

Potential spread of the invasive plant *Hydrilla verticillata* in South Africa based on anthropogenic spread and climate suitability

Julie A. Coetzee · Martin P. Hill · Dieter Schlange

Received: 9 November 2007 / Accepted: 23 May 2008 / Published online: 3 June 2008
© Springer Science+Business Media B.V. 2008

Abstract *Hydrilla verticillata* (L.f.) Royle is a submerged aquatic plant native to Asia and Australia that is highly invasive in the USA and was first recorded in South Africa in 2006. It is only known from one locality, Pongolapoort Dam in KwaZulu-Natal Province, but there are fears that it might spread to other sites. The primary vector of spread in the USA is recreational boaters and anglers. A survey at a fishing competition on Pongolapoort Dam showed that anglers travel considerable distances around South Africa (73% of water bodies were >200 km, visited by 68% of the respondents). A Threat Index for freshwater bodies throughout South Africa visited by participants of the competition was calculated showing that dams in the vicinity of the infestation were more at risk from invasion. Further, the potential distribution of the weed based on climatic matching with the region of origin showed that most of the country was suitable for establishment, with the exception of the high-lying interior of the country. Recommendations for reducing the potential spread of hydrilla in South Africa are presented.

Keywords Climate-based distribution modeling · Anglers · Hydrilla · Vectors of spread · Integrated management

Introduction

Aquatic systems throughout the world are particularly prone to invasion by exotic weed species, which negatively affect entire aquatic environments through their impacts on both the ecology and socio-economics of these systems. Historically, South Africa's waters have been invaded by a number of aquatic macrophytes that have detrimental economic and environmental effects. The worst of these include water hyacinth (*Eichhornia crassipes* Solms-Laub.), parrot's feather (*Myriophyllum aquaticum* (Vell.) Verdc.), salvinia (*Salvinia molesta* D.S. Mitchell), water lettuce (*Pistia stratiotes* L.), and red water fern (*Azolla filiculoides* Lamarck) (Hill 2003). Various control programmes have been implemented against these weeds and the majority is under acceptable control. Recently, two new submerged weeds have been identified in South African waters, hydrilla (*Hydrilla verticillata* (L.f.) Royle), rated as the worst submerged weed in the USA (Langeland 1996) and cabomba (*Cabomba caroliniana* Gray), a weed that is rapidly invading Australia, (Schooler et al. 2006). Very little is known about them in South Africa, including their current and potential distributions. Hydrilla is recorded from only one dam,

J. A. Coetzee (✉) · M. P. Hill · D. Schlange
Department of Zoology and Entomology, Rhodes
University, P.O. Box 94, Grahamstown 6140,
South Africa
e-mail: julie.coetzee@ru.ac.za

J. A. Coetzee
Agricultural Research Council, Plant Protection Research
Institute, Private Bag X134, Queenswood 0121,
South Africa

Pongolapoort Dam, in KwaZulu-Natal (Coetzee 2006), while cabomba has been cultivated by an aquatic plant dealer in the same province (Coetzee, personal observation).

Potential for the spread of hydrilla throughout South Africa is particularly worrying because of the negative impacts associated with its occurrence in aquatic systems. It is a submersed, rooted aquatic plant that is native to the Old World (Cook and Lüönd 1982), but has become a major weed particularly in the southeastern USA (Blackburn et al. 1969; Weldon et al. 1969; Haller 1982). Here it colonises a wide variety of freshwater habitats, resulting in thick extensive mats that cause significant economic and ecological damage (Langeland 1990; Balciunas et al. 2002). Hydrilla was introduced into the USA via the aquarium trade (Schmitz et al. 1991), and it is likely that this was the mode of introduction into South Africa too. Even though hydrilla has been present in central east Africa for considerable time (Mahler 1979), genetic analysis of South African hydrilla has shown that it is most closely related to hydrilla from Malaysia and Indonesia (Madeira et al. 2007), and interestingly, the majority of aquarium plants imported into South Africa come from Singapore, Malaysia (N. Stallard, personal communication).

In the south eastern USA, dense hydrilla infestations constitute the most severe aquatic problem (Center et al. 1997), affecting irrigation operations and hydroelectric power generation, while boat marinas and propeller driven boats are frequently hindered by the thick mats that form at the water's surface (Balciunas et al. 2002). Hydrilla control costs Florida, the worst affected state, approximately \$14.5 million each year and despite this expenditure, infestations in just two Florida lakes have cost an estimated \$10 million per year in recreational losses (Center et al. 1997).

Observations in the USA have shown that small-scale infestations of hydrilla initially cause no problems, but within as little as two growing seasons, may lead to system-wide infestations requiring subsequent large-scale management efforts, calling for multiple treatments extending over more than one season (Hoyer et al. 2005). Past experience has shown that it is very difficult to predict when and where hydrilla will reveal itself as a problem, and once it does become a problem, it is difficult to

forecast how long the widespread infestations will remain. In Australia, where the weed is native, it becomes weedy usually in response to the human induced problem of nutrient enhancement (Swarbrick et al. 1982). South Africa has some of the most nutrient enriched rivers and dams in the world, as a result of increasing population growth and urbanization, which increases the discharge of effluent rich in nitrates and phosphates to the aquatic environment (Noble and Hemens 1978). Many of these systems are already heavily invaded by other aquatic weeds, such as water hyacinth, and are likely to be open to invasion by hydrilla.

Studies of aquatic plant invasions in other parts of the world have shown that the spread of invasive weeds is enhanced by and directly related to recreational boating activities (Johnstone et al. 1985; Buchan and Padilla 1999; Johnson et al. 2001; Muirhead and MacIsaac 2005; Leung et al. 2006). In the USA, hydrilla is mainly introduced to new waters from reproductive fragments attached to boats, their motors and trailers. Stem pieces then root in the substrate and develop into new infestations, commonly beginning near boat ramps. Once established, boat traffic continues to break up hydrilla and spread it throughout the water body (Langeland 1996). Hydrilla may therefore spread around South Africa from Pongolapoort Dam in the same way as it has in the USA.

Pongolapoort Dam, also known as Jozini Dam, is the centre of a multimillion rand (USD 1 = ZAR 7.50) tourism industry, and is visited by thousands of tourists annually, largely anglers who aim to catch Tigerfish, *Hydrocynus vittatus* Castlenau, a major angling gamefish (Bell-Cross and Minshull 1988). The biggest tiger fishing competition in the southern hemisphere is held annually on this system, attracting anglers from all over South Africa and some neighbouring countries. Despite the presence of hydrilla on this system, the fishing competition went ahead in 2006 and 2007.

In this study, we aimed to investigate the potential for hydrilla to spread to other water bodies in South Africa by conducting a survey at the 2006 Tigerfish Competition which investigated the boating behaviour of anglers participating in the contest. Additionally, we aimed to determine the establishment potential of hydrilla based on climate by generating a predicted distribution of hydrilla using the climate matching

programme, CLIMEX, a tool used to facilitate the prediction of a species' potential relative abundance and distribution using climatic and biological data, based on observations of known geographical distribution (Sutherst 2003).

Methods and materials

A survey was conducted from 23 to 24 September 2006, at the annual Tigerfish Competition at Pongolapoort Dam (27.3537 S; 31.9063 E, KZN, South Africa). The dam, the third largest in South Africa, is 35 km in length and has a surface area of 13,500 ha. Its construction was completed in 1969 and it now irrigates more than 80,000 ha of agricultural land supporting products such as sugar cane, rice, coffee, fibre crops and various sub-tropical fruits. At the competition, 163 anglers were personally asked questions from a structured questionnaire (Appendix 1) by nine interviewers. All 163 respondents answered every question.

From these answers, the number of times the anglers used their boats on Pongolapoort Dam, dams in KZN, rivers in KZN, dams in the rest of South Africa, and rivers in the rest of South Africa was calculated. These data were then used to calculate a User Index for all the water bodies used by the respondents, giving an indication of the most popular water bodies in the country, according to the formula in Table 1.

A Threat Index for each water body was then calculated by multiplying the number of times a boat was used on a particular water body by the number of times the boat was used on Pongolapoort Dam,

according to the formula in Table 2, indicating which water bodies are at the highest risk of invasion by hydrilla, according to fishing activities. Water bodies used by boaters who did not use their boats on Pongolapoort Dam in the 18 months prior to the competition, except at the fishing competition, were excluded from this analysis. The water bodies frequented by the anglers were mapped with their associated Threat Index using ARCGIS 9.2 (ESRI, Redlands, Ca.).

The computer programme CLIMEX 1.1 was used to generate a predicted distribution of hydrilla in South Africa using the predefined physiological parameters of hydrilla obtained from the programme. An Ecoclimatic Index (EI) was generated, using the 'compare locations' function of the programme, for each weather station locality in South Africa. The EI describes the favourability of a location for a species and is scaled from 0 to 100 to represent the overall suitability of a geographical location for the propagation and persistence of the species. As such, it indicates only the gross features of a species' likely distribution (Sutherst and Maywald 1985). The CLIMEX parameter values were then used to map the potential distribution of hydrilla in South Africa.

Results

Between January 2005 and September 2006, half of the anglers interviewed used their boats only once on Pongolapoort Dam, 34% used their boats between two and five times, and only 15% used their boats more than 11 times (Fig. 1). Twenty respondents

Table 1 Example of how the User Index was calculated for each water body used by anglers at the Tiger Fishing Festival, using data for Albert Falls Dam

Answer to the question: how many times was your boat used on the water body*	b	c	d	e	f	g
A. Multiplication factor [†]	1	5	11	20	40	80
B. Albert Falls (total number of respondents) [‡]	1	1	2	1	1	1
A × B	1	5	22	20	40	80
User Index (Sum of A × B)						168

* See Appendix 1, questions 2–5

[†] Multiplication factor obtained from upper limit of the answer e.g. if the respondent answered c. 2–5 times, the multiplication factor used was 5

[‡] Frequency and number of anglers who visited Albert Falls Dam in the 18 months prior to the fishing competition

Table 2 Example of the calculation of the Threat Index for each water body used by anglers at the Tiger Fishing Competition, using data for Kosi Bay

Number of times on Pongola (individual respondents' responses)*	A. Multiplication factor [†]	Number of times on water body e.g. Kosi Bay [‡]	B. Multiplication factor [†]	A × B
e	20	c	5	100
c	5	b	1	5
c	5	b	1	5
c	5	c	5	25
c	5	c	5	25
c	5	c	5	25
c	5	c	5	25
c	5	c	5	25
c	5	e	20	100
d	11	c	5	55
d	11	c	5	55
d	11	c	5	55
d	11	c	5	55
d	11	c	5	55
d	11	c	5	55
Threat Index (sum A × B)				1625

* See Appendix 1, question 1

[†] Multiplication factor obtained from upper limit of the answer e.g. if the respondent answered c. 2–5 times, the multiplication factor used was 5

[‡] See Appendix 1, questions 2–5

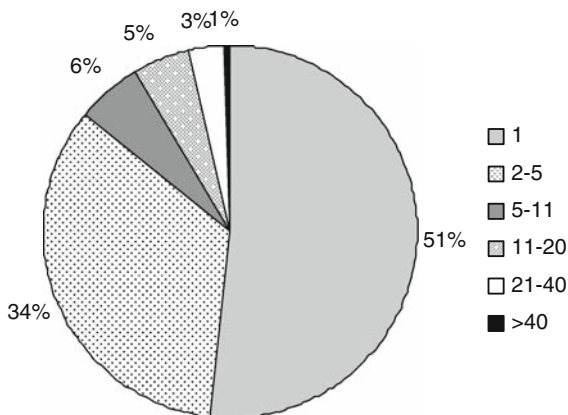


Fig. 1 The number of times respondents used their boats on Pongolapoort Dam between January 2005 and September 2006

(12.2%) never used their boats anywhere except once at the 2006 fishing competition, while 23 respondents (14.1%) only ever used their boats on Pongolapoort Dam.

Water body use was analysed by separating those in KZN from those in the rest of South Africa. Figure 2 illustrates the number of times anglers used their boats in South Africa, highlighting that dams outside of KZN are visited more frequently than other water bodies. The majority of anglers answered that they travel considerable distances, between 200 and 800 km to reach fishing destinations, which emphasizes the potential for hydrilla to spread around

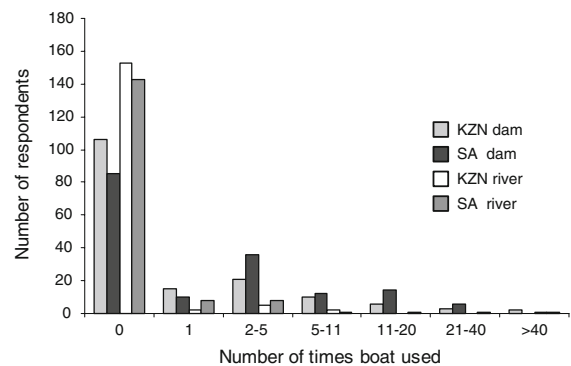


Fig. 2 The number of times respondents used their boats on water bodies in South Africa between January 2005 and September 2006

South Africa (Fig. 3). Furthermore, most of the water bodies frequented by anglers in the 18 months prior to the competition are located 200–600 km from Pongolapoort Dam (Fig. 4). The 20 most popular water bodies used by anglers at the competition, as calculated by the User Index, are shown in Table 3.

Anglers participating in the competition fished at water bodies throughout South Africa, but predominantly in KZN and Mpumalanga, in the 18 months prior to the competition (Fig. 5). In KZN, Kosi Bay had the highest Threat Index, followed by Inanda Dam, Albert Falls Dam and Midmar Dam (Table 4; Fig. 6). Jericho Dam, Loskop Dam and Nuwe Doringpoort (Witbank) Dam had the highest threat

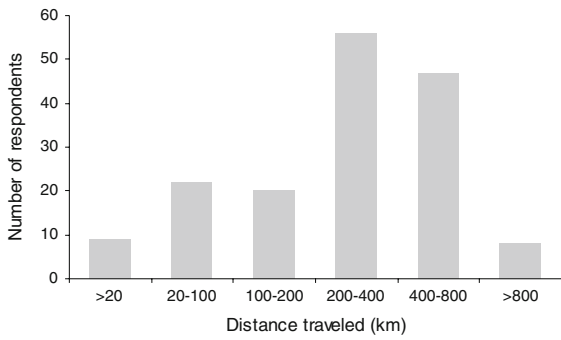


Fig. 3 The distance traveled by anglers on their last fishing trip, indicating the potential for aquatic plants to spread

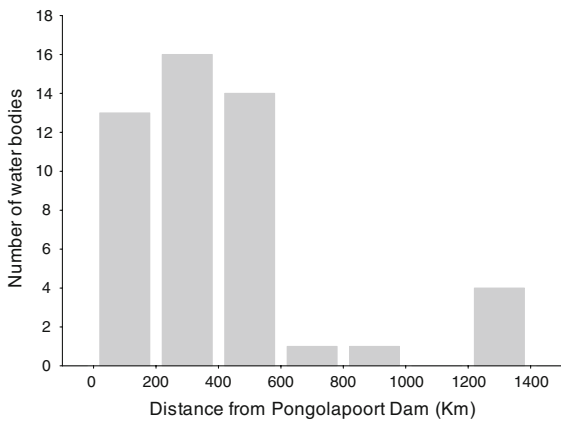


Fig. 4 The distance of water bodies visited by anglers participating in the Tigerfish Competition from Pongolapoort Dam

indices in Mpumalanga, and after Kosi Bay, the highest indices in the country (Table 4; Fig. 7). Water bodies in the rest of the country did not have indices as high as those for KZN and Mpumalanga, the highest being for Hartbeespoort Dam (Table 4; Fig. 8).

A potential distribution map of hydrilla in South Africa was created using point-based climatic data from the CLIMEX database and expressed as the EI values (Fig. 9). Locations with an EI value close to 0 are not suitable for the long term survival of the species, while an EI greater than 30 is considered very favourable (Sutherst et al. 1999). According to this predictive distribution map, only the high lying interior is excluded from where hydrilla could potentially establish. Those dams with a high Threat Index score, but a low EI score, e.g. Nuwe Doringpoort Dam, are potentially at lower risk from hydrilla establishing than those with both a high Threat Index and EI score, e.g. Kosi Bay (Table 4).

Table 3 The 20 highest User Index scores for water bodies in South Africa

Water body	User Index
Loskop Dam (MP)	340
Inanda Dam (KZN)	205
Hartebeespoort Dam (NW)	202
Nuwe Doringpoort Dam (Witbank Dam) (MP)	183
Albert Falls Dam (KZN)	168
Kosi Bay (KZN)	136
Heyshope Dam (MP)	136
Paris Dam (KZN)	110
Midmar Dam (KZN)	96
Vygeboom Dam (MP)	87
Klipfontein Dam (KZN)	83
Grootdraai Dam (MP)	82
Burnview Dam (KZN)	80
Rust De Winter Dam (GP)	71
Jericho Dam (MP)	67
Vaal Dam (FS)	64
Hendrik Van Eck Dam (Big Bend) (SW)	61
Bronkhorstspruit Dam (GP)	56
Vaalkop Dam (NW)	51
Klipkoppie Dam (MP)	46

User Index scores ranged from 340 to 1

Anglers were also asked when and how they first noticed the presence of hydrilla on Pongolapoort Dam, and the majority answered 6–12 months earlier, because the plant was caught in their propellers, anchors and fishing lines, and because they could see it from their boats. 81% of respondents replied that the presence of submerged plants harmed their fishing, 17% stated that submerged plants had no effect on their fishing, while only 2% said that submerged plants improved their fishing. 84% of respondents answered that they had noticed similar aquatic plant vegetation on dams elsewhere in South Africa.

Discussion

Identifying areas most at risk from invasion and preventing further spread is a priority in invasion biology because it usually requires less effort and money to prevent new invasions than to mitigate impacts following establishment of invasive species

Fig. 5 Distribution of water bodies throughout South Africa, and their Threat Index, visited by anglers in the 18 months prior to the Tigerfish Competition at Pongolapoort Dam

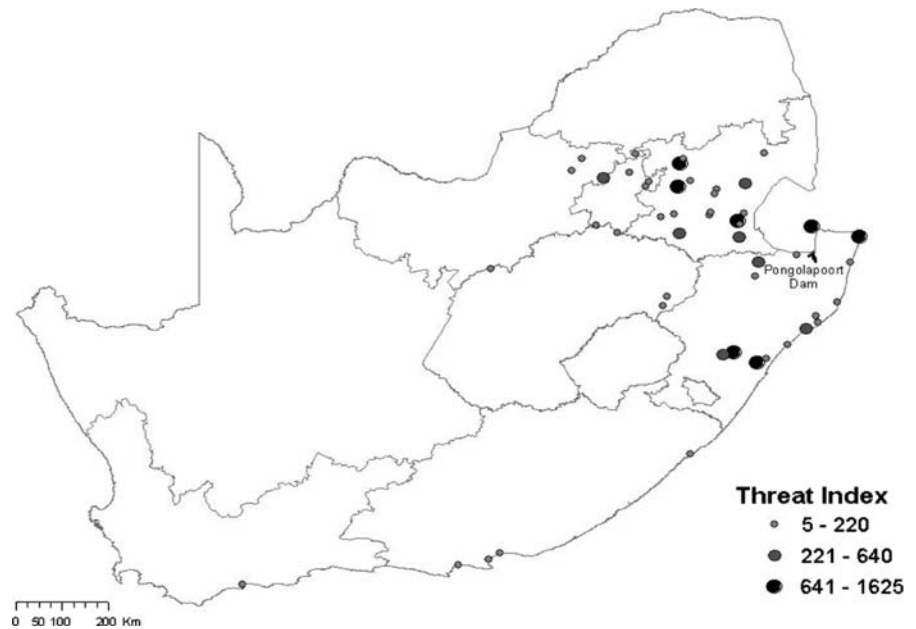


Table 4 The 20 highest Threat Index scores, distance from Pongolapoort Dam, and associated Ecoclimatic Index, for water bodies in South Africa

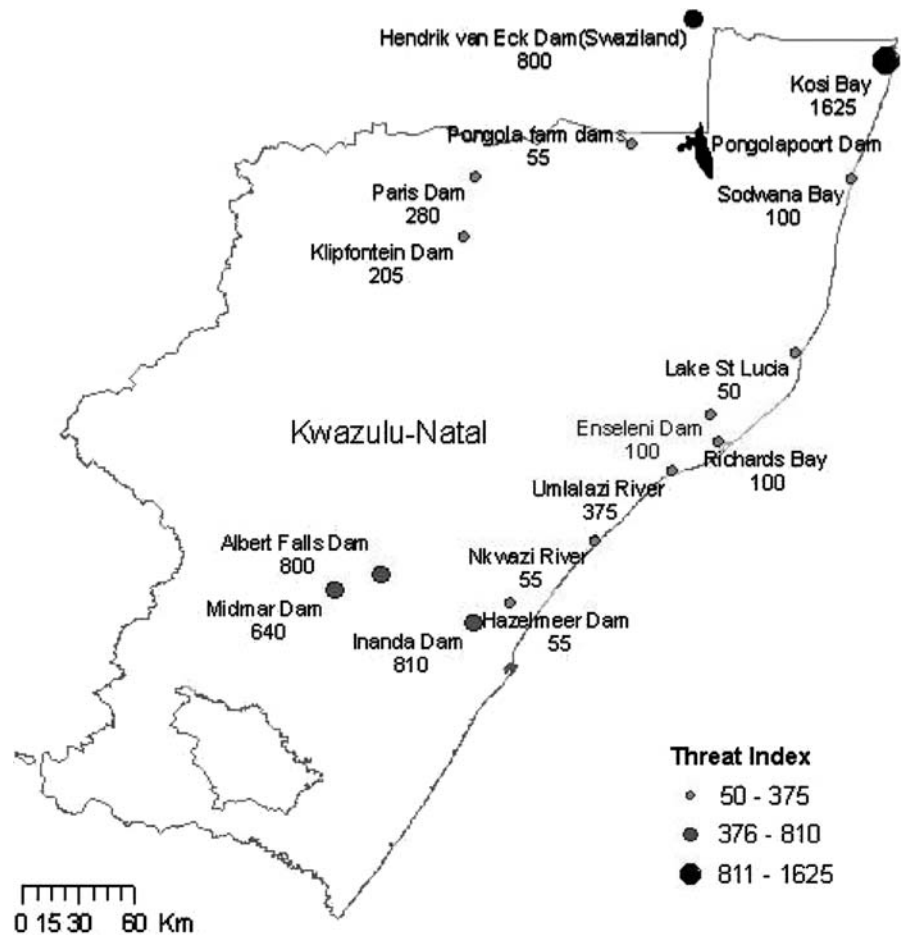
Water body	Threat Index	Distance from Pongolapoort Dam by road (km)	CLIMEX Ecoclimatic Index
Kosi Bay	1625	163	73
Jericho Dam	1145	198	28
Loskop Dam	1100	394	55
Inanda Dam	810	349	65
Albert Falls Dam	800	439	26
Hendrik Van Eck Dam	800	78	28
Nuwe Doringpoort Dam (Witbank Dam)	795	362	0
Midmar Dam	640	435	26
Grootdraai Dam	600	327	1
Hartebeespoort Dam	425	506	27
Heyshope Dam	395	161	28
Umlalazi River	375	210	73
Vygeboom Dam	320	302	64
Paris Dam	280	151	32
Vaalkop Dam	220	536	51
Middleburg Dam	220	333	0
Klipfontein Dam	205	152	10
Morgenstond Dam	200	195	28
Olifants River	200	467	55
Sodwana Bay	100	121	73

Threat Index scores ranged from 1625 to 5

(Johnson et al. 2001; Kolar and Lodge 2002; Leung et al. 2006). Reducing the threat of new invasions requires concentrating on the manner in which

humans aid the transport and establishment of species in new areas (Floerl and Inglis 2005). Ultimately, human mediated spread will determine the scale of

Fig. 6 Distribution of water bodies in KwaZulu-Natal Province, and their Threat Index, visited by anglers in the 18 months prior to the Tigerfish Competition at Pongolapoort Dam



any ecological and economic impact of a biological invasion (Lodge et al. 1998). Because recreational boaters and anglers are the primary dispersal vectors of hydrilla, understanding the potential for them to spread hydrilla from a central hub, Pongolapoort Dam, could aid in the identification of high risk areas which has important consequences for early detection, rapid response and management of these systems.

Great numbers of anglers visit Pongolapoort Dam and, according to this survey, many other water bodies throughout South Africa, increasing the risk of spread of hydrilla to these currently uninvaded systems. The results of the survey have aided in the identification of systems that are potentially at high risk of invasion as a result of angling activities in South Africa. In this study, 73% ($N = 49$) of the water bodies visited were >200 km from Pongolapoort Dam, while 68% ($N = 163$) of the respondents

visited these systems. This is a remarkably higher percentage of anglers travelling considerable distances compared to other studies, e.g. Johnstone et al. (1985) found that only 10% of boaters travelled >125 km between lakes in New Zealand; while only 0.8% of boaters moved >261 km in a study conducted in Wisconsin, USA (Buchan and Padilla 1999). Long distance dispersal events of invasive species are considered rare and stochastic (Hengeveld 1994), but when an aquatic invader is abundant in a hub and a large proportion of vectors are susceptible to colonization, it is likely to be transported repeatedly to a variety of secondary locations (Floerl and Inglis 2005). This study has shown that because South African anglers travel considerable distances to reach fishing destinations, the potential for hydrilla to spread around the country is high.

The majority of water bodies visited by anglers who partook in the fishing competition are located in

Fig. 7 Distribution of water bodies in Mpumalanga Province, and their Threat Index, visited by anglers in the 18 months prior to the Tigerfish Competition at Pongolapoort Dam

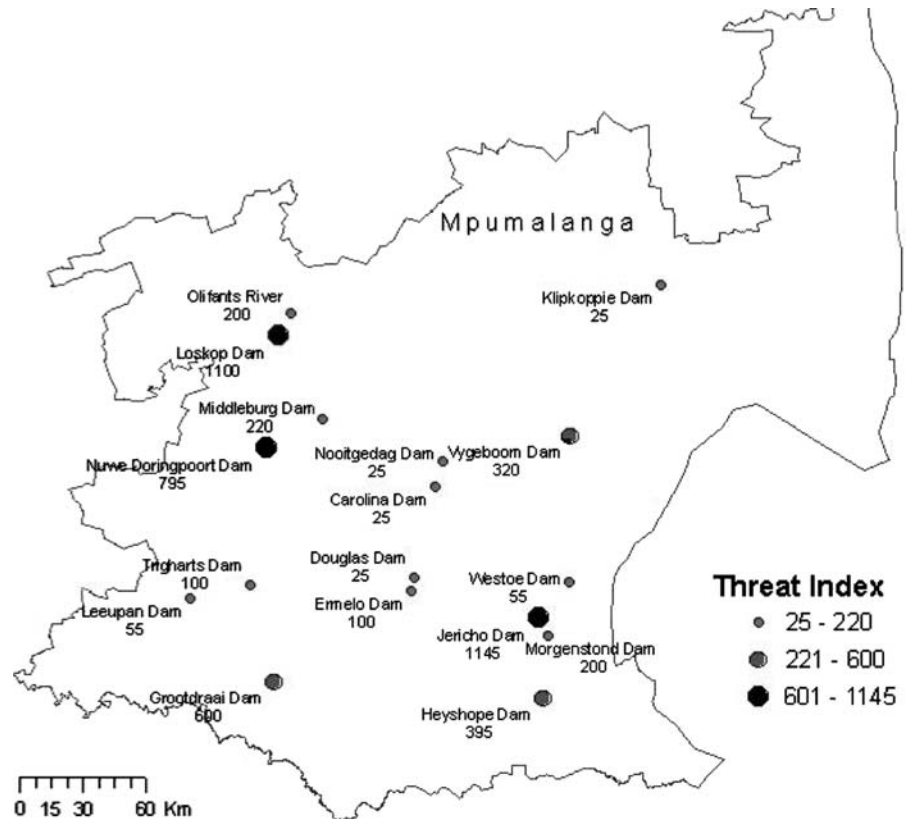


Fig. 8 Distribution of water bodies in Limpopo, North West, Gauteng and Free State Provinces, and their Threat Index, visited by anglers in the 18 months prior to the Tigerfish Competition at Pongolapoort Dam

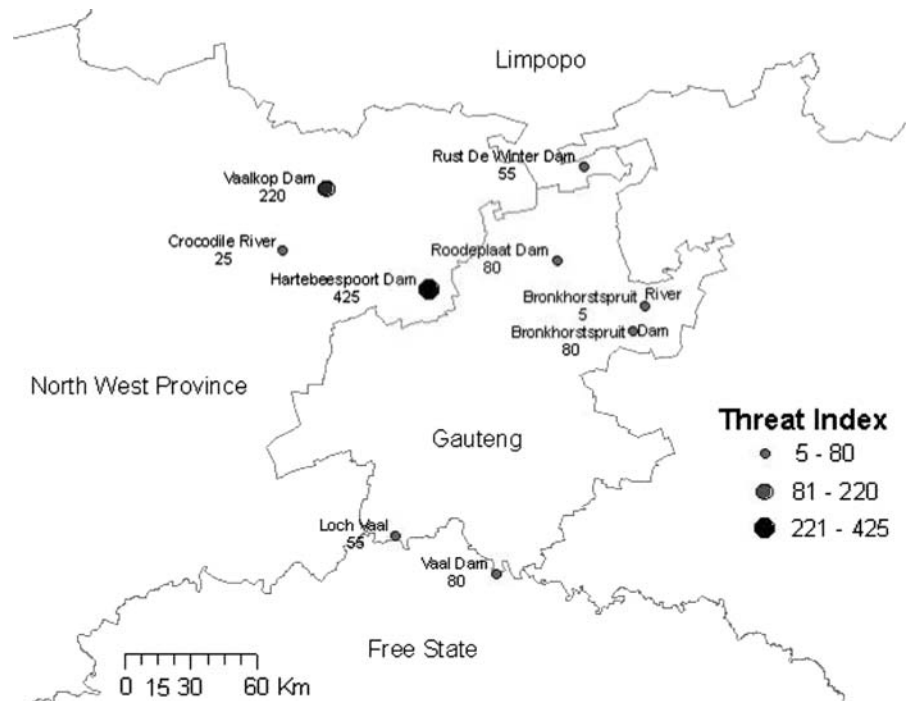


Fig. 9 The potential geographical distribution of *Hydrilla verticillata* in South Africa, as fitted by the CLIMEX Ecoclimatic Index (EI)



Mpumalanga and KZN. According to the CLIMEX model, most of these areas are suitable for hydrilla growth, indicated by high EI values. Of particular concern are those areas that have both high EIs and high threat indices, such as the north coast of KZN, where Kosi Bay has both the highest EI and Threat Index, and eastern Mpumalanga. Furthermore, the model predicts that most of South Africa is suitable for establishment of hydrilla, so should it be spread by anglers to other water bodies, its establishment will not be limited by climate.

Anglers at the Tigerfish Competition in 2006 perceived the presence of hydrilla to be detrimental to their fishing, which could have been the result of negative publicity about the presence of hydrilla in the Pongolapoort system, and low Tigerfish numbers that year as the result of cold temperatures prior to the competition (Coetzee, personal observation). Studies in the USA have shown that anglers, particularly bass anglers, prefer to fish near or in aquatic vegetation, especially submersed aquatic vegetation and are often opposed to submersed aquatic macrophyte control (Henderson et al. 2003; Maceina and Reeves 1996). On the contrary, adult Tigerfish are open water predators (Skelton 2001)

and so the presence of hydrilla on Pongolapoort Dam could be detrimental to their ecology and therefore angling activities. This could be a tool used to detract anglers from fishing amongst the infestations, thereby lessening the probability of hydrilla getting caught in anchors and motors. Despite a public awareness campaign in the region, highlighting the threat hydrilla poses to South Africa, a regional website has promoted fishing for Tigerfish on Pongolapoort Dam around the hydrilla weed beds (www.kznfishing.co.za).

In conclusion, this study has shown that there is considerable potential for hydrilla to spread from the only site in which it currently occurs to uninhabited systems around South Africa. Furthermore, should it spread from Pongolapoort Dam, its establishment is unlikely to be limited by climate according to the CLIMEX model. In order to mitigate the potential economic and ecological impacts hydrilla could have on water bodies in South Africa, management efforts should restrict the transportation of hydrilla propagules by targeting recreational boaters and anglers who frequent Pongolapoort Dam, thereby reducing the potential rate at which hydrilla could disperse to uninhabited sites.

Acknowledgements The authors thank the students from the University of the Witwatersrand who conducted the questionnaires with the anglers, in particular, Luke Schutz, Taryn Morris and Christopher Barichiev. The Invasive Alien Species Programme of the KwaZulu-Natal Department of Agricultural and Environmental Affairs, South Africa is acknowledged for funding aspects of this study.

Appendix 1

How many times was your boat used on Pongolapoort Dam in the last 18 months? (January 2005–June 2006)

- a. 0
- b. 1
- c. 2–5
- d. 5–11
- e. 11–20
- f. 21–40
- g. Other: Please specify

2a. How many times was your boat used on a dam/lake in KwaZulu-Natal, other than Pongolapoort, in the last 18 months? (January 2005–June 2006)

- a. 0
- b. 1
- c. 2–5
- d. 5–11
- e. 11–20
- f. 21–40
- g. Other: Please specify

2b. Which dam(s)/lake(s) did you use your boat on in KwaZulu-Natal, other than Pongolapoort, in the last 18 months? (January 2005–June 2006)

3a. How many times was your boat used on a dam/lake in the rest of South Africa, excluding KwaZulu-Natal, in the last 18 months? (January 2005–June 2006)

- a. 0
- b. 1
- c. 2–5
- d. 5–11
- e. 11–20
- f. 21–40
- g. Other: Please specify

3b. Which dam(s)/lake(s) did you use your boat on in the rest of South Africa, excluding KwaZulu-Natal, in the last 18 months? (January 2005–June 2006)

4a. How many times was your boat used on a river system in KwaZulu-Natal in the last 18 months? (January 2005–June 2006)

- a. 0
- b. 1
- c. 2–5
- d. 5–11
- e. 11–20
- f. 21–40
- g. Other: Please specify

4b. Which river systems did you use your boat on in KwaZulu-Natal in the last 18 months? (January 2005–June 2006)

5a. How many times was your boat used on a river system in the rest of South Africa in the last 18 months? (January 2005–June 2006)

- a. 0
- b. 1
- c. 2–5
- d. 5–11
- e. 11–20
- f. 21–40
- g. Other: Please specify

5b. Which river systems did you use your boat on in the rest of South Africa in the last 18 months? (January 2005–June 2006)

6. How far did you travel on your last boating trip by road to get your destination?

- a. Less than 20 km
- b. 20–100 km
- c. 100–200 km
- d. 200–400 km
- e. 400–800 km
- f. 800+ km

B. Plant survey

1. Have you noticed an increase in submerged aquatic plant vegetation on Pongolapoort Dam, and if so when?

- a. No increase
- b. Within the last 6 months
- c. 6–12 months ago
- d. 12–18 months ago
- e. 18–24 months ago
- f. more than 2 years ago

2. If you noticed an increase, was this because (circle as many as appropriate):

- a. the plants got caught in your propeller
 - b. the plants got caught in your anchor
 - c. your fishing line got caught in the plants
 - d. you saw the plants from your boat
 - e. you saw the plants from the land
 - f. other (please specify)
3. Does the presence of submerged plants affect your fishing?
- a. No effect
 - b. Improves it
 - c. Harms it
4. Have you noticed similar submerged aquatic plant vegetation on dams elsewhere in KwaZulu-Natal? If yes, on what dam.

References

- Balciunas JK, Grodowitz MJ, Cofrancesco AF, Shearer JF (2002) Hydrilla. In: van Driesche RG, Lyon S, Blossey B, Hoddle MS, Reardon R (eds) Biological control of invasive plants in the eastern United States. USDA Forest Service, Morgantown, pp 91–114
- Bell-Cross G, Minshull JL (1988) The fishes of Zimbabwe. National Museums and Monuments of Zimbabwe, Harare
- Blackburn RD, Weldon RW, Yeo RR, Taylor TM (1969) Identification and distribution of certain similar-appearing submersed aquatic weeds in Florida. *Hyacinth Control J* 8(1):17–21
- Buchan LAJ, Padilla DK (1999) Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecol Appl* 9:254–265. doi:10.1890/1051-0761(1999)009[0254:ETPOLD]2.0.CO;2
- Center TD, Frank JH, Dray FA (1997) Biological control. In: Simberloff D, Schmitz DC, Brown TC (eds) Strangers in paradise. Impact and management of nonindigenous species in Florida. Island Press, Washington, pp 245–266
- Coetzee JA (2006) The threat of hydrilla to South Africa. *Plant Prot News* 68:15
- Cook CDK, Lüönd R (1982) A revision of the genus hydrilla (Hydrocharitaceae). *Aquat Bot* 13:485–504. doi:10.1016/0304-3770(82)90074-2
- Floerl O, Inglis GJ (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biol Invasions* 7:589–606. doi:10.1007/s10530-004-0952-8
- Haller WT (1982) Hydrilla goes to Washington. *Aquatics* 4(4):6–7
- Henderson JE, Kirk JP, Lamprecht SD, Hayes WE (2003) Economic impacts of aquatic vegetation to angling in two South Carolina reservoirs. *J Aquat Plant Manage* 41:53–56
- Hengeveld R (1994) Small-step invasion research. *Trends Ecol Evol* 9:339–342. doi:10.1016/0169-5347(94)90155-4
- Hill MP (2003) The impact and control of alien aquatic vegetation in South African aquatic ecosystems. *Afr J Aquat Sci* 28:19–24
- Hoyer MV, Netherland MD, Allen MS, Canfield DE Jr (2005) Hydrilla management in Florida: a summary and discussion of issues identified by professionals with future management recommendations. Florida LAKEWATCH, Department of Fisheries and Aquatic Sciences, University of Florida/IFAS
- Johnson LE, Ricciardi A, Carlton JT (2001) Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecol Appl* 11:1789–1799. doi:10.1890/1051-0761(2001)011[1789:ODOAIS]2.0.CO;2
- Johnstone IM, Coffey BT, Howard-Williams C (1985) The role of recreational boat traffic in interlake dispersal of macrophytes: a New Zealand case study. *J Environ Manage* 20:263–279
- Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science* 298:1233–1236. doi:10.1126/science.1075753
- Langeland KA (1990) Hydrilla (*Hydrilla verticillata* (L.f.) Royle): a continuing problem in Florida waters. University of Florida Coop. Extension Service Circular No. 884. University of Florida, Gainesville, Florida
- Langeland KA (1996) *Hydrilla verticillata* (L.F.) Royle (Hydrocharitaceae), “The perfect aquatic weed”. *Castanea* 61:293–304
- Leung B, Bossenbroek JM, Lodge DM (2006) Boats, pathways, and aquatic biological invasions: estimating dispersal potential with gravity models. *Biol Invasions* 8:241–254. doi:10.1007/s10530-004-5573-8
- Lodge DM, Stein RA, Brown KM, Covich AP, Brönmark C, Garvey JE et al (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Aust J Ecol* 23:53–67. doi:10.1111/j.1442-9993.1998.tb00705.x
- Maceina MJ, Reeves WC (1996) Relations between submersed macrophyte abundance and largemouth bass tournament success on two Tennessee River impoundments. *J Aquat Plant Manage* 34:33–38
- Madeira PT, Coetzee JA, Center TD, White EE, Tipping PW (2007) The origin of *Hydrilla verticillata* recently discovered at a South African dam. *Aquat Bot* 87:176–180. doi:10.1016/j.aquabot.2007.04.008
- Mahler MJ (1979) Hydrilla the number one problem. *Aquatics* 1:56
- Muirhead JR, MacIsaac HJ (2005) Development of inland lakes as hubs in an invasion network. *J Appl Ecol* 42: 80–90. doi:10.1111/j.1365-2664.2004.00988.x
- Noble RG, Hemens J (1978) Inland water ecosystems in South Africa—a review of research needs. South African National Scientific programmes report no. 34. 150 pp
- Schmitz DC, Nelson BV, Nall LE, Schardt JD (1991) Exotic aquatic plants in Florida: a historical perspective and review of present aquatic plant regulation program. In: Center TD, Doren RF, Hofstetter RL, Myers RL, Whiteaker LD (eds) Proceedings of a symposium on exotic pest plants, November 2–4, 1988, Miami, Florida. United States Department of the Interior, National Park Service, Washington, D.C., pp 303–336
- Schooler S, Julien M, Walsh GC (2006) Predicting the response of *Cabomba caroliniana* populations to biological control agent damage. *Aust J Entomol* 45:327–330. doi:10.1111/j.1440-6055.2006.00559.x

- Skelton P (2001) A complete guide to the freshwater fishes of Southern Africa. Struik Publishers, Cape Town
- Sutherst R (2003) Prediction of species geographical ranges. *J Biogeogr* 30:1–12. doi:[10.1046/j.1365-2699.2003.00861.x](https://doi.org/10.1046/j.1365-2699.2003.00861.x)
- Sutherst RW, Maywald GF (1985) A computerised system for matching climates in ecology. *Agric Ecosyst Environ* 13:281–299. doi:[10.1016/0167-8809\(85\)90016-7](https://doi.org/10.1016/0167-8809(85)90016-7)
- Sutherst RW, Maywald GF, Yonow T, Stevens PM (1999) Climex: predicting the effects of climate on plants and animals. Climex 1.1 User guide. CSIRO Publishing, Victoria
- Swarbrick JT, Finlayson CM, Cauldwell AJ (1982) The biology and control of *Hydrilla verticillata*. Biotrop special publication no. 16, Bogor, Indonesia. 34 pp
- Weldon LW, Blackburn RD, Harrison DS (1969) Common aquatic weeds, 1973 edn. Dover Publications, New York 43 pp