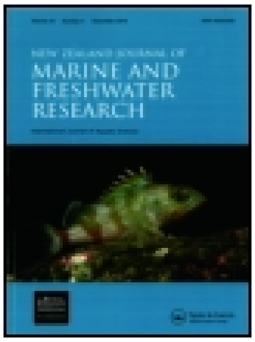

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Spread and status of seven submerged pest plants in New Zealand lakes

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Abstract The distribution of seven submerged aquatic pest plants is reported. Lake vegetation surveys recorded pest plants in 27.9% of 344 lakes, with two species co-occurring in 5.8%, and three species in 2.6% of lakes. *Egeria densa* was most frequent (15.4% of lakes), followed by *Ceratophyllum demersum* (9.0%), *Lagarosiphon major* (7.3%), and *Utricularia gibba* (5.5%). Spread since 2000 has continued for five pest plants, with 34 lakes invaded by *U. gibba* over 2004–08 alone. Early regional sites in proximity to human population centres were likely plant liberations and numerous potential founder colonies remain in garden ponds. Human activities were important for inter-lake dispersal, with the exception of bird-dispersed *U. gibba*. Significant lake associations between pest plants, and with presence of six exotic fish species, suggest common dispersal pathways and similar introduction risks. Therefore, predictions of future spread should be possible based on sources, dispersal pathways, and identifying key risk factors for lakes.

Keywords *Hydrilla verticillata*; *Ceratophyllum demersum*; *Egeria densa*; *Lagarosiphon major*; *Utricularia gibba*; *Vallisneria gigantea*; *Vallisneria spiralis*; lakes; distribution; dispersal; spread

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INTRODUCTION

Several alien submerged plant species introduced to New Zealand fresh waters meet the criteria of a pest, having substantial economic, recreational, and ecological impacts on waterways (Closs et al. 2004). Pest plant impacts are frequently realised in lake habitats, following their successful dispersal and establishment. Spread and dispersal pathways are therefore an important focus for proactive management of weeds (Champion et al. in press).

The early spread of submerged freshwater weeds is well described, with an emphasis on Rotorua Lakes (Bay of Plenty region, Fig. 1) and hydro-lakes impounded for electricity production on the Waikato River system (Waikato region) where weed impacts were first evident (Chapman 1970; Coffey 1975). Concern over the development of *Lagarosiphon major* (Ridley) Moss in Lake Rotoroa (Waikato region), and Lake Rotorua (Bay of Plenty region) led to a growing realisation of the scope for weed problems and to the first attempts at control using herbicides from 1957 (Chapman 1970).

Efforts to reduce the spread of submerged weeds within New Zealand included legislation in 1982 to prohibit the sale, propagation and distribution of "problem species" within the aquarium and nursery trade (Noxious Plant Act 1978). Subsequently, a cooperative agreement (National Pest Plant Accord—NPPA) between central government agencies, local government agencies and the Nursery and Garden Industry Association maintained the prohibited status of submerged pest plants under the provision of the Biosecurity Act (1993). Additional legislation (Section 53 of the Conservation Act 1987) also prohibited the intentional introduction of new organisms into waterways unless permitted by the Minister of Conservation. Public education about the spread of freshwater pests has been ongoing, and was recently elevated by the campaign to reduce spread of the alien diatom, *Didymosphenia geminata* (Lyngbye) Schmidt (Vieglais 2008).

In the last 10 years, various proactive measures have been taken to reduce weed spread. These include surveillance programmes and incursion response

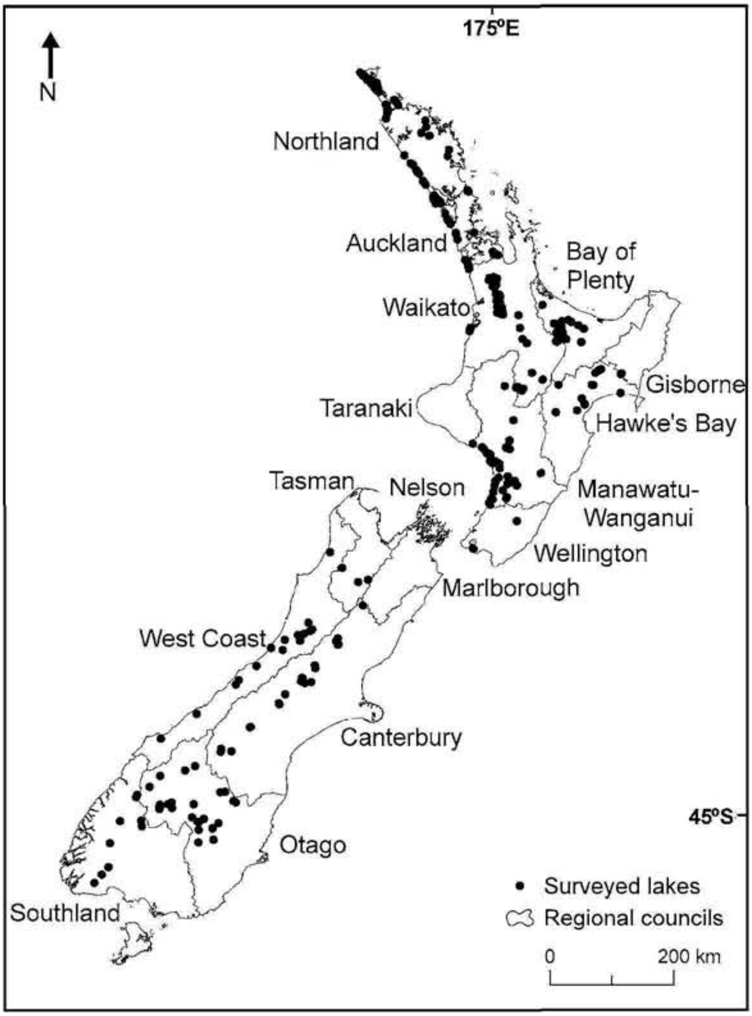

Fig. 1 Location of New Zealand lakes surveyed for pest plant presence or absence, and boundaries of regional councils and unitary authorities.

planning (Champion et al. in press) as carried out for priority lakes by five regional councils, the Department of Conservation, Land Information New Zealand, some hydro-generation companies, and Ministry of Agriculture and Forestry Biosecurity New Zealand (MAF BNZ). More recently in 2007, MAF BNZ began national eradication programmes (National Interest Pest Response) for the submerged pest plants *Hydrilla verticillata* (Linn. f.) Royle, and also *Ceratophyllum demersum* L. incursions to the South Island (New Zealand Biosecurity Institute 2007).

In the last 25 years, lake vegetation surveys have been undertaken by the National Institute of Water and Atmospheric Research Ltd (NIWA) for resource inventory and weed management purposes. Consequently, more extensive information on distribution and spread of submerged weeds is now available.

This paper reviews the spread of seven submerged pest plants over approximately 60 years from 1946 to 2008. Records from surveys provided a measure of the extent of weed presence in New Zealand lakes and their rate of invasion. Associations between pest plant species, exotic fish, and lake trophic status were explored. Finally, known pathways by which weeds spread were considered in relation to patterns of weed distribution.

METHODS

Pest plant definition

Seven submerged freshwater plant species were defined as "pests" based on the Aquatic Weed Risk Assessment Model (AWRAM) of Champion & Clayton (2000) by scoring >50 (Table 1). All are exotic and designated as "unwanted organisms" under the Biosecurity Act (1993) and prohibited from sale and distribution under the NPPA (2007). With the exception of *Utricularia gibba* L., these species do not produce viable seed in New Zealand (Champion et al. 2004). Other widespread weeds (i.e., *Elodea canadensis* Michaux, *Potamogeton crispus* L., *Ranunculus trichophyllus* Chaix, *Juncus bulbosus* L.) were not included in this analysis as they had an AWRAM score <50 (Champion & Clayton 2000) and a longer invasion history (e.g., *E. canadensis* from 1868, Chapman 1970).

Description of data sets

Pest plant presence was extracted from the Freshwater Biodata Information System (FBIS, fbis.niwa.co.nz), that holds data collated from NIWA lake vegetation surveys and other records, national herbaria, Department of Conservation and regional council pest plant databases. The first record at a lake, location or reach of river was extracted together with a locality description, grid reference, and year. Additional published sources were used where available (e.g., Chapman 1970; Cheeseman 1896). This analysis focused on naturalised sites and sites with an escape risk (e.g., garden ponds), and did not include aquaria or pet supply outlets.

Submerged vegetation data for 344 lakes (Fig. 1) collected since 1981 using the "Quick Survey Method" of Clayton (1983) indicated pest plant presence or absence. Available data for exotic fish presence and lake trophic level were included to explore pest plant associations. Lake presence of catfish (*Ameiurus nebulous* Le Sueur, 1819), goldfish (*Carassius auratus* L., 1758), koi carp (*Cyprinus carpio* L., 1758), perch (*Perca fluviatilis* L., 1758), rudd (*Scardinius erythrophthalmus* L., 1758), or tench (*Tinca tinca* L., 1758) were extracted from FBIS, and augmented by records by Rowe (2007). Trophic Level Index (TLI, Burns et al. 2000) was extracted from a lake water quality database (Sorrel et al. 2006), using the time periods of either 1990–94, 1995–99, 2000–02, or 2003–06 that best corresponded to the date of vegetation surveys.

Pest plant co-occurrence (344 surveyed lakes) and associations with the presence of exotic fish species (all data sources) were analysed using Fisher Exact test (Fisher 1954; $P < 0.05$). Simple linear regressions (Draper & Smith 1966, $P < 0.05$) were performed between lake counts for pest plant species (all data sources) and exotic fish, and a chi-square test (Conover 1980, $P < 0.05$) determined if counts of pest plant species per lake (93 surveyed lakes) differed across TLI values.

Table 1 List of freshwater pest plants in New Zealand ranked by scores >50 according to the Aquatic Weed Risk Assessment Model (AWARM) of Champion & Clayton (2000).

Species	AWRAM score
Hydrilla verticillata	74
Ceratophyllum demersum	67
Egeria densa	64
Lagarosiphon major	60
Utricularia gibba	54
Vallisneria gigantea	51
Vallisneria spiralis	51

RESULTS

Distribution and chronology of spread

Ceratophyllum demersum and *Egeria densa* Planchon were widely distributed in the North Island and extended to restricted sites in the South Island (Fig. 2A,B), *L. major* was scattered throughout (Fig. 2C) and *U. gibba* was recorded mainly from the upper half of the North Island (Fig. 3). An account of chronological spread for these species is provided below.

The remaining three species (Table 1) were less widely distributed. *Hydrilla verticillata* was first recorded in the Hawke's Bay region in 1963, and was present at lakes Tutira, Waikopiro, Opouahi and Eland. *Vallisneria gigantea* Graebner was known only from Lake Pupuke, Auckland region, since 1894 (Cheeseman 1896). Specimens cited by Healy & Edgar (1980) for Avon River (Canterbury region) and a pond at South Kaipara Head (Auckland region) were considered to be misidentifications. *Vallisneria spiralis* L. has been present in Lake Wiritoa, Manawatu-Wanganui region, since 1978 and Meola Creek, Auckland region, since 1982. From 2001 to 2008, Greater Wellington Regional Council documented *V. spiralis* from 82 sites, mostly comprising garden ponds but including Makoura Stream, Masterton. Additional sites since 2000 included ponds north of Kerikeri (Northland region), Auckland City, a Nelson Reserve, and Opawa River (Marlborough region).

Ceratophyllum demersum was first recorded in 1961 from drains and a river in Hawke's Bay (Table 2). Within 3 years it was present in Lake Ohakuri, an upper Waikato River hydro-lake. By 1980, *C. demersum* extended to lower Waikato River and adjacent Lake Waahi, had spread to lakes Rotorua and Rotoiti, and appeared in ponds in Wellington and Auckland cities (Fig. 2A). From 1980 to 1999, *C. demersum* spread within Waikato and Manawatu-Wanganui regions especially, and reached the Northland region (Fig. 2A). From 2000, the first South Island records for *C. demersum* occurred in the Tasman and Canterbury regions. Eradication programmes were subsequently implemented for these sites. Elsewhere *C. demersum* expanded in the Northland, Auckland, Bay of Plenty, Hawke's Bay, and Manawatu-Wanganui regions (Fig. 2A). In 2007, early incursions of *C. demersum* were detected in lakes Ototoa (Auckland region) and Okataina (Bay of Plenty region) with subsequent eradication measures initiated.

Egeria densa was recorded in the lower Waikato River from 1946, followed by the water bodies within its floodplain (Table 3). Subsequently, it was recorded in the Northland, Auckland, and Hawke's Bay regions. *Egeria densa* was recorded in Manawatu River and its drainage system, and had moved upstream through most of the Waikato River hydro-lakes by 1980 (Fig. 2B). From 1980 to 1999, *E. densa* expanded in the Northland, Auckland, Waikato and Bay of Plenty regions, and the first South Island sites were recorded around Blenheim in the Marlborough region, and Christchurch in the Canterbury region (Fig. 2B). Since 2000, records within the Northland, Manawatu-Wanganui and Auckland regions have increased substantially, and the first record was detected in the West Coast region (Fig. 2B). *Egeria densa* was the first Hydrocharitacean weed introduced to remote Lake Rotomahana, Rotorua district (Bay of Plenty region), and was also re-introduced to Lake Parkinson (Waikato region).

The first naturalised population of *L. major* was recorded in 1950 in Hutt Valley, Wellington (Table 4), although the plant was present at the universities of Auckland and Victoria as early as 1946 (Chapman 1970). By 1980, *L. major* had naturalised in a further 10 regions, including Lake Taupo, 8 Waikato River hydro-lakes, 8 Rotorua lakes (Bay of Plenty region), and Lake Wanaka (Otago region) (Fig. 2C). From 1980 to 1999, its distribution expanded in the Bay of Plenty and Waikato regions especially and it was recorded from the Tasman and West Coast regions for the first time (Fig. 2C). Since 2000, *L. major* has been recorded at new sites in the West Coast and Canterbury regions.

Utricularia gibba was first recorded in 1978 from a relatively isolated site at Bethells Beach (Auckland region) (Table 5). Webb et al. (1988) recorded *U. gibba* (as *U. biflora*) from "Taharoa" (probably Tawairoa Stream, Table 5) and the "Mahoenui-Waitomo Road, Waikato region" although the latter record is undated and could not be confirmed. Four cultivated records before 2000 were in the cities of Hamilton, Rotorua, Christchurch, and Auckland. The first lake sites located in 1990 were at lakes Kawaupaku and Wainamu (Auckland region). In 1999, Salmon (2001) found *U. gibba* at Lake Waikaremu in the Northland region and by 2004 it was present in 12 nearby lakes at Waipapakauri and Aupouri Peninsula (Fig. 3). Since then, an additional 22 lake sites have been recorded in the Northland region, including records from Pouto Peninsula from 2006, with further naturalised sites in the Auckland and Waikato regions (Fig. 3).

Rates of spread to lakes

Cumulative spread based on all available lake records showed different patterns for four pest plants (Fig. 4). The incidence of *L. major* increased relatively steadily, although rates were higher over 1965–75. *Ceratophyllum demersum* and *E. densa* showed steady initial increases, with higher incidence of *E. densa* in the mid to late 1980s and both species since 2000. The recent spread by *U. gibba* from 2004 onwards was confirmed from earlier surveys of the 31 invaded lakes, which did not record the plant pest in 1984/85 (11 lakes), 1988 (8 lakes), 2001 (11 lakes), and 2004/05 (10 lakes).

In the last 25 years, 34 new weed incursions were detected from 19.5% of the 118 lakes re-surveyed during this time.

Current lake status for pest plants

Overall, the seven pest plants were recorded from 27.9% of 344 surveyed lakes, with 5.8% recording two species and three species from 2.6% of lakes. The most frequent species was *E. densa* (15.4%). *Ceratophyllum demersum* was the next most frequent pest plant (9.0%), then *L. major* (7.3%) and *U. gibba* (5.5%). The remaining three pest species were recorded from ≤1% of surveyed lakes.

Table 2 Location and year of first observation for *Ceratophyllum demersum* with records listed sequentially by date and location, except where sites are grouped to clarify patterns of spread or invasion sequences. (AUK, Auckland; BOP, Bay of Plenty; CAN, Canterbury; HKB, Hawke's Bay; MNW, Manawatu-Wanganui; NTH, Northland; TAS, Tasman; WAI, Waikato; WEL, Wellington.) Lake names in bold.

Region	Year	Locality
HKB	1961	Two Napier City drains, drain to Tukituki River
WAI	1963	Waikato River at Mihi Bridge, **Ohakuri** (1964)
WAI	1966	**Atiamuri**, **Whakamaru**, **Maraetai**, **Arapuni**, **Karapiro**, **Waipapa** (1972)
WAI	1968	**Ngaroto**
WAI	1974	**Waahi**
AUK	1975	Pond—Glen Innes
BOP	1975	**Rotorua**, **Rotoiti** (1977)
WAI	1977	Waikato River between Mercer and Meremere
WEL	1979	Pond—Newlands
WAI	1981	**Taupo**, **Aratiatia** (1982)
BOP	1982	**Matahina**
MNW	1982	Moutoa flood way, Koputaroa drains, Manawatu River
HKB	1982	**Rotokaha**—Tinaroto
MNW	1983	Tank at Plant Health and Diagnostic Station—Levin
WAI	1983	Waitoa Canal—Kopuatai
WAI	1985	**Whangape**†
NTH	1985	**Ngakeketa**
WAI	1987	**Otamatearoa**
HKB	1987	**Pohue**, **Thompsons** Lagoon
BOP	1988	**Tarawera**
WAI	1990	Hamilton Gardens
MNW	1991	Swamp adjacent to Tokomaru River
WAI	1992	Maramarua River
MNW	1992	**Omanu** and adjoining pond
WEL	1995	**Wairarapa**, adjoining stream, drains, lagoons (2000)
MNW	1997	**Wiritoa**
AUK	1999	**Kereta**, **Kawakatai**
WAI	1999	**Rotoaira**
MNW	2000	Marton Stream
NTH	2001	Awanui River, **Heather**
TAS	2002	Blue Creek and Moutere River, four ponds—Motueka
NTH	2002	Drain into Kaihu River
MNW	2002	**Waitawa**, **Kopureherehere** (2003)
HKB	2002	Taipo and Tannery Stream—Napier, **Oingo** (2003)
HKB	2002	Grange Creek—Haumoana, Awanui and Karamu Stream—Havelock North
TAS	2003	Quarry pond*, Thawleys pond*—Mapua, Dirous pond
HKB	2003	**Rotoroa**—Putere, **Shagfood**—Tinaroto
MNW	2003	**Omanuka** Lagoon, **Koputara**, **Sandtoft**
MNW	2003	**Mattocks** Pond adjacent to Manawatu River
NTH	2004	**Kihona**
NTH	2004	**Waimimiha North**, **Split**
NTH	2004	**Te Werahi**
AUK	2005	**Okaihau**
NTH	2005	**Roto-otuauru**—Pouto
BOP	2006	**Rotoehu**
CAN	2006	**Centennial**—Timaru
AUK	2007	**Ototoa**
BOP	2007	**Rotomahana**, **Okataina***
HKB	2008	**Rotonuiaha**—Putere, **Green**—Tinaroto
WAI	2008	Waihekau Stream—Waitoa

*Eradicated.
†Vegetation decline.

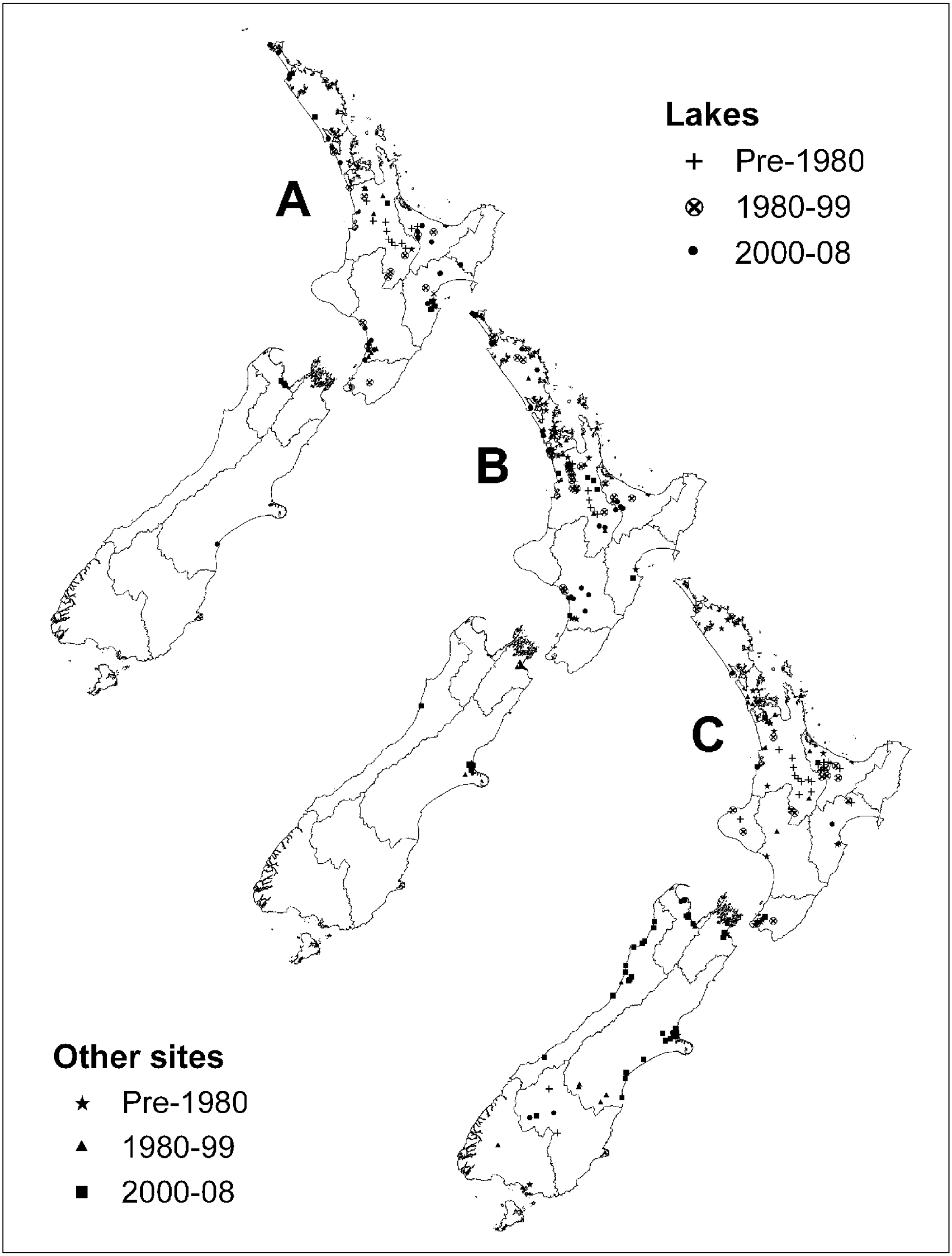

Fig. 2 Distribution of: **A**, *Ceratophyllum demersum*; **B**, *Egeria densa*; and **C**, *Lagarosiphon major* based on the date of first record and differentiating lakes from other sites. Regional boundaries indicated.

Table 3 Location and year of first observations for *Egeria densa* with records listed sequentially by date and location, except where sites are grouped to clarify patterns of spread or invasion sequences. (AUK, Auckland; BOP, Bay of Plenty; CAN, Canterbury; HKB, Hawke's Bay; MAR, Marlborough; MNW, Manawatu-Wanganui; NEL, Nelson; NTH, Northland; OTA, Otago; WAI, Waikato; WST, West Coast.) Lake names in bold.

Region	Year	Locality
WAI	1946	Waikato River—Mercer, Waikato River—Rangariri (1958) **Whangape**† (1950)
WAI	1958	**Hotoananga**†, **Kimihia**†, Kimihia wetlands (1986), **Pikopiko**† (1990)
WAI	1958	Whangamarino and Maramarua River
WAI	1958	Te Onetea Stream, **Waikare**† (1968), **Ohinewai**† (1983)
WAI	1959	Waihou River—Hauraki Plains
HKB	1961	Napier City
AUK	1963	Western Springs, Motions Road Creek (1973)
NTH	1964	Awanui River—Kaitaia
AUK	1964	Dam at Te Hana, Hoteo River (1972)
WAI	1965	**Karapiro**, **Maraetai** (1966), **Wakamaru**, **Waipapa**, **Arapuni** (1972) **Atiamuri** (1982)
MNW	1968	Stream near Shannon, **Moutoa floodway**, Manawatu River (1977)
AUK	1974	**Pupuke**, Smales Quarry (1977), Creek—Browns Bay Reserve (1978)
WAI	1976	**Parkinson***, **Parkinson** (2005)
WAI	1977	**Rotopotaka**†, **Rotoroa**†—Hamilton
WAI	1983	**Rotomanuka**†, **Ngaroto**† (1984)
BOP	1983	**Rotorua**, **Rotoiti** (1987), **Tarawera** (1988), **Pupuwharau** (1990)
NTH	1983	**Omapere**†, **Owhareiti** (1984)
WAI	1984	Waitoa Canal—Kopuatai
NTH	1985	**Rotoroa**, **Waiparera** (1988)—Waipapakauri
WAI	1986	**Rotongaro**†, **Rotongaroiti**†
WAI	1987	**Puketi**, **Rotoiti**
AUK	1987	**Whatihua**, **Pokorua** (1988)
WAI	1987	Farm pond at Opito Bay—Coromandel
BOP	1987	Pond at Lake McLaren, **McLaren** (1988)
CAN	1989	Kaiapoi gravel pit—Waimakariri River*
MAR	1989	Tuamarino, Opawa and Wairau River, Grovetown Lagoon, Blind Creek
WAI	1989	**Waahi**
AUK	1989	Garden Stream—Kelston
AUK	1990	Pond—Great Barrier Island
AUK	1990	Ponds—Waimauku
WAI	1991	**Gin**, **Mangakaware**, **Okowhao**†, **Rotokauri**†
WAI	1992	Pond—Taupo
NTH	1993	Wairua River
AUK	1996	Waitakere River and Te Henga Swamp
AUK	1997	Stream to Wairoa River—Clevedon
MNW	1997	**Wiritoa**, **Virginia**
CAN	1997	Pond—Lincoln*
CAN	1999	Kerrs reach of Avon River*, Dallington reach of Avon River (2004)
BOP	2001	**Okareka**, **Rerewhakaitu**
MNW	2001	Foxton
NTH	2001	**Heather**—Waipapakauri
NTH	2001	**Rotokawau**, **Roto-otuauru**—Pouto
NTH	2002	Waitiki Stream—Te Paki, **No Name**, **Te Werahi**—Aupouri Peninsula (2004)
WAI	2002	Harbour Marina, Kinloch Marina—**Taupo**
HKB	2002	Awanui Stream—Havelock North
CAN	2002	Pond—Coutts Island*, pond (2003)
MNW	2003	**Centennial**—Palmerston North
MNW	2003	**Koitiata**, **Vipan**, **William**, **Maungarataiti**, **Maungaratanui**
WAI	2004	**Tutaeinanga**
WST	2004	Ponds—Punakaiki
NTH	2004	**Split**—Waipapakauri
CAN	2004	Pond—Bottle Lake Plantation*, pond—Christchurch
AUK	2005	**Okaihau**, **Wainamu**, **Pehiakura**, **Kawaupaku** (2007)
NTH	2006	**Waro**
BOP	2007	**Rotomahana**
NTH	2008	**Stanners Road Dam**
WAI	2008	Waitoa River—Waharoa, Waiomau Stream—Tirau, Piako River, Waimai Stream—Raglan

*Eradicated.
†Vegetation decline.

Table 4 Location and year of first observations for *Lagarosiphon major* with records listed sequentially by date and location, except where sites are grouped to clarify patterns of spread or invasion sequences. (AUK, Auckland; BOP, Bay of Plenty; CAN, Canterbury; HKB, Hawke's Bay; MAR, Marlborough; MNW, Manawatu-Wanganui; NTH, Northland; OTA, Otago; STH, Southland; TAR, Taranaki; TAS, Tasman; WAI, Waikato; WEL, Wellington, WST, West Coast.) Lake names in bold. (*Eradicated; †vegetation decline.)

Region	Year	Locality
WEL	1950	Waiwhetu Stream, ditch (1953), Taita pond (1974), Mawaihakona Stream (2003)—Hutt Valley
AUK	1953	Western Springs
MAR	1955	Opawa River, drain, Witherlea Park (1963), Spring Creek (2001)—Blenheim
BOP	c.1955	**Rotorua**, **Rotoiti** (1957), Kaituna River (1963)
WAI	1958	Waikato River—Rangariri, Waikato River—Mercer, Mangatawhiri River
WAI	1958	**Rotoroa**†—Hamilton
TAR	1960	**Ratapiko**
CAN	1961	Avon River—Hagley Park, pond—New Brighton (1972), pond—Burwood (1993)
HKB	1964	Karamu Stream, main highway—Hastings
WAI	1963	**Atiamuri**
WAI	1966	**Taupo**, **Ohakuri**, **Whakamaru**, **Maraetai**, **Karapiro**,
WAI	1968	**Aratiatia**, **Waipapa** (1970), **Arapuni** (1972)
MNW	1969	Wanganui
HKB	1969	**Whakamarino**, **Waikaremoana*** (1999), **Pohue** (2003)
NTH	1970	Wairoa Stream—Kerikeri, Mangamutu Stream—Kaikohe
NTH	1970	**Waiparera**
AUK	1970	Pond—Waitoki
BOP	1970	**Tikitapu**, **Okataina**, **Tarawera**, **Rotoehu**, **Okareka** (1971), **Rotoma** (1973)
WAI	1970	Wairere Falls—Mokau River
STH	1972	Waihopai River , Oreti Beach (1988)—Invercargill
OTA	1972	**Wanaka**, **Roxburgh** (1974), **Dunstan** (2001)
AUK	1974	**Pupuke**
WEL	1977	Ngauranga Gorge, pond—Newlands (1979)
CAN	1981	Doctors Creek*, Pond—Hakataramea (1983)
BOP	1981	**Aniwhenua**, **Matahina** (1981)
TAR	1981	**Rotokare**
AUK	1982	Stream below Mangatawhiri Dam, drain near Pukekohe (2005)
WAI	1982	**Ngahewa**
WAI	1982	**Otamangakau**, **Rotoaira** (1985)
BOP	1983	**Te Rotoronui**, **Rerewhakaaitu** (1988), **Pupuwharau** (1990)
MNW	1983	Raetihi Stream—Ohakune
WEL	1984	**Wairarapa** and wetlands
WAI	1987	Pond at Opito Bay—Coromandel
BOP	1987	Pond at Lake McLaren
NTH	1988	**Ngatu**—Waipapakauri
TAR	1989	Waipu Lagoon—New Plymouth
WAI	1989	**Waahi**
AUK	1990	Ponds—Waimauku
CAN	1991	Omarama, Buscot Station (1995), **Benmore** (2001)
WAI	1992	Pond—Taupo
STH	1993	Pond*—Manapouri
TAS	1993	Richmond Nursery, Pearl Creek (2003)
AUK	1996	Stock trough—Henderson Valley
AUK	1996	Waitakere River and Te Henga swamp
WST	1999	Cobden Lagoon, Kamaka drains & creeks (2000), Moonlight Creek (2003)—Greymouth
WST	2000	Pond—Haast, pond—Hokitika (2003), Pond—Barrytown (2003)
TAS	2000	Motueka drain, dams and waterways—Lower Moutere (2001), Devlin's Dam (2002)
NTH	2000	**Phoebes—**Pouto
WAI	2001	**Taharoa**
MAR	2001	Stream—Picton
TAS	2001	Dam and pond, **Killarney** (2002)—Takaka
CAN	2002	Bells Creek, Edmonds Park pond (2005), Parklands pond (2006)—Christchurch
WST	2003	Granity, Karamea, Little Wanganui, Birchfield drains, ponds and creeks (2004)
WST	2003	Carters Beach, Punakaiki
CAN	2003	Washdyke Lagoon, drains—Timaru, Sir Charles Creek (2004)—Waimate
CAN	2003	Temuka, Tamitakahi Stream (2005), side creeks of Ashburton River (2007)
CAN	2003	**Rotokohatu**, pond (2005)—Bottle Lake Plantation, pond (2006)—Belfast
CAN	2004	Pond—Prebbleton, water-race into pond (2005)—Rolleston
CAN	2004	Drain—Kaiapoi, pond and water race near Waimakariri River (2005), Kaiapoi River (2006)
OTA	2007	Frankton Arm—**Wakatipu***, upper Kawarau River (2008)

Pest plant associations

Analysis of co-occurrence for pest plant species within 344 surveyed lakes (Table 6) indicated a strong association between *C. demersum* and *E. densa*, but *L. major* was also associated with each of these species, as was *U. gibba* with *E. densa*.

Simple linear regression showed the number of pest plants per lake ($n = 150$) significantly increased with increasing number of exotic fish species present ($P < 0.001$, $r^2 = 0.149$, $y = 0.3557x + 0.3313$, d.f. = 95). With the exception of perch, there was a higher than expected association between the presence of exotic fish and at least one pest plant species (Table 7). Significant associations ($P < 0.05$) indicate that lakes in which exotic fish were recorded were more likely to have the pest plant present (Table 7) than lakes not known to have the fish species (data not shown).

Based on 93 surveyed lakes with both weed and TLI data, the widespread species *L. major*, *E. densa* and *C. demersum* spanned the TLI classes of oligotrophic to supertrophic/hypertrophic, while all occurrences of *U. gibba* were from eutrophic lakes. Overall, significant differences ($\chi^2 = 10.92, P < 0.05$)

Table 5 Location and year of first observations for *Utricularia gibba* with records listed sequentially by date and location, except where sites are grouped to clarify patterns of spread or invasion sequences. (AUK, Auckland; BOP, Bay of Plenty; CAN, Canterbury; NTH, Northland; WAI, Waikato.) Lake names in bold.

Region	Year	Locality
AUK	1978	Creek—Bethells Beach, Waitakere River
BOP	1984	Cultivated—Rotorua
WAI	1985	Cultivated at Ruakura Research Station—Hamilton
WAI	1985	Tawairoa Stream—Kawhia
AUK	1986	Dam—Kumeu, ponds—Waimauku (1990)
CAN	1988	Pond—Cashmere
AUK	1988	Dam—Whatipu
AUK	1990	**Kawaupaku, Wainamu**
AUK	1993	**Kereta**
AUK	1996	Kauri Point—Auckland City
AUK	1997	Pond—Wainui
NTH	1999	**Waikaremu**—Kaimaumau
NTH	1999	**Omapere**
AUK	2003	Dam—Puhoi
NTH	2004	**Ngatu, Rotokawau, Carrot, Ngakapua, Heather, Rotoroa**—Waipapakauri
NTH	2004	**Austria, Te Arai, Waihopo**—Aupouri Peninsula
NTH	2004	**Waiparera, Morehurehu** and **nearby**—Aupouri Peninsula
NTH	2005	**Freidrich**—Baylys Beach
NTH	2005	Maitai pond—Karikari Peninsula
WAI	2005	Pond—Coromandel
NTH	2006	**Roto-otuauru**—Pouto
NTH	2006	**No Name**—Aupouri Peninsula
NTH	2006	**Owhareiti, Waro**, Wairoa River cut-off—Hikurangi
WAI	2006	Pond at Te Uku—Raglan
WAI	2007	Pond—Whatawhata
AUK	2007	**Ototoa, Mangawhai Dune**
AUK	2007	Dam—Ararimu Valley
NTH	2007	**Rotokawau, Kahuparere**—Pouto
NTH	2007	**Te Paki Dune**—Aupouri Peninsula
NTH	2007	**Little Gem, West Coast**—Waipapakauri
NTH	2007	**Vineyard**—Karikari Peninsula
AUK	2008	**Tomarata**
NTH	2008	**Wahakari, Yelavich**—Aupouri Peninsula
NTH	2008	**Rotopoua, Humuhumu, Phoebes**—Pouto
NTH	2008	**Kai-iwi, Taharoa**
NTH	2008	Wetland—Tangiteroria
NTH	2008	**Stanners Road Dam**—Kerikeri
NTH	2008	**Waiporohita**—Karikari Peninsula
WAI	2008	Whangamarino Wetland

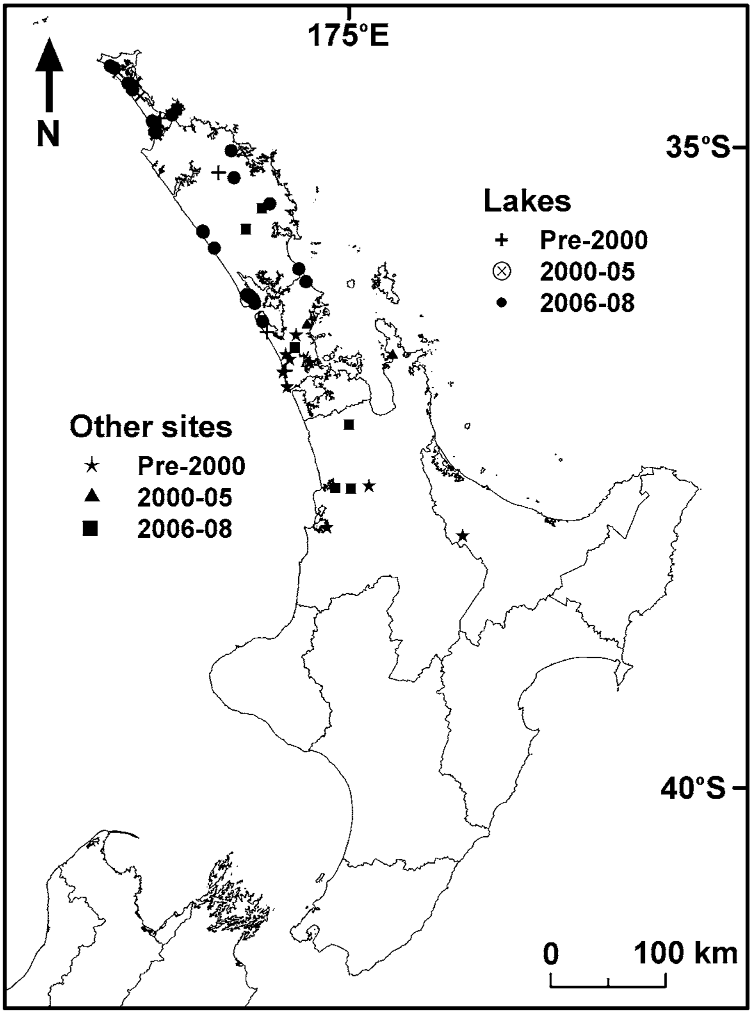

Fig. 3 Distribution of *Utricularia gibba* based on the date of first record and differentiating lakes from other sites. Regional boundaries indicated.

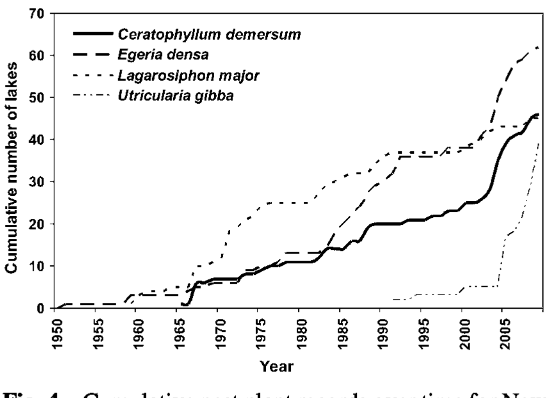

Fig. 4 Cumulative pest plant records over time for New Zealand lakes based on the year of first record.

existed between the proportions of lakes with pest plant presence within each trophic category (Table 8), with a sharp reduction in pest plant presence in the most eutrophied lakes.

DISCUSSION

Current pest plant status

There remained regions and numerous lakes where weeds were still scarce or unrecorded; such as the more remote South Island lakes in Fiordland (Southland region) and inaccessible lakes in Northland. In most instances, pest absence appears owing to lack of successful dispersal rather than unsuitable habitat. In these lakes, there are few environmental barriers such as low alkalinity, hypereutrophy, water level fluctuations over 5 m, or strongly geothermal or saline-influenced waters that might restrict weed invasions (Johnstone et al. 1985; Johnstone 1987).

On the contrary, *C. demersum*, *E. densa* and *L. major* span wide trophic, altitudinal and temperature ranges, e.g., *C. demersum* was recorded from shallow, warm Northland lakes to Lake Rotoaira (Waikato region), which at 564 m a.s.l. has winter water temperatures of approximately 5°C (James et al. 1999). Temperature tolerances for *C. demersum* range from ice cover to optima of 5–30°C (Spencer & Wetzel 1993), and for *E. densa* from ice cover to optima of 10–25°C (Di Tomaso & Healy 2003). These pest species could proliferate almost anywhere in New Zealand given reported lake temperatures of c. 0–10°C in winter and 20–35°C in summer (Green et al. 1987).

Weed distributions indicated by first weed records were modified by subsequent eradication or vegetation decline events (Tables 2–3). Eradications included use of grass carp to remove *H. verticillata* from Lake Eland (Clayton et al. 1995) and *E. densa* from Lake Parkinson (Rowe & Champion 1994),

Table 6 Co-occurrence of pest plant species (% lakes) based on surveys of 344 New Zealand lakes (FBIS 2008). Bold values show occurrence as sole pest species. Statistically significant values shown (Fisher Exact test $P < 0.05$).

Species	HV	CD	ED	LM	UG	VG	VS
Hydrilla verticillata (HV)	**100.0**	0.0	0.0	0.0	0.0	0.0	0.0
Ceratophyllum demersum (CD)	0.0	**41.9**	26.4 $P < 0.001$	28.0 $P < 0.01$	10.5	0.0	100.0
Egeria densa (ED)	0.0	48.4 $P < 0.001$	**54.8**	36.0 $P < 0.05$	42.1 $P < 0.01$	100.0	100.0
Lagarosiphon major (LM)	0.0	22.6 $P < 0.01$	17.0 $P < 0.05$	**48.0**	10.5	100.0	0.0
Utricularia gibba (UG)	0.0	6.5	15.1 $P < 0.01$	8.0	**52.6**	0.0	0.0
Vallisneria gigantea (VG)	0.0	0.0	1.9	4.0	0.0	**0.0**	0.0
Vallisneria spiralis (VS)	0.0	3.2	1.9	0.0	0.0	0.0	**0.0**
Total lake no.	4	31	53	25	19	1	1

Table 7 Frequency (%) of co-occurrences between exotic fish presence and pest plant species based on all available records. (CD, *Ceratophyllum demersum*; ED, *Egeria densa*; LM, *Lagarosiphon major*; UG, *Utricularia gibba*.) Statistically significant values shown (Fisher Exact test $P < 0.05$).

Species	Pest plants absent	CD	ED	LM	UG	Total lake no.
Catfish (*Ameiurus nebulous*)	33 $P < 0.05$	36 $P < 0.05$	61 $P < 0.001$	33	3	33
Goldfish (*Carassius auratus*)	32 $P < 0.001$	40 $P < 0.001$	43 $P < 0.001$	35 $P < 0.05$	10	63
Koi (*Cyprinus carpio*)	18 $P < 0.05$	45	64 $P < 0.05$	18	9	11
Perch (*Perca fluviatilis*)	44	25	25	28	6	32
Rudd (*Scardinius erythrophthalmus*)	28 $P < 0.01$	42 $P < 0.01$	42 $P < 0.05$	28	22 $P < 0.05$	36
Tench (*Tinca tinca*)	8 $P < 0.01$	54 $P < 0.05$	38	23	31	13
Total lake no.	77	32	37	36	15	150

Table 8 Percentage of New Zealand lakes with pest plant presence within each trophic category with range in trophic level index (TLI) values.

Trophic status (TLI range)	Lakes with pest plants (%)	Total lake no.
Microtrophic (<2)	0.0	5
Oligotrophic (2–<3)	18.8	16
Mesotrophic (3–<4)	30.0	20
Eutrophic (4–<5)	48.6	37
Supertrophic/hypertrophic (5+)	13.3	15
Total lake no.		93

whereas vegetation decline events (Champion 2002) are known for 26.4% of the lakes invaded by *E. densa*.

Dispersal pathways

Early naturalised records were frequently in widely distributed population centres, indicative of aquaria liberations (Chapman 1970). The first regional records for *C. demersum* comprised Napier City (Hawke's Bay region), Glen Innes (Auckland region), Newlands (Wellington region) and Levin (Manawatu-Wanganui region); *E. densa* included Napier, Kaitaia township (Northland region) and Western Springs (Auckland region); and *L. major* included Hutt Valley (Wellington region), Western Springs (Auckland region), Opawa River in Blenheim, and Hagley Park (Canterbury region). Several such sites recorded more than one species; at Napier (*E. densa* and *C. demersum*), Western Springs (*E. densa* and *L. major*), Newlands (*L. major* and *C. demersum*), and Taupo township (Waikato region) (*L. major* and *E. densa*). These patterns are consistent with introduction to New Zealand via the aquarium and pond plant trade (Champion & Clayton 2000), and the aquarist trade in *E. densa*, *L. major*, *C. demersum*, and *V. gigantea* before 1982. For instance, the 1963 record for *C. demersum* at Lake Ohakuri was thought to originate from an upstream thermal pond known to contain released sub-tropical fish (Howard-Williams et al. 1987).

Hydrilla verticillata was not in the aquarium trade and this fact, together with the geographic isolation of sites, has constrained its spread. The *Vallisneria* species have a basal growth meristem that requires transplanting entire plants for establishment (Coffey & Clayton 1988), explaining their limited distribution. Although both *Vallisneria* species were banned from sale and distribution in 1982, revision of legislation in 1993 removed the prohibited status of *V. spiralis* (Champion 2005). Subsequently, a number of naturalised sites detected since 2000 represented plantings as culture sources for the aquarium and pond plant trade. In response, a prohibited status was re-instated in 2007 (NPPA 2007).

Egeria densa escaped from a pond adjacent to Lake McLaren (Bay of Plenty region) (Howard-Williams et al. 1987) after probable introduction as contaminants on planted waterlilies. Similarly, contaminated waterlilies were suggested for the original infestation of *U. gibba* at Bethells Beach (Salmon 2001). More recently, *U. gibba* was found as a contaminant of aquarium plants traded in the Waikato region (authors' pers. obs.) and entry to ornamental ponds such as at Whatawhata might be explained by this pathway.

Even since 2000, new records have been detected from garden ponds for *E. densa* and *L. major* in Christchurch and the West Coast, and inspections of properties in Motueka (Tasman region), the site of the first South Island record for *C. demersum*, also revealed four pond populations (Rees 2005).

The associations between pest plant species, and with exotic fish, indicate they share dispersal pathways and/or that lakes share risk factors for introductions. A similar finding that *C. demersum* tended to occur with one or more Hydrocharitacean weeds was attributed to a shared dispersal mechanism (Johnstone et al. 1985). As both pest plants and exotic fish are largely reliant upon human activities for dispersal between isolated lakes (Champion et al. 2002) some association might be expected. However, an alternative explanation is that illegal fish liberations involve the release of weed incidentally transported from source locations, intentionally included to buffer fish during transport, or as packing for fish ova (e.g., Johnstone et al. 1985). Weed transfer is also known with fishing activities or equipment, with *L. major* first noted on illegal fishing nets in Lake Rotoaira (Forsyth et al. 1985). Spread from the first South Island site for *C. demersum* at Moutere River (Tasman region) to ponds in the area followed their use as holding ponds by a local eel fisher after fishing the river (Rees 2005). Both the latter and a more recent Timaru (Canterbury region) incursion of *C. demersum* were associated with the presence of the exotic fish rudd. Other examples of *C. demersum* spread facilitated by eel fishing are the Lake Wairarapa complex (Wellington region) and Lake Roto-otuauru, Pouto Peninsula (Northland region) (authors' pers. obs.).

Downstream dispersal via vegetative fragments occurred for *L. major*, *E. densa* and *C. demersum* within the Waikato River system (Coffey 1975); through lakes Rotorua and Rotoiti to Kaituna River (Chapman 1970); *L. major* from Lake Wanaka to lakes Dunstan and Roxburgh (Clayton 1988); *E. densa* and *C. demersum* through Manawatu River and associated drainage system; and *E. densa* within the Wairau River (Marlborough region) system. Transport with back-flows into lakes situated on river floodplains were likely for lakes Whangape and Waikare on the Waikato system, and oxbows on the Manawatu River such as Mattlocks Pond. Similarly, escape from ornamental ponds to downstream waterways is known for *E. densa* at Lake McLaren (Howard-Williams et al. 1987) and more recently *L.*

major from Buscot Station to Ahuriri River and Lake Benmore (Otago region) (authors' pers. obs.).

Transfer of weeds between lakes with contaminated equipment was confirmed by Johnstone et al. (1985) who correlated the distribution of five submerged weeds within 107 North Island lakes with boating or fishing activities. The early record (1969) of *L. major* at isolated Lake Whakamarino probably originated when equipment was sourced from the Waikato hydro-system by the then New Zealand Electricity Department. Float planes operating routine flights between lakes Ohakuri, Rotorua and Matahina (Waikato and Bay of Plenty regions) in the early 1980s were also observed to carry fragments of *C. demersum* (authors' pers. obs.), and a contaminated weed harvester from Blenheim was probably the initial source of *E. densa* in Avon River. More recently, weed cutting boats have been responsible for weed transfer between catchments in the Bay of Plenty and Hawke's Bay regions, and are likely to have contributed to *C. demersum* records in the lowland drainage systems and streams around Napier and Havelock North.

Bird mediated dispersal of the vegetative-reproducing plants considered in this analysis was ruled out by Johnstone et al. (1985) because their spread patterns were not random or proximal in nature but instead were linked to recreational use. For example, Lake Waikaremoana remained weed free for 30 years despite close proximity to invaded Lake Whakamarino. In contrast, *U. gibba* dispersal to isolated lakes (e.g., Aupouri and Pouto peninsulas) and the Whangamarino wetland was almost certainly by wildfowl transfers of seed (and possibly fine entangling stems).

Exponential spread of *U. gibba* in Northland since 2004 may represent a second, more vagile form. Salmon (2001) recognised a "far north form" from Lake Waikaremu in 1999 that pollinated readily and released abundant seed. Suspected to be a waterfowl-mediated introduction from eastern Australia, this form was predicted to spread rapidly (Salmon 2001). A "West Auckland form" extending south from South Kaipara and exhibiting limited pollination and seed set (Salmon 2001) has been associated with the slower spread within that region despite a longer invasion history.

Future spread

Legislative initiatives have limited the "propagule pressure" of pest plants for natural sites, but spread to lakes continues and a wide range of lakes remain vulnerable to invasion. Plant exchange followed by aquarium/pond liberations are the most important long-distance dispersal mechanism and potential founder colonies of weeds exist in garden ponds especially within population centres. Human activities are the main vectors of spread from lake to lake, but waterfowl are implicated in the rapid spread of *U. gibba*. A current knowledge of pest distribution and proximity to priority areas for protection will be important for proactive management (Champion et al. in press). Associations between pest plants, and also with exotic fish, suggest they share pathways and/or vectors. If key risk factors for lakes are identified, the vulnerability of water bodies, and future pest spread, may be predicted.

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