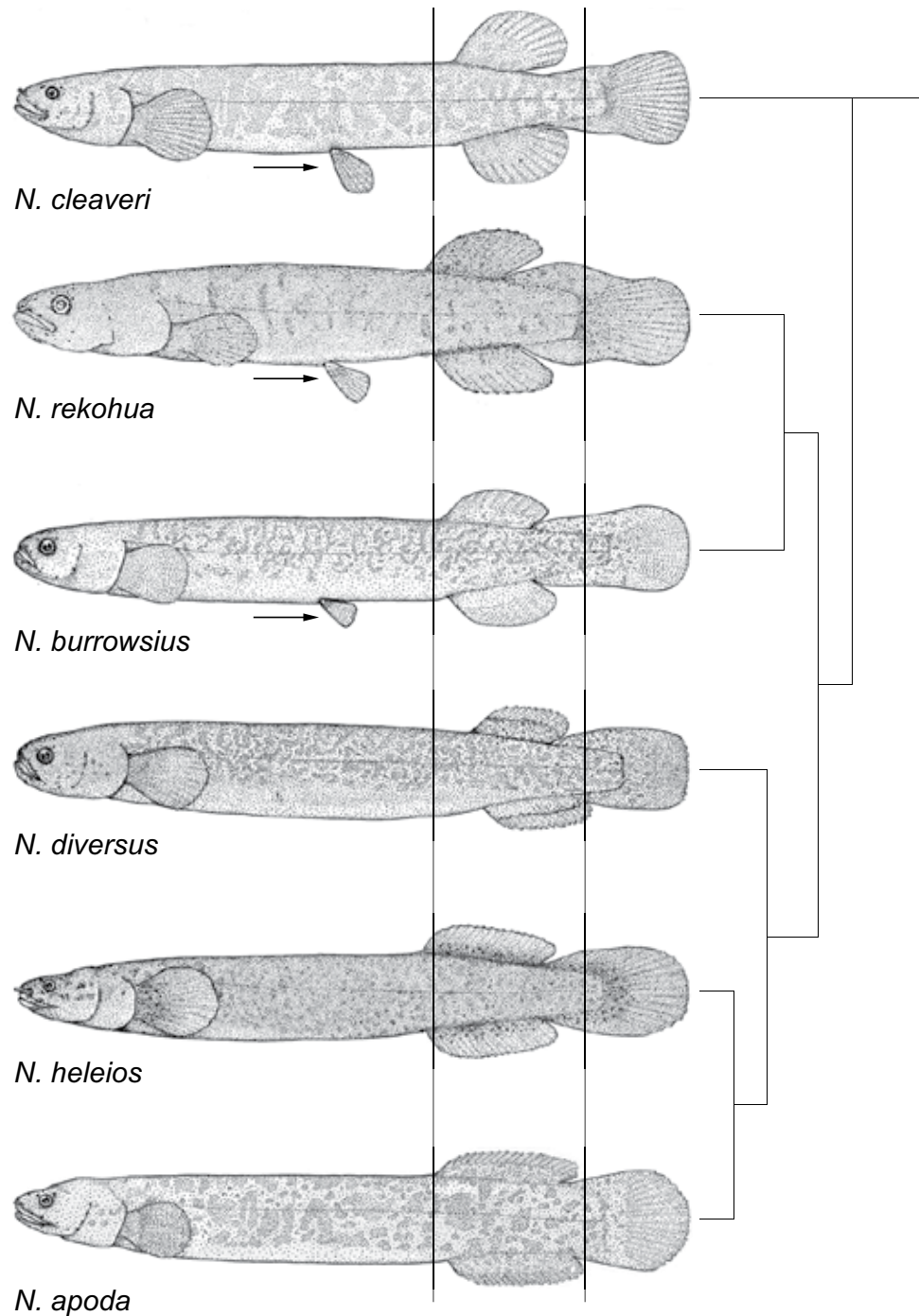


Figure 3. Placement of *Neochanna* species in a transformation series from *Galaxias*-like species at top to anguilliform species at bottom. Shown are taxonomically representative drawings by R.M. McDowall of the six species of *Neochanna*:
N. cleaveri—79 mm TL*,
N. rekobua—120 mm TL,
N. burrowsius—108 mm TL,
N. diversus—110 mm TL,
N. heleios—92 mm TL,
N. apoda—110 mm TL.
 Arrows indicate presence of pelvic fins. Vertical lines emphasise fin reduction and fin elongation. Lines at far right are indicative of phylogenetic relationships (see Waters & McDowall 2005)
 * = total length.



When all of the various physical attributes apparent in the *Neochanna* species are examined, *N. cleaveri*, *N. rekobua*, and *N. burrowsius* are the least specialised, i.e. the most 'galaxiform'. Their retention of pelvic fins (as in *Galaxias* species) likely means they are relatively proficient at swimming in open and flowing waters. At the other end of the spectrum, strong anguilliform characteristics, such as the lack of pelvic fins, occur in *N. diversus*, *N. heleios*, and *N. apoda*. Furthermore, *N. apoda* have strongly developed muscles in a robust head and an *Anguilla*-like muscular dome behind the eyes (Fig. 3; Davidson 1949; McDowall 1997a); all features that are likely to be useful when burrowing through debris in shallow wetland habitat.

Recognition of this transformation series provides an important insight into the *Neochanna* genus, and not only defines morphological and phylogenetic relationships, but also indicates evolutionary selective pressures that act on fish in wetland habitats (McDowall 1997a; Waters & McDowall 2005). Importantly, viewing *Neochanna* species as a transformation series may provide a framework within which other ecological and biological differences can be more fully understood. We thus suggest its use in the formulation of research hypotheses and to guide conservation efforts, especially relating to recently described species where direct study is limited. In this literature review, instances where research can be related to the transformation series are highlighted. However, little comparative research has been conducted between species of *Neochanna*, and single species studies have used a variety of different methods. This hinders rigorous comparisons and hypothesis testing. The intention of this review is to emphasise likely general patterns within the genus with the aim of stimulating further research.

1.3 BACKGROUND TO NAMES

Neochanna were called a 'peculiar, elusive, tenacious fish that seems more a product of Hollywood than New Zealand' by Young (1996: 14.). Indeed, in the 1800s, a Mr G.G. Fitzgerald (quoted by Roberts 1872: 457) 'thought [*Neochanna*] to have fallen from the sky' and it was widely believed that *N. apoda* actually disliked freshwater (Günther 1867). The idea developed as specimens of *N. apoda* were being found buried in the ground (mostly in areas which had only recently been drained). Thus, it was with surprise that live *N. apoda* were first exhibited swimming actively in water (Hector 1869). Our understanding of *Neochanna* species has advanced greatly since the 1800s, but the somewhat misleading common name of 'mudfish' has remained.

There are different Maori names for *Neochanna* species from different areas and dialects (Strickland 1990). *Kōwaro* has most often been applied to *N. burrowsius* (e.g. DOC 2000a); whereas *Haubau* is predominantly used for *N. apoda* (McDowall 1990). However, the Waitangi Tribunal uses *waikaka* (also spelled *waikaakaa*; Strickland 1990), interpreted as meaning 'water-cunning', for all *Neochanna* species (Pond 1997).

Various common English names for New Zealand native fish species have been used (McDowall 1996a), with *Neochanna* species sometimes called 'mud-eels' and 'spring-eels' (McDowall 1990). The common names black, brown, and Canterbury mudfish are now in regular usage. However, several common names have been used to refer to the recently discovered *N. beleios*. Ling & Gleeson (2001), when describing *N. beleios*, applied the common name 'Northland mudfish' because of its restriction to central Northland and the likelihood that its presence predates that of *N. diversus*. However, McDowall (2000) proposed the common name 'burgundy mudfish' as a descriptive reference, rather than one based on geographic location. The use of common names linked to specific locations or areas can lead to unnecessary misunderstandings. For example, Tasmanian mudfish (*N. cleaveri*) have been found on the Australian mainland (Jackson & Davies 1982), Canterbury mudfish have been found in Otago (Jellyman et al. 2003) and *N. beleios* is not the only *Neochanna* species in Northland. Nonetheless, the Chatham mudfish (*N. rekobua*) is unlikely to be found elsewhere. Recently, Hardy et al. (2006) suggested the common name of *N. cleaveri* be changed from 'Tasmanian mudfish' to 'Australian mudfish'.

The scientific genus name *Neochanna* was established by Günther (1867) and is derived from the Greek *neos* (new) and *channes*. *Channa*, the snakehead (Channidae, Perciformes) is an Asian genus that includes species with a swim bladder modified for air breathing and which are known to aestivate when their habitat dries up (McDowall 1990). *Neochanna* fish were initially described as lacking pelvic fins until McDowall (1970) recognised that *N. burrowsius* had osteological characteristics more akin to *N. diversus* and *N. apoda* than forms of *Galaxias*. Several species now assigned to *Neochanna* were earlier placed in *Galaxias*, *Lixagasa*, *Paragalaxias*, or *Saxilaga* genera (Table 2; Stokell 1945, 1949; McDowall 1970, 1997a; McDowall & Frankenberg 1981; Waters & White 1997)

The species name of *N. apoda* is from the Latin and Greek *a* (without) and the Greek *podos* (foot), and refers to the absence of pelvic fins (McDowall 1990). *N. diversus*, derived from the Latin, meaning 'separated', was so named by Gerald Stokell (1949) as specimens differed from *N. apoda* (McDowall 1990). Ling & Gleeson (2001) named the species *N. beleios* from Greek, meaning 'dwelling in a marsh'. The species name of *N. rekobua* relates to the Mori name for the Chatham Islands (Mitchell 1995). Whereas, W.J. Phillipps (1926a) named *N. burrowsius* after Mr A. Burrows, who forwarded a specimen collected from a creek on his farm, near Oxford, Canterbury; rather than in reference to its alleged ability to burrow (McDowall 1990).

1.4 HISTORY OF DISCOVERY AND STUDY

Following publication of Günther's (1867) description of *N. apoda*, a number of reports were made to members of the New Zealand Institute regarding similar fishes in the Bay of Islands, Newmarket in Auckland, and Rangitikei (Hector 1869; Roberts 1872). It was then realised that these observations were of different species, *N. apoda* and *N. diversus*. Since then, the genus *Neochanna* has accumulated species gradually, as they have been discovered or reclassified. Despite their occurrence in populated agricultural areas, *N. burrowsius* and *N. diversus* were not described formally until 1926 and 1949, respectively (Phillipps 1926a; Stokell 1949). In the 1990s, distributional survey work on *N. diversus* led to the finding and description of *N. beleios* in 2001 (Gleeson et al. 1997, 1998, 1999; Ling 1998; Ling & Gleeson 2001; Ling et al. 2001). Most recently, a fish originally described by Mitchell (1995) was recognised by McDowall (2004) as belonging to the genus. This is *N. rekobua* (Chatham mudfish).

In the 1900s, initial studies on *Neochanna* species were conducted by Phillipps (1923, 1926a, b, c) and Stokell (1938). In response to a belief that the extinction of *N. burrowsius* was imminent, all available information on this species was summarised by Skrzynski (1968). However, the biggest leap in knowledge and understanding of *Neochanna* species so far has resulted from the work of G.A. Eldon (McDowall 1991; Winterbourn 1991). Eldon made observations of *N. apoda* on the West Coast (Eldon 1968) and in the Wairarapa (Eldon 1978b), and of spawning in captivity (Eldon 1971). He studied the habitat, life-history, ecology, and diet of *N. burrowsius* (Eldon et al. 1978; Eldon 1979a, b, c), methods of catching *Neochanna* (Eldon 1992), keeping them in aquaria (Eldon 1969), and their conservation management (Eldon 1988a, 1989a, b, 1993). G.A. Eldon also wrote popular articles aimed at increasing general awareness of these fish by the public (e.g. Eldon 1978a, 1979d, 1983, 1985, 1986, 1988b).

The first university thesis on *Neochanna* was written at the then Victoria University College, Wellington, by M.M. Davidson, who examined the anatomy of *N. apoda* and reported on maintaining fish in aquaria (Davidson 1949, 1951). Later, both P.L. Cadwallader and A.S. Meredith studied *N. burrowsius* while postgraduate students at the University of Canterbury. Although Cadwallader (1973) found insufficient viable study populations to produce a thesis, he published his preliminary studies (Cadwallader 1975a). Meredith studied and published papers on the physiology of *N. burrowsius* (Meredith 1981, 1985; Meredith et al. 1982; Wells et al. 1984).

In the Waikato area, F.V. Thompson published notes summarising 9 years of observations on *N. diversus* (Thompson 1987). After this study there was a pause in *Neochanna* research until J.D. McPhail's work while on study leave at the University of Waikato. A series of studies focused on *N. diversus* followed, including investigations into habitat requirements, interactions with *Gambusia affinis* (mosquito fish), and physiology (Barrier 1993; Barrier & Hicks 1994; Dean 1995; Hicks & Barrier 1996; Barrier et al. 1996; Davidson 1999; McPhail 1999; Willis & Ling 2000; Perrie 2004). Additionally, A. Perrie (2004) investigated aspects of the ecology and physiology of *N. beleios*. Also during this period, theses by G. Butler (1999), K. Francis (2000a), and N. Grainger (2000) investigated the distribution, habitat requirements and threats to *N. apoda*, and L. O'Brien (2005) studied the ecology, habitat, and life-history requirements of *N. burrowsius*. Studies of the genetic characteristics of *Neochanna* populations have been conducted (Gleeson et al. 1997, 1998, 1999; Waters & White 1997; Davey et al. 2001, 2003; Waters & McDowall 2005) and their biogeography widely debated (Stokell 1938; McDowall 1970, 1990, 1996b, 1997a, 1998b, 2004; Jackson & Davies 1982; Main 1989; Koehn & Raadik 1991; Waters & White 1997; Waters et al. 2000; Ling & Gleeson 2001; Waters & McDowall 2005).

2. Distribution and biogeography

Neochanna species are distributed throughout much of the low-lying, poorly drained parts of New Zealand's landscape (Fig. 2). All *Neochanna* species have distinctive distributions (McDowall 1997a), and even *N. beleios* and *N. diversus* do not co-occur, despite the former occurring within the range of the latter (Kerr & McGlynn 2001; Ling & Gleeson 2001). The distinct distributions of New Zealand *Neochanna* species reflect relatively recent geological and landscape events and processes (late Tertiary to Recent). Examples include the reduction and increase of land area during the Oligocene (30 million years before present (ybp)) resulting from marine transgression and regression, mountain building (orogeny), the presence or absence of land bridges, and volcanism (McDowall 1996b, 1997a).

New Zealand *Neochanna* species likely originated from a single ancestral stock, such as a diadromous species originating in Australia, which would have arrived via transoceanic dispersal (McDowall 1970, 1997a; Waters & McDowall 2005). Indeed, ancestral traits are retained by *N. cleaveri*, which has a diadromous life history in the form of larval migration (Fulton 1986; Koehn & Raadik 1991; McDowall 1997a, 2006). A marine ancestry is also supported by physiological

studies, which have demonstrated high blood ion levels and euryhaline osmoregulation in *N. burrowsius* (Meredith 1985). In New Zealand, diadromy was abandoned by the invading stock, with subsequent geographical isolation between populations contributing to speciation (McDowall 1998b; Waters & McDowall 2005). A number of questions regarding the ancestry and derivation of *Neochanna* remain, however, especially with the inclusion of recently recognised species (Ling & Gleeson 2001; McDowall 2004; Waters & McDowall 2005). The following subsections outline the current distribution and general biogeography of each species, with reference to survey work.

2.1 *Neochanna rekobua*

Neochanna rekobua is currently the only endemic galaxiid in the Chatham Islands (Mitchell 1995; McDowall 2004). It is known only from around lakes Tuku a Taupo and Rakeinui in the south of Chatham Island, but is likely to also occur in other small lakes and wetlands in the vicinity (Fig. 2; Mitchell 1995; McDowall 2004). Surveys of Chatham Island by Skrzynski (1967) and Rutledge (1992) failed to find *N. rekobua*, despite Skrzynski speculating that suitable habitat for a *Neochanna* species was present. Because of its recent description and the Island's remoteness, targeted survey work on *N. rekobua* is in its initial stages (DOC 2004a). Recent phylogenetic analysis indicates a close genetic relationship with *N. burrowsius* and suggests that the ancestor of *N. rekobua* may have retained a diadromous life-history for longer than other species (Waters & McDowall 2005)

2.2 *Neochanna burrowsius*

Successive orogenic events formed the Southern Alps, which have acted as a barrier, isolating *N. burrowsius* on the east coast of the South Island. As the Southern Alps have eroded, the Canterbury Plains have gradually formed (late Pliocene – Present) through the deposition of outwash gravels. *Neochanna burrowsius* has dispersed throughout these low-lying plains, as far north as the Ashley River, and as far south as the Waitaki River (McDowall 1997a; Davey et al. 2003) They have been found in 16 catchments on the Canterbury Plains (NZFFD records) (Fig. 2).

Various areas throughout the Canterbury Plains have been surveyed repeatedly for *N. burrowsius* (e.g. Skrzynski 1968; Cadwallader 1973, 1975a; Eldon 1979a; Harraway 2000). However, areas of suitable habitat are now generally small, fragmented and modified, and thus easily overlooked. Jellyman et al. (2003) located *N. burrowsius* on the southern side of the Waitaki River, extending the known distribution of the species into North Otago. Many areas have also had general habitat values and attributes assigned under various large-scale habitat classification schemes to assist management (e.g. Taylor 1996; Taylor & Champion 1996; Lavender 2001).

2.3 *Neochanna diversus*

The current distribution of *N. diversus* suggests an association with proto-North Island land areas that remained above sea level during Pliocene marine transgressions. *Neochanna diversus* may already have been in these areas before marine transgression occurred (McDowall 1997a). Its absence from eastern and southern parts of the North Island has been attributed to volcanism and marine transgression, respectively (McDowall 1997a). *Neochanna diversus* currently occurs in remnant infertile wetlands from Otakairangi in the south of Northland, to Parengarenga Harbour in the north (Kerr & McGlynn 2001). Significant populations occur in the Waikato region, with an extensive population in the Whangamarino Wetland system and Kopuatai Peat Dome (Barrier 1993; Ling 2001). In all, *N. diversus* occurs in at least 17 catchments throughout its distribution (NZFFD records).

Surveys of *N. diversus* have been conducted by Town (1981), Thompson (1987) and Barrier (1993) in the Waikato, and by Kerr & McGlynn (2001), and McGlynn & Booth (2002) in Northland. Recently, several populations have been found in the Auckland region (DOC 2004b). Survey and genetic work has also been conducted by Gleeson et al. (1998, 1999) and Ling & Gleeson (2001) leading to the identification and description of *N. heleios*.

2.4 *Neochanna heleios*

Neochanna heleios is restricted to wetlands around Kerikeri, Ngawha and Lake Omapere on the Kerikeri volcanic plateau in central Northland (Fig. 2; McDowall 2000; Ling 2001). The close genetic affiliation of *N. heleios* and *N. apoda* suggests that a common ancestor may have been more widely spread in the past and that its distribution was greatly reduced, leaving what is now *N. heleios* isolated on the Kerikeri plateau, before the establishment of *N. diversus* in Northland.

Survey work by Ling & Gleeson (2001) led to the description of *N. heleios*, and Kerr & McGlynn (2001) and McGlynn & Booth (2002) have focused on distribution and management options for this species. Surveys of wetlands (DOC 2000c, d, 2001a), many of which occur in a mixture of conservation and private land, have been conducted in catchments known to contain *N. heleios*.

2.5 *Neochanna apoda*

Neochanna apoda is the most widely distributed *Neochanna* species. Its distribution suggests that it dispersed north from the South Island's West Coast across a land bridge during a Pleistocene marine regression c. 20 000–10 000 ybp (McDowall 1997a). The current distribution of *N. apoda* in the North Island is consistent with the presence of confluent river systems present at that time, while its southern limit appears influenced by late Pleistocene glaciations (Main 1989; McDowall 1996b, 1997a).

The known distribution of *N. apoda* was greatly extended by the surveys of Eldon (1968, 1978b) on the West Coast and in the Wairarapa. More recently, survey and monitoring work has been carried out in the lower North Island. Surveys by Caskey (1996, 1997, 1998, 1999, 2000, 2002) which are reported on by DOC

(1999b, 2000e, f, g, 2001b, 2002), were centred on the Stratford area in Taranaki. Rebergen (1997) undertook surveys in the Wairarapa; Francis (2000a) worked in the Wairarapa, as well as the Manawatu and Rangitikei River catchments. New populations have also been found by Horizons Regional Council and Massey University personnel in the Lake Horowhenua catchment and Santoft Forest (Horizons Regional Council 2004). On the West Coast, Butler (1999) found that *N. apoda* were locally common throughout the species' somewhat restricted and increasingly disrupted distribution. Grainger (2000) conducted fieldwork on German Terrace in the vicinity of Westport, while Eastwood (1997, 2001), and Eastwood & Butler (1999) focused on *N. apoda* habitats around Hokitika. A further survey throughout the general Franz Josef area found *N. apoda* as far south as The Forks Pakihi, adjacent to the South Okarito Forest (DOC 2000d).

3. Habitat

Considering the extensive modification of the low-lying parts of New Zealand's landscape, it is difficult to assess how current *Neochanna* habitat use reflects historic preferences (Meredith 1985; McDowall 1998a). Remnant habitat may reflect areas that were difficult to drain rather than that which contained the most productive aquatic ecosystems. Yet studies of *Neochanna* species have typically included descriptions of perceived 'ideal' habitat, usually based on the most unmodified habitat in which particular species persist today. Although descriptions of remaining habitat are illustrative, they may not be sufficient to enable identification of specific requirements, or to guide restoration actions. Regional differences in vegetation type and landscape characteristics also mean that generalisations of *Neochanna* habitat requirements cannot be made easily. Nonetheless, it is possible to detail many of the general environmental conditions typifying 'suitable' habitat for each species. The following subsections provide general habitat descriptions for each species, and then examine the hydrology, vegetation, soils, and water quality of their habitats in more detail. Where possible, comparisons are made between species. This is followed by information on the use of modified habitat and ontogenetic shifts in habitat use.

3.1 HABITAT DESCRIPTIONS

3.1.1 *Neochanna rekobua*

Chatham Island is largely covered by deep peat bogs and swampy scrubland of *Dracophyllum* spp. Skrzynski (1967) recognised that this sort of environment would provide suitable habitat for a *Neochanna* species, and was surprised when none were found. In subsequent surveys, *N. rekobua* were found along the debris-strewn shores of isolated peat lakes and their outlet streams (Mitchell 1995; DOC 2004a; McDowall 2004).

3.1.2 *Neochanna burrowsius*

Eldon (1979a) described ideal *N. burrowsius* habitat as still or very slow-flowing, meandering, swampy streams with deep pools that retain water for long periods after flow ceases. However, *N. burrowsius* have been found in a variety of habitats, which Eldon (1979a) described as seepage streams, spring streams, dams, farm ponds, scour holes, and stockwater races. The diverse range of habitats in which *N. burrowsius* are now found may be, in part, a consequence of the removal of extensive wetlands from the Canterbury Plains (Skrzynski 1968; McDowall 1998a) which has forced *N. burrowsius* to occupy whatever habitat remains that they can tolerate.

3.1.3 *Neochanna diversus*

Neochanna diversus has been described as an obligate occupier of seasonally dry, marginal areas of infertile peat bog wetlands (Barrier 1993; Dean 1995; Kerr & McGlynn 2001). It has been found in old kauri (*Agathis australis*) gum swamps and diggings (McDowall 1980a). Barrier (1993) and Hicks & Barrier (1996) found that four variables could be used to identify *N. diversus* habitat in the Waikato (Table 3): water depth during summer and winter (< 40 cm), low turbidity and little disturbance or modification (as indicated by surrounding vegetation). Barrier (1993) found *N. diversus* in habitats classified as swampy streams, wetlands and drains, but none in lake margins, ponds, dams, and lagoons.

3.1.4 *Neochanna beleios*

Because it has only recently been described (Ling & Gleeson 2001), few studies have been conducted on *N. beleios*. Perrie (2004) described *N. beleios* habitat on the shore of Lake Omapere as having a canopy of manuka (*Leptospermum scoparium*) with an understory of emergent rushes. *Neochanna beleios* has also been found at the outlet of Lake Omapere, which had nutrient-rich flowing water and riparian cover dominated by flax (*Phormium tenax*) and raupo (*Typha orientalis*; Kerr & McGlynn 2001).

3.1.5 *Neochanna apoda*

Eldon (1968) classified *N. apoda* habitat as forest puddles, white pine (kahikatea, *Podocarpus dacrydioides*) bog, borrow pits (where material has been removed by people for use elsewhere), dune swamps, and pakihi bog, all of which were shallow and ephemeral. However, in a subsequent study, forest puddles with permanent water were found to contain the highest fish densities (Eldon 1978b). Butler (1999: 28) described a West Coast *N. apoda* habitat as 'a shaded pool of clear, tea-coloured water of approximate depth of 0.23 m above a mud substrate in swampy, native bush'. In general, *N. apoda* are uncommon within beech (*Nothofagus* spp.) forest, and more frequently associated with podocarp forest (McDowall et al. 1977). Eastwood & Butler (1999) reported that *N. apoda* had been caught in habitats described variously as pakihi, hollows, ponds, pools, puddles and drains, but rarely in creeks. Richardson (1987) associated adult *N. apoda* with kahikatea forest pools, but found juveniles were most abundant in overgrown drains.

3.2 HYDROLOGY

Neochanna species occur predominantly in low-lying areas, being limited to lake margins, wetlands and generally slow-flowing waterways. Thus, water velocity appears to be the principal physico-chemical variable determining the habitat utilised by *Neochanna* species.

Eldon (1979a) maintained that numbers of *N. burrowsius* dwindled rapidly when mid-stream velocity approached 0.33 m/s, although individuals could negotiate short distances in water of twice this velocity (Eldon et al. 1978). *Neochanna diversus*, though, occurs in more sluggish water habitats, and was not found by Barrier (1993) in places where water velocity exceeded 0.16 m/s. This difference in the types of habitat these two species occupy may relate to the differing morphology of the species, with *N. burrowsius* (which has pelvic fins) being better able to cope with higher water velocity (see Fig. 3).

Water depth also influences whether or not *Neochanna* species occupy particular habitats or sites (Table 3; Fig. 4). Eldon (1979a) described *N. burrowsius* habitat as containing deep pools, some being 1–2 m deep. O'Brien (2005) also found *N. burrowsius* in habitats containing water deeper than the habitats of other *Neochanna* species (Fig. 4). *Neochanna diversus* occurred in places where water was generally shallow (Fig. 4; Barrier 1993; Hicks & Barrier 1996). Butler (1999) and Francis (2000a) surveyed a range of *N. apoda* habitats and found most fish in water ranging from 0.15 m to 0.3 m deep (Fig. 4). This depth range is supported by Eldon (1978b), who found that *N. apoda* was normally absent from water > 0.3–0.5 m deep. These findings support the hypothesis that the morphology of *Neochanna* species relates to increasing specialisation to shallow wetlands, with species having a more eel-like body plan occurring in shallower habitats (Fig. 3).

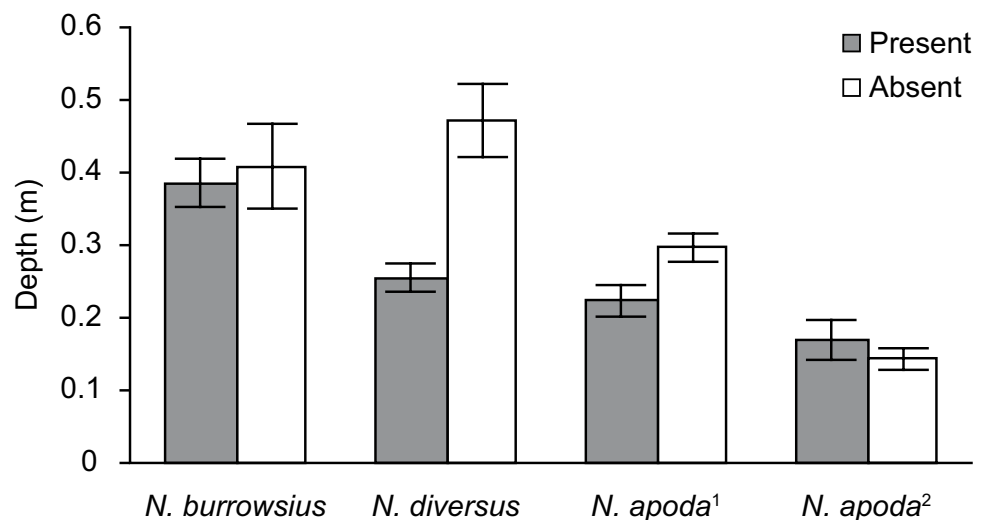
Many authors have highlighted the hydrologically disturbed nature of *Neochanna* habitats, which often experience seasonal drying and flooding, e.g. Eldon (1979a), Hicks & Barrier (1996), and McPhail (1999). Moreover, such disturbance is often viewed as important for the persistence of *Neochanna* populations, as it removes other less-tolerant fish species (Eldon 1979a; Hicks & Barrier 1996). Barrier (1993) found that 87% of sites that contained *N. diversus* dried up during summer, which removed the introduced predatory fish *Gambusia affinis* (mosquitofish). Eldon (1978b) also emphasised the importance of flood-drought cycles and the absence of other species of fish in habitats where *Neochanna* species were found. Thus, the occurrence of *Neochanna* species in habitats that dry up has been associated with their vulnerability to competitive and predatory suppression by other fish species. As Woods (1963: 36) noted, 'mudfishes do not need habitat which dries occasionally, but if they have, then other types of fish would not usually be present, so the mudfishes need have no competitors for food and shelter'.

The main factor that determines the hydrological characteristics of a site is the water source which, in turn, determines wetland type (see Clarkson et al. (2002) and Johnson & Gerbeaux (2004) for wetland definitions). *Neochanna burrowsius* inhabits small spring-fed streams, with water often sourced either from underlying aquifers or from seepage, as in small foot-hill catchments, and where scouring floods and high aquifer pressures frequently create deep pools (Eldon 1979a; O'Brien 2005). In contrast, *N. apoda* and *N. diversus* habitats

TABLE 3. SUMMARY OF RESULTS OF HABITAT INVESTIGATIONS FOR THREE *Neobanna* SPECIES. TICKS AND CROSSES INDICATE WHETHER A VARIABLE WAS STATISTICALLY SIGNIFICANT IN DETERMINING THE OCCURRENCE OF *Neobanna*. ADDITIONAL TEXT INDICATES THE NATURE OF RELATIONSHIPS AND, WHERE REQUIRED, FURTHER DESCRIPTION OF THE VARIABLE.

HABITAT VARIABLE	SPECIES AND SOURCE			
	<i>N. burrowsius</i> (O'Brien 2005)	<i>N. diversus</i> (Barrier 1993)	<i>N. apoda</i> (Butler 1999)	<i>N. apoda</i> (Francis 2000a)
Aquatic vegetation	✓Diverse submerged	✓Emergent and submerged		*Emergent
General cover	✓Macrophytes	*Wood debris	✓Foliage	
Riparian vegetation	*	✓Overhanging	*	
Tree roots/branches	✓	✓		*
Summer drought		✓		*
Disturbance rating		✓Low	*	
Water depth	*	✓Shallower	*	✓Shallower
Substrate type	*	✓Peat	*	✓Gravel
Soil type		*	*	
Conductivity	*	*	*	*
Dissolved oxygen	*	*		
pH	*	*	*	✓Low
Turbidity/clarity	*	✓Negative		*
Humic conc.		*	✓High	

Figure 4. Summary of recorded water depths (m) \pm 1 SEM for three *Neobanna* species recorded during distributional surveys. Data from: O'Brien (2005)—*N. burrowsius*; Hicks & Barrier (1996)—*N. diversus*; Francis (2000a)¹ and Butler (1999)²—*N. apoda*.



are commonly shallow pools or flooded areas created mainly by the inundation of low-lying ground by rainwater, or overflow from nearby rivers or streams during floods. For example, Hicks & Barrier (1996) classified 23% of *N. diversus* sites as having rainfall water sources only, and Francis (2000a) classified 100% of *N. apoda* sites as being of this kind. The source of water—groundwater or rainfall—influences the extent of seasonal variability in water availability, with groundwater forming the most stable habitats.

Descriptions of habitat based on seasonal patterns of water availability, flow and depth are universal and can be directly compared, in contrast to soil and vegetation descriptors, which differ depending on region.

3.2.1 Relationship between hydrological regime and *Neochanna* species body form

To assess whether the relationship between *Neochanna* species and the hydrology of their habitat hydrology conformed to the transformation hypothesis (i.e. did the most eel-like species live in the least wet or most variable habitats? see Fig. 3), we analysed habitat information for the three most studied species, i.e. *N. burrowsius*, *N. diversus*, and *N. apoda*. Descriptive data on the seasonal hydrological regimes of sites where these species had been found were collated from twelve publications (i.e. Eldon 1968, 1978b, 1979a; Cadwallader 1975a; Thompson 1987; Hicks & Barrier 1996; Eastwood 1997; Francis 2000a; Harraway 2000; Kerr & McGlynn 2001; Whareaitu 2001; Caskey 2002). This information was classified into five categories ordered along a continuum based on the extent to which sites dried up and whether they flowed or not during the wet season (Fig. 5). These categories were:

- Intermittent water (IW), where a habitat dries up completely in summer but has standing water with no flow in winter.
- Perennial water (PW), where complete drying does not occur and water may fluctuate in level, but it does not flow.
- Intermittent flow (IF), usually standing water, but some flow may occur during winter.
- Perennial flow (PF), where some flow, even if not substantial, is present year-round.
- Extreme hydrological fluctuation (EX), where sites dry up completely in summer, but flow during winter.

Thus, for example, a shallow rain-fed wetland may have intermittent water, while a deeper wetland may have perennial water. A spring-fed wetland may have intermittent or perennial flow.

Significant differences were found between the reported occurrence of the three *Neochanna* species and the five categories of hydrological regime (Fig. 6; $\chi^2 = 113$, $df = 14$, $P < 0.001$). Thus, species vary in their occupancy of different hydrological situations along the described continuum of wetness (water level) and flow fluctuation. *Neochanna diversus* was more likely to occur in habitats that dried up and was the species most often found in habitats with extreme hydrological fluctuations, which dried up in summer and flowed in winter. Although *N. apoda* was also found in habitats that dried up, it were less likely to be found at sites with flow, preferring intermittent or perennial standing water. In contrast, *N. burrowsius* was rarely found in habitats that completely dried up and showed a preference for seasonally and permanently flowing water.

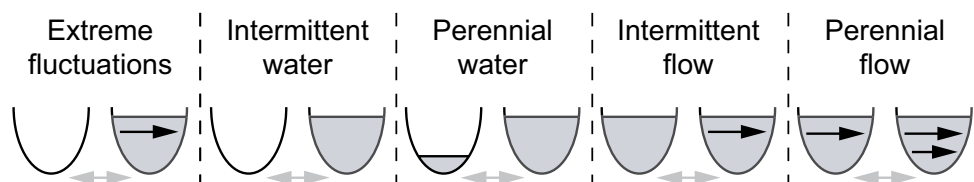


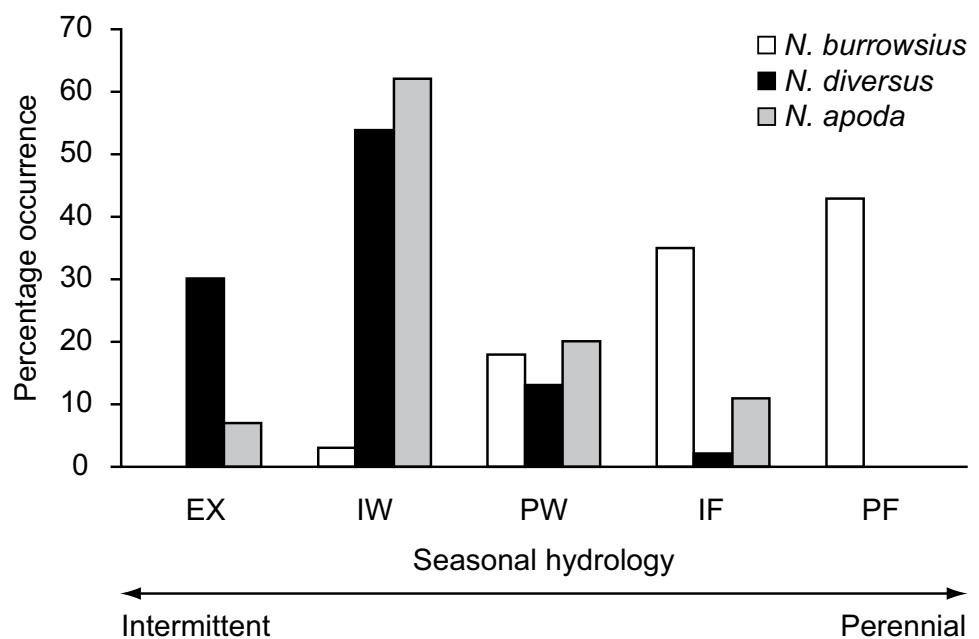
Figure 5. General classification of seasonal fluctuations in hydrological conditions typically occurring in *Neochanna* habitats. The sequence shows conditions in a habitat during summer (left member of pair) then winter (on right). The presence of water is indicated by a horizontal line and grey fill, and an absence of a line indicates habitat is dry. Water flow is indicated by an arrow, fast water flow is indicated by two arrows.

This analysis supports the conclusions of previous studies and indicates that patterns in habitat use are consistent with the placement of species in the transformation series based on their levels of morphological specialisation to hydrological situations (Fig. 3). As *N. apoda* has the most reduced fins of the species in this analysis, it is not surprising that it appears to be more intolerant of flowing water than the other two species in Fig. 6. Conversely, *N. burrowsius* has pelvic fins, which might aid locomotion in flowing water. Conservation or mitigation measures, such as assessing habitat suitability for translocation or likely effects of hydrological changes due to irrigation, should be considered on a species-specific basis.

3.3 VEGETATION

Hydrology determines many characteristics of *Neobanna* habitat. Low water velocities allow dense aquatic and semi-aquatic vegetation growth, which provides most of the habitat structure in suitable *Neobanna* habitats. The type of terrestrial vegetation present can also provide information on the level and frequency of water inundation, underlying soil type and fertility, or incidence of fire (Barrier 1993; Hicks & Barrier 1996; Grainger 2000). In addition, the presence and amount of native vegetation may reflect the level of human disturbance, as land use intensification often involves the removal of native vegetation and its replacement by introduced species. Hicks & Barrier (1996) developed a disturbance scale for the Waikato area based on terrestrial vegetation type to infer the extent of physical habitat modification. This scale ranked sites from 1 to 5, based on the abundance of native vegetation. These ranged from those where native vegetation was of 'exclusive' importance, to those where it was at 'very low' abundance and modification was ongoing. This ranking (which reflected level of disturbance) clearly discriminated habitats containing *N. diversus* from those that did not. Surface substratum was also associated with particular riparian plants. Thus, the peat soils associated with the presence of

Figure 6. Occurrence of three *Neobanna* species in habitats defined on the basis of seasonal hydrologic fluctuations. EX = Extreme fluctuations, IW = Intermittent water, PW = Perennial water, IF = Intermittent flow, PF = Perennial flow. See Fig. 5 and text for fuller descriptions of classifications. Data compiled from descriptions and measurements by various authors concerning 46 *N. diversus*, 45 *N. apoda*, and 65 *N. burrowsius* habitat descriptions (Eldon 1968, 1978b, 1979a; Cadwallader 1975a; Thompson 1987; Hicks & Barrier 1996; Eastwood 1997; Francis 2000a; Harraway 2000; Whareaitu 2001; Kerr & McGlynn 2001; Caskey 2002).



N. diversus were characteristically covered with restiad rushes (*Sporodanthus traversii* and *Empodisma minus*) and manuka, and had generally not been disturbed. However, *N. diversus* was typically absent from disturbed areas, and those with mineralised soils. Vegetation in these areas was commonly introduced crack willow (*Salix fragilis*), pussy willow (*S. reichardtii*), and grass species (*Holcus lanatus*, *Glyceria maxima* and *G. fluitans*; Hicks & Barrier 1996).

In many aquatic habitats, native submerged plants have been displaced by invasive exotic species such as watercress (*Rorippa* spp.) and monkey musk (*Mimulus* spp.). Dense aquatic plant growth impedes flow in small waterways and drains and regular mechanical removal is often required to maintain drainage (Hudson & Harding 2004). This maintenance can adversely affect *Neochanna* populations (Eldon 1978b). However, the presence of vigorously growing exotic aquatic plants may also have mitigated, to an extent, the impacts of land use changes on some *Neochanna* species. For example, when areas of wetland have been drained, *N. burrowsius* has been forced to utilise drainage ditches and habitat peripheries. By slowing water flow in channelised watercourses, aquatic plants, including exotic species, may create favourable conditions in otherwise 'atypical' habitat. Nonetheless, O'Brien (2005) found *N. burrowsius* was significantly associated with certain indigenous aquatic plant species, particularly water milfoil (*Myriophyllum* spp.), red pondweed (*Potamogeton cheesemani*), and the free-floating plants duck weed (*Lemna minor*) and water fern (*Azolla filiculoides*). The association of *N. burrowsius* with indigenous species may also be a reflection the level of disturbance (generally from agricultural activities) occurring, similar to the patterns found for *N. diversus*.

When the importance of riparian vegetation is considered, statistical analyses have not always supported general perceptions of 'preferred' habitat (Table 3). For instance, although shade was thought to be important for *N. apoda* (Butler 1999), there has been little statistical relationship demonstrated between riparian canopy cover and the occurrence of *Neochanna* species, except for directly overhanging vegetation (Table 3). The primary influence of riparian vegetation may be through the provision of complex shelter and moist refuges in the form of stumps, fallen timber, debris and irregularities in the ground, especially during dry periods (Eldon 1978a, b; Meredith 1985; O'Brien 2005). Indeed, anecdotal evidence suggests that *N. apoda* abundance declined after habitats were cleared of old fallen wood (Eldon 1978b). Overhanging margin vegetation, and aquatic emergent and submerged vegetation, also provide direct cover for *Neochanna* species (Barrier 1993; Hicks & Barrier 1996; O'Brien 2005). Complex vegetation at the water surface may be important during periods of hypoxia or when fish are feeding, and fish have been observed resting on vegetation just below the water surface (Eldon 1979a; Thompson 1987; Koehn & Raadik 1991; O'Brien 2005).

3.4 SOILS

At a large scale, the distribution of *N. diversus* and *N. beletos* has appeared to correlate with the occurrence of 'acidic peaty soils' (Ling 2001). This perception led Butler (1999) to test the hypothesis that *N. apoda* were also associated with peat soils on the West Coast. Analysis of records indicated that *N. apoda* was found predominantly on Silt-mantled Perch-gley Podzols and Acidic Allophanic

Brown Soils, with only 5.9% of occurrences being from Acidic Organic Soils, such as peat (Butler 1999; soil data converted from the New Zealand Genetic Soil Classification (Taylor & Pohlen 1962) to the New Zealand Soil Classification (Hewitt 1998) using Wallace et al. (2000)). However, Butler (1999) pointed out that the presence of *N. apoda* was still in proportion to the occurrence of peat soils on the West Coast, and that peat soils can develop in small isolated hollows, which are too small to feature on soil maps. Further, at a small scale, underlying soil categories did not predict the presence of *N. diversus* (Hicks & Barrier 1996). This was despite the importance of surface substratum type, with *N. diversus* being associated more often with peat rather than mineralised soils (Hicks & Barrier 1996). Thus, it appears that habitats with peat soils are unlikely to be specifically preferred by *Neochanna* species, and it is more likely that their occurrence in such habitats reflects their lowland wetland distribution.

3.5 WATER QUALITY

Few studies have found that water quality determines the occurrence of *Neochanna* species (Table 3). This is probably because *Neochanna* species have a broad tolerance of conditions, and reduced water quality often occurs seasonally in their habitats. Nevertheless, it is suggested that *Neochanna* prefer clean,

unpolluted water and that their presence is a good indicator of the health of water bodies (Young 1996; McDowall 1996c). Indeed, although pH and dissolved oxygen concentrations may be low in habitats occupied by *Neochanna*, the water is seldom 'foul-smelling' (Eldon 1978b, 1979a). In addition, the abundance of *Neochanna* species has been negatively related to high levels of turbidity and nutrients, conditions that often indicate the presence of human-related disturbance and inputs (Barrier 1993; Hicks & Barrier 1996; Butler 1999). Studies involving the readily measured water quality parameters pH, temperature, and dissolved oxygen are detailed in the following sections, as well as laboratory-based research into salinity tolerance.

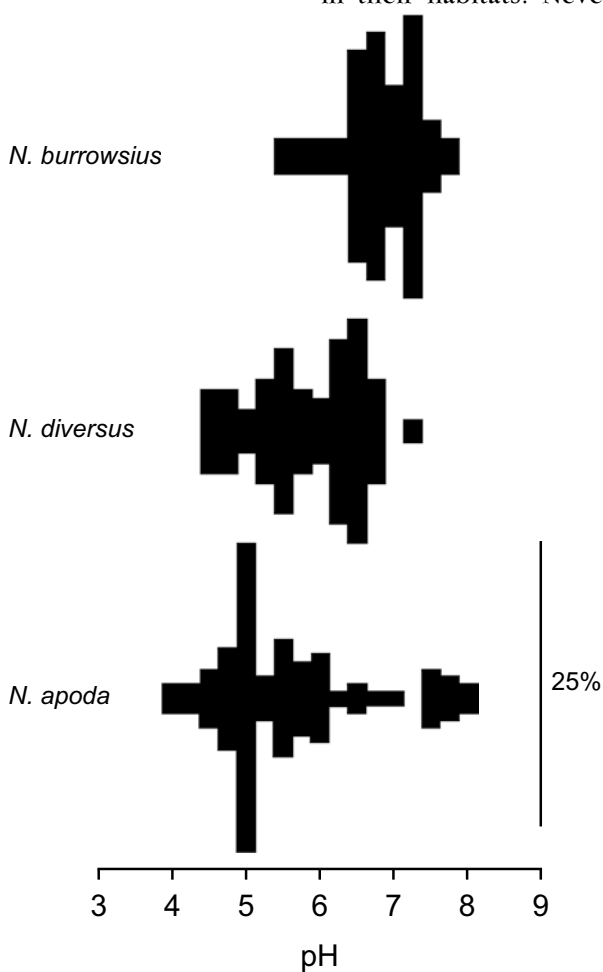


Figure 7. Occurrence (percentage frequency) of three *Neochanna* species related to habitat pH. Scale bar at bottom right indicates 25% of records. Frequency histograms were generated using 0.25 pH unit intervals. Data collated from Eldon (1979a), Dean (1995), Hicks & Barrier (1996), Eastwood (1997), Butler (1999), Caskey (1999), Francis (2000a), Grainger (2000), and O'Brien (2005).

3.5.1 pH

Analysis of available data (*N. burrowsius*: O'Brien (2005), Eldon (1979a); *N. diversus*: Hicks & Barrier (1996), Dean (1995); *N. apoda*: Butler (1999), Grainger (2000), Caskey (2000), Francis (2000a)) indicates that *Neochanna* species occur in habitats with distinct (but overlapping) pH ranges (Fig. 7). It should be noted that for *N. apoda*, all pH values greater than 7.0 were recorded by Francis (2000a) in the Manawatu and Rangitikei regions. Even here, though, habitats containing *N. apoda* had a lower mean pH (7.6) than those where *N. apoda* were absent (mean pH 8.4), suggesting a tendency for *N. apoda* to occur in habitat with lower pH. Except for these records from Manawatu and Rangitikei, Fig. 7 shows a trend that fits expectations based on the transformation series. That is, for *N. burrowsius* to occur in habitat with

higher pH values (mode: pH 7.25) than *N. diversus* (mode: pH 6.5) and *N. apoda* (mode: pH 5.0). Tolerance of low pH may be a further specialisation to life in wetlands represented by the transformation series (see Fig. 3), but the extent to which these field-based measurements reflect different underlying physiological tolerances among the species remains to be studied.

Acidity (low pH) affects fish through reproductive failure, the coagulation of mucus on gills, other forms of interference with respiratory processes (acidosis reduces blood oxygen content and impairs oxygen delivery), and electrolyte and acid-base balance (Dean 1995). pH levels can also have consequences for survival if coupled with low dissolved oxygen concentrations. Dean (1995) measured oxygen consumption of *N. diversus* at various water temperatures and pH. It was found that although *N. diversus* could compensate for increased temperature at pH 5.5 and 7, at high temperature (20°C) and low pH (4), *N. diversus* exhibited suppressed oxygen consumption. This indicated that fish were experiencing difficulties extracting oxygen from the acidic water and that conditions were approaching the limit of their tolerance (Dean 1995). *Neochanna apoda* may be more tolerant of this situation than *N. diversus*, as Grainger (2000) found *N. apoda* at pH 4.0–4.9 in habitats that also experienced high water temperatures (up to 26°C).

3.5.2 Water temperature

Neochanna species can tolerate a wide range of temperatures. Eldon (1979a) found *N. burrowsius* occurred in water temperatures ranging from 0.5–24°C and noted that habitats could freeze in winter. *Neochanna apoda* remained active and were trapped in ponds despite overnight surface ice formation (Eastwood & Butler 1999). However, Eldon (1978b) noted reduced activity in captive fish when water temperature fell below 10°C. At the other end of the scale, O'Brien (2005) recorded a daily maximum of 26°C in a shaded pool containing *N. burrowsius*. Summer temperatures measured in the Whangamarino Wetland showed that *N. diversus* routinely tolerated temperatures of 19°C (Dean 1995), and have been recorded surviving at 26°C (Thompson 1987). In *N. apoda* habitat, maximum spot temperatures of 22°C (Eldon 1978b), and 26°C (Grainger 2000) have been recorded. The temperature tolerance of *Neochanna* species may be higher than other galaxiids, as accidental overheating of *N. cleaveri* individuals indicated that the species can tolerate higher temperatures than *Galaxias maculatus* (inanga; Andrews 1991). The ability to tolerate extremes in temperature is likely to be necessary if aquatic habitats dry up, as terrestrial habitats have greater and more rapid changes in temperature (Meredith 1985).

3.5.3 Dissolved oxygen

Neochanna species have been found in habitats that experience extremely low levels of dissolved oxygen (Eldon 1979a; Hicks & Barrier 1996; Dean 1995; Grainger 2000; O'Brien 2005). For example, dissolved oxygen levels of 0.3–1.8 mg/L at the substratum surface occurred in *N. diversus* habitat (McPhail 1999). Pakahi wetland habitat containing *N. apoda* had a mean dissolved oxygen concentration of 1.4 mg/L (Grainger 2000). *Neochanna burrowsius* even persist in habitats which have periods when there is no detectable dissolved oxygen (Eldon 1979a). Extremely low levels of dissolved oxygen may be a common occurrence in adult *Neochanna* habitat. Higher oxygen levels are likely to be required for successful spawning and fry survival, however (Eldon 1993). Although *N. burrowsius* eggs

survived brief exposure to hypoxia, deformity and mortality occurred when eggs developed in water with only moderately reduced (80% of air saturation) dissolved oxygen concentrations (O'Brien 2005).

3.5.4 Salinity

Some *Neochanna* species may retain an ancestral euryhaline regulatory ability that provides tolerance to saline conditions. The ability to withstand a degree of salinity is greatest in *N. cleaveri*, and adults can be found in brackish water (Jackson & Davies 1982; Andrews 1991). Moreover, *N. cleaveri* retains a facultative diadromous life cycle, with fry able to develop at sea—as occurs in migratory *Galaxias* (whitebait) species (Fulton 1986; Andrews 1991; McDowall 1997a). For New Zealand *Neochanna* species, Meredith (1985) showed that adult *N. burrowsius* can survive for a week in up to 60% sea water, although some individuals had problems regulating buoyancy. In contrast, *N. diversus* fry showed a lower tolerance of salinity, with no fry surviving longer than 24 hours in 63% seawater (Perrie 2004). However, when fry were acclimated, by slowly increasing salinity, long-term survival in up to 54% seawater was predicted (Perrie 2004). This is a lower salinity than that tolerated by adult *N. burrowsius*, despite the expectation that fry stages would be more tolerant of salinity than adults. It is possible that salinity tolerance may be higher in less specialised (more galaxiid-like) *Neochanna* species (see Fig. 3), supporting suggestions that the common ancestor of *N. burrowsius* and *N. rekobua* initially retained a diadromous life-history (Waters & McDowall 2005).

3.6 MODIFIED HABITAT

Though it is often assumed that *Neochanna* species require unmodified 'natural' wetlands, this assumption can prove misleading (Barrier et al. 1996). Statistical analysis by Francis (2000a) indicated that *N. apoda* in the Wairarapa were associated with agricultural, rather than undeveloped land. Indeed, most *Neochanna* populations occur in water bodies surrounded by agriculturally productive land. *Neochanna* species are resilient and can persist in habitats that show little resemblance to their former natural state (McDowall 1984, 1985). Human activity can even create habitat for *Neochanna*; for example, *N. cleaveri* occupy test holes (1 m², 0.5–1 m deep) dug in the search for alluvial tin (Andrews 1991); and *N. diversus* and *N. beletos* have been found in the holes left by kauri gum diggers (McDowall 1990). Modified waterways such as drains, ditches, and water-races can, in some situations, support *Neochanna* populations of greater density than those in less-modified wetland remnants (Eldon 1978b; Hicks & Barrier 1996; O'Brien 2005). One of the highest reported catches of *Neochanna* per unit effort (68 fish per trap night) was of *N. diversus* from a roadside drain that had not been cleaned for some years (Barrier et al. 1996). The continuing process of land drainage may increasingly constrain *Neochanna* to agricultural drains and races. Eventually, as water tables lower, these may provide the only remaining suitable habitat. However, such modified habitat only represents suitable habitat when it contains aquatic plants which are often considered weeds and intensively managed. Hence, advocacy and the development of best-practice guidelines are essential if *Neochanna* populations are to persist in modified agricultural waterways.

3.7 ONTOGENETIC SHIFT

Neochanna species exhibit a well-defined ontogenetic shift in behaviour and habitat use. Larvae and small juveniles forage during the day and are pelagic and loosely shoaling until 30–50 mm long (Eldon 1979c; Thompson 1987, McDowall 1990), whereas adult *Neochanna* are benthic and cryptic (Eldon 1979d). Adults are also predominantly nocturnal, as indicated by circadian rhythms (Dean 1995). Furthermore, compared with other galaxiid species, the forebrains of *Neochanna* species enlarge to a greater extent during ontogenetic changes, which is correlated with the development of nocturnal behaviour (Cadwallader 1975b).

Ontogenetic differences in habitat use appear to occur in all *Neochanna* species. Eldon (1978b) observed that even in confined forest habitats, the type of cover used by *N. apoda* differed depending on fish size, with small fish using leaves, twigs and sticks on the forest floor as cover, and larger fish found mainly in holes under the roots of trees. Juvenile and small *N. burrowsius* were more common at the periphery of habitats, especially when population densities were high (Eldon et al. 1978; Taylor & O'Brien 2000; O'Brien 2005). In contrast, Kerr & McGlynn (2001) commented that adult *N. diversis* tended to disperse out into the extremities of a wetland, into areas which were the first to dry in summer, while fry and juvenile *N. diversus* kept to the channels, drains or natural waterways of the wetland system. Indirect morphological evidence suggests that *N. rekobua* also exhibit an ontogenetic shift in behaviour and habitat use. Unlike other *Neochanna* species, and *N. rekobua* adults, *N. rekobua* juveniles have a forked caudal fin (McDowall 2004). Together with the pelvic fins, a forked caudal fin might increase swimming ability, suggesting that juveniles are strongly pelagic. Perrie (2004) found that juvenile *N. diversus* avoided certain concentrations of conspecific odour from adults. Juvenile *Neochanna* may thus use such cues to disperse and avoid intraspecific competition, to achieve greater growth rates and larger size before summer habitat drying occurs.

3.8 SUMMARY

- *Neochanna* species occur in low-lying areas, and are generally limited to lake margins, wetlands, and other waterways with little or no flow.
- Hydrological characteristics, including water depth, source and seasonal fluctuation in water level and flow, are important determinants of habitat suitability for *Neochanna* species.
- Categorising habitat in terms of seasonal hydrological fluctuations highlighted important habitat differences between the species most studied:
 - N. burrowsius* occurs mainly in habitats with perennial or intermittent flow and is rare in habitats that completely dry up.
 - N. diversus* occurs predominantly in sites that dry up, but also occurs in sites with extreme fluctuations, drying up in summer and flowing in winter.
 - N. apoda* occurs predominantly in habitats with standing water and is rarely found where there is flow.
- Vegetation is an important feature of *Neochanna* habitat, especially aquatic and overhanging vegetation and, to a lesser extent, riparian vegetation.

- A complex habitat is required to ensure the presence of sufficient cover and moist refuges during dry periods.
- The type of vegetation at a site, especially the presence of indigenous vegetation, may reflect human disturbance and has been associated with *Neobanna* occurrence.
- Underlying soil type is generally a poor determinant of small-scale *Neobanna* distribution.
- Although tolerant of wide temperature, pH, and dissolved oxygen ranges, *Neobanna* species require good quality water, especially during breeding.
- Differences in habitat hydrology, pH and salinity tolerance support the placement of *Neobanna* species in the transformation series.
- *Neobanna* can be abundant in modified or artificial waterways.
- *Neobanna* species undergo ontogenetic shifts with larvae, juveniles, and adults utilising different types of habitat.

4. Feeding and diet

As described in section 1.2, there are distinctive trends in the teeth morphology of *Neobanna* species related to the transformation series (see Fig. 3). These differences might reflect differences in diet between species. In general, *Neobanna* species have small eyes, and the part of the brain relating to vision—the optic lobe—is proportionally reduced compared with other Galaxiidae (Günther 1867; Cadwallader 1975b). However, *Neobanna* have an enhanced olfactory sense, with elongated, tubular, and forward-facing anterior nostrils which, in conjunction with an extensive system of sensory pores, may compensate for their apparently reduced visual sense (McDowall 1997b). *Neobanna* species have the typical galaxiid primary trunk lateral line and well-developed sensory pores in the head region (McDowall 1970). Further, *N. burrowsius*, *N. diversus*, and *N. apoda* have an accessory lateral line, which may assist them to locate terrestrial prey at the water surface (McDowall 1997b). *Neobanna* species are thus well-equipped to forage under low light conditions (Cadwallader 1975b; Thompson 1987). The following subsections describe foraging behaviours and diet, including cannibalism.

4.1 FORAGING BEHAVIOURS

Adult *Neobanna* in the wild usually forage nocturnally. They are opportunistic, however, and become accustomed to feeding during the day in captivity (Eldon 1978b; Thompson 1987; L. O'Brien, per. obs.). Koehn & Raadik (1991) described foraging behaviour of *N. cleaveri* as 'browsing' around open areas, whereas Andrews (1991: 58) observed *N. cleaveri* to burrow 'vigorously through the sediment, stirring up large quantities as though searching for food'. A similar behaviour of 'grubbing' through sediment has been observed in *N. burrowsius*, with fish sometimes positioned vertically during foraging (L. O'Brien, pers. obs.). Most species have been observed feeding at the water surface, especially in

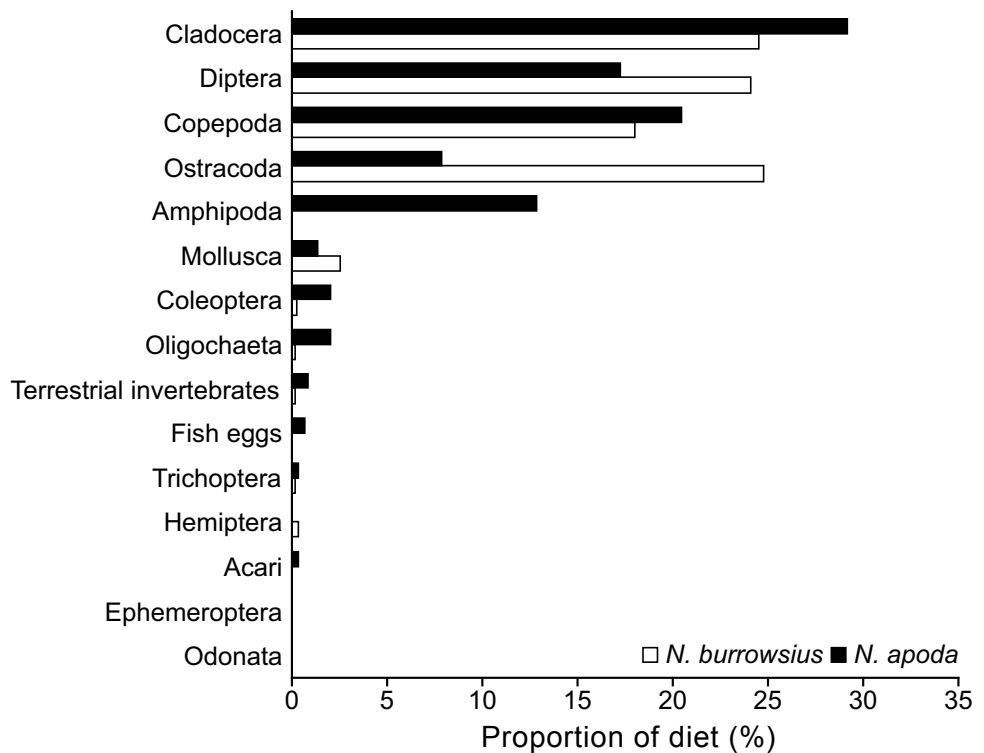
hypoxic waters (Davidson 1951; Thompson 1987; Andrews 1991; O'Brien 2005). Furthermore, Thompson (1987) noted that *N. diversus* would rest on surface weeds, possibly waiting for prey to fall on the water, as terrestrial prey items are included in the diet of *Neochanna* species (Fig. 8).

Despite their apparently reduced visual senses (McDowall 1997b), Thompson (1987) observed *N. diversus* actively pursuing prey in tanks, and Eldon (1978b, 1979b) reported that *N. apoda* and *N. burrowsius* appeared to see small active prey items. However, Eldon (1978b) also implied that *N. apoda* were sluggish and that if a prey item moved too quickly, fish could not follow the prey visually and would strike unsuccessfully. Thompson (1987) described how *N. diversus* of all sizes would coil their bodies in a manner similar to a snake, and then launch themselves forward at prey. Visual drift feeding occurs in juvenile *N. burrowsius* and *N. diversus* (Thompson 1987; L. O'Brien, pers. obs.). Thompson (1987) observed that juvenile *N. diversus* swam 'on station' throughout the day and night. They fed on 'passing morsels' in the drift, at water velocities up to 0.03 m/s. Overall, *Neochanna* species exhibit a wide variety of foraging behaviours, which differ depending on life stage, the prey species present, and habitat characteristics.

4.2 DIET

Neochanna diet usually reflects the availability of prey species and their ability to capture the prey, which in turn is influenced by habitat factors. Although they are generalist carnivores, *Neochanna* species mainly consume small, slow-moving aquatic and terrestrial prey, including earthworms (Oligochaeta; McDowall 2000). Stomach content analyses have often involved a relatively small number of samples. However, Eldon (1978b, 1979b) conducted extensive dietary

Figure 8. Summary of the main dietary components of *N. burrowsius* (sample size = 367; Eldon 1979b), and *N. apoda* (sample size = 264; Eldon 1978b). Data for juvenile and adult fish combined.



studies on both juvenile and adult *N. burrowsius* and *N. apoda* in a variety of habitats, and concluded that the results of studies with large sample sizes were similar to those from studies with smaller sample sizes. Diet composition data (Fig. 8) from Eldon (1978b; 1979b) indicated that the diets of both *N. burrowsius* and *N. apoda* consist predominantly of Diptera (midges; Chironomidae) larvae and micro-crustaceans (i.e. Cladocera, Copepoda, Ostracoda, and Amphipoda). Lane (1964) and Thompson (1987) also found that the stomach contents of *N. burrowsius* and *N. diversus* contained exclusively micro-crustaceans. Eldon's dietary data (Fig. 8) further showed that *N. burrowsius* consumed many snails (Mollusca), whereas *N. apoda* consumed many terrestrial items, including worms (Oligochaeta) and beetles (Coleoptera).

Other dietary patterns have also been observed. Although adult *N. burrowsius* diets were generally dominated by micro-crustaceans, Diptera were more abundant in diets during summer (Eldon 1979b). Furthermore, the diets of adult *N. apoda* were habitat- and size-dependent. Cladocera and Copepoda were usually important; but at one site, these taxa decreased in importance as fish grew, with *Paracalliope fluviatilis* (amphipod) and *Austrosimulium* spp. (sandfly larvae) becoming dominant dietary items (Eldon 1978b). The most common large food items taken by *N. apoda* were earthworms, which tended to be consumed immediately after water returned to dried wetlands and worms were driven to the ground surface. *Paranepbrops planifrons* (freshwater crayfish, koura) remains were also taken from the stomach of a single *N. apoda* from Harihari (Eldon 1978b). As prey selectivity studies (comparing diet with prey availability in habitat) have not been conducted, it is not known if the observed differences in diet are a reflection of differences in tooth morphology between species.

4.3 CANNIBALISM

Diet studies involving *N. burrowsius* in the wild have provided evidence of high levels of egg cannibalism, even though investigations were not limited to the peak spawning period (Cadwallader 1975a; Eldon 1979b). Cadwallader (1975a) found that *N. burrowsius* eggs were the third most abundant item eaten. Adults had eaten eggs at three locations, and at one site 13 fish had consumed a total of 23 eggs. In a long-term study, 1.7% of *N. burrowsius* had cannibalised eggs over a 9-month period (Eldon 1979b). Furthermore, *N. diversus* and *N. burrowsius* have been observed eating eggs during spawning activities (Perrie 2004; O'Brien 2005). O'Brien (2005) recorded that 32 ± 17 (mean \pm SE) *N. burrowsius* eggs were consumed per night in experimental tanks that lacked vegetation cover. *Neochanna apoda* eggs were also commonly taken by adults, but only one fry was found to have been eaten in the wild (Eldon 1978b). In captivity, adult *N. apoda* have cannibalised others during transport (Eldon 1969). Captive *N. diversus* have also consumed conspecific juveniles in aquaria (Town 1981; Thompson 1987). Cannibalism could, therefore, be a significant source of egg and larvae mortality in *Neochanna* species.

4.4 SUMMARY

- *Neobanna* species have small eyes, and a proportionally reduced optic lobe, but an enhanced olfactory sense and an extensive system of sensory pores, including an accessory lateral line.
- *Neobanna* species exhibit a diverse range of foraging behaviours, including surface feeding, drift feeding, and benthic foraging.
- Diets consist mainly of small, slow-moving micro-crustaceans and Diptera larvae.
- Seasonal and size-dependent differences in diet occur.
- Cannibalism of eggs and larvae is common in the wild and in captivity.

5. Reproduction

Neobanna species complete their entire life in freshwater habitats, except for some *N. cleaveri* individuals that retain a diadromous life cycle with juveniles developing in the marine environment (Fulton 1986). Sexual maturity is reached in the first year (*N. burrowsius*; Eldon 1979c), or second year (*N. apoda*; Eldon 1978b). The sexes can be differentiated, especially during the spawning period (O'Brien & Dunn 2005). Differences are similar to other Galaxiidae, with males having a pointed papilla, whereas the genital area in females is bulbous

(Cadwallader 1973). Spawning is thought to occur in the adult habitat (Eldon 1978b, 1979c). Eggs are approximately 1–3 mm in diameter (Table 4), extremely adhesive, and will initially attach to almost any surface; although they are easily dislodged by physical disturbance (Eldon 1979c). Embryos take several weeks to develop and hatch, the exact time being dependent, primarily, on water temperature and oxygen availability (Eldon 1978b; Eldon 1979c; O'Brien 2005). Newly hatched *Neobanna* larvae are 4–9 mm long (McDowall 1990), and although they have yolk sacs, they can generally consume small prey items immediately (Eldon 1978b). The following sections detail what is known about *Neobanna* species fecundity, and spawning behaviour, timing, and habitat.

TABLE 4. DIAMETER OF *Neobanna* EGGS, MEASURED BEFORE OR AFTER SPAWNING. RANGE OR MEAN VALUES GIVEN. DATA FROM CADWALLADER (1973), ELDON (1978b, 1979c), McDOWALL & FRANKENBERG (1981), PERRIE (2004), AND O'BRIEN (2005).

SPECIES	EGG DIAMETER (mm)	
	Unspawned	Spawned
<i>N. cleaveri</i>	1.3–1.5	
<i>N. burrowsius</i>	1.2–1.4	1.6–1.8
<i>N. diversus</i>	1.6	2.2
<i>N. apoda</i>	2.4–2.6	

5.1 FECUNDITY

An important reproductive characteristic among *Neobanna* species is the relationship between fecundity and body length (Fig. 9). *Neobanna burrowsius* produces substantially more eggs than *N. diversus* and *N. apoda*, and its fecundity is similar to that of the migratory galaxiid species (Cadwallader 1975a). In general, there is a tendency for a trade-off between fecundity and egg size in fish (i.e. many small eggs or a few large eggs) because of constraints on energy and body volume available to the gonads (O'Brien 2005). While fecundity is straightforward to determine, egg size is often based on eggs dissected from gonads, potentially