The conservation ecology of Canterbury mudfish

(*Neochanna burrowsis*)

**DOCTORAL THESIS SUMMARY**

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A pool on Dog Kennel Stream, South Canterbury in 1998 that contained an abundance of Canterbury mudfish fry.

‘It is a paradox of our times that a creature which can grow and breed in such a tiny scrap of habitat is so rare’ Eldon (1986, p. 19).
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Abstract

The Canterbury mudfish (*Neochanna burrowsius*; Galaxiidae) is a small, acutely threatened freshwater fish endemic to South Island, New Zealand, which has traits related to its historic occurrence in the wetlands of the Canterbury Plains. These wetlands have been largely transformed into productive agricultural land, with consequent fragmentation and local extinction of *N. burrowsius* populations. *N. burrowsius* now persists primarily in agricultural waterways across these increasingly drought-prone plains. I examined aspects of *N. burrowsius* habitat, inter-specific interactions, and reproduction of importance for their conservation. Field studies focused on four sites identified as important remnant *N. burrowsius* habitats. These were distributed across the latitudinal range of *N. burrowsius* and encompassed different hydrological and agricultural disturbance regimes, and fish communities.

Distributions of *N. burrowsius* within each site were patchy. Furthermore, the location of *N. burrowsius* aggregations within sites was temporally variable, and was influenced by changes in habitat quality and the presence of predatory fish. Predatory fish also affected *N. burrowsius* activity and abundance. At sites with intermittent flow that regularly dried up, successful strategies of drought survival were dependent on the size of *N. burrowsius*. Comparisons between populations indicated differences in size structure, individual growth, recruitment, deformities, disease, and parasitic infection. Experimental investigations highlighted the behavioural and physiological plasticity of *N. burrowsius*’ responses to competition, environmental conditions during spawning, and the ability of embryos to tolerate hypoxia that likely aid survival in wetland habitats. Macrophytes were also revealed to be a key element in *N. burrowsius* habitat, with particular macrophyte species associated with different *N. burrowsius* life stages. They also provide spawning substrate critical to the survival of eggs.

This research indicates that hydrological disturbance and the presence of predatory fish likely had a greater effect on population characteristics than the presence of competitors, geographical location, and direct agricultural disturbance. Thus, recognising these factors will be critical in the conservation of *N. burrowsius*. 
General introduction to *Neochanna burrowsius*.

Freshwater fish stocks are declining worldwide (Moyle 1995; Warren et al. 2000); yet endemic fish species receive relatively little research or conservation attention (LeCren 1990; Maitland 1995; Johnston 1999). Often less is known about rare or threatened fish species, than those that are more common, or are valued as a human food resource (LeCren 1990). Increasingly, the paucity of information available for many species is a barrier to determining appropriate conservation actions (Hicks & Reeves 1994). Ichthyologists have been implored to address this problem. Pister (1999) stated that it was the professional responsibility of researchers to participate in the preservation of freshwater fishes. Indeed, unless knowledge is improved it will be difficult to solve the increasing conflict between conserving fish species and the human need for land and water resources (May & Brown 2002). In New Zealand, this tension is pronounced in the lowland plains of the east coast, where extensive areas of wetland have been drained, and irrigation is now required to improve land productivity (McDowall 1998; Morgan et al. 2002).

Globally, and in New Zealand, the extent of lowland wetlands has contracted, largely due to anthropogenic disturbance (Wilson 1982; Lemly 1994; Cromarty & Scott 1996; Bourne 2000; Jenkins et al. 2003). New Zealand has lost an estimated 90 % of its wetlands in the last 150 years (Johnson & Gerbeaux 2004), yet wetland drainage still occurs legally, albeit at a much slower rate (ECan 2002). Continued wetland loss is of concern as the structural complexity of wetlands and their unique hydrology, can provide important refugia for endemic fish, especially from introduced predatory fish (Chapman et al. 1996, 2002). In New Zealand, wetland loss has directly threatened the persistence of species in the genus *Neochanna* (Galaxiidae; McDowall 1982, 1998; DoC 2003).

*Neochanna* contains six species, five of which are endemic to New Zealand. *Neochanna* occur throughout most of the low-lying areas of New Zealand in allopatric distributions. The focus of this thesis, Canterbury mudfish (*N. burrowsius*) occurs on the alluvial Canterbury Plains on the east coast of South Island, New Zealand.
**Conservation and research**

*N. burrowsius* was originally described by Phillipps (1926), from a sample sent to him by Mr A. Burrows, of West Oxford. A further specimen collected from Ashburton was reported by Stokell (1938). By this time, the Canterbury Plains had been transformed from vast wetlands into productive farmland. Although much of the evidence is anecdotal, *N. burrowsius* is likely to have been prevalent in these former wetlands (McDowall 1998). By the late 1960s there was serious concern for *N. burrowsius*’ persistence, and thus Skrzynski (1968) published all known information on the species, entitling his paper ‘a vanishing species.’ Skrzynski (1968, p. 695) concluded that ‘it seems unlikely that Canterbury mudfish will continue to survive on the Canterbury Plains with the land continually being modified.’ Subsequent authors have emphasised this point, e.g. Cadwallader (1975), Eldon (1979a, 1993), and McDowall (1998). Indeed, local extinction has been on-going; Skrzynski (1968) listed nine locations where *N. burrowsius* specimens had been collected, but re-confirmed their occurrence in only four. Cadwallader (1973) found *N. burrowsius* in 13 locations, but failed to locate any in a seven previously occupied habitats. Whereas, Eldon (1979a) located 20 *N. burrowsius* populations, however also noted one or two local extinctions. Several of these populations are now also thought extinct (Eldon 1993).

G. A. (Tony) Eldon started study on *N. burrowsius* in 1975 and published as a series of papers on their habitat and inter-specific relationships (Eldon 1979a); diet (Eldon 1979b); and breeding, growth, and aestivation (Eldon 1979c); and their response to a severe drought (Eldon et al. 1978). During the 1980s, research attention was directed to the physiological adaptations of *N. burrowsius* (Meredith 1981, 1985; Meredith et al. 1982; Wells et al. 1984). Further, during the 1980s efforts were being made to establish new populations of *N. burrowsius* (Eldon 1983, 1986, 1988a, b, 1989; Eldon & Field-Dodgson 1983). The 1990s saw an increased effort to manage the species with conservation guidelines being written (Eldon 1993). *N. burrowsius* was noted as a taonga (treasured) species in the Ngāi Tahu Deed of settlement, 1997, clause 12.14 (Te Rūnanga o Ngāi Tahu & Her Majesty the Queen 1997). Further, a protective covenant was placed on an area containing *N. burrowsius* in Dog Kennel Stream, South Canterbury (Gray 2000). Recent research into the genetic population structure of *N. burrowsius* found low levels of genetic diversity, further highlighting its vulnerability (Davey et al. 2003). Currently, *N. burrowsius* is classified by the Department of Conservation as an acutely threatened species that is Nationally Endangered (Hitchmough 2002), and included in a threatened species recovery plan (DoC 2003). Recently, a report detailing the captive management of *Neochanna* species was published (O’Brien & Dunn 2005).
**Biological background**

![Image](image_url)

Figure 1. Canterbury mudfish (*N. burrowsius*).

*N. burrowsius* are small (< 160 mm), scaleless, cylindrical fish, with anguilliform locomotion, laterally placed pectoral fins, reduced pelvic fins, and a fleshy caudal peduncle (Figure 1; McDowall 1990). It is thus considered morphologically adapted to cluttered wetland habitats, with an ability to move through dense vegetation (McDowall 1990). *N. burrowsius*, like many other Galaxiidae, has an amphibious nature (Meredith 1985). Placed in hypoxic water *N. burrowsius* will gulp air and readily leave the water if conditions exceed their physiological tolerances (Meredith 1981). *N. burrowsius* have high rates of cutaneous respiration and a low resting metabolic rate, resulting in a tolerance of emersed conditions. Thus, they can survive at least one month out of water in laboratory conditions (Meredith 1985). These traits have allowed *N. burrowsius* populations to persist in spring- or seepage-fed wetland pools and streams with fluctuating water levels and flow. In the wild when habitats have dried up, *N. burrowsius* have been found in holes within soil banks, among tree roots, under logs and vegetation, and in subterranean cavities (Eldon et al. 1978; Eldon 1979a, c).

*N. burrowsius* are a non-territorial, non-migratory fish. During early spring females scatter up to several thousand eggs amongst vegetation at the water surface (Eldon 1979c). Fry and juvenile fish are pelagic and diurnal, whereas adults are nocturnal, benthic, and cryptic, thus they are rarely seen by the casual observer (Eldon 1979c). *N. burrowsius* have traits common in species found in disturbed environments, such as high fecundity, early sexual maturity (0+; Eldon 1979c), and a tendency to disperse and colonise new habitat (Eldon et al. 1978). By virtue of these traits, *N. burrowsius* has persisted despite its wetland habitat and the hydrology of the Canterbury Plains being radically and irreversibly changed.
The Canterbury Plains

The Canterbury Plains were formed by the deposition of outwash gravels transported from the Southern Alps by large braided rivers, which shaped extensive alluvial fans. These gravels created confined aquifers as the materials deposited during glacial periods were overlain by oceanic deposits during interglacial marine transgressions when sea levels were higher (Fitzharris et al. 1992). These processes have led to the development of artesian springs and aquifers which occur across the plains. Four large braided rivers bisect the plains, being fed by alpine lake systems close to the main divide (Figure 2). Thus, these river systems often receive orographic rainfall that does not reach the easterly plains, and have high base flows. Annual rainfall on the east coast is often less than 700 mm, resulting in a moisture deficit during both summer and autumn (Fitzharris et al. 1992). This low rainfall meant that between the large alpine river systems, smaller rivers with foothill catchments rarely had the flow to maintain a channel to the sea, continuously. Connection to the sea was also impeded by long stretches of gravel bars and dunes formed as wave action piled alluvial gravels against the shore (Fitzharris et al. 1992). Furthermore, the east coast of the South Island is gradually tilting due to movement of tectonic plates, resulting in the formation of high cliffs along sections of the coast (McDowall 1998). These factors acted to retain what little rainfall reached the plains in coastal wetland and lagoon systems that extended the length of the Canterbury Plains. In addition, depressions between the alluvial fans of the main rivers collected water, forming inland wetlands that were drained by ephemeral watercourses such as the Selwyn River, which flows into Lake Ellesmere; and the Hinds River (Davis 1984; Fitzharris et al. 1992). Jobberns (1927, p. 93) commented on these inter-fan depressions that ‘being by structure adapted to the accumulation of ground water and the surface silts from the higher surrounding land, these localities comprise some of the richer lands of the [Canterbury] Province, and some have had to be reclaimed from an original swampy condition by artificial drainage.’ It was within these extensive inland depressions and coastal wetlands that *N. burrowsi* was likely to have been common and some populations still persist in remnants of such habitat (Figure 2).
Figure 2. Drainage network of the South Island, New Zealand overlaid with locations of recorded *N. burrowsius* populations. The Canterbury Plains is apparent from predominantly parallel waterways. Records were obtained from the New Zealand Freshwater Fish Database (NZFFD; McDowall & Richardson 1983) downloaded on the 16 May 2005 and mapped using the Freshwater Fish Database Assistant 5.1 (Jowett 1998). Locations shown include many known to have gone locally extinct, but do not include translocation populations. Inset shows complete outline of South Island.
**N. burrowsius habitat fragmentation**

To understand the current plight of *N. burrowsius*, it is important to consider the historical changes to its habitat. Before human arrival, much of the Canterbury Plains were covered with podocarp forest dominated by kahikatea (*Dacrycarpus dacrydioides*) in wetland areas. These lowland swamp forests were removed by Polynesian fires and were replaced by scrub, tussock and wetland vegetation (McDowall 1998). Early settlers described much of the expansive plains as ‘interminably monotonous’ ‘as far as the eye could see’ covered with ‘impenetrable bogs’ (McDowall 1998). However, the flat expanse of the Canterbury Plains proved irresistible to early settlers, who invested considerable effort into transforming the landscape. Conversion was surprisingly rapid, for example much of the area between the Ashburton and Rangitata rivers was changed from a ‘dismal swamp’ to highly productive farmland in 15 years by a Mr John Grigg of Longbeach (McDowall 1998). This was achieved by digging extensive channels and laying nearly 250 km of tiled field-drains (McDowall 1998). However, the greatest change was the channelisation of the Hinds River so that it drained directly to the sea, where once it dispersed into a vast wetland near the coast (McDowall 1998). It is not known if Mr Grigg found *N. burrowsius* while draining this wetland, however they have persisted there. This area provides a graphic example of the extent of *N. burrowsius* habitat fragmentation (Figure 3). As McDowall (1998, p. 37) commented *N. burrowsius* ‘latitudinal range is still about the same as it originally was, but it is now restricted to pathetic residual fragments of wetland that survive, scattered across the often dry and parched Canterbury Plains.’ This fragmentation may have occurred faster than existing stochastic processes of extinction, meaning that an ‘extinction debt’ is likely to be present. The concept of extinction debt relates to the temporal lag between habitat fragmentation and subsequent local extinction due to stochastic processes (Hanski & Ovaskainen 2002). Fragmentation can also lead to reduced genetic diversity with consequences, such as reduced fitness and accumulation of deleterious mutations (Wang et al. 2002; Gaggiotti 2003). This situation is compounded in *N. burrowsius* because they have low intra- and inter-population genetic diversity, with some populations having no detectable nucleotide diversity (Davey et al. 2003). Although the loss of genetic diversity does not necessarily indicate an immediate threat, it may be detrimental to long term persistence. Importantly, a population may lose the capacity to adapt to novel selection pressures as the ability to respond to changing conditions is proportional to the diversity of underlying genetic traits (Gaggiotti 2003). Thus, continued fragmentation and habitat change are likely to be detrimental to *N. burrowsius’* long term chances of persistence.
Figure 3. A case study of habitat fragmentation that has occurred in the Longbeach area between the Ashburton and Hinds rivers, south of State Highway 1. Left = modified 1800s Black Map, Middle = New Zealand Freshwater Fish Database records of *N. burrowsius* as at 1 November 2004 overlaid with the stream network of the area, Right = distribution of *N. burrowsius* as at 15 November 2004 overlaid with an orthograph of the area (Environment Canterbury unpublished data). Note the presently channelised lower section of the Hinds River which now discharges to the South Pacific Ocean.
Ideal habitat

Skrzynski (1968, p. 694) concluded that ‘it now seems impossible to determine the original habitat’ of *N. burrowsius*. This fact has been widely recognised, however the nature of *N. burrowsius*’ original habitat has been discussed, frequently (Eldon 1979a; Meredith 1985; McDowall 1990). Many of the first specimens were collected from habitats after they had dried up (Phillipps 1926), thus, Skrzynski (1968, p. 694) ‘assumed that it occupied isolated waters which dried periodically.’ However, Eldon (1979a) debated this point and emphasised the similarities between *N. burrowsius* habitat and tropical hypoxic wetlands where air-breathing fish also occur. Moreover, Meredith (1981, 1985) showed that *N. burrowsius* exhibited physiological and behavioural adaptations most likely to have evolved in swamp forest pools where hypoxia was frequent, and that it showed little adaptation to habitats that completely desiccated. Yet, *N. burrowsius* occur frequently in seasonally harsh environments where low dissolved oxygen and the near absence of water during summer exclude many other fish species. Despite this, *N. burrowsius* is considered a ‘clean water species’ requiring generally high water quality (McDowall 1998).

*N. burrowsius* habitat is predominantly spring fed wetlands, with water sourced either from hill seepage, or groundwater, often supplied by an adjacent river. Due to the proximity of hills and rivers these sites frequently experience scouring floods capable of creating pool habitat (Eldon 1979a; personal observation). Eldon (1979a) described ideal *N. burrowsius* habitat as still or very slowly flowing, meandering, ‘swampy streams with deep pools that retained water for long periods after flow had ceased.’ Similarly, Skrzynski (1968) described suitable habitat as ‘a small creek with very little flow (about 0.1 cusec), which had deep pools with flax and rush cover, and a mud bottom.’ However, *N. burrowsius* has been found in a variety of habitats, including seepage streams, spring streams, dams, farm ponds, scour holes, stockwater races and possibly, subterranean habitat (Eldon 1979a). This diverse range of habitats in which *N. burrowsius* is found, may in part be a consequence of the considerable modification of its habitat, whereby *N. burrowsius* are forced to occupy whatever habitat remains. Indeed, in many areas *N. burrowsius* now occurs only in the channels used to drain its former wetland habitat. Thus, although *N. burrowsius* may be a wetland specialist by virtue of its morphological and physiological adaptations (Meredith 1985; McDowall 1997), often the habitat that it now occupies cannot be described as wetland.
**Current threats**

In less than 40 years most wetlands on the Canterbury Plains were converted to farmland (McDowall 1998). Today, there is little visible evidence of these wetlands and the hydrology of the plains has altered, leaving many formerly waterlogged areas experiencing seasonal soil moisture deficit and resulting in an increase in both the frequency and severity of drought disturbance (Sagar & Jellyman 1985; McDowall 1998). This has lead to many fish strandings (e.g. Hicks 1982; Sagar 1985; Jellyman 1989; Main & Meredith 1999). As McDowall (1998, p. 39) concluded, ‘the ultimate irony is that the formerly extensive wetlands of Canterbury are now highly productive farmland whose full potential can be realised only by irrigation.’ *N. burrowsius* is vulnerable to increased water abstraction for irrigation as the spring-fed habitats that it occupies are most sensitive to reductions in groundwater levels (Morgan et al. 2002). However, the influence of water abstraction on larger river systems is often given greater consideration, with water resources being balanced between agricultural and river systems, rather than small waterways. This has generated a new threat as *N. burrowsius* often occur in small stock water race systems. It has been estimated that the efficiency of these stock water races, i.e. the percentage of the abstracted water actually consumed by stock; can be as low as 3 % (Morgan et al. 2002). A strong case has been put forward to remove or pipe these watercourses to ease pressure on the in-stream values of larger rivers and free up water allocation for other uses (Morgan et al. 2002). Thus, the increasing human need for water is continuing to threaten *N. burrowsius* populations, both indirectly via water abstraction lowering groundwater levels and directly as agricultural water networks are piped to increase water use efficiency.

Several other aspects of waterway management are also likely to threaten *N. burrowsius*. Any activity, such as drain maintenance and stock grazing, that removes in-stream vegetation also removes cover and spawning substrate required by *N. burrowsius* (Eldon 1979c). Stock access can also cause compaction of substratum, and break down banks, which may reduce refuge for *N. burrowsius* (Eldon 1993). Another issue is that *N. burrowsius* is considered to have low competitive ability because it occurs on its own in the majority of recorded sites (Eldon 1979a; Meredith 1985). Changes in hydrologic regime caused by irrigation, and channelisation or realignment of remaining habitat, may affect *N. burrowsius* via the presence of other fish species. Thus, actions that increase baseflow, velocity, and connectedness, may result in habitats being more suitable for other species, and/or removal of dispersal barriers to predatory shortfin eel (*Anguilla australis*; Eldon 1979a).
Thesis outline

My general aim in this thesis was to examine the conservation ecology of *N. burrowsius*; to explore methods of assessing habitat quality and population persistence; and to identify factors limiting population growth. This thesis is written as a series of manuscript style chapters with one collated reference list and a final summary chapter. The thesis has been separated into four sections covering a variety of topics considered important to the conservation of *N. burrowsius*. The initial section includes three chapters on aspects of survey methodology. These chapters cover the capture methods used for *N. burrowsius*, and examine methods of monitoring population decline, and habitat suitability. The second section comprises two chapters assessing the dynamics and health of *N. burrowsius* populations occurring in remnant habitats spread across its distributional range. These chapters compare a number of measures used to assess individuals and their populations, including, size, density, biomass, average condition and growth, as well as, ecto-parasite and infection loadings. The third section consists of chapters examining two common limiting factors for *N. burrowsius* populations, i.e. drought disturbance and inter-specific interactions. The final section contains three chapters examining reproductive characteristics. These chapters evaluate the importance of environmental conditions on *N. burrowsius* spawning, and examine survival and development through the early life stages of *N. burrowsius* as eggs, larvae and fry.

Study sites

Eldon (1993, p. 7) stated that ‘four locations are considered to be very important in terms of supporting mudfish populations.’ These four populations are the central focus of studies in this thesis and were briefly described by Eldon (1993). Unfortunately, in-depth field investigations involving conservation species are inevitably restricted due to the rarity of individuals or populations. Indeed, the paucity of sufficiently large populations hampered earlier field studies of *N. burrowsius*, e.g. Cadwallader (1973); with Skrzynski (1968, p. 688) commenting that ‘no established population, which could be studied in detail, has been found.’ Although I visited and sampled numerous remnants of *N. burrowsius* habitat, data from only the four important sites described by Eldon (1993), were examined in detail in this thesis (Figure 4; Table 1). These sites contained persistent and sizeable populations, and are assumed to be representative of *N. burrowsius*’ remnant habitat and its ecological situation, allowing valid generalisations to be made.
Table 1. Location of the four study sites in Canterbury.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Altitude (m)</th>
<th>Distance inland (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Te Roto Repo o Tawera</td>
<td>43.29</td>
<td>172.08</td>
<td>310</td>
<td>75</td>
</tr>
<tr>
<td>Hororata Spring</td>
<td>43.59</td>
<td>172.04</td>
<td>140</td>
<td>60</td>
</tr>
<tr>
<td>St Andrews Drain</td>
<td>44.52</td>
<td>171.20</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Dog Kennel Stream</td>
<td>44.88</td>
<td>171.03</td>
<td>100</td>
<td>16</td>
</tr>
</tbody>
</table>

Figure 4. Location of *N. burrowsius* studies sites across the Canterbury Plains. Modified from NIWA (2004).
General site characteristics

The four study sites examined in my thesis were located across the distributional range of *N. burrowsius* (Figure 4, Table 1). All four sites were isolated or seasonally disconnected from the South Pacific Ocean. The intensity of agricultural land-use and level of stock access differed amongst sites. However, in all cases, sites were less intensively managed than surrounding farmland. The fish community in sites was depauperate, with no more than three species ever being found, i.e. *N. burrowsius*, upland bully (*Gobiomorphus breviceps*), and *A. australis*.

Mitochondrial DNA analysis of the population structure of *N. burrowsius* identified two evolutionary significant units (ESUs): Mid Canterbury and South Canterbury (Davey et al. 2003). In my study, both ESUs were represented by two populations. The four sites can also be ranked along a continuum of hydrological and morphological characteristics, with sites ranging from perennial to intermittent, and from streams to interlinked pools (Figure 5). The sites are also representative of the ecological and agricultural situation *N. burrowsius* commonly occupies. Two sites contained *A. australis*, and two sites contained *G. breviceps* populations; two sites perennially flowed and two sites flowed intermittently, and two sites had much lower levels of agricultural pressure than the other two (Table 2).

The various factors, i.e. ESU, hydrological regime, presence of other fish species, and the level of agricultural influence, are likely to have different strengths, and *N. burrowsius* is likely to respond to them differently. Thus, by comparing pairs of sites (as in Table 2), in relation to population responses, it may be possible to identify factors that are likely to be structuring or limiting *N. burrowsius* populations. However, some abiotic and biotic characteristics were confounded (Table 2). I know of no natural site that contains both *N. burrowsius* and *A. australis* that does not also experience intermittent flow and regular desiccation.
Table 2. Study sites arranged to illustrate the similarities between pairs of sites, in terms of evolutionary significant unit (ESU), hydrological regime, presence of other fish species, and the level of agricultural influence. Sites in bold had low levels of agricultural influence, whereas underlined sites had high levels of agricultural disturbance.

<table>
<thead>
<tr>
<th></th>
<th>Perennial flow</th>
<th>Intermittent flow</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>A. australis</em> absent</td>
<td><em>A. australis</em> present</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mid Canterbury ESU</th>
<th>Te Roto Repo o Tawera</th>
<th>Hororata Spring</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. breviceps</em> present</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>South Canterbury ESU</th>
<th>St Andrews Drain</th>
<th>Dog Kennel Stream</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. breviceps</em> absent</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 5. Generalised study site morphology. Circles represent pool areas, and lines stream runs. Sites can be placed, left to right, along a continuum from a channelised stream with little pool area to a series of pools connected by small intermittent runs. The sites on the left had perennial flow and those on the right intermittent flow and dried up, to some extent each summer.
Chapter titles.

SECTION 1: Methods of capture, habitat assessment, and monitoring

Chapter 2: Active and passive methods in the capture of Neochanna burrowsius
Chapter 3: Methods of characterising microhabitat use of Neochanna burrowsius
Chapter 4: Methods of assessing the security of Neochanna burrowsius populations

SECTION 2: Population characteristics

Chapter 5: Neochanna burrowsius populations in perennial and intermittent systems: forced and constrained structures.
Chapter 6: Incidence of disease, parasitic infection & deformity in Neochanna burrowsius populations

SECTION 3: Abiotic and biotic factors

Chapter 7: Size-dependent strategies in the response to hypoxia and drought by Neochanna burrowsius
Chapter 8: Competition and co-existence between Neochanna burrowsius, and Gobiomorphus breviceps

SECTION 4: Reproduction and recruitment

Chapter 9: The influence of environmental conditions on the spawning and fecundity of Neochanna burrowsius
Chapter 10: The role of macrophytes in recruitment of Neochanna burrowsius
Chapter 11: Mechanisms moderating exposure to acute and chronic hypoxia in Neochanna burrowsius embryos
General discussion.

Population regulation, through density-dependent mechanisms, may be essential for long-term persistence of a population (Hixon et al. 2002). Canterbury mudfish (Neochanna burrowsius) populations at low densities are capable of rapid growth because of high fecundity (Eldon 1979c), and are regulated at high densities by mechanisms identified in this study, such as cannibalism and juvenile suppression (Chapter 5). Persistence of N. burrowsius populations in disturbed habitats also necessitates resistance to progressively adverse conditions, such as agricultural intensification, and resilience after acute disturbance, such as severe drought. Despite dire predictions of their likely demise (Skrzynski 1968); N. burrowsius has endured the agricultural transformation of the formerly wetland-dominated Canterbury Plains. This has mainly been due to intrinsic traits, including vagility and physiological tolerance to environmental extremes (Eldon et al. 1978; Eldon 1979d; Meredith 1985). However, some populations are still vulnerable and the intrinsic characteristics of N. burrowsius may be insufficient to ensure long term persistence if extrinsic processes, such as intensification of land use, continue (Chapters 4, 5 & 6). Furthermore, recent modelling of climate trends strongly suggests that drought frequency will increase by between two and four-fold by 2080 across the Canterbury Plains (Mullan et al. 2005). This is likely to lead to further extinctions of N. burrowsius populations as they are not specifically adapted to extended drought conditions (Eldon 1979a; Meredith 1985).

In this thesis I focused on N. burrowsius populations within the four most important natural habitats identified by Eldon (1993). Despite the importance of these, two sites had characteristics that suggested that the long-term security of the N. burrowsius populations they contain is in doubt. The Hororata Spring population, in particular, seems vulnerable to extirpation (Chapter 2). This habitat experienced the greatest hydrological fluctuations, high agricultural disturbance, and both shortfin eel (Anguilla australis) and upland bully (Gobiomorphus breviceps) were present. Likely as a consequence, the N. burrowsius population had a low density, small individual size, and high rates of pathogenic infection (Chapters 5 & 6). Conversely, comparison with other NZFFD records for N. burrowsius sites indicates that my Gee minnow catch per unit effort results at Te Roto Repo o Tawera and St Andrews Drain were at the upper end of those recorded previously (Figure 6a). Furthermore, the maximum length of N. burrowsius found at these two sites was greater than that previously recorded in the NZFFD (Figure 6b). Maximum N. burrowsius length is important as fecundity increases substantially with increasing size (Eldon 1979c).
Figure 6. Cumulative percentage frequency of (a), 58 *N. burrowsius* CPUE records using Gee minnow traps only, and (b), the length of the largest *N. burrowsius* recorded from 49 records obtained from the NZFFD on 16 May 2005. CPUE results and length of the largest *N. burrowsius* collected during April 2002 for sites studied in this thesis are overlaid: TT = Te Roto Repo o Tawera, HS = Hororata Spring, SA = St Andrews Drain, DK = Dog Kennel Stream. Note the NZFFD records include previous records for the sites studied in this thesis and multiple temporal entries for locations.
At each of my four study sites the fish community and the level of hydrological and agricultural disturbance was different (Table 2). In total, hydrological regime and the presence of *A. australis* had a greater effect on population characteristics than the presence of *G. breviceps*, geographical location, and agriculture (Chapter 5). Agriculture is widely recognised as an activity that can limit fish communities, due to channelisation of waterways (Portt et al. 1986), reduced water quality (Hickey et al. 1989; Eklöv et al. 1998), and disturbance from mechanical macrophyte clearance (Hudson & Harding 2004). However, I did not find strong evidence during my study that the level of direct agricultural activity occurring at the four sites studied was a significant factor structuring *N. burrowsius* populations. For instance, although the Dog Kennel Stream site was fenced and re-vegetated, it contained a *N. burrowsius* population that appeared constrained, consisting of small individuals at low density (Chapter 5). In comparison, St Andrews Drain, which was a channelised drainage ditch that received stock grazing and mechanical macrophyte clearance, contained a population consisting of large individuals at high densities. Nonetheless, pathogenic infection was more prevalent in the two sites with higher nitrate concentrations and greater stock access to the waterway (Chapter 6). High stock levels or access to waterways may increase bacteria levels and reduce water and habitat quality, leading to impaired fish health and increased susceptibility to pathogenic infection. As *N. burrowsius* is considered a ‘clean water species’ (McDowall 1998), it is likely that if water quality continues to decline at these sites this situation will worsen, possibly leading to high mortality rates and population extirpation. Another consideration is that beef cattle only began to be stocked at St Andrews Drain in 2002. It is likely that there is a lag period between habitat degradation due to stock damage and an observable change to fish populations. However, even in the short term, removal of macrophytes by beef cattle altered the within-site distribution of *N. burrowsius* (Chapter 4). Macrophytes provide essential habitat for *N. burrowsius* and the presence of particular plant species was associated with the presence of adults and eggs (Chapters 3 & 10). In some situations, plant removal may not have a detrimental effect on populations, if there is sufficient habitat remaining, or if macrophyte loss is short term because of vigorous re-growth. However, removal of the cover provided by aquatic plants, by grazing and/or mechanical removal may increase predation risk by herons (*Ardea novaehollandiae*) and limit recruitment if clearance occurs immediately prior to or during the spawning period (Chapter 10). Furthermore, the consequences of aquatic plant removal may be exacerbated if *G. breviceps* are present and displace *N. burrowsius* from remaining refuge (Chapter 8).
Consequences of drought and hypoxia

Neochanna species are associated with aquatic habitats that experience drought disturbance (Skrzynski 1968; Eldon 1979a). However, extensive and repeated drying of *N. burrowsius* habitats is likely to be a relatively recent occurrence exacerbated by wetland drainage, agricultural activities, and climatic change (Eldon et al. 1978; McDowall 1998; Mullan et al. 2005). The findings of this thesis support the views of Eldon (1979a) and Meredith (1985) that *N. burrowsius* are not particularly well adapted to surviving periods of complete or extended habitat desiccation. Instead, adaptations likely evolved to enhance survival in periodically hypoxic wetlands. Adaptations, such as air breathing and an amphibious tendency, have fortuitously promoted survival during periods of drought (Eldon 1979a; Meredith 1985). Despite none of my study sites becoming completely desiccated, as small pools of water always remained, high mortality of emersed *N. burrowsius* was recorded (Chapter 7). Further, in my field study, the occurrence of intermittent flow during summer led to delayed *N. burrowsius* spawning the following spring, as indicated by egg stage (Chapter 9). Additionally, during experimental investigations, low dissolved oxygen levels delayed spawning in *N. burrowsius* (Chapter 9). These responses would result in a reduced time available for egg development and fry growth before the onset of summer conditions. This is likely to have important consequences for recruitment in drought disturbed habitats, as individuals less than approximately 50 mm TL suffered high mortality when emersed (Chapter 7). The congeners, brown mudfish (*Neochanna apoda*) and black mudfish (*N. diversus*) that occur in habitats that routinely dry up completely, spawn in autumn (Eldon 1978; Town 1981). This earlier spawning allows a longer period of egg and fry development before subsequent re-drying of habitat. The lack of appropriate spawning times in *N. burrowsius* is thus likely to increase its susceptibility to increasing drought severity.

Inter-specific interactions

In general, it is considered that *Neochanna* spp. have a realised niche bounded by environmental factors and negative inter-specific interactions (McDowall 1990). This is likely due to the general trade-off between competitive ability and the capacity to survive environmental disturbance (Begon et al. 1990). In some circumstances, periods of hypoxia and drought are considered beneficial to *Neochanna* populations (Hicks & Barrier 1996). This is because deteriorating dissolved oxygen levels deleteriously affects co-occurring fish species to a greater extent than the physiologically more tolerant *Neochanna* (Eldon 1979a; McDowall 1990). Occurrence of *Neochanna* species in seasonally drying wetlands is common (Eldon 1978; McDowall 1990; Hicks & Barrier 1996). A
survey found that 87% of *N. diversus* sites in the Waikato experienced desiccation, affording *N. diversus* protection from introduced Gambusia (*Gambusia affinis*; Hicks & Barrier 1996). In my study, *N. burrowsius* was only found with predatory *A. australis* in sites with hydrological fluctuations and not in the more benign perennially flowing sites. Other *N. burrowsius* sites containing *A. australis* also periodically dry up (Glova & Hulley 1998). It is likely that without hydrological disturbance, *A. australis* may be able to extirpate *N. burrowsius*. Indeed, I found that the presence of *A. australis* in a habitat reduced the abundance of *N. burrowsius* (Chapters 2 & 4). Further, *A. australis* may suffer higher levels of mortality than *N. burrowsius* during drought and may not be as resilient after disturbance (Stokell 1949; Glova & Hulley 1998). Thus, it is possible that disturbance mediates co-existence of these species, in a way similar to that described by Closs & Lake (1996) for mountain galaxias (*Galaxias olidus*) and brown trout (*Salmo trutta*). However, habitat drying and hypoxia will only have ecological benefits if potential competitors or predators are present or likely to invade during more benign conditions. Otherwise drought disturbance is simply a limiting factor, as high mortality can be incurred, and it can also have deleterious effects on growth and reproduction.

Contrary to expectations, competition between *N. burrowsius* and *G. breviceps* was not as asymmetrical as suggested in the literature (Eldon 1979a; Meredith 1985; McDowall 1990). Various mechanisms promoted co-existence between *N. burrowsius* and *G. breviceps*, including temporal segregation, differing diet composition, and physiological tolerance to environmental extremes by *N. burrowsius*. However, other effects found in my study, such as displacement from refuge, increased activity, and altered energy allocation, are still likely to have consequences for *N. burrowsius* survival, fecundity and thus fitness. Furthermore, habitats dominated by silt, and not cobbles may favour *N. burrowsius* and negatively influence *G. breviceps* populations. The ratio between silt and cobble substratum is largely controlled by hydrological factors, which as mentioned, have been altered on the Canterbury Plains. Although relatively depauparate, the composition of the fish community at the sites studied changed over the course of the study, and differed from previous studies, with both local extinction and species invasion occurring. At Dog Kennel Stream in 1984 three *G. breviceps* were recorded as being caught with a hand net, along with *N. burrowsius* (NZFFD record number 6639). Eldon (1993, p. 7) described Dog Kennel Stream as containing *G. breviceps*, but that they were rare, and the waterway to be ‘free of immigration by diadromous fish’ due to downstream channelisation and dry sections inhibiting dispersal. In contrast, I did not find *G. breviceps* but captured *A. australis* at this site. Furthermore, at St Andrews Drain in 1976, *G. breviceps* and common bully (*Gobiomorphus cotidianus*) were recorded as being present, with *G. breviceps* being noted as common (NZFFD card numbers 50714
and 50715). In 1983 *G. breviceps* was still present (NZFFD card number 5662). In 1999, nine *G. breviceps* were caught, all being very large adults. But in 2002 only one large *G. breviceps* was caught, and it was considered that this population had effectively become extinct. It is likely that this was due to the lack of suitable cobble spawning habitat for *G. breviceps* at this site. These changes in fish community are likely to be a reflection of the on-going changes in the hydrology and land-use of the Canterbury Plains. The long-term effect of these changes is unknown, but they could potentially have major affects on *N. burrowsius* populations. For example, Eldon (1979a) detailed changes to the hydrology and morphology of a habitat that previously contained *N. burrowsius*, when reported on by Stokell (1949), but that contained only *S. trutta* when revisited.

**Physiological and behavioural plasticity**

In my studies *N. burrowsius* were remarkably adaptable and responsive to their environment. Both field and experimental studies found that *N. burrowsius* altered how energy resources were allocated, leading to reduced growth in length, yet maintenance or increase in body mass (Chapter 5 & 8). This occurred in response to the presence of a competitor and at sites that regularly dried up or became hypoxic, necessitating periods of emersion. In both situations it is likely that retaining condition instead of growing in length, which is largely irreversible, will allow resources to be diverted to fulfil other requirements, such as sustaining periods of starvation, avoiding inter-specific interactions and/or increased allocation to reproduction. Further, female *N. burrowsius* exposed to differing environmental conditions immediately prior to spawning were able to manipulate the trade-off between the number and size of eggs (Chapter 9). Embryos could also regulate oxygen consumption and survive short periods of extreme hypoxia (Chapter 11). Such compensatory mechanisms can mediate environmental influences, and can determine a population’s persistence in the face of disturbance (Le Cren 1965). However, reduced size is likely to have consequences for fecundity potential and fitness. Thus, in drought-disturbed habitats, mortality, suspension of growth and physiological constraints on adult size, may limit population increases via decreased total population fecundity, even though reproductive allocation remains high. Moreover, small size will mean that *N. burrowsius* remain vulnerable to predation by *A. australis*. 
Will *N. burrowsius* persist on the Canterbury Plains?

There are many aspects that generate concern for the long-term likelihood of *N. burrowsius* persistence, such as stunting, high rates of pathogenic infection, deformity, fluctuating abundances, and regional synchronicity. It is likely that *N. burrowsius* populations will be increasingly adversely affected if the frequency of droughts increase, as has been predicted (Mullan et al. 2005), or if dissolved nitrate concentrations and stock levels increase. Overall, *N. burrowsius* will only persist in the wild in perpetuity with a concerted effort and changes in behaviour on the part of humans. Since *N. burrowsius* occurs within an agriculture-dominated landscape, predominately, human actions directly influence its survival (Eldon 1979d). Early settlers spent considerable effort and capital removing *N. burrowsius* habitat, commenting that the land was ‘a sink for money’ (McDowall 1998, p. 35). Accounts describe ‘gangs of men … digging their way through the swampy peats and clays “to free the squelching soil from water”’ (McDowall 1998, p. 36). It took about 40 years of effort, but they succeeded. Today, little evidence of the vast wetlands of the Canterbury Plains remains. A similar investment, in fact most likely less, is now needed to ensure that the unique fauna that once occurred in these wetlands is retained. This study showed that even in their most important habitats, populations of *N. burrowsius* exhibited characteristics consistent with their acutely threatened status. Furthermore, simply due to the high level of population fragmentation they have experienced and their low genetic diversity, *N. burrowsius* are vulnerable to extinction. We cannot afford to lose any more *N. burrowsius* populations through the purposeful removal of habitat, for example by stockwater reticulation (Chapter 1). Nor can we afford to be inactive as water quantity and quality on the Canterbury Plains gradually declines. There is an increasing awareness that *N. burrowsius* has endured the complete transformation of its habitat and that it can persist in an agricultural setting. Thus, it may take very little to protect the species, requiring in many cases only a willingness to spend the time to understand its requirements. However, in what ever form, an investment is needed now to protect the last fragments of habitat suitable for *N. burrowsius*. Why? Possibly because species extinction would affect New Zealand’s image as a ‘clean green’ nation, the cost of which is valued at more than $500 million (MfE 2001). Or more simply, because as aptly put by Tony Eldon ‘life will be boring when all the small creatures have gone’ (Eldon 1979d, p. 19).
References


McDowall, R.M. 1998: Once were wetlands. *Fish & Game 20*: 32-39.


