



Mudfish (*Neochanna*  
*Galaxiidae*) literature review

SCIENCE FOR CONSERVATION 277



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# Mudfish (*Neochanna* Galaxiidae) literature review

Leanne K. O'Brien and Nicholas R. Dunn

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## ABSTRACT

*Neochanna* (commonly called mudfish) are small, cryptic fish of the Galaxiidae family that exhibit extraordinary survival ability and amphibious behaviour. Of the six species of *Neochanna*, five are endemic to New Zealand. *Neochanna* species show a continuum of morphological transformation from *Galaxias*-like characteristics towards an anguilliform, or eel-like body plan. This literature review examines the extent to which this transformation series may provide a framework for understanding a range of characteristics of the genus. *Neochanna* species are wetland specialists and it is likely that they were abundant in the extensive wetlands that once covered much of New Zealand. Large tracts of these lowland areas have been drained and are now productive agricultural land. Remaining fragmented *Neochanna* populations face increasing challenges as their habitat continues to change. *Neochanna* species are adaptable, however, and are tolerant of disturbance and adverse conditions, to an extent. With increased public awareness and understanding, and habitat protection, there is every chance that these unique fish will persist. Overall, the taxonomic distinctiveness, general biogeography, and genetic structure of the genus *Neochanna* is fairly well known, but many aspects of the species' physiology, biology and ecological situation require further study.

Keywords: Galaxiidae, *Neochanna*, *Neochanna apoda*, *Neochanna burrowsius*, *Neochanna cleaveri*, *Neochanna diversus*, *Neochanna beleios*, *Neochanna rekobua*, mudfish, literature review, conservation, wetlands, New Zealand

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# 1. Introduction

The ability of *Neochanna* (mudfish) species to survive periods without free surface water has long been recognised (Günther 1867; Roberts 1872). It is apparent that their amphibious nature and considerable tolerance to adverse conditions has enabled them to persist within an increasingly altered landscape. The majority of *Neochanna* populations occur in productive low-lying areas influenced by agricultural activities. This situation is unlikely to change substantially and there is a need to develop environmentally and economically sustainable solutions that address the apparent conflict between the persistence of *Neochanna* populations and intensive land and water management. Thus, advocacy and mutual co-operation between a wide range of landowners, government agencies, and contractors will be required to achieve conservation goals necessary to protect *Neochanna* populations. Importantly, the ability to address and communicate relevant issues with confidence requires a sound knowledge base.

This report reviews literature on the six currently recognised *Neochanna* species, highlighting aspects that may be important in directing future research, conservation and management initiatives. While the central focus of this review is the five *Neochanna* species that occur in New Zealand, comparisons with the Australian *N. cleaveri* (Tasmanian mudfish) are made, to emphasise generalities within the genus. Each chapter has an introduction followed by sections covering specific topics, and is concluded, in most cases, with a summary of key chapter points. The last chapter, entitled 'information gaps', provides a summary of issues that require further study and understanding. A bibliography provides literature that relates to *Neochanna* species, in addition to references cited in the text. This review presents detailed information to make accessible information that can be difficult to obtain. To explore general patterns we have utilised several review methods including general meta-analysis approaches, conversion of results into common metrics, re-analysis and categorisation of raw data, data extraction programs to enumerate graphical information, and basic statistical analysis, where appropriate. Information from the New Zealand Freshwater Fish Database (NZFFD; McDowall & Richardson 1983) extracted on 30 July 2004 has also been used. Locations (Table 1) mentioned in the text are illustrated in Fig. 1.

## 1.1 CONSERVATION STATUS

The decline of *Neochanna* species since the arrival of humans is considered to be linked to the extensive reduction of their wetland habitats (McDowall 1982, 1998a; Swales 1991). Land development activities such as the removal of vegetation and the draining of wetlands have removed large areas of *Neochanna* habitat. In addition, habitat removal has been accompanied by channelisation to increase water flow and the introduction of exotic fish species. These have reduced the suitability for *Neochanna* of much of the remaining habitat (Skrzynski 1968; Eldon 1979a; Ling 2004). The impact of wetland drainage on *Neochanna* populations has been recognised since the late 1800s. A report by Roberts (1872: 456) quoted S.E. Vollams describing the decline of *N. apoda* (brown mudfish)

in the Hokitika area: 'they are found in great numbers in making new roads through swampy land, but seem to disappear from the land on its being drained and cultivated'. Habitat drainage continues despite the historic destruction of approximately 90% of New Zealand's wetlands, and is a major and ongoing threat to *Neochanna* populations (Eldon 1978a; Swales 1991; Close 1996; DOC 2003).

Much of the evidence for a large-scale decline in *Neochanna* population abundance since people started modifying New Zealand's landscape is anecdotal (McDowall 1980a). However, there is evidence from genetic analyses that existing populations of *Neochanna* are remnants of larger populations (Gleeson 2000; Davey et al. 2003). Survey work has recorded instances of local extinction where *Neochanna* are now absent from areas where they were formerly present, e.g. Stokell (1945), Eldon (1993), Rebergen (1997), Francis (2000a). One example of this is the disappearance of *N. burrowsius* (Canterbury mudfish) populations that G.A. (Tony) Eldon studied extensively in the 1970s (Eldon et al. 1978; Eldon 1979a, b, c, 1993). On a more positive note, surveys continue to locate new populations, and have increased the confirmed distribution of several *Neochanna* species (Jellyman et al. 2003; DOC 2000b, 2004b); although such discoveries must be viewed in the context of continuing local extinctions, habitat loss, fragmentation and insufficient historic data (Eldon 1993; McGlynn & Booth 2002).

Despite the likelihood of ongoing local extinctions, not all species are in danger of complete extinction because of their presence in areas of protected wetland. For example, *N. diversus* (black mudfish) occurs in the extensive swamp areas of the Whangamarino Wetland and Kopuatai Peat Dome (Close 1996; Hicks & Barrier 1996); and *N. apoda* is present in the Koputaroa Scientific Reserve, near Levin, and Fensham Reserve in the Wairarapa (Richardson 1987; Rebergen 1997). However, species and populations that do not occur in such large, protected wetlands are extremely threatened. Emphasising this point is that many discoveries of *Neochanna* occur during drain clearance (Young 1996). The occurrence of *Neochanna* in waterways used or managed for agricultural purposes highlights the vulnerability of many remnant habitats. This is because growing pressure on water supplies for agricultural and other uses means that open agricultural drains are being viewed as less efficient than pipes for distributing water, and their closure and removal is being advocated (Morgan et al. 2002). There is widespread concern over the ability of *Neochanna* species to survive in an increasingly intensive agricultural landscape. As a result, all New Zealand *Neochanna* species have been classified as threatened under the Department of Conservation's (DOC's) threat of extinction classification system (Table 2; Hitchmough 2002; Molloy et al. 2002; Hitchmough et al. 2007). A recovery group has been formed and a 10-year recovery plan developed for the New Zealand *Neochanna* species (DOC 2003).

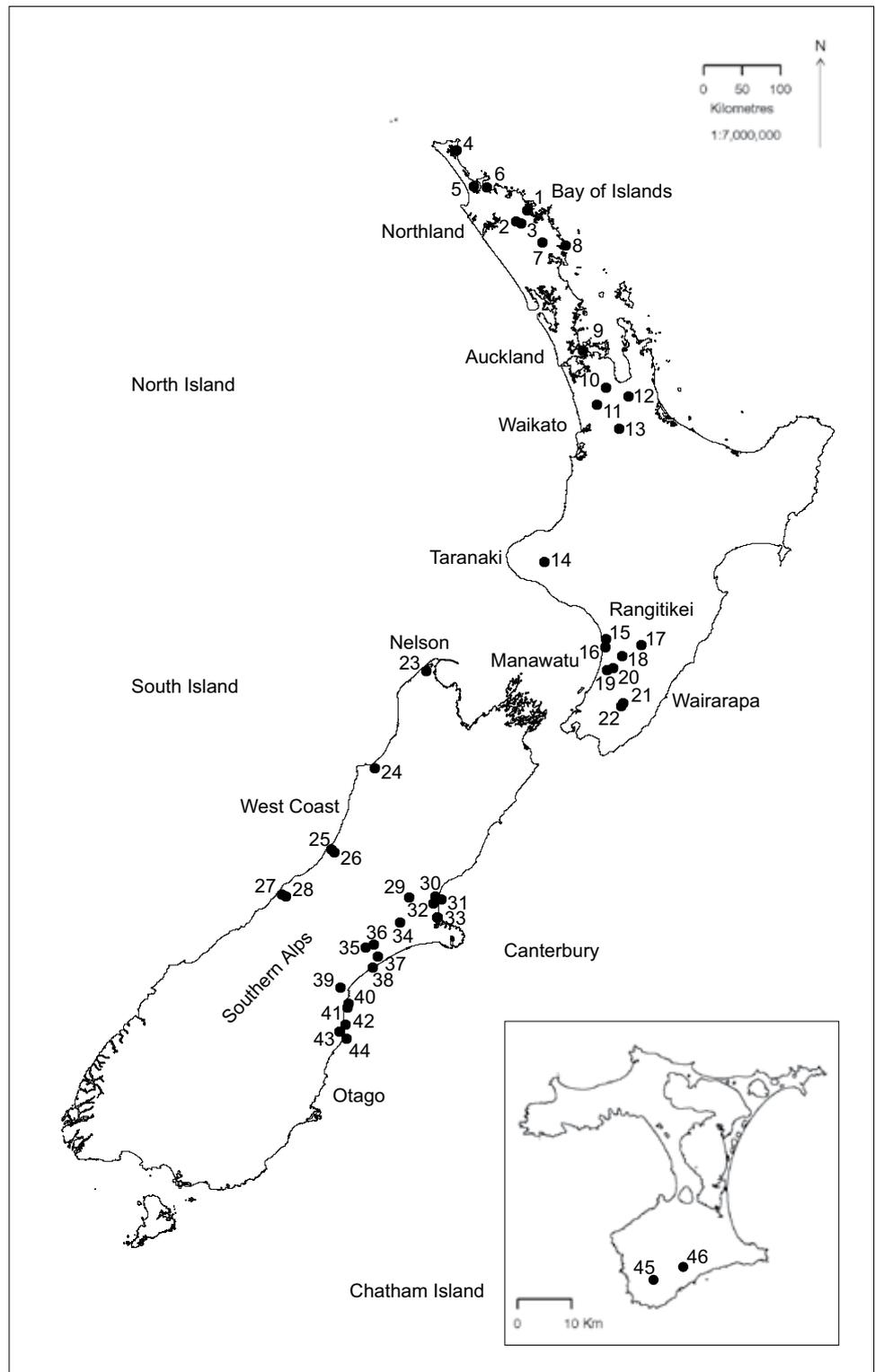
Over recent years, genetic studies and techniques have become useful tools in the conservation and management of threatened species. Genetic sequencing has been used to identify new species within *Neochanna* (Ling & Gleeson 2001), and to assign described species to the genus (Waters & White 1997). Of particular concern in the conservation of a species is genetic diversity. This issue is especially pertinent to *N. burrowsius*, which has low genetic diversity (Davey et al. 2003). Recognition of the unique genetic characteristics of populations and their importance for species conservation has led to the development of

TABLE 1. PLACE NAMES MENTIONED IN THE TEXT AND SHOWN IN FIG. 1, PLUS REGION AND *Neochanna* SPECIES PRESENT. NUMBERS ON MAP = LOCATION NUMBERS SHOWN IN FIG. 1.

MAP NUMBER	SPECIES	REGION	PLACE		
1	<i>N. beletos</i>	Northland	Kerikeri		
2			Lake Omapere		
3			Ngawha		
4	<i>N. diversus</i>	Northland	Parengarenga Harbour		
5			Waiparera		
6			Tokerau		
7			Otakairangi		
8			Ngunguru		
9			Auckland	Newmarket	
10			Waikato	Whangamarino Wetland	
11			Awaroa Stream		
12			Kopuatai Peat Dome		
13			Holland Road drain		
14			<i>N. apoda</i>	Taranaki	Stratford
15				Rangitikei	Santoft Forest
16				Rangitikei River	
17	Manawatu	Ashhurst Domain			
18	Manawatu River				
19	Lake Horowhenua				
20	Koputaroa Scientific Reserve				
21	Wairarapa	Fensham Reserve			
22	Hinau Valley				
23	Nelson	Mangarakau			
24	West Coast	German Terrace			
25	Hokitika				
26	Kaneiri				
27	Okarito				
28	The Forks				
29	<i>N. burrowsius</i>	Canterbury		Oxford	
30				Ashley River	
31			Tutaepatu Lagoon		
32			Ohoka		
33			Christchurch botanical gardens		
34			Hororata		
35			Clearwell		
36			Westerfield		
37			Willowby		
38			Lowcliffe		
39			Taiko		
40			St Andrews		
41			Otaio		
42			Buchanans Creek		
43			Dog Kennel Stream		
44			Otago	Waitaki River	
45	<i>N. rekobua</i>	Chatham Island	Lake Rakeinui		
46			Lake Tuku a Taupo		

the concept of evolutionary significant units (ESUs). An ESU is a reproductively isolated group of populations displaying unique evolutionary characteristics (Ling et al. 2001). The degree of genetic distinctiveness identified will depend on the method of analysis used. Mitochondrial DNA (mtDNA) in the D-loop region has been used most commonly to define the ESUs of *Neochanna* species (e.g. Ling et al. 2001; Davey et al. 2003). To ensure preservation of equivalent genetic

Figure 1. Location (●) of *Neochanna* species habitats mentioned in the text. Numbers refer to place names as given in Table 1.



diversity it is recommended that the same method be used to define ESUs in all *Neochanna* species. The identification of ESUs (Fig. 2), indicates that protection of a few habitats for each *Neochanna* species may be insufficient to preserve their genetic heritage.

TABLE 2. THE SIX CURRENTLY RECOGNISED SPECIES OF *Neochanna*, ONE OF SIX GENERA IN THE FAMILY GALAXIIDAE. PLACEMENT OF AUTHORITIES WITHIN PARENTHESES INDICATES THAT A SPECIES WAS ORIGINALLY DESCRIBED IN ANOTHER GENUS BUT SUBSEQUENTLY SHIFTED TO *Neochanna*.

COMMON NAME	SCIENTIFIC NAME	AUTHORITY
Chatham Island mudfish*	<i>N. rekobua</i>	(Mitchell 1995)
Tasmanian mudfish	<i>N. cleaveri</i>	(Scott 1934)
Canterbury mudfish*	<i>N. burrowsius</i>	(Phillipps 1926)
Black mudfish†	<i>N. diversus</i>	Stokell 1949
Northland mudfish*	<i>N. beleios</i>	Ling & Gleeson 2001
Brown mudfish†	<i>N. apoda</i>	Günther 1867

\* Acutely threatened species which is nationally endangered.

† Chronically threatened species in gradual decline.

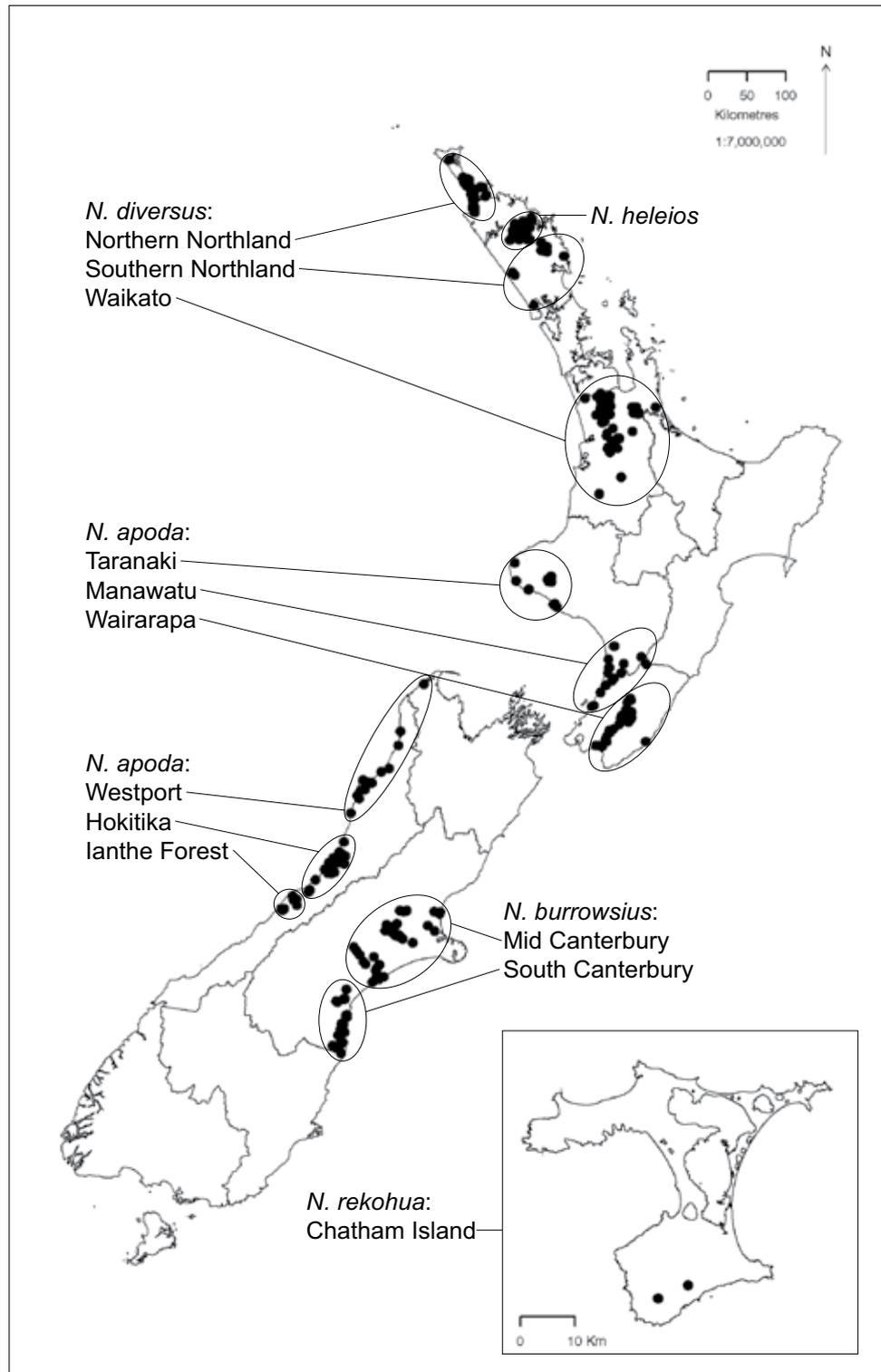
## 1.2 DESCRIPTION AND CHARACTERISTICS

*Neochanna* species belong to a group of southern hemisphere fishes known as galaxioids, which have an ancient evolutionary history (McDowall 2006). Within this group, phylogenetic studies show that *Neochanna* species are more closely related to Australian *Galaxiella* than to New Zealand *Galaxias* species (Waters et al. 2000). The general external characteristics of *Neochanna* species are a brown cigar-shaped, scale-less body, small eyes proportional to head size, large anterior nostrils, lateral pectoral fins, and a rounded caudal fin, akin to that of a stocky eel (Fig. 3; McDowall 1970, 1997a, 2000, 2004). *Neochanna* species have a distinctive swimming mode with ‘high sinuosity’ called anguilliform (eel-like) locomotion (McDowall 2003; Waters & McDowall 2005). This feature suggests an adaptation to habitats dominated by vegetation, and like *Anguilla* (Anguillidae, eel) species, an ability to live in crevices and holes, and possibly move over land (McDowall 1980b).

Based on morphological characteristics, McDowall (1997a, 2004) recognised that *Neochanna* species could be placed along a continuum indicating evolutionary transformation from a *Galaxias*-like to an anguilliform (eel-like) body plan (Fig. 3). Molecular phylogenetic analysis also strongly supports a single trajectory of progressive morphological specialisation during the radiation of *Neochanna* species in New Zealand (Waters & McDowall 2005). Two ‘sister groups’ can also be identified, comprising *N. burrowsius* and *N. rekobua*, and *N. apoda* and *N. beleios*, respectively (Fig. 3). This transformation series is interpreted as being the result of selection pressures acting on the genetic heritage of the genus, leading to increasing specialisation for existence in shallow wetlands (McDowall 2004; Waters & McDowall 2005).

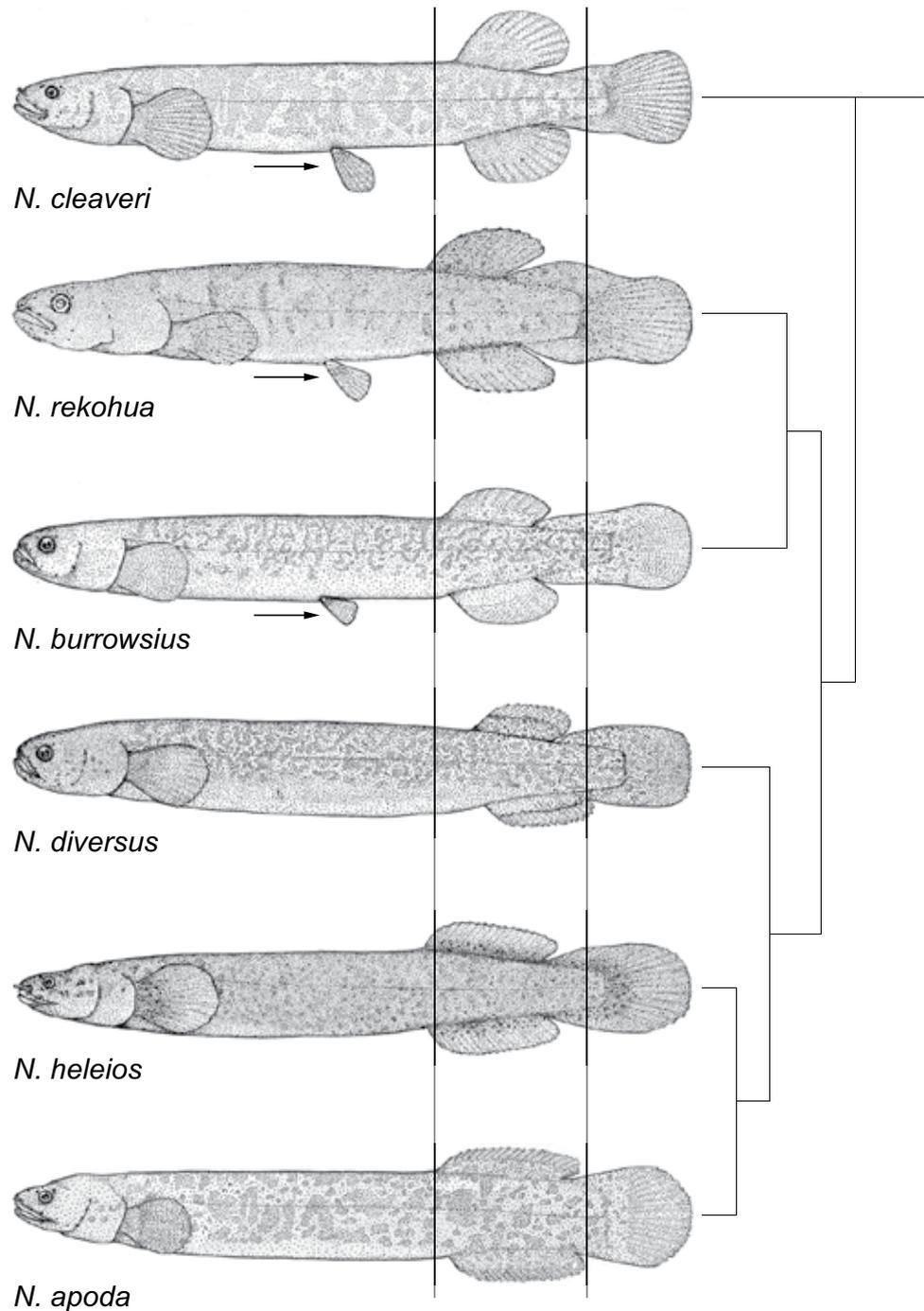
Thus, externally, there is a trend towards the development of flanges along the caudal peduncle (anterior to the caudal (tail) fin), elongation of dorsal and anal fins, increasingly fleshy fins, and the reduction and loss of pelvic fins (Fig. 3; McDowall 1980b, 1997a, 2003, 2004). Development of small fleshy fins in *Neochanna* is likely to be a response to the need for fins that do not wear or tear easily when the fish move through complex semi-aquatic or terrestrial situations, such as wriggling through forest floor debris (McDowall 1980b, 2004). In the skeleton, changes include strengthening of the cranial region, fusing of

Figure 2. Distribution (●) of *Neobanna* species with evolutionary significant units (ESUs) for each species and DOC conservancy boundaries shown. ESUs based on mitochondrial DNA in the D-loop region. Distributional data from the New Zealand Freshwater Fish Database (as at 30 July 2004). Designation of ESUs from Gleeson et al. (1997, 1998, 1999), Gleeson (2000), Davey et al. (2003), and Gleeson & Ling (unpubl. data).



caudal bones, and the reduction and loss of the pelvic girdle (McDowall 1997a, 1999a, 2004). Distinctive trends relating to teeth morphology are also apparent, including the progressive loss of endopterygoid teeth. These teeth are present, albeit reduced, in *N. cleaveri*, *N. rekohua*, and *N. burrowsius*, occur less often and are small when present in *N. diversus*, but are always absent in *N. apoda* (McDowall 1997a, 2004). The jaw teeth of *N. heleios* and *N. apoda* also differ from those of all other *Neobanna* species in being flattened and incisor-like (McDowall 1980b, 1997a; Ling 1998; Ling & Gleeson 2001).

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. beleios*.

### 2.4 *Neochanna beleios*

*Neochanna beleios* 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. beleios* 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. beleios* 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. beleios*, 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. beleios*.

### 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).

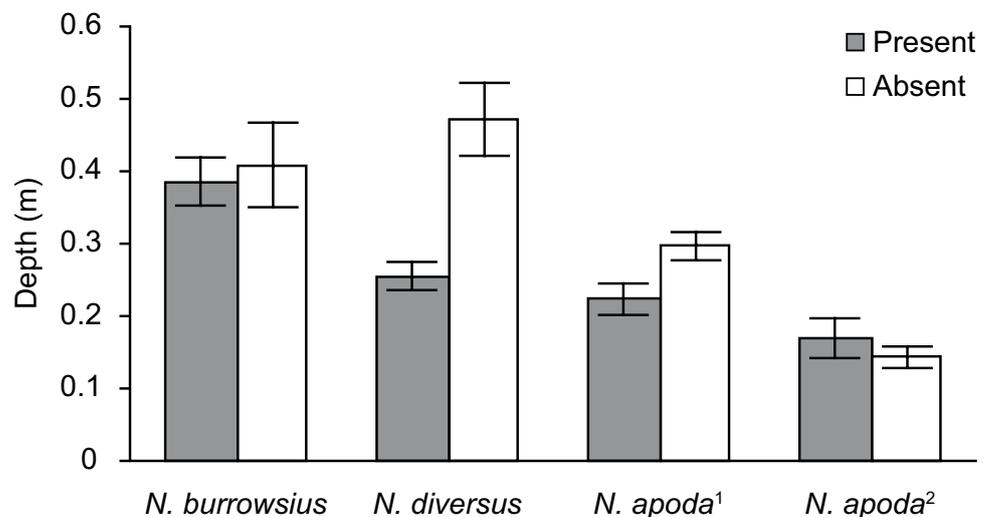
Many authors have highlighted the hydrologically disturbed nature of *Neochanna* habitats, which often experience seasonal drying and flooding, e.g. Eldon (1979a), Hicks & Barrier (1996), and McPhail (1999). Moreover, such disturbance is often viewed as important for the persistence of *Neochanna* populations, 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)<sup>1</sup> and Butler (1999)<sup>2</sup>—*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.

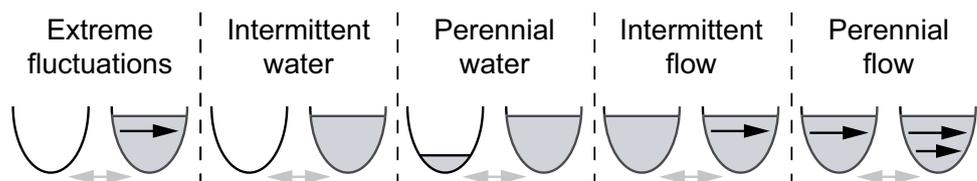


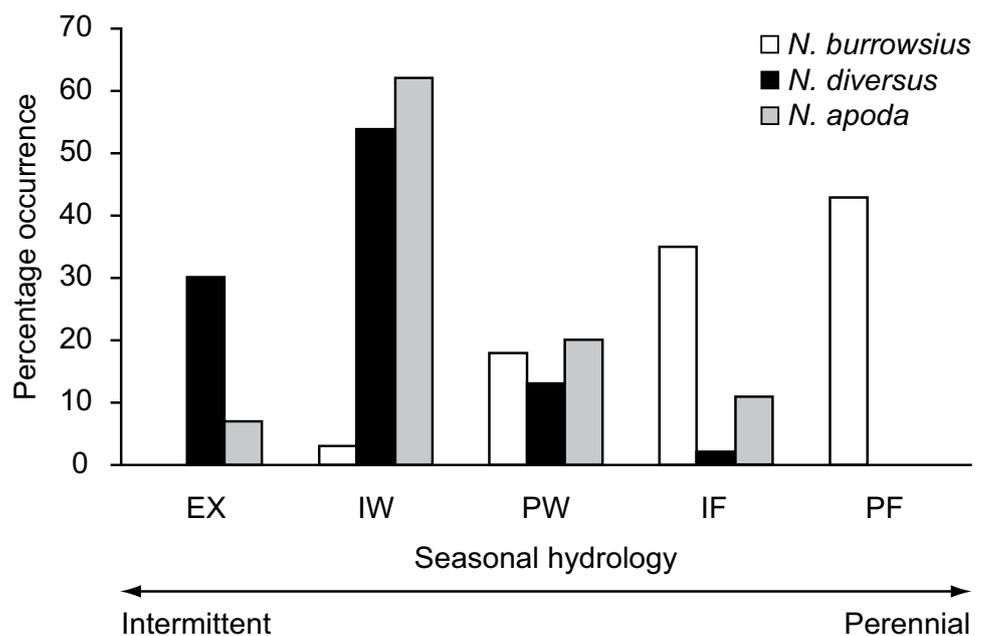
Figure 5. General classification of seasonal fluctuations in hydrological conditions typically occurring in *Neochanna* habitats. The sequence shows conditions in a habitat during summer (left member of pair) then winter (on right). The presence of water is indicated by a horizontal line and grey fill, 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 cheesemanii*), 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.

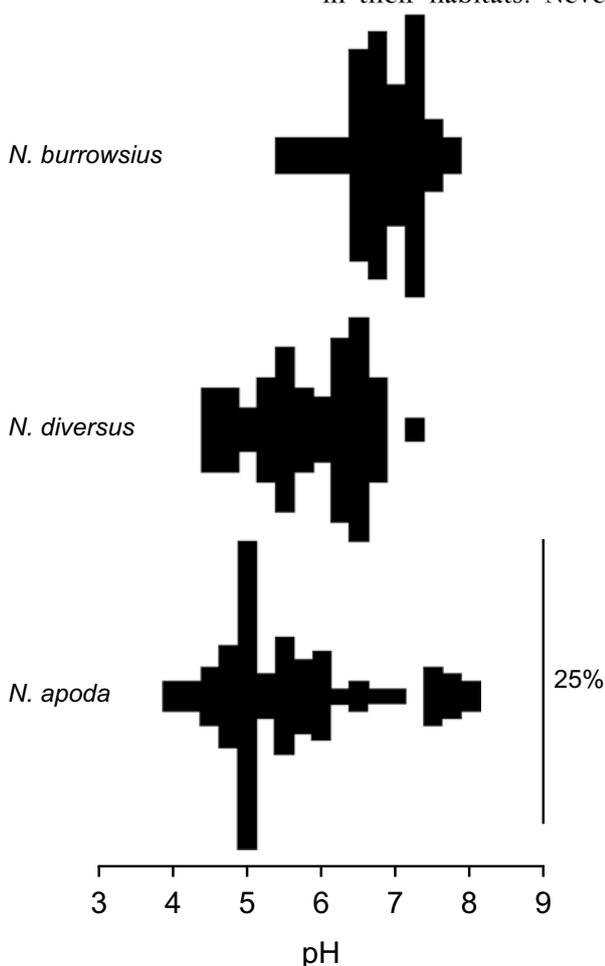


Figure 7. Occurrence (percentage frequency) of three *Neochanna* species related to habitat pH. Scale bar at bottom right indicates 25% of records. Frequency histograms were generated using 0.25 pH unit intervals. Data collated from Eldon (1979a), Dean (1995), Hicks & Barrier (1996), Eastwood (1997), 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 m<sup>2</sup>, 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

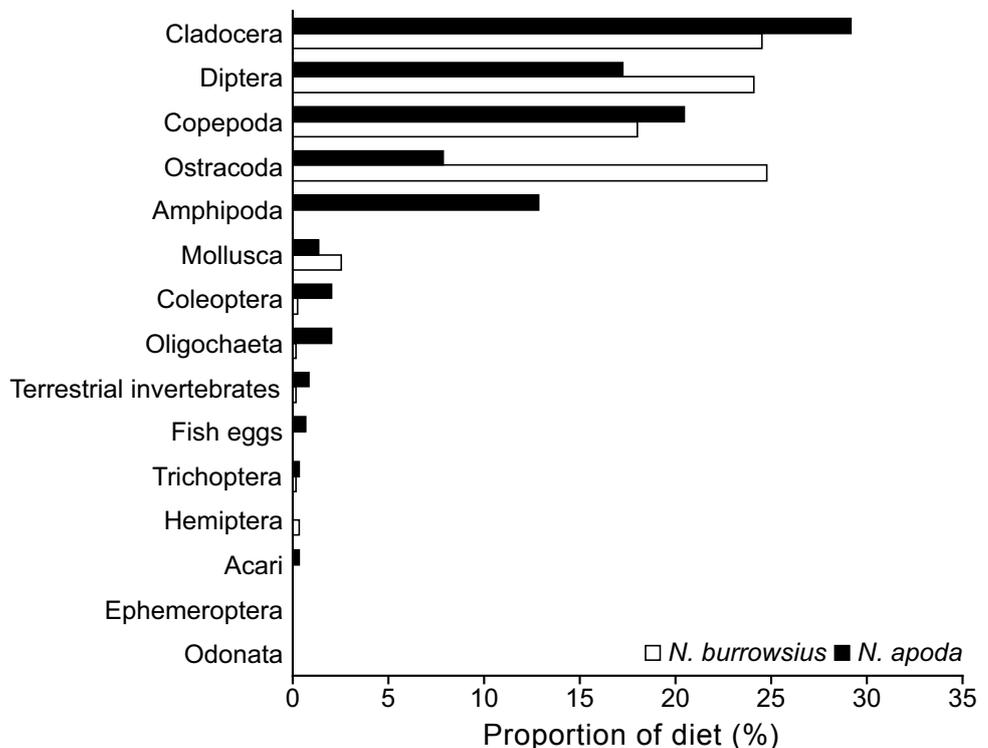
hypoxic waters (Davidson 1951; Thompson 1987; Andrews 1991; O'Brien 2005). Furthermore, Thompson (1987) noted that *N. diversus* would rest on surface weeds, possibly waiting for prey to fall on the water, as terrestrial prey items are included in the diet of *Neochanna* species (Fig. 8).

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  $32 \pm 17$  (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.

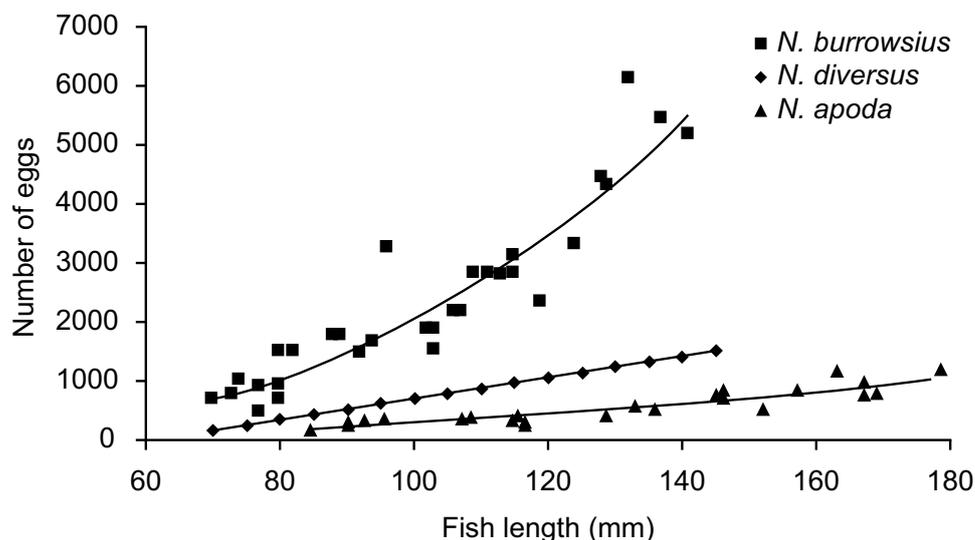
TABLE 4. DIAMETER OF *Neobanna* EGGS, MEASURED BEFORE OR AFTER SPAWNING. RANGE OR MEAN VALUES GIVEN. DATA FROM CADWALLADER (1973), ELDON (1978b, 1979c), McDOWALL & FRANKENBERG (1981), PERRIE (2004), AND O'BRIEN (2005).

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

Figure 9. Number of eggs produced by female *N. burrowsius*, *N. diversus*, and *N. apoda* related to body length. Data from Eldon (1979c)—*N. burrowsius*, Eldon (1978b)—*N. apoda*, and generated from an equation from McLea (1986) as given by Hicks & Barrier (1996)—*N. diversus*. Equations being *N. burrowsius*:  $y = 0.0027x^{2.9}$ , *N. apoda*:  $y = 0.012x^{2.2}$ , *N. diversus*:  $y = -1080 + 17.8x$ .



at different stages of development, and may differ from the size of spawned eggs after they have expanded. Although these factors introduce variation, a fairly clear sequence in egg size is nonetheless present within the genus (Table 4). The less specialised species—*N. cleaveri* and *N. burrowsius*—have smaller, and more numerous eggs, compared with *N. diversus* and *N. apoda*. Thus, fecundity and egg size also support species placement in the transformation series (see Fig. 3).

Fecundity and egg size have implications for population dynamics and the ability to respond to disturbance and environmental change. There have been several suggestions as to the underlying reasons for the considerable differences in fecundity of *Neochanna* species. Cadwallader (1975a: 26) thought that differences were likely due to ‘a less precise fertilisation process’ in *N. burrowsius* than in *N. apoda* and *N. diversus*. Barrier (1993) proposed that *Neochanna* species could be placed on a continuum of r-K selectivity. This latter framework generated conclusions based on habitat stability, with *N. apoda* in stable habitats and *N. burrowsius* in disturbed habitats where high fecundity would be important. McDowall (1970) noted that Galaxiidae as a whole demonstrate a trade-off of egg size and fecundity and that it is strongly correlated with alternative life history patterns. Migratory *Galaxias* species whose fry develop in the marine environment have numerous small eggs, whereas wholly freshwater species tend to have fewer, larger eggs (Benzie 1961, 1968; Hopkins 1971, 1979). Thus, small egg size and, consequently, high fecundity in *N. cleaveri* are likely to be linked to its diadromous life-history. *Neochanna burrowsius* may have retained this ancestral trait, which is also likely to confer an advantage in flowing waterways where eggs and fry may be swept downstream into unsuitable habitat. In contrast, *N. apoda* often spawns within tree root hollows (Eldon 1978b). In such confined situations, numerous small eggs may not be advantageous, whereas fewer larger eggs that contain abundant yolk reserves may improve fry survival by promoting rapid development. Irrespective of the mechanism, it appears that selective pressures imposed by wetland life may not only have influenced the morphology of *Neochanna* species as detailed in the transformation series, but also their reproductive strategies.

## 5.2 SPAWNING BEHAVIOUR

Relative capture rates using a variety of methods suggest that female *Neochanna* outnumber males in many populations. The ratio of males to females was 1:1, 1:1.3 and 1:1.8 for *N. apoda* at different sites in the Hinai Valley, Wairarapa (Eldon 1978b) and 1:1.1 for *N. burrowsius* at a South Canterbury site (Eldon 1979c). However, Eldon (1979c) found that male *N. burrowsius* were more readily captured in traps during the spawning period, which he suggested indicated increased activity. Spawning involves scattering eggs throughout the habitat, a behaviour that is likely to reduce their detection by predators, including other adult *Neochanna*. Spawning has seldom been observed, but appears to involve males actively chasing females (Perrie 2004; O'Brien 2005). Pairs of *N. burrowsius* also move in unison during spawning activity in a way that suggests coordinated mating behaviour (Gay 1999; O'Brien 2005). Perrie (2004) recounted spawning behaviour in the early afternoon in *N. diversus*: 'The female(s), followed by one or both males would swim into a plant thicket... The male(s) would swim alongside, nudging and pressing their bodies against the females' (Perrie 2004: 9). Prior to spawning, unusual behaviour occurred in *N. apoda*, with adults resting amongst vegetation very near the surface of the water. These congregated fish were very still and did not startle when disturbed (Eldon 1971). However, vigorous activity must also occur during spawning in *N. apoda*, as eggs have been found splashed high above the water level of aquaria (up to 24 cm; Eldon 1971). There has been debate in the literature regarding the possible occurrence of terrestrial spawning (Eldon 1971, 1978b, 1979c; Cadwallader 1975a) and spawning migrations (Eldon et al. 1978b; Eldon 1979c).

## 5.3 TIMING OF SPAWNING

Environmental cues, including changes in water temperature, increasing photoperiod, and dissolved oxygen levels, may determine when *Neochanna* species spawn (Eldon 1979c, 1993). Cadwallader (1973) also proposed that rainfall or an increase in water level was a necessary stimulus for spawning in *N. burrowsius*. Such a cue is also potentially important for species that spawn immediately after the onset of rain. However, an increase in water level could not be confirmed as an environmental cue in experimental manipulations with *N. burrowsius* (O'Brien 2005). Spawning generally occurs from late autumn (*N. apoda* and *N. diversus*) until early spring (*N. burrowsius* and *N. cleaveri*), when water levels and temperatures are optimal (McDowall 1970; Eldon 1978b, 1979c; Ling 2001). Few field surveys for *Neochanna* eggs have been conducted, and the occurrence of spawning is usually deduced from the examination of gonads of individual fish (Eldon 1978b, 1979c; Koehn & Raadik 1991), or the appearance of fry (Eldon 1978b, Thompson 1987). Females typically spawn only once per year. However, there is some suggestion that *N. diversus* may spawn in autumn and spring if conditions are suitable (N. Ling, University of Waikato, pers. comm.). Indeed, *N. apoda* fry have been observed nearly year round if water is available (Eldon 1978b). Nonetheless, it is not known whether a female

is capable of spawning twice in a season, or whether females spawn once only, in either autumn or spring. In contrast, males spend only part of their milt at a time and may fertilise the eggs of several females in a season (Eldon 1979c).

Many of the habitats in which *Neobanna* species occur dry up during summer and autumn, so there is often only a short period of time in which successful reproduction and larval growth can occur. Rainfall is unpredictable and, possibly because of this, *Neobanna* females appear to be capable of retaining eggs for many weeks in anticipation of the onset of favourable conditions (O'Brien 2005). The ability to hold eggs may be facilitated by the development of a closed ovisac, as found in *N. apoda* (Davidson 1949). *Neobanna burrowsius* were found to delay spawning when no aquatic vegetation was present, and if disturbed or in situations of poor water quality (O'Brien 2005). The ability to control spawning readiness may be most pronounced in *N. diversus* and *N. apoda*, as they occur predominantly in seasonally dry wetlands and must be ready to spawn at the onset of rain (Eldon 1978b; Thompson 1987). However, female *Neobanna* do not synchronise their spawning and, as a result, the spawning season at any particular locality can extend over several months (Eldon 1978b, 1979c; Thompson 1987; McDowall 1990; O'Brien 2005). Thus, habitat-dependent patterns of water availability mean that *Neobanna* species do not necessarily have clearly defined breeding periods.

#### 5.4 SPAWNING HABITAT

Little is known about the specific habitat requirements for spawning of most *Neobanna* species. However, as their spawning involves scattering eggs, it is likely that relatively large areas of suitable spawning substrate are required, whether these be dense aquatic vegetation, forest floor debris, moss, or, in the case of *N. apoda*, hollows under trees. Observations by Perrie (2004) of captive fish suggest that *N. diversus* prefers denser areas of aquatic vegetation for spawning. In a field study, O'Brien (2005) found that *N. burrowsius* eggs were associated with the presence of particular macrophyte species. These species typically had a complex architecture at the water surface, provided by either root hairs, e.g. *Glyceria* spp., or their general leaf structure, e.g. *Myriophyllum* spp. (O'Brien 2005). In another field-based investigation, Eldon (1978b) placed large bottomless tins into the substratum of a forested *N. apoda* habitat to ascertain the location of spawning through the enclosure of newly hatched fry. He concluded that spawning occurred within hollows amongst the tree roots that adults used as refugia during dry periods. Eldon (1978b: 26) also described sieving *N. apoda* eggs 'from gritty mud in a water-filled hollow about 300 mm in diameter formed by cattle tracks'. Thus, *N. apoda* may spawn in small shallow 'pockets' of habitat (Eldon 1978b).

## 5.5 SUMMARY

- New Zealand *Neochanna* species complete their life-histories in freshwater; however, larvae of the Australian *N. cleaveri* may develop in the marine environment.
- The number and size of eggs produced by females, of a given size, differ among the species so far studied in a way that conforms to the transformation series (Fig. 3).
- Females may outnumber males at some sites and males may be more active during the spawning period.
- Spawning has seldom been observed, but appears to involve co-ordinated and vigorous activity.
- *Neochanna* species scatter their adhesive eggs widely, but there is some evidence that they prefer particular places for spawning.
- *Neochanna* species exhibit flexibility in the timing and duration of spawning. Such flexibility illustrates the responsiveness of *Neochanna* species to their environment and is likely to enhance survival of vulnerable early life history stages.

# 6. Population characteristics

The survival, growth and fitness of each individual in a population determines general population-level characteristics, such as patterns in the density and size of the population. A ‘sustainable’ population is often identified as one containing a wide size range of healthy individuals. However, such ideal populations are seldom observed in the wild because of the interplay of abiotic factors, such as drought, and biotic factors, such as interactions with other fish. An important objective in conservation management is to determine if a population is in decline or limited by adverse factors. Population characteristics often reflect long-term environmental conditions and may be useful in guiding conservation action. This chapter provides information on recruitment, growth rates, and methods to determine density, size, and structure of *Neochanna* populations.

## 6.1 RECRUITMENT

Persistence of a *Neochanna* population requires recruitment and survival of sufficient juveniles to at least replace older individuals that die or emigrate. For *Neochanna* species, recruitment rate depends on many habitat and population characteristics, such as hydrological disturbance, habitat quality and fish density. Thus, recruitment can vary between sites and years. Drought patterns can have an important influence on recruitment success, as fry need to develop sufficiently before habitat dries up (Eldon 1978b). High water flows and flooding may also reduce recruitment, as fry are pelagic and can easily drift, or be washed out of a site into unfavourable downstream habitat (Kerr & McGlynn 2001). Interactions with other fish species, especially *Gambusia affinis*, may also influence recruitment, via predation and competition (Barrier & Hicks 1994; Kerr & McGlynn 2001; Ling 2004). Furthermore, Francis (2000a), speculated that

changes in farming practices contributed to low recruitment into some *N. apoda* populations. O'Brien (2005) also found very low recruitment, compared with the size of the adult population, in perennially flowing habitat, while populations in intermittently flowing habitats had consistently high recruitment.

## 6.2 GROWTH RATES

Generally, the growth of *Neochanna* individuals is initially rapid, and occurs mainly in the first year of life. Growth slows after fish reach reproductive maturity, at which time energy resources are diverted to reproductive activities and gonad development. In an extensive study of *N. burrowsius* populations, Eldon (1979c) calculated that in the first 10 months of growth, fish had mean monthly increments in body length (MMI) of 7–9 mm, whereas individuals 94–110 mm long had a MMI of 1.4 mm (range 0–3.8 mm). There may also be characteristic differences in growth rate between *Neochanna* species. For example, 1+ *N. burrowsius* had slower growth rates than similarly aged *N. apoda* (Eldon 1979c). Furthermore, after sexual maturity, growth slowed to a greater extent in *N. burrowsius* than in *N. apoda* (Eldon 1979c). Similarly, Perrie (2004) found *N. beleios* had lower growth rates than *N. diversus*. Site-specific growth from mark-recapture studies are compared in Table 5. It should be noted that such studies rely on the chance capture of a previously tagged fish, thus the length of time since, and timing of, capture varies. In all species, long-term estimates of growth, calculated over more than 300 days for fish > 80 mm long, are lower than short-term estimates (Table 5). This suggests that seasonal patterns in growth occur, with fish growing more during winter and spring than in summer and autumn (Eldon 1978b; Perrie 2004).

## 6.3 POPULATION DENSITY AND SIZE

*Neochanna* species can occur at high densities in suitable habitat, and records of more than 10 fish per trap occur in the NZFFD. Various methods exist to estimate population size and make assumptions of population characteristics.

TABLE 5. GROWTH RATES, FOR ADULT (> 80 mm LONG) *Neochanna* SPECIES AT VARIOUS SITES. THE AVERAGE LONG-TERM (CALCULATED OVER MORE THAN 300 DAYS) AND MAXIMUM GROWTH RATES MEASURED ARE GIVEN.

SPECIES	SITE	MEAN MONTHLY INCREMENT (mm)		PERIOD OF MAXIMUM GROWTH	SOURCE
		LONG-TERM GROWTH	MAXIMUM GROWTH		
<i>N. burrowsius</i>	Buchanans Creek	0.9*	6.9	July–Oct	Eldon (1979c)
<i>N. burrowsius</i>	Clearwell		2.5	July–Dec	Eldon (1979c)
<i>N. burrowsius</i>	Oxford	0.4†	2.5	June–Mar	Eldon (1979c)
<i>N. diversus</i>	Tekearau	0.8	3.9	July–Nov	Perrie (2004)
<i>N. diversus</i>	Waiparera	0.3†	1.4	July–Mar	Perrie (2004)
<i>N. diversus</i>	Whangamarino	0.7†	2.7	June–Oct	Perrie (2004)
<i>N. beleios</i>	Ngawha	0.3	0.7	Nov–Sept	Perrie (2004)
<i>N. beleios</i>	Omapere	0.2†	0.9	Apr–Sept	Perrie (2004)
<i>N. apoda</i>	Hinau	1.0	11.1	July–Feb	Eldon (1978b)

\* Mean value from five fish calculated over 237 and 424 days.

† Sample size >5.

While catch per unit effort (CPUE) from sampling data provides an indication, population sizes can only be truly estimated using mark-recapture techniques. In both cases, habitat area is an important factor that influences estimates of population size. Eldon et al. (1978), in a study that used multiple trapping occasions in an extensive habitat, estimated that a population of *N. burrowsius* at Clearwell (Hinds River catchment), was likely to exceed 3000 adults. Similarly, O'Brien (2005) estimated population sizes for four *N. burrowsius* sites to range from 1200 to 3100 individuals. In contrast, 98 *N. apoda* were estimated to be present in a small 30-m<sup>2</sup> pond (Eastwood & Butler 1999). Perrie (2004) obtained population size estimates for *N. diversus* that ranged up to 540 fish per site.

Perrie (2004) also found that recapture rates of tagged fish were higher on consecutive days post tagging than over longer intervals. This indicates slow mixing rates, i.e. slow dispersal of individuals out of the immediate area they were released into after capture. Eldon et al. (1978) suggested that low mixing rates could result in poor estimates of population size. A further problem is defining the extent of a population. *Neochanna* species often occur in fragments of a larger wetland or lake system and in isolated pockets of habitat which, nonetheless, are connected during high flow and flooding, and/or by actively dispersing individuals (Eldon 1978b; Eldon et al. 1978). It is important, when deciding which methods of population size estimation to use, to determine the scale at which populations are 'open' or 'closed', i.e. whether individuals are moving in and out of the area of study or not. Many studies using mark-recapture methods have found that *Neochanna* populations at study sites are open, i.e. some fish disperse widely (Eldon 1978b; Eldon et al. 1978). However, both Eldon et al. (1978) and Perrie (2004) reported that the difference between estimates, assuming either open or closed conditions, resulted in only small differences in estimated population size.

#### 6.4 AGE STRUCTURE

Determination of age of *Neochanna* fish requires the extraction of sagittal otoliths and, therefore, sacrifice of individuals. Eldon (1978b, 1979c) estimated that *N. burrowsius* and *N. apoda* live for 4-5, and 7 years, respectively. However, he suggested that *N. apoda* might live even longer, as otoliths from the largest fish he recorded were not examined. *Neochanna diversus* may be quite long-lived, as Thompson (1987) kept several alive in captivity for 8 years. By counting otolith annuli, Perrie (2004) estimated that a 114-mm-long *N. diversus* from Whangamarino wetland was 11 years old. However, *Neochanna* species exhibit differential growth patterns, with most growth occurring in the first year of life. After maturity, growth slows and otolith rings become very closely spaced and poorly defined, so counts may not be accurate. Thus, Eldon (1978b) commented that the number of rings recorded in independent counts of a single *N. apoda* otolith did not always agree, and sometimes three counts were all different. A further complication when determining age from otolith rings and check marks is that the variable seasons experienced in New Zealand result in growth patterns that relate poorly to annual patterns. Eldon (1979c) found contradictory results from otoliths of marked *N. burrowsius* of known minimum age and concluded that counts of otolith rings could not be used to determine the age of this species. Furthermore, the length of individuals is only very weakly related to their age. Perrie (2004) counted five annuli in a 105-mm-long

*N. diversus* from Whangamarino wetland, whereas an apparently similar-aged fish from Ngunguru wetland was 149 mm long. Considering the occurrence of site-dependent and seasonally variable growth rates, as well as the low reliability of otolith annuli readings, it is not possible to estimate the age of fish with any degree of confidence.

## 6.5 SIZE STRUCTURE

Another method used to estimate the age structure of a fish population is to determine how many cohorts in length-frequency data can be observed (as a high frequency of fish at certain lengths). By convention, and especially in small fish such as *Neochanna*, 5-mm length classes are recommended (Anderson & Gutreuter 1983). Examination of length-frequency histograms for *Neochanna* species is hampered by the difficulty in distinguishing cohorts after the first year because year classes merge as growth slows and becomes more variable at the onset of sexual maturity (Eldon 1978b; 1979c). The predominance of a particular sex may also influence size structure of a population. Eldon (1979c) found that *N. burrowsius* females attained a larger size than males at two different sites. This difference may be mistaken for different cohorts. In the Wairarapa, however, Eldon (1978b) found *N. apoda* males were larger than females at one site, but at two other sites there were no significant differences in the sizes of the sexes. Overall, it appears that estimation of age structure from cohort analysis is not possible for *Neochanna* species.

Nevertheless, important differences in the overall length-frequency structure of different populations has been noted by several workers. e.g. Eldon (1978b, 1979c), Francis (2000a), and O'Brien (2005). Observed structures were skewed to either the left or right, i.e. populations either had high recruitment or were mainly large fish, respectively. At a site in South Canterbury, Eldon (1979c) found 830 young-of-the-year *N. burrowsius*, and 65 adults between November and May, whereas at another site he found only 136 young-of-the-year, compared with 238 adults. Eldon (1978b) noted differences in length-frequency distributions in different *N. apoda* habitats in the Wairarapa, with fish being larger in pasture habitat than in forested habitat, even when the two kinds of habitat were adjacent. Eldon (1978b: 31) also reported that 'the largest mudfish recorded among 24 from West Coast (South Island) forest habitats was 118 mm, and the largest of 23 from West Coast open habitats was 160 mm'. Similarly, Francis (2000a) found fish attained a greater size in a roadside drain than in forest floor habitat at Fensham Reserve, Wairarapa. Eldon (1978b) suggested that differences in size attained by *Neochanna* reflected a relationship between growth rate and availability of food resources. He considered that *N. apoda* were smaller (125 mm) when only smaller prey were available (even if the site did not dry up requiring fish to cease feeding), whereas fish grew considerably larger (160 mm) when earthworms were included in the diet. O'Brien (2005) found differences in the maximum length attained by fish in intermittently and perennially flowing sites. These findings may reflect suppressed growth and stunting of fish in intermittent and ephemeral sites. Stunting may be related to starvation during habitat drying and the general availability of food resources. Habitat drying and hypoxia might also lead to selection of smaller-sized fish with lower oxygen uptake requirements (Meredith 1985).

## 6.6 SUMMARY

- Recruitment success differs greatly among populations. Drought, high water flows, habitat quality, and biotic interactions have been suggested as influencing recruitment.
- Rapid growth occurs before sexual maturity is reached at 1–2 years, and then slows considerably.
- Growth is seasonal, with more growth occurring during winter and spring.
- *Neochanna* species may exhibit characteristic growth rates, with *N. apoda* having the highest recorded growth rates and *N. beleios* the lowest.
- Estimates of population size require mark-recapture methods and may be affected by both low mixing rates and high rates of dispersal out of sites.
- Counts of sagittal otolith annuli and analysis of length-frequency structure are not reliable means of determining age in *Neochanna* species.
- Distinct population structures occur in different habitats and populations appear stunted in some situations.

# 7. Behavioural adaptations

*Neochanna* species exhibit a range of behaviours, including a diverse repertoire of foraging techniques, as detailed in section 4. However, they are most renowned for their amphibious tendencies and ability to persist in habitats that are periodically stagnant or dry up. The propensity to move over land may be a common behaviour in Galaxiidae (Woods 1963; McDowall 1990) that is especially pronounced in *Neochanna* species, especially *N. apoda* (Eldon 1978b). Main (1989) speculated that amphibious behaviour could have played a role in the dispersal of *N. apoda* into catchments after glacial retreat. Eldon (1978b: 33) reported that K.F. Maynard had observed *N. apoda* ‘splashing about all over the road’ during heavy rain; while Eastwood & Butler (1999: 4) reported that on the West Coast, *N. apoda* is referred to locally as ‘the fish with legs’. Such amphibious behaviour likely allows *Neochanna* species to persist in small, seasonally disturbed habitats. This chapter describes the behavioural response of *Neochanna* species to hypoxia (low dissolved oxygen), emersion (being out of water), and their refuge-seeking behaviours when habitats dry up.

## 7.1 RESPONSE TO HYPOXIA

Air-breathing is generally regarded as an evolutionary adaptation to hypoxia, a scenario thought to apply in the case of *Neochanna* species (Eldon 1979a, c; Meredith 1981; Dean 1995). When placed in poorly oxygenated water, *Neochanna* may move to the surface, take a gulp of air, and hold a bubble in the buccal cavity (Eldon 1979c; Meredith 1981; McDowall 1999b). Air-breathing also occurs when individuals are emersed (held out of water), with fish exhibiting distinctly distended jaws and inflated opercular regions. This is a primitive form of air-breathing more aptly described as air-gulping, as the behaviour is similar to feeding and coughing reflexes (Meredith 1985). Nevertheless, inflating the

buccal cavity with air is an efficient method of oxygen uptake (Meredith 1981). *Neochanna* will readily gulp air and do so in preference to utilising oxygenated water at the water surface (Meredith 1985; Barrier et al. 1996). When exposed to progressive hypoxia, gill ventilation in *N. burrowsius* increased in both amplitude and frequency, until the ability to compensate for declining oxygen uptake reached a threshold and air-breathing began (Eldon 1979c; Meredith 1981). Dissolved oxygen levels at which air-breathing commenced were approximately 15–30% saturation for both *N. burrowsius* (Meredith 1981) and *N. diversus* (McPhail 1999). A variety of air-breathing behaviours have been observed, indicating different strategies or progressive stages in response to increasing hypoxia (Eldon 1979c; Meredith 1981, 1985; McPhail 1999; McDowall 1999b).

During experimental conditions of declining aquatic oxygen concentration, *N. burrowsius* rose to the water surface, took an air bubble into the buccal cavity and then returned to the bottom of the tank and performed ‘burrowing like’ activities in an attempt to remain in benthic refuge (Meredith 1981). McPhail (1999) described *N. diversus* sinking to the bottom of the tank and remaining quiescent before the air bubble was expelled and the behaviour was repeated. *Neochanna diversus* continued gill ventilation while retaining the air bubble and McPhail (1999) suggested that this enabled water to pass over the air bubble. This behaviour differs from that reported by Meredith (1981), who observed that ventilation in *N. burrowsius* ceased during submerged air-breathing.

McPhail (1999) also described two distinctive postures assumed by *N. diversus* while holding an air bubble in the buccal cavity. Fish either assumed a head-up, vertical position against the glass, or a ‘cobra’ position with the head up and the anterior half of the body arched, while the posterior half of the body remained horizontal on the substratum. *Neochanna diversus*, *N. burrowsius* and *N. beleios* have all been observed ‘hanging’ at the water surface, sometimes with their head regions exposed to air (Eldon 1979c; Meredith 1981; Barrier 1993; McDowall 1999b). These fish did not expend as much energy as those that attempted to remain benthic while retaining an air bubble. Eldon (1979c) suggested that hanging at the water surface was a response to more chronic hypoxia and noted that fish were reluctant to move when disturbed. Remaining at the water surface exposes fish to increased risk of predation by birds (Barrier et al. 1996). Schooling and shoaling behaviour is a common anti-predator response in fish and may be adopted by *N. burrowsius* when air breathing at the water surface (Phillipps 1926a; O’Brien 2005).

As air breathing in an aquatic situation can be energetically demanding and potentially hazardous, *Neochanna* may attempt to leave the water before conditions become too extreme (Eldon 1979c; Meredith 1985; McPhail 1999). This was demonstrated in an experiment involving very low levels of dissolved oxygen, where some *N. burrowsius* actively left the water without establishing a regular pattern of air breathing (Meredith 1981). Meredith (1981: 19) observed that ‘fish were reluctant to return to the water and re-emerged if pushed back in’. In a series of investigations, Eldon (1978b) found that *N. apoda* would leave the water even if they were not threatened by stranding. McPhail (1999) also held the view that *N. diversus* left the water and moved to terrestrial vegetative shelter well before their habitat dried up. Pre-emptive movement in response to falling water quality would also allow *Neochanna* species to avoid being trapped in unsuitable habitat during a drought.

## 7.2 RESPONSE TO EMERSION

Movement from an aquatic to a terrestrial situation requires both physiological and behavioural adaptations. Meredith (1985) found that, during emersion, 40% of fish at any one time would lie on their dorsal surfaces with their abdomen exposed. Eldon (1978b) also noted that during experimental drought conditions *N. apoda* would sometimes lie on their backs. This behaviour may facilitate rehydration of the skin and enhance gas exchange efficiency through the skin to vital organs. The physical act of rolling may also improve distribution and mixing of water within the opercular cavities, or enhance waste excretion across the skin by allowing diffusion from different body surfaces (Meredith 1985). *Neochanna burrowsius* were thus observed to be active during emersion, changing positions frequently (Meredith 1985). Conversely, *N. diversus* moved infrequently in some studies (fish moved only 5 times in 10 weeks; McPhail 1999) but regularly in others, changing orientation, posture and location (Dean 1995; Davidson 1999). In all cases, however, *N. diversus* were responsive when touched, often reacting with vigorous activity, suggestive of an anti-predator response. Maintaining awareness would also allow fish to avoid environmental stressors by moving into better positions and seeking water when it returns (Meredith 1985). Barrier et al. (1996) speculated that while *N. diversus* may leave poor-quality water during the day when temperatures are high, they might return to feed during the night. Indeed, emersed *Neochanna* have been found with stomach contents that show little sign of decomposition (Günther 1867; Eldon 1979b). This may also explain the anecdotal observation that *Neochanna* catch rates are higher on rainy nights during otherwise drought conditions (Barrier et al. 1996).

The ability to bend into a deep, narrow U shape is also likely to be important for survival out of water (McDowall 2003). This posture allows maintenance of a dorsal-ventral position; ensuring fish do not roll onto their sides, which would affect their ability to inflate their gills. Coiling or bending behaviour also reduces the amount of exposed skin and, thus, the effective evaporative surface during emersion (Meredith 1985). In laboratory investigations, emersed *N. diversus* that were initially placed apart from each other would often end up coiled together in clusters (Davidson 1999). Similar behaviour has been observed in *N. burrowsius* and *N. apoda* (Eldon 1978b; Meredith 1985). Behaviour such as congregating in favourable microhabitats is likely to reduce desiccation during drought. Eldon (1978b) recounted how a drainage contractor with an excavator found 'pockets' or 'pods' of *N. apoda* in a grass field, and suggested that fish congregated in a few suitable refuges. O'Brien (2007) found large numbers (> 100) of *N. burrowsius* congregated in a cavity 0.5 m below the bottom of a former pond. It appeared that this subterranean cavity had been used for many years, as a large number of skeletons were also scattered about. Other searches for emersed fish have only found a small proportion of the fish known to be present there (Eldon et al. 1978; McPhail 1999).

## 7.3 REFUGE-SEEKING BEHAVIOUR

The ability of *Neochanna* species to find refuge well below ground level has been widely reported. For example, Roberts (1872: 456) described how a *N. apoda* 'was found at least eighteen inches down ... in a little chamber somewhat larger

than its own carcass. ... The chamber was dry and completely shut in from above'. Other depths recorded are 4 feet (Günther 1867), 10 feet (Hector 1869), 0.25 m (Eldon 1979c), 0.3 m (Andrews 1991), and 0.5 m (O'Brien 2005). These recorded depths suggest that active burrowing behaviour occurs; yet *Neochanna* have also been found in a diverse range of drought refuges, including car tyres and under corrugated iron (Eldon 1968, 1978a, b, 1979a, c; McPhail 1999). Selection of microhabitat during drought may therefore be largely random and opportunistic, with many fish dying in unfavourable places (Eldon et al. 1978; Eldon 1978b, 1979a, 1979c). There is also evidence from behavioural experiments that some individuals show little desiccation avoidance behaviour, such as burrowing (Eldon 1978b, 1979c). Davidson (1999) reported that *N. diversus* did not attempt to burrow into damp moss during emersion experiments. It appears, therefore, that the ability to survive drought requires an appropriate behavioural response, which may not always occur.

*Neochanna* species have well-developed muscles and bone ossification in the head region, likely an adaptation to facilitate burrowing through vegetation and damp mud (Davidson 1949; McDowall 1997a). However, there is debate as to whether *Neochanna* species are able to construct burrows, or whether they are limited to enlarging existing fractures or weaknesses in the substrate (Davidson 1951; Eldon 1978b, 1979a, c; McPhail 1999). Of 71 *N. burrowsius* that Eldon (1979a) found emersed, only 12 were in situations that bore any resemblance to burrows or a constructed refuge. Nonetheless, *N. apoda* may utilise the burrows created by *P. planifrons* (koura), although one study found that the characteristics of the burrows occupied by the two species differed slightly, with burrows containing *N. apoda* being vertical, compared with angled burrows that contained *P. planifrons* (Eldon 1968). *Neochanna burrowsius* have also been found in smooth-walled burrows and holes (Phillips 1926a; Eldon 1979a, c; O'Brien 2005). Cadwallader (1975a) observed three captive *N. burrowsius* occupying separate, small, smooth-walled chambers with tunnel entrances in a full aquarium. These burrows were located at or just above the water level, implying that *N. burrowsius* may also use burrows during non-drought conditions. However, in laboratory experiments, *N. burrowsius* and *N. apoda* failed to construct burrows, although there was some evidence of attempts (Eldon 1978b, 1979c). Burrowing behaviour has been observed in *N. cleaveri*, which commenced burrowing when exposed to conditions of hypoxia and declining water levels in an aquarium (Koehn & Raadik 1991). The behaviour consisted of the fish initially forming a vertical shaft when surface water was still present. By the time surface water had disappeared, horizontal tunnels connected to the original shaft had been constructed, and these still contained water. The fish then rested in the horizontal tunnels with their heads protruding into the water retained in the shaft, and remained in the tunnels as the substratum totally dried out (Koehn & Raadik 1991). This study demonstrated that at least one *Neochanna* species exhibits well developed burrowing behaviour. Considering the importance of this behaviour during droughts, further study to determine the extent of and requirements for burrowing is required for all New Zealand *Neochanna* species.

## 7.4 SUMMARY

- *Neochanna* species exhibit a wide range of behavioural responses that promote survival when their habitat is disturbed by drought.
- A variety of air-breathing behaviours have been observed and fish will also actively leave hypoxic water.
- When emersed, fish remain responsive and regularly move, which may enhance distribution of fluids and excretion of wastes.
- Individuals sometimes congregate in suitable micro-habitats, which may reduce water loss by evaporation and improve survival during drought.
- *Neochanna* species have sometimes been found in 'burrows' and underground cavities in the wild. However, New Zealand species have not been observed creating burrows in controlled situations (as has been observed with the Australian *N. cleaveri*) and there is debate over their ability to do so.

## 8. Physical adaptations

The ability of *Neochanna* species to persist in habitats prone to drying up has received much comment in the literature, and much has been made of this ability, e.g. Young (1996). While it is undeniable that *Neochanna* species can survive considerable periods without surface water, how they achieve this feat is poorly understood. Most studies have concluded that *Neochanna* species have few specialised anatomical adaptations to ensure survival (Meredith 1985; Dean 1995). Furthermore, although there has been much emphasis on their survival ability, field and laboratory studies of emersed *Neochanna* indicate significant rates of mortality during emersion (30–40%; Eldon et al. 1978; Meredith 1985; O'Brien 2005). The high level of mortality found conflicts with the general view that *Neochanna* species are well equipped to survive long periods without water (Dean 1995; McPhail 1999; Ling 2001). Physiological comparisons indicate that the potential to survive emersion may not necessarily be unique to *Neochanna* species within Galaxiidae (Meredith 1985). Indeed, *Neochanna* species do not have adaptations often found in more specialised air-breathing fish, such as highly modified gills (Davidson 1949; Meredith 1985; Davidson 1999), or the conversion of the swim bladder to an accessory gas exchange organ (Davidson 1949; Meredith 1985). It will be important to understand the extent to which *Neochanna* species can tolerate the absence of water if droughts become more severe as a result of climate change. This chapter details studies on characteristics of the gills, skin, mucus, blood, circulatory system, and metabolic rate of *Neochanna* species.

## 8.1 GILLS

Gills are important sites of gas and ion exchange in animals that live in water, but in the terrestrial environment, without the support of water, they may collapse and their ability to function may be reduced. Adaptations that improve gill function in air by preventing gill collapse generally lead to a reduction in gill surface area. This is due to the secondary lamellae (plate-like structures through which capillaries run) becoming shorter, broader, and spaced further apart on the gill filament (Meredith 1985; Dean 1995). Thus, a trade-off exists in that adaptations reducing gill area, which may improve survival in the terrestrial environment, may result in reduced ability to absorb sufficient oxygen from hypoxic water. How *Neochanna* species resolve these physiological constraints may provide insights into their likely survival strategies during drought.

Three studies have investigated the morphology of *Neochanna* gills (Table 6): Meredith (1985; *N. burrowsius*), Dean (1995; *N. diversus*) and Davidson (1999; *N. diversus*). Direct comparisons between these studies are difficult because of differences in the measurements made and data presented. However, it appears that morphological differences in gill structure may occur between the species studied. All studies agree that the structural components of *Neochanna* gills are not greatly reduced or modified, and resemble the gills of most other fish species, especially those of *Anguilla* species (Meredith 1985; Dean 1995). However, Dean (1995) found significant differences between *N. diversus* and *G. maculatus* in the spacing of secondary lamellae, with the latter species having long, closely spaced lamellae, whereas those of *N. diversus* are widely spaced (Table 6). On average, the secondary lamellae of *N. diversus* also appear stouter (lower height to width ratio) than those of *N. burrowsius* (Table 6). Comparisons of the bilateral (total) area of secondary lamellae also suggest that *N. diversus* may have a smaller functional gill area than *N. burrowsius* (Table 6). Thus, although more rigorous and direct anatomical comparisons are needed, *N. burrowsius* may (by having a larger gill surface area to extract oxygen from water) tolerate hypoxia for longer than *N. diversus*. Conversely, *N. diversus* may tolerate emersion better by having short, widely spaced gills. Although these conclusions need further verification, they reflect the ecological situations in which the two species are commonly found and support their placement in the transformation series (see Fig. 3).

TABLE 6. MEASUREMENTS OF SECONDARY LAMELLAE ON THE SECOND GILL ARCH OF *Neochanna* AND *Galaxias* SPECIES. MEANS ARE GIVEN WHERE PROVIDED. A DASH (-) INDICATES INFORMATION IS UNAVAILABLE.

SPECIES	SPACING ( $\mu\text{m}$ )	LENGTH ( $\mu\text{m}$ )	HEIGHT/WIDTH RATIO	BILATERAL AREA ( $\mu\text{m}^2$ )	SOURCE
<i>N. burrowsius</i>	31*	125	0.92	8800 <sup>†</sup>	Meredith (1985) <sup>§</sup>
<i>N. diversus</i>	36	102	-	-	Dean (1995) <sup>§</sup>
<i>G. maculatus</i>	22	105	-	-	
<i>N. diversus</i>	28	-	0.81	8600	Davidson (1999) <sup>‡</sup>
<i>G. maculatus</i>	22	-	-	-	

\* Measured from supplied scanning electron micrograph.

<sup>†</sup> Calculated using allometric equation relating fish size to bilateral area.

<sup>§</sup> Sample size > 10.

<sup>‡</sup> Sample size of one 88-mm-long fish.

## 8.2 SKIN

Scaleless, permeable skin is considered a precursor of the primitive adaptations that enabled fish and amphibians to leave the water permanently. The skin of *N. burrowsius* acts as an effective supplementary gas exchange surface (Meredith et al. 1982), as it also does in several *Galaxias* species (Meredith 1985). Although cutaneous respiration is a general characteristic of galaxiid fish, it appears highly developed in *Neochanna* species. *Neochanna burrowsius* were capable of absorbing a greater proportion of oxygen (43%) through the skin than were three species of *Galaxias* (16–19%) in water (Meredith 1985). In the first 4 hours they were out of water, 40% of oxygen uptake and 45% of carbon dioxide loss occurred through the skin of *N. burrowsius* (Meredith 1985). Thus, considerable respiration can still occur in *Neochanna* even if gills collapse and their ability to function is reduced.

Metabolic waste products are also excreted through permeable skin, although valuable water may be lost through this process. Overall, the skin of *N. burrowsius* and, possibly, other *Neochanna* species is permeable to gases (oxygen, carbon dioxide, and ammonia) and water, but is weakly permeable to ions (important electrolytes) and chemical metabolites (urea; Meredith et al. 1982; Meredith 1985). These characteristics have consequences for the mechanisms and strategies that enable *Neochanna* species to survive in both air and water (Meredith 1985). Importantly, *Neochanna* species are unable to regulate water loss and have not evolved any specialisations in this regard, as are found in amphibians. However, the lack of anti-desiccatory mechanisms in *Neochanna* species is likely to be compensated for by behavioural responses and an extensive mucous covering (Meredith 1985).

## 8.3 MUCUS

Although Dean (1995) did not observe mucous cells in the skin of *N. diversus*, they are most likely present, as McPhail (1999) mentioned the presence of a mucous layer on the skin of these fish. The skin of *N. apoda* contains gland cells capable of excreting mucus (Davidson 1949). Similarly, the skin of *N. burrowsius* is covered extensively with mucous cells, which exceed 50% of the skin area. Their distribution and relative density were high compared with most other fish (Meredith 1985). The proliferation of mucous cells appears central to the function of *Neochanna* skin and is considered one of the outstanding features that allows *Neochanna* to survive in air (Meredith 1985). Indeed, mucus production increases substantially in response to emersion (Meredith 1985; Dean 1995; McPhail 1999).

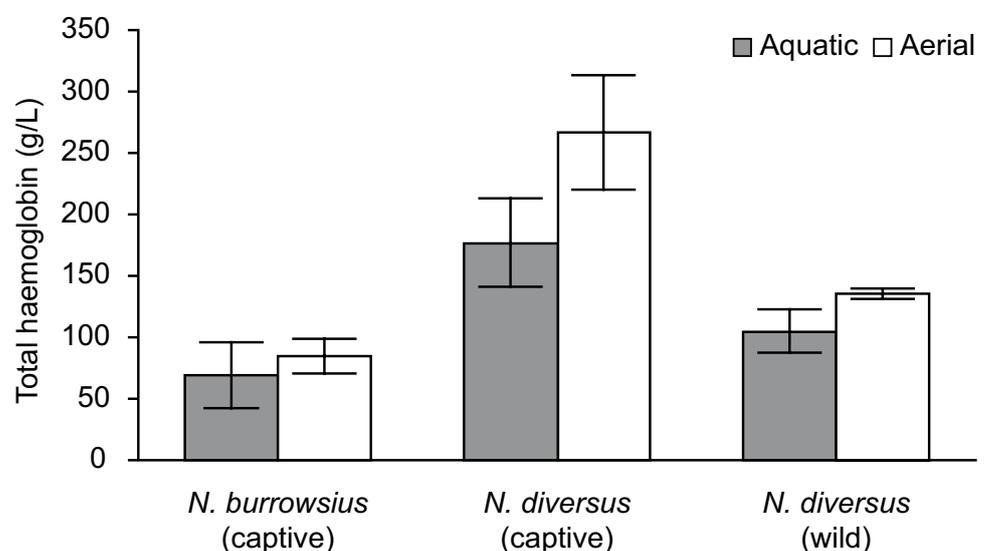
Mucus has many functions. For example, it has lubricating properties, performs protective and osmoregulatory roles, improves abrasion resistance, and is a barrier to pathogens (Meredith 1985). Importantly, mucus is hygroscopic and can store water, thus maintaining a moist layer around an emersed fish, potentially drawing and trapping water from the surrounding microenvironment (Meredith 1985). When *Neochanna* are emersed, they excrete copious quantities of mucus from their opercular apertures. This mucus may keep gill surfaces moist, thus preventing them from collapsing together, desiccating, and losing function (Meredith 1985; Dean 1999). Mucus may also aid in sealing the margins of the opercula, thus improving the retention of air bubbles in the buccal and opercular cavities when fish are air-breathing (Meredith 1985).

In some tropical aestivating fish and amphibian species, thick dried mucus can form a 'cocoon', sealing the emersed animal in a favourable microclimate. Although Hicks & Barrier (1996) speculated that *Neochanna* species formed such cocoons, there is no evidence that this occurs (Eldon 1978b; Meredith 1985; McDowall 2006). Furthermore, Meredith (1985) discussed whether a mucoid sheath, capable of resisting water diffusion, might explain the ability of *N. burrowsius* to survive for long periods without water. However, following laboratory studies, he concluded that it is unlikely to be a significant mechanism in emersed fish, as desiccation and death are likely to occur before a sufficiently protective cocoon had formed. The composition of mucus, however, may determine the effectiveness of its protective properties and osmoregulatory function, as certain types of mucus are related to amphibiousness in other fish. Several types of mucous cells are present in *N. burrowsius*, and their occurrence considered a general adaptation that has benefits for both aquatic and aerial survival (Meredith 1985).

#### 8.4 BLOOD CHARACTERISTICS

Blood (and particularly the haemoglobin it contains) is a vital part of the physiology of most animals. It is the medium by which oxygen and nutrients are transported to cells, and carbon dioxide and other waste products are excreted. Fish living in low-oxygen environments typically have haemoglobin with a high affinity for oxygen. Interestingly, the haemoglobin of *N. diversus* has a high oxygen affinity (Wells & Ling unpubl. data, quoted in Dean 1995), whereas that of *N. burrowsius* does not (Wells et al. 1984). Thus, *N. diversus* may be capable of higher oxygen uptake in situations of limited oxygen availability than *N. burrowsius*, possibly compensating for its reduced gill surface area (Table 6). The concentration of haemoglobin in blood also reflects the blood's ability to transport oxygen and carbon dioxide within an animal (Davidson 1999). Davidson (1999) measured the blood characteristics of *N. diversus* in aquatic and emersed situations and found that total haemoglobin concentration was significantly higher in emersed fish (Fig. 10). However, this may not be the case in all *Neochanna* species, as emersed and aquatic *N. burrowsius* showed no differences in blood oxygen transport properties (Wells et al. 1984).

Figure 10. Total haemoglobin (g/L)  $\pm$  SEM in the blood of wild and captive *N. diversus* (Davidson 1999) and *N. burrowsius* (Wells et al. 1984), kept or found in aquatic and aerial situations.



The ionic concentration of the blood of *N. burrowsius* was more similar to that of euryhaline marine species of Salmonidae and Anguillidae, than most exclusively freshwater fish species (Meredith 1985). This may reflect a relatively recent marine ancestry for *N. burrowsius*, as demonstrated by the diadromous *N. cleaveri* (Fulton 1986). It would be interesting to see whether similar blood characteristics are present in other species of *Neochanna*. The blood of *N. burrowsius* also has a high buffering capacity (Wells et al. 1984), a feature that may moderate imbalances generated by the accumulation of waste products. Buffering or other protective mechanisms are necessary to mitigate ammonia poisoning. Certain amino acids may play a role in this, although the mechanism is still unknown (Meredith 1985).

## 8.5 CIRCULATORY SYSTEM

Although many aspects of the anatomy of *Neochanna* species are similar to those of other fish (Davidson 1949; Davidson 1999), *Neochanna* species differ from other fish in that they have especially efficient circulatory systems (Meredith 1985). In particular, some features may represent specialisations to enhance air-breathing and survival during hypoxia. For instance, *N. apoda* have an unusual vein that may be an accessory mechanism for eliminating carbon dioxide from the brain (Davidson 1949). The heart of *N. apoda* is also different from the usual teleost type, having an incipient septum subdividing the atrium, a feature found in the South American lungfish (*Lepidosiren* species). Davidson (1949) also described numerous capillaries on the buccal surfaces of *N. apoda*. Such extensive vascularisation would increase oxygen uptake, especially when fish retain an air-bubble in the buccal cavity. Increased vascularisation has not been observed in the buccopharyngeal cavity of *N. burrowsius* (Meredith 1985) or *N. diversus* (Davidson 1999). Thus, species-specific differences in vascular systems may occur that support the arrangement of *Neochanna* species in the transformation series (Fig. 3). On this basis, *N. apoda* exhibits the greatest adaptation to air-breathing of the *Neochanna* species.

An interesting question discussed in the literature is whether *Neochanna* species are able to alter their circulatory patterns in response to environmental conditions. Investigations into ammonia excretion, respiration and skin structure have generated debate over whether *Neochanna* can change skin permeability via the constriction and dilation of blood vessels (Wells et al. 1984; Meredith 1985; Dean 1999). It has been suggested (Meredith 1985) that blood could be directed to the skin when fish are emersed (to increase gas exchange), and away from the skin in hypoxic water (to reduce oxygen loss to the surrounding water). However, there have as yet been no definitive investigations, or a general consensus regarding this ability.

## 8.6 METABOLIC RATE

Metabolic rate is an important physiological variable (commonly measured indirectly by oxygen consumption) which reflects biochemical processes and provides an indication of energy requirements and metabolic waste generation.

The metabolic rate of a fish is dependent on many factors including size, temperature, activity, and stress. For fish in captivity, holding facilities and acclimatisation times are also important in determining standard or resting metabolic rates. Unfortunately, studies of *Neochanna* species carried out so far have used a variety of fish sizes (0.5–10 g), acclimation times (30 minutes – 5 days), experimental temperatures (15–17°C), and general procedures (Meredith 1981, 1985; Meredith et al. 1982; Dean 1995). This variation complicates comparisons; nevertheless, general patterns are evident and it is possible to come to some preliminary conclusions that can be used to inform further comparative research.

In some fish, such as the lungfishes (Sarcopterygii), rapid suppression of metabolic rate occurs in response to their removal from water. This is called aestivation, and is a state similar to hibernation. Such a response to removal from water has been demonstrated in *Galaxiella*, an Australian Galaxiidae fish species found in ephemeral wetland habitats. *Galaxiella* can halve their metabolic rate within hours of emersion (Thompson & Withers 1999). There have been several studies of resting oxygen consumption of Galaxiidae under aquatic (Table 7), and aerial (Table 8) conditions (Eldon 1978b; Meredith 1981, 1985; Dean 1995; Thompson & Withers 1999). The extent of metabolic suppression is determined from comparison of these separate aquatic and aerial measurements. These studies have generated debate as to whether, in response to their habitats drying up, *Neochanna* species exhibit true aestivation, which involves significant cardiorespiratory and metabolic changes as fish enter a state of torpor.

Eldon (1978b) discussed the use of the term aestivation and concluded that *N. apoda* does not truly aestivate. Similarly, Meredith (1981) showed that Galaxiidae in general were tolerant of emersion, and that aestivation was an inappropriate term to describe the response of *N. burrowsius* to survival out of water, because they do not enter a state of torpor. Indeed, it is widely recognised that *Neochanna* species do not become fully dormant or torpid when emersed, and that they respond to external stimuli (Cadwallader 1975a; Eldon 1978b,

TABLE 7. AQUATIC OXYGEN CONSUMPTION RATES FOR RESTING *Neochanna* AND *Galaxias* SPECIES, AND *Galaxiella nigrostriata*. SAMPLE SIZES AND THE MEAN, OR RANGE, OF FISH SIZES USED ARE GIVEN WHEN KNOWN.

SPECIES	SAMPLE SIZE	FISH WEIGHT (g)	O <sub>2</sub> CONSUMPTION (μL O <sub>2</sub> /g/h)	SOURCE
<i>N. burrowsius</i>	8		47	Meredith (1981)
<i>N. burrowsius</i>	11	4–10	37	Meredith et al. (1982)
<i>N. burrowsius</i>	15	6	54	Meredith (1985)
<i>G. maculatus</i>	6	6	141	
<i>G. brevipinnis</i>	4	5	102	
<i>G. vulgaris</i>	3	5	117	
<i>G. fasciatus</i>	6	5	94	
<i>N. diversus</i>	4	0.5–1	249*	Dean (1995)
	4	2–4	218*	
	7	4–10	116*	
<i>Gl. nigrostriata</i>		0.35	48	Thompson & Withers (1999)

\* Means recalculated from extracted data and values converted using the equation:  
1 Mol O<sub>2</sub> = 22.39 L O<sub>2</sub> STPD.

TABLE 8. EMERSED OXYGEN CONSUMPTION VALUES FOR RESTING *Neochanna* SPECIES AND *Galaxiella nigrostriata* HELD OUT OF WATER FOR VARIOUS LENGTHS OF TIME BEFORE MEASUREMENT. SAMPLE SIZES AND MEAN OR RANGE OF FISH SIZES USED ARE GIVEN WHEN KNOWN.

SPECIES	FISH WEIGHT (g)	SAMPLE SIZE	DAYS EMERSED	OXYGEN CONSUMPTION ( $\mu\text{L O}_2/\text{g/h}$ )	SOURCE
<i>N. burrowsius</i>		8	8	39	Meredith (1981)
<i>N. burrowsius</i>	4-10	11	<1	57	Meredith et al. (1982)
<i>N. burrowsius</i>	6	9	<1	48*	Meredith (1985)
	6	16	28	42*	
<i>N. diversus</i>	1-6	16	1	44 <sup>†</sup>	Dean (1995)
	1-6	16	7	37 <sup>†</sup>	
	1-6	16	28	41 <sup>†</sup>	
<i>Gl. nigrostriata</i>	0.4	6	<1	21	Thompson & Withers (1999)

\* Extracted data.

<sup>†</sup> Means recalculated from extracted data and values converted using the equation:  
 $1 \text{ Mol O}_2 = 22.39 \text{ L O}_2 \text{ STPD.}$

1979c; Eldon et al. 1978; Meredith 1981; Barrier & Hicks 1994; Dean 1995; Hicks & Barrier 1996; O'Brien 2005; McDowall 2006). Thus, *Neochanna* species are unlikely to undergo the same metabolic changes in response to drought as other truly aestivating fish and may better be described as 'emersion tolerant'.

It is important to determine the extent to which *Neochanna* species are capable of lowering their metabolism, as it is indicative of their ability to survive long periods of emersion. Meredith (1981) reported that *N. burrowsius* reduced their metabolic rate by 25% during 8 days emersed, although he later found (Meredith 1985) that on being removed from water, *N. burrowsius* initially increased their metabolic rate before it settled down, after 6 hours, to a level similar to the aquatic rate. The greatest reduction in metabolic rate has been reported by Dean (1995), who calculated that *N. diversus* reduced their metabolic rate by 70–85% when emersed. Dean's (1995) study involved comparing the results of two separate experiments using different methods and fish. Crucially, Dean (1995) reported aquatic oxygen consumption rates for *N. diversus* that were 2–3 times greater than those obtained in studies of *N. burrowsius* (Table 7; Meredith et al. 1982; Meredith 1985), and were more comparable to those of *Galaxias* species (Table 7). However, it is important to note that there were calculation errors in this study (acknowledged by T. Dean, DOC, pers. comm.). It is likely that the elevated aquatic oxygen consumption rate calculated for *N. diversus* led to the apparently large difference and reduction in metabolic rate when compared with results from fish in aerial conditions. This large reduction in metabolic rate in response to emersion suggested for *N. diversus* has been widely reported in the literature as evidence of the ability of *Neochanna* species to aestivate (Barrier & Hicks 1994; Hicks & Barrier 1996; Barrier et al. 1996; McPhail 1999; Ling 2001). Considering the importance of such a physiological adaptation in enabling fish to survive drought, further examination of these results and repetition of the study are needed.

In contrast to aquatic measurements, the oxygen consumption rates measured in studies of emersed *Neochanna* species were broadly similar (Table 8). Furthermore, the values obtained for emersed *N. diversus* were similar to those of *N. burrowsius* measured in both aerial and aquatic conditions (Tables 6 and 7). It is likely that *Neochanna* species have an inherently low resting or basal metabolic rate, even in aquatic situations. Meredith (1981) observed that aquatic respiratory patterns of undisturbed *N. burrowsius*, measured by counting opercular movements, were sometimes barely detectable, and often intermittent with apnoeic pauses of 5–60 seconds, indicating low oxygen consumption and metabolic requirements (Meredith 1985). Having low metabolic rates when resting is likely to enhance the survival of *Neochanna* species during periods of starvation, hypoxia and drought.

Although metabolic rate does not appear to lower immediately in response to emersion, or a state of torpor occur, oxygen consumption rates of *N. diversus* gradually fell over 20 days of emersion (Fig. 11). After 14–21 days of emersion, *N. diversus* exhibited an oxygen consumption rate half that measured after one day (Dean 1995), although it subsequently increased (Fig. 11). Meredith (1985) did not measure the oxygen consumption of *N. burrowsius* during this period and could have missed this minimum. A gradual reduction in metabolic rate may allow *Neochanna* species to be more responsive to changes in environmental conditions. However, there may be a limit to the ability to maintain a low metabolic rate, especially in smaller individuals. After 28 days emersion, oxygen consumption rates of the smaller *N. diversus* individuals (1–2 g) increased considerably, possibly as they became stressed (Fig. 12). In general, although aestivation does not occur, it is possible that the metabolic rate of *Neochanna* species slowly lowers if fish are emersed for moderately long periods, which would promote survive without water. However, further research is required on this topic, and direct comparisons of oxygen consumption rates are needed for all species under a variety of environmental conditions and activity levels.

Figure 11. Temporal patterns in oxygen consumption  $\pm$  SEM by emersed *N. burrowsius* (Meredith 1985) and *N. diversus* (Dean 1995).

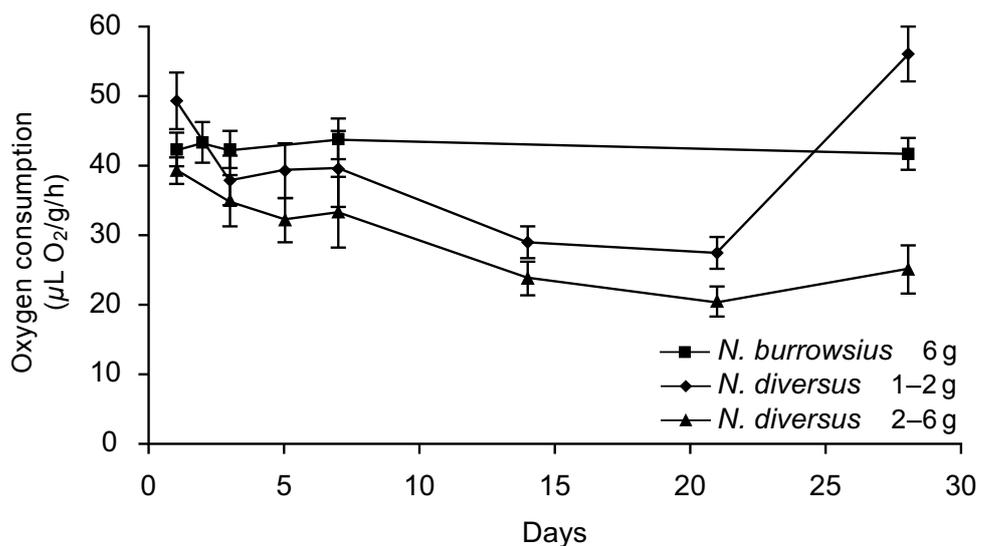
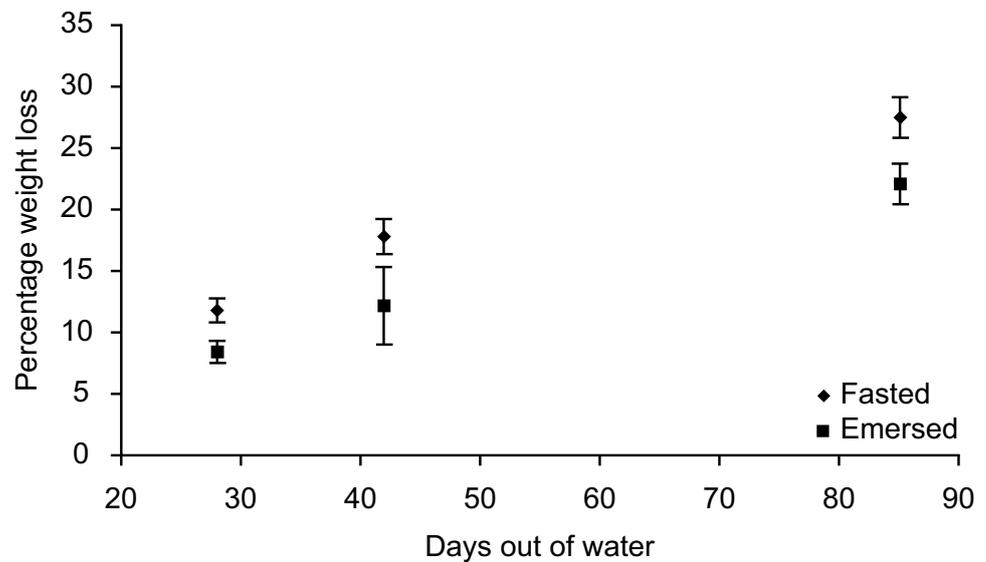


Figure 12. Results of two studies into weight loss in *N. burrowsius* and *N. diversus* held in aquatic conditions without food and emersed conditions (labelled fasted and emersed, respectively). Data from Ling (unpubl. data as cited in Dean 1995), and Meredith (1985).



## 8.7 SUMMARY

- The main characteristics of *Neochanna* species that allow survival of hypoxia and emersion are: generally small body size, inherently low metabolic rate, permeable mucus-covered skin with abundant blood vessels, an efficient circulatory system, and well-buffered blood.
- Preliminary comparisons indicate that there are differences in gill morphology, the circulatory system, and the oxygen affinity of blood, between the species studied.
- *Neochanna* species do not rapidly enter a state of torpor, indicating aestivation. Instead, their metabolic rate slowly drops when they are kept out of water and they remain responsive to external stimuli.

# 9. Survival out of water

When their habitats dry out, fish must cope with a progressive series of challenges as the quality of water deteriorates and its quantity diminishes. Survival without water poses numerous problems, including inhibited movement without the support of water, sensory perception in a different medium, passive loss of body fluids, reduced respiratory ability as gills collapse, toxic waste accumulation and food deprivation (Meredith 1985; McPhail 1999). In the terrestrial environment, *Neochanna* must tolerate abruptly changing and widely varying temperatures, desiccation, and substantial change in physiological processes such as increasing blood and tissue levels of carbon dioxide, ammonia, urea, osmolarity, as well as acid-base disruption (Meredith 1985).

*Neochanna* species exhibit the ability to tolerate severe internal disruption within the first 24 hours of emersion and this ability may be central to their survival (Meredith 1985). However, it is important to understand how *Neochanna* species prevent or control losses of essential molecules, such as water, and avoid the accumulation of toxic waste products, while maintaining respiration.

Determining the relative abilities to overcome these problems would indicate the vulnerability of *Neochanna* species to increasing drought severity. The response to drought may also be size-specific, as studies indicate that larger, adult fish may seek refuge before water recedes, and stranding may be more common in juvenile fish (Eldon et al. 1978; Eldon 1979c; McPhail 1999; O'Brien 2005). This section discusses the implications of water loss and the build up of metabolic waste during emersion and mechanisms to reduce this, as well as survival time and how this relates to fish size.

## 9.1 WATER LOSS

*Neochanna* species have a scaleless skin that is permeable to water, thus fish may suffer considerable loss of body water upon emersion. Meredith (1985) found that *N. burrowsius* were not able to restrict desiccatory water loss, as seen in amphibians. However, the mean rate of water turnover—and thus skin permeability—was not considered especially high. Nevertheless, the rate of water loss for emersed *N. burrowsius* was 2.4 times greater at 48% relative humidity than it was at 75% (Meredith 1985). At these two humidities, fish lost 10% of their initial body weight due to water loss in approximately 8 hours and 20 hours, respectively. Thus, without a mitigating mechanism, emersed *N. burrowsius* could be expected to dehydrate with lethal consequences within 48 hours (Meredith 1985). However, this estimated survival time is substantially less than that observed in the wild, so *Neochanna* species must rely on a combination of behavioural responses and habitat characteristics to avoid desiccation.

The large difference in water loss rates at different humidities highlights the importance of favourable microclimates/microhabitats in determining survival. This includes suitable conditions of ground moisture, a humid atmosphere, lack of strong air currents, cool temperature, and shielding from direct sunlight. A lack of any of these could lead to death through desiccation (Meredith 1985). However, terrestrial environments constantly fluctuate in their degree of dryness. Dehydrated *N. burrowsius* were able to regain 70% of lost body water through the skin from a damp surface within 6 hours (Meredith 1985). Thus, *Neochanna* species may survive brief periods of desiccation if regularly rehydrated from rain, dew or condensation. Further, subterranean refuges may be inundated periodically by ground water, which can fluctuate in level diurnally through expansion and contraction as temperature changes.

## 9.2 BUILD UP OF METABOLIC WASTE

Ammonia is the major nitrogenous excretory product in fish and is a highly toxic substance in alkaline conditions. However, fish can easily excrete ammonia into surrounding water, and it is only in the absence of free water that ammonia is likely to reach toxic levels in the blood. Meredith's (1985) studies of *N. burrowsius* showed that the accumulation of ammonia stabilised within 24 hours of emersion. Furthermore, levels of ammonia in the blood were low and relatively stable over 28 days of emersion. Meredith (1985) also found that in water, 80% of the nitrogen excreted by *N. burrowsius* was ammonia. However, the ammonia excretion rate measured when fish were emersed never achieved a level higher than 15% of the ammonia excretion rate in water. Thus, the remaining

85% was either excreted undetected, stored, or was not produced. If stored, the accumulated ammonia would likely kill a fish within one week if not suppressed or detoxified (Meredith 1985). Even if excreted, large accumulations of ammonia in the vicinity of a fish could be harmful to its skin surfaces unless they were protected by special mucoid compounds. However, the pH of *N. burrowsius* skin was close to neutral during emersion (Meredith 1985), which may indicate that its mucus has a buffering capacity.

Accumulated ammonia affects the acid-base status of blood and, hence, oxygen delivery. However, *Neochanna* may mitigate such acid-base disruptions through their high blood buffering capacity (Wells et al. 1984). In addition to ammonia, carbon dioxide (a by-product of respiration) levels rose in the blood of emersed *N. burrowsius*, further affecting the acid-base balance (Meredith 1985). Carbon dioxide accumulation leads to acidosis, whereas the accumulation of ammonia leads to alkalosis. Importantly, the time courses for build-up of carbon dioxide and ammonia were similar, thus their dual accumulation might have a neutralising effect, thereby reducing acid-base disruption (Meredith 1985).

### 9.3 MECHANISMS TO REDUCE TOXIC WASTE PRODUCTS

Although *Neochanna* species may be able to compensate for acid-base disruption, waste accumulation can still be detrimental. Thus, on re-immersion, *N. burrowsius* and *N. diversus* initially absorbed water, and then underwent a period of active waste excretion (Meredith 1985; McPhail 1999). As a mechanism for storing nitrogenous waste, McPhail (1999) suggested that *Neochanna* species convert ammonia into urea. Although Meredith (1985) found that 15% of nitrogenous waste in water was in the form of urea, he also found that after 8 hours of emersion, urea was not excreted by *N. burrowsius*, and after 48 hours urea had not accumulated. These results suggest that upon emersion, urea production by *N. burrowsius* was at least halved. Other methods *Neochanna* species may use for storing or detoxifying nitrogenous waste, such as amino acids, require further study.

Fish use protein as their primary source of energy for metabolism, rather than carbohydrate or lipid (as in mammals). Despite this, increases in metabolic rate can be supported by lipid metabolism. Ammonia is largely a product of protein-based metabolism; so, if fish can switch from protein to lipid or carbohydrate metabolism, the production of potentially toxic nitrogenous wastes could be suppressed. There is indirect evidence for such a change in the metabolic mechanism upon emersion. In immersed *N. burrowsius*, 72% of energy utilised for metabolism was estimated to come from protein. In emersed fish, however, only 9% was attributed to this source (Meredith 1985). Furthermore, fasting did not stimulate such a change in nitrogen excretion, which suggests that *N. burrowsius* switch their primary metabolic substrate only in response to emersion (Meredith 1985). *Neochanna burrowsius* is able to store appreciable amounts of lipids in body tissues and gonads, as shown by Eldon (1979c), who found that fat levels rose in spring and early summer. Although Meredith (1985) found no significant difference in the total lipid content of immersed, starved, and emersed *N. burrowsius*, Davidson (1999) found that triglyceride (a form of lipid) levels in the plasma of *N. diversus* were considerably lower in fish held out of water than in immersed captive and wild control fish,

suggesting the use of lipids for metabolism. Davidson (1999) also suggested that glycogen (carbohydrate) is sometimes utilised, as it is the primary energy source available to fish for metabolism when oxygen is limited. In *N. diversus*, glycogen was more concentrated in the liver than in the muscles, though emersion led to a reduction in glycogen concentration in both these tissues (Davidson 1999). Both carbohydrate and lipid metabolism could be viable solutions for limiting the production and accumulation of toxic levels of waste products during emersion.

#### 9.4 SURVIVAL TIME

In drought situations, leaving the water may be advantageous, at least in the short term. Emerged fish have lower weight loss rates than fasted (starved) fish that remain in water (Fig. 12). This difference suggests that fish that remain in water likely expend energy in unsuccessful foraging, whereas emerged fish conserve energy, due to a low metabolic rate when resting. However, Meredith (1985) found that over an 85-day period, 40% of emerged fish died at irregular intervals between 28 and 85 days, yet there was no mortality of fasted immersed *N. burrowsius*. There are accounts of *Neochanna* being able to live without water for up to six months (Eldon 1979c; Close 1996). However, it is often difficult to determine whether fish survived in situ or recolonised habitat from an adjacent area that dried up to a lesser degree (Eldon et al. 1978). Laboratory studies have indicated that some *N. burrowsius* individuals can survive emersion for 85 days (Meredith 1985), *N. diversus* for 80 days (Davidson 1999), and *N. apoda* for 63 days in controlled conditions (Eldon 1978b).

Meredith (1985) suggested that *N. burrowsius* can tolerate weight losses exceeding 50% of initial body weight. Combining available data from three studies indicates that if fish are capable of tolerating a 50% reduction in weight, some may survive up to five months (Fig. 13). Most of the variation shown in Fig. 13 is due to the initial size of fish. However, this is an extrapolation and there is little evidence that any *Neochanna* species can survive more than 3 months of emersion. Over extended periods of emersion, fish would need to metabolise much of their body tissue and lipid stores (Eldon 1979c; Meredith 1985). Gonads appear to be significant lipid storage sites in *N. burrowsius* (Meredith 1985), but there have been no studies into the effects of emersion on subsequent reproductive output. This issue is especially important for *N. apoda* and *N. diversus*, which often spawn immediately after water returns in autumn. Not only do these species need to survive, they also need to maintain sufficient spawning condition and gonadal development. Thus, there may be further adverse consequences for individual fitness when fish are forced to endure drought for many months, even if they can survive (McDowall 1999b).

#### 9.5 SURVIVAL AND SIZE

*Neochanna* may be required to utilise different survival strategies dependent on their size and the severity of drought conditions. Size influences energy reserves because there is a negative relationship between body size and metabolic rate. Smaller fish have higher metabolic rates, yet less body tissue to metabolise, which

will influence survival during periods of starvation (Meredith 1985). Furthermore, the surface area to volume ratio of fish controls efficiency of oxygen absorption through the skin, and the rate of desiccation. Thus, we would expect smaller fish to be more tolerant of immersed hypoxic conditions, whereas larger fish would be more likely to survive longer periods of emersion. Consequently, if juvenile fish have not grown sufficiently before summer drought commences, premature emersion may lead to desiccation or starvation (Eldon 1978b; McDowall 1999b). Hence, Meredith (1985) argued for the existence of an upper size limit for *Neochanna* species exposed to poorly oxygenated water, and a lower size limit for survival success during droughts.

These theoretically based conclusions have been verified by laboratory and field investigations. The combination of available data from three studies on *Neochanna* species shows a clear pattern between fish size and percentage weight lost per day (Fig. 14). Thus, fish size may be influential in determining maximum survival times during emersion. Additionally, smaller fish exhibit the greatest reduction in hepatic glycogen, an important energy source during starvation and emersion (Davidson 1999). McPhail (1999) also found significant differences in percentage weight loss between emersed adult (94–114 mm) and

Figure 13. Percentage weight loss over time for emersed fish. Combined data for various sizes of *N. burrowsius* (Eldon 1979c; Meredith 1985), *N. diversus* (Dean 1995; McPhail 1999), and *N. apoda* (Eldon 1978b). The regression line ( $\pm$  95% CI) is based on all data.

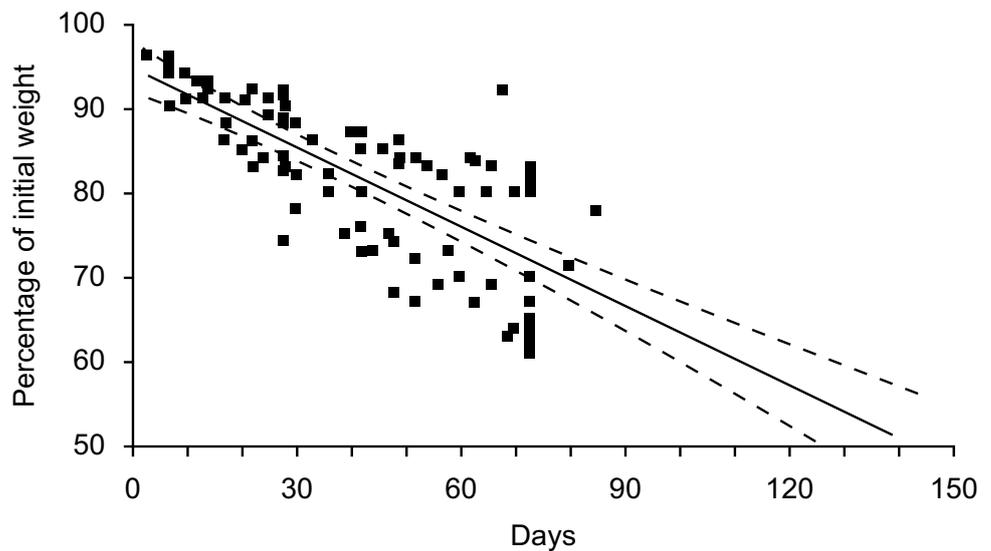
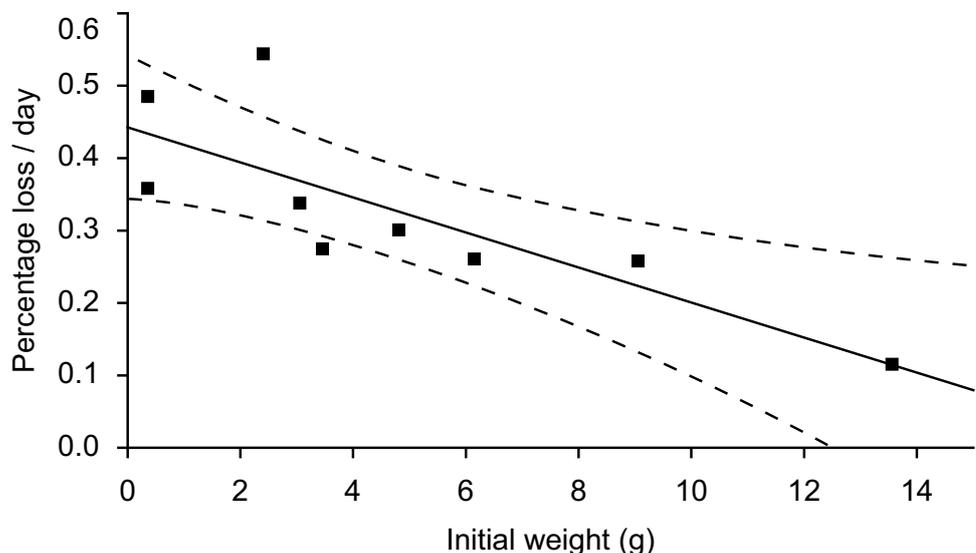


Figure 14. Relationship between fish size and weight loss during emersion. Combined data from *N. burrowsius* (Meredith 1985), *N. diversus* (Dean 1995), and *N. apoda* (Eldon 1978b). The regression line ( $\pm$  95% CI) is based on all data.



juvenile (40–60 mm) *N. diversus*. Significantly, the two juvenile fish that died during McPhail's (1999) experiment were the smallest fish (40 and 45 mm) and had lost 40–45% of their initial body weight over 73 days.

From field investigations, McPhail (1999) suggested that a difference in the average size of young-of-the-year *N. diversus* before and after a drought was due to the smallest individuals suffering the greatest mortality. There is also evidence that larger *Neochanna* may leave hypoxic water before smaller juveniles, which remain immersed. For example, Eldon et al. (1978) did not find any emersed juvenile *N. burrowsius* during a drought, despite their previous abundance. However, large numbers of juvenile fish were observed in the remaining standing water. Such size-dependent strategies in response to a drought event were quantified for *N. burrowsius* by O'Brien (2007). *Neochanna burrowsius* found emersed were significantly longer than fish found swimming freely in an adjacent remnant pool. Furthermore, individuals that had left the water but had perished were significantly shorter than surviving fish. Thus, there is an upper limit to the size of fish remaining immersed, and a lower size limit related to survival of emersion. Generally, *N. burrowsius* > 50 mm long successfully adopted a strategy of emersion, whereas *N. burrowsius* < 50 mm long remained immersed (O'Brien 2007). Consequently, the severity of summer disturbance can influence the size structure of *Neochanna* populations.

## 9.6 SUMMARY

- *Neochanna* species cannot control water loss through their skin and thus require damp refuges to avoid desiccation.
- Initial studies have suggested that *Neochanna* species may be able to switch from protein to lipid or carbohydrate metabolism, thus using different metabolic pathways to avoid nitrogenous waste accumulation during emersion.
- Studies have indicated that some *Neochanna* individuals are capable of surviving three months of emersion in controlled conditions and extrapolation of weight loss measurements indicates that it would generally take them 5 months to lose 50% of their body weight.
- Fish size and the severity of drought conditions determine successful strategies for survival. Thus, there is an upper limit to the size of fish capable of remaining immersed in hypoxic waters, and a lower size limit related to the ability to survive long periods of emersion.

# 10. Threats

Two opposing constraints are generally considered to be the most important influences on *Neochanna* populations. These are environmental extremes, drought in particular, and negative inter-specific interactions (McDowall 1990; McDowall 2006). Both constraints can be related to the hydrological regimes of *Neochanna* habitats. In hydrologically stable and benign conditions, other fish species are more likely to be present, which may result in adverse interactions. Conversely, periods of summer habitat desiccation, which may initially eliminate other fish species, may become too severe, so that *Neochanna* also suffers mortality. While these two factors are likely to pose the most common threats to *Neochanna* species, analysis of 50 items of literature indicates that a multitude of threats have been identified by authors (Table 9). Despite the recognition of threats, few studies have quantified how they influence *Neochanna* species, the extent of the threats, potential for mitigation, and the relevant importance of each threat. Such studies are needed to clarify the implications of threats, and to ensure that appropriate actions are taken to protect remaining populations and habitat. This chapter reviews threats mentioned in the literature, with sections on habitat, hydrological modification, agricultural activities, competition and predation, and factors affecting fish health.

## 10.1 HABITAT

Wetland habitats of New Zealand mainland *Neochanna* species have been reduced, fragmented, and simplified by agricultural development and land modification. Much of this habitat change occurred in the late 1800s, and has been linked to the decline in *Neochanna* populations (McDowall 1980a, 1998a; McDowall & Eldon 1996). In some areas, changes in land use continue to threaten remaining populations. The threats identified range in severity from stock access, where impacts may be temporary (but which can degrade habitat over a longer period), to the complete removal of habitat (by land and water development, for example). Some habitat changes are irreversible, and processes such as fragmentation are likely to have long-lasting effects. Activities such as peat mining may pose a substantial threat through the removal of habitat (McDowall 1980a), while proposed hydroelectric power and irrigation developments have also been identified as having the potential to affect *Neochanna* habitats (Mitchell 1995 and Tipler et al. 2002, respectively). Fire is a potential threat to some *Neochanna* habitat (Eldon 1992; Grainger 2000), but may also lead to the development of new habitat, as in the rapid formation of peat lakes after fire on Chatham Island (Mitchell 1995). At present, the main threats to *Neochanna* habitat are hydrological modification and agricultural activities.

### 10.1.1 Hydrological modification

Activities on land surrounding wetlands, such as water abstraction for irrigation and drainage improvements that lower the water table, can have adverse effects on the hydrology of wetlands and springs (McDowall 1984). Moreover, most hydrological changes have long-term consequences that are largely irreversible,

TABLE 9. SUMMARY OF THREATS IDENTIFIED IN THE LITERATURE (50 SOURCES) AS BEING IMPORTANT IN INFLUENCING THE PERSISTENCE OF *Neobanna* SPECIES. VALUES INDICATE THE NUMBER OF TIMES THE PARTICULAR THREAT IS MENTIONED IN THE LITERATURE REVIEWED.

THREAT CATEGORY AND CLASS	<i>Neobanna</i> (IN GENERAL)	<i>N. rekobua</i>	<i>N. burrowsius</i>	<i>N. diversus</i>	<i>N. beletos</i>	<i>N. apoda</i>	TOTAL
<b>Hydrology</b>							
Continual wetland drainage	3		10	9	2	10	34
Severe drought	1		11	2		3	17
Hydrological change	1		8	3	2	2	16
Irrigation	2		11	1	1		15
Channel/flow modification			11	3		1	15
Flooding			3			1	4
Groundwater level fluctuations		1	1		1	3	
Piping of irrigation water		3				3	
Proposed hydro-power scheme		1					1
Sea level rise				1			1
<b>Farming and land use</b>							
Land intensification	1		11	5	3	3	23
Drain maintenance	1		6	1		8	16
Stock access			5	1	1	8	15
Deforestation		1	3			6	10
Agricultural sprays			2	3	1	2	8
Dairy farming	1		2	1	1	1	6
Landform modification		1	1	2		2	6
Fire/fire fighting	1	1		2	1		5
Cropping			2	1	1		4
Forestry				1	1	1	3
Domestic rubbish dumping					1		1
Peat mining				1			1
Subdivision of land				1			1
<b>Population threats</b>							
Fragmentation	2		10	5	3	8	28
Small population size	2		2	2	2	3	11
Restricted range	2	1		2	1		6
Genetic diversity	1		1	2		1	5
Lack of recruitment				2	1	1	4
Disease			2				2
<b>Community influences</b>							
Interactions with other fish	1	1	11	7		3	23
Excessive waterfowl			2			1	3
Terrestrial predators			1	1	1		3
<b>Habitat quality</b>							
Invasive plant species			6	1	1	2	10
Lack of aestivation habitat			2			4	6
Lack of food resources						1	1
Lack of spawning substrate			1				1
<b>Physico-chemical properties of water</b>							
Nutrient increases			2	1	1	2	6
Reduced water quality			1	1	1	1	4
Extreme temperatures			1		1		2
Low dissolved oxygen levels		2				2	
Acidification			1				1
<b>Scientific knowledge</b>							
Insufficient knowledge	2				1		3
Scientific collection	1		1		1		3
<b>Total</b>	<b>22</b>	<b>6</b>	<b>135</b>	<b>63</b>	<b>29</b>	<b>77</b>	<b>332</b>

e.g. the transformation of the Canterbury Plains from extensive wetlands to heavily irrigated farmland (McDowall 1998a). Hydrological change can have significant consequences for *Neochanna* species. For example, drainage and increased channelisation may lead to the loss of seasonally flooded wetlands and increased water velocity, which may limit suitable habitat and displace *Neochanna* into potentially unfavourable habitat (Kerr & McGlynn 2001; O'Brien 2005). Hydrological modification may also increase the frequency and intensity of droughts. In some situations, periodic drought may act to protect *Neochanna* populations (Ling 2001), because of the higher tolerance levels of *Neochanna* species compared with other fish species (Meredith 1985; Glova & Hulley 1998). However, drought is still a stressful situation for individuals and is likely to have consequences for growth, reproduction and condition. Thus, in situations where other fish species are neither present in *Neochanna* habitat, nor likely to invade it, modifications that increase drought events are likely to threaten the persistence of populations.

### 10.1.2 Agricultural activities

The main agricultural pressures on *Neochanna* species are water quality deterioration, damage of habitat by stock, and removal of habitat by drain maintenance. Despite agricultural activity being widely recognised as affecting *Neochanna* species, few studies have investigated the responses of *Neochanna* to such disturbances. However, it has been suggested (Eldon 1978b; McDowall 1990; Eldon 1993; Hicks & Barrier 1996; Young 1996) that *Neochanna* require relatively good water quality. Increases in nutrient levels through fertiliser and stock effluent run-off influence water quality and result in changes in the structure of aquatic communities. Further, drenches and biocides intended to kill internal parasites in farm livestock do not necessarily break down in the animals, and may pass through them into receiving environments, killing non-target microbes and changing ecosystem functioning (Tremblay & Wratten 2002).

The type of livestock with access to *Neochanna* habitat is also important, as smaller animals such as sheep are usually not heavy enough to seriously pug soils, except in extreme cases (Finlayson et al. 2002). Beef cattle and dairy cows represent the most serious threats, not only because of their weight and hoof morphology, but also because of their tendency to enter small wetlands and graze on aquatic plants (Johnson & Rodgers 2003; Reeves & Champion 2004). It has been suggested (Eldon 1993; Reeves & Champion 2004) that trampling by stock in drying wetlands during summer could 'rupture' burrows and refuges, leading to desiccation of emersed fish.

*Neochanna* species require a fairly complex or cluttered habitat. This complexity is usually provided by vegetation. Unfortunately, the presence of aquatic vegetation is not always compatible with current practices of drain management. Hudson & Harding (2004) reviewed current practices, and the development of *Neochanna*-friendly drain maintenance methods was identified by DOC (2003) as a priority. Drain maintenance can have a large and long-term impact on *Neochanna* populations, as indicated by Eldon (1968) who reported that a large *N. apoda* population took at least four years to recover after the initial clearance of aquatic plants. A population of *N. diversus* also took approximately three years to re-establish in the Holland's Road Drain (Hamilton) after severe mechanical clearance, despite it once having a remarkably high density (Barrier 1993; Hicks & Barrier 1996; Barrier et al. 1996).

## 10.2 COMPETITION AND PREDATION

Analysis of NZFFD records indicates that *Neochanna* species occurred in habitats without any other fish species on more than half of the occasions they were recorded (Table 10). Although a wide variety of other fish species may sometimes co-occur with *Neochanna* species, the incidence of co-occurrence is typically low except for one or two species. It is thought that *Neochanna* species are generally intolerant of competition because of their small size, general lack of aggression, small mouth and low metabolic rate, all of which may reduce their potential to be dominant competitors (Meredith 1985). While *Neochanna* are not inherently territorial or aggressive towards con-specifics, Barrier & Hicks (1994) reported that adult *N. diversus* were aggressive towards *G. affinis*, and Eldon (1969) found *N. apoda* were aggressive when outnumbered, or in the presence of a multitude of species in aquaria (Eldon 1969). It has also been suggested (Meredith 1985) that *Neochanna* species may lack predator-avoidance mechanisms. However, when disturbed suddenly, *N. cleaveri* can jump to a height of 50–60 mm above the water before immediately diving down to the pool bottom. Fish may repeat this manoeuvre two or three times in quick succession and it is likely used to facilitate their escape from aquatic predators (Andrews 1991). Juvenile *N. burrowsius* exhibit a similar behaviour when startled, although not jumping as high (L. O'Brien, pers. obs.). The following sections provide further information on commonly occurring inter-specific interactions.

### 10.2.1 *Anguilla* species

Eels (Anguillidae; *Anguilla*) prey on *Neochanna*, including larger (120 mm) individuals (Mitchell 1995; Eldon 1978b, 1979a), and there is a surprisingly low level of co-occurrence between *Neochanna* species and eels, considering the ubiquitous distribution of *Anguilla* species (Table 10). McDowall (1982) posed the question of whether this low level of co-existence between *Anguilla* and *Neochanna* arises from *Anguilla* species having a detrimental impact on *Neochanna* populations, e.g. through predation; or whether *Neochanna* species are able to tolerate harsher conditions, and thus largely avoid interactions with other species. This is still to be fully tested. However, where *N. burrowsius* and *Anguilla* species do co-exist, small-scale patterns of distribution within sites suggest that *Anguilla* influences *N. burrowsius* abundance (O'Brien 2005). Furthermore, in sites experiencing hydrological extremes, disturbance-mediated co-existence is likely to be occurring, e.g. in Tutaepatu Lagoon, Mid Canterbury, where extreme drought in 1972 and 1998 largely eliminated the *Anguilla australis* population, whereas *N. burrowsius* is thought to have survived (Glova & Hulley 1998; Main & Meredith 1999).

### 10.2.2 *Galaxias* species

NZFFD records indicate that all New Zealand *Neochanna* except for *N. rekohua* may co-occur with *Galaxias* species (Table 10). However, the incidence of co-occurrence is low and may be habitat-mediated. For example, a survey by Eldon (1968) of thirteen sites containing *N. apoda* on the West Coast of the South Island found co-occurrence with *Galaxias* on only one occasion, despite various galaxiids being found in adjacent habitats. This co-occurrence was with two *Galaxias fasciatus* that were found in deeper parts of a pool, with *N. apoda* occupying the shallow end (Eldon 1968). Eldon (1979a) reported co-occurrence

TABLE 10. PERCENTAGE OF NZFFD RECORDS SHOWING *Neochanna* SPECIES FOUND ALONE, AND IN THE PRESENCE OF OTHER IDENTIFIED SPECIES. AS *Neochanna* MAY CO-OCCUR WITH MORE THAN ONE OTHER SPECIES AT A GIVEN LOCATION, TOTALS DO NOT NECESSARILY ADD UP TO 100.

COMMON NAME	SPECIES NAME	<i>N. burrowsius</i>	<i>N. diversus</i>	<i>N. beletos</i>	<i>N. apoda</i>
Alone		59.7	59.3	72.7	67.1
Eel	<i>Anguilla</i> spp.	0.8	4.4	2.3	0.9
Longfin eel	<i>Anguilla dieffenbachii</i>	3.4	2.2		4.2
Shortfin eel	<i>Anguilla australis</i>	6.7	21.4	15.9	11.3
<i>Galaxias</i>	<i>Galaxias</i> spp.		0.5		
Giant kokopu	<i>Galaxias argenteus</i>				0.9
Banded kokopu	<i>Galaxias fasciatus</i>		3.8	9.1	4.2
Canterbury galaxias	<i>Galaxias vulgaris</i>	3.4			
Inanga	<i>Galaxias maculatus</i>	1.7	2.2		2.8
Torrentfish	<i>Cheimarrichthys fosteri</i>		0.5		
Common bully	<i>Gobiomorphus cotidianus</i>	7.6	3.3		0.9
Upland bully	<i>Gobiomorphus breviceps</i>	23.5			1.4
Brown trout	<i>Salmo trutta</i>	1.6			0.5
Brown bullhead catfish	<i>Ameiurus nebulosus</i>		1.6		
Goldfish	<i>Carassius auratus</i>		1.6		
Koi carp	<i>Cyprinus carpio</i>		1.1		
Rudd	<i>Scardinius erythrophthalmus</i>		0.5		
Gambusia	<i>Gambusia affinis</i>		18.1	6.8	
Perch	<i>Perca fluviatilis</i>	1.7			
Koura	<i>Paranebrops</i> spp.	0.8	1.1		20.2

of *N. burrowsius* with *G. maculatus* in Buchanans Creek, South Canterbury where, during spring, *N. burrowsius* juveniles ‘mingled’ with *G. maculatus* juveniles recently arrived from the sea. It is likely that competition for food occurs in such situations.

### 10.2.3 Salmonid species

Co-occurrence of *Neochanna* and salmonid species (Salmonidae: *Salmo*, *Oncorhynchus*, *Salvelinus*) is low (Table 10), likely because of differing habitat preferences and the piscivorous nature of larger salmonids (McDowall 2006). Eldon (1979a) reported on the affect that seven *Salmo trutta* (brown trout) had on the Buchanans Creek (South Canterbury) *N. burrowsius* population, when they invaded upstream reaches during a spawning migration. These *S. trutta* consumed 19 *N. burrowsius*, whereas one *S. trutta* that had not moved upstream had only consumed invertebrates. This population of *N. burrowsius* may only have persisted because of frequent habitat drying, which removed the trout (Eldon 1993). McDowall (2006) reviewed the impacts of salmonids on galaxioid fishes, including *Neochanna* species, and highlighted the serious nature of this threat.

### 10.2.4 Coarse fish species

Only *N. burrowsius* and *N. diversus* are recorded as co-occurring with coarse fishes (Ameiuridae: *Ameiurus*; Cyprinidae: *Carassius*, *Cyprinus*, *Scardinius*; and Percidae: *Perca* species). Eldon (1979a) found *Perca fluviatilis* preyed on

*N. burrowsius* when co-occurring in pools of an intermittent stream south of Otaio, South Canterbury. *Neochanna diversus* co-occurs in Awaroa Stream with both *Ameiurus nebulosus* (brown bullhead catfish) and *Scardinius erythrophthalmus* (rudd) and with the former species in Whangamarino Wetland, Waikato (NZFFD records). It is unclear whether *N. diversus* is negatively affected by these species. This requires further investigation, as coarse fish species are implicated in reducing aquatic macrophyte cover and increasing turbidity (Chadderton 2001; Dean 2001), activities that could influence *N. diversus* habitat suitability.

#### 10.2.5 *Gambusia affinis*

The introduced fish *Gambusia affinis* (Poeciliidae), also called mosquitofish, occurs in both *N. diversus* and *N. beleios* habitats (Table 10). *Gambusia affinis* attack other fish, particularly their fins, causing mortality (Baker et al. 2004). Such behaviour has seen *G. affinis* 'implicated in the displacement, decline, or elimination of numerous native fish and amphibian species in many countries where they have been introduced' Ling (2004: 474). In New Zealand, *G. affinis* is classified as a noxious and unwanted fish species (Chadderton 2001; Dean 2001).

Kerr & McGlynn (2001) attributed the high abundance of *N. beleios* at Ngawha, Northland, to the absence of *G. affinis*. Moreover, behavioural investigations into the interactions between *G. affinis* and *N. diversus* indicated that foraging behaviour and prey capture rates of *N. diversus* altered in the presence of *G. affinis* (Barrier & Hicks 1994). Further, Barrier & Hicks (1994) emphasised that *G. affinis* could induce changes in the zooplankton community, which is an important component of the diet of *N. apoda*. However, the predominant threat arising from *G. affinis* is their predation of *Neochanna* fry. This could threaten recruitment into *Neochanna* populations, and their long-term persistence (Hicks & Barrier 1996; Ling 2004). However, *Neochanna* have a greater tolerance of seasonal dry periods, which regularly remove *G. affinis*, so co-existence within large wetland complexes is determined by hydrological dynamics. The severity of the threat posed to *N. diversus* by *G. affinis* may also be reduced by the two species spawning in different seasons, with *N. diversus* fry being abundant when *G. affinis* numbers are low (Barrier & Hicks 1994; Ling 2004). Nonetheless, use of the piscicide rotenone has been considered (Willis & Ling 2000; Ling 2003) as a means of controlling *G. affinis* numbers and thus protecting *N. diversus* and *N. beleios* populations.

#### 10.2.6 *Gobiomorphus breviceps*

*Neochanna burrowsius* often co-exists with *Gobiomorphus breviceps* (Gobiidae; upland bully) (Table 10). However, habitat separation occurs between the two species, with more *N. burrowsius* being found in macrophyte patches, and more *G. breviceps* in open areas (Eldon 1979a; O'Brien 2005). In outdoor experiments it was found that *G. breviceps* competed aggressively for space; however, competition for food resources may be reduced by temporal differences in foraging between the species, and increased foraging activity by *N. burrowsius* (O'Brien 2005). In the wild, co-existence between *G. breviceps* and *N. burrowsius* may be promoted in situations where *G. breviceps* populations are limited by factors such as environmental stress, a lack of spawning substrate, or sedimentation (Jowett & Boustead 2001; O'Brien 2005).

### 10.2.7 Frogs

There have been no specific studies into interactions between introduced frogs and *Neochanna* species, but there is some suggestion that negative interactions may occur. Eldon (1978b) found *N. apoda* fry and *Hyla ewingi* (whistling frog) tadpoles in stump holes in the same area; however, they did not appear to coexist in the same holes. Further, observations of distinct distributions in Dog Kennel Stream, South Canterbury, suggest negative interactions between *N. burrowsius* and introduced *Litoria aurea* (golden bell frog) (S. Harraway, DOC, pers. comm.). Such interactions require further study as bell frogs (*Litoria aurea*, *L. raniformis*) commonly occur in *N. burrowsius* habitat (L. O'Brien, pers. obs.). *Limnodynastes dumerilii grayi* (eastern banjo frog), discovered in Northland in 1999, may represent a future threat to *N. diversus* and *N. beleios* if it establishes and spreads. Classified as an unwanted organism, this frog can excrete a poisonous substance and breeds in wetland habitats similar to those of *Neochanna* species.

### 10.2.8 Avian interactions

Birds may influence *Neochanna* through habitat degradation or direct predation. Eldon (1993) discussed the impact that excessive numbers of water fowl can have on *Neochanna* habitat through consumption of aquatic plants. *Neochanna* eggs may also be consumed 'accidentally' by waterfowl, if they are scattered amongst vegetation at the water surface. Large flocks of waterfowl have been observed in *Neochanna* habitats by Francis (2000a) and O'Brien (2005), the latter witnessing many hundreds of waterfowl being attracted by supplementary grain to a pond prior to the duck shooting season. This influx of birds was thought to have fouled the water, leading to widespread bacterial infection of *N. burrowsius* also present in the pond (O'Brien 2005).

Evidence of *Ardea novaehollandiae novaehollandiae* (white-faced heron) predation on *N. burrowsius*, in the form of wounded dead fish, and live fish with bitten tails, was common in shallow weedy habitats (O'Brien 2005). In Canterbury, herons commonly congregate around drains following aquatic plant removal for drain maintenance (M. & H. Redworth, formerly St Andrews, pers. comm.). Thompson (1987) reported that a *Botaurus stellaris poiciloptilus* (bittern) had regurgitated a c. 100-mm-long *N. diversus*. *Halcyon sancta vegans* (kingfishers) and *Porphyrio melanotus* (pukeko) have also been implicated as predators of *Neochanna* species (Eldon 1978b; Hicks & Barrier 1996). The level of predation by birds is likely to be high in some circumstances, although the cryptic, nocturnal habits of adult *Neochanna* may mitigate this risk.

## 10.3 FACTORS AFFECTING FISH 'HEALTH'

Disease and parasitic infection can affect both growth rates and survival of individual *Neochanna* and entire populations. The prevalence of these potentially debilitating factors often varies between populations (Eldon 1978b; O'Brien 2005). Stress applied by the environment can cause outbreaks of infectious diseases in fishes. Stresses include temperature changes, low dissolved oxygen, eutrophication, sewage, and synthetic pollution (Snieszko 1974). However, fish regularly encounter pathogens in their habitats and generally have adequate

resistance to bacteria, unless weakened by stress or injury. Infection by parasites has been related to the abundance of intermittent hosts, often prey species, such as snails, which are consumed, thereby transferring the parasite to fish (Eldon 1978b; McDowall 1990).

### 10.3.1 Disease

Eldon (1978b) reported that few *N. apoda* he examined showed any outward sign of sickness. The exception was a fish caught shortly after a dry summer, which had a large bacterial (*Pseudomonas* sp.) infection. O'Brien (2005) found a higher incidence of bacterial infection in *N. burrowsius*, especially from habitat with poor water quality. The percentage of healthy *N. burrowsius* in a population with no external indication of disease or infection varied from 15% to 80%.

Determining the level of threat to *Neochanna* posed by chytrid fungus was identified by DOC (2003) as a research priority. Chytrid fungi occur commonly in both soil and water, and some are known to have severe impacts on frog populations. In tadpoles, fungi largely attack the keratin present in the skin and mouthparts, with most mortality occurring during metamorphosis into adults. Meredith (1985) found that the epidermis of *N. burrowsius* has no keratinisation, so it is possible that chytrid fungi will not threaten *Neochanna* species. However, this requires further investigation.

### 10.3.2 Parasites

Parasites are attached either internally or externally to their host. External parasites are more likely to cause the death of their host, as their own survival is not necessarily dependent on that of the host (O'Brien 2005). In fish, the most common external parasite is the ciliate protozoan *Ichthyophthirius multifiliis* (white spot or 'ich') which has caused mass mortality in fish overseas (e.g. Wurtsbaugh & Tapia 1988). External examinations by O'Brien (2005) indicated that whitespot was present in all *burrowsius* populations she studied; however, it reached a potentially epidemic level in Hororata Spring (mid Canterbury), where 50% of *N. burrowsius* captured carried at least one cyst, and some individuals carried more than 20. Eldon (1978b) examined the stomachs and gonads of *N. apoda* from several sites around the Wairarapa. The internal parasitic nematode *Hedruris sp. nigera* was prevalent in stomachs. In one population, 63% of fish examined carried a nematode, with a maximum parasite load of 14 in one individual (Eldon 1978b). The incidence of infection was related to the prevalence of amphipods, the nematodes' intermediate host, in the diet of *N. apoda*. Cysts of the digenean fluke *Telogaster opisthorchis* (Trematoda) were found in the gonads of *N. apoda* and infection rates ranged from 16% to 21% of individuals. Eldon (1978b, p. 38) also noted that 'some males were so heavily infested that at first glance they appeared to be females'. Internal parasites have not been recorded in other *Neochanna* species, most likely because only small numbers of fish have been examined (Blair 1984).

# 11. Conservation initiatives

European settlement of New Zealand resulted in rapid changes in many lowland areas. For example, J. Hector (in his letter to Günther, printed in Günther 1867: 307) stated that the type locality of *N. apoda* now lay beneath the goldfields township of Kanieri but that ‘... little more than two years ago it was a swamp covered in dense forest.’ Much of this landscape change is irreversible. However, if conservation actions are carried out now, it may be possible to preserve and restore the remaining lowland habitat of *Neochanna* species. This chapter discusses recovery plans, methods of determining distribution and conservation priority, habitat protection and restoration, reserve design, and establishing new populations.

## 11.1 RECOVERY PLANS

Guidelines towards a conservation strategy for *N. burrowsius* were produced by Eldon (1993), and a recovery plan for *N. apoda* was written by Francis (2000b). The most recent and, so far, most comprehensive plan is the the New Zealand *Neochanna* species recovery plan published by DOC (2003). This plan sets out actions thought necessary over ten years to ensure the recovery of these species. The long-term goal of this plan is ‘that the geographic range, habitat, and genetic diversity of all mudfish species are maintained and improved’ (DOC 2003: 12). Five objectives were identified for the term of the plan (2003–2013). These are:

- The protection and management of *Neochanna* habitats
- Monitoring of population trends
- Advocacy for the protection and sustainable management of habitats
- Maintenance and increase of populations
- Involvement of iwi in the implementation of the plan

Objective 4 of the recovery plan (DOC 2003) intended that the endangered species classifications of *N. burrowsius* and *N. beletios* be improved to the status of ‘Serious Decline’ or better, and that *N. diversus* and *N. apoda* remain at ‘Gradual Decline’ or improve by 2013.

## 11.2 DETERMINING DISTRIBUTION

To conserve a threatened species, it is important to evaluate its distribution and abundance using reliable measures. Unfortunately, as a species becomes increasingly rare, it becomes more difficult to detect and sample adequately. This problem is compounded for *Neochanna* species by the general difficulty in capturing them (Eldon 1992). Because of the ‘marginal’ nature of many *Neochanna* habitats, regional-scale fish surveys have only rarely found *Neochanna* species (McDowall et al. 1977; Main 1989). Comprehensive surveys targeted at *Neochanna* species have been conducted successfully throughout their ranges (section 2.3). Even so, when potentially suitable habitat is specifically sampled, the success rate for finding *Neochanna* species is seldom more than 50% (Table 11).

A variety of methods have been employed to capture *Neochanna* species, with Gee-minnow traps being the most common (Table 12). However, methods used for sampling different species have varied subtly due to differences in habitat type and surveyor preference. Other commonly used capture methods include fyke nets for *N. rekobua*, electric fishing and push nets for *N. burrowsius*, a combination of passive trapping methods for *N. diversus*, Kilwell bait traps for *N. beleios*, and hand nets for *N. apoda* (Table 12). Comparisons of data collected using different methods can be problematic. Thus, standardised methods for surveying and monitoring *Neochanna* species have been proposed (DOC 2003).

TABLE 11. PERCENTAGES OF SITES AT WHICH *Neochanna* SPECIES WERE ENCOUNTERED DURING SURVEY WORK SPECIFICALLY FOCUSED ON FINDING THEM.

SPECIES	TOTAL NUMBER OF SITES SURVEYED	NUMBER OF SITES WITH <i>Neochanna</i>	PERCENTAGE OF SITES WITH <i>Neochanna</i>	SOURCE
<i>N. burrowsius</i>	21	7	33	Cadwallader (1973)
	65	22	34	Harraway (2000)
	90	21	23	Eldon (unpubl. data)
<i>N. diversus</i>	35	4	11	McGlynn & Booth (2002)
	180	31	17	Kerr & McGlynn (2001)
	94	29	31	University of Waikato*
<i>N. beleios</i>	35	10	29	McGlynn & Booth (2002)
	180	19	11	Kerr & McGlynn (2001)
	94	3	3	University of Waikato*
<i>N. apoda</i>	26	7	27	Francis (2000a)
	31	23	74	Rebergen (1997)
	26	8	31	Butler (1999)
	14	4	29	Caskey (1996)
	7	1	14	Caskey (1997)
	33	11	33	Grainger (2000)

\* Data given in Kerr & McGlynn (2001).

TABLE 12. ANALYSIS OF COLLECTION METHODS USED TO CAPTURE *Neochanna* SPECIES AS INDICATED BY NZFFD RECORDS. VALUES ARE PERCENTAGES FOR EACH FISH SPECIES.

COLLECTION METHOD	<i>N. rekobua</i>	<i>N. burrowsius</i>	<i>N. diversus</i>	<i>N. beleios</i>	<i>N. apoda</i>
Gee-minnow trap	57.1	59.4	57.9	90.9	59.5
Passive methods combined*	14.3	6.9	13.5	2.3	8.2
Fyke net	28.6	3.0	2.3		0.5
Hand net		7.9	12.3	2.3	10.3
Electric fishing		8.9	5.3		5.6
Kilwell bait trap			5.3	4.5	7.7
Push net		8.9	2.3		0.5
Observation		4.0	1.2		6.2
Passive and active methods combined†		1.0			1.0
Spotlighting					0.5

\* Records based on a combination of net types, net/trap combination, Kilwell/Gee-minnow combination, or a combination of trap type methods.

† Records based on electric fishing/trap combinations, or net/electric fishing combinations.

Past survey work on *Neochanna* species (and freshwater fish in general) has generated site-specific point data. However, there is a growing need for detailed information on the small-scale, continuous distribution of species, particularly for planning and resource consent purposes. Thus, the management of freshwater fish using geographical mapping and modelling techniques has increasingly been recognised; for example, by Joy & Death (2000, 2002, 2004) who have successfully developed models to predict fish community composition in New Zealand streams. However, these models have predominantly focused on migratory species, and have not included rare species (occurring at < 5% of sites) such as *Neochanna*.

### 11.3 DETERMINING PRIORITY

Objective 1 of the *Neochanna* recovery plan (DOC 2003: 13) is to ‘**protect and manage habitats with key mudfish populations**’, with criteria to define key populations being listed as: preservation of large populations or habitats, unique or key scientific sites, maintenance of the geographic range, and genetic and biological diversity within each species. Priority setting has often relied heavily on the considered opinions of experts. However, quantitative methods, by which sites can be ranked to set conservation priorities, are increasingly important in conservation science (Minns 1987). The identification of effective assessment indicators, which require only basic monitoring data, will be essential for on-going conservation efforts. Increasingly, volunteer groups, non-scientific agencies, and quickly trained personnel using simple methods are conducting monitoring. This should be welcomed, as it may be a necessity for undertaking large-scale monitoring. However, it is important that the data collected yield meaningful information, in addition to the techniques being straightforward. There is, therefore, a need for transparent criteria that even persons with limited expertise can use (Minns 1987).

Ranking diverse habitats and *Neochanna* species populations is difficult. There is a tendency to rank habitats on the basis of the level of modification or agricultural influence, with ‘good’ habitat being judged to be sites that retain perceived ‘naturalness’. However, aesthetically ‘natural’ sites may not sustain the densest populations (Eldon 1978b; O’Brien 2005). For example, Barrier (1993) recorded the highest catch per unit effort (CPUE) of *N. diversus* in a roadside drain. Similarly, Francis (2000a) found the occurrence of *N. apoda* increased in areas of higher agricultural activity in the Wairarapa. Thus, population characteristics should be considered to identify key populations, as well as habitat values.

#### 11.3.1 Methods of ranking populations

It is important when assessing a population’s status that results are compared against overall standards and/or guidelines. This ensures a comparable ranking system across the entire range of habitats within a species’ range. In studies of *Neochanna* populations, the most commonly used estimate of density is CPUE data, using Gee-minnow traps and calculated as number of fish caught per trap per night. Analysis of NZFFD records using Gee-minnow traps (and which also state the effort used) indicate that the majority of sites have relatively low catch rates, i.e. 50% of populations sampled resulted in a CPUE of less than one, except for *N. burrowsius* (Fig. 15). *Neochanna burrowsius* populations consistently exhibited higher CPUE, and thus likely higher densities. This could be related to their generally higher fecundity (Fig. 9). *Neochanna diversus* populations usually yield the lowest CPUE of the mainland species (Fig. 15).

Another important characteristic of a population is the size of individuals. Maximum lengths of *Neobanna* in New Zealand, recorded as total length, are: *N. rekobua*—175 mm, *N. burrowsius*—157 mm, *N. diversus*—165 mm, *N. heleios*—134 mm, and *N. apoda*—200 mm (Eldon 1979c; McDowall 2004; NZFFD records). These differences in size attained are likely associated with differences in growth rate and/or longevity among species (section 6). Within species, adult size, especially that of females, has important consequences for population dynamics, principally because fecundity increases with size (Eldon 1978b, 1979c; Fig. 9). Thus, a population containing large females may produce a greater number of offspring, which increases the chance that some will survive, than a similar-sized population of small fish.

We suggest that *Neobanna* populations can be comparatively ranked, using the population attributes of CPUE and maximum fish length which are often recorded in the NZFFD. For example, cumulative graphs of fish density (CPUE; Fig. 15) obtained from Gee-minnow trap collections and the length of the largest fish captured (Fig. 16) could be used to rank sampled populations against the results of all other populations and sampling occasions. Specifically, this could be done by assigning a ranking, from 1 to 3, based on where the sample population fits in relation to records from other populations of that species. Rank classes are defined by the range of values, obtained from Figs 15 and 16, representing

Figure 15. Cumulative frequency of *Neobanna* population densities in terms of catch per unit effort (CPUE) using Gee-minnow traps, as given in the NZFFD at 30 July 2004.

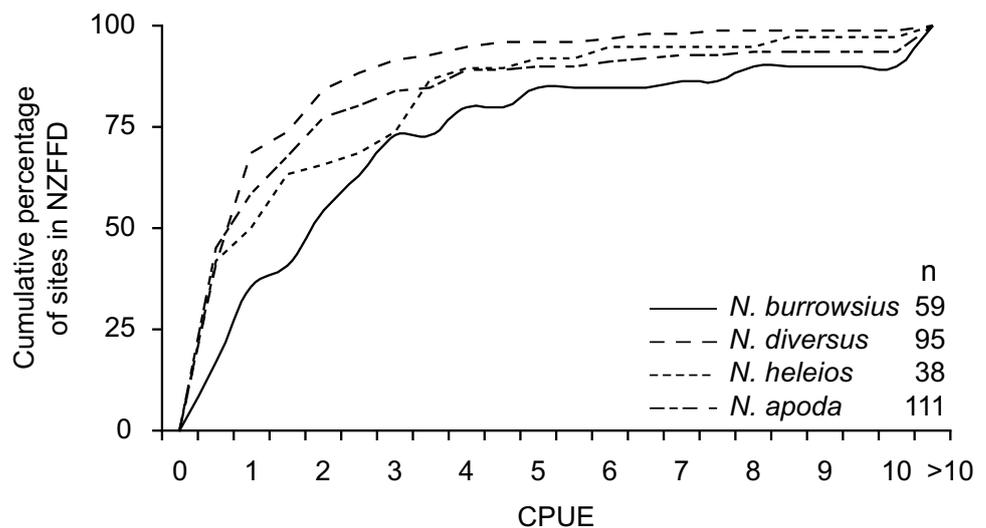
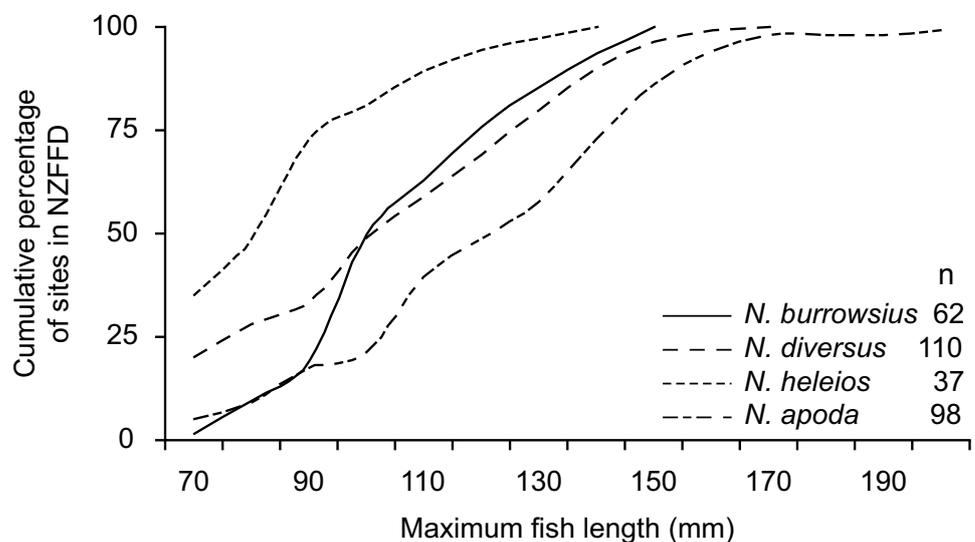


Figure 16. Cumulative frequency of maximum *Neobanna* lengths (mm) at all sites reported in the NZFFD as at 30 July 2004.



the 75–100 percentile (Rank 1), 50–75 percentile (Rank 2), and 0–50 percentile (Rank 3). This method of population assessment compares relatively well with more subjective assessments used by various authors. For example, Barrier et al. (1996) classed high catch rates for *N. diversus* as 1–8 fish per trap per night and low catch rates as 0.4, and Kerr & McGlynn (2001, p. 28) stated that ‘good sites often have greater than 4 fish per trap’. Using CPUE data presented by Hicks & Barrier (1996) as an example, the suggested classification scheme would give a top ranking to eight of the 39 sites where *N. diversus* were found, and a second ranking to five of the sites. Use of such a ranking method to identify key sites objectively is important, as highly ranked populations are likely to be a source of recruits to surrounding habitats.

#### 11.4 HABITAT PROTECTION AND RESTORATION

Many *Neochanna* populations are protected by virtue of occurring in remnant wetlands that receive some form of protection, e.g. Ashhurst Domain, Whangamarino Wetland, Kopuatai Peat Dome, Mangarakau Wetland, and Fensham Reserve. However, populations on private land remain largely unprotected. In fact, analysis of DOC’s National Database of Key Mudfish sites (DOC, unpubl. data, as at January 2004) shows that of 67 sites with land ownership given, 63% were on privately owned land. The use of covenants, such as that on Dog Kennel Stream, South Canterbury (which was the first to specifically protect a freshwater fish on private land; Gray 2000), is increasing, with 6% of sites included in the key *Neochanna* site database being under some form of protection. Although private ownership is sometimes an obstacle to conservation activities (e.g. DOC 2004a), the numbers of landowners interested in protecting *Neochanna* populations is increasing (DOC 2004b). There are many options for the protection of wetland habitat and they include both short-term and non-binding arrangements, and legal protection in perpetuity. Legal agreements (such as covenants) to protect land can be made between landowners and a number of organisations, including the Queen Elizabeth II National Trust, DOC, and local authorities. A variety of funds is also available to support conservation activities. Information on these can be obtained from DOC and local councils.

Many *Neochanna* habitats have undergone some form of restoration, mainly involving riparian planting (e.g. Caskey 2000). However, only a few studies comparing ‘restored’ and ‘control’ sites have been carried out, and one of these has suggested that dense plantings of trees and other vegetation in ‘restored’ sites may not always be beneficial to *Neochanna*. Leanne O’Brien (unpubl. data) compared *N. burrowsius* from similar pool habitats above, and within, a restored section of Dog Kennel Stream, South Canterbury, during 1999 and 2001. Juveniles from un-restored pools were generally longer and had greater condition than those in the restored pools. Although further studies are needed, this result does emphasise the importance of adequate monitoring when conducting habitat modification or restoration activities to ensure the outcomes are as envisioned and to guide future conservation efforts.

## 11.5 RESERVE DESIGN

Faunal reserves have been suggested as one way of ensuring the continued persistence of *Neochanna* species. McDowall (1984) described the appropriate criteria guiding reserve design for freshwater fish in New Zealand as naturalness, reserve size, permanence of water, absence of exotic species, absence of exploitation, and access to the sea. Although McDowall (1984) included the criterion of access to the sea primarily for diadromous species, which need access to it, this criteria is also important for *Neochanna*, but from the opposite perspective. Connections to the sea can be expected to increase the occurrence of other species which is not desirable. Reserves for *Neochanna* need to be of sufficient area to maintain the integrity of their hydrology (Close 1996; Hicks & Barrier 1996), and Hicks & Barrier (1996) considered buffer zones were needed between wetland reserves and surrounding pasture. Nevertheless, many *Neochanna* populations are able to persist in a very small habitats (McDowall 1984; Eldon 1986; Eastwood 1997), indicating that even small reserves may be effective.

The establishment of multiple, interconnected or 'complex' reserves may be desirable, as this would increase the probability of some individuals surviving severe disturbance and being able to repopulate habitat where populations have been lost. Several studies have demonstrated the ability of *Neochanna* to disperse widely and recolonise suitable habitats after disturbance (e.g. Eldon 1978b; Eldon et al. 1978; Main 1989; O'Brien 2000). Dispersal provides a mechanism whereby fish can naturally and rapidly recolonise streams following perturbation and local extinction (McDowall 1996b). Davey et al. (2003) considered that dispersal of *N. burrowsius* during flooding was an important component of its long-term persistence and that, where possible, dispersal routes between sites during flooded conditions should be identified and maintained to allow recolonisation of suitable habitats following local extinctions. Promoting the natural re-establishment of fish populations has particular advantages in that it occurs when habitat conditions are again suitable, colonising stocks are well adapted to local conditions, and it is inexpensive (McDowall 1996d).

## 11.6 ESTABLISHING NEW POPULATIONS

Throughout the world, captive breeding has brought many species back from the brink of extinction. In New Zealand, it is being used to increase population sizes, maintain genetic variability and as a source of translocation stock of threatened endemic fauna. Its potential for the conservation of threatened *Neochanna* species has been recognised and advocated, e.g. Eldon (1969, 1993) and Swales (1991), and general guidelines for the captive breeding, rearing and establishment of new *Neochanna* populations have been outlined (O'Brien & Dunn 2005). Successful captive breeding has been achieved for *N. burrowsius* (Cadwallader 1975a; Eldon 1979c; Gay 1999; O'Brien 2005), *N. diversus* (Gay 1999), and *N. apoda* (Eldon 1969, 1971). Further, Caskey (2002) and Perrie (2004) successfully reared *N. apoda* and *N. diversus* juveniles after attempts at breeding.

Some translocations of *Neochanna* species to protected sites have been successful in New Zealand, especially efforts by G.A. Eldon with *N. burrowsius* during the 1980s (Eldon 1983, 1985, 1986, 1988a, 1988b, 1989, 1993; Eldon & Field-Dodgson 1983). Initial sites included the Christchurch botanical gardens, a small pond at Ohoka, an old borrow pit at Lowcliffe, and farm dams at Taiko (Eldon 1983). By 1985, however, *N. burrowsius* were found at only two of these four sites, and the liberated juveniles in one of them were in poor condition and showed no evidence of breeding (Eldon 1985). Further translocations have also had mixed success (Eldon 1989, 1993). More recently, DOC staff translocated *N. burrowsius* to the Willowby Local Purpose Reserve (S. Harraway, DOC, pers. comm.) and to an artificially constructed 8.3-ha wetland at Westerfield (South Branch Ashburton River) in February 2002. Only the latter translocation was successful. Attempts have also been made to establish *N. burrowsius* in a restored urban waterway (Hartley 2003). In the Stratford area, Caskey (1999, 2000) applied Eldon's (1993) translocation guidelines to *N. apoda*, which occurs in fragmented agricultural habitats. A media release (Stratford Press, August 5 1998) and previous survey data (Caskey 1996, 1997, 1998) were used to locate a suitable translocation habitat where juveniles were released (DOC 1999b, 2000e, f), but despite close monitoring, the population failed to establish (Caskey 2000, 2002; DOC 2000e, f, g).

Thus, despite considerable effort, few new *Neochanna* populations have been established. This emphasises the need to focus on the protection of habitats that currently contain *Neochanna*. Further understanding is also needed of the small-scale and long-term seasonal characteristics of *Neochanna* habitats, in order to better guide the identification of potential translocation sites for each species.

## 12. Information gaps

Since the 1960s, 22 peer-reviewed, scientific articles on New Zealand *Neochanna* species have been published, seven in international journals. These articles give 50 different keywords reflecting the topics most extensively studied. The majority of these referred to species investigated and localities. Of the keywords relating to subject areas covered, **habitat** is included in six papers, **conservation**, and **air-breathing** in three, and **behaviour**, **diet**, **distribution**, **population genetics**, **spawning**, and **taxonomy** in two. A review of the literature on *Neochanna* reveals that because of their discrete distributions, most research has been on single species, by researchers from universities in the vicinity of the particular study species or population. Few comparative studies have been made, despite *Neochanna* species forming a well-defined group with interesting similarities and dissimilarities. The domination of species-specific research has led to conclusions generated from work on a few species being applied to the genus as a whole, with much speculation. Despite this, many studies emphasise that *Neochanna* species are distinct and have unique characteristics. Rather than apply overall generalities, with provisos that some species are exceptions, the present review highlights the recognition of a continuum of characteristics found among them. Further, although many common characteristics—such as drought

tolerance—have been identified, the exact mechanisms allowing *Neobanna* to persist require further study. Thus, there is a need to move from a descriptive to a mechanistic approach to research on *Neobanna* species. Understandably, the greatest information gaps are for the newly described or re-classified species, i.e. *N. beleios* and *N. rekobua*. However, further research into many aspects of basic biology and ecology is needed for all species to ensure there is adequate information to effectively undertake conservation management.

### 1 2 . 1      T R A N S F O R M A T I O N   S E R I E S

The transformation series (Fig. 3) initially proposed by McDowall (1997a) and substantiated by Water & McDowall (2005) is based on detailed knowledge of the morphological characteristics and phylogenetic relationships of the six species of *Neobanna*. The relationships are interpreted as indicating increasing adaptation to life in shallow, hydrologically fluctuating wetlands. Morphological, phylogenetic and ecological data continue to provide strong support for the placement of *Neobanna* species within the transformation series and its use as a general framework for generating hypotheses to guide further research of the genus. This review of *Neobanna* literature also supports an extension of the transformation series to include differences in life-history, fecundity, current habitat use, physiological adaptations and tolerances, and survival strategies. However, the lack of comparative research and inadequate data on many species means that definitive conclusions are not possible at present, and there is a need for:

- Comparative studies to determine the validity and generality of conclusions based on the transformation series.
- Improved understanding of the mechanisms by which particular habitats exert selective pressure on *Neobanna* species.
- Development of conservation guidelines that reflect species-specific characteristics and requirements, as indicated by the transformation series.

### 1 2 . 2      D I S T R I B U T I O N

The boundaries of evolutionary significant units (ESUs) for each species have been identified and knowledge of the geographic extent of species distributions is good (Fig. 2). Further, as *Neobanna* species are restricted to low-lying areas, their distributions are unlikely to change substantially. Further areas of investigation relating to species distributions are:

- Mapping of small-scale distributions of *Neobanna* species in wetlands and agricultural drains in a form suitable for incorporation into GIS databases, to improve conservation management.
- Resurveying of sites sampled prior to c. 1995 to assess population persistence.
- Evaluation of local extinction events since records began to determine likely rate of recent decline.
- Determination of the ability of *Neobanna* species to disperse, and identification of factors that affect dispersal rates of all life stages.

### 1 2 . 3    H A B I T A T

Investigations to date have identified general habitat characteristics for many *Neochanna* species. Species appear to occur in habitat types across a hydrological continuum, which is likely to be related to adaptations indicated in the transformation series. Further investigations could focus on:

- Understanding habitat use by *Neochanna* species at all life stages, and the importance of ontogenetic shifts in habitat use.
- Understanding the role of hydrological fluctuation on distribution, persistence, and local adaptation of *Neochanna* species.
- Developing detailed models of habitat preference for *Neochanna* species, including aspects of hydrology, vegetation (terrestrial and aquatic), and community attributes (fish and invertebrate).
- Models have been developed for some species; however, these may require further testing at a wider range of sites (if these were not included in the original model) to determine their predictive ability.
- Developing simple and quick methods for initial habitat assessment.

### 1 2 . 4    F E E D I N G

There have been few extensive studies of *Neochanna* diet, due in part to the destructive methods usually required, which limit sample sizes. However, *Neochanna* species are regarded as generalist feeders, although there are likely to be differences in diet that relate to habitat type. In particular, investigation is required into:

- The role of differences in teeth and jaw morphology in diet and feeding mode.
- How changes in habitat hydrology influence prey species composition and thus *Neochanna* growth rates.
- The ability of *Neochanna* species to change diet or otherwise compensate for the presence of competing fish species.

### 1 2 . 5    R E P R O D U C T I O N

Although reproduction is a requirement for population persistence, it has not been well studied in *Neochanna* species, especially in *N. beletos* and *N. rekobua*. This is an essential area of future study, especially as *Neochanna* species appear to differ from one another in their reproductive characteristics. Investigations should focus on:

- Determining the timing, location and type of habitat used for spawning by all species.
- Verifying that *N. apoda* habitually scatter eggs above the water line and how they achieve this.
- Investigating the role of habitat quality and environmental cues in determining spawning in *Neochanna* species.
- Investigating the fecundity and early development of all species, including egg characteristics such as size ranges and development times.

- Assessing the effect of emersion and habitat factors on subsequent reproductive output.
- Determining the length of time that *Neochanna* species can retain viable eggs and the mechanisms by which they do so.

## 12.6 POPULATION CHARACTERISTICS

Population investigations are best approached through long-term study and monitoring at particular sites, and they require appropriate funding and time allocation to ensure that this happens. There is a need to:

- Investigate the relationship between recruitment, habitat capacity and population density.
- Investigate whether there are differences in patterns of growth between species which may reflect differences in somatic versus reproductive investment.
- Confirm the occurrence of stunting and determine factors suppressing growth and adult size in populations.

## 12.7 BEHAVIOUR

Much of the information regarding *Neochanna* behaviour is anecdotal and many field observations are necessarily serendipitous. Thus, there is a need for further laboratory- and field-based behavioural studies on:

- Species-specific survival strategies, and whether all species respond equally to emersion.
- Size-dependent responses to summer stress, as different-sized fish may require different summer refuges.
- Shelter-seeking behaviour, what triggers such behaviour, and how *Neochanna* species choose specific kinds of refuges.
- How capable *Neochanna* species are at burrowing, what type of substratum is required, and where in particular habitats they are likely to burrow.
- Social behaviour during periods of increased stress or threat, and its potential to improve survival.
- Behavioural studies of *Neochanna* in low-pH waters and under progressively hypoxic conditions.

## 12.8 PHYSIOLOGY

The mechanisms that enable *Neochanna* to survive without free water for extended periods are still not fully understood. Physiological investigations have focused on *N. burrowsius* and *N. diversus*, with conclusions obtained from studies of these species often being applied to the genus as a whole. There is a need, therefore, for more species-specific knowledge. Meredith (1985), Dean (1995), and Davidson (1999) all note subjects requiring further study, including direct comparisons of oxygen consumption, metabolic rate, critical oxygen values, and gill morphology. Further, investigations must employ standardised experimental procedures and acclimation times. Topics for research could include:

- Investigations of the physiological parameters of *Neochanna* during exposure to low-pH waters.
- Whether the water permeability of mucus changes upon desiccation.
- The role of mucous substances in aiding the disassociation of ammonium ions during emersion, and maintenance of a neutral skin pH.
- Comprehensive determination of blood characteristics of fish in aquatic and aerial conditions.
- Investigations of *Neochanna* circulatory systems; in particular, blood flow to the skin, to assess the ability of the species to undergo cutaneous vasoconstriction in response to hypoxia and emersion.
- Investigation of the ability of *Neochanna* species to lower their metabolic rates on emersion, and the limits of this ability.
- Whether *Neochanna* species are capable of switching from protein to lipid or glycogen metabolism.

## 12.9 THREATS

Major threats influencing *Neochanna* populations have been identified (Table 9), but how they actually affect individuals and populations is not well understood. In particular, there is a need to:

- Quantify and understand the threats posed to *Neochanna* populations by common land management and agricultural activities.
- Investigate and quantify the impact of drain maintenance on *Neochanna* populations, including direct and indirect factors.
- Develop environmentally and economically sustainable approaches that address the apparent conflict between intensive land management and the persistence of *Neochanna* populations.
- Investigate the effect of potential competitors and predators on the persistence and health of *Neochanna* populations.
- Investigate disturbance-mediated coexistence between *Neochanna* species and potential competitors and predators.
- Investigate internal parasites and disease to fully assess the vulnerability of *Neochanna* species to these.

## 12.10 CONSERVATION

Historically, much conservation work on *Neochanna* species has been relatively ad hoc. However, since the formation of the DOC mudfish recovery group and the development of a 10-year recovery plan (DOC 2003), initiatives have become increasingly co-ordinated. There is still a need to:

- Develop guidelines for assessing *Neochanna* habitats and applying appropriate conservation actions (such as revegetation).
- Determine whether agricultural drain networks can provide dispersal corridors between small reserves to allow gene flow, particularly in *N. burrowsius*.
- Develop quantitative and transparent (but straightforward) methods by which populations can be easily ranked, that can be used to set conservation priorities.

- Determine effective assessment indicators that require only basic monitoring data, to facilitate evaluation of on-going conservation work.
- Determine what information landowners need, and develop information packs with species-specific information and best practices for interested landowner groups.
- Develop guidelines for identifying potential sites for establishing new populations.
- Improve the procedures for pre-translocation proposals and post-translocation monitoring of sites, and assimilation of knowledge to aid further translocations.
- Investigate the factors responsible for the success or failure to establish of *Neochanna* populations.

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***What is known about Neochanna species?***

*Neochanna (mudfish) are small, cryptic fish of the Galaxiidae family that exhibit extraordinary survival ability and amphibious behaviour. Of the six Neochanna species, five are endemic to New Zealand. Neochanna species show a continuum of morphological transformation from Galaxias-like characteristics towards an anguilliform, or eel-like body plan. Overall, the taxonomic distinctiveness, general biogeography, and genetic structure of the genus Neochanna is fairly well known, but many aspects of the species' physiology, biology, and ecological situation require further study.*

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