

EFFECTS OF HABITAT STRUCTURE ON DISTRIBUTION AND ABUNDANCE OF LIZARDS AT PUKERUA BAY, WELLINGTON, NEW ZEALAND

Summary: The distribution and abundance of lizards relative to habitat structure were studied at Pukerua Bay, Wellington between December 1982 and March 1988 in order to identify options for management of the habitat of the five species of lizards present. One species, Whitaker's skink (*Cyclodina whitakeri*), is a threatened species with only one known mainland population. Pitfall traps were set for 23 667 trap-days and yielded 2897 lizard captures. Highest capture rate was for common skinks (*Oligosoma nigriplantare polychroma*) and lowest rate was for *C. whitakeri*. Of the five lizard species at Pukerua Bay, *C. whitakeri* had the narrowest habitat range and was most sensitive to temperature extremes. These features, combined with predation, and habitat disturbance and degradation, have resulted in critically low numbers of *C. whitakeri*. Assessment of management options to lessen the threats to *C. whitakeri* concluded that risks from disturbance, predation and fire could best be minimised through a managed revegetation programme.

Keywords: skinks; *Cyclodina aenea*; *Cyclodina whitakeri*; *Oligosoma nigriplantare polychroma*; *Oligosoma zelandicum*; geckos; *Hoplodactylus maculatus*; vegetation; substrate; temperature; livestock; revegetation; predators; fire.

Introduction

The New Zealand archipelago supports an unusually diverse fauna of lizards when compared with temperate environments elsewhere (Daugherty *et al.*, 1990c). Before humans arrived about 1000 years ago, the highest local diversities were probably in warm lowland forests, especially those near the coast. Recent palaeoecological analyses have revealed that assemblages of up to 17 sympatric species of lizards, including at least six species of *Cyclodina*¹, were once present in Northland (Towns and Daugherty, 1994). As introduced predatory mammals spread following human colonisation, these large primeval lizard assemblages disappeared from mainland New Zealand; highest species diversities are now found on offshore islands (Towns and Atkinson, 1991; Towns and Daugherty, 1994).

Part of a coastal forest lizard assemblage has persisted at Pukerua Bay near Wellington despite extreme habitat modification. The assemblage is unique because it includes the only known remaining mainland population of Whitaker's skink

(*Cyclodina whitakeri*). Much of the Pukerua Bay site has recently been designated a Department of Conservation Scientific Reserve with the long term intention of restoring the area to coastal forest. However, because of differences in habitat use, not all lizard species present at Pukerua Bay will necessarily benefit from reforestation (East, East and Daugherty, 1995). Also, other recent environmental changes (such as the presence of introduced predators) could complicate the effects of restoration on the lizards (Towns, 1991, 1994, *in press*).

In this paper we describe the Pukerua Bay site and its lizard assemblage. We provide estimates of the population densities of each species, investigate the relationship between lizard density and environmental characteristics, discuss how reserve management could reflect the habitat needs of the lizard species, and identify how habitat management could benefit *Cyclodina whitakeri*, the rarest species in the assemblage (Towns, 1985; Molloy and Davis, 1994).

Study area

The study site was between Pukerua Bay township and Wairaka Point, on steep coastal hill sides formed from an escarpment that faces directly north and rises steeply to 160 m a.s.l. (Fig. 1). The escarpment

¹ Nomenclature for reptiles follows Robb and Rowlands (1977), Hardy (1977), Daugherty *et al.* (1990a) and Patterson and Daugherty (1995).

includes greywacke bluffs, screes and talus slopes of rocks and boulders. At the foot of some slopes are narrow talus areas (10-20 m wide) and rocks and large boulders are scattered along old beach terraces. The coastline is also rocky, with narrow beaches of rocks, stones and gravel.

By 1982, the study area had been farmed at low intensity for at least 100 years and sheep (*Ovis aries*)² had access throughout. There was also evidence of repeated fires on the northeastern cliffs. Vegetation on the escarpment and along the shoreline therefore formed a mosaic which in northeast - southwest sequence was (C. Ogle, *pers. comm.*; Department of Conservation, Wanganui, N.Z.):

1. Montpellier broom (*Teline monspessulana*)³ - Cape ivy (*Senecio angulatus*)-boneseed (*Chrysanthemoides monilifera*) shrubland and mountain flax (*Phormium cookianum*) on steep faces and burn scars.
2. Small pockets and isolated plants of puka (*Griselinia lucida*) and karaka (*Corynocarpus laevigatus*) at the foot of bluffs (sometimes with *Olearia paniculata*), and scattered along the lower slopes.
3. A remnant stand of karaka trees with the understorey eaten out by stock.
4. A patch of coastal broadleaf forest dominated by kohekohe (*Dysoxylum spectabile*) on a ridge crest with the understorey eaten out by stock.
5. Kanuka (*Kunzia ericoides*) shrubland mixed with flax on southwestern bluffs.
6. *Coprosma propinqua* shrubland intermixed with pohuehue (*Muehlenbeckia complexa*), reverting grassland, scattered tree nettle (*Urtica ferox*), and occasional kawakawa (*Macropiper excelsum*) and kaikomako (*Pennantia corymbosa*) on stable slopes and along the old beach terrace.

When this study began the northeastern portion of the study area was a Recreation Reserve administered by Porirua City Council. A further 12.3 ha of escarpment adjacent to the Recreation Reserve was purchased from its owners by the Crown in 1984 and a sheep-proof fence was completed by March 1987. Wandering goats (*Capra hircus*) entered the study area for the first time in 1986 and are now periodically culled. Few stock have entered the Crown area or the Recreation Reserve since March 1987.

Lizards present

Five species of lizard persist at Pukerua Bay:

1. Common gecko (*Hoplodactylus maculatus*): a nocturnal species that is geographically and ecologically ubiquitous and may comprise several cryptic species (Daugherty, Patterson and Hitchmough, 1994). The Pukerua Bay taxon is common throughout the North Island and northern South Island (R. Hitchmough, *pers. comm.*; Victoria University of Wellington, N.Z.).
2. Common skink (*Oligosoma nigriplantare polychroma*): a widespread diurnal species that is part of a complex of closely related species revised by Patterson and Daugherty (1990). The complex shows a high degree of morphological, ecological and genetic diversity (Daugherty *et al.*, 1990b), but genetic analyses indicate no evidence of more than one taxon at Pukerua Bay (C.H. Daugherty, *pers. comm.*; Victoria University of Wellington, N.Z.).
3. Brown skink (*Oligosoma zelandicum*): a diurnal species present only in the southern third of the North Island and in the northern South Island (Pickard and Towns, 1988). In the Wellington and Manawatu areas *O. zelandicum* is frequently sympatric with *O. n. polychroma*, but *O. zelandicum* has the narrower habitat range (Gill, 1976).
4. Copper skink (*Cyclodina aenea*): like all species of *Cyclodina*, confined to the North Island where it is the most widespread species in the genus (Pickard and Towns, 1988). It is one of New Zealand's smallest lizards and is regarded as both crepuscular and diurnal (Porter, 1987).
5. Whitaker's skink (*Cyclodina whitakeri*): apart from the Pukerua Bay population, was known only from three offshore islands that lack introduced mammals (Towns and Robb, 1986), but is now being reintroduced to islands from which predators have been removed (Towns, 1994). *C. whitakeri* is the largest species at Pukerua Bay (up to 20 cm total length), is nocturnal, prone to cutaneous water loss (A. Cree and C.H. Daugherty, *pers. comm.*; Victoria University of Wellington, N.Z.), and uses warm moist environments, such as rocky areas and seabird burrows, as daytime retreats (Macredie, 1984; Towns, 1994).

Methods

Study sites

The main study grid was in the Crown reserve where exploratory 20 m transect lines (every 20 m along

² Nomenclature for mammals follows King (1990).

³ Nomenclature for plants follows Moore and Edgar (1970), Lambrecht (1981), Allan (1982), Connor and Edgar (1987) and Webb, Sykes and Garnock-Jones (1988).

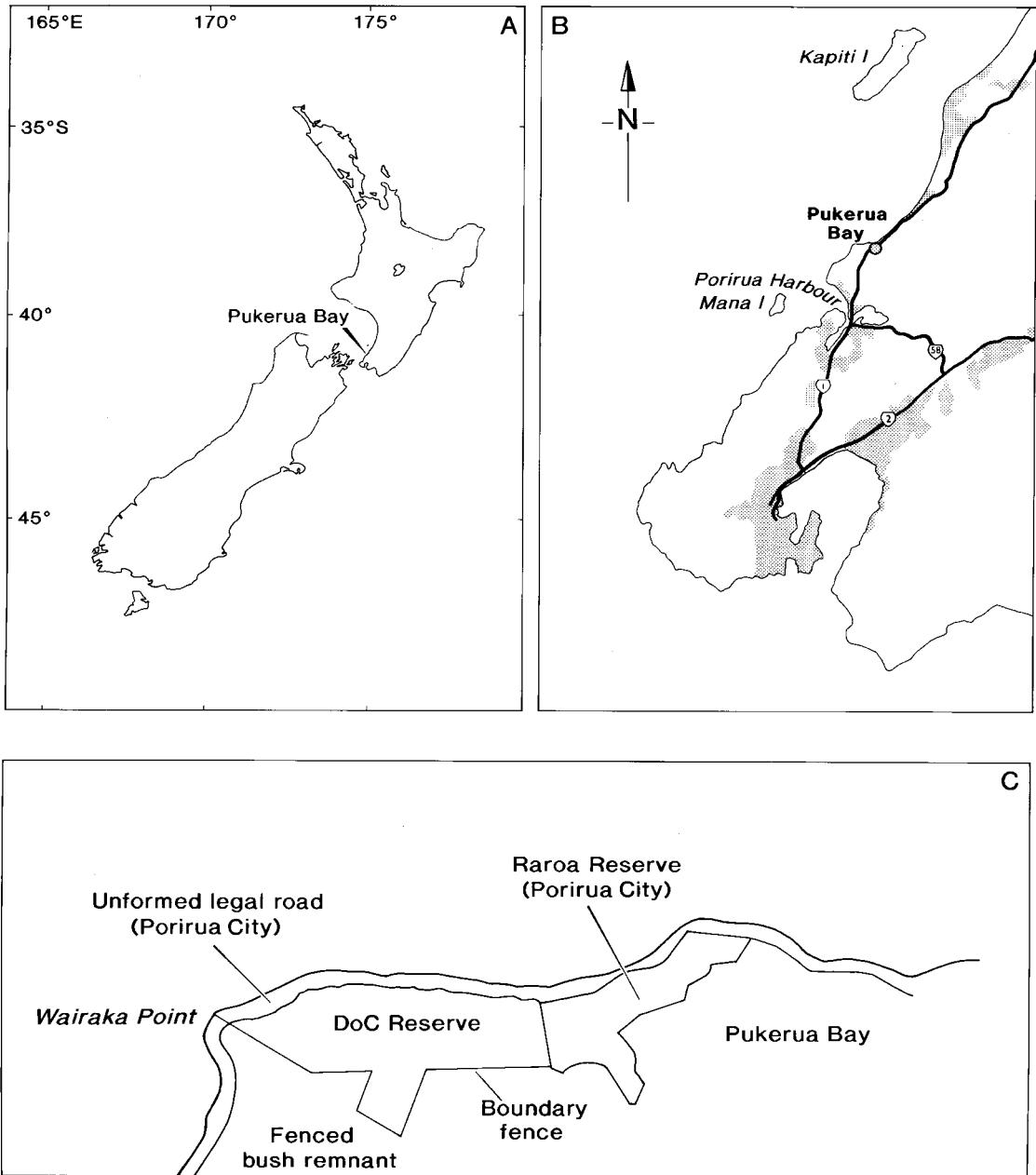


Figure 1: The Pukerua Bay study site (A); localities mentioned in the text (B), with the greater Wellington urban areas shaded; and location of the reserves (C).

260 m of lower slope and beach platform) revealed the highest frequency of *C. whitakeri* captures (December 1982 - May 1983). Regular sampling on the study grid began in December 1983 and continued to March 1988.

A second study area was established in similar habitat to the main study site (but with a southwestern aspect) between June 1983 and April 1984 at Wairaka Point 200 m south of the reserve. Trapping was discontinued because no *C. whitakeri* were caught in 885 trap-days.

The main study site was a 768 m² rectangular quadrat oriented from east to west across four exploratory transects. The quadrat and outlying transects comprised 113 pitfall traps. Most of the 79 traps within the quadrat grid were set at 4 m intervals except along the transects, where the interval was 2 m (Fig. 2). The eastern-most traps were on the edge of a clay ridge that formed a discontinuity across the rocky talus slope. All remaining traps on the grid were set into gravel or stones or a mixture of stones, gravel and loam. Precise location of the transects and study site is not given here to protect the *C. whitakeri* habitat.

All captures were by pitfall traps; those on exploratory transects were 500 ml plastic cups, whereas in the main study site traps were 4-litre paint tins (see Towns 1991). Traps were set at fortnightly intervals between December 1983 and May 1985, then reduced to August-April in 1985-1986 and December-March in 1986-1988.

Traps were baited with canned pear and usually set for 48 h. Traps into which sticks or other potential escape routes had fallen were regarded as unset. For comparison between trapping sessions, trapping effort is presented as captures per 100 trap-days (Towns, 1991).

Animals captured were permanently marked using a predetermined toeclip sequence, measured from snout to vent, weighed to 0.1 gm with PesolaTM balances, and released beside the trap.

Population estimates

Problems with unequal catchability of lizards (e.g., Towns, 1985) can be overcome partly by using extended sample periods to enable calculation of "direct enumeration" or "minimum number alive" (MNA) by summing actual number caught at time *t* and those present, not caught at time *t*, but caught subsequently (Krebs, 1966). Two assumptions required for MNA are that (a) there is no large scale migration of animals into or out of the study site between samples; and (b) that there are few deaths of animals eligible to capture (Moller and Craig, 1987).

The following data were obtained so that MNA could be calculated for lizards at Pukerua Bay in year one:

1. Mean distance moved between capture (to test assumptions on migration).
2. Size distribution for each species in each year (enables estimation of number potentially able to be captured at year one).
3. Mortality in pitfall traps (could affect the population estimates).

Density estimates were obtained by calculating MNA and the effective trapping area (ETA) for each species. ETA was calculated by adding to the trapping grid a boundary strip half as wide as the average distance between captures (e.g., Moller and Craig, 1987).

Climate data

Mobility of lizards, and hence susceptibility to capture, can be strongly influenced by ambient temperature. Temperature variation during trapping periods was measured from November 1985 to March 1988 using three max-min thermometers: one in shade at the surface, one at 0.20 m and one at 0.65 m inside PVC pipe buried in the rocky scree in the study site.

Vegetation and substrate mapping

Vegetation height, and species composition and diversity, composition of the substrate and the layer beneath the surface, were measured at the 79 pitfall trap sites in the study quadrat between 25 September and 29 October 1986. Substrates were classed as loam, clay, silt, sand, gravel (particle size <5 cm), stones (6-20 cm), boulders (>20 cm), wood and creeping vegetation. Vegetation cover was analyzed using a modification of methods for sampling tussock and shrub vegetation (Scott, 1965). At each trap site 25 measurements of vegetation height and composition, surface and subsurface substrate were obtained every 25 cm over 1 m² using a length of wire marked at 25 cm intervals inserted through a moveable frame. Maps were drawn from mean vegetation heights and species composition was determined from the first encounter at each recorded point.

Relationships between habitat characteristics and capture rates

The following habitat parameters were used in this analysis:

1. Average vegetation height at each trap site.
2. Average proportion of the different surface and

subsurface types at each trap site normalised using arcsin \sqrt{p} transformation.

Only lizard captures in December-March inclusive were used, and the final trapping season, when livestock were absent from the study area, was also excluded. Lizard capture rates were calculated by dividing the number of lizards caught by the number of days traps were set.

Analyses of distribution

Lizard captures may often reflect a Poisson process: the number of lizards caught is discrete, has a skewed distribution and the variance is proportional to its mean. For statistical analyses such data are usually square-root transformed to normalise their distribution and remove the dependence between variance and mean (Sokal and Rohlf, 1981). Unfortunately, because lizard capture rates in this study were low and often zero, the data could not be normalised by the square root transformation.

Accordingly, we used analysis of deviance assuming a Poisson error distribution (Baker and Nelder, 1978) to compare capture rates in the five study seasons during summer (December - March) and to investigate relationships between lizard captures, habitat characteristics, and ambient temperature.

Results

Relationship between vegetation and substrate

Thirty plant species were recorded within the study grid during vegetation mapping. The most widespread species were *Coprosma propinqua* (16.2%), *Ehrharta erecta* (1.2%), *Microlaena stipoides* (4.1%), *Muehlenbeckia complexa* (63.8%), and *Poa pratensis* (1.9%). Including bare ground (7.4%), these species together made up almost 95% of all first encounters.

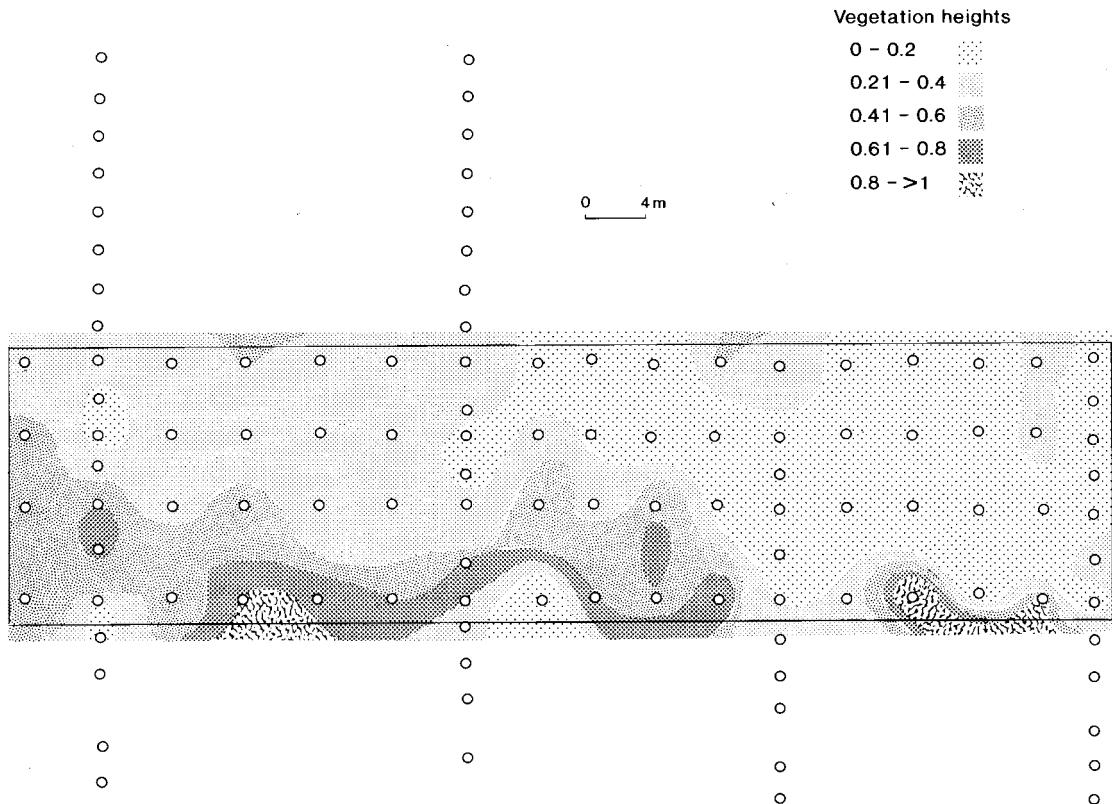


Figure 2: Layout of the study grid and transects, showing vegetation in 1986 mapped from mean vegetation heights at 79 sites. Open circles represent pitfall traps, effective trapping area for Whitaker's skink is defined by the solid line.

Vegetation in the study grid changed in relation to slope and substrate. On the northern side of the grid at the foot of the slope, vegetation on old beach terraces of loam and rounded stones had a high proportion of shrubs, predominantly *C. propinqua*. Amongst these shrubs, the more open areas contained pasture grasses such as *Microlaena stipoides* (4% of encounters) and *Sporobolus africanus* (0.3% of encounters). On the slope, vegetation was more dense at the eastern end, with extensive areas of *C. propinqua*, much of it intertwined by *M. complexa*, but also interspersed by some grasses such as *Ehrharta erecta* (1% of encounters). At the western end of the grid the substrate had a higher proportion of stones and boulders, vegetation density was lower, and *M. complexa* formed the predominant cover (Fig. 2).

Relationships between capture rates, years and seasons

Traps were set 91 times for a total of 23 667 trap-days during which 2897 lizard captures were made (including recaptures) and 1319 animals were marked and released. *Oligosoma n. polychroma* had the highest capture rate (52.6% of total captures) and *Cyclodina whitakeri* the lowest (2.7%) (Table 1).

The proportion of marked animals recaptured varied by species and season. *O. zelandicum* had the highest recorded recapture rate (49%), *C. whitakeri* the lowest of the four skink species and *Hoplodactylus maculatus* the lowest overall (Table 2). The capture rates of all lizard species varied significantly between years (Table 3), but the lowest rate of captures and recaptures for all species was in the summer of 1987-1988 (Table 2). This low rate coincided with evidence of increased predation on trapped animals and habitat changes following the removal of stock in early 1987. This season has therefore been excluded from most calculations involving mark-recapture data.

In addition to between-year variation in capture rate, continuous trapping from August 1983-May 1985 showed seasonal changes in captures (Fig. 3). The most strongly seasonal species was *Cyclodina whitakeri*. Most captures of this species (69.7%) were between December and March (inclusive).

Relationship between capture rate and temperature

No significant relationship between temperature and capture rate over summer was recorded for the diurnal *O. n. polychroma* and *O. zelandicum*.

Table 1: Mark-recapture data for lizards from Pukerua Bay between March 1983 and March 1988. Total captures include multiple captures of the same animals.

Species	No. marked	Total captures	Percentage of total captures
<i>Cyclodina aenea</i>	343	675	23.3
<i>C. whitakeri</i>	56	79	2.7
<i>Oligosoma n. polychroma</i>	649	1524	52.6
<i>O. zelandicum</i>	138	377	13.0
<i>Hoplodactylus maculatus</i>	133	242	8.4
Total	1319	2897	100.0

Table 2: Between-year variation in percentage of recaptured marked lizards at Pukerua Bay using data obtained between December and March in each season. Lizard species names are abbreviated as follows: *Cyclodina aenea* (C.a.); *C. whitakeri* (C.w.); *Oligosoma nigriplantare polychroma* (O.n.p.); *O. zelandicum* (O.z.); *Hoplodactylus maculatus* (H.m.).

Species	Season					
	1983/84	1984/85	1985/86	1986/87	1987/88	1983-87
C.a.	11	16	24	28	15	37
C.w.	13	14	20	18	0	25
O.n.p.	18	30	19	28	11	44
O.z.	20	31	54	30	0	49
H.m.	17	6	7	0	0	17
N ¹	52	56	61	112	12	

¹Number of marked animals caught in each season between December and March

Table 3: Comparison of lizard capture rates in different years by analysis of deviance. Levels of significance are denoted as <0.01 (**), <0.001 (***)

Species	F value	Degrees of freedom	P>F	Significance
<i>Cyclodina aenea</i>	21.41	4,39	0.000	***
<i>Cyclodina whitakeri</i>	4.87	4,39	0.003	**
<i>Oligosoma n. polychroma</i>	10.64	4,39	0.000	***
<i>Oligosoma zelandicum</i>	16.71	4,39	0.000	***
<i>Hoplodactylus maculatus</i>	5.01	4,39	0.002	**
Total	19.85	4,39	0.000	***

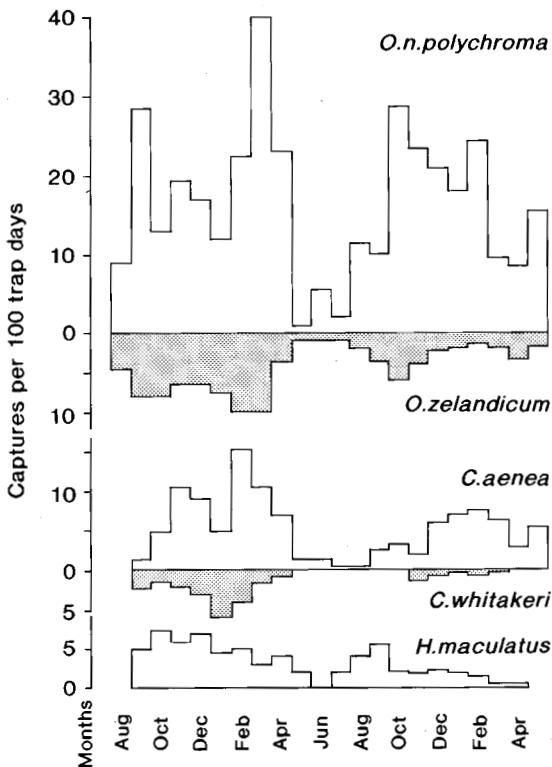


Figure 3: Seasonality of captures of lizards at Pukerua Bay over 22 months from August 1983-May 1985 with captures standardised to number per 100 trap-days.

However, capture rates of the three nocturnal/crepuscular species were significantly related to temperature (Appendix 1). *C. whitakeri* had a significant positive relationship between capture rate and all temperature measures except maximum temperature at 0.2 m depth. Both *C. whitakeri* and *C. aenea* were caught most frequently when night time (minimum) temperatures were high. In contrast, *H. maculatus* had a significant negative relationship

between capture rate and all measures of temperature; more were caught (in summer) when temperatures were low.

Relationship between capture rate and lizard behaviour

Capture rates of lizards can be influenced by territorial behaviour and/or site fidelity. Indications of site fidelity of lizards at Pukerua Bay were obtained by comparing capture frequencies (Table 4) with information on distance between captures (Table 5).

Most lizards (77.4%) were captured only once, with the highest proportion of single captures obtained for *H. maculatus* (91.9%) and the lowest for *O. zelandicum* (69.7%). The proportion of recaptures at the site (trap) of first capture was also highest for *H. maculatus* (82%) and lowest for *O. zelandicum* (56%). However, inclusion of all captures up to 4 m from first capture accounted for 93% of *O. zelandicum* movements. A very small proportion (7%) of *O. zelandicum* undertook long distance movements of up to 56 m (Table 5). This contrasts with *C. aenea*, for which only 75% of captures were within 4 m of the original trap. The remaining 25% of recaptures resulted from movements of up to 64 m, the longest distance recorded for all species.

Despite their large size *C. whitakeri* did not move widely and had the shortest recorded maximum movement (29 m) for any skink species at Pukerua Bay (Table 5).

Relationships between capture rates and habitat characteristics

Distribution of lizard captures over the study quadrat varied by species. Most captures of *O. zelandicum* were at the western end of the grid, other species were more scattered, and *C. whitakeri* and *H. maculatus* were caught too infrequently for any pattern to be determined (Fig. 4). However, it was possible to identify some relationships between

where lizards were caught and the habitat at those sites (Table 6). Each species showed different habitat relationships:

1. *O. n. polychroma*: most common where there were few boulders.
2. *C. aenea*: most common where loam, boulders and stones were abundant.
3. *O. zelandicum*: least common at sites with a high proportion of loam beneath the surface.
4. *C. whitakeri*: most common amongst stones and where there was little subsurface *Muehlenbeckia*.
5. *H. maculatus*: caught most often where there was little subsurface loam, or stones.

Negative relationships for *C. whitakeri* and *H. maculatus*, and the presence of wood (Table 6) were considered trivial because wood was rarely encountered.

Table 4: Summary of capture frequencies for each species over four seasons (December-March, 1983-1987), with percentages in parentheses. Lizard species names are abbreviated as in Table 2.

Captures	Species					Total
	C.a.	C.w.	O.n.p.	O.z.	H.m.	
1x	296 (78.7)	45 (84.9)	433 (75.7)	108 (69.7)	79 (91.9)	961
2x	53 (14.1)	6 (11.3)	81 (14.2)	30 (19.4)	5 (5.8)	175
3x	15 (4.0)	2 (3.8)	20 (3.5)	12 (7.7)	2 (2.3)	51
4x	9 (2.4)	0	13 (2.3)	3 (1.9)	0	25
5x	2 (0.5)	0	12 (2.1)	1 (0.6)	0	15
6x	0	0	7 (1.2)	1 (0.6)	0	8
7x	0	0	3 (0.5)	0	0	3
8x	1 (0.3)	0	2 (0.3)	0	0	3
9x	0	0	1 (0.2)	0	0	1
Total	376	53	572	155	86	1242

Table 5: Proportion (%) of lizards captured two or more times between August 1983 and March 1988 relative to distance from the first point of capture. Lizard species names are abbreviated as in Table 2.

Species	Cumulative % at capture distances (m)			Mean distance moved (m)	Maximum distance moved (m)	Number recaptured
	0	0-2	0-4			
C.a.	71	74	75	6.3	64	276
C.w.	75	80	85	2.4	29	20
O.n.p.	67	77	87	3.4	60	716
O.z.	56	81	93	2.0	56	204
H.m.	82	87	89	2.0	29	82
Total captures						1298

Table 6: Relationship between lizard capture rates and habitat features. Only those features with a significant relationship with lizard capture rate are included.

Species	Variable	Parameter estimate	F value	DF	Probability
<i>O. n. polychroma</i>	Boulders	-1.008	6.299	1,77	0.014
<i>O. zelandicum</i>	Subsurface loam	-0.931	4.888	1,77	0.030
<i>C. aenea</i>	Loam	2.799	92.241	1,75	0.000
	Boulders	2.463	17.170	1,75	0.000
	Stones	1.517	4.048	1,75	0.000
<i>C. whitakeri</i>	Wood	-94.000	13.864	1,75	0.002
	Subsurface <i>Muehlenbeckia</i>	-6.541	8.179	1,75	0.017
	Stones	1.517	4.048	1,75	0.048
<i>H. maculatus</i>	Wood	-151.144	8.121	1,75	0.006
	Stones	-1.336	9.656	1,75	0.003
	Subsurface loam	-3.187	30.570	1,75	0.000

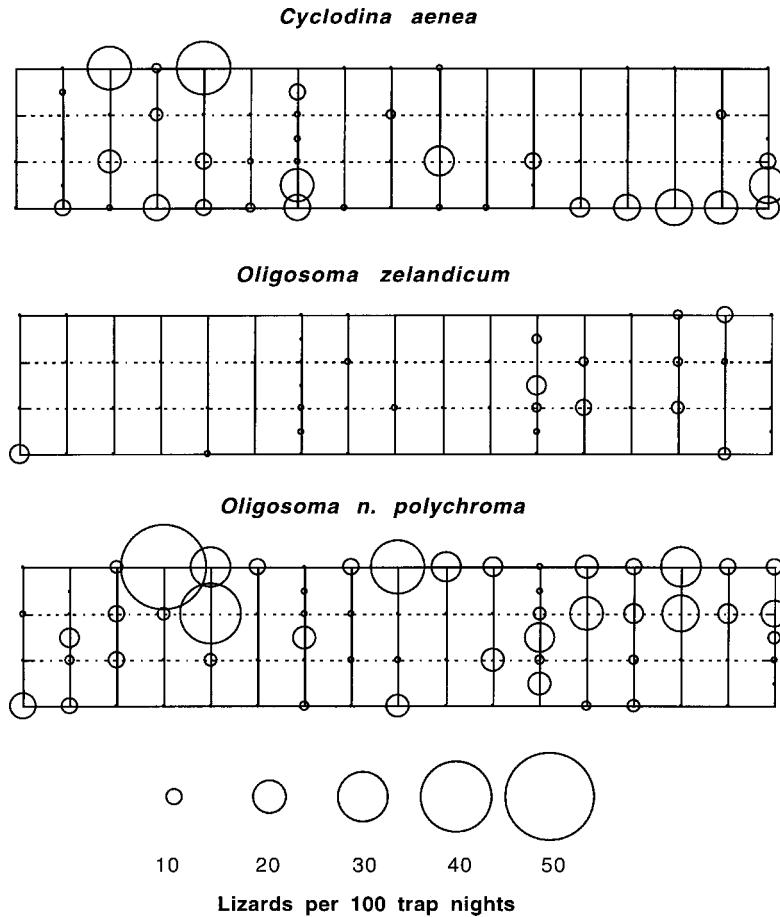


Figure 4: Proportional bubble plots showing frequency of captures by trap site for species with > 10 captures per 100 trap days on the study grid. Grid orientation as in Fig. 2.

Predation on lizards in traps

A few lizards were found dead in traps. Some were probably killed by mice (*Mus musculus*), which characteristically peeled the skin and flesh off the rear third of the lizard (Newman, 1988). Others may have been attacked by rats or mustelids which left chewed lizard fragments in the traps. In most years predation by mice was rare (0.3-1.2% mortality) and the overall death rate of lizards in traps was <5%, but in 1987-1988 mouse predation may have caused up to 7% mortality. Only one *C. whitakeri* was found dead and chewed by mice in traps (1.8% of total captures).

Population estimates

The maximum known age recorded for any of the Pukerua Bay lizards was at least 7 years for a *C. whitakeri*. However, because growth cohorts merge with age (growth rates decline as age increases), size classes used for the MNA could be identified for up to five years for *C. whitakeri* but only for four years for other species (Appendix 2). The minimum size of lizards that were included in the MNA estimates progressively increased from year one to year four. This change accounted for individuals that were born into the populations after year one. The least change of minimum size over time was for *C. aenea*;

few juveniles of this species were caught (Appendix 2). Identification of the size classes thus enabled calculation of the number of animals potentially able to have been caught in year one but not caught until up to year four (or five) (Appendix 2, Table 7).

The percentage of unmarked lizards caught diminished over time for all species except *C. aenea* where the proportion recaptured in year 4 was higher than in years 1-3 and 5 (Table 2). The MNA estimate is based on the assumption that departures from the study areas were offset by arrivals, in which case diminishing eligible size classes for the estimate would be expected. This assumption may have been violated for *C. aenea* because gains appear to have exceeded losses.

The MNA estimate was calculated from an ETA that varied between species depending on the mean distance between captures (Table 5). For *C. whitakeri* the ETA was lower than all other species (945 m²) because none was caught outside the main grid. The total area occupied by *C. whitakeri* at year one was 0.4-0.5 ha, so the population at that time probably comprised at least 260-330 animals.

Discussion

Population estimates

Population estimates are extremely difficult to obtain for lizards because their cryptic nature, territorial behaviour and the unequal catchability of different species (especially in pitfall traps) invalidate some assumptions of mathematical population models (Towns, 1975; 1985; 1991). Pitfall captures of lizards also assume that all species are retained by the traps. This appears true for the skinks, but a negative relationship between temperature and capture rates of *Hoplodactylus maculatus* was probably due to a high proportion of geckos escaping from the traps as temperatures increased (Whitaker, 1982).

At Pukerua Bay, captures were dominated by adults, a bias that increased as species size decreased. For example, adults formed over 90% of the captures of *Cyclodina aenea* and *Oligosoma n. polychroma* (Towns, 1985), yet as the two most abundant species, strong juvenile recruitment might be expected. By comparison, less than 60% of the pitfall captures of the largest species, *C. whitakeri* were adults (Towns, 1985). Such results imply trap avoidance by very small lizards. This could seriously affect population estimates and calculations of ETA if immature lizards were more mobile than adults (e.g., Whitaker, 1982).

Problems of size-related catchability are overcome to some extent by MNA estimates that use data for several years; immature lizards missed early in the sample period are likely to be caught later as adults. However, study periods extended over several years raise problems of how to determine the appropriate number of years and how to account for between-year mortality.

Some of the lizard species present at Pukerua Bay were capable of considerable longevity. Anastasiadis and Whitaker (1987) reported *Hoplodactylus maculatus* in the wild at least 17 years old, and Towns (1994) recorded *C. whitakeri* in the wild at least 12 years old. The validity of the five-year sampling period in the light of such longevity can be determined from an independent study of a translocated population of *C. whitakeri* on Korapuki Island (Towns, 1994). MNA estimates for this population (known to be a maximum of 25 animals in year one) stabilised after six years of sampling (D.R. Towns, *unpubl. data*). The five-year sampling period at Pukerua Bay may thus have slightly underestimated the numbers of *C. whitakeri*, but should have been adequate for the other skink species.

A second, and more difficult problem was mortality and emigration (net loss) between sample periods. Predation in traps (<1.5% in most years) probably over-estimates losses to predators because lizards in traps have no means of escape.

Table 7: Estimates of lizard numbers in year one calculated by MNA over four (all species other than *C. whitakeri*) or five years (*C. whitakeri*). Data used were from December to March each year and effective trapping area (ETA) was estimated separately for each species. Abbreviated lizard names are as for Table 2. ETAs for each species are as follows: *C.a.*: 1644 m²; *C.w.*: 945 m²; *O.n.p.*: 1112 m²; *O.z.*: 975 m²; *H.m.*: 975 m².

Species	Season					Total	Density/ha
	1983/84	1984/85	1985/86	1986/87	1987/88		
<i>C.a.</i>	77	76	139	118		410	2494
<i>C.w.</i>	27	8	13	13	1	62	656
<i>O.n.p.</i>	186	207	102	52		547	4919
<i>O.z.</i>	62	21	40	21		144	1477
<i>H.m.</i>	33	15	8	16		72	738

Furthermore, estimates of predation from fragments in traps cannot account for lizards removed without trace. High site fidelity of *C. whitakeri* recorded at Pukerua Bay and on Korapuki Island (Towns, 1994) suggests density estimates would adequately account for emigration by including mean distance moved between captures over the full study period in the ETA.

Because MNA under estimates population size compared with mathematical models (e.g., Moller and Craig, 1987), and the extent of the under-estimates may be difficult to determine (Krebs, 1966), their utility in population ecology might be questioned. However, when dealing with rare species such as *C. whitakeri*, the use of conservative MNA estimates is less likely to lead to inappropriate conservation management than methods that might over-estimate the population size.

Patterns of vegetation development

During the first four years of study, sheep grazed the Porirua City reserve and the area that later became the Crown reserve. Largest numbers of sheep were usually present in spring, so their grazing suppressed much of the new growth on native shrubs. The most visible changes over this period were further declines in the numbers of surviving karaka trees, suppression of binding vegetation on rocky slopes, and increased mobility of some stony substrates. More tangible changes to the vegetation began as soon as stock were excluded from the two reserves in 1987. These changes included expansion of *Muehlenbeckia* over previously bare areas, extended areas of rank grass, coppicing of karaka trees and the appearance of new karaka seedlings. Individual *Coprosma propinqua* shrubs that were browsed back by stock began expanding. Grazing has not ceased in the reserve because possums (*Trichosurus vulpecula*) and rabbits (*Oryctolagus cuniculus*) are still present.

Without further intervention, vegetation around the study grid is likely to change over the next 10 years as follows:

1. A gradual increase of young karaka trees and the development of a shrubby understorey around the existing karaka grove. The understorey is likely to include *Coprosma* species, kawakawa and possibly an outer fringe of *Urtica ferox*.
2. Increased cover of *Coprosma propinqua* on loam, but with scattered plants of puka, kaikomako, akiraho (*Olearia paniculata*), mahoe and kawakawa overtopping in places.
3. Increasing density of the *Muehlenbeckia* on stones and boulders and loam with much of it scrambling over shrub species.
4. Expansion of salt-resistant species such as taupata (*Coprosma repens*) and ngaio (*Myoporum laetum*) along the beach front.
5. Expansion of weed species such as boneseed into open areas, especially sites along the beach.

Changes in the longer term are more difficult to predict. Eventually the hill side should tend towards a coastal shrubland mosaic with pockets of emergent coastal broadleaf forest on deeper soils and dominated on the lower rocky slopes by karaka.

Effects of vegetation change on lizard habitat use

The succession towards a cover of karaka-mahoe forest merging into coastal broadleaf forest may resemble the original forest composition, but key components of this coastal system are unlikely to return. Missing from these forests are burrowing seabirds, which once must have been common, and elsewhere provide important habitat for species such as *C. whitakeri* (e.g., Macredie, 1984; Southey, 1985; Towns, 1994) and tuatara (*Sphenodon punctatus*) (East *et al.*, 1995 and references therein).

Changes in the extent and type of vegetation cover can have complex effects on the lizards and may also influence distribution of their predators (see below). Potential shifts in the distribution and abundance of lizards at Pukerua Bay will to some extent reflect the lizards' thermal requirements. The two *Cyclodina* skinks and the nocturnal *H. maculatus* rarely bask, and tend to be thigmothermic (obtain heat from warm substrates), whereas the two *Oligosoma* species are heliotherms that bask in open areas and on the surface of tangled vegetation (Gill, 1976; Werner and Whitaker, 1978; East *et al.*, 1995; Towns, *unpubl. data*). Consequently, loss of open sites through increased cover by shrubs may have little effect on *C. whitakeri*, which occupies areas with rocks, crevices and seabird burrows under scrub and forest (Macredie, 1984; Southey, 1985; Towns, 1994), and *C. aenea*, which is found in a wide range of habitats from dry coastal and inland sites, to urban gardens and dense forest (Porter, 1987; Towns, 1994). However, dense shrub and vine cover might reduce the range of suitable sites for *H. maculatus*, which otherwise occupies a wide range of habitats from open areas to forest (Whitaker, 1982; East *et al.*, 1995).

Despite their similar heliothermic habits, vegetation change may have different effects on the two *Oligosoma* species. *O. zelandicum* is often associated with environments that are moist and shaded (including forest areas) (Gill, 1976; A.H. Whitaker, *pers. comm.*; Nelson, N.Z.) and should benefit from increased cover of tall vegetation. *O. n. polychroma* is generally found in open areas, from

coastal rocky strands to native or introduced tall grasslands, and rarely enters forest (Barwick, 1959; Gill, 1976; Patterson, 1992; Newman, 1994; East *et al.*, 1995). Studies of habitat use by *O. n. polychroma* on islands indicate that, unlike *O. zelandicum*, these lizards avoid areas with shady habitats. A positive relationship between grass/herb cover and the frequency of captures of *O. n. polychroma* was recorded on Mana Island (Newman, 1994). Similar results were obtained on Stephens Island, where East *et al.* (1995) predicted a significant reduction in the numbers of *O. n. polychroma* as reforestation progressed. Consequently, increased cover by shrubs and coastal forest are likely to greatly reduce the distribution and abundance of *O. n. polychroma* at Pukerua Bay.

Capture rates of *O. n. polychroma* and *C. aenea* on Mana Island did not increase after the removal of mice despite previous observations of predation by mice on *C. aenea* (Newman, 1988, 1994). In contrast, capture rates of *H. maculatus* increased significantly on Mana Island once mice were removed. This increase was too rapid to be accounted for by increased recruitment (Newman, 1994), but could have been the result of immigration and increased survivorship of young. Both explanations implicate mice as suppressing capture rates of *H. maculatus* through interference of traps, habitat displacement, predation or all three combined. Given the potential for a complex interplay between shifts in vegetation cover and the effects of mice, declines in captures and recaptures of *H. maculatus* after removal of stock from the Pukerua Bay reserves may be attributable to increased predation from mice (or other species), whereas similar declines in capture rates for *O. n. polychroma* may alternatively (or in addition) reflect detrimental effects of increases in shrub cover.

Long term prospects for Whitaker's skink

The MNA estimate for *C. whitakeri* at Pukerua Bay extrapolates to 656 ha⁻¹, which was in the middle of the range estimated by Southey (1985) for the species in the Mercury Islands. However, this assumes equivalent densities of *C. whitakeri* throughout the inhabited area, whereas the estimate obtained at Pukerua Bay was where capture frequencies were highest. Given the restricted availability of suitable habitat (<0.5 ha), the conservative MNA estimate indicates a population of *C. whitakeri* that is vulnerable to the effects of fire and predators. Substantial increases in the number of *C. whitakeri* may be difficult to achieve at Pukerua Bay because they appear to be confined to habitats that minimise the effects of introduced

predators. However, it may be possible to improve the quality of existing habitats and thereby raise their carrying capacity for *C. whitakeri*.

We found an association between the distribution of *C. whitakeri* and the presence of stony substrates, suggesting that, with appropriate revegetation of the more extensive talus slopes of stones, rocks and boulders, the area available to *C. whitakeri* could be more than doubled. Any expansion beyond this may not be possible because of ecological and physiological constraints. However, appropriate vegetation cover around stony areas could provide suitable refuges that would be used periodically while stony slopes act as retreats during adverse conditions. This might have the effect of increasing the density of *C. whitakeri* in existing habitats.

With natural regeneration at Pukerua Bay, three key elements require consideration: habitat quality for lizards; risks from increased predator pressure; and the risk of fire. The most successful regime will be one that increases habitat quality for specified lizard species but not for their predators. The potential for fire and predation were possibly suppressed at Pukerua Bay until 1987 by grazing. However, this had particularly detrimental effects on stony talus areas that lost vegetation cover and were periodically mobilised by stock.

Natural changes after removal of grazing could, by increasing the extent of damp, shady environments, improve the habitat for species such as *C. whitakeri*, *O. zelandicum*, and possibly *C. aenea*. However, there are risks associated with laissez-faire succession. For example, low shrubs and dense *Muehlenbeckia* may rapidly develop and choke up rocky areas before taller, shade producing vegetation becomes established. Very dense, compact vegetation could detrimentally affect some areas occupied by *C. whitakeri*. The proximity of the site to Pukerua Bay township, and the large numbers of visitors, raise the fire risk within the reserve. During early succession, periodic irruptions of mice, such as that reported in 1988, are likely to be associated with proliferations of rank grasses, and could lead to increases in cats and mustelids. Trapping for rodents in the Pukerua Bay reserve during the winter of 1995 revealed no rats, many mice and the presence of weasels (*Mustela nivalis*), one of which contained *C. whitakeri* remains (C. Miskelly, *pers. comm.*; Department of Conservation, Wellington, N.Z.). Weasels are the smallest of the mustelids in New Zealand (King, 1990), and therefore have the greatest ability to penetrate bouldery areas. Reduction of the density of predators may thus hinge on control of the mice, especially if they are important in the diet of weasels.

The most effective solution could be to manipulate the revegetation process so that the effects of predators and potential fire hazards are controlled by passive means. This could be achieved by allowing natural revegetation in some areas and replanting those areas that contribute to mouse population changes (such as rank grass), high fire risk (rank grass and dry twiggy vegetation) and dense scrambling ground cover. If mouse numbers can be depressed by manipulation of the revegetation process, other predators are less likely to be attracted to the area. Lizards should also be less accessible to introduced predators than when the area was grazed because of cover provided by dense vegetation.

Regardless of the potential for management of the Pukerua Bay reserve, two problems will remain. First, *C. whitakeri* are so rare and difficult to trap, they are not a suitable species against which the effectiveness of habitat management can be assessed. More abundant and responsive species, such as *O. zelandicum* or *C. aenea*, may be the most suitable indicators of the effects of changes in the reserve on lizard abundance. Second, because of its location, the reserve can not be managed without risks. Such risks are greatly diminished when *C. whitakeri* are restored to offshore islands from which predators have been removed (Towns, 1988, 1992, 1994). However, the greater potential for establishing large populations of this species on islands should not overshadow the value of the unique community at Pukerua Bay, where, with appropriate management, *C. whitakeri* should remain a key component (Towns, 1992).

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Appendix 1: Poisson regression of lizard captures against maximum-minimum (max, min) temperatures between December and March 1985-1988 at three depths in a rocky scree slope at Pukerua Bay (conventions as in Table 3). Depths were 1 (surface), 2 (0.20 m) and 3 (0.65 m). Levels of significance are denoted as < 0.05 (*), < 0.01 (**), < 0.001 (***)

Species	Temperature measure	Regression coefficient	F	Probability	Significance
<i>O. n. polychroma</i>	Max 1	0.062	2.160	0.149	NS
	Max 2	-0.014	0.091	0.764	NS
	Max 3	0.042	0.837	0.366	NS
	Min 1	0.010	0.090	0.765	NS
	Min 2	0.014	0.188	0.667	NS
	Min 3	0.018	0.226	0.637	NS
<i>O. zelandicum</i>	Max 1	0.064	0.852	0.362	NS
	Max 2	-0.113	2.619	0.113	NS
	Max 3	0.057	0.624	0.434	NS
	Min 1	0.014	0.065	0.800	NS
	Min 2	0.020	0.156	0.695	NS
	Min 3	0.038	0.434	0.513	NS
<i>C. aenea</i>	Max 1	0.119	4.369	0.043	*
	Max 2	-0.016	0.062	0.805	NS
	Max 3	0.122	3.577	0.066	NS
	Min 1	0.116	6.359	0.016	*
	Min 2	0.111	6.565	0.014	*
	Min 3	0.151	9.720	0.003	**
<i>C. whitakeri</i>	Max 1	0.219	8.707	0.005	**
	Max 2	0.107	1.524	0.224	NS
	Max 3	0.269	9.202	0.004	**
	Min 1	0.212	12.396	0.001	***
	Min 2	0.191	11.125	0.002	**
	Min 3	0.232	12.775	0.001	***
<i>H. maculatus</i>	Max 1	-0.258	12.378	0.001	***
	Max 2	-0.168	4.433	0.041	*
	Max 3	-0.261	17.981	0.000	***
	Min 1	-0.171	8.579	0.006	**
	Min 2	-0.162	8.484	0.006	**
	Min 3	-0.184	9.685	0.003	**

Appendix 2: Data used for determining growth patterns. The snout-vent length (SVL, mm) is given for the size range of the data used in calculations of minimum number alive (year one) for each season. Cut-off points for data excluded (i.e., lizards born after year 1) were determined from growth rates of known-age animals.

		1983/84	1984/85	Season 1985/86	1986/87	1987/88
<i>Cyclodina aenea</i>	SVL range	42-57	39-57	42-57	48-57	
	Number	77	76	139	118	
<i>Cyclodina whitakeri</i>	SVL range	50-95	60-100	65-90	75-95	80
	Number	27	8	13	13	1
<i>Oligosoma n. polychroma</i>	SVL range	39-63	42-60	51-63	57-60	
	Number	186	207	102	52	
<i>Oligosoma zelandicum</i>	SVL range	36-66	39-60	48-60	57-60	
	Number	62	21	40	21	
<i>Hoplodactylus maculatus</i>	SVL range	50-65	55-65	60-65	55-65	
	Number	33	15	8	16	