

# Variability in $\delta^{15}\text{N}$ , $\delta^{13}\text{C}$ and Kjeldahl nitrogen of soils from islands with and without seabirds in the Marlborough Sounds, New Zealand

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**Abstract:** Nutrients brought to land by seabirds may provide important subsidies to terrestrial ecosystems. We measured the total Kjeldahl nitrogen (TKN) and carbon and nitrogen isotope ratios of soils from islands with and without seabirds in the Marlborough Sounds, New Zealand, to investigate one means by which seabirds may influence island ecosystem function. Isotope analysis revealed a seabird influence in island soils on the seabird-inhabited islands. However, significant differences in TKN were not related to seabird presence or absence. Pre-existing differences between the islands and high productivity even in the absence of seabirds were concluded to be the reasons for the lack of measurable seabird influence on nitrogen levels.

**Keywords:** islands; seabirds; soils; stable isotope ratios; total Kjeldahl nitrogen.

## Introduction

Large colonies of seabirds nest on islands in the Marlborough Sounds, Cook Strait, New Zealand. These birds may provide a significant marine-derived subsidy that enhances productivity (Daugherty *et al.*, 1990; Markwell and Daugherty, 2002). Marlborough Sounds islands are important sites for research and conservation, and a number of rare species and scientifically important ecosystems are found on them (Millar and Gaze, 1997). It has been suggested that seabirds are important drivers of ecosystem function on these islands (Daugherty *et al.*, 1990).

One means by which seabirds could influence ecosystem function is by the deposition of nitrogen. Plant growth throughout the world is often restricted by the supply of available nitrogen (Lee *et al.*, 1981; Killham, 1994). Nitrogen brought to land by seabirds has been shown to increase plant vigour and influence species composition (Gillham, 1956; Burger *et al.*, 1978; Lee *et al.*, 1981; Warham, 1996), and can lead to effects that ramify through island food webs (Anderson and Polis, 1999). However, guano deposition does not necessarily lead to greater nitrogen availability, as volatilisation of ammonia and other trace gases, increased immobilisation by microbes, and leaching may occur (Huntly and Inouye, 1988; Mulder and Keall, 2001).

Seabird guano is enriched in  $^{15}\text{N}$  relative to  $^{14}\text{N}$ . This is due in part to the high trophic position of seabirds (Anderson and Polis, 1999) and to preferential volatilisation of  $^{14}\text{N}$  from guano (Mizutani *et al.*,

1985). Nitrogen stable isotope ratios can thus be used to provide evidence of a marine input into a site, either currently or historically (Mizutani and Wada, 1988; Mizutani *et al.*, 1991; Hawke *et al.*, 1999). Higher (less negative) carbon stable isotope ratios have also been used as indicators of marine origin of samples (Mizutani and Wada, 1988; Ramsay and Hobson, 1991).

We compare islands with different densities of seabirds and use stable isotope analysis to determine the extent to which marine-derived nutrients brought to land by seabirds are involved in soil formation. We then measure whether this marine influence leads to significant increases in the percentage nitrogen in island soils. Thus, we quantify one component of the importance of seabirds for ecosystem function on Marlborough Sounds islands, and investigate a route whereby marine-derived nutrients subsidise a terrestrial system.

## Methods

We measured total Kjeldahl nitrogen and carbon and nitrogen isotope ratios of soils from five islands in the Marlborough Sounds, Cook Strait, New Zealand (Table 1). Seabirds were found on three of these islands, with the greatest number on Stephens Island (Takapourewa), followed by Titi Island and Nuku-waiata Island. No seabirds were seen on the remaining two, Whakaterepapanui and Maud Island (Table 1). Little blue penguins (*Eudyptula minor*) occur on all islands. Although numbers were not calculated in this study, penguin

**Table 1.** Features of sites in the Marlborough Sounds.

Island	Location <sup>1</sup>	Size (ha) <sup>1</sup>	Seabirds <sup>2</sup> (Total birds/m <sup>2</sup> )
Stephens	40°40'S 174°00'E	150	<i>Pachyptila turtur</i> , <i>Puffinus griseus</i> , <i>P. gavia</i> , <i>Pelecanoides</i> <i>urinatrix</i> (0.46–1.14)
Titi	40°57'S 174°08'E	32	<i>Puffinus griseus</i> , <i>P. carneipes</i> , <i>Pelecanoides</i> <i>urinatrix</i> (0.005)
Nuku-waiata	40°54'S 174°05'E	194	<i>P. griseus</i> (p)
Maud	41°01'S 173°54'E	309	Absent
Whakatere- papanui	40°45'S 174°00'E	61	Absent

<sup>1</sup>Data from (Millar and Gaze, (1997).

<sup>2</sup>A "p" indicates species present but in low densities. Data for Titi Island from Gaze (1982). Data for Nuku-waiata from Walls (1984) and Rufaut (1995). Little blue penguins (*Eudyptula minor*) are found on all islands.

densities appeared similar on all five islands and relatively low in relation to the other seabird species on the "seabird" islands. We collected three soil samples from each of six sites in forest (Table 2) on each island during the austral summer of 1995–1996. Sampling locations were randomly chosen based on grids within the study sites.

On two islands (Stephens Island and Whakatere-papanui) samples were also collected from open, shrubby areas (Table 2) to measure the extent of the variation in soil TKN related to habitat variation. Seabird densities were similar in the two habitats in both cases (Mean birds/m<sup>2</sup> ± 1 SE; Stephens forest 0.6 ± 0.2, Stephens shrubs 0.4 ± 0.1, Whakatere-papanui forest and shrubs 0) (Markwell, 1997, 1999).

Samples were collected from between 5 and 10 cm depth. This level was below the top layer of recently fallen leaf litter, but still above soil largely composed of parent material. The soil samples therefore contained detrital material, but were not dominated by recently fallen leaves. Soil was sealed into plastic bags. All samples were chilled at 4°C within 48 hours of collection.

Soils were hand sorted, then sieved to remove vegetation fragments. Ammonia concentration from Kjeldahl digestion of crushed soil was determined using an ammonia sensitive electrode and an Orion Microprocessor Ionalyzer. Soil samples for isotope analysis were packed in the field into plastic jars that were then filled with ethanol. The ethanol prevented rapid decomposition of organic matter and does not affect isotope analysis of soils (Mizutani and Wada, 1988). Samples were oven dried at 50°C, crushed finely, then sieved to remove large particles and vegetable matter. The resulting powders were sealed in airtight plastic jars. Stable isotope analysis was carried out at the Waikato Stable Isotope Unit, Hamilton, New Zealand. Instrument error during analysis was ± 1‰ for δ<sup>15</sup>N and ± 0.3‰ for δ<sup>13</sup>C.

**Table 2.** Predominant vegetation on five islands in the Marlborough Sounds.

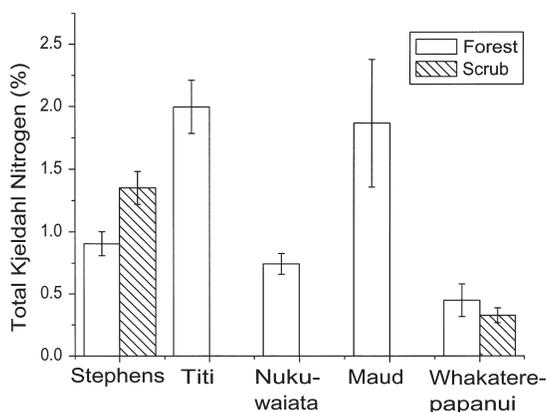
Site	Predominant vegetation
Stephens Island forest	<i>Coprosma repens</i> , <i>Melicytus ramiflorus</i> , <i>Dysoxylum spectabile</i> , <i>Hedycarya arborea</i> . Sparse undergrowth of <i>Macropiper excelsum</i> , <i>Urtica ferox</i> and <i>Solanum nigrum</i>
Stephens Island scrub	<i>Avena sterilis</i> , <i>Lolium perenne</i> and <i>Poa cita</i> interspersed with <i>C. repens</i> , <i>Muehlenbeckia complexa</i> and <i>Hebe urvilleana</i>
Titi Island forest	<i>C. repens</i> , <i>Myoporum laetum</i> , <i>Melicope ternata</i> , <i>D. spectabile</i> , <i>H. arborea</i> , <i>Pseudopanax arboreus</i> , <i>Myrsine australis</i> , <i>Melicytus ramiflorus</i> , <i>Olearia paniculata</i> . Understorey of <i>Macropiper excelsum</i> , <i>Urtica ferox</i> and <i>Asplenium bulbiferum</i>
Nuku-waiata forest	<i>D. spectabile</i> , <i>Melicytus ramiflorus</i> , <i>Rhopalostylis sapida</i> . Understorey of <i>Macropiper excelsum</i> , <i>Asplenium lucidum</i> and other small ferns
Maud Island forest	<i>D. spectabile</i> , <i>Melicytus ramiflorus</i> , <i>H. arborea</i> and <i>Laurelia novae-zelandiae</i> with <i>C. repens</i> on forest margins. Understorey of <i>Macropiper excelsum</i> and ground ferns such as <i>Asplenium bulbiferum</i> and <i>Blechnum filiforme</i>
Whakatere-papanui forest	<i>C. repens</i> , <i>Melicytus ramiflorus</i> , <i>D. spectabile</i> , <i>Hedycarya arborea</i> . Sparse undergrowth of <i>Macropiper excelsum</i> , <i>Urtica ferox</i> and <i>Solanum nigrum</i>
Whakatere-papanui scrub	<i>Avena sterilis</i> , <i>L. perenne</i> , <i>P. cita</i> with patches of <i>Phormium tenax</i> , <i>Pseudopanax arboreus</i> and <i>Cassinia leptophylla</i>

Data from K.T. Grant, M.R. East and C.H. Daugherty (Victoria University of Wellington, Wellington, N.Z. unpubl. data) (Stephens), Cannington, 1982 (Maud), Walls, 1984 (Nuku-waiata), Mazey, 1982 (Titi), and T.J. Markwell (unpubl. data) (Whakatere-papanui).

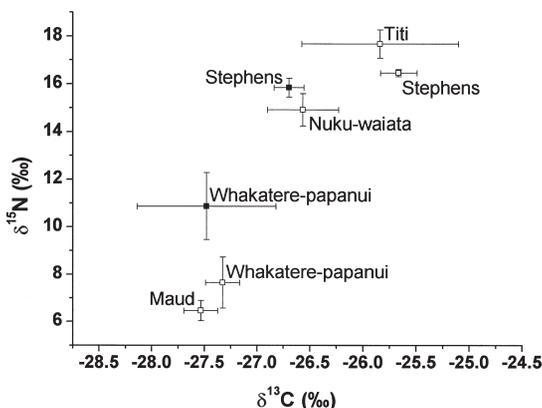
## Results

Data were found to be heteroscedastic, and non-parametric tests were used. Significant differences were found among TKN of forest soils on the different islands ( $H_{[4,57]} = 37.41$ ,  $P < 0.05$ ). Dunn's pairwise comparison revealed that the highest values were found on Titi and Maud Islands. Total Kjeldahl nitrogen of Stephens Island soils was significantly lower than that on Titi Island, but not significantly different from that of Maud, Nuku-waiata and Whakatere-papanui Islands (Fig. 1).

The TKN of soils in scrub on Stephens Island was significantly greater than that in the forest ( $U_{[38]} = 183$ ,



**Figure 1.** Mean ( $\pm 1$  SE) total Kjeldahl nitrogen on islands in the Marlborough Sounds. Open bars represent samples collected in forest; hatched bars represent samples collected in scrub habitat.



**Figure 2.** Mean ( $\pm 1$  SE)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of soils from islands in the Marlborough Sounds. Open symbols represent samples collected in forest; solid symbols represent samples collected in scrub habitat.

$P < 0.05$ ). No significant difference was seen between TKN in forest and scrub on Whakatere-papanui Island ( $U_{[12]} = 46$ ,  $P > 0.05$ ) (Fig. 1). Nitrogen stable isotope ratios of soil differed among the different islands ( $F_{[4,25]} = 106.04$ ,  $P < 0.05$ ). The greatest  $\delta^{15}\text{N}$  concentrations were seen on seabird-inhabited Titi and Stephens Islands. No significant difference was seen between Stephens Island and Nuku-waiata Island. The lowest  $\delta^{15}\text{N}$  concentrations we measured were in samples from Whakatere-papanui and Maud Islands (Fig. 2).

Soil carbon isotope ratios also differed among islands ( $H_{[4,25]} = 13.86$ ,  $P < 0.05$ ). Highest (least negative)  $\delta^{13}\text{C}$  concentrations were found on Titi and Stephens, and lowest on Whakatere-papanui and Maud islands (Fig. 2).

## Discussion

The importance of marine-derived energy and nutrients in coastal and island terrestrial systems is becoming increasingly recognised (Polis *et al.*, 1996; Polis and Hurd, 1996a, b; Anderson and Polis, 1998, 1999; Stapp *et al.*, 1999). At many seabird-inhabited sites around the world guano increases concentrations of soil nitrogen and may enhance plant growth (Hutchinson, 1950; Gillham, 1956; Burger, 1978; Ryan and Watkins, 1989; Anderson and Polis, 1999). On the islands in our study, we found evidence of a measurable marine component in the soil, however, the effects on soil nitrogen were less clear.

Sites unaffected by seabirds have  $\delta^{15}\text{N}$  values between  $-4$  and  $14$  ‰ (Peterson and Fry, 1987), but more usually between  $0$  and  $7$  ‰ (Mizutani *et al.*, 1985; Mizutani *et al.*, 1991; Clay *et al.*, 1997; Anderson and Polis, 1999; Hawke *et al.*, 1999; Hawke, 2001). Significantly higher values (between  $20$  and  $40$  ‰) can be found at sites influenced by seabirds (Mizutani *et al.*, 1985; Mizutani and Wada, 1988; Mizutani *et al.*, 1991; Anderson and Polis, 1999; Stapp *et al.*, 1999). Mean  $\delta^{15}\text{N}$  of soils from seabird-inhabited islands in this study did not reach the extreme values, but were above the range expected for seabird-free sites (Stephens forest,  $16.5$  ‰, Titi  $17.7$  ‰) (Fig. 2). The nitrogen isotopes reveal that island soils have a marine-derived component. It is likely that the nitrogen isotope ratios do not reach the extremes shown in other studies because of significant input from terrestrial sources, diluting the marine effect. The mean  $\delta^{15}\text{N}$  of soil from Whakatere-papanui scrub ( $10.9$  ‰) was above that expected for seabird-free sites, indicating the likely presence of seabird colonies on this island in the past.

Soil  $\delta^{13}\text{C}$  from sites that have not experienced seabirds is likely to be around  $-26$  or  $-27$  ‰ (Peterson and Fry, 1987; Mizutani *et al.*, 1991; Hawke *et al.*,

1999). At sites with a seabird influence, soil  $\delta^{13}\text{C}$  is likely to be closer to  $-23\text{‰}$  (Mizutani *et al.*, 1991; Hawke *et al.*, 1999). The range can be much wider;  $\delta^{13}\text{C}$  values between  $-21$  and  $-27\text{‰}$  have been recorded from seabird colonies at different sites (Mizutani and Wada, 1988). Carbon isotope ratios in our study were within this range. Greatest values were recorded on islands with the highest seabird numbers, and lowest on seabird-free islands (Fig. 2). Mean  $\delta^{13}\text{C}$  of soils from seabird islands were, however, towards the lower (more negative) end of the expected range (Stephens forest,  $-25.6\text{‰}$ , Titi  $-25.8\text{‰}$ ). Although there is evidence of marine-derived carbon input into the soil, there is also a relatively high input of terrestrially-derived carbon.

In spite of the marine input into the soils, current presence or absence of seabirds was not a reliable predictor of soil nitrogen levels. Total Kjeldahl nitrogen of soils on seabird-free Maud Island was not significantly lower than that on seabird-inhabited Stephens and Titi Islands (Fig. 1). Although significant amounts of nitrogen-rich guano are likely to be reaching the seabird-inhabited islands (Burger, 1978; Markwell, 1999; Mulder and Keall, 2001), this does not correspond directly to nitrogen in the soil. Volatilisation of ammonia and other trace gases, and leaching can lead to significant losses of guano-derived nitrogen from a soil (Mulder and Keall, 2001), while differences in nitrogen fixation rate or input of organic material can influence nitrogen content of a soil. Mulder and Keall (2001) found that soil nitrogen availability did not vary predictably with burrow density (and hence seabird abundance) within forest on Stephens Island.

It is likely that nitrogen was not limiting on any of the islands studied. The percent nitrogen was as great as that found on other seabird-influenced sites around the New Zealand coast (Leamy and Blakemore, 1960; Atkinson, 1964) and lower than that found around nests in a gannet colony (Blakemore and Gibbs, 1968).

Although greater than for most grassland soils (e.g. Brevedan *et al.*, 1996), the nitrogen level of soils from Marlborough Sounds islands was well within the range of percent nitrogen in forest soils from around the world (Vitousek *et al.*, 1982; Pastor *et al.*, 1984).

In many cases past work that has shown significant effects of seabirds on soil nitrogen took place at sites with relatively low productivity in the absence of seabirds, e.g. Antarctica (Mizutani and Wada, 1988; Ryan and Watkins, 1989), sub-Antarctic islands (Burger, 1978) or the desert islands of Baja California (Polis and Hurd, 1996b; Anderson and Polis, 1998, 1999; Stapp *et al.*, 1999). Stable isotope analysis shows that although there is marine input into the islands in this study, the soils are still predominantly terrestrially derived. It can be concluded that in the relatively productive islands of the Marlborough

Sounds, the addition of organic nitrogen from litter fall and terrestrial animals is likely to be proportionally greater than that in arid or low productivity areas. Hence the proportional importance of seabirds is likely to be less.

The importance of habitat variation in interpreting the results of this study is emphasised by the intra-island comparisons made. On Stephens Island significant differences were seen both in soil nitrogen levels, and isotope ratios of carbon and nitrogen between two physically adjacent habitats in which seabird numbers were similar. Soil nitrogen,  $\delta^{15}\text{N}$  and nitrogen cycling can be significantly influenced by habitat features such as topography and drainage (Clay *et al.*, 1997; Hawke, 2001). Such pre-existing variation between islands may have accounted for some of the differences (or lack of difference) in soil properties between the islands studied.

The classification of seabird-inhabitation of the different islands in this study is based on present occupation only. Effects of seabirds can be measured in soils for a considerable length of time after seabirds have departed (at least 300–700 years) (Mizutani *et al.*, 1991; Hawke *et al.*, 1999). Vegetation on the different islands has been modified throughout this timeframe (Cannington, 1982; Gaze, 1982; Walls, 1983; East *et al.*, 1995). Introduced predators are also likely to have had significant impact on seabird numbers. Feral cats (*Felis catus*) were present on Stephens Island between ~1895 and ~1925 (Brown, 2000). Polynesian rats (*Rattus exulans*) were present on Titi Island and Nuku-waiata but were eradicated in the 1980s and 1990s. Both Norwegian rats (*R. norvegicus*) and *R. exulans* were present on Whakatere-papanui at the time of sampling (Millar and Gaze, 1997). Historical seabird densities significantly different from those presently seen may be contributing to the trends shown in the soils on different islands.

Seabirds add a range of nutrients to the soil other than nitrogen (Atkinson, 1964; Burger, 1978; Mulder and Keall, 2001). The nitrogen provided by seabirds may not lead to changes in island soils, but other components of guano could still be influencing primary productivity, either positively by the addition of limiting nutrients such as phosphorous, or negatively by reducing soil pH. Further study is necessary to measure these factors, and to determine the importance of other roles played by seabirds, such as trampling of vegetation and digging of burrows.

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## References

- Anderson, W.B.; Polis, G.A. 1998. Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. *Oikos* 81: 75-80.
- Anderson, W.B.; Polis, G.A. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* 118: 324-332.
- Atkinson, I.A.E. 1964. The flora, vegetation and soils of Middle and Green Islands, Mercury Islands Group. *New Zealand Journal of Botany* 2: 385-402.
- Blakemore, L.C.; Gibbs, H. S. 1968. Effects of gannets on soil at Cape Kidnappers, Hawke's Bay. *New Zealand Journal of Science* 11: 54-62.
- Brevedan, R.E.; Busso, C.A.; Montani, T.; Fernandez, O.A. 1996. Production and nitrogen cycling in an ecosystem of *Ergrostis curcula* in semiarid Argentina. II. Nitrogen content and transfers. *Acta Oecologica* 17: 211-233.
- Brown, D. 2000. *Stephens Island: ark of the light*. Derek Brown, Havelock, NZ.
- Burger, A.E. 1978. Terrestrial invertebrates: a food resource for birds at Marion Island. *South African Journal of Antarctic Research* 8: 87-99.
- Burger, A.E.; Lindeboom, H.J.; Williams, A.J. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* 8: 59-70.
- Cannington, W.D. 1982. *Tom Shand Scientific Reserve (Maud Island) management plan*. Department of Lands and Survey, Blenheim, NZ.
- Clay, D.E.; Chang, J.; Clay, S. A.; Ellsbury, M.; Carlson, C.G.; Malo, D.D.; Woodson, D.; DeSutter, T. 1997. Field scale variability of nitrogen and  $\delta^{15}\text{N}$  in soil and plants. *Communications in Soil Science & Plant Analysis* 28: 1513-1527.
- Daugherty, C.H.; Towns, D.R.; Atkinson, I.A.E.; Gibbs, G.W. 1990. The significance of island reserves for restoration. In: Towns, D.R.; Daugherty, C.H.; Atkinson, I.A.E. (Editors), *The ecological restoration of New Zealand islands*, pp. 9-21. Department of Conservation, Wellington, N.Z.
- East, K.T.; East, M.R.; Daugherty, C.H. 1995. Ecological restoration and habitat relations of reptiles on Stephens Island, New Zealand. *New Zealand Journal of Zoology* 22: 249-261.
- Gaze, P.D. 1982. *A visit to Titi Island - Marlborough Sounds. 3-5 November 1982*. Ecology Division, Department of Scientific and Industrial Research, Lower Hutt, NZ.
- Gillham, M.E. 1956. Ecology of the Pembroke islands: V. Manuring by the colonial seabirds and mammals, with a note on seed distribution by gulls. *Journal of Ecology* 44: 429-454.
- Hawke, D.J. 2001. Variability of  $\delta^{15}\text{N}$  in soil and plants at a New Zealand hill country site: correlations with soil chemistry and nutrient inputs. *Australian Journal of Soil Research* 39: 373-383.
- Hawke, D.J.; Holdaway, R.N.; Causer, J.E.; Oden, S. 1999. Soil indicators of pre-European seabird breeding in New Zealand at sites identified by predator deposits. *Australian Journal of Soil Research* 37: 103-113.
- Huntly, N.; Inouye, R. 1988. Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38: 786-793.
- Hutchinson, G.E. 1950. Survey of existing knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion. *Bulletin of the American Museum of Natural History* 96.
- Killham, K. 1994. *Soil ecology*. Cambridge University Press, Cambridge, U.K.
- Leamy, M.L.; Blakemore, L.C. 1960. The peaty soils of the Auckland Islands. *New Zealand Journal of Agricultural Research* 3: 526-546.
- Lee, J.A.; Harmer, R.; Ignaciuk, R. 1981. Nitrogen as a limiting factor in plant communities. In: Lee, J. A.; McNeill, S.; Rorison, I. H. (Editors), *Nitrogen as an ecological factor: 22nd symposium of the British Ecological Society, Oxford 1981*, pp. 95-112. Blackwell Scientific Publications, Oxford, U.K.
- Markwell, T.J. 1997. Using a miniature video camera to study burrow dwelling fairy prions (*Pachyptila turtur*) and tuatara (*Sphenodon punctatus*) on Takapourewa (Stephens Island) New Zealand. *New Zealand Journal of Zoology* 24: 231-237.
- Markwell, T.J. 1999. *Keystone species on New Zealand offshore islands: ecological relationships of seabirds, rats, reptiles and invertebrates on Cook Strait islands*. Ph.D. thesis. Victoria University of Wellington,
- Markwell, T.J.; Daugherty, C.H. 2002. Invertebrate and lizard abundance is greater on seabird-

- inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. *Écoscience* 9: 293-299.
- Mazey, A.D. 1982. *Titi Island Nature Reserve management plan*. Department of Lands and Survey, Blenheim, N.Z.
- Millar, I.; Gaze, P. 1997. *Island management: a strategy for island management in Nelson/Marlborough Conservancy*. Department of Conservation, Nelson, N.Z.
- Mizutani, H.; Kabaya, Y.; Moors, P.J.; Speir, T.W.; Lyon, G.L. 1991. Nitrogen isotope ratios identify deserted seabird colonies. *The Auk* 108: 960-964.
- Mizutani, H.; Kabaya, Y.; Wada, E. 1985. Ammonia volatilisation and high  $^{15}\text{N}/^{14}\text{N}$  ratio in a penguin rookery in Antarctica. *Geochemical Journal* 19: 323-327.
- Mizutani, H.; Wada, E. 1988. Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications. *Ecology* 69: 340-349.
- Mulder, C.P.H.; Keall, S.N. 2001. Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. *Oecologia* 127: 350-360.
- Pastor, J.; Aber, J.D.; McLaugherty, C.A.; Melillo, J.M. 1984. Above-ground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256-268.
- Peterson, B.J.; Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293-320.
- Polis, G.A.; Holt, R.D.; Menge, B.A.; Winemiller, K.O. 1996. Time, space and life history: influences on food webs. In: Polis, G.A.; Winemiller, K.O. (Editors), *Food webs: integration of patterns and dynamics*, pp. 435-460. Chapman & Hall, London, U.K.
- Polis, G.A.; Hurd, S.D. 1996a. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean land interface. In: Polis, G.A.; Winemiller, K.O. (Editors), *Food webs: integration of patterns and dynamics*, pp. 275-285. Chapman & Hall, London, U.K.
- Polis, G.A.; Hurd, S.D. 1996b. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist* 147: 396-423.
- Ramsay, M.A.; Hobson, K.A. 1991. Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. *Oecologia* 86: 598-600.
- Rufaut, C.G. 1995. *A comparative study of the Wellington tree weta, Hemideina crassidens (Blanchard, 1851) in the presence and absence of rodents*. M.Sc. thesis. Victoria University of Wellington, Wellington, N.Z.
- Ryan, P.G.; Watkins, B.P. 1989. The influence of physical factors and orthogenic products on plant and arthropod abundance at an inland nunatak group in Antarctica. *Polar Biology* 10: 151-160.
- Stapp, P.; Polis, G.A.; Pinero, F.S. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. *Nature* 401: 467-469.
- Vitousek, P.M.; Gosz, J.R.; Grier, C.C.; Melillo, J.M.; Reiners, W.A. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological Monographs* 52: 155-177.
- Walls, G.Y. 1983. Activity of the tuatara and its relationships to weather conditions on Stephens island, Cook Strait, with observations on geckos and invertebrates. *New Zealand Journal of Zoology* 10: 309-318.
- Walls, G.Y. 1984. *Scenic and allied reserves of the Marlborough Sounds: a biological survey of the reserves in the Marlborough Land District, north of the Wairau River*. Department of Lands and Survey, Wellington, N.Z.
- Warham, J. 1996. *The behaviour, population biology and physiology of the petrels*. Academic Press, London, U.K.