

Breeding biology of Caspian terns (*Sterna caspia*) at a colony near Invercargill, New Zealand

MAIDA L. BARLOW*

11 Salier Crescent, Mt Stuart 7000, Tasmania, Australia

JOHN E. DOWDING

P.O. Box 36-274, Merivale, Christchurch 8030, New Zealand

jdowding@xtra.co.nz

*Corresponding author

Abstract We studied the breeding biology of a colony of Caspian terns (*Sterna caspia*) near Invercargill, New Zealand, during 1992 and 1993. The mean clutch size did not differ between years and averaged 2.04. Measurements of 147 eggs averaged 64.5 × 44.6 mm; there was no difference in size of A-eggs (1st-laid in a clutch) and B-eggs (2nd-laid) in either year, but the few C-eggs laid were significantly smaller. The incubation period averaged 27.2 days (range 26-29 days); some earlier published values of 20-22 days appear to be in error. In 1992, growth rates of A-chicks were significantly higher than those of B-chicks. Growth rates of A-chicks were significantly higher in 1992 than in 1993. Fledging occurred at 33-39 days at an estimated average mass of 527 g in 1992 and 501 g in 1993. Minimum productivity was 1.04 and 0.62 chicks fledged pair⁻¹ in 1992 and 1993, respectively. Weather during the period of chick growth was much wetter and windier in 1993 and we suggest that this reduced the ability of parents to feed chicks. Investigator disturbance, which has been implicated in lower reproductive success in some studies of Caspian terns, did not appear to have a major impact in our study. We believe this was partly because the birds were habituated to our activities and partly because of our methodology.

Barlow, M.L.; Dowding, J.E. 2002. Breeding biology of Caspian terns (*Sterna caspia*) at a colony near Invercargill, New Zealand. *Notornis* 49(2): 76-90.

Keywords Caspian tern; *Sterna caspia*; breeding biology; colonial nesting; clutch size; incubation time; growth rates; New Zealand

INTRODUCTION

The Caspian tern (*Sterna caspia*) is the largest of the terns (subfamily Sterninae) and is almost cosmopolitan. It is widespread in North America, Europe, Africa, Asia, and Australasia but is absent from the polar regions, from most of South America and the tropical Pacific Ocean, and is relatively uncommon in South-east Asia (Harrison 1983; Higgins & Davies 1996). It is not globally threatened, and the world population is probably about 50,000 pairs (del Hoyo *et al.* 1996). The range of the species appears to have decreased in some parts of Europe (Cramp 1985), while numbers and range have increased in North America (Cuthbert & Wires 1999). Other populations are considered vulnerable (del Hoyo *et al.* 1996). Some authorities (e.g., Harrison 1983) have recognised 2 subspecies, the nominate in the northern hemisphere and Africa, and *S. c. strenua*

in Australasia, but this division is not recognised by the current New Zealand Checklist (Turbott 1990) nor by Higgins & Davies (1996).

Because there are few records from the 18th and 19th century, it was suggested by Sibson (1992) that the Caspian tern may be a relatively recent colonist in New Zealand; however, the species has been recorded from a number of fossil sites in the North and South Islands (Millener 1981; Holdaway *et al.* 2001). Currently, it is widely distributed but the population is concentrated mainly in the northern half of the North Island. It is predominantly coastal but does occur inland, particularly around the central North Island lakes and on braided riverbeds in the South Island (Bull *et al.* 1985; Higgins & Davies 1996). The New Zealand population was estimated to be at most 3500 birds by Challies (1985) and its conservation status was listed as threatened by Bell (1986). A recent survey suggests 1000-1200 breeding pairs and a total population of about 3000 (Brian Bell, pers. comm.); the species is now designated

category O (threatened in New Zealand but secure in other parts of its range) by the New Zealand Department of Conservation (Tisdall 1994).

In most parts of its global range the species may breed either in colonies (often consisting of several hundred pairs) or as solitary pairs (Cramp 1985). At a few localities, breeding in loose colonies has been reported (Urban *et al.* 1986). Nearly all published studies of breeding have been conducted with colonial birds. In northern and southern temperate zones, the species breeds in spring and summer, but in tropical and sub-tropical regions it may breed at different times of the year (e.g., Milon 1950; McLachlan & Liversidge 1963; Urban *et al.* 1986). In northern Australia, there appears to be no fixed breeding season, with eggs recorded in March and May–November (Higgins & Davies 1996). Birds breeding at higher northern latitudes usually migrate to temperate or tropical areas for the winter (Cramp 1985). In New Zealand, birds breeding on the North Island coast tend to stay within 100 km of their breeding sites (Heather & Robertson 1996). Pairs nesting inland on South Island riverbeds move to non-breeding areas on the eastern coast (Pierce 1984). Birds from the Invercargill colony near the southern tip of the South Island move northwards after breeding; most winter on the east coast of the South Island 100–500 km from the colony but a few have been seen as far north as Auckland, 1170 km from the colony (Barlow 1998).

Studies of the breeding biology of Caspian terns have largely been undertaken at colonies in northern Europe and North America (e.g., Bergman 1953; Soikkeli 1973; Fetterolf & Blokpoel 1983). A number of these studies have noted that the species is very sensitive to disturbance—nests have been abandoned and productivity lowered by activities of investigators during data collection (Shugart *et al.* 1978; Fetterolf & Blokpoel 1983; Cuthbert 1988; Schew *et al.* 1994). There do not appear to have been any detailed studies of breeding in the Southern Hemisphere (Higgins & Davies 1996). Tarr (1960) outlined some aspects of breeding in Australia, but his account was based on only 20 nests observed periodically around the country over a period of 10 years. Hockey & Hockey (1980) gave a brief description of breeding during 1 season at a small colony of 15 nests in South Africa. Pierce (1984) recorded hatching success and productivity of isolated pairs breeding on braided rivers or lake shores in Canterbury, New Zealand.

We describe here the breeding biology of Caspian terns at a colony near Invercargill, New Zealand; this was an intensive study in 1992 and 1993, with limited data from other years. The colony is probably the southernmost in the world (see Harrison 1983) and is well-established. Although numbers have fluctuated, Caspian terns have attempted to breed at the

site every season for at least 30 years and possibly since the 1890s (Barlow 1998).

STUDY SITE

The colony is situated on exposed shell banks in the New River Estuary (46°29' S, 168°20' E) near Invercargill, close to the southern tip of mainland New Zealand (Barlow 1998). Terns nest on either or both of 2 shell banks on tidal flats. Both banks are narrow (c. 3 m wide) and low and are surrounded by water from mid- to high tide. They are often washed over during bad weather, resulting in some egg loss in most seasons and loss of small chicks in some seasons. In 1992 the colony nested on the bare outer shell bank; in 1993 it nested on the more vegetated inner shell bank about 600 m to the north-east.

In most years between 1964 and 1986, fewer than 10 pairs of southern black-backed gulls (*Larus dominicanus*) nested on the shell banks near the tern colony. In 1987 the number of gulls rose suddenly to about 50 pairs and again to about 100 pairs in 1988. Gulls harried the terns, and tern eggs and chicks disappeared even when no wash-outs occurred. At our request adult gulls were poisoned by staff of the Department of Conservation (Southland Conservancy) during the 1988 season and we removed the eggs of those that remained. In subsequent years fewer than 10 pairs nested near the terns; we punctured their eggs each year and they deserted. During our study in 1992 and 1993, fewer than 7 pairs of gulls nested on the shell banks each season and all deserted after their eggs were punctured.

Nearly all the Caspian terns breeding at the colony wintered north of Invercargill. The first birds returned in mid-August and numbers increased gradually until mid-October (Barlow 1998). Between 1963 and 1990, the number of breeding pairs varied between 50 and 80. In 1991, there were 70 pairs, but in 1992 only 27 pairs returned. In 1993, 47 pairs returned including some birds that had been absent the previous year. The reasons for the small number of pairs in 1992 are not clear but it is possible that low breeding success in 1991 caused some birds to desert (see Cuthbert 1988).

METHODS

Colony visits

The colony was visited almost daily from the start of egg-laying until the middle of the chick phase, then less frequently during the later stages of chick growth, fledging, and departure. Once the 1st egg had been laid, each nest was labelled by placing a flat numbered stone about 100 mm from the nest rim. Each egg was numbered with a non-toxic waterproof marker. Because of concerns about possible desertion caused by

Table 1 Weather data recorded at Invercargill Airport during the Caspian tern (*Sterna caspia*) breeding season, 1992 and 1993. A = 16-31 October (before and during egg laying), B = 16 November - 15 December (hatching and linear chick growth), and C = 1 October - 31 December (whole breeding season).

	1992			1993		
	A	B	C	A	B	C
Total rainfall (mm)	35.9	105.9	167.8	54.7	173.3	308.2
Number of days with maximum wind gusts ≥ 25 knots (46 km h ⁻¹)	6	5	32	9	17	45
Number of days with maximum wind gusts ≥ 34 knots (63 km h ⁻¹)	1	2	11	7	9	26
Number of days with hail	1	1	5	2	6	10

investigator disturbance (e.g., Penland 1981; Fetterolf & Blokpoel 1983), minimal time was spent in the colony during the first 2 weeks of laying. During the 3rd week, lengths and widths of eggs were measured to 0.1 mm with vernier calipers. Volumes were calculated from the relationship $V = 0.509 LW^2$ (Hoyt 1979). First-, 2nd-, and 3rd-laid eggs in each clutch were designated A-, B-, and C-eggs respectively.

At the beginning of each visit during the hatching and chick phases, all nests with eggs or small chicks or both were quickly covered with hats or weighted towelling squares, running chicks that could be captured were placed in cages (metal frames covered in black shade-cloth left at the site), and crouched chicks were caged. Older chicks could run more quickly and many escaped and hid in clumps of *Spartina townsendii* nearby or swam into deep water. The proportion of chicks captured on each visit varied from about 50-80%, depending on chick age (older chicks ran much faster) and the number of people (1-3) capturing them. Chicks were given a numbered metal band on the tarsus from 3 days of age. Colour bands were added at 12-14 days, when tarsi were long enough to accommodate them. In both years of this study, unique colour combinations were applied to 12 chicks and the remainder were banded with a year colour code. Young chicks were weighed to within 1 g with a 100 g Pesola spring balance; older chicks were weighed to within 5 g with a 500 g or 1 kg balance. When all chicks captured had been weighed, nest covers were removed, chicks in cages were released and we left the colony quickly. By the time we were 100 m away, adults were beginning to return to nests and chicks. The colony was not visited on days of heavy rain. Because nests and cages were covered, data collection continued in light rain but was discontinued if heavy rain began during a visit. There was some evidence that adults became more tolerant of our visits during the season. At the start of the season, adult birds would fly from nests or chicks when we were about 500 m away, but as the season progressed,

this distance reduced progressively to about 100 m and 30-40 m in wet or windy conditions.

Chick growth rates

Because we did not weigh all chicks in the colony on each visit, we could not develop complete growth curves for individual chicks. Growth rates of chicks were therefore calculated as described by Nisbet *et al.* (1995). Linear growth rate (LGR) was the slope of a regression line fitted to mass data during the period of linear growth (taken as 5-22 days for chicks in this study; see Fig. 3). LGR was calculated only for chicks with at least 5 data points during this period. A-chicks and B-chicks are the 1st and 2nd hatched in a brood of 2 or more, respectively. In comparisons of growth rates of A- and B-chicks, B-chicks were excluded from analysis if their sibling A-chick failed to hatch or died early. Asymptotic mass (AM) was the mean of at least 3 data points during the period of near-constant mass (Nisbet *et al.* 1995), which was taken as 25-35 days for chicks in this study.

Measurements are expressed as mean \pm SE_x (range; sample size). Egg measurements and growth rates were normally distributed and means were compared with paired or unpaired 2-tailed *t*-tests as appropriate. Statistical tests were computed using StatView Version 5 (StatView 1998). A probability level of <0.05 was considered significant.

Weather data

Daily weather data recorded at Invercargill Airport (46°25' S, 168°19' E, 7.5 km to the north of the colony site) were provided by the Meteorological Service of New Zealand. In Table 1, rainfall, wind, and days with hail are compared for 3 periods in 1992 and 1993: (a) 16-31 October, the period immediately before and during egg laying, (b) 16 November - 15 December, the period of hatching and linear growth for most chicks, and (c) 1 October - 31 December, which covered almost the entire breeding season. Wind speeds recorded at the Airport almost certainly

under-estimated wind speeds at the colony site, which was much more exposed.

RESULTS

Nests

Nests were simple hollows in the shellbank. Most were lined thinly with dried *Spartina* and occasionally dried seaweed. Most early nests were located on or near the crest of the shellbank, with later nests around or between them. Centre-to-centre distances of a sample of adjacent (nearest-neighbour) nests were measured late in incubation, when all nests were active. The mean inter-nest distance was $0.83 \text{ m} \pm 0.03$ ($0.35\text{--}1.24$; 53), with no significant difference between years (1992, mean = 0.78 ± 0.06 ; 1993, mean = 0.85 ± 0.03 , $t = 1.34$, $df = 51$, $P = 0.19$).

Laying

Dates of clutch initiation in 1992 and 1993 are shown in Fig. 1. Gales with gusts of 45–54 knots ($83\text{--}100 \text{ km h}^{-1}$) were recorded on 4 days between 13 and 20 Oct 1993 and a few first eggs were washed out. In 1992, the 1st egg was laid on 14 Oct; in 1993, the 1st egg found following the gales and wash-out was on 22 Oct. The mean dates of clutch initiation in 1992 ($n = 26$) and 1993 ($n = 40$) were 25 Oct and 1 Nov respectively (median dates 22 Oct and 31 Oct respectively). Dates that first eggs were found in other years at the Invercargill colony are shown in Table 2. Mean date of clutch initiation over 13 years was 14 Oct (median date 15 Oct). In 1992, 1st clutches were laid over a period of 34 days (14 Oct to 16 Nov inclusive) and there were no re-nests. In 1993 observed 1st clutches were laid over a period of 24 days (22 Oct to 14 Nov inclusive) but, as noted above, a few early eggs were washed out and this period is known to be an underestimate. Including nests from the early partial wash-out, the total laying period in 1993 was about 39 days. In other years, particularly when there were major wash-outs, laying at Invercargill was more protracted, lasting 64 and 67 days in 1988 and 1989, respectively (Table 2).

Laying intervals varied from 1–4 days (Table 3), but in most instances (46 of 60), eggs were laid 2 days apart. The average laying interval (A-B and B-C intervals combined) in both years was 2.23 days (53.6 h). Too few C-eggs were laid to allow a statistical comparison of A-B and B-C laying intervals.

Clutch size

The frequency of 1-, 2-, and 3-egg initial clutches did not differ significantly between 1992 and 1993 ($\chi^2 = 0.38$, $df = 2$, $P = 0.83$) and data were pooled. In total, there were 7×1 -egg (9.5%), 56×2 -egg (76.7%) and 10×3 -egg (13.6%) clutches and mean clutch size was 2.04. In 1993, mean clutch size at a newly-formed colony at Lake Ellesmere, 440 km to the

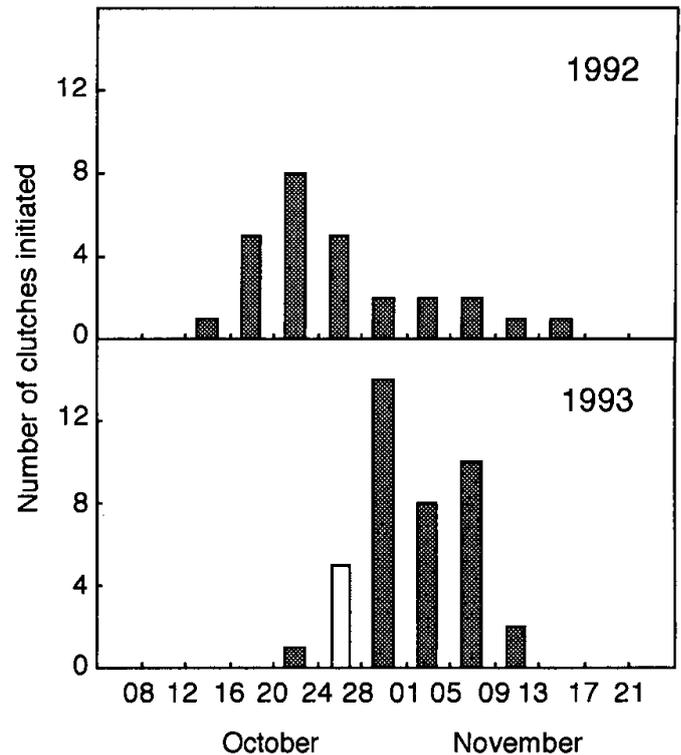


Fig. 1 Clutch-initiation dates of Caspian terns (*Sterna caspia*) at the Invercargill colony in 1992 and 1993, showing the number of 1st eggs laid in each 4-day period. In 1993, the number of clutches initiated during the period 24–27 October (open column) was estimated from hatching dates.

Table 2 Laying dates of 1st and last eggs and numbers of wash-outs at the Invercargill Caspian tern (*Sterna caspia*) colony.

Year	Date of first egg	Date of last egg	Number of wash-outs	
			Major	Minor
1964	4 Oct	9 Dec		
1966	15 Oct			
1967	21 Oct	7 Dec		
1968		4 Dec		
1969	20 Oct			
1972	11 Oct			
1974	17 Oct			
1985	1 Oct			
1986	13 Oct			
1987	23 Oct		1	0
1988	24 Oct	27 Dec	1	2
1989	25 Sep	1 Dec	3	2
1990		17 Dec	0	1
1991		15 Dec	1	2
1992	14 Oct	16 Nov	0	0
1993	22 Oct	21 Nov	0	1

north-east was 2.57 (D. Hadden, pers. comm.), which was significantly higher than at the Invercargill colony ($\chi^2 = 21.0$, $df = 2$, $P = 0.0001$).

Because different studies have reported a wide range of average clutch sizes worldwide, we tested

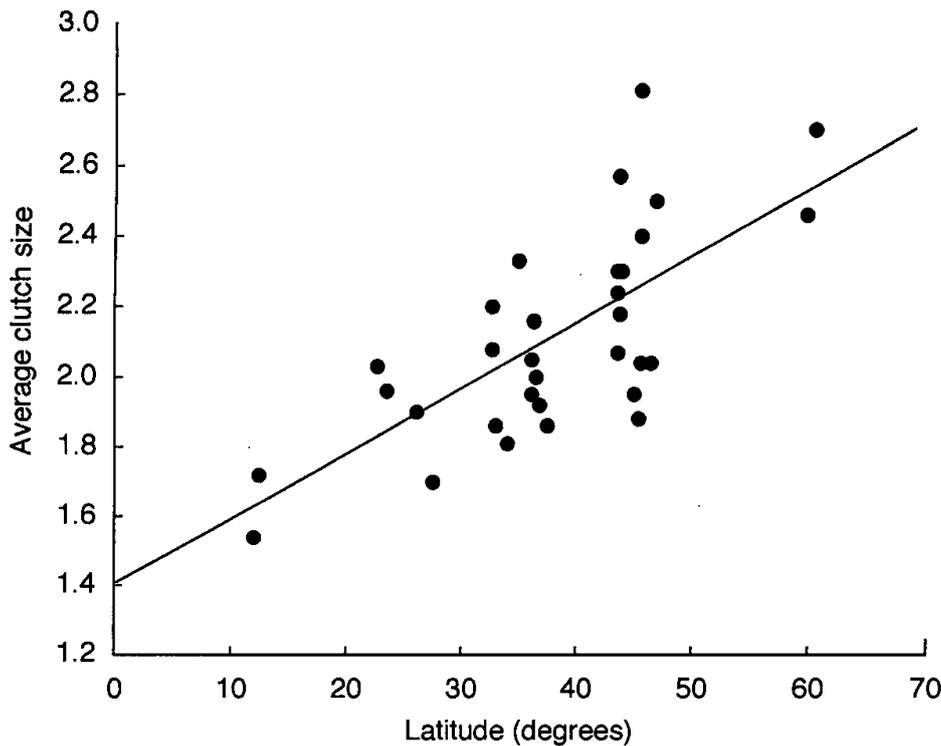


Fig. 2 The correlation between mean clutch size of Caspian terns (*Sterna caspia*) and latitude. For data and sources used see Appendix 1.

Table 3 Laying intervals at the Invercargill Caspian tern (*Sterna caspia*) colony in 1992 and 1993.

Interval (days)	Number of eggs laid	
	1992	1993
1	1	1
2	23	22
3	3	7
4	1	2
Totals	28	32

for a correlation between clutch size and latitude. There was a significant correlation ($r = 0.712$, Fisher's r to z transformation, $Z = 4.80$, $P < 0.0001$), with an increase in average clutch size with increasing latitude (Fig. 2). Data and sources used are shown in Appendix 1.

Egg measurements

A total of 147 eggs was measured. Mean length was 64.47 ± 0.19 mm (range 57.6 – 69.7 mm) and width was 44.57 ± 0.07 mm (range 42.5 – 47.1 mm). Linear dimensions and calculated volumes of A-, B-, and C-eggs in 1992 and 1993 are given in Table 4. There were no significant differences in average length, width, or volume of A- and B-eggs within clutches in 1992 (length: paired $t = 0.04$, $df = 23$, $P = 0.97$; width: paired $t = 1.99$, $df = 23$, $P = 0.06$; volume: paired $t = 1.29$, $df = 23$, $P = 0.21$) or in 1993 (length: paired $t = 1.11$, $df = 40$, $P = 0.27$; width: paired $t = 0.63$, $df = 40$, $P = 0.53$; volume: paired $t = 1.23$, $df = 40$, $P = 0.23$). Pooling data

from all A- and B-eggs within years, there were no between-year differences in average length ($t = 0.33$, $df = 135$, $P = 0.74$) or volume ($t = 1.37$, $df = 135$, $P = 0.17$), but eggs were significantly narrower in 1993 ($t = 2.23$, $df = 135$, $P = 0.03$).

There were too few C-eggs (1992, 3; 1993, 7) to allow meaningful comparisons with A- and B-eggs within years. Pooling data from the 2 years, the 10 C-eggs were on average shorter than A- or B-eggs (A, C: $t = 2.80$, $df = 80$, $P = 0.006$; B, C: $t = 2.14$, $df = 73$, $P = 0.036$), did not differ significantly in width (A, C: $t = 0.97$, $df = 80$, $P = 0.34$; B, C: $t = 1.25$, $df = 73$, $P = 0.22$) and had a lower volume (A, C: $t = 2.46$, $df = 80$, $P = 0.016$; B, C: $t = 2.19$, $df = 73$, $P = 0.032$).

Re-nests

Few data on re-nesting were obtained in 1992 or 1993 because there were no major wash-outs at the colony. In other years between 1964 and 1991, Caspian terns at Invercargill readily re-nested following loss of a clutch. Most birds re-nested if clutches were lost in October or November and a few re-nested if the clutch was lost in early December (Table 2). If wash-outs occurred later than the 2nd week of December, the affected birds normally left the colony. However, in 1988 laying continued exceptionally late, with the last egg being laid on 27 December.

Incubation and hatching

Incubation period (defined as the time between laying and hatching of each egg) was determined for 41 eggs in 1992 and for 63 eggs in 1993. The average incubation time did not differ significantly between

Table 4 Linear measurements and calculated volumes of Caspian tern (*Sterna caspia*) eggs at the Invercargill colony. Means are given \pm SE_x; A-, B- and C-eggs are 1st, 2nd and 3rd laid in a clutch, respectively.

Year	Egg status	Length (mm)	Width (mm)	Volume (ml)	n
1992	A	64.48 \pm 0.42	44.68 \pm 0.18	65.57 \pm 0.76	26
1992	B	64.53 \pm 0.48	44.96 \pm 0.17	66.45 \pm 0.81	24
1992	C	61.20 \pm 0.17	44.33 \pm 0.32	61.24 \pm 1.03	3
1992	A + B	64.51 \pm 0.31	44.82 \pm 0.12	66.00 \pm 0.55	50
1992	All	64.32 \pm 0.32	44.79 \pm 0.12	65.73 \pm 0.55	53
1993	A	64.87 \pm 0.31	44.46 \pm 0.13	65.31 \pm 0.51	46
1993	B	64.38 \pm 0.37	44.46 \pm 0.15	64.81 \pm 0.63	41
1993	C	63.40 \pm 0.88	44.23 \pm 0.25	63.11 \pm 0.76	7
1993	A + B	64.64 \pm 0.24	44.46 \pm 0.10	65.08 \pm 0.40	87
1993	All	64.55 \pm 0.23	44.44 \pm 0.09	64.93 \pm 0.38	94

A- and B-eggs ($t = 0.108$, $df = 92$, $P = 0.914$) or between all eggs in the 2 years ($t = 1.48$, $df = 102$, $P = 0.14$). Combining data from the 2 years, average incubation time was 27.2 ± 0.07 days (range 26-29 days in both years).

The fates of 54 eggs in 1992 and 97 in 1993 are shown in Table 5. The proportion of eggs that hatched did not differ significantly between years (Fisher's Exact test, $P = 0.39$). Combining the 2 years, 81% of eggs laid hatched successfully and 89% of nests hatched 1 or more eggs. The interval between pipping and hatching was determined accurately for 6 eggs, where very early pipping was recorded and recently hatched chicks (still wet) were found. The interval varied from 23-80 h, mean 42.5 h.

The mean hatching interval between A- and B-eggs (1992 and 1993 combined) was 2.21 ± 0.143 days. This was slightly lower than the laying interval (2.28 ± 0.096 days) but the difference was not significant (paired $t = 0.534$, $df = 42$, $P = 0.596$).

Following hatching, chicks remained in the nest for at least 4 days; we recorded only 2 exceptions in 95 observations, when a chick 2 days old and another 3 days old moved a few metres from their nests. These were younger siblings of a 4-day-old and a 5-day-old chick, respectively, and both broods had moved. When the oldest chick in a brood was at least 4 days old, some (but not all) broods left the nest and were found in unlined hollows nearby that we term "brood nests". These were usually just beyond the edge of the original nesting area and were lower on the shell bank and in looser shells. Distances between 11 brood nests and the original nests averaged 5.1 ± 0.91 m (range 1-10 m). Brood nests were larger and deeper than original nests and each brood nest was occupied only by the siblings or individual of a particular brood. Chicks aged 4-10 days were nearly always found in or beside the original nest or the brood nest. From day 14, most

Table 5 Fate of Caspian tern (*Sterna caspia*) eggs at the Invercargill colony in 1992 and 1993.

Fate of eggs	1992	1993	Seasons combined
Disappeared (probably predation)	3	5	8 (5.3%)
Infertile or not incubated	0	4	4 (2.6%)
Failed to hatch (early dead embryo)	4	2	6 (4.0%)
Broken or rolled from nest	0	4	4 (2.6%)
Large chick dead in shell or died hatching	1	6	7 (4.6%)
Hatched alive	46	76	122 (80.8%)
Totals	54	97	151 (100%)

chicks ran from the colony when disturbed. By day 25, most chicks were found in family groups, widely scattered on the tidal flats at mid-low tide. Others were found beside channels or hiding in vegetation. As the tide rose, all moved towards the shellbanks. There was no evidence of creching.

Hatching mass and chick growth

There was no significant difference in hatching masses of all A-chicks and B-chicks (Table 6) in either 1992 ($t = 1.00$, $df = 32$, $P = 0.33$) or 1993 ($t = 0.61$, $df = 54$, $P = 0.54$). There was also no difference in hatching masses of A- and B-chicks within clutches (1992: paired $t = 0.37$, $df = 12$, $P = 0.72$; 1993: paired $t = 0.88$, $df = 19$, $P = 0.39$). Combining A-chicks and B-chicks in each year, the mean hatching mass in 1993 was significantly lower than in 1992 ($t = 3.89$, $df = 88$, $P = 0.0002$). Two C-chicks hatched in 1992; 1 was found dead at day 2 and the other survived to fledging (as did both its siblings). In 1993, 4 C-chicks hatched but none survived beyond 5 days. In 1992,

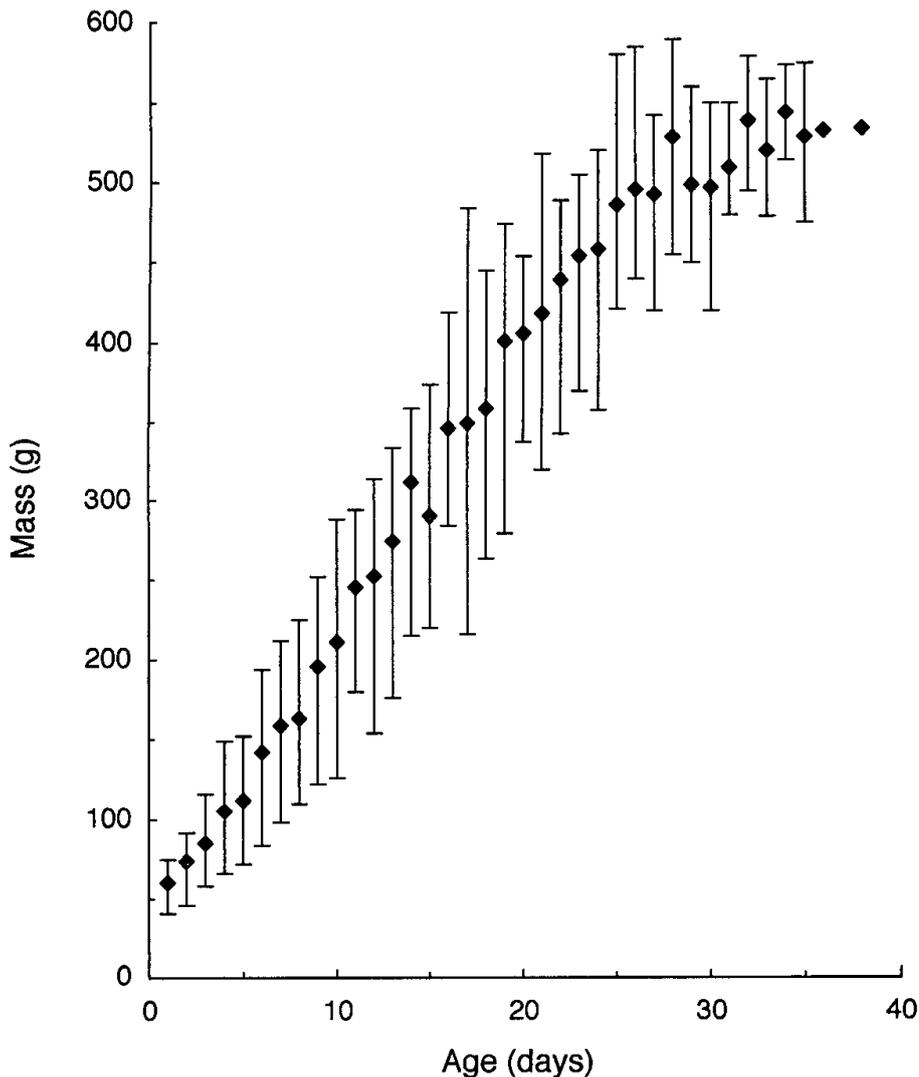


Fig. 3 Growth of Caspian tern (*Sterna caspia*) chicks at the Invercargill colony. Data from A- and B-chicks in both seasons are combined. Vertical bars show the range of values.

Table 6 Hatching masses of Caspian tern (*Sterna caspia*) A-chicks (1st hatched) and B-chicks (2nd hatched) in 1992 and 1993.

Year	Chick status	Mass (\pm SE $_{\bar{x}}$, g)	Range	<i>n</i>
1992	A	52.17 \pm 0.84	48-57	18
1992	B	53.50 \pm 1.05	48-58	16
1992	A + B	52.79 \pm 0.67	48-58	34
1993	A	49.93 \pm 0.63	44-58	28
1993	B	49.32 \pm 0.76	40-55	28
1993	A + B	49.63 \pm 0.49	40-58	56

mean age at death for 10 chicks (A-C chicks combined) was 8.4 ± 1.59 days (range 2-17 days). Eight of the 10 chicks died on or before day 10.

Mean daily masses of chicks (1992 and 1993 combined) are shown in Fig. 3. The average growth rate from hatching to 3 days was 11.7 g day^{-1} . From day 5 to day 22 (the period of "quasi-linear growth" *sensu* Nisbet *et al.* (1995)), mass gain averaged 19.2 g day^{-1} . From days 23-24, the rate of mass gain

Table 7 Mean linear growth rates (g day^{-1}) of individual Caspian tern (*Sterna caspia*) chicks in 1992 and 1993. Too few B-chicks survived in 1993 to allow comparisons.

Year	Chick status	Growth rate ($\bar{x} \pm \text{SE}_{\bar{x}}$)	Range	<i>n</i>
1992	A	20.64 \pm 0.49	18.52 - 25.00	15
1992	B	17.86 \pm 0.80	14.09 - 21.87	11
1993	A	18.37 \pm 0.65	13.73 - 22.32	14

slowed considerably and for days 25-35 it averaged 5.7 g day^{-1} .

Growth rates of individual chicks during the period 5-22 days post-hatching were calculated for A- and B-chicks in 1992 and for A-chicks in 1993 (Table 7). Mean LGR was significantly higher for A-chicks than for B-chicks in 1992 ($t = 3.12$, $df = 24$, $P = 0.005$). In 10 instances in 1992, the LGR of A- and B-chicks from the same brood could be compared. Rates averaged 2.63 g day^{-1} (12.6%) lower in B-chicks and this difference was also significant (paired $t = 2.75$, $df = 9$, $P = 0.023$). Mean

LGR of A-chicks in 1993 was significantly lower than that of A-chicks in 1992 ($t = 2.79$, $df = 27$, $P = 0.0095$). Too few B-chicks survived in 1993 to allow comparisons between A- and B-chicks or between B-chicks in the 2 years.

AM for 9 chicks in 1992 averaged 513.4 g (range 477-551 g). No chicks were weighed 3 times between days 25 and 35 in 1993, so individual AM between years could not be compared. We did, however, estimate average fledging masses from single data points collected between days 30 and 36 (the week before fledging, when masses changed little, see Fig. 3) and compared these between years. In 1992, 26 masses from 18 chicks averaged 526.5 ± 6.40 g (465-579), and in 1993, 11 masses from 11 chicks averaged 500.7 ± 14.22 g (420-575). The difference was nearly significant ($t = 1.92$, $df = 35$, $P = 0.06$). Because few B-chicks reached 30 days, comparisons of AM of A- and B-chicks were not possible.

Fledging period and breeding success

The mean fledging period for 8 chicks (1992, 6; 1993, 2) was 34.6 days (range 33-36 days). However, another chick in 1992 was not quite flying at day 38, and probably fledged on day 39.

The fates of chicks in 1992 and 1993 are compared in Table 8. In both years, some chicks had typical masses when last captured but were not seen after 10-19 days and their fates were not known. Because they were never re-captured in many visits over a 3-4 week period, we believe that most of them died. A few may have fledged. The proportion of chicks known to be dead, for which their fate was unknown and those known to have fledged differed between the two seasons ($\chi^2 = 6.86$, $df = 2$, $P = 0.032$). In 1992, productivity was between 1.04-1.22 chicks fledged pair⁻¹ and in 1993 it was 0.62-0.89 chicks fledged pair⁻¹.

Considering only broods of 2 in which both chicks hatched successfully, we also compared the proportion of A- and B-chicks known to have fledged in the 2 seasons. In 1992, 21 A-chicks hatched and 14 of these were known to have fledged; in 1993, 31 A-chicks hatched and 18 fledged. The proportion of A-chicks known to fledge did not differ significantly between seasons (Fisher's Exact test, $P = 0.57$). In 1992, 21 B-chicks hatched and 10 fledged, while in 1993, 31 B-chicks hatched and only 3 fledged (a significant difference, Fisher's Exact test, $P = 0.003$). The proportion of A- and B-chicks known to fledge within each season did not differ significantly in 1992 (Fisher's Exact test, $P = 0.35$) but did in 1993 (Fisher's Exact test, $P = 0.0001$).

Hatching success did not differ between years, but the average growth rate of chicks and productivity were lower in 1993 than in 1992. Weather data from the 2 years during the period of hatching and

Table 8 Fate of Caspian tern (*Sterna caspia*) chicks at the Invercargill colony in 1992 and 1993.

Fate of chicks	1992	1993
Known to have died before fledging	13	37
Fate unknown	5	13
Known to have fledged	28	29
Totals	46	79

linear chick growth show that this period was wetter and much windier in 1993 than in 1992 (Table 1). When there were periods of high wind, waves caused turbidity in the shallow estuary. In these conditions, and during hail or persistent rain, we noted that few terns attempted to forage in the main body of the estuary. In 1993 there were prolonged storms during hatching and when chicks were small. Between 16 November and 15 December, daily maximum gusts recorded at Invercargill Airport averaged 29 knots (53 km h^{-1}) and were almost certainly higher at the colony. During this period we recorded some adults foraging along sheltered back channels, either on foot or by flying very low and dipping.

DISCUSSION

Colony size and structure

The mean inter-nest distance of 0.83 m was within (but at the lower end of) the range of values reported in other studies of colonial Caspian terns of 0.5-3.0 m (Cramp 1985) or 0.7-4.0 m (del Hoyo *et al.* 1996). It seems likely that inter-nest distances will be influenced by limitations of space at some colonies. At a colony on a narrow island close to water level in South Africa, Hockey & Hockey (1980) recorded an average inter-nest distance of 1.23 m (range 0.65-2.90 m). The site at Invercargill was also narrow and prone to inundation, and the average spacing of 0.83 m is the lowest recorded (Cramp 1985; del Hoyo *et al.* 1996). The minimum distances we recorded (0.35 m in 1992, 0.51 m in 1993) were also below other published minima.

Clutch initiation and laying

There appears to be some variability in the dates that laying begins between years (and possibly colonies) in New Zealand. Pennycook (1949) found eggs at Washdyke Lagoon, South Canterbury, in early September in 1947 and 1948, but Pierce (1984) recorded that October was the main month for nesting (earliest completed clutch on 30 September) of birds breeding on Canterbury riverbeds and lake shores. In nearly all years, peak laying at Invercargill was in October. Only in 1989 were 1st

eggs found in late September. Washdyke Lagoon is 325 km to the north-east of the Invercargill colony and it seems unlikely that the relatively small difference in latitude (2.1°) is responsible for the difference.

The laying interval at the Invercargill colony averaged 2.23 days, which agrees with earlier reports, e.g., 2-3 days (Bergman 1953; Urban *et al.* 1986), 2 days (Tarr 1960), generally every other day (Penland 1981), and 2.3-2.7 days (Quinn, cited in Fetterolf & Blokpoel 1983). These results suggests that the value of "c. 1 day" given by Cramp (1985) is in error.

The total laying period for Caspian terns varies and seems to depend largely on whether (and when) losses occur (e.g., Shugart *et al.* 1978; Cuthbert & Wires 1999; this study). At Invercargill, the total laying varied between 34-67 days, depending on whether there were wash-outs. Some other studies have recorded similar values, such as 43-60 days in Finland (Soikkeli 1973), 57 days at the North American Great Lakes (Ludwig 1965), and about 50 days at Lake Winnipeg, Canada (Vermeer 1972). In the Great Lakes colonies, Cuthbert (1981) recorded a peak laying period for 1st clutches of 26 days and a total period (including replacements) of 86 days. However, initial nests on small skerries in Finland were laid over a period of only 18 days at 1 colony and fewer at another. Bergman (1953) suggested that intense competition for nest sites was the reason for the short laying period.

Clutch size

Variation in clutch size of Caspian terns has been well documented. First clutches vary in average size at different localities (see Appendix 1), replacement clutches are smaller than initial clutches on average (e.g., Shugart *et al.* 1978), and initial clutch size may decline substantially as the laying period progresses (Soikkeli 1973). Differences in food supply have usually been assumed to be responsible for the variation (Soikkeli 1973; Shugart *et al.* 1978), but Bergman (1953) also suggested that development of a 3rd egg may be suppressed in late arrivals at a colony.

It has been noted that average clutch size is greater in northern North America than further south on the same continent (Bent 1921; Mitchell & Custer 1986). del Hoyo *et al.* (1996) included data from Finland and concluded that clutches contain fewer eggs at lower latitudes. Our analysis (Fig. 2, Appendix 1) adds data from Africa and New Zealand. It should be noted that many of the sources used (Appendix 1) lack detail. Some values are known to be from 1st clutches only, while others probably include later clutches. In some instances sample sizes are unknown, in others incomplete clutches could have been included. In spite of these

reservations, there is a clear trend of increasing average clutch size over 10° - 60° of latitude, which includes most of the breeding range of the species. An increase in clutch size with increasing latitude is well-known in many groups of birds (Lack 1954). Seasonal changes in the availability of resources have been suggested as the most important cause of the variation (Ashmole 1963; Ricklefs 1980).

It seems likely that the latitudinal trend will be modified (and partly obscured) by annual fluctuations in food availability at a local level, suggesting that year-to-year variation in clutch size at a given colony is possible, or even likely. There was no difference between average clutch size in 1992 and 1993 at Invercargill, or in 1975 and 1976 at Grays Harbor, Washington (Penland 1981), but Fetterolf & Blokpoel (1983) recorded significant between-year differences in 1979-81 at a recently-established colony at Lake Ontario. However, they offered other explanations (increasing age and experience of the nesters and lower levels of investigator disturbance in 1980-81) for the progressive increase in clutch size. Bergman (1953) showed however, that at well-established colonies in southern Finland the percentage of 3-egg clutches (and presumably therefore the average clutch size) varied considerably between years. The large difference we detected in average clutch size between Invercargill and Lake Ellesmere in 1993 may have reflected local differences in food availability. Ludwig *et al.* (1993) also noted a large change in clutch size with time in the North American Great Lakes colonies. In the 1960s, the mean clutch at 4 colonies over 3 years was 2.68, whereas during the period 1986-1991 it was 2.15.

Although Caspian terns typically lay 1-3 eggs, supernormal clutches of 4-6 eggs incubated by female-female pairs have been reported (Conover 1983). We found no supernormal clutches.

Egg size

The average size of eggs at the Invercargill colony (64.47×44.57 mm) was similar to that of eggs from elsewhere. Bent (1921) gives values of 64.5×45 mm for 48 eggs in the United States National Museum and Bannerman & Lodge (1962) recorded mean dimensions of 64.03×44.46 mm for 100 eggs from Europe.

The relative sizes of A- and B-eggs appear to vary between studies. In our study, there were no differences between A- and B-eggs within years. Mitchell & Custer (1986) also found no difference (but measured only 8 2-egg clutches). In contrast, Quinn & Morris (1986) found that A-eggs were significantly heavier than B-eggs in 2-egg clutches (we did not weigh eggs but their calculated volume should be correlated with fresh mass), and Penland (1981) demonstrated a significant decrease in egg size from egg 1 to egg 3. We measured only 10 C-eggs but they were significantly smaller than A- or B-eggs.

Variations in egg size may be caused by a number of factors. Eggs at Invercargill were narrower in 1993 than in 1992 and hatching masses were significantly lower in 1993. The weather for the period immediately before and during peak laying (16-31 October) was wetter and windier in 1993 than in 1992 (Table 1) and it is possible that reduced food availability may have resulted in smaller eggs. Nisbet (1977) found that in the common tern (*S. hirundo*) larger eggs were laid by females with greater food intake at the time of laying. Nisbet *et al.* (1984) also found that egg mass of common terns increased with age of the parents. However, in Caspian terns Quinn & Morris (1986) noted that the A-egg fraction of total clutch mass increased as total clutch mass increased, and that increased mass of A-eggs was correlated with higher fledging success of A-chicks. They suggested that the smaller 2nd egg was caused not by depletion of resources but that the apportioning of egg mass within a clutch may be partly under the mother's control, and that laying of a smaller 2nd egg enhanced survival of the A-chick and facilitated brood reduction when food was limited. Clearly this situation did not hold at the Invercargill colony, where in each year A- and B-eggs were the same size and hatched chicks of the same mass. In 1993, when food was apparently limiting, the earlier hatching of A-chicks was obviously sufficient to give them an advantage and allow brood reduction. A- and B-eggs being the same size but C-eggs being significantly smaller at Invercargill may have been a result of resource depletion during laying.

Incubation period

Incubation periods reported in the literature vary widely. Many values given are in the range 20-22 days (e.g., Bent 1921; Serventy *et al.* 1971; Challies 1985; Cramp 1985; Higgins & Davies 1996), although primary sources give values from 24-27 days (Fetterolf & Blokpoel 1983; Mitchell & Custer 1986; Schew *et al.* 1994). Dates of first laying and hatching in 1970-72 in Finland (Soikkeli 1973) also suggest incubation periods of 24-27 days. Ludwig (1965) states that incubation is about 26 days and Håkansson (quoted in Bannerman & Lodge 1962) reported a value of c. 25 days at Gotland. The mean incubation time at a colony in Grays Harbor, Washington was 27 ± 0.4 days (Penland 1981). The value of 21 days in Australia (Tarr 1960) was based on a single nest and may not be typical. In both seasons of our study, the incubation period at the Invercargill colony averaged 27 days, with a range of 26-29 days. Most primary sources therefore suggest that incubation lasts 25-29 days and it seems likely that the range of 20-22 days quoted in several texts is incorrect, as also noted by del Hoyo *et al.* (1996), who concluded that earlier reports of 20-21 days were "erroneous".

Caspian terns begin incubation with the laying of the 1st egg (Bergman 1953; Soikkeli 1973) and hatching is therefore asynchronous; 3-egg clutches incubated until the 3rd egg hatches will be incubated about 4-5 days longer than single-egg clutches. Some (but not all) of the variation could therefore result from differences in average clutch size in different studies, but definitions of the incubation period probably also differ, although not recorded in some studies. Mitchell & Custer (1986), for example, distinguished between the incubation and hatching phases and defined the incubation period (which they recorded as 24 days) as being from the day the 1st egg was laid until the day before it pipped. Adding the pip-hatch interval we recorded, results in an incubation period (as we define it) of 26-28 days. By contrast, Ohlendorf *et al.* (1985) defined the incubation period as the day after the last egg was laid to 1 day before the 1st egg hatched.

Hatching and brood nests

Cuthbert & Wires (1999) note that the hatching interval is similar to the laying interval of 2-3 days. However, based on the hatching interval of 1.8 days quoted by Quinn & Morris (1986), they suggest that "possibly ineffective incubation of first-laid eggs may reduce [the] hatching interval". There was no indication of this in our study, in which mean laying and hatching intervals of A- and B-eggs within clutches were not significantly different.

Studies elsewhere suggest that hatching success at a colony can vary widely, depending on such factors as flooding, predation (particularly by gulls *Larus* spp.), and disturbance (e.g., Soikkeli 1973; Shugart *et al.* 1978). Combining results from 1992 and 1993, 89% of nests in our study hatched 1 or more eggs, and 81% of all eggs hatched. However, there were no major wash-outs in either year and we suspect that the values are higher than the long-term average for this colony. In the 5 seasons immediately before our study, there were 6 major and 7 partial wash-outs (Table 2). In the only other New Zealand study in which hatching success was measured, Pierce (1984) found that 28 (76%) of 37 nests of isolated pairs hatched 1 or more eggs. In 4 North American studies, 70-85% of eggs hatched (Cuthbert & Wires 1999) and in 6 Great Lakes colonies in 1991, hatching success varied from 47-85% (Ewins *et al.* 1994).

As far as we are aware, the brood nests that we recorded have not been described before, although Urban *et al.* (1986) record that at Banc d'Arguin, Mauritania, parents make a nest scrape on the ground to shelter young against the sun. Most studies suggest that chicks remain close to the original nest for some time. Fetterolf & Blokpoel (1983) noted that families remained on the original nest site until at least 14 days after hatching began, and Shugart

(cited in Cramp 1985) recorded that if chicks were completely undisturbed, they may remain at the nest until ready to fledge.

We suggest that brood nests may have 2 functions. First, being larger, deeper and lower, they probably provide more space and better shelter for growing chicks than original nests, which were mostly high on the exposed and windswept shell banks. Second, the shell banks at Invercargill were narrow and the original nests were close together. The brood nests may have functioned to spread the colony after hatching, so reducing aggression between adults guarding and feeding chicks. Whether brood nests are a result of the particular circumstances at the Invercargill colony or whether they are used at other colonies remains to be determined.

Cuthbert & Wires (1999) noted that chicks form creches and sought cover as a unit when disturbed. There was no evidence of this behaviour in our study.

Chick growth

The hatching mass of 70 g given by del Hoyo *et al.* (1996) seems very high, in comparison with the range of 40–58 g (means of 52.8 g and 49.6 g in 1992 and 1993, respectively) at Invercargill, which, however, compared favourably with means of 48.8 g and 48.2 g at 2 sites in California (Schew *et al.* 1994).

Peak growth rates in our study of 20.6 and 18.4 g day⁻¹ for A-chicks (1992 and 1993, respectively) were well below the values of 25.7 and 27.4 g day⁻¹ recorded by Schew *et al.* (1994). The only other published study of chick growth rates that we have found presented values derived by regressing chick mass against wing length (Ewins *et al.* 1994). We did not measure wing length and so these data are not directly comparable with ours.

Although hatching masses of A- and B-chicks at Invercargill were not significantly different in 1992, growth rates of A-chicks were significantly higher, which suggests that the different growth rates resulted from differences in food intake during chick growth. Nisbet *et al.* (1995) found growth rates of B-chicks to be lower and more variable than those of A-chicks in roseate terns (*Sterna dougallii*). They found that survival of A-chicks was unaffected by the presence of a younger sibling, and suggested that survival of B-chicks was probably limited by the rate at which the parents could feed the B-chick. In North America, Caspian tern A-chicks were fed more frequently and had higher fledging success than other chicks in the brood (Quinn, cited in Cuthbert & Wires 1999). Nisbet *et al.* (1995) also found that asymptotic mass of roseate tern B-chicks was lower than that of A-chicks. In our study, 2 B-chicks in clutches where the A-chick failed to hatch had high growth rates, which is consistent with competition with A-chicks for food being the main factor limiting growth of B-chicks.

Fledging

In the present study, the fledging period was typically 33–36 days, with 1 bird not fledging until at least 39 days. This is broadly in agreement with most published figures. Urban *et al.* (1986) give the fledging period as 28–35 days; Cramp (1985) gives it as 30–35 days, as do Dement'ev & Gladkov (1951) for birds at Aral Sea and in Turkmenia. Fledging at 5 weeks was recorded on the Nelson boulder bank, New Zealand (Higgins & Davies 1996) and on Gotland, Sweden (G. Håkansson, cited in Bannerman & Lodge 1962). Milon (1950) recorded 37 days in Madagascar. The only study not in agreement is that of Ludwig (1965), who stated that chicks at the North American Great Lakes fledge at 6 to 8 weeks, although he provided no data or reference to support that figure.

AM values of 566 g and 570 g in 2 Californian colonies (Schew *et al.* (1994) are considerably higher than our mean AM of 513 g in 1992 or the estimated fledging masses of 527 g (1992) and 501 g (1993). We did not weigh adults at the Invercargill colony but based on published data it appears that chicks fledged at less than adult mass. Adult masses of Australian Caspian terns vary seasonally. We can find no values for New Zealand birds at the end of the breeding season but the mean mass of Australian adults was 679 g (range 645–725 g) in January (Higgins & Davies 1996). Our estimated mean fledging mass of 519 g (1992 and 1993 combined) suggests that chicks fledged at about 72–80% of adult mass. Schew *et al.* (1994) did not weigh adults at their colonies either, but adult mass in 2 other North American studies averaged 655 g and 623 g (Cuthbert & Wires 1999), which suggests that chicks in Schew *et al.*'s (1994) study also fledged at less than adult mass.

Productivity

Although hatching success was similar in the 2 seasons, in 1993 productivity was lower, growth rates of A-chicks were lower, average fledging mass was lower, and a significantly lower proportion of B-chicks fledged than in 1992. We believe the very windy and wet weather that coincided with hatching and early chick growth in 1993 (Table 1) was an important factor in these differences, reducing the ability of parents to provision chicks. Caspian terns feed almost entirely on fish, detected by sight and caught by shallow plunge-diving (e.g., Cramp 1985; Higgins & Davies 1996). Our observations suggest that their ability to forage efficiently was reduced during windy conditions, when the estuary was turbid and flying was clearly more difficult. Pierce (1980) noted that Caspian terns were less common at Lake Wainono in winter, when the lake was turbid. In 1991, Ewins *et al.* (1994) noted that productivity at Lake Huron colonies was lower than at

Lake Ontario colonies, and that chicks were up to 29% lighter at Lake Huron than at Lake Ontario. They concluded that variations in local feeding conditions and food availability were largely responsible for the differences in reproductive success. At Lake St Lucia, South Africa, low water temperature in 1987 caused high fish mortality, lowered food availability for Caspian terns and abandonment of chicks (Cooper *et al.* 1992). In their study of roseate tern chick growth, Nisbet *et al.* (1995) suggested that differences in survival of B-chicks between colonies and in different years was mainly a reflection of food availability.

Because the fates of some chicks were not known (Table 8), we have quoted a productivity range for each year (see Results). We made many visits to the colony during the late phase of chick growth in both years without re-capturing any of these birds, so we believe that our minimum values for productivity (1.04 and 0.62 chicks fledged pair⁻¹ in 1992 and 1993, respectively) are more accurate. These values are similar to those recorded at North American colonies, where productivity is typically in the range 0.6-1.6 (Ewins *et al.* 1994; Cuthbert & Wires 1999), and at Swartkops Estuary, South Africa, where productivity averaged 0.69 from 1983-1991 (Cooper *et al.* 1992). However, most authors note that productivity can be much lower when predation is heavy or flooding occurs. Cuthbert & Wires (1999) also noted that productivity may vary greatly between years within a colony; at one Lake Michigan colony it ranged from 0.5-1.2 in a 3-year period.

Factors influencing breeding success

Although not classified as threatened worldwide, the Caspian tern is declining in some areas (del Hoyo *et al.* 1996). Apart from chick starvation caused by reduced food availability locally (e.g., Soikkeli 1973; Quinn & Morris 1986; this study), the main factors acting to reduce breeding success are flooding, predation, and disturbance (e.g., Shugart *et al.* 1978; Cooper *et al.* 1992). These factors, singly or in concert, all operate in New Zealand. The colony at Invercargill was low-lying and prone to inundation during periods of high wind and spring tides. Although very few eggs were lost to flooding during our study, many were washed out in the 5 years immediately before the study. Pierce (1984) also recorded flooding of nests on braided riverbeds. Studies elsewhere have recorded or suspected predation of eggs or chicks by mammals, including raccoon (*Procyon lotor*), skunk (*Mephitis mephitis*) and coyote (*Canis latrans*) in North America (Fetterolf & Blokpoel 1983), dog (*C. familiaris*), blackbacked jackal (*C. mesomelas*) and people (*Homo sapiens*) in southern Africa (Clinning 1978), and dingo (*C. familiaris dingo*) and feral house cat (*Felis*

catus) in Australia (Higgins & Davies 1996). We detected little predation (or human disturbance, other than our own activities) at Invercargill, probably because the colony was isolated on tidal flats and surrounded by water much of the time. However, mainland colonies in New Zealand can be affected by introduced mammalian predators; at Mangawhai, time-lapse video recording showed a feral house cat visiting the colony at night and killing chicks (G.R. Parrish, pers. comm.). Predation of eggs and chicks by herring gulls (*Larus argentatus*) and ring-billed gulls (*L. delawarensis*) has been recorded at the North American Great Lakes colonies (Shugart *et al.* 1978; Quinn & Morris 1986), and possibly by kelp (black-backed) gulls (*L. dominicanus*) in Africa (Urban *et al.* 1986). In New Zealand, disturbance of mixed colonies of Caspian terns and red-billed gulls (*L. novaehollandiae*) may result in high levels of predation of tern eggs by the gulls (Soper 1965). Oliver (1955) stated that black-backed gulls prey on eggs and chicks, but there was no evidence of serious impact in Pierce's (1984) study.

Investigator disturbance

Lowered reproductive success caused by investigator disturbance has been reported in some studies of colonial larids, including the Caspian tern (see Götmark 1992 and references therein). Recorded impacts included desertion of nests near a hide and mortality of chicks running out of their parents' territory and being killed by other adults (Penland 1981), lower hatching success and early abandonment of the nesting area by adults with chicks (Fetterolf & Blokpoel 1983), and abandonment of nests resulting from banding (Cuthbert 1988) and cannon-netting (Shugart *et al.* 1978). However, Nisbet (2000) concluded that these and many similar reports "do not withstand critical scientific scrutiny" and that published papers "systematically overstate the adverse effects of human disturbance". He notes that many observations of disturbance impacts are anecdotal or are "inconclusive in the absence of data from undisturbed control sites" (Nisbet 2000). While this may be true, we note that the absence of rigorous proof of negative impacts does not necessarily mean that such effects are not occurring. For this reason, we suggest that researchers in colonies of nesting birds should continue to adopt a precautionary approach and attempt to reduce the potential impacts of their activities where possible. As habituation may occur (see below), this approach may be particularly important in newly-established colonies, in those that have not been studied previously, and in isolated colonies that are rarely disturbed by other human activities.

Nisbet (2000) also noted that many species of colonial waterbirds, including terns (e.g., Nisbet *et*

al. 1995), can become very tolerant of repeated human disturbance. Our study supports that suggestion. Our activities at the Invercargill colony were intensive—visits were daily for much of the season, all nests were marked, all eggs were marked and measured, and all chicks were banded and weighed often—but nests were abandoned rarely (if at all) and hatching success was high in both seasons. We can be less certain about our impact on chick survival, but in 1992 at least 1.04 chicks fledged pair⁻¹ (in 1993, poor weather probably resulted in many chicks starving—see above). During our visits to the colony later in the season, many chicks 14 days and older ran to water and swam to escape (see Results). It is possible that some died as a result, but we believe that few or none actually did; these older chicks were buoyant, swam well and were invariably accompanied by an adult hovering overhead. Overall, we believe that our activities in the colony did not have a markedly negative effect on breeding success. We suggest that there were 2 main reasons for this. First, the methodology we used sought to reduce some problems reported in other studies. In particular, (a) visits were as brief as possible during egg-laying and the early stages of incubation to minimise desertion, and (b) the technique of covering all chicks in nests and caging running chicks as quickly as possible on arrival reduced the potential for chick mortality from other terns or gulls. Similar methods were used by Quinn & Morris (1986), who covered nests to reduce predation of eggs by gulls and fenced their study site to reduce mobility of chicks. At Invercargill, a few black-backed gulls nested nearby during our study, but their eggs were punctured and they deserted (see Study Site); the large gull colonies present in some North American studies (e.g., Penland 1981, Fetterolf & Blokpoel 1983) were therefore absent, and this probably helped to reduce egg and chick mortality when we disturbed the colony. Second, the colony had been visited occasionally in most seasons since 1964, and regularly (for banding of chicks and adults) during the 5 seasons immediately before our study. We believe that as a result of these visits, the birds were partly habituated to our activities. Caspian terns at Invercargill and elsewhere are normally faithful to their breeding sites (Bergman 1953; Staav 1979; Barlow 1998), making long-term habituation possible. As noted above (see Methods) there also appeared to be short-term habituation at Invercargill during each season.

CONCLUSIONS

Caspian terns have been banded in both New Zealand and Australia for many years and there is no evidence to date of any movement between the 2 countries. This suggests that the New Zealand

population may be isolated, and there are not yet sufficient demographic data to determine whether it is self-sustaining. Some estimates of productivity are available (Pierce 1984; this study) but these are insufficient to determine whether the population is stable. Using adult and pre-breeding mortality data, Ludwig (1965) calculated that average productivity of 0.6 young pair⁻¹ year⁻¹ would maintain the Great Lakes population. Productivity at Invercargill was at or above this figure in our study, but local estimates of adult life-expectancy and survival to breeding age are required before it can be assumed that this is adequate to maintain the New Zealand Caspian tern population. These data should preferably be determined at a number of widely separated sites and over a number of seasons. Given the fluctuations that are possible in productivity between years and colonies (see Discussion), further data on breeding success should also be collected at different sites over several years. In the mean time, numbers of breeding pairs and juveniles should be monitored in a sample of the larger colonies around New Zealand annually to provide warning of any decline.

ACKNOWLEDGEMENTS

We particularly thank Gary Morgan for much help with field-work, and Helen Metzger and Roger Sutton, who also helped at times. Helen Metzger provided much-appreciated hospitality and overnight accommodation for MLB on many occasions between September and December 1993. We are grateful to Trust Bank Southland Community Trust Inc. and to the Invercargill Licensing Trust for grants to the Ornithological Society of New Zealand's Southland Branch, used to defray costs of bands, postage, and photocopying. Miller Lange Ltd, Bakers, donated the metal bread-crates we adapted for use as chick-cages. The Meteorological Service of New Zealand Ltd. provided weather data. We thank Brian Bell, Nic Green, Don Hadden, Richard Parrish, Gwenda Pulham, and Michael Taylor for unpublished information, and Ray Pierce and Hugh Robertson (New Zealand Department of Conservation) and Mark Hickson (Canadian Wildlife Service) who supplied copies of some papers. For comments on the draft manuscript we thank Elaine Murphy and two anonymous reviewers, one of whom brought to our attention some useful recent North American literature on Caspian terns.

LITERATURE CITED

- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458-473.
- Bannerman, D.A.; Lodge, G.E. 1962. *The birds of the British Isles, vol. 11*. Edinburgh, Oliver & Boyd.
- Barlow, M.L. 1998. Movements of Caspian terns (*Sterna caspia*) from a colony near Invercargill, New Zealand, and some notes on their behaviour. *Notornis* 45: 193-220.
- Bell, B.D. 1986. Conservation status of New Zealand wildlife. *New Zealand Wildlife Service occasional publication no. 12*. Wellington, Department of Internal Affairs.
- Bent, A.C. 1921. *Life histories of North American gulls and terns*. United States National Museum (1965 reprint) bulletin 113. New York, Dover Publications.

- Bergman, G. 1953. *Verhalten und biologie der Raubseeschwalbe (Hydroprogne tschegrava)*. *Acta Zoologica Fennica* 77: 1-50 [in translation].
- Bull, P.C.; Gaze, P.D.; Robertson, C.J.R. 1985. *The atlas of bird distribution in New Zealand*. Wellington, Ornithological Society of New Zealand.
- Challies, C.N. 1985. Caspian Tern. p. 226 In: Robertson, C.J.R. (ed.) *Reader's Digest complete book of New Zealand birds*. Sydney, Reader's Digest.
- Clinning, C.F. 1978. Breeding of the Caspian tern in South West Africa. *Cormorant* 5: 15-16.
- Conover, M.R. 1983. Female-female pairings in Caspian terns. *Condor* 85: 346-349.
- Cooper J.; Brooke, R.K.; Cyrus, D.P.; Martin, A.P.; Taylor, R.H.; Williams, A.J. 1992. Distribution, population size and conservation of the Caspian tern *Sterna caspia* in southern Africa. *Ostrich* 63: 58-67.
- Cramp, S. (ed.) 1985. *Handbook of the birds of Europe, the Middle East and North Africa. Vol. IV. Terns to woodpeckers*. Oxford, Oxford University Press.
- Cuthbert, F.J. 1981. Caspian tern colonies in the Great Lakes: responses to an unpredictable environment. Unpubl. PhD thesis, University of Minnesota, Minneapolis, U.S.A.
- Cuthbert, F.J. 1988. Reproductive success and colony-site tenacity in Caspian terns. *Auk* 105: 339-344.
- Cuthbert, F.J.; Wires, L.R. 1999. Caspian Tern (*Sterna caspia*). Number 403 in: Poole, A.; Gill, F. (ed.) *The birds of North America*. Philadelphia, Birds of North America.
- Dement'ev, G.P.; Gladkov, N.A. (ed.) 1951. *Birds of the Soviet Union, vol. III*. Jerusalem, Israel Program for Scientific Translations.
- Dunstan, F.M.; Schreiber, R.W.; Dinsmore, J.J. 1975. Caspian terns nesting in Florida, 1973 and 1974. *Florida field naturalist* 3: 16-17.
- Ewins, P.J.; Weseloh, D.V.; Norstrom, R.J.; Legierse, K.; Auman, H.J.; Ludwig, J.P. 1994. Caspian terns on the Great Lakes: organochlorine contamination, reproduction, diet, and population changes, 1972-91. *Canadian Wildlife Service occasional paper no. 85*. Ontario, Environment Canada.
- Fetterolf, P.M.; Blokpoel, H. 1983. Reproductive performance of Caspian terns at a new colony on Lake Ontario, 1979-1981. *Journal of field ornithology* 54: 170-186.
- Götmark, F. 1992. The effects of investigator disturbance on nesting birds. *Current ornithology* 9: 63-104.
- Harrison, P. 1983. *Seabirds - an identification guide*. Beckenham, Croom Helm.
- Heather, B.D.; Robertson, H.A. 1996. *The field guide to the birds of New Zealand*. Auckland, Viking.
- Higgins, P.J.; Davies, S.J.J.F. (ed.) 1996. *Handbook of Australian, New Zealand & Antarctic birds. Vol. 3. Snipe to pigeons*. Melbourne, Oxford University Press.
- Hockey, P.A.R.; Hockey, C.T. 1980. Notes on Caspian terns *Sterna caspia* breeding near the Berg River, southwestern Cape. *Cormorant* 8: 7-10.
- Holdaway, R.N.; Worthy, T.H.; Tennyson, A.J.D. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand journal of zoology* 28: 119-187.
- del Hoyo, J.; Elliott, A.; Sargatal, J. (ed.) 1996. *Handbook of the birds of the world. Vol. 3. Hoatzin to auks*. Barcelona, Lynx Edicions.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96: 73-77.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford, Clarendon Press.
- Ludwig, J.P. 1965. Biology and structure of the Caspian tern (*Hydroprogne caspia*) population of the Great Lakes from 1896-1964. *Bird-banding* 36: 217-233.
- Ludwig, J.P.; Auman, H.J.; Kurita, H.; Ludwig, M.E.; Campbell, L.M.; Giesy, J.P.; Tillitt, D.E.; Jones, P.; Yamashita, N.; Tanabe, S.; Tatsukawa, R. 1993. Caspian tern reproduction in the Saginaw Bay ecosystem following a 100-year flood event. *Journal of Great Lakes research* 19: 96-108.
- McLachlan, G. R.; Liversidge, R. (1963). *Roberts' Birds of South Africa*. Cape Town, Trustees of the South African Bird Book Fund.
- Miller, A.H. 1943. Census of a colony of Caspian terns. *Condor* 45: 220-225.
- Millener, P.R. 1981. The Quaternary avifauna of the North Island, New Zealand. Unpubl. PhD thesis, University of Auckland, Auckland.
- Milon, P. 1950. Quelques observations sur la nidification des sternes dans les eaux de Madagascar. *Ibis* 92: 545-553.
- Mitchell, C.A.; Custer, T.W. 1986. Hatching success of Caspian terns nesting in the lower Laguna Madre, Texas, U.S.A. *Colonial waterbirds* 9: 86-89.
- Nisbet, I.C.T. 1977. Courtship-feeding and clutch-size in common terns. pp. 101-109 In: Stonehouse, B. (ed.) *Evolutionary ecology*. London, Macmillan.
- Nisbet, I.C.T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds* 23: 312-332.
- Nisbet, I.C.T.; Winchell, J.M.; Heise, A.E. 1984. Influence of age on the breeding biology of common terns. *Colonial waterbirds* 7: 117-126.
- Nisbet, I.C.T.; Spendelow, J.A.; Hatfield, J.S. 1995. Variations in growth of roseate tern chicks. *Condor* 97: 335-344.
- Ohlendorf, H.M.; Shaffner, F.C.; Custer, T.W.; Stafford, C.J. 1985. Reproduction and organochlorine contaminants in terns at San Diego Bay. *Colonial waterbirds* 8: 42-53.
- Oliver, W.R.B. 1955. *New Zealand birds, 2nd ed.* Wellington, A.H. & A.W. Reed.
- Penland, S.T. 1981. Natural history of Caspian tern in Grays Harbor, Washington. *Murrelet* 62: 66-72.
- Pennycook, C.S. 1949. Caspian tern colony. *New Zealand bird notes* 3: 129.
- Pierce, R.J. 1980. Seasonal and long-term changes in bird numbers at Lake Wainono. *Notornis* 27: 21-44.
- Pierce, R.J. 1984. Breeding success of isolated pairs of Caspian terns in Canterbury. *Notornis* 31: 185-190.
- Quinn, J.S.; Morris, R.D. 1986. Intraclutch egg-weight apportionment and chick survival in Caspian terns. *Canadian journal of zoology* 64: 2116-2122.
- Ricklefs, R.E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97: 38-49.
- Schew, W.A.; Collins, C.T.; Harvey, T.E. 1994. Growth and breeding biology of Caspian terns (*Sterna caspia*) in two coastal California environments. *Colonial waterbirds* 17: 153-159.
- Serventy, D.L.; Serventy, V.; Warham, J. 1971. *The handbook of Australian sea-birds*. Sydney, A.H. & A.W. Reed.
- Shugart, G.W.; Scharf, W.C.; Cuthbert, F.J. 1978. Status and reproductive success of the Caspian tern (*Sterna caspia*) in the U.S. Great Lakes. *Proceedings of the colonial waterbird group* 2: 146-156.
- Sibson, R.B. 1992. Some thoughts on Caspian terns in New Zealand. *Notornis* 39: 87-93.

- Soikkeli, M. 1973. Breeding success of the Caspian tern in Finland. *Bird-banding* 44: 196-204.
- Soper, M.F. 1965. *More New Zealand bird portraits*. Christchurch, Whitcombe & Tombs.
- Staaav, R. 1979. Dispersal of Caspian terns *Sterna caspia* in the Baltic. *Ornis Fennica* 56: 13-17.
- StatView. 1998. *StatView reference, 2nd ed.* Cary, SAS Institute Inc.
- Tarr, H.E. 1960. Nesting of the Caspian tern. *Australian bird watcher* 1:78-81.
- Tisdall, C. 1994. *Setting priorities for the conservation of New Zealand's threatened plants and animals, 2nd ed.* Wellington, Department of Conservation.
- Turbott, E.G. (Convener) 1990. *Checklist of the birds of New Zealand and the Ross Dependency, Antarctica, 3rd ed.* Auckland, OSNZ & Random Century.
- Urban, E.K.; Fry, C.H.; Keith, S. 1986. *The birds of Africa, vol. II.* London, Academic Press.
- Vermeer, K. 1972. Comparison of the clutch initiation of Caspian and common terns at Lake Winnipeg. *Blue jay* 30: 218-220.

Appendix 1 Data and sources used to establish a correlation between latitude and average size of Caspian tern (*Sterna caspia*) clutches (Fig. 2).

Locality	Latitude	Clutch size	Source
Guinea-Bissau	12.0° N	1.54	Urban <i>et al.</i> (1986)
Northern Madagascar	12.4° S	1.72	Milon (1950)
Swakopmund, S.W. Africa	22.7° S	2.03	Clinning (1978)
Southern Madagascar	23.5° S	1.96	Milon (1950)
Texas, U.S.A.	26.1° N	1.90	Mitchell & Custer (1986)
Florida, U.S.A.	c. 27.5° N	1.70	Dunstan <i>et al.</i> (1975)
San Diego, U.S.A.	32.7° N	2.20	Ohlendorf <i>et al.</i> (1985)
San Diego, U.S.A.	32.7° N	2.08	Kirven, in Cuthbert & Wires (1999)
Berg River, South Africa	33.0° S	1.86	Hockey & Hockey (1980)
Southern California, U.S.A.	c. 34.0° N	1.81	Schew <i>et al.</i> (1994)
North Africa	c. 35.0° N	2.33	Urban <i>et al.</i> (1986)
Mangawhai, N.Z. (1987)	36.1° S	1.95	M.J. Taylor, pers. comm.
Mangawhai, N.Z. (1993)	36.1° S	2.05	G. Pulham, pers. comm.
Kaipara Harbour, N.Z. (1995)	36.3° S	2.16	N. Green, pers. comm.
S. Kaipara Hbr, N.Z. (1987)	36.5° S	2.00	J.E. Dowding, unpubl. data
Central California, U.S.A.	c. 36.8° N	1.92	Schew <i>et al.</i> (1994)
San Francisco, U.S.A.	37.5° N	1.86	Miller (1943)
L. Ontario, Canada (1979)	43.6° N	2.07	Fetterolf & Blokpoel (1983)
L. Ontario, Canada (1980)	43.6° N	2.24	Fetterolf & Blokpoel (1983)
L. Ontario, Canada (1981)	43.6° N	2.30	Fetterolf & Blokpoel (1983)
L. Ellesmere, N.Z.	43.8° S	2.57	D. Hadden, pers. comm.
Mid-south Canterbury, N.Z.	c. 44.0° S	2.30	Pierce (1984)
L. Ontario, Canada (1991)	c. 44.0° N	2.18	Ewins <i>et al.</i> (1994)
L. Huron, Canada	c. 45.0° N	1.95	Ewins <i>et al.</i> (1994)
Northern L. Huron, Canada	45.4° N	1.88	Quinn & Morris (1986)
L. Michigan, U.S.A.	45.6° N	2.04	Ewins <i>et al.</i> (1994)
Great Lakes, U.S.A.	45.7° N	2.40	Shugart <i>et al.</i> (1978)
Great Lakes, U.S.A.	45.7° N	2.81	Ludwig (1965)
Invercargill, N.Z.	46.5° S	2.04	This study
Washington, U.S.A.	47.0° N	2.50	Penland (1981)
West of Helsinki, Finland	60.0° N	2.46	Bergman (1953)
Aland, Finland	60.7° N	2.70	Soikkeli (1973)