Aspects of the biology and ecology of variable oystercatchers (*Haematopus unicolor*) on the east coast of North Auckland, New Zealand

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Abstract: Many aspects of the ecology of the endemic variable oystercatcher (*Haematopus unicolor*) have not been studied in detail. We colour-banded and monitored a population of the species in a study area between 36°S and 37°S on the east coast of the North Island, New Zealand. Monitoring was intensive during the breeding season from 1994/95 to 1998/99, during which time we gathered information on timing of breeding, chick growth, and productivity. We also recorded measurements of adult birds and eggs. Laying of first clutches was protracted and extended from early September to mid-December. Chicks fledged at lower weights than adults and with shorter total head length and wing, but with tarsus and mid-toe within the adult range. Productivity at four core breeding sites within our study area averaged 0.42 chicks fledged per pair per year. Juveniles commonly remained with their parents on their natal territory during their first winter. From 1999, monitoring was less intensive as we continued collecting data on dispersal, age at first breeding, survival, and pair-bond retention. Natal dispersal values ranged from 0–109 km, with most birds breeding within 60 km of their natal site. As with many oystercatcher species, maturity is delayed, and birds in our study area first bred at between 4 and 8 years of age. There was a high level of mate-fidelity, with one pair-bond lasting 16 consecutive years, but divorce was not uncommon. Once established on a territory, adults were highly sedentary. Annual survival rates of adults and pre-breeders were very high, and the local population had the capacity to grow by about 5% per year. Birds breeding at low-lying sites often lost nests to flooding, and this threat is almost certain to be exacerbated by ongoing climate change.

INTRODUCTION

The oystercatchers comprise a cosmopolitan genus (*Haematopus*) of shorebirds found on all continents except Antarctica (Heppleston 1973). Currently, 11 extant species are recognised by most authorities (Clements *et al.* 2023; Gill *et al.* 2023).

The variable oystercatcher (*H. unicolor*, VOC) is one of three oystercatchers endemic to New Zealand. It is found around much of the coastline of the mainland and its off-shore islands, but is sparsely distributed in some regions and is absent from the outlying island groups (Robertson *et al.* 2007). The east coast of the northern North Island has

long been recognised as a major stronghold—there are significant numbers of pairs or individuals present in or near most of the larger east coast estuaries in Northland, Auckland, Coromandel Peninsula, and the Bay of Plenty during both the breeding and non-breeding seasons (Baker 1973a; Sagar *et al.* 1999; Dowding & Moore 2006).

All other oystercatcher species are either pied or all black, while the VOC is polymorphic, with plumage ranging from pied through a series of intermediate ('smudgy') plumages to all black (Dowding 2014). In the past, this caused confusion and resulted in a variety of taxonomic treatments, including the suggestion that intermediate birds were hybrids between pied and black species or subspecies (Oliver 1955). In some treatments, northern birds (pied, intermediate, and black) were named *reischeki*, and the all-black southern birds *unicolor*, treated either as full species (Falla 1939) or as subspecies (Baker 1972;

Heppleston 1973). Since the third edition of the *Checklist of the birds of New Zealand*, all plumage phases of *reischeki*-type birds and *unicolor*-type birds have been included in the single monotypic species *H. unicolor* (Checklist Committee 1990). The plumage phases all inter-breed freely and non-assortatively (Baker 1973b).

The VOC population reached low numbers in the early 20th century, probably in part as a result of birds being shot for food (Baker 1973a; Heather & Robertson 1996). Numbers have increased substantially since the species was afforded legal protection in 1906 (Dowding & Murphy 2001; Miskelly 2014). Some of the possible reasons for the increase were discussed by Dowding (2014). The species is currently classified as 'At Risk (Recovering)' under the New Zealand threat-ranking scheme (Robertson *et al.* 2021) and as 'Least Concern' by BirdLife International (2024). A comparison of national shorebird counts from the period 1983–1994 with counts from the period 2005–2019 suggests that the population continues to grow (Riegen & Sagar 2020). There have been no robust estimates of population size recently; however, projecting from previous estimates and taking into account the rate of increase revealed by the national counts (Riegen & Sagar 2020), there were probably about 6000–7000 individuals in the population in 2024.

The main threats to the species include predation by mammalian and avian predators, loss of nests and small chicks to big tides and storm surges, and disturbance (including crushing of nests) caused by a range of human activities in the coastal zone. The relative importance of these threats is unclear, and probably varies by location (Dowding 2014).

In the late 1960s and early 1970s, Allan Baker gathered information on some aspects of the biology and ecology of VOCs, particularly plumage changes, morphometrics and sexing, the basic features of the breeding cycle, and some aspects of behaviour (Baker 1969, 1972, 1973a, b, 1974a, b). However, his study was predominantly a comparative exercise, aimed at clarifying the systematic status of all New Zealand oystercatchers. It did not focus exclusively on VOCs (and he treated *reischeki* and *unicolor* as separate taxa), and other aspects of their biology have remained largely unstudied (Dowding 2014). Recent studies, all in the South Island, have involved colour-banding or flagging projects in the Dunedin area (Schweigman 2002), at Kaikoura (Rowe 2008, 2011, 2019), and in the Nelson area (Cook *et al.* 2007; Melville *et al.* 2020).

From 1993–2000, we marked birds with individual colour-band combinations in a study area on the North Auckland east coast and monitored them to fill some of the gaps in our knowledge of the species. In this paper we report on measurements of birds and eggs in our study area, timing of breeding, chick growth, productivity, dispersal, age at first breeding, and survival rates. We also comment briefly on current and future threats to the species.

STUDY AREA & METHODS
Study area
The greater study area extended along the North Auckland east coast from Whangarei Harbour in the north to Waitemata Harbour, Auckland, in the south (Figure 1). Within that area, birds were banded, and monitoring was most intensive, at four core sites between 36°S and 37°S at which breeding was known to occur regularly.

The Pakiri River site (36°15′S, 174°44′E) has a low-lying sand-flat around the river mouth, backed by an extensive dune system with varying densities of vegetation, predominantly marram grass (*Ammophila arenaria*). During the period of intensive monitoring (1994/95 to 1998/99), there were usually 6–8 pairs of VOCs nesting at the site. There is a campground immediately behind the nesting

area, which resulted in high levels of disturbance from people, dogs, horses, and quad bikes, particularly from late December to early February.

Omaha Spit (36°20′S, 174°47′E) forms a barrier at the entrance to Whangateau Harbour. The northern part of the spit consists of sand and shell and is stabilised by rock groynes. Low netting fences have been installed to trap sand and reduce erosion. Nearly all VOCs at this site nested on the distal section of the spit, within 700 m of the northern tip. Nesting occurred on the open beach and among the low, partly-vegetated dunes formed by the fences. During the period of intensive monitoring, 7–12 pairs nested on the spit at Omaha. Throughout the study, there was a high-water flock of juveniles and sub-adults at Omaha, typically numbering 20-40 birds. The spit is adjacent to a large inter-tidal area used for feeding by VOCs and a range of other shorebird species. Disturbance levels in the breeding area were moderately high, particularly in summer, due to the presence of a growing subdivision further south on the spit, and from recreational beach-users from further afield.

Tawharanui Regional Park (centred at 36°22′S, 174°50′E) includes a number of sandy beaches and small bays separated by stretches of rocky coastline and cliffs. Oystercatchers bred in a range of habitats; many used sandy beaches and the dunes behind them, others nested on gravel beaches or on grassy paddocks immediately behind beaches. During the period of intensive monitoring, 6–7 pairs of VOCs bred at Tawharanui.

At Wade River mouth (36°39′S, 174°44′E), VOCs nested on a low-lying chenier spit of shell and sand adjacent to a large inter-tidal area used for feeding. Initially, the spit had no vegetation and was isolated from the mainland at high water; as the study progressed, however, there was accretion of sand and gradual encroachment by mangroves (*Avicennia marina*), and the spit became attached to the mainland and progressively vegetated. During the period of intensive monitoring, 3 pairs of VOCs nested on the spit.

At the beginning of our study, all four sites were unmanaged; however, in the 1997/98 season, predator control, signage, fencing of nesting areas, and advocacy began at Omaha Spit. After most of our data had been collected, management was also instituted at Pakiri River (from 2003) and at Tawharanui (from 2004).

Methods
Juveniles and breeding adults were caught on noose-mats and unfledged chicks were caught by hand. Birds were individually colour-banded with a numbered metal band on the left tarsus, and three double wrap-around Darvic colour bands on the right tarsus. In some cases, smaller chicks were given metal bands only, and colour-bands were added later when the tarsus could accommodate three colour bands.

Monitoring was intensive from 1994/95 to 1998/99, while we collected data on clutch initiation and productivity, with the four core breeding sites normally visited at intervals of 2–5 days from late August to February. From 1999/00, visits were made at intervals of 2–4 weeks to continue collecting information on pair-bonds, survival, and dispersal. Data on chick growth were collected opportunistically throughout the study. Sightings and other observations were also provided by shorebird wardens at Omaha Spit, members of the Omaha Shorebird Protection Trust, staff and volunteers at Tawharanui Regional Park, Department of Conservation staff, and volunteer members of the Ornithological Society of New Zealand's (OSNZ) Northland, Auckland, and South Auckland branches.

All adults, eggs, and chicks measured were located between 36°S and 37°S. We measured total head length (tip of the bill to the back of the head, THL), bill length (exposed culmen), tarsus, and mid-toe & claw (MTC) with
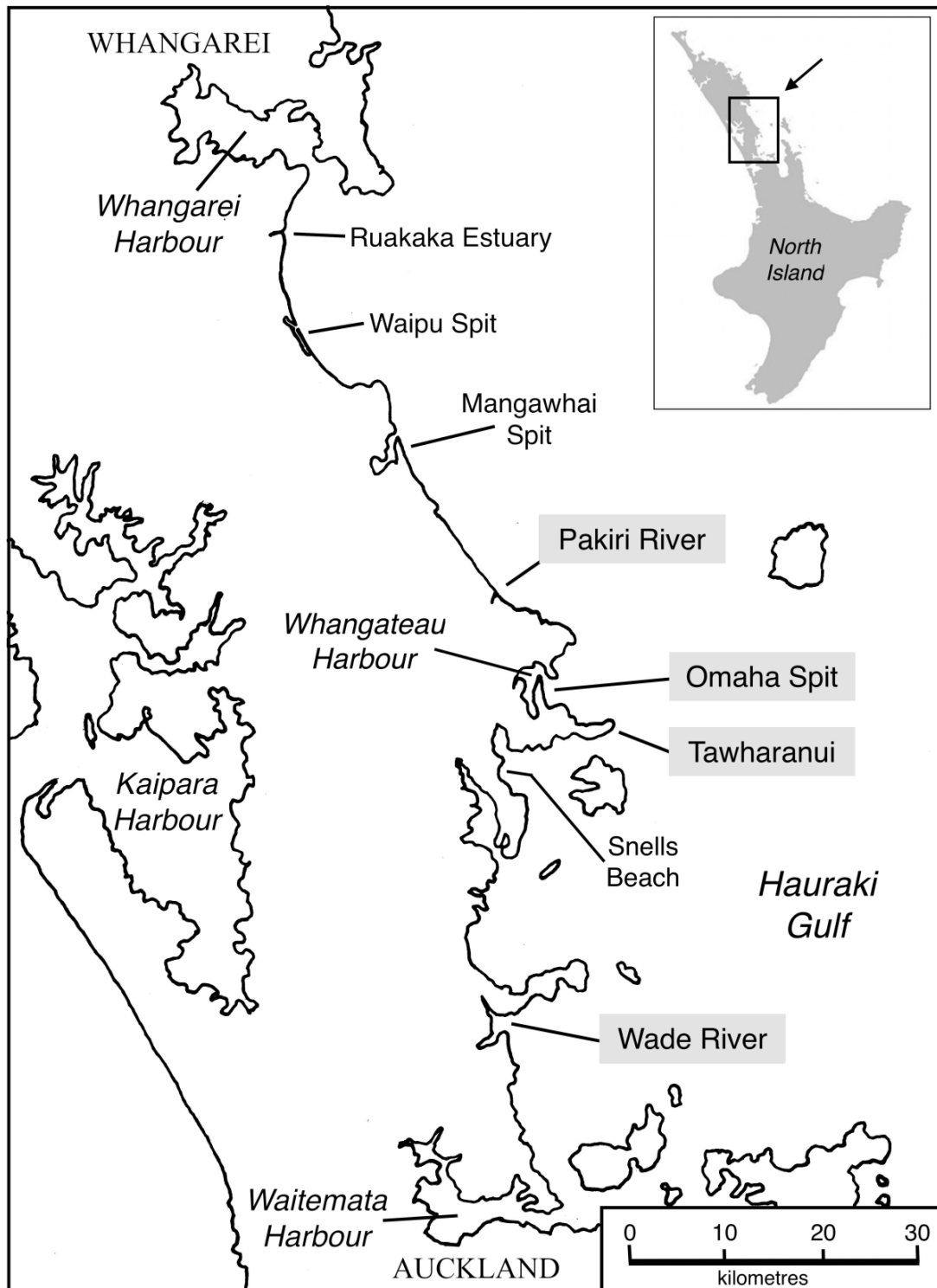
Figure 1. Map of the North Auckland study area showing the four core sites (highlighted) at which variable oystercatchers were banded, and other locations mentioned in the text.

Vernier calipers to the nearest 0.1 mm. Tail length was measured to the nearest 1 mm with calipers, and wing (flattened and straightened) to the nearest 1 mm with a wing ruler. Wing and tail measurements were excluded if the outer primaries or central rectrices respectively were in active moult. Weights of adults were recorded to the nearest 5 g using Pesola scales, and weights of chicks to the nearest 1, 2, or 5 g, depending on age. Weights of adults with incomplete clutches (i.e., birds that could have been gravid) were excluded. To reduce handling time, either during hot weather or when nests or chicks were present,

not all measurements were taken from all birds handled. Chicks were only measured when their exact hatch date was known. Maximum length and width of eggs were measured to the nearest 0.1 mm with Vernier calipers. To calculate egg volume, we used the method of Hoyt (1979) and a volume coefficient (Kv) of 0.500, the value calculated for eggs of the Eurasian oystercatcher (*H. ostralegus*) by Jager *et al*. (2000).

At Pakiri River and Omaha Spit, pairs often nested close to each other and families could sometimes be difficult to identify with certainty. Pairs used to measure productivity

therefore always had at least one bird individually colour-banded ('marked pairs'), and usually both ('banded pairs'). Determining whether chicks had fledged was made easier by the fact that VOC fledglings commonly remain with their parents for weeks or even months after fledging (see Results). In a few cases, where there was doubt about whether a large chick had fledged, the record was omitted. Productivity is therefore defined as the minimum number of chicks fledged per pair per year (CFP).

Definitions of dispersal were those of Greenwood & Harvey (1982). *Natal dispersal* is movement from the natal site to the site of first reproduction, and the subsequent movement of birds between breeding sites is termed *breeding dispersal*. *Effective dispersal* refers to either natal or breeding dispersal that is followed by successful reproduction. All dispersal values were straight-line distances measured to the nearest 1 km on Google Earth Pro. Because dispersal distributions of birds are usually highly skewed towards the origin, medians are a more useful measure of typical distances than means (Greenwood & Harvey 1982), and both are given. There were a number of occasions when birds dispersed to a site but it was not certain they had bred there before they disappeared; those records were omitted.

Occasionally, it was not clear whether an individual was breeding or not (e.g., in some cases eggs could have been laid and lost between visits). Birds were therefore only included in the analysis of age at first breeding if (a) it was certain they were breeding (eggs or chicks were seen), and (b) if we knew their location in recent breeding seasons and knew they had not bred then. These constraints reduced our sample size but resulted in a more accurate estimate of age at first breeding.

Annual survival was determined as Minimum Number Alive by recording the presence or absence of colour-banded individuals in autumn (February to April) each year. In addition to monitoring at the four core sites, dedicated searches were undertaken at other known shorebird breeding and flocking sites between Whangarei and Auckland (including Ruakaka estuary, Waipu Spit, and Mangawhai Spit) between February and April each year. Other observers contributed sightings at other times of year and from outside the greater study area. Adult survival data were collected over a 12-year period from 1994–2005 inclusive. Average adult life-expectancy in years was calculated from annual mortality (m) using the formula (2-m)/2m (Lack 1954). Generation time and the intrinsic capacity for increase (*r*) of the population in our study area were calculated using the Lotka equation (Krebs 1994). The finite rate of increase/decrease (a measure of potential annual change in the population size) λ = e^r (Krebs 1994).

Table 1. Morphometrics of breeding adult variable oystercatchers (sexes combined) in the North Auckland study area. All measurements except weight are in mm. sd = standard deviation of the mean, CV = Coefficient of Variation, n = sample size.

Measurement	Mean	*sd*	CV	Range	n
Bill length	86.3	6.4	7.36	72.7–99.6	98
Total head length	134.4	6.6	4.91	120.6–149.5	99
Tarsus length	60.0	1.9	3.12	54.4–63.7	86
Mid-toe & claw	49.4	1.8	3.56	46.0–53.1	51
Wing	282.3	7.2	2.56	268–305	47
Tail	103.9	3.7	3.58	99–113	18
Weight (g)	724.7	53.6	7.39	598–820	56

RESULTS
Morphometrics
Measurements of known adult birds (sexes combined) are shown in Table 1. We attempted to sex birds using the discriminant function derived by Baker (1974a) but were unsuccessful (see Discussion).

Measurements were made of 98 typical eggs and 2 abnormally small ('runt') eggs. Lengths of normal eggs averaged 59.9 mm (sd = 2.7, range = 54.0–65.6) and width averaged 40.4 mm (sd = 1.1, range = 37.5–42.6). The Coefficient of Variation (CV) was 4.5% for length and 2.7% for width. Elongation (length/width) averaged 1.49 (sd = 0.08, range = 1.31–1.67), and calculated volume averaged 48.8 ml (sd = 3.30, range = 39.2–56.6).

The two runt eggs were both chalky white with a very few small dark brown specks. They were from the same pair at Pakiri River in 1995; one was found on 10 November (later trampled by horses) and one was found in a different nest on 05 December. The second egg was found recently broken in the nest on 21 December and contained no yolk. Neither nest contained any normal eggs. Measurements of the runt eggs were 30.5 x 23.0 and 31.9 x 23.7 mm; the calculated volumes of these eggs were 16.5% and 18.4% respectively of the average volume of a normal egg. Both eggs were seen to be incubated, and the pair performed vigorous distraction displays when the nests were approached. The pair involved laid a clutch of normal eggs in the following breeding season.

Timing of breeding
Initiation dates of first clutches from the four breeding seasons 1994/95 – 1997/98 combined are shown in Figure 2, grouped into 7-day intervals. Of 74 known first clutches of banded or marked pairs, one (1.4%) was initiated in September, 26 (35.1%) in October, 38 (51.4%) in November, and 9 (12.2%) in December. All clutches found after 16 December laid by banded birds were replacement clutches. The 74 first clutches were from all four of our core sites (Pakiri River n = 20, Omaha Spit n = 31, Tawharanui n = 12, and Wade River n = 11). The median week of first-clutch initiation was week 7 (22–28 October) in 1994, 1995, and 1996. In 1997, the median was week 4.5 (04-11 October). This difference was significant (Mann-Whitney 2-tailed, $z = 3.327$, $P = 0.00087$).

Later observations in our study area revealed other clutches initiated in September. During the Department of Conservation's management programme for fairy terns (*Sternula nereis davisae*) at Pakiri River, a VOC nest was found on or about 07 September 2007, a full clutch of 3 eggs was laid between 05 and 12 September 2008, a 1-egg nest was found on 13 September 2008, two nests had hatched by 16 October 2009 (suggesting initiation in mid-September), and a 2-egg nest was laid in the first week of September 2010 (Eliane Lagnaz, Department of Conservation, *pers. comm.*). A clutch of 2 eggs was found at Omaha Spit on 17 September 2003 (Christine Zeiler, *pers. comm.*). Further afield, a brood of two small chicks at Onemana Beach, Coromandel Peninsula (37°09'S, 175°53'E) on 11 October 2002 (W. Hare, *pers. comm.*) indicates laying in early-mid September. The earliest clutch we have on record was at Tawharanui in 2009, when a full clutch of 3 eggs was found on 03 September (Sharon Kast, Tawharanui Open Sanctuary Society Inc., *pers. comm.*); the average interval between eggs in this species is 2 days (Baker 1969), suggesting that in this case clutch initiation occurred during the last few days of August at the latest.

Chick growth
We recorded a total of 48 sets of weights and measurements from 36 different chicks of known hatch dates. The earliest we recorded a chick flying was at age 39 days, but many could be caught by hand until about 43 days; four trapped at ages 45, 47, 48, and 50 days could all fly well enough to avoid capture by hand, suggesting that most chicks in our study area had fledged by about 44 days.
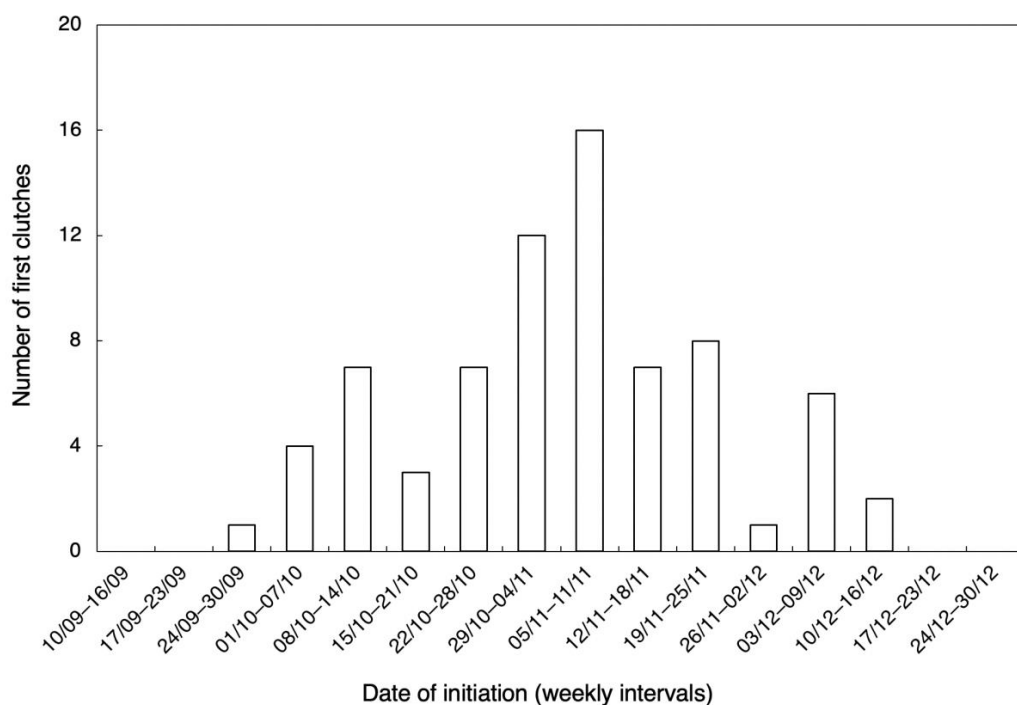
Figure 2. Timing of initiation of 74 first clutches by variable oystercatchers in the North Auckland study area. Results from 1994/95 (n = 12), 1995/96 (n = 23), 1996/97 (n = 23), and 1997/98 (n = 16) are combined and grouped into weekly intervals.

Weight
Chicks changed little in weight for several days following hatching. From 10 days to 43 days (just before fledging) weight gain averaged 12.8 g / day. Growth was most rapid between 10 and 35 days, averaging 15.3 g / day, and it then slowed before fledging occurred (Figure 3). Chicks typically fledged at between 450 and 550 g, or 62–76% of average adult weight.

Total head length
Growth in THL was the one measurement that appeared approximately linear from hatching to 43 days (Figure 4), and it averaged 1.41 mm / day. The highest value for THL that we recorded before fledging was 107.1 mm, about 80%

of the average adult value. Among the four chicks aged 45–50 days that could just fly, THL averaged 104.7 mm, or 78% of the adult average. Of the measurements we took, THL provided the greatest ability to predict age ($R^2 = 0.96$).

Wing
As with weight, there was little change in wing length for about a week after hatching. From 10–43 days (immediately before fledging), wing growth was approximately linear and averaged 5.45 mm / day (Figure 5). The greatest wing length we recorded before fledging was 216 mm, or 77% of the average adult wing length. The four chicks aged 45–50 days that were just capable of sustained flight had wing lengths of 193–220 mm (68–78% of the adult average).
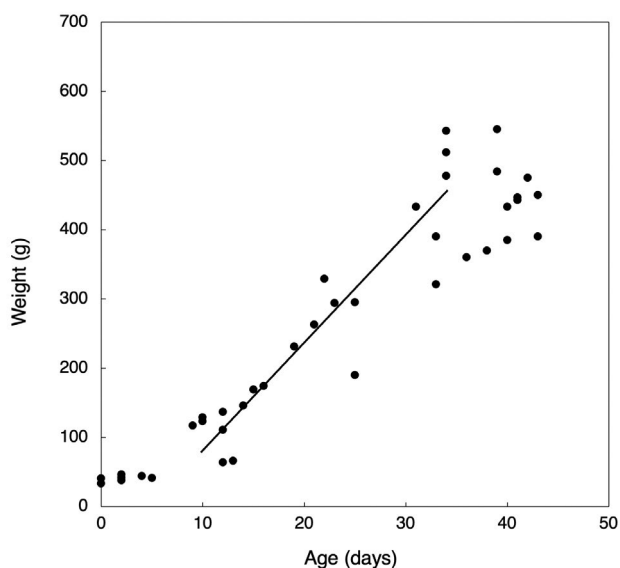

Figure 3. Growth in weight of variable oystercatcher chicks in the North Auckland study area from hatching to fledging. The fitted line shows the approximate period of fastest weight gain between 10 and 35 days.
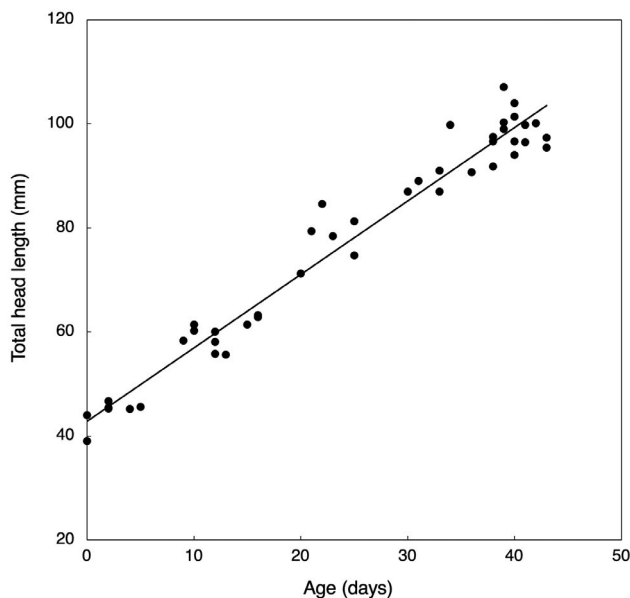

Figure 4. Growth in total head length of variable oystercatcher chicks in the North Auckland study area from hatching to fledging.
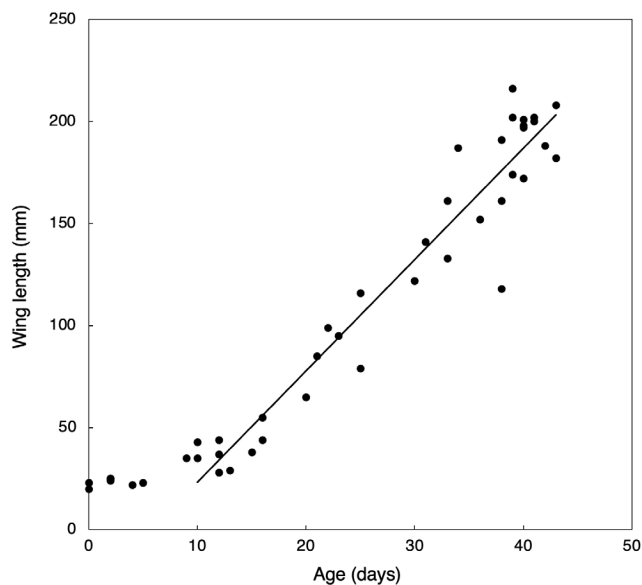
Figure 5. Growth in wing length of variable oystercatcher chicks in the North Auckland study area from hatching to fledging.

Foot growth
The feet are well developed at hatching, with tarsus length 25–30 mm, roughly 40–50% of the average adult value. From hatching to day 25, tarsus growth was approximately linear and averaged 1.0 mm / day. It then slowed markedly and chicks fledged with their tarsus length within the adult range.

Growth of MTC followed a similar pattern. It was 24–28 mm at hatch, about 50–55% of average adult length. From hatching to day 25, MTC growth was roughly linear and increased by an average of 0.75 mm / day. It then slowed substantially, and chicks fledged with MTC also within the adult range.

Variation in sibling weights
We recorded same-day weights of siblings in one 3-chick brood and ten 2-chick broods, and expressed each weight as a percentage of the weight of the heaviest chick in the brood (Table 2). There were a range of differences in sibling weights, but in seven of the ten 2-chick broods, weights were within about 10% of each other. However, we did witness occasional episodes of sibling rivalry, when a larger chick pecked at a smaller sibling or simply pushed it out of the way when a parent approached with food. Some of the intra-brood weight differences we observed may have been the result of sibling rivalry.

Post-fledging
Following fledging, some chicks remained on their natal territory, typically for 1–6 months. During this time, they were defended by their parents, and commonly still begged for food and were fed. At Omaha Spit, almost all chicks had fledged by late February; however, we regularly saw chicks still on their natal territories between March and August. In 2004, three pairs still had a single juvenile each with them on 12 September as the next breeding season approached. In the most extreme case, the pair K-5265 M-KWO and its unbanded mate had a chick that had fledged by 04 February 2002. It was recorded on its natal territory in each month through the winter; it was last seen there on 02 October (8 months after fledging), and by 22 October the parents were incubating a 3-egg clutch. After April, we only ever saw one juvenile with its parents, even when other siblings had fledged.

Table 2. Same-day weights of sibling variable oystercatcher chicks (g) in the North Auckland study area, with each weight also expressed as a percentage of the weight of the heaviest chick in the brood.

Ages (days)	Chick 1	Chick 2	Chick 3
2, 2	42 (100%)	38 (90.5%)	
4, 4	44 (100%)	41 (93.2%)	
13, 12	66 (100%)	64 (97.0%)	
13, 13	137 (100%)	111 (81.0%)	
21, 21	241 (100%)	216 (89.6%)	
21, 22	329 (100%)	263 (79.9%)	
25, 25, 23	295 (100%)	190 (64.4%)	164 (55.6%)
39, 38	446 (100%)	412 (92.4%)	
39, 40	543 (100%)	512 (94.3%)	
45, 45	505 (100%)	495 (98.0%)	
Unknown	403 (100%)	279 (69.2%)	

Table 3. Productivity (minimum number of chicks fledged per pair per year) of variable oystercatcher pairs breeding at the four core sites in the North Auckland study area.

Site (breeding seasons)	Chicks fledged	Pair-years	Average productivity
Pakiri River (1995/96–1998/99)	7	27	0.26
Omaha Spit (1993/94–1996/97)	10	35	0.32
Tawharanui (1994/95–1998/99)	15	32	0.47
Wade River (1994/95–1998/99)	14	15	0.83
Totals	**46**	**109**	**0.42**

Productivity
Minimum productivity at the four core study sites between 1993/94 and 1989/99 averaged 0.42 CFP (Table 3).

We did not attempt to quantify causes of breeding failure (and many were unknown), but two were obvious. Cat (*Felis catus*) tracks were often seen around failed nests, particularly at Pakiri River and Omaha Spit, and were also seen around two adults found freshly dead. High tides and storm surges washed out nests in low-lying areas, particularly at Pakiri River and Wade River. For example, a storm on 23 November 1995 flooded most of the nesting area at Pakiri, and four of five nests were lost. During the 1996/97 season, Cyclone Fergus passed over the study area on 30 December, followed by Cyclone Drena on 10–11 January; during that period, five of six nests at Pakiri River and all three at Wade River were lost to flooding.

We also recorded nests lost to crushing; based on tracks through the nests, they included one each lost to cattle and horses at Wade River, and three at Pakiri River, one each lost to horses, a quad bike, and people.

Productivity was highest at the Wade River site, but the average result there was particularly affected by the outcome of the 1994/95 season, when the three resident pairs fledged seven chicks between them for productivity of 2.33 CFP. Productivity was lowest at Pakiri River, possibly because in addition to being prone to flooding, disturbance levels were very high from late December onward because of the adjacent campground.

Natal dispersal
We recorded natal dispersal distances for 25 individuals, ranging from 0–109 km (mean = 27.6 km, median = 20 km). As is usual in birds, the distribution of these distances was skewed toward the origin (Figure 6, filled columns). Of the 25 birds, seven (28%) bred at their natal site, and 22 (88%) bred at or within 60 km of their natal site.
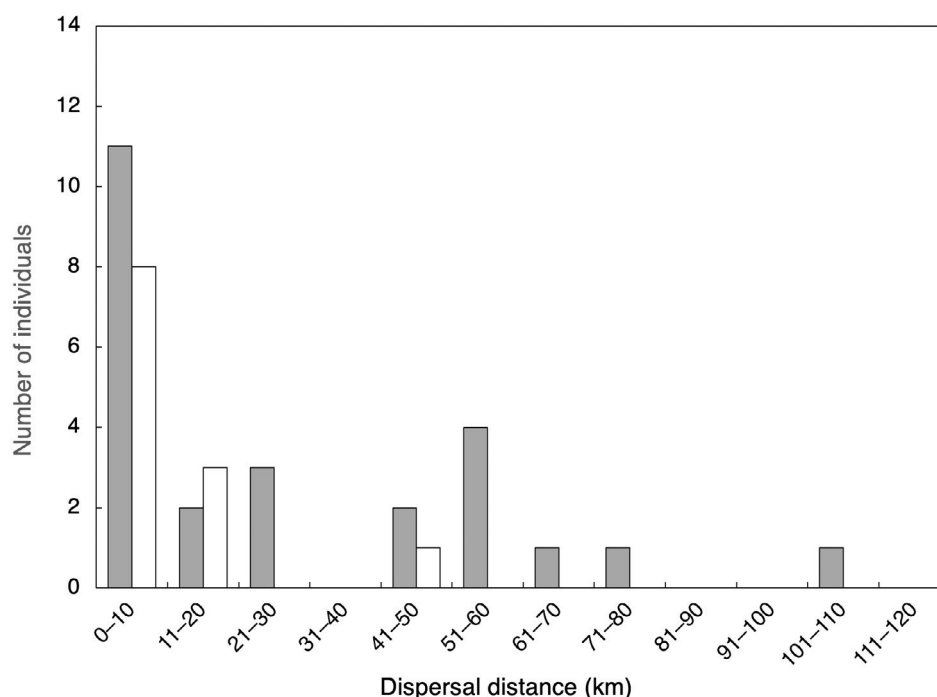
Figure 6. Dispersal of variable oystercatchers banded in the North Auckland study area. Filled columns show natal dispersal distances and open columns show breeding dispersal distances.

Age at first breeding

We recorded age at first breeding (AFB) for 18 individuals. Average AFB was 5.7 years (median = 6 years), with a range of 4–8 years (Figure 7). In three cases (two at Omaha Spit, one at Pakiri River), we recorded newly-formed pairs occupying and defending territories for a season without actually breeding. All three pairs prepared nest scrapes, displayed vigorously when we approached them, and engaged in territorial disputes with neighbouring pairs, but did not lay eggs until the following year.

Breeding dispersal and site-fidelity

We did not detect any cases of breeding dispersal by intact banded pairs. We documented 12 cases of breeding dispersal by individuals, with an average dispersal distance of 10.7 km (median = 6.0 km, range = 1–41 km). In 11 (92%) of the 12 cases dispersal distances were within 20 km (Figure 6, open columns). In three cases, breeding dispersal followed mate loss, and in seven cases it followed divorce. In two cases, the dispersing bird had an unbanded mate and we could not assign a reason for the dispersal.

Once established on a territory, VOCs in our study area showed very high site-fidelity, with adults at the four core sites generally remaining on territory year-round. We did detect occasional movements to nearby sites however, and these are summarised in Table 4. Of 58 banded breeding adults at the four sites, 44 (75.9%) were never seen away from their breeding site, and a further 10 (17.2%) were seen elsewhere only once. All of these trips appeared to be brief, and in most cases the next sighting was back at the bird's breeding site. In some cases, these movements coincided with other events. Of the two birds seen away from Omaha Spit for example, one was seen once at Pakiri River (10 km away) after its mate died and it returned to Omaha Spit within a month. The other left Omaha Spit following divorce and was found dead (of unknown causes) four months later at Snells Beach, 11 km to the south. Birds breeding at Tawharanui were more likely than birds at other sites to be detected elsewhere (Table 4), and all their movements (9 individuals, 15/15 sightings) were to Omaha, a distance of 5–7 km.
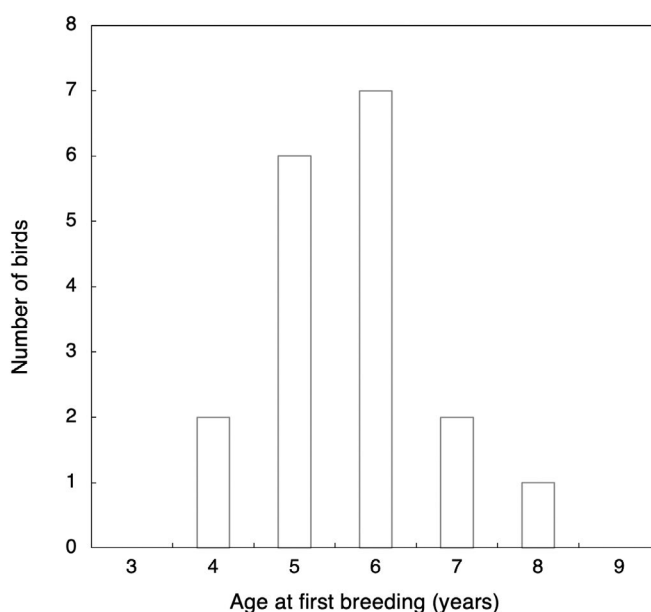

Figure 7. Age at first breeding of variable oystercatchers banded as chicks in the North Auckland study area.

Pair-bond survival

Between 1993 and 2010, 45 banded pairs were monitored for varying periods, for a total of 244 banded pair-years. Mate-fidelity was high—on average, 83% of pairs present in one breeding season were intact in the next. Three pairs were still intact at the end of the study. Of the 42 pair-bonds broken, 29 (69%) were a result of death, and 13 (31%) were a result of divorce, i.e. both birds were known alive but were no longer paired with each other. The longest pair-bond we detected lasted 16 consecutive years (K-5261 M-WRY and K-5280 M-WOW from 1994/95 to 2009/10 inclusive at Omaha Spit). We recorded seven other pair-bonds that lasted between 10 and 14 years; one was at Pakiri River, three at Omaha Spit, and three at Tawharanui.

Table 4. Site-fidelity of colour-banded adult variable oystercatchers breeding at the four core sites in the North Auckland study area, 1994–2010.

Breeding site	Number of birds	Total sightings	Sightings at breeding site	Sightings elsewhere	Number of birds seen elsewhere
Pakiri River	10	493	491	2	2
Omaha Spit	28	2668	2666	2	2
Tawharanui	12	533	518	15	9
Wade River	8	381	380	1	1
Totals	**58**	**4075**	**4055**	**20**	**14**

Survival and population trend

Annual adult survival rates in our study area are shown in Table 5. On average, survival of adults was very high (mean = 0.954, sd = 0.032) and suggested average adult life-expectancy of 21.2 years. Survival was also consistently high, with values between 0.9 and 1.0 in ten of the 11 years we measured it. Sample sizes of pre-breeders were smaller, but their survival was clearly also high: a minimum of 31 (83.8%) of 37 colour-banded fledged chicks survived to one year, 28 (90.3%) of 31 survived from one to two years of age, and 25 (89.3%) of 28 survived from two to three years of age.

Modelling our survival and productivity estimates resulted in a positive value of r (+0.0494), suggesting that our study population had the potential to grow by about 5.1% per annum. Sensitivity analysis indicated that with the very high survival rates we recorded, average productivity would have to fall below 0.22 CFP before the population started to decline. Using the same survival estimates, we calculated a generation time of 17.3 years for the species in our study area.

Table 5. Annual survival (Minimum Number Alive) of individually colour-banded adult variable oystercatchers in the North Auckland study area, 1994–2005.

Year	Number alive in year x	Number alive in year x+1	Annual survival
1994	22	21	0.955
1995	38	38	1.000
1996	55	54	0.982
1997	54	53	0.981
1998	56	54	0.964
1999	58	52	0.897
2000	59	57	0.966
2001	62	57	0.919
2002	59	58	0.983
2003	62	59	0.952
2004	61	56	0.918
Totals	**586**	**559**	**0.954**

DISCUSSION
Morphometrics

The measurements of adults we recorded are generally consistent with those previously published (Baker 1972; Marchant & Higgins 1993). However, our measurement of mid-toe was longer than Baker's because it included the claw, whereas he measured to the base of the claw (Baker 1972, Plate 8E). He also flattened the wing, but did not straighten it (Baker 1972, Plate 8F), and so our measurements of wing length were roughly 4–5% longer. Baker did not measure THL, and we note that it has a lower CV than bill length in our dataset (Table 1).

Our attempts to sex adults using Baker's (1974a) discriminant function, which requires measurement of bill length, depth, and width, were unsuccessful. We often measured both members of known breeding pairs, only to find that both appeared to be of the same sex (more often male) according to the function. Measuring bill length and depth are relatively straightforward, although values may be affected by wear of the bill tip and/or of the feathers at the base of the bill (Baker 1969; Marchant & Higgins 1993). We note that in our dataset bill length had the highest CV of all the linear measurements (Table 1). However, bill width changes quickly at the gape and we suspect our measurements of width were probably not taken at the same place on the bill as Baker's.

The egg dimensions we recorded in North Auckland (36°S–37°S) were very similar to those reported by Rowe (2008) in a sample of similar size (and using the same Kv) at Kaikoura (42.4°S). The average calculated volume of the two samples varied by only 1.67%, suggesting that there is little variation in egg size over the latitudinal range of the species.

We have found no published records of runt egg production by New Zealand birds. Runt eggs are typically produced when foreign material is present in a bird's oviduct, and albumin and a shell are deposited around the material instead of around a normal yolk. The size of the egg depends on how far down the oviduct the foreign material was located (C. Jeske, National Wetlands Research Center, U.S.A., *pers. comm.*). Runt eggs have been recorded in a wide range of species (Crick 1995), including at least three other oystercatcher species: *H. ater* (E. Nol, Trent University, Ontario, *pers. comm.*), *H. ostralegus* (C. Steel, University of Oslo, Norway, *pers. comm.*), and *H. bachmani* (B. Andres, U.S. Fish & Wildlife Service, Alaska, *pers. comm.*).

Timing of breeding

Baker (1969) noted that egg-laying by VOCs begins in October and cited the earliest record at that time as 22 October. He also commented that VOCs breed earlier in the southern South Island (October to February) than in the northern North Island (December to February). Marchant & Higgins (1993) stated that the species laid from mid-September, with a peak in November, and added "slightly later on NI", perhaps echoing Baker's comment. Our data from the northern North Island show that laying in that region also starts in September and peaks in November; in addition, we note that the clutch initiated at the end of August 2009 at Tawharanui (this study) appears to be the earliest on record nationwide. Within our greater study area, Hansen (2005) recorded an earliest laying date of 05 October at Waipu Spit, but noted that the hatch dates of some nests indicated that they were laid in September. We do not have dates for clutch initiation in the southern South Island; however, at Kaikoura, Rowe (2008) found that most eggs were laid in November and December, with the earliest on 19 October. The evidence available now

seems to suggest, *contra* Baker (1969), that breeding does not begin later in the northern North Island than in the South Island, and may even begin earlier. It is also clear from our data that initiation of first clutches can be very protracted, occurring over a period of 3.5 months from the end of August to mid-December. First-clutch initiation in our study area appeared to be significantly earlier in 1997 than in the three previous years. The reason for this is unknown, and the result should perhaps be treated with caution, given the relatively small sample size in 1997 (n = 16 clutches).

Chick growth and post-fledging

With the exception of Rowe's (2008) data on rate of increase in bill length, there appears to be no published information on chick growth in VOCs. Chicks in our study area fledged at lower weights than adults and with shorter THL and wing, but with tarsus and MTC within the adult range. From hatching to fledging, values of THL showed the closest correlation with age, and that metric appeared to be the most useful predictor of age.

Oystercatchers are unusual among shorebirds in that they feed their chicks (e.g., Ens & Underhill 2014). In some broods of two or three chicks, sibling rivalry develops, with the first-hatched chick using its size advantage to obtain more food from the parents, leading to intra-brood differences in growth rates. Sibling rivalry has been documented in other oystercatcher species, including *H. ostralegus*, *H. bachmani*, and *H. moquini* (see Safriel 1981; Groves 1984; and Tjørve & Underhill 2009 respectively). We saw cases of sibling rivalry, and a few examples of large intra-brood differences in weight that might have been caused by rivalry, but in most broods there was relatively little difference in weight.

Oystercatcher chicks of a number of species have been reported to remain with their parents for extended periods after fledging. Examples included *H. ostralegus* (see Kersten & Brenninkmeijer 1995), and the sooty oystercatcher (*H. fuliginosus*) (see Hansen *et al*. 2014). We recorded many cases of juvenile VOCs remaining with their parents for 1–6 months during their first winter, and one case of a juvenile on its natal territory for 8 months after fledging. However, the fact that many juvenile VOCs survive without staying with their parents during their first winter, suggests that post-fledging parental care is involved, rather than strict dependency. The fact that we only ever saw single juveniles with their parents after April may have been because the parents were unable to feed and guard more than one juvenile in addition to feeding themselves and defending their territory.

Productivity

Values for productivity will inevitably vary between studies, depending on a wide range of factors, including location, the length of the study, the number of pairs involved, local predation and disturbance rates, and weather events. There are a few reports of VOC productivity in the order of 1.0 CFP (Fleming 1990; Michaux 2013); however, the average at unmanaged sites, over longer periods, and with more pairs appears to be considerably lower. At Kaikoura, Rowe (2008) monitored 4–6 pairs over 8 years and recorded average productivity of 0.47 CFP. That value is similar to the 0.42 CFP that we recorded while monitoring an average of 18 pairs annually over a 6-year period.

Loss of nests to flooding was common in our study area, particularly at the two low-lying sites (Pakiri River and Wade River). Similar losses of VOC nests to big tides have been reported elsewhere (Fleming 1990; Hansen 2005; Rowe 2008). Egg loss to tidal flooding has been recorded in oystercatcher species worldwide, including *H. palliatus*, *H. longirostris*, *H. bachmani*, and *H. chathamensis* (see Lauro & Burger 1989; Lauro & Nol 1993; Tessler *et al*. 2014; Moore 2014 respectively).

Whether a given level of productivity is high enough to ensure that the population will persist depends on the survival rates in that population (e.g., Dowding *et al*. 2020). Productivity of 0.42 CFP, in conjunction with the high levels of pre-breeding and adult survival that we recorded, was potentially high enough to enable strong growth in our local population.

Natal dispersal

While there have been a number of reports of young VOCs dispersing hundreds of kilometres from their natal site, there are almost no published natal dispersal distances for the species. Baker (1974b) recorded a few examples of extensive dispersal by young birds (some of which were considered 'doubtful' by Marchant & Higgins 1993), but did not record whether breeding occurred subsequently.

Near Dunedin, one bird bred *c*. 30 km from its natal site at 5 years old (P. Schweigman, *pers. comm*.). Rowe (2019) recorded a number of his banded birds breeding at their natal site (Kaikoura); however, while some others were seen at sites distant from Kaikoura, monitoring was infrequent at those sites, and none of the birds was recorded breeding. Melville *et al*. (2020) recorded long-distance dispersal of two birds from the Nelson area, but again neither of them were recorded breeding elsewhere. Roberts & Dowding (2019) recorded a bird that bred 285 km from its natal site, but given the extended time between banding and its later identification (16 years), this distance could have consisted of natal dispersal followed by one or more breeding dispersal events.

In general, birds (including oystercatchers) show highly skewed patterns of natal dispersal, with most birds breeding relatively close to their natal site and a few dispersing longer distances (Greenwood & Harvey 1982; Paradis *et al*. 1998). Australian pied oystercatchers (*H. longirostris*) in Tasmania had an average natal dispersal distance of 9.2 km, and all bred within 30 km of their natal site (Taylor *et al*. 2014). The average in the American oystercatcher (*H. palliatus*) was 33.1 km, with a range of 3–120 km (Clay *et al*. 2014). The VOCs in our study area conformed to this general pattern, with an average of 27.6 km, and a large majority breeding within 60 km.

Natal dispersal distances can be influenced by many factors, including population density, habitat limitations, sex, timing of fledging, and flying ability (Greenwood 1980; Chu & Claramunt 2023), and could differ in different parts of a species' range. The greatest natal dispersal distance we detected (109 km) should be considered a minimum. As noted by Greenwood & Harvey (1982), studies of dispersal are often compromised by the limited size of the recovery area and may fail to detect longer-distance dispersers.

Age at first breeding

Most oystercatcher species worldwide show delayed maturation, and typically first breed at between 3 and 7 years of age (e.g., Harris 1970; Clay *et al*. 2014). In some species, breeding can be delayed further however, depending on population density and territory availability (Loewenthal 2007; van de Pol *et al*. 2014).

Among New Zealand species, South Island pied oystercatchers (*H. finschi*, SIPO) first breed at an average of 5 years (range 4–6) (Sagar & Veitch 2014) and Chatham Island oystercatchers at an average of 3.6 years (range 2–6) (Dowding *unpubl. data*). Baker (1969) assumed that SIPO breed at 3 years because they have attained adult plumage

by that age, and suggested that VOCs "probably first breed at a similar age". Cook *et al*. (2007) reported two birds breeding at 2 years old, but that event was later considered atypical (D.S. Melville, *pers. comm.*).

Our findings (average AFB of 5.7 years, range 4–8 years) appear typical of the genus. We note that the density in our study population was higher than in some other parts of the country, and average AFB may be lower in areas with lower densities. However, Rowe (2019) reported one bird first breeding at 4 years, three at 5 years, and two at 7 years at Kaikoura. Although that sample was relatively small, the range and average are very similar to the values we recorded.

We recorded three pairs having a non-breeding 'honeymoon' year before breeding, a phenomenon that has also been documented in the American oystercatcher and the black oystercatcher (Palmer 1967).

With evidence now pointing to a typical AFB of 5–6 years for VOCs, a relatively high proportion of the population will be non-breeders. Estimates of the number of mature (breeding) individuals will therefore be considerably lower than the total population estimate, a fact that needs to be considered when assigning threat status to the species (I.U.C.N. 2022; Townsend *et al*. 2008).

Breeding dispersal

There appear to be no published data on breeding dispersal by VOCs. We note that Baker (1969) used the term 'breeding dispersal' to describe the movement of birds from their wintering grounds to their breeding grounds, and not *sensu* Greenwood & Harvey (1982). Because the VOCs in our study area showed very high fidelity to their breeding sites and many had long-term pair-bonds, we recorded few examples of breeding dispersal. As with natal dispersal distances, breeding dispersal distances were skewed toward the origin. They were also shorter than natal dispersal distances on average, as is usually the case with birds (Greenwood & Harvey 1982; Paradis *et al*. 1998).

Greenwood (1980) noted that most bird species show female-biased dispersal, with males showing higher philopatry. As we could not sex birds reliably (see above), we were unable to determine whether VOCs conform to this general pattern.

Site-fidelity and movement of adults

Some oystercatcher species, such as *H. ostralegus* and *H. finschi* are wholly or partially migratory as adults (Cramp & Simmons 1983; Sagar & Veitch 2014). Others, such as *H. moquini* and *H. fuliginosus* are sedentary as adults, or only undertake short, local movements (Hockey 1983; Hansen *et al*. 2009).

VOCs are non-migratory; however, while some adults remain on their territories year-round, some adults and pre-breeders move short distances, usually to favoured estuaries, to form autumn/winter post-breeding flocks (e.g., Baker 1969; Marchant & Higgins 1993; Dowding & Moore 2006). Possible regional differences in these seasonal movements (and the distances involved) are not well understood. The breeding adults at our four core sites all remained on territory year-round, and we found no evidence that any of them moved regularly, or for long periods, during the non-breeding season. The few movements that we detected were from Tawharanui to Omaha Spit; they were brief, and occurred during and outside the breeding season. Given the proximity of the two sites (5–7 km apart), we suspect that most of these movements were short foraging trips to take advantage of the extensive feeding opportunities available in Whangateau Harbour, adjacent to Omaha Spit.

Our study area has long had a dense population of VOCs, and with national population growth continuing there may be pressure on territories locally. The very high year-round site-fidelity we recorded may be because pairs risk losing their territories if they move to a wintering site.

We note that some of the movements of previously sedentary adults occurred following mate loss or divorce, a similar situation to that described for New Zealand dotterels (*Anarhynchus obscurus*) in the same area (Dowding & Chamberlin 1991).

Pair-bonds

Almost all the birds in our pair-bond study were banded as adults in existing pairs. Some had almost certainly been in those pairs for a number of years, and so some of the pair-bond durations we recorded will be minimum values. Given the very high level of adult survival we recorded, longer pair-bonds would very likely be detected with longer monitoring. More than two-thirds of the broken pair-bonds in our study resulted from death; however, divorce was not uncommon, in spite of the statement by Marchant & Higgins (1993) that it is rare in oystercatchers. Divorce has also been documented in *H. bachmani*, where 5% of returning banded birds changed mates from one year to the next (Tessler *et al*. 2014), and in *H. chathamensis* (Dowding *unpubl. data*).

Survival and population trend

Estimates of adult survival based on return rates of marked birds can under-estimate true survival (Méndez *et al*. 2018). However, banded VOCs are large, obvious birds with large colour-bands, they are highly sedentary and approachable, and we had a large network of observers in and around our study area. Annual survival of adults in our study may have been slightly under-estimated, but it was nevertheless very high. This was not a surprise, given that a number of VOCs over 30 years of age have been recorded, many of them at Waipu Spit within our greater study area (Roberts & Dowding 2019). In *H. o. ostralegus* annual adult survival can vary markedly, particularly in colder climates with occasional severe winters that cause very high mortality (Camphuysen *et al*. 1996; Duriez *et al*. 2012). Our study area was in a temperate zone without severe winters, and adult survival was consistently high. First-, second-, and third-year survival were also high, although we acknowledge that those values are based on smaller sample sizes; we record them in the apparent absence of any other published survival data for the species. At 0.838 and 0.903, first- and second-year survival respectively were substantially higher than the values of 0.5 and 0.8 recorded in a population of *H. ostralegus* (van de Pol *et al*. 2014) and of first-year survival of 0.60 in *H. moquini* (Loewenthal 2007). Our trend data are inevitably approximate, but suggest that the population in our study area had the capacity to grow rapidly (at about +5% per annum) at the time we collected the data. That level of potential growth is consistent with the belief that the VOC population continues to increase nationally (Dowding & Moore 2006; Riegen & Sagar 2020). However, as is the case with *H. palliatus* (Clay *et al*. 2014), the rate of population growth was most sensitive to adult and sub-adult survival, which may not be as high in other parts of the VOC's range as they were in our study area.

At 0.954, annual adult survival of VOCs is considerably higher than that of SIPO (0.892, Sagar *et al*. 2002). The fact that VOCs are highly sedentary and, unlike SIPO, do not undertake an annual migration, may contribute to their higher rate of adult survival. Like the VOC, the highly sedentary *H. moquini* has a very high (and similar) rate of adult survival at 0.96 (Loewenthal 2007).

With a generation time of 17.3 years, the three-generation period over which trends are estimated for threat-ranking

purposes (I.U.C.N. 2022; Townsend *et al.* 2008) is about 52 years for this species. Our calculated generation time is much longer than the 10.35 years estimated for *H. unicolor* by Bird *et al.* (2020), where the values cited for maximum longevity and adult survival are both much too low (Roberts & Dowding 2019; this paper).

Conclusions

Many aspects of the biology and ecology of the variable oystercatcher are still not known in detail, and this endemic species provides numerous opportunities for further research. Our study has filled some gaps, particularly with regard to dispersal, age of first breeding, pair-bond retention, and survival rates, and has added to our knowledge of chick growth rates and productivity. All our results were recorded between 36°S and 37°S in the northern part of the species' range, which will allow for comparisons with data from other regions or latitudes. Given potential regional differences in climate, VOC population density, predator and competitor guilds, and disturbance levels, among other variables, it would not be surprising to see differences in demographics in other parts of the country. In addition, our productivity results were all recorded at unmanaged sites, and therefore provide a baseline for comparisons with productivity at managed sites.

Some basic information is still lacking. While the species apparently continues to increase in numbers and gives no cause for conservation concern, there is no accurate estimate of the current size of the population (Dowding 2022). This would provide a useful baseline against which to measure future change (Dowding 2014). Threats to the species include predation, inundation, and disturbance, but their relative importance is unclear (Dowding 2014). The VOC's breeding distribution is almost entirely coastal however, and current losses to inundation suggest it is likely to be further affected by sea-level rise and an increase in the frequency of storm events associated with global climate change. The vulnerability of the species to climate change has been recognised recently by the addition of the qualifier 'Climate Impact' (Rolfe *et al.* 2021) to its New Zealand threat ranking (Robertson *et al.* 2021). The adverse effects of climate change are likely to be exacerbated in some regions by an increase in disturbance levels and habitat degradation resulting from increasing development in the coastal zone and greater recreational use of the coastline as the human population grows (Dowding 2014). It has been suggested that this combination of climate change and increasing human pressure may provide the greatest future threat to oystercatcher species worldwide (Ens & Underhill 2014).

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