Variability in the breeding ecology of Australasian gannets, *Morus serrator*, at Cape Kidnappers, New Zealand

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Abstract

The Australasian gannet, *Morus serrator*, a member of the Family Sulidae, primarily inhabits New Zealand and Australian coastal waters. It is considered to be closely related to the Atlantic gannet, *Morus bassana*, in the North Atlantic, and Cape gannet, *Morus capensis*, in South African waters, with which it shares similar ecological niches.

Although often described as relatively well studied, much of our current knowledge of Australasian gannets has been derived from anecdotal observations, and irregular visits to breeding colonies. Few studies have derived information from continuous observations of known individuals over consecutive breeding seasons. Conversely, studies of Atlantic gannets, in particular, have been conducted on a far more rigorous basis. Thus, parallels drawn between the three species, and particularly Atlantic and Australasian gannets, may or may not be accurate.

This study is the first to document three complete and consecutive breeding seasons (1999-00, 2000-01, and 2001-02), using marked nests at the Plateau colony, Cape Kidnappers, New Zealand. Birds were individually marked and I investigated their breeding ecology, and in particular the annual variability in success and other breeding variables. Contrasting with previous studies, I found that the onset of egg laying differed little between years, and although laying was less synchronous in one season, it was highly synchronous in the other two seasons. This is similar to the Atlantic gannet in which the onset of laying is similar year to year, and laying is also highly synchronised. At least for the Australasian gannet, the timing of egg laying does not appear to be linked to sea surface temperature near the colony. However, both species appear to time egg laying to allow chick rearing to coincide with a predictably timed peak in prey availability. Further in depth study is required to confirm this for the Australasian gannet breeding in New Zealand. The use of back-dating to estimate the onset of egg laying from hatching dates and chick ages was also tested and found to provide a useful estimate.

Although previous studies of Australasian gannets have suggested highly variable breeding success, with almost complete breeding failures in some years, this study is the first to document this, and explore possible reasons. Previous studies have suggested human disturbance at breeding colonies as being the cause, with little evidence provided. However, I found in 1999-00, there was considerable egg and chick losses as a result of environmental conditions causing adult and chick starvation and desertion of eggs and young chicks, and productivity was only 9%. A similar pattern, although less severe, occurred in the following season, but conditions improved during the chick rearing stage resulting in 55% productivity. In 2001-02, environmental conditions were stable, resulting in high hatching success, however, an unseasonal storm resulted in considerable chick mortality, and productivity was again low at only 13%. Thus, productivity during the three seasons studied varied markedly, being very low in two of the three seasons as a consequence of environmental conditions, with no evidence of human disturbance. This is the first study which has linked the environment to variable breeding success in this species, and its findings contrast considerably with the invariably high breeding success of the Atlantic gannet. Retrospective analysis of previous Australasian gannet studies suggests this natural link between the environment and breeding success has been apparent, but not recognised, since the 1940s. Links between specific environmental factors and breeding failures are yet to be determined.

I established that calculated egg volume is a good predictor of fresh egg mass, allowing analysis of eggs through the use of linear measurements, when fresh egg mass is not known. For all seasons combined mean egg volume was 89.2 mm^3, whilst a mean incubation period of 45 days is similar to other Australasian gannet studies. Changes in specific gravity during egg development did not allow accurate determination of egg laying dates, with 12.7% of fresh egg mass being lost during development. Eggs laid both within and between seasons by individual females were highly correlated in all measures (length, width, shape, and volume). These egg measures generally showed a negative correlation with laying date, at least in the last two breeding seasons.

Egg volume was positively correlated with chick mass at hatching, although chick growth rates did not seem correlated with egg volume. However, in 2000-01, chicks that survived to fledging were significantly heavier on day-one, despite hatching from similar volume eggs. For chicks that fledged successfully, those that hatched later in the season increased in mass more slowly than chicks that hatched early. However, the reverse trend was found for wing length, possibly as a consequence of wing development being more important than mass increase.

Linked to the breeding failures in 1999-00, were low nest attendance rates by adults and the lowest recorded body mass for adult Australasian gannets in this or previous studies.

Similarly, first egg volumes in this first season were significantly lower, and fewer lost eggs were replaced. Chick growth rates also varied between breeding seasons. Early development of chicks (0-11 days) was slower in 1999-00 than in the other two seasons (slower even than chicks that did not fledge in the other seasons). Growth rates of older chicks (20+ days) that survived to fledge, however, were actually greatest in that season. This suggests that older or more experienced adults, who were better able to provision chicks through poor foraging conditions, were then able to raise faster developing chicks once conditions improved.

The evidence presented in this thesis demonstrates that the 1999-00 breeding season was a difficult one for breeding Australasian gannets at Cape Kidnappers. Furthermore, information derived from this three season study, along with analysis of historical studies, suggests that the Australasian gannet differs markedly to the Atlantic gannet in many respects. Most notable is the occurrence of pronounced breeding failures in some years, apparently influenced by environmental conditions. This seems to be a consequence of a more variable environment, involving variability in weather, oceanographic conditions, and prey availability and abundance.

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When devising the project, I sought the expertise and knowledge of one of New Zealand's most prominent seabird biologists. Christopher J.R. Robertson has been a huge influence on the entire project, from start to finish, and without his help and support this study would not have been what it is.

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During the 'extended' write-up period, a lot of people have helped me on my way, provided assistance where necessary, and the will to continue, they know who they are, and I thank them. I would especially like to say a big thank you to my parents for spurring me along and helping out where needed, and especially to my wife Adel for being so tolerant and patient. Sometimes it felt like the end was so far away, but I have received a huge amount of support, for which I am very grateful.

Preface

This thesis has been written as a series of self-contained chapters, which will form the basis of a number of papers to be submitted to refereed scientific journals. Each chapter is therefore written as a fully referenced self-contained paper, and investigates specific components of the breeding biology of Australasian gannets. Because of this, there is some overlap between chapters, but essentially they each provide new information towards different components of the breeding biology of Australasian gannets' at Cape Kidnappers.

I conducted the fieldwork, most of the statistical analyses, and have written each chapter. My supervisors have contributed throughout the thesis with help during the fieldwork, analysis, and write-up stages of the study. I have also included several appendices at the end of the thesis. Appendix 1 provides an extra analysis of egg measurements relevant to Chapter 5.

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Introduction: the Sulidae, the Australasian gannet, and Cape Kidnappers

The Order Pelecaniformes and the Sulidae

The Pelecaniformes is an ancient and diverse order to which the gannets and boobies (Family Sulidae) belong (Nelson, 1978a). Also included in the Pelecaniformes are the pelicans, cormorants and shags, darters, frigate birds and tropicbirds. All are web-footed (totipalmate) fish eaters, partly, or usually wholly marine, and between them they have evolved a wide range of feeding methods (Nelson, 1978a). However, based on the findings of Hedges & Sibley (1994), the order may contain very different taxa. Using DNA-DNA hybridisation techniques, they found that the pelicans are more closely related to the shoebill, *Balaeniceps rex*, a stork-like bird that lives in the swamps of central Africa; the boobies, gannets, cormorants, shags, and darters form a closely related cluster; the tropicbirds are not closely related to the other taxa; and the frigatebirds are closest to the penguins, loons, petrels, shearwaters and albatrosses (Super-family Procellarioidea).

The taxonomy of the Sulidae has also been strongly debated, but this now seems to be resolved (Nelson, 2002), with the formation of three separate genera: *Morus* for gannets, *Sula* for boobies, except Abbott's booby for which a third genus, *Papasula* has been proposed. Cytochrome b sequence analyses performed by Friesen & Anderson (1997) place the gannets and boobies in separate, monophyletic lineages, with Abbott's booby being basal to the gannets. They suggest the three 'groups' were distinct well back into the Miocene. This seems to strongly support splitting the family into three genera. However, Friesen & Anderson (1997) suggest that all extant lineages of boobies arose within the last 3 million years, since the beginning of the Pliocene, and that lineages leading to blue-footed and Peruvian boobies may have diverged only since the last interglacial period. The three gannets also appear to represent recent divergences (Friesen & Anderson, 1997), even though the gannet 'lineage' was distinct some time ago.

The debate has also involved whether the three gannets should be given species status or considered sub-species (or super-species) of the Atlantic gannet. Nelson (2002) now considers the gannets as a super-species, and using the genus *Morus*, defines them as *M.* [*bassanus*] *bassanus*, *M.* [*b.*] *capensis* and *M.* [*b.*] *serrator*, for the Atlantic, Cape and Australasian gannet, respectively. The implication is that the three gannets form a close knit trio, closer than any other member of the family, yet without being clear-cut species or mere subspecies.

The use of the genus *Morus* for the gannets is a change of heart by Nelson (2002), as in Nelson (1978a, 1978b) he considered them to be members of the genus *Sula*. Thus, there has been much confusion, with Northern hemisphere researchers using both *Morus* and *Sula* for the Atlantic gannet and most researchers studying the Cape or Australasian gannets choosing to use *Morus*. Counter to this, however, the Handbook of Australian, New Zealand, and Antarctic Birds (HANZAB) has included all members of the Family in the genus *Sula* (Marchant & Higgins, 1990).

I have chosen to follow Nelson (2002) and use the genus *Morus* for the gannets, and *Sula* for the boobies, except for Abbott's booby, which in accordance with the previously mentioned research, I consider to be in its own genus, *Papasula*. However, unlike Nelson (2002), I prefer to treat all three gannets as full species. This is based on several things. Firstly, recognisable differences in morphology and behavioural traits exist, whereby all three species can be clearly distinguished. Secondly, their normal breeding distributions, until recently, have not overlapped and although interbreeding now exists in low-levels at both South African Cape gannet colonies and New Zealand and Australian Australasian gannet colonies (Cape x Australasian pairings in both cases), the success of young produced is yet to be established. Thirdly, and possibly most importantly, based on evidence to date, all three species show distinct differences in their breeding ecology, including timing, breeding success, interaction with the environment, and because of this, potentially important differences in population regulation. Supporting the specific splitting of the recently diverged gannets, is the fact that several of the boobies which are given full species status, may have diverged more recently, ie. Peruvian and blue-footed (Friesen & Anderson, 1997). The recent taxonomic split of the masked booby, *Sula dactylatra*, and Nazca booby, *Sula granti* (Pitman & Jehl, 1998; Friesen et al., 2002), which until recently were considered to be one species that exhibited morphologically and ecologically distinct subspecies, also adds weight to the argument that such differences constitute genetically distinct taxa.

So, the three species of gannet and their distributions are – the Atlantic gannet, *Morus bassana*, in the North Atlantic and North Sea (Nelson, 2002), the Cape gannet, *Morus capensis*, around the southern coast of South Africa (Crawford et al., 1983), and the Australasian gannet, *Morus serrator*, in New Zealand and south-eastern Australia (Wodzicki et al., 1984; Bunce et al., 2002) (see Nelson (2002) for the most recent review of sulid distribution and population estimates).

Of the seven species of booby now considered, three are widely distributed throughout the tropics – the masked, *Sula dactylatra*, brown, *Sula leucogaster*, and red-footed boobies, *Sula sula*. The blue-footed booby, *Sula nebouxii*, has three foci, the Gulf of California and islands off Mexico, the Galápagos Islands, and the west coast of South America from northern Peru to the Gulf of Panama. The fifth, the Peruvian booby or piquero, *Sula variegata*, is restricted to the extreme north coast of Chile and islands off Peru, and the sixth, the newly described Nazca booby, *Sula granti*, breeds on the on the Nazca Plate in the eastern Pacific Ocean. The seventh, Abbott's booby, *Papasula abbotti*, breeds only on Christmas Island in the Indian Ocean. Thus, the gannets primarily inhabit the temperate zone, while boobies primarily inhabit the tropics. As far as distinguishing features of the two groups go, this could be considered the most relevant. Interestingly, until recently, none of the three gannets overlapped in breeding distribution with any other sulid, whereas every booby is sympatric with another booby species (Nelson, 1978b).

Overview of the Sulidae

Much of the basic biology of the sulids has been documented with Nelson's (1978b) comprehensive volume on the Family. Nelson's (1978a) monograph 'The Gannet' further investigates the ecology and behaviour of the Atlantic gannet, with some comparison between this and the other two gannets, and this has been slightly updated in 'The Atlantic gannet' (Nelson, 2002). These three books form the foundation to our current knowledge of the Family, and especially the gannets.

Each of the sulids is structurally very similar. They all have high aspect ratio wings and a fairly high or high wing loading, a strong conical sharply serrated beak, nostrils with no external openings, and streamlining. Each species however, has evolved to fill the particular niche it occupies. For example, they vary markedly in size and weight, from about 900 grams for male red-footed boobies, to about 3,150 g for male Atlantic gannets, with the three gannets being the heaviest (Nelson, 1978b). The Atlantic gannet is the heaviest, with Cape and Australasian following in that order (Nelson, 2002). Each of the sulids also share similarities behaviourally and ecologically, such as colonial nesting, plunge-diving, and homologous behaviours when breeding, eg. sky-pointing. But again each of these varies slightly between species. For example, although all species are colonial nesters, they vary from huge tightly packed colonies such as those of the Peruvian booby (360,000 individuals at Mazorca in 1960 (Nelson, 2002)) to the scattered arboreal nests of Abbott's booby. However, none of these similarities or differences allow gannets and boobies to fall neatly into their respective 'groupings'.

Not only have differences occurred between species, but also within some, in the form of marked sexual dimorphism (Nelson, 1978a). The least sexually dimorphic sulids are the gannets and the Peruvian booby, which have the richest food supplies (Nelson, 1978a), but both sexes also share defence of a highly competed for nest-site (masked booby also shares this trait) (Nelson, 1978b). The blue-footed booby exhibits the most extreme sexual size dimorphism, with males weighing approximately 70% of female mass (Nelson, 2002).

Estimated numbers and population change of Australasian gannets

Most (87.2%) of the New Zealand Australasian gannet population breeds within a narrow band of 4° of latitude (between 34-38°S.), and at the time of the 1980-81 census, all but three gannetries[1] (representing 0.3% of the NZ population) were north of 40°S. (Wodzicki et al., 1984) (Fig. 1). A further gannetry has since developed at Farewell Spit, with roosting birds having been recorded there in 1981, and breeding first recorded in 1983-84 (Hawkins, 1988). The gannetry has developed rapidly into several colonies with just over 2,500 breeding pairs in 2003-04 (R. Schukard pers. comm.). The establishment of additional gannetries at Cape Kidnappers (Plateau Beach (Wodzicki et al., 1984; C.J.R. Robertson unpubl. data), and on

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[1] The convention of Wodzicki et al. (1984) is used throughout this paper, in that a 'colony' represents a collection of occupied nests completely separate from any other collection, and 'gannetry' represents a collection of colonies in the same geographic location.

the mainland at Muriwai (Greene, 1999) brings the total number of gannetries in New Zealand to 29. Location of breeding sites may be related to sea-temperature, which determines spawning of fish (Wingham, 1985). The distribution and abundance of the Cape gannet has been shown to be determined by the availability of pelagic fish (Crawford & Shelton, 1978).

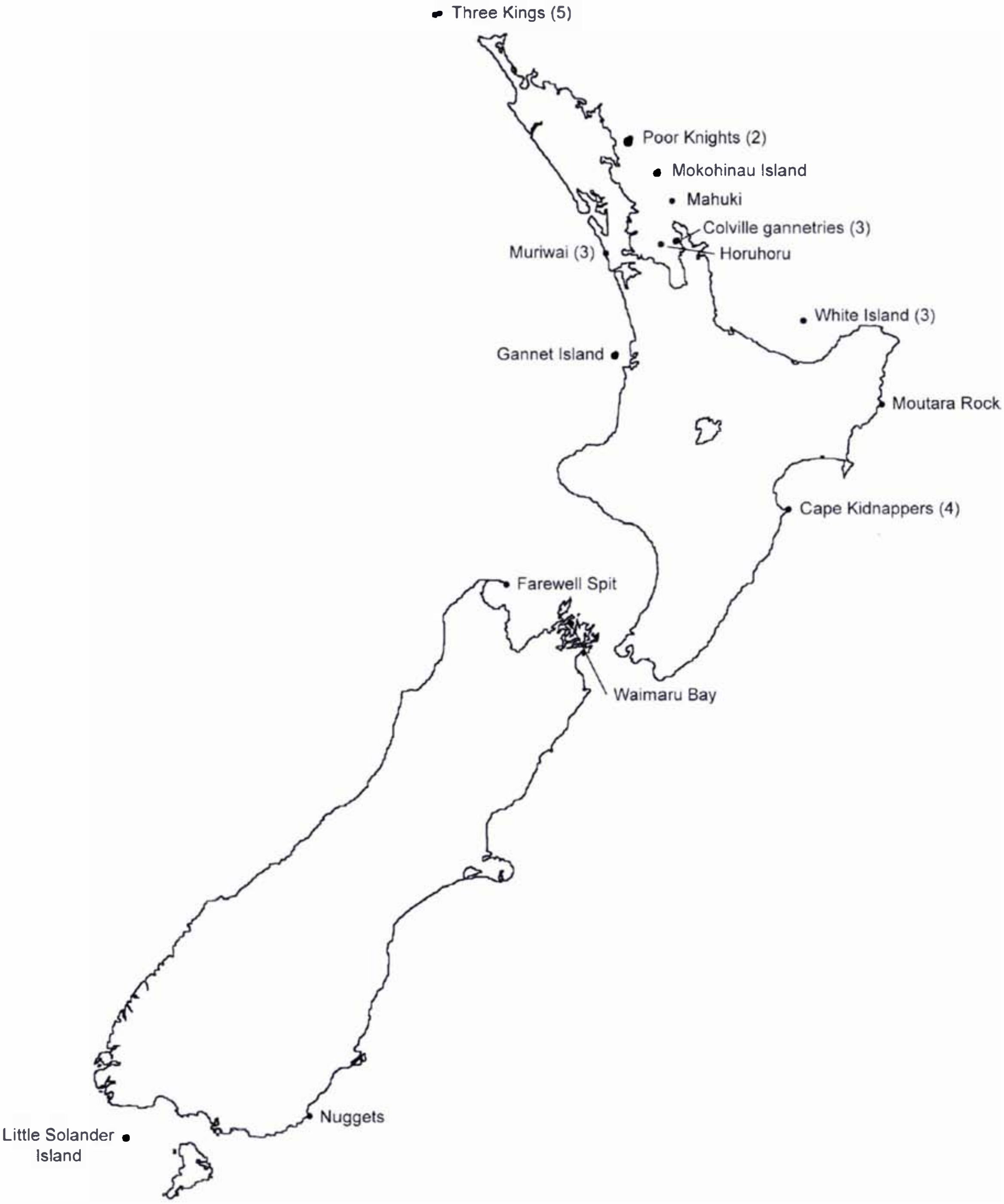

Figure 1. Location of the 29 New Zealand Australasian gannet colonies. The names of the colonies are indicated, with figures in brackets representing the number of gannetries at that location.

Changes in the Australasian gannet population, over much of the last century, are probably some of the most accurate for any seabird species. The first count of gannets breeding in New Zealand was provided by Wodzicki & McMeekan (1947), who listed 12 'breeding localities' with an estimated population of 11,777 pairs. This was based on figures from these locations over a period of years from 1926 to 1946, and included some guess work as well as actual counts. In 1946 the Ornithological Society of New Zealand (OSNZ) adopted an Australasian gannet census as a project and during the 1946-47 breeding season, 20 of the 32 known and suspected gannetries in New Zealand were visited by members. Photographs taken of 14 gannetries, by the Royal New Zealand Air Force during that breeding season were also included. Thus, during the 1946-47 season 24 gannetries were included in the first census of the New Zealand colonies. This census formed the basis for a series of papers that were published in New Zealand Bird Notes, the predecessor of *Notornis*, and Fleming (1947a) gave a full account of the census, reviewing census techniques, and describing each of the gannetries in detail. Historical information and changes in population size at some of these gannetries prior to this census are discussed. Two more gannet censuses were conducted in New Zealand, in the 1969-70 and 1980-81 breeding seasons, and these results were published by Wodzicki et al. (1984). The two latter censuses reflected far more accurate techniques, with aerial photographs forming the basis of counts. However, the change in estimated population size from 21,133 breeding pairs in 1946-47, to 37,774 in 1969-70, and to 46,004 pairs in 1980-81 reflects far more than just more accurate census techniques. Thus, the New Zealand gannet population has been steadily increasing since 1946-47 (Wodzicki & McMeekan, 1947), at a rate of roughly 2.3% per annum. We (C.J.R. Robertson, Ed Minot and I) conducted a further census in 2000-01, taking aerial photos over all New Zealand colonies (except the gannetries at The Nuggets in Otago, and Little Solander Island in the Foveaux Strait) over a period of two days in November 2000. The results of this census are yet to be analysed, but the previous rate of increase has perhaps slowed a little, to around 2% per annum (C.J.R. Robertson quoted in Nelson (2002)).

Across the Tasman, historical data for the Australian colonies are sparse, although Bunce et al. (2002) provide a recent overview of changes there. Of particular note is the almost complete demise of the Cat Island gannetry near Tasmania (Anderson, 1936; Warham, 1958; Warham & Serventy, 1978). The colony showed a drastic reduction from 5,000-10,000 birds in 1908, to a population of 14 adults and six chicks in 1977, and 12 pairs in 1980. The colony has now all but disappeared (Phillips, 1993). This decrease is attributed to predation and vandalism by fishermen and others (Warham & Serventy, 1978). Since 1980, the

Australian population has increased from 6,600 breeding pairs to approximately 20,000 pairs in 1999-2000, a rate of 6% per annum (Bunce et al., 2002). This marked increase is suggested to be due to changes in local productivity and possible changes in fishing practises. This requires further study.

Therefore, there are currently 35 gannetries, 29 in New Zealand and 6 in Australian waters. All New Zealand gannetries lie between 32–47°S., with those at the Three Kings Islands and Little Solander Island being the most northerly and southerly, respectively.

Why such a small population at the start of the century, and what has caused the increase?

The cause of such low numbers of Australasian gannets in New Zealand, at the turn of the century is unknown. The apparent increase early on, from around 11,700 pairs to 21,100 during the 1946-47 census, may have had something to do with the rigour of data collection in the first survey. However, the continued increase since 1946-47 suggests that at least some of this prior increase was real.

During the 1946-47 census and other early studies, it was suggested that disturbance at several colonies had occurred, and appeared to have been caused by humans. Little evidence for this was found, and my analysis of the breeding failures reported during these early studies (Buddle, 1947b; Hamilton, 1947; Wodzicki & McMeekan, 1947; Buddle, 1948; Fleming, 1948; Robertson & Wodzicki, 1948; McKenzie, 1949; Wodzicki & Robertson, 1953; Wodzicki & Stein, 1958; Stein, 1971), is given in Chapter 3. However, what had caused the Australasian gannet population to be so small during the early 20th Century? Several explanations are possible.

Firstly, harvesting of gannets by the Maori could have depleted numbers, and the increase we are currently seeing could therefore be the result of the population 'bouncing back' to pre-harvesting levels. Similar reasoning is given for the increase in Atlantic gannets (Nelson, 2002). Unfortunately, there is not a lot of evidence that harvesting of gannets in New Zealand occurred on such a scale that would be required to reduce numbers to the levels at the start of the century. Cheeseman (1888) quotes early voyagers after Cook as stating "that the Maoris were in the habit of crossing from the mainland at long intervals to obtain young muttonbirds or gannets" from the Three Kings. More recently Wodzicki et al. (1984) stated that "According to P. Burstall, former Conservator of Wildlife, Rotorua, Maori used to take gannets from White Island, more as a sideline to their muttonbirding activities than as a distinct activity, but after prosecution in the 1960s this practice seems to have ceased". These are the only published references I have located indicating harvesting of gannets by Maori. However, a large, fat, colonial and diurnal species such as the gannet would surely have been an easy food source. Moreover, prior to European arrival, all Australasian gannet colonies were on islands well offshore or with difficult landings. The recent colonisation (or perhaps re-colonisation?) of the mainland is consistent with previous mainland extermination.

Secondly, the increase in numbers could be in response to an increase in food availability. This is one of the more popular explanations for similar increases in other seabirds, particularly in the northern hemisphere. Several studies have documented changes in seabird numbers apparently in response to changes in prey availability and abundance (eg. Crawford & Shelton, 1978; Furness & Cooper, 1982; Crawford et al., 1992). This supports the general belief (eg. Lack, 1968) that the breeding success and population growth in seabirds are directly related to food availability. Robertson (1992) also considered this to be possible for Australasian gannets, being influenced by increases in abundance or availability of surface schooling pelagic prey species such as pilchard, *Sardinops neopilchardus*, anchovy, *Engraulis australis*, saury, *Scomberesox forsteri (saurus)*, or jack mackerel, *Trachurus novaeselandiae.* There has been an increase in inshore commercial fishing activity over the last few decades and this has included species such as barracouta, *Thyristes atun*, kahawai, *Arripis trutta*, gemfish, *Rexea solandri*, skipjack, *Katsuwonus pelamis* and albacore tuna, *Thunnus alalunga*, which prey on the fish and squid species predominant in the gannet diet (Robertson, 1992). Thus, removing large predatory fish may well have increased numbers of gannet prey species. The discards from major fisheries may also be of significant worth to Australasian gannets, as has been described in the Northern Hemisphere for Atlantic gannets and other seabirds (Garthe & Huppop, 1994; Oro et al., 1996; Oro & Ruiz, 1997).

Thirdly, changes in climate and sea conditions may have contributed to increased breeding success or adult and juvenile survival. Bunce et al. (2002) suggest that long-term changes in climate, including the prevalence of El Niño Southern Oscillation (ENSO) events, as well as the effect of fisheries, could be important in the recent increase in the Australian gannet breeding population. In New Zealand, it is also possible that a combination of all three hypotheses explains the increase in the Australasian gannet breeding population.

Australasian gannet biology: an overview

In New Zealand, gannets occur within the limit of the continental shelf (Wodzicki & Robertson, 1974). As with most other seabirds, the breeding cycle of the Australasian gannet extends over a prolonged period. Egg laying is initiated considerably earlier at more northerly gannetries, although a direct north-south gradient does not exist. Stein (1971) suggested Mahuki was the only New Zealand gannetry where egg laying is slightly ahead of Horuhoru. In relation to Horuhoru, the Colville gannetries (Motukaramarama and Motutakapu) are a week later, the Sugar Loaf (of the Poor Knights) a fortnight later, the Oaia colony off of Muriwai, a fortnight to three weeks later, and Cape Kidnappers from one month to five weeks behind. It seems likely that breeding at each location is related to local prey availability, which appears linked to sea–temperatures and the spawning of prey species (Waghorn, 1982; Wingham, 1985). Considerable differences in the diet of gannets at several of these colonies have been noted (Waghorn, 1982; Robertson, 1992).

Oliver (1930) was the first to describe the habits and distribution of Australasian gannets. Visits to colonies and observations in the 1940s provided the first insight into the breeding ecology and population status of the species in New Zealand (Buddle, 1947a; Buddle, 1947b; Bull & Fleming, 1947; Cunningham, 1947; Fleming, 1947a; Fleming, 1947b; Fleming & Sibson, 1947; Hamilton, 1947; Wodzicki & McMeekan, 1947; Buddle, 1948; Clark & Roberts, 1948; Fleming, 1948; Robertson & Wodzicki, 1948; McKenzie, 1949; Hamilton, 1950; Stein, 1950; Roberts, 1954). Several workers then studied the breeding biology of the species more closely, primarily at Cape Kidnappers (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953; Wodzicki & Stein, 1958; Wodzicki, 1967a; Wodzicki, 1967b) and in the Hauraki Gulf (Stein, 1971). Warham's (1958) study of the Cat Island gannetry off Tasmania, provides similar information for an Australian colony. These studies provided basic information on general breeding biology (egg and chick measurements, incubation and fledgling periods, breeding success), breeding behaviour, and population dynamics. Large numbers of chicks and adults were banded during these early studies, allowing assessment of dispersal and survival of the species. Considerable attention has been paid to the highly ritualised behaviour of breeding Atlantic gannets, with comparisons extending to the Australasian and Cape gannets (Nelson, 1978b; Nelson, 2002).

Undoubtedly, the most comprehensive study of Australasian gannet breeding biology to date is that by Elspeth Wingham[2] during her three-season PhD study at Motukaramarama (one of the Colville gannetries, Fig. 1) in the Hauraki Gulf, between 1978-81 (Waghorn, 1982; Waghorn, 1983; Wingham, 1984a; Wingham, 1984b; Wingham, 1985; Wingham, 1989). In more recent years there have been breeding studies at Australian colonies in Port Phillip Bay (Norman & Menkhorst, 1995; Gibbs et al., 2000; Bunce, 2001).

At Cape Kidnappers, the breeding season extends from about July to April (Wodzicki & Robertson, 1953). Adult males are the first to return to the colony (around the New Moon) in July at Cape Kidnappers (C.J.R. Robertson pers. comm.) and females return soon after. First eggs may appear at Cape Kidnappers from about the fourth week of September to the end of October (Wodzicki & Robertson, 1953). Gannets lay a single-egg clutch, although two eggs have been reported in approximately 0.75% of nests (Wodzicki & Robertson, 1953). The origin of these second eggs is uncertain (Wodzicki & McMeekan, 1947). The incubation period is on average 44 days (Wingham, 1984a), and as with other sulids the egg is incubated using the webs of the feet (Wodzicki & McMeekan, 1947). The chick hatches naked and blind, but is almost covered in thick white down within 14 days (Wingham, 1984b). By about 39 days tail feathers are just emerging, and at 55 days juvenile plumage is obvious beneath the down, which is almost gone by about 75 days (Wingham, 1984b). Chick growth is similar to that of Atlantic and Cape gannets (Wingham, 1984b). Growth is most rapid between days 20-50 and maximum weights were attained at 90 days (Wingham, 1984b). The chicks are attended and fed by both parents, with frequent small feeds at hatching, decreasing in regularity with age (Wingham, 1985). Chicks are attended continuously up until at least 48 days, after which they are sometimes left unattended (Waghorn, 1982). The nestling period appears to vary from an average of 102 days (Warham, 1958) to 108 days (Wingham, 1984b). Chicks spend from 6 hours to three days on the cliff edge, before flying from the colony (Wingham, 1984b).

After fledging from the breeding colonies in New Zealand, most juvenile Australasian gannets migrate up to 5,000 km westward across the Tasman Sea to the southern and eastern

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[2] Elspeth Wingham *nee* Waghorn

coasts of Australia (Wodzicki & Robertson, 1953; Stein & Wodzicki, 1955; Wodzicki & Stein, 1958; Stein, 1960; Stein 1961; Wodzicki, 1967a). The occurrence of juveniles or immature birds in New Zealand waters is rare, although some do remain (Stein, 1960; Stein 1961; Stein, 1962). Birds return to their natal colonies when 2-5 years old, and start breeding when 4-7 years old (Wodzicki, 1967a). Dispersal of adults during the winter appears to mainly be around the coast of New Zealand, although some may head back across the Tasman (Wodzicki, 1967a). Adult gannets occasionally use breeding colonies at night or during times of rough weather, in the months of May, June and July (Fleming & Sibson, 1947; Fleming & Wodzicki, 1952). Survival during the first few years of life is low, with 30% suggested to return to their natal colony, although the estimated life span of a bird once it is an adult is 25-28 years (Wodzicki & Robertson, 1974).

Several studies have investigated the diet of Australasian gannets in New Zealand (Wodzicki & Moreland, 1966; Wingham, 1985; Robertson, 1992) and Australia (Brothers et al., 1993; Bunce & Norman, 2000). Generally prey species appear to be inshore surface schooling species, and the most common prey in New Zealand are pilchard, anchovy, saury, and jack mackerel. Squid, *Nototodarus spp*. also seem to form an important component of the diet at some colonies during certain parts of the breeding season (Robertson, 1992). Annual variation in diet has been noted at Motukaramarama and Cape Kidnappers (Wingham, 1985; Robertson, 1992), suggesting that Australasian gannet breeding could be influenced by changes in prey abundance and availability. There are considerable differences in diet at gannetries around New Zealand (Robertson, 1992).

Atlantic and Australasian gannets – the validity of previous comparisons

Much of the literature suggests that Atlantic and Australasian gannets, and indeed Cape gannets, are similar in some aspects, but not in others. Nelson (2002) considers that in most essentials, the three gannets have similar breeding regimes. However, he does state that the Australasian gannet, although having a shorter breeding season compared to the Atlantic, is prone to considerable yearly fluctuations in attendance dates, and mean laying date. This seems to be based mainly on the work of Wingham (1984a), with use of previous studies at Cape Kidnappers (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953; Wodzicki

& Stein, 1958; Wodzicki, 1967a; Wodzicki, 1967b) and in the Hauraki Gulf (Stein, 1971). However, other than Elspeth Wingham's study (Waghorn, 1982; Waghorn, 1983; Wingham, 1984a; Wingham, 1984b; Wingham, 1985; Wingham, 1989), all previous reports on New Zealand colonies are based on infrequent visits, with periods of weeks or months between trips. Wingham (1984a) concluded that the median date of laying shows greater variability in the Australasian gannet compared to the Atlantic, and suggested this flexibility was due to a more variable, less seasonal environment.

Wingham, however, missed the entire early laying period at Motukaramarama in her first season, arriving after a massive storm caused the loss of almost all first clutch eggs. Thus, data collected in that season were based primarily on second clutches. In her second season, she also missed most of the egg laying period, and based laying dates on back-dating from hatching. The validity of this method has never been tested, and may incorporate considerable error if egg losses occur. This may well have affected the accuracy of information obtained and therefore our current knowledge of timing of breeding and egg laying. In contrast, many of Nelson's (2002) comparisons use data derived from his work conducted in the early 1960s when he lived full-time on Bass Rock, Scotland (Nelson, 1964; Nelson, 1966).

Perhaps the biggest difference in the breeding biology of Atlantic and Australasian gannets is found in breeding success. Breeding failures in the Australasian gannet have been observed, but not adequately documented in many previous studies, including those at the Three Kings (Buddle, 1947; Buddle, 1948), Mahuki (Hamilton, 1947), White Island (Robertson & Wodzicki, 1948), Cape Kidnappers (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953), Horuhoru (Fleming, 1948; McKenzie, 1949; Wodzicki & Stein, 1958; Stein, 1971), Motukaramarama (Wingham, 1984a), Farewell Spit (Hawkins, 1988), and Pedra Branca (Brothers et al., 1993) gannetries. Such events occurred at eight gannetries over 45 years, differing in the extent of failure and loss, but suggesting a widespread phenomenon. In many cases, these failures were viewed as a result of human disturbance at the colonies, with little acknowledgement that breeding failures might relate to the bad weather and/or lack of food that are a normal part of the breeding ecology of Australasian gannets (eg. Wingham 1984b). Certainly, the Atlantic gannet shows no similarity in this regard, with consistently high breeding success each breeding season (Nelson, 1966; Nelson, 2002). This led Nelson (2002) to suggest that starvation has never been evident among young in the nest, and Bass Rock gannets are immune from significant reproductive failure at the chick stage. Other interesting behaviours appear linked to this, with Atlantic gannet chicks being attended continuously until fledging (Nelson, 1966; Nelson, 2002), whilst in Australasian gannets, older chicks are often unattended (Waghorn, 1982). Interestingly, in the case of Atlantic gannets this appears to be changing in recent years, with Lewis et al. (2004) documenting what appears to be the first case of Atlantic gannets leaving chicks alone at the nest. Perhaps this is a further sign of a changing environment in the North Sea, as has been documented in other seabird studies (Hislop & Harris, 1985; Martin, 1989; Harris & Wanless, 1990; Harris et al., 1997; Harris & Wanless, 1997; Proffitt, 2004).

The growth rate of chicks is also linked to the environment in which each of these species lives. Nelson (2002) compares the growth of chicks in the three species, noting that the growth of both Cape, and particularly Australasian gannets is slower than that of Atlantic gannets. This appears fairly well documented, with the work of Wingham (1984b) and Bunce (2001) providing evidence of slower growth rates in Australasian gannets. Furthermore, Australasian gannets seem less able to raise two chicks during experimental manipulations, at least during some seasons (Waghorn, 1982; Bunce, 2001). This suggests a difference in the nature of their respective foods, whether in nutritive value per food item, crude availability or other aspect (Nelson, 2002). Environmental variability and its effect on the diet of gannets is surely part of the reason behind these differences.

Comparison of environmental variability at Atlantic and Australasian gannet colonies

Australasian gannets may live in a more variable environment than that of the Atlantic gannet (Wingham, 1984a; Wingham, 1984b; Nelson, 2002). Variability encompasses both within breeding season variability and, possibly more importantly, between breeding season variability. Yet, many of the Australasian gannet studies to date have been based around projects within a single season, or have not fully investigated the variability between several seasons in terms of breeding biology. There also appears to currently be no comparison of the amount of annual environmental variability between the Atlantic and Australasian gannet.

In terms of the environment, I use this in the broadest sense, to encompass all aspects of a gannets' physical surroundings with which it interacts. This includes climate, weather, ocean conditions, prey abundance and availability, and basically any other variable that affects the biology of these birds. Making comparisons for most of these aspects is going to be difficult, and at least for the Australasian gannet in New Zealand, there is very little information pertaining to the 'at sea' variables and prey abundance and availability. For the Atlantic gannet, however, prey availability has apparently been abundant and predictable (at least perhaps until recently) (Nelson, 1964; Nelson, 1966; Nelson, 1978a; Nelson, 1978b; Nelson, 2002). Weather is the easiest environmental factor to measure. Variability in weather, as measured at land-based weather stations, is linked to variability in ocean conditions, and therefore to prey availability and abundance.

On a very basic level I have compared the mean monthly rainfall during the egg laying and early chick stage of the breeding season at Napier, New Zealand, near Cape Kidnappers, and Leuchars, Scotland, near Bass Rock (Fig. 2). Napier rainfall data were supplied by the National Institute of Water and Atmospheric Research (NIWA) from the nearby Napier Airport Weather Station (D96484; 39° 27' S, 176° 51' E), approximately 30 km to the north-west of Cape Kidnappers. Scottish rainfall data were obtained from the Met Office (UK) website at http://www.met-office.gov.uk/climate/uk/stationdata/index.html for the Leuchars Station (72° 09' N, 34° 68' E), approximately 50 km to the north of Bass Rock.

Cape Kidnappers data from the term of this study were compared with data from 1961-63, at the time of Bryan Nelson's study. This comparison suggests that the rainfall at Cape Kidnappers is more variable during the egg and chick stage of the breeding season, than at Bass Rock.

Thus, the higher variability shown in the monthly rainfall during the breeding period, near to Cape Kidnappers, compared to Bass Rock in Scotland, suggest there could be a difference in the amount of environmental variability between the two species. The fact that the diet of Australasian gannets in New Zealand varies annually (and within seasons at some colonies), both in prey species and the timing of some prey species' appearance in the diet (Robertson, 1992), suggests that this variability is not confined to just rainfall, and that differences in oceans environment impact Australasian gannets not only directly, but through their diet. This relationship requires further study. In particular, we need information on the abundance and availability of fish species that gannets feed on in New Zealand coastal waters. The role of ENSO events in these changes also needs to be assessed, along the lines of Bunce et al. (2002) and Bunce & Norman (2000).

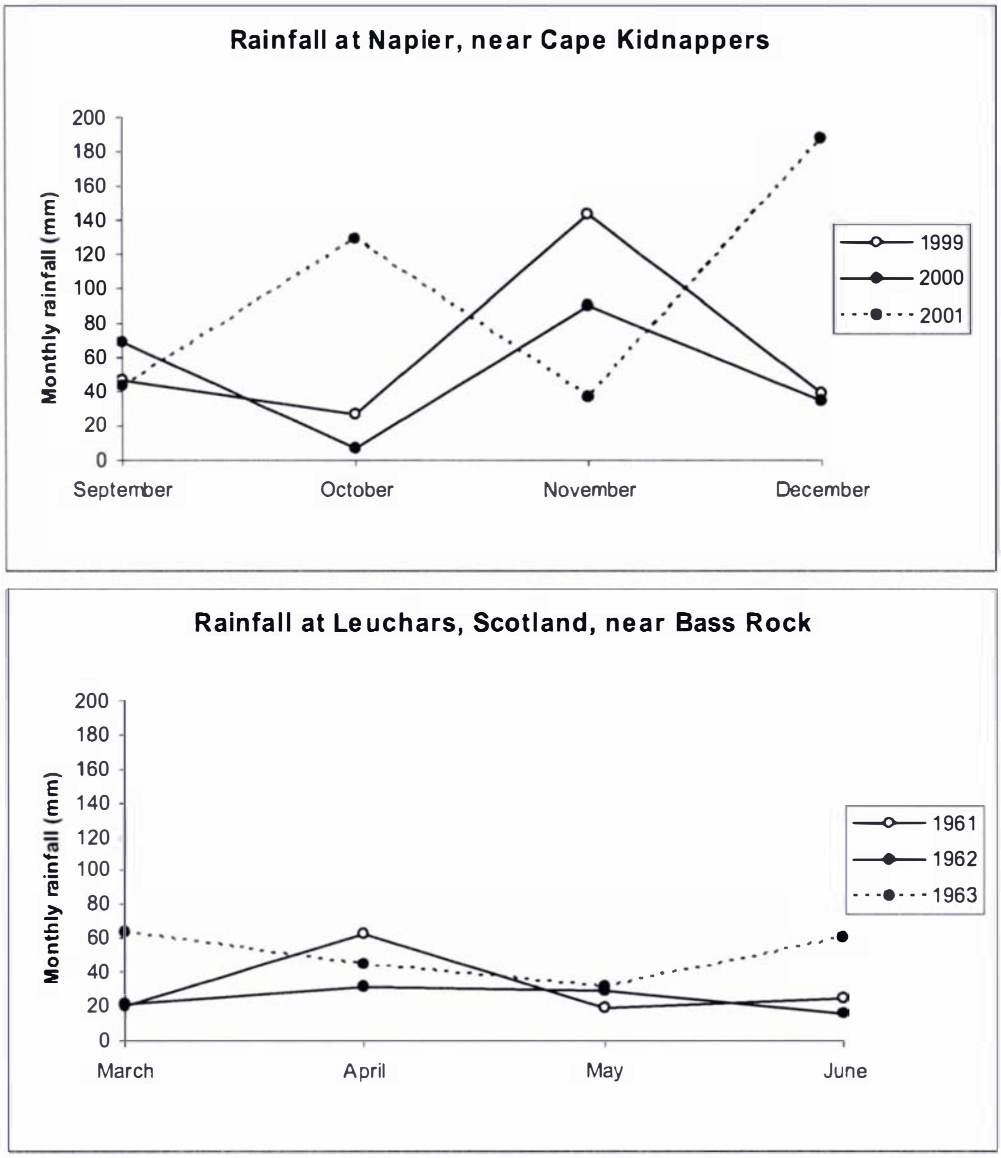

Figure 2: Mean monthly rainfall at Napier, near Cape Kidnappers in New Zealand, and at Leuchars, near Bass Rock, Scotland. Data for 1999-2001 for New Zealand, during this study are compared with data from 1961-1963 in Scotland during Nelson's work. The results show more variability in mean monthly rainfall at Cape Kidnappers during egg laying and the early chick stage, than in Scotland.

The Cape Kidnappers gannetry: a profile of the study site

Cape Kidnappers (39° 38' S, 177° 05' E) is situated approximately 20 km south-east of Napier. The gannetry currently consists of four colonies, the Saddle, Plateau, Black Reef, and Plateau Beach colonies (Fig. 3).

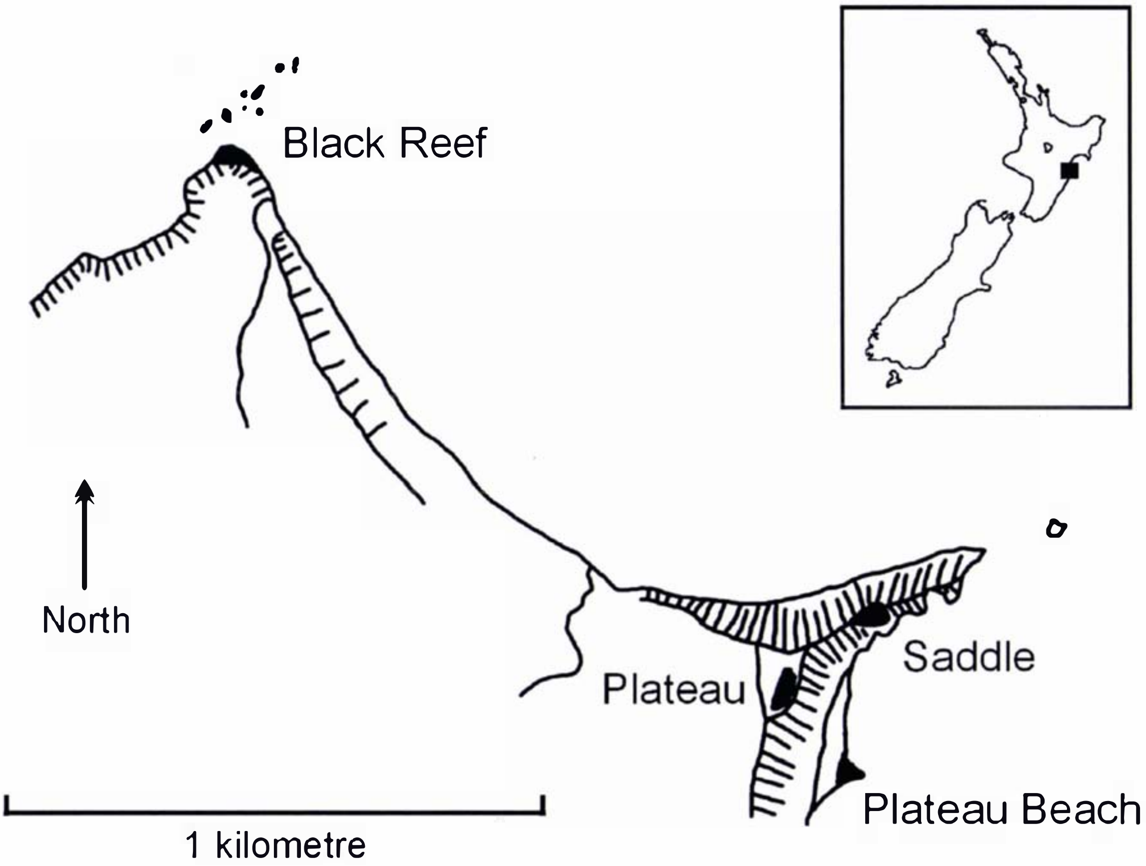

Figure 3. Map of the Cape Kidnappers gannetry showing the location of the four colonies.

A brief history of the gannetry

It is not known if a gannetry was established at Kidnappers in pre-European times, as no authentic references to a gannetry have been found in Maori tradition (Wodzicki & McMeekan, 1947). Fleming & Wodzicki (1952) summarised the history of the Cape

Kidnappers gannetry, up to the 1945-46 census, providing a brief background on the work and photographs taken at the site, which have allowed an insight into its development.

By the time of Captain Cook's 1769 voyage past Cape Kidnappers it is almost certain that there was no gannetry (Fleming & Wodzicki, 1952). Cook's voyage was made during October, by which time gannets would have been breeding. In his diary, Joseph Banks made no reference to nesting seabirds in the area (Fleming & Wodzicki, 1952). Furthermore, on 3 February 1829, Dumont D'Urville, in the 'Astrolabe', passed "not more than a league" from Cape Kidnappers, and described its appearance in some detail (D'Urville (1950) quoted from Fleming & Wodzicki (1952)). Just four days before D'Urville had recorded gannets at sea north of Cape Palliser, and noted them again near East Cape. Had a gannetry been present, it would surely have been noted.

The establishment date of the Cape Kidnappers gannetry is speculative. In 1929, H. Hill was reported to have said that he first visited Cape Kidnappers "fifty years ago" (ie. c. 1879) and that the number of gannets did not exceed 50 (Fleming & Wodzicki, 1952). The first dated report of breeding gannets was made by J.C. McLean on 19 January 1885 (Fleming & Wodzicki, 1952). His notes mention that "The gannets nest on a cliff near the Cape, about 100 nests were made of seaweed and earth...". This would have been a reference to the Saddle colony, and may have slightly underestimated the numbers, as on 21 December 1888 he calculated nearly 500 nests from their nesting density. Fleming & Wodzicki (1952) suggest that the Saddle colony was probably established about 1850. The development of the Saddle colony from 1890 through to 1945 (when the first attempt at accurately counting the gannetry was made by Wodzicki & McMeekan (1947)) can be assessed from a series of photos taken at irregular intervals. Fleming & Wodzicki (1952) give details of these photos and estimates of the number of birds breeding from these (Table 1).

So from 1879 to 1903, the Saddle colony increased at an average annual rate of 17%, well above the 3% considered to be the natural rate of increase calculated from census data and reproduction and mortality rates (Wodzicki et al., 1984; Nelson, 2002), thus, suggesting considerable immigration. From 1903 to 1931 the colony continued to increase, but at rates of less than 5% per annum, probably close to the natural increase of the colony (Fleming & Wodzicki, 1952; Bunce et al., 2002).

Table 1. Estimated number of breeding pairs of gannets at the Saddle colony, Cape Kidnappers. Counts conducted before the 1945 census were rough estimates. Most photos did not show the entire colony meaning some guess work was involved in estimating numbers.

Date of estimate	Source	Estimated breeding pairs	Reference
c. 1879	Count	< 50	Fleming & Wodzicki (1952)
January 1885	Count	c. 100	Fleming & Wodzicki (1952)
December 1888	Count	c. 500	Fleming & Wodzicki (1952)
January 1890	Photo	400-500	Fleming & Wodzicki (1952)
December 1896	Count	c. 1000+	Buller (1897)
November 1903	Photo	1226	Fleming & Wodzicki (1952)
Late 1913	Photo	1300	Fleming & Wodzicki (1952)
c. 1920	Photo	1800	Fleming & Wodzicki (1952)
1922-1923	Count	c. 2000	Cottrell (1923)
March 1930	Photo	< 2000	Fleming & Wodzicki (1952)
February 1931	Photo	< 2000	Fleming & Wodzicki (1952)
December 1945	Count	2265	Wodzicki & McMeekan (1947)
November 1946	Photo	2337	Fleming & Wodzicki (1952)

By 1945, Cape Kidnappers had developed into three colonies - the original Saddle colony, as well as the Black Reef and Plateau colonies. Again, the establishment date of the Black Reef colony is not known. However, it appears the area was not occupied by gannets before the 1930-31 season (R.H.D. Stidolph pers. comm. in Fleming & Wodzicki (1952)). The first use of this locality by breeding gannets was reported from the 1938-39 season, in the "Hawkes Bay Daily Mail", 22 July 1939 (Fleming & Wodzicki, 1952). In 1945-46, there were 376 breeding pairs scattered over five of the rocks and mainland ledges at Black Reef (Wodzicki & McMeekan, 1947).

The Plateau colony was also not in use during 1930-31 (R.H.D. Stidolph pers. comm. in Fleming & Wodzicki (1952)), although by 1934, 50 roosting birds were photographed using the area (N. Carroll pers. comm. in Wodzicki et al. (1984)). Nesting was first reported during the 1936-37 breeding season (W.B. Stewart pers. comm. in Wodzicki et al. (1984)) and there were 196 breeding pairs at the colony in 1945-46 (Wodzicki & McMeekan, 1947). The lack of hard evidence and the relatively recent citing of the pers. comm. by Stewart, has led to some confusion, with Nelson (1978b) suggesting establishment of breeding in 1945.

Gannets have used the Plateau Beach colony as a roost site since 1972-73, and from 1988 began breeding at this fourth and most recent colony (C.J.R. Robertson unpubl. data). Eggs had been laid in the 1975-76 and 1976-77 breeding seasons, but no chicks were produced (Wodzicki et al., 1984). Disturbance by stock, goats and fisherman may have prolonged the establishment of this colony.

The Saddle colony grew steadily to an estimated peak of 2,700 breeding pairs in 1970. Since then it has declined to around 2,100 pairs in 1995 (C.J.R. Robertson unpubl. data). The cause for this recent decline is the shrinking of the colony away from the eroding cliffs. The Black Reef gannetry has steadily increased to an estimated 2,500 breeding pairs in 1995, scattered over the cliffs and isolated rock stacks in this area. In recent years growth has mainly occurred on the mainland cliffs as the rock stacks have become full. The Plateau colony has also steadily grown to about 1,652 breeding pairs in 1995, and appears to have levelled off at approximately 2,000 between 1997 and 2001. The Plateau Beach colony had an estimated 345 breeding pairs in 1995, but this has steadily grown to around 916 breeding pairs in 2003 (B. Stephenson unpubl. data). This gives a total of around 6,597 breeding pairs at the Cape Kidnappers gannetry in 1995, and a rough estimate of about 7,500 at present.

The Cape Kidnappers gannetry was studied extensively from 1947 to 1964 by K. Wodzicki, with C.J.R. Robertson continuing the study since 1959. Annual ground counts have been made at the Plateau colony in the period 12-25 December since 1945 (except 1975, and estimates were derived from November and January counts made in 1955, 1956, 1958, and 1960). Aerial surveys of all colonies have been made and photographs taken during each year since 1966. A number of papers have since described population changes and various aspects of gannet ecology at these colonies (Wodzicki & Robertson, 1953; Wodzicki & Stein, 1958; Robertson, 1964; Wodzicki & Moreland, 1966; Wodzicki, 1967a; Wodzicki & Robertson, 1974; Wodzicki et al., 1984; Robertson, 1992). The data show changes in the numbers of occupied sites, distribution and density of nest sites, and contain probably the most accurate record of the development of any seabird colonies in the world.

The study site

During this study, field-work was conducted mainly at the Plateau colony, with observations of the Black Reef colony during the egg laying period. Figure 1 shows the locations of the four colonies, which are also shown in Figs. 4, 5, 6, & 7. One hundred nest sites on the seaward (eastern) side of the Plateau colony were randomly chosen and individually marked with permanent markers, whilst the colony was empty on 8 July 1999. As the nest sites were randomly chosen along the colony edge, nests varied from being right on the edge of the colony, to approximately eight metres in from the edge. Only those sites that contained nest cups or scrapes from the previous season were able to be selected. These nests were intensively monitored over three breeding seasons, 12 August 1999 - 3 April 2000, 8 August 2000 - 16 April 2001, and 2 August 2001 - 3 March 2002. They were also monitored three times during the 2002-03 breeding season. These monitored sites were situated on the opposite side of the colony to that which the public views the colony from the chain fence.

Aims of this thesis

This thesis aims to investigate the annual variability in breeding ecology of Australasian gannets breeding at a relatively undisturbed, but easily visited colony. To date, most studies of this species have occurred at sites which are logistically difficult to reach, and thus gaps in observations have led to assumptions and potential mistakes in the analysis of breeding data. Cape Kidnappers, and specifically the Plateau colony, although regularly visited by large numbers of tourists during the breeding season, fits the criteria of being easy to reach and relatively undisturbed (tourists are not allowed past chain barriers).

Previous studies have led to the suggestion that Australasian gannets exhibit a similar breeding biology to Atlantic gannets (eg. Wingham 1984a, 1984b), despite considerable periods of the breeding season being missed. Atlantic gannets appear to show very little annual variability in most aspects of their breeding biology (Nelson 1964, 1968). However, other studies in New Zealand and Australia have documented irregular breeding failures which have not been adequately accounted for, and show no similar events in Atlantic gannets (see Chapter 3). Thus, this thesis sets out to discover whether within a short-term study (three breeding seasons) annual variability in breeding biology exists, and if possible what caused this variability. The latter is of course secondary, as discovering if annual variability exists will set this species significantly apart from the Atlantic gannet, with which some currently consider it to be a super-species.

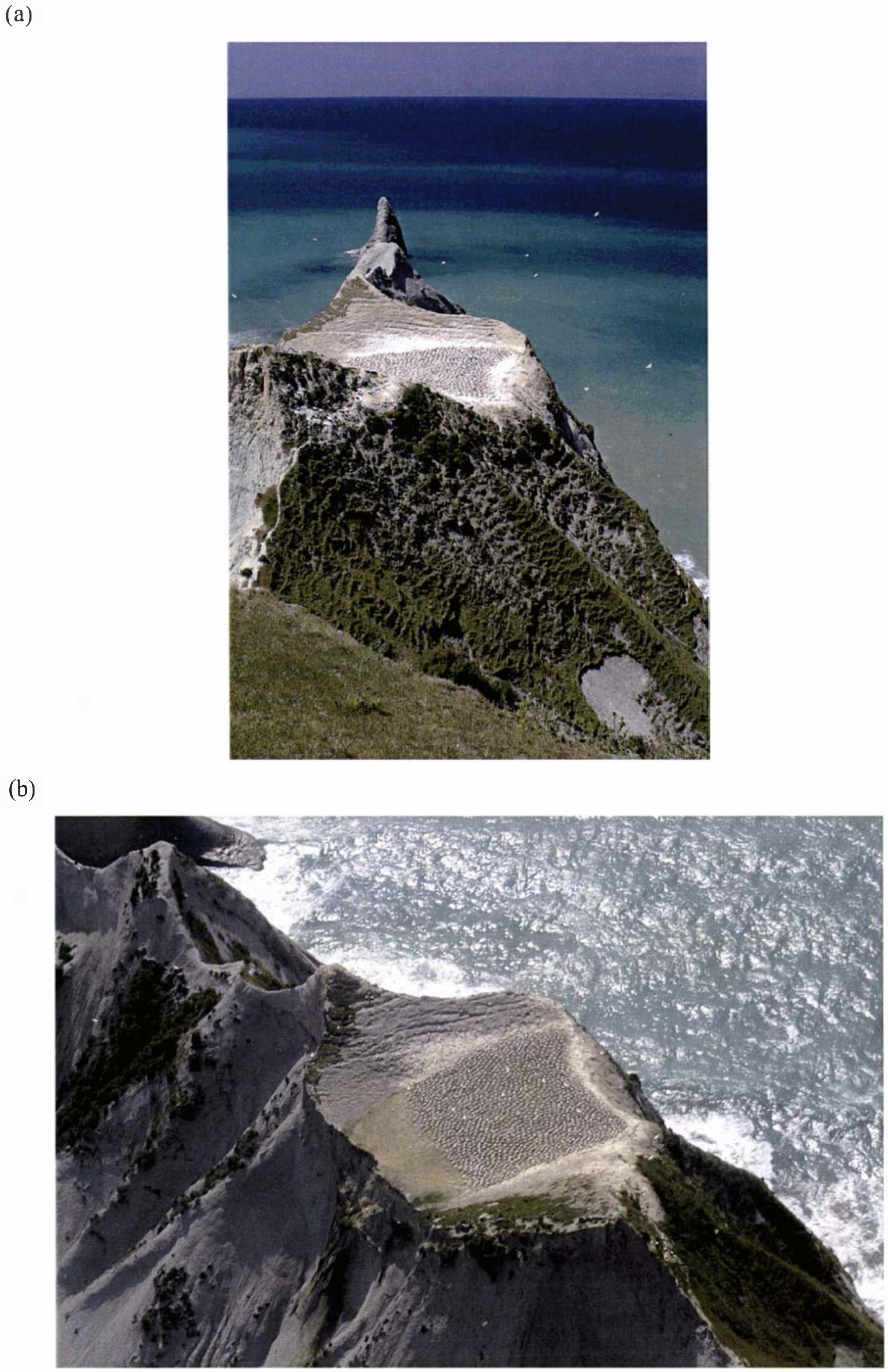

Figure 4. (a) Saddle colony photographed from the south near the lighthouse, and (b) taken from the air from a southwestern direction.

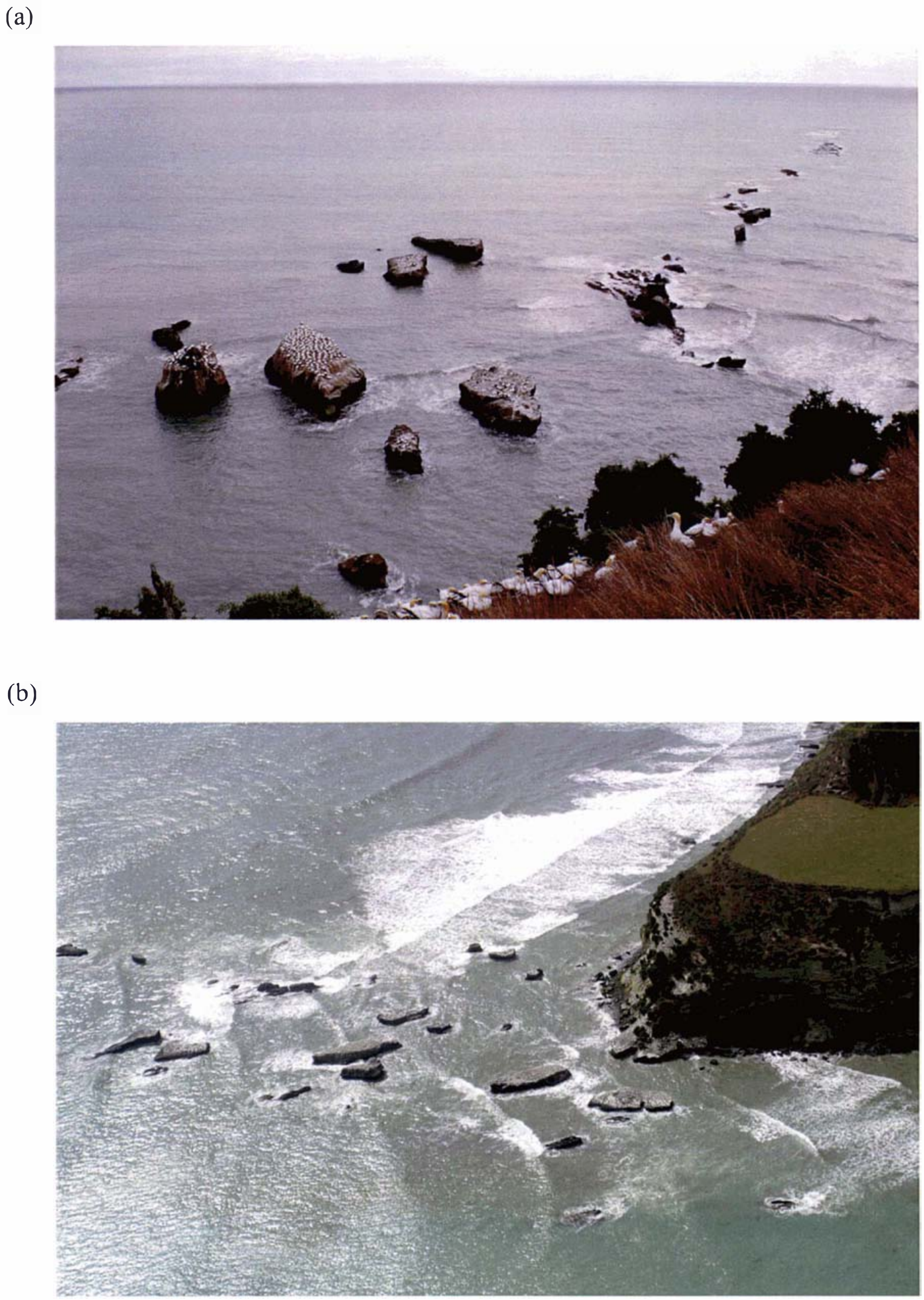

Figure 5. (a) Black Reef colony from the paddocks at the top of the cliffs, looking north, and (b) from the air taken from the west of the colony.

(a)

(b)

Figure 6. (a) Plateau beach colony from up near the Plateau colony situated to the west, and (b) Plateau colony photographed from north of the colony, showing the chain fence the public are able to view the colony from.

Figure 7. Plateau colony from the air, taken from a northwestern direction. The monitored nests are indicated, being situated on the seaward, eastern side of the colony, furthest away from the chain fence from which the public view the colony.

To investigate annual variability, I regularly monitored the one hundred nests as indicated above, over the three breeding seasons. I recorded attendance patterns by adults, date of egg laying, egg size and hatching success, incubation period, chick growth rates and fledging success, and overall breeding success and productivity. Where differences occurred between breeding seasons in any of these variables, the potential consequences and possible causes are discussed.

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2

The breeding phenology of Australasian gannets, Morus serrator, *at Cape Kidnappers*

Introduction

The Australasian gannet, *Morus serrator*, breeds around the coast of New Zealand and at several localities in southeastern Australia. Its population in New Zealand has increased markedly over the past century, with censuses suggesting an increase from 21,133 breeding pairs in 1945-46 (Fleming & Wodzicki, 1952) to 46,004, in the 1980-81 census (around 2.3% per annum) (Wodzicki et al., 1984). Since 1980, the New Zealand population appears to have continued to increase at a slightly lower rate of around 2% per annum (C.J.R. Robertson quoted in Nelson (2002)). The breeding population in Australia is estimated to have increased at about 6% per annum between 1980 and 1999, to approximately 20,000 breeding pairs (Bunce et al., 2002). The species is generally thought of as being relatively well studied (eg. Marchant & Higgins (1990)), and studies of its biology, in New Zealand and Australia, date back to the 1930s.

Oliver (1930) was the first to describe the habits and distribution of Australasian gannets. Visits to colonies and observations in the early-1940s provided the first insight into the breeding ecology and population status of the species (Buddle, 1947a; Buddle, 1947b; Buddle, 1948; Bull & Fleming, 1947; Cunningham, 1947; Fleming, 1947a; Fleming, 1947b; Fleming & Sibson, 1947; Hamilton, 1947; Wodzicki & McMeekan, 1947; Clark & Roberts, 1948; Fleming, 1948; Robertson & Wodzicki, 1948; McKenzie, 1949; Hamilton, 1950; Stein, 1950; Roberts, 1954), with reference to breeding phenology in many of these papers.

Several workers then studied the breeding biology of the species more closely, primarily at Cape Kidnappers (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953; Wodzicki & Stein, 1958; Wodzicki, 1967a; Wodzicki, 1967b) and in the Hauraki Gulf (Stein, 1971). These studies provided basic information on general breeding biology (egg and chick measurements, incubation and fledgling periods, breeding success), breeding behaviour, and population dynamics, but little information on the timing of breeding. Warham's (1958) study of the Cat Island gannetry off Tasmania, provides similar information for an Australian colony.

Undoubtedly, the most comprehensive study of Australasian gannet breeding biology to date is that by Elspeth Wingham[1] of three seasons at Motukaramarama in the Hauraki Gulf, between 1978-81 (Waghorn, 1983; Wingham, 1984a; Wingham, 1984b; Wingham, 1985; Wingham, 1989). Unfortunately, all of the first season's first eggs were missed (with a storm destroying all first clutches, and causing replacement eggs to be laid), and for the second season she missed most of the laying of first clutches. In more recent years there have been breeding studies at Australian colonies in Port Phillip Bay (Norman & Menkhorst, 1995; Gibbs et al., 2000; Bunce, 2001).

Other than Wingham's study and Warham (1958), all other studies to date have been based on one or two visits per breeding season, or visits to colonies at intervals of 1-2 weeks or more. The use of back-dating from chick ages and hatching dates to determine laying dates, has therefore been used to fill in the blanks throughout these studies. Yet, the accuracy of this technique has never been assessed. Furthermore, Australasian gannets differ markedly from Atlantic gannets, *Morus bassana*, in having highly variable breeding success from year to year (Chapter 3). This has not been fully appreciated by most workers, leading to a rather piecemeal understanding of the breeding phenology of the species, and potentially incorrect comparisons with the Atlantic gannet.

Studies of Australasian gannets show they have an asynchronous breeding system, with large annual variation in timing of breeding (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953; Nelson, 1978b; Wingham, 1984a), and this forms the basis of our current literature (eg. Marchant & Higgins (1990)). In contrast, the Atlantic gannet shows a similar onset of laying between years, and highly synchronous egg laying within colonies (Nelson, 1966; Nelson, 1978b). Because of their size, gannets have one of the smallest egg production demands on the female of any seabird species (Perrins, 1970; Ricklefs & Montevecchi, 1979). As a result, the timing of laying in both gannet species would be expected to be relatively synchronous, to take advantage of chick rearing during peak food

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[1] Elspeth Wingham nee Waghorn

abundance. At least for Atlantic gannets, a reliable, predictable, and abundant food supply is suggested to be the cause for the timing and synchrony of breeding (Nelson, 1978b). Comparison with Australasian gannets, in which chicks have a more prolonged fledgling period (Wingham, 1984b), and suffer highly variable breeding success, suggests that they do not benefit from similarly predictable peaks of food abundance. Nevertheless laying should be timed so that chick rearing coincides with the time when food is most likely to be plentiful. Alternatively, egg laying may be timed to coincide with favourable conditions for chicks at fledging time. In either case, egg laying should still be synchronous.

The aim of this study was to provide the first detailed, uninterrupted observation of breeding by Australasian gannets, over three consecutive breeding seasons. I examine how breeding phenology differs from that of the Atlantic and Cape gannet, and consider possible explanations for these differences. I also assess the use of back-dating to estimate onset of laying.

Methods

The Cape Kidnapper's gannetry (39° 38' S, 177° 05' E) is situated on the east coast of the North Island, New Zealand (Fig. 1). The gannetry consists of four Australasian gannet colonies, the Saddle (originally called Cape Kidnappers colony), Plateau, Black Reef, and Plateau Beach. Several papers have described the gannetry and its history, and changes in the breeding population have been well documented since 1945 (Wodzicki & McMeekan, 1947; Wodzicki, 1967b; Wodzicki et al., 1984; Fleming & Wodzicki, 1952; C.J.R. Robertson, unpubl. data). The birds' breeding biology in New Zealand was first documented at this site (Wodzicki & McMeekan, 1947).

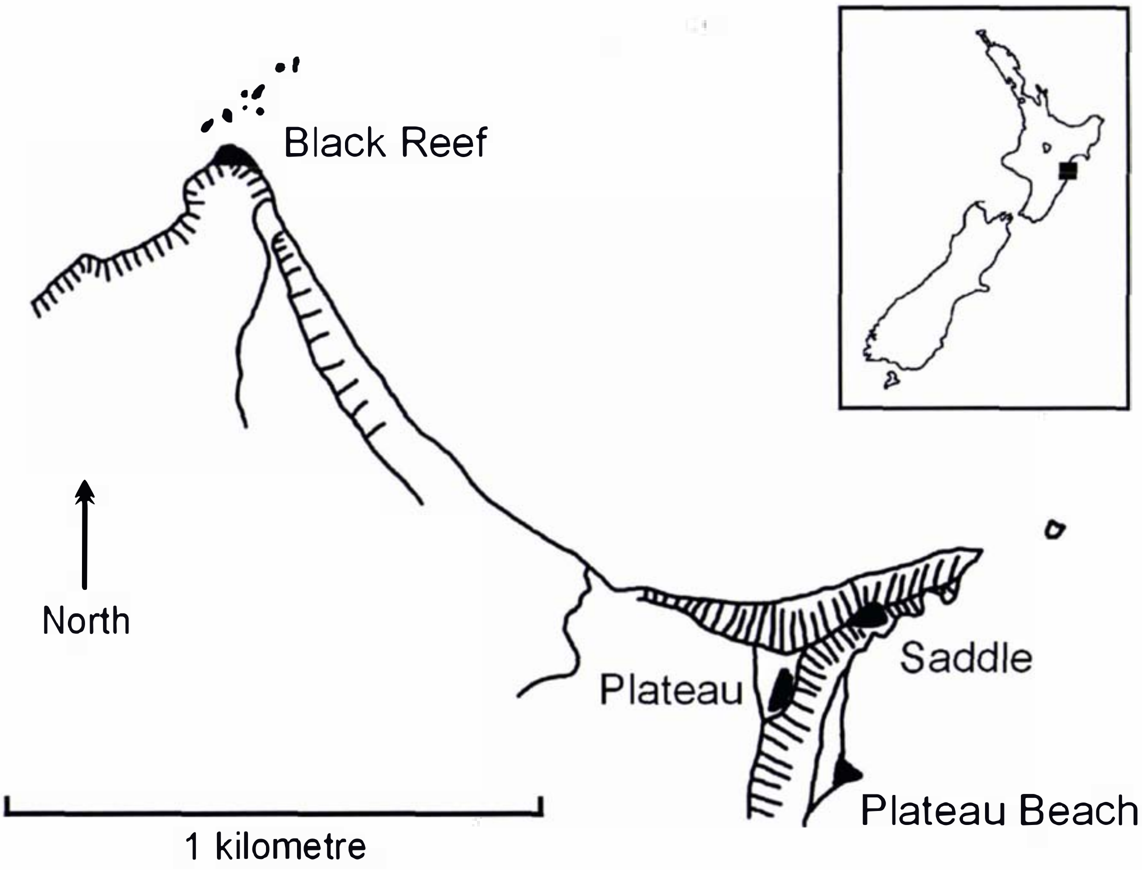

Figure 1. Location of the Cape Kidnappers gannetry, showing its orientation and the position of each of the four colonies. During this study, work was mainly conducted at the Plateau colony.

One hundred nest sites on the seaward (eastern) side of the Plateau colony were randomly chosen and individually marked with permanent markers, whilst the colony was empty on 8 July 1999 (see Chapter 1 for photos and additional information). These nests were intensively monitored over three breeding seasons, 12 August 1999 - 3 April 2000, 8 August 2000 - 16 April 2001, and 2 August 2001 - 3 March 2002. They were also monitored three times during the 2002-03 breeding season (14 November 2002, 20-21 December 2002, and 23 January 2003), to provide an estimate of laying dates for that season. Thus, data are presented for the 2002-03 season only where applicable.

To determine status of nesting attempts, nest contents, nest attendance and identity of adults, nests were checked approximately daily from September to late-December, but less frequently from December to March. Additionally, in 1999-00, the marked nests were checked three times on most Thursdays throughout the season (shortly after dawn, midday, and at the time of the normal late afternoon nest check), allowing an investigation of the time of day eggs were laid.

A nesting attempt was defined as attendance at a site by a pair, and the formation of a nest using seaweed. A 50% attendance statistic was developed, being the first date on which 50% of the marked nests were attended by an adult in each season. No more than one day was missed consecutively during the peak egg laying periods of all seasons. The date on which the first egg was laid on Rock Naught (Black Reef colony) was also determined by observing nests with binoculars. Rock Naught is one of the rock stacks which becomes surrounded by water at high tide. Approximately 240 breeding pairs use this stack annually.

All eggs were numbered with a non-toxic permanent marker (red Sharpie ® fine point) to allow eggs to be identified. Gannets lay only a single egg per clutch, with replacement eggs being laid by some birds if the first egg is lost. First clutch eggs are referred to as first eggs, whilst second and third clutch eggs are referred to as second and third eggs. The term 'all eggs' refers to first, second and third eggs collectively. The median laying date was the day on which 50% of laying had occurred, and was calculated separately for first eggs and all eggs.

Data from each season were examined to determine whether back-dating the age of chicks at the colony could accurately estimate onset of laying. As the number and age of chicks was known throughout the breeding season, three specific dates were chosen for analysis. These were 1 December, 20 December, and 30 January. By 1 December most first eggs that were successful in hatching, had hatched (98%, 92%, and 99%, in each of the three seasons respectively). The 20 December date was chosen as this is about when the annual pre-Christmas census is conducted at Cape Kidnappers (C.J.R. Robertson, unpubl. data), and 30 January was chosen as by this stage chick deaths are rare, and no fledging has yet occurred.

Sea surface temperature (SST) data were obtained from NOAA's Comprehensive Large Array-data Stewardship System (CLASS) electronic library of environmental satellite data, through their website (http://www.saa.noaa.gov/cocoon/nsaa/products/welcome). SST data for two locations close to the study site were significantly correlated ($r = 0.988$, $P < 0.0001$), therefore SST data for 39° 30' S, 177° 30' E, approximately 38 km north-east of Cape Kidnapper's in the middle of Hawke Bay, were used for analysis in this chapter.

All statistical analyses were performed using SPSS for Windows, Release 11.5.0 or 12.0.1. Capture, handling and banding of birds was conducted under the Department of Conservation New Zealand National Banding Scheme, Institutional Permit to band birds No. 0259. The Massey University Animal Ethics Committee gave permission to conduct this research, Protocol No. 98/173.

Results

Colony attendance

Attendance at the colony began in late July – early August in each season (Fig. 2), but birds were sometimes present as early as the start of July. As daily observation of the colony did not begin until close to egg laying, the exact date on which 50% attendance of the monitored nests was reached fell between 20 – 27 August 1999 and 25 August – 9 September 2000. However, in 2001 50% attendance was reached on 20 August. There was considerable variation in the number of gannets attending sites, depending on the time of day the nest check was conducted, with occupancy highest at the beginning and end of the day (B. Stephenson unpubl. data).

Egg laying

Timing of first and replacement eggs

A nesting attempt was made at all but four of the monitored nests in 1999-00, and at all nests in 2000-01 and 2001-02. The first egg was laid on 17 September 1999, 24 September 2000, 23 September 2001, and approximately 29 September 2002 (the 2002 figure is backdated from the date the first egg hatched) (Table 1, Figs. 2 & 3). There was no clear relationship between the date of 50% attendance and the date on which the first egg was laid, possibly due to a lack of precision in the date of 50% attendance.

The first second egg was laid on 18 October 1999, 26 October 2000, and 14 October 2001. These dates were 31, 32, and 21 days after the first egg was laid, in each of these seasons, again showing high consistency. The first second eggs were laid well after the median laying date (Fig. 3), after the majority of first eggs had been laid. This is mostly because very few first eggs were lost before the median laying date (see Chapter 3).

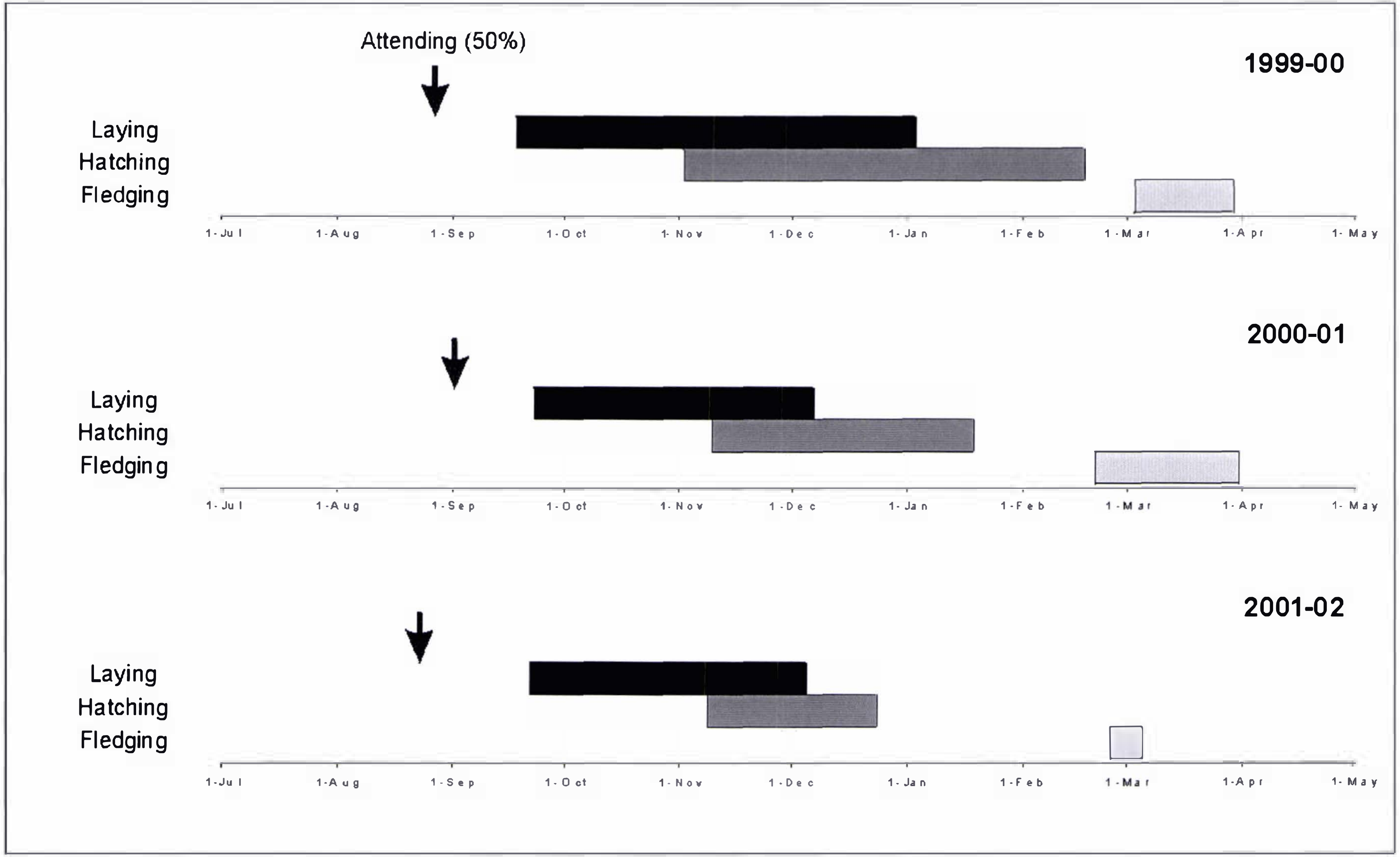

Figure 2. Breeding phenology of the 100 monitored nests at the Plateau Colony, Cape Kidnappers, during the three breeding seasons studied. The arrows indicate the approximate date at which attendance of 50% of nests was reached. Black bars show the egg laying period (both first and replacements), grey bars show the chick hatching period, and pale bars show the chick fledging period.

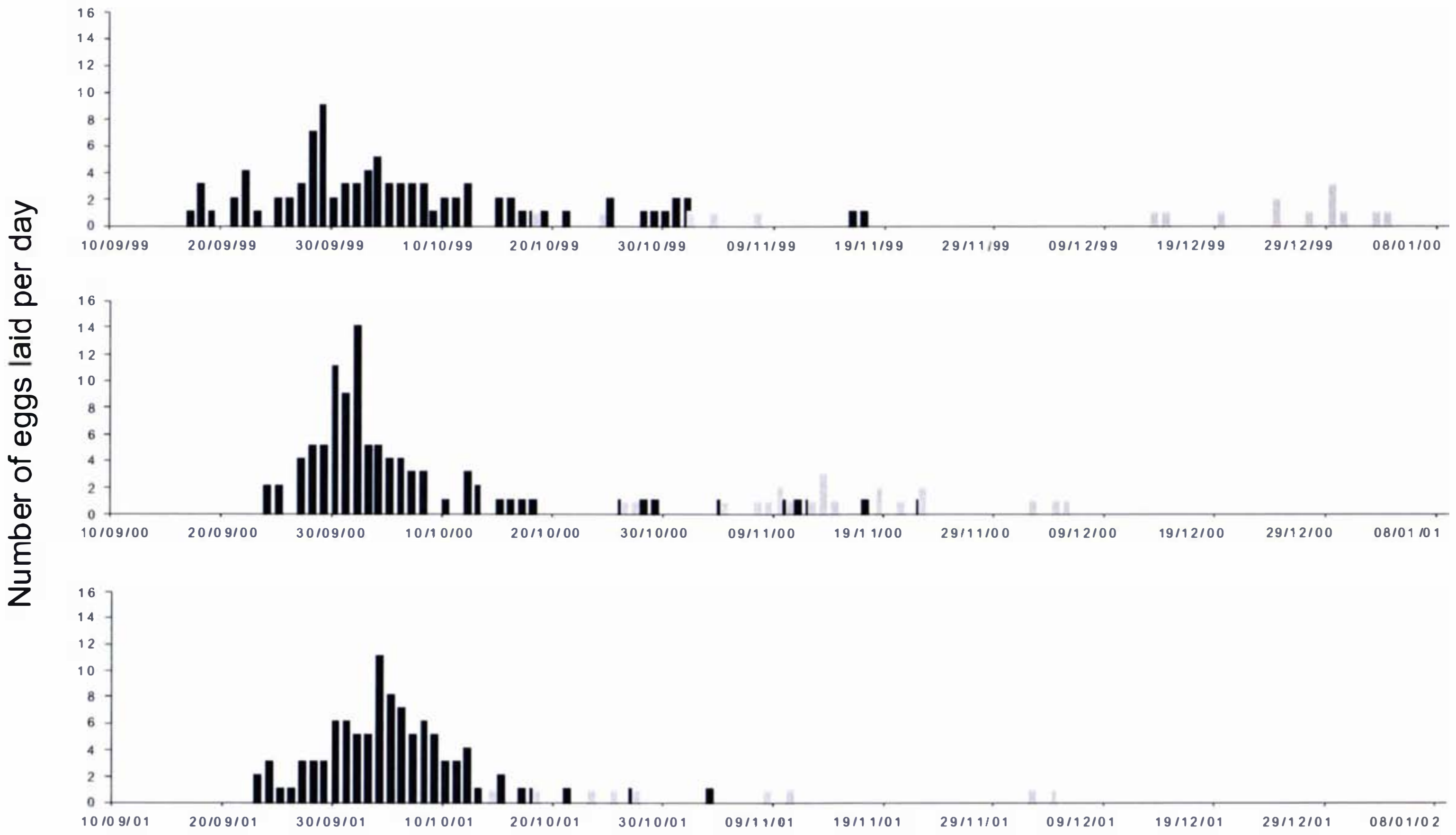

Figure 3. Number of first (solid) and second (shaded) eggs laid per day, for each of the three seasons, at the 100 monitored nests. A total of 91, 95, and 98 first eggs and 17, 21, and 9 second eggs were laid in the 1999-00, 2000-01 and 2001-02 seasons, respectively. Two third eggs, one laid in each of the 1999-00 and 2000-01 seasons, are not plotted, but were laid on 2 November and 7 November respectively. Gaps in the main laying peak are real, and not due to lack of sampling.

Table 1. Laying phenology of the 100 monitored nests, for each breeding season. First and replacement (second and third) eggs are shown. Spread of laying is given in weeks (days). The 2002-03 breeding season is included only in the all eggs section, as a distinction between first and replacement eggs could not be made. In that season the date of first egg was estimated from the age of newly hatched chicks.

Clutch	Season	No. laid	Date of first laying	Median laying date	Date of last laying	Spread of laying
First	1999-00	91	17 September	3 October	17 November	9 (61)
	2000-01	95	24 September	2 October	22 November	8 (59)
	2001-02	98	23 September	4 October	3 November	6 (41)
Replacement	1999-00	18	18 October	19 December	3 January	11 (77)
	2000-01	22	26 October	13 November	5 December	6 (40)
	2001-02	9	14 October	27 October	4 December	7 (51)
All	1999-00	109	17 September	5 October	3 January	15 (108)
	2000-01	117	24 September	4 October	5 December	10 (72)
	2001-02	107	23 September	5 October	4 December	10 (72)
	2002-01	-	c. 29 September	-	-	-

Distribution of egg laying

The number of eggs laid per day, in each of the three main seasons, follows a nearly normal distribution, but with a positive skew (Fig. 3). Mean first egg laying dates were not significantly different between seasons (One-way ANOVA $F_{2, 281} = 0.314$, NS). I tested the degree of synchrony in each season and found that 1999-00 and 2000-01 were significantly less synchronous than 2001-02 (Levene's test $F_{2, 281} = 10.0$, $P < 0.001$ and Student-Newman-Keuls test of deviate at $\alpha = 0.05$). The difference in degree of synchrony between 1999-00 and 2000-01 approached significance (Tukey HSD test of deviate, $P = 0.261$). Within three weeks from the laying of the first egg, 71%, 86%, and 93% of first eggs were laid, in each of the seasons respectively.

The spread of laying (period of time between the first and last laid egg) for first eggs was 61, 59, and 41 days for each season, respectively. When including all eggs, total spread of laying was 108, 72, and 72 days for each season. The 1999-00 season clearly stands out as being different, with egg laying being less synchronous and the laying of second eggs extending into early January. Thus, 72 days appears to be the normal spread of laying at the Plateau colony.

The median laying dates of first eggs is very consistent when visually compared, being 3 October 1999, 2 October 2000, and 4 October 2001 (Table 1). These medians are 16, 8, and 11 days after the first egg was laid, respectively. Including all eggs, the median date changes to 5 October 1999, 4 October 2000, and 5 October 2001 (Table 1), 18, 10, and 12 days after the date of first egg. Again, this shows a high degree of consistency between years.

In both 1999-00 and 2000-01, a second peak in laying occurred due to the laying of second eggs (Fig. 3). In 1999-00 this occurred between 13 December and 3 January, and in 2000-01 between 7 – 22 November. In 1999-00, this re-laying was comparatively late, with no second eggs being laid after 4 and 5 December, during the other two seasons. Of the 17 second eggs laid in 1999-00, only one produced a chick to fledging, and it was laid on 3 November, well before the peak. During 2001-02 there were few second eggs laid (>50% compared to the other two seasons), as a result of the high hatching success in that season (see Chapter 3). The laying of an egg in early January would mean fledging in early June, which is highly unlikely to be successful.

Estimating the onset of laying from chick ages mid-season

Even though large numbers of eggs were lost during the first and second seasons, accurate estimation of the onset of laying was possible using the back-dating technique (Table 2). In the 1999-00 season, the estimate made on 1 December was three days later than that actually observed through monitoring the laying of eggs. By 20 December and 30 January in that season, the estimate was five days later than the actual onset. However, this was the largest difference recorded over the three seasons, and was probably as a result of the large number of eggs lost in that season. In both 2000-01 and 2001-02, estimates on all three dates were only one day late.

Average chick age shows differences in annual laying patterns less accurately, especially late in the season. For example in 1999-00 when there were considerable egg and chick losses, the average age would indicate a peak laying period 8 days later than it actually was.

Table 2. Estimated onset of laying dates from observing the colony and aging the oldest chick at three dates throughout the breeding season. Average age of chicks on those dates is also shown, followed by range, in days. Differences between observed and actual dates are not large, suggesting that back-dating may be a useful guide.

		1 December		20 December		30 January	
Season	Onset of laying	Estimated onset	Average age, range	Estimated onset	Average age, range	Estimated onset	Average age, range
1999-00	17/09/99	20/09/99	16, 9-28	22/09/99	31, 3-45	22/09/99	65, 1-86
2000-01	24/09/00	25/09/00	15, 0-23	25/09/00	32, 7-42	25/09/00	68, 12-83
2001-02	23/09/01	24/09/09	13, 1-24	24/09/09	33, 18-43	24/09/09	77, 59-84

Laying date of individual females

To assess whether individual females laid eggs consistently early or late in the season, I examined 16 banded females that laid eggs in each of the three seasons. Females showed significant consistency, relative to the median laying date, for first eggs (One-way ANOVA $F_{15, 32} = 2.141$, $P < 0.035$). That is, females that laid early in one year, tended to lay early in the other two. This supports the findings from the colony as a whole.

Time of day eggs were laid

This study allowed investigation of the time of day that 22 eggs were laid. Fourteen (64%) were laid in the morning, roughly between 0700 and 1300 NZST, and 8 (36%) were laid in the afternoon, roughly between 1300 and 1800 NZST. Eggs did not seem to be laid at night.

Comparison of laying dates between Cape Kidnappers colonies

The first egg was laid on Rock Naught, at the Black Reef colony, on 11 September 1999, 19 September 2000 and 12 September 2001. This is 6, 5, and 11 days earlier than at the study nests at the Plateau colony, suggesting a consistent annual difference, which is difficult to explain, based on the 1500 m distance between the colonies.

Chick hatching and fledging

The first egg hatched on 3 November 1999, 8 November 2000, and 7 November 2001, with the last hatching on 18 February 2000, 18 January 2001, and 23 December 2001. All of these last eggs were from second clutches, fitting with peaks in second egg laying in each of the first two seasons. Exact fledging date of individual chicks was difficult to detect, as chicks wandered throughout the colony prior to fledging. However, chicks from the monitored nests fledged between 4 – 27 March 2000, 22 February – 3 March 2001, and 28 February – 28 March 2002. This suggests there were differences in the fledging dates of chicks between seasons, with fledging being earlier in 2000-01. This appears to be linked to breeding success, as in 2000-01 when breeding success was highest, chicks fledged earlier.

Sea surface temperature and the onset of laying

A plot of the SST data for each of the breeding seasons shows large variation through the months before and after egg laying (Fig. 4). In 1999-00 and 2000-01, SSTs on the date of onset of egg laying were similar, being 13.7°C on 17 September 1999 and between 13.5 – 14.1°C on 24 September 2000. In 2001-02, SST was between 14.5 – 14.7°C on 23 September when the first egg was laid.

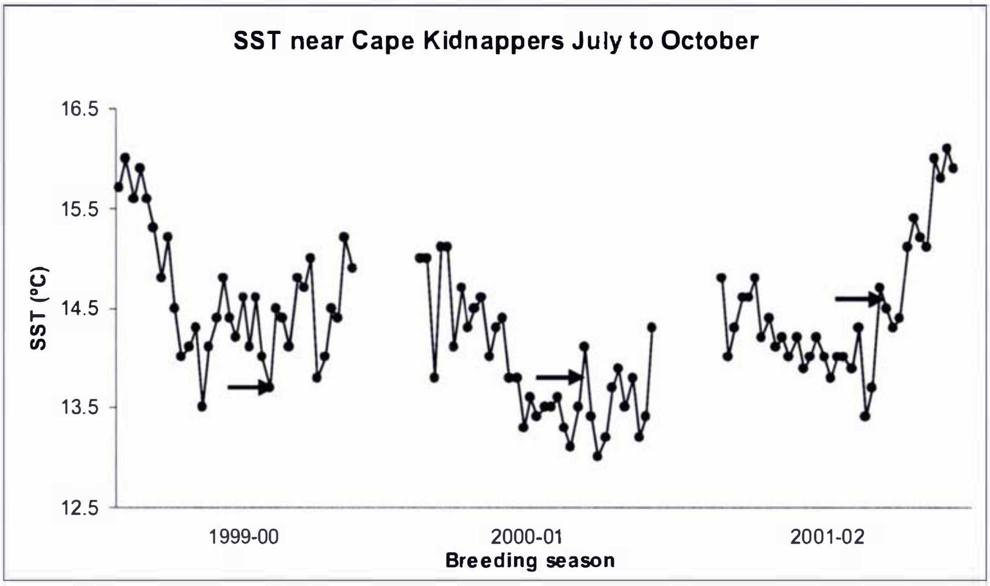

Figure 4. SSTs at 39° 30'S, 177° 30'E, throughout the months of July to October, in each of the breeding seasons. The arrows represent the onset of laying in each season at the Plateau colony.

Discussion

The data presented in this chapter, based on three consecutive breeding seasons, are the most comprehensive timing of breeding information available for Australasian gannets. They describe the breeding phenology of Australasian gannets and provide a different perspective to our current knowledge and interpretation of Australasian gannet breeding biology.

Colony attendance

Occupancy of the Plateau colony from late-July to August is consistent with previous studies at this colony (Wodzicki, 1967b; Wodzicki & Robertson, 1953). Peak numbers of birds attending the colony in the early morning and late evening has also been noted (Wodzicki, 1967b; Waghorn, 1983). At Motukaramarama, attendance was only slightly higher at 0600 hrs than 1800 hrs (Waghorn, 1983), validating the late evening nest checks in this study.

The 50% attendance statistic is a useful way of determining pre-egg attendance, and this is the first time this statistic has been calculated. In studies without marked nests it would be necessary to identify nest sites when unattended. This may be difficult in newly established colonies, where nest mounds are not yet evident.

During this study there appeared to be no correlation between 50% attendance and the onset of laying. Long-term investigation may be needed to reveal a relationship, and may be worthwhile in future studies. Similarly, in Atlantic gannets, older birds return to the colony earlier, but laying is independent of return date (Nelson, 1966). The weather and feeding conditions in the birds' wintering habitat may influence return to the colony, but evolutionary or local environmental factors may be important in determining the onset of laying (see below).

Egg laying

Onset of laying

Egg laying was initiated within a very small window, 17 – 24 September, during the three main breeding seasons studied here. In the last two seasons, the difference in the onset of laying was only one day. This is remarkably consistent, and as yet previous studies have suggested a considerable spread in the onset of laying (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953; Wingham, 1984a). The earlier onset of laying in the first season, and then only one day separating the latter two suggests that early laying in the first season, may somehow have been linked to the breeding failures observed in that season (see Chapter 3). Egg laying was also less synchronous in 1999-00 than in the other two seasons. If the first egg date for the fourth season (2002-03) is included, the onset of laying period is only increased from 7 to 12 days.

Whether regularity in the onset of laying is normal in Australasian gannets is difficult to determine. However, information that suggests it varies widely annually, apart from Wingham's study, comes from studies made through irregular visits. At Cape Kidnappers, Robertson (in Nelson (1978b)) found that first eggs usually appear in the last two weeks of September, though they may be as late as the end of October. Nelson (1978b) suggests equally significant evidence of variability between seasons in numbers of eggs and chicks at the Plateau (Wodzicki & Robertson, 1953). This, however, overlooks the considerable differences in breeding success of Atlantic and Australasian gannets (see Chapter 3). Similarly, Wingham (1984a) overlooked this when using Wodzicki & McMeekan (1947) and Wodzicki & Robertson (1953) to estimate that onset of laying at the Plateau varied between 6 September and 23 October. These dates were also based on scant descriptions of chicks from which ages were inferred.

Initiation of laying at Motukaramarama differed by 18 days in two consecutive seasons (Wingham, 1984a). Inclusion of Wingham's first season's laying has led to confusion, as most of the data for that season are based on replacement eggs following a major storm. Back-dating was used for the second season, and although this study shows back-dating may be a useful method, some of the problems are discussed below. This study made near daily visits and the results suggest the onset of laying is similar from year to year.

Over four seasons at Bass Rock, onset of laying for Atlantic gannets was within an eight day period (Nelson, 1966). However, Nelson (2002) presented evidence of a 34 day spread in the onset of laying at Bass Rock between 1961 and 1976, and the suggestion that at least at some colonies onset of laying had become progressively earlier during the past 50 years. A 16-day spread occurred at Ailsa Craig (same latitude as Bass Rock, but on the west coast of Scotland), and a 10-day spread is recorded for Bempton (south of Bass Rock on the Yorkshire coast) (Nelson, 1978b).

Thus, it seems that for Atlantic, and probably Australasian gannets, onset of laying occurs within a relatively short period between seasons. They would therefore be expected to face similar evolutionary or environmental constraints in this timing. An evolutionary constraint seems far more likely, with significant differences in environment between these two species, although despite the different environments the same constraints may exist. Supplementary fed Nazca boobies, *Sula granti*, do not adjust their laying date, but tended to produce two eggs instead of one (Clifford & Anderson, 2001), suggesting the sulids may exhibit an evolutionary constraint. Thus, gannets may have evolved the onset of laying to occur at a time which is based on predicted peak availability of food for chick rearing (Nelson, 2002), in line with Lack's (1968) theory that birds time breeding so that young are reared during peak food availability. Slight annual differences, on either side of this optimal onset of laying, may be due to local conditions in those years. Common terns, *Sterna hirundo*, initiated laying on almost the same day in two consecutive years even though food abundance differed significantly (Safina et al., 1988) and did not appear to be timed to peak prey availability (Safina & Burger, 1988). However, a long-term study of tufted puffins, *Fratercula cirrhata*, shows significant association between SST and mean hatching date, explaining the advancement in timing of breeding the puffins on Triangle Island, Canada, since the 1970s (Gjerdrum et al., 2003). Long-term studies of the breeding phenology of gannets are therefore needed to fully investigate the role of evolutionary and environmental constraints on the onset of laying in Australasian gannets at Cape Kidnappers.

Although onset of laying may be constrained, as above, the cause of the slight annual difference in onset of laying in gannets is not known. At Motukaramarama, Wingham (1984a) suggested that optimal onset of laying was mid-July, being achieved in years not affected by adverse conditions, in that or the previous season. She suggested the delay in 1979-80 was due to late departure of chicks in the previous season. My results show that the onset of laying is relatively stable at Cape Kidnappers, even following a year in which there is starvation and almost complete breeding failure (see Chapter 3).

The late departure of chicks in one year seems unlikely to affect the onset of laying in Australasian gannets in the following year. The egg of Atlantic gannets has one of the smallest demands on female resources compared to other species (Perrins, 1970; Ricklefs & Montevecchi, 1979). Eggs in this study were approximately 3.6% of female mass (see Chapter 4), similar to the 3.4 – 3.6% recorded for Atlantic gannet (Nelson, 1966; Ricklefs & Montevecchi, 1979). Atlantic gannet eggs have a relatively small yolk and very low energy per gram fresh weight (Ricklefs & Montevecchi, 1979). This suggests that the daily energy cost of forming the egg, including energy metabolised for biosynthesis, probably does not exceed 50% standard metabolic rate (SMR) (Ricklefs & Montevecchi, 1979). Even if egg production is more costly (see review by Monaghan & Nager (1997)), or limited by specific components (eg. endogenous protein (Hipfner et al., 2003)), it seems likely that females are able to recover physiologically from a late breeding season in time to initiate laying normally in the following breeding season. Even in Humboldt penguins, *Spheniscus humboldti*, which produce two broods a year, onset of laying is unaffected by date of completion in the previous season (Paredes et al., 2002).

Similarly, the first season in this study was a tough one, with food shortage and breeding failure, yet eggs were laid only seven days later in the second season. Further support that egg production places little demand on female Australasian gannets is shown, in this study, by 59-60% of females that lose an egg re-laying (in the last two seasons), some within 6 days. Likewise, Wingham (1984a) found females re-laying within a period of 13-17 days, following the complete loss of eggs in her first study season.

Onset of laying in Atlantic gannets is suggested to be linked to the super abundance of food between June and September, when Atlantic gannets are raising chicks (Nelson, 1966; Nelson, 2002). The onset of laying in Cape gannets has not been well documented. However, the availability of nesting material has been suggested to negatively affect laying date in this species (Jarvis, 1970; Crawford & Cochrane, 1990). This was based on earlier laying at a colony with higher nest cups, compared to a colony 110 km away which had lower nest cups. Cape gannets differ from the other two species in not using external material to construct a nest, but use dirt and guano from previous seasons (Jarvis, 1970).

However, the diet at these two colonies differs markedly (Berruti & Colclough, 1987), despite earlier predictions that it would be similar (Crawford et al., 1983). More recently Gremillet et al. (2004) used GPS devices to show that birds from the two colonies overlap very little in their feeding ranges, despite theoretical foraging areas with considerable overlap. Moreover, earlier laying at higher nests was also detected at the earlier breeding island, suggesting that age may have been an important factor in the difference. In Atlantic gannets, large nests tend to have eggs earlier (Nelson, 1966). This may be due to the age of the male or female at the nest, because the correlation between nest size and egg-laying is confounded by the ages of the breeders (Nelson, 1966). Therefore, availability of nesting material may not be the over riding factor controlling onset of egg laying.

Distribution of egg laying

The positively skewed normal distribution of egg laying found here is similar to that in previous gannet studies (Nelson, 1966; Wingham, 1984a). Such a distribution was not found in Cape gannets, which appear to have a positively skewed bimodal distribution (based on one season) (Jarvis, 1974).

The high degree of synchrony in egg laying found in this study was not expected, as Australasian gannets are considered poorly synchronised breeders (Marchant & Higgins, 1990). Much of the asynchrony documented to date may be because previous studies were based on infrequent visits to colonies, confounded by replacement eggs as a result of the high egg and chick losses found in this species (Chapter 3). From this study, first eggs are laid within a relatively short period, over 85% being laid within three weeks of the onset of laying (in the last two seasons). The first season was anomalous in many ways, and the higher degree of asynchrony in that season fits with it being a difficult one for breeding gannets. Egg laying in that season appears to be more asynchronous as a result of some females laying late, perhaps due to inability in predicting the peak in food availability. This may have been age related, although data to confirm this were not collected. Higher synchrony in egg laying has been found in common terns during periods of higher food abundance (Safina et al., 1988).

From this study, a 10-week spread of laying is suggested for the Plateau colony. Robertson gives 15 weeks for Cape Kidnappers, but it is not clear if this includes all colonies or just the Plateau colony (in Nelson (1978b)). The earlier laying at Rock Naught would extend the spread of laying at the gannetry. A spread of 12-13 weeks was found at Motukaramarama in 1979-80 and 1980-81 (Wingham, 1984a), whilst the Cat Island colony, off Tasmania, had a nine week spread (Warham, 1958). At Wedge Light and Pope's Eye colonies, in Port Phillip Bay, Australia, the total laying period was suggested to exceed six months, with first clutches overlapping with replacement eggs (Norman & Menkhorst, 1995). However, the longest spread of laying documented in Australasian gannets is 16 weeks at Pope's Eye, due to a severe storm occurring after most first eggs had been laid (Gibbs et al., 2000).

For Atlantic gannets, spread of laying on Bass Rock is 54-60 days (Nelson, 1966). Nelson (1978a) follows this up by saying that three quarters of Bass eggs are laid within about three weeks, and on Bonaventure Island in about two weeks (cf. 71%, 86%, and 93% in three weeks in this study). Complete spread of laying in Atlantic gannets is therefore shorter than for this study, and any other Australasian gannet colony, possibly due to the considerably lower latitude at which this species breeds, allowing a longer breeding window (although the effects of longer daylength may compensate for this). However, Australasian gannets in this study show less time between onset of laying and the median laying date, compared to Atlantic gannets. The extended laying period of replacement eggs in Australasian gannets may also be due more to the higher egg loss in this species, and the stimulus to re-lay. Higher variability in the peaks in food abundance may also be important with respect to the spread of laying in these two species. The initial three weeks of laying however, see similar proportions of the colony lay eggs in both species.

Median laying dates within the three seasons were very close, falling within two days for first eggs and one day for all eggs (including replacements). At Cape Kidnappers, Robertson states that 'the *average* age of chicks at the end of December has varied from season to season by up to three weeks' (in Nelson (1978b)). Further evidence was suggested for peak laying in several years being three weeks late, attributed to offshore winds affecting either food or nesting material (nests were poorly constructed in these years). Also during those seasons many gannet chicks died and there were extensive wrecks of other species, perhaps indicating that egg losses occurred. This may have concealed the actual distribution of egg laying during those seasons.

However, although contrary to this study, the variation in the average age of chicks suggested above, may indicate that variability in the spread of laying does occur at the Plateau colony, more than found in 1999-00. Robertson's findings were from a longer period of study, suggesting that studies of more than three years are necessary to fully understand annual differences in the laying phenology of gannets, and these could be extremely useful in understanding the complexities of timing of breeding in this species.

On Motukaramarama median laying dates varied by up to 34 days (Wingham, 1984a). However, this included the first season's data which were based almost entirely on replacement eggs. The true median in that year would have been considerably earlier. In the other two seasons, medians varied by 18 days, still more than in this study. Estimated median laying dates for first eggs at Wedge Light and Pope's Eye, varied from before 19 September and by 23 October (Norman & Menkhorst, 1995), with analysis hampered by visits usually spaced 14 days apart.

For Atlantic gannets at Bass Rock, the median laying date was within about one week over three seasons (Nelson, 1978b). Similarly, Wanless (1978) found median laying dates fell over two days in three seasons at Ailsa Craig, and Poulin (1968) showed a one day difference in two seasons at Bonaventure Island (referenced from Nelson (1978b)). Thus, Atlantic gannets and Australasian gannets at the Plateau both show a highly consistent peak in egg laying. Similarly, the median laying dates of other seabirds differ little between years (eg. snow petrels, *Pagodroma nivea* (Barbraud et al., 2000)), even in years with poor food availability (eg. Artic terns, *Sterna paradisaea* (Monaghan et al., 1992)).

Despite this, Wingham (1984a) suggested there was greater variability in median laying date of Australasian gannets compared to Atlantic gannets. She suggested this was due to a less reliable food supply and weather conditions, and this may also hold true for comparisons between Australasian gannet colonies. Reliability and predictability of the food supply, however, are two different things. From this study, I suggest that food at Cape Kidnappers is predictable (allowing fixed onset of breeding), but not necessarily reliable (meaning breeding failures in some years). Wingham (1984a) also suggested that the extended laying period of replacement eggs suggested a more equitable climate for departing juveniles. However, there is no evidence of this, and juvenile Australasian gannets disperse as far if not further than Atlantic and Cape gannets (Wodzicki, 1967a), with as many as 70% of juveniles dying (Wodzicki & Robertson, 1974). This suggests that all three species are under similar constraints during this critical stage, although this requires further study. Certainly it is evident that early fledging juveniles survive better than late fledging juveniles in Atlantic and Cape gannets (Nelson, 1966; Jarvis, 1974), but these data are not published for Australasian gannets.

Estimating the onset of laying from chick ages mid-season

Much of the current Australasian gannet literature has relied on back-dating from chick age or hatching date to determine egg laying dates. However, the accuracy of this technique has not been examined. The ability to assess onset of laying from a single visit to a colony when chicks are present would be useful, due to the difficulties of visiting these sometimes isolated colonies. The data presented in this chapter show that this technique does give a useful indication of the onset of egg laying, with accuracy over the three years being within five days. The estimation of peak egg laying, from the average age of chicks was not quite so accurate, with an eight-day difference being suggested, but still gives some indication of the egg laying distribution in that season. Thus, the accuracy of this technique differs from year to year, depending largely on hatching success and chick mortality rates. In years where egg and chick losses are high, this technique will be less accurate. The timing of these losses will also be critical, however, as losses at the start of egg laying or chick hatching will have the greatest affect due to the loss of the oldest cohort upon which back-dating is reliant.

This technique relies on an accurate estimation of the age of chicks. The error in this part of the estimation was not assessed, and depending on the experience of the observer, could be quite large. Generally the age of chicks is estimated to age classes separated by 5 - 7 days. Slight errors in observer estimates of chick age mean greater errors in the estimation of onset of laying and peak laying. Retarded growth of chicks, due to poor food availability, and heavy egg losses in the first few weeks of incubation (such as occurred during Wingham's first season), would also add considerable error to the estimates. Therefore, the technique is of use, but the results should be used with caution.

Laying date of individual females

The significant consistency in laying dates of individual females in this study fits with trends in other seabirds (Davis, 1975; Hipfner et al., 1997; Barbraud et al., 2000; Massaro et al., 2002; Paredes et al., 2002). Amongst seabirds, it is older females that generally lay earlier and produce larger eggs, at least up to a specific age (Coulson & White, 1958; Hipfner et al., 1997; Furness, 1983; Massaro et al., 2002). Similar results have been found in Atlantic gannets (Nelson, 1966; Nelson, 2002), and suggested for Australasian gannets (Gibbs et al., 2000). However, as the age of females was not known in this study, investigation of age effects can not be conducted.

Time of day eggs were laid

This is the first study to document the time of egg laying in gannets. Eggs were laid throughout the day, with more being laid during the morning than afternoon. Like most birds, gannets probably form the eggshell during the night prior to egg laying, when inactive at the nest (Perrins, 1996). Most bird species appear to lay at characteristic times of the day (see McMaster et al. (2004)), whilst in ducks the interval between eggs appears more important than the time an egg is laid (Watson et al., 1993; Esler, 1999). The only seabird for which I could find details of time of laying was the lesser black-backed gull, *Larus fuscus*, which usually lays during the early morning, before 0900 hrs (Bolton et al., 1992). There seems to be little information on the time of day seabirds lay their eggs, but this could be of interest with regard to the mating systems of these species. Although seabirds are generally socially monogamous, Australasian gannets during this study were observed to copulate with non-mates (B. Stephenson unpubl. data). Timing of laying in this species could therefore have important implications on mate guarding and extra-pair paternity.

Comparison of laying dates between Cape Kidnappers colonies

The consistent annual difference, of up to 11 days, observed between the Plateau colony and Rock Naught is puzzling, due to the distance of only 1.5 km between the colonies. However, this study is not the first to show this difference, with Wodzicki & Robertson (1953) also noting that the 'larger and older Cape Kidnappers and Black Reef gannetries are usually occupied a week or two before the first birds appear on the Plateau gannetry'. Furthermore, differences between median laying dates at the Wedge Light and Pope's Eye colonies (0.8km apart) were also noted in some years, but not in others (Norman & Menkhorst, 1995).

In Atlantic gannets, the size of the nesting group influences laying date, with larger nesting groups laying earlier than smaller groups of similar age structures (Nelson, 1966). This is thought to be due to greater social stimulation in the larger groups (Nelson, 1966; Nelson, 2002). However, the difference found here is contrary to this, in that Rock Naught has about 240 breeding pairs, compared to 1800-2100 at the Plateau colony. Environmental factors such as weather, latitude, or availability of nesting material seems an unlikely explanation, due to the close proximity of the colonies. Age and social structure may differ, with birds at

Rock Naught possibly being older, relative to the Plateau colony. Physical erosion of the site and the restricted physical size of the colony could lead to older more experienced pairs gaining nest sites ahead of later arriving younger birds. Alternatively, perhaps birds from the two different colonies, are feeding at different locations with different prey. Thus, their timing of breeding may be based around a peak in food abundance at a different location. The fact that two Cape gannet colonies situated only 110 km apart showed little overlap in foraging range, despite large overlap in theoretical foraging range (Gremillet et al., 2004), suggests this could be possible. These two explanations are easily differentiated with further study. Diet samples collected from the colonies should reveal different prey, and the use of GPS devices to determine foraging range, would allow the latter alternative to be tested.

The reasons behind different laying dates at colonies within New Zealand is also poorly understood. Laying is initiated considerably earlier at more northerly gannetries, although a direct north-south gradient does not exist. Stein (1971) suggested Mahuki was the only New Zealand gannetry where egg laying is slightly ahead of Horuhoru, with the Colville gannetries (Motukaramarama and Motutakapu) being a week later, the Sugar Loaf (of the Poor Knights) a fortnight later, the Oaia colony off of Muriwai, a fortnight to three weeks later, and Cape Kidnappers from one month to five weeks behind. It seems likely that breeding at each location is related to local prey availability, which appears linked to sea–temperatures and the spawning of prey species (Wingham, 1985). Considerable differences in the diet of gannets at several of these colonies has been noted (Robertson, 1992). More information is required on the spawning of prey species, and their seasonal abundance and availability to gannets in New Zealand. This is currently poorly understood. Nelson (1978b) suggested similar differences in timing of laying at colonies, on both the east and west of the Atlantic, were due to availability of food.

Chick hatching and fledging

Although fledging period is not directly discussed in this paper, it also appears consistent with that recorded by Wingham (1984b). Fledging of chicks at the Plateau colony during late February – March is also consistent with previous findings (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953; Nelson, 1978b). The longer fledgling period of Australasian gannets (c. 108 days) compared to that of Atlantic gannets (c.90 days (Nelson, 1966)), suggests a less abundant or more variable food source for Australasian gannets.

Why the egg laying distribution of the Australasian gannet is equally, if not more, synchronous and predictable requires further study.

Sea surface temperature and the onset of laying

The variation in SST at the time of onset of laying in each season suggests this was not an important factor in triggering egg laying. Moreover in September, the variation in SST over the 3 – 4 day period temperature was assessed, was also considerable (up to 1°C). A long-term study is probably needed to determine whether a relationship exists. Of particular importance is an understanding of how SST affects the fish species that Australasian gannets prey upon. Unfortunately there is currently very little information available for these sorts of relationships, which are almost certainly important in determining the timing and success of breeding. Not only could prey abundance be affected, but also prey availability, with prey species perhaps altering the depth at which they occur, or using different areas and thus occurring further away or closer to the colony. Mean egg laying dates in puffins, *Fratercula arctica*, at colonies in the Gulf of Maine and Norway have been negatively correlated with SST (Barrett, 2001; Diamond & Devlin, 2003).

Conclusions

This study shows that both the dates of onset of laying and median egg dates for Australasian gannets at the Plateau colony are annually consistent over the period studied. This differs somewhat from previous Australasian gannet studies, but suggests that they differ little from Atlantic gannets breeding at Bass Rock in Scotland. Moreover, the period between onset of laying and median date is shorter during this study than for Atlantic gannets, and it is mainly late laying females and replacement eggs that extend the spread of laying. Until now, the breeding of Australasian gannets was thought to be poorly synchronised, perhaps due to the way in which studies were conducted and the highly variable breeding success evident in this species. This study finds no significant differences in breeding phenology and synchronicity between the two species.

Thus, I suggest that the factors affecting the timing of egg laying in female gannets are similar in Australasia as in the Atlantic. Nelson (1966) suggests that Atlantic gannets are adapted to take advantage of a seasonally abundant and dependable food supply. I suggest that Australasian gannets are similar, and lay at a specific time, based on predictions of when future food availability will peak. However, due to a more variable environment, these peaks in food abundance may be variable, something that Atlantic gannets appear not to have had to cope with in the past. In the Australasian gannet this has lead to years in which starvation and breeding failure occur, because the predicted food supply does not arrive.

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1954). Several of these studies noted variable breeding but, the causes of this were not examined, although suspected causes were human disturbance (ie. humans approaching breeding colonies too close or taking/killing eggs and chicks) (Cunningham, 1947; Hamilton, 1947) or infertility of eggs (Wodzicki & McMeckan, 1947). Wodzicki & Robertson (1953) suggested that climatic factors and the available food supply are the only obvious factors affecting the gannets at the Plateau colony, Cape Kidnappers, citing an example of a south-easterly storm killing nearly 10% of chicks present.

Stein (1971) followed on from these studies, producing one of the most significant works, a long-term study on the Horuhoru gannetry. Although he did not provide exact information on hatching, fledging, and breeding success, variable breeding success was again evident and years of breeding failure documented. However, Stein (1971) was also not sure what caused this variability and pondered over whether this was attributable to "Man or Nature". Comment was made during his study of chicks dying from starvation, but details were not given, although this does appear to have been an important cause of chick mortality in at least one season (Stein pers. comm. in Nelson (1978)).

During the three breeding seasons 1960-61 to 1962-63, Robertson (1964) studied the Cape Kidnappers gannetry. In each of his three years, similar proportions of eggs and chicks were recorded in late-December, but details of breeding success are not given.

The most comprehensive study of Australasian gannet breeding biology is that of Elspeth Wingham[1] between 1978-79 to 1980-81, on Motukaramarama Island in the Hauraki Gulf. She documented hatching, fledging and breeding success, although the egg laying period was missed in the first two seasons. She reports the failure of all first clutch eggs in 1978-79 due to a storm with very high wind speed (Wingham, 1984a), but this was not included in estimates of hatching and breeding success. Productivity was estimated at about 61% over the three seasons (Wingham, 1984b). More recently, studies conducted from less frequent visits to Australian colonies (Norman & Menkhorst, 1995; Gibbs et al., 2000; Bunce, 2001a), have shown lower hatching, fledging and breeding success, but similar productivity compared to Wingham (1984b). Again, storms were shown to influence hatching success through loss of eggs and nests at Pope's Eye (Gibbs et al., 2000), and storms and high spring

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[1] Elspeth Wingham nee Waghorn

tides have been responsible for low breeding success at Farewell Spit in New Zealand (Hawkins, 1988).

These studies have created an impression that Australasian gannets have an annually variable breeding success, and breeding failures cause extremely low breeding success in some years. Therefore, the average breeding success in this species may be considerably less than in the Atlantic gannet with which this species is frequently compared. Yet, Nelson (1978; 2002) predicts that in the absence of disturbance, all three gannet species would share a similarly high breeding success, and that the heaviest breeding losses should occur post-fledging, although acknowledging the starvation of chicks that was observed at Horuhoru (Stein, 1971). Starvation of chicks, however, has never been properly documented during a study conducted through regular visits. Wingham (1984b) also suggests that all three species exhibit similarly high breeding success in colonies unaffected by human disturbance, and suggests this was to blame for poor success in some years in Australasian gannets.

Furthermore, a critical examination of these historical breeding failures has not been conducted. Breeding failures or significant loss of eggs and/or chicks have occurred at the Three Kings (Buddle, 1947b; Buddle, 1948), Mahuki (Hamilton, 1947), White Island (Robertson & Wodzicki, 1948), Cape Kidnappers (Wodzicki & McMeekan, 1947; Wodzicki & Robertson, 1953), Horuhoru (Fleming, 1948; McKenzie, 1949; Wodzicki & Stein, 1958; Stein, 1971), Motukaramarama (Wingham, 1984a), Farewell Spit (Hawkins, 1988), and Pedra Branca (Brothers et al., 1993) gannetries. These events occurred at eight gannetries over 45 years, obviously differing in the extent of failure and loss, but suggesting a widespread phenomenon.

The aim of this chapter is to investigate the breeding biology of Australasian gannets at the Plateau colony, Cape Kidnappers, over three seasons. The primary goal is to determine hatching, fledging, and breeding success as well as productivity at this colony, and to make comparisons with previous studies of Australasian gannets. Moreover, the causes of egg and chick loss will be documented, annual variability investigated, and, where possible, correlated with environmental conditions. This will allow comparison with the Atlantic gannet, which exhibits consistently high annual breeding success. The effect of egg volume and date of egg laying on success will also be investigated. An analysis of previous studies will be undertaken to examine more fully the poor breeding success and failures in the published literature.

Methods

The Cape Kidnapper's gannetry (39° 38' S, 177° 05' E) is situated on the east coast of the North Island, New Zealand (Fig. 1). The gannetry consists of four Australasian gannet colonies, Saddle (originally called Cape Kidnappers colony), Plateau, Black Reef, and Plateau Beach. Several papers have described the gannetry and its history, with changes in the breeding population documented since 1945 (Wodzicki & McMeekan, 1947; Fleming & Wodzicki, 1952; Wodzicki, 1967; Wodzicki et al., 1984; C.J.R. Robertson unpubl. data; see Chapter 1). Details of the birds' breeding biology in New Zealand were first documented from studies at this site (Wodzicki & McMeekan, 1947). The gannetry is currently estimated to hold approximately 7,500 breeding pairs of gannets (breeding pairs = site-occupying pairs, defined as either one or two site-holding birds occupying a nest site (Wodzicki et al., 1984), that attempt to breed annually).

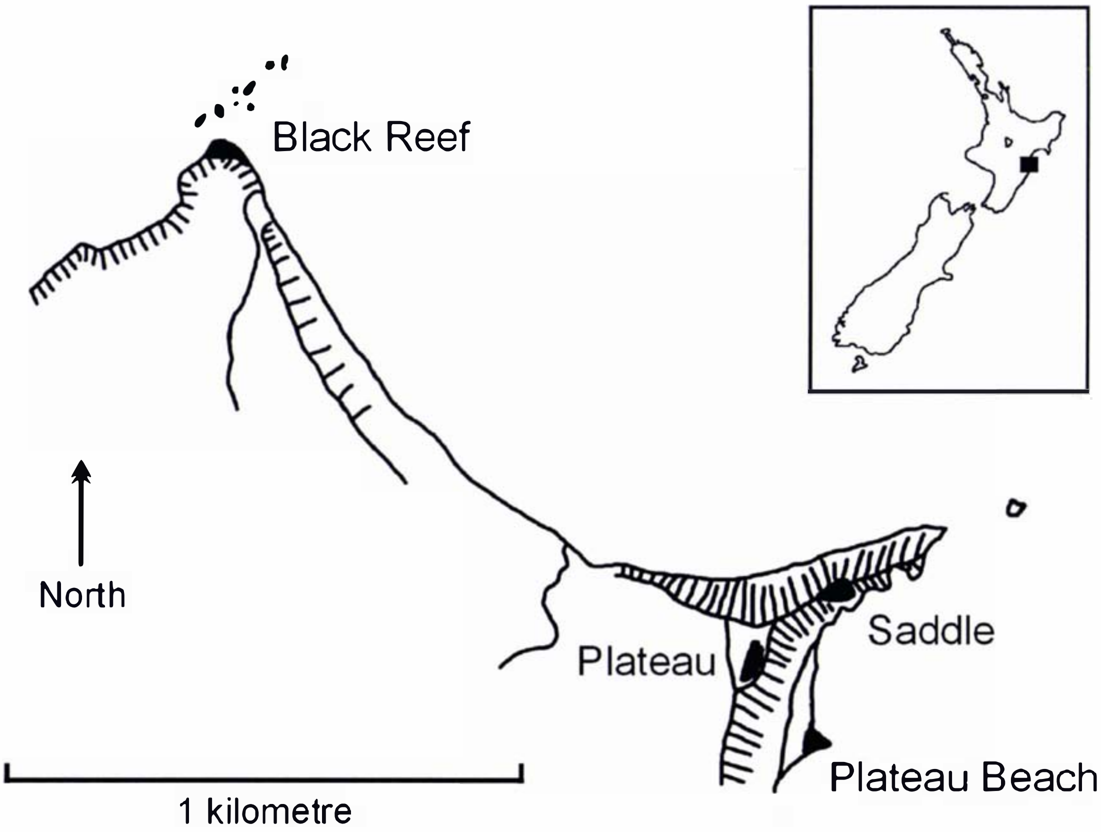

Figure 1. Location of the Cape Kidnappers gannetry, showing its orientation and the position of each of the four colonies. During this study work was mainly conducted at the Plateau colony.

One hundred nest sites on the seaward eastern side of the Plateau colony were individually marked with permanent markers whilst the colony was empty on 8 July 1999 (see Chapter 1 for photos and additional information). These nests were intensively monitored over three breeding seasons, 12 August 1999 - 3 April 2000, 8 August 2000 - 16 April 2001, and 2 August 2001 - 3 March 2002. They were also monitored three times during the 2002-03 breeding season (14 November 2002, 20-21 December 2002, and 23 January 2003) to provide an estimate of productivity during that season. Thus, data are presented for the 2002-03 season only where applicable.

To determine status of nesting, nest contents and attendance, and identity of adults, nests were checked approximately daily from September to late-December, but less frequently from December to March. A nesting attempt was defined as attendance of a site by a pair, and the formation of a nest using seaweed. Checks were more frequent during the main egg laying and chick hatching periods, with no more than one day being missed consecutively in the peak egg laying periods of all seasons. Nest checks were usually conducted towards the end of the day, and presence and identity of adults and nest contents recorded. During the three seasons, 83, 100, and 126 birds were individually identifiable by bands supplied by the Department of Conservation Banding Office. This represented 24, 29, and 39 pairs in each of the three seasons. Each adult was banded on the left tarsus with a five-number M-size stainless-steel band, and a large aluminium 'sight' band on the right tarsus. The 'sight' bands were imprinted with the last three digits of the M-band, and greatly aided the identification of adults when incubating or brooding. Adults were sexed based on behaviour at the nest, such as observation of copulation, which was often substantiated by observations of birds bringing weed to the nest (males are usually responsible for this behaviour), or females with dirty backs following copulation, or the laying of an egg.

All eggs were numbered with a non-toxic permanent marker (red Sharpie ® fine point) shortly after laying to allow eggs to be identified. Length and width (to 0.1 mm, using dial callipers) were used to calculate egg volume using the equation $V = K_V(\text{length} \times \text{width}^2)$, where the constant $K_V = 0.507$ (Hoyt, 1979). Calculated egg volume index is an accurate predictor of fresh egg weight (Chapter 4), and so is used instead of egg mass throughout this chapter. Gannets lay only a single egg per clutch, with replacement eggs laid by some birds, if the first egg is lost. First clutch eggs are referred to as first eggs, whilst second and third clutch eggs are referred to as second and third eggs. The term 'all eggs' refers to first, second and third eggs collectively.

Hatching success is the percentage of eggs that hatched of eggs that were laid, whilst fledging success is the percentage of chicks that fledged of eggs that hatched, and breeding success is the percentage of chicks that fledged of eggs laid. All values are calculated separately for first, second and all eggs. Productivity is the number of chicks that fledged from the 100 nests monitored per breeding season. To determine the effect of laying date on first egg hatching, fledging, and breeding success, the median and upper and lower quartile laying dates were calculated (median laying date being the day that the middle egg was laid on). Comparisons were then made between each quartile, with the middle two quartiles (either side of the median) being lumped together. Thus, values were calculated for first and last quartiles, and the middle two quartiles lumped, and significance tested using Chi-sq tests.

Eggs that did not hatch were classed as lost (disappeared from nests without remains, disappeared and found on the edge of the colony depredated by black-backed gulls, *Larus dominicanus*, or known deserted eggs), accidental (broken or knocked out of the nest), or infertile/addled. "Accidental" eggs were sometimes depredated, but in the case of being knocked from the nest were occasionally recovered by a neighbour. Those eggs that did not hatch after 55 days were deemed addled/infertile. The longest an egg was incubated successfully in this study was 53 days (Chapter 4).

Absolute mortality of chicks was often not determined, but chicks that disappeared from their nests and were not seen again were assumed to have died, and were also classed as lost. Thus, all deaths and disappearances of chicks are categorised as lost.

To enable comparison with previous studies at Cape Kidnappers, the percentage of nests containing eggs, chicks or empty, was determined on 20 December, in each season. Workers have traditionally visited Cape Kidnappers around this date, since 1946, to conduct nest checks and census estimates.

Hourly weather data (ambient temperature (°C), wind direction (degrees), wind speed (m/s), and rainfall (mm)) were supplied by the National Institute of Water and Atmospheric Research (NIWA) from two nearby weather stations, Napier Airport Weather Station (D96484; 39° 27' S, 176° 51' E) and Mahia Weather Station (D97192; 39° 07' S, 177° 57' E). The Napier Station (approximately 30 km to the north-west), was deemed to give representative rainfall and ambient temperature data, whilst the Mahia Station (approximately 94 km to the north-east) gave a better indication of wind direction and speed. New Zealand National Climate Summaries provided on the NIWA website and summaries of Climatological Observations for both Weather Stations were also obtained for comparison with data collected during the study.

Sea surface temperature (SST) data were obtained from NOAA's Comprehensive Large Array-data Stewardship System (CLASS) electronic library of environmental satellite data, through their website (http://www.saa.noaa.gov/cocoon/nsaa/products/welcome). Data for two locations close to the study site were obtained, the first at 39° 30' S 177° 30' E, approximately 38 km north-east of Cape Kidnapper's in the middle of Hawke Bay, the second at 40° 00' S 177° 30' E, approximately 53 km south-east of Cape Kidnappers. A very high correlation (Pearson bivariate correlation; $r = 0.988$, $P < 0.0001$), was found between the two locations, so only SST data for the first location was used for analysis in this chapter.

Unless otherwise stated, means are reported ± 1 standard deviation (SD). All statistical analyses were performed using SPSS for Windows, Release 11.5.0 or 12.0.1. Capture, handling and banding of birds was conducted under the Department of Conservation's New Zealand National Banding Scheme, Institutional Permit to band birds No. 0259. The Massey University Animal Ethics Committee gave permission to conduct this research, Protocol No. 98/173.

Results

A nesting attempt was made at all but four of the 100 monitored nests in the 1999-00 season, and at all nests in the 2000-01 and 2001-02 seasons, with first eggs being laid at 91, 95, and 98 nests, in each season respectively (Table 1). Over the three seasons, 333 eggs were laid and detected, with 109, 117, and 107 eggs being laid in each of the three breeding seasons. The number of first eggs laid did not differ significantly between seasons, although it approached significance ($\chi^2 = 4.89$, df = 2, $P = 0.087$).

Table 1. Number of nesting attempts and eggs laid (first, second, and third eggs) at the 100 monitored nests per breeding season. The number of first eggs laid per season did not differ significantly.

Season	Nesting attempts	First eggs	Second eggs	Third eggs	Total no.
1999-00	96	91	17	1	109
2000-01	100	95	21	1	117
2001-02	100	98	9	0	107
Total	296	284	47	2	333

Hatching success

Hatching success of first and all eggs varied significantly between seasons ($\chi^2 = 17.419$, df = 2, $P < 0.0001$; $\chi^2 = 18.836$, df = 2, $P < 0.0001$, respectively), being poorest in the 1999-00 breeding season, moderate in 2000-01, and high in 2001-02 (Table 2 & Table 3). For first eggs, hatching success was 48%, 64%, and 78% for each of the three seasons, respectively. In all years, first eggs had a higher hatching success than second eggs, with significant differences in 2000-01 and 2001-02 ($\chi^2 = 8.953$, df = 1, $P = 0.003$; $\chi^2 = 4.789$, df = 1, $P = 0.029$, respectively), but a non-significant difference in 1999-00 ($\chi^2 = 0.982$, df = 1, NS) (Table 2). As second eggs were not laid until 10 -24 days (mean = 16) after the first egg median date in each season (see Chapter 2), it is difficult to determine whether second eggs were less successful due to being laid late in the season, or to some other independent factor.

Table 2. Hatching, fledging, and breeding success of first, second, and all eggs for each of the three main breeding seasons studied. Productivity for the 100 monitored nests is given in the final column as a percentage.

	Season	Eggs laid (100 nests)	Hatching success	Fledging success	Breeding success	Productivity
First	1999-00	91	44 (48%)	8 (18%)	8 (9%)	-
	2000-01	95	61 (64%)	52 (85%)	52 (55%)	-
	2001-02	98	76 (78%)	13 (17%)	13 (13%)	-
Second	1999-00	17	6 (35%)	1 (17%)	1 (6%)	-
	2000-01	21	6 (29%)	2 (33%)	2 (10%)	-
	2001-02	9	4 (44%)	0 (0%)	0 (0%)	-
All	1999-00	109	50 (46%)	9 (18%)	9 (8%)	**9%**
	2000-01	117	68 (58%)	55 (81%)	55 (47%)	**55%**
	2001-02	107	80 (75%)	13 (16%)	13 (12%)	**13%**
	2002-03	-	-	-	-	**55%**[1]

[1] This is maximum productivity for this season, based on the number of chicks present during a visit to the colony on 23 January 2003. All chicks included in the above analysis were >33 days old (a further 3 chicks were <33 days old). Most chicks 40 days old are expected to fledge (see 'Fledging success' below).

Table 3. Analysis of first eggs that failed to hatch. Categories used at the bottom of the table are outlined in the methods section. Numbers given (except in parentheses) are actual numbers of eggs

Outcome	1999-00	2000-01	2001-02
Known infertile/addled	8	5	4
Disappeared	27	21	8
Disappeared and found eaten	3	3	0
Observed gull depredation at an unattended nest	0	2	0
Known deserted	2	2	0
Knocked out of nest (not recovered)	2	0	5
Knocked out of nest (recovered by neighbour)	2	0	0
Broken by adult	3	1	5
Total first eggs laid	91	95	98
Total first eggs lost	32	28	8
Total first eggs accidental	7	1	10
Total first egg hatching failures	47 (52%)	34 (36%)	22 (22%)

Variability in hatching success between seasons was mainly due to the number of eggs that were lost in each season, as opposed to accidents or infertile/addled eggs (Table 2). Distinct peaks in egg loss were evident in 1999-00 and 2000-01, but not in 2001-02 (see Fig. 9 later in this chapter). The disappearance of eggs was the biggest cause of egg loss in each of the three seasons (Table 3). In most cases, disappearance of eggs is thought to have been due to desertion by the incubating adult, and subsequent depredation of the egg by a black-backed gull.

The age at which first eggs were lost varied widely, with little discernable pattern in any season. Mean age of first eggs when lost was 26 ± 15.7, 15 ± 9.0, and 27● 16.3 days old, in each of the three breeding seasons respectively. The mean age of eggs when lost appears to reflect the period between the median laying date and the peaks in egg loss that occurred in the 1999-00 and 2000-01 breeding seasons. Egg loss in the 2001-02 season was scattered throughout incubation, with no more than one egg lost per day.

The number of addled/infertile eggs did not differ markedly between seasons (Table 3). However, as an egg could only be established as such if it remained in the nest for more than 55 days, this category may have been underestimated, especially in 1999-00 and 2000-02. It is therefore interesting to note that the number of eggs in this category was lowest in 2001-02, when the least number of eggs were lost. The 2000-01 season showed far fewer accidental egg failures (Table 3). Of the 12 eggs broken during the three seasons (9 first, 3 second), nine were <10 days old and the remaining three first eggs were 35, 43, and 53 days old. This latter egg was crushed as the chick was hatching, being the longest incubation period of a fertile egg in this study.

On four occasions during the study an adult gannet was seen standing beside a nest containing a freshly laid egg (3 times in 1999-00, once in 2001-02), but showed no interest in incubating it.

Effect of laying date and egg volume on hatching success

First egg hatching success was related to laying date (Table 4, Fig. 2). In 1999-00 and 2000-01 there was significantly lower first egg hatching success in the last quartile ($\chi^2 = 24.493$, df = 2, $P < 0.0001$; $\chi^2 = 7.260$, df = 2, $P = 0.027$, respectively). Although for first eggs in

Table 4. Success and failure rates (%) for eggs laid in each quartile in each of the three breeding seasons. The hatching, fledging, and breeding rates are given for first eggs only. Productivity is for the 100 monitored nests.

Season	Quartile	First eggs						Productivity (%)	
		Hatching (%)		Fledging (%)		Breeding (%)			
		Succ	Fail	Succ	Fail	Succ	Fail	Succ	Fail
1999-00	First	57	43	8	92	4	96	7	93
	Middle	67	33	23	77	16	84	13	87
	Last	4	96	0	100	0	100	0	100
2000-01	First	75	25	83	17	62	38	66	34
	Middle	70	30	85	15	60	40	53	47
	Last	42	58	90	10	37	63	17	83
2001-02	First	84	16	48	52	40	60	38	62
	Middle	76	24	5	95	4	96	6	94
	Last	74	26	6	94	4	96	0	100

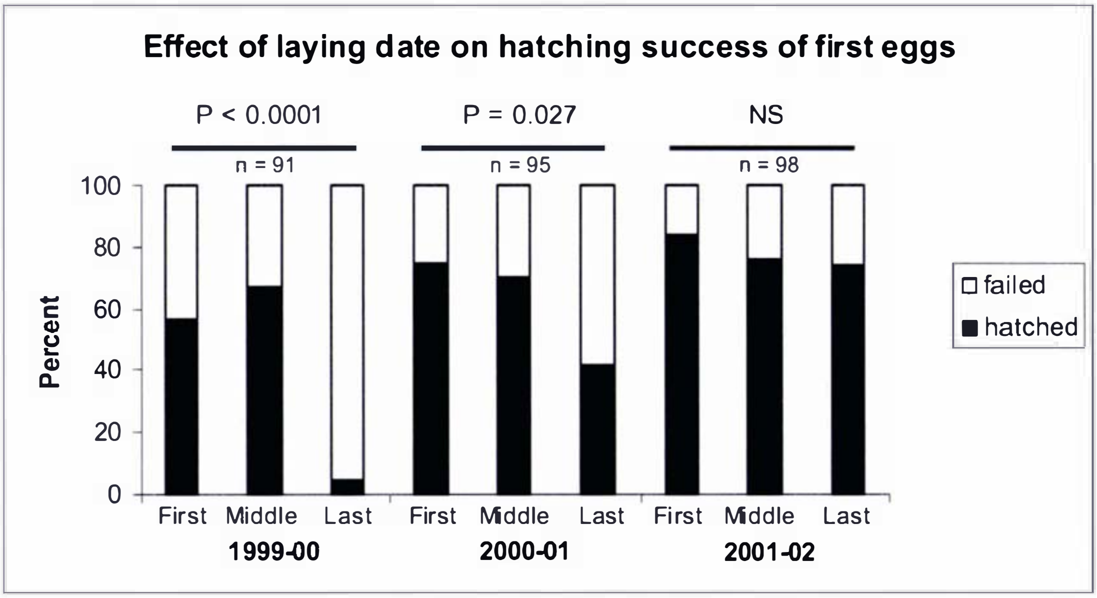

Figure 2. Relative hatching success of first eggs laid in the first, middle, and last quartiles of egg laying, for each of the three breeding seasons. Significant differences between quartiles were found in 1999-00 and 2000-01, but not in 2001-02.

2001-02, hatching success was higher in the first quartile, this difference was not significant (χ^2 = 0.84, NS), almost certainly as a result of the very high hatching success in that year (Table 2).

In both 1999-00 and 2000-01, eggs that hatched had larger volumes than those that did not (Fig. 3). This difference was significant in the 2000-01 season (t = 3.253, df = 59.25, P = 0.002). In 2001-02, a large proportion of the eggs that did not hatch were due to accidental egg failures, 10 of 22 failed first eggs (Table 3).

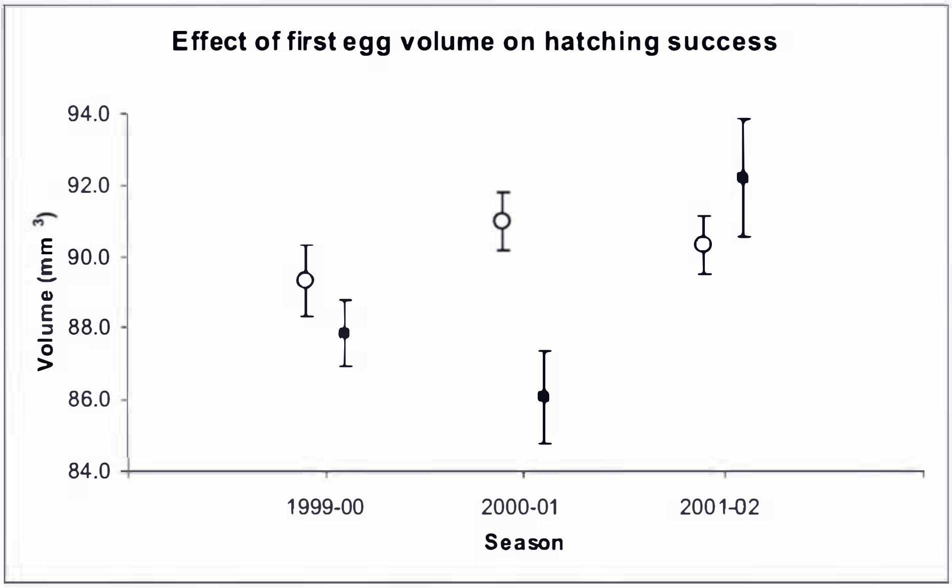

Figure 3. Mean egg volume (± 1 SE) for first eggs that hatched successfully (○) and did not hatch (■), for each of the three seasons. Sample sizes are 44 and 47 for 1999-00, 61 and 34 for 2000-01, and 76 and 21 for 2001-02, hatched and did not hatch respectively. The difference in 2000-01 is highly significant (P = 0.002).

Fledging success

Fledging success for chicks from first and all eggs was significantly different between seasons (χ^2 = 77.141, df= 2, P < 0.0001; χ^2 = 76.890, df= 2, P < 0.0001, respectively), being highest in 2000-01, and low in both 1999-00 and 2001-02 (Table 2 & 5). For first egg chicks, fledging success was 18%, 85%, and 17% for each of the three seasons respectively. In all years, first egg chicks had a higher fledging success than chicks from second eggs, with a significant difference in 2000-01 ($\chi^2 = 9.44$, df = 1, P = 0.002), but not in the other seasons ($\chi^2 = 0.008$, df = 1, NS; $\chi^2 = 0.817$, df = 1, NS, respectively) (Table 2). Overall, fledging success was highest in 2000-01.

Lack of a significant difference in first and second egg fledging success in 1999-00 may be a result of the significant chick losses from first eggs, during the peak in egg and chick loss in that season. In 2001-02, few second eggs hatched, and the storm in late December caused considerable chick mortality.

Table 5. Analysis of chicks that hatched from first eggs. Causes of mortality are considered within the text. All classes in the table are categorised as lost for the purposes of analysis throughout this paper, see Methods for an explanation of outcome.

Outcome	1999-00	2000-01	2001-02
Disappeared	11	4	18
Found dead in nest	25	3	42
Found dead, possibly due to being attacked	0	1	0
Found dead out of nest	0	1	1
Trampled in nest	0	0	2
Total first eggs that hatched	44	61	76
Total first egg chicks that did not fledge	36	9	63
Total first egg chicks that fledged	8 (18%)	52 (85%)	13 (17%)

The cause of variability in fledging success from first eggs between seasons was the high mortality of chicks in 1999-00 and 2001-02, but not in 2000-01 (Table 5). Unfortunately, it was not possible to determine the exact causes of mortality, but 1999-00 and 2001-02 showed distinct peaks in chick loss that varied in severity. In 1999-00, starvation of adults and chicks caused mortality and desertion of small chicks, leading to depredation by black-backed gulls. In 2001-02, mortality caused by starvation and desertion occurred again, but a storm in late December also caused considerable mortality.

During the study, some chick mortality appeared to have been caused by factors other than starvation and bad weather (Table 5). Small chicks from two different nests (aged 7 and 29 days) were observed alive just outside the nest cup, but were later found dead, having not been recovered by the brooding adult. The chicks were probably knocked out of the nest as one member of the pair arrived or during a fight between neighbouring birds. Similar events were observed at other nests, with a chick being aided into the nest of a neighbouring adult. In this case the adult was already brooding a chick of similar age (<7 days). A further cause of chick mortality was attack by other adults when left unattended. This was the probable cause in the death of one chick. Similarly, on several occasions unattended small chicks were trampled by non-breeding adults prospecting for nest sites.

During the three seasons, 121 chicks failed to fledge, 108 from first eggs, 13 from second eggs. All but four (3%) were between the age of 0 and 40 days (Fig. 4). Mean chick age at loss in the three seasons was 16 ± 12.2 (n = 41), 22 ± 24.1 (n = 13), 23 ± 11.9 (n = 67) days old. Once chicks were more than 40 days old they seemed able to survive bad weather, and withstand periods of poor food supply and being left unattended. In 1999-00 and 2000-01 the peak in chick age at loss was around 11 – 15 days. However, in 2001-02 this peak was at 26 – 30 days, a result of the stage of breeding during which a storm struck in late December.

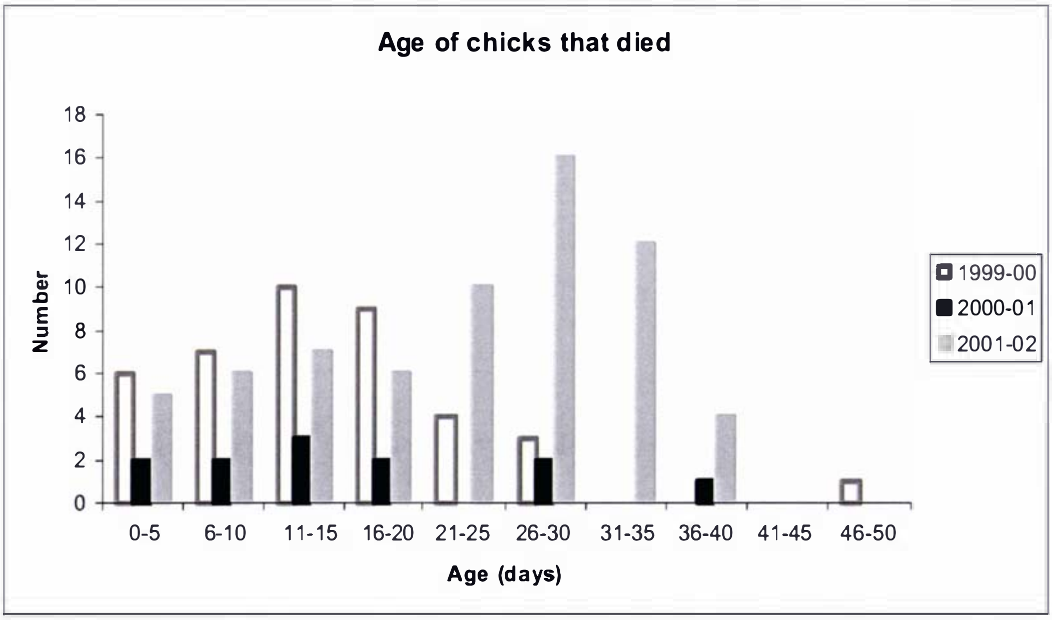

Figure 4. Age of chicks that were lost during the nestling period in each of the three breeding seasons. A further three chicks died over the three seasons, one in 1999-00 at 68 days, one in 2000-01 at 94 days, and one in 2001-02 at 74 days.

Effect of laying date and egg volume on fledging success

Laying date appeared to influence first egg fledging success (Table 4, Fig. 5). In 1999-00 and 2000-01 there was no significant difference in fledging success from each of the egg laying date quartiles ($\chi^2 = 1.719$, df = 2, NS; $\chi^2 = 0.236$, df = 2, NS, respectively), despite no chicks fledging from eggs laid in the last quartile in 1999-00. The peak loss in 1999-00 appears to have occurred when early laid first egg chicks were at their most vulnerable. The lack of significance in 2000-01 was probably due to the favourable chick rearing conditions that appeared to develop later in that season. However, in 2001-02, significantly more first egg chicks fledged from the first quartile ($\chi^2 = 19.058$, df = 2, $P < 0.0001$). Mean chick age of those that survived the storm was 36 days old (n = 13, 25 – 42), just above the peak seen in Fig. 4, suggesting older chicks had a better chance of survival.

In all years, chicks that fledged came from larger volume eggs than those that did not fledge (Fig. 6). This difference was not significant in 1999-00 or 2000-01 (t = 0.52, df = 17.6, NS; t = -0.102, df = 9.8, NS, respectively), but approached significance in 2001-02 (t = 1.516, df = 22.6, P = 0.143).

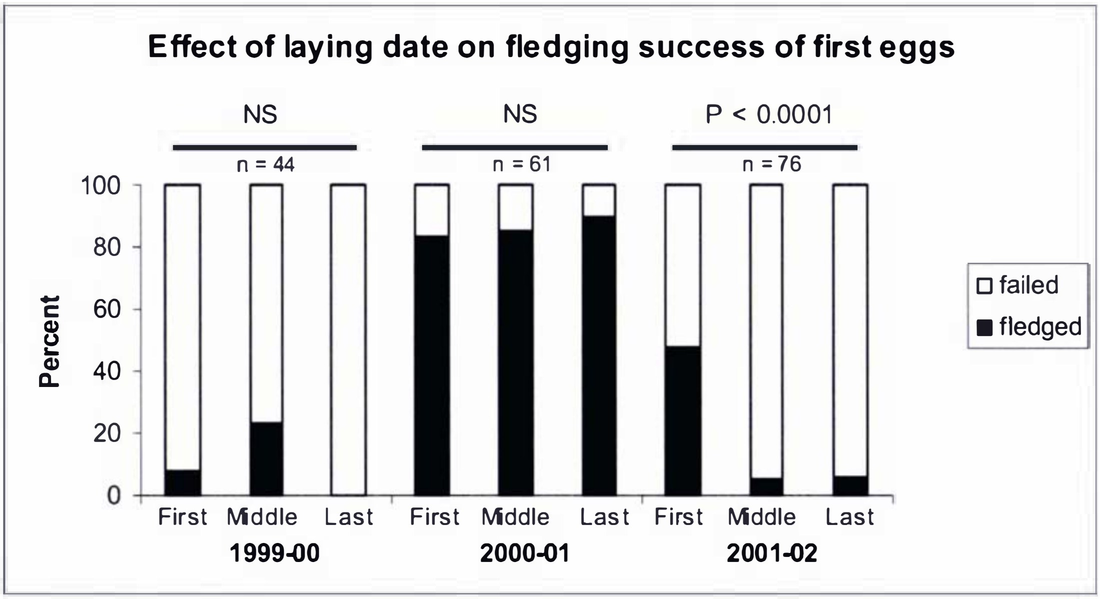

Figure 5. Relative fledging success of first eggs laid in the first, middle, and last quartiles of egg laying, for each of the three breeding seasons. Significant differences between the quartiles were found in 2001-02, but not in 1999-00 or 2000-01.

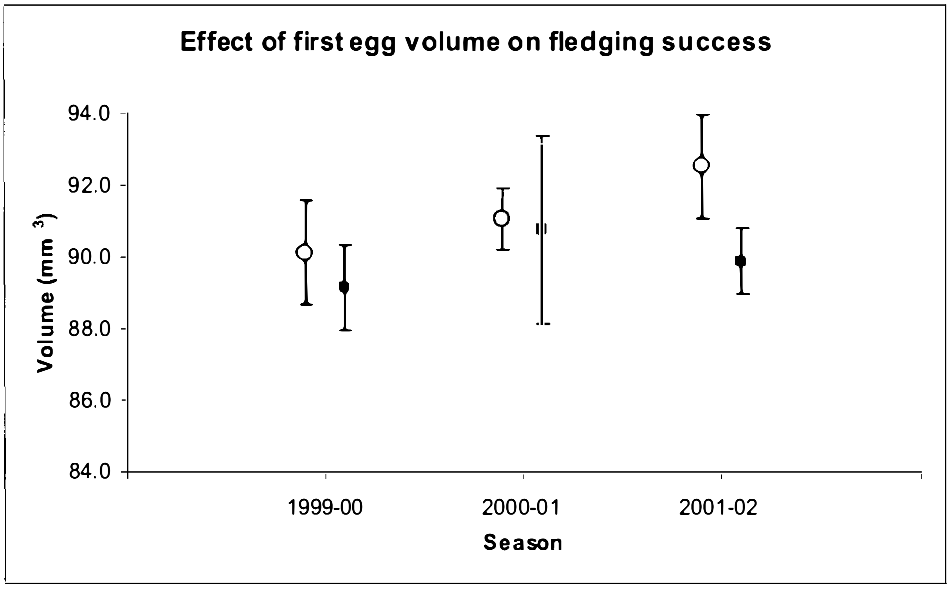

Figure 6. Mean egg volume (± 1 SE) for first eggs that fledged chicks (○) and did not fledge chicks (■), for each of the three seasons. Sample sizes are 8 and 36 for 1999-00, 52 and 9 for 2000-01, and 13 and 63 for 2001-02, fledged and did not fledge respectively. Differences were not statistically significant.

Breeding success and productivity

Breeding success for first and all eggs was significantly different between seasons (χ^2 = 63.501, df= 2, P < 0.0001; χ^2 = 58.350, df= 2, P < 0.00001, respectively), being highest in 2000-01 and low in both 1999-00 and 2001-02 (Table 2). Moreover, productivity in each of the seasons was significantly different (χ^2 = 68.068, df= 2, P < 0.00001), being 9%, 55% and 13%, respectively. Maximum productivity in 2002-03 was 55%, calculated from a visit to the colony on 23 January 2003 (Table 2).

Breeding failures in 1999-00 and 2001-02 were not a consequence of observer disturbance. The Saddle colony and rock stacks at Black Reef showed similarly poor success during those two seasons (B. Stephenson unpubl. data), yet I never entered the colonies. Disturbance at these colonies by other humans is highly unlikely, and was never observed.

Effect of laying date and egg volume on breeding success

Laying date influenced breeding success in all years, with eggs laid in the last quartile fledging fewer chicks (Table 3, Fig. 7). For first eggs, this difference was only significant in

2001-02 ($\chi^2 = 20.851$, df = 2, $P < 0.0001$), although it approached significance in 1999-00 ($\chi^2 = 5.351$, df = 2, $P = 0.069$). Breeding success of all eggs showed significant differences between the quartiles in 2000-01 and 2001-02 ($\chi^2 = 15.029$, df = 2, $P < 0.001$; $\chi^2 = 22.799$, df = 2, $P < 0.0001$, respectively), but not 1999-00 ($\chi^2 = 3.837$, df = 2, NS). The lower breeding success in 1999-00 in the first quarter appears to be a carry over effect from the hatching success.

In all three breeding seasons, the eggs that fledged chicks were greater in volume than eggs that did not fledge chicks, although this difference was only significant in 2000-01 (independent sample t-test $P < 0.0001$ – equal variances not assumed) (Fig. 8). The 2000-01 breeding season was the most productive, and although there were egg failures, 55% of nests were able to fledge a chick. Females that laid larger eggs in this season were significantly more likely to raise a chick to fledging.

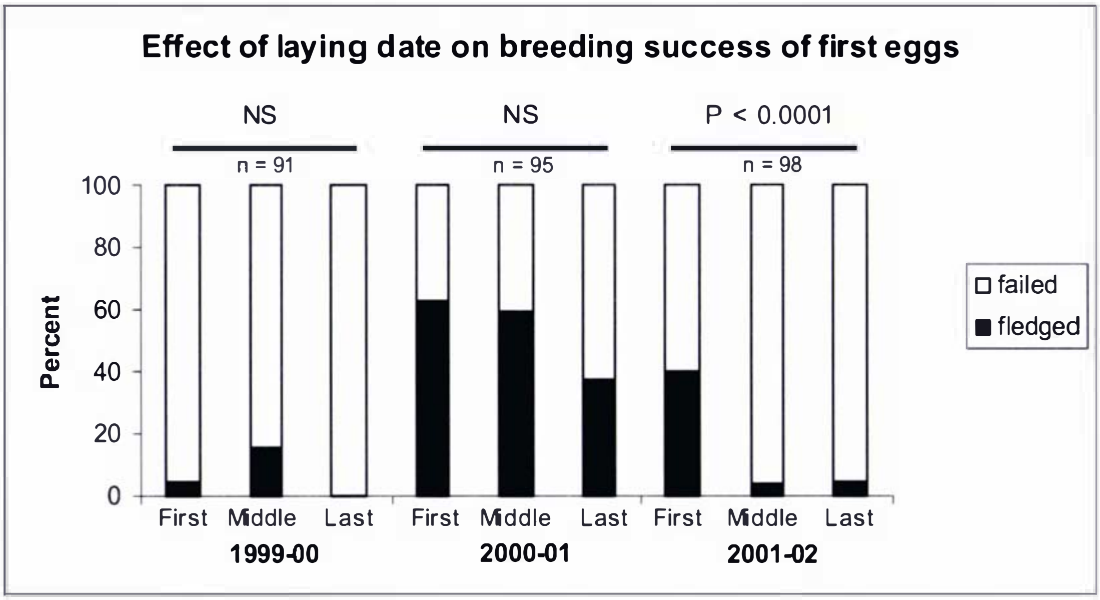

Figure 7. Relative breeding success of first eggs laid in the first, middle, and last quartiles of egg laying, for each of the three breeding seasons. Significant differences between quartiles were found in 2001-02, but not in 1999-00 or 2000-01.

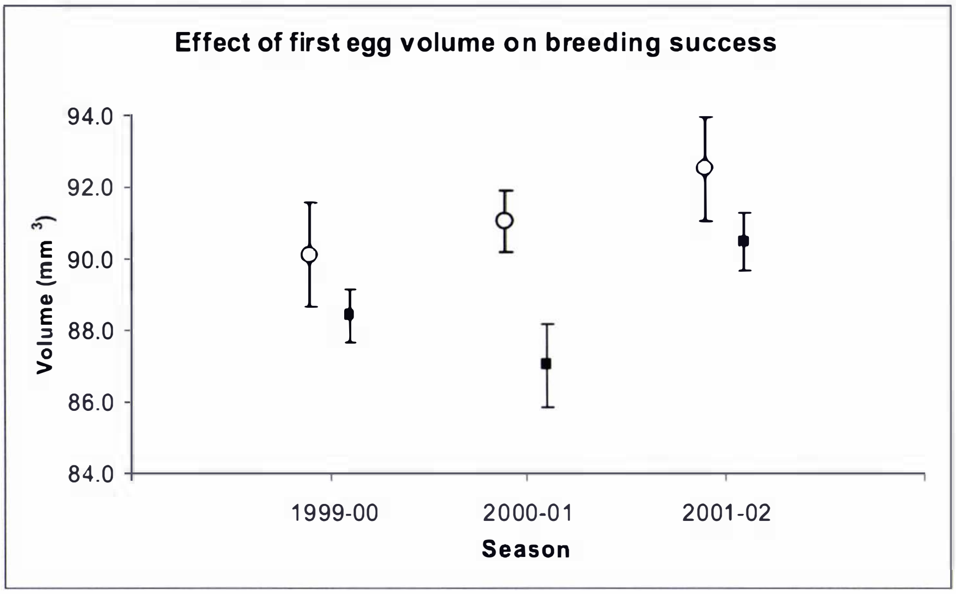

Figure 8. Mean egg volume (± 1 SE) for first eggs laid that fledged chicks (○) and did not fledge chicks (■), for each of the three seasons. Sample sizes are 8 and 83 for 1999-00, 52 and 43 for 2000-01, and 13 and 84 for 2001-02, fledged and did not fledge respectively. The difference in 2000-01 is highly significant (P < 0.007).

Peaks in egg failure and chick mortality

In all years there were distinct peaks in either egg loss, chick mortality, or both (Fig. 9). In years that peak egg loss and chick mortality both occurred, the peaks occurred together. Data presented are those for the 100 monitored nests, except where noted.

In 1999-00 peak egg loss occurred over 7 – 28 November. During this 22 day period, 27 eggs, up to three eggs per day, were lost (26 first, 1 second, 36% of the eggs initially present) (Fig. 9). This peak began just over one month after the median laying date in this season, coinciding with prolonged incubation stints by adult birds, and desertion of eggs. As mentioned above, eggs that were lost during this time were probably deserted by adults, and depredated by black-backed gulls. A sample of adult birds weighed during November and December 1999 revealed the lowest average mass recorded during the study, 2.46 kg (n = 54) and 2.45 kg (n = 61), respectively. In November 1999 one adult weighed only 1.89 kg and was very emaciated. Mean adult mass, excluding November and December 1999, was 2.62 kg (n = 121). Adult gannets appeared to be experiencing extreme food stress at this time.

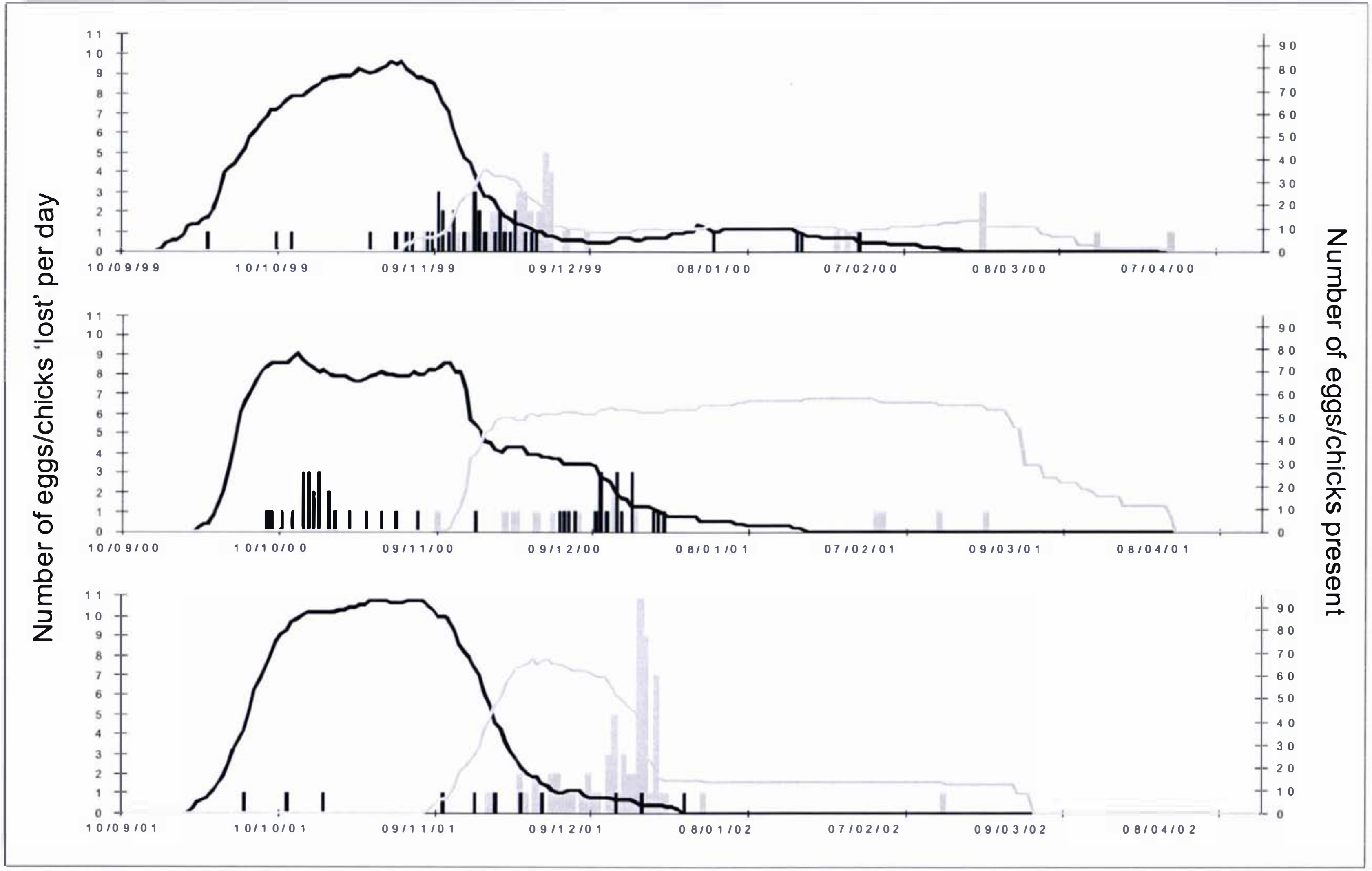

Figure 9. Seasonal analysis of the number of eggs and chicks 'lost' per day (bars) against the number of eggs present at the 100 monitored nests (lines). Numbers of eggs are indicated by black lines and bars, and chicks by grey lines and bars. This figure includes both first and second eggs. Eggs that were infertile/addled, or that failed due to 'accidents' are not included. The spike seen in chick 'losses' in the 2001-02 season, between 18-19 December, may be underestimated due to averaging the total number of 'losses' over two days.

During the 1999-00 peak in egg loss there was also a 13-day peak in chick mortality, occurring between 19 November and 1 December (Fig. 9). Three chicks were lost after the start of the egg loss, but before the main peak in chick mortality. During the peak, 29 chicks were lost, aged between 4 and 28 days old, all from first eggs (83% of the chicks present at the start of this period). Many of theses chicks were emaciated, and desertion of small chicks (<5 days old) by brooding adults also occurred. Unattended small chicks were therefore open to depredation by black-backed gulls and exposed to the weather. At this time, numerous dead chicks were removed from nests to the edge of the colony by black-backed gulls, but not always eaten. On 30 November, when the chick loss peak was nearly over, 112 dead chicks were counted throughout the Plateau colony. This is likely to be an underestimation. An estimated 30 large live chicks were all that was visible in the colony, with another approximately 30-50 small chicks under brooding adults. During 1999-00, 1796 breeding pairs were estimated at the Plateau colony.

A further 9 chicks were lost following the peak, three from first eggs and six from second eggs, with three on 22 February 2000. This secondary loss coincided with a period of rain and nine hours of higher than average wind (6.4 m/s, cf. NIWA average for February 4.6 m/s) from a generally southerly direction.

In 2000-01 two peaks of egg loss occurred, the first 7 October – 5 November, and the second 2 – 22 December (Fig. 9). The first lasted for 30 days, beginning two days after the all egg median laying date, with a total of 23 eggs being lost, up to three eggs a day (22 first, 1 second, 32% of the eggs initially present). Within this peak, 14 – 19 October, 13 first eggs were lost in 6 days. The second peak happened much later after relaying had occurred, and lasted for 21 days (Fig. 9). During this peak, 19 eggs were lost (5 first, 14 second, 59% of the eggs initially present). Although chick mortality during this season was low, chick loss was present between these two peaks, with a small peak occurring at the same time as the second peak in egg loss. Three chicks aged between 14 – 37 days old, later died in February, all from second eggs. The death of a fourth, a 94-day old chick from a first egg, was very unusual as it appeared healthy and in good condition.

In 2001-02, during the early part of chick rearing, 25 November and 23 December, emaciation and desertion of small chicks was again being observed. During this 28-day period, 64 chicks were lost, aged 1 – 39 days old (62 from first eggs, 2 second eggs, 98% of the chicks initially present). Within this period were four days of very high mortality (18 –

21 December), during which 28 chicks were lost, aged 10 – 39 days. Mortality was clearly due to the storm that struck during this time. Many of the chicks lost were too large to be sheltered sufficiently from the weather by attending adults (if actually being attended), and were too small to be able to thermo-regulate properly (average age of chicks that died during these four days was 29 days). The food stress exhibited before this bad weather was probably also a contributing factor.

These peaks in loss appear to be caused by bad weather. Certainly, the 1999 and 2000 NIWA Climate Summaries suggest that these years were more anticyclonic than normal, with 1999 being one of the most anticyclonic on record. As part of this there were more frequent easterlies over the North Island, perhaps causing the sea conditions to be rougher than normal, thus affecting the gannets' ability to feed. In 1999-00, October and November had 8 and 17 days of above average wind speeds, whilst 2000-01 had 15 and 8 days and 2001-02 15 and 15 days. Add to this the fact that November 1999 and 2000 were very wet months (173% and 70% above average monthly rainfall), whilst November 2001 had below average monthly rainfall and December 153% above monthly rainfall. The spike in very high chick mortality during four days in late December 2001 was a direct result of weather. A storm struck during 18 – 19 December, with 110.6 mm of rain falling (149% of mean monthly December rainfall in two days). A cold south-easterly to westerly wind, with speeds during the latter part of the storm, 19 – 21 December, averaged 7.6 m/s (monthly December average of 5.0 m/s). A combination of wind speed, direction, and rain is responsible for this peak in loss, and could also be a contributing factor in the losses recorded in the other two breeding seasons.

Depredation by black-backed gulls

During the peaks in loss in 1999-00 and 2000-01, eggs and small chicks were being deserted and subsequently depredated by black-backed gulls. This appeared to be the major cause of egg loss, and an important factor in chick mortality. I observed 35 cases of eggs being depredated by adult black-backed gulls from colonies at Cape Kidnappers. All but eight were in 1999-00 when this phenomenon was very common. Red-billed gulls, *Larus novaehollandiae*, were not observed to take eggs, but were frequently seen amongst the nests during the chick rearing stage when spilt regurgitations were common.

Black-backed gulls generally 'patrolled' the colony for a variable amount of time, before swooping down and taking the egg on the wing. Occasionally they landed amongst nests to pick up the egg. Only one of the 35 eggs taken was seen to be taken by a gull walking up to a nest on the edge of the colony. Thus, edge nests were not being targeted more than nests within the colony. In 18 cases of egg depredation, the placement of the egg was able to be determined. In 16 cases, the egg was taken from the nest cup, and in two, from just outside the nest cup. In all 18 cases the egg was unattended. Black-backed gulls were not observed taking eggs from attended nests, and although immature gulls were observed 'patrolling', only adults were observed to depredate eggs.

During the peak in egg loss in 1999-00 on 11 November, during 95 minutes, I observed black-backed gulls take ten eggs from the Plateau colony. Of these, at least four were from unattended nests. On 18 November, during 45 minutes, I observed depredation of another four eggs. As the eggs were broken and eaten by the gulls on the edge of the colony, I was able to determine that all four of these eggs contained well developed embryos.

No evidence of depredation by or sign of mammalian predators, such as feral cats, *Felis cattus*, or ferrets, *Mustela furo*, was found around the colony, although a brush-tailed possum, *Trichosurus vulpecula*, was found in a burrow near the colony during the study.

Sea surface temperatures near the colony

Annual patterns in SSTs are shown in Figure 10. Despite the small sample size, it is apparent that there were considerable differences in SSTs during October, November and December in each of the breeding seasons when chicks were present at the colony (Fig. 11).

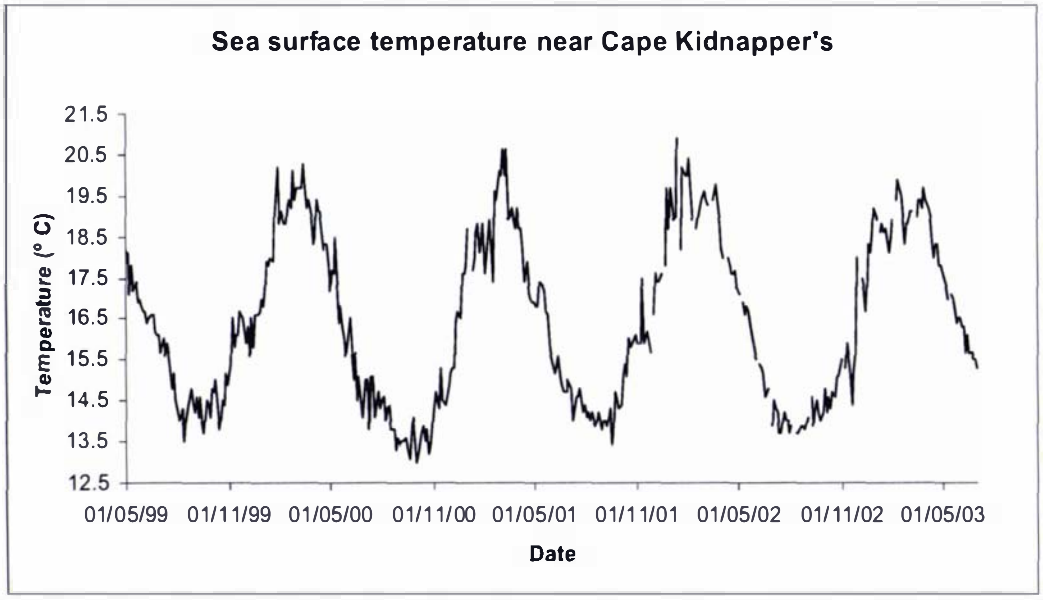

Figure 10. Annual sea surface temperature (SST) pattern near Cape Kidnapper's, taken at 39° 30' S 177° 30' E, for the duration of the study.

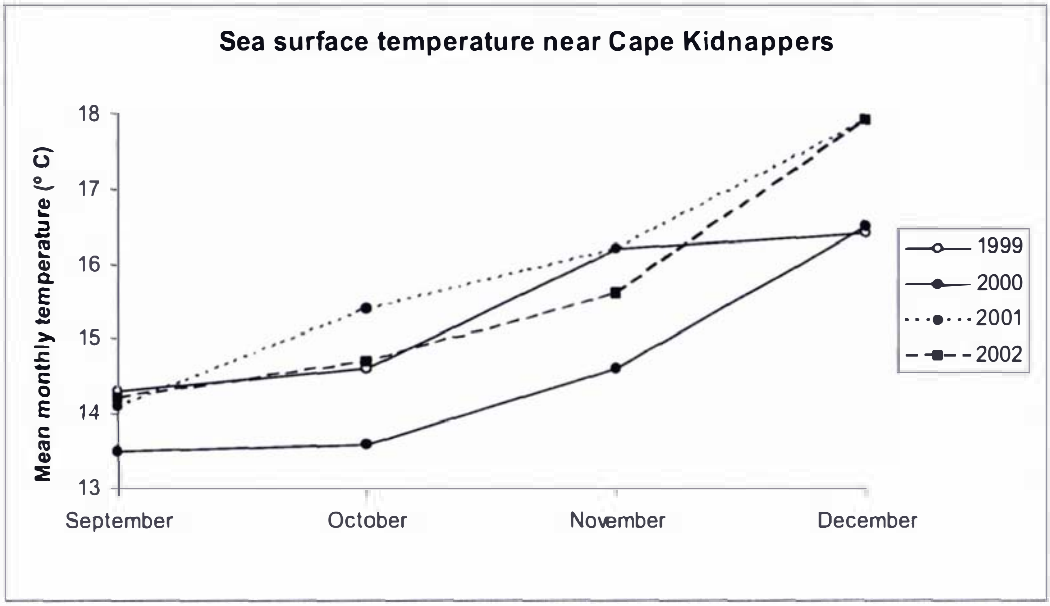

Figure 11. Sea surface temperature (SST) near Cape Kidnappers, taken at 39° 30' S, 177° 30' E, for the months September to December. This indicates a considerable difference in sea surface temperatures over the four seasons studied.

Comparison of breeding data with previous studies at Cape Kidnappers

The state of breeding on 20 December, in the four seasons studied along with productivity in that year, is shown in Table 7. As can be seen, the stage of breeding on 20 December gives an indication of what the productivity might be, but can under- or overestimate it depending on the estimation of success from eggs still present at the time. For example, in 2001-02, productivity was actually 13%, whilst on 20 December four nests had eggs and 23 had chicks, suggesting a likely productivity of above 20%. However, these data do allow direct comparison with other historical data collected at the Plateau colony, usually around this date. It suggests that caution needs to be used when using data collected at this time, to assess annual productivity.

Table 7. Nest contents at the 100 monitored nests on 20 December, and productivity, in each breeding season studied. These data allow direct comparison with historical data collected at this colony.

Season	Empty nests	Eggs	Chicks	Productivity
1999-00	84%	6%	10%	9%
2000-01	36%	11%	53%	55%
2001-02	73%[1]	4%	23%	13%
2002-03	34%	18%[2]	48%	55%

[1] 73% includes 15% of nests which contained freshly dead chicks (see later), and more chicks were to die in the following days.

[2] 18% includes 4% of eggs that were hatching on that day.

Discussion

This chapter represents the most comprehensive account of Australasian gannet breeding success and productivity to date. Most research on this species has been based on infrequent visits to colonies, thereby missing critical information. Perhaps as a result of the intensive monitoring undertaken during three breeding seasons in this study, and the timing of the study relative to environmental events, this chapter leads us to reconsider our thinking and interpretation of Australasian gannet breeding biology. The consistently high annual breeding success found in the Atlantic gannet, was not found in this species as Nelson (2002) suggested it would be. My findings indicate that the low breeding success recorded in previous New Zealand studies probably has little to do with human disturbance, and is more likely be a natural phenomenon related to environmental conditions.

Hatching success

Hatching success at the Plateau colony was very variable, with relatively low success in two of the three seasons studied. The study shows, however, that this was a result of environmental conditions affecting the behaviour of incubating adults. This is the first documented evidence of egg desertion by Australasian gannets, and this behaviour is not present in either of the other two gannet species (Nelson, 2002).

Poor hatching success leading to breeding failure has been noted in Australasian gannets before, with Wodzicki & McMeekan (1947) observing the disappearance of over 1000 eggs at Cape Kidnappers in 1945-46. Infertility of the eggs was suggested to be the ‘only logical explanation’ at the time, although it seems more likely now that events similar to those witnessed in my study were occurring. Other studies at Cape Kidnappers have suggested better hatching success. During 1960-61 to 1962-63, Robertson (1964) estimated 10 – 15% of eggs at the Plateau colony were lost and a further 5 – 10% addled, an average hatching success of around 80%. Even if this was a conservative figure, with only 55 – 58% of nests containing hatched chicks and egg loss possibly being missed, hatching success was considerably higher than in 1945-46 and in this study in at least two of the seasons. Nelson (1978) quotes Robertson as giving hatching success in six different groups at Cape

Kidnappers as 46% (459 pairs), 31% (208 pairs), 60% (150 pairs), 65% (100 pairs), 0% (35 pairs), and 7% (31 pairs), but no further details were given.

At Horuhoru, Stein (1971) suggested a hatching success of 98% for 1350 eggs, based on several visits over two months. Although almost certainly an overestimate not accounting for egg loss, it is vastly different to the 27% hatching success recorded at the same site in 1950-51 (calculated by Wingham (1984b)). For nearby Motukaramarama hatching success for all eggs was 81 – 88% (mean = 84%), and for first eggs was 81 – 85% (mean = 82%), for 1978-79 to 1980-81 (Wingham, 1984b). This fails to recognise the loss of all first clutches in a storm, and may be an underestimate in the second season due to the colony not being monitored until chick hatching. However, the 85% hatching success of first eggs in the final season of Wingham's study is higher than in any year of this study.

Similar results to my study are suggested from Australian colonies. During four seasons of study (1988-89 to 1991-92), hatching success of all eggs, was 54 – 73% at Pope's Eye (mean = 65%) and 54 – 75% at Wedge Light (mean = 64%) (Norman & Menkhorst, 1995). Similarly, in 1994-95 at Pope's Eye 63% of first eggs and 70% of all eggs hatched successfully (Gibbs et al., 2000). Again at Pope's Eye in 1997-98 and 1998-99 hatching success was 81% and 55% (n = 8) (Bunce, 2001a).

Wingham's first season was an example of how Australasian gannet hatching success can be severely influenced by weather events, as was the loss of nests and eggs to a storm at Pope's Eye (Gibbs et al., 2000). However, this hatching failure is clearly different from that recorded in this study. Compared with the Atlantic gannet, the hatching success reported above for Australasian gannets is very low. At Bass Rock between 1961-63, hatching success for Atlantic gannets was 74 – 87% (mean = 82%, n = 500) (Nelson, 1966). The 74% recorded in 1963 was the lowest ever recorded, resulting from 20% egg loss, which Nelson (1978) thought was due to exceptionally wet weather at about the time of hatching. Between 1964 and 1976 hatching success was never lower than about 85% at one part of Bass Rock (Nelson, 1966), suggesting a consistently high annual hatching success. Likewise, at Ailsa Craig hatching success was 79% and 84%, in 1975 and 1976 respectively (Wanless, 1978). The lowest rates of hatching success for Atlantic gannets come from Bonaventure Island, Canada, 40% in 1966 and 37% in 1967 (Poulin, 1968), almost certainly due to the effects of DDT and dieldrin (Chapdelaine et al., 1987). There are limited data for hatching success in the Cape gannet, although some variability was shown between two seasons, about 85% and

60% in 1966-67 and 1967-68 respectively (Jarvis, 1974). The latter was possibly a consequence of guano collection removing nest mounds prior to breeding. Thus, Australasian gannets are considerably different to Atlantic gannets in this respect, and further study is needed to determine where Cape gannets fit into the picture.

Higher hatching success of first eggs compared to second eggs, as found in 2000-01 and 2001-02, was to be expected, as the majority of first egg losses appear to be due to inexperienced adults (Nelson, 2002). Due to this inexperience, Nelson (1978) noted lower hatching success of replacement eggs than first eggs of Atlantic gannets at Bass Rock. In 2001-02 in this study, egg loss was very low, and almost half of the eggs were lost due to accidents, therefore supporting the inexperience theory. In 1999-00 it seems that due to the foraging conditions, even experienced adults were affected, and perhaps due to an improvement in foraging conditions, second eggs had a higher hatching success. This trend has been found before in Australasian gannets (Wingham, 1984a; Norman & Menkhorst, 1995; Gibbs et al., 2000), and in most cases this happened in years in which there was a catastrophic event, such as a storm or heavy rain early in the season, causing significant egg loss, but being relatively short lived, thus enabling relaying.

As observed in this study, Nelson (2002) documents females occasionally laying eggs and failing to incubate them. Atlantic gannets never normally leave eggs unattended (Nelson, 2002). He attributed this to first time breeders, however, my study suggests that in Australasian gannets this may be associated with food shortage. This behaviour was only observed in 1999-00 and 2001-02 during the peaks in egg loss, suggesting that it was food stress that caused these birds to eventually abandon the nest and egg.

Effect of laying date and egg volume on hatching success

Female seabirds that lay early are generally considered to be older or more experienced, as suggested by Nelson (1966) for Atlantic gannets, and generally lay larger eggs (Coulson & White, 1958; Parsons, 1975; Lloyd, 1979; Birkhead & Nettleship, 1981; Furness, 1983; Birkhead & Nettleship, 1987a; Birkhead & Nettleship, 1987b; Birkhead & Nettleship, 1987c; Hatchwell, 1991; De Forest & Gaston, 1996; Hipfner et al., 1997; Hipfner et al., 2003; also see Chapter 5 for further discussion). Although age of females was not known in this study, the later laying females were generally less able to hatch chicks, suggesting they were unable to cope with the environmental conditions at the time. The slightly lower success of females laying in the first quartile in 1999-00 may have been due to poor foraging conditions just before these eggs hatched. In any event, birds laying in the last quartile hatched very few chicks. However, in 2001-02 when hatching success was highest, there was no difference between early and late laying females, suggesting that even inexperienced pairs were able to incubate eggs successfully. Early breeding Atlantic gannets have a higher success, and inexperienced pairs hatched 62.5% of eggs, compared to 86% in birds breeding for at least the third time (Nelson, 1966). This difference was almost entirely due to egg loss, but also to ineffective incubation. In this study, during years when periods of stress and poor breeding conditions overlap with incubation, females that laid eggs earlier were better able to cope, incubating eggs more successfully. Similar declines in hatching success with egg laying date have been found in other seabirds, so this appears to be a common trend (Davis, 1975; De Forest & Gaston, 1996).

For Australasian gannets at Pope's Eye 'older' groups laid earlier, but egg size was not correlated with female age (Gibbs et al., 2000). This perhaps explains why a significant difference in the volume of eggs that hatched successfully compared to those that did not was only found in 2000-01. Therefore the date the egg was laid appears to be important whilst hatching success is independent of egg volume, as found in razorbills, *Alca torda* (Lloyd, 1979). Similarly, Antarctic petrels, *Thalassoica antarctica*, showed no correlation between hatching success and egg volume (Amundsen et al., 1996).

Fledging success

Fledging success in this study was also very variable between seasons, as was the cause of this variation. Several previous studies have also suggested low fledging success (see Table 8), however, the cause or extent of fledging failure has not been well documented before, and most have not adequately separated fledging failure from hatching failure. Fledging success of less than 20% occurred in two of the three seasons in this study. Notably, the 2001-02 hatching success was very high, but fledging success was very low, showing the impact of weather events and environmental variability on Australasian gannets.

Although the exact cause of death in most chicks could not be determined in this study, observations of emaciated chicks, slower growth (see Chapter 6), and high mortality during several bad weather events, suggest that starvation and exposure were the primary causes of mortality. Indirectly, food stress on adults led to high chick mortality as a result of adults leaving small chicks unattended. Fledging success has been found to exhibit the greatest response to supplementary feeding experiments, and attendance patterns and abandonment of chicks was found to be significantly correlated in kittiwakes, *Rissa tridactyla* (Gill et al., 2002). One previous study mentions starvation events in Australasian gannets (Stein, 1971), in which starvation of chicks was observed in several years (Table 8). Dead chicks have also been observed in several of the other early New Zealand studies (Buddle, 1947b; Clark & Roberts, 1948), possibly also as a result of similar starvation events. However, none of these studies adequately recorded or discussed the events.

For these starvation events, and also egg failures, weather is an important factor. Warham (1958) noted that month-old chicks were too big to be covered by the parent and became soaked during rain storms. This was a cause of considerable chick mortality in my study in 2001-02. Less severe weather induced mortality has previously been recorded at Cape Kidnappers (Wodzicki & Robertson, 1953), with nearly 10% of chicks at the Plateau colony dieing during a cold south-easterly wind. On Motukaramarama, however, no such chick losses were found, with high fledging success from all hatched eggs, 90 – 96% (mean = 94%) (Wingham, 1984b). On Cat Island, Tasmania, 16 chicks fledged from 17 hatched eggs (94%) (Warham, 1958), and at the Wedge Light and Pope's Eye colonies fledging success was also high, 76 – 97% (mean = 85%) and 82 – 95% (mean = 91%) at Wedge Light and Pope's Eye respectively (Norman & Menkhorst, 1995). Just analysing first eggs gave 75 – 96% (mean = 84%) and 79 – 96% (mean = 90%), at Wedge Light and Pope's Eye respectively. The authors felt this may have been a slight overestimate, due to some birds fledging before they could fly. At Pope's Eye in 1994-95 fledging success was 70% (Gibbs et al., 2000), with a storm killing some chicks during the early part of the season (also washed out eggs as noted above). Therefore, previous studies which provide accurate information on this variable have indicated high fledging success with little annual variation, even those which have shown the occurrence of egg losses.

Other causes of mortality recorded in both this and other studies, have been attacks on young unguarded chicks by adults, especially 'unemployed' prospecting birds (Warham, 1958), and Wingham (1984b) found most small chicks that died were smothered by parents brooding incorrectly. Mortality due to toxicity (possibly from an algal bloom) or neuropathological disease has also been observed (Wingham, 1984b), but was not noted in this study.

Most chick mortality occurred within the first month of hatching in this study, and similar results are found elsewhere (Wodzicki & Stein, 1958; Wingham, 1984b). Chicks in this early period seemed less able to cope with the food shortages. However, the storm that caused considerable chick mortality in 2001-02 mainly affected chicks aged 21-40 days old, reflecting the observation that chicks that are too large to shelter under parents are more susceptible to weather events (Warham, 1958).

The high mortality of Australasian gannet chicks is in part due to the adults' habit of leaving chicks unattended. This has been documented before (Wodzicki & Robertson, 1953; Warham, 1958; Wodzicki & Robertson, 1974; Waghorn, 1983). Waghorn (1982), however, provides the only detailed information noting that chicks were first unattended at 48 days old. She found the times when chicks were left unattended increased with age, especially in the few weeks before fledging. At 12-18 days old, Atlantic gannet chicks have acquired homeothermy at moderate ambient temperatures (Ricklefs et al., 1984), but exposure to weather events such as in 2001-02 would probably be beyond their capabilities. The mortality of chicks aged 21-40 days during the storm in 2001-02 supports this. Thus, the desertion of chicks less than about three weeks old, as seen in my study, would indicate adults were extremely stressed. Depredation of eggs and small chicks by black-backed gulls, *Larus dominicanus*, is also increased at times when the nest is left unattended.

At Bass Rock, Atlantic gannets enjoy a very high fledging success of 89 – 94% (mean = 92.3%) (Nelson, 1966). This was calculated from the same nests used to determine hatching success (1961-63). Furthermore, based on 37 years of data from Bass Rock (through to 1997), Atlantic gannets were immune from significant reproductive failure at the chick stage (Nelson, 2002). Fledging success at Grassholm, Bempton and Ailsa Craig during the 1970s was at least 90% in two to three years of study at each (Nelson, 1978; Wanless, 1978). Starvation in Atlantic gannet chicks has not been recorded (Nelson, 2002), but other factors including weather, attack by neighbours, falling (from cliff nest sites), and inadequate parental care were sources of mortality (Nelson, 1966). Prolonged rain and low temperatures caused death in some 3-5 week old chicks, although such severe weather occurs fairly infrequently and the overall mortality thus caused is insignificant (Nelson, 2002). So again there appears to be a considerable difference between fledging success in Australasian and Atlantic gannets, with the former showing considerable variability and very poor success in some years. Starvation, as well as weather events appear to be the major cause of this, and reflect the more variable environment faced by Australasian gannets. Data on fledging success for the Cape gannet are limited, although chick loss was only about 3% during two seasons (Jarvis, 1974).

Effect of laying date and egg volume on fledging success

The significant difference in the fledging success of hatched eggs between quartiles in 2001-02 shows the benefits of early egg laying. Older chicks were better able to survive the storm in December 2001. In the other two seasons there was little benefit from hatching from an early laid egg, in 1999-00 perhaps due to the timing of the food shortage, and in 2000-01 as a consequence of generally low chick mortality. Similar results were suggested by Stein (1971) who noted that in years of high egg and chick loss, the older chicks fared better. Other seabird studies reveal similar patterns. Lloyd (1979) reports that most mortality of razorbill chicks resulted from young inexperienced breeders laying late in the season. Likewise, in years of high sandeel, *Ammodytes marinus*, abundance fledging success in great skuas, *Catharacta skua*, is uniformly high in relation to adult age (Ratcliffe et al., 1998). Thus, both older and younger breeders benefited from high food abundance, suggesting no significant differences in fledging success compared to date of laying. However, in contrast to this study, birds of all ages had low fledging success during years in which sandeels were scarce. This was mainly because unattended chicks were depredated (Ratcliffe et al., 1998).

There was no significant correlation between egg volume and fledging success in any season of this study, although in 2001-02 this relationship approached significance. Several seabird studies have reported a significant relationship between egg size and fledging success. For common terns, *Sterna hirundo*, the fledging success of chicks from third eggs is significantly correlated with egg size, at least in a favourable breeding year (Nisbet, 1973). Furthermore, the fledging success of razorbills is apparently dependent on egg volume, as 75% of chicks that died did so during the first week of life, during which there was a significant difference in mass of chicks that survived and died (Lloyd, 1979). Mass in the first week was correlated with egg volume during this time (Lloyd, 1979). Parsons (1970) also found that the most important factor in determining post-hatching survival was the size of the egg. However, it may be difficult to determine whether egg size or ability of the parents is responsible without experimental manipulations as conducted in investigations of chick growth (eg. Nisbet (1978) and Hipfner & Gaston (1999)). It would be useful to conduct similar egg-swapping experiments in this species to determine the role of parental quality vs egg volume on chick survival. Other studies of seabirds with a single egg clutch have found no significant relationship between egg size and fledging success (Ollason & Dunnet, 1986; Meathrel et al., 1993).

Breeding success and productivity

This study highlights the fact that breeding success and productivity can be affected by mortality at both the egg and chick stage, and that high hatching success does not necessarily mean high fledging success. Without investigating each stage of breeding, the poor breeding success in 1999-00 and 2001-02 could have been attributed to the same factors. The low hatching and fledging success in 1999-00, and high hatching and low fledging success in 2001-02 are evidence of different processes at work.

In contrast with this study, high breeding success of first eggs at Motukaramarama shows little annual variation (74 – 81 %) (mean = 78%) (Wingham, 1984b). This was higher than for any year of my study, but does not take into account complete loss of first clutches in 1978-79. Wingham (1984b) summarised by saying that on Motukaramarama, productivity is 61%, similar to the 2000-01 season in this study, and similar to 60 – 67% in good years at Horuhoru (Stein, 1971). In Australia, similar productivity was recorded at Wedge Light 41 – 59% (mean = 51%) and Pope's Eye 41 – 55% (mean = 47%) (Norman & Menkhorst, 1995). Later, in 1994-95 at Pope's Eye breeding success from first eggs was 74%, whilst from all eggs it was 48%(Gibbs et al., 2000). Productivity appeared to be about 73% in this study, so slightly higher than in most other studies.

The Atlantic gannet had no years of breeding failure from the 1960s to early 1980s. This is in stark contrast to the Australasian gannet in this study and those outlined in Table 8 below. At Bass Rock, breeding success was 69 – 77% (mean = 74%) (Nelson, 1966). In a further 10 years of study (1965-1976), breeding success was estimated to be 80%, despite variations in weather (Nelson, 1978). Across the North Atlantic, on Bonaventure Island, breeding success was essentially the same, 69 - 77% (mean = 74%) (1976, 1979, and 1984) (Chapdelaine et al., 1987). This was after the colony had recovered from the low hatching success caused by the effects of DDT and dieldrin. Thus, breeding success was consistently high. The data for all these studies are presented as the number of chicks per 100 nests, rather than chicks fledged from eggs laid. Thus, productivity figures for these studies, using the same definitions as this study are unknown. Some of the differences between breeding estimates of Australasian and Atlantic gannets may be due to these differences in measures.

At Bass Rock 7-37% of nests with pairs attending did not have eggs laid, this value is more if empty nest sites are included (Nelson, 1978). At Grassholm, 22-30% were empty but attended, and at Ailsa Craig this figure was around 38-44%. Nelson (2002) adjusts these figures slightly, but they essentially say the same thing. That is, that a considerable proportion of nests are empty during the height of the breeding season, and many of these are apparently not included in the estimates of breeding success or productivity. Nelson (1978) suggests that in one out of four years Atlantic gannets take an involuntary rest due to change in partner. This would mean that in any season up to 25% or more of pairs could not get much past the nest building stage, and eggs if laid are almost certainly lost. This study found that relatively few pairs failed to lay eggs (9, 5, and 2% of pairs in each of the seasons respectively). This may have involved a slight underestimate due to the fact that the monitored nests were selected outside of the breeding season based on actual nest sites being visible. Thus, in most cases these were established sites which would be reclaimed by males from the previous season, or quickly taken over by males looking for a new site. As the monitored nests included sites within and on the edge of the colony, this seems unlikely have affected this result. Nevertheless, there does appear to be a significant difference between Australasian and Atlantic gannets in this respect. Moreover, changes in breeding partner were recorded during this study, with no 'rest' years being apparent (B. Stephenson unpubl. data).

Despite this, Nelson (2002) summarises more recent data for several Atlantic gannet colonies. At Fair Isle, during a period of five years (presumably in the late 1980s) breeding success (as defined in this chapter) was 48-78% (Riddiford & Harvey (1992) in Nelson (2002)). At several other gannetries (Ailsa Craig, Hermaness, Noss, Fair Isle, and Troup) figures for 'mean breeding production' are given (Murray (2000) in Nelson (2002)). Nelson (2002) was not quite sure what exactly was counted, but felt that this was total nests that produced fledging young (equivalent to productivity as defined in this chapter). The figures presented suggested 53-69% at the colonies between 1986-97, then 59-80% between 1997-99. Nelson (2002) suggested these values were extremely low, even given the fact they took into account nests in which eggs were not actually laid. Perhaps this is evidence that the breeding success of Atlantic gannets is changing, along with changes evident in other seabird species (Hislop & Harris, 1985; Martin, 1989; Harris & Wanless, 1990; Harris et al., 1997; Harris & Wanless, 1997; Proffitt, 2004).

It has been suggested that the Cape gannet shares similar breeding success to the Atlantic gannet (Nelson, 1978), although there are limited data. Jarvis (1974) found breeding success to be around 80% in 1966-67, but around 58% in 1967-68. This degree of variation in breeding success suggests the Cape gannet may be more similar to Australasian gannet than to the Atlantic gannet.

Very low breeding success and productivity in Australasian gannets is not a new finding (Table 8), but the realisation that this is a natural phenomenon has not been widely accepted. Low breeding success and almost complete breeding failure have been shown at eight gannetries, since the early gannet studies. Of note is the 1946-47 breeding season, in which similar breeding failures were evident at gannetries at the Three Kings, Mahuki, and Horuhoru. This suggests a geographically widespread phenomena, almost certainly not the result of human disturbance as suggested. The results of this study suggest that the environment, including weather and changes in food availability and abundance, have an important influence on breeding Australasian gannets.

Many of the failures documented in Table 8 are at Horuhoru. However, this is due more to Stein's (1971) long-term study at this site, and lack of data from other sites, rather than a real difference between this and other New Zealand gannetries. Information from Pedra Branca, off Tasmania, (Brothers et al., 1993) suggest similar breeding failures to those seen in New Zealand, with loss of eggs and late re-laying.

Initially, several studies suggested that human disturbance at breeding colonies was the cause of low hatching success or breeding failures (Cunningham, 1947; Hamilton, 1947). Due to a lack of critical information the suggestion that Australasian gannets enjoy high breeding success, in the absence of human disturbance, has become accepted in more recent discussions of Australasian gannet breeding biology (Nelson, 1978; Wingham, 1984b; Nelson, 2002). This is despite several studies showing the significant effects of storms on hatching success and other parts of the breeding cycle (Stein, 1971; Wingham, 1984a; Gibbs et al., 2000). However, the discovery that egg and chick desertion can be a significant factor in breeding failure is novel, and will be discussed later.

Table 8. Breeding failures and significant mortality events documented at eight gannetries in New Zealand and Australia. Many of these were during the early years of gannet study in New Zealand. Stein's (1971) long-term study showed that low breeding success at the Horuhoru gannetry was not uncommon, whilst similar long-term data for other gannetries do not exist.

Gannetry	Year	Estimate of breeding outcome	Author
Three Kings	1946-47	Almost complete breeding failure, from more than 5500 breeding pairs	(Buddle, 1947b; Buddle, 1948)
Mahuki	1946-47	Complete breeding failure	(Hamilton, 1947)
White Island	1946-47	8 January - 34-38% with eggs, 2-3% with chicks, 60-64% empty nests	(Robertson & Wodzicki, 1948)
Cape Kidnappers	1945-46	1000 eggs 'disappeared', total breeding success <16%	(Wodzicki & McMeekan, 1947)
	1948-49	10% chicks died during pre-Christmas storm	(Wodzicki & Robertson, 1953)
	1950-51	'many eggs lost' after a long period of rain	(Wodzicki & Robertson, 1953)
Horuhoru	1946-47	58% mortality of chicks, estimate 4-5% breeding success	(Fleming, 1948)
	1948-49	c.30% breeding success	(McKenzie, 1949; Stein, 1950)
	1949-50	55.6% of 840 chicks died[1], estimated 40% breeding success	(Stein, 1971)
	1950-51	c.250 chicks fledged from 1500 pairs, estimated 17% breeding success	(Stein, 1971)
	1951-52	Only 208 chicks fledged from 1500 pairs, estimated 14% breeding success	(Stein, 1971)
	1952-53	80% of 1500 chicks died	(Wodzicki & Stein, 1958)[2]
	1968-69	300 occupied nests instead of 1600, almost complete breeding failure	(Stein, 1971)
Motukaramarama	1978-79	Complete loss of first clutch during severe storm	(Wingham, 1984a)
Farewell Spit	1985-86	22 dead chicks found in January, c. 240 breeding pairs[3]	(Hawkins, 1988)
Pedra Branca	1990-91	Almost complete failure of first clutches[4]	(Brothers et al., 1993)

[1] Nelson (1978) quoted Stein as stating "starvation of small young, caused by rough weather preventing adults from feeding adequately, was an important cause of death (140 dead chicks in 1949, all between three and six weeks old, many of them clearly emaciated)."

[2] Stein apparently suggested to Nelson (1978) that 86% of chicks died during this seasons

[3] not caused by exceptionally high tides which have washed out the Farewell Spit gannetry during several seasons over the period of study

[4] deduced from two visits to the island detailing nest contents in August and late-November (see text).

Effect of laying date and egg volume on breeding success

The general trend shown by this study is for eggs laid in the last quartile to have lower breeding success than the first and middle quartiles. This difference was significant during two of the three seasons studied, and suggests an advantage to laying eggs early in the egg laying period. This is almost certainly linked to the fact that first eggs that fledged chicks were larger than those that did not. This link between first egg size and success was only found in 2000-01, when breeding success was highest, suggesting that severe conditions lesson the effect of egg volume. Thus, females are better off laying eggs as early as possible, and egg volume is either of secondary importance or a consequence of female condition.

Until now, the breeding success of gannets in relation to egg size has not been studied. However, because the Atlantic gannet has a favourable food supply, Nelson (2002) suggests there should be little if any correlation. Although not yet tested, the confirmation that a significant relationship does exist in some seasons in the Australasian gannet implies a difference between these two species in regards to food availability and abundance during the breeding season.

Peaks in egg failure and chick mortality

The peaks in egg and chick loss in this study show the important effect of environment and weather on breeding Australasian gannets. In 1999-00 the peak period of egg and chick loss overlapped, with observations of unattendance by adults, suggesting that the reason for the losses was extreme food stress in adults. This appears to have been caused by weather and possibly SSTs affecting food abundance or availability at the time. The prolonged incubation shifts during this time (B. Stephenson unpubl. data), possibly indicate that adults were flying longer distances than normal to find areas where they could feed, or needed to spend more time at a location foraging in order to be able to return to the colony. Similar trends have been found in kittiwakes during seasons in which food shortages caused similarly poor breeding success and food stress in adults (Regehr & Montevecchi, 1997). The two peaks in 2000-01 affected eggs in the first, and eggs and chicks in the second. Again, eggs were known to have been deserted and food stress in adults is thought to have been responsible. In 2001-02 a single peak occurred later in the season, following egg hatching. Thus, only chicks were affected. The occurrence of a severe storm during the latter stages of this peak caused significant chick loss, perhaps compounded by the fact that chicks were already affected by the conditions leading up to this storm.

During these peaks, the high incidence of desertion highlights the extreme food stress of the adults. Evidence for this includes desertion of eggs and chicks <5 day old, apparently longer incubation and nest attendance shifts (Chapter 5), and the low mean adult body mass recorded during these times (Chapter 5). Longer foraging trips and lower adult body mass has been associated with higher rates of nest desertion during possible periods of food shortage in blue penguins, *Eudyptula minor* (Numata et al., 2000), and Gill et al. (2002) found that supplementary feeding in kittiwakes led to shorter incubation shifts. Similarly Harris & Wanless (1997) observed the adult kittiwakes discontinue incubation, but still attend nests, during food shortage. Thus, feeding conditions directly impact nest attendance and the likelihood of desertion in seabirds. For this study, the minimum adult mass of 1.89 kg was recorded in November 1999. This is lighter than any bird recorded by Wodzicki & Robertson (1953), and is lighter than any live mass noted in Marchant & Higgins (1990). The breeding failures of Australasian gannets in 1951-52 (see Table 8) were similar to those seen in 1999-00. Perhaps similar environmental conditions were occurring.

Depredation by black-backed gulls

Depredation of eggs by black-backed gulls occurred frequently, and was a major cause of egg loss at the nests monitored in this study. Depredation of eggs also occurred at other undisturbed parts of the gannetry. Black-backed gulls took advantage of the food stress causing adult gannets to desert their eggs, with all cases of egg depredation in which the position of the egg was known, being from unattended nests.

Depredation of gannet eggs by gulls is not commonly documented in the literature. At Cat Island, disturbance by man has resulted in decimation of the colony (Anderson, 1936; Warham & Serventy, 1978). Anderson (1936) observed depredation by Pacific gulls, *Larus pacificus*, which resulted from gannets leaving nests with eggs and small chicks in response to human approach. However, despite visits to the Cape Kidnappers colonies since 1946, depredation of eggs by black-backed gulls was not detected until 1956-57 (Wodzicki & Robertson, 1953; Taylor & Wodzicki, 1958). In that year, eggs were observed being stolen from the Plateau colony on two occasions (Taylor & Wodzicki, 1958). During 1957-58, depredation of eggs from all three colonies present at the time 'became common', apparently all from unattended nests (Taylor & Wodzicki, 1958). This was believed at the time to be the first instance of gull depredation at gannet nests in New Zealand. The researchers visit to the colony may have coincided with a peak in desertion of nests by adults. If so, the depredation resulted from natural, rather than human, disturbance. It would be very interesting to know if food stress, similar to that in this study, was occurring during that breeding season.

Robertson (1964) studied the Cape Kidnappers colonies over four nesting seasons, 1959-60 to 1962-63 (26 visits of 2-8 days duration). He did not see any depredation by gulls during that study. He did note that adult black-backed gulls regularly 'patrolled' the colonies, and suggested they were looking for regurgitated food. Immature and juvenile gulls were rarely seen in the vicinity of the colonies. However, the ranger at the sanctuary reported predation on the colony margins, with eggs being taken from beneath standing birds during the greeting ceremony (Robertson, 1964). This is the only record of attended eggs being taken by black-backed gulls. Robertson (1964) suggests that egg depredation by gulls was the result of the death of one member of a pair, bad weather keeping a bird from returning or causing poor feeding conditions and desertion, or young and inexperienced breeders. Disturbance by humans was also seen to cause desertion on the edges of the colony, but he did not elaborate on the idea of desertion following poor feeding conditions. Black-backed gulls have not been seen to prey on gannet eggs or chicks at the Farewell Spit gannetry (Hawkins, 1988).

Nelson (1978) suggested that there is no evidence that unaided gulls can steal eggs from Australasian gannets. On Bass Rock, herring gulls, *Larus argentatus*, were only able to take Atlantic gannet eggs after human disturbance or freak behaviour of the gannets (Nelson, 1966), and, as starvation was never a factor in this species, eggs would not have been left unattended for any other reasons. Thus, Nelson (2002) concluded that depredation by large gulls is completely insignificant.

This study clearly shows desertion of eggs and small chicks does occur naturally as a result of food stress, and that black-backed gulls have learnt to take advantage of this situation by depredating these unattended eggs and chicks. Depredation on such a scale, with clear reasoning for its occurrence, has not been documented before.

Sea surface temperatures near the colony

Sea surface temperatures around Cape Kidnappers showed a consistent seasonal pattern, being lower in the winter (around 13.5°C) and higher in summer (around 19.5°C). However, there were marked annual differences, particularly during November and December, when mean monthly sea surface temperatures varied between years by as much as 1.6°C. The effect of such differences on the feeding ecology of gannets is unknown. Gannets at Cape Kidnappers are known to feed mainly on pilchard, *Sardinops sagax*, anchovy, *Engraulis australis*, saury, *Scomberesox saurus*, Jack mackerel, *Trachurus novaezelandiae*, and squid, *Nototodarus* spp., and these species also form the main part of the diet at other breeding colonies (Wodzicki & Moreland, 1966; Robertson, 1992). All of these fish species are surface schooling, and all except saury occupy coastal waters out to the shelf edge (Robertson, 1992). Saury have a more oceanic distribution which normally extends inshore to about the shelf edge but can sometimes occur closer to the coast when slope water extends up onto the outer shelf (Robertson, 1992). Thus, even slight changes in sea surface temperature may impact the distribution, abundance, depth at which these species occur, and thus their availability as food items for gannets.

The effects of changes in SST on the food supply of some seabirds has been documented. Mickelson et al. (1992) found that for blue penguins, *Eudyptula minor*, breeding in Bass Strait, Australia, lower sea temperatures led to heavier adults, earlier laying, more chicks per pair, and heavier chicks. Earlier breeding led to more chicks per pair and consequently the ability to raise a second clutch (Mickelson et al., 1992). Presumably the cooler waters result in slightly higher concentrations of nutrients or chlorophyll or more fish on which little penguins feed (Mickelson et al., 1992). Although not directly related to SST, other studies have shown links between feeding rates and sea conditions (wave height, wind speed). A significant negative relationship between the feeding rates and sea conditions has been shown in guillemots (Birkhead, 1976). Similarly, for sandwich terns, *Sterna sandvicensis*, and common terns, fishing success and capture rates were higher during moderate sea conditions, than calm conditions, but decreased when sea conditions became rough (Dunn, 1973). Similar effects of sea conditions could be occurring with Australasian gannets, with 1999 and 2000 being the most anticyclonic on record (NIWA Climate summaries), and this is worthy of further study.

Comparison of breeding data with previous studies at Cape Kidnappers

The analysis of nest contents on 20 December in each season revealed large annual differences in the number of nests with eggs, chicks and empty/weedy nests. Even the number of nests still containing eggs at this stage of the breeding season varied markedly from 4% to 18% of nests. Although not providing an accurate estimate of productivity, a count at this stage of the breeding season does indicate failures that have occurred up to that point. This is very useful, in the case of egg and early chick failures, when almost all such failures would have occurred by this stage. The only failures that might occur after this date and affect the colony are severe storm events, such as observed in 2001-02. If periods of food stress were to occur after this date, then they would be less likely to affect first clutches, as most chicks would be older than 30 days, and better able to cope. However, they could affect second clutches, especially eggs (see below). Care should be taken in using this information to derive a season's productivity.

The results of this study are consistent with previous information from Cape Kidnappers (Table 9). As already noted above in Table 8, there was considerable breeding failure in 1945-46 (Wodzicki & McMeekan, 1947). In late-December 1945, 81% of nests still had eggs, indicating considerable egg loss and replacement laying. Supporting this was the

Table 9. State of breeding at the Plateau colony in late December (Wodzicki & Robertson, 1953). These counts were conducted between 16 – 22 December in each year, and thus are comparable with the data derived from my 20 December data. Figures presented are percentages of nests from the Plateau colony, with the number of breeding pairs indicated by n.

	Nest contents			
Season	Eggs (%)	Chicks (%)	Empty/weedy nests (%)	n
1945-46	81.1	0.5	18.4	196
1946-47	25.8	37.4	36.8	155
1947-48	47	36.5	16.5	230
1948-49	45.2[1]	54.8	-	210
1949-50	15	75.5	9.5	220
1950-51	9.7	62.1	28.2	230
1951-52	54.3	26.4	19.3	237

[1] 45.2 includes both empty nests and eggs.

presence of few chicks, which were either well developed or just hatched. Breeding failures persisted, as almost all eggs present at this time also failed.

The 1947-48 and 1951-52 seasons also appear to stand out from the other years, still with a high percentage (>20%) of eggs present. Of note was Stein's (1971) discovery of very poor breeding success at Horuhoru in 1951-52 as well, and he mentions spring gales as a possible cause. Unfortunately, he did not appear to visit Horuhoru during 1947-48, and no information for other colonies is available.

Conclusions

As yet it is not possible to link reproductive failures and egg and chick losses to any specific environmental factor. This study, however, shows that a relationship does exist, and suggests that environmental variation between breeding seasons is an important influence on Australasian gannet breeding success. In light of the findings of this study, many of the previous breeding failures at gannetries within New Zealand and Australia are likely to have been due to such environmental variation, rather than human disturbance or infertility as posed by some early studies. It is unlikely that Australasian gannet colonies undisturbed by humans have a consistently high annual breeding success, comparable to Atlantic gannets. These two species are clearly living within different environments. The Australasian gannet appears to live in a variable environment, and has been affected by similar breeding failures to those recorded in this study, within the last century. The Atlantic gannet lives in a less variable environment where annual breeding success is high and varies little from season to season. Despite this, both species have increased throughout this period at similar rates.

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4

Australasian gannet, Morus serrator, *eggs at Cape Kidnappers, New Zealand: size characteristics and changes during development*

Introduction

The Australasian gannet, *Morus serrator*, is endemic to the Australasian region. The most recent population census in 1980-81 estimated 46,004 breeding pairs in New Zealand, and a further 6,600 breeding pairs estimated at colonies in Australia (Wodzicki et al., 1984). This population has gone through a marked increase during the past century (Wodzicki et al., 1984), with the population in Australia still increasing rapidly (Bunce et al., 2002).

The Australasian gannet has been studied at several colonies, both in Australia and New Zealand. The Cape Kidnappers gannetry is perhaps the most studied, as for some time it was the only mainland gannet colony in the world. Basic breeding biology at this colony was first investigated in 1945 (Wodzicki & McMeekan, 1947), with further work and annual counts continued to the present (Wodzicki & Robertson, 1953; Wodzicki & Stein, 1958; Wodzicki, 1967a; Wodzicki, 1967b; C.J.R. Robertson, unpubl. data). Wingham (1984) examined the breeding biology and egg characteristics of Australasian gannets at Motukaramarama Island, Hauraki Gulf. Investigation of basic egg characteristics has also been undertaken at the recently established colonies in Victoria, southeastern Australia (Norman & Menkhorst, 1995; Gibbs et al., 2000). The breeding biology and egg characteristics of the Atlantic gannet, *Morus bassanus*, have been well studied (Nelson, 1978; Nelson, 2002), but little has been published on the egg characteristics of the Cape gannet, *Morus capensis*.

Australasian gannets lay single egg clutches, but replacement eggs are common, and second replacement eggs rare (Nelson, 1978; Wingham, 1984). Both sexes incubate the egg, using the webs of their feet wrapped around the egg (Wodzicki & McMeekan, 1947), and both adults raise the chick. The incubation and fledgling periods are both prolonged, approximately 44 days for incubation and 108 for the fledgling period (Wingham, 1984). The basic characteristics of eggs at the two Australian colonies (Norman & Menkhorst, 1995; Gibbs et al., 2000) and at Motukaramarama (Wingham, 1984) and Cape Kidnappers (Wodzicki & McMeekan, 1947) have been documented. However, Wingham's study was the only one in which first and second clutches were accurately separated, and for which fresh egg mass was known. Wingham (1984) found no correlation between first and second egg length and width, and no significant difference between first and second egg length and width, although first eggs were slightly larger than second eggs. Norman & Menkhorst (1995), however, found that first eggs were of similar length, but significantly narrower, on average, than replacement eggs. Similarly, Gibbs et al. (2000) found that first eggs were smaller and lighter than replacement eggs, but again differences were not significant. Thus, there appear to be differences between eggs at Australian and New Zealand colonies. It remains to be discovered if these differences are the result of infrequent study visits, or real geographical variations.

As the Australian colonies are on man-made platforms, access is difficult and unlike the New Zealand island colonies, it is not possible to stay for prolonged periods. Therefore, the studies at these sites are based on infrequent visits up to two weeks apart. Thus, it would be useful to develop accurate methods for estimating an egg's fresh mass and also its age, from which expected hatching/laying dates can be estimated. So far, neither of these methodologies has been investigated in Australasian gannets. The development of an accurate predictor of fresh egg mass would be of particular use in determining annual and site specific differences in fresh egg mass, as well as determining changes in individual females' eggs relative to age. Several workers have shown that volume estimates derived from linear measurements allow accurate determination of fresh egg mass in other species (Wooller & Dunlop, 1980; Birkhead & Nettleship, 1984). It would be useful to know whether this technique can be used to determine fresh egg mass for Australasian gannet eggs. Changes in specific gravity for predicting laying or hatching dates has also been used in a number of studies (O'Malley & Evans, 1980; Wooller & Dunlop, 1980; Keedwell, 2002), with varying success. An assessment of the accuracy of the technique was also conducted by Collins & Gaston (1987) who suggested that it was possible to compute a confidence interval for the mean date of laying for a colony using the technique, where egg laying was synchronous. Egg dimensions have been used to successfully estimate egg volume and fresh mass for a number of species (Wooller & Dunlop, 1980; Birkhead & Nettleship, 1984; Hipfner, 1997).

As yet, we know little about annual variation in egg characteristics, effects of female age and condition on egg size, effects of egg size on chick growth and survival, and geographical variation in egg size and production costs, in Australasian gannets. Deriving a technique for accurate assessment of egg mass from linear measurements will enable many of these questions to be answered, without the need for intensive daily observations of breeding colonies.

The aims of this chapter are therefore to investigate the egg characteristics of Australasian gannet eggs at the Cape Kidnapper's colony. This is 1) to specifically develop an accurate method for predicting fresh egg mass from measurements of egg length and width, and 2) to test the utility of changes in specific gravity of eggs in ageing eggs. An accurate measure of volume that directly relates to fresh egg mass, will allow annual comparisons of egg volume through one annual visit to the colony. Being able to accurately estimate egg age from specific gravity of an egg would also allow the approximate onset of laying to be calculated for that year. I also aim to investigate the relationship between first and second eggs, and compare the egg characteristics found in this study with previous studies, both in New Zealand and Australia.

Methods

I examined 328 Australasian gannet eggs, from three consecutive breeding seasons (1999-00, 2000-01, 2001-02) at Cape Kidnappers, New Zealand (39° 38' S, 177° 05' E). Gannets lay only a single egg per clutch, but some females lay replacement eggs. Of the 328 eggs examined 283 were from first clutches, 43 from second clutches and 2 from third clutches. Between year comparisons of eggs are given in Chapter 3.

Egg size characteristics

Eggs were numbered with a non-toxic permanent marker (red Sharpie ® fine point), and length and width (to 0.1 mm, using dial callipers) and mass (to 1 gram, using a Pesola 300 g spring balance) were determined. Fresh egg mass was available for 195 eggs (59.5%) which were weighed and measured on the day they were laid (180 first eggs and 15 second eggs).

For all 328 eggs I calculated egg shape as width/length x 100 (see Coulson, 1963; Preston, 1974; Brooke, 1978; Gibbs et al., 2000). For the same eggs, egg volume was calculated using the equation $V = K_V(\text{length} \times \text{width}^2)$, where the constant $K_V = 0.507$ (Hoyt, 1979). Hoyt (Hoyt, 1979) gives a value of 0.507 for the brown booby, *Sula leucogaster brewsteri*, a value similar to other seabird species listed. The relationship between calculated egg volume and fresh egg mass was investigated using only first clutch eggs.

Incubation period, specific gravity and water loss

Date of laying and hatching, and fresh egg mass were known for 106 first eggs. Incubation period (I) was the interval between laying and hatching dates. Predicted incubation period (I_{pred}) was calculated for the same 106 eggs, using the equation $I_{pred} = 12.03W^{0.22}$ (Rahn & Ar, 1974), and compared with observed values.

Of the 195 eggs for which fresh egg mass (W) is available, 46 eggs were reweighed before the first star fractures appeared (between 5 - 41 days after laying). Observed daily water loss (MH_2O_{obs}) for each egg was calculated as the difference in egg mass between first and last egg weighing. Predicted mean daily water loss (MH_2O_{pred}) was calculated using the equation $MH_2O = 0.015W^{0.74}$ (Rahn & Ar, 1974). Comparisons between observed and predicted values are made. The specific gravity of eggs (g/cm^3) was calculated by dividing egg mass (g) by egg volume (cm^3).

As the fate of all eggs was known, eggs were classed either as successful (hatching and producing a chick) or unsuccessful (including eggs broken, lost or infertile, see Chapter 3 for further details). Successful and unsuccessful eggs were analysed to see if changes in specific gravity and water loss were different.

Unless otherwise stated, means are reported ± 1 standard deviation (SD), whilst standard errors (se) are reported in tables. Correlations conducted were Pearson bivariate correlations, and all statistical analyses were performed using SPSS for Windows, Release 11.5.0. Capture, handling and banding of birds was conducted under the Department of Conservation's New Zealand National Banding Scheme, Institutional Permit to band birds No. 0259. The Massey University Animal Ethics Committee gave permission to conduct this research, Protocol No. 98/173.

Results

Egg size characteristics

Mean egg length and width for all eggs was 77.6 ± 2.9 mm and 47.6 ± 1.5 mm respectively (n = 328) (Table 1). Mean shape and volume indices for all eggs was 61.4 ± 2.6 (%) and 89.2 ± 7.1 (mm^3) respectively (n = 328). Mean fresh mass for all eggs weighed on day 0 was 98.8 ± 7.4 g (n = 195). Based on an average female mass in September (n = 16) of 2.71 ± 0.21 kg, eggs were 3.6% of female mass.

Table 1. Mean (± 1 se) length and width and calculated shape and volume are shown for first, second and third eggs. Values are also shown for all eggs combined. Range of measurements and indices are also given for all eggs.

	First eggs	Second eggs	Third eggs	All eggs	Range
n	283	43	2	328	328
Length (mm)	77.7 ± 0.2	76.9 ± 0.5	79.8 ± 0.1	77.6 ± 0.2	67.8 – 86.5
Width (mm)	47.6 ± 0.1	47.1 ± 0.2	48.4 ± 1.3	47.6 ± 0.1	42.8 – 50.8
Shape (%)	61.4 ± 0.2	61.4 ± 0.5	60.7 ± 1.7	61.4 ± 0.1	53.8 – 71.6
Volume (mm^3)	89.5 ± 0.4	86.7 ± 1.1	94.8 ± 5.0	89.2 ± 0.4	69.2 – 108.7
n	180	15	1	196	196
Fresh egg mass (g)	99.0 ± 0.6	97.3 ± 2.2	100	98.8 ± 0.5	78 - 118

Using the fresh mass of first eggs (n = 180), the calculated egg volume index was found to be a highly significant predictor of egg mass ($r = 0.979$, $P < 0.001$) (Fig. 1).

Width and length of all first clutch eggs showed a highly significant positive correlation ($n = 283$, $r = 0.248$, $P < 0.0001$), with a high degree of variation (Fig. 2). However, if the three seasons were analysed separately, then there was a significant positive correlation in the 2000-01 and 2001-02 seasons (2000-01, $r = 0.361$, $P < 0.0001$; 2001-02, $r = 0.245$, $P = 0.015$), but not in the 1999-00 season (1999-00, $r = 0.120$, NS). Width and length of second and third clutch eggs showed a non-significant positive correlation ($n = 45$, $r = 0.44$, NS). When the three seasons were analysed separately, a significant positive trend was found in the 1999-00 season (r = 0.665, P = 0.003), a non-significant negative trend in the 2000-01 season (r = -0.112, NS) and a non-significant positive trend in the 2001-02 season (r = 0.354, NS).

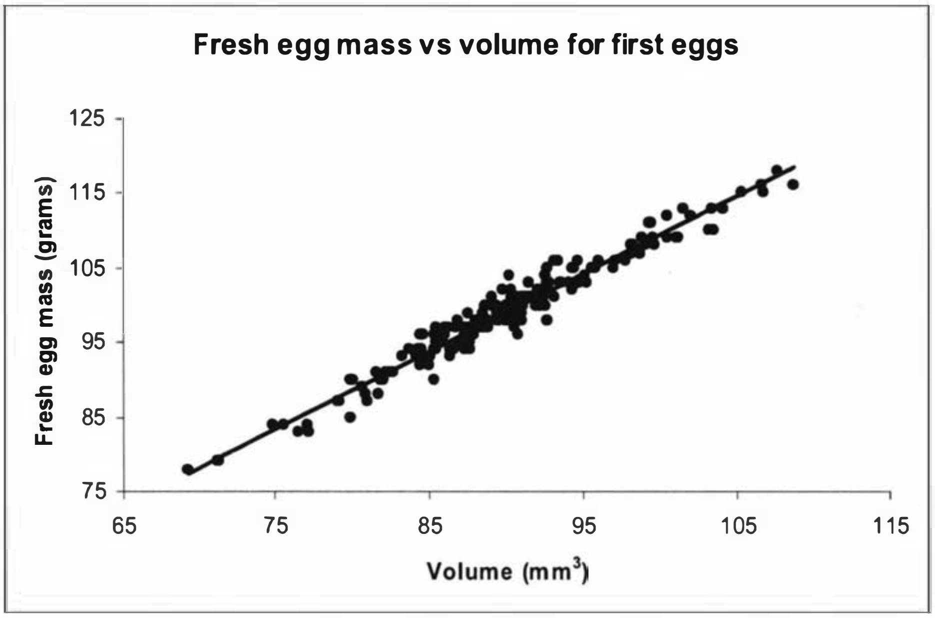

Figure 1. Fresh egg mass of first eggs from all three seasons, plotted against the volume (see text for equation used). The positive relationship is significant (n = 195, $R^2 = 0.96$, $P < 0.001$).

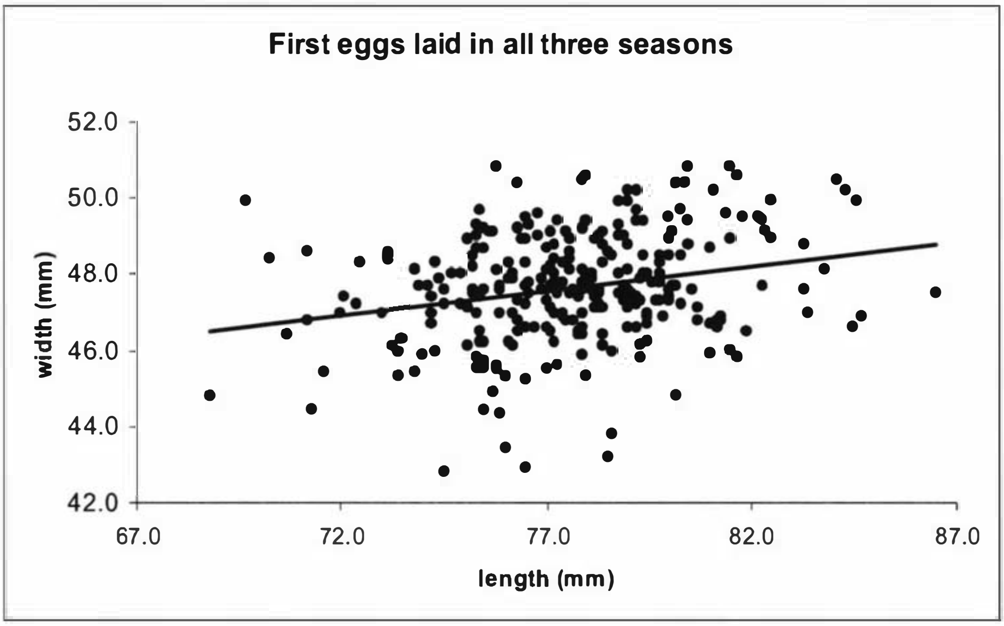

Figure 2. First egg length and width showed a significant positive correlation over the three breeding seasons (n = 283, $R^2 = 0.062$, $P < 0.0001$).

There were 42 nests for which both first and second eggs were measured (Table 2). All first and second egg measures were highly correlated ($P < 0.001$, length $r = 0.709$, width $r = 0.584$, shape $r = 0.650$, volume $r = 0.650$). First and second egg length and shape were similar (paired t-test, $t = 1.183$, NS; $t = 0.685$, NS). However, both width ($t = 2.683$, $P < 0.01$) and volume ($t = 2.702$, $P < 0.01$) of first eggs were significantly larger. Fresh egg mass was available for first and second eggs from 15 nests, and again this was highly correlated ($r = 0.784$, $P < 0.001$), and first eggs were larger than second eggs, although this only approached significance ($t = 1.951$, $P = 0.071$).

Table 2. Mean egg measures for first and second eggs (± 1 SE). There were 42 nests at which both the first and second eggs were measured, and 15 nests at which fresh egg mass was determined. Paired sample t-tests were used to determine if differences were significant.

	n	First eggs	Second eggs	Diff
Length (mm)	42	77.2 ± 0.5	76.8 ± 0.5	NS
Width (mm)	42	47.6 ± 0.2	47.1 ± 0.2	**0.01**
Shape (%)	42	61.8 ± 0.4	61.5 ± 0.5	NS
Volume (mm^3)	42	88.9 ± 1.0	86.6 ± 1.1	**0.01**
Mass (grams)	15	98.7 ± 1.9	95.7 ± 2.4	**0.001**

Individual females were not observed to lay two egg clutches in any of the breeding seasons. Only single egg clutches were laid in all nests monitored. In 1999-00 two eggs were knocked out of monitored nests by incubating adults and were recovered by neighbours. These were the only cases of nests found with two eggs.

Incubation period, specific gravity and water loss

Incubation period (I) of eggs was 45.0 ± 0.7 days (n = 106) (Table 3.). However, one egg that hatched was incubated for 53 days, and the most prolonged incubation period of an infertile/addled egg was 123 days. Fresh mass of the same 106 eggs gave a predicted incubation period (I_{pred}) of 33.0 ± 0.5. Differences between the actual incubation period (I) and predicted incubation period (I_{pred}) are highly significant (Table 3).

Of the 46 eggs reweighed more than 4 days after being laid, 32 were categorised as successful and 14 as unsuccessful. Specific gravity of both successful and unsuccessful eggs decreased linearly during the incubation period (Fig. 3). There was no significant difference between changes in specific gravity for successful and unsuccessful eggs (independent samples t-test; t = 0.187, NS). Eggs that had died would not be expected to decrease in specific gravity at the same rate as developing eggs. However, eggs categorised as unsuccessful in this study, may have included developing eggs that were lost as well as infertile or addled eggs. It was not possible to predict egg age accurately from the specific

Table 3. Observed and predicted values (± 1 SE) for water loss and incubation period. n = 32 for water loss and 106 for incubation period. See text for details of equations used to calculate values.

Variable	Observed	Predicted
Daily water loss (MH_20) (g/day)	0.279 ± 0.010	0.451 ± 0.021
Water loss to day 43, based on MH_20 (g)	12.015 ± 0.430	19.377 ± 0.161
Fraction of water loss to pipping (F) (%)	12.7 %	15.0 %
Incubation period (days)	45.0 ± 0.1	33.0 ± 0.1

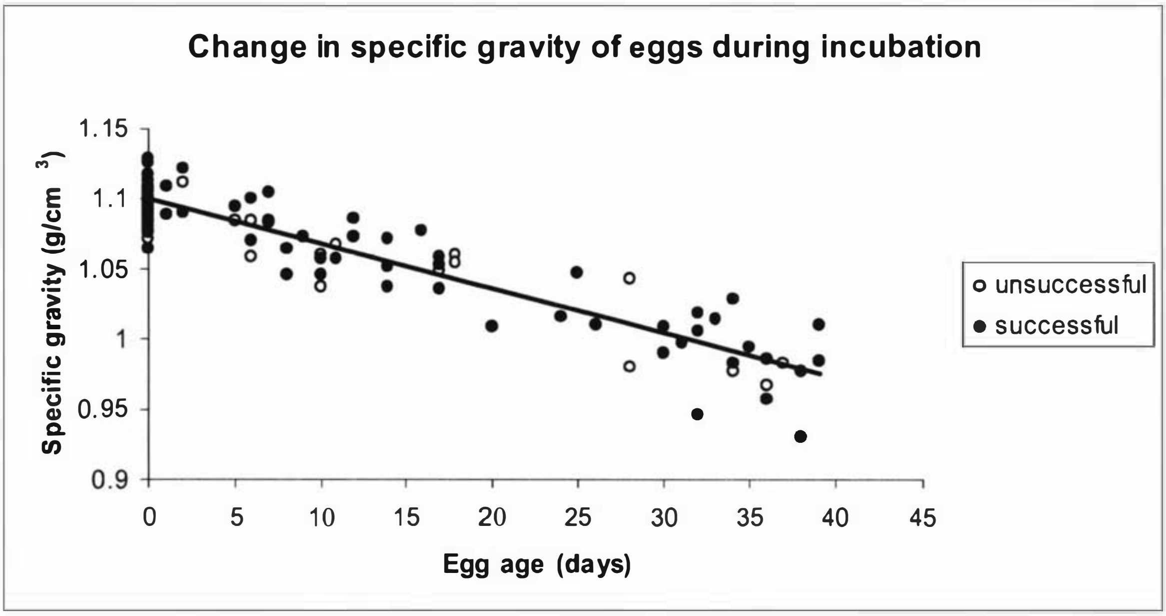

Figure 3. Change in specific gravity of 46 eggs (32 successful, 14 unsuccessful) during incubation. As there was no significant difference in change in specific gravity of successful and unsuccessful eggs, the trend line fitted is for both combined y = -0.0032x + 1.0989, R^2 = 0.8453. The plot contains some repeated measures of the same eggs, and equations and trend lines are fitted with these points.

gravity of eggs. The accuracy of prediction can be assessed using inverse predictions from the linear regression (Zar, 1999). Using this method, an egg with a density of 1.05 g/cm^3 has a predicted age of 16.1 ± 11.4 days (± 95% CI), whilst an egg with a density of 1.0 g/cm^3 has a predicted age of 31.3 ± 11.5 days (± 95% CI).

The 32 successful eggs had an average estimated water loss of 0.279 ± 0.057 grams per day, 12.015 ± 2.430 grams up until day 43 (eggs usually pipped approximately 48 hours before hatching) (Table 3). Average estimated water loss of the 14 unsuccessful eggs was 0.275 ± 0.113 grams per day, which would be an estimated 11.814 ± 4.874 grams up until the 43rd day. As can be seen, these values differ significantly from the predicted water loss values of 0.451 ± 0.020 g per day. If predicted incubation period and predicted water loss are used to calculate the mean fraction of water loss to pipping, 15.0 % of the egg's fresh mass is lost during incubation, rather than the observed mean of 12.7 % of fresh egg mass for the 32 successful eggs (Table 3). These differences are significant (paired sample t-test, $t = 5.33$, $P < 0.001$).

Discussion

Egg size characteristics

The Australasian gannet egg measurements presented here are in line with those from earlier work in New Zealand (Cape Kidnappers (Wodzicki & McMeekan, 1947); Motukaramarama (Wingham, 1984)). Eggs from Australian colonies are similar in dimension, although slightly larger (Pope's Eye and Wedge Light (Norman & Menkhorst, 1995); Pope's Eye (Gibbs et al., 2000)). Wingham (1984) suggested that at Motukaramarama, mean fresh egg mass was 99.83 g, approximately 1 g heavier than in this study. This was suggested to represent 4.25% of female mass, equating to an average female mass of 2.35 kg. It is not stated at what time of the year females were weighed. This study found that eggs were 3.6% of female mass, determined in September, when eggs are being laid. Thus, the size of the egg relative to female body mass found here was very similar to the 3.4 – 3.6% recorded for the Atlantic gannet (Nelson, 1966; Ricklefs & Montevecchi, 1979).

This study shows that egg volume is a good predictor of fresh egg mass. Similarly significant relationships between volume and fresh egg mass were found in four Alcid species (Birkhead & Nettleship, 1984; Hipfner, 1997) and in silver gulls, *Larus novaehollandiae* (Wooller & Dunlop, 1980). Determining fresh egg mass requires daily observations of nests. This can be time consuming in seabirds which generally lay during a period of weeks, whereas volume derived from linear measurements can be determined regardless of the state of incubation. Many aspects of the biology of bird eggs can be predicted from their mass (Hoyt, 1979), and thus a significant relationship between volume and fresh egg mass means that volume can be used instead. Egg volume and mass has frequently been used to investigate effects on hatchling mass, chick growth, and chick mortality (Parsons, 1970; Nisbet, 1973; Davis, 1975; Ricklefs et al., 1978; Birkhead & Nettleship, 1982; Furness, 1983; Bolton, 1991; Nisbet et al., 1995; De Forest & Gaston, 1996; Nisbet et al., 1998; Hipfner & Gaston, 1999; Hipfner et al., 2001a). The relationship between egg volume and age or breeding experience of the female, geographical position of the breeding colony, and date of laying, has been widely studied (Richdale, 1957; Coulson & White, 1958; Coulson, 1963; Nelson, 1966; Parsons, 1972; Davis, 1975; Lloyd, 1979; Mills, 1979; Mills & Shaw, 1980; Birkhead & Nettleship, 1981; Runde & Barrett, 1981; Furness, 1983; De Forest & Gaston, 1996; Hipfner et al., 1997; Massaro et al., 2002). Egg volume, as calculated in this study, can now be used to investigate similar questions about Australasian gannet breeding biology.

The lengths and widths of first clutch eggs are significantly positively correlated, but this does not hold for second and third clutch eggs. This may be a consequence of the smaller sample size of second (n = 43) and third (n = 2) eggs, and the larger variability found in these eggs. However, this could also be a real phenomenon. Eggs from Motukaramarama showed a similar trend, with first egg length and width being significantly correlated, but replacement eggs showing no correlation (Wingham, 1984). Wodzicki & McMeekan (1947) did not analyse their egg data in this way, but I performed a correlation of their egg lengths and widths. Although not significant, it approached significance (r = 0.156, P = 0.056). However, their work was conducted 16-19 December, by which stage a considerable proportion of eggs may have been replacements. If length and width of replacement eggs are not correlated, then this may explain why their data only approached significance. High correlations between various measures of individual females' eggs were found in the four species of Alcid studied by Birkhead & Nettleship (1984). However, reasons for the difference in the present study's first and replacement eggs are unclear. Length and shape of first and second eggs were similar, whilst the volume and width of first eggs were significantly larger. This suggests that the length of eggs is fixed for individual females, and width and volume varies depending on the females' condition or decision of when to lay the egg. Thus, replacement egg length and width does not have the same positive correlation that first eggs do. In contrast to this finding, Gibbs et al. (2000) showed that both volume and shape of Australasian gannet eggs were highly correlated between first and second clutches. Perhaps during that single season, food resources were abundant enough to allow females to quickly re-lay similarly proportioned eggs. Supporting this is the fact that replacement eggs were actually larger in mass than first eggs, although this was not fresh egg mass as visits to the colony were not daily.

As in this study, Wingham (1984) found mean length and width for first eggs at Motukaramarama were larger than second eggs, although neither measure was significantly different. Studies in Australia provide contrary evidence, with Norman & Menkhorst (1995) finding that first eggs were of similar length, although on average very slightly shorter, but were significantly narrower than replacement eggs. Norman & Menkhorst (1995) did not investigate differences in volume or fresh mass. Similarly, as mentioned above, Gibbs et al.

(2000) found that first eggs were on average, smaller and lighter than replacement eggs, although these differences were not significant. Both of these Australian studies, however, derived data from irregular or less than weekly visits to colonies. This may well have influenced the results because, if first clutch eggs were lost before detection, replacement eggs would be analysed as first clutch eggs. For both this study and Wingham's (1984) study, this sort of error is unlikely because of the higher frequency of visits to the colony.

Many studies have noted smaller replacement eggs compared to first clutch eggs (kittiwakes, *Rissa tridactyla*, (Runde & Barrett, 1981); common guillemot, *Uria aalge*, (Birkhead & Nettleship, 1984); thick-billed murres, *Uria lomvia*, (Birkhead & Nettleship, 1982; Birkhead & Nettleship, 1984; De Forest & Gaston, 1996; Hipfner et al., 1997; Hipfner et al., 2001b; Hipfner et al., 2003); razorbills *Alca torda* (Lloyd, 1979; Birkhead & Nettleship, 1984; Hipfner et al., 2001b)). Removing maternal effects, Birkhead & Nettleship (1984) found a marked seasonal decline in egg volume, probably due to females minimising the delay in re-laying. The relative sizes of first and second clutch eggs may be related to egg production costs for females, and may be specifically limited by egg components such as endogenous protein (Hipfner et al., 2003), or females may be re-laying smaller eggs rather than waiting to produce a larger egg, as the trade-off between larger eggs and earlier chicks may be important (Birkhead & Nettleship, 1982). Birkhead & Nettleship (1984) concluded that for Alcids, the rate at which a female can produce an egg is much lower than the rate at which a chick can grow. Thus, in years where food is not super abundant, gannets may be laying smaller eggs more quickly, in preference to producing larger eggs later.

Females rarely, if ever, lay two egg clutches. In the two cases of apparent two egg clutches, both were due to neighbours eggs having been recovered accidentally. Wodzicki & McMeekan (1947) suggested that two egg clutches are due to two eggs being laid by the female in that nest, in around 0.75% of nests. Jarvis (1974) also suggested that in Cape gannets two-egg clutches were most likely to have been laid by a single female, and used assumptions about the age of eggs in surrounding nests to support this argument, with little evidence. This study suggests that the laying of two eggs by a single female is unlikely, at least in Australasian gannets.

Incubation period, specific gravity and water loss

The incubation period observed in this study is consistent with other studies, although the egg that was successfully incubated for 53 days, was incubated for 3 days longer than the longest incubation period recorded by Wingham (1984). Wingham (1984) recorded eggs hatching after only 37 days, however, I did not observe eggs hatching before day 44. An incubation period of 43.6 days was given by Nelson (1978) for the Atlantic gannet, which incubates a slightly larger egg. Atlantic gannet chicks also develop more rapidly than Australasian gannet chicks (c. 90 days compared to c. 108 days), suggesting physiological differences between the species. The prolonged incubation periods of some pairs incubating infertile eggs is also consistent with other studies (Wingham, 1984; Gibbs et al., 2000).

Eggs lose weight throughout incubation as a result of water loss (Drent, 1970; Rahn & Ar, 1974). Thus, specific gravity of all eggs will decline from laying to hatching. This change in specific gravity has been used to predict hatching or laying dates for individual eggs from a range of species (silver gulls (Wooller & Dunlop, 1980); white pelicans, *Pelecanus erythrorhynchos*, (O'Malley & Evans, 1980); black-fronted terns, *Sterna albostriata*, (Keedwell, 2002)), with varying success, and Collins & Gaston (1987) discussed and assessed its use for predicting colony-wide laying dates. In this study, the specific gravity of Australasian gannet eggs declined at a constant rate throughout incubation, as in these previous studies. Due to the relatively synchronous laying in Australasian gannets (see Chapter 2), by randomly sampling a number of nests, this technique could be used to estimate onset of egg laying at the colony, as suggested by Collins & Gaston (1987). However, the methodology used in this study proved to be too coarse to accurately predict the age of individual eggs, as in Keedwell (2002). The use of scales with a finer resolution of mass would perhaps allow an egg's specific gravity to be determined more accurately, allowing more accurate determination of egg age. However, despite weighing white pelican, eggs to 0.1 g (roughly 0.0006 % of fresh egg mass, compared to 0.01% in this study) and calculating a specific volume equation for this species, O'Malley & Evans (1980) still encountered errors of up to 6.5 days in predicting average hatch dates of sub-colonies, and larger errors for individual eggs. Thus, if egg laying across colonies is synchronous the method can provide an approximation of average laying dates (O'Malley & Evans, 1980; Collins & Gaston, 1987), but it is of little use in determining hatching dates for individual eggs.

This study also found, perhaps surprisingly, no difference in changes in specific gravity between successful and unsuccessful eggs. Perhaps this is because many unsuccessful eggs may have been developing normally, and were classed as unsuccessful due to being lost, deserted or depredated, rather than actually being infertile or addled. A larger sample, in which only known addled or infertile eggs are analysed, would be needed to understand specific gravity changes in these eggs.

Nelson (1978) suggests 9-13% of the egg fresh mass is lost during incubation in the Atlantic gannet. In this study, the calculated value of 12.6%, to day 43 is very similar. Nelson also suggests that the Sulidae have prolonged incubation periods relative to the size of their eggs, longer than auks, gulls, penguins and geese laying eggs of roughly the same size. So the significant differences between observed and predicted values for incubation period and water loss in this study are not a surprise, but suggest that the general equations used to make these predictions (Rahn & Ar, 1974; Ar & Rahn, 1980; Ar & Rahn, 1985), are of little use in this Family. Thus, compared with the eggs of average species, Australasian gannet eggs take longer than would be expected to incubate, and their rate of water loss is lower. The use of their webbed feet to incubate the egg (Wodzicki & McMeekan, 1947), may account for some of the difference in water loss values. Whittow et al. (1989) suggest that this method of incubation offers greater resistance to loss of water vapour from the eggs of red-footed boobies, *Sula sula*. The thickness of the egg shell, greater than that in other eggs of this size, could also be important (Nelson, 1978; Whittow et al., 1989). Ar & Rahn (1985) have shown that the growth rate of embryos is proportional to the number of pores, the water vapour conductance of the shell, the water loss in the nest, and the rate of oxygen consumption at the pre-internal pipping stage.

Furthermore, Whittow (1980) suggests that ecologically, prolonged incubation in seabirds is associated with either pelagic feeding habits or a tropical environment, with both factors possibly related to food supply. Although the gannets do not quite meet the criteria that Whittow (1980) uses to define 'long incubation' (outside of the 95% confidence limit of the predicted value, based on egg weight (Rahn & Ar, 1974)), they are very close, and five of the six boobies do fall outside these limits. This suggests that long incubation in the Family may not just be constrained by environment, but may also be due to a taxonomic constraint. The fact that all members of the Family also have extended fledgling periods, again with the gannets having the shortest period, seemingly related to the long incubation period, which is possibly also constrained by both the environment (climate, prey abundance and availability, weather) and taxonomy. Supporting this is the fact that after the gannets, the fastest growing chicks are those of blue-footed and Peruvian boobies, both of which take advantage of super abundant food in good years.

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5

Annual variability in the breeding biology of Australasian gannets, Morus serrator, *at Cape Kidnappers: I adult attendance and egg size*

Introduction

The Australasian gannet, *Morus serrator*, is a colonial breeding seabird of inshore waters, characterised by a high annual adult survival rate, deferred breeding, and laying of a single-egg clutch (Wodzicki & McMeekan, 1947; Stein, 1971; Nelson, 1978; Norman, 2001). The species breeds around the coast of New Zealand and at several localities in southeastern Australia. Despite being described in recent works as well known (Marchant & Higgins, 1990), there is much still to learn about the breeding biology of this species.

Gannets are large and obvious colonial breeders, and have been the subject of a number of studies, based mostly around irregular visits to breeding sites (see Chapter 1 for a review). These studies have not focussed on annual variation in attendance patterns and egg size, and thus, links with annual comparisons of breeding success have not been made. Apart from Wingham (1984b), who studied the Motukaramarama gannetry for three incomplete seasons (1978-79 to 1980-81), Chapter 3 provides the first complete record of breeding success at an Australasian gannet colony over three seasons. It provides an analysis of hatching, fledging, breeding success, and overall productivity for 100 monitored nests, clearly showing that in some years breeding success was very low (<13% in two of three seasons). Even in the year in which breeding success and productivity were highest (47% and 55% respectively), performance was lower than that of the Atlantic gannet. Nelson (2002) suggests that the [Atlantic] gannet's generally favourable food supply indicates there should be little if any correlation between egg size and success. In contrast, I show in Chapter 3 that there was a significant relationship between egg volume and both hatching and breeding success, in the season in which breeding success was highest. Thus, there could be direct benefits for females laying larger eggs. Young from large eggs hatch with large yolk reserves that might help them through periods of food shortage soon after hatching (Parsons, 1970). For my study, hatching mass was positively correlated with egg volume and also hatching and breeding success (Chapter 3 & 6). Therefore, females should maximise egg volume. Similarly, in thick-billed murres, *Uria lomvia*, egg size was positively correlated with the rate of early wing-feather growth (Hipfner et al., 2001a). The murres, however, appear to have a trade-off between spending more time developing a larger egg, and laying an egg earlier (Birkhead & Nettleship, 1982). In a similar way, laying date also influences breeding success in Australasian gannets (Chapter 3).

Currently there are few data available on either intra- or inter-seasonal variability in egg size for any of the three gannet species. In Atlantic gannets, earlier eggs tend to be heavier than later ones (Nelson, 1966), and in Australasian gannets annual differences in egg length and width exist (Wingham, 1984a), although differences in egg volume have not been assessed.

In this chapter, I investigate annual variation in egg volume, at the Plateau colony, Cape Kidnappers, over three breeding seasons. I monitored nest attendance to determine if there were differences between breeding seasons, and relate this to variations in egg size and breeding success. I examined the eggs of known individual females in each of the three seasons, as well as at 100 monitored nest sites. The differences in first and replacement eggs are described and I analyse the delay between egg loss and replacement. This research provides baseline information for further work, particularly those examining the factors influencing the timing of egg laying by individual females.

Methods

The Cape Kidnapper's gannetry (39° 38' S, 177° 05' E) is situated on the east coast of the North Island, New Zealand (Fig. 1). The gannetry consists of four Australasian gannet colonies, Saddle (originally called Cape Kidnappers colony), Plateau, Black Reef, and Plateau Beach. Several papers have described the gannetry and its history, and changes in the breeding population have been well documented since 1945 (Wodzicki & McMeekan, 1947; Fleming & Wodzicki, 1952; Wodzicki, 1967; Wodzicki et al., 1984; C.J.R. Robertson unpubl. data). Details of the gannets breeding biology in New Zealand were first documented from studies at this site (Wodzicki & McMeekan, 1947). The gannetry is currently estimated to hold approximately 7,000 breeding pairs of gannets (breeding pairs = site-occupying pairs, defined as either one or two site-holding birds occupying a nest site (Wodzicki et al., 1984), that attempt to breed annually).

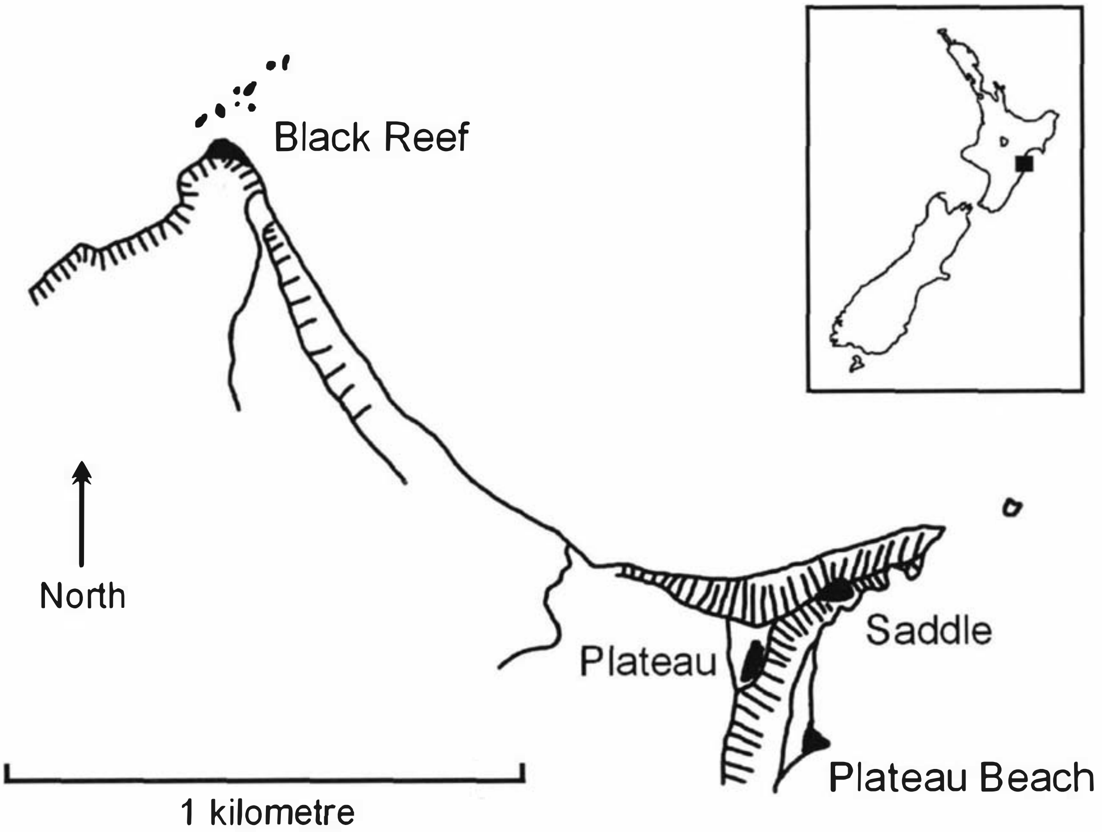

Figure 1. Location of the Cape Kidnappers gannetry, showing its orientation and the position of the four colonies. All work conducted in this study was carried out at the Plateau colony.

One hundred nest sites on the seaward, eastern side of the Plateau colony were individually marked with permanent markers whilst the colony was empty on 8 July 1999. These nests were intensively monitored over three breeding seasons, 12 August 1999 - 3 April 2000, 8 August 2000 - 16 April 2001, and 2 August 2001 - 3 March 2002.

To determine the status of nesting attempts, nest contents, daily nest attendance and identity of adults, nests were checked approximately daily from September to late-December, but less frequently from December to March. A nesting attempt was defined as attendance of a site by a pair, and the formation of a nest using seaweed. Checks were more frequent during the main egg laying and chick hatching periods, with no more than one day being missed consecutively in the peak egg laying periods of all seasons. Nest checks were usually conducted towards the end of the day, and at this time the presence and identity of adults and nest contents recorded.

During the three seasons, both members of 24, 29, and 39 pairs carried bands and were individually identifiable. An additional 35, 42, and 48 birds were also banded, but their mates were not banded. Bands were supplied by the Department of Conservation Banding Office, and each adult was banded with a five-number M-size stainless-steel band placed on the left tarsus, and a large aluminium 'sight' band on the right. The 'sight' bands were imprinted with the last three digits of the M-band, and greatly aided the identification of incubating or brooding adults. Adults were captured either by hand, or using a shepherd's crook placed around the neck of the bird. At the time of banding, adults were weighed to the nearest 20 g using a Bonso 15 kg digital scale. Adults were also captured and weighed opportunistically during the three seasons. Banded birds were sexed based on behaviour at the nest, such as observation of copulation, which was often substantiated by observations of males bringing weed to the nest, or females with dirty backs following copulation, or the laying of an egg.

All eggs were numbered with non-toxic permanent marker (red Sharpie ® fine point) shortly after laying, to allow eggs to be identified. Length and width (to 0.1 mm, using dial callipers) were used to calculate egg volume using the equation $V = K_V(\text{length} \times \text{width}^2)$, where the constant $K_V = 0.507$ (Hoyt, 1979). Calculated egg volume index is a highly significant predictor of fresh egg mass (Chapter 4), and so is used instead of mass throughout this chapter. Egg shape was also calculated as width/length x 100 (see Coulson, 1963; Preston, 1974; Brooke, 1978; Gibbs et al., 2000). Gannets lay only a single egg per clutch, with replacement eggs being laid by some birds, in the event that the first egg was lost. First clutch eggs are referred to as first eggs, whilst second and third clutch eggs are referred to as second and third eggs. The term 'all eggs' refers to first, second and third eggs collectively. Eggs that did not hatch were classed as lost (disappeared from nests without remains, disappeared and found on the edge of the colony depredated by black-backed gulls, *Larus dominicanus*, or known deserted eggs), accidental (broken or knocked out of the nest), or infertile/addled. "Accidental" eggs were sometimes depredated, but in the case of being knocked from the nest were occasionally recovered by a neighbour. Those eggs that did not hatch after 55 days were deemed addled/infertile.

Unless otherwise stated, means are reported ± 1 standard deviation (SD). All statistical analyses were performed using SPSS for Windows, Release 11.5.0 or 12.0.1. Capture, handling and banding of birds was conducted under the Department of Conservation's New Zealand National Banding Scheme, Institutional Permit to band birds No. 0259. The Massey University Animal Ethics Committee gave permission to conduct this research, Protocol No. 98/173.

Results

Egg laying and colony attendance

A nesting attempt was made at all but four of the 100 monitored nests in the 1999-00 season, and at all nests in the 2000-01 and 2001-02 seasons, with first eggs being laid at 91, 95, and 98 nests, in each season respectively (Table 1). Over the three seasons 109, 117, and 107 eggs were laid and detected, for a total of 333 eggs. The number of first eggs laid at the 100 nests in each season approached significance (Table 1). Hatching, fledging and breeding success are outlined in Chapter 3.

Table 1. Number of nesting attempts and eggs laid (first, second, and third eggs) at the 100 monitored nests per breeding season. The number of first eggs laid did not differ significantly between seasons (χ^2 = 4.89, df = 2, NS), however, the number of second eggs laid approached significance (χ^2 = 5.65, df = 2, P = 0.059).

Season	Nesting attempts	First eggs	Second eggs	Third eggs	Total no.
1999-00	96	91	17	1	109
2000-01	100	95	21	1	117
2001-02	100	98	9	0	107
Total	296	284	47	2	333

Daily attendance patterns of adults at the 100 monitored nests varied greatly over the three seasons (Fig. 2). Comparison of daily attendance patterns by month, between seasons was considered acceptable because median laying dates at the colony did not vary significantly during the three seasons (Chapter 2). In 2000-01 and 2001-02 daily nest attendance peaked in November, with one bird being present at 94% nests in both years. This dropped in December to 78% and 71%, respectively. The overall pattern was different in 1999-00, when peak attendance occurred in October (88%), dropping to 73% in November and only 65% in December. For some reason, overall daily attendance patterns were lower in 1999-00 than in the other two seasons. Variability in daily nest attendance by one adult was also greater during September and November in 1999 (as indicated by the error bars in Fig. 2) than in the other two seasons. It should be noted that September to December is when the peak in breeding occurs (see Chapter 2).

Daily nest attendance by two birds peaked early in the season, during September in all years, decreasing through October and November. This is during the pre-egg stage and the early part of incubation. In both 1999-00 and 2001-02 daily nest attendance by two birds increased slightly in December. This is largely due to failed breeders, with 79% of attendance by two birds being at nests that had already failed in 1999-00 and 88% in 2001-02. The increase therefore seems to be due to the pair not having dependent young, and therefore to less demands on feeding requirements. In 2000-01, when breeding success was highest, fewer nests had two birds attending during December.

In 1999-00 there was higher non-attendance early in the season before eggs were laid. In September, during pre-egg laying and the early stage of incubation, an average of 30% of nests were unattended. Similarly, in October, after egg laying had begun, but before the

Table 2. Mean daily nest attendance (%) by one bird for the 100 monitored nests during the September to December period. The figures in the total column are the actual mean percentage daily attendances of nests by one bird. The figures in the pre-egg, egg or chick, failed and re-laid, and failed and did not re-lay are mean percentages of the total one bird attendance. * signifies values <1%.

		Total	Pre-egg	Egg/chick	Failed and re-laid	Failed and did not re-lay
1999-00	Sept	60 ± 5.2	83	17	0	*
	Oct	88 ± 0.9	21	76	3	*
	Nov	73 ± 3.1	4	86	2	8
	Dec	64 ± 2.2	5	25	9	61
2000-01	Sept	82 ± 1.2	91	9	0	0
	Oct	89 ± 0.9	17	76	6	1
	Nov	94 ± 0.5	6	85	7	2
	Dec	78 ± 3.1	2	92	*	6
2001-02	Sept	79 ± 2.3	95	5	0	0
	Oct	90 ± 2.0	17	80	3	*
	Nov	94 ± 0.7	*	96	2	2
	Dec	71 ± 4.0	1	70	0	29

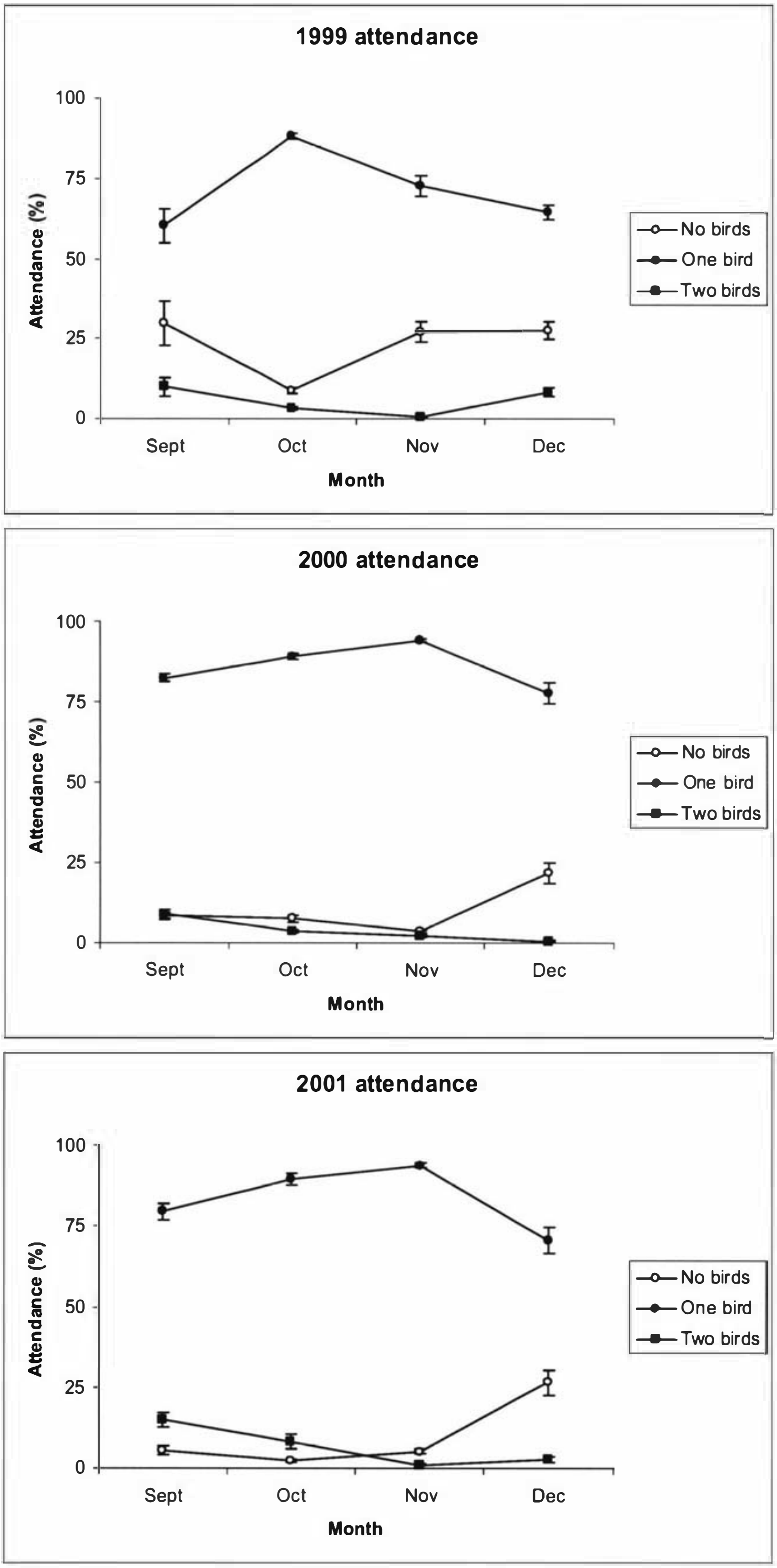

Figure 2. Mean daily attendance patterns at the 100 monitored nest sites at the Plateau colony, during the months of September through to December, in each season. These months represent the egg laying and incubation period of the colony. Attendance figures are percentages of the 100 nests. Error bars indicate 1 SE.

peak in egg loss had occurred (see Chapter 3), an average of 9% of nests were unattended. This is compared with 8% in 2000-01 and 2% in 2001-02. The significant loss of eggs during November 1999 led to a sharp rise to 27% in November, which was not seen until December in the other two seasons. The increase in nests not being attended in November 1999 was mainly due to failed breeders, with 74% of unattended nests being due to a failed breeding attempt, although some re-laid. Likewise, the increase in unattended nests in December during 2000-01 and 2001-02 is due mainly to failed breeders, 68% and 82% respectively. The remainder of unattended nests are made up of nests at which eggs were not laid, or unattended eggs or chicks.

Adult mass

During this study, data on adult mass were not collected frequently. That makes it difficult to analyse intra-seasonal variations. However, the data collected do show fluctuations in the inter-seasonal masses of adult birds attending the Plateau colony (Fig. 3).

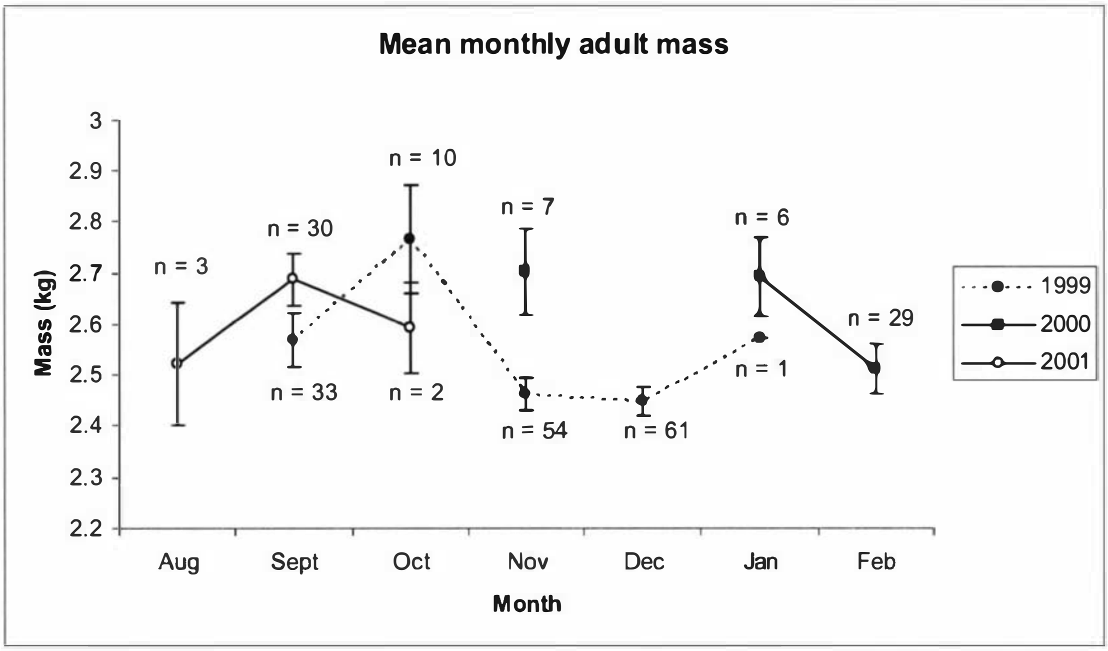

Figure 3. Mean monthly adult mass (± 1 SE) (male and female combined) during the three seasons at the Plateau colony. Of the differences in mean adult mass between years, only those in November 1999 and November 2000 were significantly different (Independent samples t-test; September t = -1.97, df = 57.5, P = 0.054; October t = 1.24, df = 4.8, NS; November t = -2.6, df = 7.7, P = 0.031), although the difference between September 1999 and 2001 approached significance.

Mean adult mass was slightly lower in September 1999 than September 2001, approaching significance, whilst the higher mean mass in October 1999 compared to October 2001 was not significant (Fig. 3). However, lower mean mass in November 1999 compared to November 2000 was significant (Fig. 3). The mean adult masses recorded in November and December 1999 were the lowest recorded in this study, being 2.46 kg (n = 54) and 2.45 kg (n = 61). In November 1999, one adult weighed only 1.89 kg, and was very emaciated. Mean adult mass, excluding November and December 1999, was 2.62 kg (n = 121).

Adults of known sex differed markedly in mass, with females weighed at the same time as males generally being heavier (Table 3). On six out of seven days, when more than one male and more than one female were weighed, mean male mass was lighter than female mean mass. Minimum mass for males and females during the study was 2.0 kg in September 1999 and 2.2 kg in November 1999, respectively. Maximum mass for males and females was 2.8 kg in February 2001 and 3.2 kg in September 1999. Due to small sample sizes statistical comparisons between male and female weights were not conducted.

Table 3. Mean adult male and female mass on the same day during the three breeding seasons. Mean female mass was greater than mean male mass on all but one day.

	Male		Female	
	N	mean	n	mean
15/09/99	4	2.42	5	2.77
25/11/99	4	2.50	2	2.42
03/12/99	3	2.45	2	2.52
27/11/00	2	2.52	5	2.78
05/02/01	2	2.75	2	2.85
08/02/01	2	2.41	3	2.81
13/09/01	2	2.42	5	2.66

Variation in egg size – intra- and inter-seasonal trends

Mensural data were collected for 328 of the 333 eggs laid and detected during the study (Table 4). Of the five eggs not measured, 1 was a first egg in the 2001-02 season and 4 were second eggs in the 2000-01 season. Apart from inclusion in Table 4, the two third eggs laid during the study are not included in further analyses.

Intra-seasonal trends

First egg length and width showed a negative correlation with laying date, in all seasons, except for length which increased slightly in 1999-00 (Appendix 1). Therefore, females that laid early in the season tended to lay eggs that were longer and wider. This affected the shape index and volume similarly, with early females laying eggs with a larger shape index and volume (Appendix 1). No trends in 1999-00 were significant, however, in 2000-01 the negative correlation for width, shape, and volume was significant, as was the negative correlation for width and volume again in 2001-02 (see Appendix 1 for significance levels). This suggests that the 1999-00 season was unusual, with a lack of a significant negative trend at least for egg volume, found in the other two seasons.

Table 4. Mean (± 1 SE) length, width, shape and volume of first and second eggs for each season, and for all eggs measured in all three breeding seasons. There was no significant difference in any measure between years for first (One –way ANOVA length $F_{2, 280}$ = 2.48, NS; width $F_{2, 280}$ = 1.14, NS; shape $F_{2, 280}$ = 0.45, NS; volume $F_{2, 280}$ = 2.45, NS), or second eggs (One –way ANOVA length $F_{2, 40}$ = 0.698, NS; width $F_{2, 40}$ = 1.237, NS; shape $F_{2, 40}$ = 1.961, NS; volume $F_{2, 40}$ = 0.471, NS).

	First eggs			Second eggs			All eggs[1]
	1999-00	2000-01	2001-02	1999-00	2000-01	2001-02	
n	91	95	97	17	17	9	328
Length (mm)	77.4 ± 0.3	77.4 ± 0.3	78.2 ± 0.3	77.6 ± 0.6	76.6 ± 0.8	76.0 ± 1.8	77.6 ± 0.2
Width (mm)	47.5 ± 0.1	47.6 ± 0.2	47.8 ± 0.2	47.0 ± 0.3	46.9 ± 0.4	47.8 ± 0.4	47.6 ± 0.1
Shape (%)	61.5 ± 0.3	61.6 ± 0.2	61.2 ± 0.3	60.5 ± 0.4	61.3 ± 0.9	63.1 ± 1.4	61.4 ± 0.1
Volume (mm^3)	88.6 ± 0.7	89.2 ± 0.7	90.7 ± 0.7	87.1 ± 1.9	85.4 ± 1.4	88.1 ± 3.0	89.2 ± 0.4

[1] includes all first, second and third eggs

Inter-seasonal trends amongst individual females

Egg measurement data, for all first and second eggs, indicate no significant difference in first and second eggs between seasons (Table 4). Further investigation of these inter-seasonal differences was undertaken using data collected from 16 individual females that laid an egg in all three seasons, and another 12 females that laid only in 2000-01 and 2001-02.

Firstly, using a Pearson bivariate correlation analysis, the eggs from each female were highly consistent in all measures, between all seasons (Table 5). That is, females that laid large eggs in one year, laid large years the next year. Note, however, that correlations between 1999-00 and any other year were lower, suggesting again that this year was anomalous and showed more variation.

Table 5. Pearson bivariate correlation analysis of egg measures from the same 16 individual females, over the three breeding seasons. All measures were significantly correlated with female in each of the seasons.

	1999-00 and 2000-01		2000-01 and 2001-02		1999-00 and 2001-02	
	Correlation	Significance	Correlation	Significance	Correlation	Significance
Length	0.797	**0.0001**	0.886	**0.0001**	0.814	**0.0001**
Width	0.816	**0.0001**	0.830	**0.0001**	0.804	**0.0001**
Shape	0.765	**0.001**	0.834	**0.0001**	0.683	**0.004**
Volume	0.839	**0.0001**	0.871	**0.0001**	0.833	**0.0001**

Secondly, a highly significant year effect on egg volume was found, with eggs in 1999-00 being significantly smaller in volume than in 2000-01 (Fig. 4). An analysis of the 12 females that laid in both 2000-01 and 2001-02 also revealed a significant difference in first egg width and volume between years (Wilcoxon related samples test, $z = -2.394$, $P = 0.017$; $z = -2.589$, $P = 0.01$). These females, however, laid larger volume eggs in 2001-02 than in 2000-01. Thus the two samples suggest different results which is puzzling, and this will be discussed later (Fig.4).

I analysed the first eggs from the 28 females from 2000-01 and 2001-02 to determine if breeding success in one season influences the change of egg volume in the following season. Too few pairs produced chicks in 1999-00 to allow an analysis of effects on egg volume in 2000-01. However, there was no effect of fledging success on the change to volume of first eggs in 2001-02 (Independent samples t-test $t = 0.665$, df= 17.1, NS).

Within season comparisons of first and second eggs for individual females

I also obtained data on first and second eggs laid by the same female within each of the seasons, with 17 in 1999-00, 17 in 2000-01, and 8 in 2001-02. Note that the females in this analysis were not necessarily the same individual females used in the inter-seasonal analysis.

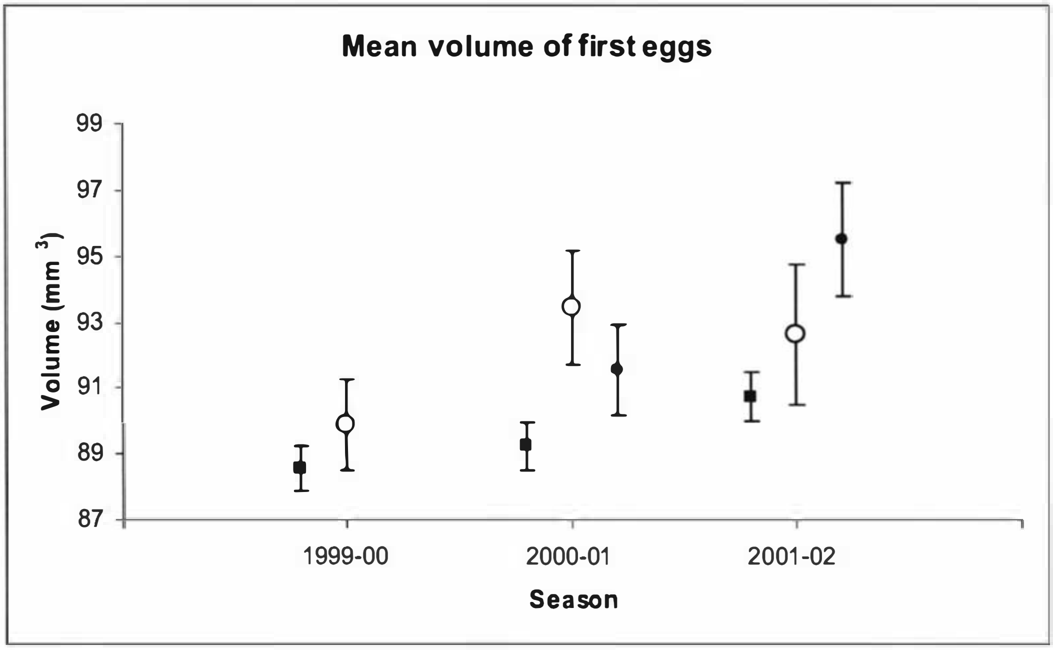

Figure 4. Mean volume (± 1 SE) of first eggs from all nests (■), from 16 individual females that laid in all seasons (○), and 12 individual females that laid only in 2000-01 and 2001-02 (●). Sample size for first eggs from all nests is 91, 95, and 97. The difference in the 16 individual females between 1999-00 and 2000-01 was highly significant (One-way ANOVA $F_{2,15} = 5.92$, $P = 0.007$).

Firstly, there is a significant correlation between first and second eggs in all measures in all years, except for width and volume in 1999-00, and shape in 2001-02 (Table 6). This high degree of correlation was expected following the significant correlations in first eggs of females laid over successive seasons.

Secondly, both width and volume showed a significant difference between first and second eggs, but only in 2001-02. In this season first eggs were significantly larger than second eggs in both measures (Fig.5). This is the season in which hatching success was the highest (Chapter 3), suggesting that females that replaced lost eggs in this season were not able to re-lay eggs of similar size. There was no significant difference in length and shape of first and second eggs (Table 7).

Table 6. Pearson bivariate correlation analysis of first and second eggs. Figures in bold are those in which a significant correlation was found.

	Measure	n	Correlation	Significance
1999-00	Length	17	0.745	**0.001**
	Width	17	0.173	0.506
	Shape	17	0.561	**0.019**
	Volume	17	0.468	0.058
2000-01	Length	17	0.741	**0.001**
	Width	17	0.692	**0.002**
	Shape	17	0.705	**0.002**
	Volume	17	0.741	**0.001**
2001-02	Length	8	0.770	**0.025**
	Width	8	0.888	**0.003**
	Shape	8	0.635	0.091
	Volume	8	0.867	**0.005**

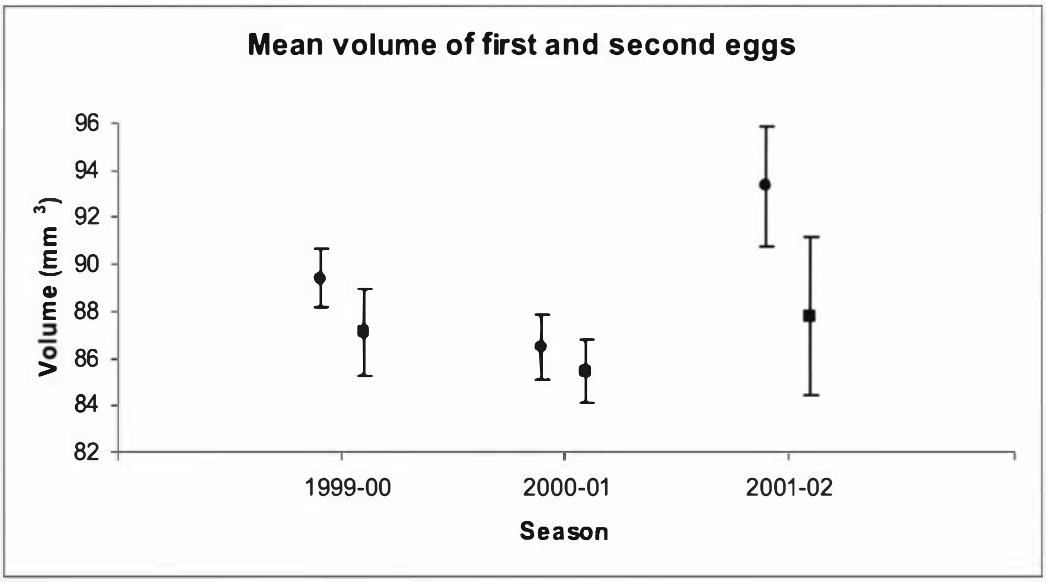

Figure 5. Mean volume (± 1 SE) of first (●) and second (■) eggs, from the same female, for all three seasons. The difference in the 2001-02 season was significant (Wilcoxon related samples test, z = -2.10, P = 0.036). Sample sizes were 17, 17, and 8, in each season respectively.

Table 7. Wilcoxon related samples analysis of first and second eggs from each of the three seasons, for all measures. Sample sizes were 17, 17, and 8 for each of the three seasons respectively.

	1999-00		2000-01		2001-02	
	Z	Significance	Z	Significance	Z	Significance
Length	-1.086	0.277	-0.595	0.552	-1.262	0.207
Width	-1.243	0.214	-1.422	0.155	**-2.383**	**0.017**
Shape	-0.450	0.653	-1.207	0.227	-0.840	0.401
Volume	-1.207	0.227	-0.923	0.356	**-2.100**	**0.036**

Egg replacement and delay period

In all years, second eggs were laid in response to the loss of first eggs (Table 8). In two cases, third eggs were apparently laid, once in 1999-00 and once in 2000-01. The third egg in 1999-00 was lost after 1 day, but the third egg in 2000-01 fledged a chick.

Table 8. Number of first eggs that did not hatch per season, and the number of second eggs that were laid in response. First eggs that did not hatch were made up of lost and "accidental eggs" (see methods for definition), but excluded infertile eggs. The number of second eggs laid in response to the loss of chicks is also given.

	No. of first eggs lost and "accidental"	No. second eggs laid in response (% re-laid)	No. second eggs laid in response to chick 'loss'
1999-00	39	9 (23%)	7
2000-01	29	20 (69%)	1
2001-02	18	9 (50%)	0

The number of second eggs laid at the 100 nests varied between seasons and approached significance (see Table 1 for significance levels). However, the number of second eggs laid in response to the loss of first eggs did differ significantly between years (χ^2 =14.51, df = 2, P = 0.001) (Table 8). In 1999-00 only 23% of first eggs lost or accidentally lost were replaced with second eggs. In 2000-01 and 2001-02 this was 69% and 50%, respectively.

Thus, during 1999-00 when adults were extremely food stressed, females seemed unable to re-lay. This analysis did not include infertile/addled eggs, as the presence of such an egg meant adults were not predisposed to re-laying.

Definite dates of egg loss or accident and subsequent re-laying, allowed the delay period to be calculated for 31 nests. There was no significant difference in delay period between seasons (Fig. 6), being on average 25.0 ± 9.5 days (n = 31).

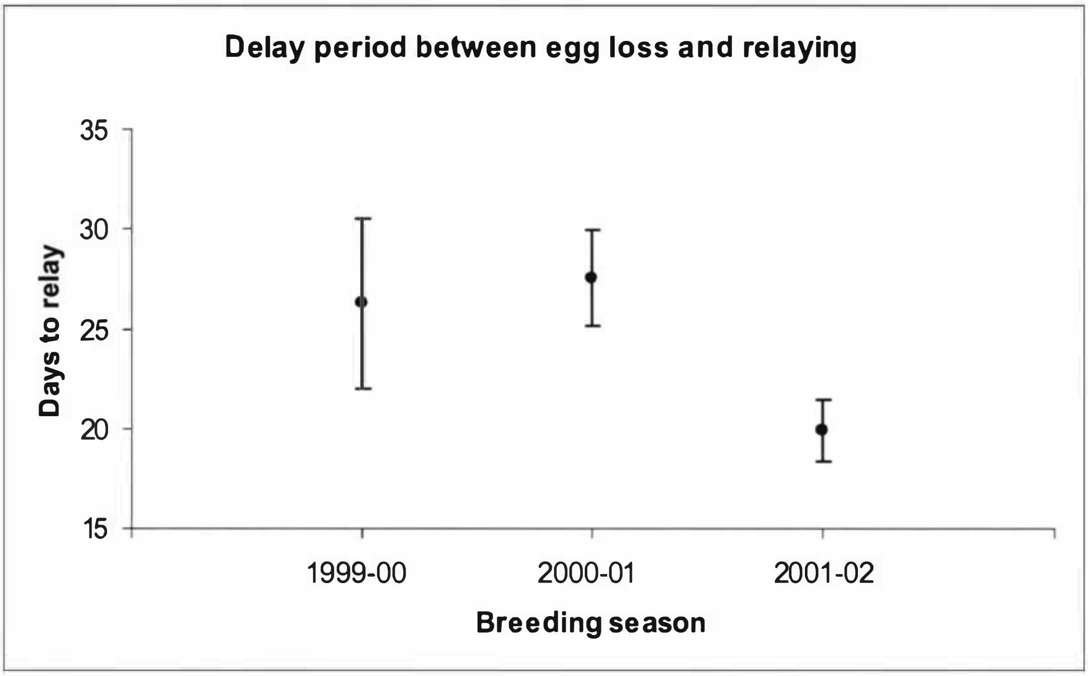

Figure 6. The delay period (in days) between the loss of first eggs and laying of a replacement egg. The differences between seasons were not significant (One-way ANOVA, $F_{2,28} = 1.979$, $P = 0.157$). Sample sizes were 8, 14 and 9, in each of the seasons.

Combining the data for all three seasons, there was also a significant positive correlation between the age of the egg when lost and the re-laying interval (Fig. 7). The shortest delay period was 6 days for an egg lost after 2 days incubation, and the longest was 50 days for an egg incubated for 10 days. The longest period that an egg was incubated for before being lost was 43 days old, and it was replaced after 40 days. Eight second eggs were laid in response to the loss of chicks produced from first eggs, and a weak negative correlation with chick age when lost, was evident (Pearson bivariate correlation r = -0.300, NS). Mean re-laying interval of second eggs in these cases was 35.0 ± 6.3 days (n = 8). The oldest chick that died and was replaced with a second egg was at least 17 days old.

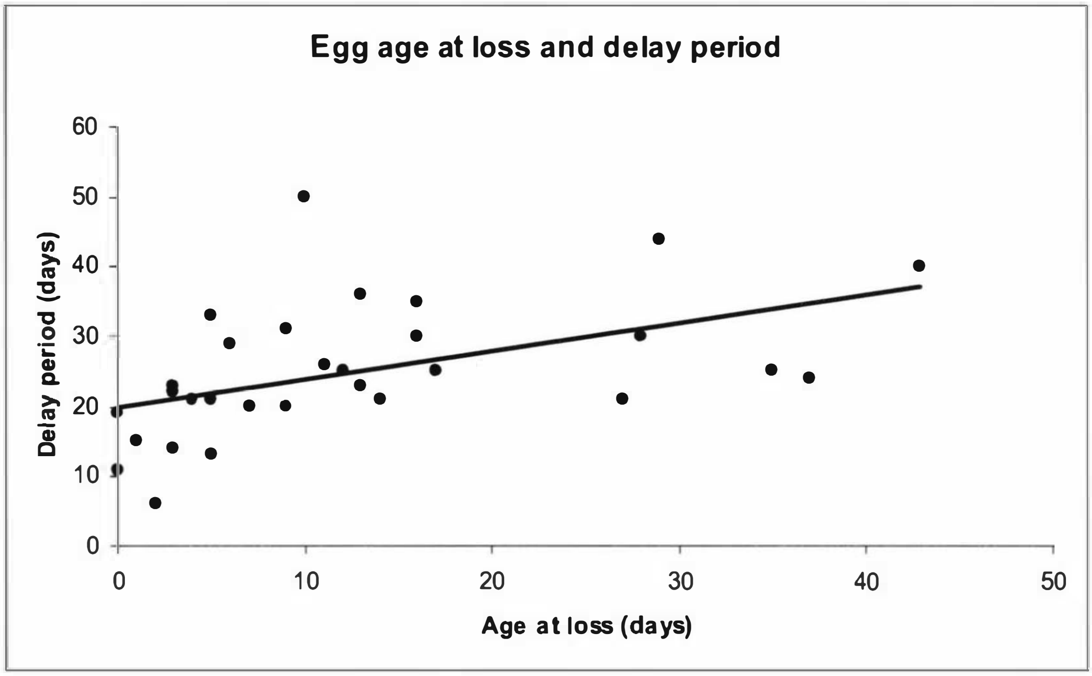

Figure 7. Delay period to replacement compared to the age of the egg when lost. A significant positive correlation exists (Pearson bivariate correlation r = 0.482, P = 0.006, n = 31).

First eggs that failed to hatch, but were replaced, were larger in volume than those that failed and were not replaced, in all seasons (Fig. 8). First eggs that failed, and were replaced were also not as old as eggs that were not replaced, in all seasons (Fig. 9). None of the differences in egg volume were significant, but in 2000-01 and 2001-02, the differences in egg age were significant. That is, in 2000-01 and 2001-02, eggs that failed and were replaced were not as old as those that failed and were not replaced. This means that if females had incubated for longer before loosing the egg, they were less likely to re-lay. Whether this was because it was too late in the season, or females were in poorer condition by this stage, cannot be determined from the limited data presented here.

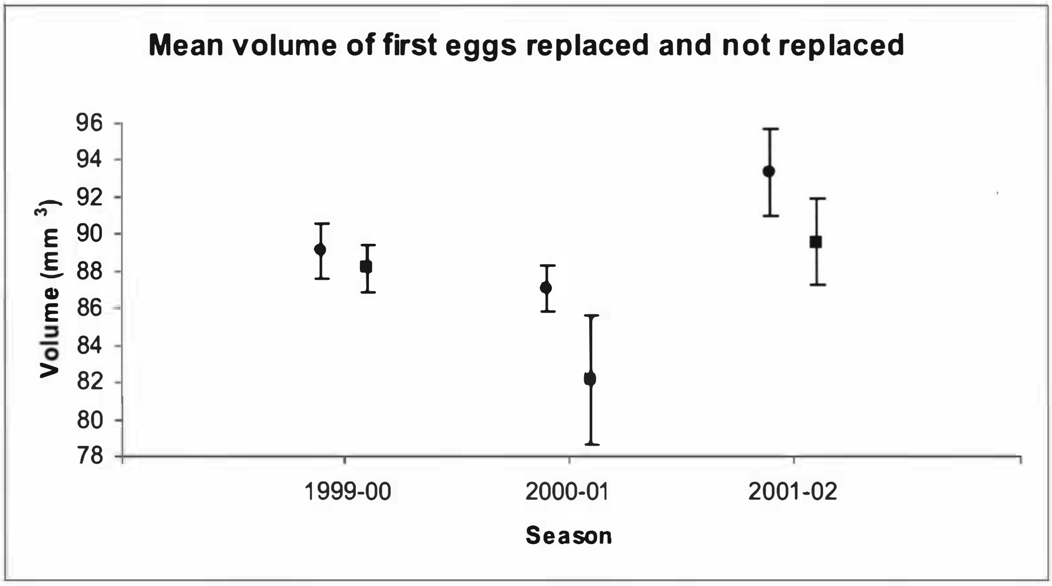

Figure 8. Mean volume of first eggs that failed and were replaced (●), compared to those that failed and were not replaced (■). The analysis only includes eggs that failed, so does not include replacement eggs following chick deaths. None of the differences within years were significant (Mann-Whitney test 1999-00 z = -1.150, NS; 2000-01 z= -1.697, NS; 2001-02 z = -1.348, NS). Sample size for replaced eggs is 9, 20, and 9 and for not replaced eggs is 30, 9, and 9, in each of the seasons respectively.

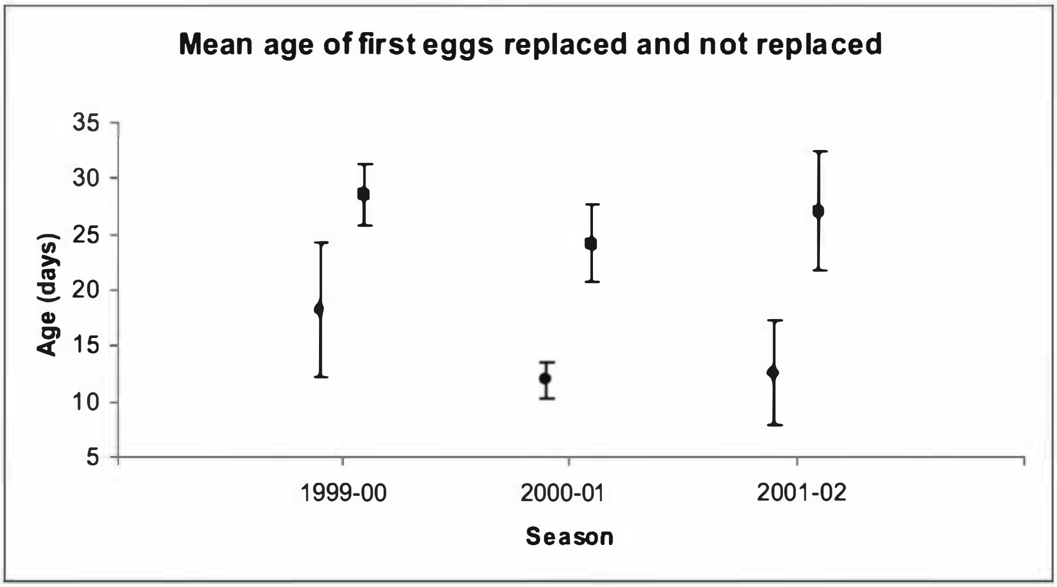

Figure 9. Mean age of first eggs that failed and were replaced (●), compared to those that failed and were not replaced (■). The analysis only includes eggs that failed, so does not include replacement eggs following chick deaths. The difference in age of eggs replaced and not replaced in the 2000-01 and 2001-02 seasons is significant (Mann-Whitney test 1999-00 z = -1.417, NS; 2000-01 z= -2.759, P = 0.004; 2001-02 z = -1.949, P = 0.05). Sample size for replaced eggs is 9, 20, and 9 and for not replaced eggs is 30, 9, and 9, in each of the seasons respectively.

Discussion

Australasian gannet nests were monitored at the Plateau colony, Cape Kidnappers, for three breeding seasons, 1999-00, 2000-01, and 2001-02. Compared with the other two seasons, 1999-00 attendance by adults was low, mean adult mass was low, egg size was small, egg replacement rates were low, and the delay period between loss of eggs or chicks and replacement high. This suggests, as did the prolonged laying period (Chapter 2), lower breeding success (Chapter 3), and lower chick growth rates (Chapter 6), that 1999-00 was a difficult year for breeding Australasian gannets.

Egg laying and colony attendance

Gannets are annual breeders, and have not been observed to have 'rest' years in which they do not breed (Nelson, 1978; Waghorn, 1983; Nelson, 2002). For the Atlantic gannet, however, one in four years on average is an involuntary rest year due to the bird changing mates, nests sites, or both (Nelson, 2002). In this study, a low, but variable number of pairs did not lay eggs at the 100 monitored nests in each of the three seasons. There are two likely explanations for this. The pair bond may have been broken through divorce or death, or the pairs at these nests may not have attempted to breed due to environmental conditions in that breeding season. It seems likely that environmental conditions were the causal factor, as in the first season of this study, during which there was poor breeding success (Chapter 3), starvation and poor condition of chicks and adults, and generally low attendance rates of nests, fewer pairs laid eggs.

Attendance of nest sites by Australasian gannets is known to vary diurnally and seasonally (Fleming, 1948; Wodzicki & Robertson, 1953; Wodzicki, 1967; Waghorn, 1983; Greene, 1999). Similar trends are evident in the Atlantic gannet (Nelson, 2002). However, changes in attendance, with reference to breeding success and other breeding variables, is not well known.

This study showed considerable variation in attendance patterns between seasons. During the pre- and early-egg laying stage in September 1999, fewer nests were attended by one bird than in 2000-01 and 2001-02. This suggests that even during the early stage of the breeding season, adults were being affected by environmental conditions, which then developed more fully during the breeding season, causing nutritional stress, desertion and loss of eggs and chicks in November and December, and very low breeding success. The period leading up to egg laying has been suggested to be the most energy consuming for the Atlantic gannet (Nelson, 2002). This is due to the considerable competition for nest sites, and the time invested by male gannets in guarding their site. Females will also be undergoing development of eggs and reserves for prolonged periods of incubation. Although the levels of aggression in Australasian gannets are less than Atlantic gannets, males still spend a considerable proportion of their time attending their sites. Similar to the findings of this study, Waghorn (1982) found that attendance by two birds was most common prior to egg laying and again later during chick rearing. As seen in this study, attendance by two birds was low during the incubation period.

Australasian gannet pairs whose breeding attempt had failed, either at the egg or chick stage, often left their nests unattended. This differs markedly to Atlantic gannets in which unattended sites are rare, at this stage of the breeding season, or any other time (Nelson, 2002). This study showed that even in seasons when breeding success was good, on average around 25% of nest sites are unattended in December.

Attendance by one bird was also significantly less during the egg and chick stage in 1999-00 compared to the other two seasons, peaking in October, prior to the considerable egg and chick losses and desertion that occurred in November and December (Chapter 3). In both 2000-01 and 2001-02, peak attendance by one bird was during November. Thus, nest attendance was linked with breeding success. When breeding failure occurred, nests were attended less frequently. In other seabirds, attendance rates and change overs are affected by supplementary feeding. Kittiwake, *Rissa tridactyla*, chicks from adults that received supplementary feeding had shorter incubation shifts (Gill et al., 2002). Moreover, once chicks hatched there was significantly lower attendance by unfed birds. Thus, attendance may be related to environmental conditions, in particular to feeding conditions. In general, low attendance rates are an indication of poor feeding conditions, especially during the chick rearing stage when high demands are placed on foraging adults.

Australasian gannets have been noted previously to leave chicks unattended (Warham, 1958; Wodzicki & Robertson, 1974; Waghorn, 1982; Waghorn, 1983). Wodzicki & Robertson (1953) noted that at 28 days chicks are still attended, whilst Warham (1958) first noted the absence of an attending adult at nests containing chicks 52 and 80 days old. Waghorn (1982) found chicks aged 48 days and over unattended, and found the times when chicks were left unattended increased with age, especially in the few weeks before fledging. At Cape Kidnappers, chicks are often left unattended at about 84 days, once their juvenile plumage has developed (Wodzicki & Robertson, 1974), and this may occur considerably earlier in some years. At 12-18 days old, Atlantic gannet chicks have acquired homeothermy at moderate ambient temperatures (Ricklefs et al., 1984), probably similar to Australasian gannet chicks. Thus, the desertion of chicks less than three weeks old would suggest adults are extremely stressed, as chicks left unattended at this stage are vulnerable to cold or heat. Depredation of unattended eggs and small chicks by black-backed gulls, *Larus dominicanus*, is also a threat (Chapter 3).

Until recently, the propensity for the Australasian gannet to leave chicks unattended appeared to be one of the major ecological differences between it and the Atlantic gannet. As demonstrated above, Australasian gannets do not continuously attend chicks through to fledging. Furthermore, attendance of nests and young by both members of the Australasian gannet pair is far less common than the 15% of daylight hours in Atlantic gannets at Bass Rock (Nelson, 2002). Atlantic gannets attend their chicks unremittingly throughout the entire fledging period (Nelson, 1964). This is almost certainly related to the foraging ecology of the two species, relating to prey availability and abundance, which in the Australasian gannet necessitates foraging by both parents in order to meet the increasing demands of chick growth. The effect of a longer day-length during the nestling period of the Atlantic gannet due to breeding at a lower latitude compared to the Australasian gannet, has not been examined and may also influence chick growth and fledging success. Nelson (1978; 2002) observed that Atlantic gannet chicks are attended through to fledging and used this as evidence that adults could easily feed chicks throughout the nestling period. Moreover, experimental twinning experiments have demonstrated that Atlantic gannets can successfully raise twins (Nelson, 1964), whilst Cape and Australasian gannets seem unable to do so in most cases (Jarvis, 1974; Waghorn, 1982; Bunce, 2001).

More recent observations show that continuous attendance of chicks through to fledging does not always occur in the Atlantic gannet (Lewis et al., 2004), possibly as a result of changing environmental conditions in the North Atlantic. The effects of such changes have been observed in other smaller seabird species over the past few decades (Hislop & Harris, 1985; Martin, 1989; Harris & Wanless, 1990; Hamer et al., 1991; Danchin, 1992; Harris et al., 1997; Harris & Wanless, 1997; Proffitt, 2004). During 2001 and 2002 at Bass Rock, nests that contained chicks, were left unattended on 14% (female) and 19% (male) of foraging trips (Lewis et al., 2004). This indicates a considerable change at this breeding colony between the 1960-70s studies of Nelson and Lewis et al. The availability or abundance of food, at least in 2001-02, was presumably lower, necessitating foraging by both adults. Nelson (2002) suggests that systematic study of the number of unattended chicks in Atlantic gannet colonies, every few years, would be a non-intrusive way to measure food availability and to compare colonies.

Associated with this, it has been speculated that the lower levels of aggression in Australasian gannets allow them to leave young unattended, whereas a higher aggression level in Atlantic gannets is prohibitive, as young left alone at the nest are attacked (Nelson, 1978). Nelson (1966) observed Atlantic gannet adults killing unattended chicks. It would be interesting to know if aggression levels in Atlantic gannets have dropped with the increase in unattended young, and perhaps the distance between nests could be an indication of this. Atlantic gannets, which are by far the most aggressive of the three gannets, have inter-nest distances of approximately 80 cm (from several colonies) (Nelson, 2002). Australasian gannets, being intermediate in aggression levels, are 79 cm apart at Cape Kidnappers (Wodzicki & McMeekan, 1947) and 86 cm at Motukaramarama (Wingham, 1984a), with the possibly larger inter-nest distances suggesting less competition for nest sites. The Cape gannet, which shows the lowest level of aggression (pers. obs.), has only 56-58 cm between nests (Rand (1963) in Nelson (1978)). Nelson (2002) suggests that Cape gannets are more aggressive than Australasian gannets, but the inter-nest distances clearly suggest otherwise, as do my observations at colonies of both. If Atlantic gannets continue to leave chicks unattended in order to spend more time foraging, then aggression levels at the breeding sites might be expected to decrease in order to lower the risk of chick deaths through adult aggression.

Adult mass

Surprisingly, there are few published data on the normal adult mass of Australasian gannets, and mass change throughout the breeding season. Wodzicki & Robertson's (1953) data from unsexed birds suggest that the mass of breeding birds decreases during the latter part of the chick period. Little information also exists for the Atlantic and Cape gannet. Nelson (2002), however, suggests that Atlantic gannet adult mass is highest upon arrival back at the colony following winter, and that while mass continues to decrease during the pre-egg stage as a consequence of prolonged site attendance, adults do not loose weight whilst feeding their "voracious young". Adult Cape gannets, on the other hand, are described as typically losing mass during the breeding season (Navarro, 1992). Patterns of within season changes in adult mass are not evident from this study. However, in 2000-01, when breeding success was highest, adult mass appeared to remain constant during the early part of chick rearing, but dropped later in the season. Thus, the pattern of adult mass change appears to be another important difference between Australasian and Atlantic gannets, seemingly related to food availability and abundance. Further work on all gannet species is needed to document changes in the mass of breeding adults during the breeding season.

More importantly, this study suggests that there was variation in the mass of breeding adults between seasons. In 1999-00 adult mass was lower than in the other seasons, supporting the suggestion that breeding adults, during November and December 1999, were clearly under going food stress and were probably emaciated, whilst feeding young chicks. These results are consistent with concurrent breeding failures (Chapter 3) and low levels of nest attendance.

Differences in the mass of the two sexes are not known for Australasian gannets, and those for Cape gannet appear limited (Rand (1959) in Nelson (1978)). In this study, males were generally lighter than females. For the Atlantic gannet, Nelson (1978; 2002) states that sexes are alike in size, although males are slightly larger, reversing the trend in the family as a whole. Nelson (1978) suggested that caution should be used in comparing mass of the two sexes as males lose more weight during the early part of the breeding season when competing for sites. However, even during the late chick stage in this study, females were generally heavier than males. Male Atlantic gannets are larger than females due to the high degree of nest site competition and aggression (Nelson, 2002). Thus, the lower levels of aggression and competition in Australasian gannets may account for the reverse in mass differences observed in this study compared with Nelson's. This needs further investigation and has important implications for the feeding ecology of the species and possible niche separation. Based on culmen and tarsus measurements, Lewis et al. (2002) suggest that Atlantic gannets are sexually monomorphic. Even so, significant differences in the foraging behaviour of males and females were observed (Lewis et al., 2002). Similar behaviours are likely to be occurring in Australasian gannets, with sexes perhaps feeding in different areas at different times.

Variation in egg size – intra- and inter-seasonal trends

Currently there is little information available on the variation of egg size within and between breeding seasons, for any of the gannets. This study provides critical information on these variables for the Australasian gannet.

Intra-seasonal trends

The significant negative trend in egg volume during the laying period in two of the three seasons was expected. Negative trends in egg size with laying date have been documented in many seabirds (Lloyd, 1979; Mills, 1979; Runde & Barrett, 1981; Birkhead & Nettleship, 1982; Furness, 1983; Hipfner et al., 1997; Hipfner et al., 2003), including Atlantic (Nelson, 1966) and Australasian gannets (Gibbs et al., 2000). This is generally considered to be due to female age, with older females laying larger eggs earlier in the season (Coulson & White, 1958; Nelson, 1966; Lloyd, 1979; Birkhead & Nettleship, 1981; Furness, 1983; Birkhead & Nettleship, 1987a; Birkhead & Nettleship, 1987b; Birkhead & Nettleship, 1987c; Hatchwell, 1991; De Forest & Gaston, 1996; Hipfner et al., 1997; Ratcliffe et al., 1998; Hipfner et al., 2003), although Massaro et al. (2002) showed that the egg size of yellow-eyed penguins, *Megadyptes antipodes*, increased with age, but laying date was independent. Furthermore, both Mills (1979) and Runde & Barrett (1981) suggested that the changing availability of food could be an important factor in egg size, and Lloyd (1979) suggested that age alone was not responsible for the size differences in eggs and that some variation may be due to intrinsic differences in the birds' breeding condition. However, although Gibbs et al. (2000) found the 'older' groups laid earlier, egg size was not correlated with female age. As the age of females was not known in this study, the relationship between egg volume and female age could not be investigated, and further study is warranted to determine the exact relationship between age of the female, and the volume and date an egg is laid.

In 1999-00 when environmental conditions caused disruption to much of the breeding season, this normally negative trend was not found. Thus, it seems that even early laying females, most probably older more experienced birds, were not able to lay their normally larger eggs, compared to females that laid eggs later in the season. This is supported by the lower consistency in the egg size of individual females, between seasons, when 1999-00 was compared with either of the other two seasons. Moreover, as the total laying period during this season was more prolonged, it seems that some females delayed laying, possibly also confounding the normal negative correlation in egg size. Regehr & Montevecchi (1997) found similar results during food shortages in kittiwakes, with no negative correlation of egg volume with laying date and suggested that this was possibly a consequence of food constraints in the pre-laying period.

Inter-seasonal trends amongst individual females

This study found no significant differences in egg measures between seasons for the 100 monitored nests. However, although not significant, females did lay progressively larger volume eggs each season. This was expected, with 1999-00 obviously being a very difficult season, and 2000-01 also showed some periods of food stress early in the season. Finally, 2001-02 showed little food stress during the egg stage of the season.

However, the analysis of the eggs from the 16 individual females did reveal a significant difference in egg volume. Again, this supports the suggestion that 1999-00 was a difficult season, with eggs in that season being significantly smaller than those in 2000-01. This seems difficult to explain in light of the previous non-significant findings. So too does the difference between the two groups of individual females analysed in the 2000-01 and 2001-02 season. One possible explanation is that all but one of the 16 females had the same mate during each of the three breeding seasons. Therefore, the female was in an established pair bond that may well have had an effect on the size of the egg she produced. The mate and site fidelity for the other 12 females, is not known, and changes in partnership could have biased results from that sample. Moreover, for the colony as a whole, such effects as well as environmental conditions, and changes in age structure with addition of young breeders, could be influencing egg size throughout the colony. Changes in conditions during the laying period could also have been affecting particular classes of females, thereby influencing egg size. Increasing sample size over several seasons, with known age birds would be necessary to understand fully what is occurring here, and help understand the role of female quality in determining egg size and timing of laying.

Annual variation in the length and width of Australasian gannet eggs was found at Motukaramarama (Wingham, 1984a), but differences in egg volume were not analysed. Annual differences in measures of Atlantic and Cape gannet eggs have not been described. However, annual variation in egg size, particularly egg volume has been shown in several other seabird species (Lloyd, 1979; Regehr & Montevecchi, 1997; Ratcliffe et al., 1998), and these differences have often been related to environmental conditions, including prey availability. Food shortage in kittiwakes has been associated with late breeding, a low proportion of pairs laying, and small eggs and clutches (Regehr & Montevecchi, 1997). Furthermore, egg volume was suggested to be a useful assessment of conditions in the pre-laying period. Likewise, Ratcliffe et al. (1998) found clutch volume of great skuas, *Catharacta skua*, was positively correlated with sandeel, *Ammodytes marinus*, biomass. Thus, the small eggs at Cape Kidnappers during 1999-00 again supports the suggestion that in this year food shortages were the cause of breeding failures and disruption.

The highly consistent measures of eggs from individual females between seasons was further evidence that eggs did indeed belong to those females, and a similarly high degree of individual consistency in egg volume has been found in many species of seabirds (Coulson, 1963; Lloyd, 1979; Furness, 1983; Hipfner et al., 1997; Hipfner et al., 2001b; Hipfner et al., 2003), both between and within years.

Annual variation in egg size is related to breeding success. Larger volume eggs are significantly more likely to hatch and produce fledging chicks in at least in some years (Chapter 3). This occurred during 2000-01 when breeding success was highest, and large-scale breeding failures did not occur. Food shortages, however, were still evident during the early stages of the breeding cycle and may still have affected egg size. Therefore, annual variation in egg size shows that females should breed more successfully if they are able to produce larger eggs, despite difficult foraging conditions. This certainly warrants further study in Australasian gannets, with the role of female age and condition needing to be related to egg size. The effects of mate and nest site should also be investigated, as should the effects of egg size on post-fledging survival and fecundity of birds.

Within season comparisons of first and second eggs for individual females

The first and replacement eggs of individual females were similar within each season, as well as between seasons as shown above. Consistency in egg size has been shown previously for Australasian and Atlantic gannet (Ricklefs & Montevecchi, 1979; Gibbs et al., 2000).

Although consistent in size, the volume of first and second eggs laid by individual females in 2001-02 when egg losses were low, was significantly different. Thus, females were unable to lay similarly sized eggs a second time round, during a season in which conditions were good. This may have been because females were young or inexperienced (Nelson, 2002). Alternatively, in that season poor quality females may not have been more likely to lose eggs and then re-lay smaller eggs. In kittiwakes, first clutches were of similar size and shape whether or not the females laid replacement clutches, suggesting that age alone was not controlling the decision to re-lay (Runde & Barrett, 1981). Yet, the reasons for a lack of a significant difference in size between first eggs and second eggs in the other two seasons, when egg losses were higher, is more interesting. This is especially so in 1999-00, when considerable egg losses occurred. Despite the stress that breeding birds were undergoing at this time, females that re-laid were able to produce a replacement egg of similar, although slightly smaller size (but see egg replacement below). In many cases, the first eggs were deserted (Chapter 3). However, why would a pair desert an egg, and then re-lay a short time later? There are several possible explanations. Firstly, perhaps the males are involved in the desertion of eggs, and females are far less prone to this behaviour. Thus, when an egg is no longer present, the female is stimulated to lay another egg. Secondly, conditions could change quite quickly between the desertion of the egg and the laying of the replacement. This seems unlikely, because in 1999-00 eggs were being deserted and laid concurrently. Thirdly, birds may have reached a point at which they can no longer incubate the egg, but after desertion and therefore, lower rates of attendance and possibly increased foraging, the female is at a point where laying a replacement egg is possible. And lastly, social stimulation may be such that females that have lost an egg are motivated to re-lay, regardless of their physical condition.

There have been few comparable studies documenting differences in first and second eggs in gannets. Wingham (1984a) found that first eggs were slightly, but not significantly larger than second eggs in both length and width, but no analysis of volume was undertaken. Conversely, at the Pope's Eye and Wedge Light colonies, Australia, replacement eggs were both longer and wider than first eggs, but only width was significant (Norman & Menkhorst, 1995), and later at Pope's Eye, replacement eggs were slightly, but not significantly, larger in volume than first eggs (Gibbs et al., 2000). Although these studies suggest a difference between New Zealand and Australian studies, considerably more work needs to be done before this can be confirmed. In particular, nests at Australian colonies need to be monitored more frequently. Intriguingly, both Australian studies showed larger replacement than first eggs. Atlantic gannets were also shown to lay slightly larger second eggs (length, width, shape and mass), although the differences were not significant, and birds attending the nests were unbanded (Ricklefs & Montevecchi, 1979). The reasons for larger replacement eggs compared to first eggs could be as simple as improvements in foraging conditions during this time. This could be related to the timing of breeding. In the early part of the season it may be important to lay early, even if the egg is small. There currently appears to be no information on the differences of first and replacement eggs in Cape gannets, but in other seabird species there is clear evidence for reduced size in replacement eggs (Lloyd, 1979; Runde & Barrett, 1981; Birkhead & Nettleship, 1982; Hipfner et al., 1997; Hipfner et al., 2003).

Egg replacement and delay period

Significantly fewer females laid replacement eggs in 1999-00, and this fits well with the poor conditions in that season. It seems that only those females in good condition were able to re-lay. This may also help to explain the lack of a significant difference in the volume of first and replacement eggs, as seen above, and hatching success (Chapter 3) of first and second eggs, in that season. In the other two seasons the percentage of females re-laying was a lot higher, similar to those found in other Australasian gannet studies (Wingham, 1984a; Norman & Menkhorst, 1995; Gibbs et al., 2000).

The mean delay to re-laying recorded in this study is in line with the 8-34 days recorded by Wingham (1984a). Nelson (1978) quotes Robertson as saying that [at Cape Kidnappers] some, perhaps most birds, replace eggs which are lost before late December. On Horuhoru lost eggs are replaced in about four weeks (Stein, 1971). Wingham (1984a) found a negative correlation between age of eggs when lost and the re-lay interval, although this was not significant and the sample size was small (n = 9). This contrasts with the significant positive correlation between egg age when lost and re-lay interval found in this study. At Pope's Eye, Gibbs et al. (2000) found no apparent relationship between re-laying interval and age at loss, for eggs or chicks.

Atlantic gannets show similar replacement patterns at Bass Rock, replacing eggs in 6-32 days, usually about 21 days (Nelson, 1966). However, Atlantic gannets do not seem to re-lay if an egg is lost more than 25 days after incubation has started (Nelson, 1966). This was suggested to be due to the fact that there is little natural egg loss in this species to justify a strong tendency to re-lay. This seems unlikely, as if incubation and chick rearing in Atlantic gannets presents as little difficulty as Nelson suggests, then most females should still be in good enough condition to re-lay, whether egg loss is normal or not. Perhaps in Atlantic gannets only very poor quality females that are unable to re-lay, lose their eggs in the first place. Alternatively, egg losses may not have been recorded often enough during his study to accurately determine the rates of re-laying, or perhaps environmental influences such as changes in day-length are prohibitive.

Wingham (1984a) was the first to record re-laying following the loss of a chick. Atlantic and Cape gannets are not known to do this, although for the latter this may be due to a lack of published information. Adams & Walter (1991) reports that Cape gannets occasionally re-lay following successful breeding. This needs further study, however, because replacement eggs did not produce another chick to fledging. I recorded eight eggs laid in response to the loss of a chick, the oldest chick being at least 17 days old, 9 days older than previously recorded (Wingham, 1984a). The small sample size in this study probably means that the negative correlation between chick age when lost and re-lay interval is of little meaning. Wingham (1984a) found a non-significant positive correlation, but again sample size was limited (n = 15). No other studies of Australasian gannets recorded re-laying intervals.

Generally, lost eggs that were replaced in this study were larger in volume than those eggs that weren't replaced, although differences were not significant. Similarly, in kittiwakes no significant differences were found between the volume of those eggs lost and replaced, and those lost and not replaced (Runde & Barrett, 1981). For Australasian gannets, Gibbs et al., (2000) found no difference in the proportions re-laid after loss of egg, young chick (≤ 8 days), or older chicks (> 8 days), but did find that older birds replaced proportionately more eggs than younger birds. Similar results have been found in other seabirds, showing that older/more experienced females have a higher capacity for re-laying (De Forest & Gaston, 1996). Other studies have suggested re-laying is independent of age or more common in females in better condition (Runde & Barrett, 1981; Houston et al., 1983). However, Hipfner et al. (2001b) found that in both razorbills, *Alca torda*, and thick-billed murres there was little relationship between egg size and probability of relaying, whilst Lloyd (1979) found the frequency of egg replacement declined as the season progressed. Again further work is needed to understand what influences whether or not a female Australasian gannet will re-lay following the loss of an egg.

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6

Annual variability in the breeding biology of Australasian gannets, Morus serrator, *at Cape Kidnappers: II chick growth*

Introduction

The Australasian gannet, *Morus serrator*, is a colonial breeding seabird of inshore waters, characterised by high adult survival, deferred breeding, and laying of a single-egg clutch (Wodzicki & McMeekan, 1947; Stein, 1971; Nelson, 1978b; Norman, 2001). The species breeds around the coast of New Zealand and at several localities in south-eastern Australia. Despite being described in recent works as well known (Marchant & Higgins, 1990), there is still much to learn about the breeding biology of this species, particularly the role of annual environmental variability on eggs and chicks.

The growth of seabird chicks can vary both temporally and geographically and may be sensitive to local availability of marine food resources (Harris, 1969; Dunn, 1975; Nelson, 1978b; Lloyd, 1979; Birkhead & Nettleship, 1981; Ricklefs et al., 1984). Furthermore, Cairns (1987) predicted that a reduction in prey availability at a seabird colony would, depending on its severity, affect several distinct parameters of breeding performance ranging from changes in adult activity budgets and colony attendance apparent with only slight reduction in food supply (eg. Uttley (1992), and Olsson & Brodin (1997)), to reduced chick growth rates and breeding success (eg. Ricklefs et al. (1984), and Navarro (1991)), and an increase in adult mortality under more restricting conditions. Spectacular reproductive failures involving pervasive starvation of chicks, abandonment of breeding colonies, and occasionally, widespread mortality of adults, have been associated with El Niño conditions (Schreiber & Schreiber, 1984; La Cock, 1986) (Barber & Chavez, 1983; Anderson, 1989; Crawford & Jahncke, 1999).

Although starvation is suggested to have never been the cause of chick mortality in the Atlantic gannet, *Morus bassana*, (Nelson, 1964; Nelson, 1966; Nelson, 2002), environmental variability appears to cause starvation of Australasian gannet chicks in some years (Stein, 1971; Nelson, 2002; Chapter 3). Furthermore, experimental studies have shown that although Atlantic gannets can cope with the addition of an extra chick (Nelson, 1964), Cape gannets, *Morus capensis*, and Australasian gannets generally appear unable to rear two chicks successfully (Jarvis, 1974; Waghorn, 1982; Navarro, 1991). To test this, Bunce (2001) conducted experiments at Port Phillip Bay, Australia,by giving supplementary food and creating twinned chicks in two breeding seasons. He discovered that the ability of adults to raise both chicks varied between seasons. Those chicks that were provided with additional food attained greater maximum mass, and twinned chicks were generally of poorer quality, had slower development, attained lower maximum masses, and had low survival rates. This suggests that gannets, at least in Port Phillip Bay, utilise a variable food supply, and in some years the population may be food limited. In comparison, the Atlantic gannet, which is described as having an abundant food resource, has, at least in the past, enjoyed an invariably high breeding success, and apparently raises its single chick with ease (Nelson, 1964; Nelson, 1966; Nelson, 2002). In Australasian gannets, variable attendance of nest sites during the breeding season and differences in the volume of eggs between seasons, has also been detected (Chapter 5), yet the effects these differences have on chick development has not been investigated in this species. Young from large eggs hatch with large yolk reserves that might help them through periods of food shortage soon after hatching (Parsons, 1970), and although the relationship between egg size and chick development requires further testing (see review by Williams (1994)), some studies, that have corrected for other factors, have suggested a significant positive correlation (Nisbet, 1973; Nisbet, 1978; Thomas, 1983; Bolton, 1991; Magrath, 1992; Hipfner et al., 2001). In Australasian gannets, egg volume is positively correlated with hatching and breeding success (Chapter 3). Therefore, females should lay eggs of the largest volume possible to maximise chick development and fledging success.

There is further evidence of high annual variance in chick growth. Wingham (1984b) found that the fitted growth curves of Australasian gannet chicks differed between her three study seasons, being more constant in one year than the other two. She suggested that this was due to food supply being more abundant in that year, or weather being more settled allowing parents to forage regularly. It is not known whether such variability exists in Atlantic gannet chick growth, but the growth rates of blue-footed booby, *Sula nebouxii*, chicks have been shown to have significant heterogeneity among breeding locations (Ricklefs et al., 1984). They suggested that growth rates of chicks are sensitive to rapid changes in oceanic currents and foraging conditions.

In assessing the survival and development of chicks it is often difficult to take account of those chicks that die early in the fledgling period. However, the first few weeks of life are an important period, as parents must make the behavioural transition from incubation to feeding chicks (Nisbet et al., 1998). Perhaps accordingly, chick mortality is often concentrated in the early part of the growth period (Nelson, 1966; Wingham, 1984b; Chapter 3). Yet most studies to date have fitted data to non-linear sigmoid curves or mass near fledging (Nelson, 1964; Ricklefs, 1967; Montevecchi et al., 1984; Wingham, 1984b; Navarro, 1991; Gibbs et al., 2000; Bunce, 2001), something that is not possible if chicks die early in the nestling period. Thus, I investigate the growth of chicks during the early period of development to determine whether there is a difference between chicks that fledge and those that do not.

This chapter investigates annual variation in colony wide and individual chick development, at the Plateau colony, Cape Kidnappers, over three breeding seasons. The three principal questions asked are 1) does the egg mass or laying date affect growth and survival of chicks? 2) is there a difference in early development of chicks that subsequently fledge versus those that do not? 3) is there annual variation in the growth rates of chicks? I then make comparisons with general trends in other seabirds.

Methods

The Cape Kidnapper's gannetry (39° 38' S, 177° 05' E) is situated on the east coast of the North Island, New Zealand. The gannetry consists of four Australasian gannet colonies, Saddle (originally called Cape Kidnappers colony), Plateau, Black Reef, and Plateau Beach colonies (see Chapter 1 for a full description of the study site). The gannetry and its history, and changes in the breeding population have been well documented since 1945 (Wodzicki & McMeekan, 1947; Fleming & Wodzicki, 1952; Wodzicki, 1967; Wodzicki et al., 1984; C.J.R. Robertson unpubl. data). Details of the birds' breeding biology in New Zealand were first documented from studies at this site (Wodzicki & McMeekan, 1947). The gannetry is currently estimated to hold approximately 7,500 breeding pairs of gannets (breeding pairs = site-occupying pairs, defined as either one or two site-holding birds occupying a nest site (Wodzicki et al., 1984), that attempt to breed annually). This study was conducted at the Plateau colony during three breeding seasons, from 1999-00 to 2001-02. During the study, census data were used to estimate a breeding population of 1800 – 2100 breeding pairs over the three years (C.J.R. Robertson unpubl. data).

One hundred nest sites on the seaward, eastern side of the Plateau colony were individually marked with permanent markers whilst the colony was empty on 8 July 1999. These nests were intensively monitored over three breeding seasons, with many adults being individually banded, and the date of egg laying and hatching known for almost all eggs (see Chapter 4). I refer to each breeding season (ie. 1999-00, 2000-01, and 2001-02) as a season, rather than a year, to avoid confusion throughout this Chapter. Mensural data were collected for each egg, and length and width (to 0.1 mm, using dial callipers) used to calculate egg volume using the equation $V = K_V(\text{length} \times \text{width}^2)$, where the constant $K_V = 0.507$ (Hoyt, 1979). Calculated egg volume index is a highly significant predictor of fresh egg mass ($r = 0.979$, Chapter 4), and is used instead of mass throughout this chapter.

Of the one hundred nests, 70 were randomly selected to have chicks weighed and measured regularly. The day a chick hatched was designated as day-zero. Initially, a schedule of handling every second day, until the age of 30 days, and then every third day from day 31 on was designed. However, weather and other constraints such as disturbance and time spent in the colony, meant that the schedule could not always be followed, and thus chicks were not weighed and measured as often as scheduled. The high loss of eggs and chicks in the 1999-

00 breeding season, and the considerable chick loss in the 2001-02 breeding season, meant that sample sizes were not as large as planned (see Chapter 2).

Chicks were usually handled and measured in the late afternoon. Chicks did not leave their nest before the age of about 40 days, after which they increasingly wandered from their nests, returning when their parents were present. However, chicks always returned to their nests to be fed by adults, and thus were still individually identifiable before banding, which was usually conducted at about 45-50 days of age. As chicks became older and more mobile a 'shepherd's crook' was used to capture the chicks without creating too much disturbance. However, during the 1999-00 and 2001-02 breeding seasons, when few chicks survived and adults were not actively maintaining nest sites, capturing chicks caused too much disturbance. Thus, in these seasons the handling of chicks ceased earlier. The sex of chicks was not known.

To obtain mass, small chicks were weighed using a 300 g or 1,000 g Pesola spring balance, and larger chicks were weighed using a 2,500 g Pesola spring balance or a 5 kg Bonso electronic scale. Measurements were made to the nearest 1 g for chicks less than 300 g, 5 g for chicks between 300 g and 1,000 g, and 20 g for chicks above 1,000 g. Chicks were weighed in clean plastic bags of an appropriate size, and these were replaced regularly as they became torn and/or soiled. Balances were calibrated at least once per season and were tared at regular intervals (the electronic scales tared on start-up). During handling, chicks sometimes regurgitated food, and this occurred more frequently if the chick had not been handled regularly. If chicks did regurgitate a meal, then this was added to the chick mass recorded.

Mensural data collected from chicks and analysed in this chapter were wing length (from the carpal joint to the tip of the wing or longest primary, flattened chord), bill length (tip of bill to base of bill), and head width (width just behind the post-orbital process). All measures were taken with dial callipers to 0.1 mm. Wing length was measured using dial callipers until primary feathers erupted, and then taken using a stop rule, to the nearest 1 mm.

It was difficult to fit data from each chick to a complete growth curve as has been done in previous studies (Nelson, 1964; Ricklefs, 1967; Bunce, 2001). The large degree of variation in the mass of chicks also meant that fitting their growth to a non-linear regression was difficult, based on the data collected. Instead, I estimated two growth parameters that could be determined from the irregular data. Linear growth rate (LGR) and asymptotic mass (AM) as outlined by Nisbet et al. (1995) were used to compare each of the four measured variables, between individuals and between breeding seasons. LGR is the slope of a regression line fitted to mass data during the quasi-linear period of a chick's growth. For Australasian gannet chicks in this study, different periods of growth were used for the analysis of LGR for each measure. For mass the period 20 – 60 days was used, whilst for wing length, quasi-linear growth was during feather development, from 40 – 90 days. Primary feathers normally erupted at about 42 – 44 days of age. For bill length the period 5 – 40 days, and for head width 10 – 40 days, were used. Only chicks with at least three data points during this period, and where the regression line had an R^2 greater than 0.9, were used. LGR is then presented for each measure as the mean daily increase in the measure (mm or g).

AM is the mean of all masses measured during a period of near constant mass. This was a little more difficult to determine, as the weight of gannet chicks in this study varied greatly. However, for the purposes of this study the AM parameter was calculated from 2 or more data points derived from chicks of age 64 days or older. LGR and AM were calculated only for those chicks that survived to fledging.

Unless otherwise stated, means are reported ± 1 standard deviation (SD). All statistical analyses were performed using SPSS for Windows, Release 11.5.0 or 12.0.1. Capture, handling and banding of birds was conducted under the Department of Conservation's New Zealand National Banding Scheme, Institutional Permit to band birds No. 0259. The Massey University Animal Ethics Committee gave permission to conduct this research, Protocol No. 98/173.

Results

Effects of egg volume on chick development

To reduce disturbance on newly hatched chicks, only fourteen chicks were weighed on day-zero, over the three breeding seasons. Mean hatching mass for these chicks was 72.9 ± 5.9 g, and was significantly positively correlated with egg volume (Pearson correlation; r = 0.665, P = 0.009) (Fig. 1). As sample sizes in each of the three seasons were small, a comparison between seasons was not conducted.

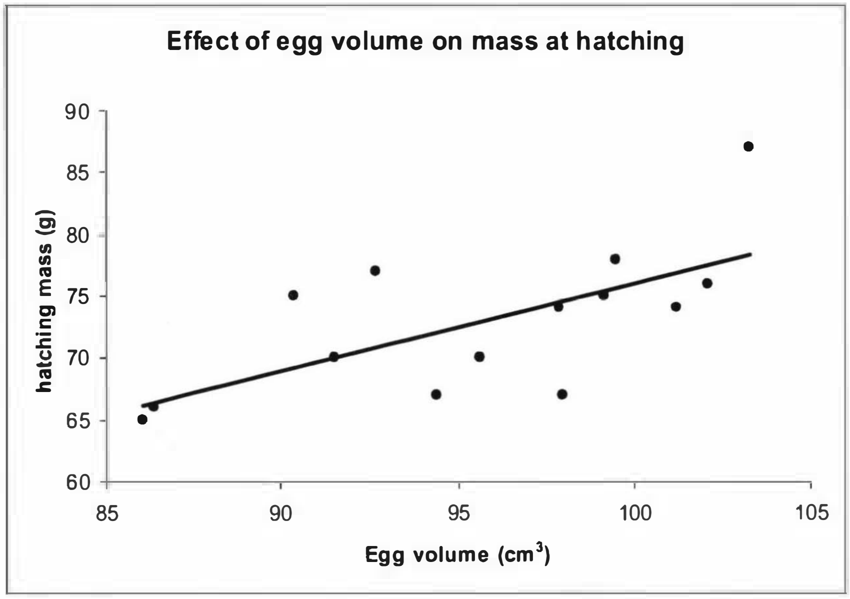

Figure 1. Correlation between egg volume and the chick mass at hatching. This positive correlation was significant (r = 0.665, P = 0.009).

Analysis of linear growth rate (LGR) for chicks that fledged, compared with egg volume, was also undertaken (Table 1, Fig. 2). Mean daily mass, wing length, bill length, and head width LGR all showed a slight negative correlation with egg volume, when all seasons data were lumped, but these correlations were not significant (Table 1). I also analysed measures from each season separately, but no results were significant. However, mass and wing length LGR both showed a near significant correlation with egg volume in 1999-00, despite the limited sample size.

Asymptotic mass (AM) was also analysed with respect to egg volume, with no significant correlation found in any season, although there was a generally positive trend (Table 1). However, in 2001-02 a nearly significant positive correlation between AM and egg volume was found.

Table 1. Pearson correlations between egg volume and chick linear growth rate (LGR) for each measure, and asymptotic mass (AM), for each of the three seasons. No correlations were significant, although mass and wing length approached significance in 1999-00, as did AM in 2001-02 (shown in bold).

	All seasons			1999-00			2000-01			2001-02		
	r	P	n	R	P	n	r	P	n	r	P	n
Mass	-0.119	0.416	49	**0.806**	**0.053**	**6**	-0.206	0.235	35	0.411	0.312	8
Wing length	-0.123	0.414	46	**0.800**	**0.056**	**6**	-0.096	0.594	33	-0.568	0.184	7
Bill length	-0.128	0.370	51	-0.483	0.332	6	-0.258	0.134	35	0.481	0.159	10
Head width	-0.105	0.469	50	0.080	0.880	6	-0.077	0.661	35	-0.519	0.152	9
AM	0.032	0.857	35	-0.246	0.690	5	-0.091	0.674	35	**0.771**	**0.073**	**6**

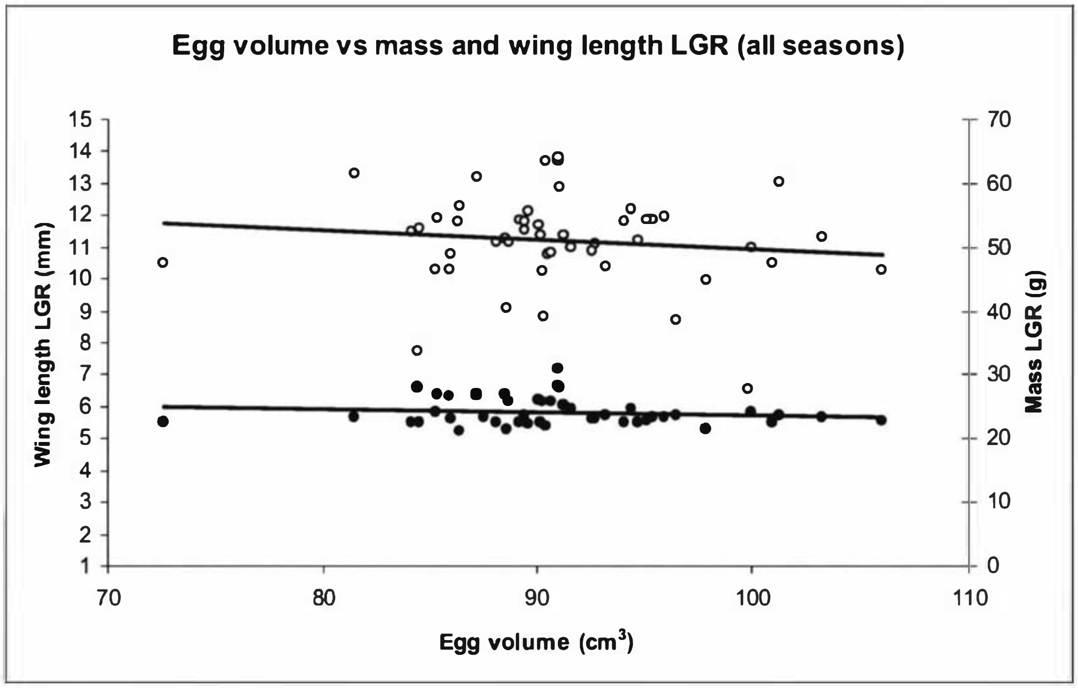

Figure 2. Egg volume against mean mass (○) and wing length (●) linear growth rate (LGR). Data for all breeding seasons were included in the analysis. Although a weak negative correlation is shown for each measure, these correlations were not significant (see Table 1).

Development of chicks in relation to date of laying

The effect of egg laying date on the outcome of chick fledging success has already been discussed (Chapter 3). However, the effect of egg laying date, standardised as days before or after the median laying date, on the subsequent growth of chicks is presented here (Table 2, Fig. 3). This was only calculated for those chicks that fledged successfully. Mean mass LGR showed a negative correlation with date of laying, and this correlation was significant in 2000-01 (Table 2). Thus, eggs laid later produced chicks that gained mass more slowly than chicks from earlier eggs. Analysing all three seasons' data together also showed a significant negative correlation (Table 2). In contrast, in 2000-01 wing length LGR showed a significant positive correlation with the date the egg was laid. That is, chicks that hatched from eggs laid following the median laying date had faster wing growth than those before the median laying date. Again, the trend was significant when data from all seasons were lumped (Table 2). When the estimated 90-day wing length (taken from wing length LGR) was compared with date of laying, this also showed a highly significant positive correlation The only other significant trend was with head width LGR in 1999-00 which showed a positive correlation. Bill length and head width LGR showed no correlation in 2000-01 (Fig. 3). There was no significant trend for AM in any of the seasons, although it was negative in each season (Table 2, Fig. 4). However, when all three seasons' data are lumped, there is a near significant negative trend, suggesting that chicks that hatched from later laid eggs, fledged at a lower AM. The fact that no significant difference in AM was found between seasons supports the lumping of data from all three seasons.

Table 2. Pearson correlations between egg laying date and chick linear growth rate (LGR) for each measure, and asymptotic mass (AM), for each of the three seasons. Significant correlations are indicated in bold.

	All seasons			1999-00			2000-01			2001-02		
	r	P	n	r	P	n	r	P	n	r	P	n
Mass	**-0.355**	**0.012**	**49**	-0.544	0.265	6	**-0.380**	**0.024**	**35**	-0.251	0.550	8
Wing length	**0.295**	**0.046**	**46**	-0.153	0.773	6	**0.712**	**0.0001**	**33**	0.201	0.666	7
Bill length	0.153	0.285	51	0.689	0.130	6	-0.069	0.693	35	-0.345	0.329	10
Head width	-0.037	0.800	50	**0.888**	**0.018**	**6**	0.100	0.569	35	0.561	0.116	9
AM	-0.306	0.074	35	-0.457	0.440	5	-0.268	0.205	24	-0.595	0.212	6

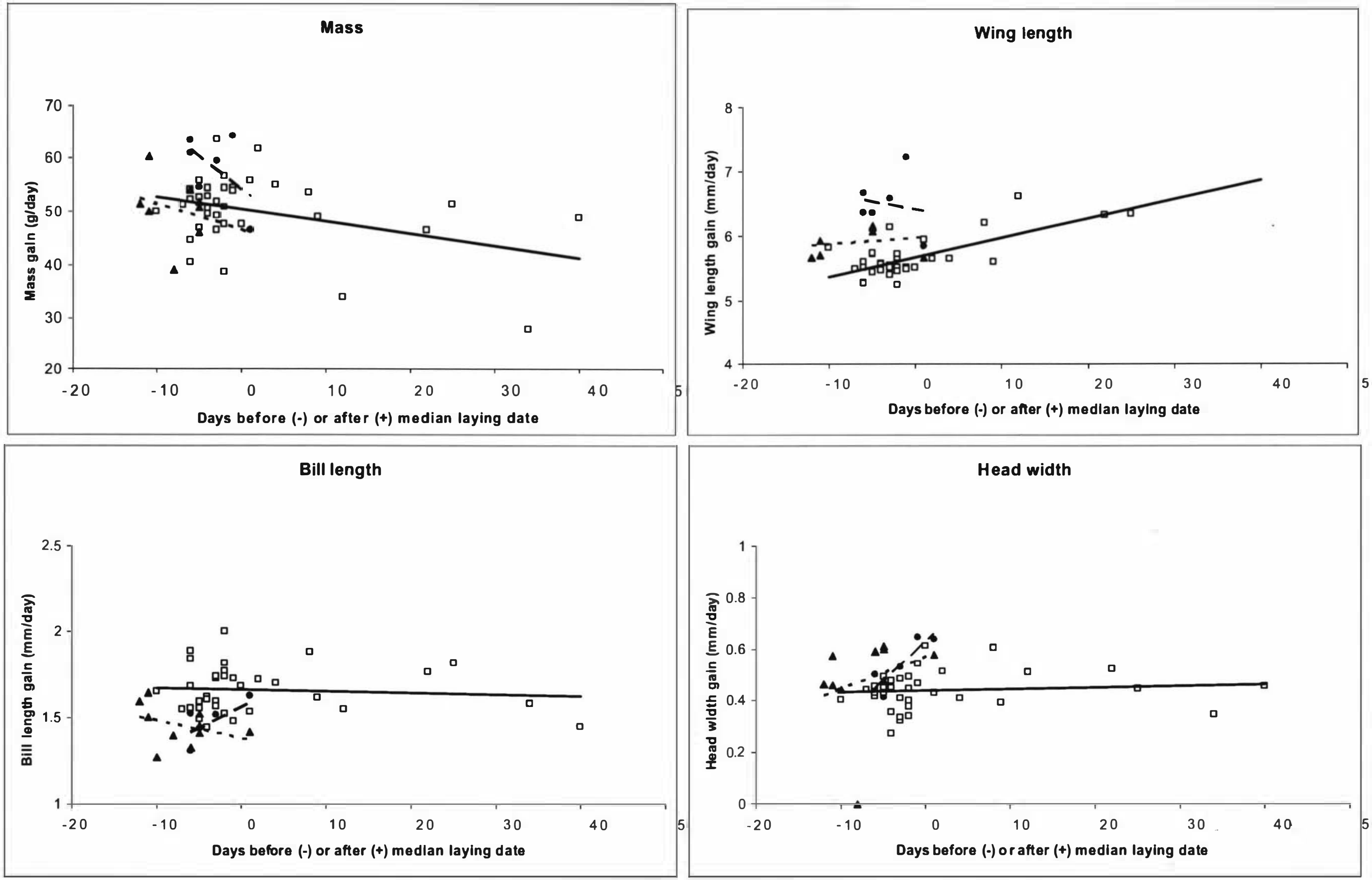

Figure 3. Growth measures compared to laying date. Each season is indicated by separate symbols, with circles for 1999-00, squares for 2000-01, and triangles for 2001-01. Regression lines are – – – for 1999-00, —— for 2000-01, and - - - for 2001-02. The negative correlation with mass in 2000-01 and positive correlation with wing length in 2000-01 were significant. These results also meant that overall a negative correlation for mass was found when all data were lumped, as was the positive correlation with wing length. The only other significant result was the positive correlation with head width in 1999-00.

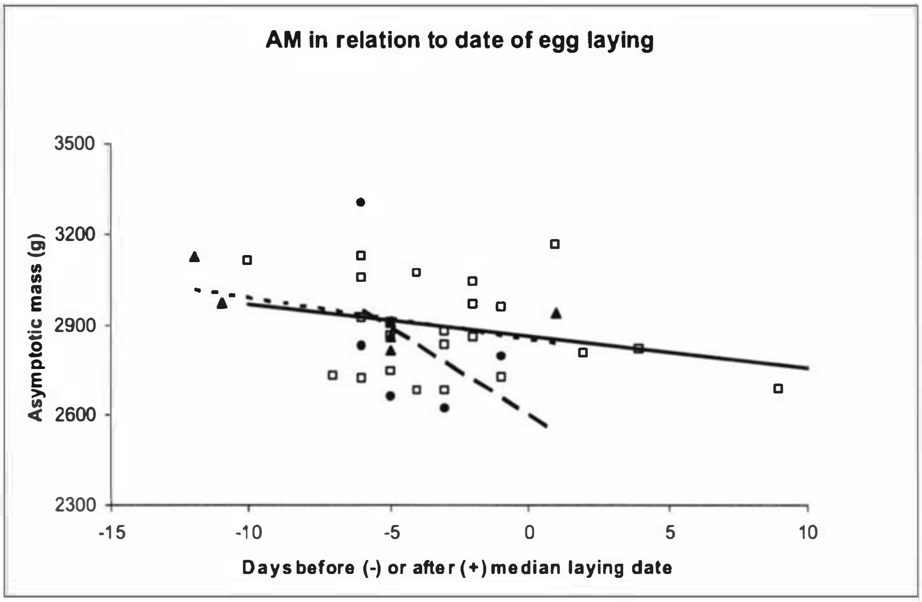

Figure 4. Asymptotic mass (AM) of chicks that fledged, in relation to laying date. Each season is indicated by separate symbols, with circles for 1999-00, squares for 2000-01, and triangles for 2001-01. Regression lines are – – – for 1999-00, —— for 2000-01, and - - - for 2001-02. There was no significant correlation in any season (see Table 2).

Relationship between mass at hatching and fledging success

Mass of chicks on day-one was investigated with respect to whether or not the chick subsequently fledged (Fig. 5). In both 1999-00 and 2001-02 there was no significant difference in the day-one mass of chicks that fledged compared to those that did not (Fig. 5). However, in 2000-01 there was a significant difference, with chicks that survived to fledging having significantly heavier day-one mass (Fig. 5). In both 1999-00 and 2001-02 there was very high chick mortality, due to starvation in 1999-00, and a combination of starvation and weather in 2001-02 (Chapter 3). In 2000-01 chick survival was considerably higher, with 81% of the chicks that hatched fledging. Therefore, in that season when there were good conditions during the chick rearing period, those chicks that were heavier on day-one were more likely to fledge.

In an attempt to understand the significant difference in 2000-01, I compared day-one mass with egg volume for chicks that fledged vs those that did not fledge (Fig. 6). This comparison was conducted for data from all three seasons combined, and separately for the 2000-01 data. Both analyses showed that even though chicks hatched from similar volume eggs, those chicks that went on to fledge were already of a greater mass by day-one, than those chicks that did not fledge. Unfortunately, the sample sizes in 2000-01 were very small (Fig. 6), but the trend shown is similar to that when the data for all three seasons are analysed together.

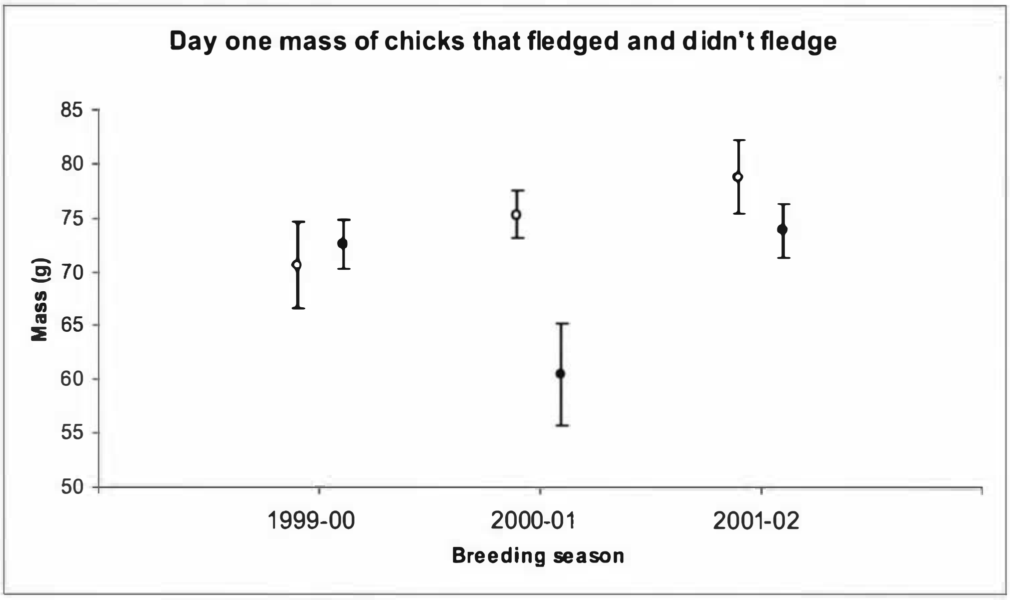

Figure 5. Mean day-one mass (± 1 SE) of chicks that fledged (○) and did not fledge (●), for each of the three seasons. Sample sizes were 5 and 18, 6 and 4, and 5 and 13 for each of the seasons, fledged and did not fledge, respectively. The difference between the fledged and did not fledge day-one mass in 1999-00 and 2001-02 was not significant (independent samples t-test; t = 0.410, NS; t = -1.170, NS), however the difference in 2000-01 was significant (independent samples t-test; t = -2.869, P = 0.041).

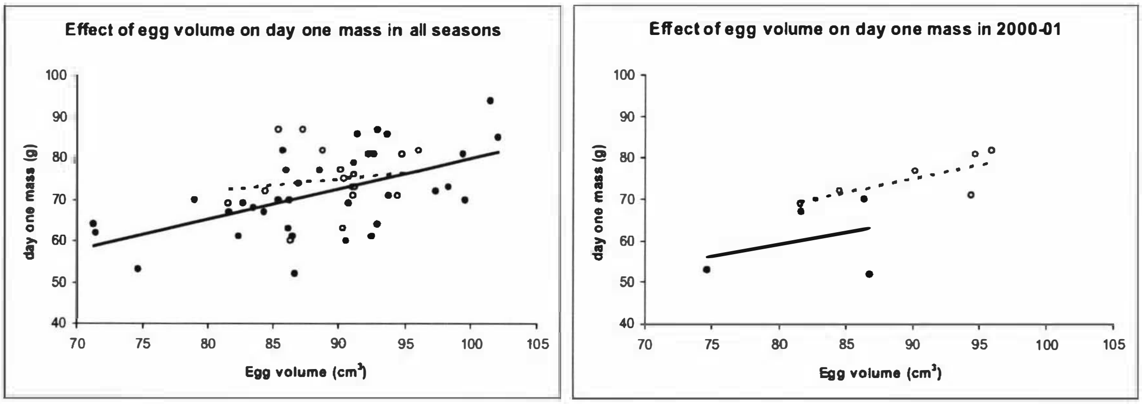

Figure 6. Egg volume vs day-one mass, for chicks that fledged (○) and did not fledge (●). 2000-01 showed a significant difference in day-one mass of chicks that fledged and did not fledge (Fig. 5). Linear regressions are fitted (dashed for fledged, solid for did not fledge) and were R^2 = 0.023 and R^2 = 0.331 for all seasons, fledged and did not fledge respectively, and R^2 = 0.533 and R^2 = 0.115 for 2000-01, fledged and did not fledge respectively.

Differences in mass increase between chicks that fledged and did not fledge

I analysed the mass of 0 – 11 day old chicks that fledged and did not fledge, in each breeding season (Table 3, Fig. 7). In 1999-00 chicks that fledged had slower development between 0 – 11 days, than chicks in the other two seasons. For chicks that did not fledge, the difference is not so apparent except for 2000-01 when growth was slightly higher than in the other two seasons. On average, chicks that fledged in 2000-01 and 2001-02 were approximately 100 g heavier at day 11 than chicks that did not fledge in all seasons. Moreover, in 1999-00 chicks that did fledge were actually growing at a rate slower than chicks that did not in all three seasons, and were still slightly lighter at day 11. The sample size of chicks used in this analysis is too small to perform statistical analyses between seasons.

Table 3. Second order polynomial regression equations from the data presented in Fig. 7. R^2 values are also presented, with all regressions showing values above 0.9 except for those chicks that did not fledge in 1999-00.

	Equation	R^2 value
Fledged		
1999-00	$y = 1.55X^2 - 2.30X + 86.98$	0.92
2000-01	$y = 1.79X^2 + 5.50X + 67.76$	0.98
2001-02	$y = 1.95X^2 + 4.46X + 75.56$	0.99
Did not fledge		
1999-00	$y = 1.22X^2 + 4.20X + 67.47$	0.80
2000-01	$y = 1.10X^2 + 8.55X + 52.47$	0.96
2001-02	$y = 1.22X^2 + 4.02X + 69.30$	0.99

Annual variation in chick LGR

There was a significant season effect on the LGR of all measures (Table 4, Fig. 8), and although the differences were similar for most measures, they were not the same. Mean mass LGR was highest in 1999-00, with 2000-01 and 2001-02 having similarly lower mean mass LGR (Fig. 8). The results were similar for wing length LGR, which was significantly higher in 1999-00 and again similarly lower in the other two seasons (Fig. 8). Mass and

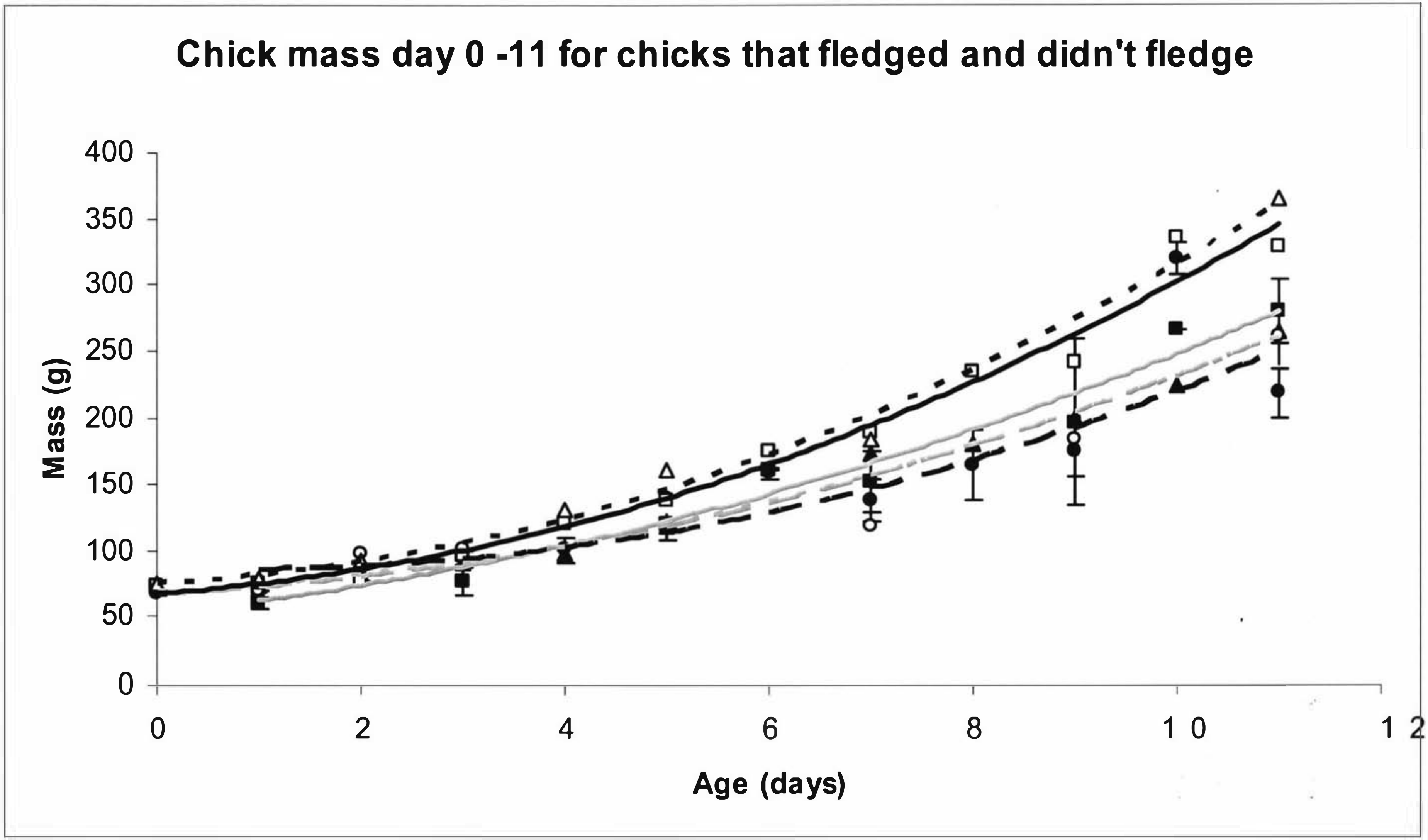

Figure 7. Chick mass day 0 – 11 (± 1 SE) for those that fledged and did not fledge, in each of the three seasons. Mean mass is indicated for each season, with circles for 1999-00, squares for 2000-01, and triangles for 2001-01. Fledged chicks are indicated by hollow symbols, chicks that did not fledge by solid symbols. The regression lines fitted are second order polynomial regressions, and equations and R^2 values are given in Table 4. Regression lines are – – – for 1999-00, —— for 2000-01, and - - - for 2001-02, being black for those chicks that fledged and grey for those that did not. Note the 2001-02 regression line is drawn but is almost the same as 1999-00.

wing length LGR were significantly positively correlated in 1999-00 (Pearson correlation r = 0.868, P = 0.25), but no other seasons had significant correlations (2000-01 r = -0.308, NS; 2001-02 r = -0.648, NS; all seasons combined r = 0.186, NS). However, for both bill length and head width 2000-01 was clearly different to 1999-00 and 2001-02, although bill length LGR was greater in 2000-01 and head width LGR was lower in 2000-01.

However, these results are contrary to those suggested for chick mass development in the period 0 – 11 days (see above). This suggests that in the early stages of development, growth was actually slower in 1999-00 than the other two seasons, but during later development (LGR; 20 – 60 days) chick growth in 1999-00 was more rapid than in the other two seasons.

Table 4. Mean LGR for each measure ± 1 SE (n). ANOVA between seasons conducted on these data showed a significant difference in all measures, as indicated in bold.

Measure	F	P	1999-00	2000-01	2001-02
Mass	$F_{2,46} = 3.688$	**P = 0.033**	58.18 ± 2.73 (6)	50.06 ± 1.18 (35)	50.42 ± 2.17 (8)
Wing length	$F_{2,43} = 16.543$	**P < 0.0001**	6.50 ± 0.18 (6)	5.68 ± 0.06 (33)	5.90 ± 0.08 (7)
Bill length	$F_{2,48} = 12.703$	**P < 0.0001**	1.48 ± 0.04 (6)	1.66 ± 0.02 (35)	1.45 ± 0.04 (10)
Head width	$F_{2,47} = 7.538$	**P = 0.001**	0.53 ± 0.04 (6)	0.44 ± 0.01 (35)	0.53 ± 0.02 (9)

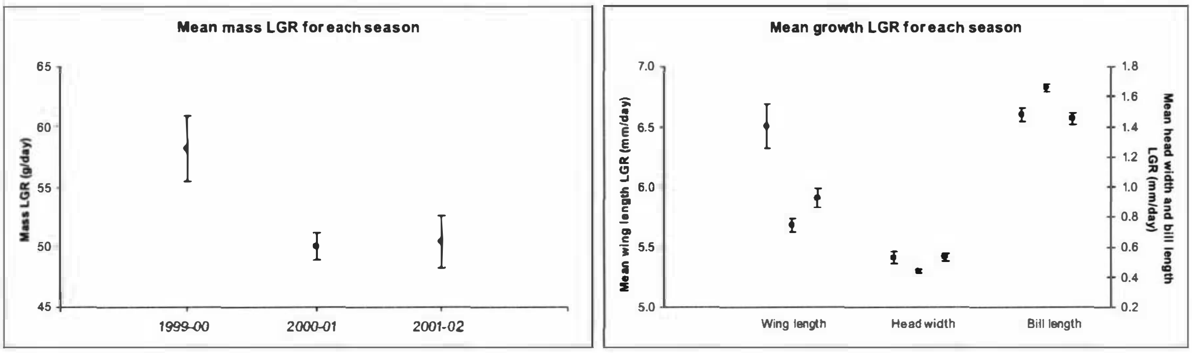

Figure 8. Mean mass and wing length, bill length, and head width LGR (± 1 SE) in each of the three breeding seasons. Samples sizes and significance are given in Table 4.

To understand the degree of variability in both mass and wing length LGR between seasons, I analysed mean R^2 values for both (Table 5, Fig. 9). There was a significant annual difference in the R^2 values for wing length LGR, but not for mass LGR. A post-hoc Tukey HSD test confirmed that the significant differences were between wing length LGR in 2000-01 and both 1999-00 ($P < 0.0001$) and 2000-01 ($P = 0.014$). This suggests that in 2000-01 wing length growth in individual chicks was less variable, than in the other two seasons, although this significant difference may not be biologically important.

Table 5. Mean R^2 value for mass and wing length LGR ± 1 SE (n). ANOVA between seasons conducted on these data showed a significant difference in wing length LGR, as indicated in bold, but not in mass LGR.

Measure	F	P	1999-00	2000-01	2001-02
Mass	$F_{2,42} = 0.240$	$P = 0.788$	0.947 ± 0.012 (6)	0.959 ± 0.007 (33)	0.956 ± 0.109 (6)
Wing length	$F_{2,42} = 15.162$	**$P < 0.0001$**	0.991 ± 0.002 (6)	0.997 ± 0.000 (33)	0.994 ± 0.001 (6)

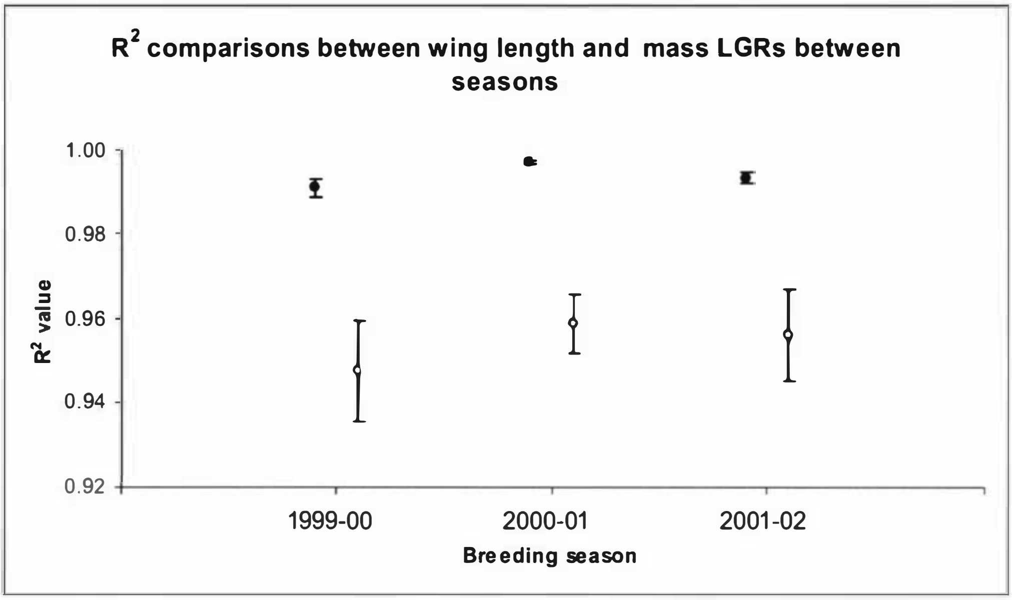

Figure 9. Comparison of the R^2 values for both wing length (●) and mass (○) LGR (± 1 SE) in each of the three breeding seasons. Samples sizes and significance are given in Table 5.

Asymptotic mass (AM) was also calculated for 5, 24, and 6 chicks in each of the three seasons (Fig. 10). The AM in each of the seasons was 2,841.5 ± 272.4 g, 2,892.3 ± 155.7 g, and 2,934.5 ± 108.6 g in each of the three seasons respectively, clearly showing a larger variation in 1999-00 than in the other two seasons. AM was not significantly different between seasons, however, the AM of chicks fledging in 1999-00 was lower than in the other seasons (Fig. 10). Furthermore, a Pearson correlation between AM and mass LGR, showed that there was no correlation in any season (1999-00 r = 0.318, NS; 2000-01 r = 0.095, NS; 2001-02 r = 0.390, NS; all seasons lumped r = 0.061, NS).

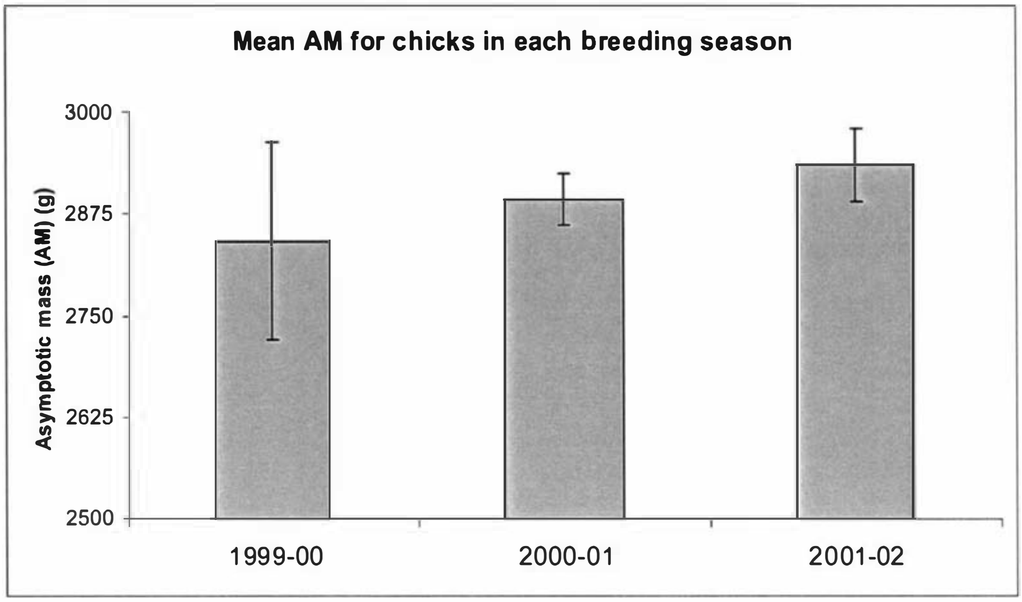

Figure 10. Mean chick asymptotic mass (AM) (± 1 SE), calculated from the average AM for individual chicks in each of the three breeding seasons. Sample size was 5, 24, and 6 chicks in each breeding seasons. Differences between seasons were not significant (Oneway-ANOVA, F = 0.413, NS).

Discussion

This chapter investigates the trends and patterns found during the development of Australasian gannet chicks. The chick growth data presented in this chapter are consistent with previous Australasian gannet studies in which basic chick growth has been assessed (Wingham, 1984b; Gibbs et al., 2000; Bunce, 2001). These previous studies have not, however, considered annual variation in chick growth, and relationships between egg volume and chick growth parameters are not adequately described. This study is the first to look at annual variability in the development of Australasian gannet chicks, and the effects of egg volume and egg laying date, providing a useful platform for further study.

Effects of egg volume on chick development

As expected, the hatching mass of chicks was strongly correlated with egg volume, as found in other seabirds (Parsons, 1970; Ricklefs et al., 1978; Birkhead & Nettleship, 1982; Furness, 1983; Amundsen et al., 1996), and Australasian gannets (Gibbs et al., 2000). The high variability in the relationship observed in this study may have been due to the length of time between hatching and being weighed, with some chicks possibly having received more food than others. Mean hatching mass of chicks in this study was slightly higher than chicks from Pope's Eye, Australia (Bunce, 2001). Unfortunately, Bunce (2001) does not give egg volumes as well as hatching mass, so a comparison cannot be made.

Fledging success is not significantly linked to egg volume (Chapter 3), although chicks that fledged generally hatched from larger volume eggs. Thus, based on the relationship between egg volume and chick hatching mass, the latter would not be expected to have a significant effect on fledging success. The non-significant correlations between LGRs for all chick measurements and hatching mass, further supports this. However, near significant correlations between egg volume and both mass and wing length LGR, suggest that in very poor seasons, such as 1999-00, egg volume may be important in the subsequent growth rates of chicks. In 2001-02, when chick mortality was high, egg volume also had a near significant positive correlation with AM. Therefore in seasons with very poor foraging conditions, chicks hatching from larger volume eggs may have more rapid growth and better survival. Mixed results have been documented with regard to this relationship, with early studies suggesting a positive relationship (Parsons, 1970; Davis, 1975; Lloyd, 1979; Gaston & Nettleship, 1981). Other studies, however, have suggested that whilst larger chicks hatch from larger eggs, their development does not differ from smaller chicks (Furness, 1983). More recently, a review of egg size and composition, and its effects on offspring fitness, suggested there is little unequivocal evidence in support of a positive relationship between egg size and offspring fitness in birds (Williams, 1994). However, of those studies reviewed, five out of 40 controlled for other characters, and reported significant residual effects of egg size on chick growth (ie. roseate tern, *Sterna dougalii*, (Nisbet, 1978) and European blackbird, *Turdus merula*, (Magrath, 1992)) and chick survival (ie. common tern, *Sterna hirundo*, (Nisbet, 1973), lesser black-backed gull, *Larus fuscus*, (Bolton, 1991), and kittiwake, *Rissa tridactyla*, (Thomas, 1983)). Clearly, seabirds featured strongly and since then further studies have been conducted, but still the relationship is unresolved.

During one season at Pope's Eye, Australia, Australasian gannet chicks from replacement eggs were significantly larger in mass through development, right through to fledging (Gibbs et al., 2000). These chicks hatched from eggs that were slightly larger than first eggs, although the difference was not significant. Gibbs et al. (2000) also found that chick mass relative to the average growth curve, was significantly correlated to egg volume. However, this and other studies could be biased by a parental effect rather than an effect of egg volume. Thus, it could be that better quality pairs lay larger eggs and are more likely to re-lay (Gibbs et al., 2000), and also forage more successfully for a growing chick (Lloyd, 1979). To differentiate between the effect of parental foraging ability and the effect of egg volume, experimental manipulations of eggs between nests are required, thereby removing the parental quality effect. Such experimental studies have provided mixed results. In thick-billed murres, *Uria lomvia*, wing growth is positively correlated with egg volume (Hipfner & Gaston, 1999). However, although hatching mass is positively correlated with egg volume, mass growth rate was not, even though mass at certain periods was heavier for larger volume eggs, this seemed to be a carry over of hatching mass. Likewise, Amundsen et al. (1996) found no effect of egg size on body mass of Antarctic petrel, *Thalassoica antarctica,* chicks after 3 days from hatching. However, recent studies on roseate terns again found a significant dependence of both mass LGR and AM on egg mass and hatch date (Nisbet et al., 1995).

Thus, the near significant trend in egg volume and mass and wing LGR and AM recorded in this study during some seasons warrants further study. Furthermore, experimental egg manipulations would allow the distinction between the effects of parental quality and egg volume on these variables.

Development of chicks in relation to date of laying

Unlike egg volume, significant effects of egg laying date on the fledging success of chicks were found in at least 2001-02 (Chapter 3). During this season there was high chick mortality as a result of poor foraging conditions and a severe storm. In 1999-00 when poor foraging conditions caused starvation, and 2000-01 when chick mortality was low, there was no effect of egg laying date on fledging success.

Egg laying date did have a significant effect on mass and wing length LGR in 2000-01, but in this season there was no effect of egg laying date on fledging success (Chapter 3). For mass LGR, the negative correlation was somewhat expected, decreasing during the laying period. Other studies have shown similar relationships (Birkhead & Nettleship, 1982; Gibbs et al., 2000). Australasian gannet chicks at Motukaramarama were less likely to be above average in mass later in the season, although this was a result of less reliable food supply later in the season (Wingham, 1984b). However, birds laying later in the season are thought to be younger and less experienced (Chapter 5), so this could also be a contributing factor. Wingham (1984b) found that the growth curves for wing and bill length from early, middle and late-hatched chicks were similar, although late hatching chicks fledged at slightly younger ages. A reduction in the fledging period of Atlantic gannets has also been noted (Nelson, 1964), although Wanless (1978) suggested this may have been due to disturbance at the colony and normally chicks would fledge when older and later in the season. In razorbills, *Alca torda*, there is a negative seasonal trend in hatching mass, following egg volume, but growth rates are not related to hatching date (Lloyd, 1979).

While mass LGR was negatively correlated with laying date, there was a significant positive correlation of wing length LGR with laying date. This was unexpected and seems difficult to explain. Why would mass LGR decrease, whilst the wing length LGR increases? This could be due to the different age period over which LGR was determined for each measure. Mass LGR was analysed through days 20-60, whilst wing length LGR was analysed for days 40-90. Or it could be due to chicks later in the season putting as much of their growth into wing length as possible, in an effort to fledge on time. To test this would require further work, in which early and later hatching chicks would be measured right through to fledging, with their age and wing length at fledging being recorded. This chapter, however, suggests that chicks may actually have been able to fledge at earlier ages based on estimates of day 90 wing lengths, which were longer in chicks that hatched from eggs laid later.

The lack of significant relationships for either wing or mass LGR measure with laying date in 1999-00 and 2001-02 may be due more to the high chick mortality occurring in those seasons, and thus the small sample size. Of importance is the fact that no chicks fledged from eggs laid more than one day after the median.

The negative correlation found between AM and date of laying, although not significant, may have been important. When the data from all seasons were lumped a near significant trend was found. The previous work by Wingham (1984b) also suggests that chicks fledge younger and possibly lighter later in the season, and similar results are found in other seabirds (Lloyd, 1979; Birkhead & Nettleship, 1982).

Therefore, further work on the effects of date on chick development needs to be done, and again experimental manipulations are needed to remove the parental quality effect. Analyses should also be controlled for the effects of egg volume. However, it appears that egg laying date does affect chick growth and survival, although the role of parental age and experience are also involved. There have been few studies documenting the relationships between chick growth and parental age (Ricklefs, 1967). However, Gibbs et al. (2000) suggest that chicks of younger Australasian gannets have lower rates of mass increases than average for the first 40 days post-hatching. They also suggest that these chicks then fledged at lighter masses to those produced by intermediate age breeders, but that older breeders have chicks that are again lower in mass, as in Wooller et al. (1990). As fledging mass influences post-fledging survival in Cape gannets (Jarvis, 1974) and other seabirds (Hedgren, 1981; Harris & Rothery, 1985; Harris et al., 1992), the same can probably be said for Australasian gannets, although this remains to be tested.

Relationship between mass at hatching and fledging success

Although a correlation between egg volume and fledging success was not evident (Chapter 3), analysis presented in this Chapter found a significant correlation between chick mass at day-one and fledging success in 2000-01. The lack of significance in 1999-00 and 2001-02 could again be due to the very high chick mortality in those seasons.

The results from 2000-01 either suggest that calculated egg volume was not sufficiently accurate (or perhaps composition of eggs rather than volume is important), or that changes between hatching and weighing at day one were important. Unlike in herring gulls, *Larus argentatus*, (Parsons, 1970), the yolk size of Atlantic gannet eggs is independent of fresh egg mass (Ricklefs & Montevecchi, 1979). Thus, egg composition could well vary between eggs independent of egg volume. Variation in egg mass may result from physical condition, hormonal status, or the size of the female oviduct (Ricklefs & Montevecchi, 1979). Perhaps of more importance is the foraging ability of the parents and therefore their chick provisioning ability within that first day of hatching. If some adults are better able to feed their chick during this period, then their chick should have enhanced initial growth and post-hatching recovery. This has important implications on breeding experience and foraging ability, and may well account for the shortening of incubation spells close to hatching (Nelson, 1966; Waghorn, 1982). Those adults that adjust their incubation spells correctly, presumably more experienced pairs, will be timing their foraging trip and return to the colony to feed a newly hatched chick. Therefore, this appears to be a critical stage for the chick, supported by the fact that most chick mortality occurs between 1 – 20 days (Wingham, 1984b; Chapter 3). The fledging success of chicks based on their mass at hatching has also been positively correlated in other seabird studies (Parsons, 1970; Lloyd, 1979). Perhaps associated with this, Nelson (2002) suggests that the larger egg size of Australasian compared to Atlantic gannets reflects a less certain food supply for the adults, with chicks benefiting from hatching with more food resources. However, this was based incorrectly on relative egg size, using Wingham's (1984a) data which suggested Australasian gannet eggs were 4.25% of adult mass. In this study average fresh egg mass was 98.8 g (3.6% adult mass) (Chapter 4), whilst at Bass Rock for Atlantic gannets average fresh mass was 104.5 g (3.4%) (Nelson, 1966). Therefore, this study shows less of a relative difference between the two species, and perhaps suggests Australasian gannets are not as well adapted to their variable environment as suggested.

Differences in mass increase between chicks that fledged and did not fledge

This sort of analysis is rare, with investigation of the relationship between growth and survival requiring data from chicks that do not survive (Nisbet et al., 1998). Generally, studies of chick growth in gannets, and other species, have fitted data to nonlinear sigmoid curves or assessed mass near fledging (Nelson, 1964; Ricklefs, 1967; Montevecchi et al., 1984; Wingham, 1984b; Navarro, 1991; Gibbs et al., 2000; Bunce, 2001). As yet, there has been little attention paid to inter-annual differences in growth rates, and growth during the critical first few weeks post-hatching (Nisbet et al., 1998).

This study reveals important differences in the growth of chicks during the early stage of development. Clearly, chicks that fledged were generally heavier throughout this period than those chicks that did not fledge. Whether this is again due to a carry-over effect of egg volume, and thus hatching mass, or a parental effect relating to better chick provisioning, cannot be determined from this data. Chicks that did fledge in 1999-00 were considerably lighter throughout this period than those that fledged in both of the other two seasons. These annual differences clearly reflect the poor foraging conditions Australasian gannets were encountering during 1999-00. The peak of egg and chick losses occurred in November, with chick losses being high during the second half of the month, overlapping with the main peak in hatching and early stages of chick development (Chapter 3). As suggested above, this is a critical time for these chicks. However, of particular note is the fact that in 1999-00, chicks that did fledge were lighter throughout this period than those that did not fledge, in that season, and in the other two seasons as well. Certainly, most chicks that fledged in that season came from eggs laid during the central part of the laying period (middle quartile; Chapter 3), while later hatching chicks tended to develop at slower rates and reach lower asymptotic masses.

Chick growth in the first few days post-hatching is also a good predictor of subsequent growth and survival in roseate terns (Nisbet et al., 1998). The growth in these first few days depended upon egg mass, hatching order, hatch date and season, but not parental age after controlling for the other variables. Thus, parental quality was only important in determining egg size, and did not directly control chick growth through provisioning. This would suggest that the differences between chicks that fledged and did not fledge in this study were due to the carry-over effects of egg volume, rather than parental quality, although this remains to be tested.

Annual variation in chick LGR

The significant annual variation in all LGR parameters during this study seems linked to the variable environmental conditions faced by Australasian gannets at Cape Kidnappers. In light of previous findings of variable breeding success and egg and chick failures, seemingly linked to changes in the environment and weather events (Chapter 3), this annual variation was expected, especially following differences in the 0 – 11 day growth of chicks.

Cairns (1987) predicted that a reduction in prey availability at a seabird colony would, depending on its severity, affect several distinct parameters of breeding performance ranging from changes in adult activity budgets and colony attendance apparent with only slight reduction in food supply (eg. Uttley (1992) and Olsson & Brodin (1997)), to reduced chick growth rates and breeding success (eg. Ricklefs et al. (1984) and Navarro (1991)), and an increase in adult mortality under more restricting conditions. During this study, I was not able to assess the availability of food directly. However, the breeding failures (Chapter 3), variation in attendance patterns (Chapter 5), and differences in egg size (Chapter 5) and chick development in this study are consistent with broad scale variability in environmental conditions leading to poor foraging conditions for the birds in this study colony.

Annual variation or variation between seabird colonies, in chick growth rates has been documented in several seabird species before, and these studies have generally considered food availability and abundance to be the causal factor (Lloyd, 1979; Gaston et al., 1983; Ricklefs et al., 1984; Nisbet et al., 1995; Hipfner, 1997; Wienecke et al., 2000). In Australasian gannet chicks, relative changes in mass were weakly correlated with mean wind speed since the previous visit (Gibbs et al., 2000), and other studies have found significant relationships between the effect of wind and foraging efficiency where prey distribution, visibility and availability may be affected (Dunn, 1973; Dunn, 1975; Birkhead, 1976). In my study, the additional turbidity of the water observed along the east coast near Cape Kidnappers due to high sediment loads (pers. obs.) could have had important impacts on the foraging of gannets. Hipfner (1997) found that despite egg volumes being similar between two years, chick growth and departure age were different, suggesting changes in foraging conditions occurred after eggs were already laid. Other studies have found changes in diet of breeding birds, possibly as a result of environmental changes, but have not found associated changes in chick growth (Bryant et al., 1999).

The differences in LGR found within this study are perplexing. Unexpectedly, the mass and wing length LGR were highest in 1999-00, when there was considerable starvation and mortality of chicks (Chapter 3), as well as food stress and abandonment of sites in adults (Chapter 5). As already discussed, the lowest rate of growth for chicks aged 0 – 11 days was in 1999-00, and this is even lower than for chicks that did not fledge in the other two years. This rather contradictory result suggests that adults that were able to forage successfully for chicks through the first several weeks may have had higher fitness, or were older more experienced birds (Coulson, 1966; Ollason & Dunnet, 1978), similar to that suggested for Atlantic (Nelson, 1966) and Australasian gannets (Gibbs et al., 2000). Once the conditions improved (or competition decreased through considerable lowering of chick numbers at the colonies), they were able to forage for and raise chicks that developed at a higher rate and exhibited a higher mass LGR. Thus, in the other two seasons, average mass LGR may have been lower due to poorer quality adults lowering the mean LGR of the chicks being monitored, although similar variation in the R^2 values suggest this may not have occurred. Conditions may have been so favourable in 2000-01 that even poorer quality adults were able to raise a chick, but these developed at slower rates. In 2001-02, chick mortality was predominantly caused by the storm in late December, as well as what seemed to be poor feeding conditions in late-November, early-December. This period of poor conditions came later in the season, possibly when chicks were less vulnerable, and the storm event produced mortality that was largely independent of pair experience or quality. As the sex of chicks was not known, the influence of this of growth rates could not be investigated. This should be investigated in future research.

Atlantic gannet chicks may be able to withstand periods of starvation lasting up to 2 weeks (Nelson, 1978a; Nelson, 1978b), and analysing lipid accumulation of chicks, Montevecchi et al. (1984) suggest nestlings could easily survive extended periods without food. Therefore, the starvation seen during 1999-00 and 2001-02 must have been very severe to have accounted for the mortality in those seasons, as well as the significant annual variation in the LGR of wing and bill length and head width, bearing in mind that these are measures of morphological growth rather than mass. Poor foraging conditions must have been occurring for quite some time before desertion of eggs and chicks, and chick mortality started to occur.

Wingham (1984b) provides the only other analysis of annual variation in chick growth in Australasian gannets. She found higher variability in the growth curves of chicks during one of her seasons, compared to the other two, and suggested this indicated indirectly that food supply was more abundant in that season, or that weather was more settled allowing parents to forage regularly. However, a direct relationship was not investigated, however, and breeding success in all years of her study was high.

In this study, bill length and head width LGR showed a different pattern to mass and wing length LGR, and reasons for this are not apparent. Further work is needed to recognise which features of chick development are important to enable better survival of chicks. In the case of head width, some of these annual differences may have been due to actual body fat, as this measurement involved directly measuring across the tip of the bill to the back of the head and may well have been affected by subcutaneous fat. This measure was highest in 2000-01 when chick survival was the greatest.

Although the difference in AM between seasons was not significant, differences were detected. The AM in 1999-00 was lower than in the other seasons, yet showed more variability, even though the sample size was small (n = 5). This is interesting considering that the mass LGR in this season was significantly higher than the other two seasons. What it suggests is that chicks were increasing in mass faster, but then did not peak quite as high in mass as chicks in other seasons. The AM of chicks in this study was lower in all seasons than recorded in other Australasian gannet studies (ie. 3,650 g (Gibbs et al., 2000), 3,132 g (Wingham, 1984b)). However, the fledging age in these studies was similar to that recorded in this study.

Therefore, although variability in growth rates of Australasian gannets between seasons was recorded in this study, the differences require further explanation. It is clear that a relationship between the environmental conditions, which affect foraging success and chick provisioning, and chick development exists. The development of gannet chicks requires further study, with direct assessment of food availability and foraging success studied concurrently.

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7

General discussion

Australasian gannets have until now been considered to be the Southern hemisphere form of the Atlantic gannet, with the Cape gannet taking its place in South African waters. However, this now seems to be an ecological over-simplification. This thesis represents the most up-to-date account of one of them, the Australasian gannet, at the Cape Kidnappers gannetry. The last major work published from a New Zealand study was in the early 1980s.

The three species are morphologically very similar, and in many ways behave and live in a similar fashion, however, this has masked the realisation that they are different animals, living in different environments. The niches these birds occupy in each of their regions, whilst being ecologically similar, seem to differ more than we first realised due to complex relationships between them and their environment. This relationship is perhaps best viewed as a flow diagram, and whilst not all of the potential influences and relationships may be included, Figure 1 sets out to at least describe the major influences that gannets have evolved with and are being affected by, particularly those deemed important by this thesis.

When looking at the complex environment gannets live in, it becomes clear, even in a simplified diagram such as Figure 1, that a slight change in one variable, for example a fisheries based impact on large predator fish species, can cause a complex chain reaction. Only through detailed study of the components of this chain reaction will we ever understand the complexity of such systems, and so, this thesis has set about to answer some of the basic biological questions about how the Australasian gannet lives in and interacts with its environment, and how this environment may impact on the species. Before this study began, we knew little about what environmental factors affect this, or either of the other two gannet species. Storms at certain times of the breeding season were known to affect chicks when at a vulnerable stage through direct exposure, but complex interaction between weather, prey, and gannets were not fully recognised.

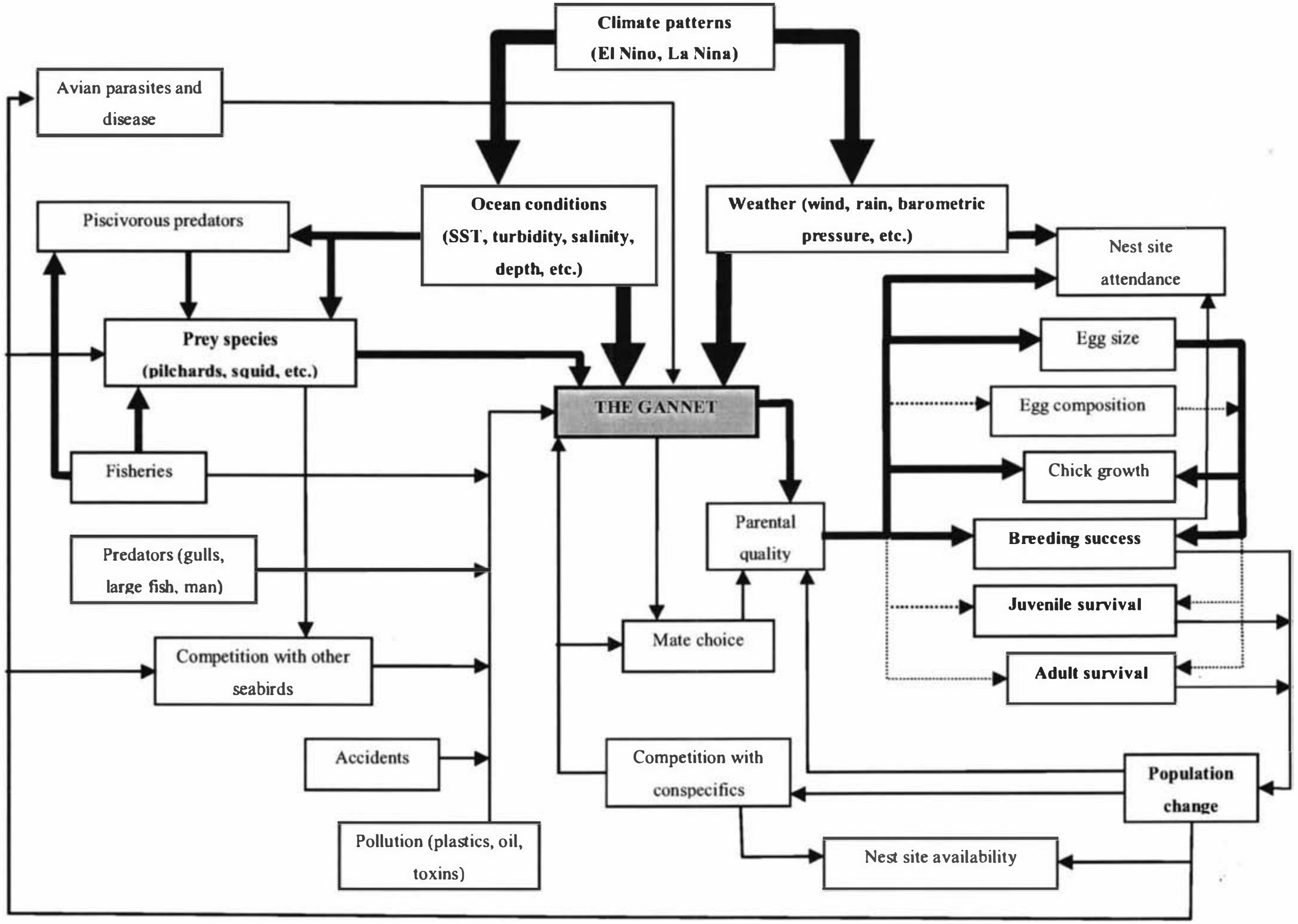

Figure 1. Flow diagram of the relationships between gannets and the environment they live in. In this case 'The Gannet' is the Australasian gannet, but could just as well be the Atlantic or Cape gannet. Rather than make the diagram overly confusing with arrows indicating relationships between every factor and every output, all are linked through 'The Gannet'. For example Avian parasites and disease could impact 'The Gannet' through changes in parental quality and therefore egg size or chick growth.

I embarked on this study with so many questions, and perhaps the greatest answer this thesis provides is to a question asked nearly 35 years ago, by one of the early gannet pioneers in New Zealand. In his 1971 paper entitled "Horuhoru revisited – longevity of the Australian gannet" (a paper which documented far more than just the longevity of the species), Peter Stein asked the question "What had happened? Was this caused by man or Nature?". This question was asked after visiting his study colony in November 1968, when breeding should have been in full swing, with an expected count of 1600 pairs. Instead only 300 nests were occupied with newly laid eggs, or chicks that were three to four weeks behind schedule. What had happened to the rest? Similar failures of breeding birds had occurred previously at other colonies, mostly blamed on disturbance by humans. Yet, there was little or no evidence of human disturbance and the environmental effects of weather, sea conditions, and lack of prey were not considered.

Rather fortuitously, the current study encountered what may well have been the worst breeding seasons observed in more than 40 years of research at Cape Kidnappers by Kazimierz Wodzicki, Rev. F. H. Robertson, and Christopher J. R. Robertson. Disturbance by humans was clearly not the answer, but environmental conditions had led to a lack of available food for the adults, leading to longer incubation and brooding stints, desertion of eggs and chicks, starvation of both adults and chicks, resulting in the considerable loss of eggs and chicks, and very low breeding success. If a visit to the Cape Kidnappers gannetry had been undertaken in November 1999, without prior knowledge of these events, a very similar picture to that which greeted Stein would have been encountered. This is the first study to document such an event in any of the three species of gannet, and sets the Australasian gannet apart from both the Atlantic and Cape gannets in this respect. In fact this sort of environmental vulnerability aligns the Australasian gannet more closely with several of the booby species, which also encounter periodic breeding failures associated with a lack of food. As yet there is no counterpart in the other two gannet species.

Previous Australasian gannet studies focussed on outlining the similarities between Australasian and Atlantic gannets. Elspeth Wingham's work was the first to suggest actual differences existed, when she suggested that Australasian gannets were far less synchronous than Atlantic gannets in their breeding habits, and she compiled evidence from other studies to support this. However, much of the evidence from previous studies came from irregular visits to colonies, and is perhaps not clear in the exact pattern that it presents. The breeding failures which occur in this species may well have affected data collected on the laying period, when compiled from irregular visits. Anecdotal observations at Cape Kidnappers seemed to suggest that egg laying varied by a matter of weeks between seasons, whilst at Motukaramarama, Wingham showed variability in laying dates, although this was compounded by egg losses. In contrast, my work shows that in the three breeding seasons studied at the Plateau colony, egg laying was initiated during a period of only a few days each year, and laying was highly synchronous. Whether this was because the environmental cue they use to time laying was consistent, or because of some physiological inflexibility, remains to be answered. Due to the contrary nature of these findings, more work is needed to establish if there is variability in the onset of laying dates and to what extent this occurs. The short-term nature of this project may be responsible for my results, or, this may be a real phenomenon which is similar to that exhibited by the Atlantic gannet. Thus, Australasian and Atlantic gannets may be similar with respect to consistent onset of laying and a highly synchronous laying period, possibly as a result of an ancestral trait shared by the two species. Alternatively, it could be that the environments these two species inhabit share at least some predictable components which constrain the timing of breeding in both species. In a seabird that breeds in temperate waters with a prolonged breeding season, there are almost certainly constraints imposed by external variables.

The assessment of onset of laying through the now authenticated technique of back-dating from chick age, may well help us to determine long-term trends in the timing of breeding. Detailed observations of colonies during the laying period would give a more accurate picture, but are time consuming, and at least five to ten years of data should be collected to understand annual variability, and to remove the effect of short-term changes. The wealth of historical data from Cape Kidnappers awaits analysis, and long-term trends should be evident within these. Analysis with respect to environmental conditions during those seasons may be possible and should be conducted. As part of this, further investigation of the distinct difference in timing of breeding between the Plateau and Black Reef colonies is needed. Is this difference a result of age structure of the colonies, or due to differences in feeding location and hence perhaps differing peaks in food availability?

In investigating the longer-term trends in the Plateau colony, and especially the timing of breeding, it may become possible to determine the factors controlling the timing of breeding. The lack of a detectable relationship between sea surface temperature and the onset of laying in this study suggests this alone is not responsible in this species. It remains to be discovered, if gannets do time the onset of breeding to certain events or peaks, what these are, and how they predict them. As suggested earlier in the thesis, I suspect that the onset of breeding is timed to some predictable event, possibly a peak in food supply during the chick rearing period, as has been suggested for Atlantic gannets. How they predict this peak, what factors affect its timing, and the variability in the amplitude of these peaks (availability or abundance of prey), remains to be discovered. The variability in the amplitude rather than the timing of these peaks is possibly responsible for the breeding failures apparent in this species, explaining why timing of breeding varies little, but breeding success does. Timing of breeding in Australasian gannets has also been suggested to be linked with calm autumnal weather conditions during the time that juveniles are fledging and therefore at their most vulnerable. This too remains unconfirmed.

The significant finding that breeding success varied enormously between breeding seasons as a result of natural events, as mentioned earlier, is probably the greatest finding of this thesis. Disturbance by humans could be effectively ruled out as a factor, and instead the blame lies with the prevailing environmental conditions during these breeding seasons. The 1999-00 breeding season is of particular importance, as in this year the fact that only 9% of breeding pairs produced a chick to fledging was the result of a lack of food. Although not measured directly, the massive loss of eggs and later the loss of eggs and chicks was primarily the result of adult birds deserting their nest sites, due to starvation. Attendance periods by adults were longer than normal, and adults were clearly emaciated and under going food stress. Later in the season, chicks could clearly be seen to be emaciated, and growth curves were affected. The reason for a lack of food was not determined, but seems related to the high number of anti-cyclonic events that occurred during 1999. Whether this caused fish stocks to be less abundant or less available, through being deeper or 'hidden' by turbid water, is unknown. Perhaps adult gannets had to travel further to access fish stocks, meaning foraging trips were longer in duration.

Atlantic gannets show no similar breeding failures, with Nelson's early work finding consistently high breeding success and no evidence of starvation or high egg and chick losses. Perhaps as a consequence of this Northern hemisphere influence, Wingham gave little attention to the complete loss of first clutches during the first year of her study at Motukaramarama, caused by a major storm. This complicated her assessment of breeding success, and although it led to only slight differences in her estimates of productivity, was still of considerable consequence to breeding Australasian gannets at that colony. Apart from the immediate impacts of the loss of eggs, other differences were noted between her study seasons as a consequence of that storm.

Although such severe storms may not be a regular occurrence in New Zealand, environmental variability is something that Australasian gannets have had to adapt to. The brief comparison of environmental variability between Cape Kidnappers, New Zealand and Leuchars, Scotland, conducted in this thesis suggests that differences may exist. Further investigation of environmental variables such as sea surface temperature, sea conditions, other weather variables, and the reliability and abundance of fish stocks would be interesting.

Accessing historical data for these environmental variables and comparing them with present data would be especially interesting in the light of current changes being documented in British seabird populations and breeding success in recent years. In the North Sea, changes in breeding success and diet of smaller seabird species (such as the auks) have been documented for several decades following changes to fish stocks, and gradually over time increased sea surface temperatures. It seems these impacts are now becoming more pronounced, and may well be starting to affect larger seabirds which have until now been able to absorb some of these changes.

During Nelson's work in the 1960s and 70s, he never observed Atlantic gannet chicks being left unattended. It seems clear that at this time, Atlantic gannets enjoyed super-abundant food in an environment that was annually consistent. This was reflected in the ability of this species to successfully raise twins, something the other two gannets seem far less able to do. As part of this, Atlantic gannets were always able to have at least one member of the pair remain with the chick, and very high levels of attendance by both members of the pair was evident. This has perhaps allowed the very high levels of aggression between neighbouring nesting Atlantic gannets to evolve, with this aggression even spilling over into attacks on chicks, sometimes resulting in the death of chicks. Conversely, Australasian gannets frequently leave their chicks unattended, and do not have such high levels of aggression. Such high levels of aggression in Australasian gannets, in which both members of the pair are forced to forage concurrently, leaving the chick unattended, would be maladaptive, as considerable chick mortality would occur. Perhaps if environmental change is occurring in the North Sea, and Atlantic gannets are now being forced to spend more time foraging, leaving chicks unattended, then aggression levels in this species will decrease. It would be interesting to monitor the level of aggressive interactions in colonies over the next few decades, to determine whether changes in aggression correlate with changes in attendance levels and foraging success. Perhaps an easy way of doing this would be to measure inter-nest distances. The nests of Cape gannets, the least aggressive of the three in my experience, are closer together than those of Australasian (medium level aggression) and Atlantic gannets (the most aggressive and widely spaced).

Study of the three species, and in particular changes that occur in the Atlantic gannet population over the next few decades may give us an interesting insight into the evolution of the gannets, and the way in which the environment has shaped their particular ecologies. By studying the Atlantic gannet, we may learn more about how the Australasian gannet has evolved to cope with a variable environment. Perhaps it is just a coincidence, that now, during this time of changing environmental conditions, Atlantic gannets are being observed to leave chicks unattended during more than just the occasional foraging trip. I suspect that this is actually a reflection of changing prey availability and abundance, and that if these conditions persist, Atlantic gannets may change other breeding behaviours, becoming more like Australasian gannets in their breeding habits. Further investigation of the levels of unattended chicks should be undertaken in the Atlantic gannet. If my suspicions are correct, I predict that as food becomes more limited, the frequency with which chicks are left unattended will increase, and at some point, starvation, decreased chick growth rates, and decreases in annual breeding success will occur. It would be of great benefit to have fisheries data which support the decrease in abundance and availability of gannet prey species in the North Sea, concurrent with these changes.

Gannets in New Zealand are opportunistic feeders. This is especially apparent from previous research at some gannetries, such as Cape Kidnappers. At several New Zealand colonies, including Cape Kidnappers, the prey that gannets feed on has been shown to change within the breeding season, but also differs seasonally between breeding seasons. In light of the 1999-00 breeding season, it is critical that we investigate the availability and abundance of the fish species gannets feed on whilst breeding in New Zealand, and determine annual variability. The variability in Australasian gannet breeding success is thus the ultimate outcome of what is happening in the environment. Unfortunately, at present this sort of fisheries data is limited for New Zealand waters.

The variability encountered in other aspects of the breeding biology of this species suggests that these birds have evolved to cope with such environmental uncertainty. The fact alone that the Australasian gannet population has undergone an extensive increase in numbers and the development of new colonies, shows that they have developed a way of overcoming significant breeding failures in some years. Cape Kidnappers itself has gone from no gannetry at all in the early 1800s, to a gannetry comprising four separate colonies, containing approximately 7,500 breeding pairs in the early 2000s. This almost certainly makes them one of New Zealand's seabird success stories. However, with such little knowledge of how the species interacts with its environment at present, we do not fully understand why it has been so successful, and therefore what future environmental change may mean for this species. Similar increases in the Atlantic gannet have also occurred. Yet, these birds seem not to have had to endure such variable breeding success. The Cape gannet, although not as well studied with regards to population change, appears to be holding its own. So why has the Australasian gannet done so well?

The key to this question seems to centre on the Australasian gannets ability to be able to overcome environmental variability. During the 1999-00 breeding season when food was limited, adult attendance at nests on the Plateau colony was lower. Thus, birds did not attend sites, especially if they had already lost their egg or chick, and presumably spent more time at sea foraging. This then allowed some birds to return to the colony, presumably once food availability had increased and relay. However, fewer birds relayed in that season, than in the other two following egg or chick loss. As mentioned above the Atlantic gannet seems to almost never leave the nest site unattended, with considerable nest site defence undertaken by males in that species, even when breeding has failed. For some reason, the Australasian gannet does not have such rigorous defence of the site, and as can be seen from the attendance data in this thesis, regularly leaves the nest site unattended if breeding has failed. It seems unreasonable to suggest that nest site availability is any more limited in the Atlantic gannet, and so reasons behind this disparity are unresolved.

During this study I used a technique for estimating the volume of eggs that correlated well with egg mass. This was useful for analyses performed during this thesis, but also means that in future, eggs of any age can be measured and a volume estimate derived, rather than time consuming observations relying on freshly laid eggs to be weighed. The analyses performed using the eggs studied in this project seem to suggest that generalised equations for incubation period and weight loss are inadequate for the genus *Morus*, and perhaps also for other members of the Pelecaniformes.

Variation in egg sizes between and within seasons was found by this study, correlating with other breeding variables, and seemingly linked to environmental variability. This is the first study to accurately document this variability over a full three breeding seasons, with eggs of a known age. That early laying females laid larger eggs than later laying females conformed to our knowledge of other seabirds. However, of note was the disruption of this pattern in the 1999-00 breeding season, even before the egg and chick losses had started to occur. Therefore, breeding birds were already being affected by the environmental conditions which were then to culminate in the desertions that occurred later in the season. Females laying later perhaps did so when conditions had improved enough for them to lay normal eggs. Similarly, in 1999-00 individual females laid significantly smaller eggs in that year compared to the next. It seems difficult to explain why egg size would vary significantly, as for a female gannet laying an egg between 3-4% of her body weight this would not seem to be a significant challenge. Perhaps the composition of these eggs holds the key, and protein analysis of eggs would be an interesting undertaking to determine if changes in egg size relate to changes in egg composition. These variables do however, seem to be linked with the environmental conditions encountered during those breeding seasons. It is important to note that females that laid big eggs one year tended to lay big eggs the next, so as well as an annual environmental affect, individual females, whether dependent on age or experience, laid similarly sized eggs relative to other females. Similar trends have been found in other species.

Furthermore, these variations in egg size and the relative date on which they were laid, both annually and on an individual basis, had consequences on egg hatching success, chick growth and fledging success. Due to small sample sizes and perhaps extreme environmental conditions in some of the seasons studied, the results in this thesis should be viewed as preliminary. However, the earlier an egg was laid, the higher the rate of chick mass linear growth rate and chick asymptotic mass. Similarly, egg volume positively correlated with the mass of chicks on day one, and chicks that were heavier on day one had a significantly better chance of fledging in at least one of the three breeding seasons. Therefore, females who produced bigger eggs, earlier in the season, were generally more likely to fledge a chick. This was disrupted by environmental events in the 1999-00 breeding season, with particular peaks of egg and chick losses affecting cohorts differently. The full effects of this are still to be examined through further data analysis. Furthermore, the effects of egg size versus parental quality are still to be investigated, with egg size perhaps being less important than parental quality. Another words good quality females lay large eggs and provision chicks well, thereby fledging more chicks. By egg manipulation experiments, moving large eggs to small-egged females and vice versa, the roles of each of these can be elucidated.

Clearly, environmental factors affected adult Australasian gannets at the Plateau colony during this study, and this in turn affected their eggs and chicks. Whether post-fledging survival and even adult survival were affected by these events remains to be determined. But, the key finding of this thesis is that there is variability in the breeding biology of the gannets at Cape Kidnappers, and this is affected almost certainly through the environmental variables outlined in Figure 1, primarily weather and prey availability and abundance. What remains is for further investigation of exactly how these external variables relate to each other, and then further investigation of the direct relationship between these and Australasian gannet breeding biology.

As an aside, we are in an interesting position, whereby we can observe how environmental variability invokes change and evolution in a species which seems not to have had to deal with it in the past. The North Sea situation may provide critical answers to some of the questions being asked in New Zealand. Will Atlantic gannets become more like Northern hemisphere Australasian gannets, living in a variable environment, where food is not predictably super-abundant? Currently there are few data on annual variability in egg size or chick growth rates for the Atlantic gannet. This sort of data should be collected, as variability in these parameters may be evident before changes in breeding success are recorded.

Clearly there must be differences in the life history parameters of Atlantic and Australasian gannets. Similar rates of population increase have been observed in both species, over much of the last century, yet considerable differences in breeding success appear evident. It is possible that Australasian gannets have been able to continue population growth, despite lower breeding success, due to lower mortality rates at the juvenile, immature, or adult stage. This could mean that if breeding success in the Atlantic gannet decreases significantly, that population increases may halt or reverse, if mortality rates in other life stages remains the same. Again these are interesting but potentially disturbing possibilities that need to be explored in future studies.

At present there are considerable differences in the ecology and breeding biology of Atlantic and Australasian gannets, in my mind supporting the consideration of the gannets as separate species. However, the general consensus as to whether they are separate or allo-species has not been reached. Perhaps they are just "gannets" in two differing environments, and much of the argument rests on which species concept one subscribes to. Will both the Atlantic and Australasian gannet continue to expand their populations, and will the Cape gannet continue to hold its own? Even for the magnificent gannet the future is uncertain.

Appendix 1

Intra-seasonal trends in egg measures

Table 1. Pearson bivariate correlation between laying date and first egg measures. Significant values are in bold. n = 91, 95, and 97 first eggs in each of the three seasons respectively.

	1999-00		2000-01		2001-02	
	correlation	significance	correlation	significance	correlation	significance
Length	0.108	0.308	-0.197	0.056	-0.119	0.246
Width	-0.155	0.142	-0.480	**0.000**	-0.253	**0.012**
Shape	-0.186	0.078	-0.229	**0.025**	-0.083	0.419
Volume	-0.068	0.519	-0.443	**0.000**	-0.250	**0.014**

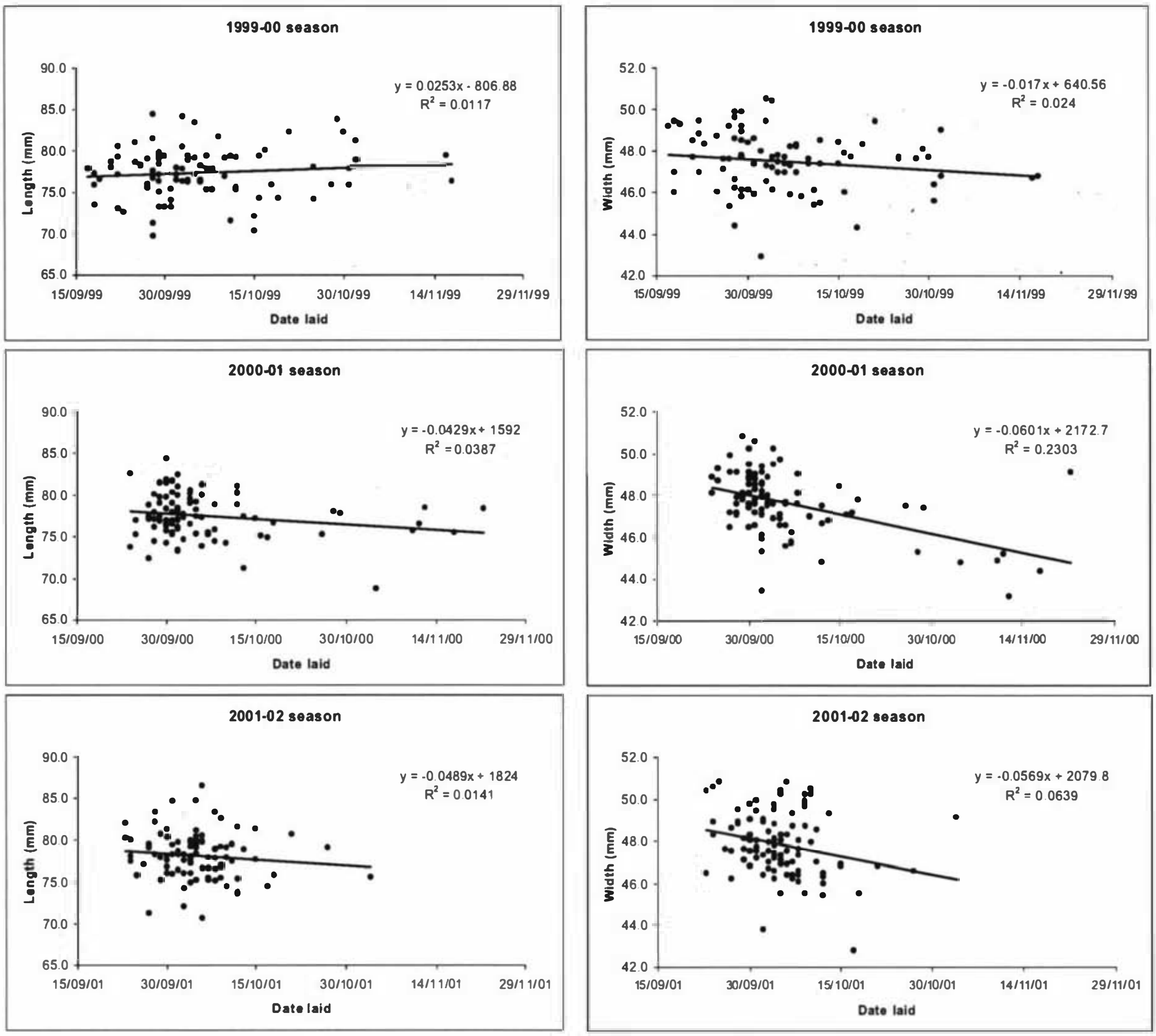

Figure 1. Length and width of first eggs compared with laying date, for each of the three breeding seasons. Negative trends in all measures were evident in all years, except for a slight positive trend in egg length for the 1999-00 breeding season. See Table 1 for significance.

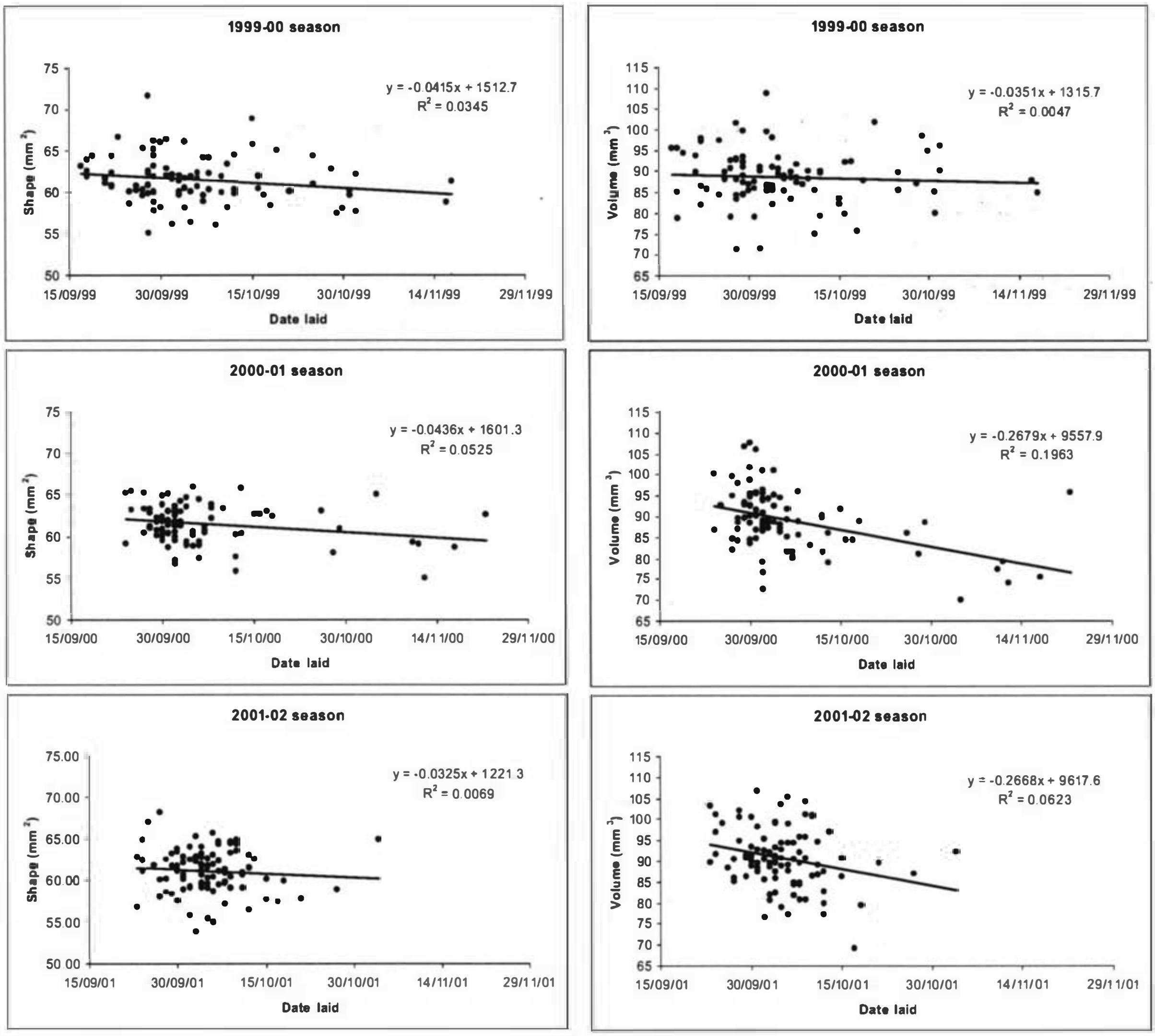

Figure 2. Shape and volume indices of first eggs compared with laying date, for each of the three breeding seasons. Negative correlations were evident in all years for both measures, with the correlation for shape in 2000-01 and volume in 2000-01 and 2001-02 being significant at P<0.05.