Habitat use and breeding performance in an inshore foraging seabird, the Black Guillemot *Cepphus grylle*.

Thomas R Sawyer BSc

A thesis submitted for the degree of Doctor of Philosophy to the Faculty of Science, University of Glasgow.

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Declaration

I declare that the work presented in this thesis has been completed by myself unless otherwise acknowledged in the text. No part of this work has been presented for any other qualification.

Thomas Sawyer
October 1999

Abstract

The choice of an appropriate habitat in which to breed successfully is a capacity likely to be subject to strong selection pressures. Studies of habitat utilisation therefore allow us to identify factors determining breeding success. In addition to their intrinsic interest, understanding of these factors plays a crucial role in developing appropriate conservation measures for species and habitat management. In marine birds however, the focus of attention has generally been only on the nesting habitat, and there is relatively little information on foraging habitats. This thesis focuses more on the latter, in an inshore foraging seabird, the Black Guillemot.

A colony of Black Guillemots, *Cepphus grylle*, was studied over two breeding seasons and data were collected on their egg laying, chick rearing and foraging behaviour. Birds were found to lay either one or two eggs, the two eggs being hatched either synchronously or asynchronously. Single eggs were found to be larger the later in the season they were laid. In two-egg clutches the second laid egg was smaller and had reduced survival. Eggs laid earlier in the season had higher fledging success in two egg clutches. Chicks hatched from larger single eggs fledged at an earlier age than those hatched from smaller eggs.

Adults providing for chicks brought a variety of food to the nest but a relatively high proportion of the predominant prey item, the butterfish, *Pholis gunnellis*, in the chick diet was associated with a high growth rate of the second chick. Adult birds catching more of this prey type travelled further to forage and made shorter dives at the foraging site.

The overall foraging distances for this colony, whilst at all times being close inshore, were higher than previously reported for inshore foragers and comparable with pelagic foraging seabird species such as the Common Guillemot in nearby colonies.

Black Guillemots showed distinct preferences for certain habitat types available in the heterogenous inshore waters at this site and their density on the water was linked to the availability of butterfish. The distribution on the water of foraging birds was consistent across both years of study but showed a degree of seasonal variation, possibly linked to the different demands of chick rearing and provisioning for adults in order to increase body condition for survival in winter. Particularly important habitats were certain distinct types of kelp, beds and these should be the focus of habitat conservation measures.

Acknowledgements

There are many people that I would like to thank, without whom this thesis would not have been possible. In the four summers that I worked on the island of Papa Westray I found the islanders to be an exceptional community of people. All of them were welcoming, helpful and charming and made me feel at home in their community. A few people deserve special mention: firstly, many thanks are due to Neil, Jocelyn and John Rendall for allowing us to work on their land, and for giving us our quota of civilisation in the form of excellent dinners, high quality conversation, games of croquet and Neil's home brew. The Rendalls of Daybreak, the Hewitson family (our footballing soul-mates), the McNabs, the Millers and the Rendalls of Backaskaill all deserve mention as well. The Community Co-op and the Church of Scotland are also due thanks; the Co-op for catering to our often bizarre needs, and the Church for renting us our salubrious accommodation. I would also like to mention Stuart Groat, who supplied us with fresh crabs and always had a friendly word for us at the pier. He will be sadly missed, as will Tommy Rendall. Very special thanks indeed must go to Jim Davidson, who, from when we first set foot on the island not only provided equipment and backup for our boating needs, but has been our mentor and a good friend as well.

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have been fewer birds captured and fewer tears of laughter. I must also thank David Donnan of SNH for making the sea surveys possible, and to David Trimble and the other MCS divers who came up to Papay.

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Chapter 1

Introduction

The study of the behaviour of living organisms – a historical perspective.

The observation of animals has been carried out in great detail since before the dawn of recorded history as testified to by the sophisticated cave paintings of 30,000 years ago. Detailed written descriptions of the behaviour of animals, such as brood parasitism by European cuckoos and the role of experience in the development of nightingale song, exist from the 4th century BC (Aristotle 1970). The discipline of ethology, the study of the behaviour of animals, is a relatively new science, although it is generally considered to have started in its modern form with the work of Charles Darwin. Ethology as a science was recognised as a significant field of scientific research when Konrad Lorenz, Niko Tinbergen and Karl von Frisch were awarded the Nobel Prize in 1973. The study of ethology in its modern form has provided us with reliable and accurate methods for describing and analysing animal behaviour, and the theoretical framework to understand and predict the response of an animal to a particular situation (Huntingford 1984). Ethology attempts to explain the causes of behaviour (what "drives" a particular response) and the effects of this behaviour (the effect it has on an individual or population). A recent offshoot of ethology is behavioural ecology, which focuses on understanding the functional significance of behaviour, and examines the demographic and life history relationship (Krebs & Davies 1997). Furthermore, an understanding of an animal's behaviour can be of practical use in understanding the complex interactions in situations where humans and animals come into contact (Monaghan 1984). Modern society has come to recognise the importance of conserving the natural environment and the animal populations that live in it, and the study of the behaviour of these animals can be extremely important in this. Of particular importance to conservation is an understanding of the manner in which an animal interacts with its environment. Central to this is the way in which an animal obtains its food requirements: that is its foraging behaviour (Clemmons and Buchholz 1997).

Foraging ecology

The finding and consumption of food to meet daily energy requirements is central to life for all animals. As the first priority, it influences all further aspects of life history by providing the energetic platform for further activity, growth and for the production of young. The pressure to find and compete for food has created the basis for much of the taxonomic diversity evident in present biological systems and is one of the driving forces of adaptive radiation (Hughes 1993). An animal must have an energy intake at least as high as the minimum amount required for survival, and this energy is quantifiable. This allows the study of the economics of foraging in terms of the costs and benefits in the currency of energy intake and loss. Behaviour can be viewed as having costs, for example travel time to an area of food and the predation risk incurred, and benefits, for example the energetic gains of different food types. The effects on energy intake of different behaviours, and different levels of costs and benefits, can be predicted and measured. The work of MacArthur and Pianka (1966) and Emlen (1966) predicted that natural selection would mould foraging behaviour whereby an animal would promote its fitness by maximising its net rate of energy gain. This was the first reference to what is now known as optimal foraging theory, the basis of behavioural modelling.

The study of seabirds in the marine environment.

The study of seabirds can be rewarding, but can pose a number of problems to the ethologist. For studies on breeding, the seabird's tendency toward large concentrated colonies of often many thousands of individuals can allow the study of many breeding pairs at once. The downside of this is that these colonies are often relatively inaccessible and situated in remote regions. Such large colonies are often extremely prone to disturbance and gaining access to the nest site has to be undertaken with extreme care. Despite this, seabird colonies have proved a fruitful place to study aspects of behaviour such as coloniality (Danchin *et al.* 1998) and the production of eggs (Monaghan *et al.* 1998, Royle *et al.* 1999).

The life history strategies of seabirds are often characterised by longevity and low annual reproductive output. This can also allow the long-term study following individuals returning to a predictable location, and looking at the effects of age and overall reproductive success.

Seabirds forage over extremely large areas on often patchy and hard to predict resources. This has made it difficult to accurately locate foraging areas and to thus draw associations between the environment and the behaviour of seabirds. The advent of remote tracking equipment such as radio telemetry, and more recently satellite tracking, has opened up a huge field of research. Devices such as these, coupled with depth recorders and gut temperature probes have shed light on the previously unknown at-sea behaviour of seabirds (Weimerskirch *et al.* 1997, Wanless *et al.* 1988b, Stokes & Boersma 1998). Data can be collected on the foraging location (Wanless *et al.* 1991), the number of dives made (Monaghan *et al.* 1994), the depth of dives (Wilson *et al.* 1991), the amount of food ingested, the underwater swimming speed (Wilson *et al.*

1996), body temperature (Culik *et al.* 1996) and the water temperature (Weimerskirch *et al.* 1995).

Such information has the potential to tell us much about the marine environment (Monaghan 1996, Montevecchi 1993), especially the abundance of fish stocks which are difficult to assess by other methods. The breeding performance and the foraging effort varies with food abundance and distribution (Monaghan *et al.* 1994, Montevecchi & Tuck, 1987). These principles can be applied to studies examining the long-term influences of climate on the populations and diet of seabirds (Montevecchi & Myers 1997).

This thesis aims to examine the relationships between an inshore foraging seabird, the Black Guillemot *Cepphus grylle*, the physical characteristics of the foraging areas it utilises and its breeding success. The study was conducted on several levels. Firstly, I examined the breeding biology of Black Guillemots at the Papa Westray colony. Information was collected on the physical characteristics and numbers of eggs and chicks (Chapters 3 & 4) as well as information on parental provisioning (Chapters 3 & 5). Secondly, the individual behaviour in relation to foraging was examined by the use of radio telemetry (Chapters 5, 7 & 10), investigating individual differences in competitive ability. Thirdly, the foraging distribution of the whole population was examined by the use of transects of the inshore waters of Papa Westray (Chapters 6, 7 & 9). Fourthly, the physical characteristics of the inshore waters, including the foraging sites, were examined (Chapters 8, 9 & 10).

Using these data I hope to be able to show that, by studying all of the important factors involved in the breeding of these birds, seabird species are dependant on very specific physical conditions and that individual birds are able to adapt behaviourally in different ways according to their ability. This can have important effects on the breeding success both for individuals and for the population as a whole. I also hope to show that the study on a population level can be useful in defining important habitats, and can be very helpful in the practical conservation of such a species.

Chapter 1

Part 2

The Black Guillemot, *Cepphus grylle.*

This member of the *Alcidae* is a small wing propelled diving seabird. It is a circumpolar species, occurring close to the ice cap at the northern end of its range. It nests under boulders, in crevasses and in burrows and lays 1-2 eggs. The Black Guillemot is shown on Figure 1.

The *Alcidae* are a family of wing propelled diving seabirds whose distribution is circumpolar in the northern hemisphere; the ecological counterparts in the southern hemisphere being the Penguins (the *Spheniscidae*). The family consists of twenty-two living species divided into thirteen genera. The family is characterised by having dense waterproof plumage; are mostly black and white, commonly with colourful bare parts and head ornaments. All alcids are skilful swimmers using their wings to "fly" underwater. Large alcids feed mainly on fish, captured by pursuit diving whilst smaller forms feed chiefly on plankton. There is a large variation in breeding biology, with nesting habitat ranging from vast colonies on exposed cliffs to single nests on the branches of trees.

Cepphus Guillemots form a subsection of the alcidae. This consists of three species, The Black Guillemot, *Cepphus grylle*, the Pigeon Guillemot, *Cepphus columba* and the Spectacled Guillemot, *Cepphus carbo*. The Black Guillemot and the Pigeon Guillemot have ranges which overlap (in the Bering Sea), the Black Guillemot occurring in both the Atlantic and the Pacific whilst the Pigeon Guillemot and the Spectacled Guillemot occur only in the Pacific.

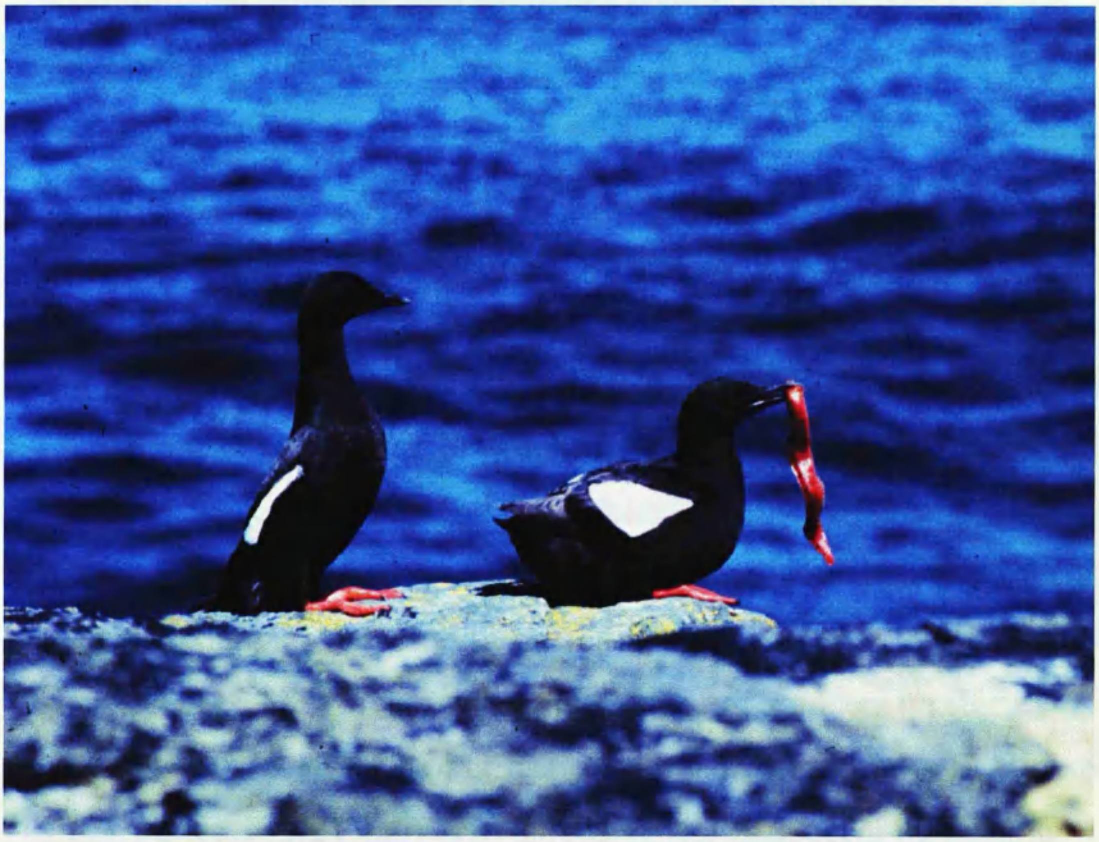

Figure 1. The Black Guillemot. Shown are two Black Guillemots on the Holm of Papa Westray. The right hand bird carries a butterfish, *Pholis gunnellis*.

Distribution

Black Guillemots occur from the edge of polar ice (>88°N) down south through subarctic into temperate coastal areas on both east and west coasts of the Atlantic, see Figure 2. It is found mainly in inshore, inlet and fjord waters and nests on adjacent coastal land. In the north of its range, the Black Guillemot commonly feeds in the gaps between drift ice and along the edge of pack ice, advancing north with the thaw. The altitude of nests can vary considerably, as can the type of nest habitat utilised. Elevations of nest sites include from near sea level across most of its range to up to 150m in Greenland (Salmonsen 1950), and 600m in Spitsbergen. Nest sites are generally found in close proximity to the sea but can occur as far as 3km inland in Spitsbergen although this is an extreme example. Nest sites occur for the most part in natural crevices such as caves, blow-holes, under fallen slabs or boulders on storm-beaches, in scree or talus or utilising rabbit burrows (Cairns 1978, Asbirk 1979, Petersen 1981, *pers obs*). Breeding sites can occur on inshore islands, or on skerries, given suitable nesting habitat.

In summer, the Black Guillemot generally stays close to the breeding colony but in winter can be found as far north as unfrozen water occurs. In the North Sea, Black Guillemots breed in considerable numbers all around the coasts of Orkney and Shetland, and in lesser numbers on the north-east tip of Scotland (Tasker *et al.* 1986), see Figure 3. During the summer birds observed in this study were entirely restricted to inshore waters in the vicinity of the breeding colony, a distribution consistent with the findings of the Seabirds at Sea Group (Tasker *et al.* 1986). In winter, dispersal was minimal, with only four sightings in four years of the study of birds in offshore waters (in this case greater than 18km).

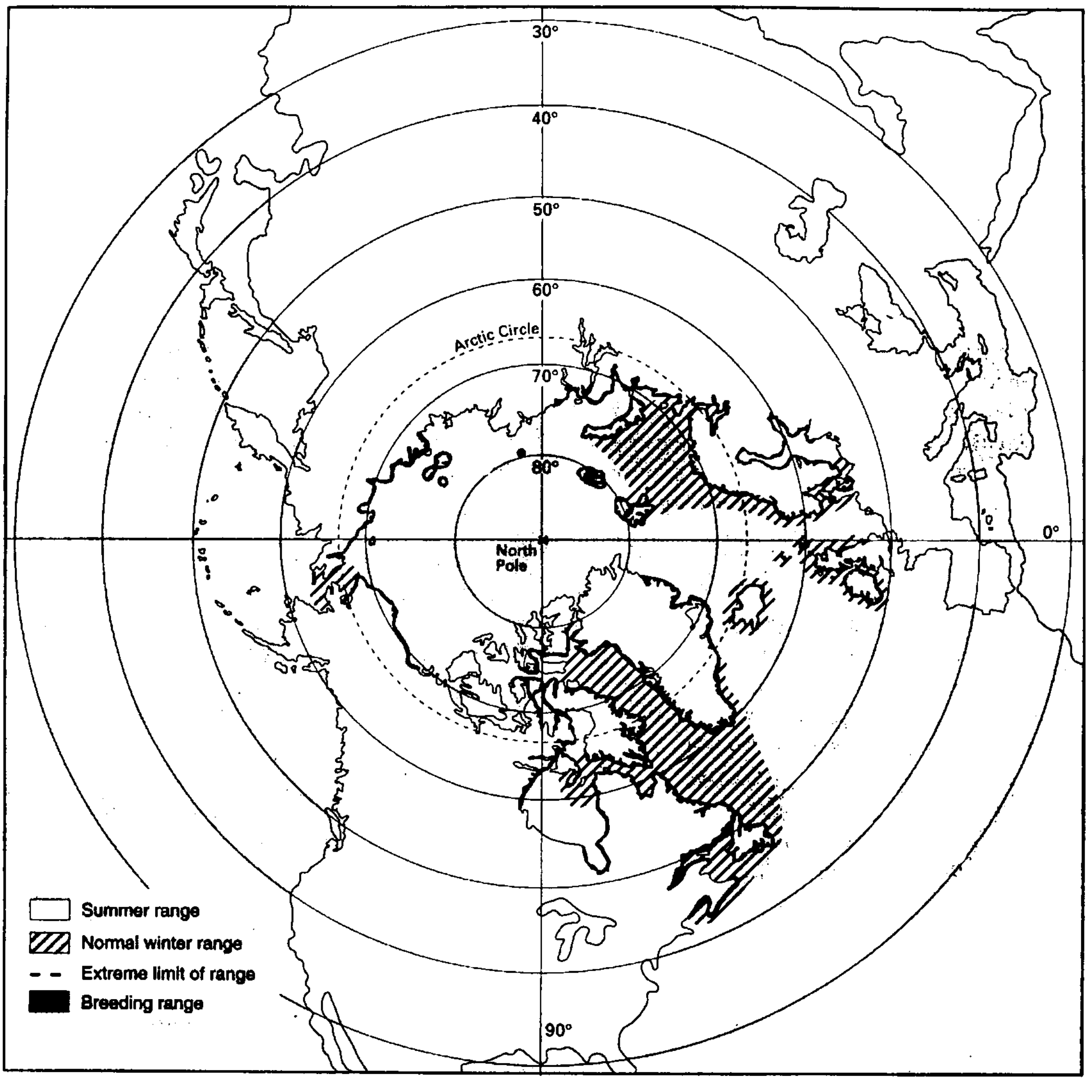

Figure 2. The global distribution of the Black Guillemot, *Cepphus grylle.*

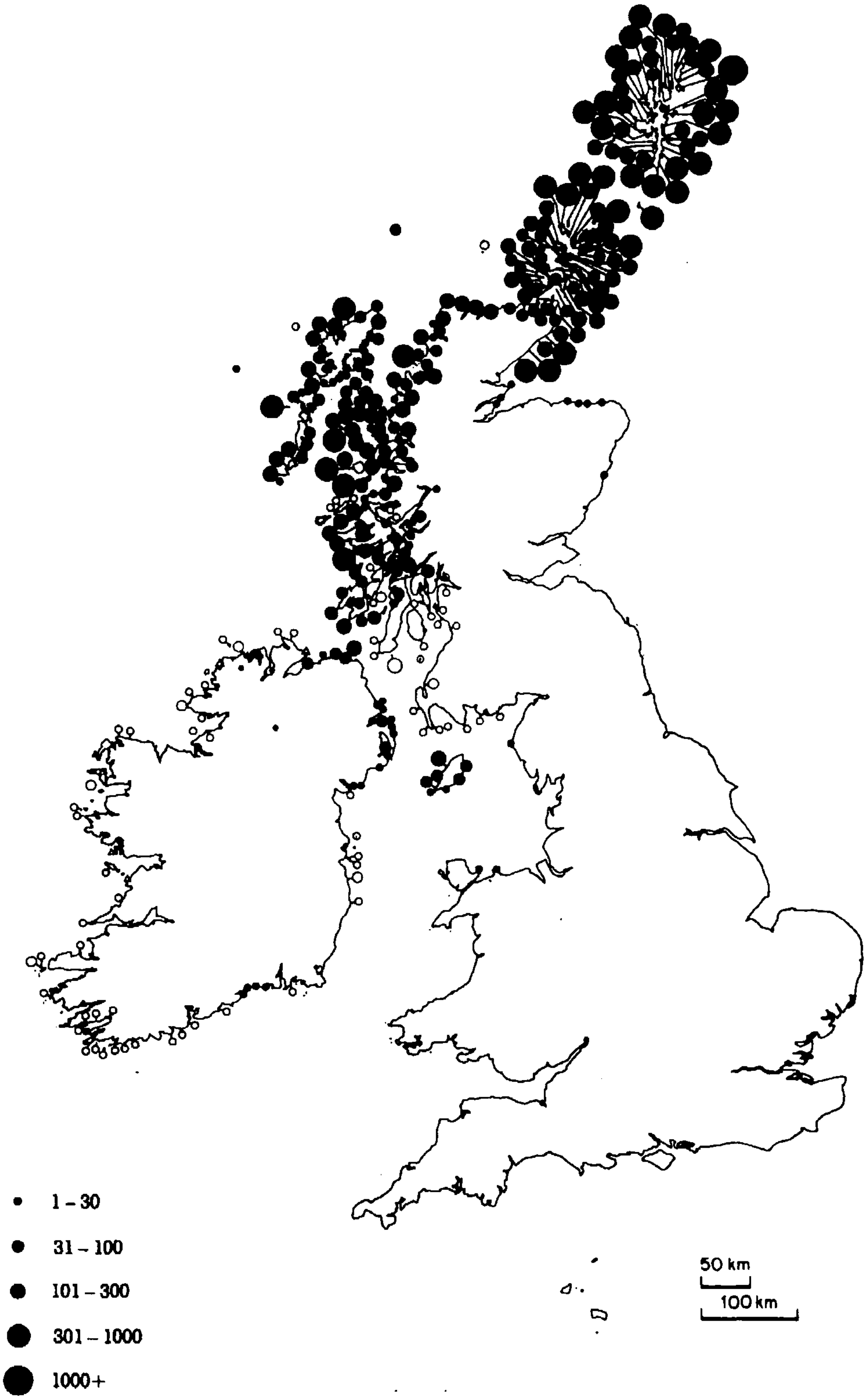

Figure 3. Distribution of breeding Black Guillemots around the British isles (after Lloyd *et al.* 1991). Closed circles were surveyed in April / May, open circles were surveyed in June.

Food

Diet varies across range. In the north (Arctic), a high proportion of the diet is made up of crustaceans whereas in the south, the diet comprises mainly of marine fish. Prey makeup can vary considerable according to availability, and birds can switch rapidly between prey types as the need arises. As a result of this there can be considerable variation in diet between populations and individuals, both spatially and temporally. Black Guillemots are pursuit divers, catching prey by diving from the surface and catching a single prey item which is eaten on the surface (*pers obs.*) or delivered to the chicks carried crosswise in the bill.

Black Guillemots are for the most part solitary foragers but there are reports of groups of birds fishing for shoaling fish co-operatively (Kaftanovski 1951). There are also reports of kleptoparasitism of conspecifics (Slater & Slater 1972; Petersen 1981). After capture, a prey item is often dropped and re-captured, sometimes involving a short dive (Storer 1952; Kozlova 1957; *pers obs.*), possibly to facilitate correct orientation in the bill for delivery to the young. Prey items are often killed before delivery to the nest; items such as hermit crabs can be shelled and the claws removed shortly after capture (Petersen 1981). Butterfish *Pholis gunnellis* delivered to the Papa Westray site have been observed to have damage marks at the back of the skull when recovered, indicating that they have been delivered dead to the chicks (*pers obs.*), although the same species has been observed being delivered alive (Petersen 1981).

Adult diet is more difficult to assess than the diet of the young. Adult birds have been observed consuming prey on the surface of the sea directly after a foraging dive (*pers obs.*). In Shetland, Ewins (1990) examined the stomach contents of 7 birds washed up on beaches.

Stomachs were found to contain evidence of *Neris,* Amphipods, *Eupagarus & Galathea,* Nematodes & Coelenterates as well as one incidence of a Butterfish, *Pholis gunnellis.*

Little is known of adult diets outside the breeding season. Sutton (1932) found crustaceans in the stomachs of 15 birds collected off Southampton Island, Hudson Bay in late February. Madson (1957) collected birds in Denmark and found two-thirds of the diet consisted of fish (gobies, herring and cod), the rest crustaceans (crabs and shrimps). Smith & Hammill (1980), collecting off south-east Baffin Island in late winter found 83% of stomachs containing larval cottid and liparid fish, 57% *Parathemisto libellula*, 43% mysids and 17% squid as well as a few other crustaceans. Ewins (1990) dissected the stomach contents of birds killed in the Esso Bernica oil pollution incident in Shetland in 1979, which occurred outside the breeding season (early spring). He commonly found in the stomachs of these birds polychaetes such as *Neris,* crustacea (*Galathea* spp.) and unidentified Reptantia, as well as gastropods and some small unidentified fish. This makeup of prey species was reflected in the stomach contents of other Black Guillemots found intact on beaches in winter in Shetland and Orkney. Black Guillemots have been observed in the pre-breeding season feeding opportunistically at fishing vessels fishing commercially for sandeels, along with other seabird species (Ewins 1989).

Nesting & breeding

Black Guillemots nest in concealed sites, commonly under boulders, in crevices, on cliffs and in caves. They will also nest in disused rabbit burrows and have been reported to use man-made structures such as fish boxes to form nest sites, for example in Norde Rønner 43% of nest sites were of this type (Asbirk 1979). Availability of suitable nest sites can be a limiting factor in this species; in Alaska, human debris has allowed the colonisation of areas which previously had no breeding Black Guillemots (Divorky *et al.* 1974).

The Black Guillemot is unusual amongst the *alcidae* in that it generally lays two eggs, although many breeding birds, particularly younger individuals, will lay only a single egg clutch. Eggs are generally laid three days apart but can rarely be as much as ten (Harris & Birkhead 1985). The chicks are semi-precocial and fledge after approximately thirty days (Harris & Birkhead 1985). The chicks are fed by both parents after the second day when they become able to thermoregulate, and are thus able to be left unattended. Chicks are reported to be enticed into the sea by the parents and starvation is likely to play a role in this, as chick weights reach a peak a few days before fledging (this study) and drop off until the chick fledges. Chicks disperse only short distances and are often at first accompanied by an adult bird.

Diving

Birds dive in shallow water, diving to the bottom to feed mostly on demersal prey. Birds have been recorded diving in water 1-8m depth (Masden 1957), 5-20m (Bergman 1971), c.10m (Belopol'ski 1957). Dive durations show some variation, dive durations quoted include 45.3s (30-75s, n=20) with a surface interval between dives of 15.1s (4-45s, n=14) (Nicholson 1930); dive duration 30-35s (25-40s), surface interval 7-10s (Bianki 1967); dive duration 30-60s, surface interval c.15s (Hyde 1937).

Threats

The main threats to Black Guillemots come from pollution and exploitation of the environment although the most serious threats to the breeding areas are the introduction of predator species such as Mink, *Mustela vison*, Rat, *Rattus norvegicus,* Ermine, *Mustela erminea* (Cairns 1985) and Otter *Lutra lutra* (Ewins 1985). The impact of human disturbance is, due mainly to the remote nature of the nesting habitat, minimal in terms of serious impact. Other threats include pollution from oil spills, the Black Guillemot being particularly vulnerable to inshore oil spills either by ingestion (Peakall & Hallett 1980) or contamination of feathers. Black Guillemots have been killed in fishing nets (Heubeck and Richardson 1980, Petersen 1981) although the examination of these has provided valuable information on the diet of adult birds in British waters (Ewins 1990).

Chapter 2

Methods

This study was conducted on the Holm of Papa Westray, Orkney. The island of Papa Westray is the furthest north-west of the Orkney islands, situated at 59°21'N, 2°53'W (see Figure 1). The study colony is located on the Holm, a small uninhabited island off the east coast of Papa Westray. This colony comprises approximately 60 pairs of breeding Black Guillemots , nesting generally under boulders on the top of the beaches on the north and east coasts of the island. This is one of the largest accessible Black Guillemot colonies in the British Isles (Lloyd *et al.* 1991). The largest concentration of nests is situated at the north end of the island on beaches facing north-east, probably due to the availability of many suitable nest sites in the boulder beaches in this part of the island (see Figure 2).

Access to the site of the colony during the study was by boat, the island being landed on each day, weather permitting, departing from a small pier on the east coat of Papa Westray. A description of the boat is given with the methods for sea surveys (this chapter). The location of the island afforded a sheltered crossing when winds were from an easterly or westerly direction, but strong wind from the south brought a large swell into the sound and frequently made the crossing dangerous. On such days travel to the study colony was not attempted, and if conditions became unfavourable during a visit, the work would be abandoned in order to evacuate the island. This required keeping a close watch on the weather and my years of experience of sailing, and working in the northern isles proved invaluable, as did keeping a close watch on national and local forecasts and studying the pressure charts. This was

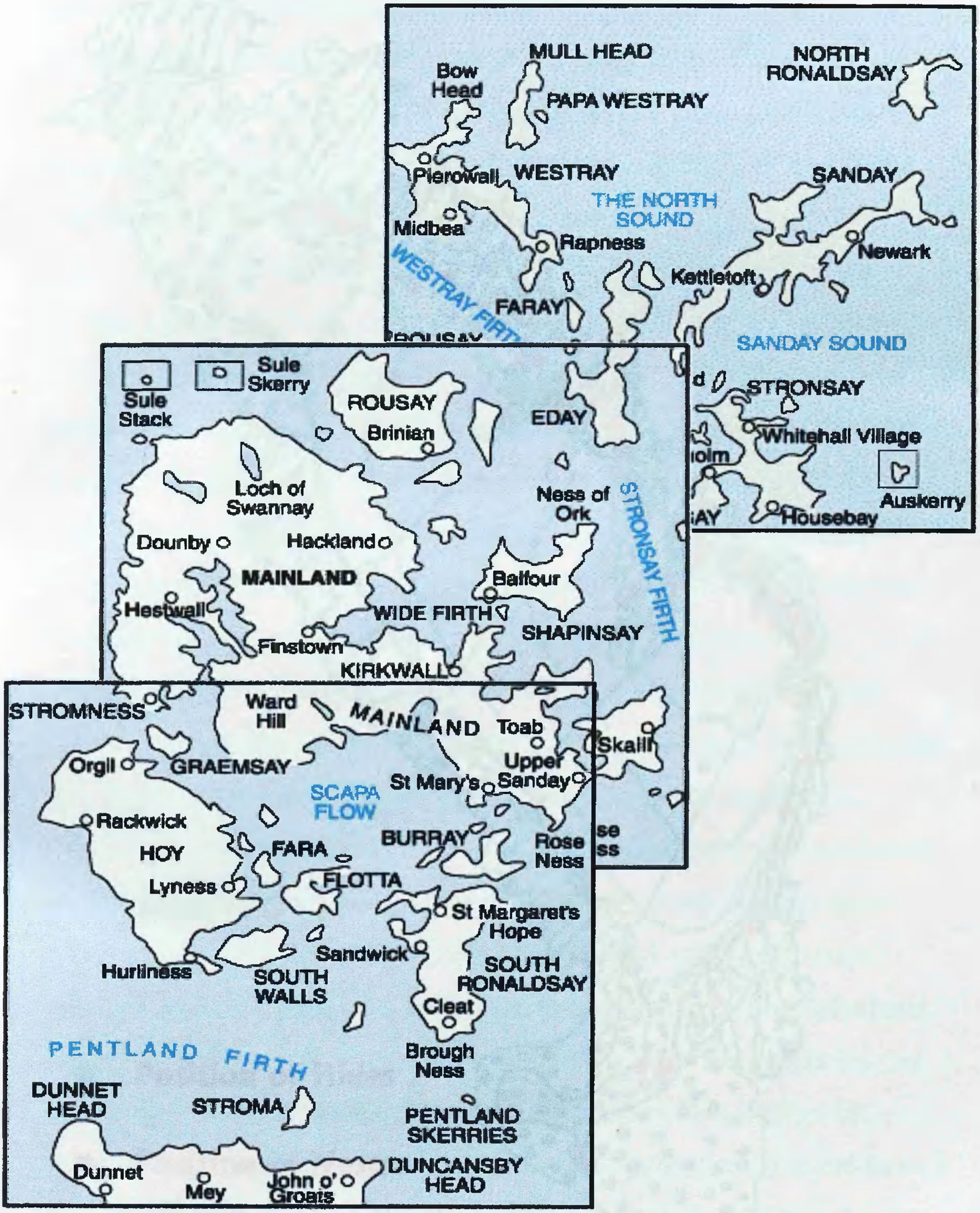

Figure 1. The position of Papa Westray in the Orkney islands. Papa Westray is located on the top left of the map.

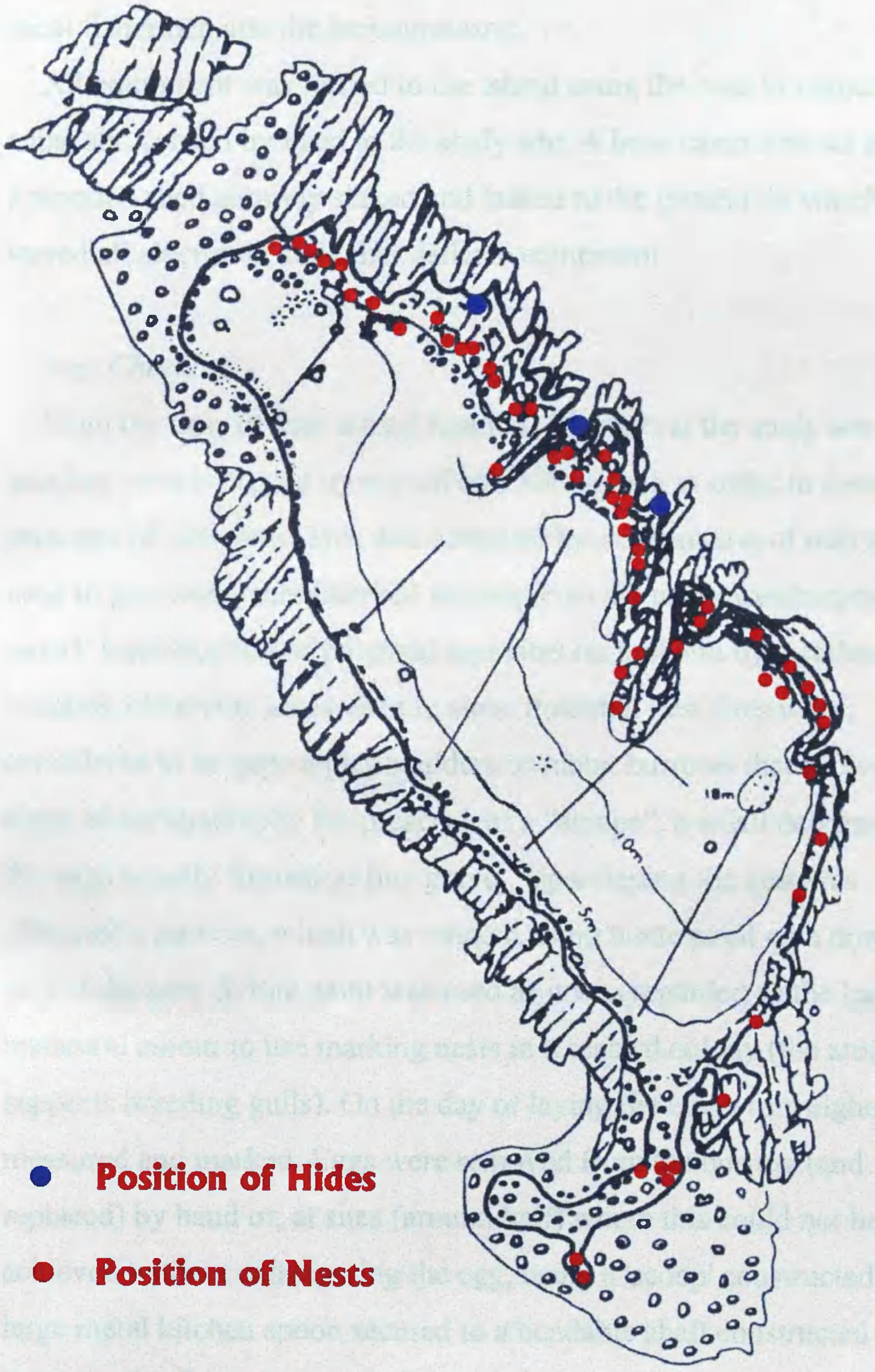

***Figure 2**. The location of nest sites and hide on the Holm of Papa Westray*

backed up with frequent discussions of the weather and local tides with local fishermen and the harbourmaster.

All equipment was ferried to the island using the boat in numerous trips, and carried by hand to the study site. A base camp was set up using a wooden shed securely staked and lashed to the ground, in which was stored all electronic and other delicate equipment.

Nest Checking.

From the time of first arrival (approx. 7th May) at the study site the beaches were surveyed by myself and Mark Cook in order to detect the presence of nest sites. This was achieved by examination of nest sites used in previous years (marked inconspicuously using weatherproof paint), identification of potential nest sites on foot and by watching the beaches, observing birds visiting sites. Potential nest sites were considered to be gaps under boulders or rabbit burrows that showed signs of occupation by the presence of a “scrape”, a small depression for the eggs usually formed in fine gravel. Upon laying the nest was allocated a number, which was marked using white paint on a prominent part of the nest. White paint was used as it was regarded as the least unnatural colour to use marking nests in a seabird colony (the area supports breeding gulls). On the day of laying the egg was weighed and measured and marked. Eggs were removed from the burrow (and replaced) by hand or, at sites (around half) where this could not be achieved without endangering the egg, using a 'scoop' constructed from a large metal kitchen spoon secured to a bendable shaft constructed from three layers of fencing wire. This device, used with care, proved effective and no eggs were lost through accidental breakage during the study. Weighing of eggs was carried out using an Ohaus portable electronic balance reading to 0.1g. Measuring of eggs was carried out both longitudinally and transversely using Vernier calipers to measure the widest part of the eggs in both directions (see Figure 3). The first laid egg was marked using a waterproof marker pen with an "a", the second marked with a "b" in order to distinguish them within clutches, and the date of laying recorded. If a nest was discovered containing 2 eggs these were marked with a "1" and a "2" to allow differentiation between the eggs and excluded from any analysis involving laying date and egg laying order. Nests were monitored daily until hatching, whereafter they were monitored every 3 days. Chicks were weighed to the nearest gramme on day of hatching if possible, without exposing them to excess cold, and at 3 day intervals where wing length, tarsus and bill length were also recorded in mm. (see Figure 4). Chicks in all but the earliest stages of chick rearing are mobile, and actively conceal themselves under and between boulders. To retrieve chicks for measuring, leg-hooks constructed from fencing wire were used. These consisted of a ~1m length of wire with the end bent through 360° to form a small crook, with the mouth just wide enough to accommodate the leg above the tarsus. No chicks were injured using these devices, and they were essential in capturing well-hidden chicks. The first hatched chick was marked using "tippex" until it was large enough to have a metal ring fitted. Checking would continue until the nest was empty. In order to obtain data on fledging, chicks that disappeared after having reached an asymptoptic weight were assumed to have fledged. The youngest age at which this was recorded was 28 days. Chicks that disappeared before this stage were assumed to have died. Many chicks were predated at the nest and evidence of this was usually visible in the form of feathers and blood near to the nest entrance and the presence of this would be recorded. Nest checks were carried out outwith the times of hide-watches

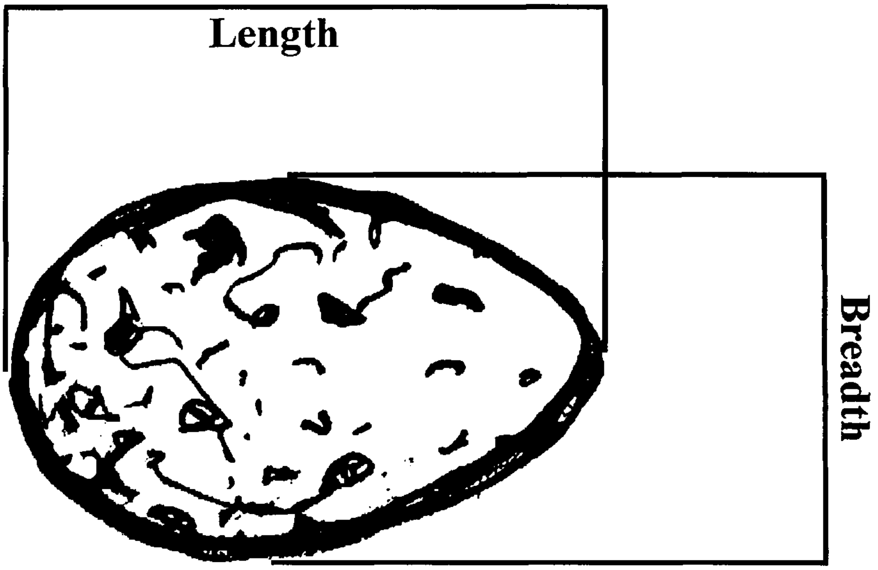

Figure 3. The axes of measurement of a Black Guillemot egg. Measurements were taken at the widest point in both directions shown.

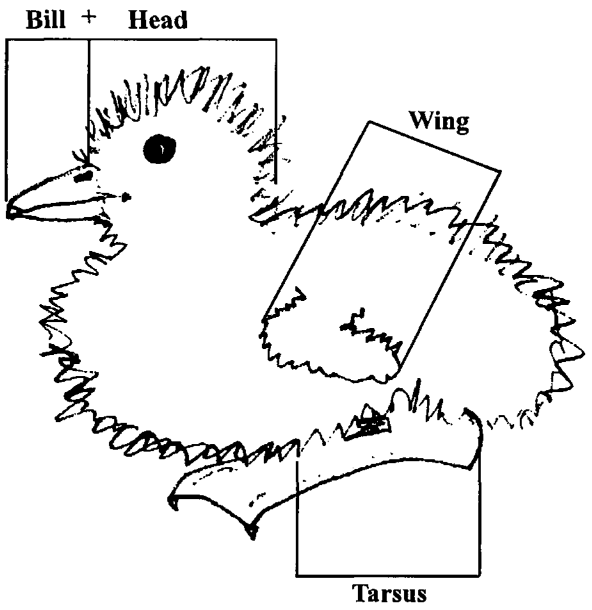

Figure 4. Chick showing measurements taken: bill, head + bill, wing & tarsus.

and I attempted to keep them to times of least Black Guillemot activity (1100-1500 hours, Ewins 1992).

Hidewatching.

3 hides were erected just above the high water mark looking up the beach towards the nest sites on the northern beaches and their locations can be seen on Figure 2. From these sites, 39 nests could be observed and it was possible to record all visits to the nest by adult birds, and the time and duration of these visits. The species of prey delivered was identified as far as possible but this was difficult due to the often rapid speed of provisioning visits to the nest. Certain prey types, however, were easy to identify, and this was true of the three main types of prey delivered. The most common prey types are shown on Figure 5. In order to collect information on the quantity and size of fish delivered to the chicks the size of prey items was also recorded. Prey size was estimated by comparing each item with the gape size of the adult carrying it, providing a measurement that can easily be converted into centimetres, given knowledge of the bill length in adult Black Guillemots (approximately 55mm in birds captured at this colony).

Hide watching was conducted in 3-hour watches, the observer allowing 10 minutes after entering the hide before starting observations to begin. The birds were relatively used to disturbance as the island was visited reasonably regularly by tourists visiting the 3500-year-old burial chamber in the middle of the island. Similarly, if a disturbance of the breeding colony occurred during a watch, the same period of time was left after the disturbance ended before the watch was resumed.

Sea Surveys.

In order to obtain information on the use of foraging sites around the inshore waters of Papa Westray it was necessary to take to the water in a

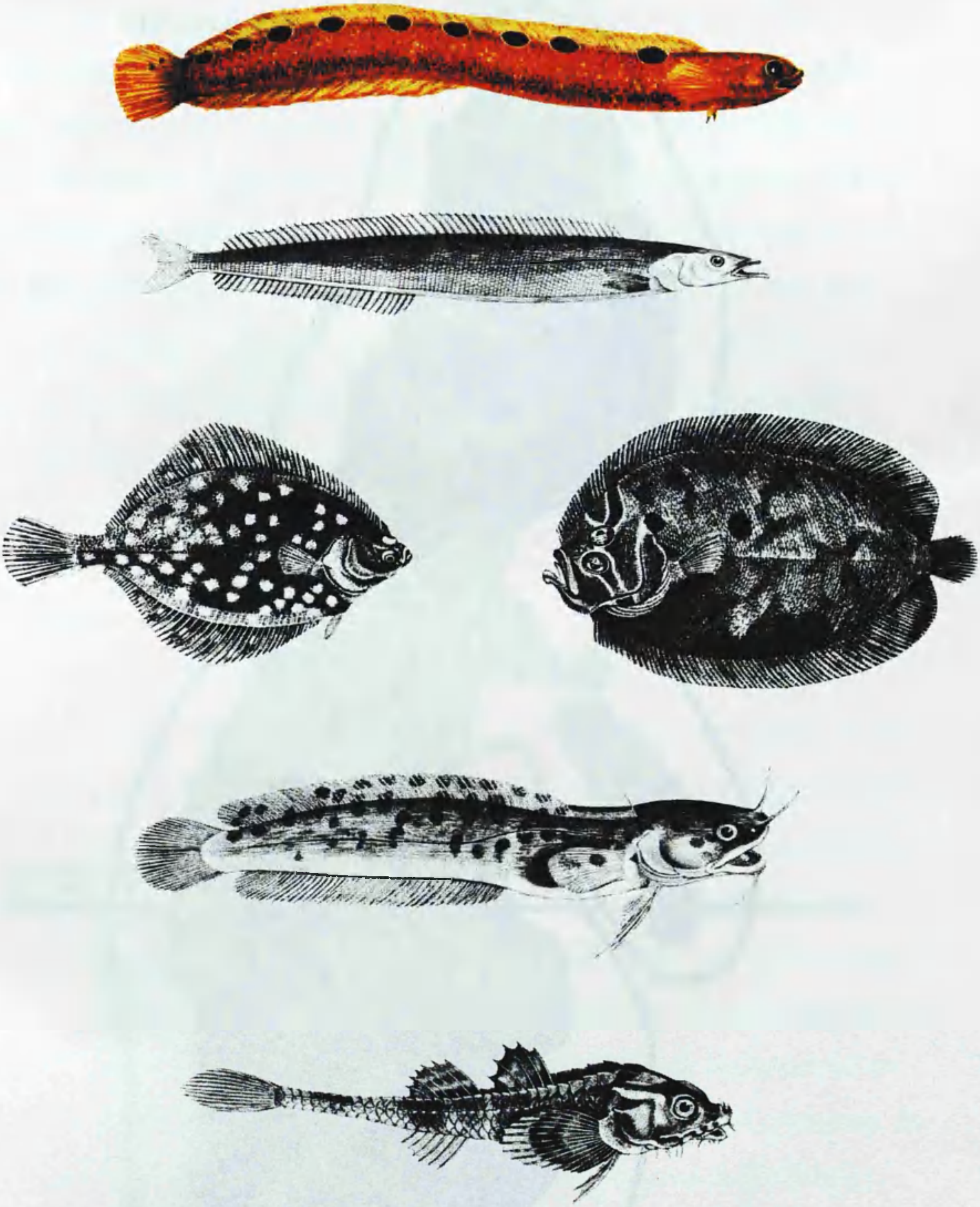

Figure 5. Some prey types of the Black Guillemot at the Papa Westray colony. Species from top; Butterfish, *Pholis gunnellis*, Sandeel, *Ammodytes spp*., Plaice, *Pleuronectes platessa* & Topknot, *Zeugopterus punctatus*, Three Bearded Rockling, *Onos mediterraneus* & Armed Bullhead, *Agonus cataphractus*.

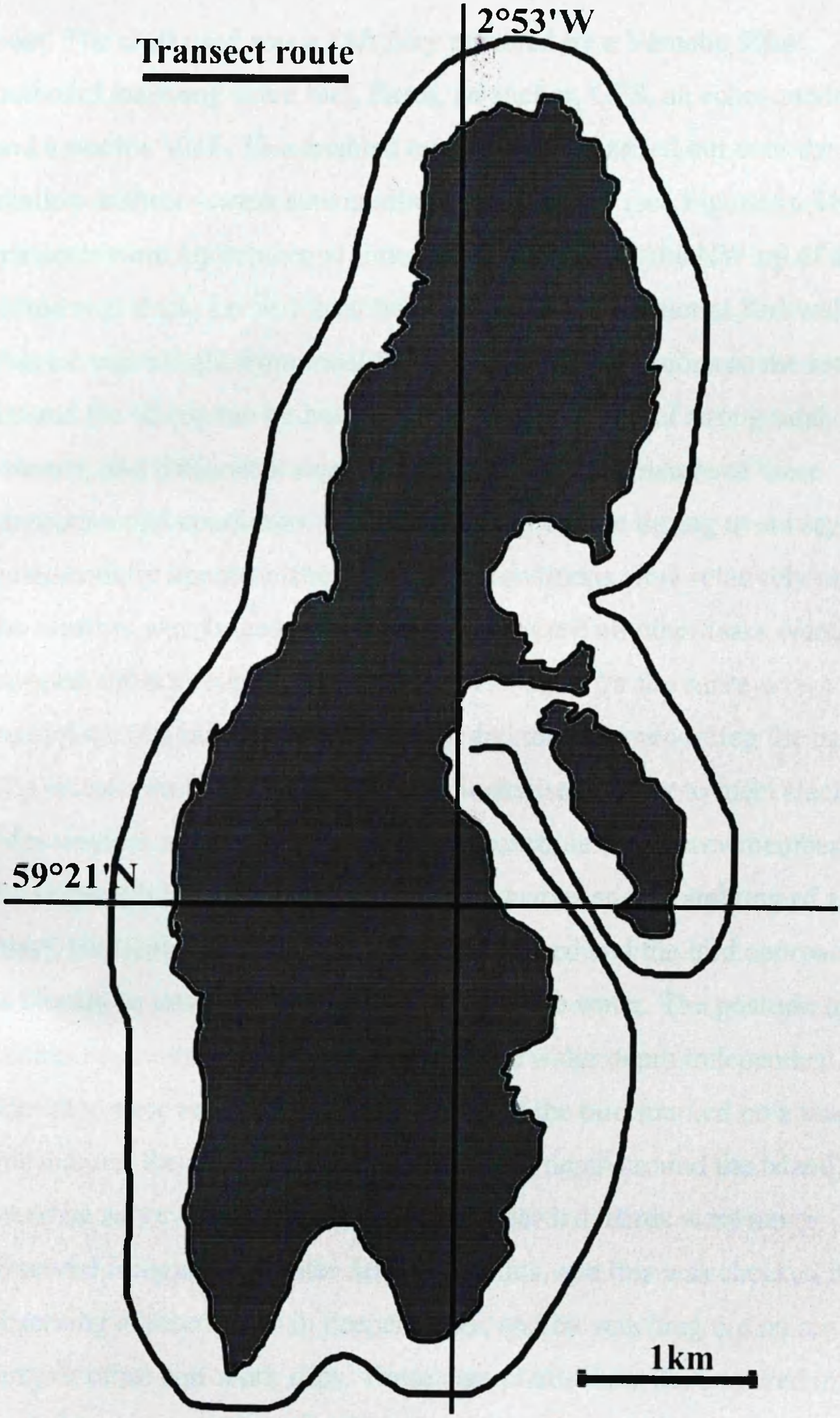

Figure 6. Transect route round Papa Westray.

boat. The craft used was a 18ft dory powered by a Yamaha 30hp outboard, carrying spare fuel, flares, an anchor, GPS, an echosounder and a marine VHF. This enabled transects to be carried out over the shallow inshore waters surrounding Papa Westray (see Figure 6). These transects were undertaken at times when the roost at the NW tip of the island was slack, i.e. at 1 hour before high and low water at Kirkwall. Advice was sought from local fishermen on the conditions as the seas around the island can be hazardous due to the nature of strong tidal streams, and lifejackets were worn at all times. The nature of these environmental conditions made it necessary for the timing of surveys to be essentially opportunistic, as suitable conditions were relatively rare. If the weather was judged to be suitable by myself all other tasks were stopped and surveys were carried out. The crew for the surveys comprised two members, one piloting and the other recording the data. The island was circumnavigated anticlockwise in order to meet slack tides without compromising the survey schedule. Each crewmember had the responsibility of watching a forward quarter and on sighting of a Black Guillemot, the speed would be decreased and the bird approached as closely as possible without putting it off the water. The position on the Global Positioning System handset and the water depth independent of tide-state were recorded and the position of the bird marked on a map. In this manner the available habitat (up to 40m depth around the island) could be surveyed and all birds present recorded. Birds were never observed foraging in greater depths than this, and this was checked by observing adjacent sites in deeper water, and by watching out on any ferry or other non-work trips. These data points were then entered into a spreadsheet using OS grid references to the nearest 10 metres.

Radio Tracking

In order to obtain information on the individual foraging behaviour of birds the technique of radio telemetry was used. This involved trapping adult birds near the nest site and attaching a transmitter beneath the tail feathers (see Figure 7) using cable ties. The birds were captured using either standing mist nets below the nest areas, by noose mats near to the nest or by "flicking". This technique involves placing a 10m mist net beneath a roost site. Two catchers would position themselves unobtrusively at each end of the net while another fieldworker chased the birds off the roost site. This was co-ordinated by radio contact, using handheld private band radios. The net was then raised just as the flying birds reached it and in this way one could catch up to 5 birds in one session. The success of this technique decreased markedly the more often it was used with birds leaving the roost site and staying away if the site was approached with a net. This was a good way to catch adult birds as it was away from the nest site and did not appear to affect the number of birds attending the roosts. Noose mats were constructed from a square of tough carpet 50 cm by 50 cm of a similar colour to the rocks at the colony. This was fitted with 36 slip nooses made from strong nylon monofilament securely attached to brass washers on the back of the carpet. The carpet was securely anchored to the ground, usually by attaching large rocks to ropes fastened to the carpet. These mats would be watched from a concealed location, often a hide, and as soon as a bird became entangled I would move to remove it. In all, the Black Guillemots at this site proved remarkably difficult to capture. Each method was quickly learned by the birds and with each time any method was used it enjoyed decreasing success, to such an extent that by the end

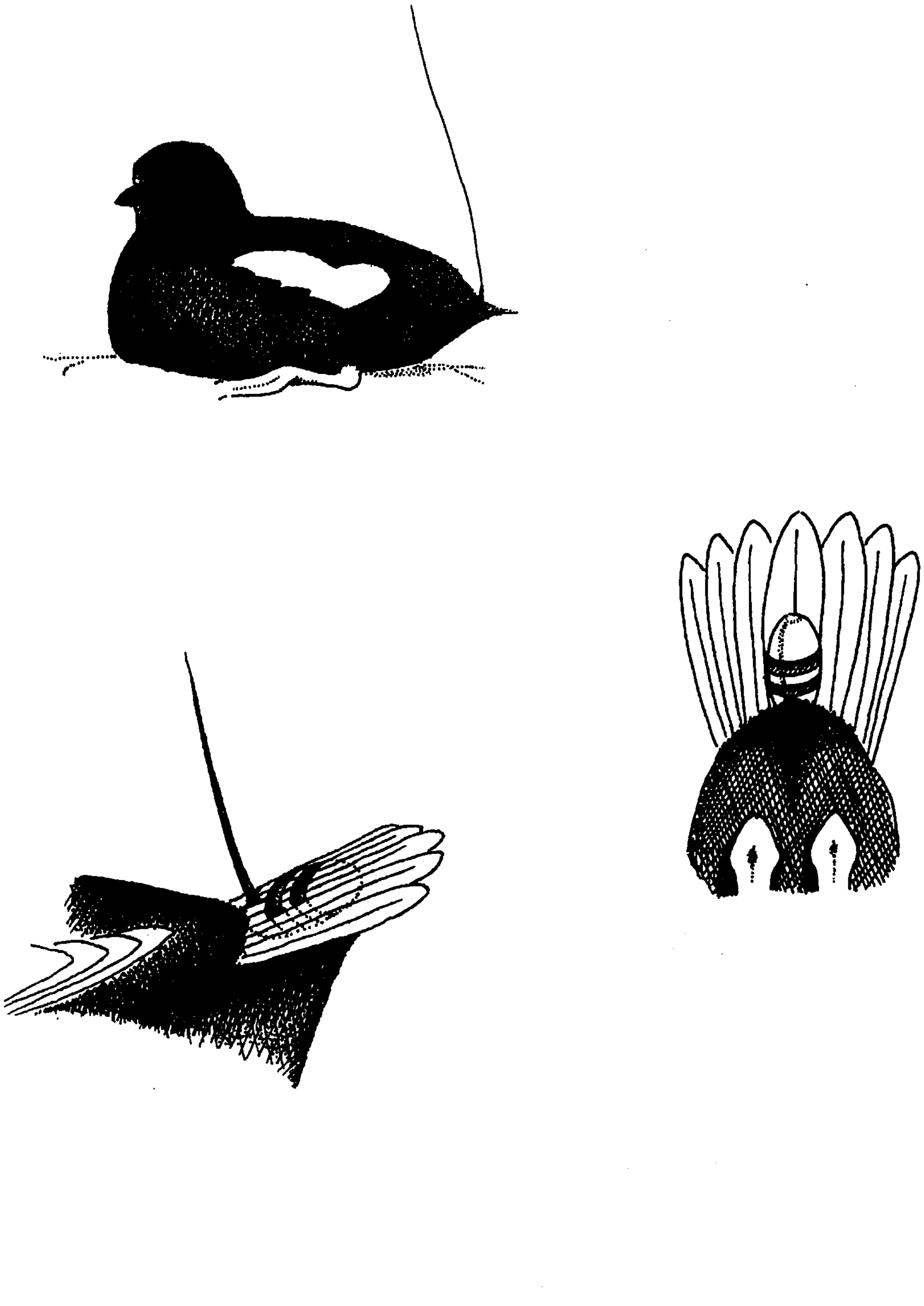

Figure 7. Attachment of radio tag to adult Black Guillemots. Top Figure shows tag in position on adult bird. Middle figure shows underside view of Black Guillemot tail with tag in position secured with cable ties. Bottom figure shows side view of tail with tag in position with tag shown dotted through tail feathers.

of the second year it was extremely difficult to catch even a few birds for attaching radio tags

The captured bird would then be measured, weighed and ringed. A colour ring combination unique to each individual was fitted to allow identification of the nest site and the activity of the individual. Three coloured Darvic rings were placed on the legs as well as a uniquely identifying metal ring issued by the British Trust for Ornithology, and the radio transmitter was attached. The tag was attached under the central 3 tail feathers and was positioned in such a way as to be partially covered by the contour feathers under the tail, thus minimising the effects of drag in the water (see Figure 7). The transmitters used were AVM single stage units, which were assembled and coated with polyester resin (Carplan two-part resin) the night before attachment. Assembling involved the attachment of a battery to the transmitter unit using conductive epoxy (RS components conductive silver epoxy) to reduce the damage to the battery of soldering directly onto the battery surface. The transmitter was then coated with a thin layer of beeswax. This was to allow the removal of the epoxy coat in the event of a tag recovery, and to assist with the waterproofing of the transmitter unit in the event of any leakage. The transmitter plus battery was then fitted with a hand made aerial constructed from 0.7mm diameter stainless steel fishing trace (used for catching sharks) sometimes referred to as "tope trace" of 50kg breaking strain. This unit was then coated with 3 thin coats of polyester resin. In order to achieve an even coat of sufficient strength to support the aerial, whilst keeping the size and weight of the tag to a minimum, the tag was dipped in mixed resin and rotated by hand until the resin set (approx. 3-4 mins). This required great concentration and manual dexterity whilst trying not to inhale the toxic fumes emitted by the resin! A layer of self-amalgamating tape was applied to the

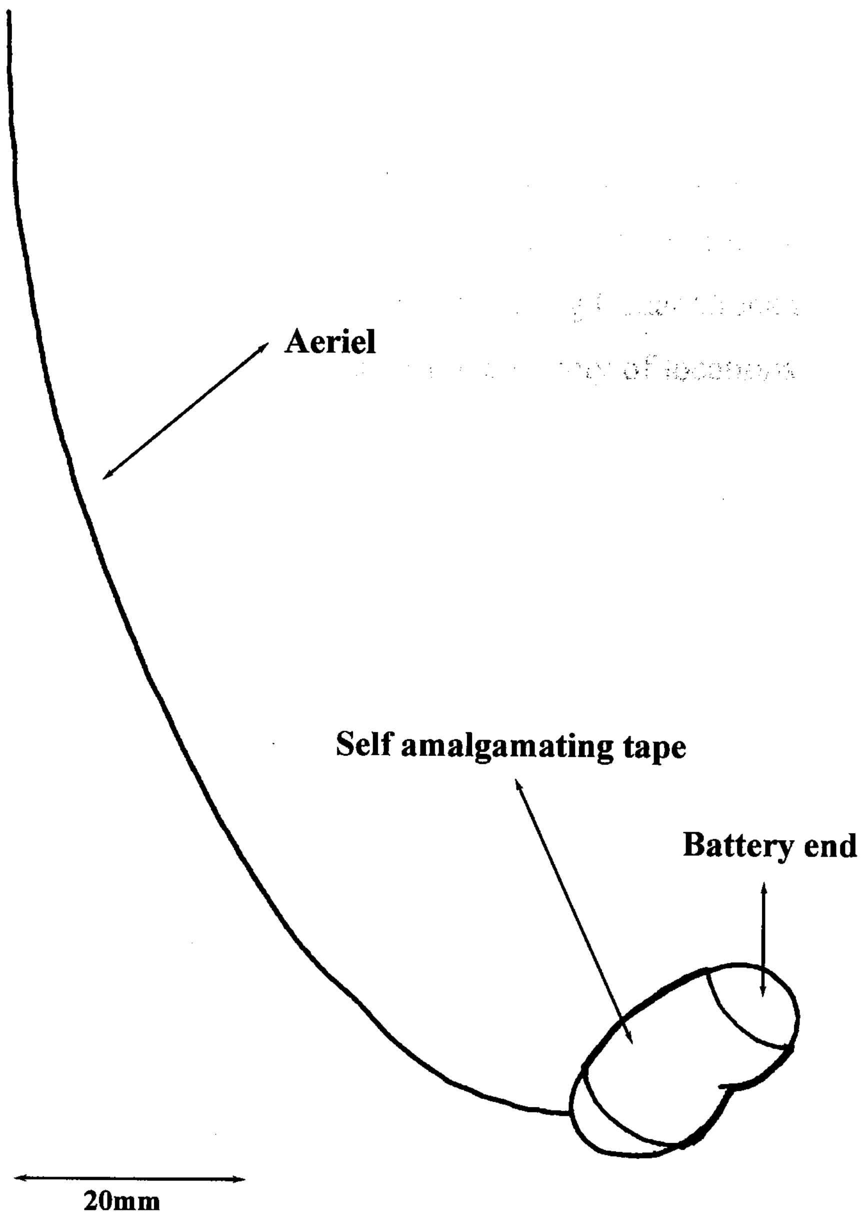

Figure 8. Completed radio tag (see text for details of construction).

completed tag in order to provide grip between the cable ties and the feathers. A completed tag can be seen on Figure 8.

Tags had a battery life of approximately 2 weeks and when completed weighed 3.5g, <1% adult body mass. These transmitters emitted a single pulse every 0.8 seconds on a specific frequency in the 173mhz waveband. These signals were picked up using Cedar Creek receivers attached to 8 element Yagi aerials from a variety of locations around the coast of Papa Westray, providing coverage of all the inshore waters. These aerials are directionally sensitive allowing accurate measurement of the magnetic bearing of the bird from the observer. The readings obtained can be used to calculate the location of a tagged bird, by triangulation (see Monaghan *et al.* 1992), or by inferring from the bearing, the signal strength and the depth of the water in the direction scanned (see Wanless *et al.* 1991). Data were collected on the location, the duration of dives (the signal cuts out underwater allowing measurement of the sub-surface interval (Trivelpiece *et al.* 1987, Wanless *et al.* 1988a, Wanless *et al.* 1988b)) and the subsequent recovery time.

Receivers were deployed as mobile tracking stations, aerials being either mounted on the roof of a landrover, or on a tripod depending on the accessibility of the chosen site. The landrover set-up involved the use of a twin aerial array connected via a null-peak switchbox (supplied by AVM) which allowed greater accuracy, 95% confidence intervals for single radio fixes was ± 1.9° of the estimated bearing, 90% of the resulting error polygons were less than 0.1km^2. Range was considered to be approximately 1 km given typical conditions. Set-ups were tested using a land-based beacon of known location to test accuracy and to calibrate bearings. Radio watches were than carried out on the chosen area of sea for periods of 3 hours with receivers scanning the frequencies of fitted tags in order to identify the location of each bird's preferred foraging site. Operators were in radio contact for the duration of tracking to allow co-ordination of tracking effort, birds being triangulated regularly and continuously followed as far as possible. On identification of a tagged bird the tracker would follow this until the signal was lost, logging dive times and taking regular bearings. At the start and finish of each radio watch the bearing of a known location land beacon was taken to calibrate the directional readings obtained during tracking. The Black Guillemot proved to be a difficult species to radio track, certainly compared to other species that I have tracked such as shags and kittiwakes. This, I believe, is largely due to the habit of foraging close in to the shore, often under cliffs making the reception of good signals often extremely difficult. Also, at this study site there were few suitable sites for tracking that were of a sufficient altitude to allow a good line of sight down onto the birds. This problem was most noticeable when waves were high. In such situations the signal from birds sitting on the water became very indistinct and the collection of good data was difficult.

Diving Surveys

In order to collect information on the underwater habitats it was necessary to carry out some form of survey of the inshore waters around Papa Westray. Initially it was expected that the Joint Nature Conservation Committee (JNCC) would be surveying the area in the summer of 1997, and I had obtained agreement that I would be able to use this data set. In the late 1996 it became apparent that this work would not be carried out during the following year and so it became necessary for me to find an alternative way of surveying the sites. I then wrote a proposal to Scottish Natural Heritage (SNH) in order to obtain funding for the charter of a dive vessel and a compressor, which was accepted. I was then able to organise a party of experienced divers with the help of the Marine Nature Conservation Society (MNCS).

The dive party consisted of 15 MNCS members and diving was carried out between 14th and 19th July 1997 from the MV Challenger. Four pairs of divers worked from the Challenger, two pairs and one three worked from the shore. In all, 56 seabed surveys were conducted in 5 days of diving (14th – 19th July). The survey sites were chosen to represent all levels of Black Guillemot usage (see Chapter 6), from the areas with the highest concentrations of foraging birds through those of low concentrations to areas which had no recorded Black Guillemots on the water. The divers were carrying out the surveys according to the methodology described in SNH document ISBN 1 85397 121 9. This is a methodology used for the surveying of the seabed by divers and involves the recording of the physical characteristics of an underwater habitat carried out in the direction of tidal flow. The surveys took the form of transects, usually of about 100m in length. The divers recorded presence of all species encountered in each habitat type encountered, the relative abundance of these, the topography of the seabed, the depth of water dived in and water state (currents and tide (in knots), turbidity (metres visibility)). The use of a relative abundance scale, as opposed to absolute numbers, for recording species corrects for differences in survey length and observer bias. The position of each survey point was accurately recorded using differential Global Positioning System (GPS) and the data sheets were sent to the marine section of the JNCC for entry into the national database. These data sets were returned to me, with each survey being allocated one or more unique habitat codes describing the habitat type.

Divers were instructed to collect information on the relative abundance of fish species, with special attention to those prey species typically delivered to the nest by Black Guillemots. The Marine Nature Conservation Review relative abundance scale was used. This is a 7-point scale from "present" to "superabundant", a standard technique in surveys of this type. This scale was used for all species observed. For each site surveyed an index of diversity was prepared for each habitat type. In all, 22 discrete habitat types were recorded across all the surveys. All surveys were carried out in good weather conditions for obvious safety reasons.

All data were entered into SPSS (version 7.0) for analysis, with spreadsheet data being manipulated using Microsoft Excel.

Further details of specific methods can be found in the relevant chapters.

Chapter 3

Breeding Performance of the Black Guillemot at the Holm, Papa Westray.

Introduction

The study of the breeding performance of animals is an important tool in understanding the selection pressures that have shaped their life history patterns. An underlying assumption of modern ecology and behavioural ecology is that lifetime reproductive success is maximised. Thus, an assessment of the breeding performance will reveal something of factors that influence the availability of resources as it is on these that the breeding performance of an animal ultimately depends.

The nature of the breeding biology of birds facilitates the measurement of reproductive output (Greenwood *et al.* 1993). Birds lay eggs, which are easily measurable in terms of their weight and size and increasingly in terms of composition of the whole egg either by use of invasive or non-invasive methods (Williams *et al.* 1997). These eggs are laid on land in a nest, a central point which allows the researcher to collect information on the adults involved, the amount of time they spend on the eggs and the total output in terms of egg numbers. The hatching of chicks can also, with regular monitoring, be accurately recorded and the chicks of many species will be accessible at the nest until fledging, so growth rates can be measured. Also, it is often possible to record the amount of food delivered to the nest by provisioning adults. The linking of reproductive output to the age of known birds has shed light on age-specific fecundity, now recognised as an important factor influencing breeding success (Hipfner *et al.* 1997).

Fluctuations in the reproductive success of birds, and in seabirds in particular, have been linked to variation in the natural environment. In seabird populations, breeding success has been linked to a number of environmental variables. Sea temperature, over fishing and prey availability have all been shown to affect the breeding success in a number of seabird species (reviewed in Montevecchi 1993).

Effects of the above are most easily detected among species that lay multi-egg clutches (Monaghan *et al.* 1989). Variation in productivity in species that lay single egg clutches is much less (Hatch & Hatch 1990), although the effects of environmental conditions can be shown by the study of variation in other aspects of their biology such as foraging effort (Monaghan *et al.* 1994).

In this chapter the breeding performance of the Black Guillemot colony on the Holm of Papa Westray over a two-year period is described. This is compared to published data on other colonies, and the factors that might influence any differences are considered.

Methods

The breeding colony on the Holm of Papa Westray consists of approximately 60 breeding pairs of Black Guillemots. This is one of the larger accessible colonies in the British Isles and had been the subject of previous studies (Gray, M.; MSc. Thesis, University of Bangor. Monaghan, P. NERC research project). The population has been consistently ringed as chicks by the RSPB on one day a year since 1983, although not all chicks hatched on the island have been ringed each year. The breeding performance was closely monitored in 1996 & 1997 in association with other studies. Information was collected on laying date, the order of laying, hatching date, growth and survival to fledging of the chicks (see Chapter 2 for greater detail).

Nest sites were identified in accessible areas; inevitably some sites, for example on ledges on cliffs, were considered too dangerous to monitor. As a result the figures for fledged birds from the colony are likely to be underestimates, although they will be in proportion with the number of nests monitored.

Table 1a. Number of nests, eggs laid, chicks hatched and fledged for 1996 and 1997 at the Papa Westray colony.

Year	No. nests	No. Eggs laid	Eggs laid per Nest	No. Chicks hatched	Chicks hatched per Nest	Chicks hatched per Egg	No. chicks fledged	No. fledged per Nest	No. fledged per egg laid
1996	62	104	1.68	78	1.26	0.75	30	0.48	0.29
1997	60	110	1.83	81	1.35	0.74	30	0.50	0.27

Table 1b. Fates of eggs for each egg type (A = first laid of two egg clutch, B = second laid of two egg clutch, S = single egg clutch) for 1996 and 1997 combined.

Egg Type	Total No laid.	% Hatched	% Predated	% Other*
A	99	81.25	6.25	12.50
B	99	70.80	7.29	21.91
S	16	81.25	0	18.75

* Other includes addled, damaged and abandoned eggs.

Table 1c. Makeup of single & two egg nests of Black Guillemot on the Holm of Papa Westray in 1996 & 1997 compared with other studies.

Year	No. Nests	% 2 Egg	% 1 Egg
1996	62	87.1	12.9
1997	60	83.3	16.7
Kent Is. (1)	49	79.6	18.4
St Mary Is. (2)	122	95.1	4.9
Flatey, Iceland (3)	935	87.4	11.4
Finland (4)	42	92.9	7.1

(1) Winn 1950, (2) Cairns 1980, (3) Peterson 1981, (4) Bergman 1971.

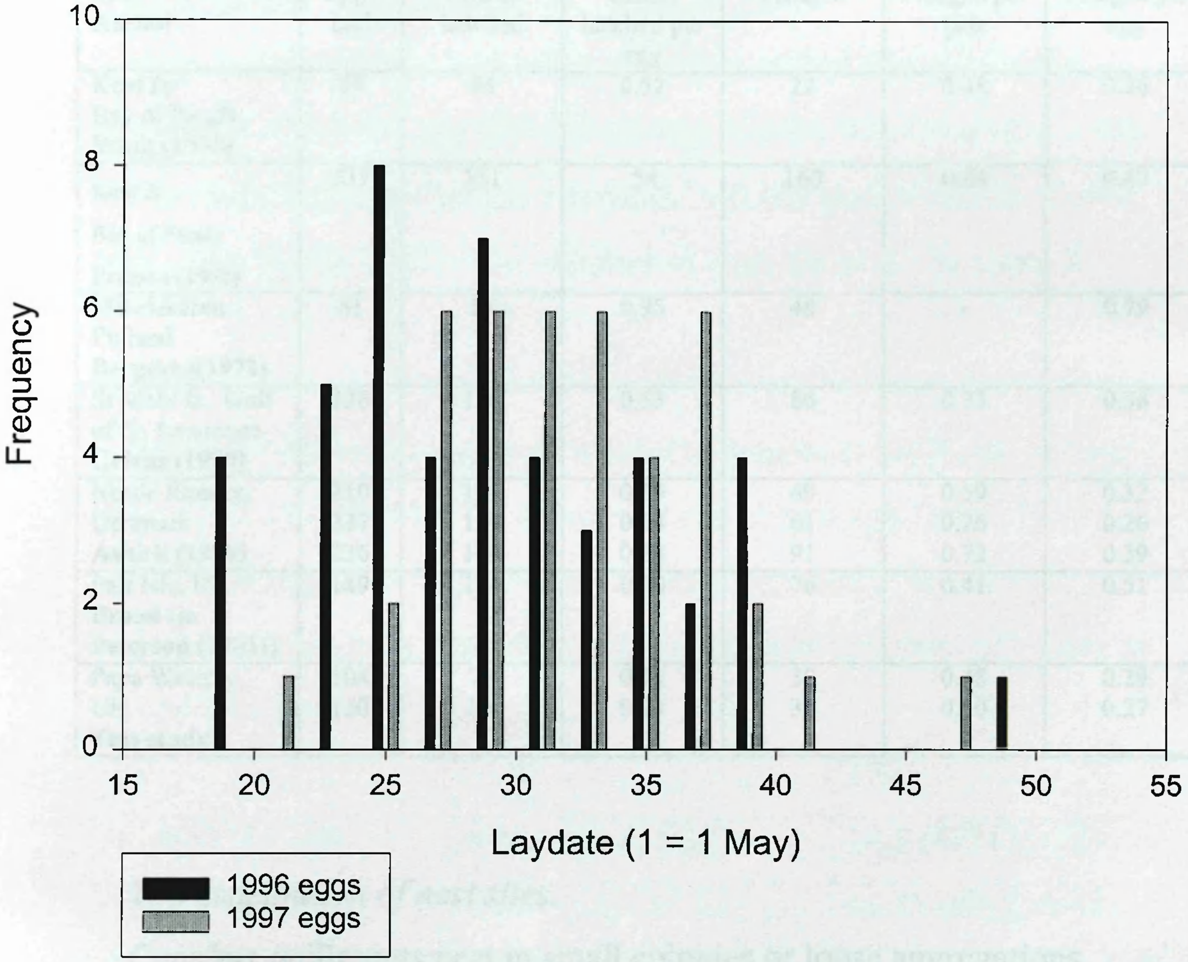

Figure 1. Frequency histogram of lay date for 1996 & 1997.

Table 2 Comparison between published data on breeding performance in different studies on Black Guillemots.

Site **Author**	Eggs laid	Chicks hatched	Chicks hatched per egg	Fledged	Fledged per pair	Fledged per egg
Kent Is. Bay of Fundy **Winn (1950)**	84	44	0.52	22	0.48	0.26
Kent Is. Bay of Fundy **Preston (1968)**	337	181	.54	160	0.84	0.47
Mikelskären Finland **Bergman(1971)**	61	58	0.95	48	-	0.79
St Mary Is., Gulf of St. Lawrence **Cairns (1980)**	238	126	0.53	86	0.73	0.36
Norde Rønner, Denmark **Asbirk (1979)**	210 237 236	125 129 149	0.59 0.54 0.63	69 61 91	0.59 0.26 0.72	0.32 0.26 0.39
Fair Isle, UK **Broad** (in **Peterson (1981)**)	149	104	0.70	76	0.41	0.51
Papa Westray, UK **This study**	104 110	78 81	0.75 0.74	30 30	0.48 0.50	0.29 0.27

The distribution of nest sites.

Cepphus guillemots nest in small colonies or loose aggregations (Belopol'skii 1957; Preston 1968; Cairns 1980, 1981). This is the case at Papa Westray with the north and east-coast of the Holm having active nests (see Chapter 2, Figure 2). Nests are predominantly of the "under boulder" type, although a number of breeding pairs inhabit burrows, some of which have been vacated by rabbits. Most of those nests that are found under boulders have a distinct "scrape", a depression in a layer of small particles of gravel on the bottom of the nest in which the eggs are laid. Those nests which had a less distinct scrape appeared to be more prone to egg damage. These nests with little or no gravel were often found to contain damaged eggs, presumably dislodged when the incubating adult left the nest.

Egg Volume

Eggs were measured and weighed on day of first discovery (see Chapter 2). From the egg dimensions egg volume was calculated using the formula: volume = length × breadth^2 × 0.467 (calculated for Puffin eggs, after Harris 1964). The volumes of eggs are given in Table 3.

Table 3. Volumes of eggs of Black Guillemots at the Holm of Papa Westray in 1996 & 1997. A = first laid egg of two egg clutch, B = second laid egg in two egg clutch, S = egg from single egg clutch. Volume is given in cc, sample size in first brackets, spread of values in second brackets.

Egg	1996	1997
Volume "A" egg	43.4 (52) (35-53)	44.5 (46) (38-72)
Volume "B" egg	42.57 (52) (35-51)	42.45 (46) (36-48)
"B" vol as a % of "A"	98.2% (52)(91-111)	96.67% (46) (62-109)
Volume "S" egg	42.26 (5) (39-45)	43.03 (10) (36-54)

For a more detailed analysis of egg laying see Chapter 4. A comparison of egg dimensions and masses between different populations of Black Guillemots are given in Table 4. The length and breadth of the"A" eggs from Asbirk's (1979) study lie outwith 2 standard errors of those laid in Shetland and Orkney (Ewins 1986, this study), while there is no difference in the dimensions of "B" and "S" eggs, or the mass of any egg type.

Table 4. Comparison of egg dimensions and masses between this study and others.

Ref.	Length (mm)		Breadth (mm)		Mass (g)		
	mean	s.d.	mean	s.d.	mean	s.d.	n
1	57.5	2.1	38.9	1.1			204
2	57.7	2.0	38.9	1.1			200
3	56.9	2.4	38.3	1.6			57
4	58.3	2.2	39.6	1.2	49.9	3.9	51
5	57.4	2.0	39.1	0.9	47.9	3.2	44
6	56.7	2.5	38.3	1.0	46.4	3.8	6
7	58.4	2.13	39.5	1.63	49.1	4.1	98
8	58.0	2.3	39.1	1.0	47.7	3.7	98
9	58.4	2.3	38.9	1.3	49.2	4.0	16

(1) *Cepphus grylle atlantis*, Denmark, 2-egg clutches, “A” egg. (2) as (1), “B” egg. (3) as (1), single egg clutches, “S” egg. (1,2,3, Asbirk 1979) (4) Shetland, 2-egg clutches, “A” egg. (5) as (4), “B” egg, (6) as (4), single egg clutches “S” egg. (4,5,6, Ewins 1986) (7) This study, 2-egg clutches “A” egg, (8) “B” egg. (9) Single egg clutches, “S” egg.

Prey types delivered to the nest.

Using data collected by watching the nest sites (see Chapter 2) it is possible to examine the composition of prey types delivered to the chick by adult birds. Certain prey types were more easily recognisable by observers, such as the Butterfish *Pholis gunnellis*, the sandeel, *Ammodytes spp.* and flatfish species, either due to their distinctive appearance, or that the frequency of delivery was high enough for observers to become skilled at identifying them accurately. The overall composition of the chick diet for 1996 & 1997 is shown on Table 5.

The predominant prey type delivered to the nest by adult Black Guillemots is the Butterfish *Pholis gunnellis* (see Chapter 5). Black Guillemot chicks are fed predominantly bottom dwelling fish across their range of a larger size than found in the stomachs of adults (Bradstreet & Brown 1985), although crustaceans, which are not delivered at this colony) feature more in chick diets in the high-arctic.

From data collected by observers from hides, it was possible to examine the feeding rate, that is, the frequency of visits to the nest by adults carrying food for chicks. The mean rate of food delivery for all nests for both years was 0.7972 feeds per hour (max. 4.0, min.0.0, s=0.6363). There was no significant difference in the feeding rate per hour between single chick and 2 chick nests (1 chick nests = 0.786 feeds/h, s.d.= 0.226, 2 chick nests = 0.755 feeds/h, s.d. = 0.286), nor was there a relationship between the rate of food delivery and the growth rate of the chicks. The rate of prey delivery did not increase with chick age. The feeding rates for the colony are shown in Figure 2.

Adult Weights.

The biometrics of adult birds caught at this site is for both sexes as no method of sexing was considered non-invasive enough as I was trying to minimise handling time and stress to the bird once captured. With the difficulty of capturing birds, it was impossible to re-trap any individuals. All weights and measurements are for adults caught on the colony during the chick-rearing phase.

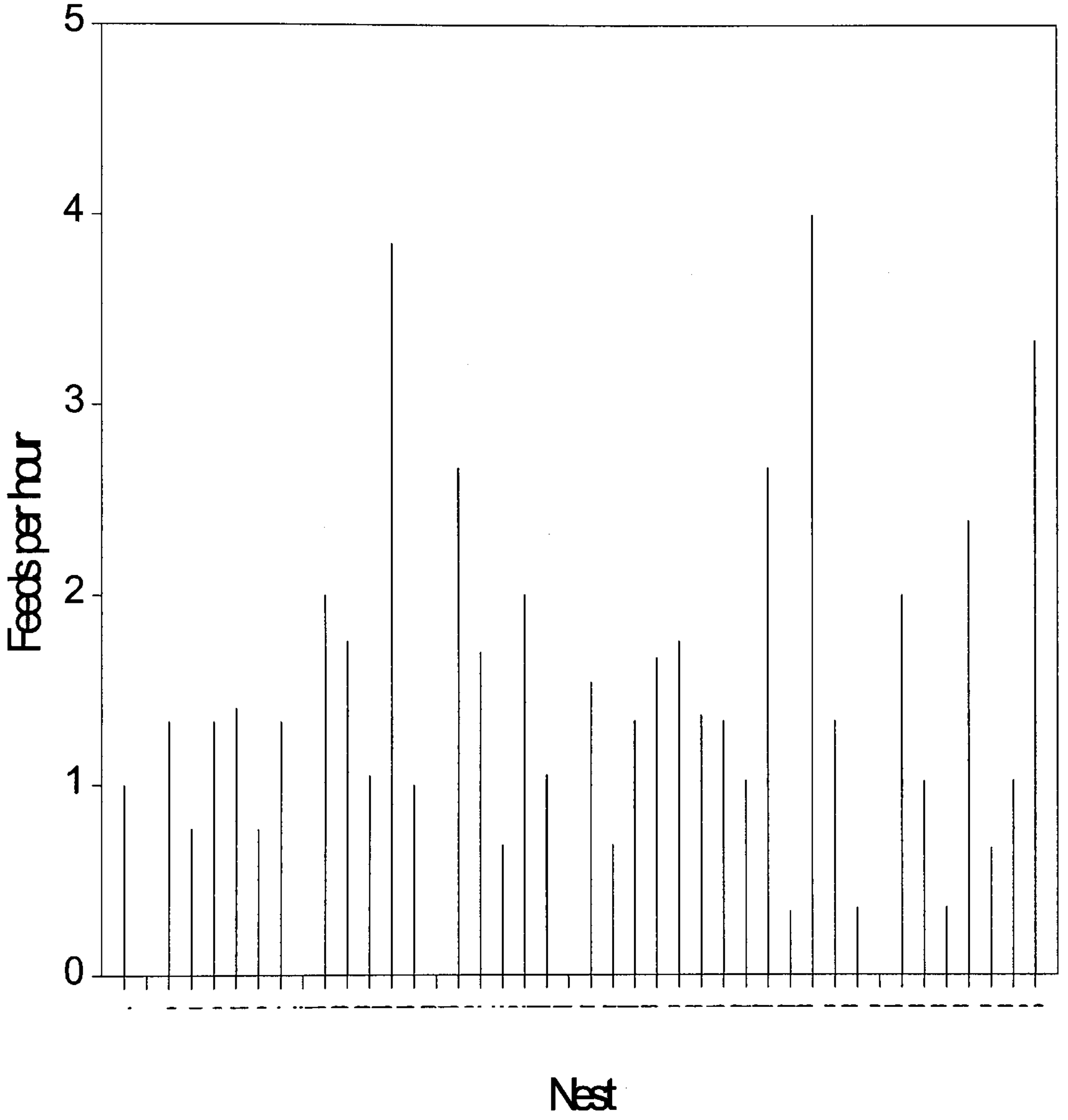

Figure 2. Feeding rates for observed nests on the Papa Westray colony in 1996.

Table 5. Prey types delivered to chicks in 4 studies.

Prey	%96	%97	Fair Isle *	Denmark **	Finland ***
butterfish	68.1	66.4	46.9	67	
sandeel	2.1	3.5	17.4	22	5
flatfish	5.3	2.1	7		
stickleback		6.2			
crustacean		0.6		2	
unidentified	24.5	20.9	2.2		
blenny				4	95
gadoids			18.4		
sea scorpions			8.1		
wrasse				7	

* Slater & Slater (1972)
** Asbirk (1979)
***Bergman (1971)

The mean weight of nine adults trapped on the colony in 1997 was 407.25g. This can be compared to weights collected in other studies on Table 6. This shows that birds trapped on the Holm of Papa Westray are of similar size, and probably of similar body condition to those breeding elsewhere. Wing lengths of birds trapped on the colony averaged 163.6mm (s.d. = 4.17, n = 9) which is similar to previously published wing lengths from birds caught in the UK during the breeding season (♂164mm, ♀163mm) (Leloup),

Table 6. Adult weights.

Study Site	♂ weight (g), (s.d.) (n)	♀ weight (g), (s.d.) (n)	Author
Spitsbergen	382, (23.4) (10)	397, (15.1) (7)	
Novaya Zemlya	385, (-) (11)	402, (-) (4)	Demantiev & Gladkov 1951
Novaya Zemlya	391, (-) (16)	412, (-) (12)	Belopol'ski 1951
Eastern Murmansk	431, (-) (78)	434, (-) (42)	Belopol'ski 1957
Denmark	376, (23.8) (40)	380, (18.2) (24)	Asbirk 1979
Jameson Land (Greenland)	408, (26.3) (17)	400, (25.4) (9)	
White Sea	348 (♂ & ♀), (-) (24)		Bianki 1967
Papa Westray	407 (♂ & ♀), (34.27) (9)		Sawyer, this study.

Conclusions

The colony on the Holm of Papa Westray shows breeding statistics similar to other studied sites, despite its relatively southerly location within the distribution range of breeding Black Guillemots. Birds at this colony are feeding their chicks on demersal fish species similar to those fed to chicks in all areas apart from colonies located in the high-arctic, although the prey delivered here can be of larger size than some other prey species (see Chapter 5). The mass of adult birds caught on the colony is high compared with birds trapped on other sites, indicating relatively good body condition of these birds. The hatching success is high, although the fledging success is relatively low compared to other studies. This lack of fledging success may be due to factors such as the high level of predation by gulls rather than this site being less able to produce young capable of fledging. These factors indicate the stability of this colony, possibly due to the predictability of the prey base (there is a regular supply of high quality food items, see Chapter 5) and the availability of productive feeding sites (see Chapter 9).

Chapter 4

Eggs and Chicks: Variation in Aspects of Black Guillemot Breeding Strategies.

Introduction

The life history strategies of seabirds are typically represented by relatively low annual reproductive rates and high adult survival. Due to these factors, and the possibility of measuring environmental influences by the study of inter-annual variation in breeding parameters, the subject has been relatively well studied by biologists (e.g. Monaghan 1996, Coulson and Thomas 1985, Wendeln and Becker 1999, Olsson and Brodin 1997, Oro *et al.* 1996).

A number of factors can effect the hatching and fledging success of an avian egg such as nest site quality (Major & Kendal 1996, Harris *et al.* 1997), the composition of eggs and the distribution of resources within a clutch (Williams, 1994, Bernardo 1996, Royle *et al.* 1999). The composition of the diet of females, in particular the protein content, can affect the size of eggs and thus the chicks (Veasey 1999).

The size of the eggs laid can have an important influence on the breeding success, and thus on the lifetime reproductive success, of birds (Bolton 1991, Hipfner & Gaston 1999, Perrins 1996). The size of the hatchling is usually closely related to egg size. The size of the eggs produced by the female has a major influence on the survival and growth rates of chicks hatched from them (Perrins 1996). Thus, chicks hatching from large eggs are at an advantage over those hatching from small eggs. Survival in hatchlings from small eggs can be significantly lower than in those from larger eggs (e.g. Nisbet 1978). The trend for large eggs producing larger chicks however, shows some evidence for decreased fledging success with the very largest eggs, which can adversely affect the fitness of the female (Perrins 1996).

Other factors affecting the breeding success of birds include the body condition of the female at time of laying (Wendeln 1997) and the timing of breeding (Moreno *et al.* 1997). The timing of breeding is likely to be affected by several factors (Svensson, 1995) and can be initiated by environmental factors such as photoperiod (Lambrechts *e*t al. 1996), the amount of rainfall (Zebra Finches, Zann *et al.* 1995) or the water level in rivers (House Wren, Finch 1991).

At the onset of the breeding season, female birds must achieve sufficient body condition to produce eggs, and to incubate them, before having to provide for the chicks in terms of foraging for chick food. Timing of breeding has been also linked to the age of the breeding birds in several seabird species (Daunt *et al.* 1999). In the Thick-billed Murre *Uria lomiva* for example, younger birds breed later and have lower reproductive success, which is the general picture that has been observed. A group of older Thick-billed Murres experimentally induced to lay later showed no reduced breeding success (DeForest & Gaston 1996), which has recently also been shown by Daunt *et al.* (1999) to be the case in the Shag, *Phalacrocorax aristotelis*. The experimental studies show that the poor performance of young birds is not simply a consequence of seasonal changes in the environment, but a result of inherent features of the younger birds. A similar study into the role of parental quality in the Thick-billed Murre showed that the effect of date is more likely to be a result of "better" birds, as birds induced to lay later showed no decrease in breeding success (Hipfner 1997). Older (more experienced) birds tend to lay larger eggs (Williams 1994), although in the Thick-Billed Murre this effect is detectable only in the first 8 years of breeding (Hipfner *e*t al. 1997). Later breeding in the Common Tern, however, is not necessarily linked to lower breeding success (Nisbet & Welton 1984).

The timing of breeding can be important, particularly if the composition of available prey is likely to change with time. It has been shown in the Blue Tit for example that breeding success is strongly linked to the availability of caterpillars (Perrins 1979, Seki & Takano 1998), which occur only for a short period of time during the breeding season.

In the Black Guillemot *Cepphus grylle*, there appears to be more variability in breeding strategy than in any other of the Atlantic Alcidae (Cramp 1985, Nettleship and Birkhead 1985, Gaston & Jones 1998). The production of two eggs allows for a number of possible permutations of egg laying and chick rearing only a single egg can be laid or two eggs can be laid, and these can be hatched synchronously or asynchronously, staggering the period of peak chick food demand. This could result in a greater variation in breeding performance. Alternatively, it may reduce variation since individuals may have more scope for adjusting reproductive demands to suit their own capacities, arriving at individually optimised strategies. Breeding in the Black Guillemot can be affected by the prey composition in the diet (Sawyer, this study). The diet choice of the Eurasian Otter, a mammalian species which feeds on very similar prey types to the Black Guillemot (McCluskie 1999), shows marked seasonal variation with an increase in the proportion of butterfish *Pholis gunnellis* (also an important prey species for the Black Guillemot), during the summer months (Heggberget 1993). Given the importance of this prey type to the growth rate of Black Guillemot chicks at the site of this study (see Chapter 5), the availability of this prey for the duration of the chick rearing phase could be crucial to the breeding success of these birds. A similar situation with respect to a key prey species was observed in the Black Grouse, *Tetrao terix* by Baines *et al.* (1996), with the availability of Sawfly larvae correlating with geographical differences in timing of breeding.

In this chapter I describe the breeding success of the Black Guillemot on the Holm of Papa Westray, Orkney, and examine the relationship between of egg size and mass and the growth and fledging of the chicks, the effect of laying date and the different influence of these factors on single eggs and two-egg clutches.

Methods

This study was conducted on the Holm of Papa Westray, Orkney. The island of Papa Westray is the furthest north-west of the Orkney islands, situated at 59°21'N, 2°53'W. The colony of Black Guillemots found here consists of nest sites formed under boulders and in disused rabbit burrows. For a full description of the site and the methods used to collect data see Chapter 2.

Data were collected by physically measuring and weighing the eggs within two days of laying. Weighing was carried out using an Ohaus portable electronic balance reading to 0.1g. Measuring was carried out both longitudinally and transversely using Vernier calipers to measure the widest part of the eggs in both directions. The first laid egg was marked using a waterproof marker pen with an "a", the second marked with a "b", and the date of laying recorded. If a nest was discovered containing two eggs these were marked with a "1" and a "2" to allow differentiation between the eggs and these were excluded from any analysis involving laying date. Laying date was recorded as being the date of appearance of the egg in occupied nest sites. Checking continued until the nest was empty. In order to obtain data on fledging, nests which became empty were checked against chick growth curves to see if the chick had been of sufficient weight to have fledged.

Egg volume was calculated using the formula: volume = length $\times$ breadth$^2 \times (0.467\times 10^{-4})$ (calculated for gull eggs, after Harris 1964).

Eggs are described here as three types. In a two-egg clutch the first laid egg is described as the "a" egg and the second laid as the "b" egg.

The egg in single egg clutches is described as the "s" egg and I was confident that all eggs described in this way were single egg clutches as opposed to two egg clutches that had lost an egg. Eggs will be described in this way hereafter.

Results

Laying Date

The mean egg laying dates for all years (1994-1997) with standard errors for each year are shown in Figure 1. For two egg clutches, the timing of laying, as indicated by the mean laying date for the "a" egg, was significantly different between years (Anova, $F_{3,161}$=7.598 $p<0.001$), the differences lying between 94 & (95 & 97), 95 & 96, tukey multiple comparisons). There was no difference in the lay-dates of the "s" egg between years. "s" eggs were laid later in all years (t-test $p < 0.001$, $t = 31.797$, 40 d.f.)

Egg size

The volume of the "s" egg showed a significant increase with lay date in all years except 1997 (Spearmans correlation co-efficient =(94, 0.786 (n = 8)) (95, 0.551 (n = 16)) (96, 0.900 (n = 5)) (97, -0.209 (n = 9)), p=(94) 0.021, (95) 0.027, (96) 0.037 (97) 0.590). The size of the "s" egg relative to the sizes of the "a" and "b" eggs for each year did not vary. There was no date or year effect on the relative volume of the "a" egg to the "b" egg. The mass of the "b" egg relative to the "a" egg was calculated as a percentage, and this was plotted against laydate (Figure 2a-d). There was no correlation between these variables in any year.

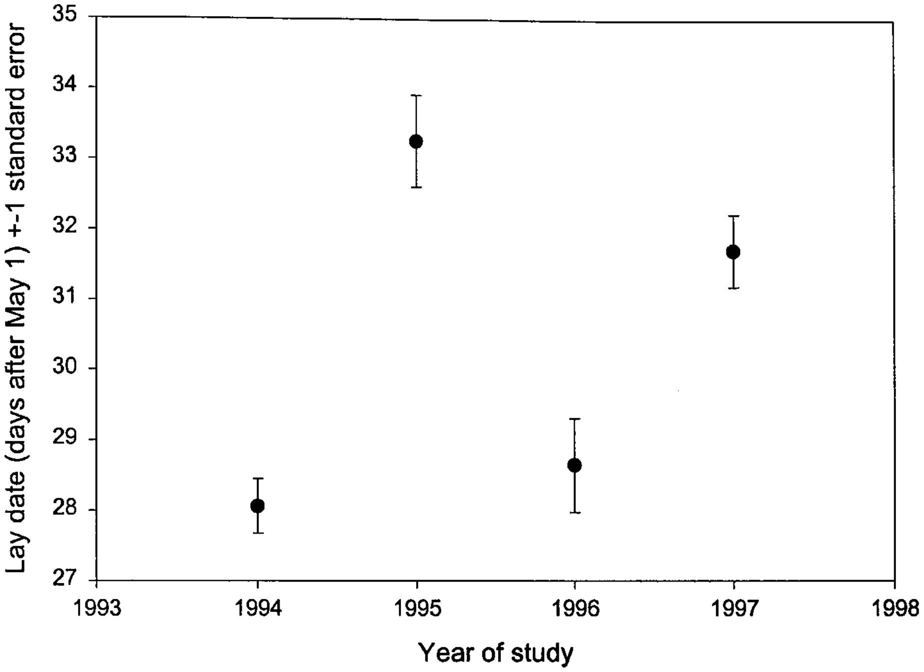

Figure 1. Mean lay dates for each year (±1 s.e.).

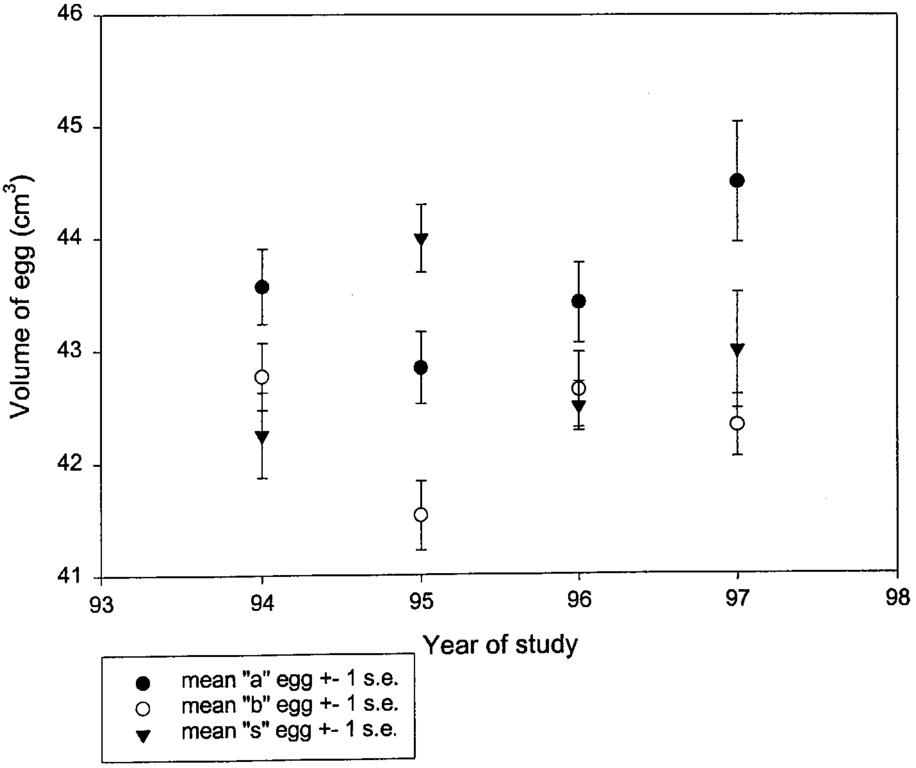

Figure 3. Mean (±1 s.e.) volumes of each egg type for each year.

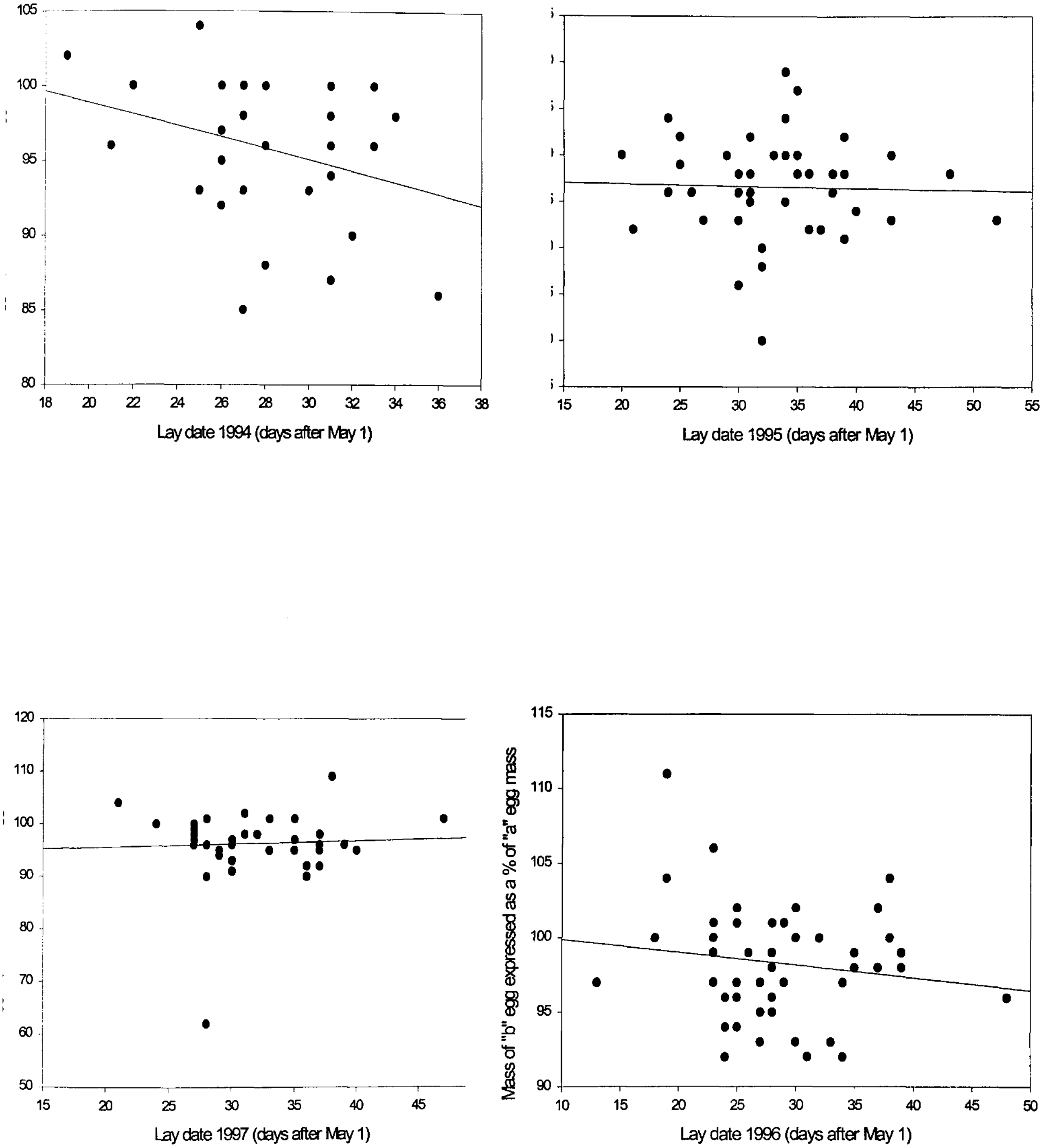

Figure 2 a-d. The relationship between the mass of "b" eggs expressed as a % of the mass of the "a" egg in the same clutch, and the laying date of the "a" egg (days after May 1).

Egg Volume

The volume of all categories of eggs showed no annual differences; the volumes of all egg categories are shown for each year on Figure 3. In all years the “a” egg was significantly larger in volume than the “b” egg (t-test, $p=0.002$). There was a difference in the volume of the “a” and “b” eggs within a clutch for all years (paired t-test $p<0.001$, $t = 6.39$,198 df), the “a” egg being larger than the “b” egg (mean “a” egg size = 43.92cc, s.e = 3.88, n = 199, mean “b” egg size = 42.51cc, s.e. = 3.06, n = 202). The relative volume and mass of the “a” and “b” eggs was not affected by laying date.

In the case of “s” eggs, the effect of laying date was more pronounced. Eggs laid later in the season had significantly higher masses in 1995 (Spearmans correlation co-efficient, 0.755, $p=0.001$) & 1996 (Spearmans correlation co-efficient, 0.812, $p<0.001$). These data on egg size can be seen in Figures 4a-d. There was no relationship between the survival of the chicks and the volume of the egg (all egg types), but the age of the “s” chick at fledging was related to the volume of the “s” egg (regression, $p = 0.007$, $r^2 = 0.53$), see Fig.5. Chicks from smaller single eggs took longer to fledge.

Egg Mass

The fresh egg masses of each egg type for each year are shown in Figure 6. The “a” egg was significantly heavier that the “b” egg for each year (paired t-test all years: $p<0.001$, $t = 9.62$, 181 d.f.), correlations between “a” egg mass and “b” egg mass (correlation co-efficient = 0.845, 180d.f.: individual years, ‘94 $p < 0.001$, correlation = 0.772, 38d.f., ‘95 $p < 0.001$, correlation = 0.773, 44d.f., ‘96 $p < 0.001$, correlation = 0.875, 49d.f., ‘97 $p < 0.001$, correlation = 0.862, 43d.f.). Laying interval had no effect on relative egg mass within clutches.

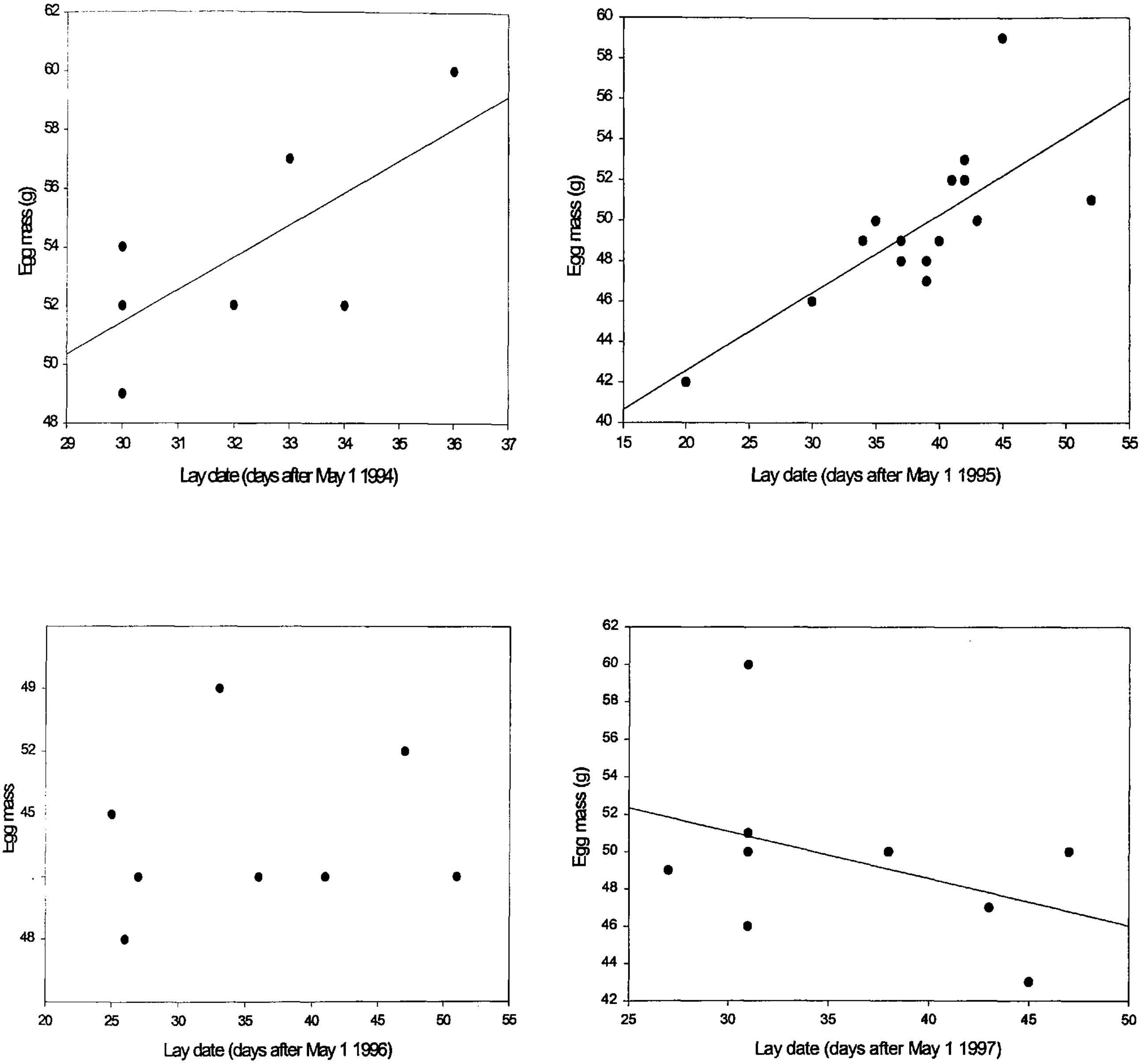

Figure 4 a-d. The mass of the "s" egg with laydate for each year (clockwise from top left 1994, 1995, 1996, 1997).

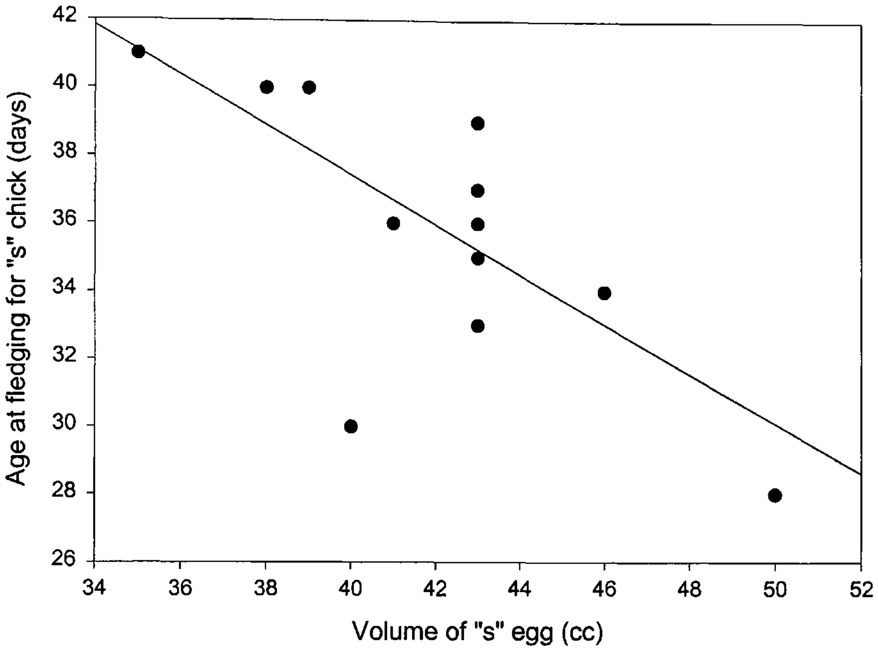

Figure 5. Relationship between single egg volume and fledging age.

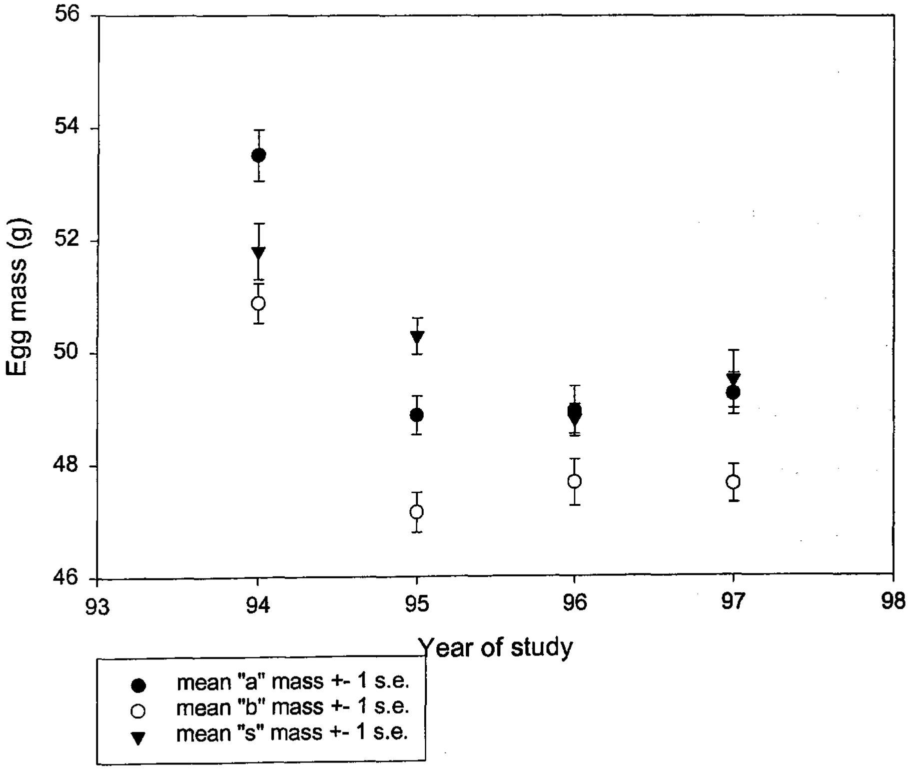

Figure 6. Mean (± 1 s.e.) masses of each egg type for each year.

Fledging success

Across all years the fledging success of chicks hatched from the "a" egg was greater than those hatched from the "b" egg ($X^2 = 7.43$, $p < 0.001$) see Table 1. Investigating the effect of the hatching date on the survival of the "b" chick (the second chick of a two chick clutch) showed an effect of laying date on the survival rates, that is the likelihood of a chick surviving to fledging. No such relationship exists for the first hatched chicks (the "a" chick). Eggs laid earlier had a greater chance of fledging (logistic regression $p = 0.001$ $X^2 = 20.420$, 3df).

Table 1. Fledging success for each egg type for all years.

Egg type	No. laid	No. hatched	No. fledged	% fledged
A	209	154	85	55.2
B	209	114	53	46.5
S	49	32	16	50.0

Discussion

The volume of the "s" egg increases with lay date. It has been proposed (Asbirk 1979) that those birds who lay a single egg are birds who are not successful enough to raise two chicks, that is, birds of insufficient foraging ability, or young birds in their first few seasons of breeding (Asbirk 1979). The data on egg volume for these type of nests supports this idea, as those birds who delay laying are able to lay larger eggs and manage to raise their chicks to fledging at an earlier age. Birds who lay a single egg and are laying earlier are laying smaller eggs, and are taking longer to raise their chicks. This suggests a lesser foraging ability, which would be reflected by both their laying a small (and thus less energetically expensive) egg and the slow growth rate of the chicks.

To isolate the effects of egg quality from parental quality, a cross fostering experiment would be required (Monaghan & Nager 1997), which was not feasible given the relatively small numbers of birds in this study area and their relatively high conservation value.

In the case of the second chick of a 2 egg clutch (the "b" chick), the hatching date (and thus the laying date) has a significant influence on the chances of survival to fledging. There was no effect of lay-date on the survival of the "a" chick, as this chick generally enjoys faster chick growth. I also found (see Chapter 5) that the effect of diet composition on chick growth was only detectable in the case of "b" chicks.

Whilst the positive effect of larger egg size on fledging success is well documented (see Perrins 1996) no such relationship was found with the Black Guillemots on Papa Westray, although there was a significantly greater fledging success from "a" eggs than from "b" eggs. This is likely to be due to the unusually high predation of chicks by gulls at this site. Chicks were usually taken between 20 and 30 days old and as such could not be included in analysis involving fledging success.

The advantages of laying later for single egg layers may be that the female is able to lay a larger egg due to the increased time taken to obtain body condition. There may be a trade-off between egg size and egg number, as greater breeding success may well be obtained from laying a single larger egg rather than two smaller ones. The effect of increased reproductive effort on the survival of the female (Perrins 1996) and the importance of laying date for the survivability of the chicks may be constraints on egg laying, making the laying of one egg later in the season a successful strategy for some Black Guillemots.

It can be seen that there is an apparent advantage to breeding earlier in the season with both single eggs and the "b" eggs being affected by laying date. Further experimental studies would be required to tease apart the factors involved.

Chapter 5

The Consequences of Prey Choice for the Breeding Success of the Black Guillemot, *Cepphus grylle.*

Introduction.

In many seabird species, breeding performance is strongly linked to the availability of one or two prey species, such as the sandeel in the North Sea (Harris & Wanless 1985) and the capelin in the North Atlantic (Lilliendahl & Solmundsson 1997) & North Pacific (Sanger 1987). This may be due to a particular fish being the most locally abundant prey type, or the delivery of a specific prey type may be optimal in terms of chick growth. In the case of a seabird foraging on the seabed or in the water column in offshore areas, there is unlikely to be a large choice of prey types compared to inshore areas high in species diversity (Gray 1997). These prey species, whilst potentially of lower energetic content (Nolet *et al.*1989) are likely to be exist in vastly higher numbers and are thus able to support much higher numbers of predators. In a species foraging in inshore areas on the other hand, there is likely to be a greater variety of available prey due to the large variety and high productivity of inshore areas. In this study, the effect of the choice of prey items was examined using an inshore foraging species, the Black Guillemot. Variation in the breeding performance of the birds allows the species makeup of chick diet to be used as a variable in examining the foraging ability of adults provisioning their chicks. Other variables useful for examining foraging ability can include information on foraging location and behaviour, collected by radio telemetry. This technique has been shown to be appropriate for species foraging in areas close to the breeding colony (Anderson and Ricklefs 1987). It is further particularly useful for collecting information on the number and duration of dives as well as location by the use of triangulation, or by inference from the signal using one receiver (Wanless *et al.* 1998).

The cost of travelling to the foraging site has been well documented as an important factor in the life history strategy of pelagic seabirds (Ashmole 1971, Ricklefs 1983). Distance traveled may vary with local circumstances, for example it has been shown that in years of poor food, North Sea seabirds can forage over greater distances than in years of good food availability (Monaghan *et al.* 1992). For seabirds such as the alcidae, the costs of flight are much higher than in non-diving seabirds (Pennycuick 1987) due to their adaptations for diving. Thus, the relative cost of increasing the travel distance may be greater in these birds. Foraging in the inshore area may thus reduce the travel distance (but see Chapter 7), and also increase the diversity of prey available, thereby increasing chick growth. However, the quality of prey may also be an important factor. In this chapter, variation in the prey species brought to chicks, and the relationship to chick growth is examined in the inshore forager, the Black Guillemot. The foraging distance and diving behaviour of adults in relation to chick diet is also examined.

Methods

Data were collected on the Holm of Papa Westray, Orkney (Chapter 2, Figure 1), during the period of May – August in 1996 and 1997. Sixty-two nest sites were located during egg laying, individually identified and subsequently monitored regularly throughout the breeding season to reveal breeding performance, chicks being weighed to nearest gram and bill, tarsus and wing length being measured to the nearest mm at 3 day intervals. Growth rates were calculated as the increase of mass in g per day for each individual chick during the linear phase of growth. The linear phase was generally between five and twenty-five days; each individual chick's growth curve was plotted to see if this was the case for all chicks before calculating growth rate. Chicks are referred to as either "A" chicks (the chick hatched from the first laid egg of a 2 egg nest), "B" chicks (the chick hatched from the second laid egg of a 2 egg nest) or an "S" chick (a chick from a single egg nest). These terms will be used hereafter.

Observation hides were erected between the high water level and the nests (located at the top of the beaches). Adult Black Guillemots carry food items singly in the bill enabling prey species identification by trained observers. The time, species and size of prey items delivered to individually marked nests were recorded during three-hour watches carried out during the hours of daylight at various points during the tidal cycle. Twenty-two nests were watched in this way from the onset of the chick-provisioning period. Information on parental foraging behaviour was collected using AVM single-stage radio transmitters operating in the 173mhz waveband. Radio tracking of adult breeders was carried out during the chick-rearing phase (25th June – 2nd August). Tags were attached to the underside of the tail feathers of sixteen adult birds caught on the colony, eleven in 1996 and five in 1997. Completed tags weighed 3.5g (>1% adult body mass). The location and duration of dives during foraging trips were recorded using Cedar Creek scanning receivers and 8 element Yagi aerials, from two mobile tracking stations. These stations were moved between different areas to provide coverage of the foraging sites, identified from boat surveys, around the coast of Papa Westray, and to collect information on individual adults foraging behaviour. For more detailed methods see Chapter 2.

Results

The effect of prey type on chick growth.

The overall prey composition in the diet of chicks at the colony is shown in Table 1. The predominant prey type delivered was the butterfish *Pholis gunnellis*, which constituted 68.9% of the observed prey items delivered to the 20 nests monitored for both years of the study. In terms of individual nests, the proportion of different prey types delivered varied considerably between pairs with some chicks receiving almost entirely butterfish, while others received predominantly Sandeels, flatfish and other prey items. Table 2 shows relevant data for 3 nests in 1996. The sizes of each type of prey delivered to the nest are shown on Figure 1. This makeup of prey was similar between years (1996: 68.1% butterfish, 1997: 66.4% butterfish) as were the sizes of prey delivered.

Table 1. Prey delivered to Black Guillemot chicks on the Holm of Papa Westray in 1996 & 1997 combined.

Prey type	No. delivered	% of total
Butterfish	923	68.89
Sandeel	32	2.39
Flatfish	57	4.25
All other	328	24.47

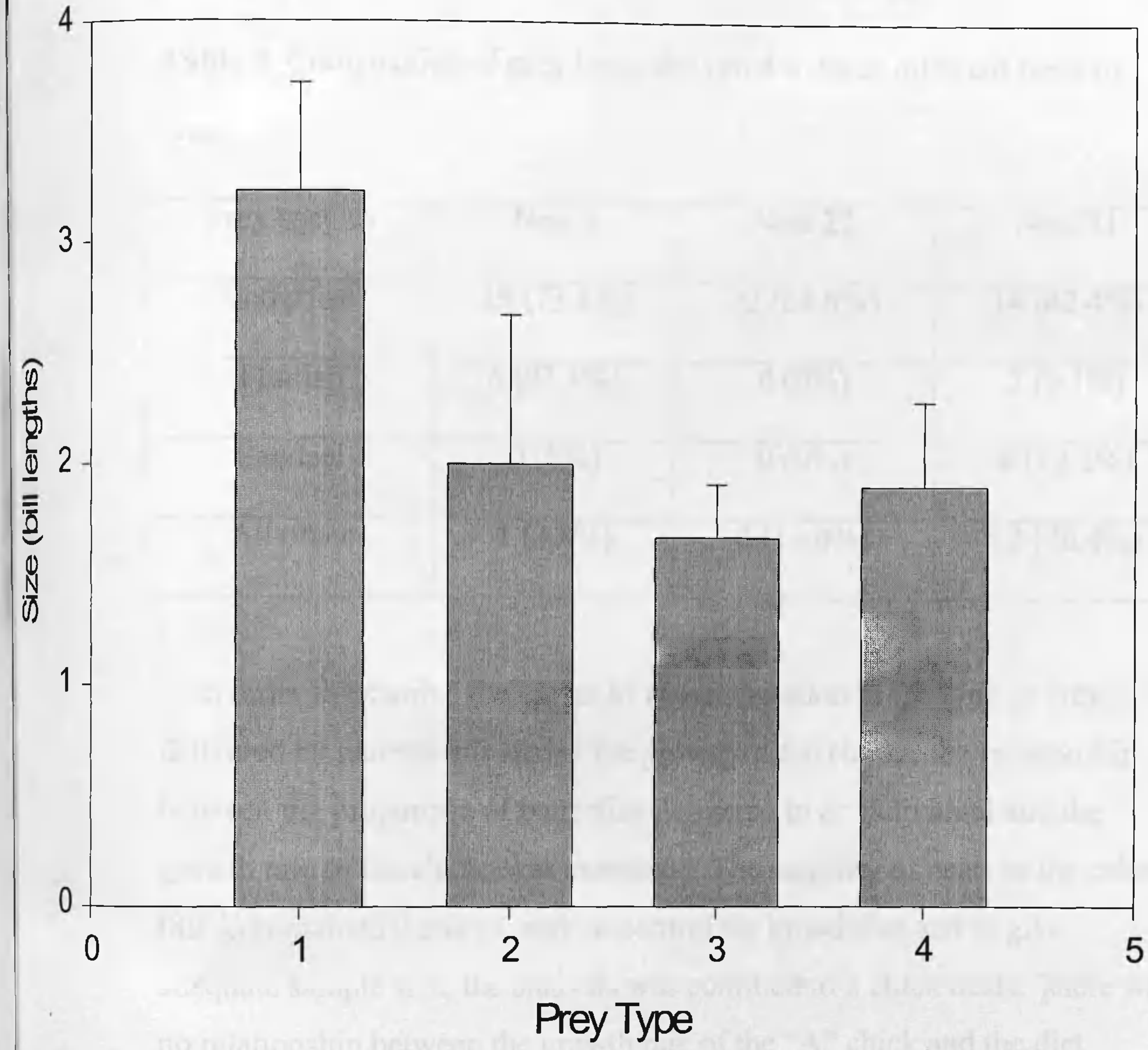

Figure 1. The size of prey types (in bill lengths) delivered to the nest by adult Black Guillemots. Prey type 1 = Butterfish, 2 = Sandeel, 3 = Flatfish, 4 = Other.

Table 2. Composition of prey types delivered to three different nests in 1996.

Prey species	Nest 8	Nest 22	Nest 71
butterfish	19 (73.1%)	22 (84.6%)	14 (42.4%)
Flatfish	6 (23.1%)	0 (0%)	3 (9.1%)
Sandeel	0 (0%)	0 (0%)	4 (12.1%)
All other	1 (3.8%)	4 (15.4%)	12 (36.4%)

In order to examine the extent to which variation in the type of prey delivered by parents influenced the growth of the chicks, the relationship between the proportion of butterfish delivered to an individual and the growth rate of the chicks was examined. The majority of nests in the colony (80%) contained 2 chicks, and, to control for brood size and to give adequate sample size, the analysis was confined to 2 chick nests. There was no relationship between the growth rate of the "A" chick and the diet composition. However, the growth rate of the "B" chicks was significantly related to the proportion of butterfish in the diet (Figure 2). The relationship can be described by the growth curve equation

$$y = e^{(2.9+(\frac{-33}{x}))} \qquad (r^2=0.696,\ f=22.92,\ 10\ \text{d.f.},\ \text{sig}=0.001)$$

In the case of single chicks, in nests in which only one egg was laid, a different relationship is seen (Figure 3). With increasing proportion of

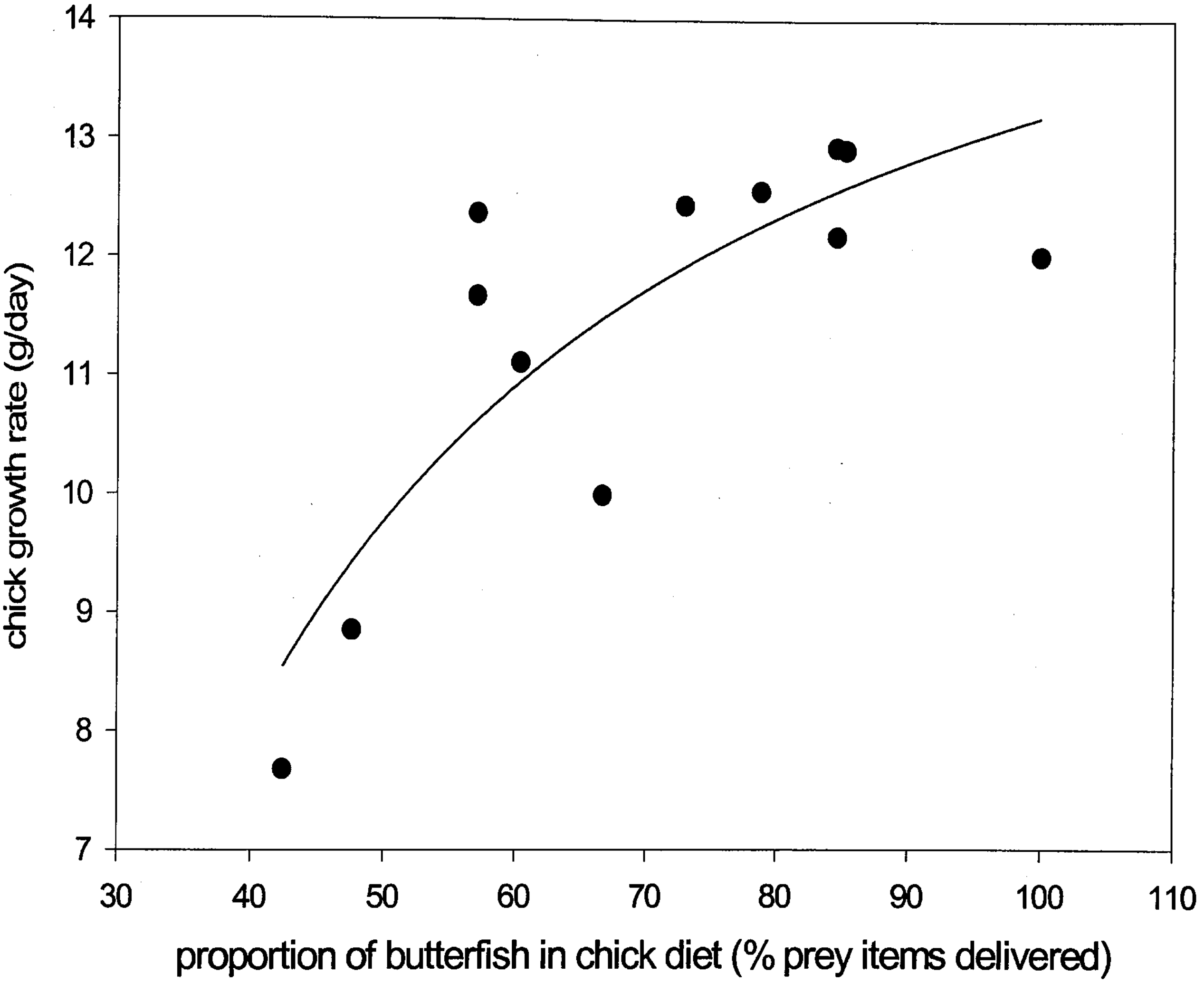

Figure 2. "B" chick growth rates and diet composition (% of butterfish in total prey delivered to nest). The curve is described by the equation

$y = 0.694 - \frac{341.65}{x}$ (r^2=0.694, p=0.0008).

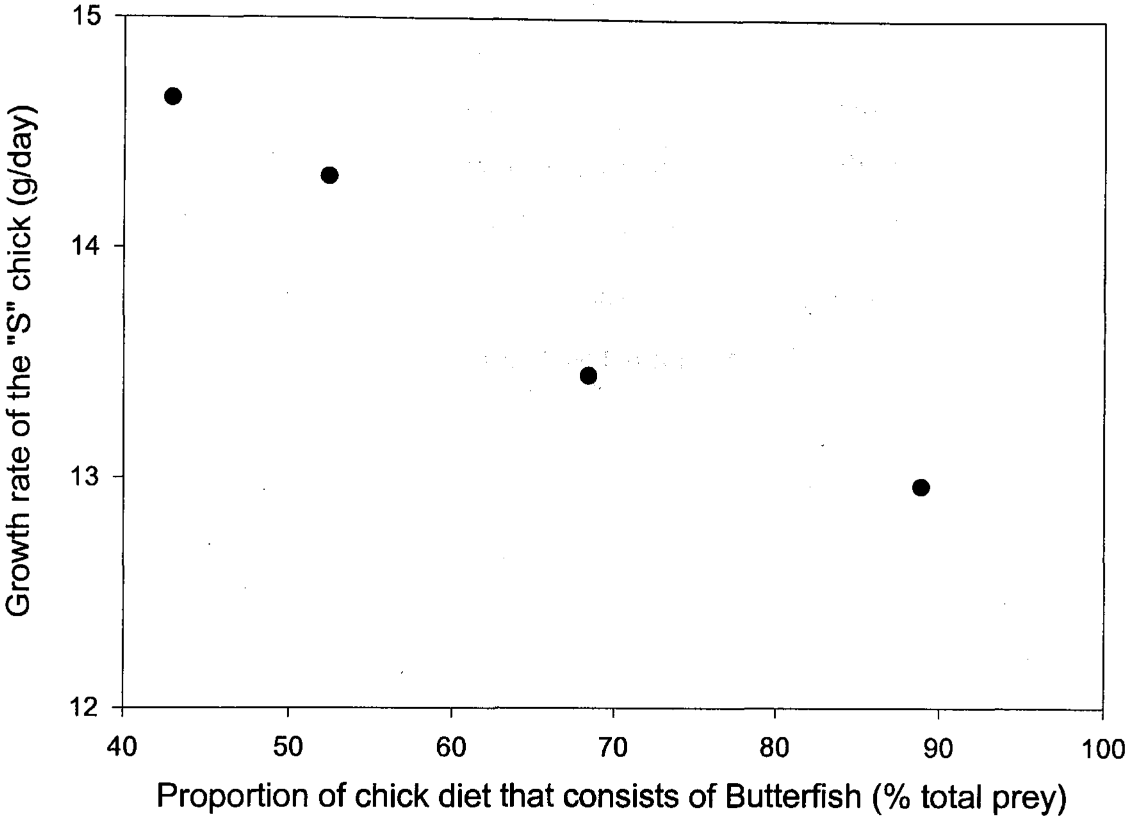

Figure 3. The growth rate of the “s” chick and the proportion of butterfish in the diet (% butterfish of total prey delivered).

butterfish, the growth rate of the chicks actually decreased markedly. While there are only 4 points, it can be seen that they follow a convincing trend.

Distance to foraging site and prey composition of chick diet.

Using the data for radio-tracked birds, the relationship between the distance traveled over the sea to the feeding site and the prey items delivered to the nest was examined (Figure 4). It can be seen that birds that are flying longer distances are delivering a higher proportion of butterfish to the nest (Spearmans correlation co-efficient = 0.693, p = 0.019).

The relationship between diet composition and dive duration.

The mean dive duration per trip decreased with increasing proportion of butterfish in the diet (Figure 5, Spearmans correlation coefficient = -0.521, p = 0.027). There was no difference between the depths of water in foraging sites at different distances from the colony (mean depth = 14.2m).

As would be expected given the relationship between proportion of butterfish in the diet and distance traveled, there is a corresponding relationship between distance traveled to the feeding site and mean dive duration (Figure 6); dive duration decreased with distance traveled (Spearmans correlation coefficient = -0.788, p =0.001).

Discussion.

From the data presented it can be seen that a diet containing a high percentage of butterfish was associated with better chick growth in the

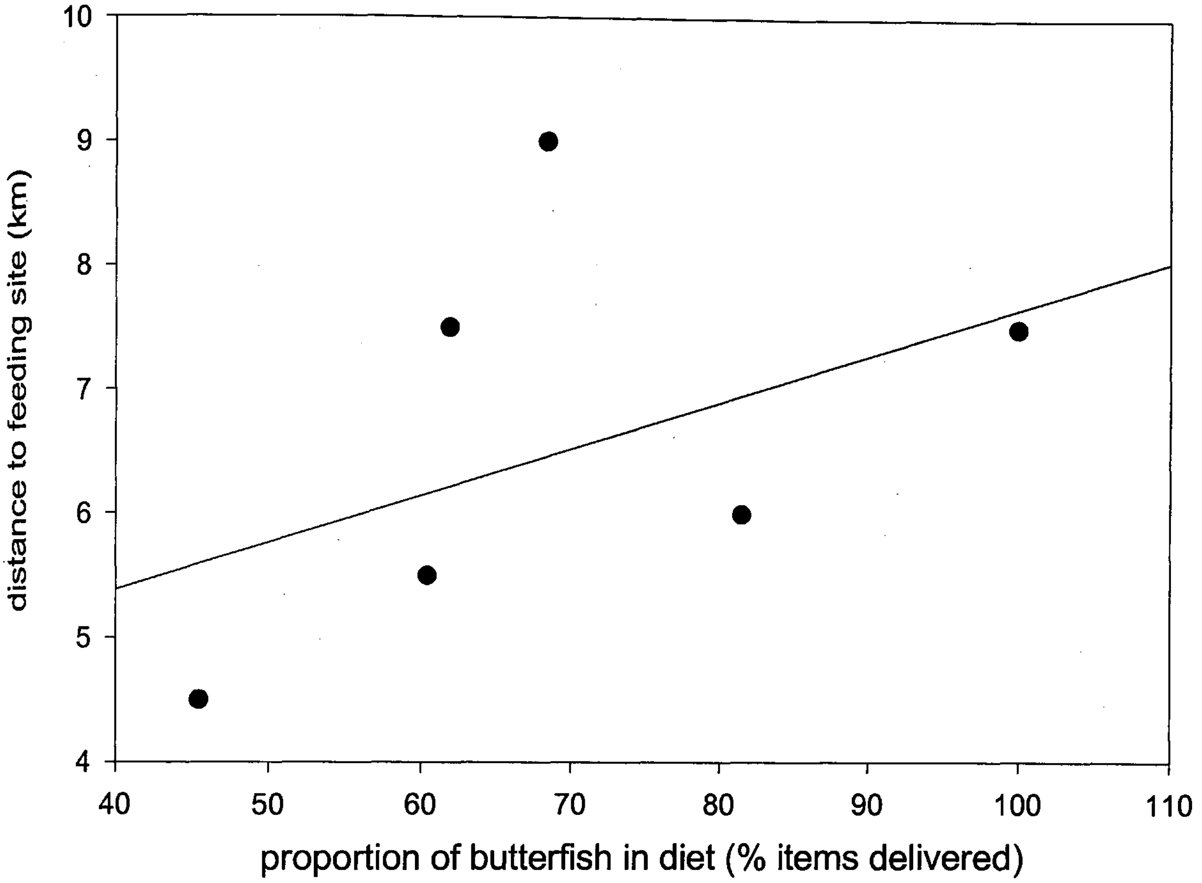

Figure 4. The distance to the feeding site and the proportion of butterfish in the diet (% butterfish of total prey delivered).

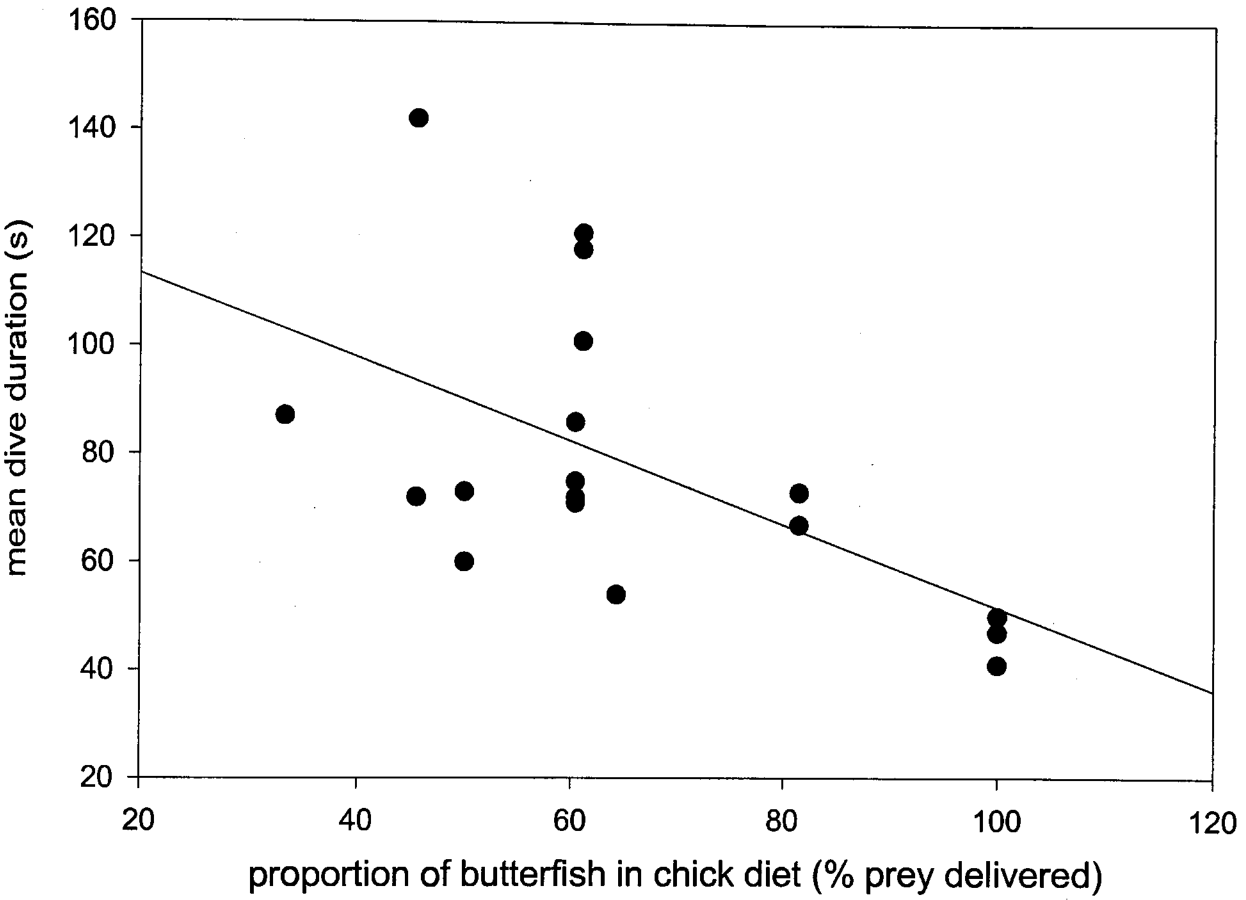

Figure 5. The mean dive duration (s) for birds from individual nests and the proportion of butterfish delivered to the nest (% butterfish of total prey delivered).

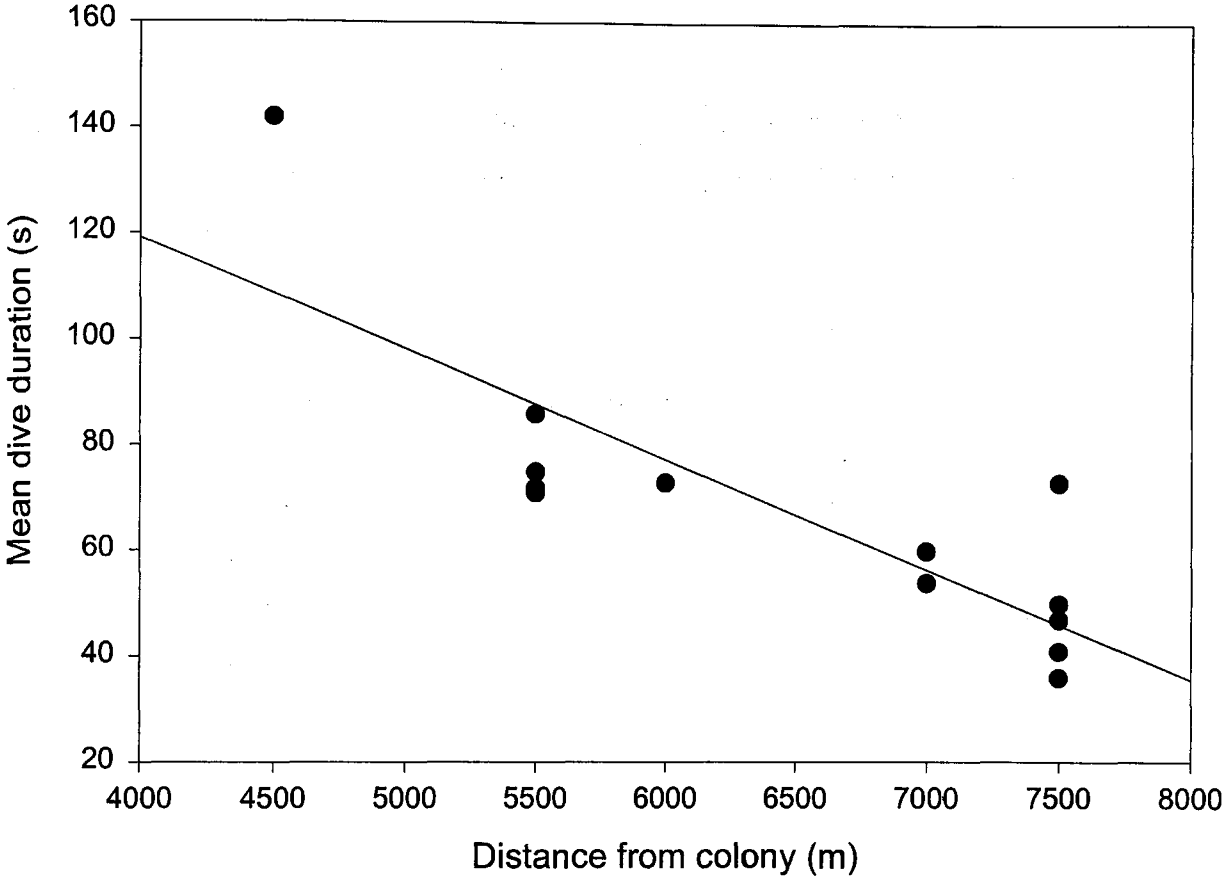

Figure 6. The mean dive duration for individual birds (s) and the distance travelled from the colony to forage (m).

second chick in two chick nests. There was no relationship between the growth rate of the "A" chick and the composition of diet. This is most probably due to the larger size of the "A" chick and its greater competitive ability during provisioning (Cook *et al.* in press, Mock & Parker 1998). These chicks, being larger, are generally first to receive a prey item and there is less variation between their growth rates than the growth rates of "B" chicks.

The butterfish, from studies of the energetic content of fish (Nolet *et al.* 1989), has a relatively high energy content compared to other prey species consumed by seabirds in the North Sea (butterfish, 5.01 kJ/g; sandeel, 4.63 kJ/g). Also, from the observation of prey delivered to nests at the study colony we have seen that the butterfish is the largest prey item commonly delivered (being on average 1.5 times the length of sandeels brought to the nest). The combination of these factors makes butterfish the most profitable prey item commonly captured and delivered to chicks by adult Black Guillemots. Given this, it can be reasonably concluded that all birds at this colony should attempt to provision their chicks on fish of this species.

From the data on foraging distance it can be concluded that the sites most rich in butterfish in suitable foraging habitat are located at a considerable distance from the colony (see also Chapters 6 & 9). The costs of flying are high for seabirds of this type (Pennycuick 1987, Nettleship & Birkhead 1985) and the distance of foraging trips associated with a high proportion of butterfish in the chick diet can be as high as 18km. Thus, if an adult bird is to profitably make trips of this length it has to be able to efficiently capture prey at the foraging location in order to maximize the amount of energy delivered per unit time spent foraging. The amount of variability in the number of dives per foraging bout between individuals at this site is high (*pers obs*, Walton *pers comm*), suggesting a considerable difference in foraging ability between adult birds. This would explain the strategy of some birds, in foraging closer to the breeding colony and capturing prey of lower energetic content, minimising the energy expenditure during foraging in terms of travel costs. The reduction of dive times by birds foraging at sites far from the colony (given no difference in depth) suggests that these birds are foraging more efficiently and are thus more able to economically forage for butterfish in these sites. If all birds were of sufficiently high foraging ability to be able to provision their chicks in this way we could expect to see all birds from the colony foraging in areas far from the colony and bringing predominantly butterfish to the nest. In the case of the "S" chick the relationship is a negative one, with increasing proportion of butterfish leading to reduced growth rates. These birds are likely to be lower quality individuals, possibly younger (Asbirk 1979), and the trade-off between distance traveled and prey quality may be different for such birds. Less efficient foraging may mean that travelling further is more costly for these birds, and not offset by the advantages of larger prey. This may represent a state-dependent difference in optimal foraging strategies, the cost and benefits of travelling different distances differing with regards to individual quality, in this case age. However, the sample size here is very small, and this requires further investigation.

Chapter 6

Sea Surveys

Introduction

The study of population ecology has developed largely separately from the study of behavioural ecology, despite the large amount of common ground between the subjects. The central theory behind behavioural ecology, that maximisation of individual fitness has shaped behavioural traits and can be related to the population consequences. The demography of a population depends on the responses of individual animals to their specific circumstances and ability as they try to maximise their lifetime reproductive success. Central to modern understanding of the behaviour of animals in relation to foraging is the concept of the ideal free distribution (Fretwell & Lucas, 1970). Distribution can be considered to be "ideal" in that individuals will attempt to maximise their fitness, and "free" in that individuals are free to move from area to area unhindered (dependent on range). The underlying assumptions of the basic model do not allow for complicated interactions between conspecifics.

The Black Guillemot is likely to be less affected by complicating factors than most species. It does not suffer heavily from predation whilst at sea so there will be little difference between patches in the risk of foraging. Its main prey species, the Butterfish, would appear to not be greatly affected by depletion. Individual fish occupy territories and if these territories are emptied they are quickly filled (Kruuk *et al.* 1988), thus, it shows a "buffer effect" (Brown 1969). There is, however, a suggestion that individual Black Guillemots themselves hold feeding territories, although there seems to be little direct evidence for this in the literature. This would mean an increase in interference by conspecifics and this would have an effect on the distribution of foragers and on the rate of depletion of prey species (Sutherland 1996). If there is interference from conspecifics then the ideal free distribution no longer applies in its simple form as individuals will no longer be "free" to move without hindrance.

The study of the spatial distribution of seabirds has been largely restricted to the study of pelagically feeding seabirds, observed from ships (Tasker *et al.* 1984, Stone *et al.* 1995). Such studies are conducted on a large geographical scale (typically measured in kilometres) looking at overall population distribution. This type of sampling is restricted mostly to transects and has a number of problems associated with it, one of the main being observer differences in sampling accuracy (Van Der Meer & Camphuysen 1996). Such studies reveal little of the fine scale relationship between the birds and the waters they are feeding upon due to the difficulty of collecting accurate data on the underwater environment in open water systems.

In the North Sea, an extensive study was carried out in the 1980's to investigate the offshore and inshore distribution of seabirds over the whole of the British waters of the North Sea. This study (Tasker *et al.* 1986) included the Black Guillemot and documented the inshore nature of Black Guillemot distribution and the surprisingly low dispersal rates of this species in British waters. Densities of birds in these studies were measured at a resolution of number of birds per square kilometre, a much coarser scale than used in this study, but a fine scale considering the amount of area covered.

This study aims to investigate the fine scale pattern of distribution over the feeding areas of an inshore foraging seabird during the breeding season.

Methods

The inshore waters of Papa Westray were surveyed from a small boat. The craft used was a 18ft dory powered by a Yamaha 30hp outboard, carrying spare fuel, flares, an anchor, GPS, an echosounder and a marine VHF. This enabled transects to be carried out over the shallow inshore waters surrounding Papa Westray. The transect route is shown on Figure 1 and was designed to cover all of the shallow inshore water (waters of up to 40m depth) although some deeper water was regularly surveyed in order to test the received wisdom that Black Guillemots do not forage at greater depths (Piatt & Nettleship 1985). These transects were undertaken at times when the roost (the area of rough tidal water) at the NW tip of the island was slack, i.e. at 1 hour before high and low water at Kirkwall. Surveys were carried out in 1996 on the 24th, 26th, 27th & 28th of June and the 1st 5th, 9th, 16th, 20th, 28th & 29th of July. In 1997 on the 29th May, the 10th & 29th of June and the 3rd, 4th, 7th, 9th & 27th of July. Advice was sought from local fishermen on the conditions as the seas around the island can be hazardous, and lifejackets were worn at all times. The crew for the transects comprised two members, one piloting and the other keeping notes. The island was circumnavigated anticlockwise in order to meet slack tides without comprimising the survey schedule. Each crewmember had the responsibility of watching a forward quarter and on sighting of a black guillemot, the speed would be decreased and the bird approached as closely as possible without putting it off the water. The position on the GPS and the water depth were recorded and the position of the bird marked on a map. In this manner, all the available habitat (up to 40m depth) could be surveyed around the island and all birds present recorded. These data points were then entered into a spreadsheet using OS grid references to the nearest 10 metres.

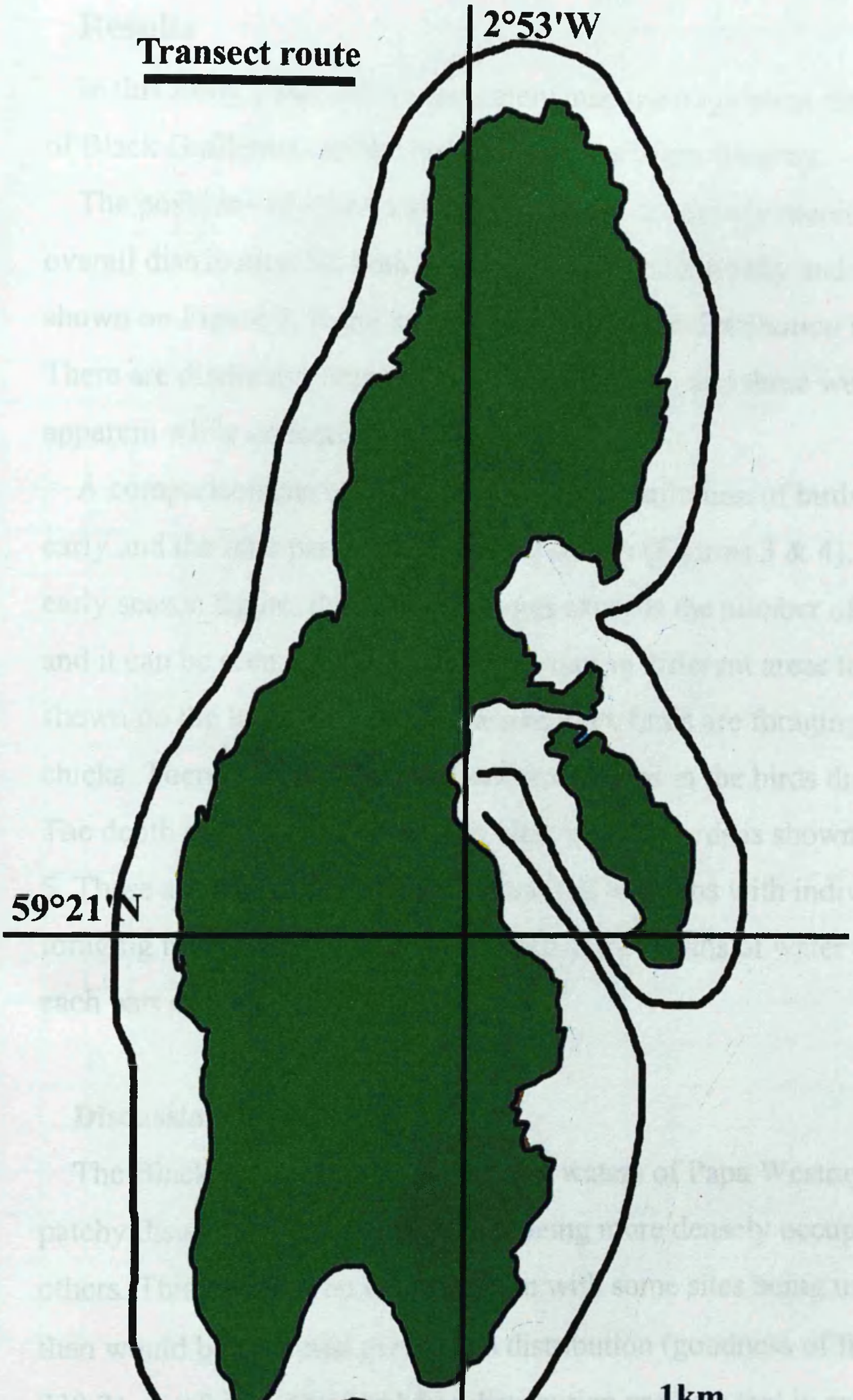

Figure 1. Route of transect around Papa Westray. Surveys were undertaken anti-clockwise.

Results

In this study I was able to accurately map the population distribution of Black Guillemots on the inshore waters of Papa Westray.

The positions of each individual bird were accurately recorded and the overall distribution for both years can be plotted spatially and this is shown on Figure 2. It can be clearly seen that the distribution is not even. There are distinctive areas of high concentration, and these were apparent while collecting the data.

A comparison can be made between the distribution of birds in the early and the later part of the breeding season (Figures 3 & 4). In the early season figure, the number of eggs exceeds the number of chicks and it can be seen that the birds are favouring different areas to those shown on the late season figure, where more birds are foraging for their chicks. There was no variation between seasons in the birds distribution. The depth of water in the foraging sites used by birds is shown on Figure 5. These are depths of the water column in locations with individual foraging birds. There was no difference in the depths of water utilised in each part of the season.

Discussion

The Black Guillemots on the inshore waters of Papa Westray show a patchy distribution, with some areas being more densely occupied than others. This distribution is not random with some sites being used more than would be expected given even distribution (goodness of fit, $X^2 = 238.21$, $p < 0.01$). The ideal free distribution predicts that in areas of high heterogeneity the spatial distribution of a foraging species will depend on the patchiness of the prey type, as well as interference from conspecifics (Sutherland 1996).

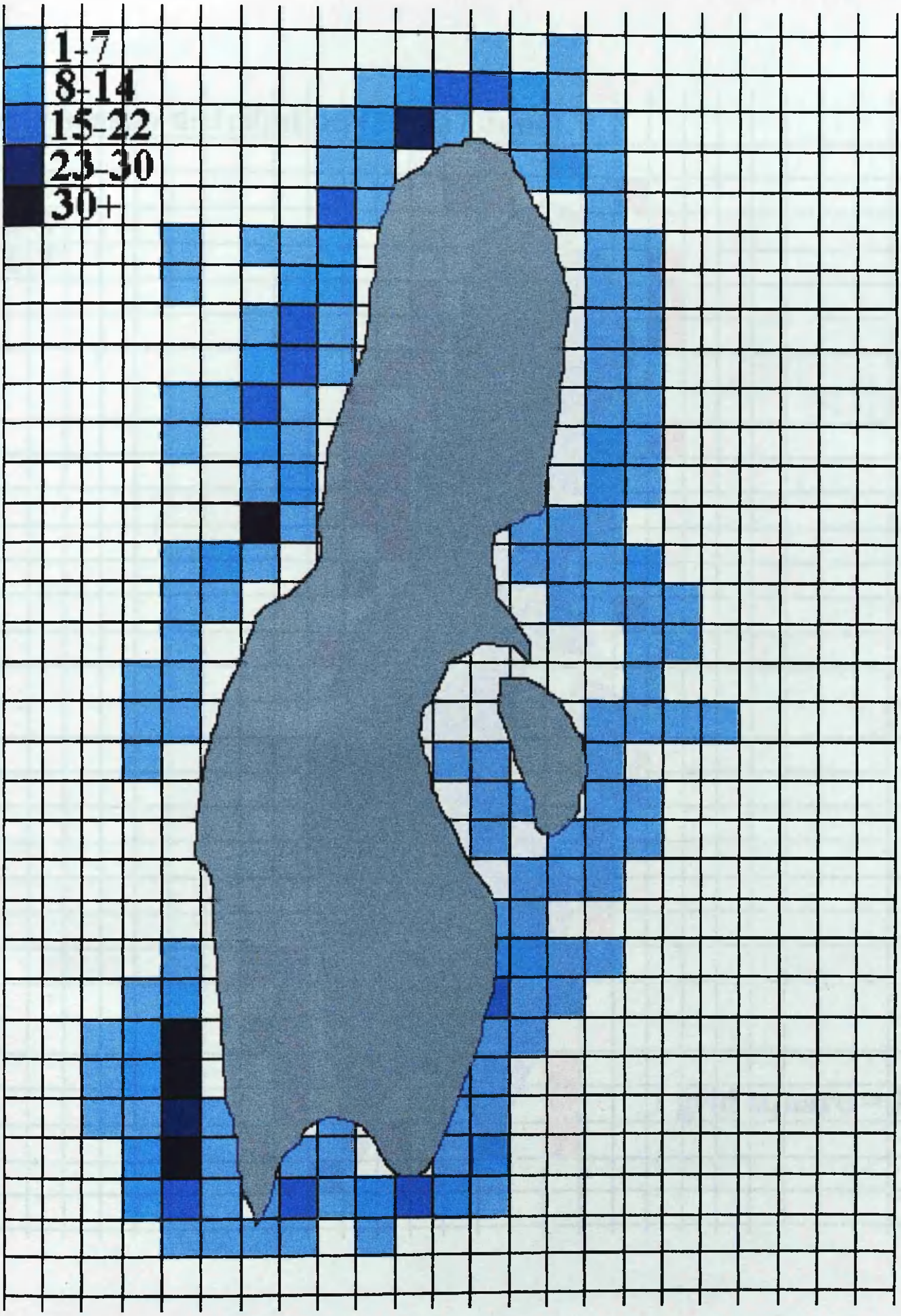

Figure 2. Overall distribution of foraging Black Guillemots on the inshore waters of Papa Westray based on surveys. Densities shown are total numbers of birds. 1 square = 250m.

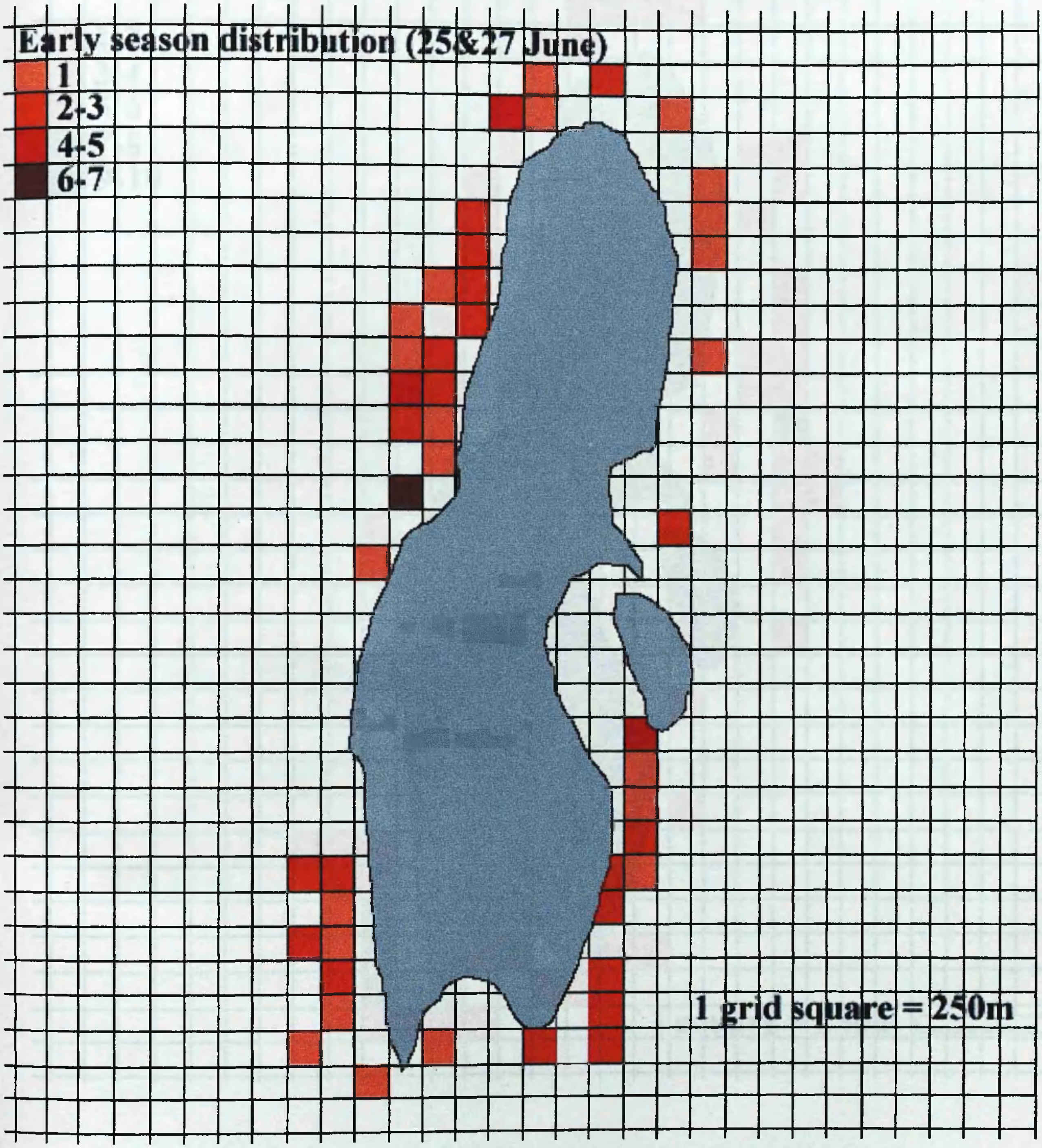

Figure 3. Early season distribution of Black Guillemots. Key for densities is shown on top left of figure (actual numbers).

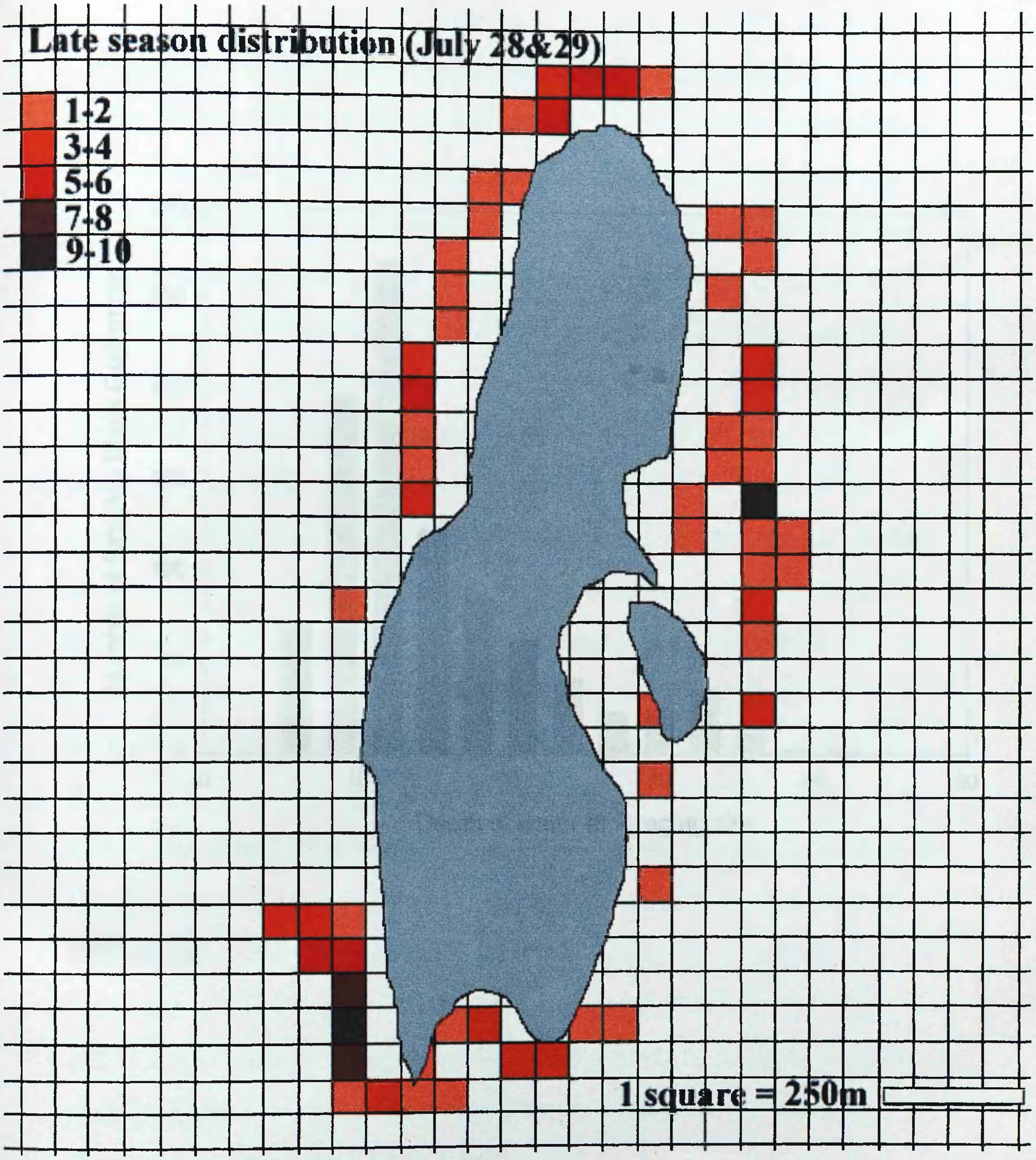

Figure 4. The late season distribution of Black Guillemots around Papa Westray (July 28 & 29). Key as Figure 3.

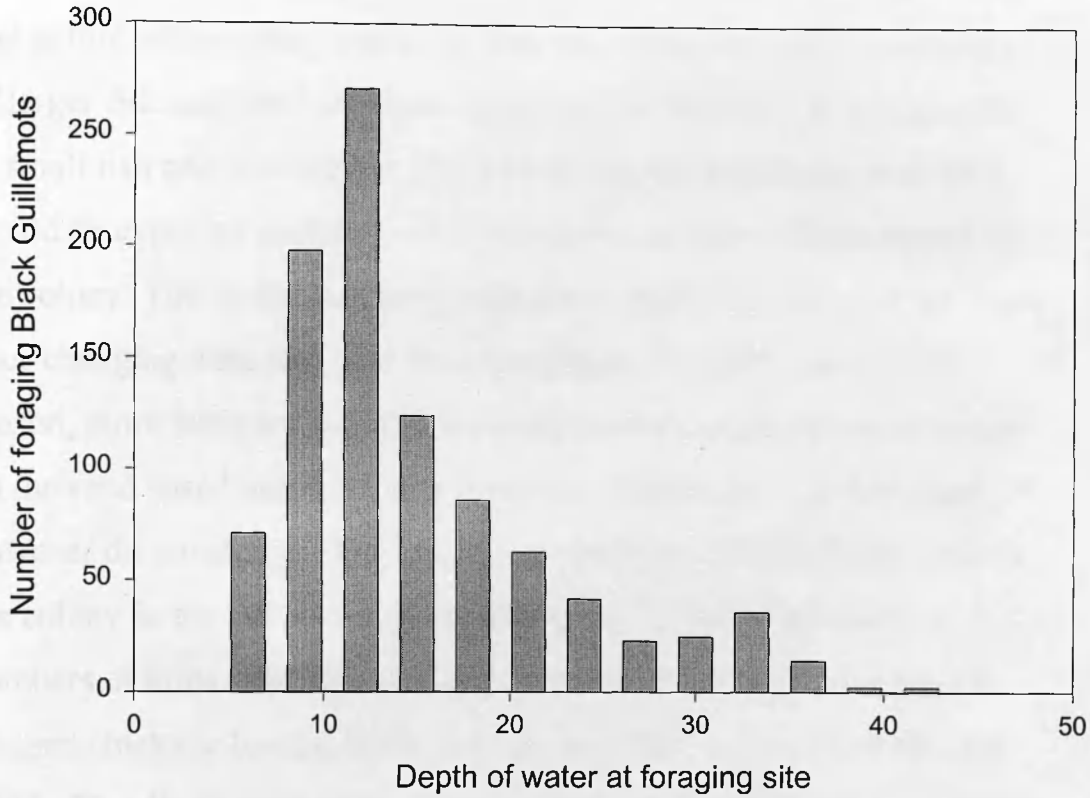

Figure 5. Depth of water used by foraging Black Guillemots located during surveys of the inshore waters of Papa Westray.

It is known that adult Black Guillemots feed on different prey to their chicks (Ewins 1986, Nettleship & Birkhead 1986), feeding themselves more on smaller fish and crustaceans which form very little of the chick diet at this colony (see Chapter 5). The bulk of the chick diet comprises of larger fish and these are likely to be found in different foraging areas to small fish and crustaceans. The distribution of adult birds, therefore, would be expected to change with the number of chicks being reared at the colony. This is the case here, with the relative importance of the main sites changing with date, and thus the number of chicks. Later in the season, more birds are going to the south-west tip of the island to forage on the sand based habitats found there (see Chapter 8). The sites used however do not change. The increase in numbers of birds found close to the colony in the late season distribution may be due to increased numbers of birds who have finished breeding, either by having already fledged chicks or having failed, are staying close to the colony (Burger 1997). The distribution of the favoured prey for the chicks, the Butterfish *Pholis gunnellis,* shows temporal and seasonal variability (Kruuk et al 1988, Quasim 1957) in distribution as well as activity. The body condition of this fish species also shows seasonal variability (Quasim 1957) and this could affect the relative profitability of foraging for this prey type (see Chapter 5). This would be very likely to influence the distribution of predators feeding upon them.

The depth of water dived in is consistent with other studies measuring the diving depth of this species.

In order to examine the feeding sites used by adults foraging for themselves, further studies would have to be conducted, surveying these inshore waters outwith the breeding season when foraging is not taking place in order to feed the chicks. Black Guillemots are unusual amongst

North Atlantic auks in that they do not disperse far from the colony during the winter months, presumably due to their dependence on shallow water food species.

The relationship between this distribution and the availability of prey and habitat around Papa Westray is examined in Chapter 9, and the foraging distances are examined in Chapter 7.

Chapter 7

Travel distance in an inshore foraging seabird.

Introduction

It is generally considered that the annual reproductive rate of seabirds is strongly linked to their feeding zones, and thereby to the energetic demands of foraging (e.g. Ashmole 1971, Lack 1968, Croxall 1987). Seabirds feeding in inshore coastal waters generally rear more than one chick, whereas those foraging in offshore (more pelagic) areas generally rear only a single chick (Nettleship & Birkhead 1985, Lack 1968). The presumed longer travel time associated with offshore foraging is thought to play a part in limiting the number of chicks that can be reared successfully within any one breeding event. The link between foraging area and annual reproductive output is considered to be well illustrated in the auks (Nettleship & Birkhead 1985). The *Cepphus* species generally forage close inshore (Cramp & Simmonds 1977, Nettleship & Birkhead 1985), and are unusual among auks in that the normal clutch comprises two eggs. This contrasts with the single egg clutch typical of the other auks that forage in more offshore areas (Nettleship & Birkhead 1985, Gaston & Jones 1998).

To date, relatively little accurate work has been carried out on the travel distances of inshore foraging seabirds. It has been assumed that those species which forage close to the shore are expending less energy in travelling to the feeding sites than those species foraging further from the shore (Nettleship *et al.* 1994). However, distance offshore is not the same as travel time. The former refers to how far the feeding area is from the nearest land-mass, while the latter refers to distance actually flown by the foraging bird from the breeding to the feeding site. Some inshore foraging species could still travel relatively long distances, albeit within the inshore area, in order to reach good feeding areas. It is important therefore to examine actual distance travelled when considering the energetic and time costs of foraging, rather than simply the distance offshore.

In this study, we identified the feeding areas used by breeding Black Guillemots *Cepphus grylle* by both counts of feeding birds from sea transects and by the use of radio telemetry to follow foraging individuals. We then compared the foraging distance as measured by distance offshore with that measured as actual distance travelled between the breeding and feeding areas.

Methods

The study site was located at a colony of approx. 80 pairs of breeding Black Guillemots situated on a small island off the east coast of Papa Westray, Orkney 59°22'N, 02°53'W (Chapter 2, Figure 1). This is the only significant concentration of Black Guillemots in the area, the nearest sizeable colony being on the west coast of the island of Westray, some 15km away from the surveyed area. Therefore it can be assumed that the majority of birds seen in the vicinity belong to the Papa Westray colony. Any birds that did in fact breed on Westray would have travelled an even greater distance to the foraging locations than we have calculated, thus our estimates of travel distances are minimal estimates. The inshore waters surrounding Papa Westray were surveyed during 1997 from a 4m dory-style boat powered by a 30hp outboard motor. We used a standard track round the island, the course of which is shown in Chapter 6, Figure 1, surveying an area approximately 1km from the island coast (validated using Global Positioning System, GPS). In this way all the inshore waters of up to 40m depth around Papa Westray were surveyed, this being the maximum observed depth of water used by foraging Black Guillemots (Nettleship & Birkhead 1985). The location of every bird observed on the surface of the water was recorded using a handheld GPS and logged. Accuracy was reported to be to the nearest 25m or less (by the manufacturers, Magellan). This was checked using traditional navigational methods; that is, by the taking of accurate bearings from known landmarks and comparing with the GPS readings at regular intervals, and it was found to be a good estimate. In all, 26 surveys were carried out during the breeding season, the number being constrained by weather and the strong tidal streams at the north west corner of the island which limited surveys to certain times (HW or LW at Kirkwall +1hr). The surveys were carried between the 25th May and the 29th July, a period covering both incubation and chick rearing at this colony.

Birds from known nests were trapped on the colony and radio tags attached beneath the central tail feathers using steel-toothed cable ties and self-amalgamating tape (see Chapter 2). Tags weighed approximately 3.5g (<1% adult body weight), and emitted a pulse every 0.8 seconds on the 173mMHz waveband. These signals were picked up using receivers attached to 6 or 8 element Yagi aerials, the accuracy of which was tested to being less than 2° direction (using null/peak switching). Birds were followed from mobile tracking stations in order to provide maximum coverage of the inshore waters surrounding the island. Tags were attached to, and data collected from, 18 birds (6 in 1996, 4 in 1997 and 8 in 1994). Tracking was carried out during the chick rearing phase (June to July) in order to collect information on chick provisioning.

Foraging sites were identified by the diving behaviour of the birds, recorded either visually or from the intermittent absence of the radio signal in the tagged individuals which indicates diving (Trivelpiece *et al.* 1986), Heath & Randall (1989)). For each foraging bird located on transects, the offshore distance was measured to the nearest shoreline point using a large scale (Ordinance Survey 1:10,000) map. Black Guillemots do not fly over the land. Travel distances from the colony were therefore calculated as the shortest possible route over the sea from the colony to the feeding site. For each radio tagged bird, the median offshore distance and median travel distance was calculated.

Results

The overall distribution of the Black Guillemots counted in the surveys, compared with the distribution of radio tagged birds is shown in Figure 1. In all, the positions of 623 foraging birds were pinpointed. Most birds were found to forage on the west coast of Papa Westray, with concentrations in both the south and the north. The offshore distance and the travel distances are shown in Figure 2a & b. There was a significant difference between the two (Wilcoxon's matched pairs, $z = -20.39$, $p<0.001$), with the median offshore distance being 300m and the median travel distance nearly 20 times greater, at 5.50km. The distribution of travel distances is bimodal, with peaks at 1000 and 6500m, but no bimodality was evident in the offshore distances.

The distribution of feeding sites used by the radio tagged birds closely matches that found in the island transects (Fig. 1). Figures 3 a & b show the frequency distribution of the median offshore distances and travel distances for each of the radio tagged birds. Again, there was a significant difference between the two (Wilcoxon's matched pairs $p<0.001$), with the median travel distance being nearly 20 times greater

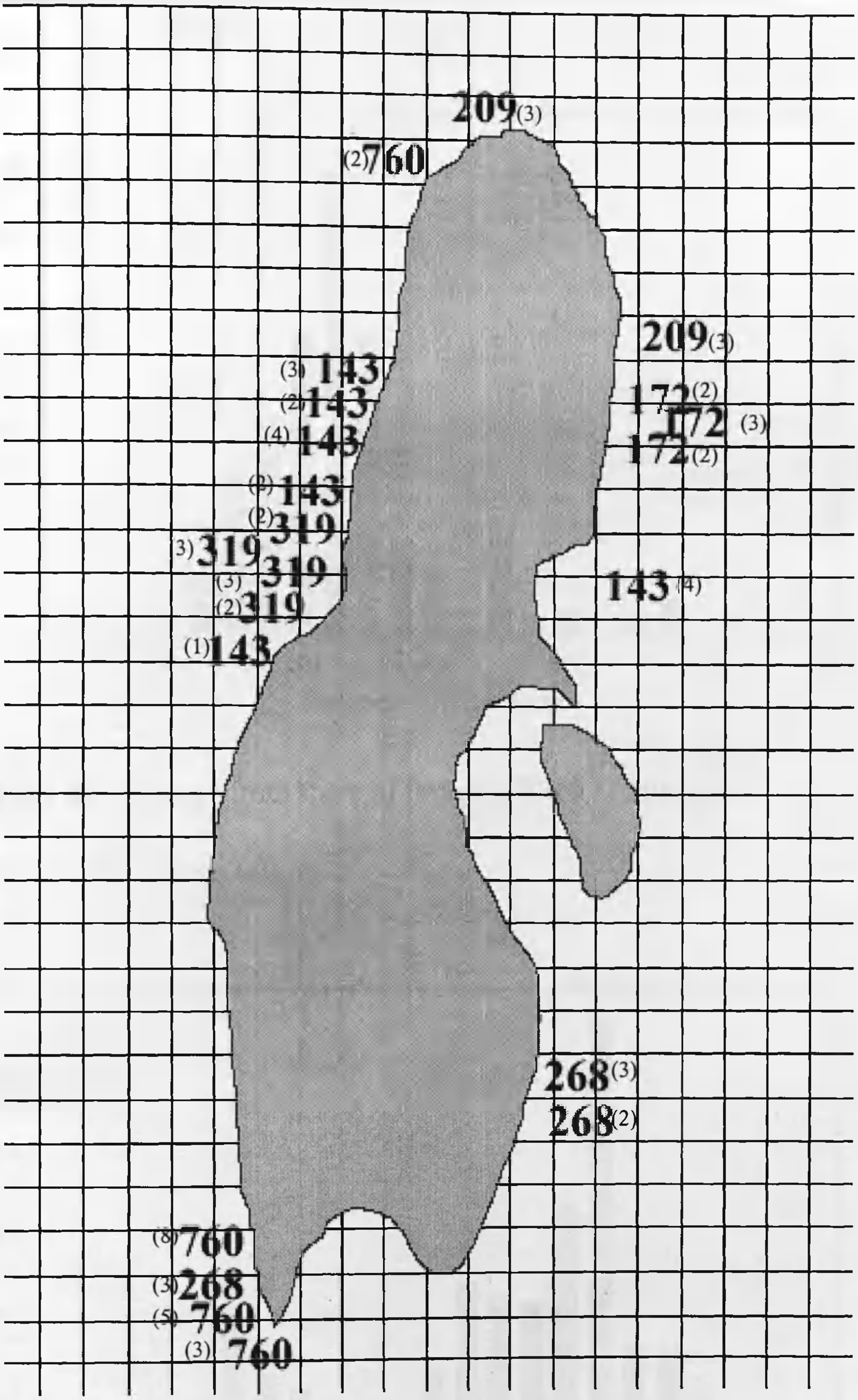

Figure 1. Distribution of radio tagged birds around Papa Westray. Numbers represent individual birds; numbers in brackets represent the number of fixes of each individual in each location. 1 square = 250m.

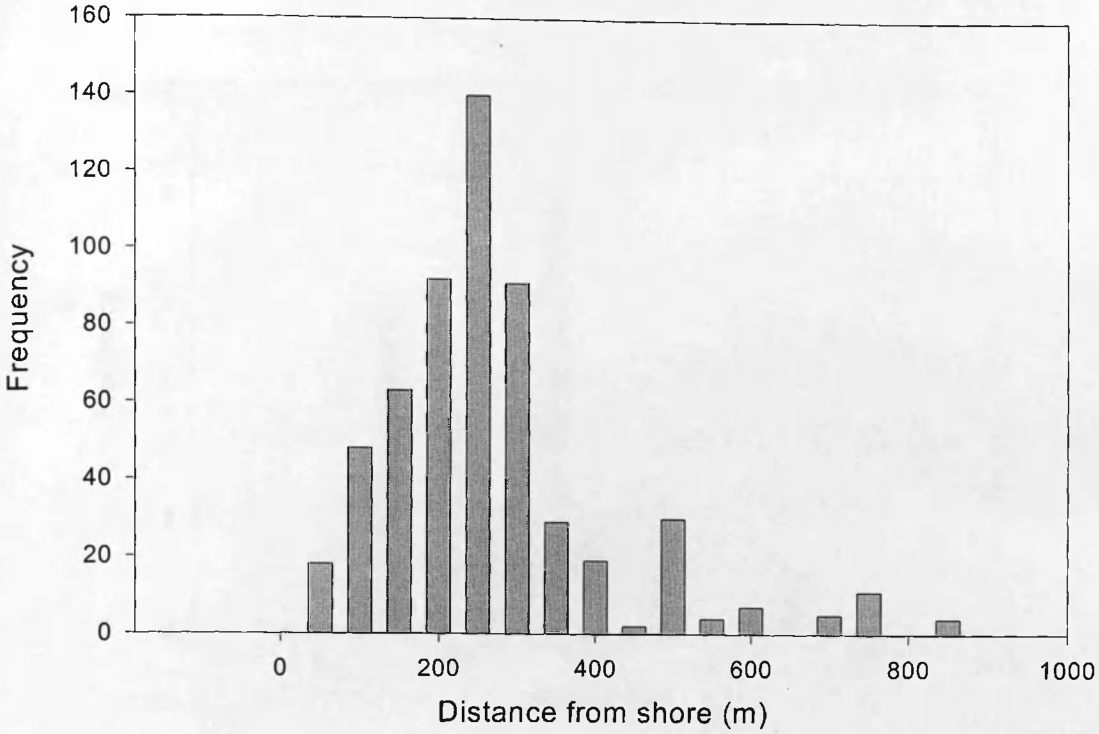

Figure 2a. Distance from shore of foraging Black Guillemots

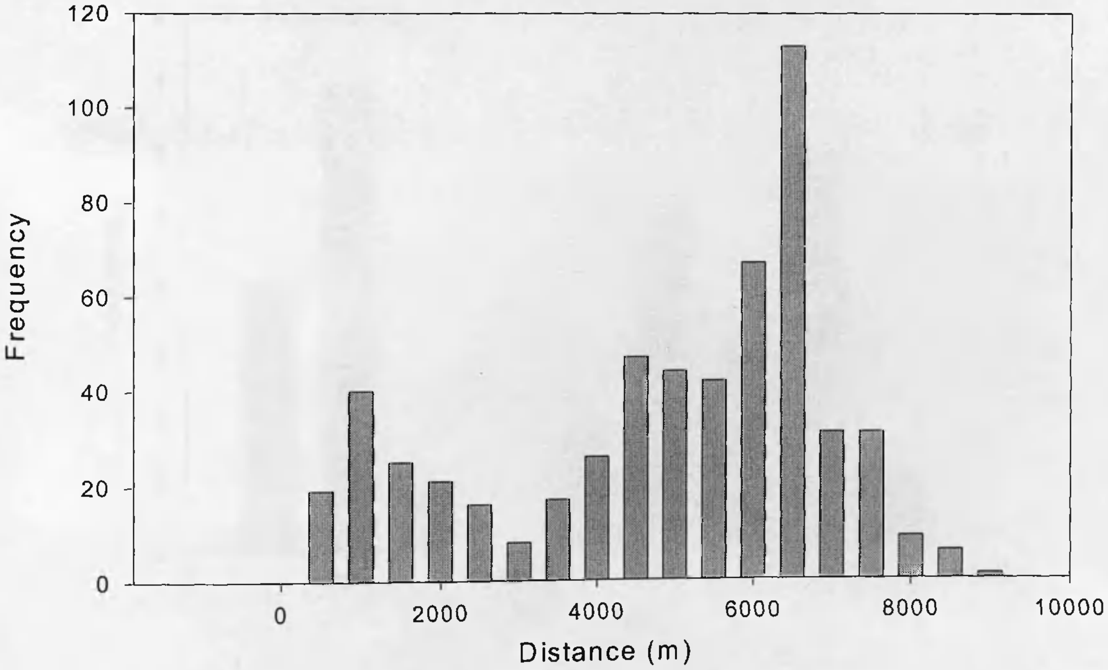

Figure 2b. Frequency histogram of distance from colony of individual birds

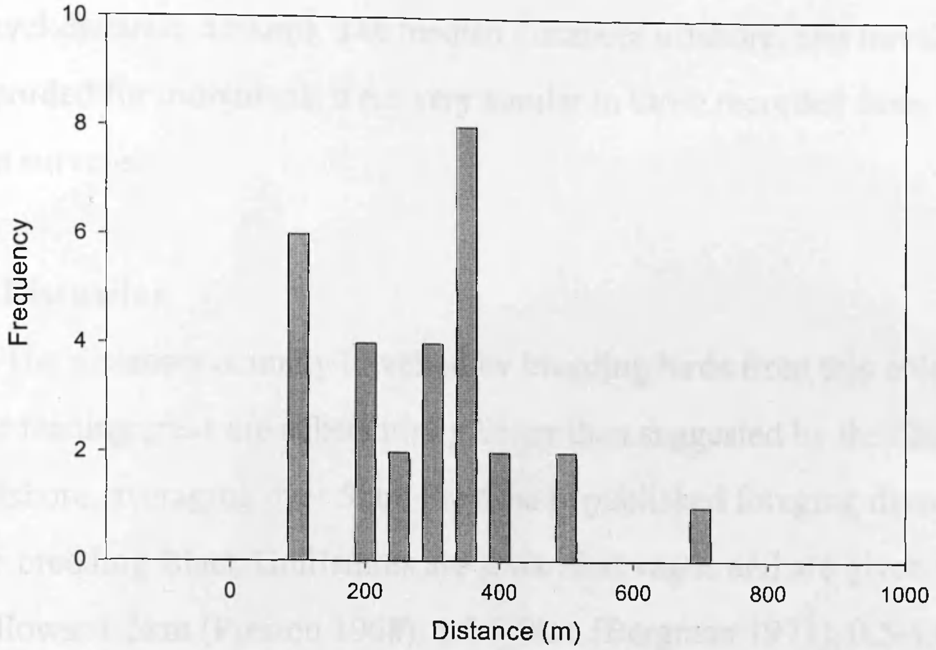

Figure 3a. Distance offshore for radio tagged birds.

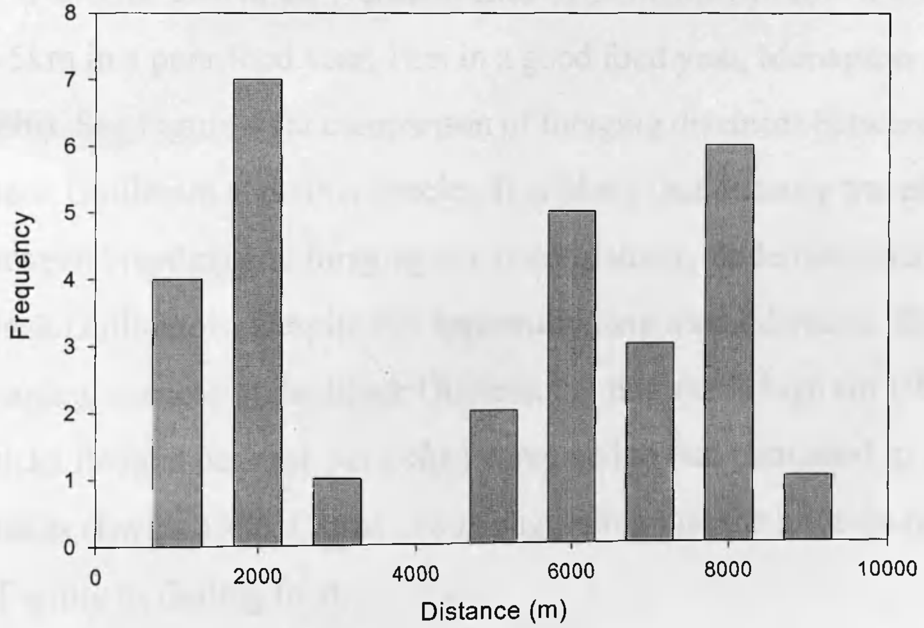

Figure 3b. Distance from colony of radio tagged birds.

than the distances offshore (median offshore distance 275m, median travel distance, 5500m). The median distances offshore, and travelled, recorded for individuals were very similar to those recorded from the sea surveys.

Discussion

The distances actually travelled by breeding birds from this colony to the feeding areas are substantially larger than suggested by the distance offshore, averaging over 5km. Previously published foraging distances for breeding Black Guillemots are somewhat vague and are given as follows: 1.5km (Preston 1968), 1.5-4.0km (Bergman 1971), 0.5-4.0km (Asbirk 1979), <2km (Bianki 1967), <7km (Nettleship & Gaston 1978). The distances flown by birds breeding on the Holm of Papa Westray are larger than most of these estimates of the foraging distance of the Black Guillemot, and comparable to that recorded for the Common Guillemot, *Uria aalgae,* also in the Northern Isles of Scotland, by radio telemetry (6.5km in a poor food year; 1km in a good food year, Monaghan *et al.* 1996). See Figure 4 for comparison of foraging distances between the Black Guillemot and other species. It is likely that distance travelled between breeding and foraging site is consistently underestimated in Black Guillemots. Despite this apparently long travel distance, the breeding success of the Black Guillemot at this site is high (in 1997, 0.6 chicks fledged per nest, *pers obs.*) compared to that published in other studies (Ewins 1986, Cairns 1980), suggesting that the birds do not have difficulty in finding food.

The distribution of foraging distances for the surveyed birds shows a degree of bimodality. Such a distribution can also be seen in the distribution of feeding sites from radio tagged birds. It is possible that

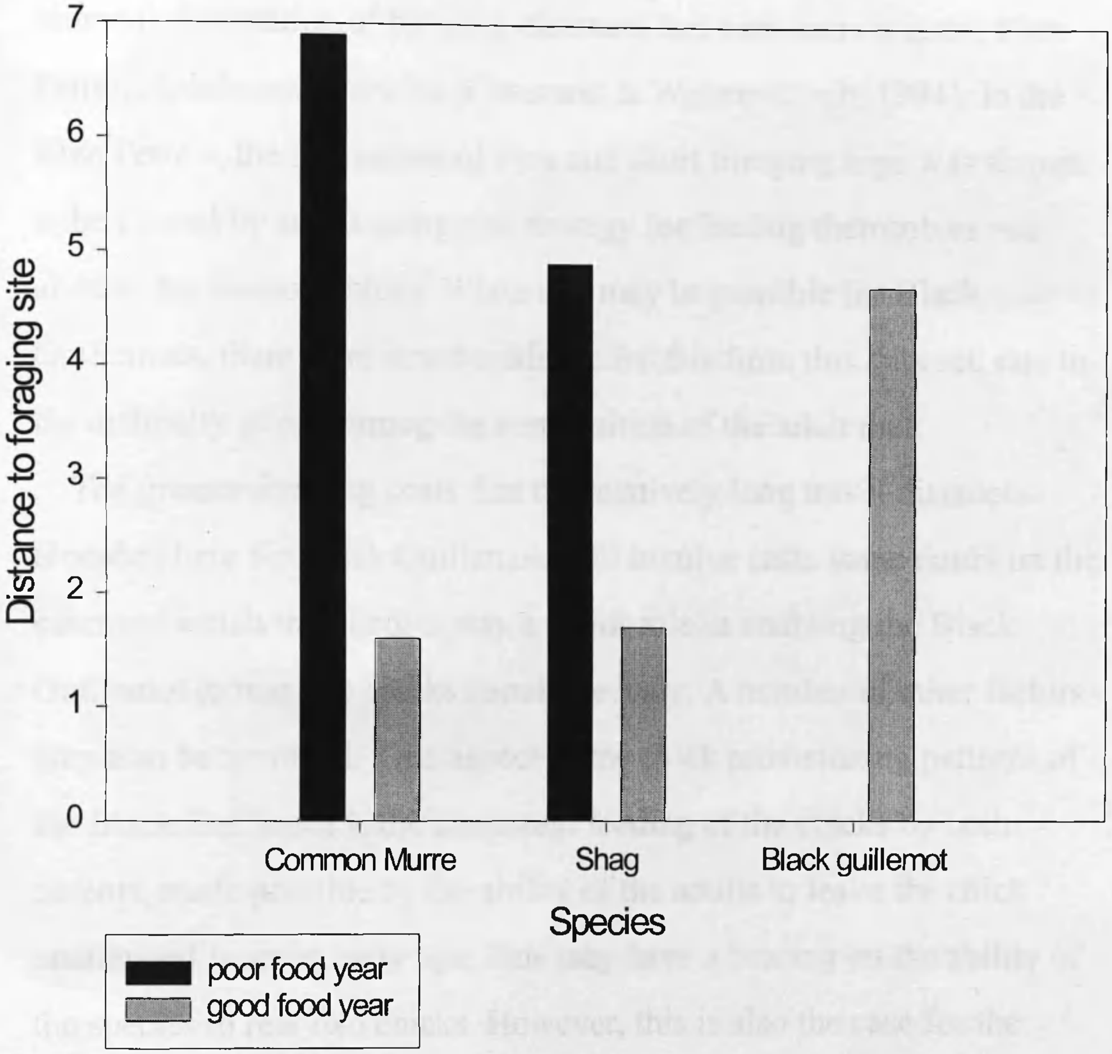

Figure 4. Foraging distance in the Black Guillemot compared with two other North Sea seabird species, the Shag Phalacrocorax aristotelis and the Common Murre Uria aalge in years of differing food availability (Shag & Murre data from Monaghan 1996).

this is due to either environmental factors such as uneven distribution of suitable foraging habitats, or, to some behavioural tendency for the birds to forage in sites both relatively near and far from the colony. Such a bimodal distribution of foraging distances has been shown in the Blue Petrel, *Halobaena caerulea* (Chaurand & Weimerskirch, 1994). In the Blue Petrels, the alternation of long and short foraging trips was shown to be caused by adults using one strategy for feeding themselves and another for feeding chicks. While this may be possible for Black Guillemots, there is no direct evidence for this from this data set, due to the difficulty of examining the composition of the adult diet.

The greater foraging costs that the relatively long travel distances recorded here for Black Guillemots will involve casts some doubt on the extent to which travel costs play a major role in enabling the Black Guillemot to rear two chicks simultaneously. A number of other factors may also be involved. One aspect of the chick provisioning patterns of the Black Guillemot is the consistent feeding of the chicks by both parents, made possible by the ability of the adults to leave the chick unattended from an early age. This may have a bearing on the ability of the species to rear two chicks. However, this is also the case for the Atlantic Puffin *Fratercula arctica,* but this species only rears a single chick and forages in relatively inshore waters. Like most North Sea seabirds, Puffins feed their chicks on sprats and sandeels (*Ammodytes spp,* Harris & Wanless 1985, Monaghan 1992), or other shoaling pelagic fish species (Harris & Hislop 1978). The Black Guillemot provides its chicks with inshore demersal species (in the case of this colony, primarily the Butterfish *Pholis gunnellis*), often of greater size (see chapter on chick diet) than sandeels and of greater nutritional content (Butterfish, 5.01 kJ/g, Watt 1991, Sandeel, 4.63 kJ/g, Hilton *et al.*

1998). *Cepphus* species generally bring larger prey to their chicks (12-15g, Gaston 1985, Cairns 1978) than Common Guillemots (8-15g, Gaston 1985, Harris and Wanless 1985), also increasing the amount of energy delivered per item. The Black Guillemot can also stagger the fledging of its two chicks thus reducing the peak demand for food items.

Another possible explanation for the increased brood size is the flight ability of the Black Guillemot, widely quoted as being one of the most able flyers of the North Atlantic alcidae. This would make flight more efficient and thus the distances involved for foraging trips would be less energetically expensive. Using Pennycuick's (1996) equations for costs of flight, we can compare the costs between the Black Guillemot, the Common Guillemot, and the Puffin. At the most efficient flying speed (23m/s for the Black Guillemot and 25m/s for the Common Guillemot) the Common Guillemot uses almost twice as much fat per km as the Black Guillemot (0.0831g/km as opposed to 0.0489g/km). The Puffin uses a similar amount of energy per km as the Black Guillemot (0.0414g/km at 22.5 m/s).

It is worth noting that the radio tagged individuals showed a large degree of site fidelity in foraging area, the same individuals returning to the same one or two foraging sites. It has been suggested that Black Guillemots hold foraging territories, and these findings would be consistent with that idea whilst not providing direct evidence.

This study clearly shows that, although the foraging areas used by Black Guillemots are relatively close inshore, the distance travelled between feeding and breeding sites is much larger, and comparable to that travelled by other auks that rear only a single chick. The apparent dichotomy between inshore and offshore foraging auks is more complex than at first sight, and the difference in reproductive output may relate to other aspects of their foraging ecology such as the nature of the prey or aspects of their diving behaviour.

Chapter 8

Diving Surveys

Chapter 8

Diving Surveys

Introduction

Spatial heterogeneity of habitat around the breeding colony is an important factor in the foraging economics of seabirds. Uneven distribution of resources can affect the amount of energy expended in foraging, due to factors such as time spent searching for profitable foraging sites, the costs of travelling to and from a suitable site and the ease of capture of prey items of differing nutritional composition. In addition, prey species diversity and abundance may vary with available foraging habitat. Such environmental factors have been shown to affect feeding performance of a number of seabird species (e.g. Carbone & Houston 1994; Monaghan *et al.*, 1994; Wanless *et al.* 1997).

Despite this, little work has been carried out relating the habitat composition of foraging sites to the behaviour and distribution of seabirds, primarily because such data are very difficult to collect, both with respect to the sites actually used by the birds, hydrographic factors and the topography of the sea bed. Most studies involve relatively large-scale measurements. One such study carried out on the Isle of May related the location of foraging Shags (*Phalacrocorax aristotelis)* to the composition of the seabed as described on existing surveys carried out by the British Geological Survey (Harris & Wanless, 1997), but even this involved relatively coarse scale information on topography.

This study is one of the first to compare the population distribution and individual behaviour of a seabird species, the Black Guillemot, to the heterogeneity of the marine environment in which it feeds. Black Guillemot facilitate such a study as the feeding sites are all within a depth range suitable for human divers (<35m), and the birds at the study site feed their chicks almost exclusively on demersal, often territorial fish prey (Cairns, 1981; Ewins, 1990; this study). This makes the sampling of prey species and other organisms in a given habitat possible due to the relatively stable nature of these resources.

In the first summer of this study (1996), an attempt was made to sample the composition of inshore fish species in different feeding areas using the technique of fish trapping. In a number of studies (Kruuk *et al.* 1988, Heggberget 1993, Beja 1995, and Watt 1995), fish traps have been used to monitor the populations inshore demersal prey species of the type captured by Black Guillemots (and in the case of these studies the Otter, *Lutra lutra*). These are funnel traps that rely on the prey species' tendency to seek out cervices, rather than baiting, to attract the fish (Kruuk *et al.* 1988). A sampling method such as this, which relies on the prey species behaviour, will carry a certain amount of bias, making inter-specific comparisons of abundance based solely on catches unreliable. Kruuk *et al.* (1988) suggested hand searches of the infra-littoral zone to obtain correct numbers of prey and then using these figures to calculate correction factors, which can then be applied to the catches from traps. The assumption here is that the population of fish at low tide (when the hand sampling is carried out) is the same as at other tide states, when the fish are caught. While this may be true for certain prey species, especially the eelpout, there is little evidence to either support or contradict this assumption for other prey species. Beja (1995) supplemented his data from fish trapping in Portugal by sampling via hand netting and angling. His results showed profound differences in the species composition and numbers obtained by different sampling methods (*Ibid.*) and suggested that none of the methods he used in fact gave an accurate representation of the overall composition of the fish population.

The kreeling method of prey sampling proved unsuitable for this study on practical grounds due to the impossibility of regularly checking the traps in adverse weather. Furthermore, those species that were captured, however, did not include representatives of the prey items fed to the chicks, these problems combined, with the unreliability of the method as discussed above led to this technique being abandoned (see also McCluskie, A. 1999).

A more suitable method of measuring prey abundance and diversity in the foraging habitats utilised by adult Black Guillemots at this colony was to use human divers. The feasibility of this was investigated on site, and after the submission of a proposal funding was obtained for this from Scottish Natural Heritage. For more detail on this see Chapter 2.

Methods

The dive party consisted of fifteen Marine Nature Conservation Society members and diving was carried out between 14th and 19th July 1997 from the MV Challenger. Four pairs of divers worked from the Challenger, two pairs and one three worked from the shore. In all, fifty-six seabed surveys were conducted in five days of diving (14th – 19th July). The survey sites were chosen to represent all levels of Black Guillemot usage (see Chapter 6), from the areas with the highest concentrations of foraging birds through those of low concentrations to areas which had no recorded Black Guillemots on the water. The locations of surveys are shown on Figure 1, and the schedule of dives is shown in Table 1 (presented at end of chapter).

The divers were carrying out the surveys according to the methodology described in SNH document ISBN 1 85397 121 9. This is a methodology used for the surveying of the seabed by divers and involves the recording of the physical characteristics of an underwater habitat. The surveys took the form of transects, usually of about 100m in length. The divers recorded presence of all species encountered in each

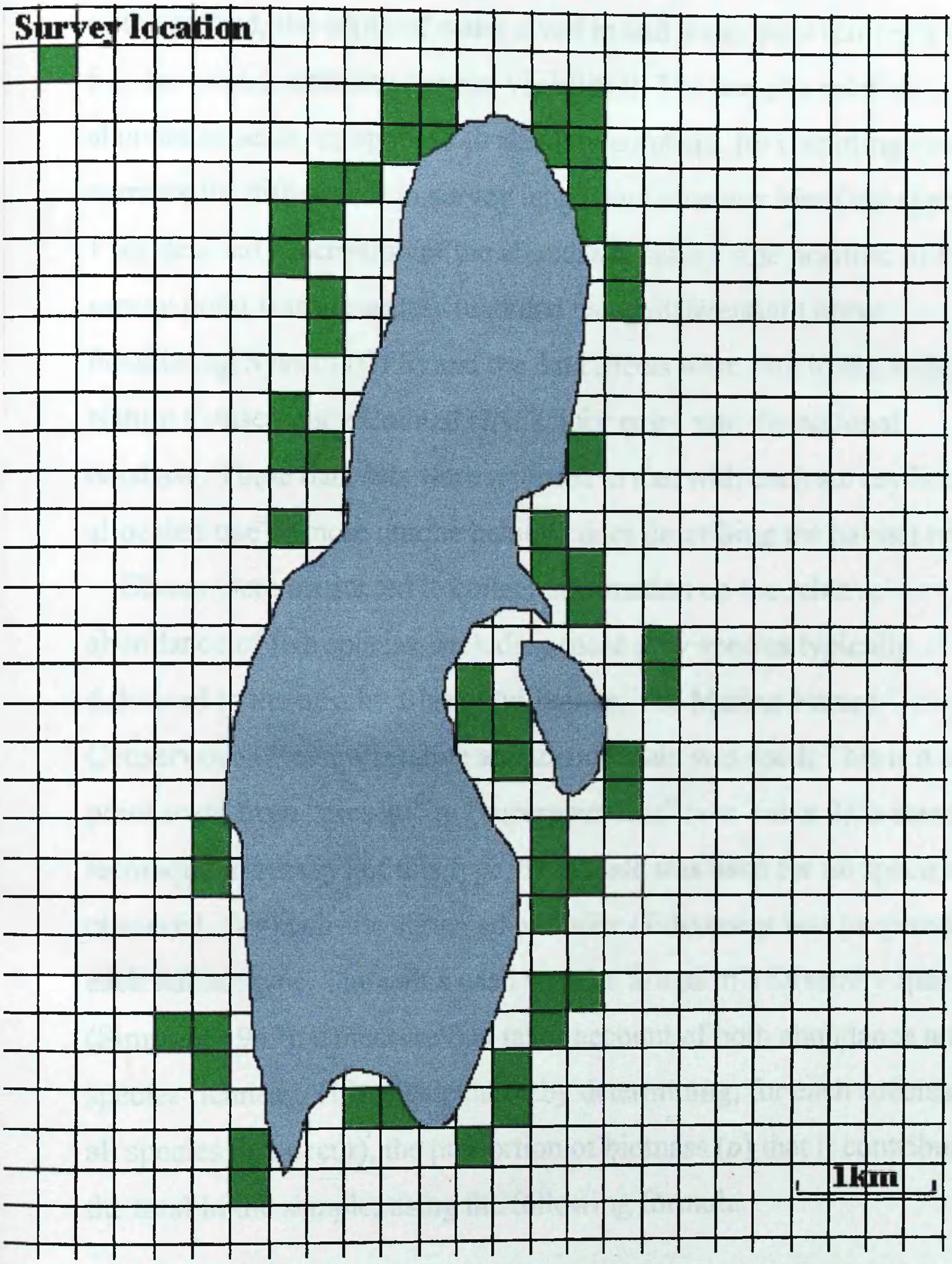

Figure 1. The locations of surveys carried out around Papa Westray. Green squares are areas surveyed.

habitat type encountered, the relative abundance of these, the topography of the seabed, the depth of water dived in and water state (currents and tide (in knots), turbidity (metres visibility)). The use of a relative abundance scale, as opposed to absolute numbers, for recording species corrects for differences in survey length and observer bias (see appendix 1 for detailed description of the abundance scale). The position of each survey point was accurately recorded using differential Global Positioning System (GPS) and the data sheets were sent to the Joint Nature Conservancy Council (JNCC) for entry into the national database. These data sets were returned to me, with each survey being allocated one or more unique habitat codes describing the habitat type.

Divers were instructed to collect information on the relative abundance of fish species, including those prey species typically delivered to the nest by Black Guillemots. The Marine Nature Conservation Review relative abundance scale was used. This is a seven point scale from "present" to "superabundant" (see Table 2), a standard technique in surveys of this type. This scale was used for all species observed. For each site surveyed an index of diversity was prepared for each habitat type. The index used was the Simpson's Diversity Index (Simpson 1949), a measure that takes account of both abundance and species richness. This is calculated by determining, for each species (of all species that occur), the proportion of biomass (*p*) that it contributes to the total in the sample, using the following formula.

$$D = \frac{1}{\Sigma p^2}$$

Table 3 shows the breakdown of habitat types and their diversities for the surveys carried out. In all, 22 discrete habitat types were recorded across all the surveys (see Table 1). All surveys were carried out in good weather conditions for obvious safety reasons.

Results

Species encountered

In total 280 different species of marine organism were recorded by divers in the 56 surveys carried out. Of these, 46 species were seaweed, 44 of the group algae, 1 lichen and 1 angiosperm. A total of 37 fish species were recorded, and a list of these is given in Table 4.

Fish prey

The prey species recorded in the surveys were those commonly delivered to the Black Guillemot chicks as observed by watching the nest site (see Chapters 2 & 5). These were butterfish *(Pholis gunnellis)*, gadoids (family *gadiodidae)*, rockling (*Ciliata & Gaidropsarus spp.*), sea scorpion (*Scorpaena scrofa*), yarrells blenny (*Chirolophis ascanii*), lumpfish (*Cyclopterus lumpus*), sandeel (*Ammodytes spp.*), leopard spotted goby (*Thorogobius ephippiatus*), sand goby (*Pomatoschistus minutus*), dragonet (*Callionymus lyra*) and flatfish species. These species along with all other fish species recorded in the surveys, are shown in Table 4. The combined abundances of these commonly delivered prey types are shown, with locations, on Figure 2.

The broad types of habitat identified are shown spatially on Figure 3. This is an oversimplification of the complex habitat systems, but serves as a useful overview of the makeup of these waters. The codes used (such as LhypR.Ft) are assigned to represent a particular biotope. A brief description of some of the more commonly encountered is given on Table 5.

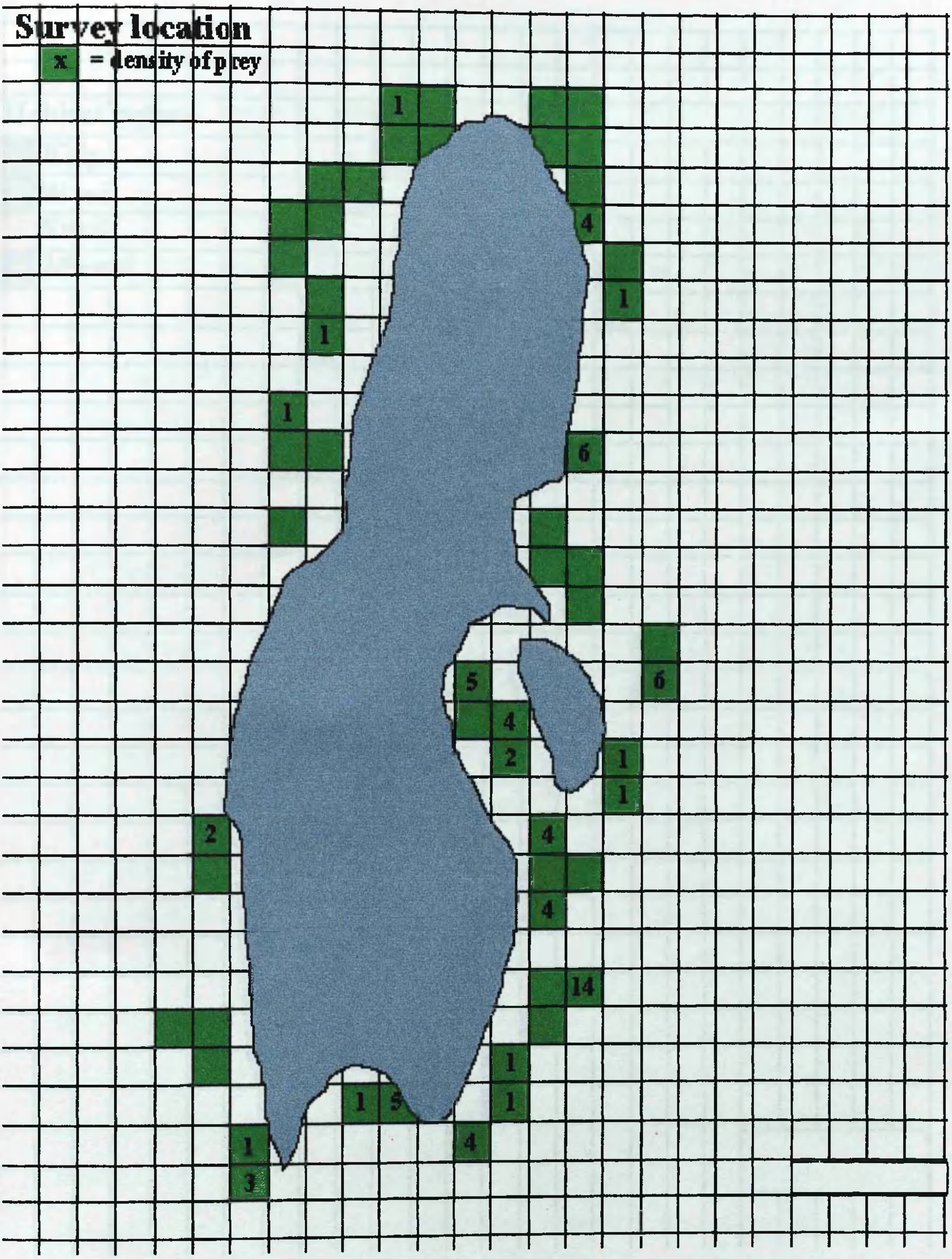

Figure 2. Areas surveyed with observed density of prey species (see text for description of species and method). 1 square = 250m.

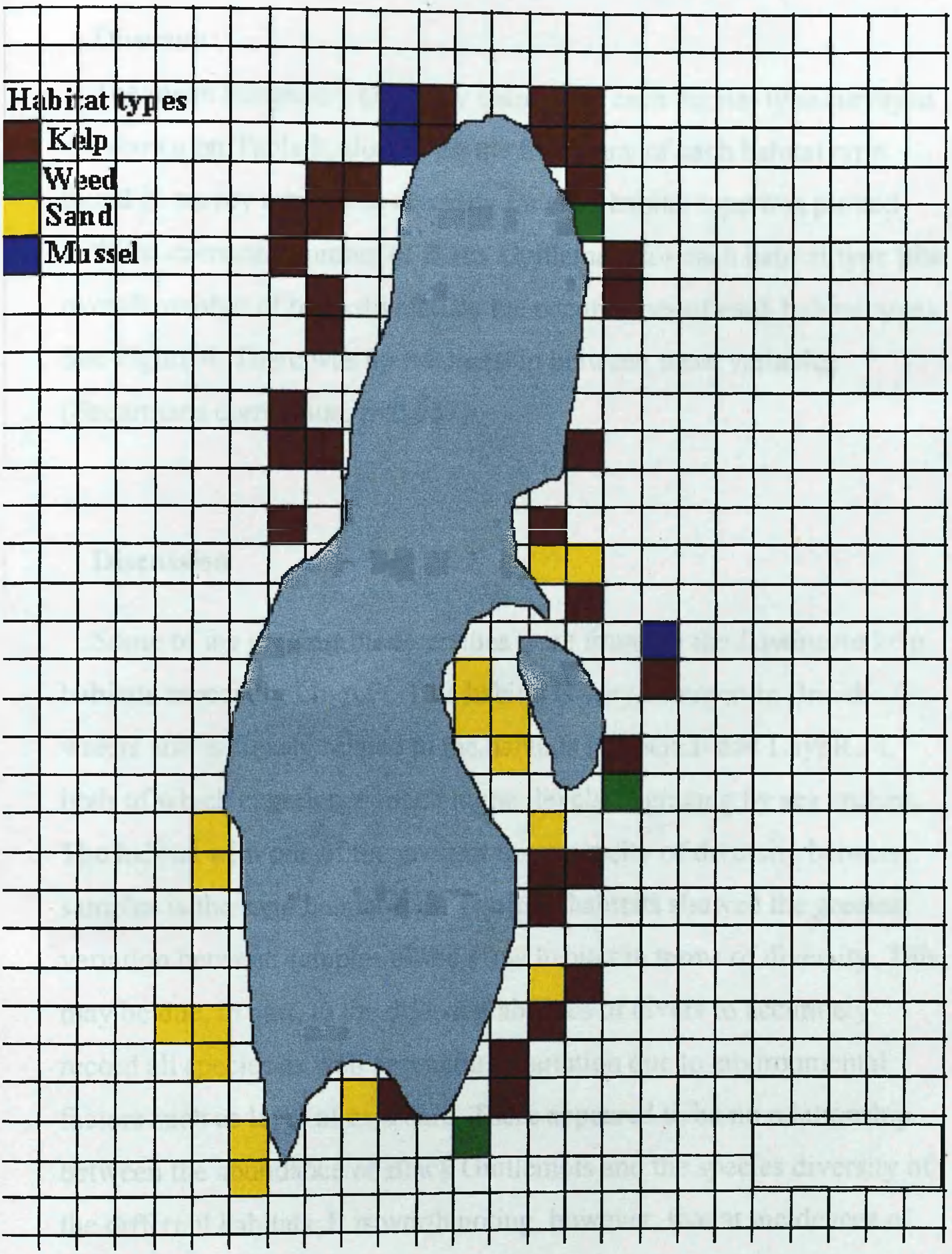

Figure 3. Basic habitat types encountered on diving surveys. 1 square = 250m.

Diversity

The mean Simpson's Diversity Indices for each habitat type surveyed are shown on Table 3, along with the frequency of each habitat type found in survey areas. The diversity for each habitat type was plotted with the corrected number of Black Guillemots for each habitat type (the overall number of birds divided by the occurrences of each habitat type). See Figure 4. There was no relationship between these variables (Spearmans correlation, p=0.537).

Discussion

Some of the greatest biodiversities were found in the *Laminaria* kelp habitats especially Lhyp.Ft. This habitat is very common in British waters and is closely related to the habitats LhypGz.F and LhypR.Ft, both of which experience much higher levels of grazing by sea urchins. The habitat with one of the greatest homogeneity of diversity between samples is the sand habitat IGS. The kelp habitats showed the greatest variation between samples of the same habitat in terms of diversity. This may be due, in part, to the differing abilities of divers to accurately record all species as well as a natural variation due to environmental factors such as level of exposure. There appeared to be no relationship between the abundance of Black Guillemots and the species diversity of the different habitats. It is worth noting, however, that at incidences of low marine biodiversity there are no foraging birds. The distribution of foraging birds is discussed in detail in the chapter on bird distribution.

The surveys include two main habitat types (as clearly seen in Figure 3), the first being kelp habitat (*L.hyperborea* and *L. saccharina*), forming

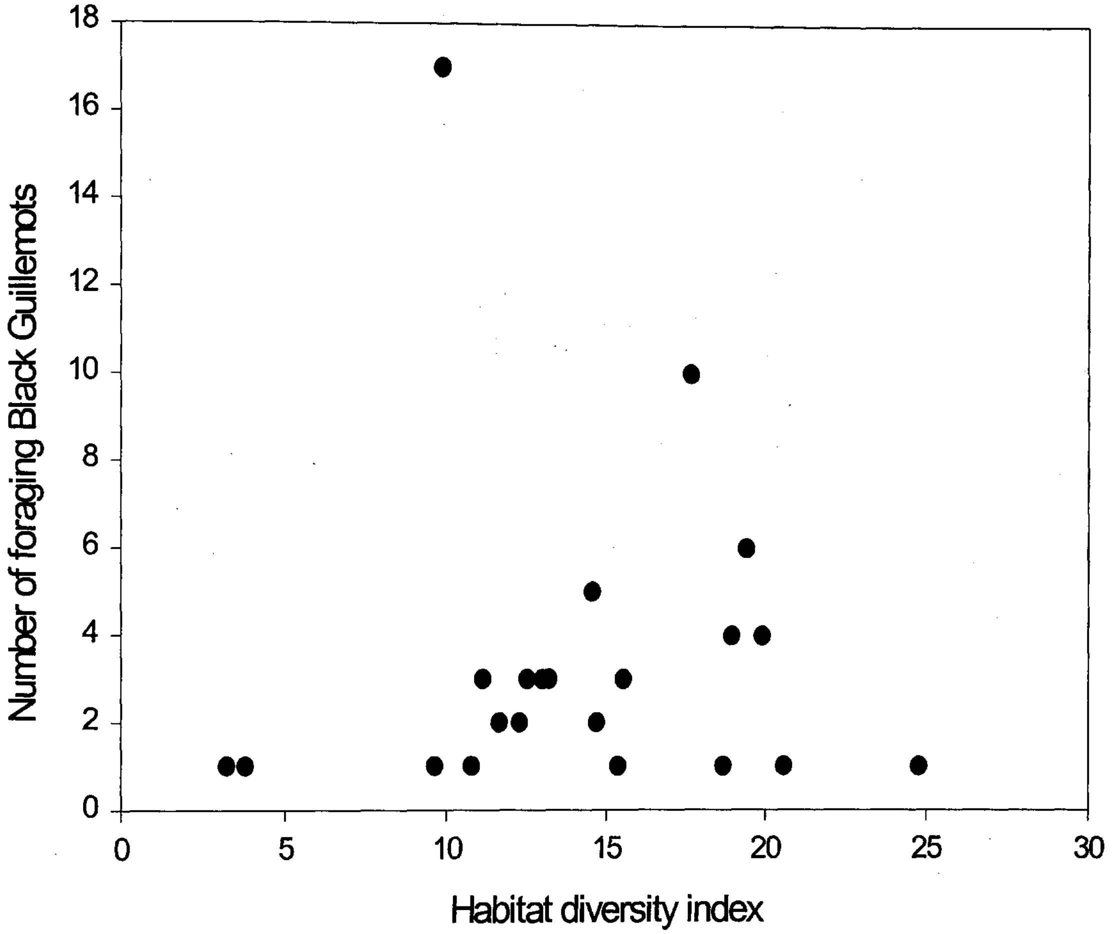

Figure 4. Diversities of surveyed sites with number of foraging Black Guillemots.

50.6% of all habitats observed, of which one, LhypR.Ft, is described as "uncommon" in British waters. This differs from other similar habitats in its lack of a dense faunal cushion generally associated with kelp beds. The second main habitat type is sand/gravel habitat (predominantly IGS, the single most common habitat in these waters), forming 24% of all habitats observed.

As we can see from Figure 3, the predominant habitat in these waters is kelp habitat, followed by sand and gravel habitats. The inshore waters of Papa Westray, particularly the north and west coast, are very exposed to the actions of waves and tide, and this is reflected in some of the habitat types found. The abundance of kelp would also be suggested by the exceptional lack of turbidity in these waters, allowing high primary productivity in shallow waters. This productivity has been noted and the island has been suggested as an ideal location of the commercial harvesting of kelp (E. Meek, *pers comm.*). The impact of this is discussed in the general conclusions. The sandy habitat on the south west side of the island is subject to very high speed tidal flow, due to the shallowness of the water, which precludes high levels of seaweed growth.

The relationship between these habitats and the foraging behaviour and breeding success of the Black Guillemot is discussed in Chapters 5 & 10.

Table 1 Dates, locations and habitats of diving surveys.

Survey Date	**Site**	**Place**	**Latitude / Longitude**	**Biotopes Present**
14.7.97	1	Fowl Craig, Papa Westray	59°22.3'N 02°51.8'W	LhypR.Ft; AlcByH; AlC
14.7.97	2	Fowl Craig, Papa Westray	59°22.5'N 02°51.8'W	LhypGz.Ft
14.7.97	3	Fowl Craig, Papa Westray	59°22.4'N 02°51.9'W	Lhyp.Ft
14.7.97	4	Fowl Craig, Papa Westray	59°22.6'N 02°51.9'W	Lhyp.TFt; AlcByH
14.7.97	5	NE of Mull Head	59°23.1'N 02°52.3'W	LhypR.Ft
14.7.97	6	North Wick Bay	59°21.9'N 02°52.1'W	IR; Lhyp.Ft
14.7.97	7	Surhoose Taing	59°21.6'N 02°52.3'W	Lhyp.Ft; FaS
14.7.97	8	Centre North Wick Bay	59°21.7'N 02°52.4'W	LsacChoR; XkScrR
14.7.97	9	South Wick	59°21.2'N 02°52.3'W	IGS
14.7.97	10	East Westray	59°20.9'N 02°52.2'W	IGS
14.7.97	11	South Wick, Southern End	59°20.7'N 02°52.2'W	IGS
15.7.97	12	W. of North Hill	59°21.7'N 02°54.2'W	LhypR.Ft
15.7.97	13	Offshore North Hill	59°22.8'N 02°54.2'W	LhypFa; LhypR.Ft
15.7.97	14	Papa Westray	59°21.9'N 02°54.2'W	Lhyp

15.7.97	15	Papa Sound	59°22.0'N 59°54.2'W	Lhyp.TFt
15.7.97	16	W. of North Hill	59°22.2'N 02°54.2'W	Lhyp.TFt
15.7.97	17	Mull Head	59°23.1'N 02°53.1'W	LhypR.Ft
15.7.97	18	W. of Mull Head	59°23.1'N 02°53.5'W	MytHAs; Mus
15.7.97	19	Mull Head	59°23.1'N 02°53.7'W	MytHAs; Mus
15.7.97	20	SW. Mull Head	59°23.1'N 02°54.4'W	MytHAs
15.7.97	21	Post Office	59°20.4'N 02°54.7'W	Lsac.Ft; Zmar
15.7.97	22	S. of Post Office	59°20.3'N 02°54.7'W	Zmar
15.7.97	23	Moclett Pier	59°19.6'N 02°53.3'W	LhypLsac.Ft; IGS
15.7.97	24	Bay of Moclett	59°19.6'N 02°53.3'W	IGS
16.7.97	25	W. of Coastguard Lookout	59°22.2'N 02°53.8'W	LhypR.Ft
16.7.97	26	W. of Mull Head	59°22.7'N 02°54.2'W	LhypFa; Mus
16.7.97	27	Off the Roost, Near Brinkwall	59°22.9'N 02°53.8'W	LhypR.Ft; AlcByH
16.7.97	28	S. of the Roost	59°22.4'N 02°54.5'W	LhypR.Ft
16.7.97	29	S. of the Roost	59°22.6'N 02°54.1'W	Lhyp
16.7.97	30	SW. Corner	59°19.7'N 02°54.9'W	IGS; LsacX
16.7.97	31	W. of Vestness	59°19.5'N	IGS; LsacX

			02°54.8'W	
16.7.97	32	W. Coast, Horse Flags Area	59°19.4'N 02°54.6'W	IGS; LsacX
16.7.97	33	SW. Papa Westray	59°20.0'N 02°55.2'W	Zmar; LsacX
16.7.97	34	Papa Sound	59°19.8'N 02°55.0'W	IGS
16.7.97	35	Bay of Burland	59°20.3'N 02°52.4'W	LhypLsac.Ft
16.7.97	36	SE. Papa Westray	59°20.1'N 02°52.3'W	Lhyp.Ft
16.7.97	37	Due E. of Holm	59°20.7'N 02°51.3'W	AlcByH; Lhyp; Oph
16.7.97	38	SE. Holm	59°21.1'N 02°51.6'W	AlcByH; Lhyp; Oph
17.7.97	39	NE of North Hill	59°19.9'N 02°51.5'W	IGS
17.7.97	40	S. of Bay of Burland	59°19.8'N 02°52.3'W	IGS
17.7.97	41	SE of Bay of Burland	59°19.8'N 02°52.4'W	Lhyp.Ft
17.7.97	42	SE. Papa Westray	59°19.5'N 02°52.5'W	Ven.Neo
17.7.97	43	S. of Bill Flag	59°19.7'N 02°52.6'W	MIR; LhypGz.Ft
17.7.97	44	E. of North Hill	59°23.4'N 02°52.2'W	Lhyp.TFt
17.7.97	45	Mull Head East	59°22.4'N 02°52.0'W	Lhyp.Fa
17.7.97	46	E. Side Between Bouden & Fowl Flag	59°23.1'N 02°52.2'W	LhypGz.Ft; AlcByH
17.7.97	47	NE. Papa Westray	59°22.8'N 02°51.9'W	LhypR.Ft; AlcByH

17.7.97	48	E. of Holm	59°20.9'N 02°51.3'W	Lhyp.Ft; Lhyp.Pk
17.7.97	49	S. Wick	59°20.6'N 02°52.0'W	IGS
17.7.97	50	S. of Holm	59°20.4'N 02°51.7'W	LhypGz.Ft
17.7.97	51	NE. of Papa Westray	59°21.1'N 02°51.3'W	IR
17.7.97	52	E. of Holm	59°21.3'N 02°51.3'W	Oph
18.7.97	53	N. of the Holm	59°21.4'N 02°51.9'W	FoR; Oph; Ant
18.7.97	54	E. Papa Westray (N. of the Holm)	59°21.5'N 02°51.8'W	LhypGz.Pk; FaAlC
18.7.97	55	S. of Head of Moclett	59°19.1'N 02°53.1'W	IGS
18.7.97	56	S. Papa Westray	59°19.9'N 02°52.7'W	LhypGz.Pk; FaAlC

Table 2 MNCR abundance scale.

MNCR code for abundance	**Description of abundance**	**Numerical equivalent**
P	Present	1
R	Rare	2
O	Occasional	3
F	Frequent	4
C	Common	5
A	Abundant	6
R	Superabundant	7

Table 3 Habitats found, their mean diversities (Simpson's diversity index, see text) for each habitat type with standard deviation, and the number of times each habitat occurred in all surveys.

Habitat	Mean Diversity	S.D.	Number of Occurrences of This Habitat
AlcByH	18.95	6.14	4
AlcC	3.77	-	1
LhypR.Ft	17.67	5.15	10
LhypGz.F	14.55	8.43	5
Lhyp.Ft	19.41	12.17	6
Lhyp.TFt	19.91	8.25	4
IR	24.77	-	1
IGS	9.86	3.70	17
LsacChoR	9.63	-	1
XKScrR	14.69	3.07	2
Lhyp	13.19	7.48	3
MytHAs	12.98	0.96	3
Zmar	15.53	2.34	3
LhypLsac	12.27	8.56	2
LhypFa	18.68	-	1
Oph	11.12	8.61	3
Ven.Neo	15.36	-	1
MIR	3.2	-	1
Lhyp.Pk	10.78	-	1
LhypGz.P	12.51	2.3	3
FoR	20.58	-	1
FaAlC	11.64	0.67	2

Table 4 Fish species encountered on diving surveys

Species	**Common name**	**Prey? (*=BG prey)**
Scyliorhinus canicula	Lesser spotted dogfish	
Ciliata mustela	5 bearded rockling	*

Gadus morhua	Cod	*
Gaidropsarus vulgaris	3 bearded rockling	*
Merlangius merlangus	Whiting	
Molva molva	Ling	
Pollachius pollachius	Pollack	
Pollachius virens	Saithe	
Trisopterus luscus	Whiting	
Trisopterus minutus	Poor cod	
Syngnathidae	Pipefish	
Scorpaena scrofa	Sea scorpion	*
Taurulus bubalis	Long-spined sea scorpion	*
Agonus cataphractus	Pogge	*
Cyclopterus lumpus	Lumpsucker	*
Ctenolabrus rupestris	Goldsinny	
Labrus bergylta	Ballan wrasse	
Labrus mixtus	Cuckoo wrasse	
Anarhichas lupus	Wolf-fish	
Chirolophis ascanii	Yarrell's blenny	*
Pholis gunnellus	Butterfish	*
Ammodytidae	Sandeel	*
Ammodytes tobianus	Lesser sandeel	*

Callionymus lyra	Dragonet	*
Gobiusculus flavescens	2 spotted goby	*
Pomatoschistus microps	Common goby	*
Pomatoschistus minutus	Sand goby	*
Pomatoschistus pictus	Painted goby	*
Thorogobius ephippiatus	Leopard spot goby	*
Phrynorhombus norvegicus	Norwegian topknot	*
Zeugopterus punctatus	Topknot	*
Pleuronectidae	Flatfish	*
Limanda limanda	Dab	*
Solea solea	Sole	*
Charadrius hiaticula		
Pleuronectes platessa	Plaice	*

Table 5 Breakdown of habitat types encountered around Papa Westray with description.

Kelp habitats	**Description**
Lhyp	*Laminaria hyperborea* dominated habitats with varying levels of exposure, urchin grazing pressure and associated communities.
Lhyp.Fa	
LhypR.Ft	
LhypGz.F	
Lhyp.Ft	
Lhyp.TFt	
Lhyp.Pk	
LhypGz.P	

LhypLsac	*Laminaria saccharina based habitats*
LsacChoR	
XkScrR	Mixed kelps (*L.digitata, L.saccherina, L.hyperborea*) with foliose red seaweed on exposed rock (MIR)
MIR	
IR	
Seaweed (non kelp)	
FoR	Foliose red seaweed
Sea Grass	
Zmar	Fine sediment with sea grass
Sand / Gravel	
IGS	Sand and gravel
Ven.Neo	Gravel with bivalve communities
Brittlestar Beds	
Oph	Brittlestars on tide swept rock
Mussel Beds	
MytHAs	*Mytilus edulus* beds in strong tides
Bare Rock	
FaAlC	Species poor heavily grazed rock
Soft Corals	
AlcByH	*Alcyonium digitatum* with bryozoan and hydriod turf. (AlcByH infralittoral, AlcC circalittoral)
AlcC	

Chapter 9

The use of foraging sites by Black Guillemots

Introduction.

Spatial variability in the density of foraging animals and the interactions between predators, prey and the environment are fundamental themes in ecology. Seabirds are predators that are patchily distributed while foraging at sea. This distribution of marine birds and other predators has been partially explained by patchiness in the distribution of their prey and thus by the birds selection of foraging habitats where prey can be most profitably obtained. The linking of the distribution of seabirds with hydrographical features has met with varying success. Those studies that have taken place have tended to concentrate on the effects of fisheries (Camphuysen et al 1995, Camphuysen 1995,) or the physical properties of the water such as oceanic fronts (Follestad 1990, Leopold 1991, Hunt & Harrison 1990). One study conducted in the Bering Strait showed that the distribution of smaller alcids was related to water column structure (taken to be an indication of underwater shear currents), wheras the distribution of larger alcids showed no relationship with the water column structure (Haney 1991). This study was conducted on an area of uniform bottom topography making separating the effect of the physical state of the water column on the distribution from other potential environmental factors possible. Other studies have shown the importance of haloclines, thermoclines and pycnoclines to the distribution patterns of seabirds (Haney & McGillivary 1985), but little has been done on a population scale on inshore waters involving the necessary repeated surveys carried out on the same area throughout a breeding season.

A major factor controlling the distribution of seabirds is likely to be the availability of food. On a coarse scale, seabird distributions can to a large extent be explained by hydrographic structure as discussed above, but the underlying cause of their distributions is most likely to be determined by prey availability (Pocklington 1979, Hunt & Schneider 1987). The use of hydroaccoustic techniques to determine abundance of nekton has been utilised and these data related to overall seabird abundance (Parrish et al 1998). Another factor in the distribution of seabirds may be the tendency to aggregate independently of food supply, for example, Guillemots are often found forming large rafts of non-foraging individuals in the vicinity of the breeding colony (Parrish 1995, Burger 1997).

Habitat selection obviously can have profound consequences. The choice of a particular habitat has the effect of placing an animal in a particular environment, and this can effect selection on a particular genotype (Partridge 1978). The study of habitat selection has largely been concentrated on terrestrial animals, as the variation in available habitat is easily seen and measured. In marine systems however, such variation is not easily seen and is much more difficult to measure. Marine systems have huge variability in the amount of different types of habitat available in often a small physical area and shallow water areas have higher variation than deeper waters (Gray 1997), largely due to the input of energy in the form of light.

Determining the suitability for foraging of a habitat can be complex. While the rate of acquisition of prey will ultimately depend on prey density, there may often be other important factors. In herbivores, plant quality is often more important than abundance. In the Oystercatcher, *Haematopus ostralegus*, the preference for foraging site depends on shell thickness (influencing the ease of handling), prey size and the muddiness of the substrate (habitat quality) (Goss-Custard et al 1992) rather than overall density of prey.

The feeding distribution of a seabird in the breeding season will show a different pattern to truly free ranging foragers due to the need to return to a central place, that is, the returning with food to the breeding colony in order to provision the chicks.

The overall distribution of foraging Black Guillemots can be related to the seabed habitats foraged upon as measured by the diving surveys (see Chapter 8). The density of birds can be examined for both seasons (1996 & 1997), and the distribution in both early and late season compared.

Methods

Sea surveys were conducted by carrying out transects as shown in Chapter 6, Figure 1. These transects allowed coverage of all the inshore waters of Papa Westray up to a depth of 50m, the maximum depth in which Black Guillemots are found to forage (Piatt & Nettleship 1985). For greater detail on the methodology used for these surveys see chapters 2 & 6. In order to obtain information on habitat and density of prey species, diving surveys were undertaken at a variety of sites around the inshore waters of Papa Westray, at sites of varying Black Guillemot density. For a more detailed description of this methodology see Chapters 2 & 8. Divers recorded information relevant to discerning habitat type (information on topography, vegetative cover, exposure and relative densities of all species encountered) and the relative densities of Black Guillemot prey species. The use of a relative abundance scale, as opposed to absolute numbers, for recording species corrects for differences in survey length and observer bias. Data from these surveys were sent to JNCC and returned to me in Dbase format (see Chapter 2 for details). These data were then manipulated in Excel and some analysis was carried out using SPSS.

Results

The relative use of different habitats is shown on Table 1. See Chapter 8 for description of the habitat types. The habitat type that features at the top of the list is the sand and gravel habitat IGS. The three sites that have the highest percentage of foraging Black Guillemots of those sites surveyed, in each 250m x 250m square, contained11.91% of the total foraging population. The overall percentage of Black Guillemots using IGS sites across all surveys was 14.11%. In the case of kelp habitats (*L. hyperborea* based), these formed the next most heavily used habitats. The top 10 sites contained 24.68 of all foraging birds; of these, *L.hyp.* habitats contained 11.44%.

Of all the surveys that corresponded with areas used as foraging sites, the total percentage of birds that use these sites was 38.74% over 41 sites. Fifteen survey sites were in areas that were not used by Black Guillemots. An index of relative importance of different habitats was created by totalling the percentage of birds found overall in each habitat type, and dividing this by the area covered by this habitat. This corrects for the abundance of different habitat types. The results of this are shown in Table 2. This table, by ranking the importance of different habitats shows which habitats are most important to foraging Black Guillemots.

The relative abundance of suitable prey types for Black Guillemots were combined to give an index of overall prey availability for each site surveyed. Those sites with observed prey were plotted against density of feeding birds in order to see if prey availability influenced predator density. There was no relationship between density of all prey items and bird abundance, but the data for those areas in which butterfish were found showed a relationship between the abundance of butterfish and the number of foraging Black Guillemots (Spearmans correlation co-efficient = 0.730, p = 0.040. see Figure 1).

Discussion

Foraging Black Guillemots at this site are presented with a wide choice of habitat types within their foraging range. From the data presented it can be clearly seen that they are discriminating between habitats and show distinct preferences for certain types. Of these types of habitats, Lhyp.TFt makes up little of the surveyed areas, but carries high numbers of birds unlike similar habitats LhypFa and Lhyp.Pk, the latter differing in the greater amount of wave exposure it is subjected to. Lhyp.TFt is described as "uncommon" by the MNCR report on British coastal habitats and seems to occur only in the Northern Isles, Outer Hebrides, Sealochs in the west of Scotland, Pembrokeshire and West Ireland. These are the areas which support all the breeding Black Guillemots in the United Kingdom and it would be interesting to investigate whether this habitat is as heavily selected in other breeding locations. The most heavily used habitat, the sand and fine gravel habitat IGS, is also the most abundant single habitat in the area. It is interesting that the greatest concentrations of birds on this habitat occurred in an area in the south-west of the island where divers reported seeing high densities of fish one particular area. Another habitat whose use far exceeds its availability is Ven.Neo, a habitat characterised as beds of small mussels *Mytilus edulus*. This site, found in the north-west of the island, consisted of kelp beds surrounding areas of seed mussels (approx. 5mm long) which could be conceviably eaten by adult Black Guillemots.

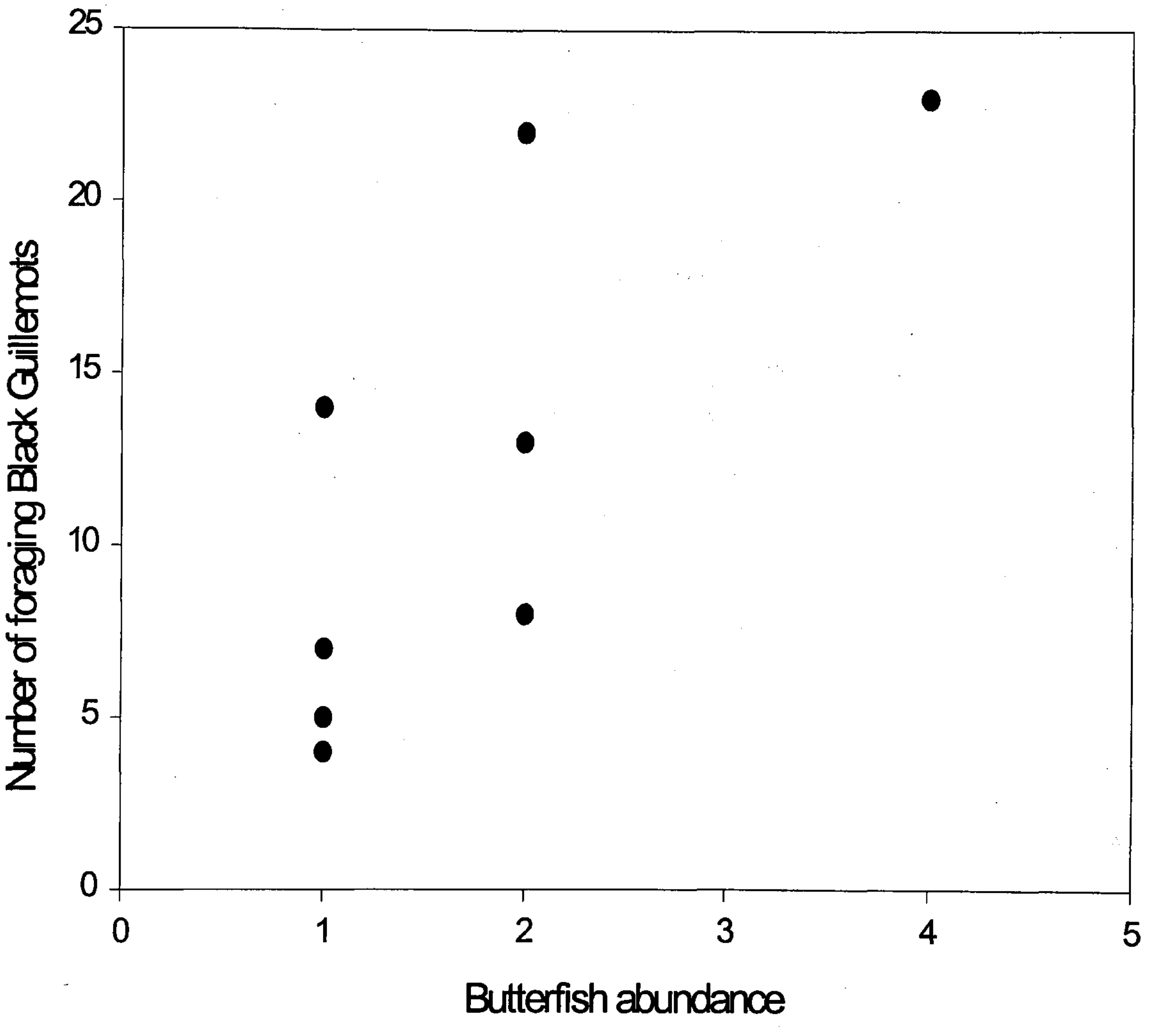

Figure 1. The abundance of butterfish and the density of foraging Black Guillemots (Spearmans correlation co-efficient = 0.730, p = 0.040).

It is also possible that such boundaries between kelp and open substrate could facilitate foraging, but analysis attempted on this proved fruitless.

Table 1. Survey number with habitat type, the number of birds observed on the habitat at that site and the % of the number of birds observed overall that was observed on that site.

Survey	Habitat	Total number of Black Guillemots	%Total Black Guillemots observed
30	IGS	44	4.19
34	IGS	43	4.1
31	IGS	38	3.62
17	LhypR.Ft	24	2.29
36	Lhyp.Ft	23	2.19
13	LhypR.Ft	22	2.1
15	Lhyp.TFt	22	2.1
25	LhypR.Ft	16	1.52
18	MytHAs	14	1.33
16	Lhyp.TFt	13	1.24
42	Ven.Neo	9	0.86
5	LhypR.Ft	8	0.76
32	IGS	8	0.76
35	LhypLsac	8	0.76
44	Lhyp.TFt	8	0.76
55	IGS	8	0.76
12	LhypR.Ft	7	0.67
14	Lhyp	7	0.67

19	MytHAs	7	0.67
33	Zmar	7	0.67
56	FaAlC	7	0.67
56	LhypGz.P	7	0.67
27	LhypR.Ft	6	0.57
51	LhypGz.P	6	0.57
20	MytHAs	5	0.48
41	Lhyp.Ft	4	0.38
43	LhypGz.F	4	0.38
49	IGS	4	0.38
3	Lhyp.Ft	3	0.29
4	AlcByH	3	0.29
4	Lhyp.TFt	3	0.29
50	LhypGz.F	3	0.29
1	AlcByH	2	0.19
6	IR	2	0.19
29	Lhyp	2	0.19
54	FaAlC	2	0.19
2	LhypGz.F	1	0.1
10	IGS	1	0.1
11	IGS	1	0.1
24	IGS	1	0.1
38	AlcByH	1	0.1
46	LhypGz.F	1	0.1
52	Oph	1	0.1

Table 2. Relative importance of each habitat type recorded on all surveys. For a description of the method of calculation of corrected

usage see text. # of occurrences is the amount of times overall during the diving surveys the habitat was encountered.

Habitat	Corrected usage by Black Guillemots †	# of occurrences of each habitat
IGS	1.085385	13
Lhyp.TFt	1.025	4
Ven.Neo	0.86	1
MytHAs	0.826667	3
LhypR.Ft	0.791	10
Lhyp.Ft	0.476667	6
LhypLsac	0.38	2
Lhyp	0.286667	3
Zmar	0.223333	3
LhypGz.P	0.19	3
LhypGz.F	0.098	5
Oph	0.033333	3
AlcByH	0	4
AlcC	0	1
FaAlC	0	2
FoR	0	1
IR	0	1
Lhyp.Pk	0	1
LhypFa	0	1
LsacChoR	0	1
MIR	0	1
XKScrR	0	2

†= % of Black Guillemots using a given habitat divided by the number of occurrences of this habitat.

Habitats with a 0 in the corrected usage column occur only in areas with no foraging activity.

Chapter 10

The Examination of Foraging Behaviour in Relation to Feeding Site

Introduction

The consequences of habitat selection for diving seabirds are little understood. Many important factors affecting their life history are likely to be physical, such as location of food, and therefore measurable, as well as less easily measured factors, such as foraging ability. In the case of a bottom-feeding seabird diving on diverse habitat types it is expected that there would be tradeoffs in terms of the costs of distance traveled to the foraging site, the depth of the water column in these sites, and the benefits in terms of profitable prey captured (Ydenberg & Forbes 1988, Carbone & Houston 1994, Monaghan *et al.* 1994, Zwarts *et al.* 1996). Once captured, different prey have different costs associated with handling time (Wanink & Zwarts 1996) and if transported back to the young, different costs associated with this. There is also likely to be regional and seasonal variation in the amount of prey available within distinct habitat types (Kruuk *et al.* 1988), making the selection of profitable foraging areas more crucial.

For the Black Guillemot, *Cepphus grylle*, like other avian divers, its feeding performance is influenced by a variety of environmental factors such as water depth, bottom substratum, prey density and size. The Black Guillemot is a single prey loader, carrying prey items singly in its bill to the nest site to be fed to chicks. Its choice of foraging habitat, however, unlike many other species, is unlikely to be influenced by differing risk of predation. Mortality rates of adult Black Guillemots, like many other seabird species, are low (Cramp 1985), although it will extend the distance flown in order to avoid flying over the land (often the shortest distance) where it is more vulnerable.

The Black Guillemot is a very suitable species for an investigation into the factors affecting choice of foraging habitat. It feeds inshore, mostly in shallow water, and feeds on non-shoaling demersal prey species (Nettleship & Birkhead 1985). These factors allow the measurement of many physical characteristics of the foraging site, and the depth of water in foraging sites will be a true indication of the depth of the water column traveled through to forage.

In this study the effects of substrate type on diving behaviour and the relative costs of travelling to different habitat types at this site are examined.

Studies such as these are important because it enable resources available to a species to be assessed, and can potentially improve our understanding of factors that control feeding distribution, which could have important applications in the conservation of key habitats.

Methods

This study was carried out on the Holm of Papa Westray, Orkney (59°21'N, 2°53'W). For the identification of habitats, a diving expedition was organized consisting of 15 members of the Marine Conservation Society. A successful application for funding was made to Scottish Natural Heritage, providing a dive vessel, compressor and skipper for a week in the middle of July. Fifty-six sites were surveyed at a variety of locations in the inshore waters surrounding Papa Westray using the Seasearch for inshore diving surveys methodology (SNH publication, see Chapter 2). Survey positions were selected within the Black Guillemot diving range (5-40m) and in areas of varying Black Guillemot density (see Chapter 6). These data were returned to the JNCC for entry into the national database, and each site was given a habitat code and description.

In order to collect information on the diving behaviour, radio tags were fitted to adult birds caught on the colony (see Chapter 2 for more detail on trapping methods). The tags used were single stage transmitters operating in the 173mhz band, supplied by AVM. The completed tags weighed approx. 3.5g (<1% adult body mass) and were attached underneath the central tail feathers (for more detail see Chapter 2). The signals were picked up on Cedar Creek receivers from two tracking stations that were moved around the coast to provide maximum coverage. Dive times and subsequent surface pauses were recorded as well as, when possible, bearings from both stations for triangulation to provide information on dive location (for more detail see Chapter 2).

In order to provide information on chick diet, hides were erected on the breeding colony and the nests monitored in watches of three-hour duration. Prey items delivered to the nest are carried in the bill. Data collected were prey type, prey size, prey fate and time. From these the proportion of butterfish delivered was calculated.

Using the data from the diving surveys, habitats were split into two categories; those with a kelp based habitat and those habitats based on sandy substrates (see Chapter 8 for full detail of the surveys), using the codes assigned to the habitats by the JNCC.

Results

The distribution of the two habitat types around the island of Papa Westray is shown on Figure 1. The distances to each surveyed site of these main groups of habitats were estimated to see if there was a difference in

Figure 1. Habitat distribution around Papa Westray. This map was created from diving surveys combined with observation from boats and discussions with local fishermen.

travelling distance for individual birds between kelp and non-kelp habitats identified as feeding sites. Travel distance was calculated as the minimum distance over the sea between the breeding colony and the surveyed site (a visual representation of the distribution of different habitats can be seen in Chapter 8). There was no difference between the two habitat types in terms of distance from the breeding colony (t-test n.s. $t = 0.485$) for those sites surveyed. Whilst the distances are not different, the travelling time to the bottom for the birds, that is, the depth of water in these sites differed between kelp and non-kelp sites (t-test $p=0.001$, $t = 3.673$), the kelp habitat being used for foraging is found in deeper water. Despite this, there was no significant difference on the duration of dives between these habitat categories. In effect, assuming a constant descent rate, this means a difference in the time available for foraging on the bottom, less time being available in kelp based habitats. There was no significant difference in the recovery time after a dive (the dive interval divided by the subsequent surface pause) between the two habitat types.

As butterfish were by far the most abundant prey type delivered to Black Guillemot chicks at the study colony (see Chapters 3 & 5), and the proportions of prey types show large inter-individual variation, the proportion of Butterfish delivered to the nest was used as a variable in comparing the foraging behaviour of radio tagged individuals. In order to see if there was a relationship between the proportion of Butterfish delivered to the nest and the average distance traveled to the foraging site, the relationship between these two variables was examined (see Figure 2). There proved to be a strong relationship between the two (Spearmans correlation co-efficient: 0.639, $p=0.019$). Parent birds bringing a higher

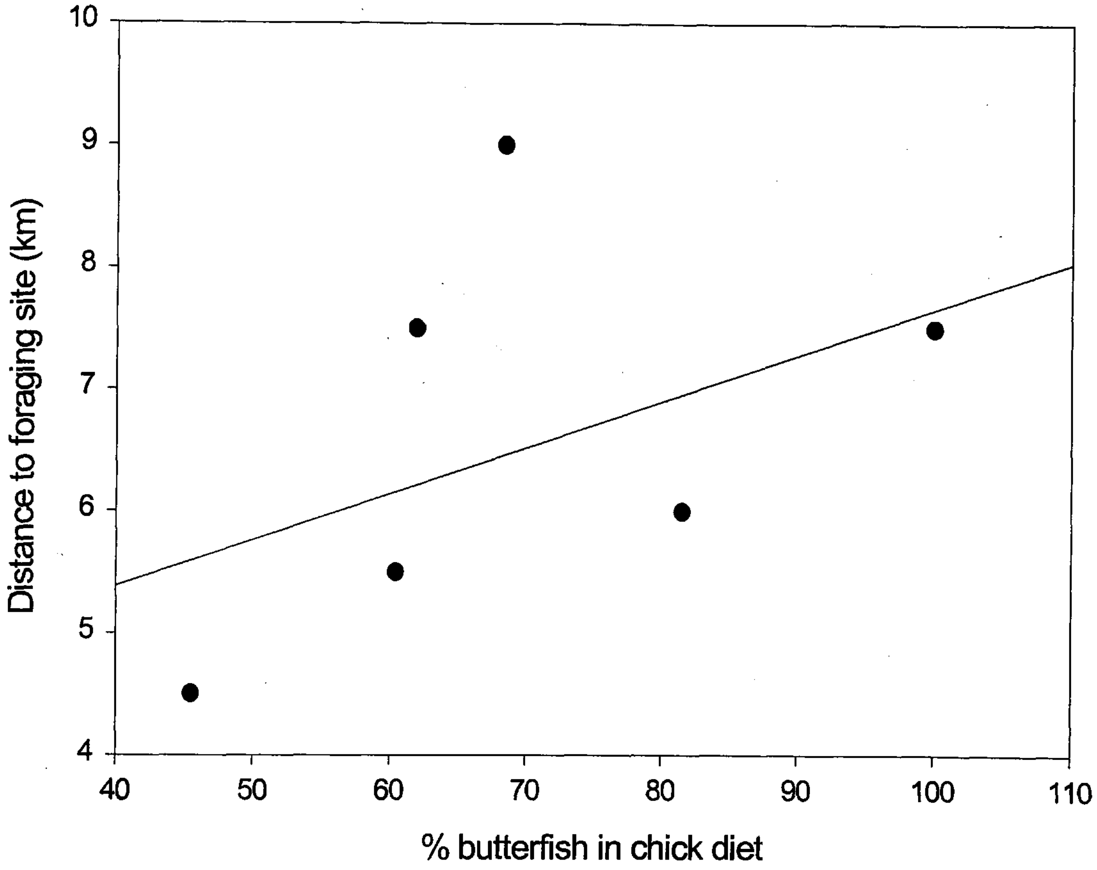

Figure 2. The distance to the feeding site and the proportion of butterfish in the chick diet (% total prey delivered).

proportion of butterfish to the nest had a higher travel distance. There is a strong relationship between mean dive duration and percentage of butterfish in the diet (Figure 3). This is highly significant (Spearmans, correlation coefficient -0.781, p = 0.005). Birds catching more butterfish made shorter dives.

There was no significant relationship overall between dive duration and ratio of recovery time to dive time either within or between habitats.

If the relationship between dive duration and distance flown to feeding area is examined, there at first appears to be no significant relationship. However, if trips of less that 3km are excluded from the analysis (this area may include a high proportion of non-foraging birds (Parrish 1995, Burger 1997)), a significant relationship emerges. Birds flying further to feed are making shorter dives (Spearmans correlation coefficient –0.788, p = 0.001). See Figure 4.

Discussion

Kelp and non-kelp habitats are not any different in terms of distance from the colony, bird foraging dive duration and after-dive recovery time. Kelp habitat occurs in deeper water and thus, given that there is no difference in dive times, allows birds shorter actual foraging time (prey encounter time), given a constant travelling speed through the water. Thus, it must be either easier to catch prey in these habitats (to offset the decreased time available for foraging on the bottom) or that such sites yield more profitable prey in terms of energy per prey item.

We have seen that birds delivering a higher proportion of butterfish (a prey species occurring mostly in habitats with good cover such as kelp

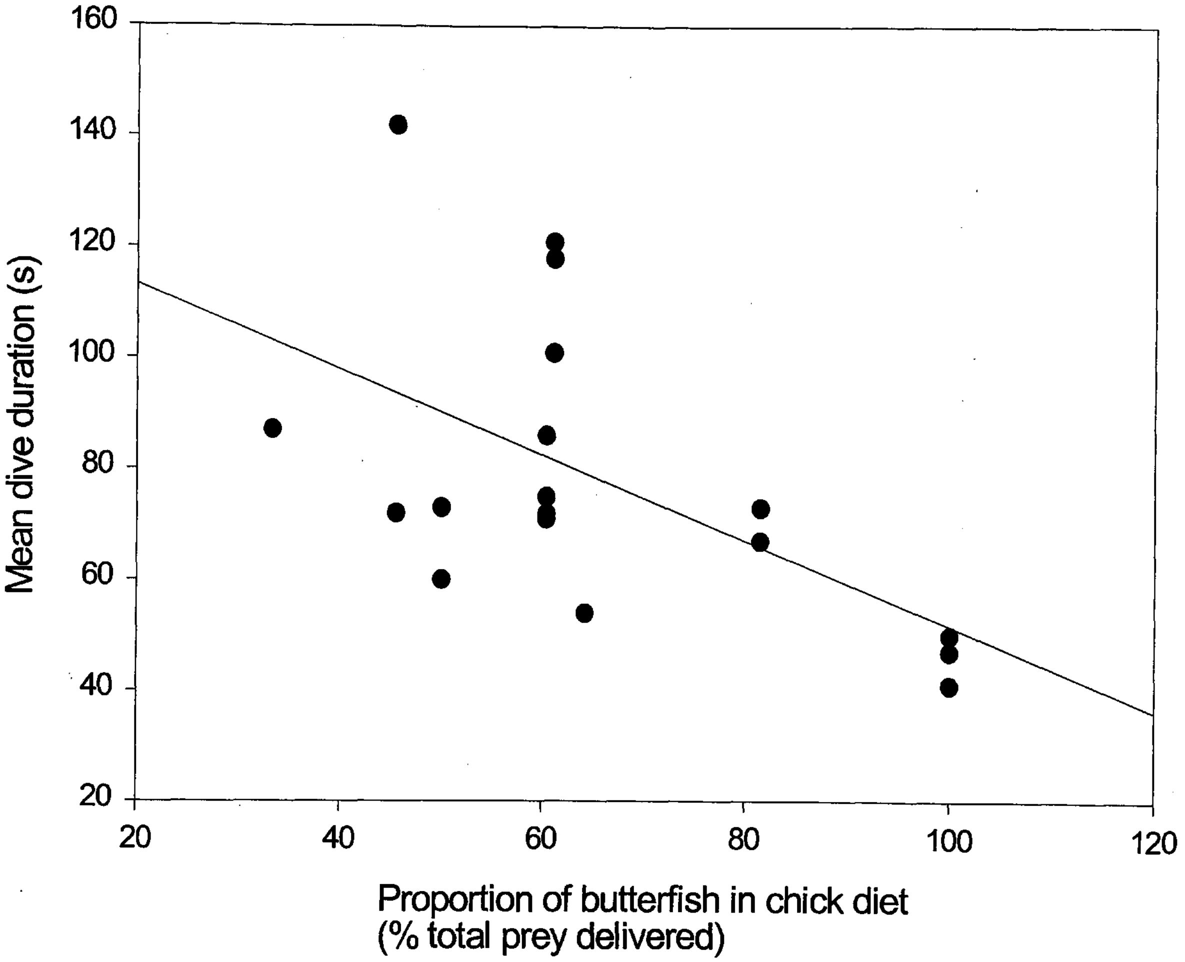

Figure 3. The mean dive duration (s) for birds from individual nests and the proportion of butterfish delivered to the nest (% butterfish of total prey delivered). Number of birds = 8.

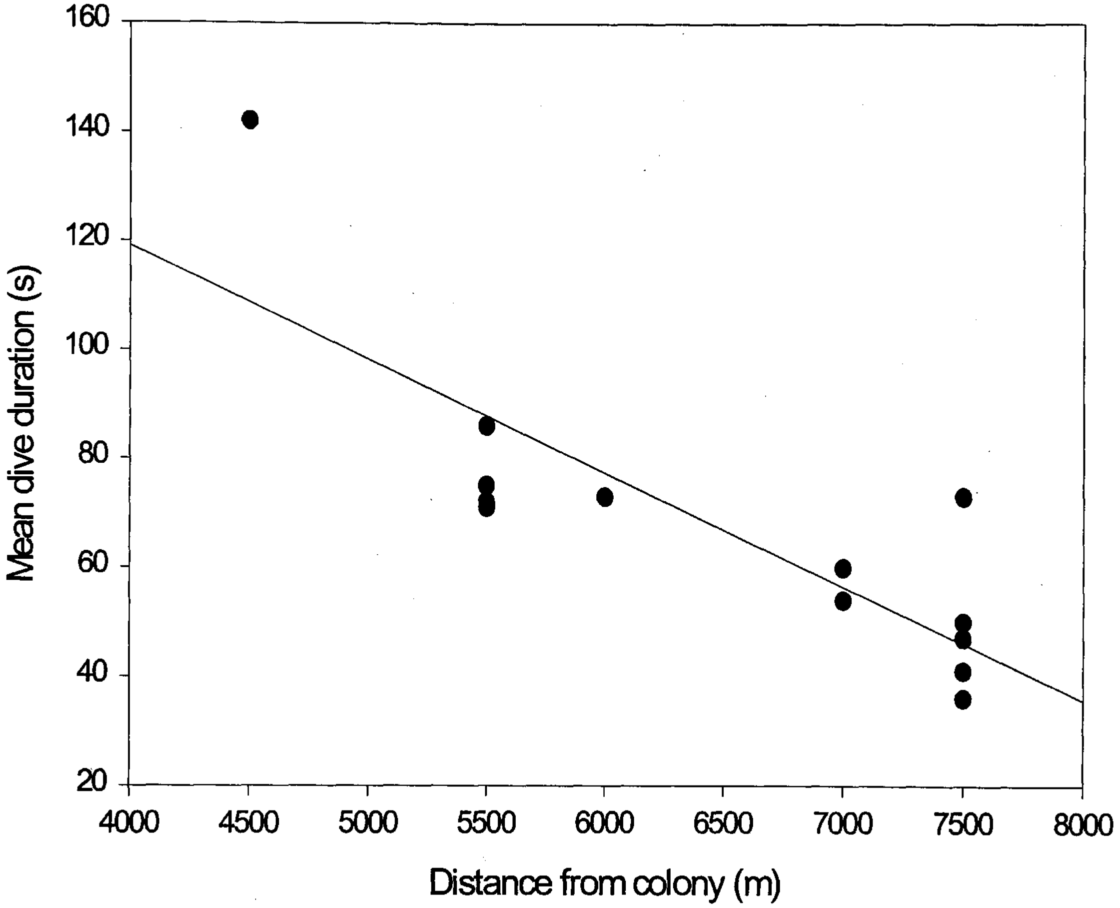

Figure 4. The mean dive duration for individual birds (s) and the distance travelled from the colony to forage (m).

beds) to the nest enjoy faster chick growth rates, (see Chapter 5). It would appear that there is some advantage in flying further to more productive feeding grounds as it is from these further sites that a high proportion of butterfish are delivered. Birds doing so (flying further) are making shorter dives, but take longer to recover from them. The butterfish has a high energy content per unit weight (butterfish, 5.01 kJ/g, Watt 1991, Sandeel, 4.63 kJ/g, Hilton *et al.* 1998) and also is the largest prey item commonly delivered to the nest site.

It is possible that the energetic demands of foraging in thick kelp habitat are greater than the demands of foraging in a more open habitat. Little is known about the exact method of capture used by birds foraging in habitats like kelp beds. The butterfish, the main prey species fed to chicks at this site, is known to live mainly amongst kelp holdfasts and amongst rocks at the bottom of kelp beds (Quasim, 1957) as well as amongst rocks associated with other seaweeds (Cheetham and Fives 1990). This microhabitat is not the most accessible of habitats, particularly in areas where the tide may flatten the kelp against the substrate. The dive durations recorded for the Black Guillemot (mean 61s, s.d 22s, max 116s) are generally higher than those reported previously for other alcids (Dovekie, mean 27s, max. 68 (Salomonsen 1950); Thick-billed Murre, mean 55s, max 224 (Croll *et al.* 1992); Razorbill, 48.7s, max 52 (Bradstreet & Brown 1985), Pigeon Guillemot, mean 36-87s, max 144s. This will give the Black Guillemot more time underwater to investigate such habitats.

It has been suggested that species of bird feeding primarily on non-schooling demersal prey may perform relatively long dives and spend longer recovering between dives (Ydenberg & Guillemette 1991). It is possible that underwater swimming speeds (quoted as 1.2-2m/s for the

Black Guillemot in Uspenski 1956) vary between habitats and this may account for the differences in diving behaviour between habitat types. In order to access bottom dwelling fish in thick kelp forest it would be necessary to penetrate this thick cover and this may entail considerable cost for the foraging bird. This would make foraging in kelp habitat more energetically expensive while being potentially more rewarding in the type of prey captured in habitat of this type (see Chapter 5).

Chapter 11

Discussion

This study has aimed to measure some of the variables affecting the breeding performance of Black Guillemots. Data were collected on breeding parameters such as laying date, size and number of eggs as well as date on hatching and growth rate of the chicks. The amount and type of food delivered to the nest was recorded, and the foraging effort of adults was measured by radio telemetry. In addition, the overall distribution at sea was mapped and samples of underwater sites were surveyed by divers. Although using an inshore foraging species breeding in burrows had obvious advantages over colonial species nesting in the open and foraging further offshore, studying Black Guillemots proved very demanding. Sample sizes are relatively small, access to the breeding site was very weather dependent, and the species proved difficult to catch and difficult to radio-track (see Chapter 2). One important variable that has not been measured is the adult, as distinct from the chick, diet. This is likely to have an important impact on the use of foraging areas, but by measuring the overall distribution of birds in the early season before many chicks have hatched I was able to locate the main areas potentially important for the provisioning of adults. Previously published data on adult diet (Ewins 1990) in Shetland showed adult Black Guillemots were eating invertebrates of the type associated with (but not exclusively) sandy and mud habitats such as *Neris* spp as well as crustacea such as Galathea, found in algal habitats such as Lhyp.Ft (see Chapter 8).

With these variables I have covered the majority of the measurable factors affecting the breeding biology of these birds.

The "b" egg of a two-egg Black Guillemot clutch is usually smaller than the "a" egg, and it is the chicks from this egg that are more likely to enjoy slower growth and are less likely to fledge. Breeding statistics from this colony compare favourably with those from other studies in other locations (see Chapter 3).

Egg production is costly for the females of all bird species and forms a major lifetime cost in terms of energy required (Monaghan & Nager 1997). For a breeding strategy to be stable, it would be expected that the number of eggs would be kept to the minimum possible, given that there is a trade-off between reproductive effort and longevity (Perrins 1996). Seabirds are typically long lived and have low annual reproductive output (Newton 1989), and thus there is no requirement for large clutch sizes.

If two eggs are relatively easy to produce for Black Guillemots than why do young birds produce only one? The decrease in reproductive output is common in young birds (DeForest & Gaston 1996), and increased early costs in terms of egg production can adversely affect the foraging performance of the female (Monaghan & Nager 1997). Egg weight in the Black Guillemot is in accordance with the observed relationship between egg weight and adult mass in the Alcidae (Birkhead & Harris 1985). This, however, is a relationship between egg weight and body mass in species that predominantly lay a single egg, and the relative cost of egg production will be higher overall with this species.

What reasons might there be for Black Guillemots to lay two eggs? Black Guillemots are unusual amongst north Atlantic auks in laying two eggs. Their ecology differs in two main areas, the type of nest habitat and their foraging ecology. The nesting biology of the Black Guillemot can potentially explain the ability to lay two eggs, or rather in inability of other north Atlantic alcids to lay two eggs. The use of concealed nest sites allows the chicks to be left unattended from an early age, and this allows both the adults to forage throughout the chicks rearing period. This is also the case for the Puffin, which lays a single egg in all cases

(Harris 1984). The eggs of the Black Guillemot are also very tolerant of being left unattended (Harris & Birkhead 1985), allowing both parents to forage for themselves during the incubation period, improving their body condition before the demanding chick-rearing period. This is in contrast to the Common Guillemot, which nests in high densities on exposed cliff faces. The nest site for this species consists of nothing more than a ledge and, if left unattended, the egg or chick would be lost. This means Common Guillemots will only lay one egg, that is, they are constrained by nesting habitat. This is also a possible reason for the early fledging displayed by this species. Other auk species who lay two eggs are the Pigeon Guillemot, Xantus' Murrulet and the Ancient Murrulet. All these species have nest sites that can be left unattended. Of the other North Atlantic alcid species, only the Puffin lays its eggs in covered nest sites, and it also seems to be able to leave its egg for long periods (Harris 1984). This species also has two brood patches so would be physically equipped to incubate two eggs, so another explanation must be found as to why the Puffin lays only one egg. Puffin chicks attain a higher fledging mass as a proportion of adult body mass than the Black Guillemot chick. This may be a adaptation to the greater dispersal distances after fledging of the Puffin chick, as Black Guillemot chicks stay close to the colony after fledging (Brown 1985, *pers obs*.). Another difference between the Black Guillemot and other auks, and a similarity between the Black Guillemot and the Pigeon Guillemot is the foraging ecology. These species are inshore foragers, and forage on prey species likely to be more predictable in their abundances (Gray 1977, Bradstreet & Brown 1985). Whilst Common Guillemots may have shorter travel distances and trip length in seasons of high prey abundance, the situation in a season of low food abundance is different, with long trips of high foraging effort (Monaghan *et al.* 1992). This means that Common

Guillemots are, by virtue of laying only one egg, able to successfully rear a chick every season. Common Guillemots are able to lay replacement eggs, as are Black Guillemots, but in this situation the demand of food for the chick will be the same, albeit later in the season. The variation in food supply for the Black Guillemot, being more stable, allows capable birds to successfully raise two chicks each year. It is worth noting that current life history strategies are not necessarily perfectly adapted to current ecological conditions and may be a remnant of adaptations to past circumstances.

The laying strategy gives the Black Guillemot a number of options in incubation and raising chicks. Apart form the choice of laying one or two eggs, two egg clutches can be incubated either as an asynchronous or a synchronous clutch. In the case of the asynchronous hatching brood, the peak demand for food is likely to be less severe as chicks will be staggered in their time of peak demand for food. Synchronous hatching broods will have chicks of more similar size and whilst the peak demand for food will be greater, the chick rearing period will potentially be shorter.

The composition of the prey brought to the nest has important consequences for the growth rate of the chicks. It is advantageous for adult Black Guillemots to provision their chicks on butterfish, providing the energetic demands of foraging are met (see Chapter 5). Black Guillemots at the Papa Westray colony travel over greater distances than previously associated with inshore foragers (see Chapter 7). As birds at this colony have as high a breeding success as other colonies, this distance appears to be compatible with successful breeding, and such travel distances are probably common in the Black Guillemot.

The distribution of foraging birds on the inshore waters of Papa Westray is not even. Certain areas are more heavily favoured than others, and this is constant across both years of surveying and within seasons. The degree of seasonal variation in the distribution of adult birds can be explained by the differing demands of foraging for chick rearing, and for feeding for themselves, the diet composition for adults and chicks being different.

Adult Black Guillemots catching predominantly butterfish, the best prey type for their chicks, have to travel to the furthest foraging areas from the colony. Birds diving in these areas are making shorter dives in water that deeper than the water in other areas. It is more energetically expensive to fly long differences to forage but, providing the bird is of sufficient foraging ability, such a strategy can be profitable. This view is supported by the observation that single egg layers (younger and less able birds) fail to gain the benefits of attempting this strategy.

The waters around Papa Westray show a large amount of variation in habitat type. This diversity of habitat shows a wide range of diversities within habitats, and a large amount of variation in available prey types.

Black Guillemots favour distinct habitat types for foraging both for themselves and their chicks. These types have very different topography, exposure, vegetative cover and fauna, but both would appear to be equally important in terms of bird density.

Protective legislation for populations of breeding seabirds has historically been centered on the protection of the breeding colony area, i.e. the nest sites themselves being protected from disturbance and exploitation. While this is an important aspect of conservation legislation, it is obvious that a lack of protection of the foraging areas required for feeding both the adults and the chicks would render any protection of the breeding area pointless. Adult birds have to attain breeding condition in time for the breeding season (the timing of which is essential – see Chapter 4), the production of eggs is well documented as being demanding (Monaghan & Nager 1997), as well as being able to provide prey at a sufficient rate to develop chicks to the fledging stage. This species, in particular, by producing two eggs (unlike all other north Atlantic Alcids) is exposed to greater relative energetic demands in the run up to the breeding season.

Given the above, it is essential to attempt to identify what, in terms of foraging areas, is required for the successful breeding of this species. From the data presented in Chapter 6 it can be seen that the distribution of these birds is far from random. The birds are selecting specific foraging areas at different times of the season, and these appear to be of certain distinct habitat types, as discussed in Chapter 9.

The most likely threat to foraging sites in this area, apart from pollution as would be caused by an oilspill, would be the commercial harvesting of kelp. The shallow waters surrounding this island are of high productivity and have been identified as potential sites for the harvesting of kelp. From the information collected on the distribution, and the habitat type, it would be possible to show that, provided those areas and habitats which are protected, such harvesting could be carried out in certain areas without adversely affecting the breeding performance at this colony, provided these areas are of habitat types not important to the foraging of this species.

Historically, the main focus of seabird conservation measures has been protection of their breeding colonies (Lloyd *et al.* 1991). Protective legislation designed to prevent the disturbance of these areas has not been accompanied by similar legislation to protect the feeding or wintering areas. In the case of many seabirds, this is a result of the nature of the feeding and wintering sites. Birds that forage on pelagic shoaling prey such as sandeel, capelin or sprats are, by virtue of the biology of their prey species, distributed over large areas of sea and their foraging locations are hard to predict. Such situations are not conducive to the framework of protective legislation, as such legislation is geared towards covering easily defined physical areas. The alternative in such situations is to protect the prey species as a whole, a situation unlikely to be politically tenable when the prey species is a commercially harvested species.

In the case of an inshore foraging seabird the situation becomes easier to manage. Such species tend to feed in distinct and measurable areas on more sedentary, often territorial prey species whose distribution is limited to the availability of suitable habitat. When such habitat has been identified as an important resource for species considered to be of international importance or in decline, it will be easier to put in place legislation to protect the physical feeding site.

The Black Guillemot is one such inshore foraging species (see Chapter 1). In the British Isles, its distribution is limited to northern and western coasts, and its numbers are small compared to other seabird species. Its dependence on inshore coastal foraging habitats will have an influence on the density of its breeding colonies; the availability of resources within an economically viable foraging distance is much less than the potential availability of prey in an open water system. This said, the inshore habitats are, human disturbance notwithstanding, likely to be more stable in terms of prey availability and the seabird population is, as a result, also likely to be more stable from year to year. The numbers of Black Guillemot in Norway have been in decline for a number of years. There has been an increase in the number of Mink *Mustela vison* And predation by these is considered to be responsible for the decrease (Tasker *et al.* 1986). The Black Guillemot is particularly susceptible to predation by mammals due to the accessible nature of its nest site.

A major conclusion of this thesis is that the Black Guillemot is selective in terms of the habitats it utilises, despite the large distances often travelled to get to such sites. Important habitats for the Black Guillemot are those that provide important prey species, the most important of which during chick rearing at this site is the butterfish *Pholis gunnellis*. Those habitats that are important are found in areas of high Black Guillemot concentration and consist of both kelp and sand habitats. There are distinct habitat types which are important to the breeding colony on the Holm of Papa Westray and these are concentrated in specific areas some distance from the colony (see Chapter 9). These areas are at the north-west and the south-west tips of the island.

In terms of the ability to conserve such a species, knowledge of these factors would make it easier to protect specific essential areas. I have shown that certain types of habitat are more important than others, and that certain distinct habitat types, often within a broader habitat description, are more important. The kelp habitats I have identified as being important often occur in close proximity to other similar, but less important in terms of foraging density kelp habitats. Kelp beds, particularly in the clear productive waters of the North Sea, are a commercially viable commodity and their harvesting for the production of alginate could be a potential threat to Black Guillemots. Research of the type I have carried out into the identification of the most important habitat types and areas used by foraging birds could potentially allow the harvesting of kelp to be carried out outwith key foraging areas. The targeting of these specific areas could be carried out instead of banning human interference over a wider area (for example a circle 10km from the colony). These "potentially exploitable" areas could consist of large sections of water which show no signs of Black Guillemot, or any other species deemed worthy of conserving, use. It is the identification of key habitats like this that a balance can be struck between reactionary over protection (which has a tendency, at least in Scotland, to cause resentment towards legislators from local people) and over exploitation of the natural environment.

The foraging ecology of the Black Guillemot differs from other North Atlantic Alcids (as I have said perhaps *ad nauseum* throughout this thesis) in that it forages on shallow inshore waters on demersal and often territorial prey. This is likely to be more predictable in availability than shoaling pelagic prey types, particularly in the case of the butterfish, the principal prey species of the Black Guillemot. This species holds small territories in areas of rocky substrate, often in kelp beds. If the territory holders are removed the territories are quickly filled by other butterfish, presumably a floating population who will occupy vacant territories in order to breed. This would make the availability of prey a very predictable resource for the Black Guillemot, providing the depletion of territories is carried out at a rate less than or equal to the rate of replenishment. In terms of the theory of foraging, this factor is likely to be a limiting factor in the sustainable density of foraging birds, and would explain the large foraging range of this species. Authors studying the Black Guillemot have suggested that individuals hold foraging territories but the evidence for this is largely circumstantial, although in my work I did find that some individuals showed a large amount of fidelity towards foraging sites.

The Black Guillemot is unusual in the Alcidae in that it winters in inshore waters close to the natal colony. Most other species occur far out to sea in the winter months, living a pelagic lifestyle. The ecology of the Black Guillemot however seems to favour foraging in shallow water at all times of year and its winter diet consists largely of bottom dwelling invertebrates.

The main conservation threats to the Black Guillemot are, not in order of priority, as follows...

Introduced species.

Mammalian predators such as Mink and Rats accessing nest sites (Craik 1997, Asbirk 1978).

Pollution, oil and chemicals.

Black Guillemots are particularly susceptible to inshore oil spills, largely due to the short range of their winter dispersal and their dependence on inshore foraging areas (Tasker *et al.* 1986, Lloyd *et al.* 1991).

Pollution in the form of human disturbance of the nest sites could be a potential problem for this species (Cairns 1980) (although some populations seem more tolerant of this than others).

Commercial exploitation of foraging areas.

There would appear to be no problem with fishing. Unlike other seabirds, the prey species of the Black Guillemot are of no commercial importance. However, the potential for the farming of kelp for the production of alginate in shallow productive cold water areas could effect the foraging sites necessary for provisioning of chicks in the breeding season.

This work has aimed to show that the little studied use of the local foraging environment is important for seabird populations, and that the ability of individuals to adapt to local variation of this environment can have an effect on their breeding success. Unfortunately some questions remain; the effect of the adult diet on breeding performance, the proportion of time spent by adults on feeding themselves and the sites important for this type of foraging are unknown, and may have effects on the breeding strategy chosen. Little also is known on the used of habitats outwith the breeding season. Given more manpower, better quality information could be gathered on the amount of energy expended overall in foraging bouts, and the surveys of the sea bed could be undertaken in more detail and covering more sites to look further into the availability of prey species.

Further research into this area may shed light on these questions, and further improve our understanding of the importance of marine habitats to the species that feed in them and to allow protection of such important areas.

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The author (right) surveying the inshore waters of Papa Westray ably assisted by Dr. Rob Field. The island is the background is the Holm, the location of the black guillemot breeding colony.