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CORMORANTS AND THE LOCH LEVEN TROUT FISHERY

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Faculty of Biomedical and Life Science, University of Glasgow

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I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is of my own composition. No part of this work has been submitted for any other degree.

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August 2002

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I worked part-time on this project for five years and most of the initial data analysis and writing-up was conducted when I was recalled to the Royal Navy to fly on the Search and Rescue Helicopter Flight at Prestwick. After the morning training flight I

would sit in the ready-room for the rest of the day, with my lap-top and field notes, typing away, whilst hoping I would not be interrupted by some unfortunate climber falling off a mountain or a pilot crashing his aeroplane. Occasionally my fellow crew members would make the mistake of asking what I was working on so busily, and as I tried to explain I could see their eyes glaze over in incomprehension, quickly followed by the onset of disinterest. However, they remained polite and continued to fly with me despite my aberration, and for their tolerance, support, fortitude and above all their humour in the face of adversity, I am eternally grateful.

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Summary

1. Perceived conflicts between piscivorous birds and commercial freshwater fisheries are common, and such a perception exists at Loch Leven, a wetland of international importance for nature conservation and a famous commercial brown trout *Salmo trutta* fishery, where Great Cormorants *Phalacrocorax carbo* have been shot in large numbers. This thesis describes the foraging behaviour of cormorants wintering on Loch Leven. It summarises changes in wintering numbers over a 32 year period, and reviews data on fish populations, fish stocking rates, angling catches and angling effort in order to seek evidence of detrimental impacts of cormorants on the fishery, and beneficial effects of large-scale cormorant shooting. Finally, this thesis considers turnover within the wintering cormorant population, and its implications for cormorant control.

2. Cormorants spent most of the time roosting, and a single peak of feeding activity occurred early in the morning. Compared to early or late winter, cormorants showed higher foraging activity during mid-winter. Both solitary feeding and flock feeding were recorded, with flock feeding predominating. Solitary feeding was distributed over a wide area. The intensity of flock feeding was less evenly distributed, with 36% of grid squares not used. Overall, 78% of flock feeding activity took place in 23% of grid squares and 59% took place in 13% of grid squares. The best predictor of both solitary feeding and flock feeding intensity of use was mean water depth. Mean water

depth was also the best predictor of winter brown trout distribution, although winter brown trout distribution was not a predictor of either solitary feeding or flock feeding intensity of use.

3. During the life of a flock, the mean distance covered was 3,757m, with a mean duration of 68min, and a median flock speed of 1.02 m s^{-1}. Flock size declined over time until the flock dwindled away, or all remaining birds flew *en-masse* to roost. The decline of individual flocks followed linear and cubic curve profiles.

4. On some occasions, flocks re-visited the same area on several sequential days, whilst on other occasions they foraged over different areas. They also sometimes revisited the same location several times during a single flock-feeding event.

5. Cormorants conducted from one to five foraging trips per day, with adults conducting fewer trips than first-winter birds, and individual trips lasting up to 395 min. Cormorants conducted up to 495 dives per foraging trip, with adults diving for less time than first-winter birds, and significant variation between individuals.

6. Median dive durations ranged from 25 to 27 s, and median surface interval ranged from 6 to 9 s, both with significant differences between individuals.

Dive duration and surface interval decreased during a foraging trip, but showed no reduction with increasing number of trips. Dive duration or surface interval did not vary with water depth. Dive duration and surface interval did not vary between solitary feeding and flock feeding.

7. Foraging time and number of dives per foraging trip were higher at Loch Leven than at other sites. Surface interval was shorter than at other sites. The lack of evidence of a link between water depth and dive duration contrasts strongly with other sites.

8. Since 1968, the number of cormorants wintering on Loch Leven has risen ten-fold, with the principal increase occurring around 1988. This increase is in line with the trend for Great Britain as a whole, but higher than that for Scotland. Variations in angling catch showed no correlation with changes in cormorant numbers, but the brown trout catch as a percentage of the loch's population has declined by about two thirds.

9. There was no evidence of detrimental impacts of cormorants on the trout fishery. Catch per unit effort remained relatively stable despite the cormorant increase, and the principal determinant of the size of angling catch was angling effort. The proportion of brown trout found to be wounded by cormorants was low.

10. There was no evidence of a reduction in wintering cormorant numbers, or of an increase in angling catches, as a consequence of shooting large numbers of cormorants.

11. Multiple cormorant counts suggested large-scale movements of birds, which was confirmed by observations of groups arriving and departing. Short-range radio tracking revealed intermittent absences, with individuals present for 51% of the time. Satellite telemetry indicated that birds mostly ranged within 45km of Loch Leven, with occasional journeys further afield. The wintering cormorant population within 45km of Loch Leven exceeded 2,000, of which Loch Leven held 10%. There was evidence of movement between sites during the winter, with reductions on marine and estuary sites and increases on rivers and stillwaters. This is consistent with optimal foraging theory and demonstrates that the Loch Leven wintering population is drawn from a wide area. High turnover within the population reduces its amenability to control, and would account for the ineffectiveness of shooting as a mitigation measure.

12. The above conclusions question the assumption that serious economic damage to commercial and recreational open-water fisheries is attributable to cormorants. Furthermore, they question the validity of shooting cormorants for fishery protection purposes on large, open water wintering sites.

Chapter 1

GENERAL INTRODUCTION

INTRODUCTION

This study addresses a difficult problem with worldwide relevance, namely the perceived conflict between freshwater fisheries and piscivorous birds. The word "perceived" is used advisedly, because the conclusion that damage is caused to commercial and recreational fisheries by cormorants is based largely on assumption and interpretation rather than on quality evidence. Furthermore, because the traditional response to such a perception has been to kill large numbers of birds, this has inevitably lead to polarisation of opinion within the scientific community and in the wider world, and to the promotion of overly simplistic views. A study such as this, which describes the foraging behaviour of piscivorous birds on a commercial trout fishery, seeks evidence of their detrimental impact, and reviews the effectiveness of shooting as a control measure, is therefore of particular relevance to the current debate.

Loch Leven is located in east central Scotland between the Forth and Tay estuaries, as shown in Fig. 1. It was judged to be a suitable site for this study for a number of reasons. Firstly, it has been a recreational trout fishery since 1873 and has comprehensive records of catches, fish stocking and angling effort. It is also a famous fishery, one of the largest in Britain, hosting national and international competitions, and has a high public profile. Research work carried out on Loch Leven is therefore liable to wide exposure, and may exert influence on the wider debate about fishery-cormorant conflicts.

FIGURE 1:   LOCATION OF LOCH LEVEN STUDY SITE

Secondly, it is a wetland of international importance for its breeding, wintering and migratory waterfowl populations. During the summer it holds the largest concentration of breeding duck in Britain and during the winter provides a refuge for many thousands of swans, geese, ducks and other water birds (Wright, 1994). As a result it has been subject to research, survey and monitoring for many years and has extensive long-term ecological records.

Thirdly, it holds the largest concentration of wintering Great Cormorants *Phalacrocorax carbo* in Scotland, with a peak of 800 recorded in 1991, making it the ninth largest wintering population in Britain. For many years a conflict has been perceived to exist between the recreational trout fishery and the wintering cormorant population, and as a consequence, cormorants have been shot in large numbers. Finally, there is high level of cooperation between the loch's fishery and conservation staff, which enables the open exchange of information and opinions, and facilitates the initiation of cross-discipline studies.

Background to this study

In 1995, Loch Leven was proposed as a potential Special Protection Area (SPA), by the Scottish Office Agriculture Environment and Fisheries Department (SOAEFD), now Scottish Executive Rural Affairs Department (SERAD). This brought unregulated cormorant shooting on the loch to an end, prompting objections from the fishery interests who applied to SOAEFD for a licence to shoot cormorants in order to control their numbers. In assessing the licence application, it became apparent that there was a lack of evidence on the possible impact of cormorants on fish stocks and angling, and also on the scope for exercising control over cormorant numbers. In order to be credible, the concept of control requires firstly that an appropriate acceptable number must be determined as a target to which the numbers should be reduced, and below which their impact is acceptable in terms of damage to the fishery interests. In addition, that target must be demonstrably achievable, i.e., cormorant numbers must be capable of being controlled.

Some Scottish cormorant breeding sites are also designated as SPAs, and analysis of ringing returns showed that birds from these sites winter on Loch Leven. This raised the possibility of birds protected on breeding ground SPAs by the strongest UK and European legislation, being legally shot on Loch Leven, another SPA, with potentially serious consequences for protected populations. Indeed, declines in breeding cormorants on some SPAs in northwest Scotland had already been attributed to the impact of shooting (Russell *et al.,* 1996).

The uncertainty and lack of evidence, and the risk of compromising SPA designations, persuaded SOAEFD and Scottish Natural Heritage (SNH) to initiate an investigation into cormorant impacts on the trout fishery, and that investigation forms the basis for this thesis.

THE GREAT CORMORANT

The genus *Phalacrocorax* contains 27 or 28 species distributed mainly along temperate and tropical marine coasts and inland waters, with some species extending to the Arctic and Antarctic. The birds are medium to large-sized underwater pursuit swimmers, characterised by hooked bills, long necks, elongated bodies, short rather rounded wings and long, normally wedge shaped tails. Their plumage is generally dark with a metallic sheen, and most species show some seasonal variation. Their feathers are not completely waterproof and they are frequently seen drying their wings in a typical spread-eagled posture (Harrison, 1983).

The Great Cormorant *P. carbo* has a discontinuous distribution from North America, through northwest Europe, Asia and Africa to Australasia, and its range overlaps with many other cormorant species. Six sub-species are listed including *P. c. sinensis* found in Eurasia, *P. c. marroccanus* found in NW Africa, *P. c. lucidus* found in Africa, and *P. c. novaehollandiae* found in Australia and New Zealand. The subject of this study, *P. c. carbo,* is found in Labrador, Nova Scotia, Newfoundland and the Gulf of St. Lawrence, the Faeroes, Norway, Ireland and the British Isles (Harrison, 1983).

In Scotland *P. c. carbo* overlaps in distribution with the Shag, *P. aristotelis,* which is almost exclusively marine, and these species can be readily distinguished in the field. Although *P. c. sinensis* has become well established in England (Sellers *et al.*, 1997), it is much less common in Scotland. It is somewhat smaller than *P. c. carbo,* and has a different shaped gular patch, but this may not be readily distinguished in the field.

The biometrics of cormorants shot and caught at Loch Leven indicate that the wintering population comprises almost exclusively *P. c. carbo* (Carss & Marquiss, 1992).

During the summer *P. c. carbo* breeds at coastal sites around Scotland, and at one inland site in Dumfries (Sellers *et al.*, 1997). In addition, non-breeders may summer at inland sites, with a maximum of 30 at Loch Leven during 1998. During the winter, the birds disperse to coastal and inland sites, and arrive at Loch Leven in large numbers from October onwards, with peak numbers usually recorded in February.

Recent advances in modern technology, such as developments in radio and satellite telemetry, have enabled more detailed research into cormorant foraging behaviour. However, most of these have focussed on salt water (e.g. Gremillet, 1997; Gremillet *et al.*, 1998; Gremillet *et al.*, 1999a; Gremillet *et al.*, 1999b; Kato *et al.*, 1999; Lariccia, 1997 and Wilson & Wilson, 1988). Those studies which have investigated cormorant behaviour on fresh water (e.g. Doherty & McCarthy, 1997; Hughes *et al.*, 1999) have been in more temperate areas, and thus intensive studies of behaviour at a freshwater site in Scotland, such as Loch Leven, add considerably to the general knowledge base.

LOCH LEVEN

Loch Leven is the largest lowland freshwater loch in Scotland, covering some 1,330 hectares with an average depth of 3.9 metres (Fig. 2). It is located in Kinross. In terms of its nature conservation interest, it is subject to two international and two national designations:

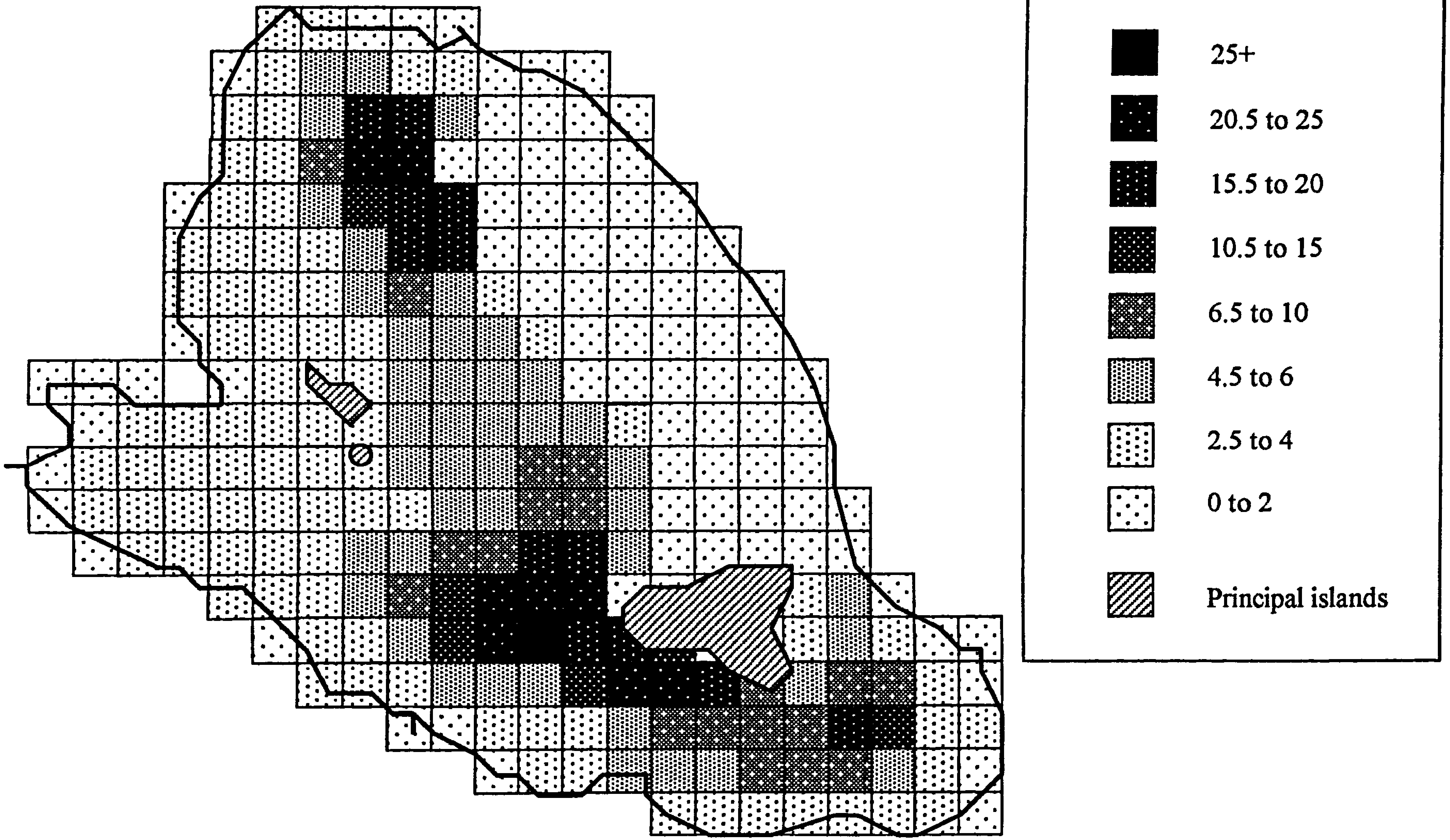
Special Protection Area

The European Union has passed two Directives of particular relevance to this study, namely the Birds Directive (Directive 79/409/EEC on the Conservation of Wild Birds) and the Habitats Directive (Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Flora and Fauna). The Conservation (Natural Habitats &c) Regulations 1994 (The Habitats Regulations) transpose these Directives into British law. Guidance on their implementation in Scotland is contained in Scottish Office Circular 6/1995.

Amongst other obligations, the Birds Directive requires Member States to take special measures to conserve the habitat of regularly occurring migratory species to ensure their survival and reproduction, bearing in mind their breeding, moulting and wintering areas and staging posts along their migration routes. The special measures include the classification in particular of the most suitable territories as SPAs for the conservation of these species.

Loch Leven qualified for designation on account of its populations of breeding wintering and migratory wildfowl. Among the qualifying criteria, under Article 4(2)

FIGURE 2: LOCH LEVEN MAXIMUM WATER DEPTH IN 250 X 250 METRE GRID SQUARES



of the Birds Directive, Loch Leven regularly supports an internationally important assemblage of wintering waterfowl, which includes nationally important wintering populations of migratory cormorant. Following consultations on the site's potential SPA status in 1995 the Secretary of State for Scotland subsequently classified it as a SPA. It is Government policy therefore that Loch Leven is accorded the highest conservation status under British and European Law, and accordingly its bird populations should be afforded the highest level of protection.

Ramsar Site

On 6 September 1973, the United Kingdom signed the Ramsar Convention on Wetlands of International Importance, and Loch Leven was one of 13 sites ratified by the British Government. Under Article 3 of the Convention, the government agreed to formulate and implement their planning so as to promote the conservation of the wetlands included in the List. Loch Leven qualified as a Ramsar site as a particularly good example of a naturally eutrophic loch. It supports characteristic flora and fauna, including nationally important wintering populations of cormorant.

Site of Special Scientific Interest

In 1956 Loch Leven was first notified as a Site of Special Scientific Interest (SSSI). In the Nature Conservation Review of 1977 it was accorded Grade 1 status, and it was re-notified as an SSSI in April 1985. The basis for its notification was its ornithological, botanical and entomological interests and the citation commented that Loch Leven is an outstanding site for wintering and breeding wildfowl in Britain.

National Nature Reserve

Loch Leven was proposed as a Nature Reserve in 1949 by the government's Scottish Wildlife Conservation Committee and in 1959 it was designated a proposed National Nature Reserve (NNR). In March 1994 it was declared a NNR under a Nature Reserve Agreement with the owner.

The trout fishery

Loch Leven is also managed as a commercial Brown Trout *Salmo trutta* fishery, and is one of the largest in Scotland with forty-four angling boats for hire. The angling catch has always been subject to wide fluctuation, but has declined markedly in recent years (Duncan, 1994). As a result, the fishery's management have established a stocking regime of Brown Trout and Rainbow Trout *Oncorhynchus mykiss* with a view to enhancing the angling catch (Montgomery, 1994). In addition to trout, the loch holds natural populations of Perch *Perca fluviatilis*, Pike *Esox lucius*, Three-spined Stickleback *Gasterosteus aculeatus* and Eel *Anguilla anguilla*, none of which are subject to commercial exploitation.

Water quality

The loch is naturally nutrient rich, but additional inputs from the surrounding agricultural land and from sewage effluent from adjacent settlements have lead to increased eutrophication, with dense, sometimes toxic, algal blooms occurring regularly. As a consequence, there have been detrimental changes in macrophyte and invertebrate communities (Fozzard, 1994). As a result of recent efforts, the inputs of the controlling nutrient, phosphorus, have been greatly reduced, with a view to re-establishing a more natural water quality in the loch (Anon., 1999)

THE CORMORANT-FISHERY CONFLICT

Interest in the perceived cormorant/fishery conflict is widespread, particularly throughout Britain, Europe and North America. Because of the claims of economic loss to commercial fisheries, the conflict has become subject to intense scrutiny, and this is reflected in a series of conferences convened to discuss the issues. Consequently, much of the published literature is to be found in dedicated journal issues and conference proceedings.

The perception of damage

The consumption of commercially important fish species by cormorants is not disputed, and at Loch Leven it has been shown that they take Brown Trout and Rainbow Trout, as well as Perch and Stickleback (Carss & Marquiss, 1992, Carss & Marquiss, 1994). However, there is no evidence that by doing so they deprive commercial or recreational fishermen of their catch (Carss, Marquiss & Lauder, 1997).

In a review, Van Eerden *et al.* (1995) concluded that impact studies showing detrimental effects of fish predation by cormorants in natural water bodies are scarce, and Kirby *et al.* (1995) concluded that scientific data on the impacts these birds have on fisheries is lacking and without this any conflicts will be difficult to resolve. Furthermore, in respect of recreational fisheries, no study has quantified the scale of losses to fisheries in relation to overall production. Hence "seriousness" has not been determined, and it is not known whether, in the absence of cormorant predation, the harvest or catch for anglers would increase (Kirby *et al.*, 1997).

Obtaining evidence

Many studies have addressed aspects of the perceived conflict, but evidence of impacts has proved difficult to obtain (Marquiss & Carss 1994, Marion 1997). In Italy, Voloni (1997) attempted to estimate fish consumption by cormorants and possible impacts on aquaculture production in the Po Delta. He found that whilst estimates of biomass removed by cormorants appeared to be relevant, many other factors directly influenced fish survival and growth, and it was difficult to discriminate the effects of cormorant predation.

Adamek *et al.*, (1997) analysed questionnaires sent to fisheries in Europe in an attempt to evaluate the status of cormorants on fisheries and quantify the scale of damage. They estimated losses of over 4 million ECU, based on claims made by fisheries but these were not supported by any proof of such damage. Complaints made by anglers were frequently found to lack any data on fish stocking and yield, and were thus considered to be unreliable. In England Feltham & Davies (1997) found biases in angling catch on the River Ribble, which raised questions on the validity of the common practice of using changes in angling catches as indicators of fish stocks and predation impacts.

Evidence for and against serious damage

On the River Bush in Ireland, Warke & Day (1995) considered the impact of cormorants to be particularly significant on older Salmon *Salmo salar* parr. However, they also described changes in cormorant foraging habits towards marine species, which reduced the incidence of inland foraging by cormorants, despite high smolt runs. In 1991, when cormorant numbers foraging inland were low, they estimated the cormorant predation rate as possibly as high as 47%. However, this was based on the stomach contents of only seven shot cormorants, of which only four contained Salmon parr. This is considerably fewer than the sample size of 12 to 15 described as adequate by Marquiss & Carss (1997) as a result of analysis of stomach contents of cormorants shot on the River Tweed in Scotland. Marquiss & Carss considered such small samples have a large margin of error. In calculating total impact it was assumed that all birds would have fed solely on the river, each taking 425g of almost exclusively salmonids. The possibility that the birds might feed in more than one location was not considered, despite the acknowledgement that cormorants often overfly the river on their way to feed on Lough Neagh, and may stop on the river to feed. The conclusion that cormorants may have taken up to 47% of the smolt is clearly speculative.

Also in Ireland, Kennedy & Greer (1988) used similar techniques to Warke & Day (1995) and estimated that cormorants may have caused predation rates of 51-66% of wild smolts and 13-28% or reared smolts, but these results are subject to the same weaknesses of small sample sizes and questionable extrapolation. In Ireland Macdonald (1987) reported levels of predation of 5.8-13.1% of migrating smolts, but provided no evidence to support his findings. Despite these shortcomings, Warke &

Day (1995), Macdonald (1987) and Kennedy & Greer (1988) are all quoted as evidence of heavy cormorant predation on salmonids in an advisory report to Government Ministers (Dunnet, 1996).

In Ireland, Doherty & McCarthy (1997) investigated the foraging activities and diet of cormorants on the River Shannon. They concluded that cormorants do not represent a serious threat to the Brown Trout fishery. They did, however, express some concern over possible impacts on a developing Eel fishery, but noted that Eel mortality also occurred due to hydroelectric turbines, and that cormorants fed heavily on injured eels that were easier to catch.

In France, Marion (1997) compared the diet of breeding cormorants and captures by fisheries at the largest inland colony in France, at the Lake of Grand-Lieu. He found that less than 5% to 28% of the commercial fishery yield was taken by cormorants, and with fish densities of about 210 & 278 kg ha^{-1}, cormorants took 6 kg ha^{-1}, or 3% whilst fishermen took 30 kg ha^{-1}, or 15%, but the cormorant impact was probably overestimated. The 3% impact was similar to other assessments, and a decrease in captures by fishermen did not seem due to cormorant predation. There were possible cormorant impacts on Pike & Tench *Tinca tinca*, but most fish taken were of non-commercial size. Impacts on Eel and non-commercial species were considered to be negligible.

In the Netherlands, Van Dam (1997) reviewed interactions between cormorants and commercial fisheries on the Ijsselmeer. He found that cormorants took about 12.7 kg ha^{-1} of fish, and the bulk comprised non-commercial species. Predation of commercial species was just under about 2.8 kg ha^{-1}, and consumption by cormorants of Eel, the most important commercial species, was less than 5% of the commercial catch. Cormorant predation of small Perch was similar to losses due to discarding of dead fish in the fyke-net bycatch, and compensatory mortality effects might operate. Losses of Perch to cormorant predation and to fyke net bycatch were both similar to the commercial catch, and predation of small fish by cormorants probably depresses the commercial catch, as does the bycatch. Pikeperch *Stizostedion lucioperca*, the least important commercial species, were also caught in comparable quantities by cormorants, fyke nets and commercial fishermen.

In the Netherlands, Dirksen *et al.* (1995) investigated cormorant prey choice and fish consumption in shallow eutrophic freshwater Lakes Wolderwijd and Veluwemeer from October to March. They found that cormorants strongly preferred small shoal-living size classes of fish, and overall prey takes were 3.7 kg ha^{-1}, or about 1.8% of the stock of Wolderwijd of 210 kg ha^{-1}. Following the removal of 36 kg ha^{-1} of fish from Wolderwijd as part of a water quality restoration project, cormorant predation rate there increased to 12.5 kg ha^{-1}, or 11% of the total stock present in September, whilst on Veluwemeer it was 2.1 kg ha^{-1}. They found little conflict between cormorants and fisheries over eels, and no conflict over Roach and Pike.

In the Netherlands, Marteijn *et al.* (1997) compared the total fish consumption by cormorants with fish stocks in lakes and large rivers. Consumption in gravel pits was 35 kg ha^{-1}, or 8-9% of available stock. They concluded that although predation could be serious on fish farms, on larger, natural waters the consumption of commercially valuable fish was often limited, and fishermen's complaints of cormorants consuming large amounts of commercially valuable fish were often unjust.

Also in the Netherlands, Van Eerden and Zijlstra (1997) investigated the diet of cormorants and their possible impact on fisheries. They found that for the largest part of their diet cormorants relied on common fish species without any economic interest. They considered the direct impact of removal of commercially important fish of marketable size and found no evidence of serious damage. They considered the indirect impact of removal of immature fish of commercially important species to be potentially the most likely cause of damage. However, they concluded that high natural mortality of immature fish and compensatory mortality mechanisms would act as a buffer, and possibly fully compensate the effects of cormorant predation.

In Germany, Keller *et al.* (1997) found that fish production losses at a Carp *Cyprinus carpio* farm had risen from 12% to 26.4% since the arrival of cormorants, which represented substantial damage. They recommended preventative measures such as cross-wiring with selective shooting of persistent individual birds if damage continued. However, on large pre-alpine lakes they found no recognisable influence of cormorants on fisheries production, and concluded there was no necessity to control cormorants. On reservoirs and gravel pits they found no evidence of effects of cormorants on fish yield, although there was potential for some impact on cyprinids and Perch, but control measures were not justified. They considered that there could possibly be some impact on small isolated stagnant waters, where defensive measures may be appropriate. On large rivers a large influence of cormorants on fish yields could not be demonstrated, and the need for cormorant control was not justified. On small rivers it was judged that there could be some cormorant impact on Grayling *Thymallus thymallus* and possibly Barbell *Barbus barbus*, but insignificant impacts on other species, and protection of Grayling spawning areas was supported.

In Bavaria, Keller (1995) and Keller (1997) estimated that during November to February a maximum of 1.8 kg ha^{-1}, or 3.3% of the annual fish production of Lake Chiemsee, was taken by wintering cormorants, compared with 28% by commercial fishermen. For individual species, 3.3% of the commercial catch of Whitefish *Corregonus* spp were predated, compared with 6.2% for Pike *Esox lucius* and 22.3% for Eel. On the lower Inn River he calculated cormorant predation as 6.3 kg ha^{-1}, or 21% of annual production, whilst anglers consumed about 64% of annual fish production. He concluded that serious damage to either commercial fisheries or anglers was unlikely to occur, although there could be some competition with anglers.

In Germany Kieckbusch & Koop (1997) examined the diet of cormorants wintering in Schleswig-Holstein. They found that half the birds fed on the Baltic, and social fishing birds, which formed the bulk of the inland population, fed predominantly on small shoaling fish of little or no economic importance. However, solitary fishing cormorants took economically important fish species such as Eel, large Perch and Roach, and they concluded that damage was possible on sites where solitary fishing was practiced.

In Italy, Donati *et al.* (1997) assessed the impact of piscivorous birds on intensive sea bass *Dicentrarchus labrax* farms, and concluded that they suffered serious damage from cormorant predation, but demonstrated the benefits of protective netting of ponds. They also found that predation increased with the intensity of fish farming stocking, and damage could be reduced through modified management practices.

In Sardinia, Addis *et al.* (1995) assessed cormorant impacts on fisheries and estimated predation as 77 kg ha^{-1}. However, this was based on only one count carried out in January, and assumed all birds were present for 180 days. Schenk (1997) calculated a maximum cormorant predation of 50 kg ha^{-1}, acknowledging this was too high as it was assumed that all feeding took place on wetlands and no allowance was made for feeding at sea. This figure was equated to between 30% and 60% of total annual production, but used production figures of 80-150 kg ha^{-1}, calculated for French Mediterranean lagoons by Duncan *et al.* (1988).

In Switzerland, Staub (1997) attributed falls in Grayling yields by 60 to 90% to a switch by cormorants from feeding exclusively on lakes, to also feeding on Swiss rivers from 1983 onwards. However, Suter (1997) reviewed the use (and abuse) of fisheries data in assessment of cormorant impacts. He noted that although the coincidence of low or decreasing angling yields with presence of cormorants had been taken as proof of cormorant depletion, there had been little or no assessment of cormorant diet or foraging activity, and little justification for the use of fish catches as indicative of stock size. At a Rhine trial site, he found that cormorant predation was positively correlated with Grayling yield. Variations in growth rate, age structure and age at first maturity were not correlated to cormorant predation but to the presence of strong cohorts of young Grayling, which itself determined the intensity of cormorant pressure.

In northeast Poland, Mellin & Mirowska-Ibron (1997) investigated the diet of cormorants and concluded that they caused damage on fish farms, but not on natural lakes. Also in northeast Poland, Stempniewicz & Grochowski (1997) assessed the diet of cormorants in a breeding colony. They found that the bulk of fish taken by cormorants were of small size classes and of species which were of little, or at best moderate, economic value. They concluded that cormorants had little economic impact.

In Hong Kong, Walthew (1997) assessed the impact of cormorant predation of pond fish during February and March. He concluded that significant damage to fish stocks was unlikely on farms following traditional single-age fish culture, but could become a problem if a trend towards mixed-age culture continued.

In England, Davies & Feltham (1997) investigated fish wounding by cormorants and found many with healed wounds suggesting that a proportion of fish may recover from cormorant attacks.

Possible benefits of cormorant predation

Some authors have argued that cormorants may bring benefits to wetlands, particularly with widespread eutrophication of fresh water, and this should be balanced against any negative impacts. De Nie (1995) found coarse fish standing stocks of 1000 kg ha^{-1} in eutrophic waters, where they form stable populations of small fish, feeding heavily on zooplankton. He concluded that social fishing by cormorants is an effective response to changes in the composition of fish populations.

Reducing predation of zooplankton by coarse fish may increase zooplankton grazing of phytoplankton, and thereby improve water quality.

Leah (1980) investigated the role of cormorants in effecting changes in limnology, and concluded that cormorant predation resulted in a drastic reduction of planktivorous fish, which led to a clear water phase in a hypertrophic lake. Marteijn *et al.* (1997) considered the trophic role of cormorants and concluded that they have positive effects. They concluded that cormorants can promote water quality by removing bottom-feeding fish, which would otherwise stir up sediments, resulting in the re-suspension of nutrients and consequent algal growth.

Van Eerden *et al.* (1995) considered cormorants to be beneficial to improving water quality by preying on Bream *Abramis brama* and taking larger cyprinids than are taken by Pike, and through their ability to hunt shoals of zooplanktivorous fish in turbid water by social fishing. Veldkamp (1995) investigated the diet of cormorants and concluded that by taking large quantities of zooplanktivorous fish including Bream, small Roach and Perch, Ruffe *Gymnocephalus cernus* and Smelt *Osmergus eperlanus*, cormorants may exert a positive influence on water quality by reducing overexploitation of zooplankton.

Dirksen *et al.* (1995) investigated prey choice and fish consumption in shallow eutrophic freshwater lakes and concluded that cormorant predation was favourable to biological management as they particularly targeted cyprinids and Ruffe, which were considered detrimental to water quality. Marion (1997) investigated fish availability and cormorant diet, and suggested that by limiting planctivore species like Bream and

Roach in eutrophic lakes where fisheries unbalance the fish community, cormorants may have a positive effect on water clarity.

Van Dam (1997) investigated interactions between cormorants and commercial fisheries and surmised that there may be compensatory benefits of cormorant predation through better growth and survival of remaining fish. Carss & Marquiss, 1997) investigated cormorant diet and concluded that removal of small Trout might be an overall benefit to a Brown Trout fishery because reduction in density can lead to enhanced growth of survivors and so fewer but substantially larger fish. Van Dobben (1952) investigated cormorant diet and concluded that cormorants selective predate *Ligula* infested Roach.

EFFECTIVENESS OF CORMORANT CONTROL

Persecution of cormorants has been practiced for many years and continues despite the lack of evidence of adverse impacts. In 1991, the French government allowed shooting of cormorants at fishponds despite the lack of evidence of impacts and the failure to take account of other major influences on fish populations including abnormal drought, natural mortality and compensatory mortality (Marion, 1997a). In Great Britain, Kirby *et al* (1995) stated that although some illegal shooting still takes place, it appears to be much less prevalent than it once was. However, Kirby *et al* (1997) stated that numbers killed legally have ranged from 400 to over 800, 96.6% of them in Scotland, and illegal shooting is also severe. McKay *et al.* (1999) assessed the effectiveness of killing cormorants on four sites in Britain. Whilst on some sites there was no effect, in other cases there did appear to be a reduction in numbers. However, this was of short duration, and there was no evidence of long-term benefits. Furthermore, the perceived short-term benefits were questionable, in that it was difficult to differentiate between the impacts of shooting and other coincidental factors, such as changes in water level and turbidity.

In Poland, Dobrowolski & Dejtrowski (1997) reviewed the impacts of cormorants on fish stocks and proposed that minimisation of conflicts was only possible through relatively intense shooting. They stated that issuing permits for even a weak population control is of great importance as it ensures a mental comfort to fish pond managers, but shooting to vent fishery managers' frustration is described as unjustified and illegal by Kirby *et al.* (1997).

In Schleswig-Holstein, Kieckbusch & Koop (1997) described a Management Plan aimed at resolving the conflict between cormorants and fisheries, and noted that approval of shooting as mitigation was based on a political compromise between ministries. Damage was anticipated on the basis that some solitary fishing cormorants took some fish of commercial value, rather than proof of any detrimental impact. Since 1985 fishery managers have been authorised to kill eight cormorants each year at fishponds. Since 1992 fishermen have been authorised to kill birds on professionally used lakes with the aim of scaring them away rather than reducing their numbers.

In Sardinia, Schenk (1997) described how fish production from wetlands was reduced by pollution from about 415 kg ha^{-1} in the 1950,s to 336 kg ha^{-1} in 1968 and 223 kg ha^{-1} in 1979/80. This puts other issues such as cormorant predation in context and raises the question as to what the real problems are. The dramatic Europe-wide reduction in the number of commercial freshwater fishermen was attributed to water pollution, river construction for shipping and field settlement, changes in consumer habits and low prices for farmed fish.

There is little evidence that killing cormorants is an effective mitigation measure either by reducing cormorant numbers or increasing fish catches. Furthermore the practicability and cost-effectiveness of such control is open to question as where cormorants consume a low proportion of commercial fish, very large numbers of birds would have to be removed to gain even modest increases (Carss & Marquiss, 1997). Shooting is widely used in Britain and yet there has been no attempt to assess the effectiveness of shooting in reducing cormorant damage on open waters. Indeed there is no scientific evidence that the removal of predators through killing reduces bird abundance in a particular area or has resulted in an increase in fish yields. Since cormorants are highly mobile there is every chance that removed individuals will be replaced quickly by others, making shooting futile (Kirby *et al.*, 1997).

In Poland, Przybysz *et al.* (1997) assessed the effectiveness of shooting and concluded that although killing of cormorants in order to control their numbers has been carried out since 1987, no decline in numbers has been detected. This was confirmed by Dobrowolski & Dejtrowski (1997a), who reported that over five years 833 cormorants were shot outside the breeding season in one area in Poland, but there was no decrease in the number of cormorants. In total in Poland 5,335 were shot legally, with no reduction in numbers, which continue to increase (Dobrowolski & Dejtrowski (1997b).

AIMS AND STRUCTURE OF THIS THESIS

It is apparent that there is a lack of information on cormorant foraging behaviour on northern freshwater sites. There is also a lack of evidence of cormorant impacts on open water fisheries, and a question over the effectiveness of cormorant control measures. These factors hinder resolution of perceived conflicts and the work conducted at Loch Leven, presented in this thesis, may therefore serve to take these issues forward. **Chapter 2** describes the foraging behaviour of Great Cormorants on Loch Leven, assesses the intensity of use of different areas and considers the factors that may influence foraging activity. **Chapter 3** describes in detail the diving behaviour on Loch Leven and compares it with findings from other sites. **Chapter 4** reviews data on angling catches, cormorant numbers and cormorant shooting in order to detect detrimental impacts of cormorants on the trout fishery. It also reviews data on cormorant numbers, cormorant shooting and angling catches, in order to detect beneficial effects of the shooting and thus assess the effectiveness of control measures. **Chapter 5** uses multiple daily cormorant counts, short-range radio tracking and satellite telemetry to assess the rate of turnover within the wintering population, in the context of the apparent lack of effectiveness of control measures. **Chapter 6** summarises the results from previous chapters and considers their wider application.

Chapter 2

FORAGING BEHAVIOUR OF CORMORANTS WINTERING ON LOCH LEVEN

ABSTRACT

In various localities, foraging behaviour of wintering cormorants *Phalacrocorax carbo* has been observed to change over recent years, in particular with the development of social or flock fishing. This has been attributed to feeding on shoals of coarse fish, and proposed as a response to eutrophication causing increased coarse fish stocks, reduced underwater visibility and loss of macrophytes. This paper describes the foraging behaviour of cormorants on Loch Leven, a wetland of international importance for nature conservation and a famous commercial brown trout *Salmo trutta* fishery, where a conflict with cormorants is perceived to exist. Loch Leven was surveyed on 557 occasions to determine the numbers and distribution of wintering cormorants. In addition, fifty-nine flock feeding events were studied in detail and the timing, position and movements of the flock were recorded. Fish abundance and distribution on Loch Leven was investigated through gill net sampling.

Cormorants spent most of the time roosting, and a single peak of feeding activity occurred early in the morning. Compared to early or late winter, cormorants showed higher foraging activity during mid-winter. Both solitary feeding and flock feeding were recorded, with twice as many birds flock feeding as solitary feeding. Water clarity did not appear to influence the frequency of flock feeding. Birds were not observed to feed at night.

Feeding distribution was recorded on a grid comprising 269 squares measuring 250 m by 250 m. Solitary feeding was distributed over a wide area with a principal concentration west and south of the largest island, and other concentrations in the north and south-east. The intensity of flock feeding was less evenly distributed, with 36% of grid squares not used. Overall, 78% of flock feeding activity took place in 23% of grid squares and 59% took place in 13% of grid squares. Solitary feeding and flock feeding intensity of use increased significantly with mean water depth, as did winter brown trout abundance. Solitary feeding increased significantly with distance from the loch shore or island shore.

The commencement of flock feeding was concentrated in seven adjacent grid squares, which accounted for 25% of flock feeding initiations, and 13 adjacent squares accounted for 32% of initiations. The mean distance covered by feeding flocks was 3,757m, with a range from 600m to 8,490m. The mean duration of flock feeding events was 68min, with a range from 13 to 135min. The median flock foraging speed was 1.02 m s^{-1} and speed in the most frequently used squares was significantly higher than in other squares. Flocks with a size of the order of 250 to 450, tended to lose about 1.5% of birds per minute for the first 40 minutes, after which the rate of loss doubled to 3%. Flock size declined until the flock dwindled away, or all remaining birds flew *en-masse* to roost.

INTRODUCTION

Cormorants have been shown to be flexible foragers, taking both benthic and pelagic fish of a wide range of species (e.g. Lekuona & Campos, 1997, Gremillet *et al.,* 1998). The behaviour of foraging birds has been found to be related to the type of prey and the conditions under which they are hunting, and may therefore be indicative of the possible impact on the foraging site (Voslamber *et al.,* 1995). A flock feeding strategy where many birds hunt together has been variously described as flock fishing (e.g. Hughes *et al.,* 1999), social fishing (e.g. Lekuona & Campos, 1997), mass fishing (e.g. Van Eerden & Voslamber 1995), and co-operative fishing (e.g. Glanville, 1992). In recent years it has been observed to occur regularly at Loch Leven, as has solitary feeding, where birds forage independently.

Foraging timing

Hughes *et al.,* (1999) found that cormorants feeding on inland stillwaters in England fed mainly in the early morning. These trends mirrored those of fish-capture rates, suggesting that cormorants fed mainly at times when fish were most vulnerable to capture. The proportion of birds present that were feeding was similar at large and small stillwaters at around 35%. The trend in the level of feeding was also similar with an early morning peak in feeding activity and a gradual decline over the rest of the day. After feeding, most birds did not leave the sites but loafed before eventually going to roost towards sunset

Hughes *et al.,* (1999) concluded that cormorants spent very little time feeding. On average, radio-tracked birds spent just 32 minutes per day feeding at Grafham Water in winter and 29 minutes in summer. However, during a period of cold weather, birds at Rutland Water and Eyebrook Reservoir spent more time feeding, with averages of 104 minutes per day at Rutland and 69 minutes per day at Eyebrook. Cormorants fed during discrete dive-bouts lasting on average only 16 minutes and containing 25 dives, engaging in between one and five dive-bouts per day.

Solitary feeding

In the Netherlands, a decrease in the proportion of solitary fishing cormorants was recorded over the 1980s (Van Eerden & Voslamber, 1995), and in the 1990s only a minority of cormorants were observed to use this technique (Dirksen *et al.,* 1995). However, in French coastal waters, Gremillet *et al.,* (1998), found that cormorants practised solitary feeding on 95% of feeding trips. Solitary feeding was considered by Van Dobben (1995) to be more effective than flock feeding when cormorants are hunting for eels *Anguilla anguilla* partly buried in sediments on the bed of a water body. Under these conditions, the disturbance caused by a flock of cormorants was considered likely to cause the eels to retreat into the sediments and become unavailable to foraging birds. Voslamber *et al.,* (1995) concluded that solitary feeders on the Ijsselmeer tend to feed in deeper water as flock feeding cormorants are unable to push shoals of fish up from these depths into clear higher water layers where they can be caught. They also suggested that only the higher quality birds may have the experience and skill to use solitary fishing techniques as a profitable alternative to flock fishing in early spring, when pre-breeding demands and the consequent need for elevated food intake are high. Noordhuis *et al.*, (1997) suggest that in deeper, clearer water larger fish are easier to catch by solitary feeding cormorants. In Germany, Kieckbusch & Koop (1997) described how solitary feeding was practised on the Baltic coasts and small lakes, and the eel and other large fish such as perch *Perca fluviatilis* and roach *Rutilus rutilus* were the main prey.

Flock feeding

Flock feeding, although now widely reported from the European continent, has rarely been reported in Great Britain (Hughes *et al.*, 1999). Van Dobben (1952) studied cormorants in the Netherlands from 1938 to 1942, and observed flock feeding only once. Voslamber & van Eerden (1991) noted that during the 1960s, flock feeding was recorded incidentally on the border lakes, initially comprising some hundreds of birds. Flock feeding on the Ijsselmeer was described as having shown a marked increase during the period 1970 to 1975 (Van Eerden & Voslamber, 1995). Van Eerden (1988) reported that more than 90% of cormorant foraging on the IJsselmeer occurred in huge flocks. Van Dobben, (1995) described flock feeding as having become the rule by 1995. Flock feeding was described as the most common technique used by cormorants in two shallow eutrophic freshwater lakes (Dirksen *et al.*, 1995). Groups of several hundred were regularly observed, with occasional groups of up to a thousand. Van Eerden & Voslamber (1995) recorded flocks of up to ten thousand individuals on the Ijsselmeer, comprising adults and recently fledged young.

In Schleswig-Holstein, Germany, Koop (1997) reported that flock fishing was first recorded in the area on lake Großer Plőner in 1983. As total numbers of cormorants increased, so did the proportion of flock feeding birds, and it became the predominant foraging strategy. Kieckbusch & Koop (1997) described huge concentrations of flock feeding cormorants on large lakes in Germany, where they predominantly took small shoaling fish such as ruffe *Gymnocephalus cernus*, perch and smelt *Osmergus eperlanus*. Koop (1997) also reported that flock fishing had not been recorded around the Danish breeding colonies, although Danish birds had been observed flock fishing on migration, and on lake Großer Plőner during the summer. In Switzerland, Suter (1991) described flock fishing as the main feeding type where shoals are hunted, with flocks of up to 800 on Lake Zurich and over 2,000 on Lake Zug. In Spain Lekuona & Campos (1997) reported that flocks of feeding cormorants comprised 78.7 +/-53.3 individuals. The successful switch from solitary feeding to flock feeding has been cited as one of the reasons for the sustained increase in the Dutch breeding cormorant population (Zijlstra & Van Eerden, 1991). However, Koop (1997) reported that the Danish breeding population had increased even though flock fishing had not been recorded around the breeding colonies.

The flock fishing technique was described in detail by Voslamber & van Eerden (1991) and by Van Eerden & Voslamber (1995). They described two distinct flock movement patterns: line hunting and zig-zag-hunting. The authors associated line-hunting on its own with fishing for small fish such as smelt. Cormorant flock speed was about 1 m sec^{-1}, equal to the fishes' burst speed enabling the cormorants to quickly exhaust their prey.

When hunting larger fish (15cm+), the authors interpreted line-hunting, during which time foraging success was found to be much lower, as a means of concentrating and exhausting the fish, in order to be able to catch them during the subsequent zigzag-hunting phase when cormorant speed increased to about 1.33 m/sec. The large size of the water body and the flat bottom were considered to favour flock feeding, as fish were unable to escape into crevices or stands of vegetation.

Van Dobben (1991) described social fishing as resulting in exhausting a shoal of pelagic fish. He attributed this change to increased water turbidity reducing underwater visibility, to loss of submerged aquatic vegetation, to changes in fish populations towards more shoaling species, and/or to increases in cormorant numbers inducing the need for a different foraging strategy. Van Eerden & Voslamber (1995) concluded that the behavioural switch from solitary feeding to flock feeding resulted from decreased underwater visibility resulting from eutrophication, and a change in fish populations towards higher numbers of smaller fish. Veldkamp (1991) attributed social fishing to eutrophication and algal blooms, with the resulting loss of submerged aquatic vegetation making very efficient social fishing possible. He noted that a substantial number of birds might switch to solitary foraging of species such as eel, if the weather renders conditions suitable.

De Nie (1995) assessed changes in European fish populations and concluded that as a result of eutrophication, some water bodies had attained very high standing stocks of fish. They comprised a small range of fish species, forming unstable populations of small individuals, which in open water fall easy prey to cormorants hunting in flocks. De Nie considered flock fishing to be an effective response by cormorants to changed feeding conditions, with reduced underwater visibility, an increase in biomass and changes in the composition of fish populations as a result of eutrophication and other human impacts on aquatic ecosystems. Van Eerden & Voslamber (1995) considered that flock feeding was only rewarding at high prey fish densities, and higher stocks of small fish render sites particularly attractive to cormorants. The general increase in turbidity and reduction in underwater visibility was also considered to have favoured flock feeding. Adjacent areas where the water was relatively clear, with Secchi disc readings of 2 to 6 m, had not been subject to comparable levels of flock fishing. Furthermore, when the Secchi disc reading on the Ijsselmeer increased to 1.5 m, flock feeding stopped completely and birds left to fish elsewhere. They judged that optimal visibility for flock feeding was indicated by Secchi disc readings of 50 to 80 cm.

Suter (1991) considered social fishing to be a counter-strategy to balance the anti-predator effects of shoaling fish, and also possibly as a mechanism to enhance the chances of finding shoals. On other sites where social fishing is less common and flocks are smaller, foraging focuses on a greater variety of solitary or group-living fish, rather than shoaling species. Voslamber & van Eerden (1991) attributed the onset of flock fishing possibly to the increase in cormorants to the point where a critical minimum number was reached, although earlier high numbers did not result in such flock fishing. Alternatively, the authors concluded that social fishing resulted from a reduction in underwater visibility due to eutrophication and algal blooms, and due to large-scale dike works affecting water flow. They suggest that a flock can concentrate their prey, and push deep-lying fish up into shallower, lighter water, where they are more vulnerable.

Hughes *et al.,* (1999) reported that cormorants were commonly observed flock feeding in groups of 3 to 480 birds and the incidence of flock feeding increased as cloud cover increased, suggesting that flock feeding may have improved foraging efficiency on cloudy days. Flock feeding was thought to be an adaptation by cormorants to exploit the rich stocks of relatively small, pelagically shoaling cyprinids in turbid eutrophicated lakes. In Schleswig-Holstein, Germany, Koop (1997) reported that flock fishing only occurred during the summer, and resulted from stratification of the water column. Shoals of fish became concentrated in the shallow oxygenated surface layer, and although the lake is deep, they were unable to escape into the depths due to the lack of oxygen. Once mixing occurred as a result of autumnal storms and stratification was disturbed, flock fishing ceased and most cormorants left the site. In French coastal waters, Gremillet *et al.,* (1998), found that cormorants practised flock feeding on only 5% of feeding trips, when they fed exclusively on pelagic fish. In Spain Lekuona & Campos (1997) concluded that flock fishing allowed shorter dives, higher feeding success and, in contrast to other findings, larger prey than solitary feeding.

Foraging distribution

In Switzerland, Suter (1991) noted that fishing cormorants were not evenly distributed over Lake Zurich and there were areas that were hardly ever visited, whilst other areas attracted large fishing flocks. Echo sounding often revealed that there were no shoals in places not visited by cormorants, but heavily used areas did not necessarily have large densities of solitary fish, but shoals were usually present. Suter (1997) found that the distribution of feeding cormorants within a deep lake correlated with the presence of large fish shoals, but not with numbers of fish less densely packed. In shallow lakes no such relationship was found.

Van Eerden & Voslamber (1995) recorded the location of flock fishing on Lake Ijsselmeer and found no systematic pattern of distribution, with great differences from day to day. They concluded that wind was the principal determining factor in the location of social fishing, due to its effect on upwelling of sediments and the aqueous mud layer, and thus reduction in underwater visibility. They suggested that deteriorating visibility reduced the attractiveness to foraging cormorants, and 40 cm Secchi disc depth was considered to be an absolute lower limit for flock fishing.

This paper presents data on foraging behaviour at Loch Leven in the light of evidence from other sites. It reports the timing of foraging, and compares solitary and flock feeding behaviour. This paper also reports the variation in intensity of foraging on the loch and the physical and biological factors that may influence it. It describes the track, speed, distance and duration of flock feeding events, the size of flocks and the rate of decline.

METHODS

During the late winter of 1996/97 and the winter of 1997/98, whole-loch surveys were conducted on Loch Leven two or three times a day to determine the number and distribution of feeding and roosting cormorants. Loch Leven is not a difficult place to count cormorants, with sufficient elevated observation points accessible by four-wheel-drive vehicle to enable the whole site to be overlooked without disturbing the birds, and cormorant roost and loafing sites are well known. Each count.was conducted by one of four principal observers, using a Kowa TSN-1 telescope with 30x magnification, and it took up to two hours to make a circuit of the observation points and complete the count. There was therefore some scope for error due to unobserved bird movements during a count, but these counts are assumed to have a generally high degree of accuracy.

In total, 243 surveys were conducted between 23 December 1996 and 11 April 1997, and 314 surveys were conducted between 8 September 1997 and 2 April 1998. It became apparent that two different feeding behaviours could be identified, flock feeding and solitary-feeding, the most prominent of which was flock feeding. In order to further investigate this behaviour, detailed tracking of feeding flocks was conducted during the winter of 1997/98 and during December1998. The tracking took the form of visual watches by an observer throughout the hours of daylight, and although flock feeding did not occur every day, 59 flock feeding events were observed intensively from a series of elevated positions adjacent to the loch shore. The position of the flock was determined through reference to clearly identifiable prominent points on the loch shore and islands.

Where there was an extensive area of open water, marker buoys were laid to provide additional reference points, and their positions were identified using a hand-held GPS set. The observer was mobile, and was thus able to move to alternative observation points as a flock moved towards the limits of accurate position plotting. The distance and time interval between timed map positions was noted, and any particular events such as the flock commencing or ceasing feeding, or flying en masse to another location were noted.

The accuracy of field observations was tested at the start of the survey programme, in order to determine the appropriate recording format. An independent observer anchored buoys at various positions on the loch and their position was recorded using a hand-held GPS set. The survey observers were then tasked to estimate the buoy's position and record it on a map, which was compared with the GPS position. Maximum error was found to be 250 metres, with most observations correct to 100 metres. On this basis, a 250m X 250m grid record map was produced, as illustrated in Fig. 1, and used in the field by all observers. Compilation of these records of cormorant solitary feeding and flock feeding enabled mapping of areas used at different intensities. In addition, the intensive tracking of individual flocks enabled the compilation of alternative distribution maps compiled throughout the life of the flock.

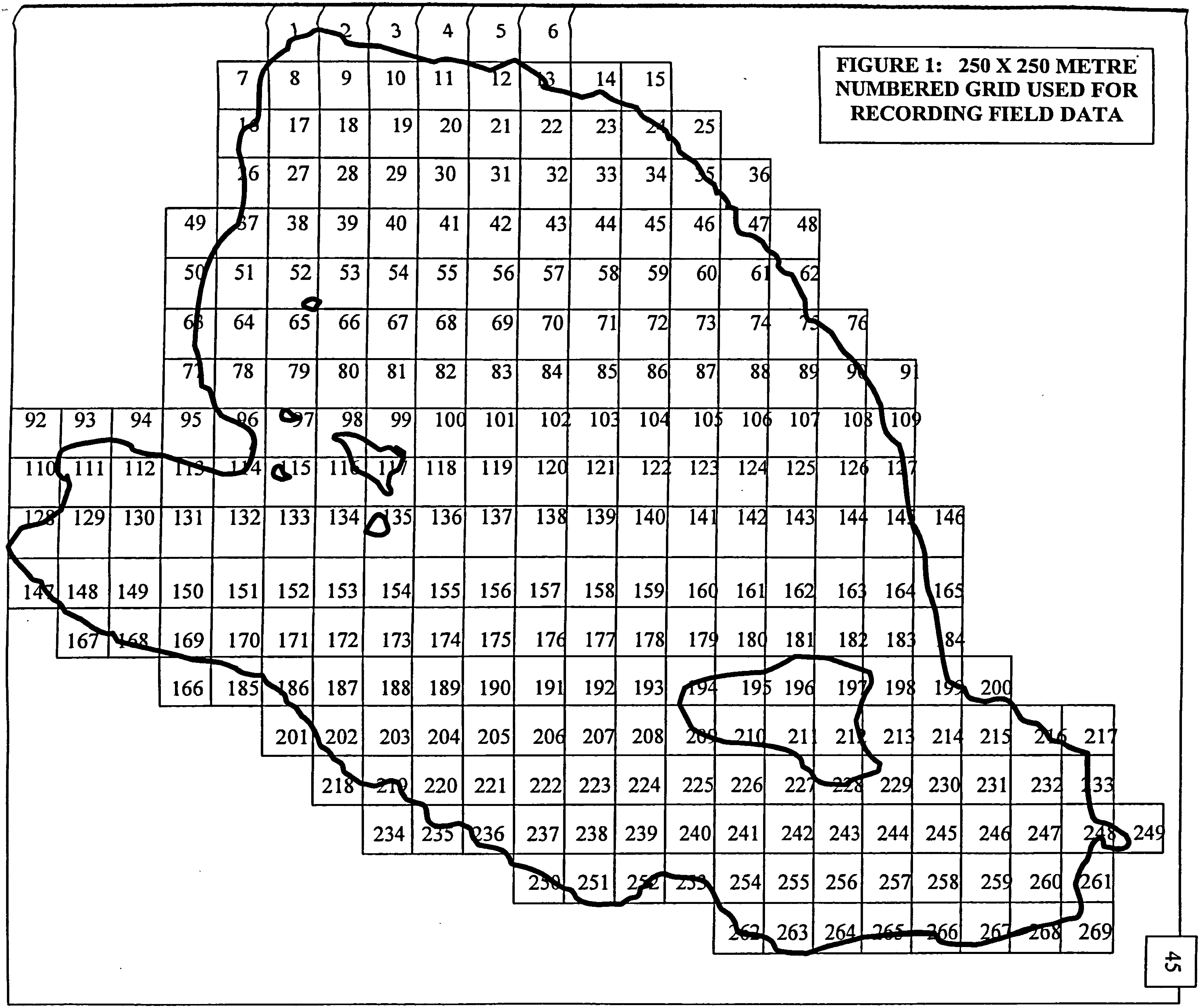


FIGURE 1: 250 X 250 METRE NUMBERED GRID USED FOR RECORDING FIELD DATA

The number of cormorants comprising each flock was usually determined by a count whilst the birds were swimming in extended line before commencing diving. On occasions, such as where a feeding flock flew en masse to another location, intermediate counts were achieved. Also, on those occasions where a flock dispersed to roost, a final count could be achieved as they left the feeding site. To supplement these data, counts of numbers of birds departing during two-minute intervals were made, repeated at 5-minute intervals, to record the rate of decline in flock size.

Birds were regularly observed to surface with fish grasped in their bills and would often quickly swallow them before diving again. However, when a bird surfaced with a fish in close proximity to other cormorants, there would frequently be aggressive competition from neighbours attempting to steal the fish, and the captor bird would flap across the water surface to a clearer area before attempting to swallow its prey. Attempts were made to determine the success rate of dives by scanning through the flock and recording the number of birds surfacing with and without fish. However, observation and field trials suggested that the commotion created by a cormorant surfacing with a fish was far more likely to be observed than the surfacing of an unsuccessful bird, which quietly appeared and dived a few seconds later. It was considered likely that such observations were heavily biased with under-reporting of unsuccessful birds, and as a result these results were disregarded.

Nine cormorants were captured with cannon nets and fitted with TW3 short-range radio transmitters, supplied by Biotrack. The transmitters were fitted on the underside of the two central tail feathers to which they were attached with cable ties. Three transmitters were fitted on each of 17 March, 7 October and 21 December 1997, and were tracked manually with a Yagi antenna and a Mariner M57 receiver, which gave an audio and visual indication of signal receipt. The behaviour of tracked birds could be deduced from monitoring transmissions, i.e. when roosting, loafing or resting on the water the signal was steady, and when flying it became stronger and steady. When feeding, the signal became regularly intermittent as no transmissions were received whilst the bird was underwater, so the start and end times of feeding could be determined. The activity of radio-tracked birds was monitored during the hours of darkness from a building 1.7 km from the roost site, via an antenna on mast elevated five metres above ground. A Philips VKR 6860/01 video camera was set up to record the receiver in video and audio, and was set on time lapse to record for four seconds every two minutes. Thus records for a fifteen-hour night could be reduced to 30 minutes of videotape which was reviewed each morning and examined for any changes in activity. Using this method, 420 hours of over-night cormorant activity were monitored, at weekly intervals from September to April 1997/98.

The distribution of fish in the loch was investigated through gill net sampling, as described by Alexander *et al.* (1999). In June to August 1998, 246 brown trout were caught by a team from Glasgow University Field Station, Rowardennan, and the University of Stirling Institute of Aquaculture. Thirty-five sites were sampled using Lungrens of Sweden “Nordic” type multi-mesh gill nets, 30 m long with twelve panels from 5 mm to 55 mm half mesh size. They were set in a range of depths, and five pelagic zones were also sampled using vertically set nets. In February and March 1999, 424 brown trout were caught. Twenty-four sites were sampled using Collins multi-mesh Survey Gill Nets, 60 m long with twelve panels from 8 mm to 50 mm half mesh size, set on the bottom in a range of depths. In addition three pelagic zones were sampled with vertically set nets.

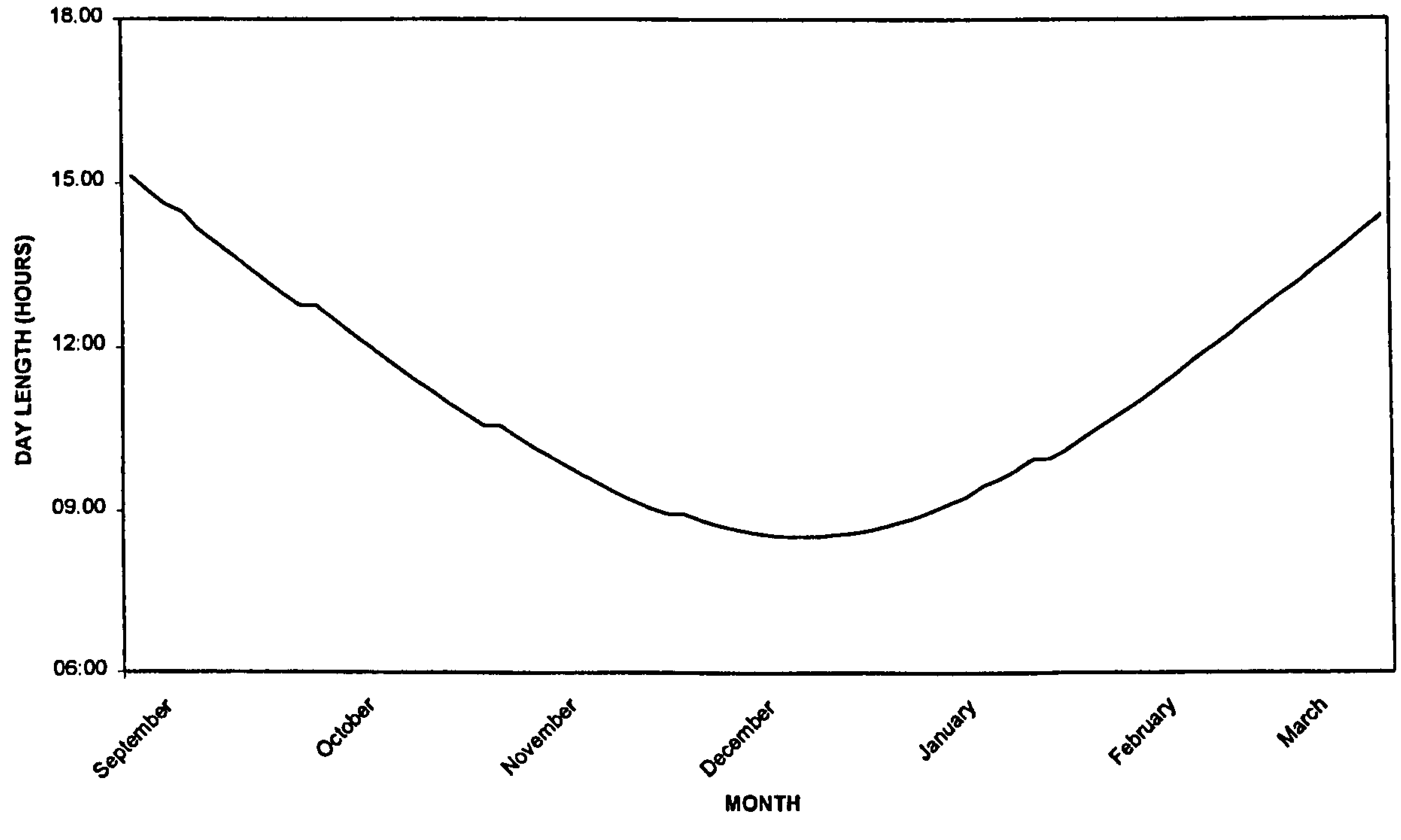
In order to measure water clarity, Secchi disc readings were obtained from the same sampling site, situated in open water 500 metres south of the southernmost of the small islands shown in Fig. 1, on 29, 28 and 26 occasions from September to April during the winters of 1996/97, 1997/98 and 1998/99 respectively. In addition, in order to investigate variation of clarity across the loch, Secchi disc readings were obtained from 50 randomly selected grid squares on 14 February 1999.

Data on times of sunrise and sunset were obtained from the Admiralty Nautical Almanac for the relevant years. Data on water depths within grid squares were extracted from the bathymetric survey map of Loch Leven prepared by the Department of Geography, University of Edinburgh, in March 1971. Information on sediment types was extracted from unpublished data held at Loch Leven NNR.

Data were subjected to a range of statistical tests using "SPSS 10.0 for Windows". In order to quantify feeding activity, percentages of active birds, i.e. those on the water and not loafing or roosting, from the whole-loch surveys were arc-sine transformed in order to normalize their distribution, and means were calculated for each hourly period.

However, this takes no account of changes in day length which, at this latitude (56° 12' North), measured as the period between "Start of Civil Twilight" and "End of Civil Twilight", can vary from 15 h 8 min in September, to 8 h 32 min in December, and 14 h 25 min in March (Fig. 2). In order to take account of this, each day was divided into ten equal periods, which ranged in extent from 1 h 30 min in early September to only 51 min in December. The percentage of birds active during each of the ten periods was calculated for each day, and means were calculated for each period.

FIGURE 2: CHANGE IN DAY LENGTH DURING WINTER, SEPTEMBER TO MARCH - BEGINNING OF CIVIL TWILIGHT TO END OF CIVIL TWILIGHT



RESULTS

1. General Feeding Behaviour

Diurnal activity levels

Most cormorants spent most of the time roosting and feeding took up a relatively short part of each day (Fig. 3). There was a peak of activity early in the morning, with 37% active between 0800 and 0900, followed by a gradual decline towards mid-day. The proportion of active birds increased during the afternoon to 25%, and then fell as all birds were observed to be roosting or going to roost. On average, 30% of cormorants were likely to be active at any one time during daylight hours.

FIGURE 3: DIURNAL VARIATION IN THE MEAN PERCENTAGE OF ACTIVE BIRDS BETWEEN 0700 AND 1659 GMT, SEPTEMBER TO MARCH, WITH STANDARD ERROR BARS

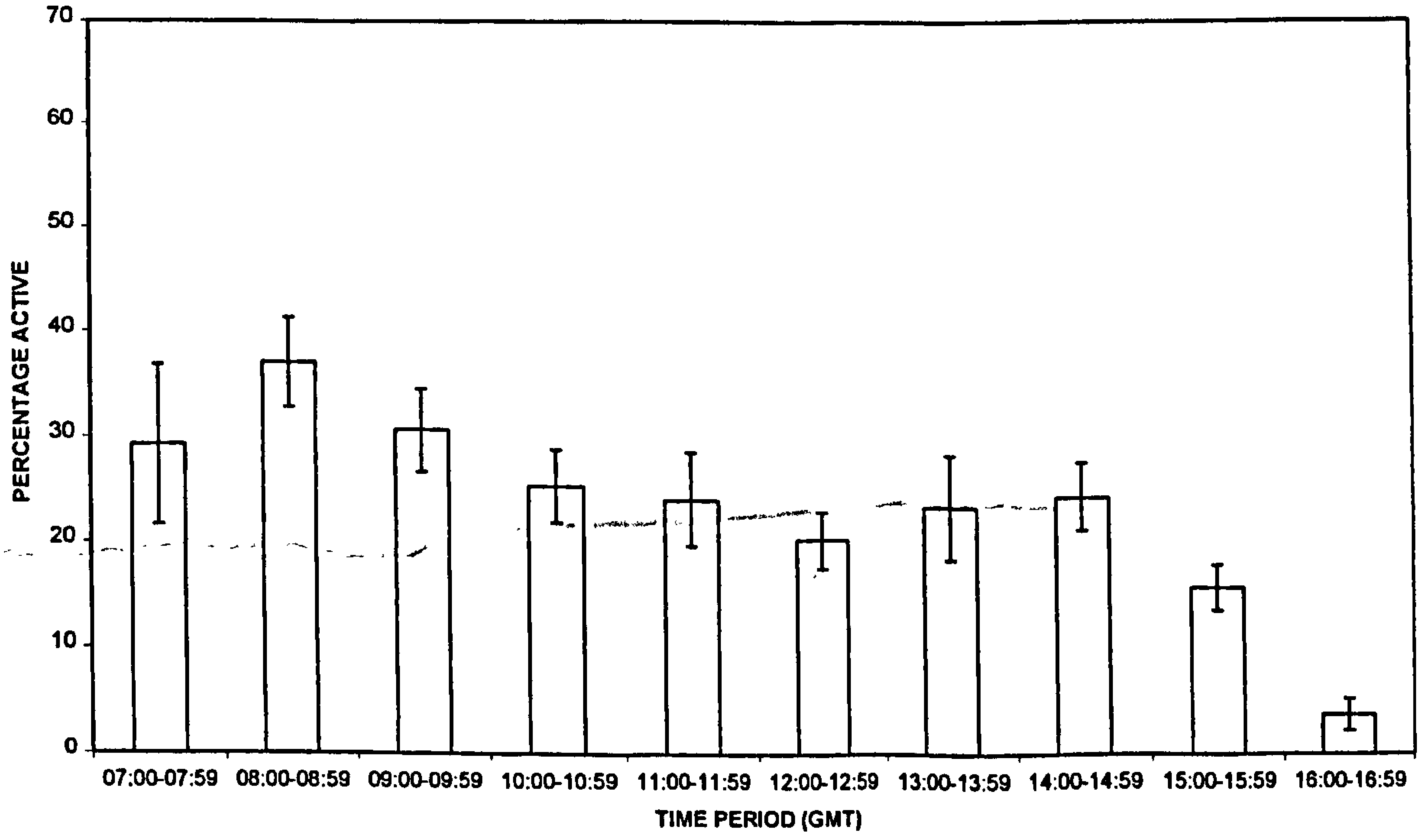
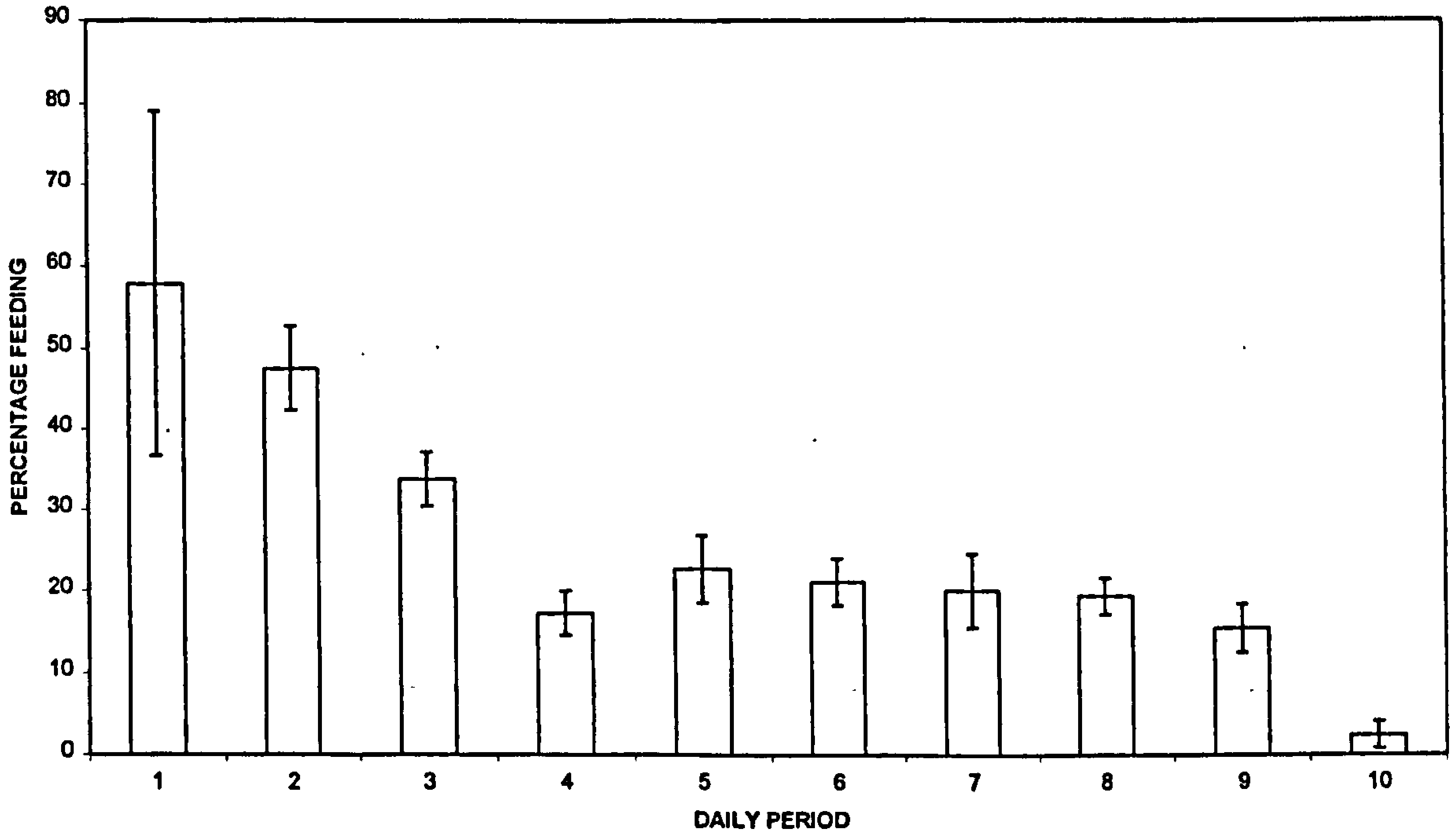


FIGURE 4: DIURNAL VARIATION IN MEAN PERCENTAGE FEEDING IN TEN EQUAL PERIODS, WITH STANDARD ERROR BARS



Correcting for changes in day length (Fig. 2) shows a stronger variation in activity (Fig. 4) with a strong peak of activity during the fist part of each day. From a peak in period 1 of 58% active, there is a steady decline to a low of 17% in period 4. During the afternoon numbers active fluctuate around 20%, until the final period when birds go to roost.

Monthly variation in activity levels

Analysis of monthly variation in activity levels during the winter (Fig. 5), suggests that birds were very much more active during the mid-winter months. The proportion of active birds increased from means of less than 10% in September to 43% in January, after which they decreased to 12% in March. Some of this variation can be attributed to difference in day length. However, it may also be attributable to increased foraging activity during colder weather, when energy demands on the birds may be elevated, or fish may be harder to catch. The data were converted to the equivalent activity level for a standard 14-hour day, by multiplying the mean percentage active by the day length in hours, and dividing by 14. Thus, 50% active during a 7-hour day would convert to 25% active during a 14-hour day. The relative intensities are shown in Fig. 6. The pattern is similar to Fig. 5, but the scale of difference is reduced considerably. It is however apparent that, all other things being equal, during January cormorants are active for three times as long as they are in September and October.

FIGURE 5: CHANGE IN MEAN PERCENTAGE OF CORMORANTS ACTIVE DURING THE WINTER, WITH STANDARD ERROR BARS

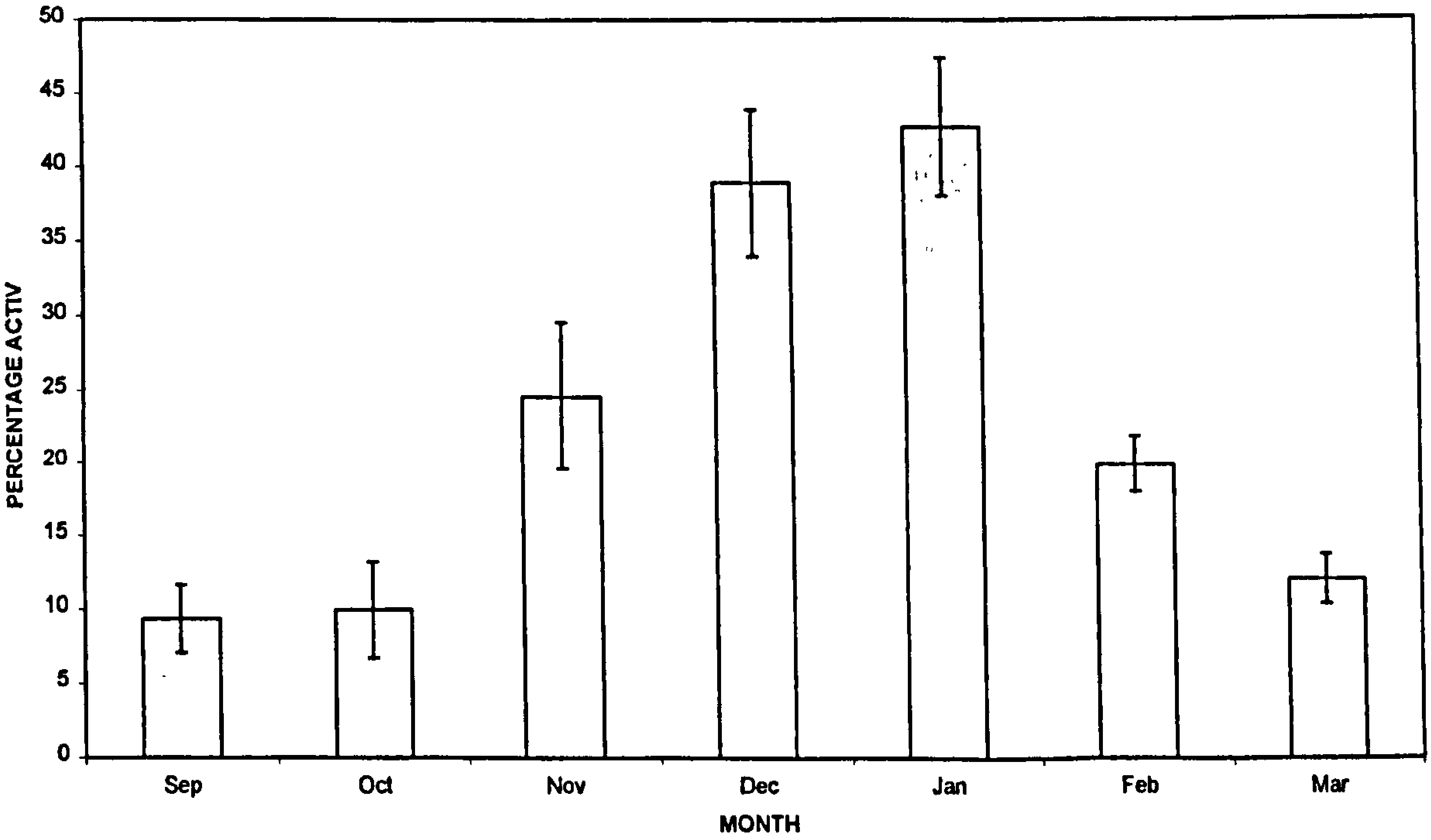
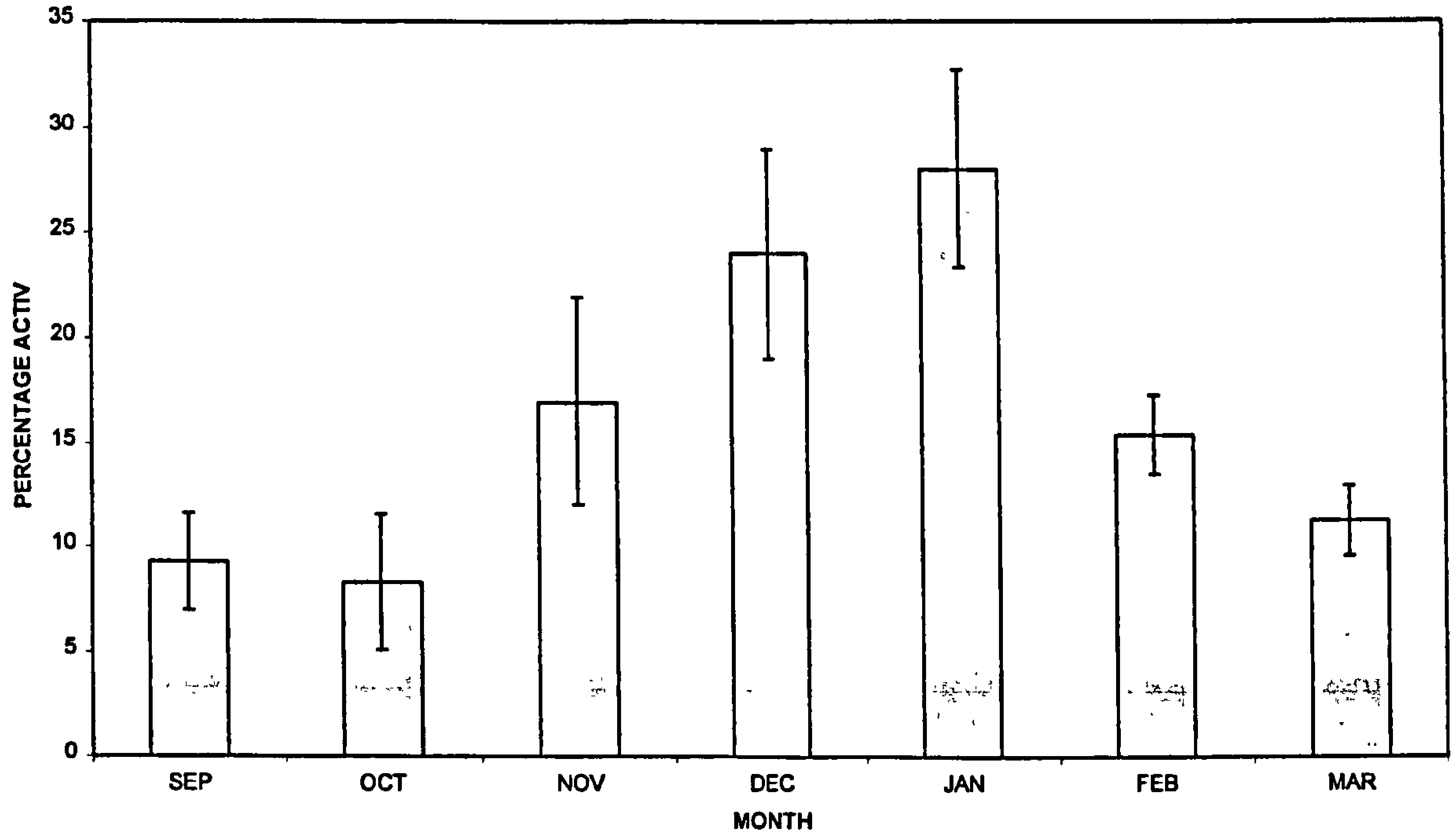


FIGURE 6: CHANGE IN MEAN PERCENTAGE OF CORMORANTS ACTIVE DURING THE WINTER, CORRECTED TO STANDARD FOURTEEN HOUR DAYLENGTH

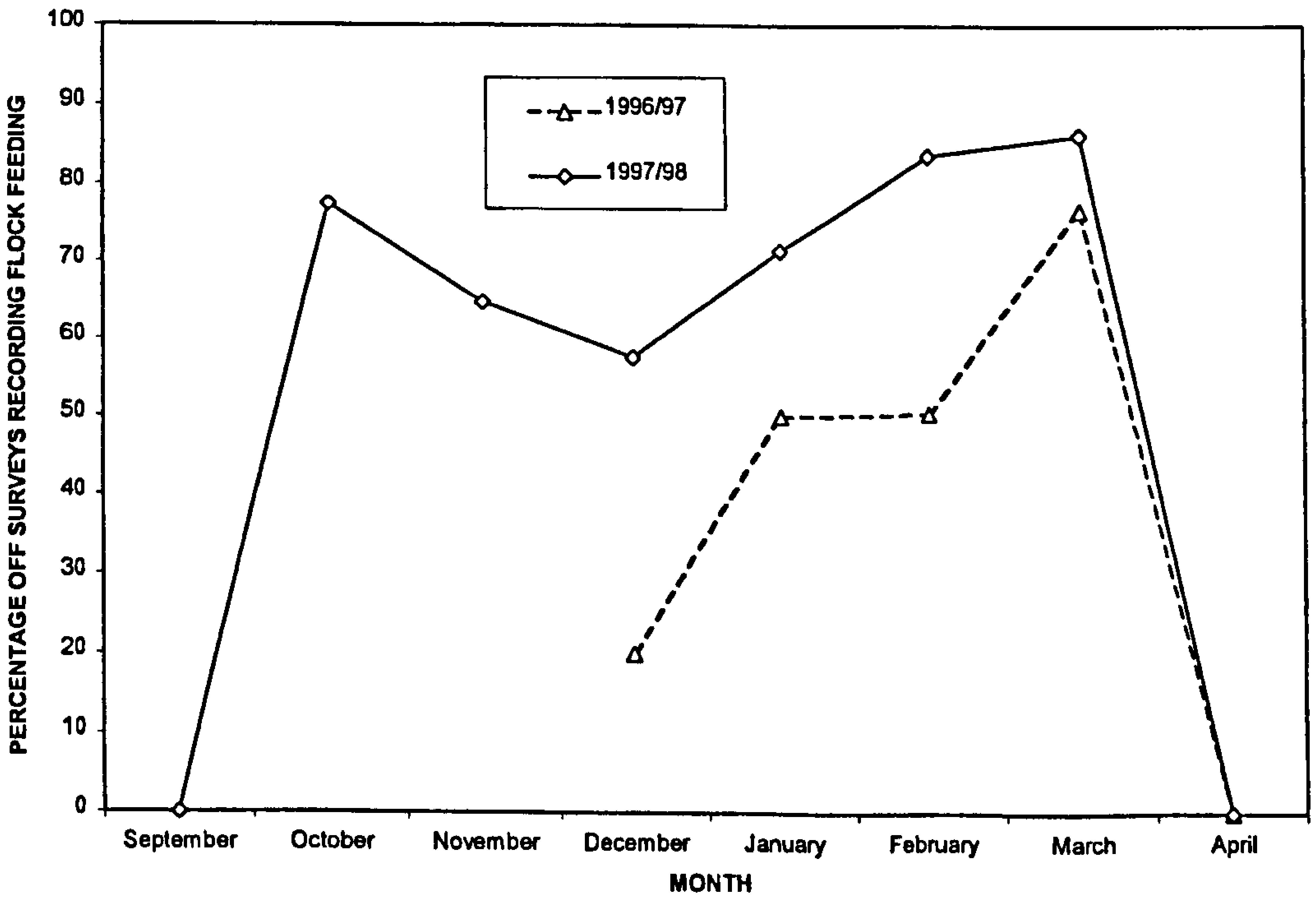


Feeding behaviour

Field observations indicated two cormorant feeding techniques: solitary feeding and flock feeding. Solitary feeding involved single cormorants or a few scattered individuals, diving alone with no apparent directional movement and no interaction between individuals. Flock feeding involved between 23 and 450 birds moving across the loch as a cohesive group, with a definable but changing direction. When the flock was actively diving, there was a constant turnover of birds surfacing, pausing briefly on the surface before diving again, and a trickle of birds flying from the rear of the flock to the front. On occasions the whole flock became airborne and flew to another feeding area where flock feeding re-commenced.

Analysis of data from the whole-loch surveys indicated that 64 % of individual cormorant feeding was conducted in flocks. Whereas solitary feeding was recorded on all whole-loch surveys, flock feeding was recorded on only 44% of occasions. Furthermore, there was variation in the frequency of occurrence of flock feeding between months and between years (Fig. 7). Flock feeding was not recorded in September 1997 or April 1997 and 1998. It was infrequent in December and at a peak in October, February and March. The variation between winters was evident in December, January and February, when flock feeding occurred much more often in 1997/98 than in 1996/97. The greatest difference was in December 1996, when flock feeding was only one third as frequent as in 1997.

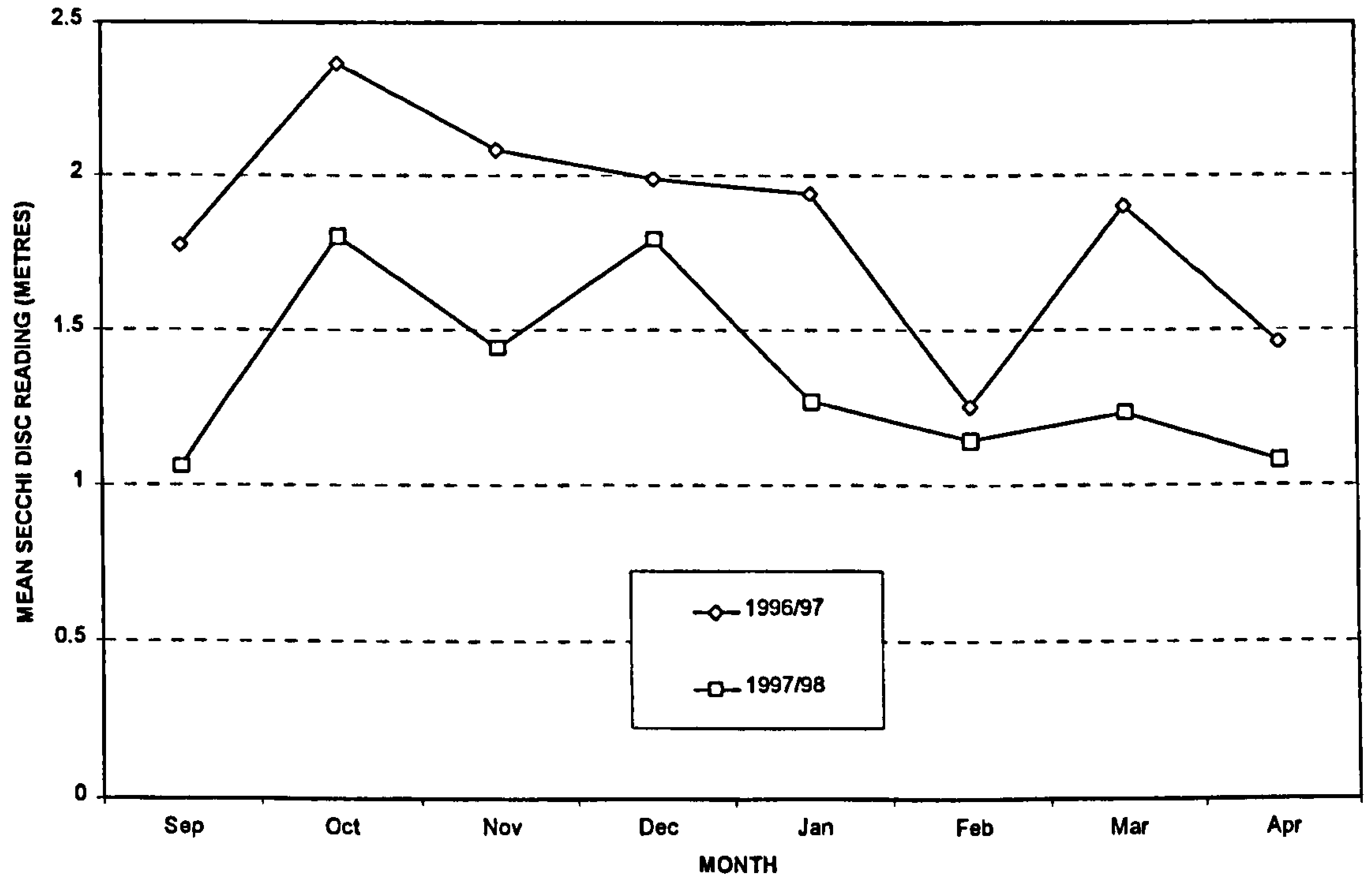
FIGURE 7: CHANGE IN FREQUENCY OF OCCURRENCE OF FLOCK FEEDING DURING WINTERS 1996/98 AND 1997/98



Water clarity

Water clarity for three winters is shown in Fig 8; it is apparent that it varied between one and 2.4 metres, and was greatest during the 1996/97 winter.

FIGURE 8: MEAN MONTHLY SECCHI DISC READINGS FOR WINTERS 1996/97 & 1997/98



The difference between Secchi disc readings for the 1996/97 and 1997/98 winters is significant ($z = 9.03$, $p < 0.001$), and it might be anticipated that this would influence the frequency of flock feeding. However, regression analysis shows no significant relationship between mean monthly Secchi disc readings and the proportion of birds flock feeding. It is apparent from Figs 7 & 8 that in December 1996 & 1997, whilst the percentage flock feeding were very different at 20% and 57% respectively, the mean Secchi disc readings were similar at 2.0 and 1.8 metres. Furthermore, in March, whilst the percentages flock feeding were similar at 77% and 86% respectively, the Secchi disc readings were very different at 1.9 and 1.2 metres.

Night time activity

During 420 hours of night time monitoring of four radio-tracked birds, steady signals were received throughout, indicating the birds remained stationary on their roosts. This suggests that cormorants on Loch Leven feed only during daylight hours.

2. Cormorant Feeding Distribution

Solitary feeding from whole-loch surveys

Solitary feeding was recorded in 207 grid squares, 77% of the total (Fig. 9). Solitary feeding was concentrated in a broad strip running south-eastwards in the south-central part of the loch. A block of 24 squares comprising Sq 117, 135 & 136, 154 to 156, 173 to 177, 190 to 193, 205 to 210 & 225 to 227, representing 9% of the squares, contained 46% of all solitary feeding observations. There was a secondary concentration in the northern area around Sq 30, and a small concentration in the south-east corner around Sq 245. Otherwise, solitary feeders were thinly scattered over much of the rest of the loch.

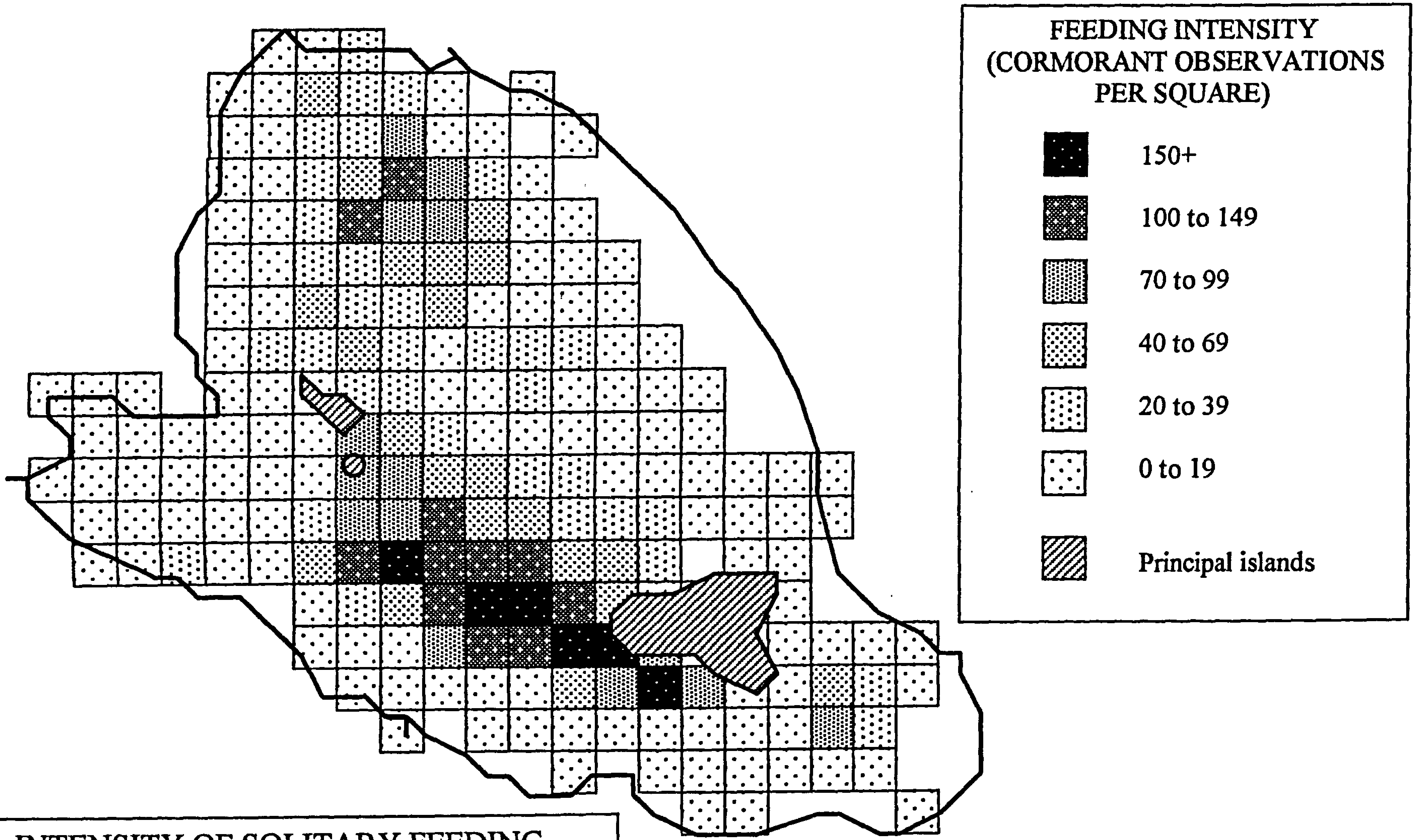


FIGURE 9: INTENSITY OF SOLITARY FEEDING DERIVED FROM WHOLE-LOCH SURVEYS

Flock feeding from whole-loch surveys

During whole-loch surveys, flock feeding was recorded in 122 grid squares, 45% of the total (Fig. 10). Flock feeding showed a major concentration in the south-central part of the loch, where four adjacent squares, Sq. 176, 190, 191 & 206, held 17% of all flock feeding observations. A block of 16 squares from Sq 155 to Sq 207, encompassing the four above, which represent 6% of all squares, held 39% of observations. There was a small concentration in the north in two adjacent squares 31 & 42, but otherwise flock feeding observations were thinly scattered. Furthermore, over half of the squares contain no flock feeding observations.

Flock feeding from intensive flock tracking

During intensive flock tracking, flock feeding was recorded in 171 squares, 64 % of the total. The distribution of flock feeding cormorants, derived from the total number of birds entering each square during all flock feeding observations is illustrated in Fig. 11. There is a general concentration to the south-west, south and south-east of the large island, and very little activity in the northern half of the loch. Of the 171 squares used, 94 (55%) held less than 1,000 birds.

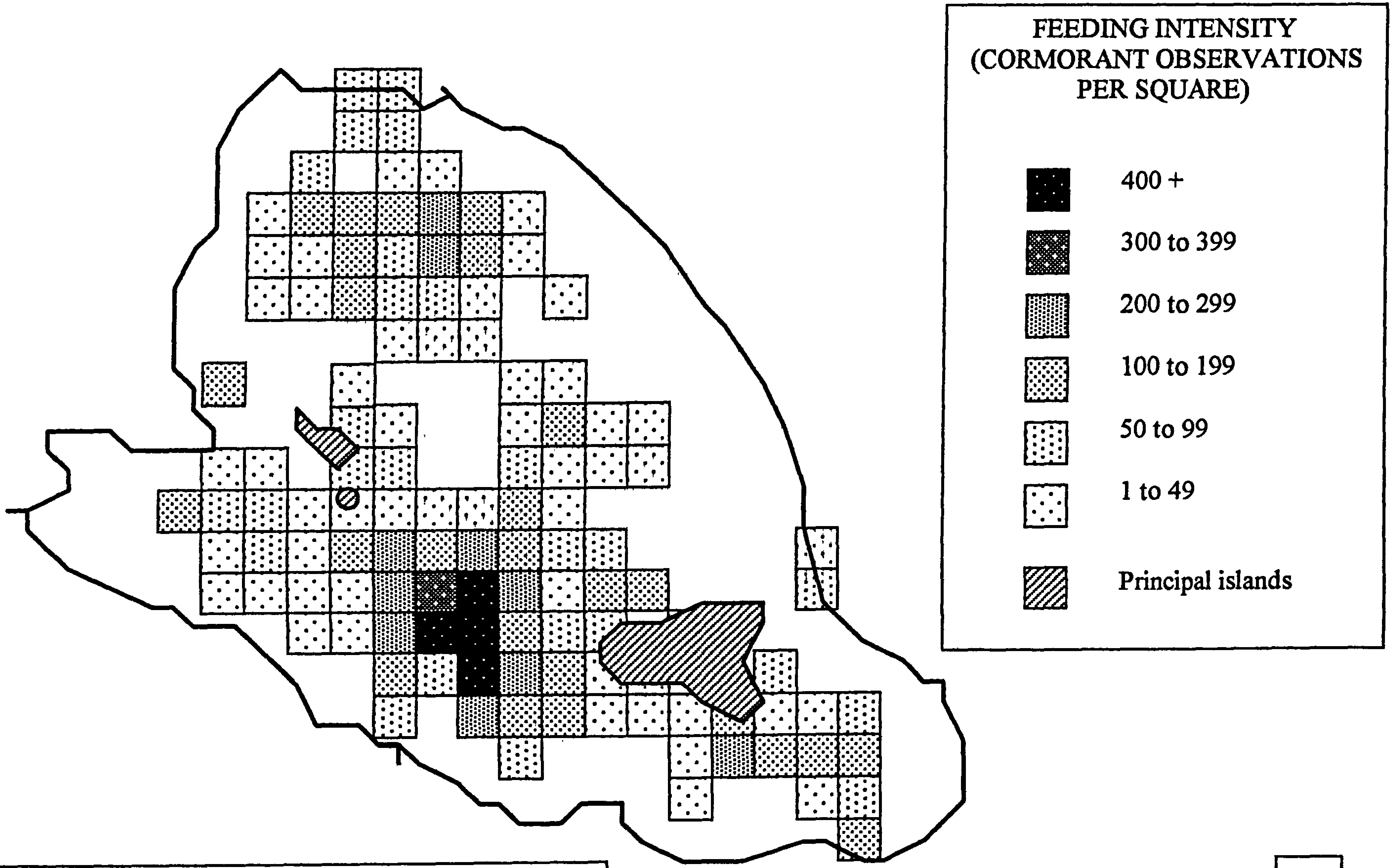


FIGURE 10: INTENSITY OF FLOCK FEEDING DERIVED FROM WHOLE-LOCH SURVEYS

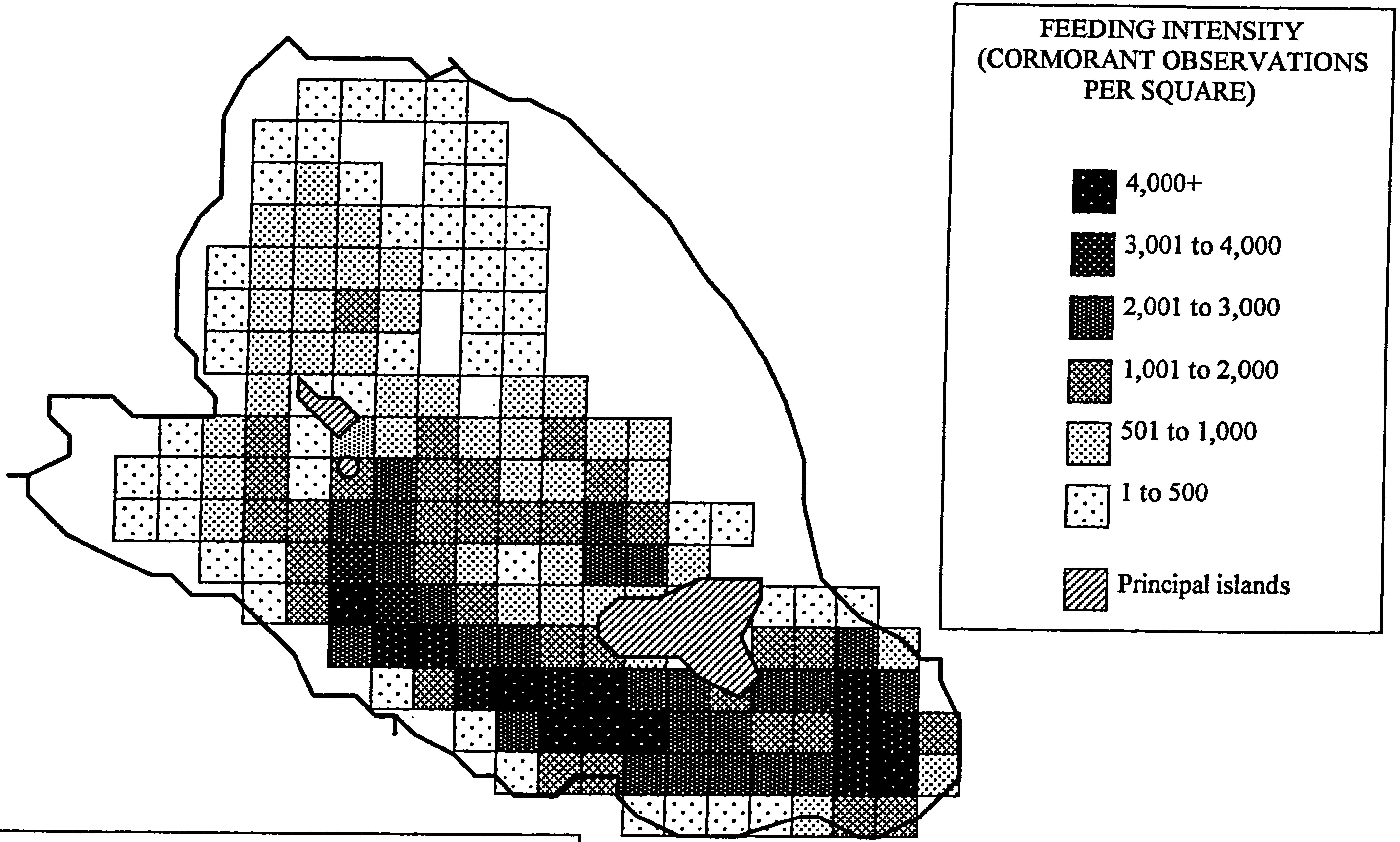


FIGURE 11: INTENSITY OF FLOCK FEEDING DERIVED FROM FLOCK TRACKING – TOTAL NUMBER OF BIRDS ENTERING GRID SQUARE

Cormorant use of grid squares in relation to physical parameters

It should be recognised that statistical tests generally assume the independence of individual data, but this is not strictly true for spatial data such as the grid squares described above. For example, birds in one square may only move to another by passing through adjacent squares. Furthermore, adjacent squares share a mutual boundary, and are therefore inevitable more similar to each other, than to more distant squares. These inherent weaknesses require that the results of statistical analysis of such data be treated with some caution.

Forward stepwise multiple regression analysis of grid square physical parameters was conducted on all grid squares, for solitary feeding and for flock feeding, using count data obtained during the 557 whole-loch surveys. In both cases, the dependent variable was the total number of birds observed in the square during all surveys. The independent variables comprised minimum, mean and maximum depth, minimum distance from the loch shore, and minimum distance from the loch or nearest island shore.

For solitary feeding, three steps were found to be significant, and the best predictor of feeding intensity was mean depth ($F_{1,256} = 359.6$, $p < 0.001$, adjusted $R^2 = 58.2\%$). Inclusion of distance from the loch shore, and also distance from loch or island shore, was significant ($F_{2,255} = 189.5$, $p < 0.001$, $R^2 = 59.8\%$, & $F_{3,254} = 138.4$, $p < 0.001$, adjusted $R^2 = 62.0\%$, respectively).

For flock feeding, only two steps were found to be significant, and the best predictor of feeding intensity was mean depth again ($F_{1,256} = 125.3$, $p < 0.001$, adjusted $R^2 = 32.6\%$). Inclusion of Maximum depth was also significant ($F_{2,255} = 73.3$, $p < 0.001$, adjusted $R^2 = 36.0\%$). The relationship between mean depth and intensity of use for feeding is illustrated in Figs. 12 & 13.

FIGURE 12: LINE FIT PLOT FOR GRID SQUARE MEAN DEPTH AND SOLITARY FEEDING INTENSITY

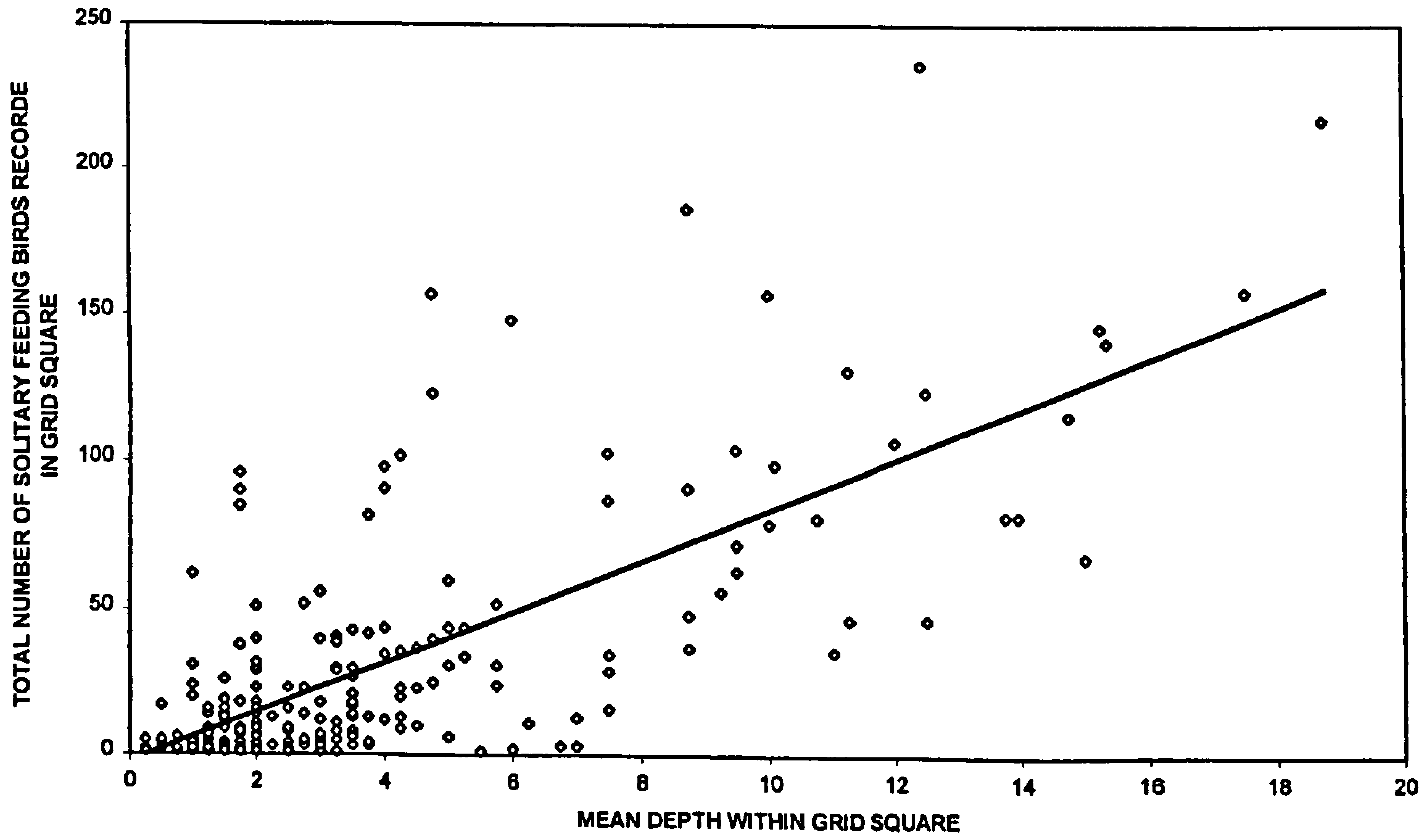
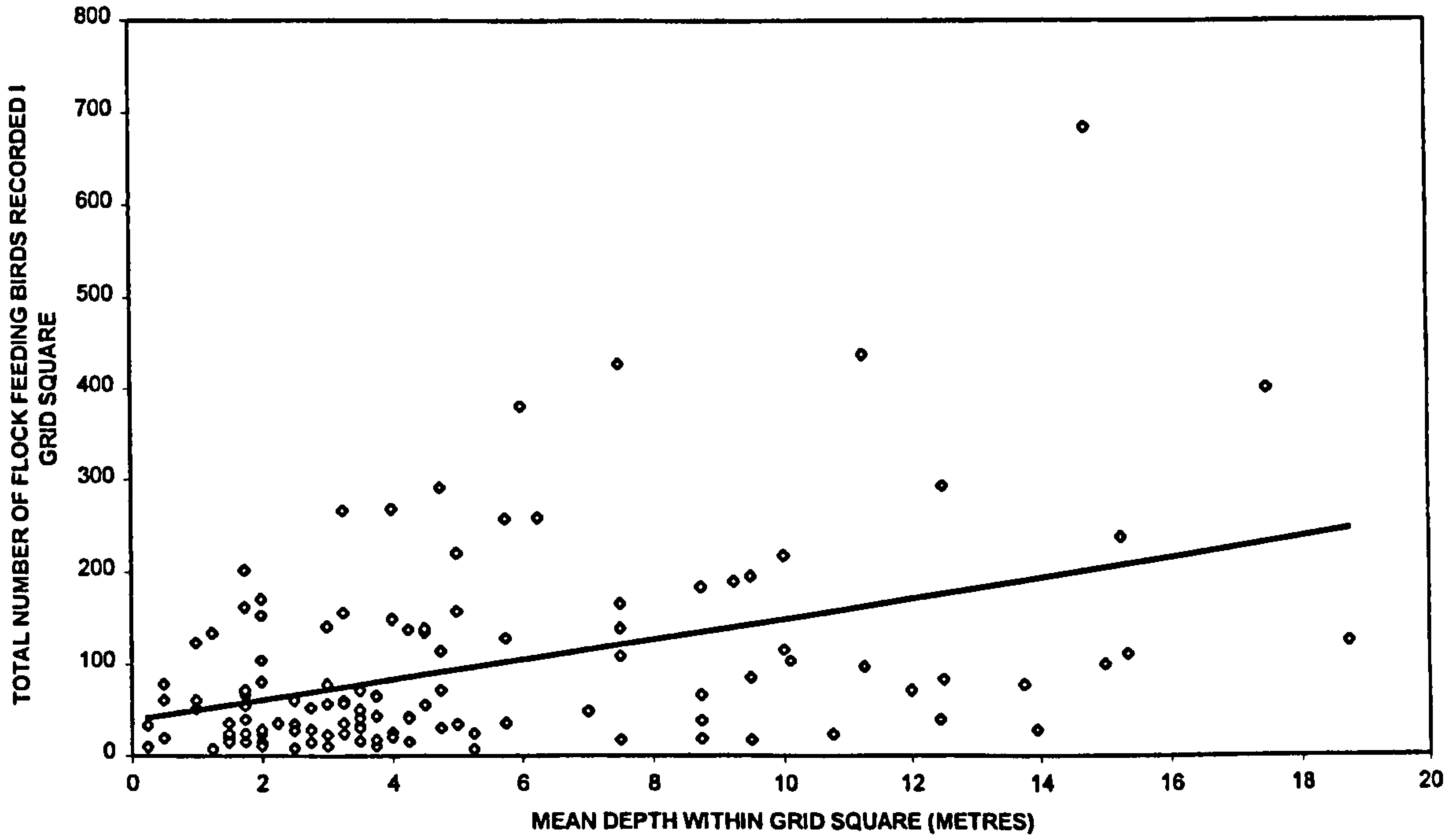
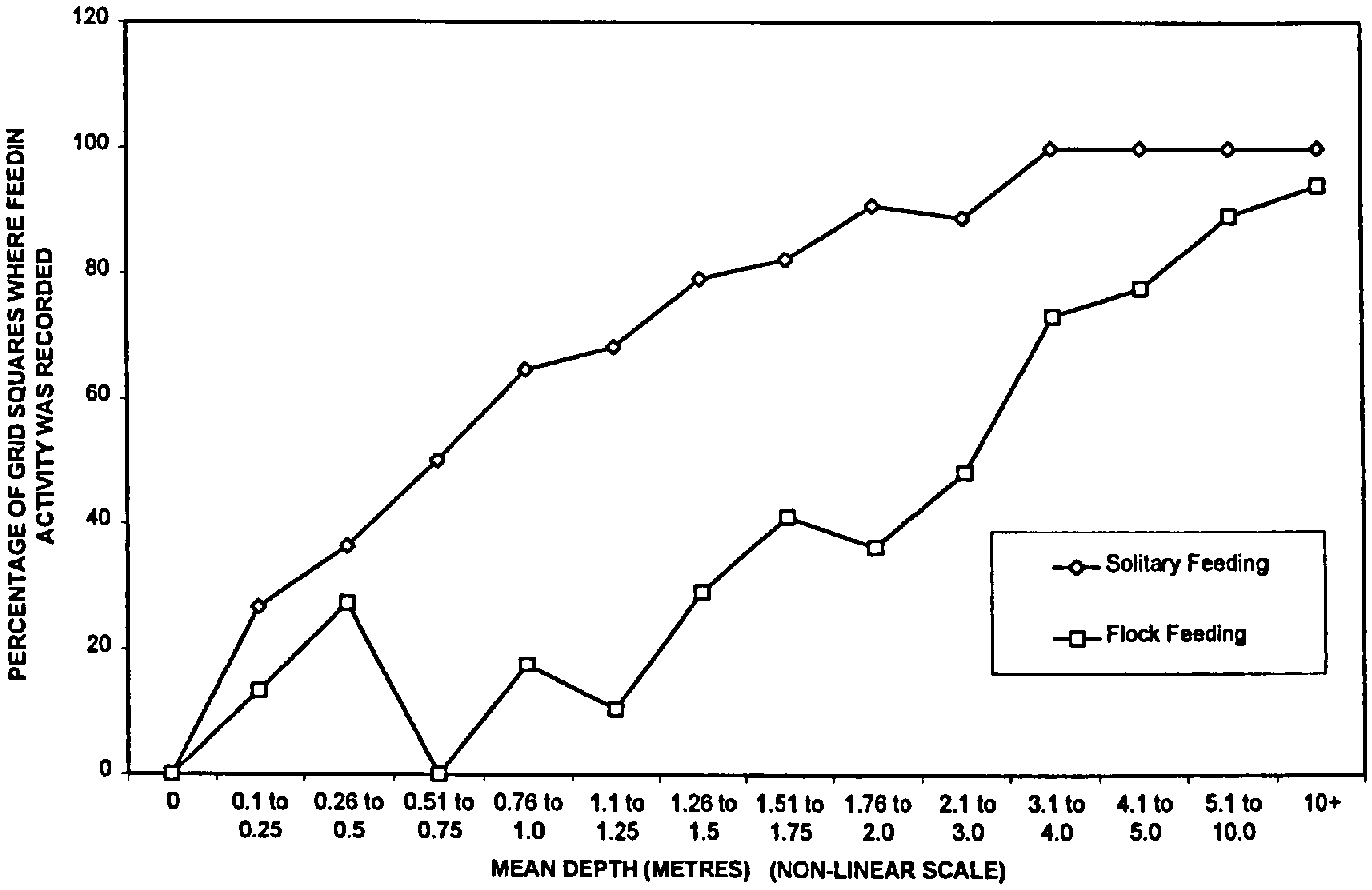


FIGURE 13: LINE FIT PLOT FOR GRID SQUARE MEAN DEPTH AND FLOCK FEEDING INTENSITY



The percentage occupancy of grid squares of different mean depth is illustrated in Fig. 14, and clearly demonstrates the increase in occupancy with increasing mean depth for both solitary and flock feeding. The strongest preference is for squares of over 2 m mean water depth. The mean water depths in squares which were not used was 0.9 metres for solitary feeding, compared to 1.9 metres for flock feeding, and the mean depth of squares not used for feeding during any surveys was 0.7 metres. Solitary feeding occupied more squares in total, and those additional squares comprised deeper water, suggesting that the most unattractive waters are those with least water depth.

FIGURE 14: PERCENTAGE OF GRID SQUARES OCCUPIED IN DIFFERENT MEAN DEPTH ZONES DURING SOLITARY AND FLOCK FEEDING



Variation in intensity of use of grid squares in relation to water clarity

The Secchi disc survey of 50 sample points on 14 February 1999 revealed a range from 90.5 to 128.5 cm, with a mean of 118 cm, and a marked variation across the loch (Fig. 15). Water clarity was greater in the south-western half, gradually deteriorating to the north-east. This is likely to reflect the effects of wave action caused by the prevailing south-westerly wind, stirring up sediments as the fetch increases and water depth decreases. The area of reduced visibility on the southern shore probably reflects the impacts of agricultural activities, causing the release of suspended sediments to enter the loch via farm ditches. It is apparent that the clearest waters covered both deep and shallow areas, and water clarity appeared to be independent of depth.

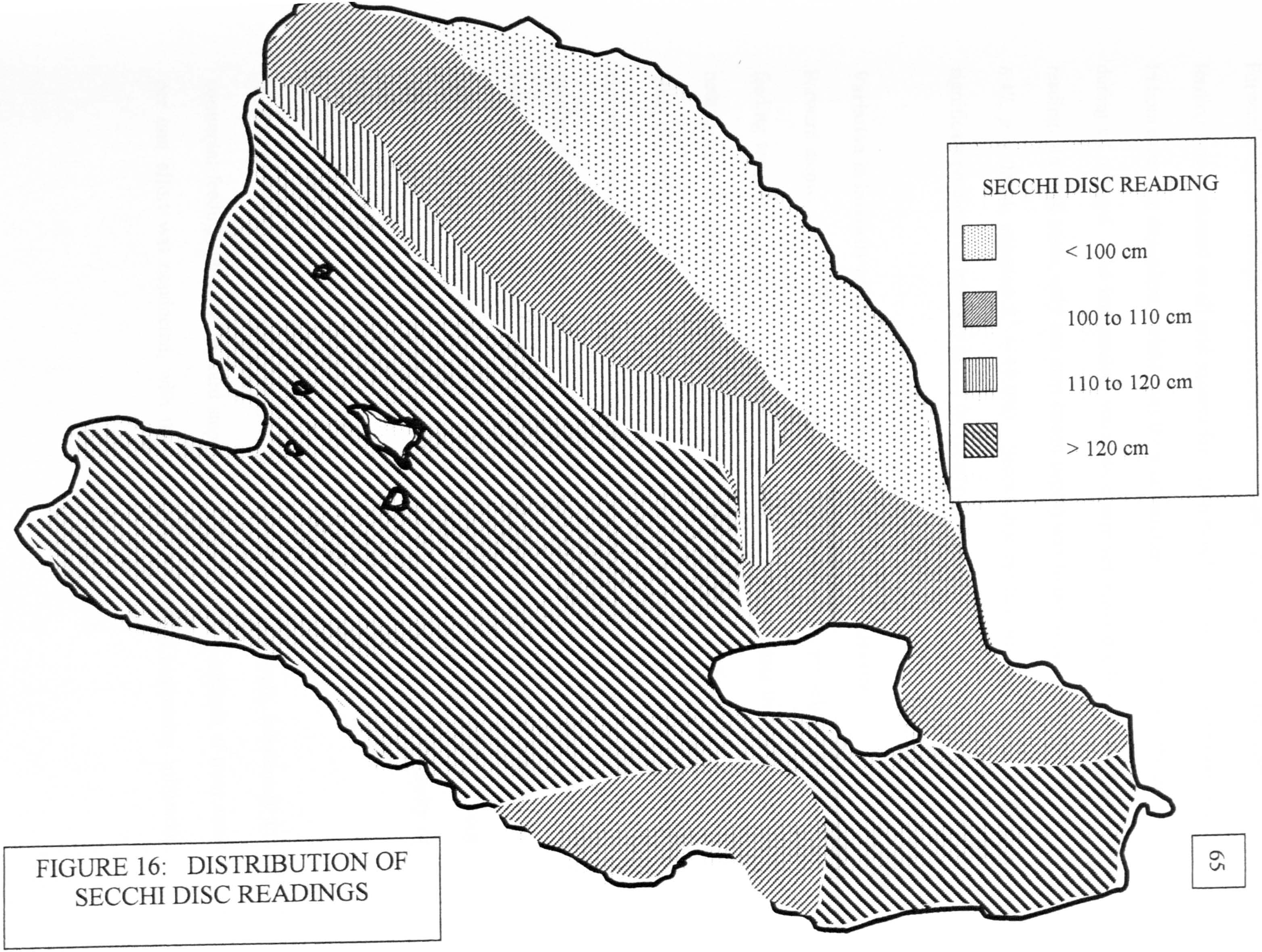


FIGURE 16: DISTRIBUTION OF SECCHI DISC READINGS

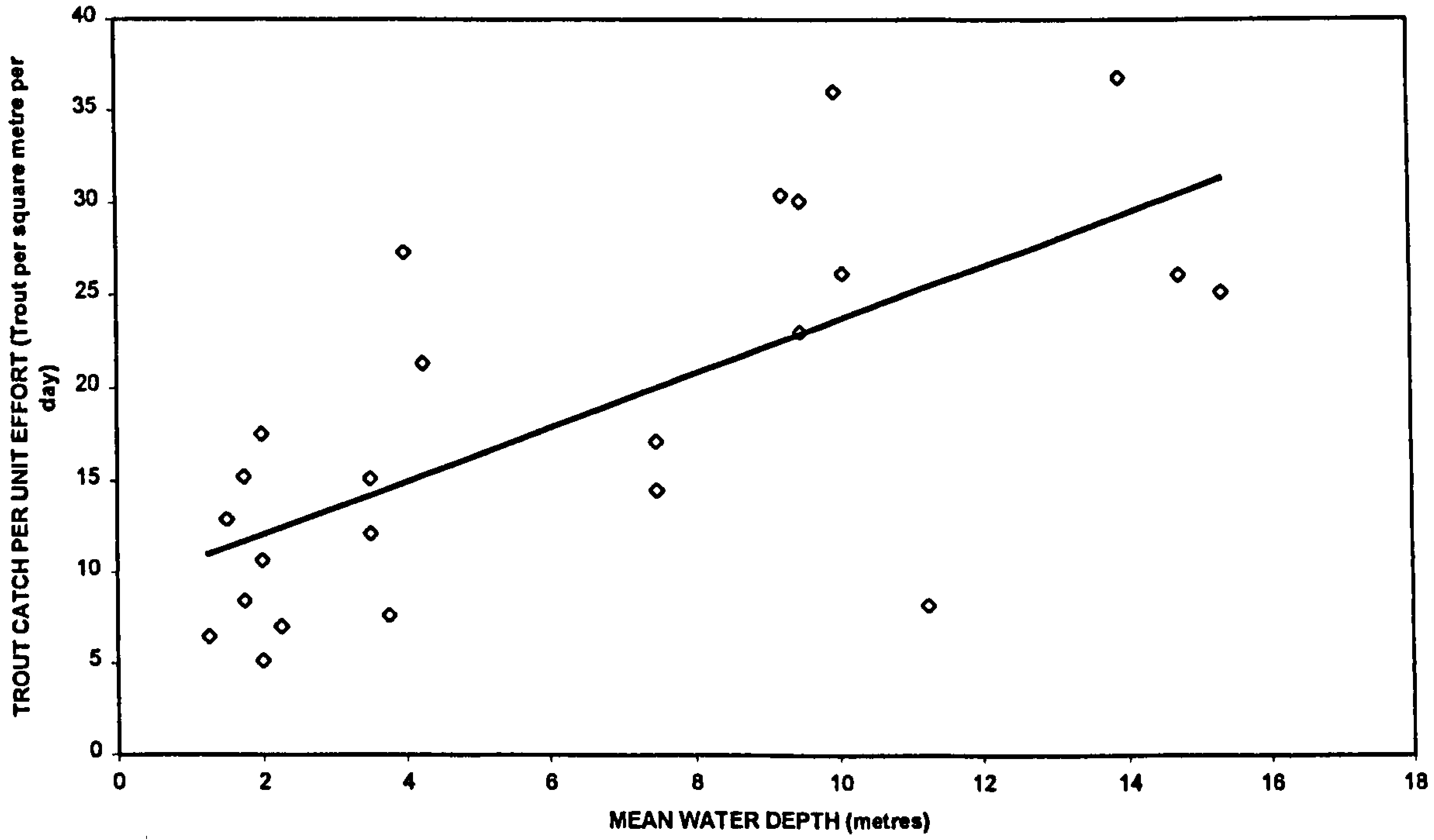
Forward stepwise multiple regression analysis of intensity of use for solitary and flock feeding was conducted on all grid squares for which Secchi disc readings were available. In both cases, the dependent variable was the total number of birds observed in the square during all surveys. The independent variables comprised mean depth and Secchi disc reading. In both cases, only one step (mean depth) was found to be significant ($F_{1,48}$ = 6.47, p = **0.014**, adjusted R^2 = 10.0%). Secchi disc reading was not found to be a significant predictor of intensity of use for cormorant feeding.

Variation in intensity of use of grid squares in relation to fish density

Forward stepwise multiple regression analysis of intensity of use for solitary and flock feeding was conducted on all grid squares for which fish sample data from winter gill-netting were available. In both cases, the dependent variable was the total number of birds observed in the square during all whole-loch surveys. The independent variables comprised mean depth, number and weight of gill net trout catch per unit effort and of number and weight of gill net perch catch per unit effort. In both cases, only one step (mean depth) was found to be significant ($F_{1,22}$ = 20.9, $p <$ **0.001**, adjusted R^2 = 46.4% for solitary feeding, $F_{1,22}$ = 10.8, p = **0.003**, adjusted R^2 = 29.9% for flock feeding). Trout and perch catch per unit effort were not found to be significant predictors of intensity of use for cormorant feeding.

In order to further investigate the relationship between mean water depth, fish density and cormorant feeding intensity, forward stepwise multiple regression analysis of trout catch per unit effort was conducted, with the independent variables comprising minimum, mean and maximum depth, minimum distance from the loch shore, and minimum distance from the loch or nearest island shore. Two steps were found to be significant with mean depth the best predictor of trout catch ($F_{1,22} = 20.0$, $p < 0.001$, $R^2 = 45.2\%$), illustrated in Fig. 16. Inclusion of distance from the loch shore was also significant ($F_{2,21} = 18.9$, $p < 0.001$, $R^2 = 60.9\%$). Thus, mean water depth appears to be the best predictor of both cormorant feeding and fish density.

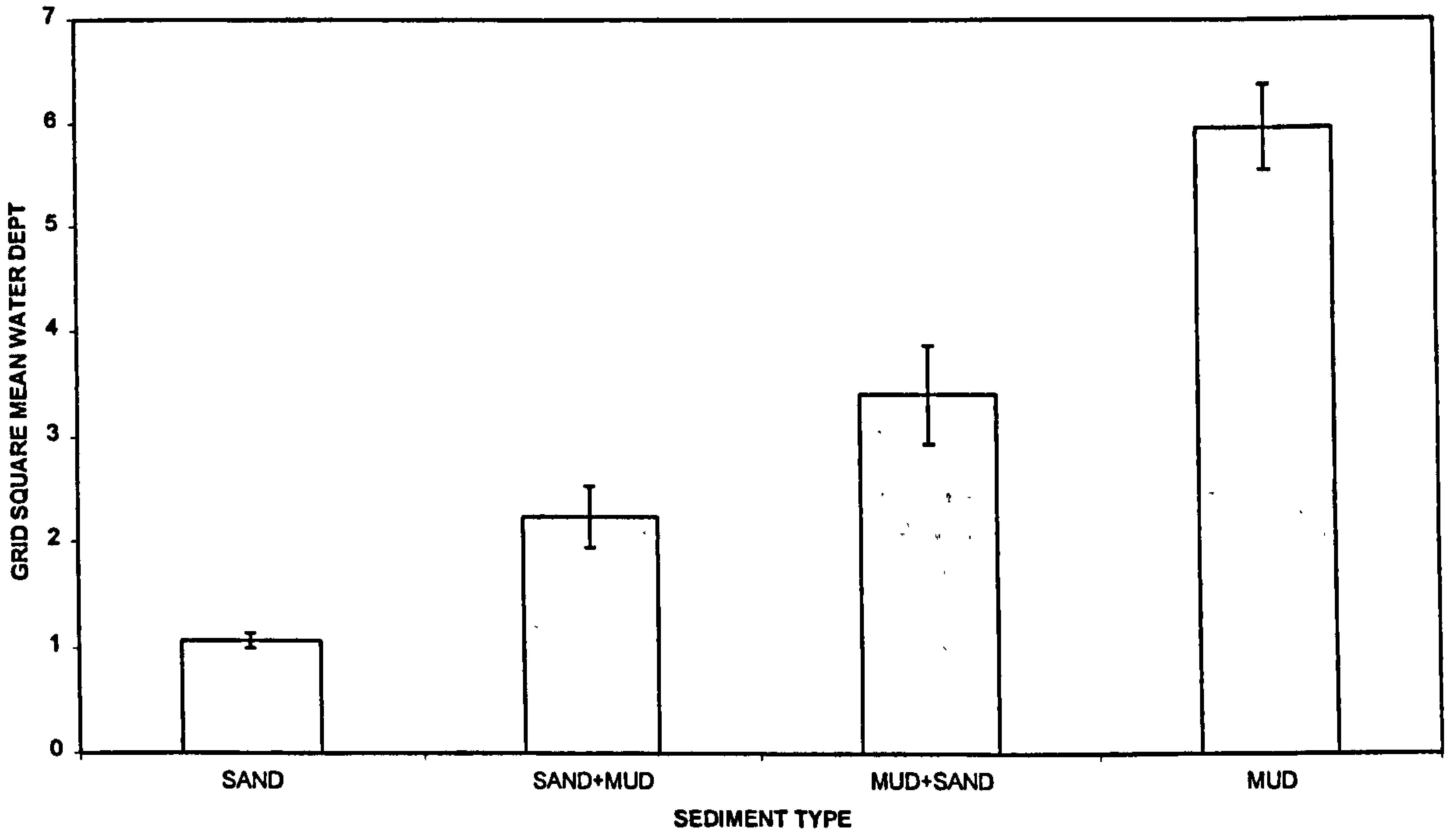
FIGURE 16: VARIATION IN WINTER GILL NET TROUT CATCH PER UNIT EFFORT WITH MEAN WATER DEPTH



Sediment types

Sediment types in individual grid squares were identified as "sand", "sand with mud" (i.e. mixed, with sand>mud), "mud with sand" (i.e. mixed, with mud>sand) and "mud". It became apparent from comparison with bathymetrical data that these four sediment types were closely associated with zones of different water depth (Fig. 17).

FIGURE 17: SEDIMENT TYPES AND GRID SQUARE MEAN WATER DEPTH WITH STANDARD ERROR BARS



Mean depths were not normally distributed, and contained vales of zero, so were $\log_{10}+1$ transformed. A one-way ANOVA test was conducted on mean depths for each sediment type, and the results were significant ($F_{3,254} = 105.98, p < 0.001$). Tukey test showed that all differences were significant ($p < 0.001$), apart from that between "sand with mud" and "mud with sand". It was therefore concluded that sediment type was largely a function of water depth, so no comparisons of cormorant distribution data with sediment type were conducted.

3. Flock Feeding Behaviour

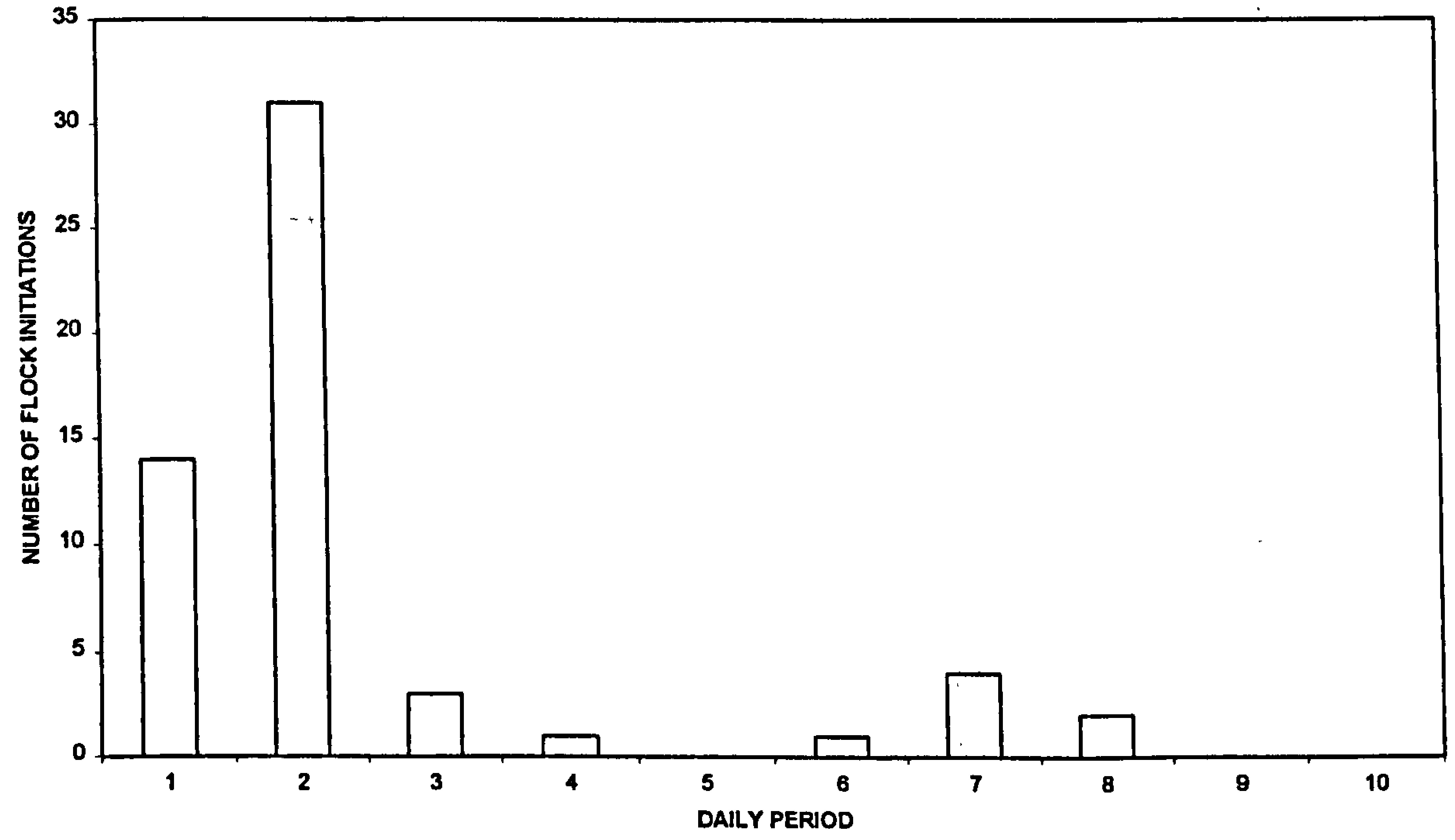
Flock formation and behaviour

Flocks usually began to form early in the morning, shortly after first light. At first a few birds would gather together on the water and swim in company with no clear direction, to be gradually joined by increasing numbers as the bulk of the birds left their roosts. Once a flock was formed, they would typically swim on the surface with heads held high, in a distinct direction for between 5 and 55 minutes (mean 16.6 minutes) without feeding, and in this fashion would cover between 120 and 1500 metres (mean 574m). On some occasions the flock would become airborne and fly for one or two minutes covering between 1000 and 3000 metres (mean 2385m) before settling again on the water. The flock generally swam in an extended line ahead, and a few birds near the front would commence diving, to be followed by the rest of the flock. They did not all dive together, and at any time there would be birds underwater, surfacing, on the surface and diving. As birds surfaced they would either dive almost immediately or swim strongly forwards before diving again. As birds fell back towards the rear of the flock they would often fly briefly forward to land at the front of the flock and commence diving again. Thus the flock progressed mainly through swimming, though with a trickle of birds flying from the rear to the front of the flock.

Time of initiation of flock feeding events

The timing of flock feeding initiation, defined as the time when diving *en-masse* began and not including time spent swimming as a flock or of sporadic diving beforehand, is illustrated in Fig. 18. Again, in order to allow for variation in day length, each day was divided into ten equal periods, and it is evident that 80% of events commenced in the first two periods. After a lull around mid-day, there was secondary phase of feeding, but of much lower intensity than during the early morning.

FIGURE 18: DIURNAL VARIATION IN TIMING OF FLOCK FEEDING INITIATION OVER TEN EQUAL PERIODS



Location of flock feeding event initiation

The first four grid squares entered by each feeding flock were extracted from the event record maps and data from all events were consolidated to give totals for each grid square. Fig. 19 shows the totals for 93 grid squares entered at the start of the events. There is clearly a concentration in the east central area, and the block of thirteen adjacent

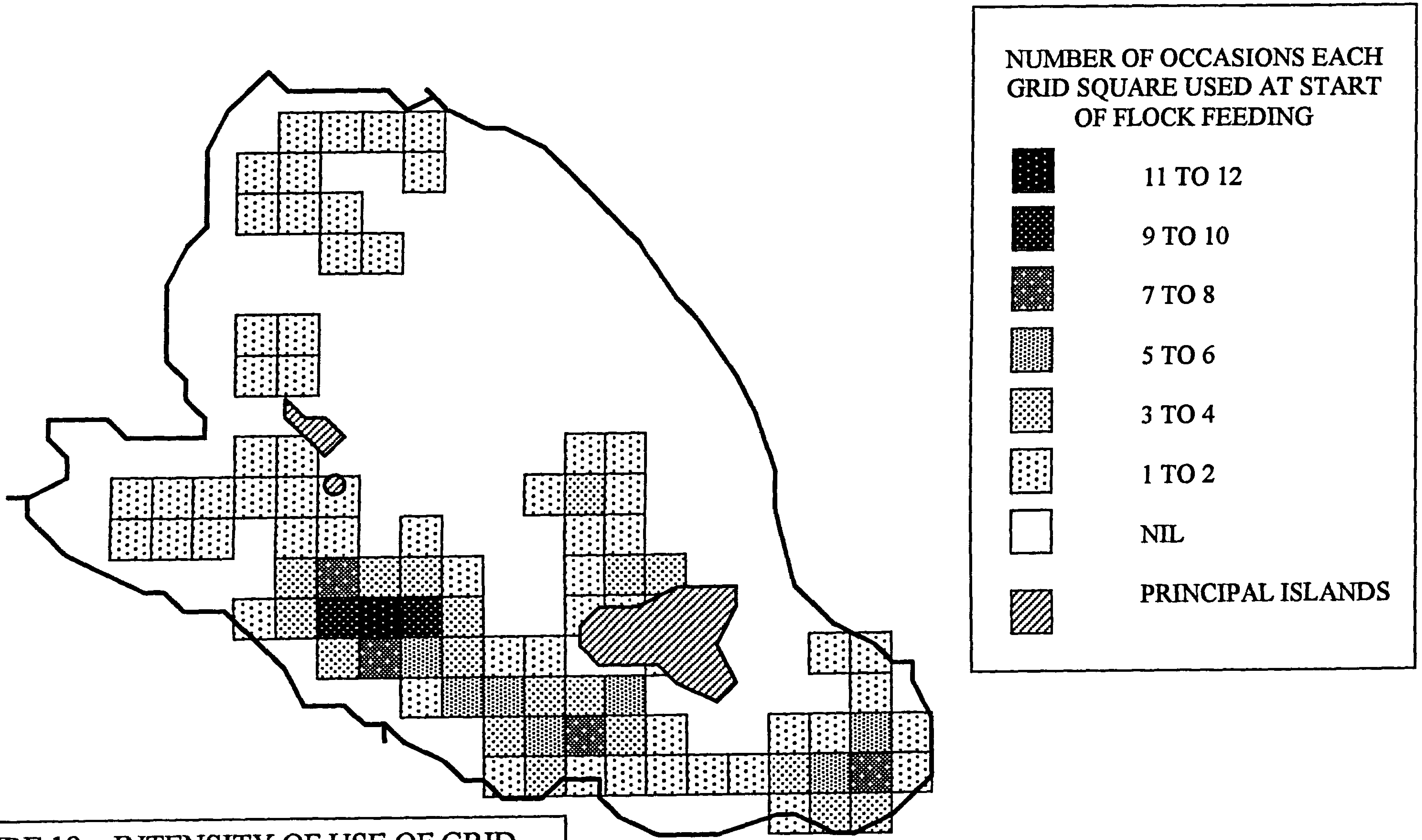


FIGURE 19: INTENSITY OF USE OF GRID SQUARES FOR INITIATING FLOCK FEEDING

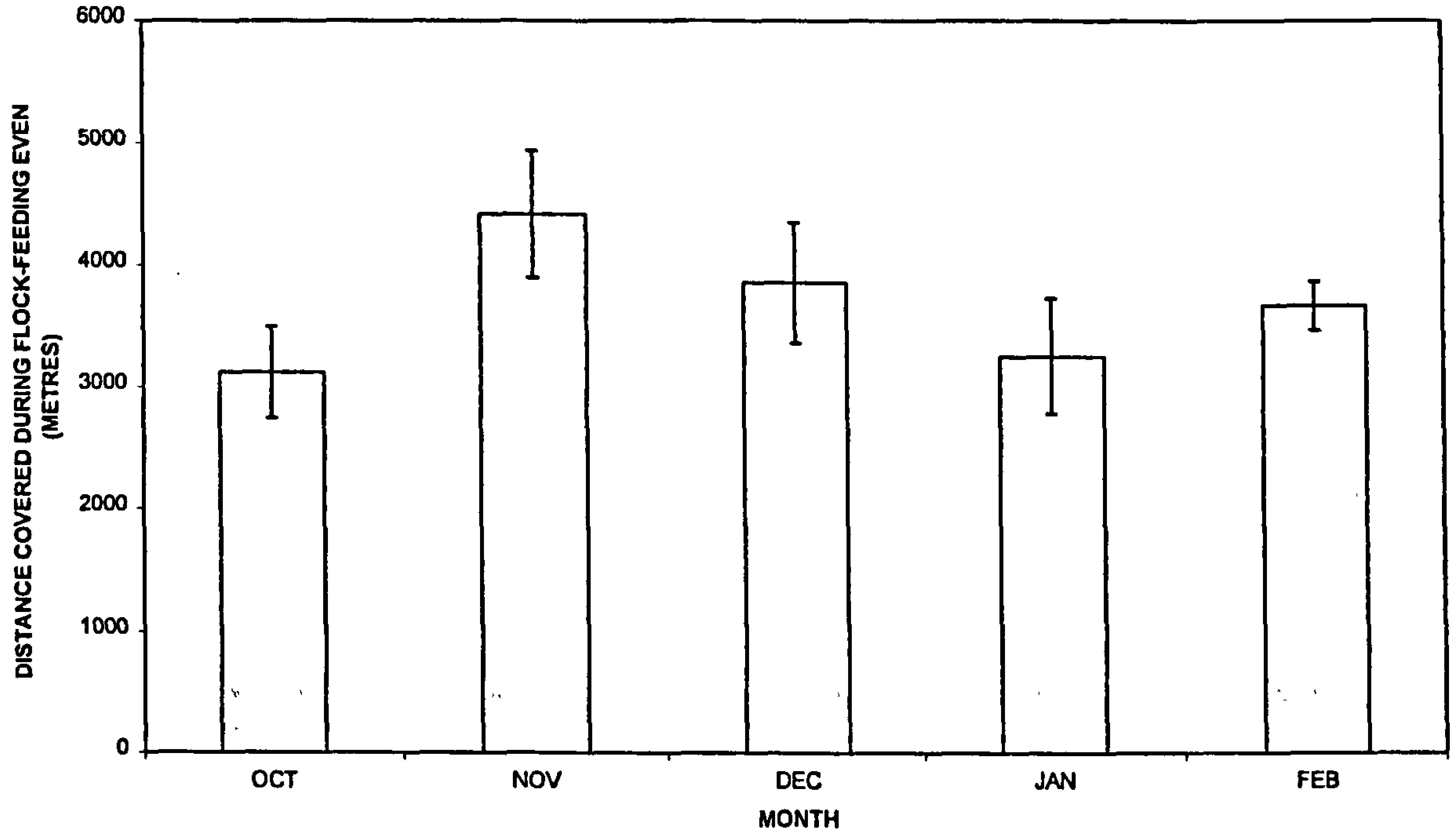
grid squares comprising 172 to 175, 187 to 191, and 203 to 206, account for 32% of flock feeding initiations, although they represent only 4.8% of all squares. There are smaller concentrations to the south of the main island around Sq. 240, and in the south-east corner around Sq. 260.

Forward stepwise multiple regression analysis of grid square physical parameters was conducted on all grid squares. The dependent variable was the total number of occasions when the square comprised one of the first four grids used during the commencement of flock feeding. The independent variables comprised minimum, mean and maximum depth, minimum distance from the loch shore, and minimum distance from the loch or nearest island shore. Two steps were found to be significant, and the best predictor of flock initiation was minimum depth ($F_{1,256} = 16.3$, $p < \mathbf{0.001}$, adjusted $R^2 = 56.0\%$). Distance from the loch shore was also significant ($F_{2,255} = 13.3$, $p < \mathbf{0.001}$, adjusted $R^2 = 88\%$).

Distance covered by feeding flocks

The distance covered during each flock feeding event was measured from the event record maps, omitting distances covered whilst not actively diving and whilst flying between feeding sites. Data from seven occasions when recording was interrupted were omitted, e.g. where the flock disappeared into a fog bank whilst still actively diving. The mean distance covered by all the recorded events was 3,757m, with a range from 600m to 8,490m. There was some variation between months (Fig. 20).

FIGURE 20: MONTHLY VARIATION IN DISTANCE COVERED DURING FLOCK FEEDING EVENTS - OCTOBER TO FEBRUARY - WITH STANDARD ERROR BARS

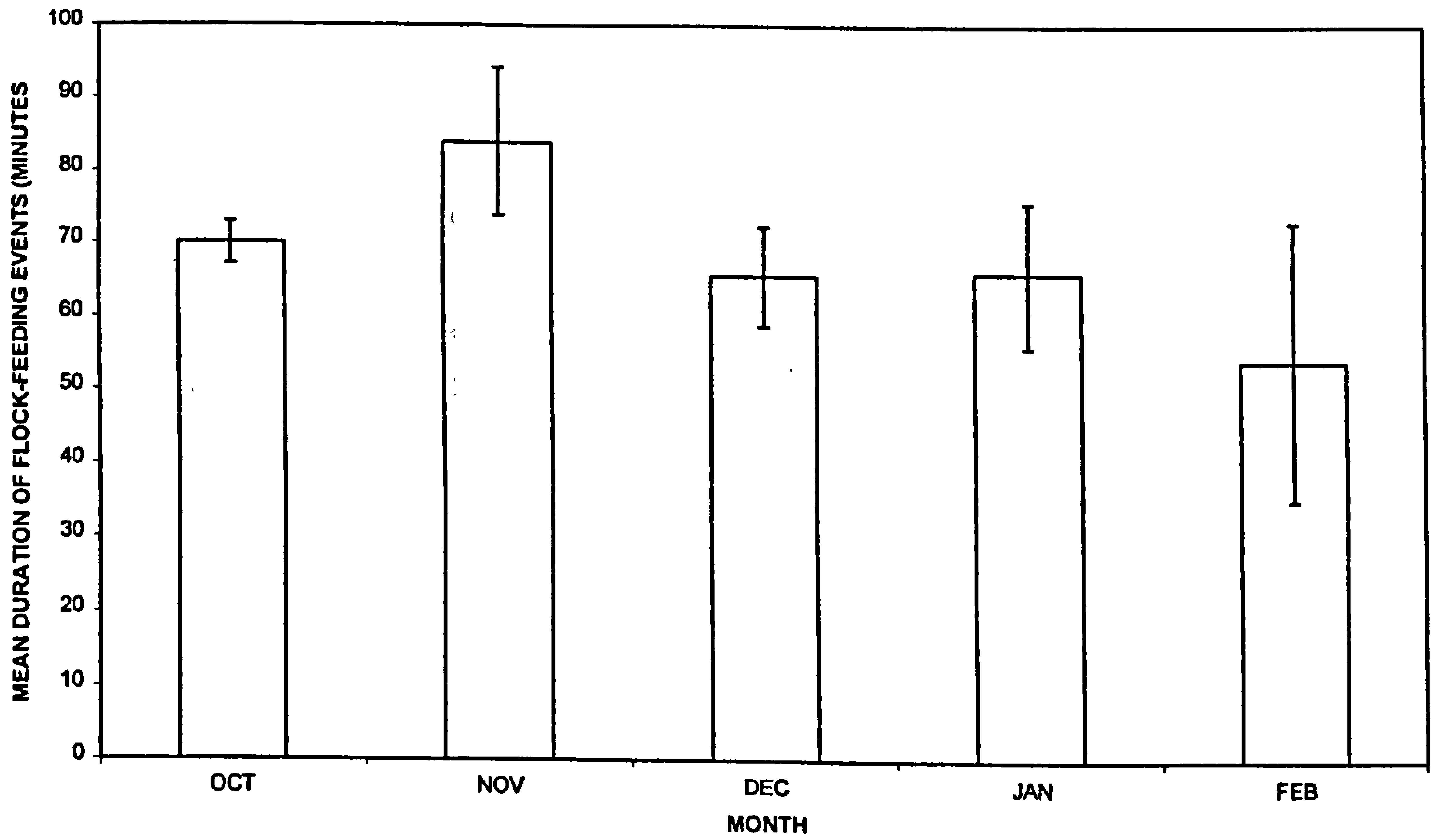


The March sample was too small to permit analysis. Although the mean distance covered in November is large, a one-way ANOVA test shows that the inter-month differences are not statistically significant. It was postulated that a larger flock might cover a greater distance, so distance covered was compared with flock size on flock formation, but regression analysis showed no significant relationship.

Duration of flock feeding events

The duration of flock feeding events was derived from the feeding start and stop times recorded on the event maps, omitting time spent not actively diving and whilst flying between feeding sites. Five records where times were not adequately recorded were excluded from analysis. The mean duration of all the recorded events was 68min, with a range from 13 to 135min, and Fig. 21 shows the variation in duration of flock feeding events. The November duration is higher than in other months, but one-way ANOVA shows that the month-to-month variations are not statistically significant. The March sample is too small for analysis.

FIGURE 21: MONTHLY VARIATION IN DURATION OF FLOCK-FEEDING EVENT - OCTOBER TO FEBRUARY - WITH STANDARD ERROR BARS



It was postulated that a larger flock might feed for longer, and flock feeding duration was compared with flock size on flock formation, but regression analysis showed no significant relationship.

Foraging speed during flock feeding events

The speed of progress of the flock was determined by measuring the distance covered between timed locations and dividing it by the time elapsed. Thus speeds could be calculated for different sections of the flock's track and allocated to individual grid squares or groups of squares. Over all the flock feeding events recorded, which exceed 60 hours in total duration and covered some 200km, speeds of between 0.25 m s^{-1} and 5.3 m s^{-1} were recorded for individual squares (Fig. 22). The median speed was 1.02 m s^{-1}. Medians of speeds each month are illustrated in Fig. 23.

FIGURE 22: DISTRIBUTION OF GRID SQUARE FLOCK SPEEDS

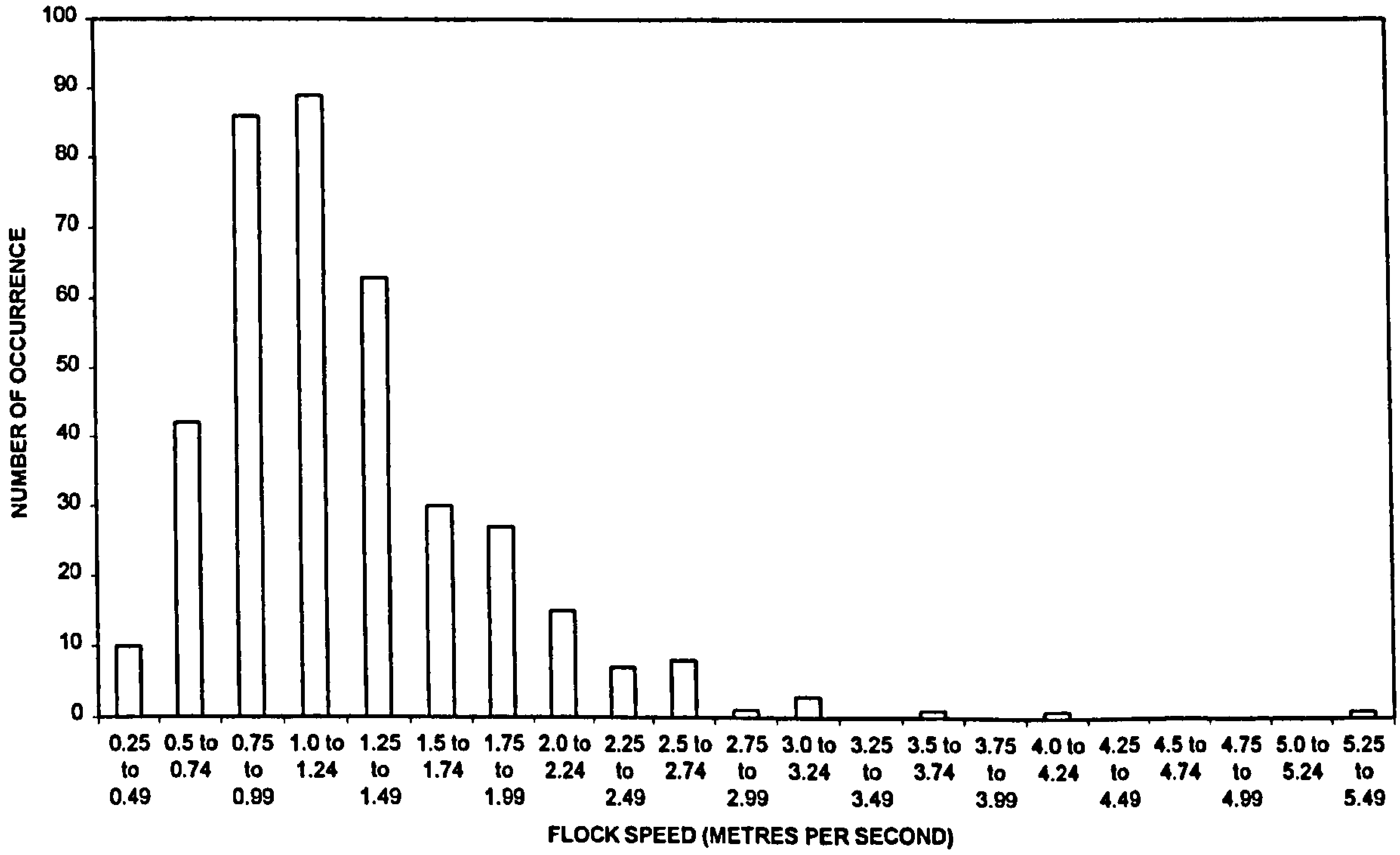
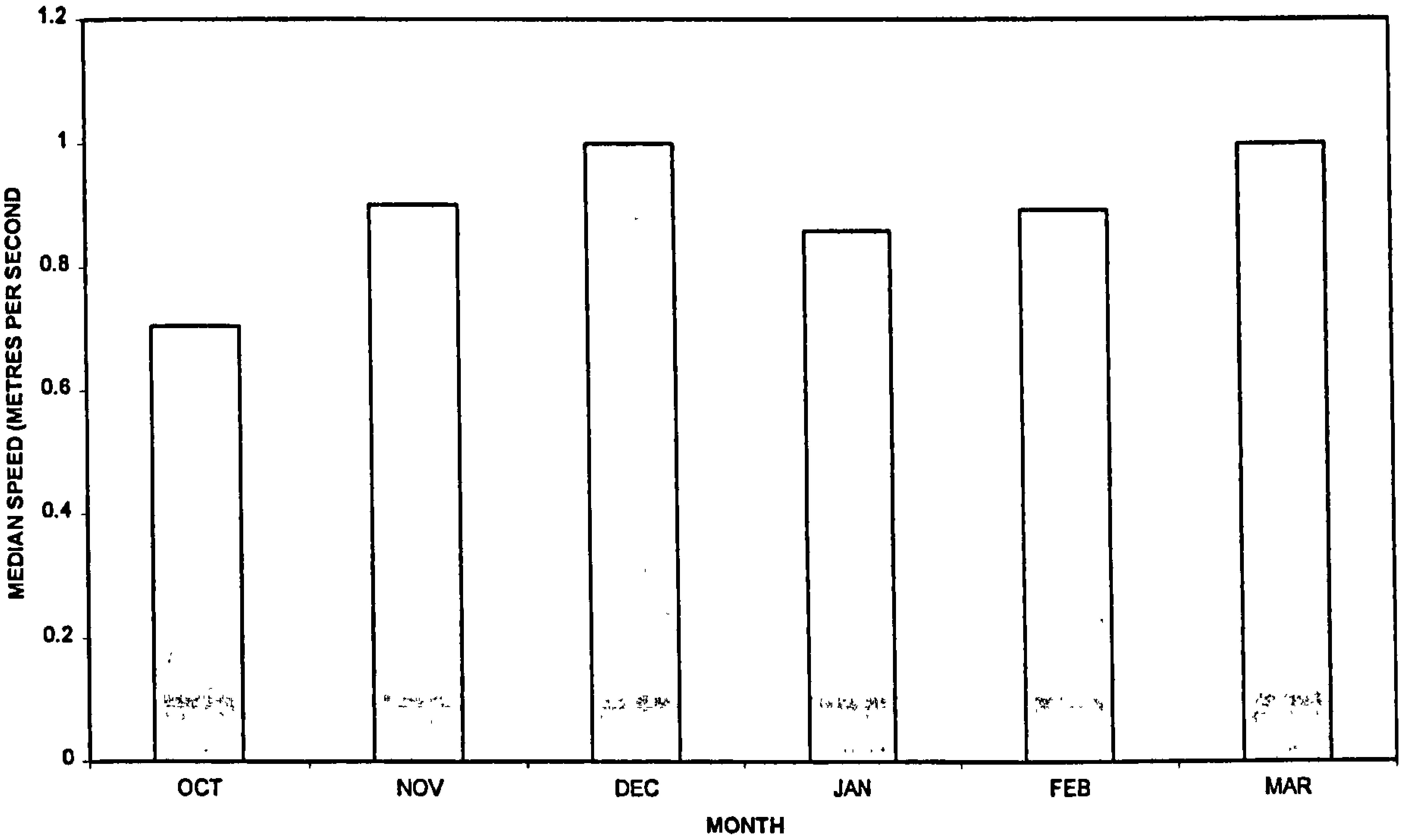


FIGURE 23: MONTHLY VARIATION IN MEDIAN FLOCK SPEED



Speeds were $\log_{10}$ transformed in order to normalize their distribution and a one-way ANOVA test demonstrated that inter-month differences are not significant.

Flock speeds of all flock feeding events were consolidated to produce a median flock speed for each grid square that had recorded three or more observations (Fig. 24). There appears to be general concentrations of squares with speeds exceeding 1.25 m s^{-1} running in a broad belt from north of the smaller islands, through the centre of the loch to the south of the larger island. The four squares with the highest median speeds of up to 2.5 m s^{-1} are contiguous, and all have sample sizes of between seven and nine observations. By contrast, there is a block of 17 squares in the central south-west area, running from Sq. 172 to 238, where the median speed in all squares is less than 1 m s^{-1}.

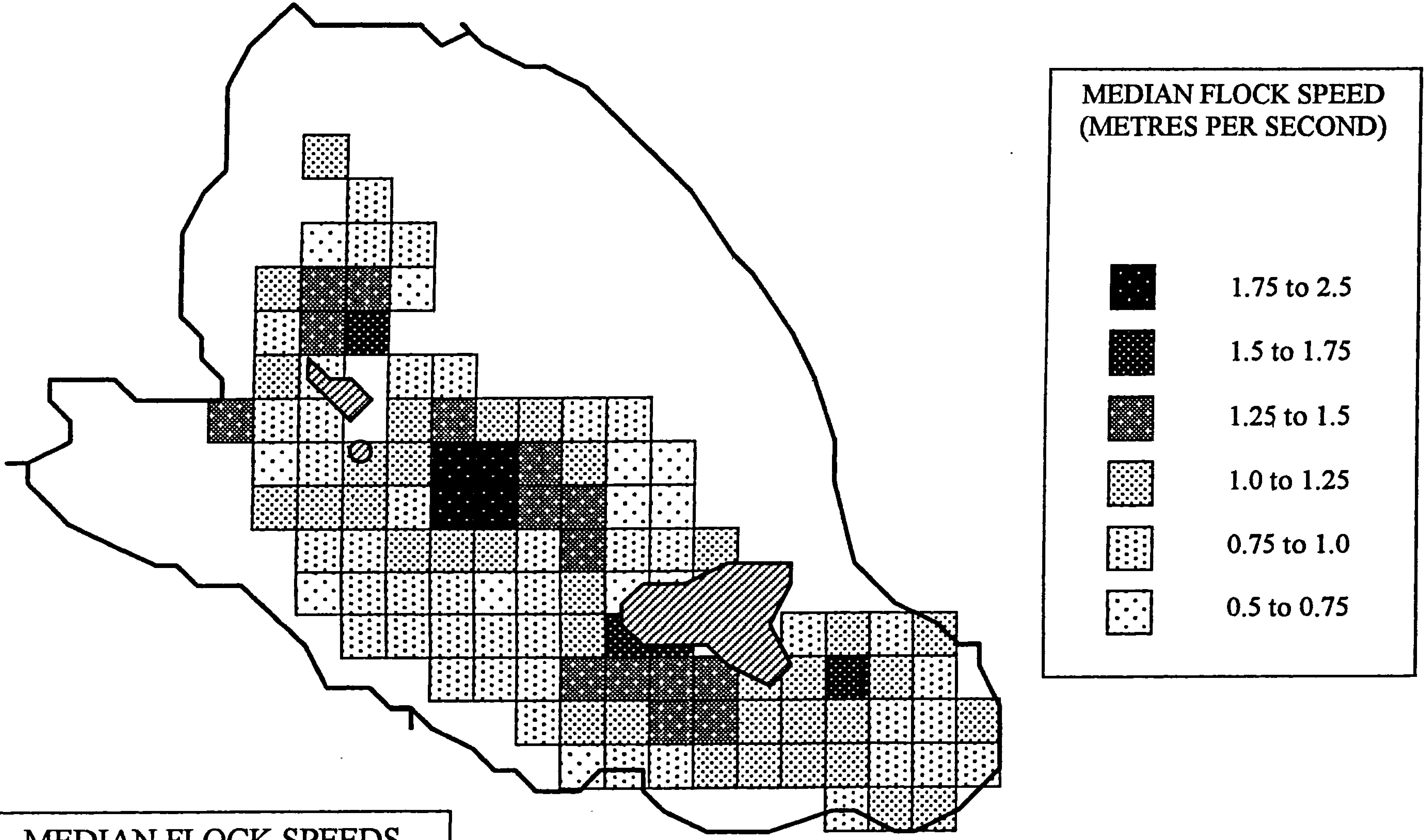


FIGURE 24: MEDIAN FLOCK SPEEDS DERIVED FROM FLOCK TRACKING

Regression analysis of median speed and intensity of use for flock feeding showed no significant relationship.

Size of flock during flock feeding events

The frequency of occurrence of different flock sizes, counted at flock formation, is shown in Fig. 25. There is a range from 25 to 450, and an uneven distribution. Field observations noted that within a few minutes of commencing flock feeding, birds began to depart for roosting and loafing sites. Although some of these departures were offset by new arrivals, these were relatively few, and the bulk of birds making up a flock arrived at the start of the event. Thereafter, the general pattern was one of gradual decline, which continued either until the flock gradually dwindled away, or until some critical point was reached when all the remaining birds became airborne together, and flew en-masse to roost.

Fig. 26 shows the flock size profiles for 5 sample flock-feeding events, which were subject to curve estimation analysis. Flock 4 showed a steady decline throughout, falling from 390 to 0 over 70 minutes, and fits a linear profile ($F_{1,13} = 440.5$, $p < 0.001$). Flocks 3 and 5 also showed a steady decline, from 270 to 205 and from 440 to 240 over 25 and 35 minutes respectively, and both fit a linear profile ($F_{1,4} = 173.4$, $p < 0.001$, $F_{1,6} = 103.6$, $p < 0.001$ respectively). However, both flocks then suddenly dispersed as all the remaining birds departed. Flocks 1 and 2 also declined in size, but showed an acceleration in the rate of decline after 45 and 55 minutes respectively, and both flock profiles fit a cubic curve ($F_{1,10} = 69.4$, $p < 0.001$, $F_{1,11} = 147.4$, $p < 0.001$ respectively).

FIGURE 25: FREQUENCY OF OCCURRENCE OF DIFFERENT FLOCK SIZES

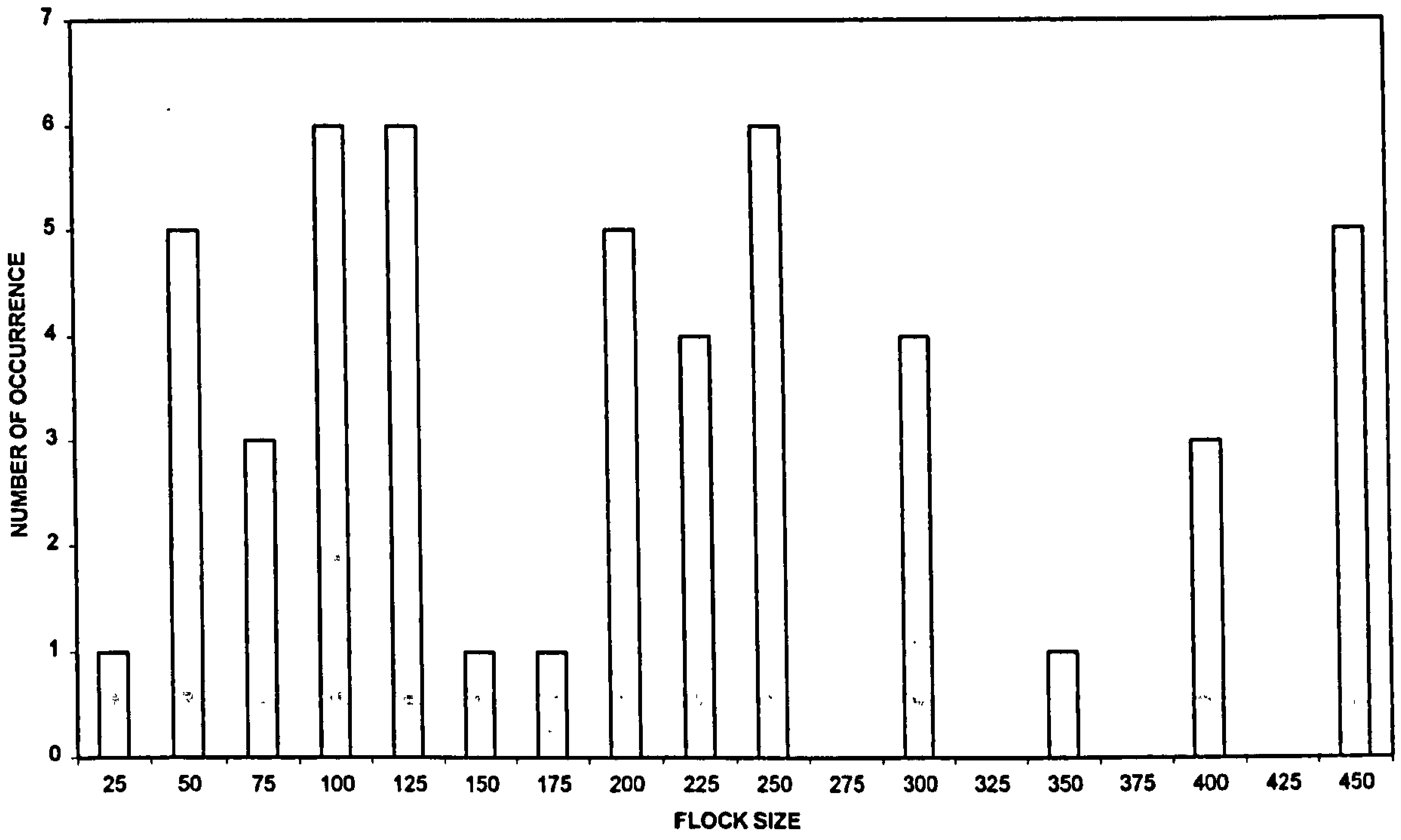
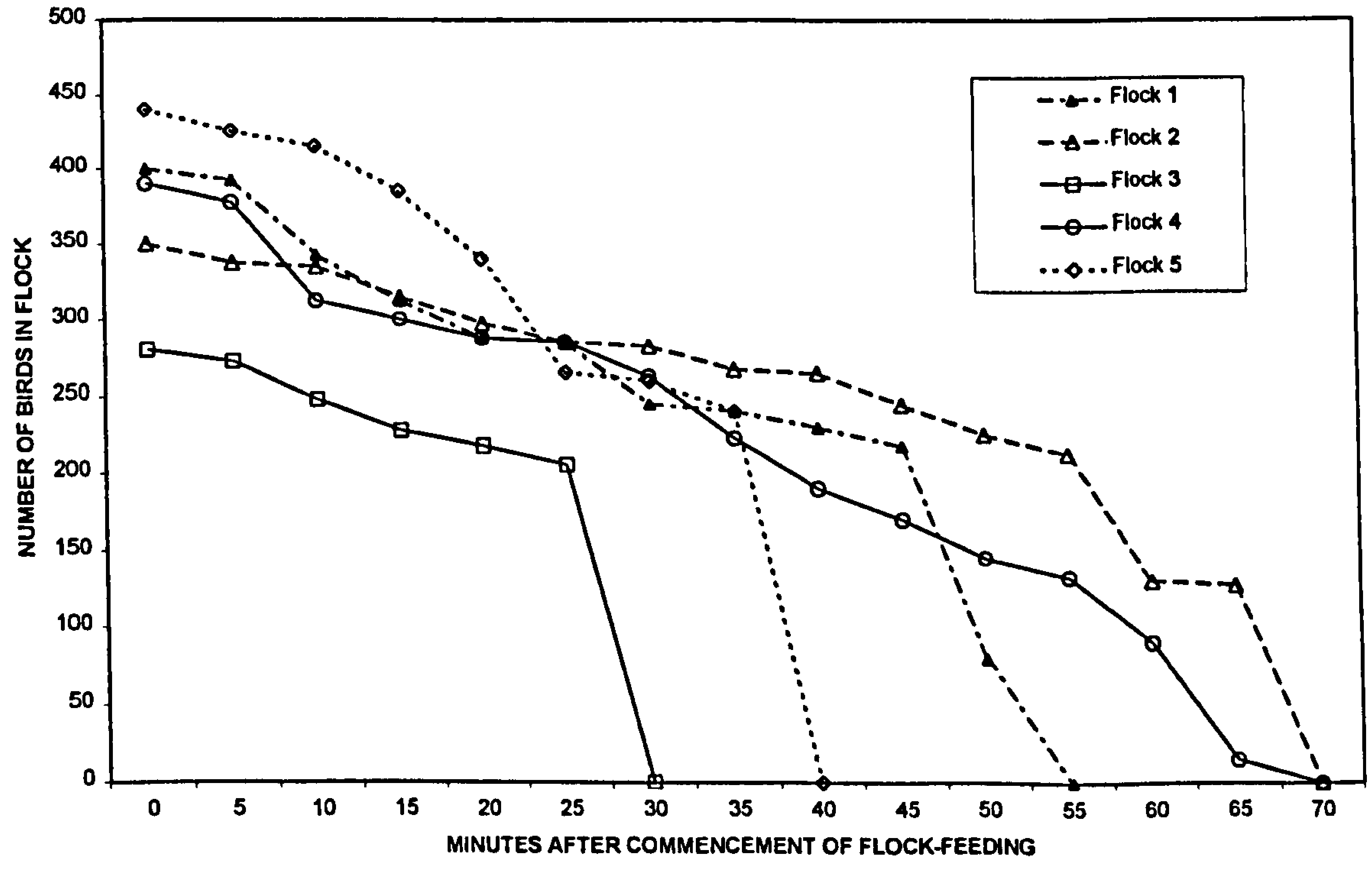


FIGURE 26: CHANGE IN FLOCK SIZE OVER TIME - FIVE SAMPLE FLOCKS



On those occasions when more than one flock feeding event was recorded in a day, the flock size was compared between earlier and later events. It was found that size declined from a mean of 232 for the first event to 179 for the second event, but the difference was not significant.

Flock feeding tracks

There was considerable variability in the tracks followed by feeding flocks, but at times some discernible patterns were evident. On occasions, the feeding flock would return to the same area for several days, sometimes following very similar tracks (Fig. 27). This repeat pattern was only observed in the southern part of the loch. By contrast, during other periods there was no return to the same area, and sequential flock feeding events visited completely different areas (Fig. 28).

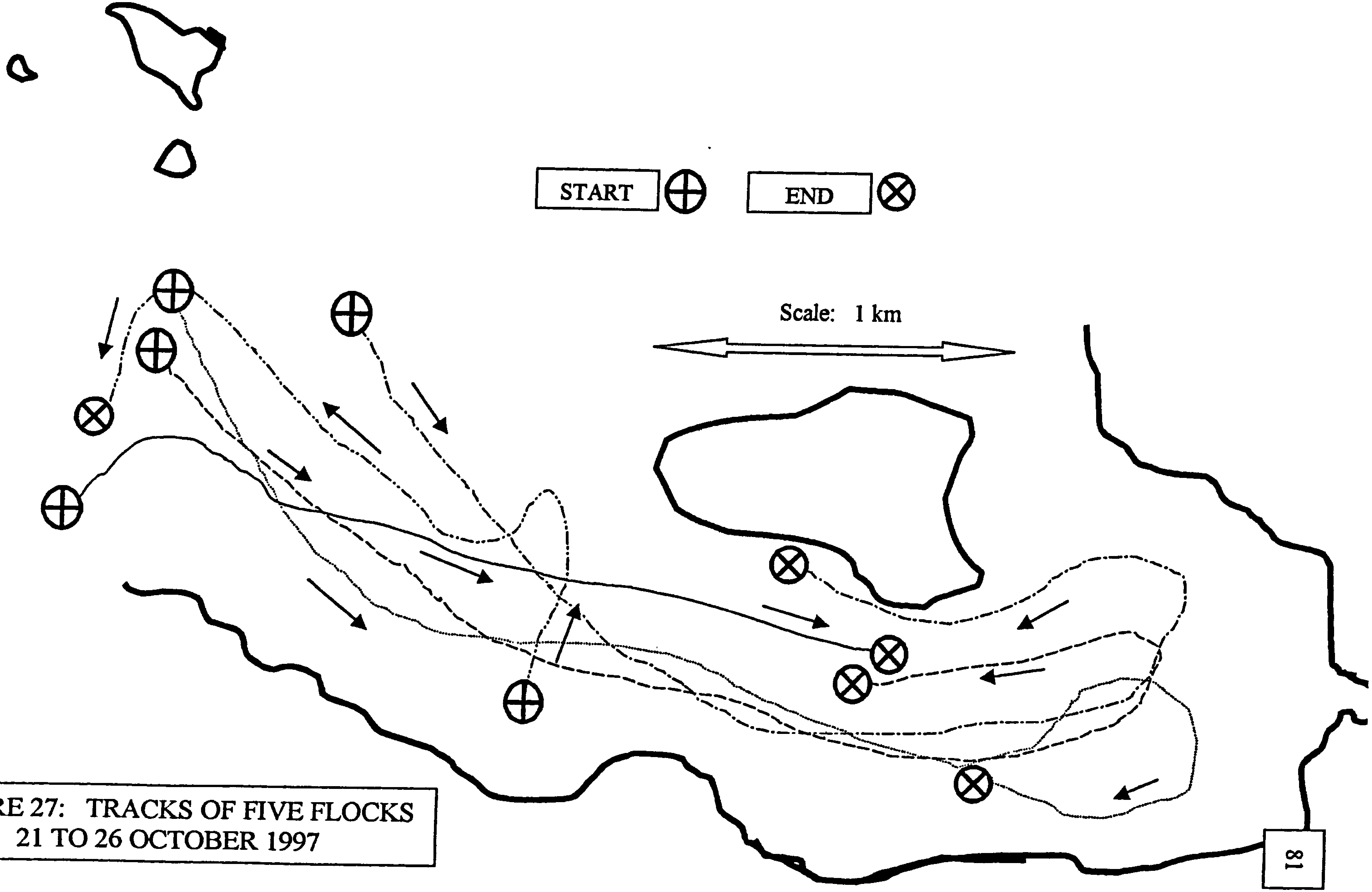


FIGURE 27: TRACKS OF FIVE FLOCKS
21 TO 26 OCTOBER 1997

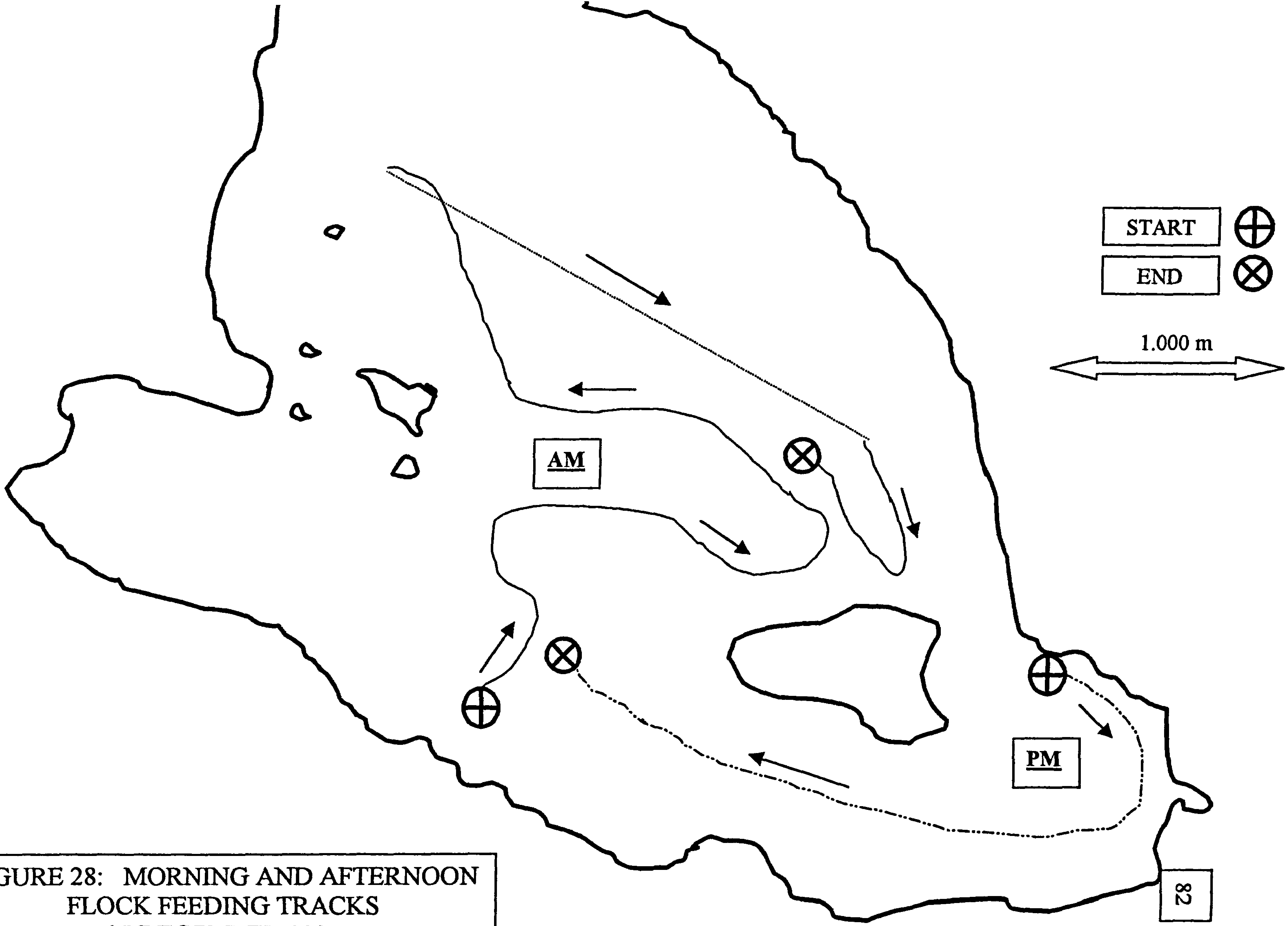


FIGURE 28: MORNING AND AFTERNOON FLOCK FEEDING TRACKS 15 DECEMBER 1997

Whilst most flocks swept through an area only once during a flock feeding event, there were occasions where a flock returned to sweep the same area again. This occurred particularly in two locations: the south-east corner of the loch (Fig. 29), and to the north-west of the large island (Figs 30).

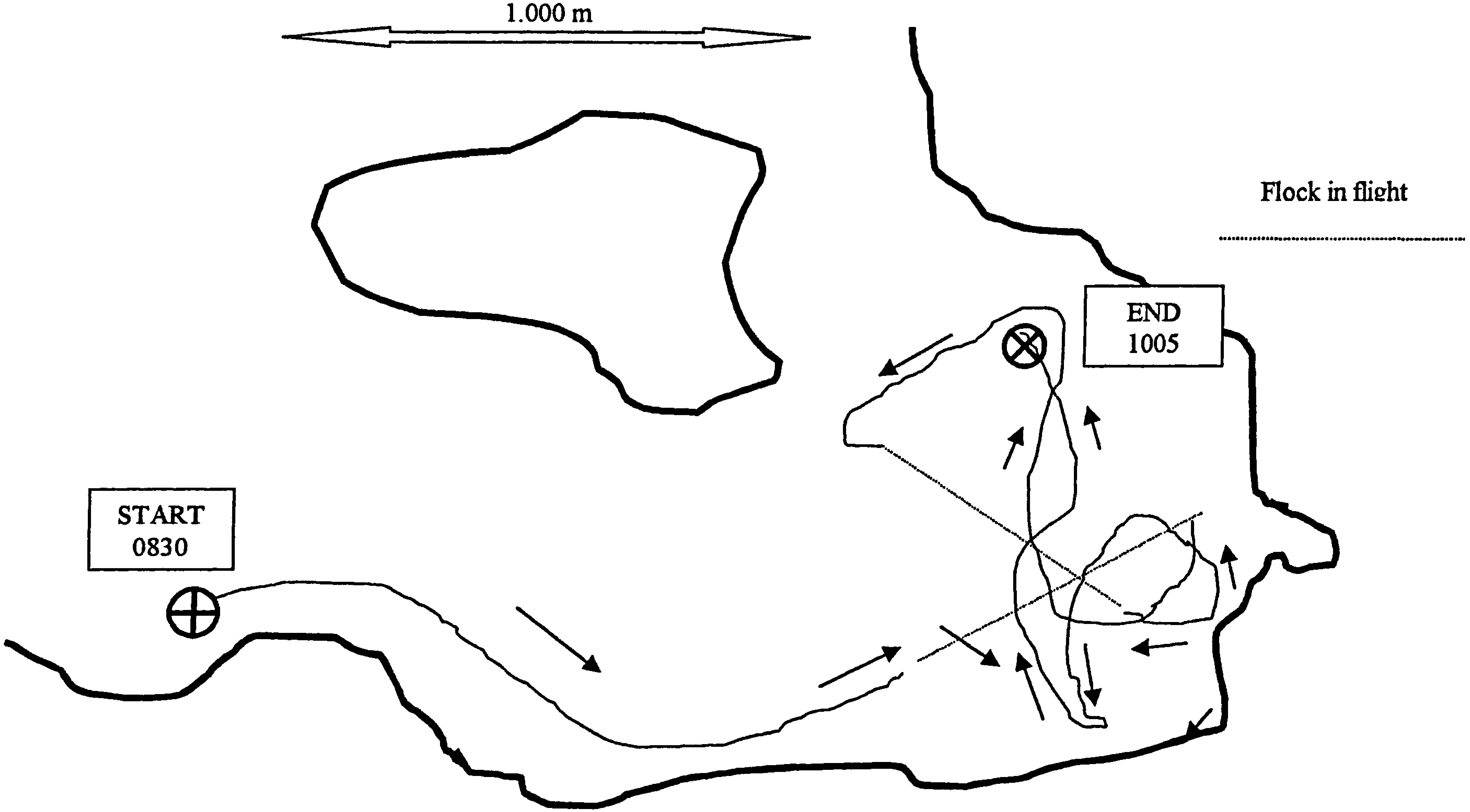


FIGURE 29: TRACK OF FEEDING FLOCK
10 DECEMBER 1998

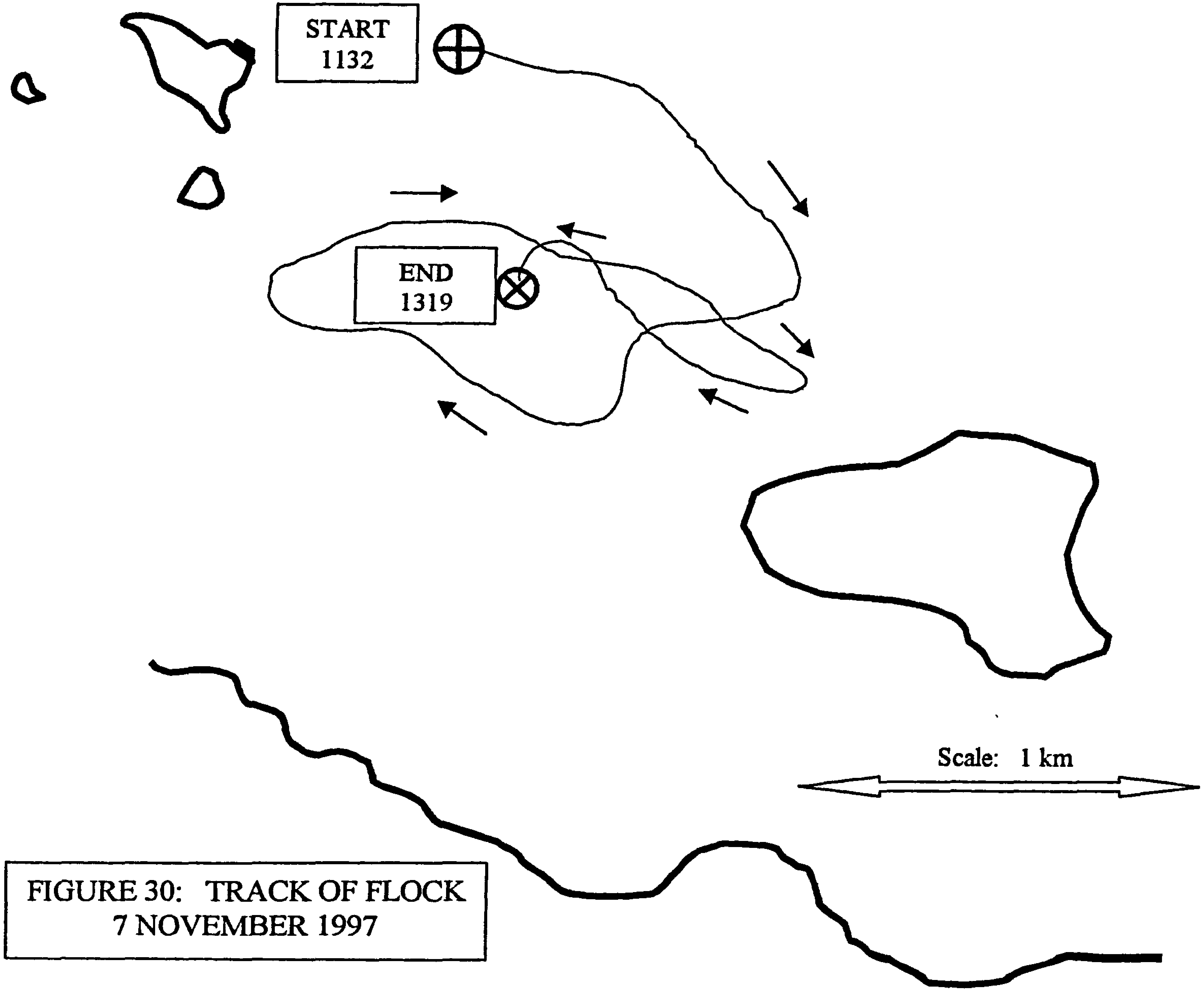


FIGURE 30: TRACK OF FLOCK
7 NOVEMBER 1997

DISCUSSION

Feeding times

The importance of taking account of changing day length across the winter, when considering foraging activity patterns, is clearly illustrated in the differences between Figs 1 & 3. Fig. 3, which divides the daylight hours into ten equal periods, shows a distinct peak of activity early in the morning, particularly during the first two periods, which is not apparent in Fig. 1. This concurs with the findings of Hughes *et al.*, (1999), but not with Van Eerden & Volslamber (1995) who reported that flock feeding in May continued at high but varying levels throughout the period from 0600 to 1800. This difference may reflect changes in demands between wintering and breeding seasons.

The proportion of birds actively foraging in the early morning (60%) was less than the 70% or more reported by Hughes *et al.*, (1999) at both Grafham and Frampton. However, unlike Loch Leven, birds regularly commuted from other roosts such as Paxton to feed at Grafham, and for an accurate comparison, with Loch Leven, both roosting numbers at these sites and feeding numbers at Grafham would have to be combined. Furthermore, the numbers foraging at Frampton and Grafham were only about 10% and 50% respectively of those at Loch Leven. The decline in foraging activity at Loch Leven to around 20% for the rest of the day is similar to the pattern at Frampton, but not at Grafham where there was a marked peak late in the day with up to 70% feeding. However, this peak occurred 16 hours after dawn, which suggests it happened outwith or on the fringes of the winter period when day length was shorter than 16 hours, and again it may reflect changes in demands between wintering and breeding seasons.

The increase in foraging activity during the mid-winter months, even allowing for shortening day length, is an interesting phenomenon, which is not reflected in the findings of Hughes *et al.,* (1999) at Grafham where there are erratic peaks and troughs from month to month with no evident pattern. At Frampton there is some superficial evidence of an increase in foraging activity in mid-winter, but if day length were allowed for, this trend would disappear. The marked increase in activity, with birds more than twice as active in December and January suggest increased energy demands, reduced foraging success, or a combination of both.

The mean total time spent foraging at Loch Leven, ranging from 1.4 hours per bird in September to 3.9 hours in January, is very much higher than the 0.5 to 1.75 hours recorded by Hughes *et al.,* (1999) during particularly cold weather. Similarly, the duration of single flock feeding events, exceeding two hours at times, was surprisingly long, as was the distance covered, at up to 8.5 km. These findings may indicate that longer foraging times are a response to high energy demands associated with the higher latitude and colder winter weather in Scotland, or may indicate reduced foraging success at Loch Leven compared to other sites.

The lack of evidence from radio tracking of nighttime activity by cormorants suggests that the findings of this study reflect an accurate picture of foraging behaviour, and agree with the general perception that cormorants do not feed at night (e.g. Cramp & Simmons, 1977).

Flock feeding and solitary feeding

The preponderance of flock feeding over solitary feeding during the winter is apparent, with major switches in behaviour evident in October 1997 and April 1997 & 1998. As described by Volslamber and van Eerden (1991), the onset of flock feeding may result from the increase in the number of foraging birds available to the point where flock feeding becomes economically viable. Similarly, the ending of flock feeding may reflect falling numbers. Additionally, or alternatively as described by Suter (1991), flock feeding may reflect changes in prey behaviour, with fish shoaling and moving into deeper water, when flock fishing represents a more effective capture technique. The potential for switching between flock feeding and solitary feeding, as described by Veldkamp (1991), is evident in the differences in proportions recorded between the 96/97 and 97/98 winters.

Flock feeding was the prevalent feeding technique on Loch Leven, even though water clarity was always considerably higher than the 50 to 80 cm Secchi disc readings, described as optimal by van Eerden and Volslamber (1995). Furthermore, for much of the study period water clarity exceeded 150 cm, described as an upper limit for flock feeding. In addition, unlike the findings of Koop (1997), flock feeding continued throughout the winter months when there is extensive mixing of the water column at Loch Leven, and no stratification (Bailey-Watts *et al.*, 1994). Despite the evidence from elsewhere, there is no evidence that water clarity had any influence on cormorant foraging technique on Loch Leven.

Feeding distribution

The markedly uneven distribution of cormorant feeding on the loch, with many areas not exploited and others subject to concentrated foraging activity, suggests the strong influence of physical and/or biological factors in determining feeding profitability. The variation between feeding techniques, with solitary feeding notably wider spread across the loch compared to flock feeding, suggests that the two feeding techniques may be influenced by different factors. The area used most regularly for flock formation lies in deep water at the north-western limit of the most intensively hunted part of the loch, which extends 4 km to the south-east. It also lies 700 m south-south-east of the principal cormorant roost site on the small circular island. The area therefore probably represents the most energy-efficient start point for foraging, offering the shortest flight distance with access to the most productive feeding areas.

Factors determining distribution of feeding intensity

Water depth is clearly a strong determinant factor, with both solitary and flock feeding concentrated in deeper water. Solitary feeding took place over more of the loch than did flock feeding, and tended to include the remaining deeper water areas. The least attractive areas had least water depth, and many shallow areas were unexploited. The most significant predictor was mean depth, particularly for solitary feeding, suggesting a preference for both deep minimum and maximum depths, rather than those areas with steeply sloping sides that descend into deep water. This concentration in deep areas of what is otherwise a shallow lake contrasts with the findings of Voslamber *et al.*, (1995) who suggest that the disturbance from a flock of cormorants attempting to hunt a deep hole in a shallow lake is likely to disperse shoals of fish rather than concentrate them into vulnerable groups.

Distance from the loch shore may also influence solitary feeding, but is likely to be generally related to water depth, with deeper areas tending to lie further offshore. Thus a preference for deep water may also result in an offshore distribution. By contrast, flocks showed no preference for offshore areas, and were regularly observed feeding in close proximity to the shore, as illustrated in Figs. As a species the cormorant has a history of persecution by fishery interests, and this behaviour may reflect an adaptation, with cormorants more willing to risk a closer approach to land whilst in company with large numbers of others. Alternatively, variation in distance from shore may simply be a consequence of variation in water depth, with flocks foraging in shallower areas that are generally closer to the shore.

The concentration of cormorants in deeper water contrasts with the findings of Hustler (1992) who found that due to buoyancy constraints in the Reed Cormorant *Phalacrocorax africanus*, feeding in deeper water increased commuting time, reduced bottom time, and lead to reduced feeding success. This suggests that cormorants should feed as shallowly as possible, and that a balance must be struck between minimum depth and maximum prey availability. It is therefore likely that prey concentrations are a principal determining factor in the apparent preference of cormorants for foraging in deeper water on Loch Leven. As shown above, the data presented in this paper do not demonstrate that winter trout distribution exerts a significant influence on cormorant foraging distribution. However, according to Thorpe (1974 & 1974b) Loch Leven trout leave the shallow littoral areas during the winter, and are thus concentrated in deeper water when wintering cormorants are present. This is confirmed for both trout and perch, by the multiple regression analysis, which shows mean depth as the principal determinant of fish distribution. Thus, it is likely that cormorants forage in the deeper areas because the fish are there, even though a direct correlation is not evident, possibly as a result of the relatively small number of fish net samples.

Water clarity does not appear to be a determining factor, and this is not surprising given that both solitary and flock feeding are concentrated in deeper water where light levels are very low. It is compatible with the conclusions of Voslamber *et al.*, (1995) who consider that prey detection in deeper water is likely to be by touch rather than visually, due to low light levels, which suggests an adaptation to hunting a relatively immobile hibernating prey, and/or one found at a high density.

Flock feeding behaviour

The median flock foraging speed of 1.02 ms^{-1} compares closely with the line-hunting speed reported by van Eerden and Volslamber (1995) associated with the hunting of small shoaling fish. However, there were sufficient occasions where speeds of 1.33 ms^{-1} or more were recorded to suggest that on occasions flock feeding cormorants on Loch

Leven may be hunting larger fish, whose capture outweighs the additional energy requirements of faster swimming.

The considerable variation in flock sizes is in line with records from other sites, although the largest flock recorded on Loch Leven was 450, rather than the thousands recorded on some European sites. The departure to roost of some birds within a few minutes of commencing feeding, suggests that they are able to quickly fulfil their food requirements, whereas other birds may forage for another hour or longer. This may reflect differences in the foraging efficiency of individuals, e.g. adults versus immatures, as suggested by Hughes *et al.,* (1999). The gradual dwindling away of some flocks, compared to the sudden dispersal of others, suggests that the profitability of flock feeding may vary considerably, and a trigger point beyond which flock feeding is no longer viable may change from day to day.

The track followed by foraging cormorant flocks may be considered in the light of optimal foraging theory. The repeated return of feeding flocks to the same area on subsequent days suggests that, during some periods, foraging success was sufficiently consistent and profitability was sufficiently high to sustain repeated visits. Similarly, the return to the same area of the loch during a single flock feeding event, suggests a response to falling foraging success on leaving that area. However, on other occasions, the flock's behaviour suggests that foraging success was inconsistent, profitability had declined below a threshold level, and the flock's response was to sample different areas. These patterns of behaviour are consistent with an optimal foraging strategy.

Chapter 3

DIVING BEHAVIOUR OF CORMORANTS WINTERING ON LOCH LEVEN

ABSTRACT

Short-range radio tracking was used to investigate the diving behaviour of wintering great cormorants *Phalacrocorax carbo* on Loch Leven, Scotland. In 59 days of tracking, a total of 7,388 individual dives were timed during 113 feeding bouts by 6 birds.

Great cormorants conducted from one to five foraging trips per day, with adults conducting fewer trips than first-winter birds. Individual foraging trips lasted up to 395 min. Not all the time on the water was spent actively foraging, and diving lasted for up to338 min per day, with adults diving for much less time than first-winter birds. Time spent foraging per trip decreased during the day with the number of trips. Cormorants conducted up to 495 dives per foraging trip, and there was significant variation between individuals. The number of dives per trip decreased as the number of trips increased. Cormorants conducted up to 529 dives per day, and adults conducted fewer dives than first-winter birds.

Median dive durations ranged from 25 to 27 s, and median surface interval ranged from 6 to 9 s, both with significant differences between individual Cormorants. Dive duration and surface interval decreased during a foraging trip, but showed no reduction with increasing number of trips. Dive duration and surface interval varied during the winter, but with no clear pattern. Dive duration and surface interval did not vary with water depth. Dive duration and surface interval did not vary between solitary feeding and flock feeding. Following observed fish capture, mean surface interval before diving again was 24.5 s. Dive duration: surface interval ratios ranged from 2.79 to 4.34. Mean time spent underwater per foraging trip for was 45 & 46 min

for adults, and 57 & 65 min for first-winter birds. Mean times spent underwater per day were 72 & 80 min for adults, and 110 & 138 min for first-winter birds.

Foraging time and number of dives per foraging trip were higher at Loch Leven than at other sites. Dive duration at Loch Leven suggests benthic feeding, with no evidence of switching between benthic and pelagic prey. Surface interval was shorter than at other sites. The lack of evidence of a link between water depth and dive duration contrasts strongly with other sites. The significant differences in diving behaviour of individual birds highlights the variability between data sources inherent in this type of study, and emphasises the need for adequate sample sizes when drawing broad conclusions.

INTRODUCTION

Great cormorants *Phalacrocorax carbo* capture their prey underwater and diving represents up to 42% of the total daily energy expenditure (Gremillet *et al.*, 2000). Cormorants take benthic and pelagic species (e.g. Lekuona & Campos, 1997, Gremillet *et al.*, 1998), and their diving behaviour has been related to the type of prey and the conditions under which they are hunting, and may therefore be indicative of the possible impact on the foraging site (e.g. Voslamber *et al.*, 1995). Unlike other diving seabirds and marine mammals, cormorants do not show common adaptations to minimise heat loss, such as the development of a waterproof plumage or the deposition of a thick layer of subcutaneous fat (Gremillet *et al.*, 1999a). The cormorant plumage is wetable, which leads to poor insulation (Gremillet & Wilson, 1999), and consequently loss of body heat is likely to lead to an increase in energetic costs and therefore in predation pressure on fish stocks (Draulans, 1988).

Cooper (1985) summarised cormorant diving patterns, and a number of recent studies have extended knowledge of the diving behaviour of *P. carbo*, covering both freshwater and saltwater sites. Gremillet (1997) studied cormorants breeding on the Chausey Islands, France. Also on the Chausey Islands, Gremillet *et al.*, (1998) timed a total of 5,871 dives in an area with very little variation in bottom depth, and Gremillet *et al.*, (1999b) timed 3,531 dives on 40 foraging trips. Hughes *et al.*, (1999) studied cormorants on freshwater sites in England and Wales throughout the year. Doherty & McCarthy (1997) studied cormorants foraging near a hydroelectric plant on the river Shannon in Ireland and Lariccia (1997) studied wintering cormorants feeding in Italian coastal lagoons and timed 1,559 dives in 91 dive bouts. Kato *et al.*, (1999) studied diving behaviour of *P. albiventer* in the subantarctic and *P. filamentosus* in Japan. Wilson & Wilson (1988) studied solitary diving patterns of four cormorant species in South Africa.

This paper reports on great cormorant diving behaviour on Loch Leven, describing the length and frequency of foraging trips, number of dives, dive duration and surface interval. It considers how these vary between individual birds and change with time, water depth, temperature and foraging technique.

Foraging trips

For breeding birds, Gremillet (1997) reported an average of two feeding trips per adult, per day, each lasting for means of 172 min for males and 184 min for females, with a mean flight time of 11 min. The mean time spent underwater on a single feeding trip was 30 min for males and 44 min for females. As demand for food increased with brood age, adults maintained the same time spent underwater (i.e. actively hunting prey) each trip, but the number of feeding trips per day increased. Hughes *et al.*, (1999) reported that on average, birds spent just 32 minutes per day feeding at Grafham Water in winter, but during a period of cold weather, birds at Rutland Water and Eyebrook Reservoir spent more time feeding, with averages of 104 and 69 minutes per day respectively. Cormorants foraged during one to five discrete dive bouts each day (mode = 2), and each dive bout lasted between 1.6 and 51.4 minutes (mean 15.77 min +/-0.57). Dive bout length varied between sites, particularly in mid-winter, with the longest at Eyebrook/Rutland. At Rutland, the maximum water depth was over 24 m, there was high biomass, and it was postulated that longer dive bouts resulted from birds searching for shoals in deeper water in poor light.

Number of dives per foraging trip

Gremillet *et al.*, (1998) reported a mean of 94 dives per bout +/- 84. Gremillet *et al.*, (1999b) found that birds conducted from 2 to 320, median 42, dives per trip. Hughes *et al.*, (1999) reported 3 to 80 dives per bout, with a mean of 24.7 +/- 0.9, with no effect of age on the number of dives per bout.

Dive duration

For *P.c. carbo* in Scotland, Cooper (1985) reported a mean dive duration of 32.6 s, with a maximum of 71 s, and in Nova Scotia, a mean dive duration of 51 s. Gremillet *et al.*, (1998) reported mean dive duration was 28 s, s.d. +/- 21. For flock fishing, which was assumed to be in pursuit of pelagic prey, dive duration was only 10 s +/- 6, whilst for mixed pelagic and benthic diving trips the mean was 31 s +/- 26. The standard deviations of dive times within a dive bout were relatively wide and there was some evidence of a bimodal distribution deriving from benthic and pelagic dives. Gremillet *et al.*, (1999b) reported individual dives lasting from 16 to 152 s, median 40 s. Hughes *et al.*, (1999) reported that dive duration ranged from 9.2 to 38.2 s, mean 24.2 s +/- 0.3. Doherty & McCarthy (1997) reported dive times of 15 s, s.e. +/- 7 for birds feeding on eels damaged by turbines, 25 s +/- 9 for birds feeding on undamaged eels, and 22 s +/- 12 for unsuccessful dives. Lariccia (1997) reported dive durations from 0.6 to 80 s, with a mean of 18.43 s. Hughes *et al.*, (1999) reported that median dive duration increased as dive bout duration increased, and was relatively constant as the number of dives in the bout increased, except above 50 dives per bout when dive duration declined. Dive duration was higher in the winter than the summer. Median dive duration increased as median surface interval increased, following a logarithmic curve and levelling out.

Surface Interval

For *P.c. carbo* in Scotland, Cooper (1985) reported a mean surface interval of 11.7 s and in Nova Scotia, 13.9 s. Gremillet *et al.*, (1999b) reported a median surface interval of 11 s. Hughes *et al.*, (1999) reported surface intervals from 3.2 to 42 s, with a mean of 11.9 s +/- 0.3. Hughes *et al.*, (1999) reported that the surface interval decreased as the number of dives in the bout increased, but there was no relationship between surface interval and duration of dive bout. Surface interval was longest in mid-winter. Cooper (1985) reported a dive duration: surface interval ratio of 3.67:1.

Diving depth

Gremillet *et al.*, (1999b) reported the median maximum dive depth was 6.1 m, with an overall maximum depth of 32 m. Birds spent from 16 to 88 s descending, median 24 s, and a median of 16 s on the bottom. Sixty-four percent of dives were benthic, and 36% pelagic. For benthic feeding *Phalacrocorax carbo*, Wilson & Wilson (1988) found dive duration (T) was highly significantly positively correlated with water depth (D), with the relationship defined as $T = 4.53D + 10.1$. Gremillet *et al.*, (1999b) reported that dive duration was strongly positively related to maximum dive depth, and individual birds showed clear preferences for distinct depth zones. There was only a weak relationship between surface interval and maximum dive depth, suggesting that the birds do not exceed their aerobic dive limit.

Radio tracking

Radio tracking has been regularly used for determining dive bout and individual dive duration and surface interval, e.g. Gremillet *et al.*, (1998), Gremillet *et al.*, (1999b), Hughes *et al.*, (1999). The possibility of the transmitter affecting a bird's behaviour, although not recognised in some studies (e.g. Guicking *et al.*, 2001), has been subject to investigation. Hughes *et al.*, (1999) found that cormorants fitted with radio tags were foraging in a similar manner to untagged birds, and there was no significant effect on diving behaviour of carrying a radio tag. Siegfried *et al.*, (1977) found no significant effects on the physical condition of African black ducks *Anas sparsa* carrying radio packages, nor on their habitat selection and use, behaviour or ability to escape predators. However, the authors did record increased preening activity, particularly during the period after the transmitter was fitted. Gessaman & Nagy (1988) found that high performance homing pigeons *Columba livia* worked substantially harder and longer during a long distance flight when wearing harnesses and transmitters. Gessaman *et al.*, (1991) found that tippler pigeon (*Columba* spp.) flew for shorter periods and used water faster when wearing harnesses and transmitters. Based on the observations of Hughes *et al.*, (1999), this study assumes no impact of the transmitters on cormorant behaviour, but in the light of other findings, the possibility of unobserved impacts can not be can not be discounted

The aim of this chapter is to describe cormorant diving behaviour at Loch Leven, seeking evidence of temporal and seasonal variation, differences between adults and first-winter birds, and between individual birds, and to compare data from Loch Leven with that from other sites.

METHODS

Nine cormorants were fitted with short-range radio transmitters. They were captured using conventional cannon nets with dimensions of either 18 m X 9 m or 27 m X 14 m, depending on the size and nature of the capture site. The first capture site used was a gravel "spit" on the north side of the largest island, which was exposed during periods of seasonally low water and used as a daytime loafing site by cormorants. The second site was a steep gravel beach on the south side of the large island, which was used as a daytime loafing site when higher water levels covered the offshore gravel bank. A third site used by the cormorants at the westernmost tip of the large island was a flat grass area above a gravel beach where they temporarily retreated during periods of strong west winds. Cannons and nets were set on site a few days before catching in order to give birds time to become accustomed to them. The site was monitored closely by telescope from the loch shore for several days, in order to assess the number of birds and their pattern of loafing behaviour. Once sufficient birds were consistently using the site, the date of the capture attempt was determined.

As the cormorant is a large, long-necked bird, and roosts in a vertical posture, the cannons were set to fire at a high angle in order to avoid injury to them. The cannons were set for the net to reach a height of 1.7 metres at an extension of three metres distance. The net was set 2 metres back from the likely position of the nearest bird, thus allowing a two-metre danger area in front of the net. Whilst this protected the cormorants it had the disadvantage of allowing some birds to escape from the catching area before the net descended on top of them. For example, on 7 October 1997 of 19 birds in the catching area at net firing, 13 were caught, and on 21 December 1997 of 20 birds in the catching area at net firing, 12 were caught.

The capture team was in place before first light on the day of the catch attempt, concealed in camouflaged hides to avoid disturbance. The cannons were fired at an appropriate time when the birds were settled and no new birds were attempting to gain access to the sites, thus avoiding undue movement or repositioning by the birds. Upon firing the capture team ran forward to lift the net clear of the water and extract the birds. Once removed from the net the cormorants were held in hessian sacks whilst awaiting processing. Surplus birds were released onto Loch Leven after ringing and measuring, and the others were released after the radios were fitted.

Nine cormorants were fitted with TW5 short-range radio transmitters, supplied by Biotrack. The transmitters were fitted to lie on the underside of the two central tail feathers to which they were attached with cable ties. Three transmitters were fitted on each of 17 March, 7 October and 21 December 1997. They were tracked manually with a Mariner M57 receiver and Yagi antenna, and all birds were checked for presence or absence at Loch Leven two or more times each day.

The behaviour of individual birds could be deduced from received transmissions, i.e. when roosting, loafing or resting on the water the signal was steady, and when flying it became stronger and steady. When feeding, no signals were received whilst the bird was underwater, so with the aid of a watch, the length of individual dives and the length of the surface interval between dives could be determined, as well as the start and end times of each feeding bout. In 59 days of tracking, a total of 7,388 individual dives were timed during 113 feeding bouts by six birds. Dive times were very strongly normally distributed, but with a small proportion of outliers. The outliers were considered dubious, due to the risk of multiple-dives, i.e. where the bird had surfaced briefly, and unnoticed, between dives. Accordingly, 37 records lying outside three standard deviations of the individual bird mean dive durations were disregarded. They comprised 0.5% of total dives recorded. In addition, 7,034 surface intervals between consecutive dives were recorded, and were also found to be strongly normally distributed, but with a small proportion of outliers. The outliers were considered dubious, as on occasions a bird was observed to spend time on other surface activities, such as handling and swallowing fish or swimming forward to the front of a feeding flock. Accordingly, 177 records lying outside three standard deviations of the individual bird mean surface intervals were disregarded. They comprised 2.5% of total surface intervals recorded.

The position of the bird was determined through reference to clearly identifiable prominent points on the loch shore and islands. Where there was an extensive area of open water, marker buoys were laid to provide additional reference points, and their positions were identified using a hand-held GPS set. The observer was mobile, and was thus able to move to alternative observation points as a bird moved towards the limits of accurate position plotting. For plotting purposes, the loch was divided into 250 x 250 m grid squares and data on water depths within each square was extracted from the bathymetric survey map of Loch Leven prepared by the Department of Geography, University of Edinburgh, in March 1971. Dry-bulb air temperature data were provided by the Meteorological Office recording station at Loch Leven.

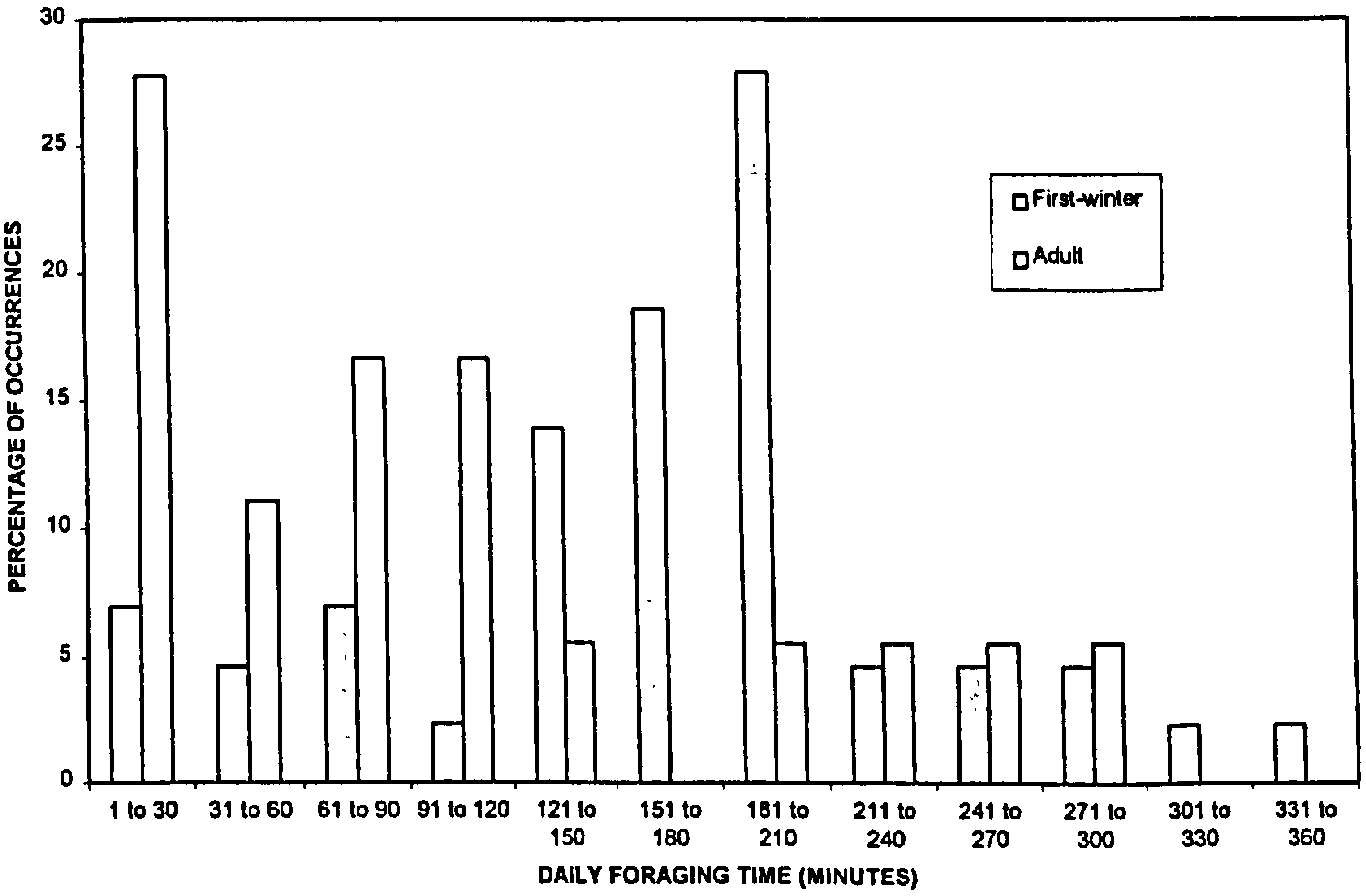
RESULTS

Foraging trips

Cormorants wintering on Loch Leven conducted from one to five foraging trips per day. Adults conducted an average of 1.47 trips per day whilst first-winter birds averaged 1.92, and this difference is significant ($z = 3.011$, $p = 0.001$). Foraging trips lasted from 2 min to 395 min, but one-way ANOVA shows that differences between individuals are not statistically significant.

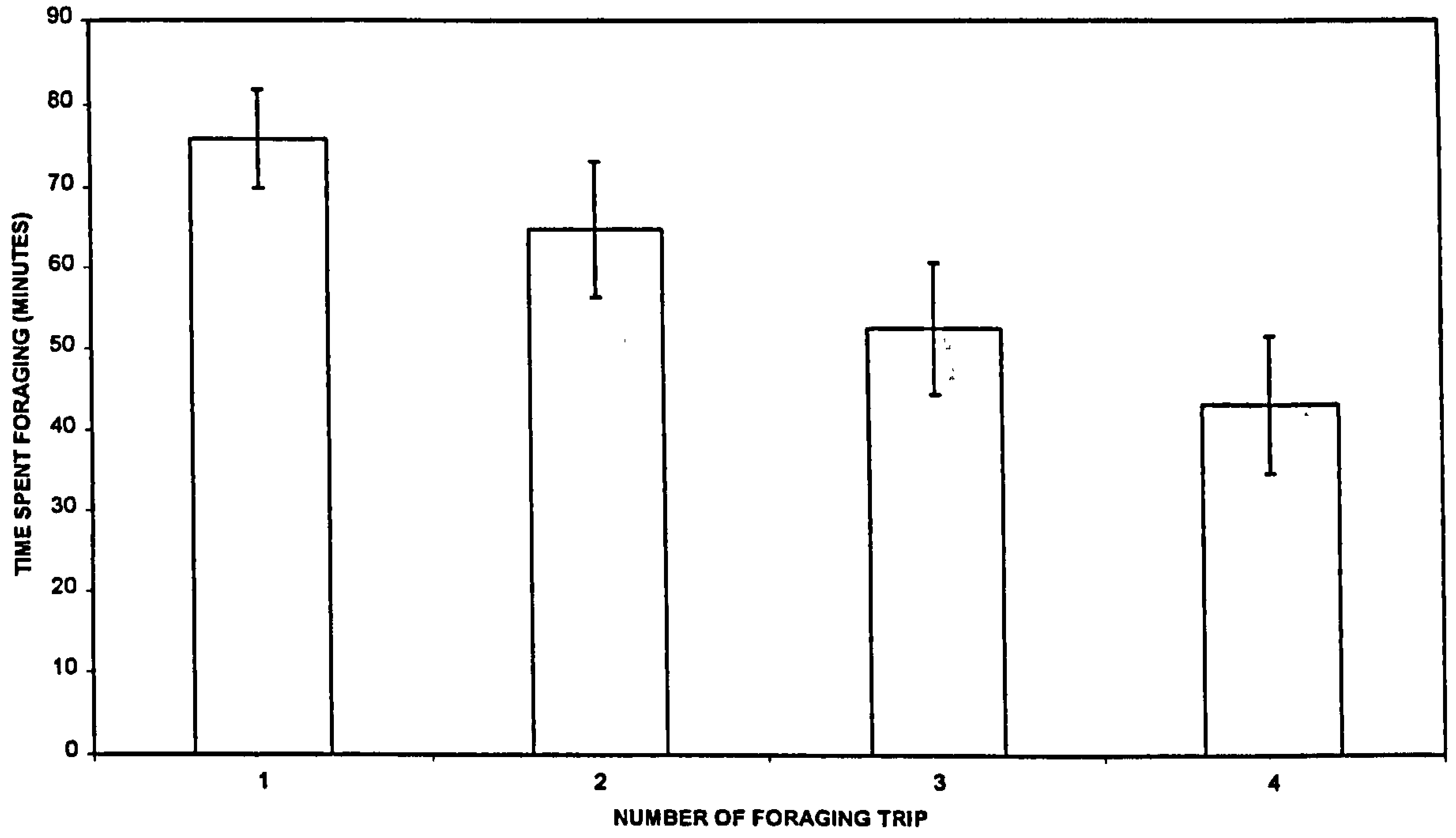
Not all the time on the water was spent actively foraging, and diving sequences lasted from 2 min to 300 min per trip, with adults spending less time diving per trip (mean 59 min, median 57 min) compared to first-winter birds (mean 70 min, median 61 min) but this difference is not significant. In total, diving lasted for between 4 min and 5 h 38 min per day (Fig.1), with adults diving for much less time (mean 98 min, median 68 min) compared to first-winter birds (mean 165 min, median 175 min), and this difference is significant ($z = 2.983, p = 0.001$).

FIGURE 1: VARIATION IN DAILY FORAGING TIME - FIRST-WINTER BIRDS AND ADULTS



On most days, birds conducted more than one foraging trip, and the time spent foraging decreased with the number of trips, as illustrated in Fig 2. However, one-way ANOVA shows that these differences are not statistically significant.

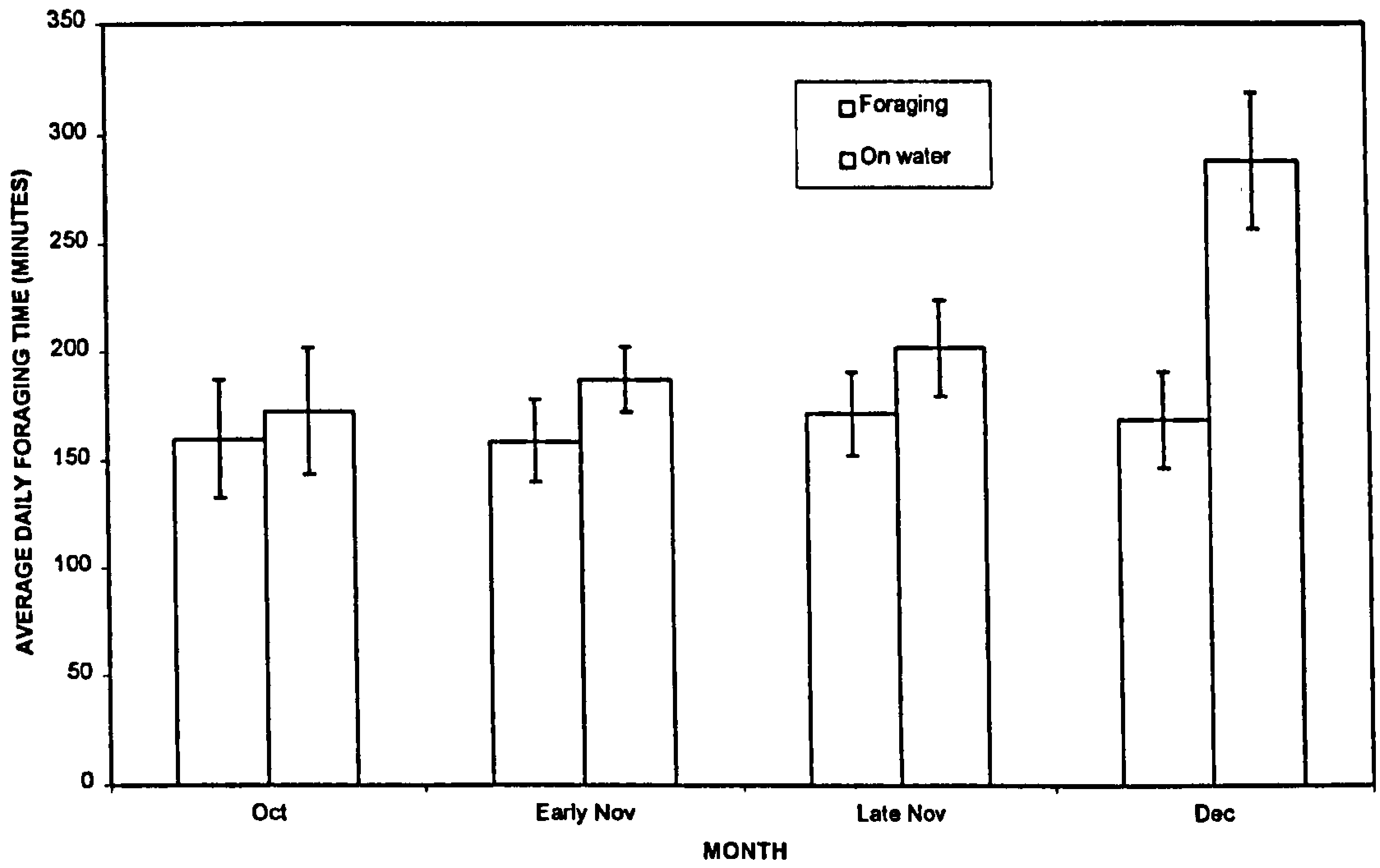
FIGURE 2: VARIATION IN TIME SPENT FORAGING PER TRIP WITH INCREASING NUMBER OF TRIPS - WITH STANDARD ERROR BARS



Regression analysis showed no significant effect of daily dry-bulb air temperature on time spent foraging.

Whilst there is little variation in the total daily time spent foraging from October to December, the time spent on the water shows an increase (Fig. 3). Following $\log_{10}+1$ transformation, a one-way ANOVA test was conducted on time spent on the water but not foraging during October, early and late November, and December by first-winter birds. The results were significant ($F_{3,39} = 8.74$, $p < 0.001$). Tukey test showed that differences between December and all three other periods were significant ($p = 0.002$).

FIGURE 3: VARIATION IN DAILY TIME FORAGING AND TIME ON WATER - OCTOBER TO DECEMBER - FIRST WINTER BIRDS, WITH STANDARD ERROR BARS



Birds loafed and roosted on site and spent relatively little time in flight, with a daily mean of 6 min and a range of between 3 min and 14 min per day.

Number of dives per foraging trip and per day

Cormorants on Loch Leven conducted a mean of 116, median 105, dives per foraging trip, with a range from 3 to 509. The numbers of dives per trip were normally distributed for individual birds. One-way ANOVA showed that differences between individual birds are not significant. The number of dives per trip decreased as the number of trips increased, from a mean of 126 on the first trip to 71 on the fourth (n = 59, 39, 14 & 5 respectively), but one-way ANOVA showed that these differences are not significant. The total number of dives per day by an individual bird ranged from 8 to 529, mean 226, median 226, and one-way ANOVA showed that differences between individual birds are significant ($F_{3,58} = 3.01$, p = **0.038**). Tukey test showed that differences between one adult (8.2) and one first-winter bird (9.1) were significant (p = **0.050**).

Dive duration for individual birds

Dive duration distributions for four birds with the largest data sets are illustrated in Table 1 and Figs 4 to 7. One-way ANOVA showed that differences between individual birds are significant ($F_{3,7629}$ = 10.29, $p < 0.001$). Tukey test showed that differences between an adult (5.7) and a first-winter bird (6.7) were significant (p = **0.039**), and differences between two first-winter birds (6.7 & 9.1) were significant (p < **0.001**)

TABLE 1: SUMMARY DIVE DURATION DATA FOR FOUR CORMORANTS

Radio No.	Age	Median Dive (s)	Mean Dive (s)	95% Conf.
5.7	Ad	25	24.3	0.73
8.2	Ad	27	26.2	0.69
6.7	1W	27	26.8	0.33
9.1	1W	26	25.7	0.22

FIGURE 4: DIVE DURATION DISTRIBUTION - CORMORANT 5.7 (ADULT)

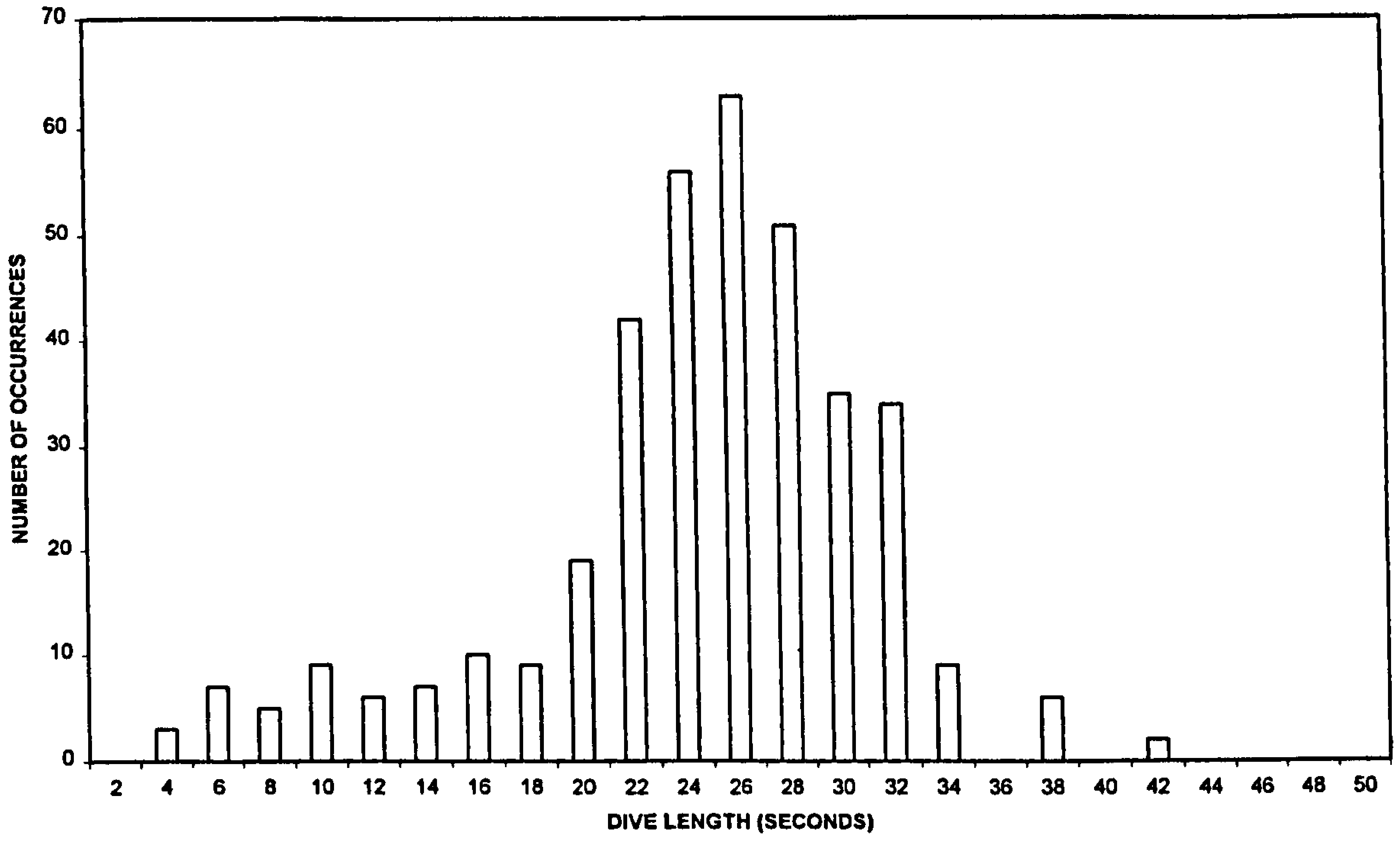


FIGURE 5: DIVE DURATION DISTRIBUTION - CORMORANT 8.2 (ADULT)

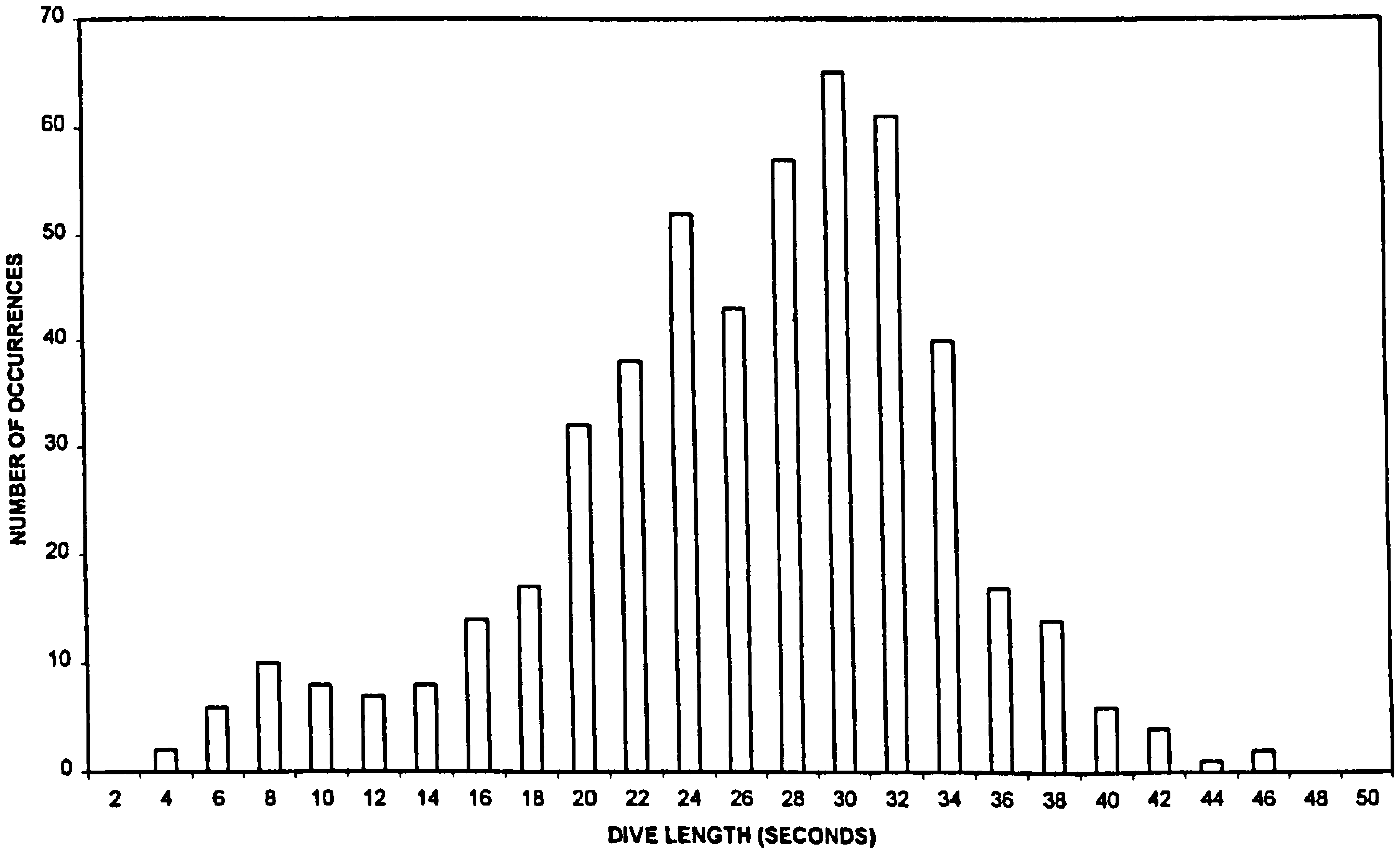


FIGURE 6: DIVE DURATION DISTRIBUTION - CORMORANT 6.7 (FIRST-WINTER)

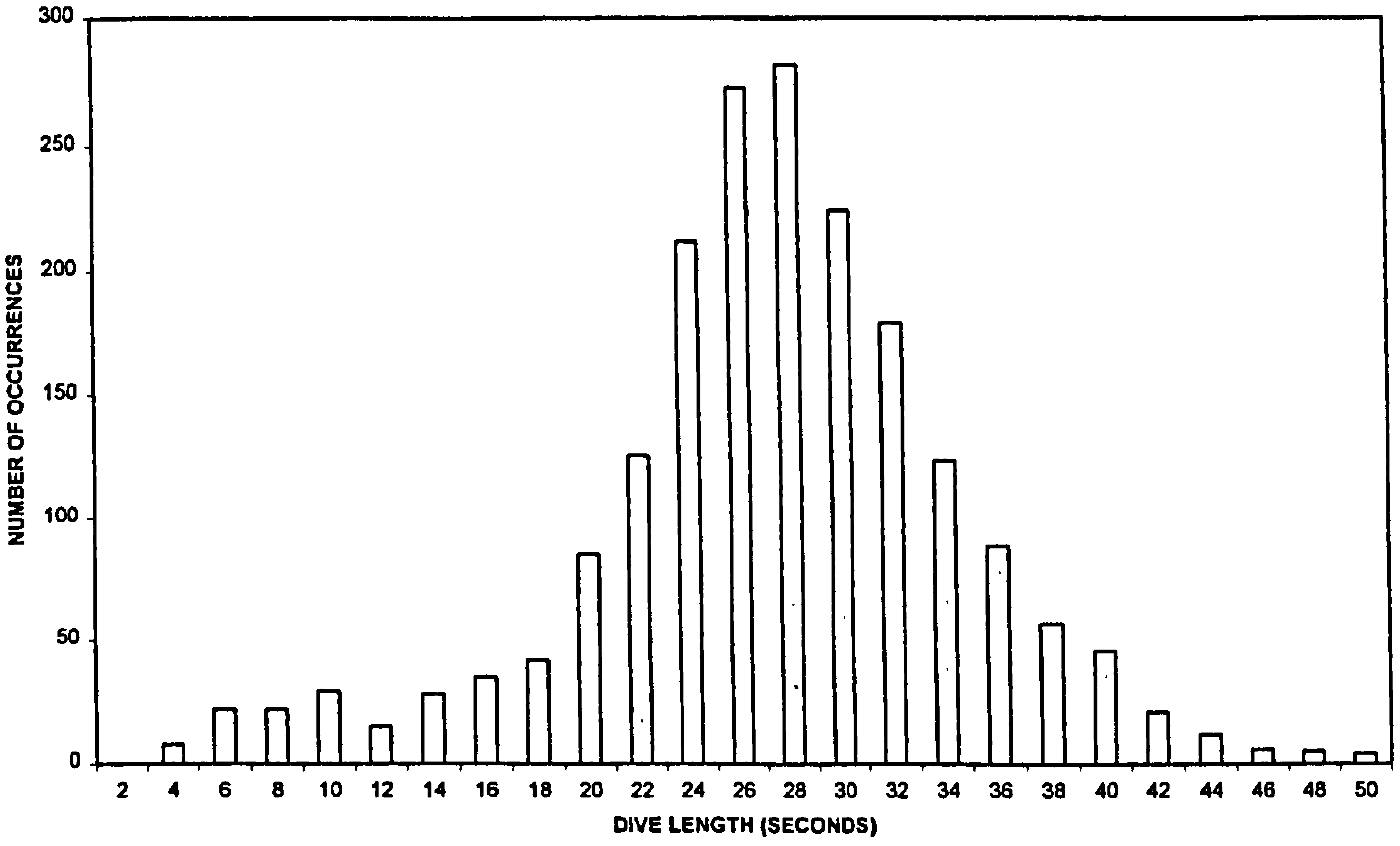
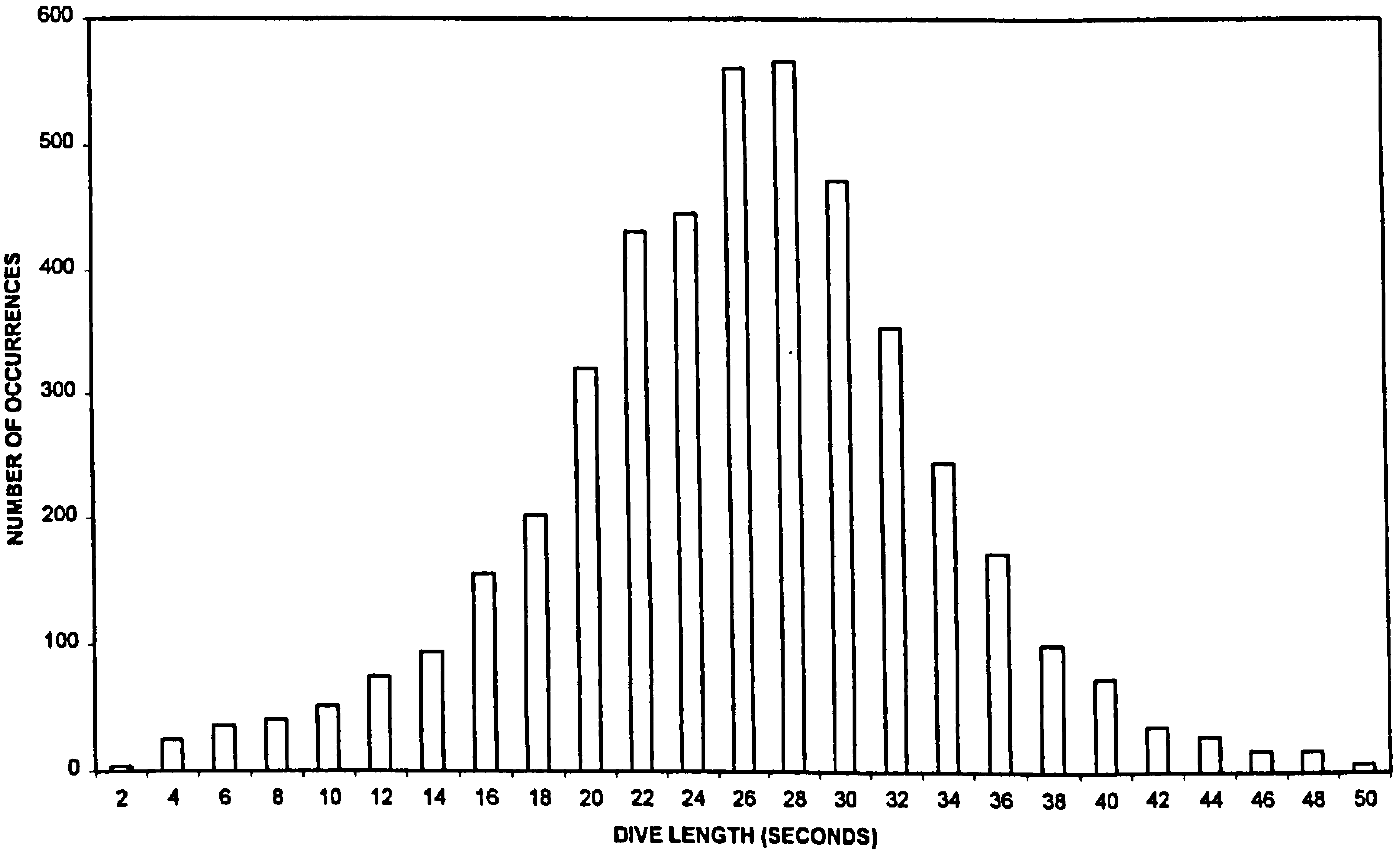


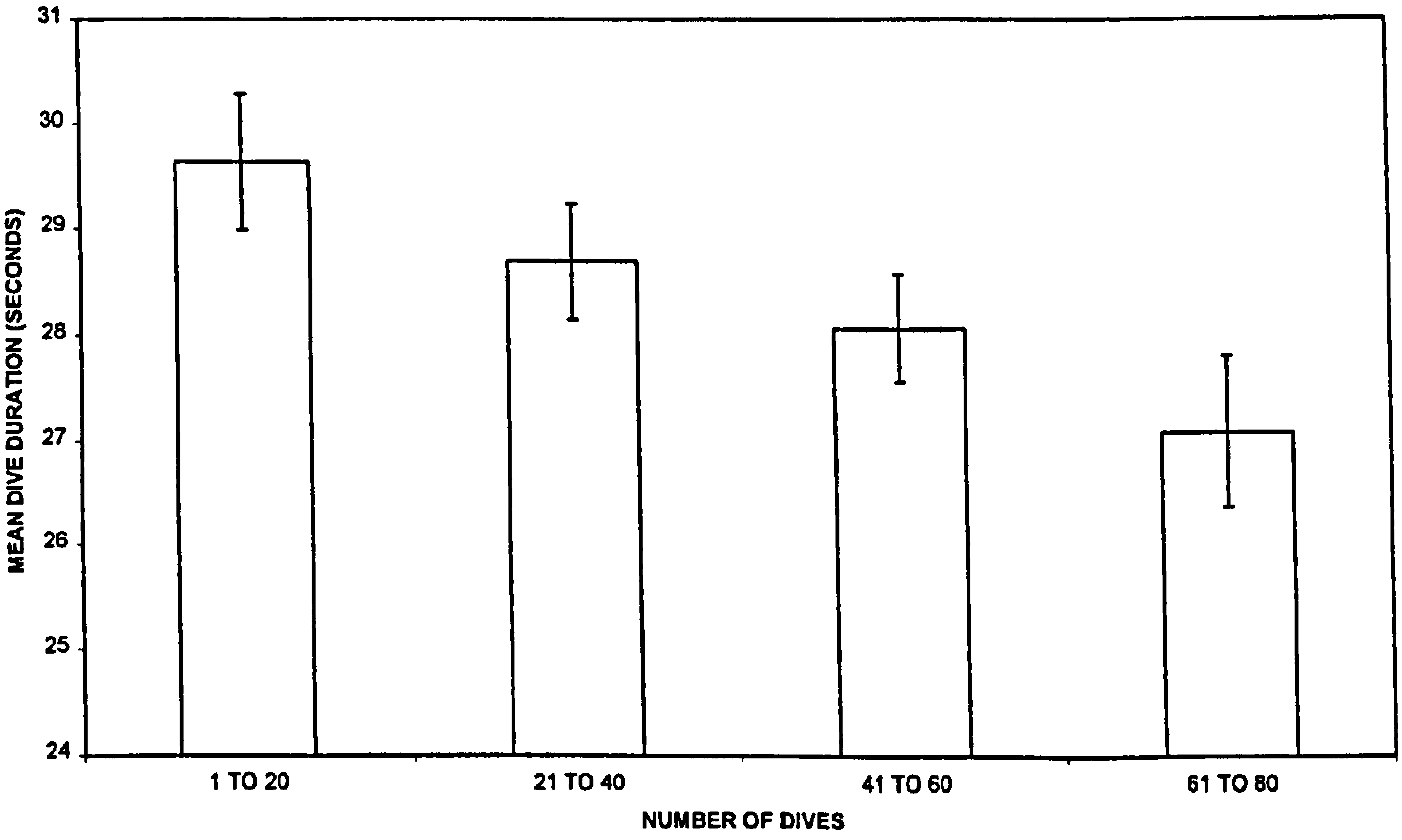
FIGURE 7: DIVE DURATION DISTRIBUTION - CORMORANT 9.1 (FIRST-WINTER)



Variation in dive duration during extended diving sequences

Data from extended diving sequences (up to 80 dives) were divided into four sets (dive numbers 1 to 20, 21 to 40, 41 to 60 & 61 to 80), and means were calculated for each set. The apparent decrease in dive duration during such extended diving sequences is illustrated in Fig. 8. One-way ANOVA showed that differences are significant ($F_{3,445} = 2.941$, $p = 0.033$). Tukey test showed that only the differences between the duration of the first set of 20 dives were significantly longer than the fourth set of twenty dives ($p = 0.023$).

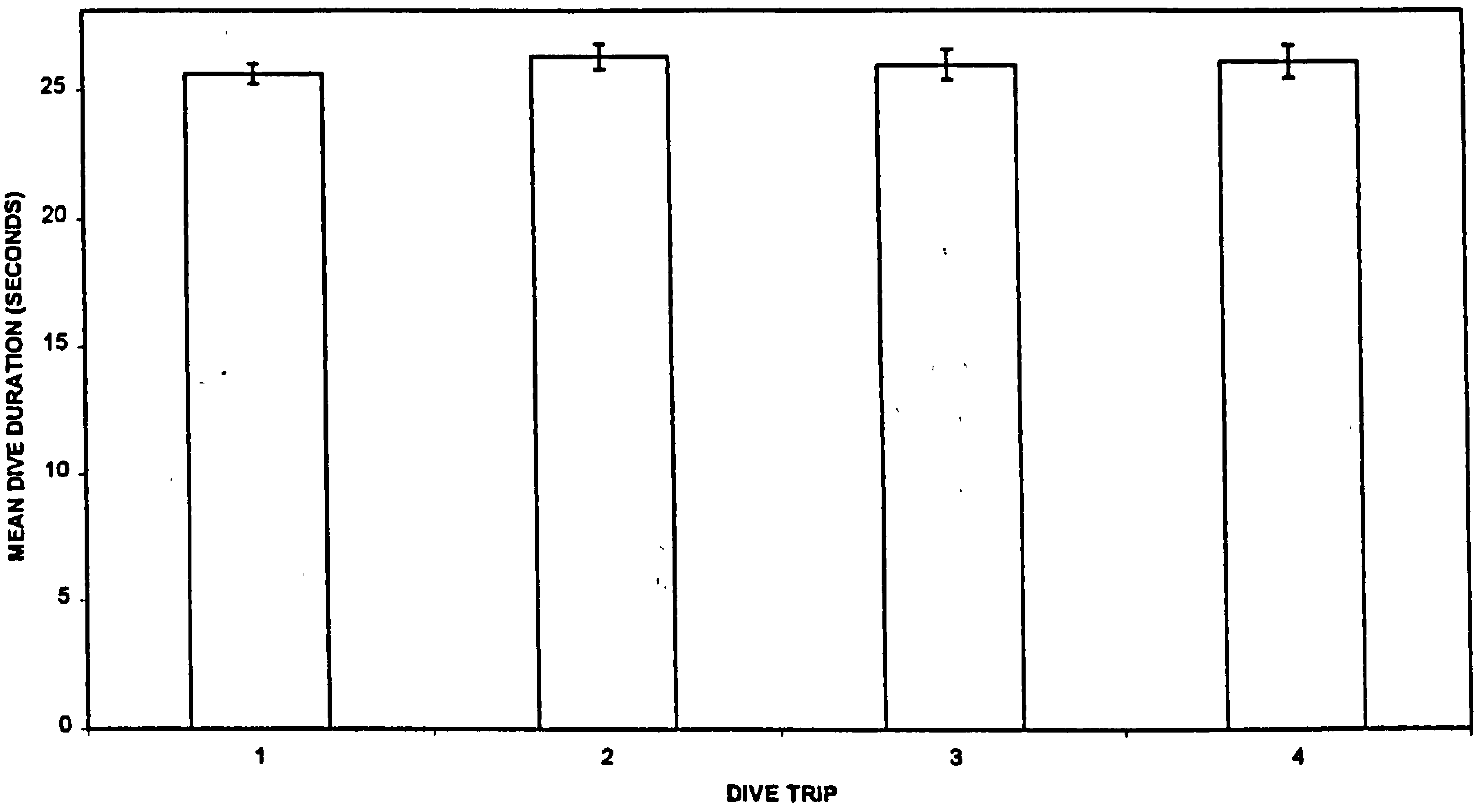
FIGURE 8: DECREASE IN DIVE DURATION OVER LONG DIVING SEQUENCES, WITH STANDARD ERROR BARS



Variation in dive duration with increasing number of dive trips

Using data for Cormorant 9.1, Fig 9 shows no reduction in dive duration with increasing number of dive trips. One-way ANOVA showed that differences between trips are not significant.

FIGURE 9: VARIATION IN MEAN DIVE DURATION WITH INCREASING NUMBER OF DIVE TRIPS, WITH STANDARD ERROR BARS - 200 RANDOMLY SELECTED DIVES FROM EACH SET OF TRIPS - CORMORANT 9.1



Variation in dive duration during the winter

A decline in dive duration during the winter is illustrated in Fig. 10 for the bird with the largest data set, Cormorant 9.1. One-way ANOVA showed that differences between periods are significant ($F_{5,4535} = 13.64$, $p < 0.001$). Tukey test showed that differences between late October and all other periods apart from mid November, are significant ($p <$ or $= 0.001$), and the difference between early and late November is also significant ($p = 0.006$). However, a different pattern was evident in the diving behaviour of Cormorant 6.7, as illustrated in Fig. 11. One-way ANOVA showed that differences between periods are significant ($F_{3,1900} = 26.77$, $p < 0.001$). Tukey test showed that differences between mid October and both early and late November were significant ($p < 0.001$), as were differences between late October and both early and late November ($p < 0.001$). Later in the winter Cormorant 8.2 showed some apparent variation in dive duration (Fig. 12), but the differences between periods are not significant.

FIGURE 10: VARIATION IN DIVE DURATION OF CORMORANT 9.1 FROM LATE OCTOBER TO MID DECEMBER, WITH STANDARD ERROR BARS

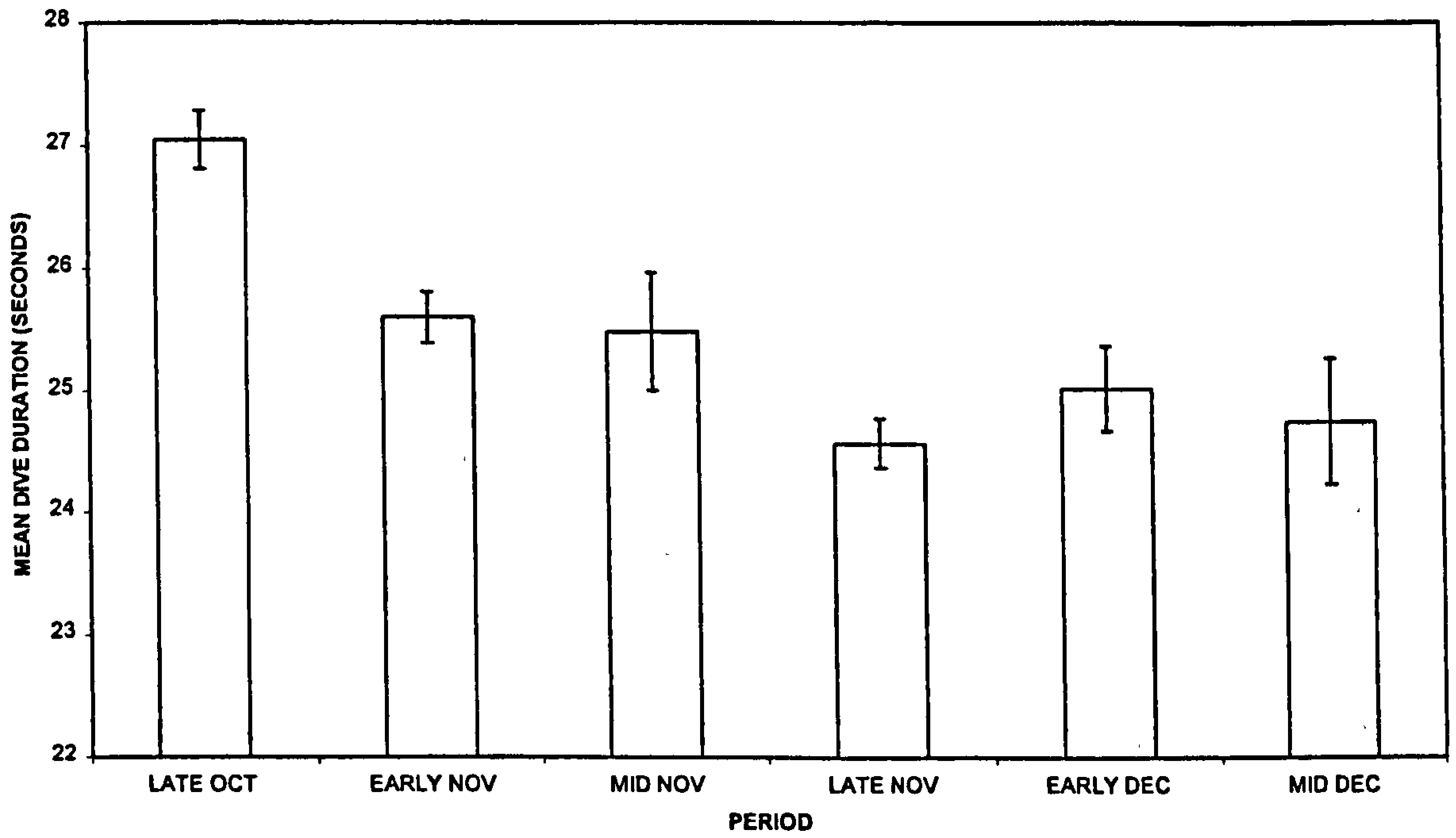


FIGURE 11: VARIATION IN DIVE DURATION OF CORMORANT 6.7 FROM MID OCTOBER TO MID NOVEMBER, WITH STANDARD ERROR BARS

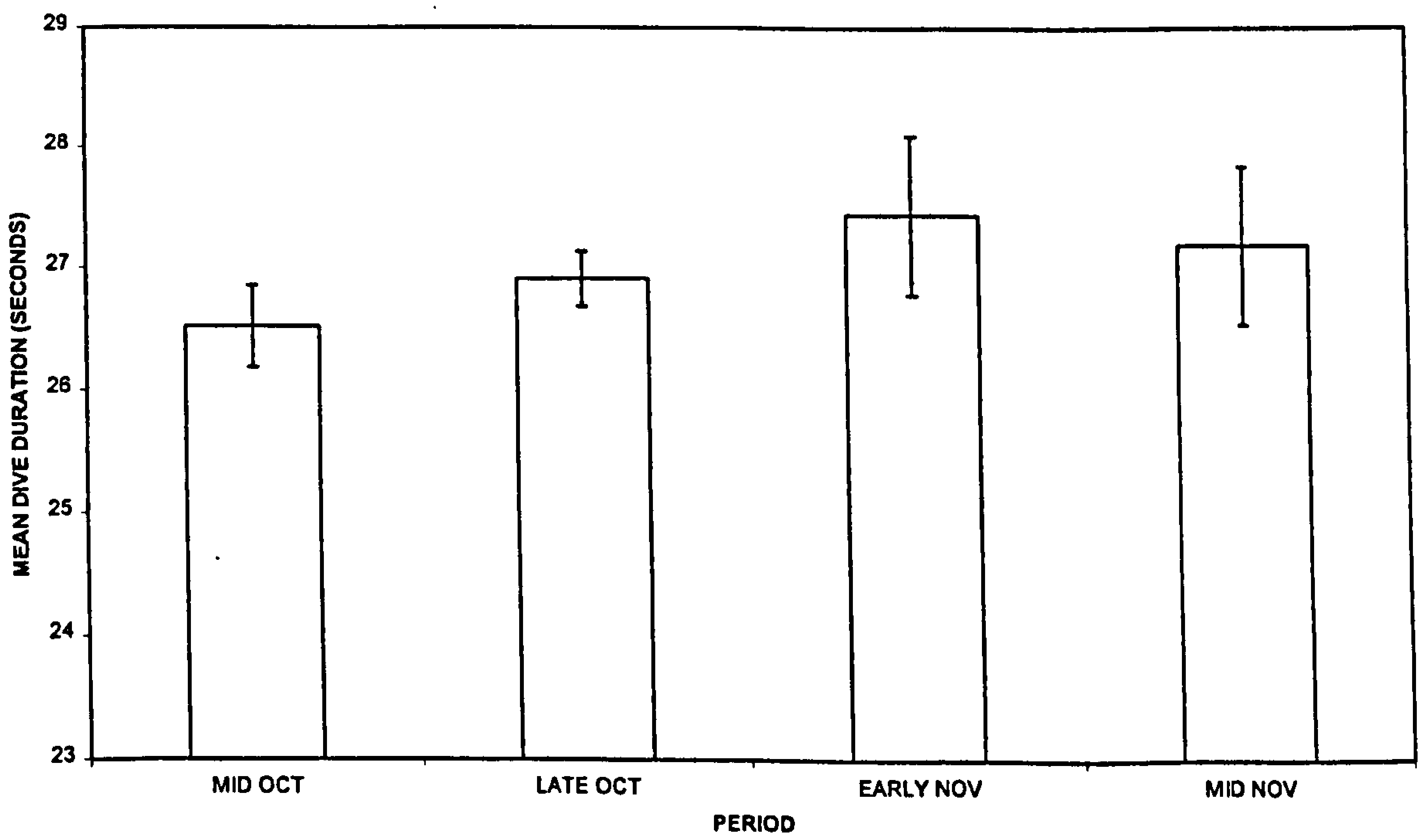
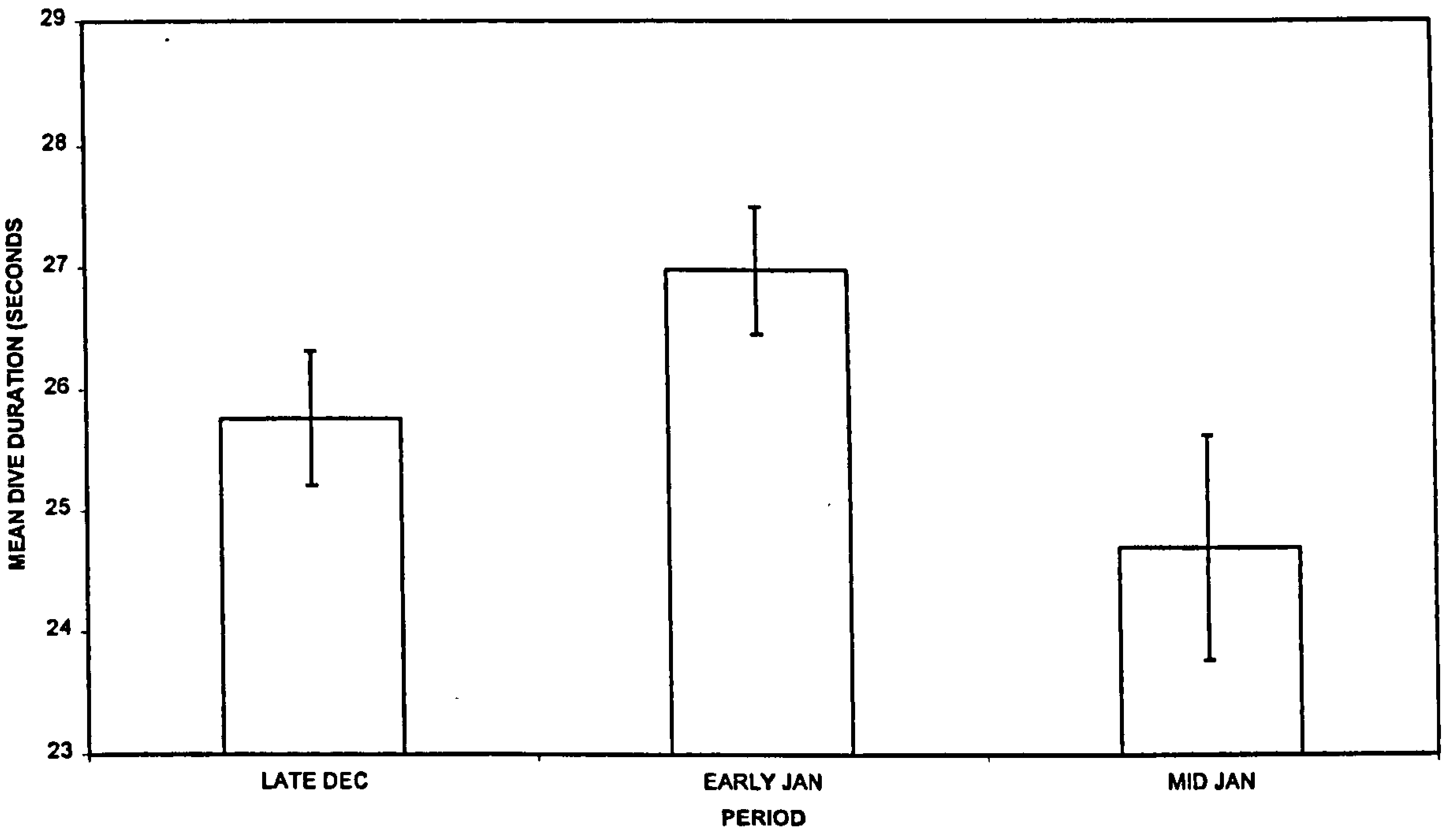


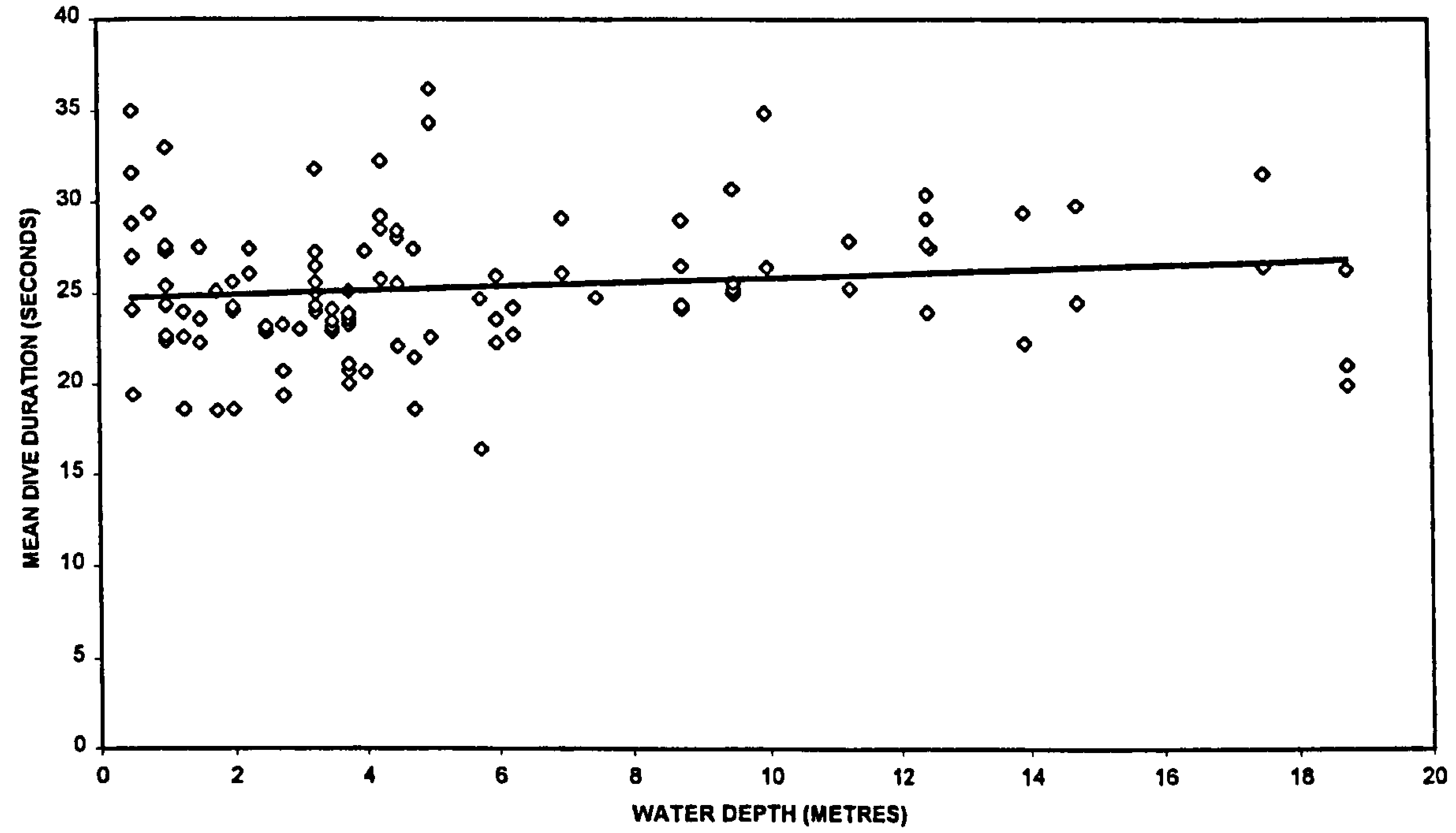
FIGURE 12: VARIATION IN DIVE DURATION FOR CORMORANT 8.2 FROM LATE DECEMBER TO MID JANUARY, WITH STANDARD ERROR BARS



Variation in dive duration with water depth

A line fit plot for water depth and mean dive duration for Cormorant 9.1 is illustrated in Fig. 13. The same pattern of a very slight apparent increase in dive duration with water depth was also evident for Cormorant 6.7, with a more pronounced increase for Cormorant 5.7 (Fig. 16), and a very slight decrease for Cormorant 8.2 (Fig. 17). However, regression analysis indicates that none of these relationships are significant, and dive duration does not appear to vary with water depth.

FIGURE 13: LINE FIT PLOT OF WATER DEPTH AND MEAN DIVE DURATION - CORMORANT 9.1



Variation in dive duration between solitary and flock feeding

Sufficient dives were recorded for Cormorant 6.7 to enable a comparison between solitary and flock-feeding dives for an individual bird. Comparison of 291 solitary dives and 1,952 flock-feeding dives produced mean dive durations of 27.70 s (SE 0.43) and 26.85 s (SE 0.17) respectively, but the difference is not significant.

Variation in dive duration between birds foraging together

On six occasions, Cormorants 9.1 and 6.7 were observed to be foraging in the same flock, and groups of ten dive times were recorded alternately. Mean dive times were 25.45 s (SE 0.38) and 26.63 s (SE 0.35) respectively, and a two-tailed "*z*" test showed the difference is significant ($z = 2.236, p = \mathbf{0.026}$). On two occasions, Cormorants 8.2 and 5.7 were observed to be foraging in the same flock, and groups of ten dive times were recorded alternately. Mean dive times were 24.71 s (SE 0.53) and 22.78 s (SE 0.64) respectively, and a two-tailed "*z*" test showed the difference is significant (z = 2.330, $p = 0.019$). The differences within these pairs are comparable with differences illustrated in Table 1 for all dives, but the difference between Cormorants 5.7 and 8.2 was not then significant.

Surface Interval

Surface interval summary data for four birds with the largest data sets are presented in Table 2, and distributions are illustrated in Figs 14 to 17.

TABLE 2: SUMMARY SURFACE INTERVAL DATA FOR FOUR CORMORANTS

Radio No.	Age	Median SI (s)	Mean SI (s)	95% Conf.
5.7	Ad	9	9.35	0.37
8.2	Ad	7	7.85	0.29
6.7	1W	8	8.14	0.14
9.1	1W	6	6.79	0.08

One-way ANOVA showed that differences between individual birds are significant ($F_{3,7252} = 83.55$, $p < 0.001$). Tukey test showed that differences between all individuals, except that between Cormorants 8.2 and 6.7, are significant ($p < 0.001$).

FIGURE 14: SURFACE INTERVAL DISTRIBUTION - CORMORANT 5.7 (ADULT)

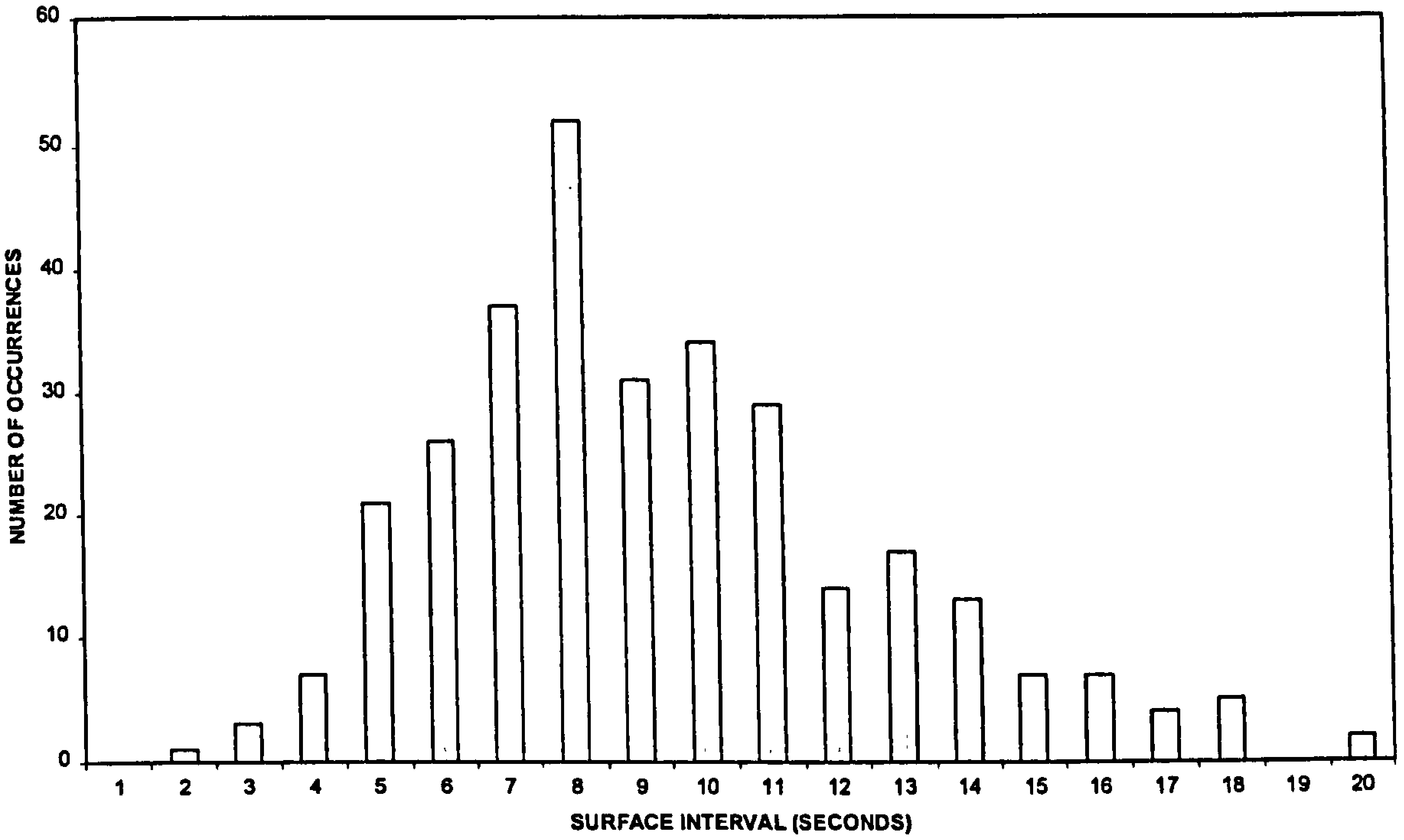


FIGURE 15: SURFACE INTERVAL DISTRIBUTION - CORMORANT 8.2 (ADULT)

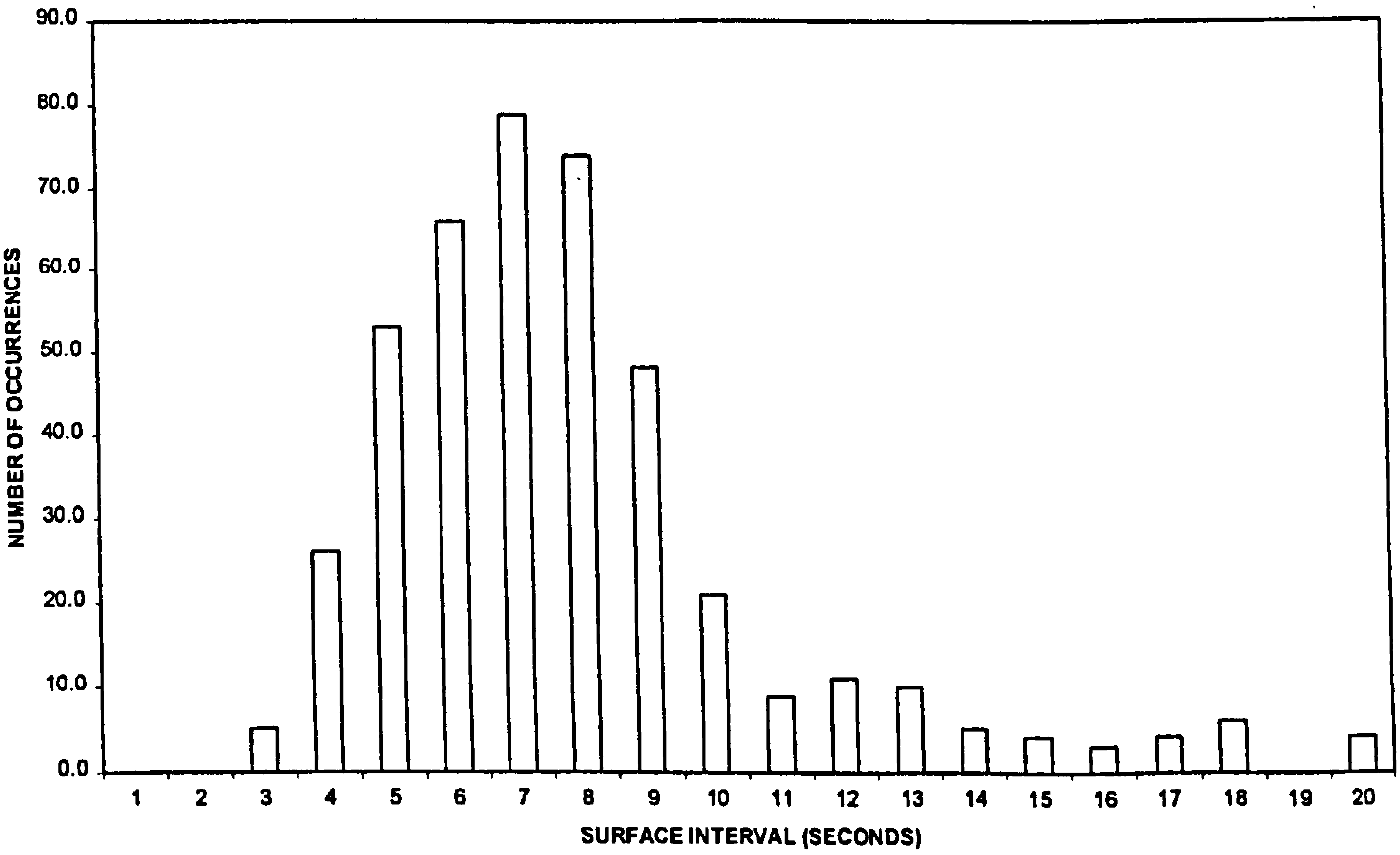


FIGURE 16: SURFACE INTERVAL DISTRIBUTION - CORMORANT 6.7 (FIRST-WINTER)

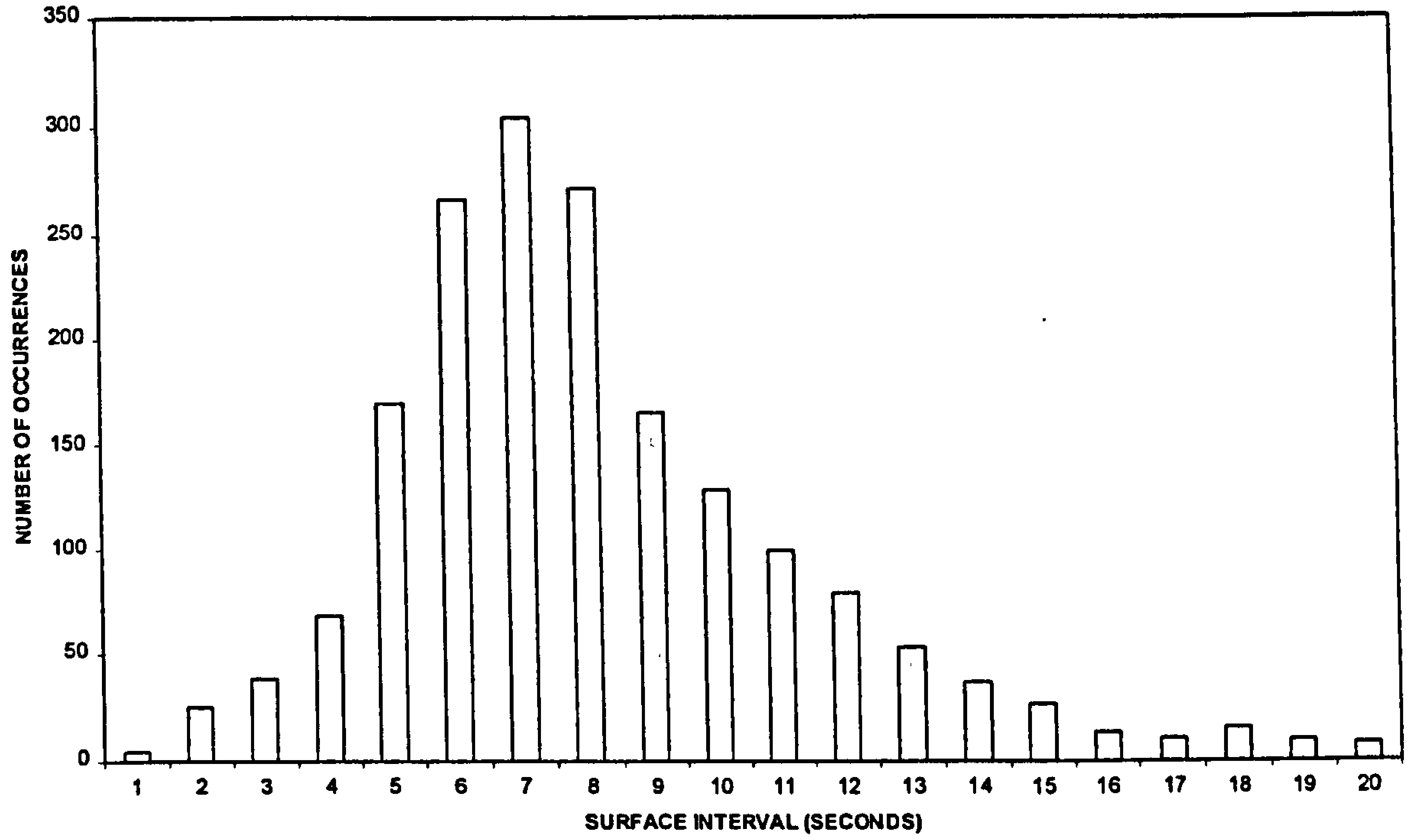
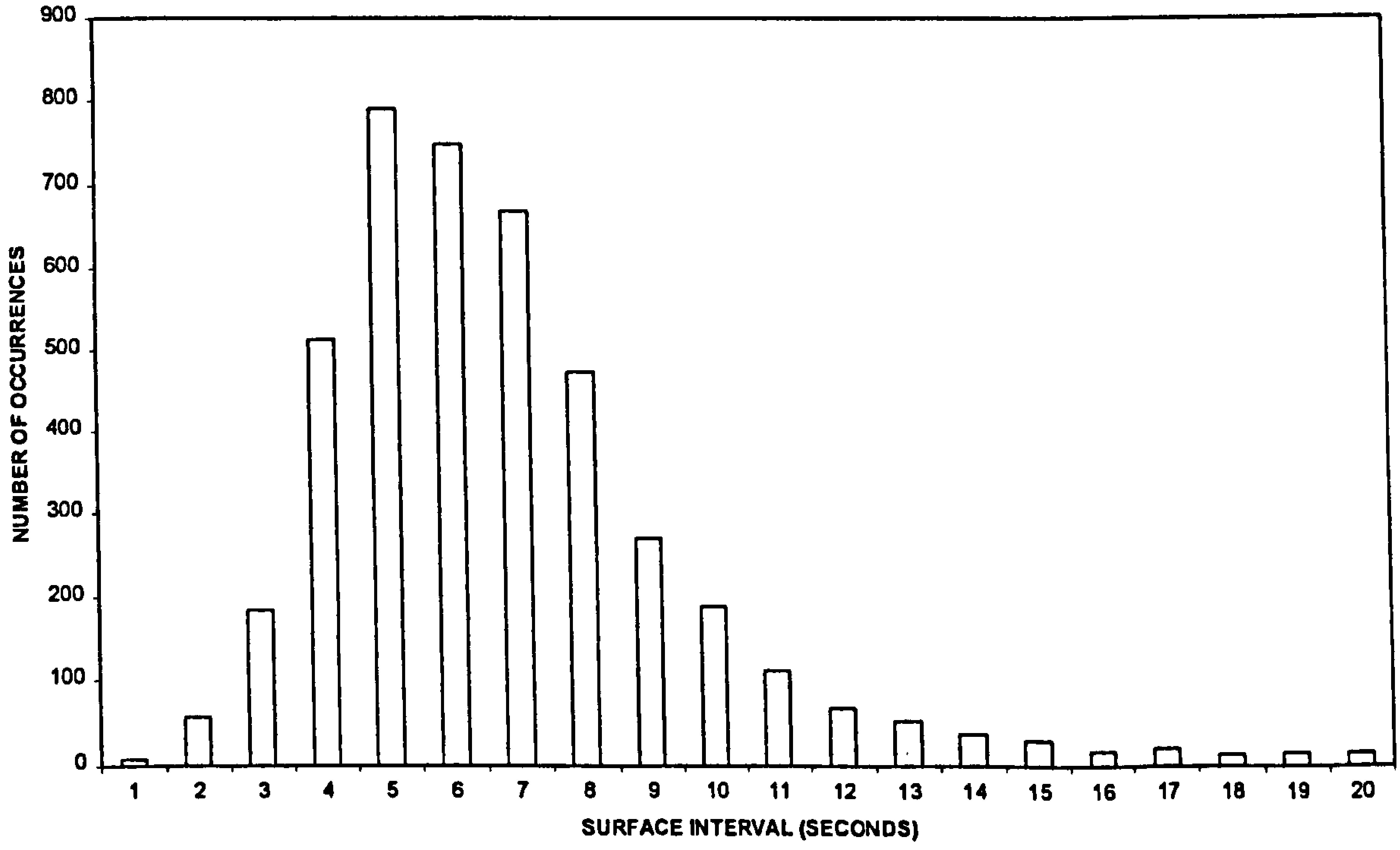


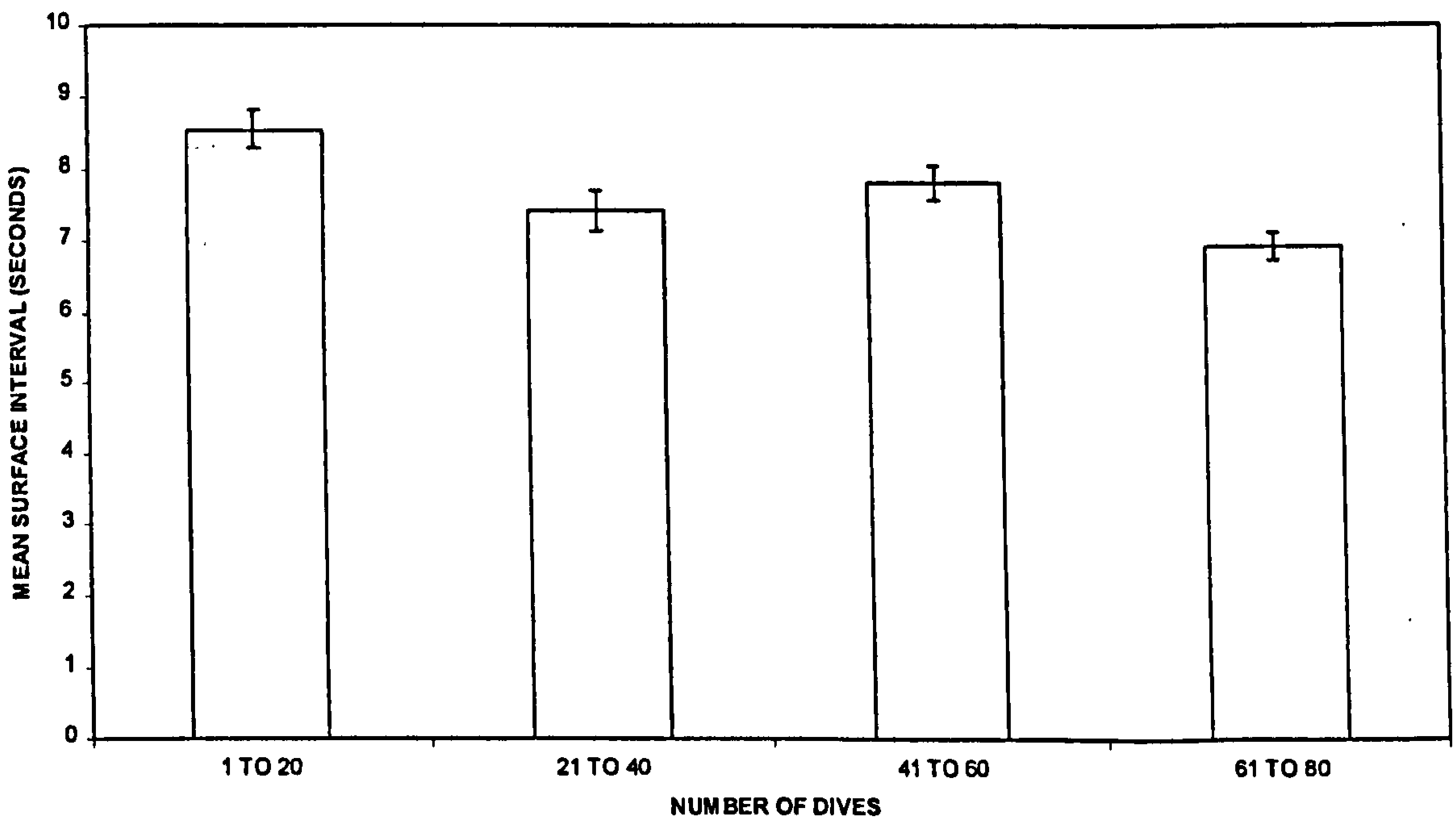
FIGURE 17: SURFACE INTERVAL DISTRIBUTION - CORMORANT 9.1 (FIRST-WINTER)



Variation in surface interval during extended diving sequences

Surface interval data from extended diving sequences (up to 80 dives) were divided into four sets (following dive numbers 1 to 20, 21 to 40, 41 to 60 & 61 to 80), and means were calculated for each set. The apparent changes in surface interval during such extended diving sequences are illustrated in Fig. 18. One-way ANOVA showed that differences are significant ($F_{3,452} = 7.26$, $p < 0.001$). Tukey test showed that the difference between surface intervals following the first set of 20 dives and the second twenty dives is significant ($p = 0.007$), as is that between the first and the fourth set of twenty dives ($p < 0.001$).

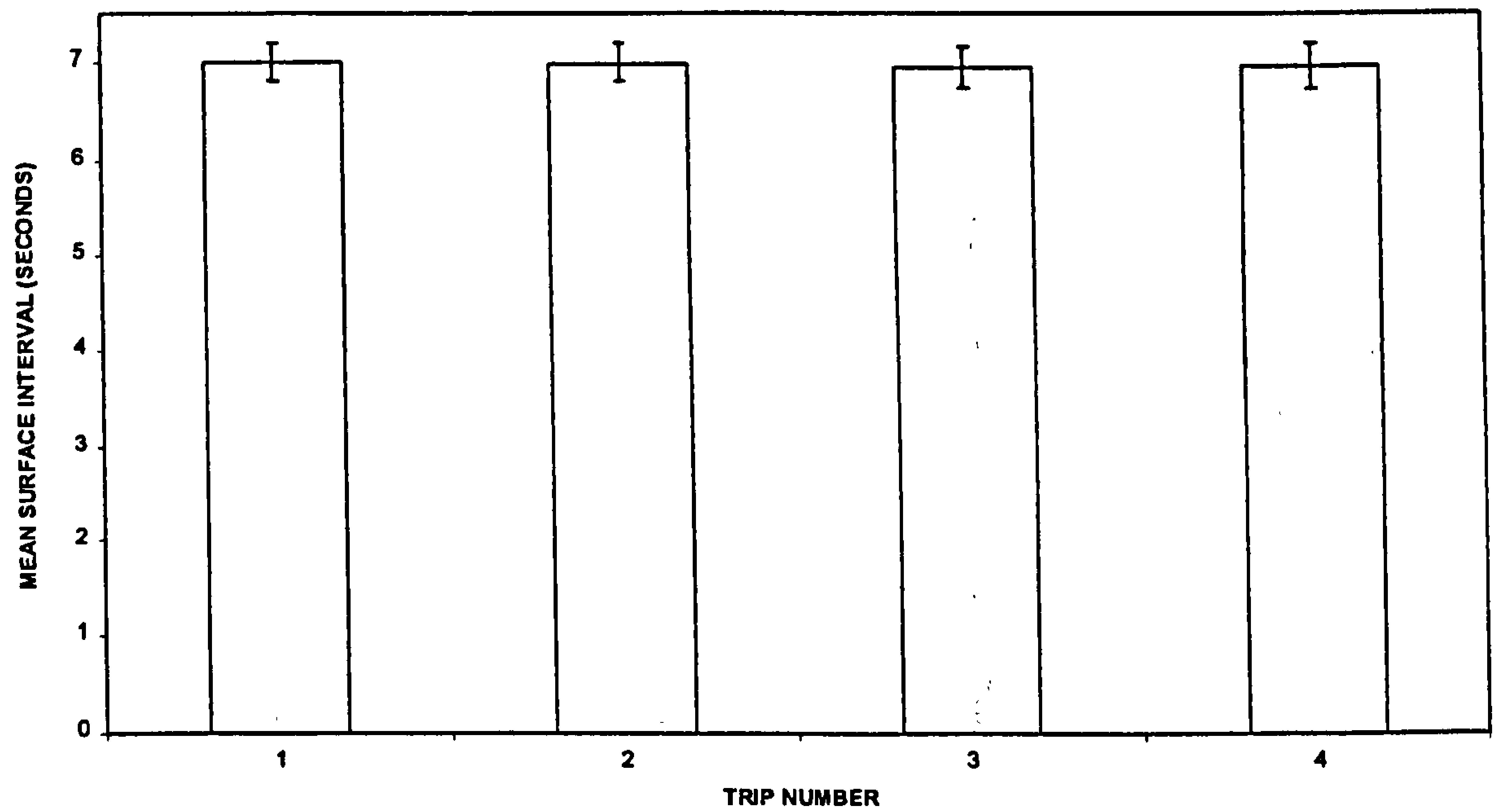
FIGURE 18: CHANGE IN SURFACE INTERVAL OVER LONG DIVING SEQUENCES, WITH STANDARD ERROR BARS



Variation in surface interval with increasing number of dive trips

Using data for Cormorant 9.1, Fig. 19 shows no variation in surface interval with an increasing number of dive trips. None of the differences between trips are significant.

FIGURE 19: VARIATION IN MEAN SURFACE INTERVAL WITH INCREASING NUMBER OF DIVE TRIPS, WITH STANDARD ERROR BARS - 200 RANDOMLY SELECTED DIVES FROM EACH SET OF TRIPS - CORMORANT 9.1



Variation in surface interval during the winter

Changes in surface interval during the winter are illustrated in Fig. 20 for Cormorant 9.1. One-way ANOVA showed that differences between periods are significant ($F_{5,4347} = 5.03$, $p < 0.001$). Tukey test showed that differences between late October and all other periods except mid December, were significant (p = **0.002, 0.033, < 0.001, 0.025** respectively).

Data for Cormorant 6.7, are illustrated in Fig. 21. One-way ANOVA showed that differences between periods are significant ($F_{3,1871} = 16.70$, $p < 0.001$). Tukey test showed that the difference between mid October and late November is significant (p = **0.001**), as are the differences between late October and both early and late November (p < **0.001**). Later in the winter Cormorant 8.2 showed some variation in surface interval (Fig. 22), but the differences are not significant.

FIGURE 20: VARIATION IN SURFACE INTERVAL OF CORMORANT 9.1 FROM LATE OCTOBER TO MID DECEMBER, WITH STANDARD ERROR BARS

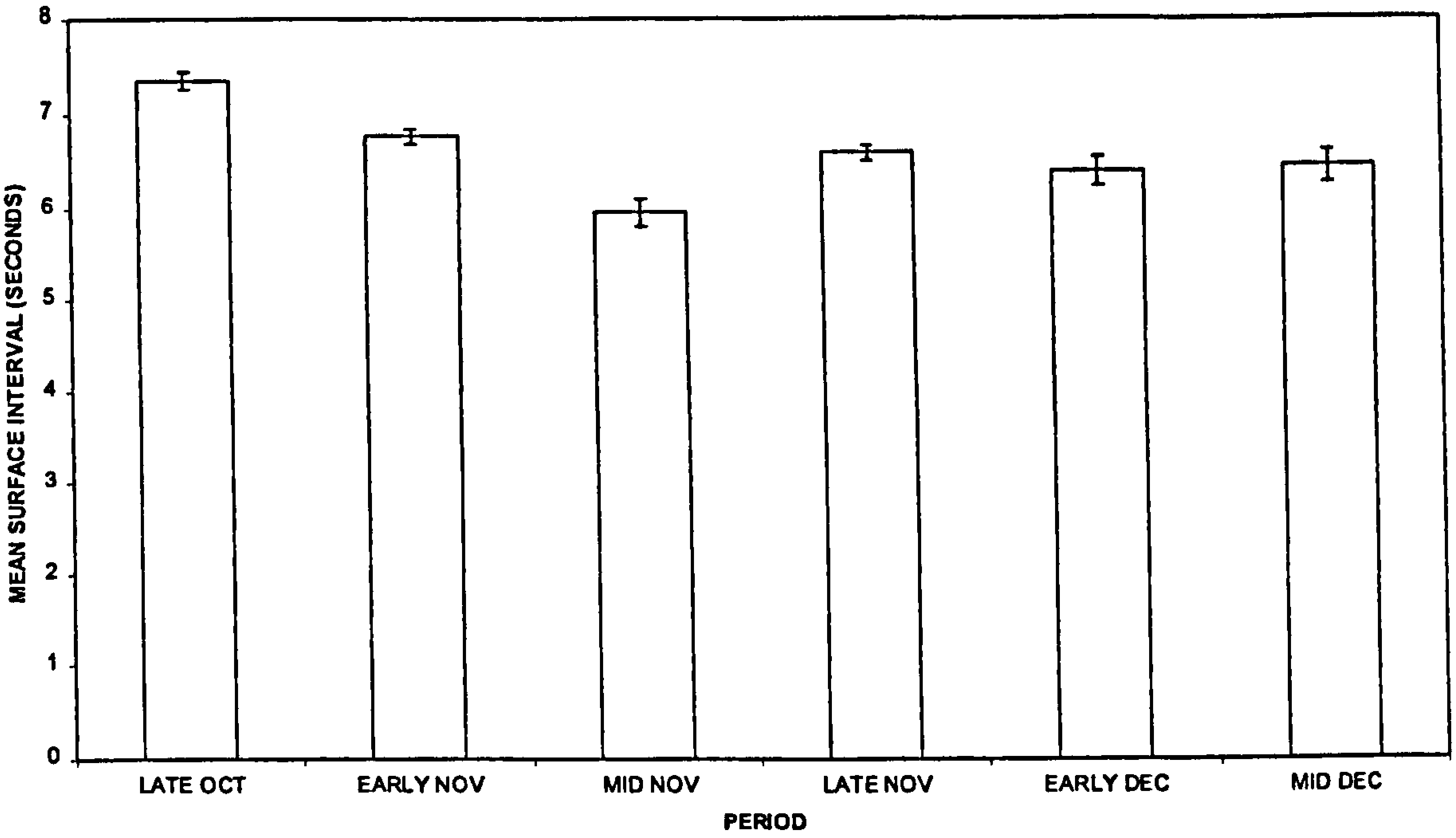


FIGURE 21: VARIATION IN SURFACE INTERVAL OF CORMORANT 6.7 FROM MID OCTOBER TO MID NOVEMBER, WITH STANDARD ERROR BARS

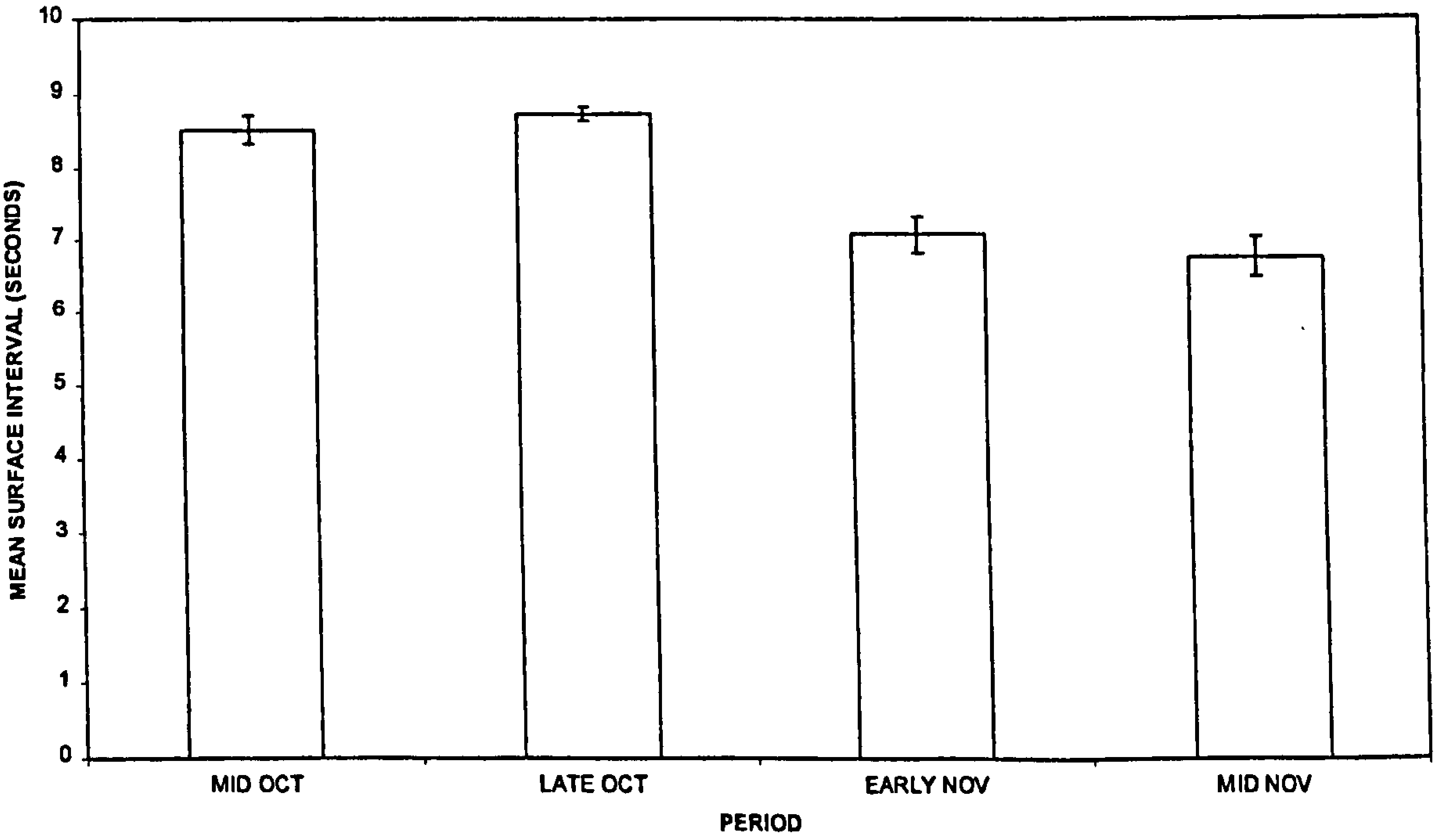
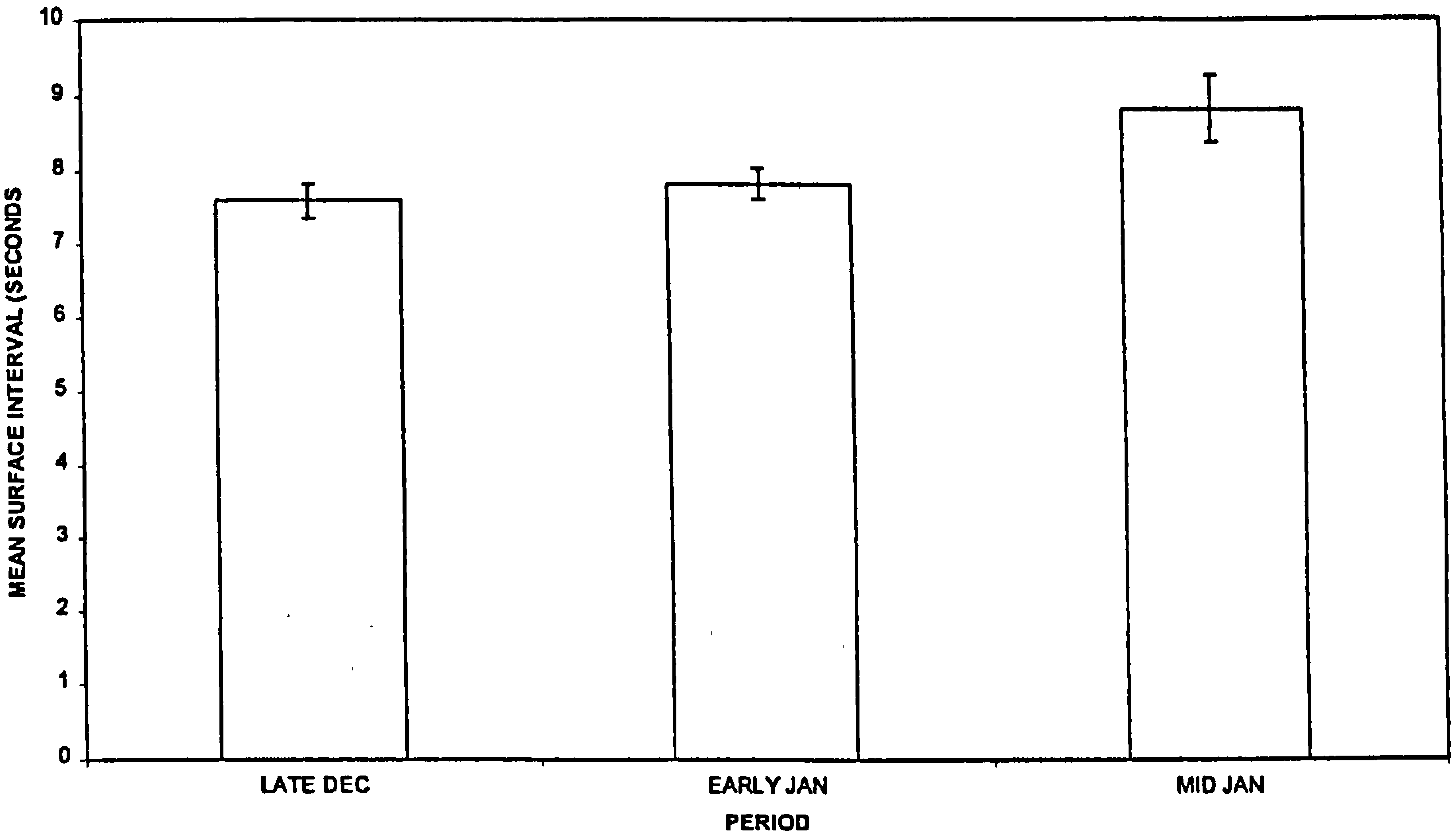


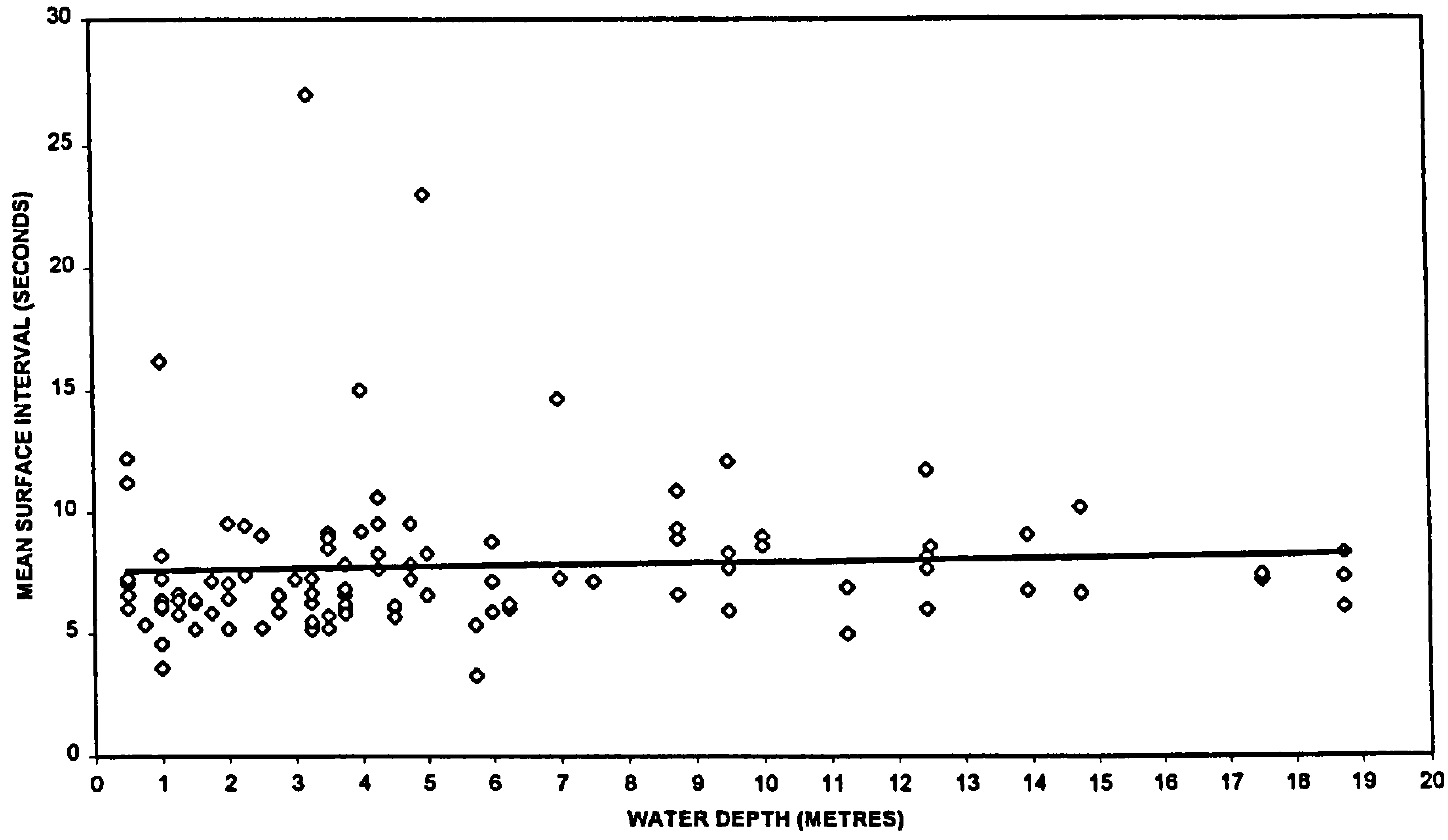
FIGURE 22: VARIATION IN SURFACE INTERVAL FOR CORMORANT 8.2 FROM LATE DECEMBER TO MID JANUARY, WITH STANDARD ERROR BARS



Surface Interval and water depth

A line fit plot for Cormorant 9.1 shows the relationship between mean surface interval and mean water depth (Fig. 23), but regression analysis shows that this is not significant. Regression analysis of similar data for cormorants 5.7, 6.7 and 8.2, also indicates that these relationships are not significant.

FIGURE 23: LINE FIT PLOT OF WATER DEPTH AND MEAN SURFACE INTERVAL - CORMORANT 9.1



Variation in surface interval for solitary and flock feeding

Comparison of 278 solitary surface intervals with 1,796 flock-feeding surface intervals by Cormorant 6.7, produced means of 8.58 (SE 0.21) and 8.16 (SE 0.08) respectively, but the difference is not significant.

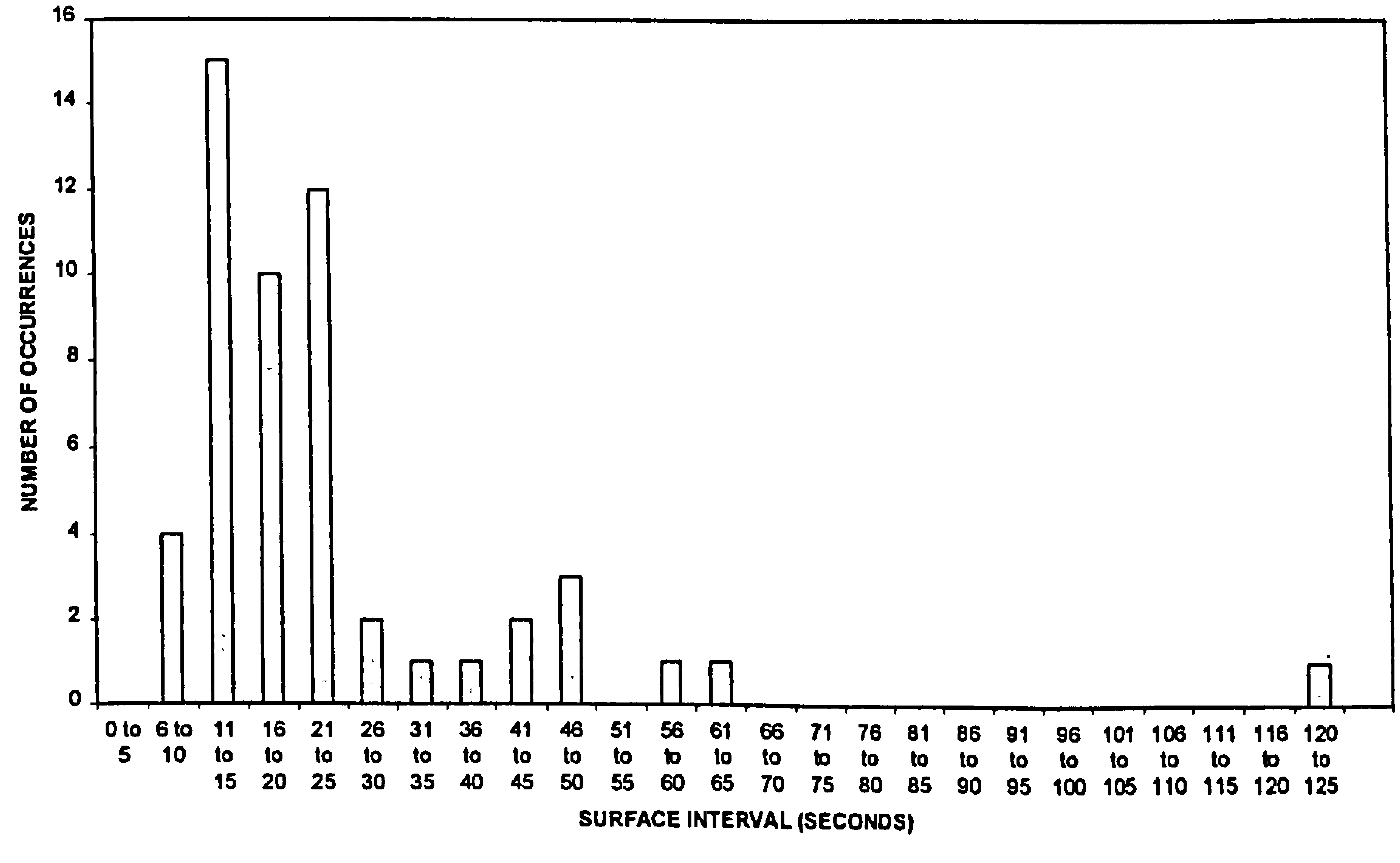
Variation in surface interval for birds foraging together

On six occasions, Cormorants 9.1 and 6.7 were observed to be foraging in the same flock, and groups of ten surface interval time were recorded alternately. Mean surface intervals were 7.00 s (SE 0.26) and 7.42 s (SE 0.28) respectively, and a two-tailed "*z*" test shows the difference is not significant. On two occasions, Cormorants 8.2 and 5.7 were observed to be foraging in the same flock. Mean surface intervals were 7.46 s (SE 0.33) and 10.18 s (SE 0.68) respectively, and a two-tailed "*z*" test showed the difference is significant ($z = 3.760, p < 0.001$).

Variation in surface interval following fish capture

On 62 occasions, birds were observed to surface with a fish, which was swallowed on the surface. On 54 of those occasions they then dived again, and on 8 occasions they ceased fishing and departed to roost. The mean surface interval before diving again was 24.5 s (median 19 s), (Fig. 28). The mean surface interval before taking off from the water and flying to roost was 147 s (median 120 s).

FIGURE 24: SURFACE INTERVAL FOLLOWING FISH CAPTURE

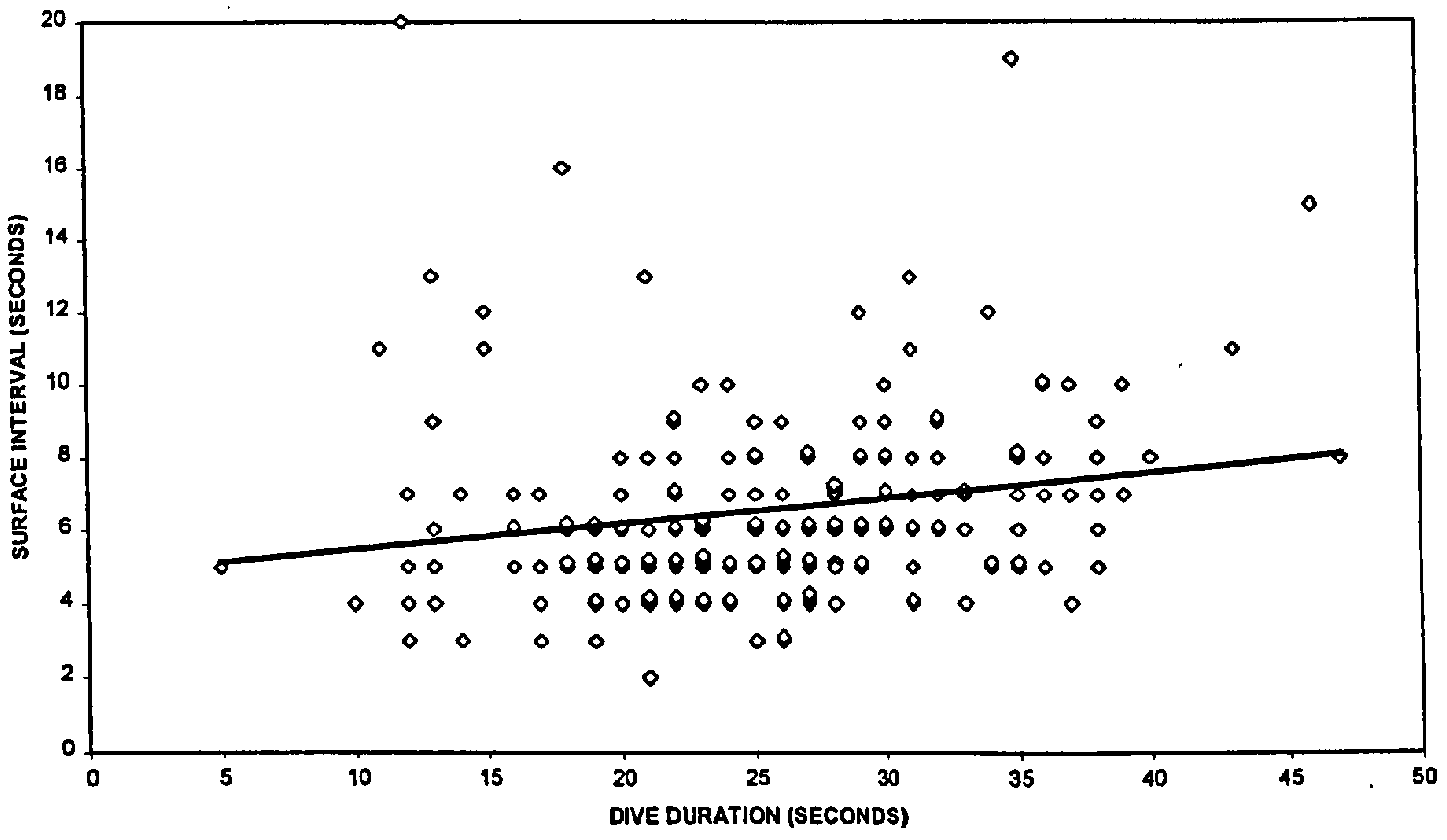


Relationship between dive duration and subsequent surface interval

As there are too many individual data points to illustrate effectively in a single chart, Fig. 25 uses 200 randomly selected dives to demonstrate the relationship between dive duration and subsequent surface interval for Cormorant 9.2. Regression analysis of all data indicates that the relationship is significant ($F_{1,4279} = 126.35$, $p < 0.001$, adjusted $R^2 = 28\%$). Significant relationships are also apparent for Cormorants 5.7

($F_{1,342} = 42.04$, $p < 0.001$, adjusted $R^2 = 10.7\%$) and 8.2. ($F_{1,448} = 4.490$, $p = 0.035$, adjusted $R^2 = 8\%$), but not for Cormorant 6.7.

FIGURE 25: LINE FIT PLOT OF DIVE DURATION AND SUBSEQUENT SURFACE INTERVAL - 200 RANDOMLY SELECTED DIVES - CORMORANT 9.1



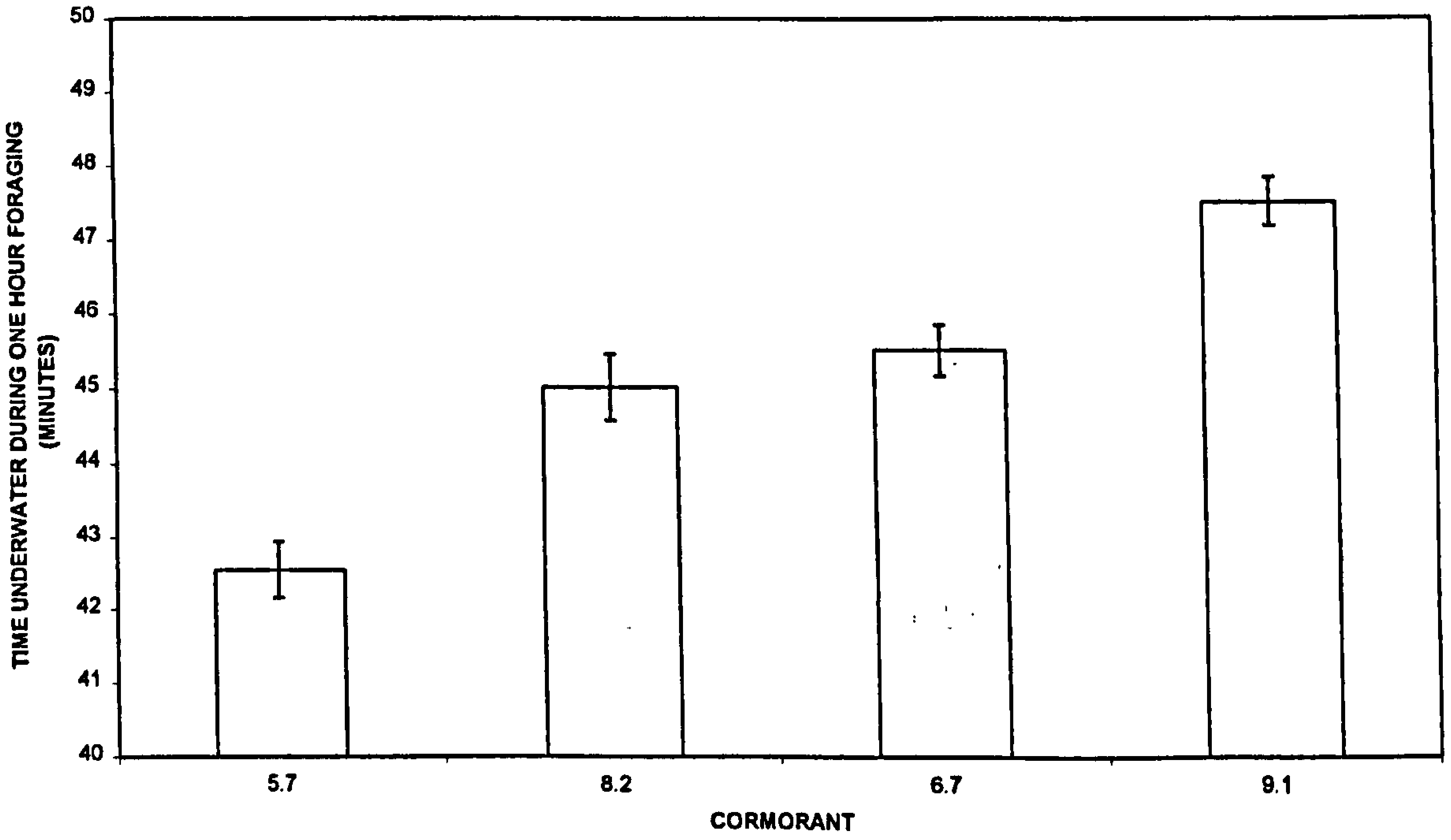
Duration of individual dive sequence

By summing the duration of each dive and its subsequent surface interval, the length of the diving sequence duration may be determined. This was similar for Cormorants 5.7, 8.2 and 6.7 with means of 35.41 s (SE 0.60), 35.13 s (SE 0.45) and 36.11 (SE 0.21) respectively. However, 9.1 mean dive sequence was 32.50 s (SE 0.13). One-way ANOVA showed that differences are significant ($F_{3,6933} = 80.90$, $p < 0.001$). Tukey test showed that differences between 9.1 and all three other cormorants are significant ($p < 0.001$).

Variation in proportion of time spent underwater when foraging

By comparing dive sequence duration with dive duration, the proportion of time spent underwater during an hour of constant foraging was calculated each bird (Fig.30). One-way ANOVA showed that differences are significant ($F_{3,6933} = 55.04, p < 0.001$). Tukey test showed that differences between 9.1 and all three other cormorants are significant ($p < 0.001$), as are differences between 5.7 and both 8.2 and 6.7 ($p = 0.025$ and $p = 0.002$, respectively)

FIGURE 26: VARIATION IN MEAN TIME SPENT UNDERWATER DURING ONE HOUR OF CONSTANT FORAGING BY INDIVIDUAL CORMORANTS - WITH STANDARD ERROR BARS



DISCUSSION

Foraging trips

The Loch Leven results agree with those of Hughes *et al.*, (1999) in terms of the number of foraging trips. The difference between adults and first-winter birds suggests greater efficiency at foraging by adults, who are able to catch sufficient prey in a much shorter time. Trip duration is considerably greater at Loch Leven than that reported from Grafham Water (Hughes *et al.*, 1999), with adults foraging each day for about five times as long, and first-winter birds for over six times as long. This may be explained in part by less favourable foraging conditions at Loch Leven, with deep water and poor visibility resulting in greater search time. However, the scale of the difference suggests that there may be other factors such as prey density, which influence foraging time. There is some evidence that foraging time increases as temperature decreases, in accord with the findings of Hughes *et al.*, (1999), but this is derived from a single bird and was not apparent in three others tested.

The progressive decrease in the duration of sequential foraging trips may be a result of success on preceding trips, with the demands of subsequent trips reduced and satiation achieved earlier. The bird may be "topping up" on food, which takes sequentially less time that starting in the morning with an empty stomach. Alternatively, the bird may simply tire more rapidly on later foraging trips as a result of earlier exertions, and this is considered below in the context of dive duration.

The finding that total daily foraging time does not increase during the winter contradicts the conclusion in Chapter 1 that, compared to early or late winter, cormorants were up to three times more active during mid-winter. This may largely be explained by the differentiation between time foraging and time on the water, with the earlier conclusion based on the results of a series of spot-checks of the loch, where birds on the water were assumed to be "active". From studies of individual birds, this chapter shows that although time spent on the water does increase from October to December, time spent actively foraging does not increase. Birds simply spend more time on the water, not actively foraging.

Diving

The number of dives per foraging trip is higher at Loch Leven than at other sites, which is to be expected given the longer foraging trip duration. This also explains the difference between total number of dives per day for adults and first-winter birds. Although adults conducted fewer dives than first-winter birds, this difference was not significant, which accords with the findings of Hughes *et* al., (1999) that there was no age effect. However, the variation between two birds indicates the importance of taking into account individual variability.

Mean dive duration at Loch Leven, of around 26 s, compares fairly closely with mean durations reported by Gremillet *et al.*, (1998), Hughes *et* al., (1999), and Doherty & McCarthy (1997) when referring to uninjured prey. However, they are considerably shorter than those reported for Scotland, and only half those reported for Nova Scotia, by Cooper (1985). They are also considerably shorter than those reported by Gremillet *et al.*, (1999b). Mean dive durations at Loch Leven are two and a half times longer than those reported for flock fishing by Gremillet *et al.*, (1998), even though flock fishing is the principal feeding behaviour at Loch Leven. They are also considerably longer than dive durations reported by Lariccia (1997), and by Doherty & McCarthy (1997) when referring to injured prey. If the suggestion by Gremillet *et al.*, (1998) that shorter dives indicate foraging for pelagic prey, is correct, the times recorded at Loch Leven suggests benthic feeding. There is no evidence of a bi-modal distribution of dive durations, resulting from switching between benthic and pelagic prey, as described by Gremillet *et al.*, 1998. The significant differences in diving behaviour of individual birds highlights the variability between data sources inherent in this type of study, and emphasises the need for adequate sample sizes when drawing broad conclusions.

Surface interval

The surface intervals on Loch Leven of between six and nine seconds are considerably shorter than those reported by Cooper (1985) (11.7 s and 13.9 s), Gremillet *et al.*, (1999b) (11 s), Hughes *et al.*, (1999) (11.9 s). This suggests that recovery time between dives is shorter on Loch Leven, even though in the case of Hughes *et al.*, (1999) dive durations are similar. The significant variation between individuals, with Cormorant 9.1 median surface interval only two-thirds of that of Cormorant 5.7, probably reflects individual foraging strategies, fitness or experience.

Variation in dive duration and surface interval over time

The decline in dive duration over an extended diving sequence does not concur with the findings of Hughes *et al.* (1999) and suggests a gradually reducing foraging efficiency, with shorter dives resulting in a lower proportion of the dive spent actively hunting and a greater proportion spent commuting between the surface and hunting depth. Commuting time appears to comprise the largest proportion of the dive

(Gremillet *et al.*, 1999b) so even a small reduction in dive duration could have a high impact on the remaining foraging time. The reducing dive duration implies a gradual decline in fitness of the individual bird as it tires during a foraging trip. The decline in surface interval over an extended diving sequence is also evident, but less pronounced, and concurs with the findings of Hughes *et al.*, (1999). It also reflects significant variation in individual behaviour. The finding that neither dive duration nor surface interval varies between sequential foraging trips suggests that the bird is able to recover its diving capacity between trips. The possibility that the bird tires more quickly on later foraging trips is supported by this lack of variation in mean dive duration, suggesting that the bird works through the normal range of dive durations during each foraging trip, but does so in a shorter time on later trips.

The variations in both dive duration and surface interval across the winter, demonstrated by three birds with the largest samples, illustrates individual behaviour patterns that do not necessarily reflect changes in behaviour in the cormorant population as a whole. It is likely that individual birds are responding in different ways to the various external factors that may affect their hunting success, and to their own hunting experience.

Variation in dive duration and surface interval with water depth and feeding behaviour

The lack of evidence of a link between water depth and dive duration contrasts with the strong correlation found by Gremillet *et al.* (1999b) and Wilson & Wilson (1988). On Loch Leven there appears to be no difference in dive duration between diving in two metres or twenty metres of water. In the light of this finding, the lack of a link between water depth and surface interval would be anticipated, and the fact that one bird did demonstrate such a link illustrates individual variation. The lack of variation in dive duration or surface interval between solitary feeding and flock feeding, evident for Cormorant 6.7, suggests that the individual followed similar dive profiles for both types of foraging. The significant variations in dive duration and surface interval between two individuals foraging in company reinforce the individual nature of their behaviour patterns.

Relationship between dive duration and surface interval

There is no evidence of the logarithmic curve described by Hughes *et al.* (1999). The dive duration: surface interval ratios were roughly comparable with the findings of Cooper (1985) and Gremillet *et al.* (1999b), but considerably greater than that suggested by Hughes *et al.* (1999).

It is apparent that cormorants wintering on Loch Leven forage for much longer each day than they do elsewhere, which suggests that it is considerably harder to achieve an adequate prey capture rate. The dive durations suggest that the birds are principally benthic foragers, despite the anomaly over flock feeding dive durations. Although cormorants may appear as a cohesive group, particularly when flock-feeding, they retain strong elements of individuality which significantly influence their behaviour. Thus individual variation is evident in different lengths of foraging trips, dive durations and surface intervals, changes with time, etc., and in the differences in behaviour between Loch Leven and other sites. This emphasises the impact individual behaviour may have on data gathering, and the need for adequate sample sizes to support deductions.

Chapter 4

IMPACT OF CORMORANTS ON THE LOCH LEVEN TROUT FISHERY AND THE EFFECTIVENESS OF SHOOTING AS MITIGATION

ABSTRACT

Perceived conflicts between piscivorous birds and commercial freshwater fisheries are common in the United Kingdom and abroad. Such a perception exists at Loch Leven, a wetland of international importance for nature conservation and a famous commercial brown trout *Salmo trutta* fishery, where cormorants *Phalacrocorax carbo have* been shot in large numbers. This paper summarises changes over a 32 year period in the number of cormorants wintering on Loch Leven, and reviews data on fish populations, fish stocking rates, angling catches and angling effort in order to seek evidence of detrimental impacts of cormorants on the fishery. It also seeks evidence of beneficial effects of large-scale cormorant shooting.

The number of cormorants wintering on Loch Leven has risen ten-fold, with the principal increase occurring around 1988. This increase is in line with the trend for Great Britain as a whole, but higher than that for Scotland. Variations in angling catch showed no correlation with changes in cormorant numbers, but the brown trout catch as a percentage of the loch's population has declined by about two thirds. Catch per unit effort remained relatively stable despite the cormorant increase, and the principal determinant of the size of angling catch was angling effort. The proportion of brown trout found to be wounded by cormorants was low, at 0.4% in June/August 1998 and 4.7% in February/March 1999. There is no evidence of a reduction in wintering cormorant numbers, or of an increase in angling catches, as a consequence of shooting large numbers of cormorants.

The above conclusions question the assumption that serious economic damage to commercial and recreational open-water fisheries is attributable to cormorants, and furthermore, they question the validity of issuing licenses to shoot cormorants for fishery protection purposes.

INTRODUCTION

Background

For centuries, fishery managers have persecuted cormorants and other fish-eating birds. It is perceived that cormorants consume large quantities of exploitable fish, wound fish that may then be un-saleable or die, and cause stress in fish and abnormal behaviour resulting in reduced availability to anglers (Russell *et al*, 1996). However, despite all the research so far published, there is still little scientific evidence for detrimental effects of cormorants on fish populations in fresh water bodies (Carss, 1997). Furthermore, there is little evidence of any beneficial effects of shooting cormorants for fishery protection purposes (e.g. Kirby, Holmes & Sellers, 1996, Russell *et al*, 1996), and research which aims to address these issues is therefore of particular importance. This paper reviews data gathered between 1968 and 2000, and tests the following hypotheses:

(a) Increased cormorant numbers have damaged the Loch Leven trout fishery by depleting the trout population and reducing angling catches.

(b) Shooting cormorants on Loch Leven is an effective mitigation measure, resulting in reduced cormorant numbers and increased trout catches.

Increases in cormorant numbers throughout Europe have been well documented, (Blanco, (1994), Van Eerden & Gregersen, (1995) and Kirby, Gilburn & Sellers (1995)). There is concern amongst fishery managers, and governments have responded by funding investigations into the impacts of cormorants on freshwater fish stocks, (Russell *et al.*, 1996). In Scotland, cormorants are given statutory protection under the Wildlife and

Countryside Act, 1981, which implements European Community Directive 79/409/EEC on the Conservation of Wild Birds (The Birds Directive). Additionally, some Scottish cormorant breeding sites are designated as Special Protection Areas under European Community Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Flora and Fauna (The Habitats Directive). In November 1994 Loch Leven was notified as a potential Special Protection Area under The Habitats Directive on account of its populations of breeding, wintering, and migratory wildfowl, which includes a nationally important wintering population of migratory cormorant. This notification ultimately lead to the cessation of cormorant shooting on Loch Leven and the initiation of this study.

Cormorants and Loch Leven

Loch Leven is located in east-central Scotland and covers 1,330 hectares with an average depth of 3.9 metres. Cormorants were not included in the British national waterfowl census until 1986/87 when the national increase in numbers was already under way, so the national data set is of a relatively short span. However, at Loch Leven, which was established as a National Nature Reserve in 1964, there are longer-term records of cormorant numbers. These data show that Loch Leven holds the largest inland wintering cormorant population in Scotland, with a peak of 800 recorded in 1991.

The status of cormorants at Loch Leven was summarised by Allison, Newton & Campbell (1974) who described it as present throughout the year but not breeding, with up to 60 birds present from January to March. The species is recorded on the loch from as far back as 1791, and as present in very large numbers in the 1940s with reports of over 200 birds. Carss, Marquiss & Lauder (1997) reviewed cormorant counts from 1981 to 1995, and illustrated the increase in the population from a winter mean of around 50, to over 200 birds.

The Loch Leven trout fishery

The loch has supported a commercial fishery for at least 680 years. In 1873 angling replaced netting as the means of exploitation (Thorpe, 1974) and it has developed into a famous brown trout fishery. Catches have fluctuated between 9,000 and 40,000 since the 1960s, reaching an all-time low of 2,700 in 1992 when particularly severe algal blooms affected the loch and the fishery was closed for the season.

As a result of concern over declining catches, artificial stocking of native brown trout commenced in 1983. Each year since, spawning adult trout have been caught in the surrounding burns, stripped of eggs and sperm, and their progeny reared in ponds adjacent to the loch. Each spring, having reached a length of about 120 mm, the juveniles have been released into the loch, with a view to their achieving a catchable size by the following spring. In addition, stocking of introduced rainbow trout *Oncorhynchus mykiss* commenced in 1993. The commercial trout fishery has detailed records of fish stocking, angling effort and catches, which renders Loch Leven well suited for a study of cormorant impact on the fishery.

The size of the brown trout population has been estimated on several occasions during the past 30 years, though obtaining an accurate estimate on a water body as large as Loch Leven is very difficult. From 1968 to 1971 Thorpe used a capture/recapture method (Thorpe, 1974,b) and in 1993 O'Grady used a gill netting technique developed in Ireland but not validated in Scottish waters (O'Grady, Gargan & Roche, 1993). In 1998 Alexander used a combination of gill netting, trawling and hydro-acoustics (Alexander *et al.*, 1999).

Over recent decades nutrient enrichment from point-source and diffuse pollution has resulted in a deterioration of water quality and episodes of dense blooms of blue-green algae, such as those in 1992 and 1994 (Bailey-Watts *et al.*, 1994). This has had direct consequences for the fishery by making the loch a less attractive place for fishermen, and on occasions by raising fears of possible toxic effects of the algal blooms. It has also resulted in wide fluctuations in pH levels, which may influence fish survival.

Fish predation by cormorants

Analysis of the stomach contents of cormorants shot for fishery protection purposes has shown that they do take trout of a catchable size for anglers. Carss & Marquiss (1992 & 1994) showed a general shift from a perch *Perca fluviatilis* dominated diet in the 1970s to a brown trout dominated diet in the 1980s and 1990s. The three-spined stickleback *Gasterosteus aculeatus* appeared in the diet from 1989 and rainbow trout appeared from 1993. In 1999 Alexander *et al.* (1999) reported a change in the loch's fish population with the resurgence of perch, and in the netting samples perch heavily outnumbered brown trout. Many perch showed signs of cormorant wounding.

Carss & Marquiss (1992 & 1994) showed that brown trout taken by cormorants were predominately in the 16 to 35 cm length range, with about half of them of a catchable size for anglers. Rainbow trout were predominately in the 26 to 40 cm range, and most of them were of catchable size. However, although the potential for economic loss to the fishery from cormorant predation was identified, Carss & Marquiss (1992) concluded that this was far from established. Carss, Marquiss & Lauder (1997) surmised that bird predation had no detectable effect on angling harvest, but did not demonstrate this through statistical analysis of cormorant and fishery data.

METHOD

Cormorant counts

Data on numbers of cormorants wintering on Loch Leven during September to March from 1968/69 to 1999/2000 were extracted from field notebooks (Allison, A. unpublished data; Wright, G. unpublished data), and from monthly National Waterfowl Census records. Loch Leven is not a difficult place to count cormorants, having sufficient elevated observation points to enable the whole site to be overlooked, and roosting and loafing sites are well known. Counts were conducted by professional field staff, and although there was some scope for error due to unobserved bird movements, the counts are assumed to have a reasonably high degree of consistency. In order to confirm this, the results of overlapping counts by different observers were compared. Annual indices of cormorant abundance in Great Britain, Scotland and south-east Scotland from 1986/87 to 1999/2000 were obtained from the Wildfowl and Wetlands Trust.

The cormorant count sequences were not complete for 11 of the 32 winters; of the maximum of seven counts, five winters were missing one count, two were missing two counts, three were missing three counts and one was missing five counts. Two options were considered in order to take account of these gaps. Firstly, stability of numbers between October and March was assumed, and a mean of the recorded counts for each winter was used as a substitute for any missing monthly counts. Thus a simple annual mean was calculated.

Secondly, using data from all years with complete count records, the percentage of the annual total occurring in each month was calculated. In years when counts were missing, these percentages were applied to the known counts in order to provide estimates for the missing data. A mean of each year's counts, both known and estimated, was then calculated and thus an alternative annual mean was derived.

Both methods were tested for accuracy by deleting known counts from winters with complete data sets, substituting estimates calculated using each method and comparing the calculated means with the actual mean. The data to be deleted were selected at random, and this was carried out twice for each winter. The procedure was repeated for each of one to five missing monthly counts, and the resultant total error was calculated. Count data were summarised to provide a profile of changing cormorant numbers over the period.

Fishery data

Details of fishing effort, fish catches and fish stocking from 1968/69 to 1999/2000, and records of cormorants shot on Loch Leven from 1981/82 to 1999/2000, were obtained from Loch Leven Fisheries. Wintering cormorant numbers were then compared to fish stock data in order to explore possible relationships by means of correlation analysis. Catch per unit effort (CPUE) data were compared with wintering cormorant numbers, and the size of fish catches was compared with angling effort. Stocking of rainbow trout from 1993 changed the nature of the fishery, and this complication was addressed by separately analysing catch data for the years prior to 1993.

In June to August 1998, 246 brown trout were caught by a team from Glasgow University Field Station, Rowardennan, and the University of Stirling Institute of Aquaculture. Thirty-five sites sampled were using Lungrens of Sweden "Nordic" type multi-mesh gill nets, 30 m long with twelve panels from 5 mm to 55 mm half mesh size. They were set in a range of depths, and five pelagic zones were also sampled using vertically set nets. All fish were examined for signs of cormorant damage as described by Russell *et al.* (1996) and the lengths and weights of all fish were recorded.

In February and March 1999, 424 brown trout were caught. Twenty-four sites were sampled using Collins multi-mesh Survey Gill Nets, 60 m long with twelve panels from 8 mm to 50 mm half mesh size, set on the bottom in a range of depths. In addition three pelagic zones were sampled with vertically set nets. All fish were examined for signs of cormorant damage as described by Russell *et al.* (1996) and the lengths and weights of all fish were recorded. Damage was classed as "fresh" where it was obvious that the wound had been inflicted recently, or "old" where there were signs of healing.

Cormorant diet

On 7 October 1997 and 21 December 1997, whilst catching cormorants using cannon nets, fish regurgitated by captured birds were collected from the netting site. They were identified to species, weighed, measured and an estimate was made of the percentage already digested. From December 1998 to February 1999, regurgitated cormorant pellets containing undigested fish remains were collected from the principal roost on Reed Bower Island. In order to remove the pellet sac and clean the contents, each pellet was placed in a petri dish in a solution of 90 gm of "Biotex" to 1 litre of water. When clean, they were washed with fresh water and filtered through an "Endecotts" certified laboratory test sieve with a mesh size of 300 microns. The remains were returned to the petri dish and placed in a drying oven to remove liquid.

When dry, the remains were examined with a USSR 6M-51-2, 8.75 power, binocular microscope, in order to identify the species of fish from which they originated. In order to aid this process, whole perch, brown trout and three-spined stickleback were also digested using Biotex solution and sample remains were prepared for each species. The items used to differentiated between species included scales, vertebrae, otoliths, idem, pharyngeal bones and prae operculum. Species presence was recorded for each pellet, but no attempt was made to measure the size of fish remains in order to calculate the original fish size.

Cormorant shooting

Records of cormorants shot on Loch Leven from 1981/82 to 1999/2000 were obtained from Loch Leven Fisheries. The number shot was compared to the number present during the same and subsequent winters in order to explore possible impacts of shooting on the wintering population. The number of cormorants shot was also compared to the number and weight of fish caught, and CPUE, for the following summer, in order to explore impacts of shooting on the success of the fishery.

RESULTS

Cormorant wintering population on Loch Leven, 1968 to 2000

The cormorant count sequences are not complete for some winters, and the gaps are shown in Table 1. Data sets are complete for all winters not listed.

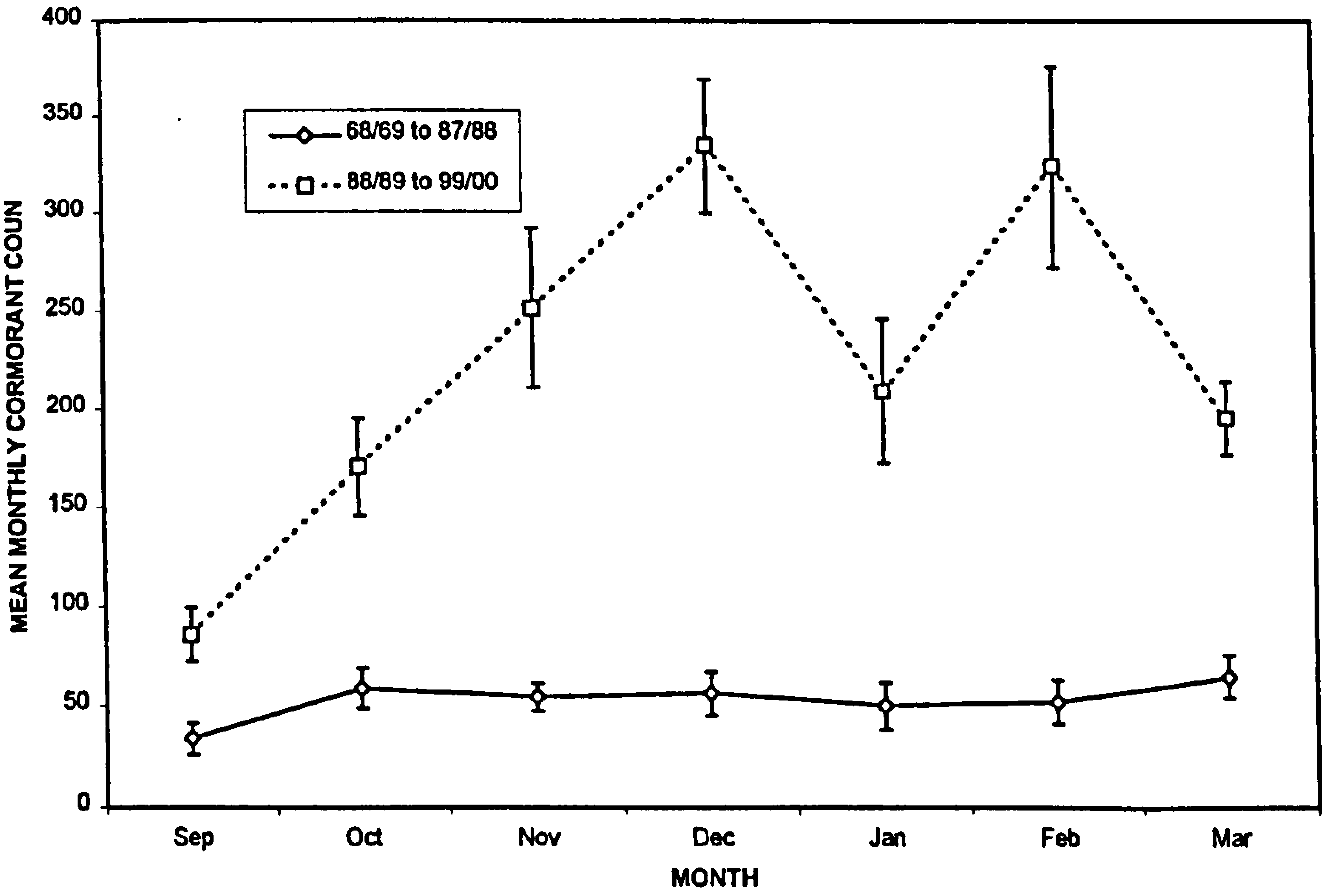
TABLE 1: OCCURRENCE OF GAPS IN MONTHLY CORMORANT COUNTS FOR WINTERS 1968/69 TO 1999/2000

Winter	68/69	69/70	70/71	72/73	74/75	78/79	79/80	80/81	90-91	92-93
Month										
Sep		x	x	x				x		
Oct		x	x				x			
Nov	x						x	x		
Dec	x	x				x	x	x		
Jan					x					
Feb	x						x			
Mar							x		x	x

The two methods tested to take account of these gaps were based on the use of a simple mean of the recorded counts for each winter, and on the use of a percentage of the annual total normally occurring each month. It was found necessary to split the data at 1988 as the monthly percentages differed markedly before and after the increase in cormorant numbers, as illustrated in Fig. 1. This indicates that prior to the increase the wintering population remained at about the same number from October to March. Post-1988, numbers have increased most during the mid-winter months, with distinct peaks in December and February showing increases of over 400% and over 500% respectively.

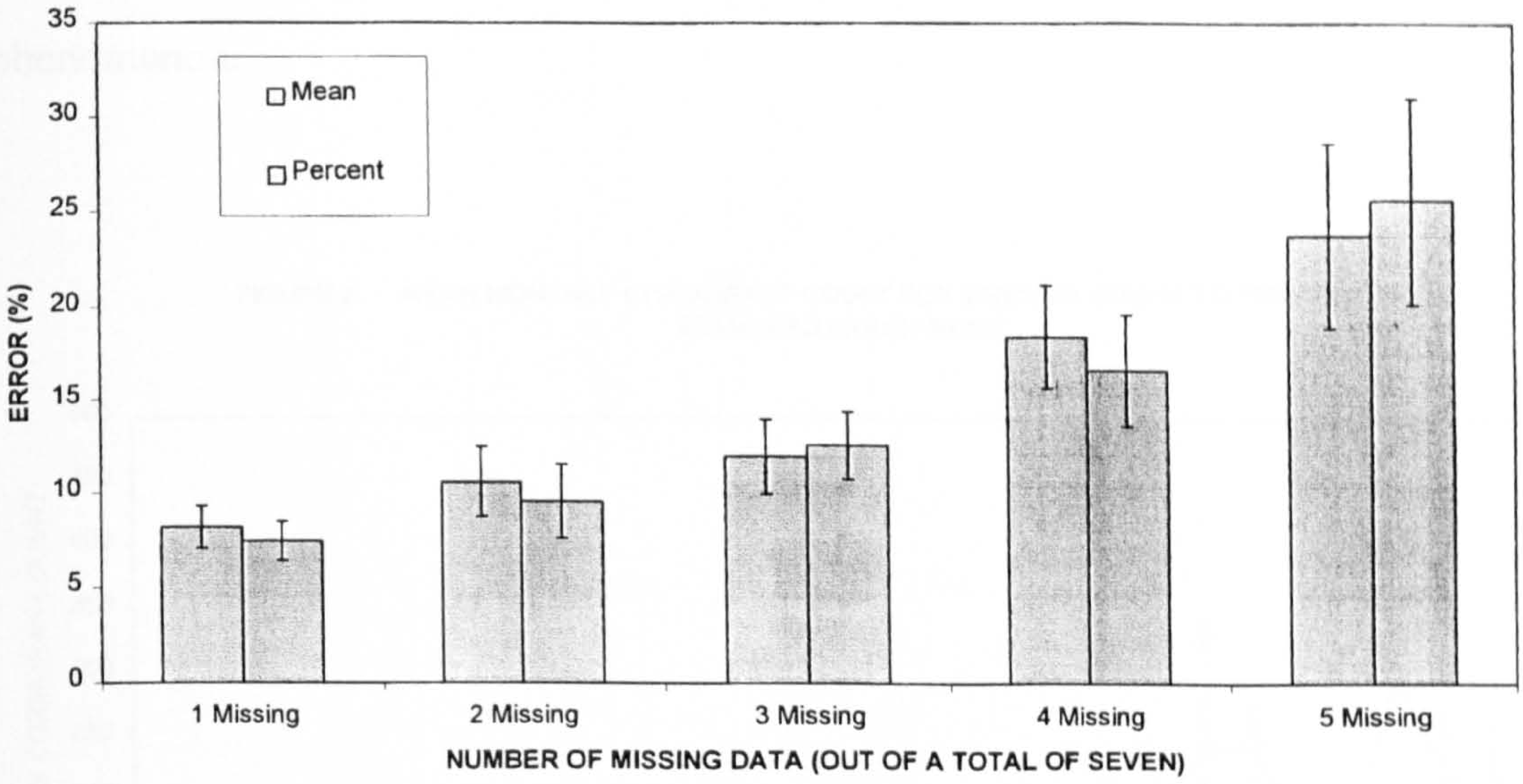
These later counts are more volatile with wide error bars, showing considerable variation between months and between winters.

FIGURE 1: MEAN MONTHLY CORMORANT COUNT FOR WINTERS 1968/69 TO 1987/88 & 1988/89 TO 1999/2000, WITH STANDARD ERROR BARS



Both methods were tested for accuracy by deleting known counts from 12 winters with complete data sets, substituting estimates calculated using each method and comparing the resulting means with the actual annual mean. The results are illustrated in Fig. 2.

FIGURE 2: COMPARISON OF PERCENTAGE ERROR IN PREDICTED MEAN MONTHLY CORMORANT COUNT WITH INCREASING NUMBER OF MISSING COUNTS, USING SIMPLE MEAN AND USING PERCENTAGES TO PREDICT MISSING DATA, WITH STANDARD ERROR BARS

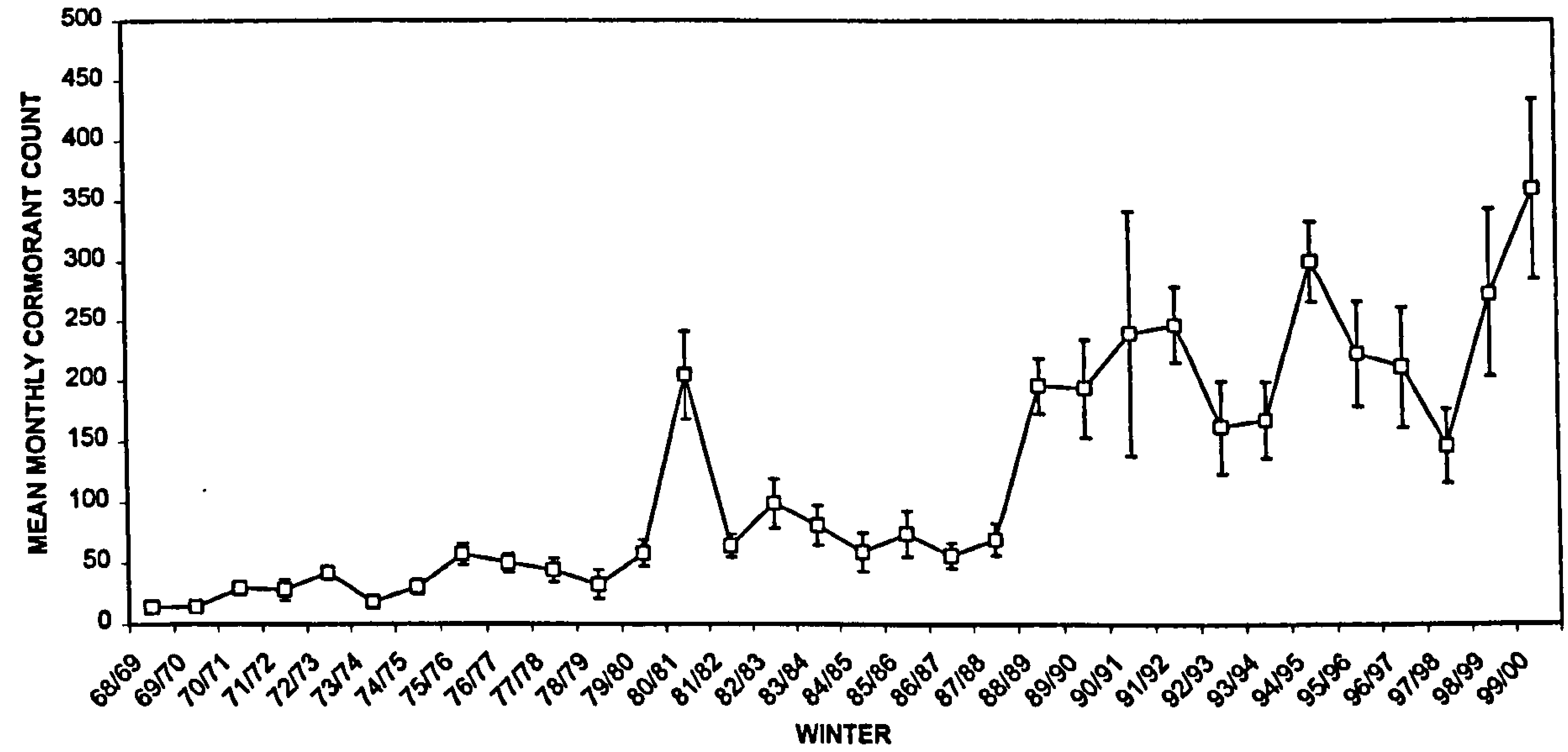


The method using a monthly percentage was found to be marginally more accurate so this was used in further analysis. The total error for up to three missing counts was found to be less than 13%, but increased to over 25% for five missing counts.

Changes in wintering cormorant numbers

Changes in the mean monthly cormorant count over the period, together with standard error bars, are shown in Fig. 3. This illustrates a substantial increase in cormorant numbers, equivalent to an annual growth rate of 12.5% up to the peak in 1994/95, or an annual growth rate of 10% taken over the whole period. Between 1987/88 and 1994/95 the annual increase was 23%, which may be compared with average annual increases of 12.6% for estuaries and 24.8% for gravel pits reported by Russell *et al.* (1996). It is also evident that there was a short-lived increase of considerable magnitude during the winter of 1980/81. Together with the reference made earlier to a large number present during the 1940s (Allison, 1974), this demonstrates that cormorant numbers have long been subject to fluctuation, and the current large wintering population is not an entirely new phenomenon.

FIGURE 3: MEAN MONTHLY CORMORANT COUNT FOR WINTERS 1968/69 TO 1999/2000, WITH STANDARD ERROR BARS



Cormorants were not included in the British national waterfowl census until 1986/87 when the increase was already under way. However, indices for Great Britain, Scotland, and south-east Scotland are available since then and in Fig. 4 they are compared with the index for Loch Leven for the period 1986/87 to 1999/2000. It is apparent that the two Scottish indices are closely comparable and relatively stable at double the 1986/87 index. The G.B. index is also relatively stable at between three and a half and four times the 1986/87 index, whilst the Loch Leven population has increased by a similar amount but shows considerable volatility.

FIGURE 4: CHANGES IN CORMORANT INDICES FOR GREAT BRITAIN, SCOTLAND, SOUTH EAST SCOTLAND AND LOCH LEVEN FOR WINTERS 1986/87 TO 1999/2000

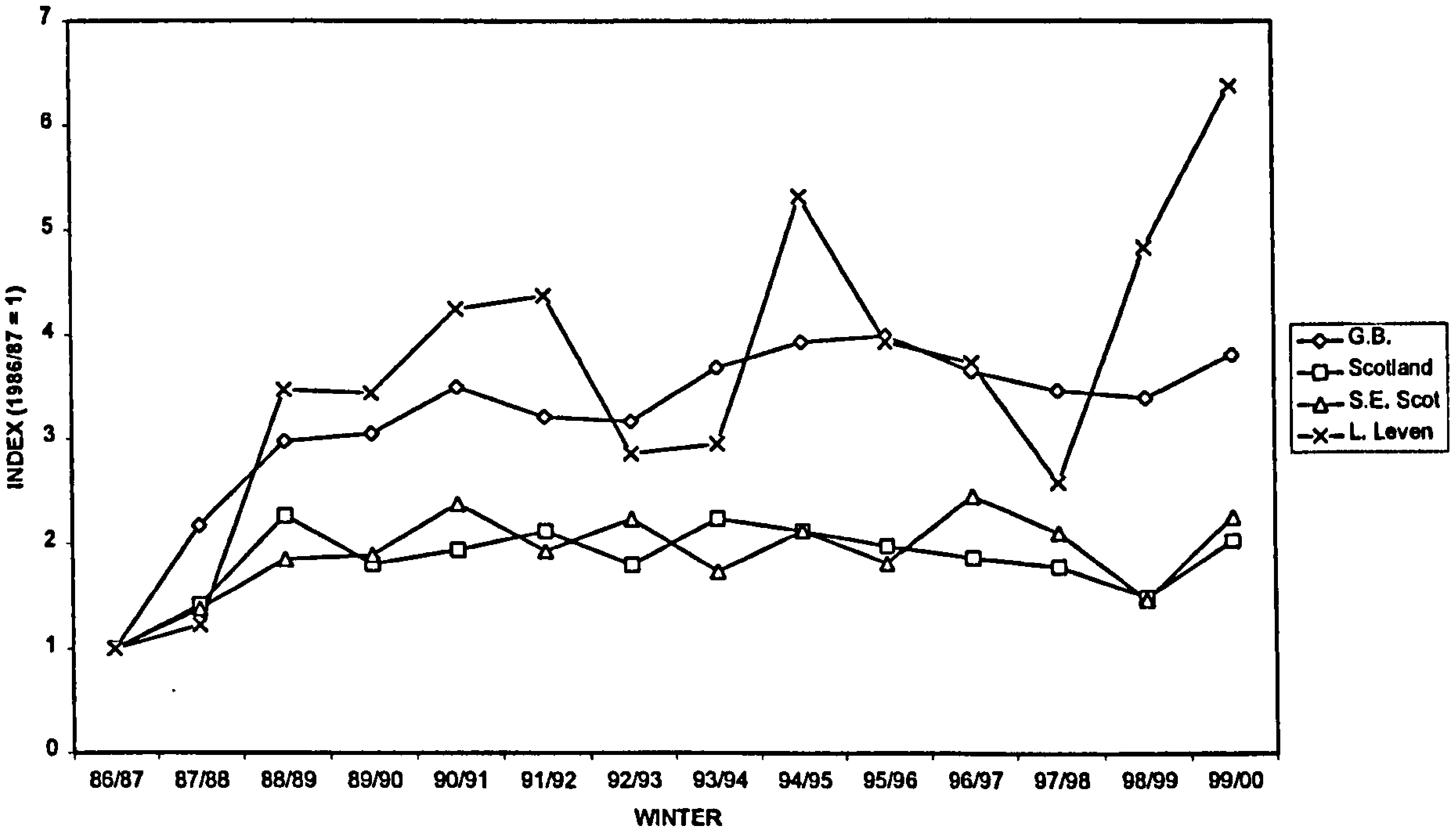
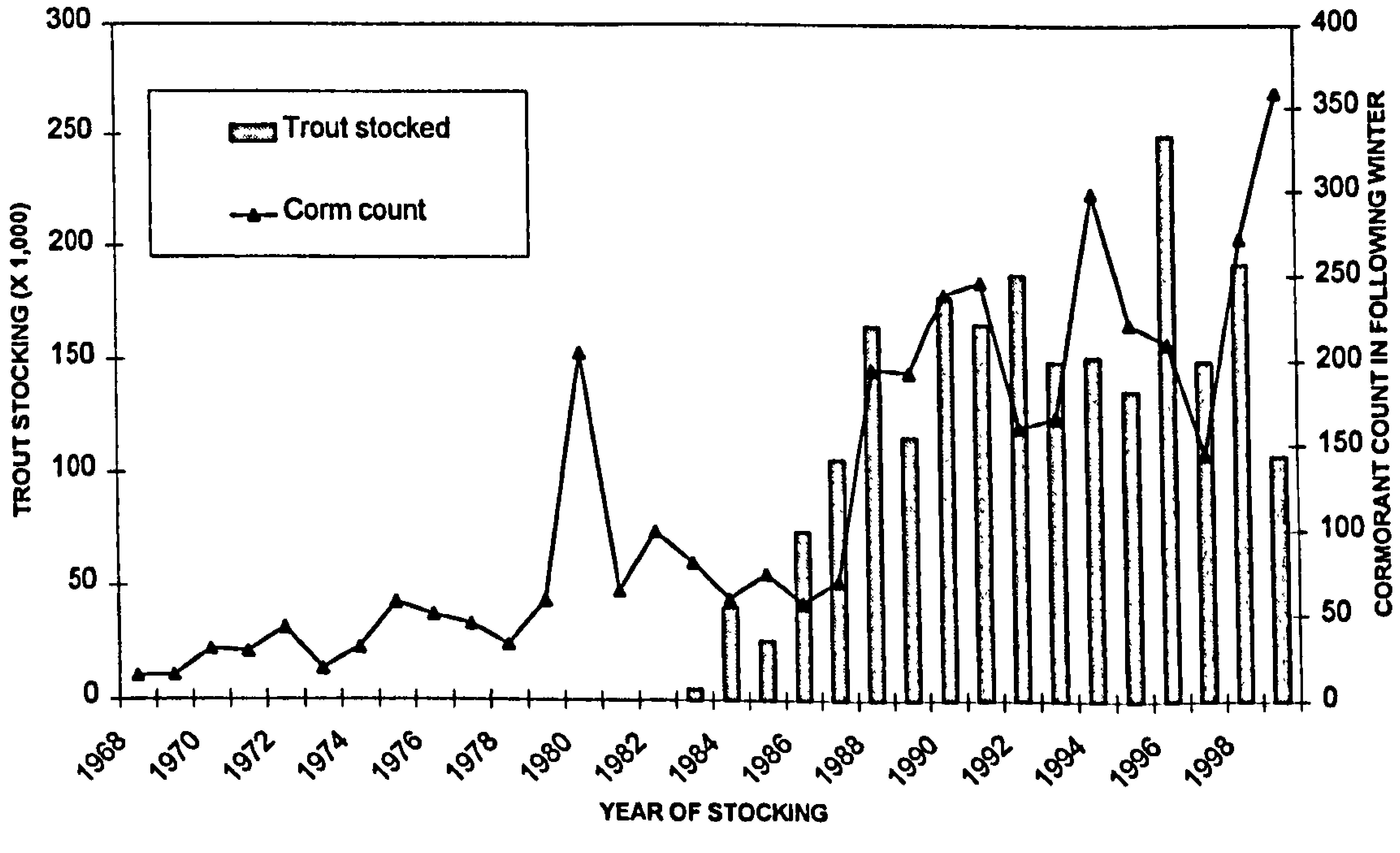


FIGURE 5: BROWN TROUT STOCKING AND MEAN MONTHLY CORMORANT COUNT DURING FOLLOWING WINTER



Trout stocking

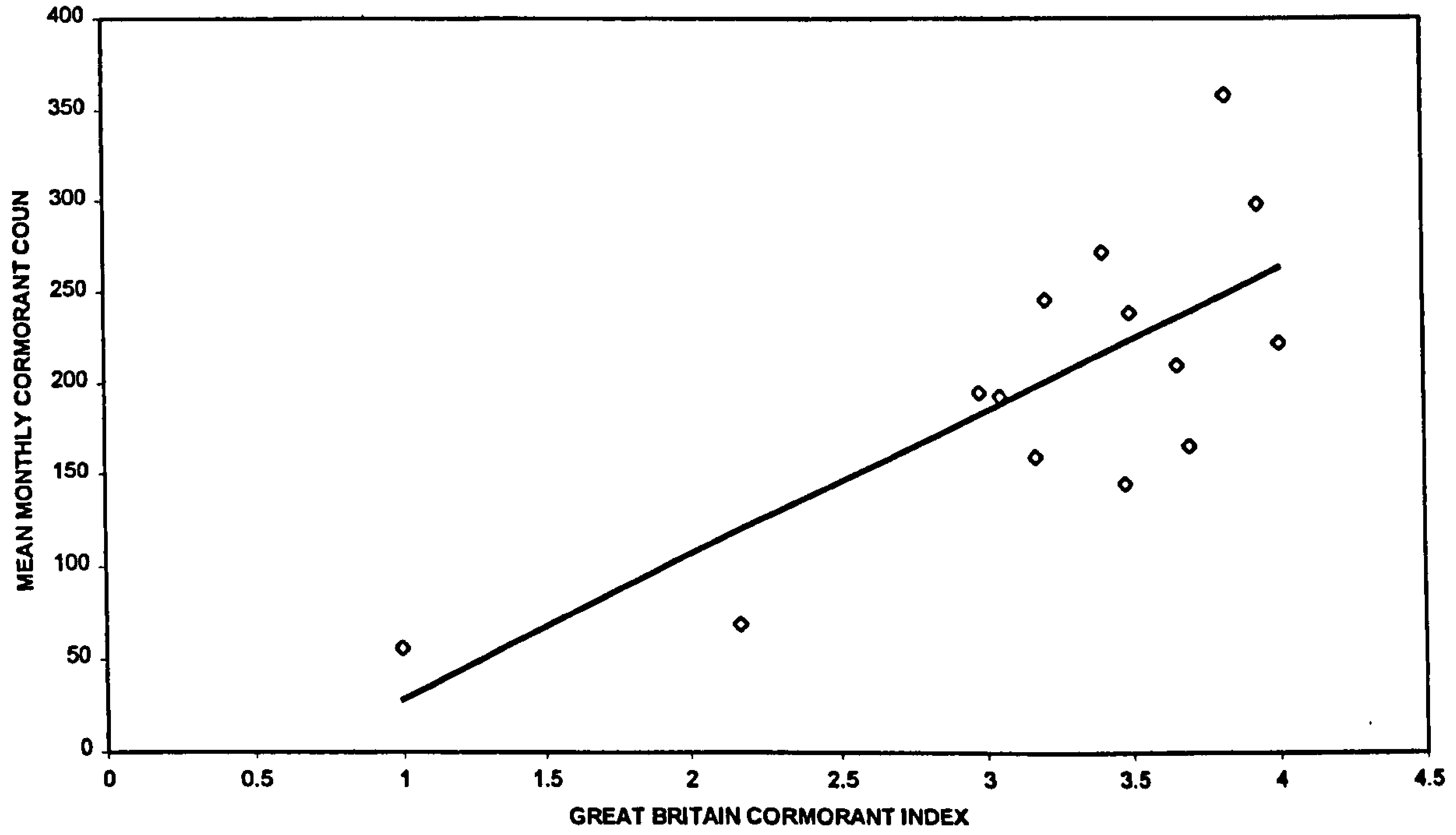
Fig. 5 shows annual brown trout stocking rates for Loch Leven, together with the mean monthly cormorant count for the following winter.

Factors affecting Cormorant numbers

Brown trout stocking began before the increase in cormorant numbers, and although nation-wide increases in cormorant numbers have been well documented (e.g. Kirby, Gilburn & Sellers, 1995), it has been postulated that the local increase at Loch Leven reflects a direct response to the stocking policy. In order to test this hypothesis, forward stepwise multiple regression analysis of cormorant counts was conducted using trout stocking, and the GB, Scotland and SE Scotland Indices as independent variables. Only one step, the GB Index, was found to be significant ($F_{1,12} = 16.09, p = \mathbf{0.002}$, adjusted $R^2 = 53.7\%$). The relationship is illustrated in Fig. 6.

These time-series data are not entirely independent, in that birds counted in one year are likely to form a component of subsequent years. Thus the results should be treated with some caution. In addition, time series tend to have a "noise" effect, which may mask longer-term trends, and this may be smoothed to some extent by using moving means. Repeating the above analysis using 5-year moving means produces similar results, with just the GB Index found to be significant ($F_{1,8} = 29.65, p = \mathbf{0.001}$, adjusted $R^2 = 76.1\%$).

FIGURE 6: LINE FIT PLOT FOR GREAT BRITAIN CORMORANT INDEX AND MEAN MONTHLY CORMORANT COUNT



Comparison of year-to-year fluctuations shows the proportion of occasions when a rise in trout stocking was followed by a rise in cormorant numbers, or a fall in trout stocking was followed by a fall in cormorant numbers, total only 50%. On the other occasions a rise or fall in trout stocking was followed by the opposite trend in cormorant numbers. The 23% annual increase in wintering cormorant numbers over the period compares closely with the UK figure of 24.8% for gravel pits reported by Russell *et al.* (1996). Therefore, the results do not argue strongly for a causal relationship between trout stocking and cormorant numbers, suggesting instead that Loch Leven Cormorant numbers reflects national influences.

Trout population and the angling catch

Table 2 contains trout population estimates, derived from Thorpe (1994), O'Grady *et al.*, (1993) and Alexander *et al.*, (1999), together with catches for the subsequent summer. The 1998 mark-recapture results were derived using the Lincoln Index (Lincoln, 1930), as modified by Bailey (1951), and the standard deviation was estimated using Bailey's method. All population estimates have fairly wide confidence limits and methods differ, so the results are not directly comparable. For example, the 260 mm+ size class quoted in 1998 does not equate precisely to the age 3+ class quoted from 1968 to1971, as this length would omit perhaps 20% of the age 3 class, which themselves comprise about 50% of the whole age 3+ class (Thorpe 1974,b). The 1998 total of 48,000 could therefore reasonably be increased by 10% in order to equate approximately to age 3+. This would effectively reduce the catch as a percentage of the population from 8.6 to 7.8%.

The population estimate quoted in 1998 using the mark/recapture method, should, in theory, be more directly comparable with the 1968 to 1971 results. However, it includes fish as small at 162 mm, which are below the normal age 3+ size. Assuming the structure of the trout population is the same as the netting/sonar results (Alexander et al., 1999), this population estimate could be reduced by 75% to equate approximately to age 3+, and the angling catch would comprises about 3% of this population.

Notwithstanding the difficulties in comparing the results in Table 2, there is no evidence that brown trout populations in the 1990's were any smaller than they were in 1968 to

1971, and indeed, they may be larger, despite the increased cormorant numbers. Therefore, from the available fish population data, there is no evidence of a decline in the trout population attributable to the increased wintering cormorant numbers. It is however apparent, that the angling catch as a proportion of the catchable trout population has declined considerably, possibly by as much as 90%, suggesting that other factors may be limiting the angling catch.

TABLE 2: LOCH LEVEN BROWN TROUT POPULATION ESTIMATES AND ANGLING CATCHES

Year	**Month**	**Method**	**Population estimate**	**Age/size range**	**Angling catch**	**Percent caught**
1968	Apr	Mark/recapture	126,665	Age 3+	37796	29.8
1969	Apr	Mark/recapture	103,497	Age 3+	20605	19.9
1970	Apr	Mark/recapture	114,526	Age 3+	20331	17.8
1971	Apr	Mark/recapture	52,737	Age 3+	9571	18.1
1993	Mar	Netting	440,000	≤477 mm	13150	
1993	Mar	Netting	186,000	Age 3+	13150	7.1
1998	Jun-Aug	Netting/sonar	217,000	162 mm+	4122	
1998	Jun-Aug	Netting/sonar	48,000	260 mm+	4122	8.6
1998	Jun-Aug	Mark/recapture	555,000	162-260 mm	4122	(3)

Cormorant impacts on fish populations during the 1998/99 winter

CPUE data from gill net sampling of June to August 1998, before wintering cormorants arrived, may be compared with data from February/March 1999 when some 270 cormorants had been present for five months, as shown in Table 3. Netting effort was considerably higher in February/March as it was assumed that fish stocks would have been depleted. However, net CPUE was virtually identical for both trout samples at 0.2 trout m^{-2} per 24 hours, showing no evidence of a detrimental impact on the brown trout population over the winter. By contrast, the net CPUE for perch declined by 94% between samples, suggesting a dramatic reduction in the size of the population, possibly attributable to cormorant predation.

TABLE 3: GILL NET CATCH PER UNIT EFFORT BEFORE AND AFTER 1998/99 WINTER (MEAN CORMORANT COUNT SEPTEMBER 98 TO MARCH 99 = 270)

Brown trout

Catch date	**Net area set (m^2)**	**Mean time set (h:m)**	**No. fish caught**	**No. fish per m^2 per 24 h**
Jun-Aug 1998	1,800	16:53	246	0.194
Feb-Mar 1999	2,160	23:15	424	0.203

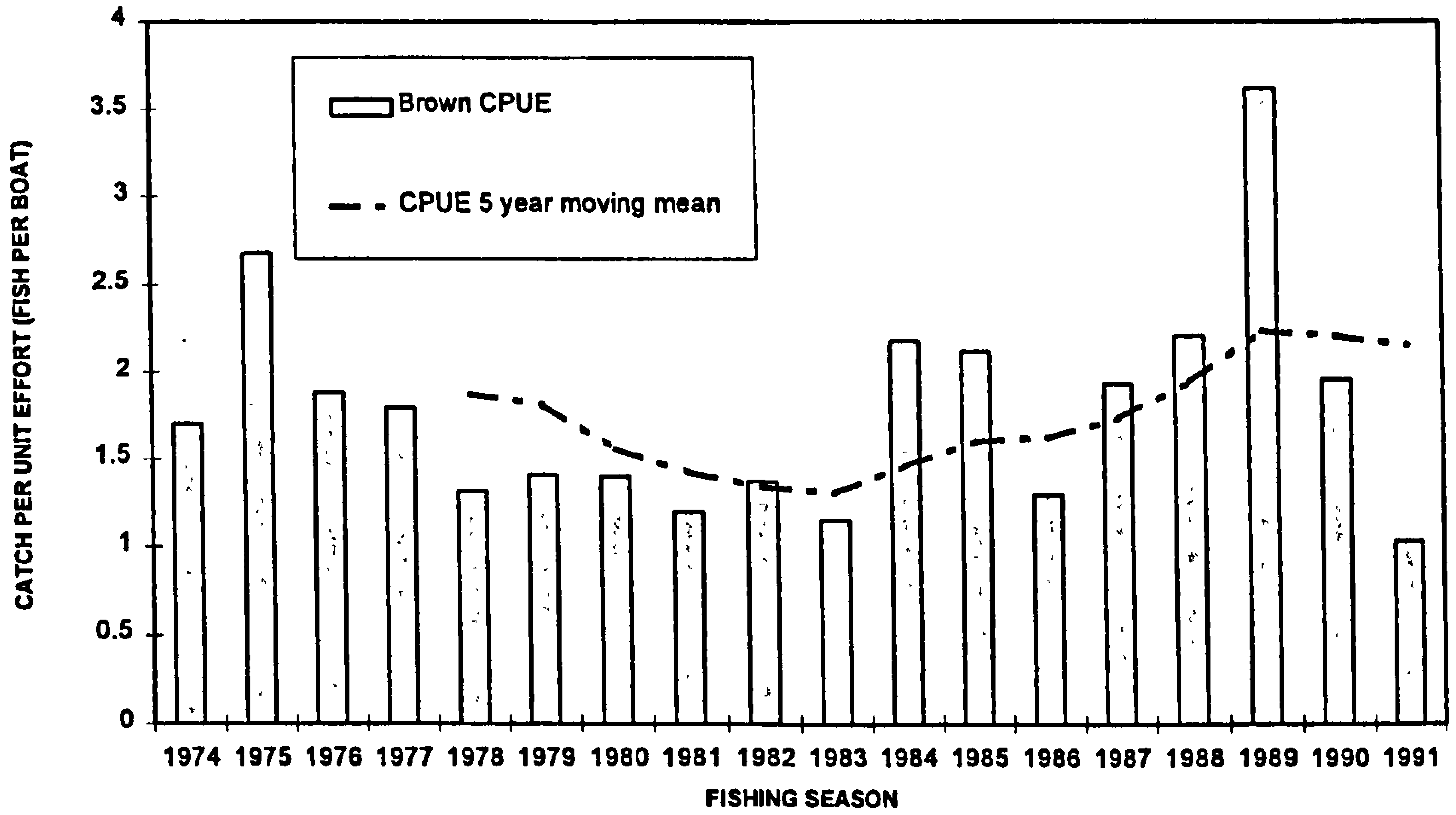
Perch

Catch date	**Net area set (m^2)**	**Mean time set (h:m)**	**No. fish caught**	**No. fish per m^2 per 24 h**
Jun-Aug 1998	1,800	16:53	567	0.448
Feb-Mar 1999	2,160	23:15	59	0.028

Factors affecting angling catch

Fig. 7 shows fluctuations in the brown trout CPUE for fishing seasons 1974 to 1991 (before rainbow trout stocking began) with a five-year moving mean.

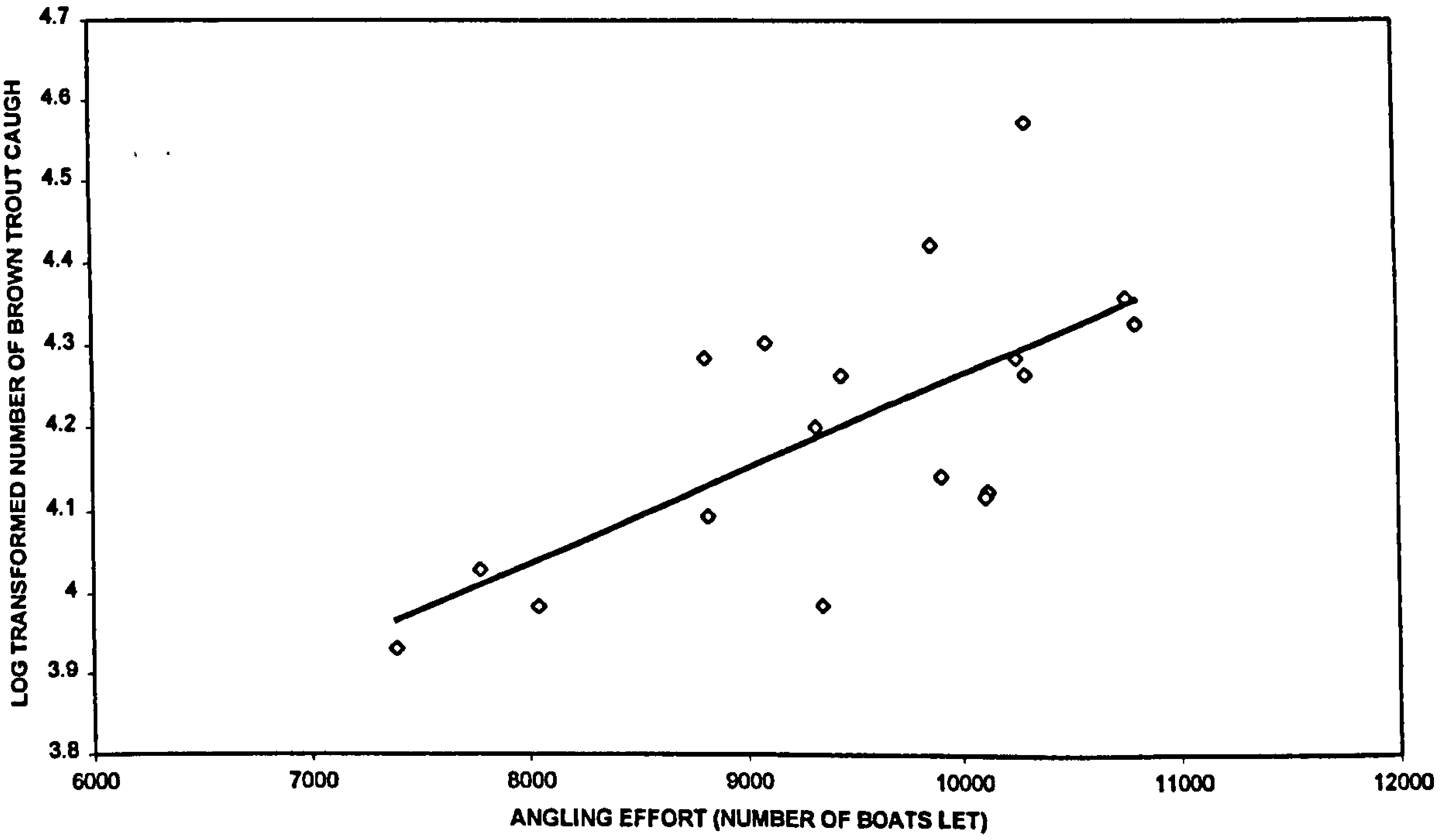
FIGURE 7: BROWN TROUT CATCH PER UNIT EFFORT, 1974 TO 1991



Whilst the mean monthly cormorant count increased from less than 20 to over 200, CPUE fluctuated around 1.8 fish per boat throughout the period. Although the lowest CPUE coincided with the highest preceding mean monthly cormorant count in 1991, the highest CPUE recorded in 1989 followed the second highest mean monthly cormorant count.

Nevertheless, it has been argued that cormorant numbers are adversely affecting angling catches, and in order to test this hypothesis, forward stepwise multiple regression analysis of angling catch was conducted for the years 1974 (when angling effort was first recorded) until 1992 (after which rainbow trout stocking began). Brown trout numbers caught and brown trout total weight caught, were dependent variables. Brown trout stocking from the same year and from the preceding year, angling effort the same year and Cormorant counts from the preceding winter were independent variables. For brown trout numbers caught, only one step, angling effort, was found to be significant ($F_{1,17}$ = 13.19, p = **0.002**, adjusted R^2 = 40.4%). Similarly, for brown trout weight caught, only angling effort was found to be significant ($F_{1,17}$ = 13.45, p = **0.002**, adjusted R^2 = 40.9%). The relationship between brown trout numbers caught and angling effort is illustrated in Fig. 8.

FIGURE 8: LINE FIT PLOT FOR ANGLING EFFORT AND NUMBER OF BROWN TROUT CAUGHT



It has also been postulated that if over-wintering cormorants are taking large numbers of trout, they may be having a detrimental effect on the commercial viability of the fishery by causing an increase or decrease in the mean weight of brown trout caught, as higher cormorant numbers selectively remove particular size classes of fish. However, regression analysis of mean brown trout weight and cormorant numbers the previous winter showed no significant influence.

Wounding of trout by cormorants

Of the 246 brown trout caught in July to August 1998, only one fish was found to be wounded, a proportion of 0.4%. This contrasts with a sample of 567 perch caught at the same time of which 21.5% showed signs of cormorant wounding. Individual trout ranged in weight from 9.1 g to 2.36 kg, median 165 g, and in fork length from 95 mm to 602 mm, median 217 mm. At the time there were between twenty and thirty cormorants summering on the loch.

Of the 424 brown trout caught in February and March 1999, eleven were identified as having old wounds and nine as having fresh wounds, giving an overall proportion of 4.7% wounded fish. Individual trout ranged in weight from 18.8 g to 1.77 kg, median 267.5 g, and in fork-length from 119 mm to 575 mm, median 305 mm. At the time there were around 200 cormorants wintering on the loch.

Cormorant diet

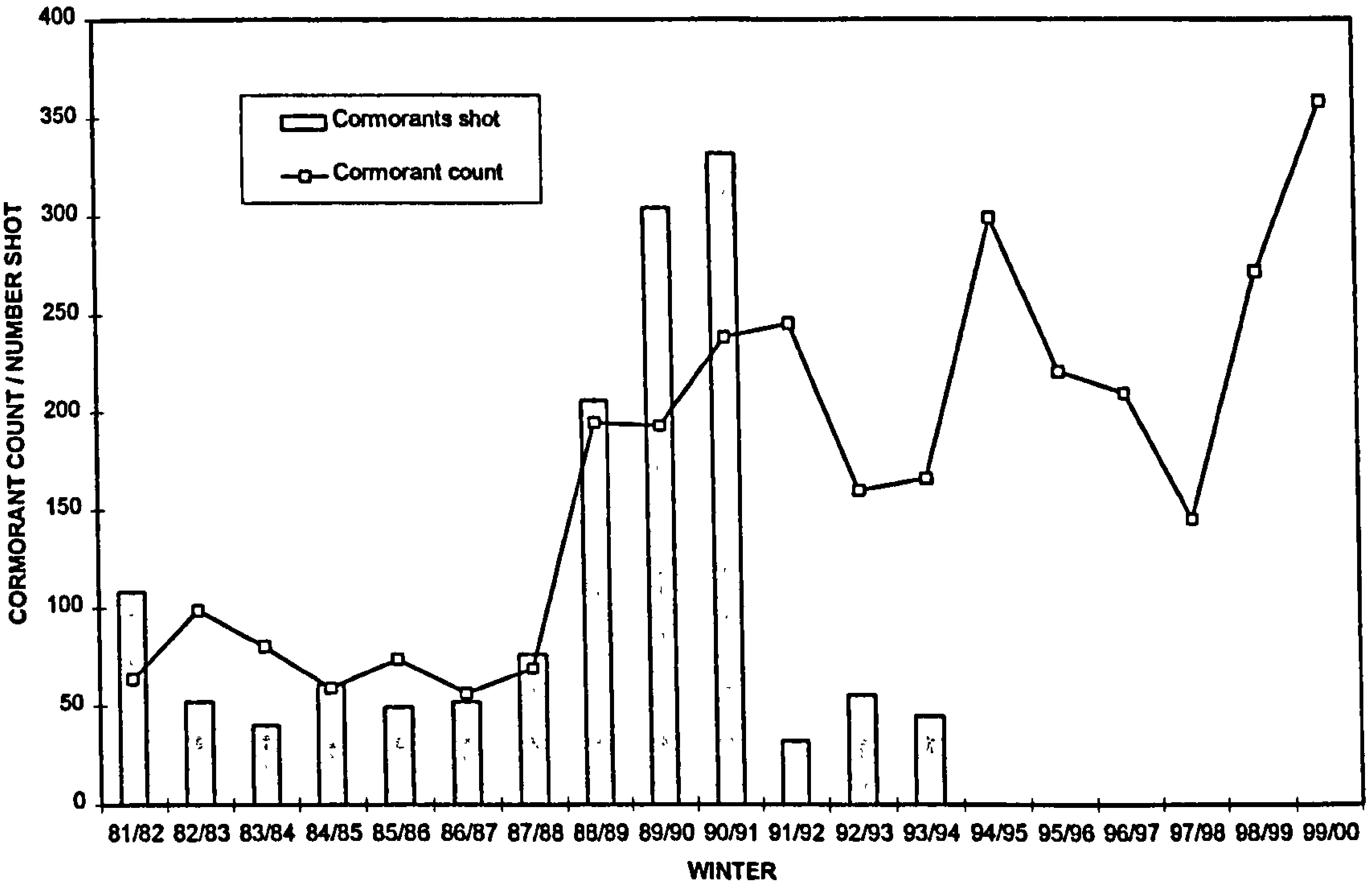
The composition of the two samples of fish regurgitated by cormorants during cannon netting differed markedly. On 7 October 1997, regurgitates from 13 birds comprised 35 perch, one trout and 58 three-spined sticklebacks. The perch ranged in weight from 2 to 200 gm, with a median of 60.5 gm., and perch length ranged from 4 to 24 cm, with a median of 15 cm. The single trout would have weighed about 100 gm and the sticklebacks averaged 6.7 gm. By contrast, on 21 December 1997 the regurgitates from 12 birds comprised 12 trout and four sticklebacks, with no perch. The corrected trout weights, allowing for estimated digestion, ranged upwards from 6 gm, with a median weight of 76 gm, and seven of the 12 were less than 100 gm. Three were between 100 and 200 gm, one around 350 gm, and one may have originally exceeded 1 kg, although it was partly digested. The lengths ranged from 8 to 30 cm, with a median length of 18 cm.

The collection of cormorant pellets between December 1998 and February 1999 proved to be difficult. The birds tended to roost high in trees at the water's edge, and most pellets either disintegrated on impact with lower branches or on the rocks below, or fell into the water. Of 81 pellets collected, 29 were found to be empty of fish remains, and 11 pellets contained fish remains that could not be identified to species. Six pellets contained both perch and trout, 13 contained only perch and 21 contained only trout. Three pellets contained two or more perch and two pellets contained two or more trout. One pellet contained remains from a large number of roach *Rutilus rutilus*.

The effectiveness of attempts to control cormorants at Loch Leven

The number of cormorants shot each year since 1981/82 (when records began) is illustrated in Fig. 9, along with the mean monthly cormorant counts.

FIG 9: MEAN CORMORANT COUNT AND NUMBER OF CORMORANTS SHOT - 1981/82 TO 1999/2000



Over 1400 cormorants have been killed since 1981/82, with over 700 killed during the three winters 1988/89 to 1990/91. Beneficial effect of shooting should have become apparent through a consequent reduction in wintering cormorant numbers and/or an increase in fish catches. Multiple regression analysis was conducted, using cormorant counts as the dependent variable, and the number of cormorants shot during the same winter and each of the three preceding winters, as independent variables. No significant relationship was evident.

Although up to 170% of mean numbers present were shot in a winter, there is no evidence of the anticipated beneficial effect of reduced numbers of cormorants or higher catches. However, there are many other factors which might have influenced cormorant usage of Loch Leven at the same time as the shooting, and masked or partially masked any beneficial effect. It could be argued, for example, that had shooting not taken place, cormorant numbers would have been even higher and angling catches lower. It could be speculated that small changes in the rate of turnover could have confounded the beneficial effects of shooting. It would require the development of a fairly sophisticated modeling process to take account of all such possible factors, and determine what may have been the actual effect of the shooting. Such modeling is beyond the scope of this thesis, but what is clear is that despite the intensive shooting, the numbers of cormorants were not reduced to an acceptable level, and the angling catches did not increase to the desired level.

Multiple regression analysis was also conducted on data from 1982 to 1999, using brown trout number and weight, CPUE brown trout number and weight, and the total number of both brown and rainbow trout, as the dependent variable. The number of cormorants shot during the same winter and each of the three preceding winters, were the independent variables. No significant relationship was evident. Therefore, there is no evidence of any beneficial effect of improved angling catches as a result of large-scale cormorant shooting.

DISCUSSION

Cormorant shooting

Despite the general protection afforded by the Wildlife and Countryside Act, cormorants may be shot for the purpose of preventing serious damage to fisheries, and to this end licenses may be issued in Scotland by the Scottish Executive Rural Affairs Department (SERAD). This raises the possibility of birds protected on breeding and wintering grounds by UK and European legislation, being legally shot elsewhere, with potentially serious consequences for protected populations. This is a particular issue in Scotland as declines in breeding cormorants in north-west Scotland, including on some Special Protection Areas, may reflect the impact of shooting (Russell *et al.*, 1996). Of the 400 to over 800 cormorant killed legally in Great Britain each year, 96.6% were killed in Scotland (Kirby *et al.*, 1997). The liberal approach to issuing of licenses by SERAD, formerly Scottish Office Agriculture, Environment and Fisheries Department (SOAEFD), and the apparent secrecy which surrounds the evidence presented in support of the licenses, has caused controversy, and the difference in the positions taken by SERAD and the Government's own conservation body, Scottish Natural Heritage, has been called into question (Cosgrove, 1997).

Applicants for licenses to shoot cormorants are required to provide evidence to support their claim that serious damage is occurring. Marquiss & Carss (1994) argue that damage cannot be considered serious if it cannot be measured. They also argue that to justify a license to kill birds, losses have to be shown to be the result of bird predation. In practice, hard evidence of serious damage attributable to cormorants has proved elusive, and instead, it has been argued, licenses are issued on the basis of anecdotal information, which is subjective, and circumstantial evidence, which is often misleading and almost always ambiguous or inconclusive (Marquiss & Carss, 1994). In effect, the presence of cormorants in the vicinity of a fishery is deemed synonymous with serious damage occurring. This general assumption may be based on inappropriate comparisons with artificial situations or interpretation of results from poorly planned experiments lacking in scientific rigour. For example, experiments conducted in Canada which attempted to demonstrate the beneficial effects of culling large numbers of sawbills, kingfishers and other birds, have been heavily criticized for their simplistic interpretation of results (Marquiss & Carss, 1994, Russell *et al.,* 1996).

In addition, on the River Bush in Ireland, Kennedy & Greer (1988) deduced that cormorants could have taken 51-66% of wild salmon *Salmo salar* smolts, based on a sample of only six cormorant stomachs, two of which were empty. The very high predation rate was calculated by assuming that all birds seen on the river would have consumed 425g of almost exclusively salmonids, every day for a month during the smolt run. Similarly, Warke & Day (1995) estimated the cormorant predation rate on salmon parr as possibly as high as 47%, based on the stomach contents of only seven shot cormorants, three of which contained no salmon parr. They made the same assumptions as Kennedy & Greer, despite the acknowledgement that cormorants often overfly the river on their way to feed on Lough Neagh. Biases in the sampling method, and the possibilities that birds might leave with less than a full stomach, feed in more than one location, or that their prey might vary across the catchment were not considered. In both cases the samples were considerably smaller than the 12 to 15 described as adequate by Marquiss & Carss (1997), as a result of analysis of stomach contents of cormorants shot on the River Tweed in Scotland. Also in Ireland, Macdonald (1988) estimated that cormorants took 5.8-13.1% of migrating smolts based on "direct observation of feeding birds", but no data were provided to support this conclusion. Despite these shortcomings, the above results are quoted as evidence of heavy cormorant predation on salmonids in an advisory report to Government Ministers, (Dunnet, 1996).

After a license is issued, there is no obligation on licensees to demonstrate any beneficial effects of cormorant shooting, and together with the lack of evidence of serious damage, this exposes weaknesses in the implementation of legislation. Marquiss & Carss (1994) argue that if birds are killed and a subsequent increase in fish abundance or fish catches cannot be detected, then killing cannot be said to prevent serious damage. Furthermore, killing cormorants at an ailing fishery, and thus being seen to "do something", may divert attention from more taxing issues such as improved marketing of the fishery or tackling water quality issues, even though they may have a far greater impact on fishery economics than avian predation.

Cormorant damage on Loch Leven

The Loch Leven data on wintering cormorant numbers, fish catches, fish stocking, angling effort and cormorant shooting offer a unique opportunity to explore long term inter-relationships between these factors on an internationally important wetland and commercial trout fishery. The past practice of shooting cormorants has been based on the assumption that cormorant presence leads inevitably to damage to the fishery, and declining trout catches have been cited as evidence of serious damage. However, this analysis of the Loch Leven data shows no evidence of any detrimental effect of wintering cormorants on angling catches, and thus no evidence to support the assumption that they are causing serious damage. Furthermore, CPUE was relatively stable despite the increase in cormorant numbers, and there is strong evidence that the principal factor in determining angling catch is angling effort, which is likely to be influenced by many external factors, including increased competition from other fisheries. Hypothesis (a) (Increased cormorant numbers have damaged the Loch Leven trout fishery by depleting the trout population and reducing angling catches) is therefore rejected.

The evidence that despite the huge increase in cormorant numbers the trout population is now no smaller, implies that cormorants are not depressing the trout population. The large reduction in the percentage of the trout population caught by anglers suggests some behavioural change that renders trout less susceptible to fly fishing, such as a switch to benthic rather than surface feeding in response to changes in the invertebrate community and reduced water clarity as a result of eutrophication. Alternatively it may reflect angler response to the availability of rainbow trout, changes in angling techniques and a reduced effort to catch brown trout. Furthermore, the fact that only 8%, perhaps as few as 3%, of catchable brown trout are now caught suggests that shooting cormorants will have no beneficial effect, as the trout catch is apparently limited by factors other than the number available in Loch Leven.

This lack of evidence of detrimental effects of wintering cormorants on trout catches is broadly in line with recent findings on other large freshwater bodies. Doherty & McCarthy (1997) concluded that cormorants do not represent a serious threat to the Lough Derg brown trout fishery. Keller (1995) concluded that serious damage to commercial fisheries was unlikely to occur, although there could be some competition with anglers. Keller *et al.* (1997) found no recognisable influence on fish populations and fisheries in large pre-alpine lakes, reservoirs, gravel pits and large rivers. Kieckbusch & Koop (1997) concluded that social fishing by cormorants took predominantly fish of little or no economic importance, but damage was possible on sites where solitary cormorants fished for eel *Anguilla anguilla.*

Van Dam (1997) found cormorants took only 5% of the commercial catch of eels. He also found that almost equal quantities of perch were caught commercially, as were killed and discarded as eel-fishery by-catch, and as were taken by cormorants. Dirksen *et al.* (1995) found little or no conflict with commercial fisheries. Marteijn *et al.* (1997) concluded that the consumption of commercially valuable fish is often limited, and fisherman's complaints of cormorants consuming large amounts of commercially valuable fish are often unjust. Van Eerden and Zijlstra (1997) found no evidence of serious damage. Marion (1997) found that cormorants took about 3% of fish stocks, that impacts were negligible on eels and non-commercial species, but could be more important on tench *Tinca tinca* and pike *Esox lucius*. Mellin & Mirowska-Ibron (1997) concluded that cormorants caused damage on fish farms but not on natural lakes.

Stempniewicz & Grochowski (1997) found the bulk of fish taken by cormorants were of small size classes and of species that were of little, or at best moderate, economic value, and concluded that cormorants had little economic impact.

It has also been argued that compensatory mechanisms and competition from other predators may act to limit the survival of prey species regardless of predation by cormorants. Van Eerden and Zijlstra (1997) considered the indirect impact of removal of immature fish of commercially important species to be potentially the most likely cause of damage, but concluded that high natural mortality of immature fish and compensatory mortality mechanisms would act as a buffer, and possibly fully compensate the effects of cormorant predation. Piggins (1958) reported that sea trout *Salmo trutta* were the most severe predator of salmon smolts. He also suggested that other predators were behaviourally adapted to exploit smolts, with, for example, the invasion of the estuary by predatory sea fish timed to coincide with the smolt run. Larsson & Larsson (1975) estimated that burbot *Lota lota* ate 30% of 550,000 smolts released. Larsson (1985) also recorded high levels of predation of smolts by pike, and estimated the total proportion taken by all predators as 50% to 70% of 660,000 released.

It is clearly important to isolate the particular impacts of predation from external effects in order to come to a judgement as to whether that predation is indeed causing serious damage. Lindroth (1965) found correlations between climatic conditions in the sea and long term fluctuations in survival of salmon smolt to adult stages, and postulated that the causative agent must act in the sea. The impact of climatic factors was also identified by

Derby & Lovvorn (1997) in their investigation into trout survival in U.S.A., where they found that although trout were predated in large numbers by piscivorous birds, over-winter survival limited trout recruitment regardless of bird predation.

Angling effort

The evidence that angling catch is principally determined by angling effort suggest that the decline in Loch Leven's trout catches may, in part, reflect an increasingly competitive angling market, rather than the impact of cormorant predation. According to East of Scotland Water (ESW), which controls around thirty trout fisheries, whilst demand for angling has been static, there has been an increase in availability. This has lead ESW to increase their marketing effort, and whilst rainbow trout fishing is holding its own, brown trout fishing remains in decline (S. Manson, pers. comm.). At another major trout fishery, Rutland Water in England, managed by Anglian Water, trout angling has declined over the period 1980-1995, but has stabilised over the past five years at the time when cormorants were at their most numerous (D.E. Moore, pers. comm.). This suggests that the Loch Leven fishery is not alone in experiencing a decline in demand, and examples of increased competition in the vicinity of Loch Leven include the development of fisheries at Heatheryford and Lochore Meadows, and in the Ochil and Lomond Hills.

Trout wounding

The finding that 4.7% of gill-netted brown trout showed signs of cormorant damage in late winter, an increase from 0.4% at the start of the winter, demonstrates that cormorants are wounding trout of a catchable size for anglers. However, the large sample size and low percentage wounded, and the fact that some wounds were old and apparently healing, suggest that wounding is unlikely to have a major impact on the fishery. Furthermore, there is a possibility that some trout were wounded whilst in the gill nets which were set for an average of 23 hours each. It is known that cormorants may take fish from nets or fish traps (Russell *et al,* 1996), one cormorant was found drowned in a gill net, and two fish close together in a net had multiple wounds.

Cormorant diet

The samples of regurgitated fish and cormorant pellets are too small for meaningful statistical analysis, but nevertheless they do provide some useful information. They indicate that during the study period the Loch Leven cormorant diet principally comprised trout and perch, possibly in proportions of 60:40, with some three-spined sticklebacks and roach. This contrasts with the findings of Carss & Marquiss (1992 &1994) who concluded that cormorant diet had switched from one dominated by perch to one strongly dominated by trout. Given the apparent reappearance of perch in the loch in large numbers, this may simply reflect the opportunistic nature of cormorant foraging behaviour, and their ability to switch between prey as profitability varies. The importance of perch in the diet of cormorants is also evidenced by the high proportion of perch showing signs of cormorant wounding, and by the steep decline in the population over the winter indicated by netting samples.

There may be some seasonal variation in prey selection, with dominance of trout over perch in pellets and regurgitates most apparent in December. However, sample sizes are small and this could equally reflect the cormorant's ability to switch between days, with the October regurgitate sample reflecting a "perch" day and the December sample reflecting a "trout" day. The finding of one pellet full of roach remains, which could not have originated from Loch Leven, indicates that not all birds that roost on the loch necessarily feed there.

The size of trout taken was considerably smaller than was previously reported by Carss & Marquiss (1992 & 1994) who found that most of the trout taken were large enough to be kept by anglers, with median lengths of 25 and 29 cm. They commented on the lack of small trout in the cormorant diet despite their availability in the loch, suggesting that cormorants were selecting for the larger fish. However, the trout in the regurgitate sample had a median length of 18 cm, and only three were of catchable size for anglers. This may reflect changes in the age/size structure of brown trout, with increased availability of smaller fish or reduced availability of larger fish. By contrast, perch size, with a median length of 15 cm in October, was considerably larger than the medians of 5 cm in November/December and 14 cm in January February previously reported by Carss & Marquiss (1992 & 1994). This may reflect changes in the age/size structure of the perch population, with increased availability of larger fish.

Shooting of Cormorants

The Loch Leven data show no beneficial effects in terms of reduced cormorant numbers or improved fish catches as a result of large scale shooting, which raises questions as to the validity of issuing licenses for cormorant control. Hypothesis (b) (Shooting cormorants on Loch Leven is an effective mitigation measure, resulting in reduced cormorant numbers and increased trout catches) is therefore rejected. Shooting is widely used in Britain as a mitigation measure and yet there has been no previous attempt to assess the effectiveness of shooting in reducing cormorant damage. Indeed there is no scientific evidence that the removal of predators through killing reduces bird abundance in a particular area or has resulted in an increase in fish yields. Since cormorants are highly mobile there is every chance that removed individuals will be replaced quickly by others, making shooting futile (Kirby *et al.* 1997). The finding that large scale shooting of cormorants on Loch Leven had no beneficial effects in terms of reduced cormorant numbers or improved fish catches is broadly in line with findings from elsewhere. In Poland, Przybysz *et al.* (1997) concluded that although cormorant killing had been carried out since 1987, no decline in numbers has been detected. Dobrowolski & Dejtrowski (1997) reported that 5,335 cormorants were shot legally, with no reduction in numbers. Shooting to provide mental comfort to fishery managers (Dobrowolski & Dejtrowski 1997) or to vent a fishery managers' frustration is unjustified and illegal (Kirby *et al.* 1997).

The Loch Leven data, compiled over 32 years, are considerably more detailed than those available for many comparable sites where a cormorant/fishery conflict is perceived to exist. However, analysis of the data provides no evidence to support the perception of serious damage attributable to cormorants. Furthermore, there is no evidence of any beneficial effects of cormorant shooting either through reduced cormorant numbers or increased trout catches. The above conclusions question the assumption that serious economic damage to commercial and recreational open-water fisheries is attributable to cormorants, and further, questions the validity of issuing licenses to shoot cormorants for fishery protection purposes.

Chapter 5

TURN-OVER IN A WINTERING CORMORANT POPULATION: IMPLICATIONS FOR MANAGEMENT

ABSTRACT

Optimal foraging theory suggests that cormorants should aggregate in areas where profitability is highest, whilst continuing to sample other sites in order to be able to respond to changing profitability. Such behaviour would induce turnover within the population wintering on a site, and thereby reduce its susceptibility to control through shooting. Earlier work on Loch Leven showed that shooting was ineffective in reducing the number of cormorants present during the winter.

Multiple cormorant counts suggested large-scale movements of birds, which was confirmed by observations of groups arriving and departing. Short-range radio tracking revealed intermittent absences, with individuals present for 51% of the time. Satellite telemetry indicated that birds mostly ranged within 45km of Loch Leven, with occasional journeys further afield. The wintering cormorant population within 45km of Loch Leven exceeded 2,000, of which Loch Leven held 10%. There was evidence of movement between sites during the winter, with reductions on marine and estuary sites and increases on rivers and stillwaters. This is consistent with optimal foraging theory and demonstrates that the Loch Leven "population" is drawn from a wide area. High turnover within the population reduces its amenability to control, and would account for the ineffectiveness of shooting as a mitigation measure.

INTRODUCTION

Optimal foraging theory

Optimal foraging theory concerns the decisions an animal makes when harvesting food, including choices about where to feed, how long to feed there, how to best cover the feeding area, and what information should be gathered about alternative food sources (Krebs 1978). The rationale behind this approach is the assumption that animals will tend to forage efficiently, because natural selection will favour those most efficient at exploiting their food resource in order to survive difficult conditions and maximise reproductive success.

Various studies have shown that animals prefer the most profitable types of food and will actively select a prey item which gives the highest net food value, allowing for the energy costs of handling and digesting it and the energy expended in searching for it. In a feeding area where such prey are abundant it will be profitable for a predator to become more selective, ignoring lower quality food items and restricting its diet to a narrow range of the high quality prey. Furthermore, where food items are not evenly distributed, but are concentrated in particular areas it is anticipated that predators will tend to aggregate in locations where profitability is highest.

However, the profitability of any foraging area is likely to change over time as a result of prey depletion by the predator, or as a result of seasonal or diurnal patterns of prey availability. Foraging profitability in deteriorating conditions is then subject to diminishing returns, and in order to cope with such a change it is advantageous for a predator to have sampled other less profitable areas. It is then able to respond quickly to deterioration by switching to what was a second best area. Predators must decide how many foraging areas to visit and how long to spend there before moving on, and in order to do this they need information on the profitability of a variety of areas. There are energetic costs of travelling between foraging areas and of sampling poor areas, and these must be balanced by the need to obtain sufficient food as well as continually updating estimates of profitability in a fluctuating environment.

Cormorants and Loch Leven

The cormorant *Phalacrocorax carbo* is a top predator that winters on Loch Leven in large numbers. Optimal foraging theory suggests that individual cormorants should sample other foraging sites within a reasonable distance based on the energy costs of travel, and should switch to feeding elsewhere when profitability is higher. In addition, cormorants wintering elsewhere would be expected to visit Loch Leven in order to sample its profitability, and to remain there if this was higher than their previous experience. In practice, these processes would be apparent from the behaviour of individuals departing and arriving, and from changes in overall numbers as relative profitability between sites changed and birds switched from one to another. The effect would be to create a continuous but variable rate of turnover within the wintering population.

The increase in cormorant numbers wintering in Britain is well documented, e.g. Kirby, Gilburn, & Sellers (1995), and has resulted in concern over the possible impact of higher cormorant numbers on commercial fishery interests, (e.g. Carss & Marquiss 1997, van Eerden & Zijlstra 1997). Shooting is commonly employed as a mitigation measure, but to be effective, it requires that the population is sufficiently discrete to be amenable to control measures. Turnover within a population would reduce its amenability to such control, and in practice, attempts to control cormorant numbers by shooting on open water fisheries have met with little success (e.g. Marquiss & Carss 1994, Mellin & Mirowska-Ibron 1997).

There appears to be considerable variability in the degree of site fidelity shown by cormorants. Cramp and Simmons (1977) considered cormorants to be individually nomadic outside the breeding season, but Sellers and Sutcliffe (1987) believed that they showed a fair degree of winter site fidelity both within and between seasons. Yésou (1995) estimated that the number of individuals using his study site was 3.9 to 6.2 times higher than the highest mid-month count. Despite turnover, he found the small number of long-staying birds to be markedly site-faithful, with very little evidence of intermittent attendance. Buchheim (1997) found a large number of short staying birds, but strong site fidelity amongst the long-stayers. These reservations suggest that foraging strategy may vary from bird to bird as well as being a function of environmental conditions.

From analysis of ringing recoveries, Coulson & Brazendale (1968) concluded that dispersal of cormorants from breeding to wintering grounds was colony-specific. They showed that birds wintering in south-eastern Scotland were drawn principally from south-west and north-west Scotland, the Orkney Islands and the Farne Islands. This is supported by ringing recoveries at Loch Leven, which include birds ringed in south-west and western Scotland, northern Scotland and Orkney, and the Forth and Farne Islands. Coulson & Brazendale (1968) also showed that the logarithm of the number of birds wintering within a particular distance of the colony was linearly related to that distance. This suggests the possibility that if shooting depletes the number in a particular area, it may be balanced by immigration, as other birds redistribute themselves in order to maintain the dispersal pattern.

Loch Leven is a famous trout fishery as well as a wetland of international importance for breeding and wintering waterfowl. It is a National Nature Reserve, Ramsar Site and Special Protection Area, and long term fishery and bird records facilitate the study of fishery/cormorant interactions. Until 1995, cormorants were shot in large numbers for fishery protection purposes, despite the lack of evidence of impacts on the fishery, or of beneficial effect of shooting.

This paper considers the cormorant's foraging behaviour, reviews evidence of turnover within the Loch Leven population, and tests the following hypothesis:

(c) High turnover amongst the wintering cormorant population of Loch Leven reduces its amenability to shooting an a means of population control

METHODS

Four principal observers conducted multiple cormorant counts, three times each day for 106 days in October and November and February to April during the winters of 1996/97 and 1997/98. In addition, two counts per day were completed for 55 days during December and January. Loch Leven is not a difficult place to count cormorants, with sufficient elevated observation points to enable the whole site to be overlooked, and cormorant roost and loafing sites are well known. Each count was conducted by one person and took up to two hours. There was therefore some scope for error due to unobserved bird movements during a count, but these counts are assumed to have a generally high degree of accuracy. Individual observer performance was analysed by comparing mean counts of pairs of observers conducted during overlapping periods. Casual observations of Cormorant arrivals and departures were also recorded, together with the direction from which they originated or in which they departed.

Eighteen cormorants were captured in order to fit them with short-range radio or long-range satellite-tracked transmitters. They were captured using cannon nets, either 15 m X 15 m or 15 m X 30 m, depending on the size of the capture site. The first capture site was a gravel bank off the largest island, which was exposed during periods of seasonally low water and used as a daytime loafing site by cormorants. The second site was a steep gravel beach on the large island, which was used as a daytime loafing site when higher water levels covered the offshore gravel bank. Dummy cannons and ropes were laid on a site for several days before a catch attempt, in order to give birds time to become accustomed to them. The site was monitored closely by telescope from the loch shore for several days, in order to assess the number of birds and their loafing behaviour pattern. Once sufficient birds were consistently using the site, the date of the capture attempt was determined. The nets were set under the cover of darkness when the cormorants had departed for their nighttime roost.

As the cormorant is a large, long-necked bird, and roosts in a vertical posture, the cannons were set to fire relatively high to avoid injury. They were aimed at a height of 1.7 metres at a distance of three metres, with a two-metre danger area in front of the net. Whilst this protected the cormorants it had the disadvantage of allowing some birds to escape from the catching area before the net descended on top of them. Thus on 7 October 1997 of 19 birds in the catching area at net firing, 13 were caught, and on 21 December 1997 of 20 birds in the catching area at net firing, 12 were caught.

Once laid, the net and ropes were lightly camouflaged with dry grass to resemble a drift line on a beach and the cannons were camouflaged with tussocks of long grass and sedge. The capture team was in place before first light and was concealed in camouflaged hides to avoid disturbance. The cannons were fired from a nearby dug-out, and after firing the capture team ran forward to lift the net clear of the water, back onto the beach. The cormorants were removed from the net and held in hessian sacks whilst awaiting radio fitting. No injuries to cormorants were recorded, although the capture team suffered lacerations from their hooked bills. After the radio was fitted and the adhesive was dry, the birds were released back onto the loch.

Nine cormorants were fitted with TW3 short-range radio transmitters, supplied by Biotrack. The transmitters were fitted on the underside of the two central tail feathers to which they were attached with cable ties. Three transmitters were fitted on each of 17 March, 7 October and 21 December 1997. They were tracked manually with a Mariner M57 receiver and Yagi antenna, and all birds were checked for presence or absence at Loch Leven two or more times each day. The transmitters estimated operating life was 4.5 to 6.5 months (Biotrack), increasing with decreasing temperature.

Nine cormorants were fitted with PTT 100 satellite-tracked radio transmitters, supplied by Microwave Telemetry, and fixed to the bird's rump with epoxy resin. Six transmitters were fitted on 7 October 1997, two on 21 December 1997 and one on 4 February 1997. In addition, one transmitter was not fitted to a Cormorant, but was reserved for accuracy checks and allowed to transmit from known locations. All transmitters were set to transmit for eight hours per day, stepping forward one hour each day so that over 24 days the full 24 hour period would be equally covered. They transmitted a series of identification signals at intervals, and were tracked by the Argos satellite system. It required the receipt by the satellite of four identification signals to enable an accurate position fix. All transmitters were set for the Loch Leven altitude of 100 m.

Once the area over which Loch Leven birds ranged was established, monthly cormorant counts obtained from the Wildfowl and Wetlands Trust were collated for 179 marine, estuary, river and still water sites within that area. Marine sites comprised rocky shore areas on the Fife and Lothian coastlines. Estuary areas include the Forth upstream of the Forth Road Bridge, the Tay upstream of the railway bridge, and smaller areas including Tentsmuir Point, the Eden Estuary and Aberlady Bay. Rivers included the Forth upstream of Fallin, the Avon, Carron, Teith and Devon tributaries, the Tay upstream of the Earn mouth and the Earn. The location of these sites is indicated in Figure 1. In addition, there are over 100 large and small still waters scattered through the area. Twenty-nine major sites (including Loch Leven) held 40% of all cormorants and had adequate data sets to enable monthly variation in cormorant distribution between habitat types to be explored.

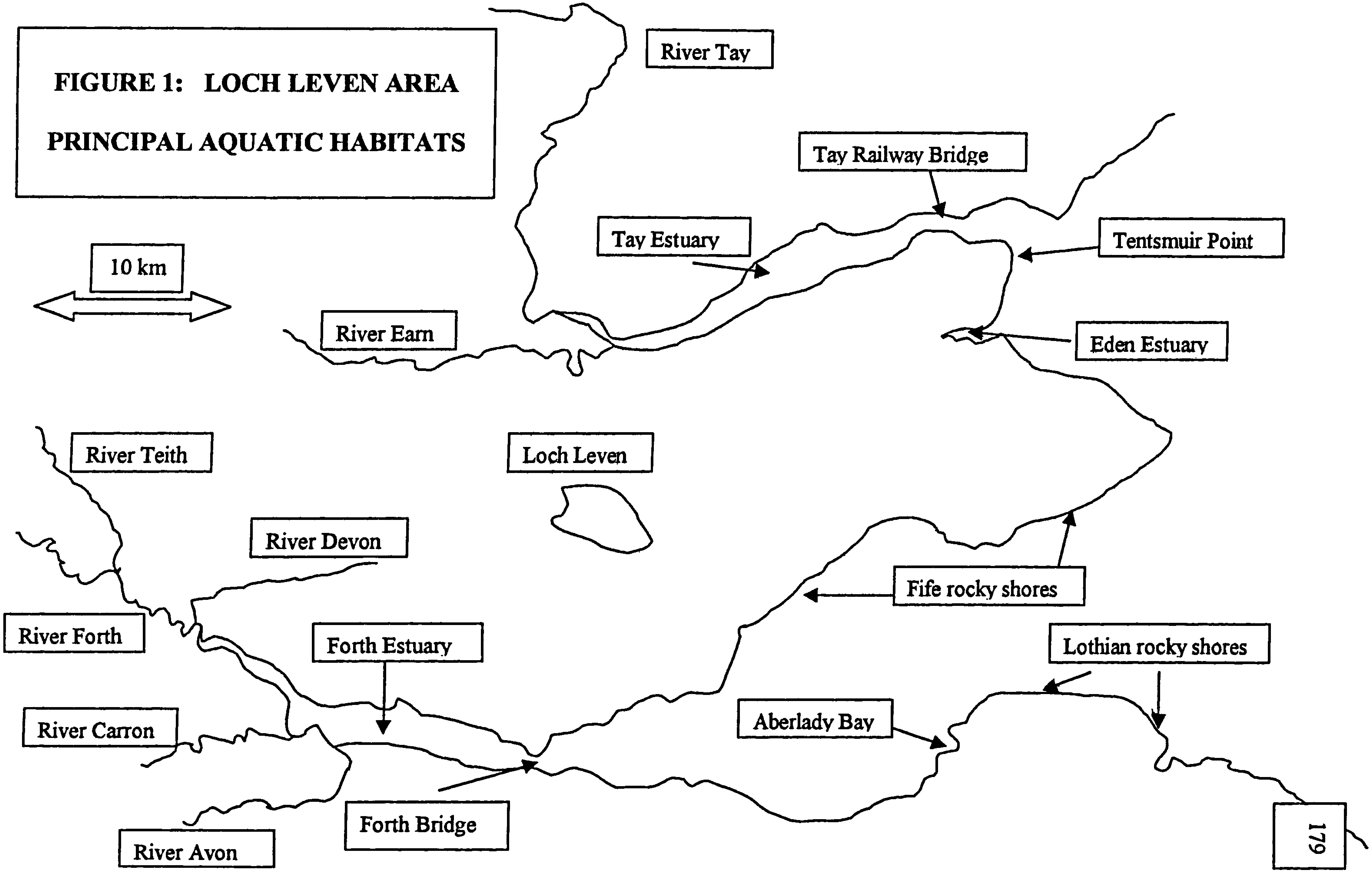


FIGURE 1: LOCH LEVEN AREA

PRINCIPAL AQUATIC HABITATS

RESULTS

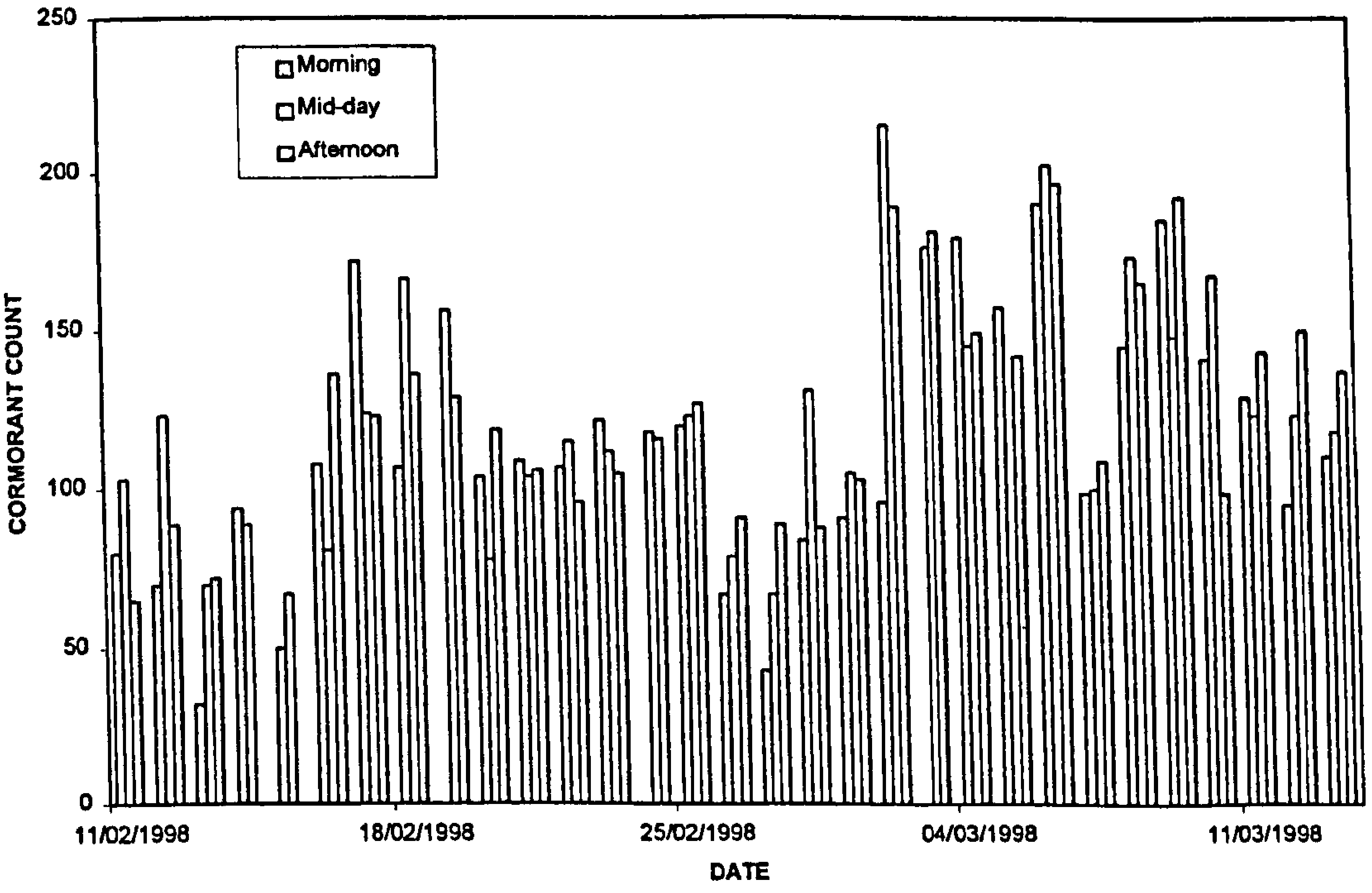
Observer analysis

Counts by pairs drawn from the four individual observers, conducted during overlapping periods, were compared by means of paired "*t*" tests. The counts varied up to 8.85% of the lower count, but none of the differences were statistically significant. This suggests that day-to-day differences in excess of this were likely to reflect true changes in numbers present.

Multiple counts

Fig. 2 shows multiple counts over a 31-day period, and illustrates fluctuations within and between days. There are periods where numbers were relatively stable, such as from 21 to 25 February, but on 2 March 120 birds arrived and on 6 March 100 departed.

FIGURE 2: WITHIN-DAY AND BETWEEN-DAY FLUCTUATION IN CORMORANT COUNT - 11FEB 98 TO 13 MAR 98



Diurnal variation

Mean values were calculated for each of the morning, mid-day and afternoon counts on 106 days when three counts were completed, and for each of the morning and afternoon counts on 55 days when two counts were completed. The means with standard error bars are illustrated in Figs 3 and 4. Although there is some variation between the means, ANOVA showed that these differences are not significant.

FIGURE 3: DIURNAL VARIATION IN MEAN CORMORANT COUNT WITH STANDARD ERROR BARS - THREE COUNTS PER DAY FOR 106 DAYS

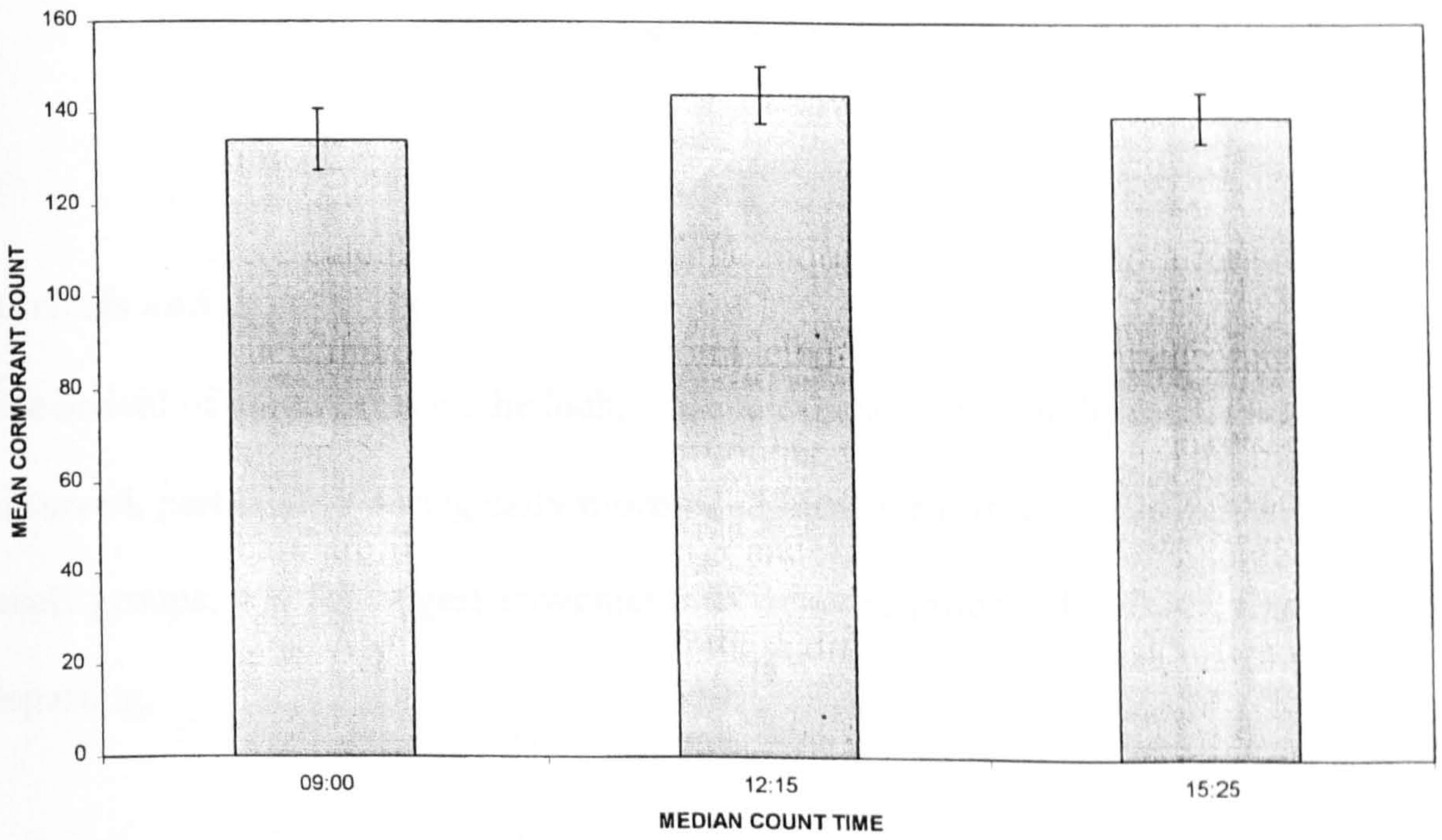
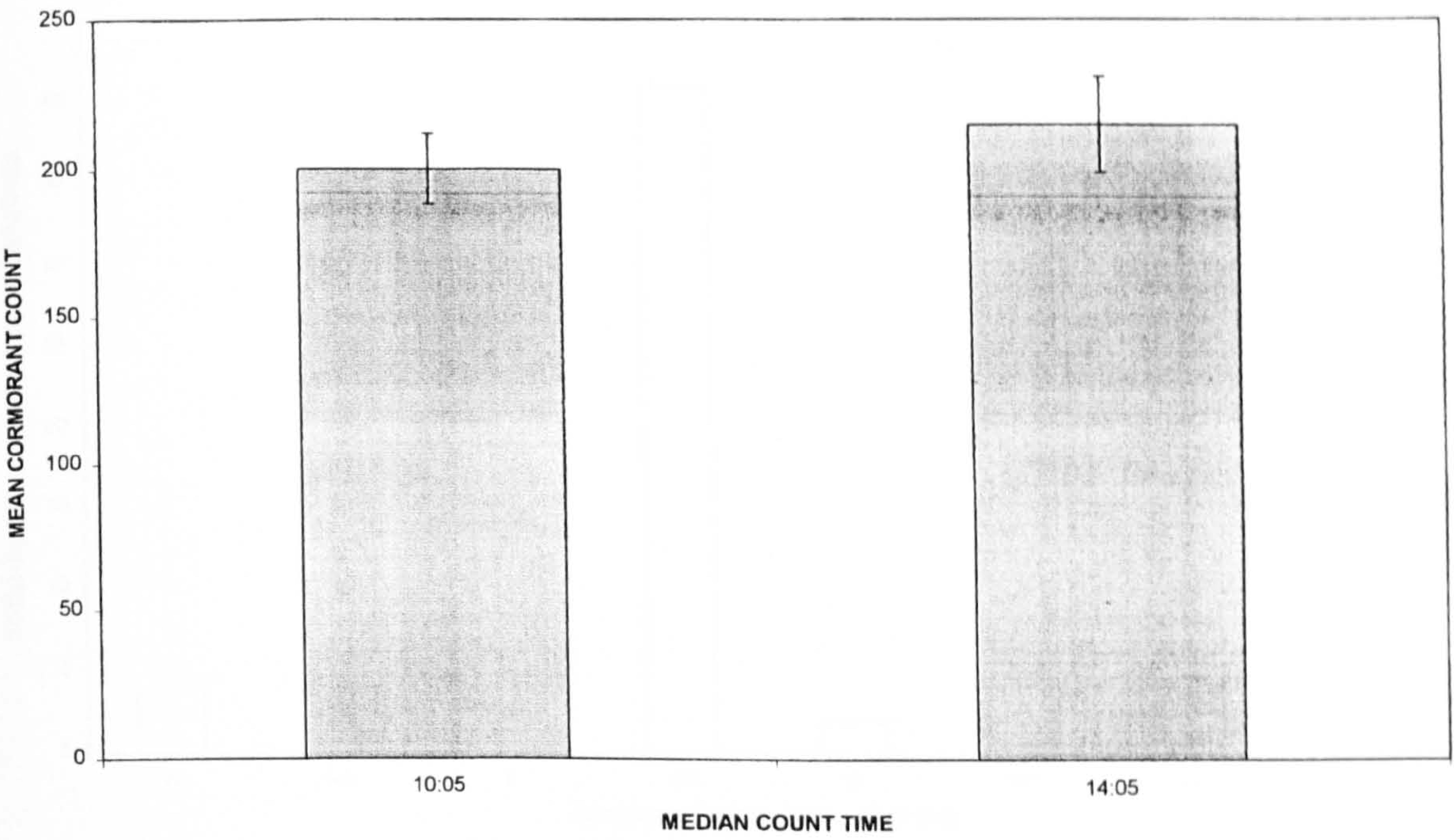


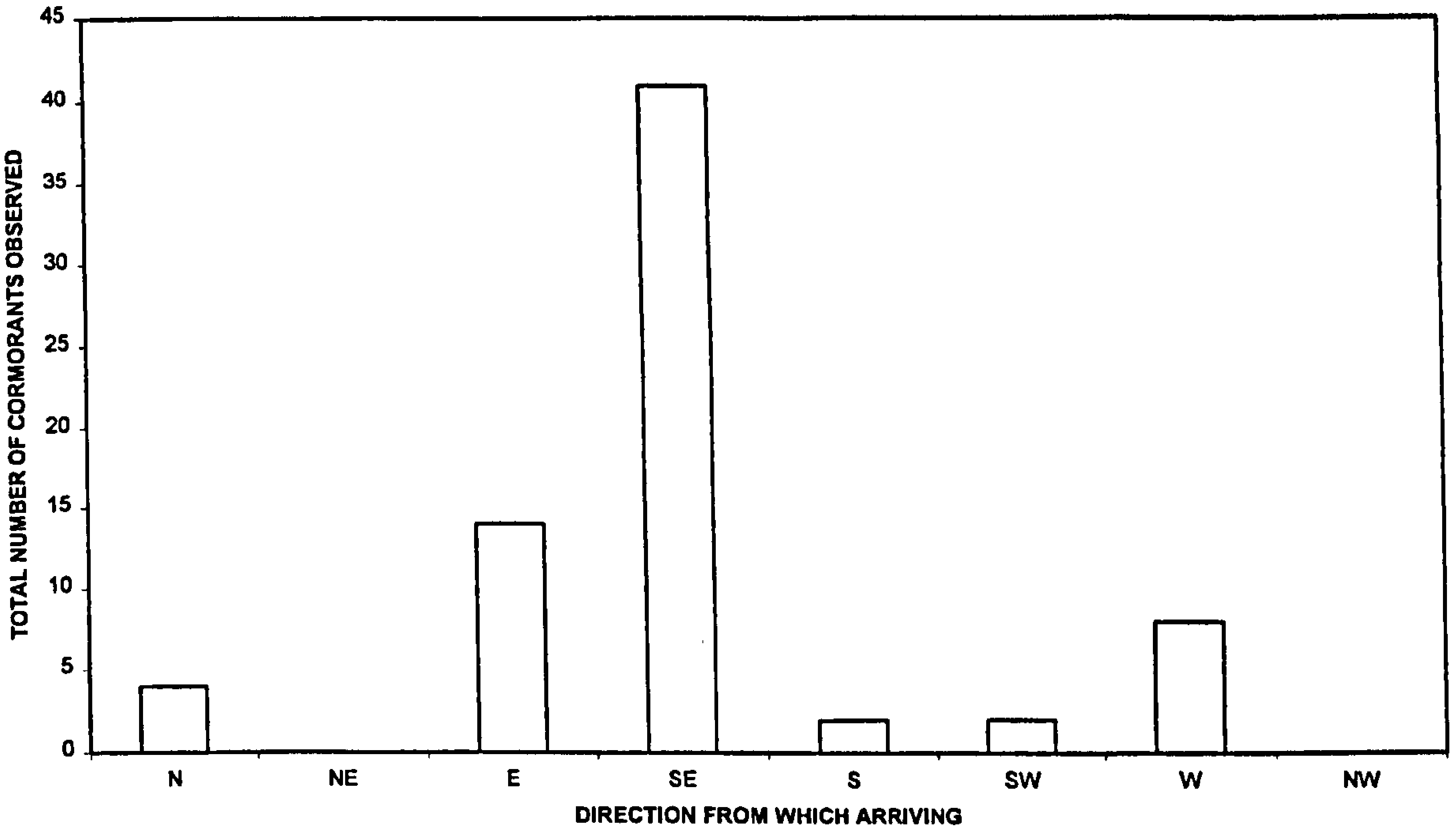
FIGURE 4: DIURNAL VARIATION IN MEAN CORMORANT COUNT WITH STANDARD ERROR BARS - TWO COUNTS PER DAY FOR 55 DAYS



Arrivals and departures

The arrival of cormorants on the loch, and their departure from the loch, was regularly observed, particularly during early mornings. Most birds travelled as individuals or in small groups, but the largest movements comprised groups of 320 arriving and 140 departing.

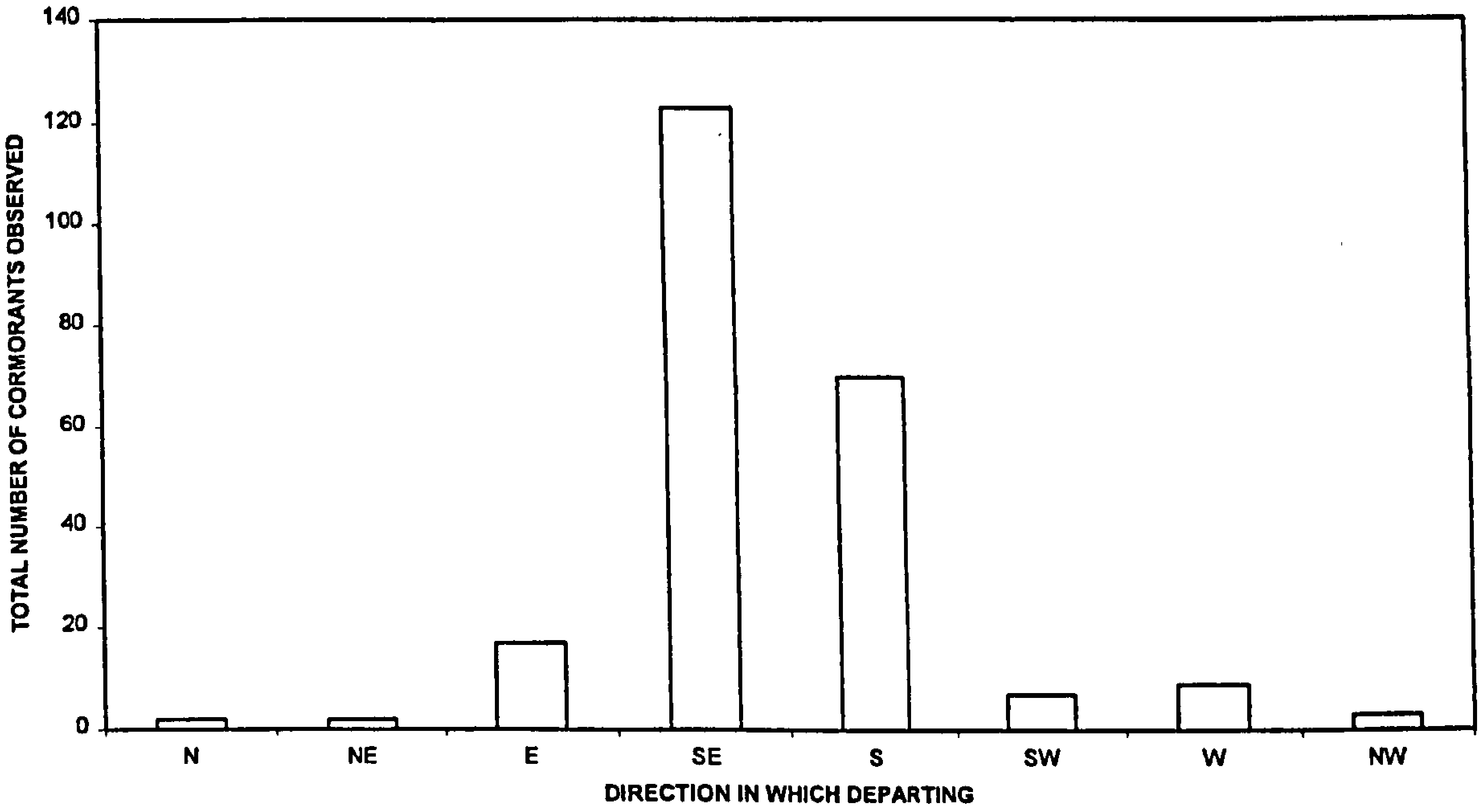
FIGURE 5: DIRECTION OF OBSERVED INDIVIDUAL AND GROUP CORMORANT ARRIVALS
(DOES NOT INCLUDE A GROUP OF 320 ARRIVING FROM THE SOUTH EAST)



The directions from which Cormorants arrived, and in which they departed are illustrated in Figs 5 and 6, but the two largest movements mentioned above, which were from and to the south east, are not included.

Arrivals originated largely from the east and south east, and departures were principally to the south east and south, but these birds were not followed beyond the loch so it is not known for how long these directions were maintained. No attempt was made to estimate the overall rate of turnover, due to the manpower required to systematically cover 20 km of shoreline and the apparently sporadic nature of Cormorant movements.

FIGURE 6: DIRECTION OF OBSERVED INDIVIDUAL AND GROUP CORMORANT DEPARTURES
(DOES NOT INCLUDE A GROUP OF 140 DEPARTING TO THE SOUTH EAST)



Short-range radio tracking

The proximity of elevated sites around the loch greatly facilitated radio tracking and strong signals were consistently received. When a radio transmitter was not located on a particular day but was located at some time afterwards, it was assumed that the bird had been temporarily absent from the loch. Following receipt of the final transmission, it was recognised that the bird could have died, left the loch, lost the radio, or the radio could have failed. Therefore, no assumptions were made as to the reason, and deductions were based only the period from release to the final transmission

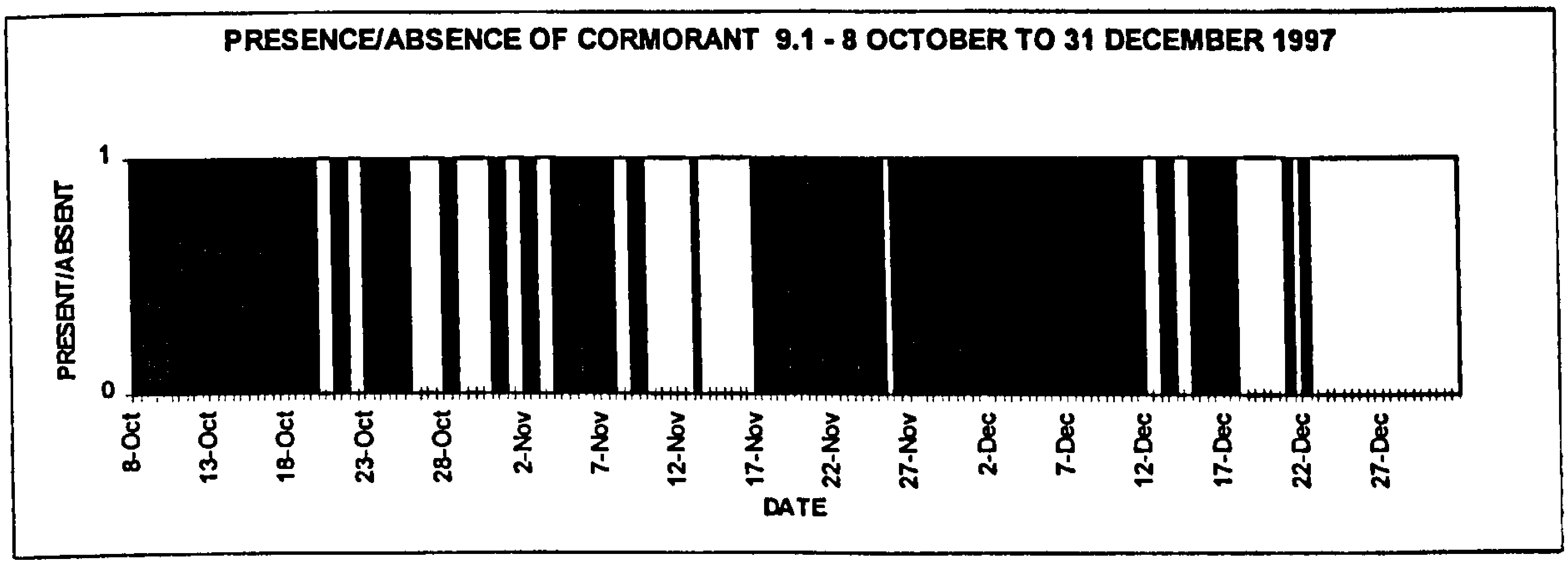
Of the three birds fitted with radio transmitters in March 1997, one bird was never located after the day on which it was captured and released. The second bird stayed for six days but was apparently absent for one day during that time. The third apparently left after six days before returning two days later, and stayed for between five and eight more days, the uncertainty being due to a receiver problem.

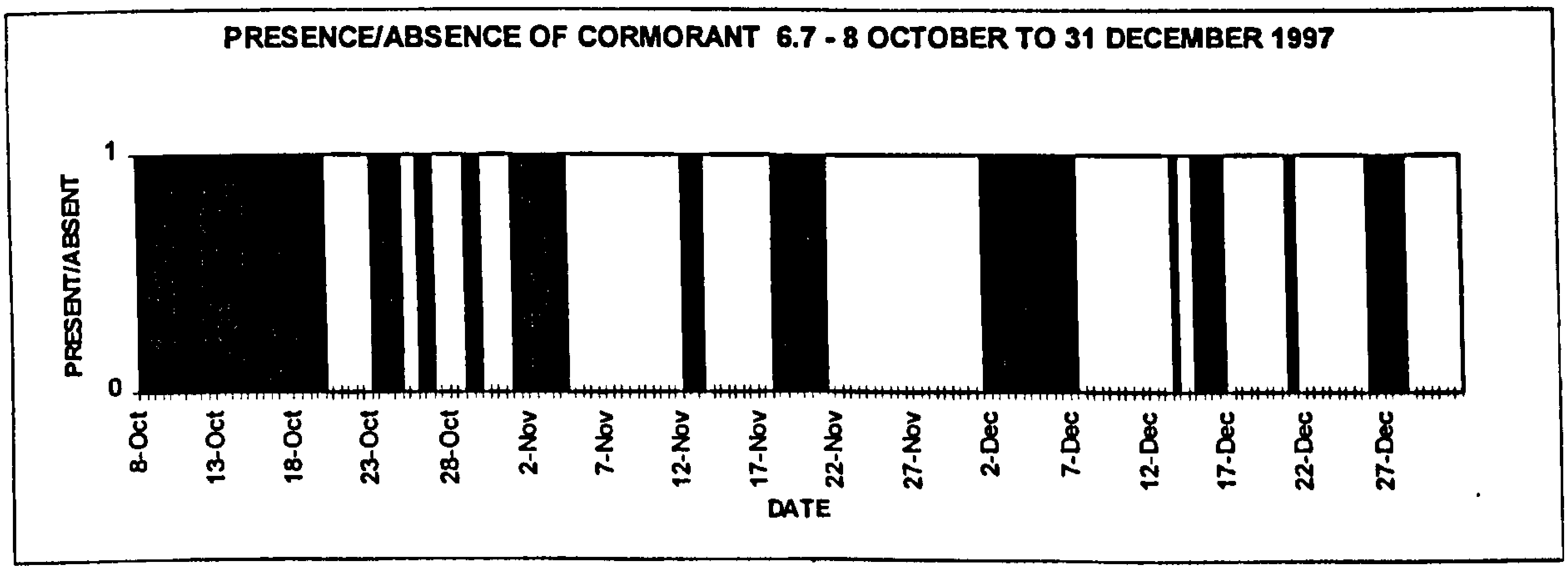
Of the three birds fitted with radio transmitters in October 1997, one transmitter was apparently defective, delivering a relatively weak signal even when in full view. Tracking of this bird was therefore deemed to be insufficiently reliable for proving presence/absence. The other two birds were tracked until December, and were present for 71% of 76 days, and 41% of 82 days. Their presence and apparent absence is illustrated in Fig. 7.

Of the three birds fitted with radio transmitters on 21 December 1997, one was present for four days but was not located afterwards. The others were present for 76% of 29 days and 28% of 94 days, as illustrated in Fig. 4. Although there was no concerted effort to track departing birds away from Loch Leven, Cormorant 5.7 was located several times on the Forth Estuary. On two occasions it was also tracked departing with other birds in the early morning and flying to feed on another freshwater site before returning to the loch later the same day.

The longest period for which a transmitter was tracked was 94 days, so transmitter life is not thought to have limited minimum stay results. When presence and assumed absence data are compiled for all birds, the total time present represents 51% of 303 days. This suggests the number of individuals using the loch is at least two times the mean population counted. It was not possible to determine the actual length of stay of individual birds, as time spent on the loch before the radios were fitted was not known and birds may have remained beyond the date when radios failed. However, the period over which transmissions were received may be used to indicate a minimum length of stay. The mean minimum length of stay for all nine birds was 43 days (SE 12.99). Allowing for 51% attendance, over the seven months from September to March this suggests that the number of individuals using the loch may be up to 9.7 times the mean count, which over the past ten winters is 233. These figures allow an estimate of the mean number of individual cormorants using the loch of between 466 and 2,260.

FIGURE 7: PRESENCE/ABSENCE OF RADIO-TRACKED CORMORANTS 9.1 & 6.7, WITH CORMORANT COUNT DATA 8 OCTOBER TO 31 DECEMBER 1997





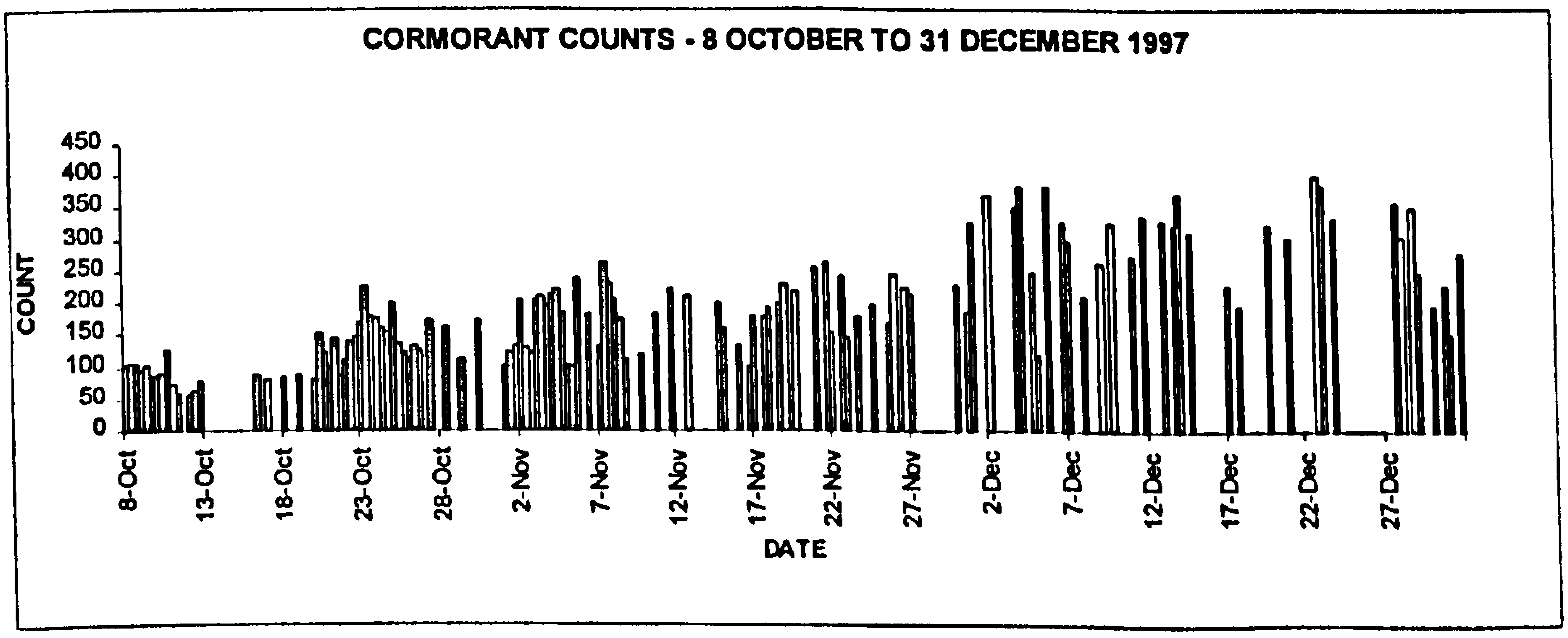
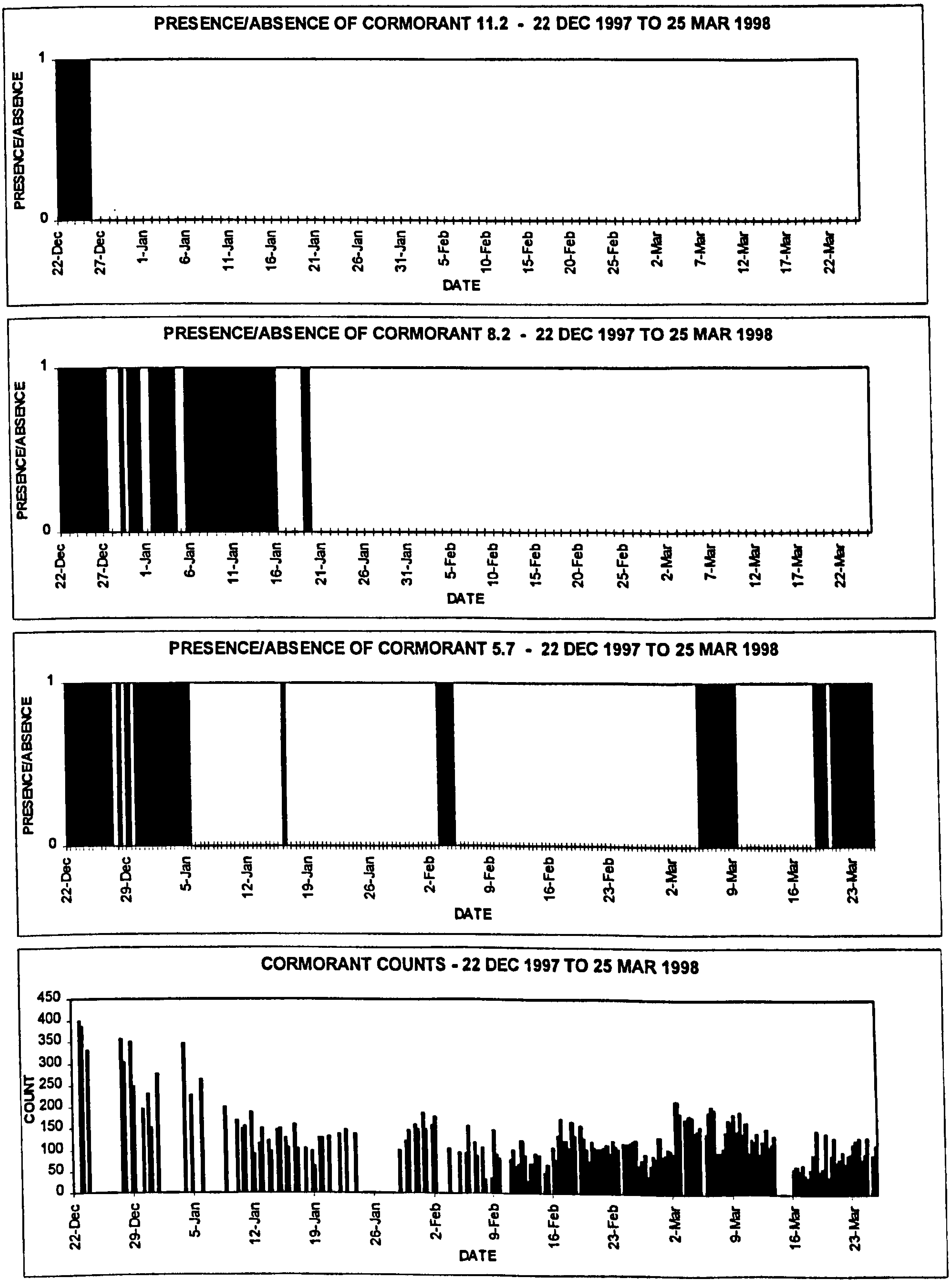


FIGURE 8: PRESENCE/ABSENCE OF RADIO-TRACKED CORMORANTS 11.2, 8.2 & 5.7, WITH CORMORANT COUNT DATA: 22 DECEMBER 1997 TO 22 MARCH 1998


PRESENCE/ABSENCE OF CORMORANT 11.2 - 22 DEC 1997 TO 25 MAR 1998

PRESENCE/ABSENCE OF CORMORANT 8.2 - 22 DEC 1997 TO 25 MAR 1998

PRESENCE/ABSENCE OF CORMORANT 5.7 - 22 DEC 1997 TO 25 MAR 1998

CORMORANT COUNTS - 22 DEC 1997 TO 25 MAR 1998

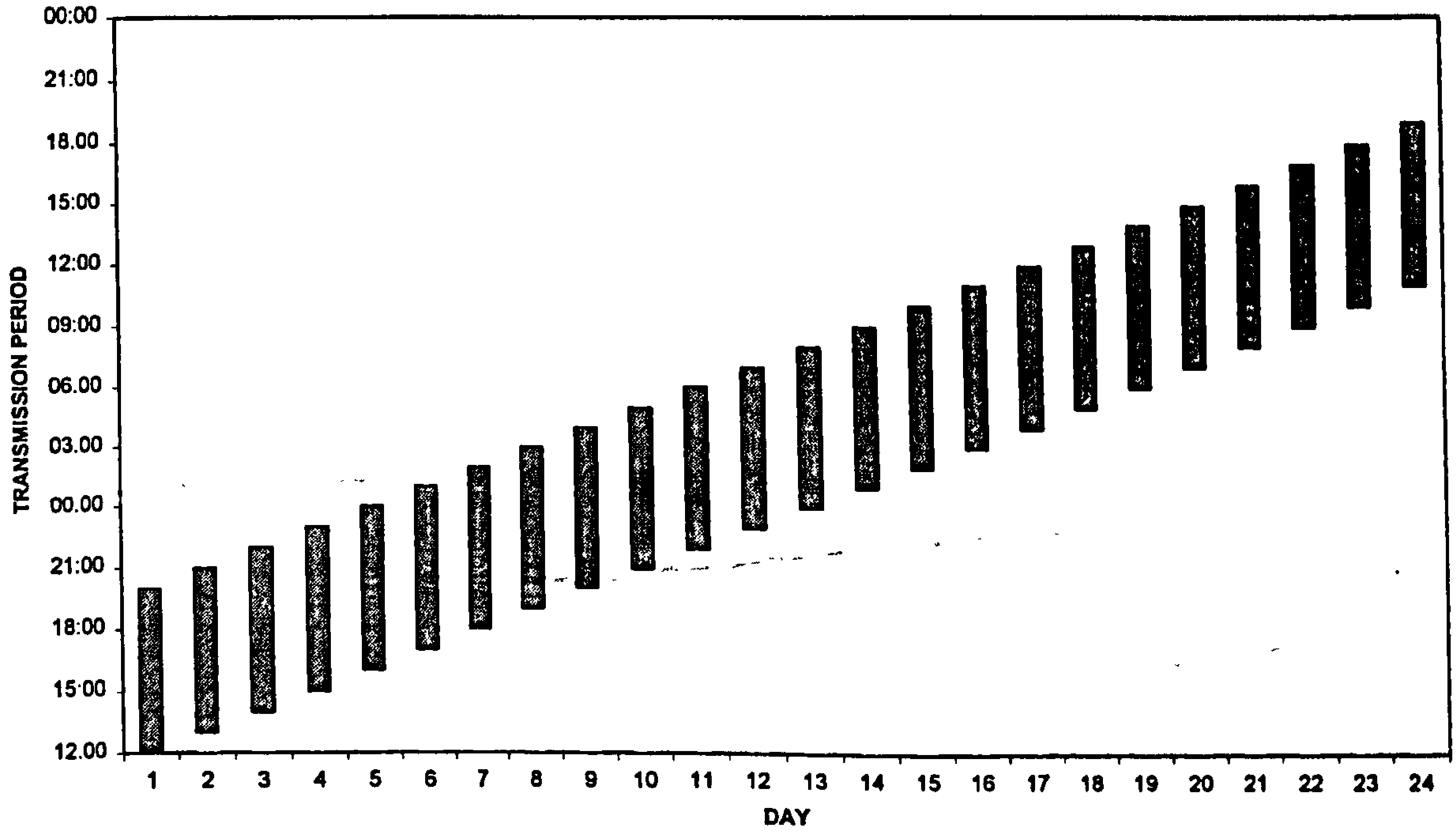
Satellite telemetry

The nine transmitters provided location data for from 13 to 56 days, with a mean of 27 days. A total of 564 fixes were recorded, but their accuracy depended on the number of sequential transmissions received by the satellite. Thus, 198 Class B fixes were based on only two transmissions received and were relatively inaccurate. 153 Class A fixes and 150 Class 0 fixes were based on three and four transmissions received respectively, but the actual accuracy could only be quantified as 1,000 m or less for 63 Class 1,2 and 3 fixes based on four transmissions received.

Timing of receipt of satellite fixes

The timing of receipt of transmissions was determined by three factors; the transmission cycle of the satellite transmitter, the orbiting pattern of the satellite, and the activity of the birds. The transmitters were designed to transmit for eight hours then switch off for 17 hours, ensuring that the transmissions covered the whole 24 hour period equally, over 24 days, as illustrated in Fig 9. Once the results were received, it was discovered that the actual transmission cycle settings varied considerably.

FIGURE 9: PLANNED CYCLE OF TRANSMISSION PERIODS OVER TWENTY FOUR DAY PERIOD



Four transmitters were set more or less correctly, as shown in the sample fix record of transmitter 470 in Fig 10. This transmitter cycles through twice during its life and covered the whole of the twenty-four hour period. However, it was found that transmitter 463 was set to switch off for only 15.5 hours, so it cycled in the reverse direction so slowly that it failed to cover the whole 24 hours, as shown in Fig 11. Furthermore, four transmitters were found to be set to switch off for 16 hours, so they maintained the same transmission time for each day and failed to cycle through the 24 hour period, as shown for transmitter 471 in Fig 12.

FIGURE 10: ACTUALTIMING OF FIXES FROM TRANSMITTER 470 - 7 OCTOBER TO 19 NOVEMBER 1997

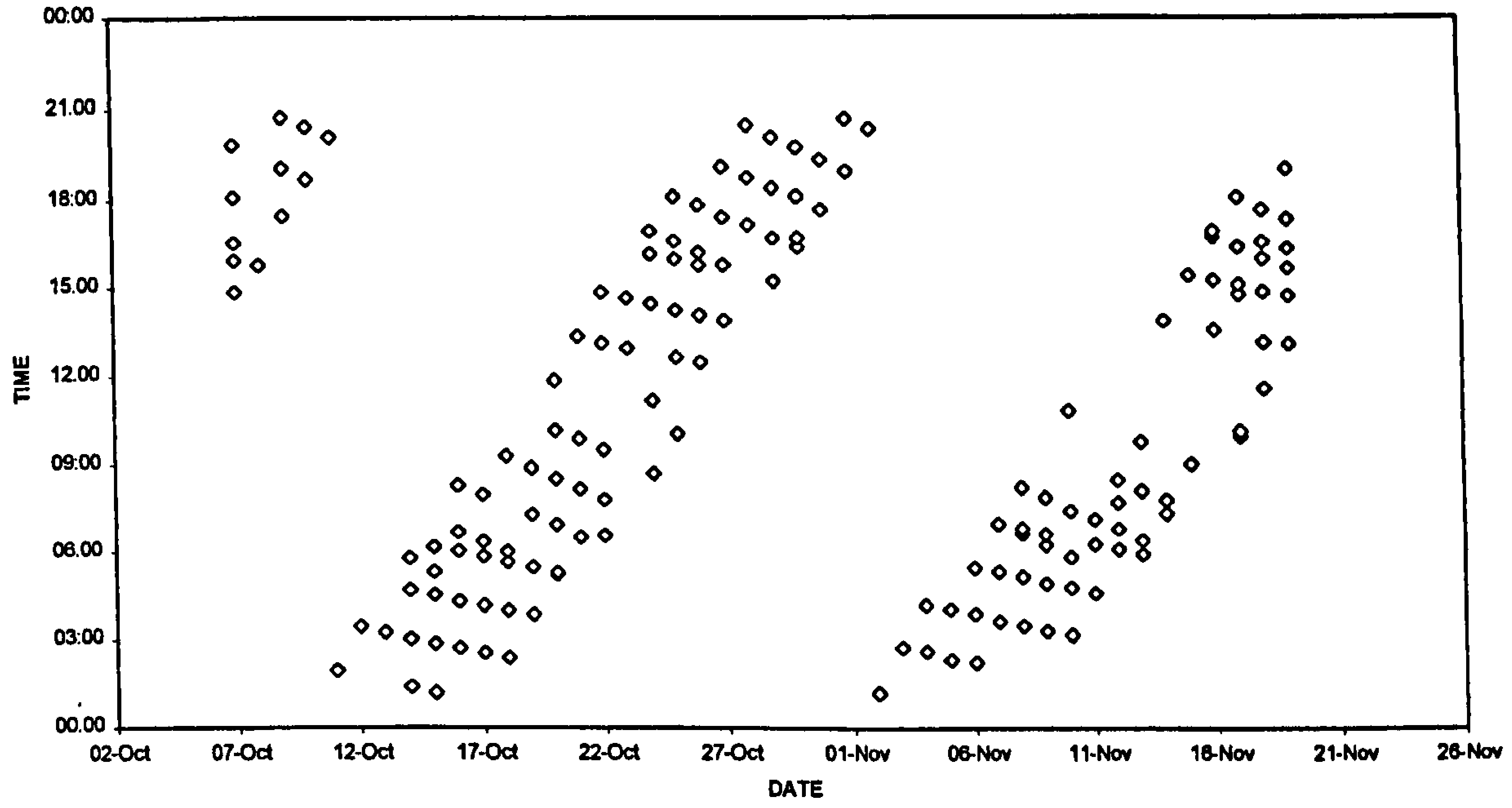


FIGURE 11: ACTUAL TIMING OF FIXES FROM TRANSMITTER 463 - 4 FEBRUARY TO 11 MARCH 1998

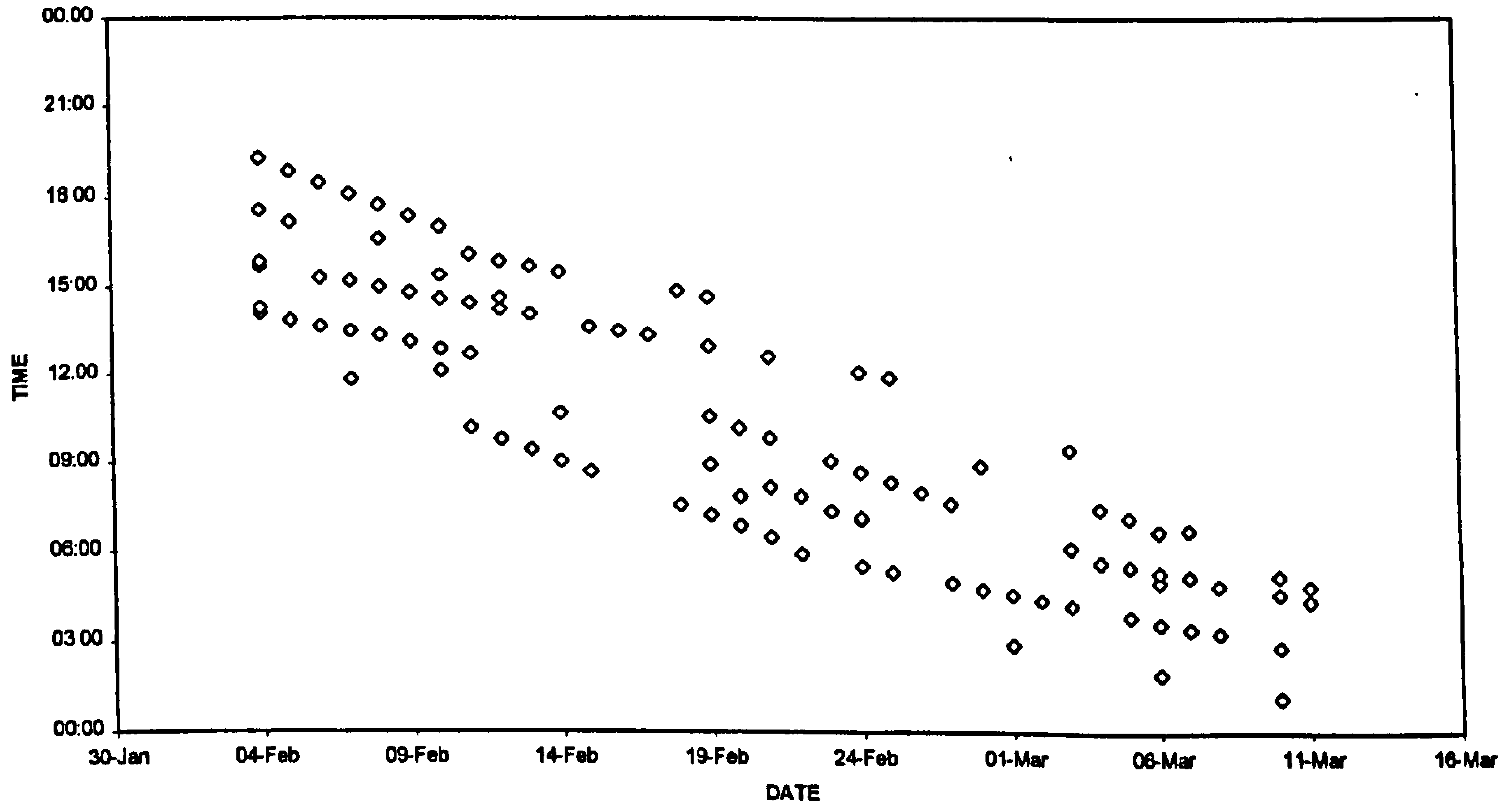
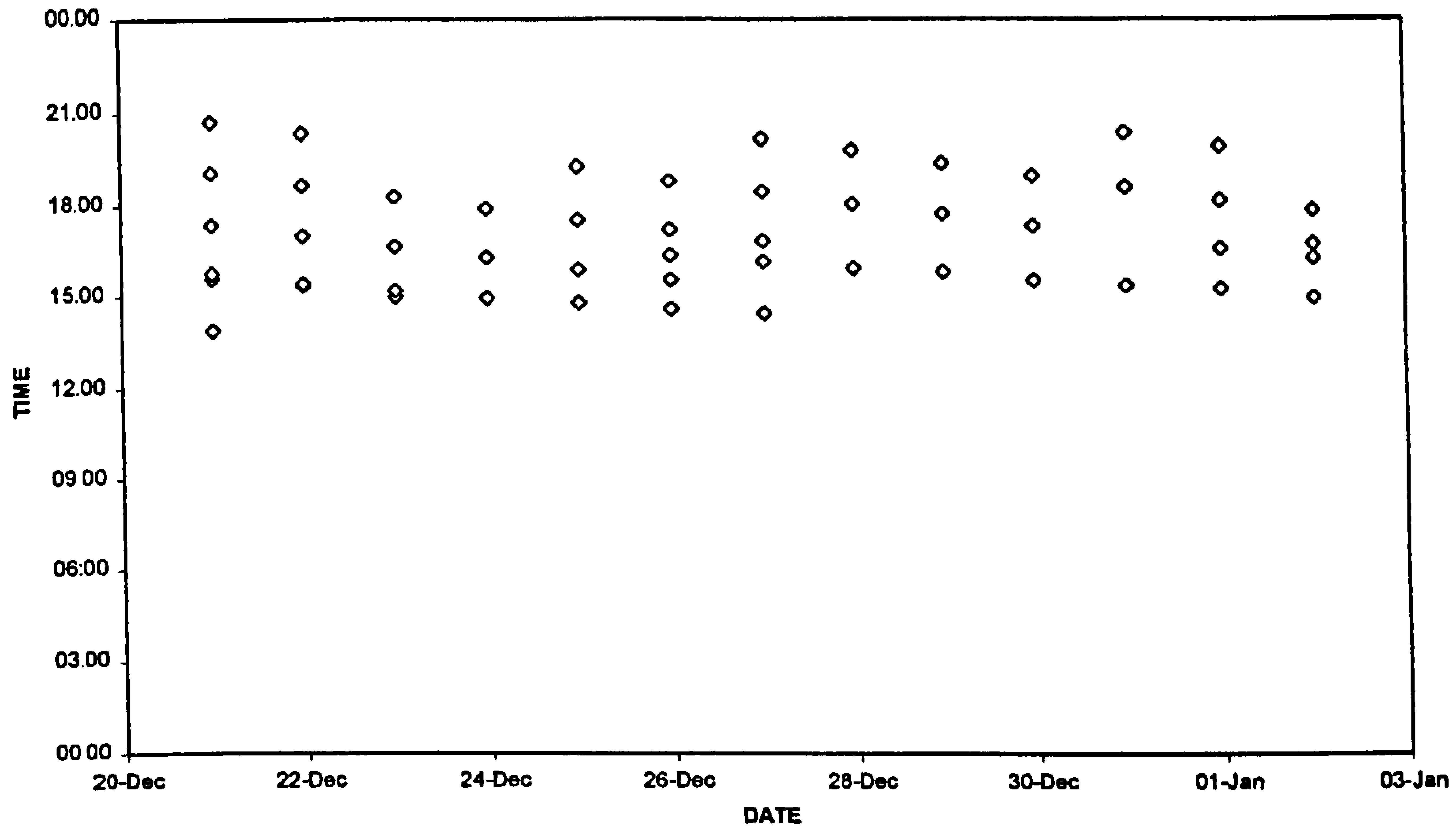


FIGURE 12: ACTUAL TIMING OF FIXES FROM TRANSMITTER 471 - 21 DECEMBER 1997 TO 2 JANUARY1998

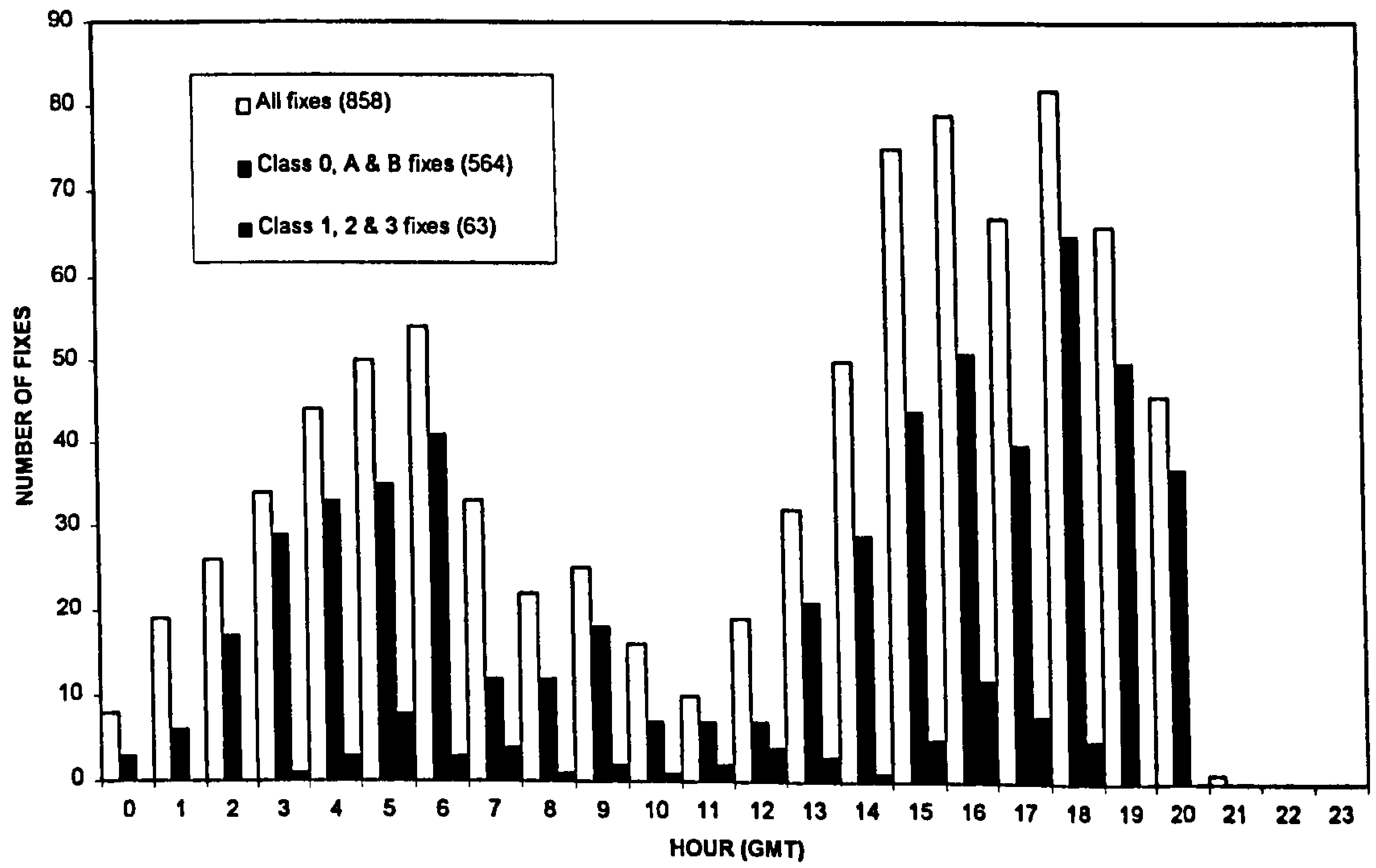


Two receiver satellites orbit between the north and south poles every 102 minutes, progressing westwards with each orbit, and between them scanning the whole of the earth's surface twice in each 24-hour period. As a satellite approaches overhead of a particular location, there is a window of up to 14 minutes, average 10 minutes, when a fix may be obtained before the satellite moves beyond range. In addition, depending on latitude, a variable number of preceding and succeeding orbits may also bring the satellite within range to obtain a fix as it passes to the east or west. This number is at a maximum at the poles where every orbit passes through the overhead, and at a minimum at the equator (Anon, 1996). At the latitude of the study area, 56° 12' north it was possible to be covered by up to five satellite orbits within the eight hour transmission period, and it was possible to obtain two fixes within the time window when each satellite was in range. The overhead times for the study area were estimated as 0700 and 1900.

When a bird is at roost whilst the transmitter is active, the signal stands a good chance of being detected by a passing satellite. However, when a bird is actively diving, the transmission cycle is constantly interrupted as the aerial becomes submerged, and given the short time window when the satellite was within range, this reduces the likelihood of receiving sequential transmissions, and thus of obtaining a fix.

As a result of the combination between transmission cycles, orbiting pattern of the satellite and bird activity, marked diurnal variation was found in the timing of fixes, as shown in Fig 13.

FIGURE 13: DIURNAL VARIATION IN RECORDING OF SATELLITE FIXES



The peak times for receiving fixes were between 0400 and 0600, and between 1500 and 1900, which coincided with times when Cormorants were likely to be at roost. However, very few fixes were obtained between 0700 and 1200 when Cormorants were likely to be most active. The likely effect of these factors is to bias fixes to times when cormorants were roosting rather than feeding, so the results may effectively underestimate the area over which the birds ranged if they returned to Loch Leven to roost. The bias in fix timings is equally apparent for different classes of fix.

Flight speed between fixes

Calculation of apparent flight speed between consecutive fixes indicated speeds of up to 985 ms^{-1}, which was clearly implausible. As a result, 59 occasions where the speed exceeded 20 ms^{-1} were scrutinised. Where high speeds were paired, i.e. they were recorded on the way to a fix, as well as from that fix, the fix was deleted. Where a fix was at the beginning of a sequence, and the speed to the second fix was high, but from the second to the third was plausible, the first fix was deleted. Where a fix was at the end of a sequence and the speed to it was high, but the speed to the penultimate fix was plausible, the final fix was deleted. Where a high speed was recorded between two fixes, both of which had plausible speeds immediately before or after, both fixes were deleted unless one had a known accuracy (i.e. class 1, 2 or 3), when the least accurate fix was deleted. When two fixes were recorded at very short time intervals, i.e. during the same satellite pass, and the distance between them was small, but sufficient to result in a high speed, both fixes were retained. As a result, a total of 41 fixes were deemed to be biologically implausible, and were discounted. Of these, 34 were Class B, five were Class A and two were Class 0, which suggested that Class B fixes were much less accurate.

Tracking of individual birds

The satellite tracking record of all nine birds are shown in Figs 14 to 22, with fixes joined in temporal sequence. Cormorant 465 was tracked for 26 days and most fixes are within 50 km of Loch Leven. The distribution suggests the bird was largely resident on Loch Leven but left occasionally to visit other sites for brief periods. Cormorants are largely confined to coastal areas and fresh water bodies, but the north easterly fix is 120 km offshore. Although plausible in terms of flight speed between positions, this Class B fix appears to be biologically dubious. Cormorant 466, which was tracked for only 13 days, appeared to remain within about 50 km of Loch Leven, apart from another dubious Class B fix 100 km offshore.

FIGURE 14: SATELLITE TRACKING OF CORMORANT 465:
7 OCTOBER TO 1 NOVEMBER 1997

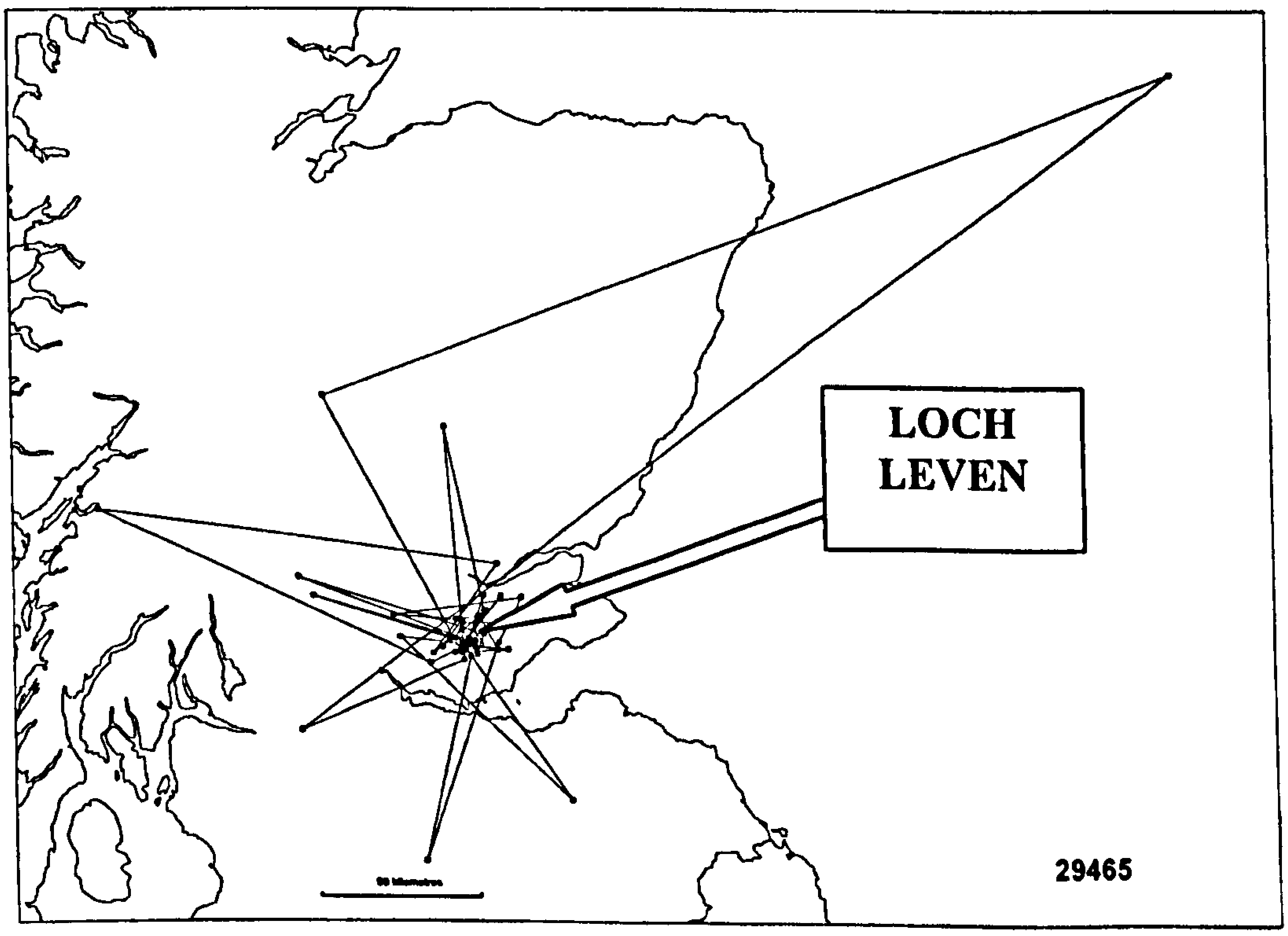
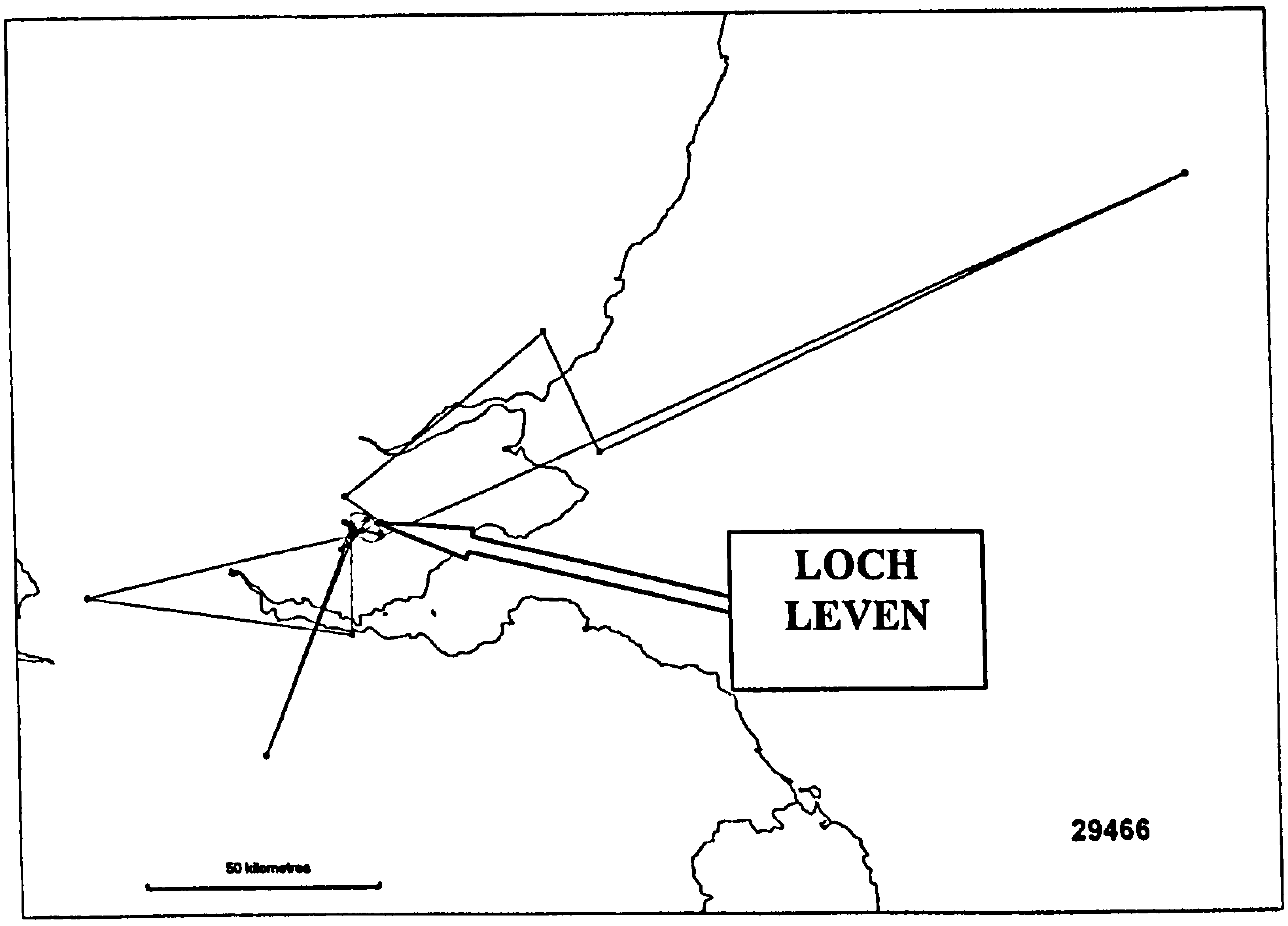


FIGURE 15: SATELLITE TRACKING OF CORMORANT 466
7 OCTOBER TO 19 OCTOBER 1997



Cormorant 467 was tracked for the longest period of 56 days and most fixes are within 50 km of Loch Leven. Again there is a dubious Class B fix, 80 km offshore to the south east. There are however two fixes, Class A and B, obtained on consecutive days, 300 km to the north in inshore waters near the north coast and the Orkney Islands, which are judged to be plausible. Similarly, two consecutive Class 0 fixes were obtained 130 km to the west, and are also judged to be plausible.

Cormorant 468 was tracked for 24 days and all but 4 fixes lie within 50 km of loch Leven. Cormorant 469 was tracked for 18 days and all fixes lie within about 50 km.

FIGURE 16: SATELLITE TRACKING OF CORMORANT 467:
7 OCTOBER TO 1 DECEMBER 1997

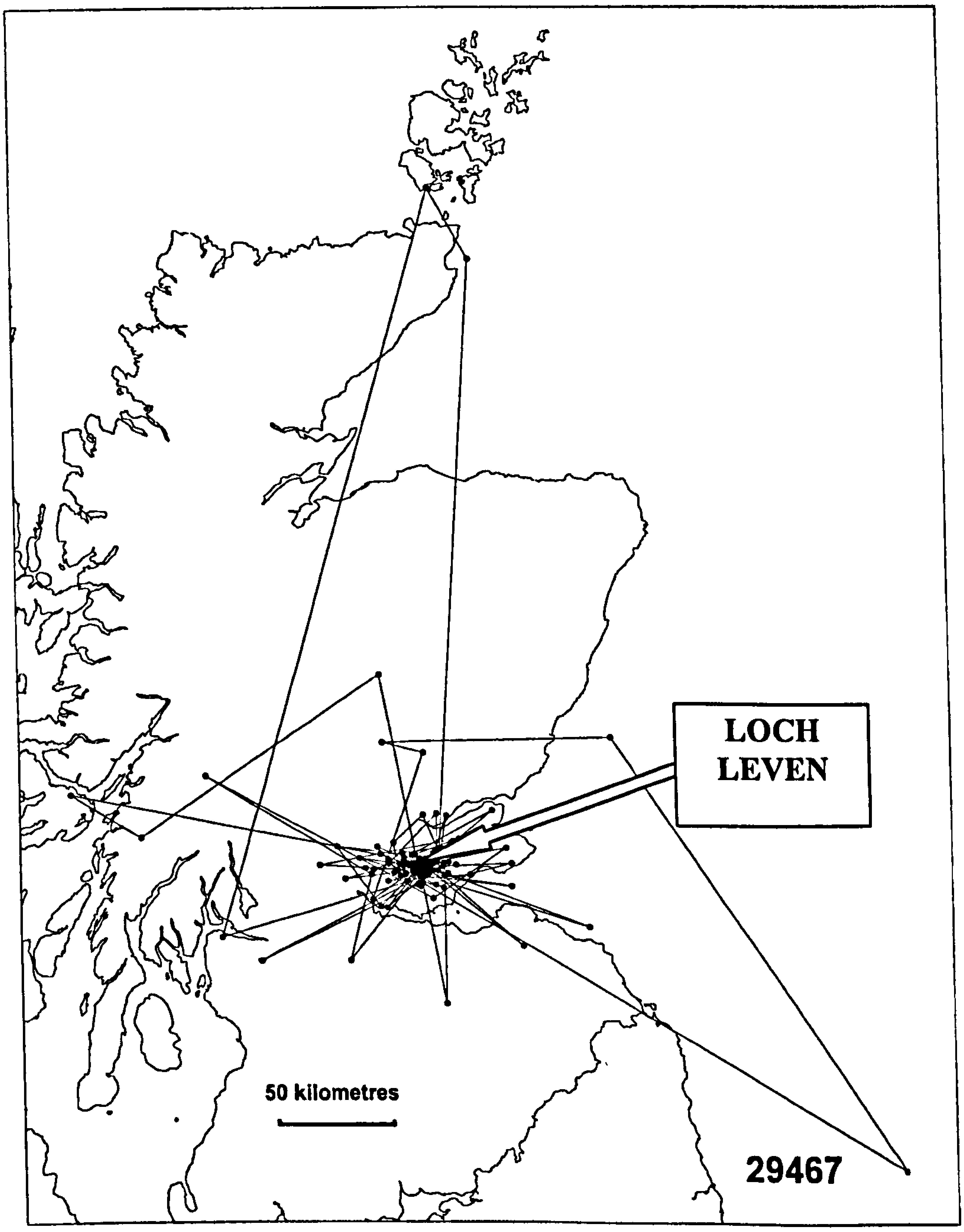


FIGURE 17: SATELLITE TRACKING OF CORMORANT 468: 7 OCTOBER TO 30 OCTOBER 1997

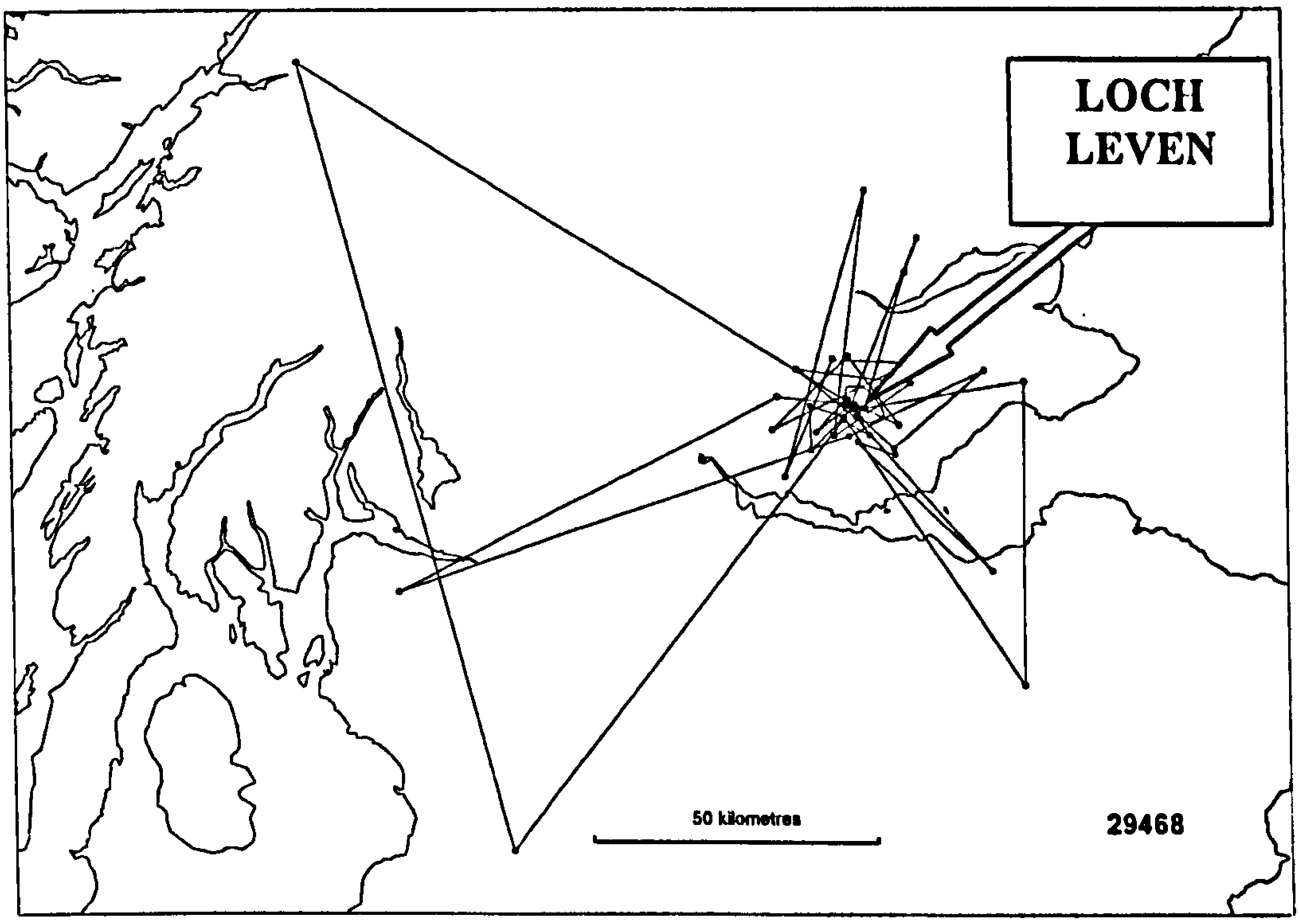
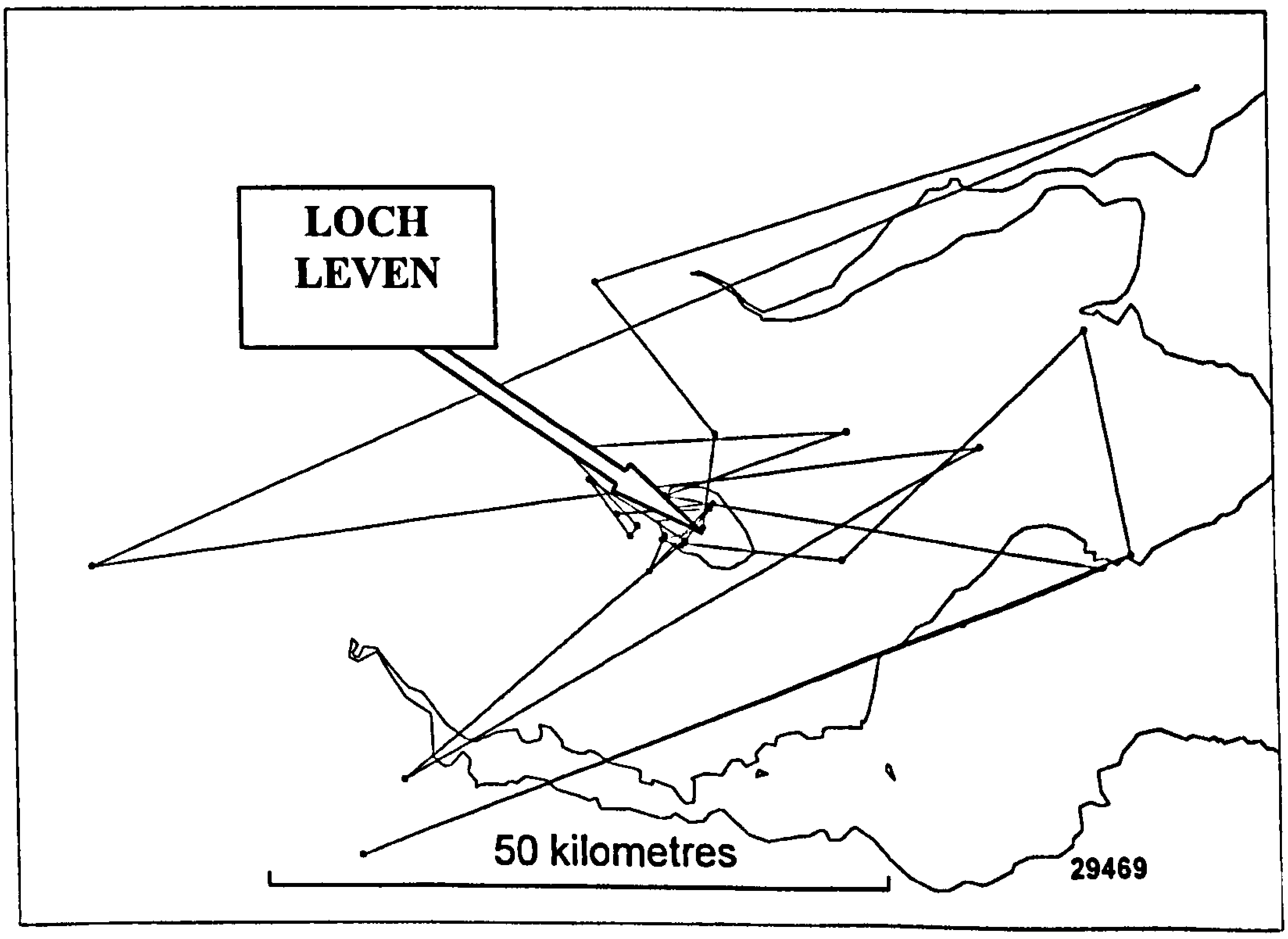


FIGURE 18: SATELLITE TRACKING OF CORMORANT 469: 7 OCTOBER TO 24 OCTOBER 1997



470 was tracked for 44 days and most fixes are located within 40 km of Loch Leven, including the Forth and Tay estuaries. In addition, three consecutive Class B fixes recorded over two days located the bird 150 km to the west, and these are judged to be plausible. Cormorant 471 was tracked for only 13 days and spent most of the time in south-east Scotland, but the last two fixes, Class B and 0, place the bird near the west coast in the vicinity of Loch Lomond. Cormorant 472 was tracked for 25 days and all but six fixes are located within 50 km of Loch Leven, particularly around the Forth estuary.

FIGURE 19: SATELLITE TRACKING OF CORMORANT 470:
7 OCTOBER TO 19 NOVEMBER 1997

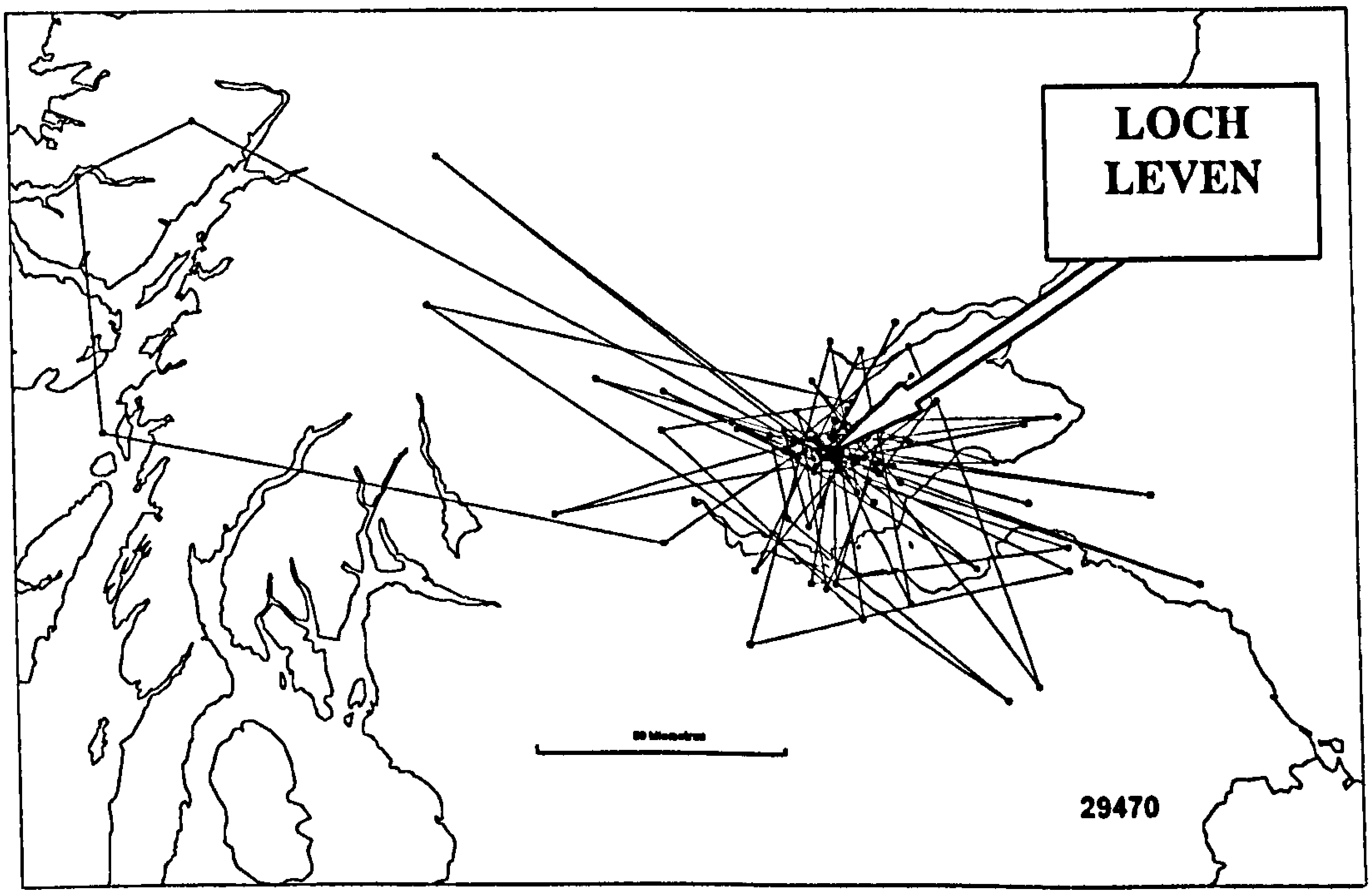


FIGURE 20: SATELLITE TRACKING OF CORMORANT 471: 21 DECEMBER 1997 TO 2 JANUARY 1998

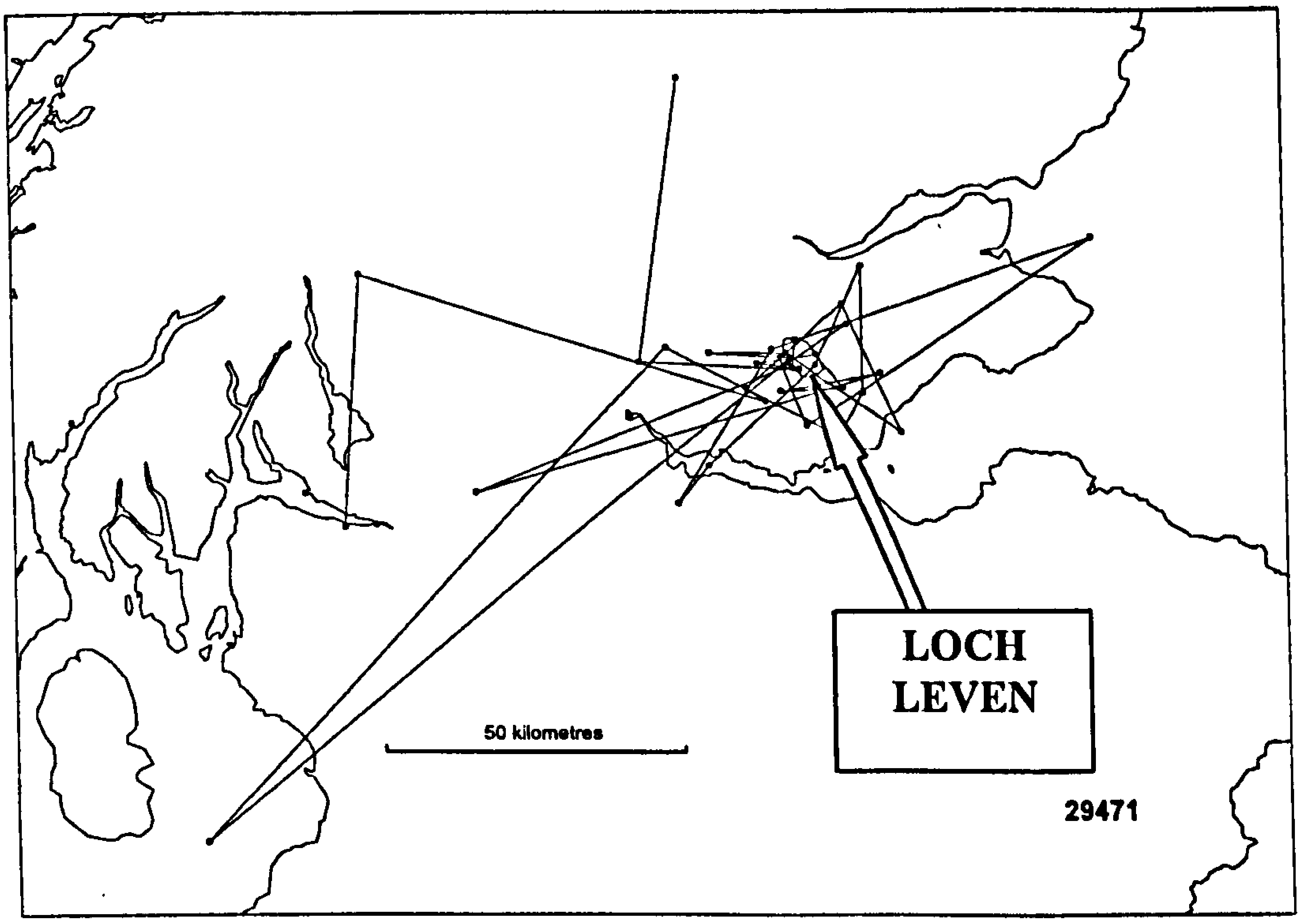
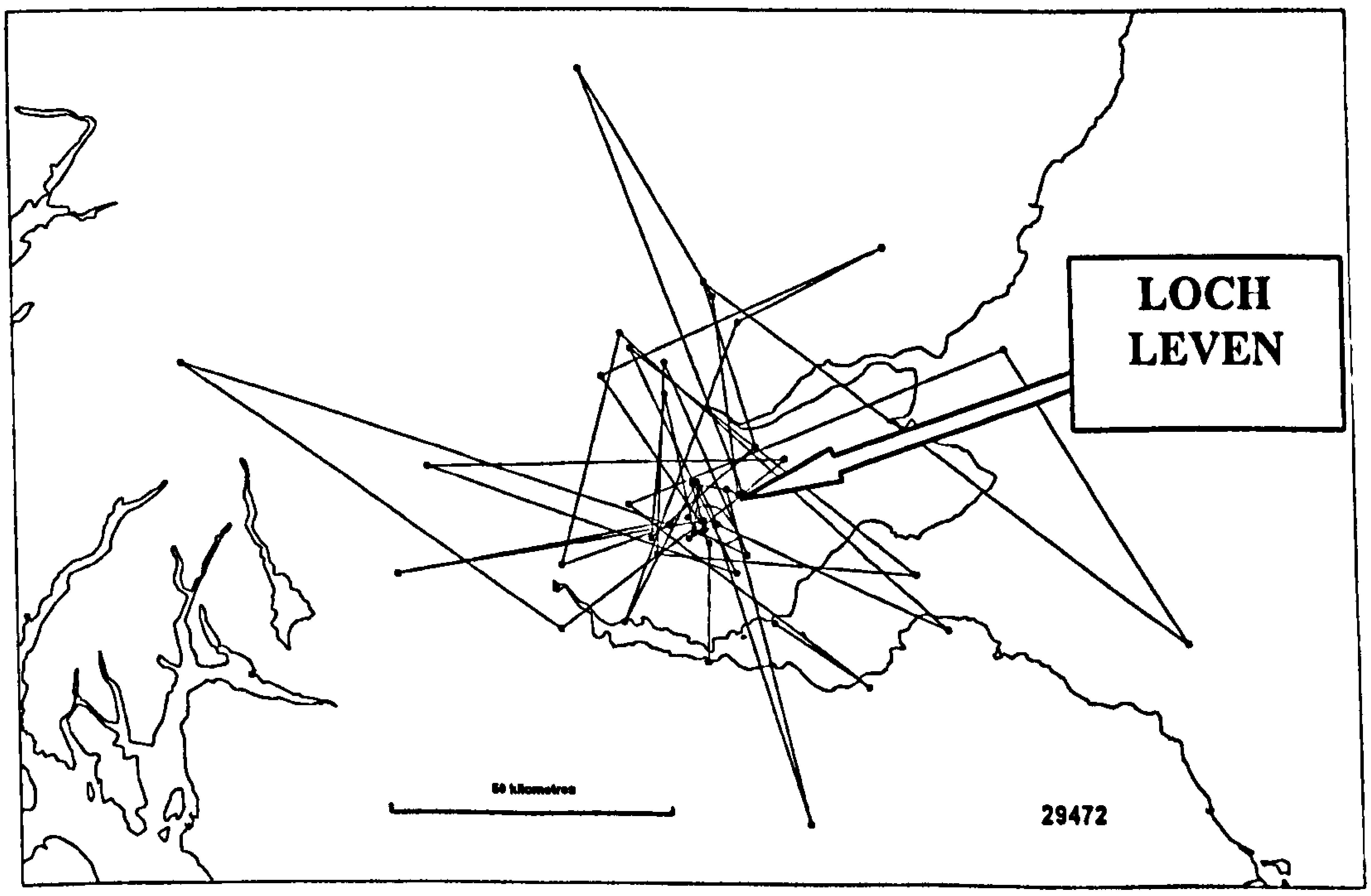
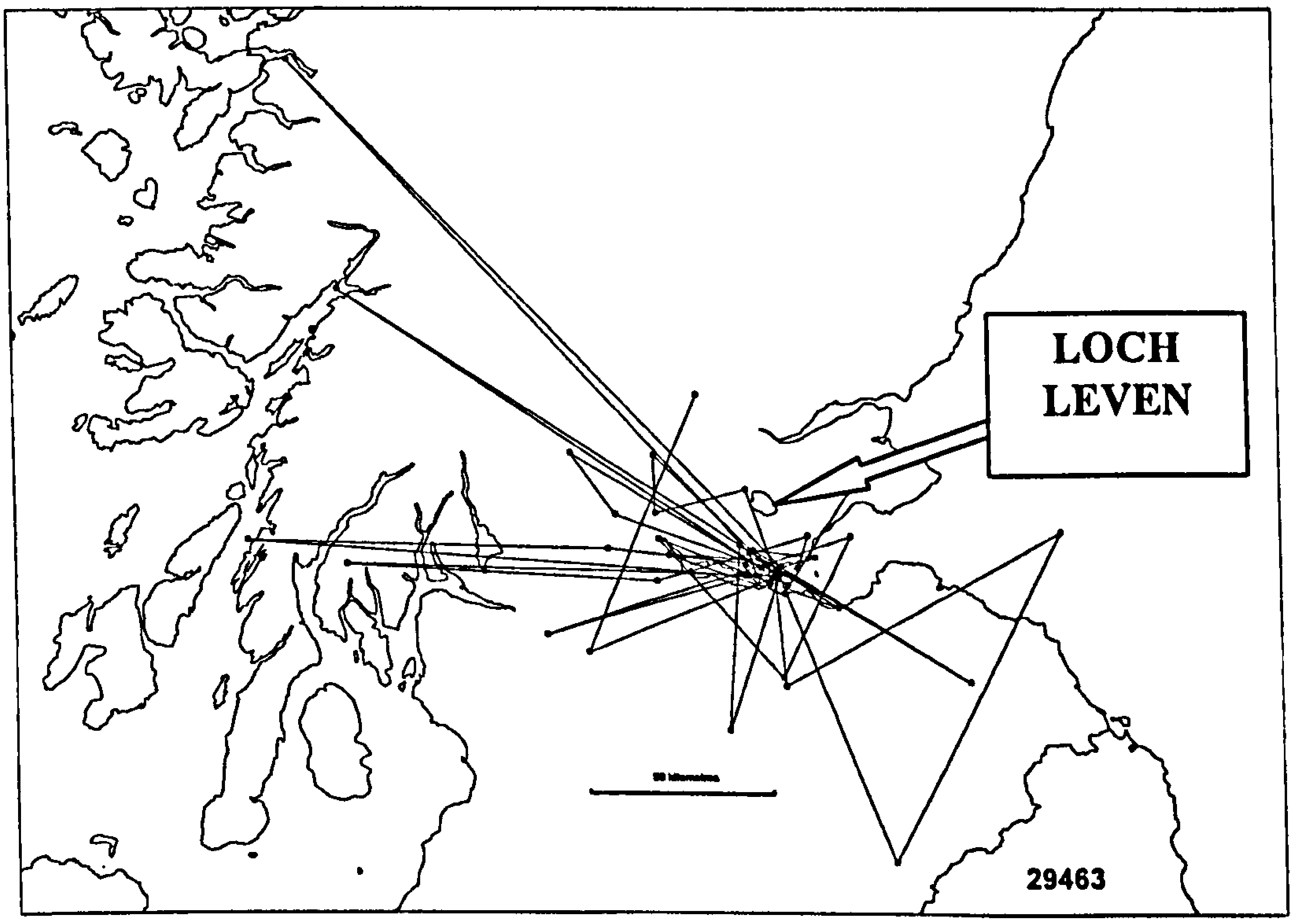


FIGURE 21: SATELLITE TRACKING OF CORMORANT 472:21 DECEMBER 1997 TO 14 JANUARY 1998



Cormorant 463 was tracked for 36 days and was only recorded in the vicinity of Loch Leven on one occasion following capture. It appeared to spend most of the time in the vicinity of the Forth estuary 25 km to the south, apart from four visits to the west coast.

FIGURE 22: SATELLITE TRACKING OF CORMORANT 463:
4 FEBRUARY TO 11 MARCH 1998



Fix accuracy

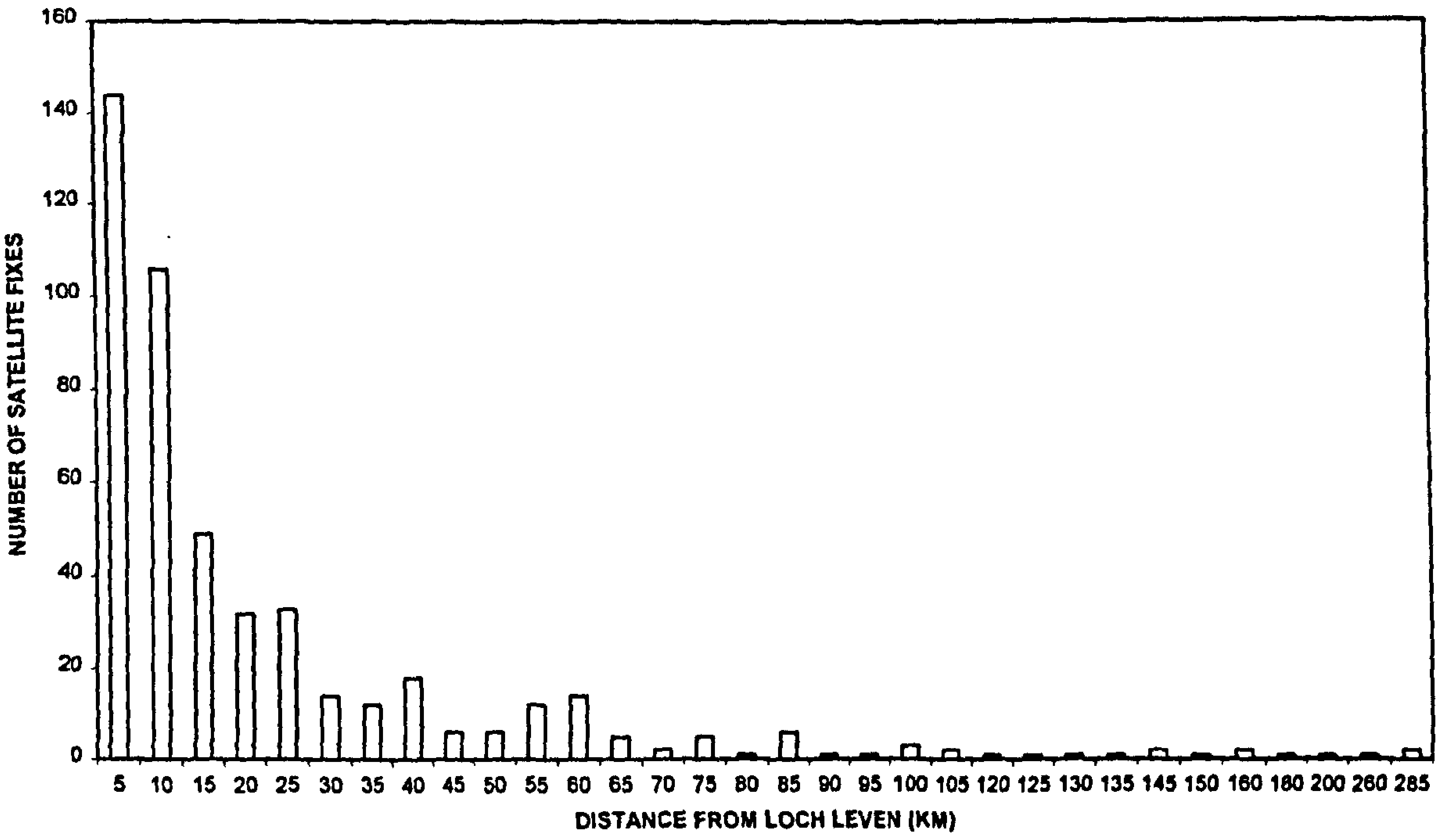
Transmitter 464 was set to transmit from known locations within the study area in order to check the accuracy of different classes of fix. However, the battery was found to have failed and no useable fixes were obtained.

Fix distances from Loch Leven

Figure 23 shows a plot of the numbers of fixes in bands of 5 km from Loch Leven. It shows that 50% of fixes occur within 10 km, and 90% occur within 60 km. Curve estimation accurately fits an inverse curve to the plot (F = 1217.7, R^2 = 95.6%, df = 56), with a formula of:

Fix number = -4.473 + (800.3/distance km)

FIGURE 23: DISTRIBUTION OF SATELLITE FIXES WITH RESPECT TO DISTANCE FROM LOCH LEVEN



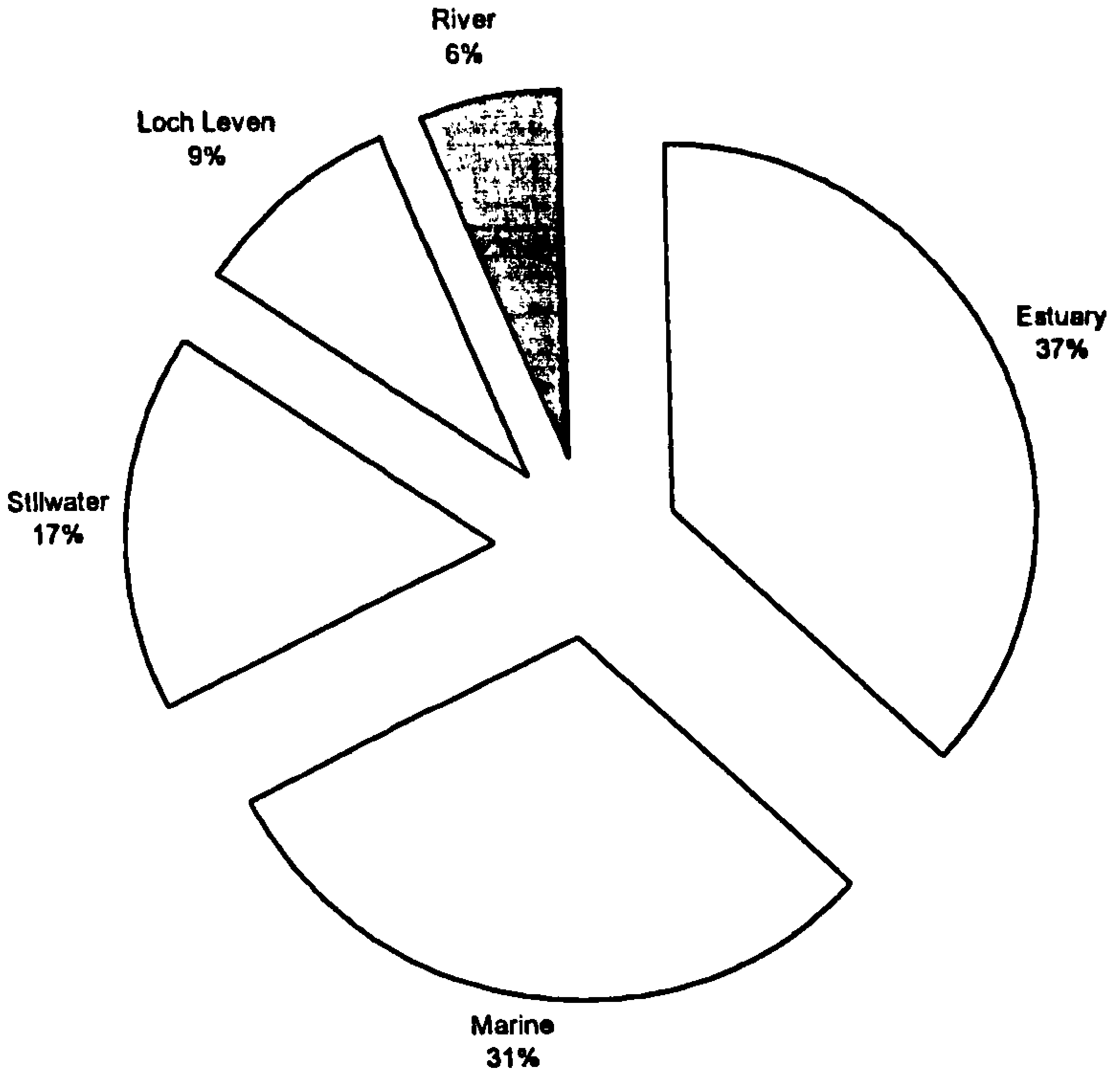
Although the accuracy of the cormorant fixes, particularly those of Class 0, A and B, have to be treated with some caution, the general pattern appears to be of birds spending most of the time within about 50 km of Loch Leven particularly on the Forth and Tay estuaries. They occasionally ranged up to 300 km, as far afield as the north and west coasts, before returning to the local area.

Taking all birds together, the 63 Class 1, 2 and 3 fixes with errors of 1000m or less give a maximum range from Loch Leven of 44km. A circle of radius 45km from the centre of Loch Leven would thus incorporate all the accurate fixes, plus 92% of Class 0 fixes, 89% of Class A fixes and 70% of Class B fixes. Such a circle may reasonably be regarded as encompassing the normal home range of Loch Leven birds, although they do travel further at times.

The wintering cormorant population within 45 km of Loch Leven

Mean winter cormorant counts from 179 sites within 45km of Loch Leven totalled 1,635. However, not all sites in the area were counted and coverage was 61% for estuaries, 42% for major rivers and 60% for still waters. Counts also covered 72% of the marine coastline, but not offshore areas. Average densities were calculated for each habitat (i.e. cormorants per km of river, hectare of still water, and km of coastline) and applied to uncounted areas to provide a correction to the count total. Cormorant density on Loch Leven was judged to be atypical so it was omitted from the density calculation for still waters. When corrections were applied, a total area cormorant population of 2,317 was estimated, of which the Loch Leven mean comprised 9%. This excludes offshore marine areas beyond counting range of observers on the shore.

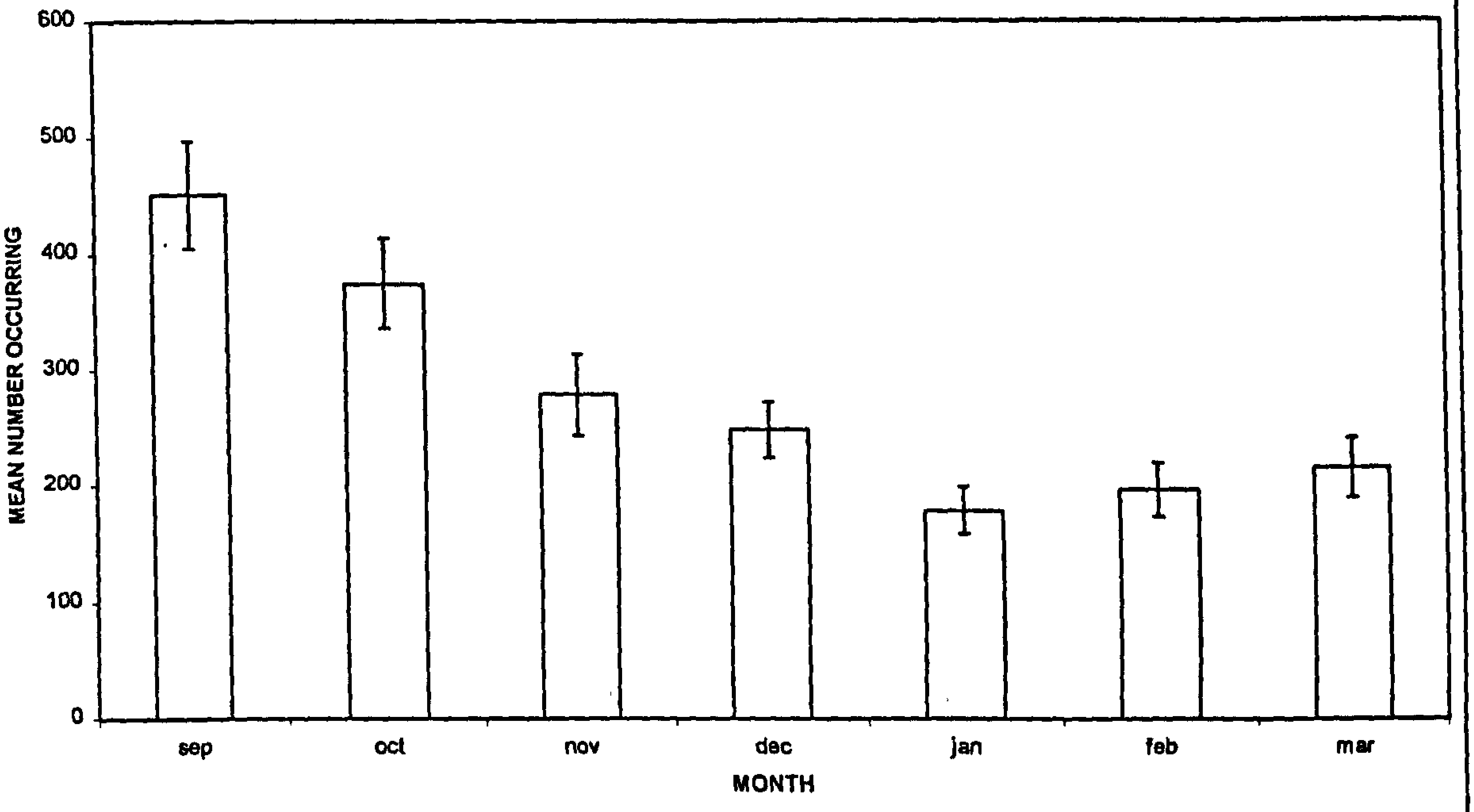
FIGURE 24: DISTRIBUTION OF WINTERING CORMORANTS BY HABITAT TYPE WITHIN 45 KM HOME RANGE - WINTERS 1987/88 TO 1998/99



The overall distribution of cormorant counts with respect to habitat types is illustrated in Fig. 23. It is apparent that the majority of birds are found on salt water sites, and rivers hold relatively few birds. Analysis of monthly data across the winter showed that though there was considerable variation between sites some trends were clearly defined.

On marine sites there was a decline of over 50% during the first half of the winter, as shown in Fig. 24. The count data for the seven sample sites are not normally distributed, so were log transformed prior to one-way ANOVA. The results were significant ($F_{6,327} = 6.73$, $p < 0.001$). Tukey test showed that differences between September and December to March were significant ($p = 0.023, < 0.001, < 0.001, = 0.003$ respectively). In addition, differences between October and January & February were significant ($p = 0.001, = 0.016$ respectively).

FIGURE 25: MONTHLY MEAN NUMBER OF CORMORANTS OCCURRING ON SEVEN MARINE SITES WITHIN 45 KM OF LOCH LEVEN - WINTERS 1987/88 TO 1998/99, WITH STANDARD ERROR BARS



On Estuaries there were declines in some sites early in the winter but increases in others, and a secondary peak occurred in December. However, in the second half of the winter there was a further decline to only one third of the September level, as shown in Fig 25. The count data for the eight sample sites are not normally distributed, so were log transformed prior to one-way ANOVA. The results were significant ($F_{6,381} = 7.87, p < 0.001$). Tukey test showed that September to December populations were significantly larger than January ($p < 0.001$, = 0.006, = 0.049, = 0.012 respectively), and March ($p < 0.001$, = 0.003, = 0.020, = 0.007 respectively). In addition, September, October and December populations were significantly larger than February ($p < 0.001$, = 0.019, = 0.043 respectively).

FIGURE 26: MONTHLY MEAN NUMBER OF CORMORANTS OCCURRING ON EIGHT ESTUARY SITES WITHIN 45 KM OF LOCH LEVEN - WINTERS 1987/88 TO 1998/99, WITH STANDARD ERROR BARS

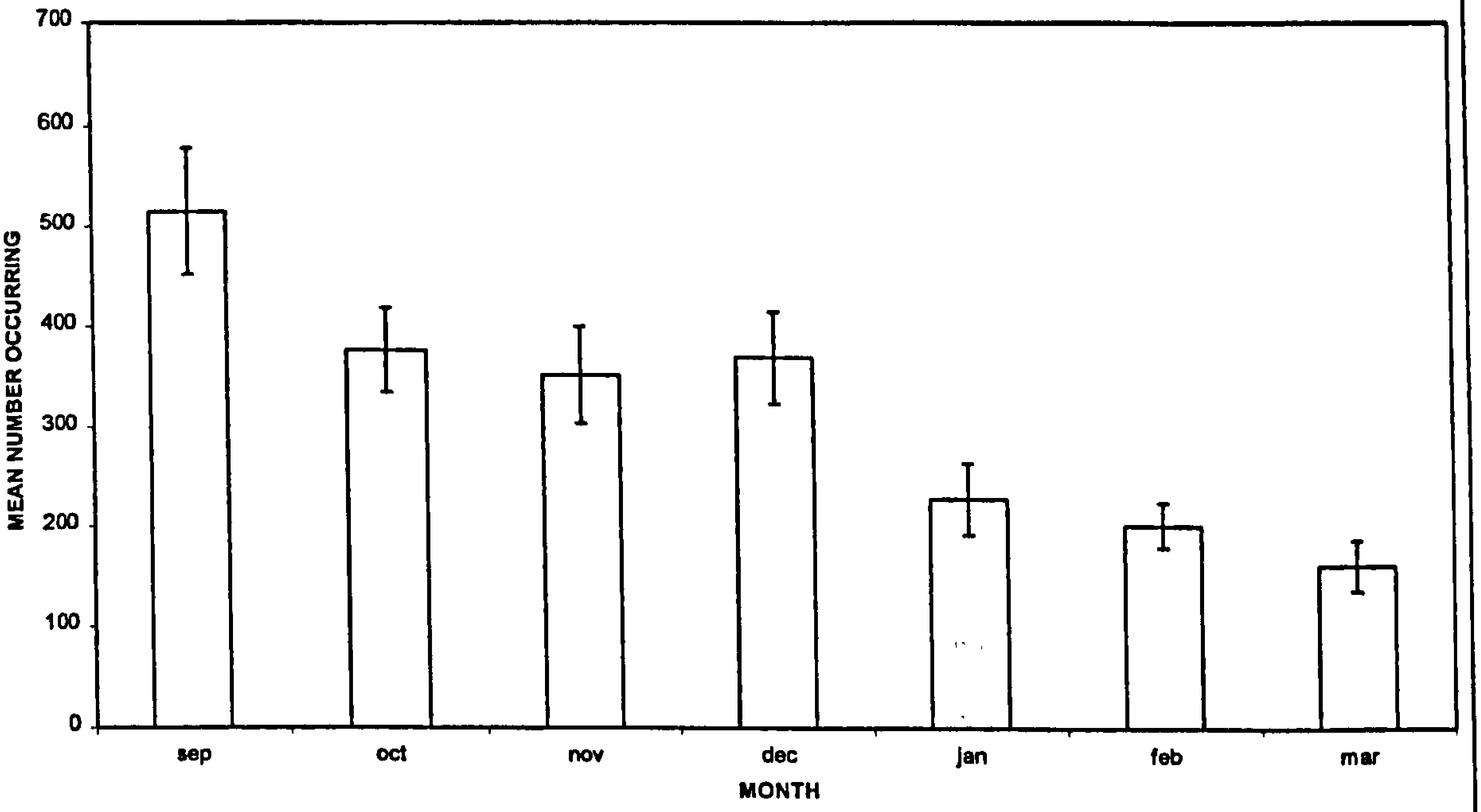
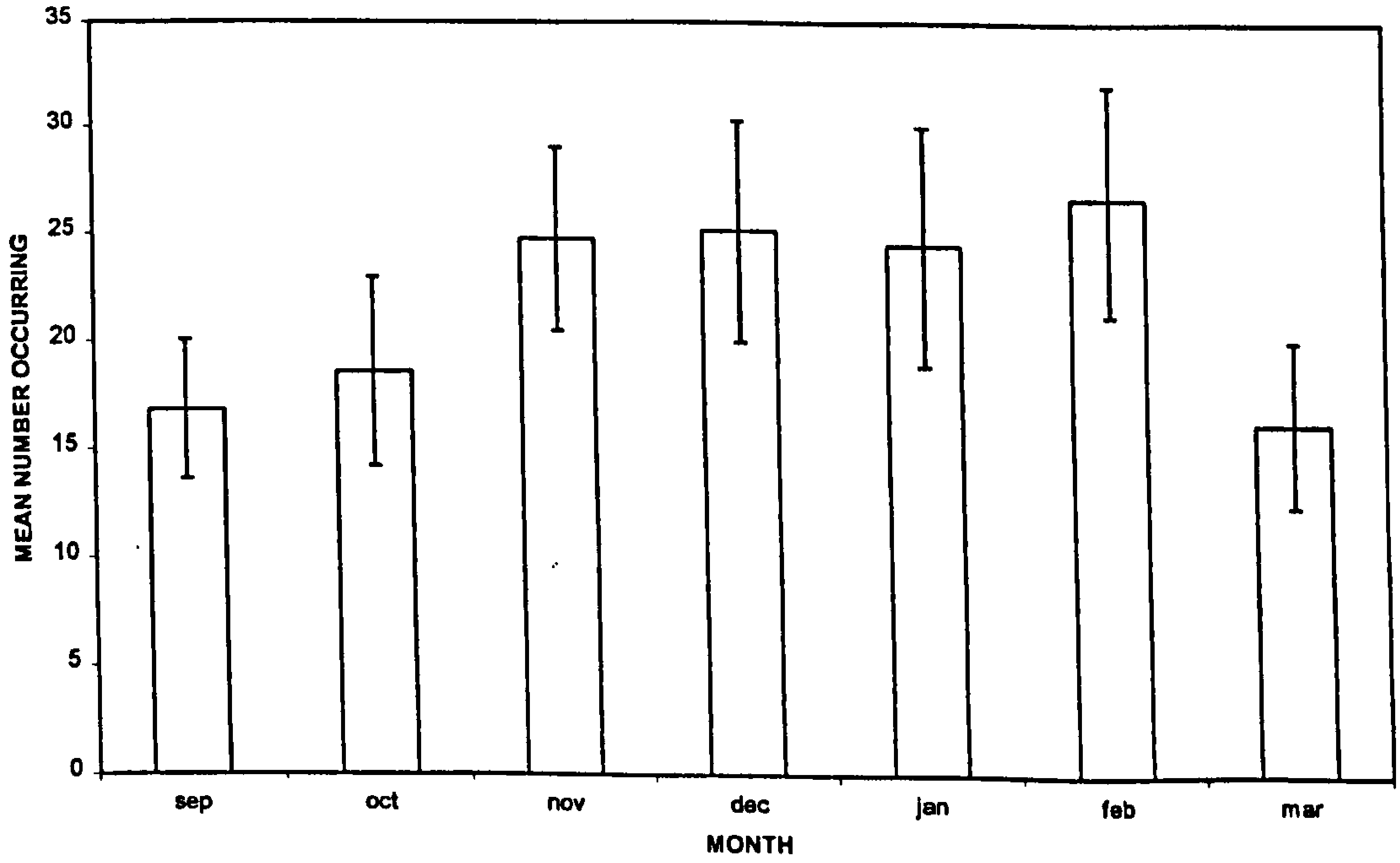
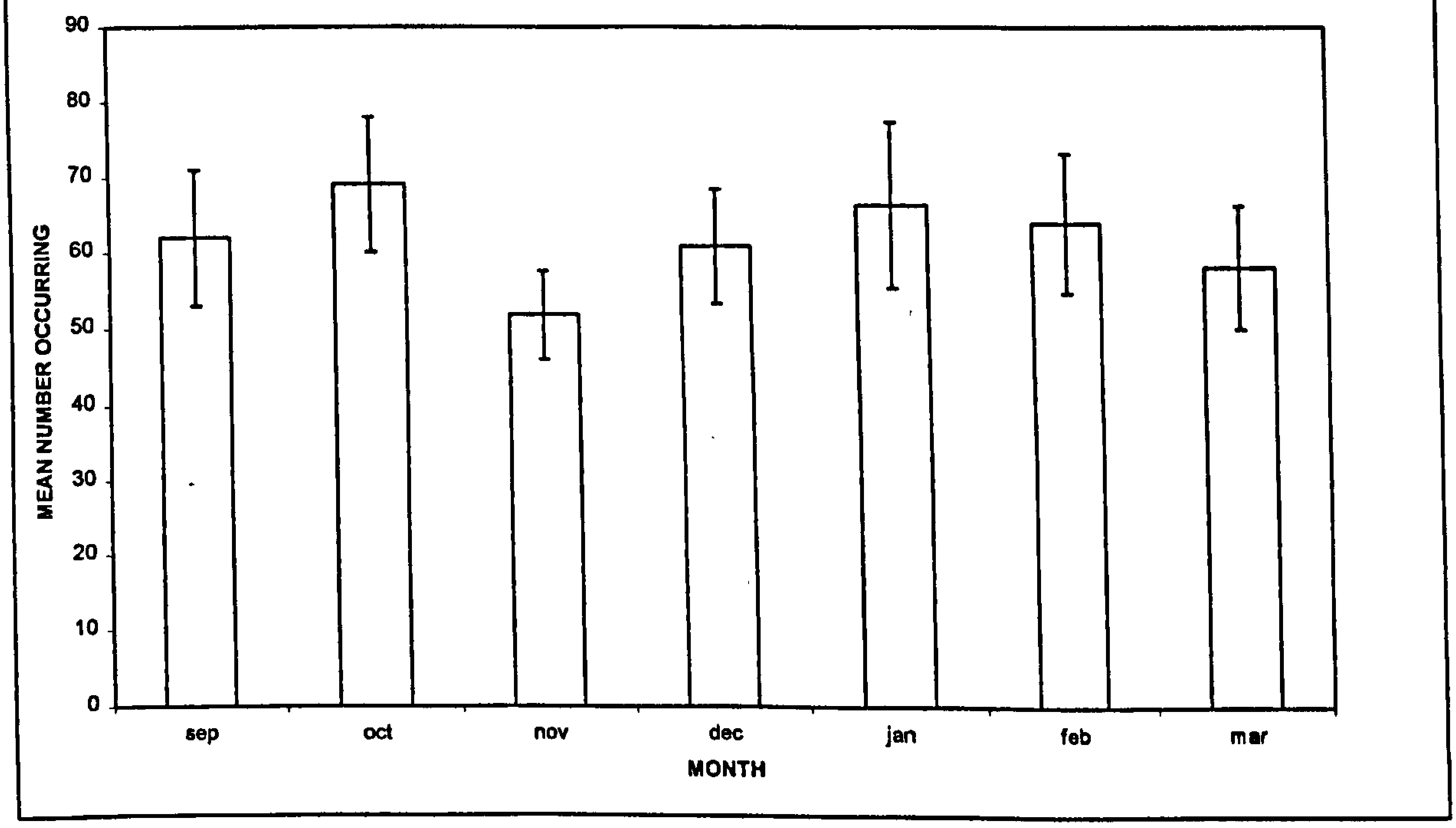


FIGURE 27: MONTHLY MEAN NUMBER OF CORMORANTS OCCURRING ON SIX RIVER SITES WITHIN 45 KM OF LOCH LEVEN - WINTERS 1987/88 TO 1998/99, WITH STANDARD ERROR BARS



River sites showed a gradual increase from September to a peak in February, followed by a sharp decline in March, as shown in Fig. 26. However, following log transformation of data from the six sample sites, one-way ANOVA showed none of the inter-month differences were significant. Freshwater sites, other than Loch Leven, showed no particular pattern, as shown in Figure 27, and, following log transformation of data from the six sample sites, one-way ANOVA showed none of the inter-month differences were significant.

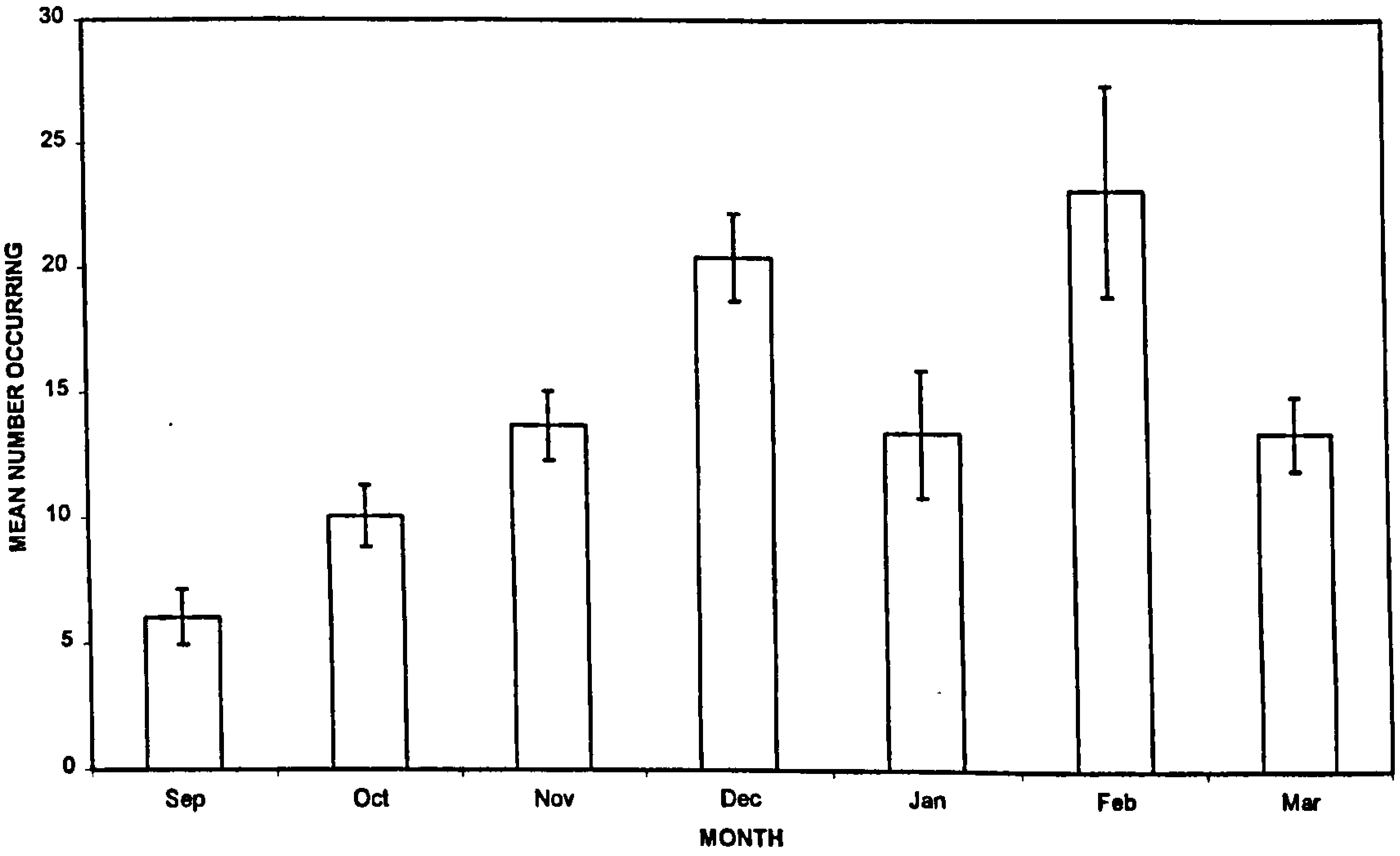
FIGURE 28: MONTHLY MEAN NUMBER OF CORMORANTS OCCURRING ON SIX STILLWATER SITES WITHIN 45 KM OF LOCH LEVEN, BUT NOT INCLUDING LOCH LEVEN - WINTERS 1987/88 TO 1998/99, WITH STANDARD ERROR BARS



Numbers on Loch Leven increased throughout the first half of the winter to an initial peak in December. There was a sharp decline in January followed by a similar peak in February, then a marked decline in March, as shown in Fig. 28. The Loch Leven data were normally distributed, and one-way ANOVA showed that monthly differences were significant ($F_{6,88} = 5.56$, $p < 0.001$). Tukey test showed that

September populations were significantly smaller than November, December and February ($p = 0.029, < 0.00, < 0.001$ respectively), and the October population was smaller than in December ($p = 0.049$).

FIGURE 29: MONTHLY MEAN NUMBER OF CORMORANTS ON LOCH LEVEN - WINTERS 1987/88 TO 1998/99, WITH STANDARD ERROR BARS



Overall, there was a general decline in total numbers on these sites as winter progressed, falling from over 1,100 to around 700. The decline on saltwater sites during the first half of the winter was accompanied by an increase on Loch Leven.

DISCUSSION

In an optimal foraging context it could be assumed that cormorants wintering at Loch Leven would continually sample a range of alternative sites, and would stay away when more profitable areas were available. Furthermore, cormorants wintering elsewhere would be expected to visit Loch Leven in order to sample its profitability, and to remain there if this was higher than their previous experience. These processes would result in turnover within the wintering population, which would reduce its amenability to control by shooting.

The multiple counts provide clear evidence of large fluctuations in cormorant numbers with the population halving or doubling in less than 24 hours. This is confirmed by visual observations of large and small groups of cormorants arriving and departing. Short-range radio tracking revealed intermittent rather than constant presence of individual birds, a different situation from that reported by Yésou, (1995). In addition, tracking of one individual indicated short-term absences of a few hours as well as longer absences, and the overall presence/absence results may underestimate such short-term absences.

The accuracy of satellite fixes from the type of transmitter used in this study has been subject to evaluation by Britten, Kennedy & Ambrose (1999). The mean distance from the true location for transmitters set for the correct altitude was found to be 6.4 km for Class 0 fixes, with a maximum distance recorded of 15.8 km. For Class A fixes, the mean distance was 4.1 km, with a maximum of 9.7 km, and for Class B fixes the mean distance was 35.4 km, with a maximum of 285 km. They also found

4.5% of fixes to be biologically implausible, compared to 7.3% in this study. It may therefore be assumed that the Class 1,2,3,0 and A fixes resulting from this satellite telemetry study do reflect the movements of cormorants with a reasonably accuracy on this scale. Class B fixes, even though biologically plausible, should be treated with some caution, and probably disregarded given the possible inaccuracy. The use of a 45 km circle as indicative of a wintering cormorant "home range" is a reasonable assumption, given the accuracies of the fixes on which it is based.

It is apparent from satellite telemetry that Loch Leven birds travel through central Scotland and as far as the west and north coasts, but activities are concentrated in eastern Scotland, particularly within 45 km of the loch. This range incorporates the marine and estuarine areas of the Firths of Forth and Tay, lowland river systems and upland and lowland freshwater lochs. The actual number of cormorants passing through is probably nearer the upper end of the estimate from radio tracking of between 466 and 2,260, as the population was not detectably depleted by the shooting of up to 370 birds each winter. The estimate of the wintering population within 45km of Loch Leven of 2,317 is 10 times the Loch Leven mean, and close to the upper end of the estimate from radio tracking of the number visiting Loch Leven. Cormorant distribution changes markedly during the winter with changes apparent in all habitats and a general move from salt water to fresh water sites. This movement into fresh water sites in mid winter suggests greater foraging success in fresh water later in winter, despite generally lower temperatures.

These results are consistent with optimal foraging theory, with birds leaving Loch Leven to sample other sites, birds visiting from elsewhere to sample Loch Leven, and overall changes in distribution between habitats, which are presumably in response to changes in foraging profitability. They do not support the concept of a discrete Loch Leven population, amenable to manipulation and control, which raises questions regarding the justification for killing birds on Loch Leven.

Given the scale of turnover, shooting as mitigation is unlikely to be effective. Many shot birds would have left anyway, and new arrivals compensate for those killed. To be effective, control measures would have to apply to the wider population of over 2,000, and the scale of shooting required to deplete it to a level where cormorants no longer winter in significant numbers at Loch Leven is likely to prove unacceptable. Furthermore, this wider population may not itself be a discrete entity, and there may be interaction with birds wintering beyond 45km, so depletion through large scale shooting may simply be compensated for by immigration. The evidence suggests that due to their foraging behaviour, cormorants are not sufficiently sedentary to enable the effective use of shooting as a site-specific mitigation measure. Hypothesis (c) is therefore accepted.

Chapter 6

GENERAL DISCUSSION

Introduction

The interactions of predator and prey are among the most topical in ecology, and predators are almost invariably controversial because different groups view them from different perspectives. Recently published material demonstrates that the successful management of predators depends invariably on understanding adequately the exact ecological context in which predator-prey interactions take place and in which problems arise (Ormerod, 2002). Furthermore, with predator-related issues growing rather than diminishing, there will be an increasing demand for ecologists to provide the understanding required to offer and evaluate sound management practices.

Resolution of the commonly perceived conflict between piscivorous birds and open-water fisheries requires the quantification of the scale of damage so caused, the determination of its significance, and the development, where necessary, of effective countermeasures. The achievement of these aims is hampered by the lack of persuasive evidence, and the principal objective of this study is to take the debate forward. With thirty-two years of cormorant counts, extensive fishery records comprising fish population estimates, angling catches, stocking data and angling effort, and the additional information on cormorant behaviour presented in this thesis, Loch Leven now possesses what is arguably the most comprehensive data set for any freshwater cormorant wintering site in Britain. It could be argued that if the persuasive evidence cannot be obtained at Loch Leven, there is even less chance of obtaining it elsewhere.

Cormorant population dynamics

It is useful to consider the Loch Leven wintering cormorants in the context of some recognised population models. It might be anticipated that density-dependent factors, such as fish population size or roost site availability, would act to limit the size of the cormorant population. However, the pattern of cormorant counts on Loch Leven shows no sign of levelling off, and does not suggest that numbers have yet reached a peak. Furthermore, as the wintering cormorants rely on a non-renewing food supply, i.e. the trout and perch populations, increasing cormorant numbers must result in increased rates of depletion of their prey. In a situation where a site has reached its carrying capacity, intake rates would inevitably fall, eventually dropping below the threshold level necessary for survival. At this point, birds would be expected to leave, or risk starvation (Newton, 1998). Loch Leven shows no evidence of this, with cormorant numbers generally increasing through the winter, again suggesting that the site is below its carrying capacity, and density dependent factors are not limiting the cormorant population.

Nevertheless, the failure of intensive shooting to reduce the wintering population shows that shot birds are being replaced by new arrivals, which suggests the possibility of some density-dependent or other effect. It may be that Loch Leven is more attractive to cormorants than other wintering sites, and a reduction in cormorant density at Loch Leven results in the recruitment of birds from these poorer habitats, which effectively act as buffers to the Loch Leven population (Newton, 1998).

If these cormorants were distributed in accordance with an "ideal free distribution" (Fretwell, 1972), all birds would have equal competitive abilities, and would be free to move between sites and settle wherever the fitness benefits seemed greatest. Thus they should distribute themselves in a way that conferred equal profitability amongst individuals (Krebs & Davies, 1987). The higher quality, more profitable habitats would support more birds than the poorer habitats. This could be achieved either through cormorants distributing themselves amongst the sites and remaining there in numbers balanced by profitability, or by cormorants constantly circulating between sites, but spending less time in the poorer habitats. The "ideal free distribution" may indeed reflect the behaviour of the Loch Leven cormorants, with birds circulating amongst the sites (as evidenced by radio and satellite telemetry), and redistributing from other sites to Loch Leven in response to increased profitability, resulting from the loss of birds to shooting.

The alternative, of an "ideal despotic distribution" (Newton, 1998), where cormorant distribution determined by "resource defence" (Krebs & Davies, 1987), is less convincing. In this case, some individual cormorants would be dominant, taking precedence and preventing others from settling where was best for them. Cormorant dominance behaviour has been identified on roost sites (Reymond & Zuchuat, 1995), and could theoretically act to limit the ability of less dominant birds to use Loch Leven. However, this is likely only if roost site competition caused birds to leave the site, which Reymond & Zuchuat suggest is unlikely. Furthermore, the principal cormorant feeding method of flock-feeding depends on the presence of relatively large numbers of birds, operating in apparent cooperation, where the influence of dominant individuals is not evident.

It may be that all of Scotland's wintering cormorants together form a distinct metapopulation, or a part of a wider one, as originally conceived by Levins (1969). In this scenario, the pattern of cormorant occupancy of individual sites continually changes in response to local reductions (e.g. by shooting) and site immigration. In effect, the entire population exists in a constantly shifting pattern of site occupancy (Newton, 1998). In the case of the Loch Leven cormorant wintering population, despite extensive culling in the recent past, the population as a whole continues to grow. This is not an isolated occurrence, and it has been recognised that the planning of culling programmes by wildlife agencies has not always taken into account the multiple factors responsible for the population dynamics of colonies and the effects of culls. By way of an example, extensive culling of gulls at a site failed to reduce the numbers at the metapopulation level, due to constant emigration (Bosch *et al.,* 2000).

Recent analysis of the effects of cormorant culling on a Europe-wide scale, highlights the need to consider the population as a whole, rather than only those birds visiting a particular site. It also demonstrates the scale of action required, and the need for objective analysis of its cost-effectiveness. In response to an increase in the population of Great cormorants *Phalacrocorax carbo sinensis* in northern Europe, widespread culling, took place in several countries. Frederiksen *et al.* (2001) reported that culling 17,000 cormorants a year had not achieved the aim, and increasing it to 30,000 still had only a limited effect. The authors concluded that culls probably have had a limited effect on cormorant populations. Furthermore, they also concluded that a reduction in the number of cormorants may not lead to a similar reduction in conflicts, and actions to control damage rather than cormorant populations are likely to be more cost-effective.

Wider applicability of Loch Leven results

In reviewing the findings presented in this thesis, the question arises as to the validity of their wider applicability, beyond the shores of Loch Leven. The findings are most likely to be directly relevant to sites where general physical and biological attributes are comparable with Loch Leven, i.e. on other large, open water fisheries. Such sites are liable to suffer similar types of perceived conflict. They are also likely to experience the same difficulties in assessing the actual impacts of cormorants, and in differentiating between traditional perception and reality in terms of adverse effects. However, they are unlikely to have available the scale of resources, in terms of manpower and material, deployed at Loch Leven during this study period. Nor are there likely to be such comprehensive long-term records of cormorant numbers, angling effort and catch, numbers of birds shot, etc., which render Loch Leven suitable for this study. The process of data gathering and analysis is therefore likely to be considerably more difficult, and the justification for control measures consequently elusive. Thus the interpretation of the Loch Leven findings in the context of comparable sites is likely to be prove a valuable option for the site manager.

Applying the lessons learned at Loch Leven may enable site managers to recognise the complexity of the issues and importance of other factors in limiting the angling catch. The Loch Leven data challenge that traditional simple arithmetical approach of "400 cormorants present for six months, each eating a third of their weight a day in trout, equal a loss of 50,000 trout to the fishermen". This approach fails to take account of any compensatory mortality effects, which might mitigate the loss of trout to cormorants, or of other factors that may serve to limit the angling catch. Furthermore, the evidence presented here does, demonstrates that wintering cormorants do not feed exclusively on Loch Leven. This study shows, that despite the huge increase in cormorant numbers, there is no evidence of a decline in the trout population, but the decline in angling catch as a proportion of the trout population is clearly evident. The data demonstrate the stability of catch-per-unit-effort over the years of cormorant increase, and the importance of angling effort as the principal determinant of angling catch. Indeed, Loch Leven fails to demonstrate any significant adverse impact of cormorants.

Where control measures are considered for other large, open water recreational fisheries, it may be anticipated that there will be similar difficulties in demonstrating any beneficial effect, either in terms of reduced cormorant numbers or increased angling catch. The same factors which limit the effectiveness of cormorant shooting on Loch Leven, e.g. high turnover within the cormorant population, the existence of large open water areas to retreat to during shooting, etc., may also apply, and shooting is likely to prove equally ineffective as a means of cormorant control. Thus, the interpretation of Loch Leven findings may enable other fishery managers to avoid wasting resources on futile attempts at control measures, and encourage a closer focus on those more relevant factors that influence commercial viability.

By contrast, on small fisheries where stocking is entirely artificial, and where angling catches and other losses can be more accurately quantified, it may be possible to assess the particular impacts of cormorants, and determine if they are indeed limiting catches (e.g. Dieperink, 1995). Indeed, it may be anticipated that cormorants are more likely to have a demonstrably negative impact on such a fishery, and control measures may be more appropriate. Furthermore, where it is determined that cormorants are a limiting factor, control measures, including non-lethal methods, may be much more effective where the site is small and birds can not retreat to open water to escape its effects, but can be effectively driven from the site. Thus, assessing the effectiveness of control measures may be much easier on very small sites, and the applicability of the Loch Leven findings is more limited.

The perceived conflict between cormorants and commercial fisheries is not unique, and there are other examples of bird species in conflict with commercial and recreational interests throughout the world (e.g. Walthew, 1995, Derby & Lovvorn, 1997). Aspects of the applicability of the findings from Loch Leven may therefore be considered in a wider context, and three further examples of conflict are discussed below: the perceived conflicts between geese and agricultural crops, between eiders (*Somateria mollissima*) and mussel (*Mytilus edulis*) farmers, and between hen harriers (*Circus cyaneus*) and grouse (*Lagopus lagopus scoticus*) shooters. All these examples are drawn from Scotland to illustrate the diversity of such problems, even on a relatively small spatial scale.

Geese and agricultural crops

Conflicts between geese and farmers have been recognised for centuries (e.g. Kear, 1990). In Scotland, the damage is usually caused by migratory flocks of Pink-footed geese *Anser brachyrhynchus*, Greylag geese *Anser anser*, and Barnacle geese *Branta leucopsis,* which breed in northern latitudes, and migrate to Britain for the winter (Owen *et. al*, 1963). Damage typically takes the form of consumption and loss of crop, but may also comprise physical damage to the crop or to the soil structure. Crops most usually affected include grass for grazing or silage production, winter cereals, oilseed rape and vegetables (Kirby *et. al*, 1999).

Although not without difficulties, the assessment of the significance of perceived damage, and of any limiting effects of goose grazing on agricultural output, is relatively easy. The conflict takes place on terrestrial areas, which are more amenable to study, and occurs in two dimensions rather than three. Thus, using simple fieldwork techniques, numbers of geese can be counted, time spent feeding can be measured, and the area over which the geese feed can be plotted (e.g. Percival, 1988). Due to the fast passage of grazed material through the goose's digestive tract, droppings can be collected on the site and dried, and the food items consumed can be identified and quantified (e.g. Owen, 1975, Bedard & Gauthier. 1986). Thus the quantity of crop consumed by the grazer may be determined with some precision.

It is also possible to establish control areas within fields likely to be grazed, from which geese are excluded, but which are in other respects comparable with the grazed areas (e.g. Percival & Houston, 1992). The difference in crop yields from grazed and ungrazed areas may be compared, and the impact of goose grazing determined with some precision. Thus Percival (1988) showed some significant declines in silage yield attributed to grazing by barnacle geese, although other authors also suggested possible beneficial effects of goose grazing (e.g. Kear, 1963, Bazely & Jeffries, 1985). Fortunately, unlike fish, cereals and grasses do not move around the field, and the confounding effect of behaviour of the food itself does not arise. Furthermore, the effects of other grazers, which might confound the assessment of goose damage, are relatively easy to identify and quantify, through fencing of domestic livestock and field observations of the activities of deer etc.

It is therefore relatively easy to assess any damaging (or beneficial) effects of goose grazing, and thus provide convincing evidence in support of any proposal to institute control measures. Unlike the situation on Loch Leven, on sites where goose control measures are implemented, typically involving shooting or scaring, there may be some success in preventing further grazing, with a consequent reduction in damage (e.g. Patterson, 1991). Furthermore, any beneficial effects of the control measures will be relatively easy to demonstrate, through defining an acceptable level of grazing, and measuring the success in achieving it. However, the cost-effectiveness of such control measures may render them uneconomical, and the establishment of sacrificial feeding areas or compensation schemes may prove a more acceptable alternative (Patterson & Fuchs, 1992).

The benefits of shooting and scaring may also prove to be a very local effect, as geese are quick to habituate to control measures and respond accordingly (Inglis, 1980). For example, they may respond by grazing an alternative crop, which represents partial success where that crop is less valuable or not so vulnerable to damage. But they may also graze other valuable crops, so the damage is displaced rather than prevented. They are also likely to attempt to return to particularly attractive crops, despite control measure, lethal or otherwise, whose effect is likely to be relatively short-lived. Geese may graze in increasingly close proximity to scaring devices, and unless they are constantly reinforced, following the initial success, control measures are eventually likely to fail (e.g. Kirby *et. al*, 1999).

Whilst the applicability of the Loch Leven findings in the goose versus agriculture conflict, is likely to be limited, there are lessons on the behavioural similarities between cormorants and geese, which reduce their susceptibility to control measures. They both form large flocks, and are relatively wary. They are both opportunistic feeders, quick to adapt to changing fortunes and from their roost site they range over a relatively wide area (e.g. Percival *et. al*, 1997). Their populations are not static, but move around the country during migration and dispersion, so there may be an element of turnover within both species (Owen *et. al*, 1963). Control measures aimed at reducing their overall numbers are also likely to prove similarly unsuccessful, unless practised intensively and extensively (e.g. Summers & Hillman, 1990, Patterson, 1991).

Eiders and mussel farms

A more recent conflict has arisen with the establishment of mussel farms in coastal marine areas, and the perception by farmers of economic loss through predation of their growing stock by eiders (e.g. Dunthorn, 1971, Galbraith, 1992). As with the cormorant-trout conflict, feeding takes place in three dimensions and out of sight underwater, so actual feeding behaviour is determined through deduction rather than direct observation. Again, the eider is a flocking bird, which moves slowly and is relatively easy to count, and the general location and timing of bouts of active feeding are relatively easy to determine, as the bird dives underwater to feed (Furness, 1996). Analysis of droppings is not practicable as the birds defecate in the water, and roosting rocks may be some distance away. However, although they also take echinoderms and crustacea, the main prey of eiders is likely to be mussels (Ross, 2000).

Farmed mussels may be cultured on suspended ropes or on the seabed. Suspended culture is practiced in Scotland, and the mussels are typically attached to vertical ropes suspended in the sea from a line of buoys, or suspended in a dense grid from a floating raft (Ross, 2000). Thus, there is scope for the construction of cages around a group of ropes and the establishment of control areas from which eiders are excluded, but which are in other respects comparable with exposed ropes. Assuming that no other predators such as Goldeneye (*Bucephala clangula*) are attacking mussels on the exposed ropes, the "before" and "after" comparison of enclosed and exposed ropes following a period of eider activity, enables an assessment of damage, and is unlikely to be confounded by mussels moving of their own volition.

Thus the assessment of damage is relatively easy, and enables a reasonable assessment of the need for eider control actions. Furthermore, given the eider's behaviour, the effectiveness of control measures such as deliberate boat disturbance, lasers and underwater playback systems, can be relatively easily assessed (Ross, 2000). However, such control measures may have only a local effect, and, as with geese, the effect may simply be to displace the predators onto another part of the mussel farm, or to another farm, rather than onto naturally occurring and less valuable food sources. In addition, the effectiveness is likely to diminish with time, and longer-term success will depend on regular reinforcing of the control measures (Ross, 2000). Overall, the findings from Loch Leven are likely to have limited applicability to this conflict.

Hen harriers and grouse moors

Red grouse have been is serious decline for many years and this has coincided in part with an increase in populations of hen harriers (e.g. Barnes, 1987). As with Loch Leven brown trout and cormorants, a long-term decline in one species has been attributed to the increase in another (e.g. Etheridge *et al.*, 1997), and lethal control measures have been widely used by keepers of heather *Calluna vulgaris* moors. These measures include nest destruction and the killing of adults, which have had a significant negative impact on densities of breeding harriers (Etheridge *et. al*, 1997). Recent analysis showed that the survival and breeding success of female hen harriers were much lower on grouse moors than on other upland land management classes in Scotland, a difference attributed to persecution of hen harriers by humans on grouse moors (Green & Etheridge, 1999).

Unlike cormorants, where the conflict with fisheries arises during the winter, hen harriers come into conflict with grouse moor managers principally during the summer breeding season (Redpath, 1991). At this time of year the harriers are not gathered in groups, but are dispersed across the moors. Thus the conflict relates to the impact of individual birds over a defined hunting territory surrounding its breeding site. The habitat in which they hunt is to some extent three-dimensional and difficult to observe, but breeding birds carry prey items back to the nest, when they may be observed, and an assessment made of they quantity and species subject to predation. Once the range of species being taken is established, the density of the prey can be assessed through established field survey techniques (e.g. Redpath & Thirgood, undated). Providing confounding factors, such as fox predation, natural grouse mortality, and other compensatory effects are accurately known, a reasonably accurate assessment may be made of the predator's impact. For example, in the "Langholm Study", researchers concluded that spring harrier predation of adults reduced breeding density by about 30%. Furthermore, grouse chick predation by harriers reduced their survival rate by 30% (Redpath & Thirgood, undated).

Where control and management measures, including non-lethal means such as prey substitution or diversionary feeding, are instigated, their effectiveness in reducing impact on grouse may be assessed. For example, Redpath *et al.,* (2001) reported that supplementary feeding with dead rats and poultry chicks during the nesting period had a clear impact on hen harrier provisioning, and could reduce the number of grouse chicks taken. In addition, the importance of habitat management may be illustrated by studies such as Thirgood *et al.,* (2002), who reported that grouse densities were higher and overwinter losses of grouse to predation were lower on areas with greater cover of heather.

Thus, the problem is somewhat simpler than the Loch Leven situation, and reasonably accurate data is more readily obtainable. However, there are parallels in terms of the importance of other factors in the long-term decline of sporting bags, and habitat degradation through over-grazing by sheep and consequent loss of heather on grouse moors (Redpath & Thirgood, undated), may be equated to water quality degradation through eutrophication on Loch Leven (Bailey-Watts *et al.*, 1994). As a result of the differences described above, the applicability of the Loch Leven study to the grouse-hen harrier conflict, is clearly very limited.

Conclusion

Perhaps the most valuable lesson from the Loch Leven study lies not in the detail of the findings themselves, nor in the particular conflict investigated, but rather in the challenge the findings present to the traditional perception that if large numbers of predators are feeding on a valuable resource, they must be causing damage. The Loch Leven study found no evidence that this is true, but rather that other factors are much more important. Furthermore, wrongly identifying the cause of a problem, and focussing on addressing it, may work against the long-term interests of the manager by wasting valuable resources, and by diverting attention from the real issues. The Loch Leven lesson is therefore particularly valuable in that it uses information from a site with possibly the most comprehensive long-term data sets, and seeks to differentiate between perception and reality. The lack of evidence in support of the traditional perception should therefore serve as a warning to those considering other apparent conflicts, particularly where the long-term data set is weak.

The general approach adopted at Loch Leven, in seeking first to identify and quantify impacts on the fishery, and secondly to measure the effectiveness of control measures, has wide applicability. The approach adopted here could form the basis for similar impact investigations, whatever the particular species involved. Any such investigation should focus on the particular objective of the site – e.g. improving angling catches - and seek evidence of significant damage attributable to the species of concern, which limits the ability to achieve that objective. The argument in this case is not as to whether or not cormorants take catchable fish, nor how many they take, but whether their predation limits the angling catch and prevents the achievement of the management objective. Where the predatory species is not a limiting factor, there is no justification for control measures.

Similarly, when investigating the effectiveness of control measures, the approach should also focus on achieving the objective of the site. Where predation is perceived to be a limiting factor, any control measures should serve to reduce the predatory species to an acceptable level, and thereby result in the achievement of the objective. If the control measures do not achieve these ends, they cannot be justified, and the basic principles underlying this investigation can be applied to any conflict of this type.

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