Scale-dependent Habitat Utilisation of Cormorants (*Phalacrocorax* spp.) in Eastern Australia

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The work contained in this thesis, except where otherwise acknowledged, is the result of my on investigation.

Signed: [redacted]

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ABSTRACT

The objective of this project was to determine factors influencing changes in the distribution of cormorants (Great *Phalacrocorax carbo*, Pied *P. varius*, Little Black *P. sulcirostris* and Little Pied, *P. melanoleucos*) in eastern Australia. The approach taken was to make comparisons among species at multiple spatial scales, identifying differences in temporal and spatial variability of resources in arid and coastal environments. Observations ranged from small (10^{-3} km^2) to large (10^3 km^2) spatial scales, and analyses centred on processes that influenced foraging patterns. Sampling was also done at temporal scales from hours to years. An important aspect of this project was the comparison of distribution and behaviour of each species in coastal estuaries and the comparatively variable interior, to assess changes to the scale of habitat utilisation in regimes of differing predictability. The specific aims of the project were 1) to characterise behaviour, distribution and associations with environmental variables at three distinct spatial and temporal scales 2) to investigate the role of environmental variability on the scale of habitat use and 3) to develop a dynamic conceptual model of cormorant movements based on choices made at different scales.

At a small spatial scale, differences in flock size were found between inland and the coast. Great and Pied Cormorants formed large groups inland and foraged singly or in small groups on the coast, most often in association with seagrass. By contrast, in both environments, Little Black Cormorants formed large feeding flocks and Little Pied Cormorants foraged singly. Flocking of Great and Pied Cormorants inland was interpreted as being a behavioural adaptation to murky water in which individuals use conspecifics for information and this would not be necessary in high-visibility coastal areas. By contrast, in coastal areas, cormorants focused on seagrass beds for foraging where the probability of encountering prey may be high. The crustacean prey of Little Pied Cormorants is often associated with high habitat structure, and may be easy to find by a solitary Little Pied Cormorant and flocking in this case would confer no advantage.

Surface times inland for all species support this conclusion: for all species except Little Pied Cormorants, surface intervals were significantly higher than those predicted to repay an oxygen debt from diving. The implication is that Great, Pied and Little Black Cormorants in unpredictable situations are on the surface longer to gain information about the location of food from conspecifics.

At an intermediate scale, I investigated the association of non-breeding cormorants with habitats in coastal and inland New South Wales. Abundance of cormorants on the coast was measured in five habitat types, along a gradient from an exposed oceanic environment to sheltered backwaters. Inland, distributions of cormorants were measured in two lake systems, with habitat types specific to location. Abundance of cormorants exhibited considerable variation at the replicate level and sites within identical habitat types at all locations in both environments, indicating that cormorants were clumped at a scale smaller than that of a habitat. On the coast, cormorants occurred near seagrass, and the relationship was stronger than any other. By contrast, cormorants in the interior were highly aggregated and not associated with any recognisable habitat features. These results agree with conclusions from small scale observations: cormorants on the coast use seagrass beds (a relatively coarse-grained cue) to locate prey on the coast and the behaviour of conspecifics (a precise cue) in less predictable inland wetlands.

For large-scale patterns, I used 13 years of aerial survey data, collected by the New South Wales National Parks and Wildlife Service, to investigate patterns of abundance and aggregation of cormorants in 1400 wetlands across the eastern half of the Australian continent. Temporal variability in abundance of cormorants in relation to aridity was investigated by comparing areas east or west of the Great Dividing Range and using years separated by rainfall level. Cormorant distribution at the landscape scale was highly variable among years and species, although the ranges of all species overlapped completely. For all species, abundance through time was low, but punctuated by periodic high spikes in abundance and correlations between yearly abundances of cormorants and environmental variables were rare. The most important trend in population size was a decrease in abundance between 1987 and 1990, corresponding to the wettest periods in the sampling period. This suggested that during wet periods, cormorants spread to smaller temporary wetlands. Cormorants also occupied a small proportion of the wetlands that existed. However, patterns among species also differed with respect to environment and wet versus dry years. Populations at the inland lakes studied fluctuated considerably through time, demonstrating sporadic periods of high abundance, interspersed with periods of low abundance and there was a general positive trend between the amount of variability in percent fill of a wetland and frequency of correlations in abundance among species and with water area. Behaviour and habitat utilisation by cormorants probably filters patterns at larger scales, creating high variability in the system.

Cormorants in eastern Australia are successful in environments that differ radically in their predictability. Their ability to survive appears to be related to their ability to make choices at a number of scales in succession. The sequence of decisions can be modelled conceptually as a loop, bringing cormorants from inland to the coast and back again, making decisions based on information at different scales. As a cormorant approaches an inland lake it uses features of the landscape to assess enough about the lake to land. Once at the lake, it gauges small scale resource quality by comparing its instantaneous rate of food intake to other places it has been. Upon leaving the lake, a cormorant must reverse the process and sample at a larger scale, assessing habitat quality once again over the region. If the cormorant perceives resources to be abundant inland, then it will find a new lake in which to forage, and repeat the process of smaller scale habitat assessment. If prospects inland are not good, the cormorant will fly to the coast. Once on the coast, it will find an estuary, making the decision to land based on stationary habitat features such as seagrass more than on conspecifics. Again, the cormorant will assess its microhabitat by assessment of small scale variables. If resources are less than the environmental average, it will leave to find another more productive location, following the same sequence of scales as inland. However, if the cormorant receives cues indicating abundance of resources inland, it may leave the estuary, irrespective of its quality, and fly inland once again, using large-scale information, completing the cycle by making decisions in a hierarchy of spatial and temporal scales. The generality of this model has yet to be tested, however it is likely that many mobile species can be viewed in this way.

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QUOTES

Mike Kingsford #1	"I thought we talked about this before."
Mike Kingsford #2	"What is this, yet another Dorfman atrocity?"
Richard Kingsford	"This is the voice mail of Richard Kingsford. If I'm not at my desk, I'm probably away at a meeting. Please leave a message."
Tony Underwood	"Eric, you have to go away and learn how to formulate a hypothesis."
Sean Connell	"It's all happening."
Charlotte Taylor	"It's all go."
Warrick Angus	"Unreal."
Piers Ettinger-Epstein	"Is this oxtail soup low-fat?"
Eric Dorfman #1	"Bronwyn, stop playing with your hair."
Eric Dorfman #2	"I'll have a large, strong, soy, café latte and a croissant."
Peter Banks	"I'll have another long black and a quiche."
Malcolm Haddon	"I'll have a cappuccino and one of those chocolate whatsits."
Bronwyn Gillanders	"I'll have a cappuccino ... ~~I think my cake is off. Do you want it~~?"
Jason Cummings #1	"I'll have a large latte and a slice of cheesecake ... Can you make it a bit bigger?"
Jason Cummings #2	"Thesis schmesis."

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CHAPTER ONE

GENERAL INTRODUCTION

A goal of population ecology is to understand features of the environment that influence the distribution of organisms. The relationship between distribution and environment is commonly investigated by correlating one or more environmental measures (e.g. resource abundance, Peters 1994) with a measure of organisms (e.g. abundance) across space or through time. The strength of these correlations may differ radically with spatial and temporal scales of observation (Dayton and Tegner 1984; see review by Schneider 1994), therefore, a fuller understanding of influences on distribution can be gained through multi-scale studies.

The value of multi-scale studies may be demonstrated with a hypothetical example of a species occupying an area, A (Figure 1.1). When the spatial scale of observation (= observational area, O) is small (O << A), the length of time an animal spends within O will be short, as it travels through A on trajectory t. The likelihood that an animal will give birth or die in this period is necessarily small, so changes in distribution account for the majority of the variation in abundance within O. Similarly, replicated snapshots in time when O is small will produce many observations in which the species is absent and a few where it is present (see Brown *et al.* 1995). As O approaches A, more of t is represented in each sample, consequently, the species spends more time under observation and births and deaths become important. Finally, when O = A (unlikely in a field study), every possible location of the species is under observation, such that changes in distribution are effectively non-existent, and the only variation in abundance is due to births and deaths. Thus, scale of observation changes the relative importance of dispersal and net population growth and several scales are required to produce an adequate picture. In the field, factors such as competition (e.g. desert rodents, Bowers and Brown 1992; musk oxen *Ovibos moschatus*, Schaefer and

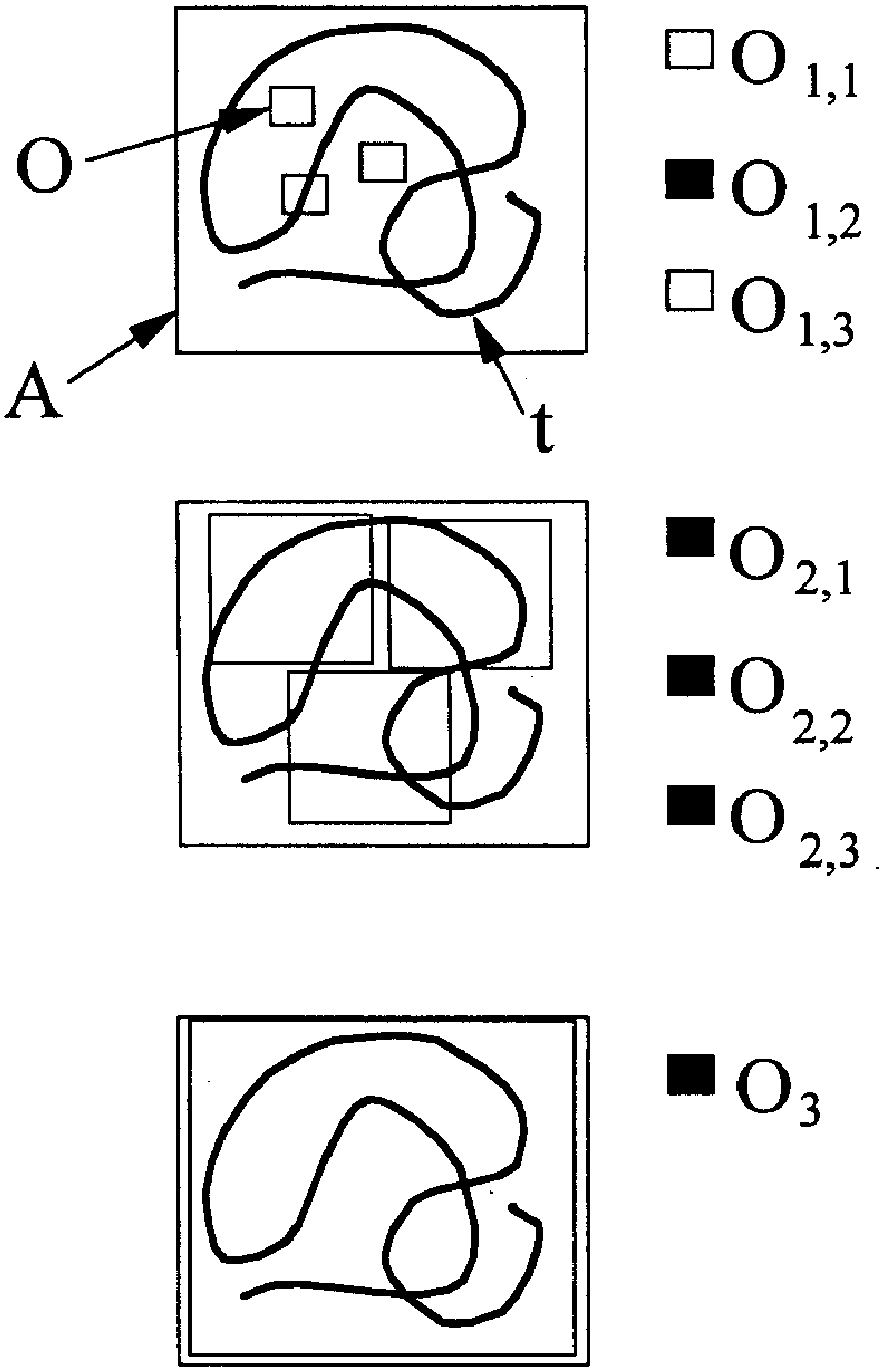

Figure 1.1. The relationship between observation area (O) and cause of variation in numbers of a species. The line t represents the species trajectory through area A. Subscripts of O represent observation size and replicate, respectively. Closed and open squares next to observations indicate presence and absence of the species in an observation, respectively. Subscript numbers represent scale and observation number, respectively. See text for explanation.

Messier 1995), predation (e.g. Knots *Calidris canutus*, Piersma *et al.* 1993; limnetic fishes, Kitchell *et al.* 1994) and habitat utilisation (e.g. cape porcupines *Hystrix africaeaustrialis*, deVilliers *et al.* 1994) have demonstrated scale-dependence.

Observational scale is also important as a number of methods exist to study variation in abundance and distribution of animals, each of which is most effective at a different scale. These include monitoring and surveys of populations (e.g. timber wolves *Canus lupus*, Mladenoff *et al.* 1995; neotropical migratory birds, Sherry and Holmes 1996), tracking individuals using radio-tags (e.g. cottontail rabbits *Sylvilagus floridanus*, Trent and Rongstad 1974, southern flying squirrels *Glaucomys volans*, Fridell and Litvaitis 1991) or biochemical markers (e.g. blue gropers *Achoerodus viridis*, Gillanders 1995) and direct observation (e.g. Red-capped Plover *Charadrius ruficapillus*, Abensperg-Traun and Dickman 1989). Each approach focuses on a specific aspect of a study animal's response to environmental variables and requires observations at a scale which is specific to the question at hand. As such, conclusions are constrained to spatial and temporal scales which are consistent with the observations from which they arise. A study at a given temporal or spatial scale will have a characteristic window of vulnerability, such that certain sources of variation may be overlooked. Use of hierarchical sampling designs that encompass a range of temporal and spatial scales can give a more complete picture of the overall response of a species to environmental variables. This is because sources of variation missed at one scale may become obvious at another (e.g. Schneider 1993).

Although multi-scale investigation is an approach that can be used with any organism or community (see Schneider 1994; Sutherland 1996), animals that are dispersive (see Chapter 2 for definition) are especially interesting because of the range of environmental conditions to which they may respond: local or broad, or a combination of both. For example, on the scale of Hokkaido Island in Japan, differences in the distribution of two species of charr (Pisces: *Salvelinus leucomaenis* and *S. malma*) are well explained by latitude (Fausch *et al.* 1994). At a regional scale, however, there was an interaction between latitude and altitude, both of which affected water temperature. Within a single watershed, the interaction became more complex including, at the scale of an individual pool, a dominance hierarchy between the two species.

Birds are particularly interesting animals for scale-based studies because flight diminishes the limitations on movement experienced by organisms restricted to land or water (e.g. fishes in isolated rock pools). Some bird species migrate across the globe, travelling further than any other type of animal, including the great whales (Dorfman and Smith 1995). This also makes them challenging to study. For example, Canada Geese (*Branta canadensis*) utilise different resources at different points along their migratory routes (McLandress and Raveling 1981), thereby increasing the potential for environmental effects at different scales.

Schneider (1993) modelled environmental effects on foraging seabirds in the Bering Sea at spatial scales from 10^{-1} km to 10^{3} km. At the smallest scale, species-specific flocking behaviour closely tracked spatially dynamic prey. On larger scales (10^{2} km), relationships were related more to geographic and hydrographic features than to prey distribution. At the largest scale, gradients of seabird abundance were related to breeding distribution and coastal configuration (see also Schneider and Duffy 1985, Schneider and Piatt 1986). Seabird distribution was associated with a variety of competing forces, each operating at a different spatial and temporal scale.

Birds that disperse should be especially able to take advantage of shifting resources, because their movements are not constrained by the exigencies of breeding at a certain location. This expectation is consistent with field data. Nomadic Pink-eared Ducks (*Malacorhyncus membranaceus*) in central Australia used wetlands flexibly, shifting their distribution and abundance to coincide with the most productive habitat and breeding when flooding triggers production of sufficient food (Kingsford 1996) . 'Opportunistic nomadism' has been demonstrated for a number of Australian birds (e.g. Australian Pratincole *Stiltia isabella*, Budgerigar *Melopsittacus undulatus*, Pied Honeyeater *Certhionyx variegatus*, Crimson Chat *Ephthianura tricolor*; see review by Schodde 1982). Dispersive birds should thus be particularly fruitful as study animals for scale-based studies, because the potential effect-size on changes in distribution and behaviour is likely to be large.

In this study, I explore aspects of resource utilisation of cormorants (Great *Phalacrocorax carbo*, Pied *P. varius*, Little Black *P. sulcirostris* and Little Pied, *P. melanoleucos*) in eastern Australia, making comparisons among species. The cormorants of Australia are characterised by a high degree of flexibility in diet (see Barker and Vestjens 1987), breeding and dispersal. This study focuses on their foraging and non-breeding association with resources at multiple scales, in a variety of habitats, ranging from temperate marine to the arid interior of the Australian continent.

Cormorants are opportunistic foragers, feeding according to prey availability in the environment (Kennedy and Greer 1988, Trayler *et al.* 1989). Although they are primarily piscivorous, they consume a wide variety of other animals including ducklings (Fisher 1963), frogs (McNally 1957), various insects (e.g. Odonata, Hemiptera, Coleoptera; Vestjens 1975; Vestjens 1977) and crustaceans (e.g. the yabby, *Cherax destructor*; Miller 1979). The ability to shift food sources increases a forager's ability to respond to changes in environmental conditions (Krebs and Davies 1987) and decreases the chance of starvation (Houston and MacNamara 1985).

Breeding can also be flexible. For example, Brandt's Cormorants (*P. penicillatus*) in California attain sexual maturity according to resource abundance, allowing individuals to take advantage of the most favourable periods (Boekelheide and Ainley 1989). In addition, Brandt's Cormorants exhibit low interannual mate fidelity, low site fidelity, and abandon or skip breeding during unfavourable conditions (Boekelheide and Ainley 1989). These life history characteristics appear to be adaptive to the highly variable conditions produced by the California Current. Such information does not exist for cormorants in Australia, but events, such as changes in food availability, are connected to gonadal maturation in Little Pied and Little Black Cormorants (see Miller 1980) and breeding of these species and Great Cormorants appears to follow wetland flooding (Llewellyn 1983).

Dispersal by cormorants within Australia is also highly variable and can be related to body size (see van Tets *et al.* 1976; Llewellyn 1983). Methodological problems with these studies, however, prevent detailed interpretation. The primary problem is that the results rely on casual sightings and tag returns by members of the public, and thus observations of the distances cormorants travelled are confounded with the density of humans available to return the tags. Although Little Pied Cormorants were suggested to be the least dispersive of the species (van Tets *et al.* 1976; Llewellyn 1983), one individual was recovered 2,900 km to the north, in Papua New Guinea (Llewellyn 1983), suggesting that more rigorous sampling designs were required. In addition, most of the birds that were recovered were dead (Llewellyn 1983). Even assuming that birds that are ill or starving will still move in the same direction as healthy birds, their trajectories would have been cut short when they died, making the construction of vector diagrams (Llewellyn 1983) especially inappropriate. Despite these problems, it is clear that all species readily travel distances of hundreds to thousands of kilometres (van Tets *et al.* 1976; Llewellyn 1983; Blakers *et al.* 1984) throughout the Australian continent (see Chapter 2).

As they disperse, individual cormorants frequently visit coastal and arid inland environments of Australia (Purchase 1969; van Tets *et al.* 1976; Brooker *et al.* 1979; Draffan *et al.* 1983). The latter vary widely in predictability and suitability. In the arid zone (the area west of the Great Dividing Range, GDR, that is not influenced by coastal rainfall), temporary wetlands appear briefly after local rainfall events, flooding vegetation and creating a food-rich environment for the prey of cormorants (fish and crustaceans). Because weather patterns are highly variable in this region (Pittock 1975; Stafford Smith and Morton 1990), the location and duration of suitable wetland habitat changes unpredictably through time. In addition, turbidity of inland wetlands (Kirk 1986) may conceal the location of prey, or areas of high habitat structure with which prey associate (Luckhurst and Luckhurst 1978; Bell *et al.* 1988; Roberts and Ormond 1987; Diehl 1993; Anderson 1994). The location and quality of food resources in the arid interior will be highly unpredictable in space and time. Observations of numerous Great and Pied Cormorants which had died, probably of starvation, near a recently-dried wetland with no fish (R. T. Kingsford pers. comm.) support a lack of certainty with regard to prey availability in the arid zone.

By contrast, permanent water in marine and coastal freshwater habitats is hydrologically more stable through time (Carter 1988). This combined with comparatively high water clarity (Carter 1988) allows cormorants to assess differential habitat quality (Trayler *et al.* 1989) for detection of fish.

There are another five chapters in this thesis, in addition to the General Introduction. In Chapter 2 (General Methods), I define the terminology of scale as used in this thesis and detail the study species and field sites. The chapter also reviews the literature on Australian cormorants. In particular, the aim of the review is on the generalist diet and flexible movement patterns, which result in differential patterns of distribution and abundance.

The studies in this thesis are organised in a hierarchy from smallest scale observations to largest. A basic premise of my research is that contributions of dispersal and behaviour to cormorant distribution exist as a nested hierarchy (*sensu* Allen and Starr

1982), in which patterns at a given scale are produced by events at the scales below. This is similar to the approaches employed by many researchers investigating scale-dependent phenomena (e.g. Brown and Orians 1970; Andersson 1980; Davies 1984; Gauthreaux 1985; Sutherland 1996). However processes at finer scales often do not completely predict patterns at larger scales, because of measurement error and stochastic behaviour (Allen and Starr 1982). In addition, the events at larger scales also constrain the behaviour at smaller ones, by defining parameters under which processes at smaller scales may act (Allen and Starr 1982). For instance, grazing by herbivores (a small scale phenomenon) may contribute to patchiness at a landscape scale, but climate (a large scale phenomenon) may also define the species' range. I therefore consider the relationship of events at different scales to be hypothesis-generating, but not strictly predictive.

In Chapter 3, I describe the behaviour of foraging cormorants, to determine environmental variables that could act as cues to the location of prey in regimes of differing predictability. I observe behaviour in coastal estuaries and in wetlands of western and central New South Wales, measuring dive and surface times, the substrate over which an individual dives, flock size and the destination of flights from water.

In Chapter 4, I investigate habitat association of non-breeding cormorants in coastal and inland habitats of New South Wales. Distribution related to foraging may be mediated by resource variability (Regelmann 1984, Gillespie and Caraco 1987) and is often scale-dependent (e.g. Schneider and Duffy 1985). I therefore predict a relationship between scale, habitat variability and the resource requirements of a given species, using a nested hierarchical design. I study the relationship between geographical features and cormorant abundance and behaviour, in coastal estuaries and some of the comparatively variable wetland systems of western New South Wales.

For landscape-scale patterns, in Chapter 5, I use 13 years of aerial survey data, collected by the New South Wales National Parks and Wildlife Service (NPWS, CSIRO and other state conservation agencies), to investigate patterns of abundance and aggregation of cormorants in 1400 wetlands across the eastern half of the Australian continent. I consider species-specific responses to water and to other species, the role of spatial and temporal variability and the importance of small-scale wetland variables. Of particular interest are landscape-scale constraints on the habitat selection examined in Chapter 4. I also attempt to gain an understanding of shorter-term patterns at a large scale by using a second set of aerial survey data (Kingsford *et al.* 1994), comprising 16 three-monthly counts of cormorants at 29 wetlands in northwestern New South Wales.

Scale itself is a thoroughly human construct (Allen and Starr 1982); nature is not divided into discreet hierarchies, but exists as a web of effects across scales. In an effort to address this complexity to some degree, each data set includes some subdivision of scales within the phenomenon explored. In Chapter 6, the General Discussion, I consider species-specific differences in behaviour and distribution and explore links between scales, developing a hierarchical model based on decision theory.

CHAPTER TWO

GENERAL METHODS: CLASSIFICATION, NATURAL HISTORY, STUDY AREAS AND TERMS USED

2.1. Classification of *Phalacrocorax.*

Researchers have suggested several phylogenetic trees for the cormorants (Phalacrocoracidae; e.g. Matthews 1927; Peters 1931; Carcraft 1985; Siegel-Causey 1988). However, assessment of the relative merits of these classification schemes is beyond the scope of this study. For consistency with other Australian authors (e.g. Blakers *et al.* 1984; Slater *et al.* 1989; Marchant and Higgins 1990), common and scientific names used in this thesis correspond with those recommended by the RAOU (updated 1994):

Phalacrocoracidae			
	Phalacrocorax		
		carbo	Great Cormorant (ssp. *carboides*)
		varius	Pied Cormorant
		sulcirostris	Little Black Cormorant
		melanoleucos	Little Pied Cormorant
	Leucocarbo		
		fuscescens	Black-faced Shag[1]

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[1] At the time of writing, Black-faced Shags are classified in a separate genus, however, Christidis and Boles (1994) classified this species as a member of *Phalacrocorax*, and this classification is becoming more widely accepted.

2.2. Natural History of Cormorants in Australia

2.2.1. General

Distribution and movements

Cormorants are widespread throughout coastal and inland waterways of Australia. All share a similar distribution (Figure 2.1, adapted from Blakers *et al.* 1984), although latitudinal gradients within species create differences in community structure. Little Pied and Little Black Cormorants are more abundant toward the north of their distribution, however Little Black Cormorants appear to be increasing their range in Tasmania (Blakers *et al.* 1994). Great Cormorants are generally more common at temperate latitudes (Harrison 1983) and in Australia, are not known to breed north of 20°S and frequently breed in Tasmania (Marchant & Higgins 1990). All species breed in western New South Wales and south western Western Australia.

Dispersal patterns vary among species (Table 2.1), however all are highly nomadic, travelling in response to localised flooding (Llewellyn 1983) to find food. Cormorants may breed wherever water levels are sufficient to facilitate production of abundant food, (Miller 1979; Miller 1980) and in the interior of Australia, this may occur throughout the year (Stafford Smith and Morton 1990).

Diet and foraging flock sizes

Cormorants consume a wide variety of aquatic and semi-aquatic organisms (Barker and Vestjens 1987) and are visual predators that pursue their prey (Hustler 1992), consuming species that are highly mobile (e.g. fishes Miller 1979; amphibians Serventy *et al.* 1971; juvenile waterfowl Fisher 1963 Storr 1965) or epibenthic (e.g. crustaceans Miller 1979). Plant material has also been recorded in stomach contents of cormorants (e.g. Hill 1925; McKeown 1934; Lavery & Haysome 1963; Hall 1974), but was probably ingested incidentally or was within the stomachs of the prey.

Cormorants feed singly or in groups of varying sizes. Flocking behaviour varies among species and, to some extent, with local conditions (Marchant and Higgins 1990). Little Black Cormorants often form feeding aggregations (Serventy 1939, Wheeler 1943, Miller 1979) whereas Little Pied Cormorants rarely do (Wheeler 1946, Vestjens 1975). Great and Pied Cormorants exhibit a high degree of variability in flocking (Marchant and Higgins 1990; pers. obs.).

Mortality

Causes of mortality in cormorants have not been widely discussed in the literature. Environmental toxicants (e.g. polychlorinated biphenyls) reduce breeding success (Fox *et al.* 1991; van den Berg *et al.* 1992), but do not appear to be a major source of adult mortality (Fox *et al.* 1991). Predation on adult cormorants has only rarely been documented. Single sightings of predation on a cormorant by a tortoise (Suborder Cryptodera) have been made in India (Sivasubramanian 1986) and by a black-backed jackal (*Canis mesomelas*) in Namibia (Hiscocks and Perrin 1987). In Australia, cormorants have been found in stomach contents of Whistling Kites *Milvus sphenurus* and Wedge-tailed Eagles *Aquila audaux* (Marchant and Higgins 1990). Crocodiles *Crocodylus porosus*, goannas *Varanus* spp., feral cats *Felis catus* and dogs *Canis familiaris* are potential predators, although it has not been documented. The infrequency of reports of predation on cormorants suggests that occurrence is haphazard and not likely a major influence on populations.

By contrast, nest predation, primarily by crows and ravens (Corvidae) is likely to be of great importance and may be a limiting factor for cormorant populations in the United States (Grant 1970; Post 1988) and Australia (Dorfman and Read 1996).

Large numbers of dead cormorants on the edges of lakes in arid Australia (R. T. Kingsford pers. comm.) suggest that starvation is also a potentially important cause of mortality.

2.2.2. Great Cormorant *Phalacrocorax carbo*

Description

The Great Cormorant (Figure 2.2) is the largest phalacrocoracid in Australia (Table 2.1). It is glossy black with a turquoise sheen, with a light cream or white throat patch that extends onto the sides of the face below and behind the eye. Breeding plumage has the addition of a small crest and white thigh patch. The face and gular region have prominent yellow bare skin and the legs and feet are black.

Australian distribution and habitat

Great Cormorants are widely spread throughout the Australian continent, around the coast and on permanent inland wetlands (Marchant and Higgins 1990). They favour deep permanent lakes and major rivers (Hobbs 1961), dams (Corrick 1981) and lake margins (Vestjens 1977). They are found less frequently in shallow, ephemeral wetlands and meadows (Gosper 1981). The roles of salinity and turbidity have been suggested to play a part in influencing their distribution (Kingsford & Porter 1994). Physical structures, such as trunks or branches may be important habitat features in these areas (Fjeldså 1985), but they are not an absolute requirement (pers. obs.) and few data are available. Great Cormorants will also roost on the ground near lake shorelines and on rocks at the seashore (pers. obs.).

In eastern Australia, Great Cormorants nest in trees or other vegetation in inland habitats (Hobbs, 1961; Vestjens 1977; Corrick 1982), or amongst rocks on offshore islands (Falla *et al.* 1981). After breeding, they are highly dispersive, travelling between the coast and inland breeding areas (Marchant and Higgins 1990). Movements towards areas of flooding have been suggested within a single catchment (Woodall 1985) as well as in large catchment systems such as the Murray-Darling Basin in central New South Wales and Victoria (Llewellyn 1983).

Some Great Cormorants disperse very widely (Table 2.1). Mark-recapture data have demonstrated individuals to move between New South Wales and Western Australia (van Tets *et al.* 1976), between South Australia and Tasmania (Llewellyn 1983) and between mainland Australia and Macquarie Island (Blakers *et al.* 1984).

Feeding behaviour and diet

Great Cormorants can feed in large flocks of up to 10,000 individuals where food is plentiful (Hobbs 1961). They are primarily piscivorous (Table 2.1) and prey are principally medium-sized mobile species, such as perch (Therapontidae; Serventy 1939) and carp (*Cyprinus carpio*, Cyprinidae; Hobbs 1961). The size of prey is restricted by the pharyngeal aperture of the cormorant (2.6 x 5.7 cm; Trayler *et al.* 1989). Great Cormorants also consume insects (e.g. the giant water bug *Diplonychus rusticus*, Hemiptera; Vestjens 1977) and crustaceans (e.g. yabbies, *Cherax* spp.; McNally 1957). Successful foraging has been recorded in very turbid water (visibility < 10 cm; Barlow and Bock 1984).

Breeding

Breeding of Great Cormorants has not been well studied in Australia. Great Cormorants breed primarily in the cooler, wetter south eastern portion of the continent as well as Tasmania, and breeding is not known to occur north of 20° S (Blakers *et al.* 1984). Great Cormorants nest on the rocky shore on cliffs, islets, human-built structures (Marchant and Higgins 1990), along water courses, and in loose nests made of sticks (Fletcher 1915) in trees about 1 - 3 metres off the ground (Marchant and Higgins 1990). The breeding habitat of Great Cormorants in Australia is similar to that of the species in Britain and Europe (Lack 1945).

Populations of Great Cormorants occasionally undergo irruptions (Blakers *et al.* 1984), followed by long-distance dispersal (Llewellyn 1983) and frequently starvation (Blakers *et al.* 1984), of juveniles. Environmental mechanisms associated with breeding or changes in population have not, however, been well addressed for this species (but see Briggs *et al.* 1997). Clutches generally range from 3 to 5 eggs (Marchant and Higgins 1990).

2.2.3. Pied Cormorant *Phalacrocorax varius*

Description

Pied Cormorants (Figure 2.3) are almost as large as Great Cormorants (Table 2.1) and are black dorsally and white ventrally, with a sharp demarcation between the two colours. Wings are black on both surfaces, but the upper wing coverts are lighter with a bronze sheen. The forehead, crown and nape are black. White extends to, or just above, the eye. The face is bare: beige or yellow in front of the eye, bright blue eye ring, gular pouch, chin and triangle above the gape are bright pink. The eyes are green and the legs and feet are black.

Australian distribution and habitat

Pied Cormorants occur in the Murray-Darling Basin and throughout coastal Australia, except Tasmania. Although Pied Cormorants are capable of long-distance movements (e.g. 869 km; Blakers *et al.* 1984), they are probably the least dispersive of the Australian Cormorants (Table 2.1; Llewellyn 1983), however, there are few comparative data.

Pied Cormorants feed in a wide variety of foraging habitats. Pied Cormorants inhabit inland lakes, swamps and rivers, as well as coastal habitats (Marchant and Higgins 1990). In these areas, Pied Cormorants forage in open water, away from habitat structure, such as vegetation or lake margins. In New Zealand, Pied Cormorants forage most frequently 100 - 300 m from shore, in a depth between 1 and 6 m (Stonehouse 1967).

Pied Cormorants breed on the rocky coast in Western Australia and Queensland and in other areas they breed in trees bordering water or on islands (Marchant and Higgins 1990). Breeding has been most frequently reported in Western Australia near Perth and in South Australia, near Adelaide (Blakers *et al.* 1984), however they have also been observed breeding at Lakes Numalla and Wyara, in Southwest Queensland, (Kingsford and Porter 1994) and in Sydney (pers. obs.).

Feeding behaviour and diet

Pied Cormorants forage singly or in groups ranging in size from a few individuals (Marchant and Higgins 1990) to hundreds and even thousands (Marchant and Higgins 1990). The diet is similar to that of Great Cormorants, primarily comprising medium to small, fast-moving fishes such as atherinids, clupeids and mugilids (Table 2.1; Serventy 1939). In inland habitats, bony bream (*Fluviatilis richardsonii*; Dorosomidae) and goldfish (*Carassisus carassius*; Cyprinidae) are important prey species (McNally 1957). Marine habitats have, however, been more completely studied, consequently a greater variety of prey has been identified. Pied Cormorants on the coast take a wide variety of prey, including juvenile Port Jackson sharks (*Heterodontus portjacksoni*; Heterodontidae); pipefishes (Sygnathidae); parrotfishes (Labridae) and several crustaceans such as school prawns (*Metapenaes macleayi*) and blue swimmer crabs (*Neptunus pelagicus*; Serventy 1939).

Breeding

The breeding biology of Pied Cormorants in Australia is poorly known. They may breed in very large colonies (up to 20,000 individuals) on the coast of Western Australia, however breeding on the east coast is limited (Blakers *et al.* 1984). Pied Cormorants may nest on the ground, using sticks, seaweed and rubbish as nesting material (Marchant and Higgins 1990) or in trees, creating nests out of twigs and branches (pers. obs.). A typical clutch consists of 2-4 eggs (Norman 1974).

2.2.4. Little Black Cormorant *P. sulcirostris*

Description

Little Black Cormorants (Figure 2.4) are small (Table 2.1) and entirely black, sometimes with a glossy purple sheen and a thin, lighter line along the throat. During breeding, the iris is bright green and a small ring of bluish tubercles develop around the eye. The bill, legs and feet are black.

Australian distribution and habitat

Little Black Cormorants are widespread along the coast, except along the Great Australian Bight, to the south. They occur in the Murray-Darling Basin in southern New South Wales and northern Victoria and inland eastern Western Australia (Blakers *et al.* 1984). Little Black Cormorants commonly inhabit wetlands, pools, semi-permanent and permanent swamps with open water (Miller 1979; Gosper 1981; Fjeldså 1985).

Foraging behaviour and diet

Little Black Cormorants forage most commonly in flocks (Marchant and Higgins 1990), with flock sizes ranging from a few individuals to well over a thousand

(Miller 1979). Although quantitative data are few, Little Black Cormorants appear to cooperate to capture prey (Serventy 1939; Miller 1979; Marchant and Higgins 1990). Several complex foraging patterns have been described: a flock moves slowly through the water, with rear birds continually flying towards the leading edge (Miller 1979); leading birds in a flock encircle a school of fish before all the flock members begin to feed (Serventy 1939); a flock spreads out in a line across a tidal inlet channel, to intercept fish leaving on a flow tide (Marchant and Higgins 1990). On rare occasions, Little Black Cormorants hunt singly for crustaceans hiding along the banks of estuaries (McNally 1957).

The diet of Little Black Cormorants is similar to that of the large cormorants, with the addition of many small fishes (~100 mm), such as the glass perchlet (*Velembassis jacksoniensis*; Centropomidae; McKeown 1944) and the mosquito fish (*Gambusia affinis*; Poecilidae; Miller 1976). Two introduced species, carp and redfin perch (*Perca fluviatilis*; Percidae), are especially important. Pest-removal programs centred on carp and redfin could have an adverse effect on this species (Miller 1979), although the density of Little Black Cormorants may be artificially high due to the abundance of these introduced species.

Breeding

Most of the information on breeding of Little Black Cormorants comes from one study (Miller 1980) in central New South Wales. Little Black Cormorants nest in unvegetated wetlands, primarily in fresh water (Miller 1980; Briggs *et al.* 1997), sometimes in association with other species (e.g. Little Pied Cormorants; pers. obs.). Gonadal maturation is stimulated by rainfall, and reproduction does not occur during drought (Miller 1980). Nesting may occur with other species (e.g. Australian Darters *Anhinga melanogaster*; Marchant and Higgins 1990). Breeding aggregation size has not been investigated, however feeding flocks may reach 1500 individuals (Miller 1979), indicating a potential for large nesting colonies. Little

Black Cormorants nest in the tops of trees up to 30 m high, constructing platforms from sticks, leaves and grasses (Marchant and Higgins 1990). Clutch sizes are unknown.

2.2.5. Little Pied Cormorant *Phalacrocorax melanoleucos*

Description

Little Pied Cormorants (Figure 2.5) are small (Table 2.1), with black back, crown, upper and lower wings and feet. The feathers of the back and upper wing coverts may be lightly outlined with buff. The breast, neck and brow are white. A few black feathers may appear on the breast. A crest is present in breeding individuals. The bill is yellow, and the lining of the mouth bright pale-blue. The iris is dark brown. A naked patch of skin in front of the eye is grey and the gular pouch is orange.

Australian distribution and habitat

Little Pied Cormorants occur throughout Australia, except for the Great Sandy Desert. Movements are not seasonal (Marchant and Higgins 1990) but may be related to local food availability (Whyte 1981). Inland, they may gather at drying pools to capture trapped fish (Hobbs 1961) and on the coast, inhabit estuaries and sheltered embayments, typically roosting on human-made structures (pers. obs.).

Foraging behaviour and diet

Little Pied Cormorants typically forage singly (Marchant and Higgins 1990), but occasionally form groups (Wheeler 1946; Gosper 1981), sometimes in association with Little Black Cormorants (Serventy 1939; Carruthers 1969) and egrets (*Ardea* spp. Bolger and Wall 1959). They feed primarily in sheltered coastal waters and inland swamps and waterways, concentrating their efforts in shallow water where their prey are most abundant (Vestjens 1977; Miller 1979; Morton *et al.* 1993).

The diet of Little Pied Cormorants (Table 2.1) differs somewhat from those of the other species. They may consume a large proportion of crustaceans; sometimes close to 90% of the diet (Miller 1979). Crustaceans commonly taken are small epibenthic species, associated with slow moving water, or high habitat structure, e.g. the snapping shrimp *Aphdus edwardsi*, spider crab *Helicarcinus australis* (Serventy 1939) and yabby *Cherax destructor* (Miller 1979).

Little Pied Cormorants also eat a wide variety of terrestrial insects, such as grasshoppers (Orthoptera; Lavery and Haysom 1963) and beetles (Coleoptera; McKeown 1944) and fish from at least 25 families (Barker and Vestjens 1987), including Cyprinidae (McKeown 1944), Atherinidae (Serventy 1939), Apogonidae (Lavery and Haysom 1963) and Mugilidae (McNally 1957, Serventy 1939).

Breeding

Little Pied Cormorants nest in freshwater lakes, billabongs and along the banks of rivers (Miller 1980). Breeding sites occur patchily throughout the interior of south eastern Australia, and occur to a lesser degree south west of Australia (Marchant and Higgins 1990). Little Pied Cormorants are intermediate among the Australian cormorants in the distance dispersed after breeding (Llewellyn 1983), although further records of exceptional movements by individuals (e.g. Hattah, Victoria, 2,900 km north, to Arufi, Papua New Guinea; Blakers *et al.* 1984), indicate that more study is needed. Nests are a loose platform of sticks and bark, lined with leaves (Marchant and Higgins 1990). Few data exist on clutch size. Three to seven eggs have been reported (Marchant and Higgins 1990).

2.3. Study Areas

In this chapter, descriptions are give for study locations that either appear in more than one chapter, or that contribute to understanding of the system as a whole. Because several study sites are nested within a given study region, information on study locations are presented in a hierarchy from largest (Table 2.2). This is not, however, the order in which they appear in chapters 3-5. For clarity, coastal sites are listed first. When maps appear in this chapter, they are not repeated in future chapters. Maps that explain details of sampling methods are left to relevant chapters and a description of study locations in the Northwest region of New South Wales is given in Chapter 6.

2.3.1. Locations

Eastern Australia

Landscape-scale data for this study were collected from the eastern-most portion of the mainland of Australia, from approximately 138°E, eastward to the Pacific Ocean. This boundary is defined by the study area covered by the waterbird survey, conducted by the New South Wales National Parks and Wildlife Service (Braithwaite *et al.* 1986). The area is bisected unevenly by the Great Dividing Range. The land east of the range, influenced by coastal conditions, generally experiences high rainfall (~ 1000 mm/yr; Australian Bureau of Meteorology (ABM) 1995). West of the Great Dividing Range, the land is more arid. Although average rainfall varies considerably from place to place, it is generally much lower than on the coast (~ 400 mm/yr, although there is considerable variation; ABM 1995). There is also an overall trend of more seasonal rains and higher temperatures in the tropical north leading to aseasonal rains and lower temperatures in the temperate south (ABM 1995).

Eastern Australia contains many hundreds of thousands of wetlands, varying in size from less than one hectare to many thousands (e.g. Yantabulla Swamp; 37,200 ha; Kingsford *et al.* 1994). West of the Great Dividing Range, unregulated wetlands undergo a drying and refilling cycle which may take from one to three years, depending on the size of the wetland (Mabbut 1977). Continuous turnover of nutrients through wetting and emptying make these wetlands of great importance to waterbirds (although more-so for herbivorous ones; Braithwaite *et al.* 1986).

The east coast of Australia is approximately 2,800 km long and punctuated by numerous estuary systems (e.g. Broken Bay). Coastal seagrass meadows, which provide food for cormorants (Trayler *et al.* 1989), tend to be more productive in terms of fish in summer, because a higher biomass of grass provides more shelter for juvenile fish (Pollard 1984). Seasonal pulses in productivity appear to be the general case for seagrass meadows (Alcoverro *et al.* 1995) and for fishes that recruit to estuaries (Neira *et al.* 1992; Gillanders 1995). Seasonality has also been demonstrated in other elements of the coastal food web of eastern Australia (Underwood 1981).

The greater Sydney region

Although heavily developed, the Greater Sydney Region (Figure 2.6) still contains extensive habitat for cormorants. Cormorants may also benefit from human presence, through creation of roosting and nesting habitat (Dorfman and Read 1996). The Sydney region contains four major estuary systems: Port Hacking, Botany Bay, Port Jackson (Figure 2.7.) and Broken Bay (Figure 2.8.). Broken Bay, with the associated Hawkesbury River, Pittwater and Brisbane Water contains the largest amount of undisturbed habitat in the area.

These areas are tidal, but have input from urban runoff. Most undisturbed waterways are lined with grey mangrove (*Avicennia marina*) or sclerophyllous forest. Most shallow channels are lined with a mosaic of seagrass and sand patches and the deeper boat channels are dredged. The community of the soft-bottom benthos varies considerably in space (Morrisey *et al.* 1992a) and time (Morrisey *et al.* 1992b), as does the faunal assemblage in seagrass beds (Pollard 1984) and the nearshore rocky reef (Holbrook *et al.* 1994).

Cormorant habitat on the Sydney region consists primarily of sheltered bays and creeks where sufficient roosting sites (e.g. pier pilings and oyster racks) and foraging habitat (e.g. seagrass beds) occur. Cormorants also occur on the rocky shores in small numbers. All species occasionally nest on human-made islands in urban lakes (e.g. Dorfman and Read 1996).

Homebush Bay

Homebush Bay and the adjacent Bicentennial Park is located along the Parramatta River, which flows to Port Jackson (Figure 2.7). Although the bay has been highly modified, important features for cormorants remain, including habitat for roosting (an exposed shipwreck and pilings) and for foraging. The floor of Homebush Bay is covered by anoxic mud (Berents 1993). Despite this, the area contains fish, including abundant gobies (e.g. *Gobiopterus semivestitus*) and sea mullet *Mugil cephalus*, as well as flathead *Platycephalus* spp. and yellowfin bream *Acanthopagrus australis* (Berents 1993).

Bicentennial Park is built on an estuary that was reclaimed from its use as a landfill site. The park now contains salt marsh habitat, mangrove forest and tidal creek, about 2 km long. There is also an artificial, 4 ha lake with a island of approximately 1 ha, on which stands of *Casuarina* have been planted. Although a study conducted shortly after reclamation described a "striking" lack of crustaceans in the estuary area (Berents 1993), estuarine fauna has more recently become established (pers. obs.).

All species of cormorant and Australian Darters have bred in small numbers on the island in the artificial lake (Dorfman and Read 1996), as have Black Swans; Eurasian Coots *Fulica atra*; Dusky Moorhens *Gallinula tenebrosa* and Pacific Black Ducks (*Anas superciliosa*; Dorfman unpubl. data). Fish have not been collected from the lake, however, Australian Darters have caught fish there (pers. obs.) and egested pellets from cormorants on the island contain otoliths of leatherjackets (Monocanthidae; Dorfman unpubl. data).

Patonga Creek

Patonga Creek (Figure 2.8) is located in Brisbane Water National Park, along the Hawkesbury River, in the Broken Bay estuary system. It is about 5.5 km long and at high tide provides approximately 130 ha of habitat. Patonga Creek is rimmed by mangroves in its southern extent, giving way to mixed sclerophyll forest to the north. Extensive oyster production occurs on the creek, providing considerable roosting habitat for cormorants.

The bottom of Patonga Creek consists of patches of seagrass (*Zostera marina*) meadow and sand, interspersed with boulders. Low tide exposes sand islands in the centre of the creek, but all seagrass beds are submerged by at least 10 cm of water. Fish caught during this study include leatherjackets (Monacanthidae); toadfishes (Tetraodontidae); sea mullet *Mugil cephalus* and blackfish *Girella tricuspidata*.

Breeding by waterbirds has not been observed on Patonga Creek, however White Breasted Sea Eagles *Aquila audax*; Whistling Kites *Haliastur sphenurus* and Azure Kingfishers *Ceyx azurea* all bred there during this study (Dorfman unpubl. data). Non-breeding populations of Sacred Ibis *Theskiornis aethiopica*; Great Egrets *Ardea alba*; Royal Spoonbills, Australian Darters and Mangrove Bitterns *Butorides striatus* have also been observed there.

Lake Altibouka (Lake Salisbury)

Lake Altibouka (29°49'S, 142°45'E; Figure 2.9) has an area of 565 ha when full. Water flows into Lake Altibouka mostly from the Southwest along a system of small creeks, which drain the Yancannia Range to the Southeast. It is a salt lake, and salinity increases as the lake dries. The lake dried out completely in December 1987 and March 1990 (Kingsford *et al.* 1994).

The lake is surrounded by sandhills and clay flats, upon which grow abundant chenopods (old man saltbush *Atriplex nummularia*; black bluebush *Maireana pyramidata*) and other flowering shrubs (e.g. spotted fuschia *Eremophila maculata*; sandhill wattle *Acacia ligulata*). The lake is surrounded by pinrush and samphire *Halosarcia pergranulata* and supports a large standing crop of aquatic macrophytes. The lake supports populations of bony bream *Nematoalosa erebi* and yellow-belly Macquaria ambigua and during floods, the desert tree frog *Litoria rubella* (Kingsford *et al.* 1994).

Because Lake Altibouka fills regularly, it is an important area for birds. Over 40,000 birds have been sighted there at a single time (Kingsford *et al.* 1994). Black Swans sometimes breed there in large numbers (133 nests) and the lake can also support breeding of Red-capped Plovers *Charadrius ruficapillus*; Grey Teal *Anas gracilis* and Maned Ducks *Chenonetta jubata* (Kingsford *et al.* 1994).

Lake Menindee

Lake Menindee (32°30'S, 142°20'E; Figure 2.10) is a large (~ 7000 ha) lake, the water level of which has been regulated since 1960. It is part of a system of five major lakes and numerous ponds and channels, which is fed by the Darling River. The lakes serve as the major source of water for Broken Hill, 110 km to the Northwest and are also a water source for communities downstream, including

Adelaide. Lake Menindee is filled most of the time, but in 1994 was allowed to dry. The floor of the lake became covered with grasses and low shrubs, which provided organic material for fish and invertebrates in 1995, when the lake was refilled. The lake bottom is otherwise homogenous mud, littered with branches and fallen trees (pers. obs.).

The only permanent feature within Lake Menindee is Snake Island, which has an area of approximately 1 ha. The island was observed casually in 1994, and no evidence of past nesting by cormorants was found (although active nests of Little Corellas *Cacatua pastinator* occurred there). In 1995, Pied Cormorants carrying nesting material were observed flying in the direction of Snake Island, but the lack of a boat prevented a survey.

Roosting habitat consists of dead trees (black box *Eucalyptus largiflorens* and river red gum *E. camaldulensis*), the bases of which stand submerged in water. These trees were alive prior to the 1960 regulation of the lake, when periodic drying allowed the tree roots to aerate. Cormorants were more commonly found roosting in these trees than in any other area. The shores of the lake are surrounded by river red gum and grasses, but the Lake Wetherell outlet channel (Figure 2.8) also includes *Phragmites australis* and rafts of *Persicaria lapthifolum*.

Fish caught here during 1995 included bony bream, juvenile carp and goldfish and an unidentified species of goby (Gobeidae). In 1994, the dry lake bed contained many drifts of dead adult carp. No other fish remains were found.

Lake Waitchie

Lake Waitchie (30°10'S, 144°00'E; Figure 2.11) is a small (140 ha) freshwater lake, which receives water from the Paroo River, filling from the south. Some water is delivered from the north by an unnamed creek, but probably contributes relatively little. The lake always had water during this study, although during dry times, the northern neck dried out (Kingsford *et al.* 1994). There is no extensive river management in the catchment. Harvesting of water upstream on the Paroo River may reduce the level of flooding of Lake Waitchie and impact on its contribution to waterbird numbers.

Lake Waitchie is surrounded by river red gum and black box *Eucalyptus largiflorens*, with some dead trees in the middle of the lake. Pinrush *Cyperus gymnocaulos*; small knotweed *Polygonum plebeum*; native liquorice *Glychorrhiza acanthocarpa*; *Brachychome heterodonta*; *Glinus lotoides*; *Senecio cunninghamii*; spear thistle *Cirisium vulgare* and *Dentella minutissima* grow on the floor of the lake bed as it dries. Yellow-belly and Australian smelt *Retropinna semoni* were caught in this lake in May 1989 (Kingsford *et al.* 1994).

Lake Waitchie is a regular breeding site for Yellow-Billed Spoonbills *Platalea flavipes* and may be typical of several wetlands along the Paroo River. Other species which have bred there are Royal Spoonbills *Platalea regia*; Pacific Herons *Ardea pacifica*; White-faced Herons *Ardea novaehollandiae*; Black Swans; Australian Darters *Anhinga melanogaster* and Pacific Black Ducks *Anas superciliosa*, though all species nest there in low numbers (Kingsford *et al.* 1994).

2.4. Terms and abbreviations

Terms to define features of an organism's surroundings have been subject to exceptional variability in the ecological literature. Because this study uses a hierarchical approach to investigate features of cormorants' *milieu*, common terms may be subject to misunderstanding and are defined in the context of this thesis.

2.4.1. Terms

Dispersal

For the purposes of this thesis, 'dispersal' is defined as a movement from one place to another. This is distinct from 'juvenile dispersal', in which young leave the area of their birth and which often exhibits a gender bias (see Krebs & Davies 1987). It is also distinct from 'migration', in which is implied temporal periodicity and a relation to climate or regionality.

Environment

"Environment" has been defined as "An organism's surroundings, both living and non-living, including temperature, light intensity, and all other species that influence the focal organism" (Purves *et al.* 1992: G10). However, in the context of a hierarchical treatment of spatial scale, this definition does not seem particularly useful. In this study, "environment" is used to differentiate coastally influenced areas from those in the rain shadow west of the Great Dividing Range. Thus, the term is roughly equivalent to "biome" ie "A major division of the ecological communities of Earth, characterised by distinctive vegetation" (Purves *et al.* 1992: G4), although in the present work, the primary delineation is based on amount and variability of water (Stafford Smith and Morton 1990). Environmental patterns of distribution of cormorants have a spatial scale of approximately 10^3 km^2.

Habitat

The term "habitat" has been used to describe a great many natural phenomena, and is especially poorly defined with regard to habitat utilisation. "Habitat" has been used as a measure of characteristics of the environment, such as water chemistry of wetlands, at a scale of 6 x 10^3 km^2 (Merendino and Ankney 1994). It has also been used simultaneously to refer to broad-scale plant communities and to the area of a single tree (de Villiers *et al.* 1994), or at once to a river course and to different successional states along the river (Rosenberg 1990). A definition of "the environment in which an organism lives" (Purves *et al.* 1992: G13) is similarly unhelpful, especially given the definition of "environment" (above), by the same authors. In this thesis, "habitat" is used as a subdivision of "environment", based primarily on physical structures. For cormorants, the spatial scale of a habitat is approximately 10^1 km^2. For example, in the coastal environment, habitats include the open coast, headlands, embayments and creeks.

Microhabitat

"Microhabitat" is largely determined by the behaviour of individuals, and so changes considerably with body size and mobility of the study species. However, there is a positional component to the term, as it is used by most researchers. "Microhabitat" has been used to describe a particular vegetation type in which a species feeds or shelters (e.g. seagrass, Leber 1985; bamboo, Rosenberg 1990). It has also been used to describe the position of refugia, however in this context has been used synonymously, and concurrently, with "habitat" (e.g. blennies *Acanthemblemaria,* in coral crevices high above, or near to, the reef surface, Clarke 1992). Although "Microhabitat" has also been specifically distinguished from "foraging substrate" (e.g. Rosenberg 1990), the term has also been used to describe it (e.g. Pacific Reef Herons *Ardea sacra* foraging on coral flats and in beach wash, Rohwer 1990). In this thesis, "microhabitat" is used as a subdivision of habitats, to delineate foraging substrate. For instance, creek habitats are divided into microhabitats of seagrass and sand.

Site

"Site" is used as a sampling unit, and makes no reference to spatial scale or to the nature of use of a given location.

2.4.2. Abbreviations

Abbreviations are made for common terms (Table 2.3). Except for GDR (the Great Dividing Range), abbreviations are only used in tables and figures.

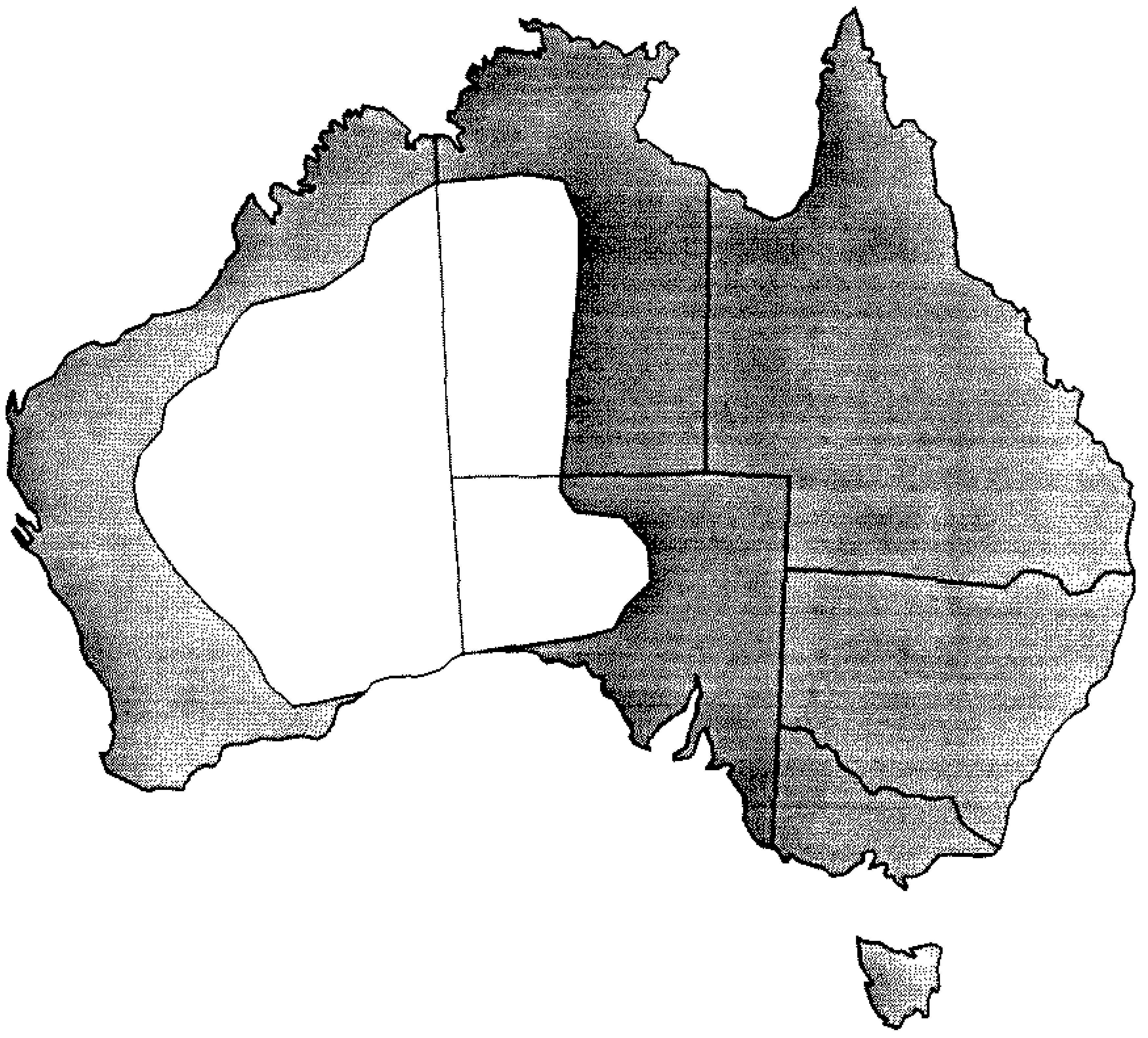


Figure 2.1. Generalised distribution (shaded area) of cormorants in Australia. (After Blakers *et al.* 1984).

Figure 2.2. The Great Cormorant *Phalacrocorax carbo* Photo: Nature Focus

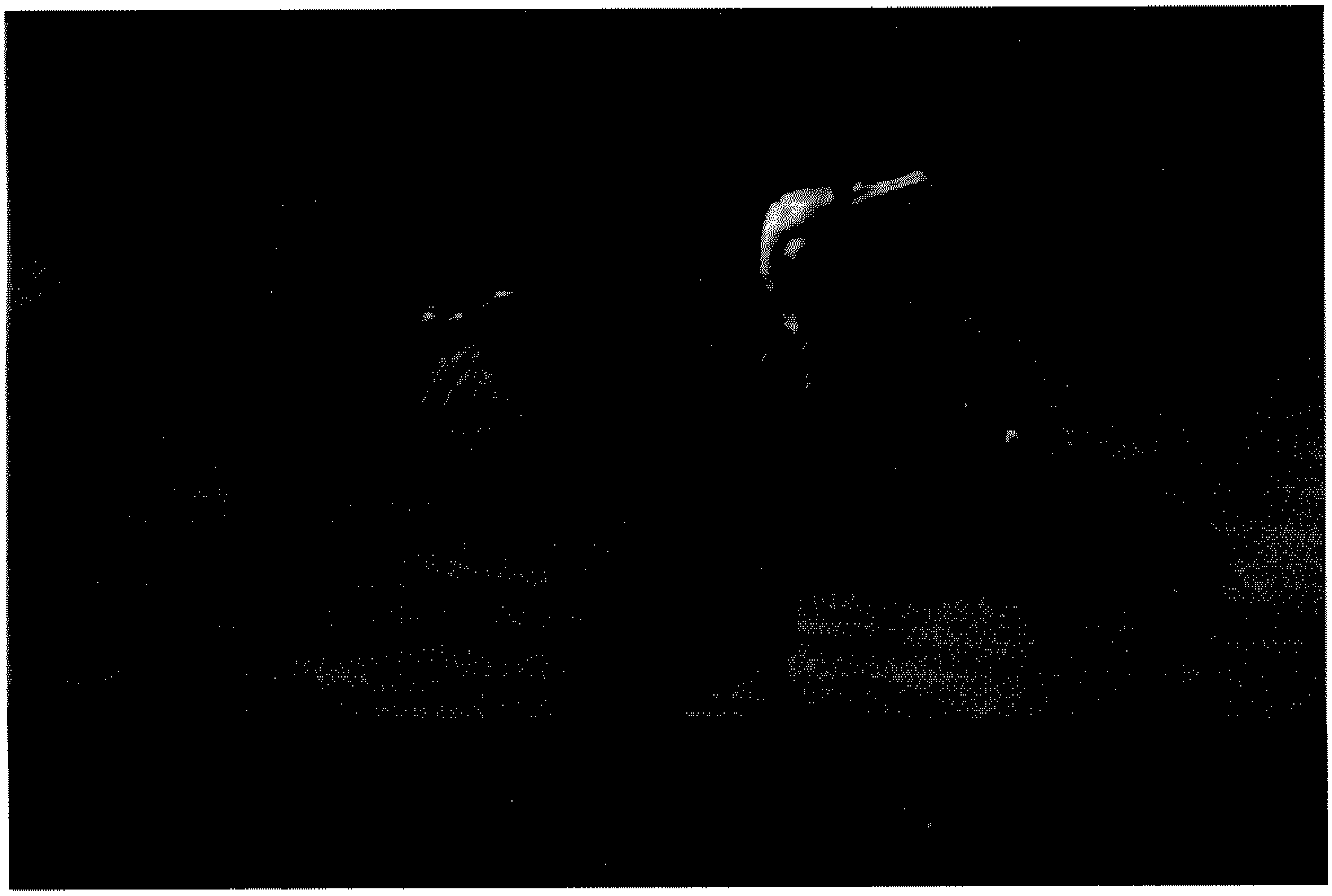


Figure 2.3. The Pied Cormorant *Phalacrocorax varius* Photo: Nature Focus

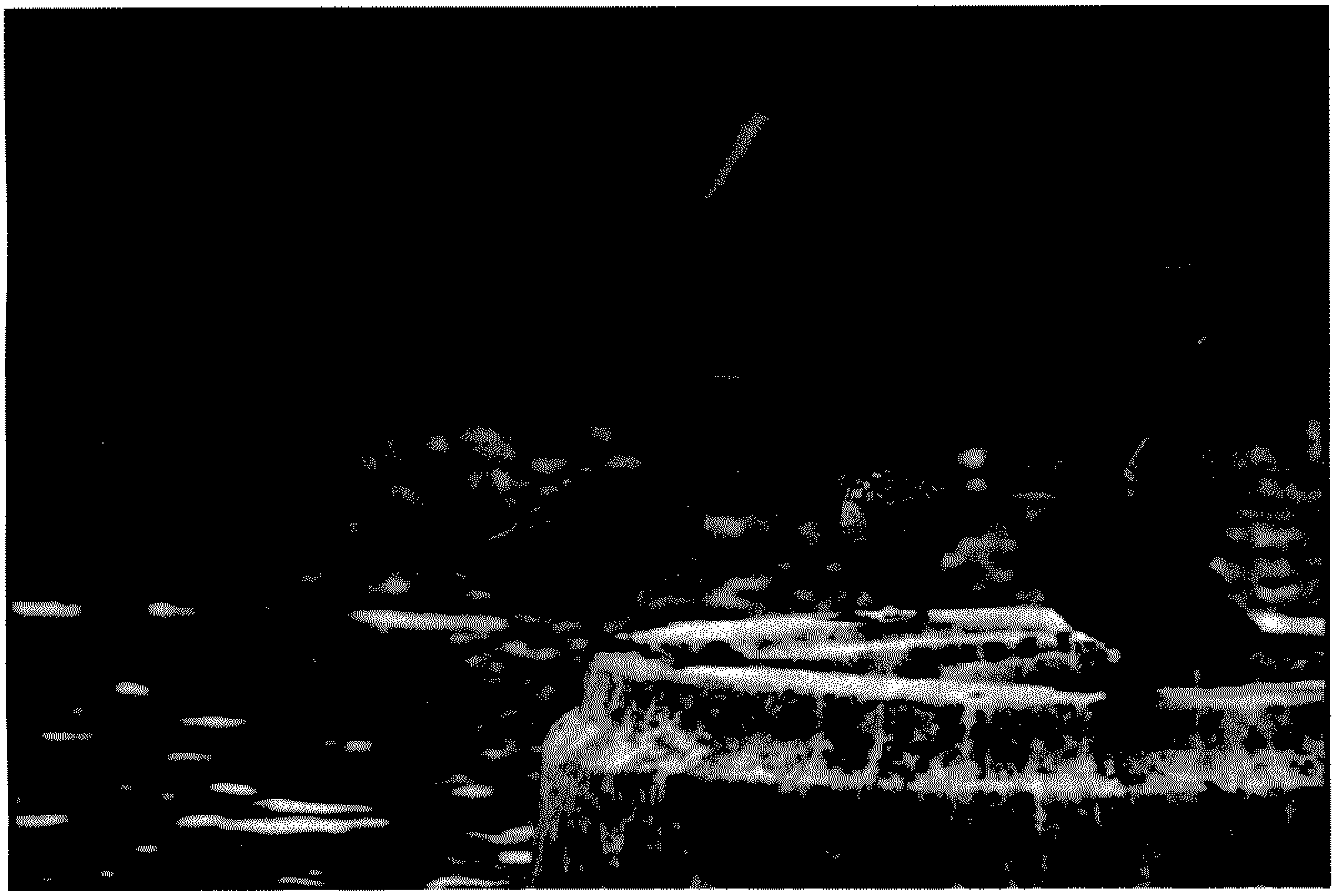


Figure 2.4. The Little Black Cormorant *Phalacrocorax sulcirostris*
Photo: E. Dorfman

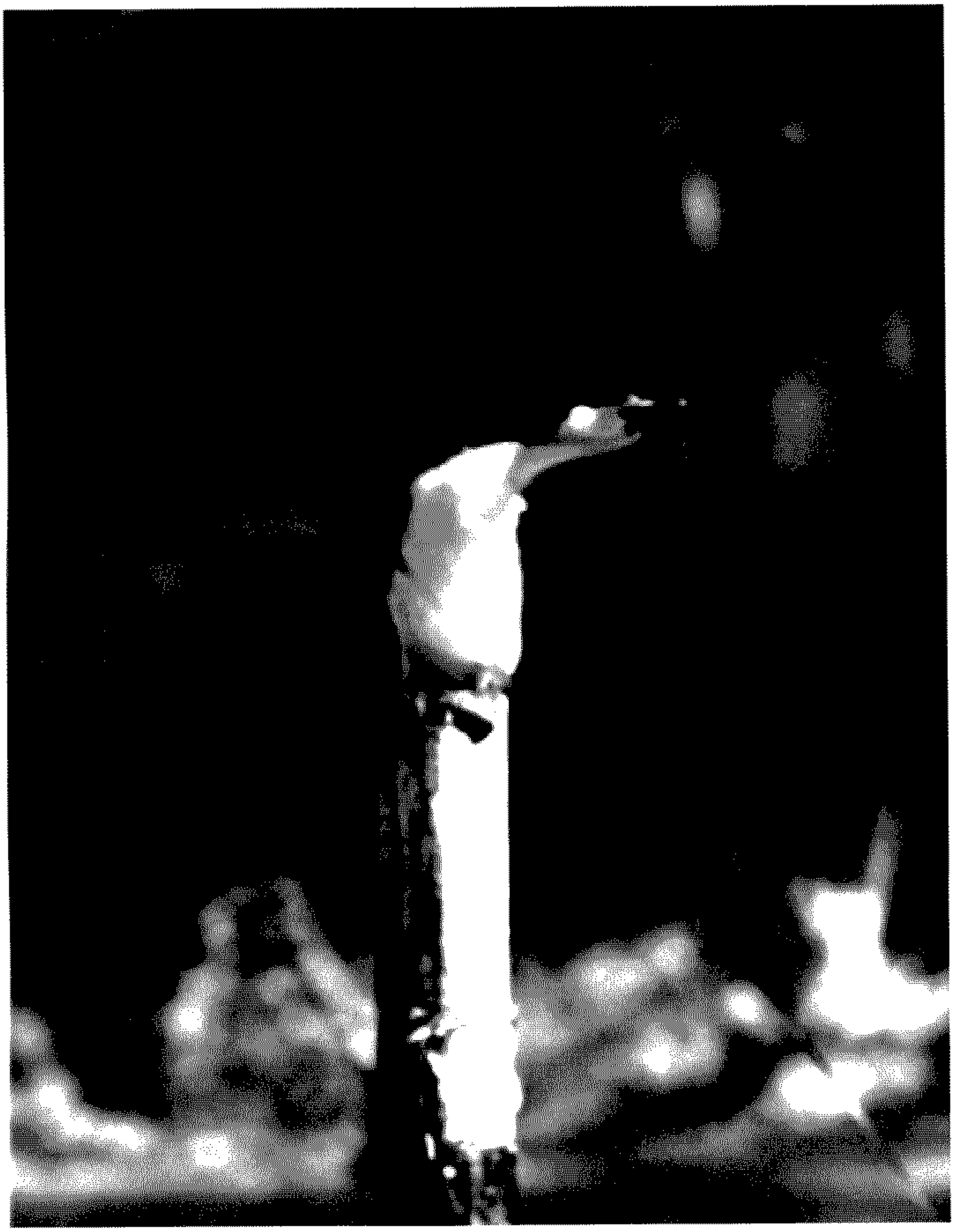


Figure 2.5. The Little Pied Cormorant *Phalacrocorax melanoleucos*
Photo: E. Dorfman

Table 2.1. Comparison of morphology, juvenile dispersal and diet of Great (GRC); Pied (PCO); Little Black (LBC) and Little Pied (LPC) Cormorants. Juvenile dispersal values reflect the longest post-fledging movements recorded. Actual maxima are likely to be greater. Similar studies on adult birds have not been conducted. Sources: [1]Marchant and Higgins (1990); [2]Llewellyn (1983); [3]Miller (1979).

Species	Standard Length[1] (cm)	Wingspan (cm)[1]	Weight (g)[1]	Juvenile Dispersal (km)	Most important prey taxon by weight
GRC	80-85	130-150	2000-2500	~2500[1]	Fishes[1]
PCO	65-85	110-130	1300-2200	322[1]	Fishes[1]
LBC	55-65	95-105	520-1210	~1500[1]	Fishes[3]
LPC	55-65	85-90	410-880	2900[2]	Crustaceans[3]

Table 2.2. Study areas used in this thesis. Asterisks are placed beside place names for which descriptions are given in this chapter. Descriptions of other sites are given in their relevant chapters.

- EASTERN AUSTRALIA*
    - COAST
        - Greater Sydney Region*
            - Port Jackson
                - Athol Bay
                - Diamond Bay
                - Homebush Bay*
                - Long Nose Point
                - Magdala Creek
                - North Head
                - Queenscliff Beach
                - Rose Bay
                - South Head
                - Wolsely St. Wharf
            - Broken Bay
                - Box Head
                - Broken Bay
                - Coal and Candle Creek
                - Dead Horse Point
                - Hawkesbury Head
                - Long Island
                - McMasters Beach
                - Newport Beach
                - Ocean Beach
                - Patonga Creek*
        - The Broadwater Lake
        - Lake Illawarra
    - INLAND
        - Northwestern New South Wales
            - Darling River
            - Glenprarie Station
            - Lake Altibouka*
            - Lake Cawndilla
            - Lake Menindee*
            - Lake Waitchie*
            - Lake Wetherell
            - Pejar Dam

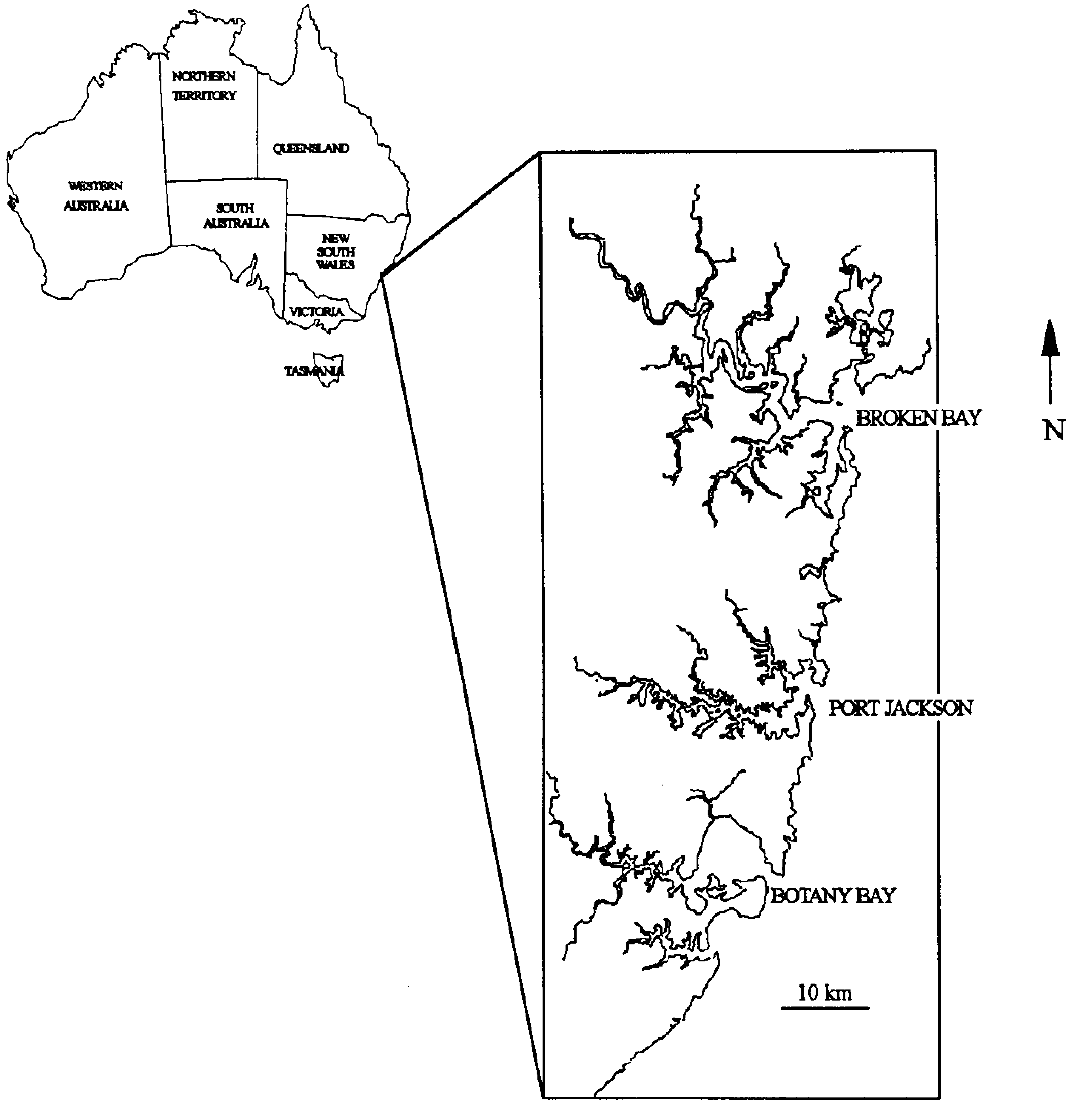


Figure 2.6. The greater Sydney Region after West *et al.* (1985).

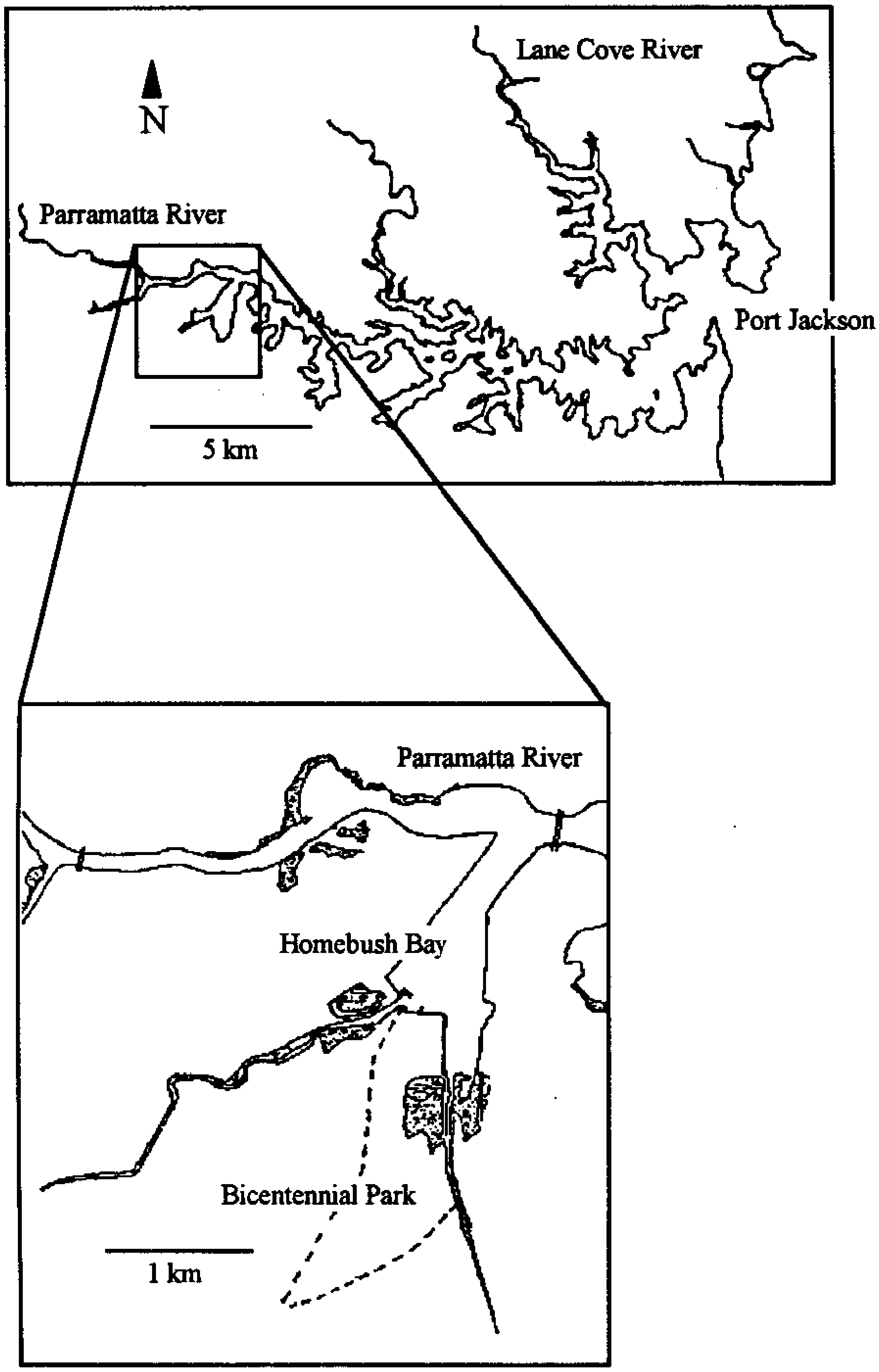


Figure 2.7. Port Jackson (inset), Homebush Bay and Bicentennial Park after West *et al.* (1985). Shaded areas indicate presence of mangroves.

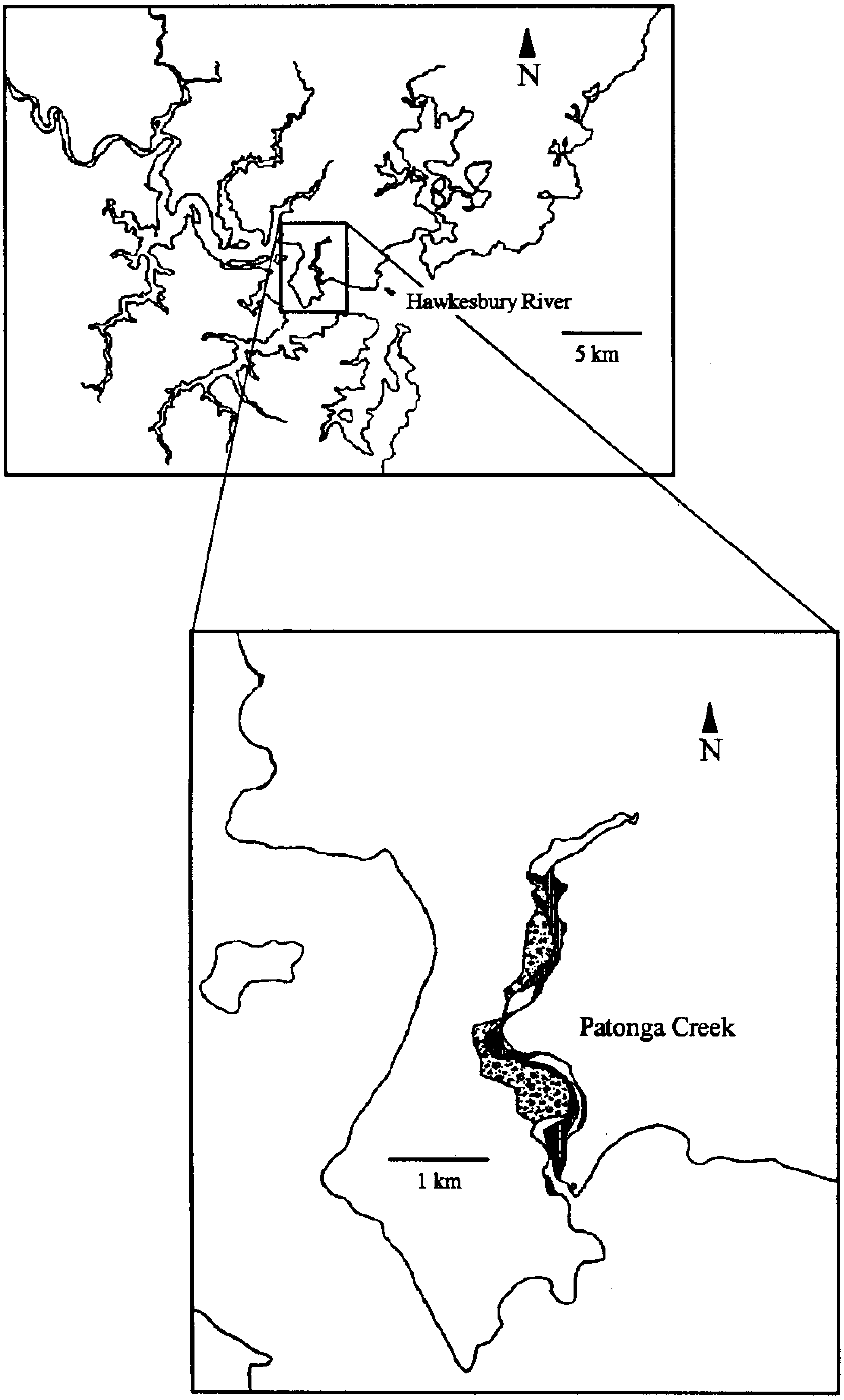


Figure 2.8. Broken Bay (inset) and Patonga Creek after West *et al.* (1985). Hatched, stippled and clear areas of Patonga Creek represent areas of seagrass, mangrove and sand, respectively.

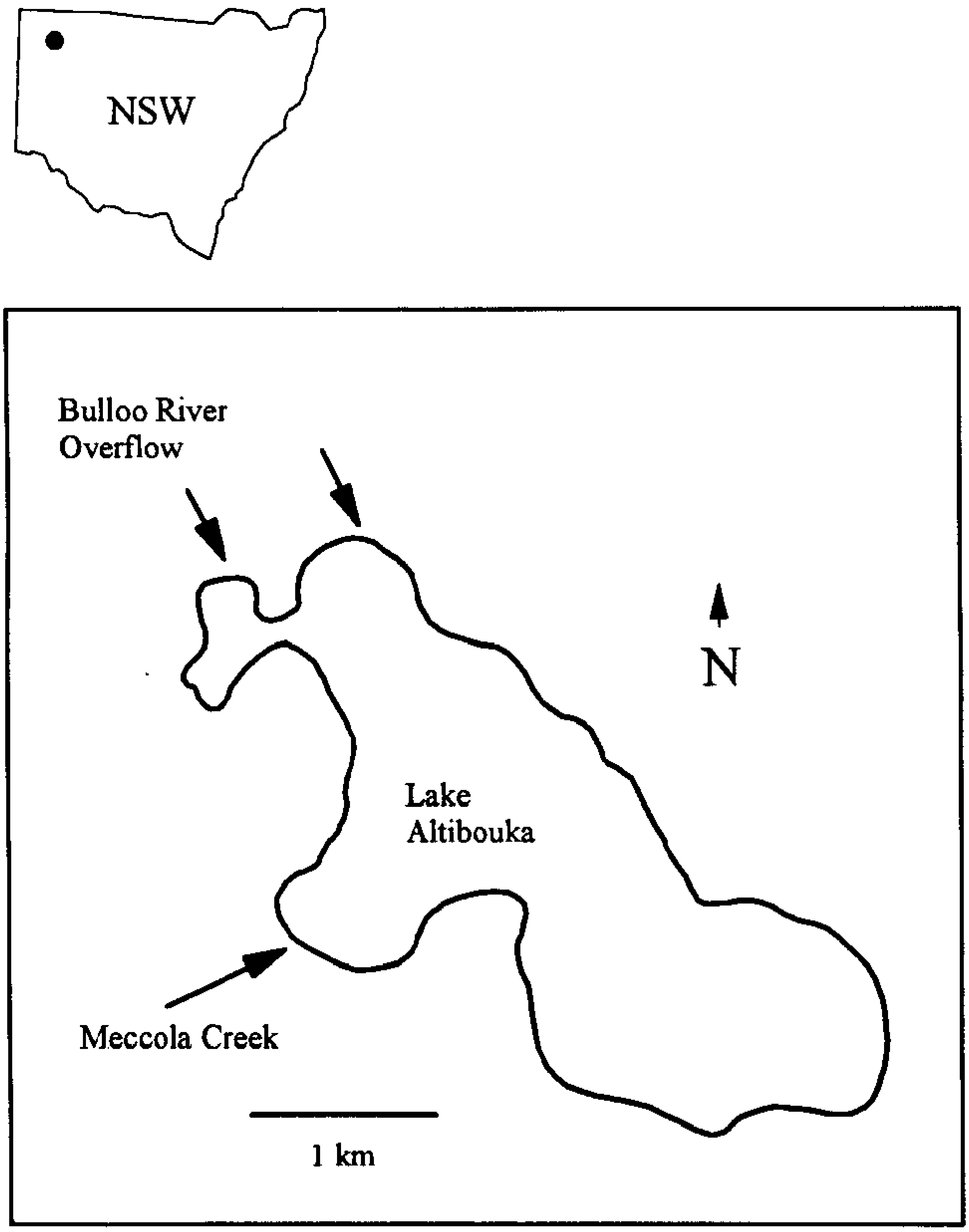


Figure 2.9. Lake Altibouka after Kingsford *et al.* (1994).

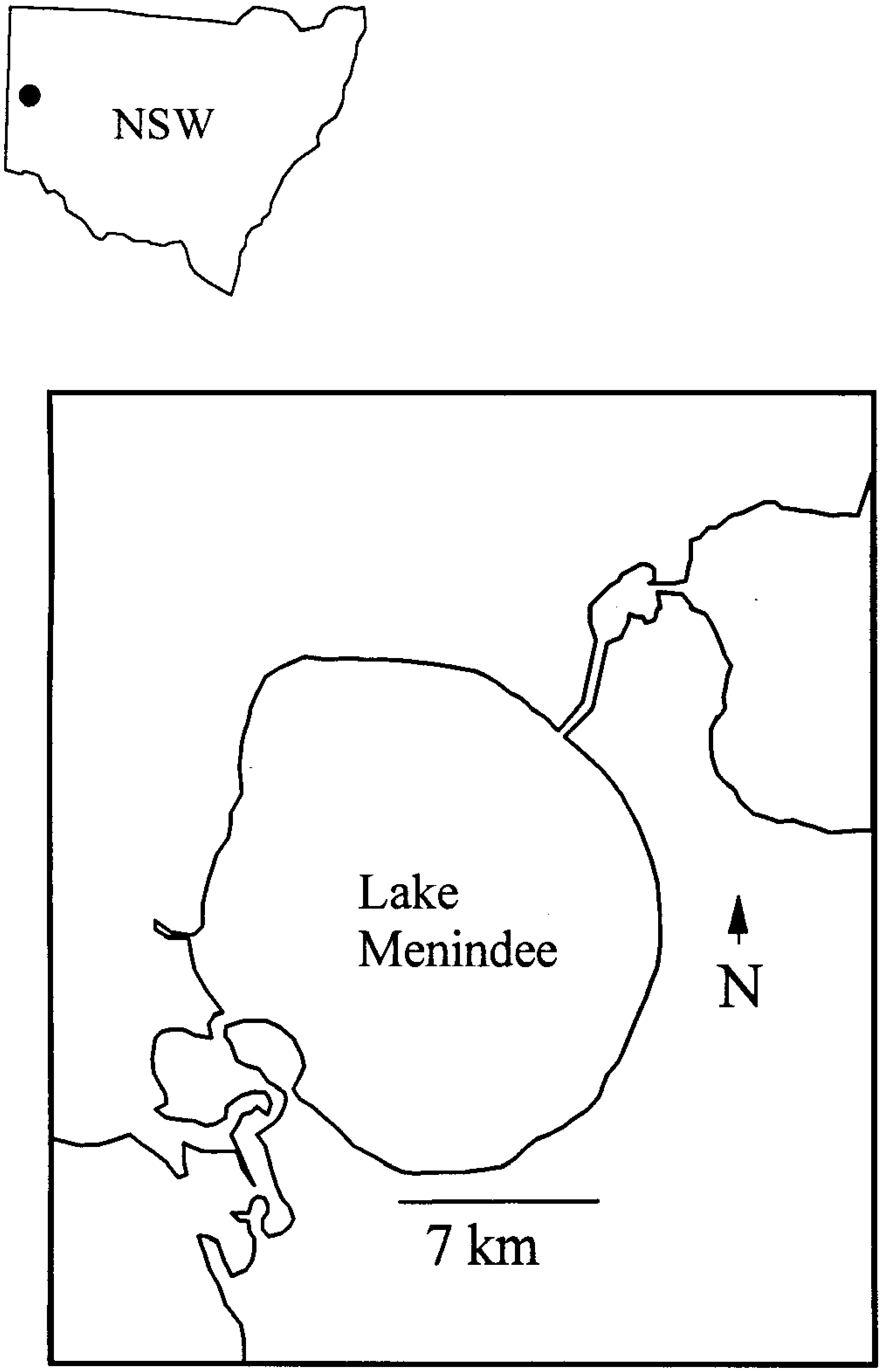


Figure 2.10. Lake Menindee after Kingsford *et al.* (1994).

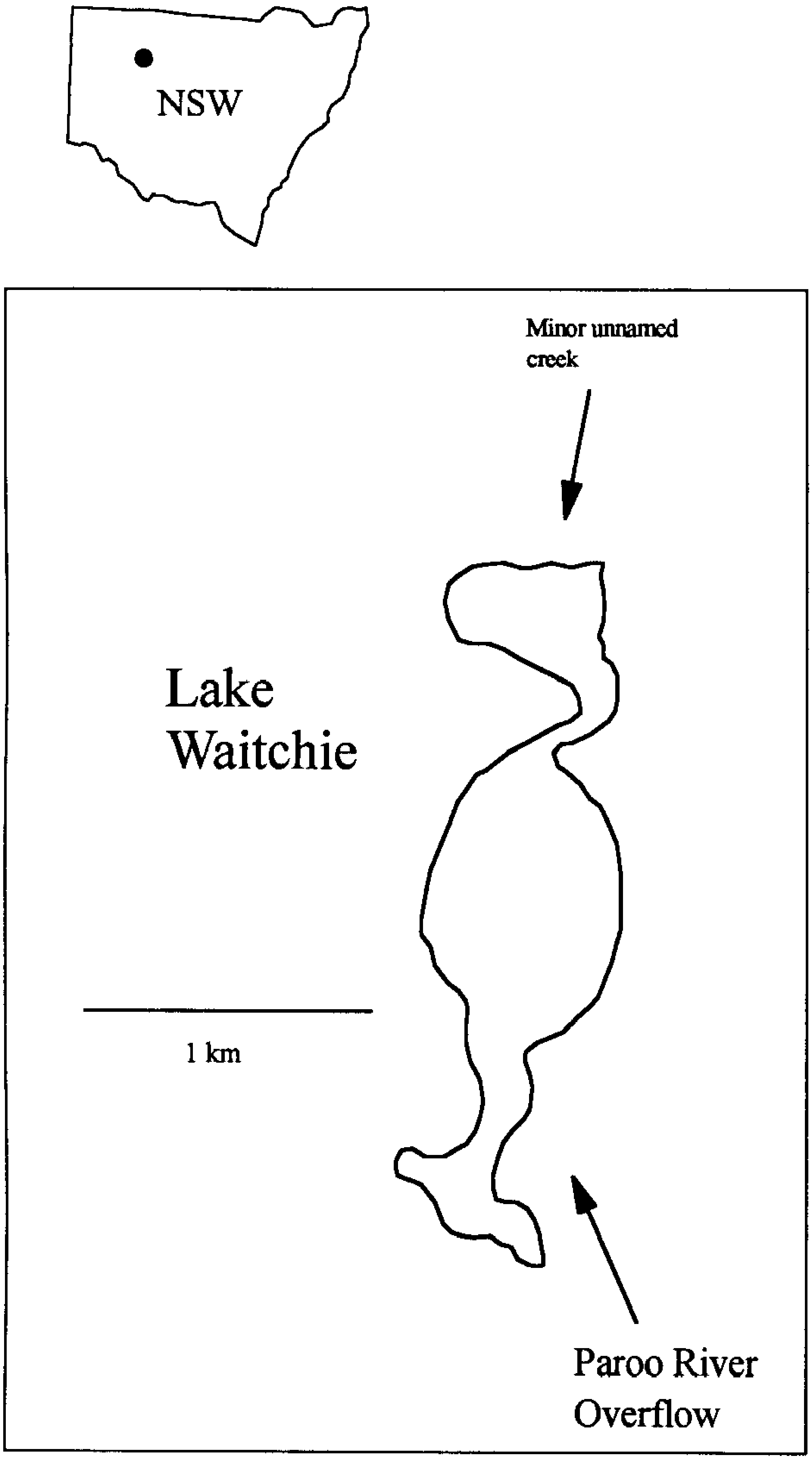


Figure 2.11. Lake Waitchie after Kingsford *et al.* (1994).

Table 2.3. Commonly-used abbreviations used in tables and figures of this thesis. Statistical terms are explained as they occur.

Abbreviation	
D	Dry
E	East
GDR	Great Dividing Range
GRC	Great Cormorant
I	Intermediate
LBC	Little Black Cormorant
LPC	Little Pied Cormorant
PCO	Pied Cormorant
W	West
W	Wet

CHAPTER THREE

FORAGING BEHAVIOUR AND MICROHABITAT USE

3.1. Introduction

Foraging behaviour occurs at the smallest possible scale of observation of animal distribution. At this scale, distribution is influenced by information cues that lead a forager to the precise point at which it captures prey. For cormorants spatial and temporal scales of cues for prey capture are on the order of centimetres to meters^2 and seconds to minutes, respectively (pers. obs.) and information at this scale comes to a forager from the presence of prey, the physical surrounds or from conspecifics or members of a feeding guild (see also Curio 1976). Each mechanism for finding prey has distinct costs and benefits and different circumstances may favour different behaviours.

The presence of prey is a common and direct source of information to predators, who may recognise the prey's movement, pattern or silhouette (such as the legs of insects; Robinson 1970). Cormorants undoubtedly recognise prey by sight (see Hustler 1992), however, in an area of high habitat structure (such as a seagrass bed), fish and crustaceans are cryptic and may only be detected just prior to capture. Thus, cormorants may not always locate prey immediately upon diving, and need to search. Some predators may "hunt by speculation" (Curio 1976), sampling the habitat in a more or less haphazard fashion, capturing prey opportunistically. This method is employed by a number of waterbirds (e.g. some storks Ciconiidae; Kahl and Peacock 1963). When prey leave behind, or associate with, predictable signals, predators can focus their search on the signal rather than on the prey. For example, Herring Gulls (*Larus argentatus*) learn to seek shore crabs (*Copsychus malabaricus*) during a falling tide, based on shallow domes in the sand above the crabs' burrows (Shaffer 1971). Cormorants in estuaries frequently associate with seagrass beds (Trayler et. al 1989; pers. obs.), suggesting that the presence of a bed may serve as a cue to the location of prey.

Conspecifics are another cue to foraging animals (Ward and Zahavi 1973). Information transfer among flock-foraging individuals has been demonstrated for a variety of taxa, particularly birds (e.g. Great Blue Herons *Ardea herodias*, Krebs 1974; Little Egrets *Egretta garzetta*, Cezilly *et al.* 1990; White Ibises *Eudocimus albus*, Smith 1995; Starlings *Sternus vulgaris*, Templeton and Giraldeau 1995a; 1995b;1996). In general, individuals can enhance their rate of food intake by observing the success of others and using it to assess the relative quality of different foraging patches. In addition to increased information, aggregation may also aid in detection of predators (e.g. Yellow-eyed Juncos *Junco phaeonotus*, Caraco *et al.* 1980; moose *Alces alces gigas*, Molvar and Bowyer 1994), although this is probably not important for Australian cormorants (see Dorfman and Read 1996).

Potential benefits of aggregation come, however, at the cost of competition (e.g. musk oxen *Ovibos moschatus*, Schaefer and Messier 1995), resource depression and aggression (e.g. Mallards *Anas platyrhynchos*; Harper 1982). Increased competition may in turn cause consumers to take greater risks in finding food (e.g. common shrews *Sorex araneus*, Barnard and Brown 1985a).

Foraging cormorants probably rely on direct observation, habitat structure and conspecifics as information cues. The relative importance of each information source is likely to depend primarily on the distribution of resources. Individuals should forage alone when food occurs in many randomly distributed patches of poor quality, and group foraging will be favoured when food is clumped or as variation in quality among patches increases (Barta and Szép 1991). Because of the costs of flock-foraging (e.g. competition), individuals should forage alone when food is obtainable without aggregating (Ekman and Rosander 1987). This model is consistent with field observations of foraging birds (Quelea *Quelea quelea*, Ward 1965; Great Blue Herons *Ardea herodias*, Krebs 1974) and cormorants should favour solitary foraging when circumstances permit.

Because cormorants are visual predators (see Hustler 1992), the prey's accessibility is likely to be related to the ease with which it can be seen. Thus, increasing variability in the position of prey, and visual filters (e.g. low water visibility) should decrease predicability (e.g. Elköv and Diehl 1994). Coastal wetlands differ from inland wetlands on both counts. In estuaries with seagrass, fish abundance is higher in seagrass beds than in intervening patches of sand (Pollard 1984), allowing cormorants to narrow their search. In addition, clear water (average Secchi depth = 200 cm; pers. obs.) aids foraging efficiency. By contrast, some freshwater inland wetlands have very little aquatic vegetation because of reduced light levels due to high turbidity (Kingsford and Porter 1993), and the vegetation that does occur, tends only to last for about six months (Briggs and Maher 1985). In addition, many fishes in inland wetlands tend to school (Merrick and Schmida 1984) and can be dispersive (see Glover 1982). Thus, cormorants foraging inland have few direct cues, either from the prey or physical structures with which prey associate (see also Chapter 4), thus flock foraging may be the most profitable response.

In this chapter, I present a general model for the foraging behaviour of cormorants under regimes of differing predictability. Cormorants foraging in coastal estuaries can find food using direct cues (ie. seagrass and the presence of prey), and therefore feed singly or in small groups. Inland, prey is more difficult to find, so cormorants forage in large flocks in order to gauge patch quality (or location) by the success of guild members (conspecifics, congeners and Australian Pelicans). Monitoring the success of guild members is possible because these species swallow their prey at the surface (pers. obs.).

Foraging behaviours of Great, Pied, Little Black and Little Pied Cormorants were observed on the coast and on inland lakes to test hypotheses arising from this model. Foraging flocks were predicted to be larger on inland lakes than on the coast, benefiting from increased search effort. However, cormorants frequently congregate inland to breed (Blakers *et al.* 1984) and sub-populations are larger in the interior (see Chapter 5).

Because increased foraging flock size might be solely a function of higher abundance of cormorants in the arid zone, it was necessary to show that differences were due to behaviour, not merely abundance.

Information transfer should be evident in differences in foraging behaviour, and individuals inland were expected to spend more time assessing each other, relative to those foraging on the coast. In murky water, cormorants could only assess the behaviour of conspecifics at the surface, so dive and surface behaviours were also investigated, testing the hypothesis that surface interval would be longer when cormorants forage in flocks than when they forage alone.

A test of this hypothesis is, however, potentially confounded. Cormorants foraging inland may also have longer dive intervals because prey is obscured by cloudy water and cormorants need to spend longer searching. Longer dive intervals may lead to longer surface intervals, as cormorants repay their oxygen debt (e.g. Wanless *et al.* 1993). It was therefore necessary to separate these effects by testing differences in surface times which were over and above that dictated by associated dive times. This was done by testing differences in surface times of cormorants flock-foraging inland against expected times derived from the relationship of surface-to-dive times for cormorants foraging singly on the coast. Longer than predicted surface intervals would be an indication that cormorants were spending more time on the surface than necessitated by aerobic requirements. It is unlikely that cormorants sit on the water for any other purpose than foraging, because they become wet to the skin with long exposure to water (Casler 1973), which would lead to the risk of hypothermia. Thus, longer than predicted surface intervals are assumed to be indicative of increased information transfer.

A given surface interval may, however, compensate either for the following (Cooper 1986) or preceding (Lea *et al.* 1996) dive. These patterns are referred to as "anticipatory" and "reactive" breathing, respectively, and appear to differ with species

(Lea *et al.* 1996). To be able to analyse the relationship between dive and surface times, it was first necessary to establish whether, for each species, the relevant dive was the preceding or following one. This was done by correlating observed dives with preceding and proceeding surface intervals (see Wanless *et al.* 1993; Watanuki *et al.* 1996).

The spatial dynamics of foraging flocks must also be considered, because there is a potential for confounding edge effects (Elgar 1989). Increased vigilance on the periphery of an aggregation is a general pattern for group-foraging birds and mammals (e.g. Barnacle Geese *Branta leucopsis,* Black *et al.* 1992; wildebeest *Connochaetes taurinus,* Burchell's zebra *Equus burchelli,* warthog *Phacocheroerus aethiopicus,* Scheel 1993). Heightened vigilance is often assumed to result from individuals at the periphery being at greatest risk of predation, but there are many confounding factors including intraspecific competition, food or patch distribution and quality, distance from cover and a variety of social factors (Elgar 1989).

Although, predation on adult cormorants may be less important in limiting populations than other effects (e.g. starvation and nest predation, Post 1988; Dorfman and Read 1996), flocking could be an innate behaviour, responding to predation that may have occurred in the past. The behaviour of relocating individuals was used to distinguish between information transfer and predation avoidance. If individuals used the success of conspecifics as foraging cues, they would be predicted to relocate toward the epicentre of the flock, when success rate of central individuals appeared high. However, if increased vigilance were primarily to avoid predators, cormorants forced to be on the periphery by dominant individuals in the centre should orient their attention in the direction of an incoming predator: namely away from the flock. In this case, unsuccessful cormorants on the periphery might relocate frequently to increase the chance of finding an undetected patch or to make an unreliable target for a predator, but would not be predicted to orient back into the flock.

In addition, individuals on the periphery of a flock typically have a lower success rate than those in the centre (e.g. Krebs 1974) and thus stand to gain most by assessing the behaviour of guild members (Ward and Zahavi 1973). Although individual success rate could not be measured, the hypothesis was tested that surface times were longer for individuals on the edge of a foraging flock than for those in its centre. Peripheral individuals were also expected to relocate frequently, once some 'giving up' threshold (*sensu* Charnov 1976) had been surpassed.

Finally, to investigate further the model that cormorants in coastal estuaries use seagrass as a foraging cue, the hypothesis was tested that cormorants dive more frequently into seagrass beds than over sand. Cormorants were predicted to be more abundant in stretches of estuary containing higher cover of seagrass.

3.2 Materials and Methods

3.2.1. Flock sizes in coastal and inland environments

Flock sizes for each species were taken from observations made in other parts of this study (see Chapters 4 and 5). A flock of cormorants was defined as a single cormorant, or group of 2 or more individuals acting in concert, in any activity. For each species - environment combination, a sub-sample of 80 flocks was chosen randomly from all observations. The data were sub-sampled because different species-environment combinations contained different numbers of samples. Eighty was the lowest common denominator. Coastal locations comprised those along the Parramatta and Hawkesbury Rivers (Chapter 4) and inland locations comprised those from Lakes Altibouka, Waitchie and Menindee (Chapter 4), supplemented by raw data on group size from aerial survey records from NSW NPWS (Chapter 5). Although this was not an optimal method of recording flock size (because of potential bias in aerial surveys against small flocks), the patchy distribution of cormorants meant that some species-environment combinations (e.g. Little Pied Cormorants inland) were logistically difficult to obtain. A Kolmogorov-Smirnov test was used to analyse differences in frequency distribution of flock-sizes between the two environments for each species, and among species within an environment (coastal and inland).

3.2.2. Dive and surface patterns

Sampling at Patonga Creek

Foraging cormorants were observed from shore along Patonga Creek, between January 1993 and June 1996. Data were collected by two people. The first person observed cormorants with hand-held binoculars and 'called out' behaviours as they occurred. The second person carried a stop-watch and recorded the first person's observations, as a time sequence. Each cormorant was observed for at least 2 minutes, until it was lost from view (maximum = 22 minutes).

The microhabitat in which cormorants foraged (sand or seagrass) was also recorded. Seagrass beds were clearly visible from shore. At high tide, patches of submerged pneumatophores of the grey mangrove (*Avicennia marina*) were available as microhabitat, but no cormorants were observed in association with them and the areas were excluded from analysis. The categories of "seagrass" and "sand" were therefore considered comprehensive as well as mutually exclusive.

Sampling at Lake Menindee

Lake Menindee and surrounding water bodies (Figure 2.10) were surveyed for cormorants in October 1994 and June 1995. Cormorants were observed by eye, 8 x 30 binoculars or with a 45x spotting scope. Behaviours were recorded with the method described above. In the first trip, the basin of Lake Menindee was dry and without cormorants, allowing an assessment of the vegetation and topography of the lake floor.

Each species of plant observed was recorded in an *ad hoc* fashion and some unknown species were collected for later identification. Water level in Lake Menindee is regulated for use by Broken Hill and by downstream water for Adelaide (Chapter 2), and refilling was imminent.

Individuals on the periphery and within a flock were treated separately. The centre of a flock was typically dense and well-defined, and a distinction could easily be made between those within a flock and those on the edge. Peripheral individuals were typically at least 100 metres away from the centre.

Analyses

Analyses were performed for all species at Patonga Creek and Lake Menindee. Differences in average dive and surface times between environments were tested with Student t - tests for each species. All Student - t tests were preceded by F-tests, to evaluate homogeneity of variance. Relationships of dive duration to the preceding and proceeding surface intervals were tested for each species by calculating Pearson linear correlation coefficients.

Patterns in inland surface times in relation to that predicted by patterns in inland dive times was tested by creating a set of expected values based on a linear regression of surface to dive times on the coast. The null hypothesis was that the relationship between surface and dive times was the same in both environments. Results of the correlation described above determined whether preceding or proceeding dives were used to generate expected values. Differences between observed and expected inland surface times were tested with a Student t - test for each species. These tests were one-tailed, because the hypothesis tested in each case was that surface times inland were longer than (as opposed to different from) the length they needed to be to meet physiological requirements.

For Great and Pied Cormorants at Lake Menindee, differences in surface time were tested between birds that were actively foraging in a feeding aggregation and those that could see the aggregation but were not in it. Differences were tested with a Student t-test.

3.2.3. Flocking Behaviour

Flocking behaviour of Great and Pied Cormorants was observed from shore with the naked eye or 8 x 30 binoculars. Foraging flocks were observed for four 10-minute periods, counting the destination of flights made by individual cormorants from the water. A Chi^2 statistic was used to test differences between the frequency of destinations of flights made by cormorants in the water irrespective of their position with relation to the flock flock. The null hypothesis that no differences exist between frequency of flights to a given destination (water, roost or elsewhere). The category "elsewhere" included the land, human constructions or out of sight. Orientation with respect to the flock of flights made from water to water were also recorded and tested with a Chi^2 statistic. The null hypothesis was tested that no difference in water to water flights existed with respect to orientation to the flock.

3.2.4. Surveys of Patonga Creek

On twenty-one occasions between January 1993 and June 1996, all of Patonga Creek (about 5 km) was surveyed for cormorants. The survey was conducted from a two-person canoe along a standardised survey route (Figure 3.1). It was possible to see the full width of Patonga Creek from every point along the survey line. The only entry point for the canoe was near the mouth of the creek, to the south (Figure 3.1), therefore all surveys were conducted from the south northward, to avoid potential disturbance to the cormorants.

Cormorants in flight were counted only if they were seen travelling southward, past the canoe. It was assumed that cormorants flying north would be counted subsequently on the survey. Cormorants were unlikely to fly from the top of Patonga Creek to another creek system, because the area is bordered by steep cliffs and forest, which appeared less attractive as a fly-way than the watercourse. For each cormorant observed during canoe trips, time, location and behaviour were recorded on a map. Maps reflect total observations of each species (ie. data are pooled), to illustrate overall patterns, uncomplicated by variation among observations. Cormorants at the surface were also recorded as either over seagrass and sand.

Analyses of microhabitat use were performed separately for each of the three species (Great, Little Black and Little Pied Cormorants) observed at Patonga Creek during this portion of the study. Differences between frequency of dives through seagrass or above sand were tested with a Chi^2 Goodness of Fit statistic, testing the null hypothesis that cormorants dived with equal frequency over both substrates. The expected ratio of dives over each substrate was determined by percent cover of seagrass in Patonga Creek. Percent cover was assessed using a map of the floor of Patonga Creek (West *et al.* 1985) and corroborated with aerial photographs taken by the New South Wales Department of Land and Water Conservation.

In addition, data on flock size for Little Pied Cormorants were stratified by behaviour (roosting or foraging) and differences between behaviour and among trips were analysed as a two-factor analysis of variance (ANOVA). Surveys were sub-sampled to space trips more than one month apart, to minimise the chance of the same individuals being observed more than once. Seven surveys were used and from these, four occurrences each of roosting and foraging were sub-sampled randomly ($n = 56$ observations). A Cochran's test was used to test for homogeneity of variance. This was not significant (Cochran's $C = 0.0461$; df = 2), indicating that transformation of the data was unnecessary. Stratification of data on flock size was not possible for other species, because of low frequency of occurrence.

3.3. Results

3.3.1. Flock sizes in coastal and inland environments

Frequency distributions of flock sizes for all species on the coast (Figure 3.2) and inland (Figure 3.3) were skewed towards a greater frequency of smaller flocks. However, in the interior, most individuals were members of large flocks, and on the coast, most individuals were single or members of small flocks (Table 3.1a). No flock larger than 75 individuals (Little Black Cormorants; Figure 3.2) was observed on the coast during this study. Frequency distributions of flock sizes were significantly different between coastal and inland environments for all species except Little Pied Cormorants (Table 3.1b). On the coast, frequency distributions were significantly different among species for only one combination (Pied vs. Little Pied Cormorants; Table 3.1c), but in the interior, distributions invariably showed strong significant differences among species (Table 3.1d).

Average flock sizes for Great, Pied, Little Black and Little Pied Cormorants were also higher and considerably more variable inland (80.3 ± 191.4; 37.1 ± 174.0; 27.7 ± 120.2; 3.0 ± 4.4, respectively) than on the coast (3.8 ± 6.0; 6.9 ± 8.7; 4.9 ± 9.6; 2.4 ± 3.2, respectively). Variation in the values above is reflected by standard deviation.

3.3.2. Dive and surface patterns at Patonga Creek and Lake Menindee

Surface and dive patterns were superficially similar among species (Figure 3.4). Dive times were slightly shorter for Great and Pied Cormorants than for Little Black and Little Pied Cormorants in both environments. Consistent with prediction, dive and surface times for all species were significantly longer inland than on the coast (Table 3.2).

Significant correlations between surface and dive times were found both at Patonga Creek and the Lake Menindee system, however the relationship differed among species (Table 3.3). Dive times of Great and Pied Cormorants were correlated only with surface times preceding them, whereas dive times of Little Pied Cormorants were correlated only with following surface times, so Great and Pied Cormorants were considered anticipatory breathers, whereas Little Pied Cormorants were considered reactive breathers. No foraging bouts of Little Black Cormorants contained significant correlations because their propensity to forage in flocks made sampling individuals difficult and only 11 bouts contained sufficient data to test the relationship (Table 3.3). In the absence of sufficient information for this species, further analyses were based the relationship between dive times and the preceding surface intervals (ie. they were considered anticipatory breathers). This choice was made because the foraging behaviour of Little Black Cormorants appears to share more characteristics (e.g. prey and flock size) with Pied and Great Cormorants than with Little Pied Cormorants. Frequency of significant correlations was low for all species and was often driven by only one or two data points (Figure 3.5).

Relationships between surface and dive times on the coast were similar among species (GRC: $R^2 = -0.005$, $n = 130$, $y = 0.05x + 6.13$, $P = 0.581$; PCO: $R^2 = 0.213$, $n = 179$, $y = 0.16x + 1.13$ $P < 0.001$; LBC: $R^2 = -0.006$, $n = 170$, $y = -0.004x + 4.00$, $P = 0.927$; LPC: $R^2 = -0.041$, $n = 202$, $y = -0.02x + 6.14$, $P = 0.563$), however, because regression coefficients for coastal and surface times were only significant for Pied Cormorants, the relationship was only treated as a true prediction of inland surface times for this species, and as a suggestion for Great, Little Black and Little Pied Cormorants, in need of testing in the future. Nonetheless, surface times inland for all species except Little Pied Cormorants were significantly higher than those predicted by the relationship between coastal dive and surface times (Table 3.4; Figure 3.6). Great and Pied Cormorants on the periphery of a foraging flock had significantly longer mean surface times than those in the centre (Table 3.5).

3.3.3. Flocking Behaviour

Although Pied and Great Cormorants fed in mixed aggregations, they may have a different foraging strategy. Both species moved within feeding aggregations but Great Cormorants were more mobile. Each Great Cormorant made a flight on average every 3.57 min and each Pied Cormorant made a flight on average every 7.94 min (calculated using total flights x total individuals^{-1} x min^{-1}, n = 210 and 102 obs, respectively). Pied Cormorants within an aggregation appeared to move forward by swimming whereas Great Cormorants flew to the head of the flock, landing on the position held by the foremost Pied Cormorants. This aspect of flock dynamics was not quantified.

As predicted, foraging Great and Pied Cormorants flying from the water flew significantly more frequently to another location in the water than to a roost (χ^2_{GRC} = 29.34, *df* = 1, n = 153 P < 0.001; χ^2_{PCO} = 62.48, *df* = 1; n = 74, P < 0.001; Figure 3.7). No observations were made of cormorants flying to a location other than water or roost. Also as predicted, Great and Pied Cormorants flying from water to another location in the water did so significantly more often towards the feeding aggregation than away from it (χ^2_{GRC} = 63.70, *df* = 1, n = 57, P < 0.001; χ^2_{PCO} = 25.14, *df* = 1, n = 29 P < 0.001; Figure 3.8).

On Patonga Creek, the only synchronised foraging behaviour observed was by Little Black Cormorants, which fed singly or in groups of 2 to 75 individuals (mean, S.D. = 5.1 ± 12.1 individuals). Roosting in groups was, however, commonplace for all species.

3.3.4. Microhabitat use at Patonga Creek

Great and Little Black Cormorants occurred less frequently and at fewer locations than Little Pied Cormorants (Figure 3.9) on Patonga Creek and Pied Cormorants were virtually absent. Frequency of occurrence for all species was especially high at two locations on the creek, one about 1 km and another approximately 5 km from the mouth

(Figures 3.9). These locations had high percent cover of seagrass and large oyster racks for perching, from which cormorants could see a reasonable distance in both directions along the creek. Cormorants were observed roosting almost exclusively on oyster racks, dead trees that had fallen into the water or in live mangroves, as opposed to taller trees or on the ground.

The floor of Patonga Creek was covered by 30% seagrass and 70% sand and all species were more abundant in stretches of Patonga Creek with a high percent cover of seagrass (Figures 3.9). Great Cormorants had the highest incidence of diving over sand, however, all species measured dived over seagrass meadows significantly more than over sand ($\chi^2_{GRC} = 189.1$, *df* = 1, n = 129 dives $P < 0.001$; $\chi^2_{LBC} = 189.1$, *df* = 1, n = 129 $P < 0.001$; $\chi^2_{LPC} = 189.1$, *df* = 1, n = 28, $P < 0.001$; Figure 3.10).

The distribution of roosting and foraging behaviours of Little Pied Cormorants on Patonga Creek was consistent over all trips, irrespective of the size of the flock or of the local population. Roosting was always more common than foraging, although both behaviours were observed by groups of over 10 individuals (Figure 3.11). Significant differences in behaviour of Little Pied Cormorants were encountered on Patonga Creek and this was consistent among trips (Table 3.6).

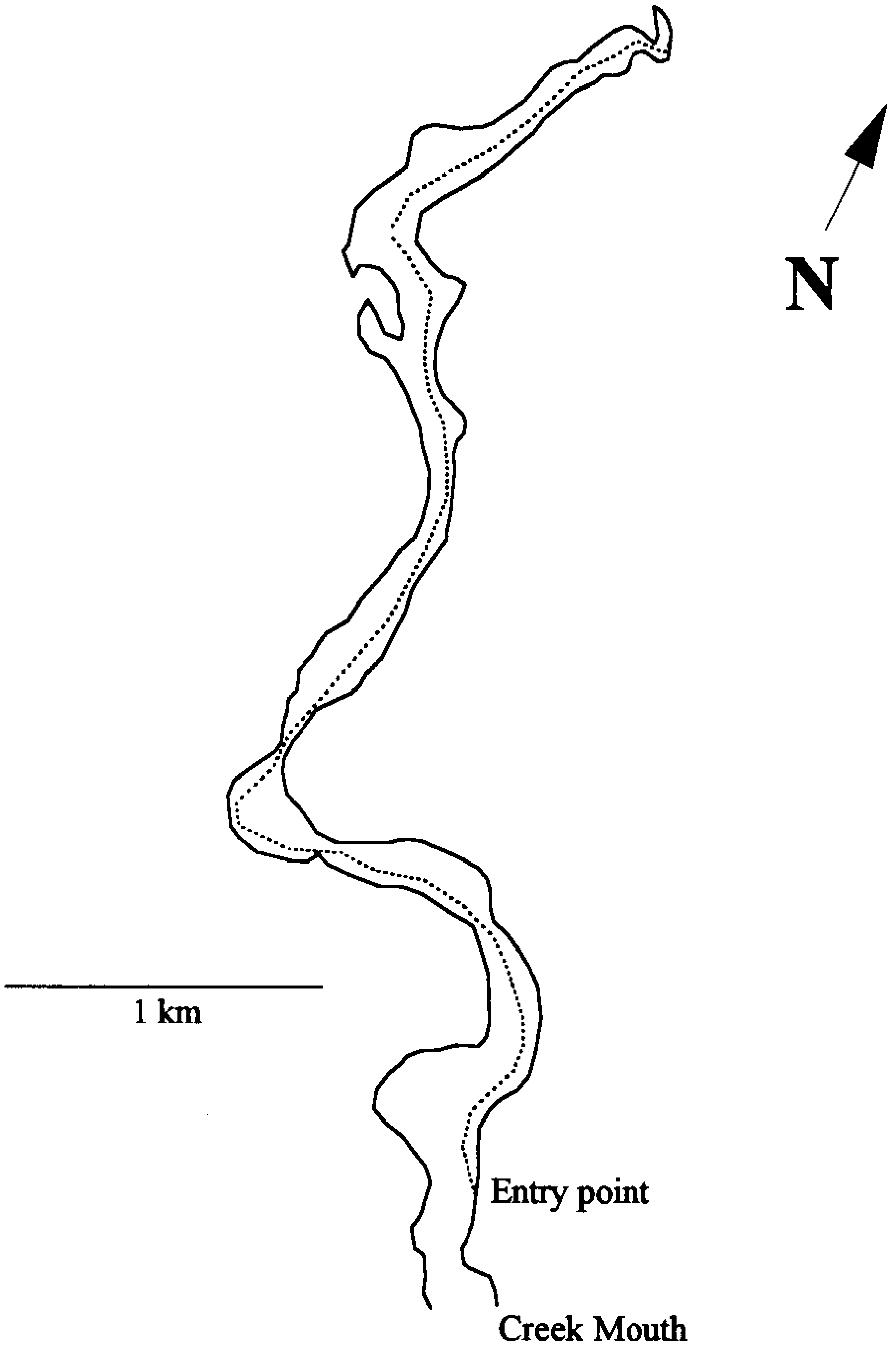


Figure 3.1. Survey line on Patonga Creek. See Figure 2.8 for a map of the region.

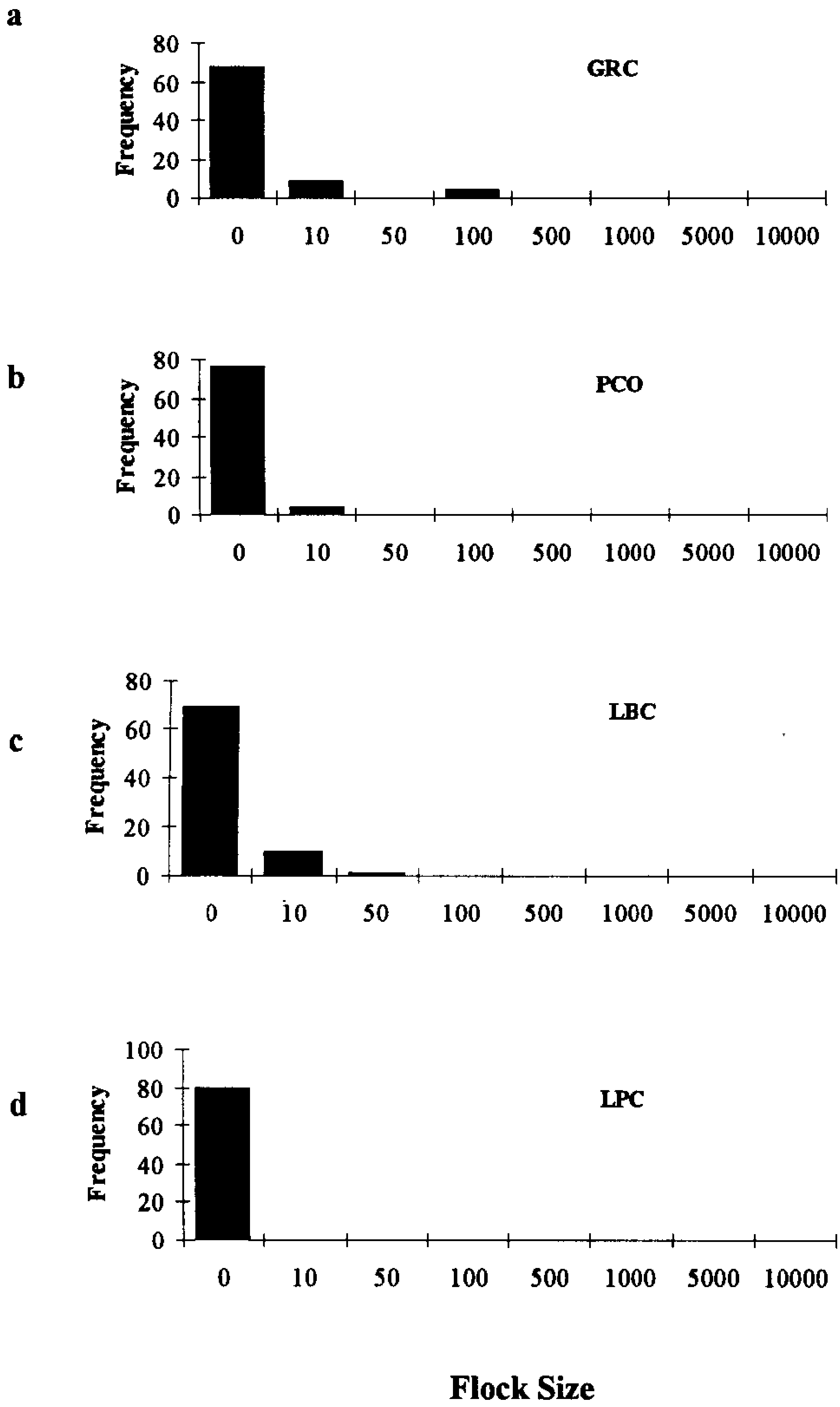


Figure 3.2. Flock size frequencies for Great (a), Pied (b), Little Black (c) and Little Pied Cormorants (d) in the coastal environment.

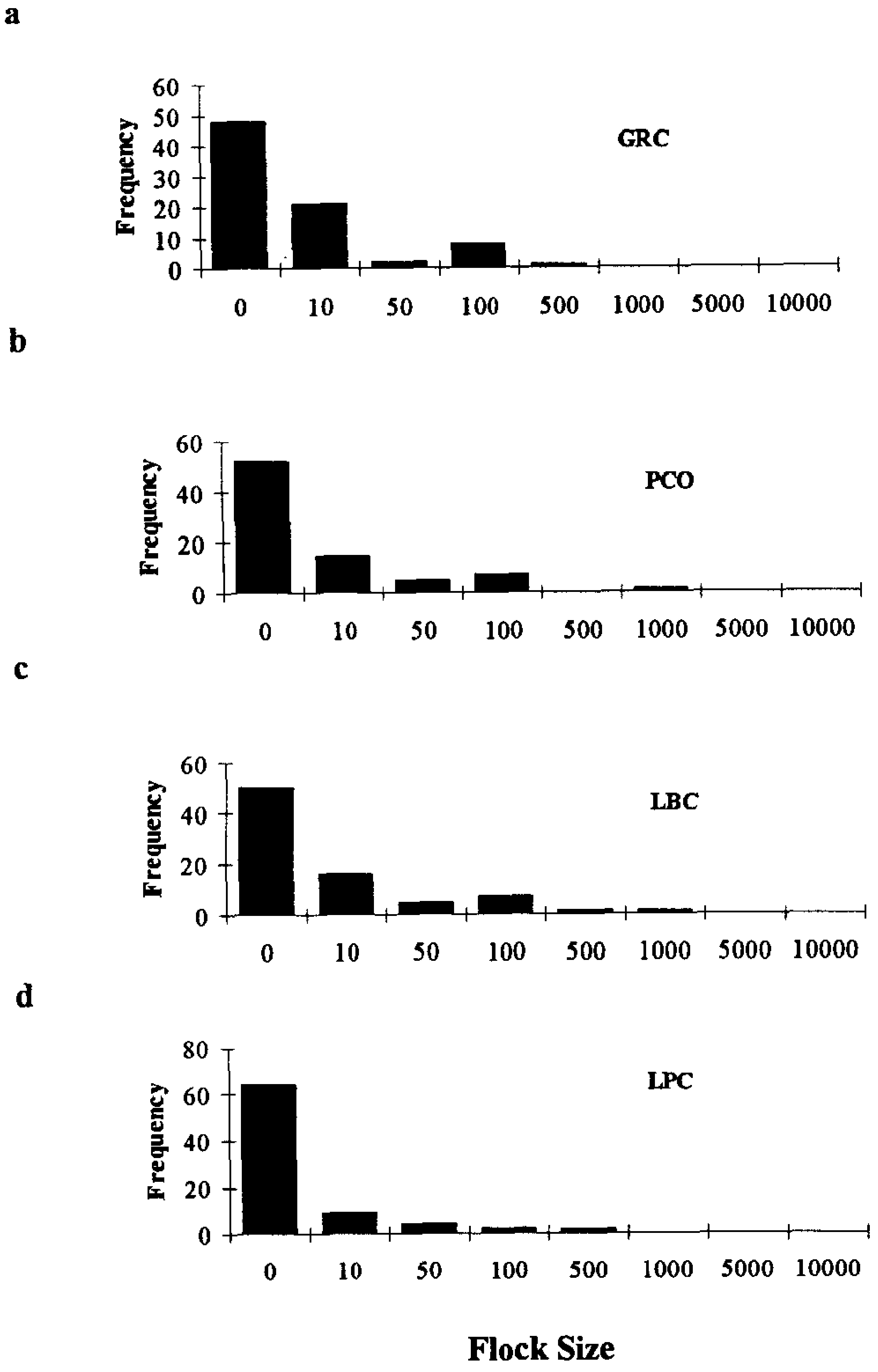


Figure 3.3. Flock size frequencies for Great (a) Pied (b), Little Black (c) and Little Pied Cormorants (d) in the inland environment. Note that the X-axis is discontinuous.

Table 3.1. a) Ninetieth percentile of flock sizes on the coast and inland from the frequency distributions in Figures 3.1 and 3.2 (e.g. 90% of Great Cormorants on the coast occurred in flocks of 20 or less. b - d) Kolmogorov-Smirnov tests of flock size frequency distributions for each species between coastal and inland environments (b) and among species on the coast (c) and inland (d). Significance values are reported in 3.1b, and elsewhere are represented by single or double asterisks for $P < 0.01$ and $P < 0.001$, respectively. Only K values are given in figures 3c and 3d.

a

Species	Coast	Inland
GRC	20	1000
PCO	30	500
LBC	50	1000
LPC	15	25

b BETWEEN ENVIRONMENTS

Species	K	P
GRC	0.875	0.001
PCO	0.573	0.001
LBC	0.241	0.05
LPC	0.074	n. s.

c AMONG SPECIES, COAST

	GRC	PCO	LBC	LPC
GRC	0.000			
PCO	0.175	0.000		
LBC	0.063	0.159	0.000	
LPC	0.125	0.293*	0.164	0.000

d AMONG SPECIES, INLAND

	GRC	PCO	LBC	LPC
GRC	0.000			
PCO	0.312**	0.000		
LBC	0.667**	0.460**	0.000	
LPC	0.914**	0.728*	0.296**	0.000

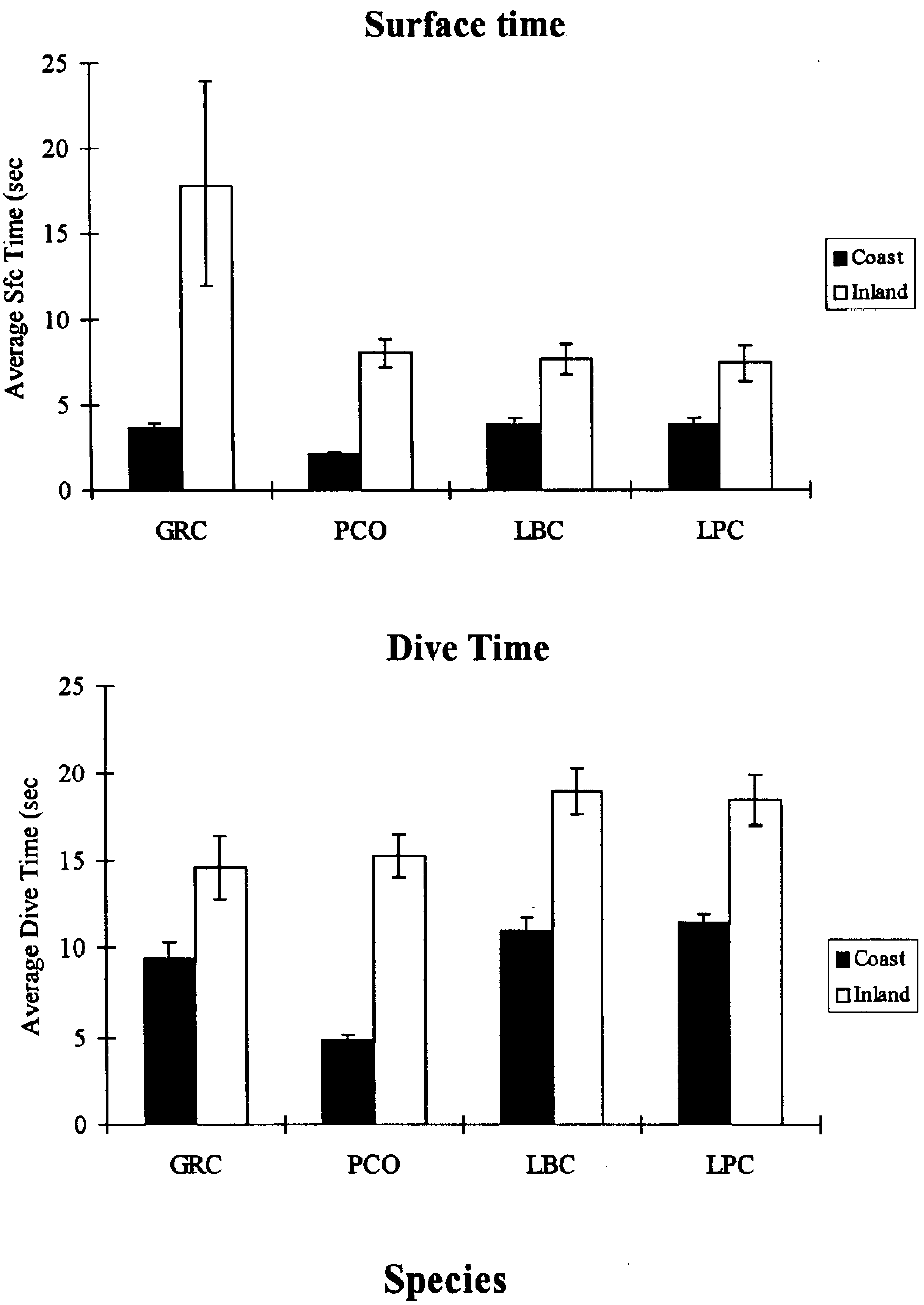


Figure 3.4. Surface and dive times (± SE) for cormorants on the coast and inland.

Table 3.2. F-tests (*F*) between variances and Student t-tests between means of dive (a) and surface (b) times of cormorants inland and on the coast. Suffices (c and i) refer to coastal and inland environments, respectively. An asterisk beside the result of an F-test, refers to significance at P < 0.05.

a Dive Times

Species	*F*	Mean(c)	Mean(i)	t	df	P (one tailed)
GRC	2.03*	9.48	14.64	-2.61	65	0.01
PCO	3.98*	4.89	15.25	-8.03	43	0.001
LBC	1.45*	10.99	18.97	-4.54	234	0.001
LPC	2.34*	11.46	18.50	-4.52	81	0.001

b Surface Times

Species	*F*	Mean(c)	Mean(i)	t	df	P (one tailed)
GRC	19.24*	2.12	17.90	6.92	174	0.001
PCO	281.68*	3.59	7.97	2.38	62	0.01
LBC	1.04	3.77	7.62	-4.13	252	0.001
LPC	3.75*	3.41	7.38	7.35	1051	0.001

Table 3.3. Frequency of correlated surface times before and after dives in coastal habitats. (For example, twenty-nine dive bouts were analysed for Little Pied Cormorants and of these, dive times were never correlated with surface intervals preceding and in four cases were significantly correlated to dives following.)

		Significant Correlations ($P < 0.05$)	
Species	Bouts Sampled	Surface Before	Surface After
GRC	10	1	0
PCO	12	2	0
LBC	11	0	0
LPC	29	0	4

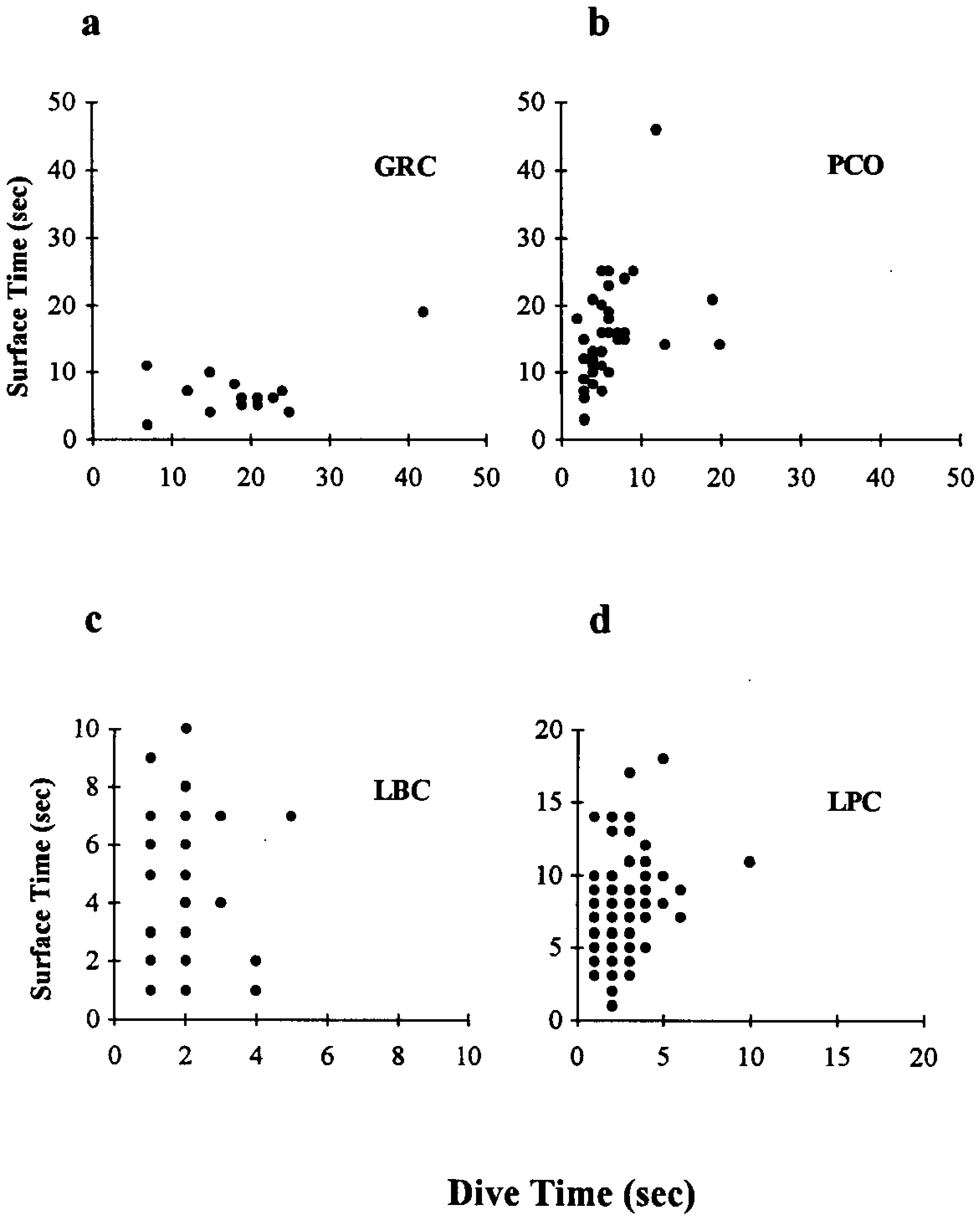


Figure 3.5. Relationships, irrespective of environment, within a single bout, between surface and dive times for Great (a), Pied (b), Little Black (c) and Little Pied Cormorants (d). Plots depict the relationship between dives and preceding (GRC; PCO) or following surface intervals (LBC; LPC), based on the relationship between dive and surface times for each species (Table 3.3). Note differences in axis scales among species.

Table 3.4. F-tests (*F*) between variances and Student t-tests between means of observed (o) and expected (e) surface times (in seconds) of cormorants foraging inland. Expected times were derived from relationships between dive and surface times for cormorants on the coast. An asterisk beside the result of an F-test, refers to significance at P < 0.05.

Species	*F*	Mean(o)	Mean(e)	T	df	P (one tailed)
GRC	8459.35*	17.90	6.84	-1.84	62	0.05
PCO	67.10*	7.97	3.63	-0.508	179	0.001
LBC	16889.58*	7.62	3.96	-4.13	39	0.001
LPC	1091.95*	7.38	5.91	-1.53	49	0.07

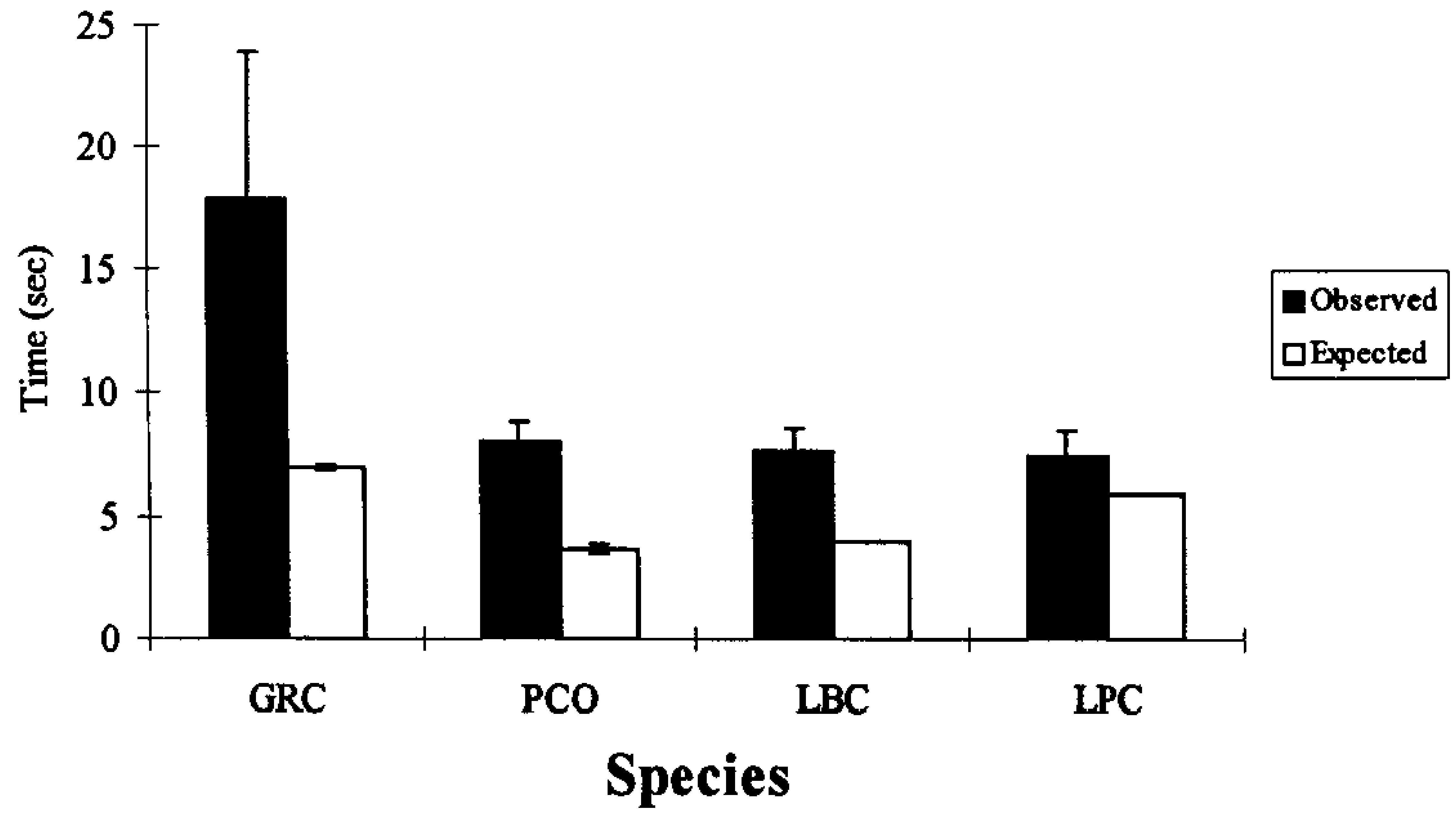


Figure 3.6. Differences between observed inland surface times and those expected by the relationship between coastal dive and surface times. Abbreviations in solid capitals (GRC, PCO, LBC, LPC) refer to species and lower case suffices (o, e) refer to observed and expected values, respectively. Error bars represent standard error.

Table 3.5. Student t-tests surface times (sec) of Great and Pied Cormorants on the periphery (p) and within (w) foraging flocks at Lake Menindee. An asterisk beside the result of an F-test (*F*), refers to significance at $P < 0.05$.

Species	*F*	df	Mean(w)	Mean(p)	t	P (two tailed)
GRC	211.43*	62	3.48	17.90	-2.40	0.05
PCO	24.25*	186	3.88	112.26	-4.75	0.001

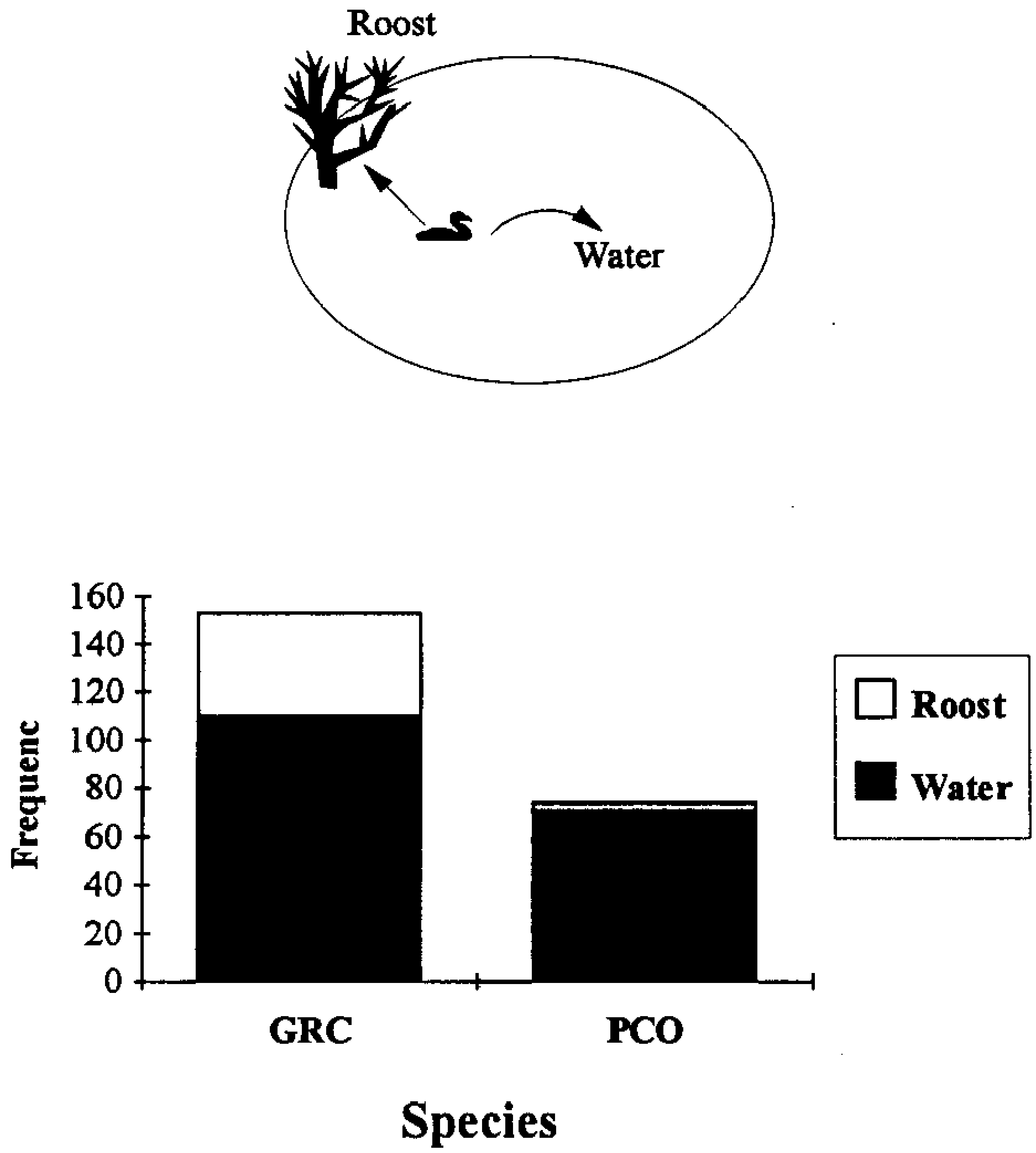
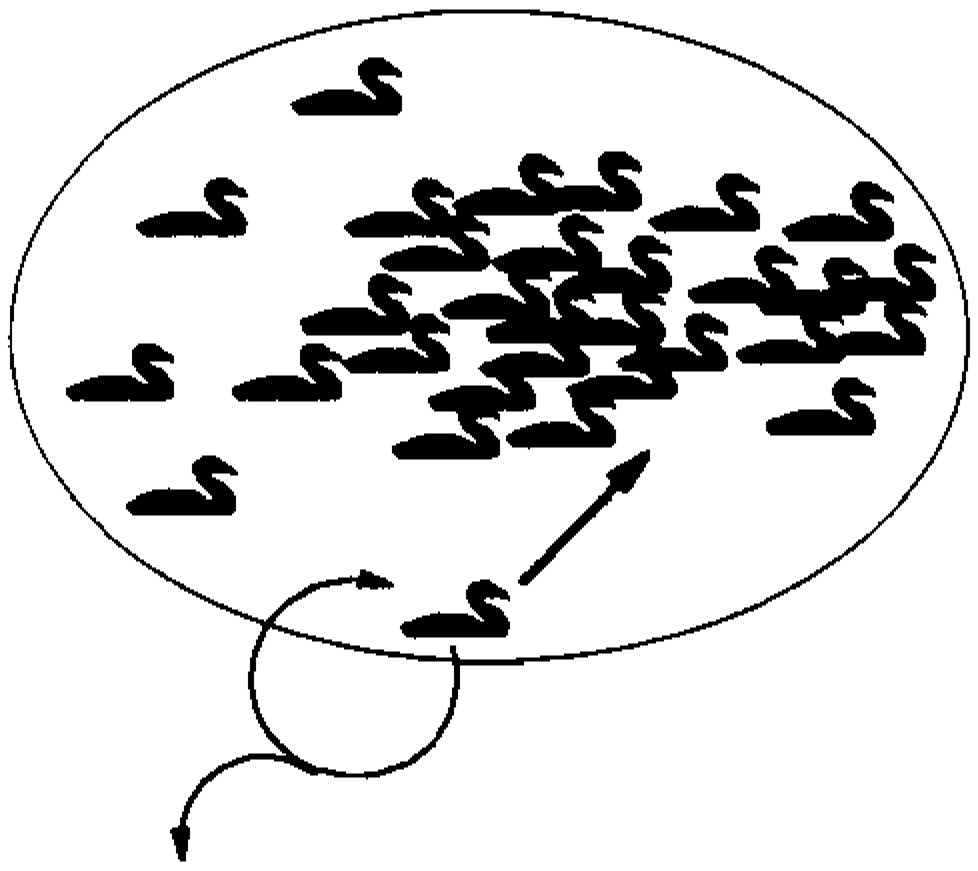


Figure 3.7. Frequency of flights made from water to roosts and to water from water at Lake Menindee.



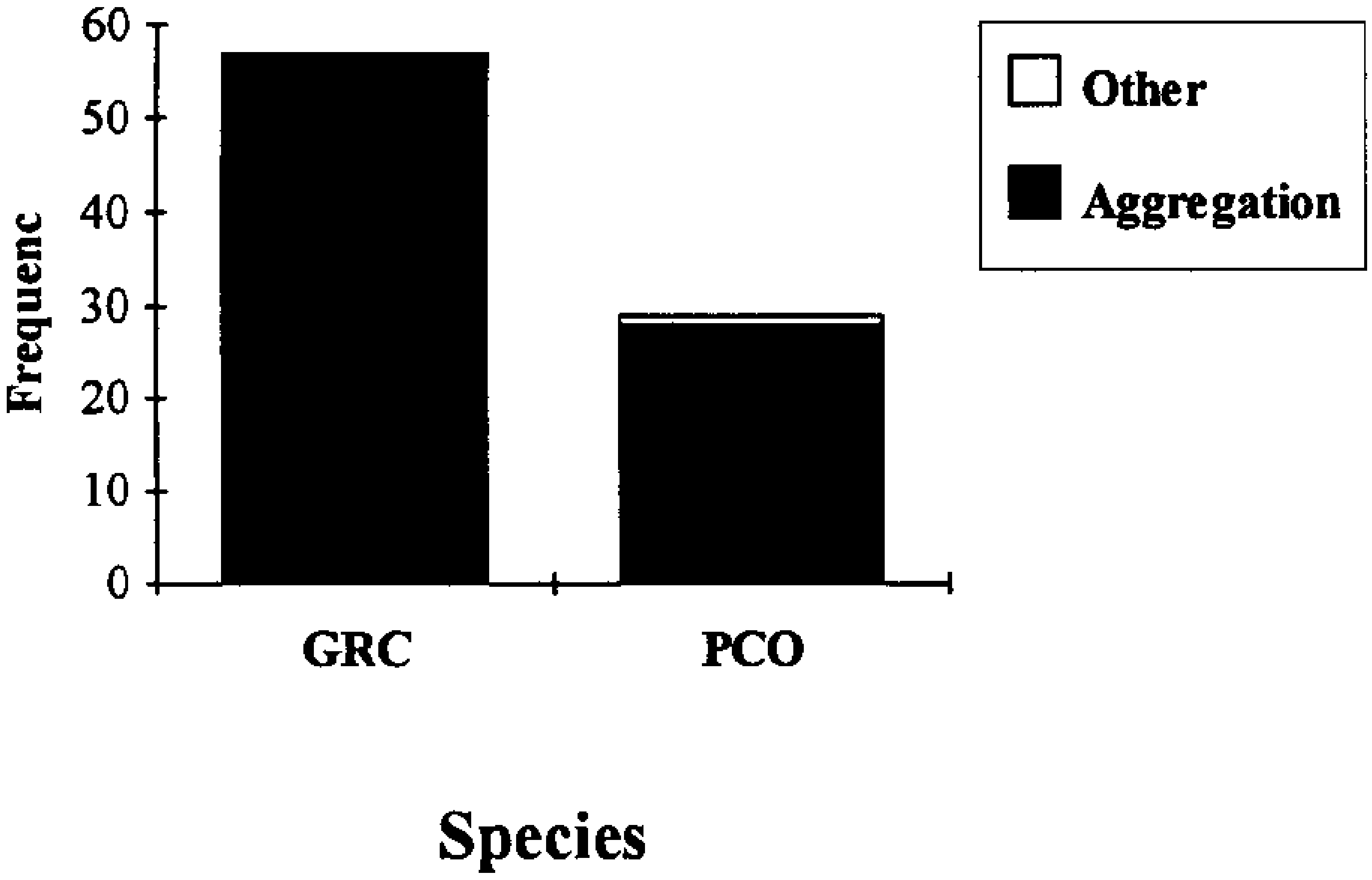


Figure 3.8. Frequency of flights made from water towards the feeding aggregation and elsewhere at Lake Menindee.

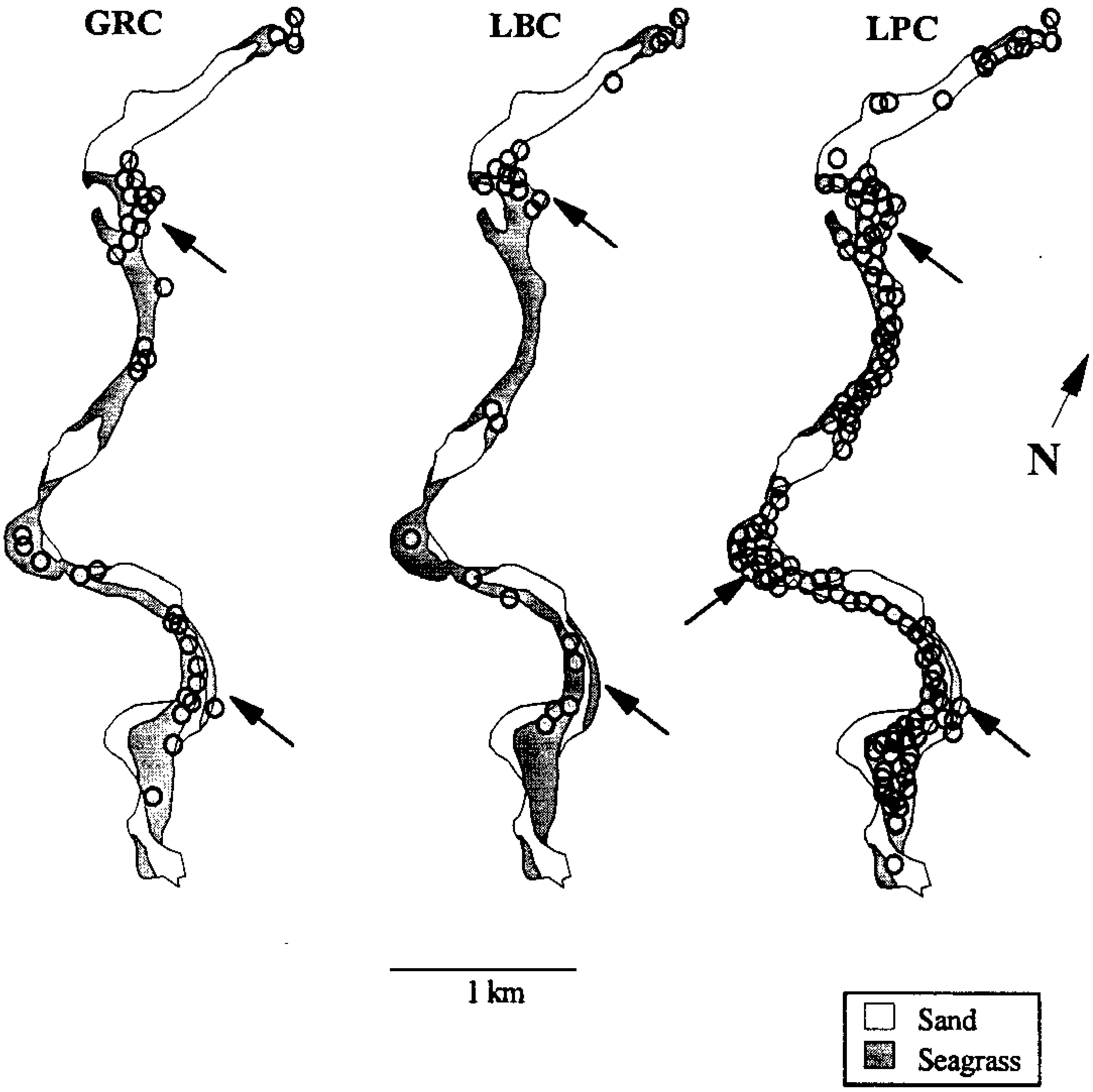


Figure 3.9. Distribution of foraging and roosting Great, Little Black and Little Pied Cormorants on Patonga Creek. Circles represent locations where foraging cormorants were observed, irrespective of flock size. Arrows indicate areas of high frequency of occurrence. n = 46, 227 and 95 individuals, respectively.

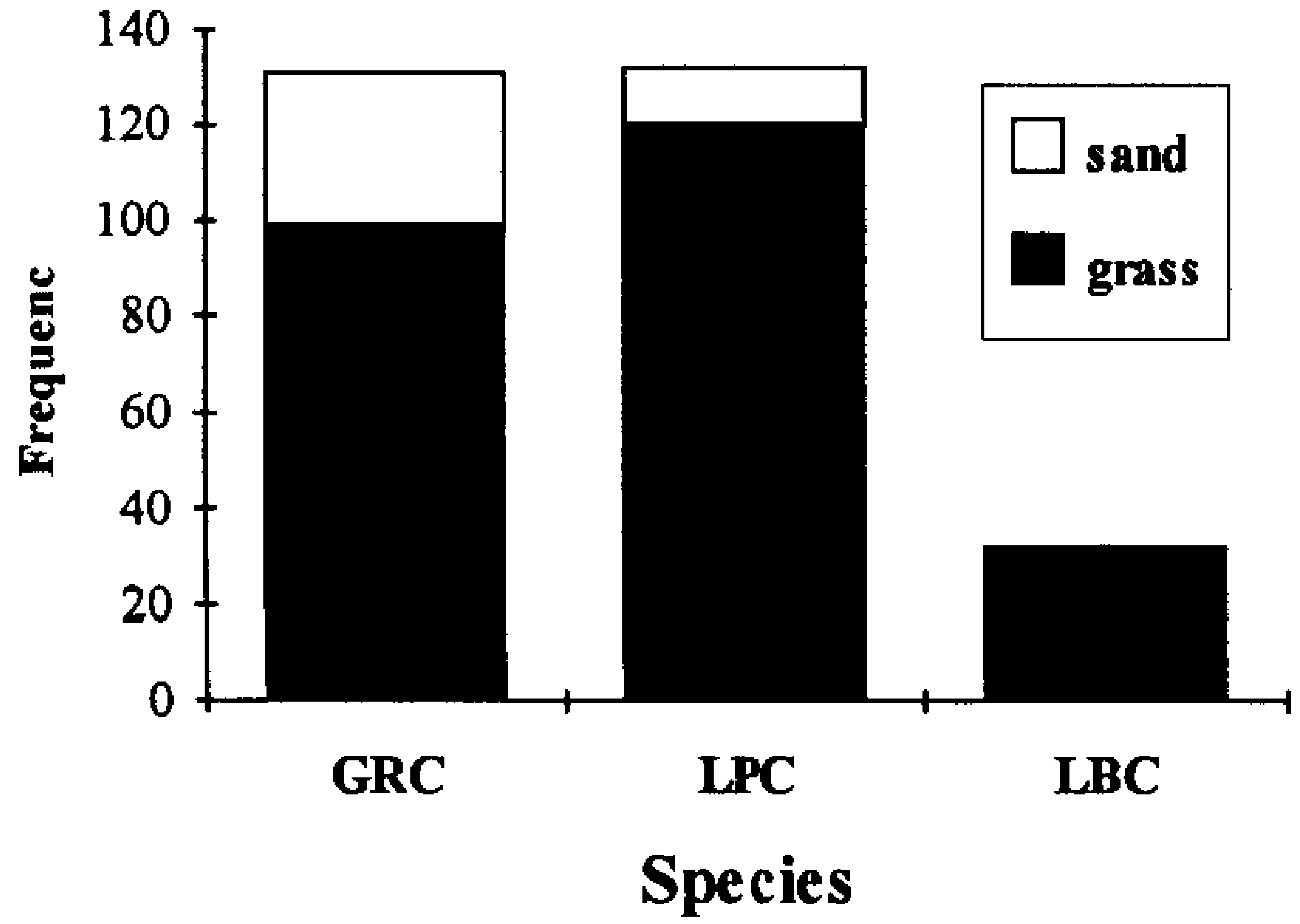


Figure 3.10. Frequency of dives over seagrass or sand at Patonga Creek, for Great, Little Pied and Little Black Cormorants.

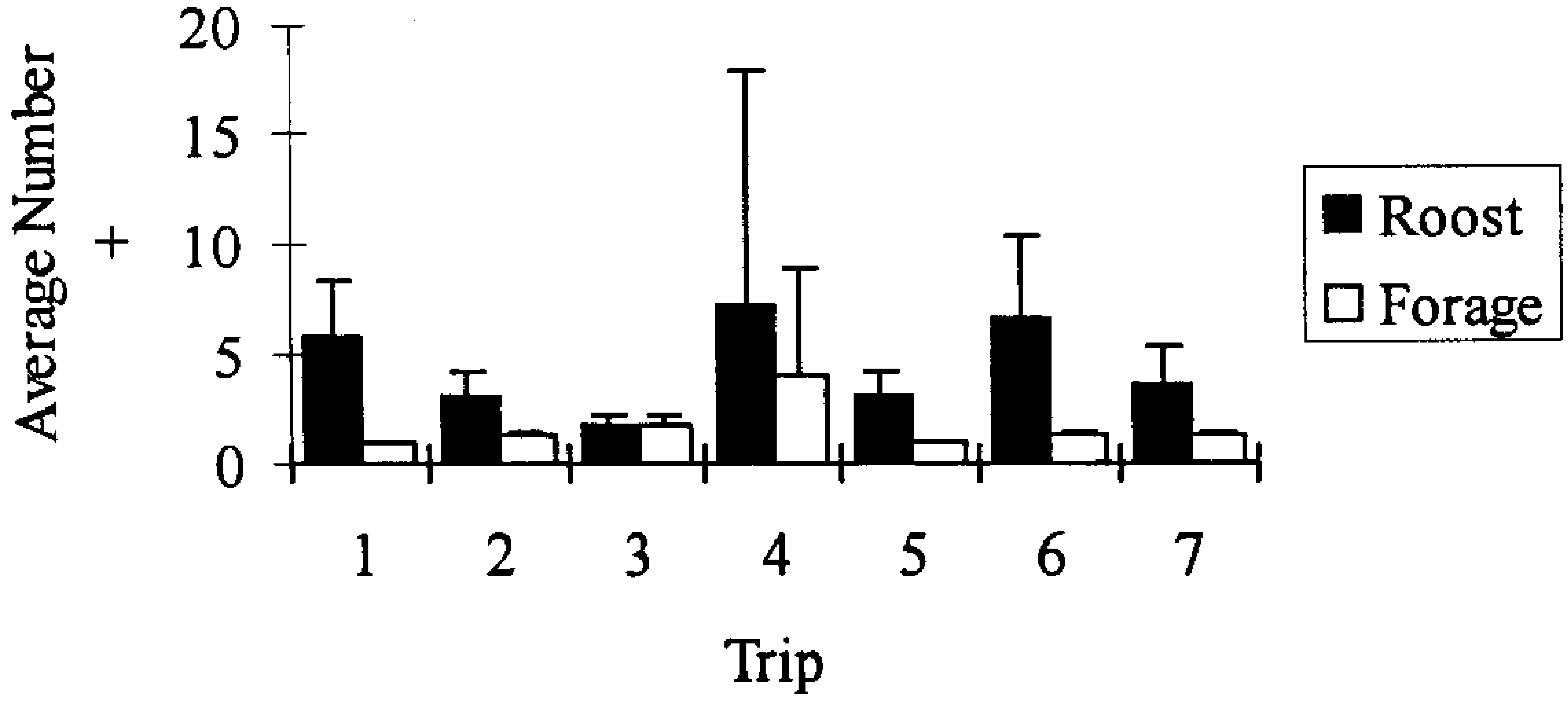


Figure 3.11. Average number of cormorants in seven trips engaging in roosting or foraging behaviour. Data in each trip are averaged over four random observations. Error bars represent Standard Error.

Table 3.6. Analysis of variance in relation to behaviours (roosting and foraging) of Little Pied Cormorants on seven trips along Patonga Creek. Abbreviations used: degrees of freedom (df), Mean Square (MS), *F*-ratio (F), Mean Square denominator (*F*vs), behaviour (beh) significance of the F test at P < 0.01 (**).

Source of variation		**df**	**MS**	**F**	***F*vs**
1	trip	6	15.351	2.317	3
2	beh	1	105.875	15.981**	3
3	trip*beh	6	6.625	0.382	4
4	residual	42	17.363		

3.4 Discussion

3.4.1. Foraging behaviour in environments of differential predictability

Cormorants occupy a wide range of habitats, from predictable coastal to unpredictable inland wetlands. With a focus of four species, this study provided an opportunity to investigate a model for habitat utilisation and behaviour across a set of species which occupy the same foraging guild. The model predicts that as cormorants move from a predictable coastal environment to an unpredictable inland one, their foraging strategy should change. The need for information transfer should drive the species to flock more in unpredictable conditions than in the predictable environment. Species varied considerably in their adherence to this model, resulting in three distinct foraging strategies: flock only in unpredictable circumstances (consistent with the general model; Great and Pied Cormorants); flock rarely (Little Pied Cormorants) or flock most of the time (Little Black Cormorants; see Figures 3.1 and 3.2; Table 3.1). Species-specific foraging behaviour appears to arise from a combination of proximate and ultimate mechanisms in which responses to local conditions are superimposed onto innate patterns of behaviour.

Great and Pied Cormorants

The importance of flocking in an unpredictable environment has been exhibited by Great and Pied Cormorants and is described elsewhere (Serventy 1939). Foraging patterns of these species were consistent with the model: individuals associated with conspecifics when prey were distributed unpredictably and foraged singly when it was possible to find prey alone. Communal hunting is thought to be adaptive when prey is either too large to capture singly (Curio 1976) or is difficult to locate (Templeton and Giraldeau 1995a). The facultative association with conspecifics exhibited by Great and Pied Cormorants may therefore be a mechanism for increasing search effort in the face of an unpredictable distribution of prey. This conclusion is supported by observations of a number of species (e.g. Laughing Gull *Larus atricilla*, Hatch 1970; African lion *Panthera leo*, Caraco and Wolf 1975; Little Egrets *Egretta garzetta* Kersten *et al.* 1991).

However, Great and Pied Cormorants also demonstrated a high degree of behavioural plasticity, changing their search strategy in relation to prevailing conditions. Situation-specific foraging behaviour and food choice has been exhibited by other species as well. For instance, American White Pelicans (*Pelecanus erythrorhynchus*) employ a number of foraging strategies, including sit-and-wait, coordinated and uncoordinated flocks and following schools of fish, adjusting their behaviour to changes in the type of prey and local circumstances (McMahon and Evans 1992). Other species also demonstrate behavioural plasticity in foraging (e.g. moose, Edenius 1993; walleye Pisces: *Stizostedion vitereum*, Bryan *et al.* 1995) indicating that it may be a capability common to many animals.

However, the importance of these finding lies not so much with a change in behaviour as with a shift in the nature, and the scale, of the microhabitat cue that releases foraging behaviour. On the coast, seagrass beds are stable, even static, relative to the length of time cormorants undertake a bout of foraging (see Bell and Westoby 1986a, b and c; Gray 1991a and b), and therefore present a fixed source of information. Great and Pied Cormorants foraging in a seagrass bed receive information about the probable location of fish within tens of metres (see Bell *et al.* 1988; Ferrell and Bell 1991) and this information source may last for months with very little change (see Pollard 1984). Although imprecise, the cue is apparently sufficiently reliable to maintain an association between foraging Great and Pied Cormorants and seagrass.

By contrast, foraging flocks are highly dynamic and individual foraging success in this situation appears to involve speculative hunting, combined with continuous sampling for the exact spot the event of prey capture by a con-specific. Information that narrows the search for prey occurs at a small scale: about 1 m^2 and 20 seconds, substantially more precise than information from a seagrass bed. The difficulty of finding inland prey, critical to the model, is also supported by the high frequency with which cormorants relocated while foraging at Lake Menindee (Figure 3.7). Thus, the high mobility of fishes in inland waters (Glover 1982) apparently requires prompt, fine grained information, and cormorants using foraging areas in both environments must be able to switch between two fundamentally different foraging strategies.

Little Black Cormorants

Little Black Cormorants did not follow predictions of the model, foraging most often in flocks, regardless of environment (Table 3.1). Flock foraging appears to be usual with Little Black Cormorants (e.g. Serventy 1939; Serventy *et al.* 1971; Miller 1979), and this may be related to individual hunting potential as well as prey type. Even a group of 30 Little Black Cormorants may not be able to prey on schooling fish as effectively as a group of 100 (Serventy *et al.* 1971). Furthermore, their foraging behaviour appears to be somewhat more coordinated and complex than that of the other species (e.g. Serventy 1939), suggesting that Little Black Cormorants are highly adapted to, or even reliant on, group foraging for active hunting as well as information transfer.

Little Pied Cormorants

Little Pied Cormorants were the most consistently solitary foragers of all the species, irrespective of environment. This species therefore conformed to the model's predictions only on the coast, a fact which may be best explained by food habits. The diet of Little Pied Cormorants comprises a large proportion of crustaceans (Barker and Vestjens 1987) and a single species, the yabby (*Cherax destructor*) can comprise up to 94% of the monthly average intake (Miller 1979). Crustaceans avoid predators by seeking refugia in freshwater (Söderbäck 1992) and estuarine (Gray 1991; Worthington *et al.* 1992) habitats. The main prey species of Little Pied Cormorants should therefore be associated with physical structures in both inland as well as estuarine habitats, and resource predictability for this species is probably no different in either environment. This would tend to negate an advantage of group foraging. Moreover, because conspecifics are potential competitors, group foraging is probably disadvantageous. Thus, solitary foraging may be a result of active avoidance of conspecifics, at least during non-breeding periods.

Notwithstanding the benefits of foraging singly, Little Pied Cormorants may derive a benefit from communal roosting, resulting in larger roosting flocks, as evidenced by larger comparative roost sizes for every flock size on Patonga Creek (Figure 3.11). Predator avoidance is important to some species of birds (Gadgil 1972), although there were no obvious predators in the study area. Nevertheless, flocking at night may provide Little Pied Cormorants some protection from the occasional predator or harassment by other species such as Sulphur-crested Cockatoos (*Cacatua galerita*; pers. obs.).

3.4.2. Surface behaviour, dive patterns and oxygen requirements

The main reason for investigating dive patterns was to search for evidence that differences in flock size were related to information transfer. As predicted, dive times for all species were significantly longer inland than on the coast, for water of approximately the same depth (Table 3.2). This is as expected, because fish in murky water are likely to be more difficult to catch, requiring longer search time underwater.

Assuming, however, a linear relationship between dive and surface times on the coast (Kramer 1988), all species except Little Pied Cormorants were at the surface longer than they needed to be to compensate for increased dive times (Table 3.4; Figure 3.6). These dives were probably well within their aerobic threshold (demonstrated by the infrequency of correlated dive and surface bouts; Table 3.3). It has already been established that cormorants in the water are foraging (see Casler 1973), so time at the surface is most likely to be spent watching con-specifics. And so, peripheral individuals, probably watching conspecifics, had significantly longer surface times than those at the centre of the flock (Table 3.5).

The notion of cormorants profiting from time spent at the surface is at variance with the prevailing ideas about diving in aquatic birds. The view has been that diving animals should spend only enough time at the surface to replenish their oxygen levels and that any more time would be wasted (Kramer 1988; Ydenberg and Clark 1989). This idea has been extended to cormorants, either explicitly (Lea *et al.* 1996) or implicitly, by terming time spent at the surface as "rest" (Stonehouse 1967; Cooper 1986; Trayler *et al.* 1989) or "recovery" (Wanless *et al.* 1993) periods. It assumes that cormorants do not obtain information at the surface about the location of their prey, possibly introducing bias into optimisation models of cormorant foraging (e.g. Wanless *et al.* 1993).

Cormorants are assumed to compensate for any oxygen debt acquired from diving by the surface interval directly preceding or proceeding it, hence the terms "anticipatory" and "reactive". Results of correlations between surface times before and after dives support conclusions of Lea *et al.* (1996) that Great and Pied Cormorants are reactive breathers and Little Pied Cormorants are anticipatory breathers (Table 3.3). Little Black Cormorants did not show a significant relationship, but sample sizes were small.
Lea *et al.* (1996) concluded that breathing was related to foraging behaviour. Species that probe the bottom for small prey (e.g. Little Pied Cormorants) could not predict the duration of each dive and would be unable to compensate beforehand. In contrast, species that feed in open water would be able to predict the amount of oxygen required for the proceeding dive. Foraging patterns of Little Black Cormorants lie somewhere in between the two (Miller 1979), which may help to explain the lack of clear patterns.

Table 3.6. Average dive and surface times for Great, Pied, Little Black and Little Pied Cormorants in this and previous studies. Time periods are rounded to the nearest second.

Species	Dive	Surface	Depth/Habitat	Source
GRC	21	7	1-8 m Estuary	Stonehouse (1967)
	39	9	no information	Cooper (1986)
	9	2	1-2 m Estuary	this study
	15	8	1-2 m Inland	this study
PCO	11	5	1-2 m Estuary	Stonehouse (1967)
	19	11	2-3 m Estuary	Stonehouse (1967)
	17	8	1.2 m Estuary	Trayler *et al.* (1989)
	25	8	2 m Estuary	Trayler *et al.* (1989)
	5	4	1-2 m Estuary	this study
	15	18	1-2 m Inland	this study
LBC	13	4	1.2 m Estuary	Trayler *et al.* (1989)
	19	8	2 m Estuary	Trayler *et al.* (1989)
	11	3	1-2 m Estuary	this study
	19	8	1-2 m Inland	this study
LPC	13	4	1-2 m Estuary	Stonehouse (1967)
	16	5	2-3 m Estuary	Stonehouse (1967)
	6	3	1 m Estuary	Trayler *et al.* (1989)
	13	5	1.2 m Estuary	Trayler *et al.* (1989)
	11	3	1-2 m Estuary	this study
	19	8	1-2 m Inland	this study

Although most aquatic birds and mammals dive aerobically (Butler and Jones 1982), anaerobic diving can be favoured (Ydenberg and Clark 1989). Western Grebes (*Aechmorphus occidentalis*) intersperse bouts of high activity with periods of rest or low activity, possibly recovering from aerobically costly bouts during the latter (Ydenberg and Forbes 1988). Anaerobic dives are longer and so are favoured when prey occur in dense, mobile, hard-to-find concentrations, because more time under water allows fuller exploitation of the prey before it disappears (Ydenberg and Clark 1989). Thus, bouts of diving may incur an oxygen debt which is compensated for later. This could have been the case with cormorants in this study, and would not have been apparent from observations of behaviour. Per-bout compensation would be difficult to test on cormorants *in situ*, because cormorants must also leave the water periodically to dry out, so it must be retained as an alternative hypothesis.

Patterns of foraging for the four species of cormorant showed that predictability has a strong influence on foraging behaviour, although species respond differently. Behavioural patterns associated with habitat features (including conspecifics) may in turn influence habitat use and distribution (e.g. Sutherland 1983; Turchin 1991) on a larger scale. In the next chapter, I use patterns of behaviour of cormorants to form predictions about habitat use in coastal and inland wetlands of New South Wales.

CHAPTER FOUR

HABITAT SELECTION IN ENVIRONMENTS OF DIFFERING VARIABILITY

4.1. Introduction

At an intermediate scale (10^0 - 10^1 km^2 and one day - three years), foraging behaviour of individuals can often be translated into patterns of habitat selection (see Sutherland 1996). Animals should select foraging patches which offer concentrations of resources that are higher than the environmental average (Charnov 1976), and by extension, should select habitat based in part on the density of profitable patches. Although other factors such as competition (e.g. Fretwell 1970; Fretwell and Lucas 1970; Harper 1982; Houston and MacNamara. 1988) and predation (e.g. Page *et al.* 1985; Brown *et al.* 1994) can also influence habitat selection, the distribution of resources is clearly an important structuring force. Habitat selection related to foraging has been demonstrated in theory (e.g. Sutherland 1983; Rosenzweig 1985; Shettleworth *et al.* 1988; Powell 1989; Possingham 1989, 1992) and practice, through empirical studies on animals that vary considerably in mobility (e.g. larval lepidopterans, Grez and Gonzalez 1995; marine ichthyoplankton, Kingsford 1995a; desert rodents, Kotler *et al.* 1994; coyotes *Canis latrans,* Shivik *et al.* 1996; red kangaroos *Macropus rufus,* McCarthy 1996; near-arctic and neotropical migratory birds, Winker *et al.* 1992).

Habitat selection may also be influenced by resource variability, although responses vary with species. For example, rodents in arid Australia may become restricted to refugia during periods of resource depletion (Morton *et al.* 1995). Other species (e.g. feral pigs *Sus scrofa*) cannot endure extreme fluctuations in habitat quality and undergo localised extinctions (Choquenot 1994). Animals may also alleviate the effect of changing resource abundance by seeking easily-discernible habitat variables that are associated with high quality patches. For instance, the distribution of Red-capped Plovers (*Charadrius ruficapillus*) in salt lakes of Western Australia is better explained by abiotic features of the environment, such as slope of shore and aspect, than by the distribution of food, suggesting that shoreline features provide the birds with increased access to concentrations of prey (Abensperg-Traun and Dickman 1989).

The importance of a given resource may not, however, be equal at different spatial or temporal scales. This has been demonstrated for a variety of taxa (e.g. marine birds, Schneider 1993; the lacertid lizard *Algyroides marchi*, Rubio and Carrascal 1994; Cape porcupines *Hystrix africaeaustralis*, de Villiers *et al.* 1994). Animals selecting suitable habitat may therefore be required to assess the array of choices at a number of scales. Patterns of abundance may logically result from an interplay between scale and variability, such that relatively course-grained (ie. larger scale) information is sufficient for detection of resources in a stable environment, whereas precise (ie. smaller scale) information is required in environments in which the distribution of resources changes extensively or quickly. Cormorants gather information from seagrass beds, a relatively course grained feature, in a stable coastal estuary, but use the foraging success of flock-members, a fine-grained cue, in the relatively unpredictable waters of an inland lake (Chapter 3).

The general aim of this chapter is to relate the foraging patterns found in Chapter 3 to habitat selection at larger spatial and temporal scales, taking habitat variability and predictability into account. If cormorants within a coastal estuary use seagrass beds as a foraging cue, it may be predicted that they will co-occur with seagrass at a larger scale. However, cormorants are highly mobile and readily move among foraging and roosting sites at distances of a kilometre or more within the course of a day (pers. obs.). In addition, factors such as boat traffic (pers. obs.) and patchiness of fish within seagrass meadows (e.g. Ferrell and Bell 1991) may also influence their distribution. An investigation into habitat selection, should therefore incorporate information from the type of habitat in which seagrass grows in addition to more precise information about the presence of seagrass at individual locations.

Seagrass meadows occur in sheltered soft bottomed habitats and are affected by irradiance (Kirkman and Cook 1982) temperature (Bulthius 1987), salinity (Walker 1985) and nutrient levels (Short 1987), thus habitats, such as creeks, river channels and bays which offer distinct regimes of depth, nutrients and sedimentation should differ in their attractiveness as habitat for cormorants.

Inland, however, aquatic macrophytes usually grow in clear water, which is normally too saline to support fish (Kingsford and Porter 1994). In addition, the presence of large flooding rainfall events and flooding that occur unpredictably in space and time across the landscape (Stafford Smith and Morton 1990) mean that even gross geographical features, such as local catchments, may provide little predictive power. Therefore, when cormorants visit arid regions, they may be predicted to be less closely coupled to stationary environmental features than when they are on the coast.

In this chapter, I measure abundance and behaviour of cormorants in relation to geographical features, in estuarine habitats in the greater Sydney region and in wetland habitats in lakes of arid New South Wales. However, because cormorants may use different habitats for different activities (e.g. roosting, foraging and nesting habitats of Australian Pelicans *Pelecanus conspicillatus* can be in different locations; R. T. Kingsford pers. comm.), I also measured frequency of behaviour in each habitat type within each environment.

4.2. Materials and Methods

4.2.1. Pilot study: cormorant abundance and behaviour in estuaries, in relation to tidal state and time of day

Because tidal state and time of day can influence movements of fish (e.g. Kingsford and MacDiarmid 1988) as well as water visibility, a pilot study in coastal estuaries was conducted to determine the effect of these variables on the distribution of cormorants.

Broader - scale sampling could then be done without confounding time, tide and spatial variation. Data on abundance and behaviour were collected at five sites in the greater Sydney region (Figure 2.6), where casual observations suggested that cormorants were abundant, at two tidal states (High: one hour before to one hour after high tide and Low: one hour before to one hour after low tide) and three times of day (early 1000 - 1200; mid 1200 - 1400 and late 1400 - 1600; see Table 4.1, Design A). Prior to sampling, tide markers were placed at each study site and a calculation was made of the time lag in comparison to local tide charts. Adjusted tide charts were used for the remainder of the study. Dawn and dusk were excluded from the sampling, because cormorants in all locations spent much of this time travelling between night-time roosts and day-time foraging locations (pers. obs.).

The number of each species was recorded as well as a behavioural state (Section 4.2.3) for each individual during each replicate count. Each replicate was conducted for five minutes. This period of time was chosen as a balance between ensuring that all cormorants were observed and minimising the opportunity for a change in abundance during sampling. Cormorants were observed using hand-held 7 x 35 binoculars.

The study was conducted twice, about 12 months apart (May - June 1994 and 1995) and data were analysed using a four-factor analysis of variance (ANOVA; Table 4.1). Each species was treated separately. No test existed for the main effects: time, tide or the interactions between the two, therefore data were pooled if differences between sampling period were not significant at $P > 0.20$ (Underwood 1997; Table 4.1, Design A). This enabled tests of the main factors to be made. Because Great Cormorants were observed only rarely during this study (six individuals in 120 observations), they were excluded from the analysis. Data were heterogeneous and so were transformed using $\ln(x+1)$ (following Underwood 1981). Variances were still heterogeneous for all species after transformation (Cochran's $C_{PCO} = 0.165$; $C_{LBC} = 0.226$; $C_{LPC} = 0.119$). The significance was therefore set to $P < 0.01$ (Underwood 1997).

4.2.2. The influence of geography and habitat type on patterns of abundance

The greater Sydney region

Habitat utilisation by cormorants was measured in two estuary systems (Broken Bay/Hawkesbury River and Port Jackson/Parramatta River; Figure 2.6.) in the greater Sydney region. Abundance of cormorants was measured in five habitat types (Open Coast, Headland, Bay, River Channel and Creek; Table 4.2a), which were chosen to represent a gradient from an exposed oceanic environment to a sheltered backwater (Table 4.2b).

See the pilot study (Section 4.2.1) for methodology of observations. A partially hierarchical design was used (Table 4.1, Design B). All habitat types were sampled in each estuary system. Variances appeared highly heterogeneous, so data were transformed using ln(x + 1), following Underwood (1981). Cochran's tests indicated that the variances were still heterogeneous (C_{GRC} 0.25; C_{PCO} 0.40; C_{LBC} 0.25; C_{LPC} 0.23; df = 3) and the significance level was set to $P < 0.01$ (Underwood 1997).

Because seagrass is an important feature of foraging behaviour of cormorants, an additional analysis was performed to compare abundance of cormorants between sites with and without seagrass. Abundances in five sites with seagrass (Patonga Creek, Magdala Park, Athol Bay, Rose Bay and Broken Bay, Figures 2.7 and 2.8) were compared to five sites without (Ocean Beach, Dead Horse Point, Long Island, Wolseley Street and Long Nose Point, Figures 2.7 and 2.8). Differences were tested with a Chi^2 test. Because of low frequency of occurrence of all species, the test was performed for all species combined.

Lakes Menindee and Waitchie

Cormorants were counted in all habitats that were found at Lakes Menindee and Waitchie (Figures 2.10 and 2.11, respectively) and collection methods for habitat utilisation inland were the same as for that on the coast. Inland environments did not provide the array of choices for sampling available on the coast. Habitats were more homogeneous, allowing for fewer factors. Also, geographical entities were physically smaller in the inland environment (e.g. a lake margin is smaller than the shoreline of a bay). This meant that there was not enough space to sample three non-overlapping replicates that were large enough to be biologically meaningful, and so two were used. Finally, each inland lake system provided habitat types that were unique to the site (Table 4.3a) and habitat types were only roughly comparable between the two, although the design was similar for each (Table 4.1b, Design C). The habitats used represented a complete coverage of available types in each location (Table 4.3).

Data for Little Black Cormorants were not analysed, because they were only sighted on three occasions at either lake, for a total of five individuals. Little Pied Cormorants were not observed during this study, although the species was observed in the area the previous year (see Chapter 3).

4.2.3. Behaviour

The behavioural state (swimming, roosting and flying) of each cormorant was recorded for each sampling design. A cormorant's behavioural state was regarded as the first behavioural category observed, irrespective of any change in behaviour during the observation period. Cormorants did not breed during this study, so reproductive behaviours (see Blakers *et al.* 1990) were not included as possible categories of behavioural state.

Behavioural states were mutually-exclusive and general, to avoid confusion during sampling. "Swimming" was any activity in the water, and although almost exclusively associated with foraging, cormorants occasionally flapped vigorously in the water. "Roosting" was any activity off the water, in which the cormorant was not flying. This included drying and sunning with wings outstretched; preening; sleeping and loafing (*sensu* Smith 1991). Flying included both long-range movement flight and relocation from one swimming or roosting spot to another (ie. metres to 100s of metres). Differences in behaviour among habitat types were analysed separately for each species using a Chi^2 test. Behaviours or habitat types which were not recorded for a given species were not included in the analysis. With the exception of Pied Cormorants at Lake Waitchie, cormorants from inland lakes were so patchily distributed that Chi^2 tests were not possible because of the high frequency of zero-values. At this location, it was not possible for Pied Cormorants to roost on open water, so this category was excluded from the analysis.

4.3. Results

4.3.1. Pilot study: the influence of time and tide

Great differences in abundance were found among locations for Pied and Little Black Cormorants, but no influence of state of the tide or time of day was detected for any species (Table 4.4). This pattern was clear, based on changes in rank abundance between tides and among times of day for particular species (e.g. Pied Cormorants, Location 3, 1993 and 1994; Figure 4.1). It was concluded that time of day and/or tide would not have a predictable influence on the results of broad-scale sampling designs. Significant differences were only found for location, even after pooling (Table 4.4). Variability was high within a set of replicates (Figure 4.1), indicating that cormorants were clumped at a scale smaller than that of a habitat.

4.3.2. Habitat utilisation

Great variation in abundance of cormorants was found among habitats at coastal and inland sites. On the coast, all species were rare or absent from open coast and headland habitats (Figure 4.2). Although there appeared to be variation among sites within a habitat (e.g. Bay), this was not detected with ANOVA because variation at the replicate level was high. Great and Pied Cormorants were highly clumped and showed all of the variability at the replicate level (Table 4.5; Figures 4.2a and b). Little Black and Little Pied Cormorants both demonstrated significant differences at the site level (Table 4.5; Figures 4.2c and d) and Little Pied Cormorants exhibited significant differences at the level of geography (Table 4.5).

The more exposed habitats were rarely used, however use of the estuarine habitats, Bay, River Channel and Creek, varied among species. Great, Little Black and Little Pied Cormorants were spread throughout the estuarine habitat types, whereas Pied Cormorants were confined to Bays and River Channels and this pattern was consistent for both estuaries (Table 4.5; Figure 4.2). Significant interactions at the level of site for Little Black and Little Pied Cormorants and near significant interaction for Great Cormorants ($P = 0.055$; Table 4.5) suggests that, for these species, the importance of habitat is dependent on qualities of individual sites.

Inland, Great Cormorants were less spread among habitats than Pied Cormorants, although both were highly aggregated, (Figure 4.3) and showed no variability at the level of habitat, sampling period or site (Table 4.6a). Lack of variation at these levels was strongly influenced by aggregation (Figure 4.3), which created high variability at the level of replicate. Although not significantly different, live trees contained more Great and Pied Cormorants than any other habitat (Figure 4.3), and this may have been preferred roosting habitat, irrespective of other patterns of use within Lake Waitchie.

At Lake Menindee, flocks of Great and Pied Cormorants showed no variation among habitats, but differences among sites were significant (Table 4.6b; Figure 4.4) and there was no interaction with sampling period. Much of the variation came from a single mixed foraging flock of about 700 Great Cormorants, 300 Pied Cormorants, (as well as 200 Australian Pelicans and 50 grebes) that occurred near the Menindee inlet channel. At this site, schools of bony bream (*Fluviatilis richardsonii*) had congregated, apparently feeding on plankton or microalgae emanating from the inlet.

When Little Black Cormorants were observed at Lake Menindee, they were always associated with foraging flocks of other cormorants in open water or near the lake margin. The Little Pied Cormorants that had been in the area the previous year roosted in association with other cormorants, but foraged singly underneath floating rafts of the semi-aquatic vascular plant, *Persicaria*. In this period, all cormorants occurred in Lake Cawndilla, at the head of the channel that leads into Lake Menindee inlet from the north (Figure 2.10).

4.3.3. Behaviour

For inland and coastal environments, in almost all habitats, roosting was the most common activity observed (Figures 4.5, 4.6 and 4.7), although differences among species were evident. All species except Little Pied Cormorants displayed significant differences in frequency of behaviour in different coastal habitats (Table 4.7; Figure 4.5). The only behaviour observed on the open coast during this study was flying, however cormorants do occasionally roost and swim along sheltered rocky shores (pers. obs.). Patterns of behaviour were roughly the same for headlands as for the open coast, although cormorants occasionally roosted there as well (Figure 4.5). Swimming was best represented in creek habitats, both in terms of proportion and frequency, although roosting in this habitat was still the principal activity (Figure 4.5).

Cormorants swam and roosted at coastal sites with seagrass significantly more often than at sites without seagrass (Figure 4.7; $Chi^2_{swim} = 15.38$, $Chi^2_{roost} = 12.41$, df = 1, $P < 0.001$). Flying was not significantly different between the two types of site (Figure 4.6; $Chi^2_{fly} = 0.26$, df = 1, n.s.).

Pied Cormorants at Lake Waitchie demonstrated significant differences in the frequency of behaviour at different habitat types ($Chi^2 = 31.57$, df = 6, $P < 0.001$), however the relative frequency of roosting was high enough to swamp the potential effects of behaviour on habitat type (Figure 4.7).

Table 4.1. Sampling designs used in this chapter. An asterisk (*) denotes fixed factors. In designs B, C and D, "Time" denotes occasion of sampling. "{}" indicates a nested factor and "x" denotes an interaction.

DESIGN A: DISTRIBUTION IN RELATION TO TIME AND TIDE

Source of Variation	Levels
Sampling period	2
Time of Day*	Early 1000-1200; Mid 1200-1400; Late 1400-1600
Tide*	High, Low
Location	Five randomly chosen locations
Replicates	2: non-overlapping 5-minute observation periods

DESIGN B: HABITAT UTILISATION ON THE COAST

Source of Variation	Levels
Estuary	Port Jackson, Broken Bay
Habitat*	Ocean, Headland, Bay, River Channel, Creek
Site{Estuary x Habitat}	Two randomly chosen locations
Time{Site{Estuary x Habitat}}	2
Replicates	3

DESIGN C: HABITAT UTILISATION AT LAKE WAITCHIE

Source of Variation	Levels
Geography*	Open Water, Dead Trees, Live Trees, Shallows
Site{Habitat}	Two randomly chosen locations
Time	2
Replicates	2

DESIGN D: HABITAT UTILISATION AT LAKE MENINDEE

Source of Variation	Levels
Habitat*	Open Water, Lake Margin, River Channel
Site{Habitat}	Two randomly chosen locations
Time	2
Replicates	2

Table 4.2. Definitions of habitat types (a) and sites (b) for study of habitat utilisation on the coast. Note that definitions are meant for this study only and do not imply generality.

a

HABITAT TYPE	DEFINITION
Open Coast	A strip of land connecting the shore with oceanic waters.
Headland	An outcropping of land at the mouth of an embayment.
Bay	An area of water open to the coast, mostly enclosed by land.
River Channel	A tidal watercourse connecting fresh inland waters with the open coast.
Creek	An estuarine tributary of a river channel, which is diluted by freshwater drainage from land.

b

COAST

Habitat Type	Port Jackson	Broken Bay
Open Coast	Diamond Bay	Newport Beach
	Queenscliff Beach	McMasters Beach
Headland	North Head	Box Head
	South Head	Hawkesbury Head
Bay	Rose Bay	Ocean Beach
	Athol Bay	Broken Bay
River Channel	Long Nose Point	Long Island
	Wolseley St. Wharf	Dead Horse Point
Creek	Magdala Creek	Patonga Creek
	Homebush Bay	Coal & Candle Creek

Table 4.3. Habitat types (a) and study sites (b) for study of habitat utilisation inland. Note that habitat types are defined by the structures available at a given location and do not imply generality.

a

HABITAT TYPE	DEFINITION
Open Water	The area of a lake, at least 100 metres from the bank.
Lake Margin	The area of a lake between the bank and 100 metres out.
Dead Trees	In dead trees or in the water immediately adjacent to them.
Live Trees	In live trees or in the water immediately adjacent to them.
River Channel	An area of running water, uninterrupted by pooling.
Shallows	An area of lake in which the water depth is 0.75 m or less. Supersedes other categories.

b

INLAND SITE 1: LAKE WAITCHIE

Habitat Type	Site
Open Water	South East Side
	North West Side
Dead Trees	Eastern Margin
	Western Margin
Live Trees	Northern End
	Southern End
Shallows	Northern End
	Southern End

INLAND SITE 2: LAKE MENINDEE

Habitat Type	Site
Open Water	Pamamaroo Inlet
	Pamamaroo Outlet
Lake Margin	Menindee Lookout
	Lake Wetherell Outlet
River Channel	Menindee Inlet Channel
	Darling River

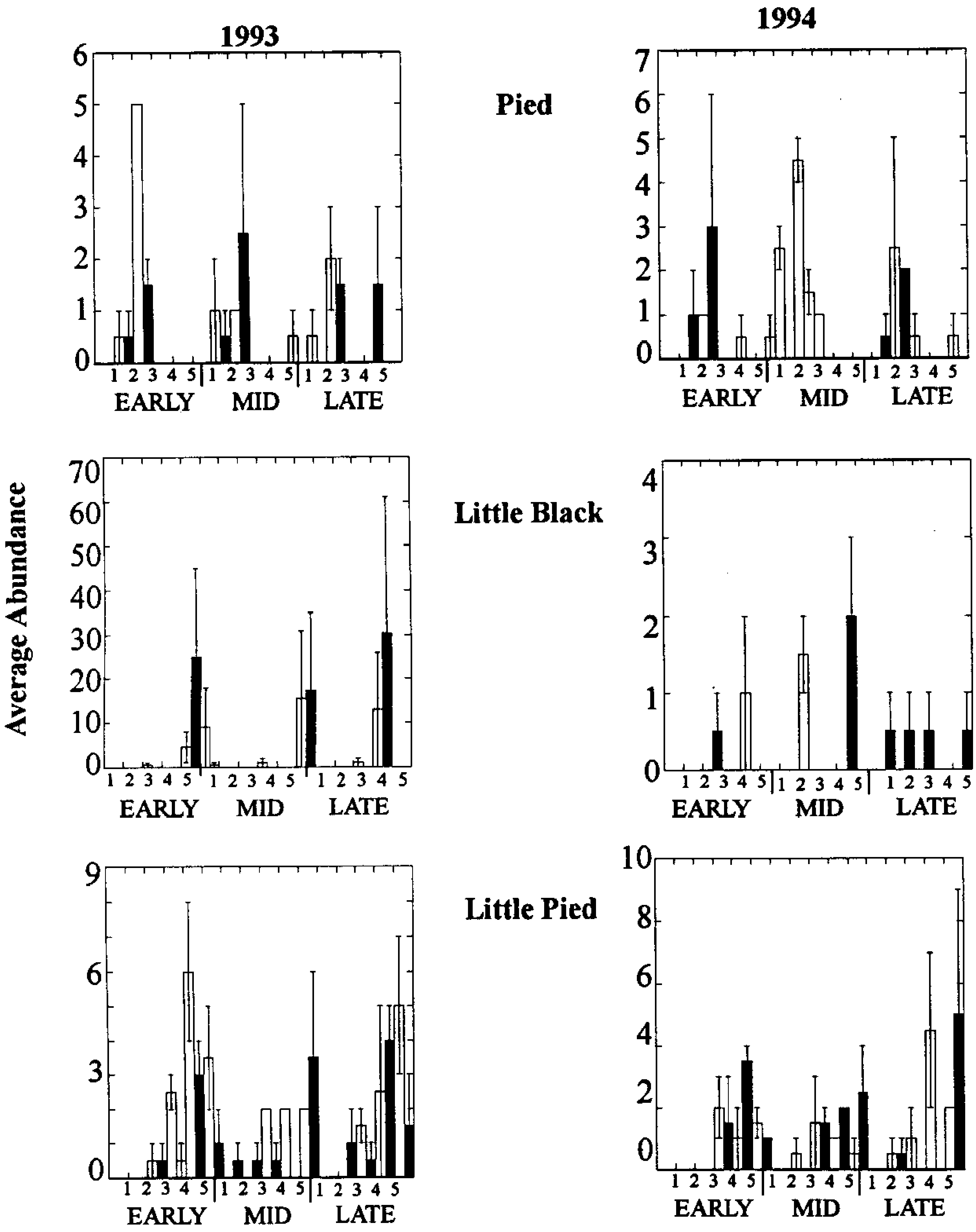


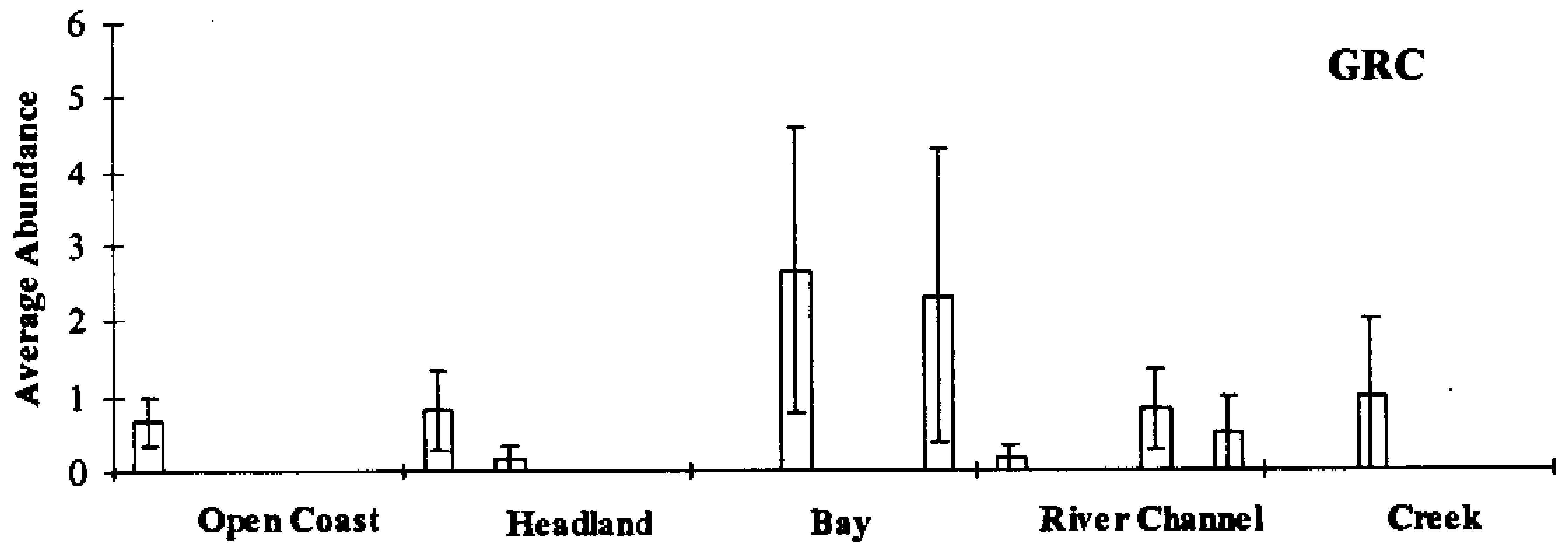
Figure 4.1. Average abundance of Pied, Little Black and Little Pied Cormorants in relation to time of day and tidal state. Numbers on the X-axis represent locations: 1=Oatley; 2=Shag Pt.; 3=Besnville; 4=Patonga; 5=Saratoga. "Early", "Mid" and "Late" refer to times of day. Shaded and empty bars represent high and low tides, respectively. Note that SE, represented by error bars, is very low for some replicates.

Table 4.4. Analysis of variance of abundance in relation to time of day and tidal state. Abbreviations used: degrees of freedom (df), Mean square (MS), F-ratio (F), Mean square denominator (Fvs), year (yr), time of day (tim), tidal state (tid), location (loc), significance of the F test (*). Significant differences are only shown for $P < 0.01$.

Source of variation		df	PCO		LBC		LPC		*F*vs
			MS	*F*	MS	*F*	MS	*F*	
1	yr	1	0.340	1.994	389.174	2.315	4.193	5.517	8
2	tim	2	0.256	0.358	1.887	0.517	3.976	5.409	5
3	tid	1	1.466	14.878	30.420	1.273	1.770	0.298	6
4	loc	4	21.302	125.014*	185.667	1.079	30.660	40.336*	7
5	yr*tim	2	0.715	0.818	3.649	0.035	0.735	0.609	14
6	yr*tid	1	0.099	0.389	23.889	0.456	5.936	2.079	13
7	yr*loc	4	0.170	0.166	172.031	2.406	0.760	0.347	16
8	tim*tid	2	0.991	0.229	6.773	1.255	2.004	1.400	11
9	tim*loc	8	0.534	0.611	90.796	0.882	2.856	2.366	14
10	tid*loc	4	0.568	2.247	56.448	1.078	1.062	0.372	13
11	yr*tim*tid	2	4.320	1.736	5.395	0.249	1.432	0.258	15
12	yr*tim*loc	8	0.874	0.849	102.954	1.440	1.207	0.551	15
13	yr*tid*loc	4	0.253	0.246	52.378	0.733	2.855	1.304	16
14	tim*tid*loc	8	0.497	0.200	13.276	0.612	1.372	0.247	16
15	yr*tim*tid*loc	8	2.489	2.419	21.703	0.304	5.549	2.533	16
16	Residual	60	1.029		71.504		2.190		

Table 4.5. Analysis of variance of abundance in relation to geographical features on the coast. Abbreveiations used: degrees of freedom (df), Mean square (MS), *F*-ratio (*F*), Mean square denomenator (*F*vs), estuary (est), geographcial feature (geog), sampling period (per). Significant differences are only shown for $P < 0.01$.

	Source of variation	**df**	**GRC** **MS**	***F***	**PCO** **MS**	***F***	**LBC** **MS**	***F***	**LPC** **MS**	***F***	***F*vs**
1	est	1	0.048	0.600	0.001	0.031	0.191	0.488	0.000	0.000	5
2	geog	4	0.053	1.070	0.072	1.353	0.331	1.082	0.401	14.437*	4
3	est x geog	4	0.050	0.619	0.053	2.407	0.306	0.780	0.028	0.159	4
4	site {est x geog}	10	0.080	2.737	0.022	0.771	0.392	28.417*	0.174	9.039*	5
5	per{site{est x geog}	10	0.029	0.695	0.029	2.087	0.014	0.814	0.019	0.539	6
6	Residual	90	0.042		0.014		0.075		0.036		



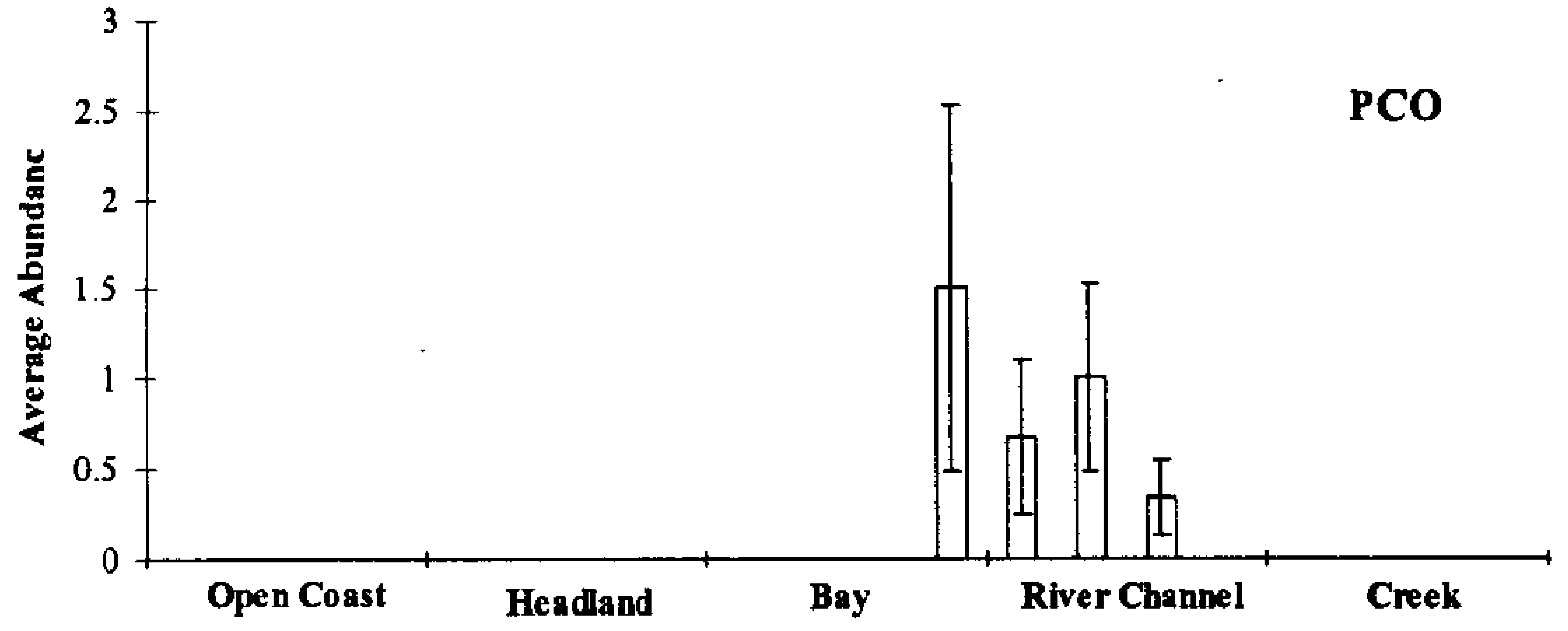
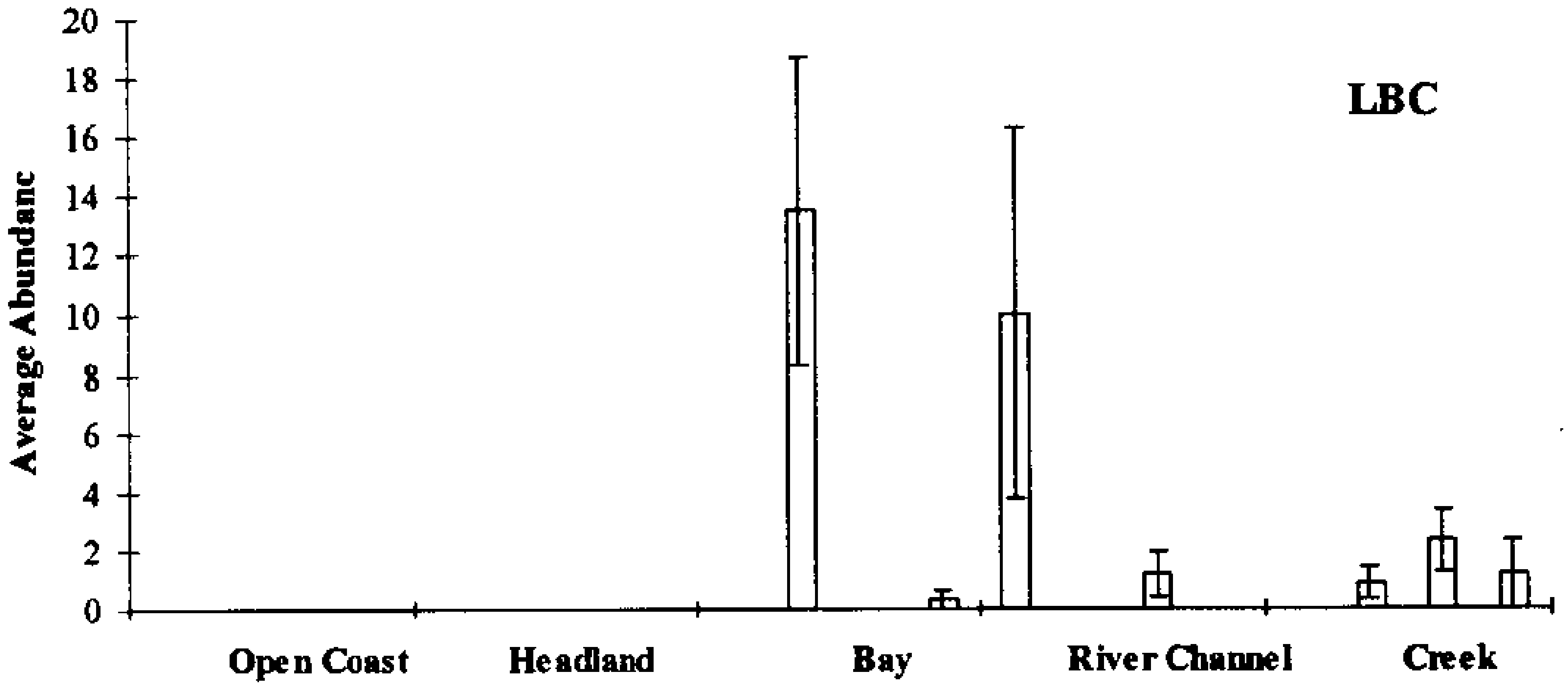


Figure 4.2. Abundance of cormorants in the greater Sydney Region, in relation to habitat and site for Great (GRC) and Pied (PCO) Cormorants. Bars represent individual sites (n = 6 observations per site, pooled by time) within a habitat. There are four sites per habitat type. Error bars indicate standard error.

continued ⇨



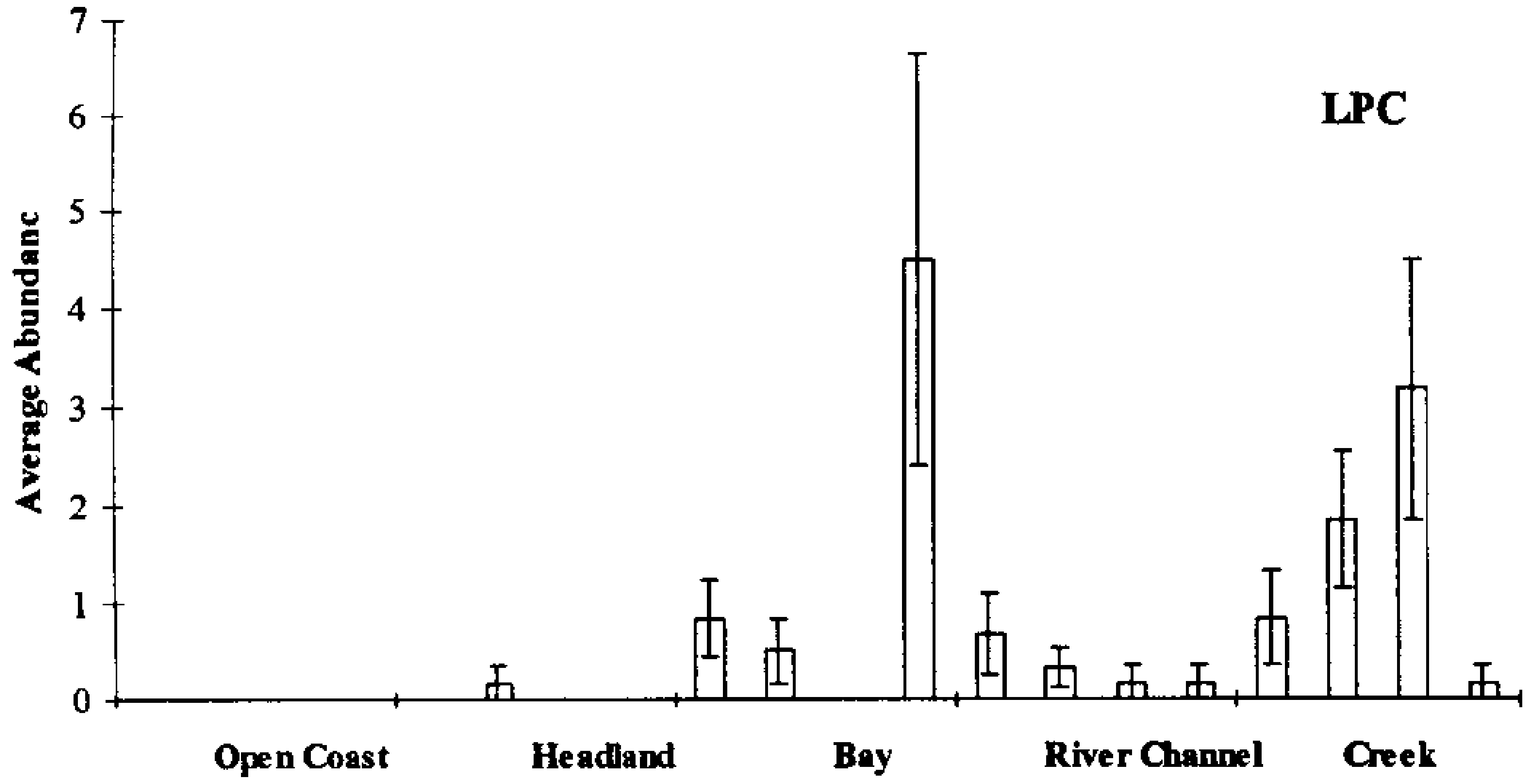
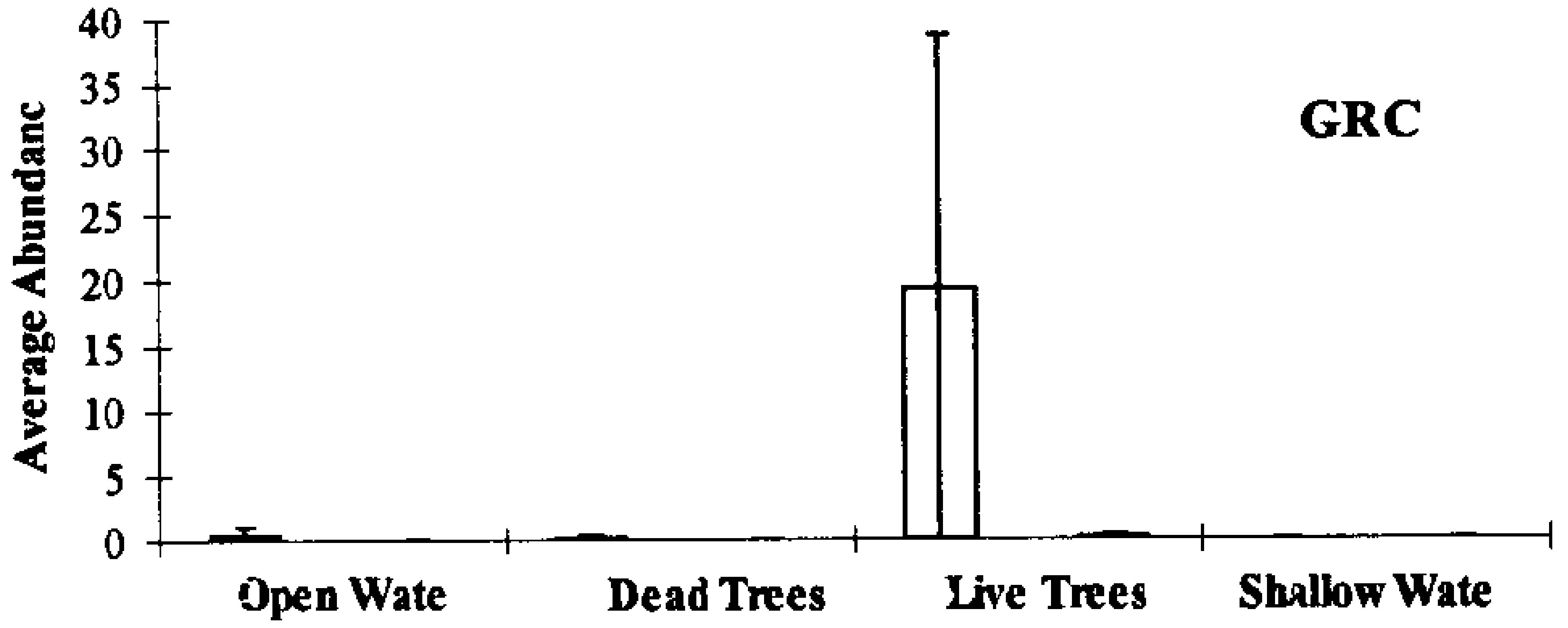


Figure 4.2. Abundance of cormorants in the greater Sydney Region, in relation to geographical entity and site for Little Black (LBC) and Little Pied (LPC) Cormorants. Bars represent individual sites (n = 6 observations per site, pooled by time) within a habitat. There are four sites per habitat type. Error bars indicate standard error.



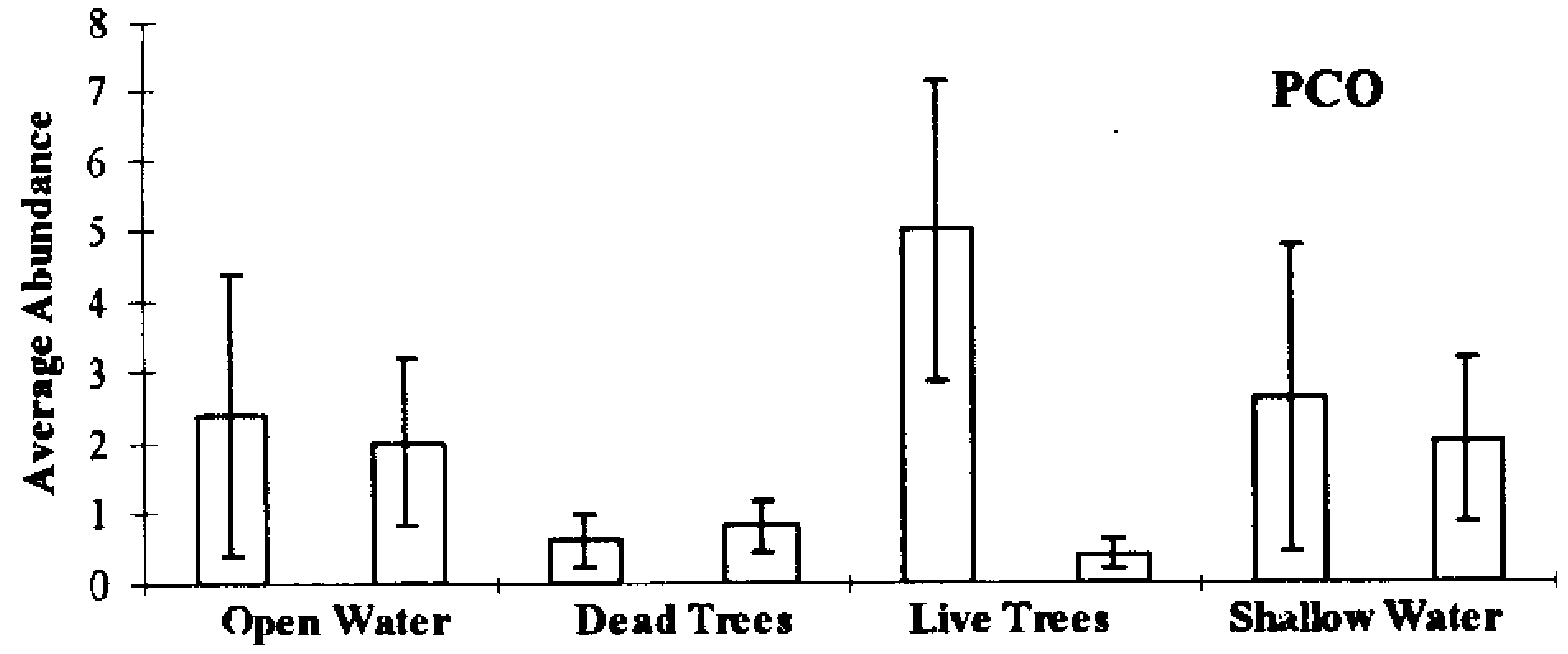


Figure 4.3. Abundance of Great and Pied Cormorants at Lake Waitchie. Bars represent individual sites (n = 4 observations per site). There are four sites per habitat type. Error bars indicate standard error.

Table 4.6. Analysis of variance of abundance in relation to geographical features in the arid zone: Lake Waitchie (a) and Lake Menindee (b). Abbreviations used: degrees of freedom (df), Mean square (MS), *F*-ratio (*F*), Mean square denominator (*F*vs), habitat type (hab), sampling period (per). F and Fvs terms in brackets indicate tests that were possible after pooling. Significant differences are only shown for $P < 0.01$.

a. Lake Waitchie

			GRC		PCO		
Source of variation		**df**	**MS**	***F***	**MS**	***F***	***F*vs**
1	hab	3	0.094	(0.521)	0.005	(0.061)	(4)
2	site{hab}	4	0.074	0.587	0.129	2.263	6
3	per	1	0.016	0.123	0.005	0.083	5
4	hab x per	3	0.094	0.745	0.082	1.428	5
5	site{hab} x per	4	0.126	1.258	0.057	0.384	6
6	Residual	32	0.100		0.149		

b. Lake Menindee

			GRC		PCO		
Source of variation		**df**	**MS**	***F***	**MS**	***F***	***F*vs**
1	hab	2	3.372	(0.757)	0.515	(0.299)	(4)
2	site{hab}	3	4.452	494.670*	1.722	13.348*	5
3	per	1	0.001	0.111	0.324	1.673	5
4	hab x per	2	0.011	1.222	0.129	0.664	5
5	site{hab} x per	3	0.009	0.053	0.194	0.880	6
6	Residual	12	0.163		0.224		

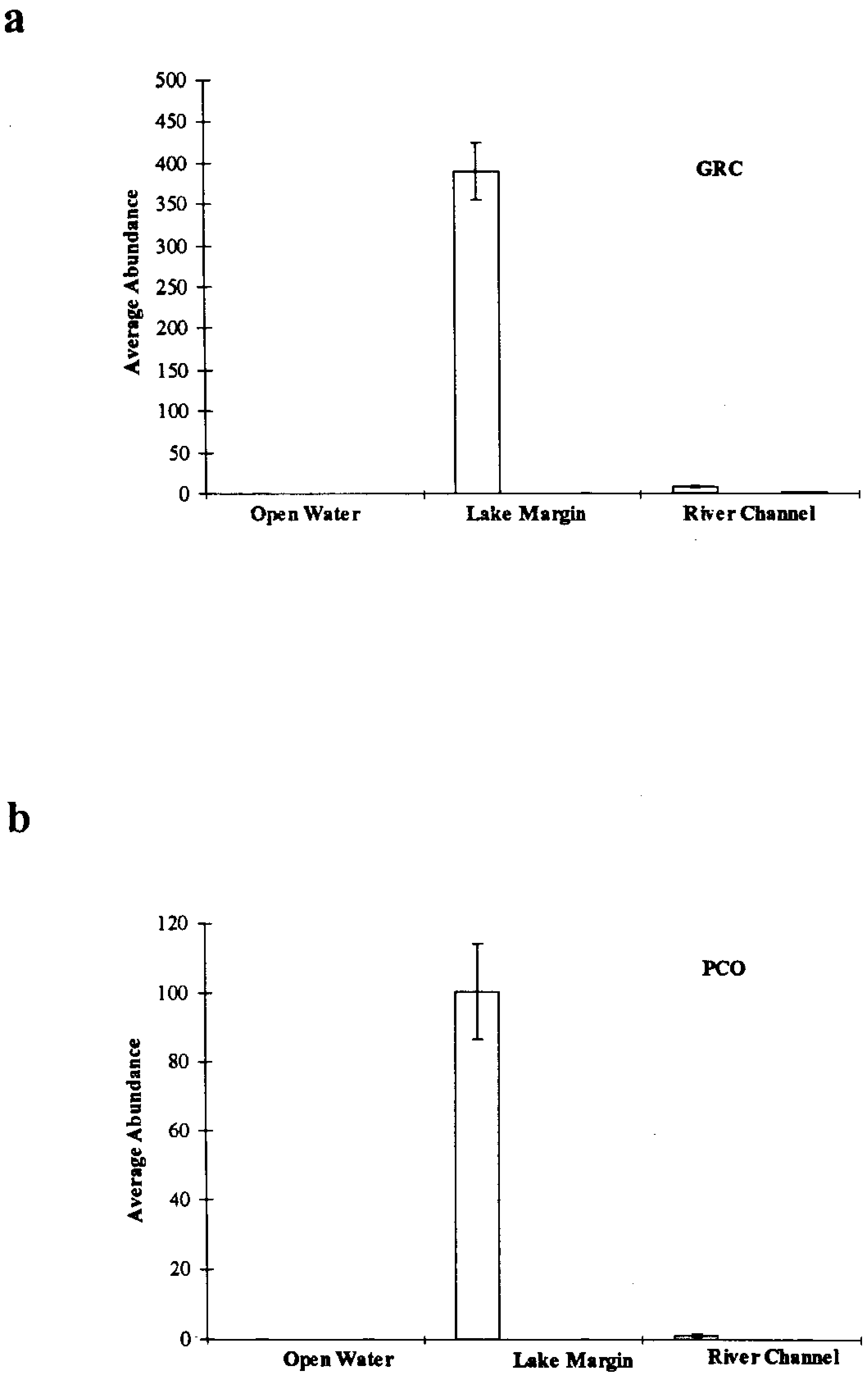


Figure 4.4. Abundance of Great and Pied Cormorants at Lake Menindee. Bars represent individual sites. (n = 4 observations per site pooled by time). Error bars indicate standard error.

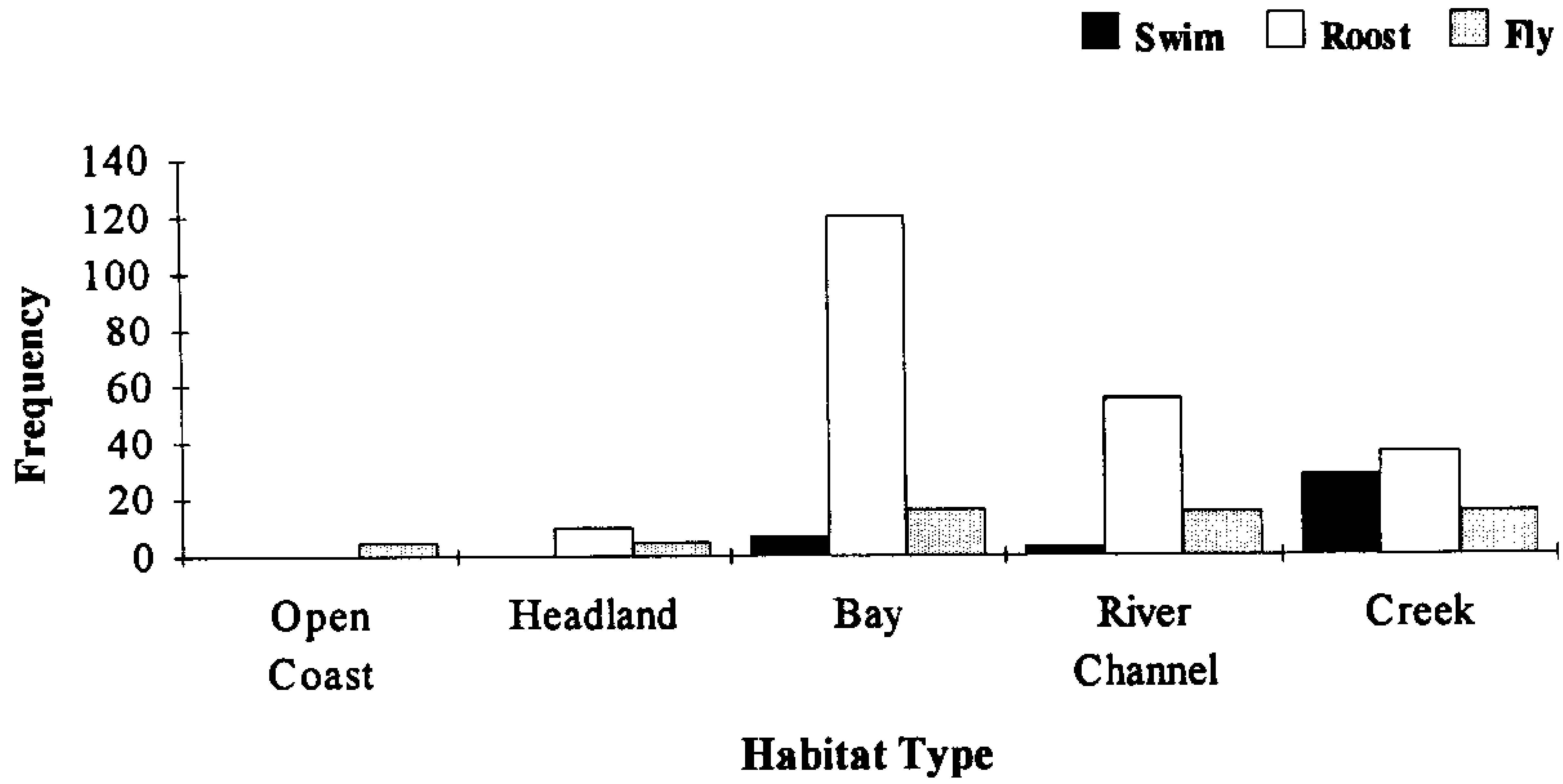


Figure 4.5. Frequency of behaviour in different coastal habitats.

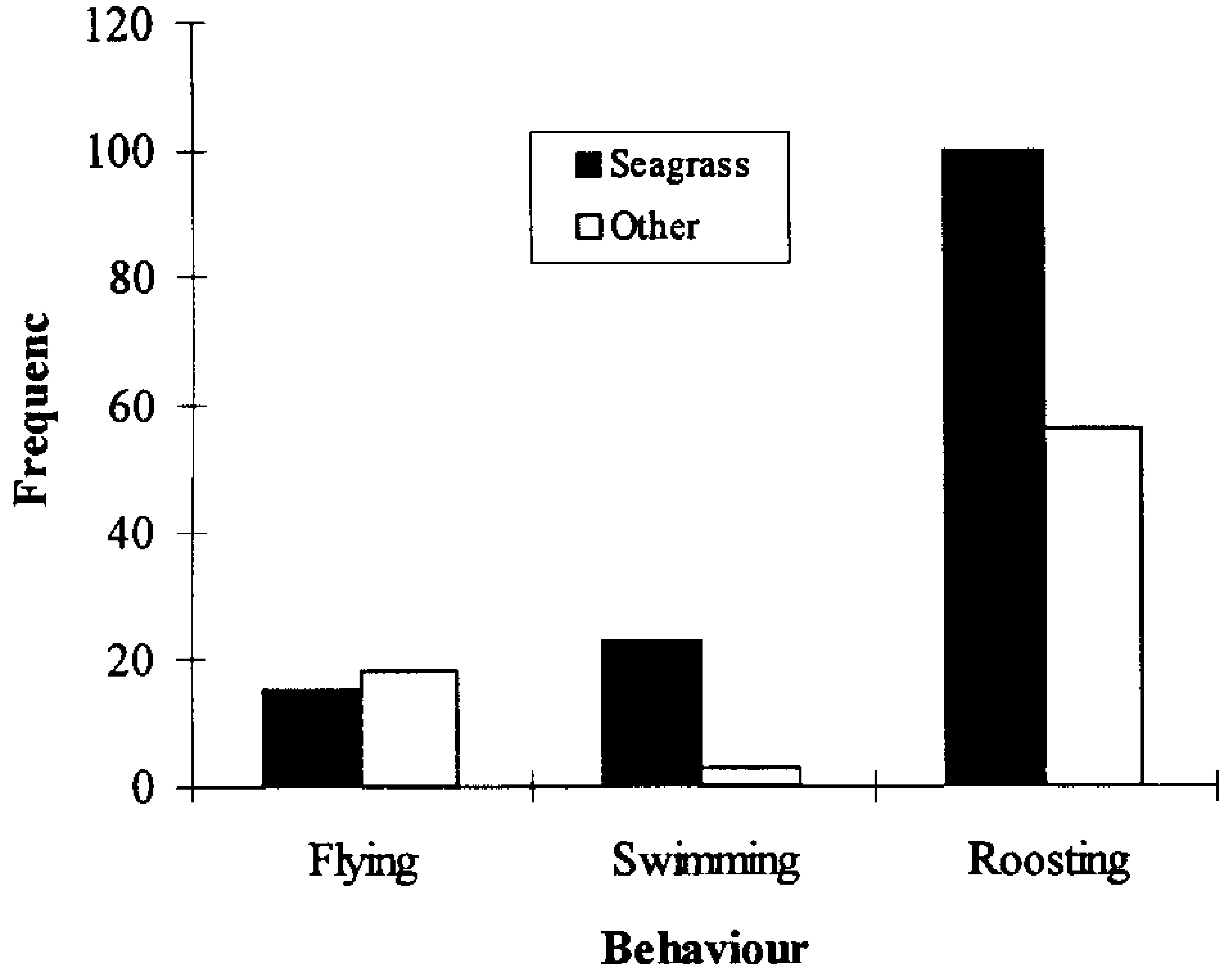


Figure 4.6. Frequency of behaviours in sites with and without seagrass.

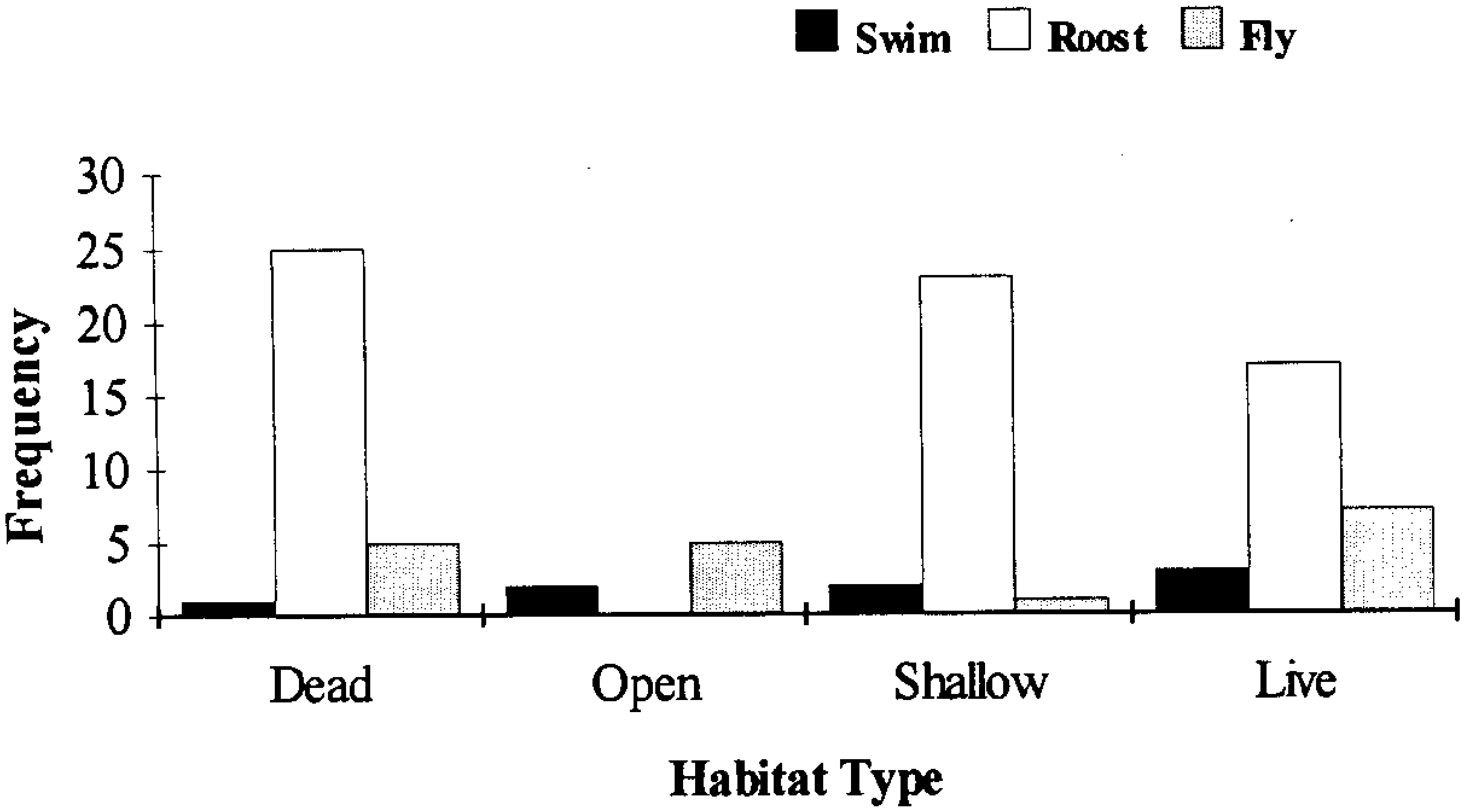


Figure 4.7. Frequencies of behaviour of Pied Cormorants in different habitat types at Lake Waitchie. See text for description of habitats.

Table 4.7. Chi-square tests of differential behaviour in different habitats. Habitat - behaviour combinations that were not observed for a given species were excluded from the analysis. Abbreviations: Creek (C); River (R); Bay (B); Headland (H); Open Ocean (O); Fly (*F*); Roost (*R*); Swim (*S*).

Species	Habitats	Behaviours	df	χ^2	P
GRC	C, R, B, H, O	*F, R*	9	21.84	0.01
PCO	R, B	*F, R, S*	5	20.59	0.001
LBC	C, R, B, H	*F, R, S*	11	97.92	0.001
LPC	C, R, B, H, O	*F, R, S*	14	10.88	n. s.

4.4. Discussion

4.4.1. Habitat selection by cormorants

Patterns of habitat selection demonstrated in this chapter follow clearly from foraging behaviour characterised in Chapter 3. On the coast, cormorants foraged and roosted around seagrass (Figure 4.6), and the relationship was stronger than any effect of time of day, tide (Table 4.4), broad-scale geography (Table 4.5) or the propensity to aggregate (Figure 4.2). By contrast, cormorants inland were highly aggregated (Figure 4.4) and not associated with any discernible habitat features (Table 4.5).

Many birds travelling between foraging locations cannot sample resource abundance directly and must select sites based on an appearance of food availability. For example, Black Swans *Cygnus atratus*, Grey Teal *Anas gracilis* and Australian Pelicans *Pelecanus conspicillatus* sometimes land on the galvanised roofs of buildings in the outback, which resemble bodies of water on moonlit nights (Davies 1984). Cormorants on the coast can easily detect seagrass meadows are easily detectable from the air (pers. obs.) and may play a role in initial habitat selection, in addition to dictating more refined choices of foraging location (Chapter 3). Although assemblages of fish are distributed patchily throughout seagrass meadows (Ferrell and Bell 1991), fish tend to be more abundant in seagrass than out of it (Pollard 1984), so meadows would provide a consistent, if imperfect, habitat cue.

Inland, the presence of water itself is likely to be the most important cue during dry periods, as large numbers of cormorants congregate even in unproductive wetlands when water is scarce (R. T. Kingsford pers. comm.). How waterbirds find water, especially at a distance, is unclear. It is possible that they possess some remote sensing system (Frith 1959), although they may also find water during the normal course of nomadic movement (Schodde 1982). During periods of flood, when choice of foraging location is far greater, aggregations such as those described here may help individuals make a selection, in addition to providing the population base for a breeding colony, should resources be sufficient for reproduction (e.g. Proserpine Dam, Queensland, R.T. Kingsford pers. comm.)

The distribution of foraging cormorants within an inland lake appears to be related to the location of patches of food discovered by chance. Birds may distribute themselves according to where they perceive resources to be (e.g. forest passerines, Holmes and Schultz 1988) and, being mobile, should have the ability to coincide closely with resource distribution. However, fish in turbid lakes are undoubtedly difficult to detect, so the distribution of cormorants may be more indicative of cormorants' perception, than actual resource distribution. Allelomimesis (in which the behaviour of an individual affects, and is affected by, the behaviour of the group in a positive feedback loop) may be the mechanism by which decision-making of individual cormorants is translated to collective patterns of distribution within and among inland lakes. If one cormorant is observed foraging successfully, more will join it. This will continue until the birds form a dense flock that moves as a unit across the lake in search of schools of fish (see Chapter 3). Allelomimetic behaviour has been demonstrated in social insects, fishes, birds and mammals, and in some cases produces distributions that miss high concentrations of resources, through the momentum of recent group activity (see review by Deneubourg and Goss 1989).

In this study, high variation in abundance at the level of replicates and sites, coupled with low variation at larger spatial scales (Table 4.6), may be evidence for allelomimesis. An important consequence of this is that if Great, Pied and Little Black Cormorants in inland wetlands act allelomimetically, then differences in the scale of aggregation among lakes (e.g. Lakes Menindee and Waitchie) may be a function of abundance, rather than differential responses to local conditions. In other words, small aggregations are apparent at the level of replicate, large aggregations at the level of site, but the process that produces them is likely to be the same.

Behaviours on the coast and inland were independent of habitat type. As with distribution, behaviour of cormorants on the coast clearly showed that they forage in areas where seagrass is abundant (Figure 4.6), irrespective of geographical features (Figure 4.5). Higher frequency of swimming near seagrass was as predicted, although the comparatively high rates of roosting observed were unexpected. Frequency of roosting may reflect time or energy budgets, the need to thermoregulate (Hennemann 1983), rest (see Hustler 1992) or perhaps digest food. Roosting is associated with foraging at least to the extent that it is generally interspersed with bouts of swimming (pers. obs.), so on the coast, a high incidence of roosting near seagrass strengthens the link between seagrass meadows and foraging cormorants.

4.4.3. Scale of habitat selection

In this study, habitat selection by cormorants was associated with physical variables at spatial scales ranging from 10^{-1} to 10^{3} km^{2}. There was a fundamental difference between the scale of habitat selection on the coast and inland. On the coast, a continuum of scales appeared in a hierarchy. Landscape features allowed cormorants to focus their search effort on estuaries as opposed to exposed areas. Seagrass meadows allowed them to refine their search to productive sites and individual seagrass beds indicated the most likely position of a food item (see also Chapter 3). Cormorants' use of the same seagrass beds for information at different scales is made possible by responses by fish to variation in seagrass characteristics at the scale of individual seagrass beds (Bell and Westoby 1986a) estuaries (Bell *et al.* 1988) and bays (Bell and Westoby 1986b).

By contrast, in the inland environment, the hierarchy of scales seemed to be discontinuous. Landscape-scale variables may indicate the location of potential concentrations of prey (ie. wetlands), but, high temporal variability in wetland productivity, coupled with mobile prey, introduce stochasticity into the system at smaller scales and cormorants are limited in their ability to assess the exact location of prey. In apparent contrast to the coastal environment, cormorants were more closely coupled to landscape patterns than to those at a foraging scale, which has also been shown for other species (e.g. Red-capped Plover *Charadrius ruficapillus*, Abensperg-Traun and Dickman 1989).

Irregularity in habitat quality has been theorised to favour the evolution of nomadism, especially for birds (Schodde 1982; Davies 1984), although other animals also demonstrate this pattern (e.g. mule deer *Odocoileus hemionus* in arid North America, Rautenstrauch and Krausman 1980). Resource patchiness has also been suggested to favour coloniality (Brown and Orians 1970) and it is common for many species of birds to congregate in the arid zone when conditions are favourable (e.g. Braithwaite *et al.* 1986; Kingsford and Porter 1993; Morton *et al.* 1993).

In this study, behaviour of individual cormorants combined to create patterns of habitat utilisation. Distribution of birds across a landscape scale can be influenced by local habitat utilisation (e.g. migrant songbirds, Sherry and Holmes 1996) as well as phenomena, such as climate, that originate at a broad scale (e.g. Double-crested cormorants *P. auritus* and Anhingas *Anhinga anhinga*, Henemann 1983). In the next chapter, I explore influences on distribution of cormorants across eastern Australia, in the context of local and broad-scale phenomena.

CHAPTER FIVE

LARGE-SCALE PATTERNS OF DISTRIBUTION IN EASTERN AUSTRALIA

5.1. Introduction

At a large-scale (ie. 10^2 -10^3 km^2), distributions of populations can often be related to movements of individuals among patches (e.g. Hanski 1994b; Sutherland 1996; see also Opdam *et al.* 1994). If animals choose habitats based on the density of productive patches (see Chapter 4), then resource dynamics should be evident in the distribution of populations over time (e.g. Brown and Orians 1970; Davies 1984; Yom-Tov 1989; Weins *et al.* 1993). For non-territorial species, limited resources and differential competitive ability may cause some individuals to disperse from an area and others to remain (Gauthreaux 1985). Dispersal is risky, because the chance of finding a suitable patch may depend on unreliable cues (e.g. Templeton and Giraldeau 1996), and foragers may expose themselves to predation risk (e.g. Kotler *et al.* 1992). Dispersal should therefore be undertaken only when the chance of survival or reproduction at a current patch is less than the chance of a patch of sufficient quality elsewhere (Weissburg 1986). An increase in environmental uncertainty should lead a greater proportion of the population to move (Real and Caraco 1986).

Relationships between resources and movements of many Australian waterbirds fit well into this model. Waterbirds may relocate to find water, food and sites for reproduction. In arid Australia, Grey Teals *Annas gracilis* forage in open water and grass swamp habitats (Briggs 1979) preferring temporary, saline wetlands (Norman 1983; Kingsford and Porter 1994). Because these wetlands dry out regularly, the distribution of Grey Teal populations changes frequently (e.g. Norman 1983; Kingsford and Porter 1993; see also review by Briggs 1992). Breeding occurs after flooding (Norman 1983; Briggs and Lawler 1991) as recently-filled wetlands become productive (see Maher 1984; Briggs and Maher 1985). During drought, Grey Teals move into refugia either on the coast (Norman 1983; Woodall 1985) or on permanent wetlands (Lawler and Briggs 1991). These refugia are generally of poorer quality, but temporally more consistent than temporary wetlands (Norman 1983). Asynchronous arrival at refugia may be due to differential reproductive success among individuals at breeding sites (Norman 1983), but this has not been tested.

Cormorants may also move inland from the coastal areas to breed during times of flooding (Purchase 1969; van Tets *et al.* 1976; Brooker *et al.* 1979; Draffan *et al.* 1983; Llewellyn 1983; Woodall 1985), although the mechanisms by which they detect rainfall are poorly understood (see Schodde 1982). For instance, in the Alligator Rivers region of the Northern Territory, Little Pied Cormorants are negatively correlated with water level and Little Black Cormorants occur sporadically (Morton *et al.* 1993b). In the Richmond Valley, New South Wales the reverse is true (Gosper *et al.* 1983). Moreover, cormorant populations may respond to water on both local scales (Great and Little Black Cormorants, Whyte 1981; Great, Pied and Little Black Cormorants, Llewellyn 1983), and regional scales (Little Black Cormorants, Gosper *et al.* 1983; Pied Cormorants, Woodall 1985; Great Cormorants, Morton *et al.* 1993b). Thus, a number of factors occurring at different scales are likely to influence cormorant distribution simultaneously. However, it is difficult to sample a large scale with the temporal frequency required to address every question. Similarly, intensive study of one or a few locations cannot distinguish changes in abundance from shifts in distribution (see Chapter 1). Comparison of local and regional information, coupled with site-specific data, can provide new insight into the movements of cormorants.

In this chapter, I relate data on abundance of cormorants to the dynamics of water within wetlands and at a landscape scale, using a combination of aerial survey data collected by the New South Wales National Parks and Wildlife Service and ground counts at several wetlands in New South Wales. The aerial survey data consisted of counts from two studies. The first data set comprised the first 13 years of an ongoing survey, collected on a yearly basis, extending across the eastern half of the continent, covering about 10% of the land surface area (about 1400 wetlands; see Braithwaite *et al.* 1986; Kingsford *et al.* 1997). The second data set came from an aerial survey covering 30 wetlands within the northwest region of New South Wales, collected every three months for four years (Kingsford *et al.* 1994). Ground counts were undertaken at two wetlands near the coast (Patonga Creek and Homebush Bay) and one inland (Lake Altibouka), representing finer grained temporal changes than were observable at a larger spatial scale.

Extending from information on behaviour and habitat selection (Chapters 3 and 4), I present a general model for dispersal of cormorants through eastern Australia. In this model, individuals or small groups of cormorants remain spread along the coast, or congregate on low-quality permanent refugia during drought. During wet periods, populations move away from refugia into temporary freshwater (see Kingsford and Porter 1994) or coastal wetlands. When cormorants enter a flooded region, they sample a number of wetlands opportunistically, comparing quality and settling on the most productive one (see Charnov 1976).

This model generates predictions at a number of scales. Over eastern Australia, cormorant populations on the coast were predicted to be high in dry years and low in wet years, fluctuating in opposition to those inland. By extension, fluctuation of the populations of all species are predicted to be highly correlated at a large scale because the presence of water inland would attract all species equally, despite differences in the use of habitats (Chapter 4) and microhabitats (Chapter 3; see also Trayler *et al.* 1989).

Within arid northwest New South Wales, cormorant populations inland were predicted to coalesce during dry periods and spread during flooding. Those species that flock inland (Great, Pied and Little Black Cormorants) were predicted to be more highly clumped during flooding than Little Pied Cormorants, which forage singly or in smaller groups (see Chapter 3). As a corollary, cormorant species that flock should use a smaller percentage of the total number of wetlands because comparatively few water bodies can accommodate large numbers of birds. Abundances of cormorants were predicted to be positively correlated with wetland area, because a larger water body is more likely to contain sufficient resources to accommodate a large number of individuals. Cormorants were also predicted to be more strongly correlated to water level at fluctuating wetlands than at permanent ones because of the increased productivity provided by drying and refilling (see Maher 1984) and wetland richness can enhance fish production (Welcomme 1979)..

This effect should also be more pronounced in arid conditions (inland and in dry years) because the pool of choices (per unit area) is smaller. If cormorants use a small proportion of the total number of wetlands, the question arises as to whether the set of wetlands used remains the same from year to year. Because many inland wetlands dry out regularly and most coastal wetlands do not, an individual wetland inland is predicted be of less long-term importance to cormorants than one on the coast.

5.2. Materials and Methods

5.2.1. Sampling

Aerial surveys: eastern Australia

Data for Great, Pied, Little Black and Little Pied Cormorants were from an ongoing aerial survey program, conducted by the New South Wales National Parks and Wildlife Service, with other state conservation agencies, to monitor populations of waterbirds in eastern Australia. Surveys were flown in October each year, lasting about four weeks

(R.T. Kingsford pers. comm.). Data included in this thesis were from surveys flown in 1983 through 1995.

Aerial surveys were flown on survey bands that covered the eastern portion of the Australian continent. Ten survey bands, each 30km wide, were flown at regular intervals of 2° of latitude (~ 200 km apart), from 38°30'S to 20°30'S. This represented approximately 10% of the land surface area of eastern Australia (Table 5.1; Figure. 5.1). Survey bands varied in length; the western limit of each band was 136°00' E, except bands 1 and 2, where it was the coast; the eastern boundary was the east coast. Inland regions (ie. those west of the Great Dividing Range) comprised about 80% of the total survey (Figure 5.1). An attempt was made to survey all wetlands larger than 1 ha within each band, as well as those smaller than 1ha on an *ad hoc* basis.

Counting methods depended on the configuration of a given wetland. Total numbers were counted on wetlands of 50 ha or less and on large lakes, braided rivers and floodplains, a system of transects was used, following Caughley *et al.* (1977). See Braithwaite *et al.* (1986) for further details of the sampling design. No data were available for Pied Cormorants in 1983.

Aerial surveys: northwest New South Wales

Data were taken from a survey for waterbirds (Kingsford *et al.* 1994), in which researchers flew surveys for waterbirds on 30 lakes. These surveys began in March 1987 and were repeated every three months until December 1990, for a total of 16 replicate counts over the four year period. The survey included parts of the three most westerly river systems in the state: the Warrego River, the Paroo River and the Bulloo River in New South Wales (Figure 5.2). Aerial surveys were flown in a Cessna 206 aircraft, at a height of about 30 m at a speed of about 170 km hr^{-1} over the water approximately 150 m from the edge of the lake (where waterbirds concentrate; Kingsford *et al.* 1994).

When the entire lake could not be counted because of practical problems of manoeuvrability of the aircraft, the percentage of the lake edge counted was estimated at the time of the aerial survey and this figure was used to extrapolate counts for the whole perimeter. Counts were usually ≥ 50% of the lake. See Kingsford *et al.* (1994) for further details of sampling methods.

Over the course of several years, flooding regimes in this area typically include the full range of rainfall levels, and storm events can be severe (Mabbut 1977). Small lakes seldom have water for more than a year, but larger ones (e.g. Lake Eyre) may last for three years (Mabbut 1977). Heavy rainfall may occur at any time of year, providing runoff to fill downstream wetlands. Median annual rainfall decreases from about 300 mm in the east to about 140 mm in the west (Goodrick 1984). Most of the area is reasonably flat, varying from 72m to 200 m altitude, which creates a spatially complex runon/runoff pattern of drainage (Stafford Smith and Morton 1990).

In addition to the lakes surveyed, the study region contains many floodplains and river channels, which filled during flood, and many thousands of small wetlands fringed with canegrass *Eragrostis australasica* and black box *Eucalyptus largiflorens* (Kingsford *et al.* 1994). Although these were not surveyed, their presence should not substantially influence patterns of cormorant abundance on the lakes in the study, because analyses of these data are based on a regional perspective.

Ground counts: Patonga Creek

Temporal variability between the two environments was investigated at short (weeks) to long (years) time scales by comparing variability of seasonal and yearly averages at two coastal locations (Patonga Creek, Figure 2.8 and Homebush Bay, Figure 2.7) and one location inland (Lake Altibouka, Figure 2.9).

At Patonga Creek, 57 surveys for cormorants were made on the lower 25% (about 1.5 km) of the channel, from a 150 metre length of the eastern shore. Counts were made between January 1993 and January 1996. Abundance of each species was recorded. Each survey took about 25 minutes to complete, travelling northward on foot. It was not possible to see the entirety of the shoreline during the survey. Therefore, cormorants flying northward were not counted, because it was not known if they would subsequently land within the survey area and be recounted.

Ground counts: Homebush Bay

Forty-seven surveys for cormorants were conducted at Homebush Bay between February 1992 and June 1996. Surveys collected during this study were supplemented by others gathered by experienced volunteers at the park at the same time. Surveys included the ornamental pond in the associated Bicentennial Park (at which there was a nesting colony; Dorfman and Read 1996), the tidal channel and the head of Homebush Bay (Figure 2.7). The survey was completed from an observation tower and all other observations were made from the ground.

Each survey took about one hour, but most of this time comprised travelling between observation spots. Differences in geography between Homebush Bay and Patonga Creek precluded standardising by area, so the time spent in observation was kept to 25 minutes to standardise sampling effort.

Ground counts: Lake Altibouka

Data from Lake Altibouka were collected under the aegis of a survey program for waterbirds conducted by the New South Wales National Parks and Wildlife Service. Between three and five observers counted birds at any one time. Surveys were conducted using a 50x spotting scope and birds were counted with the aid of a mechanical counter. Because counts were made from the ground, the lake was divided into three sections and daily counts from each section were summed. An implicit assumption was that movement of birds from one section of the lake would be reasonably low within the time required to conduct the counts. This was possible because the lake was reasonably small (< 2 km; Chapter 2). To reduce the chance of double counting, cormorants that moved during observation were discounted.

Surveys were made on three consecutive days, every three months (= 4 sets per year in March, June, September and December), from September 1990 through September 1996. However, because Lake Altibouka was dry at the beginning of the survey, only data from March 1992 were analysed, for a total of 57 counts. It was not possible to standardise surveys at Lake Altibouka with those at the coastal sites.

Inland rainfall

Rainfall data were taken from the Australian Bureau of Meteorology's *Monthly Rainfall Review* from the end of December 1991 through October 1996. Data from five reporting districts were included: Far Southwest, Far Northwest, Lower Darling, Upper Darling and Southwest Plains (Districts 45 through 49; Figure 5.3). Districts were chosen to represent a sampling area in which rainfall was most likely to affect dispersing cormorants. The southern edge of the study area was the Murray River, used by Gosper *et al.* (1983) to predict abundances of waterbirds in the Richmond Valley, New South Wales. The area also included the region around the Warrego River, New South Wales and Queensland, which was used by Woodall (1985) to predict fluctuation in numbers of waterbirds near Brisbane, Queensland. The sampling area included Lake Altibouka, in addition to the upper third of the Murray-Darling Basin.

5.2.2. Analyses

Methods of analysis are presented in a hierarchy from largest to smallest spatial scale, irrespective of the scale at which the data were collected.

Eastern Australia

To test differences in patterns of abundance between coastal and inland, each survey band was divided into two, representing areas east or west of the Great Dividing Range (GDR), based on the mid-point of the GDR (Table 5.1). Inland regions included some mountainous regions west of the centre of the GDR. Survey Bands 1, 2 and 10 were excluded from statistical analyses, although they are described. This is because, on these survey bands, the distance from the western boundary to the east coast was greater than the distance to the coast in other directions (Figure 5.1). Some birds on Bands 3 and 4 could have travelled westward to Spencer Gulf and Gulf St. Vincent.

Mean wetland area among years was 329,000 ha for all bands. In analyses that distinguished between wet and dry periods, dry years were those in which the total wetland area for the survey (estimated during sampling, see Braithwaite *et al.* 1985) was less than 0.5 SD below the mean (243,000 ha). Years in which the total wetland area was greater than 0.5 SD above the mean (415,000 ha) were considered wet. Years in which the water level fell between these two figures were considered intermediate. The years 1983, 1984, 1989 and 1990 were wet, 1986, 1988, 1993 and 1995 were intermediate and 1985, 1987, 1991, 1992 and 1994 were dry (Figure 5.4). Intermediate years were not used in analyses of abundance versus rainfall, to maximise chances of detecting rainfall effect.

Differences in yearly abundance between coastal and inland areas of eastern Australia, were tested with a Spearman rank correlation for each species. Spearman correlation matrices were used to test co-occurrence of species and the relationship to water level (ha of water per survey band) within environment (inland and coast). Ranked tests were to compare species because population sizes among species differed considerably, making relative proportions a better representation than abundance.

Northwest New South Wales

An indication of clumping within northwest New South Wales was obtained by using the northwest aerial survey data to calculate the coefficient of variation (CV) for the abundance of each species over all wetlands filled in each time period. The relationship between rainfall (as indicated by monthly rainfall for reporting districts 46 and 47, Figure 5.3) and CV for cormorants was tested for each species using a Pearson correlation (n = 16 time periods). Because cormorants may have taken some time to change their distribution in response to rainfall events, rainfall was calculated for both the time period of observations and a one month period, beginning two months before each survey (e.g. August rainfall was calculated for a November count).

Individual wetlands

The dispersion of cormorants among wetlands was determined for each species using a cumulative frequency curve of abundance versus number of observations. Differences among species were investigated by calculating the number of observations containing 90% of the individuals of a species. Differences between 90th percentile values were tested with separate Chi-square contingency tables for wet versus dry years and inland versus the coast for each species. Expected values were weighted by the number of observations in each category and Yates corrections were used in all cases. Because of the dynamic nature of wetland filling and drying (eg Briggs and Maher 1985) and the high degree of nomadism exhibited by cormorants (see Marchant and Higgins 1990), it was assumed that yearly counts at a given wetland were independent.

A subset of wetlands was constructed comprising wetlands that had ranked in the top seven, in terms of abundance, in at least one year (1983 - 1995) within the survey. These were termed "active" wetlands. Use of the seventh wetland as a cut-off in ranking was arbitrary, but was set, based on preliminary analysis, with the intention of including most of the large aggregations in a year while excluding most of the singletons. A separate subset was constructed for each species. Non-parametric Kolmogorov-Smirnov statistics were used to test differences in frequency distributions of active wetlands among species and on the coast versus inland.

The relationship of cormorant abundance to the area of wetlands was tested with a Pearson correlation for each species in 50 wetlands chosen randomly from the survey. Tests included only wetlands that were 100% full (estimated at the time of counting; see Braithwaite *et al.* 1986), to avoid potential confounding with the dynamics of filling and drying.

The relationship of cormorant abundance to variability in wetland fill was examined using data on abundance of cormorants over 13 years at Lake Menindee, Lake Illawarra, Pejar Dam, The Broadwater Lake and Glenprairie Floodplain (Table 5.3). These wetlands represented a range of variability in regimes of filling. Changes in cormorant abundances were related to variability in wetland area with a Pearson correlation for each species in each wetland.

Because logistic constraints precluded intensive sampling at more than three locations, low replication within environments made quantitative tests among sites inappropriate. In addition, the opportunistic nature of sampling did not permit treatment of the data with a time series analysis such as temporal autocorrelation. Comparisons of temporal patterns between environments were therefore made on a visual basis.

5.3. Results

5.3.1. Eastern Australia

Cormorant distribution and density (individuals per km of survey band) varied considerably, among years, survey bands and species (Figures 5.5 a-d). Great Cormorants appeared to shift their distribution from the southern survey bands in the early 1980s northward in the 1990s and density was punctuated by periodic disproportionate spikes (Figure 5.5) and fewer individuals of all species were observed between 1988 and 1990, both on the coast and inland (Figures 5.6 a and b, respectively). The distribution of Pied Cormorants overlapped considerably with that of Great Cormorants, although densities were lower (Figure 5.5). Pied Cormorants also showed a subtle shift to the north through time, however spikes in density were not as high as for Great Cormorants, suggesting lower overall abundance and making distribution patterns more difficult to interpret (Figure 5.5). Little Black Cormorants had the lowest overall density and populations focused around central survey bands (Figure 5.5). Shifts in distribution for Great and Little Black Cormorants corresponded with the completion of Proserpine Dam, Survey Band 10, in 1991 (Figure 5.7; R. T. Kingsford pers. comm.). Little Pied Cormorants were generally widely spread throughout the survey, however, this species formed a large aggregation (556 individuals) in 1994 at Myall Lake, Band 4. Little Pied Cormorants were consistently most numerous on Survey Band 4 and, after 1990, on Survey Band 5 (Figure 5.5). Populations of all species showed a decrease in density between 1987 and 1989.

Yearly abundances of cormorants were never correlated with those of the same species in a different environment (Table 5.5a) and rarely correlated with water or other species within an environment (Table 5.5b). However, the few significant correlations that occurred were consistent with prediction. Abundances of Great Cormorants on the coast were significantly negatively correlated to changes in water level and, inland, abundances of Great Cormorants were significantly positively correlated with those of Pied Cormorants and Little Black Cormorants (Table 5.5b; Figures 5.8a and b).

5.3.2. Northwest New South Wales

Rainfall at each observation period differed markedly from that of the observation from two months earlier. The two sequences appeared to be fluctuating in opposition (Figure 5.9), although the negative correlation was not significant (Table 5.6a). No seasonal pattern of rainfall was evident, despite intermittent fluctuations (Figure 5.9). Three-monthly patterns appeared almost as variable as annual patterns (Figure 5.10)

Coefficients of variation (CV) differed substantially among species (Table 5.6b). Great and Little Black Cormorants were highly clumped, Pied and Little Pied Cormorants were more spread, but considerable variation existed within this pattern. Correlations between current or lagged rainfall and CV were not significant for any species (Tables 5.6a). The coefficients of variation of some species were highly correlated over time (Table 5.6a), however, all relationships were driven by a single count (Lake Altibouka, March 1988; Figure 5.11) and abundances of all species were very low at other times. It was therefore difficult, using this data set, to ascertain the strength of the relationship among species.

5.3.2. Patterns at individual wetlands

In general, cormorants occupied a small proportion of the wetlands that existed (e.g. Figure 5.12), however, patterns among species differed with respect to environment and wet versus dry years (Table 5.7). Significant differences existed in the number of wetlands used by 90% of the Great, Pied and Little Pied Cormorants observed in this study. The greatest differences appeared between wet and dry years for Great

Cormorants, whereas no obvious pattern existed for Pied and Little Pied Cormorants (Table 5.7)

Most wetlands that ranked in the top seven in terms of abundance for any year did so only once during the study, and this was true on the coast as well as inland (Figures 5.13 a and b, respectively). Kolmogorov-Smirnov tests of frequency in the top ranking seven wetlands were not significant between environments (Table 5.8a) or among species within environment (Tables 5.8 a and b). With the exception of Lake Illawarra, the few wetlands that ranked in the top seven for nine years or more for any species (Table 5.8d) were dams in which water level was regulated and which were likely to contain permanent populations of fish (R. T. Kingsford pers. comm.). Populations at these lakes fluctuated considerably through time (Figure 5.14), demonstrating sporadic periods of high abundance, interspersed with periods of low abundance, in a similar way to other water bodies such as Proserpine Dam and Lake Altibouka (Figures 5.7 and 5.11, respectively).

Size of wetland and abundance of cormorants (n = 50 observations) was significantly positively correlated for Pied ($r^2 = 0.321$, $P < 0.05$) and Little Pied Cormorants ($r^2 = 0.699$, $P < 0.001$), although the former appears driven by one or two points (Figure 5.15). This relationship was not significant for Great or Little Black Cormorants ($r^2 = 0.068$ and 0.086, respectively).

Patterns of fill of individual wetlands varied considerably, from 100% filled through time (The Broadwater Lake), to mostly dry, punctuated by periods of high fill (Glenprairie Floodplain; Figure 5.16). There was a general positive trend between the amount of variability in percent fill of a wetland and frequency of correlations in abundance among species and with water area (Figure 5.16; Table 5.9). No significant correlations in abundance existed with area of water or among cormorants at the tidal wetlands (The Broadwater Lake and Lake Illawarra, Tables 5.9a and b; Figures 5.17 a and b, respectively), this was because there was great variation in abundance of cormorants, despite no variation in lake area (Figures 5.16 c-e).

At Pejar Dam, and Lake Menindee, positive relationships occurred between single pairs of species (Tables 5.9c and d, respectively), driven by intermittent spikes of high abundance in both cases (Figures 5.17c and d, respectively). At Glenprairie Floodplain, all species were significantly positively correlated with water area and with one another (Table 5.9e), although the strength of the relationship was still supported by a single spike in abundance (Figure 5.17e), corresponding to a period of high water in 1984 (Figure 5.16).

As with counts taken with other frequencies, abundances of all species through time from intermittent counts at Patonga Creek, Homebush Bay and Lake Altibouka were highly variable (Figures 5.18 a-c). Patterns were typified by intermittent spikes in abundance and every species was absent from each site at least once during observations. No obvious differences occurred among sites, except that maxima were generally highest at Lake Altibouka and least at Patonga Creek. Rank abundance among species was dependent on location, but Little Black Cormorants were most numerous in all cases. Both they and Great Cormorants were more numerous than Pied and Little Pied Cormorants in all locations. No obvious association existed between inland rainfall and abundance of any species at any location (Figures 5.18 a-c).

Table 5.1. Survey bands used in this study, their latitude, the longitude at which the Great Dividing Range (GDR) crosses the band, and the closest urban area where the band reaches the coast in New South Wales (NSW) or Queensland (QLD).

Survey Band	Latitude	GDR Longitude	Closest Coastal Town
3	34°30'	148°00'	Woolongong NSW
4	32°30'	148°00'	Newcastle NSW
5	30°30'	150°00'	Coff's Harbour NSW
6	28°30'	151°00'	Byron Bay NSW
7	26°30'	153°00'	Nambour QLD
8	24°30'	144°30'	Bundaberg QLD
9	22°30'	145°30'	Port Clinton QLD

Band	**GDR Cutoff**	**Westernmost 'Coastal' Wetland**
3	148°00'	Warragamba Reserve
4	148°00'	Cudgegong River
5	150°00'	Namoir Lagoon
6	151°00'	Milkami Lagoon
7	153°00'	Noosaville Lagoon
8	144°30'	Thornleigh Creek
9	145°30'	Lake Dunn

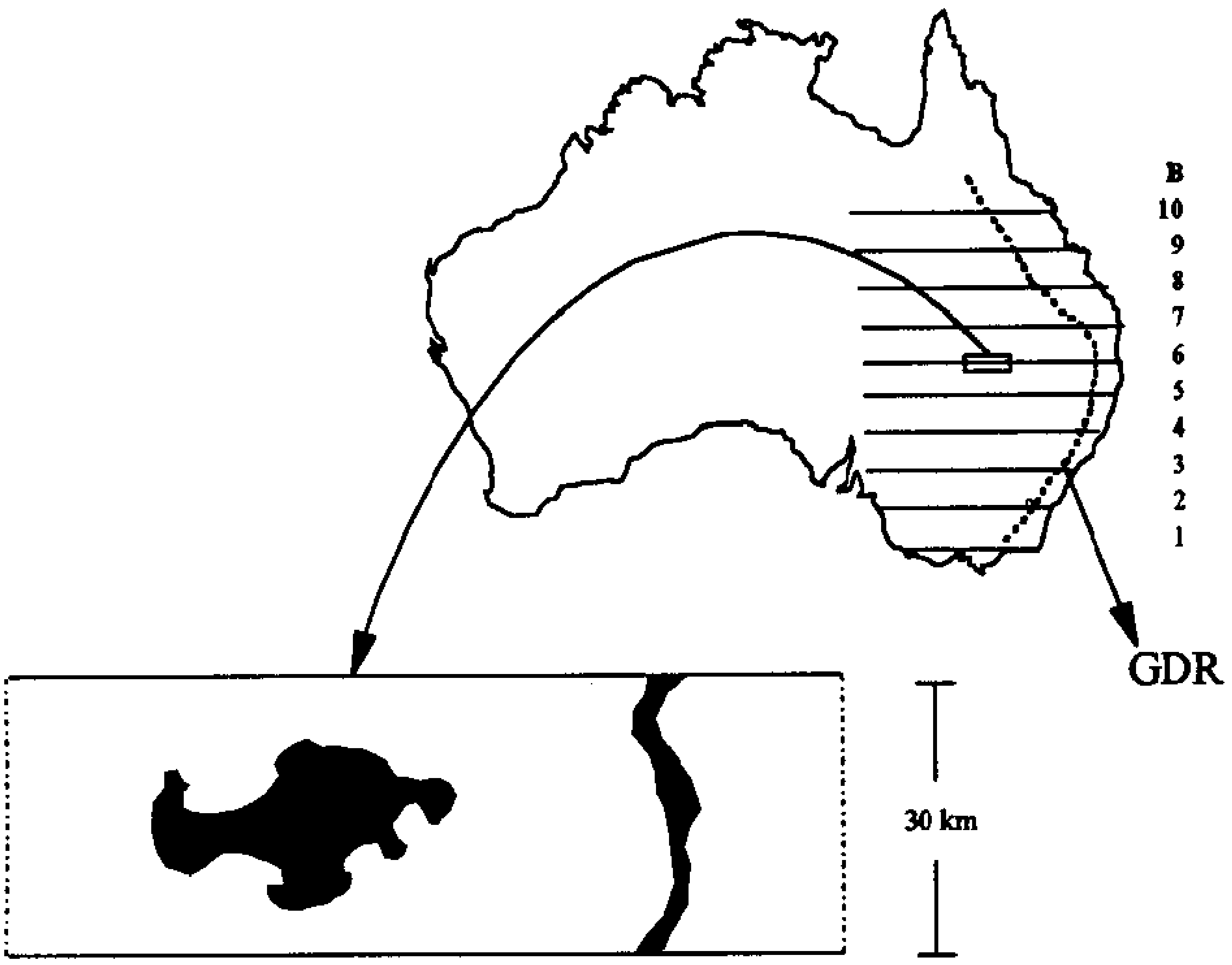


Figure 5.1. Aerial surveys for waterbirds, conducted by the New South Wales National Parks and Wildlife Service, 1983 - 1995. Surveys were conducted on 10 aerial survey bands (B), which were 30 km wide. The dotted line indicates the mid point of the Great Dividing Range (GDR). After Kingsford *et al.* 1997.

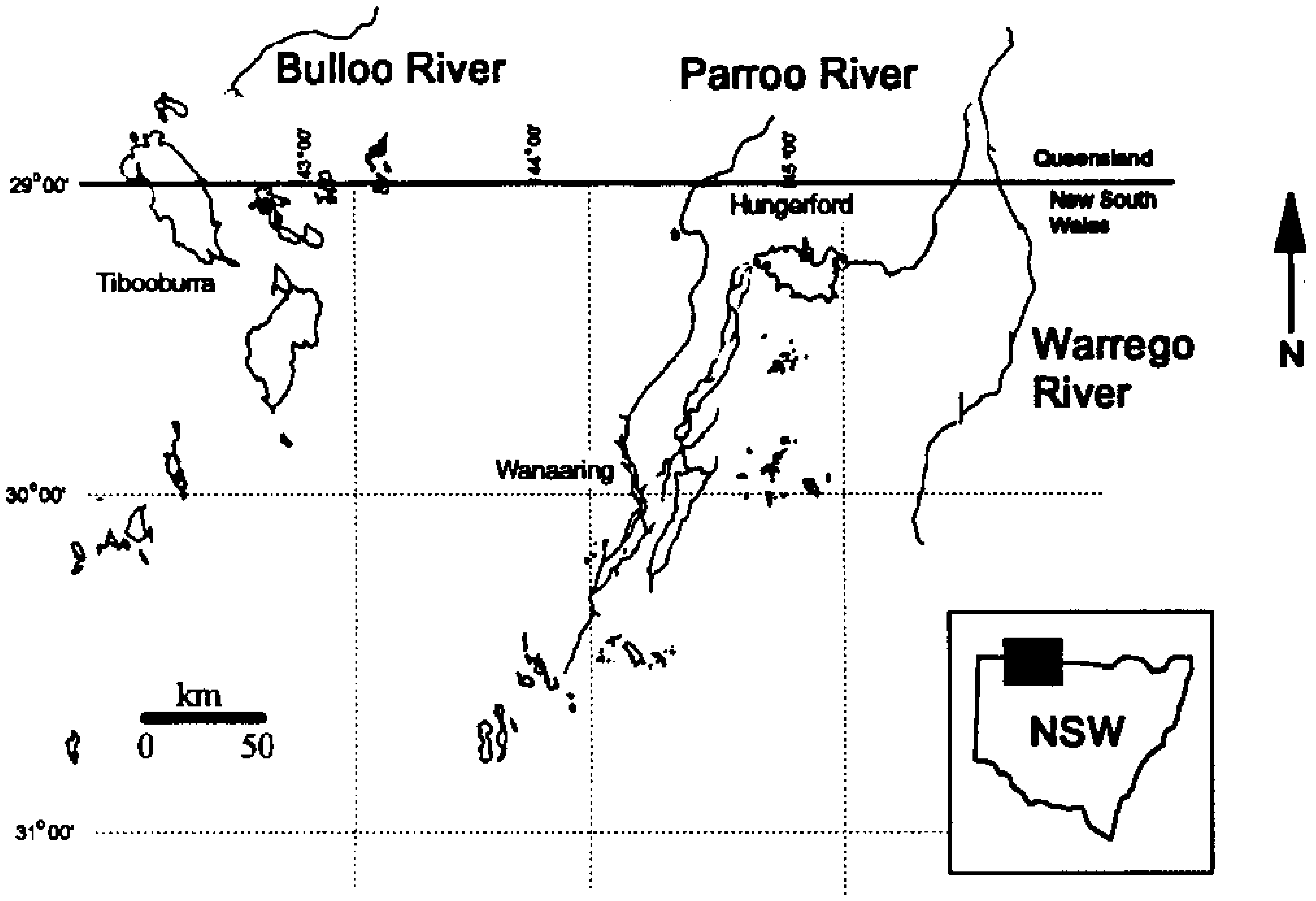


Figure 5.2. The north-west region of New South Wales, showing main watercourses (after Kingsford *et al.* 1994).

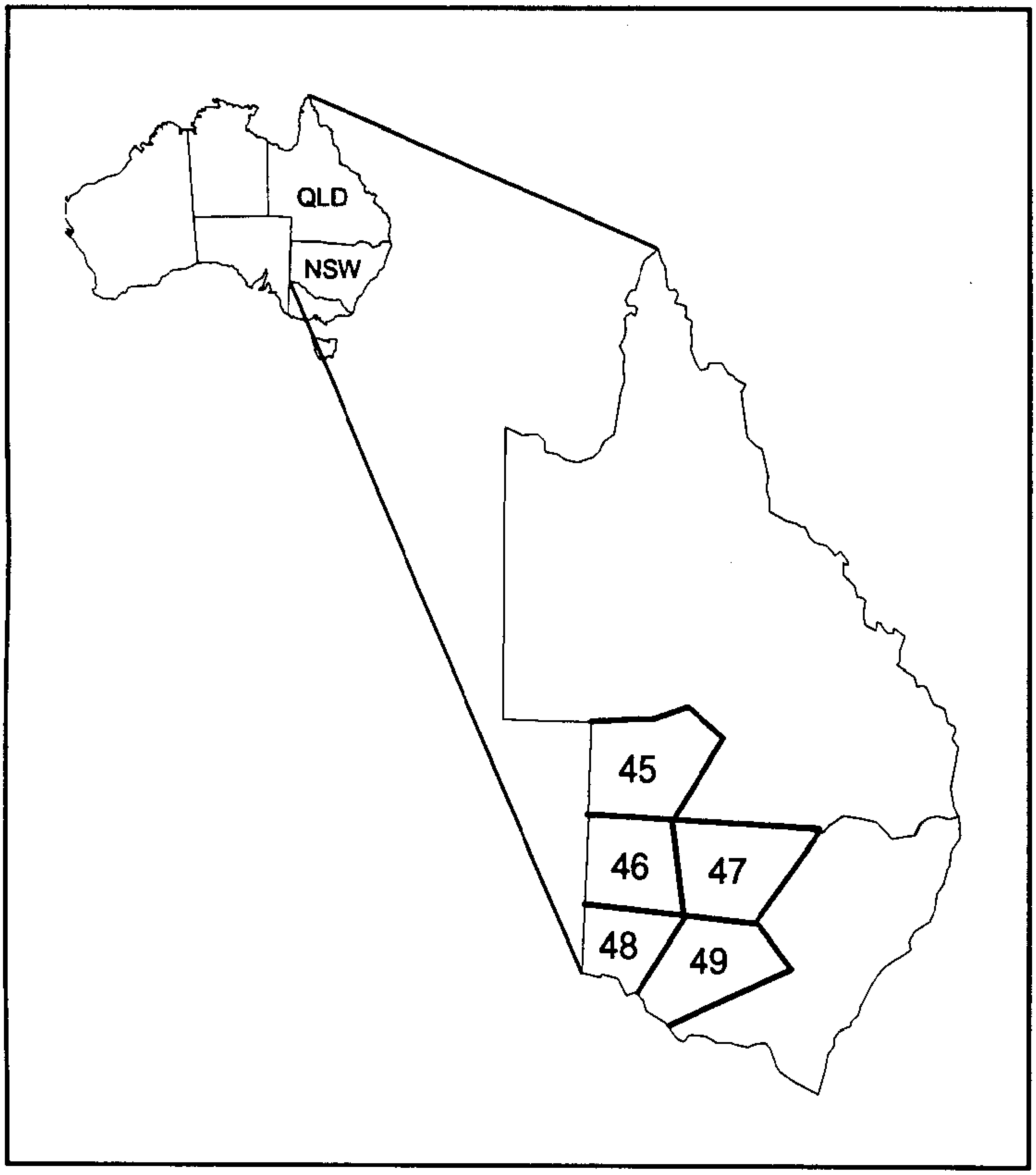


Figure 5.3. Rainfall Reporting Districts. Numbers correspond to those used by the Monthly Rainfall Review, published by the Australian Bureau of Meteorology.

Table 5.3. Wetlands used for detailed analysis of abundance through time.

Wetland	Lat (°S)	Long (°E)	Area (ha)	Description
Pejar Dam	34°37'	149°42'	10,000	Within pastoral land, bordered by aquatic vegetation & few trees. Used as a water supply for local communities. Human activity low.
The Broadwater Lake	32°55'	152°28'	22,770	An estuarine lake that lies within Myall Lakes National Park. Human activity seasonal; mostly recreational fishing.
Glenprairie Floodplain	22°58'	149°54'	33.400	Near the coast, but in a rain shadow. Water level fluctuates greatly. On pastoral land. Human activity, low.
Lake Illawarra	34°52'	150°83'	34,750	Tidal; narrow entrance limits flushing. Some commercial development on shore. Human activity high; includes water sports; recreational & commercial fishing.
Lake Menindee	32°37'	142°32'	47,100	Water level kept artificially high; acts as storage for Broken Hill and irrigation. Human activity sporadic; mostly recreational fishing. See Chapter 2.

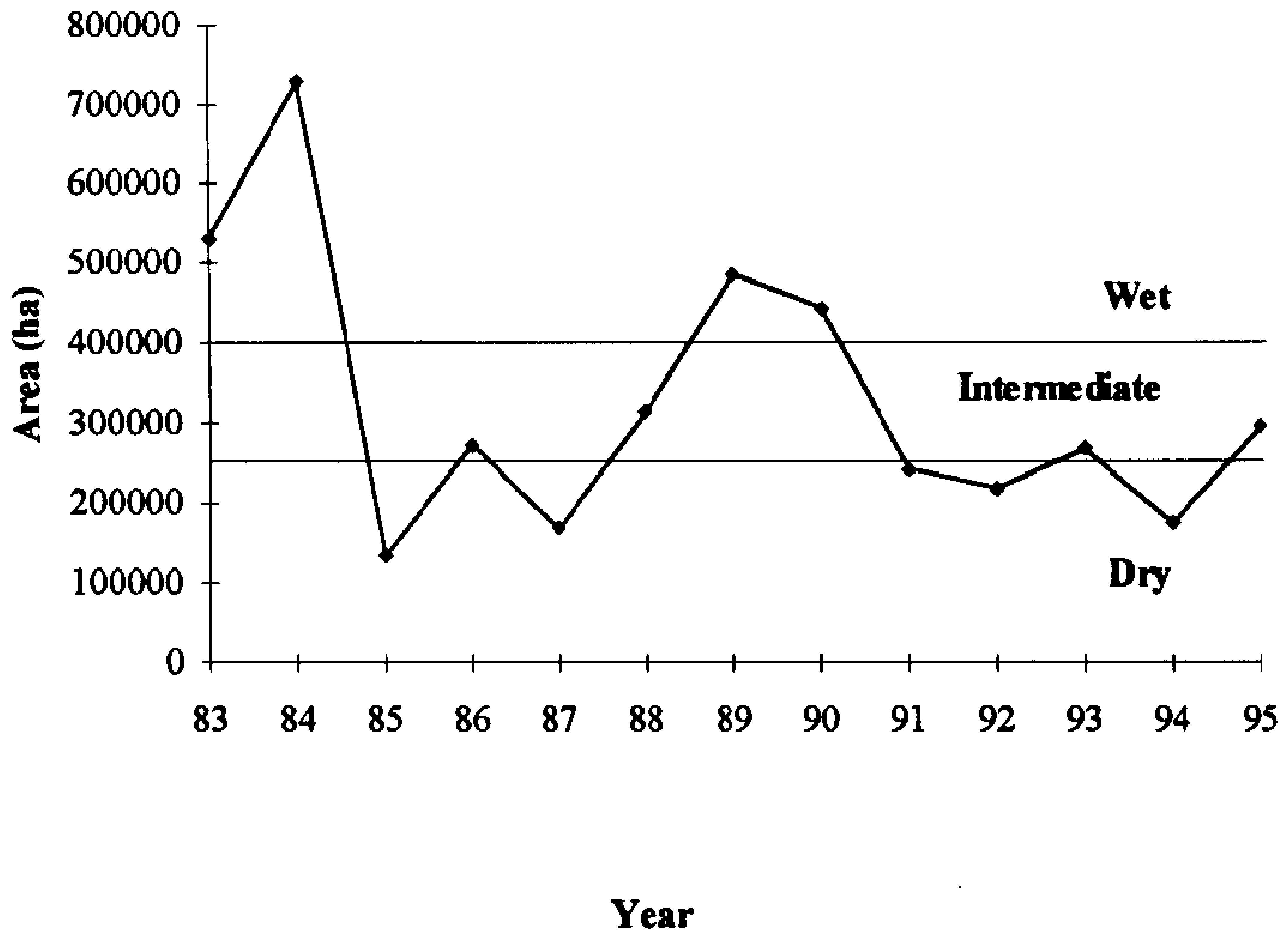


Figure 5.4. Area of water on the survey (ha). The years 1983, 1984 1989 and 1990 were considered wet, 1986, 1988, 1993 and 1995 were considered intermediate and 1985, 1987, 1991 and 1992 were considered dry.

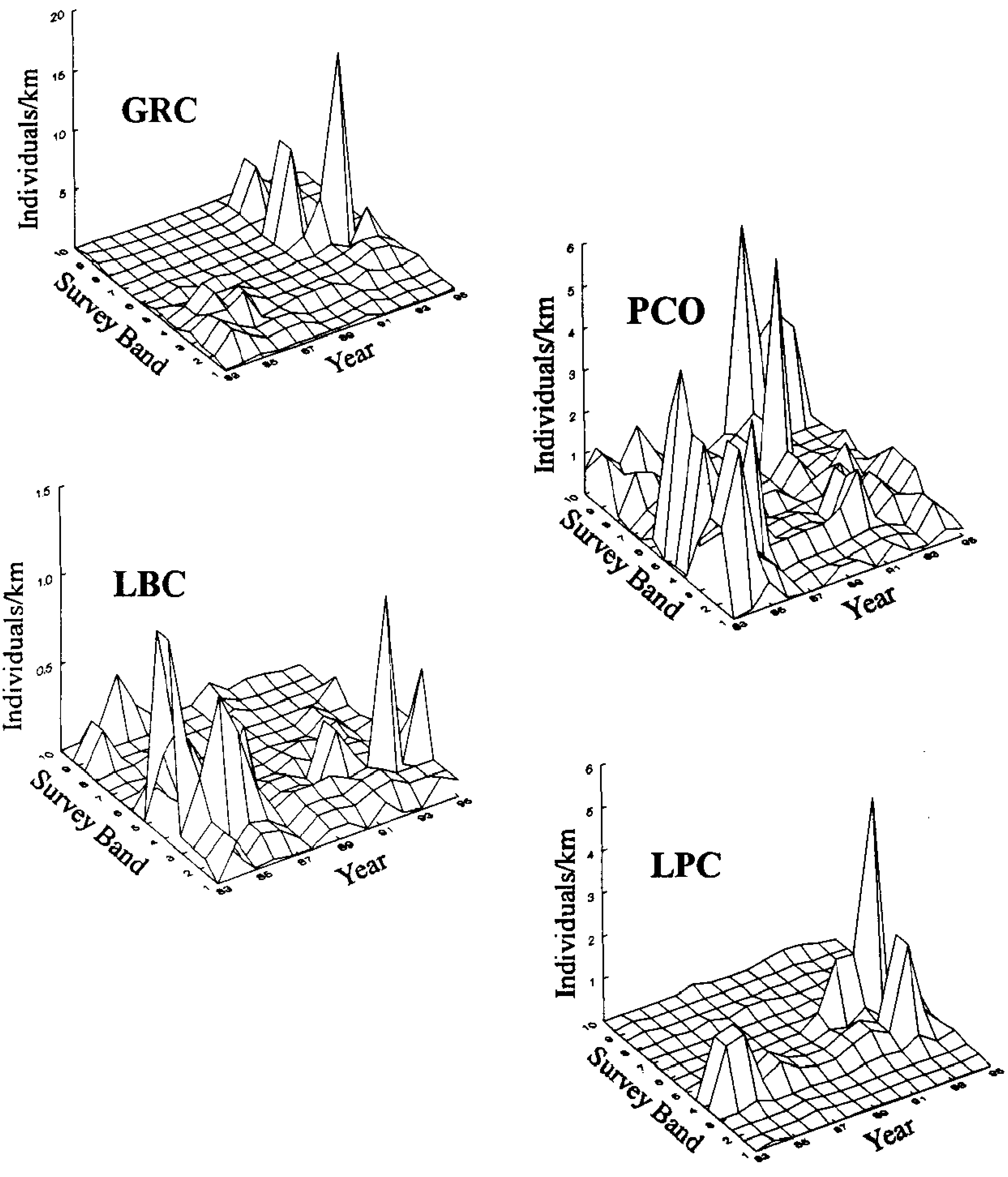


Figure 5.5. Density (individuals per km of survey band) of cormorants on 10 survey bands between 1983 and 1995. Note differences in z axes.

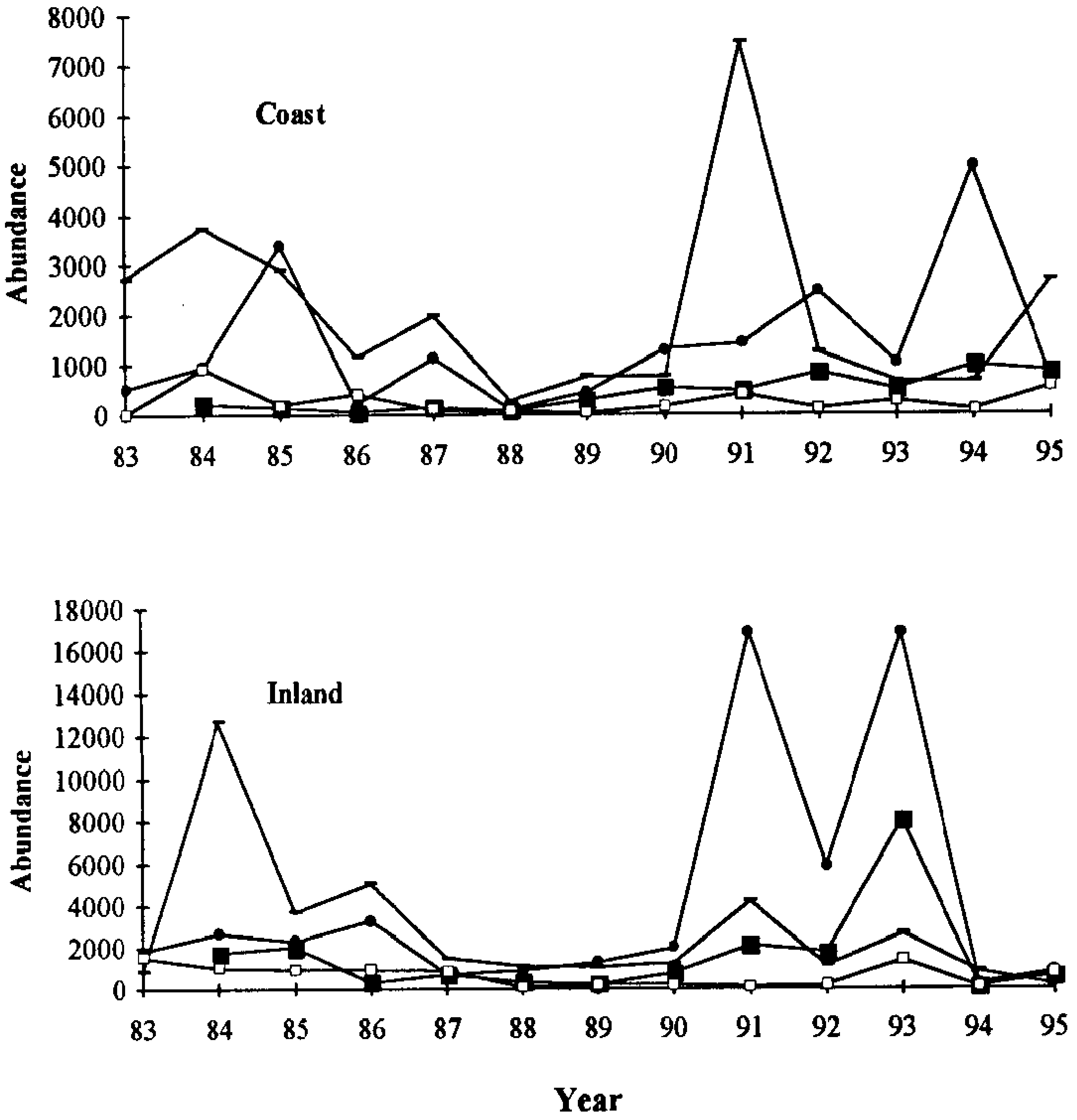


Figure 5.6. Abundances of cormorants observed by aerial survey inland and on the coast. Symbols indicate Great (•), Pied (■), Little Black (-) and Little Pied (□) Cormorants.

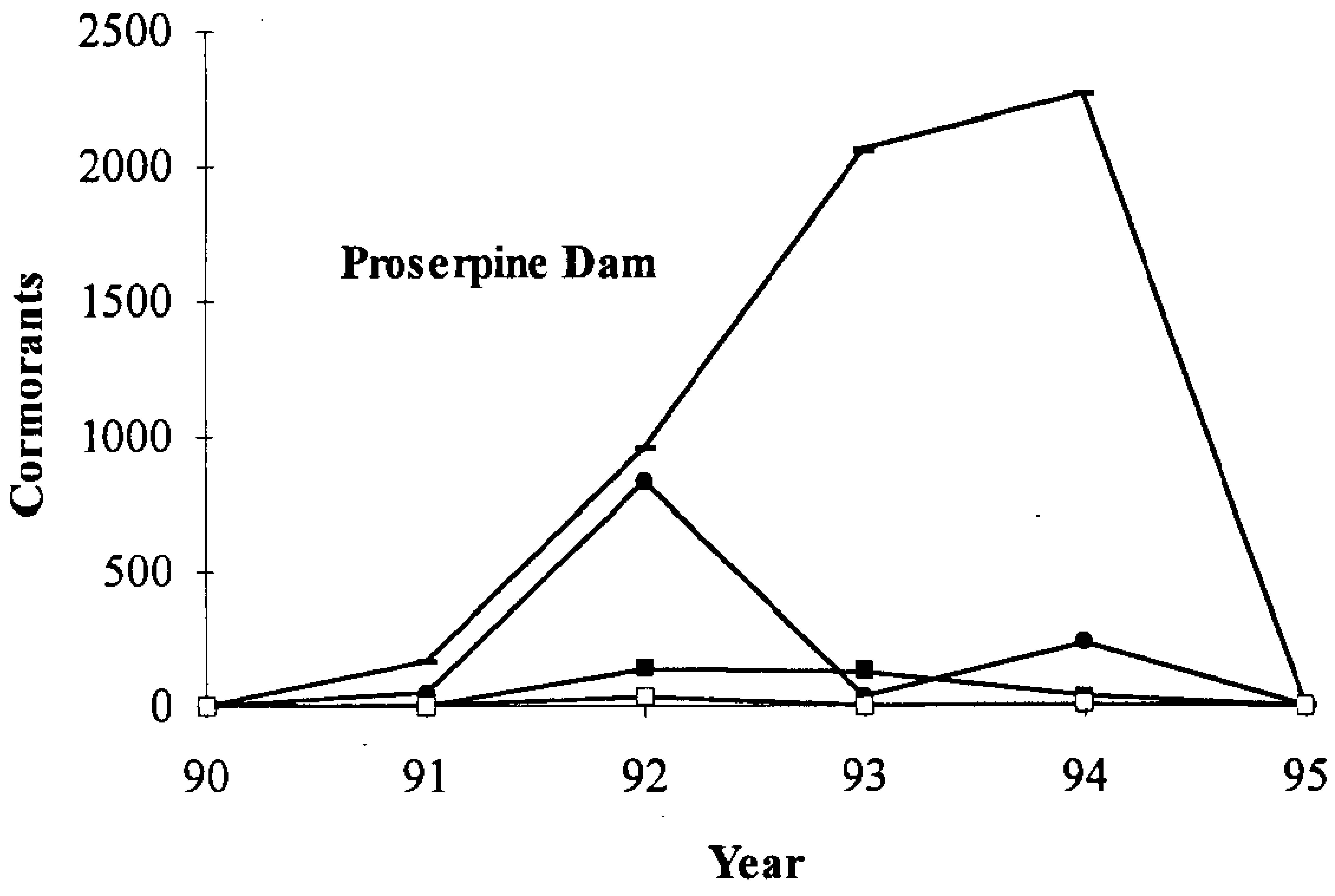


Figure 5.7. Abundance of cormorants over time at Proserpine Dam between its completion (in 1991) and 1995. Symbols indicate Great (•), Pied (■), Little Black (-) and Little Pied (□) Cormorants. Cormorants were nesting between 1991 and 1994 (R. T. Kingsford pers. comm.).

Table 5.5. Spearman rank correlations: a) coefficients for abundance of each species of cormorant over time between environment (ie. inland vs. the coast) and b) matrices for occurrence of species with each other and with water level (as indicated by rainfall), within environment. An asterisk beside a coefficient indicates significance at $P < 0.05$.

a) Between environment

Species	n (years)	Spearman's ρ
GRC	13	0.159
PCO	12	0.021
LBC	13	0.418
LPC	13	0.203

b) Among species within environment. n for correlations involving Pied Cormorants is 12 years; for other species it is 13.

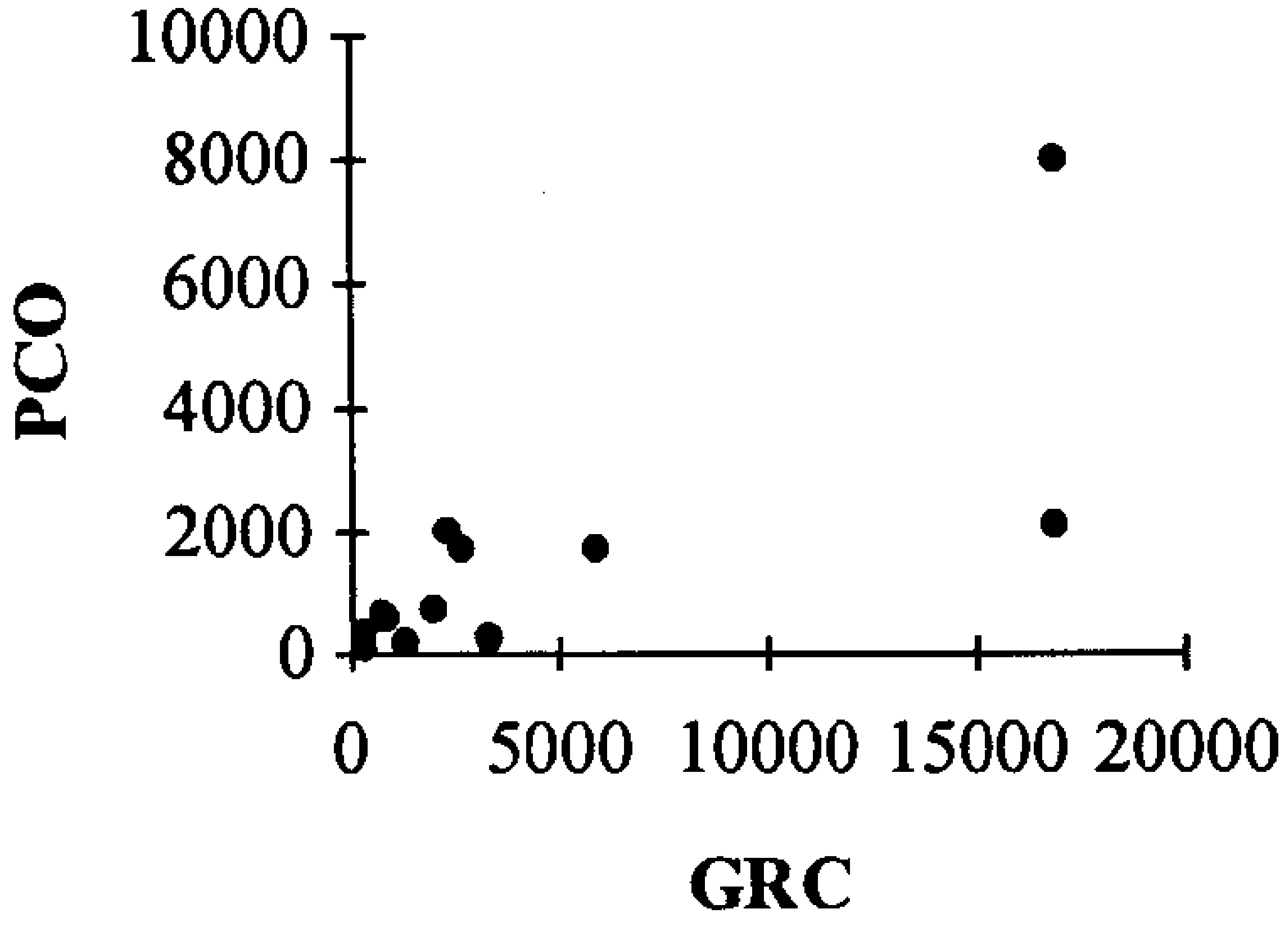
COAST

	GRC	PCO	LBC	LPC	Water
GRC	1				
PCO	0.503	1			
LBC	0.220	-0.084	1		
LPC	0.132	0.028	0.500	1	
Water	-0.638*	-0.205	-0.087	-0.090	1

INLAND

	GRC	PCO	LBC	LPC	Water
GRC	1				
PCO	0.748*	1			
LBC	0.681*	0.531	1		
LPC	0.335	0.371	0.341	1	
Water	-0.050	-0.216	-0.076	0.425	1

a



b

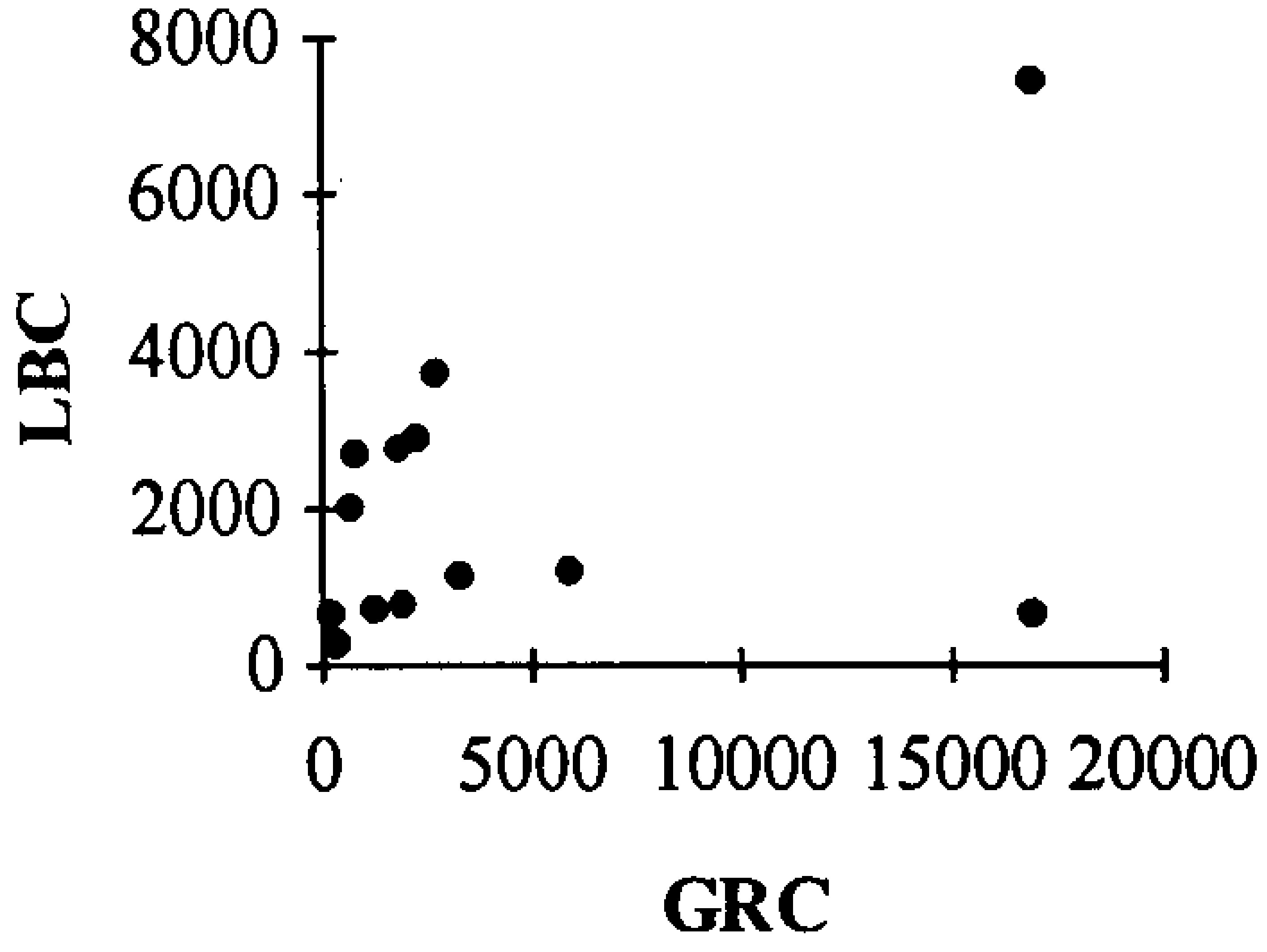


Figure 5.8. Significant correlations of abundance among species inland. n = 12 and 13 years (a and b, respectively).

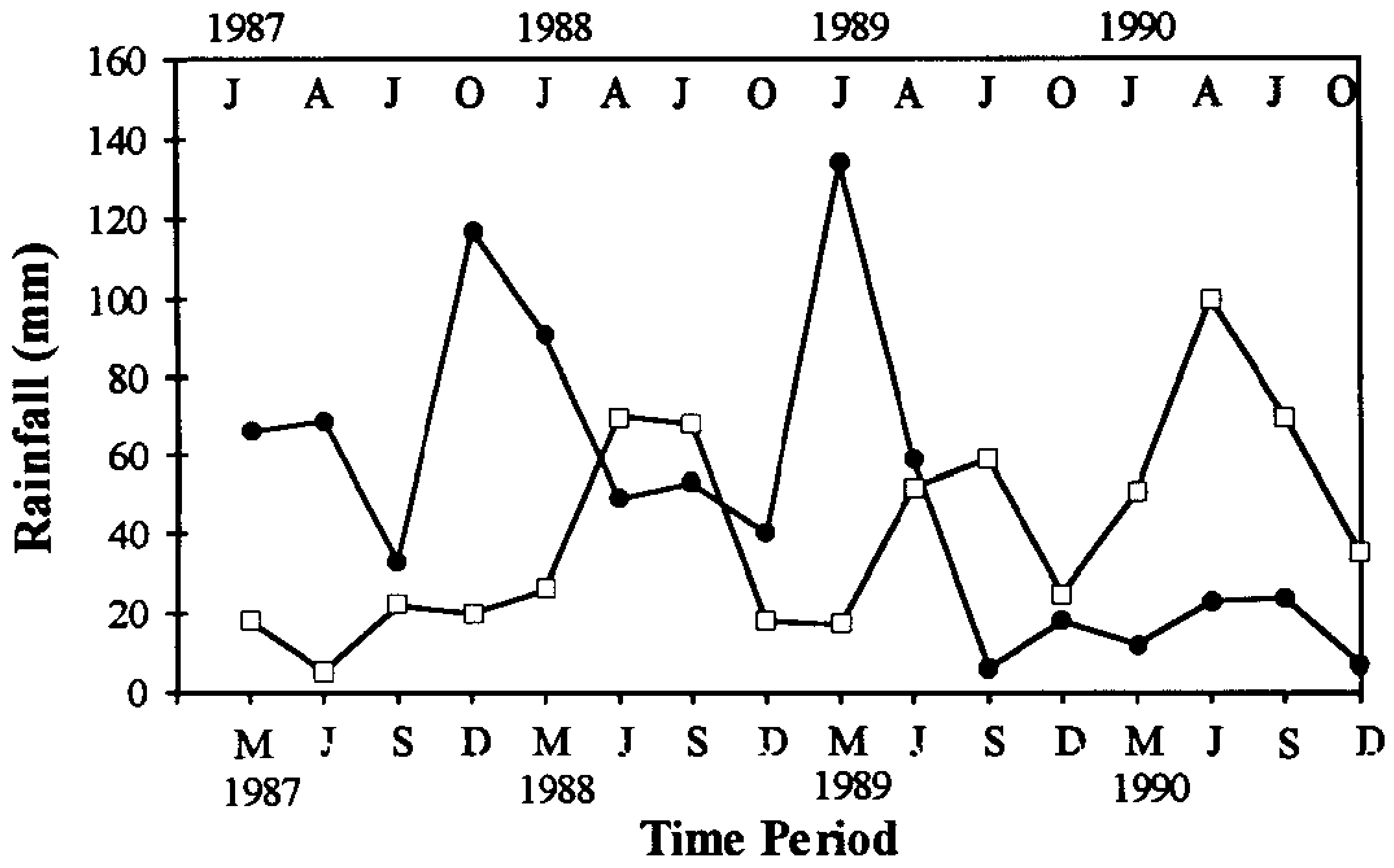


Figure 5.9. Rainfall in the Northwestern Region (Australian Bureau of Meteorology Reporting Districts 46 and 47; Figure 5.3) in 16 time periods. On both graphs, data are separated by three months. Open squares (□) represent the period between January 1987 and September 1990 (upper axis) and filled circles (●) represent the period between March 1987 and December 1990 (lower axis; ie. each datum of the latter set falls two months before the corresponding datum of the former; upper axis). Dates represented by closed circles correspond to aerial surveys.

Table 5.6. a) Pearson Correlations between coefficients of cormorant abundance in northwest New South Wales among species through time, with regional rainfall at the time of sampling ("rain") and two months prior ("rain2"; n = 16 surveys). Asterisks (**) indicates significance at *P*< 0 .001. b) CV for all observations of each species in northwest New South Wales.

a

	GRC	PCO	LBC	LPC	rain	rain2
GRC	1					
PCO	0.137	1				
LBC	0.968**	0.076	1			
LPC	0.993**	0.342	0.994**	1		
rain	-0.1187	0.0511	-0.1893	-0.2497	1	
rain2	-0.320	-0.468	-0.273	-0.266	-0.466	1

b

Species	CV
GRC	100.12
PCO	36.19
LBC	151.43
LPC	12.94

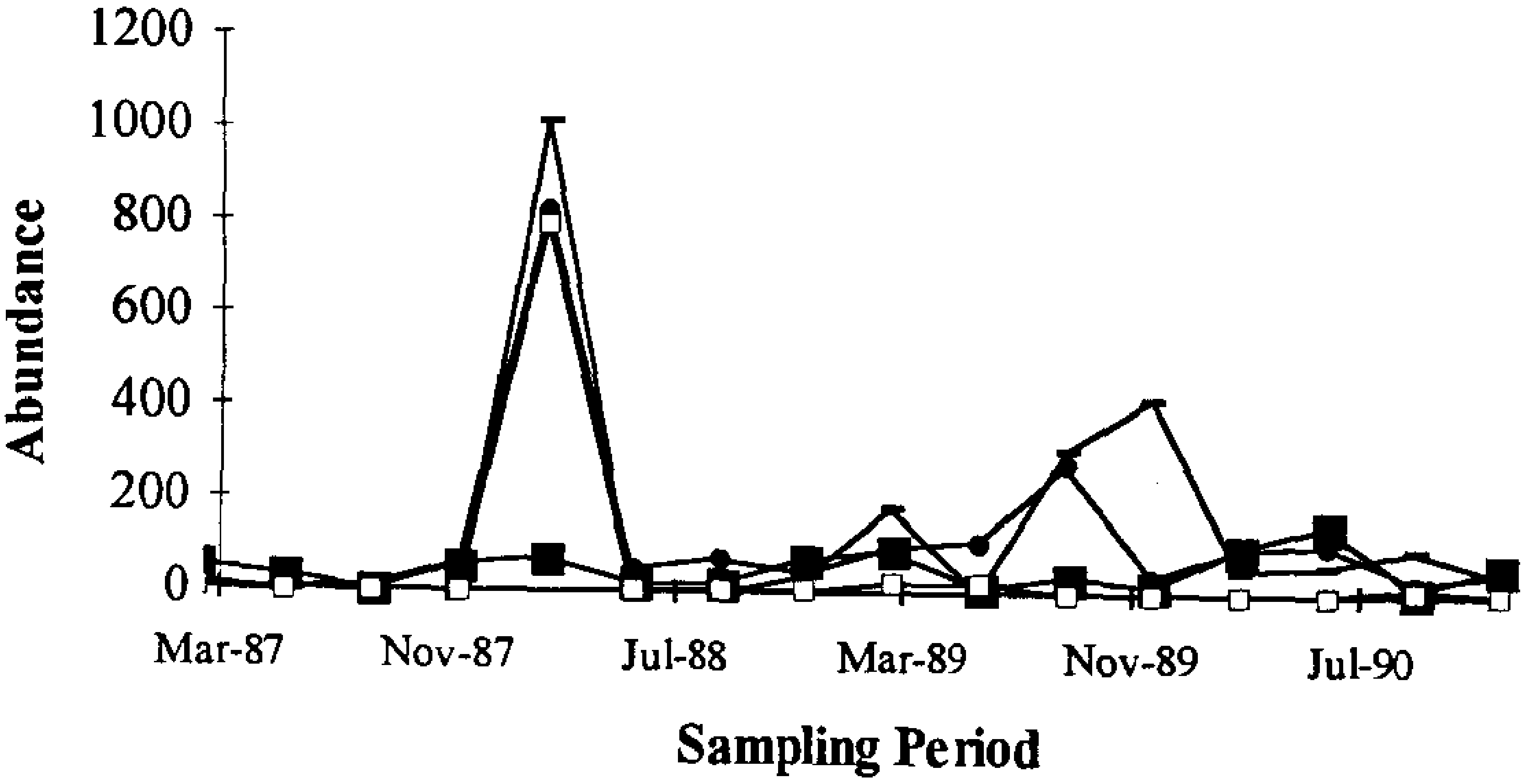


Figure 5.10. Abundance of cormorants over time in northwest New South Wales. Symbols indicate Great (•), Pied (■), Little Black (-) and Little Pied (□) Cormorants.

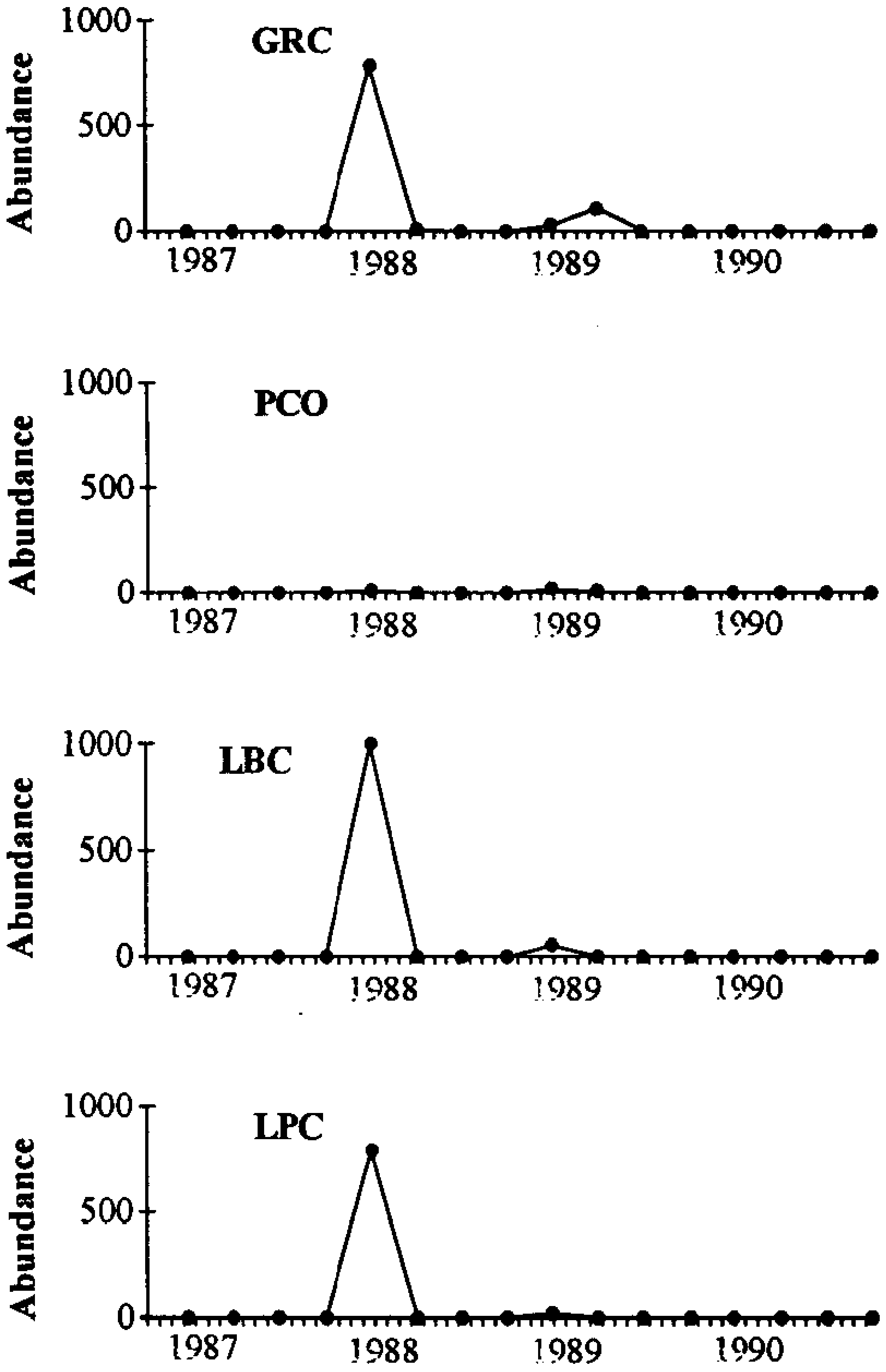


Figure 5.11. Abundance over time of cormorants at Lake Altibouka, sampled by air in three-month intervals.

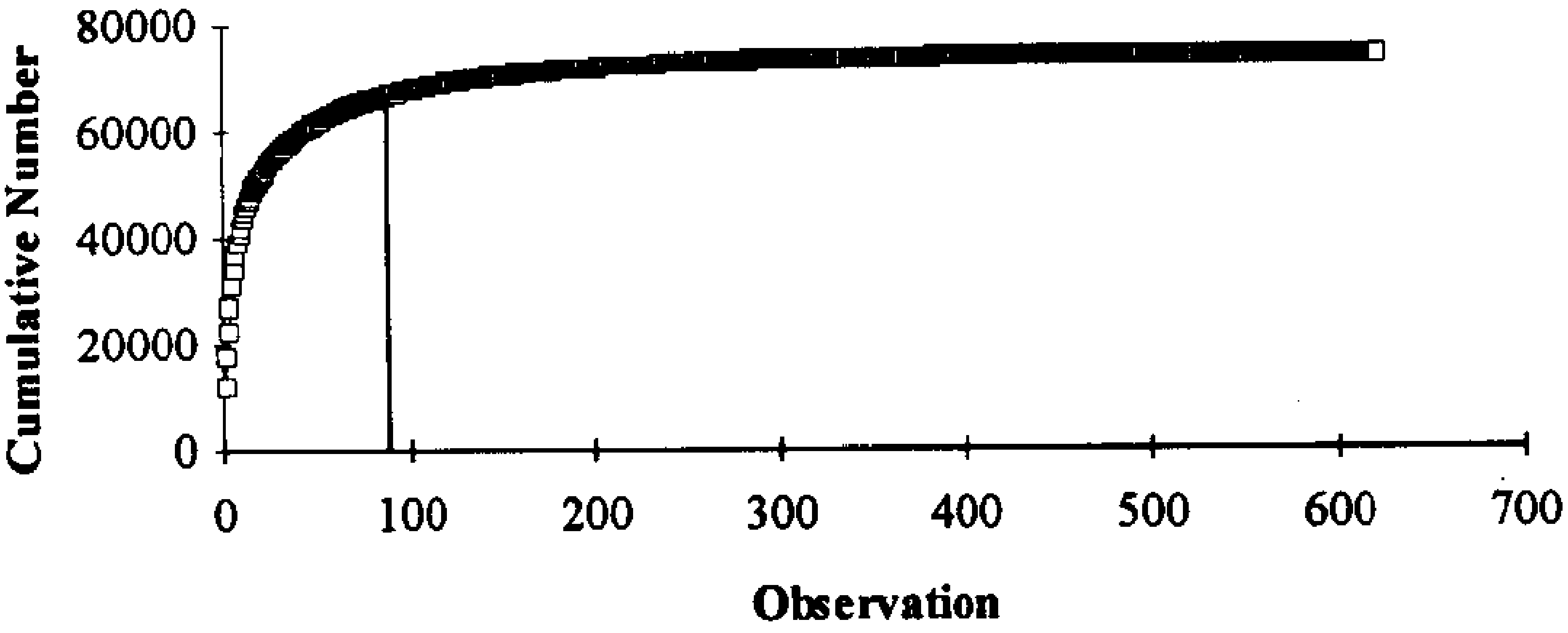


Figure 5.12. An example of a cumulative curve for abundance versus observation: Great Cormorants over eastern Australia (inland and coast, in all years). Ninety percent of the 54,682 Great Cormorants observed were in 96 wetlands (14% of 659 wetlands).

Table 5.7. Chi-square contingency tables for each species, testing differences in the number of wetlands used by 90% of individuals, between coastal and inland environments, and dry and wet years. Values presented are Observed \ Expected. One and two asterisks (* , **) indicate significance at $P < 0.05$ and $P < 0.001$, respectively. Yates corrections were used in all cases.

GRC		Inland	Coast	χ^2
	Wet	35(31)	30(16)	21.71**
	Dry	17(35)	13(12)	

PCO		Inland	Coast	χ^2
	Wet	19(18)	17(13)	4.385*
	Dry	24(33)	19(21)	

LBC		Inland	Coast	χ^2
	Wet	27(29)	20(18)	0.84
	Dry	32(29)	20(22)	

LPC		Inland	Coast	χ^2
	Wet	15(19)	12(12)	4.33*
	Dry	10(15)	19(13)	

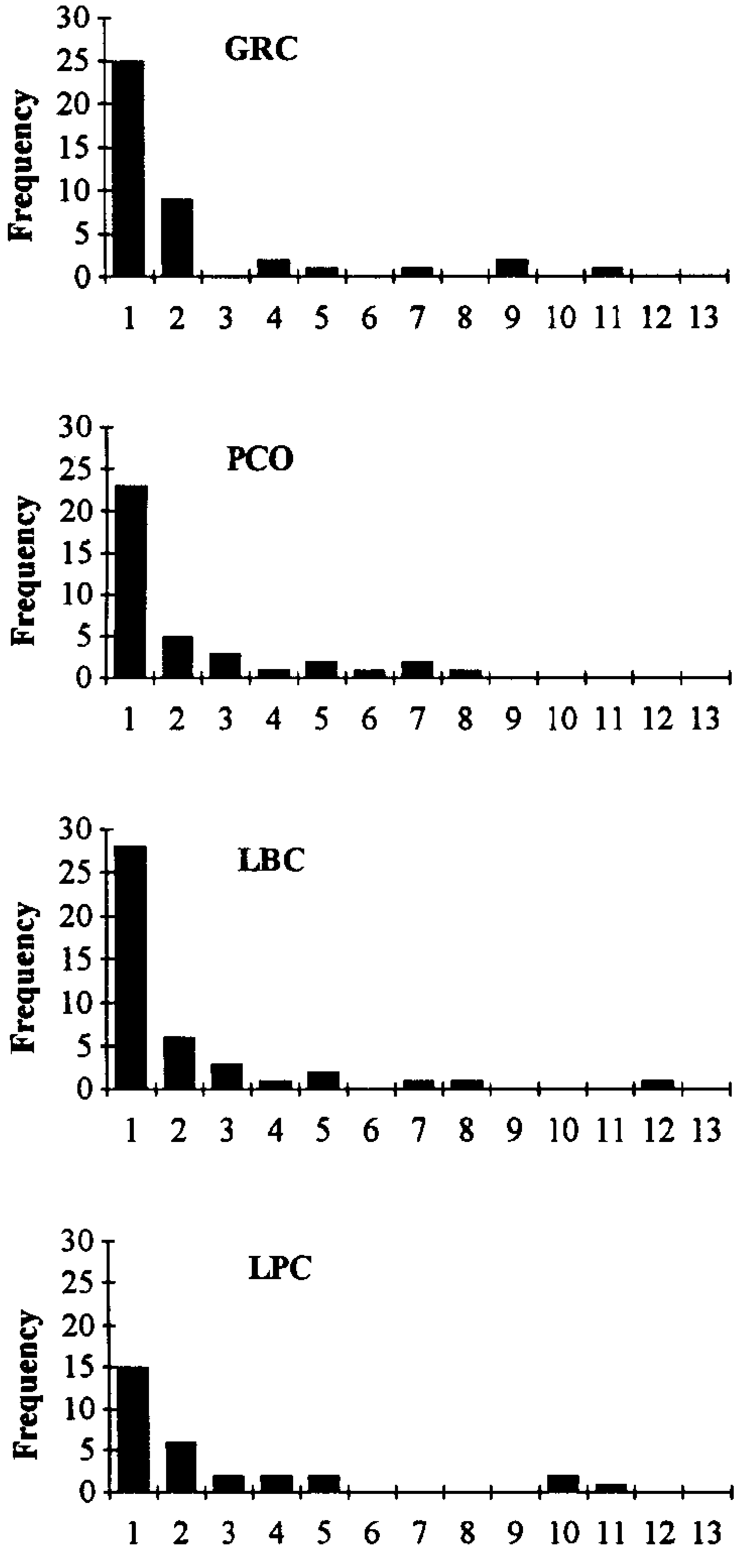


Figure 5.13a. Frequency with which coastal wetlands ranked in the top seven in terms of abundance for each species.

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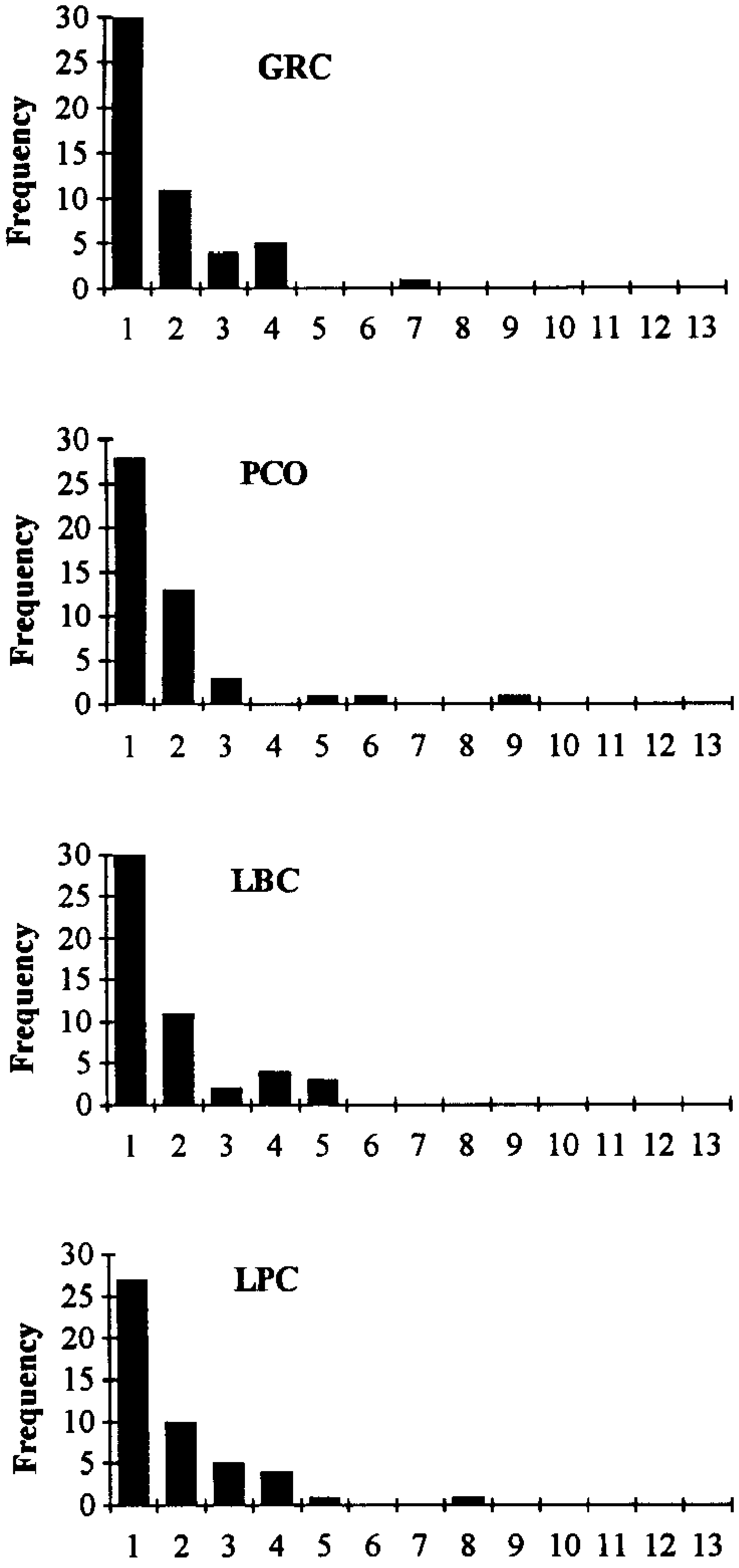

Figure 5.13b. Frequency with which inland wetlands ranked in the top seven in terms of abundance for each species.

Table 5.8. Kolmogorov Smirnov (*D*) results for differences in frequency with which wetlands ranked in the top seven in terms of abundance of cormorants between environments (a) and among species on the coast and inland (b and c, respectively). No result was significant. d) Identity of wetlands that ranked in the top seven for 9 years or more for any species, including the wetland's name, survey band, maximum area and number of years in which it ranked in the top seven.

a Between environments

Species	*D*	*P*
GRC	0.143	> 0.15
PCO	0.143	> 0.15
LBC	0.214	> 0.15
LPC	0.143	> 0.15

b Among species on the coast

Species	GRC	PCO	LBC
PCO	0.071		
LBC	0.071	0.071	
LPC	0.143	0.071	0.143

c Among species inland

Species	GRC	PCO	LBC
PCO	0.143		
LBC	0.071	0.143	
LPC	0.071	0.143	0.071

d Top ranking wetlands

Species	Name	Band	Area (ha)	Years
GRC	Burrandong Reserve	4	6060	11/13
	Split Rock Dam (Reservoir)	5	200	9/13
PCO	Lake Cawndilla	4	8600	9/12
LBC	Coolmunda Dam	6	1640	12/13
LPC	Burrendong Reserve	4	6060	11/13
	Coolmunda Dam	6	1640	10/13
	Lake Illawarra	3	3475	10/13

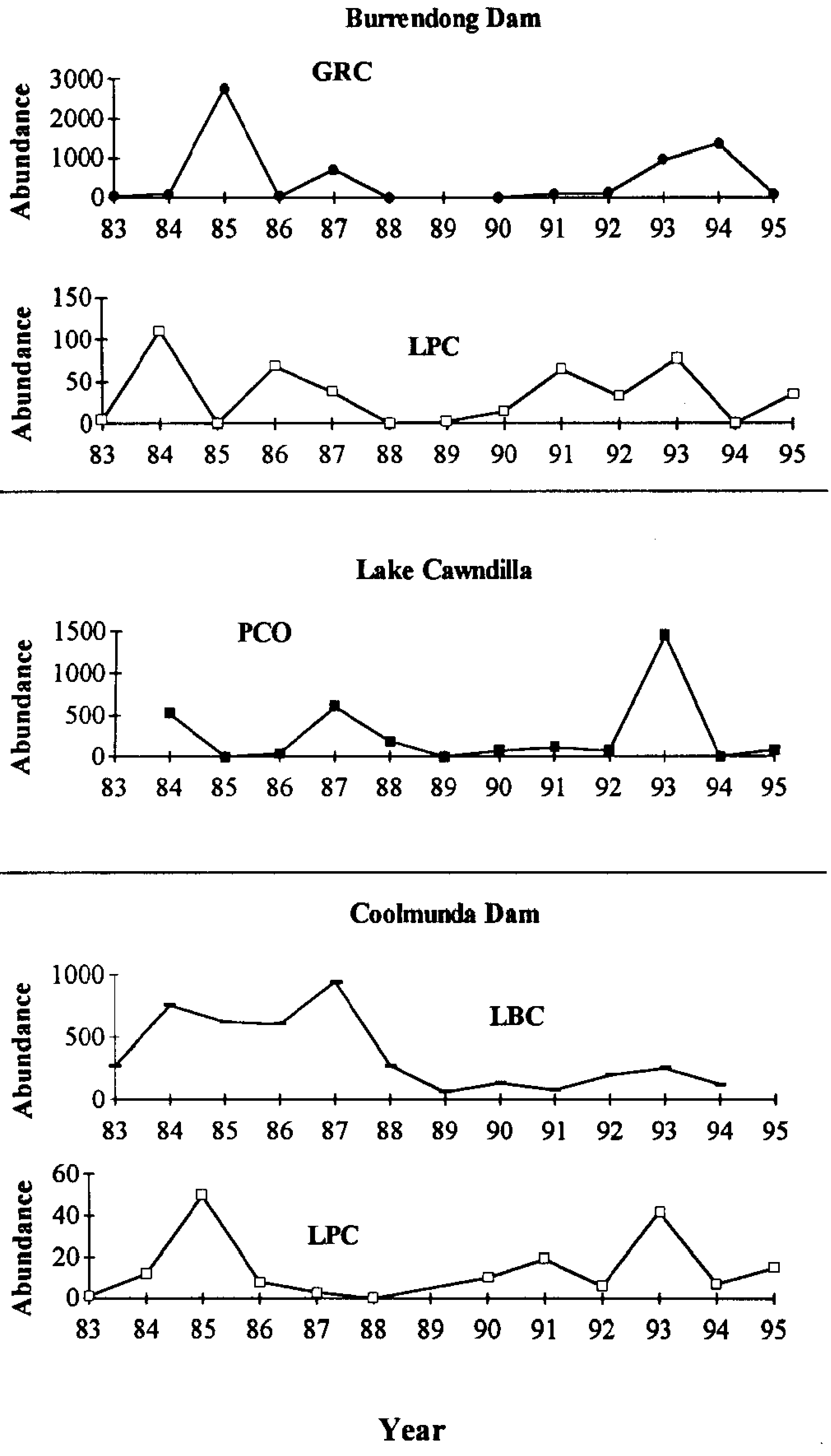

Figure 5.14. Yearly abundance of species at wetlands that ranked in the top seven for ≥ 9 years. See Figure 5.17a for yearly abundance at Lake Illawarra.

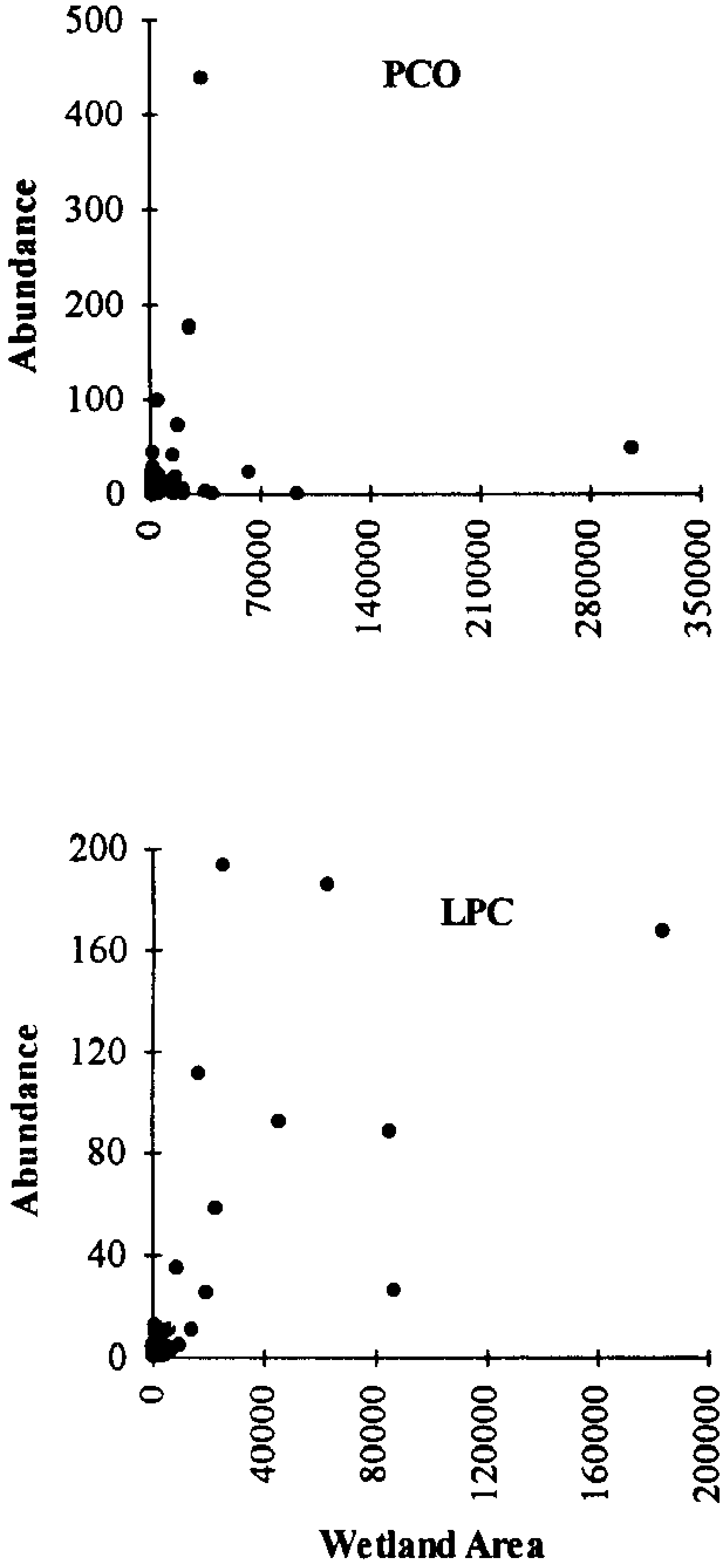

Figure 5.15. Relationship between abundance of Pied and Little Pied Cormorants to wetland area (ha$\cdot 10^{-1}$ of wetland surface area).

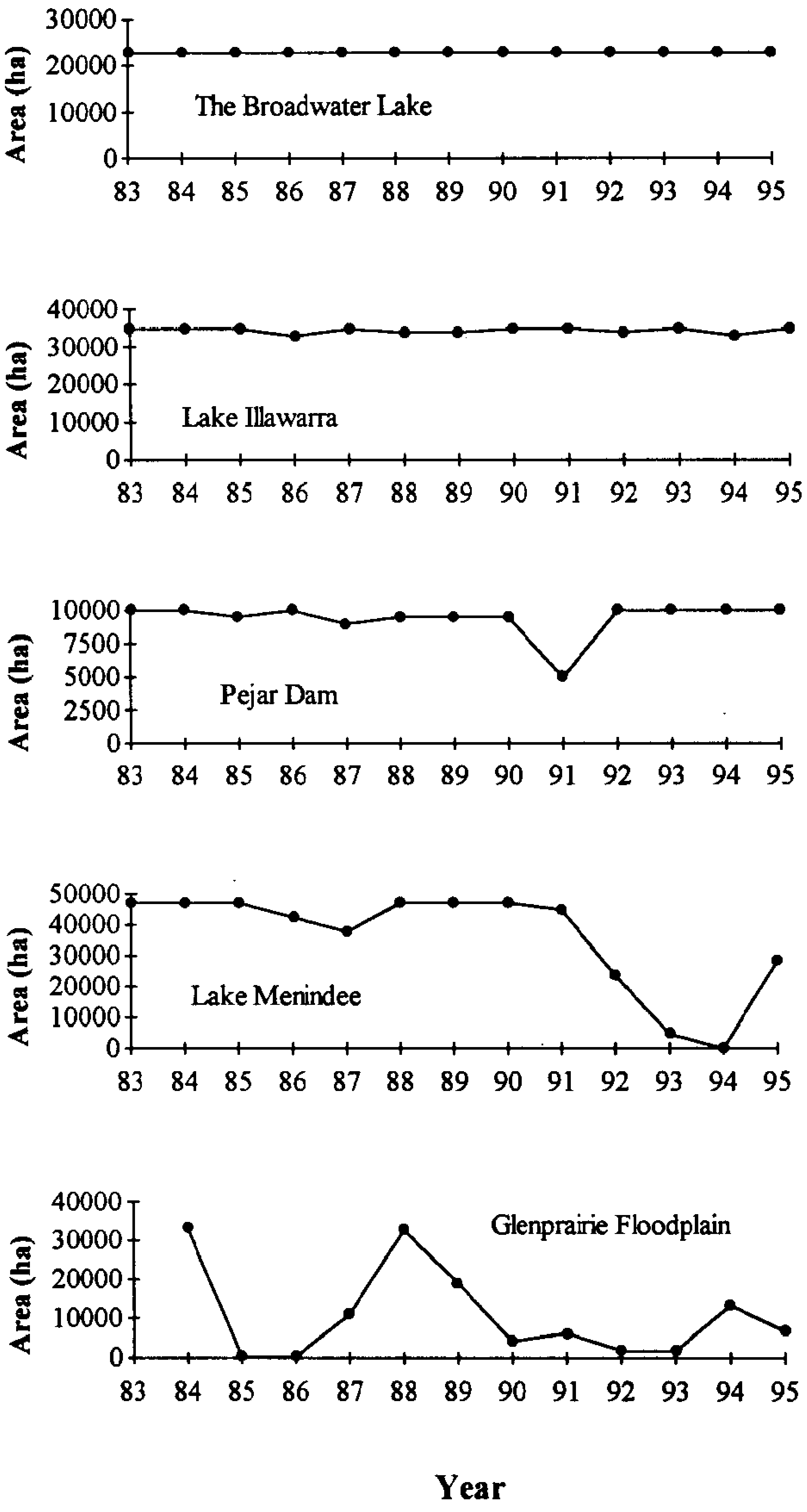

Figure 5.16. Change in wetland area for The Broadwater Lake, Lake Illawarra, Pejar Dam, Lake Menindee and Glenprairie Floodplain.

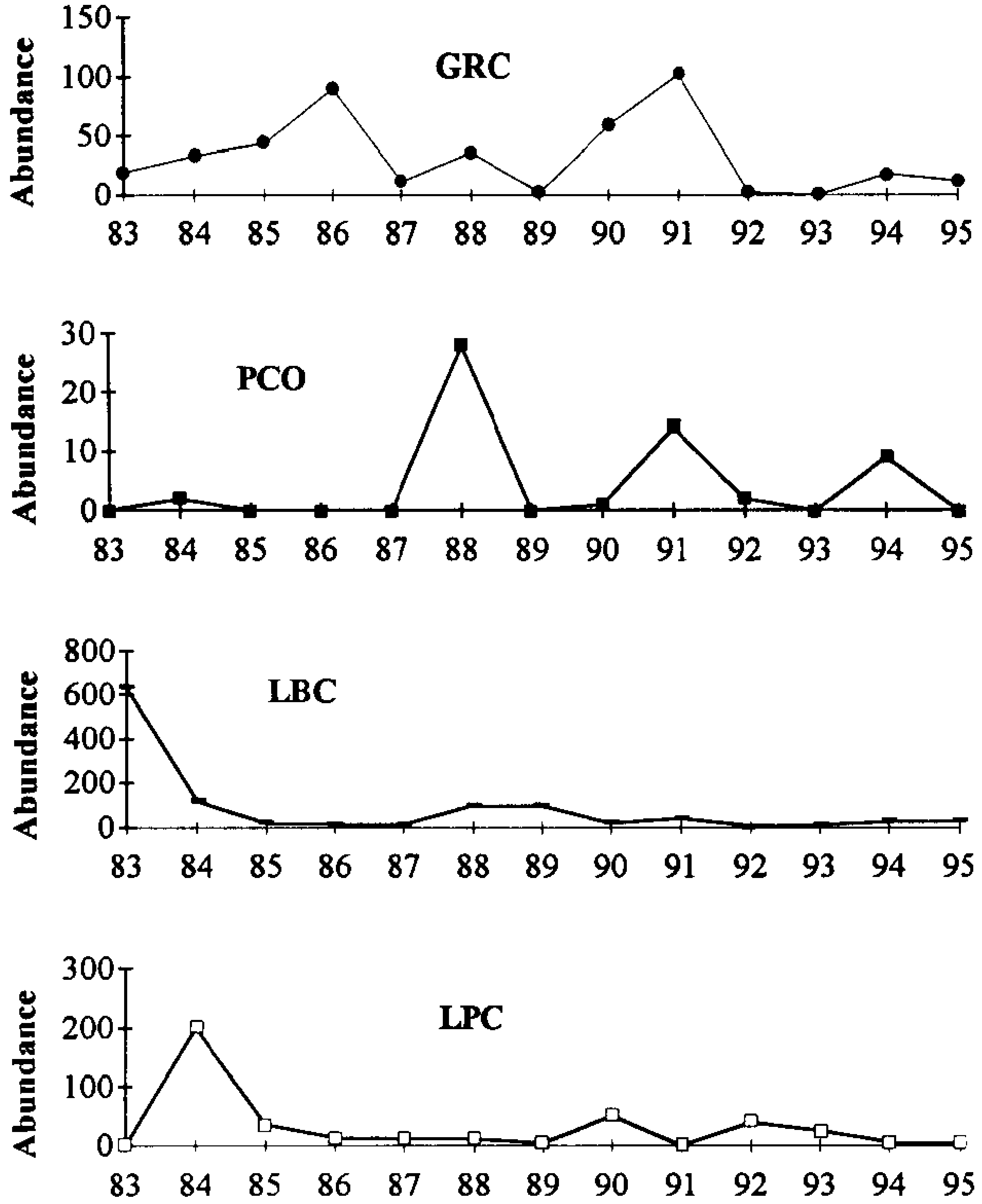

Figure 5.17a. Yearly abundance of cormorants on Lake Illawarra.

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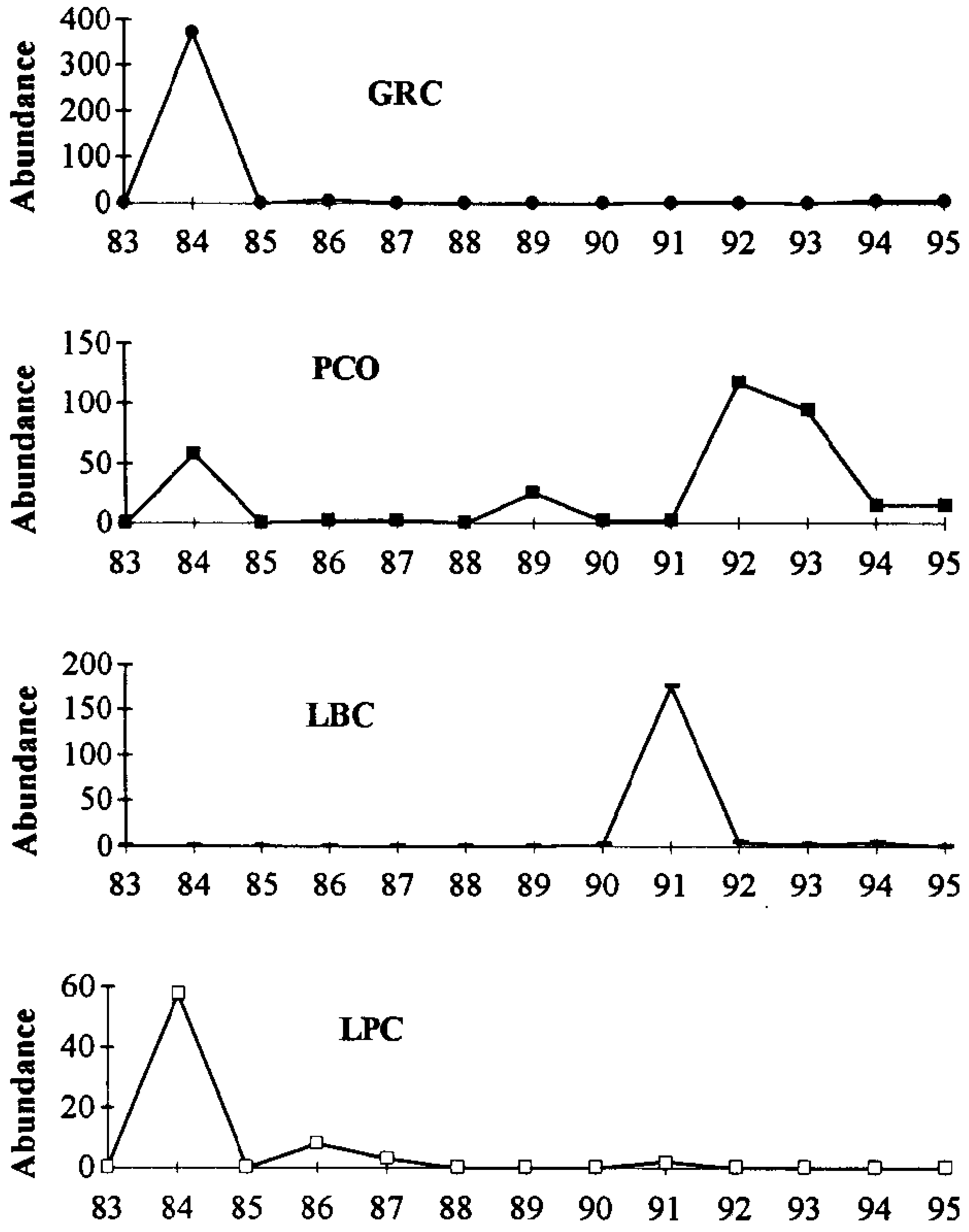

Figure 5.17b. Yearly abundance of cormorants on Broadwater Lake.

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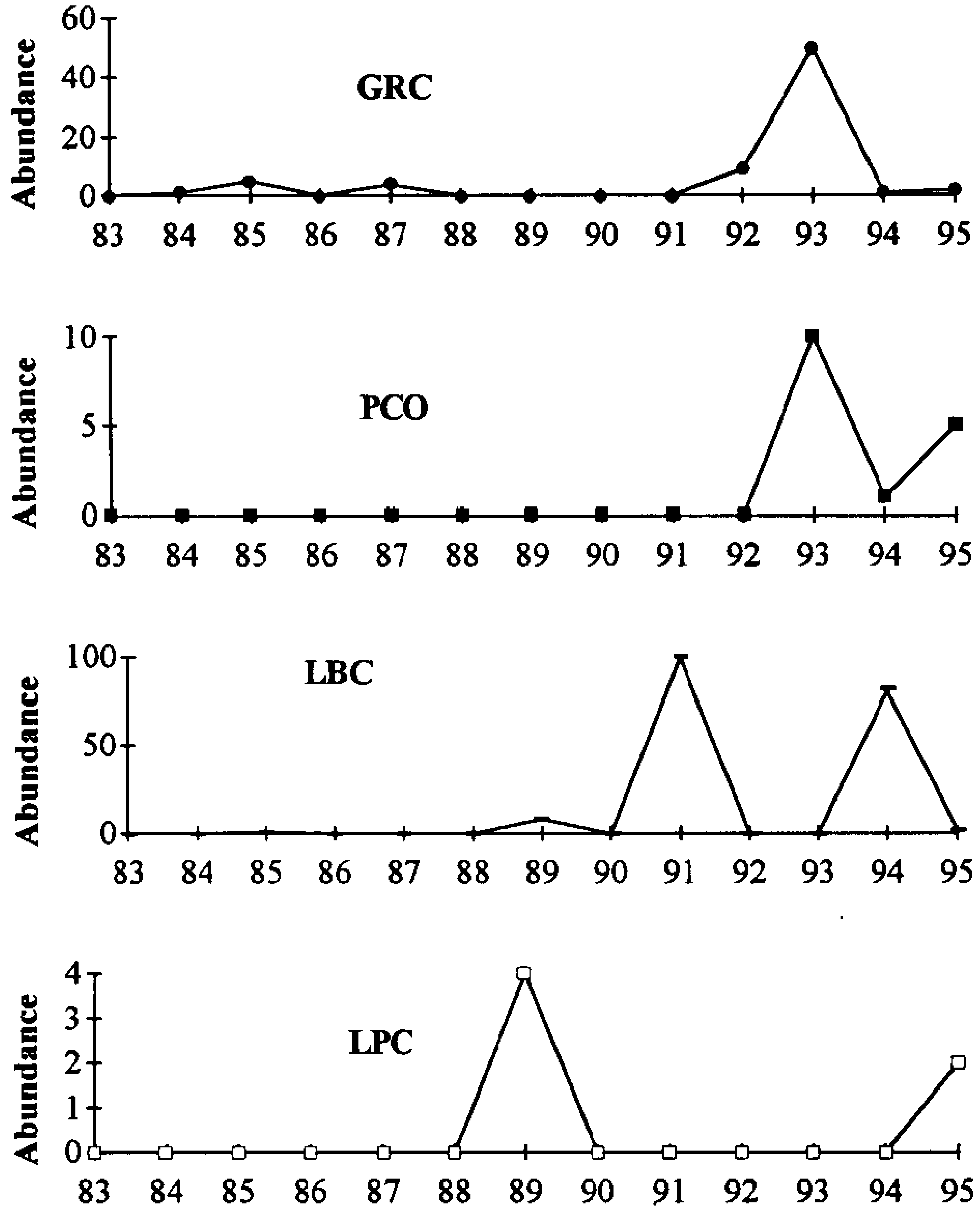

Figure 5.17c. Yearly abundance of cormorants on Pejar Dam.

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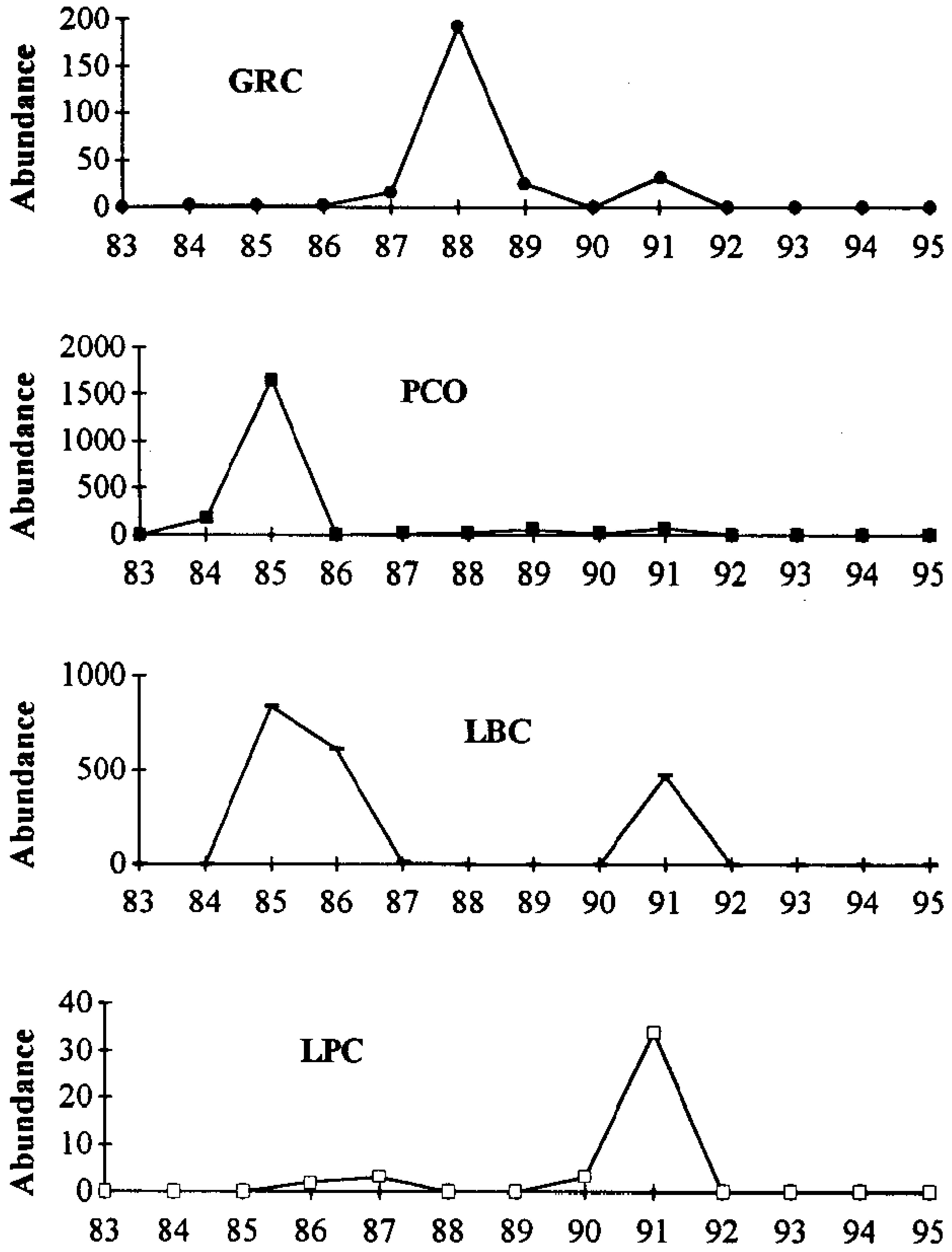

Figure 5.17d. Yearly abundance of cormorants on Lake Menindee.

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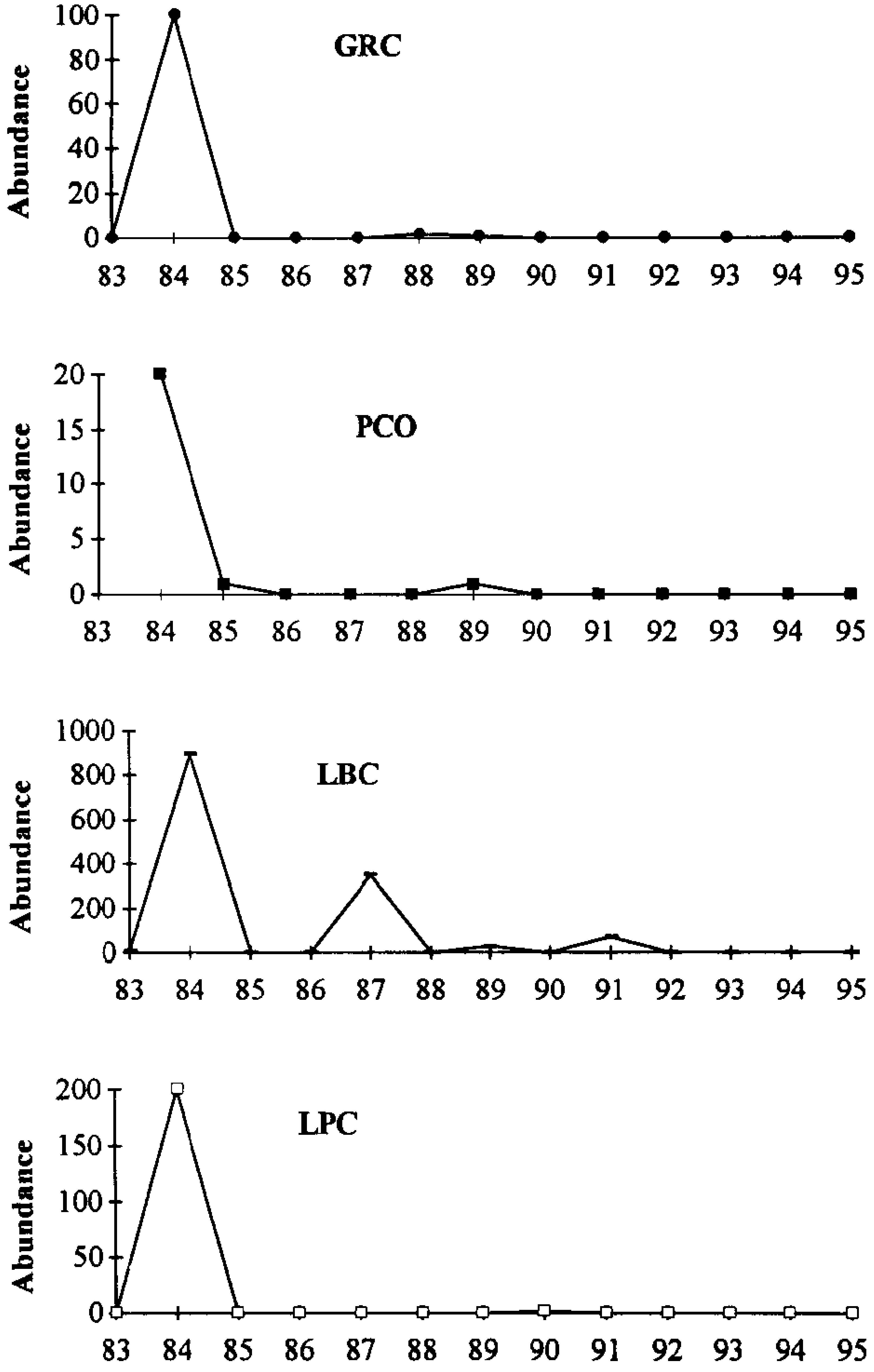

Figure 5.17e. Yearly abundance of cormorants on Glenprairie Floodplain.

Table 5.9. Correlation coefficients for cormorants and wetland area at The Broadwater Lake (a), Lake Illawarra (b), Pejar Dam (c), Lake Menindee (d) and Glenprairie Floodplain (e) between 1983 and 1995. An asterisk next to a coefficient indicates significance at $P < 0.05$. Coefficients for wetland area at Glenprairie Station reflect data since 1984 only.

a The Broadwater Lake

	GRC	PCO	LBC	LPC	Area
GRC	1				
PCO	0.24562	1			
LBC	-0.0902	-0.1604	1		
LPC	0.9914	0.20973	-0.0738	1	
Area	-0.0745	-0.0813	-0.0905	-0.1029	1

b Lake Illawarra

	GRC	PCO	LBC	LPC	Area
GRC	1				
PCO	0.2673	1			
LBC	-0.1328	-0.0585	1		
LPC	-0.0008	-0.1529	-0.0614	1	
Area	-0.0827	-0.2305	0.2028	0.2433	1

c Pejar Dam

	GRC	PCO	LBC	LPC	Area
GRC	1				
PCO	0.9*	1			
LBC	-0.18	-0.12	1		
LPC	-0.15	0.061	-0.11	1	
Area	0.17	0.203	-0.7	0.087	1

d Lake Menindee

	GRC	PCO	LBC	LPC	Area
GRC	1				
PCO	-0.097	1			
LBC	-0.1175	0.711*	1		
LPC	0.04448	-0.0814	0.33943	1	
Area	0.27253	0.25013	0.30934	0.19356	1

e Glenprarie Floodplain

	GRC	PCO	LBC	LPC	Area
GRC	1				
PCO	0.998*	1			
LBC	0.927*	0.923*	1		
LPC	0.999*	0.998*	0.927*	1	
Area	0.617*	0.603*	0.584*	0.601*	1

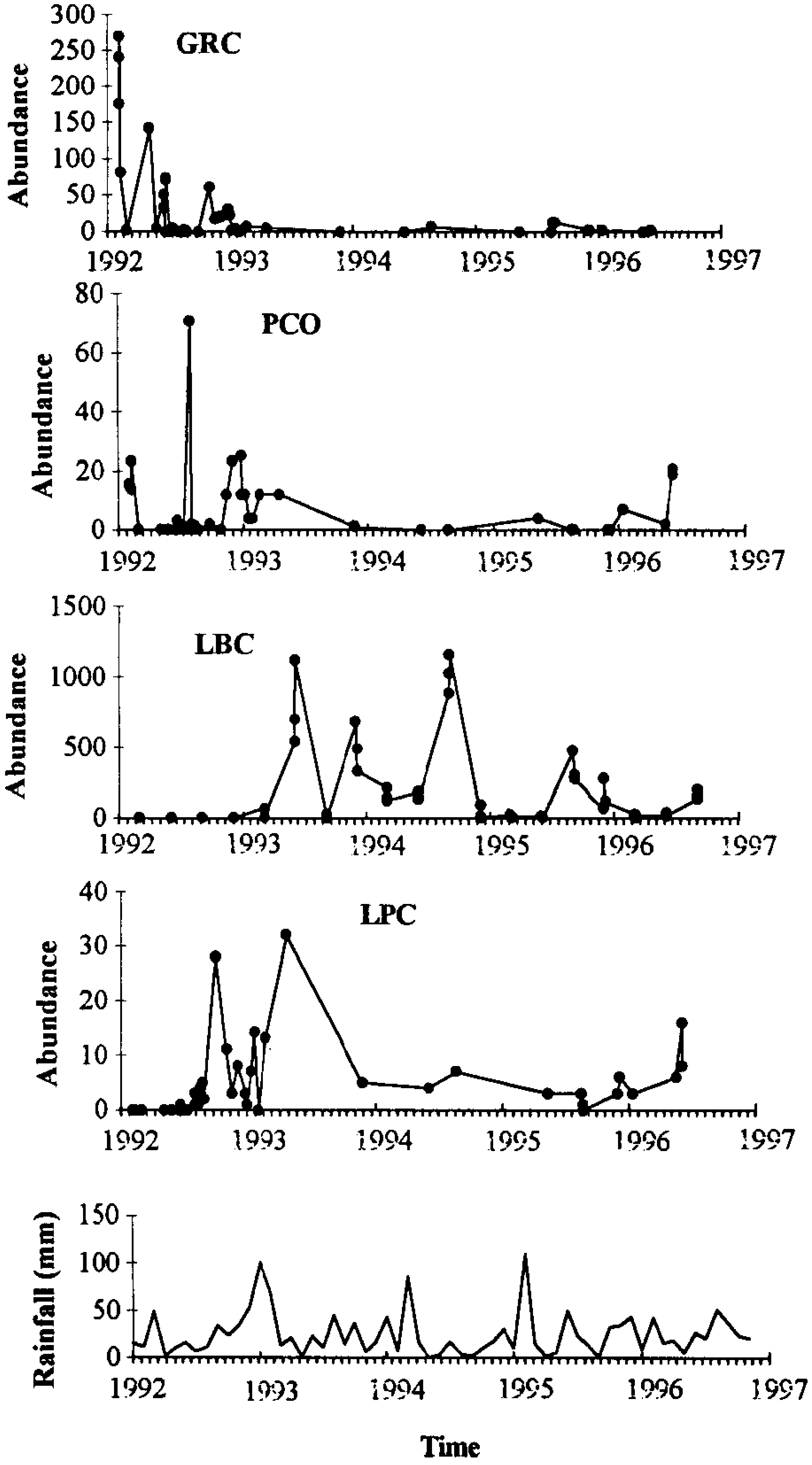

Figure 5.18a. Abundance at Homebush Bay for each species and inland rainfall. Graphs illustrate patterns between 1/1/92 through 31/10/1996.

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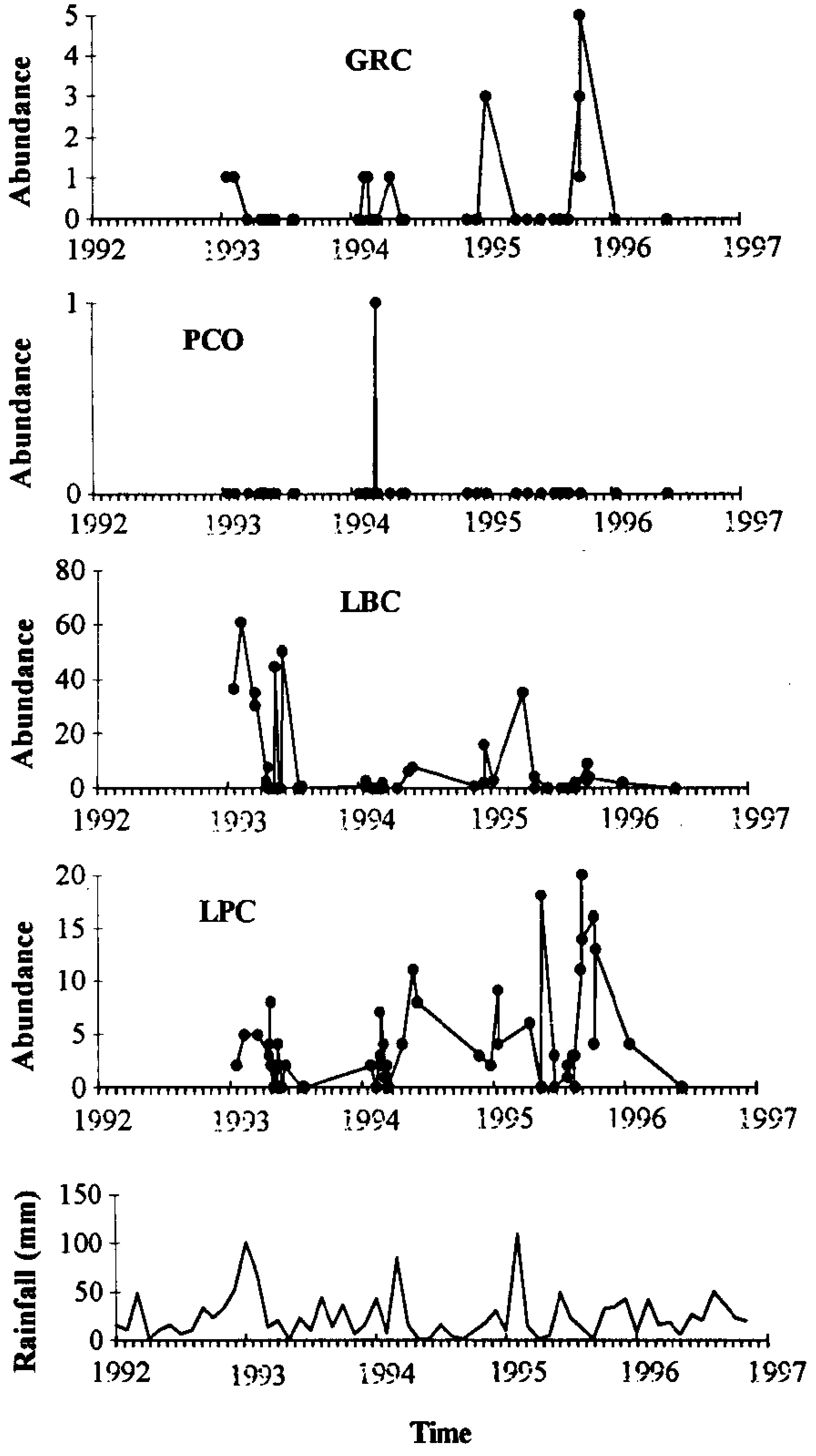

Figure 5.18b. Abundance at Patonga Creek for each species and inland rainfall. Graphs illustrate patterns between 1/1/92 through 31/10/1996. No data are available for Patonga Creek in 1992.

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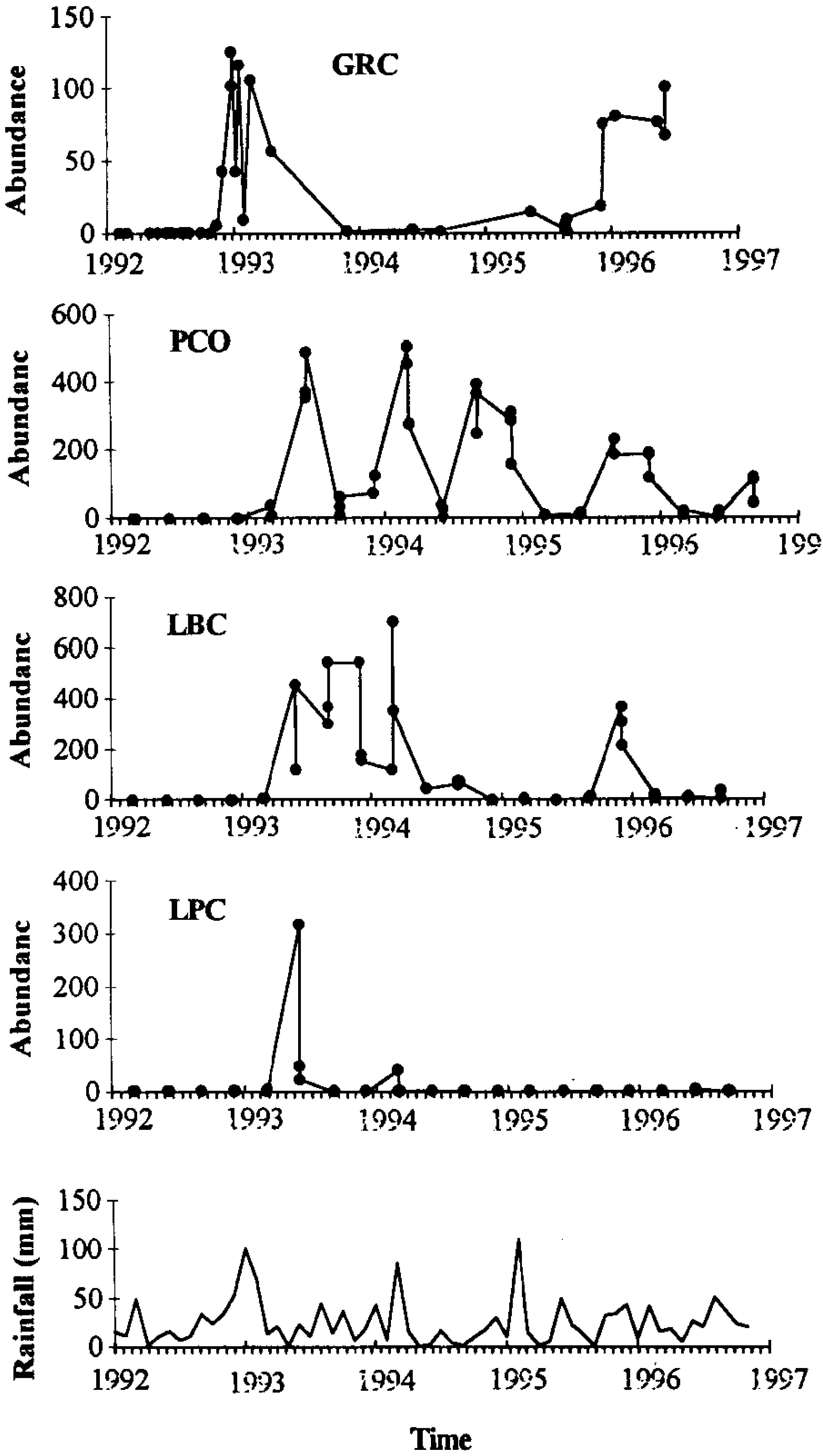

Figure 5.18c. Abundance at Lake Altibouka for each species and inland rainfall. Graphs illustrate patterns between 1/1/92 through 31/10/1996. Note continuance from Figure 5.10.

5.4. Discussion

5.4.1. The relationship of cormorants to water and variability

The most obvious pattern in this study was high temporal variability in abundance, irrespective of species, environment, rainfall or scale of observation and from intensively sampled wetlands (e.g. Figure 5.15) to yearly snapshots of the landscape of eastern Australia (e.g. Figure 5.5). The pattern for most species was typified by variability in the system, created by low abundance through time, interspersed with sporadic high peaks. All species therefore appear to be highly dispersive while seeking sites for foraging and reproduction.

Despite a high degree of patchiness in abundance, several results support predictions from the model presented in this chapter. A basic tenet of the model was that populations of cormorants disperse during wet periods and contract during drought. Across eastern Australia, low numbers were observed on the coast and inland (Figure 5.6) during one of the wettest periods of the survey (Figure 5.4). High variability and low overall abundance made significant correlations rare (only for GRC on the coast; Table 5.5), but the coefficient was negative in almost all cases. Additional evidence comes from relationships between rainfall and CV in abundance in northwest New South Wales. Although rainfall is a coarse predictor, negative relationships (although not significant; Table 5.6a), again suggest that cormorant populations disperse during wet periods. The power of the statistic may have been lessened by low frequency of peaks, indicating that a substantial data set is required for studies of this nature.

Observations at Lake Altibouka also support the model and suggest that this area may act as a refuge during drought. The only appreciable numbers of cormorants during sampling in northwestern New South Wales occurred at Lake Altibouka during a dry period (March 1988, Figures 5.9 and 5.11), and although inconclusive, this clumping (ie high numbers of birds on an individual wetland) during drought is consistent with the model. All the peaks in inland rainfall (>75 mm in a month) also coincided with low abundance of cormorants at Lake Altibouka. Ground counts from this wetland (Figure 5.16) could not be combined with aerial surveys, because of differences in visibility between the two methods, however, it appears that, with a three-monthly sampling design, 10 years sampling at a temporary wetland (in this case 1987 to 1997; the Lake was dry in 1991 and not graphed) is the minimum required to obtain sufficient population peaks to allow reliable comparisons of this type.

Although spikes in abundance occur sporadically, and are therefore difficult to test, they are important to the system because populations of cormorants appear to be highly aggregated most of the time. The percentage of wetlands used by 90% of any species of cormorant (e.g. Figure 5.11) was never more than about a third, and as low as a tenth of the wetlands that exist (Table 5.7). It is tempting to think that use of a small proportion of wetlands means that individual wetlands would be important continually. This might also be expected from other species (e.g. Shags *P. aristotelis*, Potts 1969; Double-crested Cormorants *P. auritus*, Léger and McNeil 1987; Brandt's Cormorants *P. penicillatus*, Boekelheide and Ainley 1989), or for Great Cormorants in other regions (e.g. Northern Ireland; Warke *et al.* 1994) that return every year for decades to the same breeding sites.

In eastern Australia, however, the temporal scale on which this occurs appears to be longer for most of the sites observed in the aerial survey. Irrespective of their position in relation to the coast, most wetlands that ranked in the top seven in terms of abundance did so only once in 13 years (Figure 5.12) and only five wetlands ranked in the top seven for nine years or more (Table 5.8), although most of these are important breeding sites (R. T. Kingsford pers. comm.). Cormorants probably live about 10 years (see Boekelheide and Ainley 1989), which suggests that the period sampled by the eastern

Australian aerial survey would encompass the life of all but the oldest individuals. During a 13 year period, it is apparent that abundant resources seldom occur in the same place. Thus, environmental conditions may permit reproduction only a few times within the lifespan of a cormorant, so, successful breeding is likely to be a combination of remembering location of past resources and learning how to find new resources reliably.

Water level in each of the five consistently important wetlands is regulated, and with the exception of the estuarine Lake Illawarra, all of these were small to medium sized dams in which permanent populations of prey could be expected (R. T. Kingsford pers. comm.). Regulation of wetlands and water channels, which is often detrimental to wildlife because of lowered productivity (e.g. Briggs *et al.* 1997; Thoms and Sheldon 1997), can in some cases be beneficial to cormorants, or at least irrelevant. Great Cormorants in Europe have greatly increased, due in part to wide-spread eutrophication favouring short-lived fishes which are the preferred food of Great Cormorants (Warke and Day 1995). Similarly, 'artificial wetlands' in the form of channel catfish (*Ictalurus puncatus*) hatcheries have contributed to dramatic increases of Double-crested Cormorants along the Mississippi Delta in the U.S.A. (Glahn and Stickley 1995). The data presented here, and a preference of Little Pied and Little Black Cormorants for wetlands with heavily regulated water regimes during later stages of flooding (S. Briggs pers. comm.), suggest that controlled water bodies are also important to cormorants in eastern Australia (see also Briggs *et al.* 1997). Analysis at a landscape scale (e.g. with aerial survey data) would aid understanding the potential influence of artificial wetlands on populations of cormorants.

Nevertheless, abundance of cormorants at the frequently highly ranked wetlands fluctuated as dramatically (Figures 5.13 and 5.16a) as those in other locations, suggesting that there is little fundamental difference between these and other wetlands. Cormorants in eastern Australia thus appear to be highly mobile, irrespective of patterns of change in their resources, although a highly fluctuating resource provides better conditions (e.g. Glenprairie Floodplain, Table 5.9). This conclusion casts doubt on Llewellyn's (1983) assertion that abundance of cormorants in a given location can be forecast.

Patterns of dispersion may also affect an observer's perception of abundance at a large scale (see Chapter 1). In this study, Little Pied Cormorants were estimated to be the least abundant of the species across eastern Australia (Figure 5.6), yet they are thought to be the most common cormorant in inland Australia (Serventy 1939). In this study, Little Pied Cormorants were also the least aggregated species (Table 5.6), which agrees with observations of small flock sizes (Chapter 3). However, they frequently use wetlands smaller than 1 ha (Serventy 1939), and many occurrences may have been missed. Similarly, low abundances of all species were observed between 1988 and 1990 (Figures 5.6 and 5.7), during a time of intermediate to high rainfall (Figure 5.4). During these wet periods, cormorants may have spread to small wetlands undetected by the aerial surveys. These results are also consistent with the model, although an intensive program of telemetry would be required to demonstrate this aspect conclusively.

One result that was not predicted by the model was the similarity in dispersal patterns for all species between inland and the coast. Qualitative patterns were similar for abundance across eastern Australia (Tables 5.5a and 5.8) and in individual wetlands (Figures 5.15 a-c). This was particularly unexpected for Great and Pied Cormorants which demonstrate a stronger tendency to flock inland (Chapter 3). Small- and meso-scale features (such as aquatic macrophytes; Chapter 4) apparently elicit similar responses in both environments. Although cormorants demonstrate irruptions in other areas (e.g. eastern Britain, Potts 1969) and use coastal and inland sites for different portions of their life cycles (e.g. Warke et al. 1994), it is difficult to compare the eastern Australian system with others because of inherent unpredictability of resources (see Stafford Smith and Morton 1990) which influences many aspects of these species' natural history. For instance breeding of cormorants, which is seasonal elsewhere (e.g. eastern Canada, Léger and McNeil 1986) is initiated by the onset of rain (as evidenced by water level and food availability) in Australia (Miller 1980). Dispersal patterns of cormorants in eastern Australia may therefore be more comparable to those of other mobile animals in this region, such as red kangaroos (*Macropus rufus*) that increase their movements during drought (Norbury *et al.* 1994) and expand their foraging habitat after rain (Priddel 1988).

To gather information about widely distributed resources, cormorants must sample their environment. Relative unpredictability of the environment, and the risk associated with using a particular resource patch, depends to some extent on the ease with which a forager can assess resource variability (Regelmann 1984). Thus far, any means by which cormorants could obtain information would be beneficial. It has been suggested that aquatic birds have a mechanism for detecting the presence of water at great distances (Frith 1959), contrasting with an alternative model in which they find water through the course of normal movements (Schodde 1982). Results from this chapter support the latter idea and this leads to questions about how cormorants might reduce *apparent* variability as they sample the environment.

5.4.2. Large scale sampling by cormorants

Shettleworth *et al.* (1988) present a theoretical model of foragers choosing between two food sources, one which is of mediocre quality, but stable, the other which fluctuates between periods of extreme highs and lows. In their optimal model, a forager should sample the fluctuating resource as often as necessary to ascertain its quality and use the stable but mediocre resource only when the fluctuating one is low. There are costs associated with each choice. Foraging in the stable area incurs a cost if the variable area has high resources ("overrun cost") and incurs the cost of missing food at the stable area if they sample the variable area when resources are low ("sampling cost"; Shettleworth *et al.* 1988). They tested their model on captive pigeons (*Columba livia*) choosing between feeding stations in which levels of grain were adjusted according to the model's parameters. Shettleworth *et al.* (1988) found the pigeons to behave near optimally, suggesting that pigeons maximise reward rates on a moment-by-moment basis, picking at random from a remembered distribution associated with each alternative.

Decisions made by cormorants travelling through eastern Australia may be analogous to pigeons choosing between feeding stations, providing the risk associated with sampling at a large scale is not prohibitive. Shettleworth *et al.* (1988) kept their study animals in a small cage, so the only potential cost to investigating the variable resource was sampling cost. However, sampling the variable resource for cormorants also incurs the potential risk of starvation, which can occur in 12 days without food (Potts 1969), and dispersing cormorants are sometimes subject to high mortality (as much as 65% in Shags dispersing through Britain, Potts 1969). Although this suggests that there is a great deal of error associated with the quest for food, it is difficult to believe that dispersing cormorants have no way of detecting the quality and location of resources beyond the scale of a single wetland or habitat (Chapter 4).

Cormorants can fly at an altitude of 2000 metres or more as they travel among wetlands (R. T. Kingsford pers. comm.) and while doing so should be able to observe 150 km in every direction (see Emlen 1975) at all times, not withstanding visual acuity and cloud cover. Cormorants attain flying speeds of at least 30m/s (pers. obs.), and therefore could observe over 22,000 km^2 in 5 hours of sustained flying. In addition, a decrease in angular velocity of the apparent ground movement would give cormorants more time to inspect the landscape below (see Emlen 1975). Thus, cormorants do appear to be able change the scale of observation, thus reducing apparent variability and making the model of Shettleworth *et al.* (1988) potentially useful in understanding this system. In addition, the ability to sample large areas quickly reopens the question of whether cormorants may assess rainfall from a distance using visual cues (e.g. swollen or muddy rivers), possibly in combination with more haphazard movements. The necessary next step in testing this model further would involve satellite telemetry. Individual or groups of cormorants could be predicted to relocate frequently among wetlands, but with directed movement towards more productive regions and non-breeding flocks could be predicted to coalesce and disband quickly, depending on resource availability.

In this chapter, the population sizes of cormorants were demonstrated to be highly variable, attaining high peaks against a background of low abundance. It appeared that populations of cormorants relocate frequently, regardless of the specifics of location. In the General Discussion I integrate information on behaviour, habitat selection and dispersal to develop a scale-dependent model of resource use by cormorants in eastern Australia.

CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSION

6.1. Scale-dependent habitat utilisation by cormorants in eastern Australia

The objective of this study was to investigate scale-dependent habitat use by cormorants in eastern Australia, by identifying differences in resource variability in arid and coastal environments. Observations ranged from small (10^{-3} km^2) to large (10^3 km^2) spatial scales, and a descriptive approach, combined with mensurative experiments was used to examine processes that influenced foraging patterns. The specific aims of the thesis were 1) to examine the scale of information cues for cormorants foraging in environments of different regimes of predictability, and 2) to investigate the ways in which foraging behaviour can be scaled to habitat utilisation and distribution across the landscape of eastern Australia. In this chapter, I review the information collected, use decision theory to develop a scale-based conceptual model for resource use, discussing differences among species. I also consider how environmental variability may dictate scales of sampling by foragers.

Foraging cormorants appeared to use environmental cues (e.g. presence of seagrass beds) that allowed them to narrow their search for prey, although the strength of these cues changed with scale (Table 6.1). At the smallest scale, distribution of cormorants was related to environmental features that indicated the precise location of prey (Chapter 3). At an intermediate scale, cormorants were more abundant in areas where foraging cues (ie. foraging conspecifics or seagrass beds) were more prolific (Chapter 4), or where a complex interaction of processes (e.g. rainfall, drainage, aquatic plants) had created abundant resources (Chapter 5). All species in this study demonstrated high variability in abundance, and behaviour was often dependent on local environmental conditions. Abundance, distribution, behaviour, and interspecies associations varied considerably through time and space at every scale of observation. Moreover, variability of wetlands in terms of the degree to which they were filled appears to be an influence.

Table 6.1. Scale-dependent associations with the location of foraging, generalised to all species of cormorant in this study.

SCALE	**MAIN EFFECT ON FORAGING LOCATION**	
	Coast	**Inland**
Small	Position of seagrass	Behaviour of guild members or presence of aquatic macrophytes
Intermediate	Presence of seagrass	Presence of guild members or macrophytes
Large	No obvious effect	Wetland variability

These results are consistent with the literature on population dynamics of cormorants in eastern Australia (e.g. Gosper 1981; Woodall 1985; Kingsford and Porter 1993; Morton *et al.* 1993b), however differences exist among species. Many of these appear to be related to diet, and most strongly apparent at intermediate and small scales. For instance, no relationship existed between wetland size and abundance of cormorants for Great, Little Black and probably Pied Cormorants (Chapter 5), the species that form large flocks, pointing to a selective advantage to flocking for species that concentrate on mobile prey (see also Van Eerden and Volsamber 1995). Little Pied Cormorants, however, were more abundant in larger wetlands, suggesting that individuals of this species space themselves out when occupying positions within a wetland. This is a pattern supported by the spread of Little Pied Cormorants' foraging positions on Patonga Creek (Chapter 3) and their low coefficient of variation across northwest New South Wales (Chapter 5), however it remains to be tested specifically.

In this study, cormorants appeared to sample their surroundings at a number of scales, but it is only small-scale sampling (i. e. that at which prey is captured) that gives a true indication of habitat quality for an individual. Sampling by cormorants at larger scales suffices only to narrow the search. Even the success of a conspecific (Chapter 5, see also Van Eerden *et al.* 1995) would provide an imperfect view of prey availability, especially for inexperienced or weak individuals. Provided cormorants are able to detect resources at a given wetland, the rate of food intake of a cormorant is probably the most important factor in determining the decision to remain (and possibly reproduce) at a site, or leave (see Charnov 1976) and ultimately produces high variability at a landscape scale.

6.2. Multi-scale resource sampling by foragers

6.2.1. The hierarchy of decision making

One difficulty with multi-scale studies is that the scale of observation often dictates sampling method, making comparisons among scales problematic. In studies of highly mobile animals, it is often undesirable, or impossible, to manipulate natural systems to detect an effect using a single design (see Wootton 1994) and a mensurative approach is important. Hierarchy of decision making is a useful 'common currency' (*sensu* Schneider 1994) by which behaviour and distribution can be combined at different scales.

Holling (1992) provided a model for scale-dependent decision making, using storks, ibis and egrets (Ciconiiformes) in Florida. These birds may relocate to wetlands over 1000 km from their birthplace, using coarse-grained assessment of an area region including the Everglades of southern Florida and lakes of northern Florida and the Carolinas. At a finer scale, foraging areas (home ranges) are decided within a few hundred kilometres over the period of about a year, based on instantaneous rate of food acquisition and wetland characteristics. At a still finer scale, decisions concern finding habitats within foraging areas, where food is concentrated. This foraging distance, about 20 km, is where wading birds must travel each day in search of suitable wetlands. Within a habitat, wading birds must choose appropriate patches, at the scale of 10s of metres and about an hour and, finally, decisions are made about the prey themselves. The spatial and temporal extents of foraging, about 1 metre and less than a minute, respectively, are set by the predator's ability to respond to prey.

Holling (1992) presented a graphical representation of this model (Figure 6.1), which defines the 'universe' in which these birds make decisions.

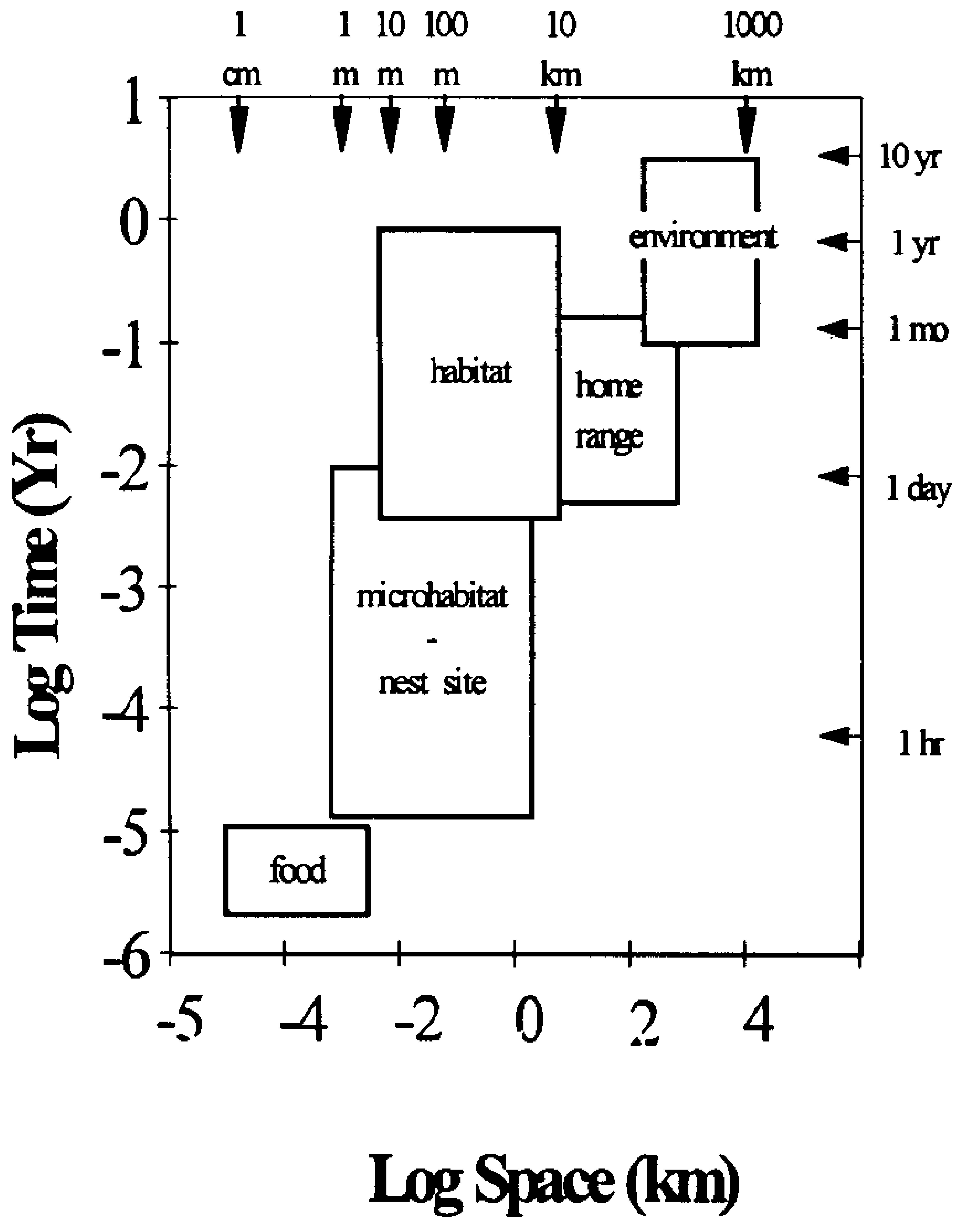

Figure 6.1. Scales in the hierarchy of decisions made by cormorants. Adapted from Holling (1992).

The hierarchy of scales in decision making by cormorants is probably similar to that of ciconiiforms, although the spatial extent of each scale is probably larger for the former, because they are more mobile (see Marchant and Higgins 1990). For instance, a cormorant may chase a fish more than 20 metres through a kelp forest (pers. obs.), an act which encompasses a larger space than that used in the sit-and-wait style of most ciconiiforms.

Holling's (1992) graphical approach delineates scales of decisions made by foragers, however, decision making is also temporally dynamic, as evidenced by the utility of Markov chains in quantifying behavioural series (see Hines *et al.* 1983). As foragers search through their environment, choosing foraging habitats that contain a high density of productive microhabitats, they must alternate among scales. If a cormorant feeding on a lake encounters a consistently low rate of return, it will leave the area in search of a new foraging location (e.g. Volsamber *et al.* 1995), making a predictable switch from small-scale to large-scale sampling. In the section that follows, I use information collected in this thesis to develop a graphical model for foraging cormorants that builds on Holling's (1992) work, incorporating the dynamics of sampling at different scales.

6.2.2. A dynamic model of hierarchical sampling by cormorants

The model (Figure 6.2) is a loop in which the arbitrary starting point is a cormorant arriving inland from the coast (1)[1]. As it approaches a lake it uses features of the landscape to assess enough about the lake to land (2). This may be the reflection of the

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[1] Numbers correspond to elements in Figure 6.2.

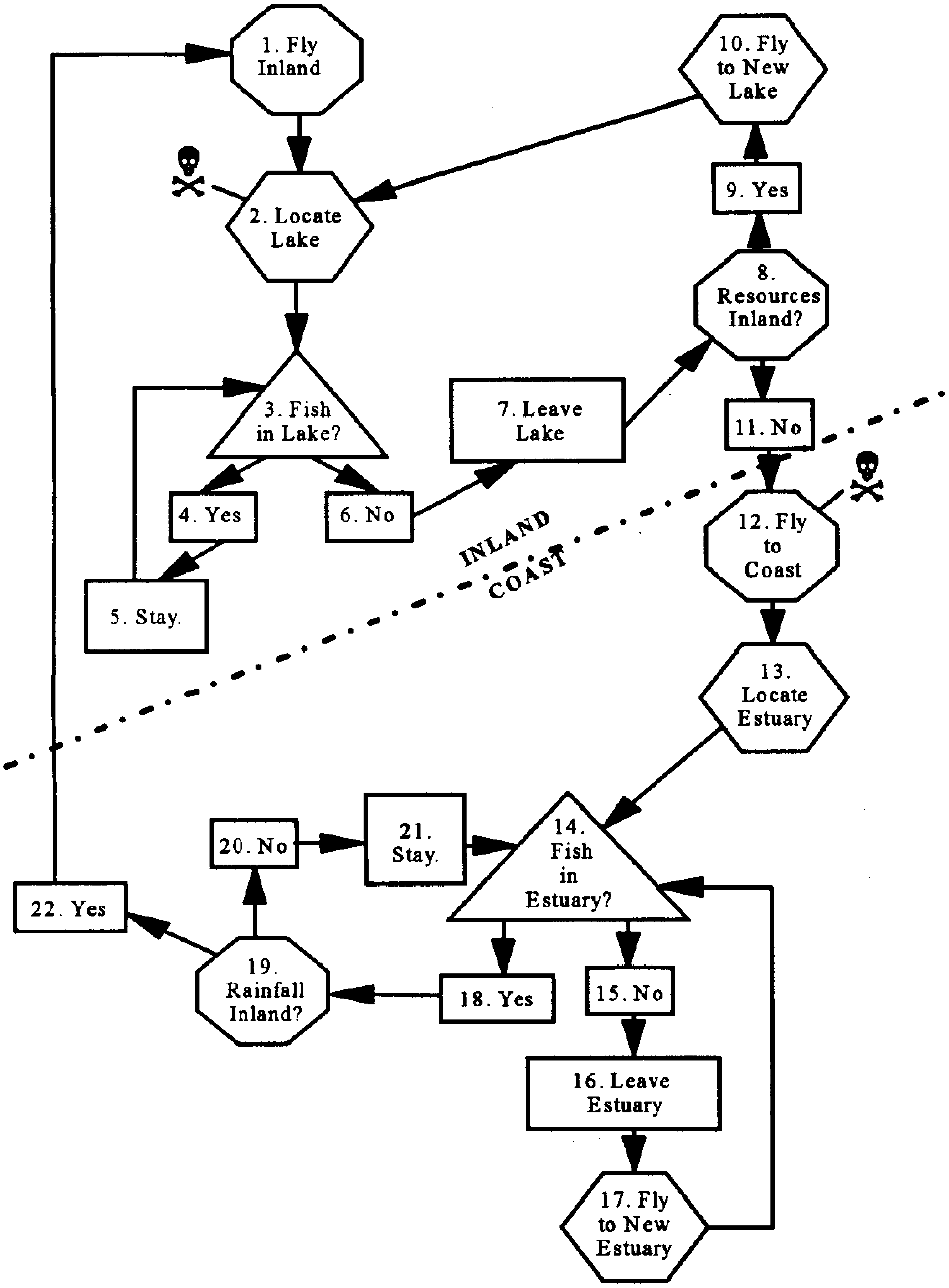

Figure 6.2. Flow diagram of the process of decision-making occurring at different spatial scales. Octagons, hexagons and triangles indicate assessment of large, intermediate and small scales, respectively. Small rectangles indicate the outcome of sampling by cormorants and large rectangles indicate an action taken. A Jolly Roger (☠) indicates elements of the model associated with high mortality (and hence, high risk).

sun or moon (see Schodde 1982), vegetation or presence of conspecifics (Chapter 4). Once at the lake, the cormorant gauges small scale resource quality by comparing its instantaneous rate of food intake to other places it has been (see Charnov 1976; 3). If it is successful (4), it will stay (5), for as long as resources remain. Once fish stocks have declined (6), either through hunting by cormorants (e.g. Craven and Esther 1987) or by abiotic features, such as wetland drying (see Glover 1982), cormorants will leave the lake (7). If resources remain abundant for long enough, cormorants will breed. For Great, Pied and Little Black Cormorants, gregariousness may also influence arriving at, and leaving a wetland.

Up to this point, the cormorant has made a succession of choices which decreases with scale at every step (Figure 6.2). Upon leaving the lake, it must reverse the process and sample at a larger scale, assessing habitat quality once again over the region (8). If the cormorant perceives resources to be abundant inland (9), then it will find a new lake in which to forage (10), and repeat the process of smaller scale habitat assessment (2). If prospects inland are not good (11), the cormorant will fly to the coast (12). Although the dichotomy (8) is presented as straightforward, individuals within a population do not necessarily behave in the same way. Great Cormorants in western France may pass through or remain faithful to overwintering sites, with no apparent distinction in their health or experience (Yésou 1995), possibly indicating a difference among individuals in the predisposition to disperse.

Once a cormorant reaches the coast (12), it will find an estuary, making the decision to land (13) based on stationary habitat features such as seagrass more than on conspecifics (Chapter 4). Once again, the cormorant will assess its microhabitat by hunting (14). If resources are less than the environmental average (see Charnov 1976; 15), it will leave (16), to find another more productive location (17), following the same sequence of scales as inland (1-10). If fish do occur in the estuary (18), the cormorant may still derive a benefit from leaving, if resources inland have improved sufficiently to breed.

Therefore, the cormorant probably monitors conditions inland (19), although the mechanism for doing this remains unknown (Chapter 5; see also Schodde 1982). The series (14,18,19,20,21), reflects a behavioural loop in which a cormorant samples two food sources, one mediocre but stable, the other fluctuating between extremes of high and low quality (see Shettleworth *et al.* 1988; Chapter 5). If the cormorant receives cues indicating abundance of resources inland (22), it will leave the estuary, irrespective of its quality, and fly inland once again (1), completing the cycle by making decisions in a hierarchy of spatial and temporal scales. Although some aspects of this model could not be tested here, its basic structure is formed from the information collected in this thesis and supporting information from the literature, and further predictions may form the basis for future studies.

6.3. Further research

6.3.1. Marking and tracking individuals

A difficulty in comparing data on abundance from aerial surveys to environmental phenomena is that one may be unable to separate out small scale events that dictate short term movements, potentially resulting in poor correspondence between variables (Type II error). A direct link is therefore needed. Radio or satellite telemetry allows movements of foragers to be coupled simultaneously with fine-grained events and processes that encompass a large spatial extent (e.g. coyote *Canis latrans* predation on domestic sheep *Ovis aries*; Shivik *et al.* 1996). Telemetric methods would be useful in studying cormorants in eastern Australia. For instance, arrivals and departures of cormorants could be measured directly in relation to foraging success. Moreover, satellite telemetry would be necessary to gather unequivocal information about movements to and from the coast in relation to rainfall.

6.3.2. Consequences to survival and reproduction

Data from this thesis suggest that cormorants may be more mobile than they need to be to track their resources, especially on the coast (Chapter 5). Cormorants could be balancing the risk of starvation incurred from remaining at a location in decline against the risk of starving through failure to find a new wetland containing food. Alternatively, they may be inherently highly mobile, irrespective of the state of resources. Either strategy would have consequences to reproduction as well as survival.

Waterbirds may 'miscalculate' by remaining at a wetland too long after resources have declined, becoming too weak to relocate, eventually starving (e.g. Black Swans *Cygnus atratus*, Lake Wyara, QLD, 1993; pers. obs.). Reproduction may also be initiated too late after a temporary wetland has begun to dry, leaving juveniles to starve or dehydrate before they are old enough to leave (e.g. Australian Pelicans, Lake Wyara, 1993; pers. obs.). The consequences of different choices are more important inland, because cormorants are more likely to starve (R.T. Kingsford unpubl. data), and to reproduce, in the interior.

Following the fate of individuals, through a combination of mark-resight, telemetry and nest tagging, would provide the opportunity to test the ability of cormorants to optimise their foraging decisions with respect to the distribution of resources. In addition, the consequences of those decisions to survival and reproduction could be measured directly.

6.3.3. Other aquatic birds

In this thesis, the purpose of comparing the behaviour and distribution of four species was to gain an understanding the effect of changing resources on birds that rely directly on bodies of water. It would be productive to compare activity patterns of cormorants to other large waterbirds inhabiting eastern Australia. For instance, Australian Darters

Anhinga melanogaster, closely related to cormorants, have a diet that overlaps with that of Little Pied Cormorants, (see Barker and Vestjens 1987). Darters also forage singly, occupying similar inland habitat types (see Marchant and Higgins 1990), although the population is substantially smaller (e.g. Kingsford *et. al.* 1996). Differences in thermoregulatory ability also suggest that members of the genus *Anhinga* may be better suited to the tropics and less suited to temperate regions than are members of *Phalacrocorax* (Hennemann 1983). Darters might exhibit the same variability in distribution as cormorants, but occur more densely toward the north of their range, so that landscape-scale patterns of association among species would change with latitude.

Similarly, comparisons with large herbivorous birds such as Black Swans may aid in understanding this system. The range of Black Swans is similar to that of cormorants (Blakers *et al.* 1984), but patterns at individual wetlands differ. The clear water of saline wetlands, which promotes the growth of aquatic plants (Kingsford and Porter 1994), appears to be better for swans, but too salty to support fish (Bruton 1985) and so are less important to cormorants (Kingsford and Porter 1994). Because some inland wetlands undergo a change from fresh to salt water as they dry (see Glover 1982), populations of Black Swans in wetlands that salify with time might fluctuate with a time lag behind populations of cormorants, although on a larger scale, the effect would probably be obscured by high mobility of these species. The sequence would not be predicted on the coast or in wetlands that remain fresh because differentiation of resources would not cycle predictably through time, and cormorants and swans frequently co-occur in these areas (e.g. Briggs 1979; Whyte 1981; Gosper 1983; Fjeldså 1985).

6.4. Conclusion

Addressing the processes by which foraging animals gather information at different scales, and the way in which they switch from one scale to another are stimulating fields of research which have not yet been widely addressed. It is especially interesting for Australian waterbirds, which disperse widely over a highly heterogeneous landscape. In this study, cormorants were found to be highly mobile opportunists using information at a combination of scales, and these were influenced by environmental variability and predictability. In highly unpredictable environments, small-scale, precise cues (such as the behaviour of conspecifics) appear to be required for cormorants to forage successfully, whereas in more predictable environments, slowly changing, less precise cues are sufficient.

In eastern Australia, survival and reproduction of cormorants appear to be closely linked to the ability to travel between inland and the coast, therefore, the ability to adjust the scale of response appears to be highly adaptive. The generality of this idea, and its applicability to other species would form a fertile basis for future investigations.

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