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Between a Rock and a Hard Place: Conserving the Broad-headed Snake in Australia's oldest National Park

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The broad-headed snake (*Hoplocephalus bungaroides*) is recognised as one of the most endangered reptiles in Australia. This study examined the distribution of the broad-headed snake in Royal National Park in order to devise measures to conserve the species in this Park. Loose rock on rock outcrops provides vital shelter sites for the broad-headed snake. Surveys were conducted by searching under loose rock at 26 rock outcrop sites distributed throughout the Park. Sites were categorised as disturbed or undisturbed based on proximity to roads and walking trails which are extensive in the Park. Broad-headed snakes were found at nine sites, representing a significantly greater proportion of undisturbed sites. This suggests that the distribution of the snake was influenced by disturbance. Quantification of the loose rock habitat revealed little difference between disturbed and undisturbed sites. Thus, either the methods of quantification were inadequate or broad-headed snakes simply avoid sites classed as disturbed. Further studies are needed to assess ongoing habitat disturbance in this Park, to review all walking tracks that are located close to suitable snake habitat and to assess the feasibility of recovering sites that are presently disturbed.

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KEYWORDS: broad-headed snake, *Hoplocephalus bungaroides*, endangered, Royal National Park.

INTRODUCTION

The conservation status of Australian reptiles was recently reviewed (Cogger et al. 1993). Scores were given to species based on their population size, population stability, distribution, reproductive rate and ecological specialisation. The broad-headed snake (*Hoplocephalus bungaroides*) received a total score suggesting that it was the second most endangered snake in Australia. The availability of information required for the conservation of the species was poor and it was concluded that the species should have a high priority for research and monitoring (Cogger et al. 1993). Indeed, the species is accorded the highest conservation status by the New South Wales *Threatened Species Conservation Act* 1995 and is also listed by the Australian *Endangered Species Protection Act* 1992. It has been formally recognised as endangered in NSW since 1974.

The geographic range of the broad-headed snake is one of the smallest for an Australian elapid snake and is virtually confined to the region of the Sydney basin (Longmore 1989; Swan 1990; Cogger 1992). Within this region it is broadly distributed across many National Parks, including several of considerable size and some that are Australia's oldest. However, detailed information on the distribution of the broad-headed snake is absent and its presence within such conservation areas does not guarantee long term survival due to the close proximity of the greatest concentration of Australia's human population. The ultimate goal for recovery of the species is to ensure that viable populations are maintained across the reserve system (Cogger et al. 1993).

The broad-headed snake has become threatened due to habitat destruction caused by urban expansion, bush rock collection (Hersey 1980; Shine and Fitzgerald 1989) and possibly removal of hollow-bearing trees that provide summer retreat sites (Webb and Shine 1997a). Loose sandstone rocks on rock outcrops offer shelter to broad-headed snakes and their prey, and therefore comprise a vital habitat component (Hersey 1980; Webb 1996; Webb and Shine 1997b). Despite extensive collection of bush rock for garden ornamentation in areas around Sydney, neither the severity of this problem nor its solution is known. Natural replacement of this habitat component may take millennia (Webb 1996). Thus, studies on the species should document the availability of the loose rock habitat throughout its range.

Royal National Park, Australia's oldest National Park, was chosen as an example of a conservation reserve where the status of the broad-headed snake needs to be determined. This Park has been declared for over 100 years and has the greatest recreational use of any in which the snake occurs. Therefore, this Park should provide a good model for examining the management requirements of the snake. The present study aimed to: i) determine the distribution of the broad-headed snake in Royal National Park, ii) assess the influence of disturbance on the habitat of the snake, and iii) provide recommendations for the management of the snake in this Park.

METHODS

Study Area

This study was conducted in Royal National Park (Royal NP) which has an area of approximately 17000 ha. The Park is located about 24 km from the Sydney GPO and forms the southern boundary of the Sydney metropolitan area. Continuing urbanisation has virtually isolated the Park from other bushland areas; links with Heathcote National Park to the west are tenuous, as the two Parks are separated by the Princess Highway (and associated urban development along the western boundary) and by the Sydney-Wollongong Freeway along the south-western boundary. The eastern boundary is the coastline.

Royal NP consists of four broad habitat types: heathland, woodland, open forest and closed forest. Heathland is the most extensive habitat type in the Park with open forest dominating the gullies and ridges on the western and southern sides of the Park, and woodland occurring between these two habitats. Closed forest is mostly confined to the gully along the Hacking River. A wildfire in January 1994 burnt through about 95% of the Park (Whelan et al. 1996) with only the closed forest surviving unburnt.

Survey Sites

Areas that contained potential habitat for the broad-headed snake were identified from topographic maps and traverses of the Park. Selection of survey sites was based on the presence of rocky ridges, rock ledges or outcrops that contained loose rock and which had a north through to west aspect. These aspects are favoured by snakes as they receive the late afternoon sun during the cooler months of the year, which is beneficial to these nocturnal snakes (Webb 1996). Many sites contained disjunct patches of rocky habitat but the area searched at each site was approximately equal to a transect 200 m x 30 m. Sites devoid of any loose rock were not chosen. Adjacent sites were chosen only if they were separated by at least 300 m.

A total of 26 sites were identified as appropriate for survey. A further 14 sites were examined but could not be used because they were virtually devoid of loose rock (probably due to past anthropogenic disturbance). Sites were chosen to adequately represent

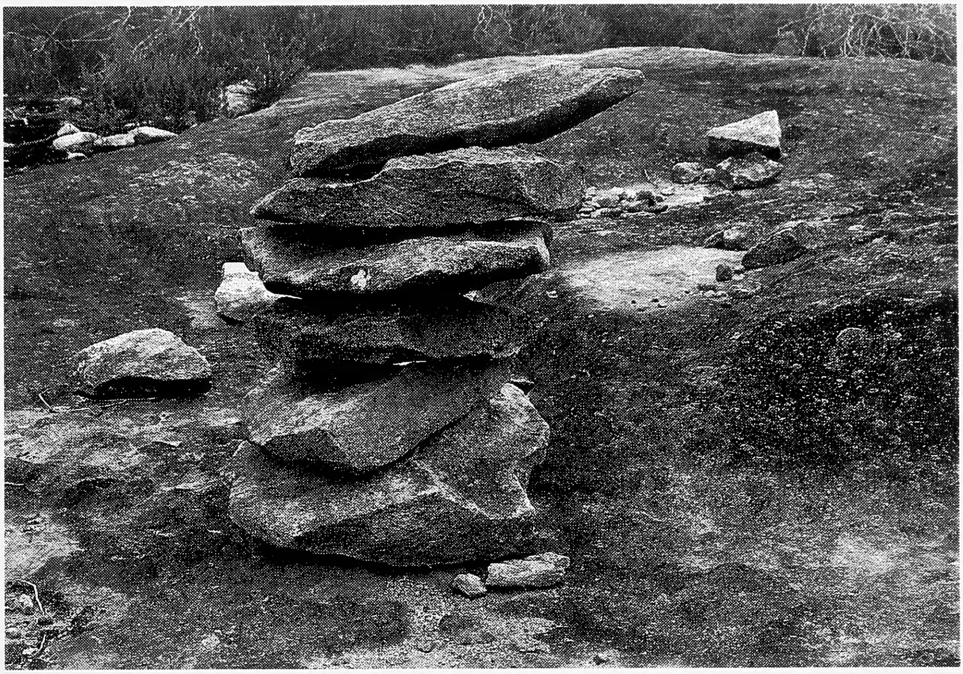

Figure 1. Disturbance of the loose rock habitat — indicated here by a rock pile apparently constructed by hikers.

two broad habitat types, forest and woodland-heath (an ecotone between woodland and heath), where broad-headed snakes have been recorded previously. Forest was represented by 15 sites and woodland-heath by 11 sites. All sites were affected by the 1994 fire.

All sites were placed into one of two categories (disturbed or undisturbed) based on their potential for disturbance. Disturbed sites were arbitrarily defined as those that were located within 300 m of a road or walking trail. The long period of recreational use of the Park (>100 years) may make it more difficult to recognise more than the most obvious signs of rock disturbance (e.g. camp fires), so an operational definition was needed. However, this definition is consistent with the criteria used by Schlesinger and Shine (1994), based on several types of recognisable disturbance to a rock outcrop (see Fig 1). The present definition could be applied objectively and allowed consistency through time, so that intermittent disturbance to outcrops during the survey period would not require that they be switched to a different category. Because of the high public use of the Park and its age (dedicated in 1872), most sites were placed in the disturbed category. A total of 17 disturbed and nine undisturbed sites were identified for surveys.

There are a number of factors that could affect the presence of snakes on rock outcrops other than the level of habitat disturbance. The main factor appears to be temperature. Radio-tracking studies of broad-headed snakes approximately 100 km south of Royal NP established that the cooler months of the year are the most appropriate time to look for snakes sheltering under loose rock (Webb 1996; Webb and Shine 1997b). Thus, surveys of outcrops were only conducted between late April and mid-September. Even within this period, temperatures varied substantially and may have influenced the detection of snakes. Also, it was not known whether rain would affect the use of loose rocks by snakes, so surveys were not conducted during periods of heavy and continuing rain. To maximise the chances of detecting snakes a survey strategy was employed whereby every site was surveyed on three different occasions, with a minimum of 2 weeks between repeat surveys at the same site. Surveys were conducted between April 1995 and July 1997.

Surveys consisted of walking through a site and searching for snakes under loose rock by one or two people. Care was taken to ensure that the same rocks were not searched twice when two people were present. Rocks that lay on a rock base were the focus of the survey. Rocks that were embedded in the soil, located in wet areas or which did not lay flush with the substrate were not considered suitable. Many rocks in these categories (>100) were lifted during the survey but were never found to conceal broad-headed snakes. No attempt was made to search adjacent rock crevices. Several factors were recorded during each survey of a site: the time taken to survey the site (the elapsed time multiplied by the number of people searching), the total number of suitable rocks that were lifted, the number of these rocks that sat neatly on a bare rock substrate (>50% bare), and the number of reptiles encountered under the rocks. Only rocks of >10 cm length were included. All snakes found under rocks were captured, measured, and for broad-headed snakes, given a small but distinctive cut on the ventral scales so they could be identified if recaptured.

Habitat Measurements

The availability of loose rock was quantified in two ways. Firstly, the number of rocks turned during each site survey was recorded. The number counted in each survey was averaged over several surveys at a site. This was done because it was not possible to precisely mark out a survey transect at each site, nor was it known whether the number of rocks at a site would change temporally. Secondly, the abundance and size distribution of rocks at each survey site were sampled in three quadrats, each measuring 5 x 10 m. These measurements were made at each site during the latter part of the snake survey. The method for this followed that of Schlesinger and Shine (1994) but differed in a few respects. The quadrats were placed at each end and in the middle of the survey area. The length, width and thickness of all rocks >10 cm diameter were measured and the number of these rocks that lay directly on a rock substrate was counted.

RESULTS

Snake Survey

Each of the 26 sites were surveyed three times. Broad-headed snakes were detected at seven forest sites and two woodland-heath sites (Table 1). This result shows that the broad-headed snake could be found in each habitat type, and that all sites could be used to examine the influence of habitat disturbance. There were nine sites categorised as undisturbed (U) and 17 sites categorised as disturbed (D). The amount of time (min) spent searching sites was equivalent ($t=0.67$, $P=0.51$) for both categories (mean±s.e.; U = 28.0±3.2, D = 25.6±2.0). Broad-headed snakes were located at five of the undisturbed sites and two of the disturbed sites following three surveys to each site; this distribution was significantly dependent on the disturbance category ($G=5.61$, $P<0.025$). A broad-headed snake was also found at disturbed site C in 1994. A fourth survey was made to four of the forest sites and a broad-headed snake was detected at one undisturbed site (H) where none had been detected in the three earlier surveys. In contrast, the small-eyed snake (*Rhinoplocephalus nigrescens*) was detected at 10 of the 26 sites (Table 1), and its distribution was independent of disturbance category ($G=1.68$, $P>0.1$). Six of the sites in which broad-headed snakes were located during the three visits were located in the southern part of the Park. However, separate analysis of these data showed a significant influence of site disturbance on the distribution of broad-headed snakes ($P<0.02$) but not on small-eyed snakes ($P>0.75$).

TABLE 1

Snake survey data for Royal NP. Habitat was Forest (F) or woodland-heath (W), and disturbed (*) or undisturbed. Values (except BHS, SES) are means of three repeat surveys. Rocks = the number of rocks turned; good = the number of rocks sitting on a rock substrate; BHS = broad-headed snake; SES = small-eyed snake. Values for BHS and SES show the number of snakes for each of 3 surveys (values in brackets are snakes detected outside the 3 surveys). Geckos and skinks are the number encountered under rocks.

Site	Habitat	Time (min)	Rocks	Good	BHS	SES	Geckos	Skinks
AA	F*	24	49	27	0/0/0	0/0/3	6.3	0.7
A	F	36	43	15	1/0/0	1/0/0	3.0	0.7
B	F*	22	34	8	0/0/0	0/1/1	0	0
C	F*	20	25	5	0/0/0 (1)	0/0/0	0	1.3
D	F*	43	67	21	0/0/0	0/0/1	3.3	0
E	F	19	24	11	1/0/0	0/0/0	0	0.3
F	F	49	82	18	0/0/0	1/3/0	5.0	0
G	F	26	45	18	0/1/0	1/0/0	1.0	0
H	F	17	31	10	0/0/0 (1)	1/0/0 (2)	0.3	0.3
I	F	26	54	13	1/0/0	2/0/0	1.3	0.7
J	F	26	52	13	0/1/0	0/0/0	0.7	0.7
K	F*	30	37	9	0/0/0	0/0/0	2.3	2.0
KK	F*	21	47	13	0/0/0	0/0/0	1.0	1.0
L	W*	14	15	7	1/1/0	0/0/0	1.3	0.3
M	W	27	68	16	0/0/0	0/0/0	1.3	1.7
N	W*	25	56	15	0/0/0	1/0/0	0.7	0.7
P	W*	41	65	20	0/0/0	0/0/0	1.7	0.7
Q	W*	29	53	12	0/0/0	0/0/0	0.3	0.7
R	W*	20	38	8	0/0/0	0/0/0	4.0	2.0
S	W*	30	51	19	1/0/0	0/0/0	2.3	0
T	W*	21	70	19	0/0/0	0/0/0	1.0	0.7
U	F*	19	58	20	0/0/0	0/0/0	0.3	0
V	W	26	69	14	0/0/0	0/0/0	2.7	2.0
W	F*	37	62	19	0/0/0	0/1/0	5.3	2.3
WW	W*	16	48	11	0/0/0	0/0/0	0.7	0.3
Y	W*	23	69	21	0/0/0	0/0/0	4.7	0.3

Broad-headed snakes in all but one instance chose rocks that had a dry, bare-rock substrate underneath. The rocks (n=11) varied from 3–11 cm in thickness (mean±s.e., 6.4±0.7 cm), from 46–134 cm in length (70.4±7.4 cm) and from 30–67 cm in width (43.1±3.9 cm). Small-eyed snakes chose rocks that often contained soil and leaf litter underneath and although similar in thickness, the rocks were smaller in size to those of the broad-headed snake. These rocks (n=13) were 2–11 cm (6.0±0.6 cm) in thickness, 22–83 cm (50.5±4.7 cm) in length and 17–46 (32.6±2.5 cm) in width.

Loose Rock Habitat

The availability of rocks surveyed varied among sites from 24 to 82 (Table 1). The number of rocks that had a rock substrate underneath varied from 5 to 27 among sites. When these values are averaged over site categories, the total number of rocks surveyed at the undisturbed sites (52.0±6.2) was equivalent (t=0.34, P=0.74) to that surveyed at the disturbed sites (49.6±3.8). The number of rocks with a rock substrate that was surveyed at the undisturbed sites (14.2±0.9) was equivalent to that at the disturbed sites (14.9±1.5).

The data recorded from the three 5 x 10 m quadrats were also consistent with the above data on rock abundance at each site (Table 2). The total number of rocks per three quadrats was equivalent at undisturbed sites (29.8±1.3) and disturbed sites (31.6±2.3). A similar number of rocks sitting on a rock substrate was counted at undisturbed sites (7.8±1.5) and disturbed sites (8.7±1.0).

TABLE 2

Rock habitat measurements at each site. * = disturbed sites. Total rocks = the number counted in three 5 x 10 m quadrats. Suitable thickness = the number of rocks within the range (3–11 cm) selected by broad-headed snakes. Suitable LxW = rocks within the range of length (46–134 cm) and width (30–67 cm) selected by snakes. Suitable LxWxT = rocks with suitable length, width and thickness. Values in brackets show the number that were sitting on a rock substrate.

Site	Total Rocks	Suitable Thickness	Suitable LxW	Suitable LxWxT
AA*	40 (7)	27 (4)	7	4 (2)
A	31 (10)	26 (9)	6	6 (2)
B*	39 (7)	29 (4)	8	4 (0)
C*	21 (6)	15 (3)	3	3 (2)
D*	33 (5)	31 (5)	1	1 (0)
E	29 (8)	22 (5)	9	6 (2)
F	28 (9)	25 (8)	8	8 (2)
G	36 (18)	30 (15)	10	10 (7)
H	33 (2)	30 (2)	5	5 (0)
I	28 (6)	25 (5)	3	3 (1)
J	33 (6)	28 (2)	5	5 (1)
K*	32 (15)	31 (15)	3	2 (1)
KK*	46 (20)	41 (18)	7	5 (5)
L*	20 (4)	17 (3)	2	2 (1)
M	26 (4)	23 (4)	2	2 (0)
N*	37 (10)	35 (9)	3	3 (2)
P*	26 (5)	23 (4)	4	4 (2)
Q*	31 (6)	25 (6)	3	2 (1)
R*	20 (7)	18 (6)	9	8 (3)
S*	17 (4)	14 (2)	2	2 (0)
T*	31 (10)	28 (9)	12	11 (6)
U*	32 (11)	28 (9)	6	5 (2)
V	24 (7)	19 (7)	5	5 (3)
W*	24 (10)	15 (5)	4	2 (1)
WW*	47 (10)	42 (9)	1	1 (1)
Y*	41 (11)	34 (9)	9	9 (1)

The dimensions of rocks selected by broad-headed snakes (including 6 adults and 3 juveniles) were used to devise an index of rock suitability at each site. It was assumed that the ranges in rock size (see above) reflected a size preference by snakes. Comparing the numbers of rocks within the thickness range of those selected by broad-headed snakes revealed no difference between undisturbed sites (25.6±1.4) and disturbed sites (26.4±2.0). If only those within this grouping that had a rock substrate are counted, the number of rocks potentially preferred by broad-headed snakes was not different at undisturbed sites (6.6±1.5) compared to disturbed sites (6.9±1.0).

The abundance of rocks at each site within the range of length and width selected by snakes was compared from the quadrat data (Table 2). This showed that the number of rocks was greater for undisturbed (5.9±0.9) sites compared to disturbed sites (4.9±0.8) but the difference was not significant (t = 0.75, P = 0.46). Comparing those in this group that also had the appropriate thickness revealed no significant difference (t = 1.36, P = 0.18) between the undisturbed sites (5.6±0.8) and the disturbed sites (4.0±0.7). The number of rocks in this group with a rock substrate was equivalent between the undisturbed sites (2.0±0.7) and the disturbed sites (1.8±0.4).

Availability of Potential Prey

The number of lizards seen under rocks was quite variable across all sites (Table 1). A lower number of geckos (*Oedura lesueurii*) was recorded at undisturbed sites (1.7±0.5) compared to disturbed sites (2.0±0.5) but the difference was not significant (t = 0.49, P = 0.63). The number of small skinks (various species) was equivalent between the undisturbed (0.7±0.2) and disturbed sites (0.8±0.2).

DISCUSSION

Snake Distribution

The broad-headed snake like many endangered vertebrates is not an easy animal to study due to its rarity. This necessitated devising a standard survey method that could be applied in any area where information on relative abundance and distribution was required. Three visits to a site with suitable habitat was arbitrarily chosen and reflected a trade-off between survey intensity at a site, and the number of sites to be surveyed. Snakes were found at sites during the first or second survey except in two cases when they were found outside the three surveys. Thus, two searches several months apart may suffice when a general index of presence or absence is needed. Weather conditions are likely to influence the detection of sheltering snakes. Dry sunny conditions the week before and during the survey appeared the most appropriate.

Although the locations of broad-headed snakes were distributed quite broadly across the Park, there was a concentration in the southern part of the Park. This may reflect either a greater expanse of forest, which has been suggested to be the snake's preferred habitat (Swan 1990), or may reflect lower levels of disturbance. Roads and walking tracks tend to be located in gullies in the southern part of the Park but close to ridges in the northern part of the Park. However, data analysis revealed that broad-headed snakes in the southern part were significantly influenced by site disturbance while small-eyed snakes were not.

The detection of single broad-headed snakes at eight survey sites (two were detected at a ninth site) suggests that either the density of snakes was extremely low or that lifting of rocks at a site created disturbance that the snakes avoided. Although the latter cannot be ruled out, it is likely that the snakes were at very low density in Royal NP given the extensive area and large number of rocks surveyed. This low density could be the result of recent wildfires in the snake's habitat. Broad-headed snakes often use tree hollows as retreat sites during summer (Webb 1996; Webb and Shine 1997a), making them vulnerable to summer wildfires. This could have led to the death of many snakes in January 1994 when fires swept through 95% of the Park. Low reproductive and growth rates (Webb 1996) would keep their abundance at low levels for many years.

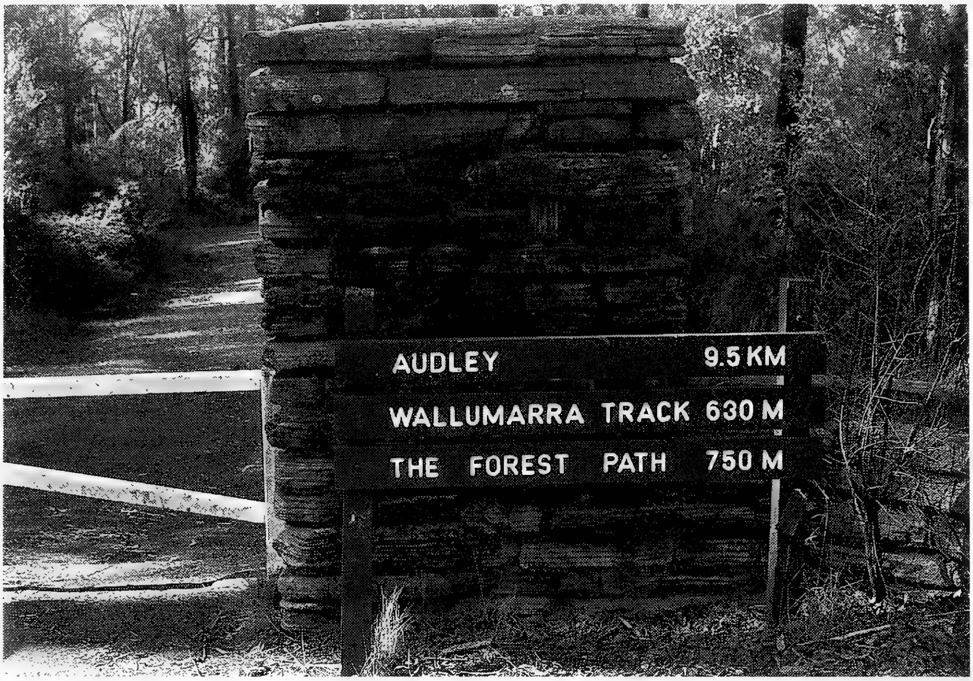

Figure 2. The gateway marking the southern end of Lady Carrington Drive constructed last century from loose rock of a size suitable for broad-headed snakes.

Habitat Disturbance

There was an influence of disturbance on the distribution of the broad-headed snake. Other studies have suggested that disturbance of its habitat may result from bush rock collection for garden ornamentation or from logging (Shine and Fitzgerald 1989; Schlesinger and Shine 1994; Webb and Shine 1997a; Shine et al. in press). These forms of disturbance may be of less concern within well-patrolled National Parks like Royal NP. Interestingly, several historic rock walls in the Park are constructed from rocks approximating the dimensions of those preferred by broad-headed snakes (Fig. 2). This may explain the dearth of loose rock at some of the 14 sites rejected from inclusion in this study.

Disturbance of the habitat of the broad-headed snake is extensive within Royal NP, has multiple causes and is an ongoing process. One disturbed site where a snake was observed was vandalised by the construction of two small rock gardens for growing cannabis. One undisturbed site was in the process of being vandalised in a similar way when visited for the third survey. The people responsible reported displacing a snake resembling a broad-headed snake at the former site. A walking trail adjacent to another disturbed site had been partly constructed from loose rock suitable for snakes. In yet another area, such rocks had been used to form a drainage channel. Disused camp fires constructed with such rocks were seen at several sites.

The influence of disturbance on the measured variables of the loose rock habitat was not strong. The number of rocks did not differ between disturbed and undisturbed sites. When the dimensions of rocks selected by snakes were considered, the undisturbed sites contained only marginally more of the "preferred" rocks than the disturbed sites. Snakes may simply avoid sites where human recreational activities are at a high level such as would be predicted for the disturbed sites. The rarity of broad-headed snakes at disturbed sites could also be a result of snake collectors that removed broad-headed snakes from easily accessible sites. The latter explanation is quite likely given that this species is valued by amateur herpetologists in Sydney (Hersey 1980; Shine et al. in press) and that Royal NP was a well-known collecting site (J. Webb pers. comm.). Recolonisation of sites cleared of broad-headed snakes may be very slow due to their low reproductive and growth rates. This species gives birth to 1–5 young every 2–3 years (Shine 1983; Webb 1996).

Active management for the broad-headed snake should be given a high priority in Royal NP. However, few areas in the Park contain undisturbed habitat. Many areas of suitable habitat are either traversed by walking trails or in close proximity to walking trails. Hence, protection of the broad-headed snake's habitat will always be difficult. Given that this snake is critically endangered it is not realistic to ignore its management requirements in this National Park no matter how small the local population of snakes might be.

Management of Broad-headed Snake Habitat

Studies have found that thin (<15 cm thick) loose rocks exposed to direct sunlight are used extensively by broad-headed snakes during the cooler months of the year (Webb 1996; Webb and Shine 1997a). By choosing these rocks, snakes can remain active by maintaining their body temperatures within their preferred range (see Huey et al. 1989; Webb 1996; Webb and Shine 1998). This would allow snakes to feed over longer periods of the year to maximise their levels of growth and reproduction (Huey et al. 1989). In areas where loose rock has been destroyed, snakes may be forced into hibernation for a long period of the year which may restrict reproductive output. Thus, such areas may only be able to support low densities of snakes and their prey. This may have adverse consequences if maintained over long periods of time for isolated populations such as that in Royal NP. It is assumed that the time period for natural replacement of loose rock is millennia (Webb 1996). This indicates that active management of the snake's habitat is required.

An obvious outcome of the present study is the need to examine ongoing disturbance of the loose rock habitat within Royal NP. A short-term study should be initiated that provides an assessment of continued disturbance to the loose rock habitat. This could be done by establishing sites where loose rock is experimentally placed on rock shelves at disturbed and undisturbed locations. The locations of these rocks would be precisely mapped at the beginning and end (e.g. 12 months later) of the experiment. This would allow an assessment of the level of ongoing disturbance and an insight into the feasibility of recreating this habitat component to benefit the snakes. Such a study should also consider the potential to increase the abundance of the snake's prey species through managing the loose rock habitat.

Given the paucity of broad-headed snakes in Royal NP and the extent of ongoing habitat disturbance, similar surveys are now required in other National Parks around Sydney to examine the suitability of the habitat for this endangered species. This information is fundamental to conserving this species but presently no such information is available (Cogger et al. 1993). A recent study included many off-Park areas (see Shine et al. 1998). Surveys could establish a baseline of the distribution and abundance of the broad-headed snake that could be used by Park managers in future years to monitor the local status of the species. For example, the present study provides baseline data on the distribution of broad-headed snakes in Royal NP. It is recommended that surveys be conducted every five years at fixed sites to provide an assessment of the status of the population. Such a frequency should minimise any disturbance caused by these surveys but consideration should be given to whether such surveys have an impact on broad-headed snakes.

Given the low reproductive rate of the broad-headed snake, the loss of snakes to either wildfire or snake collectors will have a severe impact on population stability. The extensive use of tree hollows by broad-headed snakes in summer (Webb and Shine 1997a) necessitates consideration of active fire management to protect snake habitat from summer wildfires. Control fires in buffer zones or burning snake habitat in the cooler months when snakes are not in tree hollows should be considered. It is not clear at present how to protect snakes from collectors but this may be achieved by ensuring that rock outcrops are not too accessible. The present study found that snakes were more frequently detected at undisturbed sites, demonstrating the need for active management to ensure such sites remain undisturbed. A comprehensive review of all walking trails with some rationalisation such as the closure of particular walking tracks will be needed. It may also require specific fire management to promote dense vegetative growth near tracks to discourage hikers from walking beyond track boundaries. A program of public education should be initiated in Royal NP to increase public awareness of the vulnerability of this snake to habitat disturbance (e.g. to discourage construction of camp fires). This could be used to encourage reporting of people who may interfere with the snake's habitat.

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Carbonate Sedimentology of the Late Early to Middle Devonian Limestone Members of the Yarrimie Formation, Manilla, NSW

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The Sulcor and Moore Creek Limestone Members of the siliciclastic and volcaniclastic Yarrimie Formation occur east of Manilla, NSW. The limestones are exposed in two continuous belts on the eastern limb of the Yarramanbully anticline. The Sulcor Limestone Member at Yarramanbully is late Emsian in age and is a northern equivalent of the Sulcor Limestone Member near Attunga. The Moore Creek Limestone Member is middle to late Eifelian to possibly early Givetian in age. It is a northern equivalent of the Moore Creek Limestone Member near Attunga and near Tamworth. In both units the base is not exposed and the top of the older limestone is erosional; the top of the younger limestone is covered or faulted, and possibly erosional in the north. A number of disconnected small limestone bodies in the vicinity are interpreted as tectonic fragments, olistoliths and clasts in megaconglomerates.

All limestones are of shallow marine origin; the older Sulcor equivalents were deposited in shallow quiet water, the younger Moore Creek equivalents include basal reworked sediments changing upwards to massive shallow marine carbonates. In both limestones a deepening upward trend is observed and there is some indication that the northern limestones where deposited in shallower water than the southern ones, suggesting deposition on a bathymetric gradient.

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KEYWORDS: Devonian, Emsian, Eifelian, Givetian, Tamworth Group, Yarrimie Formation, Moore Creek Limestone Member, Sulcor Limestone Member, carbonate sedimentology, biostromes.

INTRODUCTION

Scattered limestone bodies largely of Devonian age are abundant in the Tamworth Belt of NSW (Fig. 1). Limestones belonging to the Emsian to Givetian Sulcor and Moore Creek Limestone Members of the Yarrimie Formation are exposed in the Yarramanbully region (Fig. 2) approximately ten kilometres east of Manilla (NSW) extending southward over six kilometres.

The purpose of this paper is to document recent geological mapping and sedimentological studies of the limestones in the Yarramanbully region. The area was mapped on 1:25 000 scale airphotos. The field data were transposed onto the 1:25 000 scale topographic map (map sheet KLORI 9036–II–N; Central Mapping Authority of NSW) (Fig. 3). Sections were measured through key locations with good exposure and minor deformation.

GEOLOGICAL SETTING

Large limestone bodies informally known as the Yarramanbully limestones of the Yarrimie Formation (Chappell 1961; Crook 1961; McMinn 1977, 1982) are exposed on

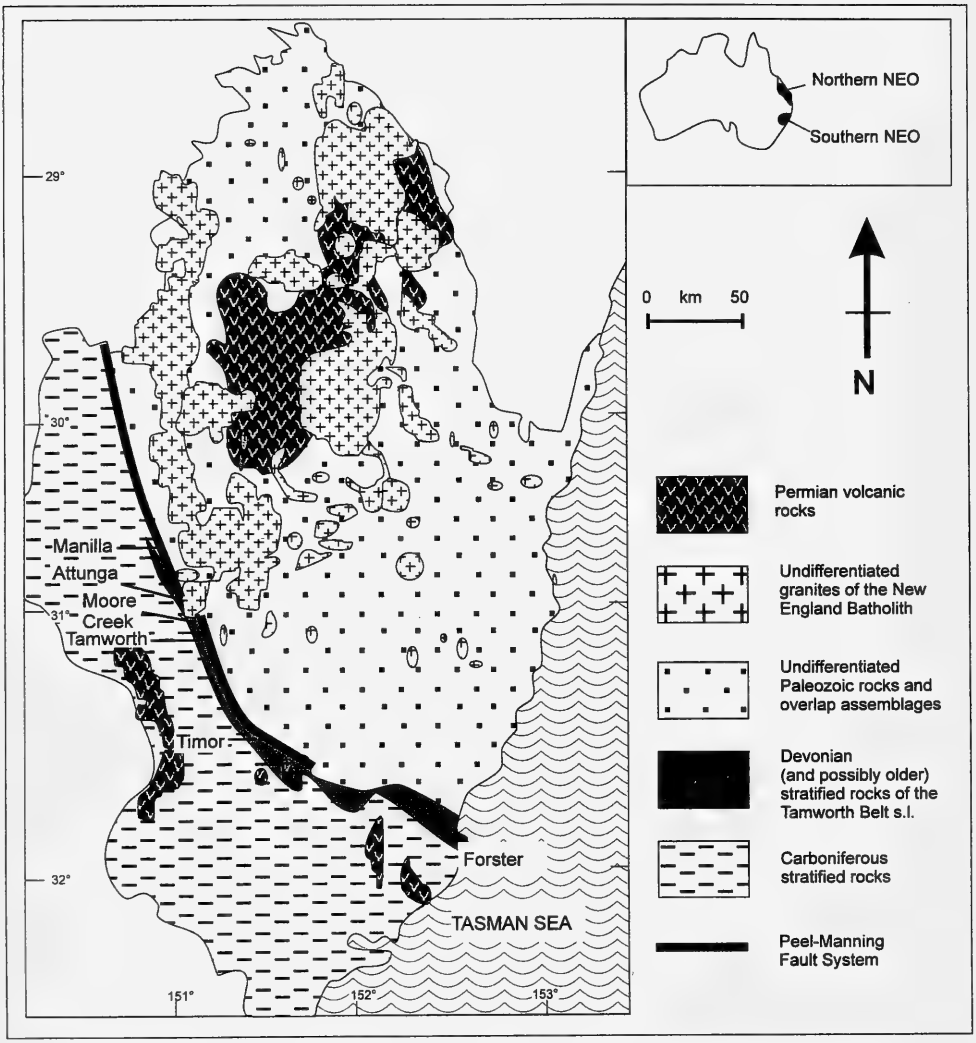

Figure 1. Simplified geological map of the southern New England Orogen (NEO) with locations mentioned in the text.

the eastern limb of the Yarramanbully Anticline (Voisey 1958) (Fig. 3). The anticline is faulted at or near the hingeline and older rocks are exposed on the eastern limb than on the western limb (Fig. 4).

The stratigraphic sequence begins with the lower Yarramanbully limestone, herein referred to as the Sulcor Limestone Member (Crook 1961), which is exposed over a distance of approximately 3.5 kilometres with a regionally consistent NNW-SSE strike. Its base is truncated to the west by a north-south trending fault. The limestone dips to the southeast at moderate angles and is complicated by folding and faulting. Folding has thickened the limestone particularly in its northern and central parts; its true thickness probably does not exceed 200m. To the south it ends abruptly along a steeply SW dipping fault (GR Klori 916 926). The top of the lower limestone is eroded with conglomerates forming up to 25m thick and 500m wide channels incising the uppermost beds of the

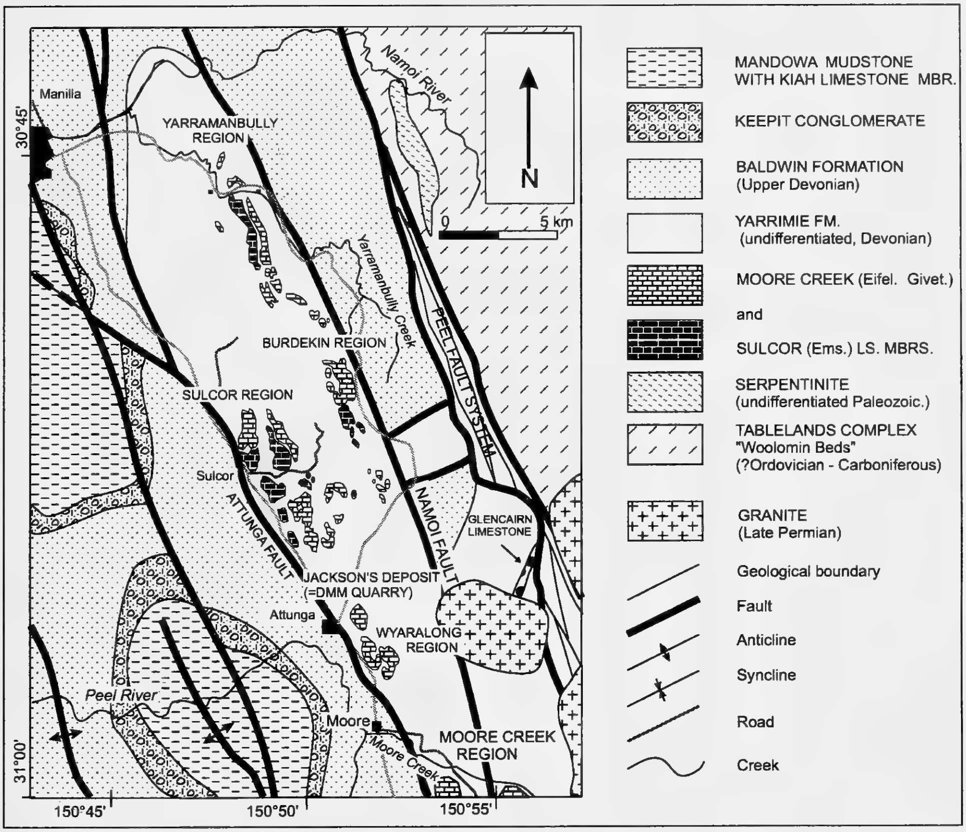

Figure 2. Simplified geological map of the Attunga region locating the limestone bodies. Geology based on 1 : 250 000 Geological Series Sheet Manilla (SH 56–9) published by the N.S.W. Department of Mines, 1966.

succession. A fault separates the lower limestone and overlying siliciclastic sediments from those underlying the upper limestone member. It hence appears that the Sulcor Limestone Member is a fault-bounded block. Chappell (1961) commented that many of the limestone bodies in the Tamworth Belt are limited by faulting. Pedder (1967: 138) commented, that Crook (1961) determined the Sulcor coral *Phillipsastrea maculosa* from the Silver Gully Fm. southeast of Tamworth. This implies that the Silver Gully Fm. (which underlies the Yarrimie Fm. in the type section at Silver Gully) is probably in part younger than the Sulcor Limestone Member. Hence the Sulcor Limestone may be regarded as a member of the Silver Gully Fm. The stratigraphy of the Tamworth Belt limestones and volcaniclastics is currently under review (Mawson and Talent in prep.; E. C. Leitch pers. comm. 1997).

Above the lower limestone follows the lower Yarrimie Formation with 100m to 350m of wavy bedded bioturbated silicified siltstones, mudrocks, and minor arenites and conglomerates (Fig. 5A). The actual limestone/siliciclastic contact is nowhere exposed but interbedded siltstones and grainstones have been found immediately above the contact in the central part of the outcrop area. The lithologies of the lower Yarrimie Formation are very similar to those seen below the Moore Creek Limestone Member at Wyaralong (Pohler and Herbert 1993) and Jackson's Deposit (Mawson and Talent 1994). Manser (1968) observed a similar sequence below the Timor Limestone and felt that it

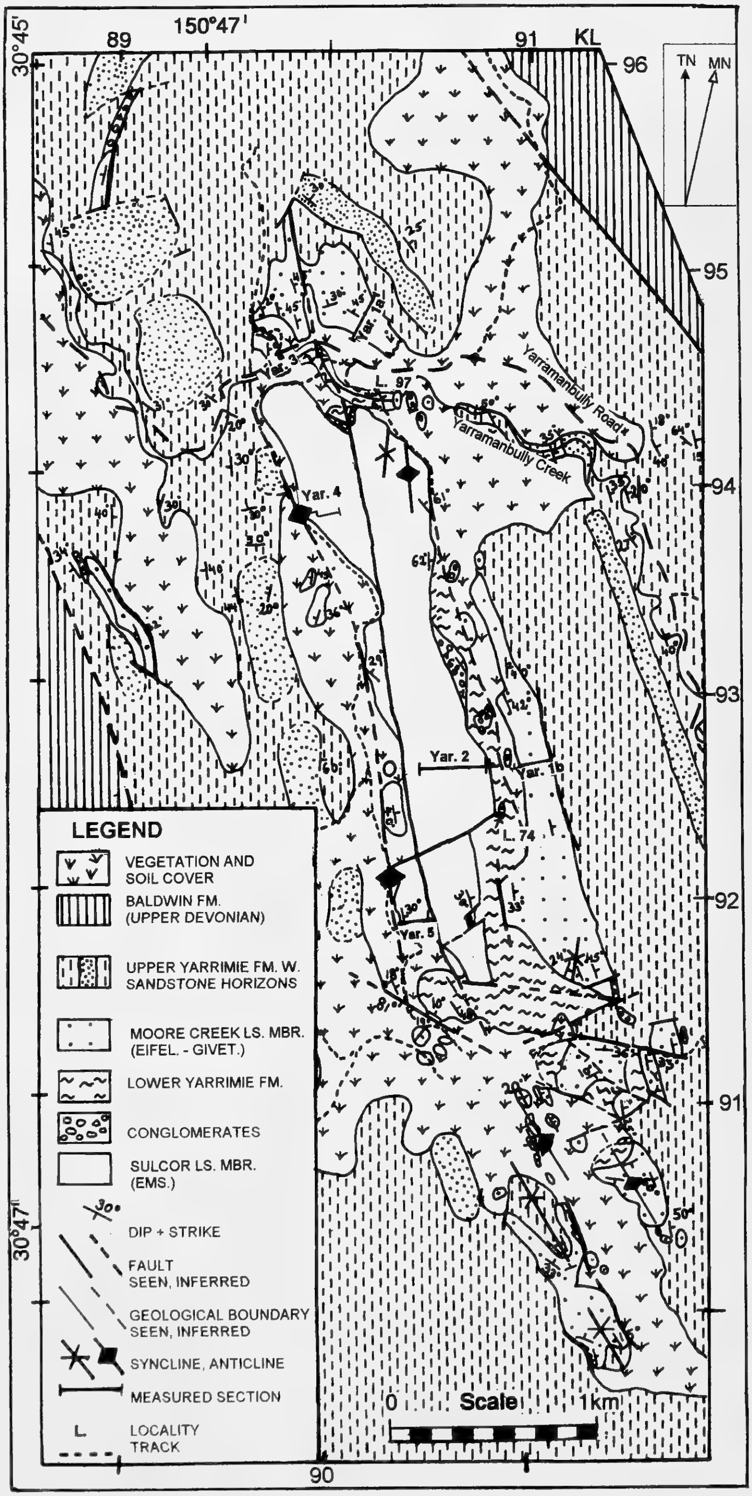

Figure 3. Geological map (based on topographic map 1:25 000 Klori 9036–II-N) of the Sulcor and Moore Creek Limestone Members and adjacent sediments in the Yarramanbully region.

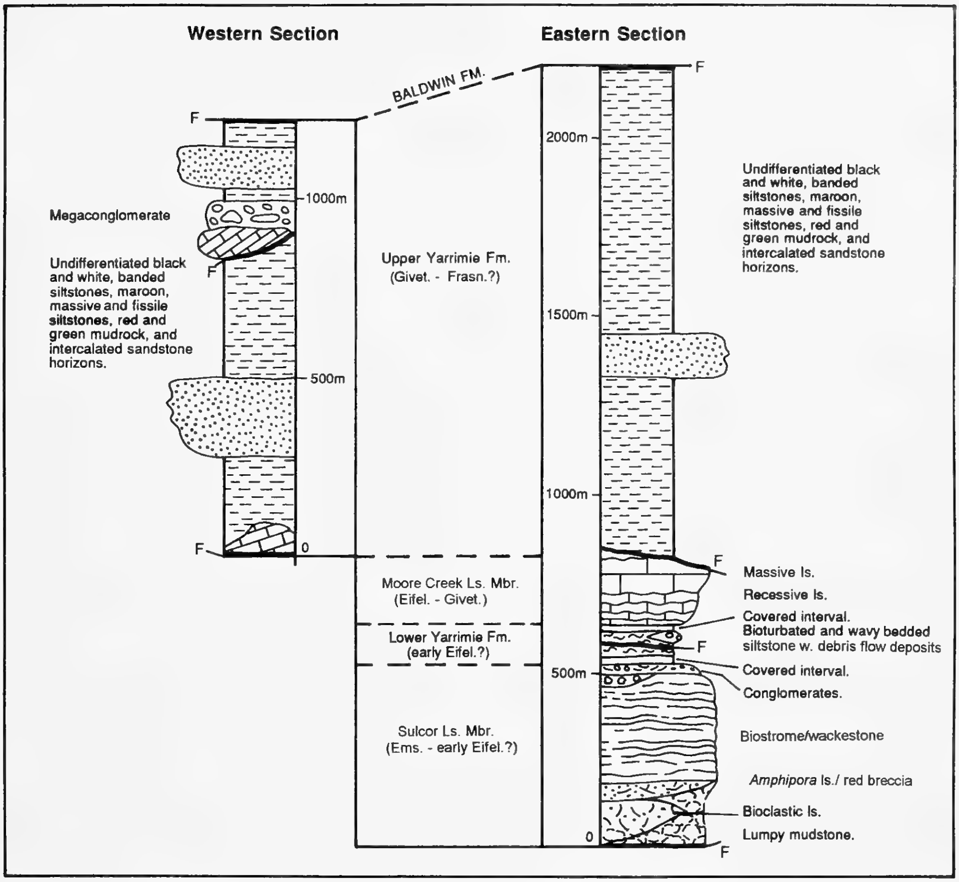

Figure 4. Generalized composite sections of the Yarrimie Formation with limestone members east and west of the anticlinal hinge. Thicknesses are apparent and estimated for some intervals.

was sufficiently different from the upper Yarrimie Formation to warrant sub-division of the formation. He referred the lower sequence to the Lilberne Beds and the upper mixed volcaniclastic/siliciclastic sediments to Busches Formation. This sub-division of the Yarrimie Formation appears to also be valid in the northern part of the Tamworth Belt. However, because the Yarrimie Formation was defined earlier (Crook 1961) it takes precedence over Manser's definitions and his Lilberne Beds and Busches Formation should possibly be assigned member status within the Yarrime Formation. In addition it is possible that the lower Yarrimie Fm. is in part age-equivalent to the Silver Gully Fm. southeast of Tamworth (Pedder 1967). The lithologies, however, are quite different and therefore Mawson et al. (in press) referred to the lower Yarrimie Fm. as "unnamed unit", pending clarification of the stratigraphic relationships.

The lower Yarrimie Formation is succeeded by the Moore Creek Limestone Member up to 200m thick, extending over six kilometres from north to south in a number of laterally discontinuous and fragmented limestone bodies. The most continuous exposures are located in the northern and central eastern part of the map area.

The base of the upper limestone is not exposed. The top appears to be erosional in the north, where sporadic ferruginous red breccias occur; in the central part some of the

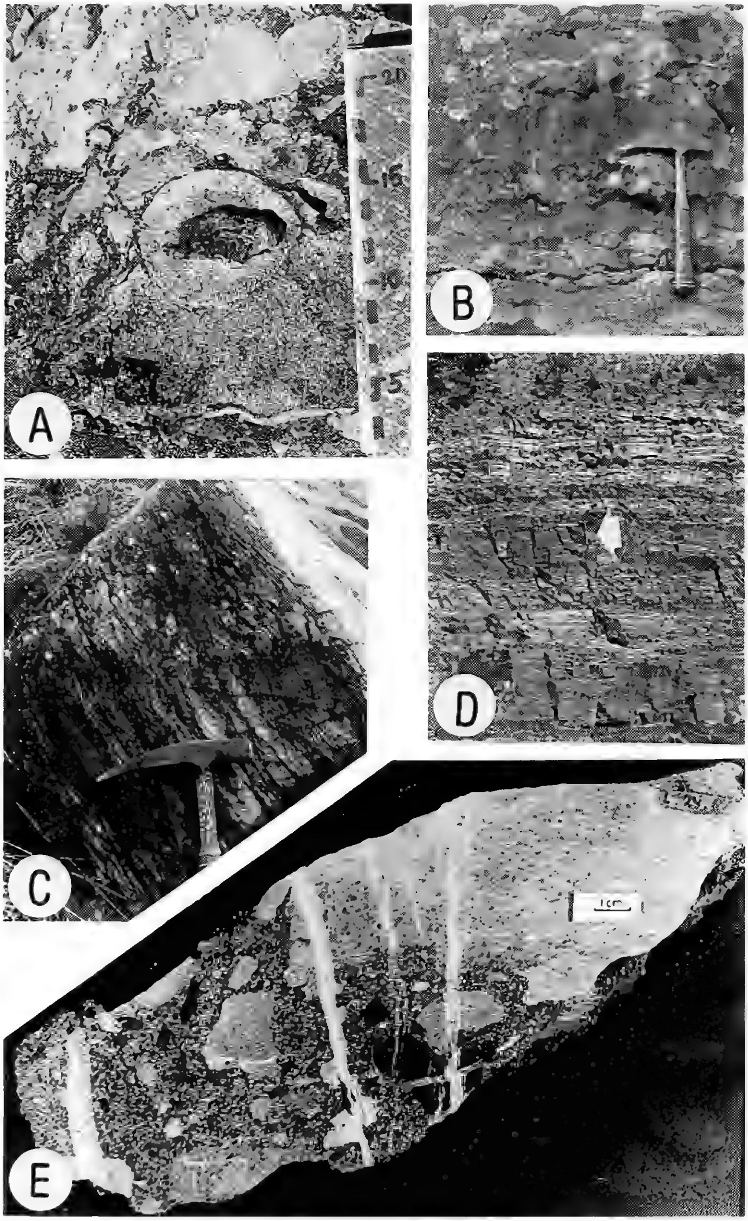

Figure 5A. Conglomerate in the lower Yarrimie Formation (central part of Yarramanbully area at L. 74, see Fig. 3 for location). Light grey rounded limestone clasts are set in a silicified siltstone matrix. Note corallite of *Pseudamplexus princeps* in centre. Figure 5B. Nodular to bedded limestone found near the top of the Sulcor Limestone in the bed of Yarramanbully Creek at Yar. 3 (see Fig. 3 for location). The lighter coloured sediment between the nodules is red and green mudrock to siltstone. Figure 5C. Mylonitic limestone in loose block adjacent to the fault at the hinge of the Yarramanbully anticline, limiting the limestones to the west (GR Klori 903 947). Figure 5D. Black and white banded siltstones, thick bedded and fissile siltstones characteristic of the upper Yarrimie Formation in the bed of Yarramanbully Creek below Yarramanbully Road. Note scale provided by geological hammer (arrow). Figure 5E. Polished slab of clasts and matrix found in the megaconglomerate unit north of “Cashel”. Light grey clasts are limestone, dark clasts are red mudrock. Small white grains are in part feldspar laths.

upper sequence is missing due to faulting, or is covered. To the south the limestone is complexely folded, faulted and fragmented. Basal and top contacts are commonly sheared and/or the limestone bodies are not in stratigraphic order (Fig. 3).

Above the limestone follows the upper Yarrimie Formation with an apparent thickness of over 1.5km. The sequence consists of maroon massive and fissile siltstones, tuffaceous black and white banded siltstones, red and green silicified mudrocks and intercalated coarse sandstones. Figure 5D illustrates a characteristic succession at Yarramanbully Creek. A fault separates the Yarrimie Formation from overlying sediments assumed to be time-equivalent with the Baldwin Formation (McMinn 1982).

As mentioned above, the eastern limb of the Yarramanbully anticline is separated by a fault from the western limb. This fault can be inferred at GR Klori 903 947 where mylonitic limestones occur in loose blocks adjacent to the fault (Fig. 5C). The fault continues in a southward direction along the base of the lower limestone and disappears under drift at the end of the limestone outcrop.

The sequence on the western limb probably belongs to the upper Yarrime Formation suggesting that it is down-faulted. A number of small west-dipping limestone outcrops occur immediately to the west of the faulted anticlinal hinge. They contain corals such as *Pseudamplexus princeps* and lithologies (i.e. echinoderm grainstone) characteristic of the Sulcor Limestone Member. They are overlain to the west by upper Yarrimie siltstones and sandstones and hence are not in stratigraphic order. They may represent small faultblocks which were emplaced adjacent to the larger fault structure to the east.

Two disconnected limestone bodies in the northwest (GR Klori 891 965) and far west (GR Klori 890 931) (Fig. 3) are associated with conglomerates (Fig. 5E) and surrounded by upper Yarrimie lithologies suggesting that they are either blocks in megaconglomerate units or faulted-in slivers of older lithologies. Faults can be seen or inferred limiting the northern outcrop at the base and to the north; the southwestern outcrop is faulted to the south and probably at the base were loose blocks of mylonitic limestone occur. The age of these two large masses has so far not been ascertained because no conodonts were recovered (R. Mawson pers. comm. 1995). The lithologies are not similar to those of the eastern limestone outcrops or elsewhere in the area.

Marshall (1968) suggested that the limestone bodies on the western limb of the anticline are of mixed age based on the co-occurence of *Phillipsastrea linearis* (Hill) and *Sociophyllum* n. sp. Pedder. The latter coral was also found in the present study along with a number of *Phacellophyllum* sp. (J. Pickett pers. comm. 1994). The presence of a mixed coral fauna is consistent with the conglomeratic nature of the unit.

Disconnected limestone outcrops in the southern part of the map area are commonly faulted and folded with a sheared base. Their lithologies suggest that they are fragments of the Moore Creek Limestone Member. Most are not in stratigraphic order but are over- and underlain by upper Yarrimie Formation suggesting that they are either tectonic fragments or olistoliths.

BIOSTRATIGRAPHY

Chappell (1961) was the first to investigate fossils from limestones in the Yarramanbully region. He reported the presence of abundant *Pseudamplexus princeps* (Etheridge) south of Yarramanbully Creek and suggested that these rocks are correlative to the Sulcor Limestone. Marshall (1968) also found *P. princeps* in the lower Yarramanbully limestone in addition to a number of other rugose corals namely *Phillipsastrea linearis* (Hill), *Trapezophyllum coulteri* Hill, *Tipheophyllum* n. sp., *Phacellophyllum* sp., *Plasmophyllum* sp., and *Thamnophyllum* sp. All of these rugose corals were previously reported by Hill (1943) and Pedder (1967, 1970) from the Sulcor

Figure 6. Facies distribution in the Sulcor and Moore Creek Limestone Members at Yarramanbully. For distribution of soil and vegetation, upper Yarrimie Formation and areas further south see Fig. 2.

Limestone Member. Phillip and Pedder (1967) concluded that late Emsian is the latest occurrence of *P. princeps*.

Marshall (1968) reported a different coral fauna from the conglomerate at the top of the lower Yarramanbully limestone with *Macgeea touti* Pedder and other corals of Pedder's (1967, 1970) Sulcor Fauna C. Numerous corals were collected from the conglomerate for the present study but *M. touti* was not found. However, the limestone facies which contains Fauna C at Sulcor (thinly bedded biostromal boundstone with silicified tabular and laminar stromatoporoids and tabulate corals) is missing at the top of the Yarramanbully limestone. It is likely that the conglomerate contains eroded remains of the topmost unit of the sequence with the youngest faunas. *M. touti* occurs in an interval straddling the Emsian/Eifelian boundary (Philip and Pedder 1967).

Conodonts from the upper Yarramanbully limestone were investigated by Mawson et al. (1988, p. 500). Their measured and sampled section in the valley of Yarramanbully Creek commences at grid reference 94609021 on the New South Wales Central Mapping authority 1:25,000 topographic map Klori, 9036–II-S. The conodont fauna recovered indicates the section to begin in *australis* Zone (mid Eifelian). At 14.7m above the base of the section, the incoming of *Polygnathus eiflius* is indicative of *kockelianus* Zone (late Eifelian). This age is consistent with that given for portion of the Moore Creek Limestone cropping out in the vicinity of Attunga and Tamworth (e.g. Philip 1967; Mawson and Talent 1994; Klyza 1995; and Mawson et al. 1997).

CARBONATE LITHOFACIES

The facies of the Sulcor and Moore Creek Limestone Members were mapped in the northern part of the area based on 1:25 000 scale aerial photographs, enlarged to 1:10 000 (Fig. 6). Several sections were measured through both limestones on the eastern limb of the Yarramanbully anticline and through the two limestone bodies exposed on the western limb (Yar. 1–4). Locations and designations are indicated on Figure 3; stratigraphic columns of selected sections are illustrated in Figs 7, 9, 10 and 12. Units are described in ascending order beginning with the Sulcor Limestone Member. Terminology used for descriptions is that of Dunham (1962), Folk (1962), Pettijohn (1957), and Grabau (1903, outlined in Folk 1968).

Sulcor Limestone Member

Coarse bioclastic limestone

This lithofacies crops out along the track to the SW end of the Sulcor Limestone Member (GR Klori 901 938). Its base is not exposed, the top is conformably overlain by the dark lumpy wackestone. The facies cannot be followed laterally to the south because it is cut off by a fault. To the north it interfingers with the lumpy wackestone facies. It is at least 100m thick at Yar. 4 where it forms massive outcrops of light grey to grey rudstone or biosparrudite interbedded with and grading upwards into finer-grained lithologies (Fig. 7). The basal calcarenites and calcirudites are composed of diverse very coarse sand- to pebble- sized fossil fragments; thin sections show the fossil debris to be dominantly derived from echinoderms, with subordinate stromatoporoids, *Stachyodes*, rugose and tabulate corals, algae and brachiopods. Lithoclasts of wackestone are rarely found. The finer-grained lithologies are packstones and grainstones with fine to medium sand-sized allochems with a higher mud fraction and stylo-flaser bedding but otherwise similar composition. Near the top of section Yar. 5 (not figured) occur finer-grained bioclastic limestones above the lumpy wackestone indicating that this lithology is not restricted to the base of the lower limestone.

Many of the fossil fragments have micritic envelopes, particularly the echinoderm and shell fragments. In many cases the original structure of a skeletal fragment has been completely obliterated by recrystallization, leaving only a mosaic of coarse crystalline calcite surrounded by a thin rim of micrite. Most components are rounded to subrounded, with low sphericity, and poor sorting.

Interpretation

Rounding and lack of lime mud between components suggests high water energy. However, micrite envelopes are caused by microbial decay (Bathurst 1966, 1975; Alexandersson 1972) and this degradation may have contributed to their roundness. The

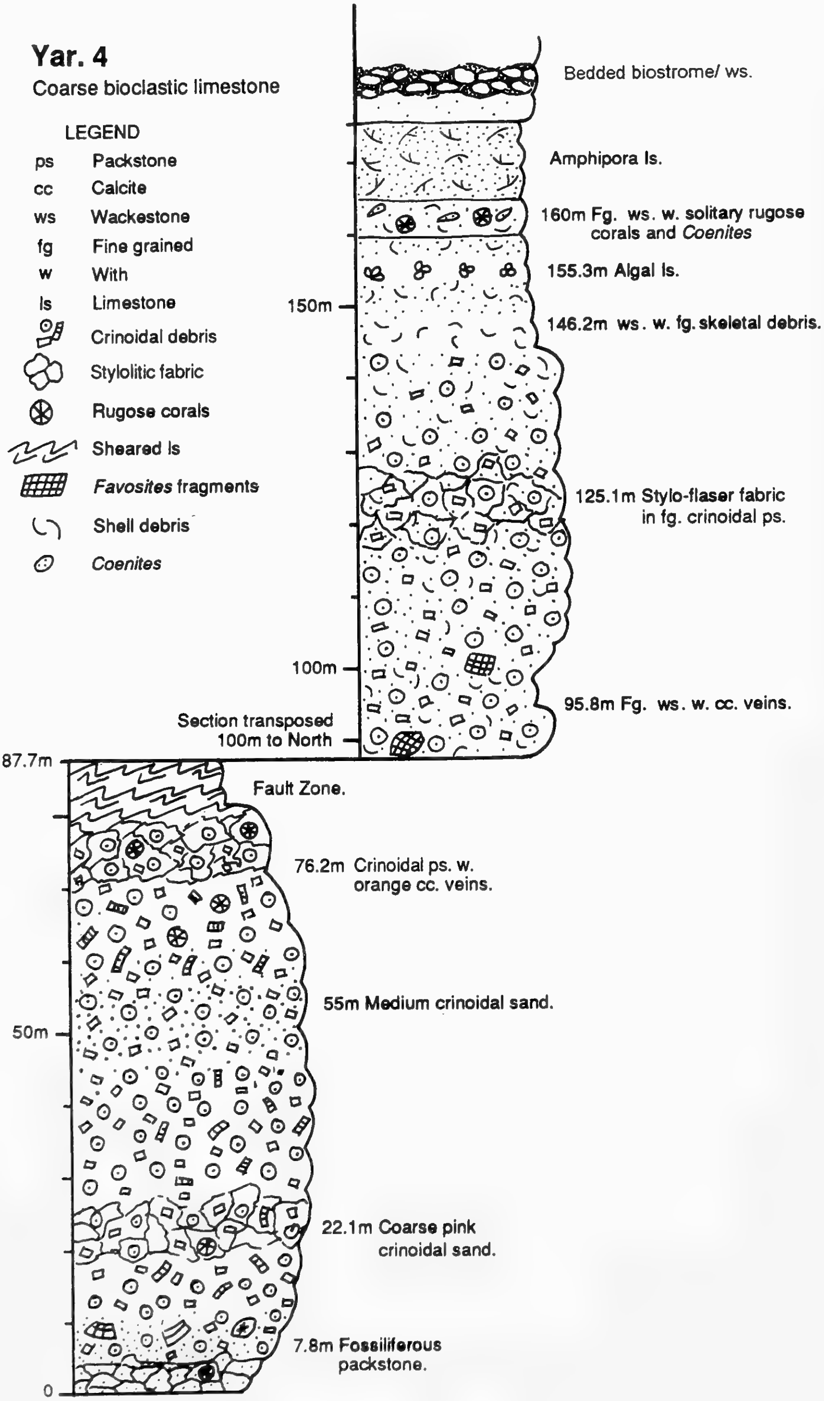

Figure 7. Section Yar. 4 through the basal echinoderm rudstone and grainstone, Sulcor Limestone Mbr. (see Fig. 3 for location).

amount of neomorph spar and dusty inclusions in the ground mass suggests that originally the limestone contained more mud (Bathurst 1975). Hence water energy may have been lower than indicated by the present texture and composition. The sediment is almost entirely composed of debris from baffling and frame-building organisms. Its large size and lack of sorting suggests that no distant transport occurred, but that breakdown and reworking was close to their life position. The extensive replacement of early aragonitic and calcitic cements suggests that the sediment was exposed to meteoric or even vadose diagenesis. The sporadic occurrence and lateral discontinuity of the sediment implies a lenticular outcrop pattern. It may be that the bioclastic limestone formed in shoal areas colonized by crinoids and other organisms below and interfingering with the lumpy wackestone facies.

Lumpy wackestone

The lumpy wackestone lithofacies crops out along the track towards the SW end of the lower limestone and is best exposed at location Yar. 5 (GR of base KL 916 919). The base of the unit is in most places not exposed, except at the northern end of the outcrop where it overlies the bioclastic limestone. The upper contact with the bedded biostromal limestone is conformable but in some places difficult to pinpoint because the transition marked by increasing fossil content is gradual. The limestone is composed of lime mud with varying but typically minor shell and echinoderm debris. It is grey with weathering but dark grey to black on fresh surfaces. It has a flasery, lumpy appearance due to stylolitization with stylolites delineating small (1–5cm long, 1–3cm thick) limestone lenses. The most common biogenes are solitary horn-shaped rugose corals; towards the top small tabulate corals, alveolitids, *Amphipora* and stromatoporoids appear. The lack of bedding is due to bioturbation (Bambach and Sepkoski 1979).

Interpretation

The high mud content and lack of structures indicative of wave action suggest that the sediment was deposited in quiet water. A sample processed for total organic carbon content from this lithology and the overlying dark *Amphipora* limestone gave a low value of 0.1%. It is likely that the organic material is not preserved due to heating of the rock during burial diagenesis (P. Hoffmann pers. comm. 1997). The initial organic content cannot be determined anymore and the dark colour is probably now caused by high content of disseminated sulfides. This points to dysaerobic bottom conditions with sufficient oxygen to support the burrowing infauna. At greater sediment depth oxygen levels decreased and some detritic material escaped oxidization. The silty and argillaceous material seen on stylolitic seams suggests an original, though modest content of fine-grained terrigenous material. The sediment probably formed a soft substrate. No evidence is seen for early lithification, slow sedimentation, encrustations or discontinuity surfaces. Water depth is difficult to estimate in the absence of sedimentary structures or fossils as depth indicators. The palaeoenvironment could have been a deep shelf below fair weather wave base or the subtidal portion of a somewhat restricted marine basin.

Amphipora limestone

The *Amphipora* limestone, up to 30m thick, is best exposed at GR Klori 918 935. It is difficult to trace along strike because of structural complications and weathering; to the north and south it disappears and is obviously not laterally continuous but a subfacies within the lumpy wackestone which it overlies and interfingers with. It is succeeded by bedded biostromal limestone or by stylobreccia with red mud matrix.

The *Amphipora* limestone weathers to a dark grey colour, fresh surfaces are almost black. *Amphipora* skeletons are concentrated in 30–50cm thick banks, interbedded with equally thick beds of fine-grained dark lime mudstone or wackestone. The fossils are randomly oriented with no readily detectable palaeocurrent direction (Fig. 8C).

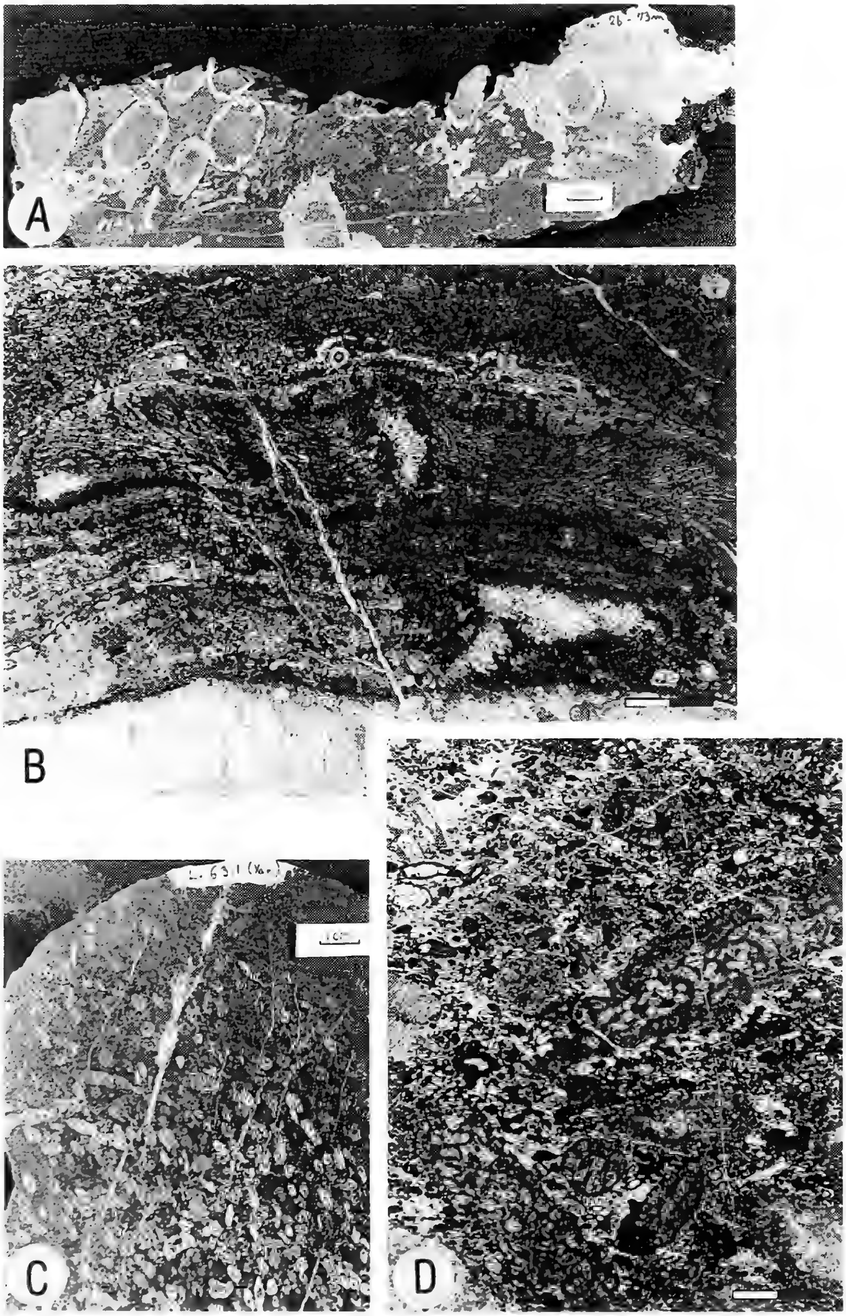

Figure 8A. Cross-sections of several colonies of *Yakutiopora* oriented parallel to bedding plane from biostrome/wackestone facies at Yar. 2, Sulcor Limestone Mbr. (Fig. 3 for location). Polished and etched slab. Scale bar is 1cm. Figure 8B. Thin section photomicrograph of partly silicified *Alveolites* colony growing on stromatoporoid. Note *Wetheredella* colony in the lower left of the stromatoporoid. Yar. 2, biostrome/wackestone facies. Scale bar is 2mm.Figure 8C. Polished slab of *Amphipora* limestone collected from Amphipora limestone unit, northern part of Sulcor Limestone Member. Figure 8D. Thin section photomicrograph of *Amphipora* coenostea set in a matrix of fine to medium grained peloidal calcarenite. Scale bar is 2mm.

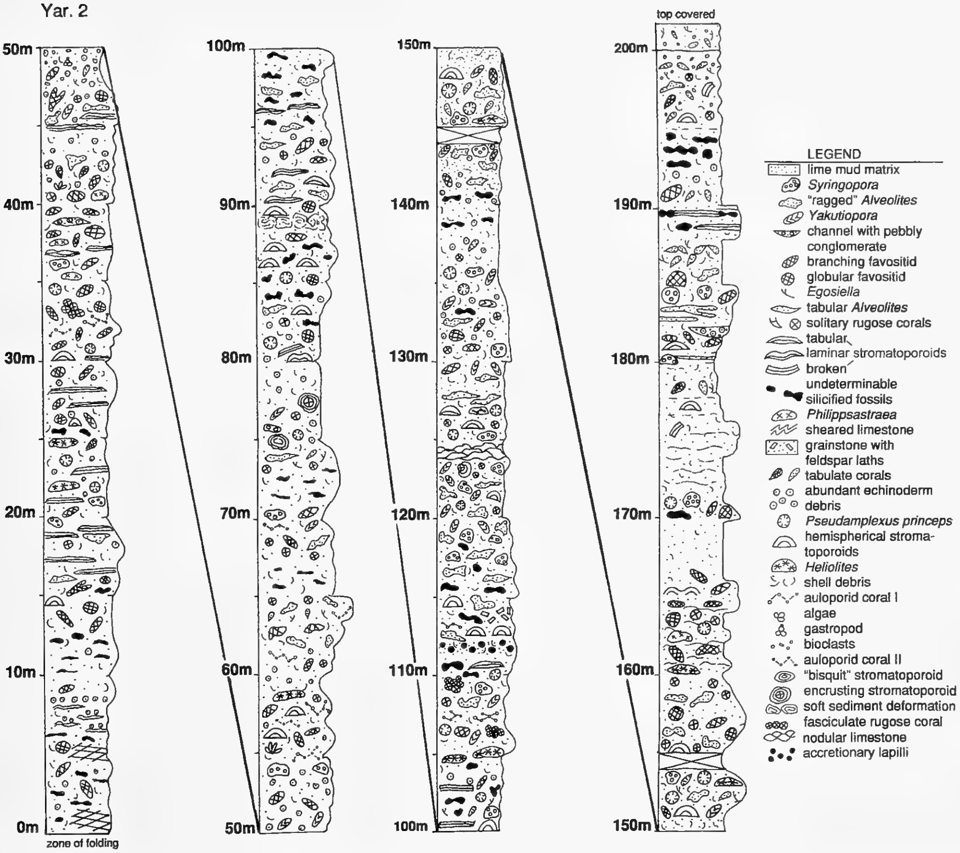

Figure 9. Section Yar. 2 measured through the central part of the Sulcor Limestone Member (see Fig. 3 for location).

In thin section the *Amphipora*-rich intervals can be classified as bafflestone and biopelmicrite (Fig. 8D). The dominant components are *Amphipora* skeletons and minor numbers of small solitary rugose corals enclosed in poorly washed, poorly sorted sand composed of medium to fine sand-sized peloids. Subordinate allochems include cortoids (=coated grains), fine shell debris, microskeletal debris and irregularly shaped algal lumps.

Fossils other than *Amphipora* include ostracods, brachiopod and echinoderm fragments, abundant small undetermined shelly fossils (single-chambered foraminifera?) and algal fragments.

Interpretation

Amphipora lived in very shallow quiet lagoons (Fischbuch 1968; St.Jean 1971) and has been reported from many such paleoenvironmental settings (Gogolczyk 1956; Gutkin and Rodchenko 1968; Jenik and Lerbekmo 1968; Fischbuch 1970; Harvard and Oldershaw 1984; Soja 1990). The accompanying components and fossils are consistent with this interpretation.

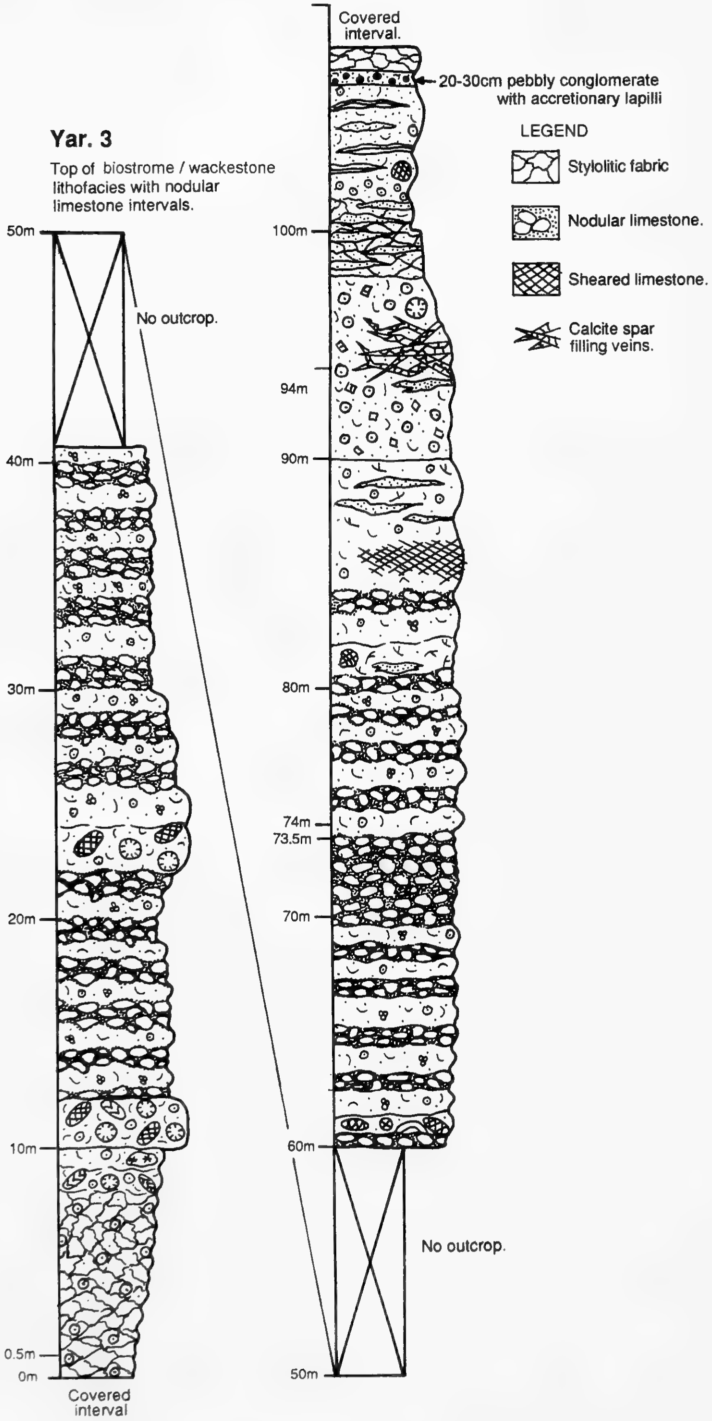

Figure 10. Section Yar. 3 through the Sulcor Limestone Member measured in bed of Yarramanbully Creek (see Fig. 3 for location; see Fig. 9 for detailed legend).

Biostrome/wackestone facies

This facies consists of pavements of tabular and laminar stromatoporoids and alveolitids interbedded with skeletal wackestone and floatstone with ramose tabulate corals. The unit is at least 150m (true thickness) thick and occupies most of the outcrop area of the Sulcor Limestone Member at Yarramanbully (Fig. 9). The sequence is well-bedded with bed thicknesses varying between 0.2m and 0.5m. It has gradual contacts with the underlying *Amphipora* limestone and dark lumpy wackestone, the upper contact with conglomerate is erosional. The limestones weather dark grey, while fresh surfaces are commonly almost black.

The lithology of the sequence is best exposed in the bed of Yarramanbully Creek at Yar. 3 (Fig. 10). Here well-washed rocks show interbedded nodular and wavy-bedded lime mudstone or wackestone (Fig. 5B) with partings of red or green mudstone.

The unit is richly fossiliferous but many of the fossils are obliterated by silicification and are seen as irregular crusts with ragged outlines emphasized by a yellow weathering siliceous rim. The 1–15cm high and 5–30cm long ragged crusts are mainly formed by alveolitids, whereas pavements are dominantly tabular stromatoporoids (Fig. 11C). Other common fossils are tabulate corals with large branching forms such as *Yakutiopora* (Fig. 8A) and favositids, fasciculate colonies of *Syringopora*, massive favositids and heliolitids, and small ramose tabulozoa of *Coenites*-type.

Rugose corals are represented by abundant *Pseudamplexus princeps* (Fig. 11D) and infrequent colonies of fasciculate and massive compound forms such as *Phacellophyllum* (Fig. 11B) and *Phillipsastrea* respectively. Sponge spicules are common but sponge skeletons are rarely preserved. Large framework-building organisms comprise between 30% and 70% of the rock volume and it is hence justified to regard the lithology as an organic build-up facies. The biogenes are embedded in a matrix of skeletal or peloidal lime mud. Fossil allochems are dominantly ostracods, filamentous shells, sponge spicules, calcite spheres, fragments of gastropods and trilobites, crinoid ossicles and fragments, debris from corals, bryozoans and stromatoporoids and, most prominently, thalli of udoteacean and dasycladale algae (Mamet and Pohler in press). Other components include peloids and cortoids. The lime mud to allochem ratio of the matrix ranges between 40 : 60 and 50 : 50.

One of the most striking features of the biostromal unit is the prolific occurrence of epibionts. Successive encrustations of thin (1–5cm) crusts of stromatoporoids or alveolitids are particularly widespread (Fig. 8B). Usually several different genera and species are involved in building encrustations which may be 10cm to several metres long. Also very abundant are diverse epibionts growing on the large tabulate and rugose corals. Corallites of *P. princeps* with an overgrowth of *Syringopora* (Fig. 11D) are a common occurrence. Other associations include growth of stromatoporoids, bryozoans or *Wetheredella* on various rugose corals, stromatoporoids on an indeterminate recrystallized encrusting organism, auloporid corals and *Trypanopora* on *Yakutiopora* and stromatoporoids. Commonly the overgrowth involves two or more different participants.

Interpretation

The biostrome/wackestone facies has been documented in detail in Pohler (1998) and is therefore only briefly addressed herein.

The growth forms of the coralline hydrozoans and tabulozoa forming thin pavements have been described from low energy backreef, reef and forereef environments in Australia's Canning Basin (Playford and Lowry 1967; Playford 1980). In the Devonian of Europe laminar stromatoporoids have been reported from forereef environments (Braun et al. 1994), reef (Jux 1960) and backreef environments (Krebs 1968, 1971; Lecompte 1970). Several researchers (Cook 1995; Yong-ji Zhen 1994; A.I. Kim pers. comm. 1993) consider the association of *Yakutiopora* and other branching tabulozoa with tabular and laminar stromatoporoids and alveolitids to be characteristic of shallow

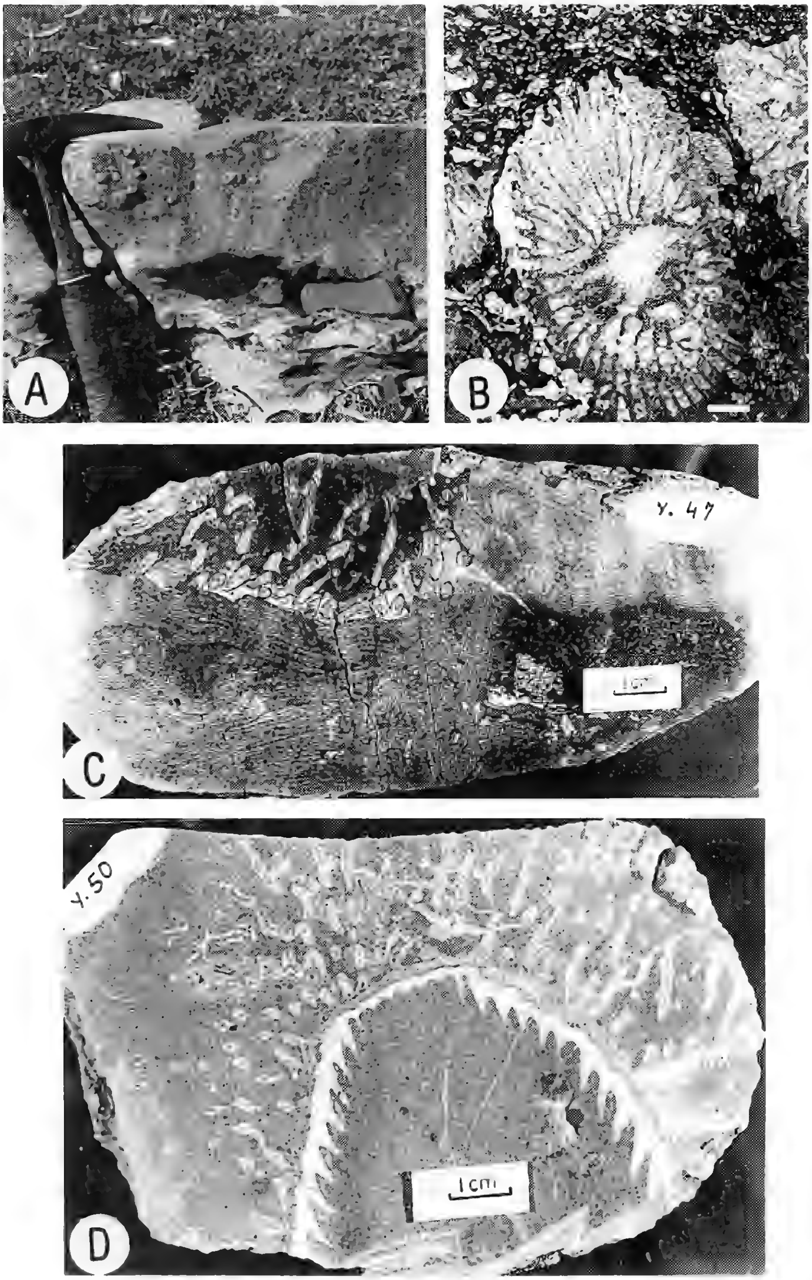

Figure 11A. Pebbly conglomerate (30cm thick) with accretionary lapilli in the creek bed of Yarramanbully Creek at the top of section Yar. 3, Sulcor Limestone Mbr. (GR Klori 902 945). Note high sphericity of lapilli. Figure 11B. Thin section photomicrograph of undetermined fasciculate colony of *Phacellophyllum* sp. which is characteristic of the biostrome/wackestone facies at section Yar. 2 (Sulcor Limestone Mbr.). Scale bar is 1mm. Figure 11C. Tabular stromatoporoid with *Syringopora* colony on top. The surrounding dark sediment is skeletal wackestone. Polished slab from biostrome/ wackestone facies at section Yar. 2. Figure 11D. Polished slab of *Syringopora* colony and juvenile rugose coral on *Pseudamplexus princeps*. Note thin stromatoporoid encrusting corallite. (Section Yar. 2).

lagoons. The abundance of lime mud (suggesting low energy), and the rich ostracod fauna and algal flora seem to support this interpretation.

In the Yarramanbully biostromes no hardgrounds are readily recognizable. In some cases a pronounced difference between sediment underlying and overlying a stromatoporoid colony can be seen, suggesting that a change in sedimentation occurred, possibly associated with a lag and induration or lithification of the surface prior to colonization. The occurrence of early carbonate cements is suggested by the remnants of aragonite needles seen in some samples. In one case a colony of *Syringopora* seems to grow contemporaneously with aragonite cements on the surface of a stromatoporoid colony (Fig. 11C). However, the presence of skeletal debris and lime mud between stromatoporoid laminae suggests that loose sediment was present and interfered with the growth of the colony. In addition, many tabular colonies are broken along vertical fractures apparently caused by differential compaction. The fractures are filled with the surrounding muddy skeletal sediment which must have been still soft in order to fill the gaps. Fractures filled with calcite spar are rarely seen.

It must be concluded that much of the sediment was colonized while still soft, and that the tabular and laminar growth could be a “snow shoe” adaptation designed to prevent the organism from sinking into the mud. Scrutton (1997) suggested that Paleozoic reef-building organisms were adapted to soft substrate. He considered the laminar and tabular growth forms of tabulate corals indicative of quiet deep water (>50–60m). Bertling (1996) suggested that the flat plate-shaped morphology of Jurassic hermatypic corals in northern Germany is an adaptation to low light intensity at depth at or below storm wave base. Some Recent hermatypic coral genera (e.g. *Montastrea*, *Porites, Siderastrea*) adapt to growth in deeper water by forming crustose or foliose growth forms. *Acropora* is said to form encrusting colonies under not further specified extreme conditions and generally foliose and encrusting corals are observed in low energy conditions (Milliman 1973; Sorokin 1995). Cockbain (1984) noted that in the Devonian Reef Complexes of Western Australia large massive tabular corals are common in reef margin and reef flat subfacies, whereas tabular and laminar growth forms grew on slopes and appear to be a particularly stable growth form.

Lack of light could also be due to cloudy water caused by siltation. The corals were obviously able to remove sediment from their surface. The “ragged” outline of some tabular alveolitid corals suggests that partial mortality due to sediment coverage occurred affecting the fringes of the colonies. Recovery from partial mortality also occurs in Recent corals, but constantly high turbidity tends to kill corals as can be observed in many reefs. Hence sediment coverage must have been sporadic because very flat colonies would be easily burrowed by mud and their shape was not conducive to quickly remove sediment from the surface. The bedded nature and increasing silicification of the biostrome/ wackestone also points to low sedimentation rates. Laminar and tabular growth of corals and stromatoporoids was probably not caused by low illumination due to turbid water but is rather an adaptation to increasing water depth.

Conglomerates

In Sulcor Limestone Member two types of conglomerates can be distinguished: a) a conglomerate with lithoclasts and b) a pebbly conglomerate with lapilli.

a) Conglomerate with lithoclasts: In the central part of the limestone body a conglomerate up to 30m thick, with subangular to subrounded carbonate and mudrock lithoclasts covers the surface of the biostrome wackestone. The conglomerate is graded with clast sizes decreasing up section. The largest clasts observed are 30cm across. The conglomerate decreases in thickness to the north.

b) Pebbly conglomerate with lapilli: A 30cm thick pebbly conglomerate occurs in the bed of Yarramanbully Creek (Yar. 3, GR Klori 902 945) (Figs 10 and 11A). The pebbles are 0.5cm–2cm in diameter, very well rounded with high sphericity and composed of siltstone with a vaguely laminated fabric reminiscent of pisolites. The matrix is a coarse to medium sand comprising a mixture of calcitic skeletal debris and volcaniclastic grains, including pyroxene, albite, and pumice. A similar pebbly conglomerate occurs in section Yar. 2c at 112m (Fig. 9). Here the pebbles are yellow-stained and cracked. A similar lithology with red siltstone pebbles occurs at Sulcor (only in loose blocks) and in the Sulcor Limestone Member in the Burdekin region (Fig. 2).

Interpretation

a) The lithoclastic conglomerates are graded suggesting that they were deposited from waning flows. The lenticular cross sections imply that channeling occurred. The increase of terrigenous material is commonly observed when shorelines become exposed due to a relative fall in sea level. As previously discussed the limestone clasts in the conglomerate are supposedly time-equivalent to the uppermost Sulcor Limestone Member. The nature of the conglomerates suggests that exposure of the shoreline occurred with subsequent erosion. This was probably caused by a fall of relative sea level as a result of either tectonic or climatic changes. The palaeogeographic setting of the limestone in a presumed forearc basin was favourable for synsedimentary tectonic events.

b) The roundness and composition of the pebbles in the pebbly conglomerate is characteristic of accretionary lapilli (R.H. Flood pers. comm. 1994; H. Noll pers. comm. 1998). In contrast to ordinary lapilli, which are clasts, accretionary lapilli are aggregations of fine ash particles. Most likely they are formed through condensation of water vapour within a highly concentrated hot pyroclastic flow or an ascending eruptive column. Water droplets acted as aggregation nuclei by making the ash particles stick together. Vapour is abundant in phreatic eruptions, occurring when the volcanic heat vaporizes a waterbody (Schumacher and Schmincke 1991). Accretionary lapilli are found in subaqueous and reworked deposits, e.g. in the Devonian Lenneporphyr of Germany (Heyckendorf 1985).

The increase of volcaniclastic material, some of it from air falls, may be interpreted as a result of renewed volcanic activity. The composition of the other volcanogenic components in the lapilli conglomerate suggests a basaltic rather than andesitic source (P. Conaghan pers. comm. 1994). The conglomerate is certainly an event horizon, but it is not clear whether one or several of these events occurred, because the horizon cannot be followed along strike to demonstrate lateral continuity.

Lower Yarrimie Formation

The conglomerate unit a) described above forms the top of the Sulcor Limestone Member. The contact with the fine-grained siltstones, siliceous mudrocks and conglomerates of the lower Yarrimie Formation is nowhere exposed contributing to the problematic nature of the relationship between siliciclastic and carbonate units. White (1988) who studied the lower Yarrimie Formation (the Lilberne Beds of Manser 1968) at the Timor anticline concluded that they are submarine fan deposits. This interpretation is also implied by lithologies and sedimentary structures of the unit below the Moore Creek Limestone Member at Jacksons Deposit (pers. obs. 1994). Exposed contacts between the Moore Creek Limestone Member and the lower Yarrimie Formation show in many cases shear zones implying bedding parallel faults. This structural displacement is likely to occur during deformation of rocks with different competence.

Moore Creek Limestone Member

The Moore Creek Limestone Member is about 200m thick and composed of two distinctive units: (1) a lower recessive weathering unit, and (2) an upper massive unit (Fig. 12).

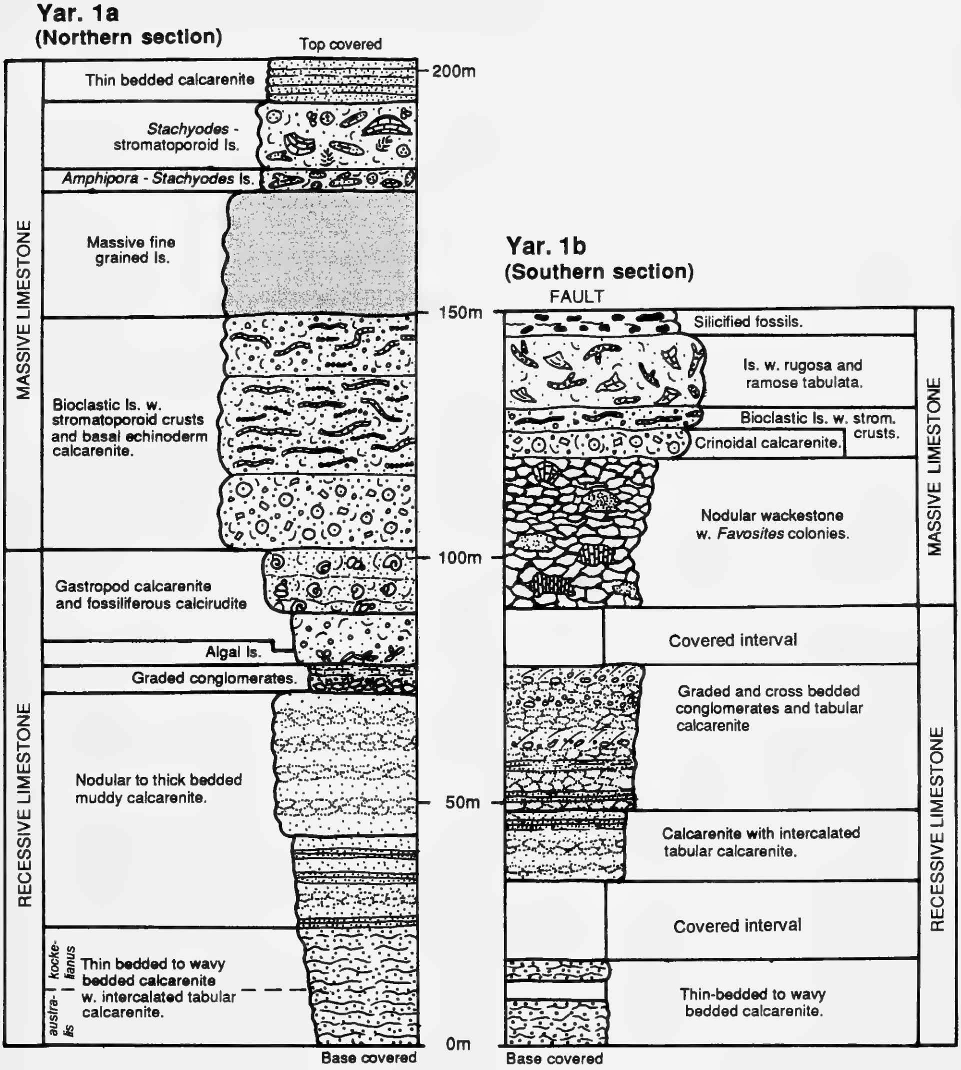

Figure 12. Measured sections Yar. 1a and Yar. 1b through Moore Creek Limestone Mbr. (see Fig. 3 for location).

The lower recessive weathering unit is characterized by a sequence of a) thin-bedded to wavy-bedded calcarenites with intercalated tabular limestone intervals, b) nodular to thick-bedded calcarenites and c) graded conglomerates, d) algal limestone, e) fossiliferous calcirudite and gastropod calcarenite.

The upper massive limestone in the north comprises a) bioclastic limestone with thin fossil crusts and basal echinoderm calcarenite, b) massive fine-grained limestone, c) *Amphipora–Stachyodes* limestone, d) *Stachyodes*- stromatoporoid limestone, and e) thin-bedded calcarenite. Southward the massive limestone sequence begins with f) nodular wackestone with *Favosites* and *Heliolites* colonies, followed by a basal echinoderm calcarenite and bioclastic limestone. Following above are: g) a bioclastic wackestone with rugose and tabulate corals and h) bedded wackestone with silicified fossils. Facies b) to e) are not developed in the south where instead facies f) to h) occur (Fig. 12). Only the bioclastic limestone with stromatoporoid crusts and basal calcarenite is common to both sections in the massive limestone unit.

(1) Lower recessive limestone unit

1a) Thin-bedded to wavy-bedded calcarenite with intercalated tabular calcarenite lithofacies

The Moore Creek Limestone Member at Yarramanbully begins with a five metre thick unit of poorly exposed 10–15cm thick beds of calcarenite with 3–5cm thick siltstone partings. The basal contact with the underlying siliciclastic unit is not exposed and the thin-bedded limestones grade upward into wavy-bedded muddy calcarenites (Fig. 14D).

The basal thin-bedded calcarenites are composed of coarse to medium sand-sized crinoid debris with very little muddy matrix. They become more vaguely bedded with 2–10mm thick partings upsection. Coarser and finer-grained beds of muddy calcarenites are intercalated and separated by wavy partings. Fossil debris is dominantly derived from crinoids; minor amounts of rugose corals and stromatoporoid fragments are also present. Around 20m up-section in Yar. 1a the amount of large silicified fossil fragments increases and partings become more pronounced. At 25.4m (Yar. 1a) 0.5–2m thick tabular bedded intervals occur. They are formed by thin (3–6cm) beds of fine calcareous and lithic sands separated by 0.5–2cm thick, dark brown siliceous ridges with a high content of siliceous silt-sized mud (Fig. 13C). The ridges outline occasional low-angle cross bedding.

Large stromatoporoid (up to 50cm diameter) and favositid colonies as well as centimetre-sized rounded mudstone pebbles are sometimes enclosed. The calcarenites have a characteristic yellow tinge from weathering of chlorite-replaced labile grains of probable volcaniclastic origin. The tabular limestones occur in 0.8m or larger intervals.

1b) Nodular to thick-bedded lithofacies

This facies begins gradually above Unit 1 and is composed of dark wackestone with light coloured echinoderm debris forming 5–20cm thick beds separated by 1–3cm thick partings which upsection become thicker and form nodular horizons. Overturned colonies of favositids and stromatoporoids can be found in some horizons (Fig. 13B).

1c) Graded conglomerate lithofacies

Graded conglomerates occur in sections Yar. 1a and Yar. 1b. Several conglomerate horizons occur in Yar. 1a between 72.1m and 78.1m. The thickest conglomerate is 50cm thick but because of the recessive weathering exposure is poor and thicker beds may be present. Each conglomerate is formed by rounded limestone pebbles, coarse fossil debris (stromatoporoids, favositid colonies, etc.) and smaller brown mudrock clast. The largest clasts are 20cm in diameter and well rounded with high sphericity. They occur usually near the base of each bed. Mudrock pebbles are usually less than 5cm in diameter and rounded but with low sphericity (Fig. 14C). Up-section the pebbles gradually decrease in size and are capped by the tabular calcarenites described above (Figs 13A, D). Deposition was apparently gradual and continuous for each graded unit because no breaks can be seen between different grain sizes. The conglomerates are laterally continuous but decrease in thickness and grain size along strike.

At Yar. 1b coarse conglomerates were not seen but several finer-grained units with decimetre thick rudites occur between 48m and 75m and may be correlative in part to the same unit in Yar. 1a. The rudites are comprised of sequences beginning with small rounded pebbles followed by cross-bedded grainstone with mud drapes and, finally, bedded grainstone without apparent sedimentary structures. They are intercalated with tabular limestone and fine grained calcarenites.

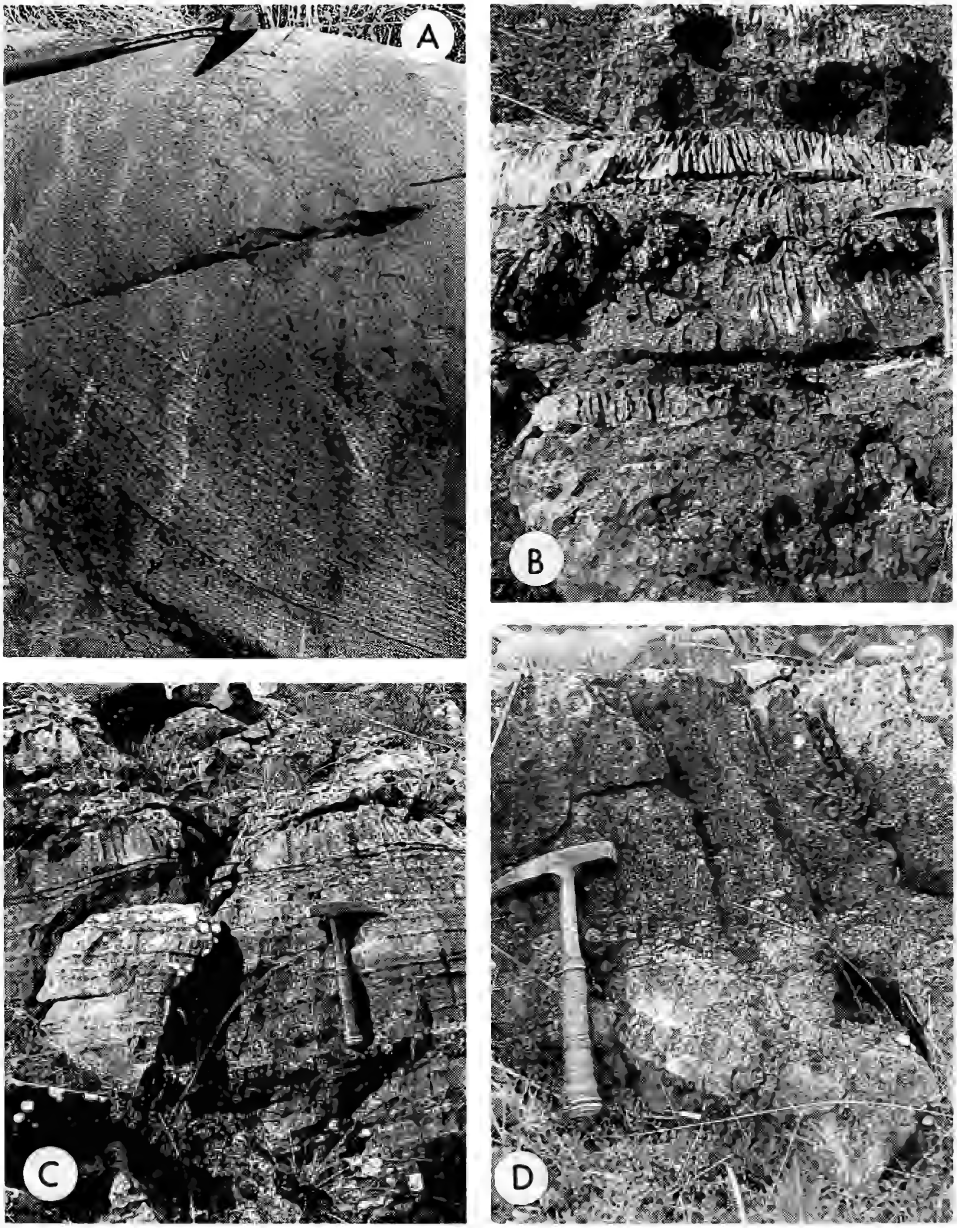

Figure 13A. Graded conglomerate with channel cutting into cross-bedded calcarenite below. At base a second graded conglomerate unit (lower left of photograph). (Moore Creek Limestone Mbr.; L. 97; Fig. 3 for location). Figure 13B. Overturned *Favosites* and stromatoporoid colonies in the nodular to thick bedded calcarenite. Section Yar. 1a, Moore Creek Ls. Mbr. Figure 13C. Platy calcarenite at section Yar. 1a with weathering resistent ridges of silicified mudrock or siltstone. Note nodular limestone above the tabular calcarenite interval. Figure 13D. Graded conglomerate at section Yar. 1a.

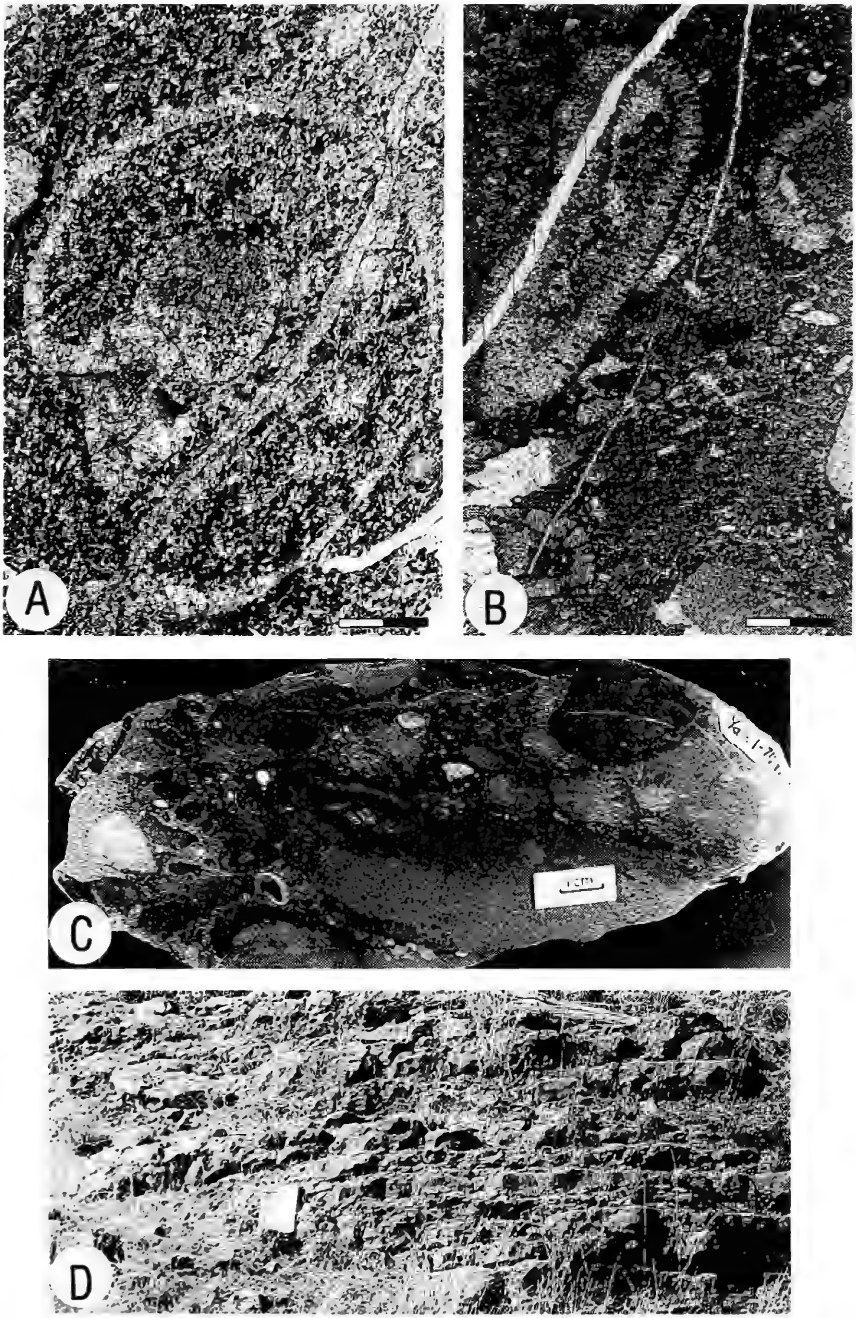

Figure 14A. Thin section photomicrograph of low-spired gastropod with shell completely replaced by calcite in fossiliferous calcarenite lithofacies. Section Yar. 1a, Moore Creek Limestone Mbr. Scale bar is 2mm. Figure 14B. Thin section photomicrograph of algal limestone at section Yar. 1a with *Couvinianella*. Scale bar is 2mm. Figure 14C. Polished slab from graded conglomerate lithofacies. Clast are rounded limestone pebbles, coarse fossil debris and smaller brown mudrock clasts. Section Yar. 1a, Moore Creek Limestone Mbr. Figure 14D. Basal thin-bedded calcarenite with siltstone partings north of section Yar. 1b, Moore Creek Ls. Mbr., Fig. 6 for location.

The matrix of the coarse conglomerates is composed of mixed siliciclastic and carbonate grainstone with much replacement by chlorite and neomorph calcite spar.

To the west in a small gully occurs a conglomerate with large, rounded lime mud pebbles overlain by cross-bedded mixed siliciclastic/carbonate sand. The beds appear to be fining upwards and in one instance the conglomerate can be seen to cut into the underlying mixed sand (Figure 13A).

The unit containing the conglomerates and tabular calcarenites can be followed throughout the map area and beyond and is hence an important marker horizon.

1d) Algal limestone

A less than 1m thick limestone bed with dasycladale algae occurs above the conglomerate unit at 79m at Yar. 1a and at the base of the northwestern side of the Moore Creek Limestone Member (GR Klori 903 947) (Mamet and Pohler in press). It contains poorly preserved thalli and molds of *Couvinianella*, a genus of dasycladacean algae described by Mamet and Préat (1992) (Fig. 14B). The outcrop is not continuous and the algae may have had a patchy distribution.

1e) Fossiliferous calcirudite and calcarenite lithofacies

The sequence is sandwiched between a short interval of algal limestone at its base and the massive limestone at its top. At section Yar. 1a it begins with 8.4m of vaguely bedded bioclastic limestone with abundant coarse fossil debris derived from stromatoporoids, *Alveolites*, and tabulate corals. This coarse unit is followed by 13.6m of wavy-bedded, yellow weathering, fine-grained calcarenite with shell-rich beds or pods of gastropods and brachiopods (Fig. 14A). This latter sequence is usually recessive and hence poorly exposed. The gastropods are low- and high-spired forms, their shells completely replaced by calcite. Trilobites and tabulate corals are also present. The matrix and surrounding calcarenite is composed of fine-grained, well-sorted peloids and rounded shell debris. The yellow weathering colour probably stems from iron oxide leached from chlorite(?) which replaced labile grains derived from volcanic tuffs.

Interpretation

Lithofacies 1a–c and e are all characterized by a largely bioclastic composition with a high percentage of lithoclasts of presumable terrigenous and/or volcaniclastic origin. The thin-bedded calcarenites at the (exposed) base of the Moore Creek Limestone Member show no cross bedding or grading; the wavy calcarenites are similarily devoid of those features. Both lithologies are moderately well sorted with a high mud content suggesting lack of winnowing. Probably transport for some distance occurred to achieve the sorting. Combined with a lack of sedimentary structures and textures indicative of traction or turbidity currents the depositional environment was probably deep subtidal (i.e. below fair weather wave base).

The tabular limestones show occasionally a pinching-out of recessive calcarenites. Grading may be expressed in the higher relief ridges caused by silicification of fine-grained argillaceous material. Weathering of volcanic tuffs to clay can form silica as a by-product (Pollock 1988). Unfortunately the rocks are too weathered to resolve their original composition by means of light microscopy. The lack of bioturbation and resulting destruction of bedding suggests that the sediment was deposited suddenly or was inhospitable for infaunal burrowers. The relatively good sorting was probably achieved by transportation, and the occasional incorporation of clastic debris along with the pinching of beds points to erosion. These parameters are suggestive of storm deposits or distal turbidites.

Flat tabular strata were defined by McKee and Weir (1953). Imbrie and Buchanan (1965) summarized the different settings where this type of stratified sediment has been observed to form: on beaches, supratidal mud flats and oolite shoals at low tide. The flat sand laminae (sheet deposits) found on supratidal mud flats were interpreted as storm deposits (Shinn and Ginsburg 1964). Similar sediments on Anticosti Island (Quebec) and Bell Island (Newfoundland) are also associated with storm deposits (pers. obs. 1989, Brenchly et al. 1993).

The graded conglomerates (1c) are characterized by rounded mudrock and limestone clasts, graded bedding, occasional cross bedding and channeling. These features are also typical of both turbidite deposits and tempestites. The roundness and composition of the clasts points to a land-to-sea direction of transport, because well-rounded clasts are usually indicative of lengthy transport or erosion and are typically found in the beach zone or at river mouths. Medium-size gravels (6–20 cm) are moved on the beach and some, together with sand, are transported into deeper water during storms (Reineck and Singh 1980). This mechanism could account for the wide distribution of the facies which can be followed southward as far as the Sulcor area. There is some indication for a sloping bottom higher up in the sequence (see below) which could support an interpretation of the graded and tabular strata as turbidites, but the great extent of the facies without facies change lends support to the interpretation as storm deposit.

The nodular to thick-bedded muddy calcarenites (1b) are very similar in composition to the wavy-bedded calcarenites and a similar environment is indicated. The nodular interbeds are probably caused by a rhythmically increased influx of terrigenous fine-grained sediment or decreased carbonate production. Bioturbation destroyed the bedding and later compaction and diagenetic unmixing may have caused the nodular fabric. The increased number of large colonies of frame-building organisms indicates a renewed colonization of the substrate by organisms other than crinoids. Maybe a decreasing amount of the terrigenous sands was the cause.

The algal limestone (1d), though not laterally continuous, is a good indicator of shallow quiet water within the photic zone. The dasycladale alga *Couvinianella* was also found in the Wyaralong limestone to the south (Pohler and Herbert 1993) at approximately the same level.

The fossiliferous calcirudites (1e) suggest increased organic diversity in a nearby area. The gastropod calcarenites are typical of shallow quiet water.

(2) Upper massive limestone unit

2a) Bioclastic limestone with fossil crusts

The unit is a massive grey limestone with characteristic thin wavy crusts of stromatoporoids and tabulate corals in a coarse bioclastic matrix. The sequence is over 47m thick at Yar. 1a, though much thinner at Yar 1b with conformable contacts to over- and underlying strata. The stromatoporoid crusts are 0.1–1cm thick and 2–10cm long (Fig. 15C, D). Most are redeposited but a few of the larger ones appear to be in situ. *Actinostroma, Hammatostroma,* and *Keega* are known to form thin crusts (Riding 1974). The stromatoporoid crusts are accompanied by thin lattice-shaped crusts, probably the initial layers of alveolitid corals (Fig. 15C). The crusts are associated with large *Favosites* colonies, small nodular (dislodged?) *Heliolites* (Fig. 15D), and tabular and ragged stromatoporoid and *Alveolites* colonies respectively. Large in situ fossils and fossil fragments are set in a poorly washed matrix of peloidal to skeletal packstone with abundant debris of echinoderms, ostracods, trilobites, brachiopods and algae. Intervals of coarse fossiliferous floatstone to rudstone are intercalated with better-sorted relatively unfossiliferous packstone and grainstone on a decimetre scale.

2b) Massive fine-grained limestone

The massive grey limestone is exposed in section Yar. 1a where it is 26.1m thick. It has gradual contacts with over- and underlying lithologies and is characterized by a mottled appearance and small (mm-thick and cm-long) spar-filled fissures. The mottling is

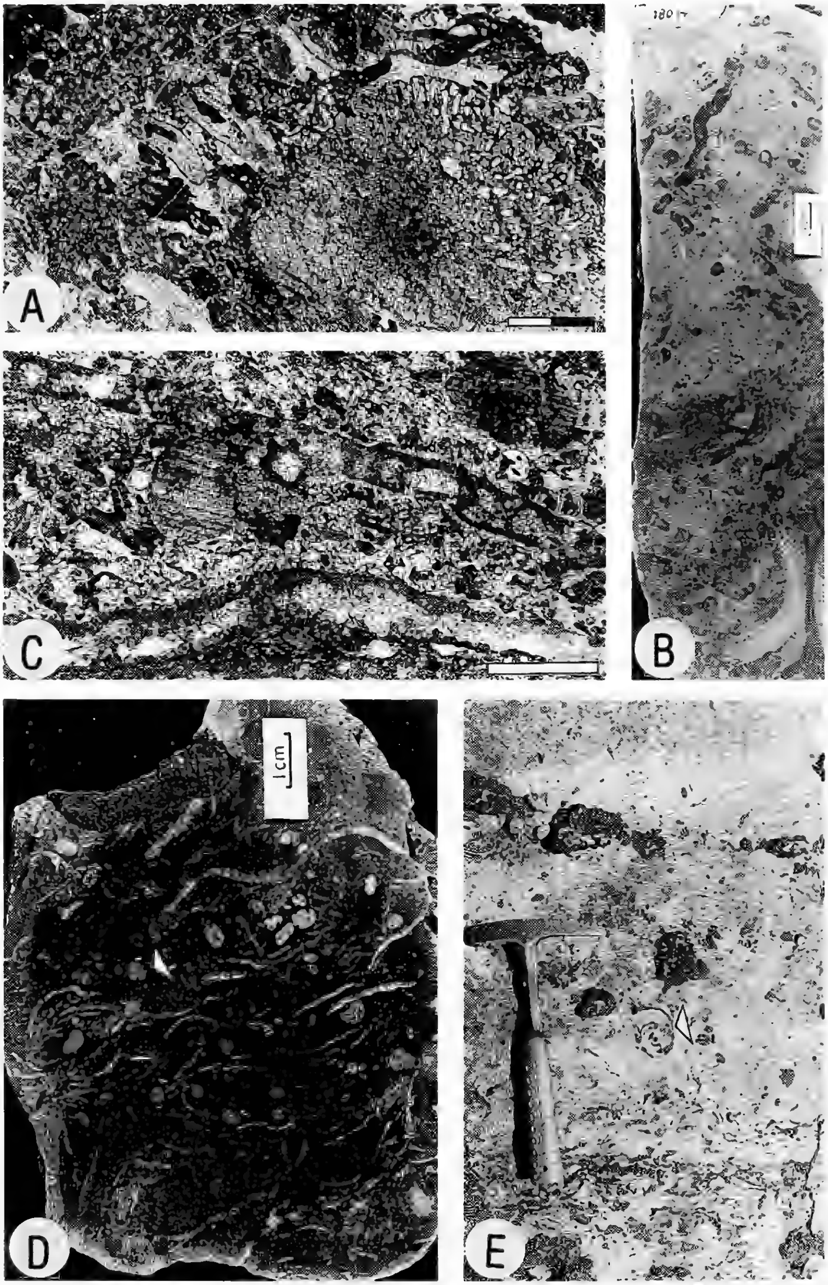

Figure 15A. Thin section photomicrograph of the *Amphipora–Stachyodes* limestone at section Yar. 1a. Moore Creek Ls. Mbr., Fig. 6 for location. Scale bar is 2mm. Figure 15B. Polished slab of *Amphipora–Stachyodes* limestone at section Yar. 1a. Figure 15C. Close-up of basal layer of alveolitid corallites from the sample Yar. 1a — 118.7m. Section Yar. 1a, Moore Creek Ls. Mbr., Fig. 6 for location. Scale bar is 0.5mm. Figure 15D. Polished slab with crusts of stromatoporoids, alveolitids (see Fig. 15C for close-up) and rounded *Heliolites* fragments (arrow) from the bioclastic limestone interval at section Yar. 1a. Figure 15E. Bedded wackestone with silicified nodules. Note goniatite to right of hammer and shell beds near base of picture. Top of section Yar. 1b, Moore Creek Ls. Mbr., Fig. 6 for location.

caused by limestone lumps (1–5cm in diameter) separated by yellow or reddish stylolitic argillaceous partings. The sediment is composed of lime mud with dark shell debris (ostracod shells) and solitary rugose corals. Patchily distributed are packstone to grainstone lenses, more coherent mudstone intervals (20cm or more across) and fossiliferous areas with *Alveolites* fragments and crinoid stems up to 3cm long. Poorly preserved *Amphipora* are scattered throughout.

2c) *Amphipora–Stachyodes* limestone

Above the massive fine-grained limestone follows a thin (1.5m) bafflestone to rudstone composed of densely-packed skeletons of *Amphipora* and *Stachyodes costulata* Lecompte (Fig. 15A, B). The skeletons are not in life position and show no preferred orientation indicating lack of current sorting. The matrix is a poorly washed peloidal packstone to wackestone with only minor skeletal debris.

2d) *Stachyodes*–stromatoporoid limestone

This 15m thick massive interval is composed of stromatoporoid and *Heliolites* colonies and associated *Stachyodes* in a matrix of bioclastic calcarenite to calcirudite with abundant algal fragments and echinoderm debris. Broken thalli of codiacean and dasycladale algae are present. The matrix is poorly washed and poorly sorted. Many of the large frame-building fossils are overturned but some appear to be in situ.

2e) Thin-bedded calcarenite

The top of the limestone succession is formed by a 9m thick interval of bedded fine to medium sand-size calcarenite.

2f) Nodular wackestone with *Favosites* and *Heliolites* colonies

Nodular wackestone is composed of oval lumps of bioclastic wackestone (3–5 cm long) set in a pink-grey matrix. The lump:matrix ratio is approximately 3:1. The basal contact with recessive limestone is covered, the upper contact with echinoderm calcarenite is gradual. The unit in section Yar. 1b is about 34m thick. It contains intermittently large (up to 40 cm diameter) in situ *Favosites* and globular *Heliolites* colonies. Bioclastic content includes minor crinoidal and brachiopod debris.

2g) Bioclastic wackestone with rugose and ramose tabulate corals

This unit is approximately 17m thick at section Yar. 1b. It is composed of bioclastic limestone with stick-like tabulate corals (abundant) and bryozoans (uncommon), rugose corals, favositids and brachiopods.

2h) Bedded bioclastic wackestone with silicified fossils

The bioclastic wackestone is characterized by large (5–8cm diameter, up to 20 cm long) lumps of silicified fossils (?). Nowhere could the origin of the lumps be ascertained but the overall shape resembles branching favositids seen in the Sulcor Limestone Member. At section Yar. 1b the unit is cut off by a fault and is only about 4–6m thick; further south it is much thicker and well bedded with abundant shell debris. At one location a goniatite of the genus *Tornoceras* was found (Fig. 15E) indicating a late Eifelian to early Givetian age of the succession (T. Becker written comm. 1997).

Facies 2f)–2h) are restricted to the southern outcrops of the Moore Creek Limestone (section Yar. 1b).

Interpretation

The bioclastic limestone with fossil crusts (2a) is composed of poorly sorted and sub-rounded bioclastic components suggesting that it was not transported far. The fossil crusts are difficult to evaluate. Playford and Lowry (1967, p.72) illustrate a sample of calcirudite with a thin stromatoporoid layer from the late Devonian Saddler Limestone (Canning Basin, W.A.). The Saddler Limestone is a forereef deposit with abundant bioclastic and biogenic components. It is possible that the stromatoporoids are fragments of larger animals or that they are dislodged juvenile colonies which attempted to colonize the unstable forereef slope. In the Moore Creek Limestone Member the stromatoporoid crusts are associated with larger colonies of in situ low hemispherical forms and other frame builders. This suggests that the crusts may also be at least partly in situ, and that they either could not grow larger because they became dislodged, or that they are dwarfed or bizarre forms which are sometimes found in hostile environments (St. Jean 1971). A coarsening of the bioclastic debris up-section without change in overall composition possibly indicates that the source area was closer. Deposition was probably in a shallow subtidal environment possibly on a sloping surface which formed an unstable substrate. This interpretation is consistent with a decreasing thickness of the unit to the south (Yar. 1b) where instead a fine-grained nodular wackestone with in situ coral colonies exists. This facies (along with facies 2h) can be followed to the southeastern corner of the Yarramanbully region. Although lacking good indicators of water depth it was probably deposited in the subtidal zone in quiet water. Both facies 2g) and 2h) were probably deposited in a similar environment. It is not clear how they relate to the section north of Yarramanbully Creek because no interfingering of the different facies can be observed due to lack of outcrop. Facies 2f)–2h) indicate a deepening upward trend progressing from nodular wackestones to bedded siliceous limestone with goniatites.

The massive fine-grained limestone (2b) with *Amphipora*, ostracods and scattered small rugose corals was probably deposited in a very quiet, possibly lagoonal, environment. As discussed above, *Amphipora* lived in shallow marine lagoons and the *Amphipora–Stachyodes* limestone (2c) was probably deposited in such an environment.

The overlying *Stachyodes*–stromatoporoid limestone with its matrix of diverse bioclastic algal debris suggests a well oxygenated marine environment within the photic zone.

The fine-grained calcarenite (2d) at the top of the sequence may be correlative to the calcarenite at the top of the Wyaralong limestone where it heralds the burial of the limestone by increasingly more siliciclastic turbidites.

The massive limestone unit begins with a large thickness of bioclastic limestone followed by fine-grained limestone with few fossils and finally a biogene-dominated limestone. Overall the sedimentation is that of a shallow marine environment, the trend being initially shallowing upwards until deposition of the *Amphipora–Stachyodes* limestone. *Stachyodes*–stromatoporoid limestone and fine-grained calcarenite seem to indicate deepening again. In the scree of the slope at Yar. 1a red ferruginous breccias with fitted clasts can be occasionally found suggesting that an erosional surface similar to that in the Wyaralong limestone is also present at the top of the Moore Creek Limestone. This erosional surface, however, has not been observed in situ.

SUMMARY AND CONCLUSIONS

The Sulcor and Moore Creek Limestone members are exposed on the eastern limb of the Yarramanbully anticline and in a number of structurally displaced bodies south of the main exposures. On the western limb younger rocks of the upper Yarrimie Formation occur, including a megaconglomerate incorporating a 300m long and 100m wide limestone block. The western limb of the anticline is downfaulted along a fault trending approximately parallel to the axis of the anticline at or near the hinge line.

The two continuous limestone belts on the eastern limb of the anticline are of different age. The lower limestone contains corals of late Emsian to possibly earliest Eifelian age and is hence time-equivalent with the Sulcor Limestone Member of the

Yarrimie Formation. The upper limestone is Eifelian to possibly Givetian in age and time-equivalent to the Moore Creek Limestone Member. The two limestones are separated by a belt of siliciclastic and volcaniclastic sediments with debris flow deposits incorporating late Emsian fossils and limestone clasts. These sediments are assigned to the lower Yarrimie Formation and are similar in lithology to those underlying the Wyaralong limestone and Jacksons Deposit. They also resemble the Lilberne Beds below the Timor Limestone Member. The contacts between lower Yarrimie Formation and lower and upper limestone members are nowhere exposed and can therefore not be evaluated with confidence.

The Moore Creek Limestone Member is overlain by brown massive and fissile siltstones, green sandstones and black and white banded siltstones of the upper Yarrimie Formation.

The Sulcor Limestone sequence begins in the north with coarse bioclastic limestone, followed by grey and black stylo-nodular mudstone to wackestone and *Amphipora* limestone. The overlying biostromal limestone comprises the thickest and most continuous unit (up to 200m). The sequence is terminated by an erosional event which is recorded by deposition of conglomerates incising the upper limestone surface. The different lithofacies are all of shallow water aspect and, with the exception of the bioclastic limestone, are quiet water deposits. The transition from *Amphipora* limestone and bioclastic limestone to bedded and partly silicified biostrome wackestone indicates a deepening upward trend consistent with the late Emsian transgression shown in Johnson et al. (1985). The restriction of the shallow water lithofacies such as the bioclastic limestone and the *Amphipora* limestone to the northern part of the map area suggests that deposition took place over a bottom sloping to the south. A bathymetric gradient is also evident in the overlying Moore Creek Limestone Member at Yarramanbully (see below) and at Wyaralong (Pohler and Herbert 1993).

The lithoclastic conglomerate that terminates the Emsian sequence could represent a gravity flow deposit which settled on top of the limestone after it was transported down slope into a basin, thus implying that the whole of the Sulcor Limestone is an olistolith. The lack of fossil data in the surrounding Yarrimie Formation hampers interpretation.

Alternatively it may indicate exposure of Sulcor Limestone to the west (?) causing erosion of biostrome wackestone and of volcaniclastic sediments. There is no indication of a karstic surface at the top of the Sulcor Limestone Member at Yarramanbully, rather the sequence records deepening upwards. This scenario would be consistent with the development of a fault scarp in the Late Emsian caused by rifting or renting of the basin floor. If the overlying lower Yarrimie Formation is in stratigraphic context it records continuing subsidence. With the data at hand it is impossible to decide whether the Sulcor Limestone Member at Yarramanbully is a fault-bounded block or an olistolith.

The Moore Creek Limestone Member begins with recessive weathering, muddy echinoderm calcarenite with high volcaniclastic content. Whether this stems from airborn tuffs or from reworked tuff horizons cannot be decided. An influx of graded conglomerates with silicified mudrock and well-rounded limestone clasts indicates erosion and reworking in the beach zone and redistribution of beach gravels by storms across the shelf area. These deposits can be traced southward, where the conglomerates are finer grained and cross-bedding becomes more prominent. The overlying algal limestone and fine-grained gastropod calcarenites confirm very shallow water as a depositional environment.

Massive bioclastic limestone with encrusting stromatoporoids and tabulate corals follow above the recessive unit. They suggest beginning stabilization of the depositional environment which enabled bottom dwelling organisms to colonize the substrate. Calciclastic components decrease further upsection with deposition of a massive fine-grained mudstone, presumably a shallow lagoonal sediment. The low fossil content implies a somewhat hostile environmment. *Amphipora–Stachyodes* limestone above indicates re-establishment of a thriving bottom community. This trend continues with deposition of the overlying *Stachyodes-* stromatoporoid limestone. Its rich algal flora indicates a shallow marine environment. Thin-bedded calcarenites form the uppermost unit of the Moore Creek Limestone and may be the first indication of termination of limestone deposition. The contact with the overlying siltstones of the upper Yarrimie Formation is not exposed. Rare occurrence of ferruginous limestone internal breccia in slope scree suggests that another erosional event occurred similar to that seen at the top of most other limestone bodies in the Tamworth Belt.

The Moore Creek Limestone further south (documented in section Yar. 1b) was probably deposited in somewhat deeper water. Particularly the bedded bioclastic wackestone with silicified fossils indicates deeper water than the presumably coeval massive limestones to the north. The southern limestone also records a deepening upward trend (beginning with deposition of the nodular wackestone) more clearly than the northern counterpart. It can be concluded that the Sulcor and Moore Creek Limestones where deposited on a sloping bottom that deepened to the south and that termination of limestone deposition coincides with relative rise of sea-level.

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Food Items Brought Home by Domestic Cats *Felis catus* (L) Living in Booderee National Park, Jervis Bay

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MEEK, P.D. (1998). Food items brought home by domestic cats *Felis catus* (L) living in Booderee National Park, Jervis Bay. *Proceedings of the Linnean Society of New South Wales* **120**, 43–47.

Cat owners kept records of the food items brought home by domestic cats living in two adjacent villages surrounded by Booderee National Park, NSW. During a 12 month period food items brought home by seven cats comprise eleven native and three introduced species. One endangered bird was recorded although mammals were the largest prey group.

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KEYWORDS: Domestic cats, *Felis catus*, prey, food items, Jervis Bay, predication.

INTRODUCTION

Predation by feral and domestic cats *Felis catus* (L) has been identified as a contributing factor in the decline of some wildlife populations (Eberhard 1988; Potter 1991; Dickman 1996). However, quantitative evidence of ecological impacts caused by cats is mainly concentrated on island ecosystems (Taylor 1979a; Apps 1983; Fitzgerald and Veitch 1985). In the terrestrial environment cat and fox predation can combine with other negative ecological impacts in their effect on fauna, therefore masking the impact of each predator. Isolating and quantifying these impacts require long term experimental investigation, and research of this nature has not yet been undertaken.

The impact of cat predation on wildlife has been raised as a social and ecological issue in the 1990's and an Australian synopsis has been provided by Dickman (1996). Claims of domestic cats causing the decline and extirpation of birds, reptiles and small mammals in urban and semi-urban environments has initiated a number of investigations that have attempted to fill in some of the gaps in our knowledge of the predatory behaviour of domestic cats. In Adelaide, Paton (1990) surveyed 421 cat owners (700 cats) and identified prey caught by cats to determine the number captured and the species diversity. The survey revealed that 62% of cats brought home birds, 59% mammals, 34% reptiles and a small number of frogs and insects. Trueman (1991) estimated in his Tasmanian cat owners survey, that 65,000 native animals and 76,000 introduced animals were killed by cats each year. In a study similar to Paton (1990), Barratt (1997) surveyed the owners of 214 cats in suburban Canberra to determine the prey returned home by domestic cats. It was revealed that approximately 75% of cats hunted, with the largest prey group recovered being introduced rodents (64%), followed by native birds (14%), introduced birds (10%) and a small proportion of reptiles and frogs. These studies have focused on cats living in urban/disturbed areas and in the case of Barratt (1997) the proportion of introduced prey (~75%) to native prey (~25%) is probably representative of the relative abundance of fauna that would be expected in most disturbed urban environments.

This paper reports on the prey brought home by a small number of domestic cats living within a National Park in NSW.

MATERIALS AND METHODS

Jervis Bay Territory (approx. 150°43′E, 35°09′S) is located approximately 200 km south of Sydney on the coast of New South Wales and is an area of 7700 hectares. The landscape is predominantly Permian sandstone with wind blown sand dunes. There are six main vegetation communities (Ingwersen 1976) with heath covering the largest area in the Territory (Williams 1995). Twenty one native non-volant mammals have been recorded in the Territory. The most abundant small mammal species are the Brown Antechinus *Antechinus stuartii* and the Bush Rat or Mootit *Rattus fuscipes*. Six species of vertebrate pests co-habit the area (Meek and Nazer 1995), including the European red fox *Vulpes vulpes*, the cat *Felis catus* and the dog *Canis lupus familiaris*.

In this study, cat owners in two adjacent villages (HMAS Creswell and Jervis Bay Village) within Booderee National Park were asked to collect animals brought home by their domestic cats during 1994. The purpose of the investigation was to supplement a larger study aimed at radio tracking cats to determine whether cats were hunting in the surrounding National Park (Meek unpub. data). The owners (n=6) of seven cats agreed to collect specimens. They were asked to record the prey items brought home, and behavioural information including; when the cat brought the specimen home, whether the prey was alive or dead and if it had been partly eaten by the cat. The owners contacted me to retrieve the specimens which provided an opportunity for accurate taxonomic identification. The study did not aim to quantify the impact of cat predation, only to determine the prey items brought home. The assumption was made that prey brought home was caught by each cat and did not reflect the actual prey killed because this was impossible to determine without stomach analysis and behavioural observations.

The survey was conducted over a 12 month period although several cat owners, including the most efficient hunting cat, left the area during the study. Efforts were made to encourage new participants in the study but all were reluctant to assist.

RESULTS AND DISCUSSION

Thirty five specimens were brought home by cats in the study comprising eleven native and three introduced species (Table 1). Native mammals were the largest prey group (49%), followed by introduced mammals (26%), native birds (19%) and reptiles (6%). One bird species (Ground Parrot, *Pezoporus wallicus*) caught by cats is listed as a vulnerable species on Schedule 2 of the Threatened Species Conservation Act (1995).

Most of the prey were caught at night, particularly mammals (Fig. 1), and 34% of prey were found partially eaten by the cats. It was impossible to determine the number of prey killed, cached or killed and eaten by the cats.

The results of this survey indicate that cats residing in natural bushland do hunt native wildlife, in particular mammals. However, these results only represent a small number of cats in a population and the method used only allows for generalisations to be made about cat predation. The data can not be used to comment on population impacts. These results concur with Leyhausen (1979), Churcher and Lawton (1987), Fitzgerald (1988), Barratt (1997) and Meek and Triggs (in litt.) that small mammals are a favoured food item of the cat. As expected, the proportion of native species to introduced species in this study is contrary to the findings of Barratt (1997). In his study, cats in the urban areas of Canberra returned with more introduced than native animals which reflects the difference in species composition between urban and natural habitat.

TABLE 1

Prey items brought home by domestic cats in Jervis Bay Territory

Status	Prey Class	Common Name	Species name	Frequency n	Frequency %
Native					
	Mammal	Brown Antechinus	*Antechinus stuartii*	3	8.6
		Dusky Antechinus	*Antechinus swainsonii*	2	5.7
		Sugar Glider	*Petaurus breviceps*	5	14.3
		Ring Tail Possum *	*Pseudochirus perigrinus*	4	11.4
		Bush Rat	*Rattus fuscipes*	3	8.6
	Bird	Ground Parrot	*Pezoporus wallicus*	2	5.7
		Red Wattle Bird	*Anthochaera carunculata*	1	2.6
		Southern Emu Wren	*Stipiturus malachurus*	1	2.6
		Grey Shrike Thrush	*Colluricincla harmonica*	1	2.6
		Crimson Rosella	*Platycercus elegans*	2	5.7
	Reptile	Skink	unknown	2	5.7
Total				***26***	***74.3***
Introduced					
	Mammal	House Mouse	*Mus domesticus*	5	14.3
		Ship Rat	*Rattus rattus*	2	5.7
		Rabbit	*Oryctolagus cuniculus*	2	5.7
Total				***9***	***25.7***

* killed by unidentified cat.

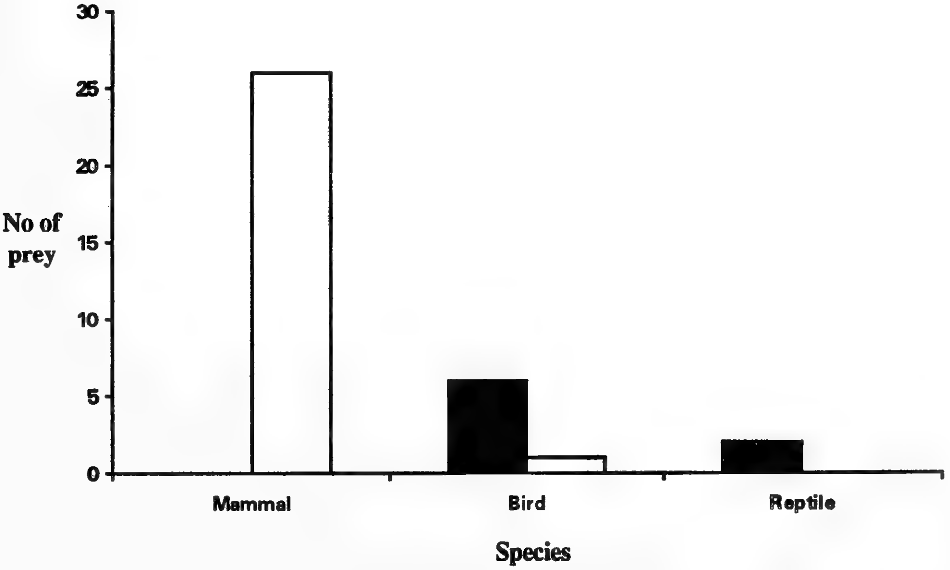

Figure 1. Time of day when prey were brought home (n=35 prey) by domestic cats in Booderee National Park 1994. Open bars = number of prey brought home in the day; solid bars = number of prey brought home at night.

Information provided in this study suggests that cats in Jervis Bay are taking fewer prey items home (5 prey/cat/year) than cats in Adelaide (54 prey/cat/year) (Paton 1990). This wide differentiation in figures is most likely a result of three main factors; the small number of cats in this study, the different survey techniques used between the studies and the removal of cats from this study when their owners left the villages. Efforts were made to bring new cats into the study, however many owners were concerned that the evidence would be used to prevent the ownership of cats within the National Park.

Cats are often described as opportunistic hunters (Turner and Meister 1988; Dickman 1996; Barratt 1997), although observations in this study suggest that individual cats can also specialise in hunting preferred species. Two of the cats in this study showed an apparent tendency for hunting particular species; one cat was an extremely successful mouser (*Mus domesticus* and *Rattus rattus*) while another was an efficient hunter of sugar gliders *Petaurus breviceps*. This form of individuality was also observed in cats from Canberra (Barrett, D. pers comm. 1995) and the behaviour has been discussed by Turner and Meister (1988).

Barratt's (1997) view is that there is a potential threat to patchily distributed wildlife by cats in new residential developments and he recommends night curfews to reduce the impacts on mammal species. Similar threats are posed by cats residing in close proximity to natural bushland, particularly to species with low abundance or that are at risk of extirpation. This view is not supported by Jarman and van der Lee (1992) who believe that domestic cats are a potential threat to wildlife, but consider they pose little threat to endangered species. The combined results of my study, that of Barratt (1997) and unpublished tracking data by this author confirm that domestic cats will hunt in natural bushland and will hunt and kill wildlife (including endangered species). However, the implications of this predation on population abundance of species is unclear. As a precautionary measure it is recommended that free-roaming cats are restricted from wandering in areas where there are threatened native wildlife.

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Pollen Loads Collected from Large Insects in Australian Subtropical Rainforests

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Pollen loads on insects >9 mm in length, collected principally from the flowers of subtropical rainforest trees, were examined. Primary sites of pollen lodgement on the integument of approximately 60 species of Coleoptera, Diptera and Hymenoptera (Icheumonoidea, Sphecoidea, Vespoidea) were recorded. Hooked setae were recorded for the first time from the beetle genus *Cacochroa* (Cetoniinae-Scarabaeidae).

Although most insects carried mixed pollen loads the low incidence or absence of pollen from non-conspecific plant taxa ('foreign' pollen) indicated temporal foraging constancy for some species. Insects foraging on Myrtaceae generally carried large pollen loads with little or no foreign pollen. Wasps exhibited considerable variation in the amount of pollen carried. Beetles in the families Buprestidae, Cerambycidae and Scarabaeidae (subfamily Cetoniinae) carried mixed pollen loads, derived from a number of plant taxa, but often in substantial quantities, indicating that Coleoptera are potentially important pollinators of mass-flowering rainforest trees with generalist pollination ecologies.

The foraging behaviour and surface vestiture of individual insect taxa influence pollen loads and sites of pollen deposition on the bodies of insects. All insect taxa examined were observed to make frequent inter-plant movements and undertook relatively long distance inter-plant flights and, consequently, may be important in contributing to outbreeding in fragmented populations of rainforest trees.

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KEYWORDS: Coleoptera, Diptera, wasps, pollen, pollination ecology, subtropical rainforests, rainforest fragmentation.

INTRODUCTION

The majority of mass-flowering Australian subtropical rainforest trees appear to be capable of being pollinated by members of a taxonomically diverse assemblage of insects (Williams 1995) and as such are part of the majority of angiosperms which "are generalists in their pollinator requirements" (Ollerton 1996). Most insects visiting Australian subtropical rainforest trees are less than 6 mm in length (Williams 1995), and insects in this size group have been shown to transport pollen and to act as pollinators of a number of Australian tropical and subtropical rainforest plants (Hamilton 1897, House 1985, 1989, Armstrong and Irvine 1989, Williams 1995). Although large ecologically specialised bees are pollinators of some Australian rainforest plants (e.g., Gross 1993), the capacity of ecologically unspecialised larger insects (here arbitrarily characterised as species >9 mm in body length) to transfer pollen in Australian rainforest communities has not been investigated. The decision as to which insects can be considered large is a subjective one but individual insects longer than 9 mm become conspicuous to the casual human observer.

Large insects constituted less than 6 percent of the number of individuals and species of anthophilous insects sampled in Australian subtropical rainforests by Williams 1995. Large insects were absent in many samples from a number of study plants

(Williams 1995). Although larger species make up a small proportion of the flower-visiting fauna, their potential for relatively long-distance inter-plant movements may have important consequences for the reproductive success of disjunct or isolated plants. This may be particularly important for plants possessing small entomophilous flowers as such plants are not regularly visited by bats or birds (Williams 1995) which might otherwise act as long distance pollen vectors. The capacity of a vector to transport pollen is related to body morphology and behavioural patterns (e.g., foraging movements, orientation and contact with floral structures, grooming). The presence of compounds on the exine (e.g., pollenkitt) may facilitate adherence to the vector (Faegri *et al.* 1992) but the role of exine sculpture in facilitating pollen transport is unclear (Williams and Adam in press).

Historically, bees (Apoidea) and Syrphidae (Diptera) have been considered as more efficient and specialised collectors of pollen and, consequently, pollinators of flowering plants, than other insects (see Holloway 1976, Armstrong 1979, Roubik 1989, Williams and Adam 1994). The foraging behaviour of eusocial Apidae is well documented (Faegri and van der Pijl 1979, Appanah 1982, Appanah, Willenstein and Marshall 1986, Adam, Fisher and Anderson 1987, Bernhardt and Thien 1987, McAlpine 1988, Bertin 1989, Roubik 1989, Williams and Adam 1994, 1997) but the pollination contributions of other bee families are varied and some groups, for example the Colletidae, may contribute little to reproductive success in plants (see Armstrong 1979, Faegri and van der Pijl 1979, Steiner 1985, Bernhardt and Thien 1987, Williams and Adam 1994). Proenca and Gibbs (1994), however, record pollination of the tree *Siphoneugenia densiflora* Berg (Myrtaceae), in a Brazilian savannah woodland, by the colletid *Ptiloglossa* sp.. Numerous species of aculeate or 'higher' wasps (Vespoidea, Sphecoidea) visit some rainforest plants (Williams and Adam 1995) but their role in pollination has been little investigated.

Although a number of beetle families possess dense or long vestiture (Crowson 1981) Coleoptera have been regarded as 'smooth-bodied' and not likely to be effective pollinators (Percival 1965, Ashton 1969, Armstrong 1979, Archibold 1995). Archibold (1995), for example, citing Faegri and van der Pijl (1979), stated that "Pollen does not readily adhere to the smooth bodies of beetles and their clumsy action usually restricts them to open, bowl-shaped blossoms which offer little reward of nectar or pollen".

Increased surface vestiture, palynophilic (pollen-collecting) setae and frontoventrally placed pollen retaining punctation and foveae, and possibly medial pits and grooves on the disc of the head and elongated mouthparts (as in the *Castiarina* 'producta' spp. group of Coleoptera-Buprestidae), are considered derived apomorphic characters in anthophilous Coleoptera (Holloway 1976, Gardner 1989). Such pollen retaining structures in various pollinivorous Coleoptera may have evolved as food collecting surfaces (Crowson 1981), but may also permit transport of pollen between plants so that insects possessing these structures have the potential to act as pollinators.

Here we present data on pollen loads carried by large anthophilous insects in subtropical rainforest remnants and associated ecotones. These data provide:

1. a test of the assertion (Archibold 1995) that superficially smooth integuments render many Coleptera unlikely pollinators,
2. for those insects carrying pollen, an indication of pollen load capacity and principal sites of pollen deposition on the integument, and
3. an indication of fidelity or constancy of potential vectors to the flower resource (this is only related to the time of sampling and does not indicate how the species may forage at other sites or times).

In addition, we briefly comment on morphological and behavioural factors that influence the amount of pollen carried by individual insects. Our investigation of pollen loads was intended primarily to determine whether individual taxa could potentially act as pollinators, rather than to assess the efficiency of individual taxa as pollinators.

METHODS

As a small component of a study of the pollination ecology of subtropical rainforests (Williams 1995), undertaken in the Manning Valley (approximately 31°52′S, 152°22′E) in coastal northern New South Wales, insects greater than 9 mm in body length were collected to determine their capacity to carry pollen. Latitudes and longitudes of study sites are given in Table 1 and descriptions of the study sites are given in Williams (1993, 1995) and Williams and Adam (1997). The majority of field collections were made between 1990 and 1993. Most specimens collected are lodged in the Australian Museum, Sydney. Insects were collected individually by hand netting as they landed upon, or fed from, flowers. To avoid pollen contamination specimens were placed separately in an insect killing jar primed with ethyl acetate and then stored separately for later examination. Specimens were examined under a binocular microscope. Insects were identified principally by comparison with material held in the Australian Museum, Australian National Insect Collection, CSIRO (Canberra), and the New South Wales Department of Agriculture (Orange).

A summary of the primary pollen deposition sites on the integument of those insects studied which carried pollen is given in the Appendix (insects listed in the Appendix represent the majority of larger-sized native taxa collected during the broader pollination study).

Most pollen was located as aggregations or discrete masses on the insect body. These aggregations were removed with a micropin and embedded in glycerine-safranin gel, to which had been added several drops of phenol to inhibit fungal growth, on a microscope slide. Slides were later examined by light microscope (at X40). The pollen loads examined were rated ‘moderate (M)’ (>100 grains), ‘heavy (H)’ (>200 grains) and ‘abundant (A)’ (>300 grains). Pollen loads <100 grains are given as approximate counts of individual grains (Table 1). Pollen composition was expressed as percent ‘home’ pollen (House 1985); i.e. pollen conspecific with the plant species from which the insect was collected. Although the shape and sculpture of pollen from different Myrtaceae species are similar, Myrtaceae pollen could be identified with reasonable certainty based upon the absence of co-flowering myrtaceous species or gross differences in grain size (such as between *Waterhousea floribunda* (F. Muell.) B.Hyland and *Tristaniopsis laurina* (Smith) P.G. Wilson & Waterhouse).

Insect taxa examined were observed to undertake frequent inter-plant movements and relatively long distance inter-plant flights between widely spaced trees. A number of additional large insect taxa, particularly in the Coleoptera (i.e. Tenebrionidae-Alleculinae, Cantharidae, Oedemeridae), occur rarely on mass-flowering subtropical rainforest trees but their inter-plant movements were observed to be far less frequent. Such species could still be important in carrying pollen between flowers in individual inflorescences. Although these relatively sedentary taxa were omitted from consideration they do collect pollen on their bodies thus reducing the pollen available for carriage by insects that undertake more frequent and relatively long distance inter-plant movements.

RESULTS

More than 60,000 insects of all sizes were collected during the three seasons, 1990–1993, in which most of the fieldwork was undertaken. Data on numbers of plant species and individuals sampled, numbers of samples collected, and frequency of large-sized insects within individual samples are given in Williams (1995). Although the number of large insects overall was less than 6 percent the proportion of large insects in individual samples varied from 0–20 percent (Williams 1995). The introduced ‘honey bee’ *Apis mellifera* frequently represented more than 70 percent of the large-sized insects collected in samples (Williams 1995).

TABLE 1

Pollen loads from large insects (excluding *Apis mellifera*) demonstrating frequent intercanopy movements (approximate pollen grain counts in three abundance classes: 'M' moderate = >100 grains, 'H' heavy = >200 grains, 'A' abundant = >300 grains; total counts given for <100 grains; number of foreign grains given in brackets; '>99' = probably all 'home' pollen with several unassignable grains; '@' = pollen count indeterminate due to grain deformation or similarity of type; 'm' = male, 'f' = female). Site codes: (1) Harrington [31°52′30″S, 152°41′00″E], (2) Manning Point [31°53′30″S, 152°40′00″E], (3) Saltwater Reserve [32°00′30″S, 152°33′45″E], (4) Lansdowne Reserve [31°47′30″S, 152°32′30″E], (5) Lorien Wildlife Refuge [31°45′00″S, 152°32′30″E], (6) Kenwood Wildlife Refuge [31°44′45″S, 152°31′30″E], (7) Wingham [31°52′40″S, 152°22′00″E], (8) Woko National Park [31°49′00″S, 151°47′00″E). Nomenclature for plants follows Harden (1990–1992)

Insect Taxa	Plant Taxa from which insects were collected	Site	Pollen load	% Home pollen
COLEOPTERA				
Buprestidae				
Castiarina acuminata Kerremans	*Alphitonia excelsa* (Fenzl) Benth.	1	6	100
C. acuminata	*Alphitonia excelsa*	1	54(1)	98
C. acuminata	*Cuttsia viburnea* F. Muell.	5	A	<30
C. acuminata	*Guioa semiglauca* (F. Muell.) Radlk.	1	M	>95
C. acuminata	*Guioa semiglauca*	1	A	>99
C. delta Thomson	*Tristaniopsis laurina* (Smith) P.G.Wilson & Waterhouse	7	A	>99
C. insignis Blackburn	*Acmena smithii* (Poiret) Merr. & Perry	4	A	100
C. insignis	*Tristaniopsis laurina*	7	H	>99
C. insignis	*Waterhousea floribunda* (F.Muell.) B. Hyland	7	A	100
C. neglecta Carter	*Alphitonia excelsa*	1	M	100
C. neglecta	*Alphitonia excelsa*	1	M	?100
C. producta Saunders	*Acmena smithii*	4	A	100
C. producta	*Alphitonia excelsa*	6	M	unrecorded
C. producta	*Guioa semiglauca*	1	A	>70
C. producta	*Tristaniopsis laurina*	5	A	<70
C. producta	*Tristaniopsis laurina*	7	M	?100
C. producta	*Waterhousea floribunda*	7	A	100
C. pulchripes Blackburn	*Cuttsia viburnea*	5	A	>95
C. ?sexcavata Deuquet	*Acmena smithii* var. *minor*	8	A	>95
C. ?vicina Saunders	*Waterhousea floribunda*	7	A	>99
Curis aurifera Castelnau & Gory	*Waterhousea floribunda*	7	A	>70
C. splendens (Macleay)	*Acmena smithii* var. *minor*	8	M	<50
C. splendens	*Waterhousea floribunda*	7	A	>99
Metaxymorpha grayi Parry	*Tristaniopsis laurina*	5	A	>99
Torresita cuprifera Kirby	*Waterhousea floribunda*	7	M	>95
Cerambycidae				
Aridaeus thoracicus (Donovan)	*Tristaniopsis laurina*	5	H	>95
A. thoracicus	*Waterhousea floribunda*	7	A	>99
Distichocera superba (Poll.)	*Tristaniopsis laurina*	5	H	100
D. superba	*Waterhousea floribunda*	7	A	>99
Hesthesis sp. nr. *bizonata* Newman	*Tristaniopsis laurina*	5	M	<30
Tragoceras spencei (Hope)	*Waterhousea floribunda*	5	A	>90
Tropocalymma dimidiatum (Newman)	*Acmena smithii*	1	H	>99

Scarabaeidae				
Cacachroa gymnopleura (Fischer)	*Waterhousea floribunda*	5	M	100
Diaphonia dorsalis Donovan	*Euroschinus falcata* J.D. Hook	3	18(1)	94
D. dorsalis	*Waterhousea floribunda*	5	A	>99
D. dorsalis	*Waterhousea floribunda*	7	A	>99
Eupoecila australasiae (Donovan)	*Alphitonia excelsa*	1	M	100
E. australasiae	*Waterhousea floribunda*	5	A	>99
E. australasiae	*Waterhousea floribunda*	7	A	>99
Glycyphana brunnipes (Kirby)	*Alphitonia excelsa*	6	M	<70
G. brunnipes	*Euroschinua falcata*	3	21(7)	33
G. brunnipes	*Tristaniopsis laurina*	5	M	>99
Polystigma punctatum (Donovan)	*Alphitonia excelsa*	1	H	>99
P. punctatum	*Tristaniopsis laurina*	5	A	>95
P. punctatum	*Waterhousea floribunda*	7	A	>99
P. punctatum	*Waterhousea floribunda*	5	A	>95
DIPTERA				
Calliphoridae				
Paramenia sp.	*Alphitonia excelsa*	1	H	>90
Nemestrinidae				
Austrogastromyia nigrovittata Mackerras	*Cuttsia viburnea*	5	A	100
A. ?punctata Macquart	*Waterhousea floribunda*	7	H	>95
Syrphidae				
Dideopsis sp.	*Alphitonia excelsa*	1	3	100
Tabanidae				
Cydistomyia nigripicta (Macquart)	*Tristaniopsis laurina*	7	9(1)	89
Scaptia auriflua Donovan	*Waterhousea floribunda*	5	M	>95
S. ?quadrimacula Walker	*Cuttsia viburnea*	5	H	>95
HYMENOPTERA				
Ichneumonidae				
Echthromorpha intricatoria (Fabricius)	*Alphitonia excelsa*	1	H	100
Pompilidae				
Chryptocheilus sp.	*Tristaniopsis laurina*	7	A	100
Scoliidae				
Campsomeris ?tasmaniensis (Saussure)	*Alphitonia excelsa*	1	83(3)	96
C. ?tasmaniensis	*Diospyros australis* (R. Br.) Hiern	5	A	<1
C. zonata Smith	*Tristaniopsis laurina*	5	A	>99
Scolia verticollis (Fabricius)	*Alphitonia excelsa*	1	H	>95
S. ?verticollis	*Tristaniopsis laurina*	7	M	>95
Scolia sp.	*Tristaniopsis laurina*	7	M	>95
Sphecidae				
Bembicinus sp.	*Alphitonia excelsa*	1	3(1)	66
Bembix promontorii Lohrman	*Alphitonia excelsa*	1	4	100
Bembix sp. 1	*Alphitonia excelsa*	1	8(@4)	@50

Bembix sp. 2	*Acmena smithii*	2	19(8)	58
Sceliphron laetum (Smith)	*Tristaniopsis laurina*	7	M	>90
Sphex ephippium Smith	*Alphitonia excelsa*	1	7(4)	43
S. fumipennis Smith	*Alphitonia excelsa*	1	48(3)	94
Tachysphex sp.	*Alphitonia excelsa*	1	96(0)	100
Tiphiidae				
Anthobosca ?signata Smith	*Alphitonia excelsa*	1	M	>95
A. ?signata	*Alphitonia excelsa*	1	A	100
A. ?signata	*Tristaniopsis laurina*	5	M	>95
Diamma bicolor Westwood	*Alphitonia excelsa*	1	73(7)	>90
Dimorphothynnus dimidiatus (Smith)	*Acmena smithii*	2	H	>95
D. dimidiatus	*Acmena smithii*	1	83(@50)	<40
D. dimidiatus	*Guioa semiglauca*	1	M	100
Hemithynnus apterus (Oliver)	*Acmena smithii*	2	22(?)	>50
H. rufiventris (Guerin)	*Tristaniopsis laurina*	5	H	>99
Rhagigaster sp. nr. *kiandrensis* Guerin	*Alphitonia excelsa*	1		?home
Zaspilothynnus sp. nr. *campanularis* (Smith)	*Alphitonia excelsa*	1	38(@9)	@76
Vespidae				
Abispa splendida (Guerin)	*Tristaniopsis laurina*	7	A	>99
Bidentodynerus bicolor (Saussure)	*Tristaniopsis laurina*	7	H	80
?*Epiodynerus* sp.	*Tristaniopsis laurina*	5	M	<60
Polistes humilis (Fabricius)	*Alectryon coriaceus*	2	8(3)	63
P. tepidus (Fabricius)	*Alphitonia excelsa*	1	M	100
Pseudabispa confusa van der Vecht	*Tristaniopsis laurina*	7	A	>99

Pollen loads from 86 individual insects, comprising approximately 60 native insect species in 13 families, were examined (Table 1). Although this number is a small proportion of the large insects the sample represented nearly all of the larger-sized native species and genera collected during the pollination study, and in most instances represented all of the individuals collected for individual taxa. None of the species or genera examined were considered to be specialist foragers as all species occurred either in several habitats or upon a variety of plant species (Williams 1995), or carried mixed pollen loads (Table 1) indicating that foraging patterns are generalised. However, the pollen loads of some taxa indicated temporal fidelity or constancy to the host plant. Although numerous individuals and taxa were observed at close range in the field, very few large insects exhibited cleaning behaviour (which would have reduced their pollen load).

Coleoptera-Buprestidae

The buprestid fauna collected from the lower Manning includes genera that are phyllophagous or, alternatively, floricolous as adults (Williams 1995). The principal floricolous genus collected was *Castiarina* (sensu Gardner 1989) (Table 1), but species of *Torresita*, *Curis*, *Metaxymorpha*, *Calodema* and *Neocuris* also occurred on flowers of rainforest trees. *Neocuris* was excluded from the genera examined for pollen loads, due to the small size of individuals (<5 mm), and although *Calodema* was observed on *Cuttsia viburnea* we were unable to collect specimens due to the difficulty of hand netting in the canopy.

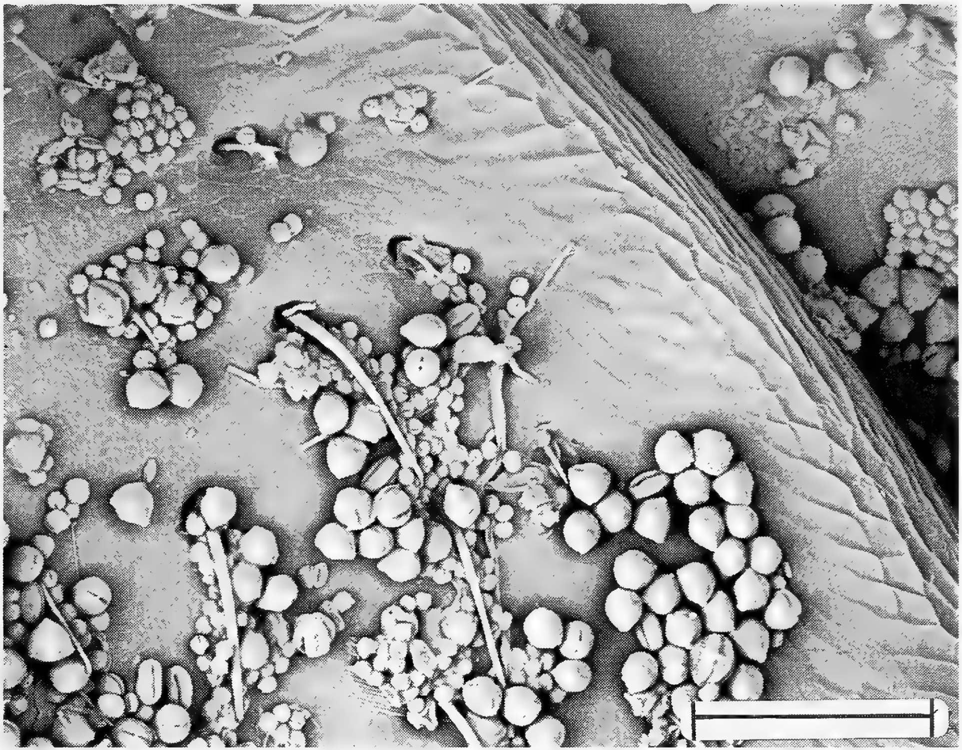

Figure 1. Mixed pollen load on the hypomeron of *Castiarina acuminata* (Buprestidae). Note almost total absence of surface sculpture at this point (scale = 100 μm).

Fifteen (60%) of the 25 Buprestidae examined had abundant pollen loads (Table 1). *Castiarina* spp. generally carried large pollen loads composed primarily of 'home' pollen. In 2 specimens of *Castiarina acuminata* Kerremans collected on *Alphitonia excelsa*, in littoral rainforest at Harrington, pollen loads were light (6–53 grains), although principally consisting of 'home' pollen. On *C. neglecta* Carter, however, loads of *Alphitonia excelsa* pollen from the same site were more substantial (M). Species collected on myrtaceous blossoms (*Acmena smithii* (Poiret) Merr. & Perry, *Tristaniopsis laurina*, *Waterhousea floribunda*) generally carried heavy to abundant pollen loads which were almost exclusively 'home' pollen. Pollen loads on *Curis* spp. collected from Myrtaceae were more variable (M-A, i.e. less than 50 to more than 90% 'home' pollen).

Although vestiture in several non-Australian buprestid genera is long and dense (e.g., *Acmaeodera*, *Julodis*) most Buprestidae possess short setae.

Placement of pollen was principally ventral and on anterodorsal areas. Major sites of pollen deposition were the frontal cavity of the head, thoracic hypomera (Fig. 1), prosternum and metasternum, and antennal and coxal cavities.

Surface punctation and vestiture on the head, pronotum and anteroventral surfaces generally, permitted the retention and transport of potentially large pollen loads (Table 1). Vestiture on the abdominal ventrites and sutures between individual abdominal segments carried significant loads. Vestiture is vulnerable to wear and abrasion which may reduce pollen carrying capacity.

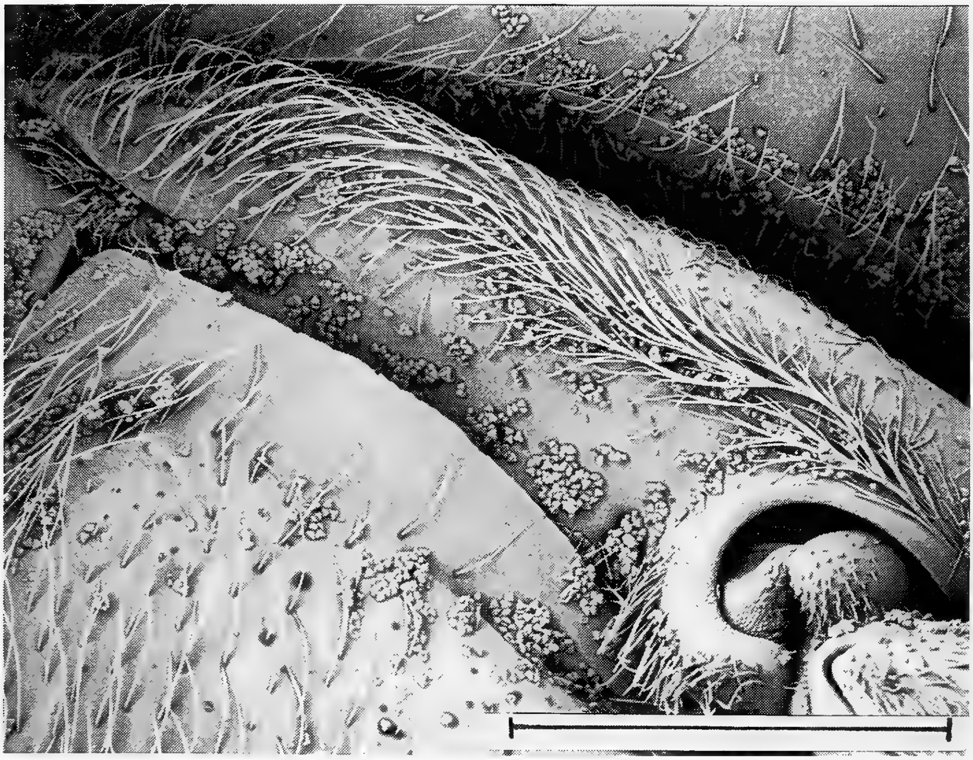

Figure 2. Pollen grains associated with the metacoxal region, *Stenoderus* sp. (Cerambycidae). Note general absence of integument sculpture or punctation at this magnification (scale = 500 μm).

Coleoptera–Cerambycidae

Although Cerambycidae are a taxonomically diverse group within the rainforest Coleoptera, most regionally-occurring species are phyllophagous (Williams 1995).

Large Cerambycidae are infrequent or spatially and temporally localised flower visitors in rainforest. Of the 5 large species collected at blossoms, only *Tropocalymma dimidiatum* (Newman) and *Distichocera superba* (Poll.), are known to be regionally restricted to rainforest (G. Williams unpublished data). Although widely distributed in coastal habitats (Webb 1987, G. Williams pers. obs.) *Aridaeus thoracicus* (Donovan) was collected only on *Tristaniopsis laurina* and *Waterhousea floribunda* at Wingham during this study.

Three (43%) of the Cerambycidae carried abundant pollen loads. Both *D. superba* and *T. dimidiatum* carried heavy or abundant pollen loads which were composed almost totally of 'home' pollen. *Aridaeus thoracicus* (H-A: more than 95 to more than 99% 'home' pollen) and *Tragocerus spencei* Hope (A; >90%) carried heavy pollen loads but the pollen load carried by *Hesthesis* sp. near *bizonata* Newman was smaller (M) and contained a high proportion of foreign pollen (<30% home pollen).

Principal placement of pollen in Cerambycidae was on the ventral and anterodorsal regions. The regions of the head, antennal and coxal cavities (Fig. 2), and mesosternum were major deposition sites. In Cerambycidae, however, the prosternum is generally reduced to a smooth convex structure, without a prominent frontal lobe or vestiture, and this reduces its capacity to function as a pollen deposition site.

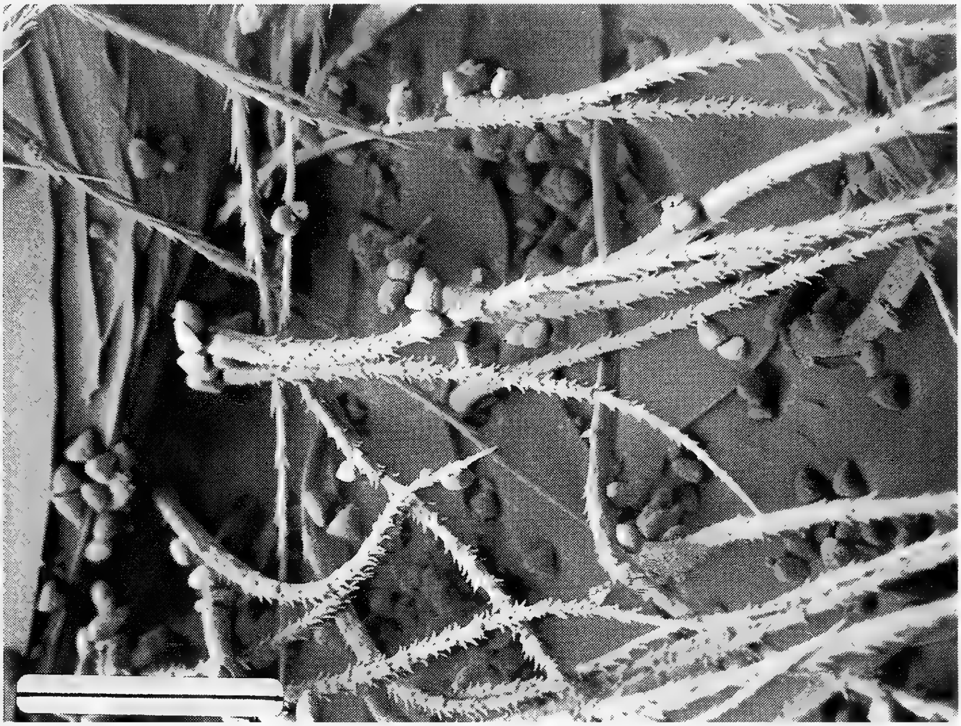

Figure 3. *Cacochroa gymnopleura* (Cetoniinae), lateral detail of hooked palynophilic setae, and pollen grains, in the vicinity of the hypomeron. Similarly hooked setae are recorded in Apoidea (see Barth [1991], plate 13) and Syrphidae (Holloway [1976], figure 8) (scale 100 μm).

Coleoptera–Scarabaeidae–Cetoniinae

Adult Scarabaeidae-Cetoniinae constitute a flower-adapted group within the otherwise predominantly phyllophagous Scarabaeidae (Lawrence and Britton 1994, Williams 1995). Cetoniinae collected comprised 5 genera, each represented by a single species.

Seven (50%) Cetoniinae carried abundant quantities of pollen. *Diaphonia dorsalis* Donovan carried variable quantities of pollen (17 to >300 grains) and this was almost exclusively 'home' pollen. *Cacochroa gymnopleura* (Fischer) carried abundant quantities of 'home' pollen only, but is a common species widely encountered on the flowers of Myrtaceae-Leptospermoideae (Webb 1987) in eastern Australia. Similarly, *Eupoecila australasiae* (Donovan) (M-A: >99%) and *Polystigma punctatum* (Donovan) (H-A: >95%) carried high 'home' pollen loads and are both widely encountered in coastal sclerophyll forests. *Glycyphana brunnipes* (Kirby) carried smaller variable loads (21 to >100: >60 to >99%). Although common on *Euroschinus falcata* J.D.Hook. (Anacardiaceae), at Saltwater, pollen loads were very low (Table 1) or could not be readily discerned under the microscope.

Although Cetoniinae generally lack the prominent integumental punctation of Buprestidae they possess long, dense setal clusters and surface vestiture which readily ensnare pollen grains (Fig. 3) (Crowson 1981).

Hooked setae were recorded on the lateroventral surface of *Cacochroa gymnopleura* (Fig. 3) during scanning electron microscopy investigation of pollen lodgement. Englund (1993) has recorded branched setae on the European cetoniine *Cetonia aurata* (L.) but

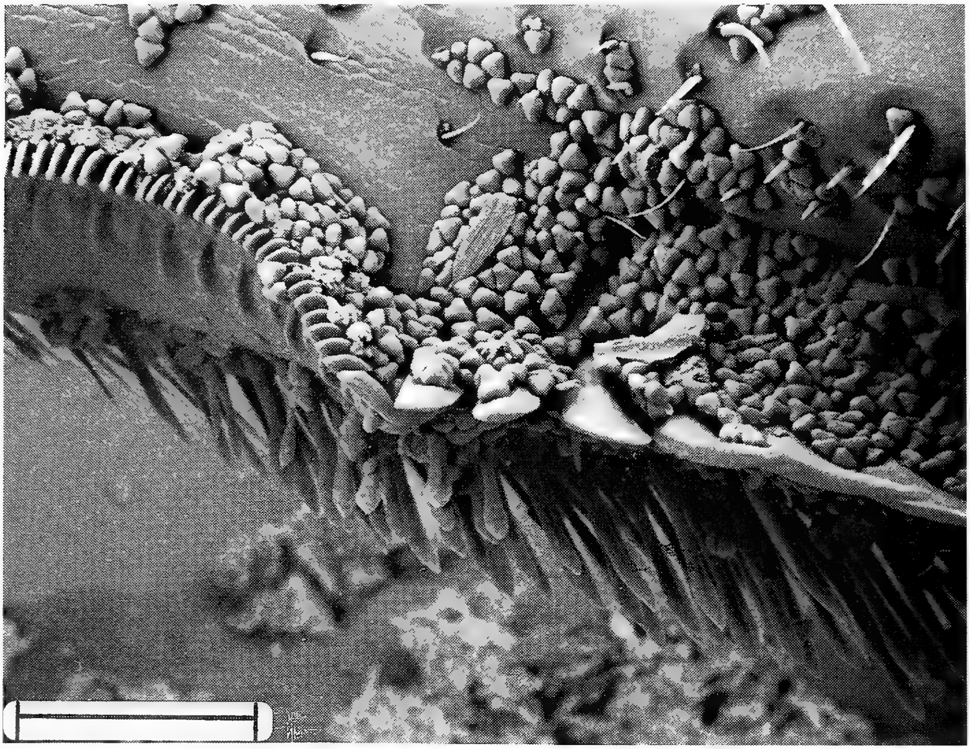

Figure 4. *Anthobosca ?signata* (Tiphiidae); detail of specialised 'pollen comb' on the first tarsomere (scale = 100 μm).

these structures have not otherwise been reported from the Cetoniinae. Crowson (1981) noted modified, plumose, hairs in the scarabaeoid genus *Amphicoma* (Glaphyridae) and hooked setae similar to those in *C. gymnopleura* have been found on the glaphyrid genus *Lichnanthe* (J.F. Lawrence pers. comm.). Hooked setae may occur more widely in pollen-feeding scarabaeoids but can be readily overlooked under normal magnification (J.F. Lawrence pers. comm.). Similarly shaped setae have been described and figured from specialised Apoidea and Syrphidae (Diptera) (Holloway 1976, Barth 1991).

The head, and lateral and ventral surfaces of the prothorax of Cetoniinae carry heavier pollen loads than other regions of the body. Unlike Buprestidae, the frons does not generally possess a pronounced frontal or vertical cavity or depression and pollen clusters are not normally associated with the frons. The clypeus however, frequently possesses large, readily discernable pollen loads. The importance of the clypeus as a site of pollen deposition probably reflects the pronounced development of this structure in Scarabaeidae generally (Carne 1957a, 1958, Britton 1970, Matthews 1972, Crowson 1981, Lawrence and Britton 1991), although some Dynastinae and Rutelinae possess a reduced clypeus (Carne 1957b, 1958).

Coleoptera potentially carry large pollen loads (54% of specimens cited in Table 1 carried abundant quantities of pollen). Feeding behaviour in anthophilous Buprestidae, Cerambycidae and Cetoniinae is similar. Species characteristically feed on nectar by inserting the head and mouthparts into the perianth or hypanthium. Short distance, inter-flower movements are undertaken without the aid of flight, by 'clambering' across and through paniculate and corymbose inflorescences. Long distance, inter-plant flights are

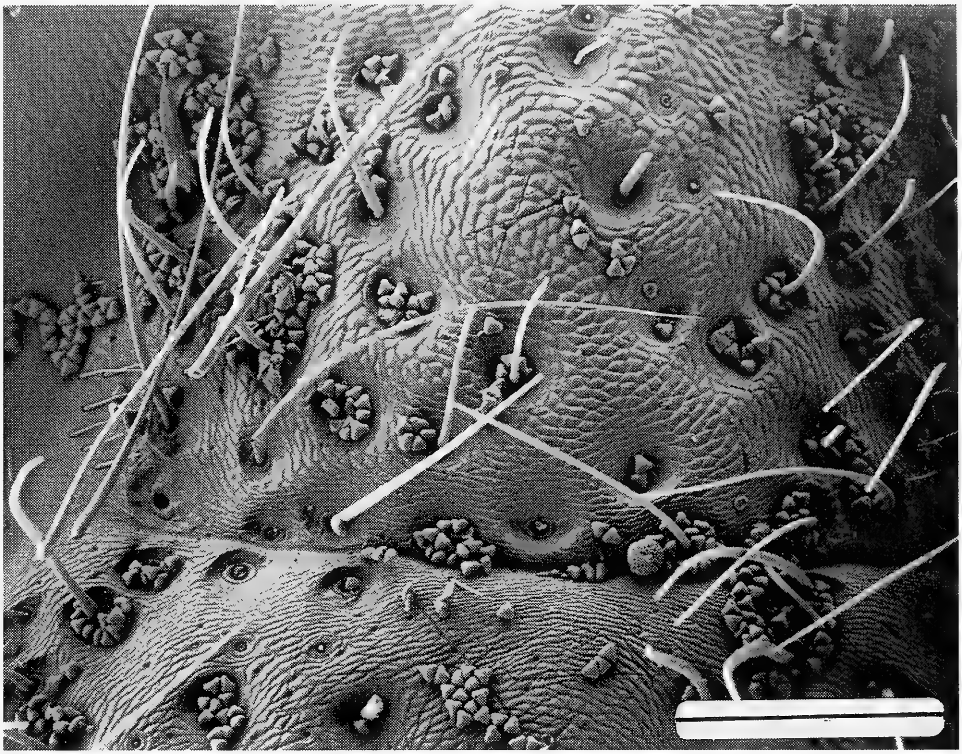

Figure 5. Pollen clusters (principally Myrtaceae) in fascial punctation, *Scolia* sp. (Scoliidae) (scale = 200 μm).

undertaken either without preceding visual warning, as in Cetoniinae, or as a response to disturbance (e.g., Buprestidae-*Castiarina*). The similarities in sites of pollen deposition on these taxonomically unrelated families is not unexpected given their generally similar foraging behaviour.

Hymenoptera (Ichneumonoidea, Sphecoidea, Vespoidea)

Pollen was found on members of the families Tiphiidae, Scoliidae, Sphecidae, Pompilidae and Vespidae (aculeate wasps), and Ichneumonidae. The Tiphiidae (6 genera, 7 spp.), Sphecidae (5 genera, 8 spp.) and Vespidae (5 genera, 6 spp.) were the most abundant larger-sized wasps frequently carrying significant (>100 grains) pollen loads. Only 18 percent of larger-sized wasps carried abundant pollen loads. This was lower than the 54 percent (n=46) of Coleoptera individuals that carried abundant quantities of pollen (Table 1).

Most wasp records were from *Tristaniopsis laurina* (Myrtaceae) and *Alphitonia excelsa* (Williams and Adam 1995). While Tiphiidae were generally common on *A. excelsa*, they exhibited variation in pollen loads (1 to >300 grains) and percentage of 'home' pollen (0–100%) carried. This variation in pollen loads did not correlate with size of individual taxa.

Variation in number of pollen grains and percent 'home' pollen was found in all families. Hymenoptera collected from *Tristaniopsis laurina*, at the Lorien study site in wet sclerophyll forest, and at the Wingham site in rainforest carried generally greater pollen loads (range Lorien M-A; Wingham M-A) and loads dominated by 'home' pollen

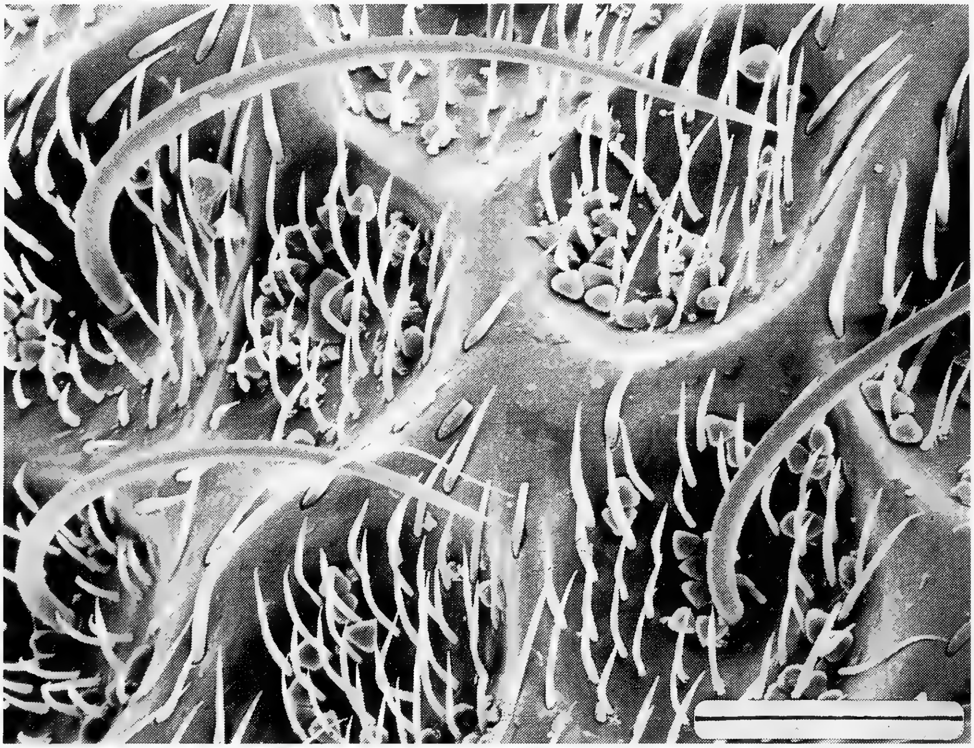

Figure 6. Detail of pollen, in lateral thoracic punctation, *Abispa* sp. (Vespidae) (scale = 100 µm).

(range Lorien less than 60 to more than 99%; Wingham 80 to more than 99%) (Table 1). In part, this is related to the relatively greater amounts of pollen available from *T. laurina* flowers (Williams 1995).

Sites of pollen deposition on large wasps were more varied than on Coleoptera (see Figs. 4, 5, 6). The head, basal antennomeres and dorsum of the mesosoma are major pollen deposition sites (the metasoma was found to carry little pollen except in the eumenine *Bidentodynerus bicolor* (Saussure)). The legs, particularly the femora and tibiae, carry pollen loads to an extent not generally paralleled in the Coleoptera. In *Anthobosca ?signata* Smith (Tiphiidae) there are specialised 'pollen combs' on the first tarsomere (Fig. 4) and these carried the largest proportion of the pollen load (functionally analogous structures are found in Apoidea and floricolous Scarabaeidae [Crowson 1981, Roubik 1989]). In *Dimorphothynnus dimidiatus* (Smith) (Tiphiidae) pollen was associated with mesepisternal grooves. In *Sphex fumipennis* Smith, *S. ephippium* Smith and *Bembicinus* sp. (Sphecidae), *Campsomeris ?tasmaniensis* (Saussure) (Scoliidae), *Rhagigaster* sp. near *kiandrensis* Guerin and *Zeleboria xanthorrhoei* (Smith) (Tiphiidae-Thynninae) the base of the forewings was the site of pollen deposition. In *Echthromorpha intricatoria* (Fabricius) (Ichneumonidae) pollen was deposited on the prementum, and malar region of the head, and was associated with the forelegs.

Robust, setose Hymenoptera-Scoliidae, and some Vespidae-Eumeninae, move across and between inflorescences in a similar manner to that of large Coleoptera. This 'clambering' method of inter-flower movement maximises physical contact between the flower and insect integument and consequently heavy pollen loads are carried, deposited widely upon the insect (Appendix).

Sphecidae undertake frequent inter-plant and inter-flower movements and remain on individual inflorescences or flowers for short periods (usually <10 seconds). For example, *Bembix* spp. generally made foraging bouts of less than 3 seconds at individual flowers. In addition, sphecids frequently feed by having their body relatively raised above most of the flower structure and this reduces contact with stamens. Although closely related to Apoidea (Naumann *et al.* 1991) sphecid behaviour differed from that of bees, which generally undertook foraging bouts involving prolonged and repeated contact with stamens. Sphecids visited only a small number of the plant species sampled. They were most frequently found on *Alphitonia excelsa*, which releases little pollen unless the petals (which initially encapsulate the stamens) are firmly depressed (Williams 1995) — which Sphecidae generally do not achieve due to light body weight and feeding posture upon blossoms.

There is no obvious explanation for the generally small pollen loads on Tiphiidae, which foraged in a similar manner to that of Scoliidae and Vespidae. These are principally slender species, exceptions being *Anthobosca ?signata* (which superficially resembles a large scoliid), and *Hemithynnus apterus* (Oliver), *H. rufiventris* (Guerin) and *Zaspilothynnus* sp. near *campanularis* (Smith). The latter 3 species however, appeared to be uncommon and were rarely collected.

Diptera

Although small-sized Diptera (<6 mm) are a very abundant component of the insect fauna visiting subtropical rainforest flowers (Williams 1995) very few large species were observed or collected. The pool of larger-sized Diptera in subtropical rainforests, from which pollinators can be drawn, appears to be small. However, entomophilous rainforest trees flowering on rainforest margins are able to recruit large anthophilous flies, such as Bombyliidae, from adjoining vegetation types.

Syrphidae are generally considered to be variously specialised oligolectic flower visitors (Holloway 1976, Faegri and van der Pijl 1979, Colless and McAlpine 1991). Few ecologically specialised Syrphidae were collected from tree blossoms (see Williams 1995) but several generalist semi-adapted genera occurred (i.e. *Psilota*, *Eristalinus*, 'Eristalis', *Helophilus*). The single syrphid examined, *Dideopsis* sp., carried few pollen grains.

The genus *Austrogastromyia* (Nemestrinidae) occurred at particular times on only two plant species (*Cuttsia viburnea* F. Muell. — Escalloniaceae, *Waterhousea floribunda* — Myrtaceae) but carried heavy and abundant pollen loads, with minimal content (<5 to 0%) of foreign pollen. Similarly, *Paramenia* sp. (Calliphoridae) carried heavy pollen loads (>90% home pollen). Pollen loads carried by *Scaptia* spp. (Tabanidae) ranged from M-H, with >95% home pollen. The tabanid *Cydistomyia nigripicta* Macquart, however, carried minimal loads (<10 grains) even though foraging upon mass-flowering *Tristaniopsis laurina*.

The anteroventral surface generally, and the head, femora and tibiae were the major deposition sites. In *Austrogastromyia nigrovittata* Mackerras the abdominal sternites, and in both *A. nigrovittata* and *A. ?punctata* Macquart, lateral prothoracic sclerites (i.e., anepisternite, sternopleura), carried pollen masses. In general, however, the dense, pilose surface of large Diptera precluded pollen accretion on the surface of the integument.

DISCUSSION

This study has shown that although large insects comprise only a small proportion of the insect visitors to subtropical rainforest flowers they are capable of transporting large quantities of pollen. More detailed studies of long distance movements by these insects, and of their effectiveness as pollinators, are required to assess the importance of large insects to the reproductive ecology of subtropical rainforest plants.

Large insects collected from Myrtaceae generally carried heavy pollen loads which consisted principally of 'home' pollen and the examination of pollen loads on insects generally indicated temporal foraging constancy by individual taxa, which would minimise pollen loss to non-conspecific flowering plants. Sites of pollen deposition on the integument of individual insect taxa were diverse and pollen loads were variable but are influenced by time spent foraging, foraging behaviour, body morphology and size of the insect, as well as quantity of pollen presented by individual flowers and plants (Williams 1995). For example, the relatively small amounts of pollen produced individually by the flowers of *Alphitonia excelsa* (Fenzl) Benth. (Rhamnaceae), and the method of pollen presentation which requires depression of the stamens and enveloping petals to release pollen masses (Williams 1995), may restrict the pollen loads found on anthophilous insects regardless of the time they individually spend foraging and the number of flowers visited. In general Coleoptera carried large amounts of pollen contrary to the suggestion that pollen does not adhere to their 'smooth' bodies (e.g., Percival 1965, Archibold 1995). It has been suggested that large Coleoptera are pollinators of trees and shrubs in a number of Australian open forest and woodland communities (e.g., Hawkeswood 1980, 1981, 1982, Webb 1986, 1987). Our results suggest this may also be true in rainforests.

Based upon the development of body vestiture, two broad groupings of taxonomically unrelated anthophilous insects on mass-flowering rainforest plants can be recognized:

1. species with sparse or poorly developed vestiture (e.g., Buprestidae, Cerambycidae, Vespidae) which generally spend individually long periods foraging on inflorescences and make inter-flower movements upon individual trees by clambering from blossom to blossom. In so doing large quantitites of pollen may adhere to the body integument;

2. species with dense, often long, setae (e.g., Sphecidae, some Diptera) that are unlikely to carry heavy pollen loads directly on the integument. Rather, individual pollen grains are ensnared by setae, or small pollen clusters may aggregate in spatially discrete regions. Whilst this later group contains species characteristically considered specialised in their foraging behaviour these generally transport small pollen loads potentially resulting in reduced contributions to reproductive success in mass-flowering rainforest plants.

The flowers of most subtropical rainforest trees conform to the entomophilous floral syndrome (Williams and Adam 1994). Birds and bats are important inter-plant and long-distance pollinators in many ecosystems but are relatively rare visitors to plants with entomophilous flowers in New South Wales subtropical rainforests (Williams 1995). Consequently, larger-sized insects that have a propensity to undertake flights to widely-separated flowering plants (even though their movements may be short compared with that of many birds and bats) may be important in the reproductive ecology of fragmented rainforest plant populations because isolated plants can suffer greatly reduced levels of pollination.

The daily movements by small insects (<6 mm), particularly those of small Coleoptera and brachyceran Diptera, in subtropical rainforests are predominantly within the crowns of individual trees, with the majority of inter-plant movements being to near-neighbours (G. Williams pers. obs). As such they are likely to promote autogamous and geitonogamous pollination in self-compatible species. The larger insects included in this study undertook frequent daily movements between trees. Such inter-plant movements are important for self-incompatible and dioecious plant species and promote out-crossing, rather than geitonogamous pollination.

Even if inter-plant movements occur at low frequency these can be sufficient to result in succesful pollination of highly dispersed plants (Frankie, Opler and Bawa 1976, Englund 1993).

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APPENDIX

Primary Pollen Deposition Sites. (**H**) head, (**T**) thorax (incl. wings in Diptera and Hymenoptera), (**L**) legs, (**A**) abdomen (in Coleoptera the elytra, for purposes of pollen deposition function as part of the abdomen).

COLEOPTERA

Buprestidae

Castiarina acuminata (**H**) frontal cavity, vertex; (**T**) mesosternum, coxal cavities, prosternum, metacoxal plate, pronotal hypomera; (**L**) procoxae, femora; (**A**) elytral striae, ventrites.

Castiarina delta (**T**) pronotal fovae, hypomera, metacoxal plate; (**A**) elytral striae, elytra generally.

Castiarina insignis (**H**) antennal cavities, frontal cavity; (**T**) prosternum, mesosternum, metacoxal cavities, metacoxal plate; (**L**) coxae; (**A**) abdominal ventrite 1, apical ventrite, anterolateral elytral margins.

Castiarina neglecta (**H**) antennal cavities, anterior margin of eye; (**T**) coxal cavities, pronotal hypomera, mesosternum.

Castiarina producta (**H**) antennal cavities, frons, genae; (**T**) prosternal lobe, pronotal hypomera, mesosternum, coxal cavities, metacoxal plate; (**L**) coxae; (**A**) ventral surface generally.

Castiarina pulchripes (**H**) vertical suture; (**T**) prosternum, prosternal and metasternal lobes, mesosternum, coxal cavities; (**L**) profemora.

Castiarina ?sexcavata (**H**) antennal cavities, vertical suture; (**T**) prosternal lobe, metacoxal plates, ventral surface generally; (**A**) ventral surface generally.

Castiarina ?vicina (**T**) anterior and basal pronotal margins, prosternal and metasternal lobes, ventral surface; (**L**) metafemora; (**A**) elytral striae, ventral surface generally.

Curis aurifera (**H**) basal margin, frontal cavity; (**T**) pronotal fossae, ventral surface generally; (**A**) ventral surface generally.

Curis splendens (**H**) frontal cavity; (**T**) dorsal and ventral punctation generally, lateral pronotal margins, coxal cavities, metacoxal plate, ventral surface generally; (**A**) dorsal and ventral punctation generally, ventral surface generally, epipleurae.

Metaxymorpha grayi (**H**) antennal cavities, scape, frons, mentum, gula; (**T**) prosternum, metasternum, coxal cavities; (**A**) epipleurae.

Torresita cuprifera (**H**) antennal cavities; (**T**) pronotum, punctation of ventral surface; (**A**) punctation of ventral surface.

Cerambycidae

Aridaeus thoracicus (**H**) antennomeres 1–4, vertex; (**T**) meso-metepisterna, mesosternum, mesocoxal cavities, ventral surface generally; (**L**) mesocoxae, basal 1/2 femora; (**A**) elytral humeri.

Distichocera superba (**H**) antennal cavities, scape, antennae generally, genae, vertical and frontal cavities; (**T**) mesosternum, coxal cavities, ventral surface generally; (**L**) coxae; (**A**) humeral calli, epipleurae, ventral surface generally.

Hesthesis sp.nr. *bizonata* (**T**) mesosternum, mesosternal cavities; (**L**) mesocoxae.

Tragocerus spencei (**H**) frons, vertex; (**T**) pronotum, metasternum.

Tropocalymma dimidiatum (**H**) frontal cavity, gulae; (**T**) mesocoxal cavity, metacoxal cavity and plate; (**L**) metacoxae.

Scarabaeidae-Cetoniinae

Cacachroa gymnopleura (**H**) head generally; (**T**) dorsal and ventral surface generally; (**L**) femora, tibiae generally; (**A**) elytra and ventral surface generally.

Diaphonia dorsalis (**H**) antennal cavities, anterior ocular margin, ocular canthi, genae, mentum; (**T**) prosternal lobe, ventral surface generally; (**L**) protibiae; (**A**) ventral surface generally, epipleurae.

Eupoecila australasiae (**H**) clypeus, antennal cavities; (**T**) anterolateral pronotal angles, prosternum, metasternal lobe, ventral surface generally; (**L**) profemora; (**A**) elytral base laterad of humeri, ventral surface generally.

Glycyphana brunnipes (**H**) clypeus, antennal cavities; (**T**) anterolateral pronotal angles, pronotal hypomera, coxal cavities, metacoxal plate, meso-metasterna, ventral surface generally; (**L**) coxae; (**A**) basal margin of elytra, epipleurae.

Polystigma punctatum (**H**) clypeus, antennal cavities, genae, labial palps; (**T**) lateral margins of pronotum, pronotal hypomera, ventral surface generally; (**L**) femora, protibiae; (**A**) sutures of abdominal ventrites, ventral surface generally.

DIPTERA

Calliphoridae

Paramenia sp. (**L**) base of protibiae, apex of profemora.

Nemestrinidae

Austrogastromyia nigrovittata (**H**) prementum, ocular margins, head generally; (**T**) sternopleura, anepisternites; (**L**) pro-meso femora and tibiae; (**A**) abdomen generally.

Austrogastromyia ?punctata (**H**) frons; (**T**) anepisternites, anteroventral surface, base of ventral wing surface (**L**) legs generally.

Syrphidae

Dideopsis sp. (**H**) head generally.

Tabanidae

Cydistomyia nigripicta (**T**) thorax generally.

Scaptia auriflua (**H**) eyes, head generally; (**T**) ventral surface generally.

Scaptia ?quadrimacula (**H**) head generally; (**T**) dorsal and ventral surfaces generally; (**L**) femorae, tibiae.

HYMENOPTERA

Ichneumonidae

Echthromorpha intricatoria (**H**) prementum, malar region; (**L**) procoxae, basal 1/2 profemora.

Pompilidae

Chryptocheilus sp. (**H**) basal margin; (**T**) pronotum, mesepimeron, mesonotum, propleuron; (**L**) trochanter.

Scoliidae

Campsomeris ?tasmaniensis (**H**) mandibles, clypeus, head generally, including antennomeres; (**T**) thorax generally, incl. wing bases; (**L**) femora, tibiae, legs generally; (**A**) gaster generally.

Campsomeris zonata (**H**) head generally; (**T**) ventral surface generally; (**L**) pro-mesofemora.

Scolia verticollis (**H**) mandibles, frons, clypeus; (**T**) thorax generally; (**L**) protarsomeres.

Scolia ?verticollis (**H**) basal antennal segments, vertex; (**T**) anterior pronotal margin; (**L**) pro-mesocoxae, femora, tibiae.

Scolia sp. (**H**) distal margin; (**T**) anterior pronotal margin, anteroventral surface.

Sphecidae

Bembicinus sp. (**H**) antennal cavities; (**T**) base of forewings; (**L**) profemora.

Bembix promontorii (**H**) vertex; (**T**) base of mesosoma.

Bembix sp. 1 (**H**) basal margin; (**T**) dorsal surface generally.

Bembix sp. 2 (**H**) head generally; (**T**) dorsal surface generally.

Sceliphron laetum (**T**) anteroventral surface generally.

Sphex ephippium (**H**) head generally; (**T**) thorax generally, base of wings.

Sphex fumipennis (**T**) lateral thoracic region generally, base of forewings; (**L**) trochanters.

Tachysphex sp. (**H**) mandibles, prementum.

Tiphiidae

Anthobosca ?signata (**H**) scape, frons, clypeus, head generally; (**L**) specialized ‘combs’ on prolegs, tibiae, metafemora.

Diamma bicolor (male) (**T**) lateral margin of prothorax; (**L**) profemora.

Dimorphothynnus dimidiatus (**H**) antennal cavities, frons, clypeus, vertex; (**T**) mesoscutum, mesepisternal grooves (ant. margin); (**L**) prolegs generally.

Hemithynnus apterus (**H**) vertex; (**T**) pronotum, mesoscutum, ventral surface generally.

Hemithynnus rufiventris (**H**) basal antennomeres, vertex, head generally; (**T**) lateral and ventral surface of mesosoma.

Rhagigaster sp. nr. *kiandrensis* (**T**) propodeum, base of forewings.

Zaspilothynnus sp. nr. *campanularis* (**T**) lateral margins of mesosoma, especially sutures, propodeum; (**A**) base of gaster.

Zeleboria xanthorrhoei (**H**) scape, frons, antennal cavities; (**T**) base of forewings.

Vespidae

Abispa splendida (**T**) ventral surface generally; (**L**) coxae, pro-mesofemora.

Bidentodynerus bicolor (**H**) head; (**T**) mesepisternum; (**A**) base of petiole, gaster.

?Epiodynerus sp. (**H**) antennal cavities, clypeus; (**T**) ventral surface generally.

Polistes humilis (**L**) protarsomeres.

Polistes tepidus (**H**) antennal cavities; (**T**) ventral surface of mesosoma generally; (**L**) prolegs generally.

Pseudabispa confusa (**H**) antennal cavities; (**T**) mesopleura.

New Species and New Records of Psocoptera (Insecta) from South Australia

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Smithers C.N. (1998). New species and new records of Psocoptera (Insecta) from South Australia. *Proceedings of the Linnean Society of New South Wales* **120**, 69–79.

Four new species of Psocoptera (barklice, booklice) are described from South Australia bringing the total known from South Australia to fifty-one. New species are *Caecilius lobatus* (Caeciliidae), *Ectopsocus exastis* (Ectopsocidae), *Ptycta trullifera* and *Tanystigma longitibia* (Psocidae). *Psocidus notialis* Smithers (Psocidae), a Western Australian species, is transferred to *Tanystigma* Smithers. Additional locality records are given for four previously recorded species.

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KEYWORDS: *Psocoptera*, *Caecilius lobatus*, *Ectopsocus exastis*, *Ptycta trullifera*, *Tanystigma longitibia*, South Australia.

INTRODUCTION

Smithers (1984) gave an account of the Psocoptera of South Australia which included forty-five species. Material collected since then is described here and knowledge of the South Australian fauna is brought up to date by making brief reference to work carried out since publication of the 1984 monograph. This can be summarized as follows. The type of *Stenopsocus striatifrons* (McLachlan) has been studied and the species redescribed and transferred to *Tanystigma* (Smithers 1987). The type locality of the species is, however, not known and its occurrence in South Australia remains unconfirmed. Badonnel and Lienhard (1988), when undertaking a generic revision of the Mesopsocidae, erected the genus *Mesopsocopsis* for *Mesopsocus reticulatus* Smithers, the only member of the family so far recorded from Australia. Rees (1994) and Rees and Wright (1995) have recorded Psocoptera associated with stored products in South Australia. Smithers (1997) has described a remarkable new genus and species of the Elipsocidae (*Yuntapsocus hollowayi* Smithers). The only known specimen, a female, is small, has a cylindrical body, is mostly colourless and has a circular, heavily sclerotized clunial plate which bears pores and specialized setae. This plate may be used to seal a tunnel or cavity or possibly provides an evaporative surface onto which secretions from the pores might be discharged. The specimen was beaten from vegetation but its pale colour and cylindrical form suggest that it is probably an inhabitant of the nests of ants or termites or burrows of wood-borers.

The present records bring the total number of species known from South Australia to fifty-one.

DESCRIPTIONS AND RECORDS

Caeciliidae

Caecilius lobatus sp. n.

FEMALE

Colouration (in alcohol)

Head pale brown with darker marks. Irregular confluent spots mesad of compound eye, across back of vertex and between antenna base and eye. A patch on each side of median epicranial suture level with upper margin of eyes. Postclypeus with brown striae. Anteclypeus pale. Labrum mostly brown. Genae pale brown. Scape, pedicel and first two flagellar segments pale brown; remainder of flagellum darker. Eyes and ocellar tubercle black. Maxillary palps brown. Mesothoracic lobes and scutellum pale brown, parapsidal sutures pale. Dorsal lobe of metathorax pale brown, lateral lobes and scutellum darker. Pleura pale brown. Legs pale brown, distal tarsal segments a little darker than rest of legs. Fore wings (Fig. 1) hyaline, faintly tinged with pale brown pattern. Hind wings hyaline. Abdomen pale, terminal structures pale brown.

Morphology

Length of body: 2.0mm. Median epicranial suture very distinct but not reaching ocellar tubercle. Clypeal shelf absent. Length of flagellar segments: f1: 0.35mm; f2: 0.24mm. Antennae short, much shorter than fore wings. First flagellar segment straight, not enlarged. Labrum without styli at distolateral angle. Lacinia (Fig. 2) narrow in basal half, broad in distal half, end broad with transverse row of small, rounded denticles. Eyes moderately large but not reaching level of vertex. IO/D: 2.1; PO: 0.71. Lower part of mesothoracic precoxal suture present, running from mesotrochantin to about two thirds of way towards episternal suture. Legs with tibiae of uniform width throughout length. Measurements of hind leg: F: 0.49mm; T: 0.81mm; t1: 0.22mm; t2: 0.08mm; rt: 2.75:1; ct: 10,0. Ctenidiobothria small, especially those nearer distal end of first tarsal segment. Fore wing length: 2.5mm; width: 0.86mm. Fore wing (Fig. 1). Pterostigma with sharp posterior angle. Stem of Rs sinuous. Rs and M fused for a short length. Cell R3 narrow, R2+3 and R4+5 diverge at a small angle. Cell R5 narrow because of proximity to R4+5 to M. Areola postica steeply arched, top of areola postica a little nearer to M than to wing margin. Wing setae well developed. Pterostigma with sparse, evenly spaced setae. Cu2 setose. Epiproct (Fig. 3) lightly sclerotized with rounded hind margin. Setae long, especially those arising from margin. Paraproct (Fig. 4) lightly sclerotized without posterior marginal cone. Trichobothrial field round, individual trichobothria large, separated by sculptured integument. Subgenital plate (Fig. 5) with hind margin transverse in median part. Pigmentation slight. Lateral apophyses absent. Setae fairly evenly distibuted, long and fine. Two folds, one on each side, run parallel with posterolateral margin, ending at lateral ends of transverse part of hind margin. Gonapophyses (Fig. 6) with ventral valve curved but with small lobe on curved part of valve. Spermatheca (Fig. 7) with strongly sclerotized sac and long glandular area.

MALE

Unknown.

Material examined

South Australia. 1 female (holotype), 5km north of Yunta, 12.xi.1994, C.N.and A.S. Smithers. Holotype in South Australian Museum.

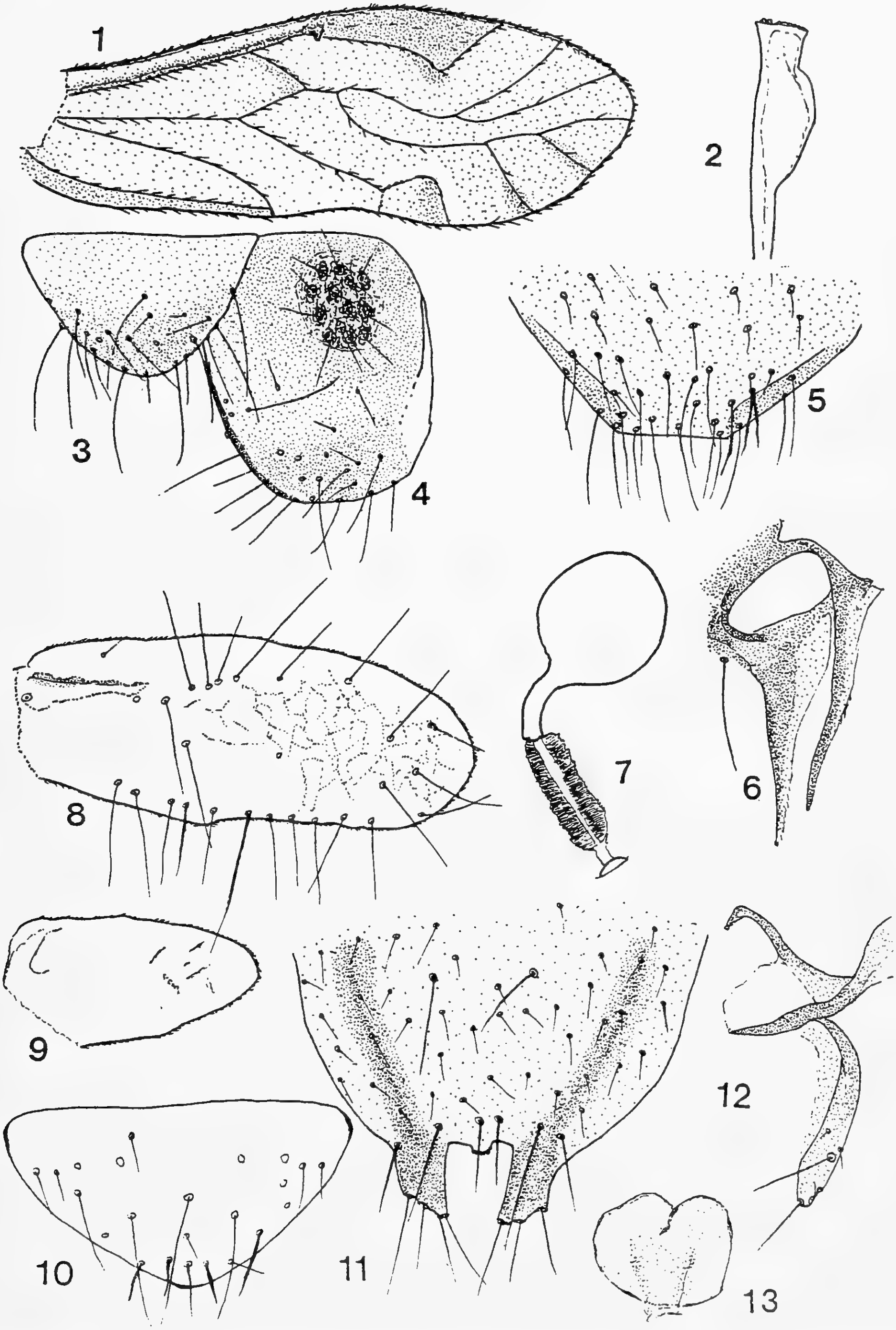
Discussion

Caecilius lobatus can easily be distinguished from other Australian species of this genus by its wing pattern which is very faint and the shape of the ventral valve of the gonapophyses in which there is a small sclerotized lobe on the curved section of the valve. There is a strong possibility that this species may later have to be placed in another genus, as is the case with most Australian species of *Caecilius*, when groups of species in this very large, worldwide, genus have been better defined.

Maoripsocus semifuscatus Tillyard

Material examined

South Australia. 3 males, 1 female, 5km north of Yunta, 7–8.v.1995, C.N. and



Figures 1–13. *Caecilius lobatus* sp.n. Female: 1) Fore wing, 2) Lacinia, 3) Epiproct, 4) Paraproct, 5) Subgenital plate, 6) Gonapophyses, 7) Spermatheca. *Ectopsocus exastis*. sp.n. Female: 8) Fore wing, 9) Hind wing, 10) Epiproct, 11) Subgenital plate, 12) Gonapophyses, 13) Sclerite of ninth sternite.

A.S. Smithers. 1 male, 15km north of Morgan, 8.v.1996, C.N. and A.S. Smithers. This species was described from New Zealand and has been recorded from New South Wales, Tasmania and South Australia.

Peripsocidae

Peripsocus maoricus (Tillyard)

Material examined

South Australia. 1 female, Cadell, 8.v.1995, A.S. Smithers. Described from New Zealand, previously recorded from New South Wales, Victoria, Tasmania, Western Australia and South Australia.

Ectopsocidae

Ectopsocus exastis sp.n.

FEMALE

Colouration (in alcohol)

Head very pale brown with darker marks. Vertex with groups of irregular spots adjacent to median epicranial suture and inner margin of compound eyes. Frons same colour as spots, i.e. darker than vertex. Postclypeus mostly same colour as spots on vertex but with an indistinct, narrow, pale line from epistomial suture to about half way to anterior margin of postclypeus. Labrum brown. Genae pale. Dark brown line from eye to antenna base. Scape and pedicel brown, flagellum paler. Eyes black. Ocelli pale, slightly darker centripetal marks. Maxillary palps pale, with brown distal segment. Thorax brown dorsally. Pleura dark brown in dorsal parts, brown along a line extending as a lateral line from antenna base to eye. Ventrally, pleura pale. Legs pale. Wing rudiments (Figs 8, 9) pale testaceous. Abdomen dorsally pale brown with suggestion of irregular darker segmental bands; laterally each segment with a dark brown spot. Abdomen ventrally pale.

Morphology

A small species. Micropterous. Length of body: 1.7mm. Median epicranial suture distinct only in upper part of vertex. Vertex somewhat horizontal, sloping into frons and postclypeus which are in same plane. Postclypeus only slightly bulbous. Head with fine setae, spaced closer than setal length. Antennae fairly short. Eyes small, placed laterally on head, well below level of vertex. IO/D: 3.4; PO: 0.6. Ocelli small, anterior ocellus about same size as lateral ocelli. Mesonotum and metanotum simple, without differentiation of antedorsum, lateral lobes and scutellum. Nota with well developed setae. Fore femur broad in relation to fore tibia. Hind legs without coxal organ. Measurements of hind leg: F: 0.33mm; T: 0.47mm; t1: 0.14mm; t2: 0.07mm; rt: 2:1. No ctenidiobothria on tarsi. Fore wing length: 0.3mm; width: 0.12mm. Fore wing (Fig. 8) reduced to a rudimentary flap without discernible venation. Surface with indistinct reticulate pattern of irregular shallow ridges in distal half. Long, finely pointed setae probably indicate positions usually occupied by veins. Margin with closely set setae. Hind wing length: 0.13mm; width 0.08mm. Hind wings (Fig. 9) without reticulate pattern and without setae but marginal microtrichia present. Epiproct (Fig. 10) very lightly sclerotized, sparsely setose with setae of various lengths arranged more or less symmetrically. Paraproct also lightly sclerotized, damaged in preparation of holotype. Subgenital plate (Fig. 11) setose, with two posterior lobes, usual sclerotized areas long and narrow, running forward from near base of posterior lobes. Lobes short and broad, inner margin straight. Posterior margin of plate, between lobes, sinuous, medially a little extended posteriorly in which area margin bears fine spicules. Three or four terminal setae on each lobe and six strongly developed setae in row across plate anterior to hind margin in addition to smaller setae on body of plate. Two somewhat longer setae occur centrally on the plate. Structure of gonapophyses (Fig. 12) difficult to interpret. Ventral valve narrow, well sclerotized and apically sharply curved. Dorsal valve membranous, supported by sclerotized rod. External valve narrow, lightly sclerotized except for a supporting rod along margin in basal half, with one long seta on body of valve and a few smaller setae near distal end. Entrance to spermatheca (Fig. 13) with well sclerotized plate.

MALE

Unknown.

Material examined

South Australia. 1 female (micropterous) (holotype), 5km north of Yunta, 12.xi.1994, A.S.Smithers. Holotype in South Australian Museum.

Discussion

Wing polymorphism, micropterty and brachyptery are relatively uncommon features in the large genus *Ectopsocus* McLachlan. Of the Australian species *E. axillaris* (Smithers) has brachypterous males. *E. edwardsi* New has micropterous, brachypterous and macropterous forms in both sexes. *E. richardsi* (Pearman) has brachypterous males and females. In *E. vachoni* Badonnel males are micropterous and females are micropterous or macropterous. *E. exastis* is known only from one female which is micropterous. It is easily distinguished from *E. axillaris*, *E. edwardsi* and *E. richardsi* in that at least some veins of the fore wings are obvious in those species whereas none are discernible in *E. exastis*. *E. vachoni* is very similar to *E. exastis* in lacking veins in micropterous specimens and in having minute spicules along the hind margin of the subgenital plate between the posterior lobes. The margin between the lobes is sinuous in *E. exastis* whereas it is transverse in *E. vachoni*. Ocelli are present in micropterous *E. exastis* but not in micropterous specimens of *E. vachoni*. In *E. vachoni* the sclerotized areas of the subgenital plate are somewhat shorter and broader than in *E. exastis,* forming a less extended “V”. The posterior lobes of the subgenital plate in *E. exastis* are longer and have fewer apical setae than in *E. vachoni* and the inner margins of the lobes quite straight. In *E. exastis* there is a well developed sclerotized structure associated with the entrance to the spermatheca, a feature reported for very few species of *Ectopsocus*.

Psocidae

Ptycta umbrata New

Material examined

South Australia. 2 females, 14km northeast of Peterborough, 7.v.1995, A.S. Smithers. Previously known from New South Wales, Victoria and other South Australia localities.

Ptycta trullifera sp. n.

MALE

Colouration (in alcohol)

Head ivory with dark brown pattern. A few large, irregular, well defined spots across back of vertex, adjacent to median epicranial suture and inner margins of compound eyes. A line from ocellar tubercle to anterior margin of eyes where they meet epistomial suture. Frons with dark anterior margin, an ivory spot on each side and a smaller median spot, otherwise dark. Postclypeal striae well defined, mostly parallel with one another, each with an isolated anterior spot near anterior margin of postclypeus. A few striae on each side curved. Labrum with dark median anterior oval mark, basad of which is a median dark spot. Anteclypeus pale. Genae ivory. First flagellar segment with brown basal half, very dark brown distally; more distal segments dark. Eyes black. Ocellar tubercle dark. Maxillary palps pale, fourth segment very dark. Meso- and metathorax mostly chocolate brown with irregular, ivory median stripe and ivory areas near wing bases. Thorax laterally dark with pale areas on mesopleura. Coxae dark. Femora pale with mottled pattern. Tibiae pale brown. Tarsi brown. Fore wings (Fig. 14) hyaline with brown marks. Abdomen pale with dark brown terminal structures.

Morphology

Length of body: 2.4mm. Head with very sparse, very short, fine setae. Antennae with fine setae, a few of which are longer than flagellar diameter. Length of flagellar segments: f1: 0.43mm; f2: 0.27mm. Eyes large, reaching level of vertex. IO/D: 1.1; PO: 0.91. Ocellar tubercle very prominent. Measurements of hind leg: F: 0.49mm; T. 1.11mm; t1: 0.29mm; t2: 0.12mm; rt: 2.4:1; ct: 19,2. Fore wing (Fig. 14) with Sc ending in R1. Rs and M meet in point. First and second sections of Cu1 almost in a straight line with one another. Fore wing glabrous. Hind wing with Rs and M fused for a length. A few very fine, very short setae on margin between R2+3 and R4+5. Epiproct (Fig. 16) lightly sclerotized with a sclerotized marginal band. Posteriorly band is thicker and the posterior margin is extended back into a small membranous lobe. Marginal band sinuous, becoming narrower anteriorly. Epiproct extended over tenth tergite as a shallowly bilobed flap. Paraproct (Fig. 15) heavily sclerotized with very well developed, curved, posterior process and narrower, ventrally directed apophysis. Trichobothrial field large. At base of paraproct is a heavily sclerotized lobe. Tenth tergite well sclerotized, narrow medially. Ninth tergite with anterior margin developed into heavily sclerotized ridge, especially laterally. Hypandrium (Fig. 18) symmetrical, deeply cleft behind to form two upturned lobes bearing apophyses. Phallosome (Fig. 17) closed anteriorly, inner parameres fused distally and expanded into flattened, broad, divided, strongly upturned lobe. External parameres membranous, each supported by a narrow sclerotized rod, each expanded distally into a delicate membranous lobe.

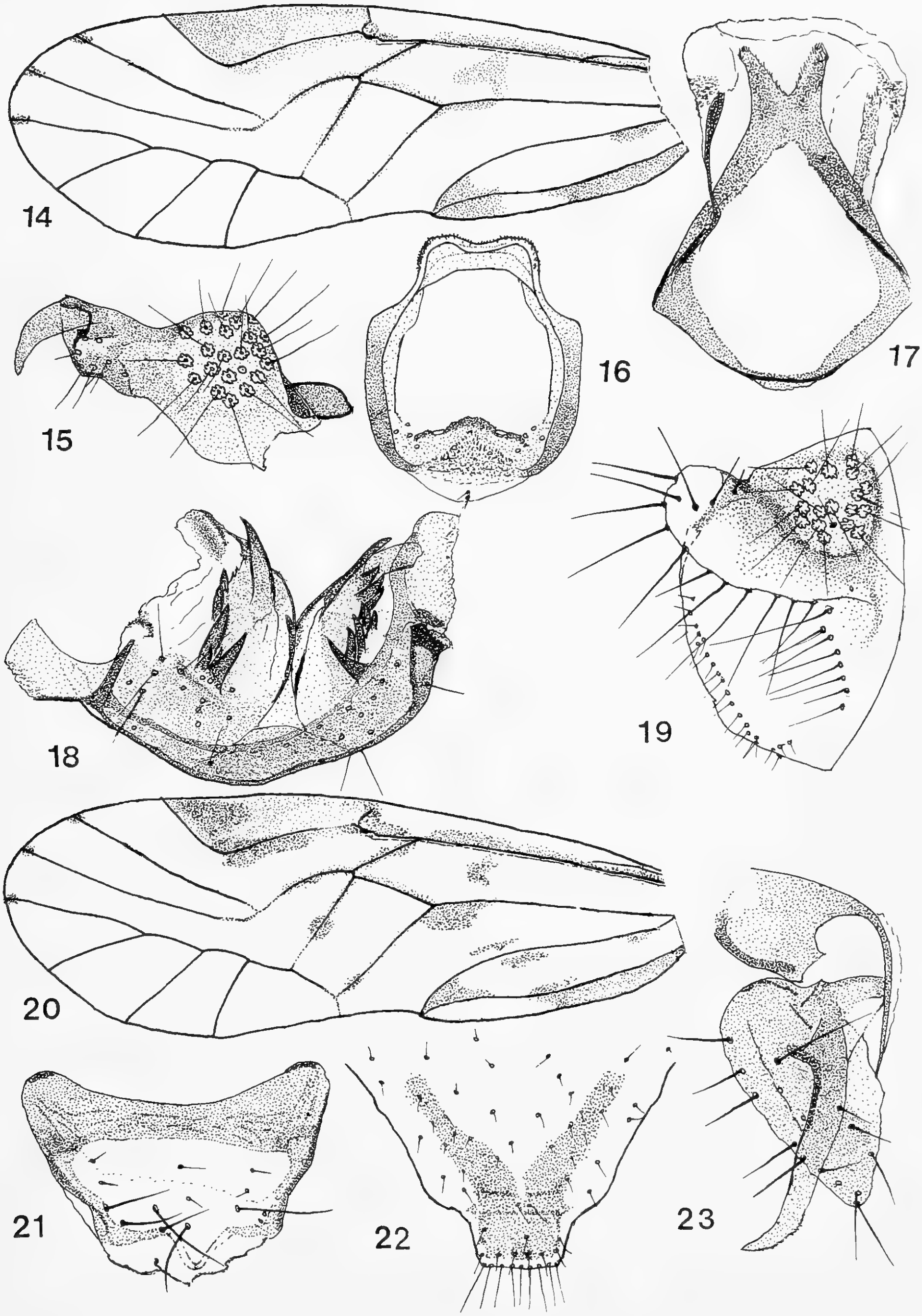
FEMALE

Coloration (in alcohol)

As in male but brown wing areas more extensive (Fig. 20).

Morphology

Length of body: 2.2mm. Length of flagellar segments: f1: 0.35mm; f2: 0.23mm. Eyes smaller than in male, not reaching level of vertex. IO/D: 2.06; PO: 0.75. Ocellar tubercle prominent but less so than in male. Measurements of hind leg: F: 0.40mm; T: 1.0mm; t1: 0.24mm; t2: 0.11mm; rt: 2.18:1; ct: 17,0. Fore wing length: 2.9mm; width: 1.0mm. Fore wing (Fig. 20) venation as in male. Hind wing length: 2.3mm; width: 0.73mm. Epiproct (Fig. 21). Paraproct (Fig. 19). Subgenital plate (Fig. 22) with short, square-ended, posterior, median lobe which has a row of ten strong marginal setae and a shorter submarginal row of only five small setae. Plate otherwise sparsely setose. Sclerotized areas of plate in form of a substantial "V". Gonapophyses (Fig. 23) with short ventral valve, dorsal valve long, narrow, tapering only near distal end. External valve somewhat transverse, of a single lobe only, of approximately same width for most of length but narrowed posteriorly, setose.



Figures 14–23. *Ptycta trullifera* sp.n. 14) Male fore wing, 15) Male paraproct, 16) Male epiproct, 17) Phallosome, 18) Hypandrium, 19) Female paraproct, 20) Female fore wing, 21) Female epiproct, 22) Subgenital plate, 23) Gonapophyses.

Material examined

South Australia. 1 male (holotype), female (allotype), 2 females (paratypes) 5 km north of Yunta, 7.v.1995, A.S.Smithers. Holotype and paratypes in South Australian Museum.

Discussion

Since the erection of *Ptycta* (Enderlein 1925) to accommodate *Psocus haleakalae* Enderlein and *Psocus distinguendus* Perkins from Hawaii and *Clematostigma schillei* Enderlein from Java many species have been added to the genus. The generic limits became somewhat obscure until Thornton (1984) studied the Hawaiian fauna, including the type species *P. haleakalae*, and redefined the genus. There is little doubt that species have been placed in *Ptycta* which are not congeneric with the type species and that these will eventually have to be reassigned to other genera. These include some Australian species, of which there are altogether at present twelve in the genus. Some of these are known only from one sex. The male phallosome in *Ptycta* is relatively simple, consisting of a ring-like structure which may be rounded or angular with short, mostly anterolaterally directed spur-like extensions. In *P. emarginata* New and *P. improcera* New the phallosome is unusual in that where the internal parameres are fused posteriorly they form an upturned plate which has a broadly divided hind margin which is finely toothed. In *P. trullifera* the phallosome has a similar hind margin but also has weakly developed external parameres, each consisting of a membranous lobe strengthened by a sclerotized rod. It can easily be recognized by this feature. In *P. campbelli* Schmidt and Thornton there is a suggestion of the rudiments of external parameres but this species lacks the upturned plate.

The Australian species of *Ptycta* can be differentiated by differences in details of the genitalia of both sexes. More obvious superficial differences are to be seen in the fore wing pattern and the relationship of veins Rs and M to one another. In particular, *P. trullifera* does not have a spot in cell R5 of the fore wing just behind the fork of Rs, and Rs and M are joined by a short crossvein. Several of the other species have such a spot, namely, the females of *P. prosta* Schmidt and Thornton, *P. emarginata* New, *P. glossoptera* New and *P. australis* Schmidt and Thornton. In all of the Australian species other than *P. trullifera* Rs and M in the fore wing are either fused for a length or meet in a point. These features, taken together with those of the genitalia should permit species identification.

Tanystigma tardipes (Enderlein)

Material examined

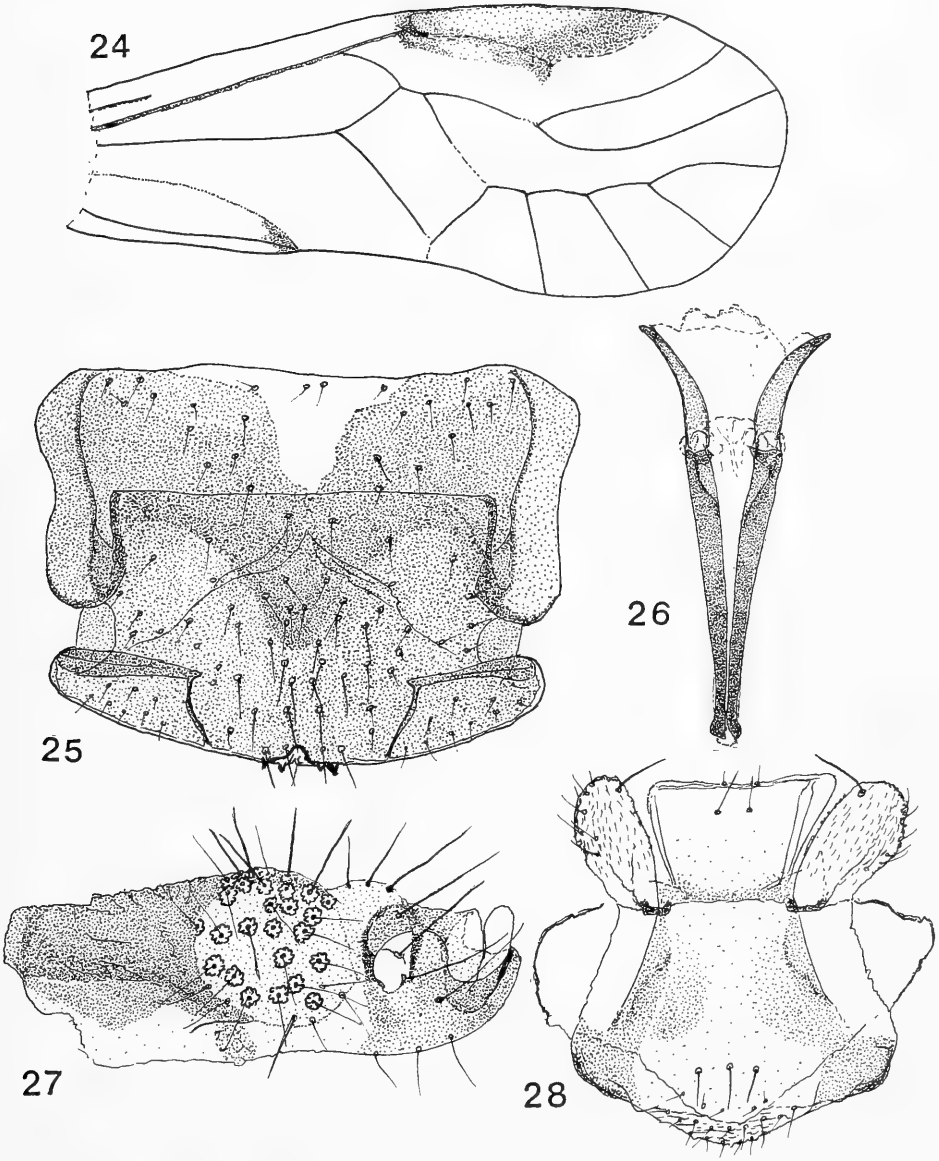
South Australia. 2 males, 2 females, 15km northeast of Morgan, 8.v.1995, A.S.Smithers. 2 males, 5 females, 14km northeast of Peterborough, 7.v.1995, A.S.Smithers. Previously known from Victoria, Tasmania and a few other South Australian localities.

Tanystigma longitibia sp.n.

MALE

Colouration (in alcohol)

Head pale grey with dark chocolate brown marks. Irregular spots adjacent to compound eyes, across back of vertex and adjacent to posterior part of dark median epicranial suture. Ocelli surrounded by dark circles. A line from lateral ocelli to antenna bases. Postclypeal striae each broken into a series of slightly elongated spots, the two middle



Figures 24–28. *Tanystigma longitibia* sp.n. Male: 24) Fore wing, 25) Hypandrium, 26) Phallosome, 27) Paraproct, 28) Epiproct.

striae complete and fused into one broader median stripe. Labrum with semicircular mark in middle of anterior part, the semicircle joined to the clypeal suture by a small spot. Frons with median stirrup-shaped mark. Dark mark between compound eye and antenna base. Genae grey. Scape, pedicel and first flagellar segment of antenna dark brown, more distal segments very dark. Distal segment of maxillary palp very dark brown. Dorsum of thorax dark with broken, irregular, pale brown, median, longitudinal stripe. Lateral lobes of mesothorax dark, sutures pale brown. A pale line along lateral part of lobe curving towards midline just anterior to scutellum. Metanotum dark with pale spot near wing base in addition to pale midline. Pleura pale with dark sutures. Fore wing (Fig. 24) hyaline except for pterostigma, postpterostigmal mark and a small brown mark in angle at nodulus. Coxae dark. Femora pale with irregular dark mottled pattern. Tibiae brown, dark near femora, tarsi a little darker. Abdomen pale, except for very dark chocolate brown terminal structures.

Morphology

Length of body: 2.4mm. Median epicranial suture not reaching ocellar tubercle. Anterior arms absent but dark line almost in position usually occupied by suture. Length of flagellar segments: f1: 0.59mm; f2: 0.59mm. Eyes moderately large but prominent, not reaching level of vertex. Inner margins diverge strongly behind. IO/D: 2.4; PO: 0.85. Ocelli large, anterior ocellus a little smaller than lateral ocelli. Antennae fine, setae fine, only a little longer than flagellar diameter. Measurements of hind leg: F: 0.54mm; T: 1.19mm; t1: 0.32mm; t2: 0.15mm; rt: 2.13:1; ct: 18,3. Ctenidiobothria well developed forming a strong comb on distal tarsal segment. Hind tibia well supplied with ctenidiobothria. Fore wing length: 3.0mm; width: 1.3mm. Fore wing (Fig. 24) glabrous. Sc ends free in costal cell. Pterostigma with short, indistinct spurvein. Rs evanescent just basad of fork. M evanescent just basad of apex of areola postica. Areola postica tall, with narrow apex, second section of Cu1a at strong angle to first. Hind wing glabrous. Epiproct (Fig. 28) with rectangular, median anterior lobe and apically rounded lobe with a rough surface on each side of median lobe. Paraproct (Fig. 27) with short, very strongly curved distal process. Trichobothrial field large, trichobothria not occupying whole area. Hypandrium (Fig. 25) broad, with lateral lobes, small median posterior emargination with two small cones on each side of the notch. Phallosome (Fig. 26) open posteriorly with parameres fused anteriorly, each ending behind in a pointed, outwardly curved distal sclerite. Membranous penial bulb slightly rugose, without sclerites.

FEMALE

Unknown.

Material examined

South Australia. 1 female (holotype), 15km northeast of Morgan, 8.v.1995, C.N.Smithers. Holotype in South Australian Museum.

Discussion

The male of *T. longitibia* differs from all other known males of *Tanystigma* species, other than that of *T. notialis* (Smithers), in having a dark spot in the angle at the nodulus. The phallosome also differs in proportions and form, especially of the distal sclerites of the external parameres which are well developed and curve outwards. The shape of the hypandrium is also distinctive. The longer form of the phallosome with its outwardly directed, simple, terminal sclerites distinguishes this species from *T. notialis,* in which the phallosome is relatively shorter and in which the distal sclerites of the external parameres are shorter and bifid. *T. notialis* is much bigger than *T. longitibia,* having a wing length of 3.9mm as opposed to 3.0mm in *T. longitibia.*

Tanystigma notialis (Smithers) **comb. nov.**

Psocidus notialis Smithers, 1972. *Australian Zoologist* 17(1):20, figs 18–25.

Psocidus notialis Smithers was described from Western Australia (Smithers 1972) and is here transferred to *Tanystigma* (*Tanystigma notialis* (Smithers) **comb. nov.**) on the basis of the form of the phallosome, hypandrium and epiproct of the male, the shape of the subgenital plate and gonapophyses of the female and the elongate form of the pterostigma in both sexes.

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Descriptions of the Colour Patterns of Juvenile Anemonefishes (Pomacentridae: *Amphiprion*) from New South Wales and the Lord Howe–Norfolk Island Region

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RICHARDSON, D.L. (1998). Descriptions of the colour patterns of juvenile anemonefishes (Pomacentridae: *Amphiprion*) from New South Wales and the Lord Howe–Norfolk Island Region. *Proceedings of the Linnean Society of New South Wales* **120**, 81–86.

The live juvenile colour patterns of all three anemonefishes with breeding stocks in New South Wales and the Lord Howe–Norfolk Island region are described for the first time. The three species, *Amphiprion akindynos* Allen, *Amphiprion mccullochi* Whitley and *Amphiprion latezonatus* Waite had similar colour patterns consisting of a dark brown or black base colouration, three white body bars, and a yellow snout and pectoral fin tips. The colour patterns of juvenile *A. akindynos* and *A. mccullochi* were not consistently separable, whereas *A. latezonatus* Waite could be distinguished from these two species due to differences in caudal and soft dorsal fin coloration. Ontogenetic changes in colour patterns are also described.

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KEYWORDS: *Amphiprion akindynos, A. latezonatus, A. mccullochi*, colour changes, taxonomy

INTRODUCTION

The anemonefishes (Sub-family Amphiprioninae) are a guild of pomacentrid fish that are obligate symbionts of certain sea-anemone species (Allen 1975). Although the adult phase colour patterns of anemonefishes are well known and described (Allen 1975, 1980, 1991; Fautin and Allen 1992) descriptions of the live juvenile phase colouration are generally lacking, particularly for those fish occurring in eastern Australian sub-tropical waters.

The present study aimed at describing the live colour patterns of all three *Amphiprion* species that have breeding stocks within New South Wales and the Lord Howe–Norfolk Island region, as a guide for field identifications. Two species of anemonefish have breeding populations in the mainland waters of N.S.W.; the tropical *Amphiprion akindynos* and the sub-tropical endemic *A. latezonatus* (Richardson 1996; Richardson et al. 1997). Unlike *A. akindynos*, *A. latezonatus* also has breeding populations in the Lord Howe–Norfolk Island region, where it co-occurs with the regionally endemic *A. mccullochi* (Allen 1991). An additional two anemonefishes have been recorded in N.S.W. mainland waters (*A. perideraion* (Bleeker) and *A. melanopus* Bleeker; see Richardson 1996), both of which are tropical vagrants that do not have breeding stocks within the eastern Australian sub-tropics (Richardson 1996). Both of these species are well described elsewhere (see Allen 1975; 1980; 1991; Fautin and Allen 1992) and are not considered further in this study.

MATERIALS AND METHODS

Field observations and collections were undertaken at fifteen locations extending from Gneering Shoals (26°37′S, 153°07′E) in southern Queensland to South West Rocks (30°56′S, 153°05′E) in northern N.S.W. Specimens held by the Australian Museum, and colour photographs of live anemonefishes, were examined at sites extending from the Gneering Shoals to Broughton Island (32°37′S 152°18′E), and Lord Howe Island (31°33′S, 159°05′E), Norfolk Island (29°01′S, 168°03′E) and Middleton Reef (29°27′S, 159°06′E).

The two anemonefish species from mainland waters (*Amphiprion akindynos* and *A. latezonatus*) were identified by monitoring changes in the colour patterns of known individuals over time at Julian Rocks (28°36′S, 153°37′E). Three to four juveniles of each species were monitored at one to two monthly intervals over a twelve month period, after which time they had reached sub-adult status and their species membership could be determined. The results of this study were validated by monitoring the ontogenetic colour change in two aquaria-reared juveniles of each species over a fourteen month period.

Juvenile *A. mccullochi* was identified and described from photographs taken *in situ* and previous taxonomic records. Since *A. latezonatus* is the only anemonefish species sympatric with *A. mccullochi* in the Lord Howe–Norfolk Island region (Allen 1991), juveniles from this region with colour patterns unlike *A. latezonatus* were considered to be *A. mccullochi*. Furthermore, the live colour patterns of juvenile *A. mccullochi* were cross referenced to the general colour patterns of preserved specimens and previous descriptions of this species (see Whitley1929; Allen 1975).

Descriptions and line-drawings of all species were made from photographs taken in the field and laboratory aquaria, specimens collected by the author (and deposited at the Australian Museum), and other specimens held at the Australian Museum (AMS). All lengths given are standard lengths (mm).

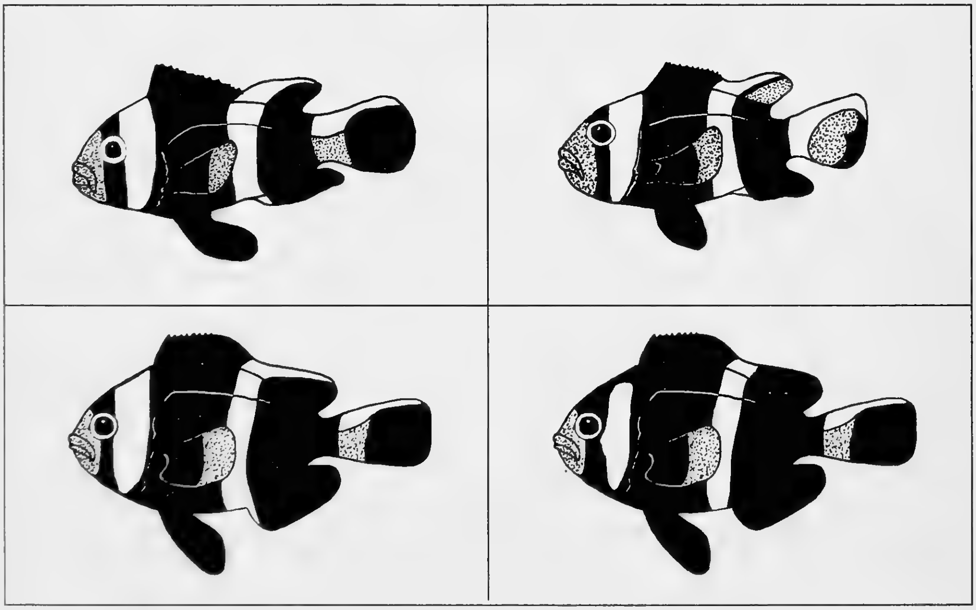

Figure 1. Juvenile colour patterns of (a) *Amphiprion akindynos*, 25 mm SL, (AMS I.37378-001, North Solitary Island); (b) *A. latezonatus*, 20 mm SL (AMS I.37378-002, North Solitary Island); (c) *A. mccullochi*, 28 mm SL (AMS IB.5497, Lord Howe Island); (d) *A. mccullochi*, 36 mm SL (AMS IA.968, Lord Howe Island). Black = black/dark brown, white = white, stippling = yellow).

DIAGNOSTICS

Generic Colour Patterns

Juveniles (i.e. post-settlement fish, varying in size from 9 to 35–40 mm SL) of all three species had a dark brown or black base colouration, with three white body bars; a white vertical head bar extending from the lower edge of the interopercule to the dorsal surface of the head, a white vertical mid-body bar and a white peduncular bar. Yellow pectoral fin pigment extended over the outer third of rays and the snout was yellow. Intra-specific variations in the colour patterns did not appear to be dependent on the anemone species inhabited.

Amphiprion akindynos (Fig. 1a)

Material Examined:

(10 preserved specimens: 13–34 mm; 11 preserved specimens: 40–97 mm). AUSTRALIA — Gneering Shoals (2: 20.0–25.5); North Solitary Island, AMS I.37378–001 (6: 13.1–19.0), (10: 40.0–97.0 mm); Broughton Island, AMS I.17246004 (2: 11.1–34.4), AMS I.37378–001 (1: 57.5). Field observations at Gneering Shoals (4: 15–25), Moreton Bay reefs (25: 10–30), Julian Rocks (>30: 10–35), North Solitary Island (>30: 10–35), and South West Rocks (6: 15–25).

Live Colour Description:

Juvenile colouration observed in specimens from 9–35 mm. Dark brown or black base colour. Head-bar usually touched the posterior edge of eye (did not touch posterior edge of eye in 2 of 10 specimens) and joined at the anterior base of the dorsal fin. Mid-body white bar usually extended over the second spine of the anal fin (1 of 10 specimens extended from just anterior of the anus), reaching over 5–6 rays of dorsal fin, and continued posteriorly along the distal edge of fin rays. The remainder of soft dorsal fin dark. The ventral half of the peduncular bar yellow; dorsal half of the peduncular bar white, with the white portion extending posteriorly along upper edge of caudal fin in 9 of 10 specimens, remainder of caudal fin dark. Yellow snout pigment touched the anterior edge of eye (just anterior of the eye in 2 of 10 specimens). Spinous dorsal fin, anal and pelvic fins dark except 14 of 90 live specimens (15–35 mm) which had yellow to light brown anal and pelvic fins.

Colour in Alcohol:

Dark brown or grey body colour and cream/grey snout, abdomen, bars and pectoral fin tips. Yellow and white pigmentation of live specimens was grey or cream in alcohol.

Ontogenetic Changes:

Brown/black base colour progressively faded to light brown/tan with increasing size, dark base colour absent in specimens >35–40 mm. Yellow snout, and caudal and pectoral fin pigmentation absent in specimens >35–45 mm, caudal fin entirely white in specimens >55 mm. In specimens > 50 mm, head bar does not join anteriorly and the mid-body bar does not touch dorsal fin, in contrast to juveniles.

Previous Literature:

Allen (1975) briefly described and illustrated a juvenile *A. akindynos* from the Great Barrier Reef. In contrast to all specimens examined in the present study, the peduncular bar of Allen's specimen (his Fig. 78) surrounded the caudal fin. Allen (1975) provided a photograph of two juvenile *A. akindynos* in an aquarium (Fig. 206); these specimens lacked yellow pigmentation on the caudal fin, in contrast to all specimens examined during the present study .

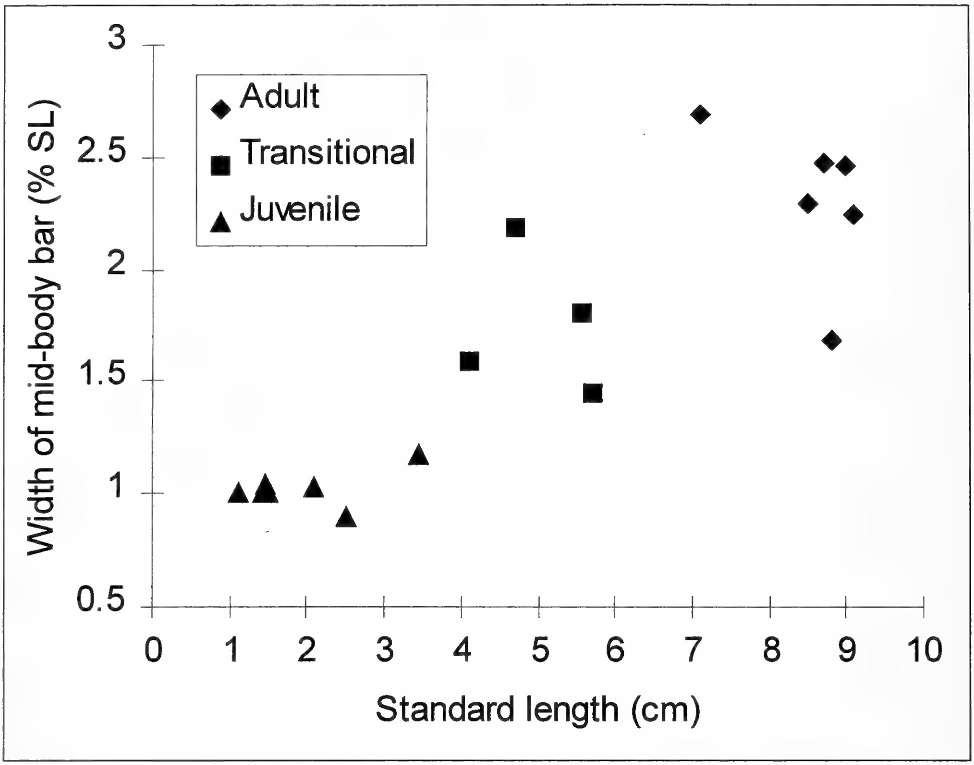

Figure 2. Relationship between mid-body bar width (expressed as a percentage of the standard length of fish) and the standard length of juvenile, sub-adult and adult *Amphiprion latezonatus* at Julian Rocks, December 1994

Remarks:

Since thorough descriptions of the live colour patterns of juvenile *A. akindynos* are lacking from the Great Barrier Reef, it is unknown whether the differences in caudal fin colouration between this study and Allen (1975) are due to geographic or random variations.

Amphiprion latezonatus (Fig. 1b)

Material Examined:

(7 preserved specimens: 11–34 mm; 11 preserved specimens: 47–91 mm). AUSTRALIA — North Solitary Island AMS I.37378–002 (7: 11.1–34.5), AMS I.19700–002 (6: 57.7–91.0); Broughton Island AMS I.17246001 (3: 41.3–71.0) . Live specimens and photographs at Lord Howe Island (1: 25), Gneering Shoals (1: 15), Moreton Reefs (1: 20), Julian Rocks (23: 15–30), North Solitary Island (18: 10–35) and South West Rocks (5: 15–20).

Live Colour Description:

Juvenile phase colouration was observed in specimens from 10–34 mm. Base colour black or dark brown. Head bar touched posterior edge of eye and joined at the anterior base of the dorsal fin (Fig. 1b). Mid-body white bar extended over the second spine of the anal fin, extending over 3–7 rays of dorsal fin, and continued posteriorly along the distal edge of fin rays. The remainder of soft dorsal fin was yellow. The peduncular bar extended ventrally across the peduncle, and along the upper margin (and posterior margin in 3 of 7 specimens) of the caudal fin. The caudal fin predominantly yellow with a surrounding black border that was more pronounced posteriorly (Fig. 1b). Yellow snout pigment touched the anterior edge of eye. Spinous dorsal fin, anal and pelvic fins dark.

Colour in Alcohol:

Dark brown to grey base colour. Yellow and white makings of live specimens were cream colour in alcohol.

Ontogenetic Changes:

Dark base colour present at all development stages. The maximum width of the mid-body bar (expressed as a percentage of standard length), a major diagnostic feature separating the colour patterns of adults from congeners, was relatively narrow in the juvenile stage but increased with increasing size (Fig. 2). In specimens >60 mm, yellow snout, and soft dorsal, caudal and pectoral fin pigmentation was absent. Specimens >45–50 mm develop a white bar on the posterior edge of the caudal fin and dark yellow pigmentation on the base of dorsal fin.

Previous Literature:

Photograph of large juvenile in Kuiter (1993).

Remarks:

The predominant yellow caudal and soft dorsal fins colouration clearly distinguish juvenile *Amphiprion latezonatus* from congeners in this geographic region.

***Amphiprion mccullochi* (Fig. 1c and 1d)**

Material Examined:

(2 preserved specimens: 9 mm; 4 preserved specimens 28–41 mm; 1 preserved specimens 83 mm). AUSTRALIA–Lord Howe Island, AMS IA.963 (1: 83.0), AMS IA.967 (1: 43.1), AMS IA.968 (1: 36.0), AMS IB.5497 (1: 28.0), AMS I.17368038 (1: 9.0), AMS 5515 (1: 9.1); Middleton Reef, I.27142024 (1: 29.0). Photographs of live specimens — Lord Howe Island (3: ~20 mm).

Live Colour Description:

Base colour black. Snout, and head and mid-body bar width varied with size of specimens. Specimens 9–20 mm (Fig. 1c); head-bar touched the posterior edge of eye and joined at the anterior base of the dorsal fin. Mid-body white bar extended over the second anal fin spine, reaching onto first 4–5 rays of dorsal fin, and continued posteriorly along the distal edge of fin rays. Yellow snout touched anterior edge of eye. Specimens 28–43 mm (Fig. 1d): head-bar was less pronounced than in small specimens, did not join dorsally and usually did not touch eye (1: 29 mm specimen, head bar touched anterior edge of eye). Mid-body white bar extended from just anterior of the anus, reaching onto first 1–2 rays of dorsal fin, and did not continue posteriorly along the distal edge of fin rays. Yellow snout pigment touched the edge of eye in the (2) 28–29 mm specimens, but not in the (2) 36–43 mm specimens.

Soft dorsal fin dark in all juvenile specimens (9–43 mm). The ventral half of the peduncular bar yellow; dorsal half of the peduncular bar white, with white portion extending posteriorly along upper edge of caudal fin, remainder of caudal fin dark. Spinous dorsal fin, anal and pelvic fins dark.

Colour in Alcohol:

Dark brown base colour with cream bars and snout.

Ontogenetic Changes:

Dark base colour present at all development stages. Only the head bar is retained in the adult stage, and is highly reduced in width and length compared to juveniles. Specimens >44 mm: yellow snout, and yellow caudal and pectoral fin pigmentation absent; caudal fin entirely white; mid-body bar absent or highly reduced. Ontogenetic colour changes in this species have not been fully documented and requires further investigation.

Previous Literature:

Whitley's (1929) description of juvenile *A. mccullochi* and the juvenile specimen (AMS IB.5497) illustrated in Allen (1975) are in agreement with the present study.

Remarks:

The juvenile colouration of small (<20 mm) *Amphiprion mccullochi* was, in most cases, identical to juvenile *A. akindynos,* with the exception that some *A. akindynos* specimens had light brown anal and pelvic fins, whereas *A. mccullochi* did not. There were, however, some distinct differences between these two species in larger juveniles (>28 mm). In this regard, the head bars joined at the anterior base of the dorsal fin in all *A. akindynos* juvenile specimens (9–35 mm) and most sub-adult specimens (35–50 mm), but did not join in *A. mccullochi* specimens >28 mm (see also Allen 1975). Furthermore, the mid-body bars of large *A. mccullochi* juveniles (>28 mm) did not extend onto the anal fin or posteriorly along the distal edge of soft dorsal fin rays, but nearly always did in *A. akindynos* juvenile specimens (9–35 mm).

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Vegetation Distribution on a Gravel Point Bar on the Wilson River, NSW: a Fluvial Disturbance Model

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BRIERLEY, G. AND CUNIAL, S. (1998). Vegetation distribution on a gravel point bar on the Wilson River, NSW: a fluvial disturbance model. *Proceedings of the Linnean Society of New South Wales* **120**, 87–103.

Vegetation distribution on a gravel point bar on the Wilson River, on the mid-north coast of New South Wales, is determined by the pattern of geomorphic units that comprise the point bar. Morphodynamic interactions between vegetation and fluvial processes vary for these differing geomorphic units, reflecting a combination of successional and hydrogeomorphic processes. Fluvial reworking by floods has created a mosaic of geomorphic units which support vegetation at differing phases of regeneration and growth. Stands of river oak on channel-marginal ridges promote gravel deposition. These features are separated by a series of unvegetated chute channels at the bar head. A range of mid-lower canopy species and more substantive ground cover are evident at the bar core and on the channel-marginal bench, where the dense vegetation cover promotes deposition of fine sands and silts. The bar core is separated from the bench by a scoured flood channel, which supports a lower diversity of vegetation. An extensive, unvegetated bar platform has developed at the apex of the bend. The primary geomorphic unit at the bar tail is an older bar platform unit which has a dense river oak monoculture. This feature has been buried by up to 1 m of sand. Reworking of materials over the point bar surface, and associated implications for vegetation distribution within the riparian zone, are described within a fluvial disturbance model.

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KEYWORDS: *Callistemon*, *Casuarina*, fluvial disturbance, geomorphic units, gravel bar, hydrogeomorphic models, *Leptospermum*, North Coast (NSW), riparian vegetation

INTRODUCTION

Over the past decade or so there has been growing recognition of the significance of riparian vegetation as a control on river character and behaviour (e.g. Hickin 1984; Thornes 1990; Hupp et al. 1995). As a general rule, streams with thick riparian vegetation cover tend to be narrower than channels with thin streamside vegetation (Andrews 1984; Hey and Thorne 1986). Alternatively, whenever vegetation spreads across the channel zone, it can induce significant instream aggradation (e.g. Burkham 1976; Friedman et al. 1996; Brooks and Brierley, in press).

In an attempt to reduce bank erosion and bed degradation, while improving the ecological and aesthetic value of water courses, vegetation management strategies now form an integral part of many community-based river management plans in eastern Australia (e.g. Raine and Gardiner 1995). The most effective strategies for river rehabilitation *work with* the 'natural' behaviour of river systems. In order to achieve this, underlying controls on the composition and distribution of riparian vegetation must be understood. Based on work performed in the northern hemisphere, two primary models have been used to account for the patterns of vegetation structure within the riparian zone. These are referred to as the successional and hydrogeomorphic models.

Autogenic ecological succession is an orderly, community controlled process that

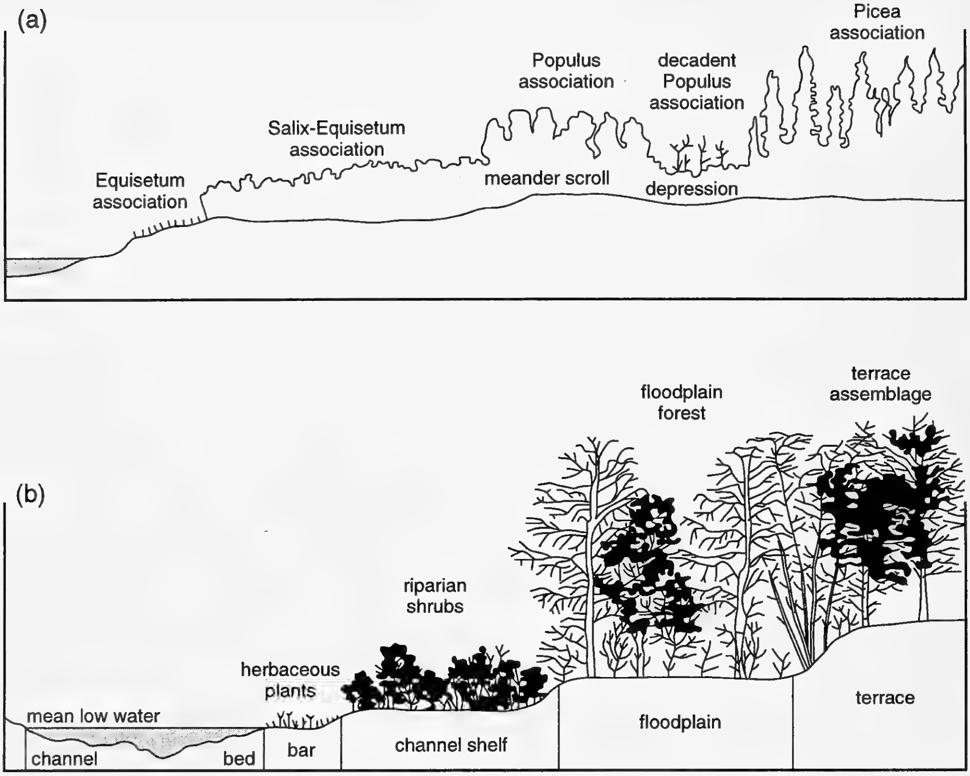


Figure 1. General models of vegetation associations along rivers. (a) The successional model of vegetation distribution across a point bar (explained in the text). The figure shows successional communities and environmental conditions along a dynamic plant succession sequence in the Mackenzie River Delta, Alaska, USA (adapted from Gill 1973). The slip-off slope of the point bar is accreting laterally to the left; (b) the hydroperiod model of vegetation distribution across differing fluvial surfaces (explained in the text). This figure shows a schematic representation of geomorphic features and associated vegetation types along Passage Creek, Virginia, USA (adapted from Hupp 1986).

occurs upon landform surfaces whose margins are periodically affected by pulses of river activity (e.g. Gill 1972; Fonda 1974; Nanson and Beach 1977; White 1979; Salo et al. 1986; Kalliola and Puhakka 1988). In rivers undergoing systematic channel migration, ‘new’ surfaces created through lateral accretion become established by ‘opportunistic’, primary colonising species (Fig 1a). These early successional communities reflect external, allogenic processes of flooding and aggradation at the point bar margin (Gill 1973). Orderly patterns of vegetation reflect phases of lateral channel shift and associated changes in the pattern of sediment deposition on the bar. Community structure changes through time, as organisms modify and gain control of the physical environment (Drury and Nisbet 1973). In this way, vegetation succession proceeds as a consequence of environmental alteration and competitive exclusion (White 1979).

The second model that accounts for the distribution of riparian zone vegetation cites external, environmental alterations as controls on the allogenic distribution of vegetation. In this hydrogeomorphic model, distinct vegetation assemblages are associated with geomorphic surfaces, the elevation and position of which determine the frequency, intensity and duration of flood inundation, sediment calibre, and the susceptibility of certain species to damage (Fig 1b; e.g. Bell 1974; Harris 1986; Hupp 1988; Hupp and Osterkamp 1985, 1996; Osterkamp and Hupp 1984; Teversham and Slaymaker 1976; Yanosky 1982).

This study tests the applicability of the successional and hydrogeomorphic models in explaining the vegetation distribution on a gravel point bar in the Wilson River, on the North Coast of New South Wales (NSW).

BACKGROUND CONTEXT: HUMAN DISTURBANCE TO RIPARIAN VEGETATION IN COASTAL NSW VALLEYS

The vegetation distribution along virtually all coastal plain rivers in NSW reflects landscape responses to the clearance of riparian zone and floodplain vegetation in the nineteenth century. Citing evidence from the lower Hunter River, along with the Manning and Nambucca catchments, Raine and Gardiner (1995) suggest that coastal rivers in NSW north of the Hunter contained stands of dense lowland sub-tropical rainforest at the time of European settlement. Channels were narrow, sinuous and relatively stable, and experienced negligible bedload transfer. Examples of the likely rainforest climax species include weeping myrtle (*Waterhousia floribunda*), watergum (*Tristaniopsis laurina*), flooded gum (*Eucalyptus grandis*), sand paper fig (*Ficus coronata*), cheese tree (*Glochidon ferdinandi*) and brush cherry (*Syzygium australe*). The rainforest also contained stands of the highly prized red cedar (*Toona australis*). Indeed, the cedar industry was one of the original mainstays of the economy in the early days of the colony (Gaddes 1990). By 1890, however, the cedar industry was all but finished in NSW, as easily accessible areas on floodplains had been logged. By this time, much of the lowland plain had been cleared of vegetation for agriculture.

Post-European clearance of riparian vegetation, altered fire regimes, depletion of the original seed base, grazing pressures and changes to river morphology have resulted in extensively modified patterns of riparian vegetation along rivers in coastal NSW. In instances where regrowth has been facilitated, it tends to be dominated by fast growing monocultures of opportunistic species, such as river oaks (*Casuarina cunninghamiana*), tea trees (e.g. *Leptospermum* sp.) and bottle brush (*Callistemon* sp.). These species can inhabit frequently flooded areas atop coarse gravel substrates. These are sites with high light levels, low nutrient availability, and low inherent fertility.

The site selected for this study records a history of opportunistic vegetation responses to channel expansion. Vegetation cover on the ‘recent’ point bar surface contrasts markedly with remnant stands of riparian vegetation at the channel margin.

REGIONAL SETTING FOR THIS STUDY

The Wilson River is a north easterly draining tributary of the Hastings River (Fig. 2). At Telegraph Point, the Wilson River drains a catchment area of 570 km^2. Headwaters are located in the Tinebank mountain ranges of the Northern Tablelands. The regional geology is dominated by mudstone, sandstone and conglomerate of the Carboniferous Boonanghi Beds.

In its upper 30 km, the Wilson River drops over 800 m to Upper Rollands Plains (see Fig. 2). At the base of the mountain range, the bedrock confined valley widens from <100 m to 500–700 m. The low sinuosity, gravel-bed channel is about 20 m wide. Downstream of Marlo Mericcan Creek confluence, the Wilson River is characterised by multiple channels with well-vegetated islands. Beyond this point, the valley widens to approximately 2 km. Various narrow (around 20 m), sinuous paleochannel threads are evident on the floodplain. The floodplain becomes increasingly swampy towards the tidal limit (around Telegraph Point).

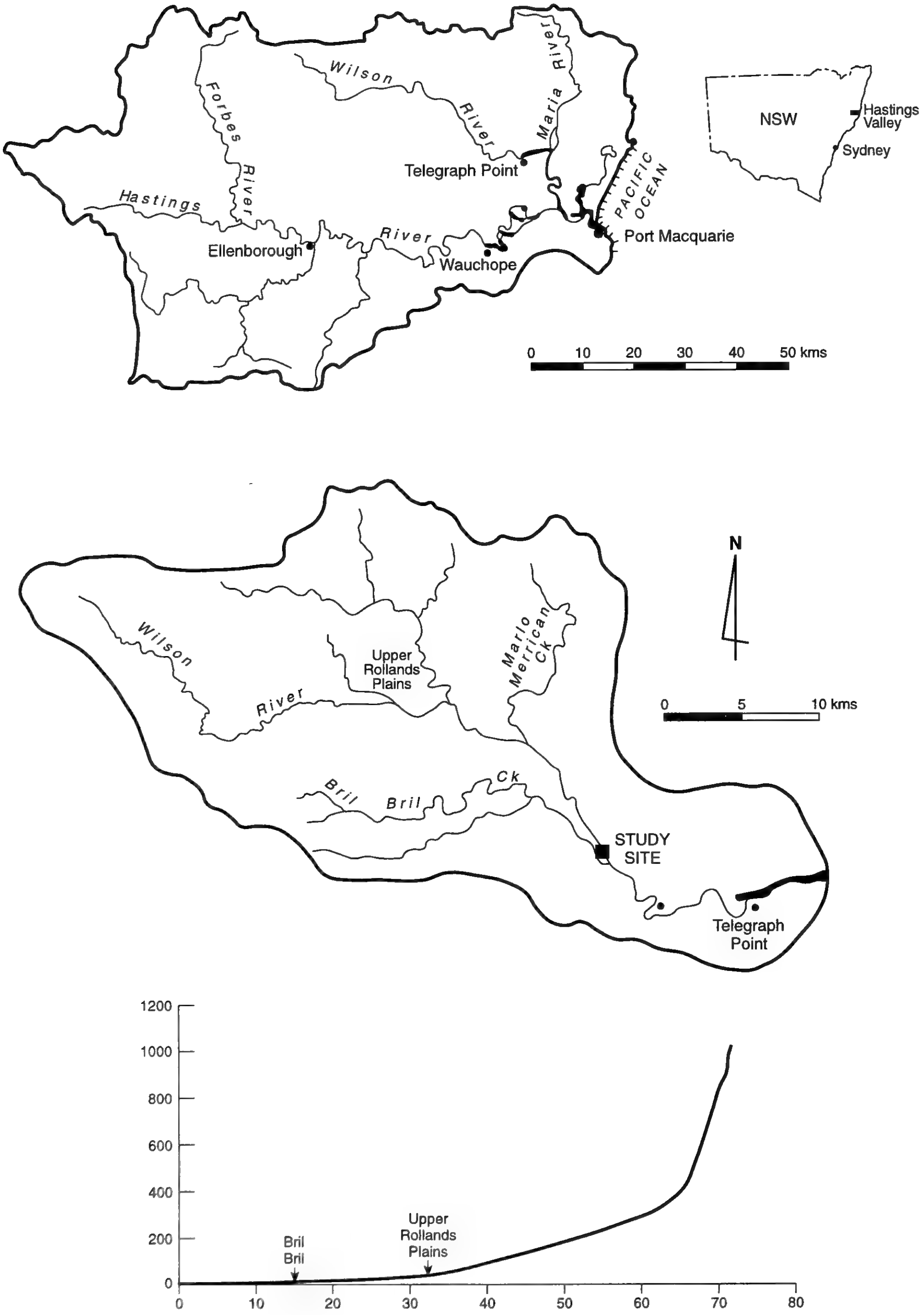


Figure 2. Location of the Wilson River and study site in the Hastings Valley.

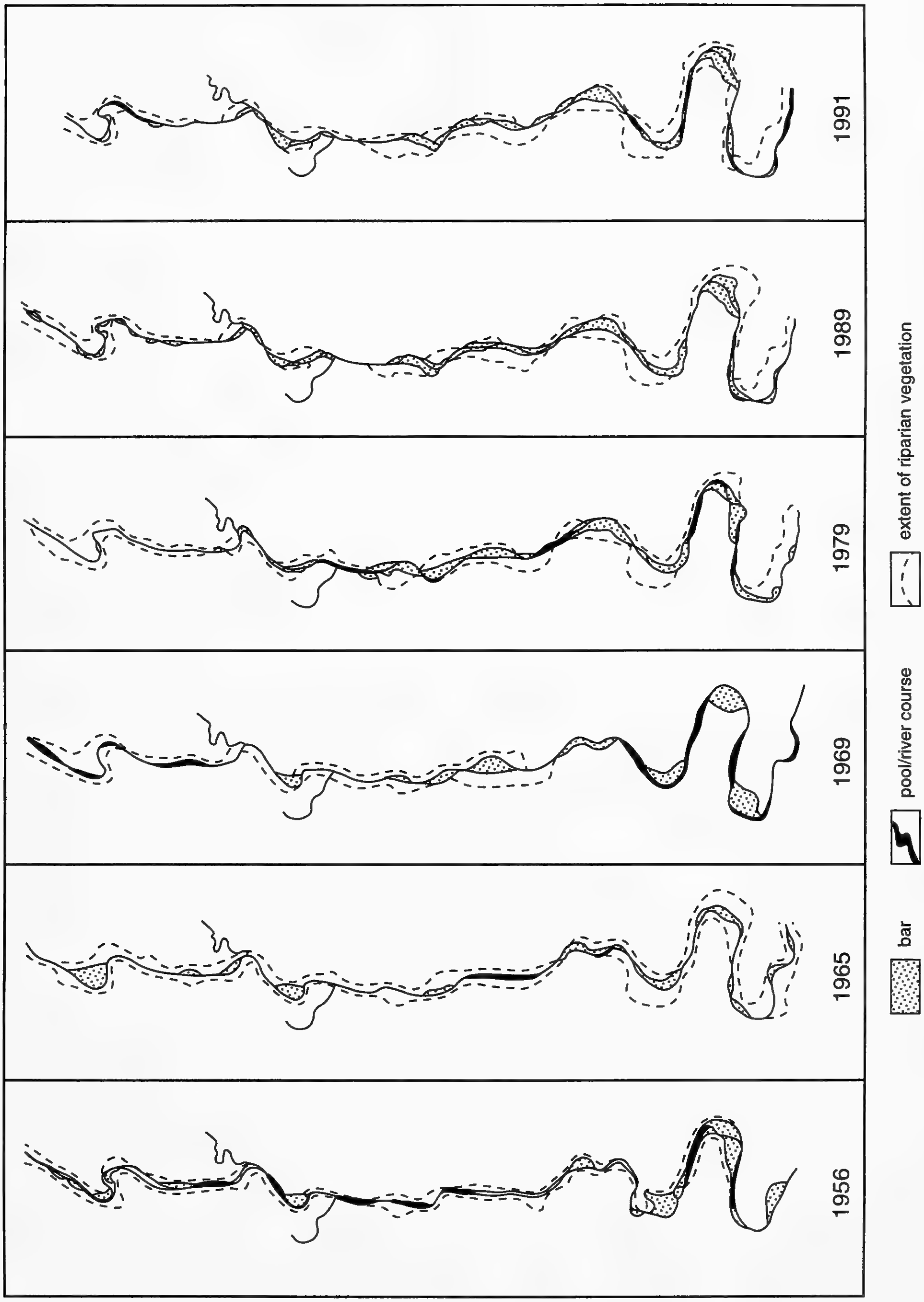


Figure 3. Air photograph interpretation of channel adjustments in the study reach (1942–1991)

Air photographs indicate that between 1942–1991 the lower course of the Wilson River has widened considerably and modified its planform (Fig. 3). At the study site, located on a large point bar approximately 600 m upstream of Bril Bril confluence, channel width increased from around 20 m in 1942 to almost 130 m in 1991. Field work in 1996 measured channel width at 170 m, indicating an increase of 750% since 1942. The channel has also incised by up to 2 m, exposing basal gravels on the concave bank. The studied point bar is approximately 150 m wide and 300 m long. The highest point on the bar surface is 2 m above the low flow channel.

Channel expansion along the Wilson River is a secondary response to bed degradation. Oversteepening of the channel bed has resulted in upstream migration of a nickpoint, and subsequent channel expansion. Widening has been especially pronounced at bends. Although the pattern of channel adjustments likely reflects an inherent, lagged response to vegetation clearance, changes in channel form have been accentuated by gravel extraction downstream of the study site. Given the enlarged channel size, low to moderate floods are more geomorphologically effective than in the past, as a greater proportion of flow is confined within the overwidened channel rather than being dispersed onto the floodplain surface. This combination of circumstances has accentuated bend expansion at the study site.

Mean annual rainfall in the area is around 1300 mm. Unfortunately, the discharge record for Wilson River is poor, with just 15 years of gauged data from the station at Avenal. These data indicate a bankfull discharge ($Q_{2.33}$) of 695 m^3s^{-1}.

METHODS

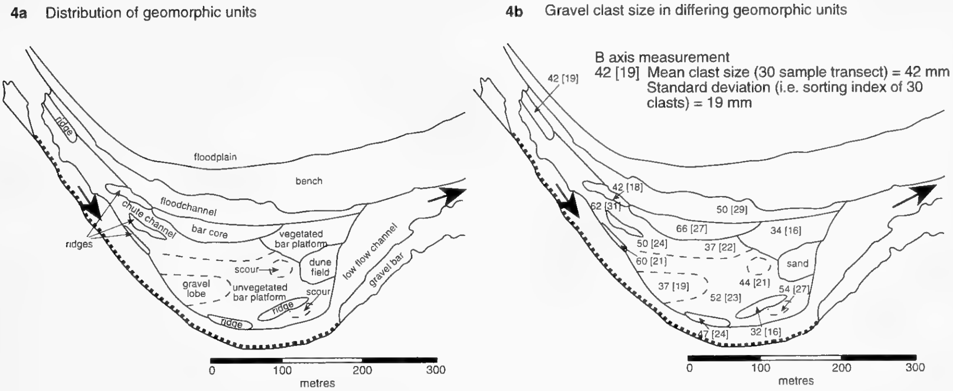
A base map of the study site was prepared at 1:12,000 scale, using an enlargement of the 1991 air photograph. Geomorphic units identified on the bar surface (*sensu* Brierley 1991, 1996) were used as the basis for a stratified field sampling technique. Nine tape and clinometer and two dumpy level transects were conducted at approximately 30 m intervals down-bar. Riparian vegetation composition, structural complexity, stem density and maturity of river oak (indicated by diameter at breast height, or DBH) were determined for each geomorphic unit. Gravel clast size was determined by b-axis measurement of 30 clasts at 1 m intervals along a line transect. For clasts whose b-axis was less than 8 mm, the nearest adjacent clast (> 8 mm) was measured. Clast shape was visually estimated as rounded, subrounded, subangular, or angular. The distribution of geomorphic units, clast size data, DBH results, and relative vegetation diversity (based on number of woody species) are summarised in Fig. 4.

VEGETATION DISTRIBUTION ON THE STUDIED POINT BAR

A diverse array of geomorphic units comprise the point bar complex (Figs 4 and 5). The morphology, position and bed material character of these units are summarised in Table 1. In subsequent sections the vegetation distribution is characterised at the bar head, mid-bar and bar tail.

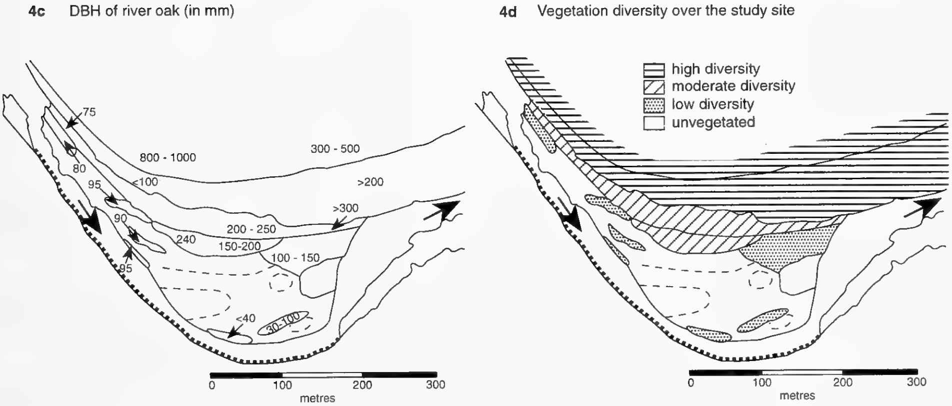
Vegetation distribution at the bar head

The bar head comprises short, parallel ridges separated by chute channels (transects A to C on Fig. 5). A large fallen tree (DBH > 500 mm) has blocked off a bank-marginal flood channel, trapping a large amount of woody debris. The flood channel widens to 40 m in mid-bar (transect E on Fig. 5), but contracts to 5 m wide at the bar tail (transect I on Fig. 5). A large bench feature, up to 2 m high and 60 m wide, marks the left bank channel margin.



4a Distribution of geomorphic units

4b Gravel clast size in differing geomorphic units



4c DBH of river oak (in mm)

4d Vegetation diversity over the study site

Figure 4. The point bar study site, Wilson River. (a) Distribution and location of geomorphic units over the bar surface; (b) clast size of differing geomorphic units over the bar surface (in mm); (c) diameter at breast height (DBH) of river oak on each geomorphic unit (in mm); (d) measure of vegetation diversity for differing geomorphic units over the bar surface, assessed as low diversity (2 or less woody species), moderate diversity (2–10 woody species), and high diversity (more than 10 woody species).

Chute channels and gravel ridges at the bar head support mainly young river oak, white sallow wattle (*Acacia floribunda*) and sporadic watergum in discontinuous bands parallel to the flood channel. Well sorted gravels have an average clast size between 40–60 mm (Fig. 4b). The DBH of river oaks is remarkably uniform across geomorphic units, ranging between 75–100 mm (Fig. 4c). There is no indication of a lateral trend in DBH of river oaks from the flood channel to the parallel ridges. Chute channels and gravel ridges at the bar head are distinctly lower than, and seemingly inset against, the left bank bench, where river oaks and distinctly older (DBH of 800–1000 mm).

Vegetation distribution in mid bar

Adjacent geomorphic units have widely varying character in the middle section of the bar, around the bar apex (transects D to H, Fig. 5). At the channel margin, gravels

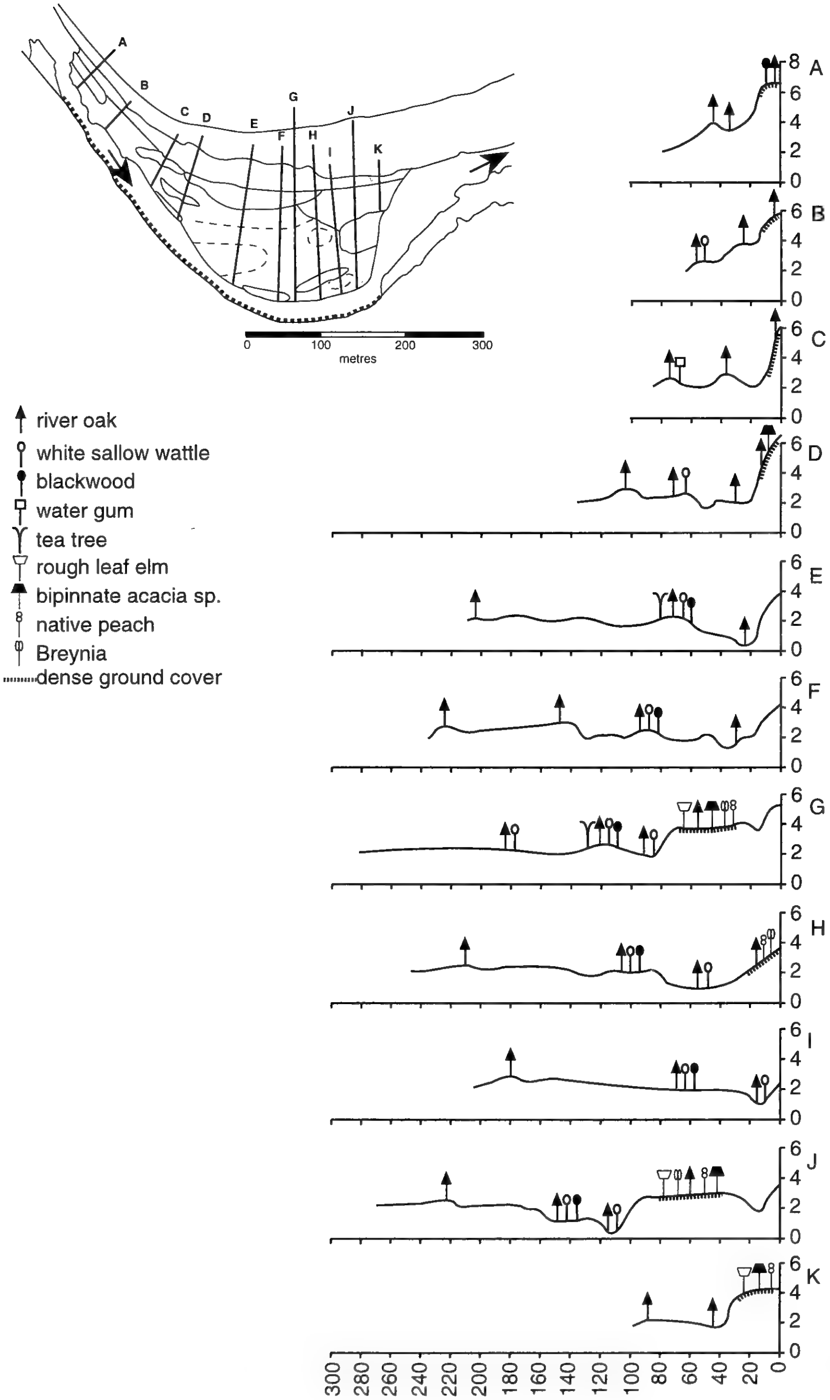


Figure 5. (a) Location of transects (A- K) across the point bar study site; (b) schematic representation of the composition and structure of vegetation assemblages on differing geomorphic units along each cross section (vegetation not to scale)

TABLE 1

Character of each geomorphic unit

Geomorphic unit	Morphology	Position on bar	Bed material character
Ridge	Linear, raised mound-like feature. Typically 5–8 m wide, < 1 m high, and < 50 m long.	Channel-margin features at the bar head or in mid-bar; may be found in a series of parallel forms, separated by chute channels.	Loose, uniform gravels with sand lenses. Average clast sizes range from 60 mm at the bar head to 30 mm at the bar tail.
Chute channel	Relatively straight, shallow channel that short-circuits the bend. Typically 10–30 m wide, < 0.5 m deep.	Primarily found at the bar head.	Loose gravels with discontinuous sand sheets. Average clast sizes range from 60 mm at the bar head to 40 mm in the gravel lobe at the bar apex.
Bar platform	Unvegetated surface, inclined slightly towards the channel. Arcuate shape, extending up to 50 m wide at the bend apex.	The dominant feature at the bend apex.	Average clast sizes range from 55 mm at the bar head to 40–50 mm at the bend apex.
Bar core	Irregularly shaped feature, with a relatively flat surface and eroded margins. Widens to > 50 m down-unit.	Separates the ridge, chute channels and bar platform from the flood channel.	Localised sand drapes (up to 50 cm thick) and scour features. Average clast size decreases down-unit, from 50 mm at the head to 35 mm at the tail.
Dune field	Irregularly shaped feature, characterised by unvegetated sand dunes. Extends up to 20 m long, 40 m wide.	Inset within the bar platform at the bar tail.	Sand.
Vegetated bar platform	Irregularly shaped feature, up to 40 m wide and 90 m long. Relatively flat surface.	Bar tail feature.	Dominated by sands up to 75 cm thick. Occasional gravels have b axis up to 35 mm.
Flood channel	Relatively straight and deep channel at the bar margin. Extends from < 10 m wide at the bar head to < 20 m wide down-bar. Depth locally increases up to 2 m deep. Irregularly scoured. Log jam at head.	Separates the complex pattern of geomorphic units on the bar surface from the bench at the left bank margin.	Prolific woody debris. Scour around trees. Generally sand-lined, but clasts in mid-bar have mean sizes of 50–65 mm.
Bench	Flat-topped feature, which widens to > 60 m down-bar. Surface drops from 4.5 m above the low flow channel at the bar head to 1 m above the low flow channel at the bar tail. Steep margin down to the flood channel and a graded slope to the floodplain.	Lines the left bank margin of the bar.	Sand and mud deposits.

have accumulated as ridges or as lobes within chute channels, locally elevating the bar margin above the older platform deposits (transects G and H on Fig. 5). Ridges lined with river oaks are not aligned parallel to the channel, as evidenced at the bar head. Gravel clasts are generally finer than at the bar head (typically 35–50 mm, Fig. 4b).

On the 'older' platform units at the core of the bar (DBH of river oaks 100–240 mm, Fig. 4c), mean clast sizes are generally coarser (between 50–60 mm), and clasts are rounder than elsewhere on the bar (up to 80% of clasts are subrounded, while the average figure for other geomorphic units is around 50%). Small gravel lobes and scour features indicate reworking of sediments at the bar core, with no linear pattern to the vegetation assemblage. The bar core supports a low open canopy of river oak and white sallow wattle, and a mid canopy of blackwood (*Acacia melanoxylon*), tea tree (*Leptospermum* sp.) and white sallow wattle. A moderate ground cover of native and exotic grasses and herbs has established. The vegetation association becomes more established towards the left bank, where mature river oaks (DBH up to 250 mm) form a tall upper canopy, with a mid-canopy of blackwood and white sallow wattle. The stem density of vegetation at the bar core is moderate to low, possibly reflecting natural thinning in response to competition for resources such as light.

In mid-bar transects the bar core is separated from the left-bank bench by a wide, sand-bedded flood channel, in which the mid to lower canopy and ground cover are poorly established. This reflects a greater degree of flood disturbance than at the bar core. Coarse woody debris caught up to 5 m high in mature river oaks (DBH around 120 mm) and white sallow wattle indicate that this is a high energy environment when floods are aligned down-valley rather than around-the-bend.

The bench surface at the left bank channel margin lies 2.5 m above the low flow channel, and has much older river oaks (DBH 300–500 mm) than adjacent geomorphic units, with wide floristic diversity and community structure. A small number of large river oaks dominate the emergent canopy. A significant proportion are dying or dead as a consequence of old age or fatal burial. Sands locally exceed depths of 100 cm on this surface. The upper and mid canopies are dominated by native species such as rough leaf elm (*Aphananthe phillipinensis*), bipinnate acacia, native peach (*Trema aspera*), breynia (*Breynia oblongifolia*), blackwood (*Acacia melanoxylon*), and a range of rainforest species. Exotic species such as lantana (*Lantana camara*), wild tobacco (*Solanum mauritianum*), stinging nettle (*Urtica incisa*) and camphor laurel (*Cinnamomum camphora*) have established a dense lower canopy and ground cover.

Vegetation distribution at the bar tail

The tail section of the bar is characterised by the most complex assemblage of geomorphic units over the bar surface (transects I to K on Fig. 5). Down-bar decline in bed material size is evident, as clast sizes at the bar tail are typically between 30–50 mm, with extensive sand deposition.

Moving away from the main channel, an unvegetated bar platform at the bar tail is transitional laterally to a narrow ridge colonised by young, partially buried river oaks (DBH 30–40 mm; occasionally up to 100 mm at the tail of the unit). Immediately behind the ridge is the downstream extension of the gravel lobe that infilled the former chute channel on mid-bar transects. As evidenced at the bar apex, this recent accumulation is higher than the adjacent bar core. The downstream end of the bar platform is highly dissected, with scour holes up to 3 m deep. Beyond these scour holes, a sand dune field has formed. Extensive sand deposition is also evident downstream of the bar core, where up to 75 cm of sand has been deposited around a dense monoculture of river oaks (DBH 100–150 mm). Significant aggradation and localised scour adjacent to the flood channel have been enhanced by dense stands of river oak, white sallow wattle and blackwood. Older river oaks (DBH > 200 mm) within the flood channel are indicative of lesser flood disturbance at the bar tail.

At the bar tail the left bank bench widens to 60 m. Surface relief varies by up to 2 m on this feature. Although this surface is less frequently inundated by low to moderate magnitude floods than adjacent units on the point bar, thick (> 1m) sand deposits indicate that flood disturbance is still a primary influence on vegetation composition, structure and survival. As observed in head and tail sections of the bar, vegetation composition and structure are more diverse on the bench than on other geomorphic units. Some river oaks have a DBH > 900 mm.

APPLICATION OF THE SUCCESSIONAL MODEL TO VEGETATION DISTRIBUTION ON THE WILSON RIVER POINT BAR

The vegetation distribution across the studied point bar has several indicators of vegetation succession. Moving away from the main channel:

1. Vegetation associations increase in complexity.
2. Species richness and structural complexity increase, reflecting a shift from disturbance tolerant species to less tolerant or intolerant species.
3. River oak, the dominant tree species across the point bar, increase in DBH (a surrogate for age).
4. Stem density decreases in more established, mature communities.

General successional trends are disrupted, however, by the irregular pattern of geomorphic units. Erosion in the flood and chute channels has defined boundaries between stands of vegetation, while deposition has created new surfaces suitable for initial colonisation. The irregularity of disturbances has created a mosaic of vegetation assemblages at different stages of colonisation and growth.

APPLICATION OF THE HYDROGEOMORPHIC MODEL TO VEGETATION DISTRIBUTION ON THE WILSON RIVER POINT BAR

The hydrogeomorphic model of vegetation distribution proposes that distinct vegetation communities are distributed upon geomorphic surfaces at different elevations above the low flow channel (Fig. 1b). On the studied point bar, the elevated channel-marginal bench contains a wider range of species, of greater age, than the remainder of the bar complex. The elevation of the bench presents a surface which is less prone to high frequency fluvial disturbances than the remainder of the bar surface. During flood stages, flow velocities on the bench are likely lower than over the bar surface, due to the lower flow depth and the dense vegetation cover. Substrate conditions on the bench are finer-grained than on the bar, and are therefore more able to retain nutrients and organic matter. Greater nutrient inputs from overlying vegetation enrich and develop the soil structure, enabling it to retain moisture more readily and consistently. Hence, these deposits have a higher fertility than the bar surface. For these reasons, the vegetation distribution on the bench comprises tall, floristically diverse species which are less flood tolerant than the vegetation cover on the bar itself.

However, elevation in itself cannot explain the pattern of vegetation over the bar. In general, the plants on the point bar are not grouped into discrete communities along an elevation continuum. Geomorphic units at differing elevations commonly have quite different substrate conditions and support different vegetation communities (e.g. the thicket of buried river oaks at the bar tail, and the stand of river oak, white sallow wattle and blackwood at the bar core). Of greater significance, however, is the recent nature of disturbance at this site, as many of the gravel accretionary surfaces that comprise the bar platform, including chute channels that are infilling with gravel lobes, remain unvegetated, yet these surfaces have a higher elevation than the diverse range of vegetation which comprises the bar core (see Fig. 5, transects G and H). At this site, where only 6 m separates the low flow channel and bankfull height, elevation of geomorphic units away from the main flow is not the dominant control on vegetation distribution.

FLOOD DISTURBANCE AS A CONTROL ON VEGETATION DISTRIBUTION

Channel expansion at the study site has presented a surface for opportunistic vegetation interaction with geomorphic processes. Most river oaks on the bar platform and

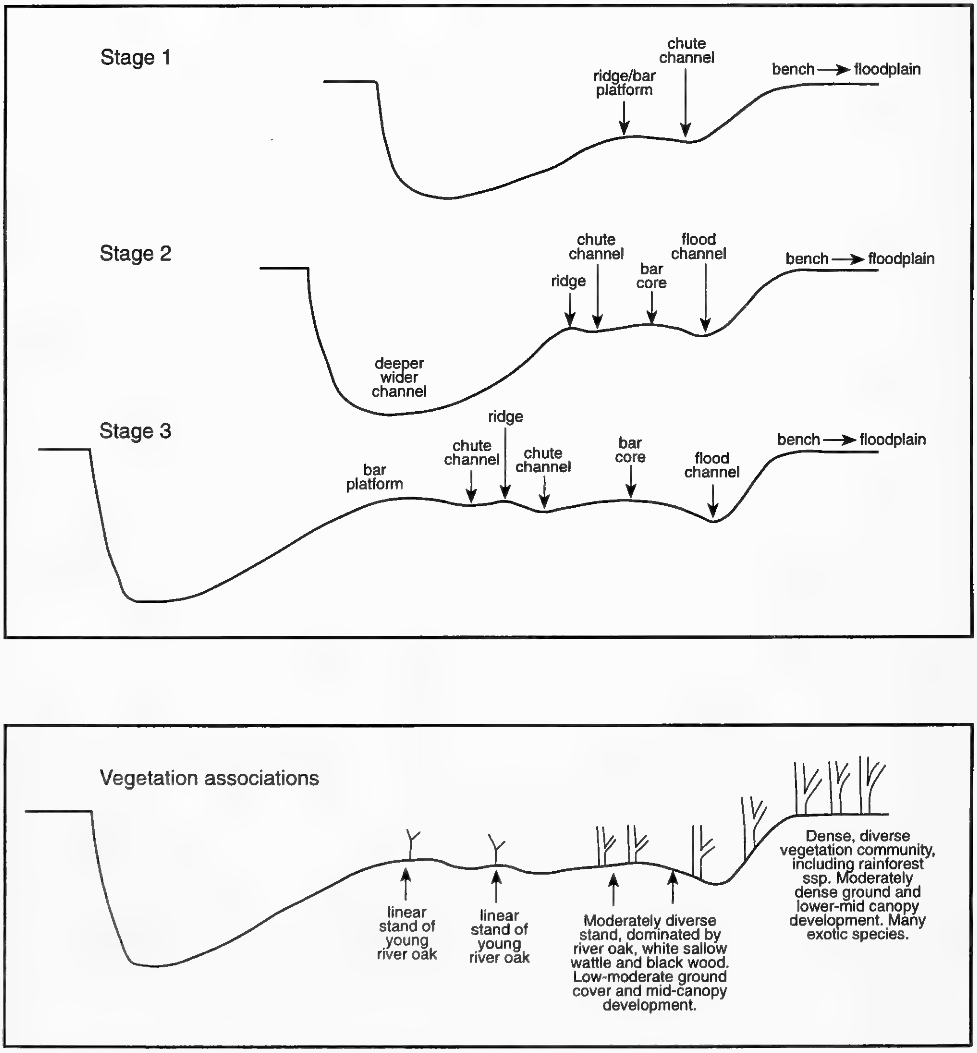


Figure 6. Evolutionary model of point bar formation associated with channel expansion at the study site (see text for explanation). Resulting vegetation patterns are shown schematically in the lower figure.

TABLE 2
Geomorphic units and their associated vegetation

Geomorphic unit	Species present	DBH of river oak	Vegetation structure (including stem density)
Ridge	River oak.	Up to 100 mm at the bar head, 30–40 mm at the bend apex and 30–100 mm at the bar tail.	Densely stemmed monoculture, typically just one-tree wide. Locally buried by gravels and sands up to 50 cm deep.
Chute channel	Unvegetated.		
Bar platform	Unvegetated, though some buried river oaks are evident at the head of the unit.		
Bar core	Low open canopy of river oak and white sallow wattle, with a mid canopy of blackwood, tea tree and white sallow wattle and a ground cover of native and exotic grasses and herbs.	Up to 240 mm.	Moderate density and diversity, with well-developed mid and lower canopies and grassed bar surface.
Dune field	Unvegetated.		
Vegetated bar platform	River oaks, with occasional blackwood and white sallow wattle.	100–150 mm.	Dense cover; virtually a monoculture of river oaks.
Flood channel	Characterised primarily by river oak, white sallow wattle and blackwood.	Less than 100 mm at the bar head, but up to 300 mm at the bar tail.	Irregularly spaced vegetation, with moderate diversity.
Bench	Upper and mid canopies are dominated by rough leaf elm, bipinnate acacia, rainforest species, native peach, breynia species and blackwood. River oaks dominate the emergent canopy. Exotic species such as lantana, wild tobacco, stinging nettle and camphor laurel have established a dense lower canopy and ground cover.	Up to 1000 mm	High diversity, with well-established upper and mid-canopies along with substantive ground cover.

associated ridges have DBH <100 mm, attesting to the recent nature of bend expansion. Channel-marginal river oaks were less than 5 years old at the time of field work, as they are not evident on the 1991 photograph.

The observed vegetation distribution reflects morphodynamic interaction between vegetation and geomorphic processes on the various geomorphic units that comprise the point bar complex (Figs 4 and 5; see Table 2). As geomorphic units are added to the point bar complex, or surfaces are modified to varying degrees during flood events of differing magnitude, the vegetation pattern changes. This, in turn, influences the geomorphic responses to subsequent flood events, resulting in a mosaic of geomorphic units with differing vegetation characteristics over the bar surface (Brooks 1994; McKenney et al. 1995). This *fluvial disturbance model* builds on the hydrogeomorphic model, applied to a lateral migration (successional) scenario.

Application of the fluvial disturbance model is accentuated in coastal valleys of NSW, where rivers have steep flood frequency curves, meaning that they experience large floods relatively frequently (McMahon et al. 1992). The geomorphic effectiveness of high magnitude floods is exaggerated by bedrock confinement of these valleys (e.g. Warner 1992; Ferguson and Brierley, in press). Responses to flood disturbance are further compounded at the study site, as channel expansion has effectively increased the frequency and duration of within-channel flows during high magnitude events.

Using DBH of river oaks as a surrogate for tree age, vegetation assemblages at different phases of regeneration and growth on differing geomorphic units provide an insight into the evolution of the studied point bar (Fig. 6). The bar core likely originated as a ridge and the adjacent chute channel subsequently became the contemporary flood channel (Stage 1 in Fig. 6). This scenario replicates ongoing processes at the bar head. Alternatively, the bar core may have evolved as a bar platform, which subsequently became separated from the bank by a flood channel.

As the channel degraded and the bend expanded, ridges developed at the channel margin associated with lateral accretion processes (Stage 2 in Fig. 6). Given their capacity to colonise and flourish under low nutrient, high light conditions, in gravelly substrates close to water, river oaks have been the primary coloniser of these ridges. River oak are able to establish and grow quickly (up to 3 m per year). When initially stabilising, there may be as many as 10–50 seedlings per square metre of alluvium, but they thin quickly through natural attrition. Deep, well spread roots resist up-rooting, while natural layering of adventitious roots enable them to survive rapid burial. Flexible, multiple stems of juvenile trees are able to bend with flow. Hence, stands of young river oak anchor the underlying gravels, enhancing deposition through increased flow resistance. Longitudinal strips of sediment accumulate in the wakes shed from initially established plants, creating a positive feedback situation of continued plant establishment in the accumulating sediment and continued sedimentation in response to the developing vegetation (Everitt 1968; Nanson and Beach 1977). Recurrence of this activity has produced a series of ridges at the bar head.

By enriching the substrate, along with its shading ability and capacity to trap sediment, river oak may facilitate the establishment of secondary colonising species (Raine and Gardiner 1995). This may well have occurred at the bar core. Species other than river oak establish between periods of inundation. Mineral substrates (particularly sands) develop structure, fabric and chemical reactivity from inputs of organic matter and nutrients from decomposing leaf litter. Edaphic developments are often reflected by the extent and composition of ground cover vegetation, such as grasses, herbaceous weeds and juvenile natives as seen on the bench at the convex bank margin.

Although the entire bar may be submerged at high flood stages, the significant degree of dissection of the bar surface, by flood and chute channels and by various scour features, indicates that extensive reworking of deposits has taken place at low-moderate flood stages. Associated with these events, there has also been extensive deposition of deposits over the bar surface, with selective deposition of sands and fine gravels at the bar tail. These factors have subsequently modified the potential for vegetative establishment and survival.

Given the enlarged channel at the study site, sub-bankfull floods have extensively modified the bar surface. For example, low-moderate magnitude events may promote infilling of chute channels and accentuate ridge development, whereas higher magnitude events may promote continued expansion of the point bar through concave bank erosion and lateral accretion. Even higher magnitude events may be aligned down-valley, activating fluvial reworking in the flood channel. Various phases of bar dissection and extension have produced a complex mosaic of geomorphic units across the bar surface, resulting in a patchy riparian vegetation community (Stage 3 in Fig. 6). Localised disturbances effectively sets succession back to the initial processes of colonisation and regeneration. This is referred to as gap phase succession (White 1979), whereby whole communities may become structurally affected as well as compositionally adapted to disturbance.

The vegetation distribution across the point bar is determined by the pattern of geomorphic units, which has produced a mosaic of plant communities of differing age and composition. These geomorphic units are subjected to flood disturbances of differing frequencies and severities. In several instances, distinct vegetation interactions can be discerned for differing geomorphic units:

1. Chute channels at the bar margin support young, sparse vegetation, reflecting recurrent phases of flood disturbance.
2. Channel marginal ridges support bands of young river oak which stabilise sediments and induce further deposition.
3. Older, more diverse stands of trees have established at the bar core.
4. Dense stands of young river oak at the bar tail facilitate sand dune deposition.
5. While the log jam at the bar head has induced some stability in the flood channel, promoting greater diversity of vegetation down-channel, flows are preferentially routed down the flood channel during high magnitude events, depositing sands in mid-bar transects and disrupting the vegetation distribution.
6. Due to their elevated position, older, less dense vegetation stands on the bench are less ‘disturbed’ than the lower point bar surface.

In this study, the geomorphic unit framework has been applied to a site which has experienced dramatic recent changes to channel geometry and planform. There are no obvious reasons, however, why the disturbance model could not be used to explain the pattern of riparian vegetation in other landscape settings (cf., Brooks 1994; McKenney et al. 1995). For example, the model is considered to be pertinent for virtually all coastal valleys in southeastern Australia.

As an postscript to this paper, the study site has subsequently been transformed by a Rivercare project. In an attempt to reduce the accelerated rate of concave bank erosion, a bed control structure has been built at the downstream end of the bend, and a bench has been constructed along the concave bank. Material for this bench was supplied from the point bar. The vegetation cover documented in this study has been removed, as the channel has been realigned along the left bank.

SUMMARY AND IMPLICATIONS

Models that directly relate riparian vegetation distribution to prevailing ecological, geomorphological or hydrological conditions *in isolation* overlook the dynamic, mutually interactive relationship between vegetation, channel morphology and hydrology. Differing vegetation assemblages on differing geomorphic units reflect variable responses of each geomorphic unit to floods of different magnitude and frequency. The pattern of geomorphic units underpins the vegetation distribution.

Prior to disturbance, it has been inferred that the riparian vegetation cover of coastal valleys in northern NSW reflected a mature phase, climax community, interspersed with patches of earlier successional plant communities (Raine and Gardiner 1995). In most valleys this situation is now reversed, with colonising species such as river oak now dominating areas that once supported diverse forest. Practical efforts at river rehabilitation in these disturbed riparian settings are increasingly focussing on revegetation strategies, framed within a 'soft-engineering' approach. Application of these approaches will be most successful if planting strategies 'work with' natural patterns of geomorphic and vegetation interaction. In general, this entails using fast growing primary colonising species at the outset, such as river oaks (*Casuarina* sp.), tea trees (e.g. *Leptospermum* sp.) and callistemon (*Callistemon* sp.). These multi-trunked species have root systems that extend below the water table, and grow in dense thickets. As such, they provide substantial resistance to flow and act as a means of gravel stabilisation. A number of sedges and rushes will perform well in conjunction with tree and shrubs on bars, benches and eroding banks. These species are effective at trapping wash load, thereby aiding the build up of cohesive materials on these surfaces. Examples include *Lomandra hystrix*, *Lomandra longifolia*, *Schoenoplectus mucronatus* and *Scirpus validus*. Full details of planting strategies are presented in Raine and Gardiner (1995).

Finally, for a fuller understanding of controls on vegetation distribution and composition on gravel point bars, a number of additional factors warrant further investigation, such as:

- Biotic processes involved in ecological succession, such as competition, inhibition and facilitation.
- Biotic responses to fluvial processes such as mechanical damage, inundation, accretion, scour and responses to variable water levels.
- Vegetation changes associated with soil development, moisture capacity, soil nutrient status, sediment size distribution and light availability.

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Ontogenetic Diet Shift and Feeding Activity in the Temperate Reef Fish *Cheilodactylus fuscus*

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The red morwong, *Cheilodactylus fuscus*, is a large and conspicuous temperate reef fish of south-eastern Australia and is a popular target of spearfishers as well as an indicator species of bioaccumulation for water quality authorities. *C. fuscus* is a benthic carnivore, feeding on crustaceans, polychaetes and molluscs. Amphipods and other small benthic crustaceans (tanaids, cladocerans, cumaceans and mysids) constitute over 60% of the diet of juvenile fish (<200 mm standard length, SL), but only 35% of the adult diet (200 to 390 mm SL), and <20% of large adult diet (360 to 500 mm SL, which were obtained from spearfishing competitions). Adult and large adult fish consume significantly greater proportions of brachyurans, molluscs and echinoderms than juveniles. Juveniles occur over turfing algae in the upper sub-tidal region to depths of five metres, and feed continuously throughout the day, with bite rates of up to 16 per minute and high gut fullness (60–100%) throughout the day. Conversely, adults occur in deeper sub-tidal habitats (between five and 18 metres), rarely feed during the day (<4 bites per minute) and adult gut fullness declines from >50% in the early morning to <18% by early afternoon. Ontogenetic and diel factors as well as habitat choice influence the diet of this cheilodactylid. The crepuscular nature of feeding in adults of this species is in contrast to several other cheilodactylids which feed during the day.

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KEYWORDS: *Cheilodactylus fuscus*, diet, diel feeding behaviour, ontogeny, temperate reef fish

INTRODUCTION

Temperate reefs provide a habitat for a diverse assemblage of fishes which obtain food and shelter from the rocky reef. High densities of attached organisms and numerous interstitial animals provide an important food source for benthic feeding carnivorous reef fishes (Russell 1983). These fishes are the most speciose, and often the most abundant group of temperate reef fishes (Berry et al. 1982; Jones 1988; Holbrook et al. 1990). On the rocky reefs of north-eastern New Zealand, Russell (1983) found 36 of the 44 species examined to be carnivores, with 29 benthic feeders, and 7 species considered to be open water feeders (Russell 1983). This pattern is repeated in other temperate reef fish assemblages, with benthic feeding carnivores being the dominant group on temperate reefs of California (Kotrshcal and Thomson 1986; Holbrook et al. 1990) and South Africa (Berry et al. 1982).

Many fish undergo an ontogenetic shift in diet which may encompass changes in the mean size of prey (Leum and Choat 1980; Schmitt and Holbrook 1984) and even in the dominant prey categories and trophic status (Werner and Gilliam 1984). On rocky reefs of north-eastern New Zealand, 11 of the 13 species for which dietary information exists show widely differing diets as juveniles compared to adults (Jones 1988 and references therein). Diets may also vary seasonally in relation to seasonal changes in prey abundance (Bell 1979; Jones 1988; Gillanders 1995), or may vary geographically (Jones 1984; Cowen 1986; Gillanders 1995).

The temperate reef fishes of New Zealand have been relatively well studied (reviewed by Jones 1988) and these studies provide some insight into the feeding ecology of Australian temperate reef fishes because of the overlap in species and family distributions. While there have been comparatively fewer studies on the diets and feeding behaviour of Australian temperate reef fishes, those that have been conducted show similar trends in feeding behaviour such as ontogenetic shift in diet (Gillanders 1995) and feeding rates (Cappo 1980), and seasonal changes in diet (Bell et al. 1978; Bell 1979; Gillanders 1995).

The family Cheilodactylidae (Perciformes) is distributed throughout the southern hemisphere and parts of Japan. It is well represented in Australia and New Zealand, being common inhabitants of temperate reefs. Most cheilodactylids are diurnally active benthic carnivores, consuming mainly gammaridean amphipods, decapod crustaceans, polychaetes and molluscs (Godfriaux 1974; Bell 1979; Leum and Choat 1980; Cappo 1980; Russell 1983; Sano and Moyer 1985; Wöhler and Sánchez 1994). Ontogenetic changes in feeding behaviour have been observed in several species including *Cheilodactylus spectabilis*, found on New Zealand and southern Australian reefs (Leum and Choat 1980); *C. nigripes*, found off southern Australia (Cappo 1980, 1995); and *C. bergi*, a demersal species from the south-east coast of South America (Wöhler and Sánchez 1994).

The red morwong (*Cheilodactylus fuscus*) is a large (up to 650 mm total length), conspicuous and abundant, temperate rocky reef fish. While not a commercially important species, it is a popular spearfishing target (Lincoln Smith et al. 1989) and has been used by local authorities as an indicator species of organochlorine and heavy metal bioaccumulation (Lincoln Smith and Mann 1989). In a study on the diet of large adult red morwong obtained from spearfishing competitions, Bell (1979) identified the species as a benthic carnivore and observed seasonal changes in diet. This study only examined stomachs (not the entire gut), of which 93% were between empty and half full, and did not investigate diel feeding periodicity, or the diet of juveniles. Bell (1979) postulated that there was little feeding during the day and concluded that further work was required on the diet of juveniles. No evidence of crepuscular peaks in feeding activity was reported for a similar species, *Cheilodactylus spectabilis* (Leum and Choat 1980), and has not been reported in studies on temperate reef fishes in California (Ebeling and Bray 1976).

The objectives of this study were to firstly investigate the feeding ecology of *C. fuscus* and compare this with the results of Bell (1979), and secondly to investigate the presence of any ontogenetic or diel shift in diet by comparing the diet of three different size groups of *C. fuscus* at three different times of day.

MATERIALS AND METHODS

Field procedure

Specimens of *C. fuscus* used for gut analysis (97 in total) were collected by handspear whilst using SCUBA from various sites in the eastern region of Sydney Harbour (mostly Middle Head and Quarantine Bay) between January and April 1993 (see Lowry and Suthers 1998 for site details and map). Fish were divided into size groups before analysis. Juvenile fish (n=20) were those <200 mm with undeveloped gonads (Schroeder et al. 1994) and an average standard length (±S.E.; range) of 155.5 mm (±3.6; 120–185) and weight of 67.6 g (±4.5; 30.8–112.4). Adult fish (n=52) were those from within Sydney Harbour, averaging 307 mm SL (±7.5; 202–390) and 569 g (±40.6; 140–1099). The sites selected for collection of fish were typical of the red morwong habitat, consisting of a boulder field, flat rock and kelp cover between 0 and 20%, in depths of 2 to 12 m. Fish were sampled during three diel periods: 0600 to 1000 h (11 juveniles, 26 adults), 1000 to 1400 h (6 juveniles, 10 adults) and 1400 to 1800 h (3 juveniles, 16 adults). Fish were placed on ice, and upon returning to shore the weight and standard length were measured before the entire intestinal tract (gut) from the stomach to the anus was removed and fixed in 10% formalin for sorting in the laboratory (see below).

The intestinal tracts (guts) of an additional 25 large adult specimens were obtained from spearfishing competitions. These competitions were held along the Sydney coast (Manly to Cronulla) and the south coast of NSW (Jervis Bay) between August 1992 and March 1993 (Lowry and Suthers 1998). Competitors leave shore at 0900 h and collect fish from inshore rocky reefs along the open coast before returning at 1300 h to have their fish "weighed in". Once fish had been weighed, the guts of specimens of *C. fuscus* were removed and preserved in 10% formalin. Because more points are awarded for larger individuals, the guts collected from spearfishing competitions were from larger fish than the adults sampled in Sydney Harbour (see above), averaging 418 mm SL (±8.2; 363–498) and 1273 g (±66.4; 850–1680).

Feeding behaviour

Adult and juvenile fish were observed at sites in Sydney Harbour and off Clovelly, approximately 10 km to the south of the Harbour along the open coast (see Lowry and Suthers 1998). Fish were observed during the day using SCUBA from a distance of 5 to 10 m with most observations lasting four to five minutes. Juveniles that were feeding and constantly moving were sometimes only observed for 30 seconds, while the behaviour of adults that were stationary for long periods was monitored for up to 6 minutes. During the observation period the number of bites made at the substratum was counted and then this was converted to number of bites per minute. Generally juveniles were not disturbed by observation and fed continuously, while adults tended to be more wary if approached to within 5 m. A correlation was performed to determine whether the number of bites per minute at the substrata was related to the period of time the fish was observed. This relationship was not significantly different from zero ($r=0.10$, $p=0.46$).

Laboratory procedure

A gut fullness ratio (C/F) was devised for use in later gut analysis. This was calculated by dividing the weight of the gut content (C) by the weight of the entire intestinal tract when full (F). Guts had a C/F value of approximately 0.8 when full, 0.4 when half full and <0.15 when empty. All guts containing food were used to determine the general diet but only guts from adults sampled in the early morning, from juveniles and from the spearfishing competitions, were used in the comparison of the diets for the different size classes. These guts ranged from half full to full (C/F of 0.4 to 0.8) with no significant difference (One-way ANOVA, $P=0.10$) in C/F values between the three size groups. The gut contents were rinsed through three sieves of 1 mm, 300 µm and 100 µm mesh sizes. The three size fractions were then drained, weighed and their volumes were measured by displacement of water in a measuring cylinder. The 1 mm and 300 µm fractions were then analysed using the points method (Pollard 1973; Hyslop 1980) and the occurrence method (Hyslop 1980). Only half of the large samples were analysed and the results were doubled to give abundances of the prey categories.

The points method provides a subjective estimate of the volume of different prey categories in the diet (Hyslop 1980). In this method of gut analysis each food category present in individual guts is assigned points based on a subjective estimate of its volume. If gut fullness is taken into account, each gut is assigned a weighting factor and then the points for each stomach are adjusted accordingly (Hyslop 1980; Harris 1985). Points for each food type are then summed over all guts examined and the results expressed as a percentage of the total number of points allocated to all food types, i.e. percentage volume (Hynes 1950; Pollard 1973; Hyslop 1980). While the points method is less accurate than more exact techniques (Pollard 1973; Hyslop 1980), it provides a means of more rapidly analysing larger volumes of material. The occurrence method simply expresses the number of stomachs containing a particular prey category as a percentage of all stomachs containing food (Hyslop 1980).

In this study an estimate of the volume of each prey category was made in a way similar to that of Choat and Clements (1992) and Gillanders (1995). The separate fractions (1 mm and 300 μm) were spread evenly over a 100 point, 10 mm grid in a Petri dish. Prey items falling on each point were identified and recorded giving a percentage proportion, or points out of 100, for each category. Whole prey items and fragments falling upon each of the 100 grid points were counted and placed into the taxonomic categories listed in Table 1. To take into account gut fullness, each gut was weighted according to the value of its gut fullness ratio and the total points for each gut were then multiplied by its weighting factor. To determine the consistency of this method eight samples were replicated and no significant differences (t-tests on major prey items, all $p>0.05$) were obtained between initial and replicated analyses. The weight and volume of the 100 μm fraction were determined, but because this fraction consisted mostly of flocculate matter and a small amount of crustacean remains it was not analysed further. While the results of the points method can be used to calculate the exact volume of particular prey items (in ml) from the volumes of the size fractions (see above), the results for this study are presented as percentage volumes obtained from the points method analysis.

The volume of each prey item was compared among groups (juvenile, adult, large adult) using a one way ANOVA and Scheffe's post-hoc test. Probability levels for rejecting the null hypotheses were adjusted by the number of prey-item comparisons made on the particular set of data ($P<\frac{0.05}{n}$). Normality was inspected from the frequency distribution, and homogeneity of variances was tested using Cochran's test. When necessary prey item points data were transformed using a $\log_{10}(x+1)$ transformation.

RESULTS

General diet

Gut analysis results for all fish with guts containing food (n=81) showed *C. fuscus* to be a benthic carnivore consuming mostly crustaceans, with smaller amounts of polychaetes, molluscs and echinoderms (Fig. 1, Table 1). The predominant crustaceans in the diet were gammaridean amphipods (average volume >30%), and brachyurans (10%). Other small Crustacea (comprising tanaids, cladocerans, cumaceans and mysids), as well as isopods, contributed 13% of the overall diet by volume. Polychaetes were the second most abundant prey item by volume after crustaceans (14%). Gastropod snails and bivalves were the most abundant molluscs by volume (4.5%), while limpets, chitons and abalone occurred in minor proportions. The echinoderm group consists of both echinoids (mostly juvenile *Centrostephanus* sp.) and ophiuroids. Algae was also present in the diet, but only in small, incidental amounts.

In terms of the level of occurrence of these major prey items in guts containing food (Table 1), amphipods and molluscs occurred in 100% of fish, isopods in 94%, brachyurans in 87% and tanaids in 51%. Polychaetes and algae occurred in 99% and 86% of guts respectively. The mean number of food items per gut was found to be 12.2 (standard error = 1.4), with the lowest number of items in any one gut being 3 (in a juvenile) and the greatest 18 (in an adult).

Ontogenetic variation in diet

Most of the 30 prey groups identified in the diet of *C. fuscus* occurred in all three size groups examined, except abalone and barnacles which were not consumed by juveniles. Some differences between the groups were observed in the occurrence of certain items. The larger molluscs (chitons, abalone and limpets), crabs, echinoderms and algae all occur in fewer juvenile guts than both adult groups, while small crustaceans (ostracods and tanaids) occur more in the diet of juveniles than in the diet of adults (Table 1). The differences in the diets of the three size groups were more obvious when comparing the proportion by volume of dietary items between the three groups (Fig. 1). Juvenile gut contents had significantly more amphipods (1 way ANOVA, $P<0.001$), small crustaceans and tanaids ($P<0.001$) than adult or large adult *C. fuscus*. Conversely, both adult groups consumed a significantly larger proportion of brachyurans and anomurans (approximately 14%) than juveniles (1%; $P<0.001$), as well as a greater proportion of echinoderms (1% in juveniles compared with 6% in adults and 7% in large adults, $P<0.05$) and molluscs (4% in juveniles compared with 7% in adults and 13% in large adults, $P<0.01$).

Some differences were also found between the diets of adult and large adult fish. Adult fish consumed a significantly greater volume of amphipods than large adult fish (approximately 31% versus 19%, $P<0.001$), and adults also consumed significantly more isopods (12%) than both juveniles and large adults which consumed similar proportions (3% and 5% respectively). The difference in diet between adult and large adult fish could be due to geographic variation in diet rather than size, as the adult fish came from Sydney Harbour while large adult fish came from a range of coastal regions outside the harbour. To investigate the possibility of geographic variation, we compared the diets of the eight largest adult fish from Sydney Harbour (335 to 390 mm SL), to the eight smallest specimens from the spearfishing competitions (360 to 400 mm SL). There was no significant difference in the volume of amphipods in the diet of similar sized adult and large adult fish ($P=0.77$), while the difference in isopods was still significant, albeit less so (from $P=0.001$ to $P=0.05$). No substantial geographic effects in diet were found amongst fish sampled from different sites in Sydney harbour or amongst fish collected from different spearfishing competitions.

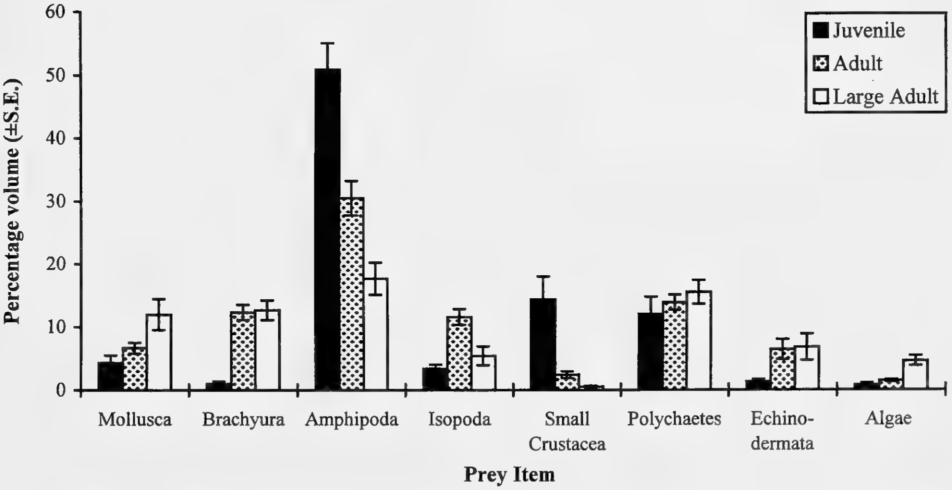

Figure 1. Mean percentage volumes (± standard error) of major prey items in the diets of juvenile (<200 mm standard length, SL), adult (200 to 400 mm SL) and large adult red morwong (350 to 500 mm SL).

TABLE 1

Percentage volume (vol.) of all prey items for the three size classes and the general diet of *C. fuscus* with percentage occurrence (occ.) in brackets. Juveniles, SL<200 mm, n=20; Adults from Sydney Harbour, 200–400 mm SL, n=26; Large adults from spearfishing competitions, 350–500 mm SL, n=25. Mean values for gut fullness (C/F ± standard error) are given for each size class.

Prey items	Juvenile		Adult		Large adult		Overall
	vol.	occ.	vol.	occ.	vol.	occ.	vol.
Mollusca	4.06	(80)	6.75	(96)	13.19	(96)	8.05
limpets	0.23	(30)	0.68	(54)	4.52	(74)	1.79
abalone	0	(0)	0.71	(35)	1.07	(43)	0.62
other gastropods	1.94	(80)	2.26	(96)	1.59	(96)	1.95
chitons	0.15	(20)	1.09	(58)	2.09	(70)	1.14
bivalves	1.74	(75)	2.01	(92)	3.92	(96)	2.55
Crustacea	70.1	(100)	59.37	(100)	40.46	(100)	56.37
Brachyura	1.07	(55)	12.17	(100)	13.11	(100)	9.27
Anomura	0.01	(5)	1.02	(46)	0.79	(35)	0.66
other decapods	0.14	(10)	1.41	(31)	0.46	(35)	0.73
Amphipoda	50.92	(100)	30.73	(100)	18.6	(100)	32.65
Isopoda	3.38	(90)	11.6	(100)	5.08	(91)	7.12
Cirripedia	0	(0)	0.05	(12)	1.71	(43)	0.57
Cladocera	3.11	(90)	2.09	(62)	0.19	(26)	1.77
Tanaidacea	9.65	(80)	0.18	(27)	0.31	(52)	2.96
Cumacea	0.89	(50)	0.04	(8)	0.01	(9)	0.28
Mysidacea	0.86	(20)	0.09	(8)	0	(0)	0.28
Other	0.06	(10)	0	(0)	0.19	(17)	0.08
Polychaeta	12.27	(95)	13.91	(100)	16.35	(100)	14.23
Echinodermata	1.25	(55)	6.32	(81)	7.60	(70)	5.27
Echinoidea	0.05	(5)	0.33	(38)	2.96	(57)	1.10
Ophiuroidea	1.2	(55)	5.99	(81)	4.64	(70)	4.17
algae	0.71	(50)	1.44	(100)	4.73	(100)	2.29
Ascidiacea	0.37	(15)	0.2	(35)	1.05	(35)	0.52
Hydrozoa	0.06	(10)	0.11	(15)	0.24	(22)	0.14
Bryozoa	0.07	(10)	0.36	(58)	2.04	(83)	0.82
Anthozoa	0	(0)	0.02	(4)	0.1	(17)	0.04
Sipuncula	0	(0)	0.15	(12)	0.07	(13)	0.08
Porifera	0.04	(5)	0.02	(8)	0.13	(26)	0.06
Pycnogonida	0	(0)	0.03	(8)	0.02	(4)	0.02
sediment	1.68	(90)	2.87	(92)	4.21	(100)	2.96
digested material	9.16	(95)	8.16	(92)	9.19	(83)	8.78
unidentified	0.23	(20)	0.14	(27)	0.57	(48)	0.30
Gut fullness	0.60±0.02		0.62±0.01		0.56±0.03		0.59±0.01

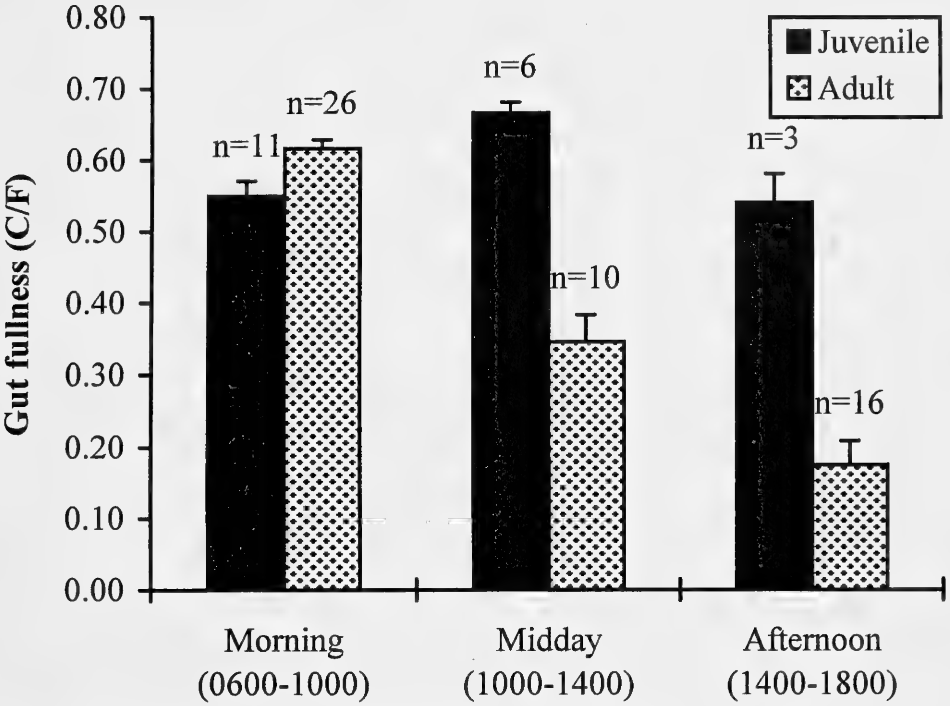

Figure 2. Gut fullness (mean C/F ± standard error) of juvenile and adult red morwong during morning (0600–1000 h), midday (1000–1400 h) and afternoon (1400–1800 h) sampling.

Juveniles and both groups of adult red morwong also displayed differences in the mean number of prey items consumed. Juveniles had an average of six prey items (range 3 to 9) while large fish had an average of nine prey items (range 7 to 13) in their intestinal tract.

Feeding periodicity and feeding behaviour

The gut fullness of juveniles sampled from Sydney Harbour were more than half full across the three diel sampling periods; morning (0600 to 1000 h), midday (1000 to 1400 h) and afternoon (1400 to 1800 h) (Fig. 2). The gut fullness ratio of juveniles sampled from the middle of the day was significantly greater, although only slightly, than C/F values from morning and afternoon samples ($p=0.03$). Adult fish sampled from early morning through midday to late afternoon were also found to have significantly different gut fullness ratios ($P<0.001$), with guts progressing from 60–90% full in the morning (C/F 0.54 to 0.77), to 0–50% during midday (C/F 0.10 to 0.50) (Fig. 2). Of the midday guts that did contain food, the foregut (stomach and beginning of intestine) was usually empty. Fish sampled late in the afternoon were, with one exception, found to be virtually empty (C/F value of approximately 0.15). The one exception to the empty guts of these late afternoon adults was a large juvenile of 210 mm SL with no gonad development whose inclusion in the afternoon sample elevated the mean C/F ratio for this period (approximately 0.20, Fig. 2).

In general, *C. fuscus* feeds by biting and sucking at the rock or algal turf with its large papillate lips, and then filtering sand and other unwanted material through the gill

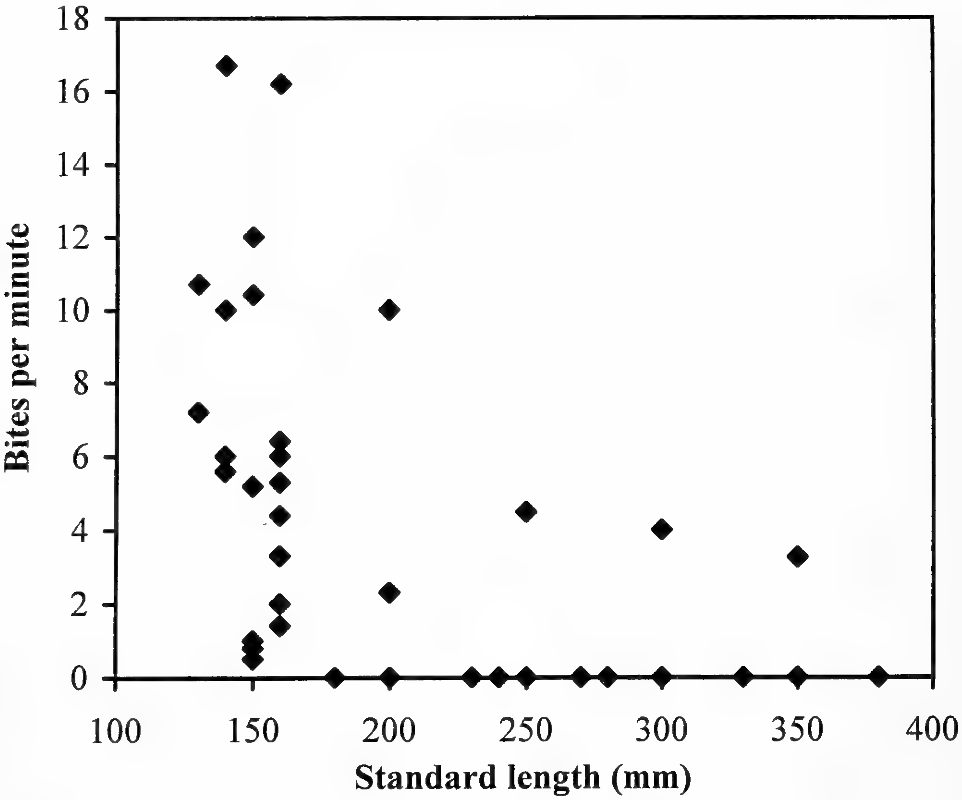

Figure 3. Number of bites at the substrata per minute for fish during daylight hours, relative to estimated standard length (n=26 juveniles, n=26 adults).

rakers and operculum. Juveniles display a different feeding behaviour to adults by feeding throughout the day, during which time adults are generally inactive. The number of bites per minute as a function of estimated length shows that juveniles feed significantly more than adults through the day (Fig. 3) (P<0.001).

DISCUSSION

General diet

Cheilodactylus fuscus is one of the larger and more important benthic feeding carnivores of temperate reefs in southeastern Australia. The main dietary components of all three size classes were amphipods, polychaetes, crabs, molluscs and echinoderms. We found a higher proportion of amphipods and a lower proportion of polychaetes, crabs and molluscs compared to that found by Bell (1979), which can be largely attributed to the significantly different diets among juveniles (<200 mm SL), adults (200 to 390 mm SL), and large adults (360 to 500 mm SL). Bell (1979) collected only large adults from spearfishing competitions which ranged from 275–415 mm SL (Bell 1979), while we found that the proportion of amphipods significantly declined even from adults to large adult fish. Inclusion of juveniles and smaller adults in dietary analysis raises the proportion of amphipods and lowers the proportions of crabs and molluscs compared to Bell's (1979) study. Another factor leading to differences between the two studies may be the amount of the gut examined. Bell (1979) examined only the stomachs (14% of gut) of which 93% were half full to empty and this may have underestimated the importance of the more common prey items in the diet. By examining the entire gut when nearly full, from adult fish collected in the early morning in this study, the majority of prey items taken during the feeding period are still present. We observed an occurrence of 100% for amphipods and crustaceans in the diets of fish regardless of size, while Bell (1979) observed an occurrence of 79% for amphipods and 89% for crustaceans.

The general diet of *C. fuscus* is similar to that recorded for other cheilodactylid fish with similar habitats. These include the banded morwong (*C. spectabilis*) from New Zealand (Leum and Choat 1980), the magpie perch (*C. nigripes*) from southern Australia (Cappo 1980), and two species from Japan (*C. zonatus* and *C. zebra*, Sano and Moyer 1985). All of these species inhabit shallow coastal regions and have diets in which amphipods dominate, and crabs, polychaetes, molluscs and echinoderms compose varying proportions of the remaining diet. These species also employ the same feeding technique as the red morwong, taking bites from algal turf, rocks and sediment then separating prey items from unwanted material. Leum and Choat (1980) found *C. spectabilis* to be a non-selective feeder, feeding on particular substrata rather than on prey items themselves. Cappo (1980) observed similar feeding behaviour in *C. nigripes* and this would appear to be true for most shallow water cheilodactylids. Our results show that adult red morwong prey on large molluscs which are most probably taken selectively from bare rocky substrate surrounding algal turf. Leum and Choat (1980) occasionally observed this behaviour in *C. spectabilis* in New Zealand.

Feeding periodicity of adults

Adult fish had full guts in the early morning which were progressively emptied throughout the day to be almost completely empty by mid-afternoon (1500 h). This implies that adults feed either nocturnally or in crepuscular peaks in activity, supporting inferences made by Lowry and Suthers (1998) who tracked adult *C. fuscus* carrying implanted radio tags. Radio-tagged fish showed significant increases in activity at 0400 to 0600 h and 1700 to 1900 h, in microhabitats well away from the normal boulder-associated habitats in which they rest during the day.

These findings contrast with feeding in other cheilodactylids. Leum and Choat (1980) found that *C. spectabilis* feeds diurnally and observed no dawn or dusk feeding peaks. Since *C. spectabilis* occupies a similar niche to that of *C. fuscus* (McCormick and Choat 1987; McCormick 1989) it is peculiar that the two species should display such markedly different feeding behaviour. Observations of *C. nigripes* throughout the day and night showed this species to also be diurnally active, sheltering in crevices and caves during the night and feeding during the day (Cappo 1980). Larger specimens of this species were found to be active earlier in the morning and later in the afternoon than smaller individuals (Cappo 1980). Both *C. zebra* and *C. zonatus* have been found to feed diurnally with the greatest amount of foraging occurring during the morning and decreasing gradually through the day with social interactions increasing greatly at dusk (Sano and Moyer 1985). While feeding in these species has been observed to begin again after sunset, data have not been collected on foraging activities through the night. *C. zonatus* has been observed "sleeping" between 2000 and 2200 h (Sano and Moyer 1985). The jackass morwong (*Nemadactylus macropterus*), a schooling species which occurs in deeper shelf waters up to 240 m (Gomon et al. 1994), feeds mostly at night, ingesting and voiding food within 24 hours (Godfriaux 1974).

Size-specific differences in diet and feeding

Juvenile *C. fuscus* consume a greater proportion of small crustaceans, in particular amphipods, while adults consume a greater proportion of large prey items such as brachyurans, molluscs and echinoderms. A similar difference has been documented for *C. spectabilis* (Leum and Choat 1980) and *Nemadactylus macropterus* (Godfriaux 1974). In some cases these changes in the diet of *C. fuscus* appear to be progressive depending on the age or size of the fish. In addition to a shift in diet, juveniles were observed to feed diurnally and those sampled throughout the day all had full guts, in contrast to the adults. Ontogenetic changes in feeding behaviour were also observed in *C. spectabilis*. Adult and juvenile *C. spectabilis* both feed during the day but juveniles spend considerably more time feeding than adults (Leum and Choat 1980). *Cheilodactylus nigripes* juveniles also were observed to feed only during the day, and to feed more frequently than adults (Cappo 1995).

An investigation into the ontogeny of prey selection of black surfperch (*Embiotoca jacksoni*) indicated that the mechanism causing ontogenetic diet shift was a group of interacting factors including morphological constraints (e.g. gape limitation), foraging behaviour, habitat selection and prey availability (Schmitt and Holbrook 1984). While consumption of large prey by juvenile *C. fuscus* is probably limited by gape, small crabs, molluscs and echinoderms do occur in their foraging habitat and are eaten (Table 1) but only in very small proportions. Juveniles of the limpet *Patelloida latistrigata* are commonly found around 5 mm length (Moran 1985) and densities of adult limpets of other species have been found around 14 m^{-2} in the shallow subtidal region (Fletcher 1987).

The main factors mediating ontogenetic diet changes in *C. fuscus* are probably those of habitat selection and resultant prey availability with morphological constraints also playing a role. As with several other temperate reef species (*C. spectabilis*, Leum and Choat 1980; *Pseudolabrus celidotus,* Jones 1984; *Achoerodus viridis*, Gillanders 1995), *C. fuscus* exhibits a size based depth distribution (pers. obs. Lowry 1997). Juveniles occur in shallow marginal zones (to depths of five metres) characterised by a greater abundance of foliose algal turf and the kelp *Ecklonia radiata*, compared to the adult habitat in deeper water (10 to 20 m) amongst large boulders and less algal turf.

The benthic fauna of coralline algal turf can include high densities of amphipods (1040 per 0.01m^2), ostracods (220 per 0.01m^2) and polychaetes (130 per 0.01m^2) but low densities of ophiuroids (Choat and Kingett 1982). They found that two species of fish feeding on this substrate (*Chrysophrys (Pagrus) auratus* and *Upeneichthys porosus*) had diets made up of these items in similar proportions (e.g. 55% amphipods, 4% polychaetes and ostracods for *U. porosus*). With increasing depth, there tends to be a decrease in the abundance and biomass of prey (crabs and shrimp), as well as a decrease in the amount of algal turf, associated with a decrease in light (Larson 1980). It may be that shallow (0 to 5 m) sub-tidal temperate regions support a greater biomass of prey for micro-carnivores than deeper (10 to 20 m) areas. Therefore juvenile *C. fuscus* may forage in the sub-littoral zone because this region provides a plentiful food source consisting of small prey items, in addition to providing protection from predators. Risk of predation is often an important factor mediating age specific patterns in habitat use (Schmitt and Holbrook 1985), and juvenile fish have often been found associated with habitats of greater structural complexity (i.e. shelter) than adults (Ebeling and Lauer 1985; Carr 1989; Holbrook et al. 1990; Levin 1991). Interactions of food abundance and predation risk have also been found to determine habitat selection by juvenile fish (Werner and Hall 1988).

Upon reaching a length of about 200 mm there was a shift in habitat use by *C. fuscus* which was reflected in diet and an accompanying change in feeding behaviour. They move to deeper regions where larger prey items (crabs, molluscs, echinoderms) are taken to replace the small crustaceans that are not as plentiful at depth. A similar ontogenetic movement into deeper water has been observed in *C. spectabilis* (Leum and Choat 1980;

McCormick 1989). *C. fuscus* differs significantly from other cheilodactylids in that adults appear to feed in crepuscular peaks (or possibly through the night), while other cheilodactylids (especially *C. spectabilis*) feed during the day and are inactive at night. These ontogenetic and diel influences on *C. fuscus* diet need to be incorporated into sampling designs of future studies. In particular, bioaccumulation studies may be confounded by the use of different size classes, which have different diets.

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The Food of Foxes, Dogs and Cats on Two Peninsulas in Jervis Bay, New South Wales

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European Red Fox *Vulpes vulpes* (L.), Dog *Canis lupus familiaris/dingo* (L.), and Cat *Felis catus* (L.) scats were analysed to assess the food, and report on the diet of these predators from two peninsulas at Jervis Bay, NSW. The main food items of *V. vulpes* comprise mammal, *Pseudocheirus peregrinus* (26.8%) on Bherwerre Peninsula, and *Rattus rattus* (37.9%) on Beecroft Peninsula. Invertebrates, vegetation and birds were also important food items of *V. vulpes* on both peninsulas. The diet of *C. lupus familiaris* consisted mainly of *Wallabia bicolor* on both peninsulas, while *P. peregrinus, Oryctolagus cuniculus* and *R. rattus* were also eaten. *F. catus* favoured mammals over invertebrates, birds and vegetation. An important finding from the survey was the occurrence of four locally endangered species; *Pseudomys gracilicaudatus*, *Sminthopsis leucopus* and *Litoria aurea* on Bherwerre Peninsula and *Rattus lutreolus* on Beecroft Peninsula. Differences in predator food preferences between Beecroft and Bherwerre reflect the differences in prey diversity on each peninsula, and supports the theory that *V. vulpes* and *F. catus* are opportunistic feeders that select the most abundant food items. In contrast *C. lupus familiaris* were more selective and favoured medium to large macropods.

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KEYWORDS: Foxes, dogs, cats, scat analysis, food items, Jervis Bay, predation.

INTRODUCTION

The diet of *Vulpes vulpes* in Australia has been studied in detail in many different ecosystems (Martensz 1971; Coman 1973; Brunner et al. 1975; Croft and Hone 1978; Seebeck 1978; Green and Osborne 1981; Triggs et al. 1984; Wallis and Brunner 1987; Lunney et al. 1990). Likewise the diet of *Felis catus* and *Canis lupus familiaris/dingo* have been studied in a number of Australian habitats (Coman and Brunner 1972; Jones 1977; Bayly 1978; Brown and Triggs 1989; Triggs et al. 1984; Brunner et al. 1991; Tidemann et al. 1994; Paltridge et al. 1997).

The diet of *V. vulpes* in natural habitat on coastal NSW has been studied by Lunney et al. (1990) and Philips and Catling (1991). In both these studies mammals were the largest food item group in the *V. vulpes* diet. Rose et al. (1994) also recorded mammals to be a significant part of the *V. vulpes* diet in Ku-ring-gai Chase National Park. Most diet studies in Australia have found that *V. vulpes* in rural Australia consume mainly *Oryctolagus cuniculus* and *Ovis aries* (Brunner et al. 1975; Croft and Hone 1978). In natural bushland other species such as *Pseudocheirus peregrinus* (Triggs et al. 1984), *Antechinus* spp and *Mastacomys fuscus* (Green and Osborne 1981) are more predominant in scats which further indicates that *V. vulpes* eat the most abundant or accessible food items in their area.

The diet of wild and feral *C. lupus familiaris* has not been widely studied in Australia, although they are implicated in many ecological impacts causing negative effects (Kolig 1973; Seebeck 1979; Kruuk and Snell 1981; Triggs et al. 1984; Delroy et al. 1986; Eberhard 1988; Flavell 1992; Barton and McEwan 1993; Meek and Nazer 1995). Analysis of *C. lupus familiaris* and *dingo* scats collected in SE Victoria by Triggs et al. (1984) found that *C. lupus familiaris* scats contained a large proportion of medium to large sized mammals such as *P. peregrinus* and *Wallabia bicolor*. Research in southern NSW recorded macropods and *O. cuniculus* as the main dietary items in the food of *C. lupus familiaris* in the coastal forests near Bega (Lunney et al. 1990).

F. catus are claimed to be opportunistic predators and diet is influenced by prey availability (Coman and Brunner 1972). Food selection in many areas is affected by seasonal changes (Jones and Coman 1981). The diet of *F. catus* is predominantly mammals in most habitats, excluding islands (Dickman 1996). *O. cuniculus* and rodents are commonly found in the *F. catus* diet in arid areas (Bayly 1978; Jones and Coman 1981) and in agricultural areas (Coman and Brunner 1972). In natural ecosystems *F. catus* focus on more abundant native species. In Victoria the *F. catus* diet mainly consisted of mammals (rats and possums), while birds, frogs and lizards are also eaten (Coman and Brunner 1972). Jones and Coman (1981) found that *Trichosurus vulpecula* and *P. peregrinus* were consumed with *Rattus fuscipes* and *Rattus lutreolus*. On Christmas Island, Indian Ocean, *F. catus* mainly prey on *R. rattus*, reptiles, birds and invertebrates (Tidemann et al. 1994). In the tropical north of Australia, native rats are an important food source (Cameron 1994), whereas *F. catus* on Macquarie Island prefer the local sea-birds and *O. cuniculus* (Jones 1977).

On our study site there are seventeen terrestrial mammal species (Appendix 1). Several native species have become extinct in the region: *Dasyurus maculatus, Isoodon obesulus*, *Phascolarctos cinereus*, and *Vombatus ursinus*. The findings in this paper are a compilation of data from scats collected over a four year period and are a useful tool in formulating management decisions regarding introduced pest and domestic animal management in the Jervis Bay Territory. The aim of this study was to collect baseline diet data on predators in the area and it was a smaller part of larger studies (Meek 1998a; Dexter and Meek 1998). The results of the investigations add further knowledge on the occurrence of native wildlife on both peninsulas and has re-confirmed the existence of several cryptic and endangered species. It is clear from this study that foxes and cats are taking locally endangered and threatened wildlife and predator population control is warranted to minimise the risk of further extinctions in the area.

MATERIALS AND METHODS

Study Site

Bherwerre Peninsula is located on the southern side of Jervis Bay (35°03′S 150°50′E) and Beecroft Peninsula is on the northern headland, approximately 200 km south of Sydney and 35 km south-east of Nowra. The total area of Bherwerre Peninsula is 7,700 hectares and that of Beecroft Peninsula is 5,250 hectares, mostly consisting of the Royal Australian Navy Beecroft Weapons Range. Parks Australia manages the majority of both Peninsulas as conservation areas. Bherwerre Peninsula is bordered by urban development to the north of the isthmus and four residential villages are located on the peninsula. Beecroft Peninsula has one residential town and is buffered from development by significant expanses of State National Park. Both peninsulas represent some of the most healthy remnant coastal habitats on the eastern seaboard, having avoided agricultural expansion and excessive development. It is likely that species diversity on Beecroft Peninsula has been modified by an increased fire regime or a Peninsula-wide bushfire that caused localised extinctions or reductions to wildlife species.

Heathlands dominate both peninsulas and are interspersed with a mosaic of swamps, sedgelands, shrublands, woodlands, littoral rainforest, and open eucalypt forest. The average rainfall for Jervis Bay is 1150 mm. May is the wettest month and September the driest. Average temperature for Winter is 15.1°C and 24°C in Summer. The predominant wind direction is north-east. The mammals of Beecroft Peninsula (see Appendix 1) have not been intensively studied although unpublished data has been referred to in Braithwaite et al. (1995). Trapping surveys have been undertaken on both peninsulas (Meek, pers. obs.). An interesting aspect of the fauna of Beecroft Peninsula is the replacement of *R. fuscipes* with *R. rattus*. Many of the arboreal mammals found on Bherwerre do not occur on Beecroft Peninsula. *Canis lupus dingo* are known to reside on Beecroft Peninsula in small numbers (Meek pers. obs.) although they are absent from Bherwerre Peninsula having disappeared about 20 years ago (Meek and Nazer 1995).

Diet Analysis

One hundred and fifty seven (n=157) fox, five dog and six cat scats were collected at random time intervals from service tracks on the Bherwerre Peninsula during 1991–93 and in 1995. Scats were discarded if it could not be determined which species they were from. One hundred and sixteen (n=116) fox, twenty four (n=24) dog and two cat scats were collected from Beecroft Peninsula in 1996. Each scat was numbered, dated and a record was made of where the scat was found. Scats were placed in plastic pots and baked in an oven at 90°C for 24 hours to kill parasite eggs. They were then soaked in water for 48 hours to soften the contents, then teased out and stored for identification. Hair was identified to species level when possible using the method described by Brunner and Coman (1974). Invertebrates were keyed out to Order. Scat content assessment was done according to the frequency of occurrence method discussed by Scott (1943). Mostly, tufts of hair were taken — comprising guard hairs, overhairs and underhairs. Skeletal material, usually teeth and claws, was also used whenever it was found as it provided valuable back-up information to hair analysis.

Stomach contents of five *V. vulpes* from Bherwerre Peninsula were examined between 1991–95. There was no quantitative analysis (volumetric) of the contents due to the small sample size although records were kept of identifiable food items.

RESULTS

Bherwerre Peninsula

In the *V. vulpes* scats, mammalian remains were found in 84.7% and birds were present in 25.5%. Twelve native mammals and four introduced mammal species were found (Table 1). The most common species were *P. peregrinus* followed by *W. bicolor*, *O. cuniculus* and *R. rattus* (Figure 1). One species, *Pseudomys gracilicaudatus*, listed as vulnerable on Schedule 2 of the ‘NSW Threatened Species and Conservation Act 1995’ was found near Wreck Bay (Meek and Triggs 1997). The range of this species is not known to extend past Sydney (Strahan 1983), although fossil records have been recovered further south and in Victoria (Watts and Aslin 1981). The hair of *Sminthopsis leucopus* was also recovered in *V. vulpes* and *F. catus* scats. This species has only been recorded on Bherwerre Peninsula by one researcher (King 1978) and has not been trapped since. Reptiles were only found in 3.2% of *V. vulpes* scats analysed.

Plant seed and vegetative material were also eaten by *V. vulpes*. The environmental weed Bitou bush *Chrysanthemoides monilifera rotundata* was eaten in winter during times of seed set. *V. vulpes* eat the fleshy berry and defecate the entire seed, usually intact (Meek 1998a). Native plant seeds were also consumed including Geebungs *Persoonia*

TABLE 1

Frequency of occurrence of items found in *V. vulpes* scats from Jervis Bay. n is the total count of each item; Frequency is the number of occurrences divided by the total number of scats.

	Bherwerre Peninsula		**Beecroft Peninsula**	
Item ingested	occurrence (n)	frequency (%)	occurrence (n)	frequency (%)
Mammal	133	84.7	110	85.3
Pseudocheirus peregrinus	42	26.8	30	25.9
Wallabia bicolor	20	12.8	7	6
Oryctolagus cuniculus	18	11.5	12	10.3
Rattus rattus	17	10.8	44	37.9
Sminthopsis leucopus	9	5.7	—	—
Petaurus breviceps	6	3.8	—	—
Perameles nasuta	5	3.2	—	—
Canis lupus familiaris	5	3.2	—	—
Rattus fuscipes	2	1.3	—	—
Cercartetus nanus	2	1.3	—	—
Tachyglosus aculeatus	2	1.3	2	1.7
Pseudomys gracilicaudatus	1	0.6	—	—
Antechinus stuartii	2	1.3	2	1.7
Antechinus spp.	—	—	2	1.7
Pteropus poliocephalus	1	0.6	—	—
Arctocephalus pusillus	1	0.6	—	—
Macropus giganteus	—	—	3	26
Homo sapiens	1	0.6	—	—
Vegetation	62	39.5	7	6
Invertebrates	55	35.0	4	3.5
Bird	40	25.5	12	10.3
Crustaceans	6	3.8	—	—
Reptile	5	3.2	1	0.9
Artificial Fibres	4	2.6	1	0.9
Soil	3	1.9	—	—
Fish	2	1.3	2	1.7
Amphibian	1	0.6	—	—
Unknown	—	—	3	2.6
Total No. scats	157		116	

spp, Blueberry Ash *Elaeocarpus reticulatus*, Apple-berry *Billardiera scandens* and Sawsedge *Gahnia sieberiana*. Numerous species of unidentified grasses were also extracted from the scats, although these seeds were probably inadvertently ingested in bird crops. Geebungs were the most abundant native plant species eaten by *V. vulpes*.

Invertebrates were an important food source of *V. vulpes*. Beetles (Coleoptera) were the most common invertebrates eaten, while grasshoppers (Orthoptera), cockroaches (Blattodea) and ants (Hymenoptera) were also consumed.

The content of *V. vulpes* scats usually included either two food items (40.1%) or one item (30.6%). Fewer scats contained three items (23.6%) and only a few contained

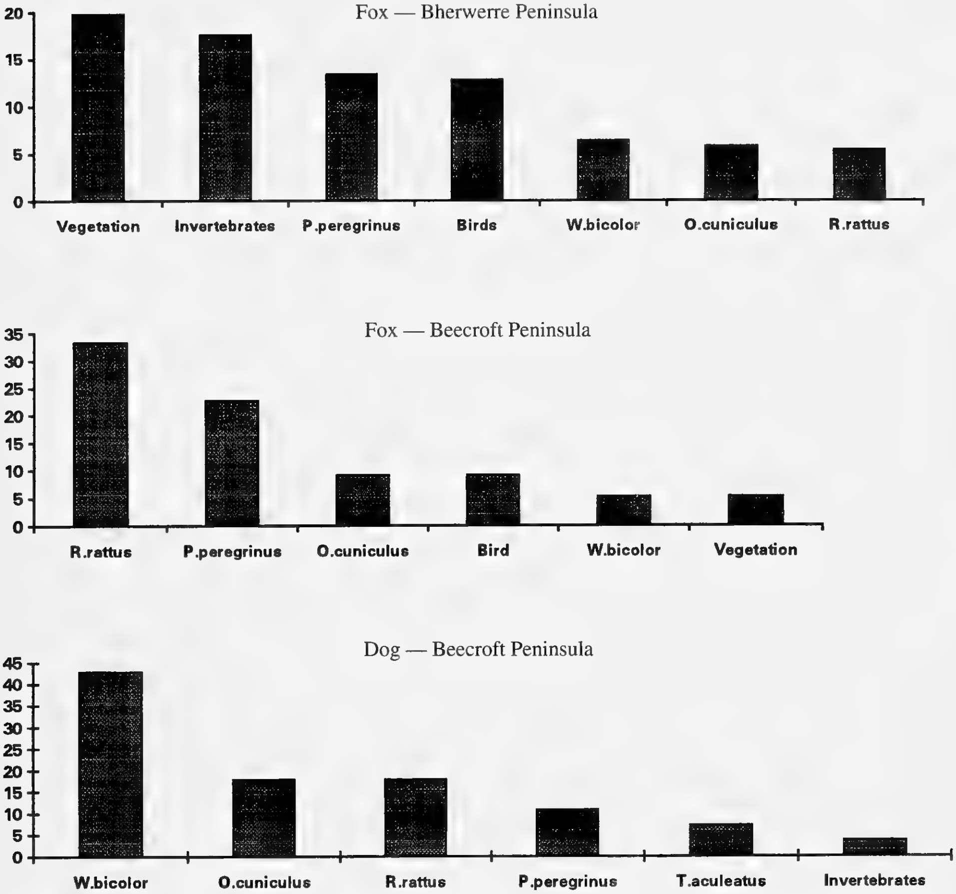

Figure 1. Composition of items in *Vulpes vulpes* and *Canis lupus familiaris* scats from Bherwerre and Beecroft Peninsulas.

four (4.5%). Two scats included small quantities of *V. vulpes* hair, most likely from grooming. Vegetation, invertebrates, *P. peregrinus* and birds were the most important dietary items, followed by *W. bicolor*, *O. cuniculus* and rats. Native species were consumed more often than introduced species.

Only small amounts of reptiles and amphibians were found in *V. vulpes* scats, however the remains of the frog *Litoria aurea* were recovered from one *V. vulpes* stomach. Other food items found in *V. vulpes* stomachs included *P. peregrinus*, *Arctocephalus pusillus*, grasses and synthetic substances.

The main food items of *C. lupus familiaris* was mammalian and invertebrate (Table 2). *P. peregrinus*, *W. bicolor*, *O. cuniculus*, *R. rattus* and *Tachyglossus aculeatus* were equally represented in the diet of *C. lupus familiaris*. Vegetation comprised a small part of *C. lupus familiaris* food intake. Mammals comprised the main proportion of the *F. catus* intake, mainly dominated by *R. rattus* while *W. bicolor* and *S. leucopus* were also recorded (Table 2). Invertebrates and vegetation were the other larger food groups in the diet of *F. catus*. Two *F. catus* scats contained 100% grooming hairs. The small sample size of dog and cat scats on Bherwerre Peninsula prevents any quantifiable assessment of the food of these species.

TABLE 2

Frequency of occurrence of items found in *C. lupus familiaris* and *F. catus* scats from Jervis Bay. n is the total count of each item; Frequency is the number of occurrences divided by the total number of scats.

	DOG			CAT	
	Bherwerre	***Beecroft***		***Bherwerre***	***Beecroft***
Item ingested	Occurrence (n)	Occurrence (n)	Frequency (%)	Occurrence (n)	Occurrence (n)
Mammal	4	22	95.7	5	2
Pseudocheirus peregrinus	1	3	13	—	2
Wallabia bicolor	1	12	52.2	1	
Oryctolagus cuniculus	1	5	21.7	—	
Rattus rattus	1	5	21.7	3	
Tachyglossus aculeatus	1	2	8.7	—	
Sminthopsis leucopus				1	
Vegetation	2	—	—	2	
Invertebrates	4	1	4.4	—	
Bird	1	—	—	1	
Frog	1	—	—	—	
Grooming hair	—	1	—	2	
Total number of scats	5	24	—	6	2

Beecroft Peninsula

In the *V. vulpes* scats collected on Beecroft Peninsula, 85.3% consisted of mammal remains. Eight mammal species including two introduced species were recorded (Table 1). *R. rattus* and *P. peregrinus* were found in the highest proportions followed by *O. cuniculus* and birds. *W. bicolor* were only found in 6% of scats. Introduced mammals were consumed more than native species on Beecroft Peninsula (Figure 1). The frequency of vegetation in *V. vulpes* diet was small. The only plant seeds found were the native Geebung *Persoonia* sp. Reptiles were recorded in low numbers and there were no frogs found in the scats collected from Beecroft Peninsula. The number of prey items in *V. vulpes* scats usually included only one food item (85.2%), with the remaining 14.8% of scats containing two items.

C. lupus familiaris scats (n=24) were dominated by mammal remains at Beecroft Peninsula, mainly *W. bicolor* then *O. cuniculus* and *R. rattus*. *P. peregrinus* and *T. aculeatus* were also eaten, as were invertebrates (Table 2). Too few *F. catus* scats were collected to make any valuable assessment of their diet on Beecroft Peninsula (Table 2).

DISCUSSION

The small sample size in this study did not allow for seasonal comparisons in diet as was undertaken by Brunner et al. (1975). As stated by Witt (1980), the diet of *V. vulpes* fluctuates over time and in order to detect seasonal preferences samples would need to be collected over several years. However, scat analysis has been shown to be useful in surveying for species not readily trapped during surveys (in Brown and Triggs 1989), although it fails to estimate the volume each species contributes to the diet and therefore assumes that all items are of equal contribution to the diet (Brown and Triggs 1989).

The range of items contained in *V. vulpes* scats in this study confirms the findings of other researchers that *V. vulpes* are extremely opportunistic in their food preferences, and have the ability to switch to the most abundant food resources (e.g. local species) available in the habitat (Brunner et al. 1975; Coman 1973; Seebeck 1978; Cavallini and Lovari 1991; Green and Osborne 1981). Insects are a prime example of an abundant food that is recorded as a spring/summer food source for *V. vulpes* (Coman 1973; Croft and Hone 1978; Seebeck 1978; Cavallini and Lovari 1991; Ciampalini and Lovari 1985).

In this study mammals were the most common dietary item. In coastal NSW Croft and Hone (1978) found that *V. vulpes* preferred birds, plants and frogs. Lunney et al. (1990) reported that *V. vulpes* in NSW coastal forests preferred mammals particularly *W. bicolor*, whereas possums and bandicoots were favoured near Sydney (Rose et al. 1994). Triggs et al. (1984) also recorded that *V. vulpes* in Croajingalong National Park preferred to eat *P. peregrinus*. These authors concluded that the high abundance of *P. peregrinus* in *V. vulpes* scats was a result of the high densities of this species in the Park. *P. peregrinus* is also abundant on both peninsulas in Jervis Bay, and this is reflected in the prevalence of this species in *V. vulpes* scats from the area. The tendency of *P. peregrinus* to forage on the ground would make them easy prey for *V. vulpes* and may be a contributing factor in the prevalence of this species in the scats. The preference for *P. peregrinus* to construct dreys close to the ground and their vulnerability to predation has been studied by Augee et al. (1996). These researchers monitored the fate of hand-reared and wild *P. peregrinus* near Sydney, and found mortality was extremely high with about 72% of possums killed by predators.

The high prevalence of *R. rattus* in the scats collected on Beecroft Peninsula also reflects the abundance of this species in the area. *R. rattus* has replaced *R. fuscipes* across the whole peninsula (Meek pers. obs.), although an unpublished study trapped *R. fuscipes* in 1988 (Braithwaite et al. 1995). It is not known why *R. fuscipes* disappeared although it has been postulated that re-colonisation of the peninsula by *R. rattus* took place after a major bushfire. The only other rat on the peninsula is *R. lutreolus* which is recorded in very low abundance and has not been trapped since 1978 (Braithwaite et al. 1995; Meek, pers. obs.).

The Long-nosed bandicoot *Perameles nasuta* was trapped at several locations on Bherwerre Peninsula during the early 1990s following the removal of foxes from certain areas (Meek and Nazer 1995; Meek pers. obs.). They were thought to have become locally extinct on Beecroft Peninsula until recently following the control of foxes on the peninsula (Dexter and Meek 1998), when they were observed at several locations (S. Hamann pers. comm.). Further surveys to confirm the re-establishment of this species are yet to be undertaken.

Scat analysis fails to adequately measure the occurrence of frogs and reptiles because the "soft" tissue is completely digested (Brunner and Wallis 1986). The only remains are usually bone fragments and unidentifiable matter which probably leads to an under-estimate of the level of predation by *V. vulpes* on these taxa. In this study the remains of *L. aurea* in one *V. vulpes* stomach of five analysed is cause for concern given the threatened status of this species (cf. Daly 1995). With frog numbers declining and many of the species threatened, *V. vulpes* predation could be a component of their demise. The question of whether *V. vulpes* is having a significant effect on frog and reptile abundance in Australia warrants further research.

Our results support comments by Coman (1973) that *V. vulpes* living in undisturbed habitat consume more native mammals than *V. vulpes* inhabiting developed or agricultural habitat. This would be the general rule since native species are more abundant. However *O. cuniculus* were the most common food item of *V. vulpes* living in Victorian forests (Brunner et al. 1975; Seebeck 1978) and National Parks (Woolley et al. 1985). *O. cuniculus* is also an important food item for *V. vulpes* in disturbed and agricultural areas of Australia (McIntosh 1963; Brunner et al. 1975; Baker and Degabriele

1987), however they are not favoured over *P. peregrinus*, *W. bicolor*, birds and insects in the Jervis Bay ecosystem. On Beecroft Peninsula *O. cuniculus* were not favoured over the more abundant *R. rattus*. The low amount of *O. cuniculus* in the diet of the fox may also be a reflection of the disjunct distribution of rabbits on both peninsulas and our failure to collect scats equally in all areas. Several of the species eaten by *V. vulpes* on Bherwerre Peninsula were not found in the diet of *V. vulpes* at Beecroft Peninsula, primarily due to a more diverse fauna on Bherwerre (Meek pers obs.).

The occurrence of *A. pusillus* in one *V. vulpes* scat collected on the beach was the result of scavenging. At night *V. vulpes* were regularly observed searching along the tide line for food and digging for Ghost crabs *Ocypode* sp. during low king tides (Meek 1998b). In one scat human hair was detected — possibly the result of an animal scavenging along a road or around a residential site where it was accidentally ingested with a food scrap.

The predominance of *W. bicolor* in the diet of *C. lupus familiaris* on both peninsulas is comparable with studies elsewhere (Triggs et al. 1984; Lunney et al. 1990). Radio-tracking data collected on the *C. lupus familiaris* of Bherwerre suggest that *W. bicolor* are favoured food and packs have been observed chasing Macropod quarry (Meek 1998b). There was a relative absence of vegetation and invertebrates in *C. lupus familiaris* scats collected on Beecroft compared to Bherwerre, which is difficult to explain. It is likely that this is due to the small number of scats collected or the influence of season on invertebrate and seed abundance.

Even though only a small number of *F. catus* scats were collected from both peninsulas it is apparent that mammals are an important food item. The consumption of medium-sized abundant mammals by *F. catus* is comparable with the data collected by Coman and Brunner (1972). The high composition of *R. rattus* in the diet of *F. catus* on Beecroft further supports the claim that they are an opportunistic predator that is influenced by prey availability (Dickman 1996). The occurrence of species with low abundance such as *S. leucopus* in *F. catus* scats is reason for some concern around the settled areas of the peninsulas.

Surveys of predator scats have provided some valuable data on the occurrence and distribution of mammals that are normally difficult to trap (Chesterfield et al. 1988; Brown and Triggs 1989; Meek and Triggs 1997). In this study one new species was found in the region (*P. gracilicaudatus*) and the existence of another (*S. leucopus*), not trapped since 1987, was re-confirmed. The analysis of scats as a survey tool in collecting baseline data on the distribution of native fauna should not be under-estimated as a management tool. It has the advantage of being relatively easy-to-collect data, comparatively cheap compared to fauna surveys and uses "predator hunting" as a survey tool. However the information gathered should only be used to determine the foods of predators. It should not be used to determine the impact upon the prey population because it: only records prey eaten (not necessarily killed); excludes cached food; and includes high frequencies of common species while rare and endangered species occur in small proportions due to their low abundance.

There are several management prescriptions that have been developed by one of these authors (P. Meek) as a result of this and other associated studies. Strategic pest management plans have been developed for both Peninsulas (Meek 1996; Dexter and Meek 1996). These plans advocate: long term fox control programs using seasonal influences on *V. vulpes* behaviour to design control strategies and maximise success; the use of a combination of control techniques; and using the "island like" nature of the Peninsulas to limit immigration. On Bherwerre Peninsula the issue of pet ownership and pet-related environmental impacts in the area (Meek 1998c) has been comprehensively addressed in a discussion paper that advocates: limits to pet numbers; ownership responsibilities; and legislation to manage pet ownership within Booderee National Park (Meek 1994).

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APPENDIX 1

List of terrestrial mammals on Bherwerre and Beecroft Peninsulas, Jervis Bay.

Species	Common Name	Abundance
NATIVE		
Monotreme		
Tachyglossus aculeatus	Echidna	High
Marsupial		
Macropus giganteus	Eastern Grey Kangaroo	High
†*Macropus rufogriseus*	Red-necked Wallaby	Medium
Wallabia bicolor	Swamp Wallaby	High
†*Petauroides volans*	Greater Glider	High
Petaurus breviceps	Sugar Glider	High
†*Acrobates pygmaeus*	Feathertail Glider	Very Low
Trichosurus vulpecula	Common Brushtail Possum	High
Pseudocheirus peregrinus	Common Ringtail Possum	High
†*Cercartetus nanus*	Eastern Pygmy Possum	Low
Perameles nasuta	Long-nosed Bandicoot	Very Low
Rattus lutreolus	Koota	Very Low
†*Rattus fuscipes*	Mootit	High
†**Pseudomys gracilicaudatus*	Karooka	Very Low
Antechinus stuartii	Brown Antechinus	High
†**Sminthopsis leucopus*	White-footed Dunnart	Very Low
†*Pteropus poliocephalus*	Grey-headed Flying Fox	High
INTRODUCED		
Vulpes vulpes	European Red Fox	Medium
Canis lupus familiaris/dingo	Dog and Dingo	Low
Felis catus	Cat	Low
Rattus rattus	Ship Rat	Medium/High
Oryctolagus cuniculus	European Rabbit	Medium
†*Lepus capensis*	Brown Hare	Very Low
Mus domesticus	House Mouse	Low

* New species recorded in this study.

† Extant only on Bherwerre Peninsula.

Abundance classifications are based on unpublished data and observations by P. Meek.

Daytime Vertical Distribution of Microzooplankton in the Hawkesbury-Nepean River

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KOBAYASHI, T., GIBBS, P. AND SHIEL, R.J. (1998). Daytime vertical distribution of microzooplankton in the Hawkesbury-Nepean River. *Proceedings of the Linnean Society of New South Wales* **120**, 129–138.

Daytime vertical distribution of 18 dominant taxa of freshwater microzooplankton was examined in mid-channel open water at North Richmond in the Hawkesbury-Nepean River, New South Wales, by measuring their densities at two depths about biweekly throughout the year. The objective was to test whether or not there was any significant depth-related distributional pattern for the dominant microzooplankton. Ten taxa were heterogeneously distributed with depth over the sampling period. Among the taxa that exhibited vertical heterogeneity, rotifers were distributed more abundantly either near the surface or in the deeper water, whereas microcrustaceans were distributed more abundantly in the deeper water. The observed vertical distributional patterns appeared to be largely independent of river flow rate. For the estimate of density of zooplankton in the water column, depth-integrated collection of quantitative samples may generally be recommended even in rivers to reduce sampling bias deriving from the likely heterogeneous distribution of river zooplankton with depth.

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KEYWORDS: regulated Australian coastal river, microzooplankton, rotifers, nauplii, *Bosmina*, density, vertical heterogeneity, river flow.

INTRODUCTION

Zooplankton may be heterogeneously distributed with depth in lakes. They may exhibit a discernible diel vertical migration (Kikuchi 1930; Zaret and Suffern 1976; Bayly 1986; Lampert 1989). In this migration, crustacean zooplankton such as large daphnids and calanoid copepods are distributed in the deeper water during the day, although there are exceptions to such a pattern (Bayly 1986).

The densities of microzooplankton may also exhibit marked vertical heterogeneity. For example, species of the rotifers *Keratella*, *Kellicottia* and *Polyarthra* are perennially surface water forms whereas species of *Synchaeta* and *Collotheca* are found mainly in the upper layer during summer but populate deeper water during autumn in a Norwegian lake (Larsson 1971). Similarly, the rotifers *Keratella cochlearis* Gosse and *Filinia brachiata* (Rousselet) mostly occupy an upper layer in a shallow English tarn during the day (Stewart and George 1988). On the other hand, the small planktonic cladoceran *Bosmina longirostris* (O.F. Müller) and nauplii are distributed near the bottom in shallow Canadian shield lakes during the day (Schindler and Novén 1971). Nauplii and copepodites of *Pseudodiaptomus* also are found near the bottom during the day in a subtropical lake in southern Africa (Hart and Allanson 1976).

In contrast to many reported patterns in the vertical distribution of lake zooplankton, little is known of the distribution in rivers. This is because in rivers, zooplankton samples are often collected at a single depth (e.g. Vásquez and Rey 1989; Thorp et al. 1994), with the assumption of uniform distribution of zooplankton with depth in rivers where the waters are presumably well mixed because of dispersion and turbulence, compared with those in lakes (Pace et al. 1992). Even when zooplankton samples are collected at different depths, the samples are combined for the depth-integrated estimate of density (e.g. Neitzel et al. 1982; Guisande and Toja 1988).

However, Brook and Rzòska (1954) report the heterogeneous distribution of dominant crustacean zooplankton species in the White Nile, by estimating the densities of these zooplankters at three depths at 15 locations. They note that the density maxima occurred at the surface for most of the zooplankton species examined, although their observation was not temporally replicated. Also, Shiel et al. (1982) dispute the assumption of uniform distribution of river zooplankton. They have described heterogeneity in both horizontal and vertical quantitative samples from the Murray River, South Australia.

Vertical distribution of zooplankton may have important ecological implications in aquatic systems, especially in relation to the spatial variability of intensity of grazing and the pattern of nutrient regeneration by zooplankton in the water column (Angeli et al. 1995 and references therein; Kobayashi et al. 1996). In the present study, daytime vertical distribution of dominant microzooplankton taxa was examined in mid-channel open water at North Richmond, by measuring their densities about biweekly at two depths throughout the year. The objectives of the present study were to determine 1) if there was any significant difference in the density of dominant river microzooplankton between depths over the sampling period and 2) if there was any significant correlation between the river flow rate and vertical distributional pattern of the dominant river microzooplankton.

MATERIALS AND METHODS

Study Site

The study site (approximately 33°40′S, 150°40′E) is located at North Richmond, about 140 km upstream of the mouth of the Hawkesbury-Nepean River, New South Wales (length of main river channel: approximately 300 km; total catchment area: 22,000 km^2) (see Fig. 1 in Kobayashi et al. 1996). Five dams and more than 13 weirs on the main river channel regulate the river flow. The study site is in the upper tidal freshwater portion of the river, about 6 m deep and 120 m wide. Data on flow rate (l s^{-1}) over Penrith weir (the closest non-tidal gauging station to North Richmond) were provided by AWT Hydrographic Services. River flow rate varied in the range 377–14,142 l s^{-1} during the study period of May 1992 to April 1993 (see Fig. 2 in Kobayashi et al. 1996).

Zooplankton Collection, Sampling and Counting

From May 1992 to April 1993, four replicate samples of zooplankton were collected about biweekly at each depth of 1 m and 4 m in mid-channel open water, with the aid of a 4.2–l Haney-type trap (Gawler and Chappuis 1987). Sampling was conducted between 1000 and 1400 h and took ~30 min to collect and filter a total of eight zooplankton samples on each sampling date. Zooplankton specimens were filtered in the field through a 35 µm mesh netting (Likens and Gilbert 1970) and preserved with a 4% buffered sugar-formaldehyde solution (Haney and Hall 1973). Further details are described in Kobayashi et al. (1996).

A 1ml width-mouth automatic pipette and a Sedgwick-Rafter counting chamber were used for subsampling and counting of zooplankton. Zooplankton was identified and counted under an inverted microscope at magnifications of x25 to x100. Preliminary counting of 5 replicate samples established that the coefficient of variation was reduced to ~0.1 when the mean number of the specimens counted exceeded 80. Therefore, the subsampling and counting were repeated until a minimum of 80 specimens of the most abundant taxon were counted. Counts included all zooplankters except protists for which testate amoebae and ciliates were counted. Zooplankton was identified by reference to the relevant taxonomic literature (primarily Koste 1978; Smirnov and Timms 1983; Koste and Shiel 1987; Bayly 1992).

In the present study, dominant zooplankton taxa were arbitrarily defined as those present in more than 50% of the total samples (total n=23), with an added mean density at depths of 1 m and 4 m exceeding 20 animals l^{-1} in at least one sample.

TABLE 1

Comparison of overall mean density of dominant zooplankton taxa between 1 m and 4 m depths at North Richmond. Overall mean density: arithmetic mean values and mean log values in parentheses are shown. Logarithmic transformation was $\log_{10}$ (animals+0.1). Log-transformed values were used for overall density comparison. Type of test performed: T, two-sample *t* test (two tailed) if there was no significant correlation in mean densities between the two depths; PT, paired-sample *t* test (two tailed) if there was a significant correlation in mean densities between the two depths. n is the sample size and p is the significance level.

Taxon	n	Overall mean density (animals l^{-1})		p	Test
		1 m	4 m		
a) Mean density at 1 m > mean density at 4 m					
Polyarthra spp. (chiefly *P. dolichoptera* Idenlson)	23	635.5(2.005)	139.1(1.528)	0.0047	PT
Proalides tentaculatus De Beauchamp	15	35.3(0.716)	15.1(0.328)	0.0101	PT
Synchaeta spp. (chiefly *S. pectinata* Ehrenberg)	23	113.4(1.725)	86.3(1.408)	0.0319	PT
Trichocerca spp.	23	29.4(1.137)	12.1(0.662)	0.0121	T
b) Mean density at 1 m is not significantly different from mean density at 4 m					
Ciliates	23	45.5(1.312)	29.4(1.143)	0.0636	PT
Asplanchna spp. (chiefly *A. priodonta* Gosse)	21	33.8(0.384)	5.7(0.163)	0.2385	PT
Brachionus angularis Gosse	17	76.7(1.261)	59.1(1.115)	0.3990	PT
Brachionus calyciflorus Pallas (long-spined form)	13	7.3(0.246)	10.3(0.323)	0.6579	PT
Conochilus dossuarius Hudson	23	64.6(0.879)	75.6(1.082)	0.1170	PT
Filinia spp. (chiefly *F. longiseta* Ehrenberg)	22	21.7(0.113)	5.4(–0.016)	0.3868	PT
Keratella cochlearis (Gosse)	23	37.5(0.593)	23.6(0.858)	0.1615	PT
Keratella tropica (Apstein)	14	4.6(–0.207)	12.5(0.463)	0.0607	T
c) Mean density at 1 m < mean density at 4 m					
Brachionus calyciflorus (short-spined form)	12	1.0(-0.665)	6.7(0.016)	0.0117	T
Bosmina meridionalis Sars	14	0.3(-0.882)	3.4(–0.169)	0.0018	T
Hexarthra spp. (chiefly *H. intermedia* Wiszniewski)	17	76.2(0.589)	88.4(1.158)	0.0487	PT
Keratella procurva (Thorpe)	18	3.2(–0.450)	7.3(0.084)	0.0035	PT
Nauplii	23	37.9(0.877)	81.7(1.267)	0.0056	PT
Copepodites	21	4.6(–0.388)	21.1(0.574)	0.0011	T

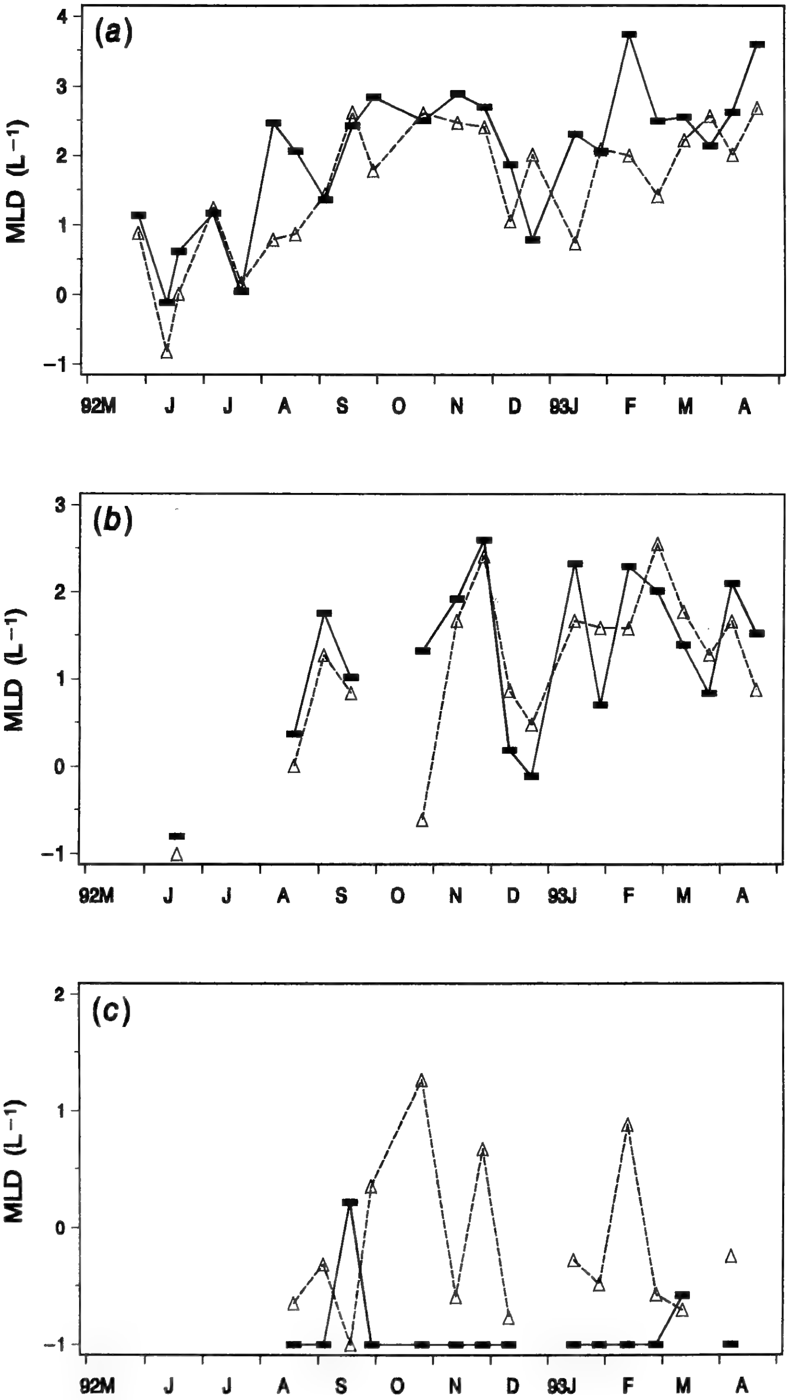


Figure 1. Examples of seasonal pattern in vertical distribution of zooplankton at North Richmond. Mean log density (MLD: $\log_{10}$ (animals+0.1) l^{-1}) is shown on each sampling date (n=3–4 on each sampling date). ■ MLD at 1m; △ MLD at 4 m. (a) *Polyarthra* spp.; (b) *Brachionus angularis*; (c) *Bosmina meridionalis*.

Statistical Analyses

Prior to analysis, density data were transformed by $\log_{10}(x+0.1)$ to stabilise the variance. The constant of 0.1 added corresponds to the lowest density value possible in the sampling and counting procedures used in the present study. The addition of the constant was necessary because some of the density values were zero. The mean log-densities of zooplankton were then calculated for each taxon at depths of 1 m and 4 m, respectively, on each sampling date. For the zooplankton taxa for which the pairwise mean log-densities were seasonally and significantly correlated between depths (Pearson product-moment correlation, $\alpha=0.05$), paired-sample *t* test (two-tailed) was applied to test the null hypothesis that the mean density difference equaled zero between the two depths over the sampling period ($\alpha=0.05$). For the zooplankton taxa for which there was no significant correlation between the pairwise mean log-densities at depths of 1 m and 4 m over the sampling period, two-sample *t* test (two-tailed) was used to test the null hypothesis. The paired-sample *t* test is more powerful than the two-sample *t* test, if there is pairwise correlation of data from the two samples. If no such correlation exists, then two-sample *t* test is the more powerful procedure (cf. Zar 1984:152).

In addition, relative density at 1 m depth (RD_{1m}, %) was estimated for each taxon on each sampling date when animal density at 1 m or 4 m >0:

RD_{1m}=(density at 1 m)/[(density at 1m)+(density at 4 m)] x 100

Spearman's rank correlation analysis was used to test if there was any significant correlation between river flow rate and the RD_{1m} for each microzooplankton taxon.

All analyses were performed using the SAS (Anon. 1989) computer programs.

RESULTS

Overall Difference in Density Between the Two Depths

A total of 18 dominant microzooplankton taxa were examined (Table 1). Seven taxa (*Polyarthra* spp., *Synchaeta* spp., *Trichocerca* spp., nauplii, ciliates, *C. dossuarius* and *K. cochlearis*) occurred throughout the study, whereas the remaining taxa were seasonal. The mean densities of microzooplankton temporarily fluctuated at both depths, but tended to correlate between the two depths (Fig. 1). A maximum mean density of 5,748 animals l^{-1} (mean $\log_{10}(x+0.1)$-density: 3.735) was recorded for *Polyarthra* spp. (chiefly *P. dolichoptera*) at a depth of 1m on 12 February 1993.

Over the sampling period, the null hypothesis was rejected for ten taxa, indicating that there was a significant difference in their overall mean densities between the two depths (Table 1). Of these, the overall mean densities of *Polyarthra* spp., *P. tentaculatus*, *Synchaeta* spp. and *Trichocerca* spp. were significantly greater at 1 m depth than at 4 m depth (Fig. 2a). On the other hand, the overall mean densities of *B. calyciflorus* (short-spined form), *K. procurva*, *Hexarthra* spp., *B. meridionalis*, nauplii and copepodites were greater at 4 m depth than at 1 m depth at North Richmond (Fig. 2c). The null hypothesis was not rejected for the remaining eight microzooplankton taxa examined, indicating that there was no significant difference in their overall mean densities between the two depths over the sampling period (Fig. 2b). Note that this does not necessarily imply that their mean densities were the same at the two depths on each sampling date.

Spearman's Rank Correlation of RD1m With River Flow Rate

On a taxon-specific basis, there was a significant negative correlation between river flow rate and RD_{1m} for the rotifers *Asplanchna* spp. and *B. angularis* (Fig. 3). An overall plot of the RD_{1m} for the examined microzooplankton against river flow at North Richmond showed no significant correlation between them (Fig. 4).

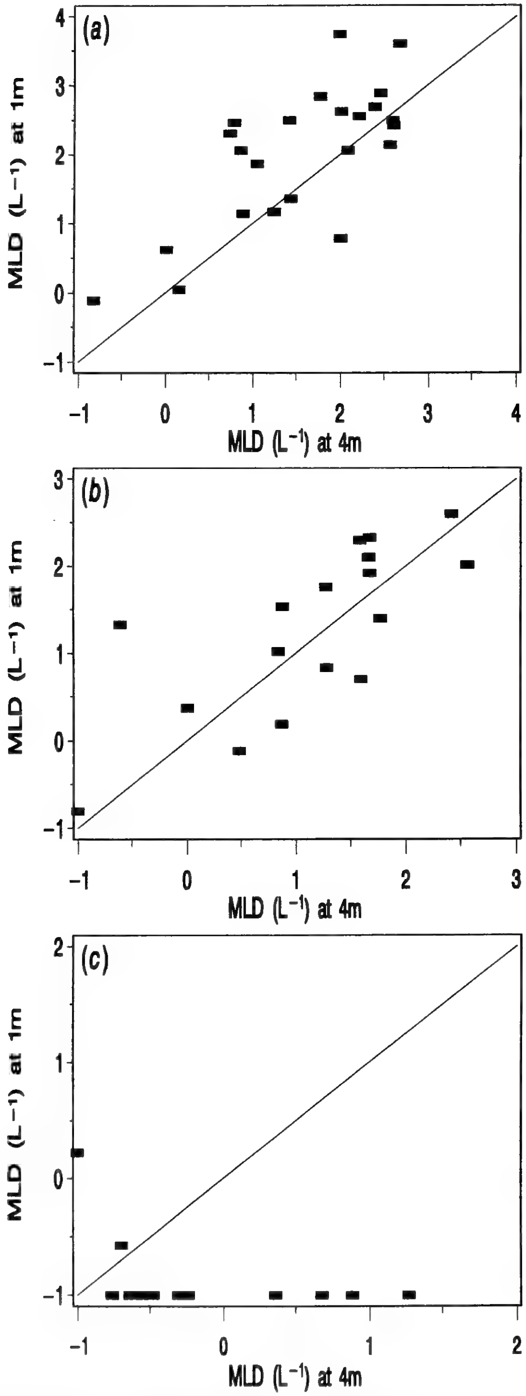
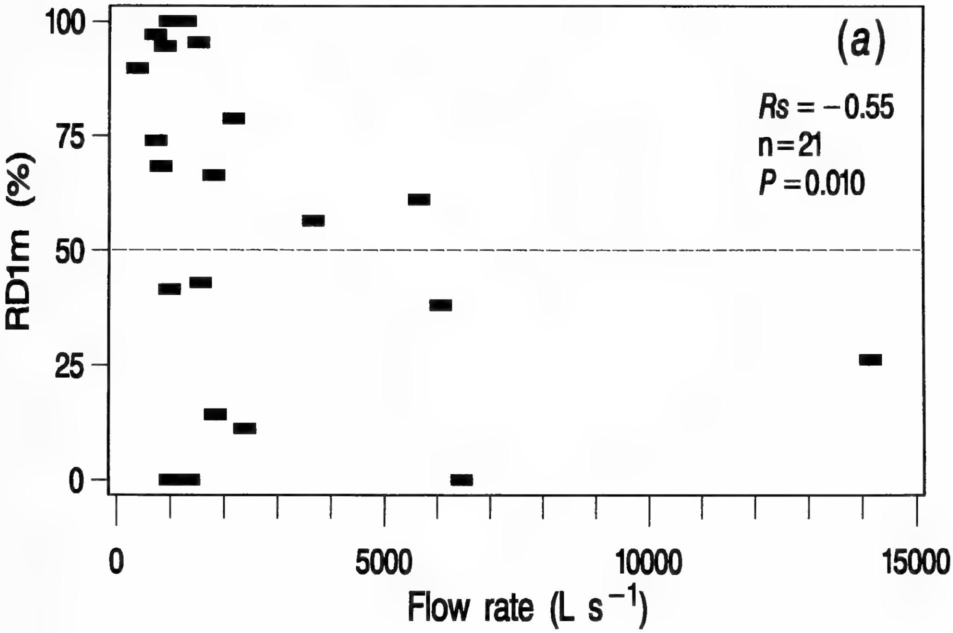


Figure 2. Examples of overall pattern in vertical distribution of zooplankton at North Richmond. Mean log density (MLD: $\log_{10}$ (animals+0.1) l^{-1}) at 1 m is plotted against MLD at 4 m. (a) *Polyarthra* spp. (overall MLD at 1 m > overall MLD at 4 m); (b) *Brachionus angularis* (overall MLD at 1 m is not significantly different from overall MLD at 4 m); (c) *Bosmina meridionalis* (overall MLD at 1 m < overall MLD at 4 m).



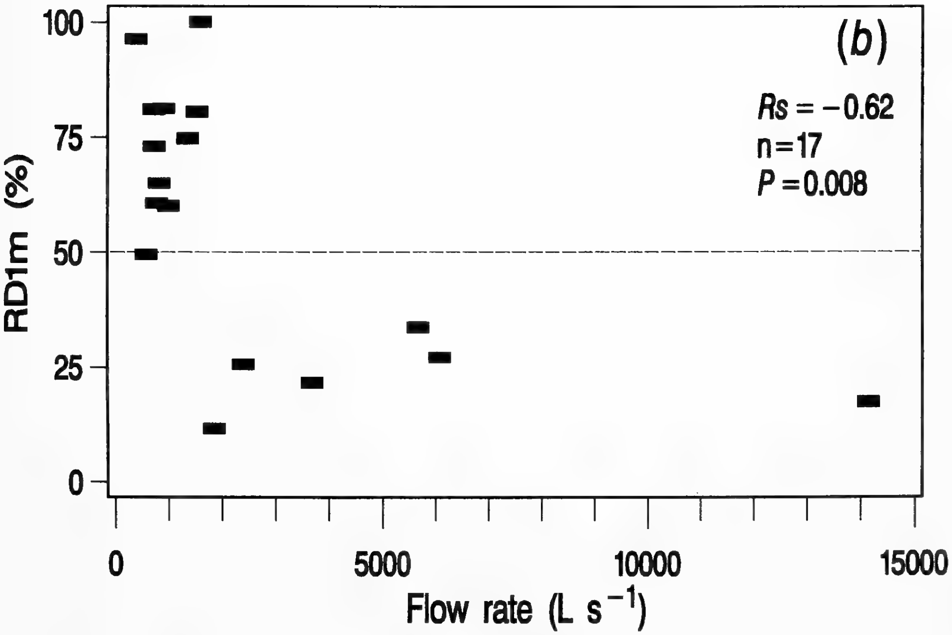


Figure 3. Significant correlation of relative densities at a depth of 1 m (RD_{1m}, %) with river flow rate at North Richmond (flow rate was measured at the gauging station over Penrith weir: see Fig. 1 in Kobayashi et al. 1996 for location of the gauging station): (a) *Asplanchna* spp., (b) *Brachionus angularis*. R_S, Spearman's rank correlation coefficient; n, sample size and p, significance level.

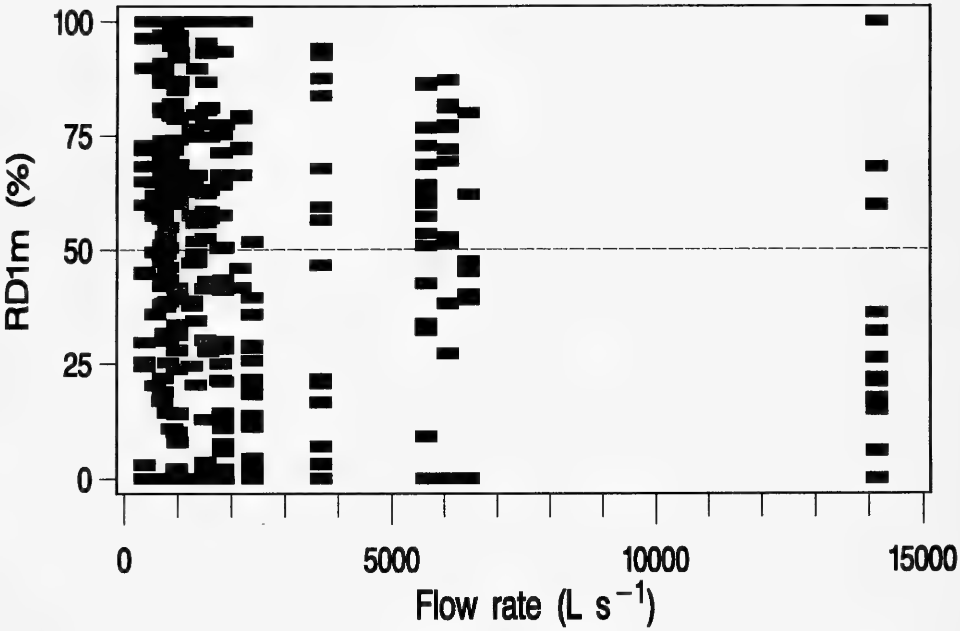


Figure 4. Overall relationship between river flow rate and relative densities at a depth of 1 m (RD_{1m}) for microzooplankton at North Richmond.

DISCUSSION

The dominant microzooplankton taxa were not necessarily uniformly distributed with depth at the studied site of North Richmond. Rotifers showed species-specific patterns in the vertical distribution, with some taxa being distributed more abundantly near the surface and the others in the deeper water. The microcrustaceans were distributed more abundantly in the deeper water. For some taxa, especially ciliates, the pooling of density may have masked possible species-specific patterns in the vertical distribution in the present study.

It is difficult to speculate whether or not the observed overall heterogeneous distribution of some of the microzooplankton taxa with depth is common in freshwater rivers because there seem to be no comparative data available from similar freshwater systems in the literature. Compared to lake microzooplankton, the surface water occurrence of *Polyarthra* spp. and the deeper water occurrence of *B. meridionalis* and juvenile copepods at North Richmond are consistent with the patterns reported for the congeneric taxa in some of the Northern and Southern Hemisphere lakes (Larsson 1971; Schindler and Novén 1971; Dumont 1972; Hart and Allanson 1976). However, the absence of consistent vertical distributional patterns for *Asplanchna* spp., *K. cochlearis* and *Filinia* spp. at North Richmond differs from the surface water occurrence of these taxa reported elsewhere (Dumont 1972; Stewart and George 1988).

The studies of the vertical distribution of microzooplankton in lakes indicate that the vertical heterogeneity of microzooplankton is often observed but the patterns of such a distribution can exhibit taxonomic variation and also temporal and spatial variation for the same taxa (Kikuchi 1930; George and Fernando 1970; Stewart and George 1988). The variability in the vertical distribution of microzooplankton may also be expected for rivers. Further inter-river comparison is necessary to verify this assertion. Nevertheless, in addition to reported horizontal (longitudinal) heterogeneity (e.g. Basu and Pick 1997; Pourriot et al. 1997), the vertical heterogeneity of river zooplankton suggests that even in rivers, depth-integrated collection of quantitative samples may generally be recommended to estimate the density of zooplankton in the water column (Brook and Rzòska 1954).

In running waters, the degree of turbulence usually increases as the mean velocity of the flow increases so one would expect greater mixing at greater flow rates. This suggests that, as a general trend, the RD_{1m} for river mirozooplankton may converge to 50% with increasing flow rate, if the vertical positions of the microzooplankton are passively determined by the degree of mixing proportional to river flow rate. An overall scatter plot of the RD_{1m} for the examined microzooplankton against river flow at North Richmond shows that this was not the case within the observed flow range in this study. On a taxon-specific basis, the RD_{1m} of two rotifer taxa were negatively correlated with river flow. These results indicate that the relative vertical distribution of dominant microzooplankton at North Richmond may largely be independent of river flow rate.

In the present study, the diel variation in the vertical distribution of microzooplankton was not investigated. For rivers, Shiel et al. (1982) conducted a 24–h study of changes in species composition and density of mid-channel winter plankton, by collecting hourly samples at a freshwater site at a depth of 3 m in the Murray River in South Australia. For the zooplankton, they noted little change in species composition overall, but a distinct change in density. They recorded a minimum of less than 20 animals l^{-1} around midnight and a maximum of 993 animals l^{-1} at dusk. Although in their diel study, the plankton samples were collected at a single depth, such temporal variation in density may partly reflect diel vertical movement of river microzooplankton. Further study is warranted to examine whether the observed patterns in the daytime vertical distribution of the dominant microzooplankton differ at night in the Hawkesbury-Nepean River.

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Altitude Separation and Pollution Tolerance in the Freshwater Crayfish *Euastacus spinifer* and *E. australasiensis* (Decapoda: Parastacidae) in Coastal Flowing Streams of the Blue Mountains, New South Wales

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The distribution of two freshwater crayfish species *Euastacus spinifer* (Decapoda: Parastacidae) and *E. australasiensis* were studied in the streams of the Blue Mountains, near Sydney. Forty sampling sites were established over a range of altitudes and upstream and downstream of sewage treatment plants. Sewage effluent was discharged directly from the treatment plants into the stream channels during the course of the study. Crayfish were sampled with electrofishing and a range of environmental variables estimated at each site. Crayfish were found at 60% of the sites sampled; *E. australasiensis* occurred at 7 sites (18%) and *E. spinifer* was found at 17 sites (42%). There were no sites in which both crayfish species occurred together. Both species occurred in small headwater streams, but *E. australasiensis* appeared to be limited to streams at altitudes above 810 m and *E. spinifer* to streams below this altitude. The actual mechanism for this altitudinal separation of the two species did not appear to be related to any particular substratum type, stream size, habitat type or cover. The highest crayfish density of either of the two *Euastacus* species recorded at any study site occurred at a site receiving treated sewage effluent. Crayfish occurred across the complete range of water quality measured at sites. The relative impact of other environmental disturbance (such as the introduction of exotic species and habitat destruction) on the conservation of crayfish populations is discussed.

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KEYWORDS: Freshwater crayfish, *Euastacus, spinifer*, *australasiensis*, pollution tolerance, altitude, Blue Mountains.

INTRODUCTION

There are 41 described species of the crayfish genus *Euastacus* (family Parastacidae) distributed throughout eastern Australia, 24 which occur in New South Wales. The biology and ecology of the majority of these species is poorly understood, with the possible exception of *E. spinifer*, which occurs near Sydney (Turvey and Merrick 1997a, b, c, d, e). The majority of *Euastacus* species have very localised distributions but a few species, such as the inland Murray River crayfish *E. armatus*, have very extensive distributions (Merrick 1993; Morgan 1997). However, even the distribution and abundance of species with extensive ranges can be reduced, probably through impacts such as habitat destruction, overfishing and pollution (Horwitz 1990).

Although the ranges of many crayfish species are restricted, they often overlap, but the co-occurrence of two species at exactly the same locality is uncommon (Morgan 1997). In general, there appears to be a narrow zone where both lowland and highland species coexist within any water course. In addition, because of the predominance of restricted ranges of *Euastacus*, it is difficult to find areas where two or more species occur over the same geological range. There have been several studies that have documented longitudinal separation within other genera of the Parastacidae. Richardson and Horwitz (1988) cite several examples of the local separation of burrowing crayfish in the genera *Engaeus* and *Parastacoides* and suggest that local topography is an important factor in separating species. There are fewer studies that show natural separation between stream dwelling crayfish in Australia. Horwitz (1994) noted that *Astacopsis franklinii* has been found in the middle and upper reaches of river systems in Tasmania which contain *A. gouldi* and suggests that some form of competitive displacement is the cause of the separation of these two species. However, Growns (1995) found no altitude separation between *A. tricornis* and *A. gouldi* in the streams of the Gog Range in Tasmania.

Two species of *Euastacus* co-occur within and around the Sydney region, *E. australasiensis* and *E. spinifer*. The distribution of *E. australasiensis* is much more restricted than that of *E. spinifer* but their ranges overlap in an area extending from near Wollongong, inland to the Blue Mountains and north to Gosford. The altitudinal range of both species is similar, from sea level to the higher parts of the Blue Mountains. Morgan (1997) suggested that the genus *Euastacus* could be divided into two main groups of species. *E. spinifer* is within the first group, which comprises species that occur at rather low altitudes and are medium to large in size. In contrast, *E. australasiensis* is part of the second group, which comprises small to medium-sized animals that generally occur at higher altitudes.

A large area of the natural range of *E. spinifer* around Sydney is now subject to urban development. Although the species also occurs in several National Parks located around Sydney these areas are known to have been modified to varying degrees and many waterways outside National Park boundaries are severely degraded (Merrick 1997). Merrick (1997) also suggested that the major threats to *Euastacus* populations were habitat destruction, fishing pressure, fires, chemical pollution, and introduced species. However, there is little information about the pollution tolerances of many crayfish species, and such information is needed for adequate management of crayfish populations.

The Blue Mountains area near Sydney is largely composed of National Parks, but urban development has increased rapidly over the last thirty years. The increasing human population in the Blue Mountains area has led to increases of urban rainfall runoff and treated sewage effluent discharge into stream headwaters. Because many sewage treatment plants (STPs) provide only secondary treatment for effluent the streams that receive these wastes have shown a deterioration in water quality (MWSDB 1987; Curry 1992; Wright 1992). These changes to water quality have caused impacts on the benthic macroinvertebrate communities (Wright 1992; Hardwick et al. 1994). In 1980, the Sydney Water Corporation (formerly the Sydney Water Board) assumed responsibility for both sewerage and water supply to the Blue Mountains area from the Blue Mountains City Council. The STPs that were a part of that sewerage system were in need of upgrading and amplification (MWSDB 1987). The Corporation began implementing an effluent management strategy for the Blue Mountains area, which included a program to remove STP effluents from the streams by diverting sewage from the small local STPs to a larger plant in the lower Blue Mountains (Currey 1993).

We sampled crayfish at sites in the Blue Mountains as a part of a three-year study commissioned to investigate the environmental effects of the Sydney Water Corporation's activities on the fish, fish habitats and fisheries of the Hawkesbury-Nepean River system (Pollard and Growns 1993; Gehrke and Harris 1996). Here we document the distribution of the two *Euastacus* species that occur in the Blue Mountains and indicate the pollution tolerances of each.

MATERIALS AND METHODS

The Blue Mountains study area is a dissected sandstone plateau lying approximately 50 km to the west of Sydney. The study area is drained by the Grose River to the north, the Coxs River to the south and west and tributaries of the Nepean River to the east. The Coxs River forms an important inflow to Lake Burragorang, the main potable water supply for Sydney (MWSDB 1987).

Most of the area lies in National Park and a strip of urban development lies along the ridge line between the Coxs and Grose River catchments. At the time of sampling there were ten STPs servicing the population of the area, some of which were overloaded and aging, with consequent impacts on water quality of streams receiving effluent (Currey 1993). Since this study, several of these sewage plants have been decommissioned.

A total of 40 sites were sampled for this study. Sites were chosen in areas upstream and immediately downstream of STPs (<1 km), far below STPs (approximately 5 km) and unimpacted reference streams. The majority of these sites have been sampled previously for their water quality characteristics (Currey 1992, 1993).

Crayfish were sampled in November 1993 using backpack electrofishing with two people. The first person operated the electrofisher, which stunned the crayfish, and these were collected by either the electrofisher operator or the second person with a dipnet. Twenty minutes of electrofishing was carried out at each site, moving upstream to cover a distance of approximately 100 m. The abundance of crayfish at each site was scored as 0 (no crayfish present), 1 (1 or 2 crayfish), 2 (3 to 10 crayfish), 3 (11 to 20 crayfish), 4 (21 to 50 crayfish) and 5 (greater than 50 crayfish).

At each site a variety of environmental variables were also recorded. These included a subjective estimate of the abundance (scale of 0 = absent to 4 = abundant) of substratum types (bedrock, boulder, cobble, gravel, sand, mud/silt, and clay), crayfish cover (rock, timber, undercuts and plant litter) and habitat types (pool and riffle). A visual estimate of average stream width and depth were also recorded for each site. The altitude of each site was obtained from 1:25000 topographical maps of the study area.

Water quality variables that were available for each site were calculated from the routine water quality monitoring data collected from the three months prior to sampling. The median values for turbidity, pH, temperature, conductivity, suspended solids, dissolved oxygen, total phosphorus, faecal coliforms, ammonium ions, total nitrogen, and the concentrations of iron and zinc were used as being indicative of the water quality of these sites that would have been affecting the populations of crayfish sampled. Sampling of the Cedar Creek site did not occur as a part of any monitoring program and as such the median values for water quality for this site were calculated from records of individual samples taken haphazardly over the past decade at this site. Water quality data were provided by Sydney Water.

RESULTS

Crayfish were found at 60% of the sites sampled (Table 1); *E. australasiensis* occurred at 7 sites (18%) and *E. spinifer* was found at 17 sites (42%). There were no sites in which both crayfish species occurred together. No crayfish were found at the remaining 16 sites (40%).

Crayfish had very low abundances below 280 m altitude. *E. spinifer* was found at sites between 145 m and 805 m and *E. australasiensis* occurred at all sites sampled between 810 m and 965 m (Table 1). Both crayfish were caught across a range of stream sizes (width and depths) and substratum types. However, both species occurred less often on sand or silt substrates (Table 2). *E. spinifer* occurred more often at sites with rock and litter cover than at other sites. Both species occurred at sites with a range of pool and riffle habitats.

TABLE 1

Subjective abundances of *E. australasiensis* and *E. spinifer* at sites (in order of altitude) sampled in the Blue Mountains. Sites are indicated as either reference (R) or located upstream (U), immediately downstream (I) or far downstream (F) of sewage treatment plants. Scores for crayfish abundance range from as 0 (no crayfish present), 1 (1 or 2 crayfish), 2 (3 to 10 crayfish), 3 (11 to 20 crayfish), 4 (21 to 50 crayfish) and 5 (greater than 50 crayfish). nd = not determined.

Site number	Site name	Type	Euastacus australasiensis	Euastacus spinifer	Altitude (m)	Width (m)	Depth (m)
1	Lynches Crk	R	0	0	15	2	0.5
2	Winmalee Crk	F	0	0	20	5	0.6
3	Fitzgerald Crk	F	0	1	145	20	0.2
4	Lennox Crk d/s STP	I	0	0	170	1.5	0.4
5	Glenbrook Crk	R	0	0	170	10	0.5
6	Valley Heights Crk d/s STP	I	0	0	175	1	0.2
7	Valley Heights Crk	U	0	0	180	1.2	0.5
8	Fitzgerald Crk d/s STP	I	0	1	180	1.5	0.2
9	Lennox Crk u/s STP	U	0	0	190	1	0.3
10	Winmalee Crk d/s STP	I	0	0	220	10	0.5
11	Springwood Crk	R	0	1	260	8	0.3
12	Leura Falls Crk d/s STP	I	0	0	280	2	0.5
13	Linden Crk	R	0	2	290	10	1.0
14	Grose River	R	0	0	315	8	1.0
15	Govetts Crk	F	0	0	315	7	1.0
16	Wentworth Crk	F	0	2	370	12	1.0
17	Cedar Crk	R	0	2	375	2	0.3
18	Grose River	R	0	0	380	8	1.5
19	Urella Brook	R	0	3	390	1.5	0.5
20	Dawes Crk	R	0	2	430	5	0.8
21	Hathill Crk	F	0	2	435	2	0.7
22	Victoria Crk	R	0	2	435	10	0.3
23	Crayfish Crk	R	0	2	445	2.5	0.6
24	Bedford Pools	R	0	3	480	10	1.0
25	Grose River	R	0	0	485	15	0.5
26	Lawson Crk	R	0	2	500	2	0.5
27	Hazelbrook Crk d/s STP	I	0	0	540	1.5	0.2
28	Megalong Crk	R	0	0	605	2	0.4
29	Back Crk	R	0	0	630	1.2	0.8
30	Podgers Glen Crk	R	0	2	660	1.5	0.3
31	Blue Mountain Crk d/s STP	I	0	2	690	1.5	0.3
32	Blue Mountain Crk	U	0	4	730	1	0.2
33	Jamison Crk	R	0	3	805	nd	nd
34	Katoomba Crk	F	2	0	810	2	0.5
35	Yosemite Crk	R	3	0	850	2	0.5
36	Leura Falls Crk	U	2	0	895	1.5	0.3
37	Katoomba Crk d/s STP	I	1	0	940	1.5	0.3
38	Hathill Crk d/s STP	I	5	0	940	1.5	0.3
39	Katoomba Crk	U	3	0	960	2	0.2
40	Hathill Crk	U	4	0	965	1	0.2

TABLE 2

Substratum, cover and habitat characteristics at sites where *E. australasiensis* (n=7) and *E. spinifer* (n=17) were recorded. Scores range from 0 = absent to 3 = abundant

Variable	*E. australasiensis*		*E. spinifer*	
	Mean	Range	Mean	Range
Substratum				
Bedrock	2.3	(0–3)	1.5	(0–3)
Boulder	0.7	(0–3)	2.1	(0–3)
Cobble	0.3	(0–2)	1.2	(0–3)
Gravel	0.4	(0–3)	1.0	(0–3)
Sand	1.6	(0–3)	2.2	(0–3)
Silt	0.1	(0–1)	0.6	(0–2)
Cover				
Rock	2.4	(0–3)	2.6	(0–3)
Timber	2.1	(1–3)	1.7	(0–3)
Undercuts	0.3	(0–1)	0.2	(0–2)
Litter	1.4	(0–3)	2.1	(1–3)
Habitat				
Pool	2.1	(1–3)	2.7	(2–3)
Riffle	1.9	(0–3)	1.9	(0–3)

TABLE 3

Water quality characteristics at sites where *E. australasiensis* (n=7) and *E. spinifer* (n=17) were recorded.

Water quality variable	*E. australasiensis*		*E. spinifer*	
	Median	Range	Median	Range
Turbidity (NTU)	3.4	(2.6–4.4)	3.3	(0.5–10.4)
Conductivity (mS/m)	7.9	(5–13.1)	12.5	(3.2–44.5)
pH	6.9	(6.5–7.3)	6.6	(5.4–7.7)
Dissolved oxygen (mg/L)	9.0	(8.6–9.6)	9.2	(8.2–10.4)
Suspended solids (mg/L)	2.6	(1.5–3.7)	2.5	(0.5–11.2)
Total phosphorus (mg/L)	0.3	(0.1–1.1)	0.5	(0 – 6.0)
Nitrates (mg/L)	2.4	(0.7–6.0)	2.0	(0–17.3)
Ammonia (mg/L)	0.1	(0.1–0.3)	0.0	(0.0–0.3)
Faecal coliforms (CFU/100 ml)	276.0	(10–1060)	66.3	(1–291)
Faecal streptococci (CFU/100 ml)	25.5	(5–73)	175.8	(1–1367)
Iron (mg/L)	0.3	(0.2–0.4)	0.2	(0.0–0.6)
Zinc (mg/L)	0.1	(0.1–0.2)	0.1	(0.0–0.2)

Crayfish occurred at 4 of the 10 sites where STP sewage effluent was discharged (Table 1). The highest crayfish density of either of the two *Euastacus* species recorded at any study site occurred immediately below the Blackheath STP on Hathill Creek. Crayfish occurred across the complete range of nutrient and faecal streptococcus levels measured at all sites. However, crayfish were absent from sites having a zinc concentration above 0.2 mg/L, turbidity greater than 11 NTU, conductivity greater than 43 mS/m, suspended solids greater than 15 mg/L, ammonia greater than 0.43 mg/L, faecal coliforms greater than 1060 CFU/100 ml and iron greater than 0.58 mg/ (Table 3). In addition, crayfish were absent from sites with recorded oxygen levels less than 8 mg/L.

DISCUSSION

We have shown that the distributions of the two species of freshwater crayfish, *E. spinifer* and *E. australasiensis*, that have similar geographical ranges are separated according to altitude in the Blue Mountain streams. The actual mechanism for the altitudinal separation does not appear to be related to any particular substratum type, stream size, habitat type or cover. Both species occur in small headwater streams, but *E. australasiensis* appears to be limited to streams at altitudes above 810 m and *E. spinifer* to streams below this altitude. However, *E . spinifer* also occurred in small to large streams. In other parts of their geographic ranges both species occur at sites just above sea level, and therefore probably occur in a wide range of habitat types, and from small to large rivers. Our findings are supported by those of Horwitz (1994) who indicated that two species of *Astacopsis* occur at lower altitudes when they do not occur within the same river as *A. gouldi*. Horwitz suggested that the mechanism for the observed altitudinal separation is due to competitive displacement between species. Confirmation of this mechanism for effective separation of species within the same stream would require experimental manipulation of populations in the field.

Both *E. spinifer* and *E. australasiensis* occurred at sites that received treated sewage effluent. However, crayfish were absent from some sites that had higher concentrations of potentially toxic substances such as ammonia and heavy metals and lower concentrations of dissolved oxygen caused by the discharges of treated sewage effluent. However, we did not find crayfish at all unpolluted sites, which indicates that *E. spinifer* and *E. australasiensis* may have been absent from these sites, which had poor water quality, for other reasons. We have only used water quality data that were collected over three months before the sampling date. The absence of crayfish at some sewage treatment plants may have been related to water released from STPs at other earlier times or accumulated toxins in the sediments.

Merrick (1995) considered that the major threats to *Euastacus* populations were habitat destruction, fishing, fire, chemical pollution and introduced species. The *Euastacus* populations in the Blue Mountains are mainly located in National Parks, and are therefore unlikely to be affected by habitat destruction. However, as the human population increases in the Blue Mountains and nearby urban areas, the threats of fire and fishing are also likely to increase. Also, introduced aquatic species such as trout are present in some streams in the Blue Mountains. There may be direct impacts of trout on *Euastacus* populations, but the threat is increased because another introduced (inland) species of crayfish, *Cherax destructor*, is commonly used as bait for trout fishing. It is likely that the introduction of both trout and *Cherax* species could contribute to the decline of *Euastacus* species. We did not locate any *C. destructor* in the Blue Mountains in this study but the species does occur in other parts of the Lake Burragorang catchment (NSW Fisheries, unpublished data). Although the current populations of *Euastacus* in the Blue Mountains appear to be viable, there is the potential for a wide variety of impacts to cause a decline in their numbers. Effective management options such as those suggested by Horwitz (1990) and Merrick (1995, 1997) are therefore required to ensure the future viability of *Euastacus* in the streams of the Blue Mountains.

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Aspects of the Reproductive Biology of Murray Cod, *Maccullochella peelii peelii*

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ROWLAND, S.J. (1998). Aspects of the reproductive biology of Murray cod, *Maccullochella peelii peelii*. *Proceedings of the Linnean Society of New South Wales* **120**, 147–162.

Aspects of reproduction in Murray cod, *Maccullochella peelii peelii*, in NSW tributaries of the Murray-Darling river system were studied. Murray cod has a distinct seasonal cycle; monthly gonadosomatic indices (GSI) and mean oocyte diameters were low between December and March, increased rapidly from June, presumably due to vitellogenesis, and were highest in October. Oocytes underwent group-synchronous development, but only one batch of yolky oocytes was spawned during the 4–5 week breeding season. Absolute fecundity ranged from 6,800 (total length, TL 480mm, weight 2.1kg) to 86,600 (1050mm, 22.7kg) eggs, and relative fecundity ranged from 3.2 to 7.6 eggs/g. Spawning was induced by a rise in water temperature to or above 20°C in spring. The presence of many consecutive year classes suggests that Murray cod spawn annually; however, between 1977 and 1980 relatively strong year classes were formed only in rivers that were at, or near flood levels during the breeding season.

No females and a few males had matured by 3 years of age. At 4 years of age, 77% of females (> 480mm, 2.1kg) and 72% of males (> 530mm, 2.3kg) were mature. All females and most males were mature at 5 years. In rivers, all cod larger than 590mm and 3.9kg were mature, but the smallest sexually-mature cod sampled from the impoundment, Lake Mulwala, was 610mm and 5.0kg. Management restrictions on the recreational and commercial fisheries for Murray cod, based on the results of this and previous studies are outlined.

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KEYWORDS: Australian inland fisheries, breeding season, fecundity, *Maccullochella*, maturation age, Murray cod, reproductive cycle.

INTRODUCTION

Despite the importance of the Murray cod, *Maccullochella peelii peelii* (Mitchell) in the inland fisheries of south-eastern Australia, and the decline in abundance and reduction in distribution since the 1950's (Rowland 1989), no quantitative study of the reproductive biology of the species in the Murray-Darling river system has been published. Gooley et al. (1995) studied the reproductive cycle and gonadal development of Murray cod in Lake Charlegrark and adjacent farm dams in western Victoria; however, this is an introduced, self-maintaining population and aspects of its biology differ from natural populations (Anderson et al. 1992; Gooley 1992).

Studies of Murray cod held in earthen ponds have provided some information on the reproductive biology of the species. Cod spawn adhesive eggs onto firm substrates such as hollow logs, pipes and clay banks in spring and early summer (Lake 1967a; Rowland 1983; Cadwallader and Gooley 1985). Lake (1967a) found that a slight 'runoff' of water into a pond induced cod to spawn, but later studies by Rowland (1983) and Cadwallader and Gooley (1985) demonstrated that spawning was not dependent on a rise in water level in ponds. Emryology and larval development in Murray cod were described by Dakin and Kesteven (1938) and Lake (1967b), and there is paternal protection of eggs during incubation (Rowland 1983). The diet and factors affecting the survival of Murray cod larvae in earthen ponds were determined by Rowland (1992). Artificial breeding techniques, including the hormone induction of ovulation and spawning have been developed (Cadwallader and Gooley 1985; Rowland 1988).

Rowland (1985) conducted research into aspects of the biology of Murray cod to provide a basis for management of the species in NSW. The reproduction component of that study is reported in this paper. Objectives were to describe the reproductive cycle and fecundity of Murray cod from tributaries of the Murray-Darling river system, and to determine the effects of water temperature and water levels on spawning, the timing and length of the breeding season, and the age and size at maturity of males and females from different populations.

MATERIALS AND METHODS

Murray cod were sampled (1978–1984) from five sites in the Murray-Darling river system (see Fig. 1 in Rowland 1998), with the exception of the Darling River, using techniques described by Rowland (1985). Some fish were sampled from the catches of professional and recreational fishers. Cod were sampled irregularly from the Murray and Murrumbidgee rivers and the impoundment, Lake Mulwala in southern NSW, and Gwydir River in the northern part of the Murray-Darling river system (Fig 1 in Rowland 1998) to determine age and size at maturity, and fecundity. In addition, data were collected from Murray cod sampled monthly from the Edward and Wakool rivers over an 11-month period between May 1983 and March 1984 to describe the gonadal cycle and to determine the breeding season. During September, October and November sampling was confined to a 10km section of the Wakool River to more closely evaluate the effects of water temperature and changes in water level on brood-fish and the breeding season.

Gonadal cycle and fecundity

Each fish was measured (TL to the nearest mm) and weighed (to nearest 10g). The gonads were removed, assigned to a stage of the Gonadal Maturity Scale (Table 1) and placed in Bodians fixative. In the laboratory, all fatty tissue and excess fluid were removed from each gonad before weighing to the nearest 0.1g. The gonadosomatic index (GSI) was calculated as the percentage of gonad weight of the total body weight; the mean monthly GSI for each sex was determined.

The tunica was removed from both ovaries of each female and all oocytes larger than approximately 0.2mm diameter were separated manually from the ovarian tissue. This was aided by vigorous shaking in Bodians fixative. No attempt was made to free the oogonia, perinuclear and other early stage oocytes. A random subsample of 100 oocytes was removed after inverting the container several times to ensure even distribution of oocytes. The diameter of each oocyte in the subsample was measured using an eye-piece micrometer. The oocytes were assigned to three size-classes based on diameter; 0.2–1.0mm; 1.1–2.0mm; >2.0mm. The total number of oocytes in each size-class in 5 adult females was expressed as a percentage frequency for each month, and a mean monthly diameter of the largest size-class was also determined.

Ovaries of mature (stage IV, Table 1) females captured in September and October were used to estimate fecundity. The ovaries were prepared as described above. All freed oocytes, and then three 3g subsamples from each female were weighed; oocytes greater than 2mm diameter in each subsample were counted. The mean number of presumably yolky oocytes (> 2mm) in the three subsamples was determined and used to estimate the fecundity of each female by direct proportion.

TABLE 1

Gonad maturity scale describing the appearance of the gonads, abdomen and vent of Murray cod.

Stage	Female	Male
I immature A	Ovaries thin, slightly rounded; pale pink, translucent; (1 and 2 year old).	Testes thin, strap-like; pale, translucent.
B	Ovaries rounded, cylindrical; pale pink, translucent; up to 80mm long, 10mm wide; sometimes white oocytes (to 1mm) visible in clear fluid; (3 and some 4 year old).	Testes thickening; opaque.
II developing virgin or recovering spent	Ovaries rounded; pale pink; oocytes (to 1mm) visible to naked eye, throughout most of ovary.	Testes flattened; pale creamy/pink.
III developing	Ovaries enlarging, rounded; occupy to ¼ body cavity; oocytes 1–2mm. Abdomen slightly rounded; vent pale pink.	Testes enlarging; creamy/pink.
IV mature	Ovaries occupy to ½ body cavity; pale/amber oocytes 2–3mm; also small (1mm) white oocytes visible. Abdomen distended; vent swollen, pink/red.	Testes enlarged, rounded on edges; white/creamy; small blood vessels on surface. Abdomen not distended; vent pale.
V running-ripe	Translucent oocytes (3mm) run freely from oviduct with pressure; ovaries pinkish/pale red, occupy > ½ body cavity. Abdomen very distended; vent swollen, red/purple.	Testes full, rounded; white; milt with firm abdominal pressure. Abdomen not distended; vent pale/pinkish, slightly swollen.
VI spent A	Partially; ovaries rounded; occupy ½ cavity, but smaller than IV and V; many large (3mm) translucent oocytes; some parts of ovaries clear; some small (1mm) white oocytes visible.	
B	Completely; ovaries rounded; occupy < ¼ cavity; red/dark pink; wall loose in recently spent females; few oocytes visible. Abdomen not distended, flabby.	Small amount or no milt on pressure; testes relatively small; creamy/pale pink; mottled appearance; walls loose; many distinct small blood vessels on surface.
VII resorbed	Ovaries < ½ cavity; walls loose; large blood vessels on surface; misshapen oocytes (2–3mm); clear and reddish patches throughout ovaries.	

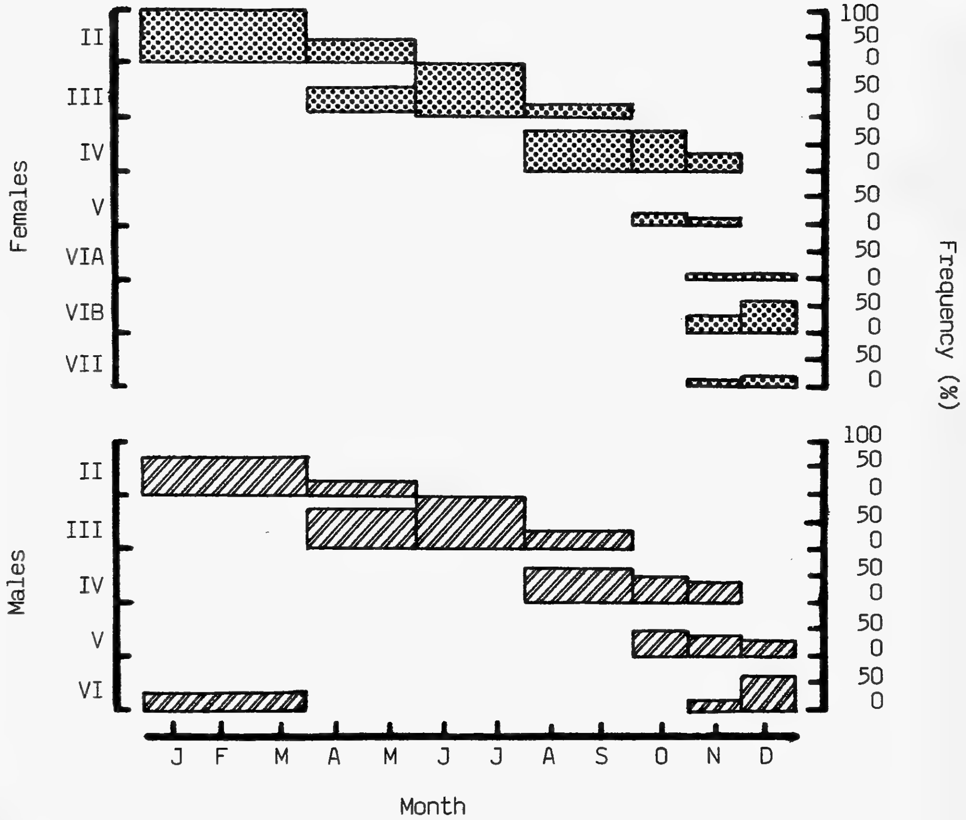

Figure 1. Seasonal changes in the relative frequency of gonadal maturity stages in Murray cod (of both sexes) from the Edward and Wakool rivers. The stages (I–VII) are described in Table 1.

Breeding season

To obtain data on the behaviour of broodfish, the duration of the breeding season and the factors inducing spawning in the wild, Murray cod were sampled using 20 gill nets (mesh sizes 10.2 - 25.4cm) and 5 drum nets (mesh size 12.7cm) from a 10 km section of the Wakool River between September and December. Water temperatures were recorded using a maximum-minimum thermometer placed permanently at a depth of 1.5m; changes in water level were recorded.

Age and size at maturity

Murray cod sampled from the Edward, Wakool, Murray and Gwydir rivers between September and December 1983, were used to determine the age and size at sexual maturity. Cod with gonads at stages IV to VII (Table 1) during this period were presumed to be mature. Otoliths and opercular bones were used to age the cod (Rowland 1985, 1998). After ageing, all fish were assigned to a year-class and the percentage frequency of year-classes from 1977 to 1980 was determined. To reduce the bias of mesh selectivity against smaller cod from the 1980 year-class, only cod captured between September and March were included in this analysis.

RESULTS

Gonadal cycle

There was a linear relationship between GSI and the percentage frequency of oocytes larger than 2mm diameter ($Y = 0.56X - 14$; $r^2 = 0.92$), indicating that GSI accurately reflects the gonadal state in Murray cod.

Most cod sampled between April and September contained gonads at stages III (developing) or IV (mature) (Fig. 1). The rapid increase in the proportion of oocytes greater than 2mm diameter, between June and October (Fig. 2) is presumably due to vitellogenesis. Mean oocyte diameters, the proportion of large, yolky oocytes, and GSI values were highest in October (Figs 2 and 3). "Running-ripe" (stage V) females and males were captured in October and November. Spent and partially spent cod were captured in November. The ovaries of fully spent females (stage VI B) contained very few residual, yolky eggs, and although an estimated 30 - 50% of oocytes remained in ovaries of partially spent females (stage VI A), most were large (3mm), spherical, translucent and ovulated, suggesting that the females were captured during spawning. By December, all females were spent or contained ovaries in which resorption had commenced. Between January and March all cod had spent or recovering gonads (stage II) and low GSI values.

Fecundity

The number of large (>2mm), yolky oocytes per female ranged from 6,800 (480mm, 2.1kg) to 86,600 (1050mm, 22.7kg). Absolute fecundity generally increased with increasing length and weight of females; however, there were large variations in the fecundity of similar-sized females (Fig. 4).

The relationship between fecundity and length is linear and represented by the equation:

$$Y = 115.17X - 48.9 \quad (r^2 = 0.90)$$

where Y = fecundity ($\times 10^3$) and X = length in mm.

The relationship between fecundity and weight is quadratic and is represented by the equation:

$$Y = -389 + 5344X - 69.5X^2 \quad (r^2 = 0.93)$$

where Y = fecundity and X = weight in kg.

The relative fecundity ranged from 3.2 to 7.6 eggs/g. The mean relative fecundity of different size-classes are shown in Fig. 5. Although only four fish were used to estimate fecundity of females over 11kg, the data suggest that relative fecundity decreases with increasing size and age in Murray cod.

Breeding season

During the period 24 September to 18 October 1983, water temperatures in the Wakool River ranged from 16 to 19°C, and pairs of mature cod (stages III or IV) consisting mainly of similar-sized males and females, were often captured in one drum net or within several meshes of each other in gill nets. The daily maximum water temperatures and the details of the reproductive condition of Murray cod captured from the Wakool River between 18 October and 5 November are shown in Fig. 6. Within 10 days of the water temperature reaching 20°C, two spent females, one "running-ripe" female, two "running-ripe" males and four mature (stage IV) females were captured. Although spent females were captured in late October and early November the first spent male was not captured until 24

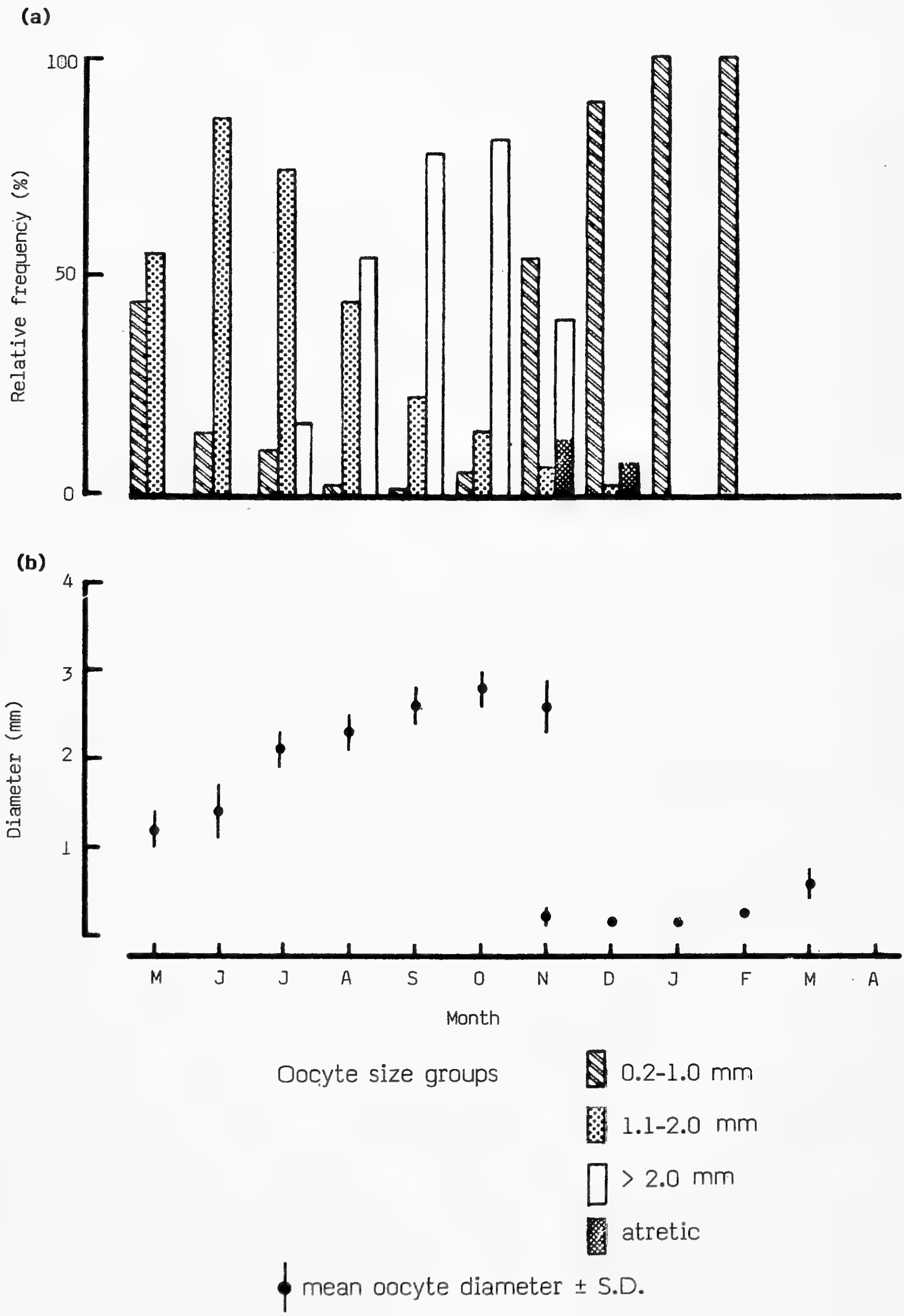

Figure 2. The occurrence of oocyte size groups during the period May 1983–March 1984, in Murray cod females from the Edward and Wakool rivers: (a) relative frequency; (b) mean monthly diameter.

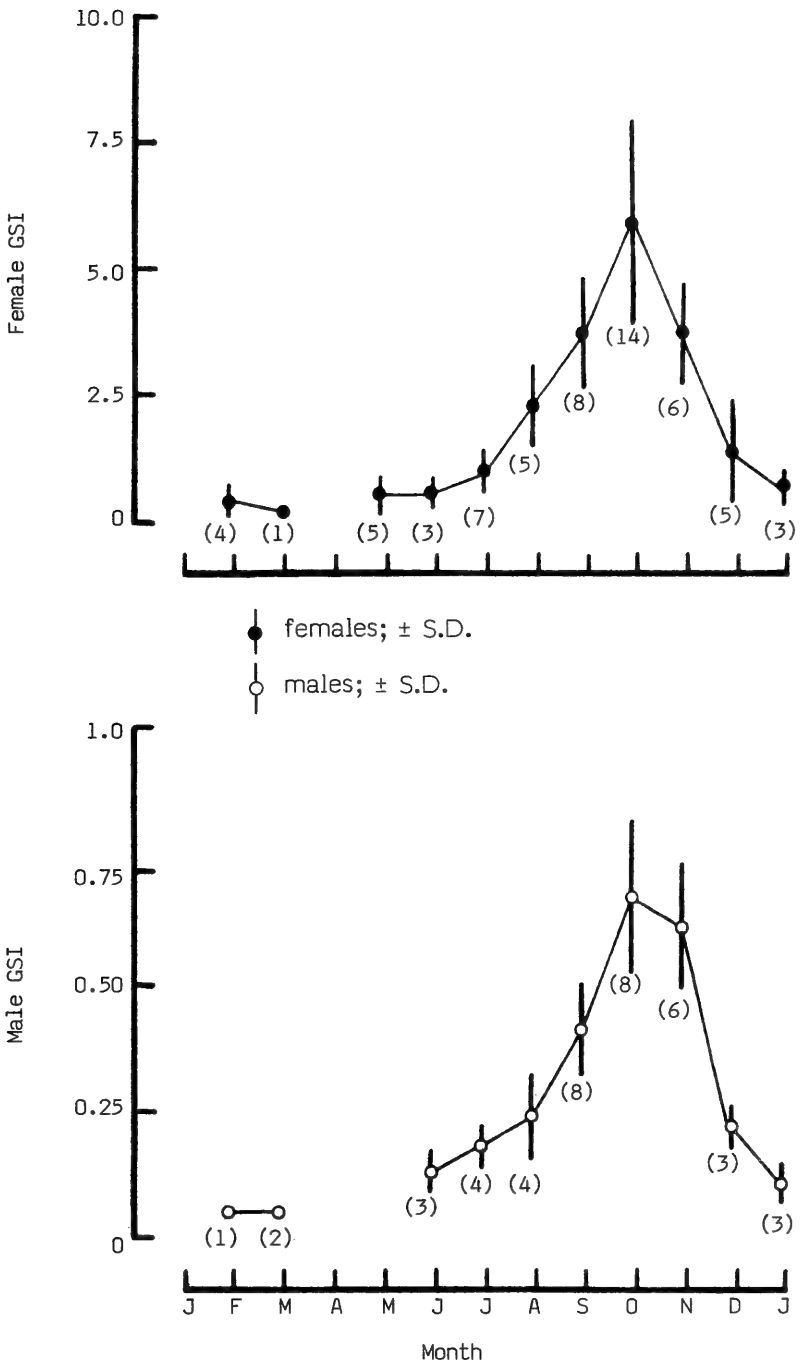

Figure 3. Mean monthly gonadosomatic indices (GSI) for the period May 1983–March 1984 in Murray cod from the Edward and Wakool rivers: (a) females; (b) males. Sample sizes in parentheses.

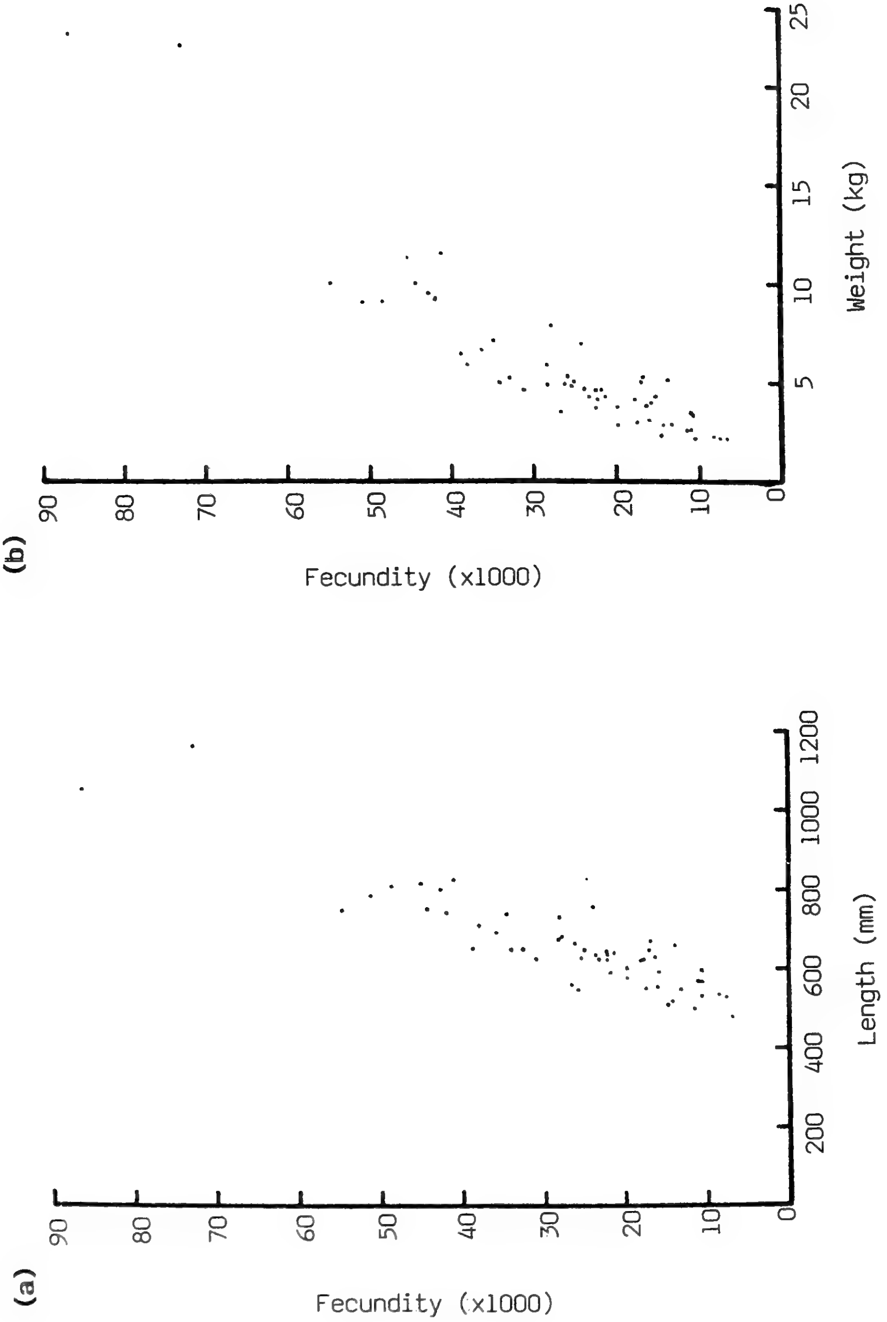

Figure 4. Relationship between fecundity and size of Murray cod females from the Murray, Edward, Wakool and Gwydir rivers: (a) related to length; (b) related to weight.

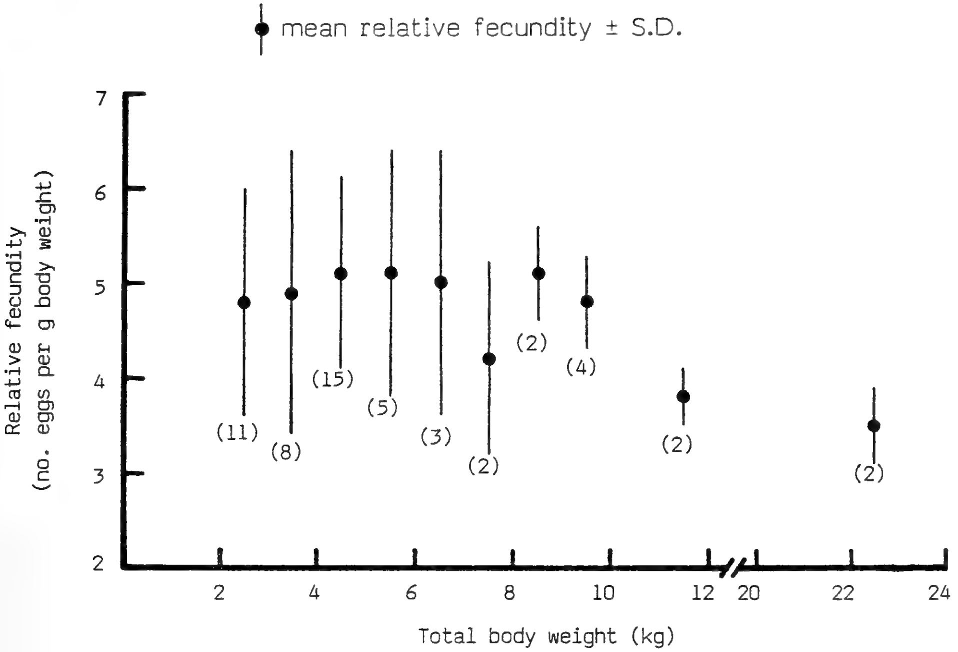

Figure 5. Relative fecundities in different size-classes of Murray cod females. Sample sizes in parentheses.

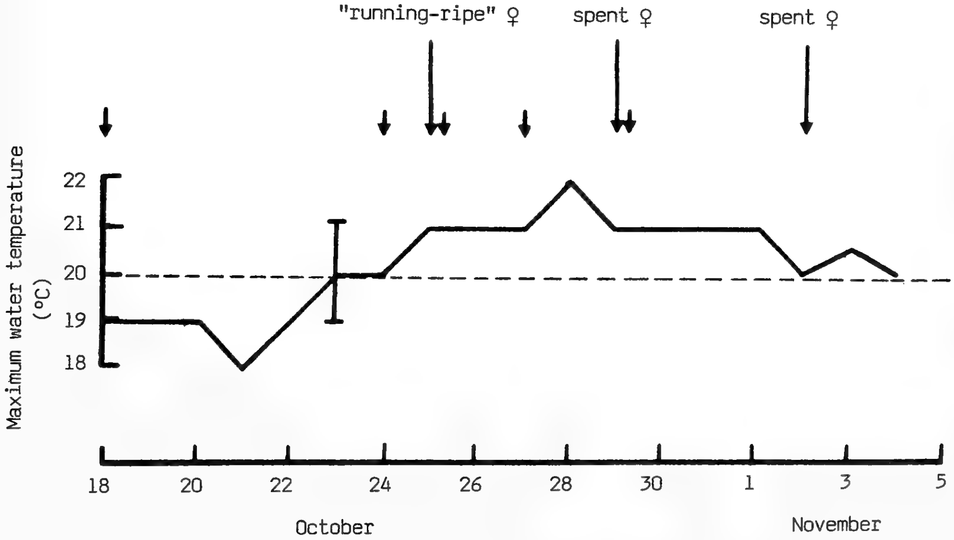

Figure 6. Water temperature and details of gonadal condition of Murray cod females captured from the Wakool River between 18 October and 5 November.

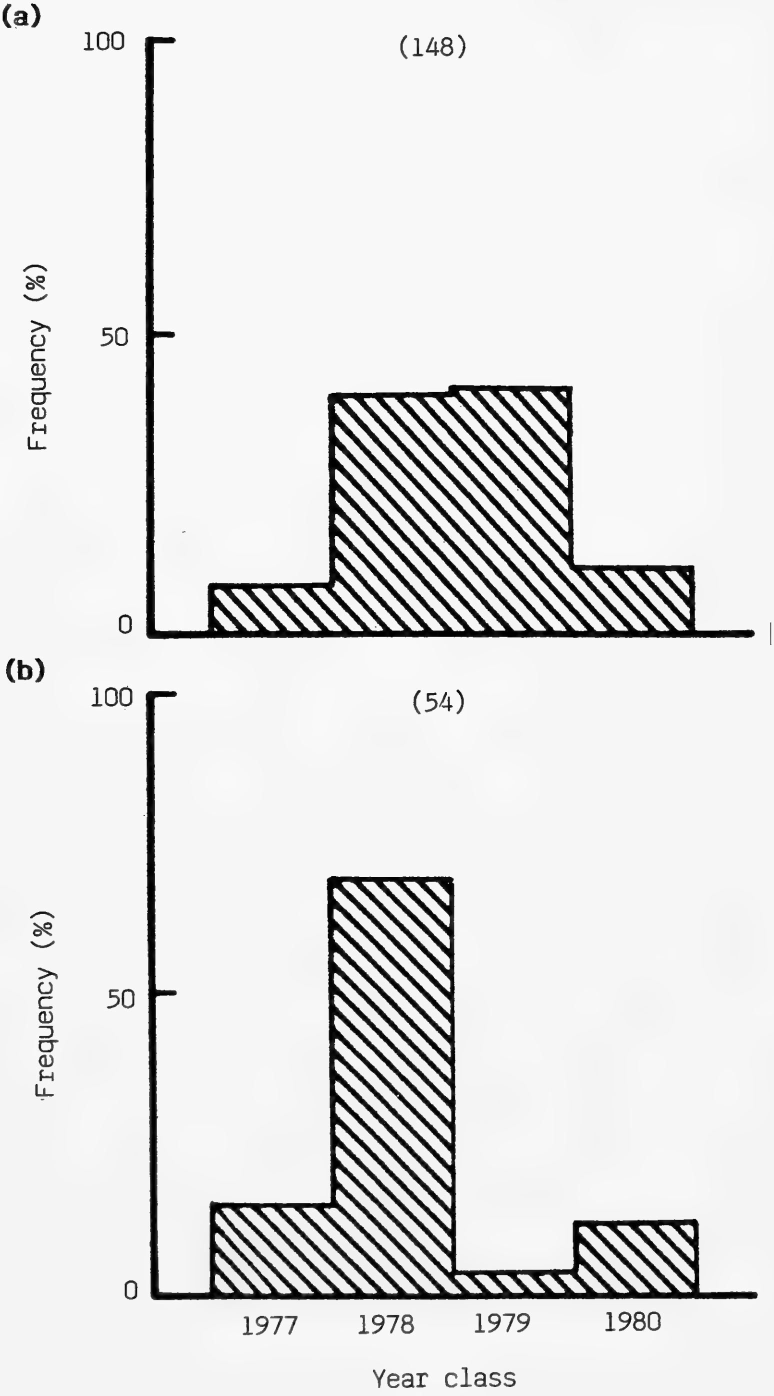

Figure 7. Recorded frequencies for four year-classes (1977–1980) of Murray cod: (a) from the Murray, Edward and Wakool rivers; (b) from the Murrumbidgee River. Sample sizes in paretheses.

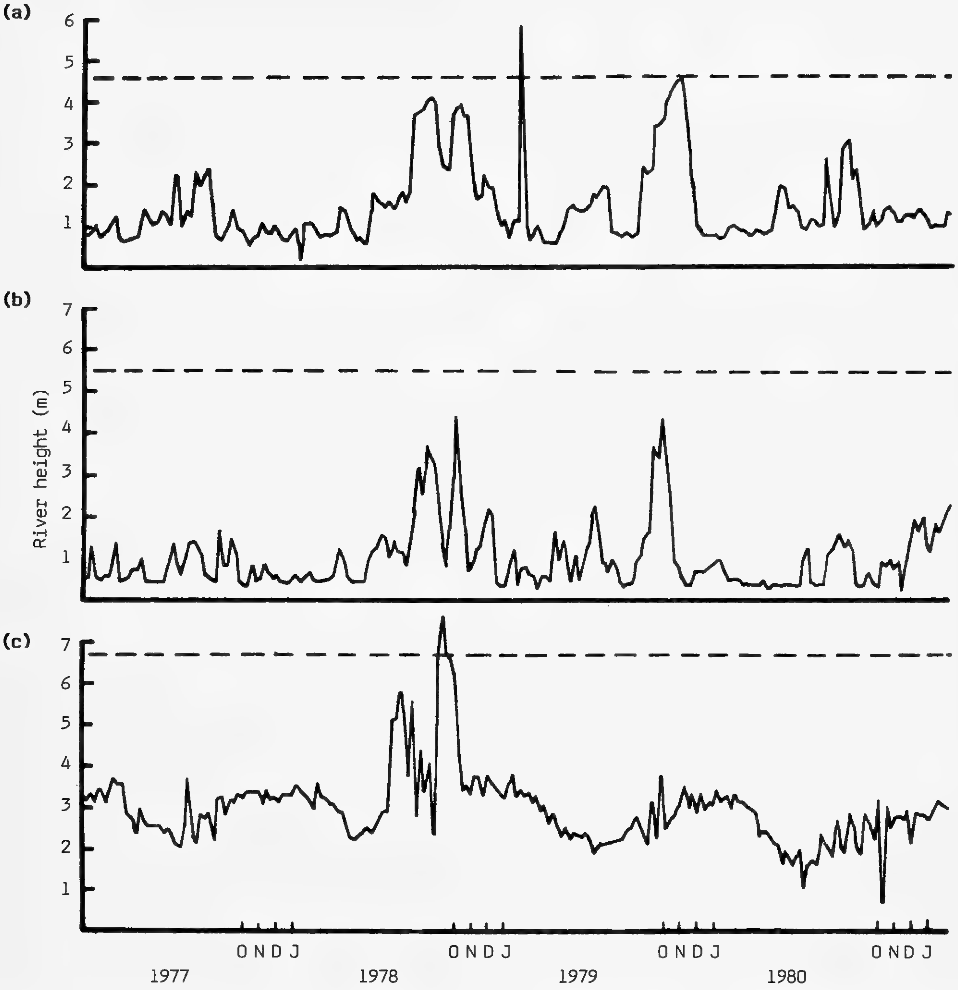

Figure 8. River heights related to flood levels (– – –) for the period January 1977 to January 1981: (a) in the Murray River (at the junction with the Wakool River); (b) in the Edward River (downstream of Stevens Weir); and (c) in the Murrumbidgee River (at Narrandera).

November. The data suggest that the actual spawning season lasted 4 to 5 weeks. Between 24 September and 24 November the water level decreased gradually by 60cm.

Mature and spent females, and "running-ripe" males were sampled from the Gwydir River between 1 and 5 October when water temperatures were 20 to 22°C. The water level in the river had been constant for approximately two weeks (Phil Forster, Bingara, personal communication).

Year-class frequencies

Murray cod representing each year-class between 1970 and 1980 were sampled from the Murray, Edward and Wakool rivers, and cod from 16 of the 17 year-classes between 1964 and 1980 were sampled from the Murrumbidgee River. The Murray cod (n = 25)

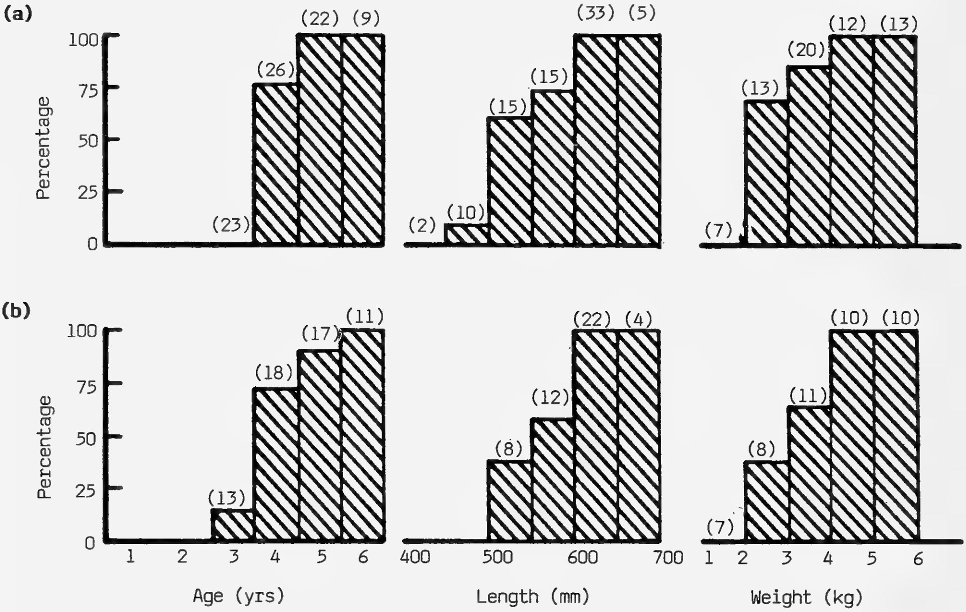

Figure 9. Percentage of mature Murray cod in each age, length and weight class: (a) females; (b) males. Sample sizes in parentheses.

sampled from the Gwydir River in October represented five year classes; 1976, 1978, 1979, 1980 and 1981. The presence of many consecutive year-classes in each river suggests that cod have spawned annually in these rivers.

The percentage frequencies of the 1977 to 1980 year-classes in the Murray, Edward, Wakool and Murrumbidgee rivers shows the 1978 year-class was strong in each river (Fig. 7). In 1978, all rivers were at or near flood level during October and November (Fig. 8). Consequently the breeding season probably coincided with flood conditions and the strong 1978 year-class is evidence for high survival of larvae under these conditions. This is supported by the presence of a relatively strong 1979 year-class in the Murray, Edward and Wakool rivers, but a poor year-class in the Murrumbidgee River (Fig. 7). In October and November 1979, the former three rivers were near flood level but the Murrumbidgee River did not rise above 3.8m at Narrandera (Fig.8). In 1977 and 1980, all rivers remained at low levels during spring and summer, and these year-classes were poorly represented in these southern tributaries.

Age and size at maturity

The percentages of mature Murray cod in each age and size-class are shown in Fig. 9. All 1 to 3 year old females were immature. One and 2 year old cod contained thin, rounded, translucent ovaries (stage IA) while those of 3 year old females were cylindrical and sometimes contained oocytes (to 1mm diameter) that were visible to the naked eye in clear ovarian fluid (stage IB) (see Table 1). Seventy seven percent of 4 year old females were mature. Immature cod of this age had ovaries with numerous, white oocytes less than 2mm in diameter (stage IB). All 5 and 6 year old females were mature. The smallest mature female sampled in this study was 480mm and 2.1kg; all females 590mm and 3.9kg or larger were mature.

All 1 and 2 year old males were immature. Fifteen percent of 3 year old cod were "running-ripe" in October and were presumed to be mature. However, the viability of the sperm from these fish was not determined and it is possible that it was non-viable and/or that these males were precocious. The smallest of these cod was 530mm and 2.3kg. Seventy two percent of 4 year old, most 5 year old and all 6 year old males were mature. All males of 585mm and 3.4kg and larger were mature.

Seven of the nine 4 year old females (77%) sampled from Lake Mulwala were mature and the smallest of these was 610mm and 5.0kg. The 2 immature females were 630mm and 5.8kg, and 640mm and 5.5kg. No 5 year old females were sampled from the lake, but all 6 and 7 year old females (n=7) were mature. Eighty percent of 4 year old males were mature; the smallest was 625mm and 5.4kg. No older males and no 3 year old cod were sampled from Lake Mulwala.

DISCUSSION

Reproductive cycle and the breeding season

The Murray cod, like many other temperate fishes, has a distinct annual reproductive cycle. Increasing GSI and mean oocyte diameters from June onwards suggest that gonadal recrudesence is initiated by increasing temperature and/or photoperiod as in many other teleosts (see Lam 1983). Murray cod exhibits group-synchronous oocyte development (de Vlaming 1983), with two or three distinct batches of oocytes distinguishable in the ovary in most months (Fig. 2a). The batch of smallest oocytes (< 1.0mm) would consist of oogonia, perinuclear and other primary oocytes for the following breeding seasons. Although two batches of larger oocytes (1.0–2.0mm; >2.0mm) are present in the prespawning ovary, previous studies by Rowland (1983, 1988) suggest that only one batch completes vitellogenesis to become the numerous, large (3.0mm), yolky oocytes that are spawned and fertilised. The fate of the intermediate batch, which presumably have not completed vitellogenesis, is not known; they may be spawned days or weeks later, or resorbed along with other ovarian material during post-spawning gonadal regression as has been reported in other species (Foucher and Beamish 1980; Mayer et al. 1990).

The reproductive cycle of Murray cod culminates in a relatively short, well-defined breeding season. Spawning is temperature-dependent and so the actual season is expected to vary latitudinally. In the current study, spawning in the southern Wakool River commenced after water temperatures rose above 20°C in late October, whereas in the northern Gwydir River spent females were caught in early October when temperatures were between 20 and 22°C. Rowland (1983) found that in four consecutive breeding seasons at the Inland Fisheries Research Station, Narrandera, most Murray cod spawned in earthen ponds when the temperature rose to or above 20°C, and cod held in ponds at hatcheries in northern NSW spawn regularly each year when water temperatures reach 20°C in late September and early October (Ray Mepham, Elsmore and Phil Forster, Bingara, personal communication). In ponds at Lake Charlegrark, near the southern limit of its natural range, most spawnings occurred during November at temperatures between 16.5 and 23.5°C (Cadwallader and Gooley 1985; Gooley et al. 1995). Conspecific populations of fishes are known to exhibit local differences in their reproductive life histories (Leggett and Carascadden 1978; Bye 1984; Mann et al. 1984) and the cooler temperature regime at this southern locality may cause the different response to the rising temperatures during spring. Other factors such as the role of photoperiod, the demography of cod in ponds and varying methods of actually measuring water temperature may also account for the variation in spawning temperatures reported.

Individual females probably spawn all or most of the largest batch of oocytes in one short period. Ovulated oocytes in the small number of "running-ripe" and partially spent females that were caught during this study (Fig. 1) were large and translucent, indicating that spawning was either occurring or imminent. Rowland (1983) found that only one of 36 females was "running-ripe" when removed from eight ponds over four consecutive breeding seasons. These observations suggest that there is only a relatively short period between ovulation and spawning.

The relatively high catch rate of cod, including pairs, in September was probably a result of increased activity of broodfish associated with spawning site selection and mating. The difficulty in catching spent males in late October and November suggests that they are not involved in normal foraging behaviour and could be protecting the eggs and possibly larvae at the spawning sites.

All Murray cod sampled in December were either spent or contained ovaries with a large number of atretic oocytes, indicating that the spawning season was complete and that in some years at least, not all females spawn. As in some other species (Lam 1983) relatively high water temperatures and long photoperiod may induce normal gonadal regression in Murray cod. The data suggest that the spawning season lasted 4 to 5 weeks.

After Lake (1967a) reported that a slight "runoff" of water into a pond was necessary to induce Murray cod to spawn, subsequent literature (e.g. Roughley 1968; Llewellyn and MacDonald 1980; Pollard et al. 1980) stated that a rising river level or flood is required for Murray cod to spawn. Further research has shown that rising water levels are not required to induce spawning in ponds (Rowland 1983; Cadwallader and Gooley 1985) or in the wild (current study). The presence of many consecutive year classes in each of the Murray, Murrumbidgee, Edward, Wakool and Gwydir rivers suggest that Murray cod spawn annually in the wild irrespective of changes in water level. However, strong year-classes are only established when the breeding season coincides with high river levels or floods (Figs 7 and 8). These data support the hypothesis that the reduced frequency, extent and duration of flooding in the Murray-Darling river system caused by the construction of dams, high level weirs and levee banks has adversely affected larval recruitment, resulting in the dramatic decline of Murray cod since the 1950's (Rowland 1983, 1985, 1989, 1992).

Fecundity

The relative fecundity of Murray cod (3.2–7.6 eggs/g) is similar to the congeneric trout cod, *M. macquariensis*, (0.6–5.9 eggs/g) (Ingram and Rimmer 1992), but low compared to some other freshwater fishes, e.g. carp, *Cyprinus carpio*, (24–198 eggs/g) and perch, *Perca fluviatilis*, (91–473 eggs/g) (Gromov 1979; Volodin 1979). Absolute fecundity (6,800–86,600) is low compared to the smaller Australian percichthyids of the genus *Macquaria*, ranging from the Macquarie perch (*M. australasica*) which spawns 50,000 to 107,700 eggs to Australian bass (*M. novemaculeata*) and golden perch (*M. ambigua*) both of which may spawn over 500,000 eggs (Merrick and Schmida 1984). The large variation in the fecundity of similar-sized Murray cod (Fig. 4) is characteristic of many species; the fecundity of different stocks of the same species can also vary markedly (Bagenal 1978). The inclusion of cod from different rivers may have contributed to this variation. There was a linear relationship between fecundity and length in Murray cod, whereas in many species this relationship is exponential (Bagenal 1978). It is possible that the small sample size of cod over 10kg obscured an exponential relationship, particularly as it appears that relative fecundity decreases with increasing size and age in Murray cod (Fig. 5).

Age and size at maturity

Age or size at maturity in fishes is influenced by various demographic and environmental factors including growth rate (Stearns and Crandall 1984). Although Murray cod grow at different rates in rivers and impoundments in NSW (Rowland 1998), sexual maturity in these populations appears to be age-dependent, with many cod mature at 4, and all females and most males at 5 years of age. However, in Lake Charlegrark, females mature at 6 years of age and a minimum size of 2.0kg, and males at 3 - 4 years and 0.7kg (Gooley et al. 1995). In some species, slow-growing fish mature at greater ages and smaller sizes than faster growing fish (Alm 1959). The reported variation in age and size at maturity between Murray cod in NSW and Victorian waters may be due, at least partly to slower growth in the colder, southern waters.

Reproductive strategies and fisheries management

In summary, Murray cod is a large, long-lived, relatively slow-growing species which has a reproductive strategy involving a long generation period, group-synchronous oocyte development, low fecundity, a relatively complex breeding behaviour, including pairing of broodfish, spawning site selection and paternal protection of the large, adhesive eggs during a relatively short, well-defined breeding season in spring.

Such fishes have a biological advantage in that potentially high larval mortality in unfavourable breeding seasons is compensated for by repeated annual spawnings over the long life span of individuals (Giesel 1976; May 1976). However, this advantage may be lost when populations decline significantly to relatively low levels, as is the case with Murray cod (Lake 1971; Cadwallader and Backhouse 1983; Rowland 1989).

Previous research (Rowland 1983, 1985, 1989, 1992, 1998) as well as the study reported in this paper have provided base-line biological data for the formulation of fisheries management policies for Murray cod. NSW Fisheries has introduced the following restrictions for the recreational fishery for Murray cod: a 3-month closed season (September, October, November) to protect cod during the breeding season; a minimum size limit of 50cm, to ensure that most fish retained by fishers have reached sexual maturity; and a bag limit of 2 fish/day and 4 in possession to reduce fishing mortality. The size limit and closed season also apply to the inland, commercial fishery; this fishery has limits on gear (type, number, mesh size) and is restricted geographically to certain waters in south-western NSW.

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Age and Growth of the Australian Freshwater Fish Murray Cod, *Maccullochella peelii peelii*

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ROWLAND, S.J. (1998). Age and growth of the Australian freshwater fish Murray cod, *Maccullochella peelii peelii. Proceedings of the Linnean Society of New South Wales* **120**, 163–180.

Murray cod, *Maccullochella peelii peelii*, were sampled over the period 1975–1984 from six tributaries and two impoundments of the Murray-Darling river system in NSW; the Murray, Edward, Wakool, Murrumbidgee, Darling and Gwydir rivers, and Lake Mulwala and Lake Burrinjuck. Age determination techniques have been validated by: analysis of seasonal changes on the margins of opercular bones and whole otoliths; by close agreement between observed and back-calculated mean lengths-at-age; and by examination of known-age fish. The sharp transition from narrow, translucent zones to broad, white zones on opercular bones, and the white, opaque zones on whole otoliths have been determined to be annuli formed each spring. Opercular bones are superior for ageing cod, particularly those older than 8 years (> 800 mm).

Murray cod is a large, relatively long-lived fish; the oldest cod was estimated to be 34 years. There was no significant difference between the growth or length-weight relationships of males and females, or cod from different rivers, but cod from the impoundment, Lake Mulwala, were significantly larger than same-aged cod from rivers. The growth in length (L) of Murray cod in rivers is described by a von Bertalanffy curve, represented by the equation: $L_t = 1369.05 \{1–\exp[–0.060(t + 5.209)]\}$. Although overall growth in length is slow ($K = 0.060$), there was no asymptote in the age-weight relationship for cod up to 30 years, indicating that Murray cod grow predominantly by weight increases after about 10 years of age. The length-weight relationship for cod in rivers is described by the equation: $W = 3.240 \times 10^{-9} L^{3.2592}$, where W is whole weight in kg and L is total length in mm.

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KEYWORDS: Australian percichthyid, ageing, growth rates, opercular bone, otolith, *Maccullochella*, Murray cod.

INTRODUCTION

The Murray cod, *Maccullochella peelii peelii* (Mitchell), is an Australian native, warmwater, percichthyid fish found naturally in the vast Murray-Darling river system (Fig. 1). It is Australia's largest, wholly-freshwater fish (growing to a maximum recorded size of 113.6 kg) and is highly valued by recreational and commercial fishers for its size and excellent edible qualities (Rowland 1989). There has been a dramatic decline in the abundance and a reduction in the distribution of Murray cod, particularly since the 1950s, and it is now relatively uncommon in many areas (Lake 1971; Cadwallader and Backhouse 1983; Rowland 1985, 1989).

Initial studies (Llewellyn 1966; Lake 1967; Jones 1974; Langtry, in Cadwallader 1977) used scales or otoliths to age Murray cod, but sample sizes were small, few age-classes were included, and the techniques used were not described or validated. More recently, Gooley (1992) and Anderson et al. (1992) used sectioned otoliths to age Murray cod from Lake Charlegrark (Victoria) and the Lower Murray-Darling basin. In both these studies ageing techniques were validated.

Rowland (1985) conducted a major research project into aspects of the biology of Murray cod, to provide essential data for the formulation of management policies for the species. The age and growth component of that study is reported in this paper. Objectives were to develop reliable ageing techniques (based on opercular bone and sagittal otolith zonation) that enable accurate assessment of age in Murray cod; to compare growth rates of Murray cod from different tributaries of the Murray-Darling river system; and to determine overall growth and length-weight relationships for the species.

TABLE 1

Details of Murray cod used for age and growth analyses

River	Sampling site	No. sampled	Total length range (mm)	Weight range (kg)
Murray	Euston Weir to junction of Murrumbidgee	45	480–1270	2.1–38.1
	Lake Mulwala*	25	610–1035	4.2–36.5
Edward and Wakool	Deniliquin to Wakool	124	415–1215	1.1–34.1
Murrumbidgee	Narrandera	81	195–1220	0.07–40.0
	Lake Burrinjuck*	4	580–1095	2.9–31.0
Darling	Bourke	26	435–1080	1.2–18.6
Gwydir	Bingara	25	167–1090	0.07–22.0

* impoundment

MATERIALS AND METHODS

Murray cod were sampled from six rivers and two impoundments in the Murray-Darling river system (Table 1, Fig. 1). Between 1978 and 1984, fish were either caught by NSW Fisheries staff using drum nets, gill nets, set lines, cross-lines, droppers or angling (see Rowland 1985) or sampled from the catches of professional and recreational fishers. Each cod was measured (total length, TL) to the nearest mm, weighed (cod <10 kg to nearest 10 g, >10 kg to nearest 100 g) and sexed. In addition, data were obtained from a further 36 cod sampled by NSW Fisheries staff between 1975 and 1978.

Ageing Structures

The bony structures from each fish were stored separately in a labeled container. Different structures were examined separately and at different times, two to four weeks apart. Each bony structure was examined independently by two people, and then re-examined 6–12 months later.

Opercular bones

Opercula were removed with the aid of a scalpel and placed in hot water for two minutes. The flesh was then easily removed, the bones separated, dried and stored. Opercular bones were placed on a black background under a desk lamp and examined with the naked eye. Opercular bones from cod, TL > 800 mm were also viewed using a binocular microscope (x20) and reflected light because of the closeness of the outer annuli. There was a sharp transition or check, between distinct white and dark bands on each bone (Fig. 2). The distances from a standard point near the fulcrum to each check and to the posterior-ventral edge of the bone were measured using calipers. The nature of the margin (black or white) of each opercular bone was noted. All observations and measurements were made on the right opercular bone, unless it was damaged.

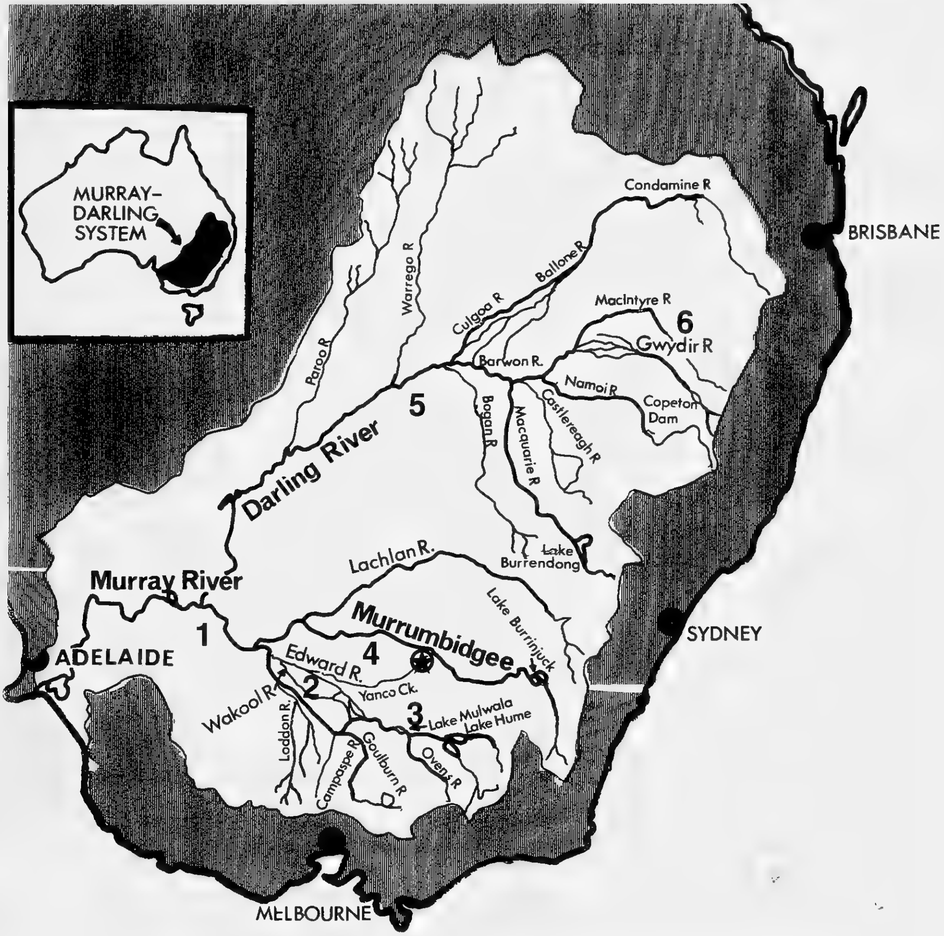

Figure 1. Localities sampled for Murray cod in the Murray-Darling river system during the period 1978 to 1984. Key to sites: 1 — Murray River; 2 — Edward and Wakool rivers; 3 — Lake Mulwala; 4 — Murrumbidgee River; 5 - Darling River; 6 — Gwydir River; star — Inland Fisheries Research Station, Narrandera.

Otoliths

Both sagittal otoliths were removed from each fish and stored dry. Otoliths were submerged, concave surface upward, in distilled water in a watchglass with a black background, and viewed using a binocular microscope and reflected light. Each otolith contained a small, distinct white focus and alternating opaque (white) and hyaline (dark) concentric zones (Fig. 3). The zones were more clearly defined on the anterior and posterior regions of the otolith. The total radius of each otolith from the focus to the medial-posterior edge, and the distance from the focus to the centre of each opaque zone along the same axis (Fig. 3) were measured using an eyepiece micrometer. The nature of the total margin, whether opaque of hyaline, was noted.

The zones were less evident in otoliths from cod, TL > 800 mm due to increased thickness of the otolith, and radii to the opaque zones were not measured in otoliths from these cod. To improve the resolution of the zones, otoliths from Murray cod, TL > 800

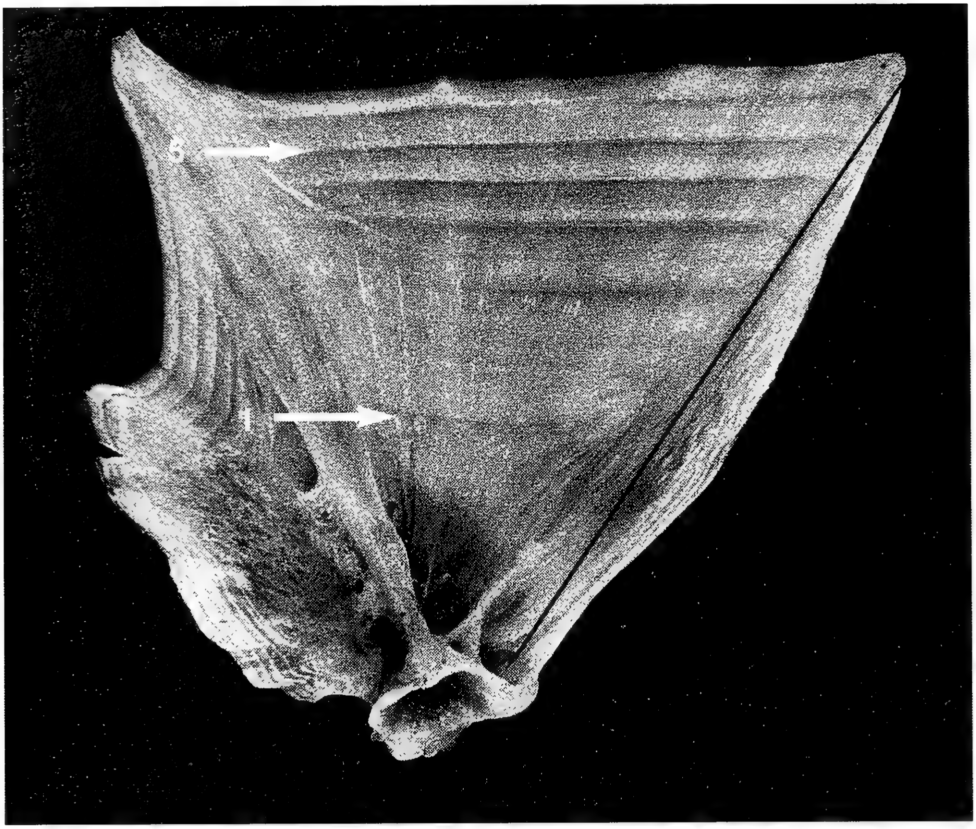

Figure 2a. Opercular bones from Murray cod used for ageing. Numbers indicate selected annuli. Distance to each annulus measured along black line. Bone (x1.5) from cod (TL 815mm, 13.3kg) sampled from Lake Mulwala in June — age 6 years, 8 months.

mm were placed in oil of clove. When the dorsal surface of the otolith was orientated towards the microscope and slightly raised, opaque and hyaline zones were distinct and could be counted along the antirostrum of the otolith.

Scales

During the initial part of the study, six non-regenerated scales were removed from midway between the anus and the closest point on the lateral line of 22 cod. The scales were cleaned in water, dried and mounted between microscope slides. The scales were examined using a binocular microscope and transmitted light.

Reference population (known-age)

Murray cod that had been artificially bred at the Inland Fisheries Research Station, Narrandera, were stocked into two 0.2-ha earthen ponds at a density of 500/ha in February 1979, and fed live food (yabbies, shrimp and goldfish) periodically. Five fish were sampled each September, November, December, February and June for the subsequent 3 years. The opercular bones, otoliths and scales of each sampled fish were examined.

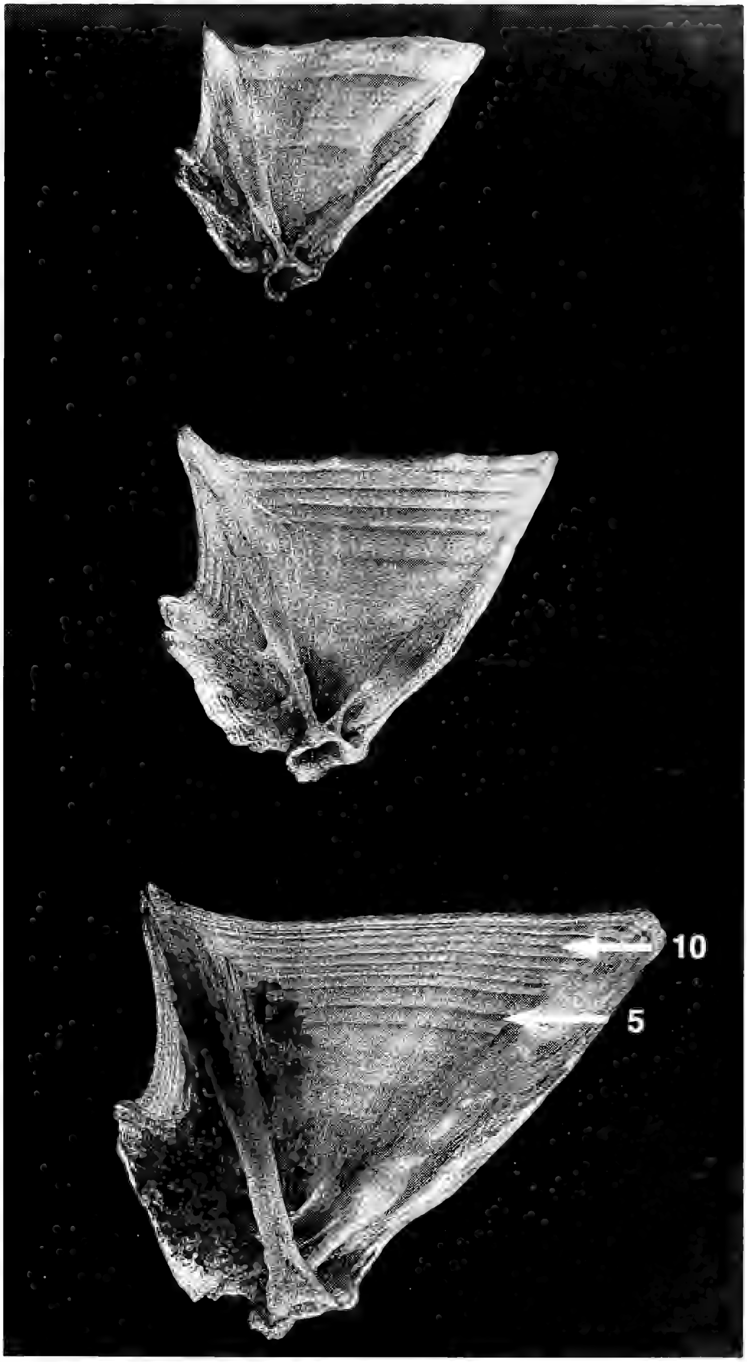

Figure 2b. Opercular bones from Murray cod used for ageing. Numbers indicate selected annuli. All bones (x0.3): top — cod (TL 580mm, 3.1kg) from the Edward River in June — age 2 years, 8 months; middle — as for (a) above; bottom — cod (TL 1085mm, 31.0kg) from Lake Burrinjuck in March — age 18 years, 5 months.

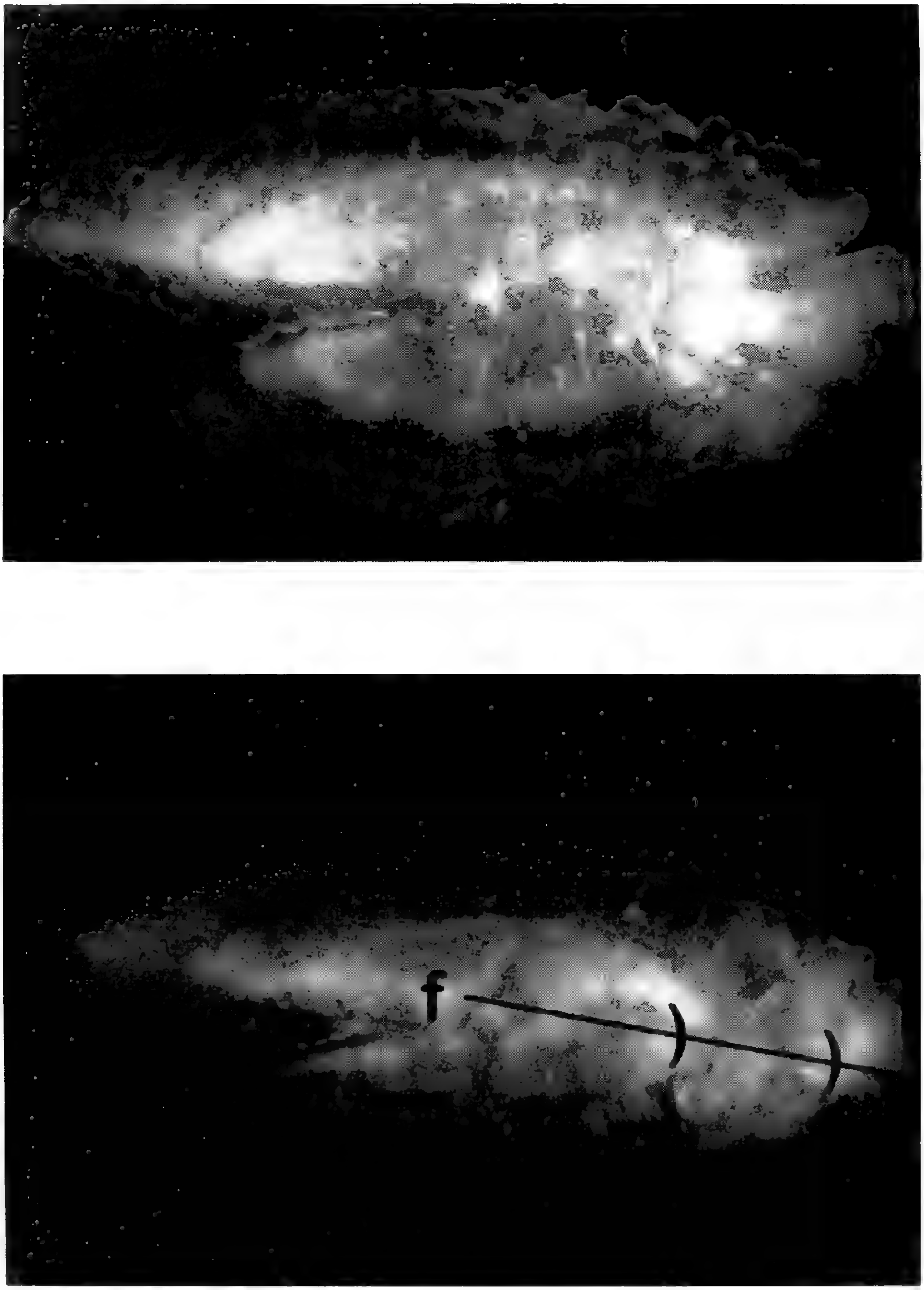

Figure 3. Sagittal otoliths (x10) from Murray cod of known age, reared in earthen ponds and sampled in February. (a) 1 year, 4 months old (TL 300mm, 0.36kg), (b) 2 years, 4 months old (TL 425mm, 1.0kg). Key to symbols: f — focus;) — centre of opaque zone.

Assigning age

Each cod was assigned an absolute age in years and months. Murray cod spawn when water temperatures rise to or above 20°C during spring (Rowland 1983, 1985, 1998) and so 1 November was defined as the birth date of cod in southern N.S.W. and 1 October for cod in the northern NSW (northern Darling and Gwydir rivers). For the calculation of mean lengths and weights at different ages, Murray cod sampled in the two months prior to an impending birth date were assigned that age. Although this is not an exact chronological age, it was considered to be biologically meaningful because it incorporates the growing and spawning seasons of each year (Barlow and Bock 1981; Rowland 1998).

Overall age and growth relationships

Comparisons between the sexes and sampling sites were conducted where sample sizes were large enough to enable statistical analyses. The mean lengths and weights of male and female cod (ages 3 to 7 years) were compared using Student's t-tests, and the mean lengths and weights of cod (males plus females; 3 to 7 years) from the different sampling sites were compared using one-way analysis of variance and Tukey's *w*-procedure (Steel and Torrie 1960).

The mean length-at-age data were fitted to a von Bertalanffy growth curve by nonlinear least squares estimation using C.S.I.R.O. Alpha Subprogram LMM2. The growth curves for males and females were compared using the likelihood ratio test of Kimura (1980).

The relationship between fish TL and opercular bone and otolith radii were determined using regression analyses, and because the relationships were linear but not directly proportional, the following equation (from Tesch 1971) was used to estimate length-at-age by back-calculation.

$$1n = \frac{Sn}{s}(1-c) + c$$

where 1n = length of fish when annulus "n" formed, 1= length of fish when sampled, Sn = radius of annulus "n", s = total radius, and c = a constant, representing the intercept of the regression line on the Y-axis

The mean lengths of cod at ages 1 to 10 years estimated from back-calculations were compared to the observed mean lengths using Student's t-tests.

The length-weight relationships for fish from rivers were determined using analysis of covariance.

RESULTS

A total of 330 Murray cod (TL, range 167–1270 mm; total weight range 0.07–40.0 kg) were sampled (Table 1).

Opercular bones

Distinct transitions from dark to white margins occurred on opercular bones of known-age Murray cod between September and November during the second and third years of growth. The opercular bones of cod less than 1 year old were pale and the change in margin type in 1 year old cod was generally not apparent until February. The margins of opercular bones from 2 and 3 year cod sampled in November, December and February were generally white, and those from cod sampled in June and September were dark.

Opercular bones from 181 Murray cod (TL, 195–1270 mm; 0.08–38.1 kg) were examined. The mean monthly marginal increments on the opercular bones of 3 and 4 year old Murray cod, and the relative frequency of the different types of margins on the bones of 3 to 20 year old cod are shown in Fig. 4.

Opercular bones of Murray cod have alternating white and dark bands that are parallel to the posterior and dorsal edges of the bone (Fig. 2). The broad, white, opaque bands which are formed during the spring and summer months gradually fade into narrow, dark, translucent bands. These end abruptly with a sharp transition or check to the next white, opaque zone. The check generally occurs in October or November and the margins of opercular bones of all cod sampled in December were white (Fig. 4). The check is considered to be an annulus.

Annuli were clearly distinguishable on opercular bones from Murray cod older than 15 years of age (Fig. 2b) and with the aid of a dissecting microscope, outer annuli on the opercular bones of cod presumed to be between 20 and 34 years old could also be counted. Ossification obscured the first one or two annuli on the bones of some of these larger cod and estimation of their age depended on knowing the approximate position of the first or second annulus on opercular bones of younger cod from the sampling site.

False checks on the opercular bones of 4% of Murray cod, were identified as an abrupt, thin transparent band in the normally broad, white band deposited between spring and autumn.

Otoliths

Otoliths sampled from known-age cod less than 1 year old were slightly opaque. By November otoliths from 1 year old cod had a distinct white, opaque zone at the margin and this was surrounded by a hyaline zone in most otoliths sampled in December and in all otoliths sampled in February (Fig. 3). During the second and third years of growth, one opaque and one hyaline zone were deposited annually, and only otoliths from known-age cod sampled in November or December had opaque margins; the remainder had hyaline margins.

Otoliths from 315 Murray cod (TL, 167–1270 mm; 0.07–40 kg) were examined. The mean monthly marginal increments on the otoliths of 3 and 4 year old cod and the relative frequency of different types of margins on the otoliths of 3 to 19 year old cod are shown in Fig. 5. The mean marginal increment was highest in September and lowest in November and otoliths from 67% of cod sampled in October had opaque or narrow hyaline margins. By November the opaque zone had been formed in the otoliths of all but 6% of fish and in January all otoliths had a relatively broad hyaline margin. No false opaque or hyaline zones were identified on otoliths.

These data indicate that the opaque zone is an annulus which is deposited in the otoliths of most Murray cod during October and November.

Ages estimated using both the otoliths and opercular bones from the same fish (TL < 800 mm), were generally in agreement (93%, n=158), but the estimated ages were the same in only 50% of fish over 800 mm (n=14). Where there was disagreement, opercular bones were used to age cod TL > 800 mm. There were no obvious differences between the formation of annuli on the otoliths and opercular bones of immature and mature cod.

Scales

Distinct checks were formed annually during October and November on the scales of known-age Murray cod. Checks were also evident on the scales of cod up to 8 years of age, and the number of checks usually coincided with the age determined using opercular bones and otoliths. However, outer checks on the scales of older cod were unclear and difficult to interpret, and there was often a high proportion of regenerated scales on cod TL > 800 mm.

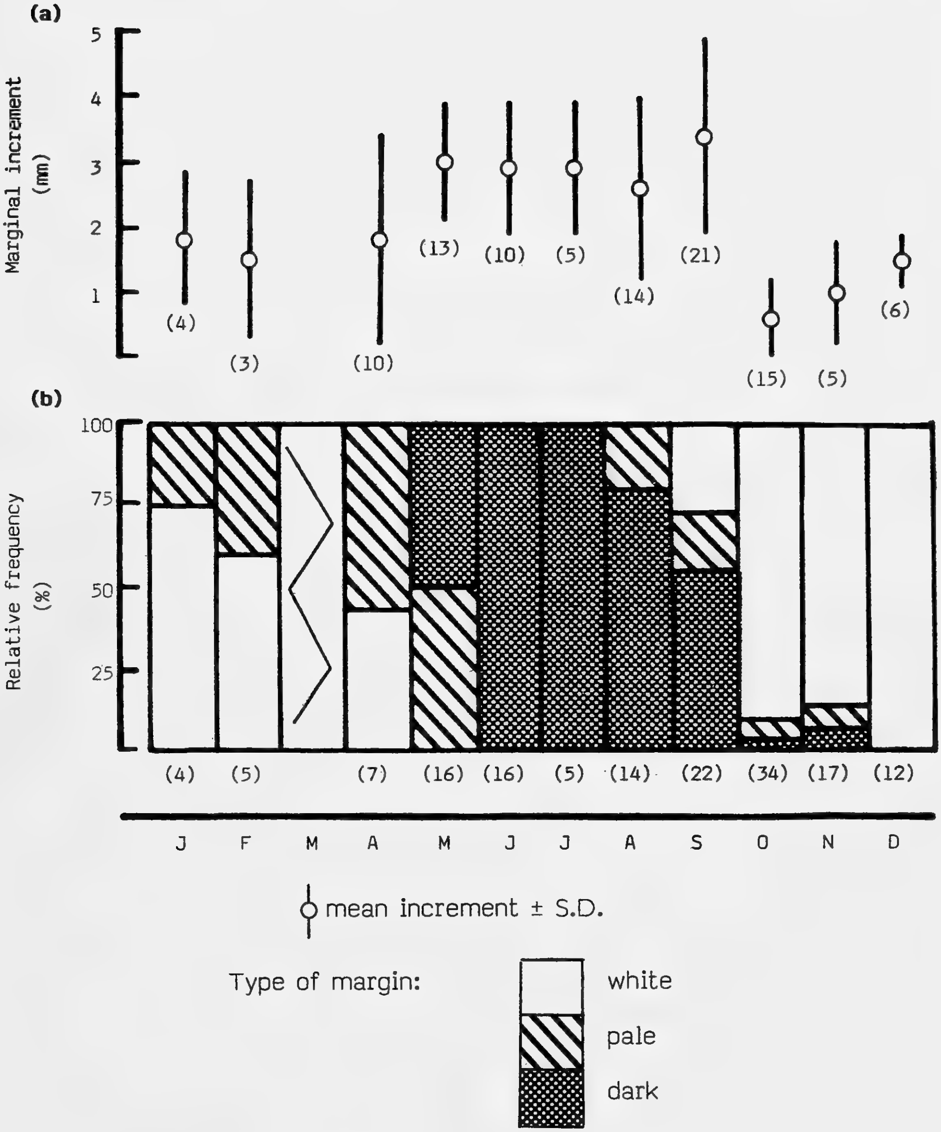

Figure 4. Size of increments and frequencies of margin types on the opercular bones of Murray cod: (a) marginal increments in 3 and 4 year old individuals; (b) relative frequency of the different types of margins in individuals from 3 to 20 years old. Opercular bones not taken from cod sampled in March. Sample sizes in parentheses.

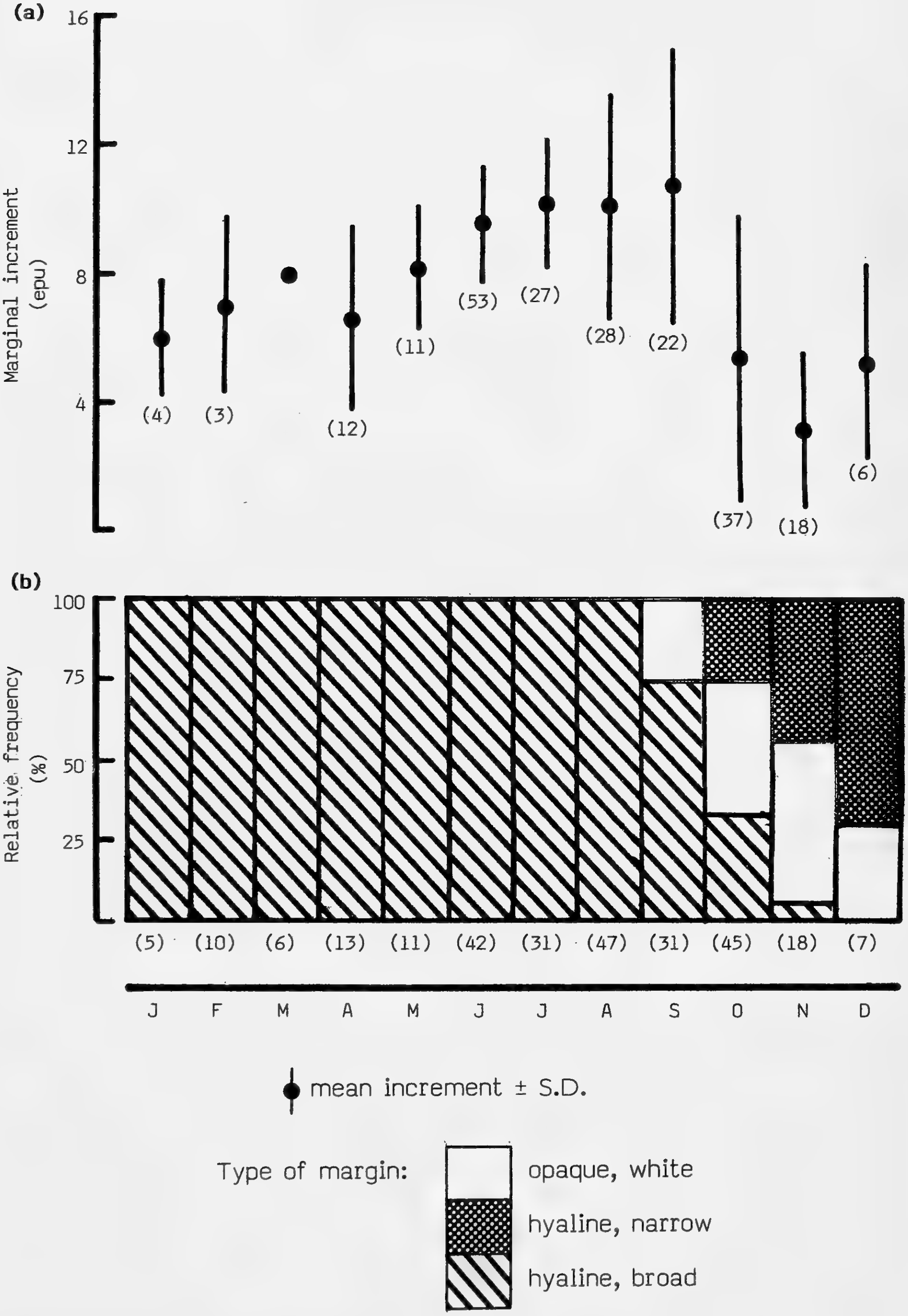

Figure 5. Size of increments and frequencies of margin types on otoliths of Murray cod: (a) marginal increments in 3 and 4 year old individuals; (b) relative frequency of different types of margin in individuals from 3 to 19 years old. Sample sizes in parentheses.

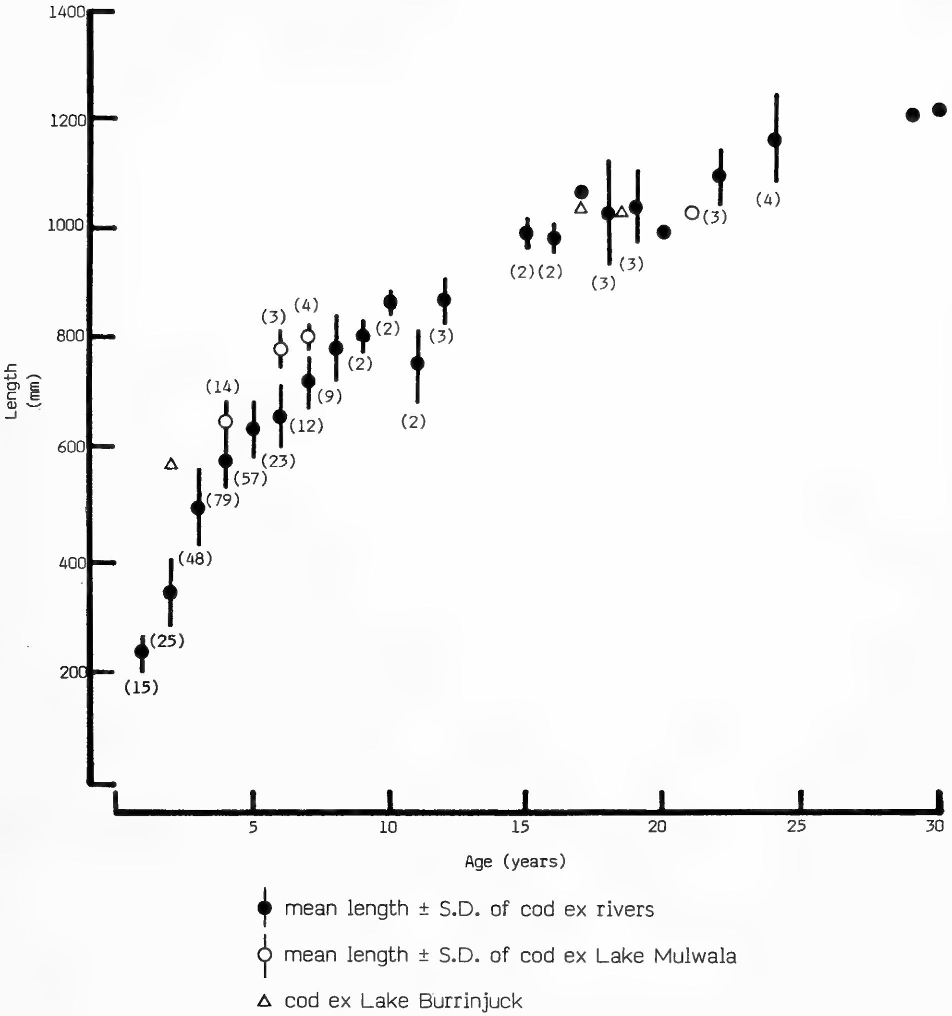

Figure 6. Total length at age in Murray cod.

Mean lengths and weights at ages

There was no significant difference (P>0.05) between the mean lengths of males and females at each site with the exception of 4 year old cod from the Murrumbidgee River. Similarly, there was no significant difference (P>0.05) between the mean weights of males and females at each site. Data from both sexes were pooled for further analyses. The mean lengths and weights of 3 to 7 year old Murray cod from different sites in the Murray-Darling river system are given in Table 2.

The mean weight of 5 year old Murray cod from the Murrumbidgee River was significantly ($P < 0.01$) lower than the weight of cod from other rivers (Table 2), but there was no significant difference ($P > 0.05$) in the mean lengths and weights of 3, 4, 6 and 7 year old cod from all rivers.

The 4, 6 and 7 year old Murray cod from Lake Mulwala were significantly longer ($P < 0.05$) than same-age cod from one or more of the other sampling sites, and cod from the lake were significantly heavier ($P<0.01$) than same-aged cod from all other sampling sites (Table 2). The four Murray cod sampled from Lake Burrinjuck were also heavier than same-age cod from rivers (Fig. 7).

The mean lengths and the mean weights of 1 to 30 year old Murray cod from all sampling sites are shown in Figs. 6 and 7 respectively.

TABLE 2

Length (L) (mm) and weight (W) (kg) of 3 to 7 year old Murray cod from different rivers and Lake Mulwala. Data are means ± s.d., with sample sizes in parentheses.

Rivers				Age (years)		
		3	4	5	6	7
Murray,	L	503±57(20)	584±50(47)	652±48(42)	662±53(18)	695±39(5)
Edward, Wakool	W	2.0±0.7(19)	3.5±1.0(47)	5.0±1.2(42)	5.4±1.5(20)	6.7±1.8(5)
M'bidgee	L	470±88(16)	560±33(14)	581±50(7)	—	746±27(5)
	W	1.8±1.1(18)	2.9±0.5(16)	3.1±1.0(10)*	—	6.8±1.2(4)
Darling	L	502±96(2)	568±36(11)	636±26(6)	651±37(5)	—
	W	2.3±1.5(2)	3.5±0.9(11)	4.3±0.6(6)	6.0±1.7(6)	—
Gwydir	L	537±36(10)	599±39(7)	583±74(2)	—	769±55(2)
	W	2.2±0.5(10)	3.6±0.2(6)	—	—	7.6±2.1(2)
Lake Mulwala	L	—	654±35(14)#	—	786±32(3)#	806±8(4)#
	W	—	5.8±0.8(14)*	—	9.6±1.5(3)*	10.9±1.8(4)*

* significantly different ($P<0.01$) within age class.
# significantly different ($P<0.05$) within age class.

Growth relationships

von Bertalanffy growth curve

The growth curves for 1 to 30 year old male and female Murray cod from rivers are represented by the equations:

$$L_{t\ (male)} = 1367.61\ \{1 - \exp\ [-0.059\ (t + 5.604)]\}$$

$$L_{t\ (female)} = 1371.84\ \{1 - \exp\ [-0.061\ (t + 4.868)]\}$$

There was no significant difference between these growth curves (X^2 [–N 1n ($^2/^2$)] = 0.3398, d.f. = 3, $P>0.01$), and the growth curve (Fig. 6) of Murray cod from rivers in the Murray-Darling river system is represented by the equation:

$$L_t - 1369.05\ \{1 - \exp\ [-0.060\ (t + 5.2090)]\}$$

Back-calculation of age

The mean lengths of 1 to 10 year old Murray cod, both observed and those determined by back-calculation are given in Table 3. Mean lengths at ages 1 and 2 were significantly ($P < 0.01$) larger than observed mean lengths; however, mean lengths at most other ages were in agreement.

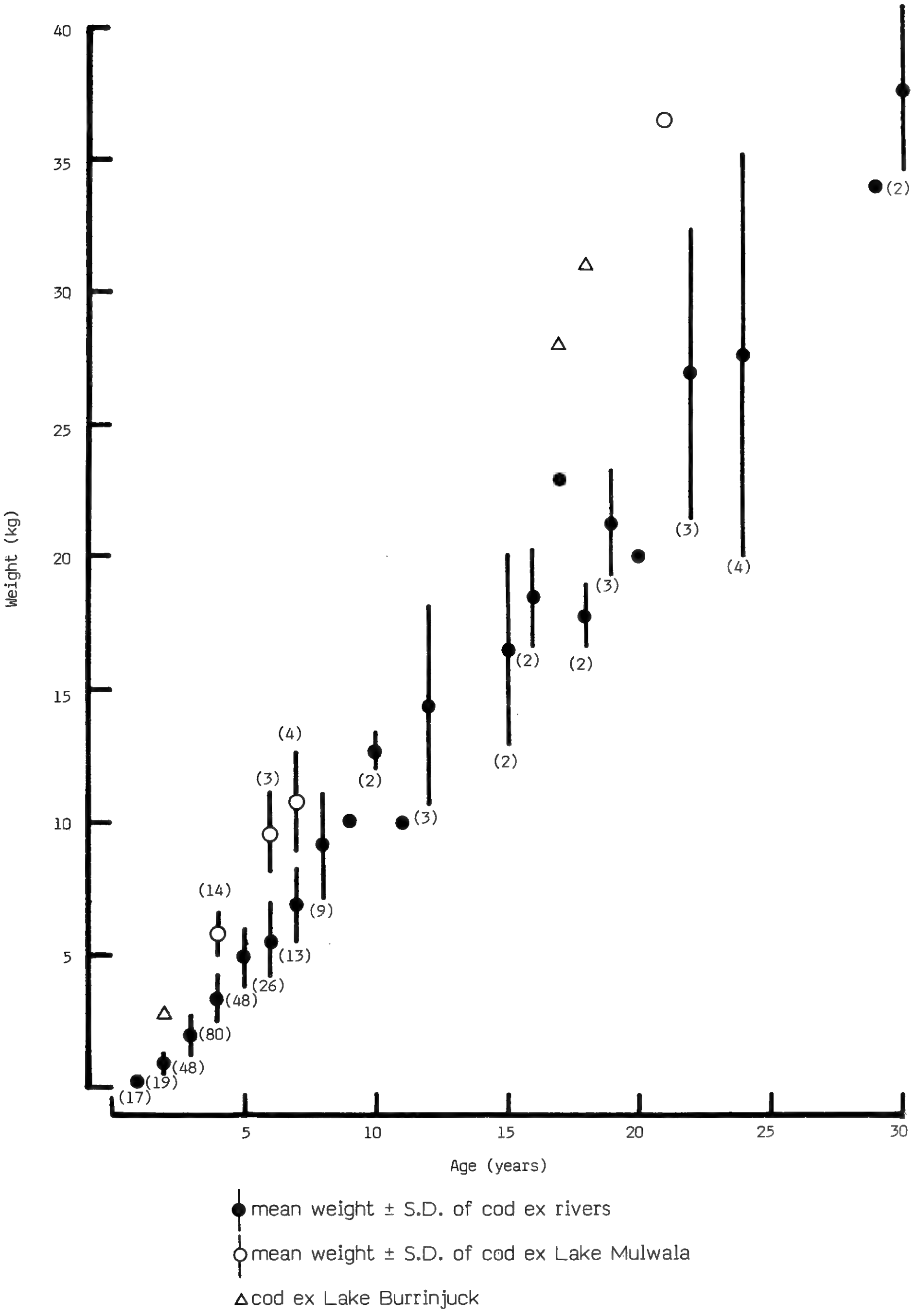

Figure 7. Weight at age in Murray cod.

TABLE 3

Observed and back-calculated mean lengths of 1 to 10 year old Murray cod.

Age (years)	Length (mm)		
	Observed	Back-calculated; otoliths	Back-calculated; opercular bones
1	236	322*	279*
2	348	429*	404*
3	499	519	512
4	579	592	580
5	639	638	613
6	663	704*	683
7	728	748	723
8	787	784	767
9	803	830	800
10	869	827	824

* significantly different ($P<0.01$) from observed mean length.

Length-weight relationships

The length-weight relationships of Murray cod from rivers and Lake Mulwala are: rivers $W = 3.240 \times 10^{-9}L^{3.2592}$ (Fig. 8); Lake Mulwala $W = 3.684 \times 10^{-9}L^{3.2592}$, where W is whole weight in kg and L is total length in mm.

DISCUSSION

Validation of techniques is an essential part of fish age and growth studies (Beamish and McFarlane 1983). The techniques for ageing Murray cod were validated by examination of the seasonal changes on the margins of opercular bones and otoliths from known-age and wild-caught fish, and by the close agreement between the observed and back-calculated mean lengths-at-age. It is possible that the differences between the observed and back-calculated mean lengths at ages 1 and 2 were due to inaccuracies in measuring the radii, or selective sampling and differential growth rates of 1 and 2 year old cod between rivers. There may also be differential growth rates of larval and juvenile cod between rivers. In 1979, the Murray, Edward and Wakool rivers, but not the Murrumbidgee River, were at or near flood level (Rowland 1998) and it was from the former rivers that many cod from a strong 1979 year class were sampled in 1983 as 4 year old fish for the age and growth analysis (Table 1). The significantly greater back-calculated mean lengths at ages 1 and 2, may reflect rapid growth of larval and juvenile cod in the Edward and Wakool rivers during the 1979 flood.

Checks are formed on both the opercular bones and otoliths of most juvenile and adult Murray cod annually during October and November, and because Murray cod breeds during these months (Rowland 1983, 1998; Cadwallader and Gooley 1985) cod can be directly aged by counting checks. There was no evidence of the subsidiary growth rings on the bony structures in Murray cod as mentioned by Llewellyn (1966), and no otoliths and only 4% of the opercular bones examined had apparent false checks.

Ageing structures

Le Cren (1947) used opercular bones to age perch, *Perca fluviatilis*, and he also found that the sharp transition from the narrow, transparent winter band to the broad,

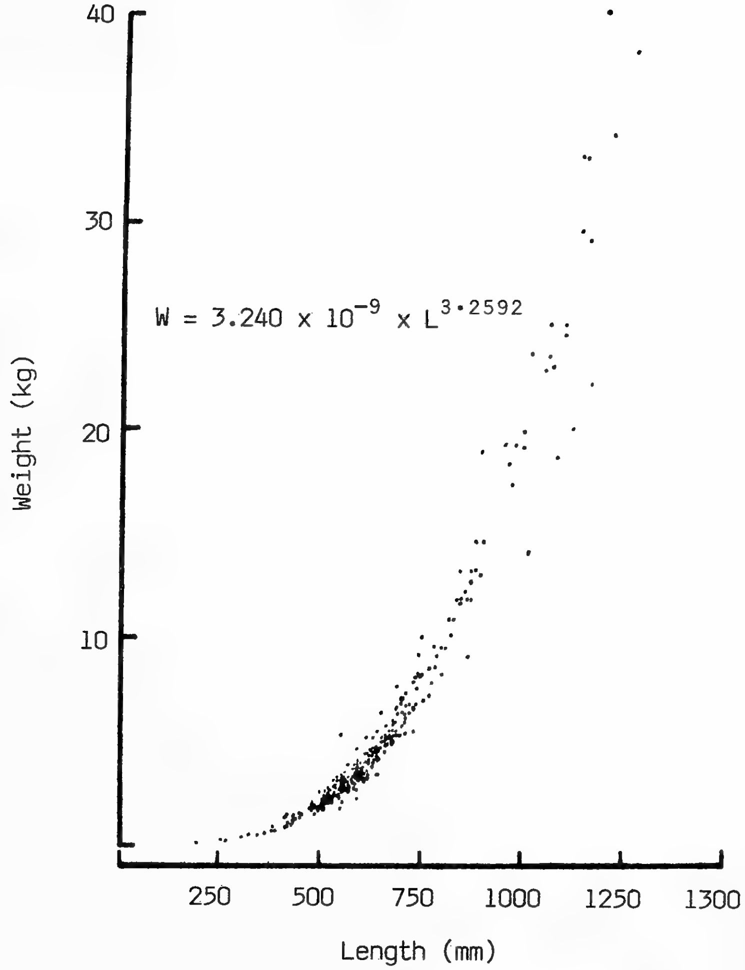

Figure 8. Relationship of total length to weight of Murray cod (both sexes) from the Murray, Edward, Wakool, Murrumbidgee and Darling rivers (n = 292).

opaque summer band was an annulus in that species. Although opercular bones are not commonly used to age fish, McConnell (1951) and Mann (1973) found opercular bones superior to other bony structures for age determination, particularly for older year-classes. Scoppettone (1988) used opercula to age the cui-ui, *Chasmistes cujus*, up to 41 years, and to demonstrate that some species of catostomids and cyprinids of western North America were older than had previously been thought. In the current study, checks could be counted on the opercular bones of Murray cod estimated to be 29, 30 and 34 years old. The use of opercular bones in these studies demonstrate that these bones are valuable in age and growth studies of long-lived fishes.

The otoliths of most fish in temperate regions consist of alternating broad, opaque zones which are formed during periods of rapid growth, generally in spring and summer, and narrow, hyaline zones formed during periods of slow growth (Jearld 1983). Previous authors have identified the hyaline zone (Jensen 1970; Dark 1975), the opaque zone

(Watson 1964; Manooch and Haimovici 1978; Johnson et al. 1983) or the distal or proximal edges of either zone (Sikstrom 1983; Moore and Labisky 1984) as annuli on the otoliths of different species of fish. In Murray cod the annulus was the opaque zone which commenced to form in otoliths in late September or early October and was generally completed by December and surrounded by part of the following hyaline zone in January. This pattern was also reported in broken and sectioned Murray cod otoliths by Gooley (1992) and Anderson et al. (1992). The increasing thickness and opaqueness of otoliths in large cod made the use of this bony structure difficult and unreliable; however, Anderson et al. (1992) were able to age cod up to 48 years (1400 mm and 47.3kg) using sectioned otoliths.

Age comparisons

Murray cod is a relatively long-lived Australian freshwater fish; the oldest cod in the current study was estimated to be 34 years. The maximum ages of cod in the studies by Anderson et al. (1992) and Gooley (1992) were 48 and 22 years respectively. These studies demonstrate that Murray cod is the longest lived percichthyid and possibly freshwater fish in Australia. The maximum reported ages of two other native percichthyid fishes are 22+ in the Australian bass, *Macquaria novemaculeata* (Harris 1985) and 19+ years in the golden perch, *Macquaria ambigua* (Battaglene 1991). These data greatly exceed the maximum age of 14 years reported by Davis (1984) for another large, Australian freshwater fish the barramundi, *Lates calcarifer* (Centropomidae).

Growth and variability

An L value for Murray cod of 1369 mm is close to 1270 mm, the maximum length observed, indicating that a von Bertalanffy growth curve adequately describes the growth of Murray cod sampled during this study. The value is also similar to that (L = 1202 mm) determined by Anderson et al. (1992). However, Whitley (1955) stated that cod grow to 1800 mm, and the 113.6 kg cod caught in the Barwon River in 1902 (Rowland 1989) would have been approximately 1750 mm according to the length-weight relationship determined in the current study. It is apparent that Murray cod can far exceed the observed and theoretical maximum sizes reported in this paper. The calculation of L depends on the number of age groups and individuals used, and a higher value of L would probably have been obtained if more cod longer than 1000 mm could have been aged and included in the calculations.

The growth rate (in length) of Murray cod is slow (K = 0.060). Long-lived fishes generally have low K values. Populations of the snowy grouper, *Epinephelus niveatus*, a fish which may attain ages of greater than 30 years, have growth coefficients of 0.063 to 0.087 (Moore and Labisky 1984). By contrast, the growth coefficient of the relatively short-lived (8 years) Australian freshwater catfish, *Tandanus tandanus*, from the Gwydir River is 0.341 (Davis 1977). It has been suggested that in marine, reef fishes the rate of attainment of maximum size reflects the trophic level and that fishes at high trophic levels have low K values compared to fish which feed at lower trophic levels (Grimes 1978; Johnson 1983). If this hypothesis also applies to fishes in freshwater habitats, the low K value of Murray cod which is the largest carnivore in the Murray-Darling river system, would be expected.

The high value of the constant b (3.2592) in the equation describing the length-weight relationship, indicates that Murray cod become more and more rotund as their length increases. This is supported by Gooley (1992) who calculated an identical value for b. Length and weight-at-age data and the length-weight relationship indicate that, after about 10 years of age, cod grow predominantly by increases in weight. From ages 10 to 30 years, there are large variations between the weights of same-aged fish and there is no asymptote apparent in the age-weight relationship of Murray cod up to 30 years of age (Fig. 7).

Murray cod from Lake Mulwala were significantly larger than same-aged cod from the rivers. Temperature is a major factor affecting the growth rate of Murray cod in farm dams (Barlow and Bock 1981) and feeding activity and therefore the growth rate of Murray cod in most Victorian waters is reduced by low water temperatures during winter (Cadwallader and Backhouse 1983). Water temperatures are generally lower in Lake Mulwala than in more western parts of the system. Lake Mulwala is upstream of the sampling sites in the Murray, Edward and Wakool rivers, and effects of the coldwater discharge from the base of Hume Weir extend to the lake (Walker 1980). The rapid growth rate of Murray cod in the relatively cool Lake Mulwala suggests that other environmental factors such as habitat type, food type and availability, and/or population size may play major roles in determining growth rate in Murray cod.

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Social Dynamics and Activity Patterns of Bottlenose Dolphins, *Tursiops truncatus*, in Jervis Bay, Southeastern Australia

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MÖLLER, L.M. AND HARCOURT, R.G. (1998). Social dynamics and activity patterns of bottlenose dolphins, *Tursiops truncatus*, in Jervis Bay, Southeastern Australia. *Proceedings of the Linnean Society of New South Wales* **120**, 181–189.

Group characteristics, activity patterns, and the occurrence of recognisable bottlenose dolphins were documented from boat surveys conducted in Jervis Bay between May 1997 and April 1998. Bottlenose dolphins were found to occur in the bay year-round, with group size ranging from a single animal up to 64 individuals (x = 15.3, SD = 14.2; median = 9, interquartile range = 18). Calves were observed during all seasons, and group size was positively correlated to the number of calves in the group. Newborns were observed only in summer and autumn. Group size was significantly different according to activities, being smaller during feeding, and larger during socialising. The most frequently recorded group activity was travelling, followed by feeding, milling and socialising. The frequency of activities changed according to season, with an increase in travelling from winter to summer and autumn, and an increase in feeding in winter and spring. A total of 103 individual dolphins were identified, with most seen in the bay either year-round or only within one season.

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KEYWORDS: bottlenose dolphins, *Tursiops truncatus*, social dynamics, activity patterns, behaviour, population structure, photo-identification, site fidelity, Jervis Bay, southeastern Australia.

INTRODUCTION

Patterns of social organisation of bottlenose dolphins, *Tursiops truncatus*, appear to be quite complex, with groups frequently changing size and composition (eg. Ballance 1990; Shane 1980; Würsig 1978). From earlier reports, habitat structure and activity patterns appear to be the main factors influencing group size, while group composition appears to be primarily based on age and sex of the individuals (eg. Shane et al. 1986; Smolker et al. 1992; Wells et al. 1987).

Bottlenose dolphins are found in all temperate and tropical waters around the world (Leatherwood and Reeves 1983). In Australia they occur throughout all nearshore waters (Ross and Crockcroft 1990), but detailed information on populations is available for only a few areas (eg. Connor and Smolker 1985, Smolker et al. 1992 for Shark Bay, WA; Corkeron 1990, 1997, Lear and Bryden 1980, for southeast QLD; Mandelc and Fairweather 1995 for Jervis Bay, NSW). Dolphin groups in Australian waters range from a mean size of only approximately 5 animals in Shark Bay, WA to about 16 off Stradbroke Island in Queensland (Corkeron 1997; Smolker et al. 1992). In Shark Bay, group size varied significantly with activity, being larger for socialising than for resting and travelling groups (Smolker et al. 1992). About 70 of these animals appear to show year-round residency near Monkey Mia in the east of the bay (Smolker et al. 1992). In Jervis Bay, approximately 200 km south of Sydney, an earlier study reported that a small group of bottlenose dolphins, which appeared to belong to a larger population, used the area as their core home range (Mandelc and Fairweather 1995).

In this paper we report initial findings from an investigation of the social structure and dynamics of these bottlenose dolphins in Jervis Bay. Specifically, we document group characteristics, activity patterns and the occurrence of recognisable individuals.

MATERIAL AND METHODS

Jervis Bay (35°07′S, 150°42′E) (Fig.1) is a relatively enclosed embayment with 102 km^2 of water surface, characterised by shallow waters, which gradually slope towards the entrance, with maximum depths reaching approximately 30 m (West 1987; Cho 1995; Holloway 1995).

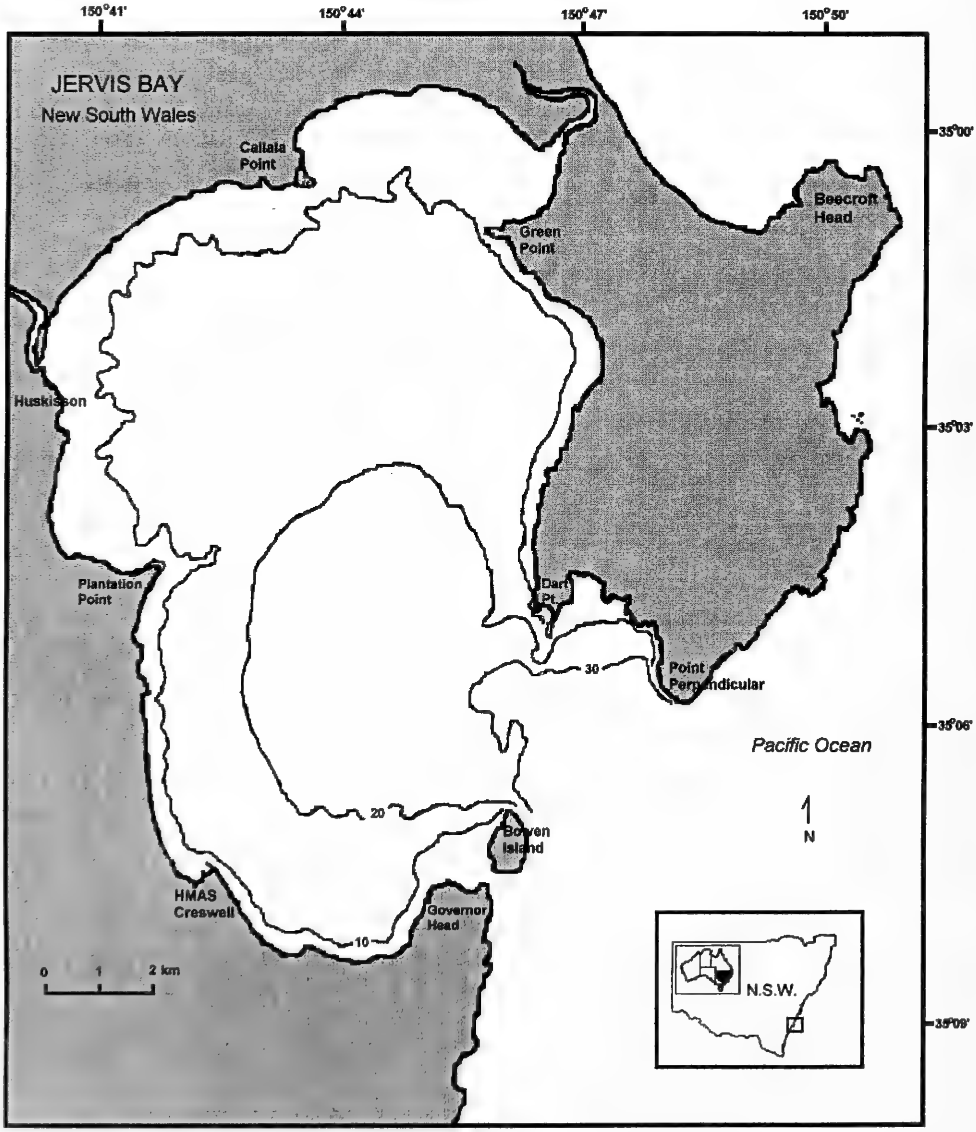

Figure 1. Map of Jervis Bay, New South Wales, Australia, showing 10 and 20 m depth contours.

Between May 1997 and April 1998, we conducted a total of 51 boat surveys in the area, for approximately 303 h of survey time and 3645 km of water surface surveyed. Routes were concentrated along the periphery of the bay, approximately along the 10 m isobath, coupled with transects crossing the middle of the bay. Consecutive survey routes in the periphery were alternated between clock-wise and anti-clock-wise directions. Effort was directed towards circumnavigating the whole bay each day with an additional transect in the middle of the bay, but surveys were curtailed or direction altered if conditions changed to a Beaufort Sea State 4 or greater. A bias towards the periphery of the bay was chosen for sampling because in a previous study dolphins were found to use waters less than 11.4 m deep nearly 90% of the time (Mandelc and Fairweather 1995). During each survey the sea was scanned 90 degrees from the bow and to each side of the boat forward of the midline (with one observer on each side) to search for dolphin groups.

When a dolphin group was encountered we recorded time of sighting, observed activity, estimated group size (including the presence and absence of calves and newborns), and attempted to photograph each individual's dorsal fin. Groups were defined as animals sighted within an area of approximately 100 m radius (Irvine et al. 1981). Calves were defined as animals between one half to two thirds the length of an adult, and newborns as individuals less than one half the size of an adult. Size comparisons could be made because both calves and newborns usually spend a significant amount of time in very close proximity to an adult. Group size was estimated by several visual counts conducted by the boat crew during the sighting. Group sizes are presented as both means and medians. Mean group sizes are presented in order to facilitate comparisons with other bottlenose dolphin studies, while medians are presented because the distribution of group size was skewed and sample sizes were relatively small. Activity patterns were defined according to Hanson and Defran (1993) and Shane (1990a) with five mutually exclusive categories: travelling, feeding, socialising, milling, and resting. Travelling groups were characterised by a uniform directional movement, with a rhythmic surfacing pattern. Feeding groups were distinguished by variable directional movement with frequent rapid dives, often exposing the fluke or tail stock. Socialising groups presented variable directional movement with body contact and splashing among individuals, and various displays and leaps. Milling groups also moved in variable directions, staying close to the surface without showing apparent surface behaviours and body contact. Resting groups were defined as animals floating or moving very slowly, with no wake observed. Activity was recorded over a 3-min interval at the time of initial sighting of a particular group (Altmann 1974). During this initial observation period, the boat remained at least 30 m from the group, in order to minimise disturbance. After this period we approached the group slowly and kept a distance of about 10 m to facilitate photo-identification of individuals. Attempts were made to photograph every member of the group at each sighting. Natural marks on the trailing edge of the dorsal fins were used to identify individual dolphins (Würsig and Jefferson 1990; Würsig and Würsig 1977).

Seasons of the year were divided as follow for analyses of seasonal occurrence of calves and newborns, and seasonal frequency of activities: autumn from March to May; winter from June to August; spring from September to November; and Summer from December to February.

RESULTS

Group characteristics

Bottlenose dolphins were observed in the bay year-round, with a total of 101 groups sighted and 1540 individuals counted. Groups varied from a single animal up to 64 individuals (Fig. 2). Mean group size was 15.3 animals (SD = 14.2) and median group size was 9 (interquartile range = 18.0).

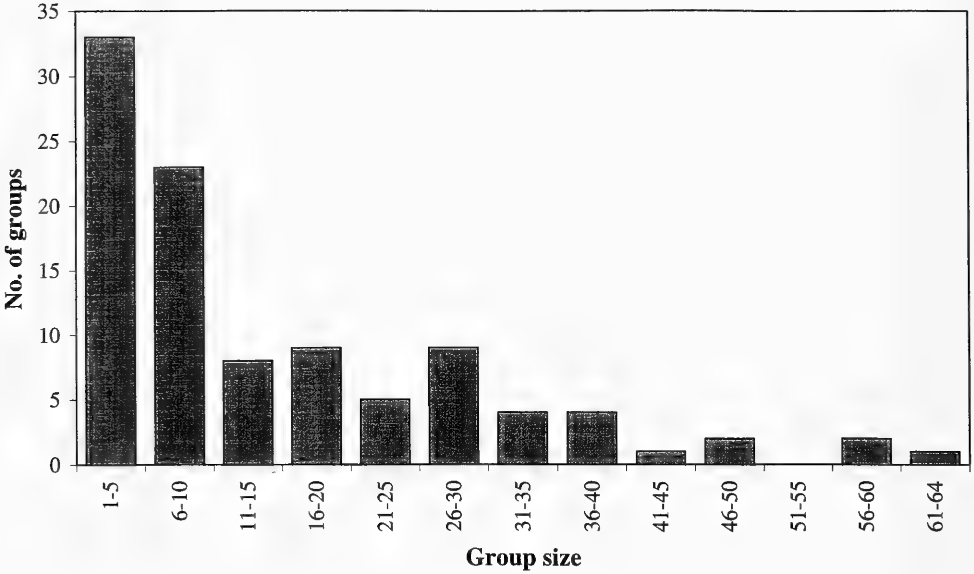

Figure 2. Frequency distribution of group size of bottlenose dolphins in Jervis Bay.

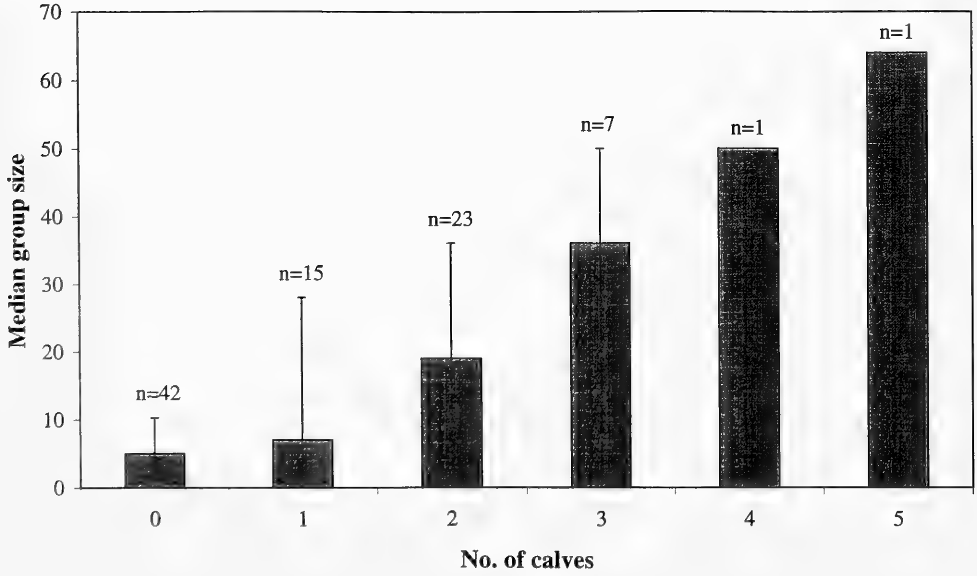

Figure 3. Bottlenose dolphin group size by number of calves seen in the group in Jervis Bay.

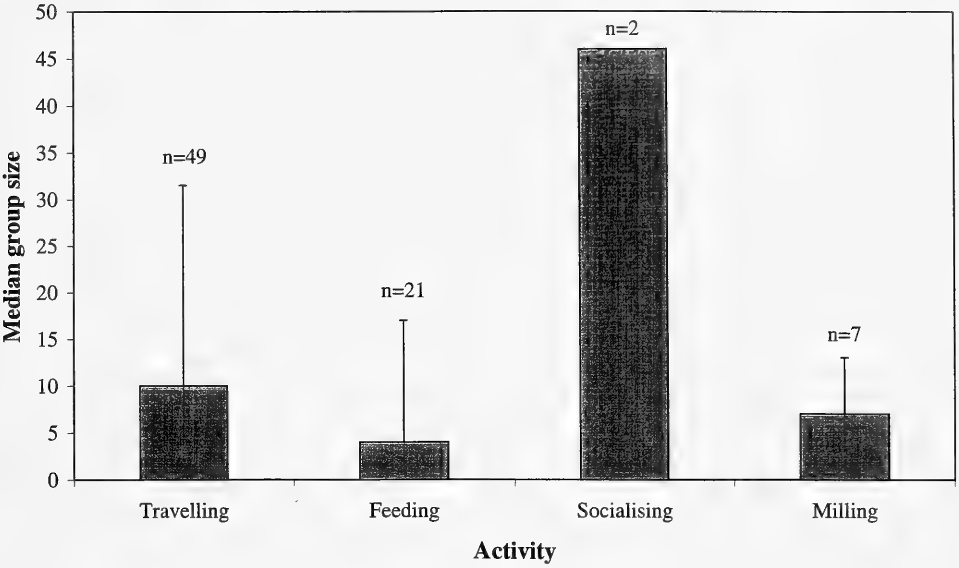

Figure 4. Bottlenose dolphin group size according to activities in Jervis Bay.

Calves were observed during all seasons, composing 5.9% (n = 91) of sighted animals. A minimum of one and maximum of five calves were observed per group. Group size was positively correlated with the number of calves in the group (Spearman $r^2 = 0.41$, $p < 0.01$, n = 89) (Fig. 3).

Newborns were observed only in summer (n = 3) and autumn (n = 1), and constituted only 0.3% of dolphins sighted during the year. On two separate occasions a single newborn was observed in a group (group sizes = 21 and 64), and once, two newborns were recorded in a group (group size = 8).

Group size varied significantly with activity (Kruskal-Wallis, $p < 0.05$, n = 79). Group size was usually larger for socialising, than for travelling, milling, and feeding groups (Fig. 4). Resting groups were never observed during the 3-min interval at the beginning of a sighting.

Activity patterns

Travelling was the group activity most frequently observed (61%), followed by feeding (29%), milling (8%) and socialising groups (4%). The frequency of travelling increased from winter to spring, summer and autumn, while feeding was more frequently observed in winter and spring (Fig. 5). Milling was not observed in spring and autumn, and socialising was only observed in summer and autumn.

Photo-identification

A total of 5796 photographs were taken, from which we identified 103 individual dolphins. The number of sightings of each of these animals varied from one to 27 (Fig. 6), with a mean of 9.6 (SD = 8.1) and median of 7 (interquartile range = 16.0). Forty-nine animals (48% of identified dolphins) were observed in the Bay at least once during each season. Thirty-seven individuals were observed in just one season (36%), 9 dolphins were observed during two seasons (9%), and 8 dolphins were observed during three different seasons (8%).

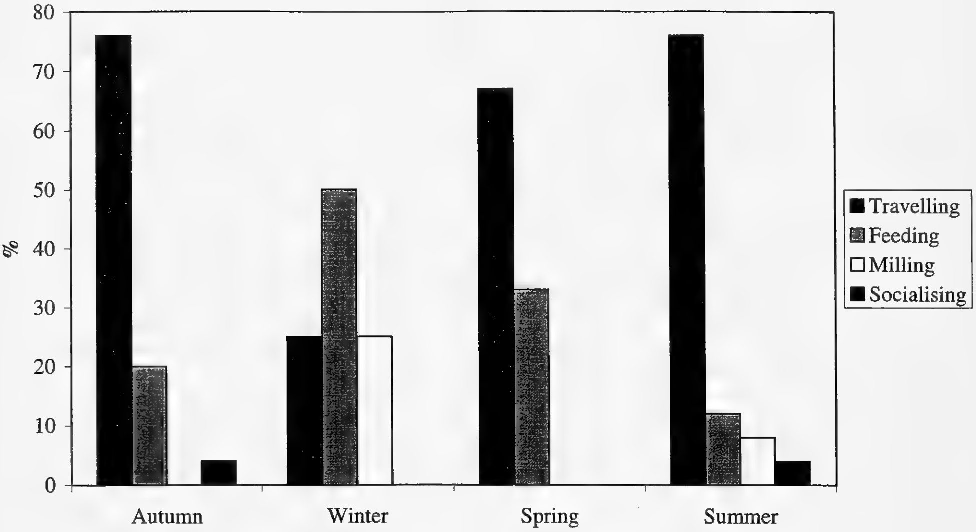

Figure 5. Frequency of activities of bottlenose dolphins by season in Jervis Bay.

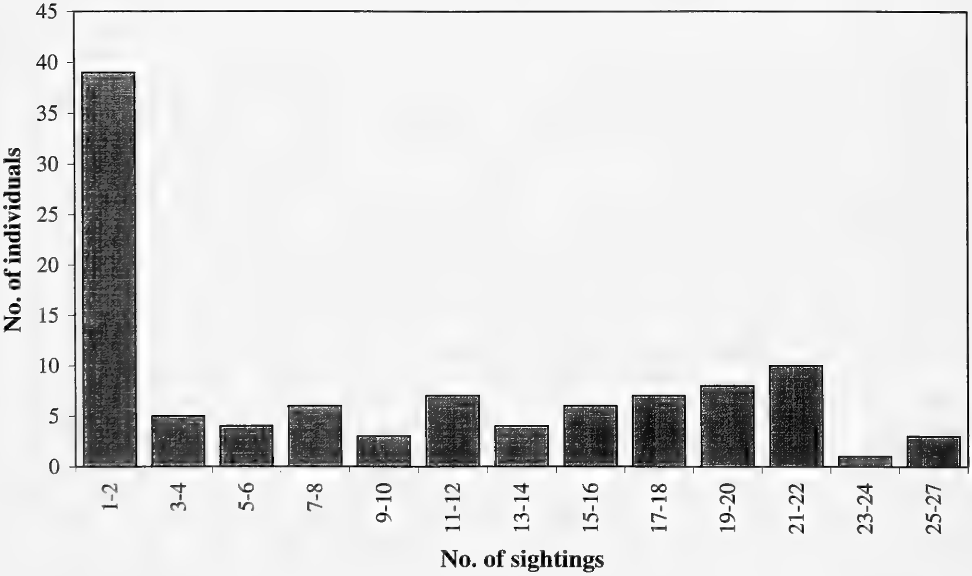

Figure 6. Frequency distribution of the number of sightings of each photo-identified bottlenose dolphin in Jervis Bay.

DISCUSSION

The size of bottlenose dolphin groups in different areas of the world is highly variable. Mean group sizes range from about 5 individuals (Irvine et al. 1981; Smolker et al. 1992; Weigle 1990) up to 140 animals (Saayman and Tayler 1973). Bottlenose dolphins in Jervis Bay coalesce in groups whose mean size is similar to those of California and southern Queensland (Ballance 1990; Corkeron 1997), but larger compared to those in Florida, Western Australia, and the Mediterranean (Bearzi et al. 1997; Smolker et al. 1992; Wells et al. 1987). While some differences in group size may be related to different definitions of exactly what a group is, it has been proposed that small groups usually occur in shallow protected habitats while large groups occur in open and deep habitats (reviewed in Shane et al. 1986, though see Scott and Chivers 1990). Bottlenose dolphins in Jervis Bay are usually found in waters less than 11.4 m deep (Mandelc and Fairweather 1995), but group size is relatively large. Predation avoidance and facilitation of location, herding and capture of schooling fish have been suggested as the main determinants of the formation of large dolphin groups (Norris and Dohl 1980; Shane et al. 1986; Wursig 1986). Large predatory sharks are not known to commonly occur in Jervis Bay (Pollard 1973; R. Chan in litt.) and cooperative feeding is rarely observed (L. Möller pers. obs.), therefore neither of these hypotheses are likely to explain the large size of groups found in the area.

In Jervis Bay approximately one half of identifiable dolphins were present in all four seasons. Hence, there is apparently a resident community of bottlenose dolphins in the area. Another one third of the dolphins identified in the Bay were seen in only one season, suggesting that the resident community may receive frequent visits of transient animals from outside. In chimpanzees, group size may increase in the peripheral areas of the community range, where encounters with individuals from neighbouring communities are most likely to occur, suggesting a defensive response by resident groups to avoid intraspecific aggression from neighbouring groups (Symington 1990). Whether a similar mechanism is operating with Jervis Bay dolphins remains to be tested.

The increase in group size with an increase in the number of calves in the group, as observed in Jervis Bay and other bottlenose dolphin populations (eg. Bearzi et al. 1997; Weigle 1990; Wells et al. 1987), has been related to potential advantages of enhanced calf assistance, protection and reduced maternal investment (Norris and Dohl 1980). However, a decrease in group size for feeding, as observed in Jervis Bay, may indicate that those benefits could be counterbalanced by reduced feeding efficiency, and that higher rates of food intake may usually not be gained through those large groups (Bearzi et al. 1997).

Observations of newborns in summer and early autumn indicate calving in Jervis Bay occurs during this period. This reflects a general pattern observed elsewhere, with calving occurring during the warmer months (Fernandez and Hohn 1998; Gruber 1981; Scott et al. 1990; Urian et al. 1996; Weigle 1990). From vessel-based work in coastal waters of southern Queensland, calves were observed in all months of the year and newborns more frequently in summer (P. Corkeron, in litt.), while from aerial surveys calves were not observed from January to March (Lear and Bryden 1980). It is possible that observers from altitude did not see calves and newborns because of their small size.

The overall activity budget of the Jervis Bay bottlenose dolphins is not dissimilar to those elsewhere, with travelling being the most frequent activity, feeding intermediate and socialising relatively infrequent. We found that there was a substantial increase in feeding in the cooler months. There are other populations worldwide that also show an increase in time spent feeding during the coldest seasons as observed for the Jervis Bay dolphin population (eg. Gruber 1981; Shane 1990b). The increase in feeding in the cooler months has been hypothesised to be related to an increase in energetic requirements with decreases in water temperature and/or to changes in prey abundance (Bräger 1992; Shane 1990a). Water temperature in Jervis Bay decreases from a mean of 22.5° C in February to a mean of 14.5° C in August (Cho 1995). Given that most species have a Q_{10} metabolic rate of 2, and that a decrease in temperature of nearly 8 degrees equates to almost a doubling of metabolic rate (Gaskin 1982), it is not unreasonable to assume increased feeding requirements in the cooler months.

The presence of newborns in Jervis Bay only during summer and autumn, considering that the gestation period of bottlenose dolphins is approximately one year (Perrin and Reilly 1984), suggest that mating in the area occurs during this time of the year.

Coincidently socialising, which has been hypothesised elsewhere to relate to calving and mating (Hanson and Defran 1993), was observed in Jervis Bay only during these seasons.

A highly variable number of sightings per individual indicate differential use of the bay by the animals, but the re-sightings of 48% of identified dolphins at least once during each season suggest that many are resident in the area. Furthermore, 36% of identified dolphins were composed of individuals observed inside the bay in only one of the four seasons, suggesting that a significant number of animals may visit the area only sporadically. While there is a possibility of simply failing to sight them, the hypothesis of migration of dolphins from the open ocean to the coast and/or from coastal waters outside Jervis Bay cannot be rejected .

ACKNOWLEDGEMENTS

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Re-interpretation of Remains of Snapper (*Pagrus auratus*) from Holocene Middens at Bass Point and Currarong, New South Wales.

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OWEN, J.F. AND MERRICK, J.R. (1998). Re-interpretation of remains of snapper (*Pagrus auratus*) from Holocene middens at Bass Point and Currarong, New South Wales. *Proceedings of the Linnean Society of New South Wales* **120**, 191–201.

The abundant remains of snapper (*Pagrus auratus*), dated at 7,000–270 years BP, from coastal middens at Bass Point and Currarong have been re-examined and analysed. By comparing measurements of a suite of head bones with extensive reference collections, standard length (SL) ranges at different levels have been determined. This re-analysis shows that size ranges and class frequency profiles are similar between lower (or pre-hook) and upper (or hook) levels at each site and, although size ranges of both sites overlap to a large degree, the mean size (SL) of Currarong individuals is higher. The populations exhibit different structures with few (13–36 %) adults at Bass Point, in contrast to ~ 88 % adults in both levels at Currarong. To test the hypothesis that angling results in an increase in size of individual snapper harvested, the pre-hook and hook level samples at each site have been statistically compared; however no significant size difference between snapper in the two levels is demonstrated. Similarly a combined comparison, with pooled data from both sites, does not show any difference in size related to the use of fish hooks.

In addition to biological, environmental or technological factors influencing target species, it is suggested that population intensification, cultural change and variation in local economies be considered when interpreting diversity or size of fish remains in late Holocene coastal sites in New South Wales. The combination of life cycle features and behavioural traits that makes *P. auratus* susceptible to over-exploitation is briefly explained.

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KEYWORDS: coastal middens, snapper remains, re-interpretation, sizing, Holocene, *Pagrus auratus*, social change.

INTRODUCTION

The significance of fish remains in archaeology has been internationally recognised for some years and major works, such as that by Casteel (1976), concentrated exclusively on this one category of faunal remains. Analyses of coastal middens in New South Wales have demonstrated both the wide diversity of foods used and the regular occurrence of fish remains (Godfree 1995; Leach 1979; Urqhart 1978). Sizing and identification of fish bones has been used to investigate seasonality of site occupation as well as the role of marine resources in the diets of coastal populations (Bowdler 1970,1976; Dyall 1982; Shawcross 1967; Sullivan 1984).

In Australia, the relatively recent introduction of angling has been linked to more efficient exploitation of marine resources and has been correlated with a gradual intensification of site occupation (Blackwell 1982; Sullivan 1984). Origins of angling technologies are still the subject of controversy (Attenbrow et al. 1997), but fishing with hooks and lines is reported to have first occurred in northeastern Australia 1,200–1,000 years ago (Rowland 1981; Walters 1988). It has been generally accepted that knowledge of

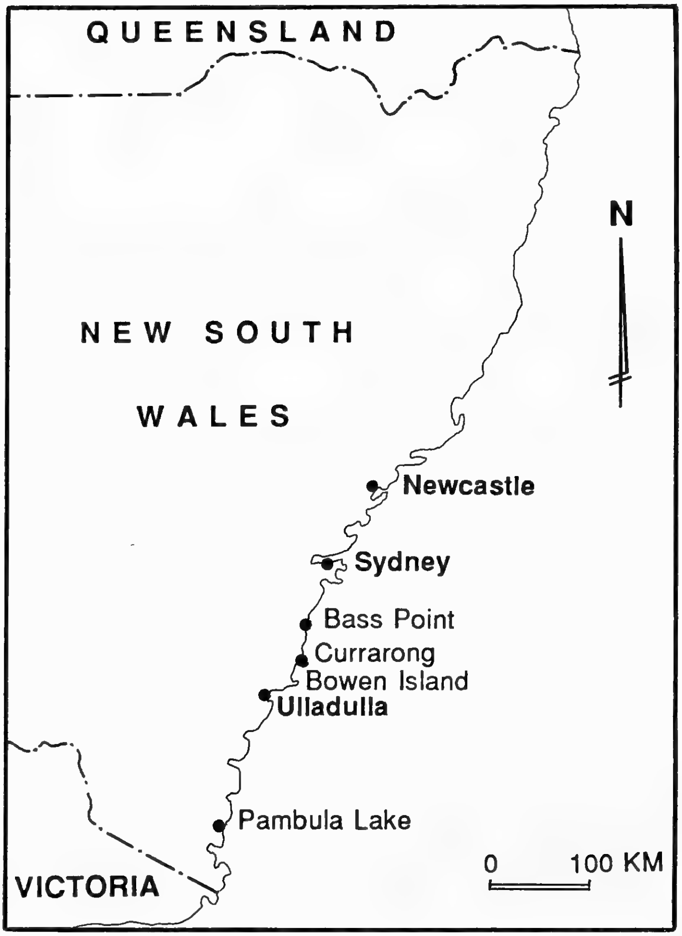

Figure 1. Locations of coastal Aboriginal midden sites studied and discussed, with regional population centres indicated for reference.

angling methods spread southwards along the eastern coast (Massola 1956), but these techniques were not adopted in some areas and alternative ideas for the transfer of this technology have been suggested (Walters 1988). Regardless of the mode of transfer it is clear that by 600–500 years BP angling was occurring in southeastern areas (Massola 1956; Walters 1988).

Two previous papers (Owen and Merrick 1994a,b) demonstrated that the findings of some local studies on fish remains in middens could be questioned on several grounds, including: small sample sizes; inappropriate measurements and analytical procedures; incomplete knowledge of the biology of target species or environmental influences on them; and over-simplistic assumptions about fishing techniques. The first paper (Owen and Merrick 1994a) investigated methods for accurate size and harvest determination; the second (Owen and Merrick 1994b) emphasised the selectivity of particular fishing techniques. This paper focuses on the suggestion by Bowdler (1970) that the introduction of angling resulted in an increase in the size of individual fishes harvested.

The snapper (formerly *Chrysophrys auratus* now *Pagrus auratus* (Paulin 1990)) has been one of the most important species in inshore fisheries of both temperate Australia and New Zealand during prehistoric and recent times (Anderson 1997; Anderson and McGlone 1992; Bell et al. 1991; Francis 1994a,b). Not surprisingly, snapper remains are reported to be abundant in middens on the south coast of New South Wales (Owen 1984; Owen and Merrick 1994b). Due to its commercial importance *P. auratus* has been extensively studied, especially in recent years (Bell et al. 1991; Francis 1994a,b; Francis et al. 1992; Hecht et al. 1996). New data on reproduction, growth rates, movement and population structure now permit a re-assessment of archaeological samples and their interpretation.

Sites, Excavations

Using size determination techniques outlined in Owen and Merrick (1994a), extensive series of *P. auratus* remains from Bass Point (34°36′S, 150°54′E) and Currarong (35°0′S, 150°50′E) have been re-assessed. These sites include faunal remains dated at between 7,000 and 270 years BP (radiocarbon dating). Details of the original excavations are described below. Localities (Fig. 1) and summary profiles (Fig. 2) from Bass Point are shown.

The Bass Point excavations (Bowdler 1970) covered a total of 7 m^2 (0.2% of total midden area) — to a depth of 1.15 m; materials recovered from 50 mm spits were sieved with a 4.77 mm mesh screen. Midden layers are distinguished on shell content and the site has been divided stratigraphically into four levels:

1. upper midden, base interface dated at 570 ± 75 years BP;
2. lower midden, base at depth of 400–450 mm;
3. grey sand (75–150 mm thick);
4. white sand (~ 600 mm thick) - top layers dated to 2,975 ± 145 years BP, base dated to 17,010 ± 650 years BP (Bowdler 1976: 254).

The three Currarong excavations, by Lampert (1971), are at the northern end of the Beecroft Peninsula and four levels (depth units) have been recognised for analytical purposes. Shelter 1 was excavated to a depth of 1.48 m and is dated at 1,970 ± 80 years BP at a depth of 1.10 m. Shelter 2 was excavated to 1.20 m and has a basal date of 5,540 ± 90 years BP. Shelter 3 was dug only to 0.9 m.

Specific objectives of the studies reported here are: to re-assess the size range of snapper in the archaeological remains at Bass Point and Currarong, using the bone size / fish length relationships derived from a comprehensive reference collection; to investigate size ranges of total samples from selected midden levels at each site; to relate size to the introduction of angling technology; to briefly discuss interpretation of fish remains in relation to population pressures, cultural change and modes of resource utilisation.

MATERIALS AND METHODS

Archaeological Sources, Measurements

Archaeological material examined was from collections held at the Department of Anthropology, University of Sydney, where the new snapper reference collection used for the size determination studies (Owen and Merrick 1994a) has also been lodged. This comparative series comprised material from 42 individuals (SL 132.5–479.5 mm). Details of preparation, bones selected, and exact measurement methods were fully documented in Owen and Merrick (1994a).

Using dividers and dial calipers, a total of eight measurements (seven head bones, sagittal otolith) were taken on archaeological collections, but only five characters (largest data sets) from three head bones (listed in Tables 1,2 and 3) were utilised in analyses. Each measurement , for the purposes of analysis, was considered to represent an individual.

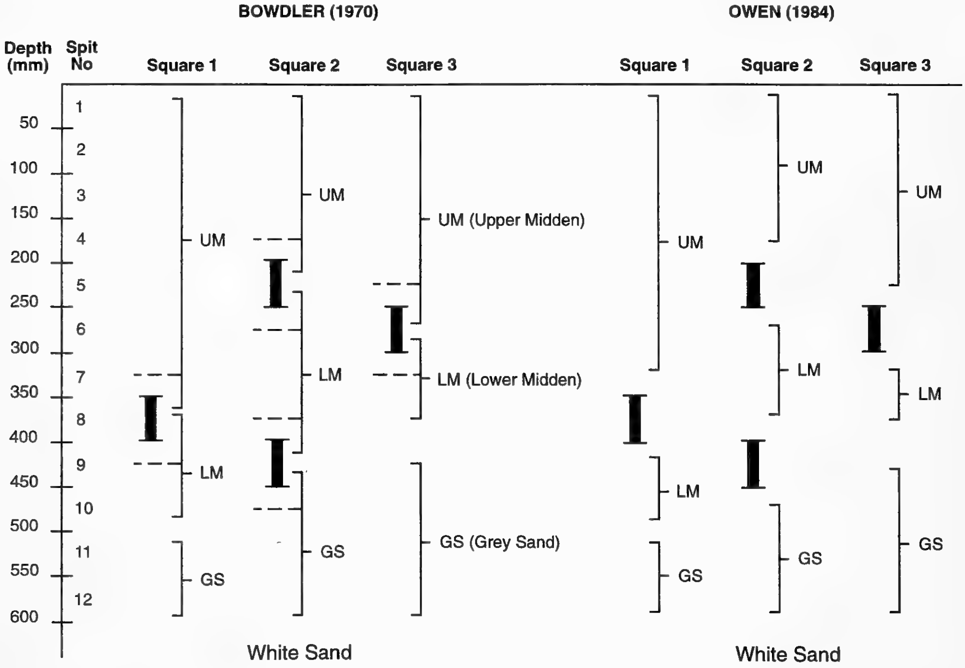

Figure 2. Midden layers exposed during two excavations at Bass Point, related to spit levels. Possible divisions between midden levels are marked (- - -) and intermediate spits not included in analyses indicated (I).

Analyses

For the linear regression analysis shown in Table 1, standard lengths (SL) for the archaeological samples were calculated to the nearest 0.1 mm. The histograms and statistical analyses have been based on total samples from upper (hook) and lower (pre-hook) levels. All specimens from intermediate areas, where there was a discrepancy between excavations (Fig. 2) or confusion about exact strata boundaries, were excluded.

For the purposes of comparing population structure the samples were divided into 40 mm size classes, from 159.95 mm to 679.95 mm, and 279.95 mm(SL) was designated as a minimal maturation size. Several two-sample t-tests (Zar 1984) quantitatively compared sizes in hook and pre-hook strata at both localities.

RESULTS

Estimated standard lengths (from each specific bone measurement) for material from different levels at both sites have been summarised in Tables 2 and 3. Length frequency histograms (Fig. 3) illustrate overall midden population structure (discussed further below) and details of t-tests are summarised in the text.

Population Structure

The total estimated size range at Bass Point was 160.6–555.6 mm SL. Figure 3a shows that an overwhelming majority (~ 87 %) of snapper harvested in recent times were in the size range 159.95–279.95 mm(SL). In pre-hook levels (Fig. 3b) about 64 % of individuals were of similar sizes; however, by extending the length range to 319.95 mm

~ 75 % of the population were included. The overall distributions of hook and pre-hook samples, although skewed, were similar with very few specimens in any size class above 319.95 mm in either level. This small number of large adults was emphasised in the histogram for the total Bass Point midden population (Fig. 3c), which shows that less than 20 % of specimens exceeded 319.95 mm.

At Currarong total estimated size range was 172.4–667.8 mm SL. The most frequent size classes at this site extended from 279.95–479.95 mm (Figs 3d and 3e) . In the hook level almost 74 % of individuals fell within this range and ~ 75 % of pre-hook specimens were in this size bracket. About 75 % of specimens, in both levels, exceeded 319.95 mm. The distribution profiles, at both levels, were similar (Figs 3d and 3e) and more regular than the Bass Point samples. This normal distribution was confirmed in the histogram for the total Currarong midden population (Fig. 3f), which shows an even normal pattern around peak frequency classes from 319.95–399.95 mm.

TABLE 1

Selected regression expressions relating specific snapper bone dimensions to standard length — calculated from *P. auratus* reference collection data (Owen and Merrick 1994a).

Bone		Bone Measurement to Standard Length(†) Relationship
Premaxilla	(process length)	$y = 0.62 + 12.47\,x$
	(jaw length)	$y = 3.12 + 9.78\,x$
Dentary	(height)	$y = 5.80 + 30.80\,x$
	(jaw length)	$y = 1.31 + 10.69\,x$
Supra-occipital	(width)	$y = 3.70 + 9.84\,x$

† Standard length (y) is calculated using the formula $y = a + bx$, when a is the constant, b the exponent and x the bone measurement.

Comparisons of Strata

The size ranges of specimens in pre-hook (179.8–555.6 mm SL) and hook (160.6–550.8 mm SL) levels at Bass Point were similar. The t-test confirmed the null hypothesis, that there was no significant difference between the mean sizes in pre-hook ($\bar{x} = 285.1$ mm SL) and hook ($\bar{x} = 254.7$ mm SL) levels

$$(\,|t| < t_{0.05\,(2)\,88},\ 0.10 < p\,(\,|t| < 1.987) < 0.20) \text{ at this site.}$$

The size ranges of specimens in pre-hook (199.5–667.8 mm SL) and hook (172.4–578.6 mm SL) levels at Currarong also overlap each other, as well as the Bass Point ranges, to a large degree. Only nine (~ 3 %) out of 292 Currarong specimens were estimated to exceed the maximum size calculated for Bass Point. Again the t-test indicated that there was no significant difference in mean size between pre-hook ($\bar{x} = 375.5$ mm SL) and hook ($\bar{x} = 384.2$ mm SL) levels

$$(\,|t| < t_{0.05\,(2)\,290},\ 0.20 < p\,(\,|t| < 1.969\,) < 0.50).$$

Figures 3c and 3f clearly show that population structure at the two sites differed. To minimise site-specific influences, data from the pre-hook layers at both sites were pooled and hook layer data were pooled for a combined comparison. Although the mean standard lengths for these pooled data sets were similar, the frequency histograms (Figs 3g and 3h) illustrate different patterns with relatively high frequencies in hook levels over a wide size range (159.95–479.95 mm SL). The t-test did not demonstrate any significant difference between mean sizes (pre-hook $\bar{x} = 357.7$ mm: hook $\bar{x} = 349.1$ mm) of the combined samples at the two levels

$$(\,|t| < t_{0.05\,(2)\,380},\ 0.20 < p\,(\,|t| < 1.967) < 0.50).$$

TABLE 2

Estimated standard lengths (nearest 0.1 mm) of *P. auratus* from the Bass Point archaeological collection (data summarised from Owen 1984).

Bone		Fish Hook Level (Upper Midden)			Pre-Fish Hook Levels (Lower Midden)		
Measurement	n	Range	Mean	n	Range	Mean	F value
Premaxilla process length	9	165.8–492.5	272.8	5	180.8–400.2	261.8	0.031<F 0.05
Premaxilla jaw length	17	162.2–396.0	230.3	5	179.8–285.4	226.9	2.124<F 0.05
Dentary height	12	187.3–523.1	278.7	10	245.9–501.5	315.0	0.750<F 0.05
Dentary length	8	160.6–550.8	268.3	6	218.3–314.6	265.6	0.046<F 0.05
Supraoccipital width	8	190.5–266.3	236.5	10	198.4–555.6	301.9	0.272<F0.05
Total measurements (Individuals)	54	160.6–550.8	254.7	36	179.8–555.6	285.1	1.066<F 0.05

TABLE 3

Estimated standard lengths (nearest 0.1 mm) of *P. auratus* from the Currarong archaeological collection (data summarised from Owen 1984).

Site,	Fish Hook Level			Pre-Fish Hook Levels					
bone	(Depth Unit 1)			(Depth Unit 2)			(Depth Unit 3)		
measurement	n	Range	Mean	n	Range	Mean	n	Range	Mean
Shelter 1									
Premaxilla									
Process length	15	224.4–511.2	369.2	10	313.0–468.8	379.3	6	276.8–397.8	367.5
Jaw length	37	230.7–498.7	359.8	31	221.9–493.8	363.4	10	243.4–442.9	334.8
Dentary									
height	44	181.2–535.4	381.9	28	249.0–667.8	390.6	16	208.9–535.4	388.3
Jaw Length	30	172.4–578.6	411.7	21	257.9–567.9	389.1	9	205.5–512.3	349.8
Shelter 2*									
Premaxilla									
Process length	2	427.7–569.9	498.8	2	199.5–511.2	427.1	1	310.5	310.5
Jaw length	6	343.2–523.1	474.9	3	202.3–377.4	296.2	1	277.6	277.6
Dentary									
height	6	187.4–452.2	328.0	5	378.3–520.0	455.7	–	–	–
Jaw length	5	188.4–508.0	377.4	4	398.0–534.8	481.6	–	–	–
Total									
measurements (individuals)	145			104			43	(=147 total for pre-fish hook levels)	

* As data from Shelter 2 were considered insufficient for a separate analysis, these measurements were combined with the more numerous data from Shelter 1.

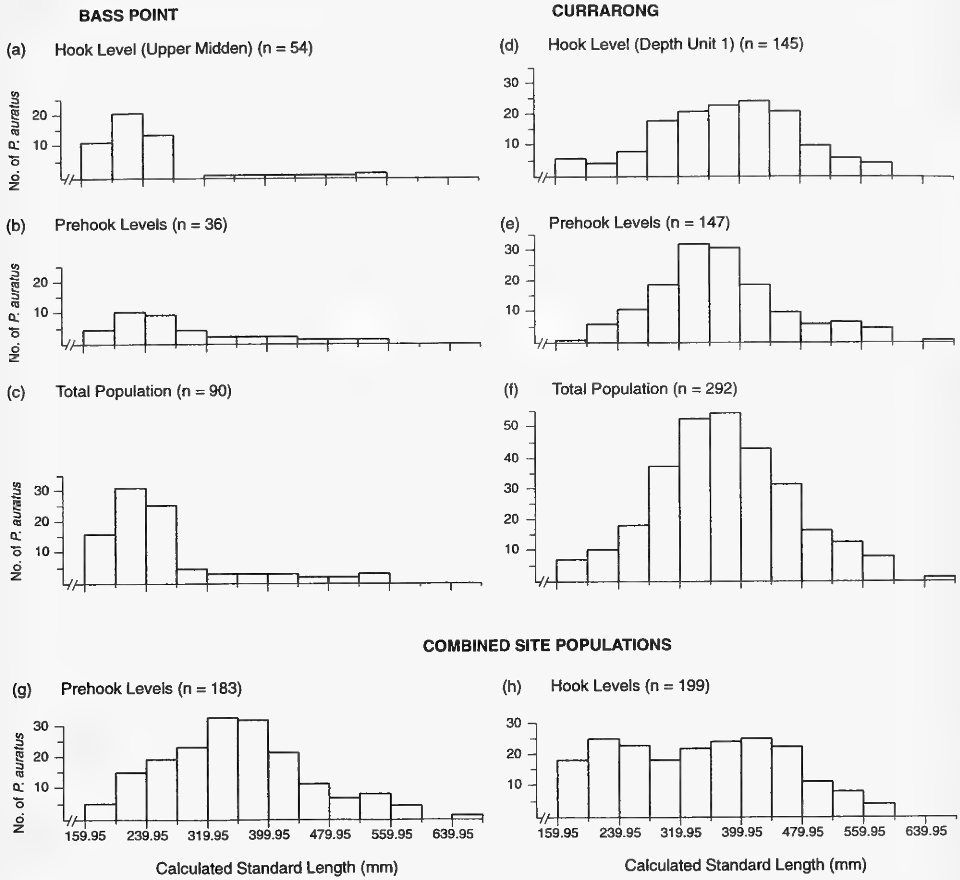

Figure 3. Relative size frequencies of archaeological snapper remains from two midden sites: (a) Bass Point - hook level; (b) Bass Point - pre-hook level; (c) total Bass Point sample, from all levels; (d) Currarong - hook level; (e) Currarong - pre-hook levels; (f) total Currarong sample, from all levels; (g), (h) combined site populations, all specimens in lower or pre-angling strata are compared with all upper or recent samples.

DISCUSSION

Although the remains measured only represent a fraction of the midden material at Bass Point and Currarong respectively, and pre-hook and hook periods differed in duration, nonetheless these samples are among the largest examined to date and the comparisons are of interest for several reasons. Previous studies (Owen and Merrick 1994a) demonstrated that a number of bone measurements can be used as accurate predictors of snapper size, but the reduced number of characters analysed here were based on the bones that occurred with the highest frequencies (largest measurement samples) at both localities. Each measurement of archaeological material had to be treated as if each bone was from a separate individual, as it was impossible to ascertain if similarly-sized paired bones were from the same individual or similarly-sized individuals. As a consequence, similar size determinations for several different bones may mean that they all came from a single individual, so the number of individuals represented may have been substantially less than the total values (n). The many factors that may influence harvests are discussed further below, but several conclusions can be drawn about the populations sampled.

Analyses

Neither the Bass Point nor Currarong samples included many large, old adults. Even the largest individuals were only about half the maximum size (~ 1200 mm: ~ 20 kg) recorded for the species (Last et al. 1983). The maturity size of 279.95 mm(SL) was selected as the point at which over 90 % of individuals were mature. Previous studies (Crossland 1977; Horn 1986) show varying percentages of maturing individuals, from ~ 50 % around 240 mm SL to 100 % at 300 mm SL, but newly mature individuals probably don't make any major contributions as breeding stock (Anon. 1984). Large percentages of snapper taken at Bass Point , in both pre-hook and hook levels, were immature with only 13–36 % adults . This suggests that the reproductive potential of Bass Point populations was limited (Anon. 1984), in contrast to Currarong where about 88 % of individuals in both levels were adults.

The size frequency profiles of the two sub-populations (hook and pre-hook groups) at each locality were similar, although the mean sizes of Currarong snapper are larger. The size ranges of *P. auratus* in pre-hook and hook layers were similar both at each site and between localities. The extended ranges at Currarong were due to a very small number of large specimens (exceeding the largest Bass Point individual) which occurred with approximately equal frequencies (~ 3 %) in both pre-hook and hook levels.

The three comparisons failed to detect any change in the mean size of *P. auratus* in connection with the use of the hook. However, a difference in the population structure at the two sites is indicated. It is impossible to explain this on present data, but contributing factors could include:

(a) more intensive harvesting at Bass Point prior to the levels (time interval) investigated, which resulted in removal of a high percentage of large adults;

(b) a genetic difference between populations with the Bass Point stocks representing a distinct genetic group that perhaps matured at a slightly smaller size. Genetic variability in other local snapper stocks, separated by similar distances, has been documented elsewhere (Smith 1990);

(c) a local difference in preferred techniques resulting in a bias towards capture of smaller, immature individuals in shallower more sheltered areas.

Technological and Cultural Change, Resource Utilisation

Despite the relatively large samples analysed, the fact that no significant differences could be established relating to the introduction of angling is not surprising. Impacts of this type of technological change would be very difficult to discern. Factors that would influence harvests, which may be reflected in midden remains, include: the many interacting biological and environmental parameters that affect growth and occurrence of fishes (Owen and Merrick 1994a); the variety of fishing techniques used concurrently and the selectivity of particular harvesting methods for target species (Owen and Merrick 1994b); and cultural change and altered resource utilisation as a result of population pressures in the late Holocene (Nicholson and Cane 1994). Whilst these studies were confined to snapper there are several general observations and recent findings which should be taken into account when analysing all coastal midden remains in south-eastern Australia.

Firstly, although individual interpretations may differ over some details, recent reviews (Lourandos and Ross 1994; Nicholson and Cane 1994) have reported a steady increase in coastal Aboriginal populations for several thousand years with accelerated growth over the last 2,000 years. This population trend resulted in increased requirements for food and intensification of site occupation.

Secondly, while it is clear that most marine and estuarine habitats were harvested, there were general cultural restraints or social differences which limited pressure on individual sources. For example, the totem system prohibited some members of the community from hunting particular species and , within a tribe, youths undergoing initiation or pregnant women were not permitted certain types of food (Kohen 1994, 1995). Whilst men fished with spears and the women usually collected shellfish, the whole community participated in other activities such as netting of seasonal schools of mullet migrating along the shoreline (Nicholson and Cane 1994; Owen and Merrick 1994b; Ross et al. 1996). The hypothesis of Bowdler (1970) linking the introduction of fish hooks and altered responsibilities, with women involved in angling while men continued fishing using other techniques, has been confirmed (Attenbrow et al. 1997).

Thirdly, the recent introduction of angling coincided with maximum pressures on food resources as well as cultural change. The concentration of population meant that demands for food were higher than at any previous time. Although Owen and Merrick (1994b) point out that angling does not normally exert a great pressure, it is cumulative, especially when combined with other techniques, and even minimal culling will dramatically reduce some species. There is also some evidence of an increased variety of species captured in recent times at other south coast sites, such as Bowen Island (Blackwell 1982) and Pambula Lake (Sullivan 1984).

Fourthly, there is evidence that coastal economies varied at different sites, depending on local resources and population movements. Coastal Aboriginal populations were not static, generally concentrating on the coast in spring or summer and then becoming more evenly distributed in winter. Sites very close to the sea were often only occupied for short periods and show a higher degree of specialisation. Whereas other sites, such as Currarong, had a mixed economy. Located at the juncture of several environmental zones (woodland,estuarine, marine) with abundant and diverse resources, the occupants at Currarong were not preferentially exploiting any particular zone or resource (Nicholson and Cane 1994).

The possibility of local over-exploitation of prehistoric coastal fisheries cannot be ignored and the snapper has a number of characteristics that make it susceptible to excessive harvesting pressure. *P. auratus* is a slow-growing, late maturing (~5 years), long-lived fish (<60 years) which appears to have limited local ranges (Anon. 1984). Although breeding is in deeper marine areas, development involves a prolonged juvenile and sub-adult phase (~ 4 years) in estuaries, to a relatively large size, before migration back to marine environments to join adult stocks. The adults are also reported to come closer inshore during an extended summer spawning season (Bell et al. 1991; Hecht et al. 1996; Roughley 1963). An aggressive nature and low diet selectivity mean that this species can be readily taken by angling, using a variety of baits (Winstanley 1984).

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