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Feeding and movement of *Anguilla australis* and *A. reinhardtii* in Macleods Morass, Victoria, Australia

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Feeding and movement of *Anguilla australis* Richardson, and *A. reinhardtii* Steindachner, were studied in Macleods Morass, Gippsland, Victoria from July 1975 to March 1977. Stomach fullness varied seasonally. Both species ingested a wide range of items with teleosts and insects forming the major group for *A. australis* and teleosts the major group for *A. reinhardtii*, which fed on a narrower range of items. No relationship between size of items ingested and size of eel was evident. Kendall rank correlation coefficients indicate that both intraspecific and interspecific differences in diets due to seasonal and size variations were usually insignificant.

Tagged eels were recaptured at the overall rate of 18·5%; of 1051 eels released, a total of 194 eels was recaptured. Maximum linear distance travelled by two eels was 3715 m while maximum days at liberty was 643 days. Home range was in the order of 400 m. No relationship between length of a tagged individual and days liberty or with distance moved was evident. Movement was closely related to fluctuations of water temperature with peaks being associated with feeding in the littoral zone of the Morass.

I. INTRODUCTION

Although detailed studies on the feeding biology of *Anguilla* spp. in the Northern Hemisphere have been published (Deelder, 1970; Ezzat & El-Seraffy, 1977; Godfrey 1957; Moore & Moore, 1976; Ogden, 1970; Pantulu, 1957), studies of Australasian *Anguilla* spp. have largely been centred in New Zealand (Burnet, 1952, 1968, 1969; Cadwallader, 1975*a*; Cairns, 1942; Hopkins, 1965, 1970; Jelliman, 1977; Kilner & Akroyd, 1978) and describe the biology of *A. australis* Richardson, and *A. dieffenbachii* Gray, predominantly in terms of interactions with introduced fishes, especially salmonids.

Studies of eel movement have until recently concentrated on monitoring either up-stream or downstream migrations normally associated with commercial exploitation, e.g. of glass-eels, or silver eels. While '. . . migration seems to be the most important phenomenon in the life cycle of the eel . . .' (Deelder, 1970), there are relatively sedentary periods within this life cycle as a consequence of a necessary physiological change, e.g. glass-eels to elvers, or during a time of growth and maturation, e.g. yellow eel phase. Investigations of movements of eels by conventional tagging methods (Aker & Koops, 1973; Burnet, 1969; Deelder & Tesch, 1970; Gundersen, 1976; Gunning, 1963; Gunning & Shoop, 1962; Hurley, 1972; Mann, 1965; Tesch, 1966, 1967, 1968, 1970) and by telemetric tracking of eels with ultra-sonic tags (Stasko & Rommel, 1974; Tesch, 1972, 1974, 1978) indicated that eels exhibit homing behaviour and occupy a definitive home range.

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Two species of Anguilla occur in south-eastern Victoria; the short-finned eel, *A. australis* and the long-finned eel, *A. reinhardtii* Steindachner. Several short-term investigations of the feeding of *A. australis* in Tasmanian rivers have recently been completed (Lake & Bennison, 1977; Sloane, 1976). Cursory observations of the diet of *A. reinhardtii* have been recorded from mainland Australia (Beumer, 1976; Stephenson, 1953).

In Victoria a small, but valuable, fishery yielding an average annual catch of 200 tonnes (1975–77) is based on the capture of both species of eel; *A. australis* constitutes 95% of this catch. An understanding of the feeding requirements and movements of eels is essential to continuing management of the present fishery and a prerequisite to eel culture. In this paper are reported the results of a 21-month study of the feeding of *A. australis* and *A. reinhardtii* and of the movements of *A. australis* based on mark-and-recapture data.

II. MATERIALS AND METHODS

Both species were collected from Macleods Morass, Gippsland, Victoria during a 21-month period from July 1975 to March 1977. The Morass is connected by an artificial drain to the Mitchell River which flows into the Gippsland Lakes complex. The drain is normally open from July to December (mid-winter to early summer). The Morass, an area of 423 ha, consists of two shallow zones located at either end of a much deeper zone (The Long Waterhole). The zones were delineated on an arbitrary basis as follows: Zone A = northern shallows (depth up to 1·2 m); Zone B = The Long Waterhole (depth from 0·30 to 5·1 m); and Zone C = southern shallows (depth up to 1·4 m), from which artificial drain flows into the Mitchell River. The Morass has been a State Game Reserve since 1966 and has been re-opened to commercial fishing for limited periods only since July 1977.

Samples were taken with fyke nets set overnight and checked by 1000 h the next morning. The nets were normally set for 2 nights each month except in January and February and October 1977, when nets were set for 3 nights each month. The positions of netting sites were recorded each time; between 8 and 16 nets were used each month. An attempt was made to collect 20 specimens of each species of eel per month for examination. Where possible the 20 specimens were representative of the size-range of the total catch. In a small system such as the Morass, where the size of the eel population was unknown, it was felt that the continual removal of more than 20 eels of each species may have an adverse effect on the population. The mesh-size of the fyke nets used was 25 mm to allow capture only of eels longer than the legal minimum size (300 mm) and also to preclude the taking of small forage fishes, thereby reducing contamination of the stomach contents of captured eels.

Surface and bottom water temperatures (from max-min thermometers set during the netting period each month), salinity, conductivity, pH, dissolved oxygen, and water level were recorded each month. Air temperatures and rainfall data were obtained.

Eels retained for examination were anaesthetized with quinaldine immediately on capture and after measuring (to nearest 1 mm) and weighing (to nearest 10 g) were killed. The alimentary tract (from oesophagus to rectum) was removed, individually labelled and preserved in 10% formalin. In the laboratory, the contents of the Y-shaped stomach were removed and examined and items were analysed by the occurrence method (Hynes, 1950; Pillay, 1952). Variations of overall diet with size and season for each species and between species were analysed by using the non-parametric Kendall rank coefficient, τ, after Siegel (1956):

$$\tau = \frac{S}{N(N-1)}$$

where S is the observed sum of the $+1$ and -1 scores allocated by inspection of the relative position of each food item in both ranks and N is the number of food items in a rank. Where tied observations occurred the formula was modified accordingly (Siegel, 1956). The significance of τ was tested by using a normal approximation to test the null hypothesis that the true value of $\tau = 0$, using:

$$z = \frac{\tau}{\sqrt{((2(2N+5)/9N(N-1))}}$$

The significance of z was determined by reference to a table of areas of the normal curve. Probability values greater than 0·05 were considered to indicate dissimilar diets; from 0·05 to 0·01 the diets were considered to be similar; and for probabilities less than 0·01, the diets were considered very similar (Cadwallader, 1975*b*).

Only *A. australis* were tagged because the total number of *A. reinhardtii* taken was too small; all specimens of the latter were retained for examination. Eels were anaesthetized, measured and weighed before tagging. Three types of anchor tags were used: yellow Floy FD-68A (55 mm long with 40 cm of tubing; black legend); red Stockbrand (Perth, W.A.) (50 mm long with 35 mm tubing; white legend); and blue ' batch ' tags (55 mm long, no tubing or legend). Dennison (Mark II) tagging guns were used to insert tags below the anterior end of the dorsal fin base with the T-bar lodged firmly behind the interneural spines. Only eels longer than 300 mm were tagged. Tagged eels were released within 5 m of original capture site. Tagging was undertaken for two periods: October 1975 to February 1976 (excluding December) and August 1976 to February 1977 (excluding November).

Most eels were tagged and released within zones A and C with relatively few tagged and released within zone B. No mortalities were recorded during the tagging operations. A small number of eels were tagged and kept in laboratory aquaria for 3 months without mortality.

Eels were recaptured throughout the study period and during July to October 1977 when the Morass was opened to limited commercial eel fishing with fyke nets of dimensions similar to those used in the study. Two returns were also made by anglers. On recapture tagged eels were re-measured, re-weighed and where possible, again released. During the study, exact recapture sites were recorded but those recaptured during commercial fishing were only recorded as being taken in Zones A, B, or C. In the analyses of recaptured eels, original total lengths (at release) are used.

Ten species of fishes were recorded from the Morass during this study, short-finned eel, *Anguilla australis*; long-finned eel, *A. reinhardtii*; Australian smelt, *Retropinna semoni* (Weber); common galaxiid, *Galaxias maculatus* (Jenyns); sea mullet, *Mugil cephalus* L; European carp, *Cyprinus carpio* L, 1758; Crucian carp, *Carassius carassius* L, 1758; pvgmy perch, *Nannoperca australis* Gunther; big-headed gudgeon, *Philypnodon grandiceps* (Krefft); and tupong, *Pseudaphritis urvilli* (Cuvier & Valenciennes).

III. PHYSICO-CHEMICAL REGIME

Zones A and C are extensively covered with emergent vegetation including Juncus, Cyperus and Typha with Phragmites and Paspalum extending from the bank well into the shallow margins. Free-floating Azolla and Lemna were also abundant in these two zones. In zone B, Juncus, Eleocharis and Typha were established in patches around the margin of this zone with submerged vegetation including Vallisneria, Elodea and Myriophyllum in the shallower, more exposed margins.

Both surface and bottom water temperatures (Table I) followed a similar seasonal pattern with lowest values recorded during winter (June–August) and highest values in summer (December–February). Maximum surface water temperatures were generally lower than mean air temperatures except during summer (1975–76) and late spring–early summer (1976) but minimum surface temperatures were always, except in June 1976, well above minimum air temperatures. Thermal stratification was minimal with maximum surface temperatures being higher than maximum bottom temperatures by 0·5–2·0° C throughout the study except during October and November 1976 and March, 1977, when maximum temperatures were inverted by 0·5–3·5° C. The Morass may be

TABLE I. Physico-chemical data, Macleods Morass, Gippsland, Victoria

Month	Temperatures (° C) Surface Water Max	Surface Water Min	Bottom Max	Bottom Min	Air(B'dale) Max	Air(B'dale) Min	D.O. (%)	pH	Salinity (ppt)	Conductivity (μmhos-18 C)	Rainfall (mm)
1975											
Jul.	14·8*	8·9*	13·9*	8·6*	16·8	5·2	—	—	—	—	22·2
Aug.	17·0	9·0	15·5	9·0	15·0	6·0	—	—	—	—	103·2
Sep.	18·0	16·0*	18·0	12·5	18·5	8·1	—	—	—	—	65·1
Oct.	16·5	12·4*	16·0	11·8*	19·3*	9·3	112	6·0	0·6	< 1000	108·3
Nov.	20·0	17·0	21·0	16·0	22·8	11·6	98	6·0	0·5	< 1000	40·7
Dec.	28·0	24·0	27·5	19·5	24·2	13·7	88	6·8	0·6	< 1000	104·5
1976											
Jan.	26·5	23·0	26·5	20·0	22·9	13·8†	68	6·8	0·8	< 1000	60·2
Feb.	29·0	22·0	28·0	22·0	24·3	15·2†	90	6·8	1·3	< 1000	23·0
Mar.	20·0	18·0	20·0	18·0	21·3	13·4†	87	6·0	1·0	1120	54·6
Apr.	21·0	14·0	20·0	13·5	20·0	10·9†	—	6·0	1·2	1210	16·0
May	18·0	11·0	18·0	11·0	15·7	6·7†	126	6·0	1·2	1190	4·6
Jun.	9·0	6·0	9·0	6·0	17·9	6·8†	95	5·5	1·2	1120	145·2
Jul.	15·0	8·5	14·0	8·5	14·9	4·7†	69	7·0	1·1	1103	18·0
Aug.	12·5	10·0	12·0	10·0	15·0	5·1†	111	7·0	1·1	1217	83·2
Sep.	23·5	13·0	23·5	13·0	17·2	6·6	93	7·6	1·0	1047	70·6
Oct.	17·0	14·0	17·5	14·0	18·0	8·7	113	6·3	1·0	1251	88·6
Nov.	22·0	16·0	25·5	16·0	20·0	10·4	—	5·9	1·0	1055	77·0
Dec.	34·0	20·0	32·0	19·0	24·1	11·6	84	6·2	0·8	1071	40·8
1977											
Jan.	23·5	20·5	23·5	21·5	25·9	13·0	—	6·5	1·0	1460	36·7
Feb.	21·5	19·5	21·5	20·5	26·0	14·7	112	6·2	1·2	1679	49·0
Mar.	26·0	21·0	27·0	21·0	24·0	11·5	85	6·0	1·5	1709	54·8

*estimated temperatures.
†max/min temperatures for Lake Entrance (30 km east of Bairnsdale).

considered as polymictic (Bayly & Williams, 1973) probably because the surface is exposed to wind action and the Morass is shallow; these factors permit the rapid rate of warming of the water after low winter temperatures.

Dissolved oxygen concentrations, pH, salinity and conductivity fluctuated during the study period but none of these factors appeared to be limiting. The water level in the Morass varied by 50–60 cm during the study period as a consequence of rainfall, evaporation and effluent (final stage) of almost 2 million l day^{-1} (J. Walker, Consulting Engineer, Bairnsdale Water Authority, pers. comm.). Highest water-levels were recorded during late winter–early spring when exposed mud-banks around the perimeter of the Morass are inundated. The removal of water for pasture maintenance by riparian landowners during the summer also accounts for lower water-levels during this season. Rainfall was highest during the winter and spring months when 65% of all rainfall during the study was recorded.

IV. FEEDING

STOMACH FULLNESS

The stomach fullness of *A. australis* varied seasonally with more empty stomachs during the autumn-winter months although a few empty stomachs were present during

TABLE II. Monthly percentage occurrence of food items in stomachs of *A. australis* stomachs

Food item	Occurrence of each item per month																			
	1975					1976												1977		
	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Hymenoptera					10												5			
Coleoptera	29	7					5					10	40	31	10	29	5	10		5
Trichoptera												10								
Diptera	5											5			5					10
Odonata		27	5	15	15											6		5		
Hemiptera	19	27	25	10	45	45	30	30	10	20		25	45	54	45	47	40	70	76	60
Lepidoptera	5																	5		
Insect (M)	5						5		5				5			6	20		5	
Copepoda		7																		
Ostracoda		7											5		5					
Cladocera												50								
Atyidae		7				10	5	5	5							6		10		
Parastacidae																27				
Penaeidae								5												
Planorbinae	14	7											5	15		6	5	15		
Bulininae	14	13		15			5					5	5	8	10	18				
Cyprinidae	24	13		5	5	15	15	25	5	20			10	23	5		10	35	19	15
Nannopercidae	10	33		5													5	10		
Galaxiidae	14	27	20	25	10	10	15	10	5	5	5	5	20		5				10	5
Retropinnidae		7	10	5										8						
Bovichthyidae			20			5			5	5		5			5					5
Anguillidae			5					5		5	5			8						5
Gobiidae	19	13	30	25		10	5	20	15	15	5	5	10	23	5	18	5			
Teleostei (M)	5	7	45	25	10	10	10	5	20	15		15	5	23	15	18	25	10	10	20
Amphibia	19	7		10	10										5			5		
Macrophytes	24	13	5	20	5	10		5	5	10		10		39	25	29	30	45	10	10
Algae		7										5	5	8	5	12	5	5	5	
Diatoms													5							
% empty	14	7	10	10	15	5	5	5	35	30	50	15	15	0	0	0	15	5	14	5
No. of fish	21	15	20	20	20	20	20	20	20	20	20	20	20	13	20	17	20	20	21	20

(M) = miscellaneous

TABLE III. Monthly percentage occurrence of food items in stomachs of *A. reinhardtii* stomachs

Food item	Occurrence of each item per month																			
	1975					1976												1977		
	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Coleoptera																		7		
Odonata																11				
Hemiptera					33											22		27	11	
Insect (M)																		7		
Atyidae					33	14	10									11				
Crustacea (M)													100							
Cyprinidae		100		100					17							11		53	56	
Galaxiidae						14	10		34									13		
Retropinnidae	50				33		10	50	17											
Bovichthyidae	50																			20
Anguillidae																22				20
Gobiidae					33		10		17					25	40	33			11	
Teleostei (M)									17				100	50	20		75	27	11	40
Macrophytes														25				40	11	20
Algae													100						11	
% empty	0	0	100	0	67	42	40	50	0	100			0	0	40	0	25	7	11	0
No. of fish	2	1	1	1	3	7	10	2	6	1	0	0	1	4	5	9	4	15	9	5

(M) = miscellaneous.

TABLE IV. Percentage of empty stomachs per month in each size-group for *A. australis* and *A. reinhardtii*

Month	310–459	460–609	Size-group (mm) 610–759	760–909	≥910
Aug.	—	25	9	0 (0)	(0)
Sep.	—	0	11	0	(0)
Oct.	—	25	0	0	(100)
Nov.	—	0	15	0 (0)	—
Dec.	—	20 (67)	7	100	—
Jan.	(0)	0 (67)	7 (0)	0 (50)	—
Feb.	(0)	0 (33)	0 (100)	25 (100)	—
Mar.	0	0 (50)	10	0	(0)
Apr.	50	43 (0)	14	50	—
May	50	40 (100)	22	25	—
June	100	55	43	0	—
July	—	13	10	50	—
Aug.	50	29	0	0	—
Sep.	0	0 (0)	0 (0)	0	—
Oct.	(0)	0 (33)	0 (100)	0	—
Nov.	(0)	0 (0)	0 (0)	0 (0)	—
Dec.	0	0 (0)	0 (100)	33	—
Jan.	0 (0)	29 (0)	14	0 (33)	—
Feb.	0	0 (0)	9 (0)	—	(100)
Mar.	(0)	13 (0)	0	50	—

the summer months each year (Table II). In *A. reinhardtii*, empty stomachs were present more often, particularly during summer (Table III). The increased number of empty stomachs in *A. australis* was related to low water temperatures during the winter months while in both species fewer empty stomachs were associated with elevated water temperatures and an increase in the area of inundated littoral zone of the Morass. Empty stomachs during summer may be the result of very high temperatures that may also reduce feeding activity in anguillids as shown by Boetius & Boetius (1967). The number of empty stomachs did not increase with increasing eel size (Table IV). The overall pattern for stomach fullness reflects the degree of movement of both species where the peaks of activity, as indicated by the higher monthly catches (Table V), were related to the presence of fewer empty stomachs.

STOMACH CONTENT ANALYSIS

Items occurring in the stomachs of both *A. australis* and *A. reinhardtii* varied during the study period (Tables II and III). Miscellaneous categories refer to fragments which were not identified. *A. australis* fed on 28 different categories while *A. reinhardtii* fed on 15 different categories of items. Within each common group of categories, i.e. insects, crustaceans, teleosts, and plant material, *A. australis* took a wider range of items than *A. reinhardtii*. In addition, molluscs and amphibians were also taken by *A. australis* but not by *A. reinhardtii*. The majority of items taken by both species were aquatic motile species with the only terrestrial items (lepidopterans and hymenopterans) taken by *A. australis*.

TABLE V. Monthly catches of *A. australis* and *A. reinhardtii*

Month	No. of nets	*A. australis* No.	*A. australis* $\overline{\text{T.L.}}$ (mm)	(range) (mm)	*A. reinhardtii* No.	*A. reinhardtii* $\overline{\text{T.L.}}$ (mm)	(range) (mm)
1975							
Jul.	8	0	—		0	—	—
Aug.	9	22	662	(545–875)	2	935	(770–1100)
Sep.	9	14	641	(460–785)	1	1220	—
Oct.	11	42	637	(375–760)	1	1000	—
Nov.	11	91	590	(322–865)	1	875	—
Dec.	16	149	602	(348–849)	3	505	(474–525)
1976							
Jan.	15*	55	685	(486–872)	7	616	(446–864)
Feb.	13*	262	631	(365–868)	10	547	(440–760)
Mar.	15	196	603	(313–893)	2	561	(549–572)
Apr.	13	83	639	(394–858)	6	617	(483–1170)
May	14	96	642	(393–817)	1	601	—
Jun.	13	36	636	(344–897)	0	—	—
Jul.	11	51	601	(342–897)	0	—	—
Aug.	14	47	593	(382–845)	1	287	—
Sep.	15	68	663	(352–853)	4	577	(503–666)
Oct.	15*	108	667	(397–868)	5	535	(439–660)
Nov.	15	20	651	(327–805)	9	608	(547–795)
Dec.	15	84	646	(375–816)	4	574	(525–653)
1977							
Jan.	15	405	625	(355–898)	15	551	(424–908)
Feb.	15	615	578	(327–895)	9	636	(486–1085)
Mar.	15	311	640	(425–885)	5	471	(430–500)

*Nets set for 3 nights.

Teleosts and insects were the major groups taken by *A. australis* while the major group taken by *A. reinhardtii* was teleosts. For both species, whole teleosts were normally taken only by specimens greater than 50 cm although scales, fish eggs, vertebrae, etc. were present in the stomachs of smaller specimens. Of the items taken by both species, only *A. australis* fed on those items that were predominant in the shallow, marginal areas of the Morass, e.g. amphibians, molluscs, lepidopterans, hymenopterans. The large amount of macrophytes, usually fragments of emergent vegetation, suggests that both species feed in the slower backwaters where such detritus settles. There was no apparent relationship between the size of prey and the size of eel as expressed by the ratio of prey length : eel (predator) length for the larger items taken (Table VI). The mean and range of these ratios also reflect the body form of the different fish species ingested with four of these, *G. maculatus*, *R. semoni*, *Anguilla* spp. and *P. grandiceps* all having elongate body forms while the cyprinids and *N. australis* have deeper compressed body forms. When smaller items were ingested, as in the occurrence of cladocerans (*Daphnia*) in July 1976, a wide size range of eels (497 to 792 mm long) fed on these.

SEASONAL VARIATIONS IN DIET

Except for the autumn–winter comparison, the seasonal diets of *A. australis* were very similar with neighbouring seasons exhibiting the greatest similarity (Table VII).

TABLE VI. Mean (and range) of the ratios of prey/predator lengths of larger items of different size-groups of *A. australis* (i) and *A. reinhardtii* (ii)

Item	310–459	460–609	Size-groups (mm) 610–759	760–900	≥910
(i) *A. australis*					
Cyprinidae	—	9·0 (—)	11·5 (—)	4·1 (2·8–6·6)	—
Nannopercidae	—	9·5 (7·8–11·0)	9·1 (7·9–10·6)	—	—
Galaxiidae	—	9·9 (5·5–16·5)	6·2 (2·1–12·7)	7·8 (4·2–11·2)	—
Retropinnidae	—	8·6 (7·2–9·9)	6·9 (—)	6·0 (—)	—
Anguillidae	—	17·2 (—)	17·6 (11·5–23·5)	21·3 (18·7–24·9)	—
Gobiidae	7·8 (—)	11·9 (5·7–15·7)	8·4 (4·0–13·5)	6·4 (3·3–9·6)	—
Amphibia	—	5·5 (—)	4·0 (—)	7·7 (—)	—
Macrophytes (*Eleocharis*)		12·1 (—)			
(ii) *A. reinhardtii*					
Cyprinidae	—	—	—	—	11·4 (8·6–14·1)
Galaxiidae	12·4 (—)	9·4 (8·9–9·7)	—	—	—
Retropinnidae	—	4·4 (2·4–7·9)	—	5·2 (4·0–6·8)	—
Anguillidae	—	—	38·2 (—)	20·8 (—)	—
Gobiidae	—	7·1 (3·5–10·9)	—	9·3 (5·7–12·8)	—

TABLE VII. Kendall rank correlation coefficients, τ, (with z values for testing significance), to compare seasonal differences within the diets of *A. australis* and *A. reinhardtii* respectively. The top portion to seasonal intraspecific comparisons for *A. australis* the bottom left portion to seasonal intraspecific comparison for *A. reinhardtii*

	Winter	Spring	Summer	Autumn
Winter	—	0·3521 (2·629)**	0·4763 (3·557)***	0·2674 (1·997)*
Spring	−0·5887 (−3·058)*	—	0·5516 (4·119)***	0·3521 (2·629)**
Summer	−0·3792 (−1·969)*	0·3714 (1·929)*	—	0·5318 (3·972)***
Autumn	−0·1536 (−0·798)	0·2003 (1·041)	0·3183 (1·654)*	—

*P=0·05–0·01; **P=0·01–0·001; ***P<0·001

The difference in the autumn–winter diets of this species was caused largely by the intake of molluscs, amphibians, and a greater diversity of insect, teleost and plant material during the winter months.

For *A. reinhardtii* however the autumn–winter and the autumn–spring comparisons were dissimilar while the remaining comparisons indicated only similar diets (P=0·05–0·01) between seasons (Table VII). The reasons for the lack of similarity is uncertain but may reflect the lower number of items taken, the lower numbers but wider size-range of specimens examined and the greater percentage of empty stomachs recorded for this species. Between the two species, the diets were very similar (P< 0·01) for all seasons except winter.

TABLE VIII. Kendall rank correlation coefficients, τ, (with z values for testing significance), to compare intraspecific differences in diet between size-groups of *A. australis* and of *A. reinhardtii*

	Size-group I (No.) (mm)	Size-group II (No.) (mm)	Corr. coeff. (*z*)
A. australis			
	310–459 (13)	460–609 (122)	0·4789 (3·577)***
	460–609 (122)	610–759 (200)	0·7123 (3·692)***
	610–759 (200)	760–900 (52)	0·4943 (3·733)***
A. reinhardtii			
	310–459 (9)	460–609 (51)	0·3834 (1·992)*
	460–609 (51)	610–759 (13)	0·3648 (1·895)*
	610–759 (13)	760–909 (7)	0·3087 (1·604)*
	760–909 (70)	⩾910 (5)	0·3087 (1·604)*

*P=0·05–0·01; ***P<0·001.

TABLE IX. Number of eels tagged per zone per length interval per tag type

Length interval (mm)	Floy A	Floy B	Floy C	Floy Σ	Stockbrand A	Stockbrand B	Stockbrand C	Stockbrand Σ	Batch A	Total A	Total B	Total C	Total Σ	% (of 1051)
310–359	1	—	—	1	2	—	—	2	—	3	—	—	3	0·3
360–409	4	—	1	5	5	—	16	21	—	9	—	17	26	2·5
410–459	10	—	4	14	22	—	45	67	1	33	—	49	82	7·8
460–509	8	—	5	13	33	—	88	121	4	45	—	93	138	13·1
510–559	9	2	3	14	51	1	71	123	9	69	3	74	146	13·9
560–609	5	4	11	20	70	4	65	139	10	85	8	76	169	16·1
610–659	8	3	9	20	71	1	51	123	11	90	4	60	154	14·6
660–709	11	6	7	14	69	3	45	117	4	84	9	52	145	13·8
710–759	3	2	4	9	74	2	24	100	1	78	4	28	110	10·5
760–809	4	—	2	6	34	1	11	46	1	39	1	13	53	5·0
810–859	2	—	1	3	12	—	4	16	2	16	—	5	21	2·0
860–900	—	—	—	—	3	—	1	4	—	3		1	4	0·4
Total	65	17	47	129	446	12	421	879	43	554	29	468	1051	

SIZE VARIATIONS IN DIET

There was no apparent relationship between the size of a particular item taken and the size of the eel. When the overall diets for the different size-groups of *A. australis* were compared for intraspecific differences, the diet of each size-group was very similar to the diet of the successive larger size-group (Table VIII). For *A. reinhardtii*, the overall diets of the different size-groups were similar (Table VIII). Comparing the overall diets of the size-groups for both species for interspecific differences, the diets for all groups were found to be very similar (P< 0·01).

V. RECAPTURES AND MOVEMENTS

TAGGING

A total of 1051 *A. australis* were tagged (Table IX). Of these, 83·6 % were tagged with Stockbrand tags, 12·4 % with Floy tags and the remainder with batch tags. Eels tagged with Stock-brand tags covered the entire length range sampled (310–900 mm); eels tagged with Floy tags were up to 850 mm long and with tags only from 510 to 800 mm in length. Of the eels tagged, 82·0 % were from 460 to 750 mm long with numbers of tagged eels in each 50 mm interval in this range being more or less equally represented. The marking of eels over a wide range such as this ensures that enough tagged eels remain available for recapture.

RECAPTURES

Between October 1975 and October 1977, 194 recaptures were made giving an overall return rate of 18·5 %. Almost all these were captured in fyke nets, either during the study (22 % of all returns) or by commercial fishing (76·8 %). No tag losses, as evidenced by open ' wounds ', were recorded but a further 7 eels were recaptured with only the tag bases remaining. In each case, the plastic tubing had broken free, leaving an exposed tag base. Returned tags, particularly the Floy type, were covered with periphyton, but the legend on the Floy tags was however distinct as long as 21 months after release. The white legend on the Stockbrand tags became indistinct in most cases after 8–9 months and tags were removed and examined under a binocular microscope before the serial number could be identified. In several recaptures the tags caused wounds but in each of these the T-bar had not locked behind the interneurals but was lodged in the dorsal musculature; all such eels were re-tagged.

Eight multiple recaptures were made with all eels being taken on two occasions (Table X). Of these, four were recaptured one day after tagging. Return rates for the Stockbrand tags were highest (21·1 %) and considerably lower for Floy tags (5·4 %) and batch tags (2·3 %).

TABLE X. Overnight and multiple recaptures of *A. australis*

Eel number	T.L. (mm)	Release date	1st Recapture	Distance moved (m)	2nd Recapture	Distance moved (m)
1	695	30.ix.76	19.x.76	⩽5	19.i.77	<5
2	764	30.ix.76	17.xi.76	⩽5	15.xii.76	400
3	779	30.ix.76	14.xii.76	85	16.viii.77	*
4	642	30.ix.76	19.i.77	⩽5	14.vii.77	*
5	750	19.x.76	20.i.77	200	16.viii.77	*
6	592	20.x.76	21.x.76	⩽5	23.ii.77	240
7	692	20.x.76	21.x.76	145	—	—
8	689	14.xii.76	15.xii.76	⩽5	20.i.77	90
9	695	19.i.77	20.i.77	⩽5	—	—
10	718	19.i.77	20.i.77	⩽5	22.viii.77	*
11	682	19.i.77	20.i.77	⩽5	—	—
12	680	19.i.77	20.i.77	⩽5	—	—
13	689	19.i.77	20.i.77	185	—	—

*Commercial returns from within original release zone.

TABLE XI. Recaptures per length interval per days liberty

Length interval (mm)	Days liberty											
	⩽5	6–50	51–100	101–150	151–200	201–250	251–300	301–350	351–400	401–500	501–600	601–700
460–509	—	—	—	5	—	1	—	—	—	—	—	—
510–559	—	—	—	3	3	8	6	2	—	—	—	—
560–609	2	3	1	4	8	7	5	1	—	—	1	—
610–659	—	2	2	4	8	6	5	3	—	—	—	1
660–709	6	6	4	2	11	17	2	5	2	—	—	—
710–759	1	2	2	1	4	12	4	3	—	—	—	—
760–809	—	3	2	1	—	4	5	3	1	—	—	—
810–859	—	—	—	—	—	1	—	—	—	—	—	—
Total	9	16	11	20	35*	57	25	17	2	—	1	1

*Includes batch tag return.

TABLE XII. Captures within zones and between zones

Release zone	Recapture zone	No. tagged	No. recaptured	% of tagged	% of recaptured
A	A	554	109	19·6	93·1
	B	—	1	0·2	0·9
	C	—	7	1·3	6·0
B	B	29	2	6·9	40·0
	A	—	1	3·4	20·0
	C	—	2	6·9	40·0
C	C	468	63	13·5	87·5
	A	—	8	1·7	11·1
	B	—	1	0·2	1·4

TABLE XIII. Linear distance moved per length interval of eels recaptured during study

Length interval (mm)	Distance (m) <5	6–100	101–200	201–300	301–400	401–500	501–1000	1001–4000
460–509	—	—	—	1	—	—	—	—
510–559	—	—	—	—	1	—	—	—
560–609	2	—	1	2	—	—	1	1
610–659	2	—	—	—	2	—	1	1
660–709	9	2	2	2	—	—	1	1
710–759	—	2	1	—	1	—	—	1
760–809	1	3	—	1	1	—	1	—
Total	14	7	4	6	5	—	4	4

The maximum period between release and recapture was 643 days. Recaptures increased to a peak at 201–250 days after release followed by a gradual decline with 97·9 % of the recaptures being made within 350 days of release (Table XI). During the study, most recaptures were made during the spring and summer months when total catches of both *A. australis* and *A. reinhardtii* were highest (Table V). Commercial recaptures were made throughout mid-winter to mid-spring with both angling returns made in summer.

MOVEMENT

Most eels were recaptured within the zones of release and may be considered as ‘ home fish ’ (Gerking, 1953) (Table XII). Only 20 eels (10·3 % of all recaptures) had moved to adjoining zones or from one end of the Morass to the other, e.g. from Zone A, through Zone B, to Zone C. These may be termed ‘ stray fish ’ (Gerking, 1953). The maximum linear distance moved was 3715 m for two eels (total lengths 620 and 715 mm) after 36 and 79 days respectively. The extent of movement is probably greater than that recorded here as only the linear distance may be measured from this type of mark-and-recapture data. Definitive home ranges (defined here as the area through which an

TABLE XIV. Days liberty of recaptured eels with linear distance moved

Distance (m)	Days liberty <5	6–50	51–100	101–150	151–200	201–250	251–300	301–350
≤5	6	5	1	2	—	—	—	—
6–100	1	4	1	—	—	—	—	1
101–200	2	1	1	—	—	—	—	—
201–300	—	1	2	2	—	—	—	1
301–400	—	1	3	1	—	—	—	—
401–500	—	—	—	—	—	—	—	—
501–1000	—	2	2	—	—	—	—	—
1001–4000	—	2	2	—	—	—	—	—

TABLE XV. Mean total length and length range per zone per month of catches (Sept. 1976–Mar. 1977)

Month	Zone	No.	$\overline{\text{T.L.}}$ (±S.D.) (mm)	Range (mm)
1976				
Sep.	A	55	675±82	432–833
	B	2	772±115	691–853
	C	11	588±126	352–762
Oct.	A	64	682±100	456–868
	B	8	681±54	607–762
	C	37	637±109	397–826
Nov.	A	10	652±102	484–805
	B	5	698±55	627–775
	C	5	601±173	327–748
Dec.	A	51	661±94	490–816
	B	7	630±86	535–790
	C	26	616±101	375–768
1977				
Jan.	A	276	640±102	355–898
	B	—		—
	C	129	592±98	366–845
Feb.	A	339	599±102	335–895
	B	12	678±105	485–815
	C	264	543±108	327–870
Mar.	A	207	629±82	425–840
	B	62	675±74	514–885
	C	42	641±97	448–865

eel normally travels (Hayne, 1949) and not implying a territory where aggressive interactions are to be considered (Gerking, 1953)) were determined for the 42 eels recaptured during the study period and the two angling returns (Table XIII). There was no apparent relationship between initial lengths of tagged eels and distance moved. Of the eels recaptured in the study and from angling returns, 81·8% had moved 400 m or less between release and recapture; the remainder moved between 501 and 4000 m.

Of the overnight recaptures, three eels (Nos. 3, 7 and 13) had moved a linear distance of between 145 and 200 m in about 24 h (Table X). One multiple recapture eel (No. 1) maintained a very limited home range during a 4 month period while another (No. 2) had a limited range (< 5 m) initially but after this the range was extended by 400 m. There was no relationship between linear distance moved and days at liberty (Table XIV) with 77·3% of eels moving 400 m or less within 150 days of liberty.

When the mean total length and length range per zone month were analysed for the period September 1976 to March 1977 (spring to early autumn), the larger sized eels were almost always taken in Zone B (the deeper water) and the smaller-sized eels in Zones A and/or C (the shallow water) (Table XV). There was a progressive decrease in overall mean size from September to February indicating the increased presence of smaller eels being retained by the fyke nets during late spring–mid summer, particularly in Zones A and/or C.

VI. DISCUSSION

FEEDING

The pattern of stomach fullness recorded here suggests that while the two species of eels feed occurs throughout the year, the intensity of feeding follows a seasonal pattern, being most intense during spring and summer months.

This pattern is similar to that reported for *A. rostrata* by Ogden (1970), Smith and Saunders (1955); for *A. anguilla* by Deelder (1970), Ezzat and El-Seraffy (1977), and Frost (1946); and for *A. australis* and *A. dieffenbachii* by Burnet (1952) and Cairns (1942). Although Burnet (1952) suggested that the number of empty stomachs increases with the eels increasing size as a consequence of a reduced feeding frequency by larger eels, this was not apparent for either species studied in Macleods Morass. The possibility that captured eels may have digested their food and therefore bias the number of empty stomachs recorded did not arise as the time between net setting and checking varied between 16 and 18 h. Cairns found that insect larvae and fish taken by eels were identifiable up to 24 and 36 h respectively after ingestion. While Sinha (1965) indicated that the digestion rates of eels may vary with size and physiological condition of the feeding eel and the size and nature of the prey, it is assumed in this study any digestion within the net-setting period was minimal. A further source of bias may be the capture of eels before they had ingested any food and thereby increasing the recorded number of empty stomachs. While the extent of bias is difficult to measure it should remain relatively constant.

The feeding of eels during June 1976, when minimum temperatures fell to 6·0° C agrees with the findings of Woods (1964) who also recorded this temperature as the lowest at which feeding occurs. Sloane (1976), however, found that *A. australis* taken at temperatures between 5° and 6° C had empty stomachs and found eels to feed only at temperatures above 12° C. The presence of many empty stomachs during the summer months is probably due to the high water temperatures recorded during this season. Boetius & Boetius (1967) found for *A. anguilla* temperatures higher than 26° C inhibited feeding; however, the nocturnal feeding habits of Australasian anguillids (Cairns, 1942; Skryznski, 1974) would minimize this effect.

In this study teleosts and insects formed the most abundant groups of ingested items in *A. australis* while for *A. reinhardtii* teleosts formed the major group. Both Lake and Bennison (1977) and Sloane (1976) found that with stream-dwelling *A. australis* in

Tasmania crustaceans and insects formed the main groups in the diet. Stephenson (1953) also reported that *A. reinhardtii* fed on teleosts (F. Dorosomatidae) while Beumer (1976) recorded this species in feeding on orthopterans, palaemonids and teleosts (F. Centropomidae). That teleosts are most important food for *A. australis* and *A. reinhardtii* appears to be a characteristic of anguillid diets, as indicated from reports in *A. bengalensis* by Pantulu (1957): on the New Zealand *Anguilla* spp. by Burnet (1952), Cairns (1942), and Phillips (1929); on *A. anguilla* by Frost (1946), Sinha (1969), and Sinha & Jones (1967); and on *A. rostrata* by Ogden (1970). In several studies where teleosts were absent from the diet or of minor importance (Hopkins, 1965; Lake & Bennison, 1977; Sloane, 1976) they were concerned with smaller eels, usually less than 600 mm, or on a few short-term samples.

A. australis had a more diverse diet consisting of 28 different items compared with 15 items for *A. reinhardtii*. This contrasts with the finding of Cairns (1942) that *A. australis* was not a diverse a feeder as *A. dieffenbachii*, the sympatric New Zealand long-finned species. There was no evidence of selection for particular items by *A. australis* although the fewer items recorded for *A. reinhardtii* may be due to selection and/or to feeding in the deeper water, (55·6% of all *A. reinhardtii* were captured in Zone B). The similarities in the overall diets, both interspecifically and intraspecifically, in most seasons and all size-groups, suggest there may be indirect competition for particular items. *A. reinhardtii* is the only species of a large number of commercial fishes in the Morass and within the Gippsland Lakes complex for which exploitation is nominal. This low exploitation, coupled with the similarities of its diet and habitat with those of *A. australis*, gives *A. reinhardtii* ecological advantages over *A. australis*, the species which forms 95% of the annual Victorian eel catch.

Cannibalism is recorded for both species and appears to be a characteristic of anguillid diets *vide* Hopkins (1970) for the New Zealand *Anguilla* spp. and for *A. anguilla* by Bertin (1956), Opuszynski and Leszczynski (1967), and Sinha & Jones (1967). There was no evidence to suggest that eels of either species changed their feeding habits markedly as they grew larger, a characteristic also reported by Sinha (1969). The range for the ratios of prey length: predator length for the larger items for *A. australis* (2·1–24·9) and *A. reinhardtii* (2·4–38·2) are similar to those recorded by Moore and Moore (1976) for piscivorous *A. anguilla*.

The wide range of items present in the stomachs of *A. australis* and *A. reinhardtii* is a characteristic of anguillid diets (Deelder, 1970; Godfrey, 1957; Moriarty, 1972, 1973; Opuszynski & Leszczynski, 1967; Pantulu, 1957; Wenner & Musick, 1975) and reflects the generalized feeding habits of this group in which the diet depends on the abundance and availability of food items.

TAGGING AND MOVEMENT

The success of anchor tags for comparatively long-term mark-and-recapture studies of anguillids is indicated by the recapture rate and the days at liberty, a maximum of 643 days being recorded. The Floy tag was most successful for the retention of the legend, and legibility whereas more eels tagged with the Stockbrand tags were re-captured. The variations in recapture rates according to the types of tag probably reflect the number of tags of each type used rather than the merits of a particular tag type. No tagging loss was recorded but the decline in recaptures after 250 days liberty suggests either that increasing tag loss occurred after this period or that tagged eels may have moved out of the study area. Tagging losses in trout, where similar anchor tags (Floy FD-67) have been used, were found to be only 5·7 and 2·0% in two trials of 7 months with no affect on survival of the tagged fish (Carline & Brynildson, 1972).

In interpreting recapture data, Williams (1957) and Gerking (1959) have emphasised that the data represent the techniques of the author as much as the behaviour of the species being studied. The overall recapture rate of 18·5% in Macleods Morass was higher than that recorded from most other mark-and-recapture studies on anguillids, e.g. 1·3 and 10·7% for *A. rostrata* by Hurley (1972) and Vladykov (1957) respectively; 2·7% for *A. anguilla* by Gundersen (1976), but was less than 23·7% by Deelder (1962) and the 23·3 and 22·2% recorded by Tesch (1967 and 1970 respectively) for ' control eels ' in their homing experiments on *A. anguilla*. The recapture rates varied seasonally for *A. australis* and reflect both the seasonal movement of this species and to a lesser extent the fishing intensity. As indicated by the overall catches of both species during the study, movement was greatest during spring to summer months and points to a close relationship between movement and water temperatures where peaks of activity were closely related to elevated water temperatures. This phenomenon has also been reported in other anguillids (Gundersen, 1976; Mann, 1965; Nyman, 1972; Sattler, 1954; Sorensen, 1951; Wenner & Musick, 1975) although these authors reported on movements of stream-dwelling eels. Smith & Saunders (1955) contend that *A. rostrata* generally avoid ' cold water ' and found the largest populations within small, warm, shallow lakes. The relative inactivity of anguillids during winter months is well-known (Adams & Hankinson, 1928; Bertin, 1956; Deelder, 1970). While ' stray eels ' were recorded only to the extent of 10·3% of all recaptures, the actual number is probably much higher.

The presence of larger eels throughout the study period coupled with an increase in the number of smaller eels during the spring and summer months support the proposition that larger eels are less sensitive to low water temperatures (Alm, 1932; Sorensen, 1951). This is further supported by the presence of smaller eels predominantly in the shallow, warmer Zones A and B whereas only larger eels were generally taken in deeper, colder Zone B. This pattern of distribution and movement is similar to that described by Nyman (1972), from laboratory experiments, who suggested that the active dispersal of feeding and fattening of yellow eels (*A. anguilla*) after a relatively inactive crowded period in the colder months is size-dependent and permits the maximal exploitation of available food resources. In the Morass, the peaks of activity coincided with the inundation of marginal areas, as a result of late winter and spring rains, where the available feeding area in the littoral zone is enlarged. This is supported by the relatively lower number of empty stomachs recorded during the spring and summer months.

From the recapture data presented here, it is concluded that the majority of *A. australis* within the Morass exhibited limited movement. The extent of this movement reflects the home range and is considered to be in the order of 400 m. This home range is markedly greater than those recorded for *A. dieffenbachii* by Burnet (1969) or for *A. rostrata* by Gunning (1963) and Gunning & Shoop (1962), but again these authors report on stream-dwelling anguillids. Larger home ranges have been reported, e.g. that of 40 km for *A. anguilla* by Mann (1965) and that of 320 km for *A. rostrata* by Vladykov (1957), and there appears to be a direct relationship between the size of a home range and the size of the body of water in which anguillids occur. The data given here suggest the situation described by Gunning (1963) in which a stream-dwelling eel selects a particular locality and may then be expected to occupy this till maturity is equally applicable for eels found in small, relatively stable lentic habitats such as Macleods Morass.

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