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HABITAT UTILIZATION AND ITS RELATIONSHIP TO GROWTH AND REPRODUCTION OF THE EASTERN LONG-NECKED TURTLE, *CHELODINA LONGICOLLIS* (TESTUDINATA: CHELIDAE), FROM AUSTRALIA

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ABSTRACT: *Chelodina longicollis* occupies a wide range of ephemeral and permanent waters in the Jervis Bay Territory of coastal New South Wales. As ephemeral waters dry up during periods of low rainfall, which may span several years, the turtles retreat to the refuge of two permanent dune lakes. High population densities in these lakes coupled with low productivity lead to a sharp decline in growth, and reproduction ceases almost entirely. Differences between the lakes in the growth rates and body conditions of turtles coincide with differences in food availability. When rainfall increases, the turtles disperse once more to the ephemeral swamps where they grow faster and are in better condition; and reproductive output is considerably greater than in the permanent water. The propensity of the species for overland migration following rain is explained by the advantages of colonizing highly productive ephemeral waters, reinforced by the severe disadvantages of remaining in the permanent water of overcrowded drought refuges.

Key words: Dispersal; Population dynamics; Migration; Dune lakes

LONG range terrestrial movements are an important component of the population dynamics of many species of aquatic turtles (Gibbons, 1970, 1986). Turtles move overland seeking nesting sites or sexual partners, in response to seasonal cues, or as habitat becomes unfavorable (Gibbons, 1986). Habitat may become unfavorable as waters recede during droughts (Gibbons et al., 1983) or when there is a reduction in available foods (Parker, 1984).

Large temporal and spatial variation in food and water availability occur regularly, often unpredictably, in ephemeral aquatic habitats. Turtles occupying such habitats could be expected to exhibit a high degree of terrestrial mobility and be capable of aestivation in order to escape unfavorable conditions and to recolonize when conditions improve. Movement between habitats presumably occurs when individuals attempt to locate suitable conditions for growth and reproduction, and this may lead to large local variation in population densities.

Eastern long-necked turtles (*Chelodina longicollis*) are distributed throughout eastern Australia (Cogger, 1975) where they occupy both permanent freshwater lakes and rivers and ephemeral ponds, rainpools, and swamps (Chessman, 1988). They can aestivate on land (Chessman, 1983) and often undertake extensive overland migrations (Anon., 1941; Chessman, 1984*a*; Stott, 1988). Female reproduction follows a cyclic pattern with nesting in the spring and early summer (Chessman, 1978; Parmenter, 1985). *Chelodina longicollis* is an opportunistic carnivore which uses its long neck in a strike and gape action (Legler, 1978; Pritchard, 1984) to secure fast-moving prey. Its broad diet includes plankton, nekton, benthic macro-organisms, carrion, and terrestrial organisms that fall upon the water (Chessman, 1984*b*; Georges et al., 1986).

In the Jervis Bay area of New South Wales, *C. longicollis* occupies a wide variety of permanent and ephemeral water

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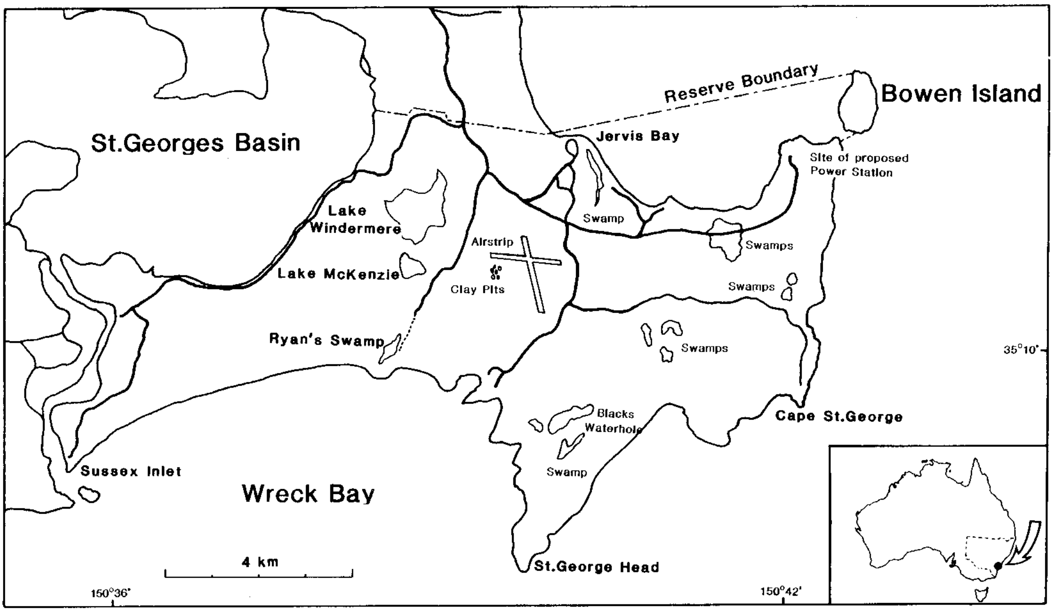

FIG. 1.—A map of the Jervis Bay Territory showing the locations of the lakes, waterholes, swamps, and place names used in this paper.

bodies that appear to differ markedly in productivity. The turtles are particularly abundant in Lakes Windermere and McKenzie (Georges et al., 1986), two permanent freshwater dune lakes. The hydrology, geology, and water chemistry of these lakes have been described (Jacobson and Schuett, 1984), but their biological characteristics have received little attention. Studies elsewhere indicate that dune lakes are typically low in nutrients and have low productivity and low biotic diversity when compared to other Australian waterbodies (Bayly, 1964; Bayly et al., 1975; Bensink and Burton, 1975; Timms, 1973). In view of this, and the low densities of *C. longicollis* in dune lakes studied elsewhere, Georges et al. (1986) considered the high densities of the species in Lakes Windermere and McKenzie to be somewhat puzzling.

We studied growth, reproduction, body condition, and population size of *C. longicollis* in Lakes Windermere and McKenzie and in a nearby ephemeral swamp, Ryan's Swamp, at Jervis Bay (Fig. 1). We used data, combined with information on movement between habitats, to construct a descriptive model of habitat use by *C. longicollis*. The model provides an explanation for the high densities of turtles in the lakes and identifies the advantages to *C. longicollis* of undertaking long and hazardous overland migrations.

STUDY AREA

The Commonwealth Territory of Jervis Bay is a peninsula about 7000 ha in area on the coast of New South Wales (approximately 150°43′ E, 35°09′ S: Fig. 1). It has a temperate climate with warm dry summers and cool wet winters. Annual average rainfall is 1264 mm (Fig. 2). The wettest months are March–June and the driest months are September–December. Average maximum temperatures range from 24 C in January to 16 C in July, and average minimum temperatures range from 17–9.5 C in the same months.

The two permanent lakes, Windermere (approximately 43 ha) and McKenzie (approximately 9 ha), are 800 m apart and were originally formed by drifting sand dunes that dammed a west flowing stream (Jacobson and Schuett, 1984). They are dystrophic with physical, biological, and

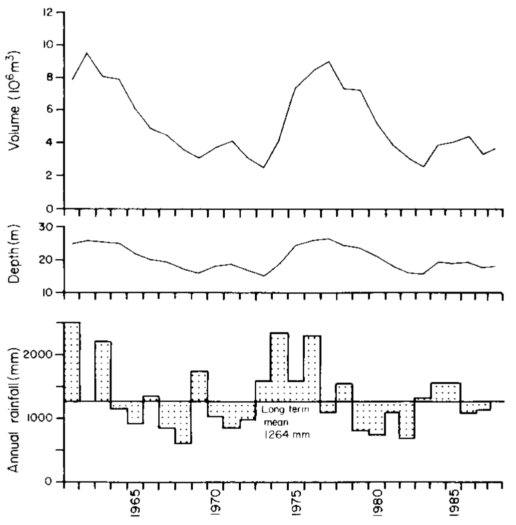

FIG. 2.—Fluctuations in annual rainfall 1961–1987 and corresponding changes in the monthly water level of Lake Windermere (after Jacobson and Schuett, 1984). The water levels of Lake McKenzie and the swamps were not monitored, but they are believed to follow a similar pattern.

chemical characteristics typical of dune lakes studied elsewhere (Bayly, 1964; Bayly et al., 1975)—dilute acidic waters with high proportions of organic material of terrestrial origin (Norris, unpublished data). They are closed, with surface inflows but no surface outflows, and isolated from the ocean and other freshwater bodies. The dark colored waters of Lake McKenzie have a higher organic load and contain a greater abundance and diversity of benthic and planktonic macro-invertebrates than the clear waters of Lake Windermere (Georges et al., 1986).

Ryan's Swamp is an isolated shallow (1–2 m) ephemeral freshwater swamp about 2.5 km south of the lakes. Unlike the permanent lakes, where emergent aquatic vegetation is limited to a few isolated stands of *Eleocharis sphacelata* and *Baumea arthrophylla*, the swamp has a dense cover of *Eleocharis sphacelata*, *Trichoglin procera*, and *Baumea articulata*.

In addition to Ryan's Swamp and the lakes, the territory has many other natural ephemeral waterbodies (e.g., Blacks Waterhole) and a few ephemeral waterbodies created during mining for fire-clay and in preparing a site for a proposed nuclear reactor (Fig. 1). All of these are used by the turtles.

MATERIALS AND METHODS

A mark–recapture program was undertaken between October 1983 and March 1987 to provide data on growth, movement, and population dynamics. Altogether, 566 turtles were marked in Lake McKenzie, 436 in Lake Windermere, and 135 in Ryan's Swamp. Six turtles were marked in Ryan's Swamp in 1983, but the site was not visited again until 1986. In Lake McKenzie and Ryan's Swamp, turtles were caught with hoop traps (Legler, 1960) baited with bread and sardines. Traps were cleared and reset at intervals of 1–3 h. In the clear waters of Lake Windermere, traps proved ineffective, and turtles were caught by hand with the aid of mask and fins. Each turtle was marked with a unique combination of filed notches in the marginal scutes and underlying bone. Population estimates were derived using Jolly-Seber analysis (Seber, 1973).

Carapace lengths (straight-line maximum) were measured with vernier calipers (±0.1 mm), and body weights were measured with Pesola spring balances and expressed in units of mass (±5 g). The sexes of turtle were not determined before 1986. In adult females, the posterior lobe of the plastron is roughly convex, whereas in males it is concave or irregular (Chessman, 1978). The reliability of the determination of sex in this way was checked with dissected animals ($n = 74$) and was 100% reliable for turtles with carapace lengths >145 mm. All turtles, except those retained for dissection, were released at their site of capture on the day of capture.

Incremental change in carapace length (CL) between captures was used as an index to growth. As captures were not always made exactly 1 yr apart, the fraction of the growing season covered by the period between captures was used to convert growth increments to growth rates. The growing season was assumed to be the 6 mo between mid-September and mid-March, as occurs in *C. longicollis* elsewhere irrespective of latitude (Chessman, 1978; Parmenter, 1976). If the period between captures spanned less than half of the growing season, the data were omitted from the analysis.

We had no means of determining when an individual arrived in Ryan's Swamp, so growth rates for these individuals were calculated using the maximum possible time that the animal could have spent in the swamp. These estimates are therefore conservative and represent the minimum growth rate possible.

Repeated measurements of individuals in the same capture period indicated that ±0.5 mm was a reasonable estimate of the accuracy of measurements of incremental growth. Individuals were classified as non-growers if they grew <0.5 mm in the period between captures and as growers if they grew >0.5 mm. The proportions of growing and non-growing individuals of each sex and in each habitat were compared in a chi-square contingency analysis (Zar, 1984).

Non-growing individuals were excluded form calculations of mean growth rates. Growth rates in Ryan's Swamp, Lake McKenzie, and Lake Windermere were compared after correcting growth rates for their dependence on body size (CL) using analysis of co-variance (Zar, 1984). The relationship between growth rate and body size was much more pronounced in juveniles than in adults, so the two groups were analyzed separately. Slopes of the regressions of growth rate on body size were first compared between bodies of water. Where the slopes were not significantly different, the elevations of the regression lines were compared to determine if the growth rates of turtles in the three bodies of water were significantly different. Differences in the growth rates of mature males and mature females were tested in a similar manner.

Fourteen male and 60 female *Chelodina longicollis* were collected from Lake McKenzie ($n = 25$), Lake Windermere ($n = 28$), and Ryan's Swamp ($n = 21$) at monthly intervals between October 1986 and March 1987, a period spanning the entire breeding season. Each was weighed and measured, then killed by intra-cranial injection of sodium pentabarbitone usually within two days, but never more than 10 days, from the date of capture.

In males, the colors of the testes and epididymes were noted, and fluids from them were examined under a phase-contrast microscope for spermatozoa. Females were palpated through the inguinal pockets to detect the presence of eggs (Ewert and Legler, 1978), and any gravid females were retained for dissection. Ovaries were weighed and corpora lutea were removed and their maximum diameters measured (±1 mm) with calipers. Ovaries were then fixed in 10% formalin, and once hardened, oocytes (>4 mm diameter) were removed and measured to the nearest 1 mm by means of a gauge containing a graduated series of holes (after Moll and Legler, 1971). Atretic follicles >4 mm in diameter were also counted; they could be distinguished from yellow developing follicles by their pink or reddish-brown color and pitted surface.

Oviducts and any subcutaneous fat in the inguinal pockets were removed and weighed (±0.1 g). Any eggs present were weighed and their maximum and minimum diameters were measured (±0.1 mm). They were incubated at 30 ± 0.5 C and at constant high but unmeasured humidity. Hatchlings were released from the eggs at time of pipping and weighed (±0.1 g).

Potential nesting sites (Chessman, 1978; Parmenter, 1976; Vestjens, 1969) were surveyed at regular intervals during the breeding season for signs of nesting activity. Surveys commenced in August 1986 at the lakes and in late October 1986 at Ryan's Swamp, and were discontinued at all localities in March 1987.

Comparison of the body condition of turtles in the different bodies of water were based on the assumption that a turtle in good condition would have a greater body mass than a turtle of the same length but in poor condition. Carapace length and body mass were log transformed (natural logs) to linearize the presumed power relationship between the two. Where the slopes were not significantly different, the elevations of the regressions between the two transformed variables were compared in an analysis of covariance (Zar, 1984) to detect significant differences in body condition between turtles from the different bodies of water and between turtles of each sex. In the absence of pronounced sexual dimorphism (Chessman, 1978; Parmenter, 1976), we assumed that males and females of the same carapace length and in the same condition would have the same body mass. Interpretation of differences in body condition for males and females depended on this assumption.

Throughout this paper, means are presented with standard errors, unless otherwise specified.

RESULTS

Sexual Maturity

In the absence of marked sexual dimorphism (Chessman, 1978; Parmenter, 1976), especially at onset of maturity, presence of sperm in the epididymes or testes was the only criterion for demonstrating sexual maturity of males. Unfortunately, absence of sperm could not be used to indicate immaturity, because the size-range of males without sperm completely overlapped the size-range of males with sperm. The two smallest males to contain sperm had carapace lengths of 145 mm and 147 mm, yielding 145 mm as the best estimate of the minimum size at maturity of males. It corresponds to the size at which males could be reliably distinguished from females on the basis of plastron shape. The age of animals with a carapace length of 145 mm is unknown.

The presence of oviductal eggs, corpora lutea, or enlarged ovarian follicles indicated sexual maturity in females. The smallest mature female had a carapace length of 162 mm whereas the largest immature female was 168 mm long, yielding 165 mm as the best estimate of the size at onset of maturity for females. Again, the age corresponding to a carapace length of 168 mm is unknown.

Female Reproduction

In Ryan's Swamp, the ovarian cycle followed the typical pattern for the species at other localities (Chessman, 1978; Parmenter, 1976, 1985). The ovaries were quiescent during the mid-summer months (December and January) when most follicles were small and larger ones (>7 mm) were regressing (Table 1). Follicles enlarged in February and March, before winter, and there was a corresponding increase in mean ovary mass. Follicles presumably continued to enlarge between March and October, as they were of preovulatory size (16–18 mm) by October.

Between late October and early November, ovaries of gravid females contained numbers of large corpora lutea (4–7 mm) that generally corresponded to the number of eggs in the oviducts (Table 1). However, one gravid female dissected in early November had 10 large corpora lutea, corresponding to the 10 eggs in the oviducts, and a further 11 corpora lutea presumably resulting from eggs laid earlier in the season. A second female with no oviductal eggs had 13 large corpora lutea and a set of smaller ones (not counted). These data provide evidence of multiple clutching by turtles in Ryan's Swamp.

No intact nests were found at Ryan's Swamp, owing to widespread predation, probably by the European fox (*Vulpes vulpes*). They have a characteristic method of slicing eggs open (Thompson, 1983*a*), and footprints and scats were found at a number of sites. The main nesting site was a flat grassed area on the western side of the swamp, but several nests were also found on a steep sandy path leading from the grassed area to a vehicle track on the top of a nearby ridge. Nesting occurred as early as mid-October, reached a peak in November and early December, and was finished by the end of December (Table 1).

Eggs of *Chelodina longicollis* are hard-shelled and ellipsoid in shape. A total of 74 eggs from 10 gravid females yielded the following mean dimensions (mean of means): egg length 30.4 ± 0.2 mm (range = 27.1–37.1 mm), egg width 19.0 ± 0.1 mm (17.7–20.6 mm), egg mass 6.4 ± 0.1 g (4.7–8.0 g). Eggs from a single clutch differed by as much as 6.7 mm in length and by 1.1 g. Egg mass, length, and width were not significantly correlated with the number of eggs in a clutch, but there was

TABLE 1.—Seasonal occurrence of ovarian follicles, corpora lutea of various sizes, and oviductal eggs for *Chelodina longicollis* from Ryan's Swamp. Data for juveniles and non-breeding females are omitted. Follicles <4 mm in diameter were present on all gonads but were not counted. Bracketed values are numbers of atretic follicles; + implies that the structures were present but not counted.

Month	Carapace length (mm)	Follicle size (mm)							Corpora lutea		Eggs
		4–5	6–7	8–9	10–11	12–13	14–15	>15	I	II	
Oct.	228.7	3	3	1	2		2		11		11
	217.3	2			1			10			
Nov.	218.0	6	4	2					10	11	10
	162.5	4					1		5		5
	224.8	16	1	4	3				13	+	
	237.9	4			1				13		13
	207.0	1	3						10		10
	209.1	1 (9)	2	2		1			8		8
	195.3	3	3	1		1	1		9		9
	175.9			1		1			7		7
	183.7	3	1	1	1				6		6
	167.1		1						5		5
Dec.	223.4	4	1		6	3					
	213.1			1		(1)					
	204.2	4									
	229.1	9	4	(1)	(1)						
Jan.	229.5										
	207.3	4	1	1							
Feb.	227.3	8	6	14	3						
	210.2	8 (3)	3	3	7						
Mar.	181.9	7	10								
	211.4	13	12	15							

a significant positive linear relationship between female carapace length and clutch size ($r^2 = 0.90$, $n = 10$, $P < 0.0001$). Clutch size can be predicted by the formula

$$\text{Clutch size} = 0.097\text{CL} - 10.9 \quad (\text{CL in mm}).$$

Clutch mass also showed a positive linear relationship to carapace length ($r^2 = 0.98$, $n = 10$, $P < 0.0001$) as did mean egg width ($r^2 = 0.54$, $n = 9$, $P < 0.05$), but mean egg length ($r^2 = 0.09$, $P > 0.10$) and mean egg mass ($r^2 = 0.1$, $P > 0.10$) did not.

Mean incubation time to pipping at 30 C was 61 ± 0.2 days ($n = 62$, range = 57–67 days). Of the 69 eggs incubated, three failed to begin development (possibly infertile) and four died at an early embryonic stage after chalking (Thompson, 1983*b*). Mean hatchling mass was 4.2 ± 0.1 g (3.0–5.2 g) and hatchling mass was positively correlated with egg mass ($r = 0.87$, $n = 60$, $P > 0.0001$).

Whereas all females from Ryan's Swamp dissected before December showed evidence of either recent or imminent ovulation, no females from either Lake McKenzie or Lake Windermere dissected at any time contained follicles larger than 5 mm in diameter. Follicles between 4 mm and 5 mm in diameter occurred in only four females from Lake McKenzie (5%) and three females from Lake Windermere (2%), and of the many turtles palpated for eggs in both lakes, only one specimen from Lake McKenzie was gravid. Masses of ovaries and oviducts were consistently higher in Ryan's Swamp than in either of the lakes. Ovarian mass also underwent an annual cycle in the swamp whereas it did not in either of the lakes. These data, together with the face that no nests were found at either lake despite extensive searches, suggest that the reproductive output of the lake populations was extremely low in 1986.

Growth

In Lake McKenzie, both mean growth rates and the percentage of turtles showing appreciable growth appeared related to rainfall (Fig. 3). In the drier years of 1984–1985 and 1986–1987, no adults grew ap-

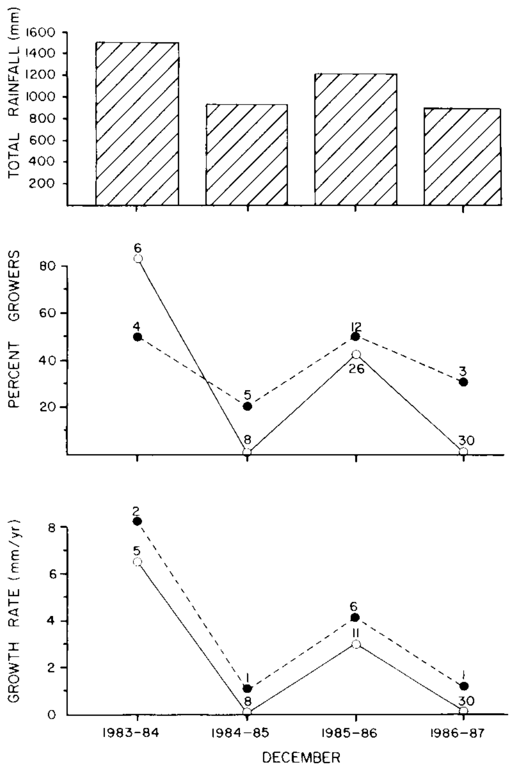

FIG. 3.—Yearly variation in total annual rainfall, the proportion of turtles that grew appreciably, and growth rates. Rainfall is calculated from 1 April–31 March of the following year to span the growing season. Dashed lines are for juveniles; solid lines are for adults. Sample sizes are given above the symbols.

preciably. Juvenile growth rates averaged 1.0 mm/yr, but only one juvenile from each of these years (20% and 30% respectively) showed measurable growth. However in 1983–1984, the wettest year of the study, 83% of adults grew appreciably with an average growth rate of 6.2 mm/yr. Fifty percent of juveniles grew in this year with an average growth rate of 8.2 mm/yr. With only 2 df, the significance of these associations between growth and rainfall could not be tested.

In general, Ryan's Swamp provided better conditions for growth than either of the lakes. All juveniles examined from the swamp grew appreciably, whereas a significantly smaller proportion (46% in each lake) of those examined form the lakes grew appreciably (χ^2 = 8.62, df = 1, $P < 0.005$: Fig. 4). Juvenile growth rates, corrected for body size, were significantly higher in Ryan's Swamp than in Lake McKenzie (F = 18.96, df = 3,42, $P < 0.0001$) and significantly higher in Lake McKenzie than in Lake Windermere (F = 4.12, df = 3,42, $P < 0.05$). Of the juveniles that showed appreciable growth, a juvenile with a carapace length of 110 mm would be expected to grow 5.7 mm in a year in Ryan's Swamp, 3.4 mm in Lake McKenzie, and 2.1 mm in Lake Windermere.

No sex-related differences in growth could be demonstrated for adults ($P > 0.50$ in all tests), so data for mature males, mature females, and unsexed adults were pooled. Only 7% of adults in Lake Windermere (n = 41) grew appreciably, significantly fewer than the 36% in Lake McKenzie (n = 41) (χ^2 = 8.61, df = 1, $P < 0.005$) and the 50% in Ryan's Swamp (n = 12) (χ^2 = 8.96, df = 1, $P < 0.005$). The percentage of adults showing appreciable growth did not differ significantly for Ryan's Swamp and Lake McKenzie (χ^2 = 0.25, df = 1, P = 0.62).

Adult growth rate was not correlated with carapace length at any locality ($P < 0.50$ in all tests). Mean adult growth rate in Lake Windermere was less than a third of that in Lake McKenzie and Ryan's Swamp (t = 2.35, df = 33, $P < 0.05$), whereas adult growth rates in Lake McKenzie and Ryan's Swamp were not significantly different (t = 0.45, df = 33, P = 0.66) (Fig. 4).

Body Condition

There was no significant difference in the body condition of juveniles from Ryan's Swamp and Lake McKenzie, but juveniles in Lake Windermere were in poorer condition than in either of the other two bodies of water (difference in elevation = 0.039: F = 13.16, df = 2,185, $P < 0.0001$). In Ryan's swamp, adult turtles (males and females combined) were in better condition than those in Lake McKenzie (difference = 0.037: F = 18.48, df = 3,361, $P < 0.0001$) and in Lake Windermere (difference = 0.072: F = 78.23, df = 3,361, $P < 0.0001$). Adult turtles in Lake Windermere were in

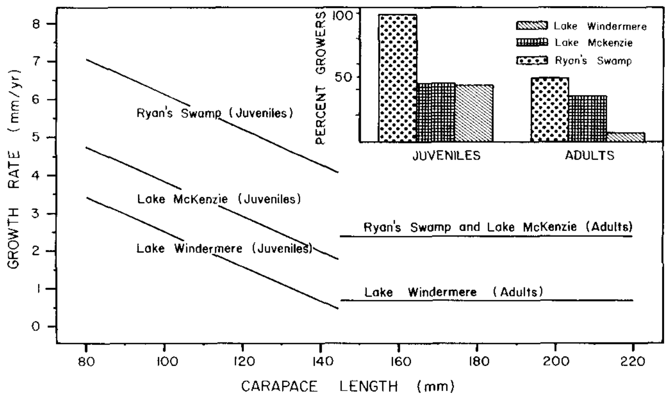

FIG. 4.—Relationship between growth rate and carpace length for juvenile and adult *Chelodina longicollis* in Ryan's Swamp, Lake McKenzie and Lake Windermere. Although diagrammatic, the magnitudes of regression elevations are accurate and only significant differences are shown. The insert shows the proportions of juveniles and adults that exhibited appreciable growth in each body of water.

the poorest condition, a finding consistent with observations made at the time of capture. Emaciated turtles were caught in both lakes, but more frequently so in Lake Windermere. These animals had sunken inguinal pockets, and the outline of the vertebrae could be seen in the neck. Many were unable to withdraw their heads into their shell when held upside down. No emaciated individuals were caught in Ryan's Swamp.

Females were in better condition than males in both Ryan's Swamp (difference = 0.049: $F = 2197.9$, df = 2,94, $P < 0.0001$) and Lake Windermere (difference = 0.062: $F = 2114.4$, df = 2,149, $P < 0.0001$) but were in similar condition in Lake McKenzie.

Dispersal

Ryan's Swamp was dry between July 1979 and April 1983. Four days after standing water was first present in the swamp, several turtles were caught there. One, found moving overland towards the swamp, was covered with fresh algae indicating that it had probably moved from nearby permanent water. In all, 18 turtles marked in Lake McKenzie or Lake Windermere were recaptured in Ryan's Swamp between October 1986 and March 1987. Fifteen of these turtles were among the 273 marked in the lakes in 1983 whereas only three of the 577 captured in the lakes in 1984 and 1985 were later caught in the swamp. This suggests that most migration occurred in 1983, shortly after the swamp first filled, though turtles continued to move to the swamp up to the end of 1985. No migration of marked individuals from Ryan's Swamp to the lakes was detected, but seven marked turtles were known to have moved between the lakes. The size range of turtles known to have moved was 127.0–219.0 mm carapace length ($n = 25$). Of the animals that could be sexed, 10 were male and five were female, yielding a sex ratio that was not significantly different from 1:1 ($\chi^2 = 1.1$, df = 1, $P = 0.25$).

Population Estimates and Sex Ratios

Population estimates for Lake McKenzie were 1440 ± 451 in October 1983, 1236 ± 309 in October 1984, 504 ± 60 in October 1985, and 405 ± 83 in 1986, declining steadily as the study progressed. The corresponding estimates for Lake Windermere were 506 ± 167, 1125 ± 473, 564 ± 155, and 551 ± 171. With the exception of the initial population estimate for Lake Windermere in October 1983, these population trends were consistent with migration of turtles from the lakes to ephemeral swamps following the end of the drought in 1983 (Fig. 2). The number of turtles in Ryan's Swamp also declined in 1986–1987, coincident with a drop in water level from 1.5 m in October to 0.8

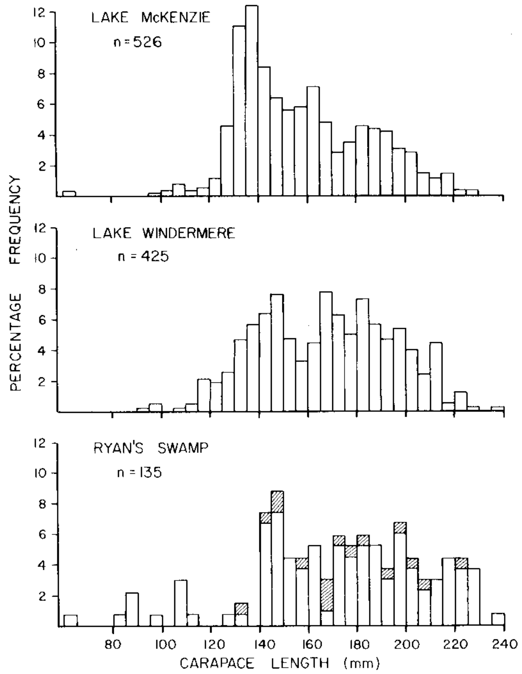

FIG. 5.—Size distributions of *Chelodina longicollis* in Lakes McKenzie and Windermere and Ryan's Swamp. The hatched individuals represent marked immigrants to Ryan's Swamp.

m in January. Population estimates for the swamp were 355 ± 138 in November 1986, 235 ± 192 in December 1986, and 94 ± 75 in January 1987.

There were no consistent trends from year to year in the size distributions of turtles from the two lakes. However, Ryan's Swamp contained a much greater size range of turtles than either of the lakes, with many more of the juvenile classes represented (Fig. 5).

The ratio of males to females >145 mm in carapace length was 51:61 in Ryan's Swamp, which is not significantly different from a 1:1 ratio ($\chi^2 = 0.72$, df = 1, $P = 0.40$). In contrast, sex ratios in both Lakes McKenzie (43:115: $\chi^2 = 31.8$, $P < 0.0001$) and Windermere (65:102: $\chi^2 = 7.8$, $P < 0.01$) were significantly biased toward females.

DISCUSSION

The turtles of Lakes McKenzie and Windermere appeared to suffer from severe food limitation. In 1986–1987, the lake populations failed to breed, and the lack of small turtles is an indication of poor reproduction in previous years. The absence of sperm in the epididymes of many mature males suggest that male reproductive processes were also affected, as other studies have shown sperm to be abundant in the epididymes of mature males throughout the year (Georges, 1983; Parmenter, 1976). Compared to turtles in Ryan's Swamp, turtles in the lakes were in poorer condition, fewer showed appreciable growth, and of those that did, growth was slower. Mortality is probably high in the lakes, though the large numbers of emaciated turtles, many of which were recaptured in poor condition throughout 1986–1987, suggests that *C. longicollis* is capable of withstanding long periods with limited food.

A comparison of the two lakes confirms that growth and body condition are related to food availability. In 1984, the summer standing crop (per unit area) of littoral macro-invertebrates in Lake McKenzie was seven times greater than that in Lake Windermere (Georges et al., 1986), representing a marked difference in food availability between the lakes. Compared to Lake McKenzie, fewer turtles in Lake Windermere grew appreciably, growth was slower, and the turtles were in poorer condition. Further indirect evidence for food limitation as the cause is provided by the close relationship between turtle growth and rainfall (Fig. 3). Freshwater dune lakes are low in nutrients, and production is driven primarily by the slow bacterial degradation of organic solids and solutes of terrestrial origin (Wetzel, 1975). Perhaps in years of above average rainfall, there is a greater than average input of organic nutrients, boosting production in dune lakes and leading to an increase in the abundance of aquatic invertebrates. Higher rainfall may also lead to an increase in abundance of terrestrial insects (Ballinger and Congdon, 1980; Bell, 1985; Dunham, 1978; Lowman, 1982; Takanaka and Takanaka, 1982).

Sex determination of chelid turtles, unlike that of most chelonian families, appears independent of incubation temperature (Bull et al., 1985; Georges, 1988; Thompson, 1988), and so temperature cannot explain the biased sex ratios in the lakes. Nor is trapping-bias a likely cause, because similar bias was evident in samples obtained by diving, and traps in Ryan's Swamp did not yield a biased sex ratio. Hoop traps were unbiased with respect to sex in other studies of chelid turtles (Georges, 1988). The most likely explanation is that males have suffered greater mortality than females in the lakes. In the absence of pronounced sexual dimorphism, the 5% difference in body mass between males and females in the swamp probably reflects the larger size of female reproductive organs, as ovarian mass ranges from 1–6% of body mass (this study) compared to 0.2–0.8% for testes (Chessman 1978). However differences in the mass of reproductive organs does not account for the 7% greater body mass of females in Lake Windermere, as maximum ovarian mass in both lakes was <0.3% of body mass. Instead sexual differences in body mass in Lake Windermere may indicate that males are more affected than females by conditions of severe food limitation. If this resulted in male-biased mortality then it would account for the female-biased sex ratios in the lakes.

Ephemeral aquatic habitats are generally highly productive environments, particularly after complete drying and refilling (Crome, 1986; Danell and Sjoberg, 1982; Kadlec, 1962; Swanson and Meyer, 1977). There are no data on production in Ryan's Swamp for comparison with that of the lakes, but in 1981, the standing crop of littoral invertebrates (per unit area) in the ephemeral Black's Waterhole (Fig. 1) was 3.7 times higher than in Lake McKenzie (Norris, unpublished data). In addition, competitors for food, such as fish (Chessman, 1984*b*), are often unable to invade the isolated ephemeral swamps. Presumed higher production in Ryan's swamp appears favorable for reproduction as seasonal variation in ovarian follicles and ovarian mass, and the production of more than one clutch per season, were consistent with the pattern described for the species at other localities (Chessman, 1978; Parmenter, 1985). Small individuals were well represented in the swamp (Fig. 5), strong evidence of substantial recruitment since the swamp refilled in 1983, as extensive overland migration by small turtles (carapace length <110 mm) is unlikely to be successful (Chessman, 1978).

Species of turtles exploiting the greater production of ephemeral waters must also overcome the problem of periodic and often unpredictable habitat loss. *Pseudemydura umbrina* of Western Australia is morphologically the most suited of all Australian chelids to survival without water (Legler, 1981), and it aestivates annually beneath litter or in burrows when the ephemeral swamps it occupies dry in the summer (Burbidge, 1981). *Chelodina rugosa* survives the annual drying of floodplain "billabongs" in northern Australia by burrowing into the substratum, and remaining inactive until the billabongs refill (Grigg et al., 1986). *Chelodina longicollis* is also capable of terrestrial aestivation (Chessman, 1983), but unlike *P. umbrina* and *C. rugosa*, it often occupies ephemeral waters that may be dry unpredictably for several consecutive years (e.g., Ryan's Swamp, Fig. 2; Hattah Lakes, Chessman, 1978). Prolonged aestivation in this species is unlikely, as laboratory studies indicate a limit of about 3 mo continuous aestivation without access to water for a 1 kg adult (Chessman, 1978).

We propose that individuals of *C. longicollis* at Jervis Bay move overland to seek refuge in the permanent waters of Lakes McKenzie and Windermere when ephemeral bodies of water become dry during prolonged periods of low rainfall. At such times, the number of turtles in the lakes would reflect the carrying capacity of both the permanent and ephemeral waters of the Jervis Bay Territory, and may well exceed the carrying capacity of the lakes alone. This explains the exceptionally high population densities in the lakes at the end of the 1979–1983 drought (Georges et al., 1986), the poor body condition and slow growth of the lake turtles, and the failure of these turtles to reproduce in 1986 and probably in earlier years. When a drought ends, as in 1983, turtles disperse from the permanent lakes to occupy ephemeral waters that become available again. The cue for these migrations may be a rising water level in the lakes or simply rainfall, as even light rain can stimulate migratory behavior in captive *C. longicollis* (personal observation). The decline in turtle numbers in the lakes between 1983 and 1986 is consistent with this dispersal phase. Turtles were observed at Ryan's Swamp within four days of the first standing water, indicating a very rapid initial migratory response.

The migratory tendencies of *C. longicollis* probably first evolved in response to selection for an ability to exploit productive ephemeral habitats in the absence of interspecific competition from fish (Chessman, 1984*b*) and other species of turtle (Chessman, 1988; Georges et al., 1986). However once populations grew to approach the carrying capacity of both the ephemeral and permanent waters of a region, individuals would have often found themselves occupying more restricted permanent water during extended dry periods, where intense intraspecific competition for food would cause a sharp decline in growth and reproductive output, as has occurred at Jervis Bay. Reproductive potential and onset of sexual maturity depend on size and not age in turtles (Gibbons, 1982), so any delay in growth while occupying a drought-refuge would have considerable consequences for reproduction of individuals. Under these circumstances, occupation of ephemeral waters would afford much greater selective advantages than could have been predicted from a comparison of production in ephemeral and permanent waters alone.

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