

Dynamics of habitat use by wading birds in a subtropical estuary:
Implications of hydrography

INTRODUCTION

The dynamics of habitat use by wading birds have been well studied for short-legged waders (Charadriiformes, Goss-Custard 1970, 1977; Holms 1970, Silliman et al. 1977, Myers 1980, Connors et al. 1981, Fleischer 1983), but are more poorly known for long-legged species (Ciconiiformes). This is especially true for marine systems where studies have focused on major environmental cycles (see Kushlan 1981 for review). Ciconiiformes (hereafter referred to as wading birds) are known to respond to major seasonal climatic changes (Henny 1972, Ryder 1967, 1978) and lunar tidal cycle^S (Brandman 1976, Krebs 1974, Bayer 1978, Custer & Osborn 1978a, Pratt 1980). Beyond the patterns imposed by these major cycles, little is known about the dynamics of habitat use by wading birds.

In the southern United States, where the annual climatic cycle is relatively minor and the lunar tidal range tends to be small (NOAA Tide Tables 1986), habitat use by wading bird populations is potentially independent of these factors. Therefore, an analysis of habitat use patterns may identify other factors that function as determinants of habitat use. In this study, I collected precise data on dynamics of habitat use by wading birds at a series of locations in a subtropical lagoonal system. These data were collected in conjunction with an analysis of habitat topography and hydrography. By combining these data, I was able to test two null hypotheses. First, in

the absence of restrictions imposed by a tidal cycle, habitat use would be independent of time. And second, in the absence of a strong annual climatic cycle (temperature) habitat use by wading birds would be constant throughout the year.

METHODS

Florida Bay is a large, shallow, lagoonal estuary situated between the southern coast of the Florida mainland and the island chain of the Florida Keys. A complex network of anastomosing, shallow mud banks runs throughout the bay (Fig. 1, Schomer and Drew 1982) providing extensive habitat for wading birds.

To provide a representative sample of habitat heterogeneity in Florida Bay, a study site was selected in each of 4 major subenvironments identified by Zieman & Fourqurean (1982, Fig. 1). The Northeastern habitat (Fig. 1, No. 1) was represented by a 6 km section of bank running from the mainland at Little Madiera Bay south east through the Park Keys. The East Central habitat (No. 2) was represented by a bank (Cross Bank) running from Plantation Key, 8 km west towards Captain Key. The Atlantic habitat (No. 3) was represented by a 4 km section of bank extending from the boundary of Everglades National Park at Bow-Legs channel to the western-most Buchanan Key. Finally, the Gulf habitat (No. 4) was represented by a triangular area (4 by 2.3 km at its base) of shallow bank bounded by Frank Key on the east, Flamingo channel on the north, and Conchie channel on the south. Each of these study sites consisted of shallow seagrass meadows with interspersed mangrove islands. The three eastern most of

these areas, Northeast, East Central and Atlantic, are largely linear in configuration reaching a maximum width of 300 m though typically measuring less than 200 m in width. The Gulf site in western Florida Bay was a wide bank measuring 2.3 km in width. The physical and floral characteristics of these sites are fully described in Powell et al. (1986).

Wading bird use of the different study sites was quantified by making systematic censuses of each area. Censuses were made from a 17 ft. open skiff that was run along the edges of the study area. Since all of the study sites were located within Everglades National Park, the wading birds were accustomed to boat traffic and were undisturbed by relatively close approach. The narrow width of the site coupled with the absence of obstructing vegetation permitted exact counts of wading birds present. Night-time data were collected with the aid of a 300,000 candle power spot light. At the East Central site, where there were no natural landmarks on the bank, it was necessary to set out transect markers (numbered PVC stakes) at 100 m intervals. These markers made it possible to plot bird locations to the nearest 25 m. During the first year of the study, one site (East Central) was censused semi-monthly at 3 h intervals for a continuous period of 72 h (24 censuses). Results from this first year indicated that a reduced frequency of censusing would accurately measure wading bird use of the study sites. Thus, during the second year, when all sites were surveyed, data were collected on randomly selected days during each of 3 2-month periods.

Under the reduced survey schedule, data were combined as either daylight or darkness. Darkness surveys were collected between 1/2 hour after darkness and midnight when nocturnal species had been found to be in greatest abundance. At one site, Gulf, tidal range was great enough to restrict wading bird presence to periods of low tide. At this site, data from low tide were used to generate bird use profiles.

To develop a hydrographic model for the study sites it was necessary to map the topography of each site. Mapping was accomplished by measuring down to sediment surface level from the naviface at slack high tide (at that time the water surface was measuring down to the sediment surface assumed to be level). These measurements were made at 20 m intervals along cross sections that ran perpendicular to the long axis of the study sites. At least 6 transects were measured on each of the 3 eastern linear sites. The Gulf site had greater topographic relief along its long axis which necessitated a depth profile for that axis in addition to two cross-sectional profiles. In order to correlate the topographic maps with tidal fluctuations, a continuous water level recorder (Leupold & Stevens Type F recorder) was placed in deep water (< 2 m) at each of the study sites. In conjunction with each recorder, 3 to 5 staff gauges were placed on each study site bank.

The translation of water level changes registered on the continuous recorder into water depths on the banks where wading birds fed was accomplished by correlating water levels at the continuous recorder with water levels at its associated staff gauges. For the eastern half of the bay where tidal change was

small, water level changes in the shallow banks were equivalent to changes at the recorders so a single correction value for each site adjusted the recorder record to water level on the bank. At the Gulf site in the western part of the bay, the water depth relationship was more complex and required separate equations for rising and falling stages (Powell et al. 1986). Equations, derived from these data, made it possible to accurately predict water depth at the staff gauges as a function of water level at the continuous recorders. Water level at the staff gauges was translated to depth on the bank through the topographic maps. Predictions of habitat availability for a particular wading bird species at a given study site were generated by solving the bank depth equations for times when levels were below maximum foraging depth of that species. Custer & Osborn (1978b) demonstrated that the water depth used by wading birds was dependent on leg length. To allow for maximum foraging access to the study sites by the various wading bird species, I used total leg length as the maximum foraging depth (Fig. 2). In addition, the model was adjusted for species that fed only during daylight or darkness.

RESULTS

Ten of the 11 species of Ciconiiformes recorded in Florida Bay foraged on the study sites (Table 1, Green-backed Herons, Eutorides striatus fed exclusively in mangrove areas so they were not a focus of this study). The 9 remaining species were present in sufficient numbers to allow statistical analysis of their distribution at one or more sites. One species, Ardea herodias,

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resides in Florida Bay as two distinct color forms one of which, the blue form, is composed of migratory and non-migratory components (Robertson & Kushlan ¹⁹⁷⁴ 1978). In view of the complexity in A. herodias population structure, the two color forms were treated separately.

The first year of study at the East Central study site demonstrated that most species were restricted to diurnal foraging. One species, Yellow-crowned Night Heron fed exclusively at night and two species fed in either daylight or darkness (Roseate Spoonbill and both Ardea color phases, Table 1). During daylight hours, wading bird presence was independent of time of day (Table 1). One of the three nocturnally active species, Ardea, and was present in slightly greater numbers between nightfall and midnight than during the rest of the night (Table 1).

Based on the wading bird activity patterns at the East Central study site, the censusing for the second year could be abbreviated. Daylight observations were made at random times throughout the day; darkness censuses were made between one-half hour after sunset and midnight, the period of greatest activity by nocturnal species.

The presence of all species, except the white form of Ardea, varied significantly with time of year (Table 2). The Blue form of Ardea showed a significant change at only the Northeast site where numbers were higher during the October-November observation period. Roseate Spoonbills were present in such small numbers during most of the year that analysis of trends was possible at only 2 sites. They were present in large numbers at the

northeast site during the October-November period and in small numbers at the East Central site during March-April (Table 2). Seasonal changes in populations of the other wading bird species were more pronounced and at 3 of the 4 sites followed a trend of greater abundance in spring than in fall (ANOVA, $P < 0.05$; Table 2). The greatest fluctuations occurred in populations of the smaller species. At the 3 eastern sites, Little Blue and Tricolored Herons, Snowy Egrets, Red-nosed Blue-Kneed Yellow-crowned Snook Snarfing Computer Whizzer, and White Ibis tended to be present in relatively large numbers only during March-April and to decline through fall (Table 2). The intermediate sized species, Great and Reddish Egrets, tended to follow this same trend at the eastern sites, but relative changes in populations were less pronounced (Table 2). At the Gulf site, seasonal trends in wading bird abundance differed from the eastern sites. Of the 4 small species, only the Tricolored Heron was present in lower numbers during the fall sampling period. The 3 remaining species were most abundant on the banks during fall (Table 2). Once again, both color morphs of the largest species, Ardea, were uniformly present throughout the year.

Water Depth Patterns

The elevation cross sections of the different study sites show that the 3 narrow banks on the eastern side of the Bay (Northeast, East Central, and Atlantic) are largely flat surfaces with relatively steep sides (Fig. 3). Therefore, at these sites availability of foraging substrate for wading birds simulated a step-function. When water levels were sufficiently low for a

species to feed, the entire bank top area was available. When the water level became greater than maximum foraging depth for a given species, most bank area became unavailable simultaneously. The Gulf study site, which is over 2 km wide, has a greater range in topography (Fig. 4). Therefore, at this site, the amount of foraging substrate available to wading birds was variable depending on water level.

From 1 to 4 years of water level data were collected at the 4 study sites between April 1981 and December 1985. The data show a complex, heterogeneous pattern of water level fluctuation in Florida Bay (Fig. 5). Three cycles with different periods were apparent in the data. Water levels exhibited a pronounced annual cycle that occurred uniformly throughout the Bay. Mean daily water levels during late summer and fall months averaged up to 30 to 45 cm deeper than during spring months (Fig. 6). A daily fluctuation in water level was recorded at each site, though the range differed by an order of magnitude among sites. Daily tide ranged from a highly irregular cycle of just a few cms at the Northeast site to a regular semi-diurnal tide of up to a meter at the Gulf site (Fig. 5). The East Central site had a daily tidal range similar to, but somewhat more regular than that of the Northeastern site while the Atlantic site was a regular semi-diurnal cycle of 20 cm (Fig. 5). The third cycle in water level fluctuations was an irregular cycle with a period of from 3 to 7 days and a mean amplitude of 21 cm ($n = 15$ in 1984). During these cycles, mean daily water level would rise for several days before dropping over several days to approximately the original

level (Fig. 7). These cycles, which occur infrequently and irregularly, appear to be largely an expression of wind effect on the shallow bay. Strong winds, particularly those associated with frontal activity, produce asymmetrical tidal movements (Allen 1942, Ginsburg, 1956, Corsline 1963, Enos & Perkins 1979). In association with cold fronts, wind direction clocks around from the fair weather easterly direction through southeasterly, when water levels tend to rise, through northwest, when there tends to be a net loss of water from the bay, before ultimately returning to the easterly tradewind (ANOVA, $P < 0.01$; Table 3).

The availability of foraging habitat for wading birds, as calculated on the basis of water level data, follows a marked seasonal cycle. At the 3 eastern sites (Fig. 8) water levels are predicted to be sufficiently low to allow all species of wading birds to forage daily during winter, spring, and early summer (Ardea, the tall species, may potentially feed both day and night, so their access to foraging sites is predicted on the basis of 24 h as opposed to 12 for the remaining species). However, by fall, water levels are consistently too deep for foraging by all species except Ardea herodias which, by virtue of its large size, is largely immune to seasonal water level changes (Fig. 8). The situation for western Florida Bay, as exemplified by the Gulf site, differs from that of the east. At the Gulf site, predicted habitat availability is far less variable and all species are expected to have access to sufficiently shallow water on the banks throughout the year (Fig. 8).

DISCUSSION

Diurnal species of wading birds in an area with little lunar tide were uniformly active throughout daylight hours. This habitat use pattern is consistent with the null hypothesis and therefore does not allow its rejection. Two species, Ardea and Roseate Spoonbill, were present as well, primarily at night. The Spoonbill feeds actively in daylight as well, but primarily at interior mangrove habitats (Allen 1942). At the eastern sites, ^{keep small} great white and great blue herons rest on nearly mangrove islands during daylight and fly onto the flats at ~~or~~ just after dusk to begin foraging. Nocturnal foraging by Ardea had been noted in other environments (Willard 1975, Bayer 1978, Pratt 1980), but only Black & Collopy (1982) quantified diurnal & nocturnal occurrences. They found Ardeas were present with equal frequency at low tide throughout the diel cycle. In Florida Bay, Ardea were present in significantly greater numbers during the first half of the night (ANOVA, $P < 0.01$), indicating that additional as yet undetermined factor(s) influence nocturnal activity patterns.

The observed seasonal dynamics of wading bird habitat use on the study sites are largely inconsistent with the predictions of the null hypothesis that, in the absence of a pronounced climatic seasonality, wading bird presence would be constant throughout the year. Wading bird use of available habitat is consistent with predictions of the hydrology model. In the eastern bay, where the model predicts seasonality in habitat availability, most species had a strong seasonal component to their presence that was consistent with the model (Fig. 9). Only the Great White Heron was uniformly present in eastern Florida Bay. They

are large and may feed any time day or night so they can be expected to have greater immunity to seasonal water level fluctuations. The seasonal variation in Great Blue Herons probably reflected seasonal migration as numbers were highest during fall months when winter residents are present. Seasonal distributions of wading birds were also consistent with habitat predictions for western Florida Bay. In conjunction with year-round habitat availability, all species were present throughout the year (Fig. 9). While most species demonstrated significant seasonal trends, there was no consistency in these trends among species.

While eastern and western Florida Bay have the same annual cycle in mean water level (Fig. 5), the predicted and observed impact of this cycle on habitat availability differ markedly for the two areas. These divergent habitat use patterns result from differences in the magnitudes of lunar tides at the two locations. In eastern Florida Bay where daily tides amount to only a few cms, a seasonally induced change in the mean water level has a greater impact on habitat availability than at the western site where the semi-diurnal tide may be greater than 1 meter. When water level in the bay reaches its maximum levels in fall, the lunar tidal range in the western bay is sufficient to lower water levels below maximum foraging level on a daily basis (Fig. 10). In contrast, the tidal range in eastern Florida Bay is so small, that even relatively minor increases in mean water level raise depths on the banks above foraging depth for the entire tidal cycle (Fig. 10). When water levels are low,

eastern bay wading birds have greater access to foraging habitat. However, when water levels are high the opposite occurs and the birds lose access to most eastern bay foraging sites.

The component of water level variability induced by wind also exerts a greater impact on habitat availability in the eastern bay. Here again, because of the small daily tides a relatively minor rise in daily mean water level can result in water depths that are too great for wading birds to forage even at low tide (Fig. 7). Thus, foraging habitat in the eastern bay typically becomes unavailable, particularly to the smaller wading bird species, for several days at a time even during the months of low mean water level (Table 4).

The occurrence of extended periods in eastern Florida Bay when water levels are too deep for most wading bird species to feed has major implications for those populations. When access to the extensive mud bank foraging sites is prevented by high water levels, the birds must either shift to alternative foraging habitats within the area or migrate. This loss of habitat occurs predictably during fall months when the annual water level cycle is at its peak. However, periods of deep water also occur unpredictably during the low water period in spring when most small wading bird species are breeding (Nesbitt et al. 1982).

Reference
Only one species, Roseate Spoonbill, migrates from Florida Bay, where it breeds in winter, north along the west coast of Florida during months when water levels are highest. The remaining 7 species (excluding Ardea must either shift to the western side of the bay (a distance of 40-50 km) or feed in areas of slightly higher elevation either on the islands within Florida

Bay or the surrounding fringe. Two of the 4 smaller species that declined in numbers in eastern Florida Bay when water levels were high, were present in greater numbers on the western side of the bay at that time (Table 2). This suggests that the response of at least some of the birds is to shift to the western sites. While this strategy may be an option for birds during the non-breeding season, the western foraging areas are probably too far away for breeding birds nesting in the eastern bay. Feeding flights by these species are generally less than 3-5 km and maximum flights are less than 30 km (Bateman 1970, Custer & Osborn 1978a, Erwin 1983, Hafner & Britton 1983). The largest known flight distance is for coastal colonies of White Ibis (Bildstein & Fredericks, ~~personal communication~~^g) that regularly fly up to 20 km and rarely 40 km to food rich inland foraging sites. A further disincentive to making long flights to the western side of the bay is that the western area also experiences high water levels (Fig. 6) and reduced foraging habitat availability (Fig. 8) when eastern bay areas are flooded. Suitable alternative foraging habitat in the vicinity of eastern Florida Bay consists of seasonally flooded areas that are kept open by high soil salinity and/or hurricane destruction of mangrove vegetation. These habitats amount to only a small fraction of the extensive bank habitat in Florida Bay.

Whether birds shift to the west or remain in eastern Florida Bay, periods of high water level, particularly when they occur during the breeding season, are undoubtedly stress periods, and the availability of alternative habitats during these periods

limits the size of wading bird populations in Florida Bay. The distribution of alternative foraging habitats may also explain the distribution of breeding colonies in eastern Florida Bay. The major colonies are situated in a ring along the eastern fringe of the bay. Moving in a clockwise direction, they include Tern Key, Porjoe Key, Butternut Keys, historically - but no longer Cowpens Key, mangrove keys adjacent to Cotton Key, Peterson Keys, Buchanan Keys, Green Mangrove Key and Barnes Key (Nesbitt et al. 1982, Powell unpublished data). All of these colonies are close to alternative foraging sites along the margins of the bay.

The dependence of wading birds on alternative, higher elevation, ^{foraging habitats} breeding sites has major management implications.

While Florida Bay itself is within Everglades National Park, most of the alternative foraging sites that fringe the bay are privately owned and in the past have been heavily impacted by human development. The destruction of these habitats has likely reduced the carrying capacity of the Florida Bay ecosystem, and future maintenance of viable wading bird populations in eastern Florida Bay will depend on preventing further loss of these areas. Maintaining viable wading bird populations in eastern Florida Bay is particularly critical to the continued survival of Eastern U.S. populations of Roseate Spoonbill and Reddish Egret. Both of these species have small populations that breed primarily in eastern Florida Bay.

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Fig. 1. Study sites in Florida Bay. Stippled areas are shallow banks used by wading birds as foraging habitat. One study site is situated in each of 4 subenvironments: Northeast (1), East Central (2), Atlantic (3), and Gulf (4).

Fig. 2. Maximum foraging depth of wading birds as determined by leg length. While wading birds generally feed at depths that are less than leg length (Custer & Osborn 1978b), leg length is here adopted as maximum depth to eliminate the possibility of under-estimating habitat availability.

Fig. 3. Bank profile data from 3 study areas in eastern Florida Bay (Northeast, 1; East Central, 2; and Atlantic, 3 sites). Each line is a cross sectional transect run perpendicular to the long axis of the bank.

Fig. 4. Topographic map of Gulf study area in western Florida Bay. Contour lines (cm) were generated from 3 cross sectional transects, one run down the long axis of the bank and 2 perpendicular to the long axis.

Fig. 5. Monthly means and mean daily range in water level at the 4 study sites in Florida Bay (Northeast, 1; East Central, 2; Atlantic, 3; and Gulf, 4.). See Fig. 1 for study site locations.

Fig. 6. Variation in mean monthly water level at 4 study sites in Florida Bay. Zero is annual mean water level for each site.

Fig. 7. Continuous water level trace from Northeastern study area showing wind related water level fluctuation during April 1984.

Fig. 8. Predicted habitat availability (mean number of hours per day) for wading birds categorized as tall, ARDEA; medium, GE & RE; and short species SE, LBH, TH, YCNH, RS, WI) at each study area in Florida Bay (see Fig. 1 for locations of study sites and Table 1 for Key to abbreviations). Habitat availability was generated by solving for hourly water depths on the foraging sites that were less than leg length for the respective species.

Fig. 9. Relationships between seasonal variation in habitat availability and wading bird presence at 4 locations in Florida Bay. The large species, Ardea (which can feed 24 hrs per day), has relatively constant access to all habitats and is uniformly present year-round. Smaller species have marked seasonal variation in access at 3 sites which is reflected in population fluctuations.

Fig. 10. Frequency distributions in hourly water levels at an eastern (Northeastern) and western (Gulf) study site during 3 months. When mean water level is low (May) wading birds have access to both feeding sites. However, when mean water level is high (October) tidal range at the eastern site is insufficient to permit access by most wading bird species to the foraging site at low tide.

Table 1. Temporal distribution of wading birds foraging on East Central study site. Species for which sufficient data were collected are Casmerodius albus, GE; Egretta thula, SE; Dichromanassa rufescens, RE; Florida caerulea, LB, Hydranassa tricolor, TH; Eudocimus albus, WI; Aiaia ajaja, RS; Nyctanassa violacea, YCNH; Ardea herodias (Blue & White combined), Ardea. Diurnal samples showed no significant differences in presence of species (ANOVA, P<0.05). Primarily nocturnal Ardea, was present in greater numbers during the first half of darkness (ANOVA, P<0.05).

		GE		SE		RE		LB		TH		WI		RS		YCNH		Ardea	
	N	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd
Dawn	33	8.4	6.5	1.6	2.3	4.2	3.5	11.9	13.1	7.6	8.9	24.5	30.7	1.6	2.5	0.0	0.1	22.4	17.6
0800-1100	25	6.6	5.8	1.3	2.2	3.8	3.0	8.1	10.1	5.4	5.2	12.6	20.6	0.7	1.4	0.0	0.2	17.9	19.8
1100-1300	16	5.5	4.6	0.3	1.0	3.9	2.6	6.8	8.9	6.5	7.5	8.1	12.0	0.5	1.2	0.0	0.0	22.6	21.7
1300-1530	17	6.7	6.4	3.0	4.9	4.7	3.9	14.3	16.2	9.5	8.7	20.0	30.3	0.4	1.0	0.0	0.0	19.8	19.1
1530-1800	29	8.0	6.2	2.3	4.2	4.5	3.2	11.7	12.3	6.6	5.9	20.4	30.3	1.0	1.9	0.0	0.3	16.1	11.1
Dusk	12	8.4	5.8	0.6	0.7	3.7	2.8	8.7	7.0	6.6	7.6	27.5	31.5	2.9	3.3	0.0	0.2	31.5	15.4
1850-2230	29	0.9	2.7	0.1	0.7	0.2	0.9	0.6	2.4	0.3	1.8	1.2	6.1	3.1	5.3	3.2	4.9	81.4	27.9
2230-0330	12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	4.1	5.0	5.2	83.0	13.5
0330-0615	21	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	2.5	4.8	3.6	7.1	58.0	22.7

Table 2A. Number of wading birds foraging at the Northeast site in Florida Bay. See Figure 1 for site location. Means with different superscripts are significantly different (ANOVA, $P \leq 0.05$).

Species	March-April			July-Aug			Oct-Nov		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
Great Egret	2.7 ¹	2.1	11	4.9 ¹	4.1	15	2.2 ¹	2.1	11
Reddish Egret	6.7 ¹	3.9	11	1.9 ¹	1.7 ¹	15	1.0 ²	1.0	11
Snowy Egret	0.0		11	0.0		15	0.0		11
Little Blue Heron	0.9 ¹	2.1	11	0.1 ¹	0.3	15	0.2 ¹	0.4	11
Tricolored Heron	9.7 ¹	7.3	11	0.5 ²	1.2	15	0.0 ²	0.0	11
White Ibis	6.4 ¹	4.0	11	0.5 ²	1.3	15	3.2 ²	10.5	11
Roseate Spoonbill	4.3 ¹	2.1	3	0.0 ²		7	24.8 ³	15.1	6
Great Blue Heron	0.7 ¹	0.6	3	0.0 ¹	0.0	7	3.3 ²	2.2	6
Great White Heron	17.0 ¹	4.0	3	13.9 ¹	1.9	7	13.3 ¹	3.7	6

What do the superscripts mean?

Spring

Table 2B. Number of wading birds foraging at the East Central site in Florida Bay.
See Figure 1 for site location. Means with different superscripts are
significantly different (ANOVA, $P \leq 0.05$).

Species	Number of Birds								
	March-April			July-Aug			Oct-Nov		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
Great Egret	10.5 ¹	7.4	12	6.9 ¹	3.6	22	2.6 ²	2.5	20
Reddish Egret	3.2 ¹	5.8	12	1.1	0.9	22	0.1 ²	0.2	20
Snowy Egret	5.5 ¹	3.9	12	0.5 ²	0.9	22	0.0 ²	0.0	20
Little Blue Heron	10.7 ¹	6.6	12	3.8 ²	5.7	22	0.3 ³	1.1	20
Tricolored Heron	8.4 ¹	6.6	12	1.1 ²	2.0	22	0.0 ³	0.0	20
White Ibis	25.1 ¹	15.1	12	12.0 ²	23.9	22	1.8 ³	6.1	20
Roseate Spoonbill	9.8	5.0	6	0.0		8	0.0		8
Great Blue Heron	2.8 ¹	2.2	6	1.9 ¹	0.8	8	2.9 ¹	1.6	8
Great White Heron	43.7 ¹	10.5	6	27.3 ¹	3.3	8	35.4 ¹	17.1	8

Table 2C. Number of wading birds foraging at the Atlantic site in Florida Bay. See Figure 1 for site location. Means with different superscripts are significantly different (ANOVA, $P \leq 0.05$).

Species	Number of Birds								
	March-April			July-Aug			Oct-Nov		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
Great Egret	5.0 ¹	3.2	8	6.3 ¹	6.5	23	1.0 ²	2.3	18
Reddish Egret	4.4 ¹	1.8	8	1.0 ²	1.3	23	0.0 ³	0.0	18
Snowy Egret	0.9 ¹	1.0	8	0.0 ²	0.0	23	0.1 ²	0.3	18
Little Blue Heron	18.7 ¹	9.5	8	1.0 ²	1.8	23	0.2 ²	0.7	18
Tricolored Heron	8.0 ¹	4.2	8	0.8 ²	1.7	23	0.0 ³	0.0	18
White Ibis	18.0 ¹	13.1	8	0.2 ²	0.7	23	0.0 ²	0.0	18
Roseate Spoonbill	1.7 [*]	2.9	8	0.0		7	0.0		8
Great Blue Heron	1.0 ¹	0.0	3	1.1 ¹	1.1	7	0.5 ¹	1.1	8
Great White Heron	14.0 ¹	6.2	3	10.3 ¹	4.6	7	5.7 ¹	3.1	8

* Present only during daylight

Table 2D. Number of wading birds foraging at the Gulf site in Florida Bay. See Figure 1 for site location. Means with different superscripts are significantly different (ANOVA, $P \leq 0.05$).

Species	Number of Birds								
	March-April			July-Aug			Oct-Nov		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
Great Egret	99.5 ¹	13.5	6	40.7 ²	10.8	6	74.5 ¹	35.3	12
Reddish Egret	0.0	0.0	6	0.0	0.0	7	0.0	0.0	12
Snowy Egret	1.0 ¹	1.5	6	0.1 ¹	0.4	7	9.7 ²	9.2	12
Little Blue Heron	41.0 ¹	11.7	6	55.4 ¹	13.5	7	105.0 ²	36.1	12
Tricolored Heron	24.4 ¹	5.9	5	15.9 ¹	6.9	7	5.5 ²	5.2	13
White Ibis	33.0 ¹	14.8	6	4.0 ²	5.2	7	68.0 ¹	44.0	12
Roseate Spoonbill	0.0		6	0.0		7	0.0		12
Great Blue Heron	13.8 ¹	1.9	6	12.0 ¹	1.9	5	10.6 ¹	5.4	11
Great White Heron	57.3 ¹	21.6	6	43.5 ¹	9.2	6	34.3 ¹	14.5	10

Table 3. Analysis of water level changes at the East Central site in correlation with wind direction. Rising tides tend to be greater than falling tides when wind is from the SE quadrant. The opposite is true when wind is out of the NW quadrant.

		X	N
NNE-E	Falling	3.59	(192)
	Rising	3.45	(185)
SSE-E*	Falling	3.06	(87)
	Rising	5.17	(88)
SSW-W	Falling	4.53	(27)
	Rising	5.12	(32)
WNW-N*	Falling	5.26	(85)
	Rising	3.76	(69)

*Rising & falling tides significantly different (ANOVA P\$0.01).

Table 4. Number of days and (greatest number of consecutive days) that water remained too deep for three species to feed at the Northeast site.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Great Egret	0	0	2 (2)	0	0	0	0	0	11 (4)	9 (4)	11 (7)	0
White Ibis	7 (4)	1 (1)	11 (6)	7 (7)	1 (1)	5 (5)	0	8 (6)	30 (30)	22 (20)	19 (7)	1 (1)
Tricolored Heron	11 (4)	6 (5)	11 (6)	8 (8)	5 (2)	6 (6)	0	20 (14)	30 (30)	26 (22)	24 (12)	4 (4)

Fig. 1

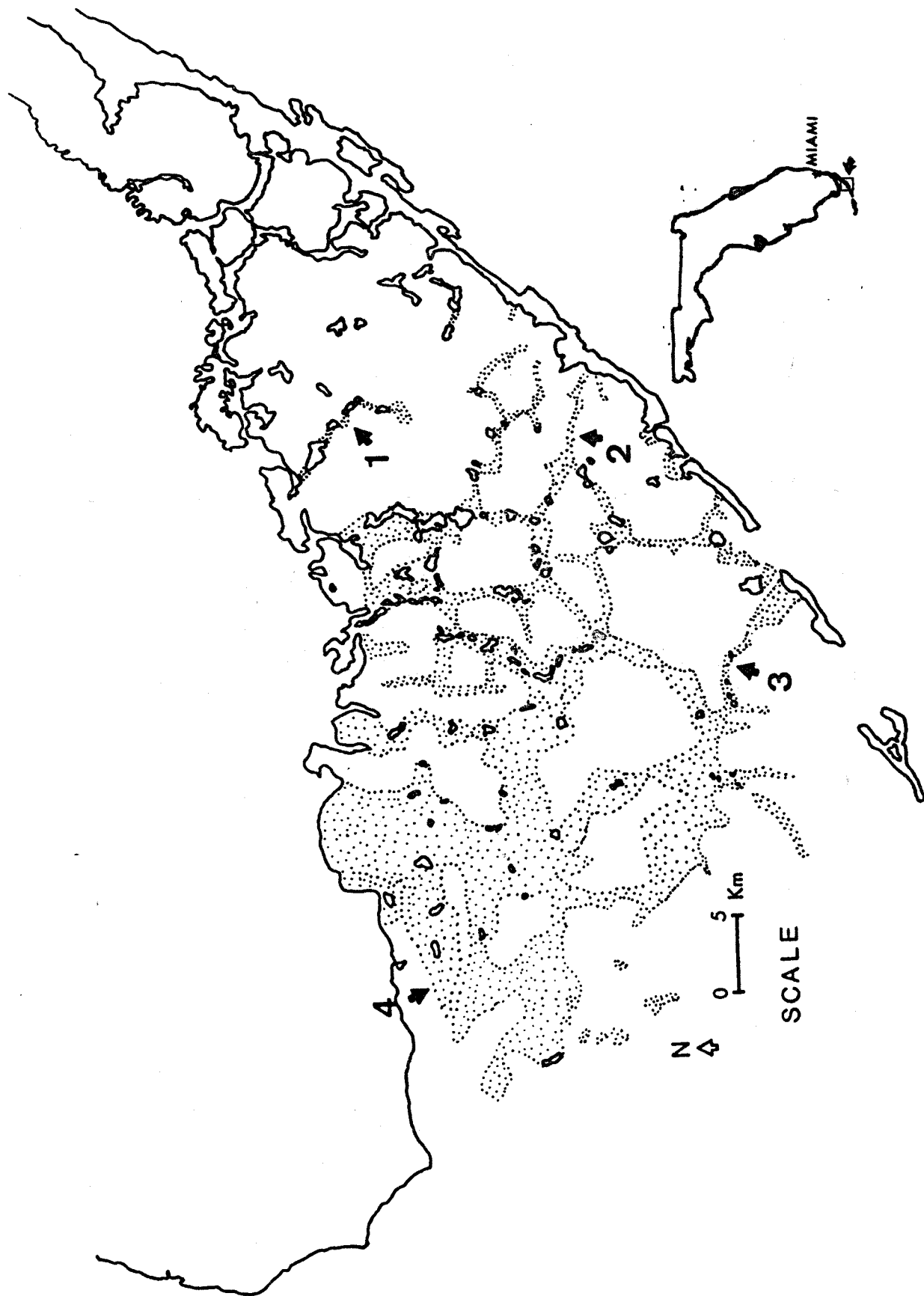


Fig. 2

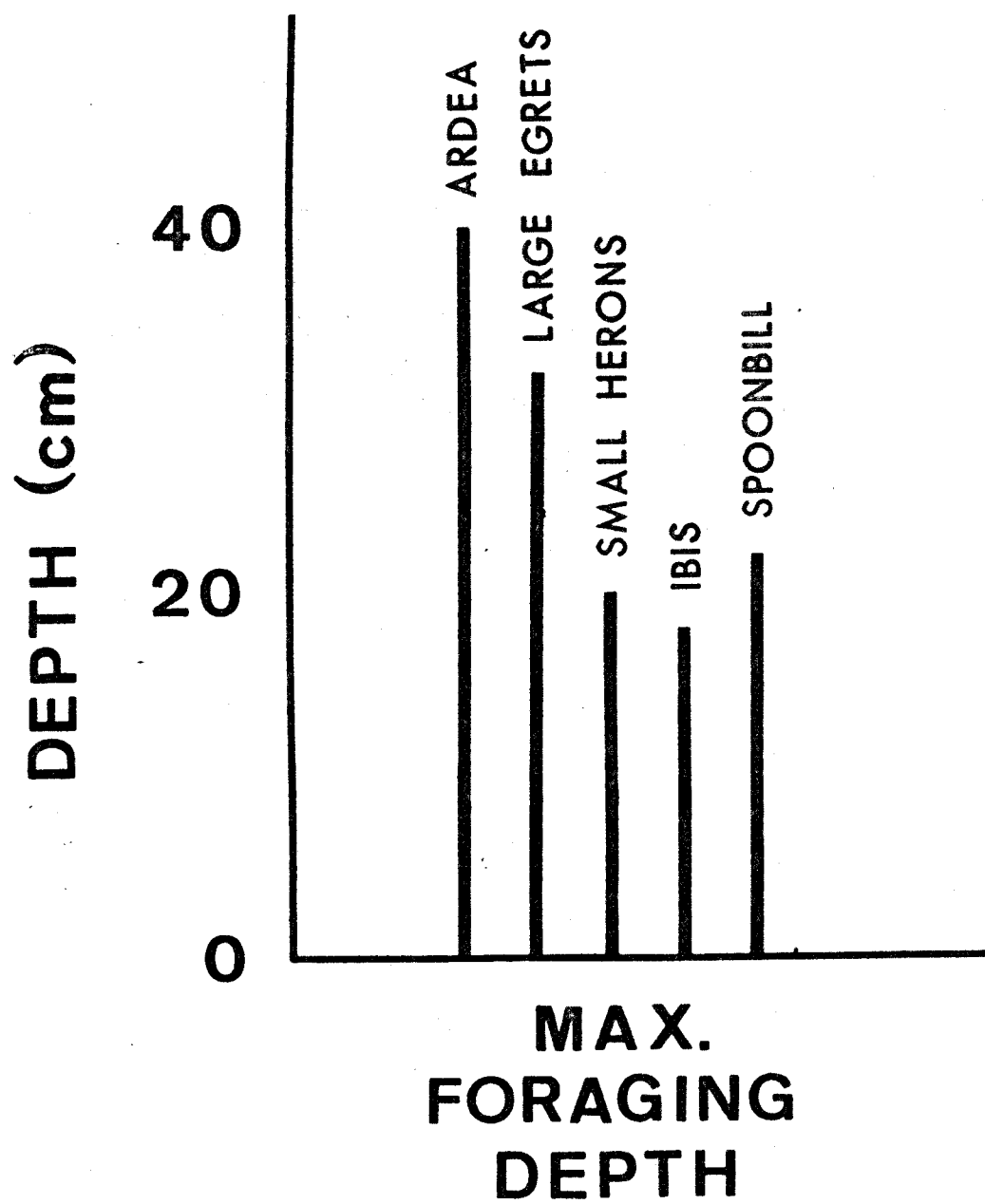


Fig. 4

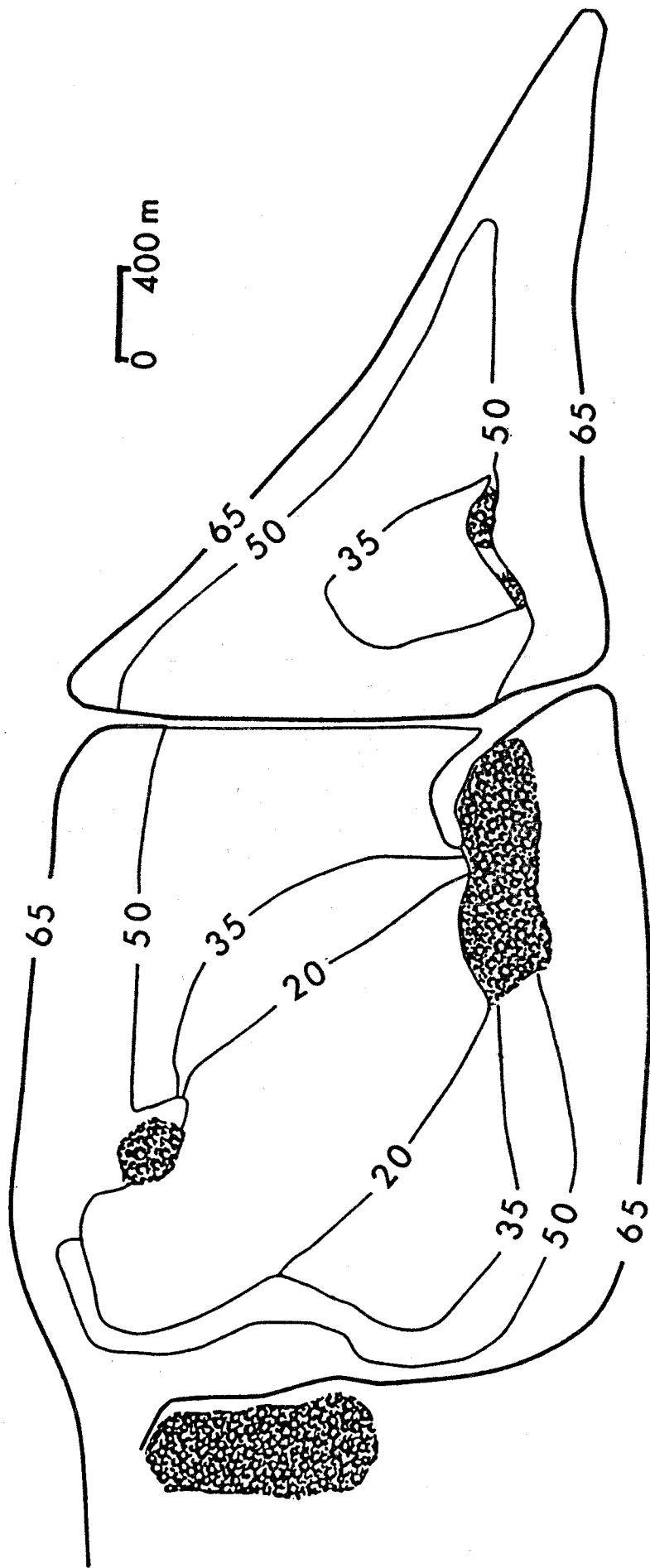


Fig. 5

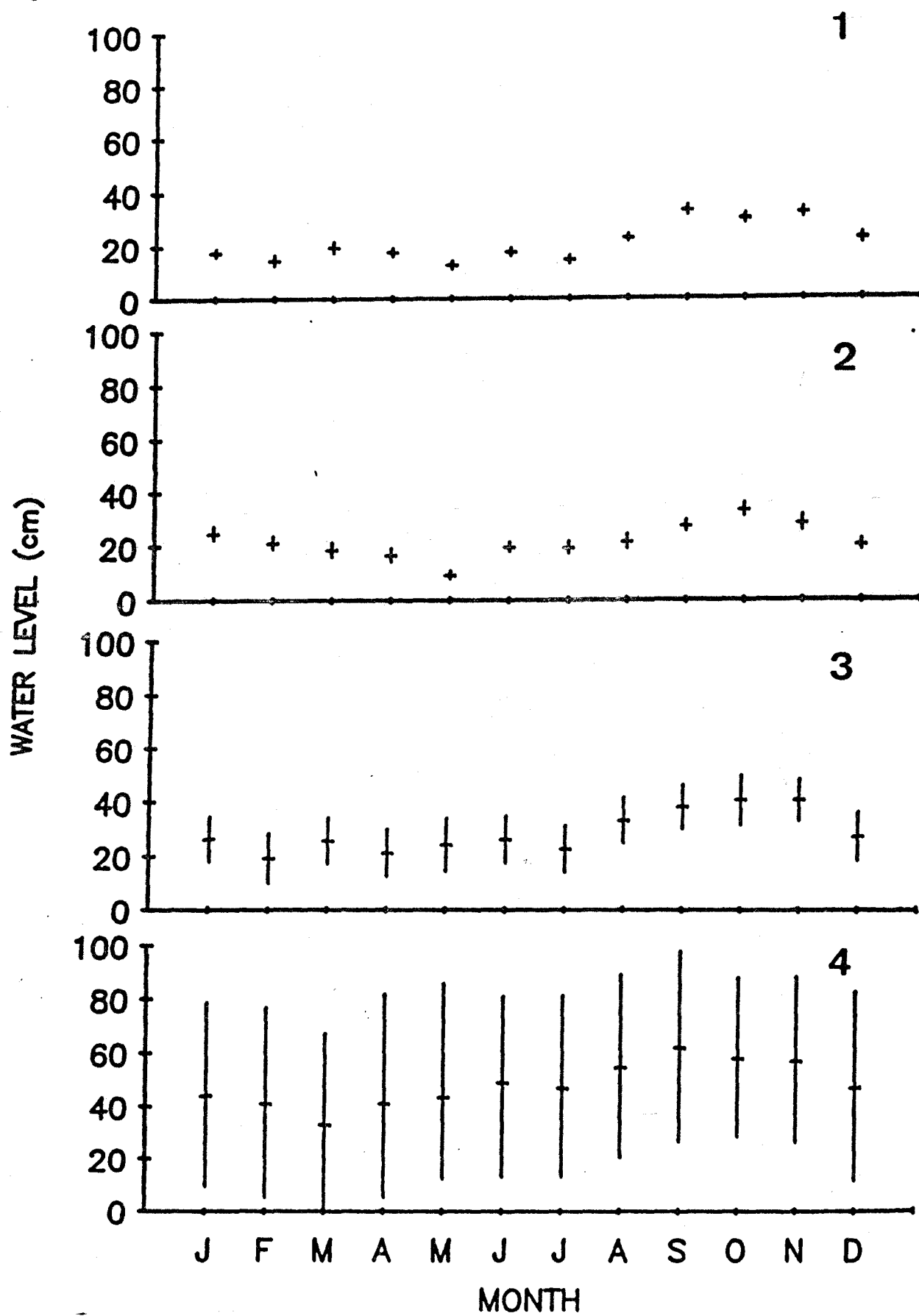


Fig. 8a Northeastern

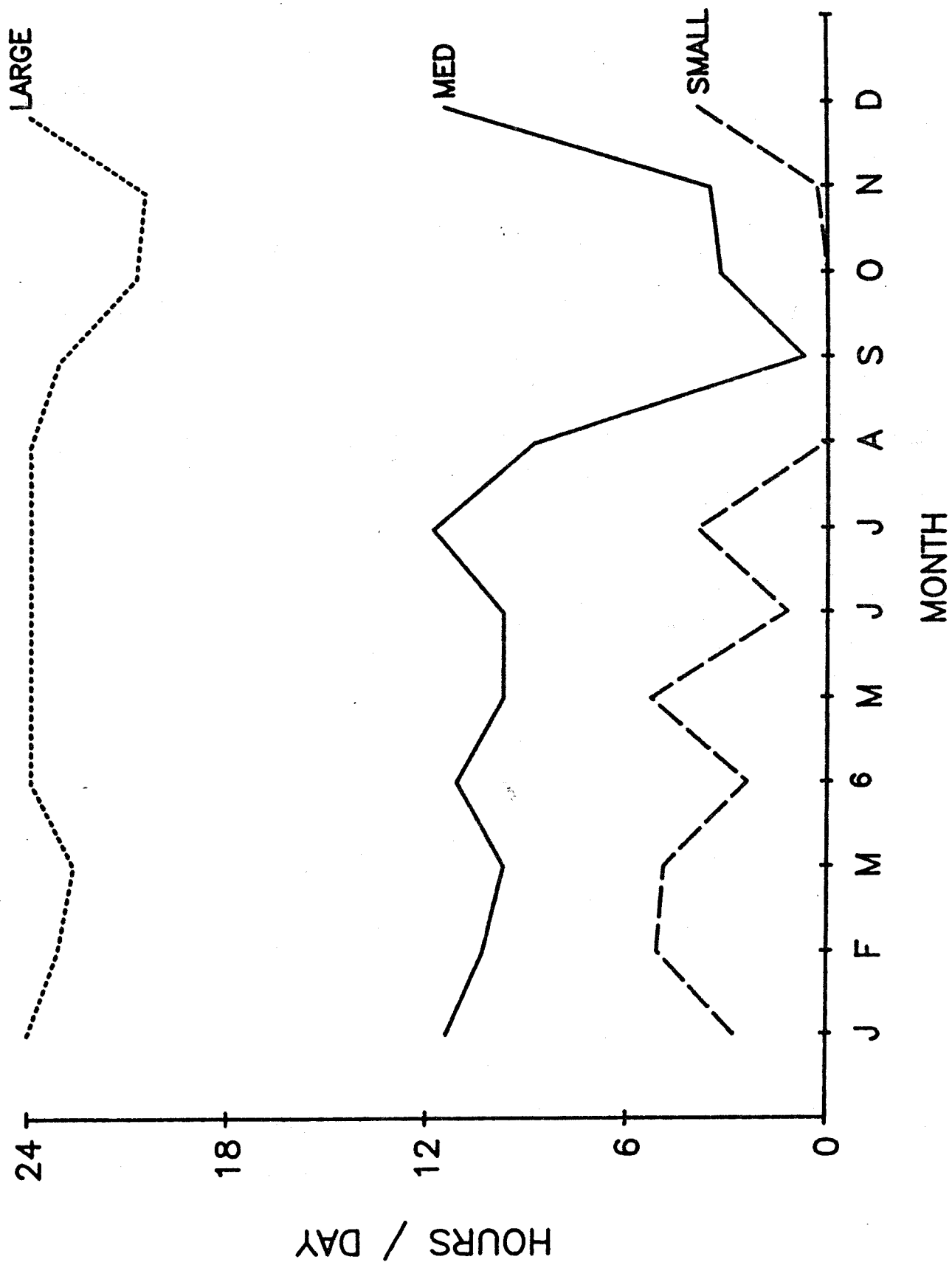


Fig. 8b East Central

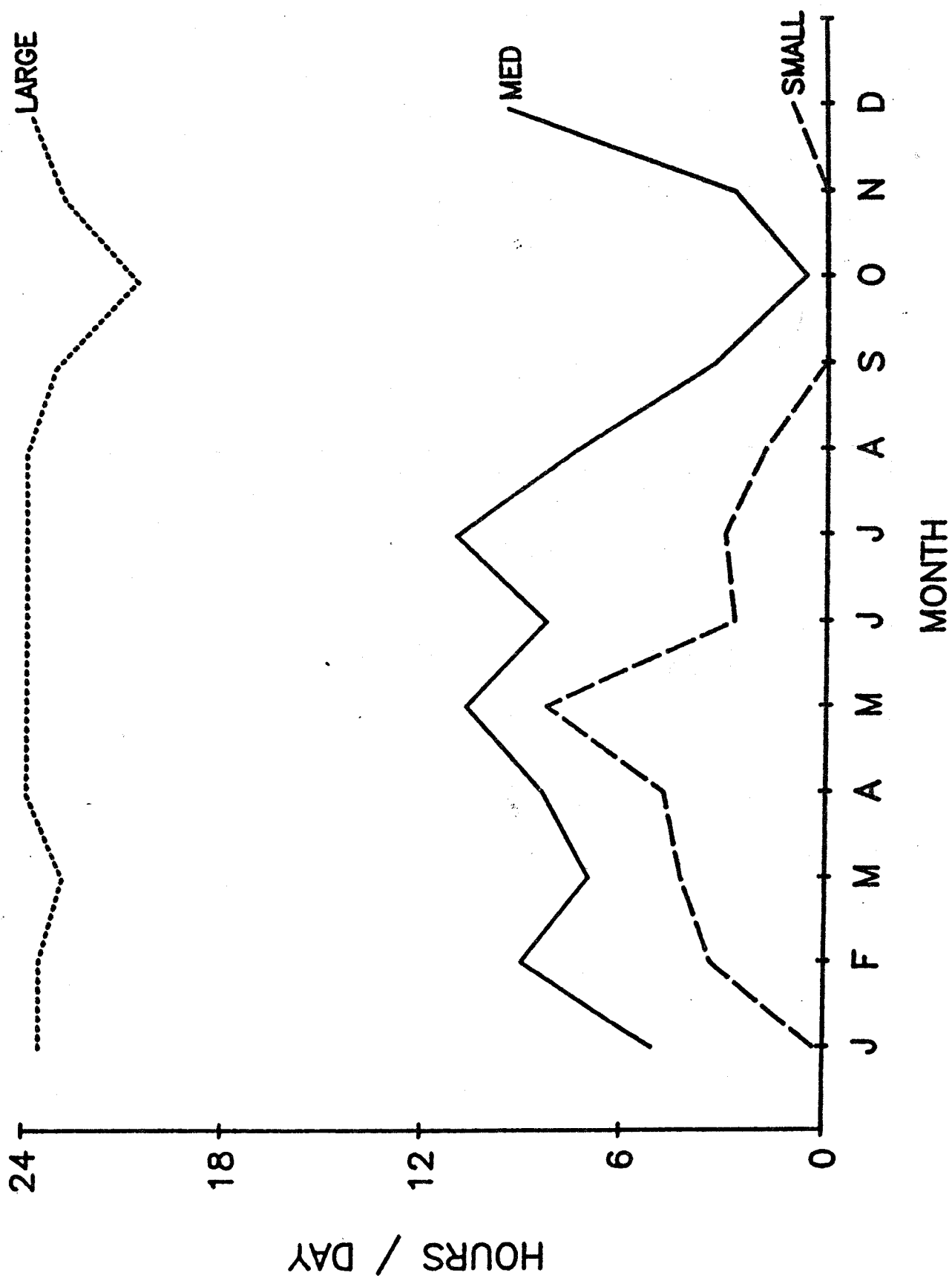


Fig. 8c Atlantic

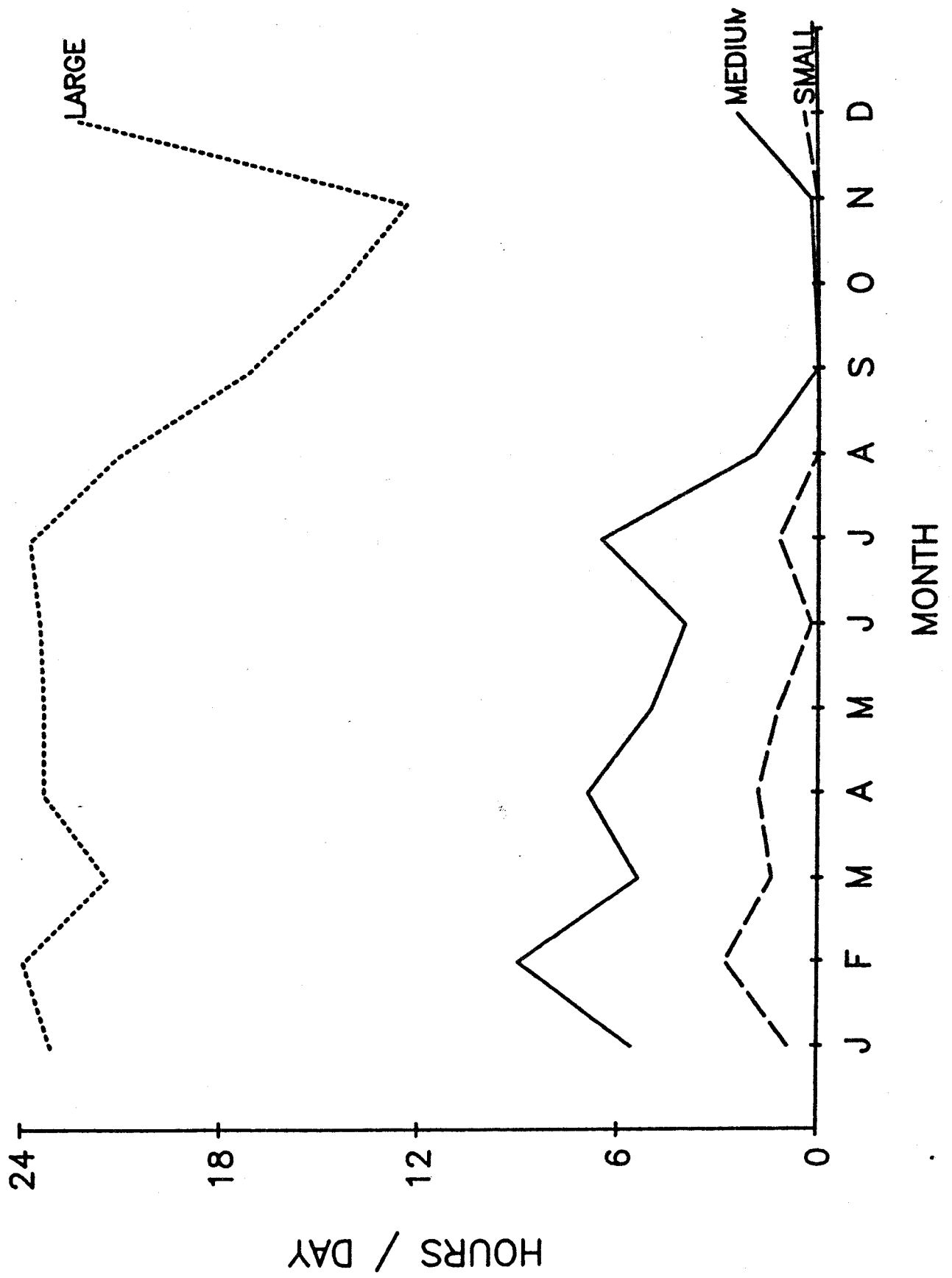


Fig. 8d Gulf

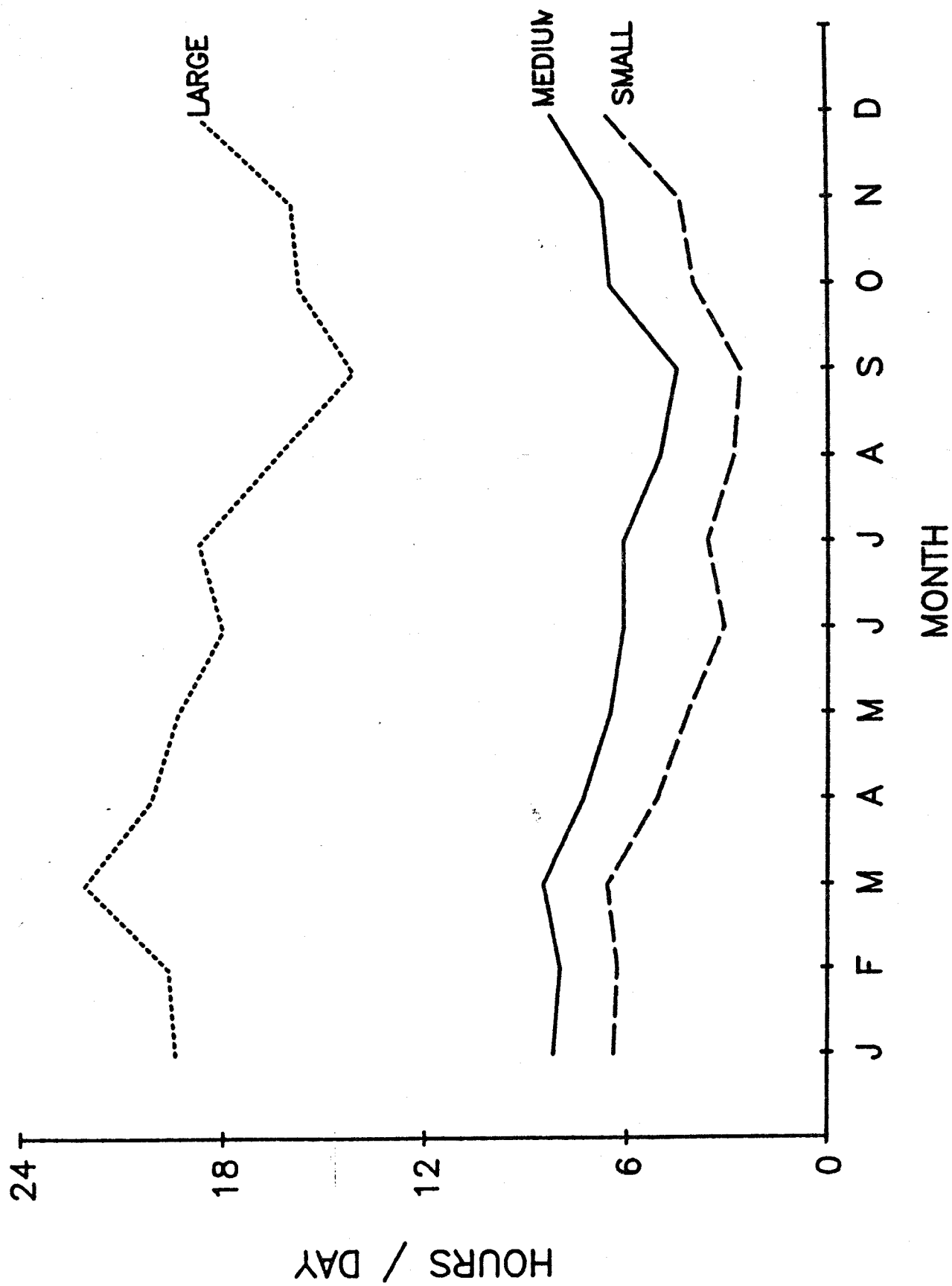


Fig. 9a Northeast site

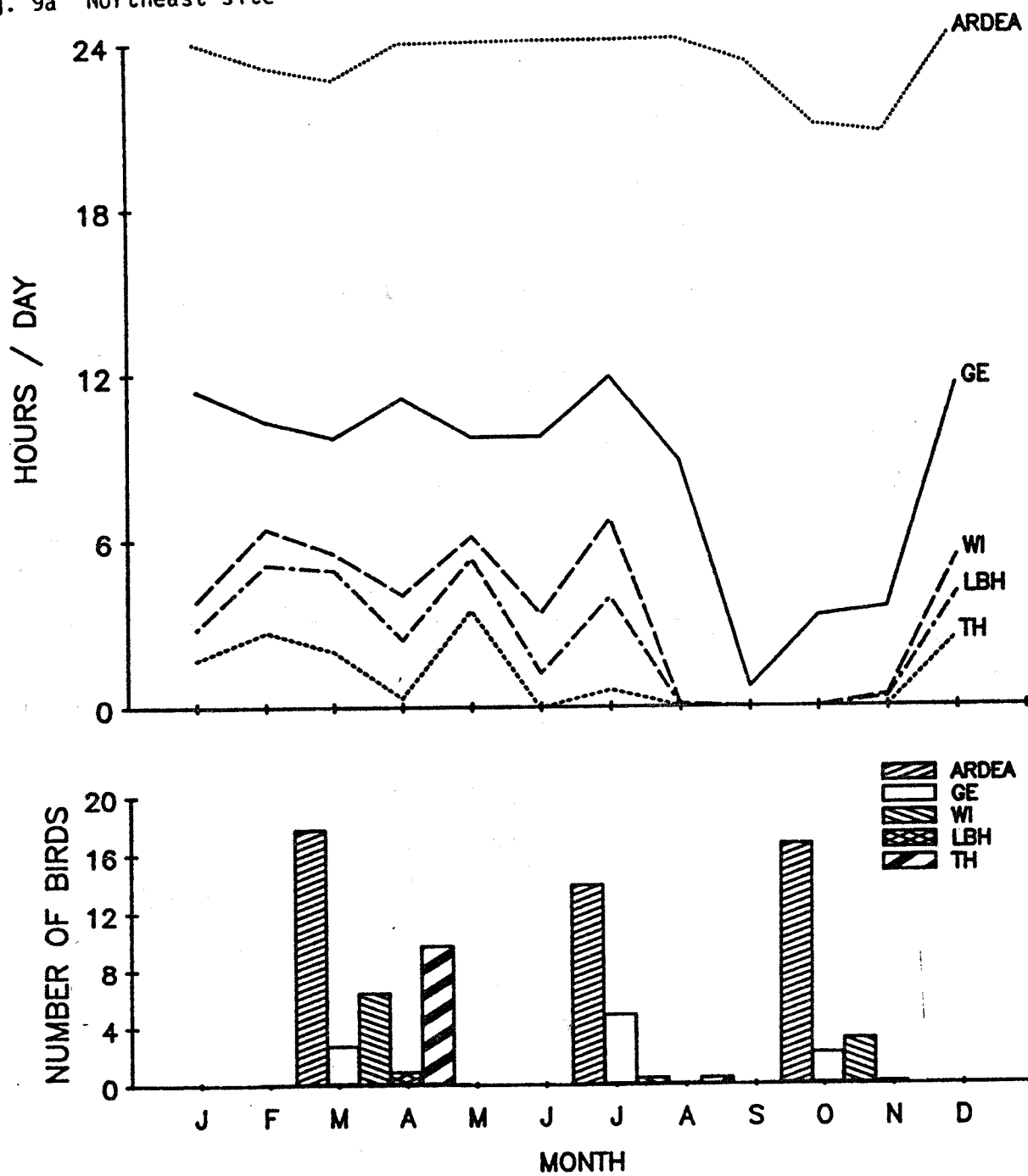


Fig. 9b East Central site

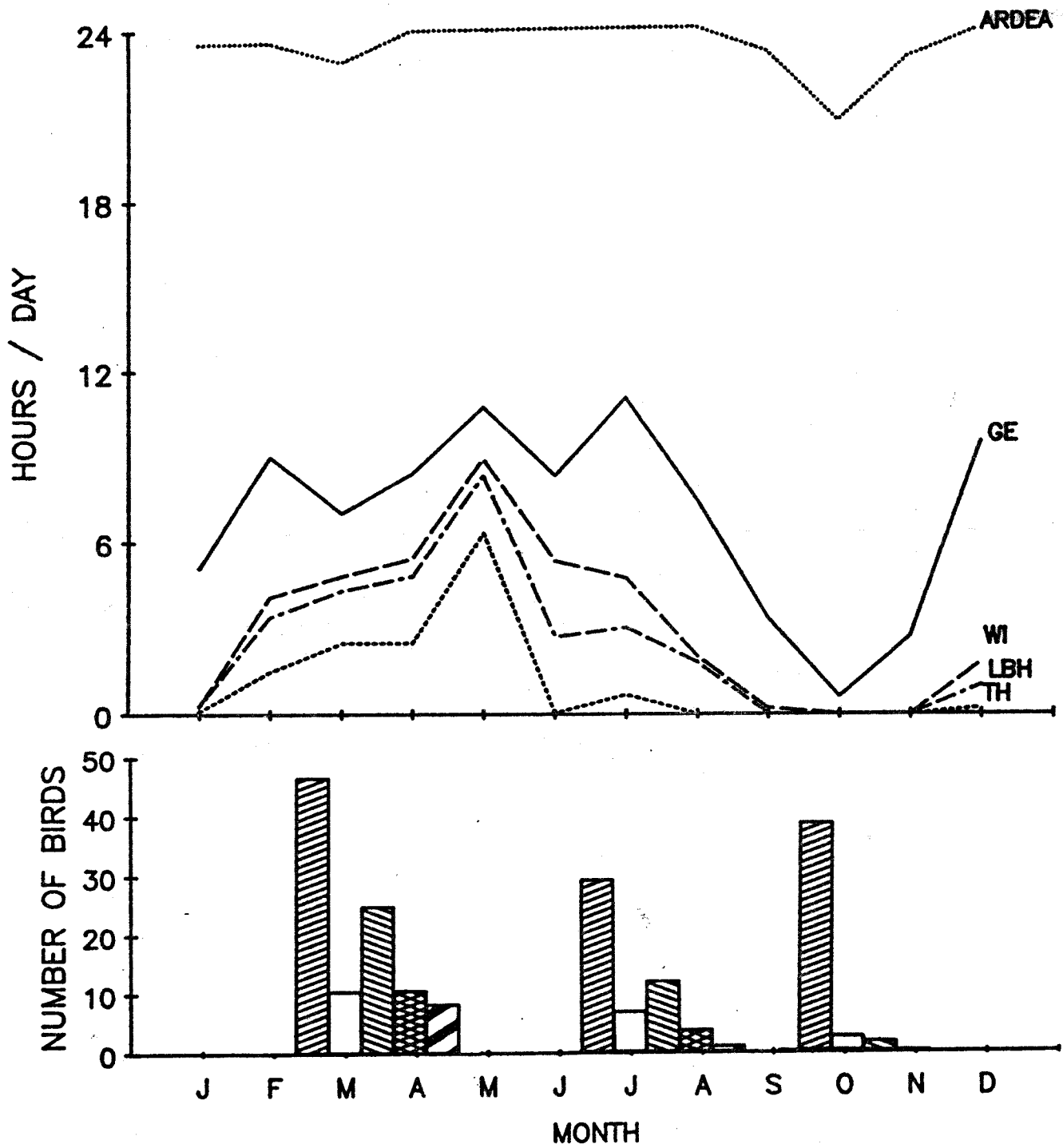


Fig. 9c Atlantic site

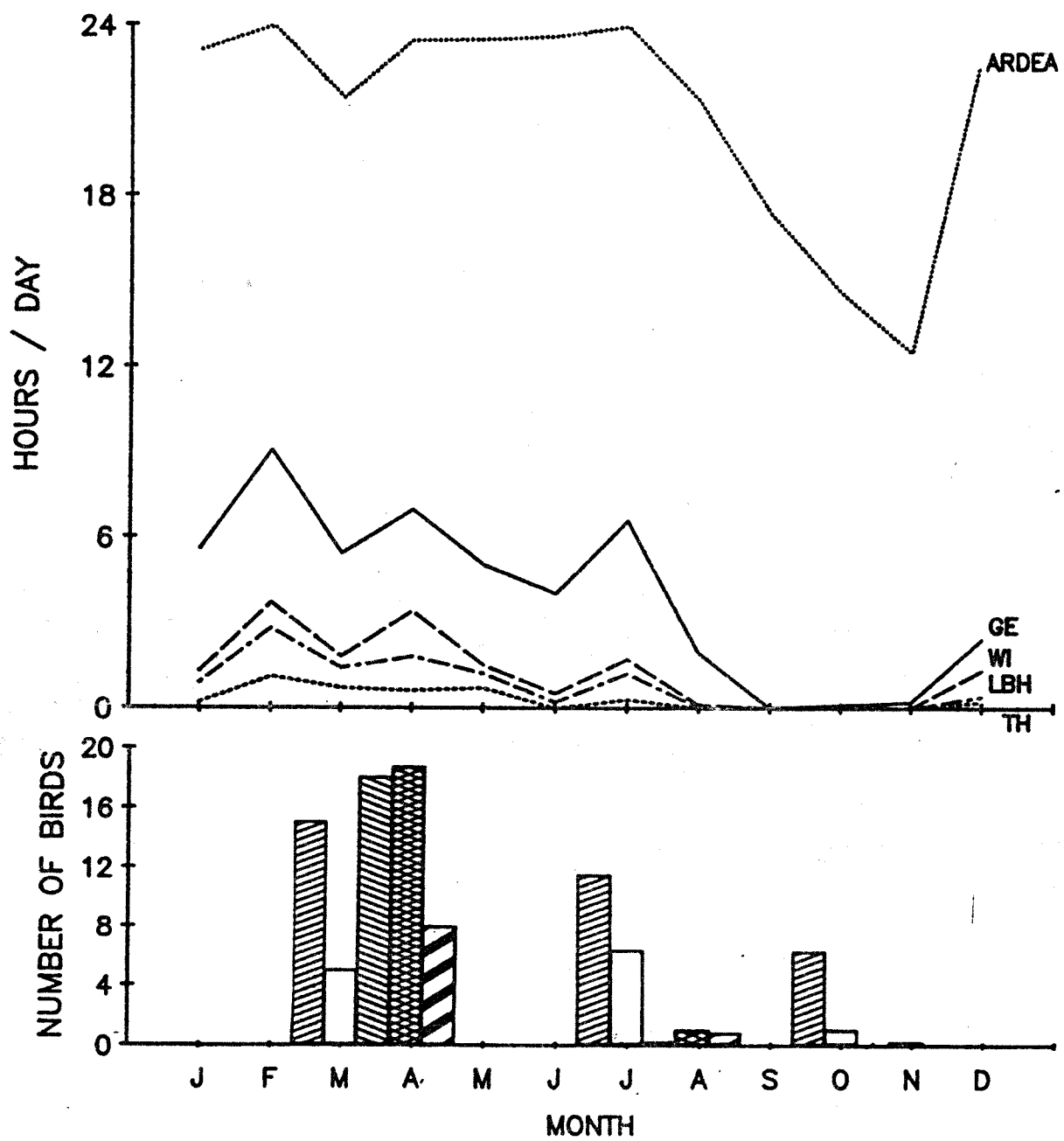


Fig. 9d Gulf site

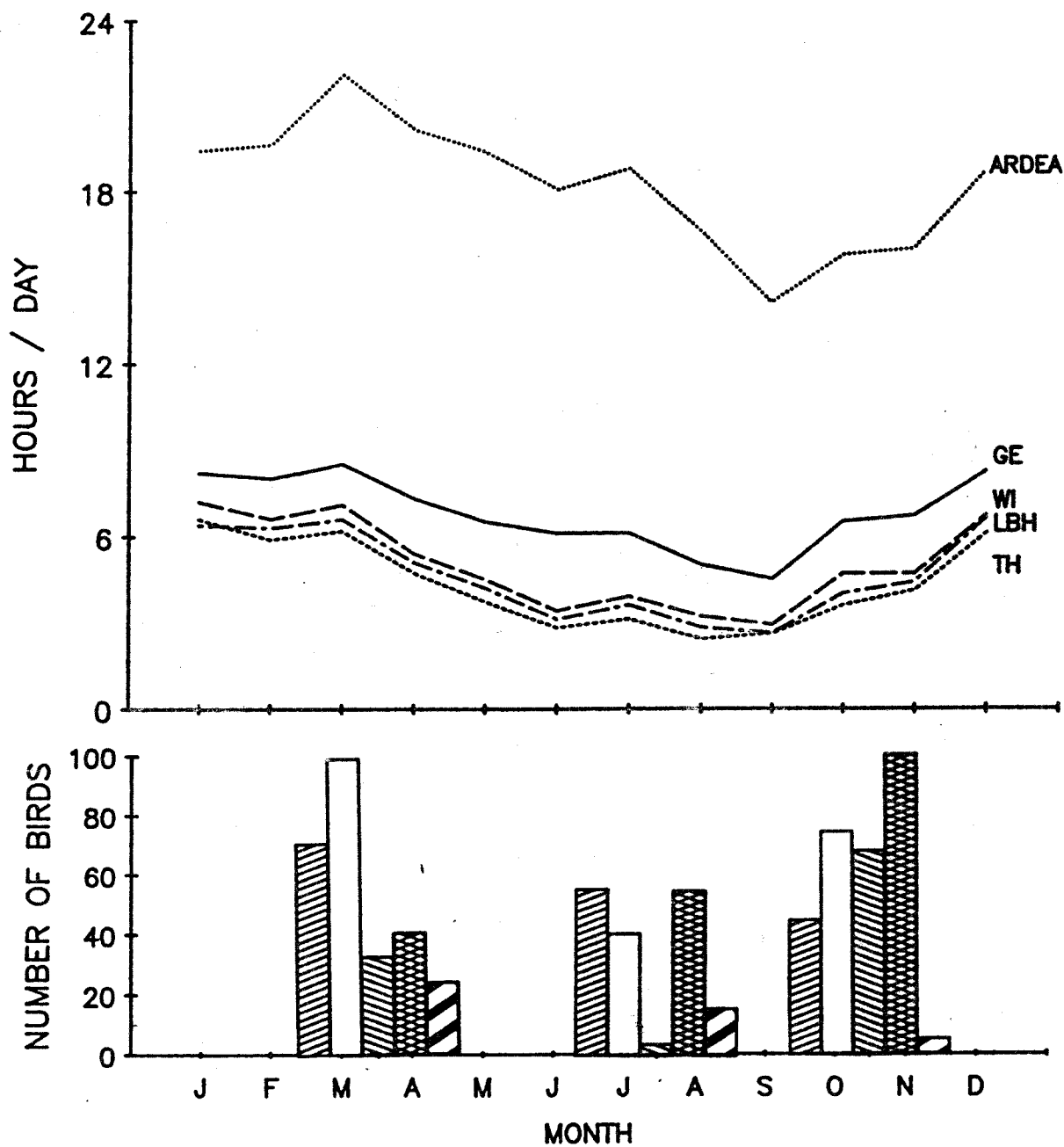


Fig. 10

