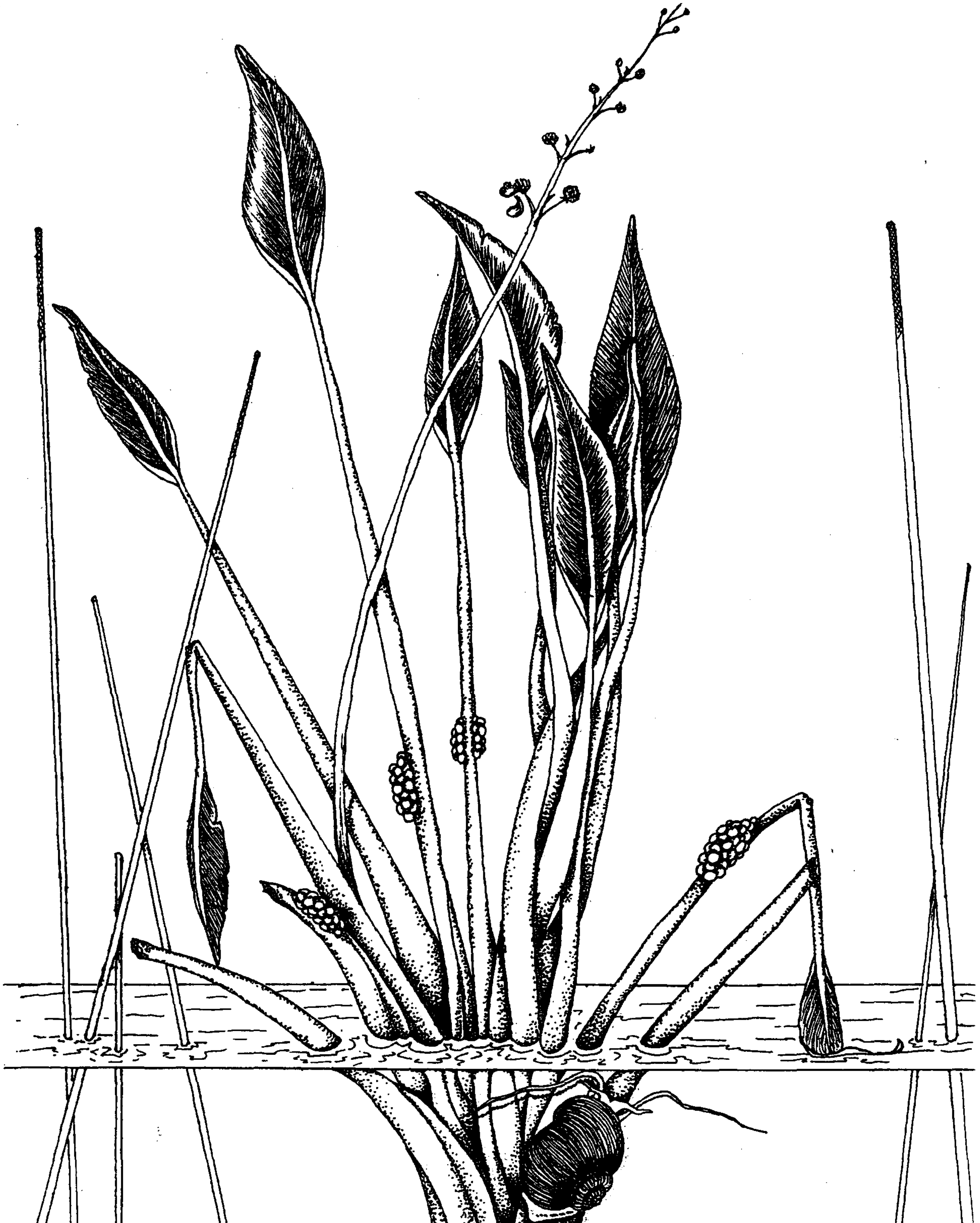
Special Publication SJ94-SP3

THE EFFECTS OF HYDROLOGY ON THE POPULATION DYNAMICS OF THE FLORIDA APPLESNAIL (*Pomacea paludosa*)



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THE EFFECTS OF HYDROLOGY ON THE POPULATION DYNAMICS OF THE FLORIDA APPLESNAIL (*Pomacea paludosa*)

by

Richard L. Turner

Florida Institute of Technology

FINAL REPORT

13 March 1994

Prepared for

St. Johns River Water Management District

under contract 91D192

EXECUTIVE SUMMARY

The Effects of Hydrology on the Population Dynamics of the Florida Applesnail (Pomacea paludosa)

by

Richard L. Turner
Florida Institute of Technology

The objective of this study was to investigate the effects of hydrology on certain aspects of the life history of the Florida applesnail (Pomacea paludosa). The Florida applesnail is an important component of the marsh food chain and nearly the sole food source for the Florida snail kite (Rostrhamus sociabilis plumbeus). The return of breeding Florida snail kites to the upper basin of the St. Johns River provides an opportunity to manage habitat for this species within its historical range. A critical factor in developing a management plan is knowledge of the biology of the Florida applesnail.

The biology of the snail is unusual. Adult applesnails live under water, but they must surface periodically to breathe air with a lung to supplement the oxygen absorbed from water by the gill. The female snail crawls out of the water on plant stems and lays eggs that hatch after a couple of weeks as small snails, which drop from the stems to the water below. The hydrologic regime of the marsh can, therefore, have a major influence on the population dynamics of the snail.

This study included field surveys and laboratory experiments. The distribution of egg clutches among and within different plant associations and the characteristics of plants that make them suitable for deposition of clutches were studied in Blue Cypress Water Management Area East. The density, thickness, and height of plant stems were measured along with the occurrence of snail eggs.

In the laboratory, the tolerance of adult snails to long-term exposure was assessed by measuring the survival of snails exposed to air at temperatures and humidities comparable to those that prevail in marshes. Some snails were provided moist sand to see if their survival might improve.

Eggs were submerged in water for various durations to assess their ability to survive flooding. The potential effect of aquatic predators on submerged clutches was evaluated by taking eggs of known ages and submerging them in the field for several days to determine if aquatic predators might decrease survival below levels expected due to flooding alone.

The major findings of this work are:

> Clutch density was highest along the edge of sawgrass stands and zero in the deep marsh plant association. Densities in maidencane and mixed shallow marshes were about one-third those in sawgrass. In all plant associations, clutches occurred preferentially on broad-stemmed species rather than on narrow-stemmed species. The species most used for egg-laying were Cladium jamaicense, Crinum americanum, Pontederia cordata, and Sagittaria lancifolia.
>
> Snails were very intolerant to aerial exposure. High mortality occurred within the first week. The Florida applesnail appears to be a weak burrower. Survival rates were not greatly increased by the availability of moist sand.

Submersion of clutches slowed embryonic development and increased mortality. Embryos that were within a few days of hatching at the time of submersion were not strongly affected. When younger embryos were submerged, none hatched, and most died in early stages of growth.

Submersion of clutches in the field increased mortality above that due to submersion alone, but factors other than predation, such as loss of adhesion and entanglement with floating debris, accounted for the losses. There was no evidence that aquatic predators were a significant factor.

Management recommendations to optimize snail habitat are:

The marsh should be managed to provide a heterogeneous community of broad-stemmed emergent plants at moderate density.

Drawdowns should be planned to minimize impacts on the snail population; summer drawdowns and annual drawdowns should be avoided.

Water level rises should occur slowly during the reproductive season (March through October), particularly during the first few months.

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INTRODUCTION

The Florida applesnail, Pomacea paludosa (Say, 1824), is the largest freshwater snail of North America (Pennak 1989). It belongs to the tropical and subtropical family Ampullariidae. Its distribution in peninsular and northern Florida makes it the northernmost species of the genus Pomacea (Haldeman 1845; Neck and Schultz 1992). The Florida applesnail is amphibious and has biphasic gas exchange: it not only obtains oxygen from water by a gill but also inhales air at the surface by its lung (Brooks and McGlone 1908). Snails reach the water's surface by ascending the stems of emergent freshwater plants. At night during egg-laying (oviposition) season, females continue the climb well above the surface and lay clutches of large pearl-like eggs in a gelatinous mass on the stem. After two or more weeks of embryonic development, juvenile snails hatch and drop from the stem into the water below (Hanning 1979).

Its large size, habitation of shallow water, and dependence on breathing at the surface make P. paludosa vulnerable to a variety of aerial and terrestrial predators as well as to fish (Chable 1947), turtles (Dalrymple 1977), and alligators (Delany et al. 1988). Semi-nomadic natives of the St. Johns River system and Seminole Indians are the only known mammalian predators of the applesnail (Wyman 1875; Moore 1892-1893; Blatchley 1932; Cumbaa 1976; WNET 1991). Avian predators in Florida include white ibis, boat-tailed grackles, limpkins, and most notably the Florida snail kite, which depends almost exclusively on the snail as prey (Snyder and Snyder 1969; Kushlan 1974; Nesbitt et al. 1974).

The return of breeding Florida snail kites to the upper basin of the St. Johns River gives an opportunity to manage habitat for this endangered bird within its historical range. The St. Johns River Water Management District has considered managing the Blue Cypress Water Management Area as kite habitat. A critical factor in developing a management plan is the accumulation of sufficient knowledge on the biology of the Florida applesnail. Many authors over the years have noted the paucity of information on this snail and the need for studies on how to manage it as prey for the kite (e.g., Martin and Doebel 1973; U.S. Department of the Interior 1973, 1980; Perry 1974; Cary 1983; U.S. Fish and Wildlife Service 1986; Kushlan 1983; Martin et al. 1983). Unfortunately, a recent review of present knowledge and attempt to develop a management plan for the applesnail revealed the persistence of large gaps in available information (Turner et al., in press).

The purpose of the study reported here was to provide data for the development of an effective management plan for the Florida applesnail in the Blue Cypress Water Management Area. The 2-yr project addressed five areas of research:

1. distribution of egg clutches among and within plant associations in the marsh;
2. characteristics of plants that make them suitable for deposition and holding of clutches;
3. tolerance of adult snails to long-term exposure;
4. physiological tolerance of clutches to submersion in water;
5. exposure of submerged clutches to aquatic predators.

MATERIAL AND METHODS

Study Sites

The field survey, studies of predation on submerged clutches, and the collection of clutches, adult snails, water, and sand used in this study were done at two locations in east central Florida. One location was a series of borrow pits at the northwestern corner of the intersection of Interstate 95 and Florida State Road 518 in Melbourne. The second location was a freshwater marsh at the northeastern corner of the intersection of Florida State roads 512 and 60, south of Fellsmere and west of Vero Beach (Figure 1).

The borrow pits, known locally but unofficially as Clear Lake (28° 07′ 24" N, 80° 42′ 28" W) and East Twin Lake (28° 07′ 20" N, 80° 42′ 58" W), are deep steep-sided lakes that were formed by the excavation of carbonate rock to build the roadbed for the interstate highway. They are rimmed by thin strands of emergent vegetation, mostly *Typha latifolia* (common cattail), *Panicum* sp., *Eleocharis cellulosa*, *Sagittaria lancifolia* (lance-leaved sagittaria), and *Pontederia cordata* (pickerelweed). Clear Lake is rectangular and covers 2.9 ha. The sides of the lake descend steeply 1-2 m before sloping more gently to deeper water. The bottom is unvegetated to depths visible from the surface. Clutch production is heaviest along the western shore, where cattails provide the main substratum for oviposition. Adult applesnails usually can be found crawling or rolling around off three beaches of the western shore and southwestern corner. *Quiscalus major* (boat-tailed grackle) was the only observed predator on adult snails, although *Lepomis microlophus* (redear sunfish) (Chable 1947; Wilbur 1969; Dineen 1974) and *Trionyx ferox* (Florida soft-shelled turtle) (Dalrymple 1977) probably eat adults; and various species of *Lepomis* probably eat hatchling snails (Snyder and Snyder 1971; N. Jaynes, personal communication, 1993).

The freshwater marsh is the Blue Cypress Water Management Area (BCWMA) East, owned by St. Johns River Water Management District. Part of the area is reclaimed agricultural land. The marsh is bounded by high levees, within which are deep perimeter canals. Water flows from the southeastern corner to the northwest, where the marsh is hydrologically connected to BCWMA West. Dense stands of common cattail outline the marsh along the perimeter canals. Most of the tract is an extensive, shallow, oligotrophic marsh subdivided by low levees that are occasionally breached between adjacent cells of the tract. Water depth generally is less than 1 m, and the substratum is clean sand, sometimes overlain with sawgrass peat. District personnel have mapped the plant associations for 1752 ha (about four-fifths of BCWMA East) based on aerial infrared photography conducted in 1989. The plant associations are dominated by emergent grasses (Gramineae) and sedges (Cyperaceae). Fieldwork of the present study showed that the vegetation in some areas of the marsh has changed since the baseline data were obtained and that boundaries and definitions of the plant associations are sometimes hard to determine in the field. The BCWMA East marsh is used by a number of wading and other bird species for roosting, nesting, and feeding. Notable among them are predators of the Florida applesnail: *Rostrhamus sociabilis plumbeus* (Florida snail kite), *Aramus guarauna* (limpkin), boat-tailed grackle, and *Eudocimus albus* (white ibis) (Snyder and Snyder 1969; Kushlan 1974; Nesbitt et al. 1974; Kushlan and Kushlan 1975).

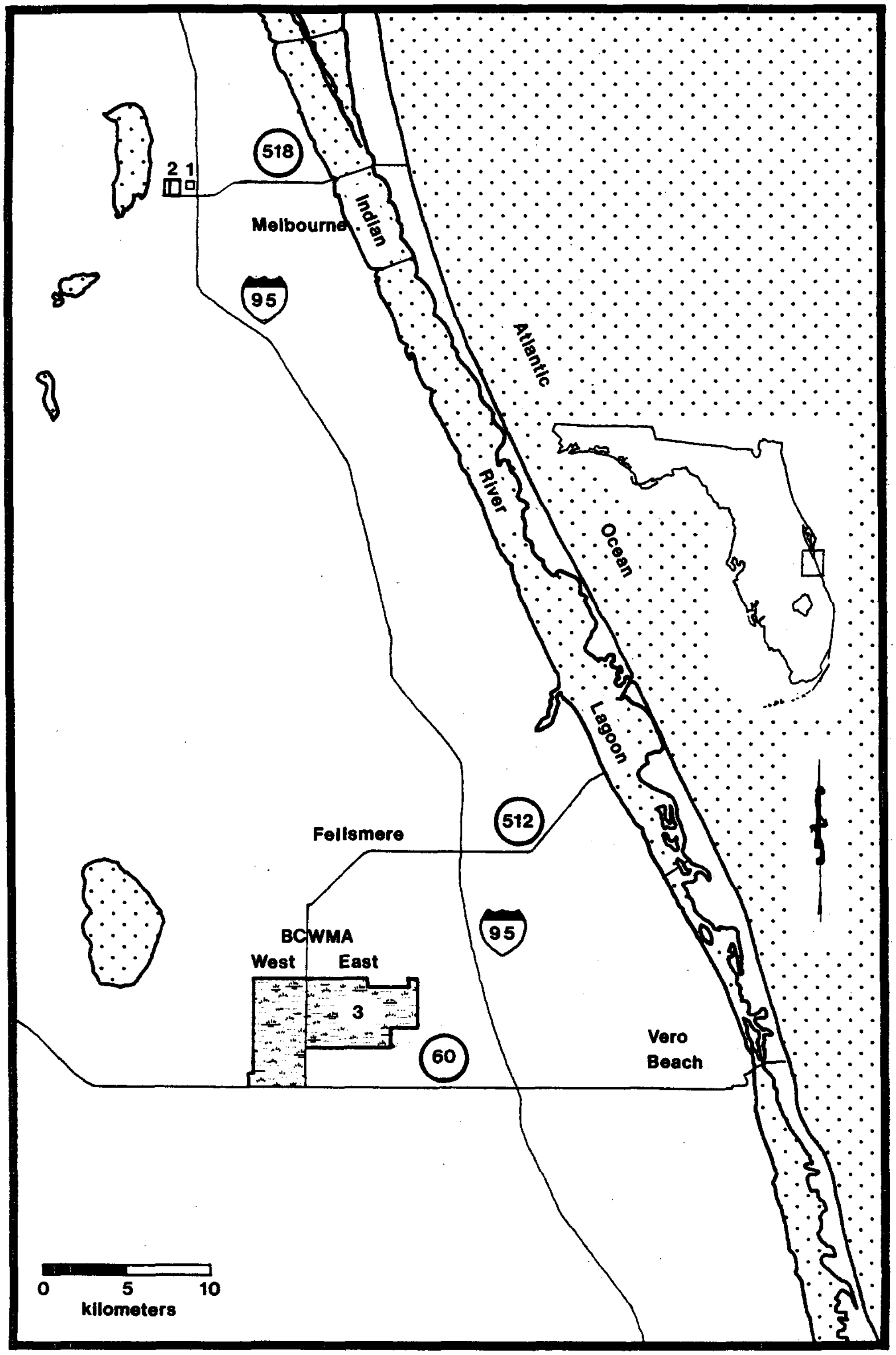

Figure 1. Locations of study sites. Field studies and collection of material for laboratory studies were conducted at three locations: 1, Clear Lake; 2, Twin Lakes; 3, Blue Cypress Water Management Area (BCWMA) East.

Field Survey

The field survey was conducted in 1992 and 1993 within the BCWMA East marsh to assess the use of emergent plant stems for oviposition by the Florida applesnail. The four plant associations, other than trees, with the highest acreages were selected for comparative analysis: maidencane marsh (519 ha), deep marsh (399 ha), sawgrass marsh (234 ha), mixed shallow marsh (233 ha). Sites were chosen that were representative of the plant association and that were suitable for application of the sampling method. Where possible, more than one plant association was sampled in a general location. As the summer drought of 1993 progressed, sampling was increasingly restricted to the western half of the tract. Sampling data for the sites are given in Appendix I (Table A).

Maidencane marsh, deep marsh, and mixed shallow marsh associations were sampled along rectilinear transect lines. Each transect line was 25.0-100.0 m long. Clutches were sampled within a 2.0-m-wide path along one side of each transect line. The plant associations were sampled within 3-10 quadrats taken at approximately 5-m (15-20-m for deep marsh) intervals along the other side of each transect line.

The sawgrass association was sampled along the irregular edges at which stands of sawgrass met other plant associations. Curvilinear transect lines 24.8-44.7 m long were laid, roughly outlining the sawgrass edge. Clutch parameters were measured along each transect line to a depth of 1 m into the stand because preliminary surveys into stands of sawgrass indicated that clutches within dense stands were rare. Parameters of the sawgrass association were measured within three quadrats, taken near the center and near the ends of each transect to a depth of 1 m into the stand.

Reproductive activity of the Florida applesnail was estimated at each site as the density of unhatched clutches, approximately representing clutch production of the previous 2 wk. Water depth and the elevation of each clutch above the water were measured as indicators, respectively, of the potential for stranding of hatchlings and for submersion of clutches with changes in water level. Clutch-bearing stems were characterized by species, stem diameter at the water's surface, usable height for oviposition above the water's surface, and number of clutches per stem to give insight on the plant characteristics required or preferred for oviposition.

Stem densities of emergent plants were estimated within a four-sided, floating, quadrat frame with inside dimensions of 1 m by 1 m. For sawgrass, a three-sided frame was pushed into the stand at water level. At high stem densities, the quadrat was subdivided into halves or quarters. Representative stems of each species of plant were selected to estimate stem diameter at the water's surface and usable height above the surface for oviposition. Water depth was measured near the center of the quadrat. Assistance in plant identification was provided by District personnel.

The distribution of clutches among stems of emergent plant species was analyzed by chi-square to test the null hypothesis that clutches were distributed in proportion to the occurrence of stems. Observed distribution of clutches on stems was determined from the clutch survey conducted along one side of the transect lines. Expected distribution was estimated from stem densities measured in quadrats taken along the other side. The test criterion was the tabulated value for chi-square at $\underline{P} = 0.05$ for $\underline{n} - 1$ degrees of freedom, for which $\underline{n}$ is the number of plant species with emergent stems in the quadrats.

Culture System

Adult snails and clutches collected from the field were held in a recirculating aquarium system in the Aquaculture Laboratory at Florida Institute of Technology, Melbourne. The two aquaria are large (60-63 cm by 175-183 cm), shallow (13-15 cm), plastic, photographic sinks cradled one above the other in a wooden frame. A holding tank located above the upper sink contains polystyrene pellets and delivers fresh water by gravity to the upper sink, from which the water flows successively into the lower sink and into the filtration compartment of a holding tank below. The filtration compartment contains broken carbonate rock overlaid with two mats of synthetic fiber. Water is delivered from the lower holding tank to the upper one by a sump pump. Water depth in the sinks is maintained at 8.5-11.5 cm by use of elevated drain tubes. A floating mercury switch in the lower holding tank prevents failure of the pump and overflow of the sinks in the event of excessive evaporation, leakage, or clogging of plumbing. This laboratory uses tap water from the City of Melbourne and treats it with chemicals and aeration for removal of chlorine before use.

Effects of Exposure on Adults

Four trials were conducted to study the ability of adult Pomacea paludosa to survive exposure in the laboratory. Adults were either subjected to fully aerial exposure or provided with water-saturated sand from BCWMA East. Aerial exposure was accomplished by nesting snails in fiber or plastic egg crates with the apertures of the shells upward to allow retention of mantle fluid. Saturated sand, from which supernatant water was decanted, was provided to a depth of about 5 cm in shallow plastic trays. Each tray held 15 snails within a uniform grid marked along the sides of the tray; one snail was placed in the center of each square of the grid with the aperture of the shell downward to allow burial or, at least, contact of the soft body with moisture in the sand.

Applesnails were collected from Clear Lake, East Twin Lake, and BCWMA East and held in the culture system for varying lengths of time. Shell length (distance along the columellar axis from the apex to the bottom of the apertural lip) was measured on each snail. Snails were marked on the body whorl with nail polish or with a 7-mm numbered circle of polyester sheet attached to the shell by rapidly setting cyanoacrylate cement. Drained fresh weight was measured on a triple beam balance.

Although specific procedures varied among trials, the general protocol for monitoring snail mortality included the following steps. The aperture of each snail was checked for a gaping or closed operculum, and the snail's position in the egg crate or grid was recorded as an indication of locomotor activity since the last observation was made. The snail was lifted and sniffed for odor. Its response during handling was noted, especially to tapping or pulling on the operculum with forceps. If the snail was agape and unresponsive, the columellar muscle or body was touched gently with a blunt probe in an attempt to elicit a response. Lack of response was taken as a sign of mortality, which was confirmed by easy removal of the body from the shell or of the operculum from the foot. Snails that were apparently alive or uncertain to be dead were returned to their assigned positions or, upon termination of a trial, to chambers with aerated water from the culture system for recovery.

The first trial was run in mid-July 1992 in an air-conditioned laboratory (22-25 C, 63-81% relative humidity) for 14 d of aerial exposure and a subsequent 9-d recovery period for surviving snails. The 46 snails were collected from Clear Lake on the morning that the trial began, and they were marked for identification with nail polish. (Polyester tags were used in the other three trials.) The second trial in May-June 1993 lasted for 29 d of aerial exposure with a 2-d recovery period in an unair-conditioned laboratory (27-31 C, 48-80% relative humidity) that roughly followed local weather parameters. The 18 snails were collected at East Twin Lake and BCWMA East during the 9 d preceding the trial and held in the culture system. The third trial, run in early July 1993, used 23 snails collected at Clear Lake on the morning the trial began and 27 collected from the lake during the previous 6 wk. These 50 snails were sacrificed after 7 d of aerial exposure in the unair-conditioned laboratory (28-31 C, 67-76% relative humidity). The fourth trial, conducted in mid-July 1993 without air-conditioning (28-29 C, 76-80% relative humidity), exposed snails with or without water-saturated sand for 7 d, followed by a 2-d recovery period for apparent survivors. Most (83%) of the 30 snails in each of the two treatment groups of the fourth trial were used within 10 d of collection at Clear Lake; the remaining snails were left over from collections made for the third trial.

Effects of Submersion on Eggs

Clutches of applesnail eggs are laid at night within an adhesive mass of extracapsular mucus (jelly) that dries within a few hours after sunrise. Clutches that are found to be invested with jelly are, therefore, within several hours of oviposition. Jellied clutches were collected at Clear Lake in August and September 1993, transferred to standard (25 mm by 76 mm), glass, microscope slides, and allowed to dry in an inclined position under full-spectrum fluorescent lighting (Daylight, General Electric Co.) at 27-32 C and 59-82% relative humidity. The upright orientation of the clutch on the original plant stem was maintained during this study. When the clutches were dry, each was placed at an incline in a beaker and allowed to incubate under a photoperiod of 12 h of light and 12 h of darkness for 14 or 21 d. During incubation, coarsely filtered lake water was added to the beakers to submerge selected clutches at ages of 1, 4, 8, and 12 d; control clutches were not submerged.

At 14 or 21 d of incubation, clutches were removed for dissection to determine the stages and viability of embryos. Stages of development included hatchlings, shelled embryos, and unshelled embryos. Shelled embryos were further staged by estimating the size as the number of full grid squares occupied by each embryo placed over graph paper with 1-mm spacing. The following criteria, from most to least reliable, were used to recognize a live embryo: heartbeat; withdrawal of the body into the shell; active epidermal ciliation; foot expanded and appressed to an intracapsular gas bubble.

Low production of clutches at the lake during the summer drought of 1993 precluded optimal experimental design: replication was low, and the clutches had to be incubated in three trials. Each trial included two control clutches, but not all possible combinations of treatments (age at submersion and day of sacrifice) were included in each trial.

Predation on Submerged Clutches

The field phase of studies on submersion attempted to assess the potential of predation to inflict mortality before death that would be expected to have occurred by submersion alone (i.e., in the absence of predators) based on results of the laboratory phase. Jellied clutches were collected from emergent stems in Clear Lake at regular intervals and held in the culture system for later use. At the start of each of two trials, therefore, clutches of several ages were available for submersion. In addition, enough jellied clutches were found in Clear Lake at the start of the Clear Lake trial to include 0-d-old (jellied) clutches. The two trials were conducted at Clear Lake and at BCWMA East. Ages for the Clear Lake trial were 0, 1, 4, 7, and 11 d; those for the BCWMA East trial 2, 6, 9, and 13 d.

Poles made from half-inch (21-mm outside diameter) polyvinylchloride (PVC) plumbing pipe were cut to 1.5-m lengths and driven vertically into the substratum. Clutches were attached by their plant stems to the PVC poles with plastic cable-ties, free ends of which were cut to reduce the chance of fouling by windblown or waterborne debris. Each pole held a pair of clutches of the same age, one clutch (aerial clutch) about 300 mm above the water level and one (submerged clutch) about 50 mm below the water level. At Clear Lake, 10 poles were set along the northern shore and secured to *Typha latifolia* with cable-ties. Water depth was 510-810 mm. Pairs of clutches were assigned to the poles haphazardly, and they were oriented toward open water. At BCWMA East (27° 40′ 21.2" N, 80° 38′ 19.2" W), 15 poles were set in two ranks, one along the sawgrass edge and the other within the nearby mixed shallow marsh and about 5.1 m from the sawgrass edge at depths of 280-440 mm. Assignment of clutches to poles was haphazard, and those on poles along the sawgrass edge faced open water.

Clutches were harvested after 3 d in June 1993 in the Clear Lake trial and after 7 d in July 1993 in the BCWMA East trial. During these trials, water level dropped about 30 mm at Clear Lake and about 20 mm at BCWMA East, leaving none of the submerged clutches exposed. Notes on gross condition of clutches and eggs were made in the field and laboratory, and eggs from the BCWMA East trial were individually dissected.

Visibility in the water column at Clear Lake was excellent: The bottom at the base of the PVC poles could be seen from the surface, and there was no macroscopic debris floating or suspended in the water. Visibility at BCWMA East was poor: *Utricularia vulgaris* (common bladderwort) and plant debris filled nearly the entire water column along the sawgrass edge and in the mixed shallow marsh; only a few centimeters of free water remained at the surface.

RESULTS

Field Survey

Fifteen taxa of emergent plant were encountered in quadrats and transects during the field survey at BCWMA East (Appendix I, Table B). Specimens of the genus *Leersia* were not identified to species, and some stems of *Utricularia* that lacked flowers were not further identified. A rare unknown grass was not found after its first appearance in samples. *Nymphaea odorata* was included only for occasional stems that were left emergent by declining water levels. The 15 taxa were clearly distinguishable as narrow-stemmed and broad-stemmed plants based on diameter and morphology. Narrow-stemmed plants, such as the spikerushes, had stems of rather uniform diameter ($\leq$ 6 mm) from base to tip and arose from rhizomes individually or in loose clusters. The broad-stemmed plants, such as sawgrass, tapered from a wide base, usually from a tight cluster of stems, and had stem diameters of at least 6 mm at the water's surface.

The four plant associations (maidencane marsh, deep marsh, mixed shallow marsh, sawgrass marsh) varied widely in the presence and densities of plant species (Figure 2, Table 1). Maidencane marsh had a high density of stems, and most were narrow-stemmed plants. In the seven transects taken in maidencane marsh, more than half the emergent stems were *Panicum hemitomon* (1-6 mm stem diameter), and one-third were *Eleocharis cellulosa* (1-4 mm). The broad-stemmed *Sagittaria lancifolia* accounted for only 7% of stems, and nine other emergent species encountered had stem frequencies less than 5%. The six transects of deep marsh were sparsely vegetated and only had two species of narrow-stemmed spikerush (1-4 mm), which were almost equally represented by stems. The six transects taken in mixed shallow marsh had the highest stem density of the four plant associations. *Eleocharis elongata* (1 mm) dominated and was followed in dominance by *S. lancifolia*, *Panicum hemitomon*, and the broad-stemmed *Pontederia cordata* (Figure 2). In addition, six species of emergent plant with stem frequencies less than 5% were recorded from mixed shallow marsh. Stem density was moderate (Table 1) in six transects taken along the edge of sawgrass stands adjacent to mixed shallow marshes of *Nymphaea odorata*, *E. cellulosa*, *S. lancifolia*, and *Utricularia vulgaris*. The broad-stemmed *Cladium jamaicense* dominated numerically, and the other eight emergent species had stem frequencies less than 5%.

No live applesnails were seen within transects, but clutches were found in all transects except those in deep marsh. Although no stem in deep marsh bore a clutch of applesnail eggs, nearby stands of maidencane, mixed shallow, and sawgrass marshes held many unhatched clutches--evidence that *Pomacea paludosa* was present and reproductively active in the vicinity during the previous 2 wk. Clutch densities in maidencane and mixed shallow marshes were similar, and they varied similarly among transects. Clutch density along the edge of sawgrass marsh was three times the density of maidencane and mixed shallow marshes and was consistently high among transects. The four plant associations contributed differently, however, to standing crop of clutches of the entire marsh because of their proportionate acreages: Standing crop in maidencane marsh was more than twice that in mixed shallow marsh, and it was more than 20 times the estimate of standing crop in sawgrass marsh.

The distribution of clutches within plant associations was not predicted by the proportional occurrence of plant stems, and there was a strong association of clutches with broad-stemmed plants. Chi-square analysis revealed skewed distributions ($P < 0.05$) of clutches among stems in maidencane, mixed

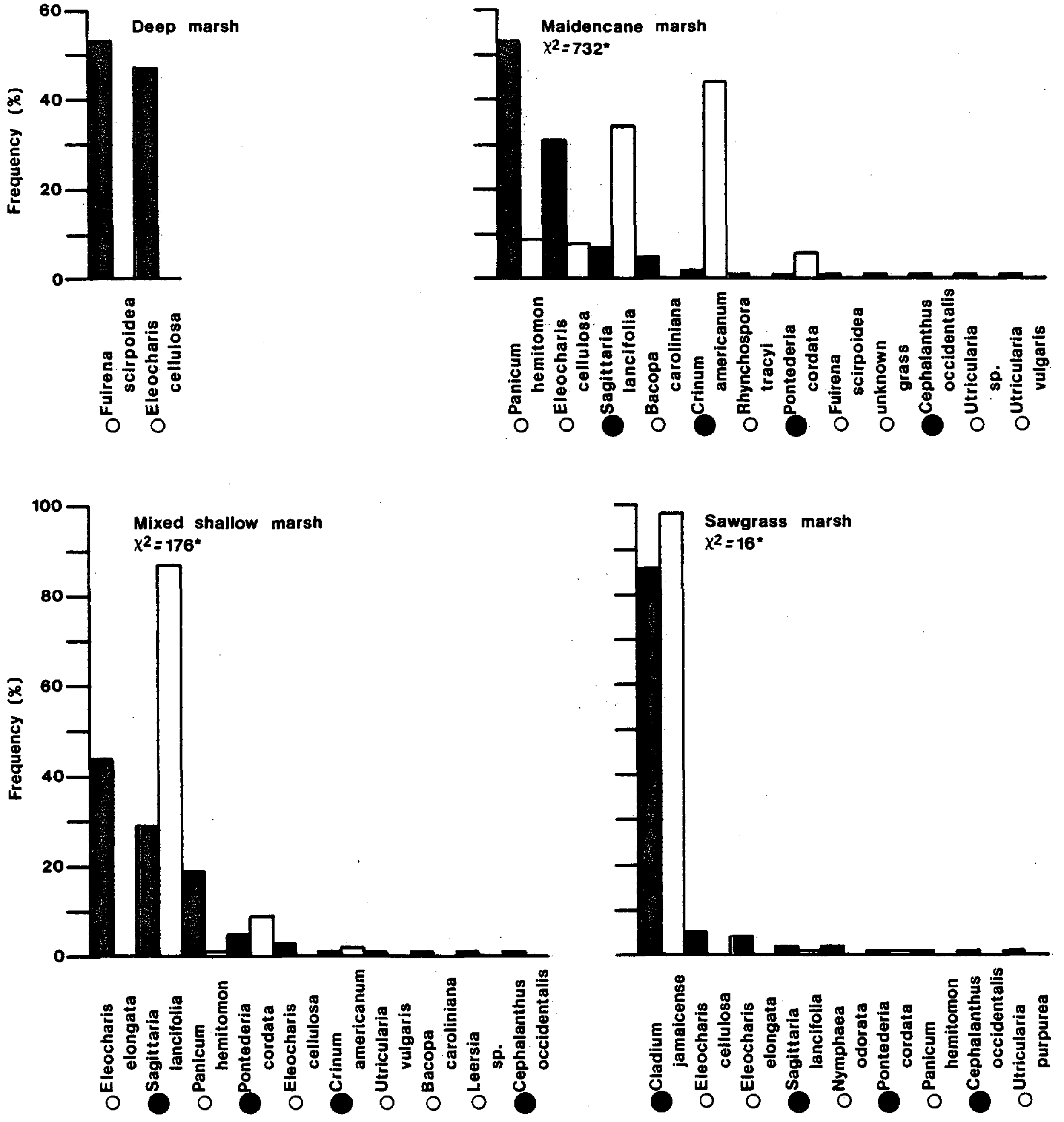

Figure 2. Frequencies of stems and clutches at BCWMA East. Frequencies of emergent plant stems (black bars) were calculated from quadrats, and those of clutches (white bars) on species of plant stem from transects. Non-zero values $\leq 1\%$ are drawn at 1%. Values for chi-square are given for comparisons of stem and clutch distributions; *, $P < 0.05$. Circles: open, narrow-stemmed plants; closed, broad-stemmed plants.

Table 1. Occurrence of clutches by plant association, BCWMA East. Stem densities are means of mean quadrat densities within each of six or seven transects per habitat. The percentage of stems that belong to narrow-stemmed species is given. Clutch densities are means of densities found in the six or seven transects sampled for each plant association. These values were converted to standing crop for each association in the entire BCWMA East marsh using the area or perimeter occupied by the association in the marsh. Also given is the frequency (%) with which a clutch was found attached to two stems (paired stems) and the frequency with which two clutches (paired clutches) were found on one stem. Water depths are means for depths in the centers of all quadrats and for depths beneath all clutches found in transects in 1993. Clutch heights are means of the transect means.

	Plant association			
	Maidencane marsh	Deep marsh	Mixed shallow marsh	Sawgrass marsh
Stem density (m^{-2})	255	18	285	151
Percent narrow stems	91	100	63	11
Clutch density (m^{-2}):				
mean	0.196	0	0.197	0.603
range	0.08-0.52	--	0.10-0.44	0.36-0.80
Area (ha)	519	399	233	234
Perimeter (km)	--	--	--	83.2
Clutch standing crop:				
area	1.02×10^6	--	0.459×10^6	1.41×10^6
perimeter	--	--	--	0.050×10^6
Stem use (%):				
Clutches on paired stems	4.5	--	1.2	0
Stems with two clutches	6.0	--	2.4	1.8
Water depth (mm):				
1993 quadrats	386	551	336	339
1993 transects	384	--	342	346
Clutch height (mm)	186	--	171	207

shallow, and sawgrass marshes (Figure 2). In maidencane and mixed shallow marshes, which were dominated by narrow stems, clutches occurred predominately on the rarer broad stems; in sawgrass marsh, dominated by broad stems, clutches occurred again on the broad-stemmed species more frequently than expected. In maidencane marsh, only 12 clutches were borne on narrow-stemmed plants. The other 57 occurred on *Sagittaria lancifolia* (mean diameter of clutch-bearing stems 10 mm), *Crinum americanum* (18 mm), and *Pontederia cordata* (8 mm). Six narrow-stemmed species comprised 63% of stems in mixed shallow marsh but carried only one clutch; the other 86 clutches were attached to *S. lancifolia* (7 mm), *P. cordata* (8 mm), and *C. americanum* (21 mm). In sawgrass marsh, most of the 116 clutches were found on the broad (17 mm), outer, oldest and dead stems that enshrouded the inner, younger, narrower stems of each culm of the dominant *Cladium jamaicense*; and the rest were attached to *S. lancifolia* (12 mm) and *P. cordata* (11 mm).

In addition to the lack of clutches in deep marsh and the high density of clutches in sawgrass marsh, two lines of evidence indicate that the plant associations differed in their availability of substratum for oviposition. The frequency of clutches deposited on pairs of adjacent stems and the frequency of stems bearing two clutches increased with dominance of the habitat by narrow-stemmed plants (Table 1). Paired stems only consisted of narrow-stemmed species, single stems of which applesnails rarely used. The patchy occurrence of rarer broad stems in maidencane marsh probably resulted in the greater use of paired stems of *Panicum hemitomon* and *Eleocharis cellulosa*. The only use of paired stems in mixed marsh was of *P. hemitomon*, and no paired stems were used in sawgrass marsh. Similarly, the rarity of suitable broad stems in maidencane marsh might explain the high incidence of repeated use of single stems for oviposition (Table 1). Two clutches per single stem was a less frequent condition in mixed shallow marsh, and it was least frequent in sawgrass marsh despite the high clutch density and low stem density (Table 1). Only broad stems bore two clutches each.

The four plant associations differed little in the protection offered to clutches against variation in water level. Although deep marsh had the greatest depth, the lack of clutches gives it only the potential as a refuge for adults during drought or drawdown. The other three plant associations were much shallower, and the shallowest (mixed shallow and sawgrass marshes) were similar in depth. In all three, depths measured in the quadrats seemed to be good predictors of depths beneath clutches. Clutch heights above the water were greatest in sawgrass marsh, and clutches were, therefore, least susceptible to submersion with rising water level; but heights in maidencane and mixed shallow marshes were not much lower. Clutches on narrow stems were attached much lower than others. In maidencane marsh, clutch heights averaged 105 mm on *Panicum hemitomon* and 69 mm on *Eleocharis cellulosa* despite the emergent heights of these species (654 mm and 480 mm, respectively). The single clutch on a narrow stem in mixed marsh was attached at 20 mm height on a *P. hemitomon* of 160 mm emergent height.

Effects of Exposure on Adults

In the first two trials, in which the locomotor activity of snails could be monitored daily, the animals ceased moving within 2 d. Periodically and sometimes after many days, however, snails would gape and extend the foot, head, and occasionally the eyes and tentacles, twisting and turning in place. More than half the animals buried themselves when provided with sand, but they typically made broad shallow wallows no more than half the shell length in depth. Secretion of an epiphragm was not observed even in snails that remained closed. A strong foul odor was invariably an indicator of death and was often accompanied by the release of fluid past the operculum; but gape of the operculum was unreliable. Also, the absence of odor was not a reliable indicator that a snail was alive. Tight closure of the operculum often confounded attempts to detect death in lieu of odor or fluid unless closed animals were purposely sacrificed, as in the third and fourth trials.

Survivorship was reduced to 50% by 6 d of aerial exposure and to 7% by 14 d in Trial 1 (Figure 3). Survivorship was higher in Trial 2, 50% of the snails surviving 25-27 d, but it dropped suddenly to 33% by 29 d (Figure 3). The third and fourth trials were conducted on the suspicion that the results of the first two trials differed because of the involvement of separate technicians making subjective decisions on odor and responsiveness of the snails. Survival of aerial exposure was much poorer in the third and fourth trials, in which animals were sacrificed after 7 d: 2% and 0-3% survival, respectively (Figure 3). Animals provided with sand in Trial 4 survived better (10-13%; Figure 3); but of the four survivors, one died during the recovery period. Only 40% of the snails buried into the sand. All four survivors had buried themselves, two of them deeper than half the shell length. The only other snail to bury deeper than half the shell length did not survive 7 d.

Effects of Submersion on Eggs

Submersion in all treatments slowed the rate of embryonic development and increased mortality (Figure 4). The severity of effects was directly proportional to the duration of submersion and inversely proportional to age at submersion.

Despite high variability in some of the data, success of hatching after 14 d was highest in the control group, and unhatched embryos in the controls were the largest in size of all groups (Figure 4). Moderate hatching occurred in clutches submerged at 12 d of age, and unhatched embryos were smaller than those of the controls. Hatching success was poor in clutches submerged at 8 d of age, and the two juveniles that did hatch fell from the uppermost eggs of one clutch that had become partly exposed due to excessive evaporation; embryos in the 8-d clutches were yet smaller. No hatching occurred in clutches submerged at ages of 4 d and 1 d, and sizes of their embryos were smallest of all groups.

Extension of incubation time to 21 d did not allow embryogenesis to progress except in control clutches and in clutches submerged at 12 d of age (Figure 4). Embryonic mortality during the first 14 d of incubation was 12% of unhatched shelled embryos, and mortality was highest in earlier stages of development. Mortality was 67% among unhatched shelled embryos of clutches incubated for 21 d.

Predation on Submerged Clutches

None of the loss or breakage of eggs in clutches submerged at Clear Lake and BCWMA East is directly attributable to predation, and most is reasonably explained by other factors. This study does, however, show that submersion of eggs increases mortality by any of several possible factors (Table 2). It also supports two conclusions drawn from submersion studies in the laboratory: Submersion does not prevent hatching by late-stage embryos; submersion suppressses hatching by mid-stage embryos.

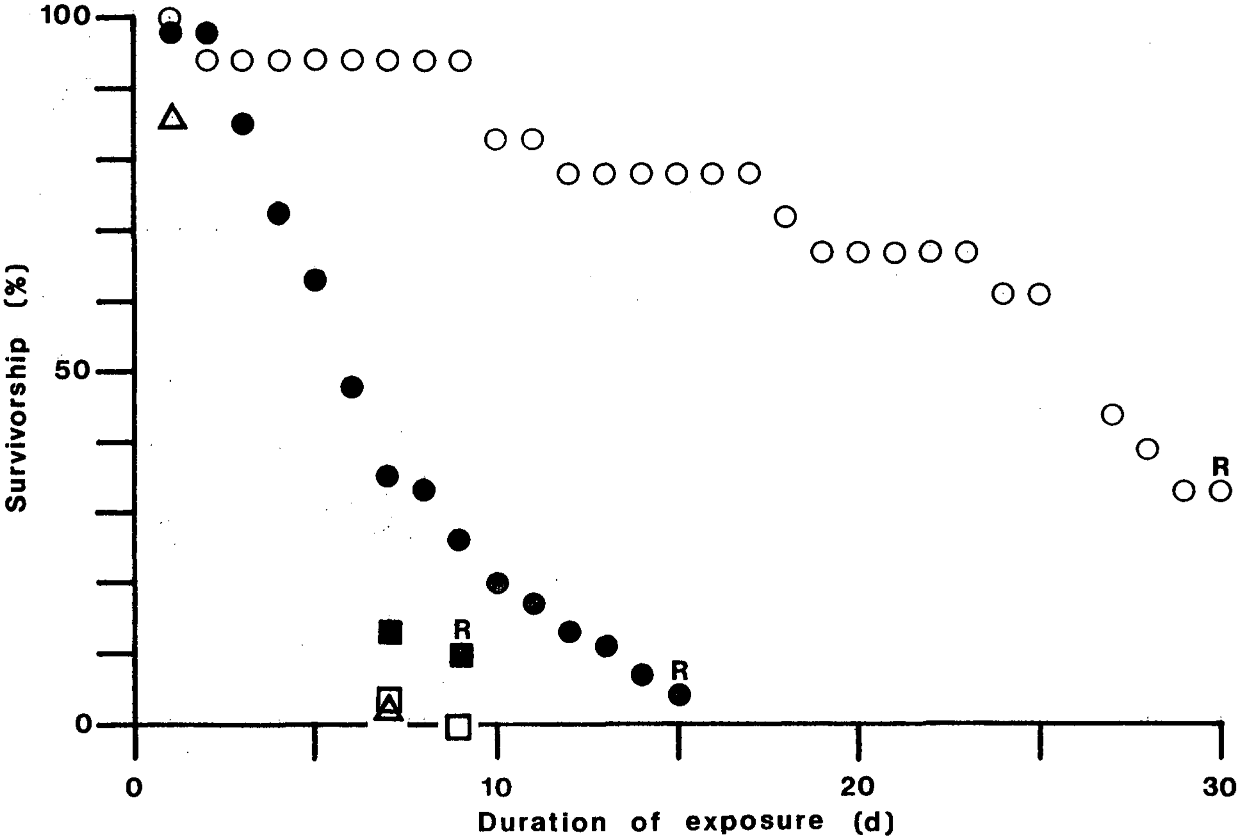

Figure 3. Effects of exposure on adult applesnails. Snails were held in the laboratory under fully aerial conditions or with sand saturated with water to evaluate their capacity to aestivate. Trials 1 (closed circles) and 2 (open circles): aerial; checked daily for mortality for 14 d or 29 d, respectively, and after 1 d of recovery (R). Trial 3 (triangles): aerial; checked for mortality after 1d and 7 d of exposure. Trial 4 (squares): aerial (open squares) and with sand (closed squares); checked for mortality after 7 d of exposure and 2 d of recovery.

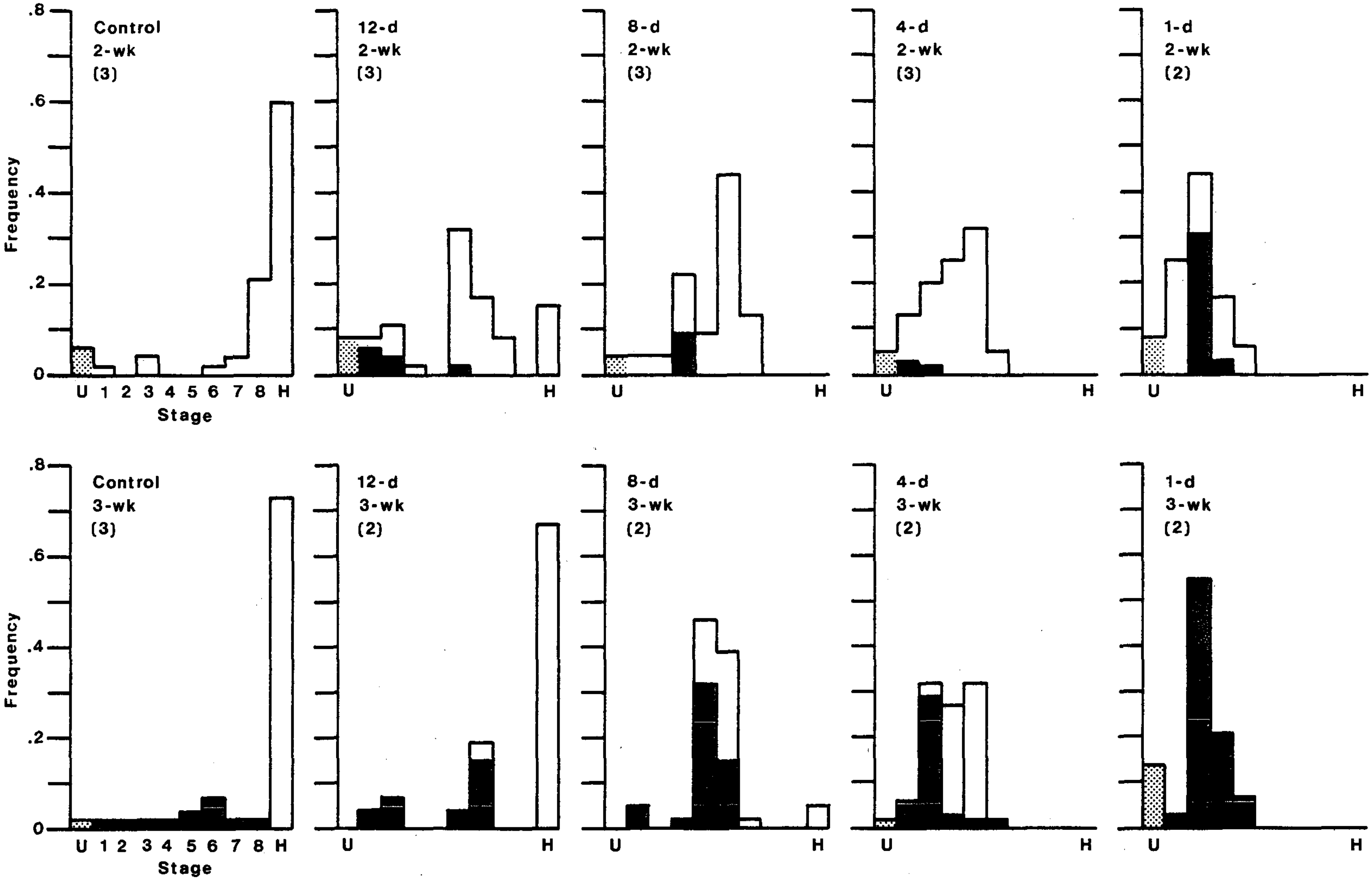

Figure 4. Effects of laboratory submersion on eggs. Eggs were sacrificed at ages 2 wk (upper row of histograms) or 3 wk (lower row) to determine developmental stage and mortality. Clutches were submerged at ages 12, 8, 4, or 1 d and remained submerged until the day of sacrifice. Controls were not submerged. Embryos were classified as unshelled (U, stippled), eight increasing sizes of shelled embryo (1-8), or hatched (H). Shelled embryos were scored as live (white parts of bars) or dead (black). Values in parentheses are the numbers of clutches used.

Table 2. Condition of clutches submerged in the field. Each submerged clutch was paired with an aerial clutch of the same age, and both were attached to a PVC pole driven into the sediment. Duplicate PVC poles were used at Clear Lake, giving two aerial and two submerged clutches at each age. At BCWMA East, four PVC poles were used for each age except 6-d-old clutches, for which three poles were used. Data do not include eggs that were damaged in handling at the start of the trial.

Age at start (d)	Percentage of eggs after 3 or 7 d in:							
	Aerial clutches				Submerged clutches			
	Whole	Lost	Broken	Hatched	Whole	Lost	Broken	Hatched
				Clear Lake, 3 d				
0	100	0	0	0	44.4	55.6	0	0
1	98.2	0	1.8	0	98.6	0	1.4	0
4	93.4	3.3	3.3	0	83.0	11.0	6.0	0
7	98.8	0	1.2	0	83.9	16.1	0	0
11	100	0	0	0	70.5	9.8	19.7	0*
				BCWMA East, 7 d				
2	96.9	3.1	0	0	90.6	6.3	3.1	0
6	86.7	0	1.3	12.0	100	0	0	0
9	54.1	1.3	0	44.6	82.3	12.9	3.2	1.6
13	32.1	25.9	0	42.0	9.9	16.8	22.8	50.5

*Control clutches in laboratory began to hatch on last day of trial.

Only 4 of the 309 eggs in 10 aerial clutches were damaged during the 3-d trial at Clear Lake (93-100% survival; Table 2). There was no evidence of hatching in aerial clutches or of damage due to recreational use of jet-propelled watercraft. Two additional eggs from one aerial clutch were lost entirely from their attachment to the plant stem. Survival of eggs in submerged clutches at Clear Lake was much lower and more variable (44-99%; Table 2). Of 362 eggs in 10 submerged clutches at Clear Lake, 19 were broken; but 12 were empty of contents (no residual yolk or albumen) and belonged to clutches for which control clutches in the laboratory began hatching on the date that this trial was concluded. Another 66 eggs were lost from submerged clutches: 40 from jellied, 0-d-old clutches, which presumably lost adhesion; 11 eggs from the PVC pole holding the aerial clutch that lost 2 eggs; 6 from a submerged clutch that presumably had begun to hatch, based on hatching of control clutches in the laboratory.

Dissection of eggs that were retrieved from the trial at BCWMA East after 7 d improved the ability to discriminate between hatching and other conditions of eggs. Survival of eggs was higher and less variable in aerial (74-99% whole and hatched eggs; Table 2) than in submerged clutches (60-100%). All but one egg were lost or crushed in a pair (i.e., aerial and submerged) of clutches on one PVC pole, indicating the occurrence of an unknown random event. Except for this pair of clutches, 8 eggs were lost and 1 broken out of 333 eggs of 14 aerial clutches; and 31 eggs were lost and 11 broken out 303 eggs of 14 submerged clutches. On the other hand, more than half of the eggs lost from submerged clutches represented an entire clutch on a pole that had become surrounded by floating debris; and 7 of the 11 broken eggs of submerged clutches were empty (no residual yolk or albumen) and belonged to clutches that had begun to hatch. Hatching rate of 13-d-old eggs was higher in submerged than in aerial clutches; and the rate for 9-d-old eggs was far poorer in submerged than in aerial clutches (Table 2).

Conclusions

Distribution of egg clutches among and within plant associations in the marsh. Clutch density was highest along the edge of sawgrass stands and zero within deep marsh. Densities within maidencane and mixed shallow marshes were about one-third those in sawgrass marsh. Within the three plant associations that held clutches, the distribution of clutches among plant stems was not explained simply by the frequency of stems among species. Limitation of suitable substratum for oviposition was indicated by the use of paired stems for oviposition and by the occurrence of two clutches on single stems. The associations in decreasing order of substratum limitation were: deep marsh, maidencane marsh, mixed shallow marsh, sawgrass marsh.

Characteristics of plants that make them suitable for deposition and holding of clutches. Clutches were strongly associated with plants having broad stems. The stems tapered from their clumped bases to their emergent tips and generally exceeded 6 mm in diameter at water level. Except for a few species with short stems and for broken stems of long-stemmed species, most available stems far exceeded the heights at which clutches were deposited, and stem height was, therefore, rarely limiting. Narrow-stemmed plants were rarely used, and clutches on them were low to the water despite the far greater height of the stem. The most suitable plants for oviposition based on frequency of use were, in alphabetical order: *Cladium jamaicense*, *Crinum americanum*, *Pontederia cordata*, and *Sagittaria lancifolia*.

Tolerance of adult snails to long-term exposure. Snails collected in spring and summer were very intolerant of aerial exposure. High mortality occurred within the first week, and the apparent survival of some snails for as long as a month seemed to be an artifact of opercula that remained tightly closed after death. Because the Florida applesnail is a weak burrower, the availability of moist sand offered little protection against exposure.

Physiological tolerance of clutches to submersion in water. Submersion of clutches slowed embryonic development and increased mortality. Embryos that were within a few days of hatching at the time of submersion were not strongly affected. When younger embryos were submerged even to 21 d of development, none hatched, and most died in early stages of growth.

Exposure of submerged clutches to aquatic predators. Submersion of clutches in the field increased mortality above that due to physiological intolerance to submersion, as determined by laboratory studies. Factors other than predation reasonably accounted for losses and breakage of eggs in the field: loss of adhesion, especially by jellied clutches; entanglement with floating debris; unknown factors that damaged also the aerial clutches; hatching. There was no evidence that aquatic predators were a significant factor.

DISCUSSION

Field Survey

Adult applesnails were rarely encountered during the field survey and never occurred within transects or quadrats. The dark shells of the few were visible against the bare sand of deep marsh, where adults were out of the reach of avian predators and out of their own reach of the surface for oviposition and, presumably, aerial respiration. Snail kites, when present, foraged successfully in more densely vegetated marsh, where casual observation yielded no adult snails during the field survey. Although no method has been found to assess applesnail populations adequately (U.S. Fish and Wildlife Service 1986; Owre and Rich 1987; Rich and Owre 1990), available estimates give a wide range of snail density for specific habitats: 32-75 m^{-2} under dense cover of the aquatic plant *Vallisneria* and < 4 m^{-2} on bare mud in a riverine population at Wakulla Springs (Bryan 1981); 0.25 m^{-2} among grasses and rushes in open water, 0.25-0.50 m^{-2} in mats of *Bacopa*, and 1-2 m^{-2} in mats of *Utricularia* in the Everglades (Kushlan 1975); 0.25-2.40 m^{-2} in five types of habitat in the Everglades (Owre and Rich 1987).

The densities of clutches in the present study ($\leq$ 0.603 m^{-2}) were well within the range found by Owre and Rich (1987) in the Everglades (0.06-1.27 m^{-2}). When clutch density is calculated for BCWMA East based on estimates of standing crops in sampled plant associations, a value for the mapped part of the marsh of 0.165 m^{-2} is obtained if clutch density is assumed to be homogeneous in stands of sawgrass and 0.087 m^{-2} if clutches are assumed to occur only along the perimeter of sawgrass stands. Estimates of standing crop in the mapped area of the marsh are 2.9 x 10^{6} clutches and 1.5 x 10^{6} clutches, respectively.

The distribution of clutches in the marsh is highly dependent on the availability of proper substratum for oviposition. Broad-stemmed plants are clearly preferred. Wallace et al. (1956) also found clutches more frequently on *Cladium*, *Sagittaria*, and *Typha* than on *Panicum* and other narrow-stemmed plants. The Florida applesnail has a broad foot, and the female must hold position on a stem in air for one or more hours to deposit a clutch of 10 to 80 eggs one at a time at intervals of 2-6 min (Couper *in* Haldeman 1845; Hepler 1974; Hanning 1979). The biomechanical requirement for broad stems is also indicated by the frequency (31%) with which clutches on narrow-stemmed species are deposited on pairs of stems and by the short distance above water level that the female climbs on narrow stems despite the emergent height of the stems. Usable substratum is lacking in deep marsh; and its availability, based on frequencies of clutches on paired stems and of stems carrying paired clutches, is somewhat limited in maidencane marsh.

Narrow stems are inferior also in the resistance they provide a clutch to submersion by rising water level. Clutch heights were similar among plant associations (171-207 mm; Table 1) probably because most clutches occurred on broad-stemmed plants, on which the ascent by a gravid female was not limited by stem diameter. In these associations, water rising at 12.2-14.8 mm/d would reach mean clutch heights over a 2-wk period. Wyman (1875) roughly estimated clutch height at up to 2 ft, and Hanning (1979) measured mean clutch height at 150 mm for 121 clutches.

Water depth below applesnail clutches is not given in the literature. Based on depths measured in the present study, plant associations seem to vary more in the resistance they provide to stranding of hatchlings on exposed substratum than to submersion of unhatched clutches. The rate of drawdown over 2 wk that would have stranded the clutches standing at the time of the field survey was 27.4-32.6 mm/d in maidencane marsh, 24.4-45.3 mm/d in mixed shallow marsh, and 24.7 mm/d in sawgrass marsh.

Effects of Exposure on Adults

The family Ampullariidae, which includes applesnails, includes members that are well known for their capacity to aestivate. Baker (1903) wrote that ampullariid snails are capable of "living for several years away from the water." In the field, Pomacea urceus aestivates for 4.5 mo (Burky et al. 1972), and Pila virens aestivates for 6 mo and, possibly, for as long as 24 mo (Meenakshi 1956, 1964). In the laboratory, Pomacea lineata and Pomacea urceus survive more than 13 mo out of water (Little 1968; Burky et al. 1972). Aestivation is anaerobic in some ampullariids and aerobic in others (Burky et al. 1972; Santos et al. 1987). During aestivation, snails lose as much as 35-62% of the wet weight of soft tissue (Little 1968; Burky et al. 1972), and humidity has no effect on weight loss or survival in Pila virens (Meenakshi 1964). Pomacea lineata is active out of water until it loses 20% of its wet weight, at which point aestivation ensues (Little 1968).

Aestivation is a cyclic activity that has been attributed often to Pomacea paludosa in the literature, but most authors have relied on anecdotal observations. Tabb (1963) referred to eyewitness accounts of applesnails "burrowing into the soft muds at the bottoms of deeper holes" during droughts; he recommended a field study on the effects of declining water level on marsh animals and a laboratory study on tolerance to desiccation and high CO_2 concentration. Wetmore (in Cottam 1942) described feeding by limpkins at Paradise Key, Florida, on applesnails buried in the mud of a wet prairie. Snyder and Snyder (1969) speculated that boat-tailed grackles might forage for aestivating snails as they do for stranded mussels.

On the other hand, there have been no substantive reports on survival of Pomacea paludosa during periods of natural drought or of aerial exposure in the laboratory. We know little of the occurrence of aestivation in the field, its importance to the snail's population biology, and its physiological mechanisms. Tabb (1963) described P. paludosa as a weak burrower in soft substrata. Snyder and Snyder (1971) described burial in sand, and burial was usually incomplete, as found in the present study. Little (1968) included limited data on hemolymph composition of P. paludosa in his study of aestivation by P. lineata; he mentioned that the former species suffered higher mortality than the latter during aestivation and attributed the difference to the poor fit of the operculum within the aperture of P. paludosa. An additional explanation could be intolerance to the increase in lactic acid concentration during anaerobiosis (Thomas and Agard 1992). In the present study, many animals closed the operculum tightly, but none formed an epiphragm of dried mucus as a seal. As for survival in the field, Sprunt (1950) described the "reeking odor of dead Pomacea snails" detected during drainage of a marsh in south Florida.

The ability of Pomacea paludosa to survive exposure is unimpressive compared to its congeners. The snails stopped crawling early in the present study, but many remained active and agape. Greater apparent survival in the first two trials than in the last two might have been due to the continued monitoring of closed dead snails that were thought to be alive in the absence of a foul odor. Nevertheless, P. paludosa suffers substantial mortality in less than 1 mo of exposure and might not survive 1 wk.

Effects of Submersion on Eggs

The large gelatinous eggs of *Marissa cornuaurietis*, in the same family Ampullariidae as *Pomacea paludosa*, are laid underwater. They swell from 3 mm diameter at oviposition to 5 mm as water is imbibed soon afterward (Michelson 1955). It is not, therefore, valid to assume that the large eggs of *P. paludosa*, with diameters of 4-6 mm (Ryder 1889; Wallace et al. 1956; Hepler 1974; Hanning 1979), would die from submersion due to physiological stress. But the Florida applesnail has probably evolved a physiological dependence on aerial incubation. More than 100 yr ago, Ryder (1889) warned that submersion kills the embryos. Other authors since have parroted his warning, and only Hurdle (1973) has offered new data. Hurdle (1973) found submersion to delay hatching but not to prevent it. Submersion loosened the extracapsular adhesive mucus after 1 wk, and 45% of clutches lost eggs by detachment within 2 wk. Unfortunately, Hurdle's (1973) clutches were of unknown ages at the start of submersion, and he gave no data on mortality within clutches. A subsequent experiment (Hurdle 1974) gave similar results, with submersion for 1 wk followed by a post-submersion period of continued embryogenesis; but no information was given on age of clutches or on mortality within clutches. In the present study, also, embryogenesis was delayed by submersion. After 3 wk, however, embryogenesis had not progressed beyond stages at 2 wk in clutches that were submerged at ages of 1, 4, and 8 d; and mortality at 21 d of incubation was high. Clutches that were submerged at 12 d of age had already achieved a moderate size of shelled embryo; some hatched within another 2 d and many by the end of the experiment at 21 d.

Many smaller embryos are capable of crawling when freed from their eggshells, but only embryos with body shells similar in size to their eggshells will hatch. The mechanism of hatching is unknown in *P. paludosa*. Hatching does not seem to be aided by weakening of the eggshell by chemical dissolution or radular scraping, for inspection by scanning electron microscopy gives no evidence for either mechanism (Turner and McCabe 1990). If hatching is size dependent, it might be accomplished by outward pressure from extension of the foot. Based on this hypothesis, submerged eggs would hatch only if they contained late-stage embryos that could achieve hatching size before death from physiological stress; and smaller embryos, competent to live if freed, would remain unhatched, lacking aid from implosion by water pressure on a weakened eggshell and the ability to extend the foot across the diameter of the egg.

Predation on Submerged Clutches

Aposematism must be an effective mechanism for protecting the large yolk-filled eggs of the Florida applesnail from terrestrial predators (Snyder and Snyder 1971; Romer 1972; Orians and Janzen 1974), for most claims of predation on its eggs are weak (Bailey 1925; Blatchley 1932; Ligas *in* Snyder and Snyder 1971; Abreu 1976; Kushlan 1978). The Cuban Zapata sparrow (*Torreornis inexpectata inexpectata*) is the only well-documented predator on eggs of the applesnail (González Alonso et al. 1986). There seems to be general agreement in the literature on applesnails (*Pomacea* spp.) that the major selective pressure for aerial deposition of clutches has been (or was) the avoidance of aquatic predators. It seems unlikely, however, that aposematism would have evolved prior to or parallel with aerial oviposition, for aposematism might have been equally as effective against aquatic vertebrates in the past as it appears to be against terrestrial predators today. Indeed, potential aquatic predators reject eggs offered to them (Snyder and Snyder 1971).

Other advantages to depositing aerial clutches might be the more favorable incubation temperature and oxygen concentration for embryogenesis; the production of larger hatchlings from larger eggs that could survive only in a well-oxygenated environment; avoidance of mechanical damage from drift material in a high-density medium and from adults climbing stems to breathe at the surface; avoidance of clutch cannibalism; reduction of microbial growth by exposure of the eggshell to ultraviolet light. None of these possibilities has been studied. Whatever the selective pressures might have been, the ability of applesnail eggs to survive submersion or for the species to evolve aquatic incubation again might be prevented by a dependence on sunlight for satisfying an acquired vitamin deficiency; for the success of embryogenesis is poor when aerial eggs are incubated in darkness (R. Turner, unpublished observations).

It would not be surprising, therefore, that clutches submerged in the field might die from physiological stress before they are eaten by predators. Damage incurred by submerged clutches in Clear Lake and BCWMA East marsh was low and could not be specifically attributed to predation. There was evidence for other causes for loss and breakage of submerged eggs, including hatching, weakened adhesion to stems, impact or snagging by waterborne debris, impact from adjacent moving stems, and unknown factors that also caused damage to companion aerial clutches.

Jellied clutches are easily dislodged from their attachment to stems upon submersion. But jellied clutches are the least likely stage in a stand of clutches to be submerged because of the height to which water level must rise in the hours between oviposition and the desiccation of extracapsular mucus. Early stages in embryogenesis also are the most unpalatable (Snyder and Snyder 1971; Romer 1972). Late-stage embryos, on the other hand, are most threatened unless they were attached to a vigorously growing stem: Water level could rise above clutch height during the 2-wk incubation period. Moreover, unpalatability diminishes as embryogenesis proceeds, and late-stage embryos are the most likely to survive submersion physiologically and to hatch under water. Submersion of clutches with late-stage embryos might increase hatchling mortality due to predation. Snyder and Snyder (1971) speculated that *Lepomis macrochirus* (bluegill) eat juvenile *Pomacea paludosa* in the field as they did in their laboratory studies. Nelinda Jaynes (personal communication) has repeatedly observed *Lepomis* spp. lying in wait beneath clutch-bearing stems in Hunter´s Lake, Hernando County, Florida, and consuming hatchling snails as they descend through the water column. Hatching might be the only stage at which submerged clutches experience substantial predation. Predation on hatchlings, whether from submerged or aerial clutches, warrants further study.

RECOMMENDATIONS FOR MANAGEMENT

Turner et al. (in press) have reviewed our present knowledge of the Florida applesnail and have discussed its management in the light of existing information. Their attempt to develop a mangement plan was hindered largely by a paucity of reliable data of direct use for management: Most studies either have not taken experimental approaches, have relied on weak correlative data, or have perpetuated untested assumptions made in earlier work. The recommendations given here draw from the data reported earlier in this document, from other observations made at BCWMA East and Clear Lake during the past 2 yr, and from re-evaluation of some existing literature.

These recommendations focus on optimizing conditions for applesnails. They rely on three assumptions: The absence of clutches does not indicate the absence of adults; if plants suitable for oviposition are absent, a population of snails cannot be maintained indefinitely, although longevity of individual snails will not be affected; growing and senescent plant stems are sufficiently persistent to exceed the duration of embryogenesis.

Recommendation 1: The marsh should be managed to provide a heterogeneous community of broad-stemmed emergent plants with a moderate density of stems.

Applesnails encounter stems at the sediment, and they probably climb stems that give a good footing. Broad-stemmed plants are favored by female _Pomacea paludosa_ as substrata for oviposition, and they probably also are used by male and female snails to access the surface of the water for aerial respiration. The short heights of clutches on narrow stems and the use of paired, adjacent, narrow stems indicate biomechanical problems of climbing by adult snails. The frequency of surface inspiration by Florida applesnails is known to be directly related to water and air temperatures and inversely related to the concentration of dissolved oxygen (Beissinger 1981; Cary 1985). Further studies on locomotory biomechanics and on selection of stems by diameter would be helpful in management, as would respiratory studies similar to those already done on animals erroneously or questionably identified as _P. paludosa_ (McClary 1964; Freiburg 1971; Freiburg and Hazelwood 1977; _see_ Turner et al., in press).

Diversity of the plant community must, however, be maintained because oviposition and aerial respiration are not the only concerns in the biology of applesnails; maintenance of a heterogeneous community is our only insurance against ignorance. We do not know, for example, the ways in which plant associations provide refugia against predation on hatchlings and older juveniles. Natural diet is poorly known, and evidence currently supports the conflicting alternatives of a macrophytic diet and a microphagous diet (Turner et al., in press). The ability of snails to navigate along the sediment and among stems might differ as growth forms of plants and their stem densities change. Stem density should not be high, for the apparent reduction in clutches within monospecific stands of sawgrass indicates difficulty in penetrating the stand by applesnails.

Applesnails are not limited by the height of emergent stems as much as the breadth of them. Clutch height is limited by the tendency of female snails to climb, not by the available height of the substratum. Sawgrass does not, therefore, give any advantage over other broad-stemmed plants in resistance to submersion by rising water levels. Again, heterogeneity of the plant community is the better choice.

Maidencane marsh is valuable as snail habitat if it contains a moderate frequency of broad-stemmed plants. Management of the marsh should minimize the acreage of maidencane marsh or encourage within it the growth of patches of suitable plants for oviposition and aerial respiration by snails. Otherwise, productivity of applesnails might be enhanced by the design and implantation of artificial structures for oviposition and aerial respiration within stands of maidencane.

Bacopa and *Utricularia* seem to be favored submergent plants for applesnails despite the apparent uselessness of their occasional, short, emergent stalks for oviposition. Research on the role of these and other plants as refugia, forage, and substrata for aerial respiration will help in planning management.

At three times the clutch density of maidencane and mixed shallow marshes, the edge of sawgrass marsh has the potential to hold a high proportion of the standing crop of applesnail eggs. It does, indeed, do this by acreage on the assumption that clutch densities along the perimeter of the stand reflect densities of the interior. Preliminary data from air-boat transects into sawgrass stands in summer 1992 indicated that clutches were rare in dense stands, and they occurred in patches of open areas in the thicket along with *Nymphaea*, *Sagittaria*, and other plants of the mixed shallow marsh. Opportunities to probe beyond 1 m in transects reported in this document did not reveal clutches farther into dense stands of *Cladium*. Estimates of standing crop based on perimeter of sawgrass marsh are probably more accurate. Based on this preliminary evidence, broad expanses of dense sawgrass probably do not favor applesnail populations. Management of sawgrass as applesnail habitat should favor perimeter over area. Although deep marsh was not used for reproduction, it might provide a refuge for a remnant of the applesnail population during drought and drawdown.

Recommendation 2: Drawdowns should be controlled by season and duration.

There is no evidence that applesnails require a period of aestivation. In fact, high mortality can be expected during the first week of exposure in late spring and in summer. Sykes (1983) concluded that snail populations were large only when areas remained flooded for more than several years, and data in Kushlan (1975) support Sykes′ conclusion.

Natural winter dry season of December through April might be less severe on snail populations for several reasons: Lower temperatures presumably decrease metabolic rates, oxygen demand, and evaporative water loss; nutrient reserves in the body would be used less; snails would be in a phase of reproductive quiescence and not on the verge of metabolic exhaustion as older snails probably are by June (Martin 1973; Hurdle 1974; Hanning 1979). Because oviposition begins before the dry season ends, oviposition will occur in deeper parts of the marsh on available substrata and will advance toward sawgrass marsh as water level rises in subsequent months. Undoubtedly, winter drought might kill many snails stranded in shallow marsh, but mortality would probably be lower than during summer drought. Studies on respiratory physiology and aestivation by snails in winter should investigate these possibilities.

The migration of applesnails into deeper marsh as water level declines might be considered, but the only studies on locomotion of *Pomacea paludosa* by Tuellner (1973) and Tuellner and Wolff (1979) examined the role of statocysts in geotaxy. Migration is, however, unlikely: if applesnails concentrated in restricted pools during winter drought, the Florida snail kite would probably have evolved the woodstork's habit of capitalizing on concentrated prey; and management for woodstorks and snail kites would not so strongly conflict.

A hydrologic cycle of winter drawdown alternating with 2-3 yr of high water would favor applesnail populations based on our present knowledge of them. Annual drawdown is likely to reduce the carrying capacity for applesnails considerably. There is little doubt that declining water levels in summer could severely impact the snail population. A regular, long-term, monitoring program should be initiated to track fluctuations in clutch production and to evaluate management practices.

Recommendation 3: Increases in water level should occur at seasons and at rates that will minimize submersion of clutches.

The warning of Ryder (1889) must be heeded: submersion of applesnail clutches kills them. Hanning's (1979) determination of the reproductive season from March through October in Lake Okeechobee also seems to hold for BCWMA East and Clear Lake. Increases in water level during this season must be permitted only with the distribution of clutch heights in mind. The distribution that exists at any time reflects recent hydrologic history: If water level is declining, younger clutches would occupy a lower broad zone on stems, and a greater proportion of them than older clutches will be submerged by subsequently rising waters; if water level is steadily rising, cohorts of older clutches will be submerged in succession. Only clutches nearest to hatching would provide some hatchlings during a period of rapidly rising water. If water level were to increase too rapidly, as much as 2 wk of clutch production in the marsh would be lost. Production during the first few months of oviposition is probably most critical, for there is evidence that the early hatchlings provide the spawning population for the autumn and following spring (Martin 1973; Hurdle 1974; Hanning 1979).

The distribution of clutch cohorts should be monitored and applied to a dynamic model that should be developed to predict mortality at known or desired rates of flooding. The challenge to effective management is the decision on what level of mortality to accept. Predation on submerged clutches, at least, need not be a consideration. Proper maintenance of levees, supervision of water-control structures, and monitoring of natural accumulation of water will be critical to successful management of the standing crop of clutches. Otherwise, rapid flooding should be permitted only in November through February.

ACKNOWLEDGMENTS

The fieldwork for this study involved familiarization with the marsh at BCWMA East, collection of clutches and adult snails for field and laboratory experiments, conduct of the field experiments of predation on submerged clutches, operation of the airboat, and conduct of the field survey. For their assistance in this work and for many hours of companionship, I thank Richard Dellinger, Mary Ann Lee, Edgar F. Lowe, Steven J. Miller, Kenneth L. Snyder (who provided an exceptional amount of assistance), and Kevina Vulinec of the St. Johns River Water Management District; Veronica S. Cusack, Kerrie A. Fallon, James M. Feltz, Kirsti L. Halvorsen, Jennifer O. Kahrs, Nancy A. Lightowler, Stacey E. McCaffree, and Michael G. Shlepr of Florida Institute of Technology; and my son William D. Turner and stepson Philip C. Tallon. A number of students at Florida Institute of Technology helped with preliminary, final, and ongoing studies on aestivation (V. Cusack), clutch submersion (J. Kahrs, Matthew L. Kinter), and exposure of hatchlings (S. McCaffree); design, construction, and maintenance of the culture system (David A. Cook, V. Cusack, J. Feltz, M. Kinter, N. Lightowler, M. Shlepr); and general maintenance and supervision of Aquaculture Laboratory (K. Halvorsen, Nikhil K. Mehta); I am indebted to them for their invaluable help. Joseph S. Straniti (Florida Institute of Technology) generously gave much of his personal, as well as professional, time to modifying the incubators for interior lighting. Junda Lin made the facilities of Aquaculture Laboratory available to me; and he and Timothy C. Tricas, both on the faculty at Florida Institute of Technology, advised me on experimental design and statistics. Robbyn R. Miller, St. Johns River Water Management District, assisted me with Lotus 1-2-3 at a critical time in managing the data for this project; and Kimberli J. Ponzio, also of the District, provided or confirmed many of the plant identifications and made several District project maps available for use in this study. In overseeing this project, Mary Ann Lee and Ed Lowe have been helpful, tolerant, and enthusiastic despite their busy schedules. Finally, special thanks go to Cammie R. Cox (Florida Institute of Technology) for her artistic rendering of the cover illustration.

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APPENDIX I

Table A. Sampling data for field survey, BCWMA East. Transect widths were 2.0 m for all locations except for mixed shallow marsh transect 1 (3.0 m) and for all sawgrass marsh transects (1.0 m).

Plant association	Transect number	Date	Coordinates ° ′ ″ N; ° ′ ″ W	Length (m)	No. of quadrats
Maidencane marsh	1	8/20/92	27 41 20.0; 80 38 0.5	30.0	5
	2	6/17/93	western third of tract	25.0	6
	3	6/17/93	same as transect 2	25.0	3
	4	7/ 7/93	27 40 1.8; 80 36 41.5	25.0	5
	5	7/ 7/93	27 39 56.2; 80 35 57.8	25.0	5
	6	7/22/93	27 40 48.5; 80 36 15.1	25.0	5
	7	7/22/93	27 40 7.3; 80 37 41.2	25.0	5
Deep marsh	1	9/30/93	27 41 12.1; 80 37 48.0	80.0	5
	2	9/30/93	27 40 44.9; 80 38 2.6	100.0	5
	3	9/30/93	27 40 15.3; 80 38 10.0	100.0	5
	4	9/30/93	27 41 19.0; 80 37 8.9	100.0	5
	5	9/30/93	27 40 52.0; 80 37 29.8	100.0	5
	6	9/30/93	27 40 30.7; 80 37 32.4	100.0	5
Mixed shallow marsh	1	7/16/92	27 41 33.0; 80 37 57.1	84.4	10
	2	8/20/92	27 41 16.4; 80 37 50.8	25.0	5
	3	8/ 6/93	27 41 5.1; 80 37 38.4	25.0	5
	4	8/ 6/93	27 40 13.3; 80 38 23.7	25.0	5
	5	8/20/93	27 40 54.6; 80 38 8.0	25.0	5
	6	8/28/93	27 40 30.5; 80 38 21.5	25.0	5
Sawgrass marsh	1	8/20/93	27 40 57.9; 80 38 15.6	41.2	3
	2	8/20/93	27 41 26.9; 80 37 47.7	44.7	3
	3	8/28/93	27 40 21.2; 80 38 19.2	42.1	3
	4	8/31/93	27 40 59.7; 80 37 24.4	24.8	3
	5	8/31/93	27 41 30.1; 80 37 8.9	25.0	3
	6	8/31/93	27 40 39.0; 80 37 26.0	25.0	3

Table B. Plants encountered in the field survey, BCWMA East. References: Stodola (1967), Godfrey and Wooten (1979), Bell and Taylor (1982), Duncan and Duncan (1987), Taylor (1992).

Scientific name	Common name	Family
Bacopa caroliniana	blue water-hyssop	Scrophulariaceae
Cephalanthus occidentalis	buttonbush	Rubiaceae
Cladium jamaicense	sawgrass	Cyperaceae
Crinum americanum	string lily	Amaryllidaceae
Eleocharis cellulosa		Cyperaceae
Eleocharis elongata		Cyperaceae
Fuirena scirpoidea	leafless fuirena	Cyperaceae
Leersia sp.		Gramineae
Nymphaea odorata	white waterlily	Nymphaeaceae
Panicum hemitomon	maidencane	Gramineae
Pontederia cordata	pickerelweed	Pontederiaceae
Rhynchospora tracyi		Cyperaceae
Sagittaria lancifolia	lance-leaved sagittaria	Alismataceae
Utricularia purpurea	purple bladderwort	Lentibulariaceae
Utricularia vulgaris	common bladderwort	Lentibulariaceae