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A comparative study of the population dynamics, life history characteristics, and physiological ecology of *Callinectes similis* and *C. sapidus* in estuarine environments of the northern Gulf of Mexico.

Pan-wen Hsueh
University of Alabama at Birmingham

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A comparative study of the population dynamics, life history characteristics, and physiological ecology of *Callinectes similis* and *C. sapidus* in estuarine environments of the northern Gulf of Mexico

Hsueh, Pan-wen, Ph.D.

University of Alabama at Birmingham, 1992

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A COMPARATIVE STUDY OF THE POPULATION DYNAMICS, LIFE
HISTORY CHARACTERISTICS, AND PHYSIOLOGICAL ECOLOGY
OF *CALLINECTES SIMILIS* AND *C. SAPIDUS* IN ESTUARINE
ENVIRONMENTS OF THE NORTHERN GULF OF MEXICO

by

PAN-WEN HSUEH

A DISSERTATION

Submitted in partial fulfillment of the requirements for
the degree of Doctor of Philosophy in the Department
of Biology in the Graduate School, The University
of Alabama at Birmingham

BIRMINGHAM, ALABAMA

1992

ABSTRACT OF DISSERTATION
GRADUATE SCHOOL, UNIVERSITY OF ALABAMA AT BIRMINGHAM

Degree Ph.D. Major Subject Marine Biology

Name of Candidate Pan-wen Hsueh

Title A comparative study of the population dynamics, life history characteristics and physiological ecology of *Callinectes similis* and *C. sapidus* in estuarine environments of the northern Gulf of Mexico

Population dynamics, life history, salinity tolerance, congeneric interactions, and diets of the blue crabs *Callinectes similis* and *C. sapidus* were compared in the Mobile Bay-Mississippi Sound estuarine systems of the northern Gulf of Mexico. Crabs were collected monthly from May 1989 to June 1990 by otter trawl or seine from four sampling sites that represented open-bay and salt marsh habitats. *Callinectes similis* and *C. sapidus* co-occured at all four sampling sites. However, with few exceptions, *C. similis* numerically dominated in open-bays, while *C. sapidus* was more abundant in salt marshes. It appeared that *C. sapidus* was forced to migrate from shallow waters into open-bays during periods of high freshwater influx. Population size structures of both blue crab populations in open-bays and salt marshes indicate that juvenile *C. similis* recruited into both salt marsh and open-bay habitats, whereas juvenile *C. sapidus* recruited primarily into salt marshes. *Callinectes similis* and *C. sapidus* appeared to have similar life cycles. Adult female crabs migrated to either coastal or offshore high-salinity waters to spawn and release crab larvae, which then re-invaded estuaries as megalopae. Juvenile *C. similis* consumed less food per day and grew slower than *C. sapidus* under laboratory conditions. In addition, *C. similis* attained a smaller maximum body size than *C. sapidus* (125 vs 190 mm CW). Female

C. similis and *C. sapidus* became sexually mature at body sizes of 60 and 100 mm CW, respectively. Consequently, fecundity and reproductive output of *C. similis* were less ($2.4-5.5 \times 10^5$ and 24-49 kJ per brood) than that of *C. sapidus* ($2.1-3.2 \times 10^6$ and 171-372 kJ per brood). Reproductive effort in *C. sapidus* may have been substantially reduced due to parasitism by the rhizocephalan barnacle *Loxothylacus texanus*, which stunts growth and inhibits gamete production. In contrast, *C. similis* were never infected by *L. texanus*. Salinity tolerance and field caging experiments suggested that population dynamics of *C. similis* in shallow marsh habitats may be regulated by salinity and congeneric predation. *Callinectes similis* was forced to migrate from shallow marshes during seasons of high freshwater influx due to their limited tolerance to low salinity. Although juvenile *C. similis* recruit into these habitats, they may suffer continuous predation pressure from the congener, *C. sapidus*. Dietary analysis indicates both blue crabs are opportunistic predators. They feed mainly on benthic macro-invertebrates, especially bivalves. Diets of *C. similis* and *C. sapidus* significantly overlap, indicating that they utilize the same food resources in areas of sympatry.

Abstract Approved by: Committee Chairman

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GENERAL INTRODUCTION

While the blue crab, *Callinectes sapidus*, is an important commercial fishery species in the United States, and has been well studied along the northern Atlantic coast, the lesser blue crab, *C. similis*, has received much less attention. Knowledge of the biology of *C. similis* is restricted to descriptive information on taxonomic classification (Williams, 1965, 1966, 1974; Franks *et al.*, 1972; Gore, 1977) and general life history (Williams, 1966; Tagatz, 1967; Christmas and Langley, 1973; Bookhout and Costlow, 1977; Norse, 1978; Overstreet and Heard, 1978a, b; Stuck and Perry, 1981; Perry, 1984; Williams, 1984). Information on the seasonal occurrence and abundance, habitat partitioning, reproductive biology, and life history characteristics of *C. similis* are lacking. *Callinectes similis* is abundant and co-occurs with *C. sapidus* in the Gulf of Mexico (P. Hsueh, pers. obs.; H. Perry, 1984).

Studies of *Callinectes sapidus* in the Gulf of Mexico are of interest not only from a comparative standpoint with *C. similis*, but because so little is known of their biology in Gulf systems (R. Orth and H. Perry, pers. comm.). The life history, population dynamics, and ecology of juvenile and adult *C. sapidus* have been well studied in coastal estuarine and bay systems on the eastern coast of North America (Churchill, 1919; Orth *et al.*, 1984; Heck and Wilson, 1987; Hines *et al.*, 1987; Wilson *et al.*, 1987). Similar studies of *C. sapidus* in the Gulf region will provide valuable comparative information. The significant differences in the physical and biotic

environments between these two geographic regions may dramatically influence aspects of the life history and ecology of *C. sapidus*.

The significance of studying the life history and ecology of *Callinectes similis* is important in several respects. First, the high abundance of *C. similis* makes it an excellent candidate for a peeler (soft shell) crab fishery. A peeler crab fishery for *C. similis* in the Gulf of Mexico could be developed through direct harvesting or using the technology of a land-based shedding system (Perry *et al.*, 1982). Secondly, *C. similis* may impact *C. sapidus* populations through species-species interactions, including indirect competition for resources such as food and habitat, or direct competition such as predation. Clearly, the potential economic benefits of a peeler crab fishery and the possible direct impact by *C. similis* on *C. sapidus* populations makes the importance of studying the biology of *C. similis* a high priority to agencies assessing and managing the blue crab fishery in the Gulf of Mexico.

Due to the large and growing commercial fishery for *Callinectes sapidus* in the Gulf of Mexico, it is important to begin to understand patterns of growth, reproductive output, recruitment, distribution and abundance in this area. The blue crab fishery in this region is fast approaching the catch levels that of the Northeast Atlantic (Steele and Perry, 1990). For example, total blue crab landings in 1987 in the Gulf of Mexico equaled 39% of the national catch, while Chesapeake Bay had only a slightly higher yield. A proper management scheme is needed to facilitate the continued acquisition of maximum yield without the risk of overfishing. Investigations on the distribution and abundance, population dynamics, and life history characteristics of *C. sapidus* will provide needed assessment information.

Although quantitative studies are lacking, *Callinectes similis* is generally thought to be restricted primarily to the more saline waters of the Gulf of Mexico, while *C. sapidus* ranges well up into brackish waters of tidal creeks and estuaries (Tagatz, 1968; Ettinger and Blye, 1981; Williams, 1984). The basis of these differences in biogeographic distribution may be related to *C. sapidus* osmoregulatory abilities. Engel (1977) examined the osmoregulatory capabilities of adult *C. similis* and *C. sapidus*. He found that adult *C. sapidus* is the better regulator of the two, in spite of both being hyperosmotic regulators of Na^+ and Cl^- at reduced salinity. In contrast, Guerin and Stickle (1988) raised juvenile *C. similis* and *C. sapidus* at salinities ranging from 2.5 to 25 ppt and found that *C. similis* could survive and grow at very low salinity (e.g. 2.5 ppt). Guerin and Stickle (1988) concluded that *C. similis* appears to have a greater physiological tolerance to low salinity than its field distribution suggests. In lieu of these conflicting studies, a comparative study on salinity tolerance of juvenile and adult *C. similis* is needed.

There are other possible reasons why *Callinectes similis* may not co-occur with *C. sapidus* in low salinity waters of estuaries in the Gulf of Mexico. Megalopae of *C. similis* may selectively settle on substrates which are associated with high salinity systems. Alternatively, megalopae may indeed settle in brackish water habitats, where they subsequently suffer greater mortality than the congeneric *C. sapidus* that may grow faster and certainly attains a larger size as an adult (Williams, 1984). If *C. sapidus* is indeed growing faster and attaining a larger body size than *C. similis*, this may afford a refuge in size from predation by fish and other predators. Habitat requirements may be similar for both species, and it is possible that due to its larger size *C. sapidus* is outcompeting *C. similis* in low salinity

waters. It is even possible that *C. sapidus* feeds on the smaller *C. similis*, as cannibalism has been well documented in *C. sapidus* (Hines *et al.*, 1987). No studies have examined potential competition for habitat or food resources between these two common portunid decapods.

There is little information available on aspects of the reproductive biology of *Callinectes similis* which comparisons can be made with *C. sapidus*. Fecundity has been estimated to range from 7×10^5 to 2×10^6 eggs in *C. sapidus* (Williams, 1984). No information is available on overall fecundity, nor the relation between body size and fecundity, in *C. similis*. In addition, it is of interest to compare the total allocation of energy to an entire brood (reproductive output) in mature *C. sapidus* and *C. similis*. Finally, it is important to examine factors which influence reproductive output such as reproductive castration through rhizocephalan parasitism.

The estuaries (Mobile Bay and Mississippi Sound) of the northeast Gulf of Mexico provide a diversity of marine environments in which comparative studies of *C. similis* and *C. sapidus* can be conducted. The seasonal and spatial salinity regimes of Mobile Bay have been documented by Schroeder and Lysinger (1979). Salinities of 15 ppt or greater occur in the lower two thirds of the Bay during periods of low river discharge (July to November). This corresponds with recruitment periods of *C. similis* and *C. sapidus* in the Mississippi Sound (Stuck and Perry, 1981). Therefore, it is likely that populations of *C. similis* recruit into Mobile Bay. It is well-known that *C. sapidus* occurs in the Mobile Bay area in great abundance (Tatum, 1982).

The main focus of the present study was to increase our knowledge of the biology of the lesser blue crab, *Callinectes similis*. Clearly, very little is known about this important, but overlooked, species. Historically, due to

problems of taxonomic identification, *C. similis* has been incorrectly lumped with *C. sapidus* (Stuck and Perry, 1981; Perry, 1984). This means that earlier population analyses overlooked *C. similis* and conclusions about *C. sapidus* may be incorrect. Because most studies of *C. sapidus* have focused on North Atlantic waters, it is also important that comparative information be gathered from the Gulf of Mexico. There are many differences between these environments which may influence aspects of the biology of *C. sapidus*. Therefore, aspects of this study will add significantly to our knowledge of *C. sapidus* in the Gulf of Mexico.

The present study will include both field and laboratory approaches in order to better understand aspects of the population dynamics, life history, and physiological and organismal ecology of *Callinectes similis* and *C. sapidus* from the Gulf of Mexico. This information is critical to the maintenance of a blue crab fishery in the Gulf of Mexico. The specific objectives of the study are to examine 1) temporal and spatial patterns of occurrence, abundance, and size frequency of *Callinectes similis* and *C. sapidus* in estuarine environments of the Gulf of Mexico, 2) characteristics of growth and reproduction in *Callinectes similis* and *C. sapidus* including growth rate, size at sexual maturity, fecundity, and allocation of energy to reproductive output, 3) the effect of parasitism by rhizocephalan barnacles on reproductive effort in *Callinectes similis* and *C. sapidus*, 4) salinity tolerance of *Callinectes similis*, 5) cannibalism and conspecific predation in *Callinectes similis* and *C. sapidus*, and 6) the respective diets of both *Callinectes similis* and *C. sapidus* from a mud-bottom habitat in Mobile Bay.

**POPULATION DYNAMICS AND LIFE HISTORY
CHARACTERISTICS OF THE BLUE CRABS
CALLINECTES SIMILIS AND *C. SAPIDUS*
IN BAY ENVIRONMENTS OF THE
NORTHERN GULF OF MEXICO**

**PAN-WEN HSUEH, JAMES B. McCLINTOCK,
AND THOMAS S. HOPKINS**

Submitted to: Marine Ecology P. S. Z. N. I.

ABSTRACT

The population dynamics and life history characteristics of *Callinectes similis* and *C. sapidus* in the Mobile Bay-Mississippi Sound estuarine system of the northern Gulf of Mexico were studied. We report that *C. similis* was numerically dominant in open-bays, *C. sapidus* was more abundant in shallow salt marshes, juvenile *C. similis* recruited into both open-bays and salt marshes, but juvenile *C. sapidus* primarily recruited into shallow salt marshes. Sex ratios of *C. similis* and *C. sapidus* were generally skewed towards higher proportions of males than females. *Callinectes similis* appears to have a life cycle similar to that of *C. sapidus*. Egg-carrying *C. similis* migrate to higher salinity waters and presumably release larvae to nearshore shelf waters, and following development they re-invade estuaries as megalopae. Juvenile *C. similis* grew more slowly than *C. sapidus*. This may be attributable to reduced feeding rates. Marked differences in fecundity and reproductive effort were found between these species. *Callinectes similis* and *C. sapidus*, respectively, produced $2.4\text{--}5.5 \times 10^5$ and $2.1\text{--}3.2 \times 10^6$ eggs and invested 24-49 and 171-372 kJ per brood. Rhizocephalan barnacle infestation by *Loxothylacus texanus* was encountered in *C. sapidus*, however, sympatric *C. similis* were free from this parasite.

INTRODUCTION

Callinectes similis Williams is widely distributed along the east coast of North America and within the Gulf of Mexico. The distribution of *C. similis* ranges along the Atlantic from Delaware to southern Florida and in the Gulf of Mexico from northwestern Florida to Campeche, Yucatan. Isolated reports of the occurrence of *C. similis* from Isla de Providencia,

Columbia and northern Jamaica have also been made (Williams, 1984). In many areas, *C. similis* co-occurs with its congener, *C. sapidus* (Tagatz, 1967; Williams, 1974; Perry, 1975; Hsueh *et al.*, in press a). Considering distributional records, there is a remarkable lack of information on population dynamics and life history characteristics of *C. similis*. This has been due, in part, to the tendency to lump individuals of both species together.

Callinectes similis and *C. sapidus* co-occur in the Mobile Bay-Mississippi Sound estuarine system (Hsueh, 1992). This provides an opportunity to compare the population dynamics and life history of *C. sapidus* with its closely related congener, *C. similis*. In addition, although the life history and population dynamics of *C. sapidus* have been well studied in coastal estuarine and bay systems on the northeastern coast of the United States (e. g., Millikin and Williams, 1984; Hines *et al.*, 1987; Hines *et al.*, 1990), little information is available for the Gulf of Mexico (see references in Steele and Perry, 1990). Significant differences in both physical and biotic factors characterize these two geographic regions and may influence aspects of life history and population dynamics.

The present study focused on the Mobile Bay-Mississippi Sound estuaries as model systems to compare aspects of the biology of *Callinectes similis* and *C. sapidus*. Aspects of the investigation included seasonal occurrence and abundance, habitat partitioning by sex and size, feeding and growth rates, size at sexual maturity, fecundity, energy invested in egg masses and reproductive castration through rhizocephalan parasitism.

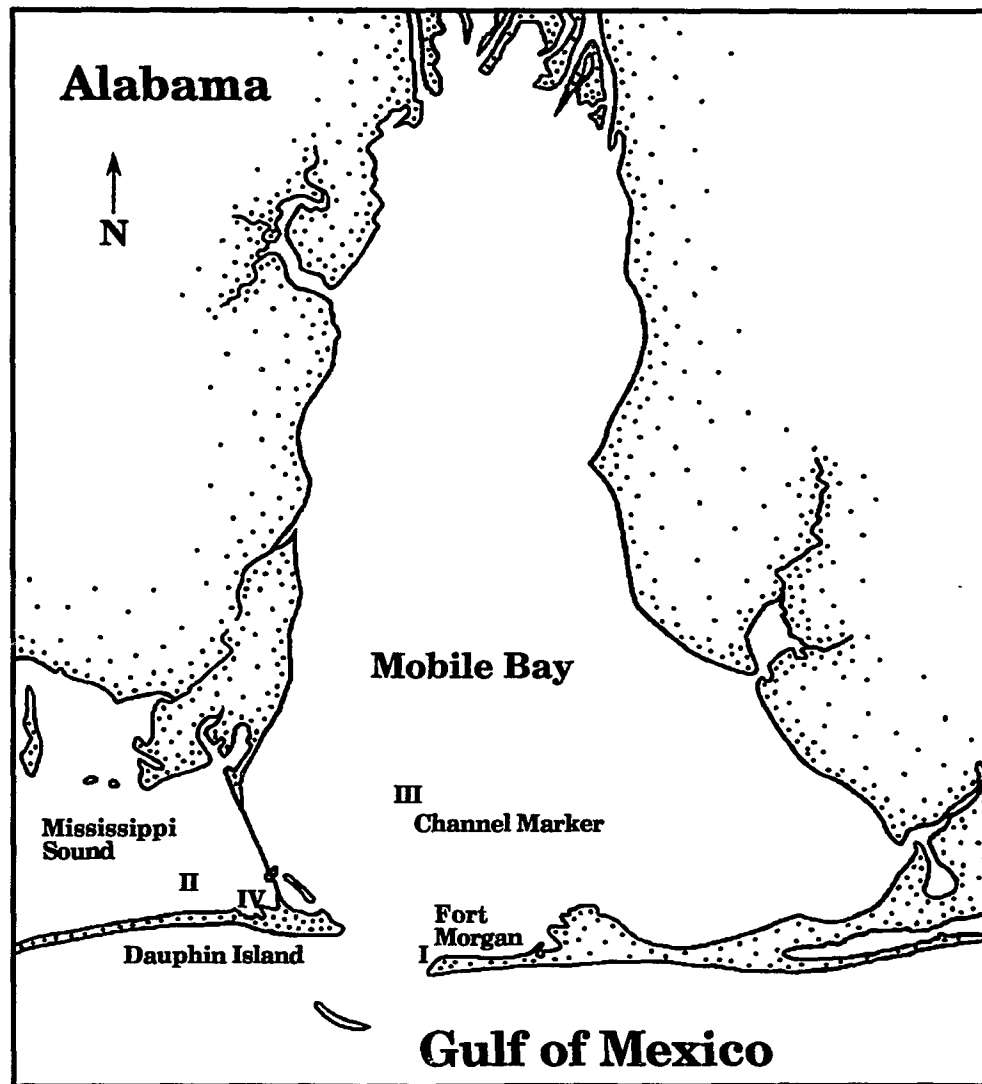
MATERIAL AND METHODS

1. Distribution, abundance, sex ratio and size frequency

Callinectes similis and *C. sapidus* were collected monthly from May 1989 to April 1991 by otter trawl (6.1-m opening and 3.0-cm mesh with 0.5-cm mesh cod end; triplicate 10-min trawls at approximately 3.6 km/hour) at study sites in Mobile Bay (Fort Morgan, 10 m depth) and east Mississippi Sound (Tall Range D, 3 m depth) (site I and II, Fig. 1). *Callinectes similis* and *C. sapidus* were also collected monthly from Channel Marker #28 in south-central Mobile Bay (site III, Fig. 1) for a one-year period (July 1990 to June 1991). Crabs at this site were collected monthly by otter trawl (7.9-m opening and 3.5-cm mesh with 2.5-cm mesh cod end; single 20-min trawl at 3.6 km/hour). Blue crabs were also collected monthly at the Dauphin Island Airport marsh using a 6-m seine (5-mm mesh) (site IV, Fig. 1). Beach seining was conducted monthly by pulling the net towards the shore over a distance of 25 m.

The sampling sites selected in this study represent a variety of habitats including open mud bottom (sites I, II and III) and salt marsh wetland (site IV). Water temperature and salinity measurements were taken during each sampling period at each site. The numbers of individuals collected, and sex and size [carapace width (CW)] were recorded for both species. A Mann-Whitney U test was used to compare abundances for each sampling date at Fort Morgan and Mississippi Sound sites (Zar, 1984). Male and female sex ratios of each species were compared using a Sign test (Zar, 1984).

Figure 1. Map of Mobile Bay and east Mississippi Sound, Alabama. Four permanent sampling sites in this study are noted in Roman numerals.



2. Feeding and growth rates, size at sexual maturity, fecundity, and energy invested in egg masses

Feeding rates of three size classes (11-20, 21-40, 41-70 mm CW) of juvenile *Callinectes similis* and *C. sapidus* were examined in the laboratory from May to July, 1989. *Callinectes similis* and *C. sapidus* were collected from Mobile Bay and Dauphin Island Airport Marsh (Sites III and IV). Crabs were held individually in 1.1 l plastic containers on racks in aquariums maintained at a constant temperature of 23 °C and a salinity of 30 ppt. Crabs were fed an *ad libitum* diet of 5% gum agar containing a 5% concentration of fish meal. Agar food blocks were pre-weighed, placed in each container for 24 hrs, and then blotted dry and re-weighed. Mean rates of food intake were compared between *C. similis* and *C. sapidus* within each size class using a Student's t-test (Zar, 1984).

Using a similar experimental protocol as in the feeding experiments, the growth rates of 10 juvenile (20-25 mm CW) male *Callinectes similis* and *C. sapidus* were examined. Wet weight and carapace width of crabs were measured at each molt interval over 100 days. An ANCOVA was employed to compare growth rates (Zar, 1984).

The size at which female *Callinectes similis* and *C. sapidus* become reproductively mature (oval-shaped abdomen) was ascertained from field collections of individuals. A total of 1800 *C. similis* and 577 *C. sapidus* were examined. A total of 390 *C. similis* and 72 *C. sapidus* male testes were examined microscopically to determine the size at which male *C. similis* and *C. sapidus* become reproductively mature.

Ovigerous *Callinectes similis* and *C. sapidus* were collected from Mobile Bay in the summer of 1989 for measurements of fecundity and reproductive energy output. The numbers of eggs produced per female was

estimated by weighing sub-samples of egg masses of twelve crabs of each species and counting the numbers of eggs under a dissecting microscope. These counts provided an assessment of the number of eggs per unit wet weight egg mass. Multiplying by the total wet weight of the egg mass, we obtained an estimate of total fecundity.

In order to calculate the total energy invested per egg mass, sub-samples of twelve egg masses of each species were analyzed for organic composition (soluble and insoluble protein, soluble carbohydrate, lipid, and ash). Protein and carbohydrate concentrations were determined using colorimetric techniques (Lowry *et al.*, 1951 and Dubois *et al.*, 1956, respectively), while lipid concentration was determined using a gravimetric technique (Freeman *et al.*, 1957). Ash was determined by placing tissues in a muffle furnace for 4 hrs at 500 °C. Energetic composition (kJ/g dry wt) was computed indirectly by multiplying the dry weight of the egg mass tissue by the level of each organic class and their energetic equivalents (Brody, 1945; Lawrence *et al.*, 1984). Total reproductive energy output was calculated by multiplying the amount of kJ/g dry wt egg mass tissue by the entire dry weight of the egg mass. The reproductive output (total kJ) of *C. similis* and *C. sapidus* was compared using a Student's t-test.

3. Parasitism

Numbers and sizes of *Callinectes similis* and *C. sapidus* infected by the rhizocephalan barnacle *Loxothylacus texanus* were recorded.

RESULTS

1. Environmental conditions

Bottom sea water temperature at all four sampling sites varied greatly with season over the study period (Figs. 2 & 3). The highest sea water temperature (35 °C) occurred at the Mississippi Sound site in August of 1989. Maximum temperature lows (11 °C) occurred at both Dauphin Island Airport Marsh and the Mississippi Sound sites in December of 1989. Sea water temperatures were generally similar at each of the four sampling sites on a given date. During the summer of 1990, however, sea water temperatures were consistently higher at the Dauphin Island Airport Marsh than the other three sites, ranging from 32 to 34 °C.

Salinity at the four sampling sites also varied with season. The lowest salinities generally occurred during the early spring (February-March) of 1990 (Figs. 2 & 3). Maximum salinity (34 ppt) occurred at the Fort Morgan site in January 1990. Minimum salinity values (1-2 ppt) were recorded at the Mississippi Sound site in February and March of 1990. Differences in seasonal fluctuations of salinity were lower at the channel site (26-32 ppt) when compared with shallower sites (e.g., Mississippi Sound site 1-26 ppt). Overall, salinities were consistently lower at the Dauphin Island Airport Marsh site than the other three sites, with values ranging from 4 to 26 ppt ($\bar{x} = 14 \pm 7$ ppt). Salinities were consistently highest at the deeper water open-bay Fort Morgan and the channel site, with values ranging from 17 to 35 ppt ($\bar{x} = 26 \pm 5$ and 30 ± 2 ppt, respectively).

2. Distribution, abundance, sex ratio, and size frequency

Callinectes similis and *C. sapidus* co-occurred at all four sampling sites. *Callinectes similis* was generally collected in significantly ($P < 0.05$)

Figure 2. Temperature and salinity at Fort Morgan, Mississippi Sound, and Dauphin Island Airport Marsh sites from May 1989 to April 1991. No data were collected in September 1989 for these three sites, and in January 1991 at the Fort Morgan and Mississippi Sound sites.

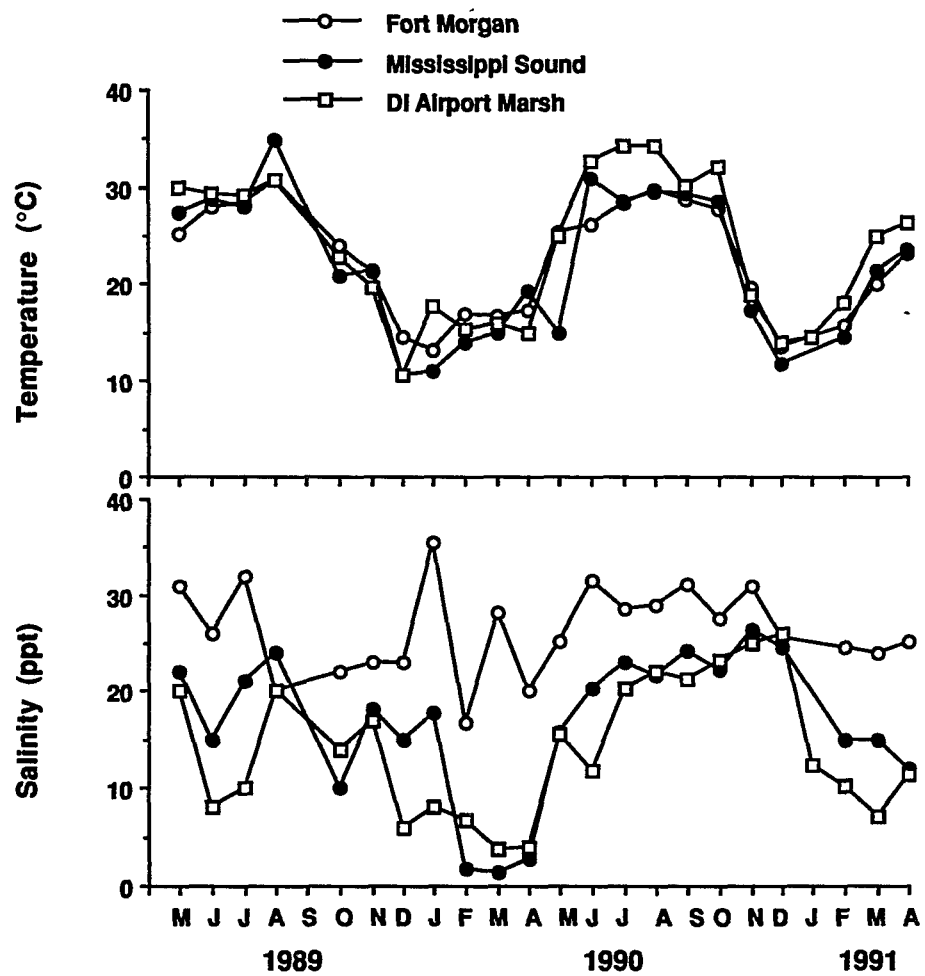
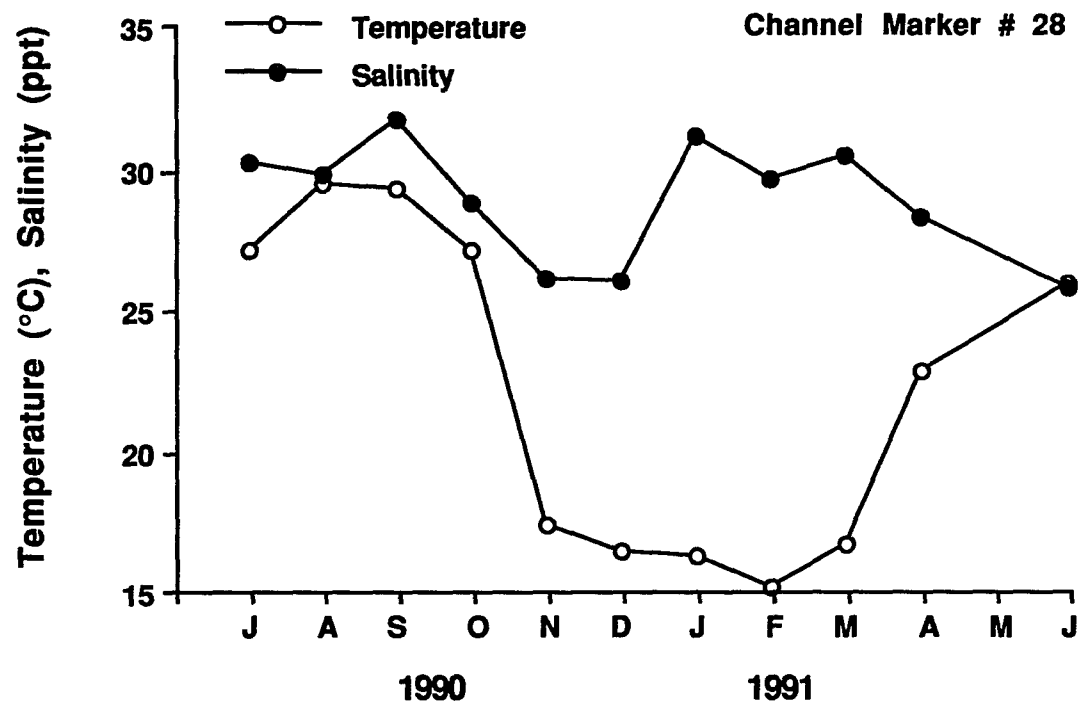


Figure 3. Temperature and salinity at the Channel Marker site from July 1990 to June 1991. No data were collected in May 1991.



greater numbers than *C. sapidus* at open-bay sites (Fort Morgan, Mississippi Sound, and Channel Marker). This trend was particularly evident at the Channel Marker site from July 1990 to February 1991, where *C. similis* accounted for at least 95% of the total crabs collected. Minor exceptions occurred in June 1989 at the Mississippi Sound site, March 1990 at the Fort Morgan and Mississippi Sound sites and April 1991 at the Fort Morgan site (Figs. 4 & 5).

Abundances of blue crabs varied over both season and site. At the Fort Morgan site, both species were most abundant during the summer of 1989 and the spring of 1990 and 1991. Peak abundances reached a mean of 71 *Callinectes similis* per trawl during the summer of 1989, and 64 and 32 *C. similis* per trawl in the spring of 1990 and 1991, respectively (Fig. 4). *Callinectes sapidus* was most abundant at the Fort Morgan site during the spring of 1990 and 1991 when abundances reached means of 30 and 43 crabs per trawl. At the Mississippi Sound site, *C. similis* peaked in abundance (\bar{x} = 89 crabs per trawl) in fall of 1989 and remained low throughout the rest of sampling period (Fig. 4). *Callinectes sapidus* had low densities throughout the entire sampling period at the Mississippi Sound site. At the Channel Marker site, *C. similis* was abundant in all seasons except spring 1991, when *C. sapidus* became abundant at this site (Fig. 5).

In contrast to open-bay sites, the abundance of *Callinectes sapidus* was much greater than that of *C. similis* at the Dauphin Island Airport Marsh during the entire sampling period (Fig. 5). Peak abundances of *C. sapidus* occurred during the summer and winter of both 1989 and 1990, and the spring of 1991. *Callinectes sapidus* was found on all sampling dates, while *C. similis* did not occur at the marsh site in the spring and

Figure 4. Mean (± 1 S.E., $n=3$) abundances of *Callinectes similis* and *C. sapidus* at the Fort Morgan and Mississippi Sound sites from May 1989 to April 1991. No data were collected in September 1989 at these sites.

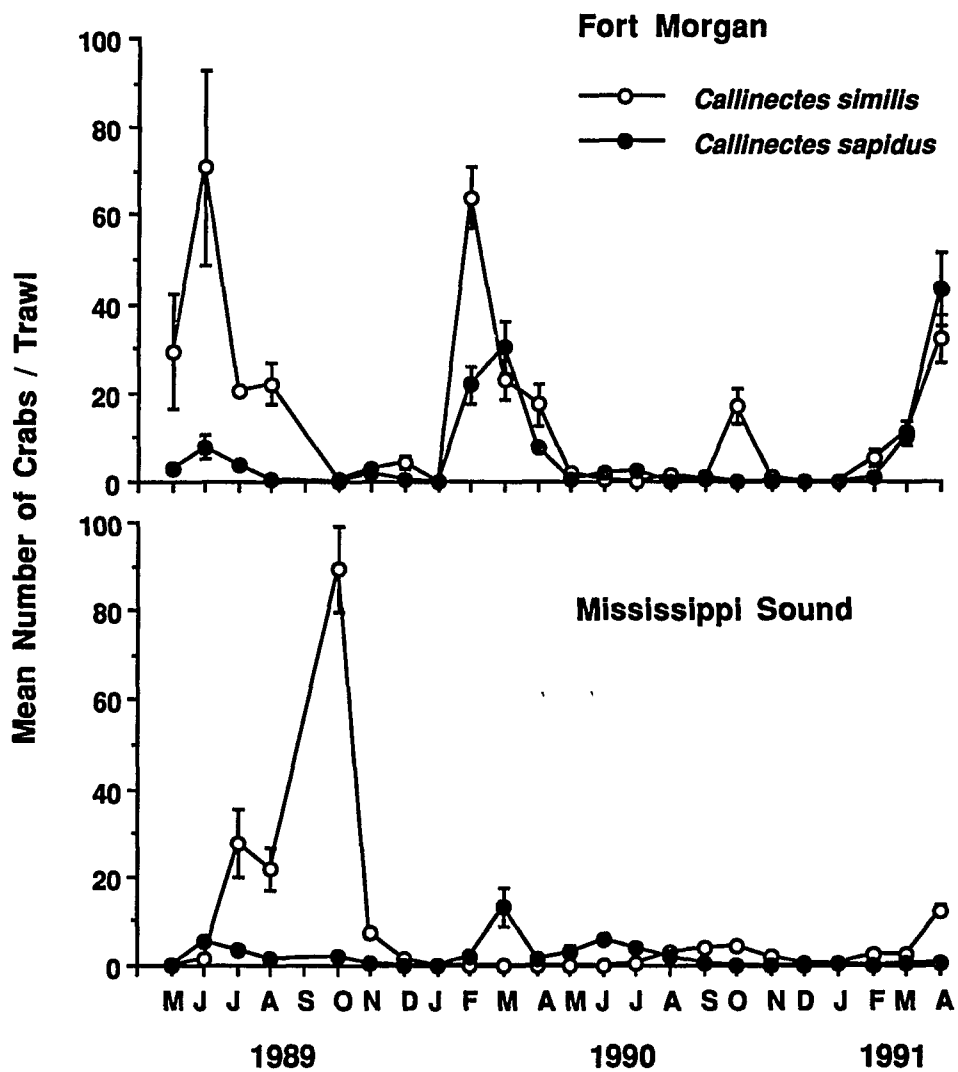
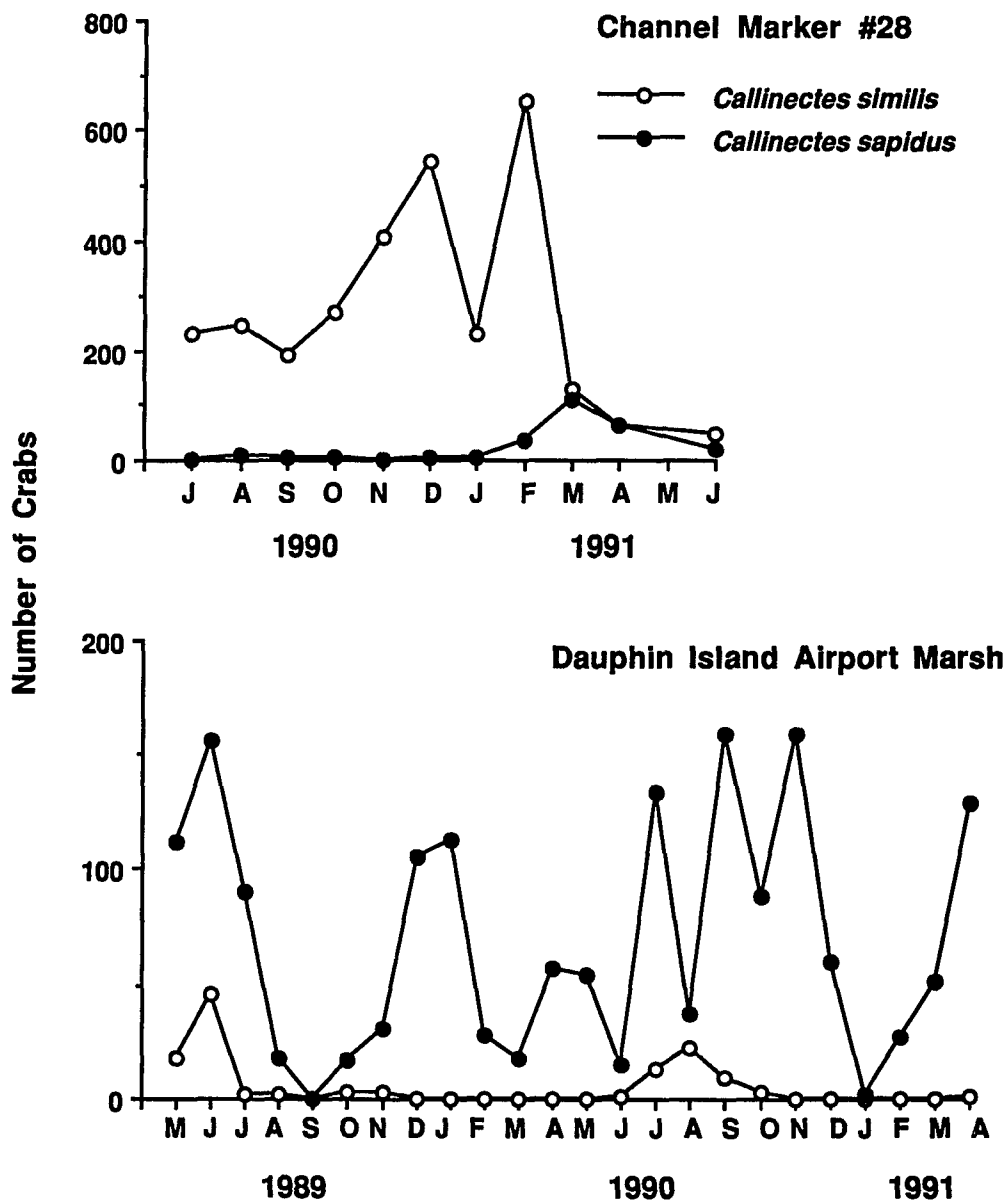


Figure 5. Abundances of *Callinectes similis* and *C. sapidus* at the Channel Marker (July 1990 to June 1991) and Dauphin Island Airport Marsh sites (May 1989 to April 1991).



winter of 1989 and 1990. Peak abundance of *C. similis* occurred in the early summer of 1989 (Fig. 5).

Sex ratios of *Callinectes similis* varied among sites (Fig. 6). Males were significantly ($P < 0.05$) more abundant at all study sites except the Channel Marker site; however, male:female ratios in open-bays were much lower than in shallow marshes. These ratios were further reduced from 2.9:1 and 2.5:1 at the Fort Morgan and Mississippi Sound sites to 1.2:1 at the Channel Marker site. Sexually mature females were collected in greatest numbers at the Channel Marker site. Only small numbers of sexually mature females were collected at the Mississippi Sound and Fort Morgan sites (Fig. 6). No sexually mature *C. similis* were collected at the Dauphin Island Airport Marsh. In the open-bays, sexually mature females were collected almost year-round with peak abundance in October of 1990 (Fig. 7). Despite numerous sexually mature females being collected from open-bay sites during the study, not a single female was carrying an egg mass.

Sex ratios of *Callinectes sapidus* also varied among sites (Fig. 6). Males numerically dominated over females ($P < 0.05$) only at the Dauphin Island Airport Marsh site. In contrast, females were more abundant than males ($P < 0.05$) at the Fort Morgan and Channel Marker sites. There was no difference ($P > 0.05$) in the abundance of males and females at the Mississippi Sound site. Sexually mature females were collected in greater numbers at the Fort Morgan and Channel Marker sites than at the Mississippi Sound site. No sexually mature females were collected at the Dauphin Island Airport Marsh. In the open-bays, sexually mature females were collected almost year-round, except for the months of November and December in 1989 and 1990 (Fig. 7). In contrast to *C. similis*, ovigerous females were collected from May to August 1989, July to October

Figure 6. Percent frequencies of males, and immature and mature females of *Callinectes similis* and *C. sapidus* at four sampling sites. Data are combined over all sampling dates. Sample sizes are given at the top of each bar.

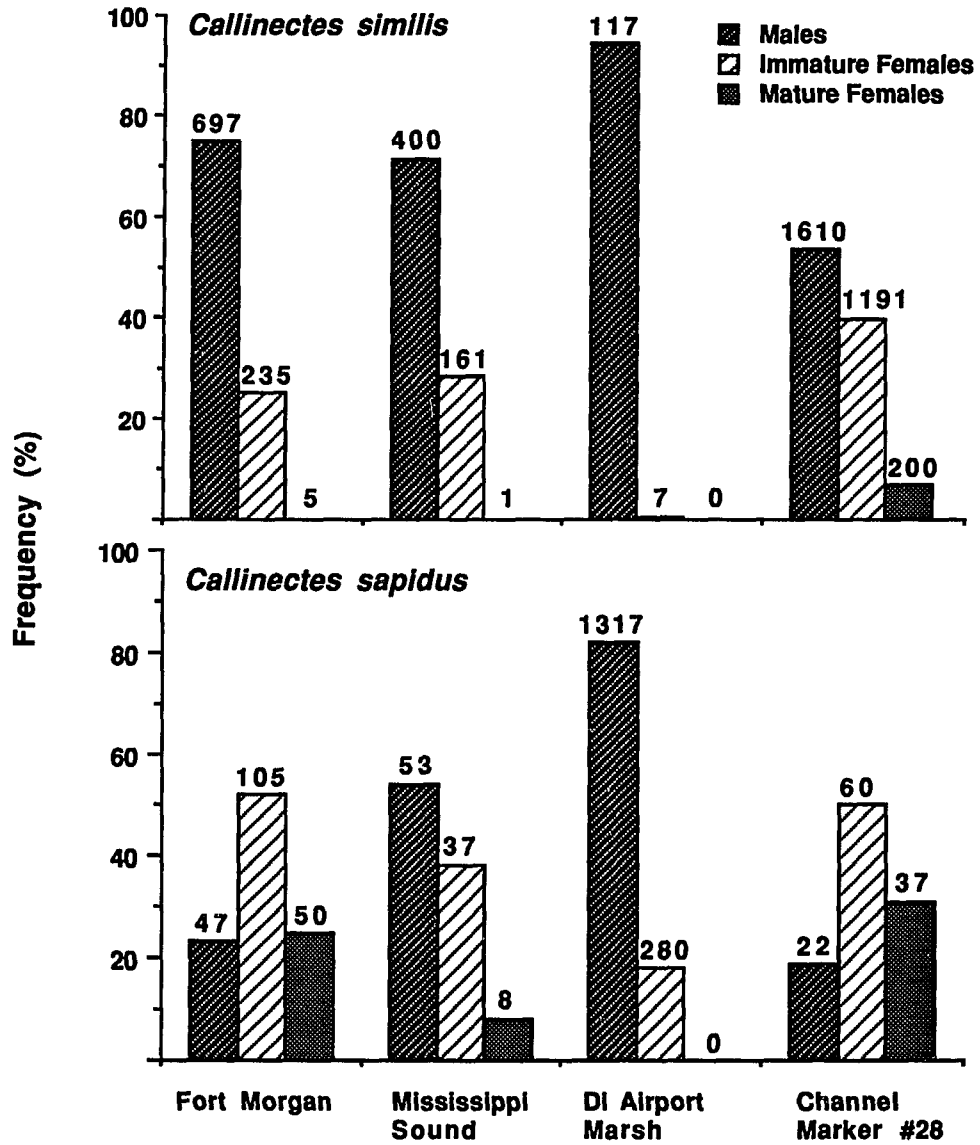
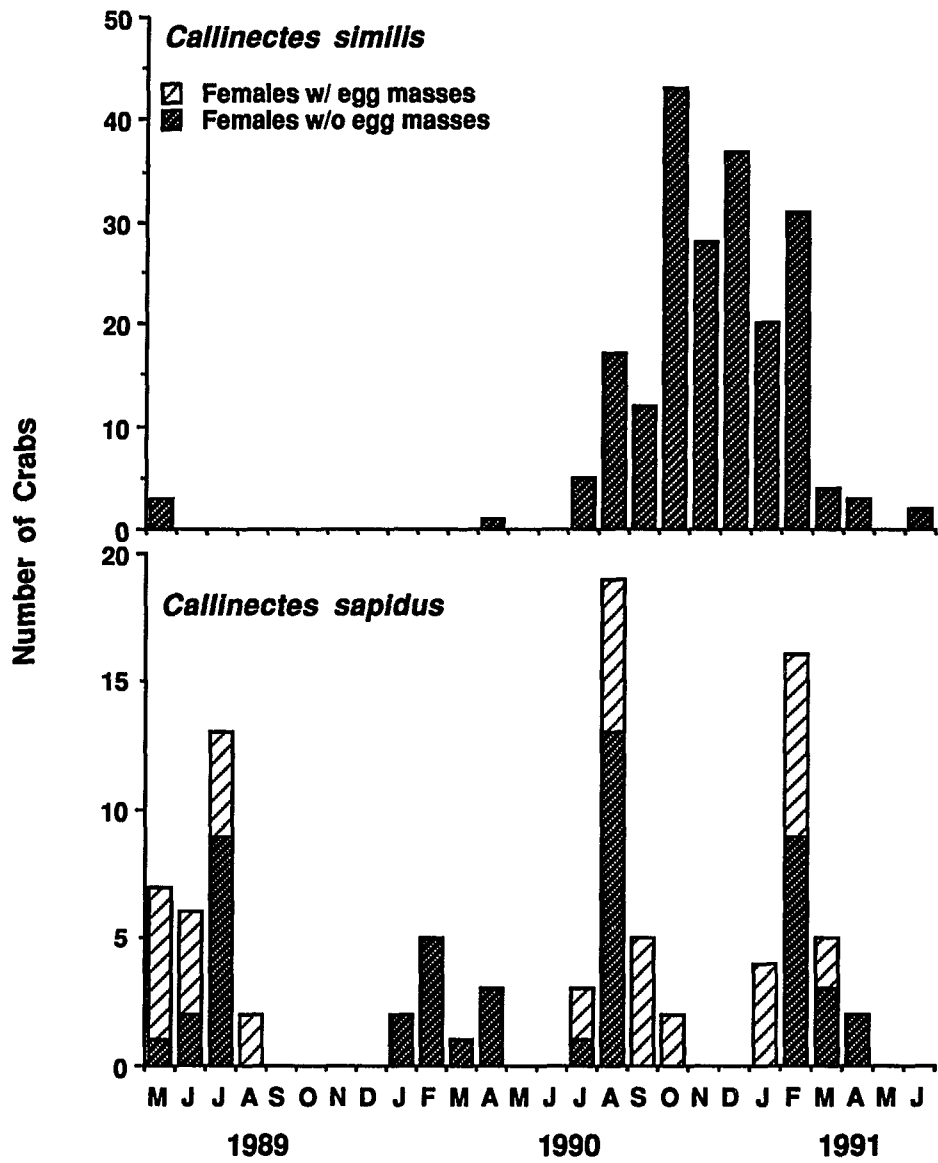


Figure 7. Abundances of mature female *Callinectes similis* and *C. sapidus* with and without egg masses from May 1989 to June 1991. Data are combined for all sampling sites.



1990, and January, 1991. The percentage of females with egg masses varied over both season and year (Fig. 7). These percentages ranged from 31 to 100% during the summer of 1989 and the summer and fall of 1990, and 44 to 100% during the months of January, February and March in 1991. Sexually mature females collected in January, February, and March 1990, and April 1990 and 1991 were not carrying egg masses.

Callinectes similis reached larger sizes in open-bays. Sizes of *C. similis* at the Fort Morgan site ranged from 4 to 107 mm CW. The largest mode occurred in the 31-40 mm CW size class (Fig. 8). At the Mississippi Sound site, sizes of *C. similis* ranged from 8 to 91 mm CW. The largest mode occurred in the 21-30 mm CW size class (Fig. 8). Recently settled *C. similis* (≤ 10 mm CW) were observed only in April, 1991, at Fort Morgan and Mississippi Sound sites. At the Channel Marker site, sizes of *C. similis* ranged from 21 to 125 mm CW. With few exceptions, the population structure of *C. similis* displayed a unimodal distribution with peak sizes in the 41-60 mm CW size classes (Fig. 9). Individuals of *C. similis* larger than 90 mm CW were collected most frequently at the Channel Marker site. The population size structure of *C. sapidus* at the open-bay sites displayed bimodal distributions with peak frequencies in the 41-50 and 141-150 mm CW size class (Fig. 10).

At the Dauphin Island Airport Marsh, *Callinectes similis* were small with a size range of 4-36 mm CW. Most *C. similis* (85%, $n=124$) collected at this site were in the 11-20 mm CW size class. Larger individuals (> 30 mm CW) were rarely observed, and individuals larger than 40 mm CW were completely absent. Sizes of *C. sapidus* at the Dauphin Island Airport Marsh were larger ranging from 5 to 187 mm CW. However, most crabs were less than 30 mm CW (Fig. 11). Recently settled

Figure 8. Size frequency distributions of *Callinectes similis* at the Fort Morgan and Mississippi Sound sites. Data is combined over all sampling dates.

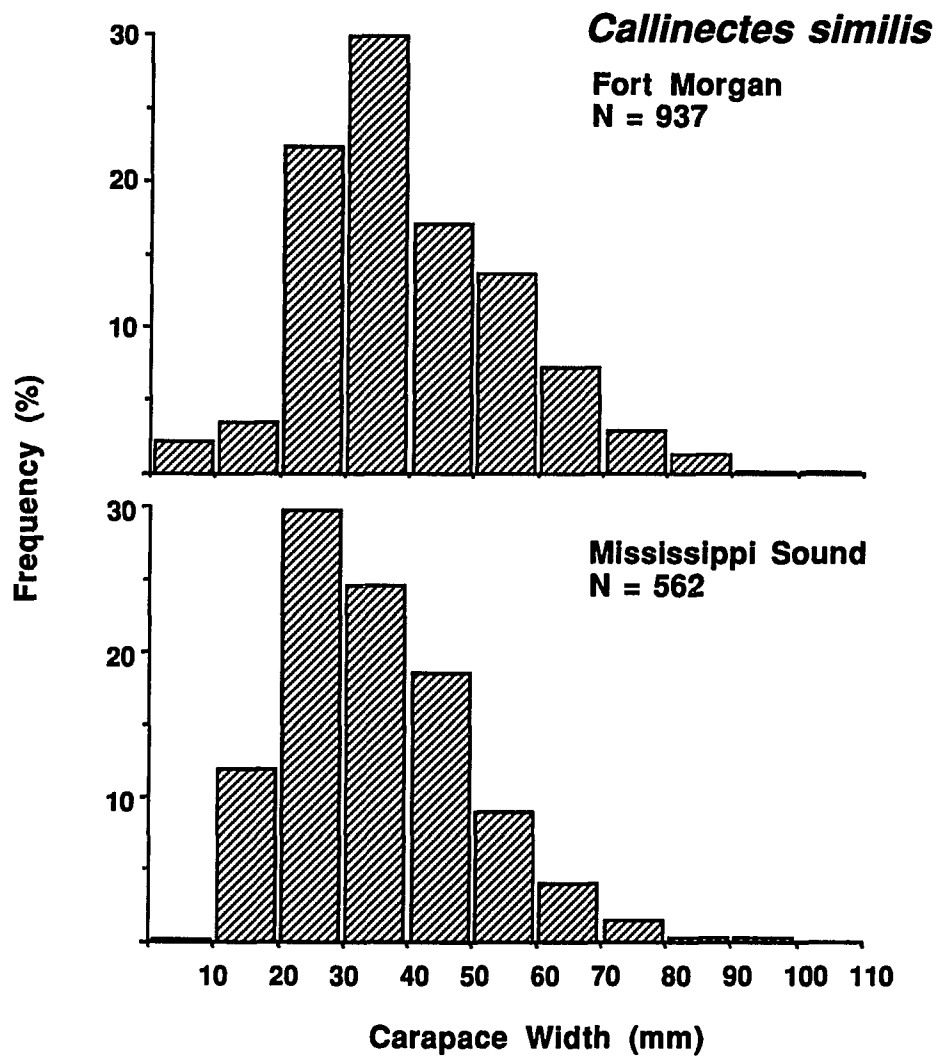


Figure 9. Monthly size frequency distributions of *Callinectes similis* at the Channel Marker site from July 1990 to June 1991. Sample sizes are given.

Callinectes similis

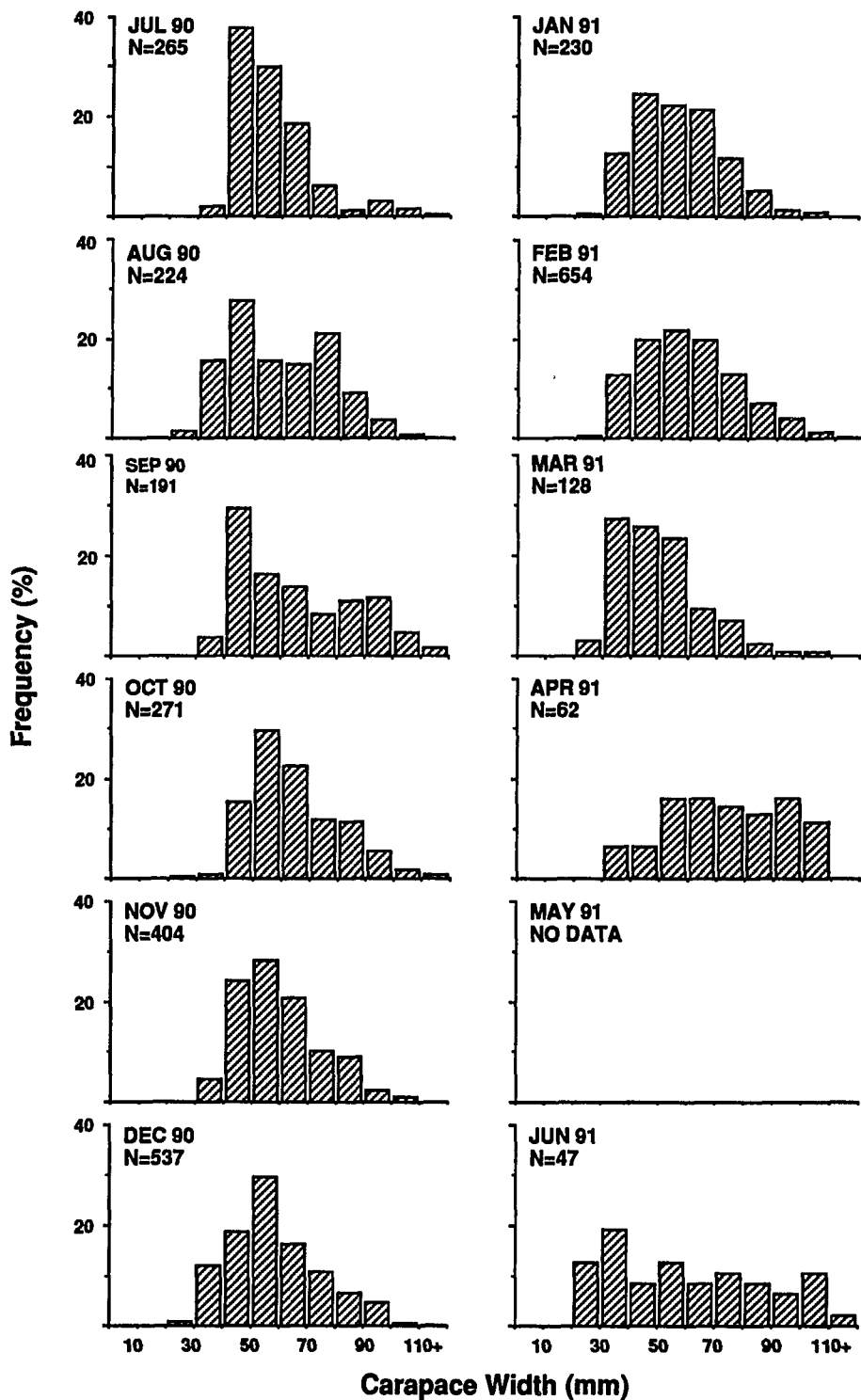


Figure 10. Size frequency distribution of *Callinectes sapidus*. Data are combined from Fort Morgan, Mississippi Sound and Channel Marker sites and over all sampling dates. Sample sizes are given.

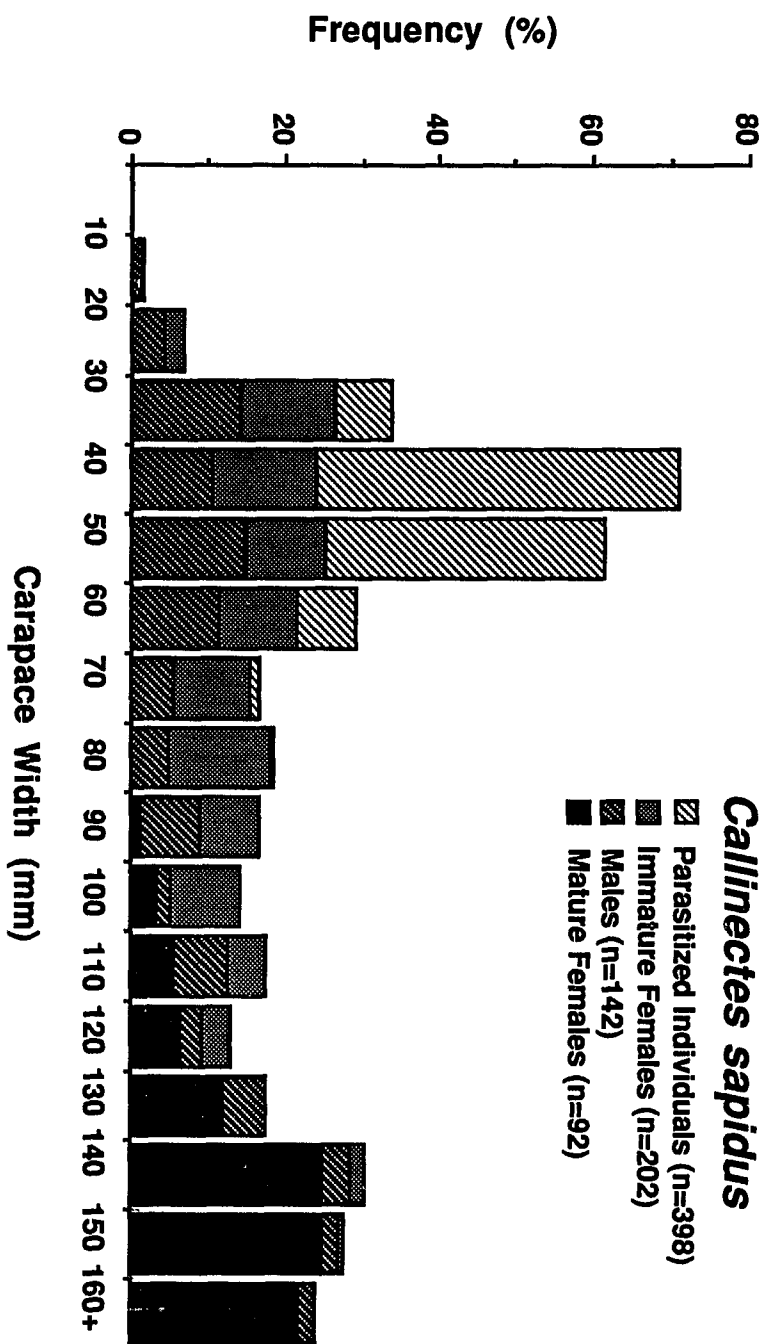
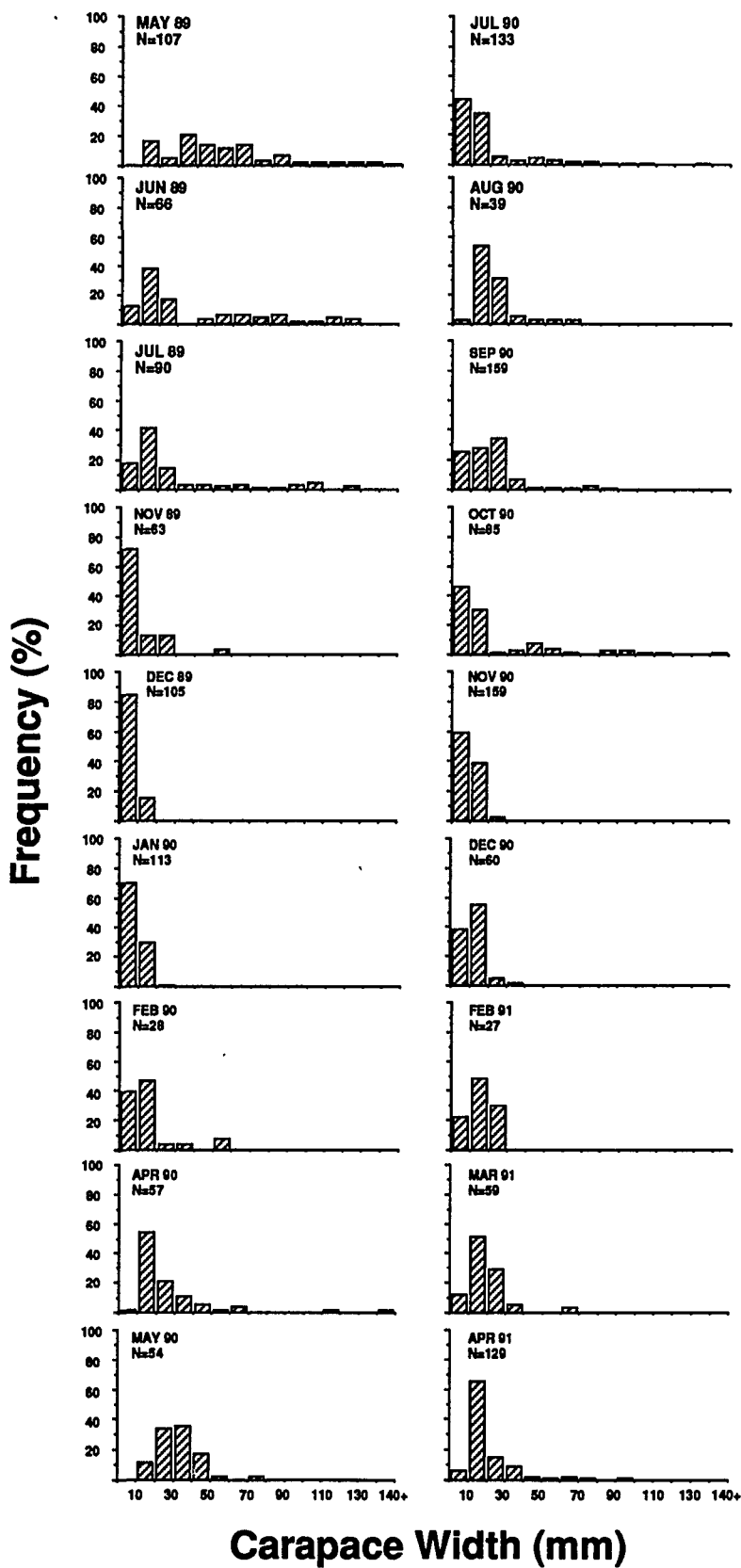


Figure 11. Size frequency distributions of *Callinectes sapidus* at the Dauphin Island Airport Marsh site. Data are presented only for months in which numbers of crabs collected were greater than 28 individuals.

Callinectes sapidus

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C. sapidus (≤ 10 mm CW) were collected almost year-round with major peaks of recruitment in the late fall and winter of 1989 and 1990 and secondary recruitment peaks in the summer of 1989 and 1990.

3. Feeding and growth rates, size at sexual maturity, fecundity and energy invested in egg masses

Callinectes sapidus had significantly higher ($P < 0.05$) mean daily food intake rates than *C. similis* in all size classes examined (Fig. 12). Mean food consumption rates of the three size classes of *C. similis* were $0.47 (\pm 0.03)$ g / day (11-20 mm CW), $0.95 (\pm 0.06)$ g / day (21-40 mm CW) and $1.45 (\pm 0.20)$ g / day (41-70 mm CW), respectively. Mean food consumption rates of the three size classes of *C. sapidus* were $1.05 (\pm 0.05)$ g / day (11-20 mm CW), $1.48 (\pm 0.09)$ g / day (21-40 mm CW), and $1.89 (\pm 0.16)$ g / day (41-70 mm CW), respectively. Growth rates of *C. similis* were significantly ($P < 0.05$) lower than *C. sapidus* (Fig. 13). Incremental changes in carapace width occurred more rapidly for *C. sapidus* than for *C. similis* (Fig. 13). Mean intermolt periods were 25 and 80 days and 42 and 87 days for *C. sapidus* and *C. similis*, respectively.

Size at sexual maturity was smaller for female *Callinectes similis* than for *C. sapidus*. The former developed an oval shaped abdomen at a minimum body size of 60 mm CW (Table 1). Female *C. sapidus* matured at a minimum body size of 100 mm CW. Size at maturity for male *C. similis* (presence of testes with active sperm) was also smaller than for male *C. sapidus*. In *C. similis*, males matured at a minimum body size of 70 mm CW, while *C. sapidus* matured at a body size of 120 mm CW.

Reproductive output, both in terms of fecundity (number of eggs produced) and energy investment (total kJ per egg mass) was much lower in *Callinectes similis* than *C. sapidus* (Table 1). Fecundity was ten times

Figure 12. Mean (± 1 S.E., n=10) laboratory food consumption rates of three size classes of *Callinectes similis* and *C. sapidus*.

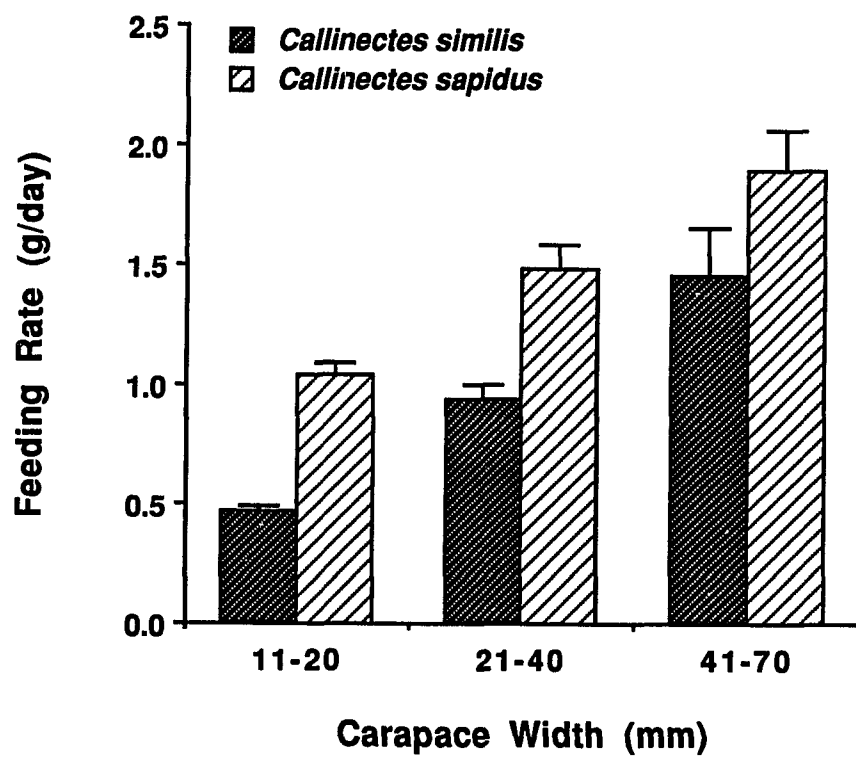


Figure 13. Mean (± 1 S.E., n=10) laboratory growth (width and weight) increments of juvenile (20-25 mm CW) *Callinectes similis* and *C. sapidus* over a 100-day period.

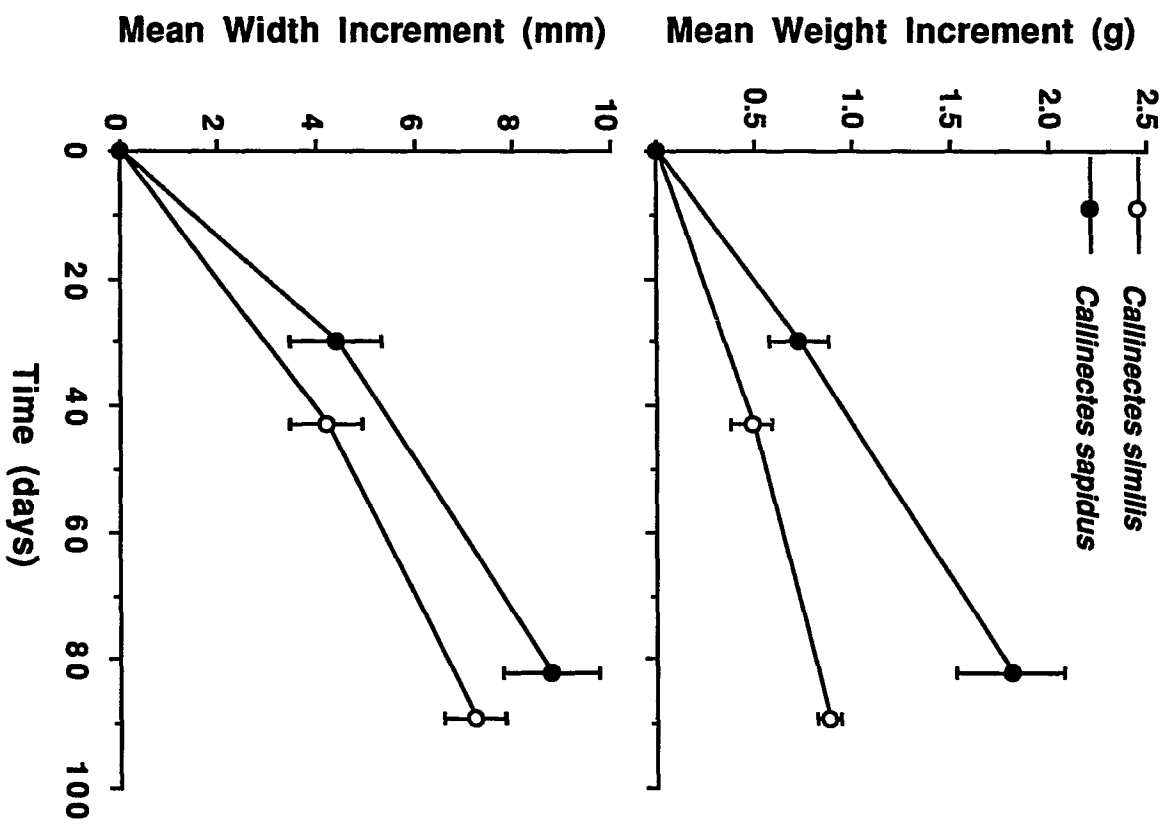


Table 1. Life history characteristics of *Callinectes similis* and *C. sapidus* from the northern Gulf of Mexico.

Characteristic	<i>Callinectes similis</i>	<i>Callinectes sapidus</i>
Maximum carapace width (CW)	125 mm	190 mm
Female size at sexual maturity (CW)	≥ 60 mm	≥ 100 mm
Male size at sexual maturity (CW)	≥ 70 mm	≥ 120 mm
Number of eggs / brood	2.4-5.5 x 10 ⁵	2.1-3.2 x 10 ⁶
Energy invested / g dry wt egg mass	25.3±0.19 kJ	24.8±0.41 kJ
Energy invested / egg mass	24-49 kJ	171-372 kJ
Parasitism by rhizocephalan barnacles	Absent	Present

lower in *C. similis* ($2.4-5.5 \times 10^5$ eggs per brood) than *C. sapidus* ($2.1-3.2 \times 10^6$ eggs per brood). Energy invested in each brood was also much lower, with only 24-49 kJ per brood invested by *C. similis* compared with 171-372 kJ per brood for *C. sapidus*. On a per gram basis, there was no difference ($P > 0.05$) in the amount of energy invested in egg production (Table 1).

4. Parasitism

Callinectes sapidus was observed to be parasitized by the rhizocephalan barnacle *Loxothylacus texanus*. Infected crab sizes ranged from 35 to 80 mm CW, with the mode of infected crabs ranging from 40-50 mm CW (Fig. 10). Incidence of infection of *C. sapidus* collected from open-bay sites was 62%, but at the Dauphin Island Airport Marsh it was less than 1%. The incidence of infection varied seasonally and interannually. At the Fort Morgan site, infected blue crabs were collected in June, July and December 1989, January-June 1990, and March-April 1991, with high percentages (95%, $n=20$) in June 1989, (57%, $n=58$) February and (40%, $n=108$) March 1990, and 70% ($n=27$) and 82% ($n=130$) in March and April 1991. At the Mississippi Sound site, infected crabs were collected in June, July, October, and November 1989, March and June-August 1990, and April 1991. Rhizocephalan infected *C. sapidus* at this site were never collected in large numbers. At the Channel Marker site, infected *C. sapidus* were collected in December 1990, and January-April and June 1991, with high percentages (76%, $n=37$) in February, 72% ($n=89$) and 56% ($n=61$) in March and April 1991. Rhizocephalan barnacles did not parasitize *C. similis*.

DISCUSSION

Both *Callinectes similis* and *C. sapidus* were widely distributed in the Mobile Bay-Mississippi Sound estuarine system. *Callinectes similis* was found to be numerically dominant in open-bays, while *C. sapidus* was

more abundant in marshes. Distinct habitat preferences of *C. similis* and *C. sapidus* may be related to differences in osmoregulatory ability (Engel, 1977; Hsueh, *et al.*, 1991; Hsueh, 1992). Based on an analysis of the ion regulating ability of both *C. sapidus* and *C. similis*, Engel (1977) suggested that *C. similis* is less tolerant of low salinity environments. In the present study, most *C. similis* occurred in the Mobile Bay Channel and at bay-mouth sites where salinity is consistently high (≥ 25 ppt) year-round. These observations suggest that *C. similis* may prefer high salinity environments. We report, however, that 22% of *C. similis* (12 to 67 CW) were collected from relatively brackish water (8-15 ppt). In addition, Hsueh *et al.* (in press b) found that both juvenile (20-30 mm CW) and adult (> 70 mm CW) *C. similis*, are able to tolerate salinity as low as 10 ppt for one week. *Callinectes similis* occurred in shallow marshes during seasons of low freshwater influx. These habitats support abundant *C. sapidus* (Darnell, 1959; Perry, 1975; Orth *et al.*, 1987; Williams *et al.*, 1990). The opportunity to utilize shallow vegetated habitats may increase survival of juvenile *C. similis*. It is well-known that juvenile *C. sapidus* utilize shallow vegetated habitats as refuges from predation (Heck and Wilson, 1987; Wilson *et al.*, 1987; Orth and van Montfrans, 1990) and possibly as a source of detrital nutrition (McClintock *et al.*, 1991).

In contrast to *Callinectes similis*, *C. sapidus* was seldom observed in open-bays except in the spring of 1990 and 1991. These periods were correlated with periods of heavy freshwater influx into the Mobile Bay, which may have forced *C. sapidus* to migrate from shallow marshes or grassbeds into open-bays. It is possible that the abundance of *C. similis* may decline when *C. sapidus* move into their habitats. Predation pressure from the more aggressive *C. sapidus* may play a role in excluding

C. similis from both marshes and open-bays. Using field caging experiments, Hsueh *et al.* (in press b) demonstrated that *C. sapidus* has a significant predatory impact on *C. similis*.

Interannual and seasonal variation in numbers of *Callinectes similis* and *C. sapidus* was observed in this study. At the Fort Morgan site, the summer peak abundance of *C. similis* in 1989 was not observed in 1990, but the spring peak abundance of *C. similis* which occurred in 1990 at this site was also observed in 1991. In a similar fashion, the summer peak abundance of *C. sapidus* at Dauphin Island Airport Marsh was observed in both 1989 and 1990, but the winter peak abundance of *C. sapidus* at this site was only observed in 1989. Interannual and seasonal variations have also been reported in *C. sapidus* from the northern Atlantic (Hines *et al.*, 1987; Orth and van Montfrans, 1987) and northeastern Gulf of Mexico (Livingston *et al.*, 1976). Factors such as food availability and recruitment success have also been suggested to cause interannual and seasonal variations in abundances of blue crabs (Orth and van Montfrans, 1987; Hines *et al.*, 1990). Although numbers of *C. similis* were reduced in the Mississippi Sound in 1990 compared to 1989, the abundance of crabs at the more stenohaline Fort Morgan site was consistent over the two year period. A stable population was even more evident at the Channel Marker site where salinity remained high (> 25 ppt).

Sex ratios of *Callinectes similis* and *C. sapidus* were generally skewed towards higher proportions of males than females. We found that female *C. sapidus* were more abundant at open-bay than shallow marsh sites. Similar skewed sex-ratio patterns have been reported by Hines *et al.* (1987) for *C. sapidus* in Chesapeake Bay. Furthermore, they noted that female *C. sapidus* were more common than male crabs in open river basin

habitats, but male crabs preferentially utilized tidal creek habitats as molting grounds. The present study indicates that the predominance of males in shallow marshes and tidal creeks is geographically widespread.

Spring and fall spawning seasons for *Callinectes similis* in Florida, North and South Carolina, and Texas estuaries have been suggested by Williams (1966) and Tagatz (1967). Low numbers of sexually mature female *C. similis* collected in Mississippi Sound indicate that females are migrating to deeper waters in Mobile Bay or into nearshore coastal waters, where salinities are relative high. Tagatz (1967) found that female *C. similis* spawn in nearshore waters of the Atlantic Ocean. Migration to higher salinity waters by sexually mature female *C. similis* is similar to that of *C. sapidus* (Millikin and Williams, 1984; Williams, 1984; Hines *et al.*, 1987). Numerous egg-bearing *C. similis* were collected from Sand Island (approximately 1 km offshore of Mobile Bay) in September, 1989 (M. Dardeau, pers. comm.). Larvae of *C. sapidus* cannot survive in low salinity environments (Costlow and Bookhout, 1959). We suggest that the larvae of *C. similis* may also be intolerant of low salinities.

Egg-bearing *Callinectes sapidus* were collected in higher percentages than male and immature female crabs at the Channel Marker and Fort Morgan bay-mouth sites. This suggests that sexually mature female *C. sapidus* behave similar to conspecifics in the North Atlantic and other regions of the Gulf of Mexico. That is, reproductively mature females migrate to the mouths of bays to extrude and carry their eggs (Darnell, 1959; Perry, 1975; Millikin and Williams, 1984; Williams, 1984; Hines *et al.*, 1987). This facilitates the release of zoeae into high salinity offshore waters where development to megalopae occurs (Epifanio *et al.*, 1984; Millikin and Williams, 1984).

Population size structures of *Callinectes similis* differ between marshes and open-bays. Only small (≤ 40 mm CW) *C. similis* occurred in shallow marshes, while *C. similis* from 4 to 125 mm CW occurred in open-bays. This indicates that juvenile *C. similis* recruit into both open-bays and salt marshes. Size frequencies of *C. similis* in open-bays indicate that pre-adult and adult *C. similis* may prefer these habitats, however, *C. similis* also recruits into shallow marshes as megalopae since megalopae and newly settled (3-10 mm CW) *C. similis* have been collected from shallow marshes (our study and K. Heck, pers. comm.). Submerged vegetation may provide refuge for newly settled megalopae and juvenile blue crabs (Orth *et al.*, 1984; Heck and Wilson, 1987; Wilson *et al.*, 1987; Orth and van Montfrans, 1990). We report that *C. similis* may utilize floating *Sargassum* spp. as habitat. Coincident with larval development in *C. similis*, *Sargassum* spp. are transported into Mobile Bay by southeasterly winds in summer months. Additionally, we report that recruits of *C. similis* may settle on colonial organisms (e.g., entoproct colonies) attached to sunken vessels or oil rig pilings in Mobile Bay.

Whereas individuals in the 40-50 mm CW comprise the most common size class at open-bay sites, size frequency distributions of *Callinectes sapidus* at the Dauphin Island Airport marsh were numerically dominated by individuals less than 30 mm CW. This suggests that marshes are nursery habitats for *C. sapidus* in the Mobile Bay-Mississippi Sound estuarine system. Similar observations have been reported in South Carolina (Mense and Wenner, 1989) and Texas (Thomas *et al.*, 1990). *Callinectes sapidus* appears to have a prolonged period of recruitment which lasts for most of the year. Moderate temperatures in the Gulf of Mexico may prolong reproductive activity. This contrasts with the

North Atlantic where recruitment occurs only in the summer and fall (Darnell, 1959; Perry, 1975; Livingston *et al.*, 1976; Perry and Stuck, 1982; Hines *et al.*, 1990). This suggests that temperature may be an important constraint on larval survival (Costlow and Bookhout, 1959; Hsueh, 1991).

Although *Callinectes similis* and *C. sapidus* are similar in appearance and have been mistaken for one another for some time (Perry, 1984), there are differences in aspects of their life history. A comparison of growth rates in *C. similis* to *C. sapidus* under identical nutrient regimes indicates that *C. similis* lags behind *C. sapidus*. *Callinectes sapidus* consumes more food per day, suggesting that *C. sapidus* is feeding more actively over a longer period of time. Not only do *C. similis* grow more slowly than *C. sapidus*, but they also reach an asymptotic size earlier. Maximum body size in *C. similis* is only 66% of that for *C. sapidus*. Moreover, size at sexual maturity is smaller in *C. similis* than in *C. sapidus*, and both fecundity and the total reproductive output (energy invested in eggs) are reduced. Fecundity of *C. sapidus* estimated in the present study was within the range ($1.75 - 4.0 \times 10^6$ eggs per brood) estimated for Chesapeake Bay populations (Churchill, 1919; Van Engel, 1958; Prager *et al.*, 1990). Fecundity is 4 to 10 times lower in *C. similis* than in *C. sapidus* ($2.4-5.5 \times 10^5$ vs $2.1-3.2 \times 10^6$ eggs per brood) and energy invested in egg production ($24-49$ vs $171-372$ kJ eggs per brood) is 3 to 15 times lower. We report, however, that the amount of energy invested per unit egg mass (kJ g^{-1} dry wt) is similar in *C. similis* and *C. sapidus* (25.3 ± 0.19 vs 24.8 ± 0.41 kJ). Hines (1982) suggested that female body size is the primary determinant of fecundity among 20 species (7 families) of brachyurans including *C. sapidus*.

The occurrence of the parasitic rhizocephalan barnacle *Loxothylacus texanus* on populations of *Callinectes sapidus* was evident. In contrast, *C. similis* was never found with this parasite (also see Williams, 1966). The basis for the differential infection of sympatric *C. similis* and *C. sapidus* is unknown. Rhizocephalan parasitized *C. sapidus* have also been found in other estuarine waters of the Gulf of Mexico (Wardle and Tirpak, 1991). Infection may be significant as *L. texanus* stunts growth and inhibits gamete production (Reinhard, 1950). Parasitic barnacles only infect juvenile *C. sapidus* ranging in size from 33 to 100 mm CW (Wardle and Tirpak, 1991; present study). Juvenile *C. sapidus* inhabiting shallow water habitats such as Dauphin Island Airport Marsh were not infected by rhizocephalans.

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**FACTORS AFFECTING THE POPULATION DYNAMICS OF THE
LESSER BLUE CRAB (*CALLINECTES SIMILIS* WILLIAMS)
IN BARRIER ISLAND SALT MARSH HABITATS OF
THE GULF OF MEXICO**

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ABSTRACT

Although adults of the lesser blue crab *Callinectes similis* are found abundantly in high salinity mid-bay waters, juveniles (< 40 mm CW) occur in abundance in barrier island salt marsh habitats of Mobile Bay, Alabama, during seasons of low freshwater influx. We have investigated factors which may regulate this pattern of distribution and abundance. Laboratory experiments exposing lesser blue crabs to 5, 10, 15, 20, 25 and 30 ppt demonstrated that juvenile and adult *C. similis* suffered 75% mortality at 5 ppt over a period of 7 days. We suggest that limited osmoregulatory ability may be one important factor which restricts juvenile lesser blue crabs from marsh habitats during extended periods of low salinity. Field caging experiments were conducted to investigate congeneric and conspecific patterns of predation in *C. similis* and *C. sapidus*. Both species were cannibalistic and adult *C. sapidus* preyed heavily on juvenile *C. similis*. Therefore, *C. sapidus* may have a significant predatory role in regulating the abundance of juvenile *C. similis* in barrier island salt marsh habitats along the northern Gulf of Mexico.

INTRODUCTION

The lesser blue crab, *Callinectes similis* Williams, is widely distributed with its congener, *Callinectes sapidus* Rathbun, in estuaries along the northern Gulf of Mexico (Perry, 1984). Nonetheless, habitat partitioning is reported to occur in these two blue crabs. *Callinectes similis* apparently prefers bay and offshore high-salinity waters, whereas *C. sapidus* dominates numerically in low-salinity estuaries and bays (Perry, 1984; Williams, 1984; Hsueh, 1992). This generally partitioned distribution is thought to be related in part to the inability of *C. similis* to

tolerate low salinity. Engel (1977) examined ion concentrations in the hemolymph of these species, and found that at 5 ppt salinity, adult *C. sapidus* are superior hypo-osmoregulators in comparison to adult *C. similis*. No difference in osmoregulatory ability was reported at higher salinities in these species.

In Mobile Bay, Alabama, juvenile *C. similis* co-occured with all age classes of *C. sapidus* in barrier island salt marsh habitats during late spring, summer and fall when salinities were 8-28 ppt (Hsueh, 1992). However, juvenile *C. similis* were not observed in marsh habitats during winter and early spring when salinities periodically fell to 5 ppt or less. Moreover, adult *C. similis* were never observed in barrier island marsh habitats regardless of season or salinity (Hsueh, 1992). Although seasonal patterns of juvenile *C. similis* in salt marsh habitats may be determined in part by salinity levels, it is likely that congeneric predation could be an important factor in regulating both juvenile and adult patterns of abundance. *Callinectes sapidus* is an aggressive predator which is cannibalistic and capable of preying upon other species of brachyurans (Hines *et al.*, 1990; Mansour and Lipcius, 1991). Although *C. similis* and *C. sapidus* co-occur in some habitats, there is no information available on their predator/prey interactions.

The present study examines the question: "Do reduced salinity and congeneric predation contribute to the limited distribution of juvenile and adult *C. similis* in barrier island salt marsh habitats containing abundant *C. sapidus*?" Furthermore, this study extends the evaluation of cannibalism in blue crabs to *C. similis*, an extremely abundant yet little studied species.

MATERIALS AND METHODS

Blue crabs were collected during the summer of 1990 in Mobile Bay, Alabama. Lesser blue crabs (*Callinectes similis*) were collected from a site near channel marker #28 and *C. sapidus* from the Dauphin Island Airport Marsh. Crabs were not fed to standardize nutritive condition, they were used for salinity and predation experiments within one and three days of their collection, respectively. The salinity tolerance of *C. sapidus* is well-known (Engel, 1977; Millikin and Williams, 1984). Therefore, we chose to examine only *C. similis*. Juveniles (20-30 mm carapace width, CW) and adults (> 70 mm CW) were collected by trawling. Ambient salinities at the sampling site ranged from 26 to 28 ppt at the time of collection. Crabs were maintained in 20 ppt seawater in a recirculating tank for 24 hrs and only healthy undamaged crabs were used in experiments.

Salinity tolerance

Partitioned aquaria (90 x 60 x 20 cm) containing 5, 10, 15, 20, 25, or 30 ppt artificial seawater (Tropic Marin) were used. Each aquarium held 12 crabs in 20 x 20 cm compartments. Juvenile (n=12) or adult (n=12) *C. similis* were transferred to each aquarium, and mortality in each salinity treatment was monitored over a 7-day period. Crabs were exposed to each salinity without acclimation. At the end of the 7-day period, crabs which survived in each salinity treatment were transferred into 1 ppt seawater for one day and mortality was monitored. No food was provided for the crabs during the 7-day experimental period. Preliminary observations indicated that non-fed crabs remain robust for at least two weeks (twice the length of the experiment). Salinity tolerance experiments for both juvenile and adult crabs were replicated once. A contingency table

analysis was used to compare differences among mortality of juvenile and adult *C. similis* exposed to various salinity treatments (Sokal and Rohlf, 1981).

Congeneric predation and cannibalism

Different combinations of sizes and densities of both *C. similis* and *C. sapidus* were deployed in rectangular 1-cm mesh cages measuring 100 x 50 x 20 cm (L x W x H). The corners of each cage were secured to the bottom using 2-cm diameter PVC pipes. The bottom of the cage was submerged approximately 5 cm into the soft sediment in order to provide crabs an opportunity to seek refuge by burrowing. Crab densities used in each cage were determined on the basis of crab size. Densities were similar to those used in a density-dependent foraging study by Mansour and Lipcius (1991) for *C. sapidus* in Chesapeake Bay. These values are considered to be equivalent to moderate to high field densities. Each deployment was replicated three times except for the small *C. sapidus*/small *C. similis* treatment which could only be conducted once due to the limited availability of crabs in this size class. Cages were deployed next to the Dauphin Island Sea Laboratory boat dock at a depth of 1 m. After 24 hrs, the numbers and sizes of surviving crabs were recorded. Evidence of congeneric predation or cannibalism was documented by counting the remains (usually the carapace) of individual crabs. Mortality rates were statistically compared between different size combinations of crabs using a contingency table analysis.

RESULTS

Salinity tolerance

Both juvenile and adult *C. similis* exposed to 5 ppt salinity showed 13% and 21% mortality, respectively, after day one of the experiment (Fig. 1). There was a rapid increase in adult mortality (linear regression, slope = 50) and a gradual increase in juvenile mortality (slope = 4.1) at 5 ppt by day 6 of the experiment. By day seven, 75% mortality had occurred in both juvenile and adult crabs exposed to 5 ppt. Juvenile and adult crabs exposed to 5 ppt salinity had significantly greater cumulative mortality than crabs exposed to all other salinity treatments. Mortality estimates of juvenile crabs in the 15 ppt salinity treatment were confounded by anthropogenic contamination of the sea water and were not included in the analyses. Mortalities of adult crabs in the 10 and 15 ppt salinity treatments were significantly greater than in the 20, 25, and 30 ppt salinity treatments ($P < 0.05$) (Fig. 1). Except for the 20 ppt salinity treatment, there were no significant differences in mortality between juvenile and adult crabs at each salinity treatment ($P > 0.05$).

Congeneric predation and cannibalism

Both congeneric predation and cannibalism were observed in *Callinectes similis* and *C. sapidus*. Larger *C. sapidus* had a significantly greater ($P < 0.05$) predatory impact than smaller *C. sapidus* on small *C. similis* (Table 1). Congeneric predation on *C. similis* by large *C. sapidus* was significantly reduced ($P < 0.05$) when *C. similis* sizes were increased from the 40-50 and 51-60 size classes to 90-100 mm CW (Table 1). Mortality of *C. sapidus* was minimal (0 to 14.3%) when caged with *C. similis* and in

1. Cumulative daily percent mortality of small (20-30 mm CW) and large (> 70 mm CW) *Callinectes similis* at six salinity treatments.

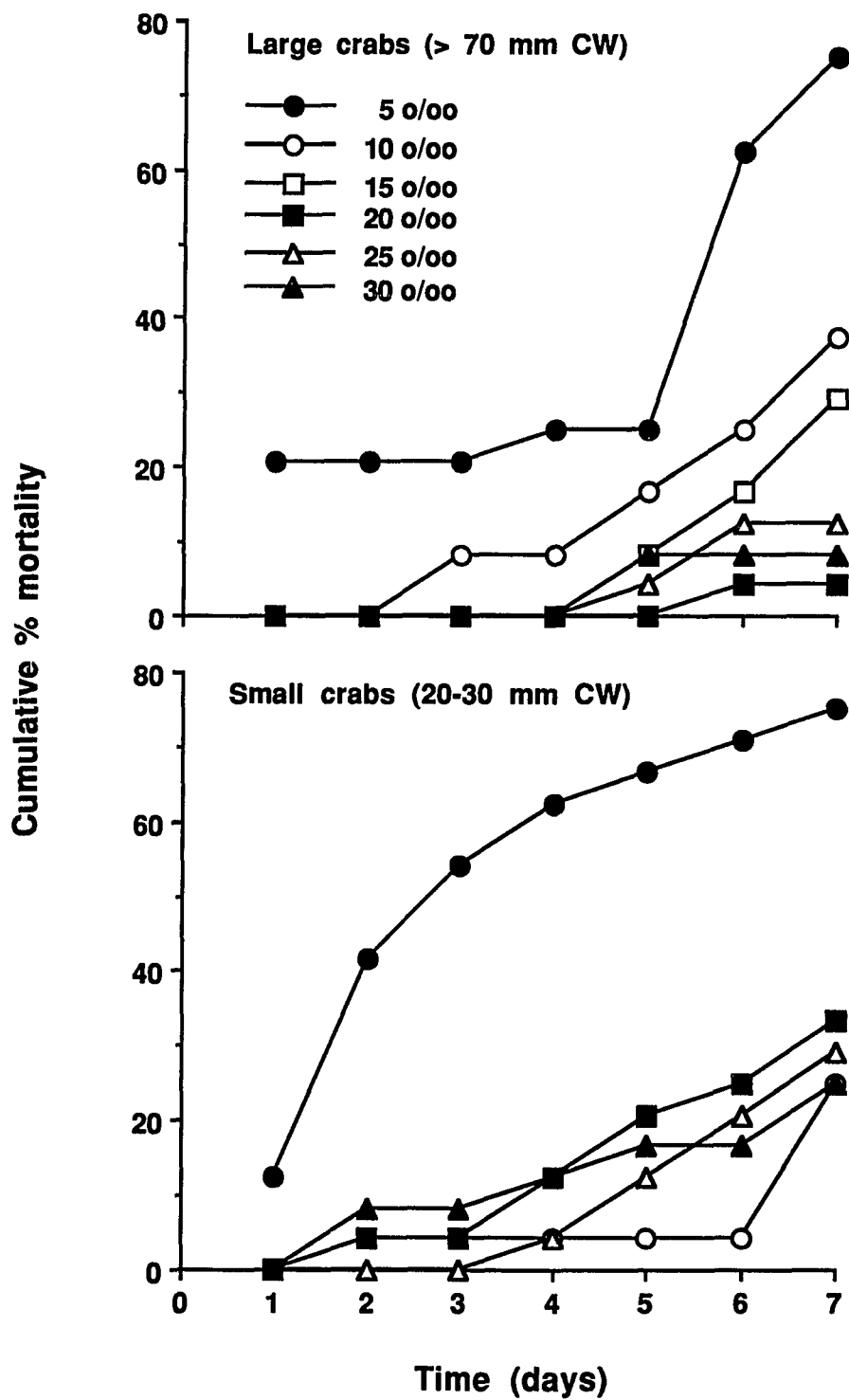


Table 1. Mean % mortality (± 1 SE) of *Callinectes similis* (lower numbers) and *C. sapidus* (upper numbers) placed in experimental cages. Short bars indicate experiments were not conducted with these size combinations.

		<i>Callinectes sapidus</i>			
		51-60	70-80	90-100	> 120 (mm CW)
<i>Callinectes similis</i>	40-50	$\frac{14.3}{0}$	—	$\frac{13.3 \pm 13.3}{43.3 \pm 7.7}$	$\frac{11.1 \pm 11.1}{80.0 \pm 8.8}$
	51-60	—	$\frac{0}{28.6 \pm 4.8}$	—	$\frac{0}{80.9 \pm 7.3}$
	90-100 (mm CW)	—	—	—	$\frac{0}{33.3 \pm 3.9}$

the larger size classes may have resulted from cannibalism (Table 1). Large *C. similis* had a relatively minor impact on small conspecifics. Small *C. similis* suffered only 23% (± 11) mortality when kept in cages with large *C. similis*. There was no mortality of large *C. sapidus* or *C. similis* when caged with smaller conspecifics.

DISCUSSION

It is well-known that salinity is an important factor in regulating the distribution of a variety of marine invertebrates (Pearse and Gunter, 1957; Teal, 1958; Gilles and Pequeux, 1983). Based on the lesser ability of *Callinectes similis* to osmoregulate in low salinity (5 ppt) sea water when compared to *C. sapidus*, Engel (1977) suggested that the distribution of *C. similis* should be limited to offshore waters where salinities range from 20 to 35 ppt. The present study provides direct evidence that *C. similis* is incapable of tolerating acute exposure to low salinities (≤ 5 ppt) over a period of seven days. Nonetheless, *C. similis* appears to be able to tolerate moderate salinities (10-15 ppt). These laboratory studies correspond with field observations on the distribution of *C. similis*. Hsueh (1992) noted that numerous juvenile *C. similis* were found in shallow estuarine waters (e.g. Dauphin Island Airport Marsh and Mississippi Sound) where salinities ranged from 8-28 ppt during seasons of low freshwater influx. Consequently, we suggest that salinity may become an important factor in regulating the distribution of *C. similis* only when it falls to 5 ppt or less.

Although no differences in salinity tolerance were found between juvenile and adult *Callinectes similis*, adult *C. similis* do not occur in shallow estuarine waters (Hsueh, 1992). This may be the result of continuous attrition of juveniles due to osmotic stress and mortality. It appears that only juvenile *C. similis* utilize shallow waters perhaps

because vegetation provides structural refuge from predators and a potential nutrient source for juvenile blue crabs as seen in *C. sapidus* (Wilson *et al.*, 1987; Orth and van Montfrans, 1990; McClintock *et al.*, 1991).

In addition to low salinity, predation may be an important factor in regulating the distribution and abundance of *Callinectes similis*. This factor has been shown to be an important determinant of population dynamics of marine invertebrates (Connell, 1961; Reise, 1977; Virnstein, 1977; Jensen and Jensen, 1985; Kennish, 1990). One apparent predator of *C. similis* in shallow marsh habitats is its congener, *C. sapidus*, which is abundant in these habitats (Churchill, 1919; Tagatz, 1968; Ettinger and Blye, 1981; Williams, 1984). *Callinectes sapidus* attains a larger body size than *C. similis* (19 vs 12 cm CW). Willason (1981) noted that the larger lined shore crab, *Pachygrapsus crassipes*, preys upon the smaller yellow shore crab, *Hemigrapsus oregonensis*, and limits its upper vertical distribution in salt marshes on the west coast of the United States. *Callinectes sapidus* is a top predator in benthic communities (Hines *et al.*, 1990). Crab remains, including conspecifics, are frequently found in the gut contents of blue crabs (Laughlin, 1982; Hines *et al.*, 1990; Hsueh, 1992). Mansour and Lipcius (1991) noted the aggressive behavior of blue crabs may result in mortality of conspecifics when individuals are held in aquariums. The results of the field caging experiments indicate that adult *C. sapidus* can prey on juvenile *C. similis*. As in any caging experiment, predation effects may be inflated. Nonetheless, blue crabs were held at reasonable densities and were provided with a refuge (i.e., burial in sediments, sensu Orth and van Montfrans, 1982). It is likely that congeneric predation is a factor which influences the abundance of *C. similis* in shallow marsh habitats of Dauphin Island.

Cannibalism within *Callinectes similis* is documented in this study for the first time. However, cannibalism does not appear to be as prevalent as may be found in *C. sapidus* (Hines *et al.*, 1990; Mansour and Lipcius, 1991). Crab remains accounted for only 5% of the total prey consumed by *C. similis*, whereas this figure was 13% in *C. sapidus* (Hsueh, 1992). A reduced level of cannibalistic behavior in *C. similis* may facilitate the dense aggregation of all age classes of *C. similis* in open-bay habitats. Moreover, aggregations of *C. similis* in open-bay habitats may be a response to intense predation by *C. sapidus* in shallow marsh habitats. Few *C. sapidus* co-occur with *C. similis* in the open-bay habitats of Mobile Bay (Hsueh, 1992).

In summary, we suggest that the population dynamics of *Callinectes similis* in shallow salt marsh habitats of Mobile Bay, Alabama, may be influenced by both salinity and congeneric predation. During the seasons of abundant freshwater influx into the Mobile Bay estuarine system (winter and early spring), *C. similis* may be forced out of shallow marsh habitats due to its inability to osmoregulate effectively. However, pulses of megalopae and juveniles of *C. similis* recruit into shallow marsh habitats during late spring, summer and fall, when salinities in these habitats are higher (Hsueh, 1992; K. Heck, pers. comm.). As juvenile *C. similis* grow, their numbers may be reduced in shallow marsh habitats as a result of predation by *C. sapidus*.

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**A COMPARATIVE STUDY OF THE DIETS OF THE BLUE
CRABS *CALLINECTES SIMILIS* AND *C. SAPIDUS*
FROM A MUD-BOTTOM HABITAT IN
MOBILE BAY, ALABAMA**

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ABSTRACT

Diets of *Callinectes similis* and *C. sapidus* collected from the same open bay locality in Mobile Bay, Alabama were investigated. Fish, bivalve, brachyuran, and gastropod remains constituted the four most common prey items for both species. The cumulative Index of Relative Importance (IRI) of these four food groups was 85% in *C. similis* and 91% in *C. sapidus*, suggesting that both *Callinectes* spp. forage primarily on these four prey groups. To examine ontogenetic shift in diets, individuals of *C. similis* were sorted into three size classes (29-50, 51-80 and 81-111 mm carapace widths) representing juvenile, pre-mature, and sexually mature stages. We found statistically significant differences in the hierarchy and proportions of the main prey types among size classes examined. There was no significant difference in the diet of male and female *C. similis*. Relatively high percentage of dietary overlap between *C. similis* and *C. sapidus* suggests that these crabs probably utilize common resources in areas of habitat overlap in Mobile Bay, Alabama.

INTRODUCTION

The lesser blue crab, *Callinectes similis* Williams, and the blue crab, *C. sapidus* Rathbun, are both widely distributed in estuaries along the northern Gulf of Mexico (Perry, 1984). *Callinectes similis* is smaller in body size than *C. sapidus*. Maximum point to point carapace widths of *C. similis* and *C. sapidus* are 12 and 21 cm, respectively (Williams, 1984). In Mobile Bay, Alabama, *C. similis* mainly occurs in open-bay habitats, while *C. sapidus* is more abundant in shallow nearshore habitats (Hsueh, 1992). However, a small number of juveniles and adult male *C. sapidus* co-occurs with *C. similis* in open-bay habitats (Hsueh, 1992). Food partitioning of these two species in open-bay habitats is unclear, while feeding habits of

C. sapidus in shallow habitats have been well examined (Darnell, 1958; Tagatz, 1968; Laughlin, 1982).

The purpose of this study was to examine whether prey are partitioned by two common blue crab species occupying the same open-bay habitat. Moreover, this study presents the first information on the diet of *C. similis*, an extremely abundant but little studied blue crab.

MATERIALS AND METHODS

Individuals of *Callinectes similis* and *C. sapidus* were collected from Mobile Bay, Alabama (30°19' N, 88°02' W) in June, 1990. Crabs were collected during daylight hours using an otter trawl with a 6.1-m opening and 3.0-cm mesh. Crabs were identified and preserved immediately in 10% buffered formalin. The foregut of each crab was removed, fixed in formalin, and stored in 70% ethanol for dietary analysis. The carapace width (CW) and sex were recorded for each individual.

Gut fullness (volume) for each individual was qualitatively estimated. Foregut contents were examined under a binocular dissecting microscope. Prey items were sorted into broad taxonomic groupings. Fish remains were identified by the presence of undigested vertebrae, scales, or intact body segments. Bivalve, gastropod, and brachyuran remains were identified on the basis of fragments of shells and carapaces. Microscopic taxa, such as cypris larvae, foraminiferans, nematodes, and ostracods, were usually intact. The unrecognizable, partially-digested organic matter was categorized as digested animal tissue (DAT). For each prey item in the foregut of each crab, a visually-estimated relative volume (%) was assigned (Williams, 1981; Haefner, 1990). Each prey item was dried at 60 °C for 24 hours, then weighed.

Dietary patterns of *Callinectes similis* and *C. sapidus* were analyzed using Percentage Points and Frequency of Occurrence indices (Williams, 1981; Wear and Haddon, 1987) and the Index of Relative Importance (IRI) (Stevens *et al.*, 1982). A Percentage Point index was calculated for each prey item by summing weighted points for each prey and dividing by the total number of points for all crabs and all foods in the sample. Weighted points were ascribed to each prey item based on the relative volume of that prey item in the foregut of each crab (see details in Williams, 1981; Wear and Haddon, 1987; Haefner, 1990). A Frequency of Occurrence Index (FO) was calculated for each prey item by dividing the number of crabs in the sample whose foregut contained a given prey by the total number of crabs in the sample. An Index of Relative Importance for each prey item was calculated as the sum of the Numerical Composition (NC) and Gravimetric Composition (GC). This value was multiplied by the Frequency of Occurrence (FO) to yield the IRI. Numerical Composition was based on the percentage of total number of prey items in the sample, while Gravimetric Composition was based on the percentage of total dry weight of all foregut contents in the sample.

A contingency table analysis was used to compare the four most abundant food items (fish, bivalves, brachyurans, and gastropods) between species. The four most abundant food items were also compared according to sex and size class for *Callinectes similis* (29-50, 51-80, and 81-111 mm carapace width; n= 36, 19, and 11, respectively). Size classes were determined on the basis of sexual maturity with individuals divided into sexually immature (juvenile), pre-mature, and sexually mature stages. Although DAT was measured, it was not considered as a prey item in the statistical analysis of diets.

RESULTS

A total of 83 *Callinectes similis* and 23 *C. sapidus* were collected from the sampling site. Of the *C. similis* collected, 65 were males and 18 were females, carapace width ranging from 29 to 113 mm. Six *C. sapidus* males and 8 females were collected. Nine additional specimens taken were sexually immature and parasitized by rhizocephalan barnacles. The sizes of *C. sapidus* ranged from 34 to 111 mm.

Sixty-four percent of *Callinectes similis* foreguts were more than half-filled with prey, while 80% had at least a trace (< 5% by volume) amount of food. Seventy percent of the foreguts of *C. sapidus* were more than half-filled with prey, while 91% had at least a trace amount of food. The sample size and frequency of *C. similis* foreguts filled by more than 50 percent met the criteria recommended by Williams (1981) for describing the diet of portunids. The sample size for *C. sapidus* was somewhat below the recommended level, but we propose that it was adequate for comparisons of main prey types.

Callinectes similis fed on a wider variety of prey than *C. sapidus* (20 vs 11 prey types) (Tables 1 & 2). However, fish, bivalves, brachyurans, and gastropods were ranked as the four most common prey items for both blue crabs. Fish was particularly abundant in the diets of both species. The cumulative values of the IRI and Percentage Points indices of these four prey items were 85 and 84% in *C. similis*, and 91 and 93% in *C. sapidus*, respectively. Statistical analysis revealed that there was no significant difference (Contingency Table, $P > 0.05$) among the four most abundant prey items of *C. similis* and *C. sapidus*.

There were significant differences (Contingency Table, $P < 0.05$) in feeding habits among the three size classes of *Callinectes similis*.

Table 1. Quantitative analysis of prey items from foreguts of 66 *Callinectes similis* collected from Mobile Bay, Alabama in June, 1990. Prey items were ranked based on Index of Relative Importance. IRI = Index of Relative Importance; FO = frequency of occurrence; NC = numerical composition; GC = gravimetric composition; Pts = percentage points; DAT = Digested animal tissue. The Index of Relative Importance of each prey item was calculated as $(NC + GC) \times FO$.

Prey Items	IRI	IRI (%)	FO (%)	NC (%)	GC (%)	Pts (%)
Fish	5861.60	48.90	87.88	23.02	43.68	48.57
Bivalves	3414.30	28.48	74.24	19.44	26.55	24.61
DAT	1441.31	12.02	60.61	15.87	7.91	7.06
Brachyurans	591.94	4.94	36.36	9.52	6.76	9.36
Gastropods	314.42	2.62	27.27	7.14	4.39	1.26
Polychaete	87.96	0.73	10.61	2.87	5.51	4.49
Crustaceans	79.68	0.66	16.67	4.37	0.41	0.23
Detritus	75.35	0.63	16.67	4.37	0.15	0.00
Sand dollars	61.08	0.51	12.12	3.17	1.87	0.95
Nematodes	22.63	0.19	9.09	2.38	0.11	0.00

Table 1 (Continued)

Prey Items	IRI	IRI (%)	FO (%)	NC (%)	GC (%)	Pts (%)
Sediment	11.69	0.05	4.55	1.19	0.01	0.00
Foraminiferans	5.92	0.05	4.55	1.19	0.11	0.27
Cypris larvae	5.55	0.05	4.55	1.19	0.03	0.00
Eggs	5.46	0.05	4.55	1.19	0.01	0.00
Bryozoans	2.61	0.02	3.03	0.79	0.07	0.02
Plant seeds	2.45	0.01	3.03	0.79	0.02	0.00
Insects	2.10	0.01	1.52	0.40	0.00	0.00
Amphipods	0.68	0.01	1.52	0.40	0.05	0.00
Squid	0.62	0.01	1.52	0.40	0.01	0.00
Ostracods	0.61	0.01	1.52	0.40	0.00	0.00

Table 2. Quantitative analysis of prey items from foreguts of 21 *Callinectes sapidus* collected from Mobile Bay, Alabama in June, 1990. Prey items were ranked based on Index of Relative Importance. IRI = Index of Relative Importance; FO = frequency of occurrence; NC = numerical composition; GC = gravimetric composition; Pts = percentage points; DAT = Digested animal tissue. The Index of Relative Importance of each prey item was calculated as $(NC + GC) \times FO$.

Prey Items	IRI	IRI (%)	FO (%)	NC (%)	GC (%)	Pts (%)
Fish	6439.39	49.87	85.71	26.09	49.04	52.21
Bivalves	2869.48	22.22	66.67	20.29	22.75	20.30
Brachyurans	1742.16	13.49	52.38	15.94	17.32	19.75
DAT	1144.50	8.86	52.38	15.94	5.91	5.68
Gastropods	662.62	5.13	42.86	13.04	2.42	1.14
Sediment	18.23	0.14	4.76	1.45	2.38	0.92
Crustaceans	7.14	0.06	4.76	1.45	0.05	0.00
Squid	7.09	0.05	4.76	1.45	0.04	0.00
Detritus	7.09	0.05	4.76	1.45	0.04	0.00
Plant seeds	7.04	0.05	4.76	1.45	0.03	0.00
Nematodes	7.00	0.05	4.76	1.45	0.02	0.00

Significant differences in prey types occurred between sexually mature and juvenile *C. similis* (Contingency Table, $P < 0.05$). The importance of fish in the diets of *C. similis* increased with increasing body size (Table 3). With the exception of juveniles, the four most common prey items were ranked in the same order of importance in the diets of *C. similis*. Juvenile *C. similis* fed mostly on bivalves, followed by fish, brachyurans, gastropods, and other prey items (Table 3). There was no significant difference (Contingency Table, $P > 0.05$) in diets between sexes in *C. similis* (Table 4). However, in diets of female *C. similis*, gastropods and brachyurans ranked as the third and fourth most important prey items (Table 4).

DISCUSSION

The high percentage of *Callinectes similis* and *C. sapidus* with foreguts more than half filled with prey suggests that both species were actively foraging at this open-bay site during the time of collection. The diversity of foods eaten by each species suggests that both species are opportunistic predators. Their diets are composed mostly of benthic macroinvertebrates, especially bivalves, brachyurans and gastropods. Our results are similar to studies of diets of other *Callinectes* spp. (Laughlin, 1982; Lipcius and Hines, 1986; Haefner, 1990; Stoner and Buchanan, 1990). Laughlin (1982) noted that *C. sapidus* fed on as many as 17 prey items, with bivalves was the primary food item. Haefner (1990) found that *C. ornatus* preyed heavily upon cerithiacean gastropods but ingested other food types when available. The importance of fish in the diets of both blue crab species in Mobile Bay is greater than that reported in diets of other *Callinectes* spp. West and Williams (1986) suggested that large (100-130 mm) blue crabs could catch longnose killifish (*Fundulus similis*) when they were caged together in predator inclusion experiments. However, the high percentage

Table 3. Index of Relative Importance values (%) for prey items from foreguts of juvenile, pre-pubatal, and sexually mature *Callinectes similis* collected from Mobile Bay, Alabama in June, 1990. DAT = Digested animal tissue.

Prey	Juvenile (29-50 mm CW) (n=36)	Pre-mature (51-80 mm CW) (n=19)	Sexually mature (81-111 mm CW) (n=11)
Fish	35.99	50.77	62.00
Bivalves	38.22	29.00	14.69
DAT	15.98	5.92	10.79
Brachyurans	6.51	3.26	2.03
Gastropods	1.58	3.47	1.16
Other	1.72	7.58	9.33

Table 4. Index of Relative Importance values (%) for prey items from foreguts of male and female *Callinectes similis* collected from Mobile Bay, Alabama in June, 1990. DAT = Digested animal tissue.

Prey Items	Male (n=49)	Female (n=17)
Fish	47.85	49.33
Bivalves	27.91	31.19
DAT	11.29	13.60
Brachyurans	6.84	1.15
Gastropods	2.72	1.93
Other	3.39	2.80

of fish in the diets of Mobile Bay blue crabs may also reflect scavenging on fish remains that are discarded by shrimp trawlers. *Callinectes similis*, and especially *C. sapidus*, include brachyurans in their diets. In some cases this included blue crabs which supports the contention that intrageneric predation and/or cannibalism is prevalent (Laughlin, 1982; Hines *et al.*, 1990; Hsueh *et al.*, 1990).

The similarity in diets between *Callinectes similis* and *C. sapidus* indicates that there is a high percentage overlap in the prey of these two species. Stoner and Buchanan (1990) also found that the diets of four tropical *Callinectes* species in Laguna Joyuda, Puerto Rico, overlapped. The high percentage of overlap in the diets of *C. similis* and *C. sapidus* suggests that both species may share available food resources in open-bay habitats of Mobile Bay.

The composition of *Callinectes similis* and *C. sapidus* diets in this study tends to reflect patterns of prey availability. In a study of the benthic infauna of Mobile Bay, Alabama, Hopkins (pers. comm.) found substrates dominated by the bivalve mollusks *Mulinia lateralis* and *Macoma mitchelli* during summer months. Bivalves were ranked as the highest of invertebrates preyed upon by *C. similis* and *C. sapidus* in Mobile Bay. Laughlin (1982) and Haefner (1990) found food items in the foreguts of *C. sapidus* and *C. ornatus* in direct proportion to their relative abundance in the environment. For example, Haefner (1990) found that a high frequency of occurrence of cerithiacean gastropods in the diet of *C. ornatus* related well to the natural abundance of these gastropods in Mullet Bay, Bermuda. Mansour and Lipcius (1991) demonstrated density-dependent foraging behavior in *C. sapidus* when offered the bivalve *Macoma balthica*.

Differences in diet among age classes of *Callinectes similis* occurred. Ontogenetic changes in diet have also been noted in other portunids: *C. bocourti* (Stoner and Buchanan, 1990), *C. sapidus* (Laughlin, 1982; Stoner and Buchanan, 1990), *C. ornatus* (Stoner and Buchanan, 1990), *Carcinus maenus* (Ropes, 1989), *Liocarcinus puber* (Choy, 1986), and *Ovalipes punctatus* (Du Preez, 1984). Laughlin (1982) noted that fish and crabs occurred more frequently in the diets of large than small *C. sapidus*. It has been suggested that feeding habits of crabs are strongly influenced by morphological changes during growth of feeding-related structures, such as chelae and mouth parts (Elner, 1980; Perez and Bellwood, 1988). Sexual feeding preference does not seem to play a role in the composition of the diet of *Callinectes similis*. Similar observations have been made for other portunids (Choy, 1986; Haefner, 1990).

Brachyurans are known to influence the distribution and abundance of prey populations (Kitching *et al.*, 1959; Muntz *et al.*, 1965; Virnstein, 1977, Seed, 1980; Perez and Bellwood, 1988). The importance of bivalves in the diets of *Callinectes similis* and *C. sapidus* indicates both species prey heavily upon these molluscs. Based on qualitative observations of the sizes of shell fragments and hinges of valves in the foreguts of crabs in this study, both species appear to feed almost exclusively on small individuals (< 1 cm shell length). Ropes (1968) noted that *Carcinus maenus* prey heavily on newly settled *Mya arenaria* which occur in abundance during the autumn in Plum Island Sound, Massachusetts. Arnold (1984) demonstrated that small (< 75 mm carapace width) and medium sized (75-125 mm carapace width) *C. sapidus* prefer 10-mm shell length *Mercenaria mercenaria*, while larger blue crabs (> 125 mm carapace width) show no preference between 10- and 25-mm shell length bivalves. Wear and Haddon

(1987) also suggested that *Ovalipes catharus*, through heavy predation on spat and juveniles may play an important role in influencing the recruitment of bivalves.

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SUMMARY AND CONCLUSIONS

This study indicates that both *Callinectes similis* and *C. sapidus* occur in abundance in the Mobile Bay-Mississippi Sound estuarine system. Although both species frequently co-occur in open-bays, *C. similis* is generally more abundant than *C. sapidus* in these habitats. Exceptions occur during months when there are large influxes of freshwater into the Mobile Bay-Mississippi Sound estuarine system. During these freshwater influx periods, *C. sapidus* may be forced to migrate from shallow habitats into open-bays. In contrast, *C. sapidus* is more abundant than *C. similis* in shallow marshes. *Callinectes similis* recruits in shallow marshes during late spring to early fall when salinities are moderate.

Distinct habitat preferences of *Callinectes similis* and *C. sapidus* may be related to differences in osmoregulatory ability. The present study suggests that *C. similis* is incapable of tolerating acute exposure to low salinities (≤ 5 ppt) over a period of seven days. Nevertheless, *C. similis* appears to be able to tolerate moderate salinities (10-15 ppt) under laboratory conditions. This may explain why *C. similis* can be found in shallow water during seasons of low freshwater influx. Consequently, salinity may become an important factor in regulating the distribution of *C. similis* only when it falls to 5 ppt or less.

In addition to low salinity, congeneric predation may be an important factor that regulates the distribution and abundance of *Callinectes similis*, especially in shallow marshes where *C. sapidus* is abundant. Field caging experiments indicate that large *C. sapidus* prey heavily upon small

C. similis. These interactions may help to explain the sharp decline of recently recruited juvenile *C. similis* at the Dauphin Island Airport Marsh. Although both *C. similis* and *C. sapidus* are cannibalistic, *C. similis* preys upon conspecifics to a lesser extent than does *C. sapidus* (Hsueh, unpubl. data). A reduced level of cannibalistic behavior in *C. similis* may facilitate the dense aggregations of all age classes of *C. similis* in open-bays. Moreover, aggregations of *C. similis* in open-bays may be a response to intense predation by *C. sapidus* in shallow marshes.

Differences in habitat partitioning were noted between sexes of both *Callinectes similis* and *C. sapidus*. Females of both species were more abundant at open-bay than shallow marsh sites, whereas males of both species dominate numerically in shallow marsh habitats. Along the north Atlantic coast and other Gulf regions, sexually mature female *C. sapidus* migrate to deeper waters, where salinities are relatively high, to extrude and carry their eggs. Survival of blue crab larvae is greater in higher salinities (> 20 ppt) (Costlow and Bookhout, 1959). It is likely that the similarity in the migration pattern of sexually mature *C. similis* with that of *C. sapidus* may be due in part to the intolerance of its larvae to low salinity. Egg-bearing *C. similis* were found only in high salinities at the mouth of the bay or in offshore waters.

Size-specific differences in habitat partitioning were also seen in both *Callinectes similis* and *C. sapidus*. Small *C. similis* were collected from both shallow marshes and open-bays, whereas large *C. similis* only occurred in open-bays (Also see Appendix). This suggests that juvenile *C. similis* recruit into both open-bay and salt marsh habitats. It is well-known that submerged vegetation in shallow habitats can provide refuge for newly settled megalopae and juvenile blue crabs (Orth *et al.*, 1984; Heck

and Wilson, 1987; Wilson *et al.*, 1987; Orth and van Montfrans, 1990). Although megalopae and juvenile *C. similis* recruit into open-bays (P. Hsueh, pers. obs.; K. Heck, pers. comm.), there is little information about how they avoid predation in these habitats. One hypothesis is that juvenile *C. similis* utilize floating *Sargassum* spp. as habitat. *Sargassum* spp. are transported into Mobile Bay by southeasterly winds in summer months, corresponding with recruitment periods in *C. similis*. Another hypothesis is that newly recruited *C. similis* may settle on colonial organisms (e.g., entoproct colonies) attached to sunken vessels or oil rig pilings in Mobile Bay. Both *Sargassum* and colonial entoprocts may provide structural refuges similar to submerged vegetation in shallow waters. A comparison of the size frequency distributions of *C. sapidus* in shallow marsh and open-bay habitats indicates that marsh habitats provide nursery grounds for young *C. sapidus* in the Mobile Bay-Mississippi Sound estuarine system.

It appears that both *Callinectes similis* and *C. sapidus* have a similar life cycle. Egg-bearing females of both species migrate to open-bay or offshore waters, where salinity is high, to release their larvae. Crab larvae are presumably transported into continental shelf waters to develop. Megalopae recruit into estuaries following approximately one month in the offshore plankton (Perry, 1984).

Recruitment duration of *Callinectes similis* is more abbreviated than that of *C. sapidus*. Recently settled *C. similis* were collected only during late spring to early fall in the Mobile Bay-Mississippi Sound estuarine system, whereas recently settled *C. sapidus* were collected almost year-round. The prolonged recruitment of *C. sapidus* is a common phenomenon in regions of the Gulf of Mexico, but not in the North Atlantic (Darnell,

1959; Perry, 1975; Livingston *et al.*, 1976; Perry and Stuck, 1982; Hines *et al.*, 1990).

As megalopae settle in estuarine habitats, juvenile *Callinectes* *sapidus* appear to grow faster than *C. similis* (Hsueh, 1992). Growth rates of *C. similis* under identical nutrient conditions were reduced when compared to those of *C. sapidus*. *Callinectes sapidus* consumed more food per day, suggesting that it is a more aggressive feeder. In addition to growing slower than its congener, *C. similis* reached an asymptotic size earlier. Maximum body size in *C. similis* was only 66% of that for *C. sapidus*. Moreover, size at sexual maturity was smaller in *C. similis* than in *C. sapidus*. The smaller body size of sexually mature female *C. similis* may be directly responsible for its lower fecundity and reproductive output (energy investigated in eggs) (Hines, 1982). Numbers of eggs produced per brood are 4-10 times fewer in *C. similis* than in *C. sapidus*, while energy invested in egg production is 3-15 times lower (Hsueh, 1992).

The influence of the parasitic rhizocephalan barnacle *Loxothylacus texanus* on reproductive efforts of *Callinectes sapidus* is marked. The incidence of infection of *C. sapidus* collected from open-bay sites was 62%. Infection is significant as *L. texanus* impacts the morphology of *C. sapidus*, stunting its growth and inhibiting gamete production (Reinhard, 1950; Overstreet, 1978). In contrast, *C. similis* was not infected with this parasite. The reason for the differential infection of *C. similis* and *C. sapidus* is unknown.

Both *Callinectes similis* and *C. sapidus* appear to be opportunistic predators. Their diets overlap considerably and are composed mostly of benthic macroinvertebrates, especially bivalves, brachyurans and

gastropods. The high percentage of overlap in the diets of both species indicates that they must share available food resources in the open-bay habitats of Mobile Bay. It is likely that these two species compete with one another when prey is limited. In addition, the potential role of *C. similis* in benthic communities as a top predator exists. *Callinectes sapidus* is known to have a significant impact on the structure of benthic communities (Virnstein, 1977). Ontogenetic shifts in diet occurred among different age classes of *C. similis*. These may be due to morphological changes during growth of feeding-related structures, such as chelae and mouth parts (Elner, 1980; Perez and Bellwood, 1988). Sexual feeding preference does not seem to play a role in the composition of the diet of *C. similis*.

Abundances and distributions of *Callinectes similis* and *C. sapidus* indicate that both species depend heavily on estuarine environments for habitat. Conservation of these estuarine environments is critical in providing necessary habitat for *C. similis* and *C. sapidus* populations and for assuring the continued success of the blue crab fishery. Despite the importance of the blue crab fishery in Alabama, there are few state regulations to limit the sizes and sexes of collected blue crabs. According to Alabama state regulations, blue crabs can be harvested when their body size is larger than 10 cm CW. This includes egg-bearing females. Male *C. sapidus* reach maturity at a size of approximately 13 cm CW. In order to adequately ensure maximum reproductive effort in male crabs, minimum harvested body size of male blue crabs should more appropriately be limited to 14 cm CW. Moreover, ovigerous *C. sapidus* can produce $2.1\text{--}3.2 \times 10^6$ eggs per brood. The mating and brooding season of females immediately follows the pubertal molt, and brooding time may last two months (Perry, 1984). Therefore, restrictions on harvesting recently molted, sexually mature

females would facilitate the maintenance of populations with high reproductive output.

The blue crab fishery in the Gulf of Mexico is comprised of both soft and hard shell fisheries. Nonetheless, both fisheries are utilizing the same blue crab resources. With a growing soft shell crab fishery in Alabama, additional demands for soft shell crabs may increase conflicts with the hard shell crab fishery. An alternative crab fishery resource, *Callinectes similis*, could reduce competition for blue crab resources between soft and hard shell crab fisheries. Male *C. similis* attain sizes larger than 10 cm CW, indicating their potential as a soft shell crab fishery resource. Ultimately, population stocks of *C. similis* in the Gulf of Mexico need to be carefully evaluated and their utility considered in light of the regenerative capacities of their populations.

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APPENDIX

In addition to the material presented in the main body of this dissertation, information on the population dynamics of the lesser blue crab *Callinectes similis* in other estuarine and coastal habitats of Alabama was gathered by Stevens Heath and his colleagues (Mark VanHoose, Robyn Mellon and Travis Powell) of the Department of Conservation and Natural Resources of Alabama. Crabs were collected from March 1989 to April 1990 at 18 sampling stations and shipped to UAB for further analysis of population size structure and sex ratio. The sampling stations were representative of the three most common habitats (sandy beach, salt marsh and open-bay mud-bottom) occurring in Alabama coastal and estuarine waters (Fig. 1). Temperature and salinity measurements were collected during the sampling period. *Callinectes similis* occurred at all sampling sites, indicating a broad range of distribution in coastal and estuarine waters of Alabama. Crabs were collected from some sites where salinities were as low as 6 ppt. Similar to the present study, differences in habitat partitioning in different size classes of crabs were noted. Crabs smaller than 30 mm carapace width were collected from all three types of habitats, whereas larger *C. similis* were absent from salt marsh habitats (Table 1). These results correspond with the present study, which suggests juvenile *C. similis* recruit into shallow marsh and open-bay habitats. In addition to size structure, sex ratios of *C. similis* in these sampling sites were similar to observations in the present study. Male crabs dominated numerically in

shallow waters (marshes and sandy beaches), but this pattern was reduced in open-bays.



Fig. 1. Map of estuarine and coastal waters of Alabama. Black circles represent sites sampled by the Department of Conservation and Natural Resources. Rectangular boxes represent sampling sites for which data is presented in the main body of this dissertation.

Table 1. Size ranges and sex ratios of *Callinectes similis* collected from 18 sampling sites in estuarine and coastal waters of Alabama. Temperature (°C) and salinity (ppt) ranges at each sampling site are presented. Data are for all sampling dates from March 1989 to April 1990. DI = Dauphin Island; GS = Gulf Shore; MS = Mississippi Sound; MB = Mobile Bay; MBCM = Mobile Bay Channel Marker. Numbers of crabs are not directly comparable among habitat types due to differences in sampling gear.

Type of Habitat	Sampling site	No. of samples	No. of Crabs	Size range (mm)	M/F ratio	T/S (°C/ppt)
Sandy Beach	DI Front Beach	3	17	3-9	14/3	22-29/6-15
	Paradise Inn	2	11	3-67	3/8	20-23/9-33
	GS State Lodge	2	2	2-3	0/1	23/29
Salt Marsh	Cedar Point	4	7	3-8	7/0	13-28/6-14
	Coden	3	17	3-8	17/0	27-30/9-19
	Point Aux Pines	4	23	3-21	20/3	14-29/6-24
	DI Airport Marsh	2	2	3-9	2/0	14-30/9-12
	MS Tall Range C	5	79	20-84	60/19	20-28/9-22
	Grand Bay	3	6	3-48	2/4	21-28/19-25
	MBCM # 57	9	351	3-111	255/96	18-28/10-23

Table 1. (Continued)

Type of Habitat	Sampling site	No. of samples	No. of Crabs	Size range (mm)	M/F ratio	T/S (°C/ppt)
Open-bay	MBCM # 23-24	7	98	28-88	48/50	19-28/20-25
	MBCM # 25-26	2	51	28-103	23/28	26-27/10-22
	MB Oil Rig	5	45	13-80	35/10	15-24/18-24
	MB Pass	4	101	31-93	54/47	17-27/28-30
	Bon Secour Bay	1	56	25-74	43/13	21/17
	Perdido Pass	1	1	54	0/1	24/32
	Mid-Perdido Bay	2	3	12-47	3/0	21/22
	Arnica Bay	5	104	11-64	60/44	17-20/18-24

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