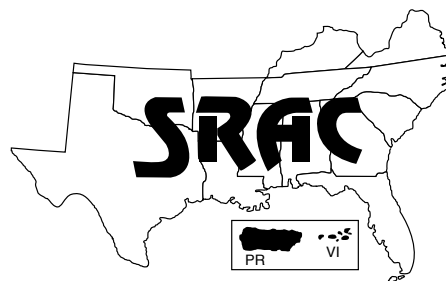




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Procambarid Crawfish: Life History and Biology

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Crawfish (or crayfish) have social, economic and ecological significance in several regions around the world, including the southern United States. Louisiana dominates the crawfish industry of North America in both aquaculture and wild capture fisheries. Crawfish also are cultivated for food in Texas, Arkansas, Mississippi, Alabama, South Carolina and North Carolina, and are consumed in these and many other states. However, there is no place where crawfish have had more impact on the economy of a region than in Louisiana, where the industry contributes well in excess of \$150 million to the state's economy annually.

Species of importance

Procambarus clarkii (the red swamp crawfish) and *P. zonangulus* (the white river crawfish) are the species of greatest commercial importance in the southern U.S. *Procambarus acutus acutus*, sometimes referred to as the eastern white river crawfish, is cultivated in several states along the east coast of the U.S. and is nearly indistinguishable from *P. zonangulus*. These crawfishes belong to the phylum Arthropoda (subphylum Crustacea), order Decapoda, and family Cambaridae. The red swamp crawfish is native to the states bor-

dering the Gulf of Mexico from Texas to Alabama, northward up the Mississippi River drainage into Tennessee and Illinois, and southward into eastern Mexico. The red swamp crawfish has been introduced in other areas of the U.S. (including Hawaii) and in at least 19 other countries in Central and South America, the Caribbean, Europe, Africa and Asia. The white river crawfish is found in the southern states along the Gulf of Mexico and northward up the Mississippi River drainage, possibly as far as the confluence of the Mississippi and Ohio Rivers. The eastern white river crawfish is found along the Atlantic coastal plain into southern New England.

The red swamp and white river crawfishes, and to a lesser extent the eastern white river crawfish, have similar ecological requirements. The red swamp and white river crawfishes often co-exist in the same native habitat or managed impoundment. Both are ecologically adapted to the annual hydrological cycles of spring flooding and summer dry periods common to large river systems and floodplains in the region. Both species construct simple shallow burrows, to which they retreat to reproduce and survive temporary dry periods. One notable difference between the two species is that, in the South, the white river crawfish is a seasonal spawner, reproducing only in the fall and winter. Red swamp crawfish may spawn at any time during the year when environmental conditions are

favorable. The red swamp crawfish produces more, but smaller, eggs than the white river crawfish. The red swamp crawfish appears to be better adapted to nutrient-rich waters and may tolerate higher water temperatures, although these differences have not been confirmed. The white river crawfish grows faster at cooler temperatures and can attain a slightly higher maximum size of about 130 grams (3.5 crawfish per pound). Anecdotal evidence indicates that the red swamp crawfish is usually more abundant in standing water habitats with low dissolved oxygen, such as swamps. Hence the common name red swamp crawfish.

Both red swamp and white river crawfishes do well in commercial crawfish ponds, and both thrive in the low-energy-input, extensive aquaculture systems used in Louisiana and other southern states. Though the abundance of each species can vary among ponds and within a pond during the 7- to 10-month production cycle, the red swamp crawfish most often dominates the catch and is the most desired species in the marketplace, particularly in Louisiana. White river crawfish are usually most numerous in ponds that have been in continuous cultivation for several years; it occasionally becomes the dominant species over time.

The factors that govern the relative abundance of the two species in production ponds are not fully understood. Research has shown that the species that enters the

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pond first in greatest numbers after fall flood-up is likely to dominate the population. Thus, if red swamp crawfish become established first after the pond is flooded, they will dominate the population and the later harvest. If juvenile white river crawfish become established before red swamp crawfish juveniles enter the population, white river crawfish will dominate the population and the subsequent catch. Despite efforts to limit the presence of white river crawfish in ponds in Louisiana (because it is less desirable in the marketplace), both species are responsive to routine culture practices and often co-exist in production ponds.

There is no evidence that red swamp and white river crawfishes cross-breed naturally, although crossbreeding and hybridization have been observed in other crawfish species. The red swamp and white river crawfishes are similar in appearance, especially at a young age, and an inexperienced observer might not be able to distinguish between the two species. Several key anatomical features are used to distinguish between them (Fig. 1).



Figure 1. Adult white river crawfish (*Procambarus zonangulus*), top left, have longer, narrower claws than red swamp crawfish (*Procambarus clarkii*), top right. Red swamp crawfish (bottom right) usually have a dark line visible on the underside of the abdomen, whereas the white river crawfish do not.

As the common names suggest, adults of the white river crawfish are off-white to tan, while the adult red swamp crawfish is red. However, color alone is not a definitive distinguishing characteristic, particularly in immature crawfish. The large primary claws or "chelae" of adult white river crawfish are more elongated and narrow than those of adult red swamp crawfish. The areola, or space on the dorsal surface where the two halves of the carapace meet, is wider on white river crawfish. Also, the white river crawfish lacks the dark stripe on the underside of the tail or abdomen that is a distinguishing characteristic of red swamp crawfish. Sex is easy to distinguish in both species. Males have two sets of hard, calcified swimmerets next to the thorax; females have a seminal receptacle (*annulus ventralis*) and oviduct openings (Fig. 2).

Life cycle

Based on their distribution in North America, the red swamp and white river crawfishes are classified as temperate species; however, aquaculturists generally regard them as having traits normally associated with warmwater species. These crawfishes are relatively short-lived in the deep

south (2 years or less), have relatively high juvenile survival rates, and can alternate between sexually active and inactive forms. *P. clarkii* can spawn year-round in the southern U.S. and females may reproduce more than once a year.

The life cycles of both red swamp crawfish and white river crawfish have evolved to allow them to adapt to the cyclical low-water dry conditions and high-water flood conditions common to their natural habitats. Commercial crawfish aquaculture simulates this hydrological cycle, but with precise control over when ponds are flooded and when they are dewatered to optimize recruitment and subsequent crawfish production. Mature animals mate in open water and the sperm are stored in a seminal receptacle (*annulus ventralis*) on the underside of the female. The female may mate with more than one male and eventually retreats to the burrow to spawn. Although spawning can take place in open water, the burrow provides protection while the eggs and offspring are attached to the abdomen. Females carrying eggs or hatchlings are highly vulnerable to predators because the attached brood prevents the typical escape response, which is repeatedly

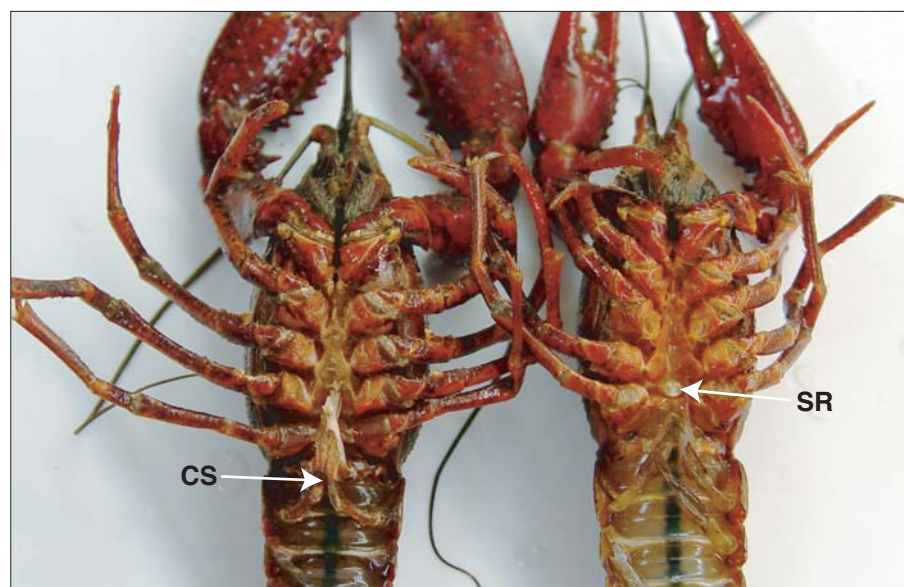


Figure 2. Males (left) can be recognized by two pairs of hard, calcified swimmerets (CS) next to the thorax and spur-like protrusions at the base of the middle set of walking legs. On females (right), the seminal receptacle (SR) can be observed on the underside of the thorax between the last pair of walking legs; with close observation, the oviduct openings can be spotted near the basal joints on the second pair of walking legs.

and rapidly contracting the tail to propel itself backward very quickly.

Crawfish can burrow for reproduction at any time of the year but do so most often in late spring/early summer in the South. Crawfish of all ages and sizes, whether mature or immature, male or female, will construct burrows or retreat to existing burrows to survive periods of dewatering. Crawfish ponds are usually drained from late April in some production systems to as late as July or August in others. Before draining, mature crawfish burrow near the water line (Fig. 3). As the water level drops, crawfish burrows follow the waterline. Some burrows are found on the pond bottom after draining, but those often contain a high percentage of non-reproductive crawfish, such as males and immatures. For unknown reasons, some individuals will not burrow as the habitat dries, while others will construct very shallow burrows that can quickly dry out and lead to death.

In mature females, eggs usually begin to develop before burrowing and complete development in the burrow. As they mature, eggs within the ovary become spherical, enlarge, and change color from white or cream to dark brown (Fig. 4). At maturity, the large, dark eggs are expelled through the oviducts, fertilized externally with sperm that have



Figure 3. Crawfish burrows appear near the water line in ponds when mature crawfish begin burrowing for reproduction. Burrows may or may not have the typical "chimney" associated with the entrance. The density of burrows in this photo is extremely high.



Figure 4. Extracted crawfish ovaries showing the various stages of maturity, from well developed on the left to immature on the far right.

been stored in the seminal receptacle, and then are attached to the swimmerets (pleopods) under the tail (abdomen) with an adhesive substance called glair. Although crawfish can survive in a very humid environment within the burrow, they must have free-standing water for spawning. The number of eggs laid varies with the size and condition of the female and usually ranges from 200 to 300. Large females (more than about 15 count, 30 g) can have more than 500 eggs.

The incubation period is temperature dependent and it takes about 3 weeks for eggs to hatch at 74 °F. Hatchling crawfish remain attached to the female's swimmerets through two molts, after which they closely resemble adults in appearance. After hatchlings become detached from the female, they tend to remain with her for several more weeks. It is critical that the female and her young leave the burrow within a reasonable time after spawning because little food is available in burrows and cannibalism and death of the young can otherwise occur.

Pond flooding, in combination with rainfall, allows crawfish to emerge from burrows. Crawfish are trapped inside the burrow by the dried soil plug at the entrance. There must be enough external moisture to soften the plug before crawfish can emerge. When burrows are flooded, crawfish can emerge, but when crawfish have burrowed above the water line on levees, they may not be able to emerge until there is heavy rainfall to soften the soil plug. It is common for the brood female to emerge with young or eggs attached to the abdomen (Fig. 5). Hatchlings quickly



Figure 5. Female with hatchlings attached to swimmerets beneath the abdomen.

become separated from the female as she moves about in open water and they disperse in the pond.

Because spawning is largely synchronized in pond-reared crawfish, production ponds are routinely flooded in autumn to coincide with peak spawning. The spawning of both red swamp and white river crawfish peaks in autumn and usually several waves of young-of-the-year emerge with pond flooding and rainfall. Continuous recruitment and differential growth result in a crawfish population of mixed sizes and age classes.

A crawfish must molt or shed its hard exoskeleton to increase in size (Fig. 6). Frequent molting and rapid growth occur in production ponds when conditions are suitable. Growth rate is affected by many factors, including water temperature, population density, dissolved oxygen levels, food quality and quantity, and genetic influences; however, environmental factors have the most influence on growth rate. Harvest size is typically reached within 3 to 5 months after hatching in the South, but it can be



Figure 6. Soft, freshly molted crawfish (top) and its cast exoskeleton (bottom).

reached sooner with optimal growing conditions.

After growing and attaining sexual maturity, both males and females stop growing. Sexually mature individuals have distinct sexual characteristics, including darker color, enlarged claws (chelae), and hardened sexual structures. Mature males develop prominent hooks at the base of the third and fourth pair of walking legs (pereiopods) and there are changes in the seminal receptacle of mature females. Mature individuals become more abundant in late spring. Females will mate after their maturity molt and begin the process of constructing burrows at the water's edge on levees.

Burrow ecology

Although procambarid crawfish can construct burrows underwater, this rarely occurs in commercial crawfish ponds in the South. One exception is when a severe cold front rapidly lowers the water temperature in shallow ponds. Then, crawfish will sometimes dig shallow burrows underwater in the pond bottom, presumably to buffer the effect of a drastic temperature decline. Normally, however, burrows are built above the water line, usually at the water's edge, and in some cases in small puddles of water away from the water's edge. Burrows must be constructed in saturated soil because the process involves creating a soil slurry, which is removed from the hole in multiple trips to form the burrow.

Procambarid crawfish dig simple, nearly vertical burrows, usually 40 inches or less in depth. Burrows are a refuge from predators and provide the moist, humid environment necessary for crawfish to survive dry periods. These species of crawfish have evolved to spawn within the protection of the burrow. Most burrows are built at night and may require several days to complete. Crawfish burrows are usually dug by an individual crawfish, with the burrow diameter determined by the size of the crawfish. The burrow extends downward into a terminal chamber that is slightly larger than the diameter of the tunnel. Water levels in burrows vary with the soil moisture condi-

tions, but it is thought that any free water in a burrow is likely to be trapped water, perhaps from rainfall seepage, rather than water seeping into the burrow from the water table. When there is no standing water in the burrow, wet mud in the chamber serves as a humidifier. This can sustain crawfish but is not conducive to spawning. The burrow walls and terminal chamber are extensively worked by the crawfish, possibly to ensure good seals. The entrance of the burrow, which often has a chimney or stack of the excavated soil, is eventually closed with a mud plug (Fig. 7). Burrow entrances at the water's edge are often hidden under vegetation or woody debris. Over time, the burrow entrance may become undetectable because of weathering and vegetative growth.



Figure 7. Active crawfish burrows will eventually become sealed with a soil plug or cap. With time and weather, and covering by vegetation, the burrow entrance may become inconspicuous.

Burrows usually contain either a single female or a male and female. Occasionally, a burrow may contain a single male or more than two crawfish. Burrows are usually occupied for several months before crawfish emerge with the presence of water. Survival during the time they are in the burrow depends on the severity and length of the dry interval (which is associated with burrow moisture), characteristics of the burrow (such as depth and soil type), and the health of the animal. Immature crawfish and crawfish forced to burrow by rapidly declining water levels may construct shallow burrows that do not retain sufficient moisture for survival during

lengthy dry periods or drought. Soil with little clay content and soil with very high clay content that cracks during severe drought may also make it difficult to survive if moisture is lost during burrow occupation.

Molting

Molting is the process by which crawfish shed their old exoskeletons to grow. Crawfish grow during short episodes of molting with long intermolt periods between each shedding episode. Young crawfish must molt about eleven times to reach maturity. A molt cycle has five major stages, but the process is actually a continuum with indistinct delineations. The *intermolt* phase is the period when the exoskeleton is fully formed and hardened. During this phase, crawfish eat and increase tissue and energy reserves. Preparation for molting takes place in the *premolting* stage. During premolt, a new underlying (soft) exoskeleton forms while minerals from the old shell are reabsorbed. During the *late premolt* period, crawfish stop feeding and seek shelter because they are particularly vulnerable to predation and cannibalism during molting. The *molting* or "ecdysis" phase involves the actual shedding of the old exoskeleton and takes only minutes to occur. The brittle exoskeleton splits between the head (carapace) and tail (abdomen) on the dorsal or back side, and the crawfish usually withdraws from the old exoskeleton by tail flipping. It is during the soft phase that the new, supple exoskeleton expands to its new dimensions. Calcification or "hardening" of the new exoskeleton takes place during the *postmolt* phase, which can be divided into two periods. Initial hardening occurs when calcium stores within the body are transported to the new exoskeleton. Calcium is stored in the body in soft tissue, in blood and, for a short period, in two hard "stones" or gastroliths (Fig. 8) located in the head on each side of the stomach. The gastroliths disappear as they dissolve and the minerals are reabsorbed after molting. The second period of shell hardening is absorption of calcium from the water. As crawfish resume feeding, further mineralization and hardening of the new exoskeleton occur.



Figure 8. Gastroliths, paired bodies formed within the wall of the foregut ("stomach") during the premolt phase, store minerals from the old exoskeleton during molting.

Molting is controlled by hormones and occurs more frequently in younger crawfish than in older ones. The amount of growth that occurs during molting and the intermolt interval (or period between molts) can vary greatly; growth is affected mostly by environmental factors such as water temperature, water quality, food quality and quantity, and crawfish density. Research indicates that genetics plays a minor role in growth. Crawfish can increase up to 15 percent in length and 40 percent in weight in a single molt under optimal conditions.

After a period of growth, both males and females molt to a sexually active phase (referred to as Form I phase) and growth ceases. In southern aquaculture ponds, frequent molting and rapid growth occur in spring because of warming waters and adequate food sources. More mature crawfish appear as the season progresses. High temperatures ($> 80^{\circ}\text{F}$) when crawfish are overcrowded and food is scarce may stimulate the onset of maturity at a smaller than desirable market size. This is referred to as "stunting." When moved to a better environment, a stunted crawfish may revert to a sub-adult form (Form II) and resume growth.

Food habits

Crawfish have been classified as herbivores (vegetation eaters), detritivores (consumers of decomposing matter), omnivores (consumers of both plant and animal matter), and, more recently, as obligate carnivores, which means that they "require" some animal matter in the diet for optimal growth and health. Crawfish have been known to ingest living and decomposing plant matter, seeds, algae, microorganisms, and an assortment of larger invertebrates. They will also eat some vertebrates such as small fish, but food resources vary considerably among habitats. Living plants, often the most abundant food resource in crawfish ponds and in natural habitats, are thought to contribute little to the direct nourishment of crawfish. Starchy seeds, if present, are consumed and may provide needed energy. They mostly eat intact fibrous plant matter when other food sources are in short supply; aside from furnishing some essential nutrients, it provides a limited amount of energy and macronutrients to growing crawfish. Decomposing plant material, with its associated microorganisms (collectively referred to as detritus), is consumed in greater quantity and has a higher food value, but detritus does not generally provide the protein and energy needed for maximum growth.

In the aquatic environment, there are many other animals that rely on microbial-rich detritus as a primary food source, including mollusks, insects, worms, small crustaceans and some small vertebrates (Fig. 9).



Figure 9. Invertebrates in crawfish ponds, fed by decomposing plant fragments, furnish crawfish with the high-quality nourishment needed for maximum growth.

These animals, when consumed by crawfish, are a source of high-quality nutrition. For crawfish to grow at their maximum rate, they must consume animal matter or other high-protein and energy-rich foods. However, they can sustain themselves for some time by eating intact and detrital plants and bottom sediments containing organic debris.

Supplemental feeds are not routinely used in most commercial crawfish aquaculture ponds. Instead, producers establish or encourage a forage crop to provide the basis of a complex food web (Fig. 10) from which crawfish derive most of their nutritional needs. Plant fragments from the forage crop provide the "fuel" that drives a detrital-based production system, with crawfish at the top of the food web. Juvenile crawfish also derive some nutritional value from residual bait associated with harvesting activities.

Water quality

Water quality management in crawfish production usually focuses on maintaining acceptable levels of dissolved oxygen. Procambarid crawfish are generally tolerant of low oxygen levels, but persistent exposure to extremely low oxygen concentrations can reduce production. Juveniles are most susceptible to chronically low levels. When dissolved oxygen remains consistently below 1 ppm throughout the day for several weeks, crawfish become sufficiently stressed that they may stop feeding. Levels consistently below 0.5 ppm may affect molting and reduce crawfish survival. Other important water quality variables are pH, total hardness, total alkalinity, iron, hydrogen sulfide content, ammonia, nitrite and salinity (salt content). Desirable values are between 6.5 and 8.5 for pH, more than 50 ppm as CaCO_3 for total hardness, more than 50 ppm as CaCO_3 for total alkalinity, less than 0.1 ppm for ferrous iron, less than 0.002 ppm for hydrogen sulfide, less than 0.06 ppm for un-ionized ammonia, less than 0.6 ppm for nitrite, and less than 6 ppt for salinity.

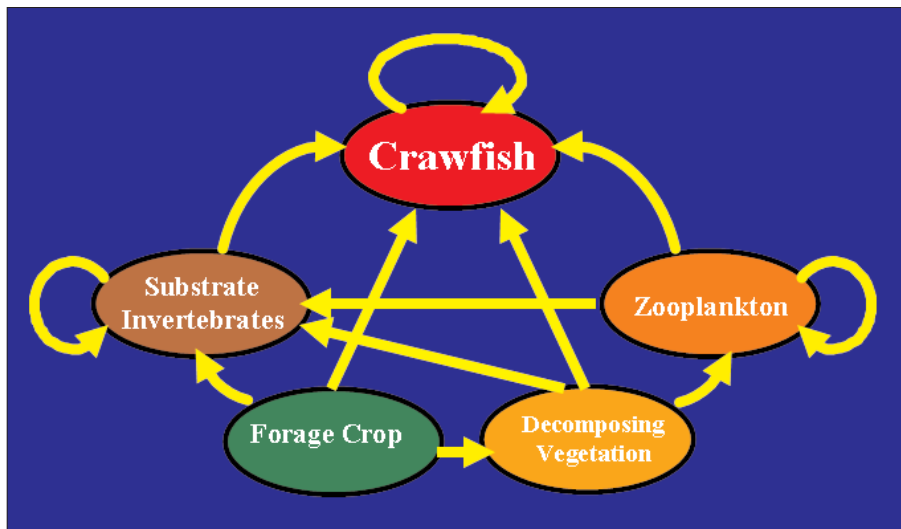


Figure 10. A simplified diagram of the nutrient pathways of the food web in crawfish ponds, with the forage crop serving as the principal fuel and crawfish at the top of the food chain.

Parasites and diseases

Serious disease problems in procambarid crawfish culture, as currently practiced in the southern U.S., have been rare. Individual crawfish are susceptible to various pathogens such as bacteria, viruses, fungi, protozoans and parasites; however, epidemic outbreaks sufficient to affect commercial production in earthen ponds have not been encountered until recently. White spot syndrome virus, the disease that has caused significant mortality on marine shrimp farms around the world, was identified

in commercial crawfish aquaculture operations for the first time in 2007. The disease occurred in Louisiana but its prevalence and impact on crawfish production is not yet known. The rarity of disease outbreaks in crawfish aquaculture is presumably due to the extensive nature of production systems. Significant disease problems are more likely to be encountered in intensive, high-density holding systems, such as purging operations and soft-shell production facilities. Diseases are also most likely to occur when temperatures are high and/or when dissolved

oxygen is low. The only practices related to disease management in the procambarid crawfish industry are those which minimize food shortages, overcrowding, and exposure to low dissolved oxygen.

All North American crawfishes are suspected to be vectors of the *Aphanomyces* fungi, or plaque fungus, which was responsible for dramatically reducing or eradicating populations of Noble crawfish (*Astacus astacus*) in many lakes, rivers and streams throughout Europe. Although known to be carriers of the fungus, North American crawfishes are not normally affected by the fungus.

Procambarid crawfish cultured in the southern U.S. are sometimes affected by other organisms that do not necessarily have an effect on production but may hinder crawfish marketability because of certain physical effects. Microsporidia—a microscopic protozoan—can infest the abdominal muscle, giving it an unattractive milky-white appearance (porcelain disease), but this is not common and has minor economic impact on the industry. Various ectocommensal organisms that attach to the exoskeleton can limit the acceptability of crawfish if the infestation is heavy, and at times buyers may refuse to accept lots of crawfish with heavily soiled exoskeletons.

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