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Synoptic Review of the Literature on the Southern Oyster Drill *Thais haemastoma floridana*

Philip A. Butler

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Synoptic Review of the Literature on the Southern Oyster Drill *Thais haemastoma floridana*[1]

PHILIP A. BUTLER[2]

ABSTRACT

This literature search identifies a majority of the publications in the period 1880-1980 concerned with the marine gastropod, *Thais haemastoma floridana* (Conrad). The southern oyster drill is an economically important oyster predator in the western Atlantic and Gulf of Mexico littoral. Major contributions of each paper to our knowledge of the drill's biology are briefly categorized. Hitherto unpublished research by the author on the snail's biology is documented.

INTRODUCTION

The drill has been the subject of sporadic investigations for more than 100 yr because of its association with the American oyster, *Crassostrea virginica* (Gmelin). In the past, field surveys and research in oyster biology were considered to be an appropriate part of the Federal mandate for assistance to the States, and much of the early work was conducted and published by Federal agencies. Since 1950, however, perhaps in recognition of the nonmigratory nature of oyster populations, Federal laboratories have been concerned only with the more generalized problems of oyster biology, and State laboratories have strengthened their oyster research and management programs.

Despite the long-continued efforts of oystermen and biologists alike to control the depredations of this pest, the southern oyster drill still prevents profitable oyster culture on about half of the estimated 3.6×10^4 ha (1,400 mi^2) of otherwise suitable oyster bottoms in the northern Gulf of Mexico. Interest in the drill's biology has increased in recent years since the recognition of its suitability for laboratory research on the osmoregulatory physiology of euryhaline species. In view of the diverse interests in the drill, it seemed desirable to gather and collate the available literature of the past century as an aid to future research efforts, and to outline major aspects of the biology of this gastropod.

Of the 173 publications cited, about 25% are the result of special surveys and summary reports by Federal scientists. Another 18% represent research efforts at State laboratories charged with shellfish management responsibilities. Other than the few technical source books listed, the remaining 25% of the citations describe research accomplished at university and museum laboratories.

TAXONOMY

There has been continuing confusion on the nomenclature of New World populations of snails belonging to the *haemastoma* complex as described by Linné. Early workers in the Gulf of Mexico area recognized that smaller drills tended to have smooth shells as opposed to the nodular large ones (Moore and Danglade 1915). Eventually, rugosity and large size as well as geographic restriction were claimed as valid subspecies characters in separating *T. haemastoma haysae* Clench (Clench 1930) from the smaller, smooth type of shell of *T. floridana* (Conrad 1837). More recently, a strongly indented suture has been cited as critical in referring the nodulose shell type to *T. haemastoma canaliculata* (Gray) (Abbott 1974). Curiously, the apparent holotype for this most recently designated subspecies is a single, entirely smooth shell of unknown provenance (Yen 1942; Abbott 1974).

It has been reported that the range of the nodulose shell type is restricted geographically to the area from northwest Florida to Texas (Abbott 1974; Burkenroad 1931; Clench 1947; Moore and Danglade 1915), but more recently it has been reported from the Atlantic coast (Hoese 1969). In Mississippi, the two shell types have been considered to be only ecological variants (Moore 1961), and others have rejected rugosity as a subspecific character (Butler 1954a; Gunter 1979). It appears that there are both smooth and knobby shells, with and without the indented suture. The situation was perhaps best summed up by Tryon (1880): "...the numerous species referred to the haemastomoid group...appear at best to be mere names for geographical groups...which invariably connect with the parent form...."

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In this bibliography, the term *floridana* is recognized as valid in separating New and Old World subspecies. References to *T. h. haemastoma* (Linné) on the eastern Atlantic coast and in southern Brazil are not included. In many of the citations a subspecific name is not listed by the authors, and the appropriateness of their inclusion in this bibliography is dependent on the geographical locale of the research.

DISTRIBUTION

The widespread distribution reported for the southern oyster drill is a result of not only its economic importance but also of the obvious aphorism that the range of specific flora and fauna is coincident with the travels of observant naturalists. The following citations are not all-inclusive but rather identify only those papers that are concerned primarily with the temporal and spatial aspects of the drill's habitat.

The apparent focus of the drill's present-day distribution in the mid-Gulf of Mexico littoral has ancient antecedents. Both smooth and nodose shells are common in million-year-old Pleistocene deposits east of the Mississippi Delta in Breton Sound (Parker 1956). Oyster shell deposits in Mississippi Sound dating back about 5,000 yr contain numerous drill shells buried 5 m below the bottom level (Butler 1954b; Demoran 1961), and shell deposits in nearby Lake Pontchartrain show this area to have been a typical oyster and drill biocoenose about 2,000 yr ago (Darnel 1962).

Drill populations have attracted attention since the close of the 19th century when declining oyster production became associated with the predatory snail (Cary 1907; Moore 1898; Moore and Pope 1910; Swift 1898b). Early faunal inventories identified the drill in Texas (Parker 1955), Louisiana (Cary 1906), and Mississippi and Florida (Vanatta 1903). More recent faunal lists cite populations in Texas (Gunter 1950; Hildebrand 1954; Pulley 1952; Strecker 1935; Whitten et al. 1950), Louisiana (Behre 1950; Harry 1942), Mississippi (Walker 1953), and Florida (Menzel 1955b; Menzel et al. 1966; Sykes and Hall 1970). The drill's range is most often given in shell books as the littoral zone extending south from Cape Hatteras, NC, about lat. 33°N, to the Gulf of Mexico, the Caribbean islands, and the northeast coast of Brazil at about lat. 5°S (Abbott 1974; Aldrich and Snyder 1936; Morris 1956; Perry and Schwengle 1955; Rehder 1954; Vilas and Vilas 1952; Warmke and Abbott 1961). Populations of the knobbed shells have been restricted in shell books to the northern Gulf of Mexico (Abbott 1974; Clench 1947; Johnson 1934; Morris 1956). Field scientists have noted the presence of knobbed shells in the coastal lagoons and offshore on the shrimping grounds in Texas at depths <20 m (Breuer 1962; Hildebrand 1954; Strecker 1935; Tunnell and Chaney 1970), and in Louisiana (Behre 1950; Burkenroad 1931; Harry 1942; Perret 1971; St. Amant 1957). They are reported also in Mississippi (Moore 1961), Alabama (Archer 1947), Florida (Butler 1954a), and, significantly, on the coast of Georgia where knobbed shells approaching the maximum sizes ascribed to Louisiana shells have been collected (Hoese 1969).

Drills with smooth shells are common in Texas bays (Gunter 1950; Ladd 1951; Moffett 1975; Strecker 1935). In Louisiana, smooth shells are much less common than the knobbed ones (Behre 1950; Harry 1942; Moore 1899; St. Amant 1938). The drill is only too prevalent in Mississippi Sound in years of high salinity (Butler 1952; Engle 1948; Moore 1913a), in Alabama (Hoese et al. 1972; May 1968), and on Florida's west coast (Butler 1954a; Dawson 1955: Finucane and Campbell 1968; Higgins 1938a; Pearse and Wharton 1938; Schecter 1943b). It has been found 8 km offshore on oil well platforms in the northern Gulf (Gunter and Geyer 1955). The drill is less common on Florida's east coast (D'Asaro 1966; Ingle 1953). In Georgia, the drill is rare (Walker et al. 1980), or only relatively abundant in a few areas (Higgins 1938a; Hoese 1969); in South Carolina it is uncommon but found occasionally in the subtidal habitat (Zingmark 1978).

The earlier presumed northern extent of the drill was in the waters of the barrier islands just south of Cape Hatteras (Chestnut 1956; Wells 1961) and on the subtidal wrecks offshore in North Carolina (Wells and Gray 1960). However, field studies in the 1950's identified living and long-buried shells in both the Virginia and Maryland sections of Chincoteague Bay on the eastern shore at about lat. 37°N (Sieling 1960). The scarcity of location records for the drill south of Texas reflects the absence of economically important oyster populations. However, intertidal collections have shown the drill to be relatively common in Panama (Birkeland et al. 1976), the Antilles (Clench 1947; Dall and Simpson 1901; Lewis 1960), and in Venezuela where dense populations were found at the entrance of Lake Maricaibo (Rodriguez 1963).

The drill is abundant along the northern coast of Brazil, both intertidally and at depths down to 35 m. It is reported south to about 450 km below the Equator in which area it is sympatric with *T. h. haemastoma* (Mathews 1968; Rios 1970; Rocha 1948). In view of the drill's planktonic larval life, it is possible that field surveys will find scattered populations of the subspecies further south in the generally favorable climate along the Brazilian coast, perhaps as far as Uruguay.

ANATOMY

Apparently there is but a single description of the gross and microscopic anatomy of *Thais*. This is reasonably complete and accurate but, unfortunately, only the abstract has been published (St. Amant 1938). Other than this Master's thesis, there are only minor contributions concerning the drill's adult structure and functions. The accessory boring organ has been described as somewhat unusual among muricids in its location atop the egg capsule gland (Carriker 1961). The dental conformation (Krutak 1977) and length of radula in relation to shell length have been detailed (Radwin and Wells 1968). There is an absence of sexual differentiation in shell morphology, and the external reproductive verge is present in both sexes but is either undeveloped or atrophied in the female (Morrison 1943). Separation of copulating pairs revealed that the penis extends at least 40 mm in males about 55 mm in shell length. The proboscis is relatively even longer (Menzel and Hopkins 1954). Chemical methods for relaxing and fixing snail tissues to facilitate anatomical studies are described (Carriker and Blake 1959).

The larval shell has been described and figured (Moore 1961). There is a dramatic change in the character of the shell as the definitive sinusigeral larva assumes the crawling habit. A thin, knifelike varix is formed that separates the smooth larval shell from the granulated adult shell. Presumably this change is the result of the termination of the planktotrophic diet. We found that in month-old drills of about 10 mm length, the shell makes up about 75-80% of the total body weight. This percentage declines to about 60% in drills >40 mm in shell length. Chemical studies of the shell identified nine amino acids in the organic matrix (Meenakshi et al. 1971).

Pharmacological studies of the secretions of the hypobranchial gland revealed the presence of a newly identified choline ester (Keyl et al. 1957; Whittaker 1957, 1960). Gland extracts were active vasodilator and hypotensive agents (Huang and Mir 1972), stimulated smooth muscle, and acted as a central nervous system depressant (Mir 1971). Methanol and acetone extracts of the gland from both shell types contained relatively large amounts of several choline esters (Roseghini and Fichman 1973). Aqueous extracts of the gland had an LD_{50} of 215 mg/kg to mice (Huang and Mir 1971).

GROWTH

Thais h. floridana is a moderately long-lived prosobranch in a taxonomic group whose life spans range from 1 to 20 yr. Early field observations of drill growth showed that those passing through 6.4 mm mesh on oyster trays had grown a minimum of 45% during the following 2-mo period (Moore and Pope 1910). Juvenile snails captured in the northern Gulf of Mexico were >21 mm long in October of their first year (Higgins 1938b). Drills with a mean length of 35 mm were captured, marked, and released in the field in south Florida; when recaptured 82 d later, their mean length had increased by about 12.2 mm (Ingle 1953). Field observations in Louisiana led to the conclusion that most drills die when 2 yr old after spawning only once (Menzel and Hopkins 1954). This was not corroborated in our Florida studies in which data indicate a minimal normal life span of 5 yr and a maximum perhaps twice as long. Six of 15 tagged snails survived in a wire mesh cage or live-car for 6 yr and were observed to deposit capsules of fertile eggs annually. During their final 3 yr, these drills decreased 15% in average shell length due to erosion of the shell spire by the boring sponge *Cliona truitti* Old. When sacrificed during the breeding season, histological examination of the three male and three female survivors showed normal gametogenic activity (Butler 1954a).

The mature larval shell or protoconch measures approximately 1.6 mm in length and has five whorls that are demarcated from the new growth of the teleoconch shell by a thin varix (Moore 1961). Veliger larvae may assume the crawling habit prior to metamorphosis and we have found them occasionally on epifaunal study plates with only three whorls and measuring about 0.7 mm in columnar length. Drills showing the new demarcation between juvenile and adult shell have been found frequently in suspended live-cars of oysters that we examine at 30-d intervals during the summer months. Some of these drills attain a length of 25 mm in a month's time and show the larval shell persisting as the terminal three or four whorls of the adult shell spire. These terminal whorls are solidified internally with shell deposits and may persist in very large or old shells.

In an extensive series of growth observations in west Florida, 600 drills of different size groups were maintained in large tanks with flowing seawater and an abundance of food (Butler 1954a). The individually numbered drills were measured at monthly intervals for 3 yr. In this protected habitat, some drills reached a length of 55 mm at age 6 mo and were larger than other drills known to be 3 yr old. Annual growth increments in the drills were markedly affected by the severity of winter temperatures in the 3 yr, but the mortality was about 12% per annum in all size groups. Length increases per annum declined from about 185% in the smallest size group, 10-19 mm, to about 10% in the largest size group that initially measured 50-59 mm in length. Male and female drills grew at similar rates throughout the experiment.

Growth rate appears to be a direct response to food consumption and ambient temperature, but individual variations under identical conditions may be significant with some individuals not growing at all seemingly under the best of conditions. Consequently, identification of individual snails is essential in experimental growth studies. We marked drills with enamel paint but this needs frequent renewing. Drills have been identified by notching the shells (Ingle 1953), and with plastic tags attached to the shells with fiber glass resin (Fischer 1979).

REPRODUCTION

In the northern Gulf of Mexico, southern oyster drills usually attain sexual maturity at the age of 8-12 mo (i.e., the first spring after their metamorphosis) and spawn in the period April through August (Engle 1945; Higgins 1938a; Hoese et al. 1972; Menzel and Hopkins 1954; Pearse and Wharton 1938). We have observed several instances, however, when 60-90 d-old drills were depositing capsules in live-cars of experimental oysters. Spawning is temperature dependent and initiated at about 21°C. Depending on the severity of winter weather in the northern Gulf, spawning may occur as early as January (Butler 1954a; Little and Quick 1976) or February (Menzel and Hopkins 1954) and continue sporadically through October. Eggs laid in unseasonably warm winter months may be killed by subsequent cold weather (Menzel and Hopkins 1954) or have larval development significantly delayed (Butler 1954a). In south Florida, spawning typically occurs throughout the year (D'Asaro 1966). Spawning usually occurs at salinity levels above 20‰ but a salinity drop from 27 to 13‰ for several days did not appear to damage the embryos. However, a decline from 27 to 4‰ killed embryos in capsules within 20 min (Higgins 1938b).

Copulation may be observed in early spring when mass spawnings occur (Butler 1954a), but solitary females lay fertile eggs subsequently and dissection of oviducts in the summer reveals masses of motile sperm (St. Amant 1938). Female drills that are held in experimental aquaria in the absence of males may deposit normal appearing capsules containing sterile eggs (Butler 1954a). Capsule size is determined by female size; large female drills in the northern Gulf deposit capsules varying from 10 to 18 mm in length and about 3 mm in width (Butler 1954a; Churchill 1920; St. Amant 1938). In warmer waters, capsules are reported to be smaller, about 6×2 mm (D'Asaro 1966). In one instance in Pensacola Bay we observed 25-mm females, not more than 2 mo old, depositing capsules 4 mm long and containing about 500 viable embryos.

The creamy white capsules are deposited with the one concave surface adjacent to the convex surface of the next capsule to form a compact mass. Capsules are attached by a short stem to a hard substrate, or in the case of mass spawnings they may be attached in tiers to underlying capsules of their own or other species (D'Asaro 1966). Capsules diagrammed as those of *T. h. floridana* from Barbados are either incorrectly identified or markedly different from *floridana* capsules deposited in other areas (Lewis 1960). Under field and laboratory conditions, capsules are deposited at the rate of 2 to 4/h (Burkenroad 1931; Butler 1954a; Higgins 1938b; St. Amant 1938) up to an observed maximum of 17 in 1 h (D'Asaro 1966). Clutches of capsules vary in number up to about 150, and several clutches may be deposited by each female during the spawning period. The gregarious habit of spawning drills leads to the deposition of thousands of capsules over a short period of time in limited space (D'Asaro 1966; Galtsoff 1964; Glaser 1904; Higgins 1938b). The eggs are fertilized in the oviduct at some point near the albumen gland before capsule formation (D'Asaro 1966). They number from hundreds to more than 6,000 in each capsule depending on the size of the female (Butler 1954a, c; D'Asaro 1966; Higgins 1938b; St. Amant 1938). The albumen gland has been described as the best histological criterion of spawning readiness (Belisle and Stickle 1978). Capsules become brown as the embryos mature but turn purple only when empty or when the developing embryos die despite statements that capsules with developing embryos may be purple (Churchill 1920; Galtsoff 1964; Moore 1913a). Under optimal conditions it would be possible for a female drill to produce in excess of 10 million eggs during her lifetime.

The egg capsules are deposited about an hour before formation of the first polar body, and larval development proceeds at rates controlled by ambient temperatures. At a mean temperature of 25°C, development requires about 2 wk (D'Asaro 1966) but may be completed in 10 d or extended to at least 39 d (Butler 1954a; St. Amant 1938). We have found no evidence of larval mortality within the capsule during the developmental period. The initial description of *Thais* embryology was based entirely on external morphological changes (St. Amant 1938), but a definitive description, based on histological sections as well, traces the organogenesis of the developing larva until the planktotrophic stage is reached (D'Asaro 1966).

Early investigators were unaware of the pelagic larval stage (Moore and Pope 1910), and it has been reported (without data) that *T. haemastoma* has a pelagic stage in subtropical waters but not in boreal areas (Thorson 1950). Others conclude in a review of stenoglossan prosobranchs that the pelagic larval stage is a genetic rather than a geographic attribute (Radwin and Chamberlin 1973). Duration of the pelagic stage is unknown. Clench (1954) believed that it had to be short in order to explain the existence of clines, but collection of pediveligers is rare until long after the onset of spawning; a free-swimming stage of not less than 2 mo seems likely (Moore 1961). Casual efforts to culture larvae through metamorphosis in vitro have been unsuccessful (Butler 1954a; D'Asaro 1966; St. Amant 1938).

Young drills of both sexes have a clearly defined verge, and about 75% initially develop a male gonad. Field surveys of drills <25 mm in length and presumably <120 d old showed a preponderance of 4 or 5 males to 2 females. Shell size is not necessarily directly related to sexual development since some of the smaller drills (16.5 mm) of both sexes had well-developed gonads, while others measuring as much as 42 mm could not be sexed either grossly or on the basis of histology. We sexed a group of 300 snails estimated to be a year old and maintained them in live-cars for 30 mo. During that period, no sex reversals were detected; however, the snails were examined only grossly.

A small verge usually persists in the adult female, and dissection of 63 Louisiana drills showed them to be fundamentally hermaphroditic with male and female ducts present but with one set undeveloped or degenerate (Morrison 1943). We randomly collected 532 presumably mature drills over a period of 3 yr in Santa Rosa Sound, FL, and on the basis of gross examination 45% were male, 49% were female, and 6% were of indeterminate sex.

BEHAVIOR

In the northern Gulf of Mexico, the activity of the southern oyster drill is limited by the critical temperature of 12°C (St. Amant 1938). Below this point, feeding stops and drills tend to disappear beneath rocks and shells or bury themselves in the substrate (Butler 1954a). The burying habit is well-established, and as much as 50% of a drill population may be buried even when temperature and salinity levels are suitable for feeding. When active, drills crawl easily on very soft mud bottoms (Burkenroad 1931); on hard surfaces, they move at rates as fast as 9 m/h (Butler 1954a; St. Amant 1938). Drills are occasionally taken from sandy bottoms in shrimp trawls (Hildebrand 1954; Swingle 1971) and are reported hitchhiking on a variety of floating objects as well as on the blue crab, *Calinectes sapidus* (Rathbun), the horseshoe crab, *Limulus polyphemus* (Linné), and sea grasses (Moore 1961). Drill larvae are effectively distributed by water currents, and their presumably lengthy planktonic existence facilitates dispersal of the species and repopulation of areas devastated by periodic low salinities. In experimental studies, we found larval movement to be continuous and basically vertical. Monitored in flow-through aquaria, larvae ascended at an observed rate of 20 cm/min.

POPULATION DENSITY

The number of drills per unit area is of obvious interest and importance in assessing potential losses on oyster grounds due to this predator. Drill populations fluctuate widely as a result of sudden environmental changes. For example, the opening of the Bonnet Carré Spillway in Louisiana appeared to have eliminated the drills in western Mississippi Sound in 1950. Yet only 2 yr later in dredged samples from this area, the volume ratio of drills to oysters was about 1 to 150 (Gunter 1953). Density surveys are of only immediate value and can cover but a limited area. Numbers in the following citations have been transposed to numbers of drills per square meter: Apalachicola, FL, in 1955, 2.7 drills (Menzel et al. 1957); Santa Rosa Sound, FL, in 1968, 222; lower Mobile Bay, AL, in 1967, 2.7 (May 1971); Mississippi Sound, MS, in 1956, 27 (Chapman 1959); west of the Mississippi River, LA, in 1936, 25 (St. Amant 1938); and, remarkably, Lake Maracaibo, Venezuela, in 1956, 1,290 (Rodriguez 1963).

In 1968 when we found the drill population on the rocky shore of the laboratory island in Santa Rosa Sound, FL, was 222/m^2, the drills averaged 33 mm in length and 1.5 g in wet weight of tissues. We estimated their biomass was the equivalent of about 3.3 t/ha.

DRILLING TECHNIQUE

The ability of *Thais* to prey on oysters has been a matter for discussion and some dissension since the turn of the century when perhaps the first experimental observations of the drill were undertaken (Moore and Pope 1910). Drills were placed in an enclosed live-car with mixed-sized oysters, and apparently only oysters of <40 mm length were killed. Oystermen as well as some biologists believed that large oysters were immune to drill attack (Churchill 1920; Moore 1898; St. Amant 1938). Later studies showed that damage to large oysters could be heavy but difficult to detect (Burkenroad 1931; Cary 1907; Moore 1899). Many oystermen failed to evaluate the importance of this pest (Baughman and Baker 1951; Burkenroad 1931; Butler 1954a; Higgins 1938a; Moore 1899). We exposed a group of 25-65 mm oysters in a live-car to 25-mm drills, and 83 oysters were killed in a 7-d period. Ten of the oysters showed no evidence of drill damage; in 65, the slitlike marginal hole was difficult to find; and only in the remaining 8 was there an obvious circular hole that was randomly located on the surface of the valves. Turn-of-the-century oystermen believed that the drill secretes an acid to bore the hole (Moore 1913b); this has been affirmed more recently (Carriker 1961). Some suggested that there is a paralytic poison to make the oyster gape (Baughman and Baker 1951; Gunter 1970; Higgins 1938a; McGraw and Gunter 1972; Moore 1898; St. Amant 1938), but a more detailed study of drill feeding indicated oysters gaped only after being three-quarters consumed (Chapman 1956).

The mechanics of radular movement during feeding are described but present no evidence of an acid or paralytic secretion (Gunter 1952a). An accessory boring organ is assumed (Garton and Stickle 1980; Radwin and Wells 1968) and identified in *Thais* and related species (Carriker 1961). The angle of the bore hole made by *Thais h. floridana* is compared with that of other species of muricids (Gates 1910). Excision of the radula and odontophore is reported to be followed by complete regeneration within 3 wk (Demoran and Gunter 1956). Early workers, unaware of the drill's planktonic stage, erroneously assumed that it was able to bore oysters as soon as it emerged from the capsule like its northern counterparts (Moore 1913a), but its ability to drill as soon as it can crawl is well documented (Butler 1953). Bore holes made by young drills gradually increase in diameter from 0.1 to 0.2 mm and are as much as 10 times as large in the adult. Some have assumed that mature drills, i.e., about 50 mm in length, no longer bore holes but simply rasp open the oyster's valves (Gunter 1979).

FEEDING SELECTIVITY

The importance of the drill as an oyster predator reflects essentially the monocultural nature of oyster farming. Given a choice, drills selectively feed on mussels, barnacles, small and then larger oysters, presumably on the basis of ease in opening rather than flavor (Butler 1954a; Hedgpeth 1953; St. Amant 1938). In an evaluation of drill attractants, we baited traps with four kinds of food. In a 2-wk period of daily inspections, 190 drills (27-44 mm long) were captured. The drills selected the different baits as follows: mussels, 35%; barnacles, 30%; oysters <30 mm long, 27%; and large oysters, 8%. The drill is an opportunist, however, and eats whatever is available including *Donax variabilis* Say (Loesch 1957), *Rangia cuneata* Sowerby (O'Heeron 1966), and *Perna perna* (Linné) (Urosa 1969). We have also observed them feeding on *Anomia simplex* Orbigny, *Crepidula plana* Say, and *Mercenaria mercenaria* (Linné). It apparently does not feed naturally on scallops or blue crabs although it is occasionally seen browsing on their epifauna.

Thais is attracted by shucked oyster meats in experimental trays and as far as 3 m downstream from them (Gates 1910; Gunter et al. 1957). It is readily attracted to oysters killed by other drills, and as many as eight drills have been observed feeding on a single oyster (McConnell 1954; Moore 1913a).

In the absence of a normal food supply, the drill readily feeds on its companions. In an experimental group of mixed-size drills that had been starved individually for a month, 26 were cannibalized in the following week when they were placed together. At the end of the week, all of the remaining drills were approximately the same size and the cannibalism stopped (Butler 1954a). Experimental data reveal that the drill stops feeding when the salinity declines to 7.5‰ (Garton and Stickle 1980). Field data indicate that feeding and other activities terminate when the temperature drops to 12°C or less (St. Amant 1938).

SALINITY TOLERANCE

The southern oyster drill tolerates a broad range of salinities but typically flourishes only in the more saline parts of the estuary (Cooley 1978). Adapted to tidal shifts in salinity patterns, it has no narrowly defined, low-salinity death point. When acclimated to a salinity of 35‰, for example, drills became immobile when the salinity declined to 15‰; but when acclimated to a salinity of 20‰, they were not harmed when the salinity declined to about 10‰ (Butler 1954a). Drills reportedly survived a gradual salinity decline to about 5‰ on Florida reefs (Higgins 1938a), although mortalities were sustained at salinities of 8-10‰ in Mississippi Sound (Gunter 1953). Experimentally, drills suffered higher mortality when suddenly exposed to a salinity of 7‰ than to 3.5‰, presumably because the lower salinity caused an immediate closure of the operculum that sealed off the drill from the environment (Schecter 1943a).

Low temperatures provide at least temporary protection for the drill, as well as the oyster, from incursions of freshwater in the spring months. Relict drill populations are preserved in pockets of more saline benthic waters when spring freshets and floods result in a superficial run-off of potentially lethal freshwater (Butler 1952). Under experimental conditions, week-old encapsulated larvae acclimated to a salinity of about 25‰ were killed after 48 h exposures to salinities of 15 and 10‰. When we exposed capsules of veliger larvae to tap water and then returned them to salt water, mortalities were as follows: 2 min, 40%; 4-6 min, 75%; and 10 min or longer resulted in a complete kill. Pelagic drill larvae reportedly tolerate lower salinities than adults, but the planktonic stage is probably the limiting factor in the distribution of drills along the estuarine salinity gradient (Gunter et al. 1974; Wells 1961).

Laboratory studies suggested that osmolality in the drill is controlled by active rather than passive tissue processes (McRitchie 1968). The amplitude of osmolality fluctuates directly with ambient salinity changes (Stickle and Howey 1975). Studies with artificial tidal cycles showed that at lower salinities, drills contracted, their oxygen consumption declined (Findley et al. 1978), and their haemolymph osmolality tended to be hyperionic at low salinities and vice versa (Hildreth and Stickle 1980).

PREDATORS

Thais must be judged an extremely successful animal in that it has no documented natural predators in the adult stage. At least five species of hermit crabs have been identified as inhabiting its shells (Cooley 1978; Fotheringham 1976), but there is no evidence that such acquisitions are other than accidental. In our studies of epifaunal setting on artificial substrates, 2-mm anemones were found containing up to 10 snail shells but it is not certain that these were *Thais*, although this snail was settling out of the plankton at the time.

In the laboratory, we found it possible to induce hermit crabs to attack the drill only by forcing the crabs to occupy shells that were too small for them. Starved drills in the laboratory will prey on each other, and the crown snail, *Melongena corona* (Gmelin), will adapt to a drill diet. Starved stone crabs, *Menippe mercenaria* (Say), will feed on them (Powell and Gunter 1968), but not the banded tulip, *Fasciolaria lilium hunteria* (G. Perry), which normally preys on other gastropods (Wells 1958). Drills are damaged in nature by commensals residing in and gradually eroding their hosts' shells, especially the boring sponge, *Cliona truitti* (Menzel and Hopkins 1954), the boring clam, *Diplothyra smithii* Tryon (Harry 1976), and the blister worm, *Polydora* spp. (Hyman 1967; Menzel and Hopkins 1954). We found that experimental drills kept in live-cars were more damaged by boring sponge than by their benthic neighbors presumably because the latter occasionally suffocate their commensals by burying in bottom muds.

PARASITES

The southern oyster drill's rather limited diet has perhaps restricted the variety of parasites which it serves as host (Cake 1975). Only 2 of 10 potential metacestode types were found in *Thais* when surveyed with 35 other gastropod species (Cake 1976, 1978). This was about the same level of infection of metacestodes found in oysters (Cake and Menzel 1980). Larval cestodes are common gut parasites in drills of both shell types examined in Texas (Wardle 1974). Only one larval trematode type was found in thousands of drills examined near Galveston, TX, although 14 others were observed in the 20 different gastropod species collected (Epstein 1972).

Cercariae of the digenetic trematode *Parorchis acanthus* (Nicoll) were reported from snails in Florida and snails of both shell types in Louisiana. The mass of cercariae effectively castrates the drill.

The adult trematode lives in the cloaca of gulls and other sea birds (Hopkins 1957; Schecter 1943b). In the northern Gulf, the natural infection rate of *Parorchis* is about 3% in *Thais* and can be increased to only about 12% experimentally (Cooley 1958). The infection rate in gulls is also low, and it was not possible to increase it experimentally (Cooley 1962). The adult polyclad *Hoploplana inquilina* Wheeler is reported from the mantle cavity of *Thais* and other snails from the western Atlantic littoral, and from Louisiana where the specimens were larger than any collected from the type locality on the Atlantic coast (Hyman 1967; Pearse and Wharton 1938; Schecter 1943b).

Of uncertain pathogenicity are protozoans we have observed frequently in sections of drill liver tissue, and a saprophytic *Labyrinthula thaisii* Cox and Mackin found on the gills of drills collected near Galveston, TX (Cox and Mackin 1974).

ECONOMIC IMPORTANCE

The extent of drill depredations on the oyster community is dependent naturally on salinity and temperature regimes. In more saline areas, their damage varies inversely with the density of the associated mussel and barnacle communities (St. Amant 1938). Under experimental conditions, a 50-mm drill ate about 85 2-wk-old spat per day, and from 1 to 5 market-size oysters per month (Butler 1953, 1954a; Menzel and Hopkins 1956). A 15-mm drill ate its own volume of oyster tissue in a 20-min period (St. Amant 1938). By extrapolation, an average drill can destroy 1,000 to 3,000 oysters during its lifetime (Butler 1954a). Estimates of the damage caused by drills in Texas varied from nil (Moore 1907) to about 90% or more in some areas (Baker 1951; Baughman and Baker 1951; Gunter 1955; Hofstetter 1959; Menzel 1955a). In Louisiana, the drill has been recognized as the most serious oyster predator (Galtsoff et al. 1935; Hopkins 1955; McConnell 1954; Pollard 1973; Van Sickle et al. 1976), and that its destructiveness increases as salinity levels increase (Dugas 1977; Padgett 1960; St. Amant 1938). Similar observations in Mississippi have been reported (Chapman 1959; Gunter 1953); Gunter and Demoran 1971; MacKenzie 1977; Maghan 1967; May and Bland 1970), and in Alabama (May 1968, 1971, 1972; Ritter 1896). In Florida, reported damage varies from negligible (Menzel and Nichy 1958) to extensive (Danglade 1917; Ingle and Whitfield 1968; Swift 1898a, b). In Georgia, production of oysters subtidally is insignificant because of the drill (Harris 1980). It is generally recognized that there can be little extension of oyster grounds into more saline areas until the development of efficient drill controls (Galtsoff 1950).

CONTROL

There is consensus that the southern oyster drill prevents profitable oyster culture on thousands of hectares of otherwise suitable grounds along the Gulf coast, but methods for controlling this predator are essentially absent. Limited control may be obtained in some areas by destruction of the drills culled when harvesting oysters (Gates 1910). So-called traps, however, permit drills to exit as well as enter and so must be emptied at frequent intervals. They are prohibitive in terms of required manpower (Butler 1954a, c). Use of seed oysters as bait in such traps is unsatisfactory because our experiments showed that while this bait attracted about 75% of the drills on a barren bottom, only about 5% were captured on an oyster reef. The often-suggested use of palmetto or yucca branches to attract gregarious drills during the breeding season is likewise too labor intensive to be practical (Burkenroad 1931; Engle 1945; Menzel and Hopkins 1954).

Suggestions to make the harvest of drills more profitable by using them for human food (Burkenroad 1931; Butler 1953; Gunter 1971) were reflected in a small fishery in Louisiana in the early 1950's. Special traps were constructed that harvested only the larger drills. The processed drill meats had an acceptable flavor but became discolored after being canned (George Seale[3]). Laboratory efforts to increase the incidence of the trematode parasite *Parorchis* in hopes of spreading this specific disease in the environment were also unsuccessful (Cooley 1962).

Inevitably, ideas for drill control have centered on the effects of contrived fluctuations in salinity regimes. It has long been noted that extensive spring freshets devastated drill populations (Breithaupt and Dugas 1979; Burkenroad 1931; May 1972; Menzel et al. 1966) as do flood waters from crevasses in the Mississippi River levee system (Gunter 1952b; Viosca 1938). It has been suggested seriously that regulated discharges from the Mississippi River could be used to control the drill on Louisiana oyster grounds (Breithaupt and Dugas 1979; St. Amant 1938). There is no question, however, that drill problems are largely overcome by culturing oysters in less saline areas (McConnell 1954).

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LITERATURE CITED

ABBOTT, R. T.
1974. American seashells; the marine Mollusca of the Atlantic and Pacific coasts of North America. 2d ed. Van Nostrand Reinhold, N.Y. 663 p.
ALDRICH, B., and E. SNYDER.
1936. Florida sea shells. Houghton Mifflin, N.Y., 122 p.
ARCHER, A. F.
1947. Oyster reefs in Alabama. Ala. Conserv., Dec. 7, 12.
BAKER, B. B., Jr.
1951. A brief report on the Texas oyster investigation. Proc. Natl. Shellfish. Assoc. 41:50-52.
BAUGHMAN, J. L., and B. B. BAKER.
1951. Oysters in Texas. Tex. Game, Fish Oyster Comm. Bull. 29, 37 p.
BEHRE, E. H.
1950. Annotated list of the fauna of the Grand Isle region. La. State Univ. Occas. Pap. Mar. Lab. 6, 66 p.
BELISLE, B. W., and W. B. STICKLE.
1978. Seasonal patterns in the biochemical constituents and body component indexes of the muricid gastropod, *Thais haemastoma*. Biol. Bull. (Woods Hole) 155:259-272.
BIRKELAND, C., A. A. REIMER, and J. R. YOUNG.
1976. Survey of marine communities in Panama and experiments with oil. EPA Ecol. Res. Serv. 600/3-76-028, 176 p.
BREITHAUPT, R. L., and R. J. DUGAS.
1979. A study of the southern oyster drill (*Thais haemastoma*) distribution and density on the oyster seed grounds. La. Wildl. Fish. Comm. Tech. Bull. 30, 20 p.
BREUER, J. P.
1962. An ecological study of the lower Laguna Madre of Texas, 1953-1959. Publ. Inst. Mar. Sci., Univ. Tex. 8:153-183.
BURKENROAD, M. D.
1931. Notes on the Louisiana conch, *Thais haemastoma* Linné, and its relation to the oyster, *Ostrea virginica*. Ecology 12:656-664.

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[3] G. Seale, Golden Meadow Fisheries Co., Golden Meadow, LA 70357, pers. commun. 30 May 1955.

BUTLER, P. A.

1952. Effect of floodwaters on oysters in Mississippi Sound in 1950. U.S. Fish Wildl. Serv., Res. Rep. 31, 20 p.

1953. The oyster predator problem. South. Fisherman, June, p. 35.

1954a. The southern oyster drill. Proc. Natl. Shellfish. Assoc. 44:67-75.

1954b. Summary of our knowledge of the oyster in the Gulf of Mexico. *In* P. S. Galtsoff (editor), Gulf of Mexico. Its origin, waters and marine life. p. 479-489. U.S. Fish Wildl. Serv. Fish. Bull., Vol. 55.

1954c. Methods for controlling the southern oyster drill. Atl. Fisherman, January, p. 17.

CAKE, E. W., Jr.

1975. Larval and postlarval cestode parasites of shallow-water benthic mollusks of the Gulf of Mexico from the Florida Keys to the Mississippi Sound. Ph.D. Thesis, Florida State Univ., Tallahassee, 434 p.

1976. A key to larval cestodes of shallow-water, benthic mollusks of the northern Gulf of Mexico. Proc. Helminthol. Soc. Wash. 43(2):160-171.

1978. Larval cestode parasites of edible mollusks of the northeastern Gulf of Mexico. Gulf Res. Rep. 6:1-8.

CAKE, E. W., Jr., and R. W. MENZEL.

1980. Infections of *Tylocephalum* metacestodes in commercial oysters and three predaceous gastropods of the eastern Gulf of Mexico. Proc. Natl. Shellfish. Assoc. 70:94-104.

CARRIKER, M. R.

1961. Comparative functional morphology of boring mechanisms in gastropods. Am. Zool. 1(2):263-266.

CARRIKER, M. R., and J. W. BLAKE.

1959. A method for full relaxation of muricids. Nautilus 73(1):16-21.

CARY, L. R.

1906. A contribution to the fauna of the coast of Louisiana. Bull. Gulf Biol. Stn. 6:50-59.

1907. A preliminary study of the conditions for oyster culture in the waters of Terrebonne Parish, Louisiana. Bull. Gulf Biol. Stn. 9:1-62.

CHAPMAN, C. R.

1956. Feeding habits of the southern oyster drill, *Thais haemastoma*. Proc. Natl. Shellfish. Assoc. 46:169-176.

1959. Oyster drill (*Thais haemastoma*) predation in Mississippi Sound. Proc. Natl. Shellfish. Assoc. 49:87-97.

CHESTNUT, A. F.

1956. The distribution of oyster drills in North Carolina. Proc. Natl. Shellfish. Assoc. 46:134-139.

CHURCHILL, E. P., Jr.

1920. The oyster and the oyster industry of the Atlantic and Gulf coasts. Rep. U.S. Comm. Fish., 1919. App. VIII (Doc. 890), 51 p.

CLENCH, W. J.

1930. A new subspecies of *Thais* from Louisiana. Nautilus 41:6-8.

1947. The genera *Purpura* and *Thais* in the western Atlantic. Johnsonia 2(23):61-91.

1954. The occurrence of clines in molluscan populations. Syst. Zool. 3(3): 122-125.

CONRAD, T. A.

1837. Descriptions of new marine shells, from upper California. Collected by Thomas Nuttal, Esq. J. Acad. Nat. Sci., Phila. Ser. I, 7:227-268. (Not seen, quoted by Clench.)

COOLEY, N. R.

1958. Incidence and life history of *Parorchis acanthus*, a digenetic trematode in the southern oyster drill, *Thais haemastoma*. Proc. Natl. Shellfish. Assoc. 48:174-188.

1962. Studies on *Parorchis acanthus* (Trematoda:Digenea) as a biological control for the southern oyster drill, *Thais haemastoma*. U.S. Fish Wildl. Serv. Bull. 62:77-91.

1978. An inventory of the estuarine fauna in the vicinity of Pensacola, Florida. Fla. Mar. Res. Pub. 31, 119 p.

COX, B. A., and J. G. MACKIN.

1974. Studies on a new species of *Labyrinthula* (Labyrinthulales) isolated from the marine gastropod *Thais haemastoma floridana*. Trans. Am. Microsc. Soc. 93:62-70.

DALL, W. H., and C. T. SIMPSON.

1901. The Mollusca of Puerto Rico. Bull. U.S. Fish. Comm., 1900, 20:351-524.

DANGLADE, E.

1917. Condition and extent of the natural oyster beds and barren bottoms in the vicinity of Apalachicola, Fla. Rep. U.S. Comm. Fish., 1916, Doc. 841, 68 p.

DARNELL, R. M.

1962. Ecological history of Lake Pontchartrain, an estuarine community. Am. Midl. Nat. 68(2):434-444.

D'ASARO, C. N.

1966. The egg capsules, embryogenesis and early organogenesis of a common oyster predator, *Thais haemastoma* (Gastropoda: Prosobranchia). Bull. Mar. Sci. 16(14):884-914.

DAWSON, C. E.

1955. A study of the oyster biology and hydrography at Crystal River, Florida. Publ. Inst. Mar. Sci., Univ. Tex. 4:279-302.

DEMORAN, W. J.

1961. Preliminary studies on the effect of the purple dye of the oyster drill *Thais haemastoma* on the oyster. J. Miss. Acad. Sci. 6:93-95.

DEMORAN, W. J., and G. GUNTER.

1956. Ability of *Thais haemastoma* to regenerate its drilling mechanism. Science 123(3208):1126.

DUGAS, R. J.

1977. Oyster distribution and density on the productive portion of the State seed grounds in southeastern Louisiana. La. Wildl. Fish. Comm. Tech. Bull. 23, 27 p.

ENGLE, J. B.

1945. The condition of the natural oyster reefs and other public oyster bottoms of Alabama in 1943 with suggestions for their improvement. U.S. Fish Wildl. Serv. Spec. Sci. Rep. 29, 42 p.

1948. Investigation of the oyster reefs of Mississippi, Louisiana and Alabama following the hurricane of September 18, 1947. U.S. Fish Wildl. Serv. Spec. Sci. Rep. 59, 70 p.

EPSTEIN, R. A.

1972. Larval trematodies of marine gastropods from Galveston Island, Texas. Tex. J. Sci. 24(3):389.

FINDLEY, A. M., B. W. BELISLE, and W. B. STICKLE.

1978. Effects of salinity fluctuations on the respiration rate of the southern oyster drill, *Thais haemastoma*, and the blue crab *Callinectes sapidus*. Mar. Biol. (NY) 49:59-67.

FINUCANE, J. H., and W. CAMPBELL, II.

1968. Ecology of American oysters in Old Tampa Bay, Florida. Q. J. Fla. Acad. Sci. 31:37-46.

FISCHER, M.

1979. The results of a tag retention study utilizing various commercial adhesives on the oyster drill, *Thais haemastoma*. La. Wildl. Fish. Comm. Tech. Bull. 28:29-34.

FOTHERINGHAM, N.

1976. Population consequences of shell utilization by hermit crabs. Ecology 57:570-578.

GALTSOFF, P. S.

1950. Latent oyster resources of Florida. Proc. Gulf Caribb. Fish. Inst. 2:15-16.

1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Fish. Wildl. Serv., Fish. Bull. 64, 480 p.

GALTSOFF, P. S., H. F. PRYTHERCH, R. O. SMITH, and V. KOEHRING.

1935. Effects of crude oil pollution on oysters in Louisiana waters. U.S. Dep. Commer, Bull. Bur. Fish., no. 18, vol. 48:143-210.

GARTON, D., AND W. B. STICKLE.

1980. Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* spat. Biol. Bull. (Woods Hole) 158: 49-57.

GATES, W. G.

1910. Oyster culture in Louisiana. Bull. Gulf Biol. Stn. 15:1-32.

GLASER, O. C.

1904. An incomplete list of the marine fauna of Cameron, Louisiana. Bull. Gulf Biol. Stn. 2(II):40-42.

GUNTER, G.

1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):7-51.

1952a. Radula movement and boring efficiency of gastropods. Nature 169 (4302):630-631.

1952b. Historical changes in the Mississippi River and the adjacent marine environment. Publ. Inst. Mar. Sci., Univ. Tex. 2(2):119-139.

1953. The relationship of the Bonnet Carré Spillway to oyster beds in Mississippi Sound and the "Louisiana Marsh", with a report on the 1950 opening. Publ. Inst. Mar. Sci., Univ. Tex. 3(1):17-71.

1955. Mortality of oysters and abundance of certain associates as related to salinity. Ecology 36:601-605.

1970. Some factors concerning the drilling apparatus and the feeding and predation of the prosobranchiate gastropods especially on other molluscs. *In*: Proceedings of symposium on Mollusca, p. 370-378. Mar. Biol. Assoc. India, Mandapam Camp, India.

1971. The molluscan resources of the Gulf of Mexico. FAO Fish. Rep. 71.2(2): 111-115.

1979. Studies of the southern oyster borer, *Thais haemastoma*. Gulf Res. Rep. 6:249-260.

GUNTER, G., B. S. BALLARD, and A. VENKATARAMIAH.

1974. A review of salinity problems of organisms in United States coastal areas subject to the effects of engineering works. Gulf Res. Rep. 4:380-475.

GUNTER, G., C. E. DAWSON, and W. J. DEMORAN.

1957. Determination of how long oysters have been dead by studies of their shells. Proc. Natl. Shellfish. Assoc. 47:31-33.

GUNTER, G., and W. J. DEMORAN.

1971. Mississippi oyster culture. Am. Fish Farm. 2(5):8-12.

GUNTER, G., and R. A. GEYER.

1955. Studies on fouling organisms of the northwest Gulf of Mexico on platform and pile. Publ. Inst. Mar. Sci., Univ. Tex. 4(1):37-67.

HARRIS, C. D.

1980. Survey of intertidal and subtidal oyster resources of the Georgia coast. Ga. Dep. Natl. Resour., Brunswick, GA, 44 p.

HARRY, H. W.

1942. List of Mollusca of Grand Isle, Louisiana, recorded from the Louisiana State University Marine Laboratory, 1924-41. La. State Univ. Occas. Pap. No. 1, 13 p.

1976. Correlation of benthic Mollusca with substrate composition in lower Galveston Bay, Texas. Veliger 19(2):135-152.

HEDGPETH, J. W.

1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci., Univ. Tex. 3:107-224.

HIGGINS, E.

1938a. Progress in biological inquiries, 1935. Rep. U.S. Comm. Fish. 1936, App. IV:381-452.

1938b. Progress in biological inquiries, 1936. Rep. U.S. Comm. Fish. 1938, App. III:1-61.

HILDEBRAND, H. H.

1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci., Univ. Tex. 3(2):229-366.

HILDRETH, J. E., and W. B. STICKLE.

1980. The effects of temperature and salinity on the osmotic composition of the southern oyster drill, *Thais haemastoma*. Biol. Bull. (Woods Hole) 159:148-161.

HOESE, H. D.

1969. Population of large oyster drills (*Urosalpinx*, *Eupleura*, *Thais*) from the southern United States salt marshes. *In* T. L. Linton (editor), Feasibility study of methods for improving oyster production in Georgia. Ga. Game Fish Comm. and Univ. Ga., 176 p.

HOESE, H. D., W. R. NELSON, and H. BECKERT.

1972. Seasonal and spatial setting of fouling organisms in Mobile Bay and Mississippi Sound, Alabama. Ala. Mar. Resour. Bull. 8:9-17.

HOFSTETTER, R. P.

1959. The Texas oyster fishery. Tex. Game, Fish Oyster Comm. Bull. 40, 38 p.

HOPKINS, S. H.

1955. Oyster setting on the Gulf Coast. Proc. Natl. Shellfish. Assoc. 45:52-55.

1957. Interrelationships of organisms. B. Parasitism. *In*: J. W. Hedgpeth (editor), Treatise on marine ecology and paleoecology. Geol. Soc. Am Mem. 67, 1:413-428.

HUANG, C. L., and G. N. MIR.

1971. Pharmacological properties of hypobranchial gland of *Thais haemastoma* (Clench). J. Pharm. Sci. 60:1842-1846.

1972. Pharmacological investigations of salivary gland of *Thais haemastoma* (Clench). Toxicon 10(2):111-117.

HYMAN, L. H.

1967. The invertebrates: Mollusca I (Vol. VI). McGraw-Hill, N.Y., 792 p.

INGLE, R. M.

1953. Notes on growth of *Thais haemastoma floridana* and *thais* (*Stramonita*) *rustica*. Proc. Natl. Shellfish. Assoc. 42:12-14.

INGLE, R. M. and W. K. WHITFIELD.

1968. Oyster culture in Florida. Fla. Dep. Nat. Resour., Educ. Ser. 5, 1962 rev., 25 p.

JOHNSON, C. W.

1934. List of marine Mollusca of the Atlantic Coast from Labrador to Texas. Proc. Boston Soc. Nat. Hist. 40(1):1-204.

KEYL, M. J., I. A. MICHAELSON, and V. P. WHITTAKER.

1957. Physiologically active choline esters in certain marine gastropods and other invertebrates. J. Physiol. (Lond.) 139:434-454.

KRUTAK, P. R.

1977. Gastropod radulae: their potential in the fossil record. Trans. Gulf Coast Assoc. Geol. Soc. 27:314-322.

LADD, H. S.

1951. Brackish water and marine assemblages of the Texas coast with special reference to mollusks. Publ. Inst. Mar. Sci., Univ. Tex. 2:125-164.

LEWIS, J. B.

1960. The fauna of rocky shores of Barbados, West Indies. Can. J. Zool. 38: 391-535.

LITTLE, E. J., and J. A. QUICK, Jr.

1976. Ecology, resource rehabilitation, and fungal parasitology of commercial oysters, *Crassostrea virginica* (Gmelin), in Pensacola Estuary, Florida. Fla. Mar. Res. Publ. 21, 89 p.

LOESCH, H. C.

1957. Studies of the ecology of two species of *Donax* on Mustang Island, Texas. Publ. Inst. Mar. Sci., Univ. Tex. 4(2):201-227.

MacKENZIE, C. L., Jr.

1977. Development of an aquacultural program for rehabilitation of damaged oyster reefs in Mississippi. Mar. Fish. Rev. 39(8):1-13.

MAGHAN, B. W.

1967. The Mississippi oyster industry. U.S. Fish Wildl. Serv. Leafl. 607, 12 p.

MATTHEWS, H. R.

1968. Notas sôbre o genero *Thais* Röding, 1798, no nordeste Brasiliero. Arq. Estac. Biol. Mar. Univ. Fed. Ceará 8:37-41.

MAY, E. B.

1968. Summer oyster mortalities in Alabama. Prog. Fish-Cult. 30(2):99.

1971. A survey of the oyster and the oyster shell resources of Alabama. Ala. Mar. Resour. Bull. 4, 53 p.

1972. The effect of floodwater on oysters in Mobile Bay. Proc. Natl. Shellfish. Assoc. 62:67-71.

MAY E. B., and D. G. BLAND.

1970. Survival of young oysters in areas of different salinity in Mobile Bay. Proc. Southeast. Assoc. Game Fish Comm. 23:519-521.

McCONNELL, J. H.

1954. The Gulf Coast conch, *Thais haemastoma*. Proc. Natl. Shellfish. Assoc. 44:76-77.

McGRAW, K. A., and G. GUNTER.

1972. Observations on killing of the Virginia oyster by the Gulf oyster borer, *Thais haemastoma*, with evidence for a paralytic secretion. Proc. Natl. Shellfish. Assoc. 62:95-97.

McRITCHIE, R. G.

1968. Effects of thermal and osmotic acclimation on an estuarine gastropod. Ph.D. Thesis, Rice University, Houston, TX, 71 p.

MEENAKSHI, V. R., P. E. HARE, and K. M. WILBUR.

1971. Amino acids of the organic matrix of neogastropod shells. Comp. Biochem. Physiol. B. Comp. Biochem. 40(4):1037-1043.

MENZEL, R. W.

1955a. Some phases of the biology of *Ostrea equestris* Say and a comparison with *Crassostrea virginica* (Gmelin). Publ. Inst. Mar. Sci., Univ. Tex. 4:69-153.

1955b. Annotated check-list of the marine fauna of the St. George's Sound-Apalachee Bay region, Florida Gulf Coast. Oceanogr. Inst. Florida State Univ. Contrib. 61, 78 p.

MENZEL, R. W., and S. H. HOPKINS.

1954. Studies on oyster predators in Terrebonne Parish, Louisiana. Tex. A&M Res. Found. Project 9, College Station, 155 p.

1956. Crabs as predators of oysters in Louisiana. Proc. Natl. Shellfish. Assoc. 46:177-184.

MENZEL, R. W., N. C. HULINGS, and R. R. HATHAWAY.

1958. Causes of depletion of oysters in St. Vincent Bar, Apalachicola Bay, Florida. Proc. Natl. Shellfish. Assoc. 48:66-71.

1966. Oyster abundance in Apalachicola Bay, Florida, in relation to biotic associations influenced by salinity and other factors. Gulf Res. Rep. 2:73-96.

MENZEL, R. W., and F. E. NICHY.

1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. Bull. Mar. Sci. Gulf Caribb. 8:125-145.

MIR, G. N.

1971. Pharmacological investigations of some poisonous and venomous marine animals of the Gulf of Mexico. Ph.D. Thesis, Univ. Miss., University, 110 p.

MOFFETT, A. W.

1975. The hydrography and macro-biota of the Chocolate Bayou estuary, Brazoria County, Texas (1969-71). Tex. Parks Wildl. Dep. Tech. Ser. 14, 72 p.

MOORE, D. R.

1961. The marine and brackish water Mollusca of the State of Mississippi. Gulf Res. Rep. 1:1-58.

MOORE, H. F.

1898. Some factors in the oyster problem. Bull. U.S. Fish Comm., 1897, 17:275-284.

1899. Report on the oyster beds of Louisiana. Rep. U.S. Comm. Fish., 1898, 24:45-100.

1907. Survey of oyster bottoms in Matagorda Bay, Texas. Rep. U.S. Comm. Fish., 1905, Doc. 610, 86 p.

1913a. Condition and extent of the natural oyster beds and barren bottoms of Mississippi Sound, Alabama. Rep. U.S. Comm. Fish., 1911, Doc. 769, 62 p.

1913b. Condition and extent of the natural oyster beds and barren bottoms of Mississippi east of Biloxi. Rep. U.S. Comm. Fish., 1911, Doc. 774, 42 p.

MOORE, H. F., and E. DANGLADE.
1915. Condition and extent of the natural oyster beds and barren bottoms of Lavaca Bay, Texas. Rep. U.S. Comm. Fish., 1914, Doc. 809. 45 p.

MOORE H. F., and T. E. B. POPE.
1910. Oyster culture experiments and investigations in Louisiana. Rep. U.S. Comm. Fish., 1908, Doc, 731, 52 p.

MORRIS, P. A.
1956. A field guide to the shells of our Atlantic and Gulf coasts, 3d ed., W. J. Clench (editor). Houghton Mifflin Co., Boston, 236 p.

MORRISON, J. P. E.
1943. Notes on the reproductive morphology of *Thais*. Nautilus 56(3):103-104.

O'HEERON, M. K., Jr.
1966. Some aspects of the ecology of *Rangia cuneata* (Gray). Masters Thesis, Texas A&M Univ., College Station, 71 p.

PADGETT, H. R.
1960. The marine shellfisheries of Louisiana. Ph.D. Thesis, Louisiana State University, Baton Rouge, 360 p.

PARKER, R. H.
1955. Changes in the invertebrate fauna, apparently attributable to salinity changes, in the bays of central Texas. J. Paleontol. 29(2):193-211.
1956. Macro-invertebrate assemblages as indicators of sedimentary environments in east Mississippi Delta region. Bull. Am. Assoc. Pet. Geol. 40:295-376.

PEARSE, A. S., and G. W. WHARTON.
1938. The oyster "leech" *Stylochus inimicus* Palombi, associated with oysters on the coasts of Florida. Ecol. Monogr. 8:605-655.

PERRET, W. S.
1971. Cooperative Gulf of Mexico estuarine inventory and study, Louisiana, Phase IV, Biology Sect. I. La. Wildl. Fish. Comm., New Orleans, p. 29-105.

PERRY, L. M., and J. S. SCHWENGLE.
1955. Marine shells of the western coast of Florida. Bull. Am. Paleontol. 26(96):1-318.

POLLARD, J. F.
1973. Experiments to re-establish historical oyster seed grounds and to control the southern oyster drill. La. Wildl. Fish. Comm. Tech. Bull. 6, 82 p.

POWELL, E. H., and G. GUNTER.
1968. Observations on the stone crab, *Menippe mercenaria* Say, in the vicinity of Port Aransas, Texas. Gulf Res. Rep. 2:285-299.

PULLEY, T. E.
1952. An illustrated check list of the marine mollusks of Texas. Tex. J. Sci. 4(2):167-199.

RADWIN, G. E., and J. L. CHAMBERLIN.
1973. Patterns of larval development in stenoglossan gastropods. Trans. San Diego Soc. Nat. Hist. 17:107-117.

RADWIN, G. E., and H. W. WELLS.
1968. Comparative radular morphology and feeding habits of muricid gastropods from the Gulf of Mexico. Bull. Mar. Sci. 18:72-85.

REHDER, H. A.
1954. Mollusks. U.S. Fish. Wildl. Serv., Fish. Bull. 55:469-474.

RIOS, E. C.
1970. Coastal Brazilian seashells. Fundacão Cidade Rio Grande Mus. Oceanogr. Rio Grande. XI, 82 p.

RITTER, H. P.
1896. Report of a reconnoissance of the oyster beds of Mobile Bay and Mississippi Sound, Alabama. Bull. U.S. Fish Comm., 1895, 15:325-338.

ROCHA, D.
1948. Subsídio para o estudo de fauna cearense. (Catálogo das especies animais por mim coligidas e notadas). Rev. Inst. Ceará, Fortaleza 62:102-138.

RODRIGUEZ, G.
1963. The intertidal estuarine communities in Maracaibo, Venezuela. Bull. Mar. Sci. Gulf Caribb. 13:197-218.

ROSEGHINI, M., and M. FICHMAN.
1973. Choline esters and imidazole acids in extracts of the hypobranchial gland of *Thais haemastoma*. Comp. Gen. Pharmacol. 4(15):251-257.

SCHECTER, V.
1943a. Tolerance of the snail *Thais floridana* to waters of low salinity and the effect of size. Ecology 24:493-499.
1943b. Two flatworms from the oyster-drilling snail *Thais floridana haysae* Clench. J. Parisitol. 29:362.

SIELING, F. W.
1960. A notable range extension of the southern drill, *Thai haemastoma floridana*, into Chincoteague Bay. Chesapeake Sci. 1(3-4):212-215.

ST. AMANT, L. S.
1938. Studies on the biology of the Louisiana oyster drill, *Thais floridana haysae* Clench. Masters Thesis, Louisiana State Univ., Baton Rouge, 116 p
1957. The southern oyster drill. *In*: Seventh Biennial Report, p. 81-84. La. Wildl. Fish. Comm., New Orleans, LA.

STICKLE, W. B., and T. W. HOWEY.
1975. Effects of tidal fluctuations of salinity on hemolymph composition of the southern oyster drill *Thais haemastoma*. Mar. Biol. (NY) 33(4): 309-322.

STRECKER, J. K.
1935. Notes on the marine shells of the Texas coast. Baylor Univ. Bull. 38(3):48-60.

SWIFT, F.
1898a. The oyster grounds of the west Florida coast: their extent, condition and peculiarities. Bull. U.S. Fish. Comm. 17:285-296.
1898b. Report of a survey of the oyster regions of St. Vincent Sound, Apalachicola Bay and St. George Sound, Florida. Rep. U.S. Comm. Fish., 1896, 22:187-217.

SWINGLE, H. A.
1971. Biology of Alabama estuarine areas - cooperative Gulf of Mexico estuarine inventory. Ala. Mar. Resour. Bull. 5, 123 p.

SYKES, J. E., and J. R. HALL.
1970. Comparative distribution of mollusks in dredged and undredged portions of an estuary, with a systematic list of species. Fish. Bull., U.S. 68:299-306.

THORSON, G.
1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. Camb. Philos. Soc. 25:1-45.

TRYON, G. W., Jr.
1880. Manual of conchology, Vol. II, Muricinae, Purpuriniae. Published by author, Phila., 289 p.

TUNNELL, J. W., Jr., and A. H. CHANEY.
1970. A checklist of the mollusks of Seven and One-half Fathom Reef, northwestern Gulf of Mexico. Contrib. Mar. Sci. 15:193-203.

UROSA, L. J.
1969. Identification of some predators of the mussel (*Perna perna*) under experimental conditions. FAO Fish. Rep. 71.1, 159 p.

VANATTA, E. G.
1903. A list of shells collected in western Florida and Horn Island, Mississippi. Proc. Acad. Nat. Sci. Phila. 55:756-759.

VAN SICKLE, V. R., B. B. BARRETT, T. B. FORD, and L. J. GULICK.
1976. Barataria Basin: salinity changes and oyster distribution. La. Wildl. Fish. Comm. Tech. Bull. 20, 22 p.

VILAS, C. N., and R. N. VILAS.
1952. Florida marine shells. Bobbs-Merrill, Indianapolis, 170 p.

VIOSCA, P., Jr.
1938. Effect of Bonnet Carré Spillway on fisheries. La. Conserv. Rev. Winter issue:51-53.

WALKER, J. F.
1953. A check list of marine invertebrates collected at the Gulf Coast Research Laboratory from 1947 through 1950. J. Miss. Acad. Sci. 4:192-207.

WALKER, R. L., M. A. FLEETWOOD, and K. R. TENORE.
1980. The distribution of the hard clam *Mercenaria mercenaria* (Linne) and the clam predators in Wassaw Sound, Georgia. Ga. Mar. Sci. Cen. Tech. Rep. 80-8, 59 p.

WARDLE, W. J.
1974. A survey of the occurrence, distribution and incidence of infection of helminth parasites of marine and estuarine Mollusca from Galveston, Texas. Ph.D. Thesis, Texas A&M Univ., College Station, 346 p.

WARMKE, G. L., and R. T. ABBOTT.
1961. Caribbean seashells. Livingston Publ., Narberth, PA., 346 p.

WELLS, H. W.
1958. Predation on pelecypods and gastropods by *Fasciolaria hunteria* (Perry). Bull. Mar. Sci. Gulf Caribb. 8:152-166.
1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31(3):239-266.

WELLS, H. W., and I. E. GRAY.
1960. Some oceanic sub-tidal oyster populations. Nautilus 73(4):139-147.

WHITTAKER, V. P.
1957. ββ-Dimethylacrylycholine, a new naturally occurring, physiologically active ester of choline. Biochem. J. 66:35.
1960. Pharmacologically active choline esters in marine gastropods. Ann. N.Y. Acad. Sci. 90:695-705.

WHITTEN, H. L., H. F. ROSENE, and J. W. HEDGPETH.
1950. The invertebrate fauna of Texas coast jetties; a preliminary survey. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):53-87.

YEN, T-C.
1942. A review of Chinese gastropods in the British Museum. Proc. Malac. Soc. Lond. 24(V):170-289.

ZINGMARK, R. G.
1978. An annotated checklist of the biota of the coastal zone of South Carolina. Univ. S. Carolina Press, Columbia, 364 p.