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Studies on oyster scavengers and their relation to the fungus disease Dermocystidium marinum

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STUDIES ON OYSTER SCAVENGERS AND THEIR RELATION TO THE FUNGUS DISEASE DERMOCYSTIDIUM MARINUM[1]

INTRODUCTION

Within the past decade there have been several studies on the biological structure of oyster reefs. These studies, however, gave few insights into the dynamics of oyster communities. The extensive studies of Hedgpeth (1953), Gunter (1955), and Parker (1955, 1959) in Texas and Korringa (1951) in Holland were largely concerned with sessile forms, and the highly motile fishes went almost unnoticed. While these studies clearly emphasized immotile organisms, the present study leans in the opposite direction.

This study started from casual observations of oyster fishes, and progressed to comparisons of mortality of oysters with activity of other members in the community. Mortality of oysters in the study area occurs predominately in the warmer months; in Chesapeake Bay this is caused by Dermocystidium marinum, a fungous parasite, and by a newly discovered sporozoan. This mortality occurs when many organisms are active in the community. Some of these oyster associates, as they are herein termed, are scavengers of dying oysters and obviously ingest cells of oyster parasites; disease causing death making the oyster available. The importance of what appeared to be interaction between members of the community and a general dependency among these members was apparent early in the study. The concept of the oyster biocoenosis is quoted widely, but has received little expansion. While this study was not concerned with the whole community, its main interest has been to show the role of fishes, crabs, and a few other scavengers in the community, especially in their relationship to the oyster, Crassostrea virginica (Gmelin 1790), and its parasitic fungus, Dermocystidium marinum Mackin, Owen, and Collier 1950.

Gathering of information on oyster fishes began with observations during other studies for the Marine Laboratory of the Texas Game and Fish Commission. Studies in Virginia were incidental to oyster mortality studies on the Eastern Shore of Virginia, with occasional observations in other parts of Virginia, Delaware, and Maryland. Many oystermen and dealers graciously gave their time, oysters, and equipment, and helped catch specimens, particularly A. M. Acuff, Ralph Clark, Elwood Gaskins, and W. E. Walker. Mr. A. M. Acuff kindly donated an oyster reef for scavenger studies. Dr. J. D. Andrews introduced the writer to the Chesapeake area and supplied much information on Dermocystidium. Dr. S. H. Hopkins provided information, advice, and assisted summer field studies. Miss Evelyn Wells provided valuable help securing references. W. T. Davis, and later R. D. Hickman and Bonnie Callaway, assisted both field and laboratory studies in Virginia. W. T. Davis drew figures 1, 2, 6, and 7. Mr. Tom K. Burton, Jr. photographed figures 3 and 4. Mr. Michael Castagna happily provided information and specimens from Chincoteague Bay. Mr. Ken Parks of the Accomack County Health Department sterilized media and equipment as well as providing numerous other considerations. For identifications I am indebted to the following specialists: copepod, Dr. David Causey,

University of Arkansas; leech, Mr. P. J. S. Raj, University of Connecticut; sponges, sea squirts, Dr. Sewell H. Hopkins, A. & M. College of Texas. All fishes and crabs were identified by the writer, ~~of this paper,~~ me.

METHODS

Data on scavengers were collected incidental to studies of oyster mortality on the Eastern Shore of Virginia, supplemented by observations elsewhere. Many fishes were collected from trays used in mortality studies and from bags of live oysters used specifically to collect oyster fishes. The presence of *Dermocystidium marinum* was determined by Ray's (1952) thioglycollate culture method. Oysters and the digestive tract of fishes were cultured by the standard method, but feces were originally cultured in petri dishes with ten cc of medium added to about 5 cc of water containing fecal material. This method has the advantage of not disturbing the feces, but enhances the growth of molds. Since this method proved generally unsatisfactory, feces were later cultured in test tubes, by adding dilute oyster serum from uninfected oysters. Fishes and crabs were fed in aquaria or small bowls on pieces of meat or whole oysters that apparently died from heavy *Dermocystidium* infections. The fish were then washed in three or more separate sterile dishes and placed in dishes with Seaside water of a salinity always near 30 ‰; or they were placed in aquaria for infection experiments. When it seemed that the fungus was incompatible with Seaside water, Bayside water near 20 ‰ was substituted.

by oyster biologists). Gunter and Geyer (1955) found *Hypsoblennius ionthas* inside "boxes" and associated with oysters from hulls and ballast tanks of boats kept in the offshore Gulf of Mexico. Andrews and Hewatt (1957) mention that clingfish, gobies, and blennies were present in their trays of oysters and quickly ate dying oysters. They did not name the species but these are *Gobiesox strumosus*, *G. bosci*, and *C. bosquianus*.

In many parts of the world fishes are associated with species of oysters, ~~as well as other~~ and with molluscs (Table 1). These associations, although widespread, have not been studied in detail, but apparently range from chance association to inquilinism to parasitism.

The most famous association between molluscs and fishes is that of the pearlfish (*Fierasfer*) which resides in the mantle cavity of the pearl oyster (*Meleagrina*). This association is usually spoken of as inquilinism, but is not always harmless, for there are records of fishes pearlised by the oyster. Schultz (1948) and Dales (1957) note that the relationship is sometimes fatal to the fish. This association is probably more complex than thought since Arnold (1953) found that early stages of *Carapus* (= *Fierasfer*) are obligate parasites because they are unable to live outside of their holothurian hosts. Along similar lines a young goby, *Gobiosoma bosci*, was reported living in the soft parts of an oyster (Nelson 1928). These gobies are normally found free-living with oysters.

Off the northeast coast of the United States young squirrel hake, Urophycis chuss (Walbaum) were reported in the mantle cavity of scallops (Welsh 1915, Nichols and Breder 1927). In gastropods, Apogonichthys is known from the pallial cavity of conchs, Strombus, in the Bahamas and Key West (Plate 1908, Hildebrand and Ginsburg 1926, Gudger 1927a).

Various blennoid, gobiid, and gobiesocid fishes are reported from reefs of oysters, and many instances are known of spawning within the shells of molluscs. Paragobiopsis ostreicola (Chaudhuri) apparently occupies such a niche in India (Chaudhuri 1916; Bhattacharya 1916) as does Gobiosoma bosci on Atlantic and Gulf coasts of the United States. P. ostreicola was described from specimens taken from oyster beds in Chilka Lake and embryos were found inside an oyster shell. Other examples are the goby, Gobius minutus, which spawns in Ostrea edulis and other mollusc shells in England (Lebour 1920), a blenny which spawns in molluscs in France (Guitel 1893), Blennius cornutus in Africa (Smith 1950), Forsterygion varium in New Zealand, and many others (Table 1). The description of F. varium spawning and parental care (Graham 1956) and that of Pholis gunnellus (Gudger 1927b) are among the best for species associated with molluscs. Undoubtedly the habit of association with molluscs and spawning in shells is very common in species which normally inhabit hard substrates. Many more examples will be found.

CRABS ASSOCIATED WITH OYSTERS

The literature of crab-mollusc associations was not extensively reviewed as it was for fishes and was largely restricted to those species associated with reefs of Crassostrea virginica.

Several groups of crabs are known to be associated with oysters. The only case of parasitism is apparently that of Pinnotheres ostreum which is beyond doubt harmful to oysters (Stauber 1945, Flower and McDermott 1952, Haven 1959). Related species of Pinnotheres occur in mussels and other molluscs.

A maiid, Libina dubia (Milne-Edwards), occurs on oysters in Virginia, but its relationship was not investigated. It is probably a scavenger as it has been observed feeding on stranded jellyfish, Dactylometra.

Two large crabs are frequently associated with oysters although they often live in other habitats. Cancer irroratus and Carcinedes menas sometimes prey on oysters in northern states. Menzel and Hopkins (1956) reported that blue crabs (Callinectes sapidus Rathbun) were scavengers of large oysters but were important predators of spat.

Mud crabs (Xanthidae) are also accused of preying on spat and they are probably important scavengers. McDermott and Flower (1952) found that mud crabs were selective feeders ~~of~~ on oysters. It is assumed that these crabs are less important than other predators; but there is little information on this matter, ~~except for~~ The stone crab, Menippe mercenaria a of southern waters, member of this family, is an important predator on oyster beds.

Mud crabs are important members of the oyster community and are probably the most abundant ~~crab~~ brachyurans found with oysters. They are alternate hosts of certain mollusc gregarines, Nematopsis, (Prytherch 1938, 1940;

(Petrolisthes armatus, an anomuran, is more abundant than mud crabs on some Gulf Coast oyster beds)

Sprague and Orr 1955). According to Feng (1958) it is not certain that the spores of Nematopsis are acquired by the scavenging habits of the crabs, although this seems most probable. McDermott and Flower (1952) and Ryan (1956) gave extensive information on the mud crabs of oyster beds in Delaware and Chesapeake Bays.

OTHER SPECIES

Of course, other animals scavenge oysters besides crabs and fishes, but there is little published. Most predators of oysters, such as Urosalpinx, Eupleura, and Thais, also scavenge. The borderline between scavenging and predation is a thin one. Another major group of organisms, annelids, are often abundant on oysters, and feed on meats.

LIFE HISTORY STUDIES

OYSTER REEF FISHES

The following fishes were those found associated with oysters on the Eastern Shore of Virginia. They are discussed in their estimated order of abundance in the area. Note that the total number of specimens taken or seen was not always recorded, but estimates of abundance of each species were recorded at every opportunity. On several occasions all oyster fishes were preserved and the numbers of these agreed generally with estimates of relative abundance.

These estimates were usually written as few when from 4 to 8 individuals were seen; many when 8-15 were seen; and abundant over 15. Fewer than four were recorded as to number. The relative abundance (Table 2) is based on these estimates. In 1961 all fishes were saved at two stations (Gulf and Swash Bay).

GOBIOSOMA BOSCI (LACÉPÈDE, 1798). According to Briggs (1958) this goby ranges from Massachusetts to Hispaniola and throughout the Gulf of Mexico. Within its range it occupies many habitats, and in some areas it is the most abundant fish on oyster reefs.

Nearly everywhere *G. bosci* has been found it is common. Joseph and Yerger (1956) list it as the most abundant goby in Alligator Harbor. Pearse and Wharton (1938) found it common in Apalachicola Bay, occurring and breeding on oysters. Kilby (1955) found specimens common in marsh pools. Mackin and Wray (1950) found it common enough in Louisiana to use spawning as an indication of a normal environment and lack of pollution. They are the only recent workers to note more than superficially the relation between oysters and fishes, although their concern was with oyster mortality; their report was not published. Bean (1891) may be the first to note abundance of *G. bosci* on oysters but his mention of it in the Potomac River has been overlooked. Nelson (1928) noted spawning of *Gobiosoma* in oysters in Delaware Bay and described the remarkable occurrence of a stunted 21 mm living gravid female in a live oyster. Innumerable early records of *Gobiosoma* may have applied to this or to different species. Ginsburg (1933) constructed a synonomy of these.

Springer and Woodburn (1960) also found *G. bosci* common on oyster reefs in the Tampa Bay area, and they pointed out that this habitat was different from those previously reported for the species. They found an ecological separation between *G. bosci* and the closely related *G. robustum* Ginsburg, the latter restricted to grass flats. In Texas the writer recorded *G. bosci* in Aransas, Copano, Mesquite, San Antonio, East, and Galveston Bays exclusively from oysters except for one collection from a rock pile. In all cases it was noted as common and often was the only such associated fish in low salinity areas in Galveston, East, and Copano Bays. *G. robustum* was found in Aransas, Copano, Mesquite, and West Bays in grass flats of *Ruppia maritima*, *Diplantheria wrighti*, and *Thalassia testudinum*. Hildebrand (1954) found *G. robustum* common in *Thalassia* flats in Redfish Bay. Although ecological separation between the two species was apparent in Texas, as in Florida, both Gunter (1945) and Simmons (1957) record *G. bosci* in grass flats in Aransas Bay and the Laguna Madre, respectively.

Even though *G. robustum* has most commonly been noted from vegetation, Breder (1942) reported it from several habitats and recorded spawning in shells. Reid (1954) first suggested ecological separation of the two species. Other authors noted *G. bosci* from grassy areas and this is the habitat listed in popular works and even monographs. Hildebrand and Schroeder (1928) found *G. bosci* in grassy areas in Chesapeake Bay, but did not record it on oysters as they did other species.

On the Eastern Shore of Virginia *G. bosci* was found in every creek (personal communication) has observed it from oysters there many times. Schwartz (1961 reports it common in Chincoteague Bay.

G. bosci is known from a few other habitats but apparently never in open waters, except during a pelagic larval stage. Nine young individuals (13-26 mm) were taken from sponges, Halichondria, Lissodendoryx, and Microciona on pilings at Wachapreague. Others were observed swimming in and out of the oscula of Lissodendoryx. Larger specimens were found in sponges in Cherrystone Creek and Burton's Bay and one (37 mm) was taken from a sponge at Wachapreague. Sponge inquilinism has not been noted for this species, but Gudger (1950) cited earlier records of other Gobiosoma from sponges and Breder (1942) reports G. robustum living in sponge beds. Small gobies were also abundant in sea squirts, Ecteinascidia turbinata Herdman, which were abundant on pilings and oysters in the Wachapreague area in the summer and fall. Joseph and Yerger (1956) reported this goby among sea squirts, Molgula and Styela, in Florida. In Occohannock Creek young gobies were often abundant among Molgula which was abundant on oysters at times in the summer. G. bosci was also observed entering the burrow of an unknown organism at Wachapreague, probably as a temporary hiding place while roaming short distances away from oysters.

Many workers found this goby in essentially fresh-water in rivers, streams, and upper parts of estuaries, (Pearse and Wharton 1938, Hubbs 1957, Renfro 1960, Raney and Massmann 1953, and others). On the other hand Simmons (1957) found it abundant in the Laguna Madre of Texas in salinities up to 45 $^{o}/oo$ and Hildebrand (1958) took one specimen from the hypersaline Laguna Madre of Tamaulipas, but he found G. robustum more common. In Virginia G. bosci was abundant in salinities as low as 2.8 $^{o}/oo$ in Messongo Creek and as high as 34.4 $^{o}/oo$ in Swash Bay. As previously noted it is the most common oyster fish on the Seaside where salinities seldom fall below 30 $^{o}/oo$. Although previous workers noted this goby's abundance in a particular range of salinities, usually in lower ranges, these seldom agreed. This probably reflects the salinity range of proper habitats in each area. In experimental work we kept all sizes and eggs in salinities over 30 $^{o}/oo$ and even though these often came from salinities of 15-22 $^{o}/oo$ there was no apparent mortality from salinity and eggs hatched normally.

On the Seaside, where tides may range as high as 4 1/2 to 5 feet, G. bosci was found in all levels of the intertidal, even in the highest Spartina marsh at low tide. Usually the fish were restricted to small pools with oysters and mussels (Modiolus demissus) but rarely one was exposed in a dead oyster. When no other hiding place is available, these fish remain hidden among oysters, even when totally exposed at low tide.

G. bosci was found over a wide range of temperatures. It was active and common in temperatures of about 10 to 31°C, but below 10 appeared to be increasingly scarce. Below 3° it was rarely seen, except for a few individuals buried in the mud and debris on the edge of oyster reefs. A single inactive specimen was taken in mud near oysters in Hungars Creek on March 2, 1960 at a temperature of 1.7°C. A single dead individual and a dead Gobiesox strumosus was taken at The Gulf on December 27, 1960 when water temperatures were 3°C and had been as low as -1.5 for the past two days. Two live G. bosci were also taken.

Spawning of G. bosci occurs inside of newly killed hinged oyster shells ("boxes"). An attempt was made to locate eggs of this species as well as those of other oyster associates in other habitats where adults occur. However, none were found. In view of the intimate parental association with the eggs and the apparent dependency for recently dead oysters (presumably for the clean surface attachment for the pedicel) it seems unlikely that spawning occurs except where mollusc mortality occurs. M. Castagna (personal communication) reports one case of spawning within the shells of Mercenaria mercenaria and Schultz (1948) reports spawning in fossil shells washed into Chesapeake Bay from Miocene cliffs. Nelson (1928) also mentioned spawning in clams.

Although others have noted eggs of G. bosci and Kuntz (1916) has described their development, breeding in hinged oyster shells has often gone unnoticed. Hildebrand and Cable (1938) described development of Gobiosoma spp. from larvae taken in tow nets, and young taken in seines. Their data on earlier stages include both bosci and ginsburgi since they did not collect eggs. Mackin and Wray (1950) noted that spawning of G. bosci in oysters occurred during high mortality periods. They found goby spawning from late March to the middle of September in Louisiana. Pearse and Wharton (1938) found eggs and young in April and July in

Apalachicola Bay. Based on examination of gonads Hildebrand and Schroeder (1928) stated that spawning takes place from June to October in Chesapeake Bay. Pearson (1941) took pelagic young of *Gobiosoma* spp. from June to October during 1929 and 1930 but he found young most abundant in July and August. Nelson (1928) reports spawning in May and June in Delaware Bay beginning at temperatures of 68°F. Schwartz (1961) reports that *G. bosci* spawns in May through July in Chincoteague Bay. Perlmutter (1938) found larvae of *Gobiosoma* spp. during June and July in Peconic and Gardiners Bay, New York. Greely (1938) reported young and gravid females in July and August from the same area.

On the Seaside of the Eastern Shore of Virginia most spawning occurred from the middle of May through the first week in June (Fig. 2). This was during the beginning of the local oyster mortality period which lasted from the first week in May through about the end of June (Andrews, *et al.*, In Press). On the bayside spawning was confined largely to the middle of June to about the middle of August, although heavy mortality of oysters continued for two months thereafter. Temperatures during spawning were from 21 to 25°C on the Seaside, but were 24 to 31°C on the bayside, except one instance in 17.5°C. Spawning seems largely confined to the beginning of the mortality period, so it seems that some factor other than availability of spawning sites determines the end of spawning. A few late spawners were always found as late as August on the Seaside.

These late cases of spawning occurred with the smallest spawning males (29-39 mm). These males were probably members of a late spawn the previous year although the smallest could be from an early spring spawning the same year. These fish (29-33 mm in August) seem to be those which were 20-25 mm in May and June. Earlier spawning males were 39-49 mm on the Seaside and 47-58 mm on the Bayside.

A few individuals, 14 to 24 mm, taken in July 1961 were the earliest appearing Seaside young of the year. They were apparently from the May-June spawn. This group was represented by specimens 25-33 mm in August but they merged with smaller gobies from a later summer spawn. Gobies as small as 15-19 mm were found as late as November 30 at The Gulf.

On the bayside fewer smaller specimens were taken, and these did not appear until August, apparently from the July spawn. This group appeared to be 20-27 mm by September. This interpretation indicates slow growth through the winter months and rapid growth in the summer. The very largest (over 50 mm) seem to be at least two years old but there ~~is~~ are not enough data to prove this.

Spawning periods were determined by recording the presence of eggs in "boxes" usually taken from trays (Fig 2), but including some from natural bottoms. A parent (in nine instances the male, others not determined) was always present with the eggs. Nelson (1928) stated that the male guarded the eggs but he gave no data. Most eggs were confined to the inner recesses of the valves, and formed a dense mat over all but the edges of both shells. Many shells contained eggs only in the cup of the valve. Many of these were eyed embryos. During spawning on the Seaside in 1960 nearly all eggs seen were brought into the laboratory for hatching, but all died within a short time. The parent was not left with the eggs, and this apparently was a prerequisite for hatching. Several later batches hatched when a parent was left in the shell. While the presence of the parent may be of some protective value, the main function seems to be to fan the eggs constantly. Eggs left without a parent soon develop a varied fauna with hydroids, crustaceans, and annelids becoming abundant. Hildebrand and Cable (1938) found that eggs of *Hypsoblennius hentzi* and *Chasmodes bosquianus* would not hatch without the male, the eggs becoming fouled with hydroids and copepods. The parent lies within the shell with its head towards the open end and fans the eggs with undulating movements of its body and alternate movements of the left and right pectoral. Operculum movements are rapid, indicating rapid respiratory rates. Two hatchings in aquaria occurred at about 0930, but time of other hatchings are not known. One instance occurred when the eggs of *G. bosci* were continually fanned for about a day previous to hatching by a single adult *Chasmodes bosquianus*. The movements of the blenny in the shell were identical to that of goby males.

When eggs with a parent were in an aquarium with a vigorous aerator, the parent remained in the shell with little activity. When suddenly placed in oxygen rich water from ~~low oxygen content~~ water of low oxygen content, these gobies will undulate their bodies and move their pectorals and opercula in a manner similar to those in "boxes" with eggs. They do not always show this motion while the water is losing its oxygen but they often do. This motion was observed in natural waters in males with eggs as well as in aquaria. These facts suggest that there is a sharp oxygen gradient in the shells caused by egg respiration that the goby is constantly trying to overcome.

Newly hatched larvae were immediately pelagic, and adult gobies readily fed on these larvae, particularly those which ventured into lower aquarium levels. No data ~~was~~ were gathered on time of development, but it took 7 days from the death of the oyster to eyed embryos in the Machipongo River at temperatures near 20°C. Salinities where eggs were taken ranged from 15.4 to 32.9 °/oo.

Gobies inside shells are invariably pale, but rapidly turn dark when exposed to light. When subject to low oxygen content and subsequent death, they turn pale except for the dark fins. The characteristic stripes of the species are usually apparent although they are difficult to see during the very lightest and very darkest phases. Other oyster fishes also have some ability to change shades. In any given light intensity, except extremes, the shading of all individuals in a single container will not be the same and will vary from dark to light, but not usually as light as is possible.

Two ectoparasites were apparent on a few fishes, all but one from the lower Bayside (Table 4). A copepod, <u>Lernaeenicus radiatus</u> (LeSueur) was found on 8 out of 75 adult and 1 out of 184 young gobies from The

Gulf in 1961 and on one specimen from Cherrystone and one from Bradfords Bay. All had from 1 to 6 parasites on the head, body, and/or all the fins. A leech, *Myzobdella lugubris* Leidy, was found on two specimens from The Gulf, both attached to the first dorsal fin at the posterior base.

Since these gobies are secretive any predators are of interest. Darnell (1958) reports the food habits of several fishes in Lake Pontchartrian, Louisiana, some of which ate *G. bosci*. Of 176 croakers (*Micropogon*) examined, *G. bosci* was present in only two. Of 101 *Lagodon rhomboides* examined only 2 had eaten gobies. Other fishes which ate *G. bosci* were *Sciaenops ocellatus* and one *Morone interrupta* (= *Roccus mississippiensis*). The habitat of *G. bosci* in the lake was not stated, but the only large shellfish population there is of *Rangia cuneata*. Of 124 *Pogonias cromis* examined by Gunter (1945) 12 had eaten *G. bosci*; one ate as many as 23 individuals. He also reported this goby from *Sciaenops ocellatus*.

OPSANUS TAU (LINNAEUS, 1766). Toadfish were found in all areas studied. Occasional adults were seen, but most specimens taken with oysters were juveniles, which seem to be the common stage inhabiting oyster reefs. *O. tau* was as widespread as *G. bosci* but was not consistently so abundant. During July 1960 young toadfish were very abundant in Occohannock Creek, probably more so than any other species.

Gudger (1910) gave an account of the life history of *O. tau* and Breder (1941) gave data on the related *O. beta* Goode and Bean. The

American species of toadfishes were compared by Schultz and Reid (1937) who considered Atlantic and Gulf populations as separate species. Recently toadfish were used extensively in experimental studies according to Dovel (1960) who describes and pictures their larval development in detail.

O. tau apparently occurs largely in the saltier areas of Chesapeake Bay (Hildebrand and Schroeder, 1928) but we have taken young in Messongo Creek after a sharp drop in salinity to 2.8 °/oo due to Hurricane Donna. Toadfish were slightly more abundant than Chasmodes (Table 2), but the difference is not large enough to be significant.

Three small toadfish (24-52 mm) were taken from sponges (Halichondria and Lissodendoryx) at Wachapreague. This species has not been reported in sponges but a picture by Klingel (1955:688) shows a toadfish hiding beneath a sponge, which appears to be Microciona, in Chesapeake Bay. Breder (1939) reported small Opsanus beta from a sponge.

Large toadfish were often abundant in oyster trays in all areas, but they were usually found associated with hiding places in the wire rather than with the oysters.

CHASMODES BOSQUIANUS (LACÉPÈDE, 1800). This blenny is represented by populations on the Atlantic and Gulf coasts separated by the allopatric C. saburrae (Springer 1959).

C. bosquianus was not usually a common fish in bayside creeks, but it was abundant in The Gulf in the fall on oysters. It was also a very common fish in Zostera marina flats at the same locality. Although recorded in every locality it was largely found in medium salinities and was taken in a range of 19.9 to 31.2 °/oo. Except for a single specimen taken in Swash Bay on October 10, 1960, none was seen on the Seaside. Specimens from oysters are available from Chincoteague Bay, where it is apparently more common (Schwartz 1961).

On the Eastern Shore this blenny is most abundant on oysters in the lower Bayside creeks in Northampton County. An estimated 19 % of fish specimens from oysters in these creeks were C. bosquianus, and it was taken or seen in 19 out of 46 collections at regular stations. Hildebrand and Schroeder (1928) noted a male with eggs at Cherrystone on May 22, 1922, and Lugger (1877) noted this species with oysters in many parts of Chesapeake Bay. Eggs in a "box" with a male were taken on August 19, 1960 from Nandua Creek. When placed in a bucket of water about half of them hatched. Like G. bosci, they were pelagic. Unlike goby eggs they covered both valves completely and were rose-orange colored. Other males with eggs in "boxes" were taken from The Gulf on August 2, 1961, and August 24, 1961 when four were taken.

The most extensive study of the life history of C. bosquianus was done by Hildebrand and Cable (1938) who found eggs in oyster shells guarded by males.

GOBIESOX STRUMOSUS COPE, 1870. Clingfish were found in several bayside creeks but they were seldom common. It was the only species other than Tautoga taken through most of the winter, and it seemed most common in the fall. Records of G. strumosus are from September 8, 1959 through January 29, 1960. Specimens appeared at The Gulf as early as August 2, 1961, however. The writer recorded a similar seasonal distribution when specimens were taken from December through March on oysters and clam shells in Texas (Hoese, 1959). Clingfish apparently have a spotty distribution since ~~it was not ever~~ they were never seen on the Seaside or in 4 out of 7 Bayside creeks (Table 2). In the other 3 Bayside creeks ~~it was not common, probably~~ they probably made up ~~accounting for~~ less than 10 % of all fish specimens. This is perhaps another species common to oysters and grass flats as Hildebrand and Schroeder (1928) took numerous specimens from grassy bottom in the Rappahannock and Patuxent Rivers. It was taken only twice in collections in grass flats in The Gulf although it was found on oysters nearby. It has also been observed with oysters on the Cape Charles Jetty.

Springer and Woodburn (1960) note that G. strumosus is often left trapped at low tide. On July 2, 1959 the writer observed an association of these fishes in a tide pool on the Gulf of Mexico beach about 20 miles ENE of Gilchrist, Texas. This area of the Texas coast forms the western extremity of the Chenier Plain and contains numerous outcroppings of clay along the beach line. Many juvenile clingfish were on the sand of the tide pool, and many were attached to outcrops of clay. Adults were found inside the empty shells of Thais in the tide pool, and juveniles were attached to the outside of the shells. Two adults were taken in a seine pulled over a submerged clay bed in the shallow surf. Although numerous collections were made over a period of months along a 60 mile stretch of this beach this was the only place G. strumosus was found.

fishes around oysters and several were found in trays from September through March with the youngest appearing in August. It was recorded from Cherrystone, Gulf, Cobb Bay, and Swash Bay.

CENTROPRISTIS STRIATUS (LINNAEUS, 1758). As soon as tautogs disappeared from Swash Bay in early April, young sea bass appeared through October 1960 and 1961. Although not recorded from oysters at The Gulf, small sea bass are caught on hook and line in the summer. All specimens seen were immature. Arve (1960) noted the association of young sea bass and oysters.

LUTJANUS GRISEUS (LINNAEUS, 1758). This snapper is apparently a regular stray to Chesapeake Bay according to Hildebrand and Schroeder (1928). One small specimen (30 mm) was taken from oysters kept at Wachapreague on November 17, 1959 and one (36 mm) was taken from an oyster tray in The Gulf on November 20, 1959.

LAGODON RHOMBOIDES (LINNAEUS, 1766). Pinfish do not seem to be common in the area. Only one small specimen (31 mm) was taken with oysters at Wachapreague on August 3, 1960. A few others were seen in sports catches in the area. The writer did not note pinfish on oysters in Texas, although they are common around rocks. Caldwell (1957:134) noted pinfish avoiding oysters at one station in Cedar Key, Florida.

LACTOPHRYS TRIGONUS (LINNAEUS, 1758). Trunkfish are apparently unreported since Hildebrand and Schroeder (1928) found a specimen at

Cape Charles. One specimen, 7 mm, was captured by S. H. Hopkins on a reef in Hog Island Bay on June 23, 1960. One each was taken from Hungars Creek and The Gulf (32 mm) during the fall of 1959.

ARCHOSARGUS PROBATOCELPHALUS (WALBAUM, 1792). Sheepshead were not recorded on the Eastern Shore except for two taken by M. Castagna in Chincoteague Bay. Uhler and Lugger (1876) report that they are widespread around oyster regions of Chesapeake Bay, but Hildebrand and Schroeder (1928) note that sheepshead have declined in abundance. Sheepshead are apparently rare on the Eastern Shore. Sheepshead are more common in Texas and are often found in the vicinity of oysters. Simmons and Hoese (1959:77) noted sheepshead from both oysters and grass flats in Texas.

MYCTEROPERCA MICROLEPIS (GOODE AND BEAN, 1879). Several specimens of gags recently reported by Hoese, et al., (1961) from the Chesapeake area were taken in association with oysters.

ORTHOPRISTIS CHRYSOPTERUS (LINNAEUS, 1766). Young pigfish were common in oyster trays in August and September 1961 in Swash Bay, Cherrystone Creek, and The Gulf.

CHAETODON OCELLATUS BLOCH, 1787. One young butterfly fish was taken from an oyster tray in Bradfords Bay on October 20, 1961. Schwartz (1961) reported four specimens from Chincoteague Bay.

SOME ASPECTS OF FISHES IN THE OYSTER COMMUNITY.

Other species will undoubtedly be added to this list. Some fishes previously noted with oysters may have been accidental, and some may be real associates. Several species listed by Pearse and Wharton (1938), for example, may not be true oyster associates but are those sometimes accidentally taken with oysters. Such may be the cause of Behre's (1950) statement that *Gobionellus hastatus* was common on oyster beds in Barataria Bay, Louisiana. The writer (Simmons and Hoese 1959) found *G. hastatus* associated with the mud bottom of Cedar Bayou where there were no oysters. Similar observations have since been made in Galveston Bay. Oysters are grown on ~~various-type~~ bottoms of various types so a great many organisms associated with these respective bottoms will be taken with oysters.

Oyster reefs are often favorite fishing spots for sports fishermen and some of these possible associations between oysters and sports fish are not clear. *Pogonias cromis* and *Archosargus probatocephalus* feed on oysters and associated organisms, but no such known relation exists for *Cynoscion nebulosus*, which is commonly fished near reefs in the Gulf of Mexico. Food habit studies of this fish indicate a preference for more open water organisms (Guest and Gunter 1958). There may be reasons other than those presented why certain fishes are attracted to reefs.

The interesting paper of Arve (1960), who increased trap catches of certain species by oyster-shell plantings, deserves comment. He found four species, *Centropristis striatus*, *Roccus americanus*, *Sphoeroides maculatus*, and *Lagodon rhomboides* more abundant on planted than open bottom. Since all his specimens were trapped, those taken on open (control) bottom, which were few in number, would tend to be those species favoring shelter. Open water species, such as Paralichthys dentatus, might be less inclined to enter a trap, as his data show, than Centropristis which is usually associated with shelter. His data do not prove that plantings in general increase the total carrying capacity of bay fishes, but that they are selective for certain species, which apparently increase. Complementary studies with other sampling methods in open waters are needed. The idea of increasing substrate to improve fishing is used by numerous states, especially offshore, but there is no scientific study to show the value of such.

It is perhaps significant that oyster fish such as Gobiosoma bosci are always taken with live oysters but never with dead shell. In May 1961 numerous individuals were taken from Wachapreague in bags of about 1/2 live oysters and 1/2 "boxes". Spawning commenced in the "boxes". In nearby bags of all "boxes" no fish were taken through June. Korringa (1951) did not note many differences between the invertebrate fauna of live and dead shells.

Fishes form a distinct and important part of the oyster biocoenosis, partly because they are the most motile forms associated with oysters. This probably accounts for the little attention paid these fishes since most swim away when oysters are lifted out of the water. Some of the few species that can be considered true oyster associates are very abundant on reefs, and most of their life history seems to be associated with oysters. These few species that are intimately associated with oysters use reefs for shelter and often feed on organisms (*Caprella*, *Gammarus*, etc.) found in the epifauna of oysters (see Hildebrand and Schroeder 1928, for analyses of stomachs of species discussed). When oysters die, these fishes become scavengers and spawn inside the clean surfaces of hinged valves.

The fishes living on reefs of *Crassostrea virginica* are similar in many parts of the United States. *G. bosci* is found commonly on oysters in Virginia, North Carolina, Delaware, Maryland, Florida, Louisiana, and Texas. It is probably common on oysters throughout their range. *Chasmodes*, *Hypsoblennius*, and *Gobiesox* are known from oysters in some of these states, and probably occur on beds in all states within their range.

These fishes living in the oyster community and spawning within hinged valves of recently dead oysters are herein considered primary oyster associates. Populations of these species apparently confine nearly all of their benthic life history to oysters as far as is known, and they are not usually abundant in open waters. They are, however, abundant in other habitats which presumably offer environmental requirements similar to oyster reefs. The fishes recorded in this category for the Atlantic and Gulf coasts are presently *Gobiosoma bosci*, *G. ginsburgi*, *Chasmodes bosquianus*, *Hypsoblennius hentzi*, *H. ionthas*, and *Gobiesox strumosus*. Besides these fishes there is a group which often are found with oysters, but seem to be more pelagic and breed elsewhere, all being larger than primary associates. This group is not well defined, but there are fishes that feed on reefs or consistently use oysters for protection, while carrying on a sizeable portion of their life elsewhere. Species now considered in this group are Opsanus tau, O. beta, Centropristis striatus, Mycteroperca microlepis, Orthopristis chrysopterus, Pogonias cromis, Chaetodon ocellatus, and Tautoga onitis. Young Opsanus spp. are often as abundant as primary associates, and these young are found side by side with gobies and blennies, sometimes in the same oyster shell. Actually, spawning habits of Opsanus are similar to primary associates, especially in the degree of parental association. But being larger they spawn in shells larger than oysters and similar large objects. This shows the difficulty of categorizing these species to the degree of their relationship with oysters, but this should serve as a basis for comparing species and further study.

One striking fact about all these fishes is that many, if not all, have populations in grass flats (Table 5). The habitat of Gobiosoma bosci has been firmly entrenched in the literature as grass flats. In Virginia these populations are found in Zostera marina and sometimes Ruppia maritima. In the Gulf of Mexico these same species are known from Ruppia, Thalassia, and Diplantheria. Petersen (1917) reported young Gobius ruthensparri and G. minutus from Zostera. In contrast, many species found in grass flats are not known from oysters. Bairdiella chrysura (Lacepede), Apeltes quadracus (Mitchill), and Lucania parva (Baird and Girard), which are common in Zostera on the eastern shore of Chesapeake Bay, have apparently never been found with oysters.

Two reasons probably explain why oyster fishes can colonize grass flats. First, grassy areas should offer protection and shelter; second, many small invertebrates used as food by these fishes are common in grassy areas as well as on oysters. Similar reasons were given by Caldwell (1957:130) for populations of pinfish, *Lagodon rhomboides*, colonizing both grassy and rocky areas. All primary associates have pelagic larval stages which offer opportunities for wide dispersal.

Similarly some xanthid crabs (*Neopanope texana*) are abundant in eelgrass. Collections in The Gulf in a *Zostera* flat always yield large numbers of these crabs. Other organisms characteristic of oyster reefs are also abundant in eelgrass. Studies of oyster drills (*Urosalpinx* and *Eupleura*) by the Virginia Fisheries Laboratory included extensive sampling in beds of *Zostera* which support large populations of small drills (MacKenzie 1961). Incidentally, these muricids are unusual members of the oyster community in that they are almost ? the only members that do not reach oysters through the plankton. Korringa (1951) pointed out that the majority of oyster associates have planktonic stages.

Many primary associates have populations in rocky areas, on piling, and on other hard substrates. Springer and Woodburn (1960) found *G. bosci* on rocks as well as oysters, and the writer noted *Hypsoblennius ionthas* on both oysters and jetties in Texas.

Physically, coral reefs in tropical and warm temperate regions seem to be the closest natural counterpart of oyster reefs. Many species within the two habitats are closely related. For example, Springer and Woodburn (1960:66) state that Opsanus beta is replaced offshore on reefs in the Gulf of Mexico by Opsanus pardus (Goode and Bean). They also list two gobies and one blenny from offshore reefs. Modification of pelvic fins as in the Blenniidae, Gobiidae, and Gobiesocidae is common to all primary oyster associates, and representatives of these same families are common on coral reefs. But coral reefs contain a much wider variety of species.

Several oyster fishes and mud crabs live as inquilines in sponges. Actually, by definition, many fish-mollusc associations are probably cases of quasi-inquilinism or commensalism and Gobiosoma bosci seems more dependent on oysters than it is on sponges. The one known instance of Gobiosoma within a live oyster considered with its normal more or less free-living habits suggest that G. bosci is barely on the free-living side of the borderline between inquilinism (parasitism ?) and free-living.

The figures for relative abundance of oyster fishes were all taken from subtidal tray oysters and in some areas this contrasted with that on natural reefs nearby. For example, at The Gulf, only 55 % of specimens from subtidal plants and trays in 1961 were G. bosci, but on native oysters it was almost the only fish present. It would seem that G. bosci is the only true oyster fish because it is the only fish found year-round on oysters everywhere and very often is the only fish present. In high salinities it dominates the intertidal zone and in low salinities the subtidal zone. This distribution of dominance follows that of native oysters (i.e.- intertidal in high salinities, subtidal in low). Coupled with the fact that this is the only species that spawns in rhythm with local oyster mortality, it appears that G. bosci has lived with oysters for a considerable period of time.

Since neither Chasmodes bosquianus nor Hypsoblennius hentzi is found with oysters until spawning season in The Gulf, they may be more closely tied to eelgrass flats where they live prior to spawning. The rarity of these species on the Seaside where eelgrass is absent supports such a conclusion, but this absence may also be due to lack of oyster mortality during the spawning season or to the lack of larger oysters for these larger associates. Gobiesox strumosus also was not found on oysters until late summer and fall, but its habitat previous to this time is not known. It is listed as a year-round oyster inhabitant by Schwartz (1961). Nevertheless, these latter species, particularly the blennies, seem to be relatively recent invaders of oyster reefs, especially in numbers, since subtidal plantings by man.

SPAWNING OF FISHES RELATED TO OYSTER MORTALITY

No oyster fish spawning was noted outside of hinged shells of oysters, and reported instances are uncommon. Since oysters form the largest mollusc community in the estuarine epifauna they undoubtedly have the most mortality and provide the most spawning sites.

In lower salinity areas where oysters are native subtidally, numerous sites are available during the spawning season. However, in high salinities oysters are native to the intertidal zone and before extensive subtidal plantings by man, spawning sites were presumably scarce. Spawning was usually found in subtidal oysters although extremely low tides rarely left the eggs exposed. It is interesting to speculate on high salinity spawning sites before the coming of man. Either a few oysters washed or were carried by ice to subtidal zones or other subtidal molluscs or oysters in intertidal pools which retain water were used. Another possibility is that spawning occurred when a series of extremely high tides failed to expose the lower levels of normally intertidal reefs. Such a case occurred in the Machipongo River during May 1960 when tides remained high for about a week never exposing a group of normally intertidal oysters. Spawning by G. bosci then commenced.

A strong correlation between the beginning of oyster mortality and spawning of Gobiosoma bosci is apparent (Fig. 2). However, a few individuals spawn relatively late in the season on the Seaside. These are all smaller gobies which may become sexually mature late in the spawning season.

Most oyster mortality on the Seaside occurs during May and June and the peak of G. bosci spawning occurs in these months with only scattered examples thereafter. On the bayside mortalities are delayed until July and do not reach a peak until late August or early September (Andrews, et al., In Press; Fig. 2). G. bosci spawning begins as early as there is mortality on the Bayside, even as early as May, but occurs largely in July and August with only scattered examples thereafter.

Therefore, spawning seems largely restricted to the beginning of the major mortality period of the region. Unless there are racial differences in Seaside and Chesapeake Bay populations, spawning is relatively independent of temperature above a certain level. This seems possible since some Bayside spawning commences as early as some mortality starts even though temperatures are far below that of the spawning peak. Also the percentage of available sites with eggs decreases with rising temperatures. G. bosci spawning in the Gulf of Mexico (Pearse and Wharton 1938, Mackin and Wray 1950) occurs as early as oyster mortality begins (March-April) along with earlier high temperatures. Whereas temperature is important to goby spawning, if only indirectly by controlling oyster mortality, spawning seems relatively independent of temperature for fishes in general.

Nelson (1928) reports spawning of G. bosci in Delaware Bay in May and June, which correlates with the spawning season on the Seaside of Virginia. He did not present any data about oyster mortality but said spawning sometimes occurred in clams. A spawning season of May to July was reported by Schwartz (1961) in Chincoteague Bay.

Pearson (1941) recorded pelagic larvae of Gobiosoma in plankton tows from June through October, 1929 and 1930 in Chesapeake Bay, but he found them most abundant in July and August. Such a distribution of larvae is expected from recent observations on spawning which indicate a peak in July and August. Spawning in 1960 and 1961 apparently was similar to that in 1929 and 1930, and this could be the result of similar mortality patterns of oysters during the four years.

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