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A REVIEW OF PUBLISHED WORK ON *CRASSOSTREA ARIAKENSIS*

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INTRODUCTION

Field research on the Asian (Suminoe) oyster, *C. ariakensis*, began in 1998 at the Virginia Institute of Marine Science (VIMS) in response to a resolution from the Virginia Legislature to initiate investigations on alternative species. All field trials have used sterile triploids. Initial research indicated promising performances in *C. ariakensis* in a variety of salinities for growth and disease resistance (Calvo et al. 2001). Research on this species continues at VIMS today, but in the meantime, the Virginia Seafood Council has run two commercial trials of *C. ariakensis* on their own with similar promising results. They have proposed a third for 2003 with about a million triploid *C. ariakensis*. The direction taken by industry clearly indicates a desire to proceed with larger and larger scale-ups of aquaculture using triploids. This notion was addressed in a symposium staged in 2001 (Hallerman et al. 2002) where the general consensus found that "it is difficult to consider the risks of aquaculture of triploid (infertile) *C. ariakensis* as separate from the risks of diploid (fertile) *C. ariakensis*. That is, there was consensus that triploid aquaculture would inevitably lead to some introduction of reproductive individuals in the Bay, with unknown outcomes for population growth." Part of the difficulty in assessing the risk of such a scenario comes from the inherent difficulty of predicting the consequences of an introduction generally. Another difficulty of assessing risk, especially for *C. ariakensis*, is the lack of information on this species.

The aim of this review was to provide an unabridged overview of the published works on this species. We may have missed some references that were obscure or indirectly referred to *C. ariakensis*. Many of the works on *C. ariakensis* were in other languages, principally Chinese. For Chinese articles, they were translated and are presented in somewhat more detail than those in English. Some were obtained while traveling to specific laboratories in China and would otherwise be difficult to obtain. We were as complete as possible given the timely need for this review.

We present the information uncritically. That is, we present the contents of the articles without analysis. Partly this is the result of space constraints. More importantly, it is unclear that data reported always apply to *C. ariakensis*. Morphologic confusion is common with *Crassostrea* species. For example, a considerable number of reports of *C. ariakensis* occur in west India and Pakistan, geographically isolated from the main populations in Japan, China, and Korea. It seems unlikely that this is the same species, but to judge so *a priori* would be to leave out this information. We expect scientists to consider the data critically and test it if appropriate.

The information we collected is organized into general categories so that one work may be cited repeatedly if it crosses categories. The content in each category in no way implies the importance of this information, merely what has been done. Conversely, categories missing information reflect the absence of data.

NOMENCLATURE

Harry (1981) described the history of the genus name *Crassostrea* Sacco, 1897 as follows: Over half a century ago Lamy (1929–1930) surveyed the living oysters and put all species in the genus *Ostrea* Linnaeus, 1758, including *Crassostrea ariakensis*. But since 1930, other authors, chiefly those interested in the commercial production of oysters (e.g., Thompson 1954), have separated *Crassostrea* from *Ostrea* on the basis that the promyal passage on the right side of the excurrent mantle chamber is closed in *Ostrea* and open in *Crassostrea*. Other differences on morphology and anatomy between these two genera can be found in Ahmed (1971 and 1975), Glude (1971), and Stenzel (1971). In this review, please note that *Ostrea* is cited from many old references.

Nomenclature is confusing for *C. ariakensis* (Carriker & Gaffney 1996) because the traditional oyster classification methods rely mainly on conchological characters, i.e., external and internal morphology of the shell, which express high phenotypic plasticity among environments (Hirase 1930). In addition, oyster eggs are fertilized in mass spawns that increase the possibility of hybridization and promote high variation (Guan & Li 1986). Therefore, species with the same name might be genetically distinct whereas the ones with different scientific names might be genetically the same. Species variously called *C. rivularis*, *discoidea*, *palmipes*, or *paulucciae* in previous literature (Carriker & Gaffney 1996) might be the same as the species we call *C. ariakensis* today. In general, it is accepted that *rivularis* is synonymous with *ariakensis*, although it is still possible that *rivularis*/*ariakensis* was misclassified in certain publications. This review includes all the available publications with the above mentioned species names.

The authorship of *ariakensis* has been credited to Fujita (1913). However, we are confused by the description of Wakiya (1930) on the origin of the name *ariakensis*. He wrote his reference as "*O. ariakensis* (Wakiya M. S.) Fujita, ... 1913." Harry (1981) assumed that "Fujita proposed the name in 1913, based on a manuscript of Wakiya." Coan et al. (1995) seemed to agree by giving the reference in a way of "Fujita, 1913... ex Wakiya MS." Who proposed the name *ariakensis* first, Fujita or Wakiya? We were not able to locate Fujita (1913), so we cannot answer that question for sure. According to our publication collection, the species name *ariakensis* was not referred to as frequently as *rivularis* before mid 1990s, but it has been widely referred to in recent publications.

The history of species name *rivularis* can be traced back to 1861, when Gould described a new species called *Ostrea rivularis*, which in Latin means "oysters in small brooks." His original description was written in Latin. Translated to English, the shells he observed were "discoid, oblong, slender; inferior valve thick, purple, with remotely radiate ribs and fortified small tubes; superior valve simple, with ramosing less purple veins; cavity minimally deep, ovate; white ash-colored broad margin, weak hinge." He emphasized "the rays of the little tubes below, and the veins

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above, are unusually clear, distinctive characters." The dimension of the observed shells was "Diam. 60; Lat. 10 millim." It "inhabits the China Seas, as indicated by shells adhering to it."

There is serious ambiguity in the source of Gould's specimen. The title of his article indicates that his description was based on the collection of "the North Pacific Exploring Expedition," whereas according to Hirase (1930), it was based on a single specimen from China in Dunker's collection. Hirase did not explain whom Dunker is except for a reference listed as Dunker (1882). Several other authors mentioned China as the source of Gould's specimen (Ahmed 1971, Galtsoff 1964), but no additional references were offered for further confirmation. Hirase (1930) also questioned the completeness of Gould's description and its value for identification because it seems based on a single specimen, which seems to be comparatively young according to its size (60 mm). Gould's description of *rivularis* and those of others (see Morphology section) are incompatible. Thus, it is quite possible that *rivularis* of Gould (1861) is different from the species we call *rivularis* or *ariakensis* today.

O. (C.) rivularis Gould has been widely applied to oysters with similar conchological characters in many Pacific coastal countries, such as Japan, China, Pakistan, and India. Its taxonomic status in each country is still muddled. A review is summarized below.

In Japan, Ariake-gaki, Suminoe-gaki, and Kaki ("gaki" in Japanese means oyster) were some common names for *O. rivularis* (Amemiya 1928). This species was once classified as *O. gigas* by Fujimori (1929) but this was refuted by Taki (1933) and Imai and Hatanaka (1949). Wakiya (1930) surmised that *O. rivularis* of his in 1915 (Wakiya 1915) and that of Amemiya (1928) was the same as *O. ariakensis*, whereas the *O. rivularis* described by Lischke (1871) seemed to be the young of *O. ariakensis*.

In Pakistan, Awati and Rai (1931) indicated two names for the same species, *O. discoidea* and *O. rivularis*. Reeve (1871) described *O. discoidea* based on specimens from Fuji Island and New Zealand, but Ahmed (1971) stated that the figure and the shell characters published by Reeve were different from that of *O. discoidea*. According to Ahmed, Reeve's *O. discoidea* is rounded and flat to the extent that it looks like the windowpane oyster, *Placuna placenta* Linne, 1758, which is abundant in lagoons of Philippines and South East Asia (Abbott & Dance 1986). Based on his own experience, Ahmed believed that *O. discoidea* is not distinguishable from *C. rivularis*.

In China, the common name for *O. (C.) rivularis* is Jinjiang-muli ("jinjiang" in Chinese means "close to river" and "muli" means oyster). One of the long-standing debates on oyster classification involves two morphologically very similar variants that occur in the Pearl (Zhujiang) River estuary. One is called "white meat" oyster and the other is "red meat." Very experienced oyster farmers can separate these two variants by external appearance and the color of the soft body. Fei (1928) believed that both are *O. gigas*. However, Zhang and Lou (1956a) identified "white meat" as *O. rivularis* and "red meat" as a variant. The "white meat" oyster is considered better than the "red meat" because of meat quality and productivity in aquaculture, thus has higher commercial value. The "red meat" oyster is apparently more resistant to harsh conditions according to observations of it in culture (Guan & Li 1986). Further investigations by other researchers revealed other differences. A comparative study on the physiologic and biochemical indexes (Guan & Li 1986), such as oxygen consumption rate, fatty acid composition, and amino acid composition, demonstrated sufficient differences in physiology to suspect that

genetic differences are likely. Anatomically, Li (1989) found a difference in the connection of the body with the gills. In "white meat" both the left and right epibranchial chamber connect with the promyal chamber, whereas in "red meat" only the right epibranchial chamber connects with the promyal chamber. He believed the two belong to two different species. A study on genetic variation using starch gel electrophoresis (Li et al. 1988) demonstrated that they should belong to different species because their genetic identity was low ($I = 0.548$). The estimated divergence time of the two is 3×10^6 years. The comparison of genetic similarities and genetic distances suggests that "white meat" is *C. rivularis* and "red meat" is probably *C. iredalei*. Guan and Zheng (1990) studied the esterase isoenzyme of the two groups by polypropylene amide gel electrophoresis and agreed that they are different species. Above all, it was generally agreed that "white meat" is *C. rivularis*, but whether "red meat" is *C. iredalei* is still unconfirmed.

MORPHOLOGY

Conchological Characters

References on conchological characters of naturally occurring *C. ariakensis* come from three countries: China, Japan, and India. References from the United States (Pacific Northwest) are also included because the seed were introduced from Japan. Reports containing conchological data are listed individually following a general review to compare and contrast characters of what are called *O. (C.) rivularis*, now *C. ariakensis*. The major conchological characters presented in these reports are size; thickness and shape of the valves; outer structure of the valves; comparison between the left and right valve; color of outer and inner surface; size and color of ligament; color, size and position of the muscle scar; and hinge structure (Table 1).

Review

In China, it is commonly observed that valves of *Ostrea (Crassostrea) rivularis* are large and thick with varying shapes, basically round but sometimes elongated into oval, oblong, and even triangular shapes. The right valve is thinner, flatter, and smaller than the left. Both valves are covered with concentric lamellae (fluted shell margins on the external shell), with fewer layers of, but stronger, lamellae on the left valve. Density and shape of lamellae varies by age class, which are thicker and more layered in older oysters (Zhang & Lou 1956a, Zhang et al. 1960). Color of lamellae or the outer surface of valves ranged from gray, yellowish brown, brown, to purple or dark purple. Dark purple coloration is apparent in *C. ariakensis* grown in high-salinity areas of Chesapeake Bay (Zhou & Allen, unpubl.). The inner surface of valves is white or grayish white, purple on the edge. The ligament area is short and wide, and the ligament is usually purple black. The muscle scar is very large, mostly oval or kidney shaped, located in the mid-dorsal area, purple or light yellow in color.

The coloration of valves and muscle scars of *C. ariakensis* described in reports from Japan is different from those from China. In Japan, the outer surface of the valves was described as cream-buff or white, streaked with radial chocolate bands, violet bands, or almost uniformly violet (Hirase 1930, Torigoe, 1981, Wakiya 1929). The inner surface of the valves was strongly lustrous or partly opalescent (Hirase, 1930, Torigoe 1981). The muscle scar was usually white or sometimes stained with olive-ocher spots or

TABLE 1.
Characteristics of oysters by citation.

Gould (1861), China, <i>O. rivularis</i>	
Valve shape size:	Discoid, oblong, slender.
Left, right valve:	Inferior valve thick, purple, with remotely radiating ribs and fortified small tubes; superior valve simple, with ramifying less purple veins; cavity minimally deep, ovate.
Shell color outer:	Purple; white ash-colored broad margin.
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	Weak.
Zhang and Lou (1959), China, <i>O. (C.) rivularis</i> , includes figure(s)	
Valve shape size:	Large and thick with various shapes, round, oval, triangle, and oblong; concentric scarce lamellae on outer surface.
Left, right valve:	—
Shell color outer:	Yellowish brown.
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	—
Zhang and Lou (1956a), China, <i>O. (C.) rivularis</i> , includes figure(s)	
Zhang et al. (1960), South China, <i>O. rivularis</i> , includes figure(s)	
Similar descriptions from the above two references are combined as follows.	
Valve shape size:	Valves large and thick with various shapes, round, oval, triangle, and oblong.
Left, right valve:	Right valve flatter and smaller than the left one, with yellowish brown or dark purple concentric lamellae on its surface. In 1 to 2-y-old individuals, lamellae thin, flat, and brittle, sometimes dissociated; on valves older than 2 ys old, flat but sometimes with tiny wavy shape at the edge; on valves several years old, thickly layered, strong as stone. Left valve is larger and thicker than right valve, stronger but fewer layers of lamellae. A few samples had inconspicuous radiating ribs or plication.
Shell color outer:	Gray, purple, or brown.
Shell color inner:	White, grayish purple on the edge.
Ligament:	Ligament purple black. Ligament groove short and wide, like an ox horn. The length from the ligament to anterior is one sixth to one fourth of shell height.
Muscle scar:	Muscle scar very large, light yellow, irregular shape, mostly oval or kidney shaped, located in the middle of the dorsal area.
Hinge:	—
Cai et al. (1979), China, <i>O. rivularis</i> , includes figure(s)	
Valve shape size:	Shells large and thick with various shapes, such as round, oval, triangle and oblong.
Left, right valve:	Right shell flatter and smaller than the left shell, with yellowish brown or dark purple lamellae on its surface. The lamellae are thin and flat, with not much layers and no radiating ribs, but usually with protuberance. The left shell is larger and thicker with irregular shape and similar lamellae as the right shell.
Shell color outer:	Yellowish brown or dark purple.
Shell color inner:	White or grayish white.
Ligament:	Ligament purple black, ligament groove short and wide.
Muscle scar:	Muscle scar large, oval or kidney shaped, located in the middle of the dorsal area.
Hinge:	No denticulate on the hinge.
Li and Qi (1994), China, <i>C. rivularis</i> , includes figure(s)	
Valve shape size:	Large variation in shell shape, usually oval or oblong.
Left, right valve:	Concentric lamellae tend to coalesce, no radiant ribs.
Shell color outer:	Light purple.
Shell color inner:	White.
Ligament:	Wide ligament groove.
Muscle scar:	Light purple.
Hinge:	—
Amemiya (1928), Japan, <i>O. rivularis</i> , includes figure(s)	
Valve shape size:	It is either circular or oval in form, pronounced elongation as found in <i>O. gigas</i> is absent.
Left, right valve:	—
Shell color outer:	—
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	—
Cahn (1950), Japan, <i>O. rivularis</i> , includes figure(s)	
Valve shape size:	Round, flat, smooth surfaced, plates thin, almost smooth, shell thick.
Left, right valve:	—
Shell color outer:	Pale pink, radiating burnt lake strikes on shells.
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	—
Hirase (1930), Japan, <i>O. (C.) rivularis</i> , includes figure(s)	
Valve shape size:	Orbicular, oval, elongated oval, though appearing somewhat subtriangular because of its rather long umbo. There are many intermediate forms, but on the whole the specimens are oval. The shell is fairly strong and thick, though not to the extent of <i>C. gigas</i> .

continued on next page

TABLE 1.
continued

Left, right valve:	The right valve is somewhat smaller. The concavity of the left valve is larger. The anterior depression of the left valve is very obscure. The lamellae of the right valve are somewhat thin and almost smooth, and distinct placcations are not apparent, but sometimes the lamellae are covered with somewhat irregularly tubular projections. It is noteworthy that smooth lamellae are more common in the young than in the adult. The color is cream-buff with many radial chocolate bands, but in adults these bands are fused into larger ones; their arrangement differs in each individual. In the left valve, the lamellae are generally indistinct, and may be close together or separate.
Shell color outer:	The common color is pale rhodonite pink with radiating "burnt lake" striae.
Shell color inner:	The inner shell surface is generally white with strong luster, sometimes with a yellowish central part.
Ligament:	The ligament is "burnt lake" or black.
Muscle scar:	The muscular impressions, elongated oblong with concave anterior side, are equal in size for the two valves and rather large in porportion to the inner shell area. The color of the impression is white, or rarely marked with olive-ocher spots; its surface is almost flat.
Hinge:	—
Imai (1978), Japan, <i>C. rivularis</i> , includes figure(s)	
Valve shape size:	Round or elliptical
Left, right valve:	The lower shell is shallow and the umbo cavity below the hinge plate is very small.
Shell color outer:	The part near the hinge plate in the upper shell is violet-brown in color.
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	—
Kira (1962), Japan, <i>C. rivularis</i>	
Valve shape size:	Has a large and rather flat shell, of which the surface bears very coarse and widely spaced concentric lamellae.
Left, right valve:	—
Shell color outer:	—
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	—
Torigoc (1981), Japan, <i>C. ariakensis</i> , includes figure(s)	
Valve shape size:	Large sized (height 200 mm × length 112 mm, Hirase 1930). Outline orbicular to long spatulate form, mostly tongue form, subequivalves. Attachment area is small to medium, commonly behind the umbonal area.
Left, right valve:	Both valves flat, but left valve weakly concave. Both valves have very faint dichotomous radial ribs, left valve more conspicuous than right valve. Growth squamae flat and stretched parallel to the grow lines. No commissural plication, or very weak even if present. Commissural shelf small to medium. Umbonal cavity shallow. No chomata. The dorso-ventral section has chalky deposits between solid shell layers and no hollow chambers. Both valves are thinner than those of <i>C. gigas</i> , so chalky layers are very thin. The parts of chalky deposits are often intruded by worms.
Shell color outer:	"White in ground" (sic) color with pale purple streaks radiating from umbo.
Shell color inner:	Chalky white or partly opalescent.
Ligament:	—
Muscle scar:	Reniform, dorso-anterior border concaved and close to ventro-posterior shell margin from the center of the valve. Lustrous white or sometimes with purple patches, particularly on right valve.
Hinge:	—
Wakiya (1929), Japan, <i>Ostrea ariakensis</i>	
Valve shape size:	Shell usually circular or oval in shape. However, its shape varies considerably according to the hardness of the bottom on which it lives. When found imbedded in soft mud it has an extremely elongated shell so that it is very difficult to distinguish it from that of <i>O. laperousi</i> found on a mud bottom of lower salinity, only differing from <i>O. laperousi</i> in having the hinge of lower valve not very long and subequal to that of the upper one. <i>O. rivularis</i> Gould has, according to the original description, its lower valve provided with radiating, tube-shaped ribs set distantly. Therefore the species in which the ribs are absent from the lower valve or only very weakly developed, if present at all, cannot be the species of Gould.
Left, right valve:	Lamellae imbricated rather compactly, lower valve concave, not provided with ribs; upper valve flat, length of hinge nearly equal to that of lower valve. Occasionally, weakly developed ribs are observed on the lower valve of the young of the species, but never on full-grown ones.
Shell color outer:	Whitish and streaked with violet, or almost uniformly violet.
Shell color inner:	Lead white; muscular impression faint, usually not specially colored but sometimes stained purple.
Ligament:	—
Muscle scar:	—
Hinge:	The hinge of the lower valve not so long as, as long as or a little longer than the breadth; no umbonal cavity below margin of hinge.
Coan et al. (1995), USA, <i>C. ariakensis</i> , includes figure(s)	
Valve shape size:	Subtrigonal, flared ventrally, heavier and more rounded than <i>C. gigas</i> .
Left, right valve:	Left valve moderately concave, with white to pale pink lamellae; right valve moderately flattend, with many thin commarginal lamellae, sometimes with dark brown to purple radial color bands. Both valves with densely layered, thin lamellae.
Shell color outer:	—
Shell color inner:	—
Ligament:	—
Muscle scar:	White to purple to olive.
Hinge:	—
Galtsoff (1964), USA, <i>C. rivularis</i> , includes figure(s)	
Valve shape size:	Orbicular strong and large.
Left, right valve:	Left, lower valve slightly concave, upper valve shorter and flat. The left valve has generally indistinct lamellae of pale pink color with radiating striae. The lamellae of the right valve are thin and most smooth, sometimes covered with tubular projections.

continued on next page

TABLE 1.
continued

Shell color outer:	The color of the right valve is cream buff with many radial chocolate bands, their arrangements greatly variable.
Shell color inner:	—
Ligament:	—
Muscle scar:	Situated near the center or a little dorsally, is white, occasionally with olive-ochre spots.
Hinge:	—
Langdon and Robinson (1996), USA, <i>C. ariakensis</i> , includes figure(s)	
Valve shape size:	This species differs from the Pacific oyster morphologically in that the shell is typically more rounded and the edges of shell layers are flat and not rippled like those of Pacific oysters (Torigo, 1981).
Left, right valve:	—
Shell color outer:	—
Shell color inner:	—
Ligament:	—
Muscle scar:	—
Hinge:	—
Awati and Rai (1931), India, <i>O. discoidea</i> or <i>O. rivularis</i>	
Valve shape size:	Shell flat and of large size, rounded, foliaceous with conspicuous lines of growth.
Left, right valve:	Lower valve lightly concave, upper valve of the same size and shape as the lower, slightly convex.
Shell color outer:	—
Shell color inner:	Clear and nacreous.
Ligament:	Ligament area small.
Muscle scar:	Oblong with a cloudy white or smoky white color.
Hinge:	No denticulations.
Rao (1987), India, <i>C. rivularis</i> , includes figure(s)	
Valve shape size:	Shallow shell cavity
Left, right valve:	—
Shell color outer:	Imai (1978) has stated that the hinge part of the shell of <i>C. rivularis</i> is violet brown in color. The coloration may be caused by ecological conditions such as luxuriant growth of seaweeds in the vicinity or other factors and should not be considered of taxonomic importance.
Shell color inner:	—
Ligament:	—
Muscle scar:	Oblong white.
Hinge:	—
Patel and Jetani (1991), India, <i>C. rivularis</i>	
Valve shape size:	Shell oval, narrow at anterior end and broader with posterior end.
Left, right valve:	Left valve has deep radial ridges from the hinge and tightly inter locked with upper right valve.
Shell color outer:	Pink to brownish with tints.
Shell color inner:	—
Ligament:	Having narrow hinge-ligament
Muscle scar:	White.
Hinge:	Having narrow hinge-ligament.

purple patches (Hirase 1930, Torigoe 1981, Wakiya 1929). Rao (1987) thought the difference in coloration might be caused by ecological conditions and therefore not considered a character of taxonomic importance. Reports from the United States are consistent with reports from Japan for coloration, which indicates that at least some part of coloration might be caused by genetic factors. *O. (C.) rivularis* from India are similarly described. Coloration of the inner surface of the valves and the muscle scar are close to Japanese reports.

Reports from Japan were often comparative between *C. ariakensis* and other species, such as *O. (C.) gigas* (Amemiya 1928, Hirase 1930, Torigoe, 1981) and *O. laperousi* (Wakiya 1929). *O. (C.) gigas* were believed to have stronger, thicker, and more elongated shells than *O. (C.) rivularis*, whereas *O. rivularis* is very difficult to distinguish from *O. laperousi* found on muddy bottom in lower salinity. *O. rivularis* differs from *O. laperousi* by having the hinge of the lower valve not very long and subequal to that of the upper one. Japanese reports agree that *O. (C.) ariakensis* has flat valves, with the left one weakly concave (Cahn 1950, Kira 1962, Torigoe 1981). Wakiya (1929) thought the various shapes of *O. ariakensis* were influenced by the hardness of the bottom because the ones with extremely elongated shells were found imbedded in soft mud. This is also a character of other *Crassostrea* spp. (Galstoff 1964).

The most confusing character through this review has been what Gould (1861), who first named *O. rivularis*, described as

remotely radiating ribs and fortified small tubes on the outer surface of left valve and veins on right valve. He emphasized that these are usually clear, distinctive characters of this species. His observation was based on a sample from China. However, no reports from China agreed with his description of such characters. Cai et al. (1979) and Li and Qi (1994) observed no radiating ribs in this species. Based on a large-scale investigation of oyster species all along the Chinese coast, Zhang and Lou (1956a) described inconspicuous radiating ribs or plication in a few samples of *O. (C.) rivularis*. Only one report from India described deep radial ridges from the hinge on the left valve (Patel & Jetani 1991), although the origin of the background specimen was unknown. From Japan, similar characteristics were described as indistinctive or occurring at very low frequency. Hirase (1930) and Galstoff (1964) mention that the lamellae are sometimes covered with tubular projections. Hirase (1930) and Cahn (1950) mentioned "radiating burnt lake strikes," which might or might not be the same feature we are discussing here. Torigoe's (1981) report said "both valves have very faint dichotomous radial ribs, left valve more conspicuous than right valve." Wakiya (1929) is more helpful in clarifying this confusion. He stated this species was "not provided with ribs...occasionally, weakly developed ribs are observed on the lower valve of young of the species (*Ostrea ariakensis*), but never on full-grown ones." Either Gould's original descriptions

were inappropriate for adult *C. ariakensis*, or he described a different species (Wakiya 1929). The latter possibility is quite high if Gould did get his specimen from China because there are around 20 oyster species there (Zhang & Lou 1956b, Cai & Li 1990, Li & Qi 1994, Guo et al. 1999), and classification based completely on morphologic characters is questionable.

ANATOMIC CHARACTERS

Review

Anatomic characters were not studied as broadly and completely as conchological ones. Reports mainly come from Japan and China. Researchers had different emphases in their anatomic studies. The only character described by more than one researcher is the mantle. Hirase (1930), Zhang et al. (1960), and Galtsoff (1964) were in agreement that the inner row of the mantle tentacles is aligned while the outer row is irregular. Details of anatomic characters are given in Table 2.

GEOGRAPHIC DISTRIBUTION

From an overview of the literature, *C. ariakensis* seems to have a wide geographical range. According to Kuroda and Habe (1952), *O. rivularis* encompassed latitudes 12–34°N, which covers the area from southern Japan to southern India. Ranson (1967) listed sources of *C. ariakensis* specimens in museums around the world, coming from Southern Japan to coasts bordering the South China Sea, including Hong Kong, Vietnam, and Sabah (formerly North Borneo), Malaysia. Several authors (Wakiya 1929, Cahn 1950, Kira 1962, Coan et al. 1995) mentioned its distribution in Korea. Anon (1996) mentioned that *C. rivularis* was also found from the Philippines and Taiwan to Thailand. Above all, this species seems to occur all along the west coast of the Pacific Ocean, from southern Japan to Pakistan (Angell 1986). Sparks (1965) even reported that *C. rivularis* was indigenous to Kenya. However, for most areas outside of Japan and China, no references are available to confirm these observations genetically as *C. ariakensis*.

Quite a few literature reports are available listing specific locations in a country where this species occurs naturally. Below we

TABLE 2.

Anatomical characteristics of oysters by citation.

Hirase (1930), Japan, *O. (C.) rivularis*

Mantle—In a specimen whose length and altitude are 96 mm and 45 mm, respectively, the mantle is united by the anterior 21 mm, or 0.22 of the body length. There is no siphon. The mantle margin is dark nigrosine violet or pinkish vinaceous, and the tentacles are arranged in two rows, the outer consisting of tentacles of irregular size and the inner of slender single tentacles. Fine tendons radiate from the posterior sides of the adductor muscle as usual.

Adductor muscle—The adductor muscle measures 20 mm in altitude and 22 mm in breadth and is suborbicular, with somewhat concave anterior face and convex posterior face. The distance between the anterior end of the adductor muscle and the anterior end of the body is 52 mm. A small portion of the posterior part of the adductor muscle is white as usual.

Heart—The pericardium, contiguous to the anterior face of the adductor muscle, is oval and measures 19 mm in altitude and 6 mm in breadth. The heart runs obliquely from the antero-dorsal corner of the pericardium to the postero-ventral corner. The ventricle and the auricles are both flesh color. The ventricle measures 8 mm in altitude and 6 mm in breadth, while one of the auricles measures 8 mm in altitude and 3 mm in breadth.

Ctenidium—The posterior end of the ctenidium curls up along the posterior face of the adductor muscle.

Alimentary system—The palps are as usually found in *Crassostrea*. The rectum begins at the dorsal region of the pericardium and ends just above the posterior end of the adductor muscle. About 3 mm of the terminal portion is free, differing from other oysters of this subgenus and shorter than in *Neopycnodonte cochlear*, whose free portion is 5 mm. The anal end has a ring. The distance between the mouth and the anus is 55 mm, its ratio to body length being 0.57.

Imai (1978), Japan, *C. rivularis*

C. ariakensis differs from *C. gigas* in that a part of the rectum and anus are away for the soft parts.

Torigoe (1981), Japan, *Crassostrea ariakensis*

Soft parts are similar to *C. gigas* but the coloration of soft parts is the palest of Japanese *Crassostrea* species.

Zhang et al. (1960), South China, *O. rivularis*

Mantle—The inner row of the mantle tentacles is aligned while the outer row is irregular.

Heart—Heart chamber is flesh pink.

Li (1989), China, *C. rivularis*

Promyal chamber—The left and right epibranchial chambers connect with the promyal chamber all together. In the cross section of this type, the ascending lamellae of the left and right outer demibranch attach to the mantle, whereas the other part of gills are free in the mantle cavity. The whole epibranchial chamber is connected with the promyal chamber. On the lateral view from the right side of the oyster, the joint of the two gills attaches to the visceral mass at and below the adductor muscle, while above the adductor muscle, the gills are dissociated so that the two rows of water tubes on the left as well as the two rows on the right of oyster body can be seen. The "white meat" Jinjiang oyster from Shenzhen Bay belongs to this group.

Nelson (1938) stated that oysters with a promyal chamber are adapted to low salinity and highly turbid waters, while oysters without it do better in high salinity, less turbid waters. Thomson (1954) had similar reports. The occurrence of the promyal construction in commonly cultured oyster species in China and their distribution are consistent with Nelson's statement. Oysters with the chamber inhabit mostly estuary and intertidal zones, where salinity and transparency are both low and the environmental factors fluctuate. The ones without the chamber inhabit mostly shallow seas with higher salinity and relatively stable environments. It is likely that the promyal chamber is an adaptation stemming from oysters moving into increasingly estuarine habitats.

Galtsoff (1964), USA, *C. rivularis*

Mantle—Margin of the mantle is dark violet; the tentacles are arranged in two rows; those of the outer row are of irregular size; the inner tentacles in a single row are slender.

summarize this information by country, from north to south along the Pacific west coast.

Japan

Kira (1962) reported distribution of *C. rivularis* roughly from central Honshu to Kyushu (Fig. 1). Honshu is the largest island of

Japan located in the center of the archipelago. Kyushu is southern most. Cahn (1950) reported the restricted range of its distribution as western Kyushu, mainly in Ariake-kai ("kai" in Japanese means sea) and Yatsuchiro-wan ("wan" means bay). It is most abundant in the inner parts of Ariake-kai, the southern coast of Fukuoka and Saga prefecture. Hedgecock et al. (1999) found a similar distribu-

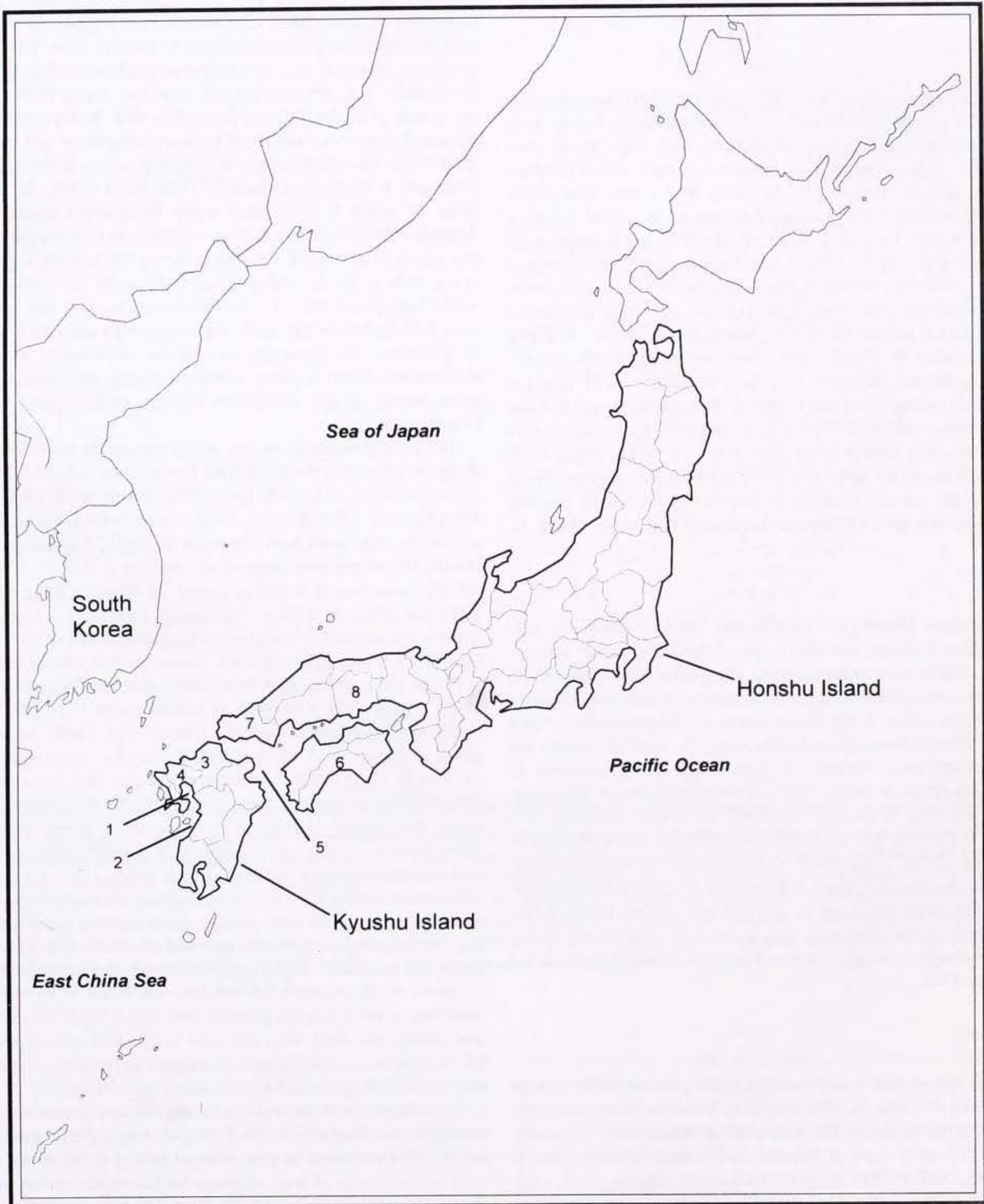


Figure 1. Locations reported with *C. ariakensis* populations in Japan. 1. Ariake-kai; 2. Yatsuchiro-wan; 3. Fukuoka prefecture; 4. Saga prefecture; 5. Shiranuhi Bay; 6. Kochi prefecture; 7. Yamaguchi prefecture; and 8. Okayama prefecture.

tion in the Ariake Bay. Ariake-kai or commonly called Ariake Bay, seems to be the most recognized natural habitat and the namesake of *C. ariakensis*, as it was mentioned most frequently (Wakiya 1929, Hirase 1930, Cahn 1950, Galtsoff 1964, Imai 1978, Hedgecock et al. 1999). In addition, Wakiya (1929) mentioned Shiranuhi Bay on the northeastern coast of Kyushu, and Cahn (1950) listed the Pacific coast of Kochi, the coast of Yamaguchi and Okayama prefecture.

China

China has an extensive coastline of about 18,000 km extending from the cold temperate north to the tropical south. Based on an extensive investigation on oyster species along the Chinese coast in 1956, *O. (C.) rivularis* was identified in each coastal province (Zhang & Lou 1959; Fig. 2). As Zhang et al. (1960) later stated, the distribution of this species covers the whole coastal region of China, with a latitudinal range of 15–40°N and a longitudinal range of 107–124°E. Table 3 lists the names of locations where *O. (C.) rivularis* has been reported. The locations underlined were considered by Zhang and Lou (1956b) as major production areas, which might not be true today. Among those, Xiaoqing River estuary in Yangjiaogou, Shandong province was specifically mentioned because a very large population of *O. rivularis* was found there. In certain localities, the population was so large that people call them "oyster hills" because individual oysters grew attaching to each other (Zhang & Lou 1956b, Zhang et al. 1960). It would be interesting to try to determine whether natural populations are still available in some locations, having possibly been shielded from exploitation because of their rarity (Table 3).

India

Although Ahmed (1971) mentioned that *C. rivularis* was distributed on both east and west coasts of the Indo-Pakistan subcontinent, other reports maintained that this species was found only on the west coast of India (Fig. 3). It was first reported along the coast of Bombay (Awati & Rai 1931). Durve (1986) gave a much wider range between Ratnagiri and Okha along the coast of Gujarat and Maharashtra area. Gujarat (Saurashtra) has a long coastline of 1500 km (Patel & Jetani 1991). Specific locations in this range were described by Mahadevan (1987) as Aramra, Poshetra, Port Okha, Porbandar, Sikka, Gagwa Creek, Singach Creek, Beet Kada, Khanara Creek, Laku Point, Gomati Creek (Dwarka), Harsad, Navibander (Madha Creek), Balapur, and Azad Island. In addition, Rao (1987) mentioned creeks of Kutch and Aramda Creek in Gujarat and Mahim, Ratnagiri and Jaytapur in Maharashtra. Durve (1986) also mentioned some trawling areas around Bahrain in the Arabian Gulf.

Pakistan

This species was found abundant on the coast of West Pakistan (Ahmed 1971; Fig. 3). The following locations have been mentioned in the literature: the coast of Sind (Ahmed 1971), Korangi Creek (18 miles south of Karachi) and Sonari (40 miles west of Karachi; Asif 1978b), Sandspit backwaters (Qasim et al. 1985, Barkati & Khan 1987, Aftab 1988), and Port Qasim (Gharo-Phitti saltwater creek system near Karachi; Ahmed et al. 1987, Barkati & Khan 1987).

ECOLOGY

Habitat

Below we summarize reports on the nature of the habitat described for *C. ariakensis* and the vertical and horizontal ranges of its distribution.

In Japan, *O. rivularis* was only reported from muddy beds (Amemiya 1928, Wakiya 1929, Hirase 1930). It generally adheres to other objects by the umbonal part of the left valve, but many specimens appear to have lived separately (Hirase 1930). Its vertical range is just above the low tide mark and closely restricted to the vicinity of the low tide line (Amemiya 1928, Wakiya 1929). Its horizontal range was determined by water temperature and salinity (Imai 1978). The salinity range of its natural habitat under ordinary conditions is 9–30 ppt (Amemiya 1928, Cahn 1950), the lower range of which is lower than many *Crassostrea* species. As Amemiya (1928) explained, these conditions are apt to change for one reason or another. For instance, during ebb tide the exposure of the beds to the air and sun inevitably make the surrounding water more saline due to evaporation. But because this species lives close to the low tide mark, exposure to high salinities is short. *C. ariakensis* can apparently tolerate low salinities as well. *O. rivularis* was found in places where the salinity falls occasionally much below 10 ppt, sometimes even in entirely fresh water (Amemiya 1928).

In China, this species occurs widely among the river estuaries along the coast. It is found from the low tide line to 7–10 m below mean low water (Zhang & Lou 1956b, Zhang et al. 1960, Cai 1966, Cai et al. 1979, Xu et al. 1992). Sometimes it could be found around the high water mark (Zhang et al. 1960). According to Lu (1994), the temperature range of *C. rivularis* is 2–35°C. Normal salinity range was reported as around 10–30 ppt (Zhang & Xie 1960, Lu 1994) or 9–28 ppt (Zhang & Lou 1956b). Optimum salinity was reported as 10–25 ppt (Zhang et al. 1960) or 10–28 ppt (Nie 1991). It was observed that *C. rivularis* could tolerate salinity as low as 1–2 ppt for a short term (Zhang et al. 1960, Zhang & Xie 1960), as Nie (1991) reported its salinity range 1–32 ppt. Pure fresh water could cause mortality (Zhang et al. 1960). An interesting exception to the normal distribution of *C. ariakensis* was reported by Chen (1991) for Northern Jiangsu. The silty coast of Jiangsu province was not originally suitable for *O. rivularis*. Actually, few oysters were found in this province. Things changed when *Spartina anglica* was introduced. It was planted discontinuously along the coast of Jiangsu province, and by 1991, it occupied 377 km of coastline and 180 km² coastal area of the province. This plantation changed the local ecology. Chen reported that this plant kept clay around its growing area and gradually formed small ridges and backwaters in that area, which he believed was a critical condition for these oysters. *O. rivularis* was found at the seaward boundary of the *S. anglica* planting area, which was between high and middle tide mark with one-third to one-half time exposure. The density of its distribution was as high as 107 per m² and the average shell height of adult *O. rivularis* was 19.5 cm.

In India, *C. rivularis* was found on both hard grounds and in muddy creeks (Mahadevan 1987, Patel & Jetani 1991). Patel and Jetani (1991) reported its preference of muddy rocks, rocks covered by 3–4 inches of mud, although we have to think that settlement preceded the mud deposits. This oyster has been found in groups of four to five large and small individuals attached to isolated rocks and coral stones that came up in trawl-nets (Durve



Figure 2. Locations reported with *C. ariakensis* populations in China. No distinction is made between aquaculture sites and natural populations. Underlined sites are considered major production areas. 1. Xindao (dao: island); 2. Andong (Dadonggou); 3. Zhuanghe; 4. Gaiping; 5. Fengnan; 6. Ninghe; 7. Beitang; 8. Tanggukou; 9. Yangjiaogou; 10. Yexian; 11. Yantai; 12. Rongchen; 13. Dingzigang; 14. Shijiusuo; 15. Sheyang; 16. Jianggang Bay; 17. Rudong; 18. Huijiao; 19. Daishan; 20. Zhenhai; 21. Dinghai; 22. Meilin; 23. Sanmen; 24. Wenling; 25. Leqing Bay; 26. Wenzhou Bay; 27. Xiapu; 28. Ningde; 29. Luoyuan Bay; 30. Huian; 31. Tongan; 32. Xiamen; 33. Longhai; 34. Haicheng; 35. Yunxiao; 36. Shantou; 37. Haimen; 38. Lanbiao, Huilai County; 39. Jiazi; 40. Jieshi; 41. Gaoluo; 42. Shanwei; 43. Qingcao; 44. Baoan; 45. Xiangzhou; 46. Tangjiahuan; 47. Nanshui; 48. Hengshan; 49. Zhanjiang Bay; 50. Qinzhouwan(Longmen); 51. Baoping Bay; 52. Boao; 53. Qinglangang; 54. Qiongsan; 55. Lofu Shan; and 56. Deep Bay.

1986) or solitary (unattached) in the littoral zone (Awati & Rai 1931). The vertical range of *C. rivularis* was described as the littoral zone (Awati & Rai 1931), sublittoral low waterline area or submerged offshore area (Durve 1986), intertidal (Mahadevan 1987, Rao 1987) or tidal region (Patel & Jetani 1991) and also at 9–15 m depth (Durve 1986).

In Pakistan, the preferred habitats of *C. rivularis* are the backwaters and creeks along the coast (Moazzam & Rizvi 1983). It seems that this species thrives in muddy environments (Ahmed

1971, Asif 1978b, Ahmed et al. 1987) and adheres to hard substrate such as stones (Ahmed et al. 1987). It occurs near the low water mark (Ahmed 1971, 1975, Ahmed et al. 1987, Barkati & Khan 1987) and the preferred tidal height for spat settlement is 0.5 ft mark (Ahmed et al. 1987).

Predators, Harmful Organisms, and Diseases

According to Zhang and Lou (1956b), in China, “red tide” is generally most harmful to oysters. It caused 50% mortality of

TABLE 3.
Locations where *C. (O.) rivularis* was reported in China.

Province	Locations Where <i>C. (O.) rivularis</i> was reported
Liaoning	Gaiping, Andong (Dadonggou), Xindao, Zhuanghe (Zhang & Lou 1959)
Hebei	Fengnan, Tanggukou, Beitang (Zhang & Lou 1959)
Tianjin City	Ninghe (Zhao et al. 1991)
Shandong	Rongchen (Zhang & Lou 1956b) Yangjiaogou, Dingzigang (Zhang & Lou 1956b, 1959) Shijiusuo (Zhang & Lou 1959) Yantai, Yexian (Zhao et al. 1991)
Jiangsu	Sheyang, Rudong (Zhang & Lou 1959) Northern coast (north of Jianggang Bay; Chen 1991)
Zhejiang	Sanmen (Zhang & Lou 1956b) Zhenhai, Daishan, Huijiano, Dinghai, Meilin, Wenling (Zhang & Lou 1959) Wenzhou Bay (Huang et al. 1981) Leqing Bay (Zhou et al. 1982)
Fujian	Xiamen (Zhang & Lou 1956b, 1959) Tongan, Haicheng (Zhang & Lou 1959) Luoyuan Bay (Xu et al. 1992) Yunxiao, Longhai, Huian, Ningde, Xiapu (Cai 1966)
Guangdong	Shanwei, Lanbiao (Zhang & Lou 1956b) Baoan, Tangjiahuan, Hengshan (Zhang & Lou 1956b, 1959) Shantou, Jiazi, Jieshi, Haimen, Nanshui (Zhang & Lou 1959) Qingcao, Gaoluo, Xiangzhou (Zhang et al. 1960) Zhanjiang Bay (Cai et al. 1992) Peal River estuary (Guan & Li 1986)
Guangxi	Longmen (Zhang & Lou 1959)
Hainan	Baoping Bay (Zhang & Lou 1956b, 1959) Qiongsan, Qinglangang, Boao, (Zhang & Lou 1959)
Hong Kong	Lofu Shan (Ke & Wang 2001) Deep Bay (Mok 1974)

cultured oysters in Baoan, Guangdong Province in 1953. Red tide could be caused by *Noctiluca* sp. diatom or the more harmful *Ditylum* sp. The carnivorous oyster drills *Thais gradata* (known as "huluo," which means tiger snail in China) and *Naticidae* sp. (known as "yuluo," which means jade snail) are also very harmful to oysters. Tiger snail can drill through the shell of a spat in 3 min and in 8 h for a 3-y-old oyster (Wu et al. 1997). Beside these, carnivorous crabs, such as *Scylla*, *Portunidae*, *Lithodidae*, sea urchin *Echinoidea*, and sea star *Aseroidea*, are also harmful to spat.

Below we list the available reports on these subject areas by publication year.

Harmful organisms to *C. rivularis* cultured in Zhanjiang Bay, Guangdong Province, China (Cai et al. 1992)

The effects of the predator *T. gradata* and *Balanus* spp. were reported in an important estuary for aquaculture. *T. gradata* was found harmful to 1-y-old oysters. Its density on oyster cultch could be as high as seven individuals/m². Mortality caused by *T. gradata* could be as high as 31%, 14% on average. *T. gradata* preferred living in groups, usually hiding in the shaded area of concrete posts. Its reproductive season was from the beginning of April to the middle of June peaking from the beginning of April to the beginning of May. Each female carried 50–100 oospores, with about 100 eggs in each oospore. Hatchability was very high, al-

most 100%. Incubation period was about 15–30 days. Barnacle *Balanus* spp. competed for setting space and food. In the worst situation, the oyster seed could be smothered with a total covering of *Balanus* spp. *Balanus* spp. set increased from the upper estuarine area toward the lower saltier regions. Highest density occurred in the low intertidal area. *Balanus* spp. larvae preferred the sunny side of a setting place.

Mass mortality putatively caused by *Prorocentrum* sp. bloom in Zhanjiang, South China (Zhang et al. 1995)

From late April to late May 1994, an episode of high mortality occurred at an *O. rivularis* farm close to the port of Zhanjiang, Fujian Province, South China. Mortality reached 98% over about 25 hectares. Water sampling and histopathological monitoring was conducted. During the outbreak, the water temperature increased from 18 to 30°C, pH fluctuated between 6.5 and 7.0, and salinity ranged 25.6–29.1 ppt. The water was blue-brown in color and all water samples revealed variable concentrations of phytoplankton, of which 96% were composed of *Prorocentrum* sp. with concentrations of 201–667 cells/mL over the period of observation. The temporal association of the mass mortality and a *Prorocentrum* bloom suggested that the bloom was probably the cause of the mortality. This assumption is supported by the histopathological findings that suggest toxicosis. In particular, the observed lesions were acute and corresponded with the outbreak.

Affected oysters were gray in color and had a softer than normal texture. The most outstanding microscopic lesion was intense accumulation of hemocytes in and around hemolymph channels, especially in the Leydig tissue. Close examination of the larger vessels revealed that hemocytes were actively infiltrating the vessel walls, as well as involved in transmigration into the Leydig tissue and the formation of intravascular thrombi. A diffuse, and less intense, hemocytosis was present in the interstitium between the digestive tubules, while a mild hemocytosis was detected in the gills. Oedematous changes were prominent around the digestive tubules and in the Leydig tissues where they were accompanied by tissue necrosis/lysis. The digestive tubules were empty and their epithelia were dysplastic, varying from low columnar to cuboidal and in some instances there was necrosis of the tubular epithelium. Brown cells were particularly prominent in the intertubular tissues. The pathology was consistent with a systemic toxicosis resulting from absorption of toxins from the digestive gland.

***Bonamia*-like parasite found in *C. rivularis* reared in France (Cochennec et al. 1998)**

C. rivularis was imported from the Haskin Shellfish Research Laboratory in New Jersey in 1994. Seven months after introduction, some mortality occurred in quarantine. Histologic examination revealed the presence of an intracellular protozoan parasite in the connective tissues of nine dead specimens. Ultrastructure analysis suggested that the protozoan might belong to the genus *Bonamia*. *Bonamia* was likely transmitted to the experimental oysters from neighboring waters, which are endemic for bonamiosis, possibly when inlet water treatment lapsed.

An intracellular procaryotic microorganism associated with lesions in *C. ariakensis* in Pearl River estuary, South China (Wu & Pan 2000)

A series of mortalities of cultured oysters have occurred in Pearl River estuary since 1992, usually from February to May. The mortality peaks at 80–90% during April and May. The diseased



Figure 3. Locations reported with *C. ariakensis* populations in India and Pakistan. India: 1. Ratnagiri (16N, 73E); 2. Balapur (not located); 3. Porbander (Porbundar), Navibander (21N, 69E); 4. Dwarka (Gomati Creek) (22N, 68E); 5. Okha, Aramda Creek, Poshetra, Port Okha, Sikka (22N, 69E). Pakistan: 1. Korangi Creek (24N, 67E); 2. Karachi (24N, 64E); and 3. Port Qasim (27N, 68E).

oysters are generally aged 2–7 y. A rickettsia-like intracellular microorganism is present in the tissue of diseased oysters.

PHYSIOLOGY

Natural Reproduction

Hermaphroditism and Sex Reversal

Crassostrea are oviparous and protandric hermaphrodites (*c.f.*, Coe 1934). The occurrence of true hermaphrodites (both sexes simultaneously) is rare. Hasan (1960) stated that hermaphrodites do not exist in *O. discoidea* (= *C. rivularis*). In a study of hermaphroditism and sex reversal in *C. rivularis* from the coast of Karachi, Pakistan, true hermaphrodites were absent (Asif, 1979). Hermaphrodites observed were actually transitional stages of the sexes and used to study sex reversal. According to Asif, gonad generally appeared in *C. rivularis* at the age of 2–3 mo at a length of 0.4–0.6 cm and 62% were male. Protandric hermaphrodites were found in summer and autumn, which indicates the time of sex reversal. The percentage of males declines gradually with increasing size as is true for other *Crassostrea* spp. Cai et al. (1992) also

claimed that sex ratio of *C. rivularis* had an obvious regular change during the reproductive season (usually summer and autumn) and the ratio of females to males increased as the oysters got older. Hasan (1960) also mentioned that individuals with undistinguishable sex are fairly common throughout the spawning season. In Asif's study, the percentage of females increased over males beyond the size class 5.0–5.9 cm.

Spawning

Importance of temperature in gonad maturity and spawning of oysters is well known. Temperature influences the development of gonad (Orton 1936, Spark 1925, Nelson 1928). Temperature also directly influences the abundance of food, which is necessary for the development of gonad (Loosanoff & Engle 1942, Loosanoff & Tommer 1948). Periodic examinations of the gonad of *O. discoidea* showed that normal growth of the reproductive products was coincident with gradual rise of water temperature and food abundance in the summer months (Hasan 1960).

The combined effect of temperature and salinity on the start of

spawning was discussed by Hornell (1910, cited from Hasan, 1960) and confirmed by Hasan (1960) through an experiment on *O. discoidea* in Pakistan. The rise in water temperature helps the development of gonad, while decrease in salinity stimulates the gonad for spawning. Cai et al. (1992) also mentioned that oyster reproduction is closely related to environmental conditions. High temperature and low salinity could cause mass spawning of *C. rivularis* in Zhanjiang Bay, Guangdong province. Hu et al. (1994) presented a more detailed and slightly different discussion in his study of *C. rivularis* spat collection in Jiulong River estuary, Fujian province. He agreed that spawning is related to the change of water temperature and salinity. Water temperature could change with wind direction or strength. Salinity could be changed by precipitation, water current, and tides. However, he seemed to believe that simply a change of water temperature and salinity could be the trigger for spawning, whether an increase or decrease. According to his observation, whenever the tide changed from neap to spring, spring to neap, or during spring tide, oysters would spawn, as long as their gonad was well developed. If the wind direction happened to change from northeast to southwest, or cold air happened to pass by, spawning would increase. He explained that a temperature change of only about 1–2°C would stimulate *C. rivularis* to spawn.

Hasan (1960) studied two natural *O. discoidea* beds at Waugudar Creek, Pakistan. Spawning starts by the first week of July when temperature was about 28–29°C and salinity about 24 ppt. Number of spawning individuals remains almost constant during August and September, much reduced in November and almost nil in December.

Several authors talked about reproduction of *C. rivularis* from China. According to Zhang and Lou (1956a), the optimum salinity for reproduction of *C. rivularis* is 10–25 ppt in China. Hu et al. (1994) reported that in Jiulong River estuary, Fujian province, gonad maturity reaches its peak from the middle of April until mid-May. Oysters spawn twice each year: spring spawn is from May to June and fall spawn, from the end of October to the beginning of December. During spring spawn, water temperature fluctuated between 20 and 30°C, salinity 5–25 ppt. Guan and Li (1986) mentioned that in Zhujiang River estuary, Guangdong province, the reproductive season is from June to September. Spawning is mainly during June and July. There might be a second spawning if appropriate environmental conditions are available. Guan and Li did not report the environmental conditions associated with spawning. Cai et al. (1992) reported that the reproductive season is generally from the beginning of April to the middle or end of June in Zhanjiang Bay, Guangdong. Environmental conditions in the study area (Shimen) are listed as follows: Annual water temperature ranged from 14 to 31.8°C. Daily water temperature changed 2 to 4°C. Water temperature was highest in June and lowest in January. Salinity ranged from 7.52 to 22.18 ppt in summer (but could drop to 0.00 ppt when flooded), 18 to 30 ppt in winter. pH ranged from 7.1 to 7.9 in summer and 7.9 to 8.1 in winter. Zhang et al. (1960) mentioned that reproduction occurred year round in South China Sea area. The reproductive peak is from late May to early September. Zhang et al. did not report environmental conditions during this time period.

According to Tanaka (1954), the spawning season of *O. rivularis* ranges from late May (20–22°C) to early September (28–26.5°C) in Ariake Bay, Japan. There are three major spawning periods during this season: early June (22–23°C), late June to early July (24–26°C), and the beginning to middle of August (30–

28.5°C). The eggs of *O. rivularis* measure 49–53 µm in diameter. The relation between salinity and developmental condition is shown in Table 4. The temperature varied from 24 to 27°C (Amemiya 1928). The above results are nearly identical to those of Huzimori (1920, cited from Amemiya, 1928).

Spatfall

The preferred tidal height of settlement for *C. rivularis* spat was reported to be at the 0.5 ft mark in Pakistan (Ahmed et al. 1987). A broader range was reported from China by Nie (1991): from the low tide line to a depth of 10 m, with the maximum setting at ± 0.4 m low water mark. Hu et al. (1994) reported the optimal water depth for spat collection is from the low tide mark to a depth of 1 m in Jiulong River estuary, China. Larvae settle 12–18 days after spawning. In southern China, spatfall occurs from June to August, the period of highest temperature and lowest salinity (Nie 1991, Cai & Li 1990).

Three reports on spatfall seasons from Pakistan are summarized below. One study was conducted at Paradise Point situated on the west coast of Karachi (Moazzam & Rizvi 1983). This is basically a rocky shore having frequent stretches of boulders and sand. The subtidal area along this shore is generally more deeply inclined than the rest of the coast. This is also a power plant site. *C. rivularis* occurs in the cooling system of the power plant, which has been made artificially "protected" and simulates conditions of a backwater environment. The environment conditions were reported as follows. Temperature dropped to its minimum of 20–22°C in December–January and reached its maximum of 28–30°C in June–July. Salinity remained fairly constant (35–36 ppt) except during the short spell of rains in July–August when salinity dropped to 28 ppt. The contents of suspended matter fluctuated between 0.003 mg/L in November and 0.116 mg/L in June. Transparency was less than 1 m in June–July. Maximum settlement of *C. rivularis* occurred in June and September–October. A considerable number were also observed in July–August.

The second report came from two natural oyster beds (Hasan 1960). One is situated between Korangi and Kadero creeks, south of the village Vagudar and about 16 miles southeast of Karachi. The other one is about 6 miles south of Dhabeji. The temperature and salinity profile were reported from Vagudar creeks. Temperature profile looks very similar to the one from the above report, except that it dropped even lower to 16–17°C in January. Salinity was reported only from April to September, with a maximum of 36–37 ppt in April–May and then dropped continuously to 21–22 ppt in September. The pattern of larval settlement of *O. discoidea* in this report is different from the one mentioned above. Settlement at Vagudar Creek occurred from July to December with mid-

TABLE 4.
Relationship between salinity and developmental condition,
according to Amemiya 1928.

Salinity ppt	Sp. gr. at 0°C	Condition
ca. 7	ca. 1.0056	Minimum salinity
8–14	1.0064–1.0112	Much too low salinity
15–18	1.0120–1.0144	Too low salinity
19–25	1.0153–1.0200	Optimum salinity
26–30	1.0209–1.0241	Too high salinity
31–33	1.0249–1.0256	Much too high salinity
ca. 34	ca. 1.0273	Maximum salinity

September being the peak period. Moazzam and Rizvi related setting failure to the presence of high contents of suspended matter in seawater during the southwest monsoon period (June–September). This high content of suspended matter is believed to interfere with larval settlement of many invertebrates in this area (Ahmed et al. 1978).

The third report came from the Ghara-phitti saltwater creek system (Ahmed et al. 1987). Spat fall occurred from April to October with peak settlement from April to July. The maximum settlement occurred during the period June 24 to July 23. No environmental conditions were given in this report.

Growth

Growth Rate

C. ariakensis is well known for fast growth. In Pakistan, *C. rivularis* spat reached the size of 0.5 mm in about one week and 2.0 cm in about 1 mo (Ahmed et al. 1987). Hasan (1960) found that a size of 3.0 cm was reached 2 mo after settlement. In about one and half years, they become ready for market. Temperature and salinity data of Hasan's study is shown in the spatfall section. In China, *C. rivularis* can grow to 10–16 cm in 2 to 3 y (Zhang & Lou 1956b). In Japan, it attains full size (20 cm) in 2 or 3 y (Amemiya 1928). The results of Fujimori's study (1929) on the growth rate of *O. rivularis* was presented in two parts: spat / young oysters and the sexual adult. Fujimori found that the growth rate of the spat varies considerably according to their time of attachment. The size of adult *O. rivularis* in Kyushu was 5.5 cm shell height at 1 y, 9.7 cm at 2 y, 12.4 cm at 3 y, 15.2 cm at 4 y, 17.9 cm at 5 yr, and 19.7 cm at 6 y. In Japan, growth was most rapid in August and September (Cahn 1950). Environmental conditions were unavailable for the above reports, if not mentioned.

Shell Dimension

C. ariakensis reaches a large size. As Cahn (1950) mentioned, the maximum size attained by this species according to the literature is 257 mm with an estimated age of 20 y. The maximum length he recorded in Japan was 240 mm. A maximum shell height of about 200 mm was reported several times from Japan and the United States (Amemiya 1928, Hirase 1930, Coan et al. 1995). According to the growth rate of adult *O. rivularis* determined by Fujimori (1929), the estimated age of such size is more than 6 y old. Generally, adult specimens reach 6–7 inches (or 150–170 mm) in height, as reported from four countries (Hirase 1936, Galtsoff 1964, Ahmed 1971, Rao 1987).

Allometric Growth

A study of the allometric (relative growth) relationship between shells and tissues of *C. rivularis* was presented by Barkati and Khan (1987) from Pakistan. Shell length was defined as the maximum distance between the tip of the anterior margin and the posterior margin. Shell width was defined as the maximum distance between the lateral margins. The following points were reported. Shell width increased faster than shell length ($r = 0.85$). Shell length increased faster than dry tissue weight ($r = 0.52$). An exponential relationship exists between shell length and shell weight with faster growth in length compared with shell weight ($r = 0.84$). Dry tissue weight increased faster than shell weight ($r = 0.74$). Condition index (the proportion of dry tissue weight to total dry weight of shell and dry tissue) increased with increasing shell length ($r = 0.41$). No linear variable was useful to accurately predict other variables due to low coefficient of correlation (r),

probably due to irregular growth in various shell dimensions (length and width).

For example, Asif (1978b) reported variation in shell growth in two populations of *C. rivularis* caused by setting density in Pakistan. One population in Korangi Creek was exploited and densities were low. Another population in Sonari was crowded. In the Korangi Creek, the oysters are attached to rocks or stones horizontally, whereas those of Sonari grow upward with the umbo downwards. Generally, the wild stock of *C. rivularis* of the Korangi Creek are round and shallow whereas the Sonari population is elongated and deeply cupped. In the majority of the Korangi Creek population, height plus width varies closely with length of the shell while in the Sonari population, shell height plus width varies twice as much as the length.

Feeding

Food Selectivity

According to Cai et al. (1992), *C. rivularis* (collected in Zhanjiang Bay, Guangdong Province, China) is a selective feeder. It preferred small articles to long-chain groups or large articles. The majority of its food is composed of phytoplankton such as *Coscinodiscus* sp., *Nitzschia* sp. and *Cyclotella* sp.

Feeding Habits

Zhang et al. (1959) did an extensive study on the feeding habits of *O. rivularis* in relation to time, tides, season (change of temperature and salinity) and suspended particles. The experiment was conducted in the Pearl River estuary and some nearby bays. Most of the sampled oysters were 3 to 4 y old at the time of examination. These oysters were collected from the wild as spat and cultivated in oyster farms. The percent of *O. rivularis* that are feeding at any given time (incidence of feeding) was not related to periods of light and darkness, nor to the periods of tides, or the density of suspended particles. Salinity and temperature did have certain influences, as summarized below.

According to examinations at five different times of the year, the highest average incidence of feeding for *O. rivularis* was a little more than 80%. It was also found that feeding time of *O. rivularis* adds up to 16–19 h everyday with irregular intervals. Feeding habits of *O. rivularis* were not related to change of sea level or direction or speed of water flow caused by tidal change.

In Pearl River estuary, feeding incidence of *O. rivularis* was highest from October to April (50–100%), when temperature ranges between 10 and 25°C and salinity between 15 and 30 ppt. During summer, the natural reproductive season of *O. rivularis*, when temperature is much higher (22–30°C) and salinity is much lower (3–26 ppt), feeding incidence is lower (0–70%). Feeding incidence seems to be more closely related to salinity according to monthly records. Although *O. rivularis* is known to tolerate low salinity, feeding rate was significantly retarded if salinity was lower than 5 ppt. Above 10 ppt, feeding was active.

Increase in suspended particles in the seawater (higher turbidity) failed to influence feeding incidence of *O. rivularis*. In this case, the authors maintained that these suspended particles served as a food source for the oysters.

Oxygen Consumption

Guan and Li (1988) did an extensive study on oxygen consumption of *C. rivularis*. A Warburg manometer was used to measure the oxygen consumption of dissected gill tissue of *C. rivularis* taken from the Shenzhen Bay Oyster Farm. Oxygen consumption

varied with the change of seawater temperature. A negative correlation was found between oxygen consumption and the oyster age. The older and heavier the oyster, the less oxygen was consumed by its gill tissue. Oxygen consumption differed significantly in different reproductive periods.

BIOCHEMISTRY

Biochemical composition

Qasim et al. (1985) determined the following biochemical parameters for *C. rivularis* from Pakistan. Water contributes 78% of soft body wet weight. Of soft body dry weight, 35.7% was crude protein, 22.5% glycogen, 23% lipid, and 11.2% total inorganic substances. These are the averages from sampling over a period of time (sample interval was not stated in the article). Higher value for lipids (31%) was reported from India (Patel 1979, cited from Qasim et al. 1985). This difference is probably the result of geographical variation, seasonal variation, or both.

Qasim et al. (1985) mentioned that the ratio between glycogen and protein changes with reproductive state of an oyster (no specific information available). Another report on biochemical indexes of *C. rivularis* from the Pearl River estuary, China (Guan & Li 1986) showed seasonal change of lipid content and its close relationship with reproductive physiology of the oysters. As the authors discussed, reproductive season in the Pearl River estuary is from June to September, of which June and July are primary spawning periods. There could be a second spawning in September if environmental conditions were appropriate. In their study, lipid content was highest in May (2.88% of wet weight), then dropped dramatically from June until it reached the lowest point 1.06% in October, the end of the reproductive season.

For protein, amino acid profile determines the nutritive quality of tissues. Such a profile of *C. rivularis* tissue protein has been reported from the Pearl River estuary, China (Guan & Li 1986) and Pakistan (Aftab 1988). There are only slight differences between the two reports. From China, specimens were tested in May, and the amino acid profiles are presented in Table 5 (Guan & Li 1986). Glutamine and asparagines are most abundant. From Pakistan, 14 amino acids were analyzed. Methionine and arginine were not detected. Glycine and aspartic acids were most abundant. Seasonal variation in bound amino acid content is shown in Table 6 (from Aftab 1988).

The shells of *O. rivularis* have been used as traditional Chinese medicine. Zhao et al. (1991) examined the content of calcium carbonate, trace elements and amino acids in shells of *O. rivularis* collected from Tianjin, Shandong, Zhejiang, and Fujian provinces. Calcium carbonate in raw shells was 92.0–95.5% and in calcined shells, 96.4–96.9%. Calcined shells have had organic materials removed. The raw shells contain large amounts of Ca, small amounts of Mg, Na, Sr, Fe, Al, Si, and traces of Ti, Mn, Ba, Cu, etc. Shell decoctions (an extract obtained by boiling the shells) contain small amounts of Ca, Na, Mg, K, and trace element of Sr, P, Pb, Zn, Ni, V, Ba, Li, Mn, Ti, Cu, Cr, Mo, As, Hg, etc. The oyster shells contain 17 amino acids. Total amino acid content amounted to 0.16 to 0.24% in raw shells.

Li et al. (1994) studied the medicinal value of "oyster complete nutritional tablet," a dietary supplement made from extracts of both shells and soft body of *O. gigas* and *O. rivularis* from South China Sea. The tablet contains a high content of eighteen amino acids, especially the eight essential to the human body. Putative benefits are attributed to the liver, kidney, spleen and intestine to a certain extent.

TABLE 5.

The amino acid compositions and their contents in *C. rivularis* sampled in May, 1984 (Guan & Li 1986).

Amino Acid	Contents in Dried Samples (%)
Alanine	2.04
Arginine	1.95
Asparagine	3.30
Cystine	0.28
Glutamine	4.06
Glycine	2.15
Histidine	0.76
Isoleucine	1.18
Leucine	1.87
Lysine	2.23
Methionine	0.57
Phenylalanine	1.05
Serine	1.39
Threonine	1.48
Tyrosine	1.34
Valine	1.32

Heavy Metals and Toxins

Lu (1994) did a preliminary study on the feasibility of using *O. rivularis* as a monitoring agent for heavy metals, like Cu, Zn, Cd, Pb, along the Guangdong coast, China. He found that profiles of Cu, Zn and Cd content in the oyster correlated with the distribution of industrial discharge along Guangdong province. Also see Ke and Wang 2001. Further investigations on the suitability of *O. rivularis* as a biomonitor of specific metals or other chemicals are presented below.

Zn

According to Lu et al. (1998a), Zn accumulated continuously in the tissues of the oyster through 12 days of exposure. Accumulation was linear with time. Loss of Zn from *C. rivularis* was not observed over 35 days of depuration. Zn accumulated less readily with increasing salinity. The author concluded that in general *C. rivularis* is a reliable indicator of Zn in marine systems.

TABLE 6.

Seasonal variation in the protein and amino acid composition of tissue protein hydrolysate of *C. rivularis* (Aftab 1988).

Component	February	May	August	November	Average
Protein % d.w.	40.56	41.25	52.50	55.00	47.33
Alanine	6.04	6.91	9.00	9.67	7.90
Aspartic acid	6.78	9.83	12.56	6.58	8.94
Glutamic acid	6.30	7.98	11.26	5.08	7.65
Glycine	13.27	11.88	6.55	9.10	12.10
Histidine	2.07	1.87	2.72	1.91	2.14
Isoleucine	2.38	1.80	3.12	2.08	2.32
Leucine	3.98	2.89	5.34	3.63	3.96
Lysine	1.59	1.74	1.44	1.28	1.51
Phenylalanine	1.75	1.30	1.94	1.55	1.63
Proline	0.46	2.05	0.79	2.40	1.43
Serine	4.07	6.01	7.82	3.51	5.35
Threonine	3.85	5.74	6.92	3.24	4.93
Tyrosine	0.85	0.60	0.91	0.79	0.79
Valine	3.64	3.75	5.55	2.98	3.98

Cd

Lu et al. (1998b) studied Cd absorption in *C. rivularis*. The content of Cd in body tissues of *C. rivularis* accumulates in linear proportion to Cd concentration in the water and to exposure time. Accumulated Cd attenuates slowly with a biologic half-life of 77 days. With increased salinity, rate of accumulation decreases while rate of Cd loss slows down. *C. rivularis* seems to be a reliable bio-monitor of Cd pollution.

Cu

Cu absorption in *C. rivularis* was examined by Lu et al. (1998c). It continuously accumulated in the tissues of the oyster through the exposure to a concentration of 100 µg/L over 12 days. Accumulation was linear with time and decline of Cu concentration was slow, with a half-life about 131 days. Rate of Cu accumulation was significantly slower with increased salinity, but rate of decline in Cu concentration was not significantly related to salinity.

Total Petroleum Hydrocarbons (TPHs)

Lin et al. (1991) looked at concentration of TPHs in the Pearl River estuary, China. TPHs in *C. rivularis* tissues decreased with time during the period leading to sexual maturity. The rate of decrease was about 0.24 µg/g, dry weight. The biologic half-life was 43 days. Aromatic hydrocarbon compounds with smaller molecular weight were released sooner from oyster tissues than those with greater molecular weight. The concentrations of TPHs in oyster tissues were not significantly related to those in waters and sediments, and not clearly dependent on the contents of lipids in oyster tissues during the study period (September 1986 until February 1987).

GENETICS**Karyotype**

So far, research on the cupped oyster species of the genus *Crassostrea* shows a common diploid chromosome number of $2n = 20$, and their karyotypes include only metacentric and submetacentric chromosomes. The proportion of these chromosome types can be different interspecifically (Leitão et al. 1999).

Chromosome number of $2n = 20$ was confirmed in *C. ariakensis* (Ieyama 1975) and in *C. rivularis* from West Pakistan (Ahmed 1973) and China (Yu et al. 1993). Yu et al. reported the karyotype of *C. rivularis* sampled in Southern China had 10 metacentric pairs. A more recent karyological study (Leitão et al. 1999) on an American population of *C. ariakensis* originally introduced from Japan shows that it consists of eight metacentric and two submetacentric (nos. 4 and 8) chromosome pairs. A variable number of one to three Ag-NORs (nucleolus organizer regions) was observed terminally on the metacentric pairs 9 and 10. About 68% of the silver stained metaphases showed Ag-NORs only on pair 10.

Polyploidy

Rong et al. (1994) reported their attempts to produce tetraploid *C. rivularis*. Newly fertilized eggs of *C. rivularis* from south China were treated with physical and chemical methods in the first three minutes before the cleavage of zygotes or at the onset of first cleavage. Induction rates of tetraploids were 28% for heat shock, 30% for cold shock, 28% for chlorpromazine treatment and 35.8% for "traditional Chinese medicine" treatment as indicated by chromosome spreads from larvae. Production of viable spat was not reported.

Hybridization

Gaffney and Allen (1993) reviewed previous hybridization reports among *Crassostrea* species and pointed out that most of reports of successful hybridization suffer from one or more of the following: 1) ambiguities in classification; 2) possible contamination during spawning; 3) absence of experimental controls for assessing the quality of gametes as well as larval viabilities; and 4) the absence of genetic confirmation of hybrid status. They conclude that there was virtually no unequivocal evidence for the formation of viable interspecific hybrids among *Crassostrea* species.

Early studies on cross-fertilization between *C. gigas* and *C. rivularis* gained little success (Miyazaki 1939, Imai & Sakai 1961), but was reported successful by Zhou et al. (1982) and Downing (1988a,b, 1991). Asif (1978a) reported successful production of trochophore larvae 4–5 h for the cross of *C. rivularis* with *C. glomerata* and *Saccostrea cucullata*. For the reasons mentioned above, these should be viewed with caution.

Hybridization of *C. gigas* and *C. rivularis* was re-examined by using specimens originally introduced from Japan to the United States (Allen & Gaffney 1993). Such crosses are of interest because of the disease resistant properties of these species (Calvo et al. 1999, 2001). In addition, the hardiness and apparent disease resistance of *C. gigas* and the high temperature, low salinity tolerance of *C. rivularis* could lead to promising variants for aquaculture, especially if the diploid is sterile. Three replicates of a 2×2 factorial mating of *C. gigas* and *C. rivularis* were produced to examine the viability of this cross. Fertilization rate, yield of 48-h-old larvae, and survival of fertilized eggs was lower in the hybrids than in pure crosses. All crosses showed similar larval growth rates, except *C. rivularis* (female) \times *C. gigas*, which grew more slowly. Isozyme electrophoresis and flow cytometry confirmed hybridization. Triploid hybrids were produced using tetraploid *C. gigas* and diploid *C. ariakensis* (Que & Allen 2002).

Hybridization between *C. ariakensis* and *C. virginica* failed (Allen et al. 1993). Cytogenetic and electrophoretic analysis revealed the formation of hybrid zygotes and larvae between *C. virginica* and *C. rivularis*, but larval survival was limited to a maximum of 10 days. Larvae stopped growing at about day 4, reaching a maximum length of about 80 µm. Studies on larval feeding using fluorescent beads indicated that growth limitation apparently was not caused by an inability to feed. Induced triploidy did not rescue hybrid failure.

Population Genetics

A number of studies have used molecular markers of various sorts to distinguish among *Crassostrea* species, including *C. ariakensis*. Among the earliest was work by Buroker et al. (1979) who estimated levels of genetic variation for six *Crassostrea* and three *Saccostrea* species based on electrophoretic variation in proteins in about 30 loci, *C. rivularis* among them. Liu and Dai (1998) used RAPD techniques to differentiate *C. talienwhanensis* and *C. plicatula* from *C. rivularis*. Li et al. (1988) used electrophoretic markers to separate four *Crassostrea* species, and concluded that the "white oyster" was *C. rivularis* and the "red oyster," *C. iredalae*.

C. rivularis was also among those used by Littlewood (1994) to establish the first phylogenetic estimates for this species based on nuclear DNA. Since then, a number of other studies employing

molecular markers have been applied to *C. ariakensis*, mostly to discriminate among species (O'Foighil et al. 1995, Gaffney & O'Biern 1996, Hedgecock et al. 1999, Francis et al. 2000). Hedgecock et al.'s study confirmed the occurrence of *C. ariakensis* in the northern regions of the Ariake Sea and re-emphasized the need for genetic confirmation for species identification.

AQUACULTURE

References to aquaculture of *C. ariakensis* come mainly from Japan and China, and are discussed accordingly.

Aquaculture in Japan

Of the five edible oysters species in Japan, only *O. gigas* and *O. rivularis* were cultured commercially (Cahn 1950). *O. rivularis* was second to *O. gigas* in commercial importance (Amemiya 1928)

According to Amemiya (1928), cultivation of *O. rivularis* began in Ariake Bay in the late 1890s and seed were later transplanted to Kozima Bay in Okayama Prefecture around 1928. An even earlier report of cultivation in Ariake Bay in the 1860s was given by Wakiya (1929). Both Wakiya and Langdon and Robinson (1996) mentioned that the culture of Suminoe oyster were conducted in the Suminoe river, Saga Prefecture from the beginning of the Meiji period in the mid-19th century. Discrepancy between Cahn and Wakiya on the start of *C. rivularis* aquaculture might rest on their definition of cultivation. Cahn (1950) described two types of culture systems at the mouth of the Suminoe-gawa ("gawa" in Japanese means river or stream), Ariake Bay, a primitive one and a more developed one. Cahn did not say when the primitive culture started, but he implied that the more sophisticated culture started after 1885. The primitive culture consisted simply of gathering natural oysters and storing the larger individuals for a short time on the bottom of the Sumino-gawa, later to be shipped to Nagasaki at the proper season for sale.

Aquaculture of *O. rivularis* began fortuitously. For some reason during the winter of 1884 these oysters were not shipped for sale to Nagasaki. The next year they were considerably larger by size and weight. From this observation, a new type of culture evolved in the local area. Young oysters about 2.5 cm in length were gathered from every possible growing place from July until March and were placed on oyster beds at the mouth of the river. To prevent loss, they were heaped close together in masses. They were washed and cleaned twice or three times each month during low tide. In April individual oysters were stuck in the mud vertically, hinge down and ventral margins uppermost. As the mud was very firm, the oysters fared and grew well. As they grew, they were thinned and replanted to give them more growing space. Growth was most rapid in August and September.

Aquaculture in China

C. rivularis is the most economically important marine shellfish species cultured in South China (Zhang et al. 1995), primarily in Fujian, Guangdong and Guangxi Province. The history of its culture in Guangdong is over 300 y old (Cai et al. 1979). The Pearl River (Zhujiang) estuary, Guangdong was considered the most famous cultivation site of this species (Zhang & Xie 1960). Some other places mentioned in the literature are Yangjiaogou, Shandong Province (Zhang et al. 1960), Leqing Bay, Zhejiang Province (Zhou et al. 1982) and in Deep Bay, Hong Kong (Mok 1974). In 1996, China produced 2.3 million tonnes of oysters from aquaculture, among which *C. rivularis* accounts for 20–30% (Guo et al.

1999). In Guangdong province, *C. rivularis* production was about 40% of total sea culture production (Qiu & Li 1983).

The primitive method of oyster culture was to improve growth and reproduction with procedures like fishing restrictions and protection from diseases and predators (Zhang & Xie 1960). The advanced method involves collecting natural spat and artificial grow-out. Modern oyster culture includes larval culture and breeding. Larval culture and breeding of *C. rivularis* larvae has been successfully accomplished on a research scale in South China (Liang et al. 1983, Cai et al. 1989) but has not been used in large-scale commercial culture. Hatchery production of seed is seen as a step to increase the reliability of seed production.

Spat collection and artificial grow-out is still the most popular. This is composed of four steps: spat collection, grow-out, fattening, and harvest. For spat collection, cultch material to collect spat was traditionally oyster shell and gravel (Nie 1991). Since the 1960s, cement plates (17–24 cm × 14–19 cm) or cement bars (40–80 cm long × 4–6 cm²) reinforced with embedded bamboo stakes were used. Stakes are used increasingly since they are easier to handle, provide more surface area, and are not so readily covered by silt. Season and location of spat fall is summarized in Physiology. Oyster larvae in the water are monitored to ensure the best time of planting the clutch. Spat collectors are placed in rows in rectangular blocks, usually 30 to 37.5 × 10³ stakes or 100 to 135 × 10³ plates per hectare. Further details follow below for specific culture techniques.

The age of harvest is generally 3.5 to 4 y (Qiu & Li 1983), but varies from 2 to 5 y depending on culture location where the environment, the specific culture technique, and even the expected market size could be different. For example, Guo et al. (1999) reported 2 to 3 y in Guangxi where oysters maintain rapid growth throughout the first 3 y and are usually harvested at a size of 10–15 cm. The culture technique used there is concrete bars or shell strings hanging on rafts and long lines. In Pearl River estuary, Guangdong, oysters were usually harvested at 3 y of age by bamboo stake culture (Zhang & Xie 1960). Cai and Li (1990) reported the period to be 3 to 5 y in Southern China.

Cai and Li (1990) summarized oyster culture techniques in China. The ancient bottom culture techniques, including bamboo stake, stone and concrete culture, are still the major methods, but farmers are becoming increasingly aware of the advantage of off-bottom culture, like the rack and raft culture. The various techniques are described below (reproduced from Cai and Li's work, 1990).

Rock (Stone) Culture

Rock culture is usually applied in areas that have hard substrate. Marble flagstones approximately 90 cm × 25 cm wide and 10-cm thick are preferred for this method. Stones may be arranged one-by-one vertically, resembling tombstones or two stones may be arranged in an "A" shape. Three stones may be arranged to form a tripod. Average spacing between stone groups is 70 cm. Another choice of rock is irregularly shaped natural boulders of 4 to 5 kg. The traditional arrangement of the boulders, called "stars in the sky," involves uniform distribution over the substrate. Two modifications were used along the coast of Guangdong and Hainan Provinces. One is called "plum blossom" with five or six boulders grouped together. Another is called "small house" with three flagstones arranged to form a shed or an upside-down "U." Both kinds of rocks are thoroughly washed and then covered in limewash 10 days before use.

In Guangdong and Fujian Provinces, the rocks are set out in early May to June or in November. Maximum spatfall is expected in May. Spat collected in June is usually subject to heavy mortality due to high temperatures and strong sunlight during attachment. Spat collected late in the season usually grew poorly because of low water temperatures. Oysters are grown to market size at the site of spat collection.

Approximately 60,000 stones are required for one hectare, and *C. rivularis* may be harvested in 3 to 5 y. Production is moderate, ranging from 750 to 3000 kg per hectare. The oysters grown on rocks are more subject to predation by starfish and other organisms than are oysters grown on stakes, so considerable time must be invested in predator control.

Concrete Culture

Prefabricated posts or tiles are a derivative of the traditional rock culture technique for the culture of *C. rivularis* and has been used since 1950 in Guangdong Province. Spatfall occurs most of the year, but optimum periods are April and May. To prevent the tiles or posts from sinking into the mud, they are removed and rearranged around May, September, and December. Concrete culture requires a 4-y cycle. Spat collection and growth occupies the first year from June to April. The second and the third years involve a cultivation period yearly from May to August. Market size is attained in 2.5 to 3 y and involves a progressive increase in the spacing of the concrete tiles or posts. The cultivation cycle is completed by a fattening period extending from September to January. For fattening, oysters are transferred from the spat collection/grow-out area to prime growing grounds, usually in the low intertidal zone. For this culture method, in Guangdong, harvest generally occurs in February to April of the fourth year, when growth rates begin to decline sharply. Expected production from the concrete method is 7.5 to 15 tons of meat per hectare.

Rack Culture

Since 1965, rack culture has been used to cultivate *C. rivularis* in Guangdong Province. The racks may be constructed of bamboo, wood, stone or concrete. Because wood and bamboo are rapidly destroyed by shipworms and stone is heavy and awkward to handle, concrete is preferred. The form of the rack varies greatly, but consists basically of members driven into the substrate to form a horizontal frame, which supports the oyster cultch 2.5 to 3 m above the substrate.

Several types of material are used for spat collection. The most popular one is punched oyster shells, separated by 3 cm bamboo or plastic spacers, and strung on 2 m lengths of galvanized wire or polypropylene line. Concrete tiles, approximately 10 cm² with a central hole, may be substituted for the oyster shell. Concrete poles between 70 and 130 cm in length may also be used. The cultch is suspended from the rack, with spacing proportional to the density of spat settlement and the character of the growing area. The number of racks accommodated varies widely between the growing sites. Production is estimated at 10 to 20 tons per hectare.

Raft Culture

According to Qiu and Li (1983), raft culture started in Japan in 1950. Since 1979, the Fisheries Research Institute of the South China Sea has conducted experimental raft culture of *C. rivularis* in Guangdong Province. The fattening period lasts from September

to May, and three crops may be harvested, because 2 mos are sufficient under optimal seasonal conditions. The ratio of meat production to shell is some 60% higher in raft-fattened oysters than in oysters harvested directly from bottom culture.

C. rivularis can be marketed in less than 3 y using rafts, and that the condition factor will be increased by more than 22% and the meat quality will be superior to oysters cultivated by the traditional bottom methods (Qiu & Li 1983). Though initial costs are higher, the increased production and working advantages of floating raft culture are apparent, and it is expected that raft culture will account for a steadily increasing share of oyster production in China (Qiu & Li 1983). Nie (1991) also mentioned that raft culture gives faster growth and a higher yield. A raft of 84 m² will produce in 2 y what 667 m² of bottom culture will in 4 y. Rafts seem to withstand typhoons better than originally thought.

DISCUSSION

C. ariakensis shares many life history traits with other *Crassostrea* species. It is clearly an estuarine species with salinity tolerances similar to *C. virginica*. Its occurrence in river systems and apparent responsiveness to salinity changes for spawning cues suggests that its reproductive strategy is somewhat different than *C. virginica*. There are indications that larval behavior differs from that of *C. virginica* (M. Luckenbach, VIMS, pers. comm.), perhaps an adaptation to fluvial existence. Many other questions about its ecology are unanswered or incomplete and a number of research priorities have been identified (Rickards & Ticco 2002). One of the principal problems with extrapolating life history from the available literature is the uncertainty over species designation. Some reports are clearly referring to *C. ariakensis*, e.g., those from southeast China where aquaculture activity is concentrated and there is a long history of working with this species. Other reports are not so clearly *C. ariakensis*, especially ones deriving from western India and Pakistan. Also because of likely morphologic confusion, the geographic range for *C. ariakensis* is incompletely described. For example, it seems likely that its range should include the coast of Vietnam, yet there seem to be no direct accounts of this. There are accounts of its occurrence as far as Borneo, the Philippines, and Thailand, but these are unconfirmed. From a practical standpoint, *C. ariakensis* from China are probably an appropriate starting stock for an introduction, should that proceed, because of similarities in latitude. From that respect, this area seems a most appropriate focus for obtaining more information on the species. Korea and Japan are possible sources as well. We did not encounter reports of *C. ariakensis* from Korea except as casual remarks. Stocks in Japan seem to be limited in abundance.

It is unclear whether *C. ariakensis* is a "reef-forming" oyster, depending on how you define "reef." Clearly, *Crassostrea* species, and oysters in general, benefit from aggregation and adults or their shells provide substrate for recruitment in subsequent generations. Some accounts of *C. ariakensis* describe "oyster hills" that would clearly qualify as reefs (Zhang & Lou 1956b, Zhang et al. 1960). Apparently, it is common knowledge among fishermen in China that *C. ariakensis* forms reefs. Other accounts have *C. ariakensis* occurring as small aggregates and singles. In our travels to China, we encountered several sites that had "natural" populations of *C. ariakensis* (Allen et al. 2002). There seem to be natural populations in proximity to Xiamen although we did not observe this first hand. They were available in the local market and reportedly from natural populations that were harvested. There are natural sets of *C. ariakensis* near Hong Kong on the shores of Deep Bay, but this

could be from culture activity in the area. Seed is imported from the Pearl River estuary, so there are likely sources of "natural" populations in the Pearl River delta system. We observed, first hand, collection (harvesting) of *C. ariakensis* adults from sections of the Shiman River near Guan Du in close proximity to Zhanjiang Ocean University. According to the diver on hand, they occur in various assemblages, mostly stuck onto available substrate such as large rocks. They also occur in the Dafeng River in Guangxi province near Beihai. There are probably many other natural populations along the coast of China. By way of caveat, it is difficult to attest to the "naturalness" of resident *C. ariakensis* populations. That is, those that we observed or heard about first hand were populations that occurred relatively deep (3–10 m) in river systems. Whether at some time in the past populations of *C. ariakensis* were distributed in higher reaches of the water column (i.e., before they were exploited over the millennia) is difficult to establish. It is also difficult to distinguish whether spat fall is from natural populations or from aquaculture operations.

There are clearly big questions concerning basic physiology in the kind of detail that exists for other congeners. *C. ariakensis* seems to exhibit growth rates that are extraordinary in head to head trials with *C. virginica*. Yet, these trials have been carried out in disease endemic areas where *C. virginica* could be sick or dying. Growth rates of *C. virginica* in, for example, the Gulf of Mexico, approach those seen in trials of *C. ariakensis* in the Chesapeake

Bay or reported growth rates from the literature. Similar knowledge gaps exist for larval biology, reproductive physiology, predation, competition, etc.

In our opinion, *C. ariakensis* is an underused resource around the world. It clearly has aquaculture applications in estuarine areas that are marginal or unsuitable to *C. gigas*, the most popular culture species. It seems hearty, fast growing, and highly marketable. Of course, utilization of this species would require introduction, as in the Chesapeake Bay. From that perspective, it would be useful to have more basic research on *C. ariakensis* with which to guide decisions about movement of this potentially valuable oyster species.

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