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The Biology and Culture of Marine Bivalve Molluscs of the Genus *Anadara*

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INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

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ABSTRACT

A review is made of the general biology, ecology, population dynamics, reproduction and culture methods of marine bivalves of the family Arcidae, subfamily Anadarinae. These cockles are harvested on a subsistence basis in many tropical, subtropical and warm temperate areas. The important species are *Anadara granosa* (L.), *A. subcrenata* (Lischke) and *A. broughtoni* (Schrenk).

Hatchery production, if economical, could overcome the considerable year to year variability in supply of spat of some species. However, the major constraint to improving productivity of culture beds is predation by gastropod drills and starfish.

INTRODUCTION

Marine bivalve molluscs of the family Arcidae, subfamily Anadarinae, are an important source of protein in many tropical, subtropical and warm temperate areas. On the Pacific coast of Colombia, *Anadara tuberculosa* (Sowerby), *Anadara similis* (C.B. Adams), *Anadara multicostata* (Sowerby) and *Anadara grandis* (Broderip & Sowerby) are all harvested on a subsistence basis (Squires et al. 1975) as is *Anadara ?cornea* (Reeve) in Fiji (Butler, unpublished data) and *Anadara senilis* (L.) in West Africa (Okera 1976). Species harvested on an intensive commercial basis include *Anadara granosa* (L.) in Malaysia and Thailand, *Anadara subcrenata* (Lischke) in Japan, and *Anadara broughtoni* (Schrenck) in South Korea. There is some culture of *Anadara nodifera* (Von Martens) in Thailand (Tookwinas 1985); *Anadara satowi* (Dunker) is fished in China and South Korea and *Anadara antiquata* in the Philippines (Toral-Barza and Gomez 1985).

Catch statistics for the most important species are presented in Table 1. Landings for species and countries not included in this table are insignificant in terms of commercial value. *Anadara granosa* is by far the most important anadarinid currently harvested, although *A. broughtoni* has become increasingly important in recent years. In Malaysia, all production of *A. granosa* takes place on the west coast of the peninsula where there are extensive tidal mudflats. Breakdowns of landings by state for Malaysia and by province for Thailand are given in Tables 2a, 2b and 2c.

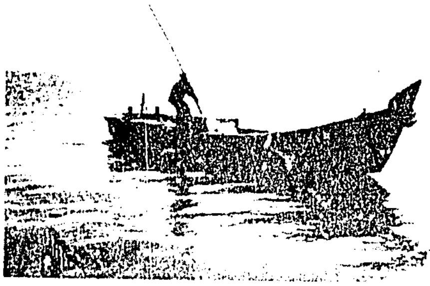
Despite the obvious importance of *A. granosa* and the growing interest in other species of the same genus as a food source, there has been very little research on the group. What little has been undertaken has usually been done on a piecemeal basis. This review collates all the information on anadarinids that is relevant to culture or fishery operations. Because of its importance, emphasis is laid upon *A. granosa*.

Table 1. Nominal catches (tonnes) of species of *Anadara* from 1978 to 1983. (Source: FAO 1984 and Korea Fisheries Administration)

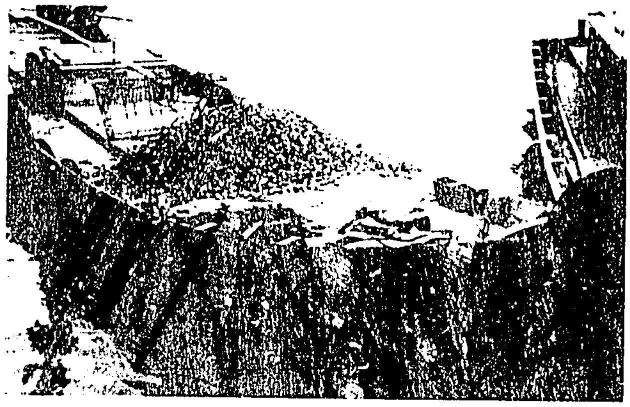
Species	Country	Nominal catch 1978	1979	1980	1981	1982	1983
A. granosa	South Korea*	5,955	5,166	5,427	4,630	7,950	5,113
	Malaysia	55,598	63,412	121,271	68,912	49,462	38,535
	Thailand	16,326	19,263	13,724	23,353	6,044	12,951
A. subcrenata	Japan	4,023	7,206	1,677	2,803	3,624	3,747
	South Korea*	395	485	973	1,483	260	–
A. broughtoni	South Korea*	665	1,548	2,301	12,193	20,339	11,047
Anadara spp.	Indonesia	40,980	32,183	32,383	37,410	29,335	27,560
	Philippines	171	1,947	44	94	151	203

*Data from annual fisheries statistics of Korea Fisheries Administration.

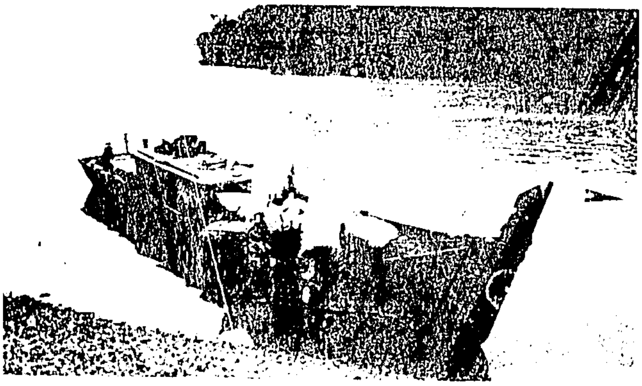
Photos by R.S.V. Pullin.



Harvesting *Anadara granosa*, Malaysia



Landing a harvest of *Anadara granosa*, Malaysia.



Bags of harvested *Anadara granosa*, Malaysia.

Sampling an *Anadara granosa* harvest for undersized shells, Malaysia.

Examining *Anadara broughtoni* in the market, Chungmu, South Korea.

Shucking cockles, *Anadara broughtoni* in Chungmu, South Korea.

Table 2a. Annual landings of *A. granosa* (in tonnes) in Malaysia by state, 1979-1983. (Source: Ibu Pejabat Perikanan (Department of Fisheries), Kuala Lumpur)

	1979	1980	1981	1982	1983
Perlis	—	132	68	128	—
Kedah	16	115	2,249	546	—
Penang	4,174	9,564	4,335	8,545	7,349
Perak	55,297	104,962	57,462	32,915	—
Selangor	3,821	6,637	4,289	7,209	8,686
Negeri Sembilan	—	—	131	—	—
Malacca	103	—	9	—	—
Johore	—	60	315	9	—
Pahang	—	—	—	116	—

Table 2b. Annual *A. granosa* seed collection by state, in Malaysia, in thousands of tins,* 1979-1982. (Source: Ibu Pejabat Perikanan (Department of Fisheries), Kuala Lumpur)

State	1979	1980	1981	1982
Perak	49	15	55	53
Selangor	19	184	167	46
Pulau Pinang	—	84	—	—
Total	68	283	222	99

*1 tin = 15-18 kg

Table 2c. Landings of *A. granosa* (in tonnes) in Thailand, by province, 1978-1983. (Source: Department of Fisheries statistics)

Province	1978	1979	1980	1981	1982	1983
Trat	—	—	—	—	20	28
Rayong	—	—	—	—	18	—
Chon Buri	—	—	—	216	137	134
Chachoengsao	—	—	—	—	1	—
Samut Prakan	—	—	—	—	2	2
Samut Sakhon	—	—	—	—	10	3
Samut Songkhram	479	1,698	153	5,455	528	5,451
Phetchaburi	1,823	3,240	1,296	1,800	1,271	3,687
Chumphon	—	—	—	160	180	195
Surat Thani	—	—	4,800	12,150	654	1,039
Nakhon Si Thammarat	—	—	900	1,620	1,256	1,041
Songkhla	—	—	—	—	—	—
Pattani	229	105	78	94	—	—
Ranong	—	—	—	—	300	36
Phangnga	44	233	54	684	517	870
Phuket	86	65	—	11	26	74
Krabi	33	218	26	162	108	333
Trang	165	264	161	575	489	58
Satun	13,467	13,440	6,256	426	527	—
Total	16,326	19,263	13,724	23,353	6,044	12,951

Throughout this review all species are referred to by specific rather than vernacular names. Nevertheless, it is worth noting some common names. Members of the subfamily Anadarinae are frequently called mangrove cockles (because they are often associated with mangroves) or bloody cockles, a reference to the fact that they possess the red blood pigment hemoglobin. *Anadara subcrenata*, which is harvested in Japan, is known locally as "mogai". In Malaysia, *A. granosa* is known locally as "kerang" (Malay), "hoy kreng" (Thai) "si-ham" (Cantonese) or "cockle" (English). The use of the term cockle probably arose because of the animal's resemblance in size and shape to the European cockle, *Cerastoderma edule*, which belongs to a different family, the Cardiidae. The term "cockle", therefore, has no taxonomic significance.

GENERAL BIOLOGY AND ECOLOGY

Abiotic Factors

ELEVATION

Most species of *Anadara* are intertidal or marginally subtidal in their distribution. In Malaysia, larval *A. granosa* usually settle on muddy shores between mean high water of neap tides (MHWN) and mean low water of neap tides (MLWN). They do not generally extend into the area above MHWN which is usually dominated by mangrove swamp forests. Peak densities of *A. granosa* are usually encountered around midtide level (MTL) (Broom 1980). However, in some areas populations of *A. granosa* may be dense subtidally. For example, in Kakinada Bay, India, the exploited *A. granosa* populations are apparently largely subtidal (Narasimham 1969). On the shores of Hong Kong *A. granosa* can be found intertidally but those appearing in the local markets are trawled from subtidal locations. The subspecies *Anadara granosa bisenensis* Schrenck et Reinhart, found in more northerly latitudes, is generally found at lower shore elevations and subtidally (Cahn 1951).

Other factors may, of course, play a part in determining the level on the shore at which larvae settle. Pathansali (1963) reported that at Penang, Malaysia, the level of mudflat colonized by *A. granosa* ranges from MTL to just above mean low water of spring tides (MLWS) while in Panchor, Perak, it is from MTL to MLWN. He ascribed this variation to the effects of different salinity regimes (see below).

The Central and South American species *Anadara tuberculosa* is also a typically intertidal organism (Squires et al. 1975) which apparently reaches its highest densities among the roots of mangrove swamp forests (Baquiero 1980), although it is unclear whether this is an entirely natural phenomenon or due to intense harvesting activity at lower shore levels not colonized by mangrove plants. The most widely exploited West African species, *Anadara senilis*, is reported to extend from the upper part of the intertidal to the sublittoral (Okera 1976). Populations of *Anadara cornea* are usually found around MLWS (Butler, unpublished data), although again it is uncertain whether this is due to persistent heavy exploitation at other shore levels. The two species which are at the center of exploitation in Japan and Korea, *A. subcrenata* and *A. broughtoni*, are found largely subtidally (Cahn 1951; Kusukabe 1959; Kanno 1966). *Anadara trapezia* (Deshayes) occurs in the low intertidal and subtidal coastal waters around eastern Australia (Sullivan 1960).

SUBSTRATE

All the species of *Anadara* that are commercially important are essentially dwellers in soft substrates. *A. granosa* can be found on substrates of sandy mud but the highest population densities are found on the soft intertidal muds bordering mangrove swamp forests (Pathansali 1966). Broom (1982a) studied natural populations of *A. granosa* at two locations on the coast of Selangor, Malaysia, and found that water content of the substrate at the study sites was 55 to 65%. There was some variation with elevation, the substrate at high shore elevations tending to be somewhat drier (Broom 1980). The proportion of particles less than 53 μm in diameter at these two sites was 80-90%. However, Boonruang and Janekarn (1983) found that a population of *A. granosa* at Phuket, Thailand, inhabited substrates with 70-80% sand (particle size greater than 63 μm in diameter). The water content of these substrates (47-51%) reflected their predominantly sandy nature. Pathansali (1966) found that in areas occupied by natural populations of *A. granosa* in Perak, the silt/clay fraction of the substrate (in this case particles less than 31 μm in diameter) was never less than 46% while 90% of the particles were less than 124 μm in diameter. Not surprisingly, these muds tend to have a high organic content. Broom (1982a) reported organic matter content (as loss on ignition at 475°C for 7 hours) to be in the range of 6 to 11% at the study sites. At both study sites, there was a black, sulphide-rich layer 3-4 cm below the mud/water interface. Boonruang and Janekarn (1983) reported organic matter in the substrates inhabited by the Phuket population as 10.7-12.9% but this probably included inorganic carbonates lost during the burning process which was conducted at rather high temperature (600°C).

Other species also tend to occupy substrates which are predominantly muddy in nature. Cahn (1951) reported that *A. granosa bisenensis* is typically an inhabitant of muddy substrates. Tanaka (1971) reported that *A. broughtoni* is found on muddy substrates in shallow waters around Japan. Kanno (1966) has shown that in Sendai Bay large dense populations of *A. broughtoni* exist only in those areas where silt is the predominant substrate, although he found no evidence of a direct relationship between silt content and density of animals.

For *A. subcrenata*, there is some discrepancy among reported substrate preferences. Cahn (1951) reported that a substrate of muddy sand (50-80% sand) is preferred and that the presence of substances for byssal attachment is essential. Kusukabe (1959) maintained that although this species may be found in sandy mud the greatest population densities are attained in mud substrates with no significant sand component. Ting et al. (1972) reported that *A. subcrenata* inhabits only predominantly muddy substrates. These substrates had a water content of 48-60% with 81-84% of particles less than 40 μm in diameter and an organic content (measured as loss on ignition) in the region of 9 to 10%.

According to Yoloye (1975) and Okera (1976), *Anadara senilis* is found in mud or sandy mud. There is no quantitative information on the composition of the sediments in which this species is found. *Anadara tuberculosa* is reportedly found in soft mud (Squires et al. 1975) rich in organic matter (Baquiero 1980). Sullivan (1960) reported that *Anadara trapezia* occurs on estuarine mudflats with very high densities ['often several dozen to the square foot'] being found in pools containing stands of *Zostera* and *Posidonia*. Dixon (pers. comm.) has found *A. trapezia* in both muddy sand and mud with no obvious correlation between density and substrate type. Low densities are sometimes found on rocky substrates.

Not all species of *Anadara* are associated with muddy substrates. In the Indo-Pacific region, *Anadara antiquata* (L.) is usually found in the sublittoral area inhabiting rocky crevices and attached to rocks and stones by a slender byssus. *Anadara anomala* (Reeve) is also found sublittorally, but in sandy substrates. *Anadara inaequivalvis* (Brugière) is found intertidally in sandy areas (Lim 1966). *Anadara cornea* is found in sandy substrates in Fijian coastal waters (Butler, unpublished data).

In relation to substrate preferences, it is appropriate to mention the extent of development of a byssus in species of *Anadara*. There is no record in the literature that *A. granosa* produces a byssus at any time and a byssus has never been observed in this species. Many other species do produce a byssus at some stage but they subsequently detach and burrow into the substrate. Cahn (1951) maintained that byssal attachment in *A. subcrenata* is so important for the spat that they will not settle in substrates which do not possess an admixture of dead shells or stones to which they can attach. The same also seems to be true of *Anadara trapezia* (Dixon, pers. comm.). Although Sullivan (1960) did not observe a byssus in *A. trapezia*, young specimens attach to the underside of pieces of gravel by a byssus. The latter is normally lost when a length of about 3 cm is attained but it may be retained if the only available substrate is rock (Dixon, pers. comm.). Kanno (1963) and Kim and Koo (1973) stated that *A. broughtoni* also attaches to hard surfaces at the spat stage. In Colombia, mangrove cockles (mostly *A. tuberculosa*) are attached by a byssus to mangrove rootlets (Squires et al. 1975). *A. antiquata* attaches to rocks by a slender byssus (Lim 1966).

SALINITY

Anadara granosa is often found at highest densities on mudflats near but not in the mouths of large rivers (Pathansali 1963; Broom 1980). During the seasons when rainfall is lower than average, the salinity of the coastal waters usually varies between 28 and 31 ppt, but in the rainy season the salinity over some beds may drop as low as 5-10 ppt during low water of neap tides or as low as 15 ppt at high water (Broom 1980). In Penang, the mean monthly range has been reported as 26 to 31 ppt with considerable tidal fluctuations and at Panchor, Perak, the majority of readings taken in one year were in the range of 18.2 to 25.9 ppt (Pathansali 1963). Exceptionally low values do not usually persist over natural beds for more than one or two weeks. This may not be the case in artificially seeded areas (see section on mortality below).

Pathansali (1963) made a study of the salinity requirements and preferences of *A. granosa* in the laboratory. He first examined feeding rates of two groups of *A. granosa* under different acclimation conditions. One group measured 13-14 mm in mean length, the other 35-38 mm. In young *A. granosa* acclimated for 16 hours to water at 29 ppt, feeding rate was not reduced at a salinity of 23.4 ppt but was reduced by 85% at a salinity of 17.6 ppt and was nil at 12 ppt. When *A. granosa* of the same size were acclimated for 16 hours to water at 12 ppt, feeding rate at 17.6 ppt was 90% of that at 29 ppt although it was negligible at 12.0 ppt. On the other hand, large *A. granosa* acclimated to water at 28.3 ppt displayed a 22% reduction in feeding rate when placed in water at 22.9 ppt and at 11.5 ppt feeding rate was negligible.

In simple salinity tolerance experiments, Pathansali (1963) acclimated five groups of *A. granosa*, ranging in size from 20 to 28 mm, to 29 ppt, then placed groups in water at 23, 17, 12 and 8 ppt, respectively, for 30 days. At 17 ppt, only 50% of the animals were active initially and there was some initial bleeding. At 12 ppt the test animals hardly responded at all initially and bled when disturbed but they gradually grew more active over several days. Test animals transferred to 8 ppt had all died by the eighth day of the test. At the conclusion of the experiment on the 30th day only two other deaths had occurred.

Pathansali (1963) also carried out an experiment to determine the effect of changes in salinity on the activity of early spat measuring 0.25 mm to 1.00 mm in length. They were transferred from water with a salinity of 29 ppt to that with a salinity of 9.3 ppt in a series of small salinity decreases. Animals were maintained for 10 minutes in each consecutive salinity. It was observed that all the early spat were very active at salinities down to 18 ppt. At 15.4 ppt, only 80% of the spat were active; at 12.8 ppt, 50% were active and at 9.4 ppt all were inactive.

It would appear that *A. granosa* is able to function relatively efficiently at salinities above 23 ppt, although young specimens seem to be able to continue normal feeding activity at a lower salinity than older specimens. Very young individuals apparently remain active at even lower salinities (down to at least 18 ppt). Although feeding efficiency and activity generally decrease substantially at salinities less than 20 ppt, *A. granosa* is capable of acclimating to salinities as low as 12 ppt, at least in the short term. These results are consistent with the known distribution of *A. granosa* in areas where the salinity is usually in the range of 26 to 31 ppt but which are subject to large, short-term fluctuations.

Other *Anadara* species appear to have similar preferences for areas with an estuarine influence. According to Cahn (1951) *A. granosa bisenensis* has a preference for areas where there is a significant freshwater influence. Okera (1976) reported that *A. senilis* is found in the lower reaches of estuaries and Yoloye (1975) reported that it lives in estuaries, creeks and lagoons. Yankson (1982) has recorded the presence of a population of *A. senilis* in a Ghanaian lagoon which experienced a rise in salinity up to 50 ppt in the dry season. Squires et al. (1975) maintained that in the mangrove shores in Colombia where *A. tuberculosa* is found, salinities fluctuate between 15 and 23 ppt but Baquiero (1980) found that populations of *A. tuberculosa* in Baja California Sur, Mexico, were subject to salinities in the range of 30-40 ppt. *A. trapezia* is also found in areas where there is an estuarine influence (Sullivan 1960). Although it is normally found in waters with a salinity of approximately 30 ppt, it will acclimate well to and reproduce in water of 22 ppt. It can also acclimate to water of 12 ppt but will not grow at such a low salinity. Tolerance of high salinities is not good and catastrophic mortality ensues if exposed for a few days to water at 40 ppt. (Dixon, pers. comm.).

According to Ting et al. (1972) *A. subcrenata* occurs in areas where the chlorinity is in the range of 16-17.8 ppt (salinity 28.9-32.1 ppt). Kusukabe (1959) cited evidence indicating that the planktonic larvae of *A. subcrenata* have a well-defined preference for salinities between 24.6 and 29.8 ppt and in the Nakanoumi, a shallow saltwater lagoon enclosed by the Shimane and Yumigahama Peninsulas, Japan, they congregate in a narrow subsurface layer of water corresponding to this salinity range.

The mode of tolerance of species of *Anadara* to large fluctuations in salinity is not known. Djangmah et al. (1979) studied the response of *A. senilis* to changes in salinity. They found that the valves remained open at salinities down to 15 ppt. However, below this salinity, the animal isolated itself from the environment by closing up. Djangmah et al. (1979) examined osmotic and ionic concentrations of the hemolymph at the same time and found that these tended to follow changes in the external medium. When the valves were open, almost perfect osmoconforming took place. It would seem that this species is capable of tolerating the changes in its internal environment that are consequent upon a change in the external environment.

TEMPERATURE

The temperatures to which species of *Anadara* are exposed vary according to their geographical range. Temperatures experienced by *A. granosa* in Malaysia are generally in the region of 29 to 32°C, the average surface water temperature range throughout the year. Subpopulations high on the shore may be subjected to considerably higher temperatures during periods of minimal water movement. Broom (1980) found that under neap tide conditions, the temperature at the water's edge on a sunny day could rise to 40°C. Also, the temperature of the mudflat may drop several degrees at night. MacIntosh (1978), working in the same area as Broom, found that in an unshaded mudflat adjacent to a mangrove forest, the temperature could fall as low as 25°C in the early morning. Boonruang and Janekarn (1983) recorded substrate temperatures in an *A. granosa* population at Phuket, Thailand, as being from 25 to 31.4°C and water temperature as 25 to 32.8°C.

Other tropical species experience temperature regimes similar to those experienced by *A. granosa*. For example, Squires et al. (1975) found that temperatures in the mud inhabited by *A. tuberculosa* in Colombia range from 26 to 37.5°C. Baquiero (1980) reported that in Baja California Sur, Mexico, sea temperatures in the region vary from 17°C in March to 27°C in August but he also maintained that within the mangrove swamps where *A. tuberculosa* occurs, temperatures range from 29.5 to 35°C. Yankson (1982) mentioned that in some lagoons in Ghana inhabited by populations of *A. senilis*, temperatures may be consistently in the region of 32 to 34°C. *A. broughtoni* and *A. subcrenata*, being inhabitants of temperate waters, are subject to a much wider range of temperatures. Ting et al. (1972) reported that waters inhabited by *A. subcrenata* may range in temperature from 6°C in February to 27°C in September. Kusukabe (1959) gave a slightly larger range of 2-5°C in winter to 28-30°C in summer for waters inhabited by the same species. *A. trapezia* has not been found where the water temperature drops below 8°C (Dixon, pers. comm.).

OXYGEN

According to Bayne (1973), *A. granosa* is subject to low oxygen tension in its natural habitat. He found that the oxygen content of seawater as it rose over a mudflat on the flood tide could be reduced from full saturation to less than 60% saturation. He also found that the temperature of the standing water on the mudflat could rise considerably during the day, thus further contributing to reduction in oxygen content of the water. In a series of laboratory experiments, Bayne (1973) found that *A. granosa* is capable of maintaining oxygen consumption in the face of declining oxygen tension although smaller individuals have less capacity to regulate than larger ones.

It is possible that the resistance of members of the Anadarinae to low oxygen tensions is aided by the fact that they contain hemoglobin and erythrocytes in the blood (Kawamoto 1928). Collet and O'Gower (1972), cited by Bayne (1973), found that this hemoglobin is peculiar in that the hemoglobin/oxygen dissociation curve shifts to the left so that the diffusion gradient of oxygen across the ctenidia may be maintained, or even increased, at higher temperatures. This would clearly be of significance for an animal exposed to low oxygen tensions and simultaneous temperature increases.

Djangmah et al. (1980) reported that *A. senilis* is also an oxygen regulator at oxygen tensions between 50% and 100% saturation. However, they found that although hemoglobins were responsible for only 34% of the oxygen uptake at 25°C, there was sufficient hemoglobin in the hemolymph to act as an effective oxygen store during prolonged exposure to anoxic conditions.

A. broughtoni and *A. subcrenata* also inhabit areas which may be subject to severe oxygen depletion during summer periods (Kusukabe 1959; Kanno 1966). An unidentified species of *Anadara* (either *A. broughtoni* or *A. subcrenata*, but probably the former) was subjected to low oxygen tensions and monitored for mortality over a 12-day period (Anon. 1980). At 80% saturation, there were no mortalities during the test period whereas at 14.6% saturation, there was 60% mortality. At saturation levels below 14.6%, all animals died within the test period.

Biotic Factors

FOOD AND FEEDING MECHANISMS

Members of the Anadarinae lack well-developed siphons. Openings of the inhalant and exhalant streams lie flush with the posterior margin of the shell and do not extend beyond it. As a result, most species do not burrow into the mud to any depth. *A. granosa* frequently lies in the mud such that the posterior end protrudes slightly above the surface. At other times, both inhalant and exhalant openings may be below the surrounding level of the mud surface in a small depression. In such a situation in the laboratory, during filtration surface mud often falls from the edges of the depression into the inhalant opening.

Given this type of habitat, it seems that as long as the mud surface is easily resuspended then *A. granosa* is likely to be gaining its nutrition from a mixture of detritus (or microorganisms attached to detritus) and benthic microalgae. Broom (1982a) has shown that on mudflats in Selangor, Malaysia, the concentration of chlorophyll *a* in the benthic layer at high tide is usually around twice the concentration in the water column just below the surface. However, at mid-ebb tide, concentrations of chlorophyll *a* are higher still, indicating that substantial quantities of chlorophyll-bearing organisms are resuspended from the substrate. Examination of the content of water samples from the benthic layer revealed that they contained large quantities of benthic diatoms and diatoms typically found in shallow coastal waters (Broom 1980). These diatoms, together with foraminiferans, are invariably found in the guts of *A. granosa* (Broom 1982a). An illustration of a typical section through the gut of *A. granosa*, displaying the presence of diatoms, detritus and a foraminiferan, is presented in Fig. 1. Broom (1982b) has also produced evidence that a dense population of *A. granosa* may significantly reduce the amount of chlorophyll in the benthic boundary layer compared with the quantity of chlorophyll in the benthic layer of nearby mudflats where no such population is present.

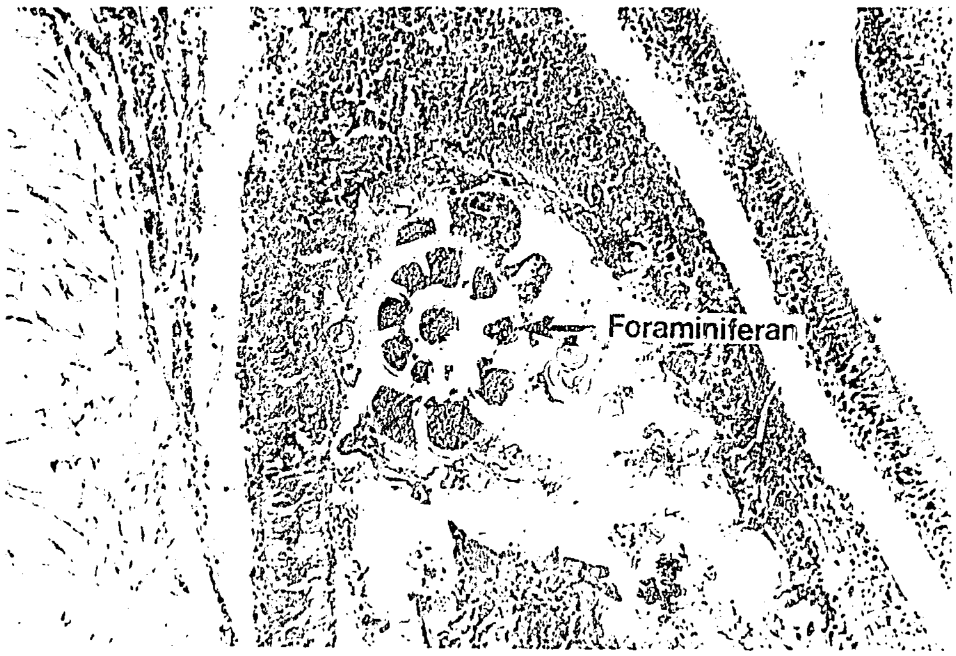


Fig. 1. A section through the intestine of *Anadara granosa* demonstrating the presence of a foraminiferan.

Reports in the literature of the likely sources of nutrition of other species of *Anadara* are almost non-existent. The only information found is a speculative reference to *Anadara cuneata* (Reeve) by Lim (1966). *A. cuneata* is a large subtidal Indo-Pacific anadarinid that establishes deep burrows in relatively firm mud (Lim 1966). The posterior end of the shell is usually a few centimeters below the surface of the mud and the burrow is usually filled with turbid water. Lim (1966) found that *A. cuneata* maintains a "diffuse" anterior inhalant water current which brings in resuspended organic particles that "probably serve as a major source of food". Those species that do not inhabit predominantly muddy substrates presumably place a greater reliance upon material produced in the water column.

As a general rule, bivalve molluscs are not particularly well adapted to filtering water with high concentrations of suspended solids. Consequently, unless they are specifically adapted for deposit feeding (e.g., tellinids, nuculanids) they tend to be excluded from soft mud substrates where there may be substantial resuspension of particulates (Rhoads and Young 1970). Many of the Anadarinae however, appear to have adapted to exploit the niche for a filter feeder that can cope with high concentrations of suspended solids. This has been demonstrated by the work of several authors as follows.

Sullivan (1960) has shown that in *A. trapezia* the coarse frontal cilia on the filaments of the ctenidia are particularly extensive, and he suggested that this is significant in determining the relative efficiency of sorting of particulate matter. He found that when the water contains a lot of sediment the coarse frontal cilia are fully active. They carry large particles ventralwards to the free edges of the ctenidia whence they are carried posteriorly in a rejection current. This is in itself unusual because in most bivalves the current along the ventral edge of a ctenidium is an anteriorly-directed feeding current. Some large particles fail to be removed by the coarse cilia. These end up in the dorsally-directed currents created by fine cilia and are directed toward the feeding grooves and thence to the labial palps. The latter possess very large, extensively ridged sorting areas and, according to Sullivan, are quite capable of sorting large quantities of relatively coarse material. Sullivan also noted that, presumably as a result of these adaptations, *A. trapezia* could continue feeding in quite heavy silt loads.

Lim (1966) compared the ciliary currents in *Anadara antiquata, A. anomala* and *A. cuneata* which, as indicated above, live in environments where they will experience markedly different concentrations of suspended solids. *A. antiquata* inhabits rocky areas, *A. anomala* inhabits sandy substrates and *A. cuneata*, muddy substrates. Lim (1966) found that on the labial palps of *A. antiquata* there were 40 transverse folds; on those of *A. anomala*, 43, and on those of *A. cuneata*, 150. He also found that the order of complexity of the labial palps was *A. antiquata* < *A. anomala* < *A. granosa* < *A. cuneata*. He suggested that this was due to the differences in the environment of the four species with *A. cuneata* having to deal with the heaviest loads. Lim (1966) noted that in both *A. granosa* and *A. cuneata* there is a strong ciliary current carrying particles collected from the outer surface of the labial palps onto the inner surface at the distal portion. This was not present in *A. antiquata* and *A. anomala* and was not observed by Sullivan (1960) in *A. trapezia*.

Yoloye (1975), working on *A. senilis*, reported ciliary currents similar to those found by Sullivan (1960) and Lim (1966). He noted that there are strong ciliary currents on the visceral mass, foot and mantle which remove silt and sand from the mantle cavity and prevent clogging of the gills. He further noted that *A. senilis* possesses particularly well-developed labial palps of considerable length (4 mm) and that these play a major role in sorting large quantities of particulates.

COMMUNITY ECOLOGY

Apart from general habitat descriptions, there is little information in the literature pertaining to the community ecology of species of *Anadara*. Detailed information has, however, been provided by Broom (1982a) for a Malaysian mudflat community of which natural populations of *Anadara granosa* formed a part, and by Boonruang and Janekarn (1983) for an *A. granosa* population at Phuket, Thailand. Broom (1982a) examined two areas on the mudflats of Selangor, Malaysia, where natural settlement of *A. granosa* occurs. Using a sampling technique which allowed collection of animals measuring more than 2 mm in their smallest dimension, he built up a picture of community composition as presented in Table 3. From this table, it can be seen that in the areas studied *A. granosa* was invariably a biomass dominant. At one natural bed, it was also a numerical dominant constituting 64% of the animals while at another, it constituted 33% of the animals (but maintained biomass dominance). Other numerically important species were a venerid bivalve mollusc, *Pelecyora trigona*, and the small gastropods *Plicarcularia leptospira* and *Cerithidea cingulata*. Broom (1982a) also took a limited number of samples using a technique which retained animals larger than 0.5 mm in their smallest dimension. This revealed that another important component of the community was the tiny gastropod *Stenothyra glabrata* which was numerically as abundant as *A. granosa* although its biomass per unit area was only 1% that of *A. granosa*.

Also indicated in Table 3 is the trophic status (observed or presumed) of most members of the natural community. Broom (1982a) classified *A. granosa* as a surface deposit feeder and *P. trigona* as a suspension feeder on the basis of the fact that the former effectively has no siphons while the latter has. However, the siphons of *P. trigona* are rather short (1 cm), and there is, therefore, a possibility that the species compete for essentially the same food source. Certainly, since both are shallow burrowers they would inevitably compete for space, and in this sense, must be viewed as competitors. The nassariid gastropods which constitute the bulk of the remainder of the community are scavengers and therefore would offer no competition.

The major predators in the community are the gastropods *Natica maculosa* and *Thais carinifera*. Although they are not very abundant in terms either of numbers or biomass, they are nevertheless important. Their impact upon populations of *A. granosa* is discussed in greater detail in the

Table 3. Composition of the community associated with two natural populations of *Anadara granosa* on mud-flats in West Malaysia. $\overline{N}$ represents mean number per 0.4 m^2; $\overline{B}$ represents mean total wet weight per 0.4 m^2. (Source: Broom 1982a)

Species	Sungei Buloh $\overline{N}$	%	$\overline{B}$	%	Kuala Selangor $\overline{N}$	%	$\overline{B}$	%	Trophic status[a]
Bivalvia									
Anadara granosa	33	64	109	97.2	63	32.9	137	79.2	SDF
Pelecyora trigona	0.36	0.7	0.03	+[b]	91	47.5	25	14.4	SF
Meretrix lusoria	+	+	+	+	—	—	—	—	SF[c]
Tellina lux	—	—	—	—	0.14	0.1	0.06	+	SDF
Tellina pudica	—	—	—	—	0.03	+	+	+	SDF
Theora opalina	0.01	+	+	+	0.01	+	+	+	SDF[c]
Orbicularia orbiculata	0.01	+	+	+	—	—	—	—	SDF
Nuculana bellula	+	+	+	+	—	—	—	—	DF[c]
Gastropoda									
Plicarcularia leptospira	12.6	24.4	1.58	1.4	28	14.6	3.90	2.3	S
Plicarcularia pulla	0.38	0.7	0.16	0.1	1.3	0.7	1.14	0.7	S
Nassarius jacksonianus	0.13	0.3	0.07	0.1	0.45	0.2	0.31	0.2	S
Nassarius plicnocostata	0.06	0.1	0.03	+	0.16	0.1	0.09	0.1	S
Zeuxis olivaceus	0.05	0.1	0.02	+	0.01	+	0.01	+	S
Thais carinifera	0.01	+	0.04	+	0.89	0.5	2.81	1.6	P
Volema sp.	+	+	+	+	0.01	+	+	+	P[c]
Natica maculosa	0.12	0.2	0.11	0.1	0.82	0.4	1.23	0.7	P
Cerithidea cingulata	4.4	8.5	0.96	0.9	2.1	1.1	+	+	G/SDF[c]
Clithon ovalaniensis	—	—	—	—	0.02	+	+	+	G/SDF[c]
Neritina sp.	—	—	—	—	0.11	0.1	0.02	+	G/SDF[c]
Scaphopoda									
Dentalium sp.	—	—	—	—	0.01	+	+	+	DF
Crustacea									
Diogenes sp.	0.41	0.8	0.11	0.1	3.3	1.7	0.93	0.5	S/P[c]
Clibanarius padavensis	—	—	—	—	0.24	0.1	0.37	0.2	S/P[c]

[a]SDF, surface deposit feeder; SF, suspension feeder; DF, deposit feeder; S, scavenger; P, predator; G, grazer.
[b]+ = $\overline{N}$ < 0.005/0.4 m^2, or $\overline{B}$ < 0.005 g/0.4 m^2 or < 0.05% of total.
[c]Presumed rather than observed trophic status.

section on mortality and predation. Vermeij (1980) has reported that the muricid *Bedeva blosvillei* is an important predator of *A. granosa* in one area of Indonesia.

The above dealt with animals collected as part of normal sampling procedures applied to the benthic community. Other animals, not sampled by the techniques used, may also be ephemeral members of the community. Such forms include skates and rays and wading birds. Pathansali and Soong (1958) stated that skates are major predators of populations of *A. granosa*. Tookwinas (1985) reported that in Thailand the catfish, *Plotosus anguillaris*, eats small specimens of *A. granosa*. The commonest species of wading bird that appears on the mudflats and that is likely to eat small bivalves is the redshank, *Tringa totanus*. Another wader is the greenshank, *Tringa nebularia*. A single greenshank caught at the edge of the mangrove swamp forest at Kuala Selangor, Malaysia, by Dr. D. Wells was found to have been feeding almost exclusively on very small *A. granosa*.

The communities found in areas at Kuala Selangor where *A. granosa* does not occur naturally but is seeded for culture purposes are impoverished compared to those occurring in areas of natural settlement. The only additional species of importance not mentioned in Table 3 but recorded by Broom (1980) at artificial culture sites is the barnacle, *Balanus amphitrite*. When it occurs, *B. amphitrite* is found encrusting the posterior end of specimens of *A. granosa* which protrude above the surface of the mud. At two sites at Kuala Selangor, artificially seeded with populations of *A. granosa*, *B. amphitrite* removed from the shells of *A. granosa* constituted 2.5% and 3.5%, respectively, of the total biomass of the community. Broom (1980) established that the degree of infestation tends to be a function of exposure as indicated in Table 4. At any one location, the degree of infestation varies with time but it may be as high as 75%, as illustrated in Fig. 2. These data are of importance because it is possible that *B. amphitrite* is an important competitor for food, bearing in mind its habitat near the inhalant siphon of *A. granosa* and the fact that it is essentially a filter feeder.

Table 4. Variation in percentage infestation of *A. granosa* by *Balanus amphitrite* in an artificially seeded population at Kuala Selangor, Malaysia. (Source: Broom 1980)

Height above chart datum (cm)	% bearing barnacles
250	0.82
230	2.23
200	9.03
185	8.56
145	7.22
130	9.97
110	13.93

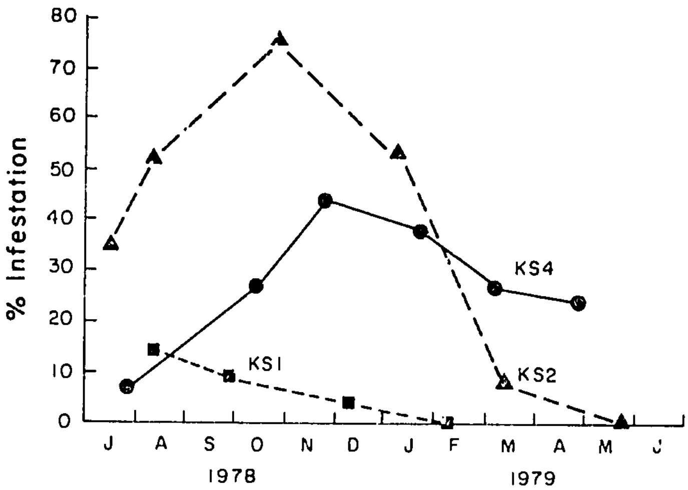


Fig. 2. Variation with time of the percentage of *Anadara granosa* encrusted with barnacles, *Balanus amphitrite*, in three different populations. All populations studied were at Kuala Selangor, Malaysia. KS2 and KS4 were artificially seeded populations on mudbanks bordering the course of the main flow of the estuary of the Selangor river. KS1 was a natural population somewhat removed from the area of the main flow. (Source: Broom 1980)

Boonruang and Janekarn (1983) described the animal community in each of three zones on the shore of Sapum Bay, Phuket, which were inhabited by *A. granosa.* Zone I extended from mean high water of neap tides to mean low water of neap tides. Zone II was from mean low water of neap tides to just above mean low water of spring tides and Zone III encompassed the remainder of the shore and sublittoral area below Zone II. Zone I was inundated about 70% of the time, Zone II 90% of the time and Zone III almost 100% of the time. Boonruang and Janekarn did not give densities of the individual species found. However, it is clear from the information provided that Zone I was dominated by gastropods, particularly *Cerithidea cingulata* and several species of nassariids including *Nassarius jacksonianus,* and *Plicarcularia pulla.* Zone II was jointly dominated by crabs and gastropods but the nassariids were rather sparse and other gastropods, particularly *Murex trapa* and *Turitella terebra,* were more important. Both Zone I and Zone II contained a species of naticid, *Natica antonii* and *Natica tigrina,* respectively. Species of *Anadara* other than *A. granosa* were also found in both zones. *Anadara nodifera* and *Anadara trocheli* (Dunker) were found in Zone I while *A. nodifera, A. trocheli* and *Anadara inaequivalvis* were found in Zone II. Zone III possessed an impoverished fauna dominated by gastropods; there were no specimens of *A. granosa* in this zone. Densities of *A. granosa* itself were relatively low compared with those found by Broom (1982a, 1983a) on mudflats in Selangor. Densities in Zone I ranged from 0.7 to 2.3/m^2 and in Zone II from 0.06 to 1.3/m^2. While harvesting helped to account for these low densities, particularly in Zone III (Boonruang and Janekarn 1983), it seems likely that the rather sandy substrate represents a sub-optimal habitat for this species.

As mentioned previously, information pertaining to the communities among which other species of *Anadara* are found is extremely limited. In fact, it is limited primarily to lists of predators. *A. granosa bisenensis* is said by Cahn (1951) to be subject to predation from ducks, sea bream *(Sparus swinhonis),* gobeoid fishes *(Taenioides rubicundus* and *Boleophthalmus pectinirostris),* blue crab *(Neptunus trituberculatus)* and drills *(Rapana thomasiana* and *Natica maculosa).* Cahn (1951) also maintained that *A. subcrenata* is subject to predation from ducks *(Anas platyrhynchus platyrhynchus* and *Aythia fuligula)* and octopus *(Polypus vulgaris* and *Polypus pang-siao),* as well as blue crab and drills. Kusukabe (1959) listed the most important predators of the spat of *A. subcrenata* as the sea bass *(Lateobrax japonicus),* eel, octopus, blue crab, drills and starfish. The starfish *Asterias amurensis* has been identified as a predator of an unidentified species of *Anadara* (probably *A. broughtoni*) (Anon. 1979, 1980). Both Cahn (1951) and Kusukabe (1959) mentioned that *Brachiodontes* sp. is an important competitor of *A. subcrenata.* Apparently, this mytilid can cause large-scale mortalities of young *A. subcrenata* by secretion of a thick mass of byssus over the bottom, suffocating the young anadarinids. This is only likely to happen where the substrate is such that *Brachiodontes* can find a suitable anchorage.

Okera (1976) was of the opinion that boreholes found in *Anadara senilis* were probably caused by *Thais callifera* and *Thais forbesi* which are quite abundant on mangrove stilt roots. He further maintained that wading birds (at low tide) and the stingray *(Trygon margarita)* and portunid crabs (*Callinectes* sp.) at high tide are other probable predators.

POPULATION DYNAMICS

Length/Weight Relationships

Length/weight relationships of a number of anadarinids are published in the literature. These are summarized in Table 5.

Table 5. Length/weight relationships of some species of *Anadara*. The relationship is assumed to take the form $W = aL^b$ where W = total wet weight (g) and L = length (mm or cm as indicated).

Species	Location	Size range	a	b	Authority
A. granosa	India	3 — 19 mm	1.9360×10^{-4}	3.2096	Narasimham (1969)
		20 — 63 mm	1.3391×10^{-3}	2.6459	Narasimham (1969)
A. granosa	Malaysia	0.75— 3.2 cm	0.245	3.295	Broom (1982c)
	Malaysia	0.75— 3.2 cm	0.215	3.373	Broom (1982c)
A. granosa	Thailand	—	0.3638	3.0438	Boonruang & Janekarn (1983)
A.g. bisenensis	Korea	— (mm)	4.327×10^{-4}	2.9374	Yoo (1971)
	Korea	— (mm)	8.145×10^{-4}	2.7284	Yoo (1971)
	Korea	— (mm)	6.031×10^{-3}	2.1532	Yoo (1971)
A. broughtoni	Korea	— (mm)	3.245×10^{-3}	2.4408	Yoo (1970)
	Korea	— (mm)	4.484×10^{-4}	2.8638	Yoo (1970)
	Korea	0.05— 1.59 cm	0.1996	2.5726	Yoo & Yoo (1974)
	Korea	1.60— 1.99 cm	0.2060	2.8400	Yoo & Yoo (1974)
A. subcrenata	Japan	—	0.236	3.2862	Ting et al. (1972)
A. subcrenata	Korea:				
	Sinan	30 — 45 cm	0.8714	2.2857	Yoo (1977)
	Baedon	30 — 45 cm	0.9012	2.1809	Yoo (1977)
	Sooncheon	30 — 45 cm	0.4713	2.6496	Yoo (1977)
	Booan	30 — 45 cm	0.7894	2.2481	Yoo (1977)

Growth

Anadara granosa in natural beds takes approximately six months to grow to 4-5 mm in length (Broom 1982a). In artificially seeded beds, it takes a further year to grow to 30 mm in length (Broom 1980) although this may vary according to local conditions. Similar growth rates were reported by Pathansali and Soong (1958) and Pathansali (1966). The former authors found that on natural beds, where the density was less than 10.5/m², *A. granosa* grew from 4-10 mm to 18-32 mm in nine months. On culture beds, at a density of 525-1,050/m², a size of 18-32 mm was attained in 10-12 months. Pathansali (1966) found that in culture beds seeded with individuals 4-8 mm long, 50% of the population achieved a length of 25.4 mm in six months. Narasimham (1969) studied a population of *A. granosa* in Kakinada Bay, India, and reported a first year growth rate similar to that observed by Broom (1982b) and Pathansali (1966) of 4.5 mm to 31.5 mm in one year. The second year growth rate reported by Narasimham, 31.5 to 49.5 mm, was much faster than that reported by other workers. However, Narasimham (1969) studied a population with three size classes and the growth rates he reported were based on modal progression. From the figures of size-frequency distribution presented, his identification of a modal group at the larger size must be treated with some skepticism. Data presented by Pathansali (1966) and Broom (1982b) indicate that the growth of *A ranosa* conforms to the von Bertalanffy model

$$l_t = L_\infty (1 - e^{-Kt})$$

where

l_t is length at time t;
L_∞ is the asymptotic length; and
K is a constant indicating the rate at which the maximum size is approached.

Broom (1982b) assumed that this model holds for sizes of *A. granosa* greater than 5 mm and estimated K and L_∞ values for a number of populations and subpopulations. He found that for the artificially seeded populations he studied, growth rates were not significantly different and overall K = 1.01 (95% confidence limits: 0.64 and 1.39) and L_∞ = 44.4 mm (corresponding extreme values 53.5 mm and 40.2 mm). Based on data provided by Pathansali (1963), similar estimates of K and L_∞ for populations studied by him have been made (Table 6). Average values of K are higher, and L_∞ values correspondingly lower, in populations studied by Pathansali compared with those studied by Broom because those studied by the former were subjected to continued harvesting which would have removed the larger individuals. This would have had the result of depressing L_∞ values and increasing values of K. However, Pathansali also provided data for what he termed "large cockles" at Batu Muang. For two of the three increments he measured, the increment is unlikely to have been distorted by size-selective harvesting and would probably provide more directly comparable estimates of K and L_∞. For this site the L_∞ value (given in Table 6) is close to that found by Broom (1982b) and although the mean K value is substantially lower, the ranges of the confidence limits

Table 6. Growth constants (K) and L_∞ values of *Anadara* species derived from published data.*

Species	Location	K (yr^{-1}) mean	u.f.l.	l.f.l.	L_∞ (mm) mean	l.f.l.	u.f.l.	Authority
A. granosa	Kuala Selangor	1.01	1.39	0.64	44.4	40.2	53.5	Broom (1982b, 1983a)
A. granosa	Jelutong	3.39	4.64	2.14	35.9	26.2	56.7	Pathansali (1966)
A. granosa	Kuala Jarum Mas	4.18	4.63	3.73	30.3	27.3	33.9	Pathansali (1966)
A. granosa	Batu Muang	2.11	3.05	1.17	29.6	20.5	53.4	Pathansali (1966)
A. granosa	Batu Muang (large individuals)	0.62	0.75	0.49	49.6	41.0	63.0	Pathansali (1966)
A.g. bisenensis	Japan	0.24	0.37	0.12	73.3	48.4	150.3	Cahn (1951)
A. subcrenata	Japan	0.68	0.83	0.53	53.6	43.8	68.9	Kusukabe (1959)

*All populations of *A. granosa* were located in Malaysia. Constants have only been derived from those data in the literature which yielded a significant fit to the model $\Delta l/\Delta t = K(L_\infty - l)$ where Δl is the small increment in the time period Δt and l is length at time t; u.f.l. = upper fiducial limit; l.f.l. = lower fiducial limit.

of the two values overlap. The growth rates cannot, therefore, be assumed to be significantly different. Judging from the corresponding ranges of L_∞, it would appear from Broom's data that specimens of *A. granosa* larger than 53.5 mm would be a very rare occurrence. Pathansali's data indicate the theoretical maximum size could be as large as 63 mm. Narasimham (1969) regularly found specimens in his samples measuring 63 mm in length. The largest specimen discovered by Boonruang and Janekarn (1983) at Phuket was 51 mm long.

The information provided by Pathansali and Soong (1958) indicated that density might have an effect on the growth of *A. granosa*. Broom (1982b), working on two natural populations, found that in one population the mean wet weight of specimens of *A. granosa* in a sample was negatively correlated with density. In a study of a second population, he found that growth in wet weight could vary enormously between subpopulations subject to different environmental conditions (Fig. 3).

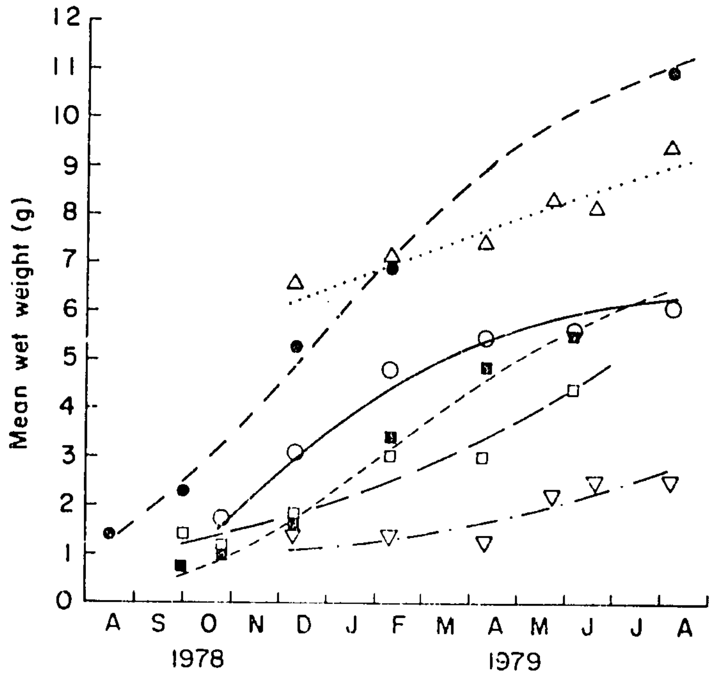


Fig. 3. Growth in mean wet weight of different subpopulations within a natural population of *A. granosa* at Kuala Selangor, Malaysia. (Source: Broom 1982b). CD = chart datum.

▽	Max density	500/m^2, 320 cm above CD, 1978 year class
△	Max density	500/m^2, 320 cm above CD, 1977 year class
○	Max density	500/m^2, 270 cm above CD, 1978 year class
●	Max density	500/m^2, 200 cm above CD, 1978 year class
■	Max density	500-1,000/m^2 including *Pelecyora trigona*, 260 cm above CD, 1978 year class
□	Max density	1,000/m^2, 220-250 cm above CD, 1978 year class.

Broom (1982b) confirmed in field experiments that both density and exposure affect the growth of *A. granosa*. Investigating the effects of density, he set up experimental plots at 250 cm above chart datum (CD) seeded at densities of 125, 625, 1,250, 1,875 and 2,500 individuals/m^2 and monitored growth by taking samples from the populations. For purposes of comparison between densities, he assumed the growth constant would be the same for all plots and, taking K to be the same as that for artificially seeded populations (1.01), he calculated the L_∞ value for each plot. The results he obtained in this manner are illustrated in Fig. 4. The relationship was best represented by the formula

$$L_\infty = 33.6 - 0.266B$$

where L_∞ is expressed in mm and B is biomass (g dry tissue/m^2). The 95% limits of confidence for the gradient of this relationship were reported by Broom (1983a) as -0.191 to -0.343 with corresponding intercept values of 31.8 and 35.4 mm. Broom (1982b) emphasized strongly that such a relationship had to be considered as site-specific, especially in view of the fact that his experiments were carried out in an area where *A. granosa* was not normally sown and did not settle naturally.

Broom (1982b) also sowed *A. granosa* at the same density ($100/m^2$) in experimental plots at 250, 200 and 150 cm above CD. Again assuming a common K value of 1.01, he calculated the L_∞ value for each population. The results obtained in this manner are illustrated in Fig. 5, which also includes a point estimated by eye, of growth in a high-shore population of *A. granosa*. Broom (1982b) argued that the most likely relationship between L_∞ and exposure would take a sigmoid form. Hence, the curve in Fig. 5. He expressed the view that once below the intertidal zone a

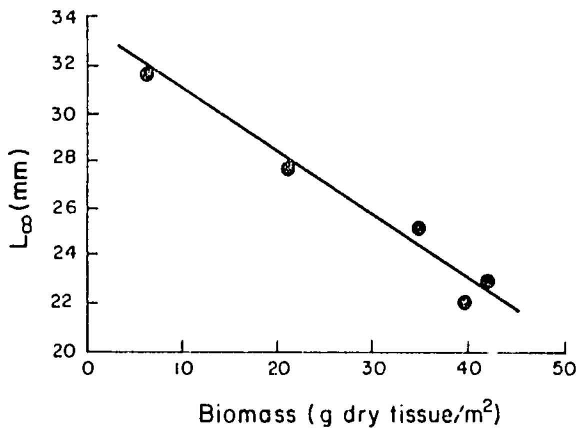


Fig. 4. *Anadara granosa*. Derived estimates of L_∞ as a function of biomass in experimental plots at Kuala Selangor, Malaysia. (Source: Broom 1982b)

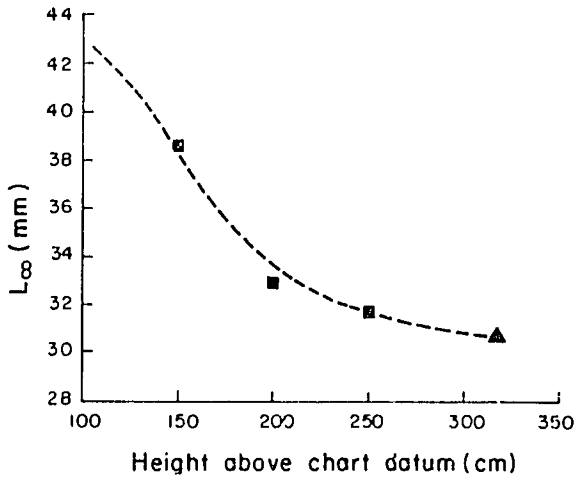


Fig. 5. *Anadara granosa*. Derived estimates (■) of L_∞ as a function of shore elevation in experimental plots at Kuala Selangor, Malaysia. ▲ is an estimate of L_∞ of one subpopulation in a natural population at Kuala Selangor. The curve is fitted by eye. (Source: Broom 1982b)

decrease in elevation would not result in an increase in feeding time and, therefore, there would be no additional effect upon growth. At higher shore levels, compensatory feeding or metabolic activity would be likely to help maintain growth in the face of increasing exposure although there is also probably a level above which growth rate declines rapidly with increasing exposure unless preceded by the death of the organism due to the increasing effects of other factors, such as thermal stress.

The subspecies *A. granosa bisenensis* exhibits a much slower rate of growth, presumably because it occurs at higher latitudes where there exist pronounced seasons. Yoo (1971) reported that in Korea the growing season extends from June to September, a size of 24 mm being achieved two years after spatfall. Data in his paper indicate that growth actually takes place throughout most of the year. The mean length of individuals in the population he studied changed from 18.5 mm in January to 24 mm in September with another 2.5 mm being added between September and the following January. The largest specimen he recorded was 41.1 mm long which accords reasonably well with L_∞ values of *A. granosa* in Malaysia. Cahn (1951) provided data on the growth of *A.g. bisenensis* in Japan from which were calculated the values of the growth constant and asymptotic size which are presented in Table 6. The table shows that the growth constant is very low and the asymptotic size rather large (although the confidence limits are wide). This confirms the view that the subspecies grows slowly. Cahn (1951) found individuals up to 70 mm long, similar to maximum recorded lengths of *A. granosa* reported by Narasimham (1969).

Data pertaining to the growth of *A. subcrenata* have been provided by Cahn (1951), Kusukabe (1959) and Ting et al. (1972). Information provided by Cahn (1951) could not be used to calculate values of K and L_∞. Overall, because of the larger size attained, growth of the species appeared to be faster than that of *A. granosa*. Kusukabe's (1959) figures were for individuals up to three years old and analysis indicated growth rates only slightly faster than those for *A. granosa* (see Table 6). Ting et al. (1972) provided data for two size groups of *A. subcrenata*. One group grew from 5-12 mm to 30-37 mm in one year; the other group grew from 23-31 to 46-49 mm in one year. This indicates growth rates distinctly faster in a seasonal environment than those achieved by *A. granosa* in a tropical environment.

A. broughtoni appears to be an extremely rapidly-growing anadarinid. Yoo (1970) maintained that under hanging culture in Korea this species grew from 4 mm to 48 mm in one year. Even in the littoral zone average growth was 32 mm to 55 mm in one year. Subsequently Yoo and Yoo (1974) monitored the growth of spat which had settled on hanging collectors and found that these grew from an average length of 0.54 mm to 10.47 mm between 17 September 1973 and 25 November 1973 but there was little growth over the winter at the end of which the mean length was only 11.08 mm. Yoo and Park (1978) studied the growth of *A. broughtoni* in the Geoje area of southern Korea for three years. In the first year, under hanging culture, the mean length of the population increased from 3.71 mm to 40.03 mm. The experimental population was then transferred to the seabed in the marginally sublittoral area and a year later the mean length was 78.86 mm. Toyo et al. (1978) provided some data on growth of an unidentified species of *Anadara* in Japan, probably *A. broughtoni*. Their data indicate that the species they studied may grow from spat to 40 mm in one year and to just below 60 mm in the next six months, a very rapid rate of growth when compared with other anadarinids.

Data on other commercially exploited species are much more sparse. According to Squires et al. (1975), *A. tuberculosa* is a slow-growing but large species. Between 34 mm and 64 mm length, recorded growth was 1 mm/month. The largest specimen found measured 110 mm. Butler (unpublished data) carried out some preliminary studies of *A. cornea* in Fiji and found some evidence that this species grows from settlement to 20 mm in less than one year but may take four years to reach 60 mm. Similar growth rates are shown by *A. trapezia* (Dixon, pers. comm.). Although a tropical species, *A. senilis* apparently exhibits seasonal variations in growth rate resulting in the formation of growth checks or rings (Okera 1976). The growth checks are formed when growth slows dramatically during the peak rainy season in July-September. The heavy rains at this time of year result in a relatively low water temperature and depressed salinity coupled with high turbidity and substratum movement, all of which are thought to have an adverse effect on growth rates and feeding (Okera 1976). Okera also reported that growth rates of *A. senilis* may vary considerably between populations and that there is some evidence that growth rates in the sublittoral are higher than in the littoral zones of the shore. In this respect, his findings are similar to those of Broom (1982b) for *A. granosa*. *A. senilis* grows to a large size. Okera (1976) found that for one population, K values were in the range of 0.27 to 0.31 with associated L_∞ values of 99 mm to 67 mm. In another population, the estimated K value was 0.22 and L_∞, 145 mm.

Mortality and Predation

Broom (1983a) monitored the decline in density of both natural and artificially seeded populations of *A. granosa* and found that in three out of four populations studied, the decline could be adequately described by an equation of the form

$$N_t = N_o \cdot e^{-Zt}$$

where

N_t is number alive at time t;
N_o is number alive at time zero and
Z is the instantaneous mortality coefficient.

Values of Z obtained for different populations at Kuala Selangor, Malaysia, are presented in Table 7. Data provided by Pathansali and Soong (1958) indicate that on culture beds in Penang and Perak a mortality of 80% could be experienced between sowing and harvest (10-12 months). This is equivalent to Z = −1.61 to −1.93/year. On occasion, culture beds of *A. granosa* may suffer sudden large-scale mortality. Liong (1979) reported that in Penang and Perak in October 1977 there were sudden large-scale mortalities (20-50%) over a period of a few days. The mortalities corresponded to a period of particularly heavy rainfall, and salinity values over the affected beds in one river mouth ranged from 2.0 ppt at the surface to 4.0 ppt at the bottom. Even though salinity varied with the state of the tide, for several consecutive days it did not exceed 14.0 ppt in an area where it was usually in the region of 30.0 ppt. From the results obtained in laboratory experiments (see section on salinity), persistent salinity values in the range of 4-14 ppt would be expected to lead to significant mortalities. Liong (1979) therefore concluded that the sudden dramatic depression of salinity was responsible for the mortality. Broom (1983a) recorded no massive mortality during the wet season in the populations he studied, but these were mainly outside the mouth of the nearby Selangor River and he never recorded a salinity less than 14.0 ppt over artificially seeded beds (Broom 1980).

Table 7. Instantaneous mortality coefficients (Z) derived from monitoring decline in density of natural and artificially seeded populations of *A. granosa* at Kuala Selangor, Malaysia. (Source: Broom 1983a)*

Site	Year	Initial density (N/m^2)	Z (per year)
KS 1	1978/79	335	−1.87
KS 2	1978/79	258	−1.77
KS 2	1977/78	125	−2.30
KS 3	1977/78	98	−1.17

*Site 1 was a natural population, the remainder were artificially seeded populations.

Broom (1983a) also conducted field experiments to determine differences in mortality rates at different shore elevations and densities. Results are presented in Table 8. At different densities (125 to $2,500/m^2$), there was no evidence of a difference in mortality rates. Broom (1983a) pointed out that this is consistent with the findings of other workers who examined mortality rates among populations of molluscs inhabiting soft-sediment shores. Broom's experiments did, however, reveal distinct differences in mortality rates at different shore elevations, with mortality likely to be greatest at low shore elevations. This he ascribed to the relatively greater degree of accessibility of low shore populations to aquatic predators, a conclusion borne out by the greater preponderance of drilled shells found at lower elevations.

Kusukabe (1959) provided some data relating to mortality among populations of *A. subcrenata*. He reported that spat sown on the seabed at $15,000\text{-}30,000/m^2$ declined to $5,500\text{-}6,600/m^2$

Table 8. Instantaneous mortality coefficients (Z) for populations of *A. granosa* in experimental plots at different densities and shore elevations at Kuala Selangor, Malaysia. (Source: Broom 1983a)

Nominal initial density (N/m^2)	Actual initial density (N/m^2)	Elevation above chart datum (cm)	Z (per year)
2,500	2,982	250	−1.44
1,875*	2,321*	250	−1.27
1,250	1,642	250	−1.44
625	986	250	−1.84
125	113	250	−0.65
100	149	250	−0.22
100	159	200	−0.57
100*	121*	150	−2.54

*The fit to the model $N_t = N_o \cdot e^{-Zt}$ was only significant in these instances.

six months later, equivalent to an instantaneous mortality coefficient of −1.83 to −3.22/year, considerably greater than that experienced by populations of *A. granosa*. Kusukabe (1959) also reported that when *A. subcrenata* is re-sown as "seed" there is likely to be 60-70% mortality before harvest in the ensuing year.

A considerable amount of information about the mortality of an unidentified species of *Anadara* (probably *A. broughtoni*) in Japan was provided by Toyo et al. (1978) and Anon. (1979, 1980). Toyo et al. (1978) reported that over two years, the average survival of spat under hanging culture was 26.6%, equivalent to an instantaneous mortality coefficient of −0.66/year, a relatively low rate of mortality. However, in field experiments using individuals with a mean length of 38 mm, much higher rates of mortality were observed. In one set of experiments in Yamaguchi, survival was monitored in cages suspended from buoys and cages fixed to the seabed. Experiments began in June and after two months, survival was in the region of 80-90%. However, in August there was sudden massive mortality so that by September survival was 15 to 33%. By December, it was 9 to 19% with no consistent differences between hanging and bottom cages. There was some circumstantial evidence that the large-scale mortality was due to a rise in water temperature to above 25°C which occurred at the same time. This was backed up by experiments in another location, Koo City, where there was a significant difference between bottom and surface water temperature (21°C as against 27°C, respectively, in August) and a corresponding difference in mortality among *Anadara* in hanging culture 2 m below the surface and those on the bottom at 23 m depth (survival after six months was 72.5% at the bottom and 47% in the hanging cages).

The survival of three size groups of this *Anadara* sp. was examined in a lower shore plot in Yamaguchi district (Anon. 1979). The experimental area dried out for about two hours on each tide. No indication is given in this report of the inherent variability in the data. However, the latter appear to indicate that there was no difference in mortality in size groups measuring 40 mm (large yr I individuals) and 56 mm (yr II individuals) with final survival after 21 days being 19% and 8%, respectively. Among the smallest size group (22 mm, small yr I individuals), mortality was more rapid and final survival after 21 days was only 1%. This was attributed to the high temperatures (up to 28°C) that occurred throughout the study during low tide periods.

At a different site in Shitamatsu, 100 m^2 areas in 13 m of water were stocked with different densities of *Anadara* sp. whose mean length was 31.3 mm. There was very high mortality in all the plots so that after 63 days there was virtually 100% mortality. This was attributed to invasion by the starfish, *Asterias amurensis*. Conversely, mortality in baskets in hanging culture, suspended a few meters above the bottom, was much lower. Out of three baskets containing *Anadara*, two were torn from their moorings after 27 days by a typhoon and floated to the surface. After 63 days, mortality in these was 65 to 75%. However, in the basket that remained in place, mortality was only 4%. Similar results were obtained in a repeat of these experiments at Koo City. Mortality on the bottom at three of the four densities (50, 20 and 10/m^2) was 100% after 39 days; at 5/m^2, it was 80% after 29 days. Conversely, in baskets suspended a few meters above the bottom, mortality was only 2 to 6% after 39 days. *A. amurensis* was again identified as the cause of massive mortality. At the beginning of the experiment, no specimens of *A. amurensis* were present in the experimental area. However, they began to move into the area shortly after it was stocked so that 18 days after stocking they were present in the highest density plot (50 *Anadara*/m^2) at an average density of 11.5/m^2. Thirty-nine days after stocking, the densities of *Asterias* dropped appreciably, and 78 days after stocking, they were present at densities of 0.02 to 0.10/m^2.

The effect upon mortality of enclosing experimental populations of *Anadara* sp. (36 mm long) in cages (mesh size not specified) on the sea floor was also examined (Anon. 1980). At one location, Shitamatsu, it was found that the survival within the enclosures averaged 52.8% after 296 days whereas in open, unprotected plots, survival averaged 11.3% at the end of the same period. The difference was thought to be due primarily to the exclusion of the starfish, *Asterias amurensis*.

In a second set of experiments, the effects upon survival of holding *Anadara* sp. under different conditions were examined (Anon. 1980), namely:

(1) in hanging baskets 8 m below the water surface with a layer of sand 5 cm thick on the bottom of the basket;

(2) in hanging baskets 12 m below the surface with a layer of sand 5 cm thick on the bottom of the basket;

(3) in hanging baskets 12 m below the surface with no sand in the basket and

(4) in cages on the bottom at 13 m.

The results thus obtained are presented in Table 9 from which it would appear that survival in hanging culture can be improved markedly by adding sand to the baskets in which batches are held and that there is a consistent trend toward decreased mortality with increased depth.

In summary, from the work of Toyo et al. (1978) and Anon. (1979, 1980), it would appear that *Anadara* sp. (probably *A. broughtoni* judging from growth rates reported in these studies) is susceptible to elevated temperatures. Mortalities among littoral populations and populations held in baskets near the surface tend to be high. Conversely, populations established on the seabed suffer

Table 9. Survival of *Anadara* sp. (probably *A. broughtoni*) when grown under varying conditions. (Source: Anon. 1980). For explanation, see text.

Date	Number alive			
	Cage at 8 m (+ sand)	Cage at 12 m (no sand)	Cage at 12 m (+ sand)	Cage on bottom (13 m)
10/6/80	100	100	100	100
21/6/80	100	100	100	100
1/7/80	100	100	100	100
10/7/80	100	100	100	100
26/7/80	100	100	100	100
11/8/80	93	93	93	93
14/9/80	55	90	88	93
9/10/80	13	54	66	76
31/10/80	11	18	35	65

from the depredations of predators, primarily *Asterias amurensis*, and good survival is only achieved by enclosing them in cages. The authors cited above also produced evidence that oxygen deficiency on the seabed is unlikely to be a factor in mortality but they suspected that this species may be more susceptible to stress during the spawning season in July/August.

Broom (1982c) presented evidence that on Malaysian mudflats the gastropod predators *Natica maculosa* and *Thais carinifera* may well be very important predators of *A. granosa*. From his data, it is evident that in the laboratory, when presented with a wide range of sizes of available prey, *N. maculosa* will consume one *A. granosa* every two days, irrespective of the size of the predator. For *T. carinifera*, the rate is a little slower at one *A. granosa* every 2.4 days. Combining these predation rates with the average predator density on the *A. granosa* beds studied by Broom (1980), it is possible to arrive at an estimate of the number of *A. granosa* per m^2 per year that might be consumed by the predators. This information is provided in Table 10 where, for comparison, the projected initial density of *A. granosa* in the study areas is also included (taken from Broom 1980, 1983a). From these data, it would seem that in two beds at least, (one natural, one artificially seeded) the gastropod populations were such that they could easily have eradicated the whole population of *A. granosa*. That the populations in question were not wiped out does not mean that the estimated consumption rates set out above are necessarily inaccurate. *A. granosa* is not the only prey species available to the two predators and there are also limits to the size of *A. granosa* that the two predators will attack.

Table 10. Projected consumption of *A. granosa* by populations of *Natica maculosa* and *Thais carinifera* found at five sites in Selangor, Malaysia, based on consumption rates in the laboratory and population densities in the field. (Source: Broom 1980, 1982c, 1983a)

Site	Projected consumption ($N/m^2/yr$) *T. carinifera*	Projected consumption ($N/m^2/yr$) *N. maculosa*	Initial density of *A. granosa* (N/m^2)
Sungai Buloh	3.8	57	86*
KS 1 78/79	341	389	335
KS 2 77/78	15	119	125
KS 2 78/79	46	10	258
KS 3 77/78	12	28	98

*Average density over 12 sampling occasions; no decline in density detected due to variability.

Broom (1982c) showed that for *N. maculosa* there is a clear increase in the preferred size of prey as the predator grows larger. However, even the largest specimens of *N. maculosa* studied by Broom in the laboratory did not normally attack prey larger than 22 mm in length and in the field, dead drilled specimens longer than 23 mm were collected only very rarely (Broom 1980). Hence, once *A. granosa* has reached a size of 23 mm, it has effectively escaped the attention of *N. maculosa*. On natural beds, this size is reached 10-12 months after spatfall. Furthermore, Broom (1983b) showed that a specimen of *N. maculosa* is probably just as likely to attack *Pelecyora trigona* (a codominant on natural beds) as *A. granosa*, particularly if it (the predator) is fairly small (less than 2 g wet weight). Since the average weight of *N. maculosa* on both natural and artificially seeded beds rarely exceeds 2 g, it seems unlikely that as many *A. granosa* would be attacked and killed as is theoretically possible while substantial numbers of the alternative prey are present.

Thais carinifera, on the other hand, may attack prey of a substantially larger size. Broom (1980) found evidence that at one artificially seeded site, a group of *Thais carinifera* containing individuals weighing up to 24 g attacked specimens of *A. granosa* measuring up to 32 mm in length. In laboratory experiments on a limited number of specimens, Broom (1983c) found evidence of definite size selection in only one out of five size classes of *T. carinifera* tested. (This was a group weighing on average 3.5 g wet weight which preferred prey in a broad size range between 12.5 and 20 mm in length). In experiments on prey species selection (Broom 1983b), *Thais carinifera* of all sizes tested (1-7 g) showed a clear preference for *A. granosa* compared with *Pelecyora trigona*. However, when faced with a choice between *A. granosa* and *B. amphitrite*, there was no evidence of any preference in four groups weighing from 0.8 to 3.1 g, but in a group with a mean weight of 5.1 g, there was a clear preference for *A. granosa*.

The behavior of the two predators is also of note. There is evidence (Broom 1982a, 1982c) that both *N. maculosa* and *T. carinifera* form aggregations which "browse" on sedentary bivalve prey. Because of this tendency, it is easy for their importance to be underestimated.

Similar information pertaining to the behavior of predators of other species of *Anadara* is very limited. Toyo et al. (1978) and Anon. (1979, 1980) stated that *Asterias amurensis* is a very important predator of *Anadara* sp. Toyo et al. (1978) maintained that a single specimen of *Asterias* measuring 76 mm can eat 22 *Anadara* in one month. In another study, experimental areas on the seabed were stocked with *Anadara* sp. (Anon. 1979). Although at the time of stocking no predators were seen, large numbers of *Asterias amurensis* gradually migrated in so that 18 days after stocking they were present at densities up to 11.25/m^2. They tended to congregate in the densest areas first then move on to the less dense plots. In a subsequent study divers removed all specimens of *A. amurensis* from the surrounding area before carrying out experimental stocking (Anon. 1980). However, within two weeks the predators had invaded the plots. *Anadara* sp. used in these experiments were usually in the region of 40 mm long indicating that *A. amurensis* may attack quite large specimens.

REPRODUCTION

Sexuality and Age/Size at Maturity

In *A. granosa* the sexes are undoubtedly separate. Broom (1983c) found evidence of hermaphroditism in only one out of 300 specimens examined. Mature gonads are usually present by the time the animal has attained a length of 18-20 mm. Age at maturity is rather uncertain. From information provided by Broom (1982a, 1982b) it would appear to be less than one year. Both Pathansali (1966) and Narasimham (1969) hold that it is 6-7 months. Broom (1983c) could find neither evidence of protandry nor any evidence of deviation from a sex ratio of 1:1. Similar findings are reported by Pathansali and Soong (1958) and Pathansali (1966).

Ting et al. (1972) reported that gonads are present in *A. subcrenata* at a length of 15 mm. The sex ratio is 1:1. Toyo et al. (1978) found that sexual maturity of *Anadara* sp. (probably *A. broughtoni*) is attained at a size of 48.3 to 52.5 mm. Squires et al. (1975) observed that the smallest mature male specimens of *A. tuberculosa* in some Colombian populations were 32 mm in length while the smallest mature female specimens were 36 mm in length. The sexes were reported as being separate but the sex ratio was not accurately determined. Sullivan (1960) reported that in *A. trapezia* the sexes are also separate. According to Dixon (pers. comm.), *A. trapezia* has a sex ratio of 1:1. There is no evidence of protandry in this species. Gonads become visible to the naked eye when the animals are 20 mm long. Butler (unpublished data) found that specimens of *A. cornea* longer than 20 mm have visible gonads at all times.

Yoloye (1974) and Yankson (1982) have investigated the sexuality of *Anadara senilis*. Yoloye (1974), working on specimens from the Nigerian coast, reported that this species is a protandrous hermaphrodite and that all young specimens become functional males when only five months old (and, judging from the information given, 18-20 mm in length). From the sixth month, many specimens appeared to be hermaphrodites and from the end of the first year the ♀:♂ ratio had become 76:24 and remained more or less constant in the adult populations. However, Yankson (1982), who studied populations in Ghana, reported a completely different situation. She found that hermaphrodite individuals occurred extremely rarely (five out of 1,448 and three out of 313 in two populations studied). There was no evidence of protandry nor, under normal conditions, did the sex ratio deviate significantly from 1:1. (In closed lagoons where, in the hot, dry season salinities rose to 50 ppt and surface water temperatures were 32-34°C the sex ratio did deviate significantly from 1:1, the actual observed ratio being close to 1:2 in favor of females). According to Yankson (1982) primary gonads begin to differentiate when the animals are 10-12 mm long and the first spawning takes place at a length of approximately 20 mm.

Spawning Periodicity

Some spawning of *A. granosa* probably takes place throughout the year (Pathansali 1966; Narasimham 1969; Broom 1983c), but there is nevertheless a clear seasonality of reproduction on the west coast of West Malaysia. In Penang, the major spawning period is from July to October with a peak in August/September. In Perak, a little further south, Pathansali and Soong (1958) deduced, on the basis of the time of appearance of larvae, that it is a little later. In Kuala Selangor, spawning takes place between September and November (Broom 1983c), and the major settlement of larvae probably takes place over a two-month period some time between early December and February (Broom 1982a, 1983c). Pathansali (1966) found some variation in the quantity of larvae in the plankton. In 1961, the greatest numbers were observed in July and August. In 1962, the period of maximum abundance was in October and in 1963, there were two peaks--one in September/October and a second in December. The second peak was thought to be linked to the spawning of *Anadara* in Perak. Boonruang and Janekarn (1983) found evidence of a spatfall at Phuket, Thailand in October/November 1979 during the transition between the wet and dry season.

The reasons for this seasonality are uncertain but seasonal salinity fluctuations in the Malacca Straits are thought to play a major role. Pathansali (1966) noted that "the seasonality in the breeding cycle seems to be closely related to salinity. In three separate years the abundance of larvae appears to correspond with the drop in salinity except for October 1961-62." Broom (1982a, 1983c) has shown that at Kuala Selangor in 1977 there was a distinct depression of surface salinity in October/November and that this coincided with a major spawning. He has argued (Broom 1982a, 1983c) that spawning is almost certainly linked in some way to the seasonal salinity depression, although it is possible that the depression of salinity itself is not the factor that serves as the spawning cue. The period of high rainfall may also depress temperatures on the intertidal mudflat and this is another possible environmental cue.

A. granosa is not the only tropical anadarinid to show some evidence of seasonal spawning. From information provided by Yoloye (1974) it would appear that the major spawning period of *A. senilis* is in October/November.

The subtropical and temperate forms all show evidence of a seasonal periodicity of spawning. *A. subcrenata* may spawn at any time between June and September (Ting et al. 1972), but the consensus of opinion is that the peak period is mid-July to the end of August (Cahn 1951; Kusukabe 1959; Ting et al. 1972). Kusukabe (1959) maintained that spawning begins when the water temperature has reached 25°C and peaks at 27°C. Cahn (1951) reported that spawning occurs when water temperature is between 22 and 28.5°C. *Anadara broughtoni* from Peter the Great Bay is reportedly reproductively inert for eight months of the year (Dzyubu and Maslennikova 1982); development of the gametes begins in May and spawning takes place from mid-July to September. Kanno and Kikuchi (1962) reported that in Japan the breeding season of *A. broughtoni* is from June to August.

Yoo and Yoo (1974) reported that in 1973 in the Geoje area of Korea, larvae of *A. broughtoni* were present in the plankton from the beginning of August to the end of September. This would appear to confirm the spawning time recorded by Kanno and Kikuchi (1962). *A. granosa bisenensis* apparently also spawns from June to August (Cahn 1951). *A. ursus* Kuroda MS begins spawning in June with peak intensity from July to early August when the seawater temperature is 24.5-27.3°C (Tanaka 1959). Sullivan (1960) reported that *A. trapezia* spawns in late summer but Dixon (pers. comm.) maintains that it spawns from spring to late summer.

CONDITION INDEX

Undoubtedly, the surest means of monitoring changes in reproductive activity is to observe histological changes. However, Broom (1983c) has demonstrated that for *A. granosa*, the dry:wet weight ratio of the flesh can be a useful indicator usually exhibiting a value of 0.17-0.18 when gonads are ripe and 0.13-0.14 just after spawning. Ting et al. (1972) found that for *A. subcrenata* a ratio of weight of fluid in the shell to total wet weight reached a peak in September (0.28), immediately after spawning, and was at a low point in May/June (0.16). Tanaka (1959) found that for *A. ursus* the ratio of wet weight of soft parts to total wet weight varied from 0.34 prior to spawning to 0.24 during the major spawning period. For *A. subcrenata*, it varied from 0.29 to 0.24.

FECUNDITY

The only information available concerning fecundity of a species of *Anadara* is that provided by Ting et al. (1972) for *A. subcrenata*. From data presented graphically, an approximate relationship as follows is derived:

$$y = 3.88x - 9.13$$
$$(n = 12, SE(b) = 1.09, F_{1,10} = 12.59)$$

where y is number of eggs (millions); x is shell length (cm); b is slope of line and F is the variance ratio.

CULTURE METHODS

Present Techniques

Only three species of *Anadara* are currently cultured to any great extent. These are *Anadara granosa*, *Anadara subcrenata* and *Anadara broughtoni*.

ANADARA GRANOSA

In Malaysia the culture of *A. granosa* proceeds as follows. After spatfall, the Fisheries Department monitors the growth of spat in their natural beds. When they fall within a size range of 4-10 mm length, the Department sanctions collection. Local fishermen then usually proceed to the mudflats at high water of a neap tide in motorized, shallow-draft boats 6-10 m long. Once over the collecting area, they drop anchor and wait for the tide to drop until the water covering the mudflats is 60 cm deep. They then leave the boat to wade through the water, taking with them a wooden sled which is illustrated in plan form in Fig. 6. The sled floats on the water and provides support for the fishermen in the difficult mudflat environment as well as forming a repository for spat collected.

The spat are collected by means of a wire basket-shaped device illustrated in Fig. 7. Most of the wire used is very light gauge being only 1-2 mm in diameter. The gap between the wires (mesh size) is approximately 2 mm. The wooden crosspiece shown in Fig. 7 is grasped by the operator and the "basket" is swept through the surface mud down to a depth of about 3 cm. The mud is sieved out by vigorous agitation in the water and the spat that are retained are tipped into the sled. Collecting continues until no standing water remains on the mudflat. When the water is very shallow the sled is used to move across the mud. The operator kneels inside on one knee and uses the other leg to propel himself along.

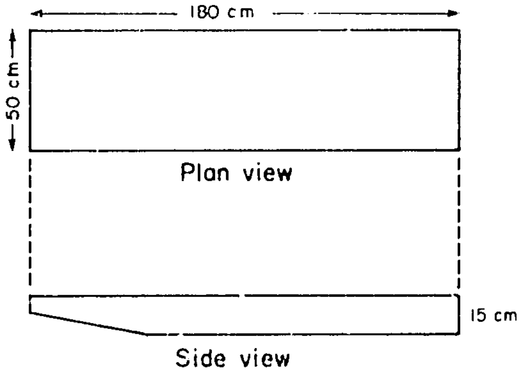


Fig. 6. Diagram of the wooden "mud sled" used by Malaysian fishermen to assist in the collection of spat of *Anadara granosa*.

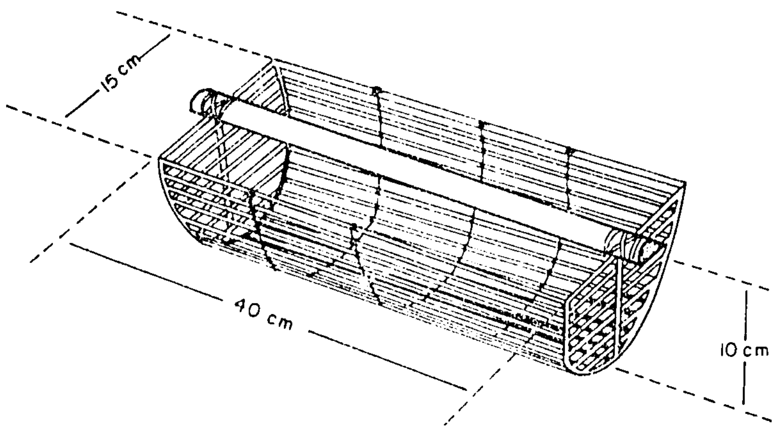


Fig. 7. Diagrammatic representation of the wire collecting basket used by Malaysian fishermen to gather spat of *Anadara granosa*.

Collection may continue for several weeks. The spat is sold both locally and to culturists up and down the coast. Much is sold to Thailand sometimes in contravention of export and import restrictions. Prior to sale the spat is sorted into different sizes. Each size commands a different price, the larger ones being more expensive on a per-individual basis because they are more resistant to crushing and dehydration and are more likely to survive the rigors of reseeding. Fishermen also make efforts to remove predatory gastropods from among the spat. Local culturists, having obtained their supplies of spat, then resow them on culture beds. It is a stipulation of the Fisheries Department that such culture beds should not be established in areas where there is normally a natural spatfall. At Kuala Selangor, the culture beds are located on the mudflats that flank the mouth of the estuary in an area of relatively high current flow and, on occasion, substantial salinity fluctuations. In other areas in Perak and Penang, the beds are established both outside and in the mouths of large rivers. However, establishment of beds within the mouth of a river carries with it the risk of sudden large-scale mortality during a prolonged period of heavy rain (see section on mortality and predation).

The culture grounds are not normally prepared in any special way. The spat are sown at densities up to 2,000/m^2 but are then thinned down as they grow, the larger specimens being removed and resown at densities of 200-300/m^2. If spatfall has been poor and supply is limited, spat may be immediately sown at the final density. Growth is monitored and after 6-9 months harvesting begins. The minimum legal length for sale is 31.8 mm and specimens which have attained this size are removed daily. The whole bed is usually fished out 12-15 months after seeding.

Both harvesting and thinning is done from a motorized, shallow-draft vessel using a dredge similar in design to that for collecting spat except that it is larger and more robust. The wire used in its construction is heavy duty, 3-4 mm in diameter. The spacing between the wires (mesh) depends on the use to which the dredge is put: for final harvesting it is wider than it is for thinning. The dredge is affixed to the end of a long pole which has usually been cut from a nearby mangrove swamp forest. The boat is usually manned by two men one of whom maneuvers it while the other thrusts the dredge into the mud and holds it there as it is dragged along. To ensure that the dredge is maintained in position while being dragged along, a rope secures the distal end to a point forward on the vessel thus relieving the operator of the near impossible task of holding it upright.

Between years it is not unusual for a culturist to allow certain plots to remain unseeded. It is the belief of many that this improves the "condition" of the ground. As mentioned in the section on food and feeding mechanism it is likely that *A. granosa* feeds on benthic microalgae to a large extent and Broom (1982b) has presented evidence that a population of *A. granosa* can significantly reduce the concentration of chlorophyll *a* in the boundary layer. Therefore, one should not be too surprised if taking a plot out of production in one year were to improve growth of *Anadara* seed in a subsequent year as the procedure would allow populations of benthic diatoms to reestablish themselves.

Tookwinas (1985) reported that culture of *A. granosa* in Thailand first took place about 75 years ago in Phetchaburi Province. Spat were collected and reseeded in bamboo-fenced areas covering 8,000 to 16,000 m^2. The culture period was one to two years. Culture continued in this fashion until 1972 when it was brought to a halt by severe pollution in the inner Gulf of Thailand.

Following the demise of *A. granosa* culture in Petchaburi Province, farmers in Satun Province began importing seed from Malaysia in 1973 to begin culture operations. The operations were successful and culture of *A. granosa* spread throughout the southern part of Thailand to the provinces of Trang, Raneng, Nakhon Si Thammarat and Surat Thani. The methods used were, and are, essentially the same as those used in Malaysia.

Despite the fact that there has been at least one recorded instance of local spatfall in Thailand (January 1983, Nakhon Si Thammarat), Malaysia remains the primary source of seed for *A. granosa* culture. Normally seed to be exported to Thailand is packed at night in 60-80 kg bags which are kept sprayed with seawater at intervals during transportation. In order to reduce mortality during the immediate post-seeding period, importation and transplantation are only done during neap tides when the culture sites are continually covered with water. Furthermore seeding is only done either early in the morning or in the evening. These precautions enable initial mortalities to be kept below 15% (Tookwinas 1985).

Initially only a part of the culture area is stocked. The stocking density, on a biomass basis, is 3,375 to 6,750 kg/ha. After three to six months the young cockles are redistributed over the whole culture area. Redistribution of the cockles is achieved by use of the mud sled described above rather than with the use of motorized vessels as in Malaysia. Harvest of the cockles takes place about 18 months after seeding. This is rather later than in Malaysia but it is accounted for by the fact that in Thailand the cockles are marketed when they reach a length of approximately 4 cm compared with 3.2 cm in Malaysia.

Harvesting is carried out in a manner similar to that in Malaysia. The dredge is operated from a 6-m boat and harvesting continues by this method until the density is reduced to 1-3 cockles/m^2. A final collection is made using the mud sled.

Despite the success in recent years of the reintroduction of cockle culture in Thailand, Tookwinas (1985) has reported that culture beds have started to deteriorate. In Muang district, Satun Province, the original soft substrate has, after five years of continuous culture, been replaced by the accumulation of the shells of dead *Anadara granosa*. The reason for this is not understood. A similar phenomenon has not generally been observed in culture areas in Malaysia but this may be because accretion on the west coast of peninsular Malaysia takes place at a sufficiently rapid pace to maintain a soft substrate even if it is mixed with dead shell (see Coleman et al. (1970) for details of accretion in this area).

Cahn (1951) reported that a similar method has been used for culture of *A. granosa bisenensis* in Okayama Prefecture, Japan. Seed cockles were collected from areas of natural spatfall in September/October using essentially the same methods as used in Malaysia, except that a slightly different collecting device was used. The seed, 5-6 mm long, were then sown in the culture areas using a flat-bottomed boat. This was manned by three fishermen, one of whom poled while the other two scattered the seed with a metal or wooden scoop. The standard amount of seed planted per unit area varied according to the size. This is indicated in Table 11 using number of individuals per liter as a proxy variable for size. The relationship between size and number per liter was as follows: average shell length 6.6 mm = 22,170/l, 9.9 mm = 6,650/l; 19.8 mm = 550/l; 33.0 mm = 110/l; 46.2 mm = 66/l.

Table 11. Culture of *A. granosa bisenensis*: relationship between size (expressed in terms of number per liter) and density at which populations are sown. (Source: Cahn 1951)

Thousands/l	Liters/ha
44 – 55	2,000
33 – 44	2,730
22 – 33	3,820
11 – 22	4,360
5 – 11	5,450
3.9 – 5	10,910
2.8 – 3.9	13,640
1.7 – 2.8	16,360
0.6 – 1.7	21,820
0.4 – 0.6	24,550

During the first year after sowing, the seed was left as it fell. In the second year it was thinned twice—in spring and autumn. Thus, the area under culture was gradually increased. Final transplantation to deeper water with a more rapid current was undertaken when the bulk of the population had reached a length of approximately 30 mm.

Harvesting was carried out in the cool season from autumn to spring. A modified hand dredge consisting of a woven metal basket net with a series of steel teeth at the lower edge was used for this purpose. The net was attached to a pole 4-5 m long. With the boat anchored, a fisherman would use the dredge to rake the surrounding sediment and retrieve the bivalves.

ANADARA SUBCRENATA

Kusukabe (1959) has described in considerable detail the methods used for culture of *Anadara subcrenata*. As with *A. granosa*, this is essentially an extensive culture method involving collection of spat followed by reseeding. The area which forms the center of the spat-collecting activity is a lagoon known as the Nakanoume in Shimane Prefecture, Japan. The lagoon is virtually enclosed by the Shimane and Yumigahama Peninsulas and has an almost flat muddy bottom covered by water up to 8 m deep (Cahn 1951).

Unlike *A. granosa*, the spat are collected using specially designed spat collectors onto which larvae settle directly. Kusukabe (1959) described the following procedure. Bamboo poles 10 m long are driven into the mud and connected by a crosspiece about 4 m long from which collectors are hung. A collector consists of gauge 19 galvanized wire to which are attached "bristles" of palm fiber about 6 m long, resembling a bottle brush. Three lengths of such wire, each 1.8 m long and looped, are bunched together to make a collector. At the beginning of a season, a few collectors are lowered every day, removed 24 hours later and examined. As soon as the number of attaching spat starts to increase rapidly, all the collectors are set out. Work continues day and night since the peak period of attachment is only 3-4 days. In 1953, an average of 97,500 spat, 90% of which were less than 2 mm long, settled on each collector.

Early work by Kusukabe in the 1940s, using spat collectors of hemp palm fiber, revealed that the larvae concentrate in a very narrow zone of the water column in the Nakanoume. Between 22 July and 5 August 1942, 78% of spat settled on the portion of the collectors between 4.5 m and 5.7 m depth. Between 31 July and 12 August, 77% settled on the portion between 3.3 and 4.5 m depth. Subsequent investigations using a hand pump revealed that the larvae were invariably found in a narrow water layer the specific gravity of which at 15 °C ranged from 1.018 to 1.022 (24.6 to 29.8 ppt). The zone was, in effect, a halocline separating the slightly brackishwater of the surface from the salt wedge underneath.

Following this discovery it became the practice to establish the salinity profile and determine the depth of the zone before setting out the spat collectors. In addition, it was discovered that the spat collection zone was effectively a band only 75 cm wide. This allowed for very efficient deployment of spat collectors and optimal allocation of resources.

Following collection the spat are transported to nursery beds in Okayama and Hiroshima Prefectures. Kusukabe (1959) reported that 60-70% of the spat fall from the collectors during transport. The culture ground is usually part of a tidal flat at a level of mean low water of spring tides. Racks of bamboo poles 60 cm high are set up and the collectors with attached spat are hung over the tops of these. Those spat that have fallen off the collectors during transportation are sown directly onto the substrate at a density of 15,000-30,000/m^2. When the spat have grown to a size of 10.3-12.9 mm, whether on the substrate or on the spat collectors, they may be used as seed for sowing on the culture areas reserved for "adults". They are harvested a year later at a length of approximately 32 mm.

ANADARA BROUGHTONI

Unfortunately, there is little information in the literature which specifically refers to the culture of *A. broughtoni*. Toyo et al. (1978) described some aspects of the culture of a species of *Anadara*, which was probably *A. broughtoni*. They maintained that young *Anadara* can be collected from culture beds in Yamaguchi Province, Japan, in September when they are 1 mm long, and transported to different districts for seeding on nursery beds. However, survival after transportation was reported as being very poor (only 6.5%) and Toyo et al. (1978) investigated ways of improving survival. Working with spat that had been raised artificially and allowed to settle on oyster shell, they found that mortality was least (0.6-2.0% after five days) if the spat could be kept immersed in seawater at 26-27 °C. Wrapping the cultch in newspaper soaked in seawater at 14-15 °C was also moderately successful, but when spat were kept at normal temperatures (25-28 °C) out of water, mortality was high, up to 55% after five days.

In Korea, spat of *A. broughtoni* are collected and reseeded at depths of 2 to 30 m on muddy substrates where they take 2-2.5 years to reach market size. Hanging culture has been attempted but when they are kept off the bottom the hemoglobin blood pigment does not develop well and this reduces the market value. In individuals raised under hanging culture the shell weight to meat weight ratio is higher (i.e., there is relatively more shell per unit weight) than in those raised under bottom culture. Furthermore the total weight per unit length is less for those under hanging culture than those under bottom culture (Yoo and Park 1978).

Artificial Induction of Spawning

Artificial induction of spawning and subsequent rearing of spat has reportedly only been achieved with any degree of success for *A. broughtoni* and *A. granosa*.

Toyo et al. (1978) reported that for a species which was probably *A. broughtoni*, over 100,000 young were raised by artificial breeding in 1970. In Yamaguchi Province one thousand million *Anadara* (probably *A. broughtoni*) were raised through artificial culture in 1977 (Anon. 1980).

The scientific basis of artificial culture of *A. broughtoni* is given by Kanno and Kikuchi (1962), Kanno (1963), Yoo (1969) and Kim and Koo (1973). Kanno and Kikuchi (1962) and Kanno (1963) found that spawning of *A. broughtoni* could be induced by repeated thermal stimulation and Kim and Koo (1973) induced spawning of "ripe" specimens by raising the water temperature from 18°C to 28°C every two hours. Yoo (1969) induced spawning by keeping individuals at a "control temperature" of 18-20°C and subjecting them to an induction temperature of 25-29°C. In all cases, "ripe" adult specimens were gathered from natural populations during the breeding season.

Following fertilization, the D-shaped larval stage is apparently attained after 20-24 hours at a water temperature of 20-25°C. Subsequent growth to settlement depends on water temperature and on the quality and quantity of food provided. Kanno (1963) provided a diet of *Monas* sp. at 1,200 5,400 cells/ml at a temperature of 23.8-27°C and found that larvae grew from 90 μm long to settlement size (235 μm long) in one month. Kim and Koo (1973) fed D-shaped larvae on *Chaetoceros calcitrans*, *Monochrysis lutheri*, *Monas* spp. and *Skeletonema costatum*. They varied the rate of feeding such that more food was provided as the larvae grew. The feeding rates were 7,000 cells/larva/day for the D-shaped veliger, 12,000 for the umbo stage and 23,000 thereafter. Growth, however, appears to have been slightly less than that reported by Kanno (1963), a length of 225 μm only being achieved after 40 days. Attachment is reported as having taken place at sizes between 180 and 270 μm. Yoo (1969) maintained larvae at 20.4 ± 1.7°C. He found the best growth was obtained by modifying the quantity of food according to the species of alga and the volume of the tank rather than the number of larvae. Thus, he found that for *Monochrysis lutheri* and *Cyclatella nana* the concentrations in the tank should be 10,000-100,000 cells/ml. For *Chaetoceros calcitrans* it should be 20,000-150,000 cells/ml. He also recommended that the cells should be cleaned (presumably by washing with sterile seawater) after spinning down in a centrifuge prior to inoculation. In Yoo's experiments larvae began to settle at a length of 260-290 μm, 30 days after fertilization.

Mortality during the "rearing" period can be high. Kim and Koo (1973) found that only 5% of the larvae survived over the 40 days for which their experiments ran. Somewhat better results were obtained by Kanno (1963) who found that in two groups of larvae, 33% and 10% survived to attachment. Kanno (1963) also provided data demonstrating the rate of growth after attachment when the spat were maintained in laboratory tanks. These data show that attached spat grew from 0.28 mm to 8.21 mm in one year.

Wong and Lim (1985) have recently reported success in artificial induction of spawning in *A. granosa*. They induced spawning by alternate immersion of sexually ripe specimens of *A. granosa* in seawater at 16-18°C and 30-32°C. Spawning took place after the second exposure to the higher temperature with the release of mature eggs (approximately 55 μm diameter) and sperm. Cell division started 10-15 minutes after fertilization and active trochophore larvae appeared after approximately four hours. The D-shaped larval stage was attained after approximately 22 hours. The larvae, feeding on a diet of *Isochrysis* sp. and maintained at a temperature of 26-30°C, reached the umbo stage after 13 days and settled after 21-22 days. Shell length at settlement ranged from 230 to 250 μm. The larvae metamorphosed into the adult form after 28-30 days. After settlement the spat were fed on "mixed brown cells" and shell lengths of 2.5 mm were attained within 30 days.

Ting et al. (1972) achieved some success in inducing spawning of *A. subcrenata* by thermal shock; immersion in a sperm-seawater suspension (for females only) and immersion in dilute ammonium hydroxide. To induce spawning by thermal shock, ripe individuals maintained at 27°C were transferred to water at 20°C (time not specified), then back to 27°C. Then the water temperature was raised to 30°C. With this treatment a 50-60% response was obtained. When immersed in a sperm-seawater suspension a 62% response was obtained. Responses of 20 to 64% were obtained by immersion in a weak solution of ammonium hydroxide in seawater (0.005-0.001N). Responses of 46% (♀) and 76% (♂) were obtained when a 0.01N solution of ammonium hydroxide was injected directly into the body cavity.

POLLUTION

To a certain extent, problems of pollution are peripheral to the main concern of this review which is the biology and culture of anadarinids. However, the potential for culture activities may be affected by local water quality and the extent of contamination by anthropogenic material is clearly important in this regard.

At present, widespread pollution of coastal waters is not prevalent in Malaysia, although local "hotspots" do exist. Sometimes these are areas quite close to culture grounds, such as Butterworth and Kuala Juru in Penang. Here, large quantities of industrial effluents are discharged daily into coastal waters constituting a source of numerous pollutants which might impinge directly upon *A. granosa*. In addition, large tracts of land in Malaysia are given over to agroindustries in the form of rubber and oil palm plantations. These are inevitably sprayed with pesticides which form part of the agricultural runoff into streams and rivers. As yet, there is no concrete evidence that the pesticides persist and are carried into coastal waters but, as several persistent organochlorines (aldrin, dieldrin, DDT and lindane) are regularly used, this is a distinct possibility (Broom 1981).

Pollutants pose a threat to culture operations for two reasons: they may have a directly toxic effect on the organism itself and they may, by virtue of contamination of the organism, render it unsafe for consumption.

Information relating to the directly toxic effects of either pesticides or heavy metals on any of the life stages of *A. granosa* is lacking, but there is some limited information on the level of a few major pollutants. Phillips and Muttarasin (1985) have carried out analyses of a range of heavy metals in marketplace samples of *A. granosa* harvested in Malaysia and Thailand. The average values ($\mu g/g$ wet weight) are summarized in Table 12. None of the levels found were particularly high, and indeed Phillips and Muttarasin (1985) concluded that "none of the samples analysed contained levels of trace elements which would indicate the existence of potential public health problems." The results of their analyses are in broad agreement with the results of the few other studies that have concentrated on *A. granosa*, with the exception that Huschenbeth and Harms (1975) detected slightly elevated concentrations of copper (5.6 $\mu g/g$).

Information on residues of organochlorines in *A. granosa* is limited to only two studies. Huschenbeth and Harms (1975) found 9 μg dieldrin/kg wet weight of flesh, 35 μg DDT derivatives/kg, 4 μg lindane/kg and 31 μg polychlorinated biphenyl compounds (PCBs)/kg in a single sample of *A. granosa* from the Phuket area of Thailand. Jothy et al. (1983) found an average of 35.5 μg DDT derivatives/kg wet weight of flesh, 3 μg dieldrin/kg and 33.3 μg PCBs/kg in six samples of *A. granosa* from Penang and Perak.

Some scattered information on concentrations of metals in other anadarinids can also be found in the literature. This is also summarized in Table 12 which is taken from Phillips and Muttarasin (1985). The levels can be considered by no means excessive although there may be a variation in the capacity of different species of *Anadara* to accumulate different metals. It should be borne in mind that many of the results are based on single samples and more information about inter-sample and interlocation variability is required before definite conclusions can be drawn.

The results outlined above give no cause for concern that anadarinids may show a particular propensity to accumulate either organochlorines or heavy metals. However, this should not be an excuse for complacency. The feeding habit of anadarinids is likely to increase their risk potential. There is little doubt that, in the natural environment, a great deal of particulate matter enters the mantle cavity of anadarinids and since some trace metals and most organochlorines associate preferentially with particulate material by surface adsorption (Phillips 1980) anadarinids are especially exposed to pollutants.

Table 12. Reported concentrations (μg/g wet weight, means) of trace elements in *Anadara* species. Data refer to whole soft parts. (Source: Phillips and Muttarasin 1985)

Species	Location or origin	n	Cd	Cu	Hg	Pb	Zn	Authority
A. granosa	Thailand	1	0.28	5.60	0.01	0.18	16.2	Huschenbeth and Harms (1975)
A. granosa	Thailand	7	0.54	1.14	<0.02	0.16	16.37	Phillips and Muttarasin (1985)
A. granosa	Malaysia	4	0.40	1.32	<0.02	0.13	19.37	Phillips and Muttarasin (1985)
A. granosa	Malaysia	6	1.91	0.51	0.02	0.46	19.2	Jothy et al. (1983)
A.g. bisenensis	S. Korea	1	0.41	0.75	0.02	1.18	—	Won (1973)
A. broughtoni	S. Korea	3	0.48	1.13	0.19	0.97	—	Won (1973)
A. inflata	Japan	1	—	—	1.76	—	—	Kitamura (1968)
A. subcrenata	Hong Kong	1	0.80	3.20	0.10	0.90	33.3	Phillips et al. (1982)
A. trapezia	Australia	4	0.19	0.19	—	0.06	3.7	Fabris et al. (1976)
A. tuberculosa	Mexico	14	—	—	0.05	—	—	Reimer and Reimer (1975)
Anadara sp.	Japan	1	—	—	0.10	—	—	Kondo (1974)
Anadara sp.	Hong Kong	1	0.70	—	0.10	0.40	—	Phillips et al. (1982)
A. granosa	India	—	—	1.63	—	—	19.99	Shah et al. (1973)

CONCLUSIONS

The picture that has emerged from this review is one of a group of bivalve species whose members have succeeded in exploiting a niche characterized by fluctuating physical variables (tidal cover, salinity, temperature, oxygen concentration) and, for suspension feeders, difficult trophic conditions (high suspended solids loads). As a broad generalization, it may be said that members of the Anadarinae are likely to be found on intertidal and marginally subtidal muddy substrates in areas where there is an estuarine influence. Geographically, they tend to be confined to tropical and subtropical areas although two of the most important cultured species (*A. subcrenata* and *A. broughtoni*) are mainly distributed in warm temperate waters. However, despite their obvious commercial importance and the fact that in many places component species are abundant and readily accessible, anadarinids are poorly researched. For this reason it has not proved possible to identify anything other than the broadest general trends regarding the biology of the different species or common approaches to culture techniques.

The nature and relative success of the culture of different species is dependent partly on habit, partly on habitat and partly on interactions with the other members of the benthic community. In Malaysia, the extensive culture of *A. granosa* has been extremely successful and it is appropriate to consider the reasons why this has been so. Of primary importance has been the existence of a fairly dependable yearly spatfall on a substrate which allows easy collection of the spat. If the species had a preference for a more sandy substrate or one which was not easily sieved it is likely that large-scale culture would never have been realized; exploitation would have been confined to harvesting natural populations as is done with *A. cornea* and *A. senilis* which inhabit substrates dominated by a larger particle size. Second, populations of *A. granosa* apparently do not experience devastating mortalities due to predation whereas species cultured in other locations (e.g., *A. broughtoni* in Japan) appear to suffer from the depredations of a wider range of predators, some of which are capable of completely destroying seeded populations.

Perhaps, the single most important factor contributing to the success of the other two extensively cultured species, *A. broughtoni* and *A. subcrenata*, is that the byssus gland is active in the spat. This has meant that it has been possible to gather the spat of both species on specially designed collectors and, equally important, has allowed large quantities to be grown under hanging culture at least for the first year. Under hanging culture they are less vulnerable to attack by predators although they may be more susceptible to any excessive rise in temperature. However, these species are usually removed from hanging culture after one year and relaid on the seabed because the byssus is not sufficiently robust to bear the rapidly increasing weight.

While it is relatively easy to identify the principal factors which have contributed to the success of culture of *A. granosa*, *A. broughtoni* and *A. subcrenata*, it is rather more difficult to identify areas of deficiency in which improvements need to be made if culture is to be more productive. In the case of *A. granosa*, small increases in productivity might be achieved if there were a better understanding of the effects of density, exposure and salinity upon growth and mortality. Research to obtain the necessary information would not be enormously expensive and would probably provide good value for money in terms of the returns. Major steps forward are, however, only likely to be made if improvements can be brought about in one or more of the following areas: 1) the total area under production, 2) the exposure of cultured populations to predators and 3) the control of the supply of spat for culture purposes.

The total area under production could conceivably be increased by adopting some form of hanging culture. This would enable utilization of the water column in permanently submerged areas and at the same time decrease exposure to predators and increase time available for feeding. However, there are several obstacles to this approach. First, *A. granosa* commands a relatively low market price and supply more or less satisfies demand at present; it is therefore doubtful that the large capital investment that would be required for a cage culture system could be justified. Second, it should be borne in mind that *A. granosa* is a burrower in soft sediments. It is uncertain how the animal would respond to being maintained in an environment where it would be unable to burrow. Third, it is not known whether the food supply obtainable from the water column would be appropriate to an animal accustomed to obtaining its nutrition from the mud/water interface.

Another advantage that might be achieved by hanging culture is isolation of the bivalves from their predators, although care would have to be taken to ensure that small gastropod predators were not introduced into the cages with the prey. However, as hanging cage culture may not be practicable, it is necessary to search for other means of minimizing predation on the mudflats. Mortality due to drills tends to be greatest on the lower shore (Broom 1983a), and there is some circumstantial evidence that drills may prefer to forage on the lower shore and only proceed to the upper shore as their preferred prey are depleted (Broom 1982c). This being so it may be possible to reduce mortality in populations of *A. granosa* by providing a sacrificial population of alternative prey. A good candidate for an alternative prey is *Pelecyora trigona* as it is often very abundant in areas where *A. granosa* settles naturally and is a relatively attractive prey for *N. maculosa*, if not *T. carinifera*. Wherever it occurs at high densities, it might be worthwhile for fishermen to gather large quantities and resow them on the downshore boundaries of beds of *A. granosa*. Drills might then attack and exhaust this sacrificial population before moving upshore to attack *A. granosa*. This would have the effect of reducing the time during which the cultured population was exposed to predation by drills and also allow individuals a period during which they could grow to a size at which they were less susceptible to attack.

There is some evidence (Broom 1982c) that predation pressure from drills decreases as salinity fluctuations increase. That is, mortality from drills decreases on beds with a progressively greater freshwater influence. This is thought to be due to the inability of the drills to cope with large fluctuations in salinity. It is possible, therefore, that mortality due to predation from drills (and presumably from fish such as skate which have little tolerance of depressed salinity) could be decreased by culturing *A. granosa* in areas where there are marked salinity fluctuations. Unfortunately, beds established in such areas run the risk of large-scale mortality if there is a period of prolonged heavy rainfall.

There can be considerable year to year variability in the supply of spat of *A. granosa*. In some years overly abundant spatfall may result in an oversupply, which results in lower incomes for those who make a living collecting spat. In other years, there may be insufficient spat. In either case the spat are available only for a period of two to three months each year. These problems will only be overcome when it is possible to produce spat in the laboratory both cheaply and on a large scale. The achievement of Wong and Lim (1985) in artificially inducing spawning of *A. granosa* represents a positive step in this direction. A word of caution must be added, however. Methods for the artificial culture of *A. broughtoni* have been well-established in Japan for over ten years. Yet Toyo et al. (1978) reported that in Yamaguchi Prefecture artificial rearing of spat, begun in 1973, was abandoned only two years after it started because the supply of spat which set naturally was more than adequate to meet demand.

In summary, it may be said that some small gains in productivity in the culture of *A. granosa* may be made by gaining a better understanding of the variation of growth and mortality as a function of exposure and density. Major gains will only be made when methods are found to prevent predators from gaining access to culture beds.

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