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THE REPRODUCTIVE BIOLOGY, POPULATION DYNAMICS, PRODUCTION AND FISHERY OF THE FRESHWATER CLAM *Galatea paradoxa* (Born, 1778) IN THE VOLTA RIVER, GHANA.

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Thesis submitted in fulfilment for the Degree of Doctor of Philosophy to the

University of Dublin, Trinity College

2010

DECLARATION

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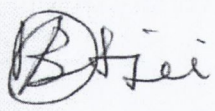

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Daniel Adjei-Boateng

October, 2010

ABSTRACT

The reproductive biology, population dynamics and production of *Galatea paradoxa* (Born 1778) (Donacidae) which is the basis of an artisanal fishery at the Volta River Estuary, Ghana, was studied from March 2008 to February 2010. Histological observation of the gonads revealed that *G. paradoxa* is gonochoristic with a dominance of females (80%) and a high incidence of hermaphrodites (9.4%). The reproductive cycle is annual with a single spawning event between July and October. Gametogenesis starts in December and progresses steadily to a peak in June-July when spawning begin until November when the animals are spent. Condition and gonadal indices showed a clear relationship with the gametogenic stages rising from minimum values in stage (I) at the start of gametogenesis to maximum values at stages (IIIA) ripe and (IIIB) start of spawning (June - August) before declining significantly to minimum values in stage (IV) spent. The synergistic effect of several environmental factors; a slight drop in water temperature, lower food availability and DO levels at the peak of the rainy season might act as cue for spawning while the slightly higher chlorophyll a levels at the start of the dry season might trigger the onset of gametogenesis in *G. paradoxa.* Oocyte diameters progressed from 3 – 9 μm at the start of gametogenesis to between 24 – 32 μm at the ripe and start of spawning stages (June –August). *G. paradoxa* is iteroparous and produces an average of 10^6 eggs a year per 40 mm female which suggests that it produces planktotrophic larvae. However, the survey did not detect any larvae in any of the plankton samples taken.

Age determination was conducted using surface ring counting, length-frequency distributions and tagging-recapture experiments. Mean lengths at ages 1 to 9 years were 15.4, 28.6, 39.8, 49.4, 57.5, 64.5, 70.4, 75.5 and 79.7 mm, respectively. All the age determination methods were successful in estimating the age of *G. paradoxa* indicating that surface ring counting is reasonably accurate for simple and rapid age estimation in this species. The population

parameters; asymptotic length (L_∞), growth coefficient (K), mortality rates (Z, F and M) and exploitation level (E) of *G. paradoxa* were estimated using length-frequency data. The L_∞ for *G. paradoxa* at the Volta Estuary was 105.7 mm, the growth coefficient (K) and the growth performance index (Ø) ranged between 0.14 – 0.18 $year^{-1}$ and 3.108 - 3.192, respectively. Total mortality (Z) was 0.65 - 0.82 $year^{-1}$, while natural mortality (M) and fishing mortality (F) were 0.35 – 0.44 $year^{-1}$ and 0.21 - 0.47 $year^{-1}$, respectively, with an exploitation level of 32 – 57 % of total mortality.

The recruitment pattern suggests that *G. paradoxa* exhibits year-round recruitment with a single pulse over an extended period (October – March) in the Volta River. Production was highest in the 3 and 4-year old cohorts with values between 62.1 and 71.6 g AFDW m^{-2} $year^{-1}$. The population production ranged between 206 and 220 g AFDW m^{-2} $year^{-1}$. The annual production to biomass ratio (P: B) of the population was approximately 1.0. Reproductive investment in *G. paradoxa* increases with age and can be described as restraint because the species allocates considerable resources to somatic growth while at the same time increasing reproductive output.

Clam fishing is an important socio-economic activity in the Volta Estuary providing employment to 503 fishers with an annual catch of 7700 tonnes and a gross income in excess of GH¢ 4,620,408 (2.3 million Euros). Commercial extinction of *G. paradoxa* is imminent as a result of overfishing and requires immediate regulation to ensure sustainability. It is recommended that a minimum landing size of 50 mm should be imposed in consultation with the traditional authorities who manage the fishery, the marketing of clams less than 50 mm should be abolished and the farming of smaller clams which is a traditional activity in the estuary encouraged.

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1.0 INTRODUCTION

1.1 Freshwater Bivalves of Africa

Africa is easily divided into six sub-regions based on the high basin-endemism of freshwater bivalves (Thieme et al., 2005). The sub-regions are: (1) Nile Basin, including Lake Turkana; (2) Atlantic basins in Western Africa; (3) Congo, including Cameroon and Gabon; (4) Southern Africa; (5) Indian Ocean basins in Eastern Africa and (6) Madagascar, including the oceanic Mascarene Islands. Africa is inhabited by two distinct freshwater mussel assemblages, the distributions of which are kept largely separate by the Sahara desert (Van Damme, 1984; Graf and Cummings, 2007). Certain European species and genera (Unionidae and Margaritiferidae) reach their southern limits in Northern Africa, from the Maghreb east to Egypt. It is only in the Nile Basin that the freshwater bivalve species of these two regions mingle. Those extralimital European taxa in Northern Africa belong to the Palearctic assemblage (Europe, Middle East and Central Asia) (Graf and Cummings, 2007).

The freshwater bivalves assemblage of Africa (85 species) consist of three families; there are two dominant families, the Unionidae (41 spp.) and Iridinidae (43), and a single, widespread species of the Etheriidae (*Etheria elliptica*). The unionid species form a heterogeneous assemblage, probably derived from at least two invasions of the Unionidae from the north (Graf, 2000). Three species are classified as members of the otherwise-Eurasian Unionidae: *Unio abyssinicus* and *U. mancus* in the Blue Nile and *Cafferia caffra* in southern Africa (Graf and O ´ Foighil, 2000; Graf, 2002).

There are, however, a few species adapted to freshwater from generally marine families. The Donacidae consist of species that are marine with the exception of two genera *Iphigenia* and *Galatea* that are freshwater and endemic to river systems in West Africa (Purchon, 1963).

Galatea paradoxa (Born 1778) belongs to the Tellinoidea and Donacidae (Purchon, 1963). It is endemic to the West African sub-region with a range that extends from the Gulf of Guinea to the Congo (Moses, 1990).

1.2 Life History of Freshwater Bivalves

The life history of freshwater bivalves is varied and depends on the family being discussed (Bogan, 2008). Freshwater bivalves of the Unionoidea, have the most specialised life histories in which the modified veliger larvae (glochidia) undergo a brief period as obligate ectoparasites on the gills, fins, or other external parts of fish (Haag et al., 1995; Haag and Warren, 1997). Glochidia, the parasitic larval stage, are brooded in the gills of female mussels until mature, then released through the siphons singly or in clusters called conglutinates (Kat, 1984). If the glochidia encounter a suitable fish host, they encyst for a few days to several weeks, metamorphose into juvenile mussels, and then drop off the fish to assume a benthic lifestyle. Glochidia encountering an unsuitable host are rejected by the fish immune system, usually within a few days (O'Dea and Watters, 1998).

Bivalves belonging to the Sphaeriidae are hermaphrodites and brood their young within the inner demibranchs without a pelagic larval stage. According to Guralnick (2004), the life histories of sphaeriid bivalves have been one of the best studied, partly because they brood their young. In *Pisidium*, one of five genera in the Sphaeriidae, offspring develop and are released synchronously. The reproductive state is therefore easily determined from a collection of adults.

Freshwater species from predominantly marine families share the life history characteristics of their marine relatives. Little information exists on the life history of *Galatea paradoxa* (Purchon, 1963; Moses, 1990; Etim and Brey, 1994). It belongs to the Veneroida, Tellinoidea

and Donacidae. Several authors have described aspects of larval development in the Donacidae (Chanley, 1969; Webb, 1986; Carstensen et al., 2010). It is assumed the life history of *G. paradoxa* is similar to *Donax* its marine relative (Purchon, 1963). The life history begins with external fertilization of gametes that are released into the water column by dioecious individuals. The oocytes of *Donax* are about 60 μm in diameter while the spermatozoa has a head diameter of 5 μm and a tail which is 40 – 50 μm in length (Chanley 1969; Carstensen et al., 2010). Larval development follows the typical sequence of successive stages for bivalve species. Within 48-hours of fertilization, a free-swimming D-veliger larva with a velum first develops, and later a probing foot that is characteristic of larva ready to settle, before metamorphosis take place (Figure 1). Larvae increase in length from 70 – 90 μm to about 250 – 340 μm in the pediveliger stage within 21 days (Chanley 1969; Carstensen et al., 2010).

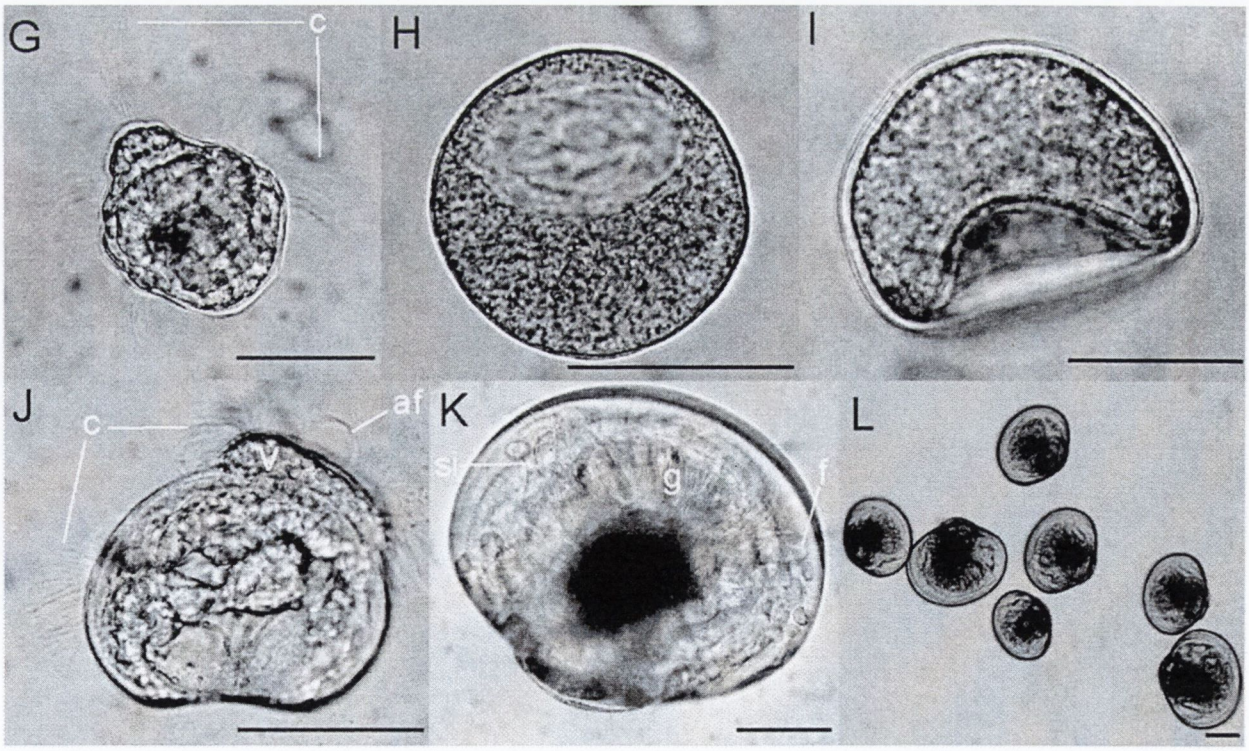


Figure 1.1 the life-history of *Donax sp.* Adapted from Carstensen et al., 2010.

(**G**) Early trochophore, ciliate (c) indicated by lines (75 μm, > 24h). (**H**) Early gastrula stage (μm, 9.5 h). (**I**) late gastrula stage (80 μm, < 24 h). (J) D-Veliger with velum (v), cilia (c), and apical flagellum (af) (K) Foot stage larvae, siphon (si), gills (g), and foot. (L) Foot-stage larvae overview (190 – 250 μm, 18 days).

The larval stage is the primary dispersal period in bivalves with planktonic larvae, however, a secondary dispersal / settlement period has been identified in other species at a much larger post larval (spat of a few mm length) stage (Beukema and de Vlas, 1989). Secondary dispersal in *Macoma balthica* is facilitated by a long thread that increases viscous drag, thus enabling the young bivalve to be carried along by relatively weak currents (Beukema and de Vlas, 1989). Transport by thread drifting results in long distance dispersal and enables settlement at a later time and greater size away from areas suitable for the small just-metamorphosed larvae (Beukema and de Vlas, 1989). Newell et al. (1991) and Beukema (1993) suggested that primary settlement requirements are different from those of growing juveniles, therefore the drifting postlarval stage is needed to transport the successfully metamorphosed postlarvae. *Macoma balthica* shifts from one type of substrate to another as a consequences of postlarval movement (Beukema, 1993), while *M. edulis* relocates from sea grass or algae to shell or rock (Newell et al., 1991).

1.3 Reproductive Cycle and Sexual Strategy of Bivalves

The reproductive cycle and spawning season of bivalves can be studied both directly and indirectly. The most reliable and widely used direct method has been studies on histological preparations and microscopic examination of histological sections of gonads (Etim, 1996; Lauden et al., 2001; Darriba et al., 2004, 2005; Drummond et al., 2006, Suja and Muthiah, 2007). Gonad smears provide a faster and direct technique of determining sex and assessing

gamete size and the stage of gamete maturity in bivalves. This technique is usually used together with histological studies (Jagadis and Rajagopal, 2007).

Indirect methods assess changes in an index that may have a bearing on the physiological state of the bivalve. The most commonly used indices are ash-free dry weight and length-weight data. The monthly monitoring of ash-free dry weights (AFDW) (Urban and Mercuri, 1998) over a period of twelve or more months is characterised by peaks and troughs, the former signifying the start and the latter the end of spawning or when the animal is spent. Periodic length-weight data (Rueda and Urban, 1998) and linear regression analysis on log-transformed data for a standard animal has been used to study the reproductive cycle. An abrupt decrease in weight between successive months may indicate a spawning event while an increase over a longer period could be interpreted as the developing phase before the spawning season.

Condition indices have been employed by a number of authors to elucidate the spawning season of bivalves (Etim and Taege, 1993; Etim, 1996, Darriba et al., 2004, 2005). However, their interpretations may be misleading as fluctuations in weight might also be caused by feeding conditions, thus independent of the reproductive cycle (Beukema and Desprez, 1986; Rueda and Urban, 1998). One can conclusively interpret a body weight cycle only in connection with studies of the gonads.

Larval survey is an indirect method used to determine the reproductive season of bivalves with a planktonic larval stage. Plankton tows are periodically conducted with nets of appropriate mesh size to monitor the first appearance, abundance and duration of larvae in the water column. Known volumes of river water are filtered through 63 μm or 70 μm mesh nets and samples immediately preserved (Cataldo and Boltovskoy, 2000). In the laboratory, sub-samples are taken, all larvae counted and the developmental stages identified under a binocular microscope. Studies on larval abundance in the plankton are usually followed by laboratory experiments to artificially spawn adult specimens of the species under investigation

to describe the stages that characterize larval development, duration and size ranges from fertilization to settlement (Cataldo et al., 2005).

Studies to date on *G. paradoxa* suggest that it largely shares the reproductive characteristics of its marine relatives. According to Etim (1996) *G. paradoxa* is gonochoristic with a few (3.5%) cases of hermaphroditism. From its external morphology, the species is not sexually dimorphic, neither could the appearance of the gonad to the naked eye help in differentiating the sexes. There are conflicting reports on the reproductive cycle of *G. paradoxa*. Earlier studies by Pople (1966) and Whyte (1982) stated that the population of *G. paradoxa* in the Volta River spawned in the dry season (December-March) when the salinity of the water averages 1 practical salinity unit (psu). However, Etim (1996) found that the stock of *G. paradoxa* in the Cross River, Nigeria, spawned at the peak of the rainy season (June – October).

According to Beukema et al. (2001), the number of eggs produced in an annual spawning season by an adult female *Macoma balthica* in the Wadden Sea increases in a non-linear manner with increasing shell length and body weight. Gamete output in bivalves is governed by their pre-spawning condition: more eggs are spawned at higher weight–at-length than at lower weight-at-length (Beukema et al., 2001). Seasonal patterns in somatic and gonadal mass indices as well as gonadosomatic ratios have been used to determine the timing of spawning and the reproductive investment of *Mya arenaria* and *Cerastoderma edule* (Cardoso et al., 2007). The gonadosomatic ratio was higher in *M. arenaria* than in *C. edule* and showed a maximum of about 20% of gonadal mass in relation to total body mass in contrast to *C. edule* with a maximum of 15% (Cardoso et al., 2007).

Sexual maturity in many bivalves is reached at 2-3 years of age (except the Sphaeriidae e.g. *Pisidium* where it is < 1 year) at varying sizes depending on the growth rate and shape of the species (Stanley and Shanks, 1983, Beukema et al., 2001). For example, *Mercenaria*

mercenaria occurring in many areas along the North Atlantic coast of the United States of America mature in three years at shell lengths between 32 and 38 mm (Stanley and Shanks, 1983). In *Gafrarum tumidum* the size at first maturity ranges between 21.4 and 23.2 mm which compares well with other venerid/arcid species (Jagadis and Rajagopal, 2007). Although annual growth rates in *Macoma balthica* in the Wadden Sea vary significantly depending in particular on the spring concentration of planktonic diatoms, first spawning occurs at two years corresponding generally with a shell length between 10 -15 mm (Beukema et al., 2001).

The reproductive cycle of bivalves is influenced by exogenous (food availability, temperature, salinity) and endogenous (nutrient reserves, hormonal cycle) variables that determine the initiation and duration of the cycle (Newell et al., 1982). Water temperature and food availability are the most important exogenous factors controlling the gonad cycle of temperate bivalves (Seed, 1976; Ruiz et al., 1992; Cano et al., 1997; Darriba et al., 2005). Gametogenesis in most temperate bivalves either commences or accelerates when ambient temperatures begin to rise thus confining the spawning of these species to the warmer periods in spring and summer (Gaspar and Monteiro, 1999). The gametogenic cycle of tropical bivalves is influenced by factors other than temperature since water temperature is relatively constant. The rainfall/flooding cycle has been found to exert a greater influence on the reproduction of tropical species (Moses, 1987).

1.4 Population Dynamics

The growth rate of bivalves is influenced by several factors including habitat type and associated abiotic variables as well as geographical latitude of habitation (Fiori and Morsan, 2004; Moura et al., 2009). Geographical latitude tends to have a profound influence on the growth rate and age of bivalves (Moura et al., 2009). For example the southernmost population of the yellow clam *Mesodesma mactroides* in Argentina (41° S) differs in age from its northern counterpart (24° S) in Brazil owing to prolonged submersion periods and a low metabolic rate as a result of lower temperatures (Fiori and Morsan, 2003). Temperate bivalves have a faster growth rate in spring and summer with a decreased rate or no growth in autumn and winter (Gaspar et al., 2004; Moura et al., 2009).

The type of habitat inhabited by a bivalve tends to influence its growth rate hence the maximum age attainable. Several authors have documented the effects of wave action on growth rates (Jones and Demetropoulos, 1968; Raubenheimer and Cook, 1990). McQuaid and Lindsay (2000) observed that *Perna perna* populations on a wave exposed shore had a faster growth rate (0.64 $year^{-1}$) compared with similar populations on a sheltered shore (0.31 $year^{-1}$). Longevity, however, was lower in the exposed population (2.59 years) than the sheltered (6.72 years), as growth rate and longevity are inversely related (Seed, 1969; Bayne, 1976; Berry, 1978).

Several methods have been used to estimate the age of bivalve populations: counting of annual growth rings visible on the surface or in the microstructure of polished and etched shells (Richardson, 2001); length-frequency distribution analysis (Anwar et al., 1990; Richardson et al., 1990); and tagging-recapture experiments (Ropes et al., 1984; Etim and Brey, 1994).

Counting of shell surface rings is a traditional method used to assess the growth rate and determine the age of bivalves (Ziuganov et al., 2000). In many bivalve species surface rings are formed annually as a result of seasonal changes in shell deposition (Richardson, 2001).

In temperate regions, bivalves show reduced growth in winter as a result of declining seawater temperatures and decreased food availability (Peharda et al., 2002). In the tropics where temperature is relatively constant, other factors such as spawning, rainfall, flooding and food may lead to reduced growth and the formation of surface rings. Storms, unusual weather patterns, disease and predator attacks can also result in the formation of surface rings, known as disturbance rings. The presence of disturbance rings can lead to an overestimation of an individual's age and underestimation of growth rates (Richardson and Walker, 1991).

The analyses of length frequency data have found wider applications in the tropics owing to its simplicity (Pauly, 1983). The age and growth rate of a species can simply be determined by collecting length-frequency data for 12 months and analysing it with user-friendly software such as Fisheries Statistics (FiSAT).

Tagging-recapture experiments are direct methods used to age bivalves and are usually applied to validate other age determining methods, e.g. shell surface rings (Sejr et al., 2002). Individuals of a known length are marked and the rate of shell deposition or growth monitored for a number of seasonal cycles and compared with earlier shell deposition rates to indicate the seasonality or otherwise of ring deposition.

Tagging studies are a major tool for assessing fisheries and studying population dynamics. Such studies often provide information about parameters that are otherwise difficult to estimate such as growth rate, natural mortality and selectivity. These capabilities make tagging studies an ideal complement to traditional age and growth rate estimation approaches.

1.5 Biomass and Production

Production and biomass studies allow the evaluation of the role of species in a community as well as comparisons among different ecosystems (Hibbert, 1976). For the sustainable management of an artisanal fishery that is based on a species with a limited distribution like *G. paradoxa* it is necessary to ascertain the production of the various cohorts in the population in order to develop a management measure that targets the less productive cohorts (Moses, 1990; King, 2000).

Biomass is the mass of an individual or a collection of animals and it increases with age (van der Meer et al., 2005). In an aquatic ecosystem, biomass generation starts with primary producers that capture solar energy and transform it into organic material for their own use with the subsequent storage of the remainder in their tissue as biomass.

Production on the other hand measures the rate at which biomass is formed or accumulated in organisms. This tends to decline with age as older organisms grow at a slower rate and a greater percentage of their energy is channelled into tissue maintenance and repair (MacDonald and Thompson, 1986). At present, the most common methods for calculating production are the increment summation method, the removal summation method, the instantaneous growth method and production estimate by the Allen curve. All these methods are based on the analysis of body weight and abundance of cohorts sampled at regular time intervals (Sprung, 1993). It has been demonstrated that all 4 methods basically lead to the same result (Gillespie and Benke, 1979; Crisp, 1984; van der Meer et al., 2005).

In many ecological studies, production is required not only for single abundant species, but also for whole communities. As collecting and analyzing field data by the methods mentioned above is extremely labour intensive, a number of empirically derived relationships are used to estimate production or to obtain a preliminary estimate of benthic production processes, when

detailed data are missing (Sprung, 1993). Banse and Mosher (1980) related the quotient of annual production to mean annual biomass of the body weight at first sexual maturity (M_s) of studied animals and found the following relation: P: B = $0.65*M_s^{-0.37}$. The application of this equation to field studies, however, encounters difficulties, because M_s is not easily obtained for rare species whose life history is poorly known (Sprung, 1993). Similarly, Schwinghammer et al. (1986) proposed an empirical relationship based on the mean annual body weight (M); P: B = $0.525 *M^{-0.304}$. The application of these empirical relationships calls for a cautious approach as P: B ratios are either over- or under-estimated since local environmental variations that affect growth are not reflected.

The proportion of an organism's energy budget that is allocated to reproduction is termed reproductive effort (Bayne et al., 1983). In general, reproductive effort increases over the adult life span in iteroparous bivalves towards an asymptote (Bayne et al., 1983). For example, when measured as the proportion of non-respired absorbed energy allocated to reproduction, there is an increase from zero to 100% over 1 to 12 years in *Mytilus edulis* (Bayne 1976; Thompson 1979). Calow (1981) investigated animal tactics of resource acquisition and allocation and compared the budgeting of energy among a variety of different species. He found that the percentage of energy allocated to reproduction was variable (Calow, 1981). Growth used between 1.2 and 53% of assimilated energy while the energy available for reproduction varied between 2 and 53%. An increase in reproductive effort with advancing age appears to be the norm in bivalve species investigated to date, although there is both interspecific and intraspecific variation in absolute values (Thompson, 1984).

1.6 General Ecology of *G. paradoxa*

The freshwater clam *Galatea paradoxa* (Born 1778) is a bivalve mollusc belonging to the Tellinoidea and Donacidae (Purchon, 1963). It is endemic to the West African sub-region with a range that extends from the Gulf of Guinea to the Congo (Moses, 1990). Despite its wide distribution little information exists on its ecology and biology (Purchon, 1963). The species prefers coarse to medium grade sandy substrates in which it burrows with only the siphons protruding into the water column (Purchon, 1963; Moses, 1990). According to Moses (1990) the density of *G. paradoxa* is directly related to the substrate type, being lower in muddy and silty deposits with high levels of vegetable debris.

Freshwater bivalves are threatened worldwide (Ricciardi and Rasmussen, 1999; McIvor and Aldridge, 2007) owing to pollution, siltation and habitat loss attributable to anthropogenic pressures such as damming, land use, loss of obligate host fish and spread of invasive species (flora and fauna). The quality of river habitats in West Africa is declining for a variety of reasons including the use of pesticides in crop plantations, siltation from mining activities and damming for hydro-electric power. Pollution, sedimentation, changing flow regime and increased water temperature threaten a range of endemic species (Seddon, 2008).

The Volta River had a seasonal flow pattern, discharging freshwater at the estuary in the wet season, with salt-water intrusion in the dry season as far as 70 km upstream (Purchon, 1963). However, the construction of the Akosombo Dam in 1964 and subsequently the Kpong Dam in 1982 on the Volta River caused an alteration of the existing biophysical and ecological processes in the river basin (Attipoe and Amoah, 1989). The alteration of the flow pattern of the river resulted in significant habitat modifications that have threatened the existence of this highly exploited species in the lower Volta.

1.7 Socio-economics of Clam Fisheries

Freshwater molluscs contributed an estimated 428, 000 tonnes out of 10 million tonnes of global inland capture fisheries in 2006, and are ranked the third most important group of species harvested from inland waters (FAO, 2009). In terms of aquaculture production, molluscs accounted for the second-largest share of 14.1 million tonnes (27 % of total production), worth US$11.9 billion in 2006 (FAO, 2009).

G. paradoxa is the basis of a thriving artisanal fishery in the lower reaches of the following rivers; the Volta (Ghana), Cross and Nun (Nigeria) and Sanaga (Cameroon) (Etim and Brey, 1994). In the lower Volta basin the clam has for decades supported the livelihood of 1000-2000 women, who fished, processed, marketed and to some extent fattened smaller clams to marketable sizes (Lawson, 1963). According to Kapetsky (1990), the clam fishery is locally very productive with yields of two to three times as much meat by weight as finfish. Furthermore, the shell has a number of important uses notably as a source of calcium in poultry feed and in lime manufacturing. The shells are also used as an alternative to stone chippings in concrete. Additionally, it is used as a pavement material to overcome muddy conditions in village compounds in the southern parts of the Volta Region, Ghana. Thus, the social and economic importance of the clam cannot be underestimated.

Landings from the clam fishery dwindled drastically from 8000 metric tonnes a year prior to the construction of the dams to a paltry 1700 metric tonnes (Kumah, 2000). The exploitation of *G. paradoxa* in the Volta River is largely devoid of all forms of management and conservation strategies apart from a closed-season from December to mid-March each year. The clam fishery in the Lower Volta has a unique traditional fattening system in which smaller clams (20 mm) are seeded to underwater farms for some months to gain weight and sold during the closed-season. Underwater farms are demarcated sites in the river that provide a

secluded environment for clams to grow under conditions which are not different from the rest of the river. In a growth trial, juvenile clams taken from the river and stocked in an underwater farm from February to early June increased in length from 3.7cm to 4.7cm. Although quite a small increment in length, it represented a 60% increase in value (Lawson, 1963). In another experiment, an increment as high as 320% in weight was recorded over a nine-month period in transplanted juveniles between 10 g and 21 g (Kumah, 2000). Attipoe and Amoah (1989) evaluated the aquaculture potential of *G. paradoxa* and concluded that it was a highly suitable species that could easily be developed into a culture-based fishery relying on juveniles collected in the wild and fattened in underwater farms.

The encouraging result on the culture potential of *G. paradoxa* has stimulated interest in its culture because *Galatea* is a delicacy in Ghana and fetches a high price on the Ghanaian market. Additionally, it is a species that could easily be integrated into the local tilapia and catfish farming systems since clams do not required external feed and can clean the environment of excess phytoplankton or suspended particulate matter through filter feeding. Integration into the existing fish farming systems will augment the income of fish farmers, especially pen culturists in the Volta River as it will utilise the same space and water resources.

1.8 Aims of the Study

Commercial extinction of *G. paradoxa* is imminent in Ghana as a result of habitat alteration and over-exploitation, with socio-economic consequences for villages, especially women whose livelihood depends on the *Galatea* fishery. One solution is to develop *Galatea* culture because:

1. There is evidence that the species is highly suitable for culture based on results from the underwater farm and transplantation experiments;

2. Suitable culture sites are abundant; and

3. There is potential for integration of *Galatea* culture into existing fish-farming systems (because of its filter-feeding habit)

The obstacles are:

1. Wild seed stock is limited; and

2. The reproductive biology, population dynamics, and growth patterns are not well understood for effective hatchery production and rearing.

In order to manage the fishery and develop the traditional fattening of clams into a sustainable clam culture it is important that the reproductive biology, population dynamics and production of *Galatea* are clearly understood.

The objectives of this study are to:

1. Determine the reproductive biology of *G. paradoxa* in the Volta River;

2. Set out the population dynamics and estimate the growth rate of *G. paradoxa*; and

3. Quantify the biomass, production and resource allocation of *G. paradoxa*.

2.0 MATERIALS AND METHODS

2.1 Study Area

The study was conducted at the estuary of the Volta River, south-eastern Ghana (Figure 2.1). The Volta River Estuary lies within the coastal savannah zone with an annual rainfall of 750–1,250 mm (Dickson and Benneh, 1977). The estuary is about 1.2 km wide at the mouth, but owing to the formation of a sandbar, the river enters the sea through a narrow opening. Two dams have been built on the Volta River at Akosombo (100km) and further downstream at Kpong (75km) from the mouth of the river. The dams, in addition to a sandbar at the mouth of the river, influence the seawater and freshwater dynamics of the estuary. Sampling was carried out at two sites seaward of the dams; Ada, the seaward limit of *G. paradoxa* distribution in the Volta River and Aveglo an area which is predominantly freshwater.

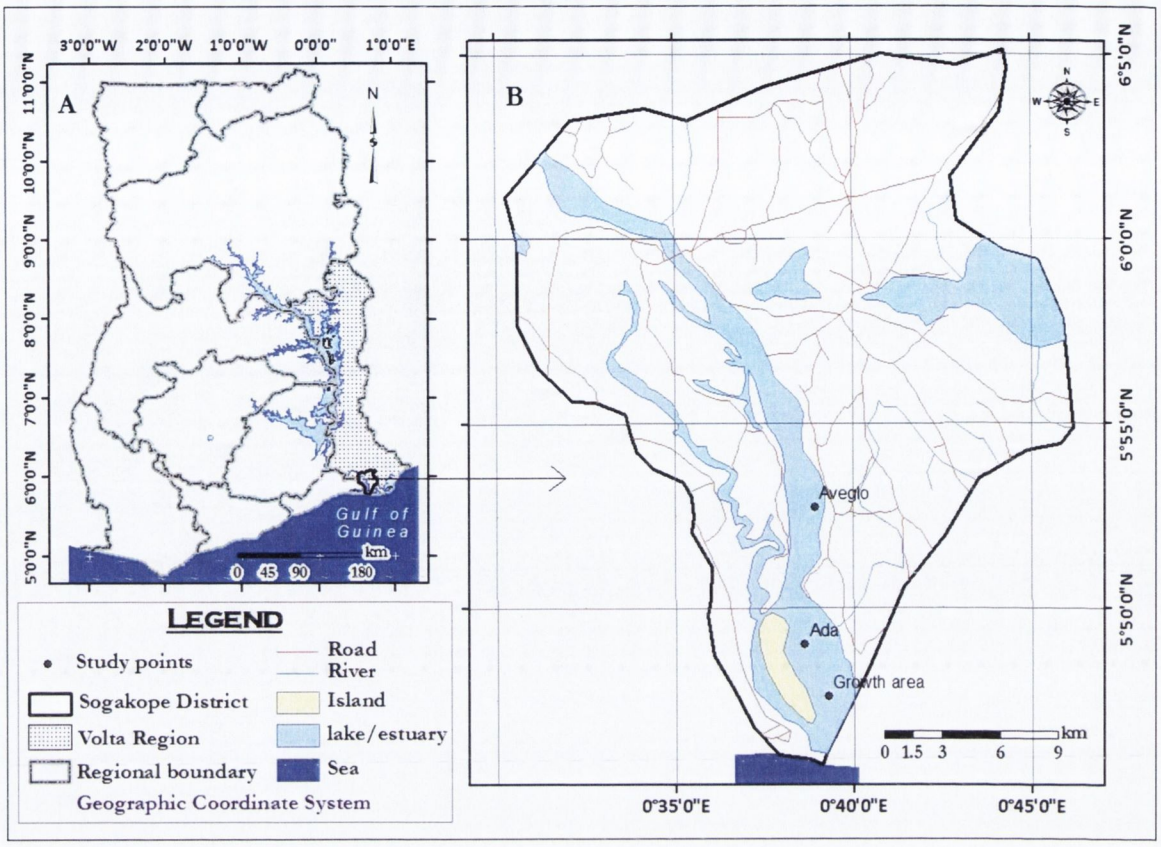


Figure 2.1 Map of Ghana (A) showing the Sogakope District (B) and the location of sampling areas (Ada and Aveglo) in the Volta Estuary. Refer to Section 2.2 for the details of the sampling areas.

2.2 Field Sampling at the Volta Estuary

The first sampling site, Ada (5° 49′ 10″ N, 0° 38′ 38″ E), was located 10 km from the mouth of the river and represents the seaward (0.03 and 1.5 psu) limit of *G. paradoxa* distribution in the Volta River. The area is generally shallow with depths between 0.60 and 2.0 m. There are patches of dense aquatic weed growth (such as *Ceratophyllum sp.*) owing to the shallowness of the area. The sediment in this area consists mainly of fine sand with patches of mud. Clam fishing in the shallow zones of this area is carried out mostly by women who search the sandy substratum for clams with their feet (Figure 2.2). When a clam is detected it is lifted between

the toes or by hand and placed in a bucket. The deeper zones are fished by men who use Hookah diving gear.

Figure 2.2 Clam fishing by women in the shallow zones at Ada, Volta Estuary, Ghana.

The second sampling site, Aveglo (5° 52′ 54″ N, 0° 38′55″ E), was situated 15 km from the mouth of the river. It is predominantly freshwater (0.03 psu) and deeper with depths between 4.0 – 6.0 m. The sediment in this area is coarse sand to gravel. Clam fishing at Aveglo is carried out by young men using Hookah fishing gear comprising compressors placed in wooden boats to provide air through long tubes and net bags. Fishers remain underwater for 30 - 60 minutes probing the sediments with their fingers for clams, which are placed in net bags and hauled into the boat with an attached rope after each dive (Figure 2.3).

Figure 2.3 Hookah fishing accessories (compressor, mask and net bag) used for clam fishing in the deeper zones at Ada and Aveglo by young men at the Volta Estuary.

2.3 Sampling Protocol

Galatea paradoxa samples were collected monthly from March 2008 to February 2010 at Ada and Aveglo from clam fishers. In order to obtain a sample covering the range of sizes in the population and eliminate any bias owing to the preference of fishers for larger clams (clams less than 20 mm are not picked by fishers), two grab samples (grab size equivalent to 0.1 m^2) were collected monthly from each site. The sediments were washed over a 1 mm sieve and any individual recovered was kept separately for density calculations and length-frequency distribution of juveniles. Samples were transported in insulated boxes with ample river water

which was refreshed every 12 hours to the wet laboratory at the Department of Fisheries and Watershed Management, Kumasi, for processing within 24 hours.

In order to determine the time of occurrence and the length of a possible planktonic larval stage of *G. paradoxa,* duplicate horizontal plankton hauls were collected monthly at Ada and Aveglo from March 2008 to May 2009 and fortnightly from June 2009 to January 2010 with a 63μm Turtox plankton net to ascertain the time larvae appeared in the water column (Johnson, 1995). The net with a ring diameter of 30 cm was equipped with a flowmeter and tows were conducted at the lowest boat speed at a depth of 1 m below the water surface for 10 minutes. The volume of water filtered was calculated from the revolutions of the calibrated flowmeter mounted in the middle of the net. The contents of the net's codend were fixed in formal saline for later analysis. In the laboratory, 2-3 drops of Rose Bengal was added to sub-samples to aid identification and enumeration of larvae. The detection and enumeration of *G. paradoxa* larvae in the plankton samples was carried out using cross-polarized light (CPL) microscopy (Johnson, 1995).

2.3.1 Laboratory Processing of *G. paradoxa*

G. paradoxa samples from Ada and Aveglo were sorted initially into three size groups (20-40, 41-55 and >55 mm) and numbered individually. The sorting and numbering was done in order to ensure that all the size groups were represented in the selection of sub-samples for subsequent processing for population dynamics, condition indices, gonad smears and histology.

2.3.1.1 Population Dynamics

G. paradoxa samples from the fishers catch in addition to those from the grab samples were processed for age and growth rate determination by the analysis of the length-frequency

distributions of the monthly samples. The shell length (maximum anterior-posterior dimension) of each specimen was measured with a pair of digital callipers (Hangzhou United Bridge Tools, Hangzhou, Zhejiang, China) (0.01mm), total weight (shell + flesh) was recorded with a Sartorius PT1200 balance (DWS, Elk Groove, IL, USA) (0.1g) after blotting the shell with absorbent paper to remove excess water and allowing the shell to air-dry for 1 hour at room temperature. The shell length and weight measurements were used to compute the population parameters of *G. paradoxa*.

2.3.1.2 Condition Indices

Using the individual clam numbers (Section 2.3.1) and the corresponding shell length–weight measurements (Section 2.3.1.1), a sample of 60 and 20 individuals were selected randomly from the three size groups and processed for condition and gonadal indices, respectively.

A sterile stainless steel knife was used to open the shell and a scalpel blade carefully used to remove the flesh of each individual (Figure 2.4). The flesh of each sample was blotted dry and weighed on a Sartorius BP 210S micro balance (DWS, Elk Groove, IL, USA) to the nearest 0.0001g (Shell-free wet weight). The wet flesh was oven-dried to a constant weight at 60°C for 48 hours and weighed to the nearest 0.0001g for shell-free dry weight.

For the determination of gonadal condition indices the gonads which are associated with the mantle were carefully excised and weighed (gonad wet weight), and the rest of the tissue excluding the gonads also weighed (tissue wet weight). The gonads and the rest of the tissue were oven-dried at 60°C for 48 hours and weighed as gonad dry weight and tissue dry weight to the nearest 0.0001g, respectively.

The shells were air-dried and weighed (shell weight) to the nearest 0.1 g and stored by month of collection to be subsequently used in age determination by counting of annual rings on the shell surface. The internal shell volume was determined by noting the volume of water from a

burette needed to fill each shell valve (Etim, 1994). The ash content of the dried body tissue was determined as the residue left after burning the sample in a muffle furnace at 550° C for 6 hours. The condition indices of each specimen were computed as:

a) Ash-free dry body weight(AFDW)/shell weight (SW) x 100;

b) Ash-free dry body weight (AFDW)/(length)^3 (L^3) x 100;

c) Shell-free wet body weight(SFWW)/total wet weight (TWW) x 100;

d) Shell-free dry body weight) (SFDW)/shell weight (SW) x 100;

e) Shell free dry body weight)(SFDW)/shell volume(SV) x 100;

f) Gonad wet weight (GWW)/shell weight (SW)x 100;

g) Gonad dry weight (GDW)/shell weight (SW) x 100;

h) Gonad wet weight (GWW)/total wet flesh weight (TWFW) x 100; and

i) Gonad dry weight (GDW)/total dry flesh weight (TDFW) x 100.

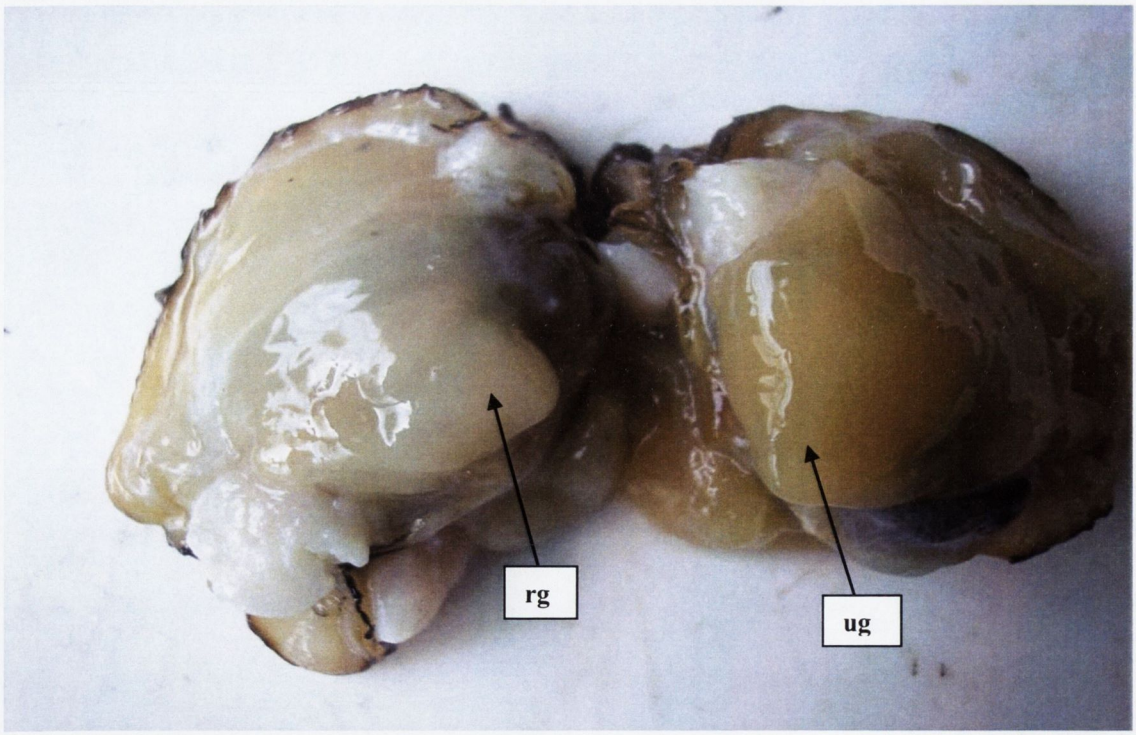


Figure 2.4 Excised flesh from 2 individuals showing a ripe gonad (rg) (left, creamy) and an unripe gonad (ug) (right, beige)

2.3.1.3 Gonad Smears

Smears of the gonad were examined under a light microscope at magnifications x10 and x40 for 12 individuals representing the range of sizes in the population to identify the sex as well as oocyte development, and progression by measuring the diameter of 30 eggs. Oocyte size was measured to the nearest μm with an ocular micrometre which was pre-calibrated with a 1 mm stage micrometer. The stages of gamete development were assigned to one of several categories after Wilson (1999):

I immature/sexes not distinguishable: no gonads seen

A first signs of gonad maturation; sexes start to be distinguishable

B gonad differentiation well advanced; sexes easily differentiated

C_1 male with spermatids; female with largely pedunculate eggs

C_2 male with sperm ducts; female eggs largely non-pedunculate, ready to spawn

D gonads almost empty but sexes still distinguishable; immediately post-spawning

2.3.1.4 Histological Examination of Gonads

The gametogenic cycle of *G. paradoxa* in the Volta River was investigated histologically by examining the gonads of 15 randomly selected individuals from each site. Sections of the gonad tissue were processed by fixing in Bouin's solution for 24 hours. The tissues were dehydrated by transferring through graded concentrations of alcohol (70-100%), cleared in a chloroform/xylene mixture, impregnated with paraffin wax at 60° C, embedded and blocked in solid paraffin, trimmed with a knife and cut with a rotary microtone at 5μm. Sections were mounted on microscope slides, stained with haematoxylin and counterstained with eosin. Slides were examined with a light microscope; first under low power (x10) to scan the entire gonad area, then under high power (x40) to assess each follicle. Each gonad sample was assessed and scored according to the scheme in Table 2.1.

Table 2.1 Explanation of the gametogenic scale and descriptive terms used in scoring the histological slides of gonad tissue. Adapted from Darriba et al. (2004).

Stage	Definition	Brief Description of gonad
0	Sexual rest	Follicles few and small. Sex distinguishable. Protogonia and gonia in mitosis.
I	Start of gametogenesis	Follicle size increases. Spermatogonia and spermatocytes in males. Oogonia and previtellogenic oocytes in females.
II	Advanced gametogenesis	Follicle size increases and occupies the entire tissue. Germinal cells in all phases of gametogenesis.
IIIA	Ripe	Polygonal follicles almost full of ripe gametes. Spermatozoa occupy most of follicle. Free ripe polygonal oocytes in the lumen.
IIIB	Start of spawning	Gonoducts with mature gametes in emission. Spermatozoa lose radial disposition. Free ripe rounded oocytes in the lumen and empty spaces.
IV	Spent	Follicle small and practically empty. Residual gametes degrading.

2.4 Age Determination in *G. paradoxa*

The age and growth rate of *G. paradoxa* in the Volta River was determined using three methods:

1. Shell surface growth rings;
2. Modal progression analysis of length-frequency distributions; and
3. Tagging-recapture experiments.

2.4.1 Shell Surface Growth Rings

Dried shells (as described in Section 2.3.1.2) were used to estimate the age of *G. paradoxa* by counting the annual concentric growth checks (narrow clear or dark zones on the periostracum) on both valves (King, 2000). Counting of surface rings was done as a double blind exercise where an independent person was trained to count the annual rings on the other valve. The mean shell length corresponding to the ages and standard deviations were calculated from the two independent counts. Increment in mean shell length from one year to the next was used as an index of growth. The age-shell length data generated was fitted to the von Bertalanffy growth function (VBGF) by the length-at-age routine in FiSAT II (Gayanilo et al. 2005) to estimate the asymptotic length (L_∞) and the growth coefficient (K).

2.4.2 Analysis of length-frequency distributions

The Bhattacharya method (Bhattacharya, 1967) available in the fish-stock assessment tool FISAT II (Gayanilo et al. 2005) is commonly used to estimate the growth parameters of a stock because it needs only length-frequency data. The length measurements recorded in Section 2.3.1.1 were grouped into shell length classes at 2 mm intervals (Tumanda Jr. et al., 1997) and analysed subsequently using FISAT II (Gayanilo et al., 2005). First, the Powell-Wetherall plot (Powell, 1979; Wetherall, 1986; Pauly, 1986) was used to obtain an initial estimate of L_∞. The L_∞ was seeded in the Shepherd's method (Shepherd, 1987) in FiSAT II to estimate K.

2.4.3 Tagging-Recapture Experiment

The growth of individual *G. paradoxa* was monitored from June 2008 to May 2009 in a tagging-recapture experiment. Wooden boxes of dimensions 50x40x15cm were filled with the sandy sediment found at the point of occurrence of the *G. paradoxa*. Fifty individuals with

shell lengths between 24 and 60 mm were selected randomly, marked by engraving a number on one side of the shell and assigned to one of the boxes. The shell length and total weight were taken, as described in Section 2.3.1.1, at the start of the experiment in June 2008 and every two months thereafter.

Data from the tagging-recapture experiment were treated as growth increment data and analysed by using the Gulland and Holt Plot (Gulland, 1959) in FiSAT II to estimate the asymptotic length (L_{∞}) which was seeded in the Munro routine (Munro, 1982) to compute the growth coefficient (K) for the data. The estimated L_{∞} and K were then fitted to the VBGF (von Bertalanffy, 1938):

$$L_t = L_{\infty}(1-e^{-k(t-t_0)}) \qquad \text{Equation 2.1}$$

Where:

L_{∞} = asymptotic length (mm);

k = the growth coefficient ($year^{-1}$);

t = the age (years); and

t_0 = age at zero length.

Based on the age-length estimates obtained for the three methods, the VBGF that describes the growth of *G. paradoxa* was estimated.

2.5 Annual Production in *G. paradoxa*

The annual production of the year classes or cohorts of *G. paradoxa* was calculated based on regression equations from the monthly samples of 60 individuals covering a range of sizes in the population as described in Section 2.3.1.2. Annual production (May 2008 to May 2009) was determined after Crisp (1984) and Wilson (1996).

$$P = \Delta B + M \qquad \text{Equation 2.2}$$

Where:

P = Production;

ΔB = change in biomass; and

M = Mortality.

For the determination of biomass, ash-free dry weights (AFDW) were obtained by loss of ignition (LOI) for the monthly samples as outlined in Section 2.3.1.2. The relationship between the AFDW (mg) and shell length (mm) was established by separate $\log_{10}$ regression for the monthly samples. The derived weight exponent β and intercept α were fitted to Equation 2.3 and applied to the mean shell length corresponding to the age of individual *G. paradoxa* and cohorts in the population at each sampling date to calculate the weight of the cohorts, which were summed to obtain the final biomass. The difference between the pre-spawning and post-spawning AFDW of the cohorts were used for the determination of change in biomass (ΔB).

$$\log_{10} Y = \alpha + \beta (\log_{10} SL) \qquad \text{Equation 2.3}$$

Where:

Y = AFDW in mg;

SL = shell length in mm; and

α, β = are the intercept and slope, respectively.

2.6 Water Quality Variables

Temperature, pH, conductivity, dissolved oxygen (DO) and salinity were measured electronically on-site with a portable multiparameter water quality meter model (HI 9828) from March 2008 to February 2010. Chlorophyll a, alkalinity, suspended particulate matter (SPM), nitrate and phosphate were measured in collected water samples in the laboratory as described below.

2.6.1 Chlorophyll a Measurement

Chlorophyll a was measured according to the standard procedure described in HMSO (1983). One litre of river water was filtered under vacuum through a Whatman GF/C filter paper to collect the phytoplankton. The filter paper was placed in a centrifuge tube containing 10 ml of methanol. The loosely capped tube was heated briefly in a water bath at 65 -70° C in a fume cupboard. The tube was removed and left for 5 minutes in the dark. The filter paper was removed from the tube after pressing it against the side of the tube to drain as much methanol as possible and the tube was centrifuged for 8 minutes at 3500 rpm to obtain a clear extract for spectrophotometric determination. Absorbance was measured after a baseline correction for methanol at wavelengths of 665 and 750 nm before and after acidification with 0.1M HCl to measure the phaeophytin concentration. Equation 2.4 was used to calculate the chlorophyll a and phaeophytin concentration in the water.

Chlorophyll a/ phaeophytin (μgl^{-1}) = $13.9[3(A_h - A_j) * v]/ d * V$ Equation 2. 4

Where:

A_h = absorbance at 665 nm;

A_j = absorbance at 750 nm;

v = initial volume of methanol in ml (usually 10 ml);

d = cell length of cuvette in cm (1cm); and

V = sample volume in litres (1L).

2.6.2 Carbonate Alkalinity or Hardness

The standard method for carbonate alkalinity determination as described in APHA (1975) was used. The method is based on the assumption that the alkalinity of water is its quantitative capacity to neutralise a strong acid to a designated pH. In the procedure, the pH value of a 50

ml sample of river water was measured while stirring gently and titrated with 0.02 N H_2SO_4 using an automatic burette to pH 4.4. The volume of acid used was then inserted into Equation 2.5 to calculate the alkalinity of the sample.

Alkalinity in (mgl^{-1}) $CaCO_3$ = ml of titrate * 20 Equation 2.5

2.6.3 Suspended Particulate Matter (SPM)

A modified procedure of loss on ignition (Allen, 1989) was used to measure the suspended organic matter in the water. One litre of river water was filtered through a pre-ashed and pre-weighed Whatman glass fibre (GF/C) filter to retain the suspended matter. The filter paper was then dried for 24 hours in an oven (105° C) and re-weighed on a Sartorius BP 210S micro balance (sensitivity 0.0001 g) to obtain the dry weight of the sample by Equation 2.6. The filter paper was placed into a dry crucible and in a muffle furnace for 4 hours at 550° C to burn the organic matter. The filters were placed in a desiccator and after cooling were re-weighed. The weight loss represents the ash-free dry weight (AFDW) of the organic particulate matter.

Dry weight of sample (g) = (DW of sample in g + filter) – (weight of filter) Equation 2.6

2.6.4 Nitrate Determination

Traditional methods for nitrate determination use cadmium columns, which can be expensive, difficult to maintain and prepare, and require a great deal of analytical technique. Nitrate concentration in the river water was monitored using the Wagtech nitrate method (Abegaz et al., 2005). Nitrate was first reduced to nitrite, the reduction stage being carried out using a zinc-based nitratest powder and nitratest tablet. The resulting nitrite was determined by reaction with sulphanilic acid in the presence of N-(1-naphthyl)-ethylene diamine to form a reddish dye. The reagents are provided in a single nitricol tablet which is simply added to the

test solution. The intensity of the colour produced in the test is proportional to the nitrate concentration and is measured using the Wagtech photometer 7100 at 570 nm.

The test was conducted by filling a graduated sample test tube with 20 ml of river water to which one spoonful of nitratest powder and one nitratest tablet were added. The test tube was capped and shaken for one minute, allowed to stand for an additional minute after which it was gently inverted four times to aid flocculation and left undisturbed for two minutes or longer to ensure complete settlement. Ten milliliters of the supernatant was carefully decanted into a test tube to which one nitricol tablet was added and crushed to ensure complete dissolution. The solution was left to stand for 10 minutes to allow full colour development. The test tube was wiped with a clean tissue paper and read at 570 nm.

2.6.5 Phosphate Measurement

The ascorbic acid method was used to determine the dissolved phosphate concentrations on filtered water samples (Strickland and Parsons, 1965). Ammonium molybdate and antimony potassium tartrate react in an acidic medium with dilute solutions of orthophosphate-phosphorus to form an intensely coloured antimony-phospho-molybdate complex. This complex is reduced to an intensely blue-coloured complex by ascorbic acid which is proportional to the phosphorus concentration. The complex which is read at 882 nm is not stable, thus analysis must be performed within 30 minutes of adding the ammonium molybdate and antimony potassium tartrate. Barium, lead, and silver interfere by forming a precipitate. The interference from silica, which forms a pale-blue complex is small and can usually be considered negligible.

2.7 Data Presentation and Statistical Analysis

Condition indices were presented graphically using the monthly mean and the standard error (SE) as estimators of the central trend of the sample. Routines in the fish stock assessment tool (FISAT II, (Gayanilo et al., 2005) were applied to the length-frequency data to estimate the population parameters (i.e., asymptotic length, growth rate, exploitation rate, natural and fishing mortality and growth performance) of *G. paradoxa.* The age groups identified by the three methods described in Section 2.4 were presented as means (± SD) in order to give the range of shell lengths corresponding to the ages. The progression of oocyte diameters and the gametogenic cycle of *G. paradoxa* (Table 2.1) were based on the majority of oocytes at a particular stage from the histological slides.

A chi-squared goodness of fit test ($\alpha = 0.05$) was used to test the hypothesis that there was an equal representation of male and female individuals in the population (totals of males and females were pooled across all sampling dates). The histological slides were also examined for any evidence of hermaphroditism, as some bivalves species are known to have both male and female gametes occurring within the same individual (Eversole, 1989). Data from the water quality variables monitored under Section 2.6 were presented as the mean and standard error. Principal component analyses (PCA) were run on the environmental variables and the gametogenic cycle of *G. paradoxa* in order to describe any correlations. Two-way ANOVA was applied to test for differences in egg numbers and biomass between sampling sites and among age groups or cohorts using the statistical software SPSS version 16.

3.0 GENERAL ENVIRONMENTAL VARIABLES

3.1 Introduction

Bivalves have a cyclical pattern of reproduction which can be divided into three phases: gametogenesis and vitellogenesis; spawning and fertilisation; larval development and growth (Newell et al., 1982). The reproductive cycle involves complex interactions between exogenous (e.g. food availability, temperature, salinity) and endogenous (e.g. nutrient reserves, hormonal cycle, genotype) variables that determine the initiation and duration of the various phases of the cycle, and thus ensure synchrony of gamete development within a population (Newell et al., 1982). Water temperature and food availability are the main exogenous factors controlling the gonad cycle of bivalves (Seed, 1976; Sastry, 1979; Ruiz et al., 1992; Cano et al., 1997; Darriba et al., 2005).

Gametogenesis in most temperate bivalves either commences or accelerates when ambient temperatures begin to rise, confining the spawning of temperate species to the warmer periods of spring and summer (Gaspar and Monteiro, 1999; Darriba et al., 2005; Serdar and Lok, 2009). The temperature at which reproductive development starts in the sea for commonly cultured species such as *Crassostrea gigas*, *Ostrea edulis, Pecten maximus* and *Tapes philippinarum* ranges between 8 and 12°C (the biological zero, b_0) for gametogenesis (Loosanoff and Davis, 1950; Lannan et al., 1980; Chavez-Villalba, 2002; FAO, 2004). Knowing the effective b_0 and the conditioning water temperature, the number of days required for conditioning can be calculated. For example, if the mean conditioning temperature is 20°C and the b_0 is 10°C, then for every day that passes the number of degree-days will increase by 20 minus 10 = 10. Thus, a 30-day conditioning period at 20°C will accrue 300 degree days and the same period at 22°C will amount to 360 degree days. This represents the minimum time

period later in spring before the stock will be ready to spawn (FAO, 2004). This knowledge has been used extensively in hatcheries to condition and spawn e.g. oysters even in winter (Chavez-Villalba, 2002).

Food availability, measured as the quantity of chlorophyll a, is an important factor that influences gametogenesis in bivalves, as in some species food availability appears to be more important than temperature (Newell et al., 1982). Villalba (1995) attributed differences in gonad development, spawning and growth rate of *Mytilus galloprovincialis* in Galician bays, Spain, to differences in food availability. The mussels from Lorbe, the northernmost site, were smaller and had a slower growth rate with only one spawning peak in early summer compared with mussels from the other sites which grew at a faster rate and had two spawning peaks. Food availability has been observed to induce a second spawning period in *Crassostrea gigas* in El Grove, Galicia, Spain, in October despite low water temperatures (16 °C). The second spawning period coincided with a major phytoplankton bloom (Ruiz et al., 1992).

In tropical species, factors other than temperature seem to influence gametogenesis and spawning as water temperature is relatively constant. The rainfall / flooding cycle has been found to influence reproduction in tropical species; e.g. in the African catfish, *Clarias gariepinus,* the onset of spawning is triggered by the flooding of marginal areas of the streams and rivers in which it lives (Moses, 1987). *G. paradoxa* is restricted to the lower reaches of the rivers in which it occurs signifying the importance of salinity in its distribution. According to Moses (1990) adult *G. paradoxa* thrives in freshwater, but larval development requires brackish conditions with an average salinity of 1psu. This chapter describes the environmental variables monitored at the estuary and their possible influence on gametogenesis and spawning in *G. paradoxa*.

3.2 Materials and Methods

The following environmental variables; temperature, conductivity, suspended particulate matter, chlorophyll a, nitrate, phosphate, pH, dissolved oxygen, alkalinity and salinity were measured at the two sampling sites (Ada and Aveglo) as described in Section 2.6.

3.3 Results

3.3.1 Variations in Environmental Variables

The environmental variables monitored at the estuary were similar for the two sites (Ada and Aveglo) and varied within a narrow range except conductivity and to lesser extent salinity which was higher at high tide (HT). Figures 3.1 to 3.10 show the variations in temperature, conductivity, salinity, suspended particulate matter (SPM), chlorophyll a, nitrate, phosphate, pH, dissolved oxygen (DO) and alkalinity, respectively, over the study period from March 2008 to February 2010. Temperature was relatively constant throughout the study period and varied narrowly between 27.3 and 29.6°C with a mean of 28.6 ± 0.8°C (n = 24).

Conductivity was fairly constant and similar at low tide with a mean of 57.9 μScm^{-1} at Ada and Aveglo. However, at high tide (HT) conductivity was higher (mean of 583.4 $\mu Scm^{-1)}$ at Ada. The maximum conductivity recorded at Ada was 2879 μScm^{-1} (Figure 3.2). Similarly, salinity was constant at 0.03 (psu) at low tide for the two sites during the period. However, at high tide values as high as 1.5 psu were recorded (Figure 3.3). The clam beds at Ada are thus exposed to different conductivity and salinity regimes depending on tide. A gradual decline in conductivity with time was noted during the sampling period.

Suspended particulate matter (SPM) fluctuated around 2.0 mg l^{-1} during the sampling period with the maximum value of 5.5 mg l^{-1} recorded in June 2008 at the peak of the rainy season. Minimum values of 0.5 mg l^{-1} and 1.1 mg l^{-1} were recorded in the dry season (January 2009)

for Ada and Aveglo, respectively. Nitrate and phosphate concentrations were very low and varied between 0.20 - 0.93 mg l^{-1} and 0.03 - 0.21 mg l^{-1}, respectively. Low nitrate levels were recorded at the peak of the rainy season (June –September).

Chlorophyll a levels were generally low during the sampling period with a mean of 6.4 ± 0.21 µg l^{-1} and 6.5 ± 0.27 µgl^{-1} at Ada and Aveglo, respectively. Although, there were periods of high chlorophyll a levels between September 2008 and January 2009, the levels fluctuated around the mean values at both sites. The pH was relatively constant around 7.0 throughout the sampling period. Dissolved oxygen (DO) concentration at both sites was similar, the values declined from 8.8 and 9.1 mg l^{-1} in March 2008 to a low of 2.2 and 1.9 mg l^{-1} in November 2008 at Ada and Aveglo, respectively. It then rose to 6.1 and 4.3 mg l^{-1} in January 2009, fluctuated around 3.8 mg l^{-1} at both sites until low values of 1.8 and 2.0 mg l^{-1} were recorded in October 2009 at Ada and Aveglo, respectively. Dissolved oxygen levels rose steadily from the low levels in October 2009 to 9.0 mg l^{-1} in February 2010 at both sites. Alkalinity was fairly constant over the sampling period, fluctuating around 50 mg l^{-1} at Ada and Aveglo (Figure 3.10).

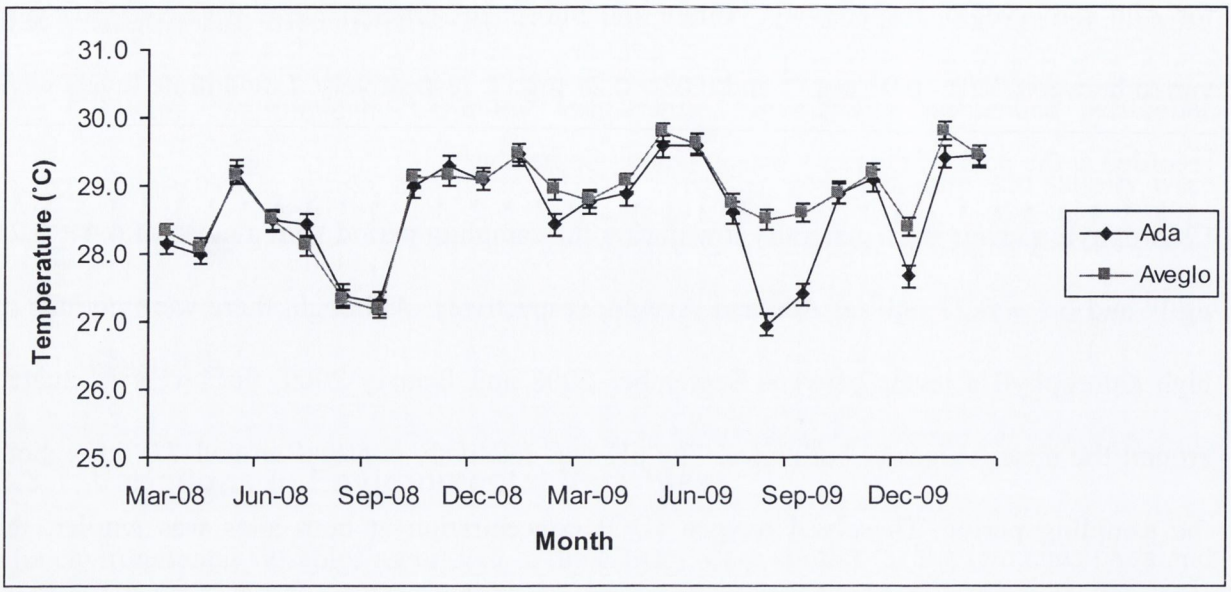


Figure 3.1 Variation in water temperature (mean ± SE) (n = 24) (°C) at Ada and Aveglo from March 2008 to February 2010.

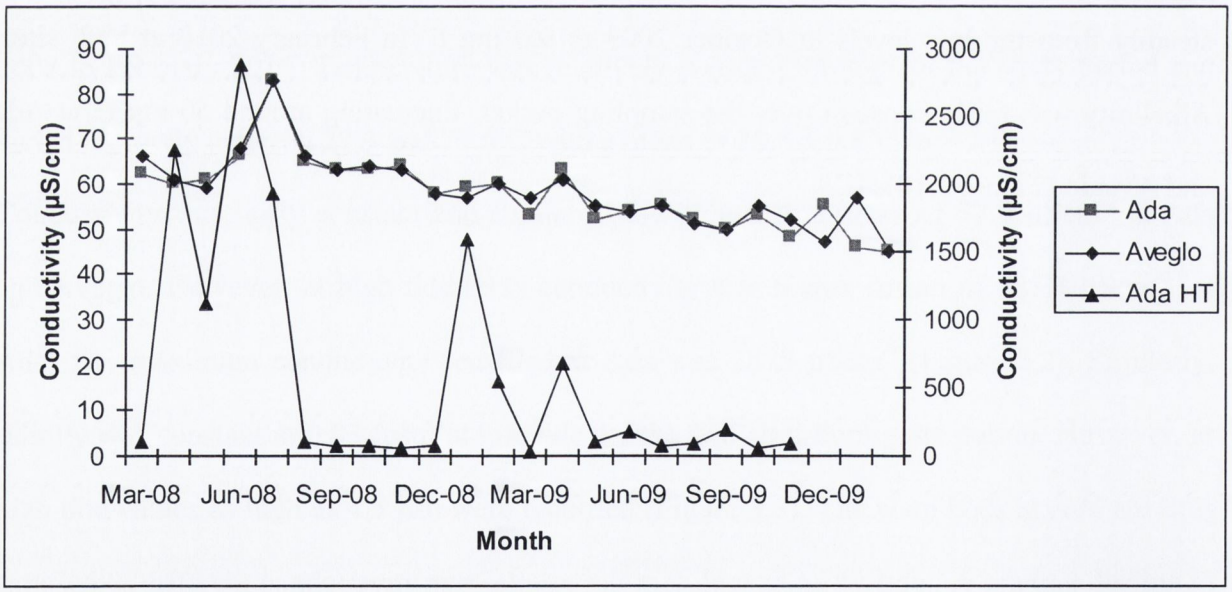


Figure 3.2 Variation in conductivity (mean ± SE) (n = 24) (μScm^{-1}) at Ada and Aveglo (left axis) and at Ada HT (right axis) from March 2008 to February 2010.

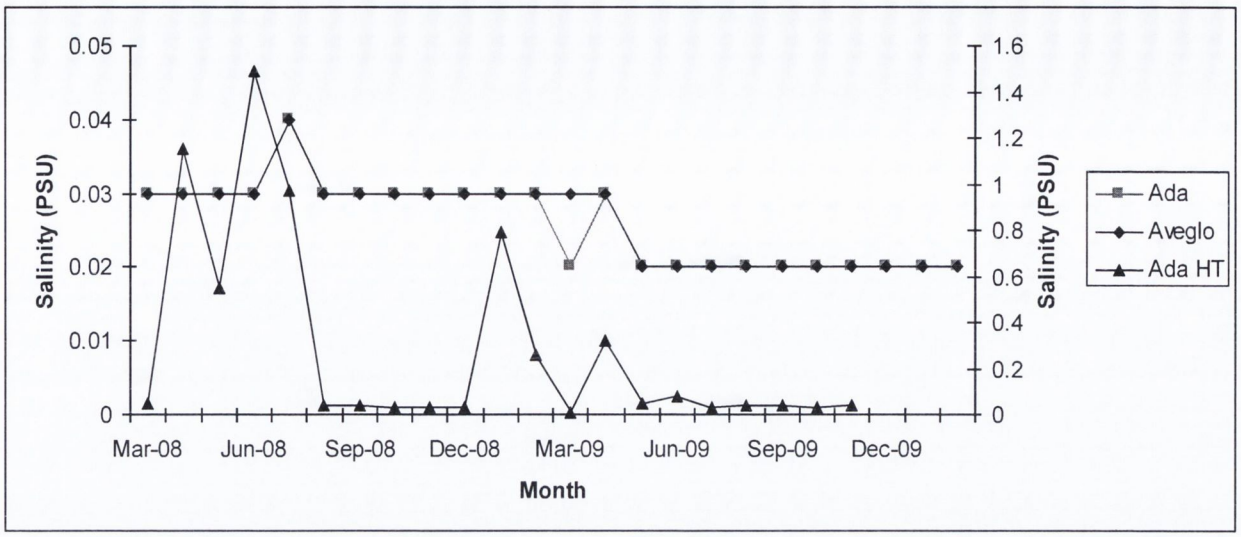


Figure 3.3 Variation in salinity (psu) at Ada and Aveglo (left axis) and at Ada HT (right axis) from March 2008 to February 2010.

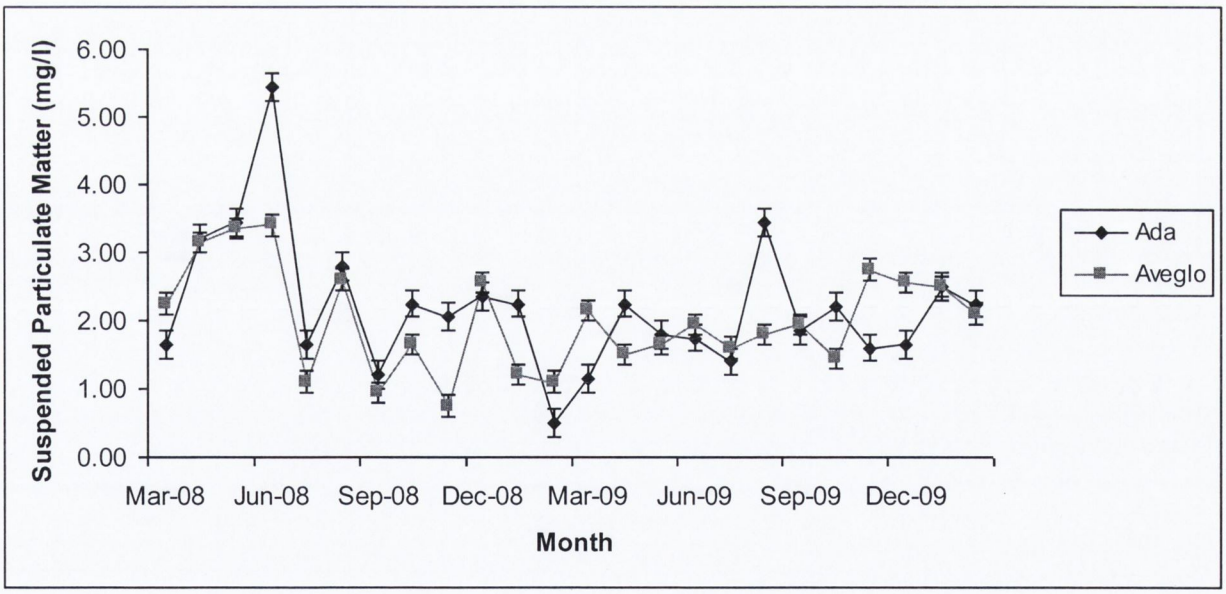


Figure 3.4 Variation in SPM (mean ± SE) (n = 48) (mgl^{-1}) at Ada and Aveglo over the study period from March 2008 to February 2010.

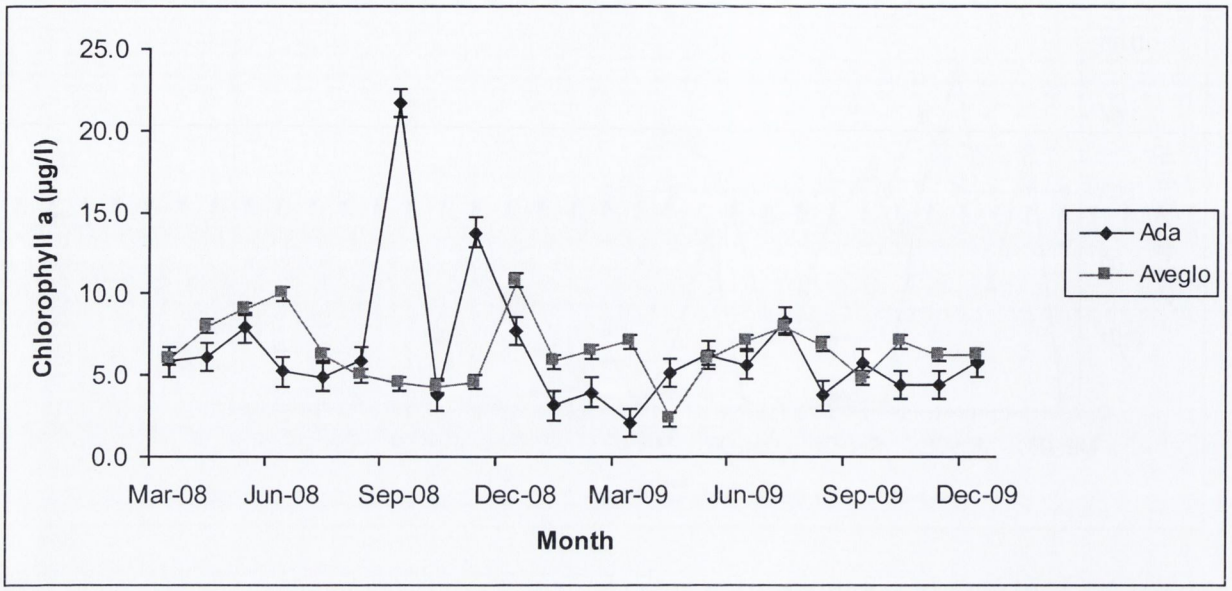


Figure 3.5 Variation in chlorophyll a (mean ± SE) (n = 48) (µg l^{-1}) at Ada and Aveglo from March 2008 to February 2010.

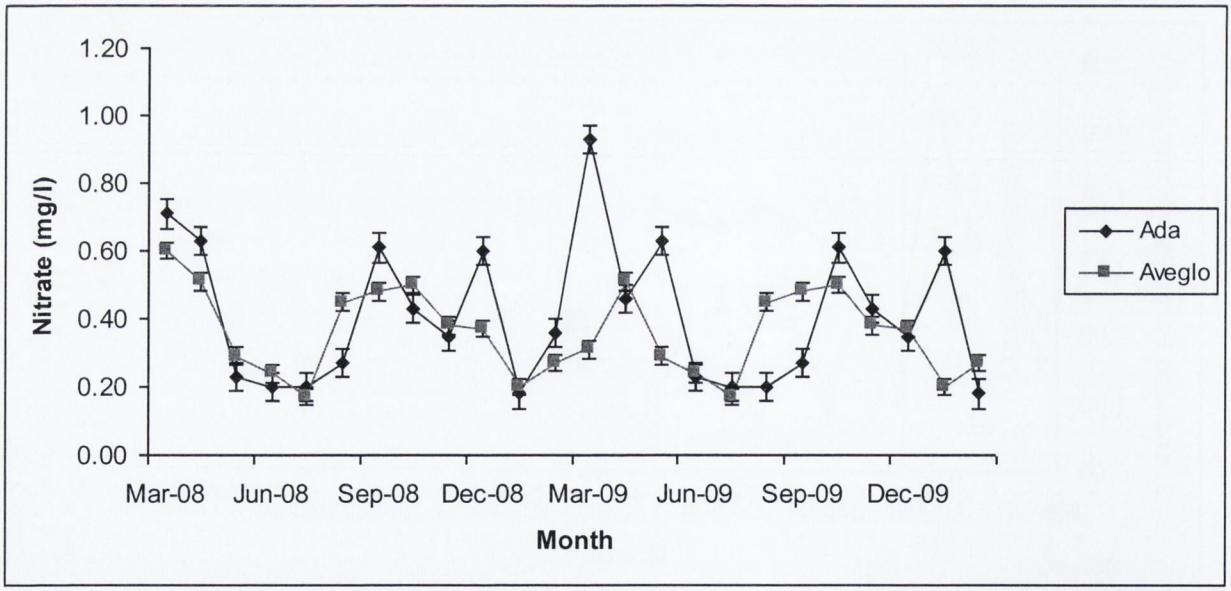


Figure 3.6 Variation in Nitrate (mean ± SE) (n = 48) (mg l^{-1}) at Ada and Aveglo from March 2008 to February 2010.

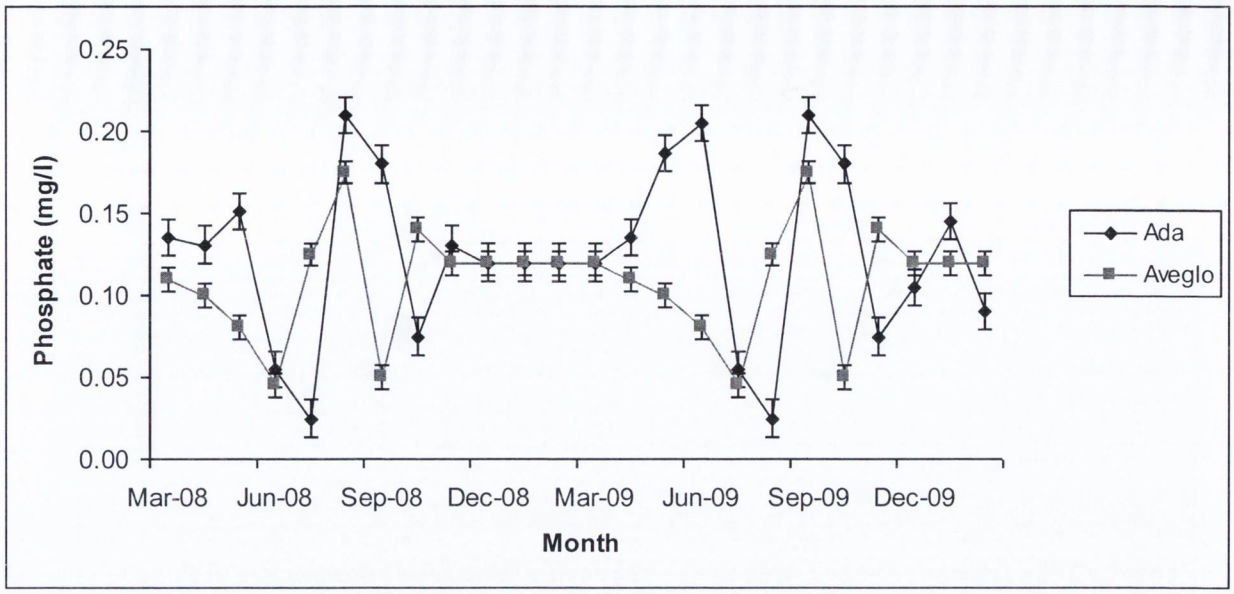


Figure 3.7 Variation in Phosphate (mean ± SE) (n = 48) (mgl^{-1}) at Ada and Aveglo from March 2008 to February 2010.

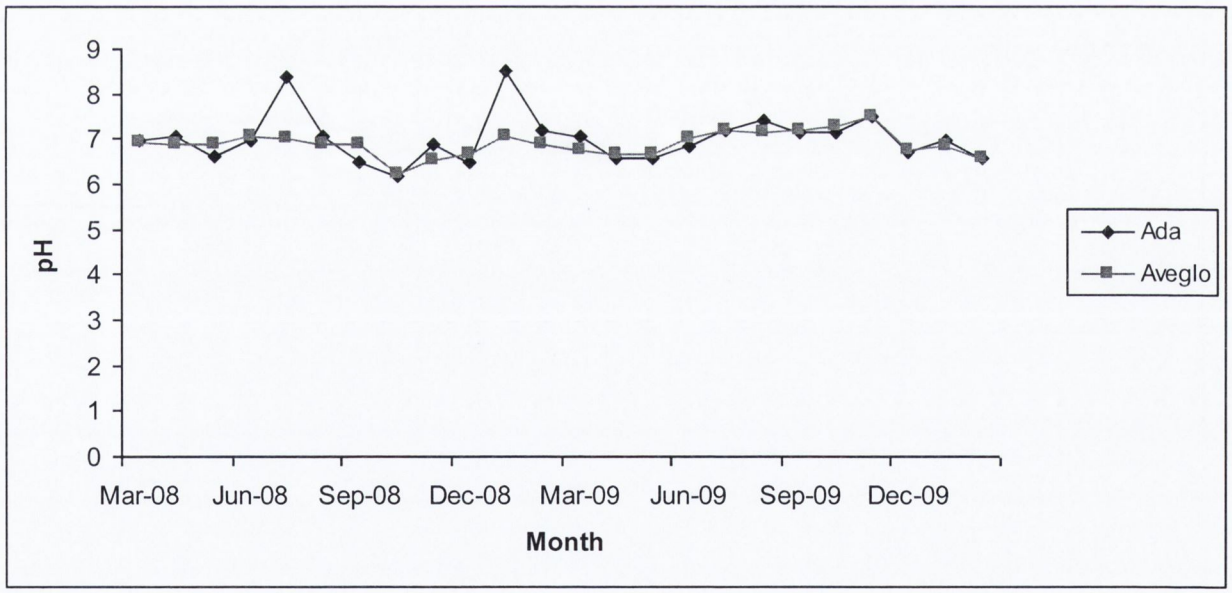


Figure 3.8 Variation in pH (n = 24) at Ada and Aveglo from March 2008 to February 2010

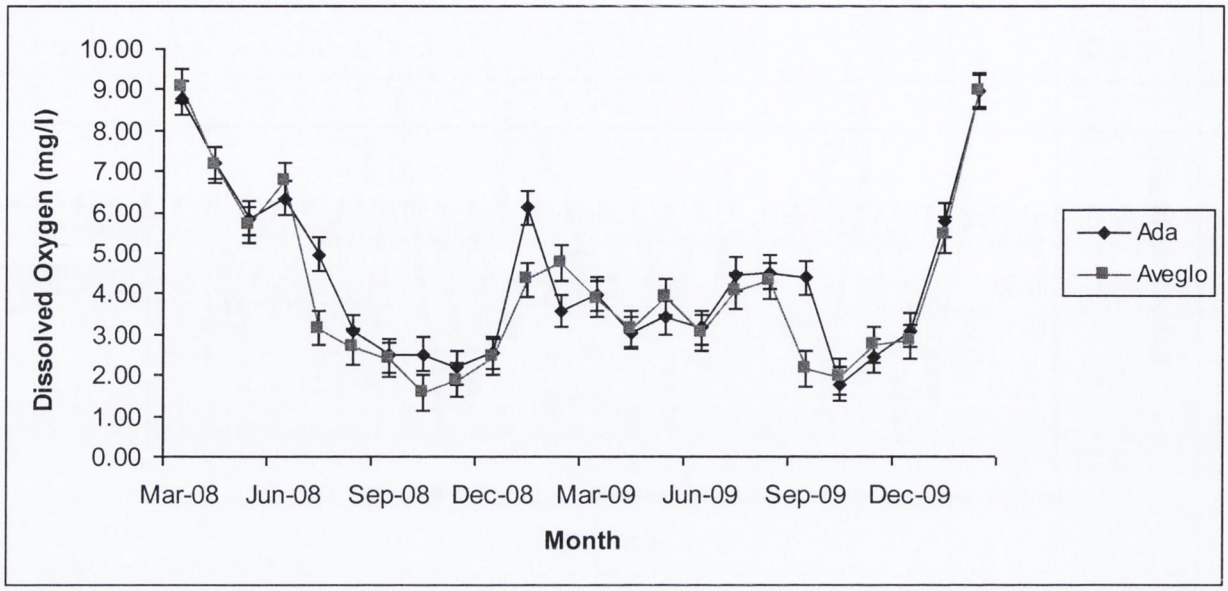


Figure 3.9 Variation in DO (mean ± SE) (n = 48) (mg l^{-1}) at Ada and Aveglo from March 2008 to February 2010.

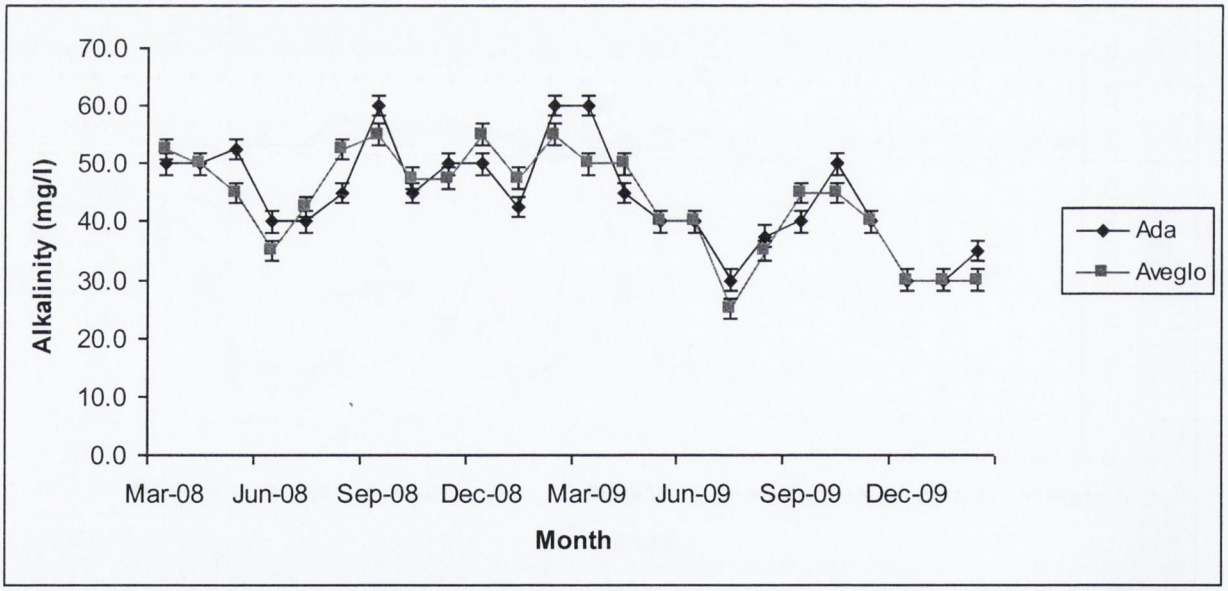


Figure 3.10 Variation in Alkalinity (mean ± SE) (n = 48) (mgl^{-1}) at Ada and Aveglo from March 2008 to February 2010.

3.4 Discussion

Gametogenesis in *G. paradoxa* commences at the beginning of the dry season in December and progresses with the onset of the rains in March-April until the animal is ripe (June-July). Spawning in *G. paradoxa* in the Volta River occurred from July to October (Chapter 4). Within its range *G. paradoxa* is restricted to the lower reaches of the rivers in which it occurs. Purchon (1963) observed that *G. paradoxa* did not occur in the lowermost 32 km from the mouth of the Volta River before the construction of the Akosombo Dam. However, there has been a significant shift in the habitat or point of occurrence of *G. paradoxa* after the construction of two dams on the Volta with the species presently occurring less than 10 km from the mouth of the Volta River (Attipoe and Amoah, 1989). In the undammed Cross River (Nigeria) the species occurs 35 km from the mouth of the river to about 150 km upstream (Moses, 1990).

The results show the influence of conductivity and salinity on the distribution of *G. paradoxa*. The estuarine water is subjected to periodic fluctuations in conductivity between 60 μScm^{-1} at low tide when the water is predominantly fresh and 2876 μScm^{-1} at high tide (Figure 3.2). The distribution of the species is tied to the range of the tide such that the point of occurrence of the species in the Volta River shifted downstream to about 10 km from the mouth of the river where the optimum conductivity/salinity zone was re-established after the construction of the dams. Moses (1990) observed that, although adult *G. paradoxa* thrives in freshwater, larval development requires brackish conditions (1 psu). The salinity requirement of *G. paradoxa* larvae as suggested by Moses (1990) is not supported by this study owing to the inability to detect larvae in the plankton. The gradual decline in conductivity observed at the estuary from June 2009 was as a result of dredging to remove the sandbar at the month of the river.

Dredging was completed in June 2009 hence the sudden drop in high tide conductivity values measured at Ada.

Temperature was relatively constant (Figure 3.1) with an average of 28.6 ± 0.8 °C at both sites over the study period hence its effects on gametogenesis and spawning might be minimal. The concept of degree-days as used in conditioning temperate bivalves cannot be applied to *G. paradoxa* owing to the relatively constant environmental temperature. The principal components analyses (PCA) did not show any strong correlations between the environmental variables and the gametogenic cycle of *G. paradoxa* as indicated by the condition indices (Chapter 4). The correlation coefficients were: conductivity 0.37; SPM 0.07; salinity -0.10; chlorophyll a 0.20; temperature -0.21 and DO -0.31. The lower DO levels recorded between September and December did not have any negative impact on the survival of *G. paradoxa.*

Table 3.1 compares some of the environmental variables measured in this study with previous studies at other stations in the lower Volta River where *G. paradoxa* used to occur. Kpong was the northern-most range of *G. paradoxa* in the pre-dam (1964) period, Sogakope is about 20 km from the mouth of the Volta River and currently is the northern-most range of the clam bed, while Ada Foah is synonymous with Ada in this study. Table 3.1 shows that the environmental variables of the river water have remained relatively stable since 1977. The high conductivity recorded at Ada Foah 520 μScm^{-1} in 1977 is comparable to the high tide conductivity of 583 μScm^{-1} recorded in this study.

Table 3.1 Summary of some environmental variables in *G. paradoxa* sites of the Volta River.

Parameter (mean ± SD)	Ada Foah• (1977-1978)	Kpong* (1995)	Sogakope† (2002)	This study (Ada)
DO (mgl^{-1})	8.0 ± 2.0	-	7.1 ± 0.4	4.2 ± 1.9
Conduct.(μScm^{-1})	520 ± 245	-	-	57.9 ± 5.2[1]
Temperature (°C)	-	28.2 ± 1.4	-	28.6 ± 0.8
Alkalinity (mgl^{-1})	44.8 ± 6.4	40.1 ± 12.9	39.8 ± 10.2	44.4 ± 9.7
Nitrate ((mgl^{-1})	6.6 ± 1.9	0.2 ± 0.1	5.6 ± 0.4	0.44 ± 0.23
Phosphate (mgl^{-1})	0.2 ± 0.1	-	0.10 ± 0.07	0.12 ± 0.05

* WARM, 1995
† GEF-UNEP, 2002
• In Andah et al., 2003

It is difficult to attribute spawning in tropical species to a single environmental trigger, however, it has been observed that most tropical species spawn during the rainy season (Moses, 1987; Etim and Sankare, 1998). Rainfall, which is directly related to the flooding and nutrient dynamics of the river, appears to be an overriding factor influencing spawning in *G. paradoxa*. During the rainy season, the estuary experiences an increase in run-off water which carries nutrients and debris from land into the river. Etim and Taege (1993) observed that during the rainy season, there was an increase in water depth of the Cross River, Nigeria, from 4 to 12 m, a lowering of conductivity and a fall in water temperature from 32 °C in March to 20 °C in July. These observations were to a small extent observed at the Volta Estuary during the rainy/flooding season. The synergistic effect of several factors; a faster current, a slight drop in water temperature, lower food availability and lower DO levels experienced at the peak of the rainy season may act as trigger for spawning in *G. paradoxa.* This observation is in agreement with Clemente and Ingole (2009) who found that spawning in *Polymesoda erosa* occurs during the mid-monsoon months of August-September when temperatures and chlorophyll a levels were low. Although, gametogenesis in *G. paradoxa* commences at the beginning of the dry season (December) when chlorophyll a levels were relatively higher (Figure 3.5), the levels recorded were not significant.

4.0 THE REPRODUCTIVE BIOLOGY OF *G. PARADOXA*

4.1 Introduction

The reproductive strategies of bivalves are varied and include the production of large numbers of planktotrophic (>10^4) and small (< 100μm diameter) eggs, as in most marine bivalve families e.g. Mytilidae (Strathmann, 1978; Bayne et al., 1983; Da Costa et al., 2008), to a relatively few large lecithotrophic eggs as occurs in the Nuculidae (Wilson, 1988; Scheltema and Williams, 2009). For freshwater bivalves, the strategies are different for the major families, e.g. members of the family Dreisseinidae (*Dreissena polymorpha)* produces numerous planktonic larvae that are distributed by water currents before settlement and attaching to substrates with byssus threads (Herbert et al., 1989; Ludyanskiy et al., 1993; Ackerman et al., 1994; Mackie and Schloesser, 1996; Orlova, 2002).

Within the Corbiculidae, there is a wide spectrum of reproductive modes ranging from development via many free-swimming veliger larvae which is typical of brackish water corbiculids such as *Polymesoda erosa, Corbicula japonica* and *C. fluminalis* (Morton, 1985a; Byun and Chung, 2001; Clemente and Ingole, 2009). Brooding in the Corbiculidae is restricted to freshwater taxa e.g. *Corbicula fluminea, C. leana, C. australis, C. africana* (Ituarte, 1994; Byrne et al., 2000; Korniushin and Glaubrecht, 2003).

Freshwater bivalves of the Unionidae have a unique reproductive strategy which combines brooding and parasitism on fish. Ova are released by females into their suprabranchial cavity in late summer or early autumn and are fertilized by sperm received through the incurrent siphon. Embryos are passed into demibranchs of the gills, where they develop into mature larvae (glochidia). Glochidia remain in the gills until their release during the following spring or summer. They are obligate ectoparasites on the fins or gills of specific fishes until they

metamorphose to the free-living juvenile stage (Zale and Neves, 1982; Haag and Warren, 1997; Garner et al., 1999)

Sphaeriids are small, hermaphroditic and ovoviviparous freshwater bivalves with a cosmopolitan distribution (Mackie et al., 1978). The reproductive state of sphaeriids is easily determined by the collection of adults. In *Pisidium*, one of the five genera in the Sphaeriidae, there is the synchronous brooding of larvae in brood pouches such that there is only one brood event per reproductive cycle (Guralnick, 2004). In *Musculium* and *Sphaerium*, although immature clams reside in pouches, brooding is not synchronous. Instead multiple brooding of different sized individuals can be found in brood pouches at any one time (Guralnick, 2004).

Bivalves exhibit either ambisexuality (hermaphroditism) or unisexuality (gonochorism). Hermaphroditism has been classified into four groups (Coe, 1943; Kasyanov, 2001):

(1) Functional hermaphroditism, where an animal concurrently develops both sperm and eggs (e.g., the ribbed scallop *Pecten irradians*). (2) Consecutive sexuality, once in the life of the bivalve, the animal undergoes a single sexual switch, usually from male to female (protandry, *Mercenaria mercenaria*). (3) Rhythmical consecutive sexuality, the animal experiences an equal number of sexual phases, changing from one sex to the other and maintaining a rhythmical pattern throughout its life (e.g. *Ostrea lurida* and *O. edulis*).

(4) Alternative sexuality, whereby animals change sex depending on season or environmental triggers e.g. *Crassostrea virginica* and *C. gigas*, respectively (Coe, 1943; Kasyanov, 2001).

Sex ratios in bivalve populations are usually close to 1:1, however, there are examples of sex ratios biased toward either females or males (Coe, 1943; Morton, 1991). Generally, there seems to be a correlation between sex ratio and habitat (Morton, 1991). Freshwater species are either hermaphroditic or gonochoristic, and the latter shows a female-biased sex ratio (Morton, 1991). Mangrove and brackish water species are gonochoristic with either a slight overall female or male bias (Morton, 1991). Marine species are usually gonochoristic with a 1:1 sex

ratio (Morton, 1991). Furthermore, for some freshwater and brackish species, the sex ratio varies with age, with the juvenile sex bias being species dependent (Morton, 1991).

The allocation of resources to either somatic growth or reproductive output in bivalves depends on the species' life-span. Short-lived bivalves such as *Pisidium* and *Kingiella chilenica* are termed semelparous because they allocate more resources to reproduction at the expense of somatic growth at a relatively smaller size. Semelparous species typically have an annual life cycle and usually die after reproduction (Morton, 1985a; Gallardo, 1993). Iteroparous species on the other hand are long-lived and tend to allocate more resources for somatic growth for a number of years before diverting resources to reproduction (Jokela, 1997). According to Browne (1978) reproductive effort is higher in semelparous species (30 %) of net productivity of the population) than in iteroparous species (18 %) and that in iteroparous species reproductive effort increases with successive breeding seasons. Species may be classified with respect to their allocation of resources either as reckless where much of the resources are allocated to reproduction at an early age or at a smaller size at the expense of somatic growth, or restraint when somatic growth is considerable relative to reproduction (Calow, 1981).

There are conflicting reports on the reproductive cycle of *G. paradoxa*. Earlier reports by Pople (1966) and Whyte (1981) indicated that the population of *G. paradoxa* in the Volta River spawned in the dry season (December-March) when salinity averaged 1psu. However, Etim (1996) found that the stock of *G. paradoxa* in the Cross River spawned at the peak of the rainy season (June –October).

Determining the seasonal patterns of gametogenic development and spawning of any bivalve species is essential for developing management strategies for the protection of spawning stock as well as ascertaining the time of larval settlement (Gribben, 2005). The reproductive cycle and spawning season of bivalves can be studied directly and indirectly. The most widely used

direct method has been studies on histological preparations and microscopic examination of histological sections of gonads (Etim, 1996; Lauden et al., 2001; Darriba et al., 2004, 2005; Drummond et al., 2006; Suja and Muthiah, 2007). Indirect methods assess changes in condition that may have a bearing on the physiological state of the bivalve. Condition indices have been employed by a number of authors to elucidate the spawning season of bivalves owing to their suitability for broodstock selection in aquaculture as well as determining when animals are in best condition for harvest (Etim and Taege, 1994; Etim, 1996; Darriba et al., 2004, 2005).

G. paradoxa has been found to be a suitable species for culture (Attipoe and Amoah, 1989), although, little information is available on its reproductive biology in the Volta River. It is imperative to ascertain the reproductive cycle of *G. paradoxa* as a first step to its sustainable management and ultimate culture. The aim of this study was to determine the reproductive cycle, sex ratios and spawning season of *G. paradoxa* in the Volta River.

4.2 Materials and Methods

The study was conducted at the Ada and Aveglo study sites from March 2008 to February 2010. A detailed description of the study area is presented in Sections 2.1 and 2.2. The methods for field sampling and laboratory processing of *G. paradoxa* for the computation of condition indices and histological examination of gonads are outlined in Sections 2.3, 2.3.1.2, 2.3.1.3 and 2.3.1.4.

In order to determine the number of eggs/oocytes spawned by a year-class or cohort and the allocation of resources to somatic growth and reproductive output as the clams grow older, regression coefficients were obtained for the monthly shell-free wet weights over shell lengths. The coefficients were fitted to the mean shell lengths of the cohorts identified in the population (Chapter 5). The gonad weight was calculated as the difference between the maximum pre-spawning and post-spawning weight of each cohort. The number of eggs spawned per year class was estimated by dividing the weight of the gonad by the mean weight of the pre-spawning egg. The weight of organic matter in *G. paradoxa* eggs were estimated from Equation 4.1 derived by Strathmann and Vedder (1977):

$$M = 6.05 \times 10^{-6} \times V^{0.747} \qquad \text{Equation 4.1}$$

Where:

V = volume (μm^3); and

M = the organic content (μg).

Egg volume (V) was first calculated by: $V = 4/3\pi r^3$, where r = egg radius (14 μm) from the pre-spawning egg diameters (24 - 32 μm, mean 28 μm). Substituting the egg volume ($V = 11.50\ \mu m^3$) into Equation 4.1 yields an egg weight of 0.0065μg

4.3 Results

G. paradoxa collected from clam fishers at the Volta Estuary over the two year duration of the study ranged between 20 to 82 mm in length. A total of 2820 individuals were sampled for condition indices.

4.3.1 Gonad Weight and Eggs Numbers

Table 4.1 presents the gonad weight as the difference between the maximum pre-spawning and the minimum post-spawning weights of a standard animal with shell lengths corresponding to 1 - 8 year old *G. paradoxa*. The number of eggs spawned per animal was estimated from Equation 4.1 and presented in Table 4.2. Assuming the difference between the pre-spawning and post-spawning weights can be wholly attributed to gonad weight, then the gonad weight generally increased with age (Table 4.1). There was no difference in gonad weights ($p > 0.05$) between the sites for the 1 to 4 year old *G. paradoxa*. However, gonad weights were significantly higher ($p < 0.05$) at Aveglo from the 5 to 8-year old *G. paradoxa* (Table 4.1).

Table 4.1 Maximum gonad weights (mg) of *G. paradoxa* individuals from 1- 8 years old with mean shell length in brackets at Ada and Aveglo.

Age/ shell length (mm)	Gonad weight (mg)	
	Ada	Aveglo
1(15.4)	200^{a}	202^{a}
2(28.6)	667^{ab}	651^{ab}
3(39.8)	1394^{bc}	1491^{bc}
4(49.4)	2236^{cd}	2184^{cd}
5(57.5)	3359^{e}	3650^{f}
6(64.5)	4569^{g}	5521^{h}
7(70.4)	5774^{i}	7487^{j}
8(75.5)	7013^{k}	9513^{l}

Values in the same row and column with different superscripts $^{a, b, c, d, e, f, g, h, i, j, k, l}$ are significantly different ($p < 0.05$).

Figure 4.1 shows that variation in gonad weight with shell length (age) of *G. paradoxa*. Gonad weight was highest at Aveglo in 2009-10, intermediate at both Ada and Aveglo in 2008-9 and lowest at Ada in 2009-10.

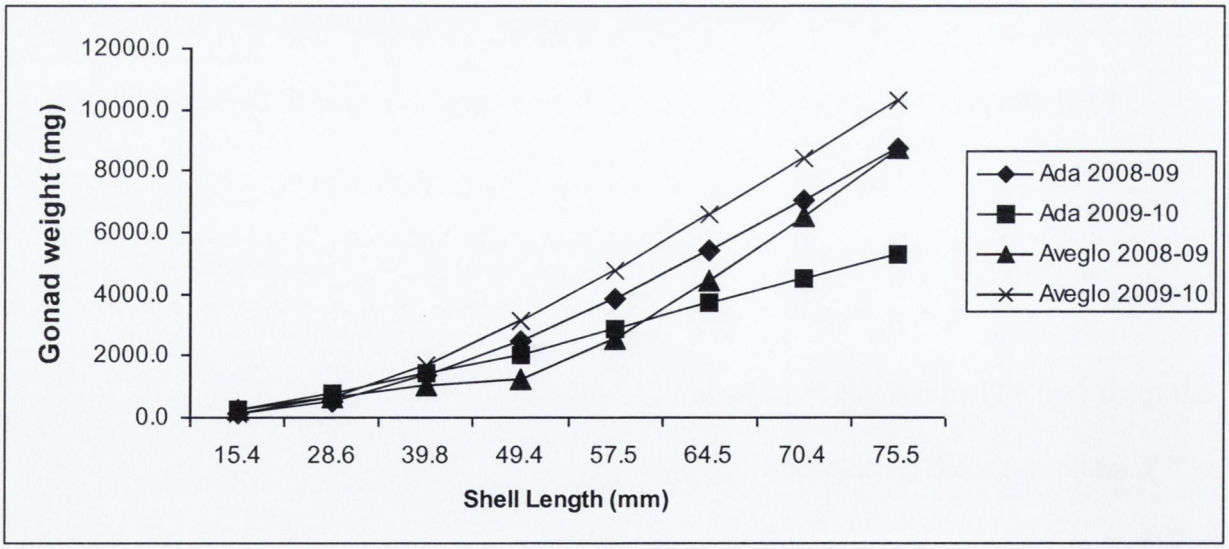


Figure 4.1 Gonad weight against the mean length of *G. paradoxa* corresponding to 1 - 8 year old individuals from Ada and Aveglo from the 2008- 2009 and 2009-2010 seasons.

The number of eggs similarly increased with age from $1.95x10^4$ in the 1-year old female of mean shell length 15.4 mm to a high value of $1.57x10^6$ in an 8-year old female (Table 4.2). There was no difference ($p > 0.05$) in egg numbers for the 1 to 4-year-old *G. paradoxa* from Ada and Aveglo. However, eggs number were higher ($p < 0.05$) from 5-year old to 8-year old *G. paradoxa* at Aveglo (Table 4.2).

Table 4.2 Number of eggs released by *G. paradoxa* individuals aged between 1- 8 years with mean shell length in brackets at Ada and Aveglo.

Age/ shell length (mm)	Egg Numbers ($x10^4$)	
	Ada	Aveglo
1(15.4)	3.1^{a}	3.1^{a}
2(28.6)	10.5^{ab}	10.0^{ab}
3(39.8)	21.3^{bc}	21.1^{bc}
4(49.4)	34.3^{cd}	33.5^{cd}
5(57.5)	51.4^{e}	55.9^{f}
6(64.5)	70.0^{g}	84.6^{h}
7(70.4)	88.4^{i}	114.7^{j}
8(75.5)	107.4^{k}	145.7^{l}

Values in the same row and column with different superscripts $^{a, b, c, d, e, f, g, h, i, j, k, l}$ are significantly different ($p < 0.05$).

4.3.2 Condition Indices

Figures 4.2 to 4.10 show the variation in condition indices over the two-year study period from March 2008 to February 2010. The seasonal patterns were consistent for all the indices from Ada and Aveglo. Figures 4.2 and 4.3 show the variation in ash-free dry weight over shell weight (AFDW / SW) and ash-free dry weight over $(\text{shell length})^3$ (AFDW / SL^3) during the study period. The indices rose from 2.83 ± 0.12 and 0.71 ± 0.03 at the start of the study in March 2008 to a peak of 5.72 ± 0.50 and 1.09 ± 0.07 respectively in August and September

2008 for AFDW / SW and AFDW / SL^3. Afterwards, the indices declined steadily to minima of 2.10 ± 0.12 and 0.47 ± 0.16, respectively, in January 2009. The same pattern repeated itself in the subsequent months of 2009, rising from the minima recorded in January 2009 to a peak of 5.47 ± 0.25 and 1.58 ± 0.23, respectively, in September 2009. Thereafter the condition indices declined steadily to minima of 2.25 ± 0.10 and 0.55 ± 0.02, respectively, in January 2010.

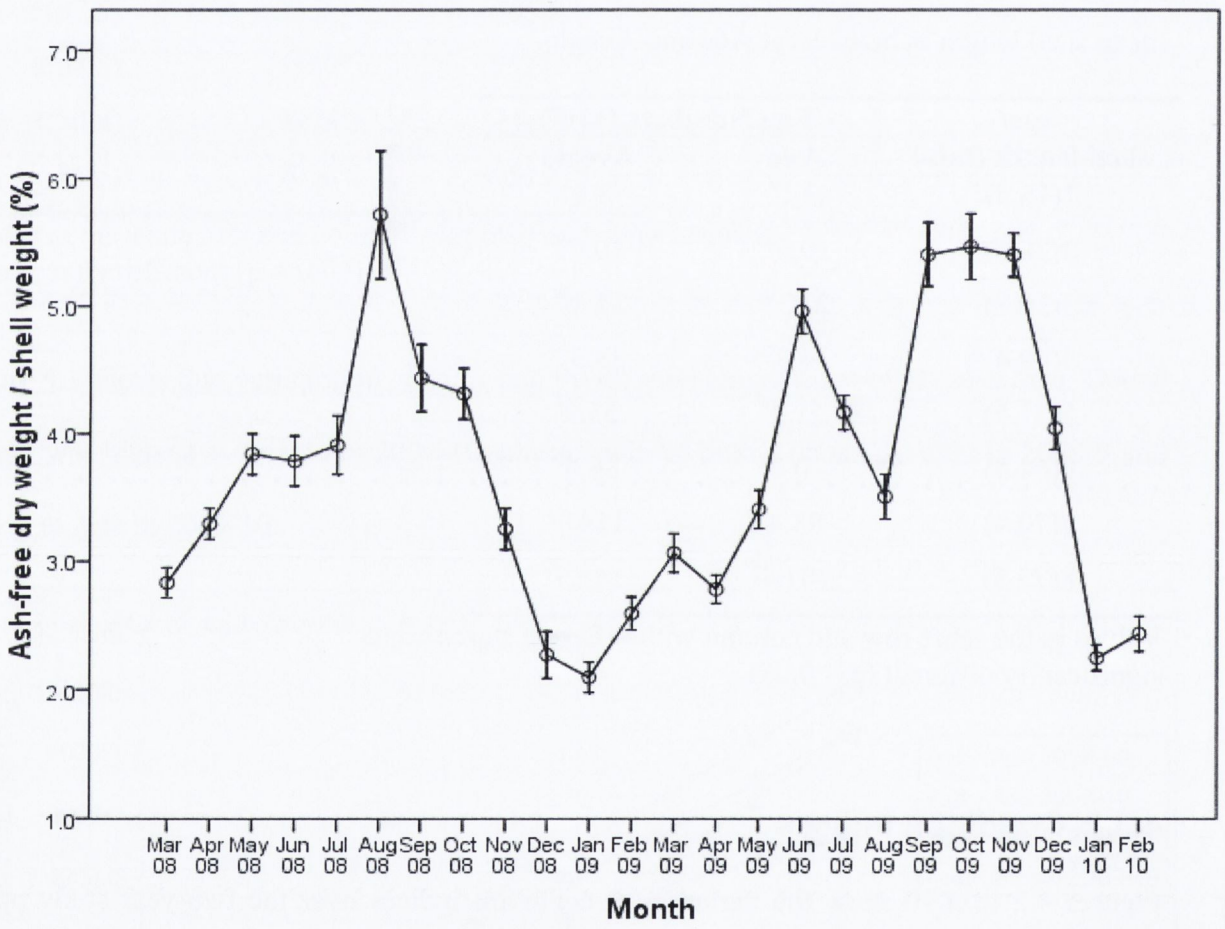


Figure 4.2 Seasonal variation in ash-free dry weight / shell weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n =1440) from March 2008 to February 2010.

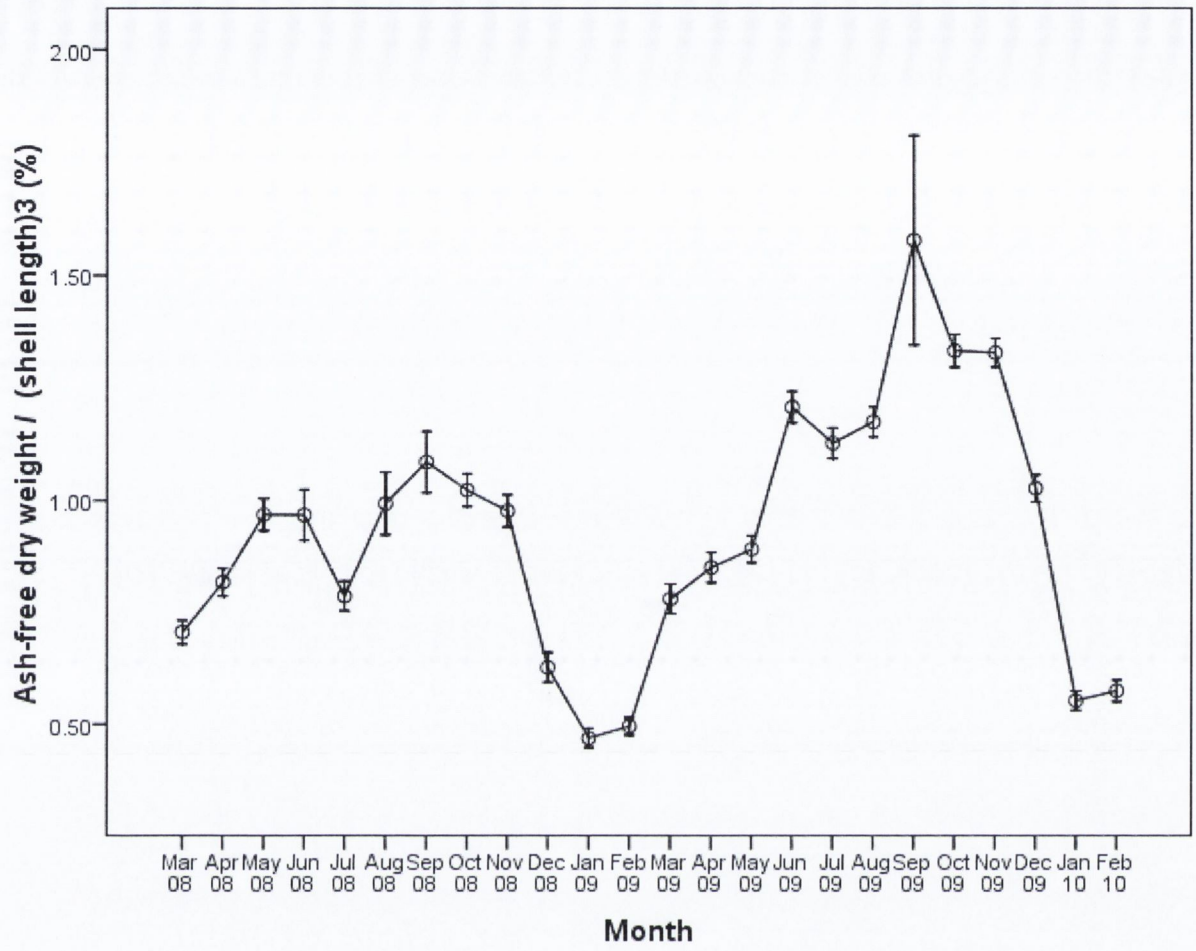


Figure 4.3 Seasonal variation in ash-free dry weight / (shell length)^3 in *G. paradoxa* from the Volta Estuary (mean ± SE) (n =1440) from March 2008 to February 2010.

Figures 4.4, 4.5 and 4.6 show the seasonal variation in shell-free wet weight over total wet weight (SFWW / TWW), shell-free dry weight over shell weight (SFDW / SW) and shell-free dry weight over shell volume (SFDW / SV), respectively. The annual patterns were consistent for the three indices over the study period. The indices rose from 11.17 ± 0.38, 5.60 ± 0.12 and 5.60 ± 0.20 respectively at the start of the study in March 2008 to peaks of 17.08 ± 0.65 in August 2008 for SFWW / TWW, 7.89 ± 0.32 in June 2008 for SFDW / SW and 11.15 ± 0.56 in November 2008 for SFDW / SV. Afterwards, there was fall in the mean of the three indices

to minima of 9.79 ± 0.27, 2.57 ± 0.11 and 4.55 ± 0.19 for SFWW / TWW, SFDW / SW and SFDW/ SV, respectively, in January 2009. The same pattern was repeated in the subsequent months of 2009, rising from the minimum values recorded in January 2009 to peaks of 19.27 ± 1.72 and 5.85 ± 0.26 for SFWW / TWW and SFDW / SW, respectively, in September 2009 and 13.19 ± 0.43 for SFDW / SV in November 2009. All the indices thereafter declined steadily to low values of 10.24 ± 0.26, 2.84 ± 0.09 and 5.61 ± 0.21, respectively, in January 2010.

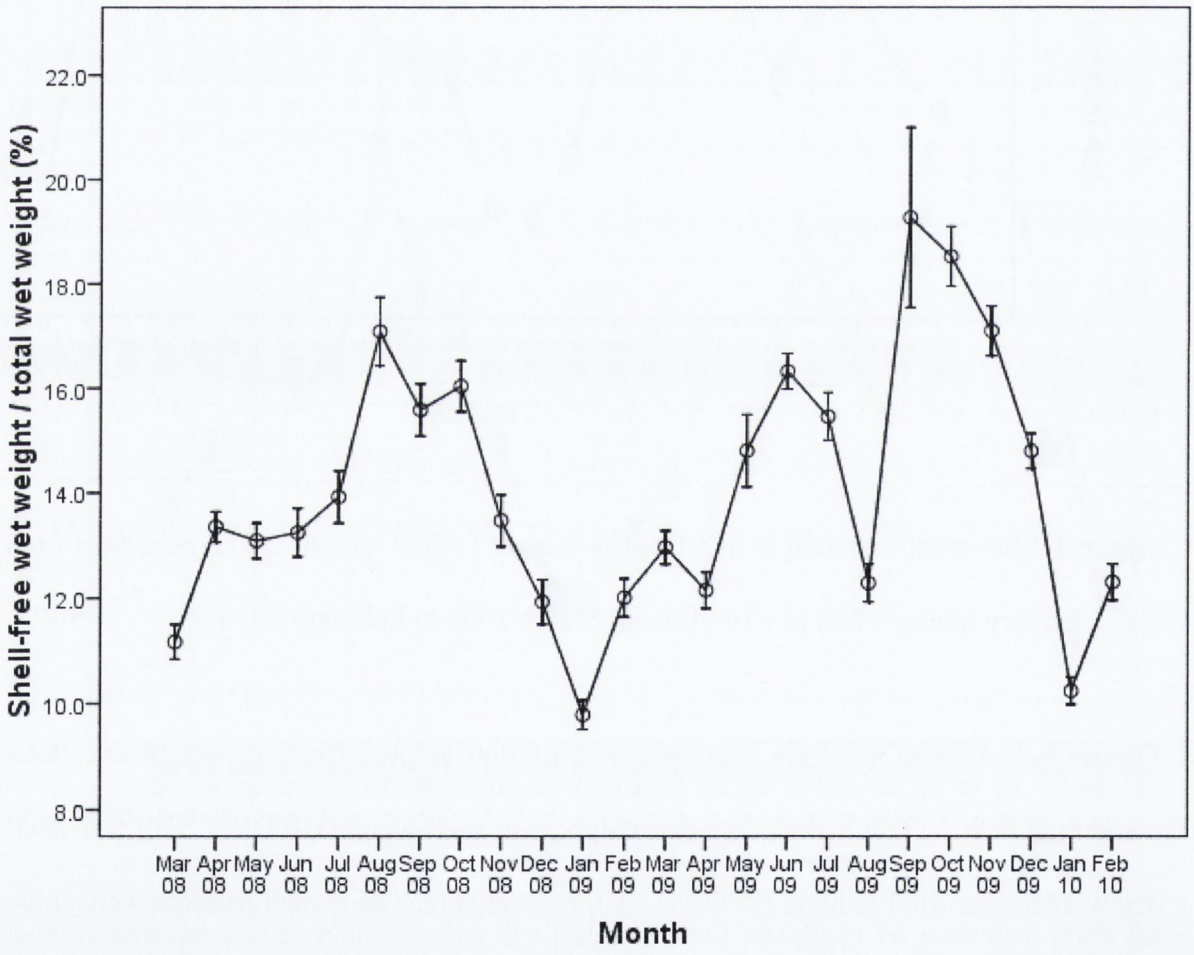


Figure 4.4 Seasonal variation in shell-free wet weight / total wet weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n =1440) from March 2008 to February 2010.

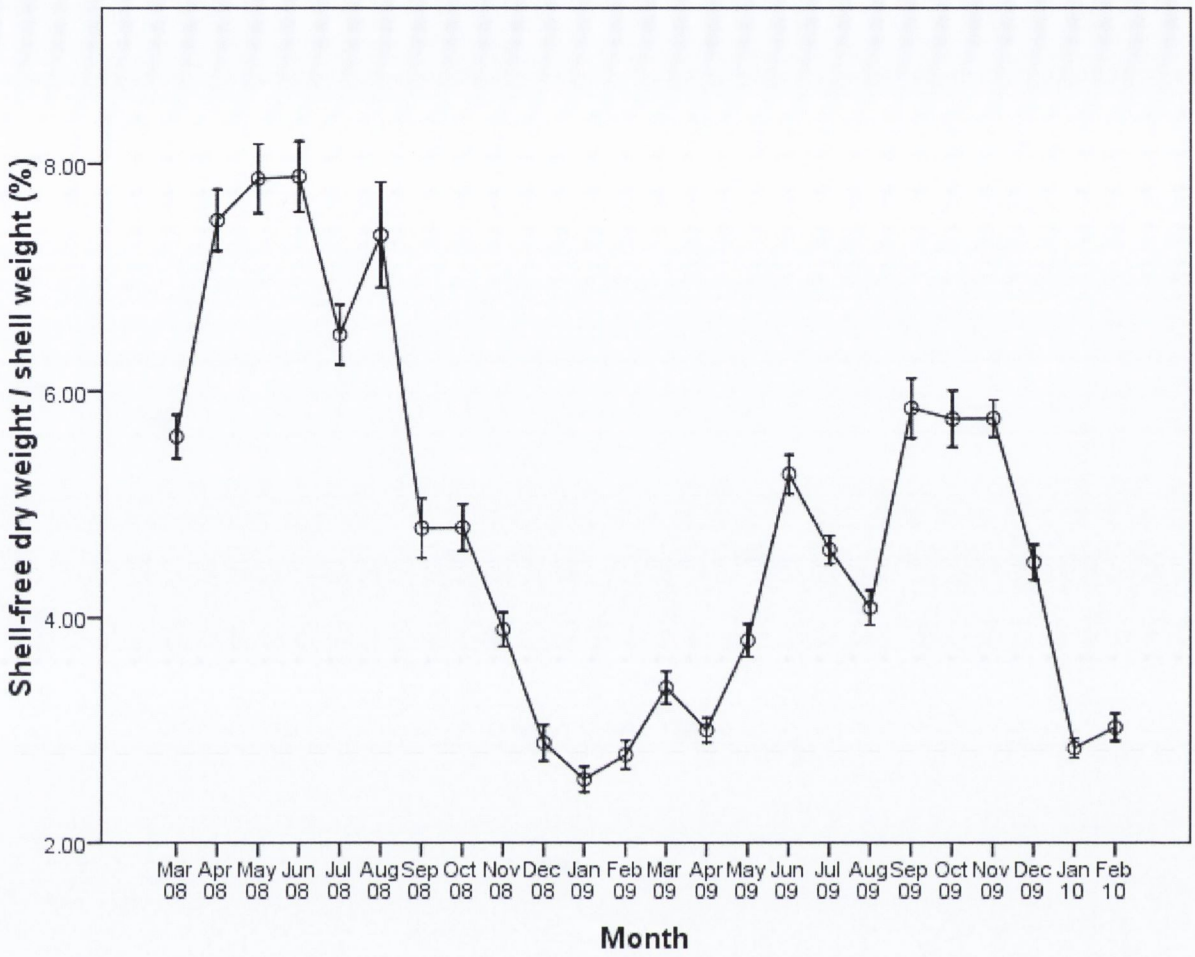


Figure 4.5 Seasonal variation in shell-free dry weight / shell weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n =1440) from March 2008 to February 2010.

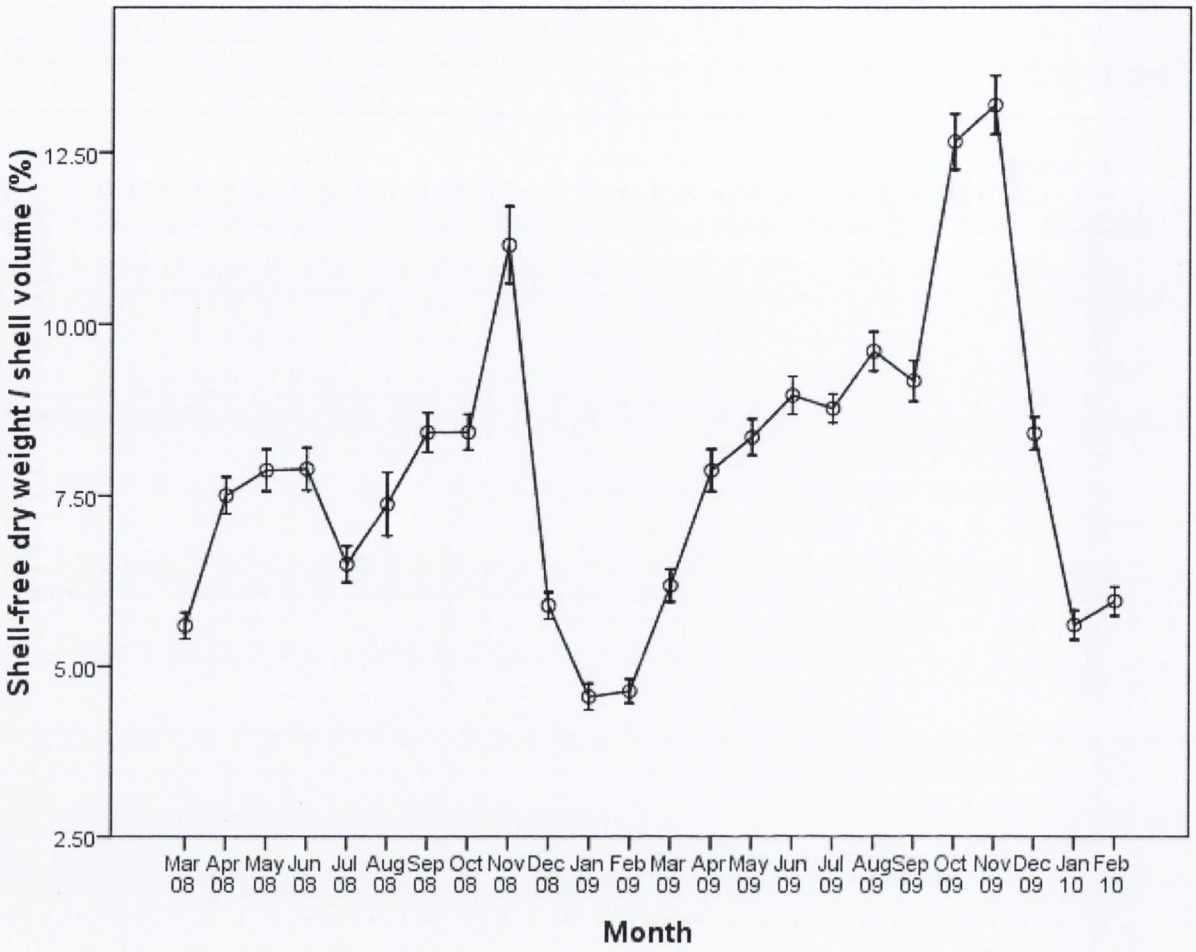


Figure 4.6 Seasonal variation in shell-free dry weight / shell volume in *G. paradoxa* from the Volta Estuary (mean ± SE) (n =1440) from March 2008 to February 2010.

Figures 4.7 to 4.10 present the seasonal variation in gonadal indices over the study period. Figures 4.7 and 4.8 demonstrate the variation in the mean gonad wet weight over shell weight (GWW / SW) and gonad dry weight over shell weight (GDW / SW). The indices rose from 2.42 ± 0.22 and 0.60 ± 0.05 in March 2008 at the start of the study to peaks of 7.36 ± 0.87 and 1.72 ± 0.21 in August 2008. Afterwards, the indices declined to minima of 2.14 ± 0.22 and 0.50 ± 0.06 respectively in January 2009. The pattern repeated itself in the subsequent sampling months of 2009 and 2010. However, the peak values of 7.21 ± 0.82 and 1.85 ± 0.22

and minimum values of 2.50 ± 0.20 and 0.59 ± 0.06 for GWW / SW and GDW / SW were recorded in October 2009 and February 2010, respectively.

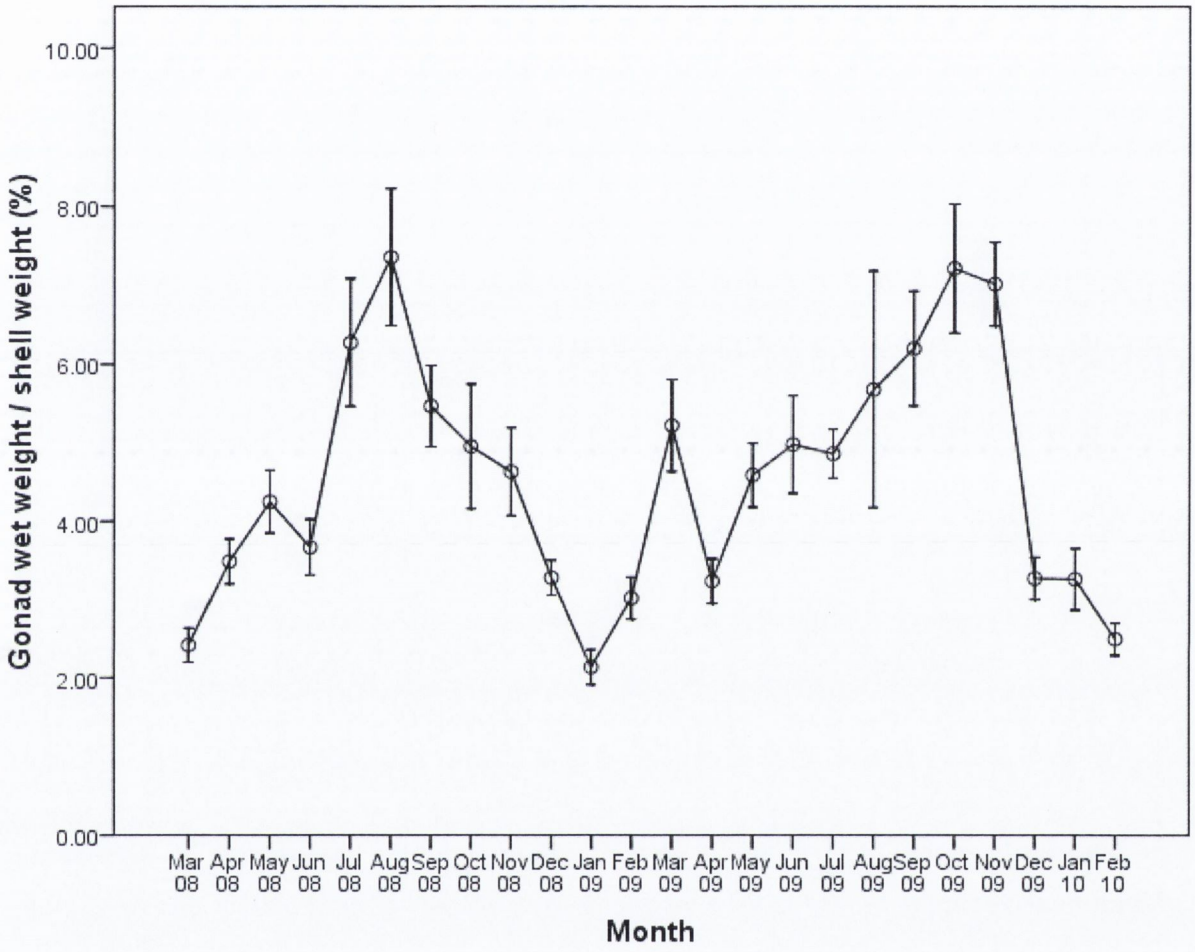


Figure 4.7 Seasonal variation in gonad wet weight / shell weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n = 480) from March 2008 to February 2010.

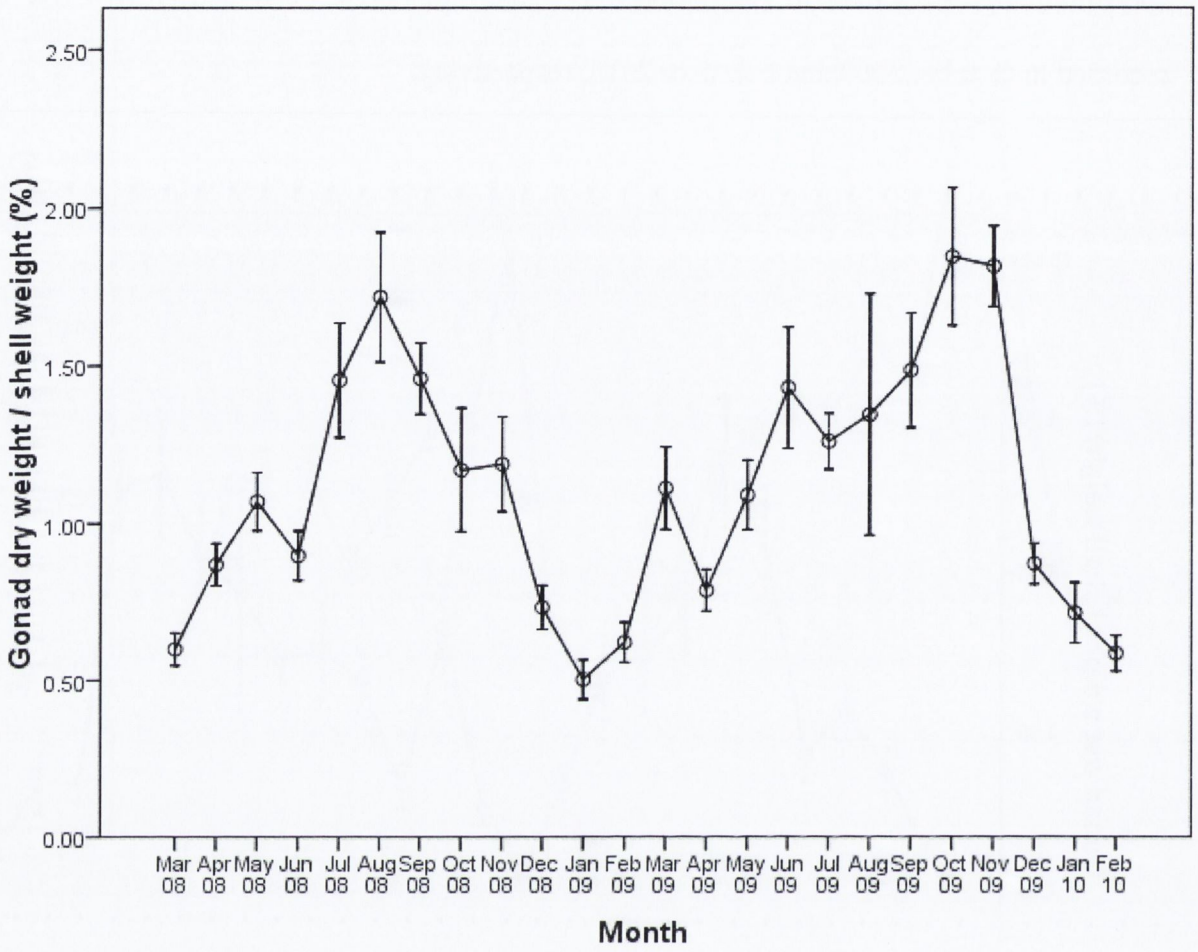


Figure 4.8 Seasonal variation in gonad dry weight / shell weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n = 480) from March 2008 to February 2010.

Figures 4.9 and 4.10 show variation in gonad wet weight over total wet flesh weight (GWW / TWFW) and gonad dry weight over total dry flesh weight (GDW / TDFW) during the study period. Figures 4.9 and 4.10 showed a trend similar to Figures 4.7 and 4.8. The indices increased from 15.16 ± 0.72 and 19.11 ± 0.81 in March 2008 at the start of the study to peak values of 29.02 ± 1.18 and 34.17 ± 1.15 for GWW / TWFW and GDW / TDFW, respectively, in August 2008. The indices declined steadily thereafter to minimum values of 17.20 ± 1.11 and 19.44 ± 1.31 in January 2009. The pattern repeated itself in 2009 although, the peak

values of 25.18 ± 1.01 and 28.11 ± 1.15 and minimum values of 15.43 ± 0.63 and 18.85 ± 0.86 for GWW / TWFW and GDW / TDFW, respectively, were recorded in October 2009 and February 2010.

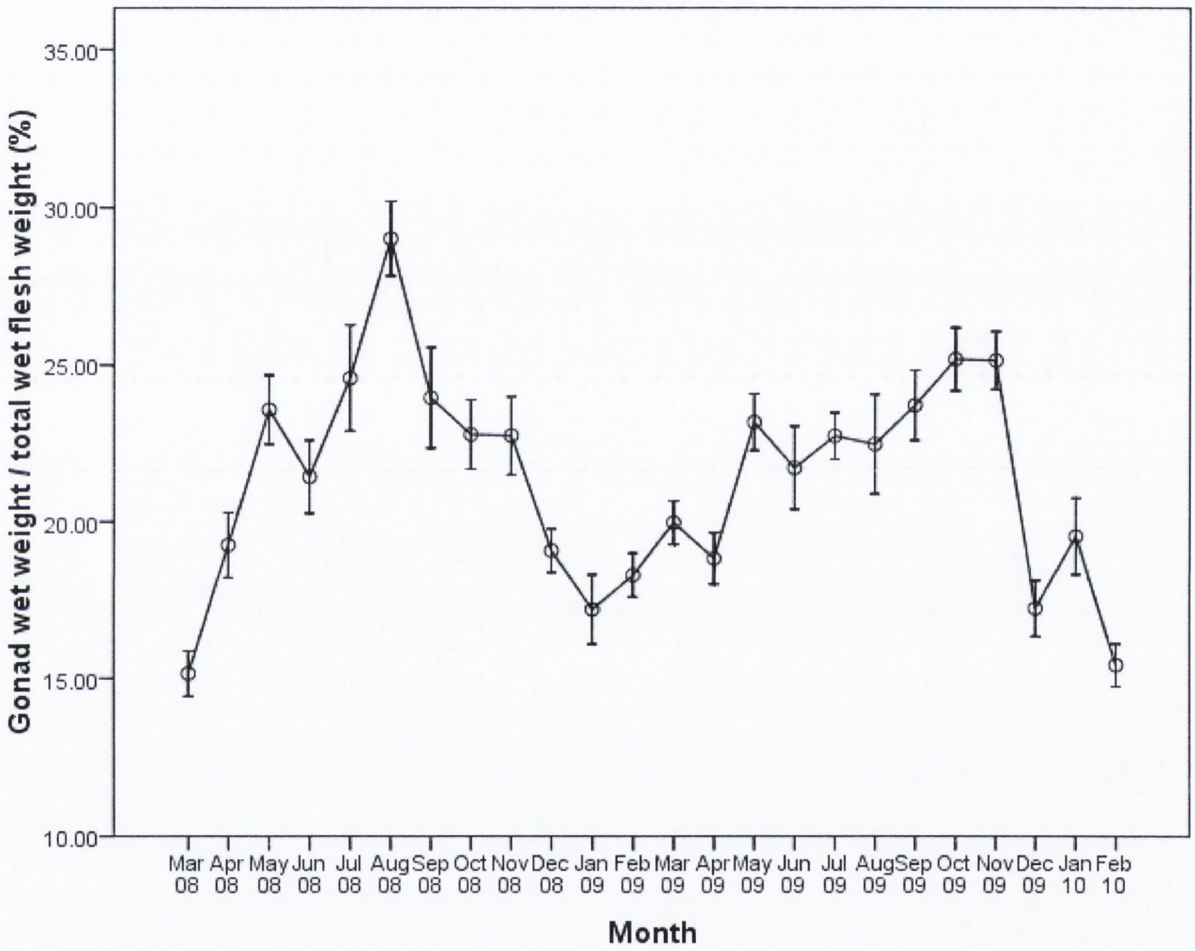


Figure 4.9 Seasonal variation in gonad wet weight / total wet flesh weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n = 480) from March 2008 to February 2010.

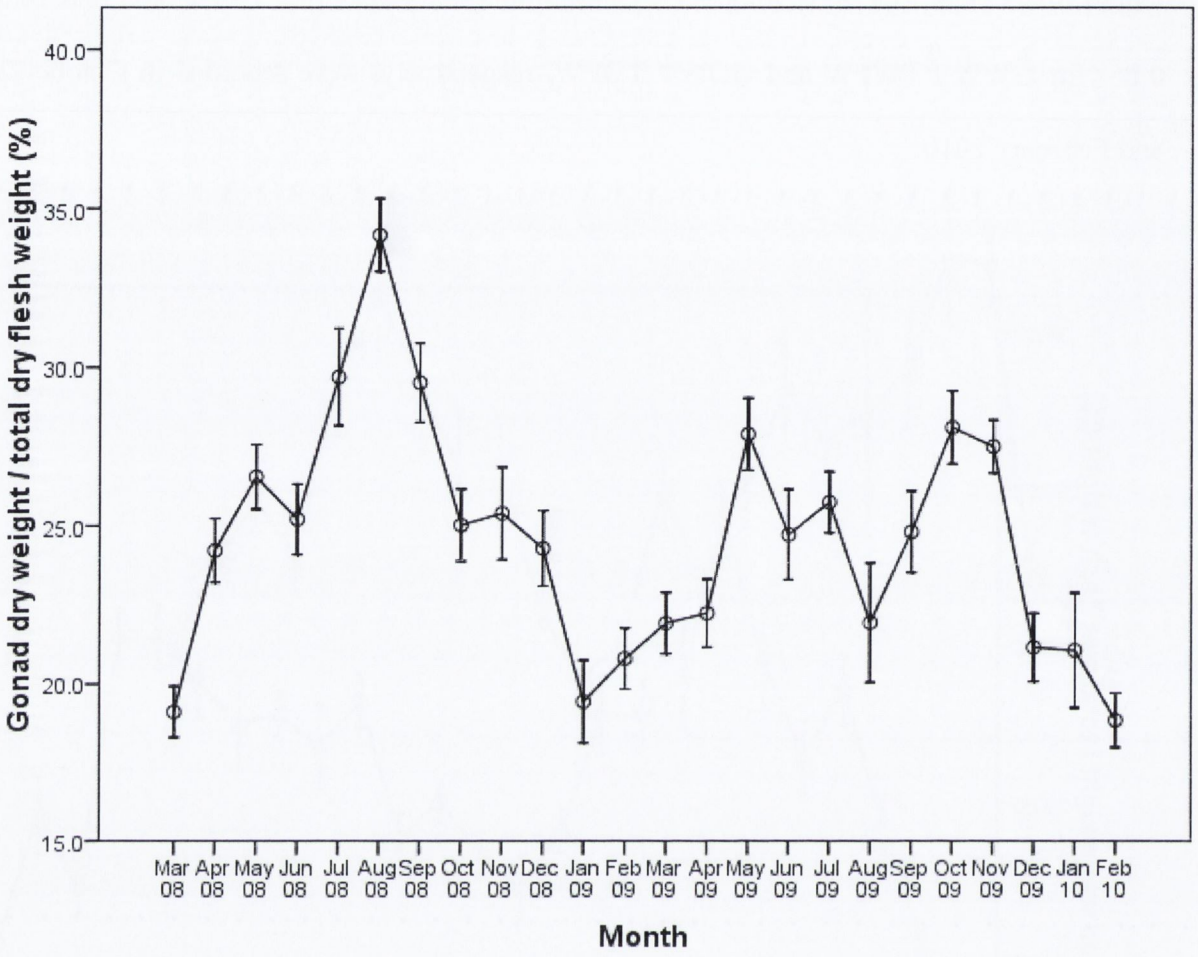


Figure 4.10 Seasonal variation in gonad dry weight / total dry flesh weight in *G. paradoxa* from the Volta Estuary (mean ± SE) (n = 480) from March 2008 to February 2010.

4.3.3 Histology

Gonad smears and histological analyses were conducted on a total of 278 specimens collected from the Volta Estuary. In all, five gonad development stages were determined: start of gametogenesis (I); advanced gametogenesis (II); ripe (IIIA); start of spawning (IIIB); and spent (IV) for males and females from histological sections as illustrated in Figure 4.13. Individuals with gonads at sexual rest (stage 0) were absent in all the sections analysed.

Except for the areas occupied by the muscular and digestive systems, most of the visceral mass consists of the reproductive system. The gonad is beige in colour when unripe (November to May) and slightly creamy when ripe (June to July) (Figure 2.4). Samples could not be sexed from the smears as all the samples analysed had female characteristics (oocytes). Males could not be distinguished until the peak of the spawning season (July –September). Oocyte diameters as shown in Figure 4.11 progressed from 3 – 9 μm at the start of gametogenesis (stage I) (December) to between 9- 18 μm at the advanced gametogenetic stage (II) (April –May). Most of the oocytes at the ripe and start of spawning stages (IIIA-B) (June –August) had diameters between (24 – 32 μm). In spent individuals, the smear contained predominantly smaller oocytes (3- 9 μm) with a few larger (12 - 24 μm) residual oocytes.

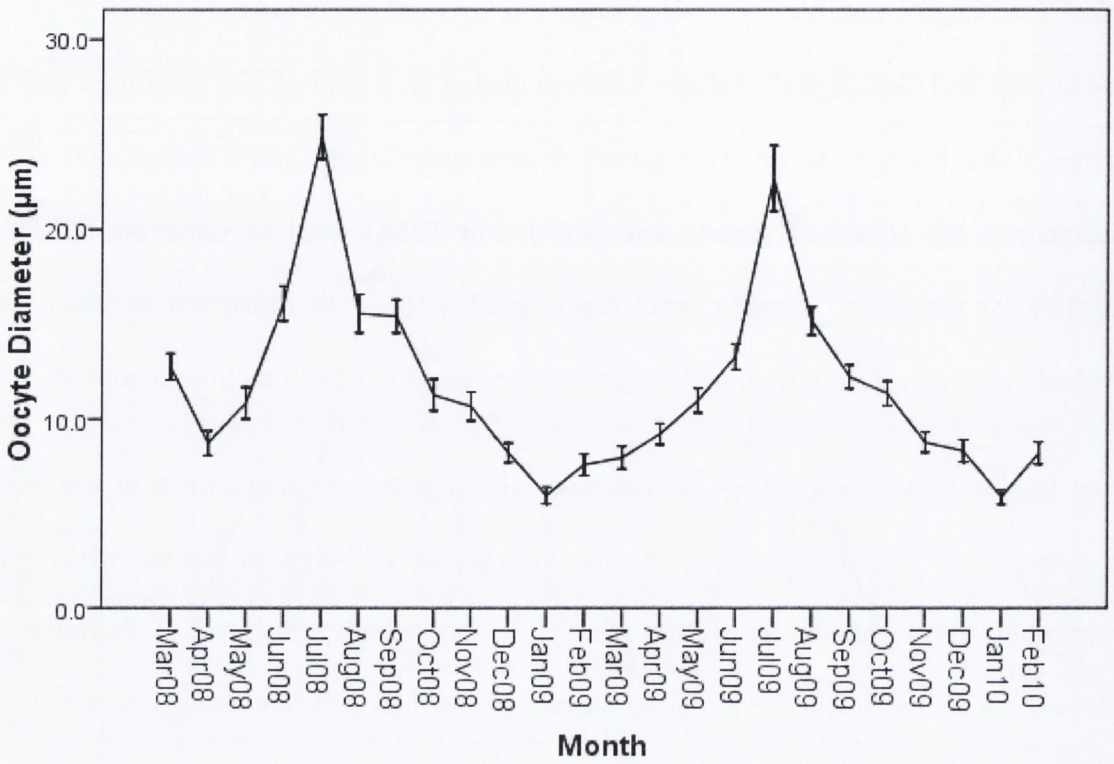


Figure 4.11 Seasonal variation in oocyte diameters (mean ± SE) (n = 720) in *G. paradoxa* from the Volta Estuary from March 2008 to February 2010

4.3.4 Sex Ratio

G. paradoxa is gonochoristic but not sexually dimorphic, external differentiation of the sexes could not be made as well as any recognisable colour difference in the gonads of males and females. Sex differentiation was only possible by microscopic examination of histological sections. The samples excluded individuals < 20 mm due to their absence from the fishery (Figure 4.12). Out of the 278 individuals examined 223 (80.2%) were females, 29 (10.4%) were males and 26 (9.4%) were hermaphrodites (Table 4.3). There was no significant relationship between site (Ada or Aveglo) and sex distribution (Chi-square with 2 degrees of freedom = 1.683, P = 0.431). However, the proportion of females in the population was

significantly higher, the overall ratio of males to females to hermaphrodites was 1: 7.7: 1 (X^2 = 275; P < 0.001, df = 2, n = 278).

Out of the 26 individuals that were hermaphrodites, almost two-thirds (17; 65.4%) had shell lengths between 20 – 40 mm (7; 26.9%) within 41 – 55 mm and (2; 7.7%) with shell lengths > 55 mm (Figure 4.12). Among the hermaphrodites there was a predominance of female over male follicles, the latter occurring mainly in the peripheral region of the gonad. The follicles were undergoing various phases of development (developing, ripe, spawning or spent) (Figures 4.14 K and L). The percentage of males in the population (10.4%) was restricted to the 20 – 55 mm shell length range. However, females were not restricted to a particular size range and occurred in all the lengths sampled. *G. paradoxa* become sexually mature at a shell length > 22 mm.

Table 4.3 Numbers and percentages of males, females and hermaphrodite *G. paradoxa* from each site.

	Male	**Female**	**Hermaphrodite**	**Total**
Ada	12 (4.3%)	115 (41.4%)	11 (4.0%)	138 (49.6%)
Aveglo	17 (6.1%)	108 (38.8%)	15 (5.4 %)	140 (50.4%)
Total	29 (10.4%)	223 (80.2%)	26 (9.4%)	278 (100%)

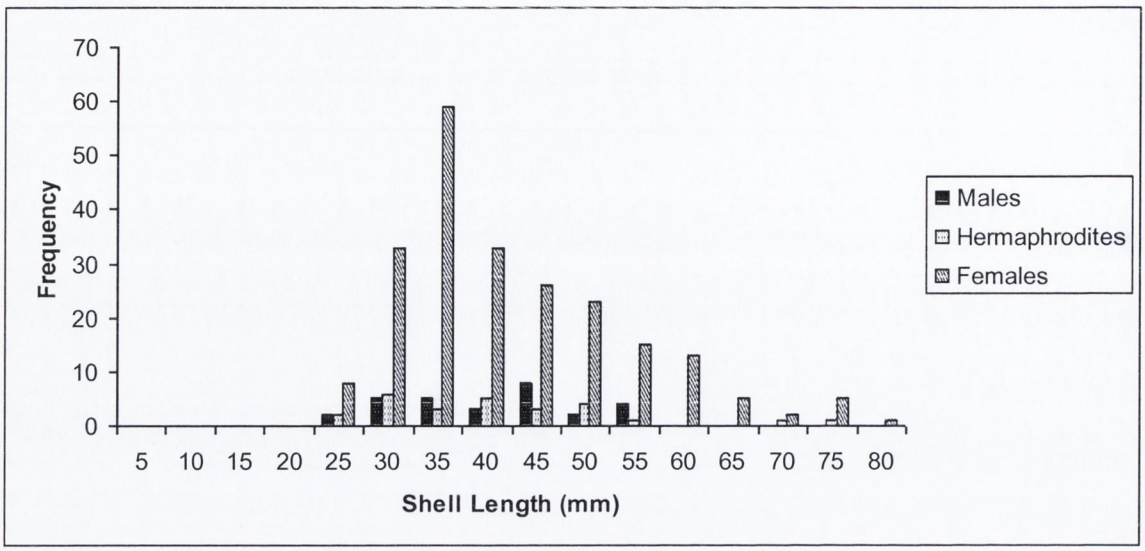


Figure 4.12 Sexual structure by length intervals of *G. paradoxa* from the Volta Estuary

4.3.5 Reproductive Cycle

Gametogenic development in *G. paradoxa* was synchronous between the sexes so a combined reproductive cycle is described. Figure 4.13 illustrates the percentage of *G. paradoxa* at the five reproductive stages. Gametogenesis in *G. paradoxa* at the Volta Estuary started in December (stage I) and progressed steadily through March to the advanced stage (II) in May (80%) to a peak in June-July when a majority (60-90 %) of the samples were ripe (IIIA). Spawning began in July with the peak of the spawning event occuring in September (IIIB). A small percentage (< 20%) of partially spent individuals was recorded in September and by November (IV) 80% of the samples was spent with about 20% at the start of gametogenesis in 2008. In 2009, spawning commenced in June (10%) and continued till November. By December, the majority of the samples were spent (80%) with 20% at the start of gametogenesis.

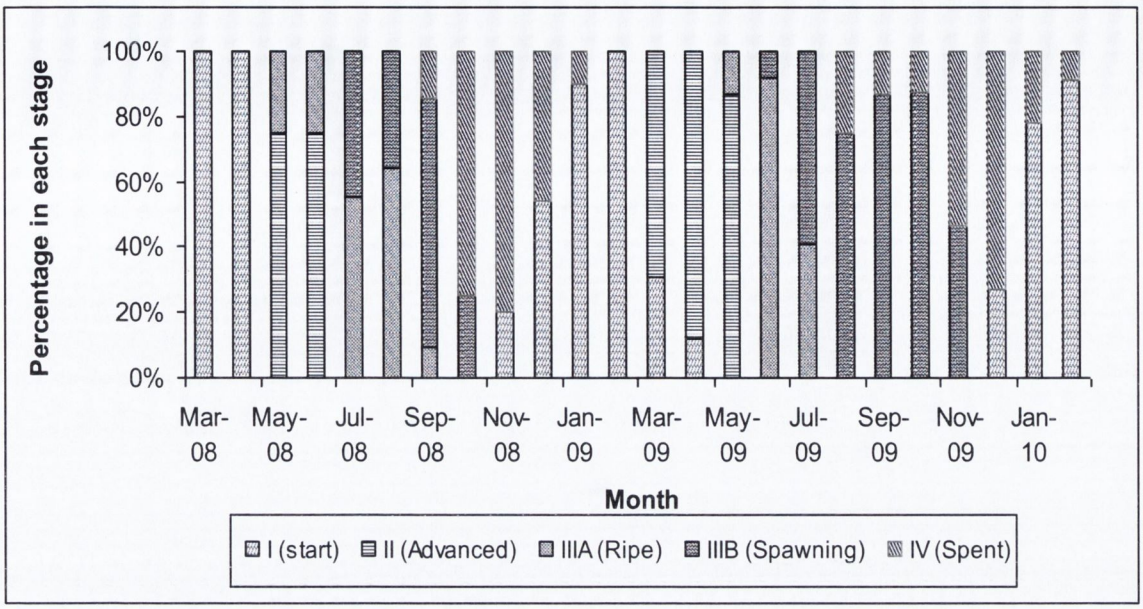


Figure 4.13. Percentage of *G. paradoxa* in various reproductive stages at the Volta Estuary from March 2008 to February 2010.

Figure 4.14 **A – L** presents photomicrographs of the male, female and hermaphrodite *G. paradoxa* at the various stages of gametogenic development.

A-E: Photomicrographs showing the gametogenic stages in the female *G. paradoxa* collected from the Volta Estuary, Ghana.

F-J: Gametogenic stages in the male *G. paradoxa.*

K and **L**: Photomicrographs showing the gonads of a hermaphrodite specimen:

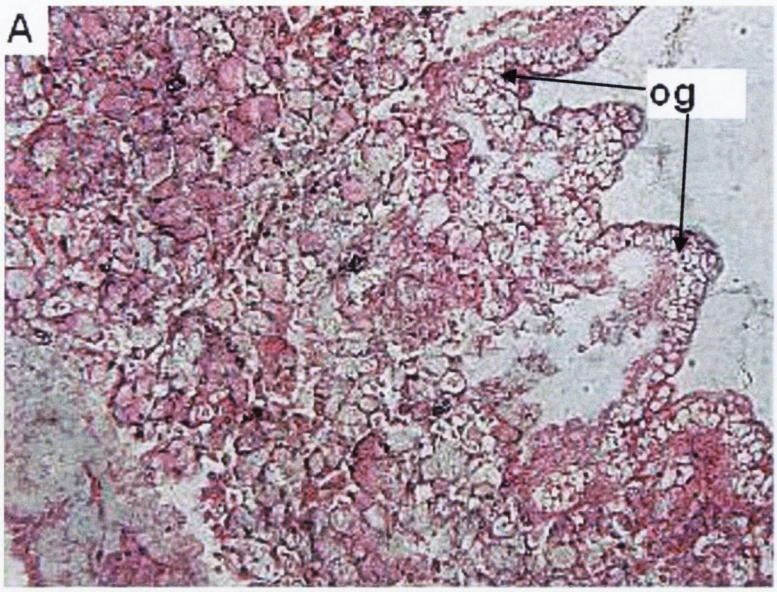
A. stage I: Start of gametogenesis (x 200). **B.** Stage II: Advanced gametogenesis (x 200).

C. Stage IIIA: Ripe (x 400). **D**. Stage IIIB: Spawning (x 400). **E.** Stage IV. Spent (x 400).

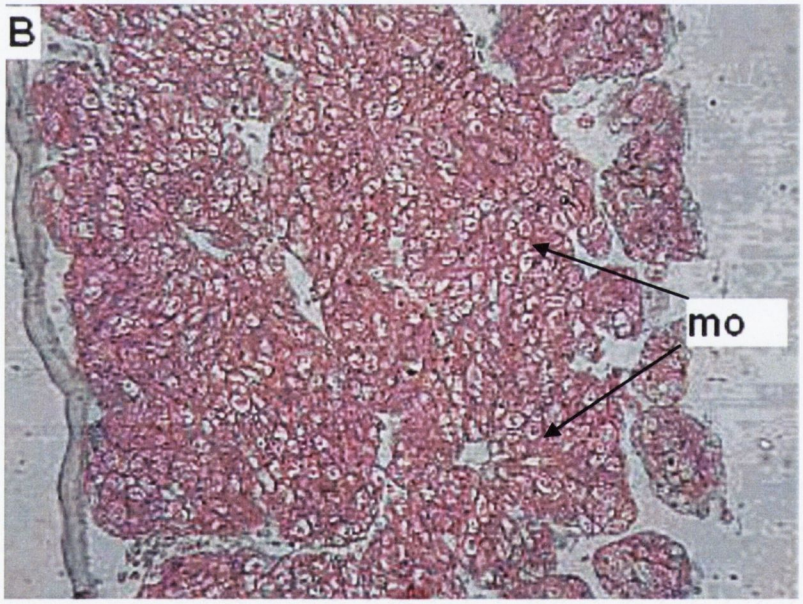
F. stage I: Start of gametogenesis(x 200). **G.** Stage II: Advanced gametogenesis (x 200).

H. Stage IIIA: Ripe (x 200). **I**. Stage IIIB: Spawning (x 400). **J.** Stage IV. Spent (x 400).

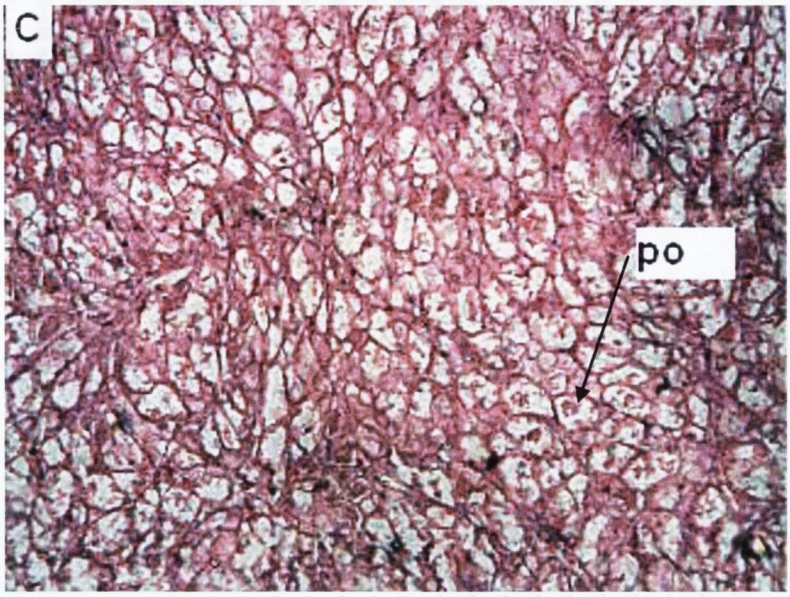
K. Ripe /start of spawning and **L**. Advanced gametogenesis (x 200)



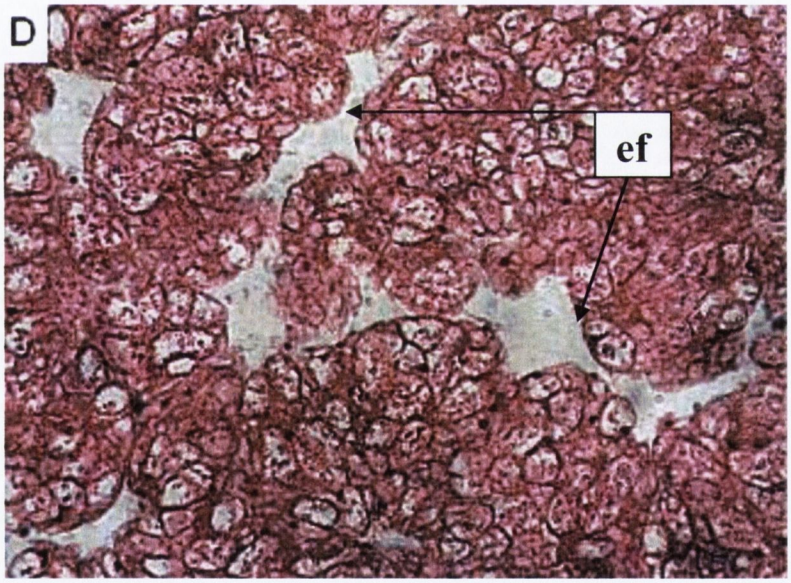
A. stage I: Oogonia (og) at start of gametogenesis(x200).



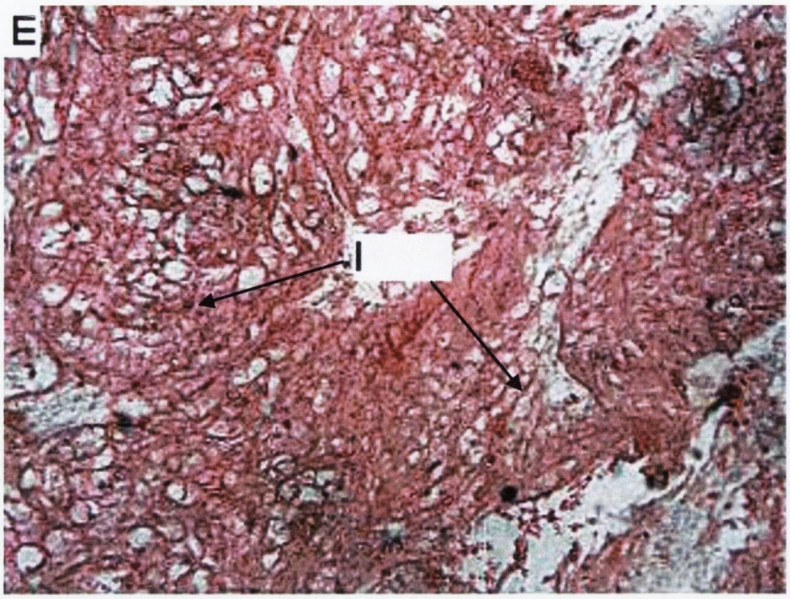
B. Stage II: Maturing oocytes (mo) assuming a polygonal shape(x200) at the advanced gametogenic stage.



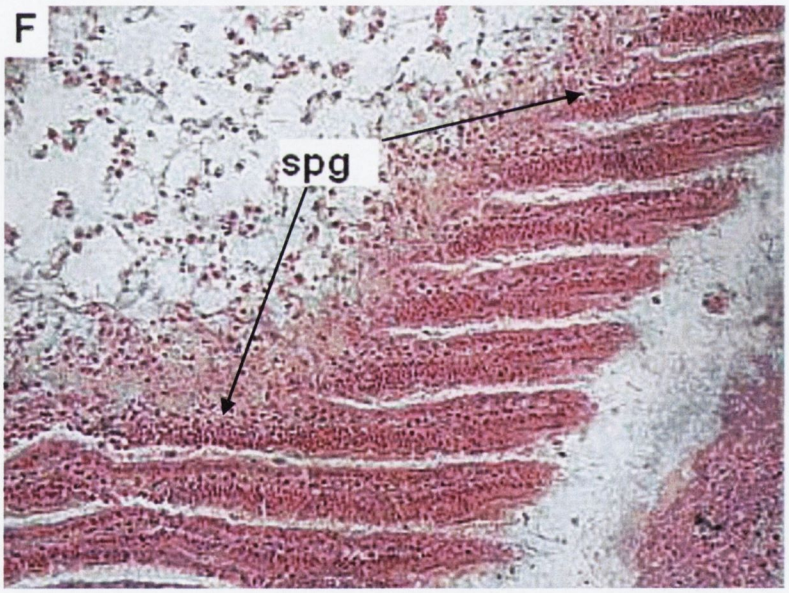
C. Stage IIIA: polygonal oocytes (po) at ripe stage (x400



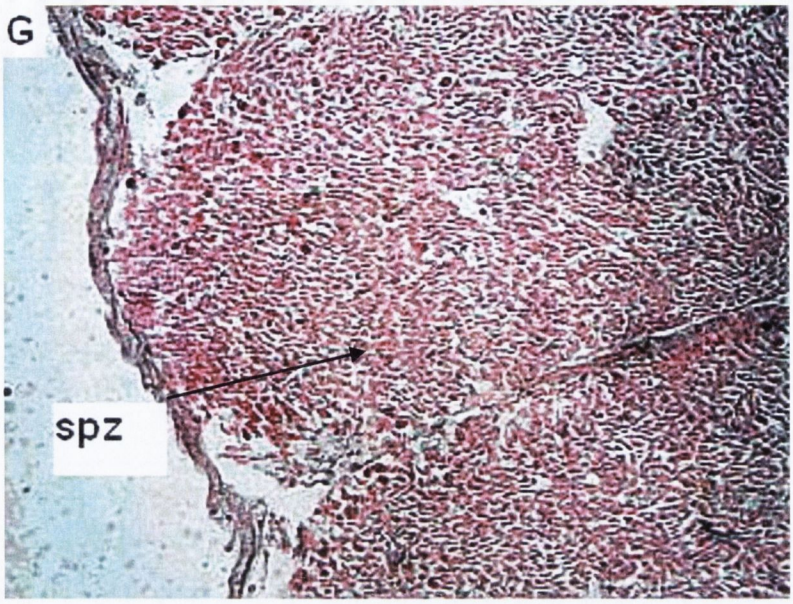
D. Stage IIIB: empty follicles (ef) following the release of oocytes at spawning (x400).



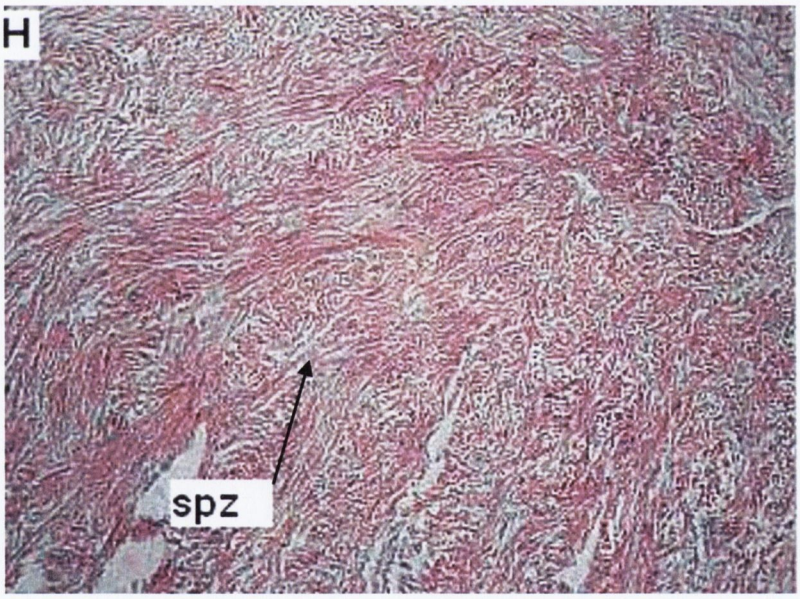
E. Stage IV: empty lumen (l) of the spent gonad with a few relict oocytes (x400)



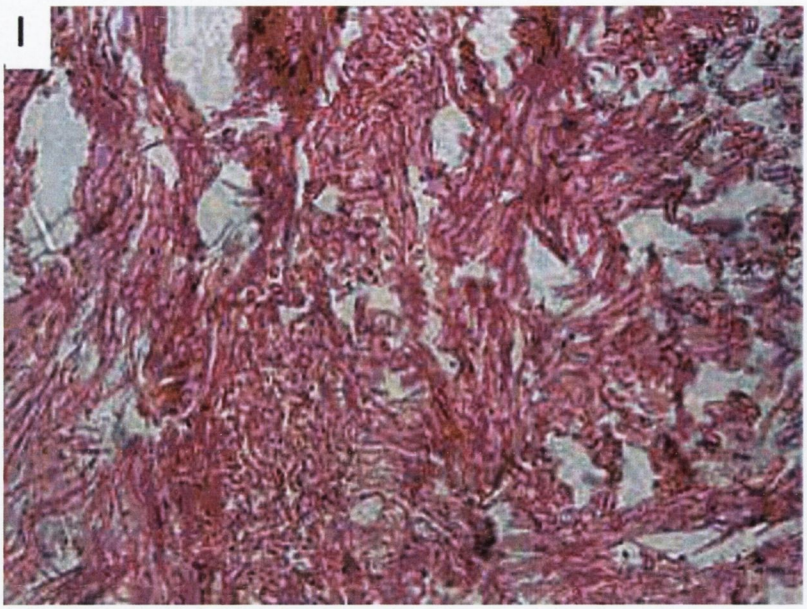
F. stage I: spermatogonia (spg) at early stages of gametogenesis (x200).

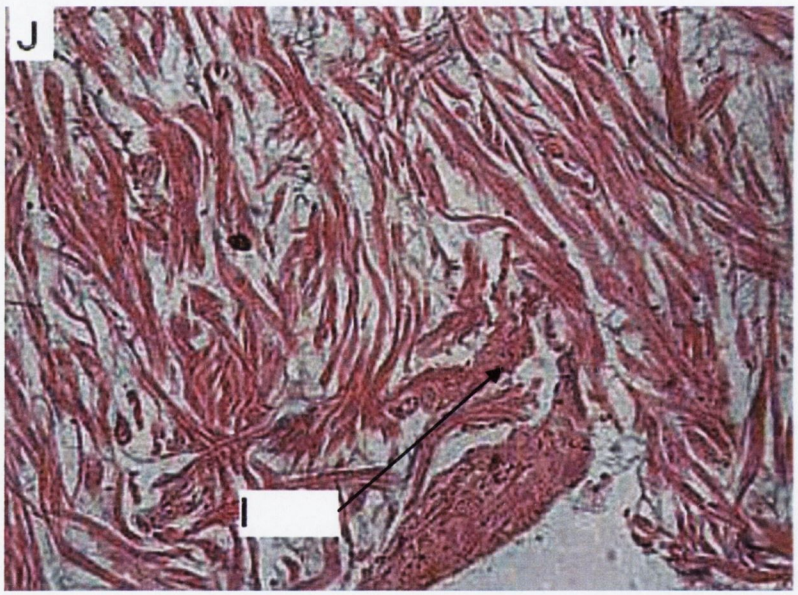


G. Stage II: maturing spermatozoa (spz) at advanced gametogenesis (x200).

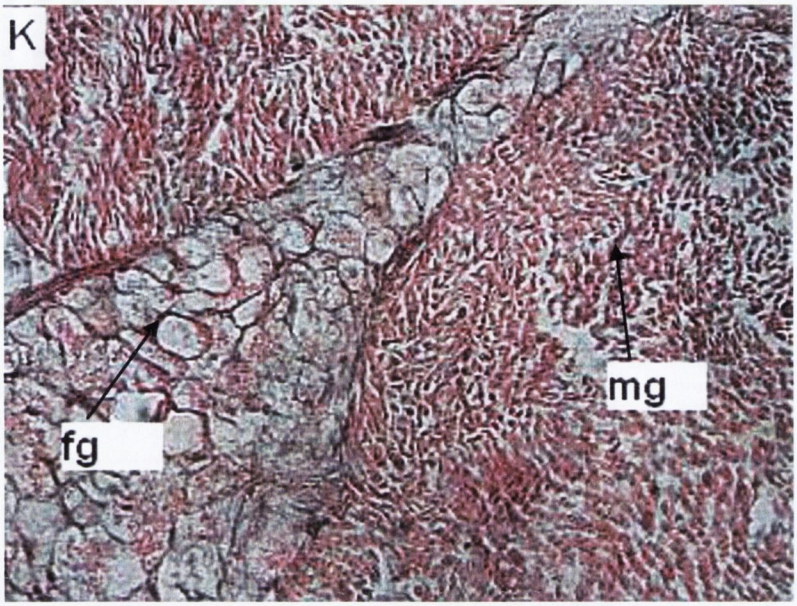


H. Stage IIIA: follicles are filled with ripe spermatozoa (spz) (x200).

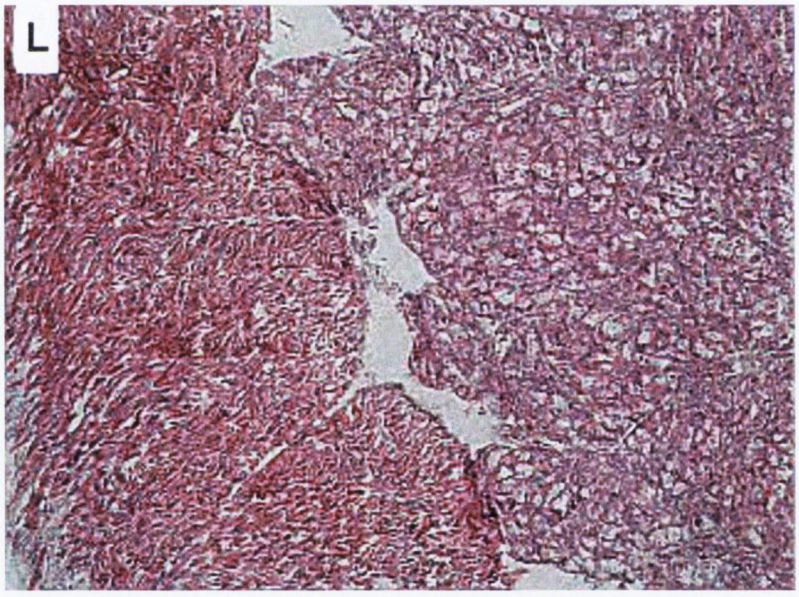




J. Stage IV: empty lumen (l) of spent male gonad with a few relict spermatozoa (x 400).



Hermaphroditic individual with female gonad (fg) and male gonad (mg)



4.3.6 Larval Survey

No larvae were found in any of the plankton samples over the two year duration of the study (March 2008 – February 2010). The sampling frequency was increased to twice a month from June 2009 to January 2010 but no larvae were detected in any of the plankton samples.

4.4 Discussion

4.4.1 Gametogenic Cycle

The results of this study on the gametogenic development and spawning of *G. paradoxa* in the Volta River are directly in contrast to earlier work (Pople, 1966; Whyte, 1981) that indicated that the species spawns during the dry season (November – March). While the triggers for the onset of gametogenesis and spawning in most temperate bivalve species are rising temperatures and food availability that normally occur during spring and summer, there appears to be entirely different triggers for *G. paradoxa* which is tropical and lives in an environment with a relatively constant temperature regime.

In Ghana, there are two climatic seasons: the rainy (April to October) and dry (November to March). The study showed that gametogenesis in *G. paradoxa* starts at the beginning of the dry season in December and progresses with the onset of the rains in March-April until the peak of the rainy season (June-July) when species is ripe. Spawning in *G. paradoxa* in the Volta River occurred from the peak of the rainy season from July - October.

The condition and gonadal indices employed in this study (Figures 4.2 to 4.10) showed a clear relationship with the five gametogenic stages. The indices rose from minimum values in stage (I) at the start of gametogenesis (December), to maximal values at stages (IIIA) ripe and (IIIB) start of spawning (June –August) before declining significantly to minimum values in stage (IV) spent (January-February). It is interesting to note that the indices increased immediately after spawning which indicates a rapid recovery and accumulation of reserves for gametogenesis. This recovery however, cannot be attributed to phytoplankton production during the dry season as the chlorophyll a levels although higher than the rainy season levels were statistically insignificant.

The pattern of gametogenesis and spawning observed in this study are in agreement with the findings of Etim (1996) who studied a population of *G. paradoxa* in the Cross River, Nigeria, using condition indices and histological methods. Etim (1996) found that the stock of *G. paradoxa* in the Cross River spawned at the peak of the rainy season from June to October. Furthermore, the results of this study are corroborated by Lawson (1963) who observed that recaptured specimens during a mark-recaptured experiment in the Volta River showed reduced growth during the flood months of July to December. It was concluded that the species was reproducing during that period.

Similarly, Clemente and Ingole (2009) observed that gametogenesis in *Polymesoda erosa* a tropical brackish water bivalve starts in October, however, active maturation of gonads commenced in January and advanced in March-April. Gonads were ripe in May with spawning occurring over an extended period from June to October.

Artisanal clam fishing in the Volta River has relied on traditionally imposed management practices to regulate the fishery for decades. One key management practice, strictly adhered to by all the clam fishers is the observance of a closed season from the end of December to March. The fishers assert that during this period the clams are lean and not palatable. As shown by this study, the timing of the closed season is based on the in-depth knowledge the fishers have acquired over the years hence the closed season coincides with the period when the animals are spent and therefore in poor condition. The clams attained their maximal flesh weight during May – July when the gonad ripens.

4.4.2 Sex Ratios and Oocyte Numbers

The sex ratio observed for *G. paradoxa* indicated significant departure from the expected 1:1 ratio. The population was dominated by females (80%) with almost equal numbers of males and hermaphrodites. The result is in agreement with the findings of Morton (1991) who observed that freshwater bivalves are either hermaphroditic or gonochoristic and when the latter is true, the sex ratio tends to be female-biased. This trend has been observed by several authors who noted unequal sex ratios in some commercially harvested clam species (Ropes et al., 1984; Rowell et al., 1990; Gribben et al., 2004; Jagadis and Rajagopal, 2007).

The unusually high percentage of females in the population could be attributed to the under-sampling of individuals < 20 mm which was a limitation to this study as the phenomenon of sex switches or protandry within the population could not be studied (Figure 4.12). Furthermore, the impact of intense fishing pressure on the larger individuals in the population might have influenced the sex ratio as larger individuals tend to be females in species that exhibit protandric hermaphroditism. Although, the males were limited to 20-55 mm in shell length and a greater percentage (92.3%) of hermaphrodites were within this length range, owing to the absence of smaller individuals, a clear trend of protandric hermaphroditism could not be indicated. This is in contrast to the observation of Rueda and Urban (1998) in their study of the freshwater clam *Polymesoda solida* in Colombia. In *P. solida*, juveniles start becoming males at 10 mm shell length and above 16 mm no juveniles were observed. At 21 mm males start changing to hermaphrodites. Afiati (2007) also observed distinct size classes during his study on the sexuality of *Anadara granosa and A. antiquata* in Central Java, Indonesia. Both species have a protandric type of development in which a primary male phase precedes the adult stage until both sexes are approximately equally represented after which sex reversal occurs. Afiati (2007) observed that the majority of the 15 – 30 mm individuals were

males, the sex ratio shifting to become 1: 1 when the animals were between 30 – 40 mm in length and by the time they attained a size over 45 mm the populations were dominated by females. The advantage of firstly being male is that some energy could be saved and redirected towards somatic growth because there is a trade-off between growth and reproduction (Seed and Brown, 1977; Calow, 1983).

Several studies have combined qualitative (examination of histological sections) and quantitative (progression of oocyte diameters) methods to show that periods of maturation and spawning tend to coincide with maximum oocyte diameter values. However, the association between oocyte diameters and the remainder of the reproductive cycle remain unclear (Heffernan and Walker, 1989; Gribben et al., 2001). In this study, mean monthly oocyte diameters (Figure 4.11) progressed from 3 – 9 μm at the start of gametogenesis (December – March) to between 24 – 32 μm at the ripe and start of spawning stages (June –August) which continues until October. In spent individuals, the smears contained predominantly smaller oocytes (3 - 9 μm) with a few larger (12 - 24 μm) residual oocytes. The progression of oocyte diameters appears sensitive to changes in the reproductive cycle and may be useful in comparing the gametogenic cycle and spawning events of *G. paradoxa* from different populations. This is in agreement with the findings of Clemente and Ingole (2009) who observed that the progression of egg diameters was a good descriptor of reproductive development in *Polymesoda erosa.*

The number of eggs produced by *G. paradoxa* ranged between 10^4 to 10^6 with an average of 10^6 per female. This suggests that *G. paradoxa* produces planktotrophic eggs and would therefore have a free-swimming planktotrophic larval stage. This is in agreement with other bivalves that produce planktotrophic eggs e.g. *Mercenaria mercenaria* (10^5 to 10^7, average 10^6) (Ansell, 1967); *Argopecten irradians* (10^5 to 10^6) (Fordham, 1970); *Polymesoda erosa* (10^4 to 10^6) (Clemente and Ingole, 2009) and *Mytilus edulis* > 10^4 (Bayne et al., 1983). The

larval survey however, did not detect any larvae in any of the plankton samples taken. The eggs of *G. paradoxa* are smaller than that of *Donax* (60 µm) and the D-shaped veliger larva of *Donax* which is about 70 µm remains in the plankton for 21 days before attaining the pediveliger size of 200 – 300 µm before settling (Chanley, 1969; Carstensen et al., 2010). The absence of the larvae in the plankton samples could be attributed to problems with the sampling methodology. Larvae were sampled by horizontal tows with a 63 µm mesh net at the slowest boat speed. The 63 µm mesh net was appropriate for sampling the veliger larvae of *G. paradoxa* assuming the larvae would be smaller in size than that of *Donax* owing to the smaller oocyte diameters. Apparently the lowest boat speed used for the tows appears too fast which led to the clogging of the net and out-welling i.e. larvae trapped in the net were forced out as a result of the faster boat speed. Owing to the challenges identified, future larval surveys would be conducted with larger mesh nets (100 - 150 µm) with the boat at a stationary position. Furthermore, vertical tows would be conducted from the mouth of the river in order to describe the early larval development and dynamics of *G. paradoxa* in the Volta Estuary.

G. paradoxa continues to grow while the number of eggs produced increases each breeding season (Table 4.2) which is typical of species with an iteroparous mode of reproduction. The mode of reproduction of *G. paradoxa* is in agreement with the finding of Browne (1978) which states that in iteroparous species reproductive effort increases each successive breeding season. *G. paradoxa* can be described as displaying reproductive restraint in terms of the allocation of resources. Individual reproductive investment as indicated by the G: P ratio (Chapter 6) increased with age from 0.90 ± 0.35% in a 3-year old individual to 43.3 ± 1.08% in a 9-year old specimen. Reproduction in *G. paradoxa* is not at the expense of somatic growth as the species invests less than 50% of its energy in reproductive output (Calow, 1981).

4.4.3 Hermaphroditism in *G. paradoxa*

The presence of hermaphrodites in bivalve species that are strictly gonochoristic /dioecious is not unusual (Sastry, 1979). Several authors have reported hermaphroditic individuals in strictly dioecious species. In a study on the reproductive cycle of *G. paradoxa,* in the Cross River, Nigeria, Etim (1996) collected specimens larger than 70 mm over a period of 32 months and found 3.5% hermaphroditism. Other studies by Darriba et al. (2005) reported the occurrence of 0.5% hermaphroditism in 883 samples of *Ensis siliqua* collected over a two-year study from the Ria de Corcubion, north-western Spain. Morton (1985b) also observed 0.5% hermaphroditism in *Polymesoda erosa* collected over a year in mangroves in Hong Kong. Similarly, Afiati (2007) reported the occurrence of less than 1.5% hermaphroditism in *Anadara granosa* and less than 1% for *A. antiquata* in a study of hermaphroditism in *A. granosa* and *A. antiquata* in Central Java, Indonesia. It was further reported that both species have a protandric type of development in which a primary male phase precedes the adult stages until both sexes are approximately equally represented (Afiati, 2007). Ceuta et al. (2010) recorded 0.4% and 0.2% hermaphroditism in *Tagelus plebeius* (Psammobiidae) and *Iphigenia brasiliana* (Donacidae) respectively from 500 samples each collected from the Cachoeira River Estuary, in Brazil.

The high incidence of hermaphroditism observed in this study (9.4%) is comparable to that recorded in *A. antiquata* (9.9%) on the Dar es Salaam coast in Tanzania (Kayombo and Mainoya, 1987). Lucas (1975) showed that the percentage of hermaphrodites amongst juvenile bivalves may be quite high, for example 23% for *Venerupis decussata* (L.), 44% for *Venus striatula* (da Costa) and 72% for *Glycymeris glycymeris* (L.). These proportions are relatively large, but, it was not reported whether those juvenile hermaphrodites survived to become adults.

Pinera et al. (2009) found an unusually high frequency of hermaphroditism in *Megapitaria squalida* collected from Bahia de la Paz (21.8%) and Bahia Magdalena (23.5%) in Baja California, Mexico. It was observed that most of the gonad tissue consisted of male follicles with oocytes located outside the follicles and toward the periphery of the gonad tissue. The high incidence of hermaphroditism in this dioecious species was attributed to stress as result of overexploitation and low population density which favours hermaphroditism (Pinera et al., 2009).

The reasons adduced by Pinera et al. (2009) could be applied to the clam fishery at the Volta Estuary. The population of *G. paradoxa* in the Volta River is threatened as a result of habitat modification and overfishing (Adjei-Boateng et al., 2010). Harvests from the clam fisheries at the Volta Estuary have increased from 1700 tonnes (Kumah, 2000) to 7700 tonnes in this study (Chapter 6). Landings are dominated by small to medium sized clams (< 55 mm) which hitherto where not harvested. These changes might have accounted for the high incidence of hermaphroditism and the dominance of females (80%) in the population. The increase in female abundance may be a strategy to ensure the reproductive success in sessile populations subjected to increasing fishing pressure and at low densities (Pinera et al., 2009). Sex reversal of small-sized males to females is common is freshwater bivalves (Rueda and Urban, 1998; Afiati, 2007). Higher exploitation rates remove the larger females from the population resulting in the reversion of more and more males at much smaller sizes to females hence the dominance of females in the population.

Little is known about the sex determining mechanism of bivalves and molluscs in general (Afiati, 2007). The male and female gametes of molluscs differentiate from sexually non-determined germ cells (Dohmen, 1983). In gonochoristic species, the differentiation of primordial germ cells into male or female gametes seems to be controlled by a neurohormone, the androgenic factor (Ceuta et al., 2010). Experiments with isolated gonads have shown that

in the absence of this factor, the cells differentiate into female gametes, while in its presence the cells differentiate into male gametes. In simultaneous hermaphrodites, like the *Helix aspersa,* the presence of an androgenic factor has been demonstrated in the male. However, the issue of how the female gametes develop is not yet known (Ceuta et al., 2010).

The phenomenon of endocrine disruption chemicals (feminisation of males) have been reported in other studies. According to Bateman et al. (2004) the appearance of oocytes in the testes (ovotestis – an intersex condition) is regarded as an endpoint of endocrine disruption in male fish and has been linked to the presence of endocrine disrupting compounds (EDC) which are thought to mimic the actions of the female sex hormone 17-ß-oestradiol, and thus disrupt natural hormonal functioning. Chesman and Langston (2006) observed a moderate (21% of males examined) incidence of intersex (ovotestis) in *Scrobicularia plana* from the Avon River Estuary, U.K. It was reported that a proportion of females in the population remained unaffected at approximately 50%, while the proportion of unaffected males dropped to 35, 33 and 28% implying that intersex is feminisation of males (Chesman and Langston, 2006). It was concluded that the level of intersex in the Avon population of *S. plana* could be attributed to (xeno) oestrogens and, thus, the presence of endocrine disrupting compounds in the estuary. The presence of endocrine disruption chemicals were not monitored during this study. The estuary is far from any sewage or sources of (EDC) therefore the high percentage of females (80%) in the population cannot be attributed to presence of such chemicals.

In conclusion, the reproductive cycle of *G. paradoxa* in the Volta River is annual with a single spawning event between July and October. Gametogenesis starts in December and progresses steadily to a peak in June-July when spawning begin until November when the animal is spent. Condition and gonadal indices showed a clear relationship with the gametogenic stage rising from a minimum at stage (I) start of gametogenesis, to their highest values at stages (IIIA) ripe and (IIIB) start of spawning before declining significantly to stage (IV) spent. The condition

and gonadal indices may prove a valuable monitoring technique in fishery management to recognise the reproductive stage of *G. paradoxa* populations as it is less expensive and time consuming than histological techniques.

Furthermore, the progression of oocyte diameters appears sensitive to changes in the gametogenic cycle and may be useful in comparing the reproductive cycle and spawning events of *G. paradoxa* from different populations. *G. paradoxa* is gonochoristic with dominance of females and high incidence of hermaphrodites in the population which may be attributed to overfishing.

It is iteroparous and produces planktotrophic eggs which average 10^6 per female. In terms of the allocation of resources between somatic growth and reproduction, *G. paradoxa* may be described as showing reproductive restraint. The data presented in this study provide valuable information on the timing and initiation of spawning events in *G. paradoxa,* which is necessary for developing sustainable management strategies and the selection of broodstock for hatchery operations.

5.0 POPULATION DYNAMICS OF *G. PARADOXA*

5.1 Introduction

The determination of the age and growth rate of bivalves is fundamental for studies on population dynamics (Neves and Moyer, 1988; Gaspar et al., 2004). Growth rate in bivalves is influenced by several factors including habitat type, environmental variables as well as the geographical latitude (Fiori and Morsan, 2004; Moura et al., 2009). While some freshwater bivalves are short-lived with their ages ranging from a few months to a maximum of 4 years in *Pisidium* (Holopainen and Hanski, 1986), others such as *Margaritifera* are long-lived and specimens over 100 years old have been reported (Bauer, 1992).

Geographical latitude has a profound effect on the growth rate and age of bivalves (Moura et al., 2009). For example bivalves occupying warmer waters tend to have faster growth rates compared with populations in cooler waters, e.g. *Callista chione* in the Mediterranean (Metaxatos, 2004) had a growth rate of 0.24 $year^{-1}$ compared with a similar population in the Atlantic ocean with growth rates between 0.15 and 0.18 $year^{-1}$ (Moura et al., 2009). Temperate bivalves have a faster growth rate in spring and summer with a decreased rate or no growth in autumn and winter (Gaspar et al., 2004; Moura et al., 2009). Among Arctic bivalves *Arctica islandica* experiences prolonged winter periods of 6 – 8 months and only a shorter warmer period with temperatures between 0 and 16°C for growth in the spring and summer (Mann, 1982). *Arctica islandica* is slow growing and long-lived, the maximum recorded age is close to 500 years, and individuals over 100 years old are abundant in the North Atlantic (Schone et al., 2005; Strahl et al., 2007).

The type of habitat inhabited by a bivalve tends to influence its growth rate hence the maximum age attainable. Several authors have documented the effects of wave action on growth rates (Jones and Demetropoulos, 1968; Raubenheimer and Cook, 1990). The effect of

wave action may be species-specific, as an increase in wave exposure may lead to either an increased (van Erkom Schurink and Griffiths, 1993), or decreased (Seed, 1968; Jørgensen, 1976) growth rate. McQuaid and Lindsay (2000) found that *Perna perna* populations on a wave exposed shore had a faster growth rate (0.64 $year^{-1}$) compared with similar populations on a sheltered shore (0.31 $year^{-1}$). Longevity, however, was lower in the exposed population (2.59 years) than the sheltered population (6.72years) as growth rate and longevity are inversely related (Seed, 1969; Bayne, 1976; Berry, 1978).

A number of methods have been used to estimate the age and growth rate of bivalve populations, including counting the annual growth rings visible on the shell surface or in the microstructure of polished and etched shells (Richardson, 2001), length-frequency distribution analysis (Anwar et al., 1990; Richardson et al., 1990) and tagging and recapture experiments (Ropes et al., 1984, Etim and Brey, 1994). Each of the methods has its advantages and disadvantages. While certain techniques may be more appropriate for one species than another, the best approach is to employ a range of methods in order to provide a more robust estimate than using one method alone (Seed and Brown, 1978).

The von Bertalanffy growth model continues to play an important role in length-based stock assessment (Gulland, 1983; Sparre and Venema, 1992). Growth parameters estimated by other methods are fitted to the von Bertalanffy growth model in order to yield a robust estimate of age and growth rate. Although the von Bertalanffy growth model has three parameters, the most important are the growth coefficient (K) and asymptotic length (L_∞). The asymptotic length is the maximum length attainable if the species were to live infinitely whereas the growth coefficient (K) is a measure of how fast the species approaches L_∞. Growth rate in bivalves is not constant throughout their life-span. It is faster at the larval stage and steadily declines as the animal approaches the asymptotic length (Moura et al., 2009). Since individual growth is a non-linear process, the comparison of growth among different organisms or

populations is difficult owing to the problem of correlation between K and L_{∞}. To overcome this problem, the overall growth performance index, phi-prime (Ø) (Pauly, 1979; Munro and Pauly, 1983) is often used to compare growth among different populations of a species.

Recruitment patterns in bivalve populations is either a single annual event, as in most temperate bivalves occurring within a short period of the year when conditions are favourable; e.g., *Mytilus edulis* in mid July (Petraitis, 1991), or over an extended period- summer to late winter or spring; e.g., *Macomona liliana* (Roper et al., 1992). In other species such as *Solemya sp,* recruitment is continuous year-round (Rainer and Wadley, 1991). Recruitment patterns are greatly influenced by climatic conditions as observed in the Wadden Sea, where higher recruitment of *Cerastoderma edule*, *Mytilus edulis*, *Macoma balthica* and *Mya arenaria* in the summer after severe winters is a common phenomenon (Strasser et al., 2001).

Growth in *G. paradoxa* according to Moses (1990), King et al. (1992), Etim and Brey (1994) and King (2000) is rapid, reaching lengths of 40 mm within the first year thereafter slowing down to about 2 mm $year^{-1}$ by the time the animal is 7 years old. These growth characteristics are shared by several marine relatives of *G. paradoxa* which are known to live for at least 10 years, e.g. *Callista chione* (Moura et al., 2009); *Venus verrucosa* (Arneri et al., 1998) and *Mercenaria mercenaria* (Peterson, 1986).

Mortality in bivalve populations consists of two parts, natural mortality (M) and fishing mortality (F). In an unexploited population total mortality (Z) is equal to natural mortality (M). Once exploitation starts, mortality owing to fishing is introduced, which in most instances assumes an important role as the exploitation level increases. In order to ensure sustainability in any fishery, it is recommended that mortality owing to fishing should not exceed 50% of total mortality i.e. F = M (Gulland, 1965). However, it has been difficult maintaining this level of exploitation even under regulated conditions. Exploitation has always gone beyond optimum or sustainable levels leading to drastic reduction in numbers or in some cases

extinction of species. For example in the *Polymesoda solida* fishery in Colombia, fishing mortality accounts for 72% of total mortality (Rueda and Urban, 1998). Similarly, in the *Modiolus metcalfei* fishery in the Philippines, fishing mortality accounts for 73% of total mortality (Tumanda Jr. et al., 1997).

Length-weight relationships usually describe a mathematic relationship between length and weight, such that one may be converted to the other. It also measures the deviation from the expected weight for a specified length of an individual or a group of individuals as indication of condition and gonad development (Le Cren, 1951). It has been found that the length-weight relationship of most organisms can adequately be described by the formula: $W= \alpha L^{\beta}$, where W = weight, L = length, α is a constant and β an exponent usually lying between 2.5 and 4.0 (Martin, 1949). For an ideal organism which maintains the same shape such that growth is uniform for all body parts, $\beta = 3$ and growth is described as isometric, a condition which is occasionally observed (Allen, 1938). In the vast majority of instances where length-weight relationships have been calculated, it has been found that $\beta \neq 3$, in that case growth is referred to as allometric where certain parts of the body grow faster than others (Gaspar et al., 2002).

Bivalves play an important role ecologically by providing food for other organisms (birds and fish) and economically as an important source of protein and raw materials (Moses, 1990; Roper et al., 1992; King, 2000). The clam fishery at the Volta River Estuary is an important source of employment and an affordable protein source to the riparian human communities (Amador, 1997). Furthermore, the clam shell has a number of important uses notably as a source of calcium in poultry feed and in lime manufacturing. Despite its commercial importance there is limited information on the population dynamics of *G. paradoxa* in the Volta River. This information is crucial for estimating sustainable exploitation rates as well as the potential of the species for aquaculture production. The present study determined the age and growth rate of *G. paradoxa* in the Volta River, Ghana, using three methods; shell surface

rings, length frequency distributions and tagging and recapture experiments, as well as recruitment pattern and mortality.

5.2 Materials and Methods

5.2.1 Age and Growth Rate

Samples for age and growth rate determination were acquired from clam fishers at the Volta River Estuary as described in Sections 2.1 and 2.2. The methods for field sampling and laboratory processing of samples are outlined in Sections 2.4, 2.4.1, 2.4.2 and 2.4.3. Age and growth rate determination was conducted by three methods, namely counting of shell surface rings, length frequency distributions and tagging-recapture experiments.

5.2.1.1 Surface Rings

Shell surface rings were not distinct for the shells to be aged immediately after sampling, however, after air drying at room temperature for a period of at least a week, the rings were discrete for aging. Size-classes of *G. paradoxa* with shell lengths corresponding to the ages of the cohorts were identified and used as a guide in the ageing process.

5.2.1.2 Length-Frequency Distributions

Cohort analysis follows the progression of a group from the time it is recruited into the fishery until it disappears. The Bhattacharya method (Bhattacharya, 1967) available in the fish-stock assessment tool FISAT II (Gayanilo et al., 2005) is commonly used because it needs only length-frequency data. The advantage of this technique is that within one year it is possible to assess any stock if sufficient length-frequency data is available.

Monthly samples (May 2008 – February 2010) were obtained from the two sampling locations, Ada and Aveglo, in the Volta Estuary (Figure 2.1). Shell lengths and total weights were taken as described in Section 2.3.1.1. The data were grouped into shell length classes at 2 mm intervals (Tumanda Jr. et al., 1997) and subsequently analysed using routines in FISAT II, (Gayanilo et al., 2005). Preliminary estimates of L_∞ and Z/K were obtained through the

Powell-Wetherall plot (Powell, 1979; Wetherall, 1986; Pauly, 1986). The final asymptotic length (L_∞) and the growth coefficient (K) were estimated by fixing the initial L_∞ from the Powell-Wetherall plot into the Shepherd method (Shepherd, 1987) in FiSAT II to estimate the asymptotic length (L_∞) and growth coefficient (K) of the von Bertalanffy Growth Function (VBGF) (von Bertalanffy, 1938): $L_t = L_\infty (1-e^{-k(t-t_0)})$, where L_∞ is the asymptotic length (mm), K is the growth coefficient ($year^{-1}$), t is the age (year) and t_0 is the theoretical age of the animal at a length equal to zero. The (t_0) was estimated by inverse VBGF: $t_0 = t + 1/K*Ln (1- L_t/ L_\infty)$

5.2.1.3 Tagging Recapture Experiment

A tagging-recapture experiment was started from June 2008 to May 2009 to monitor the growth of individual samples at the Volta Estuary to validate the age and growth rate estimates from surface rings and the length-frequency distributions. Nine wooden boxes 50x 40x15cm were used and each filled with the sandy sediment found at the point of occurrence of the species. Fifty individuals with shell lengths between 24 and 60 mm were selected randomly, individually marked and assigned to one of the boxes. The shell length and total weight of each individual were taken as described in Section 2.3.1.1 at the start of the experiment and every two months thereafter. The data from this experiment was treated as growth increment data and analysed by the Gulland and Holt plot (Gulland, 1959) in FiSAT II to estimate the L_∞ which was then seeded in the Munro routine (Munro, 1982) to compute K.

5.2.2 Recruitment Pattern

The recruitment pattern of the stock was determined from the length-frequency distribution of the grab samples by the backward projection onto the length axis of the length-frequency data of Ada and Aveglo as described in FiSAT II. The routine reconstructs the recruitment pulse from a time series of the length-frequency data to determine the number of pulses per year and the relative strength of each pulse. The input parameters are L_∞, K and t_0. Normal distribution of the recruitment pattern was determined by NORMSEP (Pauly and Caddy, 1985) in FiSAT II.

5.2.3 Estimation of Mortality Rates

Total mortality (Z) of the population was estimated from the length-frequency distribution by the length converted catch curve method (Pauly, 1984). Natural mortality (M) was estimated using the empirical relationship of Pauly (1980):

$\text{Log}_{10}\, M = - 0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$

where M is the natural mortality, L_∞ the asymptotic length, K refers to the growth coefficient of the von Bertalanffy growth function (VBGF) and T is the mean annual habitat temperature, which was (28.6 °C) at the Volta Estuary over the study period. With the Z and M estimated, the fishing mortality (F) was obtained from the relationship: $F = Z - M$, where Z is the total mortality, F is the fishing mortality and M is the natural mortality. The exploitation level (E) was obtained by the relationship of Gulland (1965): $E = F/Z = F/ (F+M)$. The growth performance index (Ø) (Pauly and Munro, 1984) of *G. paradoxa* from Ada and Aveglo was estimated using the L_∞ and K estimates in Section 5.2.1 and the Equation: $Ø = 2 \log_{10} L_\infty + \log_{10} K$

5.2.4 Length-Weight Relationships

To establish the relationship between shell length and total weight, the commonly used relationship: $W = \alpha L^{\beta}$ was applied (Ricker, 1975) where W is total weight (g), L is shell length (mm), α is the intercept and β is the slope (growth coefficient). The parameters α and β were estimated by least squares linear regression, using logarithmic data: $\log_{10} W = \log_{10} \alpha + \beta \log_{10} L$. The coefficient of determination (R^2) was used as an indicator of the quality of the linear regression. The regression coefficients for successive monthly samples from Ada and Aveglo were generated and the shell-free dry weight cycle for a 40 mm standard animal outlined.

5.3 Results

5.3.1 Surface Rings

Table 5.1 presents data on the mean shell length and the standard deviation (SD) obtained for each age as well as the length range from the counting of surface rings. The length estimates for a one year old *G. paradoxa* was 19.4 ± 4.5 mm and that for the second and third year individuals were 28.4.1 ± 7.3 and 37.1 ± 5.9 mm, respectively (Table 5.1).

Table 5.1 Mean length-at-age and the respective standard deviations (mm) along with maximum and minimum length of *G. paradoxa* obtained from shell surface rings.

			Size (mm)	
Age(years)	**N**	**Mean length ± SD (mm)**	**Minimum**	**Maximum**
1	14	19.4 ± 4.5	16.2	22.6
2	108	28.4 ± 7.3	23.3	33.6
3	94	37.1 ± 5.9	33.0	41.3
4	60	45.3 ± 5.8	41.2	49.4
5	51	49.9 ± 4.7	46.6	53.3
6	30	54.7 ± 4.6	51.5	58.0
7	18	64.4 ± 4.7	61.0	67.7
8	5	71.6 ± 2.5	69.9	73.4

The length-at-age data generated from surface rings (Table 5.1) was re-arranged to form $L_{t+1} = a + bL_t$, where L_{t+1} and L_t pertain to lengths separated by a constant time interval (1 year), a and b are constants of the Ford-Walford Plot (Walford, 1946). The seventh and eighth year old individuals were not properly aged owing to their low numbers in the population as well as the difficulty in discriminating between the rings at the shell margin in older individuals. Consequently, the Ford-Walford Plot was based on the age-length data of the first six years (Figure 5.1). From the Ford-Walford equation of $y = 0.841x + 12.79$, where $a = 12.79$ and $b = 0.841$, the asymptotic length (L_∞) was calculated as $[a / (1-b)]$ and the growth coefficient (K) =

- $\log_e b$. The estimated asymptotic length (L_∞) and growth coefficient (K) were 80.44 mm and 0.17 $year^{-1}$, respectively.

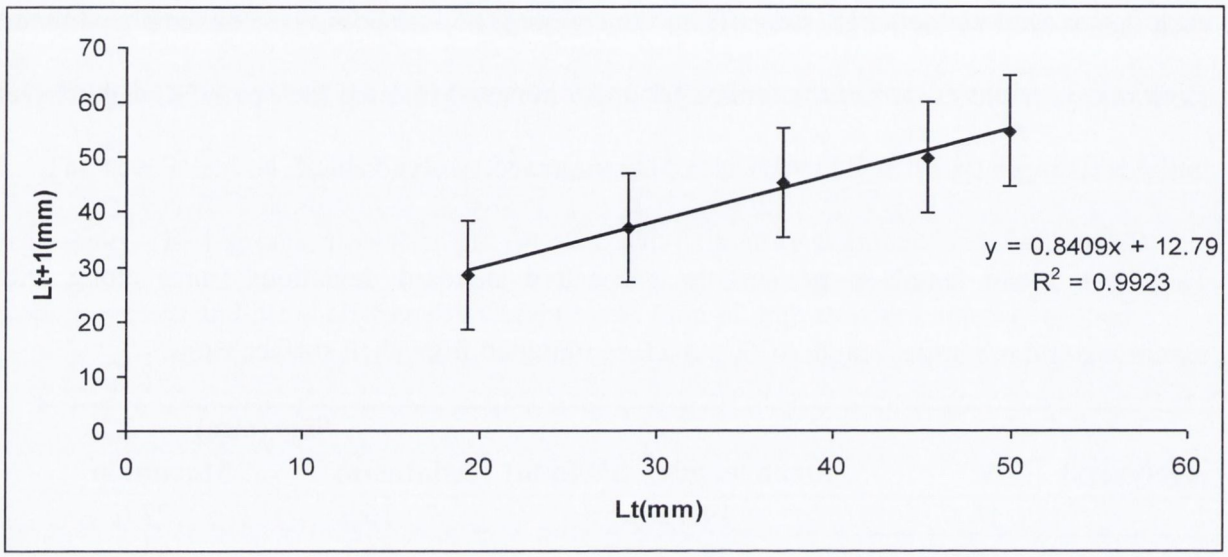


Figure 5.1 Ford –Walford Plot, using the mean length of *G. paradoxa* individuals (L_{t+1}) against L_t.

Figure 5.2 is a plot of shell length against the age of individual *G. paradoxa* determined from the counting of surface rings. From the regression equation y = 23.46Ln (x) +12.3 and that of a Ford-Walford plot, the length of 1-year-old individual from surface rings ranges between 12.3 – 12.8mm.

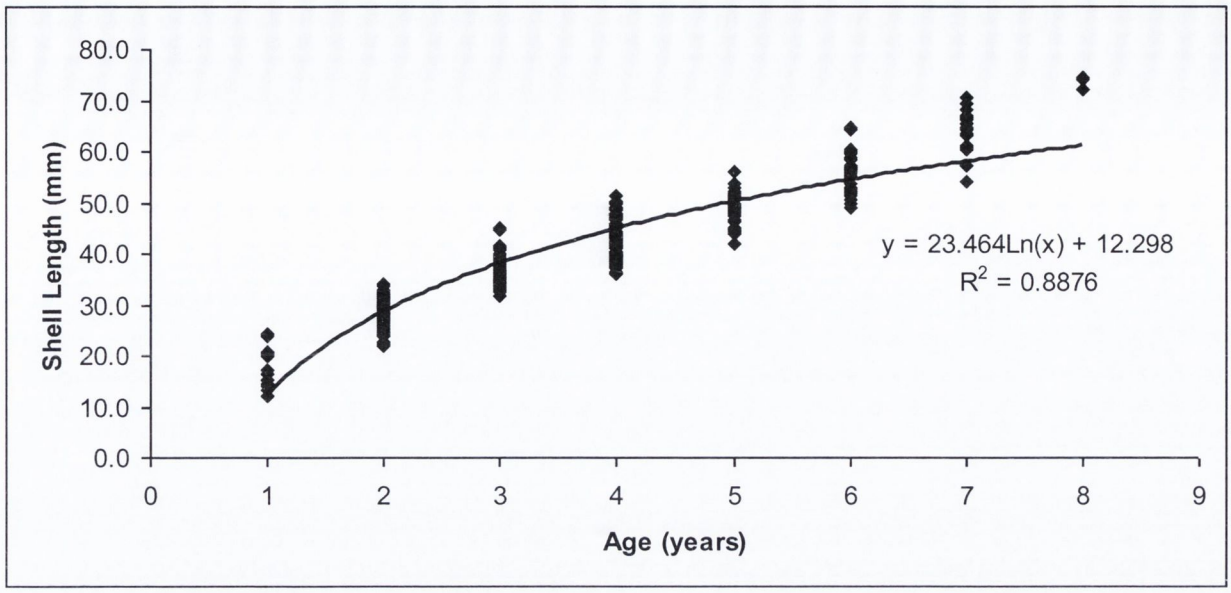
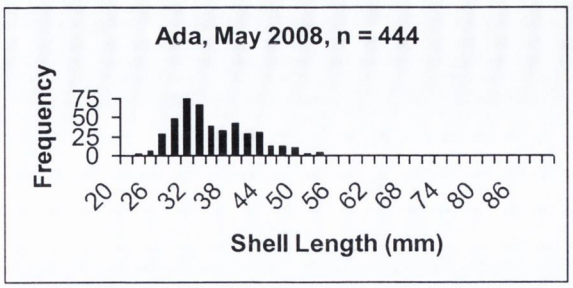


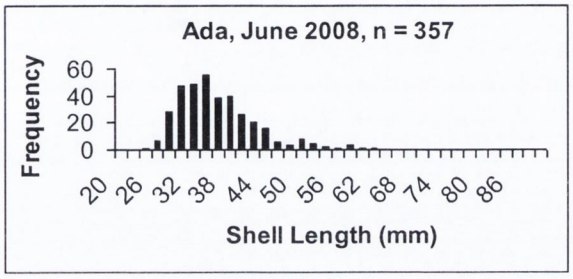
Figure 5.2 Plot of shell length against age of individual *G. paradoxa* determined from the counting of shell surface rings.

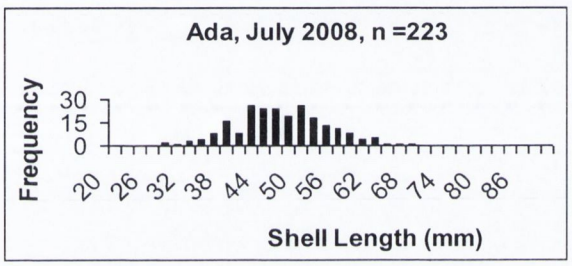
5.3.2 Length Frequency Distributions

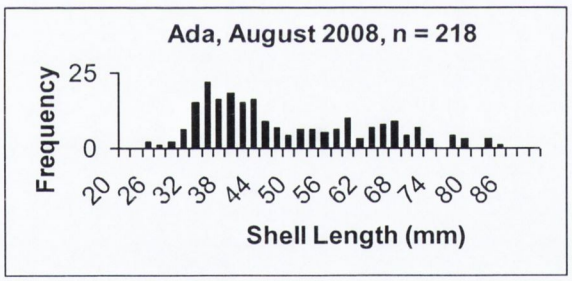
The length-frequency distributions of *G. paradoxa* samples from Ada and Aveglo are presented in Figure 5.3. Because of the fishing bias, individuals less than 20 mm were uncommon in the length-frequency distribution from the fishers catch. One could observe the movement of cohorts in the monthly samples from Ada (August 2009) and Aveglo as well as other notable shifts however, these were limited to a shell length range of 26-70 mm. The January 2009 sample from Aveglo had relatively larger individuals (Figure 5.4b). There was no difference between Ada and Aveglo with regards to the length-frequency distribution (Figure 5.3). The Bhattacharya method allowed the separation of eight cohorts. The value of the first, second and sixth years were 15.8 ± 3.0, 26.4 ± 4.5 and 55.1 ± 8.1mm, respectively. The L_∞ and K estimate for Ada was 105.7 mm and 0.14year^{-1} while that for Aveglo was 84.4 mm and 0.18year^{-1}. From the reverse VBGF, t_0 for Ada and Aveglo were -0.125 and -0.119 respectively. Figure 5.4 presents the length frequency distribution by FiSAT II of *G.*

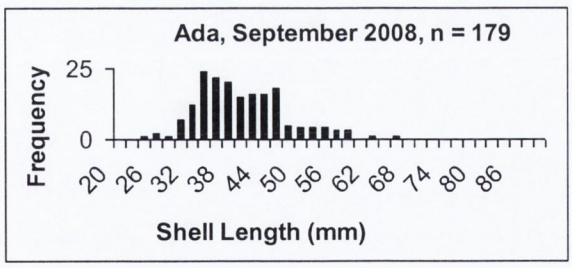
paradoxa from Ada (Figure 5.4a) and Aveglo (5.4b) with growth curves superimposed. The electronic length-frequency analysis (ELEFAN) routine in FiSAT II generated the length-frequency distribution of the monthly samples by restructuring the length-frequency data such that clearly identifiable peaks which correspond to the cohorts in the population were marked by the position of the growth curves (Figure 5.4).

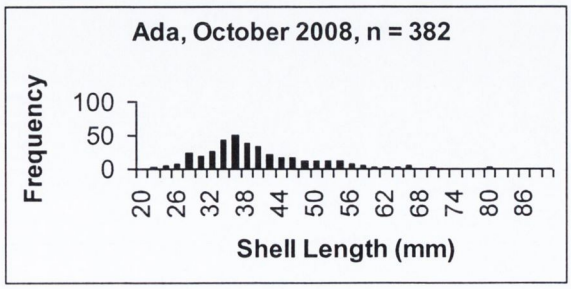

Ada, May 2008, n = 444
Frequency
0
25
50
75
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)

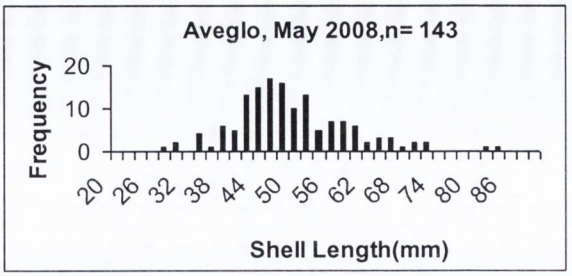

Ada, June 2008, n = 357
Frequency
0
20
40
60
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)

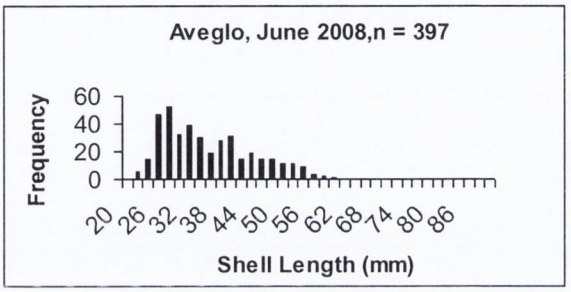

Ada, July 2008, n =223
Frequency
0
15
30
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, August 2008, n = 218
Frequency
0
25
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, September 2008, n = 179
Frequency
0
25
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, October 2008, n = 382
Frequency
0
50
100
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Aveglo, May 2008,n= 143
Frequency
0
10
20
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length(mm)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Frequency
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20
40
60
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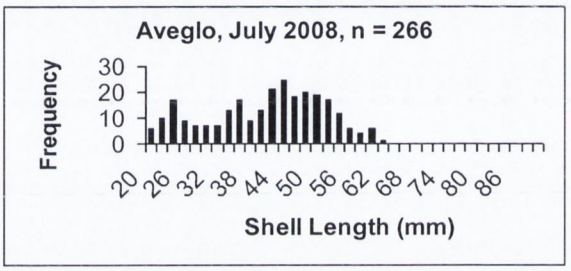
Shell Length (mm)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Frequency
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10
20
30
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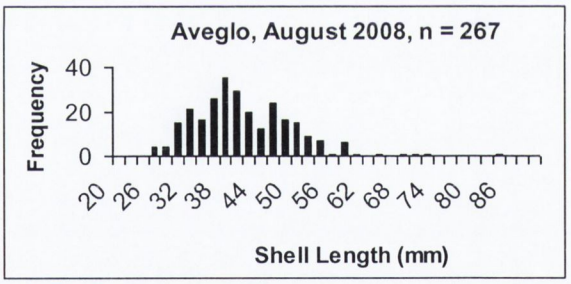
Shell Length (mm)


Aveglo, August 2008, n = 267
Frequency
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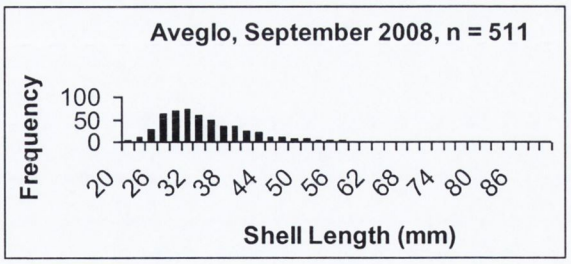
20
40
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)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Frequency
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100
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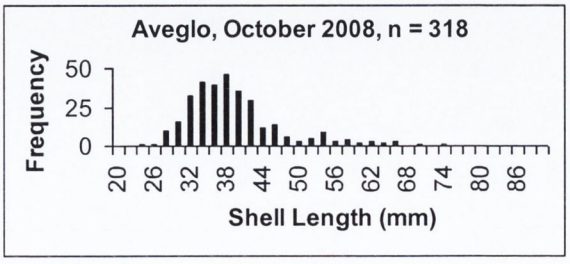
Shell Length (mm)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25
50
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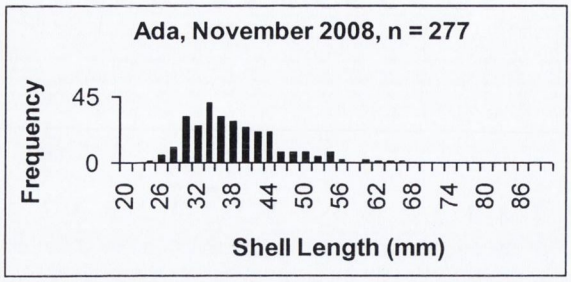
Shell Length (mm)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Frequency
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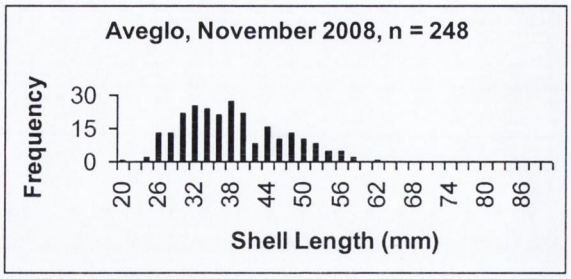
Shell Length (mm)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Frequency
30
15
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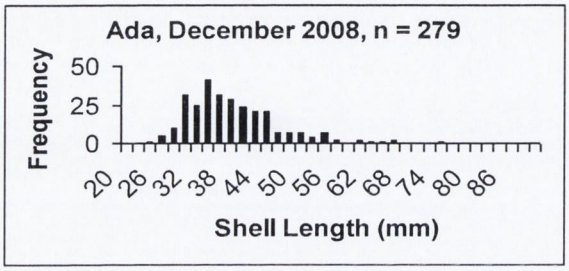
Shell Length (mm)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Frequency
50
25
0
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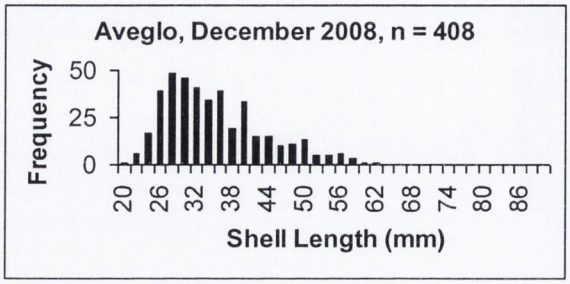
Shell Length (mm)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Frequency
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25
0
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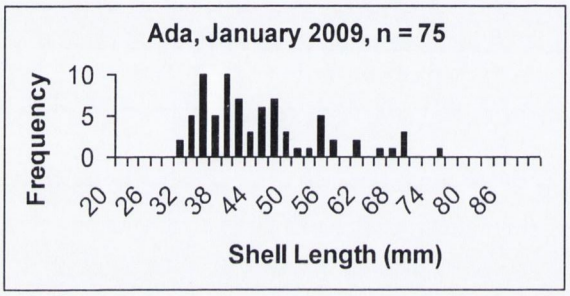
Shell Length (mm)


Ada, January 2009, n = 75
Frequency
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5
0
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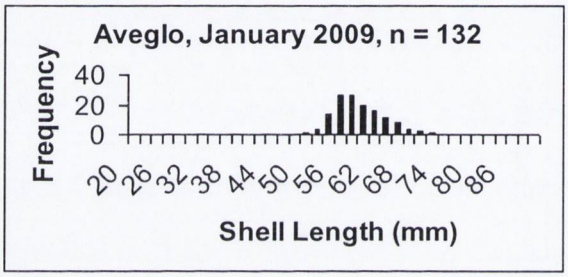
Shell Length (mm)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Frequency
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20
0
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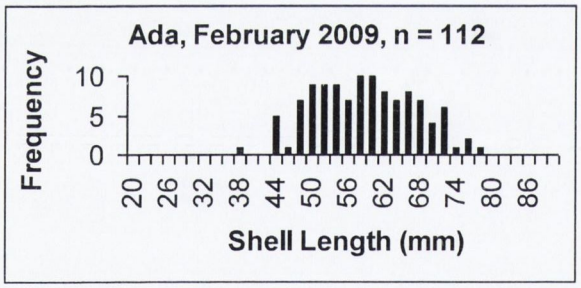
Shell Length (mm)


Ada, February 2009, n = 112
Frequency
10
5
0
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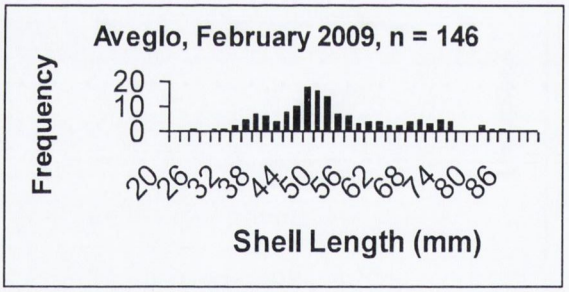
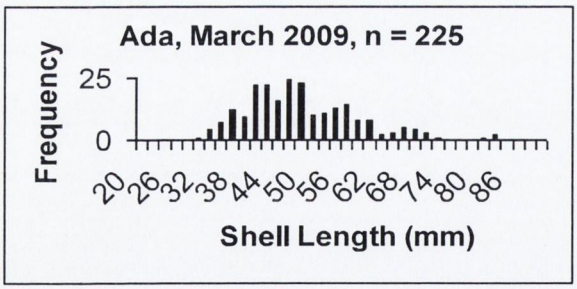
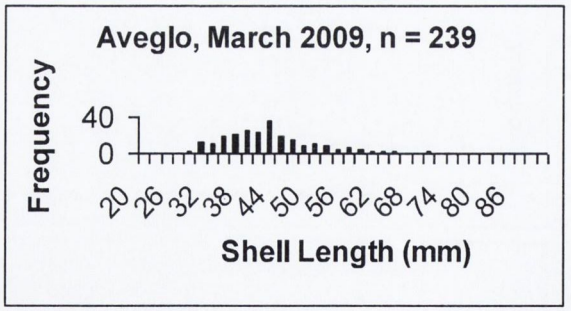
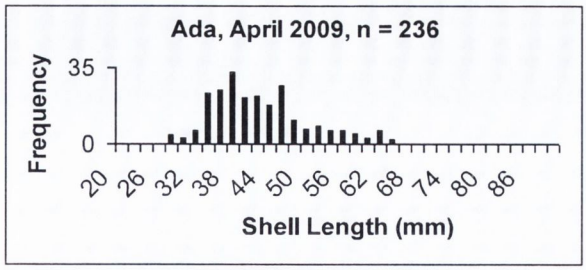
Shell Length (mm)


Aveglo, February 2009, n = 146
Frequency
20
10
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, March 2009, n = 225
Frequency
25
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Aveglo, March 2009, n = 239
Frequency
40
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, April 2009, n = 236
Frequency
35
0
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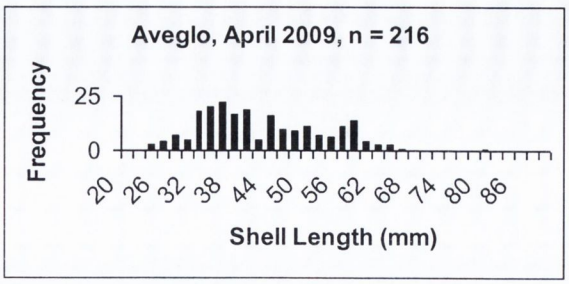
Shell Length (mm)


Aveglo, April 2009, n = 216
Frequency
25
0
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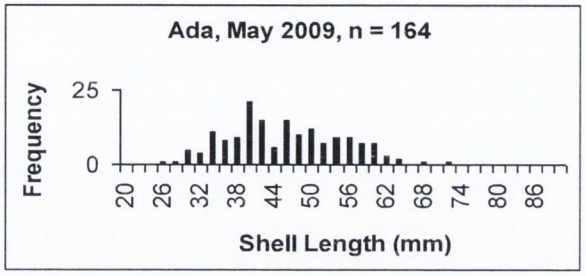
Shell Length (mm)


Ada, May 2009, n = 164
Frequency
25
0
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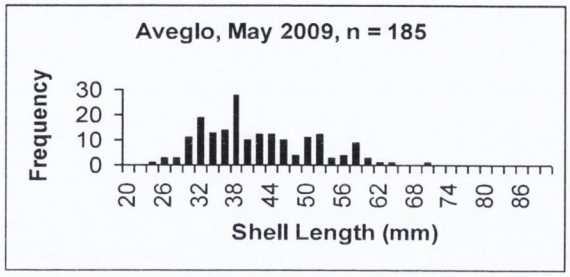
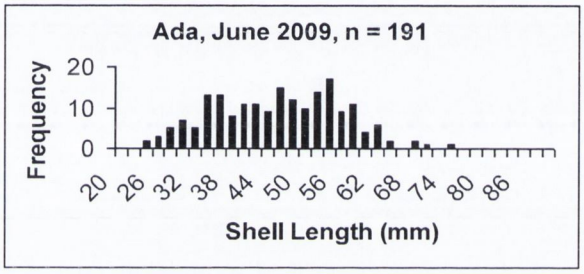
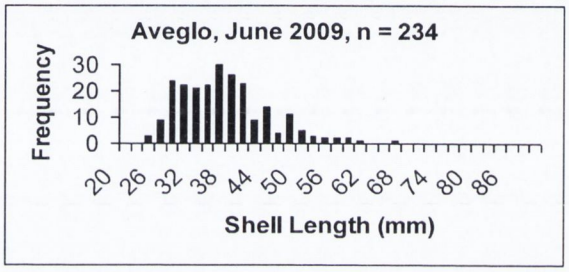
Shell Length (mm)


Aveglo, May 2009, n = 185
Frequency
30
20
10
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, June 2009, n = 191
Frequency
20
10
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)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Frequency
30
20
10
0
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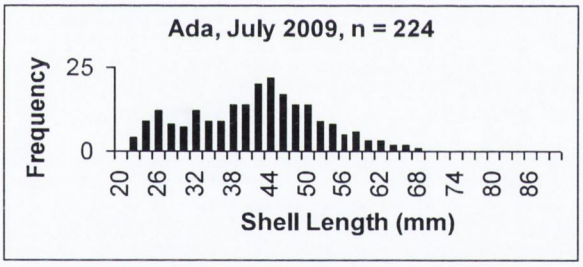
Shell Length (mm)


Ada, July 2009, n = 224
Frequency
25
0
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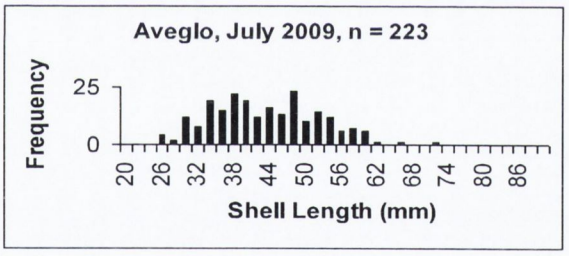
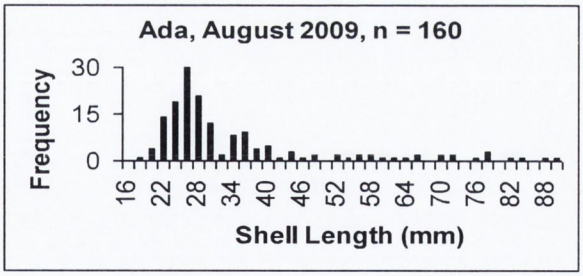
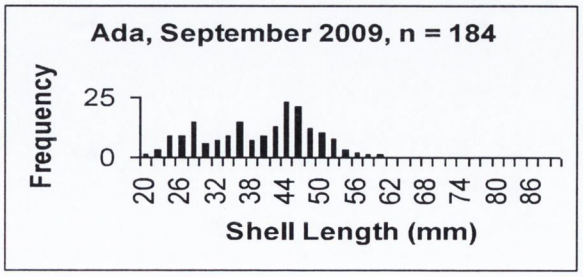
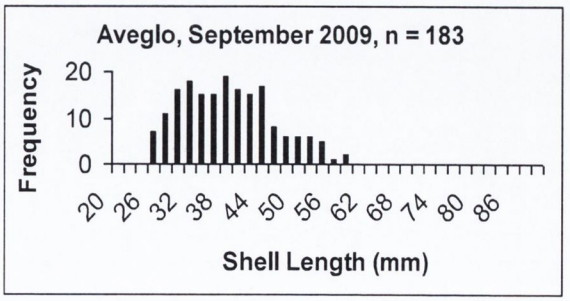
Shell Length (mm)


Aveglo, July 2009, n = 223
Frequency
25
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Ada, August 2009, n = 160
Frequency
30
15
0
16 22 28 34 40 46 52 58 64 70 76 82 88
Shell Length (mm)


Ada, September 2009, n = 184
Frequency
25
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)


Aveglo, September 2009, n = 183
Frequency
20
10
0
20 26 32 38 44 50 56 62 68 74 80 86
Shell Length (mm)

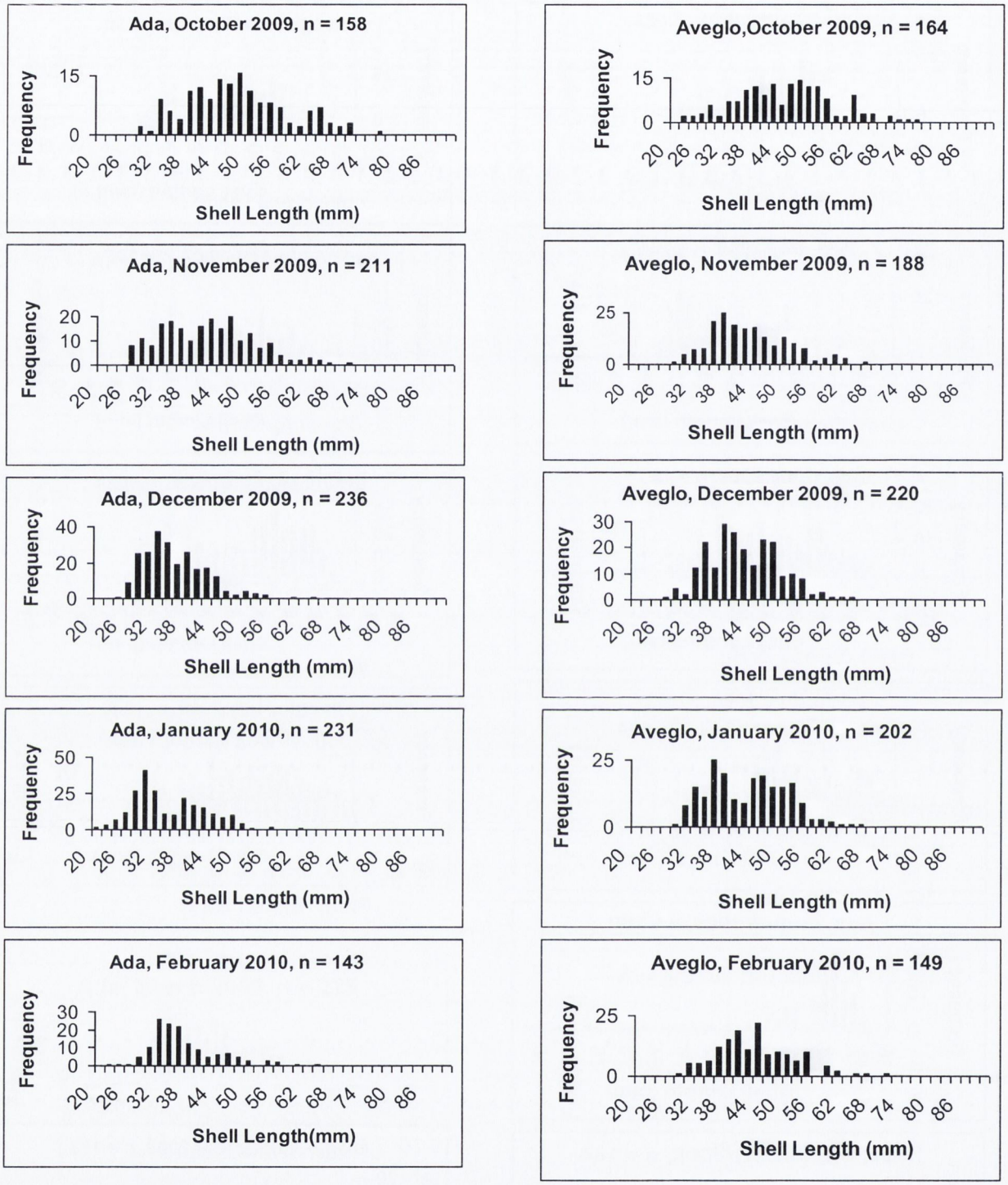


Figure 5.3 Length-frequency distributions of *G. paradoxa* samples obtained from May 2008 to February 2010 from Ada and Aveglo in the Volta Estuary.

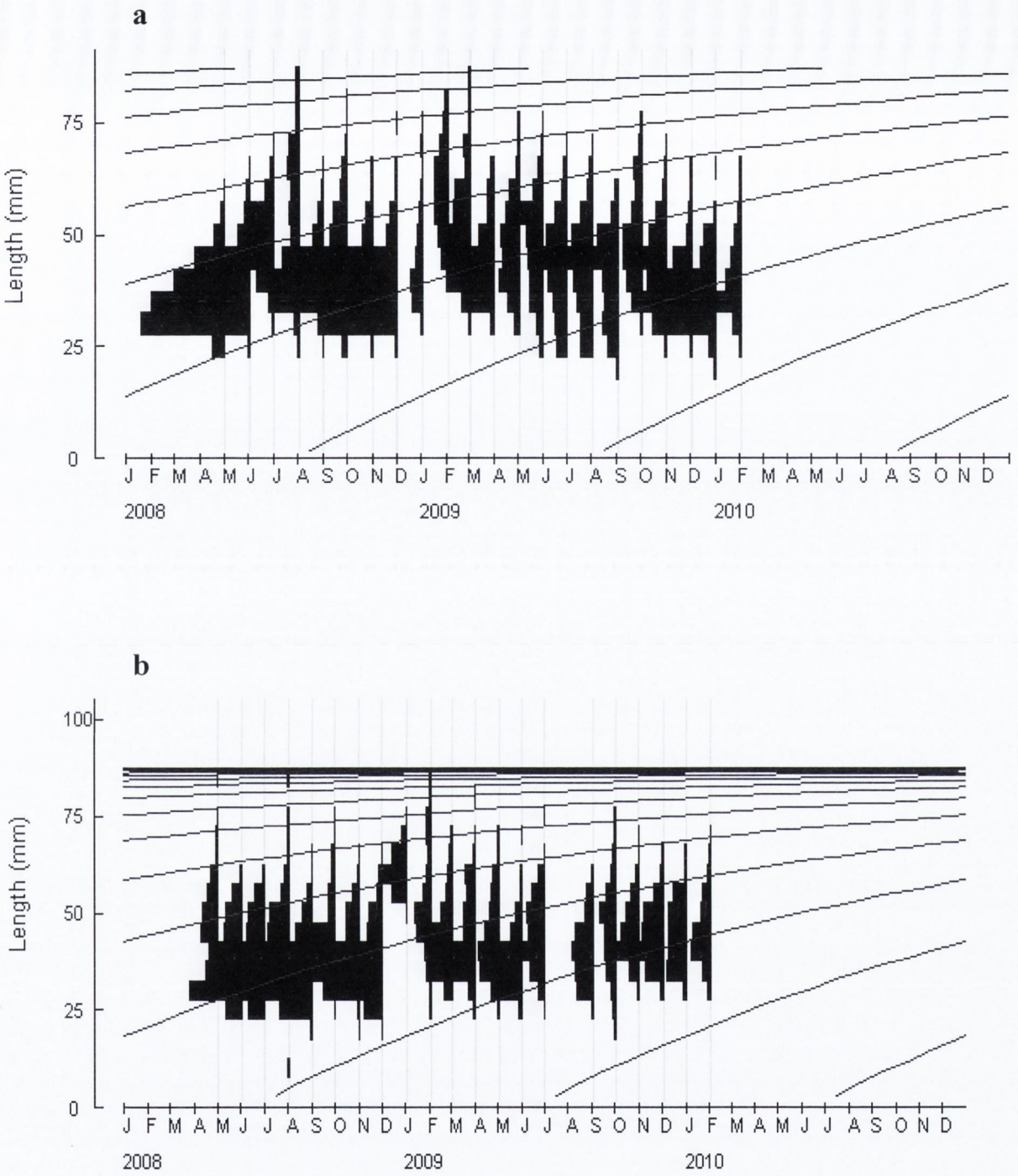


Figure 5.4 Length-frequency distributions of *G. paradoxa* from two sites at the Volta Estuary with growth curves superimposed (a) Ada (b) Aveglo

Figure 5.5 presents the length-frequency distribution of grab samples taken at Ada and Aveglo from March to December 2009. In all, 530 individuals covering a range of sizes between 5 – 60 mm were retrieved from 30 grab samples from Ada and Aveglo. The clam fishers catch is biased towards larger clams as smaller individuals (< 20 mm) are not landed. The smallest specimens (5mm) were found in grab samples between November and March at Ada (Figure 5.5a).

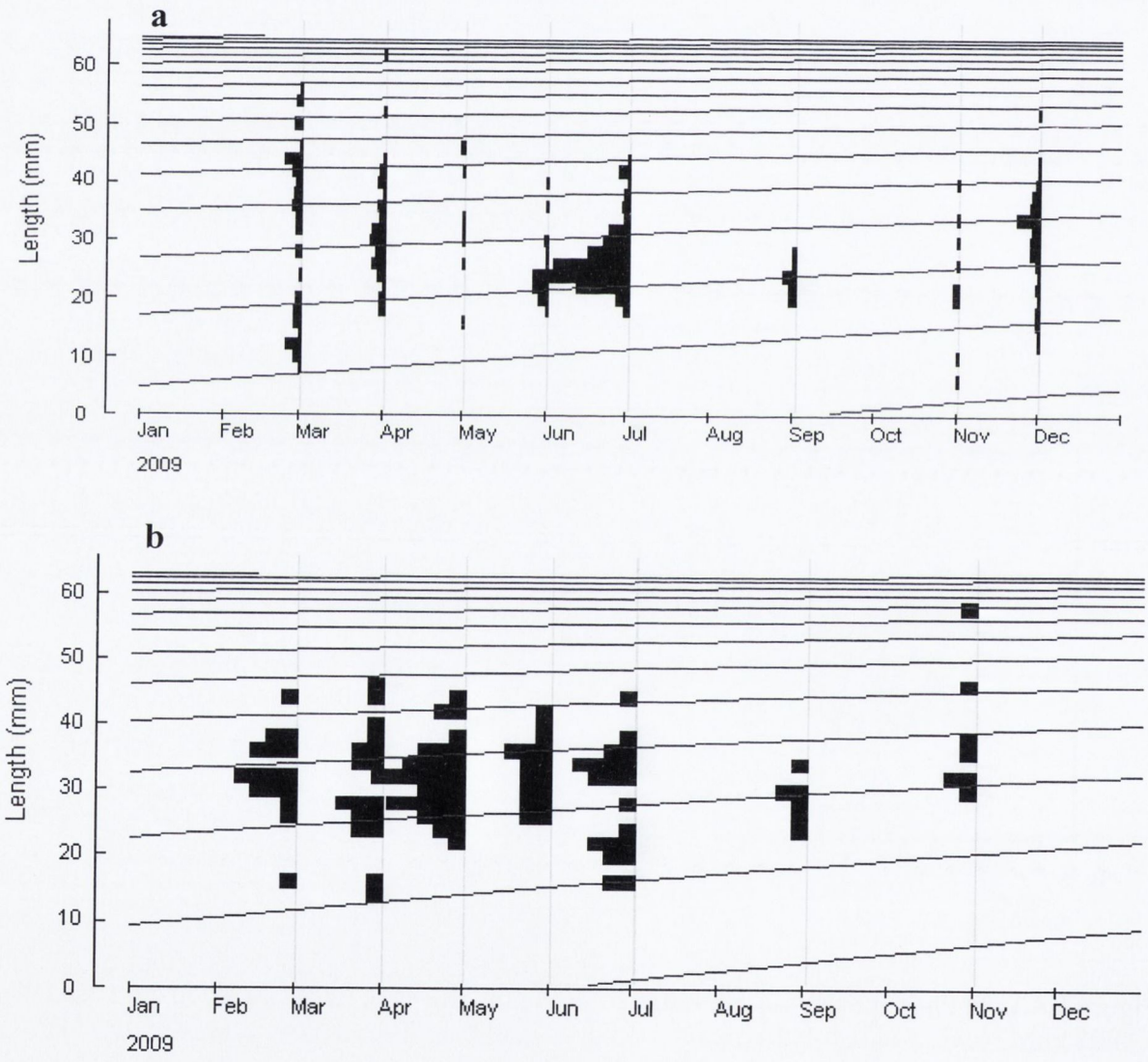


Figure 5.5 Length-frequency distributions of smaller *G. paradoxa* from grab samples taken at (a) Ada and (b) Aveglo at the Volta Estuary with growth curves superimposed.

5.3.3 Tagging-Recapture Experiment

Growth in length was about 1-2 mm a month between January and June for individuals during the tagging experiment. This, however, slowed down to about 1 mm between September and December during the spawning season and the period the animal was spent (Chapter 4). The Gulland and Holt plot generated an initial L_∞ estimate of 69.1 mm which when seeded into the Munro plot gave a K estimate of 0.46year^{-1}. The estimated L_∞ of 69.1 mm by the Munro plot was lower than the largest specimen (102 mm) observed in the estuary, hence the K value (0.46year^{-1}) was overestimated. A more realistic estimate of L_∞ and K was provided by plotting the starting lengths against the end length of individual clams in the tagging-recapture experiment at the Volta Estuary from June 2008 to May 2009 (Figure 5.6). Generally, growth was faster between March and June at a rate of 0.21 year^{-1} and slower between August and January to a rate of 0.16 year^{-1}. From the Ford-Walford plot the estimated L_∞ and K were 104.5 mm and 0.16year^{-1}.

A comparison of the age-at-length data derived from the regression coefficients from the Ford-Walford plot based on surface rings (Figures 5.1) and the tagging-recapture experiment (Figure 5.6) showed that the length of 1-year-old *G. paradoxa* ranges between 12.3 – 15.6 mm

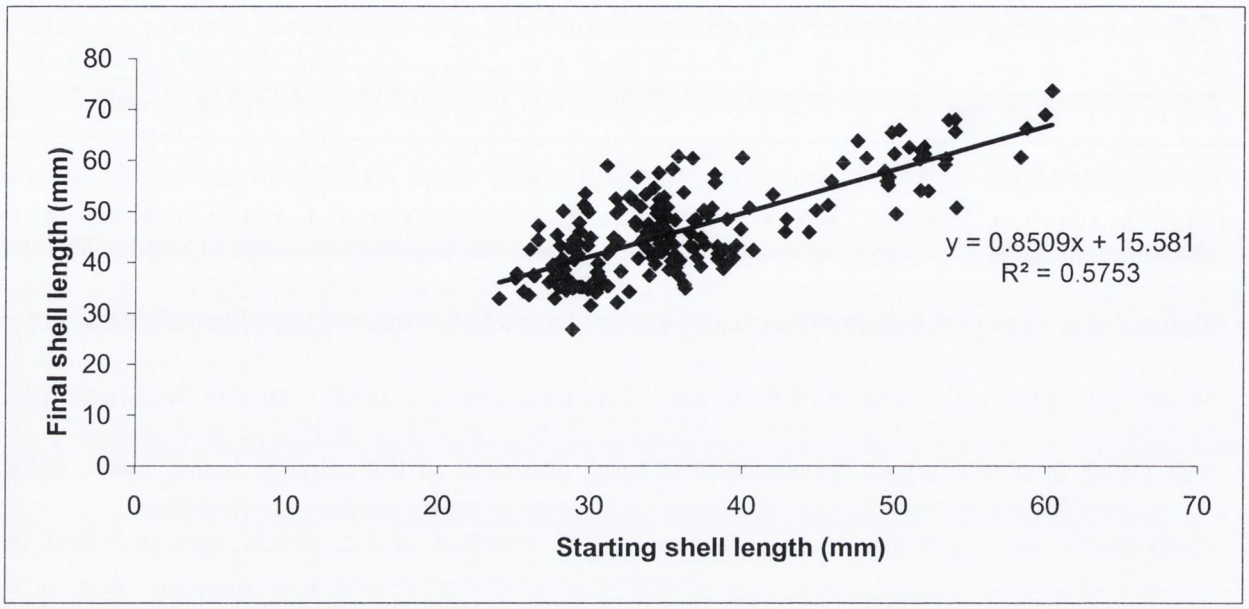


Figure 5.6 Plot of starting length against end length of individual *G. paradoxa* in the tagging experiment in the Volta Estuary from June 2008 to May 2009. Included is the regression equation used to calculate L_∞ and K.

5.3.4 Von Bertalanffy Growth Curves

The age-length estimates obtained from the three methods were fitted to the VBGF in order to describe the growth of *G. paradoxa* as shown below. Data on the corresponding age-length estimates for the three methods is presented in Table 5.2.

1. Surface rings: $L_t = 80.4\,(1\text{-}e^{-0.17t})$
2. Length-frequency distribution: $L_t = 105.7\,(1\text{-}e^{-0.14t})$
3. Tagging recapture: $L_t = 104.5\,(1\text{-}e^{-0.16t})$

The graphical representation of the growth equations are shown in Figure 5.7. The growth rate estimate (K) from the tagging-recapture experiment (K= 0.16) is similar to that from the length-frequency distributions (K= 0.14) and surface rings (K= 0.17). The asymptotic length L_∞ was lower when the VBGF parameters were estimated using data from surface rings

(80.4mm) than from length-frequency distributions (105.7mm) and the tagging-recapture experiment (104.5mm).

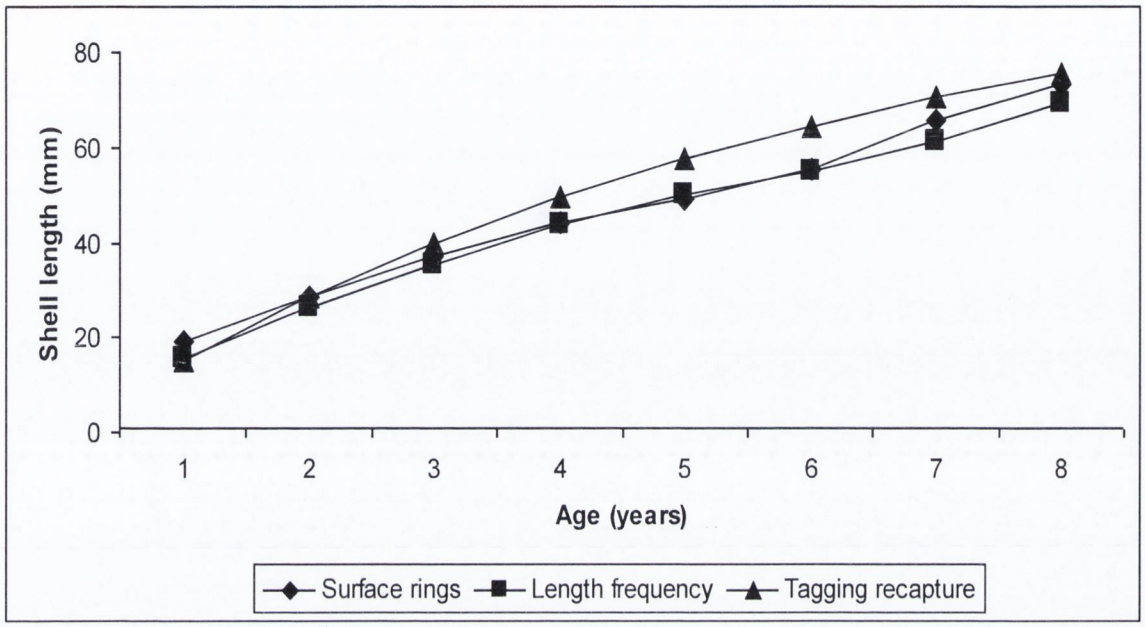


Figure 5.7 von Bertalanffy growth curves fitted using the three methods: surface rings, tagging-recapture and length frequency distributions.

Table 5.2 Mean length-at-age and SD (mm) of *G. paradoxa* obtained from surface rings, length-frequency distributions and tagging-recapture experiment.

		Method	
Age(years)	**Surface rings**	**Length-frequency**	**Tagging-recapture**
1	19.4 ± 4.5	15.8 ± 3.9	15.4
2	28.4 ± 7.3	26.4 ± 4.5	28.6
3	37.1 ± 5.9	35.1 ± 7.6	39.8
4	44.1 ± 7.6	43.6 ± 6.7	49.4
5	49.3 ± 3.9	49.9 ± 7.8	57.5
6	55.5 ± 5.3	55.1 ± 8.1	64.5
7	65.6 ± 6.0	61.3 ± 6.5	70.4
8	73.3 ± 1.8	69.1 ± 7.5	75.5
L_∞	80.4	105.7	104.5

From Table 5.2, the age-at-length data obtained from surface rings was higher ($p < 0.03$) for the 1-year-old clam compared with that from length-frequency and the tagging experiment. Additionally, the L_∞ was lower for surface rings owing to the lack of older individuals. Despite these differences the results generated by the three methods were consistent until year 4 when shell length from the tagging experiment was higher ($p < 0.01$) than the other methods.

5.3.5 Recruitment Pattern

The recruitment pattern of *G. paradoxa* at Ada and Aveglo was continuous throughout the year with a single peak. At Ada (Figure 5.8a) there was single pulse with a peak between July and September. Similarly, recruitment at Aveglo had single pulse with a peak between July and August.

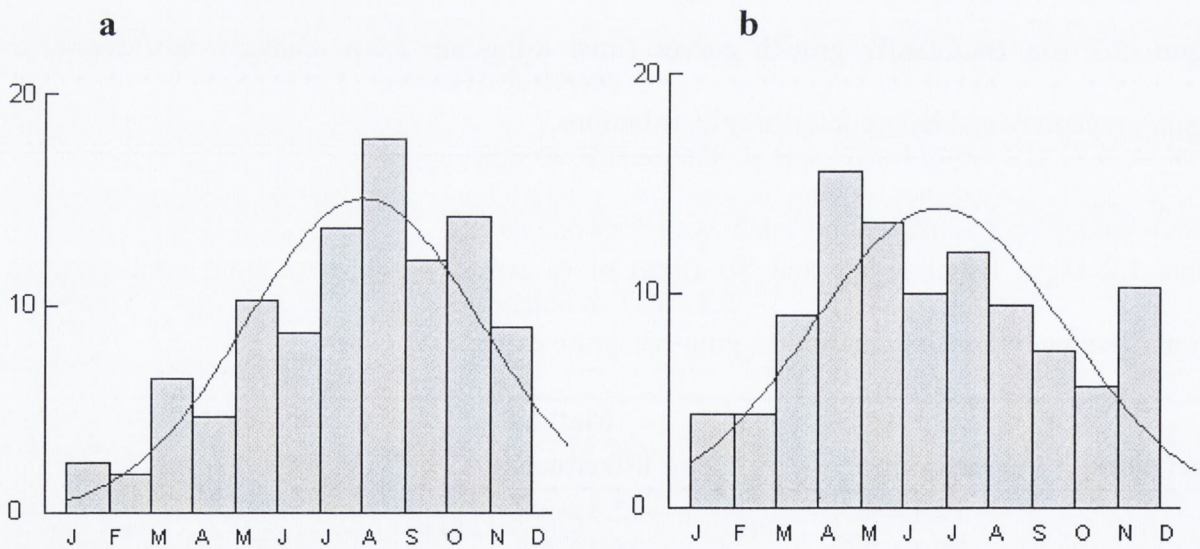


Figure 5.8 Recruitment pattern of *G.* paradoxa obtained by backward projection, along a trajectory defined by the VBGF, of the restructured length-frequency data onto a one-year timescale. The months on the x-axis were located exactly by providing the location parameter (t_0) for Ada (-0.125) and Aveglo (-0.119).

5.3.6 Mortality

The length converted catch curve analysis generated total mortality (Z) value of 0.82 $year^{-1}$ for *G. paradoxa* (Figure 5.9). Natural mortality (M) was 0.35 $year^{-1}$ and fishing mortality was 0.47 $year^{-1}$ for Ada. The exploitation level (E) of *G. paradoxa* was 0.57 (Table 5.3). For Aveglo the parameters were Z = 0.65 $year^{-1}$, M = 0.44 $year^{-1}$, F = 0.21 $year^{-1}$ and E = 0.32. Table 5.3 gives a summary of the population parameters at the two sites while Table 5.4 compares some of the estimated parameters with other studies on *G. paradoxa*.

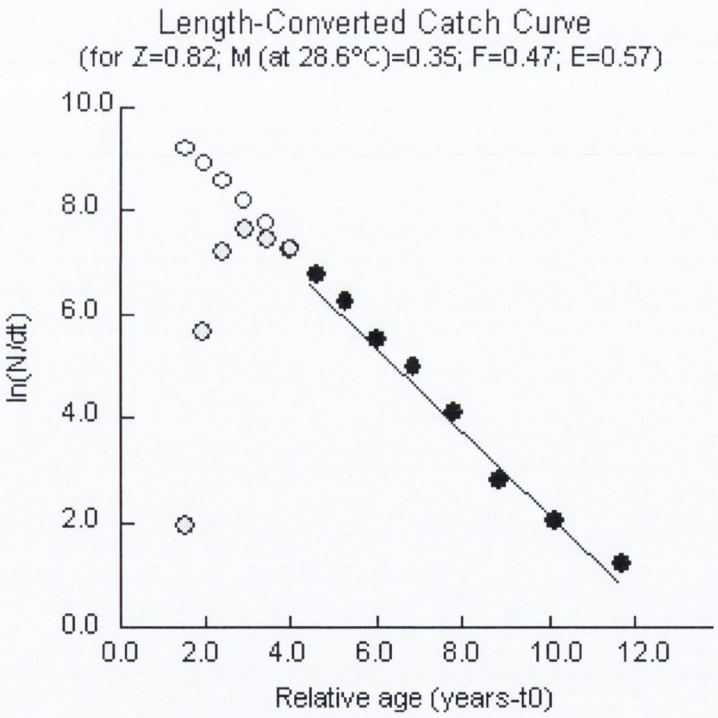


Figure 5.9 Length-converted catch curve of *G. paradoxa* from the Volta Estuary based on pooled monthly length-frequency data (grey dots). Dark data points, used for regression to generate mortality indices; grey data points, excluded from regression. White dots, portion of regression dots excluded from regression equation.

Table 5.3 Summary of population parameters of *G. paradoxa* in the Volta River, Ghana

Population parameters	Ada	Aveglo
Asymptotic length (L_∞) in mm	105.7	84.4
Growth coefficient, K ($year^{-1}$)	0. 14	0.18
Total mortality, Z ($year^{-1}$)	0.82	0.65
Fishing mortality, F ($year^{-1}$)	0.47	0.21
Natural mortality, Z ($year^{-1}$)	0.35	0.44
Exploitation level (E)	0.57	0.32
Length range (mm)	6.8 – 102.0	9.0 – 82.8
Weight range (g)	0.1 – 186.0	0.2 – 182.0
Sample number (N)	4905	5149

Table 5.4 Growth and related parameters of the *G. paradoxa* stocks in West Africa.

Location	L_∞	K	Ø	Source
Volta River (Akosombo, Ghana) 6° 16′ N	145.1*	0.75	4.198	Vakily (1992), Kwei (1965)
Volta River (Tefle, Ghana) 5° 59′ N	107.4*	0.71	3.912	Vakily (1992), Kwei (1965)
Cross River (Nigeria) 5° 11′ N	93.0	0.36	3.493	Moses(1990)
Cross River (Nigeria) 5° 11′ N	111.0	0.30	3.568	King et al., (1992)
Cross River (Nigeria) 5° 11′ N	98.9	0.83	3.909	Etim and Brey (1994)
Nun River (Nigeria)	102.0	0.25	3.415	King (2000)
Volta Estuary, Ada, Ghana	105.7	0.14	3.192	This study
Volta Estuary, Aveglo, Ghana	84.4	0.18	3.108	This study

*These values were originally given as shell height and were converted by Etim and Brey (1994.)

5.3.7 Length-Weight Relationship

The length of individuals ranged from 6.8 to 102.0 mm and total weight from 0.1 to 186.2g. The length-weight relationship for shell-free dry weight and shell length is presented in Table 5.5. Growth in *G. paradoxa* was allometric as indicated by the exponent of the regression equation which was (< 3.0) for a greater part of the study period and did not show any pattern with regards to the spawning season (Chapter 4).

Table 5.5 Regression equations and fits for successive monthly relationships between shell-free dry weight and shell length for Ada and Aveglo, Volta Estuary, from March 2008 to February 2010. Log shell-free dry weight (g) = $\alpha + \beta$. log shell length (mm).

Month	Ada				Aveglo			
	α	β	n	r^2	α	β	n	r^2
Mar 08	-4.37	2.52	60	0.73	-5.03	2.93	60	0.90
Apr 08	-4.30	2.53	60	0.81	-	-	-	-
May 08	-4.40	2.63	60	0.79	-4.96	3.00	60	0.73
Jun 08	-4.38	2.62	60	0.68	-4.46	2.69	60	0.93
Jul 08	-4.85	2.85	60	0.71	-3.92	2.36	60	0.87
Aug 08	-5.22	3.13	60	0.76	-3.12	1.90	60	0.78
Sep 08	-4.14	2.50	60	0.76	-4.05	2.43	60	0.86
Oct 08	-4.09	2.46	60	0.86	-4.36	2.65	60	0.82
Nov 08	-4.39	2.65	60	0.88	-3.78	2.25	60	0.57
Dec 08	-5.24	3.10	60	0.92	-4.83	2.80	60	0.92
Jan 09	-4.27	2.40	60	0.75	-4.02	2.35	60	0.42
Feb 09	-5.67	3.22	60	0.68	-4.24	2.46	60	0.67
Mar 09	-4.74	2.80	60	0.86	-3.50	1.99	60	0.76
Apr 09	-3.98	2.33	60	0.60	-4.28	2.55	60	0.89
May09	-4.61	2.75	60	0.81	-4.98	3.04	60	0.91
Jun 09	-4.63	2.83	60	0.89	-4.16	2.52	60	0.86
Jul 09	-3.80	2.31	60	0.90	-4.54	2.72	60	0.88
Aug 09	-4.36	2.66	60	0.94	-	-	-	-
Sep 09	-2.66	1.63	60	0.46	-3.82	2.32	60	0.74
Oct 09	-4.96	3.06	60	0.93	-3.31	2.06	60	0.71
Nov 09	-4.65	2.87	60	0.93	-4.90	3.00	60	0.89
Dec 09	-4.61	2.78	60	0.91	-4.18	2.44	60	0.69
Jan 10	-4.27	2.43	60	0.86	-4.96	2.77	60	0.85
Feb 10	-4.96	2.88	60	0.86	-4.74	2.66	60	0.83

Figure 5.10 presents the shell-free dry weight cycle of a 40 mm standard animal from Ada and Aveglo. The pattern of the shell-free dry weight cycle was similar for samples from Ada and Aveglo. At Ada, there was a gradual build up of tissue from the start of the study in March 2008 to a peak in September 2008, afterwards there was a steady decline to a minimum value of 300 mg in February 2009. The cycle was repeated in 2009, rising steadily from the minimum value of 300 mg in February to a maximal value of 900 mg in September 2009 and thereafter declining sharply to 400 mg in January 2010. There was a slight drop in tissue weight between June-July in 2008. Samples from Aveglo showed a similar trend, increasing steadily from March 2008 to a maximum value of 800 mg in August 2008 and falling sharply to a minimum value of 450 mg in December 2008. Similarly, tissue weight increased from the minimum value in December 2008 to about 800 mg in May 2009, declined briefly in June-July and then rose to a maximum value of 1000 mg in October 2009 before falling sharply to a minimum level of 300 mg in January 2010.

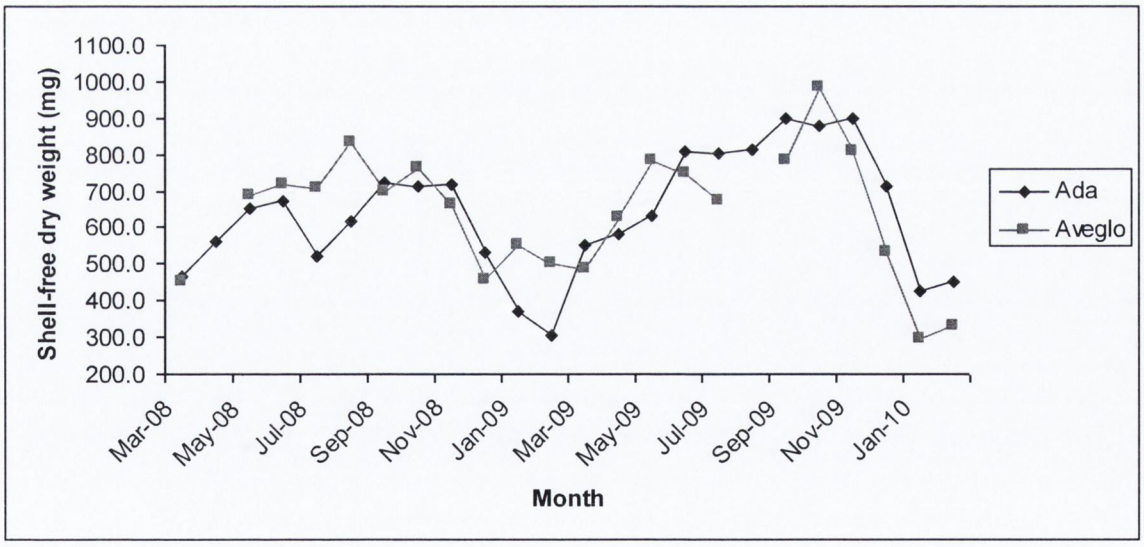


Figure 5.10 Shell-free dry weight cycle of a 40 mm standard *G. paradoxa* from Ada and Aveglo from March 2008 to February 2010.

5.4 Discussion

The population dynamics of bivalves may be studied with the objective of sustainable management and conservation (Urban, 1998; Nassar, 1999). Effective management and conservation of any fishery resource requires considerable knowledge regarding population parameters such as age and growth rate, recruitment pattern, mortalities and exploitation level of the stock (Gaspar et al., 2004; Abohweyere and Falaye, 2008).

5.4.1 Age and Growth Rate

In many bivalve species surface rings are formed annually as a result of seasonal changes in shell deposition (Richardson, 2001). In temperate regions, bivalves show reduced growth in winter owing to declining seawater temperatures and decreased food availability (Peharda et al., 2002). In the tropics where temperature is relatively constant, other factors such as spawning, rainfall, flooding and food may lead to reduced growth and the formation of surface rings. Storms, unusual weather patterns and predator attacks can also result in the formation of surface rings, known as disturbance rings (Campana, 2001; Richardson, 2001). The presence of disturbance rings can lead to an overestimation of an individual's age and underestimation of shell growth rates (Richardson and Walker, 1991). It is therefore important to distinguish between disturbance and annual rings. In this study, a combination of three different age determination methods was employed to eliminate any confusion between disturbance and annual rings.

The results show that all the three methods could be used successfully to estimate the age of *G. paradoxa.* The examination of surface rings requires the drying of the shells (for a period of at least a week at room temperature) for the rings to be clearly distinct for ageing purposes. A larger sample covering various sizes ensured that the mean and standard deviations were

representative of the different age classes in the population. The most recently deposited surface rings in older specimens were difficult to discriminate owing to their closeness as a result of reduced shell growth. The low numbers of older individuals encountered in this study resulted in the difficulty in ageing the 7^{th} and 8^{th} year old clams properly. This method is, however, relatively simple and independent of shell coloration or shape. The establishment of representative size-classes as a confirmation in allotting individuals to their respective age classes was instrumental in minimising error owing to the misidentification of disturbance rings.

A comparison of the age-length estimates obtained from the three methods showed that the estimated ages were similar for the three methods (Table 5.2 and Figure 5.7). This indicates that surface ring counting is an appropriate and reasonably accurate method for simple and rapid age estimation of *G. paradoxa*. This is in agreement with the finding of Moura et al. (2009) who reported that age estimates from the counting of surface rings was appropriate for *Callista chione* up to 10 years old. For older specimens, age was more accurately estimated from the analysis of growth lines in the cross sections of shells.

G. paradoxa is a tropical bivalve that lives in an environment with a relatively constant temperature. Spawning in *G. paradoxa,* as reported in this study (Chapter 4), is a single annual event occurring over an extended period between July and October, which coincides with the rainy/flooding season in southern Ghana. The spawning activity combined with a higher suspended particulate matter in the flood water, low food availability and reduced growth rate might cause the deposition of annual rings at this time. This observation is in agreement with the findings of Schone (2003) who observed that *Chione cortezi*, *C. fluctifraga* and *C. californiensis* at the Colorado River mouth grew more slowly when large amounts of freshwater reached the Gulf of California. The deposition of annual rings as a result of spawning activity has been observed in other studies (Jones et al., 1990; Gaspar et al., 1994).

The age-length estimates obtained in this study are in sharp contrast to the findings of King (2000) who estimated the ages of a population of *G. paradoxa* from the Nun River, Nigeria by counting surface rings. The ages estimated from his study had year 1 to 7 corresponding to mean shell lengths of 53, 64, 72, 79, 83, 89 and 91 mm, respectively. The samples for King's study were obtained from fishermen's catches which is biased towards larger clams and excluded individuals less than 40 mm in length. The age estimates were, therefore, based on the smallest length class in the commercial catch and not on the entire population. Hence, his starting length corresponds to specimen that were 4-5 years old as found in this study (Table 5.2). By assigning the starting length of 53 mm to a 5-year old individual, as shown in Table 5.2, the age-length estimates of King (2000) map directly onto that derived in this study. In order to avoid this bias, samples from fishermen catch were augmented with grab samples which captured the smallest individuals that are not normally harvested by fishermen. The age-shell length estimates in this study are, therefore, more robust compared with previous studies that were based solely on samples from commercial catches (Moses, 1990; Etim and Brey, 1994; King, 2000).

The estimated growth curves obtained from surface rings, length-frequency distributions and tagging-recapture experiment revealed that the methods provided similar estimates of growth rates until the fourth year ($\approx$ 50mm). Afterwards, the age of *G. paradoxa* was more accurately determined based on the tagging-recapture experiment than the other methods.

Asymptotic length (L_∞) is a major parameter used in evaluating the status of a population. The L_∞ value obtained for *G. paradoxa* in the Volta Estuary (105.7 mm) is close to the 107.4 mm found by Vakily (1992) who re-analysed data collected by Kwei (1965) at Tefle on the Volta River just after the construction of the Akosombo Dam (Table 5.4). Similarly, it is close to the 102 mm reported by King (2000) on the stock of *G. paradoxa* in the Nun River, Nigeria. It is, however, lower than the 145.1 mm obtained by Vakily (1992) from the re-analysed data

collected by Kwei (1965) at an upstream station (Akosombo) on the Volta River and the 111.0 mm obtained by King et al. (1992) on the Cross River stock of *G. paradoxa*. The L_{∞} estimate in this study is higher than that of Moses (1990) and Etim and Brey (1994) for *G. paradoxa* stocks in the Cross River in Nigeria (Table 5.4). The growth coefficient (K) estimate of 0.14 – 0.18 $year^{-1}$ in this study is the lowest recorded in studies on *G. paradoxa* (Table 5.4).

The growth performance index (Ø) allows inter and intra specific comparison of growth performance in bivalve species of different stocks (Abohweyere and Falaye, 2008). The Ø values of 3.192 and 3.108 obtained for *G. paradoxa* at Ada and Aveglo, respectively, are the lowest recorded for any population of *G. paradoxa*. They are also lower than the 4.198 and 3.912 values obtained by Vakily (1992) who re-analysed the data of Kwei (1965) on the stock of *G. paradoxa* from Akosombo and Tefle on the Volta River just after the construction of the Akosombo Dam. They are also lower than that reported from studies conducted (Moses, 1990; King et al., 1992; Etim and Brey 1994; King 2000) on the stock of *G. paradoxa* in the Nun and Cross Rivers of Nigeria (Table 5.4).

The low growth rate and growth performance recorded in this study could be attributed to the negative effects of habitat modification as a result of damming the Volta River. Damming has affected the nutrient dynamics and flow regime of the Volta River, resulting in the formation of a sand bar at the estuary and the growth of aquatic weeds on the clam beds (Attipoe and Amoah, 1989). The data of Kwei (1965) and (Vakily, 1992) were collected just after the completion of the dam at Akosombo with little or no effects of its impact on the physical and chemical characteristics of the river and thus on the clams' habitat. According to King (2000), the reported maximum sizes and ages of *G. paradoxa* are highly variable attributes within its geographic distribution. The different populations of *G. paradoxa* therefore display disparities in growth and longevity owing to differences in environmental factors such as substrate type, food supply, population density and physico-chemical factors of the habitat (King, 2000).

The slight differences in L_{∞}, K and Ø between Ada and Aveglo could be attributed to habitat characteristics. As described in Section 2.2, Ada is shallow with depths between 0.60 - 2.0 m, there are patches with dense aquatic weeds and the sediment is mainly fine sand with patches of mud. Aveglo, on the other hand, is deeper with depths between 4.0 – 6.0 m and the sediment is predominantly coarse sand to gravel. The shallowness of Ada allows sunlight to penetrate to the bottom of the water column thus increasing the benthic primary productivity of the area compared with Aveglo which is deeper. These slight habitat differences could explain the slightly better growth performance observed at Ada. Despite these minor differences the lifespan of *G. paradoxa* in the Volta River (10 -17 years) is within that of its marine venerid relatives.

5.4.2 Recruitment

Recruitment has been described as a year round phenomenon for tropical species because of the relatively stable and elevated water temperatures allowing year round breeding (Qasim, 1973; Weber, 1976). The recruitment pattern suggests that *G. paradoxa* exhibits year-round recruitment with a single pulse over an extended period (October – March) in the Volta River. Although, the movements of cohorts were observed in the monthly length-frequency distributions of samples from the fishermen's catch (Figure 5.3), it only gives information about recruitment into the fishery as the clams were almost 2-years old. Clam fishers do not harvest clams less than 20 mm. Therefore the recruitment pattern was best determined from the grab samples which captured the smaller individuals in the population. The smallest clams (5mm) were detected in the grab samples between November and March. Aligning this observation with the growth curves obtained from the length-frequency distributions of the

grab samples (Figure 5.5) suggests that recruitment in *G. paradoxa* occurs between October and March.

The other studies on *G. paradoxa* did not report on its recruitment pattern; however, studies elsewhere on tropical bivalves are in agreement with this finding. Al-Barwani et al. (2007) reported a continuous year-round recruitment pattern with a major peak between July-August for *Perna viridis* in the coastal waters of Malacca, Malaysia. *Modiolus metcalfei* from Panguil Bay, Southern Philippines, has a unimodal recruitment pattern with the peak of recruitment between May – July (Tumanda Jr. et al., 1997). Similarly, Mancera and Mendo (1996) reported that the recruitment pattern of *Crassostrea rhizophorae* from the Cienaga Grande de Santa Marta, Colombia, was continuous with a single peak in October –November.

5.4.3 Mortality Rates

Mortality rates at the two sites were slightly different with Ada having a higher total mortality ($0.82 year^{-1}$) compared with Aveglo ($0.65\ year^{-1}$) (Table 5.3). The difference could be attributed to the higher fishing mortality at Ada ($0.47\ year^{-1}$) compared with $0.21\ year^{-1}$ at Aveglo. Clams at Ada are, therefore, highly exploited (0.57) compared with Aveglo (0.32). This result is supported by what actually happens in the fishery. Ada is shallow (0.60 - 2.0 m) and therefore attracts a high number (three times) of fishers both manual and Hookah divers than Aveglo. The mortality values obtained in this study are in agreement with the findings of Moses (1990), who studied the stock of *G. paradoxa* in the Cross River, Nigeria. The estimated mortality coefficients of his study were: total mortality $0.82\ year^{-1}$; fishing mortality $0.50\ year^{-1}$; and natural mortality $0.32\ year^{-1}$. The exploitation level was 0.61 and Moses (1990) concluded that the stock was overfished and required immediate imposition of landing size restriction (< 60 mm) and the culture of young clams to prevent the collapse of the

fishery. King (2000) obtained similar estimates for the stock of *G. paradoxa* in the Nun River, Nigeria. The estimated coefficients were 0.80, 0.50 and 0.30 $year^{-1}$ for total mortality, fishing mortality and natural mortality, respectively. The conclusion was that the stock was overfished owing to the high exploitation level of 0.62. Etim and Brey (1994) however, obtained higher mortality values for the stock of *G. paradoxa* in the Cross River compared with Moses (1990). The estimated total fishing and natural mortality coefficients were 2.03, 1.10 and 0.93 $year^{-1}$, respectively. The exploitation level was 0.45 which is close to the optimum exploitation level of 0.50. According to Gulland (1965), the yield is optimised when F = M; thus when E is equal to 0.5. The stock of *G. paradoxa* in the Volta River is overfished as the stocks in the Nigerian rivers.

5.4.4 Length-Weight Relationships

Periodic length-weight data (Rueda and Urban, 1998) and linear regression analysis on log-transformed data for a standard animal has been used to study the reproductive cycle of bivalves. An abrupt decrease in weight between successive months may indicate a spawning event while an increase over a longer period could be interpreted as the developing phase before the spawning season. The shell-free dry weight cycle of a 40 mm standard *G. paradoxa* showed a trend of building gonad tissue prior to the start of spawning activity which occurs between July and October in the Volta Estuary (Chapter 4). The slight drop in tissue weight during June-July indicates the start of spawning in the clam with August - September being the peak of spawning in *G. paradoxa*.

Growth in *G. paradoxa* is allometric as the exponent of the regression equation was < 3 ($\beta \neq 3$) for almost the entire study period. This is in agreement with the vast majority of instances where β, in the length-weight relationships has been found to be not equal to 3 (Gaspar et al.,

2002). The large increases in gonad weight (50%) prior to the spawning period could be the reason for allometric growth in *G. paradoxa.* One would therefore have expected a lower β in the post-spawning period, that is, between November and December (Chapter 4) but this was not the case. Although, the β values were significant, varying between 1.63 and 3.10 at Ada and 1.90 and 3.04 at Aveglo, it did not show a clear-cut pattern with regards to the reproductive cycle (Table 5.5).

In conclusion, the results of this study show that age estimates from surface ring counting is appropriate and reasonably accurate for simple and rapid age estimation in *G. paradoxa.* Spawning in the population occurs between July and October with recruitment occurring between October and March. The growth rate and performance appears to be declining as a result of habitat modification owing to the negative effects of damming the river. The Volta River stock of *G. paradoxa* is overfished and requires immediate action to conserve the species. This can be achieved by implementing a minimum landing size restriction and intensifying the culture of smaller clams.

6.0 BIOMASS, PRODUCTION AND FISHERY OF *G. PARADOXA*

6.1 Introduction

Production and biomass studies are essential in the management of a fishery as it allows evaluation of the role of a species in a community as well as comparisons among different ecosystems (Hibbert, 1976). For the sustainable management of an artisanal fishery, that is based on a species with a limited distribution like *G. paradoxa*, it is necessary to ascertain the contributions made by the various cohorts to the overall population structure in order to develop a harvesting scheme that targets the less productive ones (Moses, 1990; King, 2000). Biomass is the mass of an individual or a collection of animals (van der Meer et al., 2005). In the aquatic ecosystem, biomass generation starts with primary producers that capture solar energy and transform it into organic material for their own use with the subsequent storage of the remainder in their tissues as biomass that could be harvested or transferred to other trophic levels.

Production on the other hand measures the rate at which biomass is formed or accumulated in organisms. This tends to decline with age as older organisms grow at a slower rate and a greater percentage of their energy is channelled into tissue maintenance and repair. Also, in several bivalve species, there is a shift in the allocation of available energy from somatic and shell growth to gamete production as the organism grows older (Bayne and Newell, 1983). Production has previously been viewed in the context of energy flow through trophic levels, thus, early energy flow studies used energetic measures (Kilocalories or Kilojoules) (Benke, 2010). Most estimates of production presently, whether for primary producers (autotrophs) or secondary producers (heterotrophs), are expressed as mass (grams carbon or grams dry mass).

While population biomass units are often presented as g m^{-2}, the typical unit for secondary production incorporates time (e.g., grams m^{-2} $year^{-1}$, grams m^{-2} $week^{-1}$).

Crisp (1984) outlined two components (ΔB = change in biomass; M = mortality) for measuring the total secondary production of a cohort of animals. The first is the increment-summation method which adds all the growth increments of all the members of the cohort as they occur during the period under consideration. The second is the removal-summation method which considers both the matter that leaves the cohort by mortality and the difference between the total biomass of the cohort at the start and end of the observation period (van der Meer et al., 2005).

Production to biomass (P: B) ratios are important in fishery management as it is an indicator of the quantity of material available for harvest and the size or groups that should be targeted. Since biomass and production are dependent on the growth rate of the constituent species, factors such as the density and the geographical latitude in which a species is located also influences the P: B ratio (MacDonald and Thompson, 1986). Changes in P: B ratios appear to be related to the number of year classes in the population under observation as younger year classes have higher P: B ratios than older ones (Hibbert, 1976; Robertson, 1979).

There are models based on empirical relationships for estimating the P: B ratios of species. Schwinghammer et al. (1986) proposed an empirical relationship based on the mean annual body weight (M); P: B = 0.525 $*M^{-0.304}$. Similarly, Banse and Mosher (1980) suggested an empirical relationship based on the body weight at first sexual maturity (M_s) after the equation; P: B = $0.65*M_s^{-0.37}$. Most of these empirical relationships either over- or under-estimate P: B ratios since local environmental variations that affect growth are not reflected. Thus, their adoption and application requires a cautious approach.

Calow (1981) proposed two indices for quantifying reproductive investment. The first is the Reproduction/Assimilation Index, that is the fraction of the assimilated input allocated to

reproduction and second, the model, C = 1- (A – G/R), where C = cost of reproduction, A = assimilated energy, G = reproductive output and R= respiratory energy expenditure. The outputs of both models indicate whether reproduction has imposed a cost on the organism at the expense of somatic metabolic demands. When there is no cost associated with reproduction C = 0 i.e. all the parent's metabolic demands were met. The condition C > 0 is called reproductive recklessness since the parent is put at risk by this strategy whereas the condition C < 0 is referred to as reproductive restraint since the parent does not allow reproduction to impinge on its own metabolic requirements (Calow, 1978).

In the management of a fishery that is open access, it is important to study the production of the cohorts that make up the population in order to design a harvesting strategy that ensures that juveniles have generated the optimum biomass before being harvested whilst preventing the dominance of older less-productive individuals. The *G. paradoxa* fishery is overfished (Chapter 5) and requires immediate conservation measures such as the imposition of a minimum landing size restriction in order to prevent the extinction of the species. In order to arrive at the optimum size, there is the need to measure the biomass and production of the cohorts in the population. This study therefore quantifies the biomass and production of *G. paradoxa* in the Volta River in order to provide the necessary biological information for the sustainable management of the fishery.

6.2 Materials and Methods

6.2.1 Production (P)

The production of *G. paradoxa* was calculated based on monthly grab ($0.1m^2$) samples in addition to samples from the artisanal fishery taken from Ada and Aveglo at the Volta River Estuary. The samples covered the range of sizes in the population as described in Section 2.3.1.2. Annual production from May 2008 to May 2009 was determined after Crisp (1984) and Wilson (1996) as shown:

$$P = \Delta B + M \qquad \text{Equation 6.1}$$

Where

P = Production;

ΔB = change in biomass (difference between the maximum pre-spawning and minimum post spawning weight); and

M = Mortality.

The methods for the determination of biomass (B) and change in biomass (ΔB) have been described in Section 2.5.

6.2.2 Mortality

Mortality in *G. paradoxa* was determined from the monthly samples by the decrease in percentage of individuals from the preceding cohort over a year (May 2008 to May 2009). Percentage mortality from one cohort to the next was calculated based on the geometric mean of the number of individuals in a cohort from the monthly samples over the annual period. The mean weight (AFDW) of each cohort over the annual cycle was calculated and multiplied by the mean density of the cohort at each site (Ada and Aveglo). Mortality was calculated by:

$$\text{Mortality (M)} = \sum \%\ \text{mortality}_{(C1\text{-}C2)} * \text{mean weight}_{(C1\text{-}C2)} * \text{density} \qquad \text{Equation 6.2}$$

Where:

$_{C1\text{-}C2}$ represent e.g. the mortality and mean weight of individuals from cohort 1 to cohort 2; and density = number of clams m^{-2} at Ada and Aveglo.

6.2.3 Condition of *G. paradoxa* Cohorts

The condition of *G. paradoxa* cohorts in the population was monitored by the change in their ash-free dry weight (AFDW) during the sampling period from March 2008 to February 2010. The weight exponents (β) obtained from the established AFDW – shell length (SL) relationships for each sampling date were used to calculate the AFDW for the cohorts using the mean length of each cohort.

6.2.4 *G. paradoxa* Fishery

During the field work, a survey was conducted to enumerate the fishing methods, the number of fishers engaged directly in the fishery at the estuary, catch per fisher, clam meat processing methods and the use to which the shells were put as well as management or conservation practices. The data and information collected is presented in Section 6.4.

6.3 Results

6.3.1 Biomass

In order to determine the biomass of the different cohorts in the population, the relationship between AFDW (mg) and shell length (mm) was established separately for each monthly sample from March 2008 to February 2010 (Table 6.1).

Table 6.1 Regression of $\log_{10}$ AFDW (mg) on $\log_{10}$ shell length (mm) of *G. paradoxa* from March 2008 to February 2010. (Each monthly sample consists of 60 animals).

	Ada			Aveglo		
Month	**α**	**β**	**r^2**	**α**	**β**	**r^2**
Mar 08	-4.72	2.72	0.73	-5.83	3.37	0.90
Apr 08	-4.61	2.70	0.81	-	-	-
May 08	-4.67	2.78	0.79	-5.39	3.22	0.74
Jun 08	-4.68	2.80	0.67	-5.04	3.03	0.93
Jul 08	-5.14	3.01	0.71	-5.12	3.04	0.88
Aug 08	-5.42	3.24	0.75	-3.39	2.04	0.78
Sep 08	-4.54	2.72	0.76	-4.81	2.87	0.85
Oct 08	-4.52	2.70	0.85	-4.93	2.97	0.80
Nov 08	-5.42	3.25	0.87	-4.50	2.66	0.56
Dec 08	-6.78	4.00	0.91	-7.02	4.12	0.90
Jan 09	-5.22	2.92	0.76	-4.25	2.47	0.42
Feb 09	-6.24	3.52	0.66	-4.72	2.72	0.68
Mar 09	-5.31	3.11	0.85	-4.21	2.37	0.76
Apr 09	-4.32	2.52	0.56	-4.80	2.84	0.89
May 09	-5.19	3.08	0.80	-5.74	3.48	0.89
Jun 09	-5.02	3.06	0.88	-4.65	2.80	0.86
Jul 09	-4.42	2.66	0.90	-5.10	3.05	0.89
Aug 09	-4.89	2.96	0.94	-	-	-
Sep 09	-2.97	1.80	0.47	-4.39	2.65	0.72
Oct 09	-5.33	3.27	0.93	-3.49	2.16	0.71
Nov 09	-4.99	3.07	0.93	-5.35	3.25	0.88
Dec 09	-5.19	3.12	0.90	-4.92	2.85	0.69
Jan 10	-5.58	3.20	0.87	-7.05	3.97	0.82
Feb 10	-6.39	3.72	0.85	-6.14	3.44	0.82

The mean shell lengths corresponding to the age-groups identified in the population (Chapter 5) were fitted to the regression coefficients of each monthly sample (Table 6.1) and the biomass cycle of the age-groups generated for the two year sampling period. The weight exponent β did not follow a clear trend and varied significantly ($p < 0.05$) during the study period between 1.8 and 4.0 at Ada and 2.16 and 4.12 at Aveglo. Figures 6.1 to 6.3 show the variation in biomass for individual *G. paradoxa* from 1 to 3-years old. The variation in biomass for the 1-year old clam did not show marked seasonal patterns (Figure 6.1). It started at 32.4 and 14.8 mg AFDW for Ada and Aveglo, respectively, in March 2008 and increased steadily to 49.0 and 39.4 in September 2008 for the two sites. The biomass values declined steadily until low values of 9.3 and 7.5 mg AFDW were recorded in December 2008 for Ada and Aveglo, respectively. The values then rose slowly over the following months to peaks of 54.4 and 47.5 mg AFDW in July and June 2009 for Ada and Aveglo before declining steadily to the minimum values of 10.7 and 4.6 mg AFDW in February and January 2010 for Ada and Aveglo, respectively.

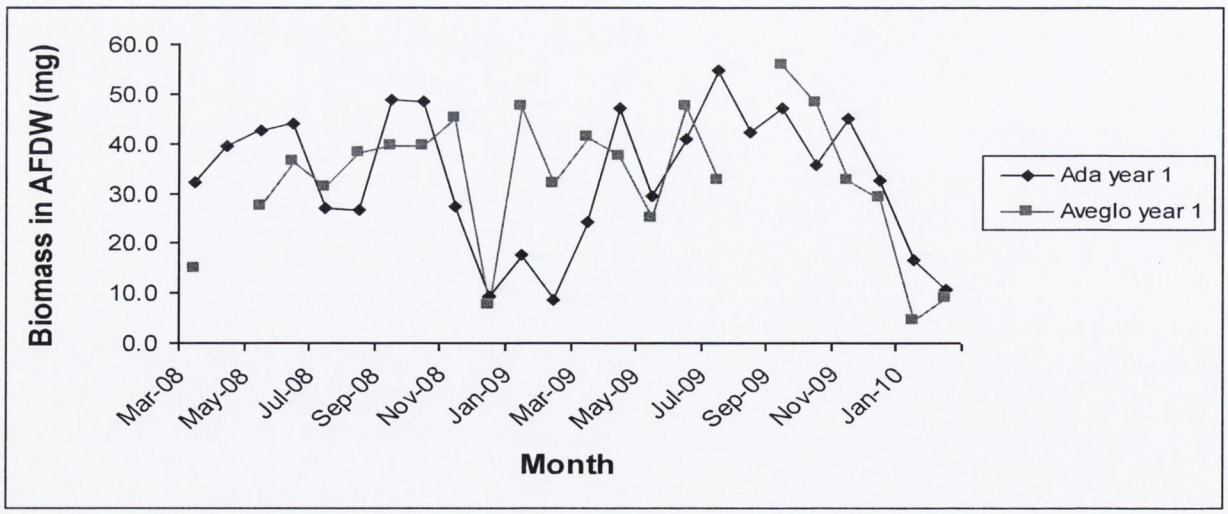


Figure 6.1 Variation in biomass (mg AFDW) for the 1-year old *G. paradoxa* at Ada and Aveglo at the Volta Estuary from March 2008 to February 2010.

Figure 6.2 shows that seasonal patterns were beginning to emerge in the biomass cycle of the 2-year old individual. Maximum biomass values of 249.9 and 237.0 mg AFDW were recorded at Ada and Aveglo in June 2008 while minimum values of 111.0 and 95.9 mg AFDW were recorded in December 2008 for Ada and Aveglo, respectively. In 2009-10, maximum biomass values of 284.4 and 269.0 mg AFDW were recorded in July and June for Ada and Avelo respectively, while minimum values of 106.6 and 53.1 mg were recorded in February and January 2010 for Ada and Avelgo, respectively.

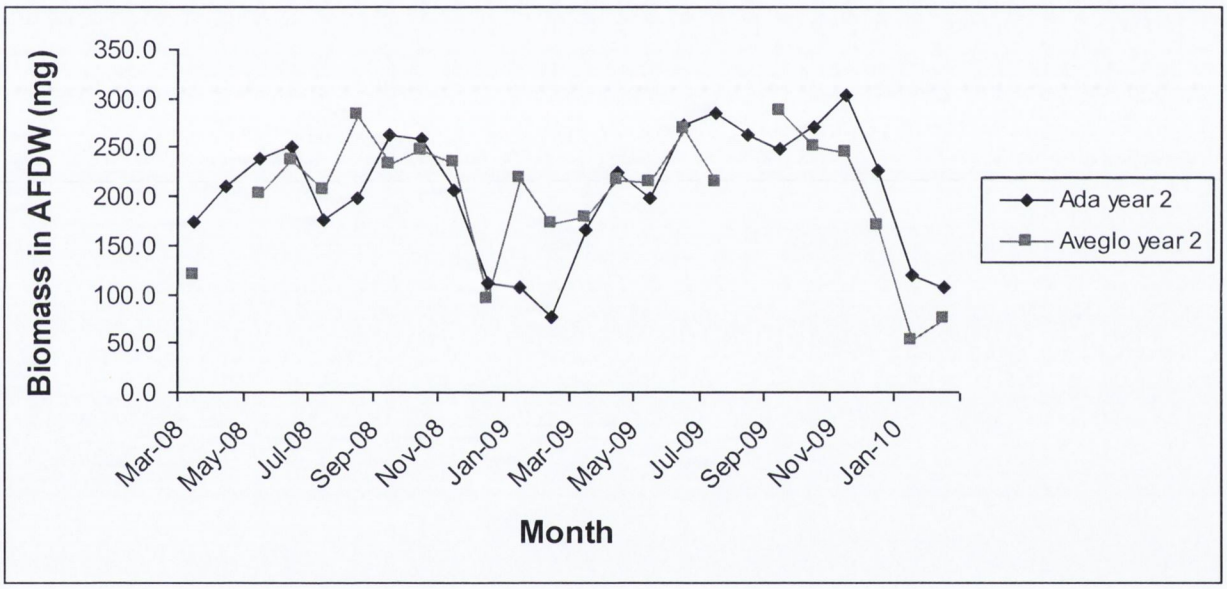


Figure 6.2 Variation in biomass (mg AFDW) for the 2-year old *G. paradoxa* at Ada and Aveglo at the Volta Estuary from March 2008 to February 2010.

Pronounced seasonal patterns were exhibited by the 3-year old individual (Figure 6.3) with maximum biomass values of 630.5 and 750.4 mg AFDW being recorded in June and August 2008 for Ada and Aveglo while minimum values of 264.4 and 373.8 mg AFDW were measured in February 2009 and December 2008 for Ada and Aveglo, respectively. For the 2009-10 season, maximum biomass values of 751.0 and 678.7 mg AFDW were measured in June for Ada and Aveglo while minimum values of 346.4 and 196.7 mg AFDW were measured in January 2010 for the two sites, respectively.

Biomass increased with age and showed strong seasonality for the 4-9 year old clams in the population with maximum biomass values occurring between June and August and minimum values between December and February for both sites in the 2008-9 and 2009-10 seasons.

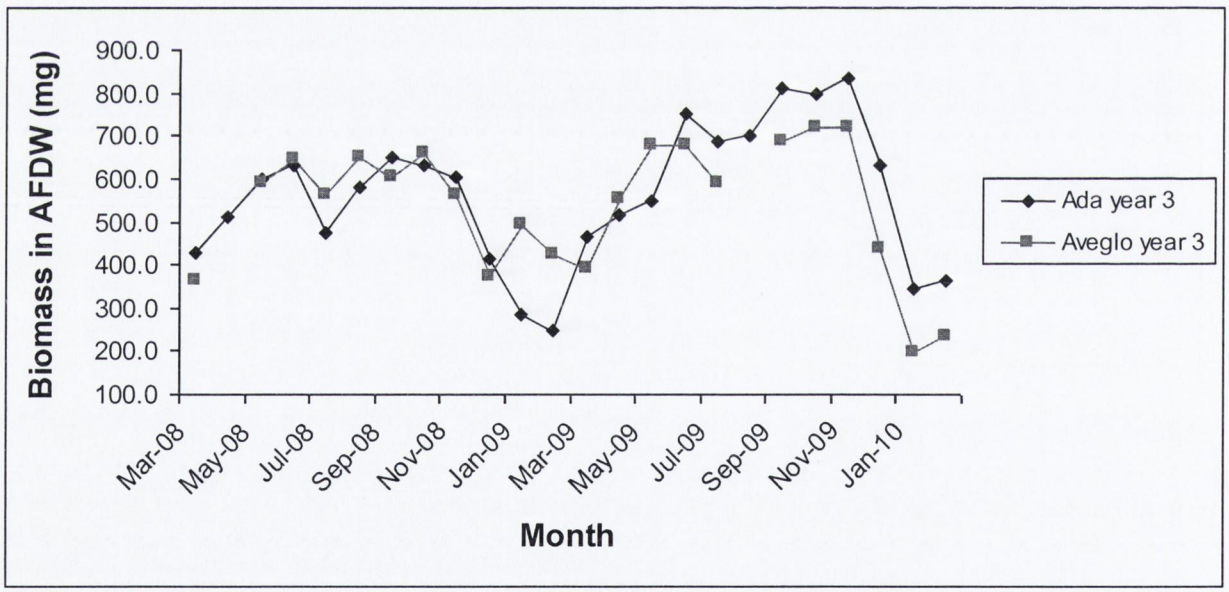


Figure 6.3 Variation in biomass (mg AFDW) for the 3-year old *G. paradoxa* at Ada and Aveglo at the Volta Estuary from March 2008 to February 2010.

6.3.2 Change in Biomass (ΔB)

In order to estimate the annual net production of *G. paradoxa* at the Volta Estuary, the change in biomass (ΔB) or standing biomass of individuals was first estimated as the difference between the maximum pre-spawning and minimum post spawning weight (Section 2.5). The change in biomass (ΔB) or standing biomass for individual clams increased from the 1 to the 9-year old *G. paradoxa* over the study period (Table 6.2). There was no difference ($p > 0.05$) in ΔB for the 1 and 2-year old individuals at Ada and Aveglo. Significant differences in ΔB between the age groups started to emerge from the 3-year old individual. By the fifth year, differences in ΔB for individuals of the same age were higher ($p< 0.05$) at Aveglo than Ada.

Table 6.2 Change in biomass (ΔB) of individual *G. paradoxa* aged 1-9 years old from Ada and Aveglo measured in the Volta Estuary.

Age	Mean shell length(mm)	ΔB (mg AFDW year^{-1})	
		Ada	Aveglo
1	15.4	39.5^{a}	35.9^{a}
2	28.6	158.4^{a}	178.5^{a}
3	39.8	394.4^{ab}	428.8^{ab}
4	49.4	700.0^{bc}	777.9^{bc}
5	57.5	1136.5^{d}	1314.2^{e}
6	64.5	1640.5^{f}	1919.9^{g}
7	70.4	2169.3^{h}	2679.9^{i}
8	75.5	2711.9^{j}	3420.9^{k}
9	79.7	3223.0^{l}	4129.6^{m}

Values in the same row and column with different superscripts $^{a, b, c, d, e, f, g, h, i, j, k, l, m}$ are significantly different ($p < 0.05$).

The change in biomass (ΔB) or standing biomass of *G. paradoxa* cohorts was calculated by multiplying the ΔB of the individual age groups (Table 6.2) by the geometric mean of the number (N) of individuals in that cohort per m^{-2} (density) as shown in Table 6.3. The ΔB for the 1-year old cohort could not be calculated owing to their absence from the fishery. ΔB increased from the 2-year old cohort to the highest value of 39,900 mg AFDW m^{-2} $year^{-1}$ in the 4-year old cohort at Ada after which it declined to 3223.1 mg AFDW m^{-2} $year^{-1}$ in the 9-year old cohort. At Aveglo, the 3 to 5-year old cohorts had the highest ΔB after which the ΔB declined to the lowest value in the 9-yeaar old cohort. The 2, 8 and 9-year old cohorts from the two sites had the lowest ΔB.

Table 6.3 Change in biomass (ΔB) of *G. paradoxa* cohorts aged 2 - 9 years old from Ada and Aveglo in the Volta Estuary.

Cohort	Mean Shell Length(mm)	ΔB (mg AFDW m^{-2} $year^{-1}$)			
		N	Ada	N	Aveglo
2	28.6	11	1742[a]	20	3570[a]
3	39.8	72	28393[c]	97	41468[d]
4	49.4	57	39900[d]	48	37,339[d]
5	57.5	21	23867[c]	29	38110[d]
6	64.5	7	11483[b]	6	11519[b]
7	70.4	6	13015[b]	3	8040[b]
8	75.5	2	5423.5[a]	2	6842[a]
9	79.7	1	3223.1[a]	1	4130[a]

Values in the same row and column with different superscripts [a, b, c, d] are significantly different ($p < 0.05$).

6.3.3 Mortality

Mortality was recorded from May 2008 to May 2009 for *G. paradoxa* at Ada and Aveglo. Percentage mortality was calculated by:

$((NC_a - NC_b) / NC_a) * 100$ Equation 6.3

Where:

NC_a = number of clams in the preceding cohort;

NC_b = number of clams in the succeeding cohort.

The average weight of the cohorts was calculated by taking the average of the monthly weights of each cohort from May 2008 to May 2009. Mortality was calculated by multiplying the number of individuals (density) in the cohort by the percentage mortality (Equations 6.3) and by average weight of the cohort. The geometric mean of the cohorts' mortality was taken as the total mortality owing to fisheries for the site. Table 6.4 presents the mortality values for the cohorts starting from the 3-year old (C_3) cohort. Mortality could not be determined for the 1-year old cohort owing to their absence from the commercial catch. Additionally, for the 2-year old cohort, mortality could not be calculated owing to the fact that there was a positive recruitment from the 2-year old to 3-year cohort in the commercial catch. Mortality was highest in the 4-year old cohort (35,284 mg AFDW m^{-2} $year^{-1}$) at Ada while at Aveglo, the highest mortality (37,686 mg AFDW m^{-2} $year^{-1}$) was recorded in the 5-year old cohort. Mortality declined from the maximum values recorded at both sites to minimum values of 4255 and 4383 mg AFDW m^{-2} $year^{-1}$ in the 9-year cohort at Ada and Aveglo, respectively. Average percentage mortality owing to fishing was 55 and 58% at Ada and Aveglo, respectively.

Table 6.4 Percentage mortality, mean weight (AFDW mg) and mortality (AFDW mg m^{-2}) of *G. paradoxa* cohorts at Ada and Aveglo in the Volta Estuary.

Cohort	Ada				Aveglo			
	N	**% M**	**Avg. Wt**	**Mortality**	**N**	**% M**	**Avg. Wt**	**Mortality**
C_3	72	20.8	476.5	7147.5	97	50.5	524.1	25680.9
C_4	57	63.2	980.1	35283.6	48	39.6	1047.1	19894.9
C_5	21	66.7	1556.1	21785.4	29	79.3	1638.5	37685.5
C_6	7	14.3	2212.8	2212.8	6	50.0	2308.7	6926.1
C_7	6	66.7	2897.6	11590.4	3	33.3	3005.3	3005.3
C_8	2	50.0	3597.3	3597.3	2	50.0	3715.9	3715.9
C_9	1	100.0	4255.4	4255.4	1	100.0	4383.4	4383.4
Total mortality		**54.5**				**57.5**		

N = number of clams per m^{-2} in the cohort
% M = Percentage mortality
Avg. Wt = Average weight of the cohort (mg AFDW)
Mortality = (mg AFDW m^{-2} $year^{-1}$)

6.3.4 Production (P)

The annual production of *G. paradoxa* at Ada and Aveglo was calculated from the monthly samples taken between May 2008 and May 2009. ΔB for each cohort was calculated from May 2008 to May 2009 as in Table 6.3 and added to the mortality values for each cohort in Table 6.4. The annual production of *G. paradoxa* at Ada and Aveglo are summarised in Table 6.5. At Ada, production increased from 34.8 g AFDW m^{-2} y^{-1} in the 3-year old cohort to the highest value of 71.6 g AFDW m^{-2} y^{-1} in the 4-year old cohort. It thereafter declined to the lowest value of 7.6 g AFDW m^{-2} y^{-1} in the 9-year old cohort. Similarly, at Aveglo, the 5- and 3- year old cohorts recorded the highest production of 67.5 and 62.1 g AFDW m^{-2} y^{-1}, respectively. Production declined from the 6-year old cohort to the lowest value of 7.6 g AFDW m^{-2} y^{-1} in the 9-year old cohort. The production of the populations at Ada and Aveglo were 206 and 220 g AFDW m^{-2} y^{-1}, respectively.

Table 6.5 Change in biomass (ΔB) (g AFDW m^{-2} y^{-1}), mortality (g AFDW m^{-2} y^{-1}) and production (g AFDW m^{-2} y^{-1}) for *G. paradoxa* at Ada and Aveglo in the Volta Estuary.

	Ada			Aveglo		
Cohort	**Δ Biomass**	**Mortality**	**Production**	**Δ Biomass**	**Mortality**	**Production**
C_3	27.66	7.15	34.81	36.43	25.68	62.11
C_4	36.30	35.28	71.58	28.15	19.89	48.04
C_5	22.74	21.79	44.53	29.80	37.69	67.49
C_6	11.30	2.21	13.51	9.31	6.93	16.24
C_7	13.12	11.59	24.71	6.34	3.00	9.34
C_8	5.57	3.60	9.17	5.39	3.72	9.11
C_9	3.36	4.26	7.62	3.25	4.38	7.63

6.3.5 Production to Biomass ratio (P: B) of *G. paradoxa*

Table 6.6 presents the P: B ratios of *G. paradoxa* cohorts and the population from Ada and Aveglo at the Volta Estuary. The P: B ratios declined with age from the 3-year old cohort (C_3) to the 9-year old cohort (C_9). At Ada, the 3- and 4-year old cohorts recorded the highest P: B ratios of 5.25 and 5.62, respectively. The P: B ratios thereafter declined to the lowest value of 0.14 in C_9. Similarly, at Aveglo the highest P: B ratio of 8.54 was recorded in C_3 after which the ratios declined steadily to 0.13 in C_9. The P: B ratio of the population (total) was similar at 0.99 and 1.02 at Ada and Aveglo, respectively.

Table 6.6 Biomass (g AFDW m^{-2} y^{-1}), production (g AFDW m^{-2} y^{-1}) and P: B ratios for *G. paradoxa* cohorts from Ada and Aveglo in the Volta Estuary.

	Ada			Aveglo		
Cohort	**Production**	**Biomass**	**P: B ratio**	**Production**	**Biomass**	**P: B ratio**
C_3	34.80	6.63	5.25	62.11	7.28	8.54
C_4	71.59	12.74	5.62	48.05	13.61	3.53
C_5	44.53	20.23	2.20	67.49	21.30	3.17
C_6	13.52	28.77	0.47	16.24	30.01	0.54
C_7	24.71	37.67	0.66	9.34	39.07	0.24
C_8	9.17	46.77	0.20	9.10	48.31	0.19
C_9	7.61	55.32	0.14	7.63	56.98	0.13
Total	**205.92**	**208.13**	**0.99**	**219.96**	**216.56**	**1.02**

6.3.6 Reproductive Investment (G: P) of *G. paradoxa*

The gonad to production ratios (G: P) of *G. paradoxa* from Ada and Aveglo are shown in Table 6.7. Reproductive investment in *G. paradoxa* was similar at the two sites and increased steadily from 1.10 and 0.60% in a standard animal with a mean length of 39.8 mm corresponding to a 3-year old clam at Ada and Aveglo, respectively, to 44.1 and 42.6% in a 9-year old clam. This shows that *G. paradoxa* invests < 50% of its energy in gonad output.

Table 6.7 Gonad to production (G: P) ratio of individual *G. paradoxa* aged between 3-9 years old at Ada and Aveglo in the Volta Estuary.

Age	Ada				Aveglo		
	ML (mm)	GW (mg)	P	G: P (%)	GW (mg)	P	G:P (%)
3	39.8	384.1	34802.7	1.10	375.6	62114.1	0.60
4	49.4	636.9	71586.9	0.89	586.5	48046.9	1.22
5	57.5	1082.9	44526.3	2.43	1027.7	67488.8	1.52
6	64.5	1614.6	13515.0	11.95	1551.6	16235.7	9.56
7	70.4	2186.5	24709.4	8.85	2112.1	9341.6	22.61
8	75.5	2784.1	9165.5	30.38	2694.4	9104.7	29.59
9	79.7	3355.5	7610.9	44.09	3248	7631.4	42.56

ML = mean length of individual clams aged 3 to 9 years
GW = gonad weight of individual clams (mg AFDW)
P = somatic production of clams (mg AFDW m^{-2} y^{-1})
G : P = gonad to somatic production ratio of clams

6.4 *G. paradoxa* Fishery

6.4.1 Canoes and Fishers

Table 6.8 shows the number of canoes/wooden boats used by artisanal clam fishers in the Volta Estuary. There were on average 251 canoes and 503 artisanal clam fishers, with each canoe operated by at least two fishers. The number of canoe clam fishers excludes the traditional hand collectors and other occasional collectors whose catch is made up of a few animals that are either sold or used for home consumption.

Table 6.8 Number of canoes and artisanal clam fishers in the Volta Estuary, Ghana

No. of canoes	Range	Mean No. of fishers	Range	Mean no. of fishers/canoe	Range
251	213-305	503	416 - 598	2	2 - 3

6.4.2 Clam Harvesting

Clam harvesting commences at the beginning of March each year after the end of the traditionally imposed closed season. Two main methods are employed; traditional hand collection and Hookah fishing. The traditional hand collection method was previously the only method for clam harvesting in the Lower Volta until the introduction of the Hookah fishing method in the 1990s. The traditional hand collecting method is limited to the shallow zones of the river and is mostly practiced by women who wade through the water, locate the clams with their feet and collect them with their hands into a container (Figure 6.4).

Figure 6.4 Women harvesting clams in the shallow areas of the Volta Estuary.

Hookah fishing is practiced solely by men who dive at the deeper zones of the river to collect the clams. The method involves the supply of air by compressors through a long hose to the fishers while submerged (Figure 6.5), allowing the fisher to remain underwater for 30 - 60 minutes. A diving mask is worn and the fingers protected with cellotape as the fingers are used to rummage the sandy sediments for clams that burrow below the surface with only their siphons protruding through the sand into the water. The fisher dives to the river bed with a net into which the harvested clams are placed.

Figure 6.5 A Hookah fisher preparing for a dive

There have been instances of compressor failures but these rarely result in fatalities as clam divers operate in waters that are less than 10 m deep and usually one diver remains aboard the canoe to alert the others of compressor stoppages. Clam fishing is restricted to a 10 km stretch of the river between Ada Foah and Agave Afedome, although there is limited harvesting of clams upstream. Figure 6.6 presents some of the accessories used and activities during Hookah fishing.

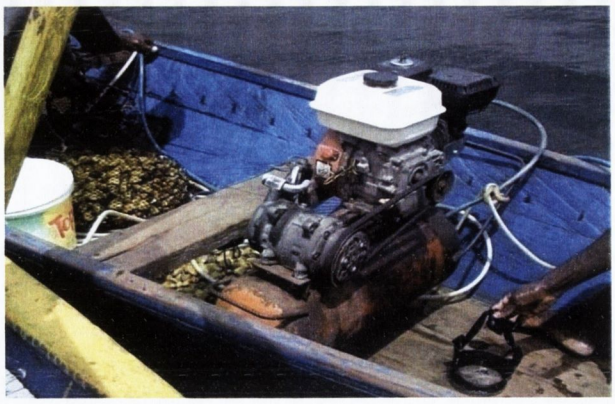


Fig. 6.6A A motorized air compressor

Fig. 6.6B The air supply hose

Fig. 6.6C Hauling the net aboard after fishing

Fig. 6.6D Unsorted clam in a canoe

Fig 6.6E Sorting the daily harvest into size classes

Fig. 6.6F A 10-litre bucket used as a measure of daily harvest and for marketing

6.4.3 Estimation of Catch and Revenue

It was estimated that an average of 130kg of clams (total weight) are landed daily per canoe (Table 6.9). The harvest largely consisted of small clams (shell length < 40 mm) which account for 43%, followed by 38% of medium sized-clams (41-60 mm) and 19% of large-sized clams

(> 60 mm). The fishery is therefore dominated (81%) by clams that are < 60 mm long. The closed-season for clam fishery is for a period of 77 days from 24th December to 11th March. Outside this period there is no fishing on Tuesdays and Sundays are optional fishing days. A clam fisher therefore works 4-6 hours a day in a 5-6 day week adding up to 236 days in a year. The estimated catch for the 251 fishing canoes is 7700 tonnes (Table 6.9). For the small and medium sized clams, a 10 litre bucketful (Figure 6.6F) sells for between 4.00- 8.00 Cedis. A 3-man boat crew on average harvest 130kg of clams which is sold for 78 Cedis (1 Cedis = 0.50 Euro). Through a chain of suppliers, clams are marketed to processors in the major towns of south-eastern Ghana.

Table 6.9 Catch statistics for artisanal clam fishing in the Volta Estuary, Ghana

Mean Catch per canoe (kg)	Range (kg)	Total Catch per day (kg)	No. of fishing days	Catch per year (kg)
130	90-170	32,630	236	7,700,680

Table 6.10 shows the categories of people employed directly in the clam fishery or ancillary activities and their average daily and yearly gross incomes.

Table 6.10 Gross incomes of categories of people employed in clam fishing or ancillary activities

Category	Revenue Day^{-1} (GH¢)	Per Year^{-1} (GH¢)
Clam fisher	26*	3,086,408
Clam processor	65	474,500
Clam Retailers	12.5	525,500
Clam shell mills		534,000
Total		**4,620,408**

*Gross income of GH¢78/canoe/day was estimated by dividing 78 GH¢ by the 3-member crew 78/3= GH¢26

6.4.4 Processing of Clam Meat

The most valuable part of the clam is the meat which is a delicacy and is processed and sold at major roadside stops. The processing method is simple and involves initial boiling to open the shells after which the meat is taken out and washed to remove sand particles. It is then skewered and fried (Figure 6.7). The main locations for the sale of fried clams are along the major highways in south-eastern Ghana at Atimpoku on the Accra-Ho Highway and at Kasseh and Sogakope on the Accra-Aflao Highway. Clam processors obtain their supply from fishers at two landing beaches at Agave-Afedome and Big Ada.

Figure 6.7 Frying of skewered clams and batch of fried clams ready for sale

6.4.5 Utilisation of the Clam Shell

The shell accounts for about 70% of the total weight of the clam. Out of the estimated 7700 tonnes of clams harvested annually almost 5400 tonnes of shells, therefore, accrue after the meat has been extracted. Locally the shells are used as a pavement material on village roads and compounds to overcome muddy conditions. Additionally, they are used in decorating buildings e.g. stairs (Figure 6.8A-B). Mills have been setup to process the shells into grit and powder for sale to other industries. Shells are purchased in truckloads mainly from Big Ada and Sogakope which are the major clam meat processing towns. The price for a truckload of shells is GH¢ 100.0 and approximately 120 bags of milled shells can be obtained from a truckload. The shells are milled at different grades of fineness depending on its intended purpose, bagged in 50 kg sacks and sold at GH¢ 4.00 per sack (Figure 6.8F). In a month, approximately 1600 bags of milled shells are produced, giving a gross monthly income of GH¢ 6400.00.

The milled shells have several uses and serve both the local and international markets. The animal feed industry, especially poultry feed producers' utilise the milled shells or grit as a source of calcium in animal feed. The milled shells are also used in the building industry in the construction of terrazzo floors. Powdered shells are used in the production of whitewash, which is cheaper than imported brands. The survey revealed that the cement industry also utilises the milled shells as a component in the production of cement

Fig. 6.8A clam shell-paved lane in a village at Big Ada

Fig. 6.8B Staircase decorated with shells

Fig. 6.8C Heaps of shells at Big Ada

Fig. 6.8D A clam shell mill at Sogakope

Fig. 6.8E A Shell Mill

Fig. 6.8F Bagged milled shells ready for sale

6.4.6 Management and Conservation of the Fishery

The most important management measure is the closed-season which commences from 24th December to 11th March each year. The institution of the closed season was in response to the small size of clam meat during this period. Aside from the closed-season, Tuesdays are non-fishing days for all fishermen. The closed season is strictly adhered to and is maintained by traditional norms and rites. The reasons for the timing of the non-fishing day are based mainly on indigenous knowledge and traditional beliefs. It also allows the fishers to market their clams as Tuesday is a market day. The clam fishery is open access as no permit is required before entry. Nevertheless, the chiefs of the Ada and Agave traditional area have responsibility to ensure compliance with the traditional laws and regulations. Apart from the traditionally imposed restrictions there are no restrictions on the quantity or the size of clam harvested.

One management strategy which has prevented the extinction of the species in the Volta River is the farming or fattening of juvenile or smaller clams. In order to supply the market with clams during the closed-season, clam fishers usually seed shallow areas of the river with small size clams for periods ranging from 6 – 8 months. This enables the clams to double their size before being harvested for sale during the closed-season. Small sized clams are seeded to shallow zones of the river demarcated by sticks. The seeding of plots with clams and their harvesting is usually undertaken by women because of the shallowness of the areas. Clams do not move more than a metre away from their seeded points and, therefore, remain within the plots of their owners.

6.5 Discussion

6.5.1 Biomass and Production

The data for the calculation of biomass and production of *G. paradoxa* were based on grab and other samples taken from the artisanal fishery which is biased as smaller clams (< 20mm) are not harvested. This notwithstanding, the density of clams and the distribution of the cohorts in the grab and fishers samples were comparable. The density of clams from the grab samples was 278 ± 250 s.d. and 110 ± 62 s.d. m^{-2} at Ada and Aveglo, respectively, compared with 75 – 511 m^{-2} from the monthly fishers' samples. The seasonal reproductive cycle of *G. paradoxa* could be identified in the cyclical changes in biomass observed during the study. At Ada, maximum biomass was recorded between June - July in 2008 and between May - June in 2009. At Aveglo, maximum biomass was recorded between May – June for the two years and minimum biomass recorded between December –February. The seasonal patterns were absent in the 1-year old cohort, started to emerge in the 2-year old cohort and were pronounced in the 3-year old cohort (Figures 6.1- 6.3). The lack of seasonal patterns in the 1-year old cohort and the appearance of patterns in the 2-year old cohort are consistent with information about the sexuality of the clam (Chapter 4). *G. paradoxa* becomes sexually mature in its second year at a minimum length of 22 mm, hence the emergence of seasonal patterns in biomass in the 2-year old cohort can be attributed to the role played by the maturing gonad. The distinct seasonality shown in the biomass cycle of *G. paradoxa* from the third year confirms earlier studies that changes in the body cycle of a cohort or standard animal could give an indication of the spawning season of a bivalve species (Etim and Taege, 1994; Etim, 1996; Darriba et al., 2005).

Although mortality for the 1- and 2-year old clams could not be calculated, as far as the fishery is concerned these age groups are not important as they are not harvested at all or form

a small percentage of landed clams. A comparison of the fishing mortality values at Ada (55%) and Aveglo (58%) with that from the length-converted catch curve (FiSAT II, Chapter 5) indicates that the fishing mortality estimated by the length-converted catch method was similar at Ada (57%) while it was underestimated at Aveglo (32%). The lower fishing mortality estimate at Aveglo could be attributed to the higher natural mortality estimate (0.44) compared with Ada (0.35). The estimation of natural mortality is difficult in practice as one is unable to factor in all the variables that account for natural mortality in a model. Estimates from models are thus, applied cautiously in management until substantiated by field data. The estimated fishing mortality from the cohorts therefore, gives a better assessment of mortality than the length-converted catch curve. It would therefore be prudent to adopt a drastic management approach to the fishery as the exploitation level has gone beyond the optimum level. The fact that more and more small clams that were hitherto not landed are being harvested necessitates a drastic approach to prevent the collapse of the fishery, thus the livelihood of the communities.

Biomass was inversely related to production in *G. paradoxa*, while biomass increased with age, production declined. Production was highest at 71.6 g AFDW m^{-2} y^{-1} in the 4-year old cohort at Ada and at 67.5 and 62.1 g AFDW m^{-2} y^{-1} in the 5- and 3- year old cohorts at Aveglo. At both sites production declined to the lowest value of 7.6 g AFDW m^{-2} y^{-1} in the 9-year old cohort. The population production was 206 and 220 g AFDW m^{-2} y^{-1} for Ada and Aveglo, respectively. The population was dominated by cohorts that were 3 to 5 years old as they accounted for 73 to 81% of production at Ada and Aveglo, respectively. The dominance of a few cohorts in the production of *G. paradoxa* is in agreement with the findings of Velez et al. (1985) who estimated 37.6 and 77.4 g m^{-2} y^{-1} dry weight in 1974 -75 and 1975-76, respectively, for the tropical clam *Donax denticulatus* in Venezuela. The production of *D. denticulatus* was attributed to the dominance of young, rapidly growing, individuals. As

demonstrated in this study, the higher production of the younger age classes in the population can be attributed to the large number of individuals in these classes and their relatively faster growth rate (MacDonald and Thompson, 1986). The dominance of a few age classes in the production of a population has been observed for *Mercenaria mercenaria* (Hibbert, 1977) in which a single year class was responsible for 75% of total population production, however, in other species, several or all the age classes may contribute significantly to production.

The annual production to biomass ratio (P: B) is used as a measure of relative productivity (Hornbach et al., 1984). The (P: B) ratio was highest in the 3 and 4 year old cohorts at 5.3 and 5.7 at Ada and in the 3-year cohort (8.5) at Aveglo. The P: B ratio dropped to the lowest values of 0.14 and 0.13 in the 9-year old cohort at Ada and Aveglo, respectively. The P: B ratios of the populations were similar for the two sites at 0.99 and 1.02 for Ada and Aveglo, respectively. The P: B ratio estimated in this study was higher than that of Moses (1990). Moses (1990) estimated a P: B ratio of 0.32 for the stock of *G. paradoxa* in the Cross River, Nigeria, based on samples collected from fishermen catches. The other studies on *G. paradoxa* (King et al., 1992; Etim and Brey, 1994; King, 2000) did not report on P: B ratios making it impossible to compare the productivity of the Volta River stock with the Nigerian stock.

Several investigations have compared the P: B ratios of bivalves from different geographic regions of the world in order to assess their productivity. Table 6.11 compares the P: B ratios of some tropical bivalves. The P: B ratio of *G. paradoxa* ($\approx$ 1.0) falls within the range recorded for tropical bivalves. It is however, lower than the minimum P: B ratio estimated for *Corbicula trigona* in Lake Aheme in Benin (Malin and Pattee, 1989).

Table 6.11 P: B ratios of some tropical bivalve species

Species	P :B	Locality	Author
Polymesoda solida	0.23	Salamanca, Island, Colombia	Rueda and Urban, 1998
Tagelus plebius	1.37	São Sebastião, Brazil	Abrahão et al., 2010
Corbicula trigona	1.9- 3.8	Lake, Aheme, Benin	Maslin and Pattee, 1989
Chione cancellata	2.65	Cariaco Gulf, Venezuela	Prieto et al., 1998
Galatea paradoxa	0.32	Cross River, Nigeria	Moses, 1990
Galatea paradoxa	0.99-1.02	Volta Estuary, Ghana	This study

Table 6.12 presents the measured P: B ratio of *G. paradoxa* and the estimated ratios by two empirical models. While the Banse and Mosher (1980) model overestimated the P: B ratio in comparison with the measured P: B, the Schwinghammer et al. (1986) model grossly underestimated the P: B ratio for *G. paradoxa* demonstrating that empirically derived relationships should be used with caution in the management of a fishery until actual measurements have been conducted.

Table 6.12 Estimated and measured P: B ratios for *G. paradoxa*

	P : B ratio	
Model	**Ada**	**Aveglo**
Measured	0.99	1.02
Schwinghammer et al. 1986	0.43	0.42
Banse and Mosher 1980	1.50	1.60

Reproductive investment in *G. paradoxa* increases with age as shown by changes in biomass, which is the difference between the maximum pre-spawning and minimum post-spawning weights (Table 6.2). Similarly, individual reproductive investment as indicated by the G: P ratio (Table 6.7) increased with age from 0.90 ± 0.35 % in the 3-year old to 43.3 ± 1.08 % in the 9-year old individual. This is consistent with the fact that the of number eggs produced by

G. paradoxa increases with age (Chapter 4). Reproductive investment in *G. paradoxa* does not take precedence over somatic growth as the animal grows older, i.e., it invests < 50% of its energy in gonad output as observed for 9-year old clam. In terms of the allocation of energy, *G. paradoxa* may be described as restrained as the increase in reproductive output with age is not at the expense of somatic growth.

6.5.2 *G. paradoxa* Fishery

Artisanal clam fishing plays an important role in the socioeconomic life of inhabitants of the Volta Estuary. The clam beds stretched for 70 km from Akosombo (100km) to Tefle (30km) from the mouth of the river prior to the construction of the dams. The number of people directly and indirectly engaged in the fishery and the methods used have been the subject of previous studies. Lawson (1963) reported that between 1000 and 2000 women were engaged in the fishery, Amador (1997) reported 111 women fishers at Battor, a fishing village on the Volta River. The current study estimated 503 fishers and 251 canoes operating between Agave Afedome and Ada Foah, the main clam fishing area at the Volta Estuary.

The annual harvest of clams was estimated at 8000 tonnes (Lawson, 1963). Pople (1966) estimated that clam harvests ranged between 4000 and 7000 tonnes per annum. The yield, however, dropped to 1400 tonnes in 1987 (Attipoe and Amoah 1989) after the formation of a sand bar at the mouth of the river. In 2000, an annual yield of 1700 tonnes was estimated (Kumah, 2000). The present study estimated an annual yield of 7700 tonnes within a restricted area of about $10km^2$. The increase in yield can be attributed to an increase in fishing effort and the introduction of air compressors which enables clam fishers to dive in deeper areas of the river and to stay underwater for longer periods searching for clams. Another reason for the higher annual yield is the landing of smaller clams. Previously, smaller clams

(< 50 mm) were not landed and fishing was restricted to shallow areas with hand collection as the only method of fishing. Diving was only possible for a few experienced divers. The methods of clam fishing have evolved over the years. Lawson (1963) reported that hand collection and diving in the shallow zones were the only method used and the clam fishery was wholly conducted by women (Lawson, 1963; Purchon, 1963).

Currently, two methods are used; hand collection mainly by women and Hookah fishing by men. The bulk of the catch comes from Hookah fishing in the deeper zones of the river where the density is high. The fishery is very important to the socioeconomic well-being of the Ada and Agave communities not only as source of food and employment but also as source of raw material (shells) for small-scale industries even beyond the estuary. Annually, it generates a gross income in excess of GH¢ 4,620,408 (2.3 million Euros).

Commercial extinction of *G. paradoxa* is imminent in the estuary as a result of habitat alteration and overfishing. There is the need to put in place a sustainable harvesting measure that will target medium to large size clams against the current situation where the catch is dominated by smaller clams. The closed season, although important as it allows the clams to recover after the spawning period, does not prevent the landing of smaller clams. A careful consideration of the production and P: B ratios showed that productivity was highest in the 3-4 year old clam after which it declined. Gamete output averaged 10% in the 6-year old clam at a mean shell length of 64.5 mm. Therefore, it would have been appropriate to fix the minimum landing size at 65 mm. However, the catch data from the fishery shows that only 19% of harvested clams are > 60 mm shell length. Fixing an unrealistic target for a fishery that is open access and community-managed would lead to illegal fishing and defeat the purpose for implementing the size restriction.

In order to prevent the extinction of the clam and to ensure that the communities continue to benefit from the fishery, it is recommended that a minimum landing size of 50 mm should be

imposed. The 50 mm size limitation corresponds to the mean size of a 4 year old clam. The 50 mm size limit was based on the fact that production was highest in the 4 year old clam (Table 6.5). Moreover, the P: B ratio (Table 6.6) declined after 4 year old cohort. The 50 mm size limit would also not unduly affect the quantity of clams landed hence, the livelihood of the fishers as would a higher size restriction (> 60 mm).

The imposition of the restriction should be done in consultation with the chiefs and traditional authorities in the two communities which have managed the fishery to date. The marketing of clams below the minimum landing size should be abolished and enforced by the traditional authorities. Secondly, the farming of smaller clams which is a traditional activity at the estuary should be encouraged so that fishers who harvest undersize clams can seed them onto their culture plots.

7.0 GENERAL DISCUSSION

The reproductive biology, population dynamics, biomass, production and fishery of the freshwater clam *G. paradoxa* in the Volta River, Ghana, was studied over 24 months from March 2008 to February 2010. *G. paradoxa* is the basis of an artisanal clam fishery in the Volta River Estuary providing a vital source of protein, employment and raw materials for industry.

7.1 The Biology of *G. paradoxa*

7.1.1 Habitat Preference

Within its range, *G. paradoxa* is limited to narrow stretches in the lower reaches of the rivers in which it occurs (Purchon, 1963; Moses, 1990; King, 2000). The habitat preference of *G. paradoxa* supports the assertion that it is a marine species that has adapted to life in freshwater (Purchon, 1963). The conductivity and salinity regime of the rivers seems to strongly influence the spawning ground of *G. paradoxa*, hence its distribution. The distribution of the species is limited by the tidal range such that dense populations are only found where the optimum salinity of 1 psu exists. Moses (1990) observed that the density of *G. paradoxa* in the Cross River was about twice in a zone with a salinity range of 0 – 1.1 psu ($13m^{-2}$) than in a more saline 0.1 -1.5 psu ($7m^{-2}$) zone. The density gradually reduced upstream from the mouth of the river and the clams were no longer found in fishable quantity after 150 km (Moses, 1990). The higher clam density ($278 \pm 250\ m^{-2}$) at Ada, which is strongly influenced by the tides, compared with Aveglo ($110 \pm 65\ m^{-2}$) in this study is in agreement with the findings of Moses (1990). Furthermore, significant movements were observed in the spawning ground of *G. paradoxa* in the Volta River during and after the construction of the Akosombo Dam (Beadle, 1981). The spawning ground shifted 30 km from the mouth of the river where the

optimum salinity of 1psu existed before the construction of the dam to 50 km upstream when the amount of freshwater allowed to flow downstream was restricted during the construction of the dam from 1960 to 1964. When the dam was completed and more freshwater was released downstream through the spillways, the spawning ground shifted to the current position of 10 km from the mouth of the river (Beadle, 1981).

7.1.2 Reproductive Cycle and Sexual Strategy

This study showed that gametogenesis in *G. paradoxa* starts at the beginning of the dry season in December when the quantity of available food was slightly higher and progressed with the onset of the rains in March - April until the peak of the rainy season (June - July) when the gonad ripened. Spawning in *G. paradoxa* in the Volta River was a single annual event starting from the peak of the rainy season July - October. Generally, tropical species tend to reproduce continuously because of the relatively stable and elevated water temperatures which allow year-round breeding (Etim and Sankare, 1998). *G. paradoxa* is an exception as data from this study as well as from the Nigerian stocks showed that there are some tropical species with a single annual spawning period, albeit over an extended period. Unlike temperate bivalves where temperature provides a strong environmental trigger for gametogenesis and spawning, there is the lack of a strong environmental trigger for gametogenesis in *G. paradoxa.*

Temperature did not have any effect on gametogenesis in *G. paradoxa* as it was relatively constant. However, the slight drop in temperature at the peak of the rainy season (June - July), together with other factors, seemed to trigger spawning in the species. Etim and Taege (1993) observed that during the rainy season, there was an increase in water depth from 4 to 12 m, a lowering of conductivity and a fall in water temperature from 32 °C in March to 20 °C in July in the Cross River. These observations were to a small extent confirmed in the Volta Estuary, at the peak of the rainy season. There was a 3°C drop in water temperature, in addition to a

fall in food availability (chlorophyll a and SPM) and dissolved oxygen. The synergistic effect of several factors; a slight drop in water temperature, lower food availability and lower DO levels experienced at the peak of the rainy season might have acted as a cue for spawning in *G. paradoxa.* This observation is in agreement with the findings of Clemente and Ingole (2009) who observed that spawning in *Polymesoda erosa* occurred during the mid-monsoon months of August-September when temperatures and chlorophyll a levels were low. Better feeding conditions at the beginning of the dry season (December) possibly triggers the onset of gametogenesis in *G. paradoxa*. The start of gametogenesis in *G. paradoxa* was synchronised with the environmental conditions such that there was an elevated food supply for gonadal tissue growth.

The sex ratio observed for *G. paradoxa* indicated a significant departure from the expected 1:1 ratio. The population was dominated by females (80%) with almost equal numbers of males and hermaphrodites. The high percentage of females could be attributed to the under-sampling of smaller individuals which could be males owing to the preference for larger individuals in the fishery. The size distribution of the sexes did not give a clear indication of sex switches or protandry within the population. In species protandric hermaphrodites, there is a single sex switch from an initial male phase to female with smaller individuals in the population being males while the larger ones are females. Although, the males were limited to 20 – 55 mm length range, the females were not limited to any particular size range and were distributed across the length range sampled. This is in contrast to the observation of Rueda and Urban (1998) and Afiati (2007) who observed distinct size classes in the sexuality of *Polymesoda solida*, *Anadara granosa and A. antiquata*. In *P. solida* there was a sex switch from a juvenile stage to a male stage before a final hermaphroditic stage (Rueda and Urban, 1998). Juveniles start becoming males at 10 mm shell length and above 16 mm no juveniles were observed. Males changed to hermaphrodites from 21 mm shell length (Rueda and Urban, 1998).

Anadara granosa and *A. antiquata* have a protandric type of development in which a primary male phase precedes the adult stage until both sexes were approximately equally represented after which a male to female sex reversal occurs (Afiati, 2007). Afiati (2007) observed that the majority of the 15 – 30 mm clams were males, the sex ratio became 1:1 when the animals were between 30 – 40 mm in length and by the time they attained a size over 45 mm the populations were dominated by females. Development as a male is considered to require less energy than as a female (Russell-Hunter and McMahon, 1975; Calow, 1983). For example, one germ cell will produce four sperm which largely consist of a nucleus surrounded by cytoplasm specialised for locomotion and penetration of the egg. In females, one germ cell will develop only to become one large oocyte with energy-rich yolk and cytoplasm. The advantage of firstly being male is that some energy could be saved and redirected towards somatic growth because there is a trade-off between growth and reproduction (Calow, 1983). It is recommended that future studies on sexuality of *G. paradoxa* should adopt sampling protocols that target the smaller clams (< 20 mm) in order for a detailed study of the sex ratios and sexual strategy of *G. paradoxa.*

7.1.3 The Life Histories of Freshwater Bivalves

The life histories of freshwater bivalves are diverse and depend on the family being discussed (Bogan, 2008). The life history strategy of a species or members of the same family may vary depending on the habitat occupied and population density e.g. freshwater corbiculids (*Corbicula leana)* are brooding without a planktonic larval stage and hermaphroditic while brackish water corbiculids (*Corbicula japonica)* are non-brooding, have a planktonic larval stage and are gonochoristic (Nanbu et al., 2008). *Margaritifera margaritifera* (Unionidae) at high densities are dioecious while at low densities females become hermaphrodites and self-

fertilising (Bauer, 1987). Species in the Unionidea combine brooding of eggs with a parasitic larval stage (glochidia). The modified veliger larvae (glochidia) undergo a brief period as an obligate ectoparasite on the gills, fins, or other external parts of fish (Haag and Warren, 1997). Bivalves belonging to the Sphaeriidae are hermaphrodites and brood their young within the inner demibranchs without a pelagic larval stage (Guralnick, 2004).

The life history strategy of *G. paradoxa* deviates significantly from the patterns typical of freshwater bivalves and appears similar to its marine Donacid relatives as well as brackish water corbiculids such as *Polymesoda erosa* with the characteristic marine bivalve reproductive traits of external fertilisation and a free-swimming veliger larva (Morton, 1985a; Clemente and Ingole, 2009). A 40 mm adult *G. paradoxa* produces an average of 10^6 eggs per year which is comparable to other bivalves that produces planktotrophic eggs e.g. *D. polymorpha, Mercenaria mercenaria*, *Argopecten irradians*, *Polymesoda erosa* and *Mytilus edulis* (Ansell, 1967; Bayne et al., 1983; Fordham, 1970; Clemente and Ingole, 2009). This suggests that *G. paradoxa* produces planktotrophic eggs and would therefore have a free-swimming planktotrophic larval stage. The larval survey, however, did not detect any larvae in any of the samples taken in the plankton. The absence of the larvae in the plankton is puzzling as the egg diameters (30 μm) and egg numbers point to a planktotrophic larva. The egg of Donax is 60 μm in diameter and the larva (> 70 μm) remains in the plankton for about 21 before settling (Chanley, 1969; Carstensen et al., 2010). The absence of the larvae in the plankton samples could be attributed to fact that the lowest boat speed used was too fast for horizontal tows with 63 μm mesh net. This might have resulted in out-welling i.e. larvae trapped in the net were forced out owing to the faster boat speed hence the absence of larvae in all the samples. Future larval surveys would be conducted with larger mesh nets (100 - 150 μm) with the boat at a stationary position. Furthermore, vertical tows would be conducted

from the mouth of the river in order to describe the early larval development and dynamics of in the Volta Estuary.

Freshwater bivalves are either hermaphroditic (*Musculium, Pisidium)* or gonochoristic (*D. polymorpha, Paxyodon syrmatophorus*) (Morton, 1991, Beasley et al., 2000). Brackish water bivalves (*Polymesoda erosa, Corbicula fluminalis*) are gonochoristic with either a slight female or male bias (Morton, 1991). The presence of hermaphrodites in bivalve species that are strictly gonochoristic is not unusual (Sastry, 1979). Several authors have reported that hermaphroditic individuals usually account for < 1% of the population in strictly dioecious species. Morton (1985a) observed 0.5% hermaphroditism in *Polymesoda erosa* in mangroves in Hong Kong. Similarly, Darriba et al. (2005) reported the occurrence of 0.5% hermaphroditism in *Ensis siliqua* from the Ria de Corcubion, north-western Spain. Afiati (2007) reported the occurrence of < 1.5% hermaphroditism in *Anadara granosa* and < 1% for *A. antiquata* from Central Java, Indonesia. Ceuta et al. (2010) recorded 0.4% and 0.2% hermaphroditism in *Tagelus plebeius* (Psammobiidae) and *Iphigenia brasiliana* (Donacidae), respectively, from the Cachoeira River Estuary in Brazil.

The high incidence of hermaphroditism observed in this study (9.4%) is comparable to what was recorded in *A. antiquata* (9.9%) on the Dar es Salaam coast in Tanzania (Kayombo and Mainoya, 1987). Pinera et al. (2009) found an unusually high frequency of hermaphroditism in *Megapitaria squalida* sampled from Bahia de la Paz (21.8%) and Bahia Magdalena (23.5%) in Baja California, Mexico. The high incidence of hermaphroditism in *M. squalida* was attributed to stress as a result of overexploitation and low population density which favours hermaphroditism (Pinera et al., 2009). The reasons adduced by Pinera et al. (2009) could be applied to the clam fishery at the Volta Estuary. Harvests in the Volta Estuary have increased from 1700 tonnes (Kumah, 2000) to 7700 tonnes today (Chapter 6). Landings are dominated by small to medium sized clams (< 60 mm). These changes might have accounted for the high

incidence of hermaphroditism and the dominance of females (80%) in the population. The increase in female abundance might be attributed to increasing fishing pressure on the larger individuals within the population (Pinera et al., 2009).

G. paradoxa may be described as showing reproductive restraint in terms of the allocation of energy for reproduction and somatic growth (Calow, 1981). Reproductive investment in *G. paradoxa* increases with age as shown by the G: P ratio which increased with age from 0.90 ± 0.35% in the 3-year old clam to 43.3 ± 1.08% in the 9-year old clam. Reproductive investment in *G. paradoxa* does not take precedence over somatic growth. That is, as the animal grows older, it invests < 50% of its energy in gonad output in a 9-year old clam. This is in contrast to the strategy of *Nucula turgida* which produces lecithotrophic eggs (100 μm) and apportions more energy to gonad output than somatic growth owing to the high lipid content of the eggs (Wilson, 1988). *Nucula turgida*, in contrast to *G. paradoxa*, shifts from restraint to recklessness with age (Wilson, 1988). The pattern of resources allocation in *G. paradoxa* is characteristic of iteroparous species e.g. the tropical scallop *Euvola ziczac* which invests ≈ 21% of total dry tissue weight as gametes (Brokordt et al., 2000).

The life-span of freshwater bivalves ranges between a few months in the Sphaeriidae (*Pisidium)* (Holopainen and Hanski, 1986) to > 100 years in the Unionidae (*Margaritifera margaritifera*) (Bauer, 1992). Age determination using surface rings is characteristic of temperate bivalves owing to the constancy in the deposition of annual rings in winter owing to low temperatures and food availability (Peharda et al., 2002). In the tropics, temperature is relatively constant, as seen in this study (28.6°C) and its effects on growth is negligible. The three methods (surface rings, length-frequency distributions and tagging-recapture experiments) used to estimate the age of *G. paradoxa* were successful. A comparison of the age-length estimates obtained from the methods indicated that surface ring counting is reasonably accurate for simple and rapid age estimation of individuals up to 4 years (≈ 50 mm)

of age. Afterwards, the age of *G. paradoxa* was more accurately determined by the tagging-recapture experiment than the other two methods. The suitability of surface rings in ageing *G. paradoxa*, a tropical bivalve, can be attributed to the constancy in the deposition of the annual rings which occurs during the spawning season. The spawning season of *G. paradoxa* in the Volta River coincides with the period of flooding which is characterised by low food availability and slightly lower temperatures. The deposition of an annual ring as a result of spawning activity has been observed in other studies (Jones et al. 1990; Gaspar et al., 2004).

The asymptotic length (L_∞) for *G. paradoxa* in the Volta Estuary (105.7 mm) is similar to that found by Vakily (1992) at Tefle on the Volta River and King (2000) on the stock of *G. paradoxa* in the Nun River, Nigeria. It is, however, lower than the 145.1mm obtained by Vakily (1992) and King et al., (1992). The L_∞ estimate in this study is higher than that of Moses (1990) and Etim and Brey (1994). The growth coefficient (K) estimate of 0.14 – 0.18 $year^{-1}$ and the growth performance index (Ø) of 3.192 and 3.108 for Ada and Aveglo, respectively, are the lowest recorded in studies on *G. paradoxa* (Moses, 1990; Vakily, 1992; Etim and Brey, 1994; King, 2000). The estimated L_∞, K and Ø of *G. paradoxa* are comparable to that of similarly sized venerid bivalves that have life-spans between 10 to 17 years: e.g. *Callista brevisiphonata* (102.2 mm, 0.17 $year^{-1}$ and 3.27) Selin and Selina (1988); *Callista chione* (98.1 mm, 0.15 $year^{-1}$ and 3.16) Moura et al. (2009) and *Mercenaria mercenaria* (94.3 mm, 0.18 $year^{-1}$) (Hibbert, 1977). The higher growth rates (Table 5.4) reported by Vakily (1992) were based on data collected just after the completion of the Akosombo Dam with little or no negative effects of the dam's impact on the habitat. The *G. paradoxa* stocks in the Cross and Nun Rivers which recorded higher growth rates than that estimated in this study are undammed (Moses, 1990; Etim and Brey, 1994; King 2000). The low growth rate and growth performance recorded in this study support the fact that damming the river has negatively affected the growth performance of *G. paradoxa*. The dams changed the flow regime of the

river and, thus, the nutrient dynamics at the estuary resulting in a lower food supply and the proliferation of aquatic weeds on the clam beds (Attipoe and Amoah, 1989).

Generally, for exploited stocks, a fishery is managed sustainably when fishing mortality (F) is equal to natural mortality (M) i.e. when the exploitation level is equal to 0.5 (Gulland, 1965). The results from this study showed that fishing mortality was higher (0.47 $year^{-1}$) at Ada compared with Aveglo (0.21 $year^{-1}$). The mean fishing mortality levels calculated directly from the commercial catch (Chapter 6) were slightly higher at 55 and 58% for Ada and Aveglo, respectively. This shows that fishing mortality has gone beyond the recommended sustainable threshold level of 50% and management interventions are required to reverse the trend. The higher fishing mortality observed in this study is in agreement with the findings of Moses (1990) who estimated a fishing mortality 0.50 $year^{-1}$ in a population of *G. paradoxa* in the Cross River. Similarly, studies by Etim and Brey (1994) and King (2000) concluded that the stocks of *G. paradoxa* in the Cross and Nun Rivers, Nigeria, were overfished and needed regulation.

7.2 Potential for Aquaculture

The suitability of *G. paradoxa* as a potential aquaculture species has been demonstrated by growth trials in the Volta Estuary (Attipoe and Amoah, 1989; Kumah, 2000) and work here on growth shows that the species has an annual growth rate of $\approx$ 10 mm. It is a species that could easily be integrated into the local tilapia and catfish cage systems since they do not require external feed and can clean the environment of excess phytoplankton or suspended particulate matter through filter feeding. Integration into the existing fish farming systems will augment the income of fish farmers, especially pen culturists in the Volta River as it will utilise the same space and water resources. Large tracts of suitable areas exist in the previous range of

the species (up to 100 km) from the mouth of the river. Moreover, the communities around the estuary are already practising a form of culture which relies on juveniles from the fishery.

There are still unresolved issues concerning the larval dynamics of *G. paradoxa* that must be addressed before hatchery production would be feasible. These could be resolved by laboratory experiments aimed at artificially spawning *G. paradoxa* broodstock collected from the estuary between May and July. The provision of a cooler period has been used to spawn tropical species such as *Crassostrea rhizophorae* in Cuba. The bivalves are held in water chilled to between 5 and 10°C below ambient temperature with an adequate food supply for a period of 4 to 6 weeks. Afterwards, they are gradually warmed to ambient conditions with a greater percentage of adults maturing gametes synchronously (FAO, 2004). Different salinity regimes could be evaluated to ascertain the optimum salinity for larval development.

The large number of eggs (10^6) per *G. paradoxa* female means fewer females would provide a large quantity of eggs needed for hatchery production. However, the low number of males in the population would mean higher numbers of broodstock have to be collected to ensure that there are enough males to guarantee successful fertilization of eggs. Until these issues are resolved, it is recommended that the farming of *G. paradoxa* should rely on juvenile clams collected from the fishery in order to develop a large pool of clam culturists before the production of hatchery raised juveniles for sale to clam culturists.

7.3 Socio-economics of *G. paradoxa* Fishery

G. paradoxa is the basis of a thriving artisanal fishery in the estuary of the Volta River. The fishery has for decades supported the livelihood of women, who fished, processed, marketed and to some extent fattened smaller clams to marketable sizes (Lawson, 1963). Apart from the meat, the shell has a number of important uses especially as a source of calcium in poultry

feed and in lime manufacturing. The shells are also used as an alternative to stone chippings in concrete. Additionally, it is used as a pavement material to overcome muddy conditions in village compounds in the southern parts of the Volta Region, Ghana.

The Lower Volta basin is predominantly rural with limited economic activities. The main occupation of the inhabitants is agriculture which is mostly subsistence crop farming and fishing. Women in the communities usually combine trading (Tuesdays) with their work on the farm. Clam fishing, therefore, plays an important role in the socio-economic lives of inhabitants of the Volta Estuary not only as a source of food and raw material (shells) for small-scale industries but also as a source of employment. An average of 503 fishers operates in the Volta Estuary with an annual yield of 7700 tonnes. This excludes the large number of subsistence fishers whose catch is usually for home consumption. Annually, the fishery generates a gross income in excess of GH¢ 4,620,408 (2.3 million Euros).

7.4 Conclusions

In conclusion, the reproductive cycle of *G. paradoxa* in the Volta River is annual with a single spawning event between July and October. Gametogenesis starts in December and progresses steadily to a peak in June – July when spawning begins until November when the clams are spent. The condition and gonadal indices showed a clear relationship with the gametogenic stages rising from minimum values at stage (I) start of gametogenesis to the maximum values at stages (IIIA) ripe and (IIIB) start of spawning before declining significantly to stage (IV) spent. The condition and gonadal indices may prove a valuable monitoring technique in fishery management to recognise the reproductive stage of *G. paradoxa* populations as it is less expensive and time consuming than histological techniques.

The progression of oocyte diameters appears sensitive to changes in the gametogenic cycle and may be useful in comparing the reproductive cycle and spawning events of *G. paradoxa* from different populations. *G. paradoxa* is gonochoristic with a dominance of females and a high incidence of hermaphrodites in the population. It is iteroparous and produces planktotrophic eggs with an average 10^6 per female per year. *G. paradoxa* may be described as restrained with regards to the allocation of resources between somatic growth and reproduction.

Commercial extinction of *G. paradoxa* is imminent in the Volta Estuary as a result of habitat alteration and overfishing. There is the need to put in place a sustainable harvesting measure that will target medium to large size clams against the current situation where the catch is dominated by smaller clams. A careful consideration of the production and P: B ratios show that productivity is maximum in the 3 - 4 year old clams, after which it declines. It is recommended that a minimum landing size of 50 mm which corresponds to the mean size of a 4 year old clam should be imposed. This should be done in consultation with the chiefs and traditional authorities in the two communities which have managed the fishery to date. The marketing of clams below the 50 mm shell length limit should be abolished and enforced by the traditional authorities. Secondly, the farming of smaller clams, which is a traditional activity in the estuary, should be encouraged so that fishers who harvest undersize clams can seed them onto their culture plots.

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APPENDICES

Appendix 1. Gametogenic stages of *G. paradoxa* showing the five stages identified and the month of collection of samples from the Volta Estuary, Ghana

month	I (start)	II (Advanced)	IIIA (Ripe)	IIIB (Spawning)	IV (Spent)	Total
Mar-08	5	0	0	0	0	5
Apr-08	2	0	0	0	0	2
May-08	0	3	1	0	0	4
Jun-08	0	3	1	0	0	4
Jul-08	0	0	5	4	0	9
Aug-08	0	0	9	5	0	14
Sep-08	0	0	2	16	3	21
Oct-08	0	0	0	3	9	12
Nov-08	3	0	0	0	12	15
Dec-08	7	0	0	0	6	13
Jan-09	9	0	0	0	1	10
Feb-09	14	0	0	0	0	14
Mar-09	4	9	0	0	0	13
Apr-09	2	15	0	0	0	17
May-09	0	13	2	0	0	15
Jun-09	0	0	11	1	0	12
Jul-09	0	0	7	10	0	**17**
Aug-09	0	0	0	3	1	4
Sep-09	0	0	0	13	2	15
Oct-09	0	0	0	14	2	16
Nov-09	0	0	0	7	8	15
Dec-09	3	0	0	0	8	11
Jan-10	7	0	0	0	2	9
Feb-10	10	0	0	0	1	11
TOTAL						**278**

Appendix 2. Environmental variables monitored at the Volta Estuary from March 2008 to February 2010.

Month/Year	Temp (° C)	pH	Cond. (µS/cm)	Salin (psu)	DO (mg/l)	Alkalinity (mg/l)	NO_3 (mg/l)	PO_4 (mg/l)	Chl a (µg/l)
Mar-08	28.2	6.99	62	0.03	8.78	50.0	0.71	0.14	
Apr-08	28.0	7.05	60	0.03	7.21	50.0	0.63	0.13	
May-08	29.2	6.63	61	0.03	5.84	52.5	0.23	0.15	6.1
Jun-08	28.5	6.99	66	0.03	6.33	40.0	0.20	0.06	6.5
Jul-08	28.4	8.39	83	0.04	4.97	40.0	0.20	0.03	7.9
Aug-08	27.4	7.04	65	0.03	3.07	45.0	0.27	0.21	5.4
Sep-08	27.3	6.48	63	0.03	2.48	60.0	0.61	0.18	5.0
Oct-08	29.0	6.19	63	0.03	2.52	45.0	0.43	0.08	5.0
Nov-08	29.3	6.89	64	0.03	2.19	50.0	0.35	0.13	4.7
Dec-08	29.1	6.47	58	0.03	2.55	50.0	0.60	0.12	3.3
Jan-09	29.5	8.50	59	0.03	6.11	42.5	0.18	0.12	4.2
Feb-09	28.4	7.20	60	0.03	3.58	60.0	0.36	0.12	10.4
Mar-09	28.8	7.07	53	0.02	3.99	60.0	0.93	0.12	4.6
Apr-09	28.9	6.56	63	0.03	3.04	45.0	0.46	0.14	4.2
May-09	29.6	6.58	52	0.02	3.41	40.0	0.63	0.19	1.7
Jun-09	29.6	6.85	54	0.02	3.18	40.0	0.23	0.21	5.0
Jul-09	28.6	7.20	55	0.02	4.48	30.0	0.20	0.06	5.0
Aug-09	27.0	7.41	52	0.02	4.53	37.5	0.20	0.03	6.3
Sep-09	27.4	7.15	50	0.02	4.4	40.0	0.27	0.21	8.3
Oct-09	28.9	7.14	53	0.02	1.78	50.0	0.61	0.18	3.3
Nov-09	29.08	7.49	48	0.02	2.46	40.0	0.43	0.08	6.3
Dec-09	27.7	6.71	55	0.02	3.1	30.0	0.35	0.11	4.2
Jan-10	29.4	6.95	46	0.02	5.79	30.0	0.60	0.15	4.2
Feb-10	29.4	6.56	45	0.02	8.97	35.0	0.18	0.09	6.3