SEASONALITY AND FISH REPRODUCTION
IN AN INTERMITTENT STREAM

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ABSTRACT

Seasonality and fish reproduction in an intermittent stream.

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During the period 1980 to 1986, the adjacent Quarahoon and Carlisle Rivers in the southwestern peninsula of Trinidad were studied with reference to seasonal effects on limnology and reproductive strategies of six fish species: *Gasteropelecus sternicla*, *Corynopoma riisei*, *Astyanax bimaculatus*, *Hemigrammus unilineatus*, *Corydoras aeneus* and *Poecilia reticulata*.

Stream flow regimes were intermittent reflecting a main dry season from January to May and a main rainy season from June to December with a minor dry period between September and November. These streams were considered long-flow intermittent streams with substantial refuge areas capable of maintaining diverse faunal assemblages. The fauna was characteristic of lentic or slow-flow conditions and was well adapted to survive conditions of stagnation and drought. Seasonal flow influenced variation of physical and chemical features and the biota. Production of plankton increased significantly during prolonged lentic periods and decreased with floods. Benthic standing crop and allochthonous input showed wide variation in both dry and rainy seasons.

Species richness of fish communities was high and may have resulted from intermediate disturbance levels and proximity to the mainland. Seasonal flow regimes strongly influenced fish population sizes, life history characteristics and reproductive strategies. Population fluctuations appeared to be due to mortality, dispersal, concentration and input of juveniles during breeding seasons. Life history traits were characteristically r-selected. Peaks of reproduction in five species coincided with the rainy seasons while *P. reticulata* bred continuously. Numbers of breeding seasons each year and their lengths varied from one short major season with rarely a second each year to long seasons twice each year. Spawning patterns also varied from a highly synchronised total spawning pattern to continuous small brood production. Maximum batch fecundities were directly proportional to species size but smaller species achieved high fertilities by multiple spawning which allowed high but variable reproductive output. Reproductive strategies were diverse but highly adaptable to fluctuating conditions.

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GENERAL INTRODUCTION

Seasonal changes in tropical regions were until recently, widely believed to be absent because of minimal variation in temperature and the duration and intensity of sunlight, all important factors determining seasonality in temperate regions (Schwassmann 1980). However, it is now well recognised that rainfall is critical in many tropical areas and the alternating wet and dry seasons have strong effects on the structure and functioning of biological communities (Dobzhansky 1950, Farnworth & Golley 1974, Krebs 1985). In addition, with increasing latitude away from the equator, the total amount of rainfall per year decreases and the seasonality of its distribution during the year varies from being almost non-seasonal at the equator to having distinct wet and dry seasons in mid-tropical latitudes (Jackson 1977). Superimposed on this general climatic scheme are the localised effects of the positions of the sub-tropical high-pressure cells, oceans, the shape and extent of land masses or seas, and varying characteristics of the trade winds and the equatorial trough. Thus, a climatically heterogenous situation exists within the tropics with some regions having a more pronounced seasonal cycle than others with respect to rainfall.

The timing of onset of animal reproduction and its duration are both closely tied to environmental variables in order to maximise reproductive success. Many tropical species belonging to a variety of groups show extended breeding seasons consistent with favourable year-round environmental conditions (reviews in Kramer 1978a and UNESCO/UNEP/FAO 1978). In contrast, many other species have well defined annual breeding cycles (Bullough 1961, review in UNESCO/UNEP/FAO 1978). Such variation in breeding may be related to studies being carried out in areas of unequal seasonal variation (Kramer 1978a, Schwassmann 1980, Hails & Abdullah 1982) or may be due to biotic factors such as competition (Bertness 1981) or varying food availability (Dobzhansky 1950, Ricklefs 1966, Karr 1976) controlling the timing of reproductive cycles. It is felt by some biologists that biotic factors play a dominant role in regulating the functioning of many tropical communities (Robinson 1978) but the role of abiotic factors may also be influential in many respects (for example Stout 1982).

The reproductive timing of tropical freshwater fishes also mirrors the variability seen in other groups. In an extensive review of the ecology of tropical freshwater fishes, Lowe-McConnell (1975) documented a range of reproductive strategies involving, among other aspects, variation in spawning frequency, fecundity, migration patterns and parental care. Throughout the review, she stressed the seasonal nature of reproduction and coincidence of the time of spawning of fish in lotic habitats with the annual rains and resulting floods. This is supported by other workers such as de Vlaming (1974), Billard & Breton (1978) and others reviewed in Lam (1983). Such timing may be adaptive since rising water levels increase available habitat, reduce predator densities and favour increased primary and secondary productivity for juvenile feeding. Kramer (1978a) pointed out that this conclusion is largely based on studies carried out in floodplains or large rivers which are both highly seasonal habitats.

Schwassmann (1978, 1980) attempted to summarise more recent studies by distinguishing between seasonal cycles of breeding in floodplain lakes and rivers and those of small forest streams. The former he described as highly seasonal environments where fish have very seasonal breeding cycles. Most of the fish in these habitats are total spawners (all eggs ripen synchronously and are spawned in one batch) in order to take advantage of a rapidly expanding and highly productive habitat. In contrast, small forest streams are permanent with no appreciable seasonal differences in water level. As a result, fish living in this habitat are multiple spawners (eggs ripen and develop in several batches during one reproductive season) and they may spawn for extended periods. However, in a detailed study of six fish species in a mildly seasonal Panamanian forest stream, Kramer (1978a) found 'considerable diversity in reproductive periodicity' (p. 982). Some species showed breeding periods coincident with the rainy season, others with the dry season, while the duration of breeding ranged from one to two days per year to almost continuous breeding. He proposed a number of hypotheses relating breeding periodicity to biotic rather than climatic causal factors. In summary, controlling factors proposed were: adult or juvenile food availability, competition for food among juveniles, competition for breeding sites, seasonality acting as a mechanism for reproductive isolation, and the phylogeny of the species. Nikolskii (1961) had also proposed previously that biotic factors could influence reproductive timing in fishes: year-round food availability would allow extended breeding periods, but conflicts over spawning grounds or food for young would result in different periods of reproduction. No data were given in support of these ideas however. In a review of seasonality in tropical fishes, Lowe-McConnell (1979) pointed out several instances where biotic factors may determine the breeding time of riverine fishes.

More recent studies of reproductive cycles in tropical freshwater fishes do not clarify the situation. Many show seasonal peaks of breeding activity coincident with the rains (Tan 1980, Hails & Abdullah 1982, Orr & Milward 1984, Cambray & Bruton 1984). In contrast however, Beumer's (1979) study of two species in a seasonally flooding Australian stream described two contrasting strategies: one species exhibiting a short well-defined spawning period coincident with the floods, the other showing a protracted spawning period over most of the year.

Some studies have elucidated the nature of the factors controlling gonad development and spawning in tropical freshwater fishes. These include field observations suggesting that floods trigger spawning activity of Indian carp (Khanna 1958), while laboratory experiments simulating rain in association with decreased pH and specific conductivity, and increased water levels, show that these variables play a definitive role in initiating gonad development and spawning in a gymnotoid fish (Kirschbaum 1975). Social factors such as pheromones or visual stimuli have also been implicated in promoting ovulation (review in Lam 1983). Lam (1983) concluded that the environmental control of fish reproductive activity is much more complex in tropical than temperate species. In addition, the proximate cues for initiating gametogenesis, spawning and gonadal regression will not necessarily be the same because of the different times of year when these activities occur. Much more information is therefore needed for tropical fishes to determine the proximate cues controlling their annual cycles, in addition to determination of the ultimate factors selecting for different patterns of seasonality in their reproduction (Kramer 1978a, UNESCO/UNEP/FAO 1978).

In summarising the ecological characteristics of fish communities in different tropical freshwater habitats, Lowe-McConnell (1975) characterised the African Great Lakes as being very stable and savanna floodplain rivers as very seasonal with upper layers of lakes and equatorial forest rivers lying between on a continuum of seasonality from stable to seasonal. She described forest rivers as showing twice yearly variation of two high and two low periods per year but rain generally occurs all year whereas floodplain rivers show one annual flood. Both show lateral flooding into the surrounding forest or savanna to increase habitat size during the wet season. Although intermittent streams were not included in Lowe-McConnell's seasonal spectrum, it can be expected that they should lie at the most seasonal end of the continuum because of their drastic flood/drought characteristics (Williams & Hynes 1977). However, compared with floodplain and forest rivers, the nature of habitat variation is quite different. For example, although the available aquatic habitat expands in the wet season, it also changes from previously lentic conditions (dry season pools) to lotic conditions. Current velocity is a major factor affecting aquatic communities (Hynes 1970) and the sudden increase in current velocity and water levels in the wet season can result in reduced fish and invertebrate populations (Stehr & Branson 1938, Paloumpis 1958, John 1964). In comparison, floodplain rivers expand laterally in the wet season onto surrounding low-lying savanna or forest resulting in an increased habitat with lentic characteristics which fish then utilise for feeding or spawning (Lowe-McConnell 1975, 1979, Welcomme 1979, 1985). In the dry season, intermittent streams are affected by drought conditions causing a rapid decrease in water level leading either to the formation of remnant pools or complete drying out. It is well documented that in these conditions increased mortality of both fish and invertebrate fauna may occur, especially if complete drying takes place (Paloumpis

1958, Larimore *et al* 1959, Williams & Hynes 1977) or when fish become concentrated into remnant pools and suffer heavy losses from aquatic and terrestrial predators (Larimore *et al* 1959, John 1964), a situation not unlike floodplain savanna pools. Lentic conditions develop at this time however, and crops of plankton, algae and other organisms adapted to stagnant conditions, as well as opportunistic species may colonise these remnant pools (Larimore *et al* 1959, Williams & Hynes 1977, Extence 1981) and secondary productivity may increase. The increase in food availability and reduction in current velocity during the dry period may be favourable for breeding for some species as compared to the wet flood season (Lowe-McConnell 1979). Therefore, although intermittent streams may show a similar range of seasonal variability as floodplain rivers, the differences outlined above may impose different selective pressures on the breeding biology of the component species.

In temperate intermittent streams, the timing of fish reproduction varies: some species spawn with the floods (normally in spring), others do not seem to have any correlation with floods, yet others spawn in the stagnant summer pools (Paloumpis 1958, Deacon & Minckley 1974, Williams & Coad 1979). Certain advantages exist for reproduction and juvenile survival in intermittent streams as compared to permanent ones including early spring breeding being possible, plentiful food and reduced predation in summer pools (Williams & Coad 1979). However John (1964) noted that prolonged drought prevented reproduction because of reduced availability of food. The duration of the breeding cycle may also be unpredictably long for such a seasonal environment. Deacon & Minckley (1974) and Williams & Coad (1979) recorded for seasonal desert and intermittent streams, that protracted breeding seasons may occur, in some cases leading to a rather complex situation. For example in the Sonoran and Mohave Deserts, stream minnows show a predominance of reproduction in spring, first by older females and later by younger ones; old females may then develop an additional complement of eggs, in some cases throughout the summer, resulting in a highly seasonal cycle for younger individuals and a protracted cycle for older individuals (Deacon & Minckley 1974).

Studies on the reproductive biology of fishes in tropical intermittent streams are few. The reproduction and development of two catfishes were studied by Orr & Milward (1984) in North Queensland, Australia. Both species showed timing of spawning coincident with the floods and there were two migrations and spawnings about a month apart for each species during the flood season.

Timing of onset and the duration of reproductive activity are only two aspects of an animal's reproductive strategy. Other aspects include reproductive effort, age of onset of reproduction, fecundity and frequency of reproduction (Moyle & Cech 1982, p. 127). Reproductive effort represents the amount of energy or time invested in the production of offspring and includes investment in gonads and secondary sexual characters as well as courtship, parental care and other reproductive behaviour. Some of the above aspects of reproductive strategies have been reviewed in some detail for tropical freshwater species by Lowe-McConnell (1975) but primarily for floodplain species. Considerable variation seems to exist in the reproductive strategies of these fishes even within the same habitat. Beumer (1979) further exemplifies this in showing that two contrasting strategies can be equally successful in the same habitat even though the species differ with respect to the timing of onset and duration of spawning, fecundity, egg size, mode of dispersal of eggs, developmental rate and stage of development at hatching.

In order to generalise however, life history theories predict that in a very variable environment such as expected in an intermittent stream, species will show characteristics of r-selection (Pianka 1970). They should have a small body size, short life span, rapid development, early reproduction, high intrinsic rate of population increase, semelparity (one period of reproduction during its lifetime), low energetic investment per offspring, and no parental care. Stearns (1976) suggested that in variable seasonal environments, the predictability of such variation would affect the life history pattern. It has been suggested that an important component of tropical seasonality is its low degree of predictability (Farnworth & Golley 1974). Although a dry season may occur every year, the time of its onset and its duration may be highly variable (Jackson 1977) and this variance will exert a powerful influence on the evolution of population characteristics (Levins 1968). In unpredictable environments, Stearns (1976) suggested that the optimal tactic would be to spread the risk of hatching too early or too late in any given cycle by generating a distribution of hatching times in the clutch that matches the historical probability distribution of the optimal date for reproduction. This concurs with ideas put forward by Nikolsky (1963) and Lowe-McConnell (1975) that multiple spawning (including partial and small-brood spawning) is advantageous as a strategy in unpredictable habitats in order to decrease the chances of one or more generations being lost due to unfavourable environmental conditions. If predictability of the conditions during the cycle is also low, the reproductive tactic should be modified further. For animals with a generation time less than the period of the cycle, the amount of expended reproductive effort should be variable and clutch sizes should be small. If the generation time is relatively long compared to the period of the cycle of environmental fluctuation, then iteroparous reproduction (more than one period of reproduction during a lifetime), and not semelparity as earlier predicted, may be expected with, again, small clutch sizes. Variable reproductive effort may theoretically be achieved by multiple spawning fishes which may vary the number of times spawning takes place during the breeding season depending on the favourability of environmental conditions (Macer 1974). Multiple spawners are quite commonly found in seasonal rivers (Lowe-McConnell 1975, Welcomme 1979, Cambray & Bruton 1984). In addition, multiple spawners have lower fecundities than total spawners in the same habitat (Lowe-McConnell 1975, Welcomme 1979), presumably concurring with small 'clutch' sizes as predicted.

In summary, certain predictions may be made on the basis of previous studies as to the nature of seasonality and its effects on the reproductive strategies of fish in an intermittent stream:

(a) Tropical intermittent streams should be highly seasonal, variable and unpredictable habitats.

(b) Seasonal variation of hydrology and biological productivity should not be of the same nature as that seen in other tropical lotic habitats.

(c) The reproductive strategies of fishes should reflect this seasonality and degree of unpredictability but may be highly variable in expression.

  (i) Life history parameters of fish should be characteristic of those of r-selected species.

  (ii) The timing of onset and duration of the breeding seasons should be cued to the most favourable period for the species and this may not be the flood season.

  (iii) Multiple spawning should occur in a high frequency of fishes due to its advantageous nature in unpredictable habitats.

In order to test these predictions, this study has the following objectives:

1. To document the physical and chemical characteristics

of the stream environment.

2. To document the differences in biological productivity between dry and wet seasons for the benthos and plankton within the stream, and the influence of allochthonous material from the terrestrial environment.
3. To determine the diversity of fish species within the stream.
4. To monitor the population demography and dynamics of six species of fish, including population fluctuations and structure, growth rates and life spans.
5. To investigate the reproductive strategies of six fish species, including size at maturation, timing of onset and duration of breeding activity, fecundity, and spawning pattern.

THE STREAM ENVIRONMENT

INTRODUCTION

Studies of tropical freshwater systems have concentrated primarily on lakes (Beadle 1974) or on large floodplain river systems such as those of the Amazon, Paraná, Niger and Senegal Rivers (Welcomme 1979). Floodplain rivers are especially interesting because of the unique interdependence of their lotic and lentic components and high fisheries production; features not readily seen in temperate rivers in their present forms (Bayley 1980). Lowe-McConnell (1975) and Welcomme (1979, 1985) thoroughly reviewed the nature of floodplain river systems with particular reference to their fisheries ecology.

Small tropical rivers and streams have not received the same attention as lakes or floodplain rivers despite the fact that they may make up a significant proportion of the aquatic habitat of important river systems such as the Amazon, in addition to being individually unique and surprisingly diverse in faunal composition (Junk 1983). Data on these small aquatic systems are scattered and pertain to isolated, often limited studies. Hynes (1970) reviewed some of the work carried out in tropical rivers and streams and attempted to integrate it into general ideas on the functioning of lotic systems. More recent work on tropical streams includes a very detailed and comprehensive study of a small Malayan river, Sungai Gombak (Bishop 1973). Other studies are geographically widespread and include those in Australia (review in Williams 1981), Africa (reviews in Davies 1979, Davies & Hart 1981, Awachie 1981, Davies *et al* 1982), Central and South America (Templeton *et al* 1969, reviews in Ziesler & Ardizzone 1979, Sioli 1984).

Hydrobiological studies in the West Indies are lacking compared to those from other Neotropical regions. Many studies are related to the taxonomy of aquatic groups (reviews in Hurlbert *et al* 1981, Hurlbert & Villalobos 1982). A few are of an ecological nature. For example in Puerto Rico Padgett (1976) investigated the processes of leaf decomposition in a small stream and Covich (pers. comm.) has continued work in this area. Hunte (1976) conducted a thorough study on the biology and ecology of three freshwater prawns in high gradient streams in Jamaica.

In the Lesser Antilles, published studies on lotic systems and their fauna have concentrated on certain islands.

The Bredin-Archbold-Smithsonian Survey of Dominica included studies on the physico-chemical nature of the aquatic habitats over a limited period of time (Hart & Hart 1969). Other lotic systems have been studied in some detail in St Vincent and St Lucia. Emphasis in these studies was largely on comparisons of different types of aquatic habitats and the zonation and distribution of aquatic fauna (Harrison & Rankin 1975, 1976 a, b, McKillop & Harrison 1980) and the population dynamics of molluscs of medical importance (Harrison & Rankin 1978, Rankin & Harrison 1979, McKillop *et al* 1981, McKillop & Harrison 1982).

In Trinidad, several studies of varying detail and emphasis have been carried out on lotic systems. These include Thornhill *et al* (1967) on the general ecology of a small portion of the Maracas River; Hynes (1971) on the longitudinal zonation of fauna in the Arima River; the Caroni River Basin Survey (Trinidad & Tobago 1976 a, b) which included analyses of the hydrology and water chemistry of the Caroni River and some of its tributaries; and Bacon *et al* (1979) who documented the physico-chemical characteristics of streams and rivers of the Nariva Swamp catchment. Unpublished studies include Carrington (1980) giving a detailed description of the physico-chemical features of the

Maracas River, and Caesar (1985) documenting the effect of siltation on the benthic fauna of a tributary of the Maracas River.

From the above review, it is clear that few studies in the Neotropical region have focused on the general ecology of an entire stream system and in particular, seasonal variation is not dealt with in many studies. Also, most of the studies conducted have concentrated on upland streams originating from high altitudes and only Bacon *et al* (1979) and McKillop & Harrison (1980) dealt with aspects of lowland streams in east central Trinidad and St Lucia respectively. Since stream flow characteristics are affected by a variety of factors such as rainfall seasonality and variability, catchment size, slope, geology, soil and vegetation (Beaumont 1975, Jackson 1977), lowland stream hydrology can be expected to vary markedly from that of upland streams and consequently affect the nature of the biota differently. In addition, the chemical composition of river water and its seasonal variation are largely determined by factors such as the amount and variability of precipitation, the nature of the bedrock and the evaporation-crystallisation process (Welcomme 1979). These factors will also vary between upland and lowland regions as well as between streams on soils of volcanic origin (the Lesser Antilles) and those of alluvial origin (Trinidad). In particular, some of the above factors may account for the phenomenon of intermittency seen in the stream under study.

Intermittent streams are defined as those which flow during the wet season but dry up during the season of drought (Ward 1975, p. 243). They are fed mainly by quickflow (channel precipitation, surface runoff and rapid interflow) but during the wet season baseflow (groundwater runoff and delayed interflow) makes some contribution when the water table rises above the bed of the stream. Such streams can be distinguished from ephemeral streams which are temporary lotic habitats fed entirely by precipitation, and perennial streams which flow continuously because of adequate year-round groundwater flow. However, many streams may be ephemeral or intermittent in their upper reaches and perennial in their lower, making it difficult to allocate them to a specific category (Ward 1975).

Intermittent streams are considered special lotic habitats having much in common with temporary lentic habitats such as temporary ponds and other small water bodies (Hynes 1970, Williams & Hynes 1976). They exhibit many features of ecological interest including the wide variety of life history strategies which may be utilised for survival by flora and fauna. Also of importance is the process of biological succession which occurs seasonally as conditions in the stream change from being lotic to lentic and eventually terrestrial (Williams & Hynes 1977). Even when the stream bed is completely dry, organisms characteristic of the soil fauna may be present (Moon 1956). Williams & Hynes (1977) also documented situations in temporary streams where there may be coexistence of closely related species with similar ecological requirements. They attributed this to be the result of either abundant food or a lack of selective pressures to promote specialisation. Intermittent streams therefore, are specialised aquatic systems bearing characteristics of both lotic and lentic environments and providing opportunities for studies of life history strategies, ecological succession and community interactions.

Both intermittent and temporary streams have received some attention in temperate moist and arid regions (reviews in Hynes 1970, Deacon & Minckley 1974, also Williams & Hynes 1976, 1977, Williams 1977, Iversen *et al* 1978). Several studies have also been conducted in the tropics, predominantly in Africa. Thornton (1980) made a preimpoundment study of the nutrient loadings and water chemistry of the Kwe Kwe River, Zimbabwe. Adebisi (1981 a, b) gave details on the hydrology and water chemistry as well as the feeding biology of the fishes of the Upper Ogun River, Nigeria. Studies on the Bandama River system, Ivory Coast, with particular reference to the taxonomy, zonation and population dynamics of the Hydropsychidae have been reported by Statzner (1982) and Gibon & Statzner (1985). A further study of the Bandama River by Lévêque *et al* (1983) thoroughly documented the hydrology and seasonal variation in phytoplankton and benthic invertebrate production in addition to the general biology and population dynamics of some fish species as part of a surveillance programme of aquatic habitats regularly treated with insecticides for the control of blackflies. In the Caribbean, McKillop & Harrison (1980) gave brief descriptions and water chemistry data for both high and low altitude temporary streams in St Lucia. However, Rzóska (1961) in a review of temporary aquatic habitats in Africa, stressed that even within the tropics climatic variation is sufficiently large to produce temporary aquatic habitats of varying permanence. This factor he asserted, is a major influence on faunal composition of such habitats.

In consequence, the objectives of this part of the study are:

(1) To determine the range of physical and chemical variation in the study site in relation to influencing factors such as rainfall and watershed characteristics, and as compared to other streams studied locally and regionally.

(2) To document the diversity of the stream fauna and the range of strategies for survival in the habitat.

(3) To determine the nature of seasonal variation and succession of stream faunas with particular reference to those aspects important in influencing the reproductive seasonality of the fishes.

THE STUDY SITE

Trinidad is the most southerly located of the Eastern Caribbean Islands lying approximately 20 km off the coast of northeastern Venezuela (Fig.1). Seasonal variation of climate generally fluctuates between a dry season (January to May and a rainy season (June to December) with a short dry period in September/October, the 'petit carême'. Rainfall is unevenly distributed over the island with annual rainfall totals ranging from over 3000 mm in the northeast

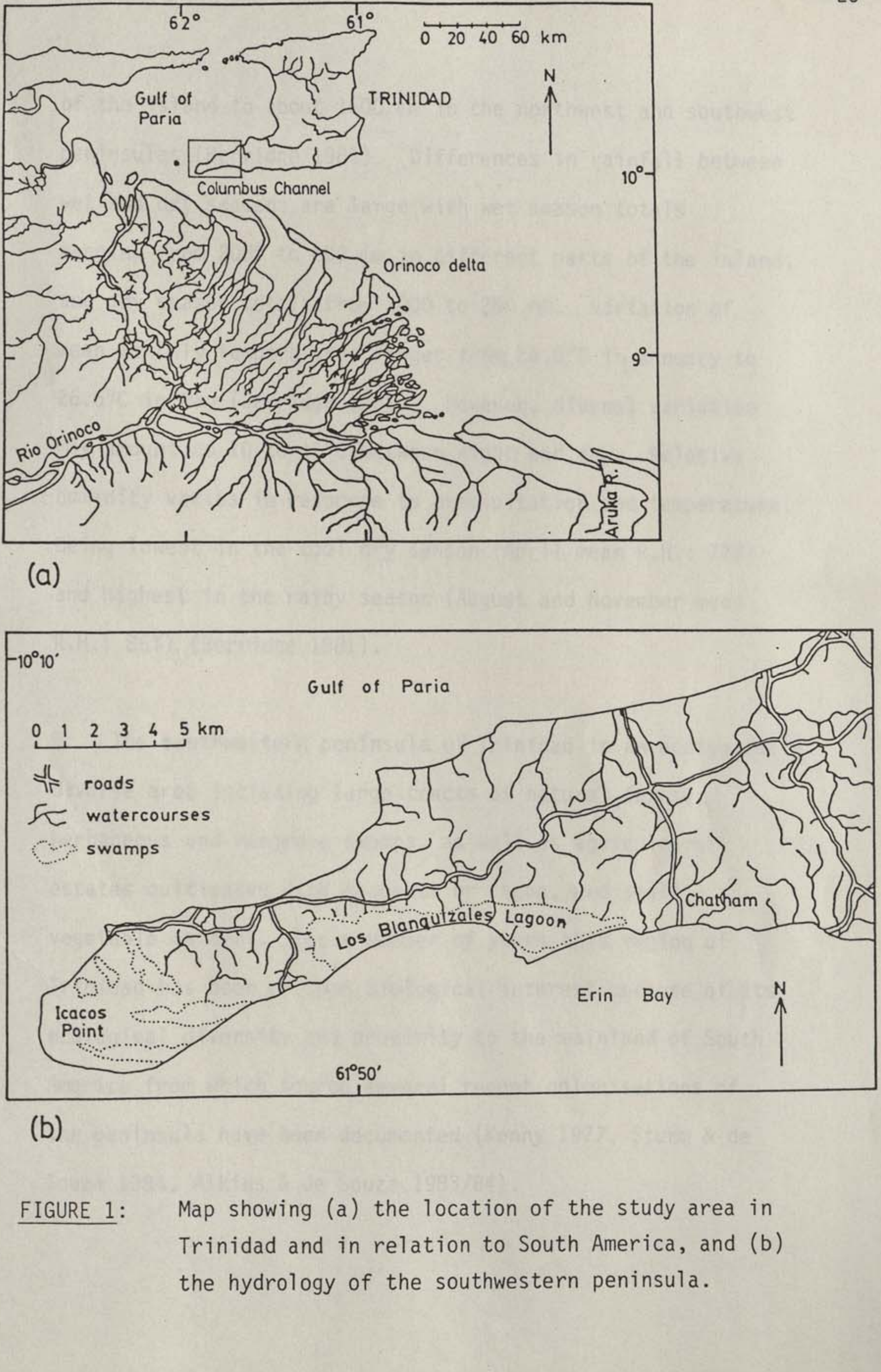


FIGURE 1: Map showing (a) the location of the study area in Trinidad and in relation to South America, and (b) the hydrology of the southwestern peninsula.

of the island to about 1500 mm in the northwest and southwest peninsulas (Berridge 1981). Differences in rainfall between wet and dry seasons are large with wet season totals ranging from 2000 to 600 mm in different parts of the island, and dry season totals from 1000 to 250 mm. Variation of mean monthly temperatures ranges from 24.5°C in January to 26.6°C in May (Berridge 1981). However, diurnal variation may amount to 10 to 15°C between night and day. Relative humidity varies in response to precipitation and temperature, being lowest in the cool dry season (April mean R.H.: 77%) and highest in the rainy season (August and November mean R.H.: 86%) (Berridge 1981).

The southwestern peninsula of Trinidad is an ecologically diverse area including large tracts of natural forest, herbaceous and mangrove swamps, as well as agricultural estates cultivated with coconuts or cocoa, and small vegetable gardens. For a number of years this region of Trinidad has been of some biological interest because of its ecological diversity and proximity to the mainland of South America from which source several recent colonisations of the peninsula have been documented (Kenny 1977, Sturm & de Souza 1984, Alkins & de Souza 1983/84).

A number of small watercourses drain the peninsula, running northward into the Gulf of Paria or southward into the Columbus Channel (Fig.1). According to Ordnance Survey maps (1977), the Quarahoon River in conjunction with its major tributaries, drains an area of approximately 16 km^2 along the Chatham Road (South) and enters the sea at two points in Erin Bay. This river has not been mapped adequately and local residents maintain that two watercourses exist: a larger more westerly one being the Carlisle River, and the smaller eastern stream being the Quarahoon River. Field checks confirm the presence of two separate watercourses and in this study they have been named according to the local residents (Fig.2). However, they are connected in their lower reaches by a series of artificial canals and ditches and are therefore not entirely independent of each other.

The catchment area of the Quarahoon and Carlisle Rivers has a gently undulating physiography with maximum elevations not greater than 60 m. Geologically, the area is formed of Pliocene sedimentary deposits, the Erin Formation, which is characterised by thick, predominantly regularly bedded sands with interbeds of grey silty clay (Barr & Saunders 1965). The clay layers may often be mixed with lignite

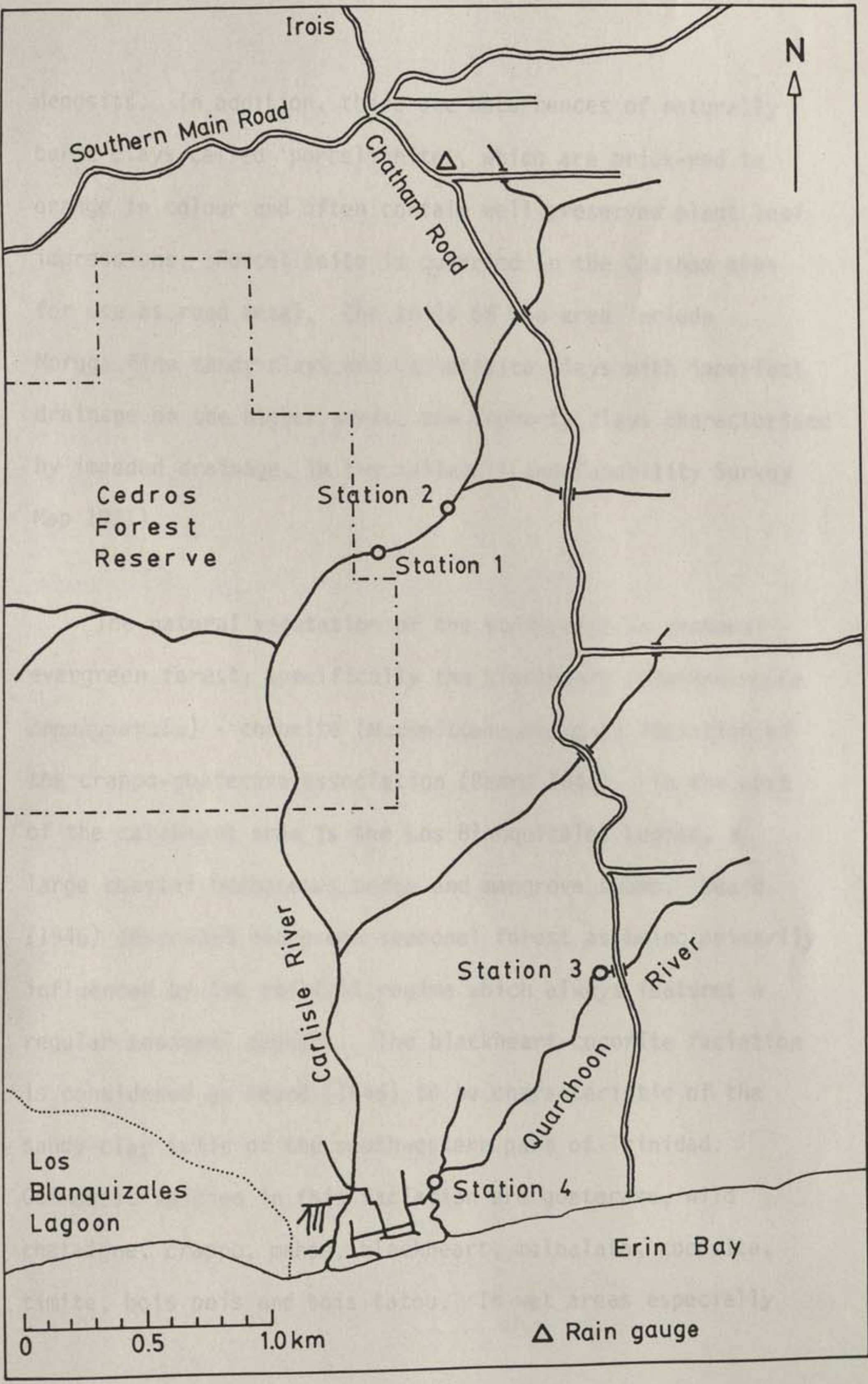


FIGURE 2: Map of the study area showing sampling stations (key as for Figure 1).

deposits. In addition, there are occurrences of naturally burnt clays called 'porcellanite', which are brick-red to orange in colour and often contain well preserved plant leaf impressions. Porcellanite is quarried in the Chatham area for use as road metal. The soils of the area include Moruga fine sandy clays and La Retraite clays with imperfect drainage on the higher areas, and Cromarty clays characterised by impeded drainage, in the valleys (Land Capability Survey Map 1971).

The natural vegetation of the study area is seasonal evergreen forest, specifically the blackheart (*Clathrotropis brachypetala*) - cocorite (*Maximiliana elegans*) faciation of the crappo-guatecare association (Beard 1946). To the west of the catchment area is the Los Blanquizales Lagoon, a large coastal herbaceous sedge and mangrove swamp. Beard (1946) described evergreen seasonal forest as being primarily influenced by the rainfall regime which always features a regular seasonal drought. The blackheart-cocorite faciation is considered by Beard (1946) to be characteristic of the sandy-clay soils of the southwestern part of Trinidad. Commonest species in this faciation are guatecare, wild chataigne, crappo, mahoe, blackheart, malbalata, cocorite, timite, bois pois and bois tatou. In wet areas especially along stream edges, dominants are crappo, wild chataigne, mahoe, wild nutmeg, bloodwood and olivier mangue with an understorey of timite (Beard 1946). Large areas of the natural forest east of the Carlisle River have been replaced by cocoa/coffee/banana or coconut plantations. During the study period, about 80 ha in the northern part of the catchment area were cleared for dairy pasture. In addition, some secondary forest and logged areas are present. However, west of the Carlisle much of the forest remains in a natural state being part of the Cedros Forest Reserve.

Both the Carlisle and Quarahoon Rivers are generally between 1 and 8 m wide with depths up to 3 m in large pools during the rainy season. The slopes of both rivers are very slight, being about 1 : 300 for the Carlisle and 1 : 200 for the Quarahoon, thus producing a sinuous meandering course along most of their length. Where they pass through cultivated areas, they receive many small drainage channels which contain water only during the rainy season. The banks of the rivers rise steeply about 2 to 3 m from the water's edge. Flow is intermittent in most years, ceasing completely during the height of the dry season when shallow stretches dry up, leaving isolated pools or chains of pools. Most of the upper and middle regions of the Quarahoon River dry up during severe dry seasons while only the upper half of the Carlisle does so.

Four sampling stations were chosen for this study: two on the Carlisle and two on the Quarahoon (Fig.2) and were representative of the range of conditions found. Only Stations 1 and 2 on the Carlisle River were sampled for the second year of the study period.

Station 1 was a shallow pool on the Carlisle River with maximum dimensions of about 10 m in length, 4.5 m width and 0.65 m depth during the rainy season. It dried out completely during severe dry seasons. Vegetation cover included the swamp immortelle (*Erythrina glauca*), fineleaf (*Pentaclethra macroloba*) and *Bactris* among other species characteristic of seasonal evergreen forest. Exposure was minimal because of fairly dense overhanging vegetation (Plates 1 and 2).

Station 2 was a deeper larger pool on the Carlisle about 25 m long in the dry season, but with maximal rainy season width and depth of 5.2 m and 2.4 m respectively. It did not dry out even during the most severe dry periods during the study and seemed to be the most northern refuge pool in the Carlisle River. This portion of the river meandered

PLATE 1: View upstream from Station 1 in May after the first rains.

PLATE 2: View downstream from Station 1 in May after the first rains.

through a cocoa estate and the banks were vegetated with cocoa (*Theobroma cacao*), immortelle (*Erythrina erythrina*) and fineleaf. Most of this stretch of stream was shaded by overhanging vegetation (Plate 3).

Station 3 was a fairly deep pool on the Quarahoon River immediately downstream of a road culvert. Rainy season dimensions were about 15 m in length, 7.3 m width and 1.1 m depth. It was reported to have been deepened for use as a cattle watering hole. During one very severe dry season in 1985, this pool dried out completely. Its banks were grassy and no large trees grew nearby thus allowing complete exposure (Plate 4).

Station 4 was brackish, located about 300 m from the sea on the Quarahoon River. At this stretch of the river, maximal width was 7.3 m and depths 1.5 m. During most dry seasons flow ceased completely and tidal influence was minimised as the river mouth became blocked by a sand bank. Vegetation cover included coconut trees, *Bactris*, swamp fern (*Acrostichum*), red mangrove (*Rhizophora*) and smaller shrubs. Banks were high and steep and because of the width at this point, the stream was relatively exposed (Plate 5).

PLATE 3: Station 2 in the late dry season (flow to left).

PLATE 4: Upstream view of Station 3 in the late dry season.

PLATE 5: Upstream view of Station 4 in the late dry season.

METHODS

Hydrology and physico-chemical characteristics

Rainfall:

Daily rainfall measurements were obtained from a guage located within the catchment area approximately 1.5 km from Stations 1 and 2, and 3 to 4 km from Stations 3 and 4. Records were obtained for the period March 1978 to July 1982 from this source. Longterm rainfall records were taken from published data (Wehekind 1955, Trinidad & Tobago 1979) based on measurements from the above and a more northerly located guage (Fig.2). Pentade analysis of daily rainfall data was carried out according to Griffiths (1959, quoted in Jackson 1977, p. 60) (Appendix 1).

Physico-chemical characteristics:

During the period from March 1980 to June 1981, certain physical parameters were measured at all four stations on a monthly basis. Each station was visited at approximately the same time of day between 0900 and 1300 hours. Radiation intensity was measured in an unshaded area at each station using a LI-COR Integrating Radiometer with pyranometer sensor. Readings were taken for three consecutive 100-second periods and a mean value calculated for the overall five minute interval. Data for the complete study period were not obtained due to malfunctioning of equipment. Air temperature, surface and bottom water temperatures were measured to the nearest 0.5°C. Depth of the water column and width of the stream channel were measured at specific points for each station. Surface current was measured in mid-channel using a flat plastic disc timed over a two to four metre distance (depending on relative current speed) and replicated five times to obtain mean current speed. Stations 1 and 2 were mapped in detail for cross-sectional shape and this was used to calculate cross-sectional area (A) as a function of width (W) and depth (D). For Station 1, A was found to be 67% (W x D), while for Station 2, A was 75% (W x D). It was assumed that because of similarities in stream bed shape, cross-sectional areas for Stations 3 and 4 bore the same relationship to width and depth as for Station 2. Discharge rates were calculated every month for which data were available using the following formula:

$$Q = A.v$$

where Q = discharge ($m^3.s^{-1}$), A = cross-sectional area (m^2) and v = current speed ($m.s^{-1}$) (Wetzel & Likens 1979).

Three surface water samples were taken at each station for determinations of (i) dissolved oxygen, (ii) biochemical oxygen demand (BOD), and (iii) general physical and chemical analysis. Dissolved oxygen samples were chemically fixed immediately in the field for a standard Winkler determination. BOD was determined from a 7-day incubation at 20°C. All water samples were submitted to the Central Laboratory of the Water and Sewerage Authority for analysis the same day or the following day after overnight refrigeration. General physical and chemical determinations included turbidity, colour, pH, specific conductance, alkalinity, hardness, nutrient and ionic composition, total dissolved solids, total solids, permanganate value and total organic carbon. Methods used were according to standard methods of the American Public Health Association except in the case of iron where an ammonium thiocyanate method was used (Lue Chin, pers. comm.).

Substrate samples were taken monthly from each station from April 1980 to June 1981 using a 5 cm diameter plastic corer to a depth of 10 cm. These were submitted to the Central Analytical Laboratory, Soils Department, U.W.I. for analysis of particle size composition and carbon content.

From July 1981 to July 1982 only Stations 1 and 2 were sampled for the above parameters with the exception of substrate samples.

Stations 2 and 4 were sampled over 24-hour periods to determine diurnal variation in physical and chemical parameters. In the dry season, samples were taken on 81/03/25-26 and 82/03/31-04/01 (Station 2) and 81/04/01-02 (Station 4), while rainy season samples were taken on 80/08/07-08 (Station 2) and 80/08/19-20 (Station 4). On each occasion the following were measured on an hourly basis: irradiance, air temperature, surface and bottom water temperatures, depth of water column and current speed. Surface water samples were taken for determinations of dissolved oxygen, pH, specific conductance and total alkalinity using the same methods as those used for monthly samples.

On 82/03/30-31 Stations 1 and 2 were mapped in detail and dissolved oxygen profiles were taken using a YSI Oxygen Meter with probe calibrated in saturated air.

Stream biota

Plankton:

Non-quantitative plankton samples were taken at each station on a monthly basis from July 1980 to June 1981 using a hand-held plankton net with a mesh size of 110 μm. Samples were returned to the lab and preserved by addition of an equal volume of buffered 4% formalin. Individual elements of the plankton were subsequently identified as far as possible and a taxonomic list drawn up.

Quantitative samples were collected from Stations 1 and 2 in order to contrast dry and rainy season plankton communities on 83/05/01 and 83/08/09 respectively. On each occasion a one litre sample of water was taken from the upper 10 cm of the water column. In the laboratory the sample was agitated to mix the contents thoroughly and four 5 ml subsamples were removed and each mixed with an equal volume of 2% buffered formalin. Preliminary tests showed that no rupturing of algal or other cells occurred on addition of the formalin. From each of the preserved subsamples in turn, a 1 ml aliquot was removed after thorough mixing and introduced into a Sedgewick-Rafter Counting Cell. Under 100x magnification the number of organisms $.ml^{-1}$ or colonies $.ml^{-1}$ for each taxon was determined according to the methods of Wetzel & Likens (1979). Numbers of colonial rotifers were estimated separately from other plankton because of their larger size and numbers of individuals $.l^{-1}$ were estimated initially. From these data the mean number of organisms $.ml^{-1}$ for each taxonomic group and the total number of organisms $.ml^{-1}$ were calculated for each station for each season. These were compared using Student's t-tests (Appendix 2).

Benthic macroinvertebrates:

Benthic invertebrate samples were taken monthly from all stations from August 1980 to July 1981. At each station, one sample of bottom detritus and sediment covering an area 625 cm² and to a depth of 5 cm was collected by hand. In September 1981 an Ekman grab became available and was used to collect a sample (225 cm² to a depth of 10 cm) from each of Stations 1 and 2 every month until July 1982. Preliminary sampling showed that benthic macroinvertebrates were confined to the uppermost layers of the substate. On return to the lab, samples were sieved through a series of sieves with mesh sizes 2.0, 1.0 and 0.5 mm. Samples were sorted visually in white enamel dishes. Live invertebrates were identified as far as possible, counted and preserved in ethanol. Time constraints prevented the replication of monthly samples for each station and these data were intended to give only a qualitative view of the composition of benthic invertebrate communities.

More quantitative sampling was conducted to contrast dry and rainy season benthic invertebrate populations. On 83/03/17 and 83/08/09, four Ekman grab samples were taken at each of Stations 1 and 2 and they were sorted in the same way as monthly samples. In addition, blotted wet weights of all live macroinvertebrates were obtained. Mean densities and biomass of benthic macroinvertebrates were calculated for each of these two stations for each season and were compared using the Student's t-test.

Larger benthic invertebrates were collected with a two-man push seine, mesh size 6 mm. In particular, *Dilocarcinus dentatus* and *Pomacea glauca* were collected monthly by seining and were preserved in buffered 4% formalin. Carapace widths and widths across the body whorl were measured for *D. dentatus* and *P. glauca* respectively for population structure analysis. *P. glauca* egg masses were also located within a constant area at each station and were counted each month.

Allochthonous input:

In order to estimate the variability in amount of allochthonous animal input falling onto the stream surface as a source of food for fishes, four 'glue boards' (Geisler *et al* 1975) were set out at each of Stations 1 and 2 for 24-hour periods on 83/04/30-05/01 and 83/08/08-09. Each tray measured 0.25 m^2, was covered with 'Tangle Trap' adhesive and was supported no more than 10 cm above the water surface to prevent inundation. On return to the lab, all animal material was removed and excess adhesive dissolved in benzene. Plant material and frass were not taken into account. All animal material was sorted to taxonomic group, counted and weighed after blotting and air drying for 1 hour. Occasional animal fragments were included with their respective taxa for weighing; only whole individuals were counted. Mean values of number and biomass of animals caught on the glue boards for each station in each season were calculated and compared using Student's t-tests.

RESULTS

Hydrology and physico-chemical characteristics

Rainfall:

Long term rainfall records for the Chatham area are shown in Table 1 while Table 2 summarises extremes of rainfall for the area. Long term monthly averages reflected a dry season from January to May with February being the driest month, and a wet season from June to December with July and August being the wettest months. The petit carême, a short dry period in the middle of the rainy season occurred between September and November. Although long term annual totals averaged 1735 mm, variability was high, ranging from 1489 to 2136 mm annual totals in two consecutive years (1974 and 1975 respectively). Monthly averages for the period during the study, indicated the occurrence of somewhat wetter than average dry seasons (110.1% 1953-77 average) with earlier and wetter than average rainy seasons at this time (110.6% 1953 - 77 average). Overall, the average annual total rainfall for 1980 to 1982 was slightly higher than those values derived from long term records (108.4% 1953-77 average).

TABLE 1: Rainfall averages for Chatham from 1933 - 1982.

Month	Average monthly rainfall (mm) 1933-1952[1]	1953-1977[2]	1980-1982[3]	1980-82 as a % of 1953-77
January	137.41	130.30	94.32	72.4
February	67.56	68.07	110.83	162.8
March	79.76	77.98	37.42	48.0
April	82.30	107.19	101.43	94.6
May	104.65	68.58	156.04	227.5
June	193.80	207.01	289.39	139.8
July	223.77	209.80	182.97	87.2
August	209.04	246.13	221.36	89.9
September	137.92	142.14	132.59	93.3
October	147.32	153.92	244.35	158.8
November	182.12	150.62	181.99	120.8
December	171.45	174.24	160.40	92.1
Average annual total	1737.11	1735.98	1882.27	108.4
Wet season average[4]	1265.43	1283.86	1413.05	110.1
Dry season average[5]	471.68	452.12	500.04	110.6

[1] : 20 year period recorded at Irois Government School, Chatham (Wehekind 1955).

[2] : 11 year period recorded at Santa Maria Estate, Chatham (Trinidad & Tobago 1979).

[3] : January 1980 - July 1982 recorded at Santa Maria Estate, Chatham, courtesy Mr B. Barclay.

[4] : June to December. [5]: January to May.

TABLE 2: Rainfall extremes for Chatham from 1953-1982.

	1953-1977		1978-1982	
	Date	Rainfall (mm)	Date	Rainfall (mm)
Wettest year	1975	2136.39	1979	2040.64
Driest year	1974	1489.64	1981	1811.53
Wettest month	77/06	496.57	80/10	447.55
Driest month	73/03	7.11	78/04	3.56
Mean wettest month	August	246.13	June	304.29
Mean driest month	February	68.07	March	40.39
Greatest in 24 hours	77/08/20	107.70	80/10/27	251.71

Sources of data as for Table 1.

More detailed illustration of rainfall just prior to and during the study period shows the range of variability in the distribution and intensity of rainfall (Figs. 3 and 4). Monthly and weekly totals for the period indicated that most of the annual rainfall occurred during the months of May to December with a drier period from January to April. However, the time of onset and duration of each season was extremely variable. An extreme situation was recorded in 1981 to 1982 where a particularly marked petit carême occurred in late 1981 and no appreciable dry season can be recognised in 1982 from these data.

Pentade analysis of rainfall data from 1978 to 1982 also illustrates the unpredictability of timing of onset and duration of each season (Fig.4). However, according to the criteria defining dry and rainy pentades (Appendix 1), a dry period did occur in early 1982. The beginning of each rainy season varied by up to three weeks from early to late May and was frequently followed by dry periods. Precipitation was also not consistent in its distribution over time with very high weekly totals alternating with drier weeks (Fig.4). Thus although wet months could be fairly clearly defined, on a more detailed analysis most of the rain falling during those months fell during one week or even on one or two days.

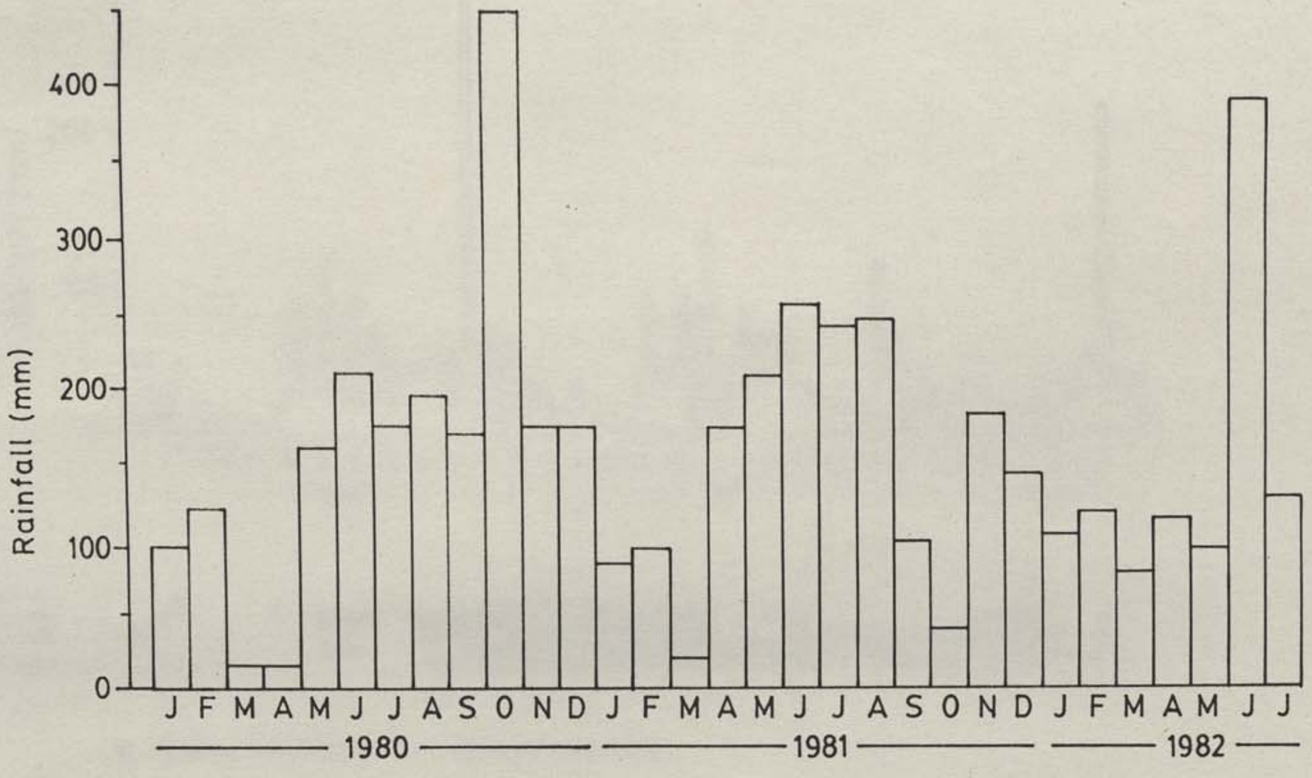


FIGURE 3: Monthly rainfall totals from January 1980 to July 1982.

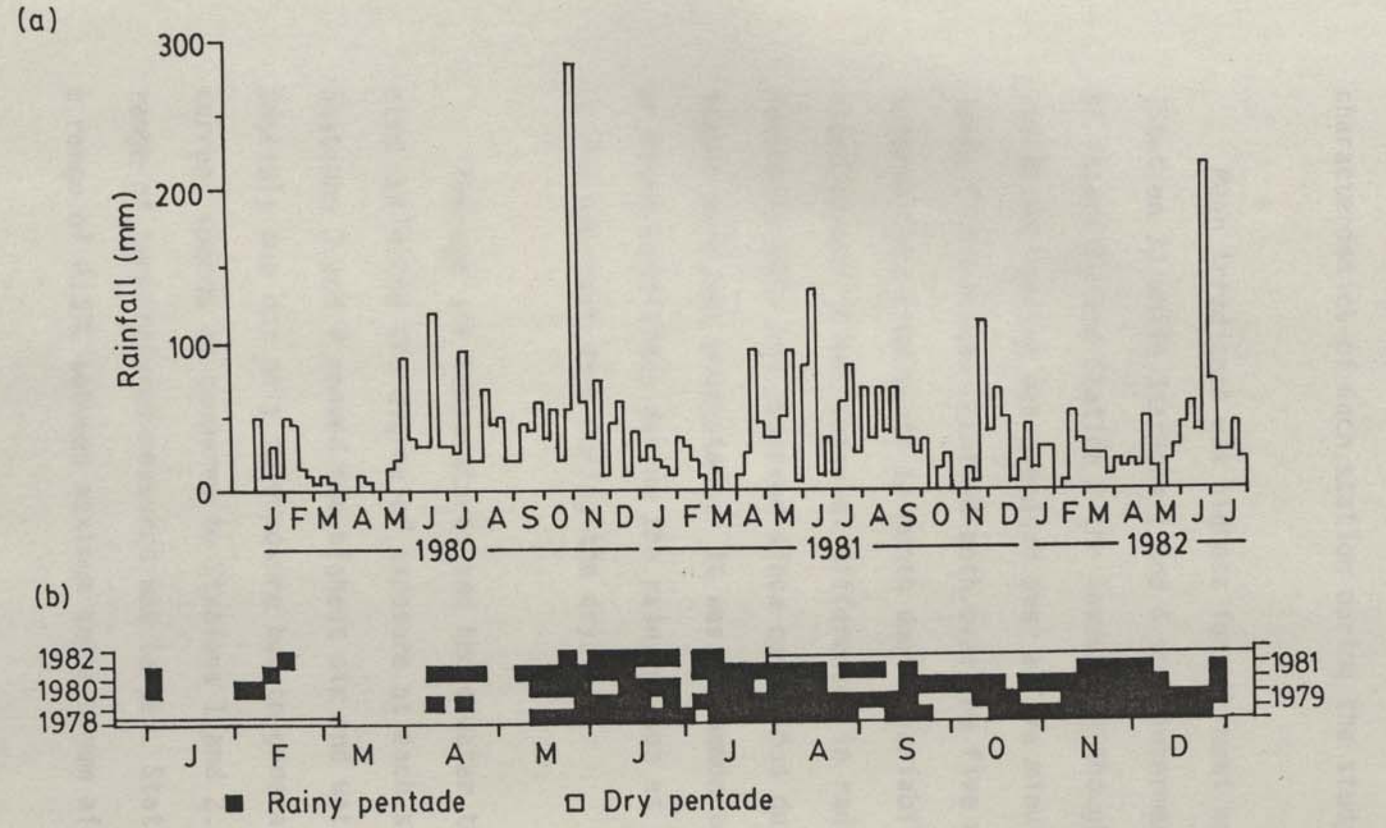


FIGURE 4: (a) Weekly rainfall totals from January 1980 to July 1982, and (b) pentade analysis of rainfall from March 1978 to July 1982.

Physical parameters:

Table 3 summarises the ranges and means of physical characteristics of each station during the study period.

Mean irradiance was highest for the most exposed site (Station 3) while Stations 1 and 4 show intermediate levels of intensity and Station 2 the lowest. Although each radiation reading was averaged over a five minute period, large fluctuations occurred both over the five minute interval and from month to month due to variability in cloud cover. Clear seasonal differences in radiation intensity were not observed since conditions during each season were not consistent. It was as common to find sunny or mixed conditions during the rainy season as it was to record overcast days during the dry.

Average air temperatures and hence water temperatures also reflected the degree of exposure at each site. Generally, Stations 3 and 4 showed the highest air and water temperatures, possibly due not only to exposure but to generally slower current speeds as compared to Stations 1 and 2. The annual range of temperatures measured was large: Station 1 showed a range of 8.5°C between maximum and minimum air temperatures

TABLE 3: Means and ranges of physical parameters for Stations 1 to 4.

Parameter	Station 1			Station 2			Station 3			Station 4		
	min	max	mean	min	max	mean	min	max	mean	min	max	mean
Irradiance ($W.m^{-2}$)	12.7	1568	303.3	14.9	508.3	209.7	148.8	1273.7	454.3	62.9	633	264.6
Temperature (°C)												
Air	24.5	33.0	28.1	24.0	32.0	27.7	25.0	32.0	29.1	26.5	34.0	30.3
Water surface	20.0	27.0	24.8	20.0	28.0	25.4	25.0	36.5	28.9	26.0	30.0	27.8
Water bottom	20.0	26.5	24.6	20.0	28.0	25.5	24.0	29.0	26.5	26.0	30.0	28.0
Depth (m)	0	0.65	0.39	0.20	2.40	0.73	0.20	1.10	0.67	0.40	1.50	0.98
Width (m)	0	5.0	3.4	2.0	7.0	3.6	3.1	9.2	5.5	3.6	8.0	5.8
Current ($cm.s^{-1}$)	0	27.0	6.9	0	14.1	1.8	0	3.5	0.8	0	3.9	1.6
Discharge ($m^3.s^{-1}$)	0	0.53	0.08	0	0.25	0.05	0	0.10	0.02	0	0.31	0.09
Colour (Hazen units)	50	350	197	50	600	231	70	1500	653	40	500	227
Turbidity (Formazin units)	15	548	71	17	250	60	44	410	131	12	120	52

recorded; Station 3 a variation of surface water temperatures of 11.5°C. Bottom water temperatures fluctuated much less than surface temperatures, the greatest range being 8.0°C at Station 2. Unlike other stations, there was a large difference between mean surface and bottom temperatures at Station 3, indicating a possible tendency towards stratification of the water column as a result of rapid heating of upper layers, slow current speeds and greater depths (Table 3).

Monthly variation of temperatures is shown for each station in Fig. 5 . Generally, water temperatures tracked air temperatures closely. Air temperatures, and to a lesser extent, water temperatures tended to show a slight increase during the middle to late rainy season consistent with higher mean monthly air temperatures at this time for the island as a whole (Berridge 1981). During the dry season months, temperatures were on occasion lower than wet season temperatures and showed large fluctuations from one month to the next. Despite this general pattern of seasonal variation in temperatures,periods of heavy rainfall were often associated with low air temperatures for example June 1980 and June 1982. Occasionally bottom water temperatures were higher

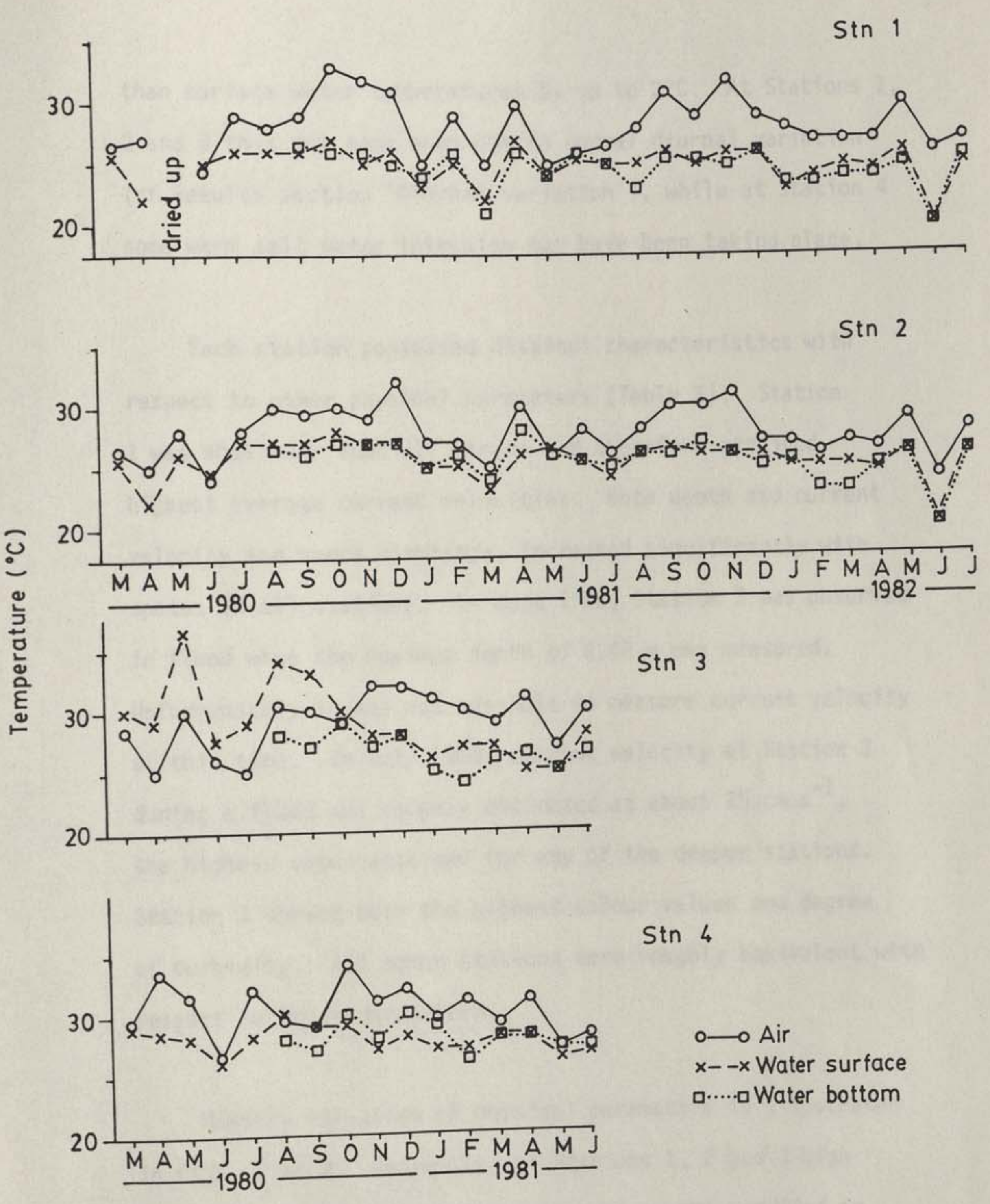


FIGURE 5: Monthly variation of air and water temperatures at Stations 1 to 4.

than surface water temperatures by up to 2°C. At Stations 1, 2 and 3 this may have been due to normal diurnal variation (cf. Results section 'Diurnal variation'), while at Station 4 some warm salt water intrusion may have been taking place.

Each station possessed distinct characteristics with respect to other physical parameters (Table 3). Station 1 was shallower than all others and therefore attained highest average current velocities. Both depth and current velocity and hence discharge, increased significantly with spates at all stations. In June 1982, Station 2 was observed in flood when the maximum depth of 2.40 m was measured. Unfortunately it was not possible to measure current velocity at this time. In July 1980, current velocity at Station 3 during a flood was roughly estimated at about 25 $cm.s^{-1}$, the highest value attained for any of the deeper stations. Station 3 showed both the highest colour values and degree of turbidity. All other stations were roughly equivalent with respect to these parameters.

Monthly variation of physical parameters is illustrated in Figs. 6 to 9. Generally, at Stations 1, 2 and 3 high levels of precipitation during the wet season resulted in increased habitat size, current velocities and discharge.

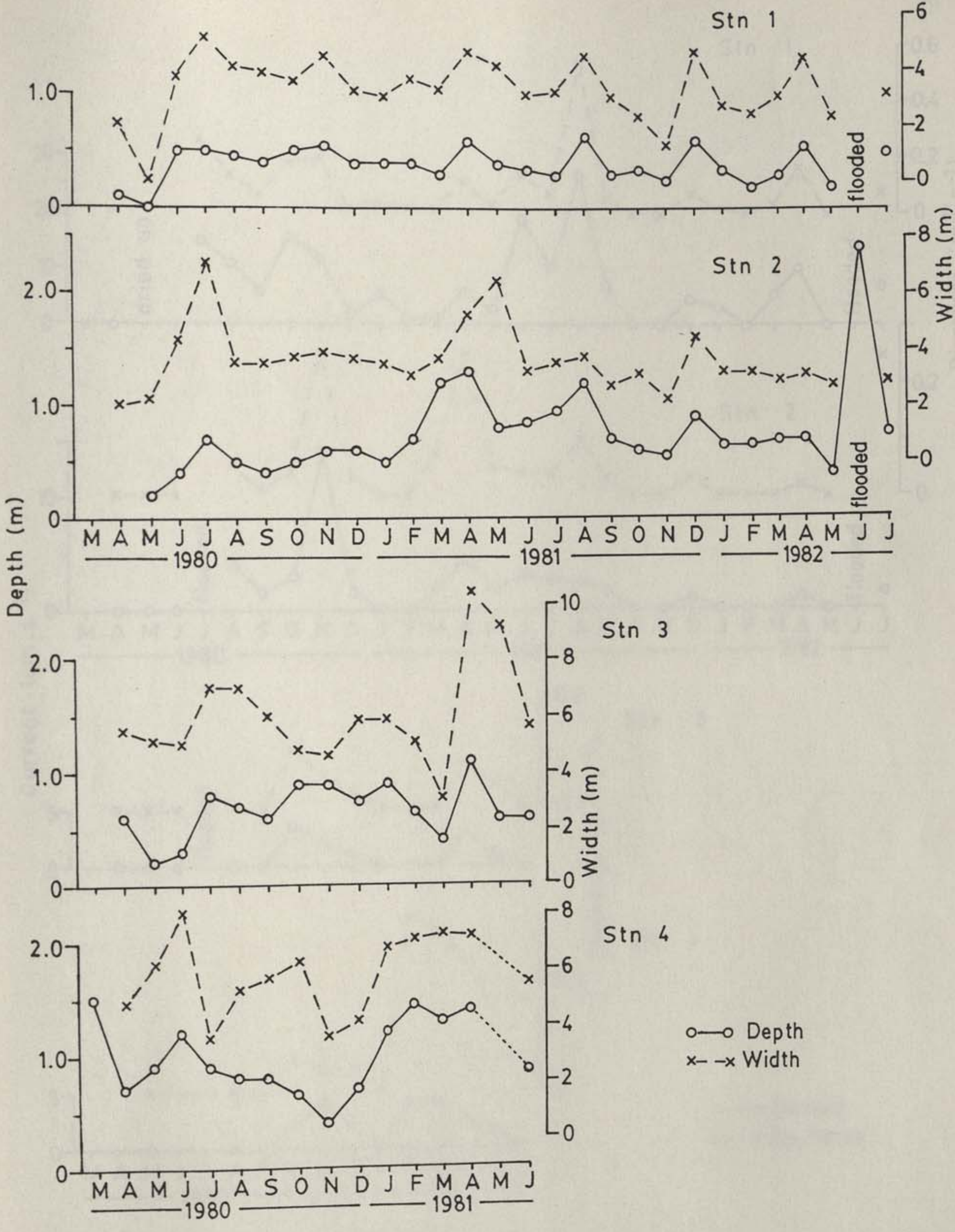


FIGURE 6: Monthly variation of depth and width at Stations 1 to 4.

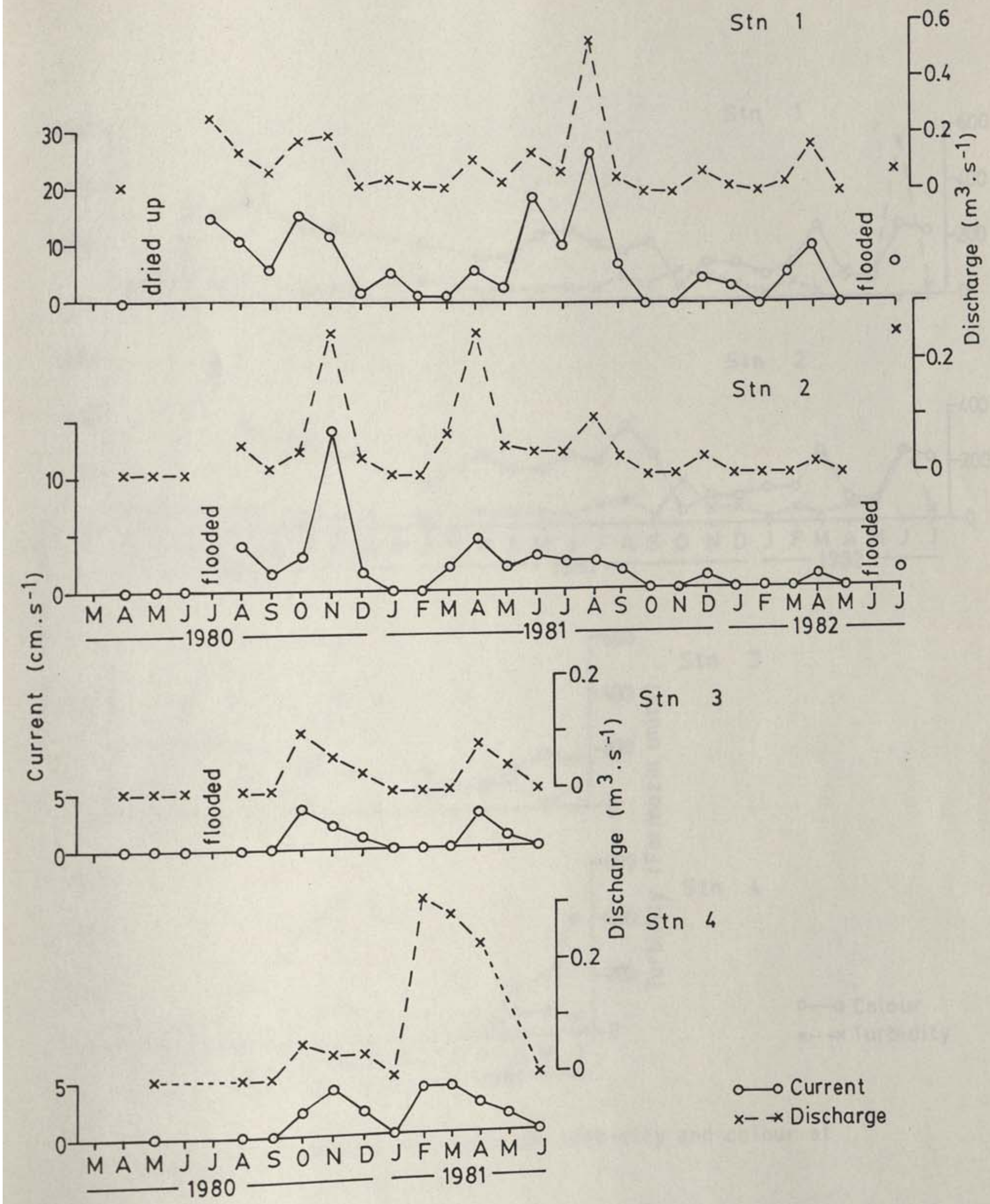


FIGURE 7: Monthly variation of current and discharge at Stations 1 to 4.

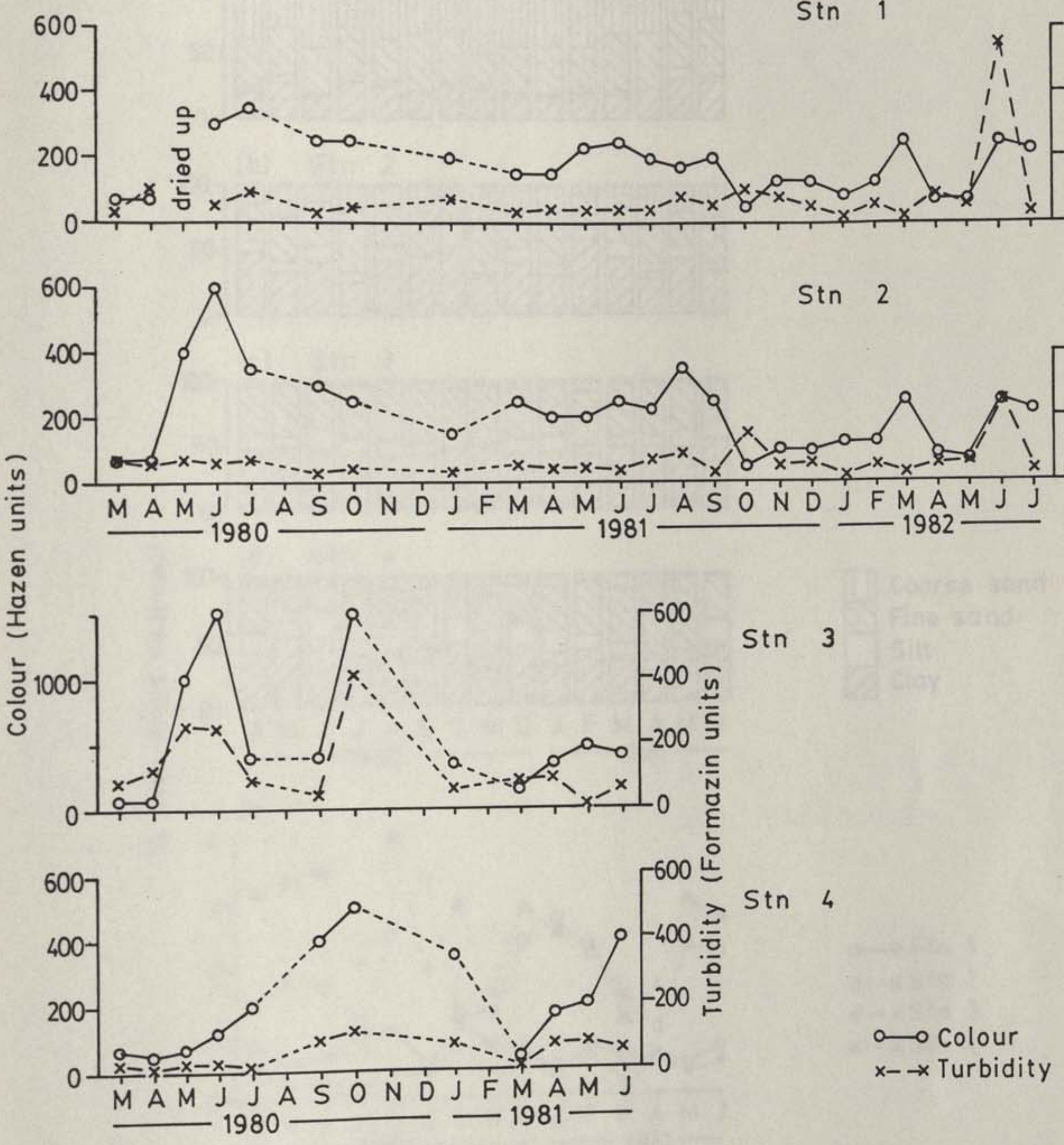


FIGURE 8: Monthly variation of turbidity and colour at Stations 1 to 4.

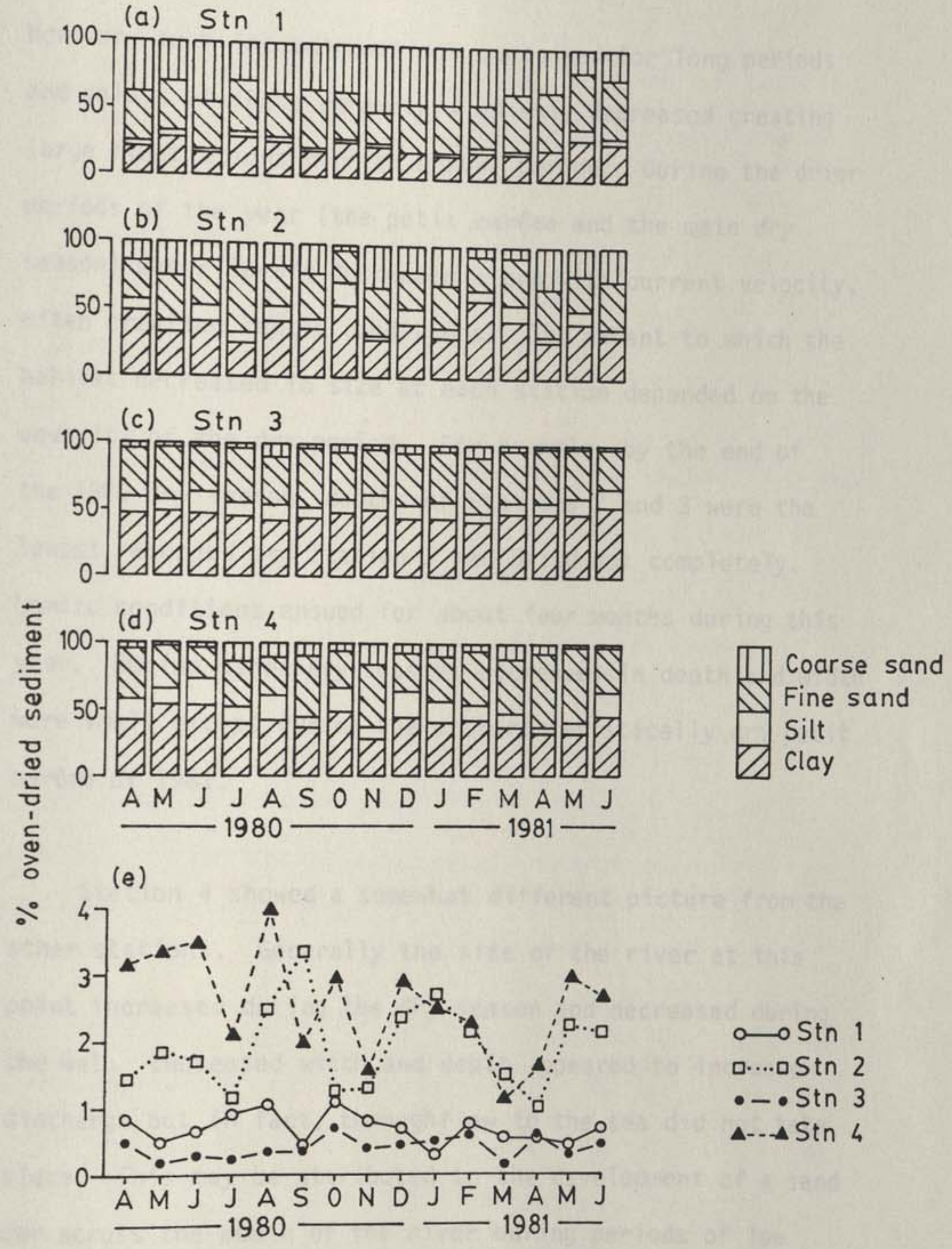


FIGURE 9: Monthly variation of (a)-(d) particle size composition, and (e) carbon content of substrates at Stations 1 to 4.

However, such increase was not sustained for long periods and values of these parameters quickly decreased creating large fluctuations over an annual period. During the drier periods of the year (the petit carême and the main dry season) water levels decreased along with current velocity, often creating lentic conditions. The extent to which the habitat decreased in size at each station depended on the severity of the dry period. For example, by the end of the 1980 dry season, depths of Stations 2 and 3 were the lowest recorded and Station 1 had dried out completely. Lentic conditions ensued for about four months during this year. During other dry seasons decreases in depth and width were small except during the uncharacteristically dry petit carême of 1981.

Station 4 showed a somewhat different picture from the other stations. Generally the size of the river at this point increased during the dry season and decreased during the wet. Increased width and depth appeared to increase discharge but in fact, throughflow to the sea did not take place. This may be attributed to the development of a sand bar across the mouth of the river during periods of low flow when discharge was insufficient to prevent the accumulation of sand moved by longshore drift into the river mouth.

This sand bar presumably prevented throughflow of water into the sea during the early rainy season when accumulation of water upstream and from runoff increased. Only after sufficient flow developed or after several spates occurred to break through the sand bar, did water levels decrease at this station.

Largely because of infrequent analyses of turbidity and colour, it is not possible to make definitive comments on the seasonal variation of these parameters. However, there appeared to be an increase in both properties with the rainy season. Although some spate events were associated with increased turbidity, this was not a consistent correlation and other factors such as increased plankton densities in the late dry season may have been contributory (cf. Results section 'Plankton').

Analysis of particle size composition of sediments allowed characterisation of sediments as follows: Station 1 - sandy clay loam, Station 2 - sandy clay, Station 3 and 4 - clay (Table 4). Mean carbon content was highest at Station 4 and next highest at Station 2 whereas Stations 1 and 3 showed substantially lower carbon contents of sediments. Such a pattern could be correlated with high

TABLE 4: Average particle size composition and carbon content of substrates at Stations 1 to 4.

	Stations			
	1	2	3	4
	% oven dried sediment			
Coarse sand (>0.2 mm)	36.2	18.9	3.7	5.9
Fine sand (0.02-0.2 mm)	37.6	32.5	38.1	38.5
Silt (0.002-0.02 mm)	2.9	9.2	10.7	13.3
Clay (<0.002 mm)	23.3	39.4	47.5	42.3
Carbon content	0.7	1.9	0.4	2.6

inputs and rates of accumulation of organic material in Stations 2 and 4 from overhanging vegetation or upstream respectively. Lower carbon levels occurred in shallow high velocity areas (Station 1) or areas lacking in input of allochthonous material from overhanging vegetation (Station 3). Substrate analyses showed little seasonal variation in particle size composition at all stations (Fig.9). However carbon content showed some variability particularly in Stations 2 and 4. At Station 2 carbon content seemed to increase in rainy periods and may reflect the increased input of organic matter from surface runoff and from upstream. Somewhat irregular variation of carbon content at Station 4 may have been due to tidal influence and accumulation of material due to blockage of the river mouth during the dry season.

Chemical parameters:

Mean values and ranges of chemical parameters measured over the study period are shown in Table 5. Generally, Stations 1 and 2 were very similar in water quality reflecting their proximity and common location on the Carlisle River as compared with Station 3 which was both physically different and located on the Quarahoon River.

TABLE 5: Ranges and means of chemical parameters for Stations 1 to 4

Parameter	Station 1			Station 2			Station 3			Station 4		
	min	max	mean	min	max	mean	min	max	mean	min	max	mean
pH[1]	5.39	7.57	6.54	5.93	7.49	6.64	5.92	7.54	6.81	6.30	7.58	6.89
Total alkalinity ($CaCO_3$)	18.0	154.0	35.1	19.8	58.0	40.6	17.0	98.0	45.6	27.0	134.0	64.1
Bicarbonate alkalinity	22.0	187.9	42.8	24.2	70.8	49.5	20.7	119.4	55.7	32.9	163.5	78.2
Specific conductance[2]	67	390	144.6	48	400	139.4	130	800	233.9	250	37,500	8,341
Total hardness ($CaCO_3$)	26.9	68.3	40.4	24.0	65.0	40.8	37.0	127.4	62.0	56.8	15,500	2,292
Calcium	2.0	12.1	6.4	2.4	16.1	6.7	4.8	15.2	10.0	8.5	400	124.3
Magnesium	2.7	12.2	5.9	0.5	12.4	5.9	2.4	22.1	9.0	7.9	1,312.2	269.2
Total iron	0.3	10.8	4.1	0.1	11.0	4.9	1.0	10.7	5.7	0.1	4.3	1.9
Soluble iron	0.2	4.0	2.1	0.1	10.2	3.2	1.9	5.0	2.9	0.02	3.9	1.4
Chloride	13.5	85.9	26.0	11.4	32.0	22.2	21.7	61.3	37.2	60.0	19,000	4,821
Sulphate	8.5	40.6	18.4	0	37.6	10.2	0	33.1	14.8	15.5	1,605	444.3
Silica (SiO_2)	6.3	27.6	15.8	5.4	36.6	17.2	9.2	21.5	16.3	6.6	24.0	16.4
Phosphate[3]	0	214.0	36.3	0	486.0	54.4	0	80.0	30.0	0	30.0	9.7
Nitrite[3]	0	22.0	5.0	0	32.0	7.3	0	50.0	17.6	0	0.02	4.7
Nitrate	0.2	20.0	2.8	0.06	16.4	2.4	0	4.3	1.5	0.2	3.7	1.0
Total dissolved solids	82	190	127.6	63	190	127.5	150	400	235.4	195	32,130	11,654
Total solids	94	340	208.7	108	430	198.9	207	940	464.4	304	32,490	12,760
Total organic carbon	2.4	22.0	13.2	9.7	24.0	15.4	21.5	59.0	34.0	0	11.5	5.8

TABLE 5: (continued)

Parameter	Station 1			Station 2			Station 3			Station 4		
	min	max	mean	min	max	mean	min	max	mean	min	max	mean
Permanganate value	3.3	14.5	8.9	3.4	14.7	10.0	4.0	18.5	13.2	0.4	16.5	8.8
BOD_7	0.3	7.7	2.7	1.1	7.4	3.4	0.4	8.3	4.3	0.6	7.3	2.8
Dissolved oxygen	0.05	14.9	5.4	0.6	16.1	3.7	0.4	10.9	5.8	1.7	13.4	3.9
% saturation O_2	0.6	180.2	63.9	6.8	192.8	45.0	4.3	136.2	75.5	21.3	170.7	49.6

[1] : pH units

[2] : µmhos

[3] : $\mu g.l^{-1}$

All other data in $mg.l^{-1}$

Station 4 showed the influence of the sea due to its proximity to the coast.

The freshwater stations were characterised by water of slight acidity, in all cases mean pH was less than 7.0 and values ranged from a minimum of 5.39 at Station 1 to 7.54 at Station 3. Mean total alkalinity values ranged from 35.1 mg.l^{-1} at Station 1 to 45.6 mg.l^{-1} at Station 3 with Station 1 showing the greatest range. Bicarbonate alkalinity values were similar to those for total alkalinity. Total hardness, measured as $CaCO_3$, was roughly equivalent for Stations 1 and 2 but was somewhat higher at Station 3. No carbonates were detected in any water samples during the study period. These waters were also of high specific conductance, means ranging between 139.4 μmhos at Station 2 and 233.9 μmhos at Station 3. Station 3 showed generally higher specific conductance attaining a maximum of 800 μmhos. Individual ions, in particular chloride and iron, were found in fairly high concentrations at all sites. Maximal chloride concentration was attained at Station 1 (85.9 mg.l^{-1}) while maximal total iron concentrations at all stations were greater than 10 mg.l^{-1}. Inorganic nutrients such as phosphate, nitrite-nitrogen, and nitrate-nitrogen occurred in moderately high concentrations. Average values ranged from 30.0 -

54.4 $\mu g.l^{-1}$ (phosphates), 5.0 - 17.6 $\mu g.l^{-1}$ (nitrites) and 1.5 - 2.8 $mg.l^{-1}$ (nitrates). At Station 3 nitrite-nitrogen was more than twice as high and nitrate-nitrogen was lower than at the other two stations. Another major constituent included silica (maximal concentration 36.6 $mg.l^{-1}$). Dissolved and total solids attained maximum concentrations of 400 and 940 $mg.l^{-1}$ respectively at Station 3. Dissolved solids made up more than 50% of total solids measured, the remainder presumably being attributable to suspended organic and inorganic solids. Both mean chemical and biochemical oxygen demands (permanganate value and BOD respectively) were highest at Station 3 (maximal values 18.5 and 8.3 $mg.l^{-1}$ respectively). Relatively high oxygen demands at all stations could partially have accounted for the relatively low mean oxygen concentrations, in addition to other factors such as lack of mixing due to low current velocities. Nevertheless supersaturation did occur occasionally. Stations 1 and 3 showed highest mean oxygen saturation values (63.9 and 75.5% respectively) as compared to Station 2 (45.0%).

Water quality at Station 4 indicated the influence of the sea with an almost neutral mean pH and higher buffering capacity (mean total alkalinity 64.1 $mg.l^{-1}$) as compared to the freshwater stations. Specific conductance was high (up to 37,500 μmhos) and this was supported by correspondingly high concentrations of individual ions. In particular calcium, magnesium, chloride and sulphate ions were found in high concentrations indicating the direct influence of sea water. Unlike the freshwater stations mean magnesium concentrations were greater than mean calcium concentrations at this brackish water site. Total and soluble iron and inorganic nutrients were found in lower concentrations than at the freshwater stations. Silica was roughly within the same range as at other stations upstream. Total and dissolved solids were found in substantially higher quantities as was expected due to higher concentrations of dissolved salts. Dissolved solids accounted for more than 90% of total solids indicating minimal quantities of suspended solids, a feature which might have contributed to generally lower turbidity values at this site. Total organic carbon was lower than upstream. Chemical and biochemical oxygen demands and oxygen saturation values were roughly within the same range as for other stations.

Monthly variation of chemical parameters for all stations is illustrated in Figs. 10 to 21 .

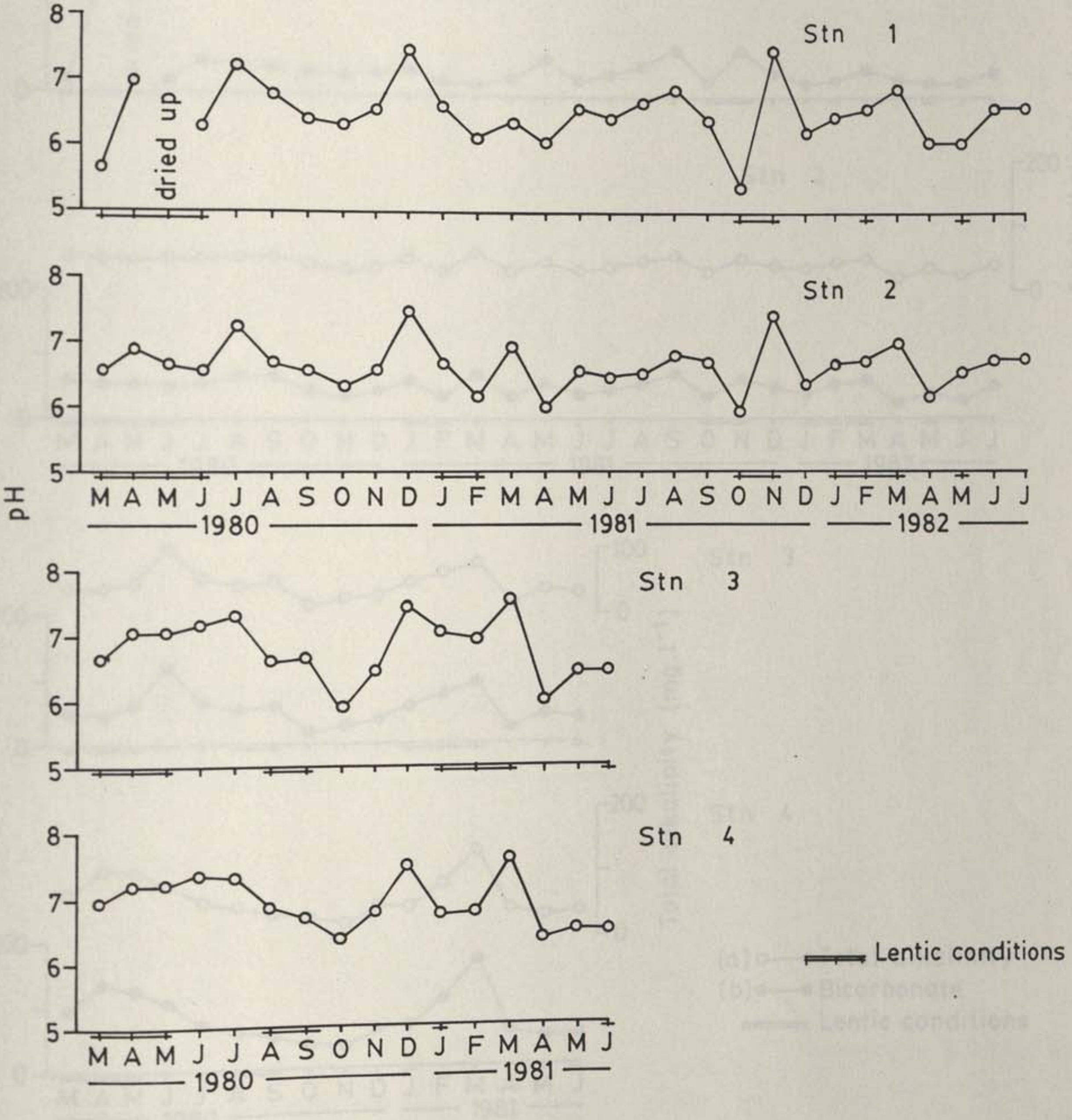


FIGURE 10: Monthly variation of pH at Stations 1 to 4.

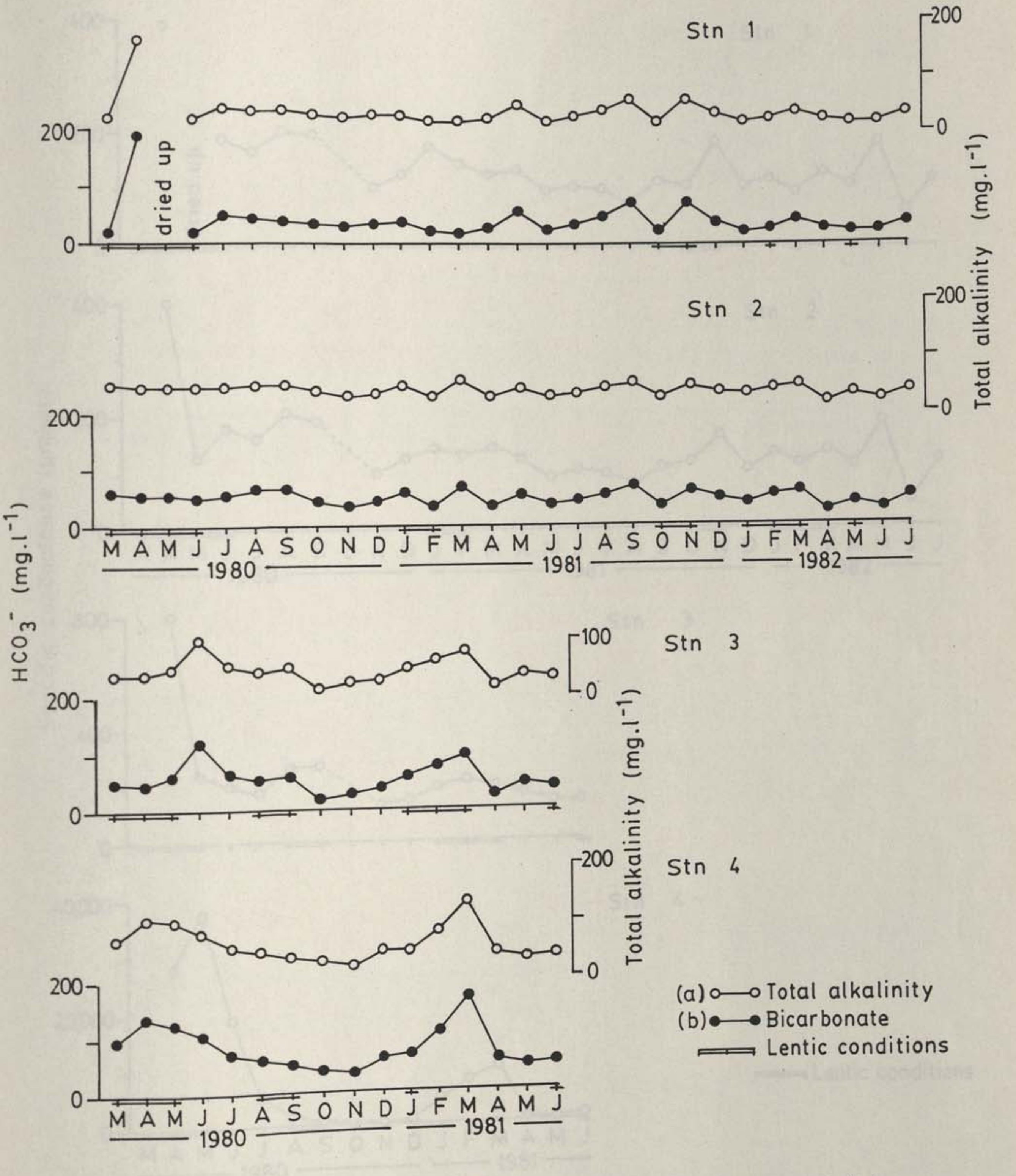


FIGURE 11: Monthly variation of (a) total alkalinity, and (b) bicarbonate alkalinity at Stations 1 to 4.

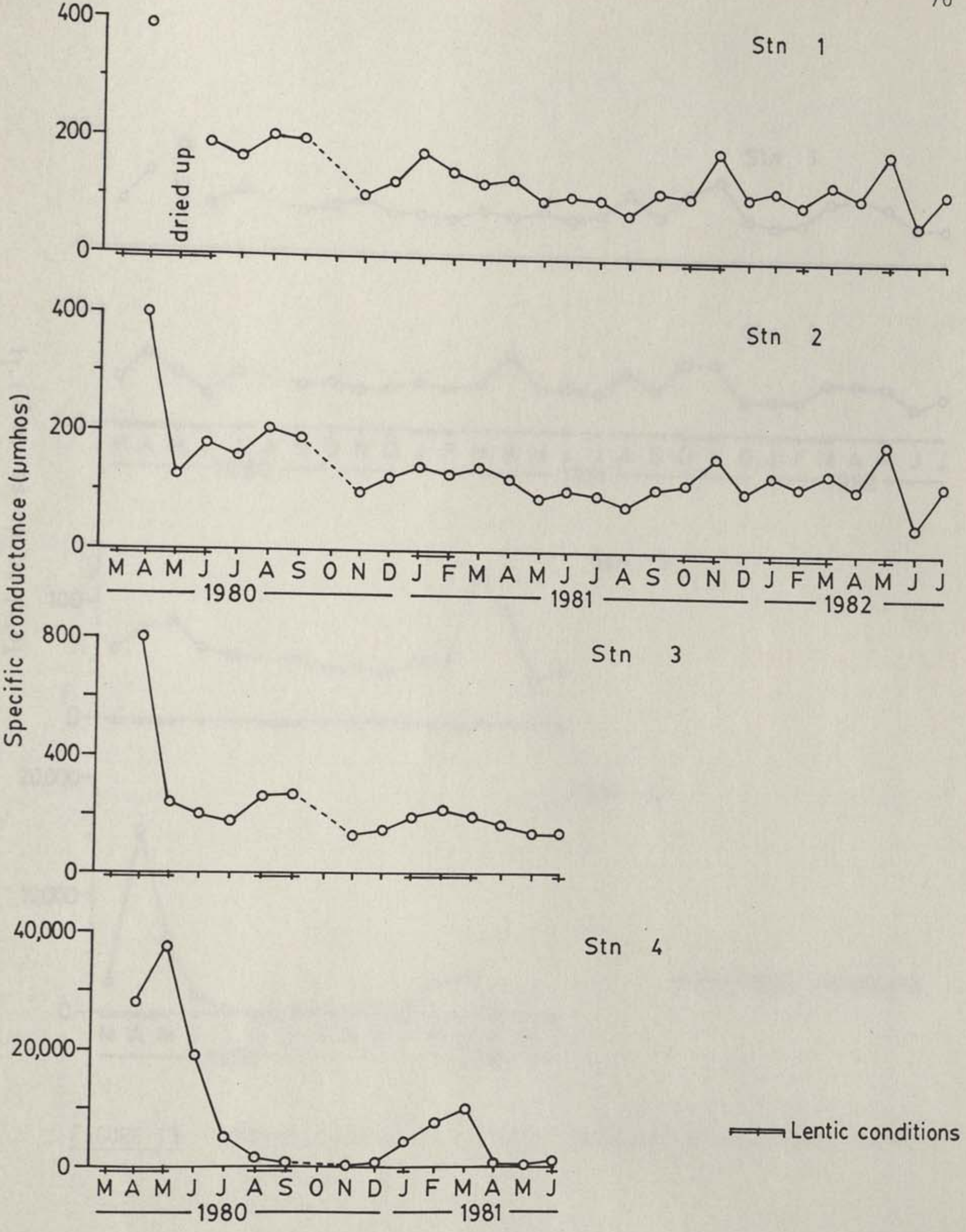


FIGURE 12: Monthly variation of specific conductance at Stations 1 to 4.

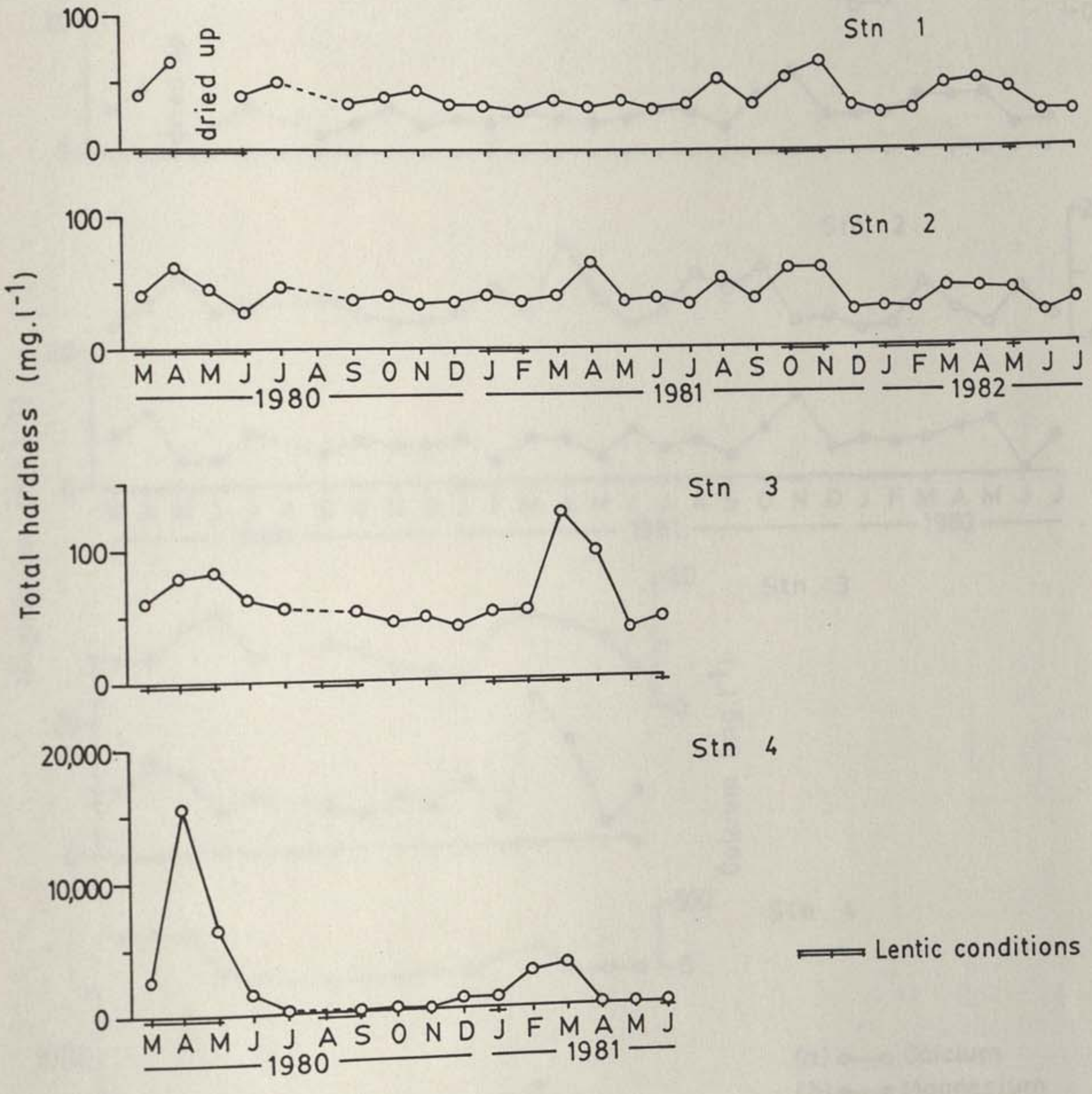


FIGURE 13: Monthly variation of total hardness at Stations 1 to 4.

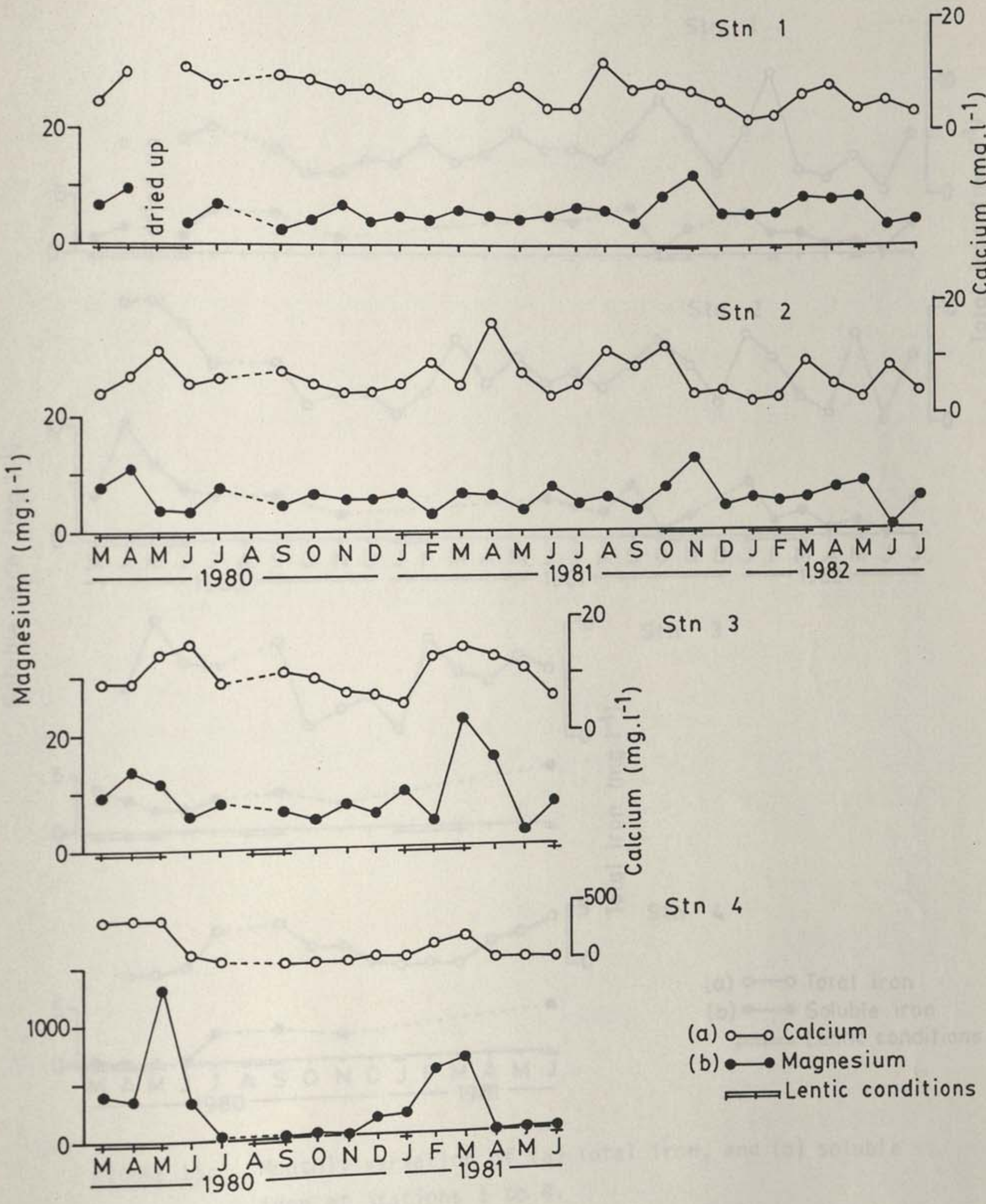


FIGURE 14: Monthly variation of (a) calcium, and (b) magnesium ions at Stations 1 to 4.

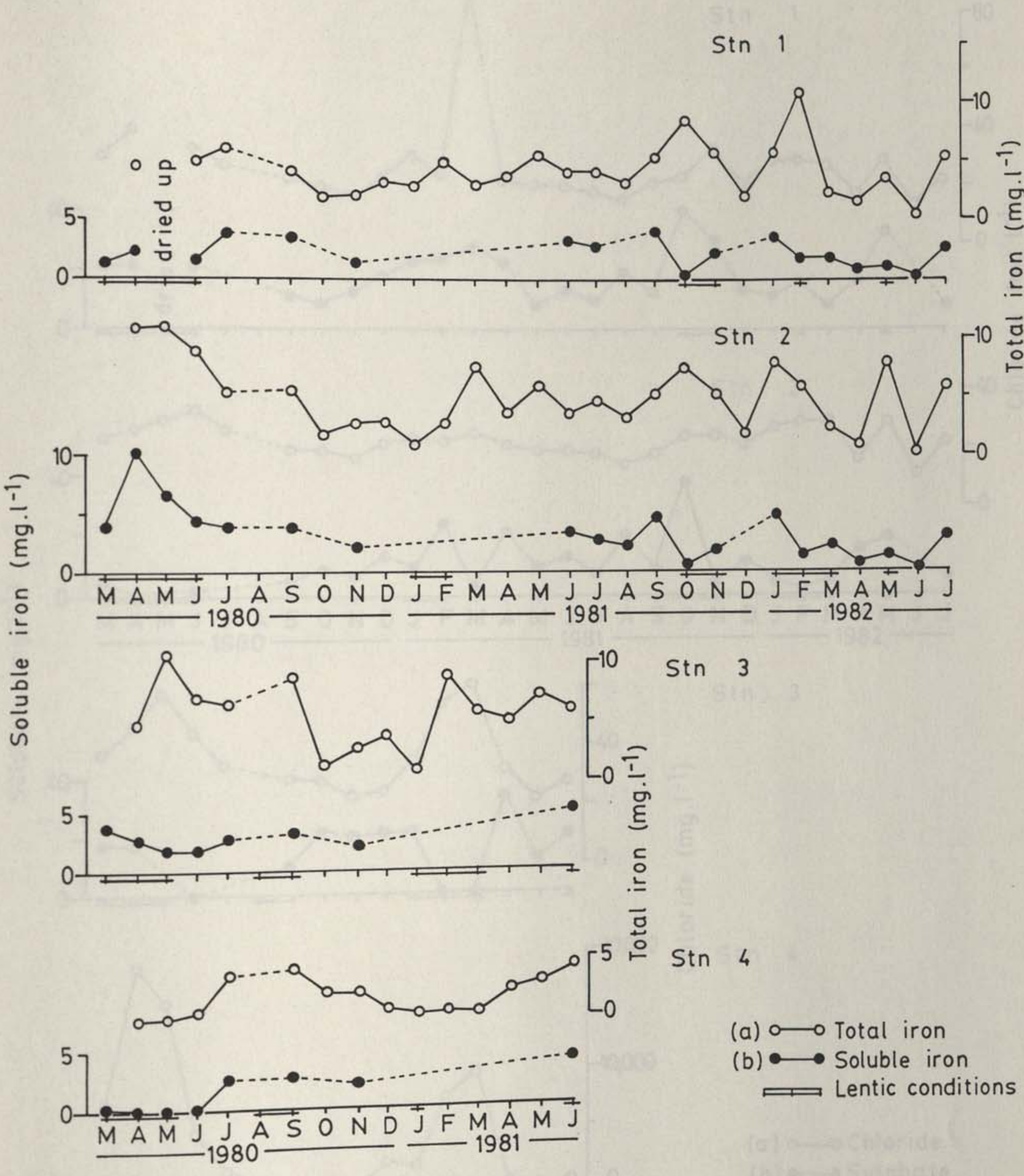


FIGURE 15: Monthly variation of (a) total iron, and (b) soluble iron at Stations 1 to 4.

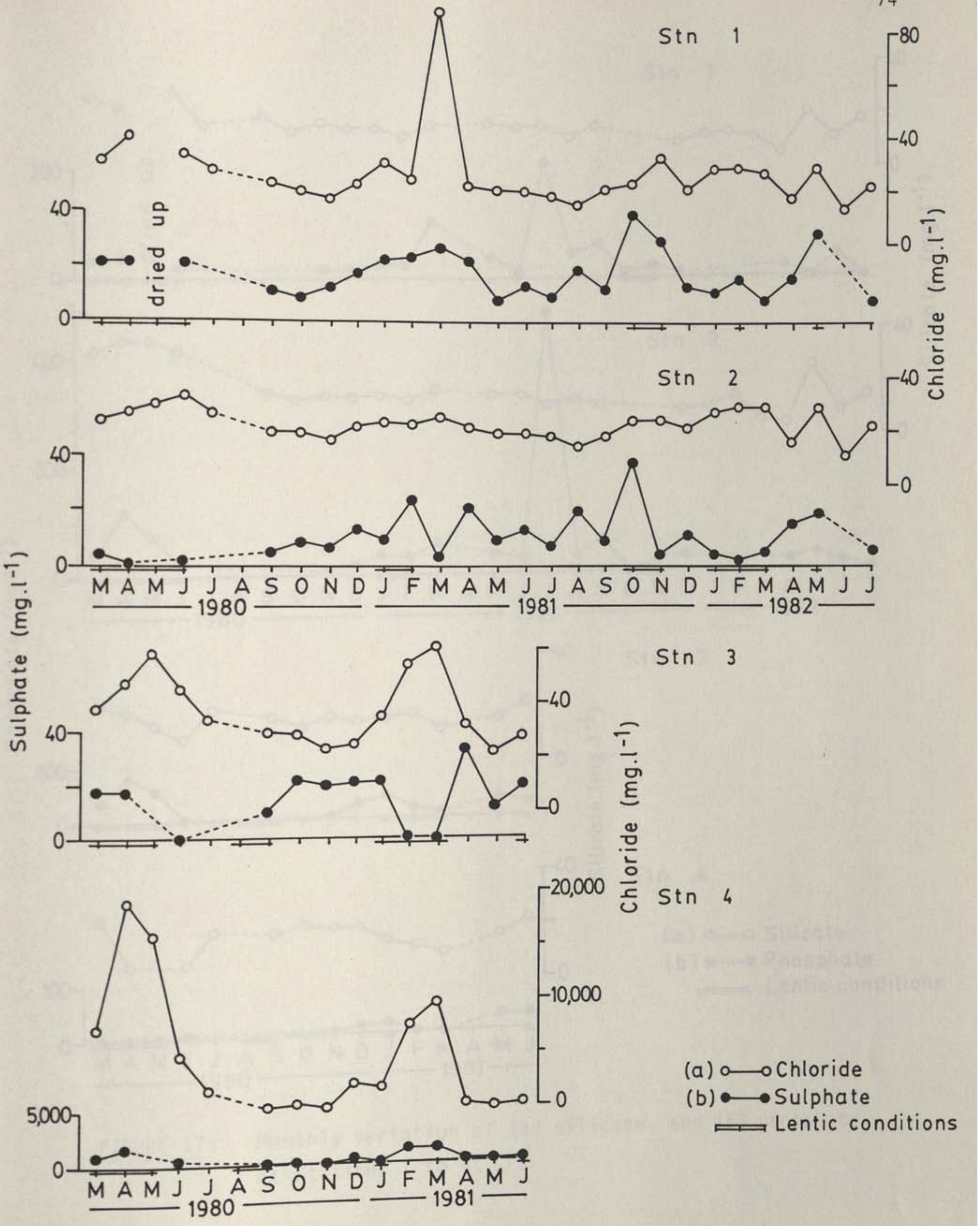


FIGURE 16: Monthly variation of (a) chloride, and (b) sulphate ions at Stations 1 to 4.

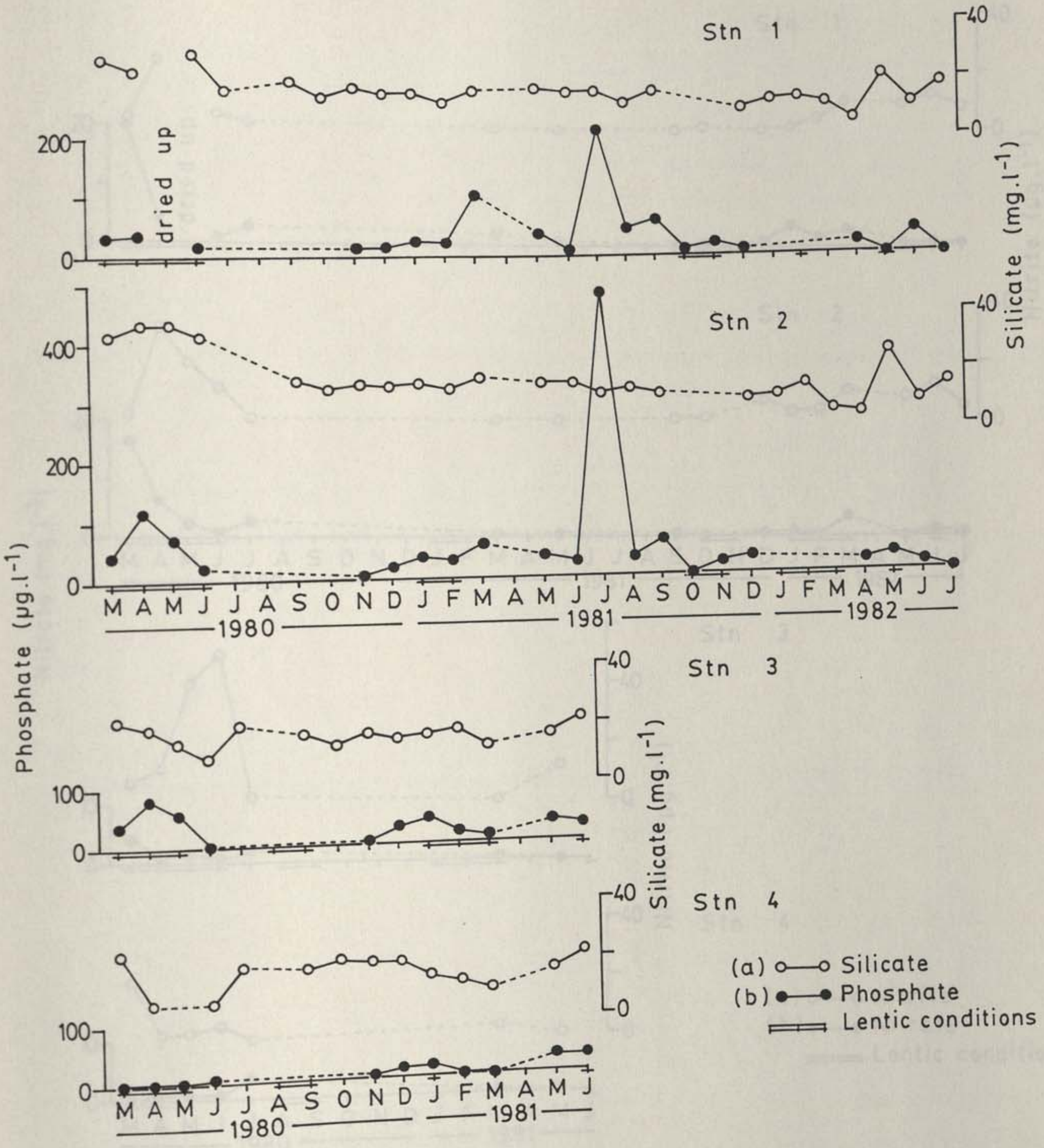


FIGURE 17: Monthly variation of (a) silicate, and (b) phosphate at Stations 1 to 4.

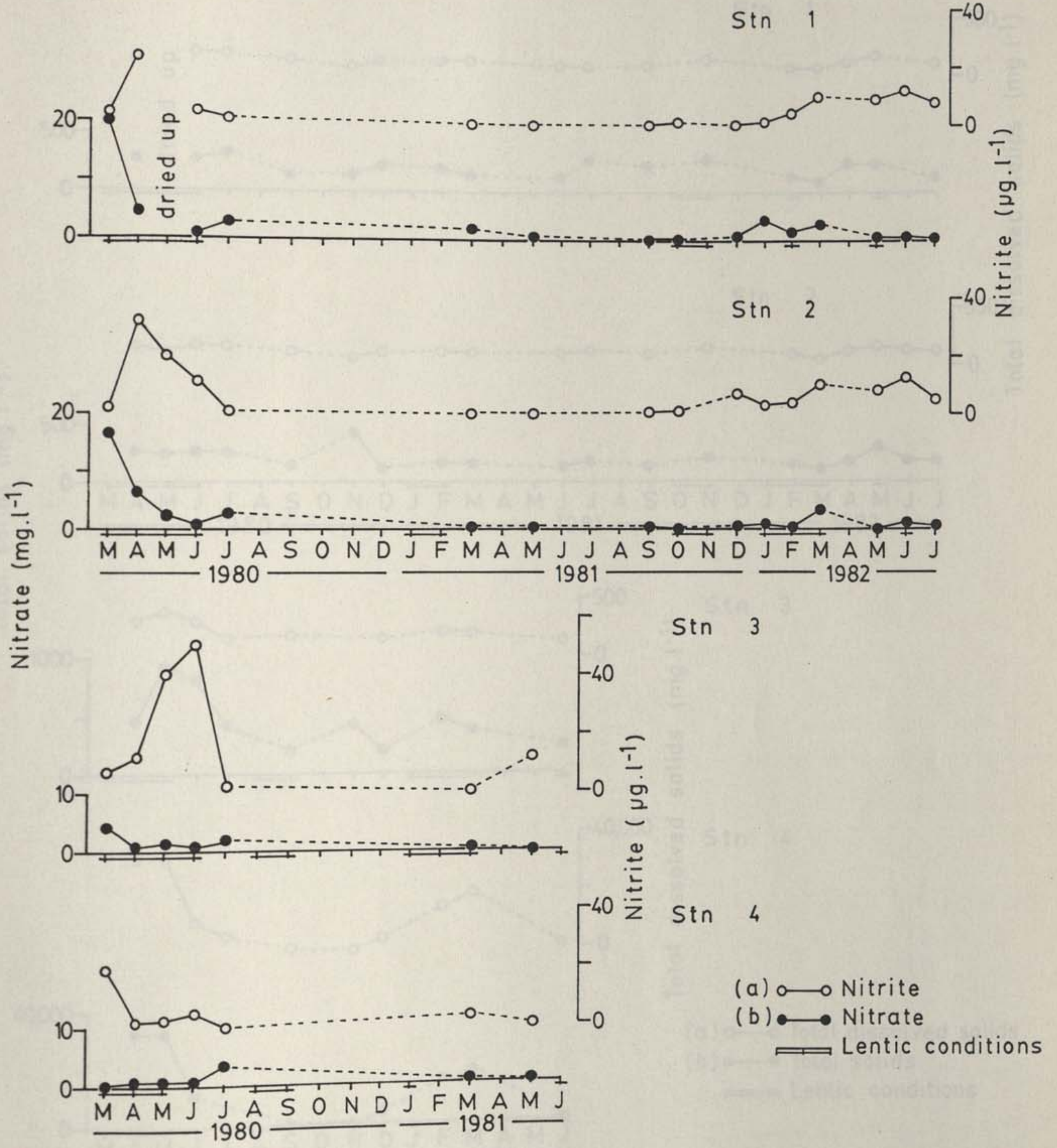


FIGURE 18: Monthly variation of (a) nitrites, and (b) nitrates at Stations 1 to 4.

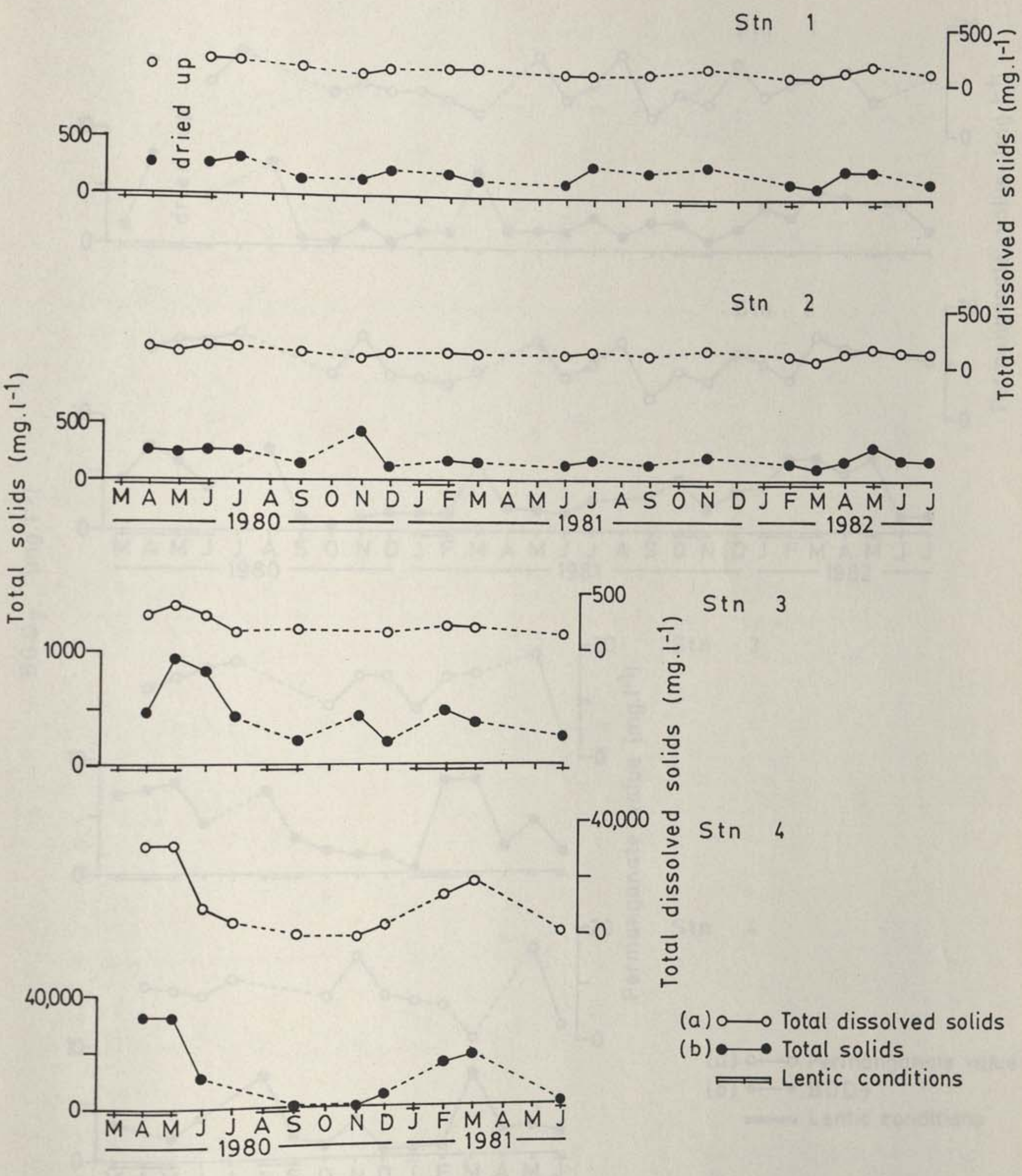


FIGURE 19: Monthly variation of (a) total dissolved solids, and (b) total solids at Stations 1 to 4.

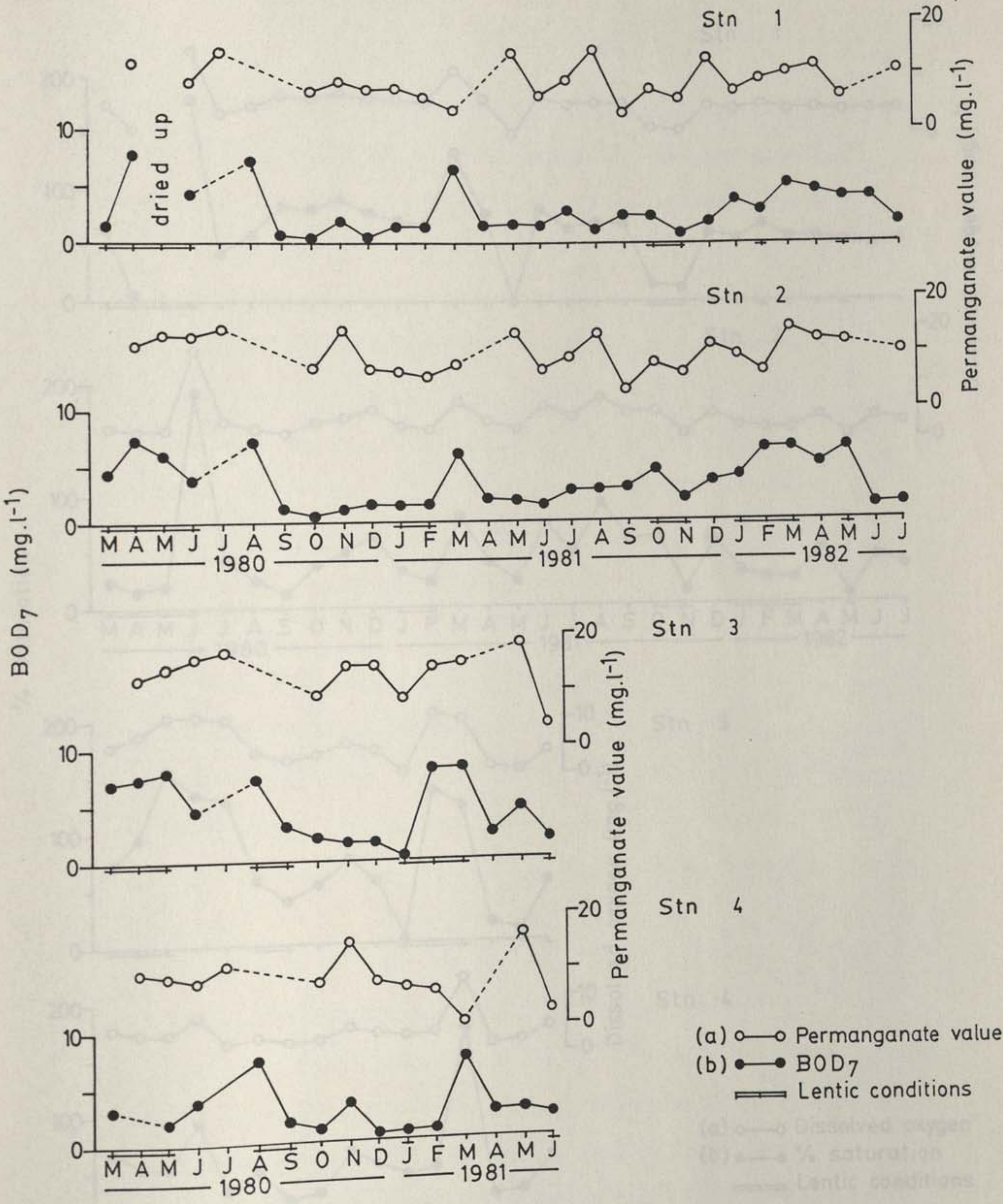


FIGURE 20: Monthly variation of (a) permanganate value, and (b) BOD at Stations 1 to 4.

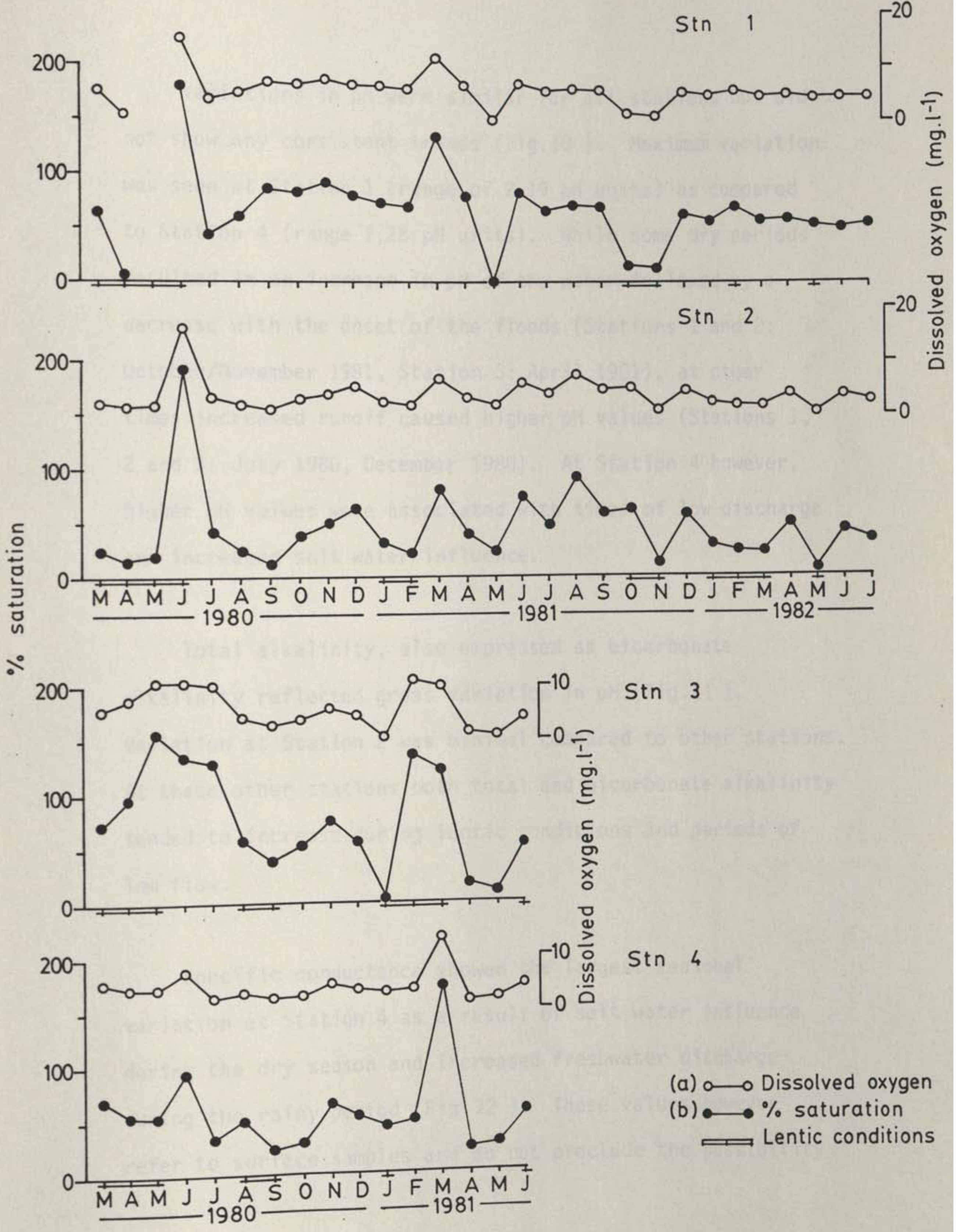


FIGURE 21: Monthly variation of (a) dissolved oxygen, and (b) percentage saturation of oxygen at Stations 1 to 4.

Variations in pH were similar for all stations but did not show any consistent trends (Fig.10). Maximum variation was seen at Station 1 (range of 2.19 pH units) as compared to Station 4 (range 1.28 pH units). While some dry periods resulted in an increase in pH of the water followed by a decrease with the onset of the floods (Stations 1 and 2: October/November 1981, Station 3: April 1981), at other times increased runoff caused higher pH values (Stations 1, 2 and 3: July 1980, December 1980). At Station 4 however, higher pH values were associated with times of low discharge and increased salt water influence.

Total alkalinity, also expressed as bicarbonate alkalinity reflected gross variation in pH (Fig.11). Variation at Station 2 was minimal compared to other stations. At these other stations both total and bicarbonate alkalinity tended to increase during lentic conditions and periods of low flow.

Specific conductance showed the largest seasonal variation at Station 4 as a result of salt water influence during the dry season and increased freshwater discharge during the rainy period (Fig.12). These values however refer to surface samples and do not preclude the possibility of salinity stratification. Station 3 attained a maximum conductance of 800 µmhos during the severe 1980 dry season with lower but still marked increases during subsequent dry periods. Although Stations 1 and 2 also showed increased conductance with lentic conditions, values were never higher than 400 µmhos which was also recorded in the 1980 dry season.

Variation in total hardness, a measure of calcium and magnesium ions expressed as $CaCO_3$, is shown in Fig. 13, while concentrations of calcium and magnesium ions are shown separately (Fig. 14). At all stations there was some tendency for hardness to increase with low flow periods. This was supported by trends shown for individual calcium and magnesium ion concentrations. Highest magnesium concentrations seemed to occur later in the dry season than calcium. While distinct increases in both calcium and magnesium ions occurred at Station 4 in the dry season, magnesium ion levels were often more than twice those of calcium.

Both total and soluble iron occurred in such concentrations for this element to be considered a fairly important chemical component of the freshwater sites. There was a slight tendency for increased concentration of total iron (predominantly insoluble Fe^{3+}) in the dry periods at these freshwater stations while at the same time decreases in soluble iron (predominantly Fe^{2+}) were observed (Fig. 15). At Station 4 iron was found only in very low concentrations except during the rainy season when discharge of freshwater with high levels of iron increased. During the dry season, most of the iron present at this brackish water station was in the insoluble form.

Both chloride and sulphate anions showed fairly clear seasonal variation in concentrations (Fig. 16). Chloride concentrations increased consistently with the existence of dry conditions attaining maximal values for freshwater sites at Station 1 during the 1981 dry season. Marked increases also occurred during low flow periods at Station 4. Of all the sites sampled Station 2 tended to be the most stable with respect to chloride concentrations. Sulphate ion levels generally increased during the dry season at Station 1 but at Stations 2 and 3 distinctly low concentrations were evident during some lentic periods (Station 2: October/November 1981), January-March 1982, Station 3: September 1980, February/March 1981).

Silica, measured as silicate, was relatively constant for all stations showing minimal seasonal variation (Fig. 17). Consistent trends were not observed although a tendency for silica levels to decrease towards the end of lentic periods was apparent at Stations 3 and 4 and to a lesser extent at Station 2.

Inorganic nutrients measured included phosphate, nitrite-nitrogen and nitrate-nitrogen (Figs. 17, 18). However analyses were irregular and as a result only tentative generalisations may be proposed. While phosphate levels increased early in the dry periods and subsequently decreased markedly at the freshwater stations, one very high value was recorded in July 1981 for Stations 1 and 2. It is unclear whether this is characteristic for flood periods since only one other flood period was analysed for phosphates (June/July 1982) or whether this was due to extrinsic factors such as fertiliser application. The latter possibility could not be assessed since analyses for associated nutrient elements were not carried out on these water samples.

Analyses of nitrites and nitrates were made too sporadically to make definitive comments on the seasonal variation of these parameters. However there seemed to be an inverse relationship between concentrations of nitrite and nitrate ions. Nitrite levels were generally highest during the 1980 dry season at all stations and decreased with the onset of the rainy season. Nitrate levels decreased during the same dry period.

As expected, variation in total dissolved and total solids reflected that of specific conductance (Fig. 19). However readings were too irregular for the full picture of events to be obtained. There appeared to be an increase in concentration of both parameters during the dry season and this was especially marked at Stations 3 and 4. The other stations were relatively stable with respect to these parameters.

Oxygen demands were recorded as chemical oxygen demand (COD or permanganate value) and biochemical oxygen demand (BOD) (Fig. 20). BOD values showed distinct increases coincident with the dry seasons and lentic conditions while COD values showed slightly different fluctuations. It appears that increased COD values occurred both towards the end of the dry periods and also during the flood period for all stations.

Monthly variation in dissolved oxygen concentrations and percentage saturation are shown in Fig. 21. Although many readings appear to be in a normal range for most freshwaters, some cases of extreme supersaturation up to more than 190% were recorded. Such readings for Stations 1, 2 and 4 were abrupt and seemed unrelated to ensuing stagnant conditions. It may be assumed that errors in methodology may have caused such aberrant values. However at Station 3, supersaturation was attained gradually over several months and seemed to follow a clear trend of seasonal variation with maximal oxygen concentrations occurring during the late dry and early rainy periods and minimal values at the onset of the dry season and during short lentic periods. This pattern coincided with the seasonal development of phytoplankton communities (cf. Results section 'Plankton') and may explain such trends in oxygen concentrations but some errors in methodology can not be excluded altogether. Although some field measurements of oxygen were made with an oxygen meter and probe, this method was unreliable at low oxygen concentrations. However, at normal oxygen levels, differences between field meter readings and Winkler analyses were relatively small. Measurements of dissolved oxygen at several points within Stations 1 and 2 showed no major spatial variation in oxygen concentrations although minor decrease with depth and increase with current speed were observed.

On one occasion on 82/06/16 the opportunity arose to make observations and obtain water samples during a flood at Stations 1 and 2. Water temperatures were low and turbidity very high as compared to values obtained at other times. Notable features of the water quality at this time were the very low specific conductance and dilution of ions such as chloride, iron and magnesium. Oxygen levels were only 50.3 and 44.1% saturation for Stations 1 and 2 respectively. Other parameters were found to lie within the range of other monthly samples taken.

In summary, the range of monthly variation of chemical parameters differed for the four stations. Variation at Stations 1 and 2 was relatively slight compared to Stations 3 and 4. Station 4 was most subject to fluctuations in water quality due to the varying seasonal influences of seawater in the dry periods and increased stream discharge in the rainy periods. Station 3 showed large fluctuations based on the alternation of lentic and lotic conditions during the year.

Diurnal variation:

Diurnal variation of physical and chemical characteristics was studied over 24-hour periods during both rainy and dry seasons at Stations 2 and 4. After sampling Station 2 on 81/03/25-26 to represent dry season conditions, inadequate chemical analyses were carried out and hourly sampling was repeated on 82/03/31-04/01. Differences in weather conditions existed between 1981 and 1982 dry seasons with 1982 being somewhat wetter, therefore data for both sampling periods are presented. Hourly variation in irradiance and surface current speed is only shown for rainy season sampling periods.

Variation in air, water surface and bottom temperatures, pH, specific conductance, total alkalinity and dissolved oxygen are illustrated for Station 2 in the rainy season sampling period (Fig. 22) and the 1982 dry season sample (Fig. 23). Air and water temperatures and dissolved oxygen content only are illustrated for the 1981 dry season sampling period (Fig. 24).

Depths at Station 2 did not change during the sampling periods being 0.5 m in the dry season and 0.7 m in the rainy

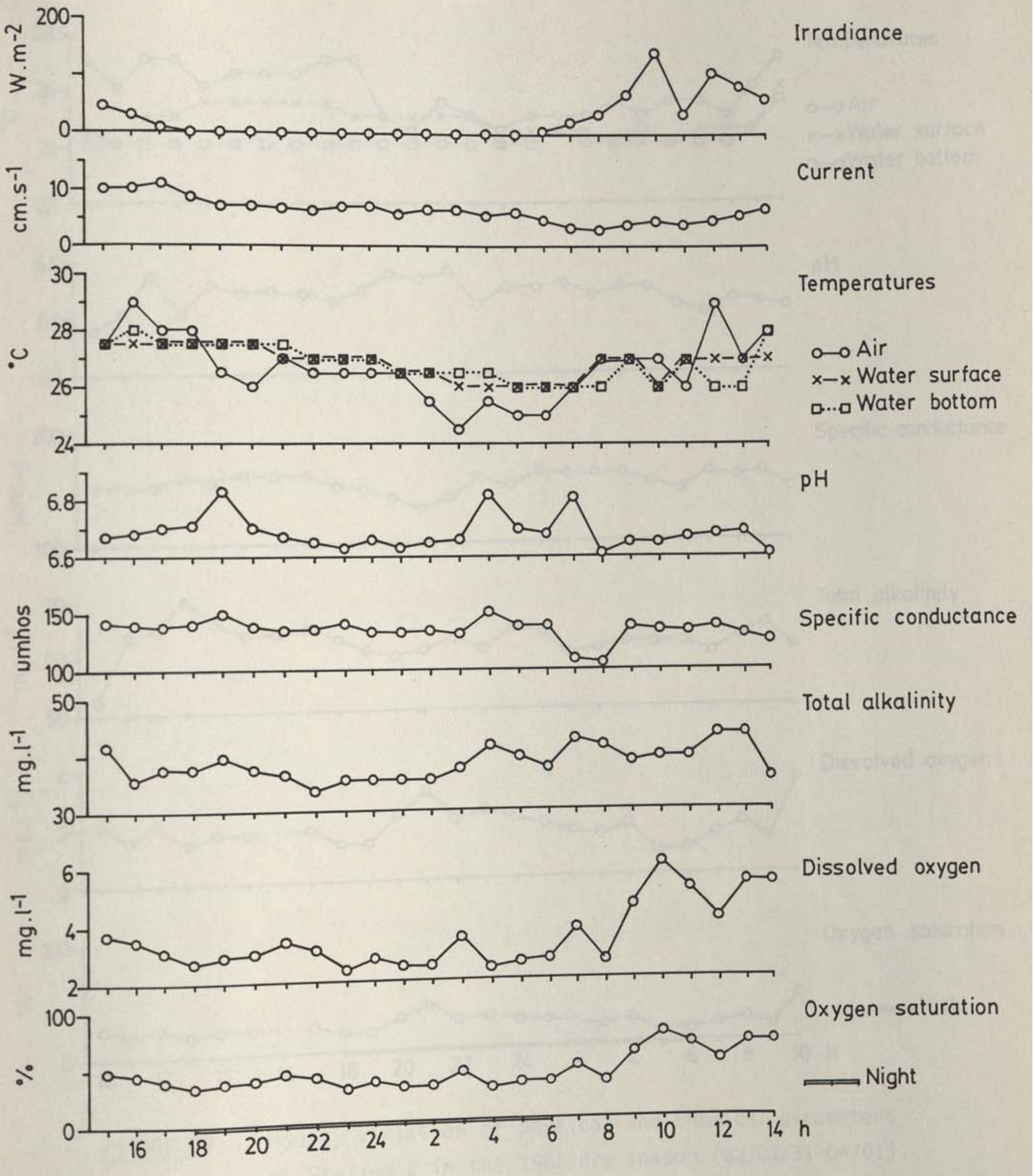


FIGURE 22: Hourly variation of physical and chemical parameters at Station 2 in the rainy season (80/08/07-08).

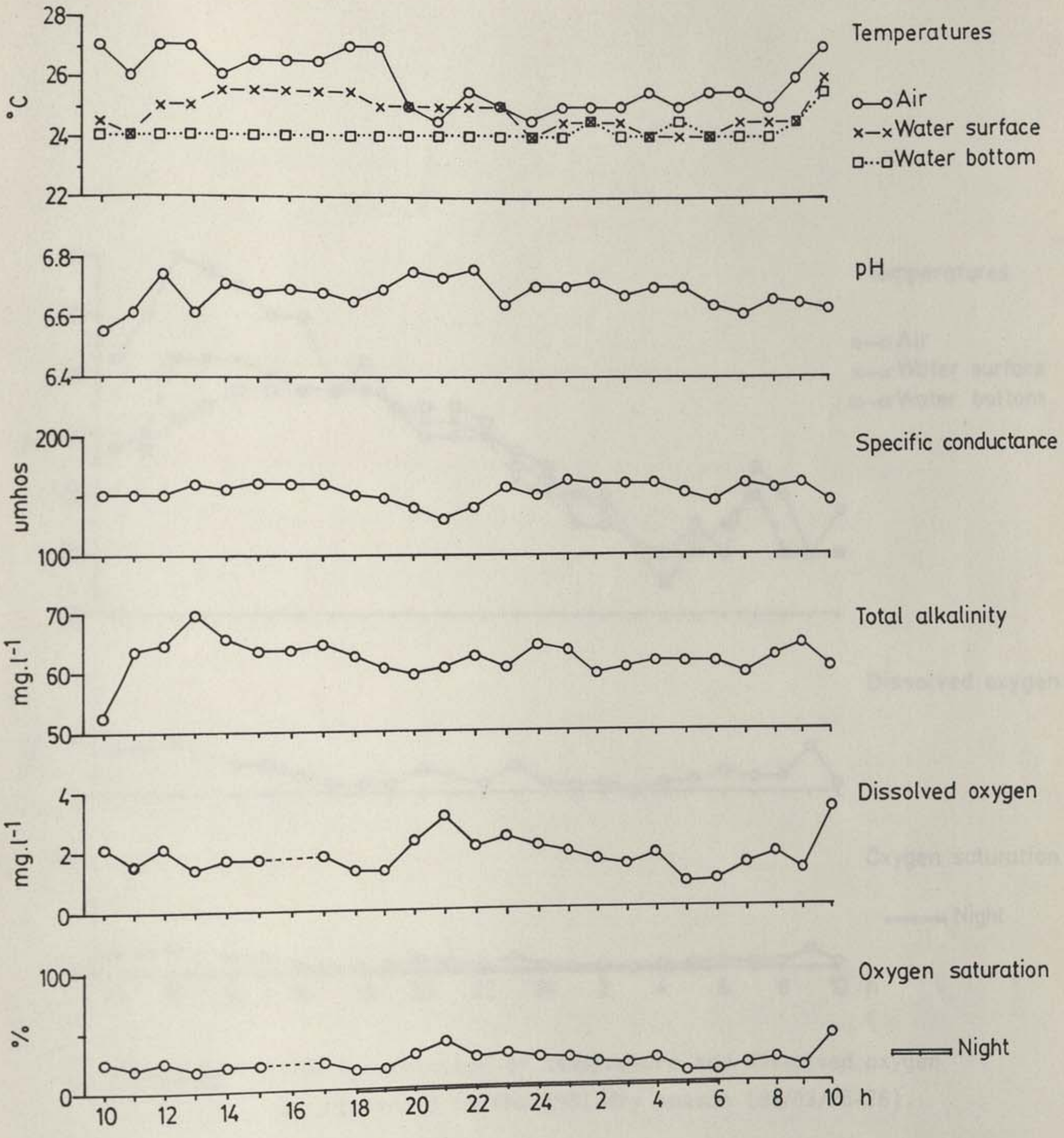


FIGURE 23: Hourly variation of physical and chemical parameters at Station 2 in the 1982 dry season (82/03/31-04/01).

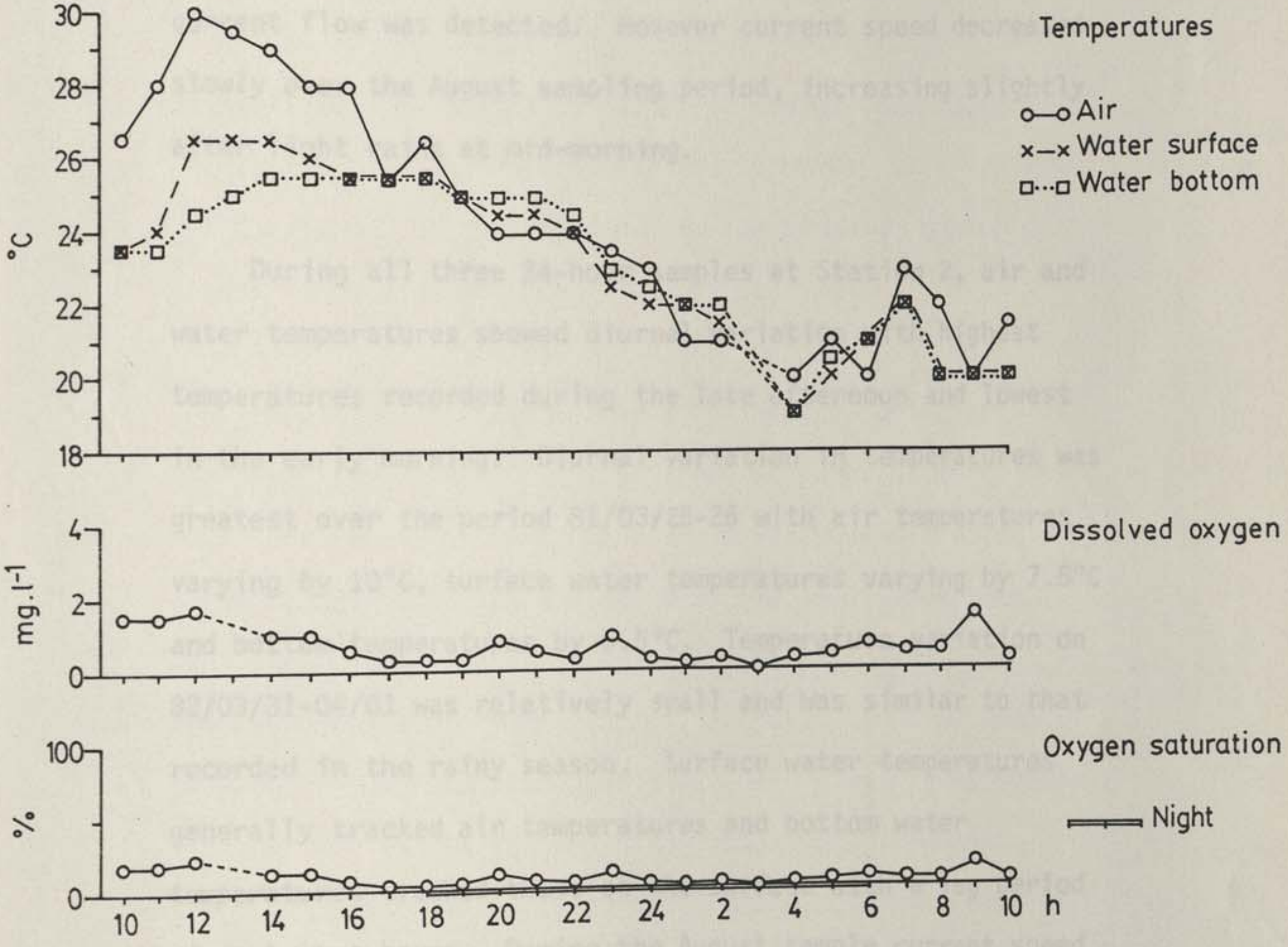


FIGURE 24: Hourly variation of temperature and dissolved oxygen at Station 2 in the 1981 dry season (81/03/25-26).

season. There was some temporal variability of irradiance over the daylight period due to changing cloud cover during the rainy sampling period. During the dry season sampling period no current flow was detected. However current speed decreased slowly over the August sampling period, increasing slightly after light rains at mid-morning.

During all three 24-hour samples at Station 2, air and water temperatures showed diurnal variation with highest temperatures recorded during the late afternoon and lowest in the early morning. Diurnal variation in temperatures was greatest over the period 81/03/25-26 with air temperatures varying by 10°C, surface water temperatures varying by 7.5°C and bottom temperatures by 6.5°C. Temperature variation on 82/03/31-04/01 was relatively small and was similar to that recorded in the rainy season. Surface water temperatures generally tracked air temperatures and bottom water temperatures tracked those at the surface with a lag period of up to two hours. During the August sample current speed seemed sufficient to ensure some degree of mixing so that surface and bottom water temperatures were very similar and equilibrated quickly. In both dry seasons some stratification in the water column occurred especially during the day when rapid heating of the upper layers occurred. During the night however stratification was less marked and on several occasions reverse temperature gradients were established with bottom temperatures higher than those at the surface. Such temperature inversions may have resulted in 'overturns' of the water column and promoted mixing of layers hence reduced stratification at night.

Specific conductance showed minimal changes over both sampling periods although some decreases occurred which could not be explained by rainfall or increased runoff (Figs. 22 and 23). Variation in pH and total alkalinity were minimal over both dry and rainy sampling periods. However dissolved oxygen content fluctuated to some extent during all three sampling periods. During the rainy season and 1981 dry season samples dissolved oxygen increased slightly during daylight hours indicating the influence of photosynthetic production of oxygen. However during the night some fluctuations occurred which may be related to overturn of the water column or equilibration of surface and bottom water temperatures, leading to a decrease of surface oxygen levels by mixing with hypoxic deeper layers (for example Fig. 23, 82/04/01:0500 h).

Diurnal variation of physical and chemical parameters at Station 4 is illustrated in Figs. 25 and 26 for rainy and dry seasons respectively. Stages of the tide as determined from Tide Tables are also indicated.

Depths remained constant during each sample period at 0.7 m and 0.8 m for rainy and dry season samples respectively. No current flow was detected during the dry season sample and only slight currents (less than 3 $cm.s^{-1}$) due to tidal influence were measured during the rainy season sampling period. Irradiance was measured only during the rainy season sample period and was maximal at midday to early afternoon decreasing drastically in mid afternoon due to overcast conditions and subsequent sunset.

Air and consequently water temperatures changed less over the 24-hour period during the rainy season sample. At this time air, surface and bottom water temperatures varied by only 8.5°C, 5.0°C and 2.0°C respectively. In contrast during the dry season diurnal variation of the same parameters was 11.5°C, 7.0°C and 7.0°C respectively. Maximal temperatures were measured during the early afternoon decreasing steadily to a minimum between 0300 and 0600 h. As at Station 2 water temperatures followed air temperatures closely with a lag

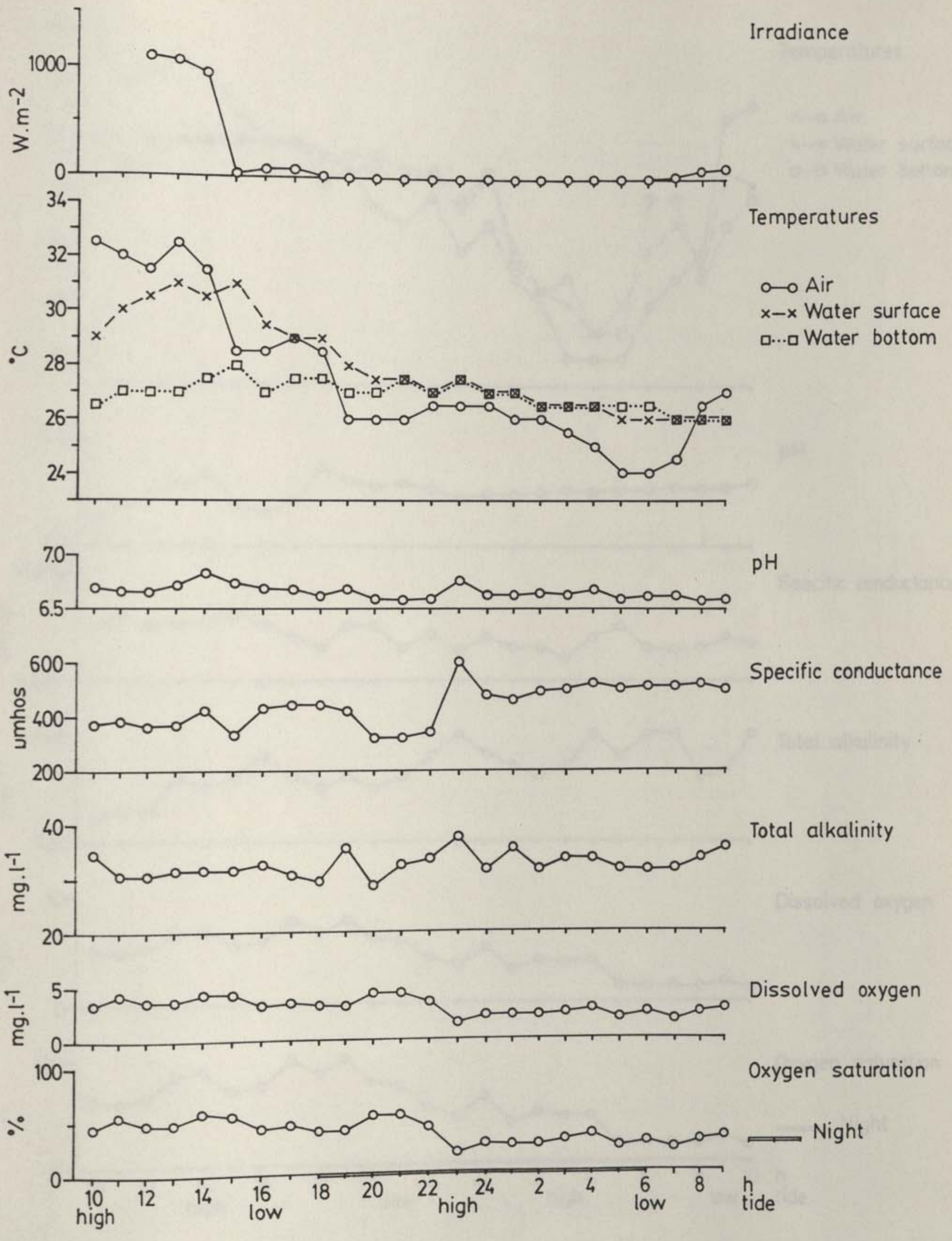


FIGURE 25: Hourly variation of physical and chemical parameters at Station 4 in the rainy season (80/08/19-20).

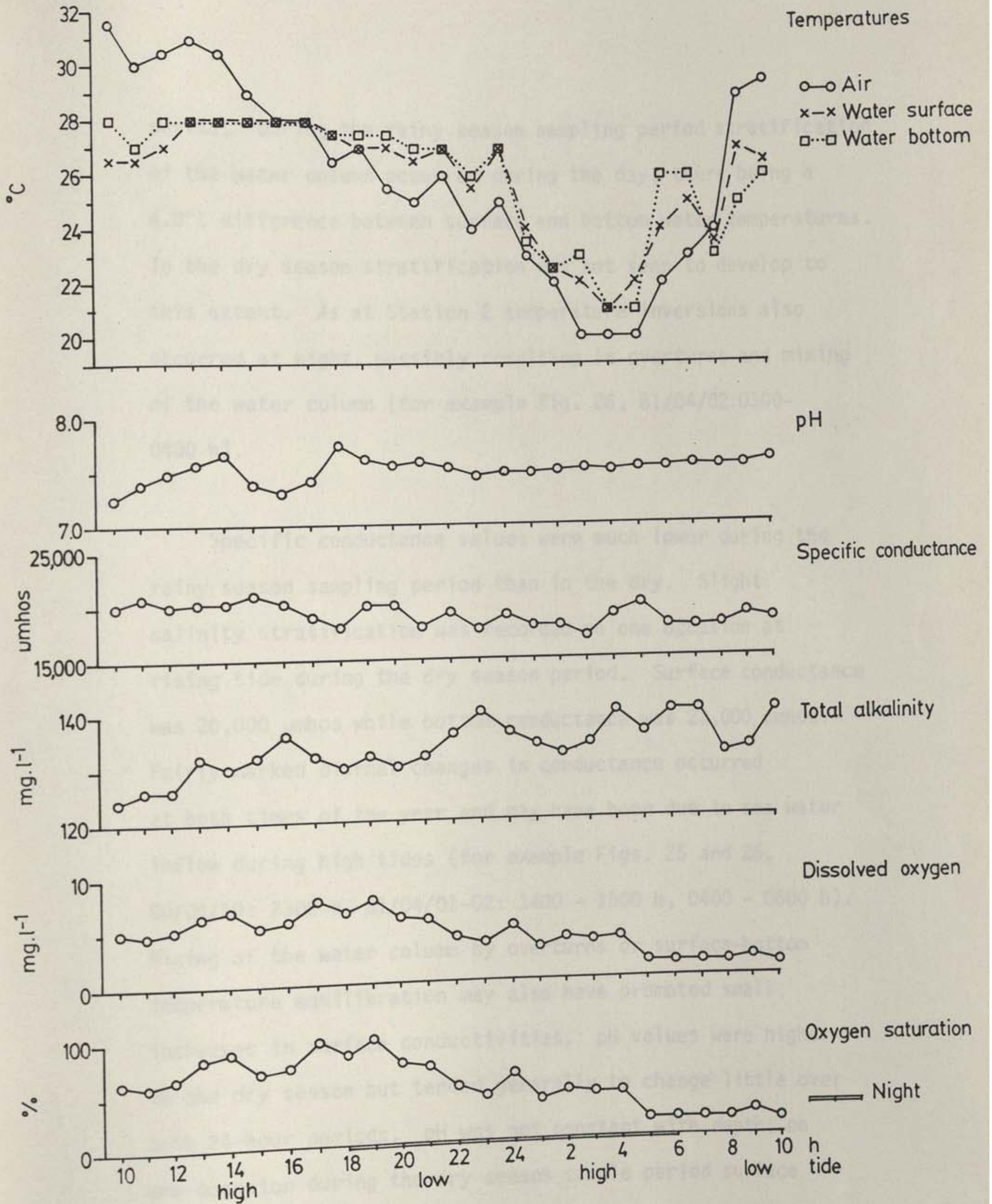


FIGURE 26: Hourly variation of physical and chemical parameters at Station 4 in the dry season (81/04/01-02).

period. During the rainy season sampling period stratification of the water column occurred during the day, there being a 4.0°C difference between surface and bottom water temperatures. In the dry season stratification was not seen to develop to this extent. As at Station 2 temperature inversions also occurred at night, possibly resulting in overturns and mixing of the water column (for example Fig. 26, 81/04/02:0300-0400 h).

Specific conductance values were much lower during the rainy season sampling period than in the dry. Slight salinity stratification was recorded on one occasion at rising tide during the dry season period. Surface conductance was 20,000 μmhos while bottom conductance was 22,000 μmhos. Fairly marked diurnal changes in conductance occurred at both times of the year and may have been due to sea water inflow during high tides (for example Figs. 25 and 26, 80/08/19: 2300 h, 81/04/01-02: 1400 - 1500 h, 0400 - 0600 h). Mixing of the water column by overturns or surface-bottom temperature equilibration may also have promoted small increases in surface conductivities. pH values were higher in the dry season but tended generally to change little over both 24-hour periods. pH was not constant with depth; on one occasion during the dry season sample period surface pH was 7.48 while bottom pH was 7.05. During this same period a sudden decrease in surface pH might have been due to mixing of surface and bottom water layers. Alkalinity was low and remained fairly constant over the rainy season sample period but was higher and fluctuated more widely during the dry season period. There was a tendency for alkalinity to increase generally during the dry season sampling period and might reflect increased inputs of carbon dioxide of respiration during the night. Dissolved oxygen levels showed diurnal variation at both times of the year with higher values during daylight hours possibly due to photosynthetic activity. Daytime oxygen saturation values were higher during the dry season sampling period.

Stream biota

General observations:

Aquatic macrophytes were not found within the study area. However algal mats did develop during slow flowing or lentic conditions in well illuminated parts of the stream and were mainly composed of *Oedogonium* and *Spirogyra* with numerous attached diatoms.

A list of benthic and other macrofauna (excluding fishes) collected during the study period at the four stations is given in Table 6 and Appendix 3. Each station supported quite rich faunas with Station 4 having a distinct brackish water fauna. In terms of the numbers of taxa represented, Station 1 showed greater diversity than all other stations, while Stations 2 and 3 were roughly equivalent and Station 4 was the least diverse. Station 1 was especially rich with respect to aquatic arthropods, particularly insects, presumably due to the more favourable flow conditions and the sandy substrate at this site.

The most commonly collected taxa at all freshwater stations included oligochaetes, particularly tubificids and occasionally naidids, the trichodactylid crab *Dilocarcinus dentatus*, aquatic insects such as the dragonflies *Perithemis mooma* and *Dythemis* spp, the water scorpion *Ranatra mixta*, the gerrid *Brachymetra albinervis*, and chironomid larvae, planorbid gastropods, *Pomacea glauca*, and sphaeriid bivalves. Ancylid limpets were common at Stations 2 and 3 but were not found at Station 1 while nematodes were always abundant at Station 3 but not elsewhere. Vertebrate and other invertebrate taxa were collected only occasionally.

TABLE 6: Summary of aquatic macrofauna (excluding fishes) collected at Stations 1 to 4 during the study period.

		Stations			
Taxon		1	2	3	4
Nematoda				x	
Nemertea		x			
Oligochaeta	- Tubificidae	x	x	x	
	Naididae	x	x	x	
	Enchytraeidae	x			x
Hirudinea	- Glossiphonidae	x	x	x	
Polychaeta	- Nereidae				x
	Capitellidae				x
Cladocera			x	x	
Ostracoda				x	
Copepoda			x	x	
Isopoda					x
Amphipoda					x
Decapoda	- Penaeidae				x
	Palaemonidae	x		x	
	Alphaeidae				x
	Portunidae				x
	Trichodactylidae	x	x	x	
Arachnoidea	- Hydracarina	x	x		
Ephemeroptera	- Leptophlebiidae	x	x		
Odonata	- Coenagrionidae	x	x		
	Calopterygidae	x			
	Aeshnidae	x			
	Gomphidae	x	x		
	Libellulidae	x	x	x	

TABLE 6: (continued)

Taxon		Stations			
		1	2	3	4
Hemiptera	- Belostomatidae	x	x		
	Nepidae	x	x	x	
	Hydrometridae	x	x		
	Notonectidae		x	x	
	Gerridae	x	x	x	
	Veliidae	x			
Coleoptera	- Dytiscidae	x			
	Gyrinidae	x			
	Hydrophilidae			x	
	Carabidae	x			
Diptera	- Chironomidae	x	x	x	
	Heleidae	x	x	x	
Gastropoda	- Planorbidae	x	x	x	
	Ampullariidae	x	x	x	
	Hydrobiidae				x
	Ancylidae		x	x	
Bivalvia	- Sphaeriidae	x	x	x	
	Mytellidae				x
Amphibia	- Bufonidae			x	
	Hylidae		x		
	Leptodactylidae		x		
Reptilia	- Chelidae		x	x	
	Emydidae		x		
	Kinosternidae		x	x	
	Crocodylidae		x	x	x

Station 4 supported a brackish water faunal assemblage with groups such as nereid polychaetes, isopods, amphipods, hydrobiid gastropods and juvenile mussels being well represented. Other crustacean fauna included penaeid and snapping shrimp and swimming crabs *Callinectes sapidus*. Terrestrial crabs on the stream banks and vegetation included *Goniopsis cruentata, Sesarma* sp, *Aratus pisonii* and *Cardisoma guanhumi*. No aquatic insects were found in this part of the stream. Caiman were occasionally seen as far as these lower stream reaches.

Plankton:

The groups represented most commonly in the plankton were algal groups with desmids, some filamentous chlorophytes and cyanophytes, diatoms and euglenoids being prominent in most monthly samples at all stations (Appendix 4). However Station 1 supported a somewhat poorer planktonic community when compared with other stations. Crustaceans such as cladocerans, ostracods, copepods (mainly cyclopoid) and amphipods were restricted in distribution being most prevalent at Stations 3 and 4. Only copepods and occasionally ostracods were found at Stations 1 and 2 and even then only rarely. While certain taxa were represented at most stations, notable exceptions were the diatoms *Coscinodiscus* and *Synedra* and the medusa of the freshwater hydroid *Craspedacusta* which were found only at the brackish water Station 4. Other restricted taxa included the colonial rotifer *Conochilus* and the previously mentioned crustaceans which were found mainly in the slower flowing deeper Stations 2 and 3.

From the monthly samples some gross variation in seasonal abundance could be recognised (Table 7). For all freshwater stations (and especially at Station 2) numbers of taxa appeared to increase in the dry season. Stations 1 and 3 showed less marked seasonal changes in terms of number of taxa collected. Certain groups occurred only in the dry season or increased in abundance at this time, for example blue green algae, desmids, euglenoids, rotifers, copepods and hydracarina. During the dry season, desmids in particular increased in abundance at Station 1 while blue green algae, euglenoids, rotifers and hydracarina predominated at Station 2. At Station 3 euglenoids were abundant throughout the dry season and also in August, while rotifers peaked in numbers in the dry season only. Also at Station 3 peaks in abundance of diatoms occurred late in the rainy season (December) and ostracods were found in large numbers in August 1980. Station 4 showed a different trend with fewer

TABLE 7: General trends in the seasonal variation of plankton composition and relative abundance at Station 1 to 4.

	Stn 1		Stn 2		Stn 3		Stn 4	
Taxon	R	D	R	D	R	D	R	D
Myxophyceae				xx		x	x	
Chlorophyceae	x	xx[1]	x	x	x	x	x	x
Bacillariophyceae	x	x	x	x	xx	x	xx	
Euglenidae	x	x		xx	xx	xx	x	
Zoomastigophorea			x	x		x		
Sarcodina	x	x	x	x	x	x	x	
Ciliata	x	x	x	x		x		
Hydrozoa								x
Rotifera	x			xx	x	xx		
Cladocera					x	x	xx	
Ostracoda			x		xx	x	x	x
Copepoda		x		x	x		xx	xx
Amphipoda					x		x	x
Arachnida		x		xx			x	

x : present

xx : common or abundant

R : Rainy season (July-December 1980, June 1981)

D : dry season (January-May 1981)

[1] : primarily Desmidaceae

planktonic taxa in the dry season. Increased abundance of diatoms occurred in the early rainy season in June and July while dense crustacean-dominated plankton samples were collected in August/September and again in January/February.

Results of quantitative sampling carried out in the 1983 dry and wet seasons for Stations 1 and 2 are shown in Table 8. Dry season samples collected at Stations 1 and 2 were not exactly comparable since Station 1 had apparently dried out and subsequently refilled with recent rains and therefore represented a newly developing planktonic community. Nevertheless both stations supported more planktonic taxa in the dry season than in the rainy season with diatoms, actinopods, rhizopods and rotifers present in addition to flagellates and ciliates found all year round. The composition of the flagellates varied from one season to the next, being almost entirely composed of euglenoids in the dry season but containing none of these in the rainy season. The rotifers, collected only in the dry season samples, were solitary species at Station 1 whereas at Station 2 colonies of *Conochilus* were common. Plankton densities varied markedly with Station 2 samples having more than 13,000 organisms.ml^{-1} in the dry season and decreasing to 27.5 organisms.ml^{-1} in the wet. Station 1 mean plankton

TABLE 8: Comparison of mean densities of planktonic organisms in dry and rainy seasons at Stations 1 and 2.

	Mean number of organisms.ml^{-1}			
	Dry season		Rainy season	
	Stn 1	Stn 2	Stn 1	Stn 2
Bacillariophyceae	2.50	2.50	0	0
Mastigophorea	1.25[1]	12907.50[1]	48.75[2]	26.25[2]
Sarcodina	17.50	20.00	0	0
Ciliata	2.50	242.50	2.50	1.25
Rotifera	3.75	7.59	0	0
Copepoda	0	0	1.25	0
Total ± Standard Error	27.50 ±7.2	13180.09 ±211.9	52.50 ±7.5	27.50 ±9.2

1 : predominantly euglenoids

2 : no euglenoids

densities increased slightly from dry to wet season from 27.5 to 52.5 organisms.ml^{-1} respectively. Comparisons of total numbers of organisms in samples showed that mean dry season densities of planktonic organisms at Station 2 were significantly higher than mean densities at the same station in the rainy season ($t = 62.02$, $df = 3$, $p<0.001$) and were also significantly higher than mean densities attained at Station 1 in both the dry ($t = 62.05$, $df = 3$, $p<0.001$) and rainy season samples ($t = 61.93$, $df = 3$, $p<0.001$). No significant differences were found between dry and rainy season mean densities at Station 1 ($t = 2.40$, $df = 6$, $p>0.05$) or between rainy season mean densities at Stations 1 and 2 ($t = 2.10$, $df = 6$, $p>0.05$).

Benthic macroinvertebrates:

Monthly samples of benthic macroinvertebrates were non-quantitative but gave a general indication of the nature of the communities and gross seasonal changes at each station (Tables 9 to 12). Certain groups such as oligochaetes (primarily tubificids), chironomids, planorbid gastropods, ancylid limpets and sphaeriid bivalves were dominant in the benthos at the freshwater stations. No clear seasonal changes in the nature of the fauna were observed at these stations. Fauna at Station 4 included primarily nereid polychaetes, isopods, amphipods, hydrobiid gastropods and

TABLE 9: Monthly variation of benthic macroinvertebrates at Station 1 (numbers.m^{-2}).

	1980					1981												1982						
Taxon	A	S	O	N	D +	J	F	M	A	M	J	J	A +	S	O	N	D	J	F	M	A	M	J	J
Nemertea							16																	
Oligochaeta	80	32	368			32	16		48	48	16	32		178	178	178	1333		89	311	178	622		133
Hirudinea										16		16		44										
Hydracarina	16																		89	133		89		
Ephemeroptera		48																	44					
Odonata		16	16						16	16									44					
Diptera																								
Chironomidae	48	80	64				16		48	48					133	44			178	578	222	44		
Heleidae	48						64			16		16			44				89		44			
Gastropoda	64								32													44		
Bivalvia	368	96	80				160		48	128		144		44			133		1022	1022	1467	2089		44
Total	624	272	528	0	-	32	272	0	192	272	16	208	-	266	355	222	1466	0	1555	2044	1911	2888	0	177

+ : No samples taken.

TABLE 10: Monthly variation of benthic macroinvertebrates at Station 2 (numbers.m^{-2}).

	1980					1981												1982						
Taxon	A	S	O	N	D +	J	F	M	A	M	J	J	A +	S	O	N	D	J	F	M	A	M	J	J
Oligochaeta	64	224	32	16		32	128	80	192	48				44		133	222	444	89	44		222		
Cladocera	16																							
Hydracarina																						44		
Odonata																						44		
Diptera																								
Chironomidae		48	32			112	96		48	32				44		311	89	267		178				
Heleidae	16					16																		
Gastropoda	32	32	32	16		16				32						89	44	89	89	178				
Bivalvia	16	64	288	224		160			16	16							44	89	44	178		44		
Total	144	368	384	256	-	336	224	80	256	128	0	0	-	88	0	533	399	889	222	578	0	354	0	0

+ : No samples taken.

TABLE 11: Monthly variation of benthic macroinvertebrates at Station 3 (numbers.m^{-2}).

Taxon	1980					1981						
	A	S	O	N	D +	J	F	M	A	M	J	J
Oligochaeta	160		48			48	160		48			
Hirudinea										16		
Copepoda			160									
Ostracoda			48									
Diptera						16						
Chironomidae	16					144	96	96	96	64		
Heleidae						16						
Gastropoda						112	32					
Bivalvia						32	16		16			
Total	176	0	256	0	-	352	304	96	160	80	0	0

+ : No samples taken.

TABLE 12: Monthly variation of benthic macroinvertebrates at Station 4 ($numbers.m^{-2}$).

Taxon	1980					1981						
	A	S	O	N	D +	J	F	M	A	M	J	J
Polychaeta	336	16	16	16			32		64	32		
Isopoda				48						32		
Amphipoda				16						48		
Gastropoda			48						144	112		
Bivalvia				16					3104	160		
Total	336	16	64	96	-	0	32	0	3312	384	0	0

+ : No samples taken.

immature mussels. The latter were found in large numbers only during dry periods.

While the data are not quantitative they do show that at certain times of the year numbers of benthic invertebrates decreased to relatively low levels, for example after spates at the beginning of the rainy season (June/July) and during some periods of low flow. At other times, numbers of invertebrates rose to fairly high densities, especially during the 1982 dry season when moderate flow was maintained at Stations 1 and 2.

Late in the 1980 dry season Station 1 dried out completely leaving only moist substrate covered with a thick layer of leaves and other detritus. A sample of this substrate and detritus contained oligochaetes, mites, hydrophilid and dytiscid beetles, dipteran larvae (including heleid midge larvae) and small planorbid snails (Table 13).

A more quantitative analysis of the benthic macroinvertebrates was made to compare dry and rainy season densities and biomass between Stations 1 and 2 (Table 14). Total densities of benthic macroinvertebrates were 1066 and

TABLE 13: List of macrofauna collected from damp stream bed at Station 1 in May 1980.

Taxon	Density (per m^2)
Oligochaeta	20
Hydracarina	176
Coleoptera	68
Diptera	
Heleidae	96
Other	400
Gastropoda	16
Total	776

TABLE 14: Comparison of mean densities and biomass of benthic macroinvertebrates in dry and rainy seasons at Stations 1 and 2.

	Mean densities (per m²)			
	Dry season		Rainy season	
	Stn 1	Stn 2	Stn 1	Stn 2
Oligochaeta	444		544	56
Hirudinea	11	78		22
Hydracarina				11
Ostracoda			11	33
Chironomidae	267		100	122
Odonata			11	
Gastropoda	56		44	967
Bivalvia	67		356	2100
Total ± Standard Error	845	78	1066	3311
	±110.3	±77.8	±184.2	±2971.5
Biomass ($mg.m^{-2}$)	1082.1	46.7	1295.4	4243.1
± Standard Error	±451.5	±46.7	±305.3	±3468.9

3311 individuals.m^{-2} for Stations 1 and 2 respectively in the rainy season. Large numbers of tubificids, chironomid larvae, planorbid snails, limpets and bivalves were present in the rainy season. In comparison oligochaetes were represented by tubificids as well as lumbriculid and naidid worms in the dry season. Dry season samples at Station 2 were practically depauperate and may have been the result of anoxic conditions developing at that time. Mean densities of dry season samples at Station 2 were significantly lower than those at the same station in the rainy season ($t = 4.15$, df = 3, $p<0.05$) in addition to being lower than those at Station 1 in the dry season ($t = 6.56$, df = 5, $p<0.01$). No significant differences in mean densities existed between dry and rainy season samples for Station 1 ($t = 1.20$, df = 5, $p>0.1$). During the rainy season, samples from Stations 1 and 2 showed no significant difference in mean densities ($t = 2.83$, df = 3, $p>0.05$).

Although densities of benthic macroinvertebrates varied somewhat, no significant differences were found in benthic biomass either between stations or between seasons (t-test, $p>0.05$ for all comparisons). Benthic standing crop varied from as low as 46.7 mg.m^{-2} in the dry season to 4243.1 mg.m^{-2} in the wet season at Station 2.

Two prominent benthic invertebrates which were also studied were the trichodactylid crab *Dilocarcinus dentatus* and the prosobranch gastropod *Pomacea glauca*. The former is unusual in that the eggs and juvenile crabs are brooded in the abdomen of the female and the latter in that it is both gill- and lung-breathing.

Monthly samples of *D. dentatus* and *P. glauca* were pooled for all the freshwater stations sampled. Ranges and means of carapace widths for *D. dentatus* are shown in Fig.27 . Juvenile crabs were present in the population at the beginning of the 1980 and 1981 rainy seasons (June-August) and also in December 1981 when particularly heavy rains occurred after a pronounced petit carême. Mean carapace width decreased at this time but increased rapidly afterwards possibly indicating rapid growth of individuals and maturation to reproduce by the following dry season. Maximum adult size attained was 51.7 mm carapace width for a male individual; maximum size of females measured was 49.6 mm carapace width. Large individuals were present in the population throughout the year but maximal size showed a slight decrease in the mid to late rainy season (October/November) possibly due to death of larger individuals at this time.

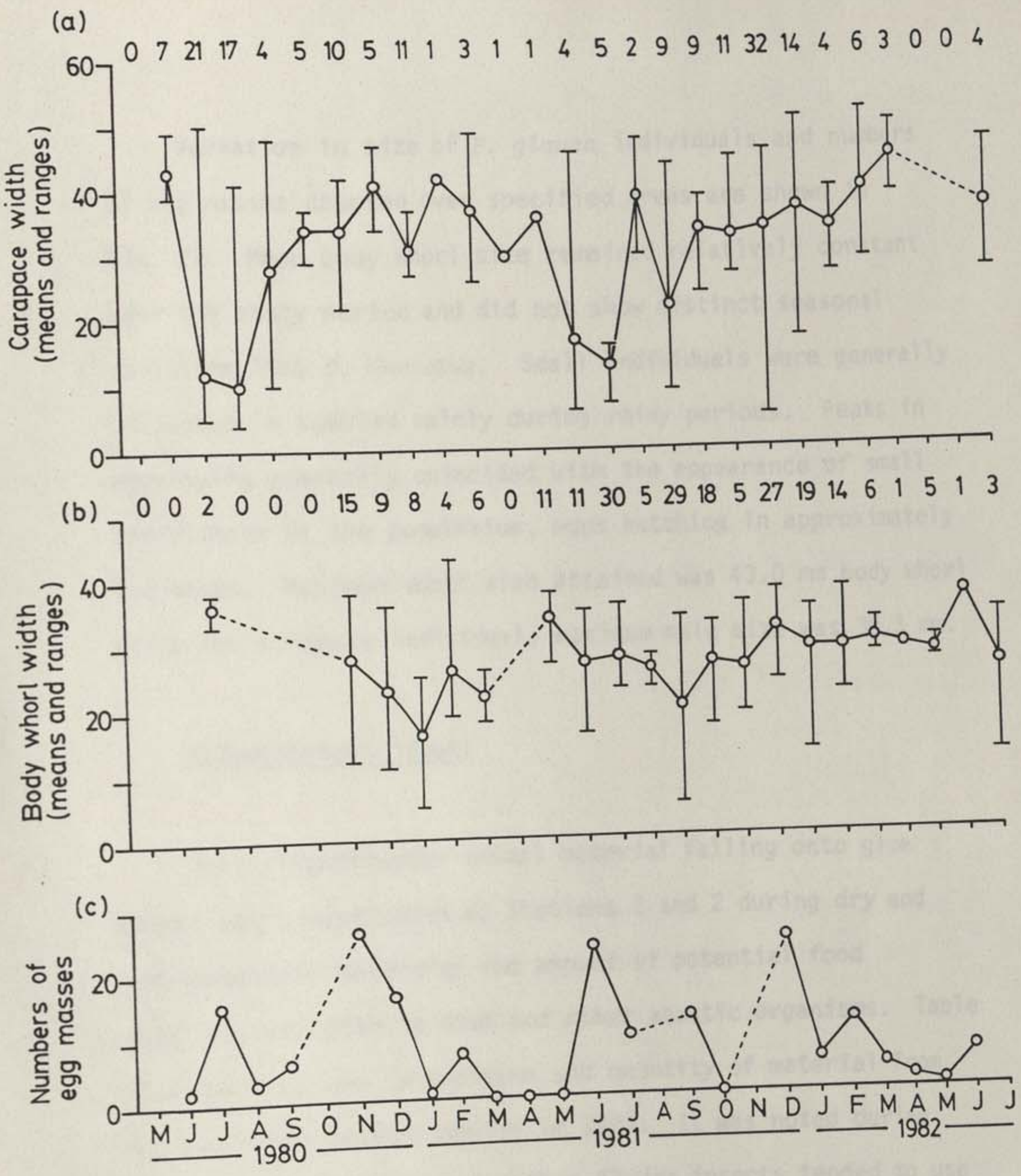


FIGURE 27: Monthly variation of size of (a) D. dentatus, and (b) P. glauca, and (c) numbers of egg masses of P. glauca at Stations 1 to 3 (numbers at top indicate sample sizes).

Variation in size of *P. glauca* individuals and numbers of egg masses counted over specified areas are shown in Fig. 27. Mean body whorl size remained relatively constant over the study period and did not show distinct seasonal variation like *D. dentatus*. Small individuals were generally collected in samples mainly during rainy periods. Peaks in egg-laying generally coincided with the appearance of small individuals in the population, eggs hatching in approximately two weeks. Maximum adult size attained was 43.0 mm body whorl width for a female individual; maximum male size was 38.3 mm.

Allochthonous input:

Only allochthonous animal material falling onto glue boards was investigated at Stations 1 and 2 during dry and wet seasons to determine the amount of potential food material available to fish and other aquatic organisms. Table 15 summarises the composition and quantity of material from dry and rainy season samples in 1983. It was noted during the 24-hour sampling period that flying insects tended to use the glue boards as a resting area thus producing over-estimates of actual 'fall in'. Nevertheless these samples generally reflect terrestrial insect abundance in the vicinity

TABLE 15: Comparison of mean numbers and biomass of organisms caught on glue boards during dry and rainy seasons at Stations 1 and 2.

	Dry season				Rainy season			
	Stn 1		Stn 2		Stn 1		Stn 2	
	no.[1]	wt.[2]	no.	wt.	no.	wt.	no.	wt.
Arachnida	4	1.1	4	2.0	4	3.6	8	16.7
Diplopoda	1	0.2	0	0	0	0	0	0
Collembola	68	3.0	1	0.1	1	0.1	0	0
Odonata	2	136.6	3	43.0	1	6.5	0	0
Orthoptera	41	133.3	0	0	4	20.1	2	0.3
Isoptera	1	0.9	0	0	0	0	0	0
Psocoptera	12	1.4	7	1.4	2	0.1	0	0
Thysanoptera	2	0.7	1	0.1	1	0.1	0	0
Ephemeroptera	0	0	0	0	31	9.2	7	2.1
Hemiptera	31	3.8	15	8.0	6	17.6	11	1.9
Coleoptera	75	99.9	54	35.7	24	22.8	77	27.7
Trichoptera	5	9.2	1	3.3	6	9.2	1	0.3
Lepidoptera	2	0.8	0	0	0	0	0	0
Diptera	846	234.1	653	125.8	743	154.3	1161	191.9

TABLE 15: (continued).

	Dry season				Rainy season			
	Stn 1		Stn 2		Stn 1		Stn 2	
	no.[1]	wt.[2]	no.	wt.	no.	wt.	no.	wt.
Hymenoptera								
ants	22	49.7	17	19.6	5	1.4	15	3.3
winged	165	22.2	75	10.5	25	2.1	39	7.5
Miscellaneous								
& unidentified	3	0.5	0	0	1	0.1	2	0.1
Total numbers	1280		831		854		1323	
± Standard Error	± 509.1		± 109.5		± 198.6		± 101.6	
Total biomass	697.4		249.5		247.2		251.8	
± Standard Error	± 227.3		± 32.2		± 72.4		± 37.1	

1 : numbers.m^{-2}

2 : mg.m^{-2}

of the stream and thus give an indication of potential 'fall in' to the stream.

The majority of organisms collected on the glue boards were terrestrial or winged insects. Dipterans were dominant in the samples both in terms of numbers and by weight, with coleopterans and hymenopterans being next most important. While most of the organisms collected were winged forms which were probably caught on landing, non-winged forms were also fairly well represented, for example spiders, collembolans, orthopterans (crickets) and ants, and these made up as much as 27% of the total sample by weight on one occasion. Some non-living animal material was also collected, for example exuviae, parts of insects and frass.

Some seasonal variation in the taxa collected was noted, for example mayflies were collected only in the rainy season samples. However, other groups do not show any conclusive variation from one season to the next. Statistically significant differences were found only between mean densities of dry and rainy season samples from Station 2 ($t = 3.80$, $df = 6$, $p<0.01$) with rainy season samples containing more organisms (as many as 1323 organisms.m^{-2}). No significant differences were found in the mean biomass of samples from different seasons or stations (t-test, $p>0.05$ for all comparisons). Maximum biomass of 'fall in' was 697.4 $mg.m^{-2}$ at Station 1 in the dry season.

DISCUSSION

The phenomenon of intermittency seen in both the Carlisle and Quarahoon Rivers under study appeared to be a result of a combination of factors, in particular precipitation regime and soil characteristics. In a classification of tropical rivers, Balek (1983) recognised four major categories of rivers based on general climatic factors, precipitation regime and geography: (i) Equatorial rivers of the humid tropics; (ii) rivers of wet and dry regions; (iii) dry climate rivers; and (iv) rivers of tropical mountains. Category (ii) includes four sub-categories based on whether the rivers are found in relatively dry or moist climates and whether located on lowlands or uplands. Generally rivers of this category show pronounced annual fluctuations in discharge due to seasonality of rainfall. Lowland rivers in relatively dry conditions may show an intermittent flow regime due to an extended dry season especially if they have small catchment areas. However, Balek (1983) noted that these lowland rivers are subject to annual rainfall totals less than 1000 mm and vegetation characteristically being dry savanna, both conditions not being met for the present study area.

Annual rainfall totals however, do not completely reflect the precipitation regime and rainfall intensity and duration during the year are important in determining runoff patterns and hence stream flow (Ward 1975). The study area was characterised by periods of intense rainfall for one to several days followed by dry periods resulting in irregularities in stream conditions. During the wet season, high water levels and stream flow were maintained and augmented by floods but during dry spells, water levels receded and current flow slowed or ceased completely. The overall pattern seen was one of irregular fluctuations in habitat size and alternation between lotic and lentic conditions at least twice per year. Small streams generally tend to be more unstable than larger ones (Hynes 1970) and in addition, variability in annual rainfall produced varying conditions of stream flow from year to year and determined the extent of drying out of the stream in successive years.

Although precipitation and climate generally have a primary influence on river regimes, the rate of infiltration through surrounding soils is also of major importance (Ward 1975). This is perhaps the single most important factor in the regulation of intermittent stream flow since it determines how precipitation will be split up into the categories of overland, inter- and ground water flow (Williams & Hynes 1977). In areas of impeded drainage where infiltration is reduced, overland or surface flow is of greater importance than inter- and ground flow thus promoting intense short term floods after periods of heavy precipitation. Ground flow may make some contribution to streamflow during the wet season but during dry periods, the ground water table recedes, lowering the level of the stream until it ceases to flow. Only a few pools remain in the channel which may then vanish due to evaporation (Williams & Hynes 1977). This situation is characteristic of areas of clayey soils with impeded drainage such as those found in the study area.

Physical characteristics of the streams under study such as temperature also showed some variability with quite large annual and diurnal surface water temperature ranges. It is generally quoted that tropical watercourses show minimal fluctuations in water temperature (Hynes 1970) and

Fittkau (1964) determined that in forest-shaded Amazonian streams, annual and daily fluctuations were roughly 1°C around a mean of 24.5°C. Other studies have documented water temperature ranges somwhat larger than this, for example Bishop (1973) measured annual ranges of up to 10°C in the lower course of the Sungai Gombak and about 5°C variation in diurnal water temperatures. Similarly, Harrison & Rankin (1976 a) recorded a diurnal range of 4.1°C for the Greathead River in St Vincent and Adebisi (1981) working on the intermittent Ogun River in Nigeria reported a range of temperatures similar to that obtained in the present study.

Factors influencing stream temperatures include substrate, turbidity, depth, exposure and altitude (Hynes 1970, Welcomme 1979). Of these, varying degrees of exposure contributed to differences seen between stations with Stations 3 and 4 showing highest water temperatures. It is unlikely that any variation occurred as a result of distance from the source of the stream since continuous flow was not always maintained and altitudinal differences were minimal. Low night-time air temperatures and the rapid cooling of surface waters in the dry season may have resulted in overturns and mixing of the water column at the stations studied. Carter (1934) in his work on the streams and swamps of Guyana, stressed the importance of inverse temperature stratification developing at night in stagnant waters in promoting mixing of the water column by overturns. He estimated that for shallow water bodies, a reverse gradient of 0.5°C or more would be sufficient to cause overturns. Such conditions were seen to exist during diurnal sampling in the dry season at the study sites and could account for reduced stratification and mixing of the water column at night, thus promoting oxygenation of deeper layers. Low surface temperatures at night have also been noted by Reynolds (1984) with respect to the generation of instability in standing water bodies in the tropics. Instability of the water column in these streams during the dry season may be an important factor in counteracting the detrimental effects of stagnation at this time of year.

Chemical composition of river waters is determined by a multiplicity of factors which inevitably impart a degree of uniqueness to each river. Nevertheless, it has been possible to estimate the 'average' chemical composition of the world's rivers as well as averages for individual continents (Livingstone 1963). Table 16 compares average concentrations for selected constituents of the world's rivers with concentrations for the freshwater stations in the study area.

TABLE 16: Comparison of selected water quality parameters of world and South American 'average' river waters[1] and those of the freshwater study sites.

Parameter$_1$ (in mg.1^{-1})	World average	South American average	Ranges and means for Stns 1-3		
			min	max	mean
Bicarbonate	58.4	31.0	20.7	187.9	49.3
Sulphate	11.2	4.8	0	40.6	14.5
Chloride	7.8	4.9	11.4	85.9	28.4
Nitrate	1.0	0.7	0	20.0	2.2
Calcium	15.0	7.2	2.0	16.1	7.7
Magnesium	4.1	1.5	0.5	22.1	6.9
Iron	0.7	1.4	0.1	11.0	4.9
Silica (as silicate)	13.1	11.9	5.4	36.6	16.4
Total dissolved solids	120	69.0	63	400	163.5

[1] : Data from Livingstone (1963)

Most notably, water samples from the study area were lacking in carbonates and to a lesser extent calcium ions, when compared to world averages. Under equilibrating conditions, weak acidity of the water allows existence of carbon dioxide of respiration primarily in the form of bicarbonates with only minimal levels of carbonates below the sensitivity of measurement (Hutchinson 1957). Low calcium levels indicate a soft water and could be partly explained by the lack of a geological source of this element in the catchment area. Chloride and to a lesser extent magnesium and sulphate concentrations are greater than world average levels and presumably indicate the proximity of the sea and influence due to wind-induced sea spray (Golterman 1975, Cole 1979). Concentrations of iron in the study streams were particularly high being seven times greater than average river water and more than 16 times greater than the levels acceptable for potable water (0.3 ppm, APHA 1971). Such high levels of iron may contribute to estimates of total hardness (APHA 1971). High levels of iron appear to be typical of many tropical waters (Payne 1986). Moderately high nutrient levels (especially nitrates) may have resulted from runoff and leachates from surrounding agricultural regions (Reynolds 1984) as well as from the nitrogen-fixing activities of leguminose plants nearby or from leachates of leaves and other organic matter immediately after falling into the stream (Bishop 1973).

Total organic carbon values at the study site (2.4 - 59.0 mg.l^{-1}) were very high compared with data for European inland waters (1 - 10 mg.l^{-1}) given by Hynes (1970). However, he acknowledged that the soft blackwaters of tropical rivers would contain much larger amounts of organic matter. Data cited by Head (1976) indicate a range of total organic carbon in rivers from 15 - 30 mg.l^{-1} with 60 mg.l^{-1} as an extreme value. Such organic load is partially and non-quantitatively measured by determining chemical oxygen demand (permanganate value) which also measures the oxygen demand of reduced compounds (Bishop 1973). Permanganate values measured at the study sites (3.3 - 18.5 mg.l^{-1}) fell within the range of values given by Hynes (1970) for lowland USSR rivers (5.5 - 20.12 mg.l^{-1}). Biochemical oxygen demands (BOD) also reflect organic loads (in addition to biological activity levels) and can be indicative of organic pollution: values between 1 - 3 ppm indicate clean water, about 5 ppm doubtful water quality, 10 ppm and greater severe pollution (Hynes 1960). BOD values measured at Chatham (0.3 - 8.3 mg.l^{-1}) indicate moderate to high organic loads. Comparatively higher total organic carbon, COD and BOD values at Station 3 in particular could be attributed to high inputs of organic material in the form of dung as this site was used as a watering hole for cattle. This is supported by high nitrite levels as compared to nitrate concentrations, a feature indicative of organic pollution (APHA 1971). Oxygen demands due to moderate organic loads and reduced mixing due to slow current speeds could account for generally low average dissolved oxygen values comparable with those found in similar waters in Indiana (Schneller 1955) and in the Amazon (Foldats 1982).

When compared with average river water composition for the South American continent (Table 16), the study site showed higher concentrations of most constituents especially sulphate, chloride and magnesium. This could be attributed to the proximity of the study site to the sea. In addition, average total dissolved solids for the study site was more than twice that for the South American continent. On the basis of more specific data water chemistry of the study area contrasted markedly with the nutrient and electrolyte-poor waters characteristic of the black and clear waters of the Amazonian region but more closely resembled that of the white water rivers (Klinge & Ohle 1964, Sioli 1964, 1975 a,b, Schmidt 1972, Furch & Junk 1980). Other mainland rivers in Venezuela are also of much lower conductivity than the streams under investigation (Lewis & Weibezahn 1976, 1981, Sanchez *et al* 1985). Stronger similarities existed between water chemistry of the study area and that of small lowland streams of St Vincent (Harrison & Rankin 1976 a) and St Lucia (McKillop & Harrison 1980). In St Lucia in particular, ranges of most water quality parameters for slow-flowing temporary lowland streams coincided extremely closely with data for the Chatham streams with the exception of higher sulphate ion concentrations in St Lucia due to the influences of volcanic fumaroles. Comparable nutrient levels (especially of nitrates and phosphates) have been recorded in mainland rivers on the eastern plains of Venezuela (Sanchez *et al* 1985).

Studies conducted locally on the Maracas River (Carrington 1980) and in the rivers flowing into the Nariva Swamp (Bacon *et al* 1979) show slight differences in water chemistry from that found at the Chatham streams. Generally the Chatham streams were slightly more acidic, lower in alkalinity and calcium ions but higher in total dissolved solids. While the Maracas River contained low concentrations of iron, some rivers entering the Nariva Swamp showed levels of total iron slightly in excess of those found at Chatham. Such high levels (especially of soluble Fe^{2+} in Chatham) may be due to the slightly acid reducing conditions existing (Cole 1979).

The estuarine nature of Station 4 imparted certain distinct characteristics indicative of marine influence on water quality at this site. In particular, higher pH and specific conductance and the resemblance of relative ion concentrations to that of sea water were apparent. In addition, certain estuarine chemical processes alter the nature of inflowing freshwater to effect changes in certain constituents such as iron, phosphates, suspended solids and total organic concentrations (Burton 1976). Dissolved iron is precipitated out largely by the influence of increasingly saline water with high pH and such activity is increased in the presence of suspended sediment (Liss 1976). Phosphate concentrations in temperate estuaries are known to be regulated to constant levels close to 37 $\mu g.l^{-1}$ irrespective of fluctuations in salinity by adsorption and release at the sediment surface, a process believed to be dependent on the presence of ferric oxides (Read 1976). Organic and fine particulate suspended material may be precipitated by the presence of dissolved salts in estuaries (Hynes 1970, Head 1976). Fine particulate suspended material becomes coagulated forming a heavy flocculent material (Burton 1976) which may settle thus allowing increased light penetration due to lower turbidity levels. Such a process, in addition to downstream transport of organic matter could account for sedimentary carbon levels up to six times greater at this site than upstream stations.

Seasonal variation in water chemistry of the Chatham streams was largely dependent on alternating lotic and lentic conditions and fluctuating levels of discharge. The latter is particularly important in all lotic environments (Golterman 1975). In particular, reduced flows and increased rates of evaporation during the dry season accounted for increased specific conductance and hardness as well as increased concentrations of individual ions such as calcium, magnesium, and chloride ions and as a result, high concentrations of total dissolved solids. Accumulation of organic matter from dry season leaf fall during times of low flow may have contributed to the existence of an organic colloid buffering system (Kleerekoper 1955) which could result in higher total alkalinities in dry periods.

When lentic conditions persisted over prolonged periods, at Stations 2 and 3 in particular, increased phytoplankton populations composed of actively photosynthesising species developed. This resulted in increased dissolved oxygen concentrations in the late dry and early rainy seasons. Under such circumstances, nutrients such as phosphates and nitrates may show declines with the passage of the dry season possibly as a result of uptake by these organisms (Hynes 1970) and by decomposing organic matter (H.B.N. Hynes 1975). High rates of photosynthetic activity could also result in increased pH values (Prowse & Talling 1958).

Times of reduced discharge were in some cases associated with increased chemical and biochemical oxygen demands and reduced dissolved oxygen levels due to accumulated organic matter, high temperatures and stagnation. As a consequence, highly reducing conditions may have developed leading to certain associated changes in water chemistry. Under reducing conditions and in association with high concentrations of electrolytes and humic colloids, increases in alkalinity, development of higher concentrations of total iron and phosphates (as a result of their release from anoxic sediments) and conversion of insoluble Fe^{3+} to soluble Fe^{2+} might occur (Hutchinson 1957, Hynes 1970, Bishop 1973). Later in the season, decreased sulphate ion concentrations due to reduction of this anion and formation of iron sulphides and hydrogen sulphide might have taken place. Fluctuations in pH would also be expected to influence features such as iron cycling with acid reducing conditions leading to the formation of soluble Fe^{2+} from insoluble Fe^{3+} in deeper water layers. Upon mixing with more oxygenated water at the surface or in the early rainy season, oxidation of iron to the insoluble form would result in precipitation or production of a flocculent brown surface film and subsequent decrease of total iron in the water column (Hutchinson 1957).

In contrast to this situation in the dry season, increased discharges during floods and generally during the rainy season resulted in dilution effects on most ions, total hardness and specific conductance, and the establishment of moderate dissolved oxygen levels. Gross seasonal changes similar to those seen in the study sites have been recorded in other tropical rivers (cf. Bishop 1973, Adebisi 1981 a, Leveque *et al* 1983) and in some local rivers (Bacon *et al* 1979).

Seasonal variation in water chemistry at Station 4 was largely dictated by increased seawater influence during times of low flow and decreased salinities in the rainy season. Such fluctuations strongly resembled those seen in brackish water outlets from the Nariva Swamp (Bacon *et al* 1979) and are consistent with what is known of chemical processes taking place in estuaries (Burton 1976).

Phytoplankton associations in the freshwater study sites may be considered according to Hutchinson's (1967) classification of temperate lake plankton, as being a euglenophyte plankton assemblage characteristically composed of dense blooms of various *Euglena* species (and in some instances *Trachelomonas* species) and found in very small and organically polluted bodies of water rich in non-humic organic matter (cf Pennak 1978). In addition, occurrence of the colonial diatom *Melosira* is indicative of eutrophic waters while there is a strong correlation between soft waters deficient in calcium and magnesium and the occurrence of large numbers of desmids (Hutchinson 1967). Hutchinson (1967) further points out that species of *Euglena* and *Phacus*, in particular can utilise ammonia as an inorganic nitrogen source as well as organic nitrogen sources, a factor possibly contributing to their abundance in the waters in the study site which were of relatively high organic content. Such euglenophyte-dominated communities have also been described for turbid swamps and pools and small creeks in Suriname (Leentvaar 1975, van der Heide 1976). Station 1 showed a relatively impoverished phytoplanktonic assemblage with desmids predominating in the dry season unlike other stations. This was a rather oligotropic community despite generally high inorganic nutrient levels but consistent with lower organic loads.

Poorly developed zooplankton communities such as those seen at the freshwater study sites, have been recorded for other Neotropical areas, for example in streams and swamps of Guyana (Carter 1934) and in Suriname (Leentvaar 1975). In contrast, very high zooplankton densities have been recorded for floodplain rivers especially in quiet backwaters or during periods of reduced flow, for example in the Blue Nile peaks of zooplankton up to 100,000 individuals.m^{-3} have been reported (Talling & Rzóska 1967). Such factors as current, high turbidity and low dissolved oxygen may act to reduce the numbers of zooplankton (Welcomme 1979), in addition to other environmental factors such as light, nutrients and temperature which limit primary productivity and hence zooplankton production (Winner 1975).

Hydrographic stability is also important in determining the development of plankton communities (Winner 1975). The development of plankton communities in rivers as compared to lakes, largely depends on the physical characteristics of turbulent flow and the turbidity due to suspended particulate loads such that only certain small, fast-growing phytoplankton species may be suitably adapted to such conditions (Reynolds 1984). Furthermore, flow rates in tropical rivers such as those of the study site are not seasonally consistent because of the alternation of wet and dry seasons and this influences the seasonal succession of plankton (Hutchinson 1967, Welcomme 1979). The reduction in flow rates at certain times of the year determines the 'age' or retention time of the water mass such that flow loses impetus, transparency increases and the biological sequence of production of phyto- and zooplankton occurs which in turn influences other stream biota (Winner 1975, Rzóska 1978).

The seasonal succession of phyto- and zooplankton at the study sites was similar to that which has been described for many large tropical rivers (summary in Welcomme 1979), that is high plankton densities at times of low water and decreases with the floods. During the floods, nutrient dilution and turbidity may act to limit photosynthetic activity and even in the dry season, phytoplankton growth may occur to the point where nutrients become limiting (Prowse & Talling 1958). Such seasonal succession may involve rapid fluctuations in abundance of species (Reynolds 1984), for example seasonal pulses of rotifers, copepods or cladocerans (Welcomme 1979) or total populations of phytoplankton may decrease to nil within a month or two (Holden & Green 1960). Lévêque *et al* (1983) described the succession of phytoplankton communities in the intermittent Bandama River in the Ivory

Coast as progressing from a diatom-dominated community (principally *Melosira, Tabellaria, Synedra* and *Navicula*) during the main floods to euglenophytes and pyrrhophytes (primarily *Cryptomonas* and *Peridinium*) just after the floods and predominantly chlorophytes throughout the dry period with a peak of blue-greens in the middle of the dry season. Holden & Green (1960) described similarly well defined succession of zooplankton communities in the Sokoto River, Nigeria with rotifers and copepods increasing in densities in the dry period and rhizopods and cladocerans becoming dominant with the onset of the floods. The effects of floods may also influence plankton composition and normally bottom-dwelling species may occur in the plankton at these times (Holden & Green 1960), for example high populations of ostracods occurred in the plankton at Station 3 in August 1980. Survival of planktonic organisms during flood periods may be accomplished by a variety of strategies, for example reservoirs of populations may survive in small backwaters or upstream (Welcomme 1979). Also many species may have diapausing eggs or other stages which survive in the bottom sediments (Moghraby 1977), for example rhizopods and rotifers such as *Conochilus* (Hutchinson 1967, Holden & Green 1960).

Brackish water plankton communities may be classified into three major categories: autochthonous (permanent residents); temporary authochthonous (introduced from outside areas by water movements and capable of limited proliferation but dependent on reinforcement from parent populations); and allochthonous (recently introduced from freshwater or open sea, have limited survival potential and are unable to propagate) (Perkins 1974). Many planktonic taxa at Station 4 seem to be allochthonous or temporary autochthonous from upstream during the rainy season, for example *Synedra, Closterium* and *Gyrosigma,* or marine, for example *Coscinodiscus*. Dominant zooplankton taxa such as cladocerans and copepods at the study site were characteristic of oligohaline estuaries such as those of the Amazon and Maracaibo Lake (Rodriguez 1974). The occurrence of diatom blooms at the beginning of the rainy season at Station 4 is consistent with what is known about increased diatom abundance in conditions of reduced salinity accompanied by high inorganic and organic nutrient concentrations (Perkins 1974). Increased populations of cladocerans and cyclopoid copepods at these times may be attributable to increased food availability, that is diatoms and organic debris respectively (Pennak 1978). Bacon (1968) also found a similar trend of increased populations of both phyto- and zooplankton during the rainy season in the Caroni Swamp.

The macrofaunal composition of the freshwater study sites was generally comparable to that of lentic rather than lotic freshwater communities described by Odum (1970) and Maitland (1978). In particular, many of the aquatic insect species found are characteristic of either littoral lentic or depositional lotic environments (cf. Merritt & Cummins 1984). Overall community composition at the study site was different from that recorded for other local areas studied, for example Maracas River (Thornhill *et al* 1969, Caesar 1985) and the Arima River (Hynes 1971), both fast-flowing clear water streams with groups such as simuliids, hydropsychids and psephenids present. Substrate was a major influential factor on the benthos at the study sites with the occurrence of such groups as tubificids, chironomids, prosobranch gastropods and sphaeriid bivalves which are commonly found in the soft substrates of slow-flowing silt-laden floodplain rivers (Welcomme 1979). The study area also bore distinct similarities in faunal composition to the periodically inundated forests along the white and mixed white/black water rivers in the Amazon (Irmler 1975, 1981). The range (0.05 - 4.2g.m^{-2}) and mean value (1.7g.m^{-2}) of standing crop of benthic invertebrates at the study sites coincided with the ranges recorded for floodplain lagoons in Africa and Latin America, that is from 0 to about 6 g.m^{-2}, and mean values about 2 g.m^{-2}

(Welcomme 1979). Irmler (1975) reported mean biomasses of benthic organisms in inundation forests to be between 0.2 and 1.8 $g.m^{-2}$ for white water forests and between 1.1 and 7.4 $g.m^{-2}$ for mixed white/black water forests.

Seasonal variation in benthic macroinvertebrate populations at the freshwater study sites was the result of two major factors: washouts due to flood events in the rainy season and stagnation and even total drying out during the dry season. Floods are major catastrophic events in streams in general (Hynes 1970, Uhlmann 1979, Fisher 1983) and their effects on population sizes, community structure and life history patterns of fauna have been documented in several tropical streams (for example Petr 1970, Bishop 1973, J.D. Hynes 1975, Stout 1981, 1982, Lévêque *et al* 1983). Consequences of floods may be quite severe in some streams, for example Siegfried & Knight (1977) reported that washouts in a California creek reduced benthic invertebrate populations by more than 85% and benthic standing crop by more than 95% resulting in decreased species diversity of the community. Such factors as substrate type, topography, faunal composition, degree of development of adaptations, and size of organisms will determine the severity of scouring and washouts on benthic fauna (Stehr & Branson 1938, Hynes 1970, Siegfried & Knight 1977). In particular, lacustrine species are unable to survive well in rivers which periodically flow swiftly (Hynes 1970).

At the study site, densities of benthic macroinvertebrates increased to high levels if low to moderate flow rates were maintained and early in the dry season. However, long periods of stagnation resulted in minimal densities of benthic organisms. Recovery was rapid when favourable conditions returned. Stagnation and drought are common occurrences of floodplain rivers (Welcomme 1979) and intermittent streams and rivers (Hynes 1970, Williams & Hynes 1977). Stagnation may produce conditions unsuitable for rheophilous species (Harrison 1966, Iversen *et al* 1978, Canton *et al* 1984); induce stratification and produce unfavourable benthic conditions (Irmler 1975, Williams & Hynes 1976); decrease habitat size (Canton *et al* 1984); and concentrate prey and predators in very small aquatic habitats (Lowe-McConnell 1975). Community composition may change, favouring certain species capable of withstanding such conditions and belonging to functional groups such as shredders and predators (Canton *et al* 1984). However such conditions may be suitable for the more lacustrine species for a number of reasons such as increased food availability in the form of algal production or accumulation of organic debris, or increased densities of prey for predators, lack of spates and increased stability of the substrate and water column, and higher water temperatures encouraging faster rates of growth and reproduction (Abell 1959, Iversen *et al* 1978, Bishop 1973, Extence 1981, Lévêque *et al* 1983, Canton *et al* 1984). In addition, migration of individuals from drying areas of stream bed into refuge pools or oviposition by adults into these last remaining aquatic habitats may actually increase population densities in such pools (Extence 1981). The above factors may have contributed to the lack of clear seasonal trends in densities of benthic organisms at some stations.

With continued drought, standing water may disappear completely and most aquatic species may die but water may persist within the substrate allowing refuge for small species capable of inhabiting these interstitial spaces (Clifford 1966). Moist substrate and leaf litter also provide suitable habitats for certain terrestrial species such as oligochaetes, dipteran larvae, scavenging beetles and ants, slugs and snails (Williams & Hynes 1976). This situation was comparable to that seen at the study site during the dry season.

With the onset of flow, recovery of the stream fauna may be rapid, for example Harrison (1966) found that after a period of drought in a South African stream, normal faunal composition in pools was attained within a month after resumption of flow and within two months in faster flowing regions. Recolonisation may be by a number of routes, for example downstream drift and upstream migration from refuge pools, vertical migration from within the substrate and aerial recolonisation via ovipositing adults (Williams 1977). The relative importance of each route will vary depending on the situation present. Williams (1977) found that vertical migration from the substrate accounted for 95% of recolonisation in a Canadian site studied, while J.D. Hynes (1975) suggested that most recolonisation in the Ghanian stream studied was via aerial means.

From the above discussion it may be seen that the effects of stagnation and drought on benthic macroinvertebrate communities may range from being detrimental to advantageous. The nature and magnitude of the effect of drought depend on the degree and duration of drought, the season of drought (for temperate situations drought coincident with adult emergence and oviposition times or major larval growth periods can be more detrimental than at other times), and the nature of the species present (Iversen *et al* 1978). Clifford (1966) summarised a classification of intermittent streams based on their temporal flow characteristics, that is short flow or long flow, and the effect of such hydrological regimes on faunal composition. In addition, other factors such as the nature of the stream bed, water table characteristics and shading effects of vegetation influence such a classification. For example, long flow streams which are reduced to isolated pools during a regularly occurring dry period may support a permanent and varied fauna and even a substantial fish population. On the other hand, a stream subject to extensive drought such that no standing water remains, in conjunction with an impervious streambed subject to high temperatures and exposure may not possess a permanent stream fauna but one limited only to adventitious and migratory species, a situation similar in many respects to a temporary stream. The extent of drought and the nature of the streambed will presumably also influence the possible routes for recolonisation.

The composition of the fauna of the stream will also determine the ability of the stream to recover, for example Harrison (1966) noted that recolonisation in his study area was rapid because the fauna was composed of species adapted to conditions of regular drought unlike streams which are subject to only occasional periods of drought such as the Welsh mountain stream studied by Hynes (1958) where many of the organisms were specialised rhithronic species. Many of the benthic and other macrofauna found at the study sites belonged to groups reported to be able to withstand periodic stagnation and even desiccation.

Adaptations of aquatic species to overcome or survive periodic drought in temporary and intermittent streams have been outlined by Hynes (1970) and he classified species into six main groups:

(i) Species which are able to tolerate extreme conditions in pools such as high temperatures and low oxygen concentrations, for example some fish and invertebrates including flatworms, crustaceans, some Trichoptera and snails. Some even take advantage of the periodical lentic conditions in order to increase survival of young.

(ii) Some species survive drying conditions by burrowing down into the substratum, for example flatworms, nematodes, oligochaetes, some amphipods and isopods, crayfish, elminthid beetles, some Chironomidae, some caseless Trichoptera, snails and mites.

(iii) Organisms may produce eggs or nymphs capable of surviving long periods of drought. Williams & Hynes (1976) document the occurrence of drought-resistant stages in many organisms studied: cysts in tubificids, copepods and triclads, and eggs of mayflies and chironomids (cf Grant & Stewart 1980). Immature forms of amphipods, ostracods and cyclopoid copepods, larvae or pupae of stoneflies, some dipterans and trichopterans, and adult enchytraeids, leeches, hemipterans, coleopterans, gastropods and fish were all found to be capable of surviving dry periods.

(iv) Species may reinvade from elsewhere, for example fishes and some aquatic invertebrates may recolonise the expanding habitat after flow resumes from aquatic refuges or insects may fly in to oviposit as soon as water reappears. The latter may be particularly important in the tropics since habitat expansion and oviposition by adult insects coincide with the beginning of the rains.

(v) Some species may occupy pools or the damp river bed only during the dry period, for example some mosquitoes, Chironomidae, beetles and bugs.

(vi) A few species appear to be highly specialised inhabitants of temporary waters such as a few snails and some Trichoptera which are capable of aestivation.

Irmler (1975, 1981) documented the range of adaptations seen in some species of the Amazonian inundation forests such as migration in the more mobile species, for example large crustacea; periods of inactivity or dormancy during the dry period in ampullariid snails and sphaeriid bivalves; increased parental care such as brooding in sphaeriid bivalves and the crab *Trichodactylus* (belonging to the same family as *Dilocarcinus dentatus* (Smalley & Rodriguez 1972)); and high reproductive potential such as seen in the sphaeriid bivalve *Eupera simoni* which matures rapidly and produces two generations per year. Sphaeriid bivalves have also been shown to have flexible life history traits to adapt to temporary waters in temperate regions (Hornbach *et al* 1980, Way *et al* 1980). Irmler (1981) also pointed out that many species found in inundation forests are preadapted to such environments and are closely related to species which can survive alternating inundation and drought. In particular, many congeners of *Pomacea glauca* are found in such habitats (Pain 1950, 1960). *P. urceus* has been studied extensively for its ability to survive under floodplain savanna conditions in Venezuela (Burky *et al* 1972, Burky 1973, 1974,Burky & Burky 1977) and in Trinidad swamps (Lum Kong 1986). *P. paludosa* is a common inhabitant of the Florida Everglades (Perry 1973, Hurdle 1974) and *P. lineata* is successful in the Amazonian inundation forest (Irmler 1981). Although the ability to aestivate and withstand droughts varies between species, other adaptations such as rapid sexual maturation and high fecundities compensate for lowered survival abilities (Irmler 1981).

The other large benthic organism studied here, *Dilocarcinus dentatus*, showed a life cycle consistent with that recorded by Stonley (1971) who noted that this species brooded eggs and juveniles from the beginning of the dry season and released young in June and July. She suggested an annual life cycle with adults dying off at the time of release of juveniles as also indicated in the present study. Brooding of eggs and juveniles is also seen in the only other local freshwater crab *Pseudothelphusa garmani* (Stonley 1971) and is commonly found in freshwater crabs in order to increase juvenile survival rates in such unstable environments (Vernberg & Vernberg 1983).

In many small streams with heavily vegetated banks such as those of the study site and the narrow upper reaches of rivers, input of material from the surrounding terrestrial ecosystem can play a major role in terms of providing food material and nutrients to the aquatic ecosystem (Cummins 1974, H.B.N. Hynes 1975). Subsequently, stream faunas play a very important role in terms of importing, producing, processing and storing such organic matter (Cummins *et al* 1983) and such a role may be essential for the retention of nutrients within tropical forest ecosystems (Dudgeon 1983). In the tropics leaf fall into aquatic habitats has been estimated as being up to 6 $t.ha^{-1}.y^{-1}$ (Welcomme 1985) and Geisler *et al* (1975) counted 56 individual pieces of material falling onto a 0.25 m^2 glue board over water during a 24-hour period. This material included mainly Culicidae and Chironomidae with lesser numbers of ants, Lepidoptera, spiders and plant seeds.

A higher abundance of insects falling onto glue boards at Station 2 in the rainy season as compared to the dry was consistent with the general trends quoted widely in the literature with regards to increased abundance of terrestrial insects at this time in the tropics. Such an increase may be due to emergence of aquatic insects (Bright 1982), increased abundance of herbivores at this time of new leaf emergence (Wolda 1978), or decreased numbers due to harsh conditions in the dry season (Janzen 1973). Nevertheless, work in some tropical areas has indicated that insect numbers may in fact show a reverse trend (Janzen 1973, Wolda 1978), an unclear periodicity (Wolda & Flowers 1985), or be dependent on the extent of seasonality of the habitat (Wolda & Broadhead 1985). In addition to the fact that there may be greater productivity of terrestrial insects during the rainy season, many insects move into moist refugia such as streams in the dry season (Janzen 1973) thus increasing in local abundance at these sites. Such factors may have contributed to the unclear trends seen in the data presented.

In summary, the general trend of seasonal variation in the streams studied showed the influence of a main dry season from January to May and a main rainy season from June to December with a short dry period falling between September and November. Lentic conditions often developed during the dry periods but did not appear to last longer than four months continuously. Drought conditions experienced were never severe enough to dry out the entire length or even the majority of the watercourses studied. Therefore, these streams may be considered to be long flow intermittent streams with substantial refuge areas and thus capable of maintaining a diverse and permanent faunal assemblage (Clifford 1966).

A general seasonal trend as outlined above was not consistent however, being highly variable from year to year in terms of time of onset, duration and intensity of any season. Lentic conditions often developed more than once each year in the same areas and not necessarily during the main dry season. This is unlike clear seasonal trends in other tropical intermittent streams where one definitive lentic period existed in each year (Adebisi 1981 a, Lévêque *et al* 1983).

Seasonality of flow was a major influence on the nature of the stream environment (both physical and chemical) and consequently on the nature and seasonal variation of the biota. However, variability in the duration and intensity of each season made it difficult to predict the nature of biotic changes. Generally however, a dense eutrophic planktonic community developed in some areas during prolonged lentic conditions and was decreased drastically with the onset of floods. Benthic standing crop and allochthonous input to the stream appeared to vary equally widely in dry and rainy seasons.

THE FISH

INTRODUCTION

The Neotropical freshwater fish fauna is the richest in the world with probably over 2000 species inhabiting the tropical regions. The greatest diversity appears to be in the Amazon basin with diversity decreasing outward to the Guianas and Venezuela in the north, the Paraná system in the south and westward to Colombia and Ecuador (Gery 1969, Lowe-McConnell & Howes 1981). The large number of species belong to relatively few basic groups, in particular the characoids and siluroids are dominant owing to the extensive adaptive radiation within these orders (Lowe-McConnell 1975). Cichlids are well represented although not as well as in Africa (Gery 1969) and the cyprinodonts are also quite important (UNESCO/UNEP/FAO 1978).

In contrast to the mainland, there are no primary freshwater fishes recorded for the West Indies north of Trinidad (Myers 1938) there being instead only secondary freshwater fishes belonging primarily to four families (Lepisosteidae, Cyprinodontidae, Poeciliidae and Cichlidae) of which the Poeciliidae is the most important (Miller

1982). In the Lesser Antilles, it appears that only four species of secondary freshwater fishes occur, that is *Rivulus hartii*, *R. marmoratus*, *Poecilia vivipara* and *P. reticulata*; the remainder of the fauna being comprised of marine invaders to freshwater (Miller 1982).

The diversity and distribution of the freshwater fish fauna of the island of Trinidad reflects its intermediate position between the mainland to the south and the West Indian islands to the north. Of a total of 76 freshwater fish species recorded for Trinidad by Boeseman (1960, 1964) only 37 are genuine freshwater species of which 32 also occur on the South American mainland. The few species which are restricted to Trinidad are relatively recent modifications of closely related continental forms (Boeseman 1960). In addition, no characoids, cichlids or catfishes have been recorded for rivers draining the north slopes of the Northern Range, instead mainly a euryhaline fish fauna similar to that of the Antilles is found in this region (Price 1955). South of the Northern Range, the island supports a fairly diverse assemblage of primary freshwater fishes comprised predominantly of characoids, a feature which characterises the island's continental origins (Kenny & Bacon 1981).

Studies on the freshwater fish of Trinidad have been largely taxonomic in nature. Boeseman (1960, 1964) gave the most recent listing of species and he also included a comprehensive historical review of past studies. Some of the earlier works included information on distribution, habitats and general biology, for example Regan (1906), Guppy (1934, 1936) and Price (1955). More recently, a detailed biological study was conducted on a species of commercial importance, *Hoplosternum littorale* (Singh 1978). This is one of the three principal freshwater species exploited commercially in the island (Kenny & Bacon 1981). The guppy, *Poecilia reticulata*, is the only other species which has been studied locally but only selected aspects of its biology have been looked at. For example antipredator adaptations in behaviour (Seghers 1973), size (Liley & Seghers 1975), colour (Endler 1978) and life history evolution (Reznick 1980, Reznick & Endler 1982) have been thoroughly investigated.

Despite the paucity of biological or ecological studies conducted locally, a certain amount of information is available on the biology of the same or closely related species on the mainland. Reviews of this literature were given in Lowe-McConnell (1975) and Welcomme (1979, 1985). The general biology of many small species has been described in the aquarists' literature, for example Tropical Fish Hobbyist series, Frey (1961) and Breder & Rosen (1966) among others. Generally, ecological studies of local and Neotropical freshwater fishes are lacking. Even in the West Indies, the only studies known are of a poeciliid, *Limia vittata* in Cuba (Barus *et al* 1980) and a recent study of *Sicydium plumieri* in Puerto Rico (Erdman 1982). In 1978 a UNESCO/UNEP/FAO review cited only four ecological studies in the Neotropical region up to that time. This situation has been improving recently (cf. Zaret 1984) but much remains to be done on fish community organisation, feeding, fish effects on their food resources and seasonality effects on breeding (UNESCO/UNEP/FAO 1978).

The species selected for this study were the six most common fishes in the study site. They were *Gasteropelecus sternicla* (Linnaeus 1758), *Corynopoma riisei* Gill 1858, *Astyanax bimaculatus* (Linnaeus 1758), *Hemigrammus unilineatus* (Gill 1858), *Corydoras aeneus* (Gill 1858) and *Poecilia reticulata* Peters 1859. With the exception of *G. sternicla* these species have been reported to be common throughout most of Trinidad south of the Northern Range (Regan 1906, Guppy 1934, 1936, Price 1955, Boeseman 1960, Nelson 1964) and *P. reticulata* has also been found north of the Northern Range

(Price 1955). *G. sternicla* was reported by Price (1955) to be restricted to the southwestern peninsula as it is 'believed to have invaded the island from Venezuela fairly recently' (p.10). Liley & Seghers (1975) also noted in their collections in the region of the Northern Range that while *P. reticulata* occurred widely from uppermost springs to lowland rivers, *C. riisei, A. bimaculatus, H. unilineatus* and *C. aeneus* were midstream or lowland river species. The widespread distribution of most of the species and their popularity in the aquarium trade makes them attractive for local study.

Another reason for the choice of the six species was the range of morphology and habits exhibited. They vary in phylogeny, size, feeding requirements, microhabitats and general reproductive biology; factors which should affect their responses to environmental conditions in the study site. Details of their biology in the wild are scattered in the literature and are minimal for many species although some information exists for their habits under aquarium conditions.

The following objectives were therefore set for this part of the study:

(1) To determine the diversity of fish species in the study site.

(2) To monitor the population demography and dynamics of the six species, in particular population structure, growth rates, life spans and population fluctuations.

(3) To investigate the reproductive strategies of the six species including timing and duration of breeding activity, size at maturation, fecundity and spawning patterns and general breeding behaviour.

(4) To determine the effects of environmental seasonality on the population biology and reproductive strategies of the six species.

REVIEW OF THE SPECIES

The six species selected for the study belonged to three orders (Characiformes, Siluriformes and Cyprinodontiformes) and four families (Gasteropelecidae, Characidae, Callichthyidae and Poeciliidae) (Table 17). They are illustrated in Plate 6.

Gasteropelecus sternicla (Linnaeus 1758)

The common hatchetfish is a small uniquely shaped

TABLE 17: Classification of the six fish species studied (after Gery (1977) and Nelson (1984)).

Class	:	Osteichthyes					
Subdivision	:	Teleostei					
Superorder	:	Ostariophysi					Acanthopterygii
Order	:	Characiformes				Siluriformes	Cyprinodontiformes
Suborder	:	Characoidei					Cyprinodontoidea
Family	:	Gasteropelecidae	Characidae			Callichthyidae	Poeciliidae
Subfamily	:	Gasteropelecinae	Glandulocaudinae	Tetragonopterinae			
Genus	:	*Gasteropelecus*	*Corynopoma*	*Astyanax*	*Hemigrammus*	*Corydoras*	*Poecilia*
Species	:	*sternicla*	*riisei*	*bimaculatus*	*unilineatus*	*aeneus*	*reticulata*

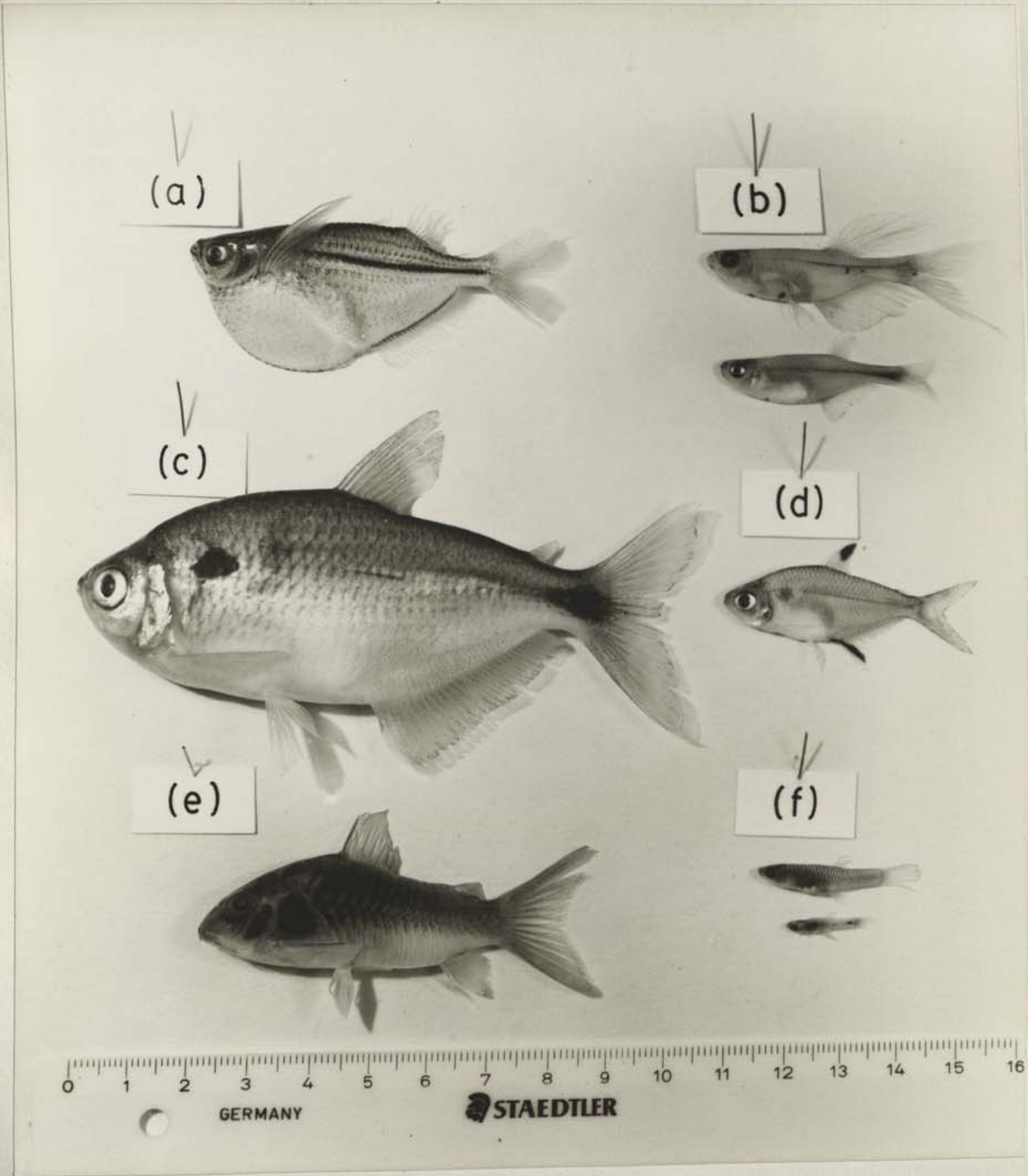


PLATE 6: The six fish species studied: (a) *G. sternicla*, (b) *C. riisei* (male above, female below), (c) *A. bimaculatus*, (d) *H. unilineatus*, (e) *C. aeneus*, and (f) *P. reticulata* (female above, male below).

characoid attaining total lengths up to 7 cm (Paysan 1975). It is predominantly surface-dwelling and has, along with other members of the family, an ability to jump and skim along the surface of the water. For this purpose it uses its well developed keel for stability and attachment of enlarged pectoral muscles and its elongated and curved pectoral fins are rapidly vibrated to create the necessary forces (Ridewood 1913, Frey 1961, Weitzman 1954, 1958). This is presumably an adaptation to escape underwater predators (Weitzman 1958). In addition to extensive morphological modifications for 'flight', the almost vertical orientation of the jaws allows for grasping organisms at the surface of the water (Weitzman 1954). While the Brazilian species, *G. levis*, and the related *Carnegiella strigata* have been bred in captivity (Stoye 1935, Stanley 1956) it appears that *G. sternicla* has not (Paysan 1975). Nevertheless this species is the commonest *Gasteropelecus* species in the aquarium trade although almost nothing is known of its biology (Gery 1977). Its geographical range includes the Guianas and Trinidad; Mato Grosso, Brazil; and the Peruvian Amazon (Gery 1977).

Corynopoma riisei Gill 1858

The sword-tailed characin is a small slender fish growing up to 6 cm in total length. It belongs to the subfamily Glandulocaudinae which is an artificial assemblage of species based on the presence of a caudal gland in males (Gery 1977). Sexual dimorphism, fairly complex courtship activities and internal fertilisation occur in many species of this subfamily (Nelson 1964). Dimorphism is extreme in *C. riisei* to the extent that the species has been described under three different genera on the basis of degree of development of males (Regan 1906, Guppy 1936). Males possess a pouch-like structure at the base of the caudal fin which is postulated to secrete a pheromone to attract females. In addition, a pair of paddle-shaped opercular extensions on the male are also used during complex courtship activities (Nelson 1964). The unpaired fins of mature males are significantly longer than in females and the anteriormost anal fin rays bear minute hooks which are necessary for sperm transfer to the female (Nelson 1964, Breder & Rosen 1966). The sperm transferred to the female are not encapsulated in a spermatheca but are held together by a viscid substance; they may remain viable for as long as 10 months or the female's lifetime (Sterba 1962, Breder & Rosen 1966). Newly laid eggs show between two and 64 blastomeres and they are laid in the early morning onto any suitably secure objects (Nelson 1964, Breder & Rosen 1966). Breeding habits and courtship behaviour in captivity were described in detail by Frey (1961), Nelson (1964, 1965) and Breder & Rosen (1966). Development of juveniles and their behaviour was described by Nelson (1964) who noted sexual differentiation at the age of 17 weeks in captivity. He also found that aggregation occurred in juveniles and sporadically in adults, and dominance hierarchies developed in groups of males.

C. riisei is generally a surface-feeding omnivore (Frey 1961, Nelson 1964). Its geographical range includes Trinidad, Venezuela and Colombia (Boeseman 1960) but the Trinidad form may be different from that of the mainland (Gery 1977).

Astyanax bimaculatus (Linnaeus 1758)

Locally called the pink-finned sardine (Boeseman 1960), this is a fairly large characid growing up to 15 cm long which is commonly found in large schools in the middle and lower layers of the water column (Paysan 1975). It has a generalised body shape which is moderately elongate with dorsal and ventral profiles symmetrical (Gery 1977). This species is widely distributed from La Plata to Panama and consists of several subspecies (Gery 1977). Studies of natural populations of this and related species have been conducted in north-east and south-east Brazil (Azevedo &

Vieira 1938, Nomura 1975 a,b,c). These studies show that the species is omnivorous including as much plant as animal material in their diet (Azevedo & Vieira 1938, Nomura 1975 b). Reproduction is seasonal coinciding with the onset of the rains and females may spawn several times during the breeding period (Azevedo & Vieira 1938, Pelizaro *et al* 1981). Sexual dimorphism is exhibited: males are considerably smaller than females and small hooks are borne on the anteriormost anal fin rays of males (Azevedo & Vieira 1938, Breder & Rosen 1966). It is unclear whether this species has been bred in captivity. Guppy (1936) described the species as being hardy and prolific and fry may be raised on prepared foods. Azevedo & Vieira (1938) reported breeding 'piabas' (tetragonopterines including *A. bimaculatus*) in captivity by inducing spawning with injections of hypophysial extract but it was not stated which species were bred. On the other hand, Sterba (1962) and Paysan (1975) reported that this species had not yet been bred in captivity. Larval development of 'piabas' was dealt with by Azevedo & Vieira (1938).

Hemigrammus unilineatus (Gill 1858)

The feather-fin is a small characid attaining maximum lengths up to 4 cm. It is similar to *A. bimaculatus* in possessing a generalised body shape and the genus is believed to have evolved from some more conservative *Astyanax*- or *Moenkhausia*-like tetra by the process of paedomorphosis (Gery 1977). *H. unilineatus* is found distributed throughout Trinidad, the Guianas and the Amazon (Gery 1977).

The species is well known by aquarists although it is inconspicuous and therefore not as popular as its more brightly coloured congeners. Azevedo & Vieira (1938) included the species in their discussion of tetragonopterines in north-east Brazil but specific comments on its biology were not made. Otherwise almost nothing is known of the habits of this species in the wild. In aquaria, individuals remain in well defined areas of the tank and are omnivorous (Paysan 1975). Males are generally smaller and slimmer than females and they have been bred productively in captivity (Frey 1961). Courtship is simple and the externally fertilised eggs appear to be spawned at the water's surface (Stolzenhain 1927).

Corydoras aeneus (Gill 1858)

Locally called the pui-pui or goldfish, this small armoured catfish is a popular aquarium species which is used as a bottom scavenger. For the past three decades there has been an export trade of this species and *Hypostomus robinii* to the temperate countries with *C. aeneus* accounting for up to 56% of the trade in 1967 when 792,783 individuals were exported (Fisheries Division 1976).

C. aeneus is relatively small, attaining maximum lengths up to 7.5 cm (Paysan 1975). Unlike other catfish, it has large eyes and short barbels and is diurnal in habits (Alexander 1965). Like several other callichthyid catfishes, *C. aeneus* is an air-breather, gulping air at the surface, using the posterior intestine as a site of gas exchange and releasing used air from the anus (Kramer & McClure 1980). Under conditions with high oxygen levels, *C. aeneus* is not a obligatory air-breather (Kramer & McClure 1980) presumably because of the increased energetic costs and increased risk of predation associated with air-breathing (Kramer & McClure 1981, Kramer 1984).

C. aeneus is commonly found in schools and they are bottom-dwelling feeding on detritus and its component fauna (Frey 1961, Paysan 1975). This species has been bred in captivity but the actual mechanism of fertilisation of the eggs is still unclear (Breder & Rosen 1966, Zukal 1982). Balon (1984, 1985) classified this species as an external egg-bearer and more specifically, a transfer brooder in which the eggs are carried for some time before deposition but after deposition it is similar to a non-guarding phytophil in behaviour. Generally females are distinguished from males by being larger with a wider body and by possessing more rounded dorsal and pelvic fins (Schofield 1957). Unlike its local relatives *Hoplosternum littorale* and *Callichthys callichthys*, *C. aeneus* does not build foam nests (Breder & Rosen 1966). Instead the female lays up to five eggs at a time into a pocket formed by the pelvic fins pressed together and sticks these onto the previously cleaned surface of the aquarium glass or plants (Frey 1961 , Breder & Rosen 1966, Zukal 1982). Several males are required to fertilise all the eggs spawned by a female (Frey 1961, Zukal 1982). Development of the eggs and fry in captivity has been described by Adams (1946), Hart (1947), Schofield (1957) and Zukal (1982) with maturation occurring not before two years (Schofield 1957).

The geographic range of the species is large extending from La Plata to Venezuela and Trinidad and westwards to Bolivia and Peru (Boeseman 1960, Frey 1961, Paysan 1975).

Poecilia reticulata Peters 1859

The guppy is the most common freshwater fish in Trinidad

(Boeseman 1960, Nelson 1964). It is very well known in the aquarium trade since it is easily bred in captivity and new exotic varieties have been selected. It has also been introduced into many tropical areas for mosquito control although its original area of distribution appears to have been rather small, that is Venezuela, the Guianas, Trinidad and Barbados (Boeseman 1960). On account of its ease of maintenance and breeding and short generation time, the guppy has been used extensively in a variety of biological studies especially laboratory-oriented ones. Despite this however,comparatively few studies have been undertaken on its biology under natural conditions in the tropics and almost nothing is known of its population dynamics and reproductive biology in nature (Kramer, pers. comm.).

The guppy is a small schooling fish attaining total lengths up to 5 cm for large laboratory-reared females (Frey 1961). Sexual dimorphism is clearly evident (Endler 1984). Males are small, slender and brightly but highly variably coloured and the anal fin rays (3-5) are modified to form an intromittent organ, the gonopodium; females are larger, more rounded in shape and are uniformly gray except for a dark spot just above the anal fin. Male coloration and intense courtship activities may play important roles in determining mating success (Farr 1980, Endler 1980, 1984, Kodric-Brown 1985) in addition to other factors such as the composition of the male group (Farr 1976, 1977) and sperm competition (Hilderman & Wagner 1954). The breeding system of guppies can be defined as a female-based polygyny where males compete amongst themselves for access to females and their sole parental contribution to offspring is in the form of gametes (Kodric-Brown 1985). The courtship display has been thoroughly described by Baerends *et al* (1955) and Liley (1966). Eggs are fertilised internally and develop within the ovary (intrafollicular gestation) but maternal-embryo exchange is limited to minerals and respiratory gases. Nutrients are supplied entirely by the stored yolk of the egg, that is they are strict lecithotrophes (Thibault & Schultz 1978, Wourms 1981). Gestation lasts between three to five weeks to produce up to 80 actively swimming young each up to 6.5 mm in length depending on the size of the female (Frey 1961, Thibault & Schultz 1978).

Wild-caught guppies from Trinidad have been shown to be benthic feeders, taking algae, organic debris and benthic invertebrates (Dussault & Kramer 1981) and the flattened head and upturned mouth are not feeding adaptations but are related to aquatic surface respiration in hypoxic habitats

(Lewis 1970, Kramer & Mehegan 1981).

METHODS

General sampling and morphometric studies

Once each month during the study period May 1980 to June 1981, each of Stations 1 to 4 was fished using a 3 mm-mesh two-man push-seine for approximately the same distance each time. Distances seined were 10 m at Station 1, 25 m at Station 2, 15 m at Station 3 and 25 m at Station 4. During the dry seasons when Stations 1 to 3 became isolated pools, the entire pool was seined. Only one pull of the seine was made each month in order to standardise fishing effort on each occasion. Accepted catch-effort methods (Youngs & Robson 1978) could not be utilised because of the relatively small fish populations in the stream and the distinct possibility of overfishing during the dry season when fish were concentrated into pools. All fish caught were collected and immediately preserved in 4% formaldehyde solution.

During the period July 1981 to August 1982, Stations 1 and 2 were seined repeatedly to collect at least 20 mature-sized individuals of each of the six species under study. This was not always possible even after seineing upstream and downstream of the stations or at other sites, for example Station 3. All juveniles were preserved and retained when caught.

In the laboratory, preserved fish from each monthly sample were identified and counted. For each of the six species under study, standard lengths (SL) were measured to the nearest millimetre from the most anterior extremity to the hidden base of caudal fin rays (Lagler 1978), and fish were weighed to the nearest milligram after blotting excess moisture (total weight, TW). They were dissected to remove the gonads which were weighed to the nearest milligram and stored in 70% alcohol for further analysis. Specimens were sexed on the basis of gonadal and secondary sexual characteristics when mature or developing; small individuals were classed as juveniles when they could not be definitively assigned to one or either sex. Data from all freshwater collections were pooled in most analyses because of the relatively small numbers of fish caught at each station.

Certain characters were noted for *G. sternicla* (greatest body depth:SL ratio), *H. unilineatus* (greatest body depth:SL ratio) and *C. aeneus* (body width at pectoral fins:SL ratio and pectoral fin spine length:SL ratio) in order to test their reliability for use in differentiating the sexes of adult specimens. Ratios for males and females were compared using a d-test after arcsine transformation of data where necessary (Sokal & Rohlf 1981).

Length-weight relationships were determined for each species using data from all individuals caught during the first year of the study. The following equation was used:

$$\log_{10}TW = \log_{10}a + b \log_{10}SL$$

where TW = total weight, SL = standard length, $\log_{10}a$ = intercept on y-axis and b = regression coefficient or slope (Bagenal & Tesch 1978). The significance of the regression coefficient was tested using F in an analysis of variance (Parker 1979, Appendix 5) and deviation from the cubic relationship tested using t_s (Sokal & Rohlf 1981, Appendix 6). The correlation coefficient, r, was also tested for significance after Clarke (1980).

Studies were made to ascertain the effects of formalin fixation on the lengths and weights of the fish as well as on the length-weight relationship. Collections of each species were made in June/July 1985 and fish were killed by chilling in water for not more than 30 minutes for the characoids and

P. reticulata and up to one hour for *C. aeneus*. Observations showed that these times were just sufficient to stop all voluntary and respiratory movements. Fish were retained in water until measurements were made (up to two or three hours maximum). Standard lengths and total weights were measured to the nearest 0.1 mm and 1 mg respectively. Fish were then fixed and preserved individually in a buffered 4% formaldehyde/freshwater solution and after 10 months they were again measured and weighed. Changes in length and weight for each individual and the average for each species were calculated and expressed as preserved measurements as a percentage of fresh measurements. Lengths and weights before and after preservation were tested for significant differences using a paired-sample t-test (Parker 1979). Length-weight relationships were determined for each species for fresh and preserved specimens separately and the regression coefficients were compared after Bailey (1981, Appendix 6).

Population studies and reproductive seasonality

For each species length-frequency histograms for all individuals collected over the study period were drawn noting the number of individuals of each length at varying gonadal development stages (Table 18 and below). From these, the

TABLE 18: Gross morphological characteristics used in the classification of maturity stages for the six fish species studied (based on formalin-fixed gonads).

Maturity stage	Male	Female
Juvenile (J)	Gonads very small or not visible; sexes indistinguishable.	
Immature (I)	Testes thin, threadlike, transparent.	Ovary small, occupying less than one-half body cavity; eggs not visible to naked eye; translucent yellow/ orange in colour.
Developing (D)	Testes translucent white, thicker than I; later opaque white or flecked, with granular surface; *P. reticulata* testis small, translucent white/pink.	Ovary larger, occupying one-half to two-thirds body cavity; opaque light yellow; eggs visible but not within mature oocyte size range.
Mature (M)	Testis very broad and thick; opaque white with smooth surface. *P. reticulata* testis large, rounded, opaque white or pink with rough surface.	Ovary occupying more than two-thirds body cavity or may be smaller; opaque deep yellow, orange or red; eggs within mature size range (Table 19). *P. reticulata* bearing ova or embryos.
Regressing (R)	Testis of similar size to M but with shrunken, flaccid appearance.	Ovary small, flabby, translucent orange/red; no or few eggs present.

TABLE 19: Mature oocyte size ranges used in classifying female reproductive state and minimum oocyte sizes used in batch fecundity estimates for the six fish species studied.

Species	Mature oocyte size range (mm)	Minimum oocyte size (mm)
G. sternicla	0.7 - 0.9	0.559
C. riisei	0.6 - 0.9	0.486
A. bimaculatus	0.6 - 0.9	0.462
H. unilineatus	0.6 - 0.95	0.486
C. aeneus	1.5 - 1.75	1.142
P. reticulata	1.2 - 2.0	1.20

minimum lengths at which sexual maturation took place were determined. Minimum lengths at which developing and mature gonads were observed (Minimum Developing SL and Minimum Mature SL respectively) were noted for each species. The length at which 50% of the individuals therein were mature was also noted for each species (Median Length at first maturity, Cambray & Bruton 1984). This had to be determined graphically in some instances.

Population structure was determined monthly by the use of length-frequency histograms based on data from all stations combined. In species where data were sufficient, growth curves were drawn using moving modes in the population structure for particularly strong and temporally distinct classes of juveniles (cohort analysis, Bagenal & Tesch 1978). In order to relate growth with age, it was assumed that reproductive maturity of these species occurred within the first year of life, a realistic assumption considering the changes in population structure over the period of study. It was also assumed that average size at maturity could be equated to the Median Length at first maturity. Once this length was assumed to be attained at 12 months of age, backward and forward projections using moving modes for different cohorts were made at one month intervals. Minimum age at maturation and lifespans were estimated from these growth curves assuming equal growth rates for males and females throughout. For species where data were sufficient, the parameters of the von Bertalanffy growth equation were determined using a Walford plot, plot of $\ln(L_\infty - l_t)$ against t, and substitution methods (Bagenal & Tesch 1978).

In order to determine the reproductive state of individuals of the six species under study, a number of characteristics were utilised. Since multiple spawning fishes may spawn a few eggs at a time for prolonged periods, gonad weight and size or gonadosomatic indices (GSI) alone are not reliable indicators of breeding activity. Females may have a few mature eggs remaining in a small ovary yet still be in breeding condition (Kramer 1978a). Therefore other characteristics such as mature oocyte diameter, secondary sexual characteristics and a limited amount of histology were utilised in addition to GSI's and gross morphological features.

Gross morphological characteristics of gonads and mature oocyte diameters used in assessing the reproductive state of the fish are summarised in Tables 18 and 19. Mature oocyte diameters were determined for each species on the basis of this size range of oocytes being the maximum observed in ovaries filling one-half to two-thirds of the body cavity. Preliminary histological studies on the ovaries of all species (except *P. reticulata*) were made to corroborate gross characteristics used. Secondary sexual characters were noted in *C. riisei*, *A. bimaculatus* and *P. reticulata* to assist in determining the degree of sexual maturation.

In reproductive analyses, only individuals of developing or mature sizes were utilised in order to eliminate juveniles and pre-reproductives from these data. Minimum Developing SL was used in the analysis of monthly variation of gonadal maturity stages for each species in order to include small first-time developing individuals in the data. However for other calculations (GSI, monthly sex ratios and condition factors) only individuals of Minimum Mature SL and above were included. Where Minimum Mature SL differed for the sexes, the smaller of the two was used. A minimum of 10 mm SL was used for *P. reticulata* because of the difficulties in sexing and weighing fish smaller than this length.

Gonadosomatic indices were calculated according to the following:

$$\text{GSI} = \frac{\text{weight of both gonads}}{\text{total weight}} \times 100\%$$

In order to assess the effects of environmental seasonality and the reproductive cycle on the condition of the fishes, condition factors were calculated according to the following equations:

$$\text{Total condition factor (CFT)} = \frac{\text{total weight (g)}}{\text{SL(cm)}^b} \times 100$$

$$\text{Somatic condition factor (CFS)} = \frac{\text{total weight - gonad weight (g)}}{\text{SL(cm)}^b} \times 100$$

where b is the regression coefficient of the length-weight relationship (Bagenal & Tesch 1978).

Mean values of GSI's and condition factors were calculated separately for males and females of each species for each month. On account of the small numbers of specimens involved, data from all stations were pooled for these calculations and in four species, data for equivalent months from successive years were combined.

Fecundity and spawning patterns

The fecundity of multiple spawning fishes is difficult to determine by standard methods of fecundity estimation (Bagenal 1978, Bagenal & Braum 1978). Where spawning occurs during a fairly well defined season it has been suggested that a count of all developing eggs (indicated by the presence of yolk or vacuoles) would give the fecundity for that season (Bagenal 1978). However, where there is continuous recruitment of large eggs from the small-sized eggs, fecundity will be much more difficult to determine (Bagenal & Braum 1978). In addition, as found by Macer (1974), a very high percentage of atretic mature eggs late in the reproductive season indicates that there may be a substantial difference between potential and actual fecundity (Bagenal 1978). Another method of fecundity estimation involves estimating the size of each batch of eggs spawned and the number of batches spawned over the total breeding season (Bagenal 1978, Gale & Deutsch 1985). In situations such as the tropics where batches may follow each other continuously over the year, fecundity must only include one batch (Bagenal 1978). In this study batch fecundities were estimated for each species except *P. reticulata* by the following methods.

Ovaries utilised for this purpose were all mature, filling a substantial proportion of the abdominal cavity, and were taken from fish caught during the study period. Ovaries were teased apart to separate the oocytes. In the case of small ovaries (from *C. riisei, H. unilineatus, C. aeneus* and some *G. sternicla*) complete counts were made of all oocytes within the largest size range of oocytes as determined from oocyte size distribution analyses (Table 19). For larger ovaries (from some *G. sternicla* and *A. bimaculatus*) a volumetric subsampling method was used with at least four subsamples being taken (Bagenal & Braum 1978). Data from Gilson's fixed ovaries used in oocyte size distribution analyses were also pooled with these data. For *P. reticulata* brood size was determined by counting all ova of mature size and/or embryos present in the ovaries of mature females caught during the study. The relationship between batch fecundity or brood size and standard length was determined according to Bagenal & Braum (1978). Statistical analyses of the relationships were conducted in the same way as for the length-weight relationships.

Investigations of spawning patterns and frequency as well as fertility (the actual number of eggs shed (Bagenal 1978)) were attempted by laboratory breeding of the six species under study. All specimens were collected from the study area and kept in aerated 85-litre aquaria which were fitted with undergravel filters. The fish were fed on prepared dried fish foods with occasional live food. An artificial spawning site was placed in each aquarium (except for *P. reticulata*) and it consisted of a 15 cm diameter glass petri dish covered with 3 mm-mesh nylon netting to which a bundle of dark green nylon yarn was attached. Observations of the fish were made every day initially and occasionally thereafter within one or two hours after dawn in order to witness courtship and spawning behaviour. Spawning sites were checked every day (usually at mid-morning) to remove any eggs that may have been spawned. This procedure was carried out until the end of the experiments. Details of specimens used in each instance and the duration of each experiment are given with the results.

Oocyte size distribution analyses were performed on ovaries over a range of maturity stages in order to investigate spawning patterns and frequency, and mature oocyte size ranges for all species except *P. reticulata*. The method utilised volumetric subsampling procedures similar to those used by Macer (1974).

Collections of female fish were made during the 1985 rainy season. They were killed by chilling and standard lengths and total weights measured. For each female both ovaries were excised, weighed to the nearest milligram and fixed in Gilson's fluid and were occasionally shaken to separate the oocytes. After a period of at least a month excess Gilson's fluid was removed and distilled water added to make up to a known volume: between 1 and 5 ml for small ovaries, up to 20 ml for larger ones. Eggs were agitated thoroughly and 1 ml subsamples taken using a 1 ml syringe. Each subsample was inserted into a Sedgewick-Rafter Counting Cell where all oocytes greater than or equal to 0.243 mm were measured and counted (usually not less than 150 oocytes). For the smaller oocytes four or five randomly chosen strips of the Sedgewick-Rafter Cell were scanned and all oocytes less than 0.243 mm were measured and counted (usually about 150 oocytes or more). For very small ovaries diluted to 1 or 2 ml, all oocytes greater than or equal to 0.243 mm were measured and counted. For larger ovaries diluted to 5 ml or more, up to four 1 ml subsamples were taken and each subsample treated as above. All oocytes were measured using an eyepiece graticule at a magnification of 40x, along their horizontal axis which was parallel to the grid lines of the Sedgewick-Rafter Cell. In two instances formalin-fixed ovaries were utilised; they were treated in the same manner as Gilson's fluid-fixed ovaries.

In order to check the accuracy of the subsampling procedure, coefficients of variation (COV) were calculated. For replicate 1 ml subsamples of *A. bimaculatus* oocytes, COV for oocytes greater than or equal to 0.243 mm was 5.22% (N = 6) while for small oocytes less than 0.243 mm COV was 7.81% (N = 10). Maximum egg sizes for the other characoids were similar to that for *A. bimaculatus* so it was assumed that sampling errors would be similar. For *C. aeneus* which had larger oocytes, COV for oocytes greater than or equal to 0.243 mm was 15.43% and for oocytes less than 0.243 mm COV was 16.27% (N = 10 in both cases). From raw data on oocyte sizes and frequency, the total number of oocytes in both ovaries were estimated and the number and percentage frequency of oocytes of each size class calculated. Using oocyte size frequency distribution histograms, the size range of the largest oocytes in mature ovaries was determined and used in batch fecundity estimations.

RESULTS

Species composition and distribution

A complete taxonomic list of fish species caught in the study area during the study period is given in Table 20. Generally the fish caught in fresh and brackish waters belonged to nine orders, 21 families and 31 species of which

TABLE 20: Taxonomic list of teleost fish collected in the Chatham streams during the study period (classification after Gery (1977) and Nelson (1984)).

Taxon	Stations			
	1	2	3	4
Characiformes				
Erythrinidae				
Hoplias malabaricus (Bloch)	x	x	x	
Erythrinus erythrinus (Schneider)			x	
Gasteropelecidae				
Gasteropelecus sternicla (Linnaeus)	x	x		
Characidae				
Brycon siebenthalae Eigenmann		x		
Triportheus elongatus Gunther			x	x
Corynopoma riisei Gill	x	x	x	
Astyanax bimaculatus (Linnaeus)	x	x	x	
Moenkhausia bondi (Fowler)[1]				
Hemigrammus unilineatus (Gill)	x	x	x	x
Siluriformes				
Pimelodidae				
Rhamdia sebae (Valenciennes)	x	x	x	
Callichthyidae				
Callichthys callichthys (Linnaeus)			x	
Corydoras aeneus (Gill)	x	x	x	
Gymnotiformes				
Gymnotidae				
Gymnotus carapo Linnaeus		x	x	
Cyprinodontiformes				
Aplocheilidae				
Rivulus hartii (Boulenger)	x	x	x	

TABLE 20 (continued)

Taxon	Stations 1	2	3	4
Poeciliidae				
Poecilia reticulata Peters	x	x	x	
P. picta Regan				x
P. vivipara Bloch & Schneider				x
Atheriniformes				
Atherinidae				x
Syngnathiformes				
Syngnathidae				x
Synbranchiformes				
Synbranchidae				
Synbranchus marmoratus Bloch		x	x	
Perciformes				
Centropomidae				
Centropomus parallelus Poey				x
Serranidae				
Epinephelus itajara (Lichtenstein)				x
Gerreidae				
Diapterus rhombeus (Cuvier)				x
Haemulidae				
Pomadasys sp				x
Nandidae				
Polycentrus schomburgkii Muller & Troschel		x		
Cichlidae				
Cichlasoma bimaculatum (Linnaeus)		x	x	
Crenicichla alta Eigenmann	x	x		

TABLE 20 (continued)

Taxon	Stations 1	2	3	4
Mugilidae				
Mugil curema Valenciennes				x
Gobiidae				
Sicydium punctatum Perugia				x
Pleuronectiformes				
Bothidae				
Citharichthys sp				x
Soleidae				
Trinectes sp				x

[1] : Collected in the middle-lower reaches of the Carlisle River only.

two species were new records for Trinidad. The most dominant families in terms of species represented were Characidae (six species), Poeciliidae (three species), Erythrinidae, Callichthyidae and Cichlidae (two species each).

Of the 19 freshwater fish species, the characids were very common at the first three stations especially *C. riisei, A. bimaculatus* and *H. unilineatus*. *P. reticulata* was also abundant. *G. sternicla* and *C. aeneus* were commonly found and especially towards the end of the study period the former species became quite abundant. *Hoplias malabaricus, Rivulus hartii* and the two cichlid species, *Cichlasoma bimaculatum* and *Crenicichla alta,* were caught occasionally as adults but during their respective reproductive periods juveniles were common. Other species such as *Rhamdia sebae, Gymnotus carapo* and *Synbranchus marmoratus* were only rarely caught possibly due to their more nocturnal habits.

Certain freshwater species were restricted in their distribution, for example *Moenkhausia bondi* was only found during an extensive seineing effort along the middle and lower reaches of the Carlisle River, an area not regularly sampled. *G. sternicla* was collected only from the Carlisle River. *Erythrinus erythrinus* and *Callichthys callichthys* were found only at Station 3. This station was situated just beside the Chatham South Road and it is possible that they were introduced there. *E. erythrinus* was only found later in the study period. Another restricted species was *Polycentrus schomburgkii* found only at Station 2 and whose distribution was probably determined by habitat preference since this pool was one of the deeper, more extensive and permanent ones in the upper Carlisle River. Pool depth and permanence most likely influenced distribution of fish at the freshwater stations since Stations 2 and 3 each supported 15 species as compared with only 10 at the shallower less permanent Station 1.

Special mention must be made of the presence of two species which were new records for Trinidad, namely *Brycon siebenthalae* and *Triportheus elongatus* (Alkins & De Souza 1983/84 , Sturm & De Souza 1984). Only two full grown specimens of *B. siebenthalae* were caught at Station 2 and extensive fishing of both the Carlisle and Quarahoon Rivers failed to turn up others. It is presumed that this species had recently colonised the Carlisle River but had not established a population. *T. elongatus* on the other hand, appeared to have been caught in the process of colonisation of these rivers. They were initially found at the mouth of a small river at Los Blanquizales Lagoon and at the mouth of the Quarahoon River in September 1981. At this time their distribution extended to approximately 300 m upstream of Station 4 (about 600 m from the river mouth). By January 1985 they were common in the middle reaches of the Carlisle River and as far as Station 3 on the Quarahoon River (about 1.2 to 1.4 km from the river mouth). A restricted range of sizes of individuals were caught, from 56 to 108 mm SL as compared to average adult size on the mainland between 200 and 280 mm SL (Goulding 1980). This suggests that these are pre-reproductives but considering the wide distribution of the species and the need for revision of the genus (Weitzman, pers. comm.), this cannot be certain without further investigation. No juveniles have been noted however. It remains to be determined whether this species has established a breeding population in the area.

The collection of *T. elongatus* in brackish water indicates that this characid has a well developed tolerance to salinities up to 12°/oo (Sturm & De Souza 1984) and a long term tolerance of salinities up to 5°/oo (Alkins & De Souza 1983/84). In April 1981 a specimen of *H. unilineatus* (17 mm SL) was found at Station 4 at a time when specific conductivity was 800 μmhos. The potential of these characids, generally considered to be primary freshwater fishes (Myers 1938), to tolerate brackish and saline waters needs to be pursued further in the light of these findings.

Of the 31 species found in the study area only 12 were restricted to brackish water at Station 4. They included *Centropomus parallelus* which occurred in most of the catches and *Poecilia vivipara, Diapterus rhombeus, Citharichthys* sp and *Trinectes* sp which were only occasionally found. Other species such as *Poecilia picta, Epinephelus itajara, Pomadasys* sp, *Mugil curema, Sicydium punctatum,* atherinids and syngnathids were uncommon or rare. However, at the mouth of the Quarahoon River schools of juvenile *M. curema,* atherinids and *Anableps anableps* were seen. Many of these species were represented by juveniles only, for example *C. parallelus, D. rhombeus, Citharichthys* and *Trinectes,* and indicated the use of this estuarine area as a nursery ground for these species.

Population studies and reproductive seasonality

General trends in population sizes of the six species studied are given first with more detailed results on morphometry, population demography and reproductive seasonality after. The quality of the data varied for the different species largely because of lack of availability of specimens at certain times.

Population fluctuations:

Despite the fact that the sampling method used for the first year of the study was only semi-quantitative, the data showed distinctive trends in the fluctuations of population sizes for the study species. During the first year of the study period, total numbers of the six species collected from all freshwater stations varied widely from one month to the next (Fig. 28). Such variation was due mainly to two recognisable factors: the effects of flow regime and the input of juveniles into the population. The former factor involved two extreme situations where increased discharge resulted in washouts and drastic decreases in fish populations (June/July, October 1980, April 1981) and on the other hand, lentic conditions and contraction of the habitat concentrated fish into pools making them more vulnerable to capture in large numbers (May 1980 at the end of a three month lentic period). Total numbers of fish caught showed a significant inverse correlation with mean discharge for Stations 1, 2 and 3 (Spearman Rank correlation coefficient = -0.567, N = 14, $p<0.05$). Substantial increases in the fish population also occurred as a result of inputs of juveniles into the

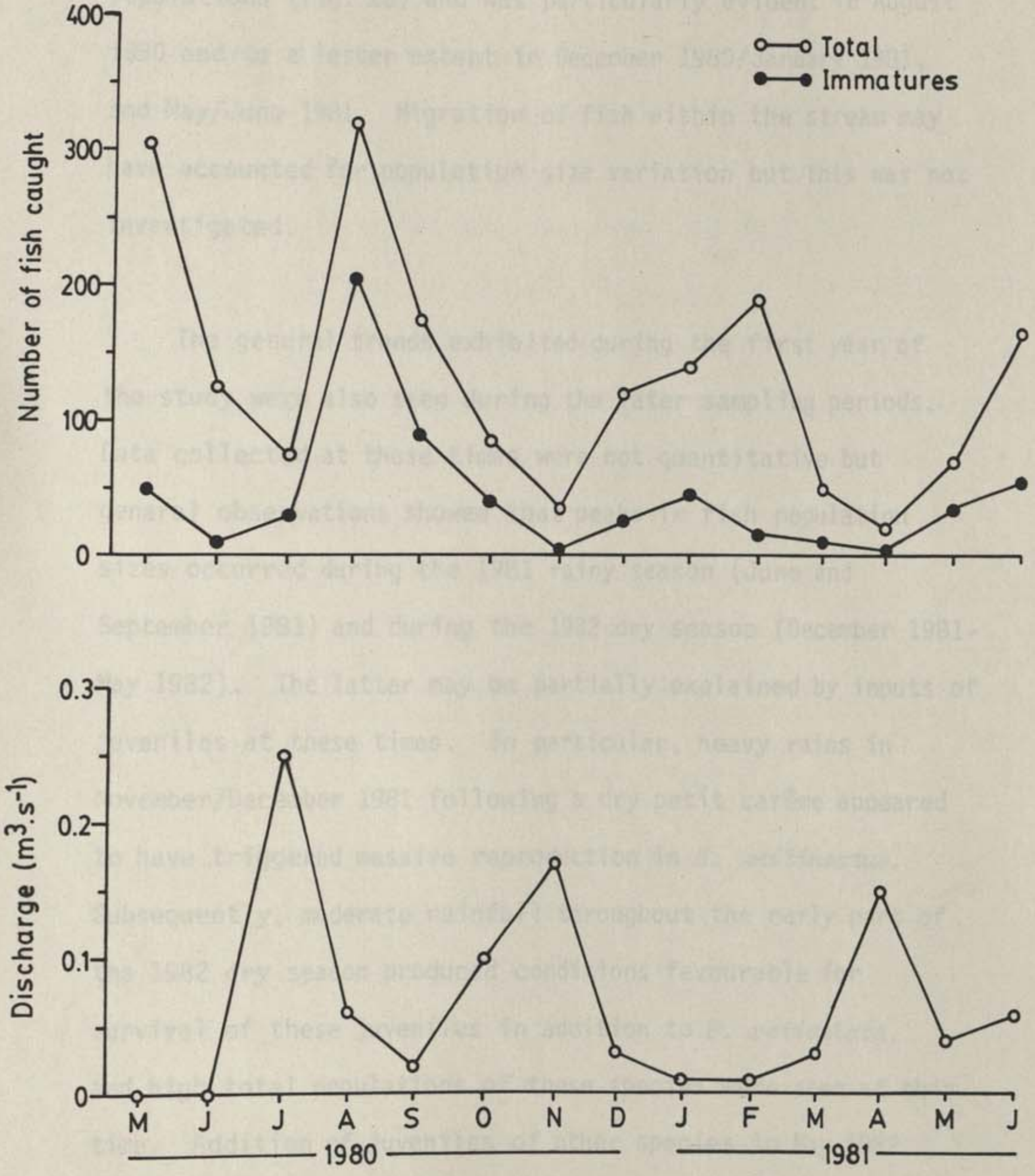


FIGURE 28: Monthly fluctuations of total fish populations in relation to mean discharge for Stations 1 to 3.

populations (Fig. 28) and was particularly evident in August 1980 and to a lesser extent in December 1980/January 1981, and May/June 1981. Migration of fish within the stream may have accounted for population size variation but this was not investigated.

The general trends exhibited during the first year of the study were also seen during the later sampling periods. Data collected at these times were not quantitative but general observations showed that peaks in fish population sizes occurred during the 1981 rainy season (June and September 1981) and during the 1982 dry season (December 1981-May 1982). The latter may be partially explained by inputs of juveniles at these times. In particular, heavy rains in November/December 1981 following a dry petit carême appeared to have triggered massive reproduction in *H. unilineatus*. Subsequently, moderate rainfall throughout the early part of the 1982 dry season produced conditions favourable for survival of these juveniles in addition to *P. reticulata*, and high total populations of these species were seen at this time. Addition of juveniles of other species in May 1982 also augmented total populations. However, nearly 400 mm of rainfall in June 1982 caused washouts and decimated the fish populations severely.

The effects of flow regime on the populations of the six species could be seen even more clearly by looking at each station separately (Fig. 29). Generally, numbers of fish caught were greater at Stations 2 and 3 than at Station 1 and this was consistent with the larger and more permanent habitat at the former two sites. Nevertheless, numbers of fish caught fluctuated widely at these two stations from month to month. At times of high discharge and floods, severe decreases in fish catches were apparent. Increases in population density occurred at times of more moderate or low discharge. A statistically significant correlation between numbers of fish caught and discharge rates was found only at Station 2 (Spearman rank correlation coefficient = -0.646, N = 13, $p<0.05$).

Analysis of the data by species allowed the determination of general population cycles for each species over the first year of the study (Figs. 30 and 31). Median catches were calculated for each species as the median value of monthly catches for all stations combined. Immatures were considered to be those individuals less than Minimum Developing SL for the species.

Numbers of *G. sternicla* caught were relatively constant

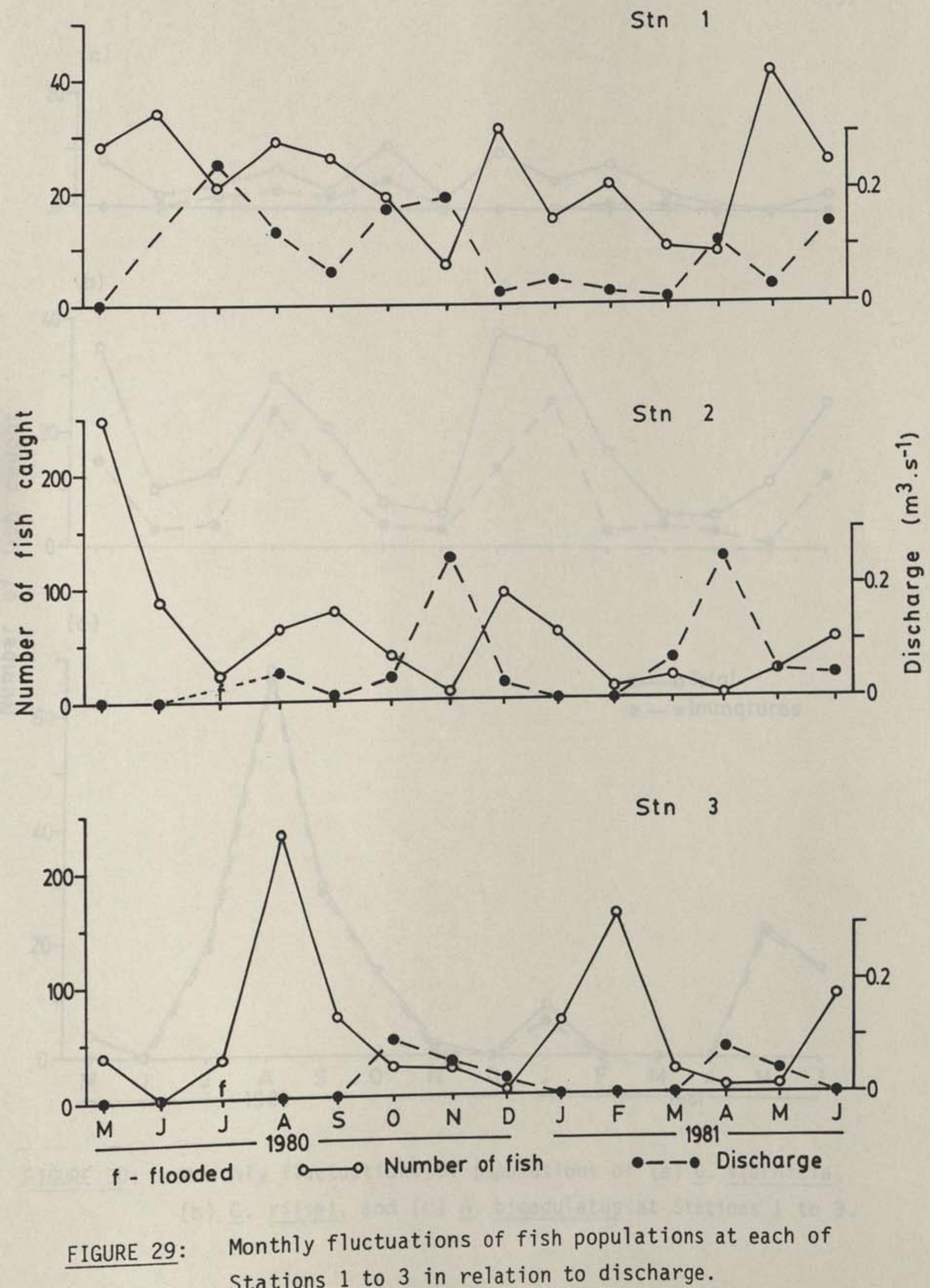


FIGURE 29: Monthly fluctuations of fish populations at each of Stations 1 to 3 in relation to discharge.

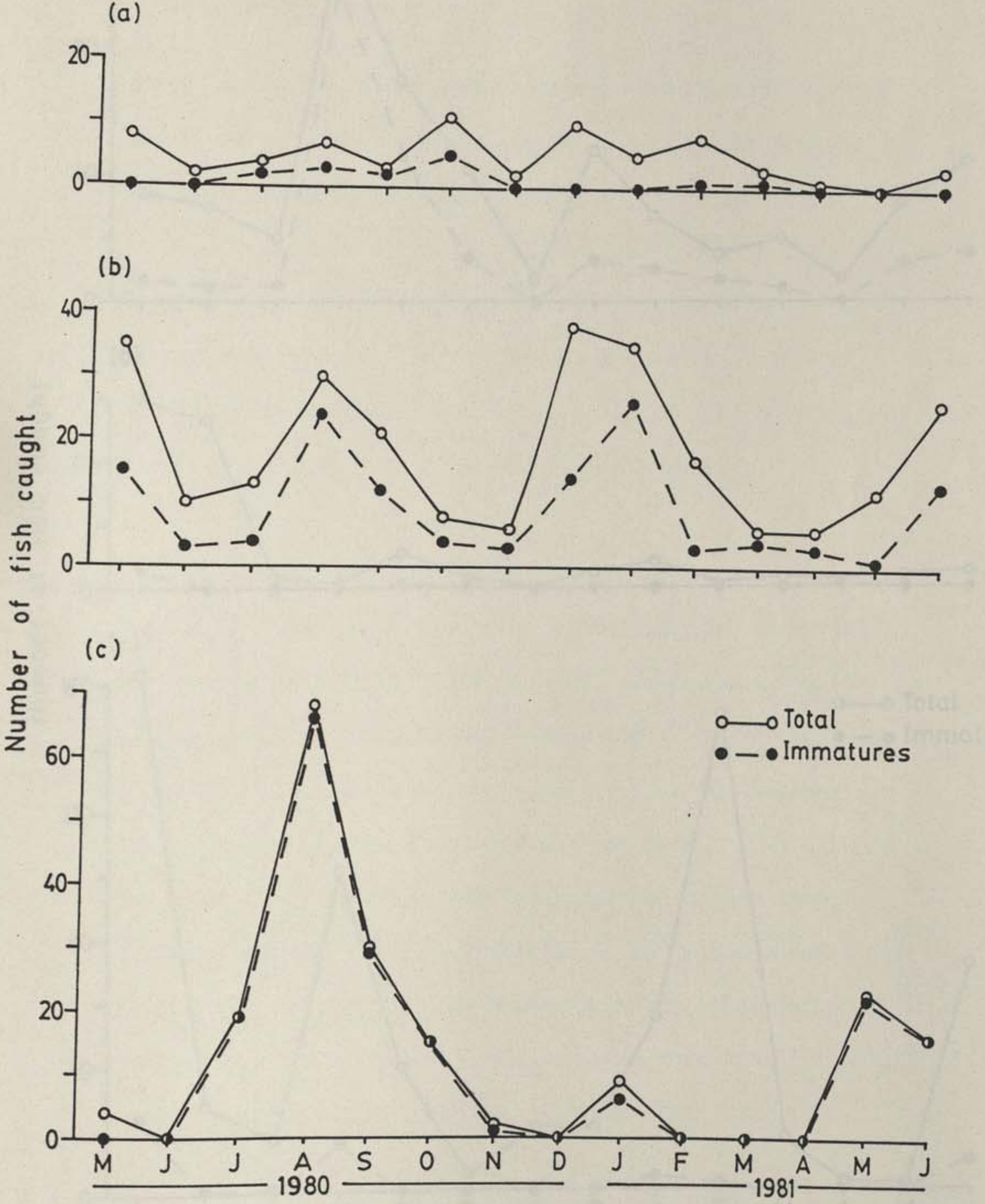


FIGURE 30: Monthly fluctuations of populations of (a) G. sternicla, (b) C. riisei, and (c) A. bimaculatus at Stations 1 to 3.

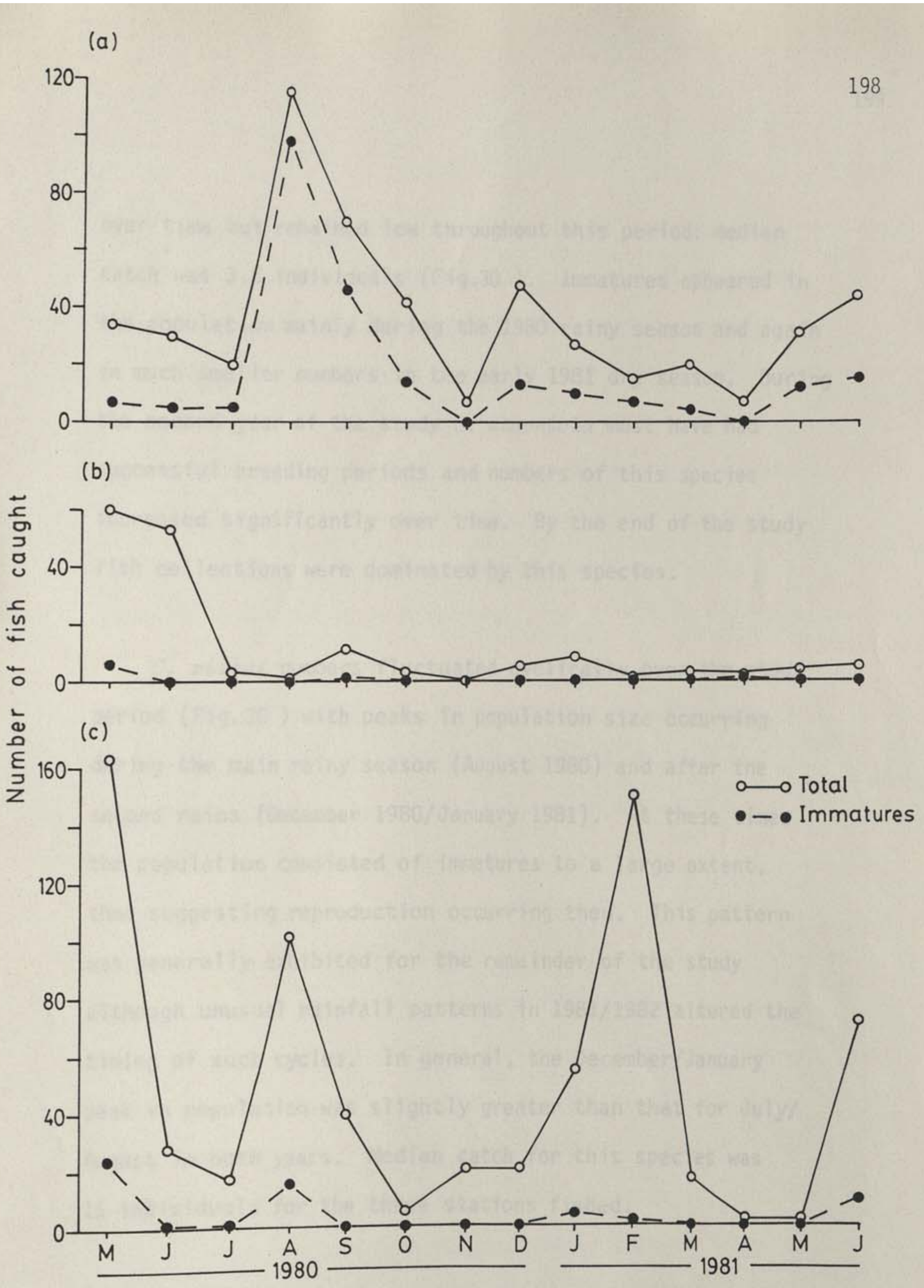


FIGURE 31: Monthly fluctuations of populations of (a) *H. unilineatus*, (b) *C. aeneus*, and (c) *P. reticulata* at Stations 1 to 3.

over time but remained low throughout this period: median catch was 3.5 individuals (Fig.30). Immatures appeared in the population mainly during the 1980 rainy season and again in much smaller numbers in the early 1981 dry season. During the second year of the study *G. sternicla* must have had successful breeding periods and numbers of this species increased significantly over time. By the end of the study fish collections were dominated by this species.

C. riisei numbers fluctuated cyclically over the study period (Fig.30) with peaks in population size occurring during the main rainy season (August 1980) and after the second rains (December 1980/January 1981). At these times the population consisted of immatures to a large extent, thus suggesting reproduction occurring then. This pattern was generally exhibited for the remainder of the study although unusual rainfall patterns in 1981/1982 altered the timing of such cycles. In general, the December/January peak in population was slightly greater than that for July/August in both years. Median catch for this species was 15 individuals for the three stations fished.

The majority of the individuals of *A. bimaculatus* caught were immature and these accounted for the population changes seen (Fig. 30). Large increases in numbers of immature individuals occurred during the first rainy season (August 1980, May/June 1981) and a minor peak occurred in January 1981 after the second rains. This pattern of major and minor peaks in numbers of immatures continued fairly regularly over the rest of the study. Adults of this species were particularly low in numbers so that trends in adult populations could not be observed. Median catch was 6.5 individuals for the three stations.

Numbers of *H. unilineatus* caught were relatively large compared with other species (median catch 30.5 individuals). Total populations varied widely as a result of input of immatures and washouts due to floods (Fig. 31). The population consisted mainly of immatures during the main rainy season (August 1980) while a smaller peak during the second rains (December 1980) consisted largely of adults with some immatures. A similar trend was seen throughout the rest of the study although a large influx of immature individuals occurred in January 1982 after particularly heavy rains in November/December 1981. Survival of these small individuals throughout the 1982 dry season was good when low to moderate flows were maintained but very heavy rains in June 1982 severely decreased the population of this and other species.

Catches of *C. aeneus* were very variable and generally low (median catch 3.5 individuals). Initially large numbers were caught but numbers declined markedly thereafter (Fig. 31). Presumably such large numbers were caught because of their concentration in the pools during a long dry season. Generally however, no clear seasonal cycle of population fluctuations was discerned.

Populations of *P. reticulata* oscillated widely over the study period with a median catch of 24 individuals for the three stations sampled (Fig. 31). Populations consisted almost entirely of reproductive individuals except in August 1980, January and June 1981 when immatures made up a minor proportion of the population. Massive inputs of immatures such as seen in some other species were not seen in this species and fluctuations were due to variation in numbers of mature individuals. Comparison of *P. reticulata* population sizes and discharge rates indicated a significant inverse correlation (Spearman rank correlation coefficient =-0.552, N = 14, $p<0.05$). Substantial decreases occurred during times of heavy rains and flooding, but populations recovered afterwards when moderate or low flows existed. Population recovery was extremely rapid on most occasions, attaining very high densities after only a month or two. In certain instances population decline began before the advent of heavy rainfall. In such cases population movements or some other type of population control mechanism or even overfishing might have been contributory.

Morphometric studies:

The six study species varied widely in terms of general body size (Table 21). *A. bimaculatus* was by far the largest species with *P. reticulata* the smallest. *C. riisei* and *H. unilineatus* were approximately equal in lengths but body proportions differed. *C. aeneus* was generally larger than *G. sternicla* but there was a substantial overlap of sizes. Males and females of all species differed in maximum sizes attained with males being smaller than females in *G. sternicla, H. unilineatus, C. aeneus* and *P. reticulata*. Maximum male size was greater than that for females in *C. riisei* and *A. bimaculatus* but in general many males tended to be smaller than females.

Secondary sexual characters made possible the determination of sex using external features in mature or even developing specimens of *C. riisei, A. bimaculatus* and *P. reticulata*.

TABLE 21: Range of standard lengths (SL, mm) and total weights (TW, g) recorded during the study period for the six fish species studied.

Species	Minimum		Maximum			
			Female		Male	
	SL	TW	SL	TW	SL	TW
G. sternicla	14	0.038	49	4.333	42	2.466
C. riisei	9	0.006	37	0.828	39	0.824
A. bimaculatus	8	0.010	76	15.757	82	17.801
H. unilineatus	9	0.011	39	1.413	33	0.857
C. aeneus	24	0.671	60	10.414	53	6.120
P. reticulata	6	0.002	25	0.394	16	0.076

However, certain differences in body proportions made it possible to distinguish sexes in the other species after some experience had been gained. Analysis of these body proportions showed that they could be used as fairly reliable external indicators of sex (Table 22). Mean body depth:SL ratio in *G. sternicla* and *H. unilineatus* showed a highly significant difference between males and females (Table 22) with females being deeper bodied than males especially when ripe with eggs. *C. aeneus* males and females differed significantly in terms of body width : SL ratio and pectoral fin spine length : SL ratio (Table 22). Females were wider bodied and possessed shorter pectoral spines than males.

Length-weight relationships for the six species are shown graphically in Figs. 32 to 34. Points were plotted for data from June 1980 to January 1981 but the line of best fit was derived from data from June 1980 to June 1981. The parameters of the length-weight relationships derived from a full year's data are expressed in Table 23. In all cases the correlation coefficients, r, were highly significant and the regression coefficients were highly significantly different from zero (F-test, $p<0.001$). Regression coefficients ranged from 3.049 to 3.515 in *C. aeneus* and *G. sternicla*

TABLE 22: Sexual dimorphism in selected body proportions for mature specimens of *G. sternicla*, *H. unilineatus* and *C. aeneus* (Based on formalin-fixed specimens).

Species	Body proportion	Sex	Mean ratio (% ± SE)	N	d[1]
G. sternicla	Body depth : SL	M	50.42 ± 0.18	65	4.987***
		F	51.89 ± 0.23	19	
H. unilineatus	Body depth : SL	M	35.13 ± 0.25	80	8.668***
		F	37.91 ± 0.21	79	
C. aeneus	Body width : SL	M	27.01 ± 0.16	80	9.249***
		F	29.14 ± 0.17	75	
"	Pectoral spine length : SL	M	27.16 ± 0.25	80	7.972***
		F	24.64 ± 0.19	75	

M : Male F : Female SE : Standard Error N : Number of specimens

[1] : ***d-test, $p<0.001$

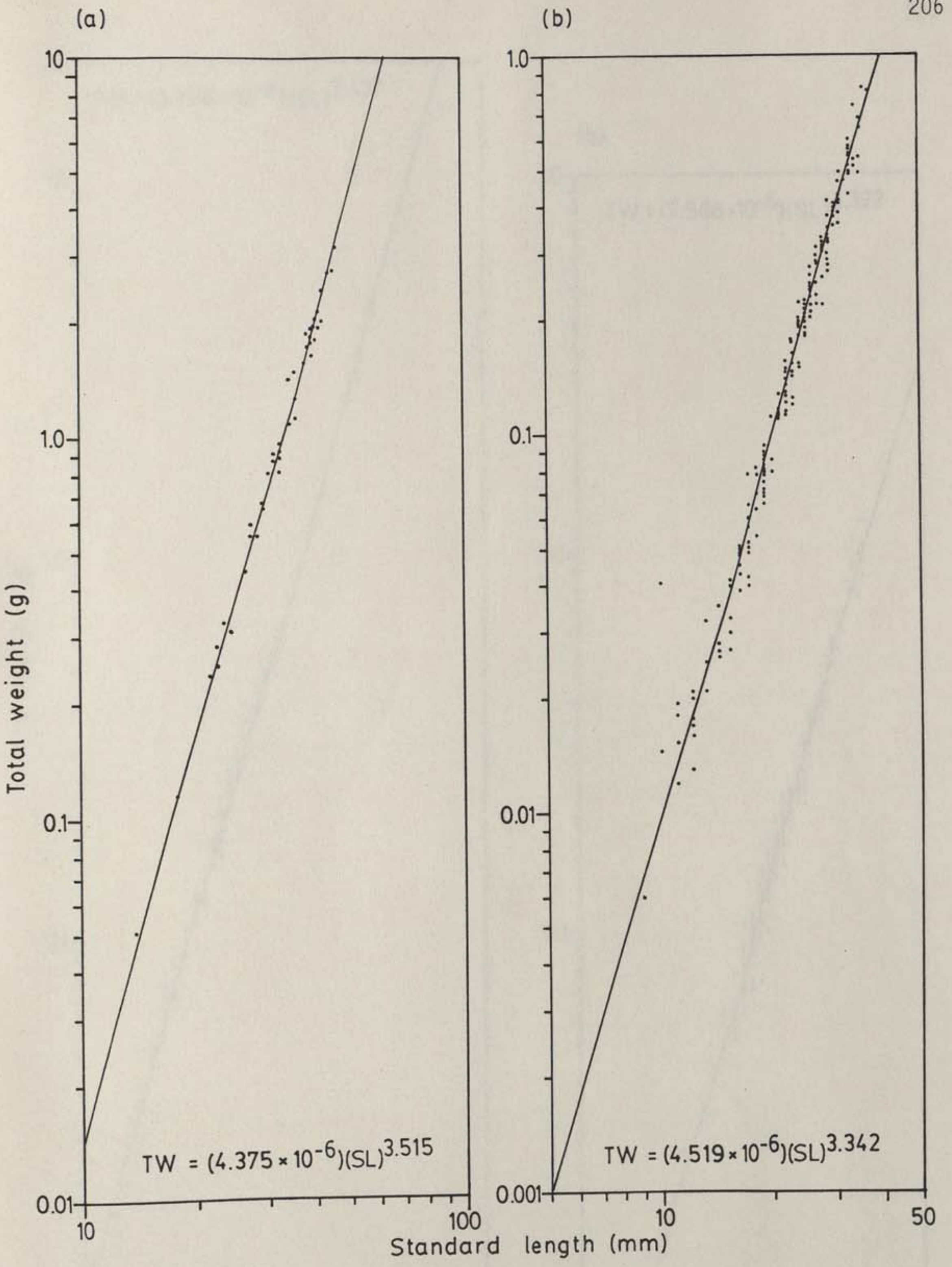


FIGURE 32: Length-weight relationships for (a) *G. sternicla*, and (b) *C. riisei*.

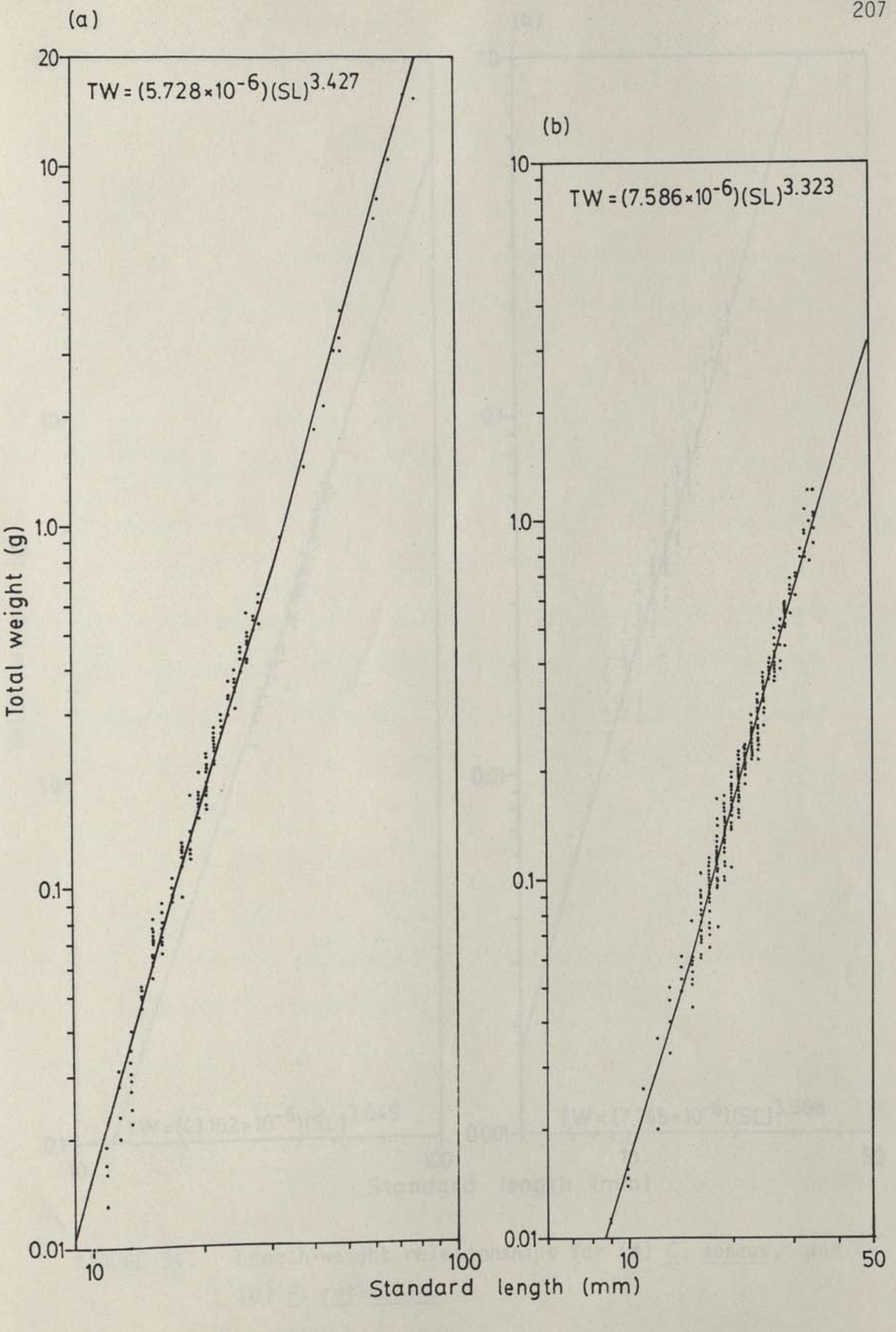


FIGURE 33: Length-weight relationships for (a) *A. bimaculatus*, and (b) *H. unilineatus*.

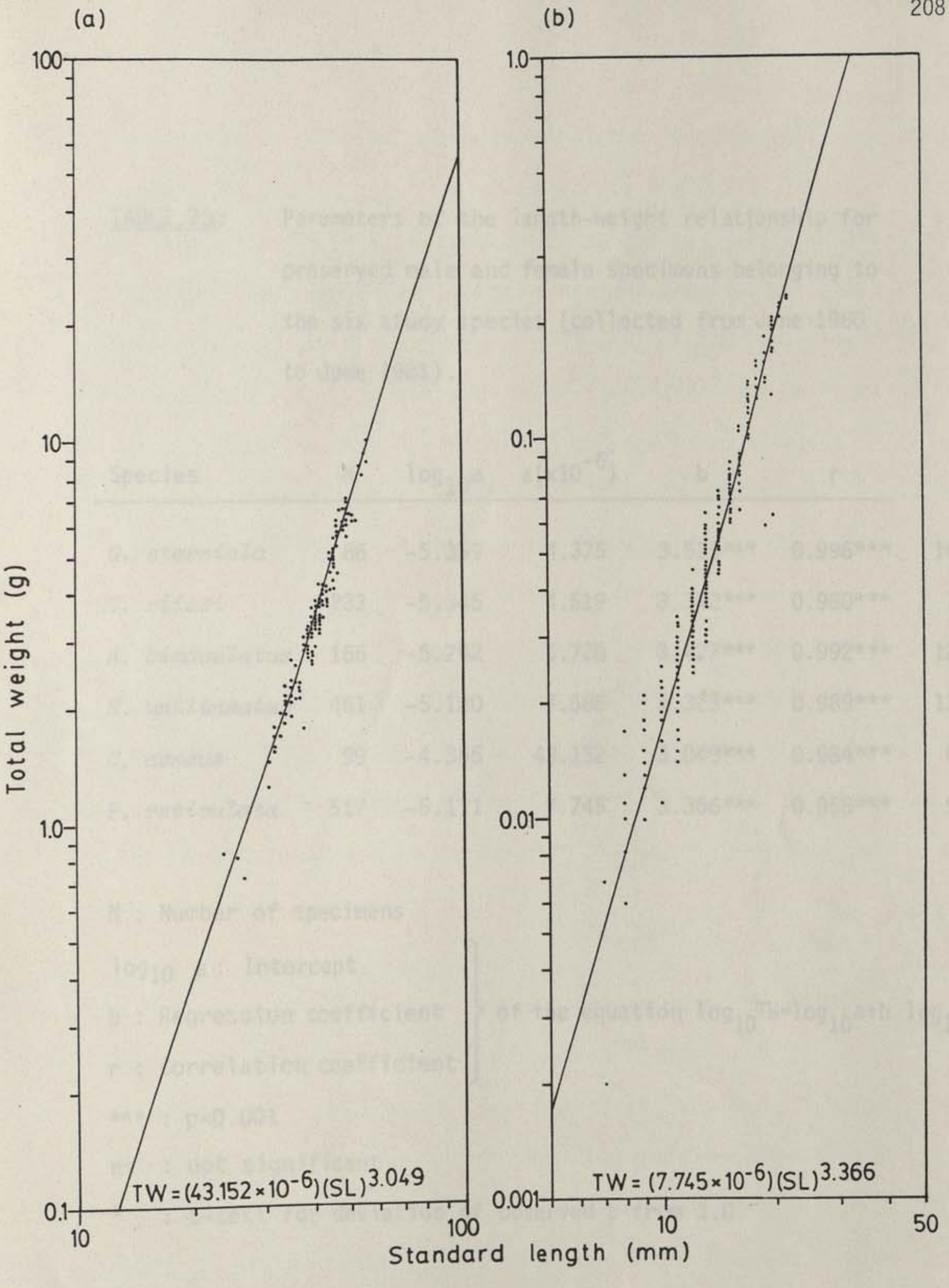


FIGURE 34: Length-weight relationships for (a) C. aeneus, and (b) P. reticulata.

TABLE 23: Parameters of the length-weight relationship for preserved male and female specimens belonging to the six study species (collected from June 1980 to June 1981).

Species	N	$\log_{10}a$	$a(\times 10^{-6})$	b	r	t_s[1]
G. sternicla	86	-5.359	4.375	3.515***	0.996***	14.905***
C. riisei	233	-5.345	4.519	3.342***	0.980***	7.714***
A. bimaculatus	166	-5.242	5.728	3.427***	0.992***	12.934***
H. unilineatus	461	-5.120	7.586	3.323***	0.989***	13.696***
C. aeneus	99	-4.365	43.152	3.049***	0.984***	0.879^{ns}
P. reticulata	517	-5.111	7.745	3.366***	0.968***	9.542***

N : Number of specimens

$\log_{10}$ a : Intercept
b : Regression coefficient } of the equation $\log_{10}TW=\log_{10}a+b\log_{10}SL$
r : Correlation coefficient

*** : $p<0.001$

ns : not significant

[1] : t-test for deviation of observed b from 3.0

respectively while the constant, a, of the length-weight equation ranged from 43.152×10^{-6} in *C. aeneus* to 4.375×10^{-6} in *G. sternicla*. For all species except *C. aeneus*, length-weight relationships were significantly different from cubic (Table 23). Comparison of regression coefficients between species showed that b for *C. aeneus* differed significantly from that for all other species (Appendix 13) and may be as a result of denser body material owing to the presence of external scale armour. Slopes of the length-weight equations for *C. riisei*, *A. bimaculatus*, *H. unilineatus* and *P. reticulata* did not differ at a highly significant level. However their intercepts did show a highly significant difference (analysis of covariance, $F = 512.31$, $df = 3/1372$, $p<0.001$). *C. riisei* had the lowest value of a consistent with its elongated and slender body form as compared to the other deeper bodied species.

Generally all species showed significant shrinkage in length as a result of formalin fixation (Appendix 7). Shrinkage in *C. aeneus* was significant (paired-sample t-test, $p<0.05$) but not as highly significant as for the other species ($p<0.001$). Average preserved lengths ranged from 96.98% of fresh length in *P. reticulata* to 99.20% for *C. aeneus*. Length decreases were more variable between specimens as compared to weight changes and this was reflected in standard errors of the means.

All fish except *C. aeneus* decreased in total weight after preservation. There was a highly significant increase in total weight after preservation in *C. aeneus* ($p<0.001$) which averaged 105.61% of fresh weight and which was greater than 110% for two specimens. Loss of weight due to preservation was not significant for *A. bimaculatus* despite average preserved weight being 98.14% of fresh weight. Many *A. bimaculatus* specimens gained weight slightly after preservation (up to 102.38%). Weight loss was highly significant for all other species ($p<0.001$) and means ranged from 94.85% for *H. unilineatus* to 97.32% for *C. riisei*.

Overall, a trend towards greater and more significant shrinkage and weight loss occurred in the smaller species as compared to the larger ones where less highly significant shrinkage or weight loss and even weight gain took place. Within each species, a similar trend was observed where smaller individuals tended to lose more weight than larger ones but this was not always consistent. These general trends agreed very closely with those seen in other experiments of this kind (Parker 1963).

The effects of formalin preservation on the regression coefficient of the length-weight relationship for each species was not significant (Appendix 8, d-test, $p>0.10$ in all cases) although d-values for *A. bimaculatus* and *C. aeneus* were relatively high. Length-weight relationships of both fresh and preserved specimens had highly significant regression and correlation coefficients. Slight differences were evident between parameters from these data and those summarised in Table 23. This was probably due to the short time span over which these experimental specimens were collected and the possibility of seasonal variation in the length-weight relationship (Bagenal & Tesch 1978).

Population demography and reproductive seasonality:

During the study period no direct evidence of reproduction was obtained for the six species under study. No spawning or courtship behaviour was actually observed in the field not through lack of time spent making observations but because of the low visibility of the turbid waters at the study sites. As a result, a range of other types of evidence had to be utilised in order to elucidate reproductive patterns for these species. These included the timing of occurrence in the population of juveniles and individuals with developing, mature or spent gonads to indicate the potential for and the existence of previous reproductive events. In addition, analyses of gonad states of mature-sized individuals using gonadosomatic indices were made.

Other species besides those being investigated were collected occasionally and gonad states were noted. Mature male and female *Callichthys callichthys* were collected in July, September and December 1980, and January 1981. *Hoplias malabaricus* were caught with mature gonads in May and June 1980 and juveniles were noted throughout the rainy season. *Cichlasoma bimaculatum* juveniles were predominant during the dry season of each year during the study whereas those of *Crenicichla alta* were found during the rainy seasons.

Each of the six species studied in detail will be dealt with separately to describe the results of this part of the study.

Gasteropelecus sternicla

Sexual maturation and growth:

Females of this species possessed developing gonads at a minimum length of 32 mm while males had developing gonads at a smaller size, 30 mm (Table 24, Fig. 35). The smallest

TABLE 24: Minimum Developing and Mature standard lengths (SL) and Median Length at first maturity for the six study species. (All lengths in mm)

Species	Minimum SL				Median SL		N	
	Developing		Mature					
	F	M	F	M	F	M	F	M
G. sternicla	32	30	33	31	38	34	119	166
C. riisei	23	26	26	26	28.5	32.5	219	246
A. bimaculatus	-	40	57	56	-	-	72	130
H. unilineatus	23	20	25	21	29	26	590	562
C. aeneus	34	31	34	34	38	35	116	145
P. reticulata	9	9	11	9	12.4	10.8	936	503

N : Number of specimens

M : Male

F : Female

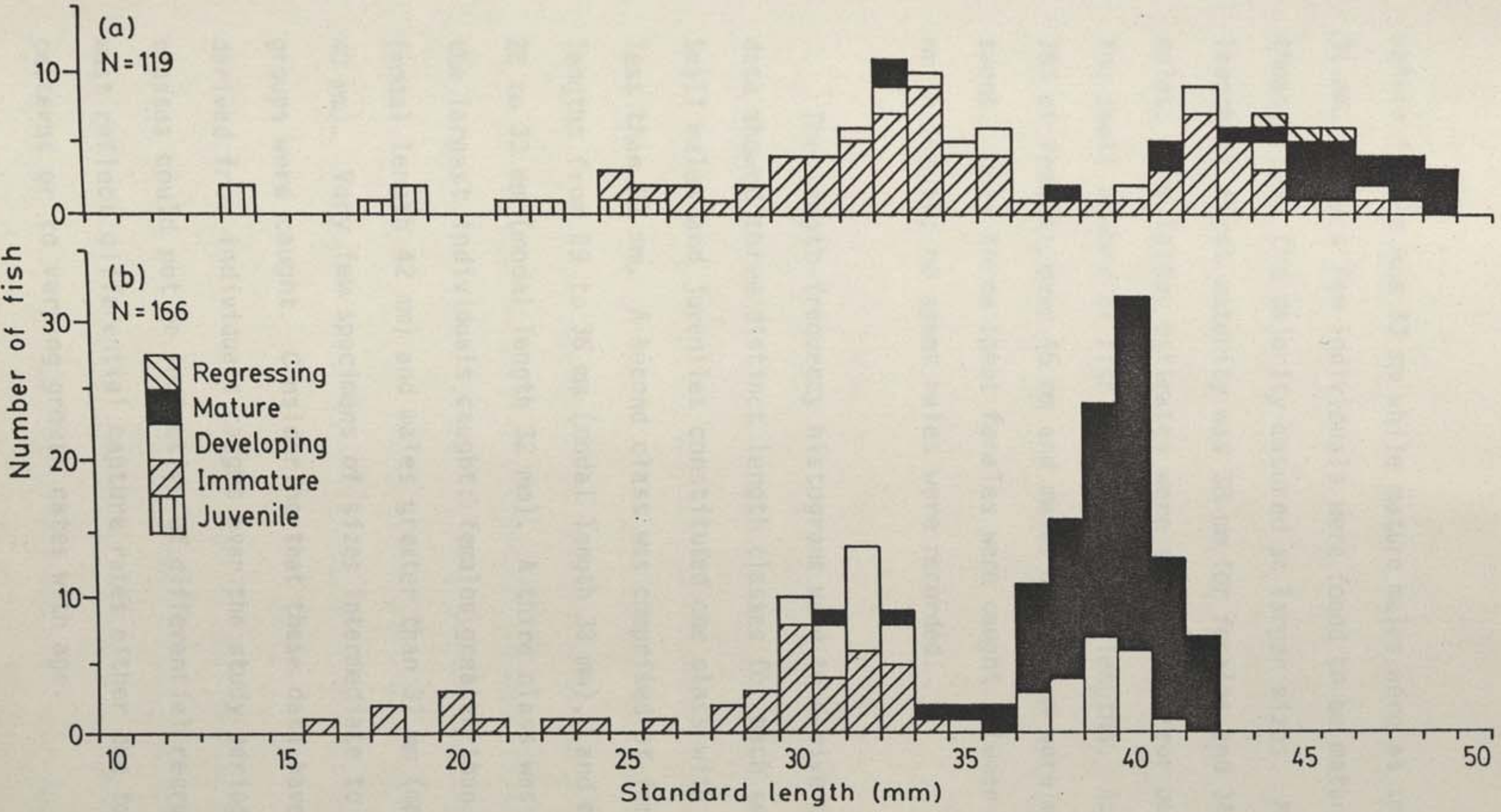


FIGURE 35: The relationship between gonad maturity stages and size for G. sternicla (a) females and juveniles, and (b) males.

mature female was 33 mm while mature males were as small as 31 mm. Only a few individuals were found to be mature at these sizes, the majority matured at larger sizes. Median length at first maturity was 38 mm for females and 34 mm for males. The latter estimates were subject to error because of the small number of fish caught at these lengths. Approximately 78% of females over 45 mm and males over 34 mm were mature or spent. Only three spent females were caught between 44 and 46 mm in length; no spent males were recorded.

The length-frequency histograms used to derive the above data showed three distinct length classes for each sex (Fig.35). Small males and juveniles constituted one class with lengths less than 27 mm. A second class was comprised of females of lengths from 29 to 36 mm (modal length 33 mm), and males from 28 to 33 mm (modal length 32 mm). A third class was made up of the largest individuals caught: females greater than 40 mm (modal length 42 mm) and males greater than 37 mm (modal length 40 mm). Very few specimens of sizes intermediate to these groups were caught. Considering that these data have been derived from individuals caught over the study period, these classes could not be indicative of differential recruitment but must reflect differential capture rates either due to migration patterns or to varying growth rates with age.

Most regular sampling was done in pool habitats and *G. sternicla* may have only entered these habitats in large numbers when ready to spawn. This could account for catches comprised of specific size classes and specimens with gonads in the developing or mature stages. However, large numbers of fish with inactive gonads were also caught within these size classes, an unlikely prospect if these areas were spawning grounds.

On the other hand, few individuals of certain lengths may have been caught because of rapid growth over that range. In this situation, the majority of individuals would have belonged to certain size classes due to their slower growth during that phase. The coincidence of the two larger size classes with the appearance of developing and mature individuals could indicate the distinct separation between growth and reproductive phases in the lifetime of this species. If this was true, then at least two separate periods of reproduction during the lifetime of each fish would be indicated.

Some evidence for growth 'spurts' alternating with slower growth rates was obtained from growth curves derived from monthly population structure data (Fig.36). Changes in population structure over time allowed the determination of

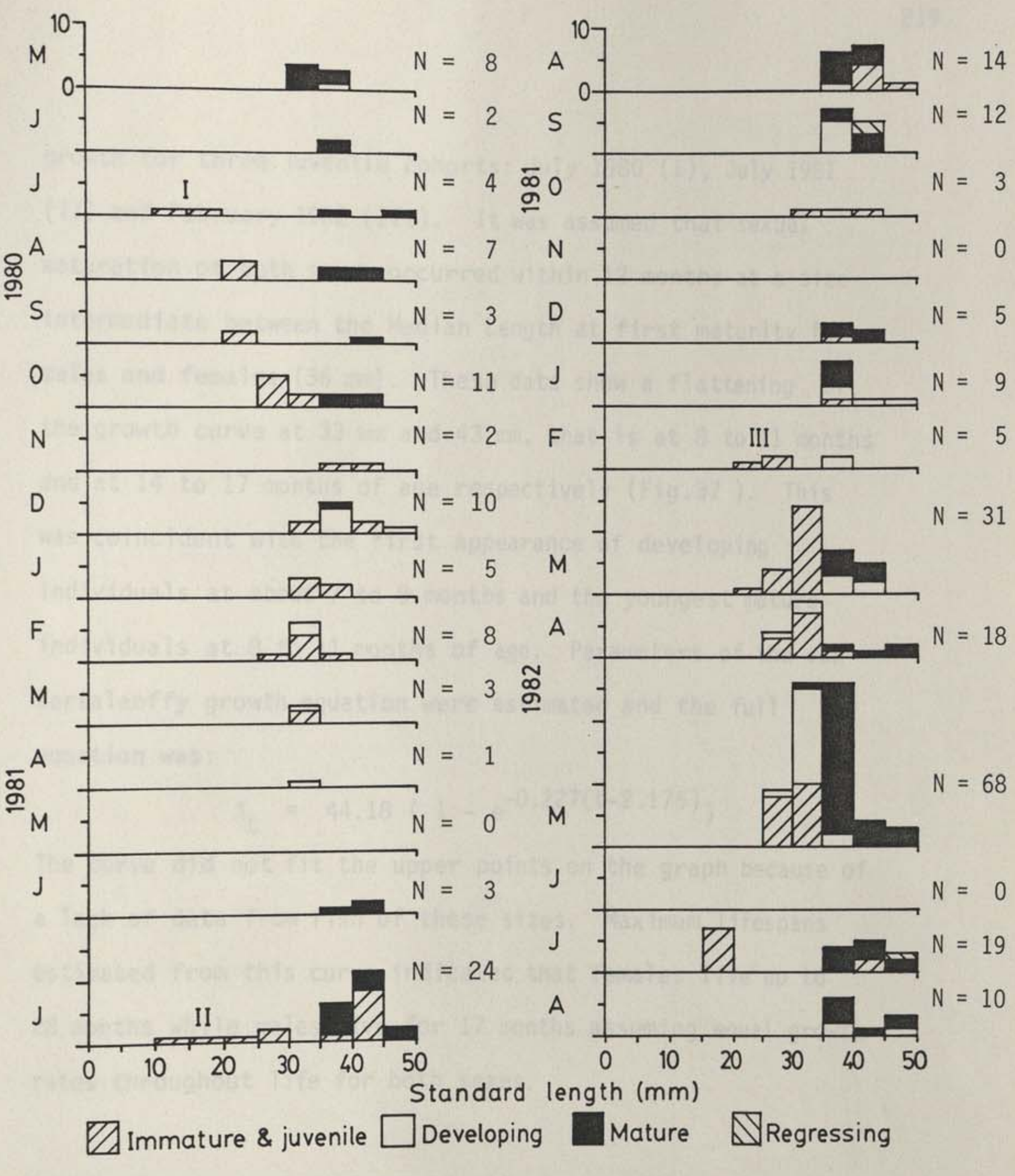


FIGURE 36: Monthly variation of population structure and the occurrence of gonad maturity stages for G. sternicla (I-III: cohorts used in growth analysis).

growth for three juvenile cohorts: July 1980 (I), July 1981 (II) and February 1982 (III). It was assumed that sexual maturation of both sexes occurred within 12 months at a size intermediate between the Median Length at first maturity for males and females (36 mm). These data show a flattening of the growth curve at 33 mm and 43 mm, that is at 8 to 11 months and at 14 to 17 months of age respectively (Fig.37). This was coincident with the first appearance of developing individuals at about 7 to 9 months and the youngest mature individuals at 8 to 11 months of age. Parameters of the von Bertalanffy growth equation were estimated and the full equation was:

$$l_t = 44.18 (1 - e^{-0.227(t-2.175)})$$

The curve did not fit the upper points on the graph because of a lack of data from fish of these sizes. Maximum lifespans estimated from this curve indicated that females live up to 28 months while males live for 17 months assuming equal growth rates throughout life for both sexes.

Population structure and reproductive seasonality:

Changes in population structure of *G. sternicla* each month indicated one major reproductive period at the beginning of the rainy season each year. Juveniles as small as 14 mm appeared in catches in July 1980, July 1981 and July 1982 (Fig.36)

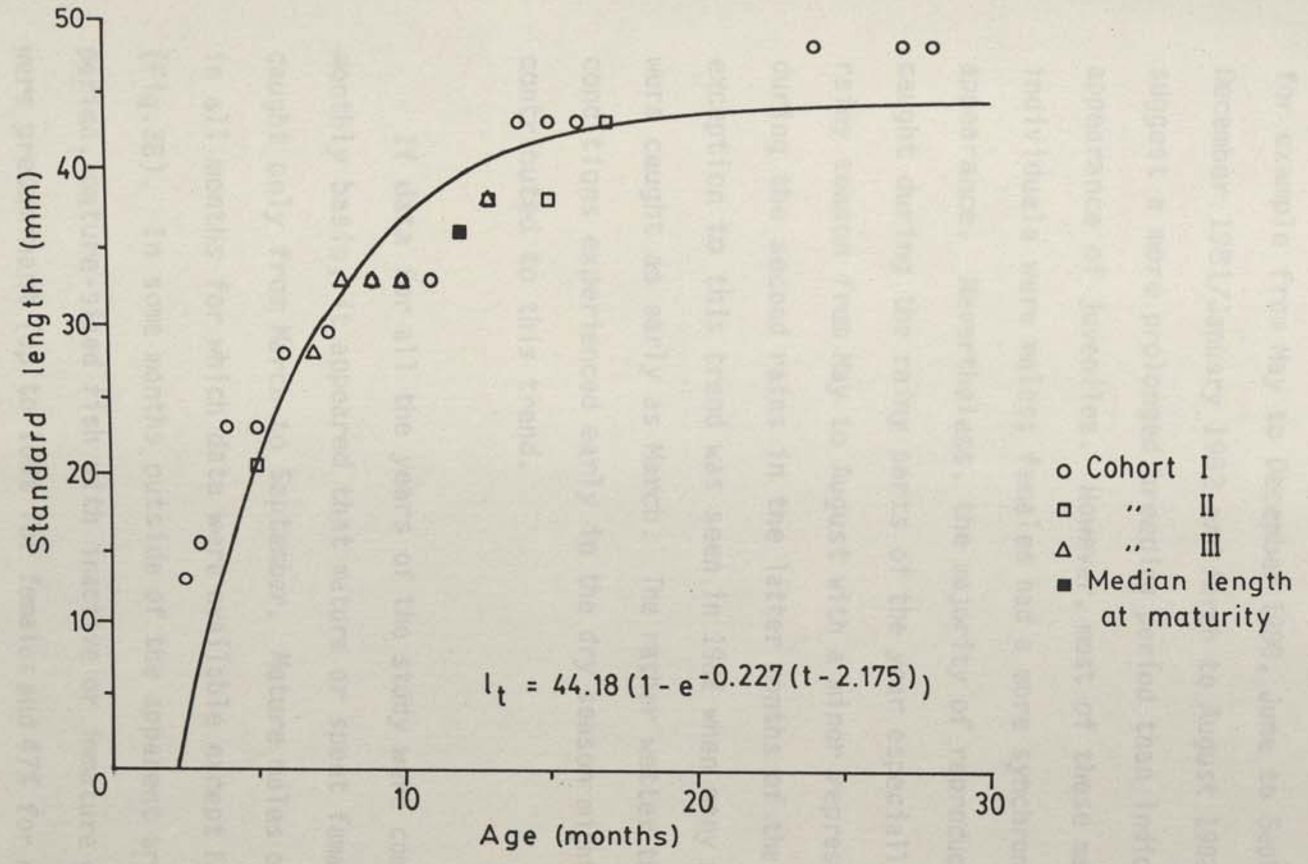


FIGURE 37: Growth curve for *G. sternicla* (males and females combined; curve fitted to von Bertalanffy equation).

suggesting an extremely regular annual reproductive cycle. The presence of mature specimens over more extended periods, for example from May to December 1980, June to September 1981, December 1981/January 1982 and March to August 1982, might suggest a more prolonged breeding period than indicated by the appearance of juveniles. However, most of these mature individuals were males; females had a more synchronised appearance. Nevertheless, the majority of reproductives were caught during the rainy parts of the year especially the main rainy season from May to August with a minor representation during the second rains in the latter months of the year. An exception to this trend was seen in 1982 when many reproductives were caught as early as March. The rather wetter than average conditions experienced early in the dry season might have contributed to this trend.

If data for all the years of the study were combined on a monthly basis, it appeared that mature or spent females were caught only from March to September. Mature males occurred in all months for which data were available except February (Fig.38). In some months outside of the apparent breeding period, mature-sized fish with inactive or immature gonads were predominant (up to 100% for females and 47% for males). The highest proportion of mature males and females was recorded in June/July. Spent females were found only in

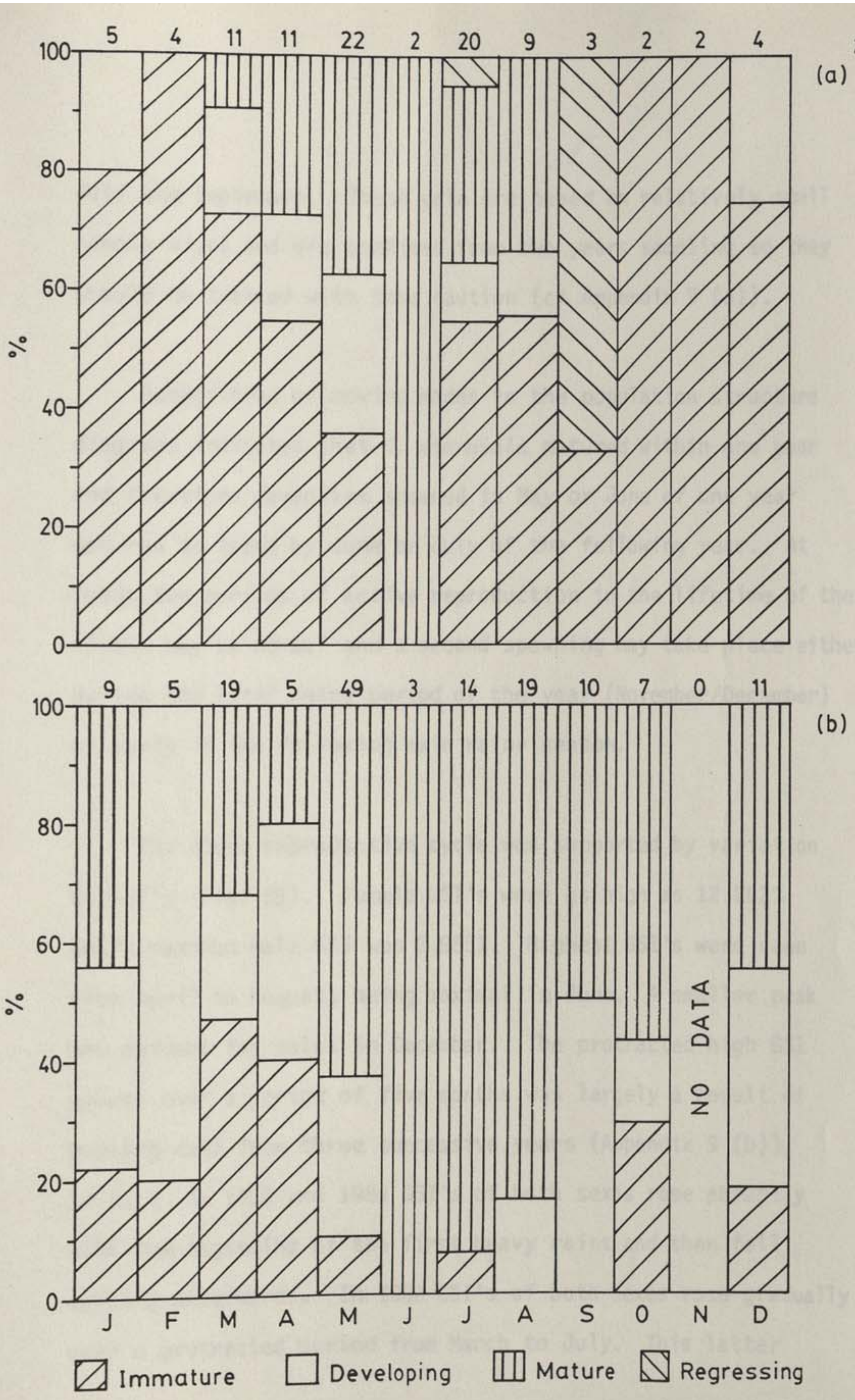


FIGURE 38: Monthly variation of gonad maturity stages for *G. sternicla* (a) females, and (b) males (numbers at top indicate sample sizes).

July and September. These data are based on relatively small sample sizes and are combined from two years sampling so they should be treated with some caution (cf. Appendix 9 (a)).

Recognition of moving modes in the population structure diagrams indicated that *G. sternicla* matured within one year and therefore juveniles spawned in May or June of one year matured to spawn by June or July of the following year. At least two periods of active reproduction in the lifetime of these fishes may be normal and a second spawning may take place either during the later rainy period of the year (November/December) or early in the following main rainy season.

The above reproductive cycle was supported by variation in GSI's (Fig. 39). Female GSI's were as high as 12.262% while maximum male GSI was 2.955%. Highest GSI's were seen from April to August, being maximal in June. A smaller peak was evident for males in December. The protracted high GSI values over a period of five months was largely a result of pooling data from three successive years (Appendix 9 (b)). In fact, in 1980 and 1981 GSI's of both sexes rose abruptly with the beginning of the first heavy rains and then fell quickly afterwards. In 1982 GSI's of both sexes rose gradually over a protracted period from March to July. This latter

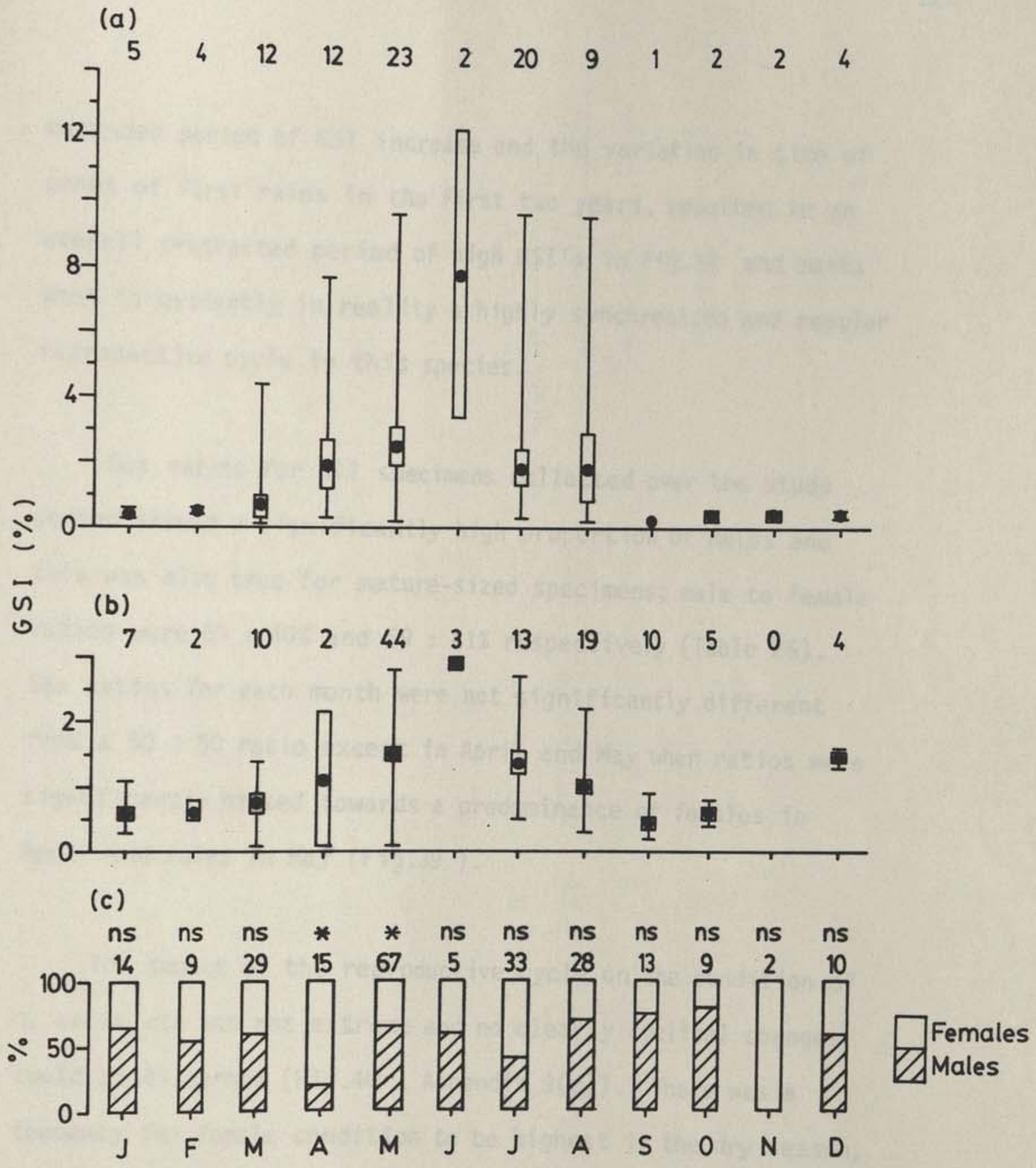


FIGURE 39: Monthly variation of GSI's for (a) females, and (b) males, and (c) sex ratios for G. sternicla (bars represent ranges, boxes represent ± 1 Standard Error; binomial test: ns - not significant, p>0.05; * - p<0.05; ** - p<0.01; *** - p<0.001; numbers at top indicate sample sizes).

extended period of GSI increase and the variation in time of onset of first rains in the first two years, resulted in an overall protracted period of high GSI's in Fig.39 and masks what is evidently in reality a highly synchronised and regular reproductive cycle in this species.

Sex ratios for all specimens collected over the study period showed a significantly high proportion of males and this was also true for mature-sized specimens; male to female ratios were 60 : 40% and 59 : 41% respectively (Table 25). Sex ratios for each month were not significantly different from a 50 : 50 ratio except in April and May when ratios were significantly biased towards a predominance of females in April and males in May (Fig.39).

The impact of the reproductive cycle on the condition of *G. sternicla* was not extreme and no clearly cyclical changes could be discerned (Fig.40 , Appendix 9(c)). There was a tendency for female condition to be highest in the dry season, decreasing gradually over the reproductive period when somatic condition decreased drastically relative to total condition. Variable fluctuations were apparent in the latter part of the year. Male condition was lowest in the dry season and increased immediately prior to breeding, during which time both somatic

TABLE 25: Sex ratios for the six fish species studied based on collections made over the study period.

	Male : Female Sex Ratio							
	All individuals				Mature-sized individuals			
Species	N	Ratio	%	χ^2	N	Ratio	%	χ^2
G. sternicla	276	1.51 : 1	60 : 40	11.36***	239	1.44 : 1	59 : 41	7.74**
C. riisei	465	1.12 : 1	53 : 47	1.57^{ns}	226	1.38 : 1	58 : 42	5.73*
A. bimaculatus	202	1.81 : 1	64 : 36	16.65***	24	1.18 : 1	54 : 46	0.17^{ns}
H. unilineatus	1152	0.95 : 1	49 : 51	0.68^{ns}	611	0.87 : 1	46 : 54	3.03^{ns}
C. aeneus	261	1.25 : 1	56 : 44	3.22^{ns}	240	1.22 : 1	55 : 45	2.40^{ns}
P. reticulata	1450	0.53 : 1	35 : 65	135.96***	1421	0.53 : 1	34 : 66	136.86***

N : Number of specimens
ns : Not significant, $p>0.05$
* : $p<0.05$
** : $p<0.01$
*** : $p<0.001$

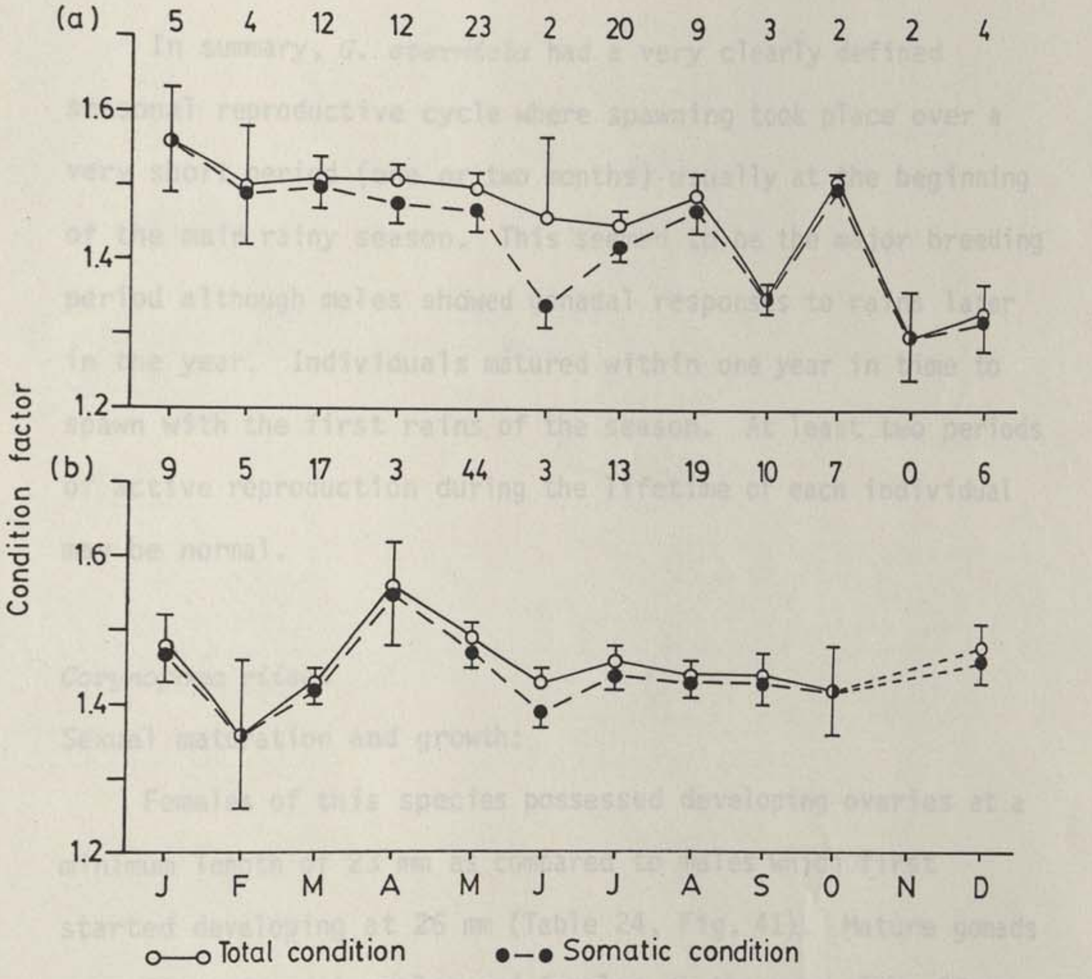


FIGURE 40: Monthly variation of total and somatic condition for *G. sternicla* (a) females, and (b) males (upper and lower bars represent 1 Standard Error for CFT and CFS respectively; numbers at top indicate sample sizes).

and total condition declined.

In summary, *G. sternicla* had a very clearly defined seasonal reproductive cycle where spawning took place over a very short period (one or two months) usually at the beginning of the main rainy season. This seemed to be the major breeding period although males showed gonadal responses to rains later in the year. Individuals matured within one year in time to spawn with the first rains of the season. At least two periods of active reproduction during the lifetime of each individual may be normal.

Corynopoma riisei

Sexual maturation and growth:

Females of this species possessed developing ovaries at a minimum length of 23 mm as compared to males which first started developing at 26 mm (Table 24, Fig. 41). Mature gonads were first found in males and females at the same size, 26 mm. Having attained a mature size, the majority of females (57%) had mature or spent gonads. However, many males grew to quite large sizes before becoming reproductively active. Several large males (up to 34 mm) had immature gonads and incompletely developed secondary sexual characters, thus suggesting delayed first reproduction. Only 38% of all the males of mature size

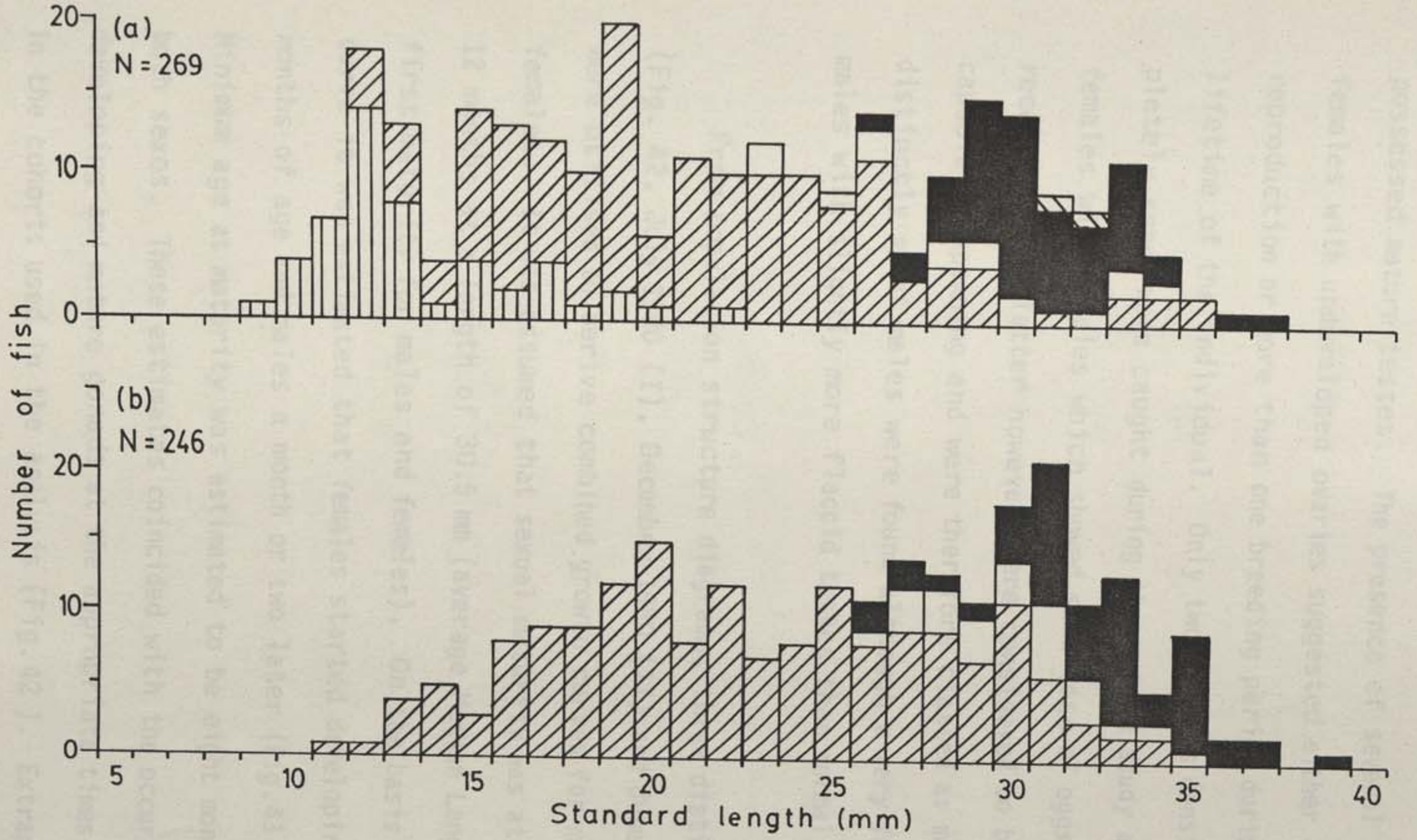


FIGURE 41: The relationship between gonad maturity stages and size for *C. riisei* (a) females and juveniles, and (b) males (key as for Figure 35).

possessed mature testes. The presence of several large females with undeveloped ovaries suggested either delayed reproduction or more than one breeding period during the lifetime of the individual. Only two females considered completely spent were caught during the entire study although many females with ovaries which showed some loss of eggs were recorded. The latter however, were considered to be still capable of spawning and were therefore classed as mature. No distinctly spent males were found although a very few large males with slightly more flaccid testes than normal were noted.

From population structure diagrams, three distinct cohorts (Fig. 42, July 1980 (I), December 1980 (II) and June 1981 (III) were utilised to derive combined growth curves for males and females. It was assumed that sexual maturity was attained in 12 months at a length of 30.5 mm (average Median Length at first maturity for males and females). On the basis of this curve it was estimated that females started developing by six months of age and males a month or two later (Fig.43). Minimum age at maturity was estimated to be eight months for both sexes. These estimates coincided with the occurrence of developing and mature gonads at the appropriate times and lengths in the cohorts used in the analysis (Fig.42). Extrapolation of the growth curve indicated a maximum life span of two years

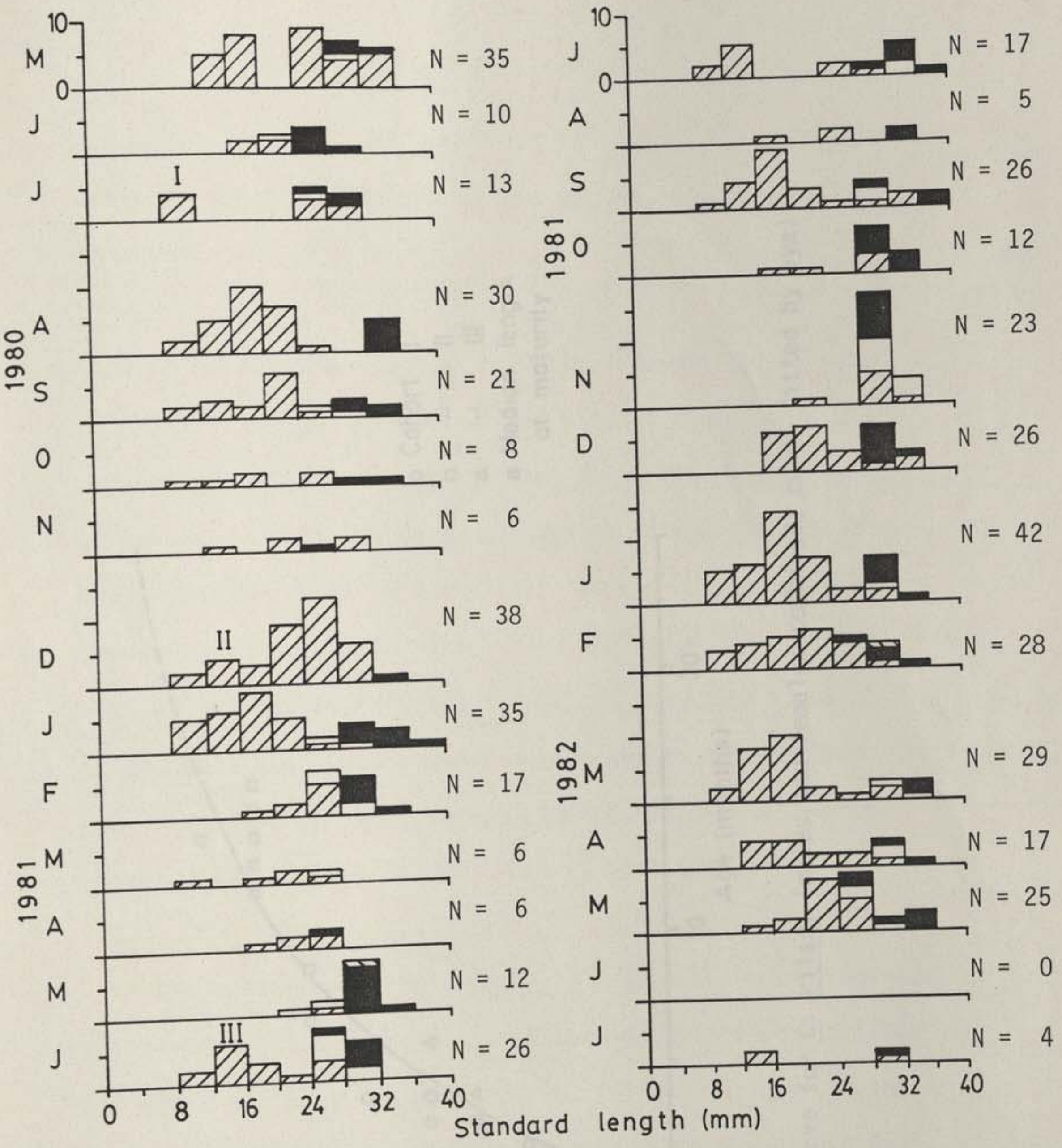


FIGURE 42: Monthly variation of population structure and the occurrence of gonad maturity stages for *C. riisei* (key as for Figure 36; I-III: cohorts used in growth analysis).

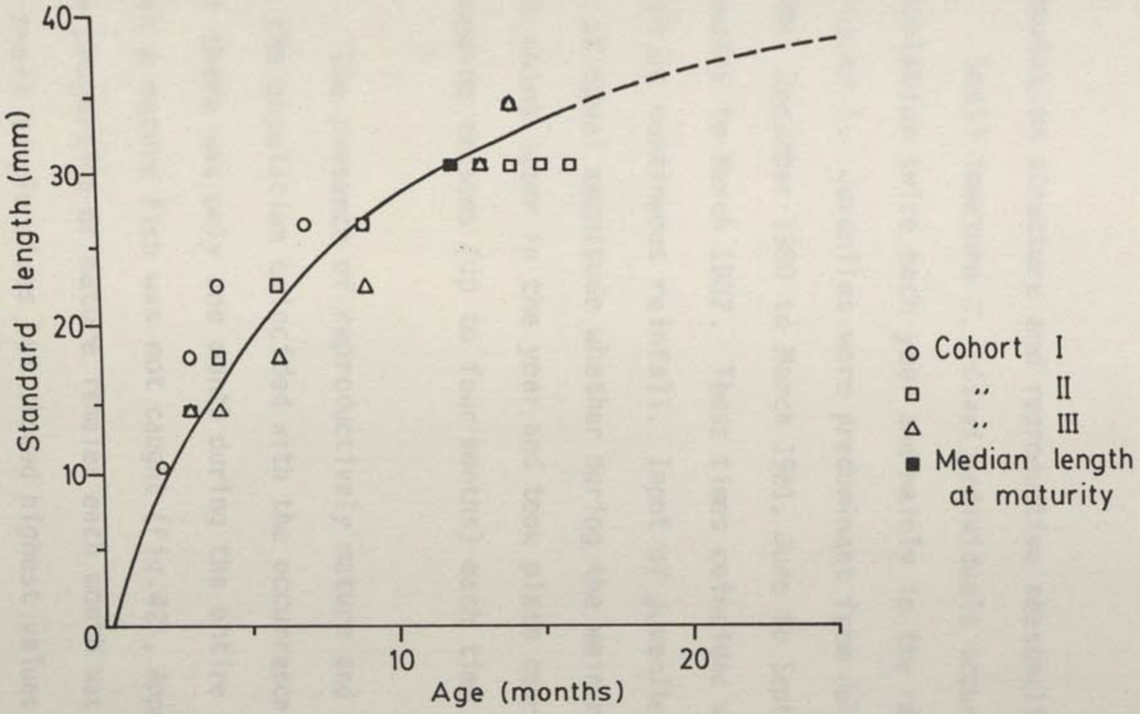


FIGURE 43: Growth curve for *C. riisei* (males and females combined; curve fitted by eye).

for males and about 21 months for females. Data were insufficient to determine the parameters of the von Bertalanffy equation.

Population structure and reproductive seasonality:

Small immature *C. riisei* individuals occurred in the population twice each year and mainly in the rainy seasons (Fig.42). Juveniles were predominant from July to October 1980, December 1980 to March 1981, June to September 1981 and January to March 1982. These times coincided with periods of high or continuous rainfall. Input of juveniles appeared to be of equal magnitude whether during the main rainy season or the rains later in the year and took place over prolonged breeding seasons (up to four months) each time.

The presence of reproductively mature and spent individuals in the population coincided with the occurrence of juveniles but there was only one month during the entire study period when a mature fish was not caught (Fig.42 , Appendix 10 (a)). The proportion of mature females each month was irregular due to small sample sizes but showed highest values (100%) in January and April, and was more than 50% in July, August and October (Fig.44). Proportions of mature males were highest in May, June, August and October (more than 50% of mature-

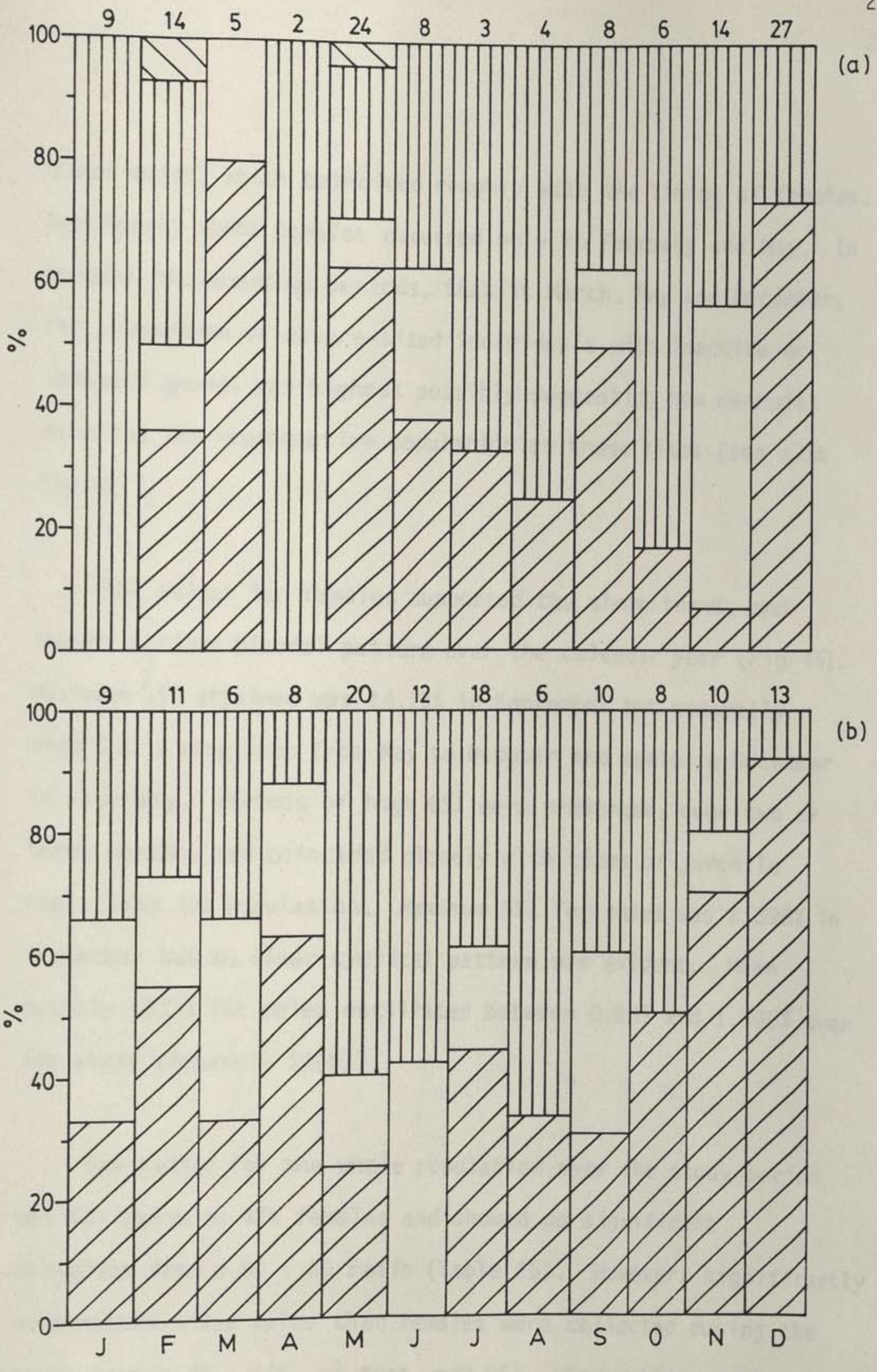


FIGURE 44: Monthly variation of gonad maturity stages for *C. riisei* (a) females, and (b) males (key as for Figure 38).

sized males) which coincided roughly with the timing of females. Completely spent females occurred only in February and May. In between the breeding periods, that is March, May and December, the proportion of mature-sized individuals with inactive or immature gonads was highest possibly suggesting new recruits entering the reproductive population at these times (see also Fig.42).

GSI values for females supported the above trends and showed a clear bimodal pattern over the calendar year (Fig. 45). Maximum GSI attained was 14.13% in September but generally high GSI's were seen from May to October and again in December to February. Periods of high GSI were prolonged, over two or three months, and coincided closely with times of juvenile input into the population. Maximum GSI for males was 2.398% in September but no clear cyclical pattern was evident. Mean monthly GSI's for males oscillated between 0.887 and 1.495% over the study (Appendix 10(b)).

Sex ratios for the whole population over the study period was 53% males to 47% females and showed no significant deviation from a 50 : 50 ratio (Table 25). However, significantly more mature-sized males than females were collected during the study (ratio 58 : 42%, χ^2 test, $p<0.05$). Sex ratios varied

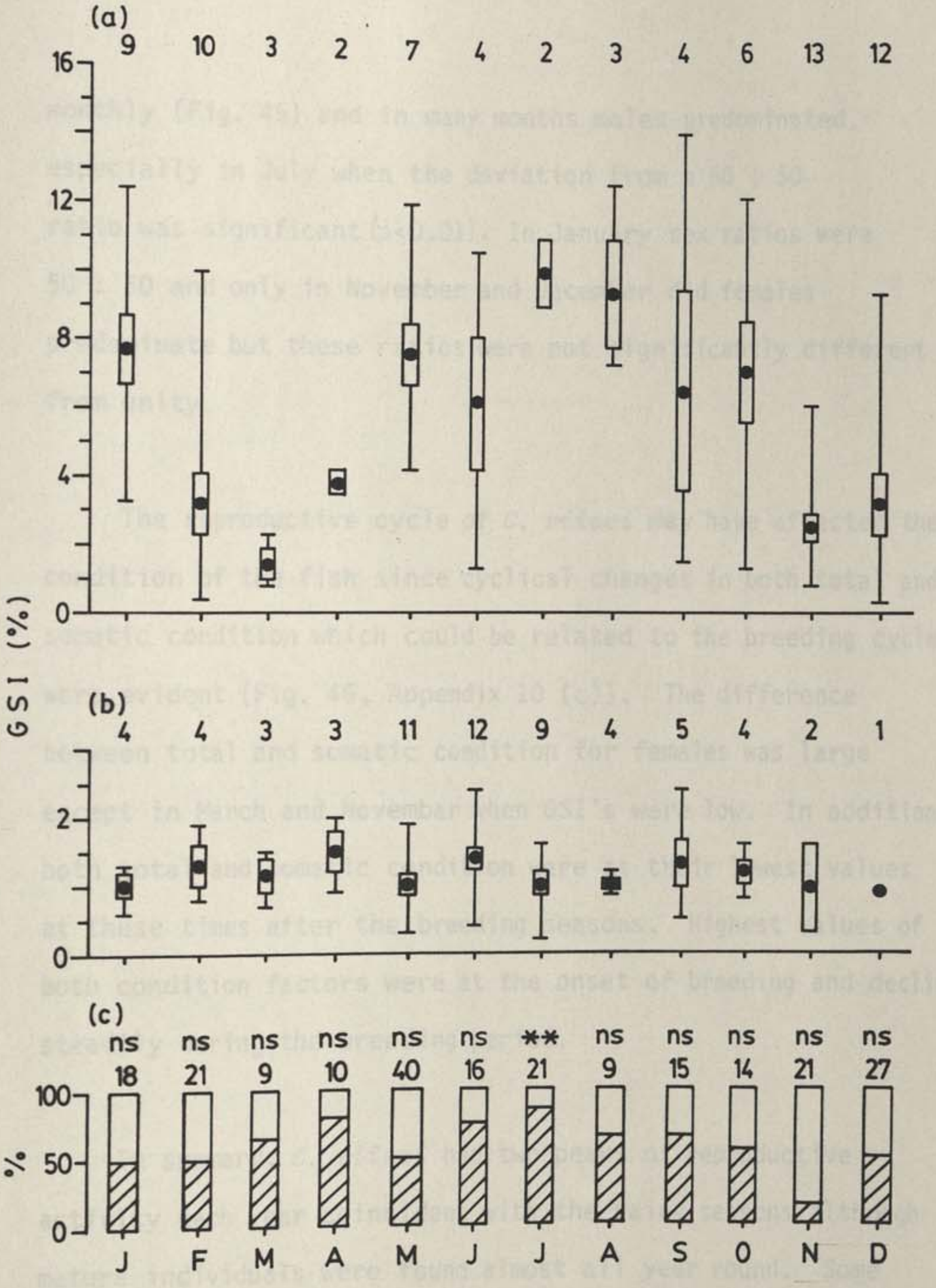


FIGURE 45: Monthly variation of GSI's for (a) females, and (b) males, and (c) sex ratios for *C. riisei* (key as for Figure 39).

monthly (Fig. 45) and in many months males predominated, especially in July when the deviation from a 50 : 50 ratio was significant ($p<0.01$). In January sex ratios were 50 : 50 and only in November and December did females predominate but these ratios were not significantly different from unity.

The reproductive cycle of *C. riisei* may have affected the condition of the fish since cyclical changes in both total and somatic condition which could be related to the breeding cycle were evident (Fig. 46, Appendix 10 (c)). The difference between total and somatic condition for females was large except in March and November when GSI's were low. In addition, both total and somatic condition were at their lowest values at these times after the breeding seasons. Highest values of both condition factors were at the onset of breeding and declined steadily during the breeding period.

In summary, *C. riisei* had two peaks of reproductive activity each year coincident with the rainy seasons although mature individuals were found almost all year round. Some juveniles which had been spawned in the earlier part of the main rainy season (May/June) could have matured by the second rainy period but it is likely that most would have matured

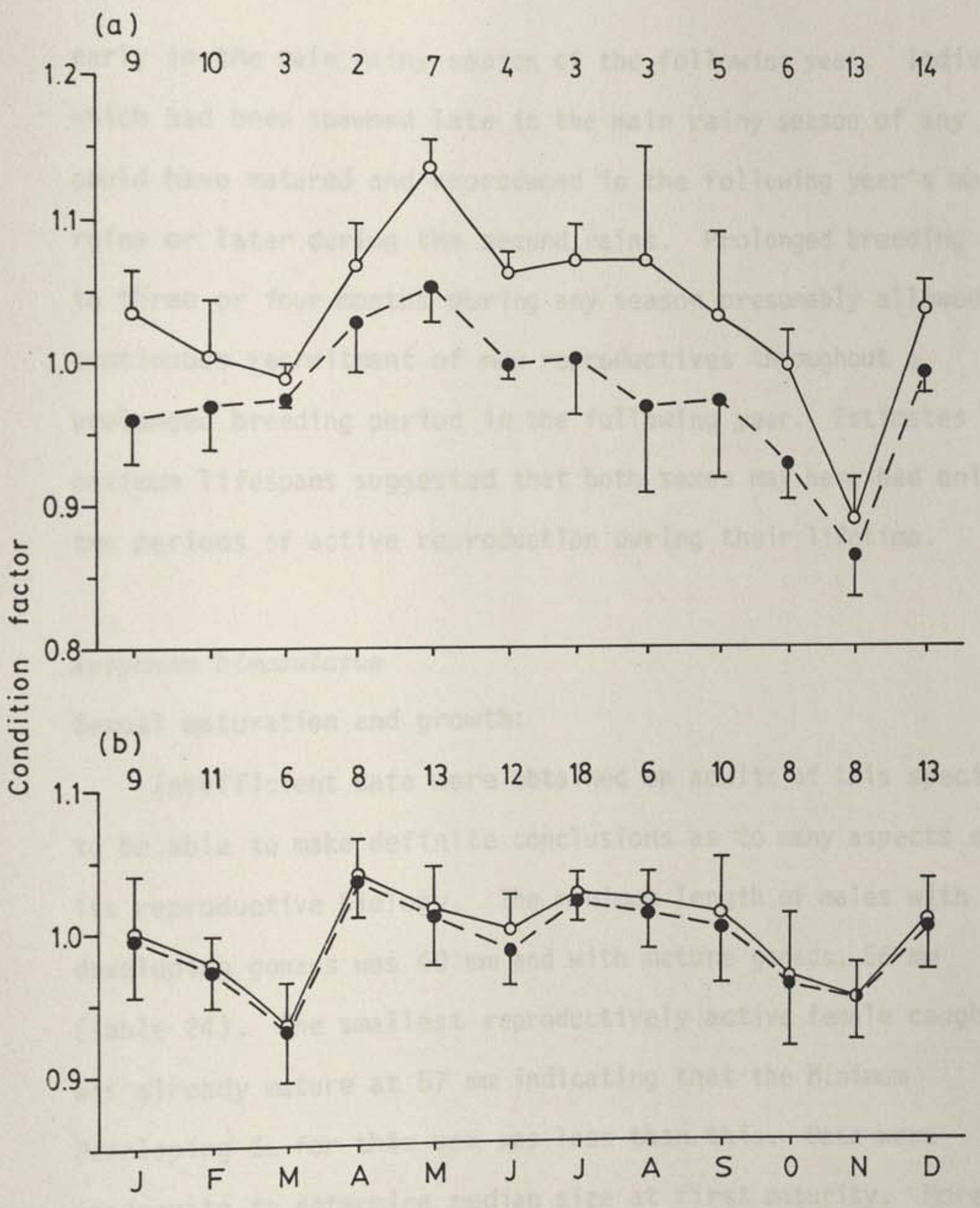


FIGURE 46: Monthly variation of total and somatic condition for *C. riisei* (a) females, and (b) males (key as for Figure 40).

early in the main rainy season of the following year. Individuals which had been spawned late in the main rainy season of any year could have matured and reproduced in the following year's main rains or later during the second rains. Prolonged breeding up to three or four months during any season presumably allowed continuous recruitment of new reproductives throughout a prolonged breeding period in the following year. Estimates of maximum lifespans suggested that both sexes may have had only two periods of active reproduction during their lifetime.

Astyanax bimaculatus

Sexual maturation and growth:

Insufficient data were obtained on adults of this species to be able to make definite conclusions as to many aspects of its reproductive biology. The minimum length of males with developing gonads was 40 mm and with mature gonads, 56 mm (Table 24). The smallest reproductively active female caught was already mature at 57 mm indicating that the Minimum Developing SL for this sex was less than this. Data were inadequate to determine median size at first maturity. More than 50% of the males of mature size were found with mature testes but only one mature female was noted from 11 of mature size (Fig. 47). No spent adults were caught.

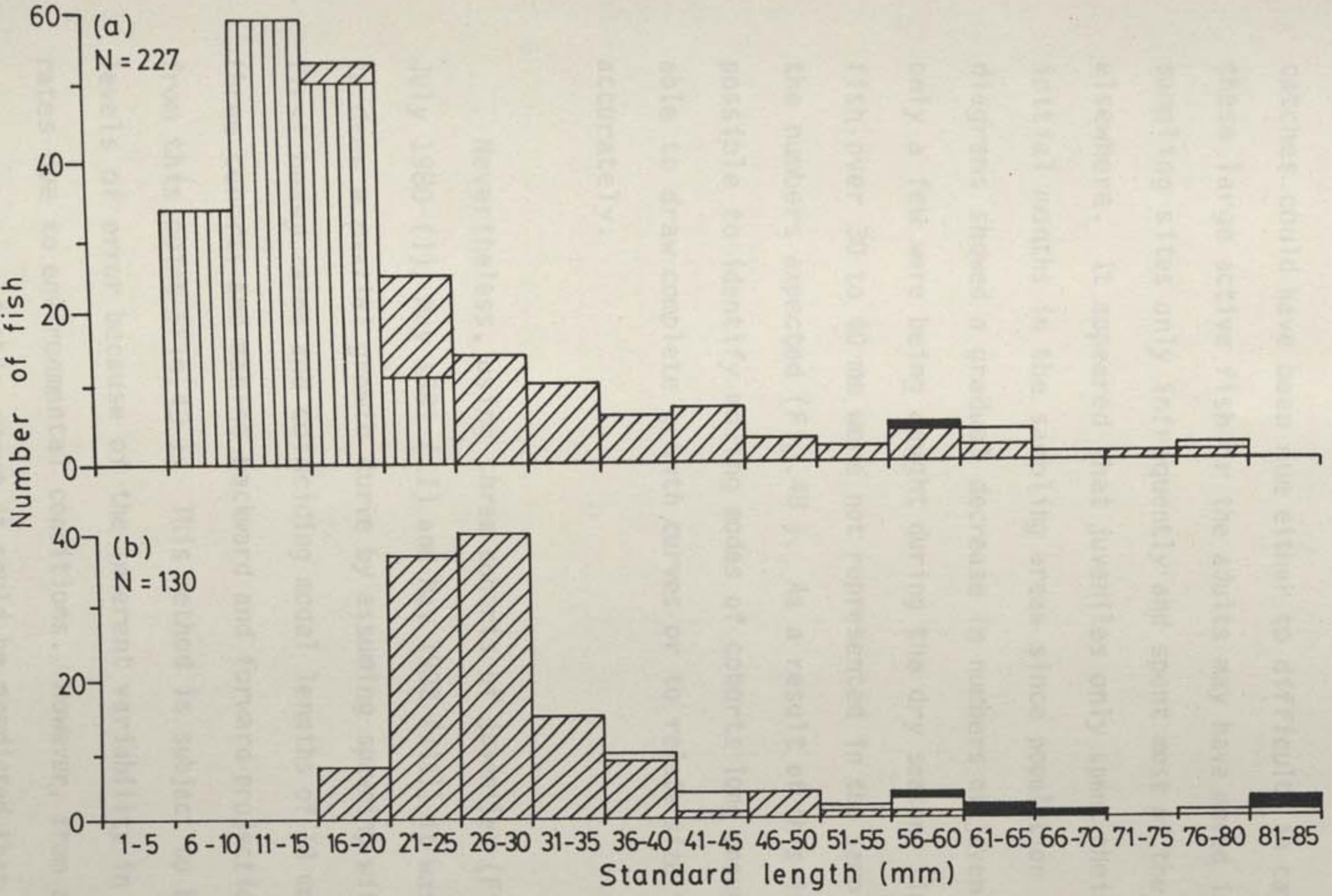


FIGURE 47: The relationship between gonad maturity stages and size for A. bimaculatus (a) females and juveniles, and (b) males (key as for Figure 35).

The predominance of juveniles and lack of adults in catches could have been due either to difficulty in catching these large active fish or the adults may have moved into the sampling sites only infrequently and spent most of their time elsewhere. It appeared that juveniles only spent their initial months in the sampling areas since population structure diagrams showed a gradual decrease in numbers of juveniles until only a few were being caught during the dry season. Immature fish over 30 to 40 mm were not represented in the samples in the numbers expected (Fig.48). As a result of this it was not possible to identify moving modes of cohorts long enough to be able to draw complete growth curves or to relate size to age accurately.

Nevertheless, using three cohorts of juveniles (Fig.48 , July 1980 (I), May 1981 (II) and May 1982 (III)) it was possible to draw a partial growth curve by assuming spawning with the first heavy rains and coinciding modal lengths of 18 mm for all three cohorts and making backward and forward projections from this point (Fig.49). This method is subject to high levels of error because of the inherent variability in growth rates due to environmental conditions. However, from a general extrapolation of this curve it could be predicted that maturity might be attained at approximately 16 months and maximum

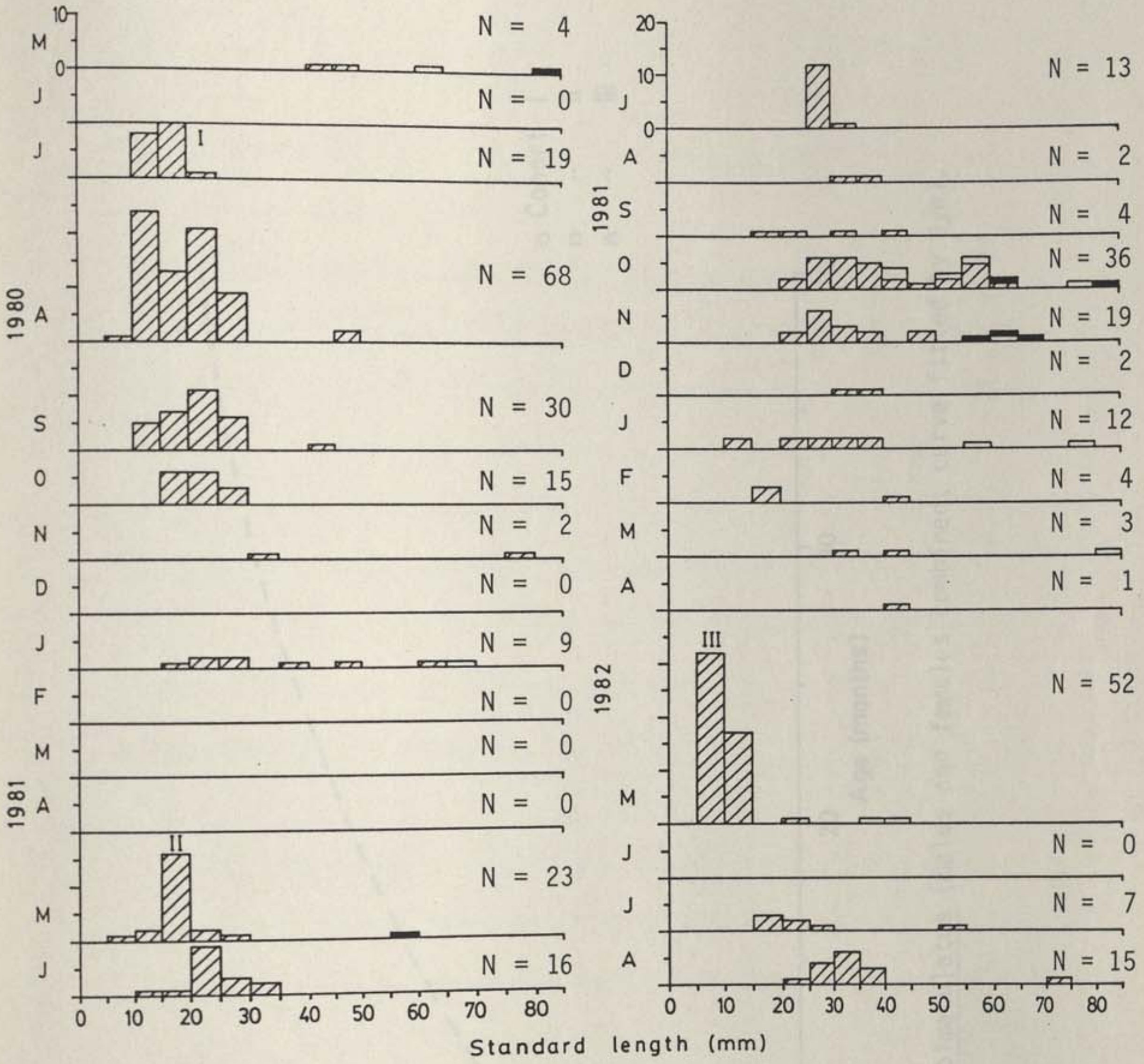


FIGURE 48: Monthly variation of population structure and the occurrence of gonad maturity stages for A. bimaculatus (key as for Figure 36; I-III: cohorts used in growth analyses).

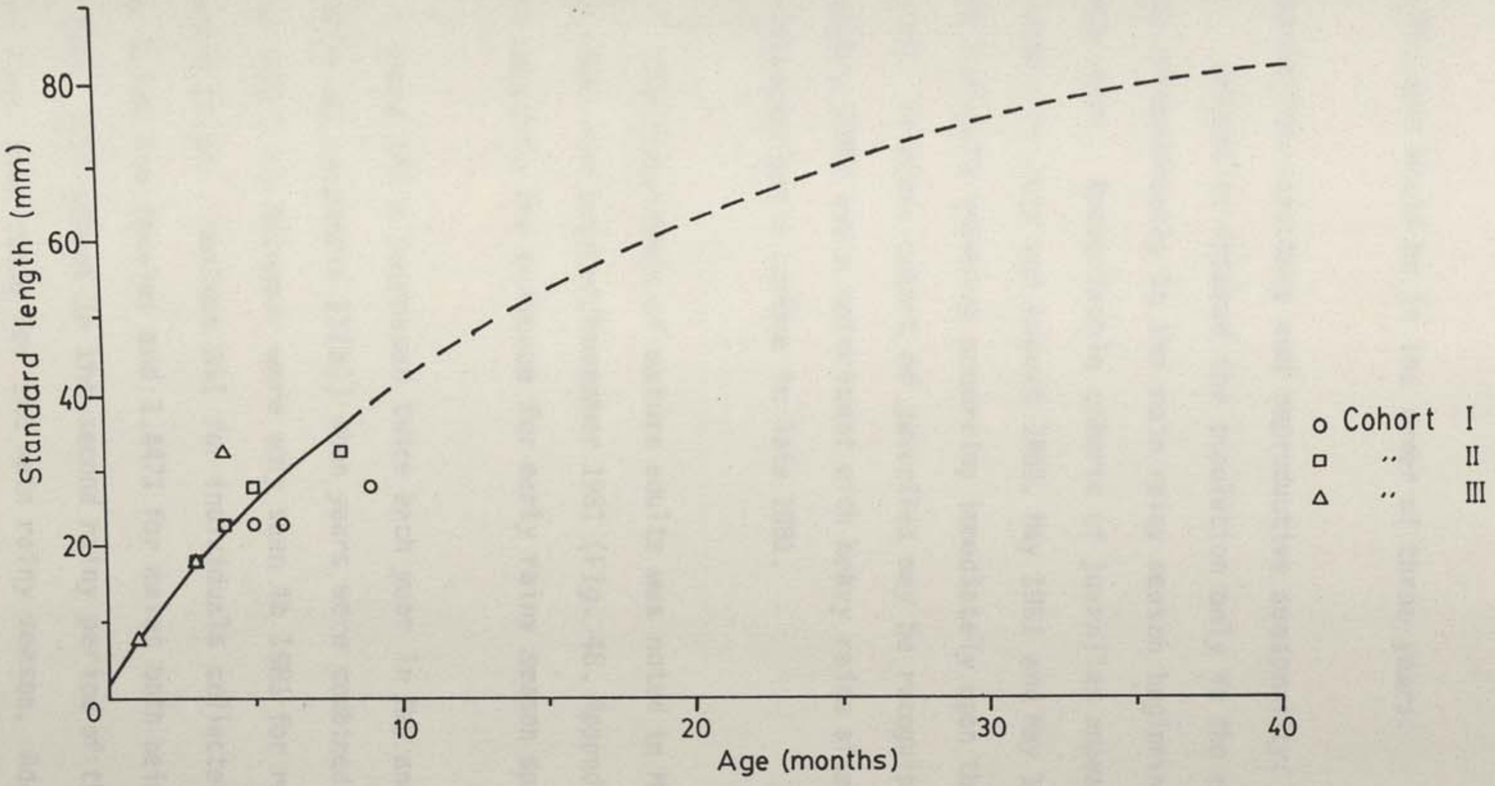


FIGURE 49: Growth curve for _A_. _bimaculatus_ (males and females combined; curve fitted by eye).

lifespans would be in the order of three years.

Population structure and reproductive seasonality:

Juveniles entered the population only in the rainy seasons and predominantly in the main rainy season beginning May/June each year. Recognisable cohorts of juveniles appeared in catches in July and August 1980, May 1981 and May 1982 (Fig.48) and indicate spawning occurring immediately upon the first rains. A minor cohort of juveniles may be recognised in January 1982 again coincident with heavy rains after a pronounced petit carême in late 1981.

The occurrence of mature adults was noted in May 1980, May 1981 and October/November 1981 (Fig. 48, Appendix 11(a)) and supports the evidence for early rainy season spawning.

Mean GSI's increased twice each year in May and November (Table 26, Appendix 11(b)) when years were combined. However, high GSI's in November were only seen in 1981 for reasons stated above. Maximum GSI for individuals collected monthly was 4.49% for females and 1.447% for males both being recorded in May. GSI values in the second rainy period of the year were less than those for the main rainy season. Additional females with well developed gonads were collected in June 1985

TABLE 26: Monthly variation of GSI's for *A. bimaculatus* (years combined).

Month	Female GSI (%)			Male GSI (%)		
	Mean	Range	N	Mean	Range	N
January	0.227	0.193-0.261	2	0.515	0.287-0.742	2
March	-	-	0	0.588	-	1
May	2.813	1.135-4.490	2	1.447	-	1
August	0.215	-	1	-	-	0
October	0.673	0.110-3.180	6	0.921	0.840-0.994	3
November	0.937	0.127-1.746	2	1.066	0.723-1.409	2

and June 1986 and GSI's of these specimens ranged from 6.77 to 14.80% (fresh weights).

Numbers of mature-sized fish collected monthly were too few to see any consistent trends or to make any definite statements about sex ratios (Appendix 11(b)). There appeared to be a predominance of females during times of breeding. For the entire population (including immature individuals) caught over the whole study period, the male : female sex ratio was 64 : 36% and showed a highly significant deviation from a 50 : 50 ratio (Table 25, χ^2 test, $p<0.001$). However, sex ratios for mature-sized individuals showed no significant difference from unity ($p>0.05$).

Trends in variation of condition factors were not very clear owing to the lack of data (Table 27, Appendix 11(c)). However, it appeared that female total and somatic condition increased in the latter half of the year after a minimum in May and were maximal in August. Male condition was maximal in January and showed minimal values during the breeding period.

In summary, *A. bimaculatus* appeared to breed after a relatively long period of growth up to two years. Breeding took place at the very beginning of the main rainy season in

TABLE 27: Monthly variation of mean total and somatic condition factors for *A. bimaculatus* (years combined).

	Females			Males		
Month	CFT(%)	CFS(%)	N	CFT(%)	CFS(%)	N
January	1.387	1.384	2	1.471	1.464	2
March	-	-	0	1.219	1.212	1
May	1.378	1.337	2	1.123	1.106	1
August	1.575	1.572	1	-	-	0
October	1.444	1.435	6	1.379	1.369	4
November	1.449	1.436	2	1.347	1.332	2

May or June and may not have lasted longer than one or two months judging from the synchronised appearance of juveniles and mature individuals in the population at these times. The major reproductive period seemed to be during the main rainy season and under certain conditions a second, minor breeding period might have occurred later in the year coincident with the second rains. Each individual might therefore have had at least one, possibly two, active periods of reproduction each year giving a total of at least two to three active breeding periods during its lifetime.

Hemigrammus unilineatus

Sexual maturation and growth:

The majority of specimens of this species which were collected were immature individuals (Fig. 50). Minimum lengths for developing fish were 20 mm for males and 23 mm for females (Table 24). Females also became sexually mature at a larger size than males: 25 mm as compared to 21 mm for males. Median length at first maturity was 26 mm for males and 29 mm for females. Of the females of mature size, 50% possessed mature gonads while 17% had developing ovaries, whereas of the mature-sized males, only 33% had mature gonads and 40% were developing. By 26 mm in length all males had either developing or mature testes but many large females (up to 35 mm) were still immature. This suggested either delayed reproduction in females or they

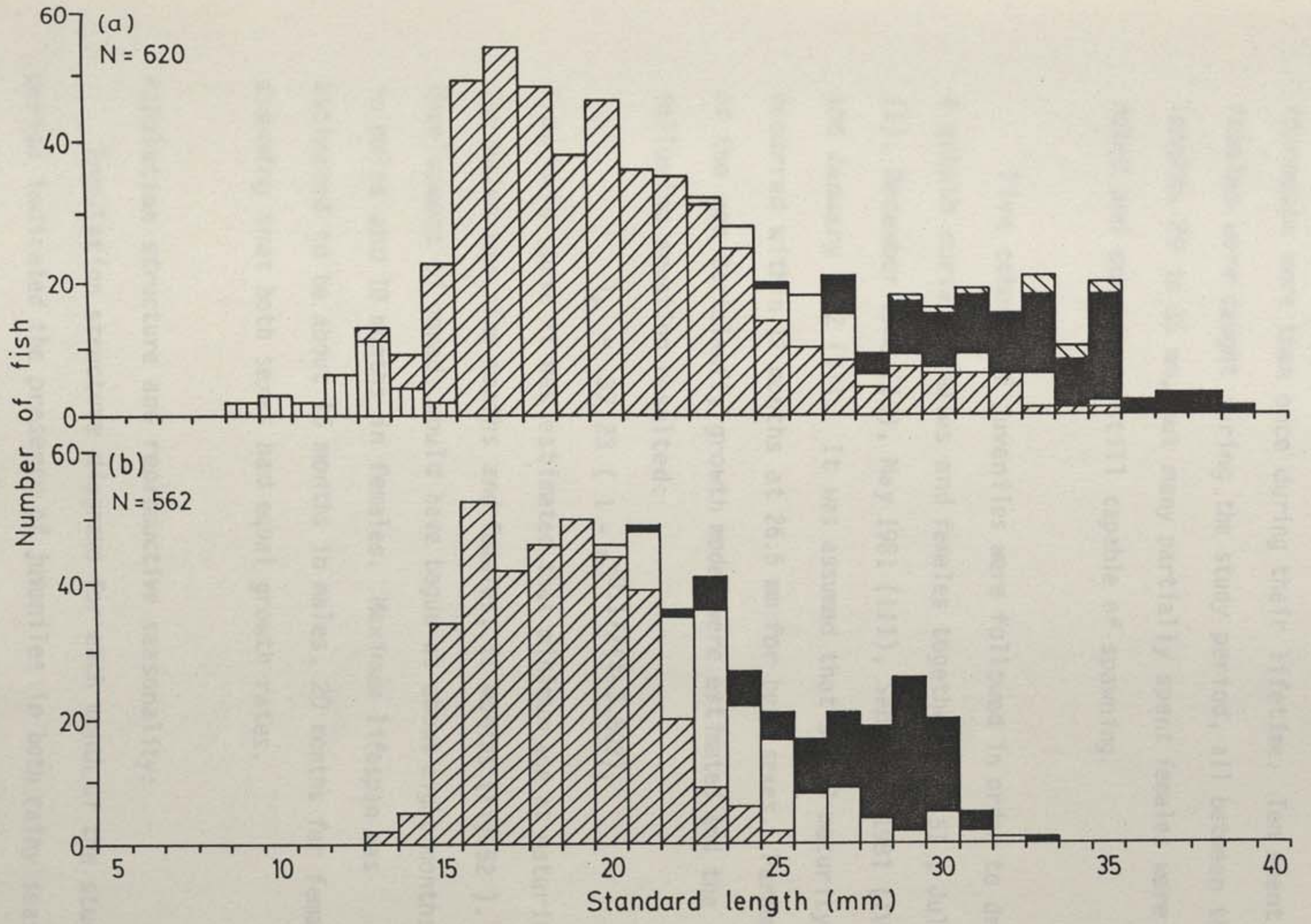


FIGURE 50: The relationship between gonad maturity stages and size for H. unilineatus (a) females and juveniles, and (b) males (key as for Figure 35).

reproduce more than once during their lifetime. Ten spent females were caught during the study period, all between the lengths 29 to 35 mm, but many partially spent females were noted and considered still capable of spawning.

Five cohorts of juveniles were followed in order to draw a growth curve for males and females together (Fig.51 , July 1980 (I), December 1980 (II), May 1981 (III), September 1981 (IV) and January 1982 (V)). It was assumed that sexual maturity occurred within 12 months at 26.5 mm for both sexes. Parameters of the von Bertalanffy growth model were estimated and the following equation resulted:

$$l_t = 37.23 (1 - e^{-0.177(t-3.802)})$$

From this curve it was estimated that minimum age at maturity for males was nine months and females, 11 months (Fig.52). Development of gonads would have begun at about eight months in males and 10 months in females. Maximum lifespan was estimated to be about 16 months in males, 20 months for females assuming that both sexes had equal growth rates.

Population structure and reproductive seasonality:

Population structure diagrams for each month of the study period indicated the presence of juveniles in both rainy seasons of each year (Fig.51). Small immature individuals were caught

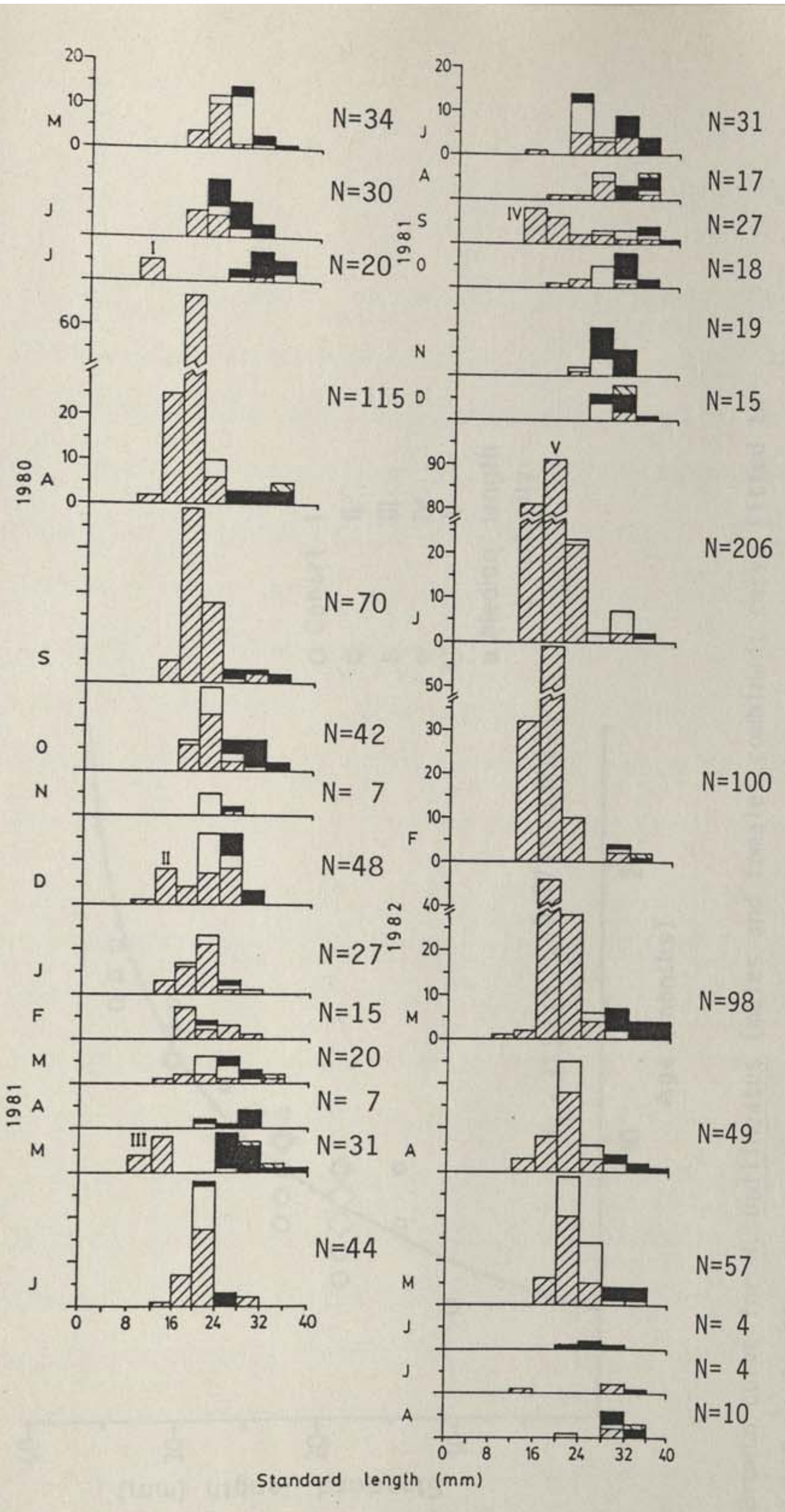


FIGURE 51: Monthly variation of population structure and the occurrence of gonad maturity stages for *H. unilineatus* (key as for Figure 36; I-V: cohorts used in growth analyses).

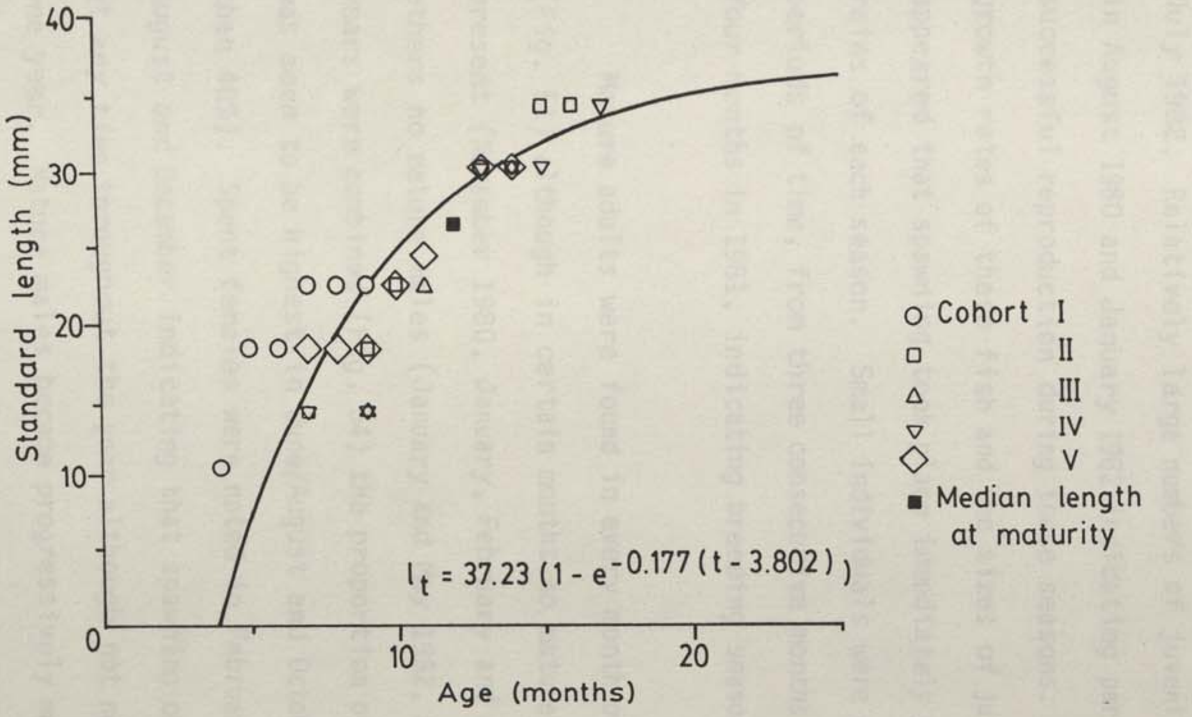


FIGURE 52: Growth curve for *H. unilineatus* (males and females combined; curve fitted to von Bertalanffy equation).

in July to September, and December 1980/January 1981, January, March, May to July, and September 1981 and January to March and July 1982. Relatively large numbers of juveniles were caught in August 1980 and January 1982 indicating particularly successful reproduction during these seasons. Considering the growth rates of these fish and the sizes of juveniles caught, it appeared that spawning took place immediately upon the first rains of each season. Small individuals were caught over varying periods of time, from three consecutive months in 1980 to over four months in 1981, indicating breeding seasons of these lengths.

Mature adults were found in every month of the study period (Fig. 51) although in certain months no mature females were present (November 1980, January, February and June 1981) and in others no mature males (January and May 1982, Fig. 53). When all years were combined (Fig. 54) the proportion of mature females was seen to be highest in June/August and October/November (more than 40%). Spent females were noted in February, March, May, August and December indicating that spawning could have occurred at any time throughout the year although not necessarily in any one year. Mature males became progressively more dominant from January to July when 54% of males of Minimum Developing SL were reproductively active. Proportions of mature males gradually decreased until September then increased in October and November again. It was noted that proportions of males and females with

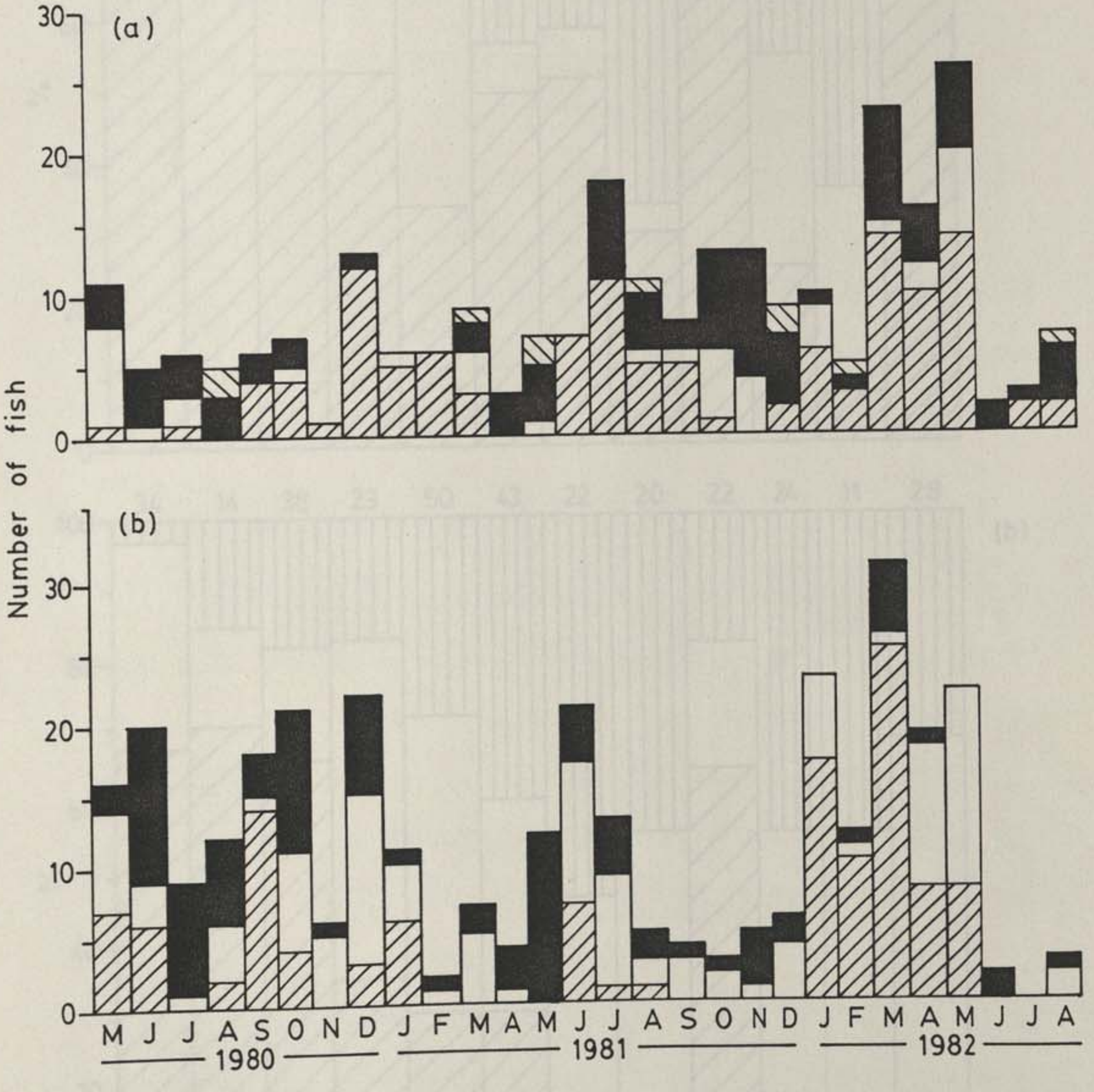


FIGURE 53: Monthly variation of gonad maturity stages for *H. unilineatus* (a) females, and (b) males over the whole study period (key as for Figure 35).

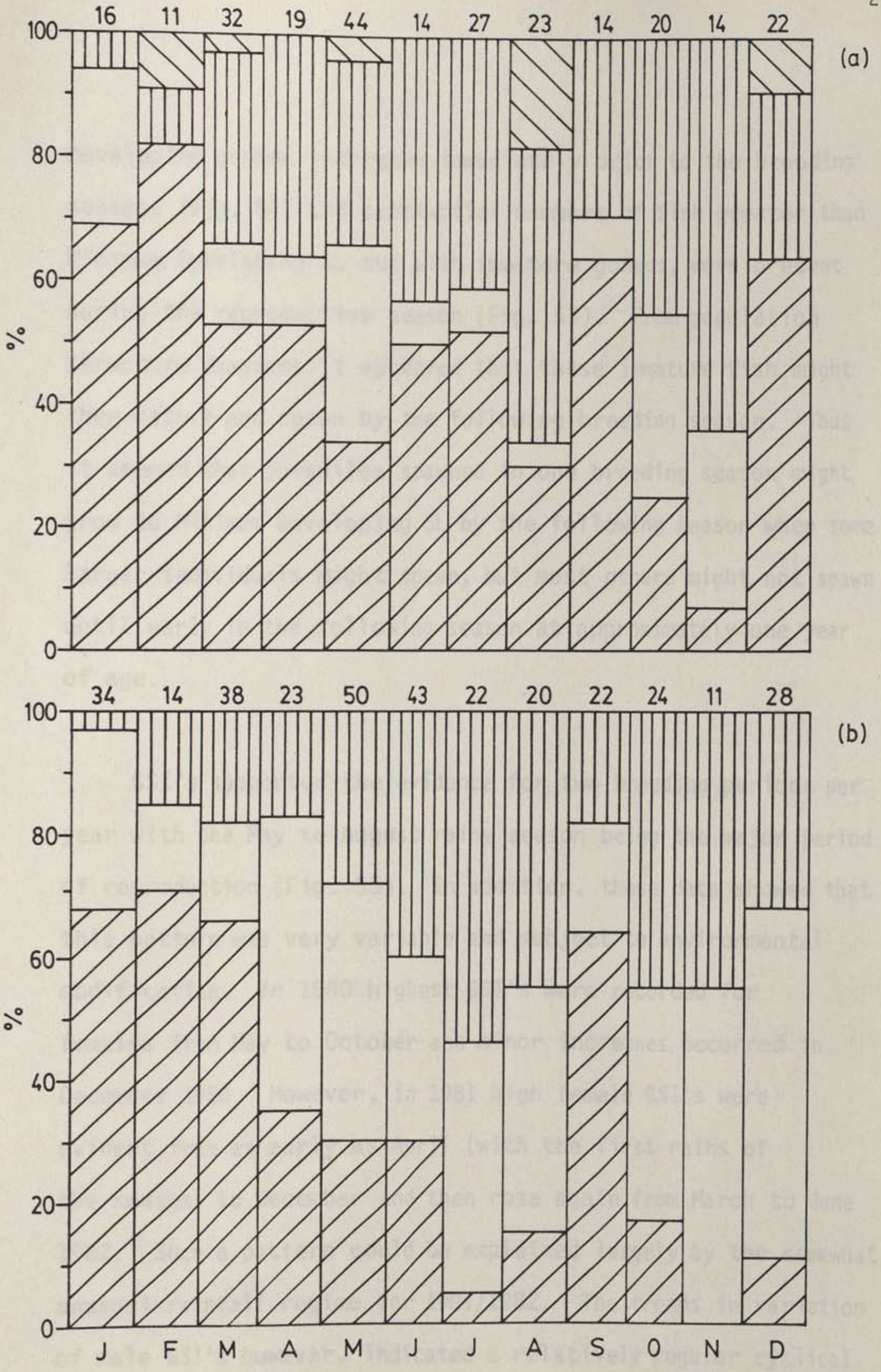


FIGURE 54: Monthly variation of gonad maturity stages for *H. unilineatus* (a) females, and (b) males over the calendar year (key as for Figure 38).

developing gonads increased immediately prior to the breeding seasons (Fig. 54) and substantial numbers of fish greater than Minimum Developing SL but with immature gonads, were present during the reproductive season (Fig. 53). From population structure diagrams it appeared that these immature fish might then mature and spawn by the following breeding season. Thus it seemed that juveniles spawned in one breeding season might grow to Minimum Developing SL by the following season when some larger individuals might spawn, but most others might not spawn until early in the following season at approximately one year of age.

GSI's supported the evidence for two breeding periods per year with the May to August rainy season being the major period of reproduction (Fig. 55). In addition, these data showed that this pattern was very variable and subject to environmental modification. In 1980 highest GSI's were recorded for females from May to October and minor increases occurred in December 1980. However, in 1981 high female GSI's were evident from as early as April (with the first rains of the season) to December and then rose again from March to June 1982. Such a pattern could be explained largely by the somewhat unusual rainfall regime for 1981/1982. The trends in variation of male GSI's however, indicated a relatively regular cyclical

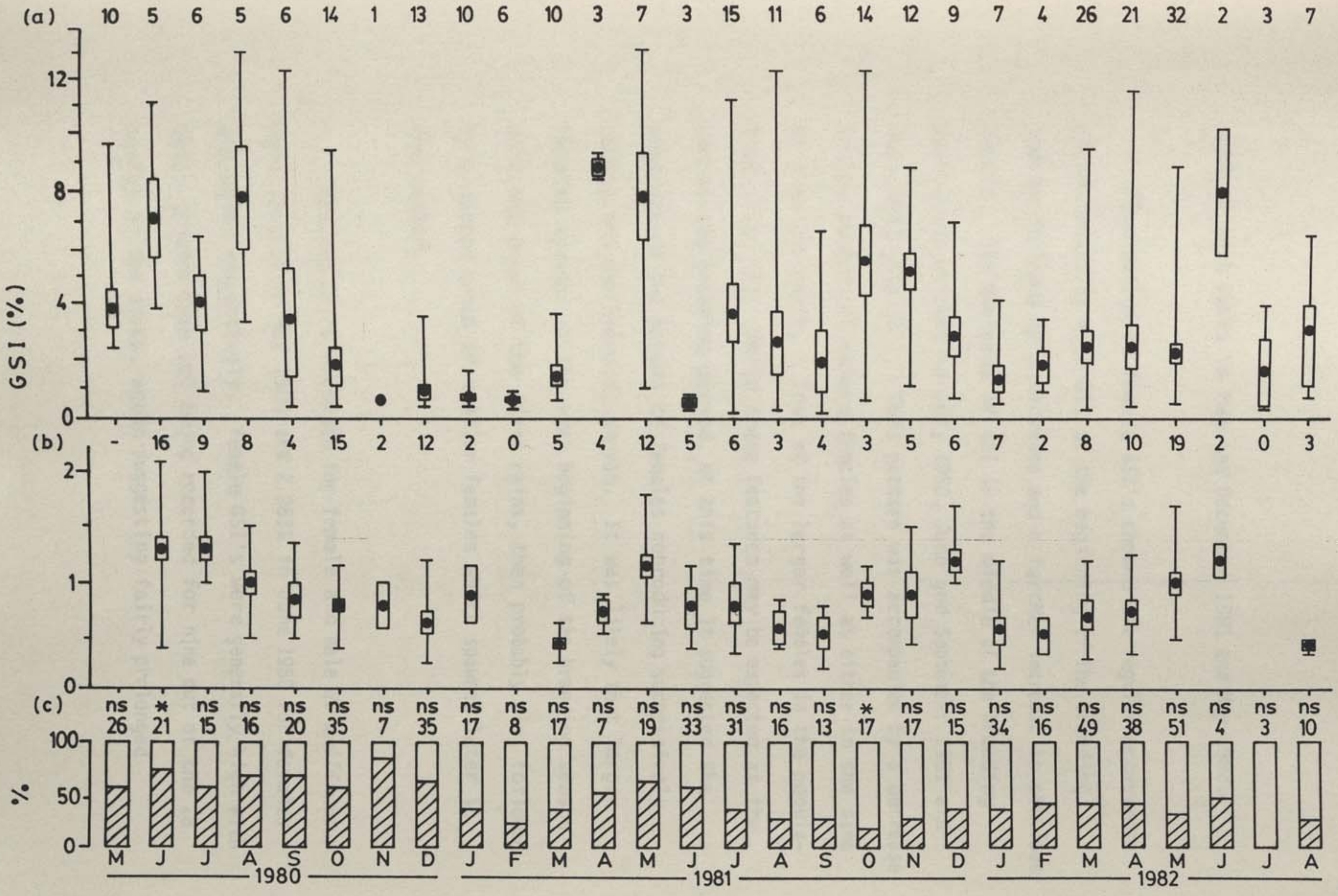


FIGURE 55: Monthly variation of GSI's for (a) females, and (b) males, and (c) sex ratios for *H. unilineatus* over the whole study period (key as for Figure 39).

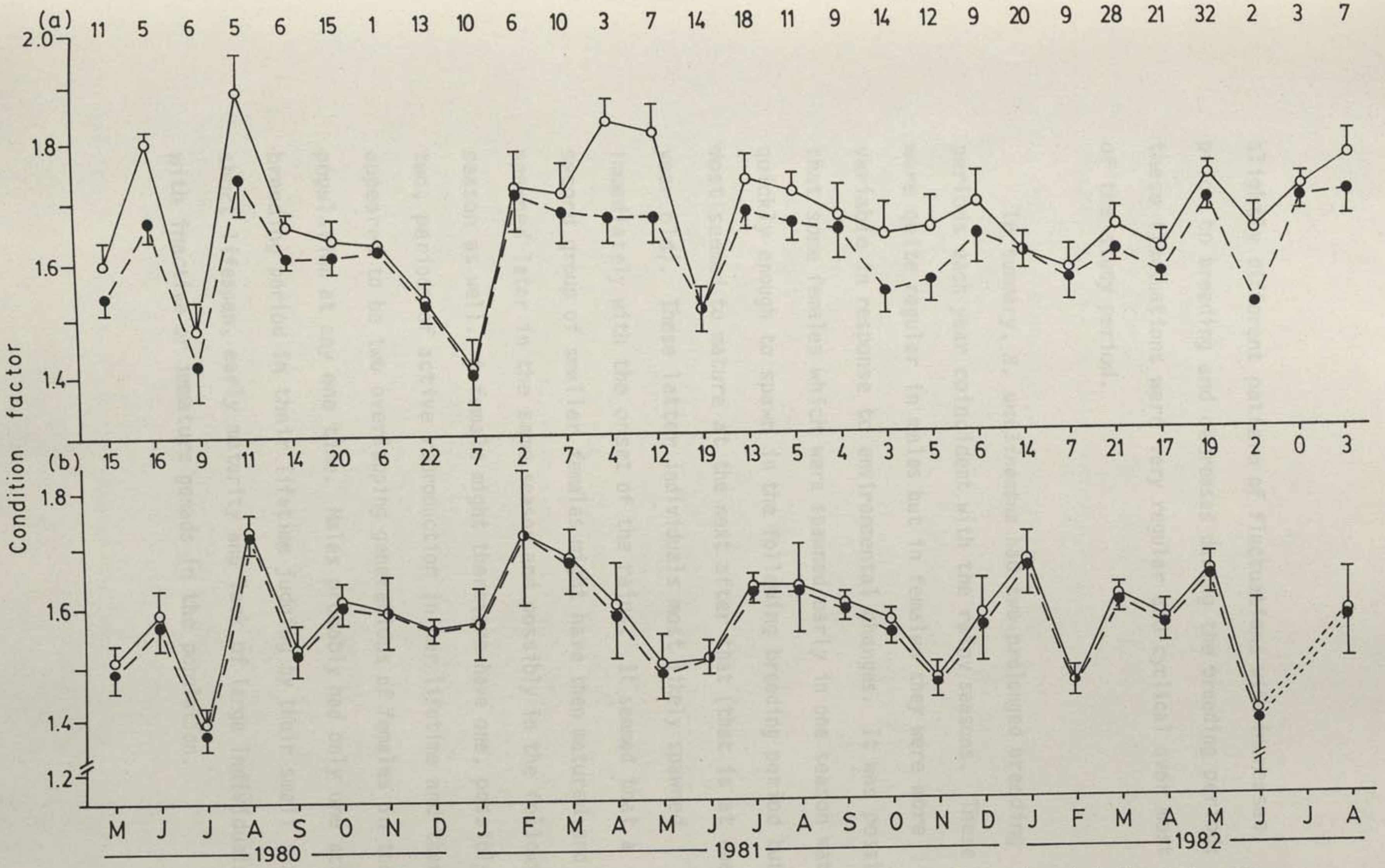
pattern with peaks in May and December 1981 and May 1982.

Fluctuation of female GSI's showed the regular occurrence of an initially high GSI at the beginning of the breeding season followed by a decrease and a further increase to previous levels. The decrease of GSI in the middle of the breeding season was evident in July 1980, June and September 1981 and July 1982 (Fig.55). This pattern was accompanied by a decrease in the numbers of mature females as well as either in the same or previous month, a loss of the larger females in the population (Fig. 51). While these features may be expected at the end of the breeding period, at this time it suggested the presence of two groups of females reproducing successively during any one breeding season. It was likely that larger females spawned at the very beginning of the breeding season with the onset of the first rains, then probably die, followed by a second group of smaller females which spawned later in the season.

Maximum GSI's recorded for female and male *H. unilineatus* were 13.101% in May 1981 and 2.083% in June 1980 for females and males respectively. Female GSI's were generally high with GSI's greater than 10% being recorded for nine out of the 28 months of the study, again suggesting fairly prolonged reproduction or continuous spawning-readiness for females.

Sex ratios for individuals caught over the study period showed no significant variation from a 50 : 50 ratio whether all individuals or only mature-sized fish were considered (Table 25). However, mature-sized fish showed a slight predominance of females over males and χ^2 value was high (3.03, $p<0.1$). Monthly sex ratios showed no significant variation from unity except in June 1980 (male : female ratio 76 : 24%, $p<0.05$) and October 1981 (male : female ratio 18 : 82%, $p<0.05$). Slightly skewed ratios were found for some other months (September, November 1980, November 1981, May, July 1982). In addition, monthly variation in sex ratios appeared to follow a cyclical pattern of higher proportions of males during breeding seasons (Fig. 55). These trends were not entirely clear-cut or consistent however.

Both male and female condition factors showed a very close correlation with the reproductive cycle (Fig. 56). Female total condition increased relative to somatic condition immediately prior to and during the breeding seasons as GSI's increased. Both total and somatic condition decreased drastically at the same time that GSI's decreased in the middle of the breeding periods. Male condition showed a



<u>FIGURE 56</u>: Monthly variation of total and somatic condition for <u>H</u>. <u>unilineatus</u> (a) females, and (b) males over the whole study period (key as for Figure 40).

slightly different pattern of fluctuations with increases prior to breeding and decreases during the breeding period; these fluctuations were very regular and cyclical over most of the study period.

In summary, *H. unilineatus* had two prolonged breeding periods each year coincident with the rainy seasons. These were quite regular in males but in females they were more variable in response to environmental changes. It was possible that some females which were spawned early in one season matured quickly enough to spawn in the following breeding period but most seemed to mature at the next after that (that is at one year old). These latter individuals most likely spawned immediately with the onset of the rains. It seemed that a second group of smaller females might have then matured and spawned later in the same season and possibly in the following season as well. A female might therefore have one, possibly two, periods of active reproduction in her lifetime and there appeared to be two overlapping generations of females in the population at any one time. Males probably had only one active breeding period in their lifetime judging by their small size, short lifespan, early maturity and lack of large individuals with inactive or immature gonads in the population.

Corydoras aeneus

Sexual maturation and growth:

Unlike some of the other species studied, most specimens of this species were reproductively active with only a few inactive or immature individuals collected (Fig.57). Minimum size of specimens with developing gonads was 34 mm for females while males started developing at a smaller size, 31 mm (Table 24). However, both males and females attained maturity at equal minimum lengths, 34 mm. Most males greater than this length were mature (70%) and 72% of mature-sized females were also mature or spent. Several large females with inactive or developing gonads were caught and could have indicated repeated spawning for females over their lifetime. Data for males showed this trend more clearly with two peaks in the numbers of males with developing testes: one at a modal length of 34 mm and another at 44 mm. This could have suggested that males undergo at least two reproductive cycles during their lifetime. Since females grew to much larger sizes than males and presumably live longer, it was not unreasonable to suggest that they may undergo more than two reproductive cycles during their lifetime. The majority of males were mature at a smaller size than females and median length at first maturity was 35 mm for males and 38 mm for females. Many partially spent females were noted but classed as mature due to the number of ova still

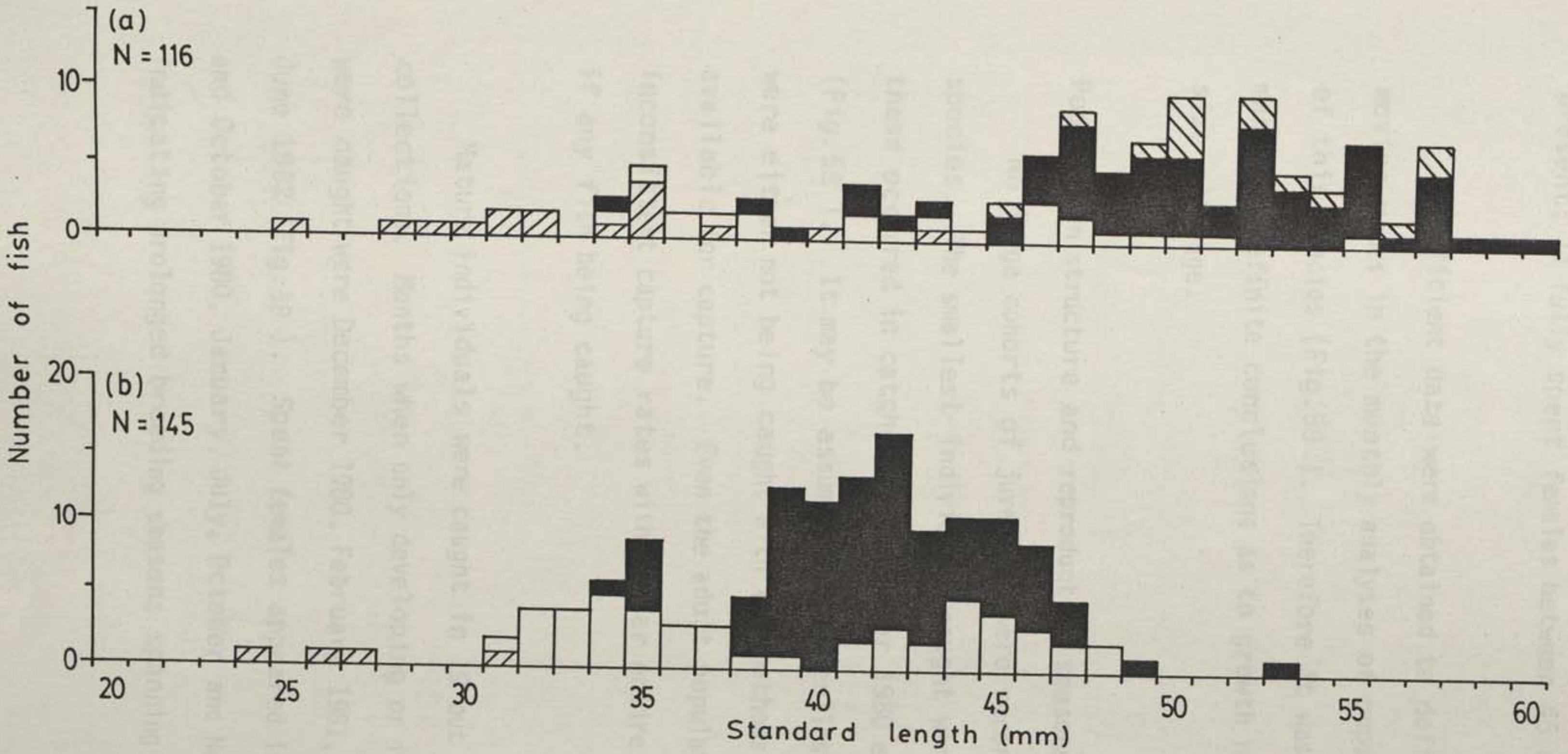


FIGURE 57: The relationship between gonad maturity stages and size for C. aeneus (a) females and juveniles, and (b) males (key as for Figure 35).

present; 14 fully spent females between 45 and 57 mm were noted.

Insufficient data were obtained to define cohorts or moving modes in the monthly analyses of population structure of this species (Fig.58). Therefore it was not possible to make any definite conclusions as to growth rates or to correlate size with age.

Population structure and reproductive seasonality:

No large cohorts of juveniles were recorded for this species. The smallest individuals caught were 24 mm SL and these occurred in catches in September 1980 and March 1982 (Fig.58). It may be assumed that juveniles of this species were either not being caught with the methods used or were not available for capture. Even the adult population showed inconsistent capture rates with either entire schools or few if any fish being caught.

Mature individuals were caught in 19 out of 23 monthly collections. Months when only developing or immature specimens were caught were December 1980, February 1981, January and June 1982 (Fig.58). Spent females appeared in May, September and October 1980, January, July, October and November 1981, indicating prolonged breeding seasons spanning both rainy

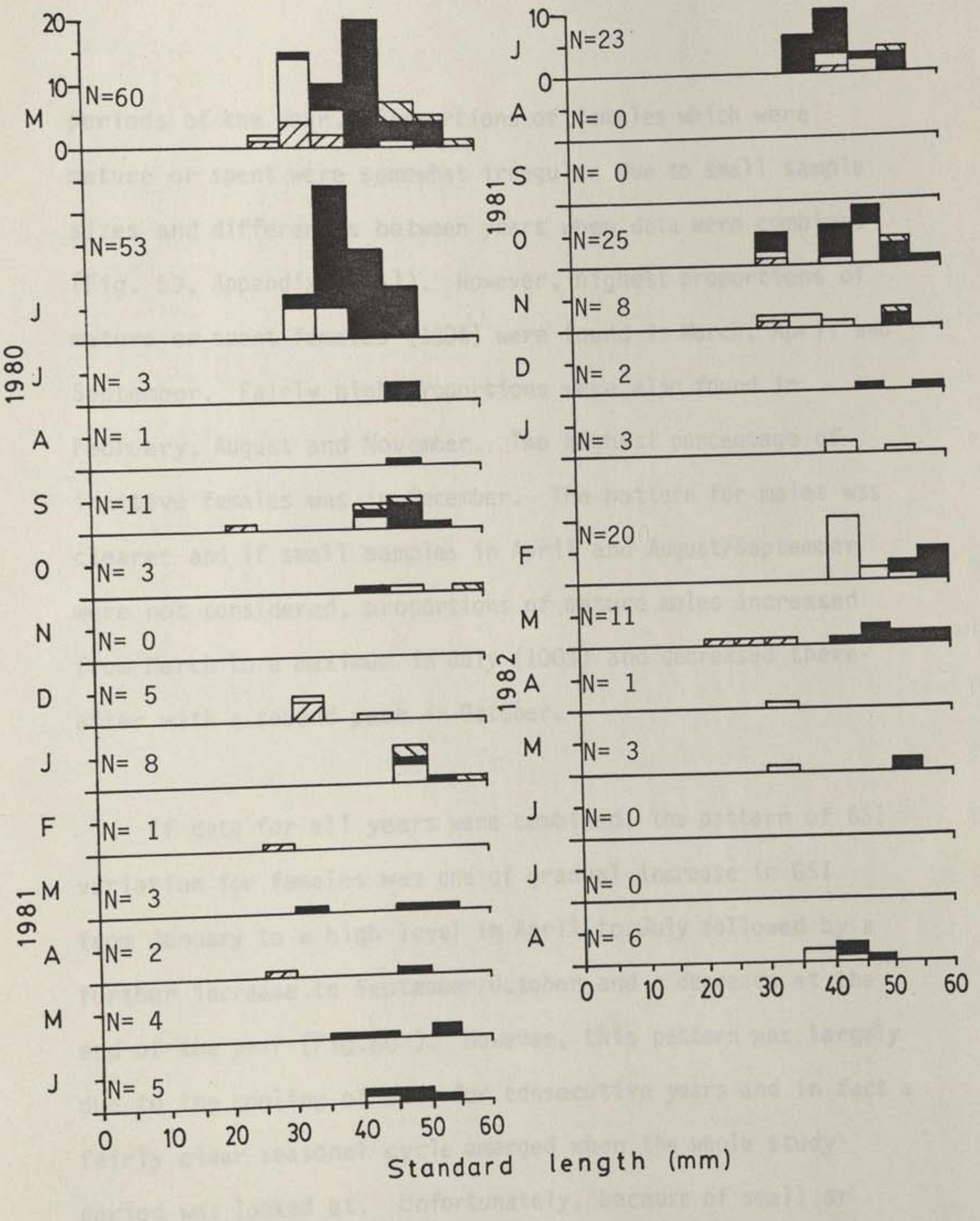


FIGURE 58: Monthly variation of population structure and the occurrence of gonad maturity stages for C. aeneus (key as for Figure 36).

periods of the year. Proportions of females which were mature or spent were somewhat irregular due to small sample sizes and differences between years when data were combined (Fig. 59, Appendix 12(a)). However, highest proportions of mature or spent females (100%) were found in March, April and September. Fairly high proportions were also found in February, August and November. The highest percentage of inactive females was in December. The pattern for males was clearer and if small samples in April and August/September were not considered, proportions of mature males increased from March to a maximum in July (100%) and decreased thereafter with a second peak in October.

If data for all years were combined, the pattern of GSI variation for females was one of gradual increase in GSI from January to a high level in April to July followed by a further increase in September/October and a decrease at the end of the year (Fig.60). However, this pattern was largely due to the pooling of data for consecutive years and in fact a fairly clear seasonal cycle emerged when the whole study period was looked at. Unfortunately, because of small or missing samples in many months the data are incomplete (Appendix 12(b)). Nevertheless, these data showed clear peaks in female GSI's from June to September 1980, April to June and

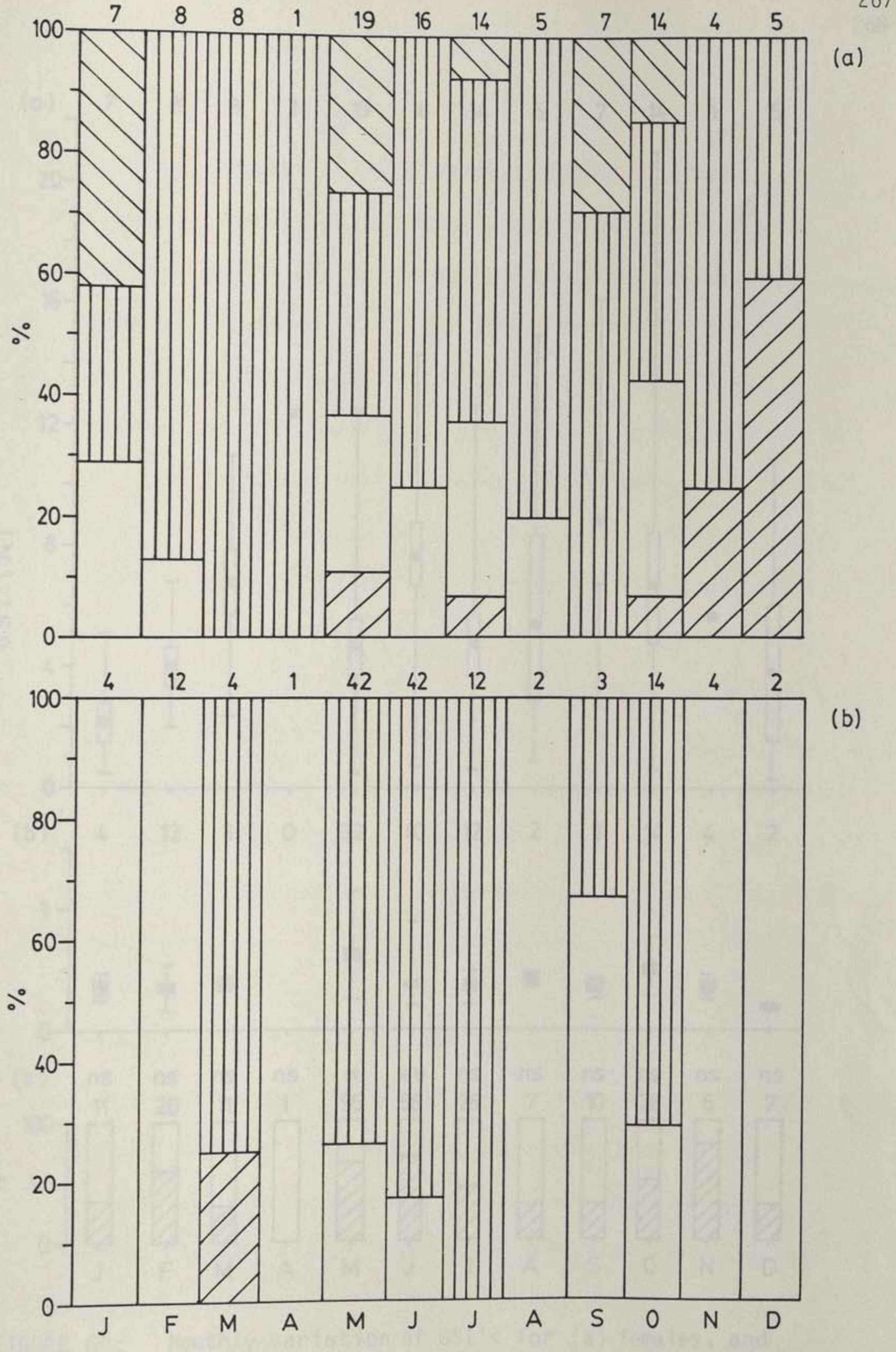


FIGURE 59: Monthly variation of gonad maturity stages for *C. aeneus* (a) females, and (b) males (key as for Figure 38).

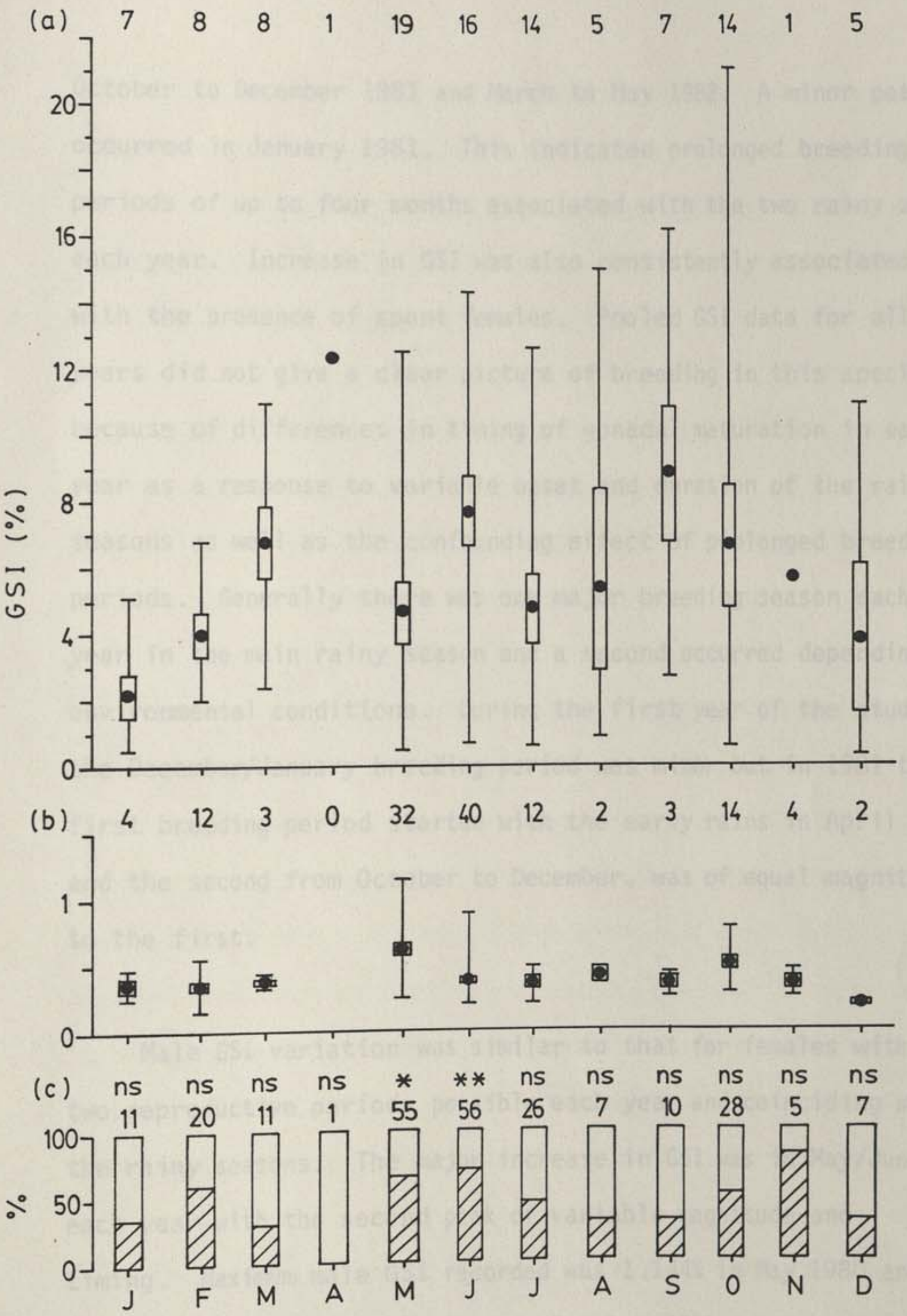


FIGURE 60: Monthly variation of GSI's for (a) females, and (b) males, and (c) sex ratios for *C. aeneus* (key as for Figure 39).

October to December 1981 and March to May 1982. A minor peak occurred in January 1981. This indicated prolonged breeding periods of up to four months associated with the two rainy seasons each year. Increase in GSI was also consistently associated with the presence of spent females. Pooled GSI data for all years did not give a clear picture of breeding in this species because of differences in timing of gonadal maturation in each year as a response to variable onset and duration of the rainy seasons as well as the confounding effect of prolonged breeding periods. Generally there was one major breeding season each year in the main rainy season and a second occurred depending on environmental conditions. During the first year of the study, the December/January breeding period was minor but in 1981 the first breeding period started with the early rains in April and the second from October to December, was of equal magnitude to the first.

Male GSI variation was similar to that for females with two reproductive periods possible each year and coinciding with the rainy seasons. The major increase in GSI was in May/June each year with the second peak of variable magnitude and timing. Maximum male GSI recorded was 1.144% in May 1980 and the female maximum was 21.169% in October 1981.

Sex ratios for specimens collected during the study were slightly dominated by males (Table 25) but this was not significant (χ^2 test, $p>0.05$). Monthly variation in sex ratios indicated significantly higher proportions of males during May and June when breeding was at a peak ($p<0.05$ (May), $p<0.01$ (June)). For the other months sex ratios did not differ significantly from unity (Fig. 60). Aquarium breeding showed that more than one male may be necessary to fertilise all the eggs of one female (Sterba 1962, Zukal 1982) and this could have accounted for such male-biased ratios.

The variation in condition factors for males and females was remarkably cyclical (Fig. 61, Appendix 12(c)). Total condition for females was much greater than somatic condition in all months of the year consistent with continuously high GSI's when data for all years were combined. Both total and somatic condition of females increased along with increasing GSI's at times of breeding and generally decreased after each breeding period. Male condition tended to decrease at the time of breeding and increased immediately afterwards.

In summary, *C. aeneus* appeared to have two breeding periods each year coincident with the rainy seasons. The first period during the main rains was generally the major breeding time while

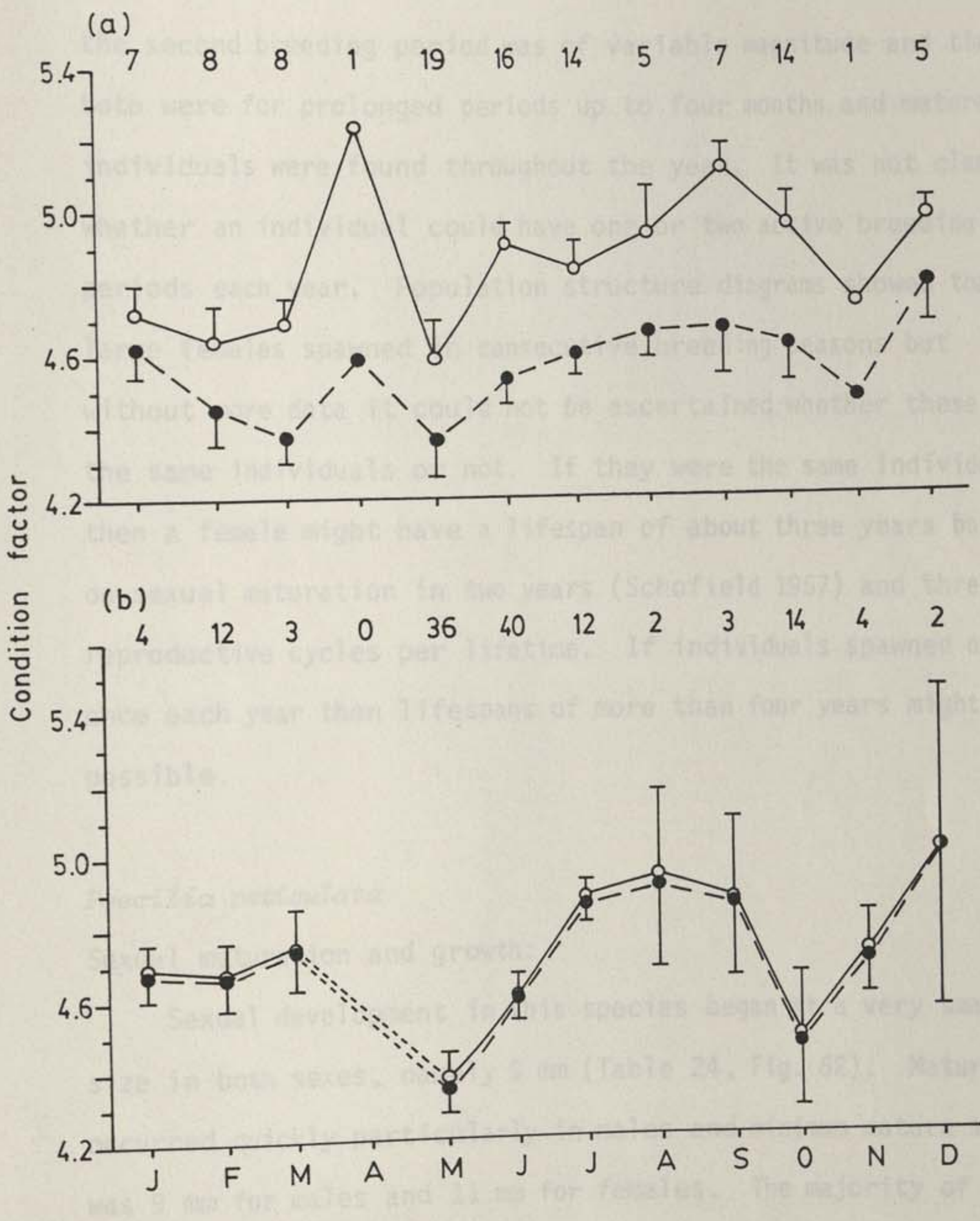


FIGURE 61: Monthly variation of total and somatic condition for C. aeneus (a) females, and (b) males (key as for Figure 40).

the second breeding period was of variable magnitude and timing. Both were for prolonged periods up to four months and mature individuals were found throughout the year. It was not clear whether an individual could have one or two active breeding periods each year. Population structure diagrams showed that large females spawned in consecutive breeding seasons but without more data it could not be ascertained whether these were the same individuals or not. If they were the same individuals, then a female might have a lifespan of about three years based on sexual maturation in two years (Schofield 1957) and three reproductive cycles per lifetime. If individuals spawned only once each year then lifespans of more than four years might be possible.

Poecilia reticulata

Sexual maturation and growth:

Sexual development in this species began at a very small size in both sexes, namely 9 mm (Table 24, Fig. 62). Maturation occurred quickly particularly in males and minimum mature size was 9 mm for males and 11 mm for females. The majority of males matured at a smaller size than females and the median length at first maturity was 10.8 mm for males as compared to 12.4 mm for females. Some males of quite large size (14 mm) were recorded as developing on the basis of gross characteristics of the testes as well as incomplete development of the secondary

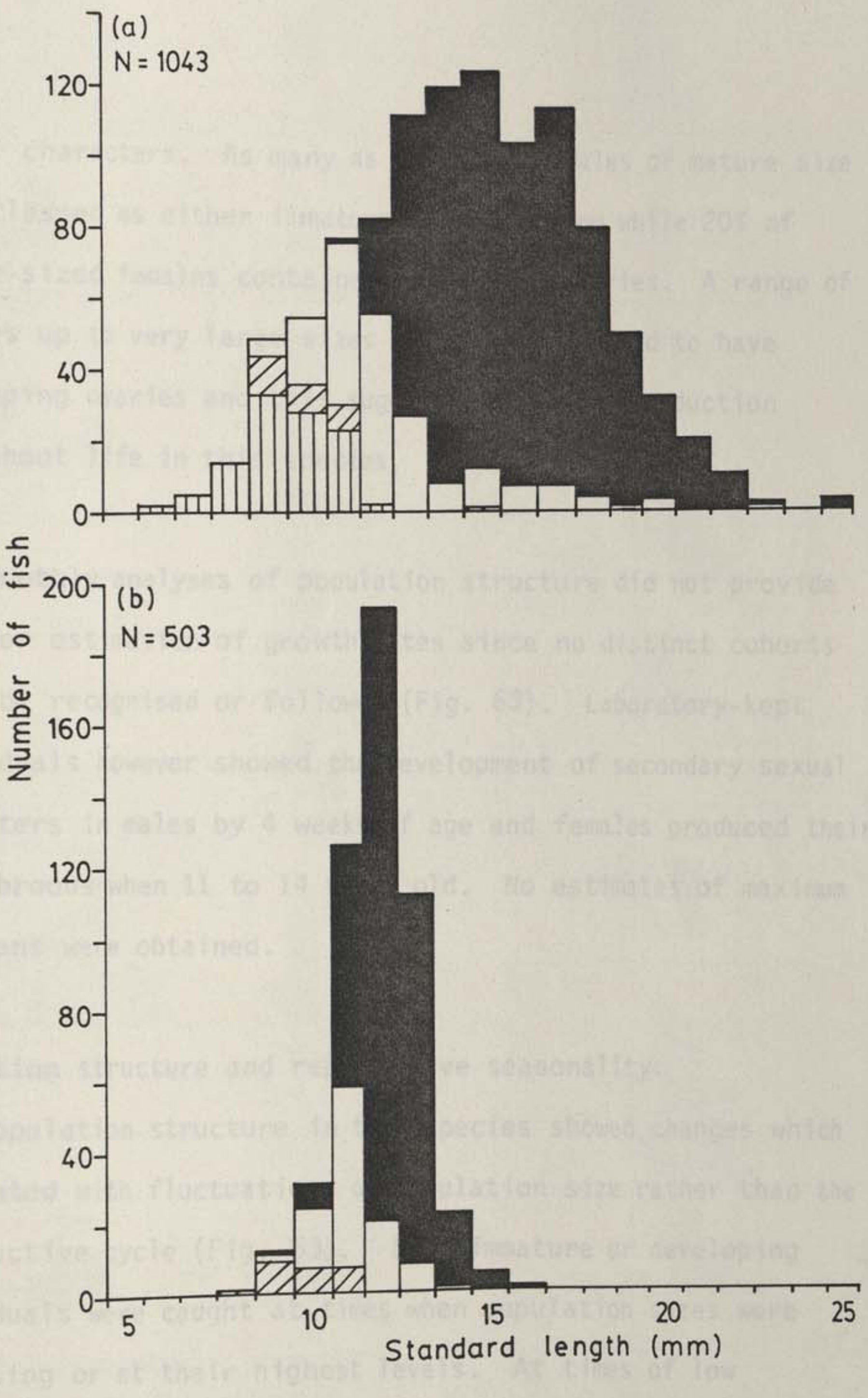


FIGURE 62: The relationship between gonad maturity stages and size for P. reticulata (a) females and juveniles, and (b) males (key as for Figure 35).

sexual characters. As many as 24% of the males of mature size were classed as either immature or developing while 20% of mature-sized females contained developing ovaries. A range of females up to very large sizes (23 mm) were noted to have developing ovaries and this suggested repeat reproduction throughout life in this species.

Monthly analyses of population structure did not provide data for estimation of growth rates since no distinct cohorts could be recognised or followed (Fig. 63). Laboratory-kept individuals however showed the development of secondary sexual characters in males by 4 weeks of age and females produced their first broods when 11 to 14 weeks old. No estimates of maximum lifespans were obtained.

Population structure and reproductive seasonality:

Population structure in this species showed changes which correlated with fluctuations of population size rather than the reproductive cycle (Fig. 63). Most immature or developing individuals were caught at times when population sizes were increasing or at their highest levels. At times of low population sizes, most of the individuals were mature and quite large; very few if any, small immature individuals were present. Population sizes were seen to fluctuate in response to stream

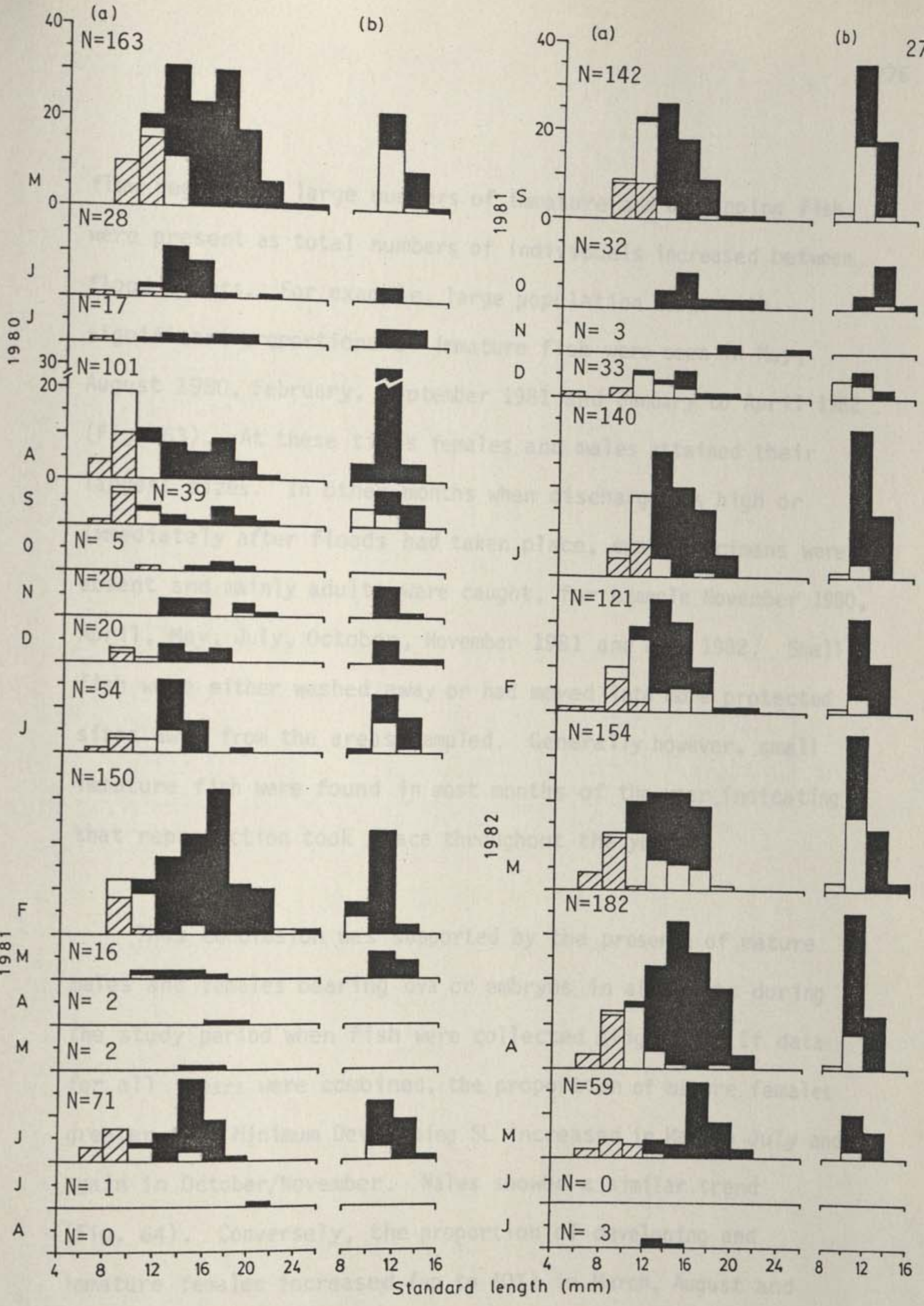


FIGURE 63: Monthly variation of population structure and the occurrence of gonad maturity stages for *P. reticulata* (a) females and juveniles, and (b) males (key as for Figure 36).

flow regime and large numbers of immature and developing fish were present as total numbers of individuals increased between flood events. For example, large population sizes with significant proportions of immature fish were seen in May, August 1980, February, September 1981 and January to April 1982 (Fig. 63). At these times females and males attained their largest sizes. In other months when discharge was high or immediately after floods had taken place, small specimens were absent and mainly adults were caught, for example November 1980, April, May, July, October, November 1981 and July 1982. Small fish were either washed away or had moved into more protected sites away from the areas sampled. Generally however, small immature fish were found in most months of the year indicating that reproduction took place throughout the year.

This conclusion was supported by the presence of mature males and females bearing ova or embryos in all months during the study period when fish were collected (Fig. 63). If data for all years were combined, the proportion of mature females greater than Minimum Developing SL increased in May to July and again in October/November. Males showed a similar trend (Fig. 64). Conversely, the proportion of developing and immature females increased (up to 40%) in March, August and December and for males in May, September and December (up to

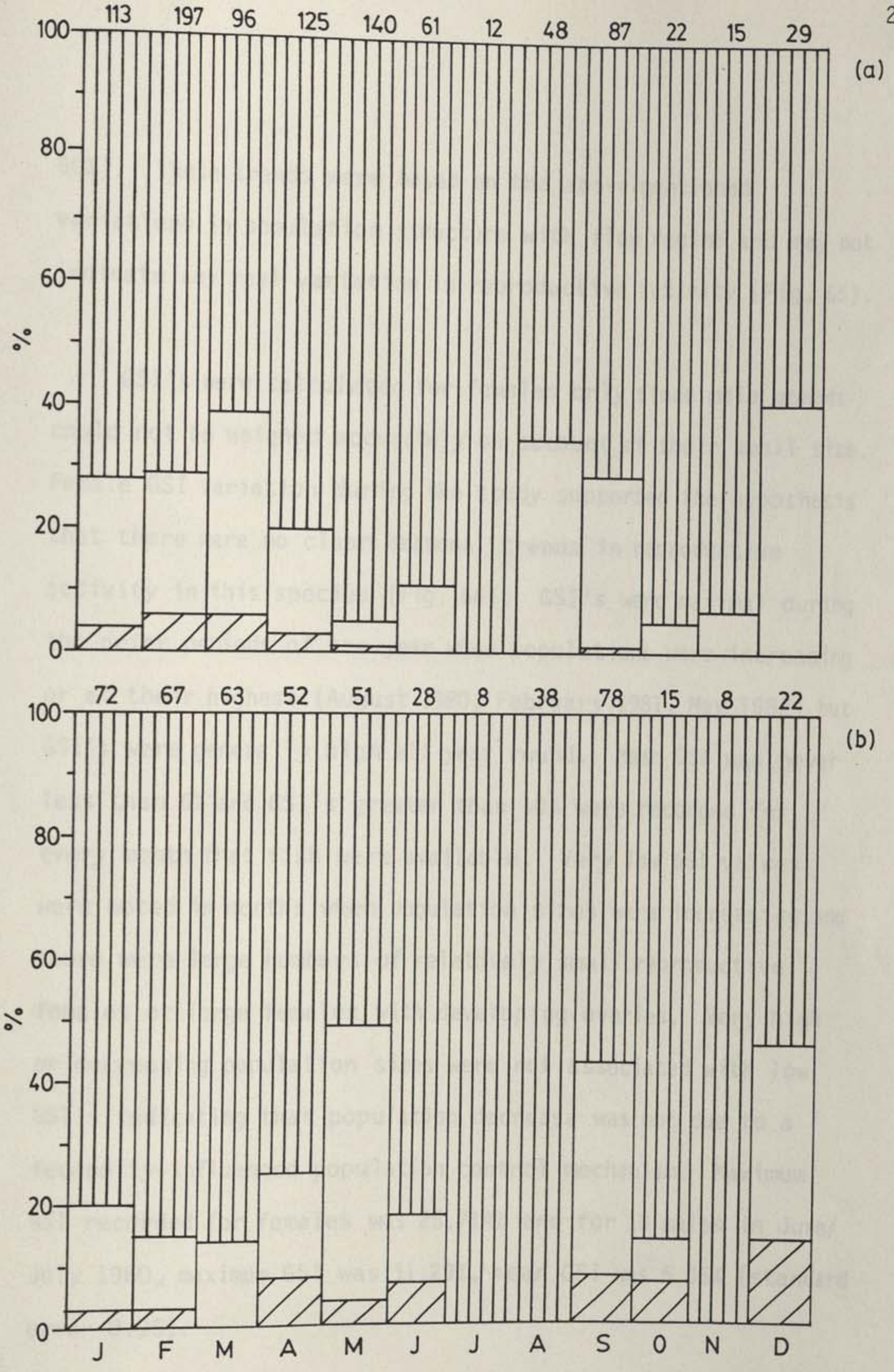


FIGURE 64: Monthly variation of gonad maturity stages for *P. reticulata* (a) females, and (b) males over the calendar year (key as for Figure 38).

50%). These trends were based on the above-mentioned variations in population structure with flow regime and may not indicate any real variation in reproductive activity (Fig. 65).

GSI's were calculated for females only since male gonads could not be weighed accurately on account of their small size. Female GSI variation during the study supported the hypothesis that there were no clear seasonal trends in reproductive activity in this species (Fig. 66). GSI's were maximal during the drier periods of the year when populations were increasing or at their highest (August 1980, February 1981, May 1982) but GSI's were generally high all year round. Mean GSI was never less than 6% and GSI's greater than 10% were recorded for every month that fish were available. Very low GSI values were noted in months when population sizes were increasing and there were large numbers of relatively small reproductive females or large females with developing ovaries. Very high or decreasing population sizes were not associated with low GSI's indicating that population decrease was not due to a fecundity-influenced population control mechanism. Maximum GSI recorded for females was 25.714% and for 10 males in June/July 1980, maximum GSI was 11.29%, mean GSI was 5.36% (standard error 0.95).

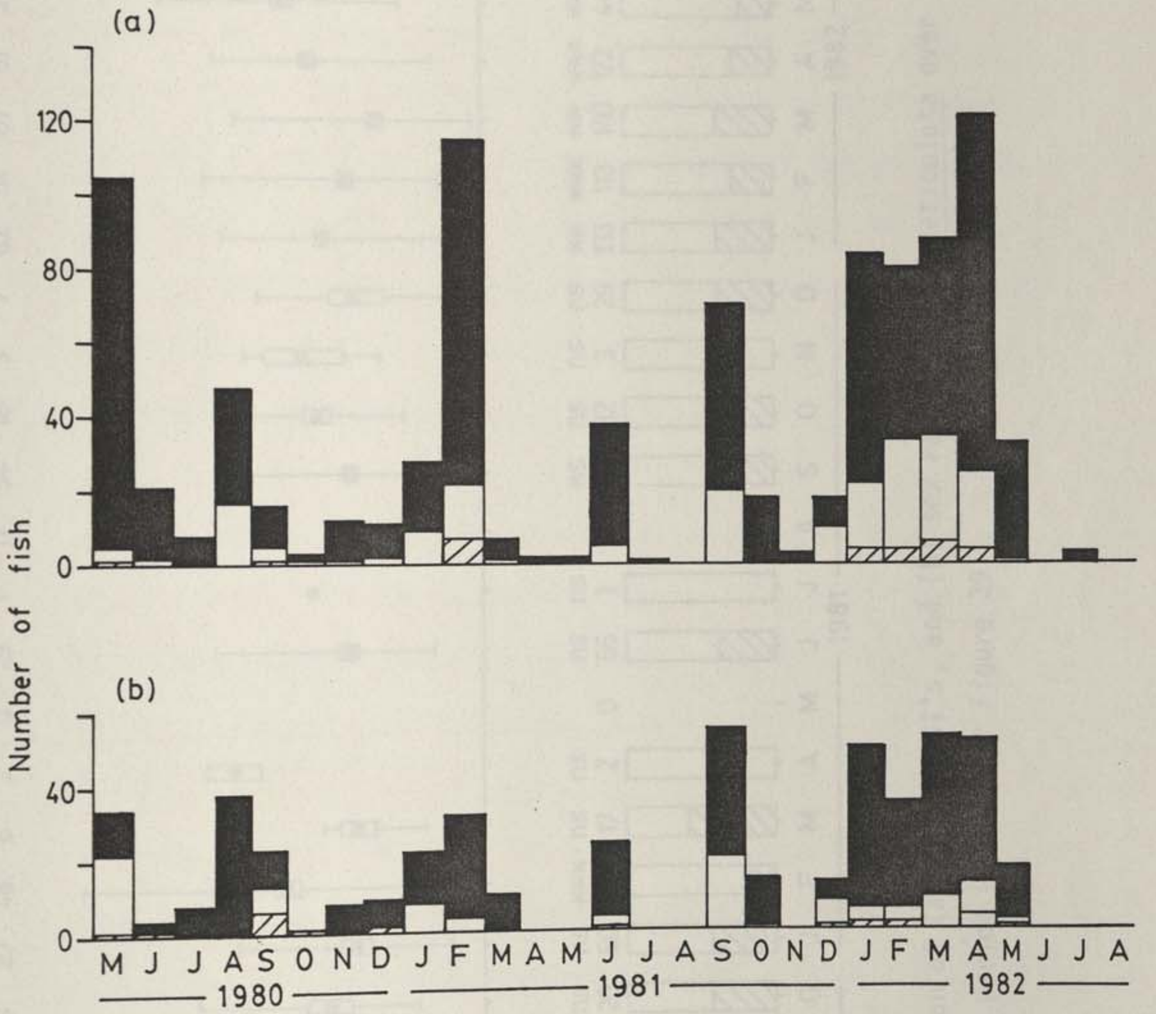


FIGURE 65: Monthly variation of gonad maturity stages for P. reticulata (a) females, and (b) males over the whole study period (key as for Figure 35).

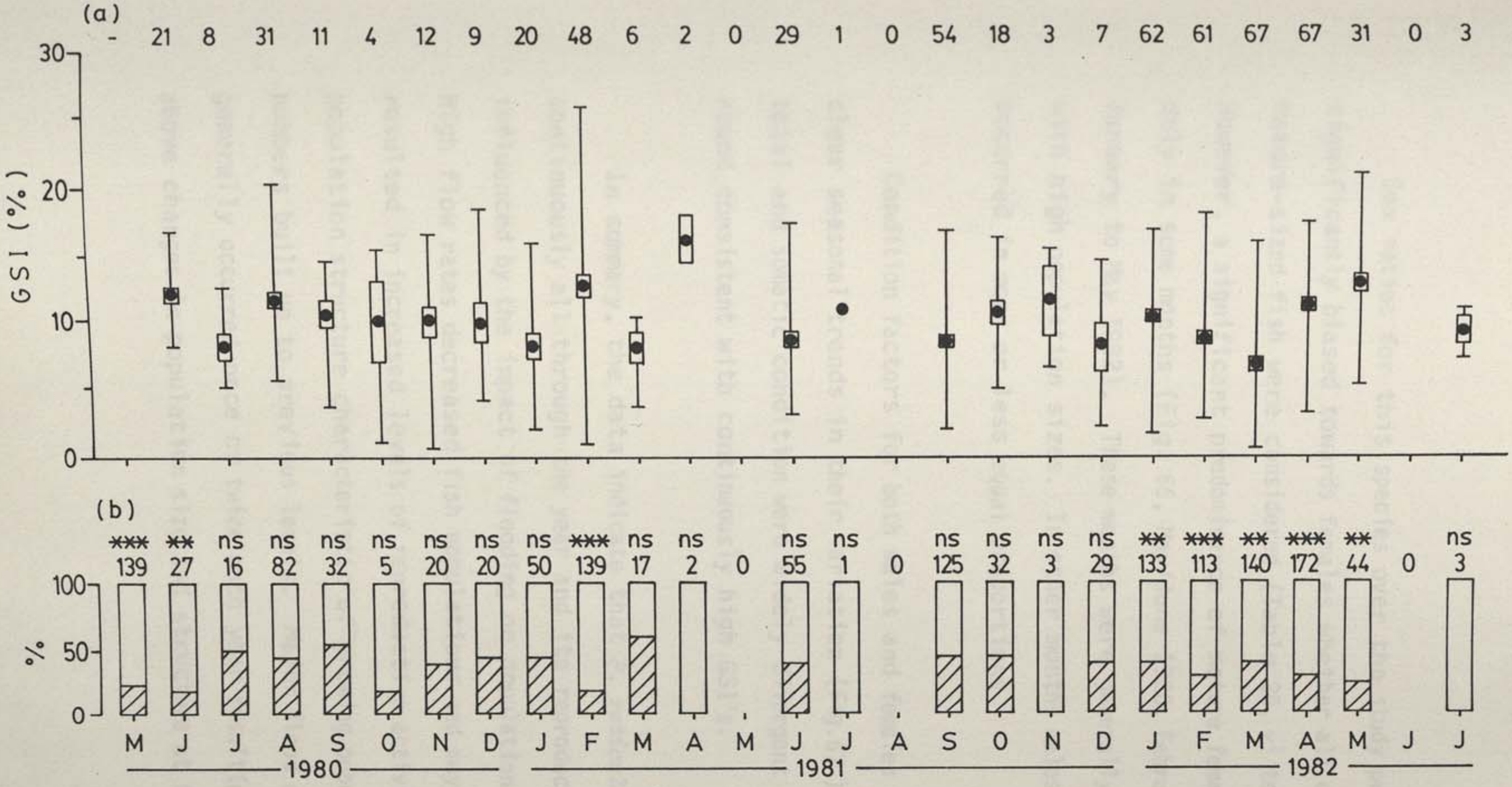


FIGURE 66: Monthly variation of (a) female GSI's, and (b) sex ratios for *P. reticulata* over the whole study period (key as for Figure 39).

Sex ratios for this species over the study period were significantly biased towards females whether all or only mature-sized fish were considered (Table 25, χ^2 test, $p<0.001$). However, a significant predominance of mature females was seen only in some months (Fig. 66, May/June 1980, February 1981, January to May 1982). These months were generally associated with high population sizes. In other months males and females occurred in more or less equal proportions.

Condition factors for both males and females showed no clear seasonal trends in their variation (Fig.67). Female total and somatic condition were widely divergent all year round consistent with continuously high GSI's.

In summary, the data indicate that *P. reticulata* reproduced continuously all through the year and its reproduction was influenced by the impact of flooding on population sizes. High flow rates decreased fish populations and may have resulted in increased levels of reproductive activity and a population structure characteristic of growing populations as numbers built up to previous levels. Major flood events generally occurred once or twice each year resulting in the above changes in population size and structure at this frequency.

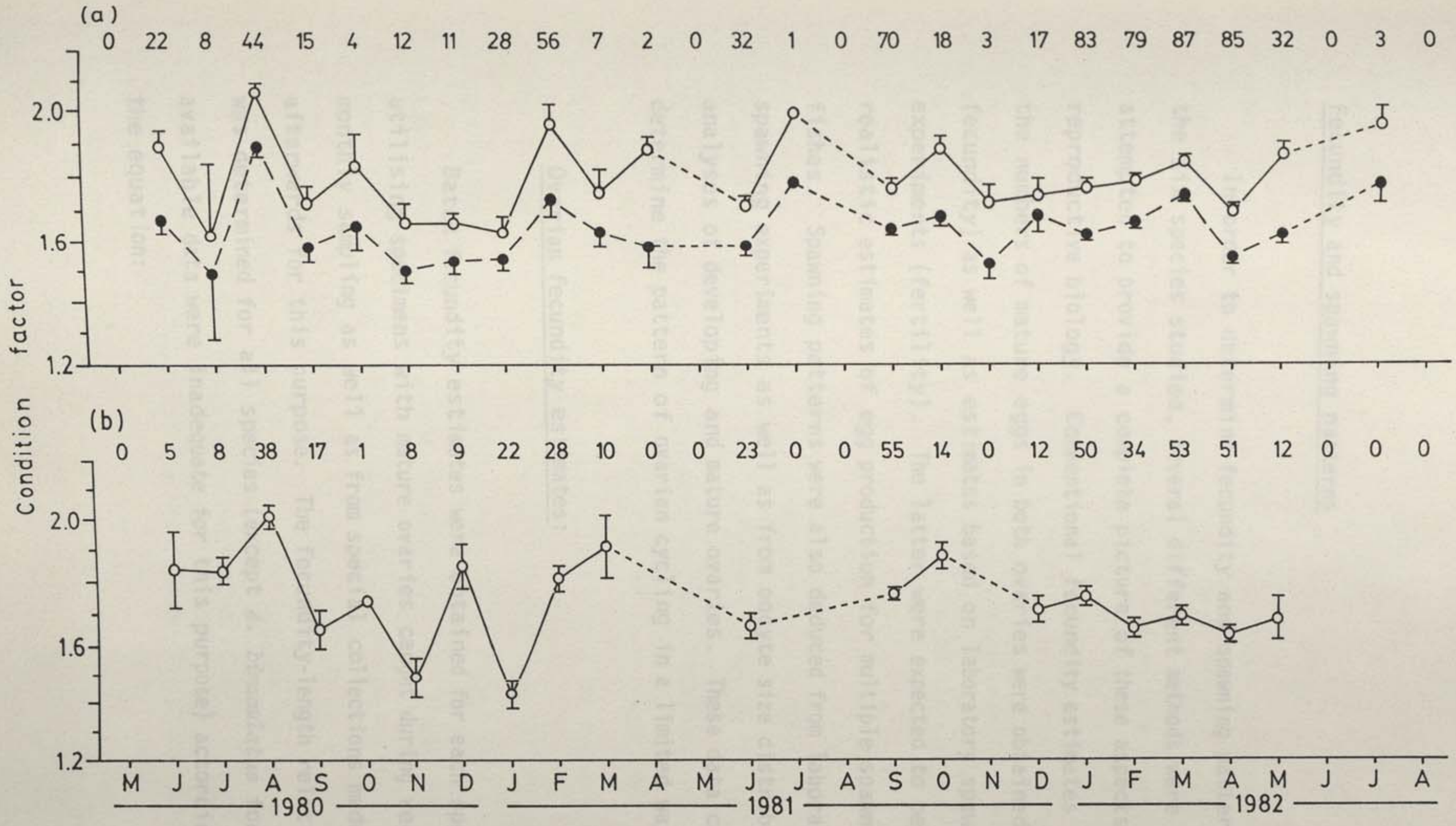


FIGURE 67: Monthly variation of (a) female total and somatic condition, and (b) male total condition for P. reticulata over the whole study period (key as for Figure 40; (b) bars represent ± 1 Standard Error).

Fecundity and spawning patterns

In order to determine fecundity and spawning patterns of the six species studied, several different methods were attempted to provide a complete picture of these aspects of their reproductive biology. Conventional fecundity estimates based on the numbers of mature eggs in both ovaries were obtained (batch fecundity) as well as estimates based on laboratory spawning experiments (fertility). The latter were expected to be more realistic estimates of egg production for multiple spawning fishes. Spawning patterns were also deduced from laboratory spawning experiments as well as from oocyte size distribution analyses of developing and mature ovaries. These data could determine the pattern of ovarian cycling in a limited way.

Ovarian fecundity estimates:

Batch fecundity estimates were obtained for each species utilising specimens with mature ovaries caught during regular monthly sampling as well as from special collections made afterwards for this purpose. The fecundity-length relationship was determined for all species (except *A. bimaculatus* for which available data were inadequate for this purpose) according to the equation:

$$\log_{10}F = \log_{10}a + b \log_{10}SL$$

where F = batch fecundity (or brood size for *P. reticulata*) and SL = standard length (Figs.68 and 69). The constants a and b (± 95% confidence limits) and the correlation coefficient, r, are given for each species in Table 28. The 95% confidence limits of b gave an indication of the spread of the points around a line of slope b and hence were used to reflect the variability of fecundity about given lengths for each species.

Determination of batch fecundities for *C. riisei*, *H. unilineatus* and *C. aeneus* were particularly difficult because of the high proportion of partially spent fish in the samples. In these cases, only ovaries which appeared full and for which the GSI values were maximal for fish of that length, were used in analyses. However, this severely limited the numbers of ovaries used in analyses for *C. riisei* and *C. aeneus* in particular. Such small samples especially over a wide size range for *C. aeneus* may have resulted in the low statistical significance of the parameters of the fecundity-length relationship (Table 28). For *C. aeneus*, there was no significant correlation between $\log_{10}F$ and $\log_{10}SL$ ($p>0.05$) and the slope showed no significant variation from zero (F-test, $p>0.05$). In addition, the slopes of the lines of best fit were much less

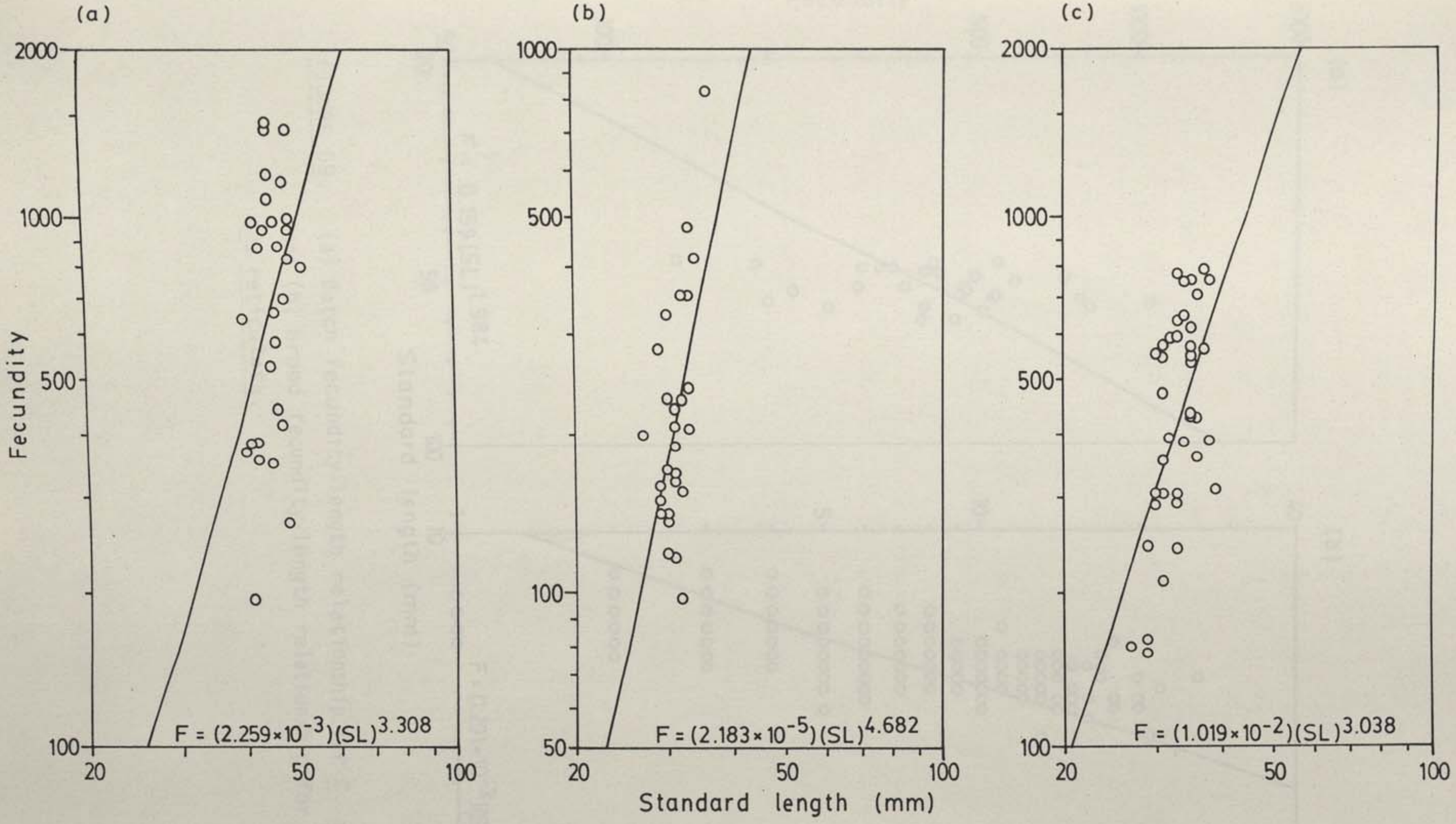


FIGURE 68: Batch fecundity-length relationships for (a) G. sternicla, (b) C. riisei, and (c) H. unilineatus.

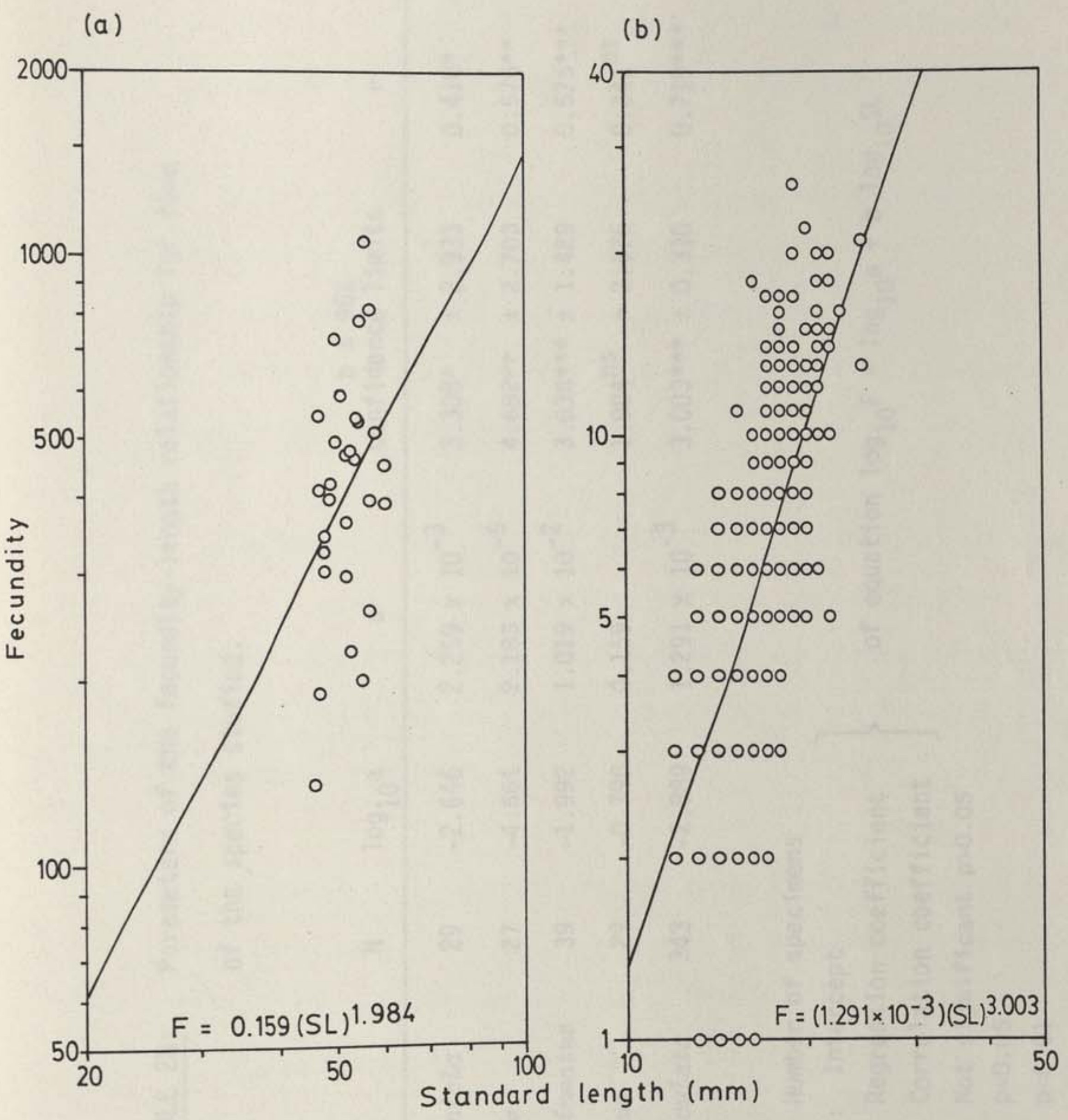


FIGURE 69: (a) Batch fecundity-length relationship for *C. aeneus*, and (b) brood fecundity-length relationship for *P. reticulata*.

TABLE 28: Parameters of the fecundity-length relationship for five of the species studied.

Species	N	$\log_{10}a$	a	b ± 95% confidence limits	r	t_s[1]
G. sternicla	29	-2.646	2.259×10^{-3}	3.308* ± 2.933	0.410*	0.216^{ns}
C. riisei	27	-4.661	2.183×10^{-5}	4.682** ± 2.703	0.576**	1.282^{ns}
H. unilineatus	39	-1.992	1.019×10^{-2}	3.038*** ± 1.429	0.575***	0.053^{ns}
C. aeneus	29	-0.798	0.159	1.984^{ns} ± 2.176	0.341^{ns}	0.961^{ns}
P. reticulata	343	-2.889	1.291×10^{-3}	3.003*** ± 0.310	0.719***	0.019^{ns}

N : Number of specimens
$\log_{10}a$: Intercept
b : Regression coefficient
r : Correlation coefficient

$$\left.\begin{array}{l}\log_{10}a : \text{Intercept}\\ b : \text{Regression coefficient}\\ r : \text{Correlation coefficient}\end{array}\right\} \text{of equation } \log_{10}F = \log_{10}a + b\log_{10}SL$$

ns : Not significant $p>0.05$
* : $p<0.05$
** : $p<0.01$
*** : $p<0.001$
[1] : t-test for deviation of observed b from 3.0.

than three in the case of *C. aeneus* and larger than three for *C. riisei* but these differences were not significant (Table 28).

Relatively low statistical significance was seen for the parameters of the fecundity-length relationship for *G. sternicla* (r, $p<0.05$; b, $p<0.05$). Small sample sizes as well as the use of ovaries which may have been partially spent or early maturing may have been contributory in this case.

The values of b for three species (*G. sternicla, H. unilineatus* and *P. reticulata*) were very close to three indicating a near cubic relationship between batch fecundity and standard length as expected. There was no significant deviation of b from 3.0 for these species (Table 28).

Variability of fecundity values about the line of best fit was comparatively high in *G. sternicla, C. riisei* and *C. aeneus* (95% confidence limits of $b > 2.0$). This was most likely due to small sample sizes and the real variability inherent in ovaries which may have been partially spent or early maturing.

Data for *A. bimaculatus* were very limited and only three fully mature females were analysed. Batch fecundities were 1948 (57 mm SL), 3075 (76 mm SL) and 6364 (70 mm SL) eggs. Maximum batch fecundity for this species was much greater than that for any of the other species investigated (Table 29). In contrast, the ovoviviparous *P. reticulata* had the lowest maximum fecundity at 26 while the other species were intermediate between these two extremes. Maximum batch fecundities were positively correlated with size for the six species ($r = 0.827$, $p<0.05$, $N = 6$).

Batch fecundities corresponded very closely with GSI for most species and in four cases, maximum fecundity estimates were for females whose GSI values were maximal for their respective species (Table 29).

Laboratory spawning experiments:

Successful spawning in the laboratory was achieved only for *C. riisei, H. unilineatus* and *P. reticulata.* Other species were maintained for prolonged periods and although courtship behaviour was observed in *A. bimaculatus* and to a lesser extent *G. sternicla,* no spawning took place. Detailed observations were made of these species on many occasions at all times of the day and night but at no time was spawning observed. Attempts were made on several occasions to replicate flood conditions by replacing tank water with fresh water but this was unsuccessful. Presumably other factors may be more relevant to inducing spawning in these

TABLE 29: Maximal batch/brood fecundities recorded for the six fish species studied.

Species	SL(mm)	GSI(%)[1]	Fecundity
G. sternicla	45	12.262	1458
C. riisei	36	14.130	833
A. bimaculatus	70	14.800	6364
H. unilineatus	37	11.521	787
C. aeneus	56	21.169	1046
P. reticulata	19	18.033	26

1 : GSI value refers to the same individual for which fecundity was determined.

species in the wild. In the case of *A. bimaculatus*, one pair showed intense but sporadic courtship activity over long periods but spawning did not occur. In this case female receptivity seemed to be low despite the persistent advances on the part of the male.

Courtship seen in *G. sternicla, A. bimaculatus* and *H. unilineatus* was simple, consisting of varying combinations of certain recognisable actions performed by both sexes such as chasing, circling and swimming parallel to each other in the same direction for short distances. In *A. bimaculatus*, after some period of chasing, the male would assume a stationary head-down or head-up position in front of or parallel to the female, meanwhile twitching or erecting the pectoral and all unpaired fins. The female remained stationary or moved slowly so that they circled each other. The male would then move away from the female with exaggerated lateral undulations of the body in a 'leading' motion. When performing circling movements, male and female on occasion oriented themselves so as to touch ventrally. During courtship in *A. bimaculatus* male coloration intensified. Considerable aggression was seen in the behaviour of this species and males often had to be removed or separated from the larger females because of the damage inflicted to them.

H. unilineatus showed courtship behaviour similar to *A. bimaculatus* with exaggerated undulatory 'leading' movements performed by males. Head-up orientation was performed by either sex or both at the same time and was followed by alternating head-down, head-up orientation creating a vertical zig-zag movement in the water. Parallel swimming, circling and chasing were also seen in this species. Male coloration varied in relation to the intensity of courtship activity.

Courtship in *G. sternicla* also included circling movements by the male around the female and when directly in front of the female rapid vibration of the male's body occurred. Chasing and leading also took place. Most of this behaviour was performed at or a few centimetres below the water's surface.

Intense and more complex courtship was seen in *C. riisei* and *P. reticulata* and it generally followed the patterns described for these species in the literature. Only very limited courtship was seen in *C. aeneus*. Spawning in *C. riisei* took place in the morning soon after dawn and up to mid-morning for periods lasting up to an hour. Spawning was not observed in *H. unilineatus* but appeared to take place either in the early morning or at dusk.

Spawning experiments with *C. riisei* were successful and in total, 11 females spawned under aquarium conditions (Table 30). Female 11 (not included in analyses) spawned only once with a clutch size of 36. Other females showed a clear 'small brood' spawning pattern.

Total numbers of eggs spawned by each female (total fertility) varied from 17 to 4987 over spawning periods ranging from 10 to 146 days. Numbers of clutches spawned per female ranged from 2 to 55. Generally, the size of the female was directly correlated with number of clutches ($r = 0.816$, $p<0.01$, $N = 9$), total fertility ($r = 0.730$, $p<0.05$, $N = 9$) and total spawning period ($r = 0.827$, $p<0.01$, $N = 9$). Eggs were spawned in clutches ranging from 1 to 266 eggs for different females. Larger females spawned larger clutches than smaller females and mean clutch sizes (ranging from 2.8 to 90.7) and maximum clutch sizes were correlated with female size ($r = 0.589$, $p<0.05$; $r = 0.796$, $p<0.01$ for mean and maximum clutch sizes respectively; $N = 10$ in both cases).

Spawning intervals ranged from 1 to 65 days and showed no recognisable periodicity in pattern varying from one female to another. For example, female 2 spawned comparatively small clutches every day for the first 18 days and subsequently spawned

TABLE 30: Summary of results of laboratory spawning experiments for *C. riisei*.

Female	SL (mm)	Total number clutches	Total spawning period (d)	Total number of eggs	Intervals between clutches (d)			Clutch sizes	
					Mean ± SE	Mode	Range	Mean ± SE	Range
F 1	38	55	146	4987	2.7 ± 0.3	2	1-14	90.7 ± 5.6	25-266
F 2	37	31	84	1565	2.8 ± 0.6	1	1-13	50.5 ± 4.5	8-107
F 3	37	28	63	1336	2.3 ± 1.0	1	1-27	47.7 ± 7.2	9-156
F 4	33	2	10	26	9.0	-	-	13.0 ± 9.0	4- 22
F 5[1]	39	10	13	301	1.3 ± 0.2	1	1- 3	30.1 ± 19.4	1-203
F 6	32	8	21	206	2.9 ± 0.5	2.5	1- 5	25.8 ± 6.6	5- 55
F 7	35	18	73	240	4.2 ± 1.3	1	1-19	13.3 ± 3.1	1- 47
F 8	35	2	27	23	26.0	-	-	11.5 ± 10.5	1- 22
F 9	35	21	74	251	3.7 ± 0.9	1	1-15	12.0 ± 2.3	1- 41
F10	35	6	72	17	14.2 ± 12.7	1.5	1-65	2.8 ± 0.9	1- 7

1 : F5 was accidentally damaged and died during the experiment

SE : Standard Error.

at more protracted intervals (Fig. 70). Female 1 however, spawned at fairly regular intervals (mean interval 2.7 ± 0.3 days) for 146 days. No peaks in spawning were recognised in the spawning patterns of either female. In other females peaks of spawning activity could be recognised being separated by prolonged periods of inactivity, for example females 3, 7 and 10 (Fig.70). Generally intervals between clutches were short with modal values between 1 and 2.5 days.

Most of the females used in these experiments died within two months of their last spawning episode. Female 1 survived more than two months after spawning ceased but no attempts at further spawning or courtship were seen.

Eggs were spawned onto the artificial weed provided and these water-hardened eggs were on average 1.106 ± 0.014 (SE) mm in diameter and weighed 0.305 mg each. A very variable proportion of these eggs failed to develop but the proportion did not result from sperm shortage. The male with female 1 died after 48 days of the experiment and was not replaced. During the remainder of the experiment, fertilised eggs were produced and hatched normally; a further period of 98 days over which 3841 eggs were spawned. Sperm were found to be stored in spermatophores in the oviduct of female *C. riisei*. Each spermatophore was slightly

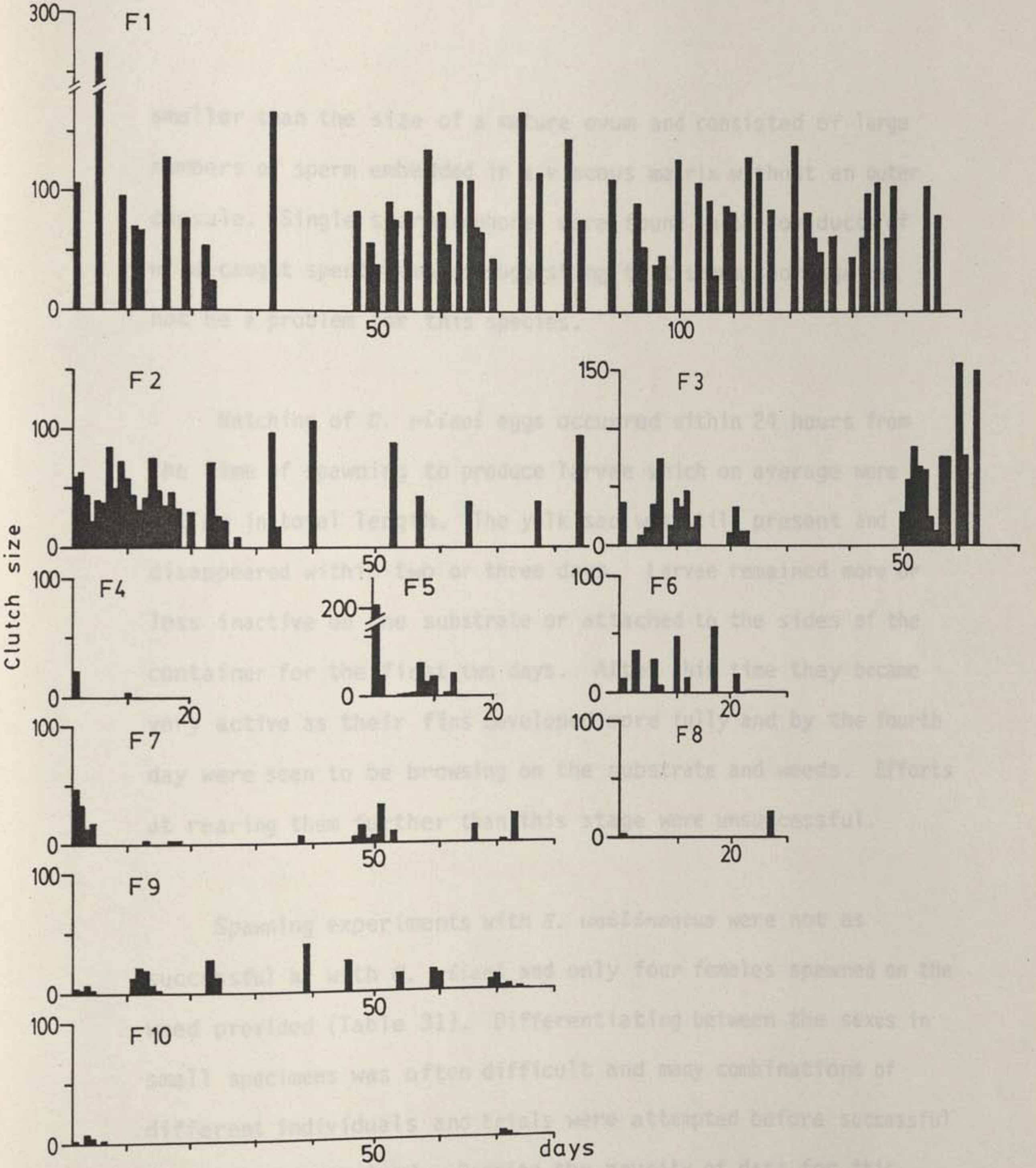


FIGURE 70: Laboratory spawning patterns for C. riisei.

smaller than the size of a mature ovum and consisted of large numbers of sperm embedded in a viscous matrix without an outer capsule. Single spermatophores were found in the oviducts of wild-caught spent females suggesting that sperm shortage may not be a problem for this species.

Hatching of *C. riisei* eggs occurred within 24 hours from the time of spawning to produce larvae which on average were 3.1 mm in total length. The yolk sac was still present and disappeared within two or three days. Larvae remained more or less inactive on the substrate or attached to the sides of the container for the first two days. After this time they became very active as their fins developed more fully and by the fourth day were seen to be browsing on the substrate and weeds. Efforts at rearing them further than this stage were unsuccessful.

Spawning experiments with *H. unilineatus* were not as successful as with *C. riisei* and only four females spawned on the weed provided (Table 31). Differentiating between the sexes in small specimens was often difficult and many combinations of different individuals and trials were attempted before successful spawning was attained. Despite the paucity of data for this species however, certain differences could be seen when compared with *C. riisei*.

TABLE 31: Summary of results of laboratory spawning experiments for *H. unilineatus*.

Female	SL (mm)	Total number clutches	Total spawning period (d)	Total number of eggs	Intervals between clutches (d)			Clutch sizes	
					Mean ± SE	Mode	Range	Mean ± SE	Range
F1	38	13	37	1014	3.0 ± 0.3	3	1-5	78.0 ± 11.3	21-163
F2	36	3	7	437	3.0 ± 0.0	3	-	145.7 ± 91.9	43-329
F3	35	6	15	97	2.8 ± 0.6	4	1-4	16.2 ± 6.3	3- 39
F4	35	2	5	64	4.0	-	-	32.0 ± 29.0	3- 61

SE : Standard Error

Total fertility of *H. unilineatus* ranged from 64 to 1014 eggs spawned over periods up to 37 days. Numbers of clutches spawned varied from 2 to 13 and average clutch size ranged from 16.2 to 145.7 eggs. Generally clutch sizes were comparable to those of *C. riisei* but were spawned over shorter overall periods with greater intervals between clutches (modal interval 3 to 4 days, mean intervals 2.8 to 4 days for *H. unilineatus*). Spawning patterns tended to indicate a gradually decreasing clutch size over the breeding period, for example female 2 (Fig. 71). *H. unilineatus* thus showed a small brood spawning pattern similar to *C. riisei* but individuals did not spawn for as prolonged periods as the latter species.

Eggs of *H. unilineatus* were approximately the same size as those of *C. riisei* and hatched within 24 hours. Larval development was similar to *C. riisei*.

Only limited breeding of *P. reticulata* was attempted due to lack of space and concentration on other species. In particular, breeding was undertaken only to obtain data on age at maturation and breeding periodicity. Periods between successive broods were found to be approximately five weeks. Since the exact time of fertilisation could not be determined, the time for brood development was not ascertained. Brood sizes varied from

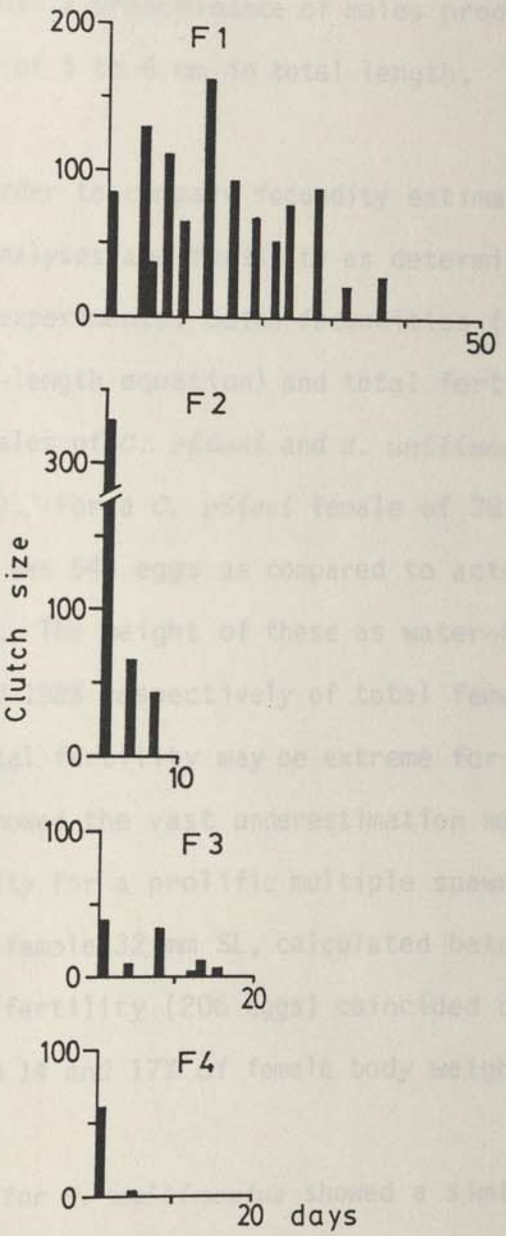


FIGURE 71: Laboratory spawning patterns for *H. unilineatus*.

4 to 11 with a predominance of males produced. Young were born at a size of 5 to 6 mm in total length.

In order to compare fecundity estimates by conventional ovarian analyses and fertility as determined in laboratory spawning experiments, batch fecundities (calculated from the fecundity-length equation) and total fertilities for different sized females of *C. riisei* and *H. unilineatus* were compared (Table 32). For a *C. riisei* female of 38 mm calculated batch fecundity was 544 eggs as compared to actual total fertility of 4987 eggs. The weight of these as water-hardened eggs amounted to 22% and 198% respectively of total female body weight. Such a high total fertility may be extreme for this species. Nevertheless it showed the vast underestimation made by ovarian estimates of fecundity for a prolific multiple spawner such as this. For a smaller female 32 mm SL, calculated batch fecundity (243 eggs) and total fertility (206 eggs) coincided closely and amounted to between 14 and 17% of female body weight.

Data for *H. unilineatus* showed a similar trend with ovarian fecundity estimates being lower than fertility for a large female but not with as great a discrepancy as seen in *C. riisei*. In the examples used, total egg weight to female body weight ratio (using the same unit egg weight as *C. riisei*) was low

TABLE 32: Comparison of batch fecundity and total fertility as numbers of eggs and as egg weight: female body weight ratio for *C. riisei* and *H. unilineatus* individuals of different sizes.

Species	SL (mm)	Batch Fecundity		Total Fertility		Fertility: fecundity ratio
		Predicted numbers of eggs	Egg weight: body weight (%)[1]	Recorded numbers of eggs	Egg weight: body weight (%)[1]	
C. riisei	38	544	22	4987	198	8.2
"	37	480	21	1451[2]	63	2.8
"	32	243	17	206	14	1.0
H. unilineatus	38	642	17	1014	27	1.6
"	36	545	17	437	14	0.8

[1]: Egg weight calculated as weight of water hardened eggs using unit egg weight recorded for *C. riisei* (0.305 mg); female body weight calculated from length-weight relationship for freshly-killed specimens (Appendix 8).

[2]: Average fertility for two females (F2 and F3).

(not more than 27%) compared to *C. riisei*. Smaller *H. unilineatus* females also showed close agreement between batch fecundity and total fertility (Table 32).

From the above comparisons, it appeared that small individuals may mature one batch of eggs and spawn all of these in several clutches over relatively short periods of time. However, larger females seemed to have a different strategy where the equivalent of several batches of eggs could be matured successively and spawned in many clutches over prolonged periods. By comparing total fertility and batch fecundities for *C. riisei* (Table 32) it may be deduced that the equivalent of from 1 to 8 batches may be matured successively and spawned almost continuously over periods of 3 to 5 months depending on the size of the female. A large female *H. unilineatus* showed less than the equivalent of two batches of eggs maturing and being spawned over a five week period.

Data on mean clutch sizes for *C. riisei* suggested that one batch of eggs could be spawned in 6 to 10 clutches. For some females which spawned in the laboratory, for example female 3 (Fig.70), numbers of clutches spawned closely together coincided with this range.

Oocyte size distribution analyses:

Oocyte size distribution studies were conducted for all species except *P. reticulata*. In most cases, ovaries which were analysed were developing, developing/mature, mature and spent. One immature ovary was analysed for *H. unilineatus* for purposes of comparison.

Gasteropelecus sternicla

Oocyte size frequency histograms for developing/mature ovaries in this species showed a large proportion of reserve previtellogenic oocytes (0.024 - 0.170 mm), an intermediate group of small vitellogenic oocytes and a smaller group of oocytes within the mature size range for this species (>0.559 mm) (Fig. 72). As maturity was attained both modal and maximum sizes of the ova within the largest size range increased. Mature ovaries were all excised from ripe-running fish and showed increasing proportions of mature-sized ova with increase in GSI. There were also comparatively more small vitellogenic oocytes within the 0.243 to 0.486 mm range in larger ovaries and in some ovaries they seemed to constitute an intermediate peak of oocytes. In the mature ovaries, there was a fairly distinct separation between mature-sized ova and these smaller

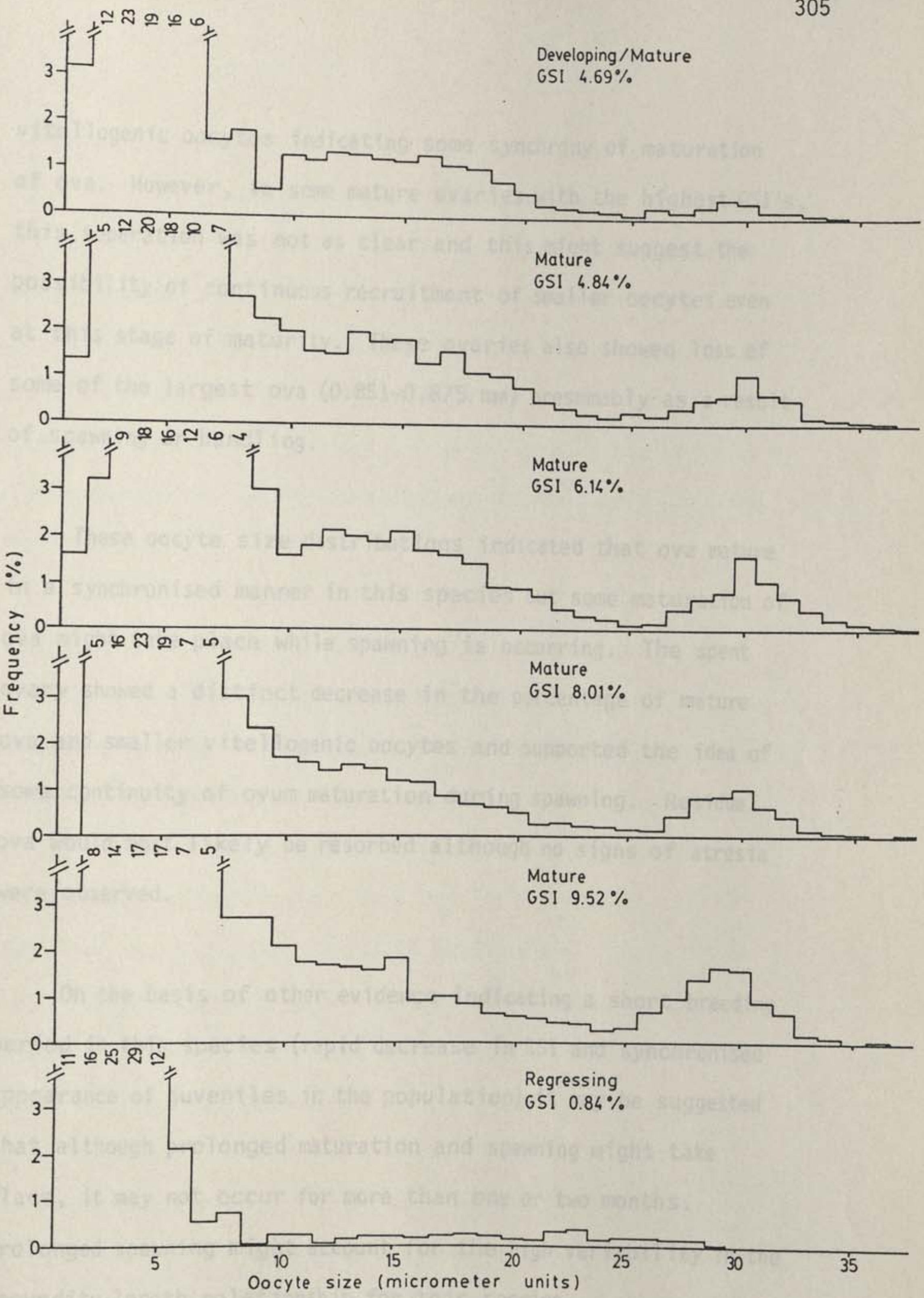


FIGURE 72: Oocyte size distribution analyses for G. sternicla (1 micrometer unit = 0.0243 mm; numbers at top represent percentage frequency).

vitellogenic oocytes indicating some synchrony of maturation of ova. However, in some mature ovaries with the highest GSI's, this separation was not as clear and this might suggest the possibility of continuous recruitment of smaller oocytes even at this stage of maturity. These ovaries also showed loss of some of the largest ova (0.851-0.875 mm) presumably as a result of spawning or handling.

These oocyte size distributions indicated that ova mature in a synchronised manner in this species but some maturation of ova might take place while spawning is occurring. The spent ovary showed a distinct decrease in the percentage of mature ova and smaller vitellogenic oocytes and supported the idea of some continuity of ovum maturation during spawning. Residual ova would most likely be resorbed although no signs of atresia were observed.

On the basis of other evidence indicating a short breeding period in this species (rapid decrease in GSI and synchronised appearance of juveniles in the population) it may be suggested that although prolonged maturation and spawning might take place, it may not occur for more than one or two months. Prolonged spawning might account for the high variability in the fecundity-length relationship for this species.

Corynopoma riisei

Analysis of ovaries from this species showed that even in mature ovaries oocyte distribution was almost continuous from small previtellogenic oocytes to mature-sized ova (Fig. 73). A small peak of mature-sized ova could be seen in the largest mature ovary. The partially spent ovary showed loss of many of the large ova while the spent ovary was lacking the majority of these as well as smaller vitellogenic oocytes; only very few ova remained.

Oocyte distribution indicated asynchronous and possibly continuous maturation of ova in time since there was no clear distinction between mature ova and smaller vitellogenic oocytes. Continuous recruitment of small oocytes into the mature size range indicated the potential for multiple spawning over a prolonged breeding period. This was confirmed with data obtained from laboratory spawning experiments. Similarly in order to maintain the high level of egg production seen in these experiments, continuous development of reserve oocytes would also have to take place.

Astyanax bimaculatus

The distribution of oocyte sizes in this species showed two main groups of oocytes: small reserve oocytes and small

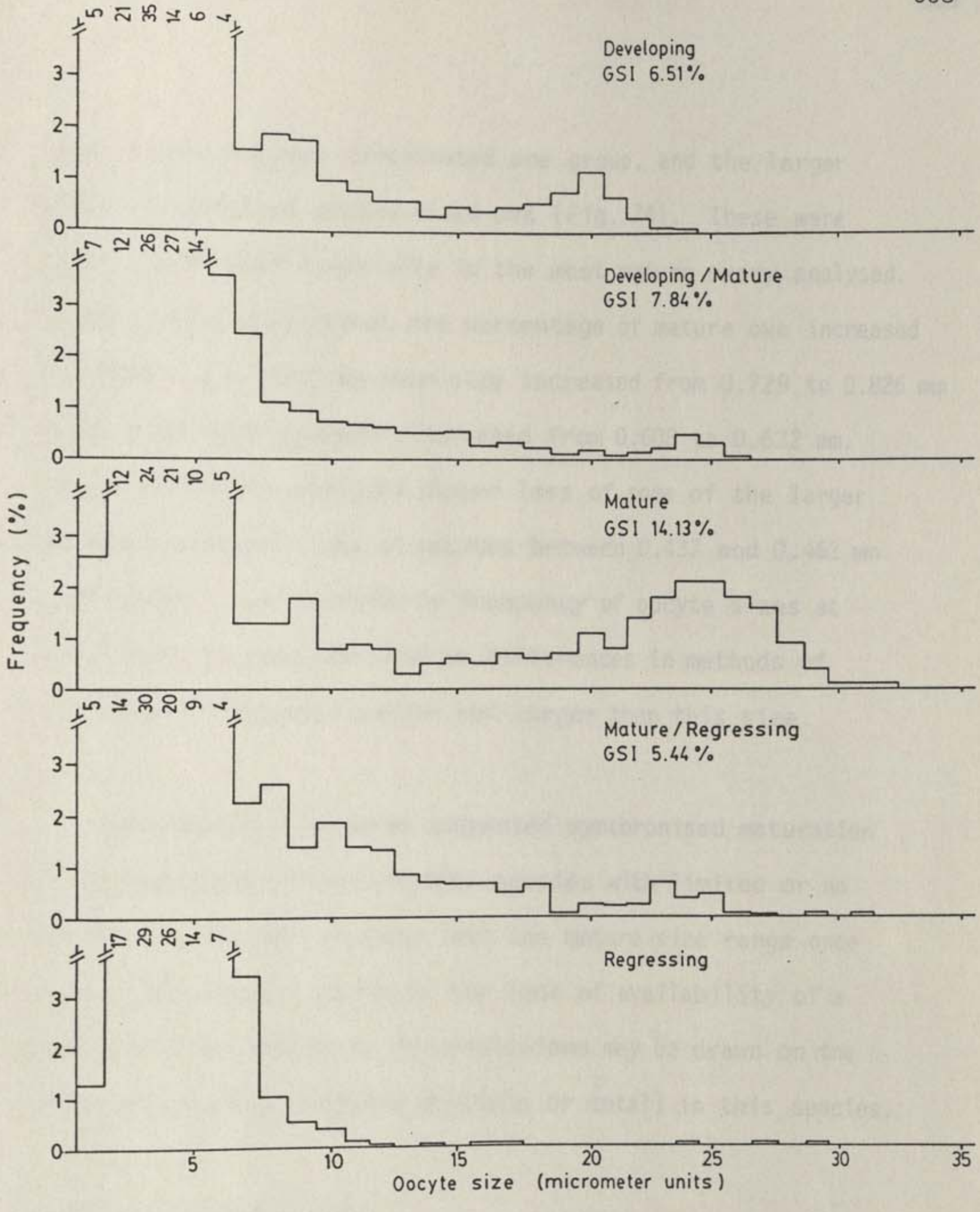


FIGURE 73: Oocyte size distribution analyses for C. riisei (information as for Figure 72).

vitellogenic oocytes constituted one group, and the larger group consisted of mature-sized ova (Fig. 74). These were clearly separated especially in the most mature ovary analysed. As maturation progressed, the percentage of mature ova increased substantially. Maximum ovum size increased from 0.729 to 0.826 mm while modal ovum diameter increased from 0.608 to 0.632 mm. The largest ovary analysed showed loss of some of the larger ova and a distinct lack of oocytes between 0.437 and 0.462 mm in diameter. The increase in frequency of oocyte sizes at 0.243 mm might have been due to differences in methods of estimation of oocytes smaller and larger than this size.

The distribution shown suggested synchronised maturation of a large number of ova in this species with limited or no recruitment of small oocytes into the mature size range once spawning has begun. Owing to the lack of availability of a spent ovary for analysis, no conclusions may be drawn on the nature of spawning (whether multiple or total) in this species.

Hemigrammus unilineatus

Ovarian size distribution analysis was difficult for this species because of lack of any developing ovaries for analysis and the difficulties in differentiating between early mature and partially spent ovaries. An immature ovary only contained

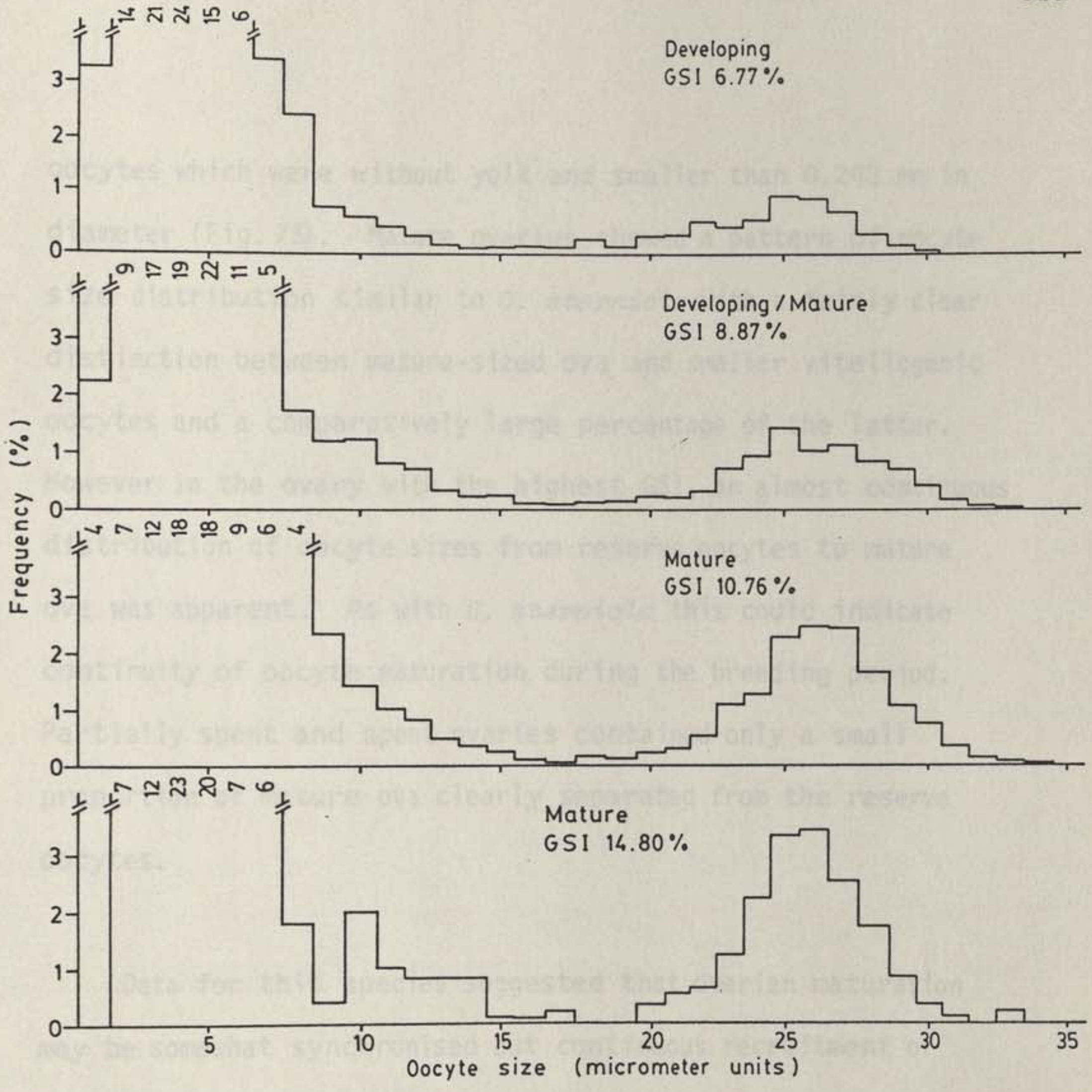


FIGURE 74: Oocyte size distribution analyses for A. bimaculatus (information as for Figure 72).

oocytes which were without yolk and smaller than 0.243 mm in diameter (Fig. 75). Mature ovaries showed a pattern of oocyte size distribution similar to *G. sternicla* with a fairly clear distinction between mature-sized ova and smaller vitellogenic oocytes and a comparatively large percentage of the latter. However in the ovary with the highest GSI, an almost continuous distribution of oocyte sizes from reserve oocytes to mature ova was apparent. As with *G. sternicla* this could indicate continuity of oocyte maturation during the breeding period. Partially spent and spent ovaries contained only a small proportion of mature ova clearly separated from the reserve oocytes.

Data for this species suggested that ovarian maturation may be somewhat synchronised but continuous recruitment of small vitellogenic oocytes during breeding is not precluded. Partially spent and spent ovaries indicated multiple spawning to some degree since all the ova were not spawned at once. Laboratory spawning experiments confirmed multiple spawning in this species with a limited number of small clutches being produced. Numbers of eggs spawned during these experiments indicated continuous recruitment of smaller vitellogenic oocytes must also take place during the breeding period in some individuals.

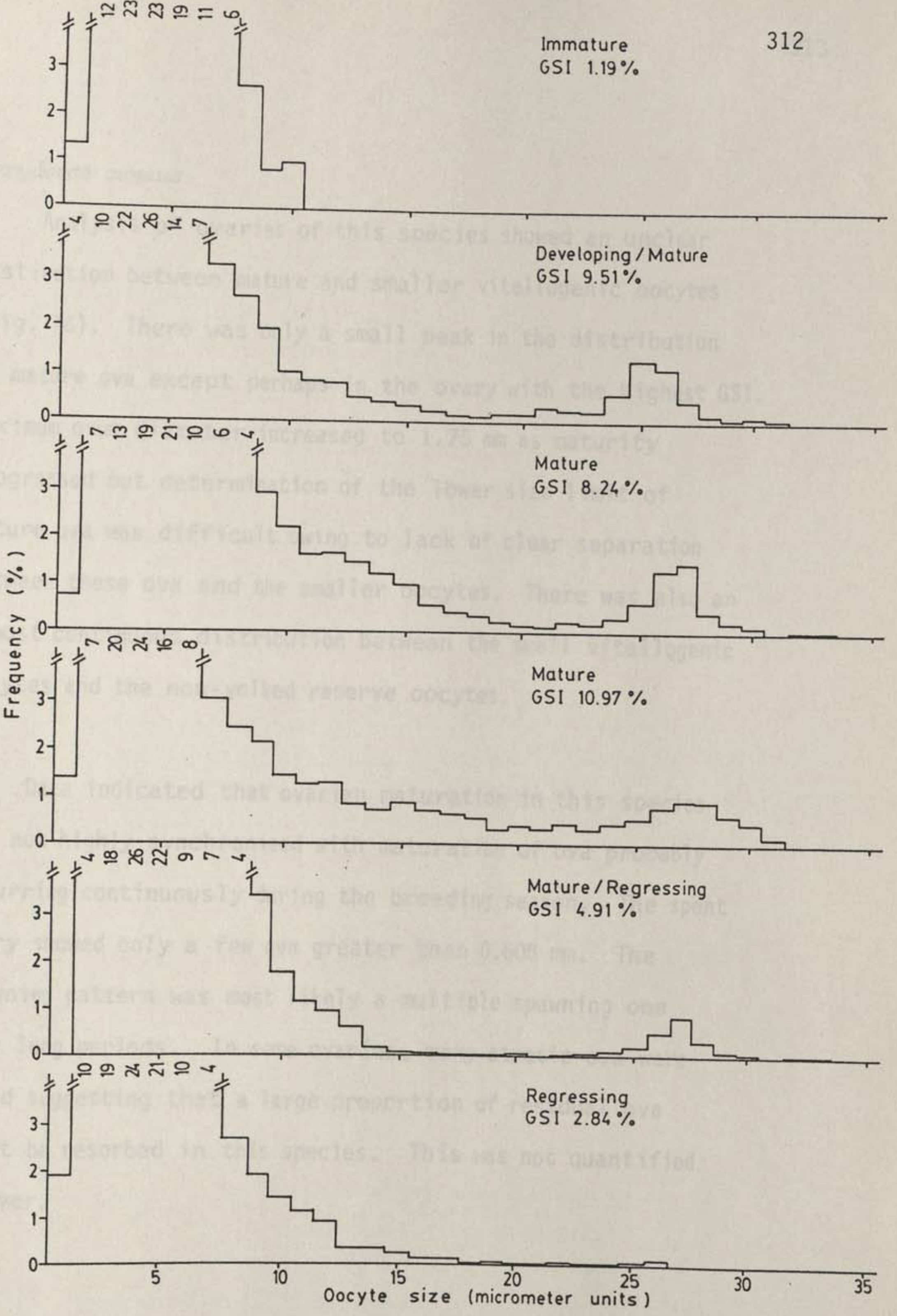


FIGURE 75: Oocyte size distribution analyses for *H. unilineatus* (information as for Figure 72).

Corydoras aeneus

Analysis of ovaries of this species showed an unclear distinction between mature and smaller vitellogenic oocytes (Fig. 76). There was only a small peak in the distribution of mature ova except perhaps in the ovary with the highest GSI. Maximum ovum diameter increased to 1.75 mm as maturity progressed but determination of the lower size limit of mature ova was difficult owing to lack of clear separation between these ova and the smaller oocytes. There was also an almost continuous distribution between the small vitellogenic oocytes and the non-yolked reserve oocytes.

Data indicated that ovarian maturation in this species was not highly synchronised with maturation of ova probably occurring continuously during the breeding season. The spent ovary showed only a few ova greater than 0.608 mm. The spawning pattern was most likely a multiple spawning one over long periods. In some ovaries, many atretic ova were found suggesting that a large proportion of residual ova might be resorbed in this species. This was not quantified however.

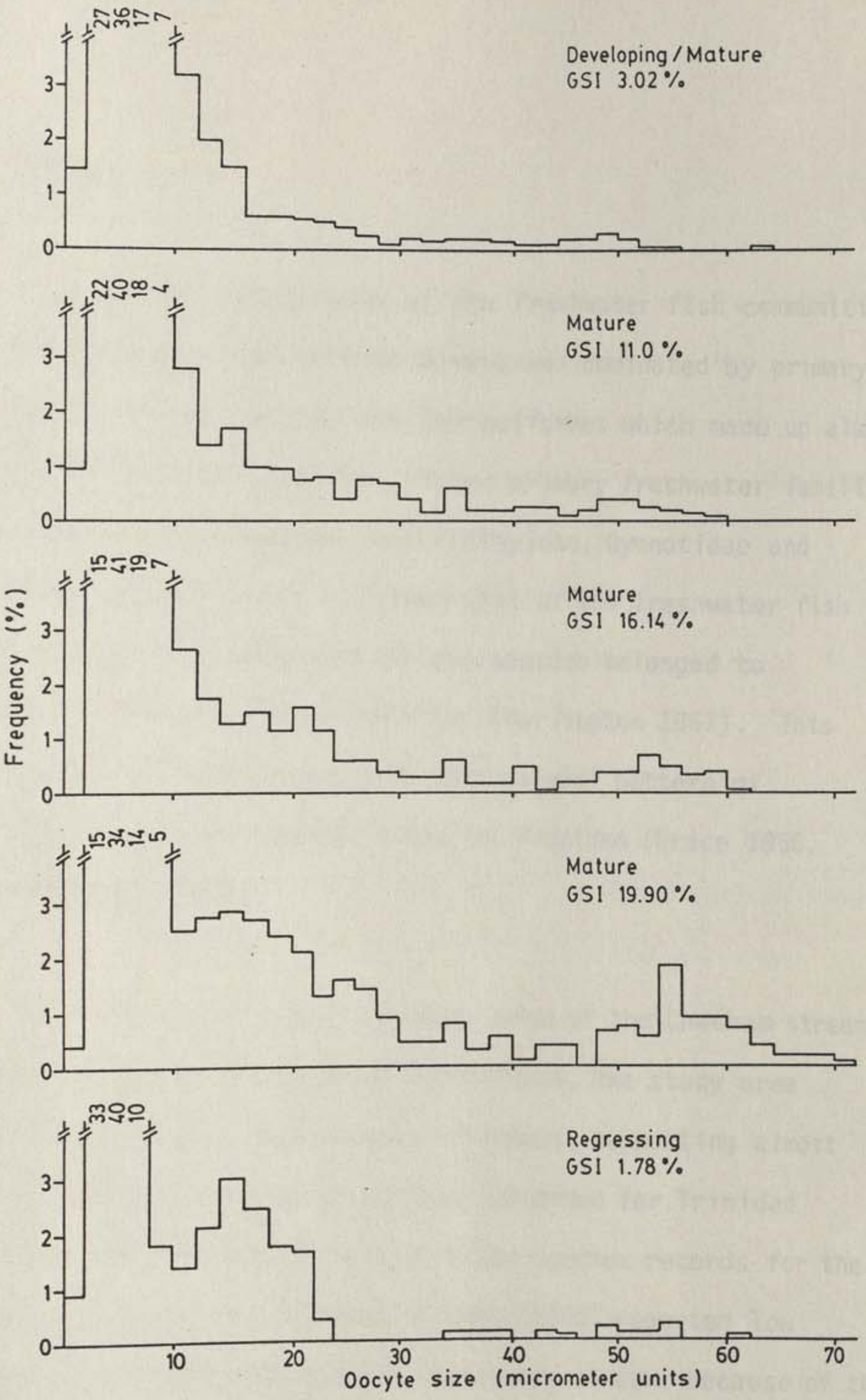


FIGURE 76: Oocyte size distribution analyses for C. aeneus (information as for Figure 72).

DISCUSSION

The species composition of the freshwater fish communities of the Quarahoon and Carlisle Rivers was dominated by primary freshwater fishes such as the Characiformes which made up almost 50% of the species recorded. Other primary freshwater families recorded were Pimelodidae, Callichthyidae, Gymnotidae and Nandidae accounting for a further 26% of the freshwater fish species while the remainder of the species belonged to secondary freshwater fish families (Darlington 1957). This composition was consistent with the general pattern of distribution of freshwater fishes in Trinidad (Price 1955, Boeseman 1960, 1964).

In spite of the small drainage area of the Chatham streams and the exacting environmental conditions, the study area possessed a notably high species richness, supporting almost half of the true freshwater species recorded for Trinidad (Boeseman 1960) in addition to two new species records for the island. In contrast, Williams & Coad (1979) reported low diversity of fishes in Canadian temporary streams because of the need for physiological tolerance or migratory patterns to withstand the harsh conditions of this habitat. A study of the Bandama River, Ivory Coast (Lévêque *et al* 1983) noted that more than 80 species were recorded for this drainage within a catchment area of 97,500 km²; approximately that predicted by species number/catchment area relationships (Welcomme 1979). However such relationships are not reliable predictors of diversity for basins of extremely small area such as the study site.

Factors which have generally been proposed to affect the species diversity of communities include time, environmental stability, spatial heterogeneity, productivity, competition and predation (Lowe-McConnell 1975, Krebs 1985). In addition, the intermediate disturbance hypothesis proposes that extreme levels of disturbance of communities would result in low species diversity whereas intermediate levels would favour increased diversity (Connell 1978, Krebs 1985). Such disturbance levels may be dictated by both frequency or intensity of disturbance (Krebs 1985). It was proposed by Sanders (quoted in Lowe-McConnell 1975) that predictable oscillations of long-term sequence could produce high levels of diversity, a situation exemplified by tropical rivers with regular cycles of flooding (Lowe-McConnell 1975, Beumer 1980). Cyclical fluctuations in conditions did occur in the streams studied although predictability was comparatively low. Nevertheless extensive refuge pools and long flow conditions may have mediated the detrimental effects associated with unpredictability or particularly harsh flood/drought conditions to promote high species richness (Clifford 1966).

A further factor which may have been contributory to high species richness at the study site was the dynamic state of local faunas in the southwest peninsula as a result of colonisation of species from the nearby mainland. Of the nine characoid fishes recorded, three were recently established colonisers and two were new records during the study period. *G. sternicla* and *M. bondi* are reported only in a restricted number of streams in southwestern Trinidad (Price 1955, Boeseman 1960) and evidence points to their being recent colonists (Price 1955). *E. erythrinus* is not recorded by Boeseman (1960, 1964) having been caught only within recent times in a small north-flowing watercourse in a drainage immediately adjacent to the Chatham basin (Kenny, pers. comm.). While not all colonist species establish populations, at least these three relatively recent arrivals have done so and a fourth *T. elongatus*, may be in the process of establishment. Faunal diversity trends in some North American river systems have been shown to be explained in part by the proximity of basins to rich source areas (Horowitz 1978).

With the exception of the above species which are of restricted distribution, all of the other freshwater species are widely distributed and common throughout Trinidad south of the Northern Range (Guppy 1934, 1936, Price 1955, Boeseman 1960). Some species are commonly found in ponds, ditches and slow-flowing watercourses, for example *G. carapo* and *C. callichthys* while others are found in middle to lower course rivers, for example *R. sebae, C. aeneus* and *S. marmoratus,* and the characids *A. bimaculatus, H. unilineatus* and *C. riisei.* In particular, *P. reticulata, C. riisei* and *A. bimaculatus* have been reported to be the three most common species in Trinidad (in order of decreasing abundance) based on analysis of the numbers of collections made by Price (1955) containing these species (Nelson 1964). In addition, Nelson showed that *C. riisei* and *A. bimaculatus* were significantly associated with each other and with three other species: *H. unilineatus, C. aeneus* and the cichlid, *C. bimaculatum.* He attributed this association to common exclusion from particular habitats, specifically those with high gradients or those tending to become brackish in the dry season.

Many of the species collected from the Chatham streams have been shown to have some ability to withstand fluctuating environmental conditions, particularly stagnation and associated hypoxia, increased predation and crowding (Carter 1935, Lowe-McConnell 1964). Air-breathing has been recorded for *E. erythrinus*, *Callichthys*, *C. aeneus* and *S. marmoratus* (Kramer 1978b, Kramer & McClure 1980) and suggested for *C. bimaculatum* (Lowe-McConnell 1964). An air-breathing ability and a capacity for overland movement (for example in *R. hartii*, *C. callichthys* and *S. marmoratus*) permits the colonisation of new habitats which may be more favourable. Use of the oxygen-rich surface water for respiration has been reported for many Neotropical fish species (Carter 1935, Lowe-McConnell 1964, Lewis 1970, Kramer & McClure 1982) including *P. reticulata* (Kramer & Mehegan 1981), and species of the genera *Hoplias*, *Astyanax*, *Rhamdia*, *Rivulus* and *Cichlasoma* in Panama (Kramer 1983). Myers (1947) and Kramer *et al* (1978) recorded the ability of *S. marmoratus* to survive in an active state without free water in burrow systems in the Amazon. Despite the capacity for many species to withstand harsh environmental conditions, species richness was greater for the deeper, more permanent pools in the streams. In addition, the larger species were found in the bigger, deeper pools comparable with other studies elsewhere (Holden 1963).

The species of the brackish water Station 4 included representatives of a euryhaline freshwater family, the

Poeciliidae, while all the other species belonged to euryhaline marine families (Miller 1982). *C. parallelus* and *M. curema* have been commonly found in brackish water habitats in Trinidad (Boeseman 1960). The use of the lower estuarine reaches of rivers as a nursery ground is relatively well documented (Beumer 1980).

Total populations of the six species studied showed wide variation over time and correlated with stream discharge rates and inputs of juveniles during the reproductive seasons. Migratory movements may have also played a role in determining population densities of certain species. Prolonged rainfall into the early part of the 1982 dry season indicated that moderate flow regimes were ideal for both reproduction and survival leading to high population sizes of most species at this time. The role of flood events in decreasing fish population sizes has been well documented in many rivers and streams which are subject to highly seasonal flows (Hynes 1970, Brown 1971, Deacon & Minckley 1974, Beumer 1980, Collins *et al* 1981). In particular, streams with narrow courses and steep banks are more likely to show the destructive effects of flooding than those with low banks or wide braided courses (Deacon & Minckley 1974). Presence of small tributaries or floodplain pools have also been shown to be important as refuges during floods in desert rivers (Deacon & Minckley 1974). Severe floods may affect adults and juveniles as well as recently spawned eggs (Paloumpis 1958, Seegrist & Gard 1972) although John (1964) maintained that young of the year were most affected due to their reduced swimming ability.

In the Bandama River, Lévêque *et al* (1983) suggested that decreases in fish catches with floods were not due to reduction in population sizes but the inefficiency of sampling methods under these conditions. Increased habitat size resulting in decreased densities of fish is also an important consideration especially in floodplain rivers where mortality is assumed to be low at the time of floods (Welcomme 1979). At the study sites, washouts due to the narrow channel were likely to have been the major cause of low catches during the rainy seasons with habitat expansion into small drainage channels playing a minor role. It was presumed that tributaries and deeper pools where current flow was reduced acted as refuges during floods. Recovery of populations after flooding was rapid as documented in other studies (for example Deacon & Minckley 1974, Beumer 1980).

In contrast, during drier periods, population densities increased primarily due to habitat contraction. Although

Shirvell (1981) postulated that stream flow was not always inversely related to fish density because behaviour such as territoriality at times of habitat contraction could act to maintain individual spacing and promote migration to other pools. Mortality did not appear to be particularly high at these times except when complete drying out of smaller pools took place. The ability of many species to withstand stagnant conditions and crowding and access to an extensive series of refuge pools most likely played major roles in enhancing fish survival unlike other situations where drought induced high mortalities in North American intermittent streams (Paloumpis 1958, John 1964) and on tropical floodplains (Lowe-McConnell 1975, Welcomme 1979).

Population sizes also fluctuated as a result of large numbers of juveniles, particularly of *A. bimaculatus*, *H. unilineatus* and *C. riisei*, entering the population during the rainy seasons once or twice each year. Highly synchronised seasonal spawning patterns of high fecundity species have been shown to lead to great fluctuations in fish populations of tropical rivers (Lowe-McConnell 1969). Lévêque *et al* (1983) also noted that failure of floods in certain years could lead to relatively smaller increases in population at these times due to a lack of a reproductive stimulus.

Population fluctuations in *P. reticulata* in particular reflected a pattern of mortality very much dictated by periodic flooding although some possibility of a density dependent population control mechanism might have existed. Reproductive capacity of female guppies in laboratory-kept populations is known to be affected by a variety of factors including photoperiod (Turner 1937), artificial illumination (Scrimshaw 1944), water temperature (Dildine 1936), food (Silliman 1948, Hester 1964), copulation frequency (Breder & Coates 1932), living space (Rose 1959, Rose & Rose 1965) and population density (Warren 1973 a, b, c, Dahlgren 1979). However, this study showed no obvious density-related changes in fecundity. In other studies, Rosenthal (1952) and Yamagishi (1976) found cyclical reproductive patterns where numbers of young increased to a maximum then decreased over time. Yamagishi (1976) attributed these to peaks in reproductive activity of successive generations of females occurring at 24 to 36 week intervals; no such trends were observed in the present study.

Relative abundances of the six species changed over the study period with *G. sternicla* becoming comparatively abundant towards the end of the study. This could be attributed to several consecutive successful reproductive seasons for this species. Evidence for such shifts in relative abundances of fish species has been widely documented for North American streams (Starrett 1951, Seegrist & Gard 1972, Deacon & Minckley 1974, Grossman *et al* 1982, Waters 1983, Schlosser 1982, 1985, Minshall *et al* 1985). These studies correlated such changes in community composition with variability in reproductive success and juvenile survival for different species due to interannual differences in hydrological regimes. Grossman *et al* (1982) after a 12-year study of an Indiana stream fish assemblage concluded that stochastic forces play a decisive role in the determination of structural and functional properties of many stream fish assemblages. Changes in relative abundance of fishes have also been noted in tropical systems, for example Holden (1963) and Lowe-McConnell (1964).

Life history parameters and reproductive characteristics of the six species studied are summarised in Table 33. Generally, individuals matured early and had relatively short lifespans. The largest species *A. bimaculatus* showed a greater estimated age at first maturation and lifespan than the other smaller species. In some species, the reproductive strategy seemed to be to maximise production of eggs or young at any favourable time of the year but usually breeding was associated with one or both of the twice yearly rainfall maxima. Reproductive timing ranged from close coincidence with the onset of the rains for

TABLE 33: Summary of life history parameters and reproductive characteristics of the six fish species studied.

	G. sternicla		*C. riisei*		*A. bimaculatus*		*H. unilineatus*		*C. aeneus*		*P. reticulata*	
	F	M	F	M	F	M	F	M	F	M	F	M
Maximum SL (mm)	49	42	37	39	76	82	39	33	60	53	25	16
Maximum TW (g)	4.333	2.466	0.828	0.824	15.757	17.801	1.413	0.857	10.414	6.120	0.394	0.076
Minimum Mature SL (mm)	33	31	26	26	57	56	25	21	34	34	11	9
Minimum mature age (mo)	8-11		8-9		16?		11	9	24[1]		2-3	1-2
Maximum life span (mo)	28	17	21	24	36?		20	16	36-48?		15[2]	
Population size variability	medium		high		very high		very high		medium		very high	
Mode of reproduction	oviparous		oviparous		oviparous		oviparous		oviparous		ovoviviparous	
Fertilisation	external		internal		external		external		external		internal	
Parental care	none		none		none		none		none		none	
Offspring size[3] (mm)	ND		3.0		2.54-2.61[4]		3.0		4.0[5]		5-6	
Mature ovum size (mm)	0.7-0.9		0.6-0.9		0.6-0.9		0.6-0.95		1.5-1.75		1.2-2.0	
Maximum GSI (%)	12.262	2.955	14.130	2.398	14.800	1.447	13.101	2.083	21.169	1.144	25.714	11.290
Maximum batch fecundity	1458		833		6364		787		1046		26	
Maximum fertility	ND		4987/season		ND		1014/season		1200/year[6]		ND	
Breeding season length (mo)	1-2		2-4		1-2		2-4		1-4		continuous	
Spawnings/season	multiple?		multiple		multiple?		multiple		multiple		multiple	
Breeding seasons/year	1, rarely 2		2		1 major, 1 minor		2		2		NA	
Breeding seasons/lifetime	3?	2?	1-2?		>2		1-2?	1?	3?	2?	up to 17[7]	

[1] : Schofield (1957) [2]: Thibault & Schultz (1978) [3]: Size at hatching/birth [4] : Azevedo & Vieira (1938) [5] : Adams (1946) [6] : Hart (1947)
[7] : Broods per lifetime, Bowden (1970) ND : not determined NA : not applicable F : female M : male

relatively short periods (one or two months in *G. sternicla* and *A. bimaculatus*) to more prolonged breeding periods during the rainy season (up to four months in *C. riisei, H. unilineatus* and *C. aeneus*) to continuous breeding (*P. reticulata*). Female GSI's were highest for *P. reticulata* and *C. aeneus* and were roughly equivalent for the other species. Generally batch fecundity was correlated with individual size and maximum batch fecundity for each species was directly dependent on species size. Batch fecundities were highest for *A. bimaculatus* and lowest in *P. reticulata;* other species had intermediate batch sizes. However, maximum fertilities for *C. riisei* and *H. unilineatus* were high and comparable with batch fecundities of the larger species as a result of the multiple spawning habit.

Data available for some of these species either locally or in other regions agreed in many respects with that from the present study. In particular, data were available for *C. riisei, A. bimaculatus* and *P. reticulata.*

Nelson (1964) reported that spawning of *C. riisei* occurred predominantly at the beginning of the rainy season in Trinidad streams although they spawned at all times of the year in the laboratory. Under aquarium conditions sexual differentiation was seen in males at 17 weeks (Nelson 1964). In comparison full gonadal maturation of males and females was observed between eight and nine months of age in the present study, but the development of secondary sexual characters began earlier in males. In addition male size may be an important factor in female choice for this internally fertilising species where female receptivity is constantly low (Nelson 1964). Since males are normally larger than females, delayed maturity to a larger size would be advantageous and enhance the male's attractiveness to females.

A. bimaculatus is also reported to be a rainy season spawner in Brazil (Azevedo & Vieira 1938, de Godoy 1975, Nomura 1975 c, Pelizaro *et al* 1981). Azevedo & Vieira (1938) described 'piabas' (including *A. bimaculatus*) spawning immediately after the first rainfall and spawning more than once during the season. Multiple spawning over a prolonged season was confirmed by Pelizaro *et al* (1981) although the source of their specimens was denoted as 'tanks in the Department of Zoology, UNESP, Sao Paulo' (p. 416). Data of Nomura (1975 c) indicated a breeding period when GSI's were high up to three months long and he concluded that this species was a total spawner.

Upstream movement for spawning was described for 'piabas' by Azevedo & Vieira (1938) and for two Brazilian subspecies of *A. bimaculatus* by de Godoy (1975) with spawning actually taking place in small tributaries or shallows. Such migratory behaviour could account for the lack of adults in catches at the study site and the movement of larger juveniles out of the areas sampled and probably into other feeding areas or larger pools downstream. Azevedo & Vieira (1938) noted female-biased sex ratios but attributed them to the inefficiency in capturing the smaller males.

Data on age and growth for *A. bimaculatus* in the present study were somewhat unreliable and seemed to contrast with Nomura's (1975 c) estimates of median length at maturity at 92.5 mm total length (TL) at two years for males and 104.0 mm TL at three years for females. However, Nomura found that the minimum size class at maturity was 65 mm TL for males and 70 mm TL for females; almost identical sizes to those recorded in the present study (56 to 57 mm SL). Further, it would not be unexpected that under more exacting environmental conditions in a smaller habitat as that of the study site, maturation might occur at a smaller size or younger age. Nomura (1975 c) noted that fecundity of *A. bimaculatus* was significantly correlated with total lengths of fish and batch fecundity estimates from the Chatham population fitted the lower portion of his fecundity-length curve. Maximum fecundity recorded by Nomura was 31,778 eggs for a 137 mm TL female. In contrast, GSI's from the present study were higher than those recorded by Nomura, that is maximum female GSI 10.90%, maximum male GSI 0.98%.

The only other species for which life history data from natural populations are available is *P. reticulata*. Liley & Seghers (1975) found that sizes of lowland stream guppies in Trinidad were smaller on average than those from upper or middle course habitats. For three lowland sites, mean SL of females ranged from 16 to 17 mm whereas male SL ranged from 12 to 14 mm. Such differences were attributed to size selective predation by large predators such as *Crenicichla alta*. Reznick (1980) and Reznick & Endler (1982) analysed this phenomenon in more detail and found that for localities where *C. alta* was the dominant predator, guppy sizes were smaller than at other sites where either *Rivulus hartii* or *Aequidens pulcher* were dominant. At *Crenicichla* sites mean male size at maturity for guppies (mean of 10 randomly chosen males) was 14.88 mm SL while minimum size of gravid female guppies (SL at which two-thirds of females therein contained developing embryos) was 14. 6 mm SL. At the Chatham sites guppy sizes were found to be even smaller than those recorded by either Liley & Seghers (1975) or Reznick & Endler (1982) namely, mean male size was 11.9 mm SL (N = 503), mean female size was 15. 1 mm SL (N = 1043) and minimum gravid female size was 12.8 mm SL (N = 1043).

Male guppy sizes are generally smaller than females as with most poeciliids due to cessation of growth of males after maturity and shunting of energy into courtship and other related activities (Endler 1984). Persistent growth of females after maturity takes advantage of increased fecundities being possible with increased body size (Miller 1979, Endler 1984). Endler (1984) also suggested that in areas of high predation or low food availability, average female body size may decrease because of the greater efficiency of small females in bearing young. At the same time however, males may also be smaller but the extent of body size reduction would not be as great as for females and under these conditions sexual dimorphism in size tends to be reduced, that is male : female size ratio approaches unity. In the present study mean male : mean female size ratio was 0.79 while mean male : minimum gravid female size ratio was 0.93. The latter ratio was lower than those quoted for areas with high predation (1.01) and areas with weak predation (0.94) by Endler (1984, from data of Reznick & Endler 1982) thus suggesting low levels of predation on guppies at the study site. From observations however, the study area supported a high diversity of potential guppy predators including *Crenicichla alta*, *Astyanax bimaculatus*, *Cichlasoma bimaculatum*, *Rivulus hartii*, *Polycentrus schomburgkii*, *Hoplias malabaricus*, *Gymnotus carapo* and *Synbranchus marmoratus* in addition to arthropod predators such as the nepid, *Ranatra* which was commonly found. Such a range of predators as well as the seasonal concentration of guppies into small pools during the dry season with these predators would in fact suggest very high levels of predation on Chatham guppy populations. Size reduction may be due more to environmental seasonality and unpredictable mortality associated with floods and drought.

Reznick & Endler (1982) also determined that guppies from *Crenicichla*-dominant sites had shorter interbrood intervals than at other sites. Their estimate of mean interbrood interval for *Crenicichla* sites was 24.1 days compared to five weeks for Chatham guppies. However, the latter estimate was based on very few samples and should be treated with some caution as a generalisation for this population.

Crenicichla-dominant sites were also found to support guppies with high brood fecundities (Reznick & Endler 1982).

For example they found the highest predicted fecundity for a 20 to 21 mm SL female was eight offspring while in the present study, guppies of the same size had a predicted brood size of 12. High fecundity could be an adaptation to compensate for high mortality from a range of potential predators as well as being a trait favoured by the seasonal conditions at the study site. Dahlgren (1979) suggested that if guppy populations frequently pass through periods of low density, genotypes for comparatively high fecundity or fertility would increase in frequency under these conditions and remain common in the gene pool at other times.

Continuous reproduction throughout the year would also increase the reproductive capacity of the species. It is generally quoted that guppies reproduce continuously (Scott 1979, Lam 1983) but all studies have been laboratory-based unlike the present one which now confirms continuous breeding in natural populations of this species. Other factors which could potentially affect reproductive capacity of guppies appear not to be important at the study sites, that is population density and food availability (Dahlgren 1979, 1980 a, b). Neither density-related reduction in fecundity nor seasonal variation in brood sizes were found; at all times brood sizes and GSI's were high. Dahlgren (1980 a ,b) stressed the very adaptable nature of this species with respect to utilising food of variable quality.

Other characteristics of the Chatham guppies compared favourably with those obtained from laboratory-bred guppies. Female age at first maturation has been recorded as 48 to 63 days (Thibault & Schultz 1978) and 25 weeks (Yamagishi 1976) compared to 11 to 14 weeks in the present study. Brood intervals reported were 21 days (Scrimshaw 1944, Thibault & Schultz 1978) while Yamagishi (1976) found most intervals between 26 to 140 days (mean interval 38.2 days) with intermittent spawnings at 59 - 66 and 90 days; intervals at the study site were about 35 days. Average female GSI's at low population densities were 9.671% (Dahlgren 1979) while mean GSI for the present study was 9.749% (N = 575). Other data not obtained in the present study but available in laboratory studies were gestation period - 25 days (Dahlgren 1979), longest period of reproduction for a female - 400 days (Thibault & Schultz 1978), maximum number of broods recorded for one female was 17 over 344 days (Bowden 1970 quoted in Miller 1979).

Population structure and many life history characteristics of the species studied were indicative of r -selected species. Fish populations were subjected to drastic density independent mortality factors such as flooding and drought with the former being particularly important. Populations of species such as *C. riisei, A. bimaculatus, H. unilineatus* and *P. reticulata* showed extreme oscillations of numbers due to alternating washouts and recolonisation and/or reproduction. Such oscillations could be environmentally influenced or inherent in the biology of the species (cf. Le Cren 1965, Lowe-McConnell 1969). Further evidence for the variable and density independent mortality these populations were subjected to was seen in changes in community composition due to stochastic influences.

Populations of species such as *C. riisei, A. bimaculatus* and *H. unilineatus* were largely comprised of recruits rather than repeat spawners as a result of their quick maturation and short life spans. This characteristic of fish populations is an r-selected trait as compared with populations of longer lived species which are comprised mainly of repeat spawners (K-selected) (Nikolsky 1963). This feature was not seen in *P. reticulata* where reproductive individuals dominated the population and may be related to the live-bearing nature of these species and the small number of young produced. With the exception of

P. reticulata, all other species produced comparatively large numbers of young each breeding season and they decreased rapidly over time suggesting high levels of early mortality (type III survivorship curve, Krebs 1985), another r-selected trait (Le Cren 1962, Pianka 1970).

Other r-selected traits are small body size, rapid development and early sexual maturity. These characteristics were seen in the species for which data were available. All the species studied were less than 100 mm SL and could be considered to be small according to Miller's (1979 b) definition. Even the largest species, *A. bimaculatus,* only attained a length of 82 mm SL as compared to sizes attained in other drainages (Guppy 1936, and personal observations). Early development was rapid with eggs of *C. riisei* and *H. unilineatus* hatching in less than 24 hours and larvae becoming free-swimming and feeding in four days. The smallest species, *P. reticulata,* matured within about two months compared to the largest species *A. bimaculatus* which appeared to mature within its second year. Monthly changes in population structure and growth curves showed maturation ages of less than one year for all the other species except *C. aeneus* for which data were inadequate to draw any definite conclusions. Rapid maturation rates such as these are typical of small species of seasonal tropical habitats (Lowe-

McConnell 1975, Welcomme 1979) as well as seasonal temperate aquatic systems (Deacon & Minckley 1974). Reduction in age at maturity is recognised as a potent mechanism for increasing growth rates of populations (Wootton 1984 a).

Overall sex ratios for populations of four species deviated from unity but no investigations were made to determine reasons for this. Likely factors include migratory behaviour of juveniles and/or reproductives (possibly in *G. sternicla* and *A. bimaculatus*), mating systems of the internally fertilising species depending on female choice, that is female-based polygyny (*C. riisei* and *P. reticulata*), and differential predation of more active colourful males in *P. reticulata* (Endler 1980). Biased sex ratios have also been recorded for other poeciliids. Female-dominated ratios occurred at times of high population densities in *Limia vittata* (Barus *et al* 1980) similar to situations in the present study. Krumholz (1948) attributed female dominance in mature *Gambusia affinis* to differential death rates of males while Milton & Atherington (1983) reported habitat preference as a factor influencing sex ratios in the same species. Experimental studies by Russian workers using guppies have suggested that brood sex ratio adjustment by females allowed production of the rarer sex thus returning population sex ratios to unity following environmental disturbances (Geodakyan *et al* 1967, Geodakyan and Kosobutskii 1969, quoted in Brown 1982). However, replication of these experiments do not confirm this phenomenon (Brown 1982). Farr (1981) also found female-biased sex ratios in laboratory strains of guppies and attributed this to long term inbreeding.

A variety of evidence including presence of mature reproductives, high GSI's and presence of juveniles pointed to a seasonal reproductive cycle for all species except *P. reticulata*. Mature individuals of *C. riisei, H. unilineatus* and *C. aeneus* were found throughout the year but peaks of reproductive activity could be inferred from high GSI's and the presence of juveniles in the population. Peaks in reproduction in these species and spawning of *G. sternicla* and *A. bimaculatus* took place during the rainy seasons. *C. riisei, H. unilineatus* and *C. aeneus* could have had two active breeding periods each year but often only one was evident for *G. sternicla* and *A. bimaculatus*. Kapetsky *et al* (1977, quoted in Welcomme 1979) distinguished three groups of fish in the Magdalena River, Colombia as those which bred once per year, those with two or more breeding periods per year and those which bred almost continuously. Breeding twice each year has been recorded by Lowe-McConnell (1975, 1979) and Welcomme (1979) in tropical systems where two flood peaks or twice yearly rainfall maxima occur. In the present study major breedings seasons twice each year were seen consistently only in the smaller species such as *C. riisei* and *H. unilineatus* which, because of their small size, fast growth rates and early maturation, had two overlapping generations each year and it was possible that some individuals, especially of *H. unilineatus*, bred twice in one year. Larger species such as *G. sternicla* and *A. bimaculatus* showed only minor peaks of breeding in the second rainy season while *C. aeneus* seemed more responsive to very high rainfall at this time. It was unclear whether the same individuals of these larger species were able to breed twice in one year. Under conditions where two breeding periods per year might occur, strategies to utilise these seasons might differ. Breeding cycles reported for *Barbus* species in Lake Victoria, Africa (cf. Payne 1975) show that two spawning periods may result from different sections of the population spawning at different times with each individual having an annual cycle, and for *Barbus apleurogramma*, fast maturation allows some young spawned in one breeding season to mature and spawn by the next season (Welcomme 1969).

Close coincidence between reproductive activity and the onset and duration of the rains each year despite the variability of the latter, indicated that the species studied must have been cued to the stimuli of high rainfall and floods to initiate reproduction. In 1980, rainfall maxima were well defined in May and October while in 1981, rains started earlier in April and again in November after a very dry petit carême. However, rainfall continued intermittently through the beginning of the dry season to February. When they occurred, peaks of reproduction of the five species coincided almost exactly with the timing of these rainfall maxima. In addition, early reproduction in April 1981 seemed to allow more time for first time maturation of young of the year of the short-lived species such as *C. riisei* and *H. unilineatus*, as well as development of gonads again in large individuals of these species and the larger species in preparation for reproduction during the second rains through to February. This could explain the particularly high juvenile abundance at this time for most species.

The most marked environmental changes seen at the study site associated with the beginning of the rainy seasons were: habitat expansion into small drainage canals as well as increases in depth and width of the main channel and reconnection of isolated pools; increased discharge and resumption of flow after stagnant conditions; water temperatures decreased with flood events but were generally slightly higher and more stable during the rainy season; increased turbidity and decreased conductivity. The stream biota showed a reduction in densities of both benthic and planktonic organisms at the beginning of the rainy season when floods occurred but benthic organisms in particular showed rapid recovery to high densities once moderate flow regimes were established.

Many previous workers have found peaks in spawning activity of freshwater fish associated with seasonal rainfall or floods but the exact nature of cues stimulating gonadal development and spawning are still unclear (Lam 1983). Factors which may affect gametogenesis in tropical fish include photoperiod, temperature, water quality and nutrition (Lam 1983). Studies of the neon tetra, *Paracheirodon innesi*, by Tay (1983, quoted in Lam 1983) demonstrated that temperature, water quality (pH and conductivity) and light intensity were important in influencing gonadal development. High conductivities inhibited gonadal development in *P. innesi* as well as in the gymnotid, *Eigenmannia virescens* (Kirschbaum 1975, 1979). This factor is of some relevance to the present study considering the high conductivities attained in contracting pools at the study area during the late dry season when gametogenesis in most species should be occurring. The ionic composition of such waters might be influential since Tay (1983) attributed the inhibitory effect to the presence of calcium ions and these were generally in low concentrations at the study site.

Photoperiod has been noted to affect gametogenesis in the guppy, *P. reticulata,* but its effect is unclear (review in Lam 1983). Gametogenesis has been enhanced in this species by increased light intensities and may be relevant in the present study to high levels of reproductive activity during the dry season when cloud cover was marginally less and leaf-fall allowed more light penetration to the stream surface. In addition, guppy populations attained higher densities at most times at Station 3 which was the most exposed site, although the additional factor of high algal and planktonic productivity at this site should not be ignored.

In contrast to the above exogenous influences on gonadal development, endogenous rhythms of reproductive activity have been proven to occur in temperate fish species and may be involved in sexual cycling in subtropical and tropical species but rigorous testing of this phenomenon is necessary (Scott 1979, Lam 1983). Nevertheless, Schwassmann (1971, 1978) and Bye (1984) suggested that an endogenous rhythm in tropical fish may take gonadal development to the final stage of maturity which is then maintained until spawning is triggered by sudden environmental fluctuations. This phenomenon would produce a relatively long-lasting phase of spawning-readiness (Schwassmann 1978) and could account for the presence of mature individuals of some species throughout the year.

Proximal factors influencing the timing of spawning events in tropical fishes appear to be associated with annual flooding but the exact stimulus is unclear (Lowe-McConnell 1975, Welcomme 1979, Scott 1979, Lam 1983). Factors involved as cues include changes in water chemistry and water temperature, dissolved substances from newly wetted soil, flow rates, food supply and availability of spawning sites among others. Lam (1983) summarised that no single factor has been identified and perhaps a consortium of factors is involved. More specific factors which induce spawning in some species may be the presence of a spawning substrate and social cues such as the visual stimulus of a mate or pheromones (Chen & Martinich 1979, Bye 1984).

In the present study the most likely stimuli for initiating spawning activity in the species studied were increased flow rates, water quality changes, particularly dilution effects, and reduced temperatures of flood waters. These factors were also influential during the early part of the 1982 dry season when reproduction of most species was apparent. In particular, the small brood spawners such as *C. riisei* and *H. unilineatus* as well as *C. aeneus* continued spawning as long as environmental conditions were favourable. Continual spawning has been noted in *Eigenmannia virescens* by Kirschbaum (1979) once water levels were constant and conductivities were low and despite the absence of stimuli which were necessary for gonadal recrudescence (that is rain simulation, rising water level and decreasing conductivity). Longer than normal spawning periods in the cardinal tetra, *Paracheirodon axelrodi*, were also related to hydrological conditions in the Rio Negro basin (Geisler & Annibal 1986). Both *E. virescens* and *P. axelrodi* are multiple spawners (Schwassmann 1980, Geisler & Annibal 1986). Therefore in some species, especially multiple spawners, environmental factors appear to act as initiators of spawning behaviour and as conditions remain favourable and constant, spawning and repeated gonadal maturation could occur.

Breeding activity was not noted in the species studied (except *P. reticulata*) during the 1981 dry season which was characteristically low in rainfall resulting in Stations 2 and 3 being stagnant for up to three months. Stagnant conditions most likely allowed a build-up of metabolites which could repress spawning. Subsequent dilution of these metabolic wastes at the beginning of the rainy season would then result in spawning (Johnson 1963, Chen & Martinich 1979). These metabolites are thought to be ammonia and are not species specific (Chen & Martinich 1979). In contrast to this situation breeding in the dry season or all year round has been recorded by Kramer (1978a), Lowe-McConnell (1979) and de Silva *et al* (1985) for streams with relatively minor seasonal variation and continuous flow all year.

Reproductive activity in *P. reticulata* was continuous throughout the study period. A comparable lack of seasonality in breeding was noted in the poeciliid, *Brachyraphis episcopi*, in Panama where no monthly variation in population structure, brood size, oocyte development or numbers of gravid females were seen (Turner 1938). Other poeciliids, *Gambusia affinis* and *Xiphophorus* spp. were found to have prolonged but seasonal reproductive cycles curtailed by temperature and photoperiod in Queensland, Australia where they have been introduced (Milton & Atherington 1983). Eight cyprinodont species in a small relatively aseasonal stream in Gabon, West Africa showed a variety of breeding strategies, some being very seasonal, others aseasonal (Brosset 1982), a situation similar to that found by Kramer (1978a) working on characins in Panama.

Condition factors of all the species studied (except *P. reticulata*), showed a fairly close correlation with seasonal influences of the reproductive cycle. Generally total condition increased relative to somatic condition with the onset of breeding due to increased gonad weights. In some species (*G. sternicla, H. unilineatus* and *C. aeneus*) and especially in females, decreases in somatic condition also occurred at this time indicating the mobilisation of somatic reserves into gonadal tissue (Le Cren 1951, Payne 1975). Both male and female condition tended to show minimal values after the reproductive period (for example in *C. riisei* and *H. unilineatus*) and in *H. unilineatus* females minimal condition factors were also noted in the middle of the breeding period when GSI's decreased. In small species such as *C. riisei* and *H. unilineatus*, very few fully spent females were found at the end of the breeding season and it is likely that death occurred soon after cessation of spawning coincident with the low condition of these individuals. Death of specimens of *C. riisei* bred in the laboratory within one or two months after spawning ceased supported this possibility. During the lengthy reproductive season however, *C. riisei* and *C. aeneus* in particular, maintained or even showed increases in condition. Cambray & Bruton (1984) reported that in species with protracted breeding seasons, the first batches of eggs may depend on fat reserves accumulated previously while later batches are derived from feeding during the breeding season.

In the small species which bred twice each year, seasonal variation in condition factors was largely determined by the reproductive cycle, a situation similar to that reported by Payne (1975) for *Barbus liberiensis* in Sierra Leone. It was not possible to investigate condition cycles of immature individuals because they matured within a year. As a result, no evidence was obtained as to whether there were any food- or metabolism-induced changes in condition over the year comparable with those of temperate fishes. Larger species which had one major peak of breeding each year showed recovery of condition after breeding (for example *A. bimaculatus*) and in *C. aeneus*, decreases in condition late in the year might have been associated with limited food availability during the second rains or possibly a second breeding period.

Variation in condition for *P. reticulata* showed no seasonal trends consistent with lack of seasonality in breeding and indicating no obvious seasonal trends in food availability or metabolism. Dahlgren (1980 a, b) suggested that *P. reticulata* possessed considerable adaptability to food sources of varying quality. Further, in a study of six cyprinodonts in Texas which all had protracted breeding periods, de Vlaming *et al*

(1978) found no correlation between monthly variation of GSI's, fat reserves and standing crops of phyto- and zooplankton.

The six species studied exhibited varying lengths of their breeding seasons: short, protracted and continuous. Generally, an inverse relationship existed between maximum batch fecundity and length of the breeding season. The species with the highest batch fecundity (*A. bimaculatus*) spawned for only one or two months each year with one major peak of spawning at the beginning of the main rainy season and rarely, a second minor spawning later in the year. *G. sternicla* had a similar reproductive pattern and its maximum batch fecundity was the highest of the other species. *C. riisei, H. unilineatus* and *C. aeneus* had more prolonged breeding periods up to four months each season and usually twice each year and all had roughly equivalent ranges of batch fecundity. *P. reticulata* produced young continuously through the year and had the smallest fecundity of all the species. Batch fecundity was positively correlated with individual size in most species and maximum batch fecundity was dependent on average species size.

Analyses of spawning patterns indicated that in species with short breeding seasons such as *G. sternicla* and *A. bimaculatus,* ovum maturation was relatively synchronised, however it could not be determined whether all the eggs were spawned at one time or in a number of sessions. Ovaries of *H. unilineatus* also indicated some synchrony of development of ova but laboratory observations showed that these ova were shed in small broods over limited periods, the length of which was dependent on the size of the female. *C. riisei* was also a small brood spawner and there was evidence of continuous maturation of ova in individuals which spawned over prolonged periods. Total egg production was dependent on female size and for large females greatly exceeded that predicted by batch fecundities. *C. aeneus* also showed evidence of continuous maturation of ova which indicated the potential for continual egg production over time although the high levels of atresia noted might suggest that not all ova produced are shed.

Data for determining spawning patterns in these species were obtained from a variety of sources such as GSI fluctuations, ovarian analyses and laboratory spawning experiments. Certain shortcomings are inherent in the use of any one of these techniques but in general they tended to corroborate each other. GSI's fell rapidly after a maximum level in species which had limited breeding periods such as *G. sternicla* but in species with prolonged high GSI levels it could not be certain whether this resulted from protracted breeding by individuals or successive waves of different individuals. GSI value alone cannot indicate whether an individual is partially spent or developing in species where the eggs are not shed all at once (Delahunty & de Vlaming 1980).

Shortcomings in the use of ovarian analyses have been noted by several workers especially in situations where the reproductive cycle of the species is not known adequately (Cambray & Bruton 1984). Macer (1974) found that histologically recognisable groups of oocytes were not equivalent to groups defined on the basis of size. In addition, only a limited number of batches of oocytes may be discernable using this method of analysis so that underestimates of potential spawnings may be made (Miller 1979 a).

Laboratory spawning experiments have one major drawback in that they can only be marginally indicative of reality since they are conducted under controlled environmental conditions and in the absence of competition and predation. Other factors such as female choice of males depending on the previous mating history of males and sperm limitation (Nakatsuru & Kramer 1982) are important in the design of experimental set ups. The effects of constant manipulation such as daily removal of spawning substrates and eggs also need to be considered although Heins & Rabito (1986) found no evidence that removal of oviposited eggs affected spawning frequency in *Notropis leedsi*.

Despite these shortcomings however, it could be concluded that for all the species studied multiple spawning (or multiple brood production in *P. reticulata*) was either observed in the study or recorded in the literature for the same species. The nature of the multiple spawning strategy exhibited was not exactly equivalent for all species however. Ovarian maturation was highly synchronised in *A. bimaculatus* but more or less continuous in *C. riisei* and *C. aeneus*. *G. sternicla* and *H. unilineatus* ovaries included one batch of mature ova which was separated, to varying degrees, from what could have been a second batch. The presence of small eggs in ovarian analyses need not indicate fractional or multiple spawning and these oocytes may eventually be resorbed (Nikolsky 1963). This might be the case in *G. sternicla* but laboratory spawning evidence showed that up to two batches of eggs could be spawned by *H. unilineatus* during a breeding period of five weeks.

The sizes of clutches spawned and intervals between clutches for each of these species also differed. *A. bimaculatus* are reported to spawn 100 to 500 eggs at a time (Azevedo & Vieira

1938) and they may have several spawning acts in one season (Pelizaro *et al* 1981) but further details were not available. Clutch size of *C. aeneus* is reported to be between 200 to 380 eggs over periods up to five hours (Hart 1947, Breder & Rosen 1966). Sterba (1962) recorded spawnings occurring at four to seven day intervals while Zukal (1982) estimated two to three weeks between spawning events. Clutch sizes for *C. riisei* and *H. unilineatus* were comparable but *C. riisei* spawned more frequently and for longer breeding periods than *H. unilineatus*.

Hails & Abdullah (1982) distinguished between three spawning types based on ovarian analyses: single batch total spawning, multiple batch spawning with two or more distinct batches of ripening eggs, and multiple batches without clear distinctions. *A. bimaculatus* seemed to fall into the single batch total spawning category although it is still unclear whether the entire batch is spawned within a short period or in several spawning acts during the season. *G. sternicla* and *H. unilineatus* seemed to fit the second category while *C. riisei* and *C. aeneus* belong to the third category but spawning patterns in *G. sternicla* and *C. aeneus* need to be confirmed. The repeated brood production of *P. reticulata* could be considered a form of multiple batch spawning with two or more distinct batches complicated by one of these 'batches' being developing embryos. Superfoetation was not observed in the present study consistent with Thibault & Schultz' (1978) observations.

The data available on breeding periodicity, batch fecundities and spawning patterns for the six species studied supported the general conclusions of Lowe-McConnell (1975) where she described total spawners as having clearly defined spawning seasons, being more fecund, producing numerous small eggs and making long migrations to do so. In contrast, multiple spawners have less clearly defined breeding seasons, produce fewer eggs at a time, often large ones and may make only local movements to spawning areas. She however associated multiple spawning, especially small brood spawning, with some form of parental care, a feature not seen in any of the species studied. Furthermore, examples of small brood spawners do not include any small species similar to those in the present study, presumably because of lack of available data at the time.

It is becoming more widely recognised that some degree of multiple spawning is of crucial importance to small fish for a variety of reasons (Nikolsky 1963, Miller 1979 b, Cambray & Bruton 1984). Most importantly it allows for considerable increases in fecundity which would not otherwise be possible due to size and nutritional constraints (Nikolsky 1961, 1963, Loiselle & Welcomme 1971, Miller 1979 b, Wootton 1984 a and others).

Enhancement of fecundity in small fish could be achieved by a reduction in egg size but a lower limit to this process is set by the increasing disadvantage suffered by smaller and less provisioned young which ultimately hatch. Miller (1979 b) estimated that the minimum teleost egg size was 0.25 to 0.40 mm in several species of gobies. In freshwater habitats, especially fluviatile ones, and where parental care is non-existent, it could be expected that minimum egg size would be much larger. Compared to north European freshwater fish species, egg sizes of *A. bimaculatus*, *C. riisei* and *H. unilineatus* were below the modal size of 1.25 - 1.75 mm diameter, while egg size of *C. aeneus* and *P. reticulata* fell within this modal class (Wootton 1979). Large egg size in *C. aeneus* was similar to that of the other local callichthyid, *Hoplosternum littorale* whose eggs were 1.0 - 1.2 mm in diameter (Singh 1978). Egg size of *P. reticulata* was dictated by endowment of large quantities of yolk for embryonic development since maternal contributions during gestation are minimal (Wourms 1981).

In species where brood size or batch fecundity cannot be increased further, increase in fecundity can be effected by repeat spawning (Miller 1979 b). This phenomenon has been reported for a variety of small fishes for example gobies (Miller 1979 b, 1984), sticklebacks (Wootton 1984 a), darters (Gale & Deutsch 1985) and minnows (Gale & Gale 1977, Gale & Buynak 1978, 1982, Heins & Rabito 1986) as well as the tropical zebra fish (Hisaoka & Firlit 1962) and poeciliids (Miller 1979 b).

Comparison of reproductive output for the above multiple spawning species is difficult owing to the different methods used in expressing the data. Miller (1979 b) calculated reproductive effort/30 days (total dry weight of offspring/ somatic dry weight of female/30 days) for several species including a specimen of *Brachydanio rerio* which produced 5,530 eggs over a five month period (data from Hisaoka & Firlit 1962) and which had a reproductive effort of 0.7725. In comparison, reproductive effort for *P. reticulata* ranged from 0.1061 to 1.504 (Miller 1979 b, Table II).

In summarising their previous studies, Gale & Deutsch (1985) proposed the use of the term 'proportional fecundity', that is the volumetric ratio of water hardened eggs spawned to the female that spawned them. In their studies, proportional fecundity for the species studied varied from 1.3 in *Etheostoma olmstedi* to 6.8 in *Pimephales promelas*. Ovarian analyses of *E. olmstedi* (Gale & Deutsch 1985) and *Notropis leedsi* (Heins & Rabito 1986) showed a pattern equivalent to Hails & Abdullah's (1982) multiple batch spawning with two or more distinct batches of ripening eggs. Continuity of oocyte distribution such as that seen in some of the species in the present study was not reflected in their data.

P. reticulata could be considered a continuous multiple spawner but when compared to the other species studied, reproductive output in the form of numbers of offspring produced, was low. However, the ovoviviparous mode of reproduction eliminates mortality from extrinsic factors during the early course of development and permits a saving in the number of offspring that need to be produced for representation in the next generation (Miller 1979 b). In addition, although superfoetation does not occur, maturation and fertilisation of ova takes place over a period of days to reduce the nutritional drain on the female than if all the ova were to be endowed simultaneously (Thibault & Schultz 1978).

Gale & Deutsch (1985) and Heins & Rabito (1986) discussed the shortcomings of conventional fecundity estimates for multiple spawning fishes in the light of their results. The former authors suggested that conventional fecundity estimates be termed 'ovarian egg counts' in order to avoid the implication that batch fecundities are true reflections of potential egg production in multiple spawning fishes. They suggested that fecundity should be measured as mean number of eggs spawned per clutch times the number of clutches per year, and such data should be obtained from captive laboratory or natural environment spawning experiments.

In addition to allowing significant increases in fecundity for small fish, a multiple spawning strategy has other advantages. It is widely recognised that several batches of eggs spawned over time reduces the chances of loss of all eggs by unfavourable conditions (Nikolsky 1963, Lowe-McConnell 1975, 1979 and others). In situations such as the study site where the beginning of the rains are unpredictable and often followed by dry spells, this is especially advantageous. Multiple spawning also allows use of a spawning site more than once each season (Cambray & Bruton 1984), reduces intra- and interspecific competition between fry (Nikolsky 1961, Cambray & Bruton 1984), may produce year classes of uniform strength (Gale & Gale 1977), and allows for control of egg numbers during the current season by continuous ovum maturation or resorption depending on ensuing conditions (Macer 1974).

The observed correlations between size and the reproductive characteristics of the six species studied raises some interesting but speculative ideas on the interaction between size and phylogeny in shaping reproductive and life history patterns of these fishes. Of the six species studied, the four characoids constituted one closely related group within which a spectrum of reproductive strategies was noted, from what appears to be relatively synchronised total spawning in *A. bimaculatus* and to a lesser extent in *G. sternicla*, to protracted small brood spawning in *C. riisei* and *H. unilineatus*. The large size of *A. bimaculatus* could provide the potential for the synchronised maturation of a large number of eggs for any one season. As a result of smaller size and a somewhat restricted abdominal cavity due to its unusual shape, that potential would be reduced in *G. sternicla*. Small brood spawning in *H. unilineatus* and *C. riisei* could be related directly to small size acting as a constraint to increased batch fecundities. The fact that *H. unilineatus* may be closely related to *A. bimaculatus* by the process of paedomorphosis (Gery 1977) might explain the relative synchrony of ovum maturation and spawning being limited to fairly short periods in the former species. In fact, Gould (1977) suggested that r-selection and early maturation could be related to the process of paedomorphosis. However, *C. riisei* being a glandulocaudine, is capable of continuous ovum maturation and spawning because internal fertilisation has allowed ovulation and spawning to be dissociated, both temporally and spatially, from male presence and mating events (Nelson 1964). The importance of size as a factor influencing the pattern of covariation of life history traits has been noted by Stearns (1983) who found that it accounted for a significant portion of ordering species onto a 'slow-fast' continuum although he did also note the effects of phylogenetic constraints on the evolution of life history traits.

In summary, the fish community at the study site could be considered to be a diverse assemblage which might be maintained by two major features of the area. The seasonally fluctuating nature of the stream in conjunction with a long flow regime and extensive refuge pools may have created an environment with intermediate levels of disturbance which maintained non-equilibrium communities of high species richness. Secondly, species richness could be related to the proximity of the study area to a source of high diversity, that is the mainland, from which continual colonisation has taken place.

The fish populations studied seemed to be strongly influenced by the seasonal flow regime at the study sites. Possible mechanisms may have been mortality, dispersal and concentration of individuals or the stimulation or inhibition of reproduction.

Life history characteristics of the six species studied reflected the impact of seasonal conditions on populations and were characteristically r-selected traits such as small size, short life spans, rapid development, early maturation and high early mortality. Biotic interactions such as predation may also have been influential, especially on the smaller species such as *P. reticulata*. Populations also showed r-selected characteristics such as high variability in size and dominance of age structure by recruit spawners.

Reproductive seasonality in most species studied was determined primarily by the flood-drought cycle which may have acted to both stimulate and inhibit breeding activity. Features associated with the floods such as increased flow and water quality changes may have been influential in stimulating reproduction. Peaks of reproductive activity coincided closely with rainfall maxima each year for all seasonally breeding species. Numbers of breeding seasons per year and their lengths varied for different species. Some species had one major breeding period and rarely, a second minor period each lasting not more than one or two months (*G. sternicla* and *A. bimaculatus*). Others consistently bred twice each year for periods up to four months (*C. riisei, H. unilineatus* and *C. aeneus*). *P. reticulata* showed continuous reproductive activity throughout the study with no obvious seasonal variation in intensity.

Variability in the seasonal regime as a result of altered timing of rainfall and stream flow were responded to by variability in reproductive timing in all seasonally breeding species indicating a high degree of adaptability in these species. The condition of fish was affected primarily by their reproductive cycles and there was no direct evidence of other factors such as food availability being highly influential.

Spawning patterns of the six species studied were variable but consistent with those described for other seasonal tropical rivers. They ranged from what appeared to be a seasonal and highly synchronised total spawning pattern in *A. bimaculatus* to continuous small brood production in *P. reticulata*. Ovarian analyses of *A. bimaculatus* suggested a total spawning pattern but no laboratory confirmation was obtained and the literature is ambiguous. Multiple spawning was confirmed in *C. riisei* and *H. unilineatus* by laboratory experiments and ovarian analyses. Some degree of multiple spawning was suggested for *G. sternicla* and *C. aeneus* by ovarian analyses but this was unconfirmed by laboratory experiments.

Maximum batch fecundities were directly proportional to the size of the species but in the smaller species high fecundity was attained by means of a multiple spawning strategy which overcame the constraints imposed by small size. Multiple spawning in turn increased the adaptability of the species by allowing variability in reproductive output and timing in addition to other advantages.

Generally, the reproductive strategies of the six fish species studied were strongly influenced by the seasonal nature of the environment. However, the strategies used were diverse and highly adaptable to the inherent stochasticity of the system.

CONCLUSIONS

At the beginning of this study several predictions were made as to the nature of the habitat and the responses of the biota to seasonal changes. An assessment of the data shows that most of these predictions made were true.

The streams studied were highly seasonal in nature with variable physical and chemical parameters which in turn influenced the biota including the fishes studied. Predictability of conditions was low with duration, onset and intensity of any season being highly variable. Hydrological patterns of the streams were equivalent to those recorded for long-flow intermittent streams with extensive refuge pools (Clifford 1966) and differed somewhat from more highly intermittent tropical streams where regular and extensive drying out was noted (Adebisi 1981 a). On the other hand, the Chatham streams were much more seasonal and were harsher environments than many small forest creeks or larger streams studied elsewhere in the tropics (for example Bishop 1973, Schwassman 1978, Kramer 1978a and others).

Biological standing crops at the study sites were variable showing no striking or consistent seasonal trends and high levels were attained in both wet and dry seasons unlike more obviously seasonal habitats such as floodplain rivers (Lowe-McConnell 1975, Welcomme 1979). Standing crops approximated those attained in some aquatic habitats on the mainland.

Life history parameters of the fishes studied showed r-selected traits as predicted including small size, short life spans, rapid development, early maturation and high early mortality. It was possible that high levels of predation may have interacted with environmental factors to emphasise these traits in some species.

Despite the range of habits, sizes and phylogeny of the fishes studied, their reproductive strategies strongly reflected the seasonality of the environment and with the exception of *P. reticulata* which bred continuously, all other species had peaks of reproductive activity in the wetter parts of the year. However, although onset of reproduction was usually cued to the rainfall maxima, duration and intensity of breeding during any season varied depending on the ensuing environmental conditions. Breeding was recorded for some species as long as conditions of flow were maintained.

Since breeding normally coincides with the most favourable time for survival of young, it could be assumed that conditions during the rainy season were favourable for survival of young in the species studied. Such factors as decreased crowding and predation pressures could be proposed as ultimate factors influencing reproductive timing in these species. Food availability could not be assessed definitively as a factor because of lack of data on adult and larval feeding habits. However, food limitation for adults did not appear to be important because of the lack of clear seasonal variation in food supply and the recorded feeding habits for many species indicate a high degree of adaptability.

Breeding was generally synchronised in most species to peak during the rainy season and massive production of young in species such as *A. bimaculatus*, *H. unilineatus* and *C. riisei* at approximately the same time may imply that swamping of predators might be an important consideration. Kramer's (1978a) proposition that phylogenetic constraints may be influential also apply to this study. Many of the species studied are also found in seasonally flooded environments on the mainland where it is advantageous to breed at times of high water. Physiological responses to initiate reproduction upon certain external cues have evolved (for example Kirschbaum 1975) and it is unlikely that such responses would change except under very strong and contrary selection pressures. In addition, inhibition of reproductive activity in stagnant pools by accumulated metabolites or high conductivity and subsequent release of inhibition by increased discharge could result in coordinated rainy season spawning.

It was predicted that multiple spawning should occur in a high frequency of fishes due to its advantageous nature in unpredictable habitats. Multiple spawning (or brood production) was definitely observed in three out of six species studied and can be tentatively suggested for the other three species on the basis of circumstantial evidence.

In addition to multiple spawning which itself allows for variable reproductive output, reproductive strategies varied depending on the number of breeding periods each year and the length of the breeding season. Obvious reproductive output in the form of amount of gonadal tissue and duration or intensity of breeding was considered but other aspects of output should also be taken into account, for example courtship and other behaviour, coloration and sexual dimorphism (Williams 1966) and these also varied between species. In general terms, the predicted overall reproductive strategy in this fluctuating habitat would be to expend high reproductive effort. However, the tactics (cf Wootton 1984 b) by which this high output was achieved differed due to phylogenetic and size constraints.

In conclusion, the six fish species studied were the most common in the Chatham streams and as such could be considered to be successful in this type of habitat. Their reproductive strategies were diverse in nature differing in timing, duration and intensity of breeding between species and in different years. In general, they were highly adaptable to the inherent stochasticity of the environment and this undoubtedly contributed to their success. In this situation, the relationship between strategy and the environment is best summarised by Dobzhansky (1950, p. 216): 'Changeable environments put the highest premium on versatility rather than on perfection in adaptation.'

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APPENDIX 1

Procedure for pentade analysis of rainfall data.

The use of pentades (5-day periods) in analysing rainfall patterns has been preferred by some workers because of the inadequacy of data based on longer periods (months or weeks) in reflecting short term rainfall variability (Jackson 1977). The onset or end of various seasons, either on average or for individual years, does not coincide with the calendar months which are often used to make generalisations about rainfall regimes. Jackson (1977) reviews the use of pentade analysis in the definition of rainy seasons, analysis of length of dry seasons and in determining the occurrence of wet and dry spells during the rainy season in various tropical regions.

The method used by Griffiths (1959, quoted in Jackson 1977) involves initially the determination of total rainfall for consecutive 5-day periods from daily rainfall data.

When the totals for three consecutive pentades are compared, the middle pentade is considered 'rainy' if the following conditions are met:

APPENDIX 1 (continued).

(i) The total rainfall for the three pentades together amount to at least 76 mm,

(ii) The rainfall amounts to 7.6 mm or more in each of at least two of the three pentades.

This procedure is repeated for successive pentades of the period under analysis.

APPENDIX 2

Tests of significance between means of two samples.

The Student's t-test was used to test for significance of differences between the means of two small samples (i.e. N_1 and $N_2 < 30$) under the condition that population variances were not assumed to be equal (Parker 1979).

The following formulae were used:

$$\frac{\bar{X}_1 - \bar{X}_2}{\sqrt{(s_1{}^2/N_1 + s_2{}^2/N_2)}} = t \text{ with } f \text{ degrees of freedom}$$

f is given by:

$$1/f = u^2/(N_1 - 1) + (1 - u)^2/(N_2 - 1)$$

$$\text{where } u = \frac{s_1{}^2/N_1}{(s_1{}^2/N_1) + (s_2{}^2/N_2)}$$

$\bar{X}_1$ $\bar{X}_2$ means of samples 1 and 2

s_1 s_2 standard deviations of samples 1 and 2

N_1 N_2 number of measurements or replicates in samples 1 and 2.

APPENDIX 2 (continued).

For comparison of means of two large samples ($N > 30$), a d-test was used (Parker 1979) where:

$$\frac{\bar{X}_1 - \bar{X}_2}{\sqrt{(s_1^2/N_1 + s_2^2/N_2)}} = d$$

APPENDIX 3

Taxonomic list of aquatic macrofauna collected at Stations 1 to 4 during the study period.

Taxon	Stations			
	1	2	3	4
Nematoda			x	
Nemertea	x			
Annelida				
Oligochaeta				
Tubificidae	x	x	x	
Naididae	x	x	x	
Enchytraeidae	x			x
Other	x	x	x	
Hirudinea				
Glossiphonidae				
Glossiphonia	x	x	x	
Placobdella			x	
Polychaeta				
Nereidae				x
Capitellidae				x
Crustacea				
Cladocera		x	x	
Ostracoda			x	
Copepoda		x	x	
Isopoda				x
Amphipoda				x
Decapoda				
Penaeidae				
Penaeus notialis Perez-Farfante				x
Palaemonidae				
Palaemon pandaliformis (Stimpson)	x			
Macrobrachium jelskii (Miers)	x			
M. heterochirus (Wiegmann)			x	
Macrobrachium sp.	x			
Alphaeidae				
Alphaeus sp.				x
Portunidae				
Callinectes sapidus Rathbun				x

APPENDIX 3 (continued)

Taxon	Stations 1	2	3	4
Trichodactylidae				
Dilocarcinus dentatus (Randall)	x	x	x	
Arachnoidea				
Hydracarina	x	x		
Insecta				
Ephemeroptera				
Leptophlebiidae[1]				
Miroculis (M.) ? fittkaui Savage & Peters	x	x		
Odonata				
Coenagrionidae	x	x		
Calopterygidae[2]				
Hetaerina caja Drury	x			
Aeshnidae[2]				
Coryphaeschna viriditas Calvert	x			
Gomphidae[2]				
Aphylla producta (Selys)	x	x		
Phyllocycla ? anduzei Needham	x			
Libellulidae[2]				
Dythemis multipunctata Kirby	x			
D. sterilis Hagen	x	x		
Macrothemis sp.	x			
Micrathyria sp.	x			
Oligoclada walkeri Geijskes	x			
Orthemis ? ferruginea Fabricius	x	x		
Perithemis mooma Kirby	x	x	x	
Hemiptera[3]				
Belostomatidae				
Belostoma malkini Lauck		x		
B. micantulum (Stal)	x			
Nepidae				
Ranatra mixta Mont.	x	x	x	
Curicta intermedia Martin	x	x		
Hydrometridae				
Hydrometra comata Torre-Bueno	x	x		
H. guianana Hungerford & Evans	x	x		
Notonectidae				
Buenoa rostra Truxal		x	x	

APPENDIX 3 (continued)

Taxon	Stations			
	1	2	3	4
Gerridae				
Brachymetra albinervis (Amyot & Serville)	x	x	x	
Limnogonus aduncus Drake & Harris	x	x		
Telmatometra fusca Kenaga	x	x		
Veliidae				
Rhagovelia ? insularis Champion	x			
Coleoptera				
Dytiscidae[4]				
Thermonectus sp.nov.?	x			
Laccophilus proximus Say	x			
Gyrinidae[4]				
Gyretes ? distinguendus Reg.	x			
Hydrophilidae[4]				
Helochares sp.nov.?			x	
Carabidae				
?Omophron	x			
Diptera				
Chironomidae	x	x	x	
Heleidae	x	x	x	
Culicoides sp.[5]	x			
Mollusca				
Gastropoda				
Planorbidae	x	x	x	
Ampullariidae				
Pomacea glauca (Linnaeus)	x	x	x	
Hydrobiidae				x
Ancylidae (2 spp.)		x	x	
Bivalvia				
Sphaeriidae (2 spp.)	x	x	x	
Mytellidae[6]				
Mytilopsis dominigensis Recluz				x
Vertebrata				
Teleostei (see separate list)				
Amphibia				
Bufonidae				
Bufo marinus (Linnaeus)			x	
B. granulosus beebei Gallardo			x	

APPENDIX 3 (continued)

Taxon	Stations			
	1	2	3	4
Hylidae				
Hyla geographica geographica Spix		x		
Leptodactylidae				
Leptodactylus podicipinus petersi (Steindachner)		x		
Reptilia				
Chelidae				
Phrynops (Mesoclemmys) gibbus (Schweigger)		x	x	
Emydidae				
Rhinoclemmys punctularia punctularia (Daudin)		x		
Kinosternidae				
Kinosternon scorpioides scorpioides (Linnaeus)		x	x	
Crocodylidae				
Caiman crocodilus (Linnaeus)		x	x	x

Specimens determined by:

1 : Dr. W.L. Peters, Florida A & M University, Tallahassee, FL, U.S.A.

2 : Prof. M.J. Westfall Jr., University of Florida, Gainesville, FL, U.S.A.

3 : Dr. N. Nieser, Tiel, The Netherlands.

4 : Dr. P.J. Spangler, NMNH, Washington DC, U.S.A.

5 : Mr. R. Martinez, CAREC, Trinidad.

6 : Dr. P.R. Bacon, U.W.I., Mona, Jamaica.

APPENDIX 4

Taxonomic list of phyto- and zooplankton collected at Stations 1 to 4 between July 1980 and June 1981.

Taxon	Stations			
	1	2	3	4
Cyanophyta				
Myxophyceae				
Spirulina, Oscillatoria, other filamentous spp.		x	x	x
Chlorophyta				
Chlorophyceae				
Desmidiaceae				
Closterium, Pleurotaenium	x	x	x	x
Zygnemataceae				
Spirogyra		x		x
Oedogoniaceae				
Oedogonium		x	x	
Chrysophyta				
Bacillariophyceae				
Coscinodiscaceae				
Coscinodiscus				x
Melosira	x		x	x
Fragilariaceae				
Synedra				x
Naviculaceae				
Navicula, Pinnularia, Gyrosigma	x	x	x	x
Protozoa				
Phytomastigophorea				
Euglenidae				
Euglena, Phacus, Trachelomonas	x	x	x	x
Zoomastigophorea	x	x	x	
Rhizopoda				
Arcellidae				
Arcella	x	x		x
Difflugiidae				
Difflugia	x	x	x	x

APPENDIX 4 (continued)

Taxon	Stations 1	 2	 3	 4
Actinopoda				
Clathrulinidae				
Clathrulina	X	X		
Ciliata	X	X	X	
Coelenterata				
Hydrozoa				
Petasidae				
Craspedacusta				X
Rotifera				
Flosculariaceae				
Conochilus		X	X	
Arthropoda				
Crustacea				
Cladocera			X	X
Ostracoda			X	X
Copepoda (Calanoida, Cyclopoida)	X	X	X	X
Amphipoda			X	X
Arachnoidea (Hydracarina)	X	X		X

APPENDIX 5.

Method used to test the significance of the regression coefficient using F in an analysis of variance (after Parker 1979).

The following table was set up with the relevant data:

Sources of variation	Sums of squares (SS)	Degrees of freedom	Mean-squares (MS)	F
Regression	$\frac{(\Sigma xy)^2}{\Sigma x^2}$	1	$\frac{\text{Regression SS}}{1}$	$\frac{\text{Regression MS}}{\text{Residual MS}}$
Residual	$\Sigma y^2 - \frac{(\Sigma xy)^2}{\Sigma x^2}$	N - 2	$\frac{\text{Residual SS}}{N - 2}$	---
Total	(Σy^2)	N - 1	---	---

where $\Sigma xy \equiv \Sigma XY - \frac{(\Sigma X)\ (\Sigma Y)}{N}$

APPENDIX 5 (continued)

where $$\Sigma x^2 \equiv \Sigma X^2 - \frac{(\Sigma X)^2}{N}$$

$$\Sigma y^2 \equiv \Sigma Y^2 - \frac{(\Sigma Y)^2}{N}$$

and X = independent variable

Y = dependent variable

N = number of samples

F has 1 / (N - 2) degrees of freedom.

The 95% confidence limits of the regression coefficient were determined as follows:

$$95\%\ \text{limits} = b \pm t_{(N\ -\ 2,0.05)}\sqrt{\frac{\text{Residual MS}}{\Sigma x^2}}$$

APPENDIX 6

Method used to compare two regression coefficients (after Bailey 1981).

The residual variance, s^2, was calculated for each set of data as follows:

$$s^2 = \frac{1}{N - 2} \left(\Sigma y^2 - \frac{(\Sigma xy)^2}{\Sigma x^2} \right)$$

The d-statistic was then computed according to the following formula for sample sizes >30:

$$d = \frac{b_1 - b_2}{\sqrt{\left(\frac{s_1^2}{\Sigma x_1^2} + \frac{s_2^2}{\Sigma x_2^2} \right)}}$$

where b = regression coefficient

other symbols are as in Appendix 5 with subscripts denoting data sets 1 and 2.

To compare the observed regression coefficient with a predicted value (b^1), the following procedure was used (after Sokal & Rohlf 1981):

standard error of b (s_b) $= \sqrt{\frac{s^2}{\Sigma x^2}}$

$$t_s = \frac{b - b^1}{s_b}$$ for n - 2 degrees of freedom.

APPENDIX 7

The effects of formalin preservation on length and weight measurements of the six fish species studied.

Species	N	Mean preserved value as % fresh ± SE		Paired-sample t-test	
		SL	TW	t_{SL}	t_{TW}
G. sternicla	51	98.33 ± 0.13	96.25 ± 0.43	13.506***	9.785***
C. riisei	53	97.52 ± 0.22	97.32 ± 0.61	11.331***	3.515***
A. bimaculatus	26	97.84 ± 0.24	98.14 ± 0.76	8.970***	0.509^{ns}
H. unilineatus	36	98.17 ± 0.17	94.85 ± 0.69	11.258***	6.934***
C. aeneus	33	99.20 ± 0.39	105.61 ± 0.64	2.219*	7.031***
P. reticulata	51	96.98 ± 0.26	94.92 ± 0.68	12.444***	7.405***

N : Number of samples
SE : Standard Error
ns : Not significant, $p>0.05$
* : $p<0.05$
*** : $p<0.001$

APPENDIX 8

The effect of formalin preservation on the parameters of the length-weight relationship for the six fish species studied.

Species		N	$\log_{10}a$	$a(\times 10^{-6})$	b	r	d
G. sternicla	(F)	58	-5.074	8.433	3.275***	0.950***	0.760^{ns}
	(P)	51	-5.309	4.909	3.427***	0.957***	
C. riisei	(F)	57	-5.335	4.624	3.305***	0.978***	0.644^{ns}
	(P)	53	-5.205	6.237	3.224***	0.990***	
A. bimaculatus	(F)	29	-4.949	11.246	3.198***	0.997***	1.082^{ns}
	(P)	26	-5.093	8.072	3.298***	0.997***	
H. unilineatus	(F)	46	-4.797	15.959	3.074***	0.984***	0.437^{ns}
	(P)	36	-4.890	12.882	3.135***	0.984***	
C. aeneus	(F)	34	-4.216	60.814	2.906***	0.986***	1.151^{ns}
	(P)	33	-4.390	40.738	3.034***	0.989***	
P. reticulata	(F)	52	-5.311	4.887	3.492***	0.988***	0.518^{ns}
	(P)	51	-5.222	5.998	3.438***	0.992***	

N : Number of specimens
$\log_{10}a$: Intercept
b : Regression coefficient
r : Correlation coefficient
ns : Not significant, $p > 0.10$

$\log_{10}a$, b and r: of the equation $\log_{10}TW = \log_{10}a + b \log_{10}SL$

*** : $p<0.001$
F : Fresh specimens
P : Preserved specimens

APPENDIX 9(a)

Monthly variation of numbers of *G. sternicla* at each maturity stage over the whole study period.

	Females				Males			
Month	I	D	M	R	I	D	M	R
1980/05		1	3				4	
06							2	
07			1				1	
08			1				3	
09	1							
10					2		4	
11	2							
12	2	1			2	4	1	
1981/01	3				2			
02	4				1	2		
03	1					1		
04		1						
05								
06			2				1	
07	9	2	2		1		6	
08	5					1	8	
09				2		5	5	
10	2					1		
11								
12	1						4	
1982/01	1	1				3	4	
02						2		
03	7	2	1		9	3	6	
04	6	1	3		2	2	1	
05	8	5	5		5	13	27	
06								
07	2		3	1			6	
08		1	2			2	5	

APPENDIX 9(b)

Monthly variation of sex ratios and GSI's for *G. sternicla* over the whole study period.

Month	Numbers M/F	Female GSI %		Male GSI %	
		Mean ± SE	Range	Mean ± SE	Range
1980/05	4/4	1.859 ± 0.54	1.075 - 3.371	1.421 ± 0.46	0.610 - 2.752
06	2/0	-	-	2.953 ± 0.00	2.951 - 2.955
07	1/1	3.901	-	0.936	-
08	3/1	9.571	-	1.078 ± 0.58	0.470 - 2.241
09	0/1	0.234	-	-	-
10	6/0	-	-	0.632 ± 0.08	0.447 - 0.834
11	0/2	0.355 ± 0.11	0.245 - 0.465	-	-
12	2/3	0.440 ± 0.02	0.402 - 0.472	-	-
1981/01	2/3	0.284 ± 0.02	0.255 - 0.316	-	-
02	3/4	0.453 ± 0.05	0.399 - 0.588	-	-
03	1/2	0.447 ± 0.08	0.363 - 0.531	0.086	-
04	0/1	1.901	-	-	-
05	0/0	-	-	-	-
06	1/2	7.811 ± 4.45	3.361 - 12.262	2.822	-

APPENDIX 9(b) continued

Month	Numbers M/F	Female GSI % Mean ± SE	Female GSI % Range	Male GSI % Mean ± SE	Male GSI % Range
1981/07	6/13	1.082 ± 0.46	0.314 - 4.916	1.019 ± 0.15	0.630 - 1.617
08	9/5	0.227 ± 0.02	0.178 - 0.301	0.950 ± 0.12	0.267 - 1.557
09	10/2	-	-	0.435 ± 0.07	0.168 - 0.924
10	1/2	0.393 ± 0.15	0.244 - 0.541	0.473	-
11	0/0	-	-	-	-
12	4/1	0.374	-	1.467 ± 0.06	1.306 - 1.582
1982/01	7/2	0.454 ± 0.16	0.295 - 0.614	0.596 ± 0.10	0.338 - 1.083
02	2/0	-	-	0.610 ± 0.14	0.470 - 0.750
03	16/10	0.704 ± 0.42	0.106 - 4.402	0.832 ± 0.16	0.073 - 1.423
04	3/11	1.939 ± 0.84	0.283 - 7.653	1.128 ± 1.03	0.103 - 2.152
05	40/19	2.613 ± 0.76	0.191 - 9.707	1.493 ± 0.11	0.130 - 2.665
06	0/0	-	-	-	-
07	6/6	3.168 ± 1.48	0.289 - 9.716	1.794 ± 0.21	1.274 - 2.667
08	7/3	1.927 ± 0.69	0.670 - 3.031	1.009 ± 0.16	0.300 - 1.494

APPENDIX 9(c)

Monthly variation of condition factors for *G. sterniсla* over the whole study period (Means ± SE).

Month	Female		Male	
	CFT %	CFS %	CFT %	CFS %
1980/05	1.397 ± 0.02	1.371 ± 0.03	1.373 ± 0.06	1.353 ± 0.06
06	-	-	1.444 ± 0.00	1.402 ± 0.00
07	1.284	1.234	1.658	1.642
08	1.451	1.312	1.437 ± 0.03	1.422 ± 0.04
09	1.376	1.373	-	-
10	-	-	1.387 ± 0.05	1.382 ± 0.05
11	1.302 ± 0.06	1.298 ± 0.06	-	-
12	1.320 ± 0.06	1.315 ± 0.06	1.470 ± 0.00	1.470 ± 0.00
1981/01	1.526 ± 0.11	1.522 ± 0.11	1.451 ± 0.07	1.451 ± 0.07
02	1.501 ± 0.08	1.494 ± 0.08	1.517 ± 0.03	1.517 ± 0.03
03	1.482 ± 0.07	1.475 ± 0.07	1.423	1.422
04	1.480	1.452	-	-
05	-	-	-	-
06	1.462 ± 0.11	1.343 ± 0.03	1.397	1.357

APPENDIX 9(c) continued

Month	Female		Male	
	CFT %	CFS %	CFT %	CFS %
1981/07	1.452 ± 0.03	1.436 ± 0.03	1.440 ± 0.02	1.425 ± 0.02
08	1.509 ± 0.05	1.506 ± 0.05	1.418 ± 0.02	1.404 ± 0.02
09	1.341 ± 0.03	1.341 ± 0.03	1.439 ± 0.03	1.433 ± 0.03
10	1.510 ± 0.01	1.504 ± 0.00	1.619	1.611
11	-	-	-	-
12	1.346	1.341	1.477 ± 0.05	1.455 ± 0.05
1982/01	1.614 ± 0.09	1.606 ± 0.09	1.487 ± 0.05	1.478 ± 0.05
02	-	-	1.128 ± 0.01	1.121 ± 0.01
03	1.513 ± 0.03	1.503 ± 0.03	1.428 ± 0.02	1.422 ± 0.03
04	1.512 ± 0.03	1.484 ± 0.03	1.560 ± 0.06	1.549 ± 0.07
05	1.523 ± 0.02	1.485 ± 0.03	1.500 ± 0.02	1.478 ± 0.02
06	-	-	-	-
07	1.464 ± 0.02	1.416 ± 0.02	1.448 ± 0.02	1.422 ± 0.02
08	1.477 ± 0.02	1.449 ± 0.02	1.471 ± 0.03	1.457 ± 0.03

APPENDIX 10(a)

Monthly variation of numbers of *C. riisei* at each maturity stage over the whole study period.

	Females				Males			
Month	I	D	M	R	I	D	M	R
1980/05	13				3	1	3	
06	1	1	1				4	
07			1		5	1	2	
08	1		3				2	
09	3	1	2			1	2	
10	1				1		2	
11			1		2			
12	17		1		6			
1981/01			5			2	2	
02	2	2	4		3	2	1	
03	1					1		
04			1		2			
05		1	6	1			3	
06	2	1	2			5	3	
07	1		1		2	2	4	
08					2		2	
09	1		1		3	2	2	
10			5		3		2	
11	1	7	5		5	1	2	
12	3		6		6		1	
1982/01			4		3	1	1	
02	3		2	1	3		2	
03	3	1			2	1	2	
04			1		3	2	1	
05	2	1			2	2	6	
06								
07					1		1	
08								

APPENDIX 10(b)

Monthly variation of sex ratios and GSI's for *C. riisei* over the whole study period.

Month	Numbers M/F	Female GSI %		Male GSI %	
		Mean ± SE	Range	Mean ± SE	Range
1980/05	7/13	-	-	-	-
06	4/1	5.351	-	1.882 ± 0.18	1.613 - 2.381
07	8/1	11.009	-	0.887 ± 0.37	0.244 - 1.583
08	2/3	9.426 ± 1.61	7.313 - 12.585	1.057 ± 0.18	0.875 - 1.240
09	3/3	7.901 ± 3.66	1.471 - 14.130	1.477 ± 0.54	0.522 - 2.398
10	3/1	1.294	-	1.217 ± 0.39	0.830 - 1.604
11	2/1	3.738	-	-	-
12	6/9	1.849 ± 1.26	0.286 - 9.397	-	-
1981/01	4/5	8.648 ± 0.60	7.116 - 10.714	0.947 ± 0.21	0.565 - 1.269
02	6/6	3.811 ± 1.47	0.429 - 10.020	0.891	-
03	1/1	0.833	-	-	-
04	2/1	3.478	-	-	-
05	3/6	8.148 ± 0.83	6.341 - 11.979	1.096 ± 0.44	0.468 - 1.932
06	8/3	6.426 ± 2.74	1.254 - 10.561	1.133 ± 0.14	0.370 - 1.546

APPENDIX 10(b) continued

Month	Numbers M/F	Female GSI %		Male GSI %	
		Mean ± SE	Range	Mean ± SE	Range
1981/07	8/2	9.029	-	1.110 ± 0.13	0.853 - 1.449
08	4/0	-	-	0.937 ± 0.01	0.927 - 0.946
09	7/2	2.439	-	1.067 ± 0.33	0.733 - 1.401
10	5/5	8.249 ± 1.16	5.974 - 12.158	1.168 ± 0.04	1.124 - 1.212
11	6/12	2.408 ± 0.43	0.775 - 6.112	0.947 ± 0.67	0.282 - 1.613
12	7/5	5.011 ± 0.67	3.593 - 6.735	0.885	-
1982/01	5/4	6.442 ± 2.11	3.349 - 12.378	1.250	-
02	5/4	2.260 ± 0.49	0.976 - 3.158	1.488 ± 0.36	0.773 - 1.882
03	5/2	1.695 ± 0.58	1.111 - 2.278	1.164 ± 0.24	0.690 - 1.500
04	6/1	4.150	-	1.495 ± 0.33	0.873 - 1.974
05	10/1	4.199	-	0.994 ± 0.15	0.299 - 1.779
06	0/0	-	-	-	-
07	2/0	-	-	1.163	-
08	0/0	-	-	-	-

APPENDIX 10(c)

Monthly variation of condition factors for *C. riisei* over the whole study period (Means ± SE).

Month	Female		Male	
	CFT %	CFS %	CFT %	CFS %
1980/05	0.827 ± 0.02	0.827 ± 0.02	0.853 ± 0.02	0.853 ± 0.02
06	1.082	1.024	0.973 ± 0.02	0.955 ± 0.02
07	1.047	0.932	1.009 ± 0.03	1.005 ± 0.03
08	1.073 ± 0.08	0.970 ± 0.06	1.011 ± 0.03	1.001 ± 0.03
09	0.981 ± 0.09	0.897 ± 0.05	0.904 ± 0.02	0.890 ± 0.02
10	0.990	0.977	0.938 ± 0.02	0.930 ± 0.03
11	1.028	0.990	1.037 ± 0.04	1.037 ± 0.04
12	1.041 ± 0.02	1.000 ± 0.02	1.045 ± 0.03	1.045 ± 0.03
1981/01	1.007 ± 0.06	0.921 ± 0.05	0.915 ± 0.03	0.980 ± 0.03
02	1.050 ± 0.05	1.007 ± 0.03	1.004 ± 0.04	1.003 ± 0.04
03	0.985	0.977	1.092	1.092
04	1.105	1.067	1.038 ± 0.02	1.038 ± 0.02
05	1.125 ± 0.01	1.034 ± 0.02	0.963 ± 0.11	0.953 ± 0.11
06	1.062 ± 0.02	0.993 ± 0.01	1.012 ± 0.04	1.001 ± 0.04

APPENDIX 10(c) continued

Month	Female		Male	
	CFT %	CFS %	CFT %	CFS%
1981/07	1.091 ± 0.04	1.040 ± 0.02	1.040 ± 0.02	1.034 ± 0.03
08	-	-	1.022 ± 0.03	1.018 ± 0.04
09	1.111 ± 0.01	1.097 ± 0.00	1.053 ± 0.05	1.050 ± 0.05
10	1.003 ± 0.03	0.920 ± 0.03	0.981 ± 0.07	0.977 ± 0.07
11	0.876 ± 0.03	0.854 ± 0.03	0.924 ± 0.02	0.921 ± 0.02
12	1.037 ± 0.03	0.984 ± 0.02	0.968 ± 0.05	0.966 ± 0.05
1982/01	1.075 ± 0.02	1.004 ± 0.01	1.071 ± 0.04	1.069 ± 0.05
02	0.938 ± 0.04	0.917 ± 0.04	0.944 ± 0.02	0.936 ± 0.02
03	0.991 ± 0.01	0.974 ± 0.01	0.902 ± 0.01	0.896 ± 0.01
04	1.037	0.994	1.038 ± 0.03	1.031 ± 0.04
05	1.220	1.169	1.033 ± 0.03	1.025 ± 0.03
06	-	-	-	-
07	-	-	1.016 ± 0.04	1.010 ± 0.04
08	-	-	-	-

APPENDIX 11(a)

Monthly variation of numbers of *A. bimaculatus* at each maturity stage over the whole study period.

	Females				Males			
Month	I	D	M	R	I	D	M	R
1980/05	1	1			1		1	
06								
07								
08					2			
09	1							
10								
11	1							
12								
1981/01	2	1						
02								
03								
04								
05			1					
06								
07								
08								
09	1							
10	7	1			4	4	2	
11	3	1					3	
12								
1982/01						2		
02	1							
03	1					1		
04	1							
05						2		
06								
07	1							
08	2							

APPENDIX 11(b)

Monthly variation of sex ratios and GSI's for *A. bimaculatus* over the whole study period.

Month	Numbers M/F	Female GSI %		Male GSI %	
		Mean ± SE	Range	Mean ± SE	Range
1980/05	1/1	1.135	-	1.447	-
11	0/1	0.127	-	-	-
1981/01	0/2	0.227 ± 0.03	0.193 - 0.261	-	-
05	0/1	4.490	-	-	-
10	4/6	0.673 ± 0.50	0.110 - 3.180	0.921 ± 0.05	0.840 - 0.994
11	2/1	1.746	-	1.066 ± 0.34	0.723 - 1.409
1982/01	2/0	-	-	0.515 ± 0.23	0.287 - 0.742
03	1/0	-	-	0.588	-
08	0/1	0.215	-	-	-

APPENDIX 11(c)

Monthly variation of condition factors for *A. bimaculatus* over the whole study period (Means ± SE).

Month	Female CFT %	Female CFS %	Male CFT %	Male CFS %
1980/05	1.285	1.270	1.123	1.106
11	1.510	1.508	-	-
1981/01	1.387 ± 0.00	1.384 ± 0.00	-	-
05	1.470	1.404	-	-
10	1.444 ± 0.04	1.435 ± 0.04	1.379 ± 0.04	1.369 ± 0.04
11	1.388	1.364	1.347 ± 0.05	1.332 ± 0.04
1982/01	-	-	1.471 ± 0.10	1.464 ± 0.11
03	-	-	1.219	1.212
08	1.575	1.572	-	-

APPENDIX 12(a)

Monthly variation of numbers of *C. aeneus* at each maturity stage over the whole study period.

	Females				Males			
Month	I	D	M	R	I	D	M	R
1980/05	2	5	3	5		10	29	
06		3	10			7	33	
07			3					
08			1					
09			5	2		2	1	
10		1		1			1	
11								
12	3					2		
1981/01		1	2	3		2		
02								
03			2				1	
04			1					
05			2				2	
06		1	2				2	
07	1	4	5	1			12	
08								
09								
10	1	4	6	1		4	9	
11	1		2	1		4		
12			2					
1982/01		1				2		
02		1	7			12		
03			6		1		2	
04						1		
05			2			1		
06								
07								
08		1	3			2		

APPENDIX 12(b)

Monthly variation of sex ratios and GSI's for *C. aeneus* over the whole study period.

Month	Numbers M/F	Female GSI %		Male GSI %	
		Mean ± SE	Range	Mean ± SE	Range
1980/05	34/15	2.827 ± 0.54	0.455 - 6.677	0.621 ± 0.05	0.243 - 1.144
06	38/13	7.870 ± 1.12	2.374 - 14.373	0.355 ± 0.02	0.193 - 0.702
07	0/3	9.682 ± 2.29	5.176 - 12.666	-	-
08	0/1	15.117	-	-	-
09	3/7	8.886 ± 2.04	2.724 - 16.338	0.348 ± 0.05	0.246 - 0.429
10	1/2	2.112 ± 1.53	0.587 - 3.637	0.277	-
11	0/0	-	-	-	-
12	2/3	0.378 ± 0.02	0.346 - 0.401	0.196 ± 0.02	0.176 - 0.216
1981/01	2/6	2.406 ± 0.67	0.483 - 5.069	0.432 ± 0.04	0.391 - 0.472
02	0/0	-	-	-	-
03	1/2	5.071 ± 1.21	3.865 - 6.277	0.357	-
04	0/1	12.372	-	-	-
05	2/2	11.832 ± 0.78	11.050 - 12.614	0.599 ± 0.01	0.587 - 0.611
06	2/3	7.066 ± 3.17	0.734 - 10.531	0.723 ± 0.16	0.558 - 0.887

APPENDIX 12(b) continued

	Numbers	Female GSI %		Male GSI %	
Month	M/F	Mean ± SE	Range	Mean ± SE	Range
1981/07	12/11	3.418 ± 0.77	0.572 - 8.524	0.365 ± 0.03	0.204 - 0.483
08	0/0	-	-	-	-
09	0/0	-	-	-	-
10	13/12	7.414 ± 2.08	0.643 - 21.169	0.506 ± 0.04	0.309 - 0.774
11	4/1	5.713	-	0.354 ± 0.04	0.256 - 0.462
12	0/2	9.052 ± 1.91	7.138 - 10.965	-	-
1982/01	2/1	0.712	-	0.298 ± 0.04	0.258 - 0.337
02	12/8	4.023 ± 0.64	1.985 - 6.819	0.340 ± 0.03	0.162 - 0.557
03	2/6	7.356 ± 1.36	2.359 - 11.033	0.387 ± 0.04	0.343 - 0.431
04	0/0	-	-	-	-
05	0/2	11.317 ± 0.80	10.519 - 12.115	-	-
06	0/0	-	-	-	-
07	0/0	-	-	-	-
08	2/4	2.966 ± 0.73	0.897 - 4.012	0.414 ± 0.06	0.358 - 0.470

APPENDIX 12(c)

Monthly variation of condition factors for *C. aeneus* over the whole study period (Means ± SE).

	Female		Male	
Month	CFT %	CFS %	CFT %	CFS %
1980/05	4.416 ± 0.12	4.293 ± 0.12	4.315 ± 0.07	4.291 ± 0.07
06	4.899 ± 0.07	4.512 ± 0.08	4.599 ± 0.06	4.582 ± 0.06
07	5.222 ± 0.07	4.714 ± 0.10	-	-
08	5.357	4.547	-	-
09	5.121 ± 0.07	4.667 ± 0.13	4.863 ± 0.22	4.846 ± 0.21
10	4.798 ± 0.02	4.697 ± 0.09	4.648	4.635
11	-	-	-	-
12	4.957 ± 0.08	4.939 ± 0.08	5.002 ± 0.45	4.992 ± 0.45
1981/01	4.771 ± 0.07	4.658 ± 0.09	4.738 ± 0.11	4.717 ± 0.11
02	-	-	-	-
03	4.798 ± 0.09	4.553 ± 0.03	4.922	4.905
04	5.238	4.590	-	-
05	5.536 ± 0.20	4.882 ± 0.22	5.205 ± 0.19	5.174 ± 0.18
06	4.964 ± 0.10	4.607 ± 0.06	4.659 ± 0.29	4.626 ± 0.30

APPENDIX 12(c) continued

Month	Female		Male	
	CFT %	CFS %	CFT %	CFS %
1981/07	4.731 ± 0.07	4.569 ± 0.07	4.869 ± 0.05	4.852 ± 0.05
08	-	-	-	-
09	-	-	-	-
10	4.990 ± 0.10	4.609 ± 0.11	4.460 ± 0.19	4.437 ± 0.19
11	4.742	4.471	4.706 ± 0.11	4.689 ± 0.11
12	5.015 ± 0.04	4.562 ± 0.13	-	-
1982/01	4.401	4.370	4.637 ± 0.10	4.623 ± 0.10
02	4.638 ± 0.11	4.451 ± 0.10	4.673 ± 0.09	4.657 ± 0.09
03	4.648 ± 0.08	4.304 ± 0.08	4.654 ± 0.10	4.636 ± 0.10
04	-	-	-	-
05	4.942 ± 0.01	4.383 ± 0.03	-	-
06	-	-	-	-
07	-	-	-	-
08	4.830 ± 0.09	4.686 ± 0.08	4.934 ± 0.24	4.914 ± 0.24

APPENDIX 13

Comparison of regression coefficients of the length-weight relationships for the six species studied.

	G. sternicla	*C. riisei*	*A. bimaculatus*	*H. unilineatus*	*C. aeneus*	*P. reticulata*
G. sternicla	-	-	-	-	-	-
C. riisei	3.060**	-	-	-	-	-
A. bimaculatus	1.833^{ns}	1.527^{ns}	-	-	-	-
H. unilineatus	4.573***	0.381^{ns}	2.554*	-	-	-
C. aeneus	7.150***	4.146***	5.878***	4.571***	-	-
P. reticulata	2.885**	-0.397^{ns}	1.210^{ns}	-0.943^{ns}	-4.715***	-

Values in the table represent the d-statistic calculated as per Appendix 6, using data summarised in Table 23.

ns : $p>0.05$
* : $p<0.05$
** : $p<0.01$
*** : $p<0.001$