Population dynamics, Biology and Ecology of the caridean shrimps; *Crangon crangon* Linnaeus, *Crangon allmanni* Kinahan and *Pandalus montagui* Leach in the Estuary and Firth of Forth, Scotland.

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DEDICATED TO MY BELOVED CHILDREN...

NATASHA AND ASANKA

DECLARATION

The work presented in this thesis is the result of my own investigations carried out at the University of Stirling, Stirling, Scotland. It has not been and not will be submitted concurrently in candidature for any other degree, in this or any other University.

S.C. Jayamanne

ABSTRACT

The population of shrimps from five stations in the estuary and one station in Firth of Forth were sampled for two years from January 1992 to investigate their population dynamics, reproductive biology and feeding ecology. Sampling was carried out at high water and low water, six times a year, by towing an Agassiz trawl, with the Forth River Purification Boards' research vessel, the 'Forth Ranger'.

Two residents, *Crangon crangon* and *Pandalus montagui*, and a migrant species, *Crangon allmanni*, were identified as the main three species of shrimps in the estuary and Firth of Forth. *C. crangon* was found throughout the estuary while *P. montagui* was confined to the lower reaches of the estuary. *C. allmanni* appeared in the estuary in October and left by June. In the Firth of Forth, *P. montagui* and *C. allmanni* were the dominant species.

The breeding cycle commenced in October, and berried females were found by December/January for all species. Berried females of *P. montagui*, and both male and female *C. allmanni*, migrated from the estuary to deeper areas, never to return. *C. crangon* females with eggs ready to hatch, spent females and larvae all occurred in the estuary. The larvae were present in the estuary from April to October. Larvae of the other two species were not found in the estuary.

All species fed mainly on polychaetes, followed by bivalves and crustaceans, which indicated a benthophagous feeding habit. The choice of food depended on the local availability of prey items, and the range of the particular shrimp species within the area; shrimps fed on prey which was abundant in their area of residence rather than moving elsewhere. The Forth Estuary is well utilized by the three species with little competition between them. Although a slow growth rate was observed in *C. crangon*, the mean condition factor indicated that the conditions in the Forth estuary were close to those normally required for shrimps.

The Forth estuary shelters three species of shrimps, with populations, varying between 1992 and 1993, of 1.6 -7.7 x 10^7 for *C. crangon*, 1.6-2.5 x10^7 for *P. montagui* and 0.7-1.0 x10^7 for *C. allmanni*. These three species contributed to the total annual shrimp production, which ranged from 5.59-17.93 tons at low water in the ratio 40:14:1. Both resident and migratory fish species benefit from this production because shrimps play a key role in the food web, forming the major link between the lower benthic invertebrates and predatory fish.

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CHAPTER 1. INTRODUCTION

INTRODUCTION

1.1. INTRODUCTION

Shrimps form an important component in the fauna of estuarine and coastal waters. The Caridea represent the dominant natant decapod group in the temperate region and replace the Penaeidea in the Southern latitudes (Allen, 1966). In all there are 2000 species of natant decapods in Europe of which about 1650 are Carideans (Smaldon, 1979). Out of these 1650, only 41 are recorded from British coastal waters. They may be found intertidally, in the shallow sublittoral zone and in abyssal depths. The estuary and Firth of Forth where the present study was based comprises large areas of intertidal mud flats, shallow sublittoral and deeper marine habitat which shelter numerous estuarine and marine fauna including caridean shrimps. Forty one species of carideans described by Smaldon (1979) from the coastal waters of Britain include two species in the Forth: *Crangon crangon* Linnaeus (= *Crangon vulgaris*) and *Pandalus montagui* Leach as recorded by Hunter (1981) and Forth River Purification Board (1978). *C. crangon* is commonly known in Europe as brown shrimp due to its colour when boiled and *P. montagui* as pink shrimp due to its natural bright pink colour. The present study found another species, *Crangon allmanni* Kinahan which had not been recorded in the estuary or Firth of Forth by previous researchers. This species is named as *C. allmanni* by Kinahan (1857), but Allen (1960) used the name *allmani*, claiming that the name given by Kinahan carries a 'capsus calami' (a spelling mistake). In the present study, the name *C. allmanni* was used in accordance with the norms of taxonomy as Kinahan's (1857) classification is the earliest known. The present study is based on the biology and population dynamics of the above three species: *Crangon crangon*, *Pandalus montagui* and *Crangon allmanni* in the estuary and Firth of Forth. It is appropriate at this juncture to review the biology, ecology and population dynamics of the above three species based on the past literature. It should be mentioned here also that although there is ample amount of literature on the life history and biology of *C. crangon*, little exists for *P. montagui* and *C. allmanni.*

1.2. LITERATURE REVIEW

1.2.1. Geographical distribution

The geographical distribution of *C. crangon* and *P. montagui* illustrated by Dore and Frimodt (1987) is shown in Fig. 1.1. *C. crangon* is common in many temperate European

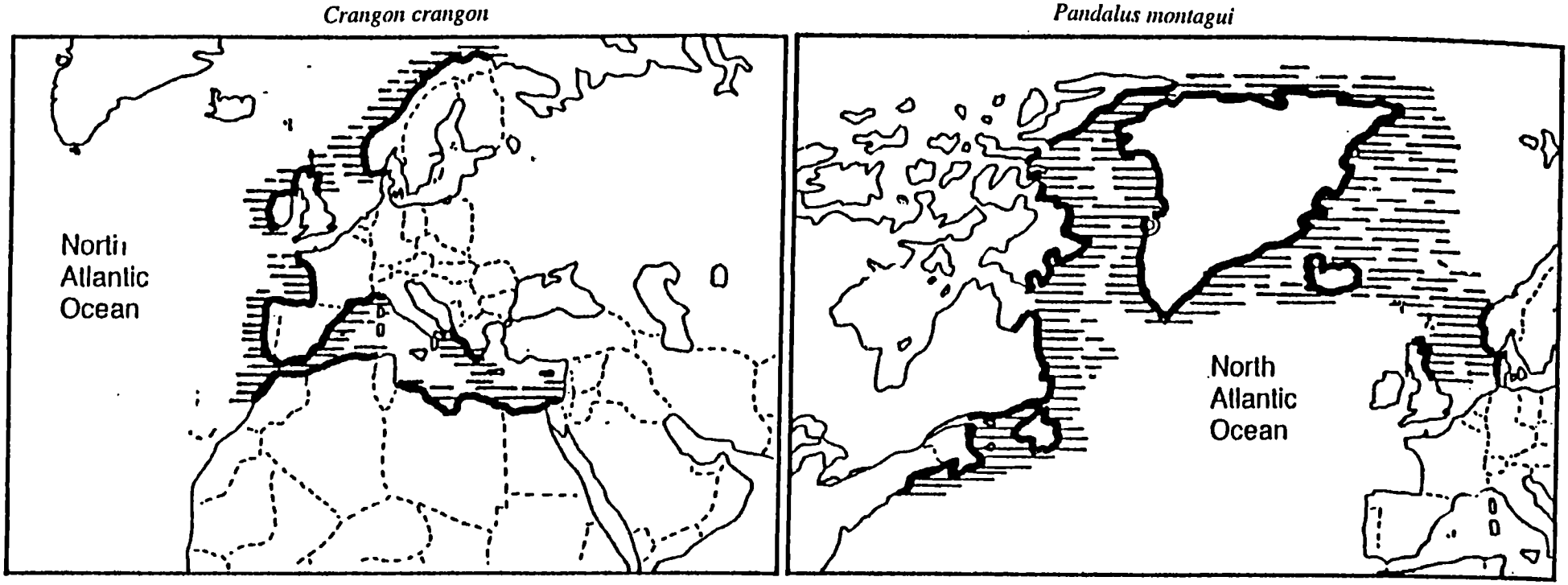


Fig. 1.1 World distribution of *C. crangon* and *P. montagui* as illustrated by Dore and Frimodt (1987).

estuaries and coastal waters and is distributed in the Eastern Atlantic from the White Sea to Portugal and Morocco, in the North sea, in the Baltic sea up to the fjords of Finland, in the Mediterranean and the Black Sea (Ehrenbaum, 1890 and Dore and Frimodt, 1987). *P. montagui* is a boreo-arctic species which ranges from the extreme north of Norway to the English channel (Mistakidis, 1957). It can tolerate a wide range of temperature (-1°C to 20°C) which enables it to extend south to latitude 40°C on the western and latitude 48° on the eastern side of the Atlantic (Squires, 1957). It is found in British Columbia (Butler, 1964); Ontario, Quebec, Newfoundland and Labrador, St. Pierre and Miguelon, New Brunswick, Nova Scotia, Prince Edward I, Greenland Belgium, Netherlands, Denmark, Norway, Sweden, Soviet Isle (Tiews, 1970); Iceland (Wollebaek, 1900) and Canada (Hudon *et al.*,1992). *C. allmanni* is restricted to the eastern boreal region of the Atlantic. It has been recorded in Iceland and throughout the North Sea and Kattegat.

All three species have been recorded from coastal area around England (Henderson, *et al.*, 1990; Webb, 1921; Lebour, 1931; Mistakidis, 1957; Allen, 1960; 1963). *C. crangon* is recorded in the English Channel, Morecombe Bay, Solway Firth, Moray Firth, Tay and Forth estuaries. *P. montagui* is recorded in Ireland and Scotland (Kemp, 1910 ; Hunter, 1981). The distribution of the species in Scottish waters as illustrated by Mason (1967) is given in Fig.1.2. *C. allmanni* was recorded from Northumberland coast (Allen, 1960).

C. crangon is a shallow water species which inhabits sandy, sandy mud and muddy substrata down to a depth of 90 m (Lloyd and Yonge, 1947; Allen, 1966) and shallow coastal areas (Boddeke *et al.*, 1991). Tiews (1970) described the depth limit of *C. crangon* as the 10-20 m line in German Coastal area but Wollebaek (1908) has observed *C. crangon* in the areas as deep as 120 m in winter.

P. montagui prefers hard bottom with small and medium stones with coarse sand and shell fragments (Mistakidis, 1957). They can be found in a depth range of 1- 430 fm (Mistakidis, 1957) and 10 fm to 50 fm (Allen, 1963; 1966).

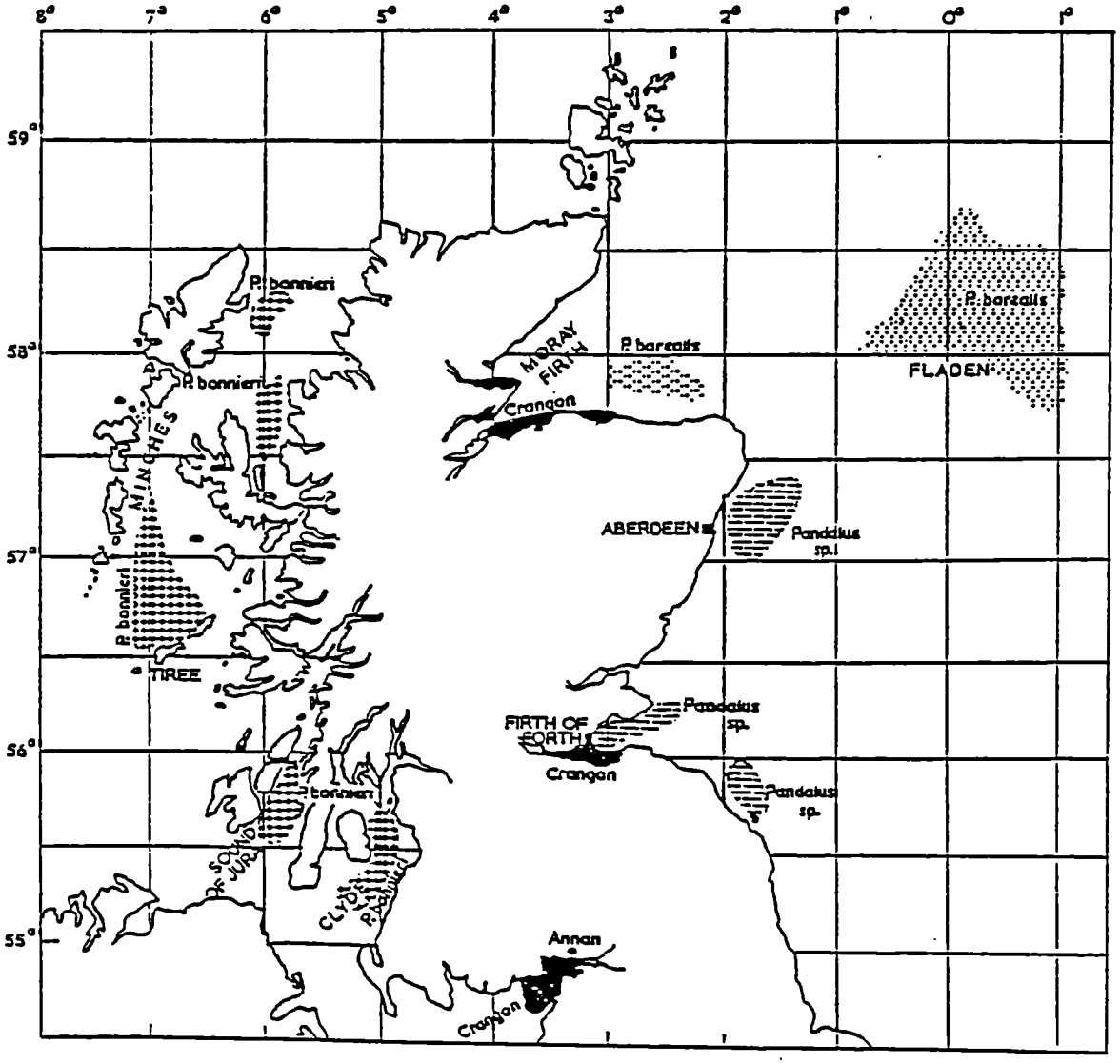


Fig.1.2 Distribution of pink and brown shrimps around Scotland as indicated by catches of research vessels of Department of agriculture and Fisheries for Scotland and the White Fish Authority (after Mason, 1967).

In contrast to the above two species, *C. allmanni* is found at all types of substrates with an exception of rocks (Allen, 1960) and at all depths below 9 fm although its normal range of distribution is between 10 to 100 fm.

1.2.2 Fishery

Crangon crangon and *P. montagui* support commercial fisheries when present in considerable numbers, but there are no records of *C. allmanni* as a fishery resource anywhere in the world. *C. crangon* supports an important commercial fishery off the coasts of Germany, Holland, Belgium, (Smaldon, 1979), Netherland coastal area (Boddeke, 1989) and Portugal (Nobre, 1936). In France, *C. crangon* fishery is considered as a fishery of minor importance (Redant, 1980), where their mortality due to fish predation is higher than the fishing mortality. Fishing effort however, appeared fairly constant during the recent years and shrimp landings showed an increasing trend (Robin, 1992). On the continental European coast, shrimps are also fished for animal feed. In Algeria, *C. crangon* forms the main part of the catches from the shrimping grounds (Ivanov, 1967) and in Italy, they are fished in large quantities and are of considerable commercial importance, being greatly esteemed as food (Soika, 1948). It is also fished on a small scale in the southern North sea and Morecombe Bay (Henderson *et al.*, 1990) and is considered as a commercially important fishery in Canada (Hudon *et al.*, 1992). In Denmark, the Faroe islands, Iceland, Norway, Sweden, Belgium and England it is considered as a fishery of secondary importance (Couture, 1961). The main fishing areas in the U.K. for *P. montagui* are the Wash (east coast), the southeast coast (including Thames estuary), Morecombe Bay and Solway Firth (Simpson *et al.*, 1970; Smaldon, 1979).

The only existing Scottish fishery for *C. crangon* is the inshore beam-trawl fishery in the Solway Firth based on Annan, in which landings of the small *C. crangon* yield around £12,000 annually in 1960's (Mason, 1967). There are records on the existence of commercial fishery for *P. montagui* in the Solway Firth in the early years of the century, but they were said to have disappeared in 1930. They were observed again in 1959 yet disappeared due to heavy fishing. *P. montagui* is not available in commercial quantities in other Scottish estuaries.

1.2.3. Life history

The life history of caridean shrimps follow the sequence of egg stage, larval stages (5-11), post larval stages and juvenile stages before reaching the final stage, adults. The newly hatched larvae of *C. crangon* measure 2 mm (Total length) which increases to 4.7 mm at the end of fifth larval stage when the animal leaves the plankton (Ehrenbaum, 1890; Havinga, 1929; Lebour, 1931). Gurney (1982) described six larval stages, one more than that been reported by the previous authors. Duration of total larval development during the spring is estimated to be 5 weeks and each larval stage found to last an average of eight days (Ehrenbaum, 1890; Thorson, 1946). Criales and Anger (1986) found strong variability in the developmental stages of *C. crangon* reared in the laboratory and identified 13 larval forms and three different developmental pathways taken by them to reach the post larval stage. Larvae of *C. crangon* are planktonic in nature and occur throughout the year (Lebour, 1931). They are present in the plankton from January to November (Lebour, 1947), and especially in spring and summer in the Plymouth coastal area. They are numerous from April to August dwindling only in February and April. The period of larval occurrence varies from the middle of May to October in the Sound between Denmark and Sweden according to Thorson (1946). Tiews (1970) finding's in the Elbe estuary agrees with Thorson (1946) and also shows that the distribution pattern of shrimp larvae depended on the system of coastal currents which transport them. Plett (1965) found that the abundance of larvae was greatest between 10 m - 20 m line decreasing considerably both in shallower and deeper areas.

At the end of fifth larval stage at an average length of 4.7 mm, *C. crangon* reaches the post larval stage, settles on the sea bed and joins the benthic food web (Boddeke, 1982). At this stage they invade tidal flats to spend their nursery stage there. Kuipers and Dapper (1984) observed an invasion of Balgzand tidal flats by *C. crangon* measuring 5 - 20 mm in length during the period from March to May. They were found to leave the tidal nursery and invade the subtidal area at a length of 30 - 35 mm (Janssen and Kuipers, 1980 ; Kuipers and Dapper, 1981). They start to reach this length in the beginning of July, with most reaching this size in August. By September most of the new generation has passed the nursery stage (Kuipers and Dapper, 1984). Adult *C. crangon* inhabit

estuaries and coastal waters. It is euryhaline and mostly found in salinities ranging from that of sea (35%) to the brackish water of river estuaries.

Larvae of *P. montagui* are liberated during spring and summer, while the adults are in the more inshore areas of their tidal range (Lebour, 1947; Allen, 1963). Newly hatched larvae are 2.4 - 3.4 mm in total length (Simpson *et al.*, 1970). They reach the post larval stage after going through 11 zoea stages at 10° C, but only 5 at 18° C. Simpson *et al.*(1970) found six developmental stages in the Firth of Clyde plankton. Björck (1913) found larvae in the Öresund from the middle of July to October. Thorson (1946) from May until August and Lebour (1947) from February to October. No information is available on the juvenile phase of *P. montagui.* Adult *P. montagui* are found in estuaries, coastal waters, fjords and in open sea at a depth range of approximately 3.7 - 5.5 m. (Mistakidis, 1957; Allen, 1963).

The larvae of *C. allmanni* were found mostly in offshore areas and the season of occurrence vary with locality, from May, Jørgensen (1923), December to August, Allen (1960) in Northumberland waters; May and July-September in Blyth and Newbiggin area (Allen, 1960); April-July in Cambois Bay (Bossanyi, 1957); January to June in Plymouth (Lebour, 1931), April to July in Kattegat (Thorson, 1946). The size of the first zoea is 2.0 mm and it reaches a size of 6.5 mm in length (Lebour, 1931) at the last larval stage.

1.2.4. Reproduction

1.2.4.1 Sex dimorphism

According to Ehrenbaum (1890), Havinga (1929) and Lloyd and Yonge (1947) *C. crangon* is heterosexual. Boddeke (1961, 1962 and 1989), however, described it as a protandric hermaphrodite which transforms from male to female after eliminating the male tissue in the gonad during copulation (Boddeke, 1961, 1989). This phenomenon was observed in individuals at a size range of 42 - 46 mm (Boddeke, 1961). Meixner (1966) disagrees with Boddeke (1961), based on his observations on *C. crangon* reared in the laboratory up to a size of 55 - 60 mm where he has found no such transformation at any stage.

P. montagui is a protandric hermaphrodite and contains varying proportions of protandrous hermaphrodites in the populations. Up to 50% of 0 - group individuals start life as males but subsequently transform to females (Mistakidis, 1957; Allen, 1963). There is no literature with regard to hermaphroditism of *C. allmanni.*

1.2.4.2 Sexual characters

The features which facilitate the determination of sex in shrimps, are generally located in the pleopods. Three external features are used to distinguish between the sexes of *C. crangon*, i.e. 1st antenna, 1st pleopod and 2nd pleopod (see Fig. 4.1 of chapter 4). In *C. crangon* of the same size, the outer branch (olfactory) of the 1st antenna has more segments and is broader and longer in males than in females (Ehrenbaum, 1890; Tiews, 1954. This character permits separation between the sexes down to the size of 30 mm in total length (Tiews, 1970). The endopodites of the first pair of pleopods serve as the second character and are shorter and microscopic in males whereas longer in females (Ehrenbaum, 1890). This character however, is not distinguishable in individuals smaller than 20 mm in total lengths, but in males it is bent in a hooked position over the joint of basipodite and exopodite (Lloyd and Yonge, 1947). This character cannot be used for exact separation of sex in animals below 40 mm in total length (Boddeke, 1961). An appendix masculina attached to the endopodite of the second pleopod (Nouvel, 1939) is the third character used to separate the sexes. The endopodites of the second pair of pleopods are biramous in males and uniramous in females. The innermost branch of the male endopodite, which is called appendix masculina, is spinous on one side, while the outer branch resembles the uniramous endopodite of the female. The appendix masculina possesses 18 strong spines along the side and tip of the ramus when fully developed Nouvel (1939). He further noted that the appendix masculina is late in developing, and observed that the ramus possess only 4 spines at a length of 35 mm in total length. According to Tiews (1970), this is the most reliable and valid character which distinguishes between the sexes down to the size of 35 mm in total length, when external dimorphism begins in the life of *C. crangon.* The separation of sex below the size of 20 mm in total length is impractical (Boddeke, 1961; Lloyd and Yonge, 1947). see Fig. 4.1 of Chapter 4.

The secondary sexual characters of *P. montagui* appear on the endopodites of the first and second pleopods. In the male the endopodite of the first pleopod bears a copulatory organ while the second pleopod possesses an appendix masculina (Mistakidis, 1957). The latter structure is absent in females, and their endopodite of the first pleopod is lanceolate in shape (Fig. 4.1). These structures can be used to separate sex down to the size of 5.0 mm carapace length, but in the animals below 4.6 mm carapace length sex differentiation becomes impossible (Mistakidis, 1957).

The secondary sexual characters of *C. allmanni* are the same as that described in *C. crangon* but there are no records of using first antenna as a character to distinguish between sexes.

1.2.4.3 Size at maturity

The length at which shrimps attain first maturity is important since it indicates the size at which the energy is shared between growth and reproduction. This feature is mostly described for females although few references refer to males (Tiews, 1954; Boddeke, 1966). The length of *C. crangon* at the attainment of sexual maturity was found to vary greatly with locality (Lloyd and Yonge, 1947). The length at first sexual maturity of female *C. crangon* was recorded as 43 mm in total length by Havinga (1929) in the Zuiderzee; 36 mm, Wollebaek (1908) in Norway; and 35 - 40 mm, Meyer-Waarden (1935) in the Bay of Jade in Oldenburg. In the Bristol channel and Severn estuary (Lloyd and Yonge, 1947), the smallest egg-carrying females measured 45 mm but in lower salinity areas of the estuary, minimum length was 47 mm. According to Kuipers and Dapper (1984), maturation takes place at a body length of 40 - 50 mm in Wadden Sea. Moore *et al.* (1979) gives the minimum size at maturity as 37 mm in the Severn estuary and states that all females attain maturity before reaching 42 mm. Henderson and Holmes (1987) found size at maturity to be 10.5 mm in carapace length, which is the minimum size at which 5% of the females are berried.

The age at maturity was found to be 1 year by Ehrenbaum (1890) in the German Coast, and also by Meyer-Waarden (1935), Nouvel-Van Rysselberge (1937) and Tiews (1954). In contrast, the respective age found at Zuiderzee, (Havinga, 1930) and Bristol Channel

and Severn Estuary (Lloyd and Yonge, 1947) was 2 years. The size at maturity for males was determined by Tiews (1954) and Boddeke (1966) as 38 mm and 22 mm respectively in Büsum area and Wadden Sea.

Age and size at maturity of *P. montagui* on the coast of England was found to be 7 months and 9 - 11 mm carapace length (Simpson *et al.*, 1970) for males. Ovary maturation was observed in early August, and female *P. montagui* appear to attain maturity by November - December. The only record of *C. allmanni* is from Allen (1960) who observed the smallest size of the berried females as 7.5 mm carapace length in Northumberland waters.

1.2.4.4 Sex ratio

Sex ratio of *C. crangon* seems to be in favour of males. Ehrenbaum (1890), Havinga (1930) and Lloyd and Yonge (1947) found relatively more males in zones of high salinities than low salinities. Tiews (1954) found more than 50% of the catches of small shrimps in Büsum to consisted of males. He attributes this high percentage of males to the age composition of the catches in which two male age groups (0 and 1) and one female age group (0-group) are represented. Sex ratios of Bristol Channel and Severn Estuary show annual cyclic changes and Henderson and Holmes (1987) explain that this is due to the existence of a single population within which differential distribution of males and females occur.

The sex ratio of *P. montagui* is influenced by the transformation of males into females. During the first year of life, 30 - 50% of *P. montagui* population mature as females (Jägersten, 1936). In the second year, some of the males transforms into females while the females continue to function as females. Thus, by the end of third year, almost all the population function as females (Mistakidis, 1957; Allen, 1963).

In *C. allmanni* sex ratio of different year groups are not available. According to Allen (1960) however, the Male: Female ratio varies from 0.15 in June to 1.38 in October in inshore populations.

1.2.4.5 Fecundity

Fecundity of caridean shrimps are generally expressed as the number of early stage eggs attached to the ventral side of the females (Havinga,1930; Meyer-Waarden,1937; Lloyd and Yonge, 1947; Jensen, 1958; Smaldon, 1979; Tiews, 1970; Boddeke, 1982; Henderson and Holmes, 1987). *C. crangon* has been found to carry up to 15,000 eggs (Smaldon, 1979). Jensen (1958) using the egg counts made by Havinga (1930) and Meyer-Waarden (1937), found a linear relationship between the number of eggs carried by the females and length of the female raised to third power ($F \alpha TL^3$). A difference between size of the summer spawned eggs and winter spawned eggs has been observed by Havinga (1930), Tiews (1970) and Boddeke (1982). The latter eggs were found to be larger than that of summer spawned eggs, and the fecundity of winter spawning females were lower than that of summer spawners. Boddeke (1982) describes the relationship of fecundity and size of the females as :

$F = 456.8 + 10.8\ TL^3$ (Winter)

$F = 495.6 + 16.4\ TL^3$ (Summer)

F = Fecundity TL = Total Length

Henderson and Holmes's (1987) findings in the Bristol Channel and Severn Estuary, however, disagrees with Boddeke's findings (1982). According to Henderson and Holmes (1987), the relationship of fecundity and size of the females in the Bristol Channel and Severn Estuary is best described by the equation

$F = 3.3\ (CL)^{2.69}$ CL = Carapace Length

and is unlikely to vary with seasons.

The fecundity of *P. montagui* varied from 136 at a size of 7.2 mm CL to 3796 at 16.0 mm CL in the east coast of England. Mistakidis (1957) also observed a direct correlation between carapace length and fecundity of *P. montagui* but has not expressed it mathematically. No substantial variation is found in the number of eggs carried at the beginning, middle and end of the breeding season (Mistakidis, 1957).

The average fecundity of *C. allmanni* varied from 400 (CL 7.5) to 2500 (CL 13.0). The maximum fecundity recorded was 7600 in a female of 17.0 CL (Allen, 1960). The relationship between CL and fecundity has also not been established for *C. allmanni.*

1.2.4.6 Spawning season

Two major spawning seasons, summer and winter have been observed in *C. crangon* by Ehrenbaum (1890), Havinga (1937) and Meyer-Waarden (1935) in the North sea. Lloyd and Yonge (1947) found a long spawning season and stated that it may probably be due to overlapping of two spawning seasons. Tiews (1954) found three spawning periods at Büsum two extending from April to August and one from November to March. According to Labat (1977), spawning occurs during the coldest months of the year (April - November) in the south along the Mediterranean coast. Henderson and Holmes (1987) found that females spawned twice a year, in January, and in late spring/early summer.

P. montagui was found to have one spawning season which starts in early November, reaches a peak in December, and continues until January or February (Mistakidis, 1957). Each female is found to lay one batch of eggs during the breeding season (Allen, 1963).

C. allmanni has also been found to spawn once a year. The spawning commences in December and continues until the beginning of July. The spawning however, is multiple with a second batch of eggs being laid as soon as the first hatch and is followed by a third smaller breeding peak (Allen, 1960).

1.2.5 Growth

The growth of shrimps are given in past literature mostly as the size at ages. Ehrenbaum (1890) estimated the age of a 60 - 70 mm (TL) *C. crangon* to be 1.5 years. Havinga (1930) determined the total length at the end of the first year as 30 - 35 mm and Meyer (1935) as 37 - 38 mm. According to Tiews (1970) female *C. crangon* reaches a total length of 33 mm at the end of the first year and grows up to 58 mm TL at the end of second year. Meyer-Waarden (1935) found that female *C. crangon* born in February reach a length of 48 mm after one year and 72 - 78 mm after the second year. According to Nouvel and Van Rysselberge (1937), female shrimps grow from 5 mm to 54.5 mm in their first year and up to 70.5 mm in the second year. Lloyd and Yonge (1947) stated that it is difficult to determine the age precisely when the spawning period is so long. According to his findings, growth rates of the two sexes are similar in the first year, but females grow faster in the subsequent year. He assumed that the females of 50 - 60 mm

length are in their third year, females over 60 mm in their fourth year, and those of 80 mm in the fifth year. He further assumed that males of 40 - 45 mm are in the second year while those of 70 mm are possibly four years old. Henderson and Holmes (1987) found a similar growth pattern for the same area except that maximum size attained, and thus longevity, had declined markedly from 5 to 3 years in females and 4 to 2 years in males. Average growth rate of *C. crangon*, as found by Boddeke (1982), was 0.40 mm/day. His calculations are said to be based primarily on the correlations between peaks in summer egg production and autumn fish yield that were highest at a time shift of four months and was not agreed upon by Kuipers and Dapper (1984). According to the latter authors, growth rate of *C. crangon* is 0.23 mm/day. Beukema (1992) disagreed with the average growth rate given by Kuiper and Dapper (1984) since it is based on the back calculations of birth date which cannot be realistic. Beukema (1992) found the average growth as 0.50 mm/day.

The maximum size attained by *C. crangon* varies from author to author (Tiews, 1970). According to Havinga (1930), female *C. crangon* reaches a total length of 91 mm, while the maximum length is 95 mm according to Tiews (1954). Maximum sizes recorded by these authors for males are 75 mm and 68 mm respectively. Boddeke (1966) also recorded the maximum lengths of *C. crangon* males as 68 mm. Lloyd and Yonge (1947) recorded maximum lengths as 80 mm for males and 70 mm for females. Maximum sizes recorded by Lloyd and Yonge (1947) are 21.3 mm (CL) for females and 18.6 mm (CL) for males and are higher than the corresponding values found by Henderson and Holmes (1987) in the same area (18.3 mm (CL) for females and 15.2 mm (CL) for males). Henderson and Holmes (1987) attribute this difference to the changes which occurred due to industrial development in the area since 1947. Males and females live up to 3 years and 2 years respectively (Henderson and Holmes, 1987; Tiews, 1954). Lloyd and Yonge (1947) stated longevity as 5 years for females and 4 years for males.

The growth rates of both male and female *P. montagui* are high during the first year of their life, but decrease during the next 2 or 3 years (Mistakidis, 1957; Allen, 1963). Males reach a carapace length of 10.0 mm during their first year while females reach a carapace length of 11.5 mm. This disparity between the sexes is maintained throughout

their life time and is due to the fact that males mature 3-4 weeks earlier than females (Allen, 1963).

There are considerable variations in the maximum size attained by *P. montagui* over their range of distribution. In the Norwegian coast and in the North sea it is 160 mm (Balss, 1926; Wollebaek, 1900), while it is 130 mm in Labrador and Newfoundland (Squires, 1957, 1961). Maximum sizes of 110 mm and 108 are reported from Maine (Scattergood, 1952) and Ungava Bay (Squires, 1957) respectively, while the lowest maximum sizes are found in Southeast England (Mistakidis, 1957) and Vancouver (Butler, 1964).

The differences between the growth rate of males and females of *C. allmanni* is not apparent in sizes less than 7.5 mm CL. According to Allen (1960) the growth rates and age are difficult to determine, due to its migratory behaviour, but it is probable that *C. allmanni* lives for 3-3.5 years. The average size of the 1-year group was estimated as 8.5 while 2-year group was 12.5 (Allen, 1960).

1.2.6 Food

Like most decapods, *C. crangon* is omnivorous but appears to prefer animal food. In western Sweden, newly recruited *C. crangon* usually feed on meiofauna mainly ostracods and harpacticoid copepods. Older stages feed on macro fauna dominated by *Corophium volutator*, *Nereis* sp., *Mya arenaria* and *Cardium edule*. Early larval stages of *C. crangon* and *Carcinus maenas*, and semi-pelagic mysids, were also eaten by older *C. crangon* (Möller and Rosenberg, 1982; 1983; Pihl and Rosenberg, 1984).

In British waters, the principal food of *C. crangon* appears to be polychaetes, especially *Nereis diversicolor*. According to Ehrenbaum (1890) and Havinga (1929), *C. crangon* mainly feed on polychaetes. Havinga (1929) further includes the algae *Ulva lactuca*, *Enteromorpha intestinalis* and in brackish water *Corophium* sp., gammarids and *Mysis vulgaris*. These food items of *C. crangon* occur in the channel and estuary along with small gastropods, bivalves and fish eggs.

In Swedish waters meiofauna and *C. volutator* are the main food for *C. crangon* throughout the season, while bivalves, *Mya arenaria*, *Cardium edule* and *Mytilus edulis* play an important role in food of *C. crangon* in July and August. Nereid species are eaten mainly in spring and early summer (Pihl and Rosenberg, 1984). According to Boddeke (1982), calanoid copepods are found to be the most preferred food in Netherland coast. Predation on 0-group plaice by *C. crangon* has been observed by Van der Veer and Bergmann (1987). They report that the minimum length of the shrimp which could feed on plaice as 30 mm. Even the larger shrimps (over 70 mm) however, could not predate on plaice bigger than 30 mm in total length.

In Dutch waters, annelids, especially *Nereis succinea* and *N. diversicolor,* form the main food of *C. crangon. Corophium* spp. are the second important food for *C. crangon* in Dutch waters. Young fish or fish larvae or molluscs have seldom been eaten by *C. crangon*, but larger shrimps always preferred worms while the smaller ones preferred *Corophium* (Havinga, 1930).

Johnson and Andre (1991), moreover, found a reduction of copepod population by *C. crangon* and agreed with Pihl and Rosenberg (1984), who state that *C. crangon* prefers harpacticoids and ostracods to foraminiferans and nematodes. Gee (1987) found that harpacticoids are the most significant diet of *C. crangon* juveniles in mud flats, while *Asellopsis intermedia* forms the diet of *C. crangon* in sand flats.

C. crangon was identified as the main predator in epibenthic fauna (Pihl and Rosenberg, 1984) in Swedish waters which exerts a great impact upon the structure and function of benthic communities. It has also been recognised as the most important carnivore in the Wadden sea tidal zone (Kuipers and Dapper, 1981).

P. montagui feeds on small crustaceans, bivalve molluscs and the tubiculous worms *Sabellaria* and *Pectinaria* (Mistakidis, 1957). According to Hudon *et al.* (1992), pelagic shrimp fed on zooplanktors while benthic shrimps contained chitinous debris, sand grains and small amount of benthic organisms. Planktonic prey were the most abundant and frequent group and included copepods, chaetognaths and hyperiid amphipods. Preference

of shrimps for these species proves that they are opportunistic feeders which take advantage of the available resources.

C. allmanni feeds predominantly on living crustacea and annelida. Mollusca, foraminifera and Ophuroidea are present in small quantities, while whiting scales were observed in some stomachs. Sand and mud also were present with the food (Allen, 1960).

1.2.7 Predators

In its turn, *C. crangon* is also predated upon by larger predators. Many species of fish are found to feed on *C. crangon.* According to Kühl (1961) and Tiews (1965) predators of *C. crangon* in the German coast include Goby (*Pomatoschistus minutus*), Armed bullhead (*Agonus catapractus*), Whiting (*Merlangius merlangus*), Smelt (*Osmerus eperlanus*), Dab (*Limanda limanda*), Short spined sea scorpion (*Myoxocephalus scorpius*), Rockling (*Ciliata mustela*), Eelpout (*Zoarces viviparus*) and Gunnel (*Pholis gunnellus*) and Sea snail (*Liparis vulgaris*).

On the Belgian coast, according to Gillis (1952), the main predators, in order of importance, are Whiting, Thornback ray (*Raja clavata*), Bib (*Trisopterus luscus*), Sole (*Solea solea*), Dab, Flounder (*Platichthys flesus*) and Plaice (*Pleuronectus platessa*). Others are Eel (*Conger conger*), Cod (*Gadus morhua*), Dragonet (*Gallionymus lyra*), Gurnard (*Frigia* spp.) and Turbot (*Scophthalmus maximus*).

C. crangon are also found to be prey of sepiolid squid (*Sepietta oweniana*) in Swedish waters (Bergström, 1985) and *Cancer magister* the Dungeness crab in U.S.A. (Stevens *et al.*, 1982).

Birds also feed on *C. crangon*, especially in estuaries. Greenshank (*Tringa nebularia*), Redshank (*T. totanus*), Avocet (*Crecurvirostra avosetta*), spoonbill are major predators of *C. crangon*, and divers, grebes and certain diving ducks also include *C. crangon* in their diet (Smaldon, 1979). Thus, *C. crangon* plays an important role in the food web, being a predator on meiofauna and smaller macrofauna and transferring the energy to vertebrates such as fish, birds and mammals.

The fishes *Gadus merlangus* and *G. luscus* are found to be the major predators of *P. montagui*. *Pleuronectus* spp., *Raja* spp., *Solea* spp., and *Cottus* spp. are also believed to feed on *P. montagui* (Mistakidis, 1957). Cod appears to be a major predator on *P. montagui* populations of Newfoundland, Grand banks and Labrador (Mikhalkovich, 1964). The seal is another predator of *P. montagui* (Squires, 1957; Seargent, 1951). Seargent (1951) found a seal with 50 specimens of *P. montagui* in its stomach in Eastern England in 1951. No reports regarding the predation upon *C. allmanni* have been found in the literature.

1.2.8 Migration

Migration of *C. crangon* into the shallower coastal waters during spring and its subsequent return to deeper saline waters at the onset of winter is a well known fact and has been reported by a number of authors (Havinga, 1930; Broekema, 1942; Lloyd and Yonge, 1947; Haefner, 1969 and Boddeke, 1975). A number of hypotheses have been proposed to explain this behaviour of *C. crangon*. There may be a causal relationship between the seasonal migrations and the osmotic capabilities of the species (Broekema, 1942). Haefner (1969) states that mature shrimps migrate to sea in winter, because they are very sensitive to the salinities below 30% at temperatures below 5° C. According to Lloyd and Yonge (1947), offshore migration is related to spawning for which adults migrate to deeper water in winter and migrate back in spring after spawning. Boddeke (1975) suggests that the migratory behaviour is related to the reproductive activities of the animals which results in the redistribution of the population.

The species also exhibits seasonal inshore and offshore migrations reportedly in relation to salinity, temperature and availability of food (Ehrenbaum, 1890; Havinga, 1929; Meyer, 1935; Broekema, 1941). The shrimps tend to bury themselves in the substrate by the daytime and emerge at night for feeding (Havinga, 1930 and Lloyd and Yonge, 1947). Hartsuyker's (1966) findings are in contrast to the above authors and reports up and down migrations on each tidal rise and fall in the Wadden sea. According to Al Adhub and Naylor (1975), *C. crangon* show peak emergence during the high tide, and the emergence period is symmetrical about the time of high tide, ensuring that the shrimps which move upstream with the late flood tide are transported downstream subsequently by the ebb tide.

Hartsuyker (1966) states that the young shrimps moving upstream closely follow the water covering the tidal flats, and that the larger animals follow with delay. At the ebb tide, larger animals leave the flats first followed by the young animals. Janssen and Kuipers (1980) disagree with Hartsuyker (1966) and report that the shrimp population shows a spatial separation between the adults that inhabit subtidal areas and the juvenile (< 2.5 cm) that are restricted to the tidal zone. According to their findings, the juvenile population does not show migration of any importance during the ebb tide.

Van Der Baan (1975) noted that the reinvasion of the estuary by *C. crangon* during spring time is closely related to temperature differences between ebb and flood water; the same holds for reverse migrations to the open sea in autumn. According to Spaargaren (1980), the seasonal movements of *C. crangon* populations are a direct result of the passive displacements which would occur when random periods of swimming alternate with periods of sinking in which no orientational behaviour of the animals is involved.

P. montagui also shows a pronounced movement into estuaries and shallow waters in spring and back into deeper waters in autumn. Occurrence of small proportions of *P. montagui* in shallow waters during the winter is also reported (Mistakidis, 1957).

C. allmanni is a migrant species which inhabit estuaries only for a part of the year (Allen, 1960). The species migrates into the estuary by autumn and leaves estuary by spring. The migration takes place at the same time period as in *C. crangon* but when *C. crangon* moves inshore *C. allmanni* moves offshore and vice versa (Allen, 1960).

1.3 THE ESTUARY AND FIRTH OF FORTH

1.3.1 General features

The estuary and Firth of Forth which lies between 55° 55′ N and 56° 15′ N and longitude 02° 50′ W and 03° 50′ W is a major geographic feature in the east coast of Scotland. The estuary starts at Stirling and runs eastwards to join the North Sea past the city of Edinburgh (McLusky, 1987a). The extent of the estuary between Stirling and bridges at Queensferry is 48 km (McLusky *et al.*, 1993) and may be divided into the head (Stirling), upper estuary (Stirling - Alloa), middle estuary (Alloa - Bo'ness) and lower

estuary (Bo'ness - Queensferry) (McLusky, 1987a). The seaward area from the Queensferry bridges to a line from Fife Ness to Isle of May is referred to as Firth of Forth and may be divided as inner (Queensferry - Leith/Pettycur), middle (Leith/Pettycur - Gullane/Earlsferry) and outer (Gullane / Earlsferry-Fife Ness / Cockburnspath) Forth (Fig 1.3).

1.3.2 Characteristics of the upper estuary

The upper part of the estuary is a narrow meandering channel from Stirling to Alloa and widens between Alloa and Kincardine Bridge. The area from Stirling-Alloa is less than 200 m in width and comprise short (5-10 m) steep intertidal areas. The total intertidal area is 1.9 km^2 and are exclusively mud and silts (McLusky, 1987b). The tidal fluctuations at Alloa and Kincardine Bridge are 5.5 m but decrease to 2.8 m at Stirling (HWOST-LWOST) (McLusky *et al.*, 1993). The area is characterised by freshwater - sea water interface and turbidity maximum (Webb and Metcalfe, 1987) and suffers from natural depletion of oxygen which is associated with such areas in estuaries (McLusky, 1989).

The upper estuary receives freshwater inflow from the River Teith (mean =23.4 $m^3 s^{-1}$), the River Forth (14.8 $m^3 s^{-1}$), and the River Allan (6.3 $m^3 s^{-1}$). These are the major freshwater inflows to the estuary and account for 70% of total inflow (62.7 $m^3 s^{-1}$) (Leatherland, 1987). Areas above Alloa are dominated by freshwater and often have salinity less than 1 ppt. Salinity of the area at 16 km below Stirling varies between 1.6 - 4.1 ppt. (McLusky, 1987b). A clear and consistent salinity gradient occurs from freshwater conditions in the upper estuary to middle estuary (McLusky, *et al.*, 1993)

The upper estuary receives large inputs of organic wastes from sewage discharges; Stirling STW, and Alloa STW, from brewery discharges; Quest International in Menstrie, discharged at Alloa, and from Kilbagie paper mill discharging via canal Burn. The Quest International alone accounts for 80% of the BOD entering the upper estuary (Dr. S. Hull, pers. comm.). The installation of treatment plant at Quest International and full biological treatment plant at Stirling STW in recent years have led to significant improvements in

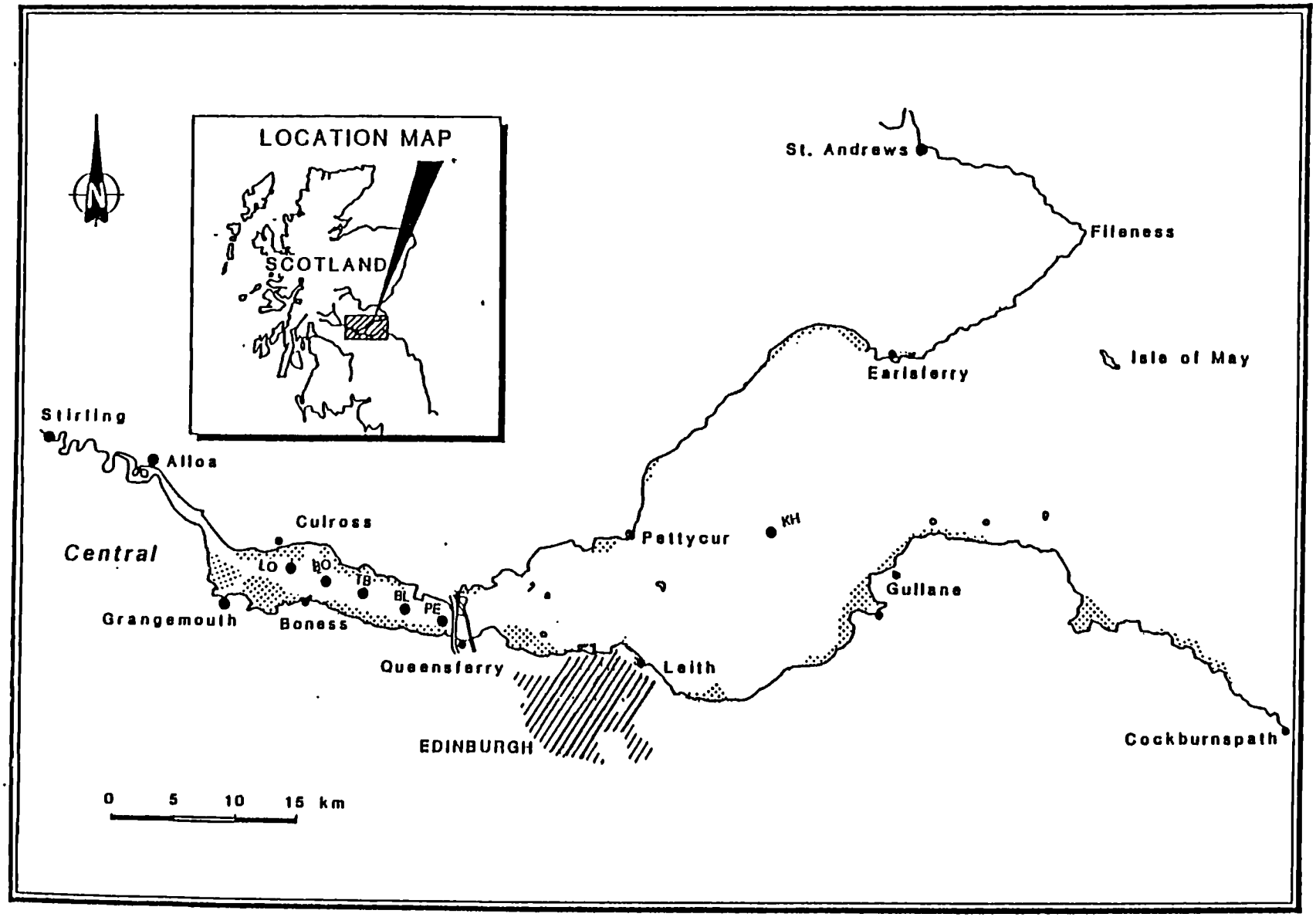


Fig.1.3 The estuary and Firth of Forth.

the water quality and the oxygen sag experienced in Alloa is not as severe as in the past (FRPB, 1991).

The sediments of the subtidal upper estuary varies from fine silt to sand. High water flows of autumn move silt in the upper estuary downstream. Sediments of both intertidal and subtidal areas are enriched with organic carbon due to high inputs of organic wastes (McLusky *et al.*, 1980; Bagheri and McLusky, 1982; Goodlad, 1983). As a result, anaerobic conditions prevail in the area supporting a depauparate fauna dominated by oligochaetes such as *Limnodrilus hoffmeisteri, Tubifex tubifex* and *Tubificoides benedini* (McLusky, *et al.*, 1980; Goodlad, 1983). Recent research however, has indicated a near 10-fold reduction in the abundance of oligochaetes in the subtidal upper estuary (McLusky, *et al.*, 1993) indicating continuous improvements in the water quality due to reductions in organic loads. Seasonal variations in the fauna are little and the species are found to be occupying approximately the same ranges throughout the year (FRPB, 1991).

1.3.3 Middle and Lower estuary

The estuary widens between Alloa and Kincardine Bridge and narrows at the point of Kincardine bridge (Fig.1.3). The extent of the estuary from Kincardine Bridge to Queensferry Bridges is 24 km, straight (McLusky, 1987b) and the water covers an area of 6057 ha at HW and 3850 ha at LW (Elliott and Taylor, 1989b). The depth of the subtidal area ranges from 1-47 m below chart datum (Elliott and Kingston, 1987). The middle and lower estuary comprise extensive mudflats; Culross and Torry Bay in the Northern shore and Skinflats and Kinneil in the Southern shore. In comparison to the steep narrow intertidal areas in the upper estuary the middle and lower estuary has flat and level mud flats which run for 2.5 km from high water to low water. The middle estuary mudflats, Kinneil, skinflats and Torry Bay alone account for 15.1 km^2 of the total intertidal area of the Forth Estuary which is 23.3 km^2. The total intertidal area of the lower estuary is 6.3 km^2 (McLusky, 1987b).

The intertidal habitats throughout the estuary are dominated by fine grained muds. In Kinneil and Skinflats which are the first intertidal flat below Kincardine 82% of the sediment is in the clay and silt fraction. At Torry Bay the sediments are coarser moving

to muddy sand and 32% of sediments in clay and silt fraction (Elliott, 1979) while in Blackness Bay has less than 10% silt and clay fraction (Anderson, 1983). The subtidal area generally consists of fine sediments which are mixtures of riverine, estuarine, and marine sands and muds with shell, clinker, fly-ash and other debris including fragmented tubes of the polychaete, *Sabellaria* (Elliott and Kingston, 1987).

The estuary has demands placed upon it by the petrochemical complex at Grangemouth, as an area receiving discharges; by the Ports Authority which dredge the main channel and discharge dredge spoil to the area; by a Power Station as an area for abstracting and receiving cooling water, by local authorities and other industries which discharge to the estuary (FRPB, 1983). The middle part of the estuary is a site of petro-chemical industries, the port of Grangemouth and a large coal-fired electricity generating station (Elliott and Taylor, 1989a). Skinflats/Bo'ness region of the middle estuary receives polluting discharges either as run-off from existing discharges at the top of Kinneil Bay, or directly from discharges in the sub-littoral areas off Bo'ness and Skinflats, as well as the Rivers Avon and Carron (FRPB, 1983). Culross receives ash discharges from Longannet coal-fired power station.

The salinity regime of the estuary varies from full seawater at its eastern limit to the freshwater- brackishwater interface in the upper estuary. There is a marked lateral variation in salinity especially in the mid region which has a shallow sub-tidal area extending from the south shore mud flats and the deeper channel along the North shore. In addition, the salinity at the western limit of the middle estuary can decrease to 0 under low tide and high river flow conditions (FRPB, 1987; Elliott and Taylor, 1989). The estuary varies between well-mixed and partially mixed states. The factors of freshwater flow, tidal range, and tidal state are primarily responsible for the changes. The well-mixed state is primarily influenced by the tidal range, because the extent of vertical mixing is determined by the stronger spring tidal currents which cause increased turbulent mixing. On the other hand freshwater flow determines the extent of landward penetration of salt (Webb and Metcalfe, 1987).

1.3.4 Intertidal fauna

Between Alloa and Kincardine Bridge the fauna becomes more diverse than in the upper part. *Nereis diversicolor, Corophium volutator, Macoma balthica,* and *Hydrobia ulvae* are found in the intertidal area. In Skinflats the most abundant inhabitant is *H. ulvae* but *M. baltica, Cerastoderma edule, N. diversicolor, Manayunkia aestuarina, C. volutator* and *Tubificoides benedini* are also found. Kinneil has Oligochaetes; *T. benedini* and *T. scoticus* and bivalves; *M. balthica, C. edule* and the gastropod *H. ulvae* as well as several polychaete species. Torry Bay has a diverse fauna with substantial populations of bivalves; *M. balthica, C. edule, Mya arenaria, Tellinids,* and others; *Hydrobia ulvae, Retusa obtusa, C. volutator, Arenicola marina, Nephtys hombergi* and *T. benedini* (Elliott, 1979; McLusky and Allan, 1976; McLusky *et al.*,1976; 1978; McLusky *et al.*, 1980; Elliott and McLusky,1985). The bay has relatively low diversity but a high productivity. In culross the diversity is similar but the abundance and biomass are lower (McLusky *et al.*, 1976). Substantial populations of *Mytilus edulis* are found here. The lower estuary has a varied fauna. Abundant patches of *M. edulis* occur in the area while other bivalves such as *C. edule, M. balthica, Mya arenaria* and *H. ulvae* are present. *N. hombergi* dominates the annelids and *A. marina,* Cirratulids and *Lanice* are among the other annelids present.

1.3.5 Subtidal fauna

The subtidal part of the upper estuary are dominated by Oligochaetes (*Limnodrilus hoffmeisteri* and *T. tubifex*) with larval forms of freshwater fauna which occur occasionally (McLusky *et al.*, 1993). The area downstream of Alloa comprises typical estuarine fauna, with Polychaetes; *Marenzellaria wireni* and *Pygospio elegans* and *Mytilus edulis* spat found in this area.

The subtidal fauna of the middle and lower estuary consists of four groups of benthic community associations (Elliott and Kingston, 1987). These includes the Polydora/Oligochaete association, in the area west of Kinneil which is characterized by *Polydora lignilciliata* and *Marenzellaria wireni* and *Tubificoides* spp. The mid estuarine area offshore of Kinneil Bay is characterized by an impoverished fauna which is represented predominantly by *N. hombergi* and *Eteone longa* which occur in low numbers.

This area indicates a stressed transition region in the estuary. The lower estuary shows two types of associations which are described as supra-estuarine associations and are characterised by many marine species such as *Dodecaceria concharum, Neoamphitrite figulus* and *Abra alba.* The northern-central part of the estuary east of Bo'ness is low in abundance and has been separated from the other part as the impoverished supra-estuarine fauna.

1.3.6 Firth of Forth

1.3.6.1 General features

The Firth of Forth is a V-shaped embayment, 50 km long, extending from the North Sea in the east to Queensferry at the Rail and Road bridges in the west. At Elie and Pettycur on the North coast and Gullane to Leith in the south coast, the V is interrupted and the middle firth is approximately circular in shape (Dyke, 1987). The outer firth is deep and saline, virtually homogenous and to all intents a part of North Sea. Salinity in the inner firth is variable due to presence of tidal drainage channels. This part consist of many sand banks.

The Firth of Forth receives freshwater inputs from the Rivers Leven, Almond, Esk, Tyne, and water of Leith and other small tributaries in North and South shore. At the seaward end the firth receives saline water of good quality from the North sea (Leatherland, 1987).

The Firth is essentially marine in nature, and deeper and wider than the estuary. The Firth receives domestic effluent inputs from the population in Edinburgh and surrounding area together with Leven area (Dyke, 1987). Sediments in the firth are usually mud or muddy sand (Elliott and Kingston, 1987).

1.3.6.2 Benthic Fauna

The largest group of benthic fauna found in the Firth of Forth consist of *Abra alba* and *Abra nitida.* A broad band from Inchkeith curving northwest into Largo Bay comprise *Pholoe inornata* which numerically dominate the fauna and *Echinocardium cordatum* and small numbers of *E. flavescens.* The inner firth is characterised by *Venus* community and *Crenella* and *Modiolus* associations.

1.3.7 Fish fauna

Fish community in the estuary has been described fully by Elliott *et al.*, (1988), Elliott and Taylor (1989a) and Costa and Elliott (1991). In total, 28 species which fall into five categories have been recorded in the estuary (Elliott and Taylor, 1989a). These include 8 residential species which spend their active life in the estuary, 3 marine species which migrate to estuary as adults, 4 marine species which use the estuary as a nursery area, 3 anadromous/catadromous species and 6 adventitious marine species with no estuarine requirements. The species; flounder (*Platichthys flesus*), whiting (*Merlangius merlangus*), eelpout (*Zoarces viviparous*), pogge (*Agonus cataphractus*) and sand goby (*Pomatoschistus minutus*) are the most dominant species (cumulative 50% of the percentage occurrences) which together with Plaice (*Pleuronectus platessa*), sprat (*Sprattus sprattus*), cod (*Gadus morhua*), herring (*Clupea harrengus*), sea snail (*Liparis liparis*), common dab (*Limanda limanda*) and fatherlasher (*Myoxocephalus scorpius*) make 90% of the recorded presence. Six of these species; cod, whiting, pogge, sand goby, eelpout and flounder feed predominantly on *C. crangon*, while feeding on *Pandulus* by *Gadus morhua* was also being noted (Costa and Elliott, 1991)

1.4 SHRIMP POPULATIONS IN THE FORTH ESTUARY

Shrimps of the estuary and Firth of Forth do not fall into the category of commercially important shellfish species. The only records of Shrimps in the estuary has been reported in a preliminary report of FRPB (1978) which described the population biology of *C. crangon* and a six month study on the shrimp population of the estuary by Hunter (1981). Hunter (1981) identified *C. crangon* and *P. montagui* as the species of shrimps found in the Forth Estuary. *C. crangon* was abundant in the area towards the mid and upper estuary, but *P. montagui* was confined to the lower estuary. His study further identified two breeding seasons for *C. crangon*, one extending from May to September and the other in December and one breeding season for *P. montagui* which falls in December. The mass migration of *C. crangon* to the sea in winter is a widely reported phenomenon (Henderson and Holmes, 1987; Tiews, 1970) but not observed by Hunter (1981), though a movement of animals towards the lower part of the estuary was observed in December. The occurrence of *C. crangon* larvae in the estuary was observed by Taylor (1980) but was not numerous.

Although not supported by direct evidence, the importance of shrimp fauna in the estuary is apparent. Food of the shrimps, copepods (Taylor, 1987), amphipods and molluscs are abundant in the intertidal and subtidal areas of the estuary (McLusky, 1987b; Elliott and kingston, 1987) and predators of *C. crangon* and *P. montagui*, such as the fishes, Cod, Whiting, Plaice, and Eelpout and the crab, *C. maenas* are also present (Howard *et al.*, 1987; Elliott and Kingston, 1987; Elliott and Taylor, 1989b). Predatory birds; Greenshank, Redshank and ducks (Smaldon, 1979) are also found in the nearshore areas (Bryant, 1987).

The fish community of the Forth Estuary are mainly supported by macrofauna and shrimps (Elliott and Kingston, 1987; Elliott and Taylor, 1989b). *C. crangon* is a preferential prey for six dominant species in the Forth estuary, and plays a central role in the estuarine ecosystem of the Forth (Costa and Elliott, 1991). The eelpout *Zoarces viviparus*, the gadoid fishes, Whiting (*Merlangius merlangus*), Cod (*Gadus morhua*), are found to feed predominantly on the *C. crangon*. The same preference has also been found for *Agonus cataphractus* and *Myoxocephalus scorpius* (Townend, 1989; Marshall, 1990). The species such as flounder and gadoids, have been found to feed preferentially on certain size classes of shrimps (Crossan, 1985; Bell, 1990). There is a strong indication that the shrimp is a vital component which links the meio-fauna and vertebrates in the food web of the fauna of Forth Estuary and thus contributes to the fish production of the Forth Estuary and Firth of Forth. Thus, any threat to the estuarine system which predominantly affect the epibenthic crustaceans such as *Crangon* will affect the resident fish populations (Costa and Elliott, 1991). Despite the importance of shrimps to the ecosystem, no proper evaluation of resources has previously been carried out in the Forth Estuary for shrimp populations.

1.5 AIMS OF THE PRESENT STUDY

The lack of proper evaluation on the resources and the population structure of shrimps in the Forth Estuary and Firth of Forth indicated the importance of commencement of a detailed study. The present study was initiated with an aim of filling the gaps in our knowledge of shrimp population of the estuary and Firth of Forth with a view of understanding their biology, population structure and ecology and their true functional

role in the estuarine ecosystem. The objectives of the study could be summarized as follows:

1. to identify and quantify the shrimp population in the estuary and Firth of Forth,
2. to describe the population structure and functioning of the shrimps,
3. to show the spatial and temporal variations in distributions and abundance of the shrimp species in the estuary and Firth of Forth and identify the extent of significance of each species,
4. to determine the growth parameters with an view of comparing with other estuaries in order to find out the deviations associated with natural or manmade perturbations,
5. to identify and quantify the contribution of shrimps to support the production of fish and maintain the ecological balance in the estuary,
6. to quantify the larval production and identify the role of environmental conditions in the life history of shrimps, and
7. to compare the functioning of the Forth estuary with other areas in terms of shrimp production.

CHAPTER 2. MATERIALS AND METHODS (in general)

MATERIALS AND METHODS (in general)

2.1 FIELD PROCEDURE

2.1.1 Sampling stations and sampling frequency

Sampling was carried out from February 1992 to January 1994, at five sampling stations in the lower Forth Estuary; Port Edgar, Blackness, Tancred Bank, Bo'ness and Longannet, and one station in the Firth of Forth; Kingstone Hudds (Fig.1.3 and Fig. 2.1) using the the FRPB's research vessel S.V. Forth Ranger IV. All sampling trips coincided with the routine demersal fish surveys of FRPB, since the shrimps occurred as a by-catch of fish sampling.

The sampling stations had been selected by Forth River Purification Board after long term research and to cover the most important areas of the middle and lower estuary. General characteristics of the estuary have been described in detail in the previous chapter, therefore, lengthy descriptions on the characteristics of the stations are avoided here. The seasonal variations in temperature (°C) and salinity (ppt), which are regarded as the most influential variables in estuarine environment, are given in Fig.2.2 (A-D) for the five stations in the lower estuary. The temperature and salinity data used here are the means of data recorded for 10 yrs (1981-1991) by the FRPB.

Port Edgar and Blackness show virtually fully marine conditions throughout the year while the salinity in the other three stations show estuarine conditions. The salinity of the area of study did not fall below 22 ppt, even during the periods where the estuary received high freshwater inputs (Fig.2.2 A and B).

Water temperature varied between 4°C in winter and 17°C in summer. In autumn and winter the temperature variation between the stations were low (Fig. 2.2 C and D). In spring and summer the shallower area of the estuary, the upper three stations, Tancred Bank, Bo'ness and Longannet exhibited temperatures higher than that of deeper waters (Port Edgar and Blackness).

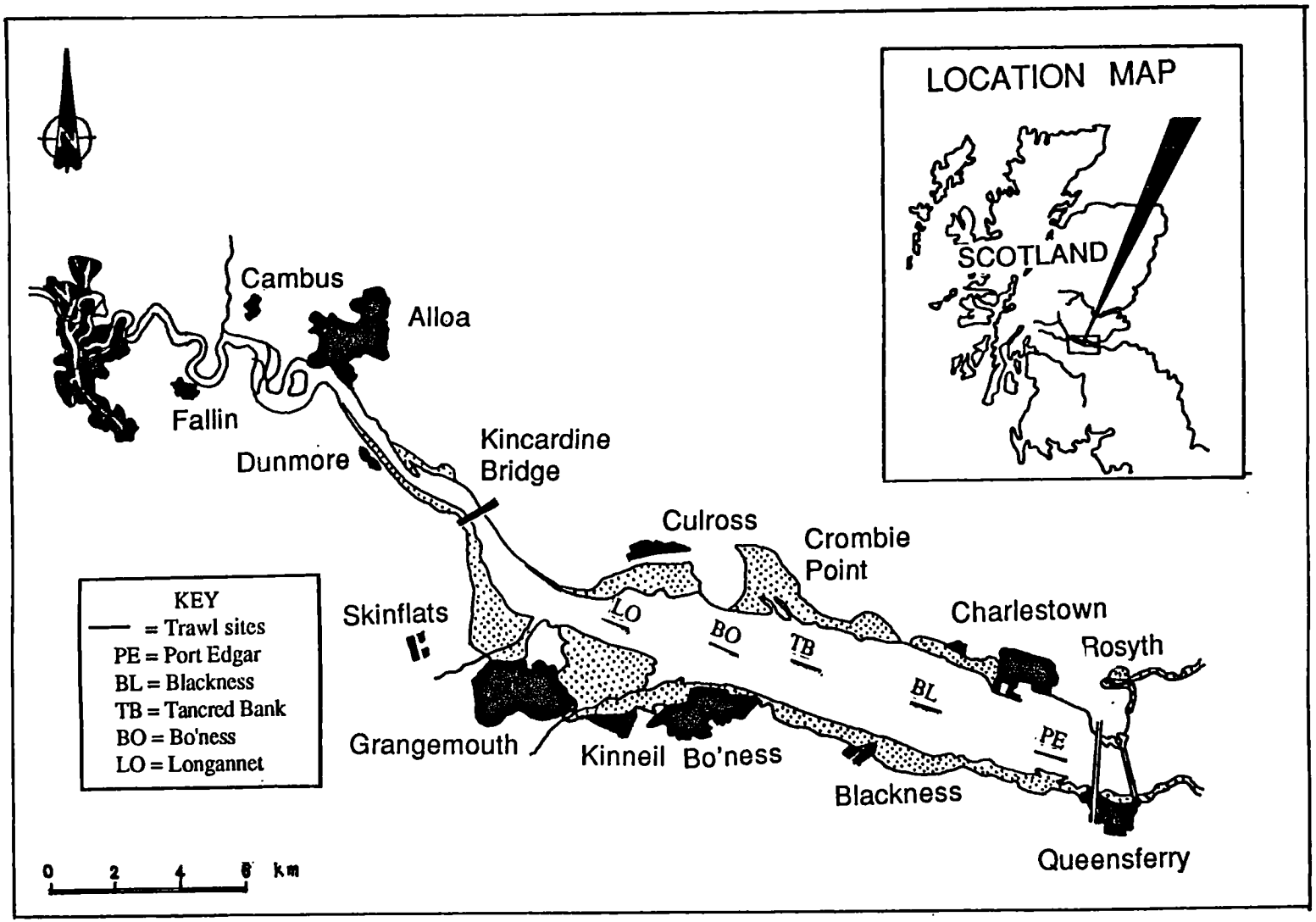


Fig.2.1 The Forth estuary showing water and shrimp sampling stations.

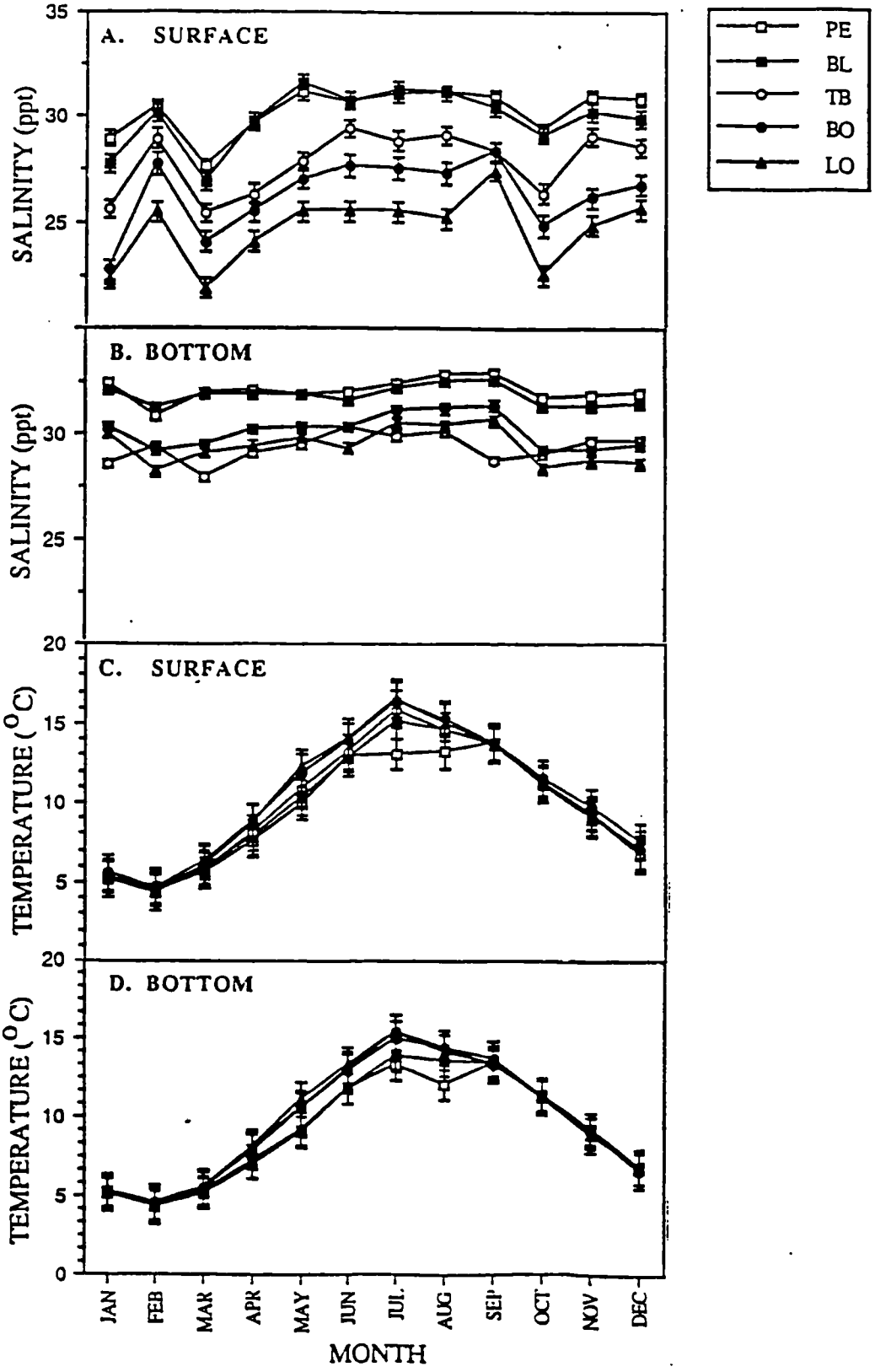


Fig. 2.2 Seasonal variations in salinity (ppt) and temperature (^{0}C) in five stations of the lower Forth Estuary. PE=Port Edgar, BL=Blackness, TB=Tancred Bank, BO=Bo'ness and LO=Longannet. The values are means of data recorded for 10 yrs. (1981-1991) by the Forth River Purification Board.

The data on depth were also obtained from FRPB and represent the mean of 13 values recorded at low water and 12 values recorded at high water during the period January 1992 to January 1994. Bo'ness is the shallowest station of the five stations studied, followed by Longannet and Tancred Bank (7.27±0.35, 8.18±0.44 and 8.91±.42 respectively). Port Edgar and Blackness are deeper areas having the depths of 14.36±0.67 m and 15.86±0.26 m respectively.

The estuary was sampled five times a year, in January, April, July, October and December, at both high and low water of the spring tide, with the routine demersal fish surveys of the Forth River Purification Board (FRPB). Additional sampling trips were made in June 1992 and 1993 to shorten the obvious interval between April and July which could have an effect on the studies. Kingstone Hudds was sampled four times in 1992 (January, April, October and December) along with surveys of the FRPB, but only twice in 1993 (January and June), due to the termination of surveys of FRPB at Kingstone Hudds. High water trawling at high water spring tide was void in December 1993 due to bad weather conditions.

2.1.2 Location of the sites

On each occasion, trawl sites were located using a standard DECCA Navigator system. The locations of the trawl at the beginning and end of the trawl and average depth of each station are given in Table 2.1.

Table 2.1- Locations of the stations at the beginning and end of trawl.

STATION	LOCATION OF STATION (LONGITUDE AND LATITUDE)		
	At the beginning	At the end	Depth below chart datum (m)
Port Edgar	56° 00.08′N, 03°25.70′W	56° 00.30′N, 03°27.30′W	14.36±0.67
Blackness	56° 00.56′N, 03°28.99′W	56° 00.85′N, 03°30.12′W	15.85±0.26
Tancred Bank	56° 01.56′N, 03°32.00′W	56° 01.87′N, 03°33.35′W	8.91±0.42
Bo'ness	56° 02.20′N, 03°35.52′W	56° 02.07′N, 03°37.28′W	7.27±0.35
Longannet	56° 02.35′N, 03°39.42′W	56° 02.35′N, 03°40.41′W	8.18±0.44
Kingstone Hudds	56° 06.55′N, 04°53.18′W	56° 06.76′N, 04°51.85′W	40.00

2.1.3 Sampling gear

An Agassiz type trawl was used as the main gear for collection of shrimps. Holme (1971) described the Agassiz Trawl as a double sided beam trawl as it was designed. It is rigged to skim over the surface of the bottom in a similar manner to a beam trawl. The Agassiz Trawl used in the present study consisted of a steel frame with a 2 meter mouth and a net made of courlene twine attached to it. The mesh size of the net was 1.3 cm (stretched) and the panel length was 4.9 m. The cod end of the net was protected by a bag-type chafer to prevent damage during towing. The passage over the ground was facilitated with the aid of rubber discs attached to the net. A plastic float attached to the middle of the headline ensured the maintenance of maximum gape during towing. The frame was connected to a winch via a single wire bridle and was towed at a speed of 2.5 knots per hour for 20 minutes. The fishing efficiency of the Agassiz Trawl was taken as 33%, the same as that of a standard beam trawl due to the similarity of the gear, following Ajayi (1983) and Elliott and Taylor (1989a).

A beam trawl of 2 m wide, 3 m net length and 1.3 cm mesh size (stretched) was used to collect shrimps from the upper estuary. A tickler chain was attached to the bottom shoes of the trawl to disturb the substratum. The beam trawl was towed by a 17 foot Dory for 0.8 km distance.

2.1.4 Sampling procedure

2.1.4.1 Shrimps

At each station, shrimps were caught by towing the Agassiz Trawl between the locations given in Table 2.1. At the end of each trawl, the catch was emptied into plastic fish boxes, washed through plastic sieves to remove the mud, and the shrimps were picked out by hand. The entire catch of shrimps was collected at each occasion, except in July and October 1992 when the catch was large. In these occasions a sub-sample was taken at random after sorting all the shrimps from the catch. Shrimps were then preserved immediately in 5% formosaline for further analysis. At Kingstone Hudds, the same Agassiz Trawl was used to catch shrimps.

In addition, the samples of shrimps collected from six stations in the upper estuary (Fig. 2.3) were provided by the FRPB. These samples were collected in July 1992, March 1993, and September 1993 and were also used for the analysis of population dynamics.

2.1.4.2 Zooplankton

Zooplankton samples were collected at each station with a standard plankton net (250 μm mesh). The net mouth was 0.5 m in diameter, and was connected to a shackle via three cords. The cod end of the net was fitted to a plastic tube with a screw cap, which enabled the easy collection of plankton. The net was maintained at a depth of 5 m below the surface by a depressor of 40 lb, at the time of towing. Zooplankton were collected by towing the net for 10 minutes, at a speed of 2.5 knots and preserved immediately in 5% formosaline.

2.1.4.3 Water temperature:

Surface water samples were collected at each station and the water temperature was measured immediately with a mercury thermometer with a range of -10°C to 110°C. The water samples were kept for the analysis of suspended solids and salinity in the laboratory.

2.2 LABORATORY PROCEDURE

2.2.1 Sample preparation and preservation

Upon arrival at the laboratory, each sample of shrimps was washed in cold water to remove the formalin, separated by species and preserved in 70% alcohol. A random sample of up to 25 shrimps per species was preserved in 90% alcohol for stomach analysis. Berried females of up to 10 per species, depending on the availability, were selected at random and preserved individually in 70% alcohol for fecundity studies. On some occasions, the same animals were used for all the biological studies. The animals taken for studies of feeding and reproductive biology were also included in the analysis of population dynamics. Remaining samples were used for studies of population dynamics. The details of the procedures used for the analyses are described in the appropriate chapters.

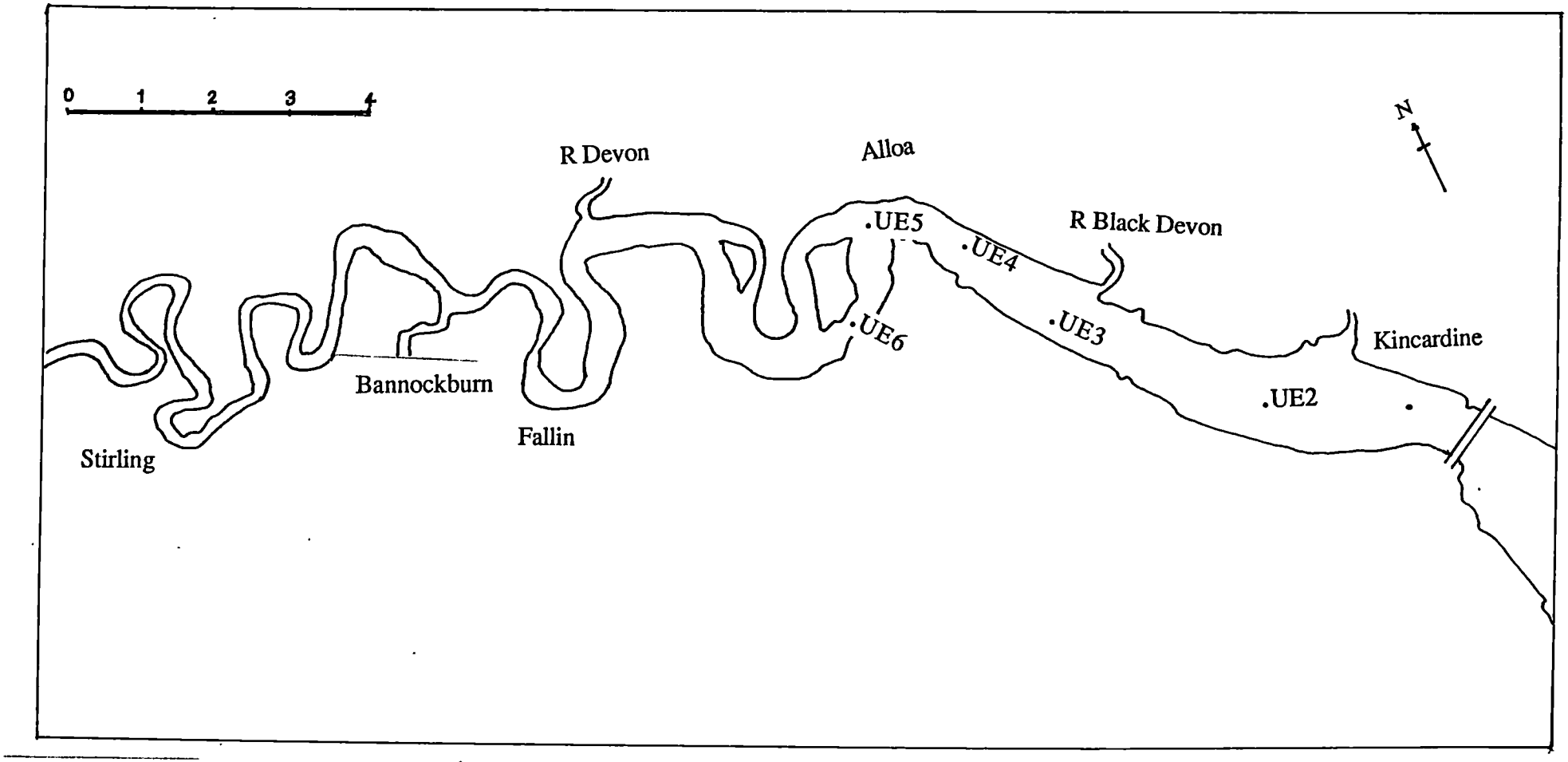


Fig.2.3 Shrimp sampling stations in the upper Forth estuary.

2.2.2 Determination of suspended solids

Suspended solids was determined according to the method described by Stirling (1985), by filtering 500 ml of each sample through GF/C filter papers with 0.47 μm pore size. Prior to determination of suspended solids the filter papers had been washed with distilled water, dried in an oven at 40°C to constant weight, cooled in a desiccator and weighed. The water sample (500 ml) was filtered through the paper by suction, and the filtrate was collected for salinity determination. Then the filter was washed with distilled water, dried at 40°C to constant weight, cooled and weighed to a precision of 0.001 g with a Mettler PC 180 digital balance. The values were recorded as mg l^{-1}.

2.2.3. Salinity

During the initial sampling (February 1992 and March 1992), a NaCl refractometer was used in determinations of salinity. From April 1992 onwards a titrimetric method was used due to the inaccuracy of the results obtained using refractometer. Determination of salinity was carried out by titrating 10 ml of sample (turbidity removed) against standardized $AgNO_3$ solution (27.25 g l^{-1}). Indicator K_2CrO_4 (100 g $^{-1}$) was used to determine the end point. Salinity was taken as the mean value of three titrations.

2.2.4 Other parameters

Wind speed and wind direction data for the period of study were obtained from the records of the Daily Weather Summaries for Edinburgh Airport, as an indication of air flow over the estuary. Data on tidal amplitude were taken from Admiralty tide tables for Rosyth. Additional data on salinity and temperature for 1980-1991 and abundance of fish throughout the period of study were obtained from the FRPB.

2.3 STATISTICAL ANALYSIS

All the statistical methods used in the present study were carried out using the software packages SPSS-X, and Minitab. Lotus 1-2-3 was used occasionally for simple linear regression and Chi-square tests. The methods employed are described in detail in the appropriate chapters.

CHAPTER 3. BIOLOGICAL RELATIONSHIPS

BIOLOGICAL RELATIONSHIPS

3.1 INTRODUCTION

The establishment of relationships amongst biological parameters is commonly practised in population biology to yield biological information (e.g.Tyler, 1973; Chambers and Milne, 1979; Norrbin and Bamstedt, 1984; Rumohr *et al.*, 1987), specially in relation to estimation of secondary production in aquatic invertebrates. As quoted by Rumohr *et al.* (1987) "the use of conversion factors reduces the tedious and lengthy laboratory work and facilitates the conversion of 'old' wet weight data to more appropriate units of biomass".

In population biology, length is the basic measurement used to describe size and therefore, growth. Accurate measurement of length in the field is however, impractical for small invertebrates such as shrimps which are numerous, and the transportation of preserved animals for later assessment is commonly employed. This procedure often results in loss of weight, shrinkage and damage to the animals concerned, and the accuracy of the results may depend upon the preservative used, the degree of damage during transportation, the duration for which the animals were kept preserved, length of time involved in measurements and the method adopted for measuring the animals. In comparison to weight, measurement of length is generally easier and quicker.

The establishment of relationships between various biological parameters and carapace length, the basic measurement for shrimps, provides efficient tools in the studies of population biology because:

a). they provide more reliable estimates due to accuracy in measurement,

b). the possibility of converting from one variable to another, and vice versa, in order to understand the different aspects of the biology where length measurement alone is not sufficient. Different analyses may demand different variables such as weight, standard length, or total length which are appropriate to fulfil the requirements of such analyses,

c). they provide an opportunity to compare the results with previous studies where

different parameter may have been used for describing size (eg: total length, standard length).

In the present study, carapace length (Fig.3.1) was used as the basic measurement and was measured in each individual at most instances. During the course of the study, it was found necessary to find out the effect of preservation on the length and weight in order to compare the present results with previous studies where different media were used for preservation. It became evident that the establishment of the following relationships was necessary for further studies on the aspects given below.

1. Effect of preservation in Ethanol on the length and weight,

2. Relationship between carapace length and total length to estimate the mortality,

3. Relationship between carapace length and other length measurements in order to find out the actual size of the prey shrimps,

4. Relationship between carapace length and wet weight/and ash free dry weight for estimation of biomass and production.

This chapter, therefore, considers the establishment of relationships between biological parameters which are being used in succeeding chapters. Through out this chapter all the weight measurements were made using a balance (Mettler PC 180) with an accuracy of 0.001 g.

Linear regressions were fitted for untransformed data or log transformed data as appropriate using ordinary least square method and the relationships were validated by the significance of the regression analysis. Comparison of sample regressions were carried out as described in Zar (1984), by comparing slopes and elevations. Student's *t*-test was used in the cases where two regressions were compared. Sum of squares for the tests were calculated from raw data using Minitab version 7.2 and the subsequent calculations were performed manually. The differences between regression lines were accepted at a

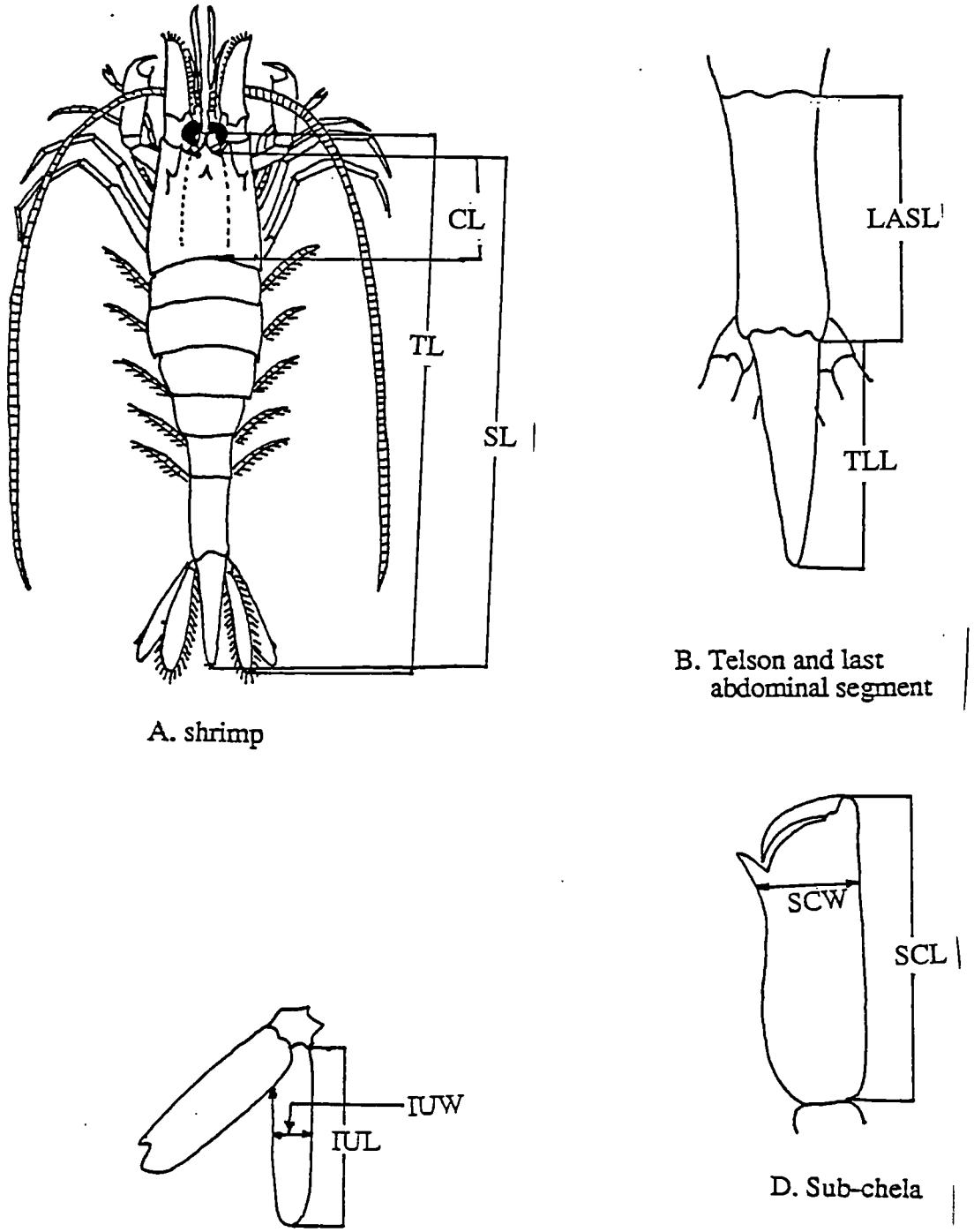


Fig. 3.1 Morphometrical measurements used in the present study. CL = carapace length, TL = total length, SL = Standard length, TLL = telson length, LASL = length of the last abdominal segment, IUL = inner uropod length, IUW = inner uropod width, SCL = sub-chela length, SCW = sub-chela width.

level of significance $p<0.05$. If the differences were not significant common regression equations were computed and were accepted as the best fit for the data. If the differences were significant, the slopes and elevations of each pair of sample regressions were compared separately and significant differences were identified (Tukey Multiple Comparison test: Zar, 1984).

3.2 EFFECT OF PRESERVATION ON THE LENGTH AND WEIGHT

The effect of sample preservation on length and weight has been emphasized by many previous researchers on larval fish (Fowler and Smith, 1983; Kruse and Dalley, 1990; Hjörleifsson and Klein-Macphee, 1992), invertebrates (Brey, 1986), and adult fish (Mathieson, 1994). Shrinkage and loss of weight due to preservation is found often in fish (Brey, 1986). The effect of preservation on the shrimps however, has not been specifically investigated. The following experiment was carried out therefore, in order to estimate the deviation of length and weight from initial length and weight due to preservation in ethanol.

3.2.1 Material and Methods

The regular procedure used throughout the study for preservation and measuring of shrimps was employed. The shrimps preserved in 5% formalin on board the boat, were washed in cold water immediately on return to the laboratory. The shrimps were then separated to three categories: small, medium and large based on the rough estimation by eye, and depending on the size range available for each species. Ten individuals per category per species were used except for *P. montagui* where 8 and 9 animals were used for small and large categories respectively due to an insufficiency of undamaged animals. The shrimps belonged to the October 1993 sampling and were selected at random from all the stations. They were then measured to an accuracy of 0.1 mm, mopped and weighed to an accuracy of 0.001 g and preserved individually in 70% ethanol. Thereafter, the shrimps were measured for length and weight at weekly intervals for four weeks following the same procedure. Results obtained were analysed using the paired *t*-test incorporated to Minitab version 7.2.

3.2.2 Results

In general, deviation of length from the initial length is not significant within the study period (Table 3.1a and Table 3.2). Medium sized *C. crangon* showed a significant shrinkage from initial length by the end of second week. Small *C. crangon* did not shrink but incresed in size after second week. No significant difference however, was observed when all the sizes were pooled. In *P. montagui* significant shrinkage was evident only in the medium size shrimps which belonged to the size range of 10.0 - 12.0 mm in carapace length while for *C. allmanni*, shrinkage was found significant in the size range 8.0 - 10.0 carapace length.

Mean weight varied significantly during the preservation ($p<0.001$). A reduction from the initial weight was highly significant in the large sizes of all the species (Table 3.1b and Table 3.2). All the size categories of *C. crangon* exhibited significant deviation from the initial weight while the weight of small *C. allmanni* were not affected by the preservation. The significant weight loss of small and medium *P. montagui* observed at the end of first week was not evident by the end of experimental period, but large and pooled *P. montagui* showed a significant loss in weight. Fig.3.2 shows the deviation of weight from the initial value for all three species with time. It is evident that the weight is affected mostly during the first week of preservation. The change in weight thereafter is insignificant (Table 3.3). The relationships between initial live weights (W_i) to preserved weights (W_p) can be described by regression lines for three species (Fig. 3.3).

3.2.3 Discussion

Comparative studies on the effect of ethanol as a preservative are few and inconsistent. Most of these studies were carried out for larval stages of fish and the shrinkage in laboratory reared larvae placed in ethanol while alive was reported to be negligible (Theilacker, 1980). In contrast, shrinkage has been reported to be greater in ethanol for net-collected larvae of *Merluccius bilinearis* (Fowler and Smith, 1983); *Stizostedion vitreum* (Glenn and Mathias, 1987) and *Mallotus villosus* (Kruse and Dalley, 1990) larvae. Hjörleifsson and Klein-Macphee (1992) observed that the shrinkage is lowest in 95% ethanol. Unfortunately, similar studies on shrimps are not available for comparison. The present findings will therefore, be useful for marine biologists working on shrimp

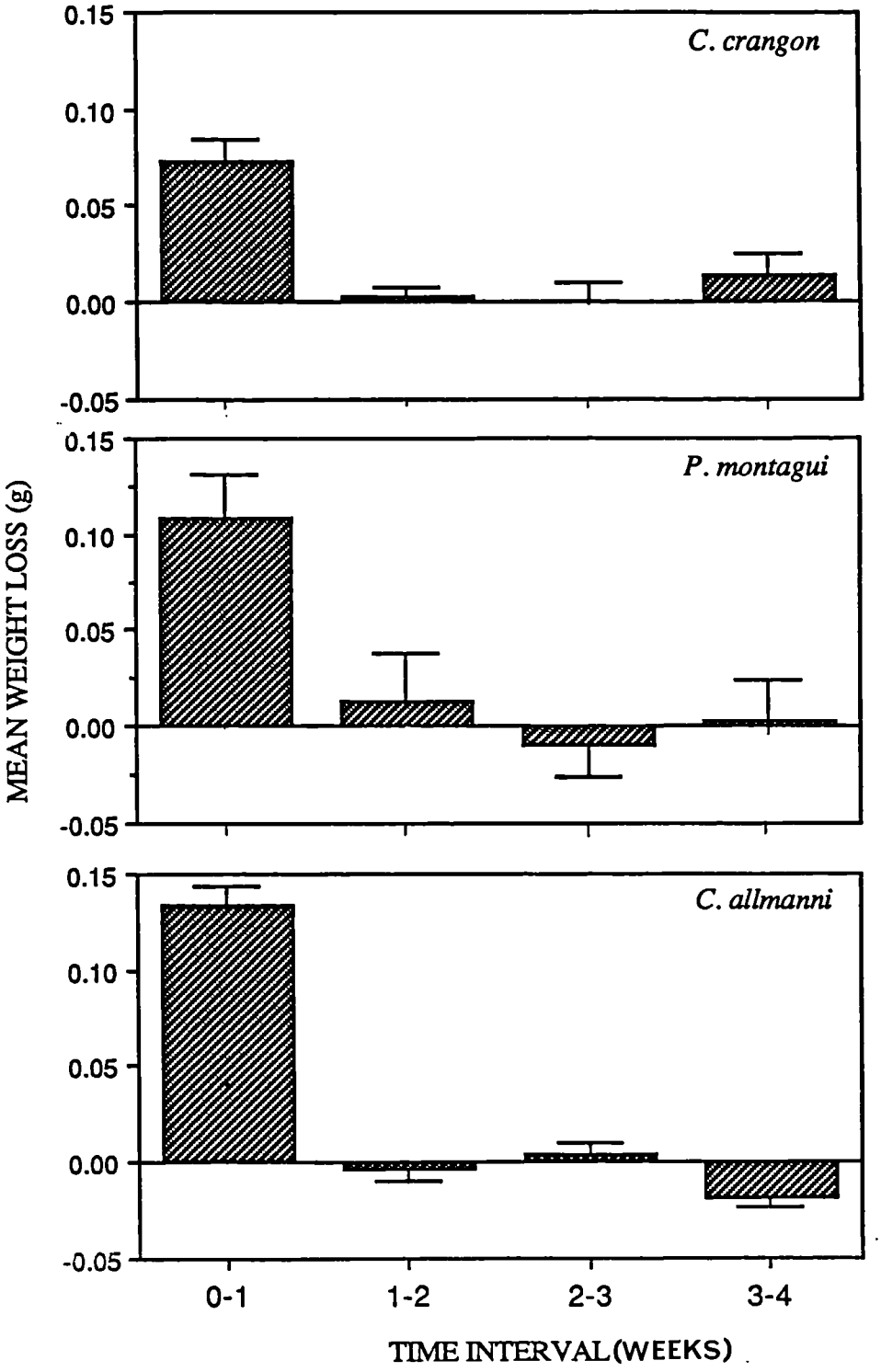


Fig.3.2 Mean weight loss±S.E. as a proportion of initial mean weight at weekly intervals in *C. crangon*, *P. montagui* and *C. allmanni*. Negative values indicate increase in mean weight.

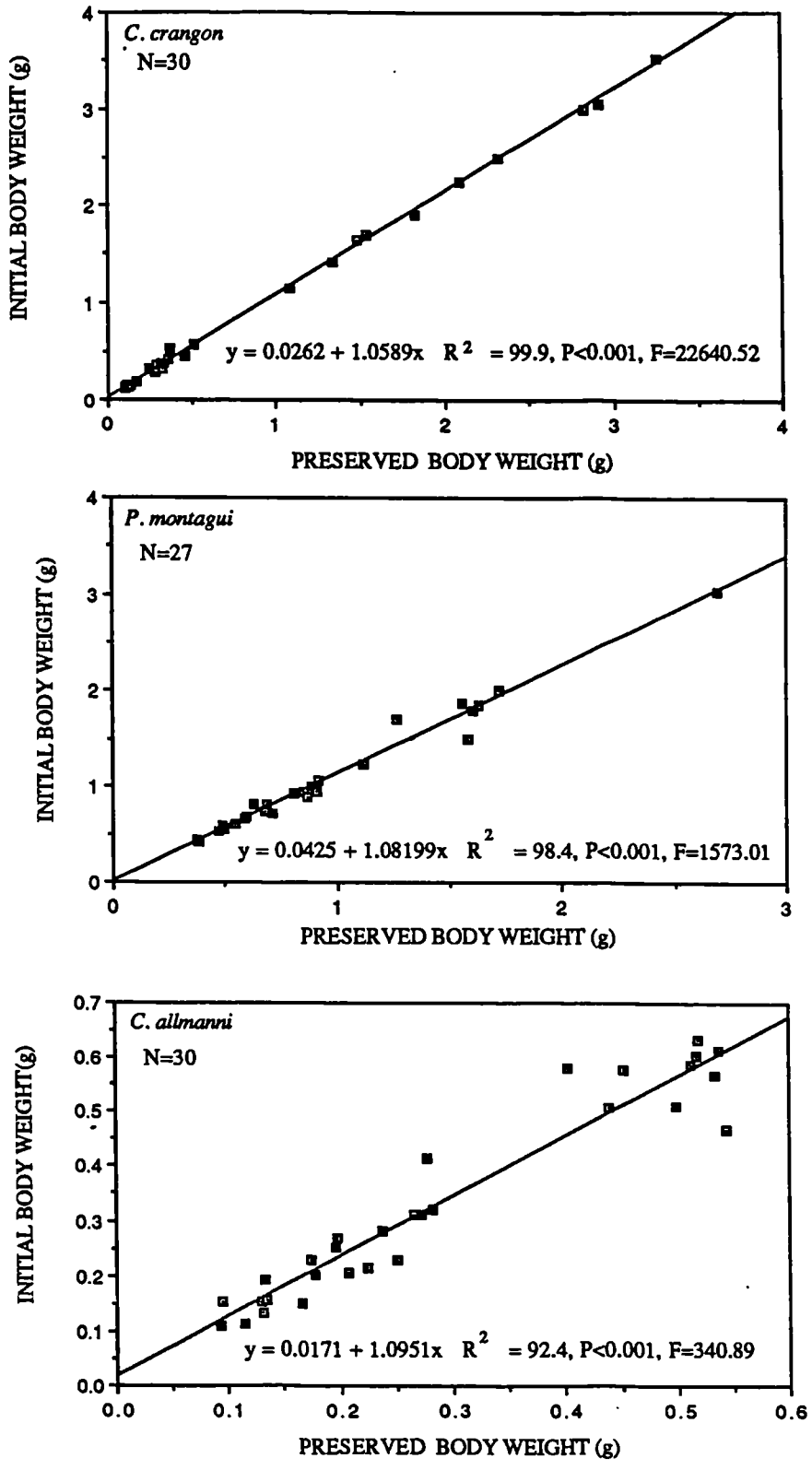


Fig.3.3 Relationship between preserved body weight (W_p) and initial body weight (W_i) in *C. crangon*, *P. montagui* and *C. allmanni* in the Forth estuary.

population studies.

Change of length of shrimps, is generally insignificant in 70% ethanol. The significance observed after two weeks in the size range 7-10 carapace length for *C. crangon* may be due to the high incidence of moulting in smaller sizes. On the other hand the large animals which moult rarely did not show significant shrinkage with time.

High variability in weight loss in large shrimps indicate that the weight loss may be due to dissolution of gonadal fat in ethanol. The yolk sac larvae of fish are also exhibited a significant weight loss as recorded by Hjörleifsson and Klein-Macphee (1992). The most important use of the studies of shrinkage or weight loss is to predict initial size and weight from preserved animals. The relationships established here for preserved shrimps were all linear with a precision of ±0.01 and could be used to obtain an estimate of initial standard weight of shrimps preserved in 70% ethanol for a period of one month.

Table 3.1(a)- Changes in mean length±S.E. of *C. crangon*, *P. montagui* and *C. allmanni* during a period of four weeks following preservation in 70% ethanol.

Species	Group	Size range (CL=mm), N	Week 0	Week 1	Week 2	Week 3	Week 4
C. crangon	small	5.0 - 6.0, 10	5.31±0.102	5.31±0.113	5.35±0.098	5.65±0.111	5.51±0.128
	medium	6.0 - 9.0, 10	7.48±0.185	7.46±0.189	7.41±0.173	7.41±0.175	7.39±0.184
	large	10.0 - 15.0, 10	12.96±0.443	13.06±0.426	12.90±0.449	12.93±0.432	12.94±0.444
	pooled	5.0 - 15.0, 30	8.58±0.618	8.61±0.626	8.58±0.619	8.66±0.596	8.61±0.607
P. montagui	small	8.0 - 10.0, 8	9.33±0.168	9.30±0.171	9.11±0.177	9.16±0.150	9.24±0.179
	medium	10.0 - 12.0, 10	10.71±0.172	10.66±0.161	10.66±0.159	10.65±0.163	10.62±0.161
	large	12.1 - 17.0, 9	13.70±0.473	13.70±0.473	13.68±0.475	13.71±0.483	13.68±0.476
	pooled	8.0 - 17.0, 27	11.30±0.390	11.27±0.392	11.21±0.402	11.23±0.402	11.23±0.396
C. allmanni	small	5.0 - 6.0, 8	5.41±0.095	5.39±0.093	5.39±0.093	5.39±0.093	5.38±0.095
	medium	6.0 - 8.0, 12	6.72±0.139	6.68±0.143	6.68±0.148	6.66±0.148	6.68±0.166
	large	8.0 - 10.0, 10	8.58±0.081	8.54±0.096	8.58± 0.082	8.51±0.094	8.50±0.081
	pooled	5.0 - 10.0, 30	6.99±0.239	6.96±0.239	6.97±0.242	6.94±0.237	6.94±0.239

Table 3.1(b)- Changes in mean weight±S.E. of *C. crangon*, *P. montagui* and *C. allmanni* during a period of four weeks following preservation in 70% ethanol.

Species	Group	Size range (CL=mm), N	Week 0	Week 1	Week 2	Week 3	Week 4
C. crangon	small	5.0 - 6.0, 10	0.149±0.008	0.124±0.007	0.130±0.008	0.127±0.007	0.127±0.008
	medium	6.0 - 9.0, 10	0.401±0.029	0.346±0.025	0.347±0.026	0.348±0.026	0.344±0.025
	large	10.0 - 15.0, 10	2.215±0.249	2.067±0.235	2.052±0.231	2.053±0.229	2.017±0.226
	pooled	5.0 - 15.0, 30	0.922±0.189	0.846±0.178	0.843±0.176	0.843±0.176	0.830±0.173
P. montagui	small	8.0 - 10.0, 8	0.603±0.054	0.522±0.030	0.500±0.320	0.514±0.035	0.534±0.042
	medium	10.0 - 12.0, 10	0.854±0.051	0.773±0.047	0.791±0.038	0.788±0.038	0.782±0.049
	large	2.1 - 17.0, 9	2.083±0.263	1.857±0.256	1.811±0.224	1.837±0.239	1.819±0.231
	pooled	8.0 - 17.0, 27	1.189±0.153	1.060±0.140	1.045±0.131	1.056±0.135	1.054±0.132
C. allmanni	small	5.0 - 6.0, 8	0.144±0.009	0.124±0.008	0.122±0.009	0.132±0.012	0.133±0.009
	medium	6.0 - 8.0, 12	0.271±0.018	0.230±0.011	0.243±0.016	0.239±0.019	0.243±0.016
	large	8.0 - 10.0, 10	0.565±0.017	0.495±0.015	0.486±0.015	0.478±0.015	0.492±0.014
	pooled	5.0 - 10.0, 30	0.335±0.033	0.290±0.029	0.292±0.028	0.290±0.028	0.297±0.028

Table 3.2- Comparison of shrinkage and weight loss with respect to the duration of preservation in *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary, Scotland as indicated by paired *t*-test. *t*-values are given in the table.

Species	Group	N	Shrinkage				Loss of weight			
			Duration				Duration			
			1 wk	2 Wks	3 Wks	4 Wks	1 Wk	2 Wks	3 Wks	4 Wks
C. crangon	small	10	0	-0.80	-7.96***	-3.72**	6.38***	2.60*	2.78*	3.54**
	medium	10	1.5	3.67**	3.28**	3.25**	3.61**	4.09**	4.15**	5.94***
	large	10	-1.63	-0.61	0.52	0.39	8.10***	7.37***	3.86**	8.17***
	pooled	30	-1.07	0	-1.91	-0.87	6.12***	5.50***	4.35***	5.54***
P. montagui	small	8	0.42	1.33	1.38	1.43	4.64***	2.20	1.49	2.90*
	medium	10	2.24	1.86	2.71*	2.86*	5.29***	1.58	1.73	2.20
	large	9	0	1.50	-0.43	0	4.47***	6.31***	5.02***	4.82***
	pooled	27	1.37	1.81	1.77	2.87	5.79***	4.84***	4.27***	4.75***
C. allmanni	small	8	1.53	1.53	1.53	2.05	2.05	2.48*	1.81	1.43
	medium	12	1.48	1.08	2.03	0.79	3.42**	5.98***	3.66**	3.88**
	large	10	1.50	0	2.33*	4.00**	3.19*	4.22***	5.01***	3.92**
	pooled	30	2.57*	1.36	3.40**	2.39*	4.72***	5.30***	5.07***	4.57***

* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$

Table. 3.3- Comparison of weight loss in *C. crangon*, *P. montagui* and *C. allmanni* between successive weekly intervals during preservation in 70% ethanol as indicated by paired *t*-test.

Species	N	Time interval	*t*-value
C. crangon	30	Week 0 - Week 1	6.12***
		Week 1 - Week 2	0.54
		Week 2 - Week 3	0.98
		Week 3 - Week 4	0.23
P. montagui	27	Week 0 - Week 1	5.79***
		Week 1 - Week 2	0.59
		Week 2 - Week 3	-0.69
		Week 3 - Week 4	0.12
C. allmanni	30	Week 0 - Week 1	4.72***
		Week 1 - Week 2	-0.26
		Week 2 - Week 3	0.24
		Week 3 - Week 4	-1.34

* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$

3.3 RELATIONSHIPS BETWEEN MORPHOMETRICAL PARAMETERS

The definition of length used for measuring size vary from animal to animal depending on the shape of the body and stability during transportation and preservation. Carapace length (CL) is regarded as the standard length measurement in studies of shrimps. Shrimps, when preserved tend to curl up beneath the abdomen and are prone to breakage during catching, transporting and measuring. Allen (1960, 1963) and Lloyd and Yonge (1947) however, used total length (TL) as the basic measurement claiming that the incidence of breakage of rostrum and telson is negligible. In the present study, it was observed that the percentage of animals with either broken telson or rostrum varied

between 5-10%. In *P. montagui*, which possesses a long rostrum, the incidence of breakage found to be higher at 10-20%. The measurement of total length in preserved shrimps was also found to be inconvenient due to difficulty in straightening the animals. Deviation from the real value tend to be high due to stretching and bending. The length of carapace on the other hand provided a better measurement since it is normally found intact.

In the present study carapace length was considered as the basic measurement for indicating the size of shrimps. The relationships between CL and TL were established for all species since it was required for mortality estimates. Measurement of other morphometrical parameters was carried out in the present study with an aim of estimating the live size of the prey shrimps found in the stomachs of the shrimps. All the shrimps identified from the stomachs were *C. crangon* and hence these relationships were established only for *C. crangon.*

3.3.1 Materials and methods

Total length (TL), Standard length (SL) and carapace length (CL) of the shrimps were measured from the tip of the rostrum to the end of the telson (TL), from the base of eye to the posterior end of telson (SL) and from the base of the eye to the posterior margin of the carapace (CL) respectively along the mid dorsal line using a Vernier calliper to a precision of 0.1 mm (Fig. 3.1). All the shrimps used were fresh and the measurements were taken immediately after returning to the lab. Relationships of CL/TL were established separately for males and females and were compared by Student's *t*-test (Zar, 1984).

The other measurements : length of telson (TLL), length of last segment of the abdomen (LASL), length of inner uropod (IUL), width of inner uropod (IUW) and length and width of sub-chela (SCL and SCW) were measured as shown in Fig 3.1. Of these, SCL, SCW, IUL and IUW were measured using a micrometer scale with a precision of 0.001 mm while TLL and LASL were carried out as described for TL, SL and CL. In total, 98

shrimps which were picked at random from all the stations from different sampling dates, were used for the analysis. Correlations between each of the morphometrical parameters with the basic parameter (carapace length) were established by fitting simple linear regressions with ordinary least square estimates.

3.3.2 Results

Regression equations computed for CL against TL clearly exhibit a linear relationship between the two sets of measurements in both male and female shrimps (Table 3.4). In *C. crangon* the slope of the relationship was similar in males and females ($P>0.05$) although the intercepts show a marked difference ($p<0.001$). This allow the computation of regression equations with a common slope for the two sexes of *C. crangon.* The difference in intercept indicates a relatively higher body length of females compared to males for a given carapace length.

The common slope observed in males and females of *C. crangon* was not exhibited by the other shrimps, *P. montagui* and *C. allmanni.* Both these species showed significantly different slopes ($p<0.001$) and hence did not allow computation of equations with common slopes for the two sexes.

Least square estimates also indicate a high correlations with carapace length against all the other morphometric measurements considered. The respective relationships are presented in Table 3.5.

3.3.3 Discussion

The relationship between carapace length and total length in shrimps has been reported by Lloyd and Yonge (1947), Van Lissa (1977) and Redant (1980) for *Crangon crangon*; Allan (1960) for *C. allmanni*, Mistakidis (1957) and Allen (1963) for *P. montagui.* These relationships compare well with the present findings (see below). No significant

Table 3.4- The relationship between CL and TL of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary. Lengths are expressed in mm.

Species	Sex	Number	Regression statistics				
			Slope (b)	Intercept (c)	Correlation coefficient (R^2)	Level of significance (p)	F-ratio
C. crangon	male	322	4.28	1.20	92.0	<0.001	1383.38
	female	578	4.10	1.69	95.3	<0.001	2429.97
C. crangon[1]	male	322	4.15	1.20			
	female	578	4.15	1.69			
P. montagui	male	142	4.21	1.65	92.1	<0.001	821.49
	female	206	2.80	12.1	90.4	<0.001	216.80
C. allmanni	male	77	3.91	9.11	84.3	<0.001	514.40
	female	82	4.61	0.71	93.2	<0.001	394.81

[1]-best fits for male and female *C. crangon* with common slope

Table 3.5- The relationship between carapace length and other morphometrical parameters of *C. crangon* in the Forth Estuary. All the lengths are expressed in mm. N=98. Relationship between CL/TL was given in Table 3.4.

Measurement of length	Regression statistics				
	Slope (b)	Intercept (c)	Correlation coefficient (R^2)	Level of significance (p)	F-ratio
Telson Length (TLL)	0.774	1.22	95.8	<0.001	2191.40
Inner Uropod Length (IUL)	0.690	1.11	92.0	<0.001	1109.06
Inner Uropod Width (IUW)	0.225	-0.23	94.2	<0.001	1588.56
Sub-Chela Length (SCL)	0.428	0.26	93.4	<0.001	1357.97
Sub-Chela Width (SCW)	0.169	-0.01	92.5	<0.001	1196.74
Last Abdominal Segment Length (LASL)	0.534	1.43	95.0	<0.001	1847.02
Standard Length (SL)	0.761	-0.598	96.9	<0.001	2986.69

differences were recorded between male and female shrimps in any of the previous studies.

C. crangon

TL = -0.510 + 4.95 CL	(r=0.94)	Van Lissa (1977)
TL = 4.372 + 4.39 CL	(r=0.998, N=1200)	Redant (1980)
TL = -0.4 + 3.82 CL	(r not given)	Henderson and Holmes (1987)
TL = 1.20 + 4.15 CL	(male)	Present study
TL = 1.69 + 4.15 CL	(female)	Present study

No regression equations were given in previous studies for *P. montagui* although a conversion factor for CL to TL was given as 4.28-4.76 (Mistakidis,1957) and 4.26 (Allen, 1963). In the present study the differences between sexes was found to be highly significant and the ratio between TL and CL were 4.21 and 2.80 for males and females respectively. TL/CL ratio for *C. allmanni* was found to be higher (4.96) in the Forth Estuary in comparison to (3.49) recorded by Allen (1963). These variations could well be due to the geographical variations, size range variation or number of animals used for the analysis. Relationships between other morphometrical parameters was not found in the literature.

3.4 ESTIMATION OF BIOMASS

Biomass can be expressed in units such as wet weight, or in units measuring living tissue only as ash-free dry weight (AFDW) or in units of energy of living tissue (Crisp, 1984). In the past, wet weight has been used routinely to estimate the biomass but the use of ash-free dry weight is recommended for estimation of production by Crisp (1984) and Rumohr *et al.* (1987). The use of AFDW excludes the non-living parts of the animal and is more appropriate for the estimation of production. In the present study, therefore, AFDW was considered as the unit of biomass and relationships between CL/AFDW for three species; *C. crangon*, *C. allmanni* and *P. montagui* were established to facilitate the conversion of CL to AFDW.

3.4.1 Materials and Methods

A sample of fresh shrimps representing the entire size range for each species; *C. crangon*, *C. allmanni* and *P. montagui* was selected at random from all the stations and analysed to estimate biomass. Sub-samples were obtained from samples of 2.2.94, 23.4.93, 23.7.93 and 18.10.93 to represent winter, spring, summer and autumn respectively. The carapace lengths of the shrimps were measured and each shrimp was placed individually in pre-weighed crucibles and weighed wet. They were then dried in an oven at 60°C to a constant weight, cooled in a desiccator and the dry weight of each individual was determined to the nearest 0.001 g. The shrimps were then combusted at 450°C for 24 hours and the ash weight was determined. The ash-free dry weight (AFDW) of the individuals was calculated as the difference between dry weight and ash weight. The procedure was repeated for each season for *C. crangon* and *P. montagui* but only for winter and autumn for *C. allmanni* since they were not caught in sufficient quantities in other seasons to sacrifice a sub-sample for determination of biomass.

The relationships between CL/WW and CL/AFDW were linearized through double logarithmic transformation. Possible differences between seasons were assessed by following the method described in Zar (1984) by comparison of slope and elevations. Samples that exhibited significant differences between the seasons were further tested for

pairwise differences using the Tukey multiple comparison test. The comparison of relationships in *C. allmanni* were carried out using Student's *t*-test.

3.4.2 Results

Table 3.6 indicates the regression equations derived for each season for *C. crangon*. The relationship between CL and AFDW exhibits a significant seasonality in *C. crangon* ($F=6.73$, $p<0.001$) although the same is not evident for the relationship between CL/WW ($F=2.57$, $p<0.1$). The Tukey multiple comparison test (Zar, 1984) revealed that the differences between the seasons are highly significant between autumn and spring although the difference of each of them with the other seasons are not significant.

Table 3.6- Log/log relationships between CL/WW and CL/AFDW of *C. crangon* in the Forth Estuary.

Season	N	Parameter	Intercept	slope	R^2	P	F-ratio
Winter	25	WW	-7.27	3.17	99.2	<0.001	2768.26
		AFDW	-9.61	3.47	97.1	<0.001	762.21
Spring	50	WW	-6.85	2.99	97.7	<0.001	2044.54
		AFDW	-10.0	3.76	88.9	<0.001	384.56
Summer	27	WW	-6.56	2.86	93.6	<0.001	366.80
		AFDW	-8.52	3.10	93.6	<0.001	368.29
Autumn	60	WW	-6.51	2.81	94.3	<0.001	3749.46
		AFDW	-8.41	2.95	92.3	<0.001	1430.59
Phil and Rosenberg (1982)		AFDW	0.3603	2.84	99.6		

P. montagui showed a significant difference for both relationships CL/WW and CL/AFDW between seasons ($F=2.841$, $p<0.05$ for CL/WW and $F=5.352$, $p<0.001$ for CL/AFDW). Tukey multiple comparison test revealed that the significant difference is only between summer and winter for CL/WW relationship (Table 3.7). Although there

was an indication of significant difference between seasons for CL/AFDW relationship Tukey multiple comparison test however, did not identify the difference.

Table 3.7- Log/log relationships between CL/WW and CL/AFDW of *P. montagui* in the Forth Estuary.

Season	N	Parameter	Intercept	slope	R^2	P	F-ratio
Winter	16	WW	-8.72	3.61	97.8	<0.001	633.30
		AFDW	-10.60	3.65	95.9	<0.001	331.37
Spring	29	WW	-8.00	3.31	95.5	<0.001	572.64
		AFDW	-10.40	3.62	95.2	<0.001	537.89
Summer	25	WW	-7.30	3.00	95.8	<0.001	587.79
		AFDW	-9.62	3.26	95.6	<0.001	565.09
Autumn	28	WW	-7.36	3.06	92.2	<0.001	273.53
		AFDW	-10.10	3.49	95.4	<0.001	478.36

The relationships between CL and WW/AFDW of *C. allmanni* between seasons were not significant (t= 1.114, t= 0.721), thus a common regression coefficients were computed for each relationship. The elevations of the regression lines however, showed a highly significant differences (t= -6.5, t= 6.28). Therefore, the following relationships with common slope but different elevations were derived to describe the relationships between CL/WW and CL/AFDW of *C. allmanni*.

Table 3.8- Log /log relationships between CL/WW and CL/AFDW of *C. allmanni* in the Forth Estuary.

Season	N	Parameter	Intercept	slope	R^2	P	F-ratio
Winter	17	WW	-7.61	3.27	92.4	<0.001	181.94
		AFDW	-10.10	3.62	84.2	<0.001	79.81
Autumn	19	WW	-6.81	2.90	92.0	<0.001	194.24
		AFDW	-9.77	3.46	91.6	<0.001	184.74

3.4.3 Discussion

The only previous record of the relationship between CL and AFDW was by Pihl and Rosenberg (1982) who described the relationship for *C. crangon* as ln AFDW = ln 2.840 CL + ln 0.3603 (r=0.996). The seasonal differences between the relationships were not considered in their study. Rumohr *et al.*(1987) emphasized that the establishment of conversion factors for the relationship between length and DW, AFDW in crustaceans is a necessity. The present findings therefore, would be useful to the European marine biologists. Since the difference between the seasons were highly significant in the present study for all species, it can be concluded that the calculation of biomass using one relationship is less appropriate than using equations derived for each season separately.

CHAPTER 4. POPULATION CHARACTERISTICS

POPULATION DYNAMICS

4.1 GENERAL POPULATION CHARACTERISTICS

4.1.1 Introduction

The present chapter focuses on three important aspects of the population dynamics of shrimps in the estuary and Firth of Forth. Firstly, it deals with the general characteristics of the shrimp population with reference to species composition, distribution, abundance and population structure. Secondly, growth and mortality are considered and finally biomass, production and population size of the shrimps in the estuary and Firth of Forth are reported.

4.1.2 Materials and Methods

4.1.2.1. Identification of species

The samples of shrimps collected from the estuary and Firth of Forth were brought to the laboratory and identification of species was carried out using the descriptions given in Smaldon (1979). *P. montagui* was separated easily from the *Crangon* species by its characteristic pink colour. The morphological features given in Table 4.1. were used to differentiate *C. crangon* from *C. allmanni.* Smaller shrimps were identified with the aid of a microscope.

Table 4.1.- Morphological differences between *C. crangon* and *C. allmanni.*

Character	*C. crangon*	*C. allmanni*
1. Colour	Dark greenish grey, distal ends of the tail fan is dark, colour change when preserved in formalin not noticeable	Light grey, no dark pigments in the tail fan, colour change to purple when preserved in formalin
2. Transparency	Exoskeleton not transparent	Exoskeleton transparent, stomach and ovaries are visible to naked eye through exoskeleton
3. Last abdominal segment	No carina	bi-carinated, dorsally

The other small shrimps found in the samples were also identified using the characteristics given in Smaldon (1979).

Determination of sex

The shrimps clearly exhibited sexual dimorphism in the adult stage and the morphological differences noted in males and females of the three species, *C. crangon*, *P. montagui* and *C. allmanni* are shown in Fig. 4.1. In the two *Crangon* species the first pleopod of the male is hooked over the basipodite of the first exopodite while the females bear a long, spatulate shaped endopodite which is offset from the exopodite. The second pleopod of the male shrimps bears a late developing appendage called appendix masculina which is absent in females. The first antenna of the males is somewhat fatter than that of the females of the same size. Sex determination in the two *Crangon* species was carried out basically using the differences in the pleopods. The third character was used as an additional feature to support sex determination in small shrimps. Sexual dimorphism was not marked in the shrimps below 5.00 mm carapace length and these were categorised as juveniles. A few shrimps below this size exhibited initiation of the appendix masculina as described by Muus (1967), but these were combined to the juvenile category since all the shrimps belong to that size class could not be sexed with certainty.

The sex determination of *P. montagui* was carried out by microscopic examination of the 1st and 2nd pleopods. The males bear a clearly distinguishable copulatory organ in the endopodite of the first pleopod which is absent in females. The endopodite of females is lanceolate in shape (Fig. 4.1). The appendix masculina described in *Crangon* species was also present in the second pleopod of male individuals of *P. montagui.* The latter character was used as a more reliable feature in determination of sex in smaller animals since the dimorphism in the first pleopod was not so conspicuous in them.

After identifying and separation of animals by species and by sex the carapace length (Fig.3.3) was measured in each shrimp in the sample/subsample to the nearest 0.01mm using a vernier calliper.

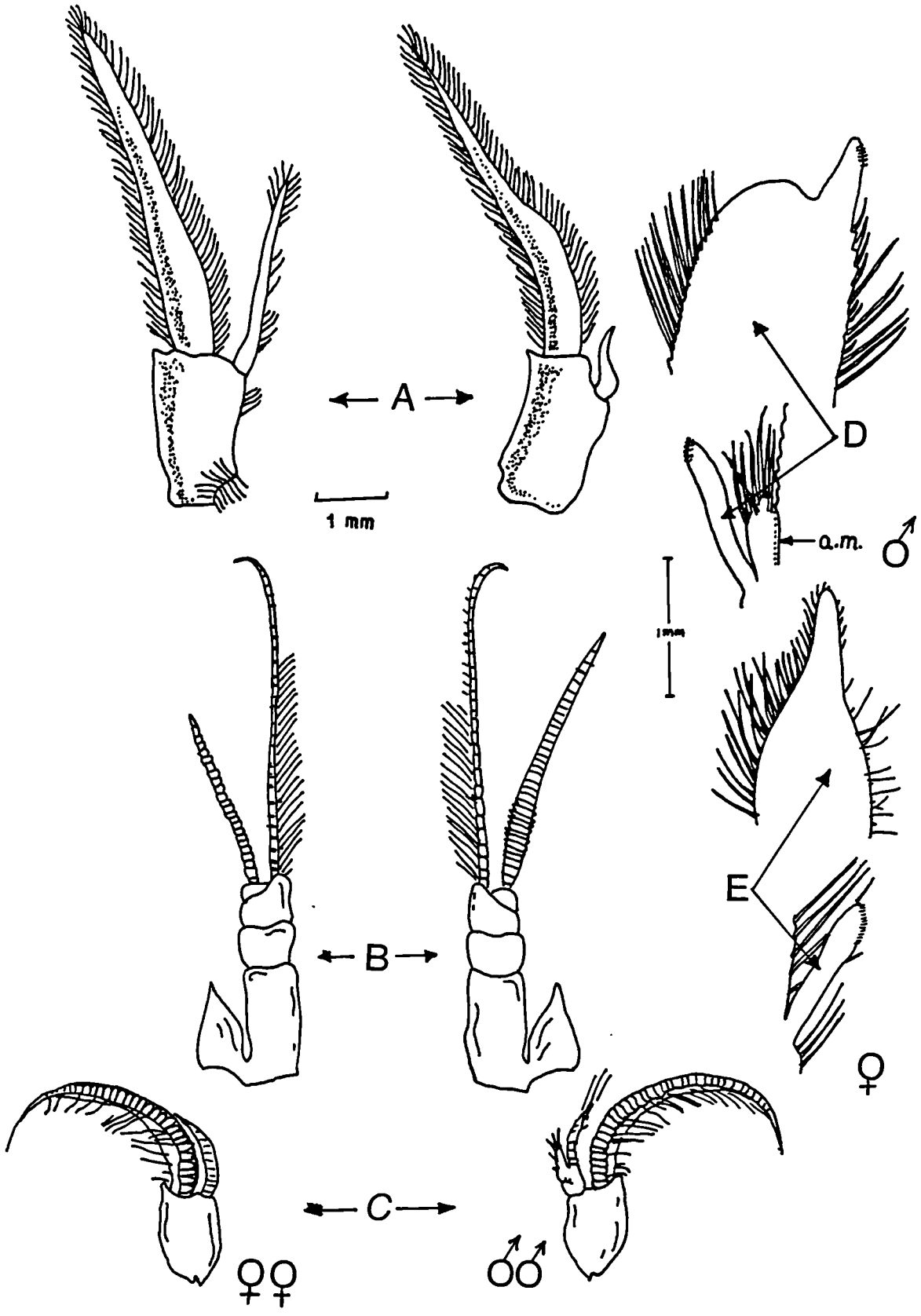


Fig.4.1 Sexual differentiation in *C. crangon* and *P. montagui*. A. first pleopod of ♂ and ♀ (from Boddeke, 1989), B. antenna and C. second pleopod (from Meyer-Waarden and Tiews, 1957; not to scale), D. endopodites of the first (upper) and second (lower) pleopods in male *P. montagui*. a.m.=appendix masculina, E. endopodites of the first (upper) and second (lower) pleopods in female *P. montagui*.

4.1.2.2. Species composition, Abundance and Distribution

Species Composition at each station, as the percentage of total number of shrimps present, was computed for both high water and low water as described by the equation 4.1.

$$\frac{N_i}{\sum_{N=1}^{1} N_i} \times 100 \qquad (4.1)$$

where N_i = Number of shrimps belong to species i (i=1,2,3)

The actual numbers of shrimps were corrected for retention efficiency of the trawl (33%), for each sampling date and station and were grouped into 1 cm size classes. The area swept by the trawl was estimated and the abundance of each species was calculated as the density ha^{-1} at each station at high water and low water. The procedure followed in the above calculation is described below.

Density $Trawl^{-1}$ (D_t) = (n x E)

where E= correction for gear efficiency (100/33), and n= original number caught

$$Density\ ha^{-1} = \frac{D_t}{A} \times 10,000 \qquad (4.2)$$

where A m^2 = area swept = 800 m x 2 m = (distance trawled x width of trawl mouth)

D ha^{-1}= 6.25 D_t

The abundance of shrimps caught at Kingstone Hudds (the only station sampled in the Firth Forth) by Agassiz Trawl, and in the upper estuary (6 stations) by Beam Trawl, were also calculated in the same manner and the respective raising factors 5.00 and 6.25 were obtained for converting the numbers to number ha^{-1}. The stations in the upper estuary and Kingstone Hudds were not sampled at the same frequency as in the major study area, but were used to provide additional information which may explain the migration and other behavioural features of the shrimp population in the major study area.

The influence of environmental parameters; salinity, temperature, suspended solids, depth and tidal amplitude on the abundance of shrimps in the major study area from PE to LO were tested using stepwise multiple linear regression analysis. Differences of abundance between HW and LW, among sampling dates and stations were examined by analysis of variance (GLM procedure).

4.1.2.3. Population structure

The population structure was established as the percentage of each category present at a particular time at a particular station. The main categories used were juveniles, males, non-berried females and berried females. An additional category transitional males was included in *P. montagui*. Only the transitionals of late stages, which are definitive were used here. Existence of transitional stages in *C. crangon* was reported by Boddeke (1985, 1989, 1991) and Martens and Redant (1986) but due to the difficulty in distinguishing such stages by examining the external features it was decided to exclude this category for *Crangon* species. The respective equations used to compute the population structures of *Crangon* species and *P. montagui* are given in equation 4.2 and 4.3 and express the each category as a percentage of total catch.

$$\frac{N_i}{\sum_{N=1}^{4} N_i} \times 100 \qquad (4.3)$$

where N_i = Number of shrimps belong to category i (i=1,2,3,4)

$$\frac{N_i}{\sum_{N=1}^{5} N_i} \times 100 \qquad (4.4)$$

where N_i = Number of shrimps belong to category i (i=1,2,3,4,5)

4.1.2.4. Mean body size

Carapace length (mm) was used as the indication of body size and the mean carapace length of each species per station per sampling was computed separately for sexes. The juvenile shrimps were allocated equally between male and female categories so that the size class would also be represented in the calculations. The normality of the population distribution was then tested by correlating the original length frequency data with normal scores using Minitab (1989). The differences between the body sizes of the population at high water and low water were then tested using one way anova by summing across the sampling dates. The differences in body size among stations were also tested in the same manner.

4.1.3 Results

4.1.3.1 Species

The caridean shrimps *C. crangon*, *P. montagui* and *C. allmanni* were the most abundant inhabitants of the shrimp community in the estuary and firth of Forth. *C. crangon* was the most common of all and appeared to inhabit the entire estuary and firth. *P. montagui* was less common and was only confined to lowermost stations, Port Edgar and Blackness, of the estuary. *C. allmanni* was only found in the estuary in certain months of the year, arriving in the estuary in October and leaving in June.

There were a few other caridean shrimps observed more rarely during the present investigations. They are listed in Table 4.2 in the order of their abundance, along with respective locations and periods of occurrence. *Pandalina brevirostris* and *Eualus pusiolus* were found regularly and the former in particular was found almost throughout the year. The occurrence of *Spirontocaris lilijeborgi* and *Pontophilus spinosus* was negligible, for instance the only two specimens of the latter was found during the entire period of study.

Table 4.2 The minor species of caridean shrimps found in the Estuary and Firth of Forth during the period February 1992 to February 1994. PE=Port Edgar, BL=Blackness, TB=Tancred Bank, BO=Bo'ness and LO= Longannet.

SPECIES	LOCALITY	PERIOD OF OCCURRENCE
Pandalina brevirostris	PE, BL, TB and BO	Throughout the year
Eualus pusiolus	PE and BL	June
Processa nouveli holthusi	TB	June
Spirontocaris lilljeborgi	BL	June
Pontophilus spinosus	KH	April and May

4.1.3.2 Species composition, distribution and abundance

C. crangon and *P. montagui* were present in the estuary throughout the year and *C. allmanni* is present from autumn to late spring/early summer (Fig.4.2). A minor proportion of *C. allmanni* was found in April in PE and BL but they were completely absent from the estuary by July. *C. crangon* comprised the bulk of the shrimps in uppermost areas, beyond Tancred Bank, in the estuary during the entire year except for presence of *C. allmanni* in relatively low proportions in autumn and winter. *P. montagui* was completely absent in the uppermost areas of the estuary despite its marginal appearance in Tancred Bank and Bo'ness at high water during June 1992 and in Longannet at high water in December 1992. *P. montagui* was present in significant proportions throughout the year in the two lowermost stations, Port Edgar and Blackness.

The distribution of *C. crangon*, *P. montagui* and *C. allmanni* in the estuary expressed as the percentage of each species occurring at each station is shown in Fig. 4.3. *C. crangon* is distributed throughout the estuary while the range of distribution in *P. montagui* is limited to the lowermost stations PE and BL. *C. allmanni* is present in the estuary only in autumn and winter and when present, their distribution extends from PE to LO specially at high water. A marked difference was observed in the distribution of *C. crangon* in summer and autumn. The majority of the population were observed at Longannet in summer while the majority aggregate at Port Edgar in autumn. This is

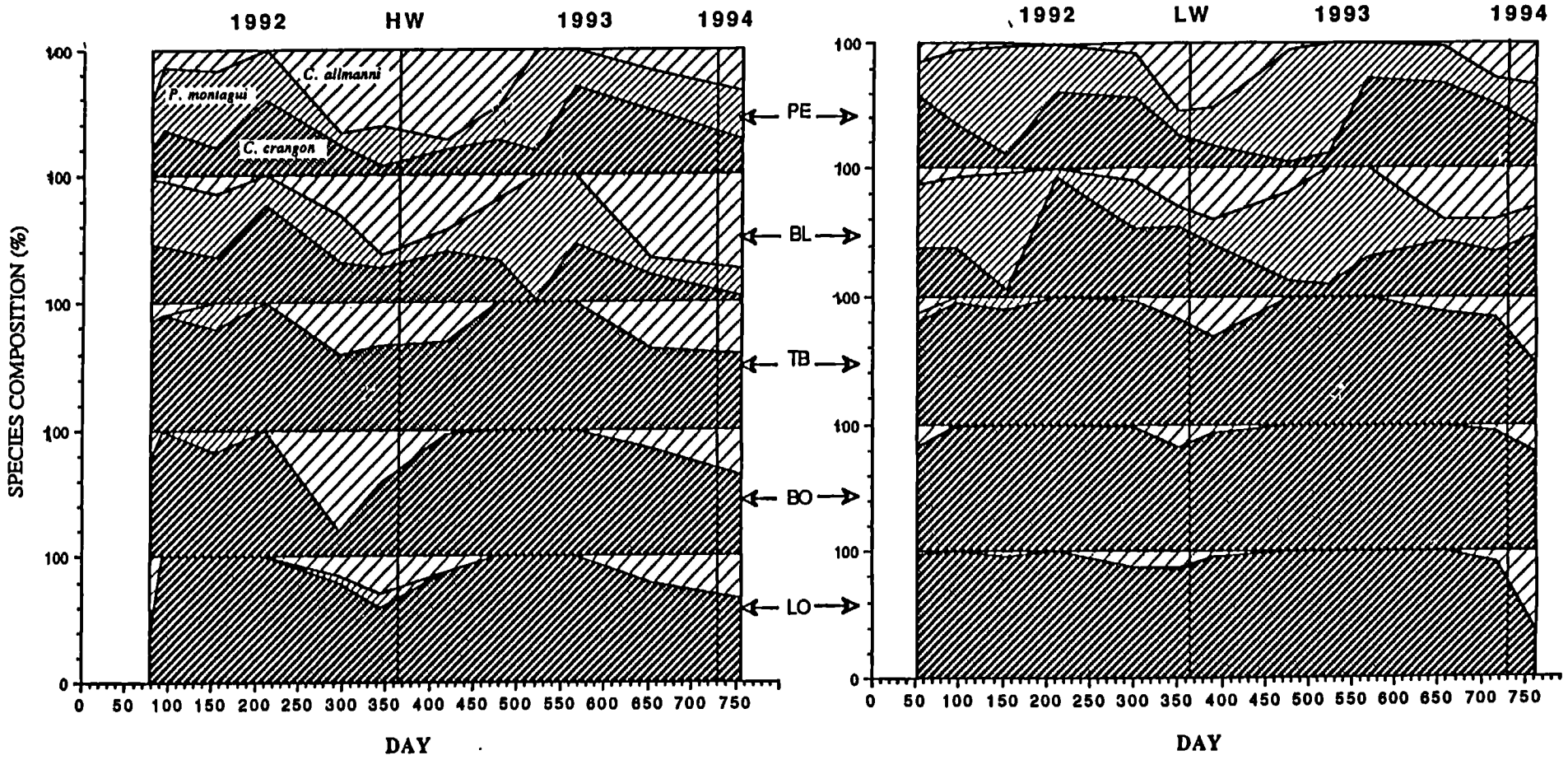


Fig. 4.2- Species composition (%) of shrimps; *C. crangon*, *P. montagui* and *C. allmanni* at five stations; Port Edgar, Blackness, Tancred Bank, Bo'ness and Longannet in the Forth Estuary. Day 1 = 1 January 1992.

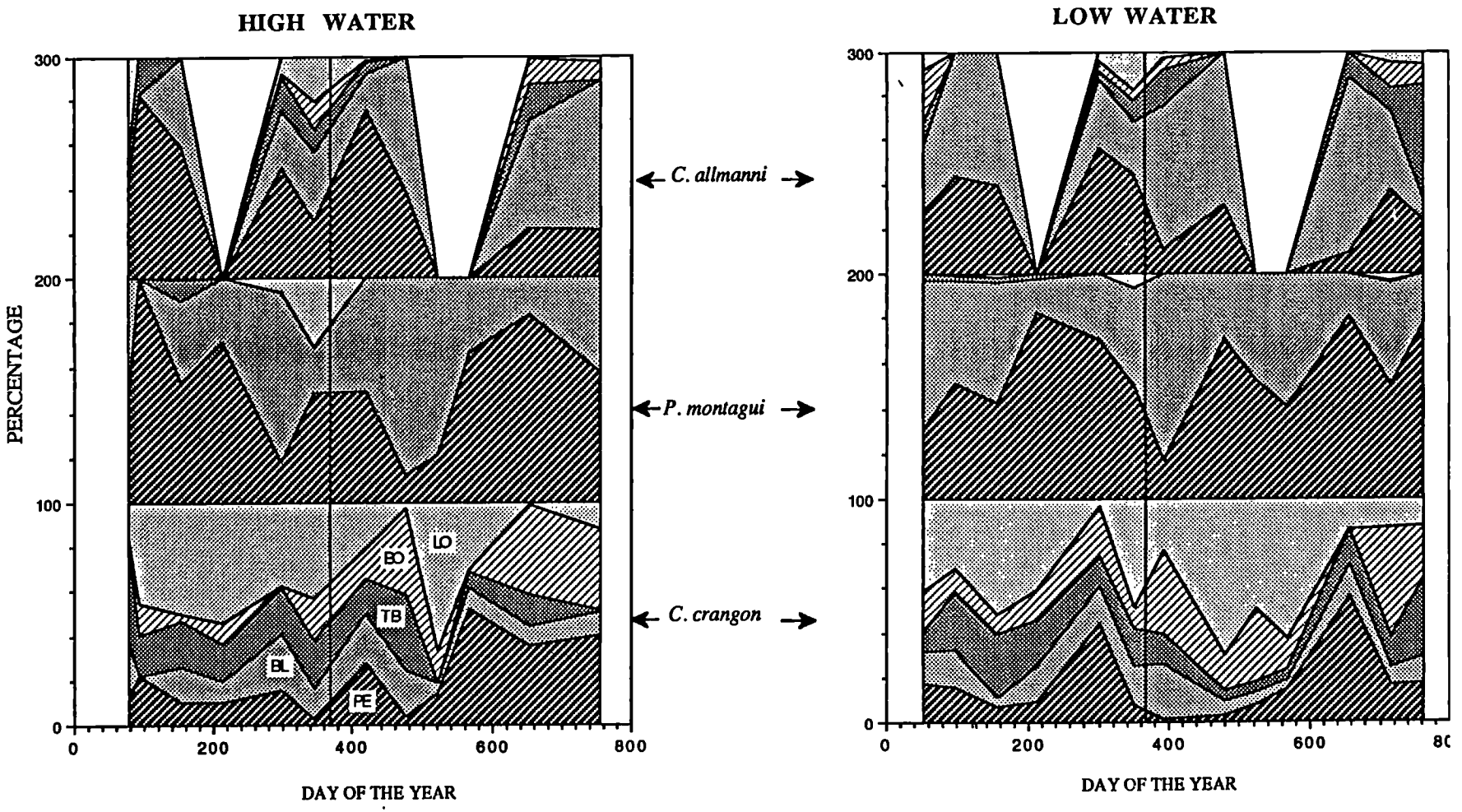


Fig.4.3- Temporal and spatial distribution, expressed as % occurrence, of *C. crangon*, *P. montagui* and *C. allmanni* at five stations: Port Edgar, Blackness, Tancred Bank, Bo'ness and Longannet in the Forth Estuary. Day 1=1st of January 1992.

clearly evident in the populations at low water. *P. montagui* also exhibits a similar variation in temporal distribution gathering at Port Edgar in autumn.

The species composition at Kingstone Hudds as indicated by figure 4.4 shows a marked difference from to the stations in the estuary. *C. crangon* was absent here in most of the year. It was observed only in two out of six trawls and all the shrimps found in these occasions are berried females carrying eggs which are close to hatch. *P. montagui* and *C. allmanni* were abundant throughout the year in Kingstone Hudds and the dominance in the catch varied seasonally. *C. allmanni* dominated the catch in late winter while *P. montagui* dominated the other seasons. In June the catch of both species is negligible in both years and comprised 2 specimens each of *P. montagui* while only one specimen of *C. allmanni* was observed in 1993.

In contrast, *C. crangon* was found to be the sole species of shrimp in the upper estuary stations, which extend from Kincardine Bridge to Longareach. It was found in all the stations sampled in the estuary up to Longareach (see Fig. 2.3 for locations of the stations).

The changing abundance of shrimps exhibited a similar trend in both years although the actual abundance was about 10 times higher in 1992 (Figures 4.5, 4.6 and 4.7). *C. crangon* is undoubtedly the most abundant species in the estuary showing about a 4 to 5-fold higher mean abundance than the other two species during most of the times of the year. The general trend in the variation of the abundance of *C. crangon* was similar in all the stations except for the drastic fluctuations observed between low and high water in some stations. The highest abundance of *C. crangon* observed in 1992 was 170,456 individuals ha^{-1} and was recorded at Longannet in July. In 1993 the highest abundance, 21,819 individuals ha^{-1} was recorded at Bo'ness in October. The lowest abundances recorded in 1992 and 1993 were 168 ha^{-1} at Bo'ness and 56 individuals ha^{-1} at Blackness respectively. The maximum abundance of both *P. montagui* and *C. allmanni* was observed in October at PE and were 27462 individuals ha^{-1} and 23387 individuals ha^{-1} respectively.

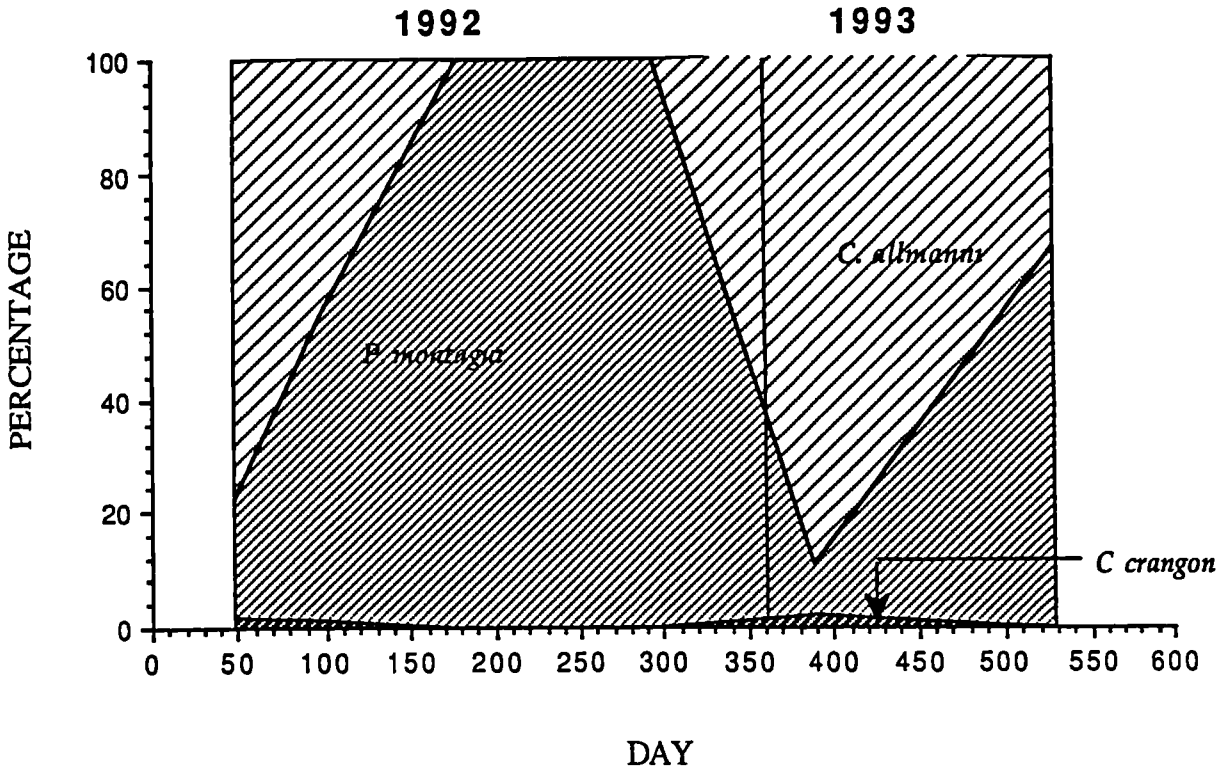


Fig 4 4 - Species composition (%) of shrimps, *C crangon*, *P montagui* and *C allmanni* at Kingstone Hudds, Firth of Forth Day 1=1 January 1992.

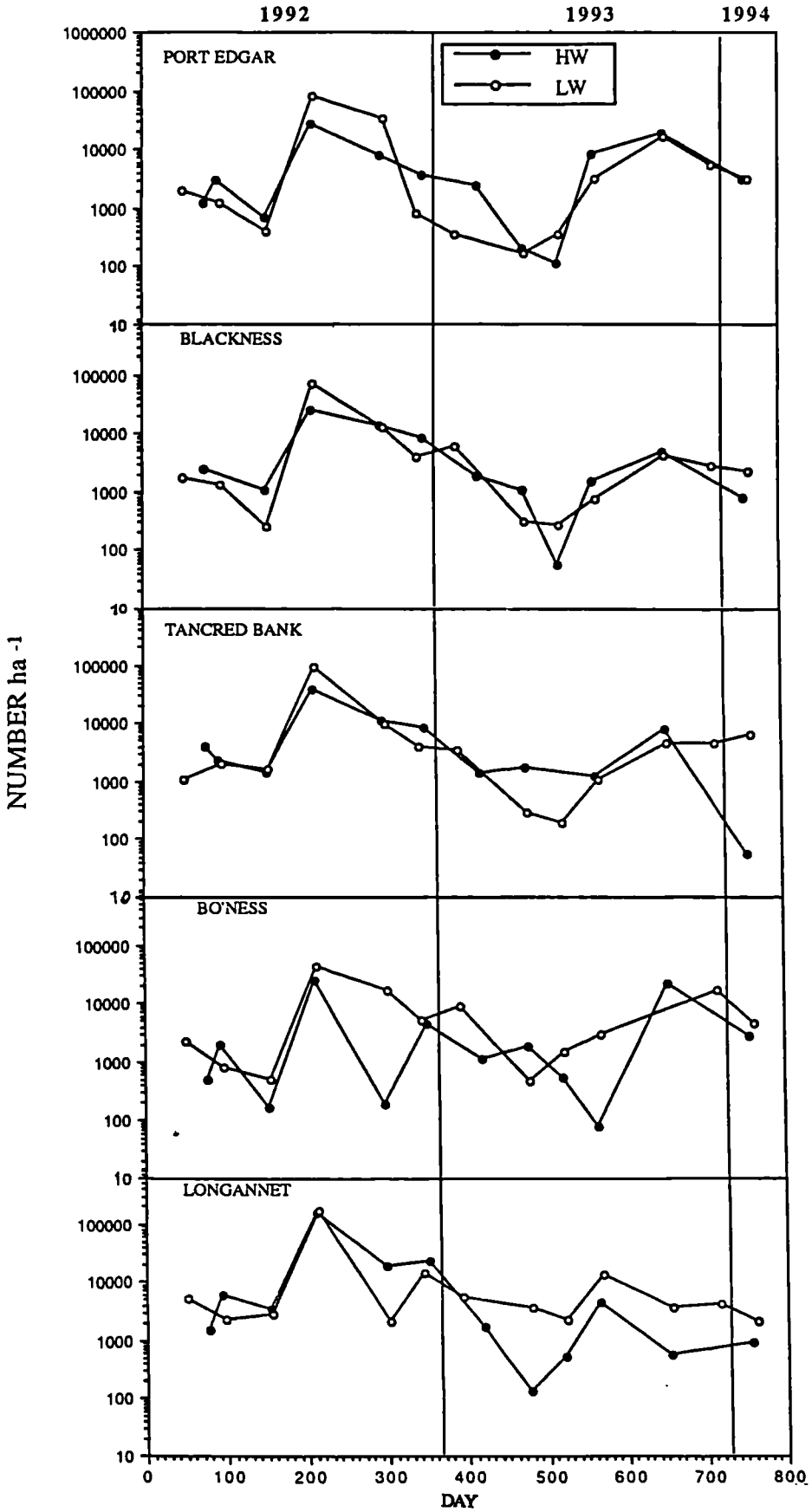


Fig.4.5- Temporal and spatial variations in the abundance (numbers ha^{-1}) of *C. crangon* at five stations in the Forth Estuary at high water and low water. Day 1=1st of January 1992.

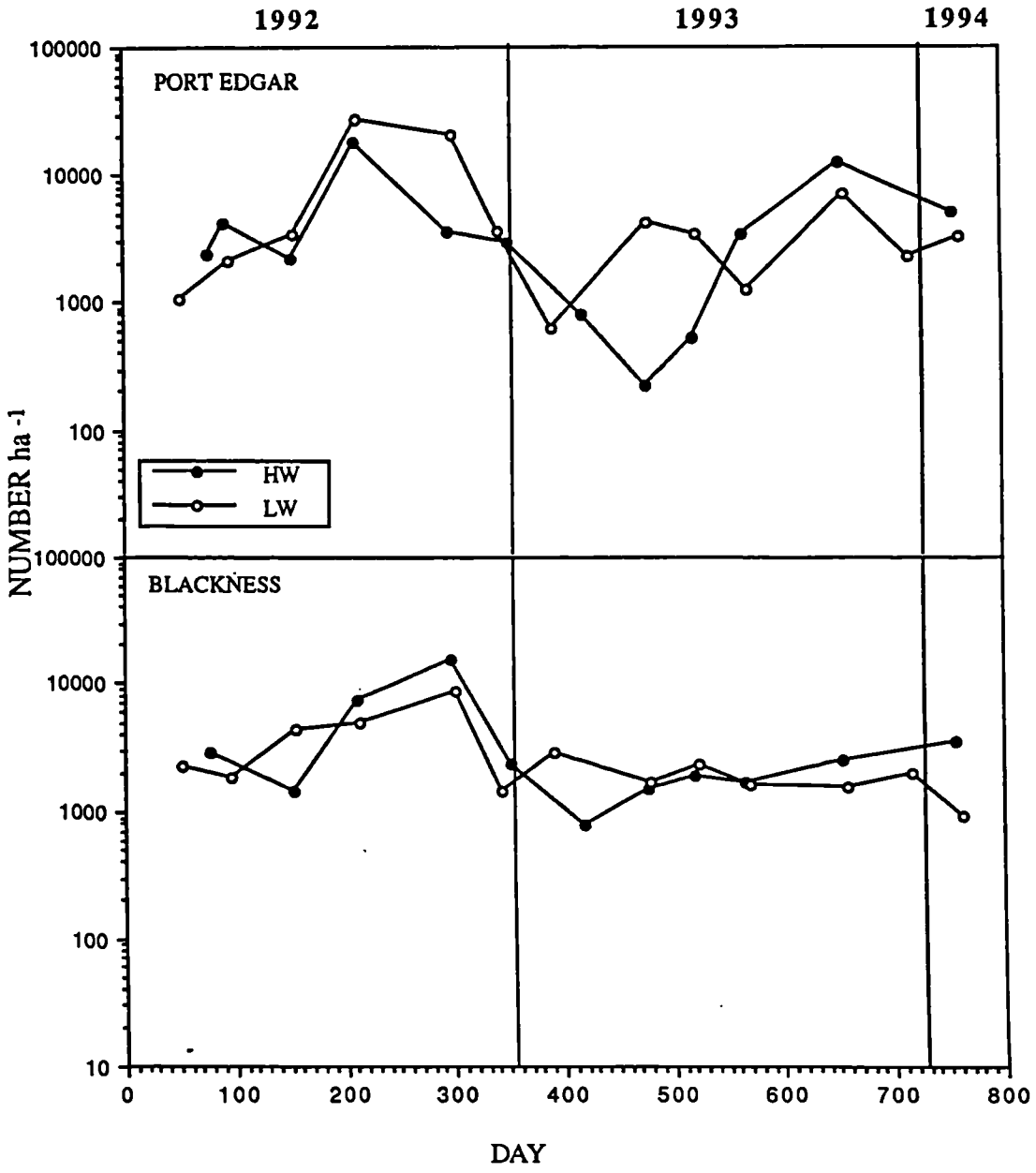


Fig.4.6- Temporal and spatial variations in the abundance (numbers ha^{-1}) of *P. montagui* at Port Edgar and Blackness at high water and low water in the Forth Estuary. Day 1=1st of January 1992.

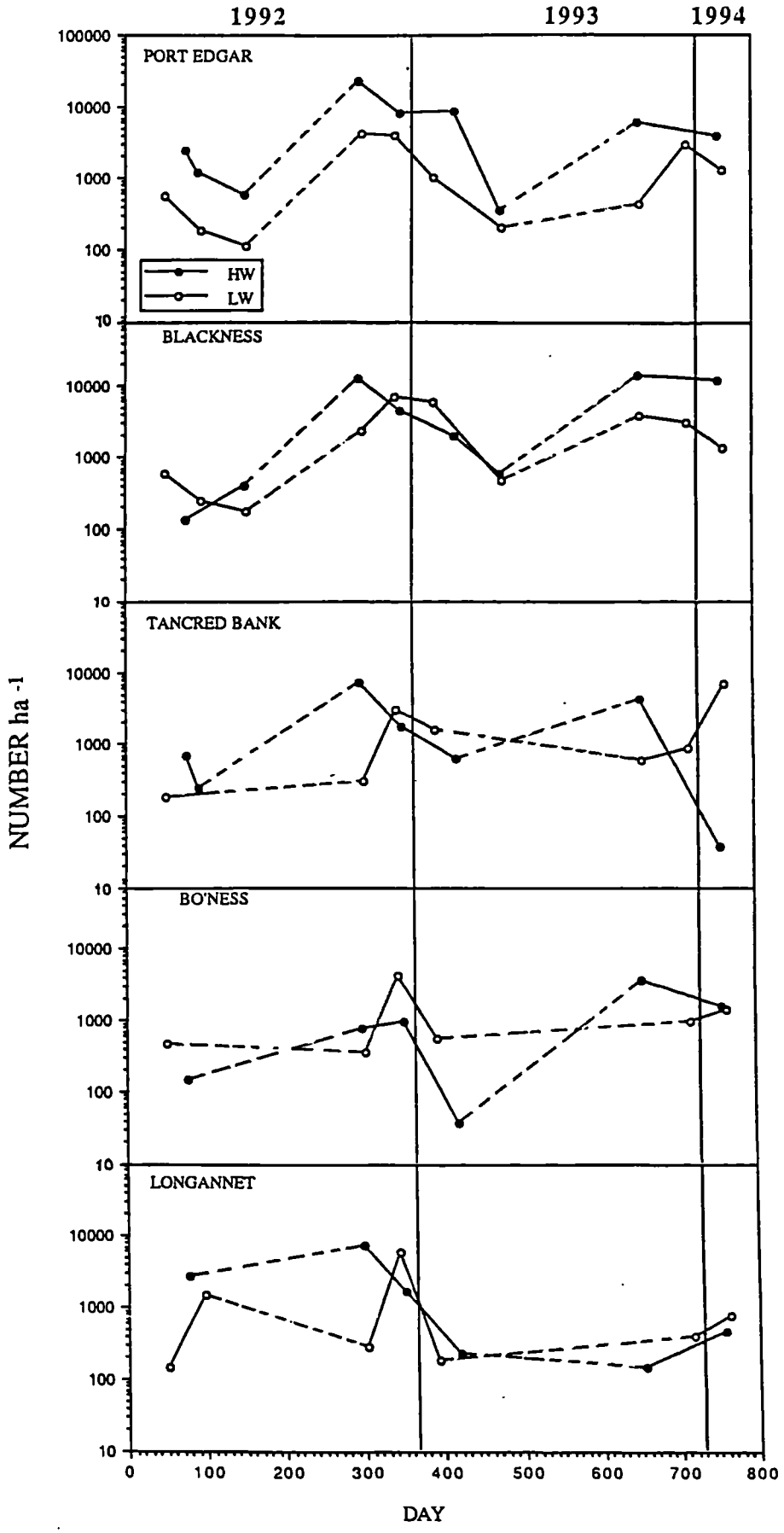


Fig. 4.7- Temporal and spatial variations in the abundance (numbers ha $^{-1}$) of *C. allmanni* at five stations in the Forth Estuary at high water and low water. Day 1 = 1st of January 1992. Broken lines indicates the period of absence of *C. allmanni* in the estuary .

The abundance of *C. crangon* was relatively low in the first 6 months of the year in all the five stations in the estuary (Fig 4.5). This low abundance was evident in both low and high waters in the two years sampled. The maximum abundances were observed in July, 1992 in low waters in all the stations. In 1993 this peak was shifted to October and further the high abundances were observed in high water except at Port Edgar where the peak was in July during low water. The differences in the abundance between the stations and between low and high water are not marked at most instances of sampling. This was further evident by the analysis of variance which showed no significant differences in the abundance of *C. crangon* either among stations ($F = 0.94$, $p > 0.05$, d.f. = 4) or between HW and LW ($F = 0.66$, $p > 0.05$, df = 1). The variation in the abundance among the dates of sampling was found significant ($F = 8.49$, $p < 0.001$, df = 20)

The abundance of *P. montagui* also showed similarly increasing trends towards the latter half of the year to *C. crangon* (Fig. 4.6). The highest abundances were recorded in July and October 1992 and October, 1993. The former were in low water and the latter in high water. Here again no conspicuous differences can be seen in the abundances at the two stations and at low and high water. This was revealed by the analysis of variance where the differences in the abundance among the stations ($F= 1.77$, $p > 0.05$, df = 1) and between low and high water ($F= 0.41$, $p>0.05$, df = 1) were not significant. Further, the analysis of variance indicated no significant difference in the abundance among the dates of sampling ($F=1.96$, $p<0.05$, df=20) which is not apparent from the 1992 data but is perhaps due to the poor abundance of *P. montagui* throughout 1993 at Blackness and most of the months at Port Edgar.

The abundance of *C. allmanni* follows a different pattern compared to *C. crangon* and *P. montagui* because it disappears from the estuary at certain times of the year (Fig 4.7). The abundance of *C. allmanni* was high in December and January in most of the samples. They then completely disappeared by April in the uppermost stations, Tancred bank, Bo'ness and Longannet, and by July from the entire estuary. The analysis of variance indicated no significant difference in the abundance among the five stations ($F= 2.10$, $p>0.05$, df = 4) nor between high and low water ($F= 0.93$, $p>0.05$, df = 1). The

difference in the abundance of *C. allmanni* among sampling dates was significant (F= 5.60, $p < 0.001$, df = 20).

The overall abundance of shrimps in the Kingstone Hudds was less than in the estuary, in particular, the abundance of *C. crangon* was negligible (Fig. 4.8). The peak abundance of *P. montagui* was observed in April, 1992 and for *C. allmanni* in January 1993 and amounted to 3226 individuals ha^{-1} and 10635 individuals ha^{-1} respectively. The lowest abundance was observed in June where the catch was almost negligible.

In the upper estuary peak abundance of shrimps occurred in July at UE3 (South Alloa) (Fig.4.9). Shrimps were found up to UE6 (Longareach) and the low abundance in Longareach can be considered as the upper estuarine limit for *C. crangon.* The peak abundance was observed in July at UE3 during the three days of sampling and was 56585 individuals ha^{-1}.

Stepwise multiple linear regression indicates that temperature is the only environmental variable which has a significant effect on the abundance of *C. crangon* while no variable played a significant role for *P. montagui.* The salinity, however, was significant at the level of $p<0.1$, and may be an influential factor for *P. montagui.* For *C. allmanni* depth showed a significant effect at 0.05 level of significance and tidal amplitude at 0.1 level of significance (Table 4.3).

Table 4.3- Level of significance of students t-test on β values of the variables (n=102).

	C. crangon		*P. montagui*		*C. allmanni*	
Variable	t	p	t	p	t	p
Temperature (C°)	2.65	0.009****	-0.16	0.875	-1.58	0.118
Salinity (ppt)	0.27	0.788	2.04	0.059*	-0.49	0.628
Suspended solids(gl^{-1})	-1.08	0.283	0.62	0.540	-0.36	0.723
Depth-(m)	-0.82	0.416	-0.37	0.711	2.50	0.014**
Tidal amplitude(m)	-1.40	0.169	-0.82	0.419	1.94	0.055*

* = $p<0.1$, ** = $p<0.05$, *** = $p<0.01$, **** = $p<0.001$

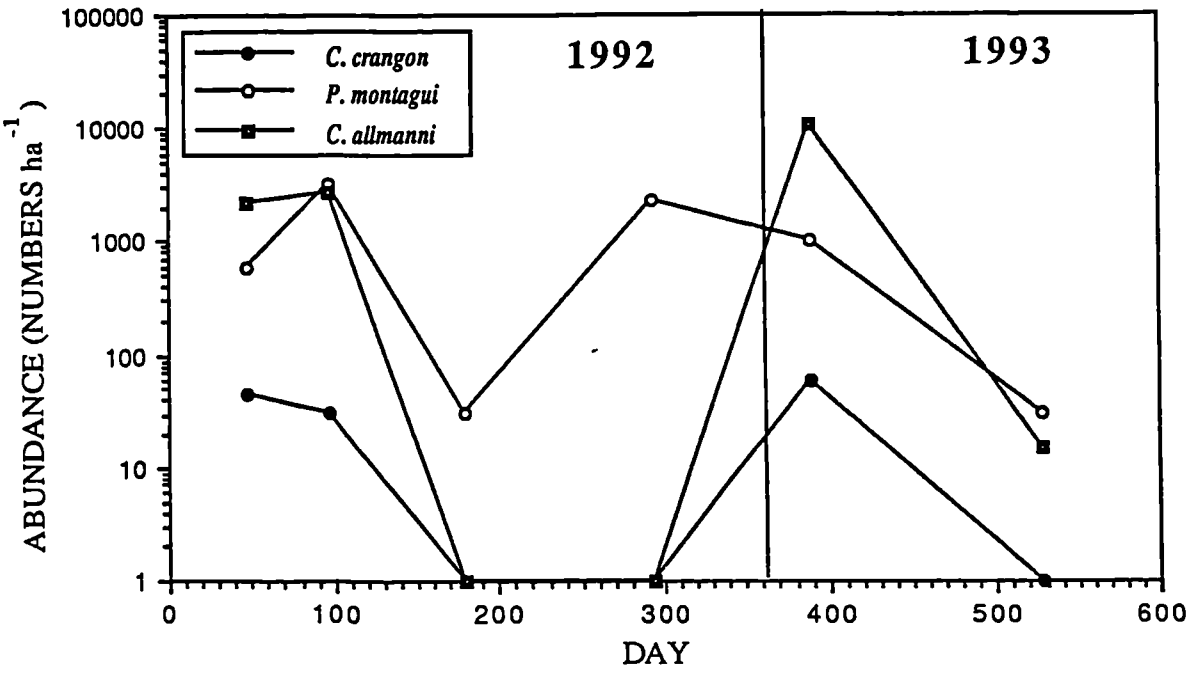


Fig.4.8- Temporal variations in the abundance (numbers ha^{-1}) of shrimps; *C. crangon*, *P. montagui* and *C. allmanni* at Kingstone Hudds, Firth of Forth. Day 1=1st of January 1992.

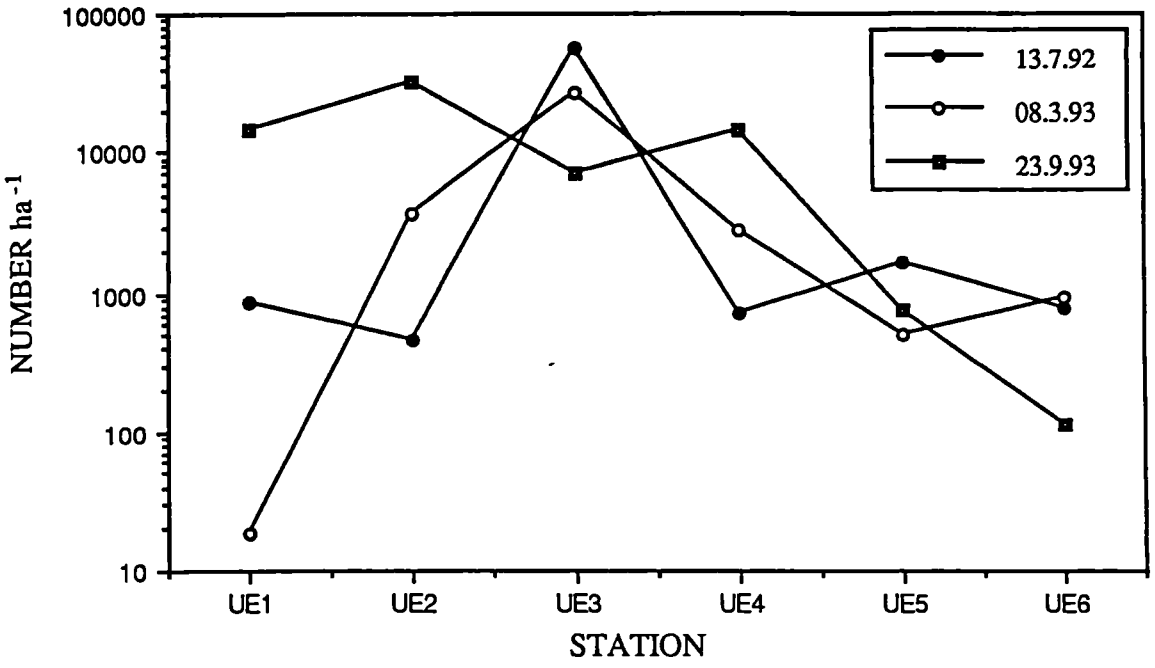


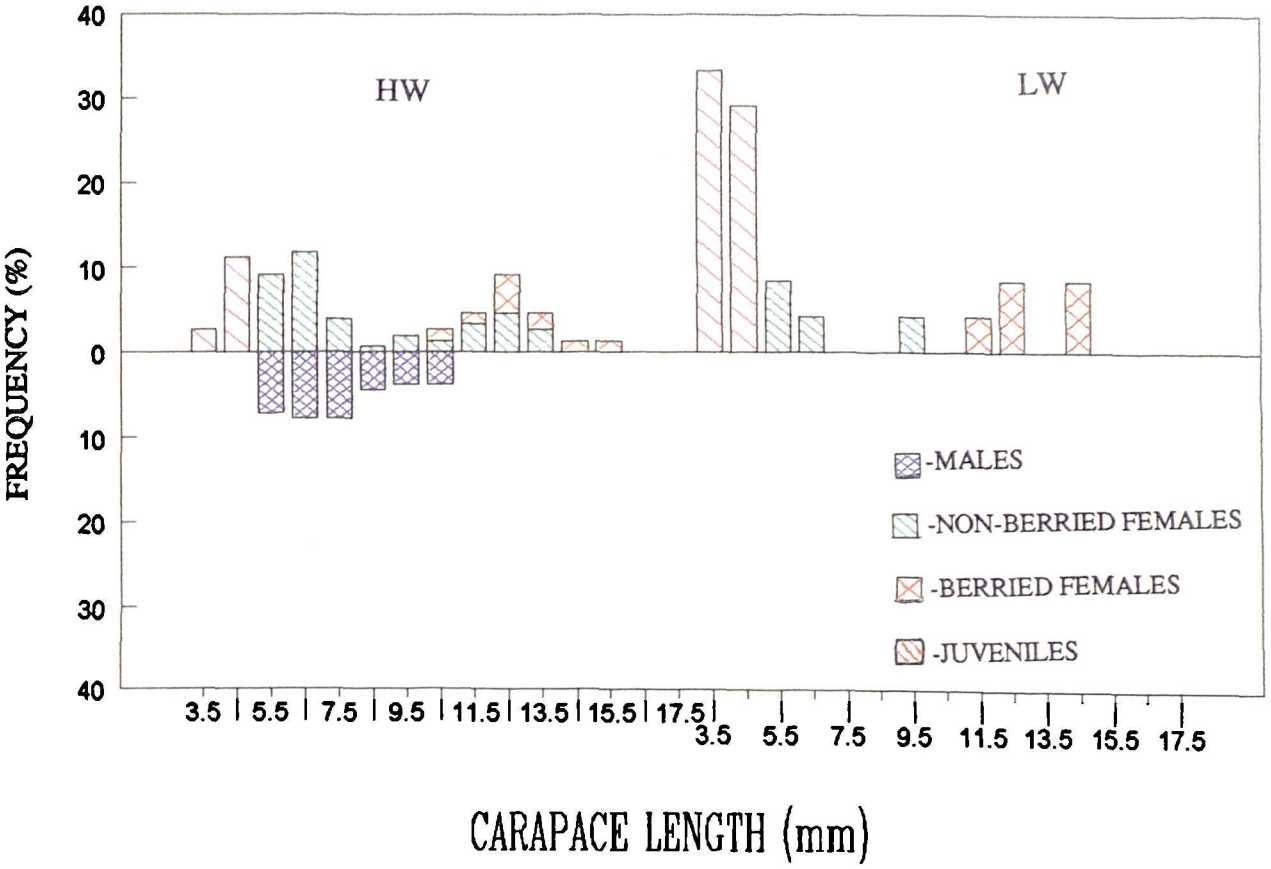
Fig. 4.9 - Spatial variation in the abundance (numbers ha^{-1}) of *C. crangon* in the upper Forth Estuary, at three sampling occasions at high tide.

4.1.3.3 Population Structure

The population structure of *C. crangon* is illustrated in Figures 4.10 and 4.11 for 1992 and 1993 respectively. The juveniles of *C. crangon* were observed in the population in January, July, October and December in all the stations in 1992. In 1993, they appeared in all the stations in July and October, but the percentages of juveniles present at Blackness, Tancred Bank and Bo'ness in October were negligible. In December, 1993, juveniles were observed only at Tancred Bank and Bo'ness and in small percentages (Fig. 4.10 and 4.11). The juveniles comprised 6-10% of the population in 1992 and 20-40% of the population in 1993. Berried females were found in the estuary all year round except in October. They appeared in very small numbers in December, and increased in proportion reaching their peak abundance in June. In both years, higher percentages of berried females occurred at Bo'ness and Longannet indicating that the berried females prefer upper areas of the middle estuary to lower areas for egg development. In July, berried females were not present at Longannet but were present in the other four stations in small percentages. The size range of the berried females varied from 8.5 to 15.5 mm in the five stations in the lower estuary. The males and females exhibited a difference in size range, females ranging from 3.5 - 17.5 mm in carapace length and males ranging from 3.5 - 13.5 mm in carapace length. Absence of males larger than 11.5 carapace length was marked in June and July. The male population in June and July clearly showed the disappearance of some length classes from the population. This is marked in the size range greater than 10.5 mm and the male population present in the estuary during this period was represented by size classes of 3.5-7.5 mm.

There was no difference observed in the population structure between HW and LW although seasonal variations were evident. The most marked variation among the stations was the aggregation of berried females to uppermost stations of the lower estuary. Higher percentages of juveniles were observed at high water indicating their movements from intertidal nursery areas to subtidal areas with high tide.

In the upper estuary, juveniles of *C. crangon* were found in high proportions on 13.7.92. Juveniles penetrated up to UE6 (Longareach) and were high in proportion from UE4-UE6. They were found again in September at UE3 (South Alloa) and UE5 (Bannockburn) in



Key to colour codes and axes in Fig.4.10 - Fig.4.17, based on Bo'ness, July 1993 (Fig.4.11).

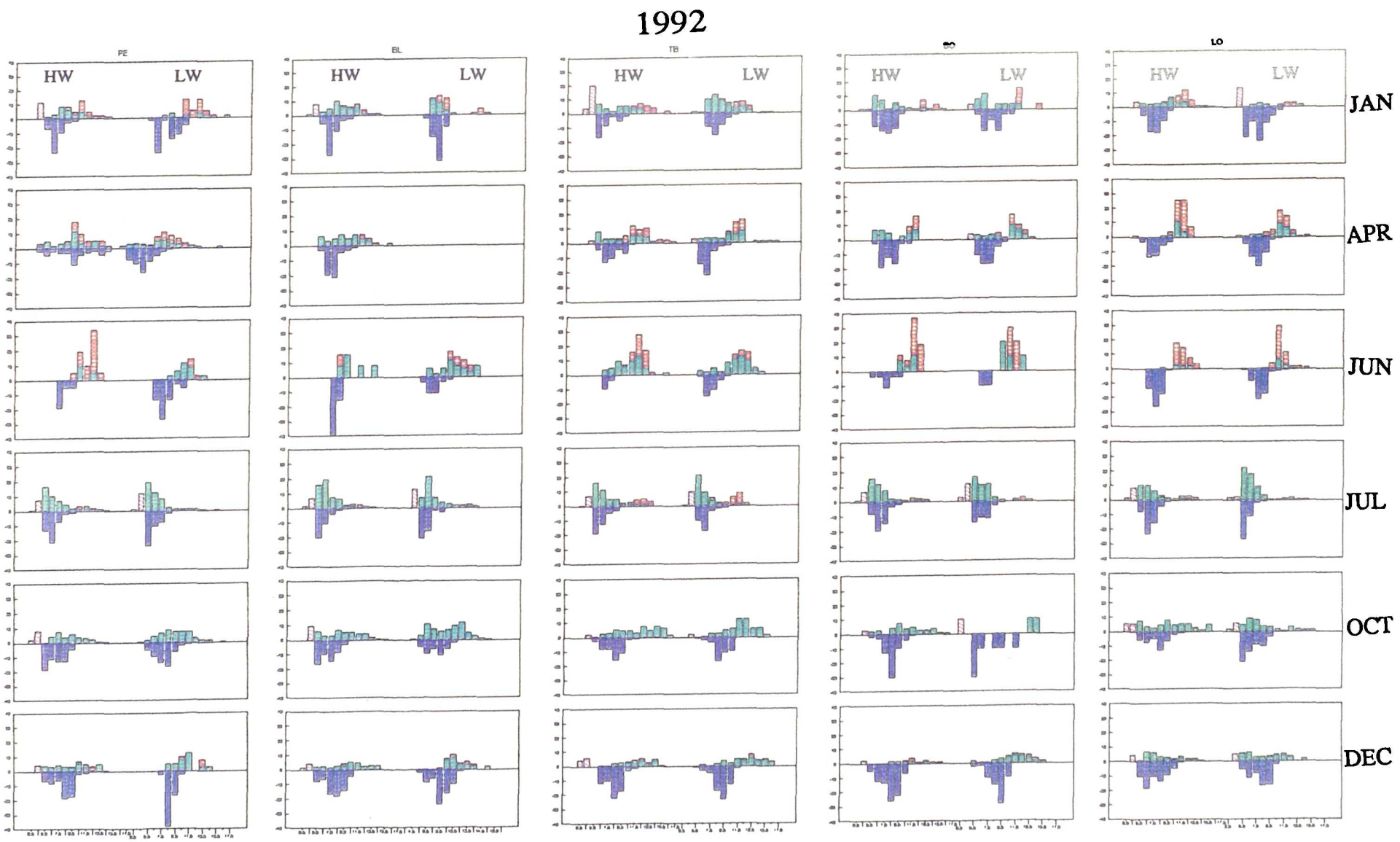


Fig.4.10 Temporal and spatial variations in population structure(%) of *C. crangon* at five stations at high water and low water in the Forth Estuary in 1992.

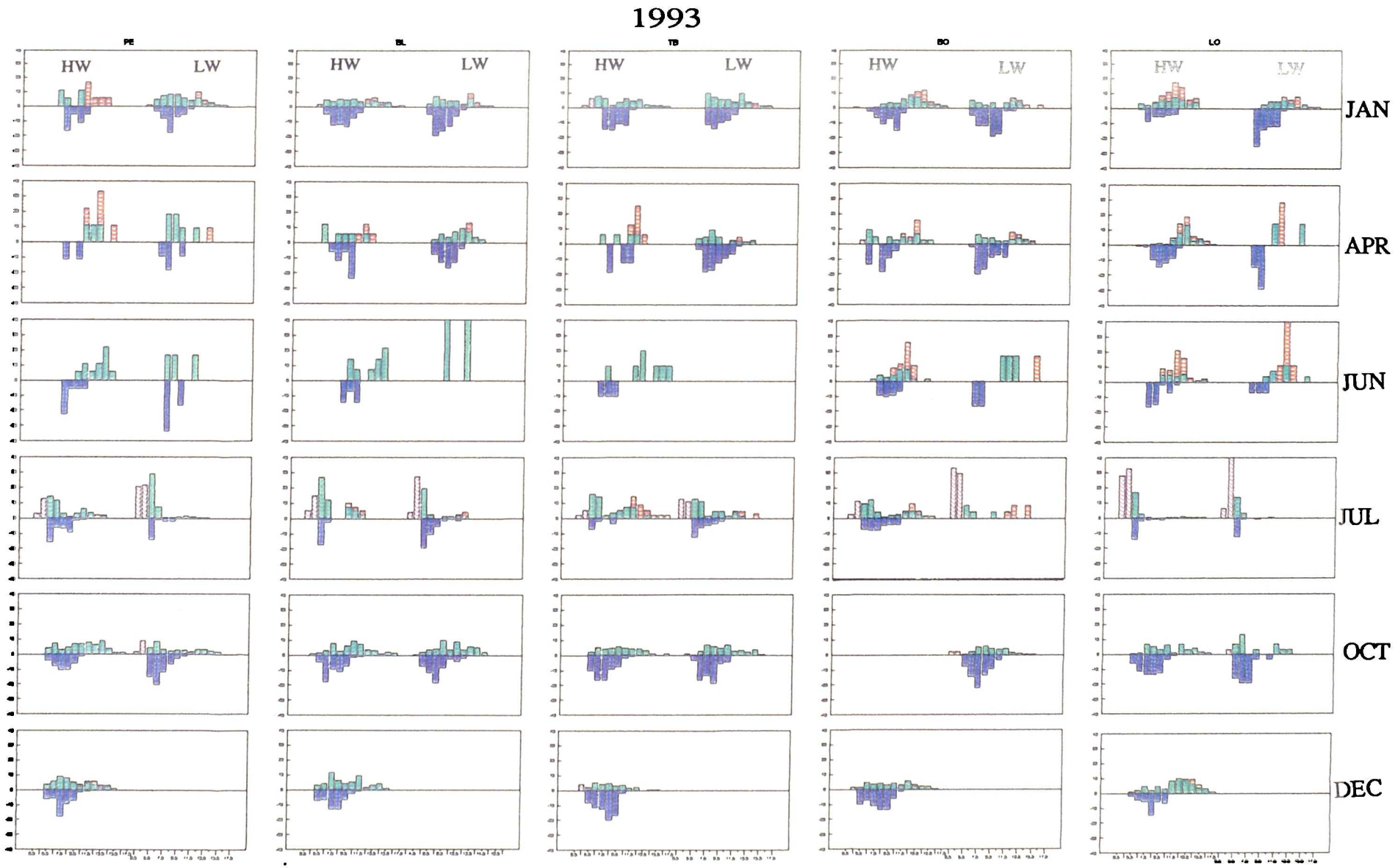


Fig.4.11 Temporal and spatial variations in population structure(%) of *C. crangon* at five stations at high water and low water in the Forth Estuary in 1993.

low proportion. Berried females were found only up to UE2 (Airth) on 13.7.92 and ranged from 10.5-13.5 mm in carapace length. In March samples they were present but not as abundant as in June (Fig.4.12). The wide size range of 3.5-15.5 mm in UE1-UE4 narrowed to 4.5-10.5 mm in the uppermost stations UE5 and UE6. Particularly, the size range in males at UE5 and UE6 was restricted to smaller size classes, 5.5-8.5 mm in carapace length. Generally, the percentage of females was higher than that of males in the upper estuary.

In KH *C. crangon* males were not found at any time of the sampling period. All the very few females found there were berried females.

The changing population structure of *P. montagui* for two years are illustrated in Figures 4.13 and 4.14 respectively. The abundance of juveniles of *P. montagui* was almost negligible accounting for only 6 specimens during the entire period of investigation. Berried females occurred only in December and January and ranged from 10.5-17.5 mm in carapace length. Transitionary males appeared in the samples in April and July but were less common in June. The size range of transitionals varied between 8.5-12.5 mm. In 1992, no transitional males were observed in the samples taken in June, but they were present in the samples of June in 1993. Transitional males disappeared from the population by October. The size range of females varied from 3.5-17.5 mm in carapace length while in males it varied from 3.5-13.5 mm. The *P. montagui* population in July 1992 separates to two clear cohorts which were however, not evident in any month of the following year. *P. montagui* population structure shows no marked difference either between high and low water or between the two stations it occurred.

The population of *P. montagui* at KH (Fig. 4.15) comprised males of a narrow size range (8.5-10.5 mm) while females ranged from 8.5-15.5 mm in carapace length. In April, all the males were in transitional stages. Berried females were observed in all the samples except those collected in June. All the females were in berry in January and ranged from 8.5-15.5 mm in carapace length while berried females of April comprised 50% of the female population with the same size range. The population was almost absent at KH in

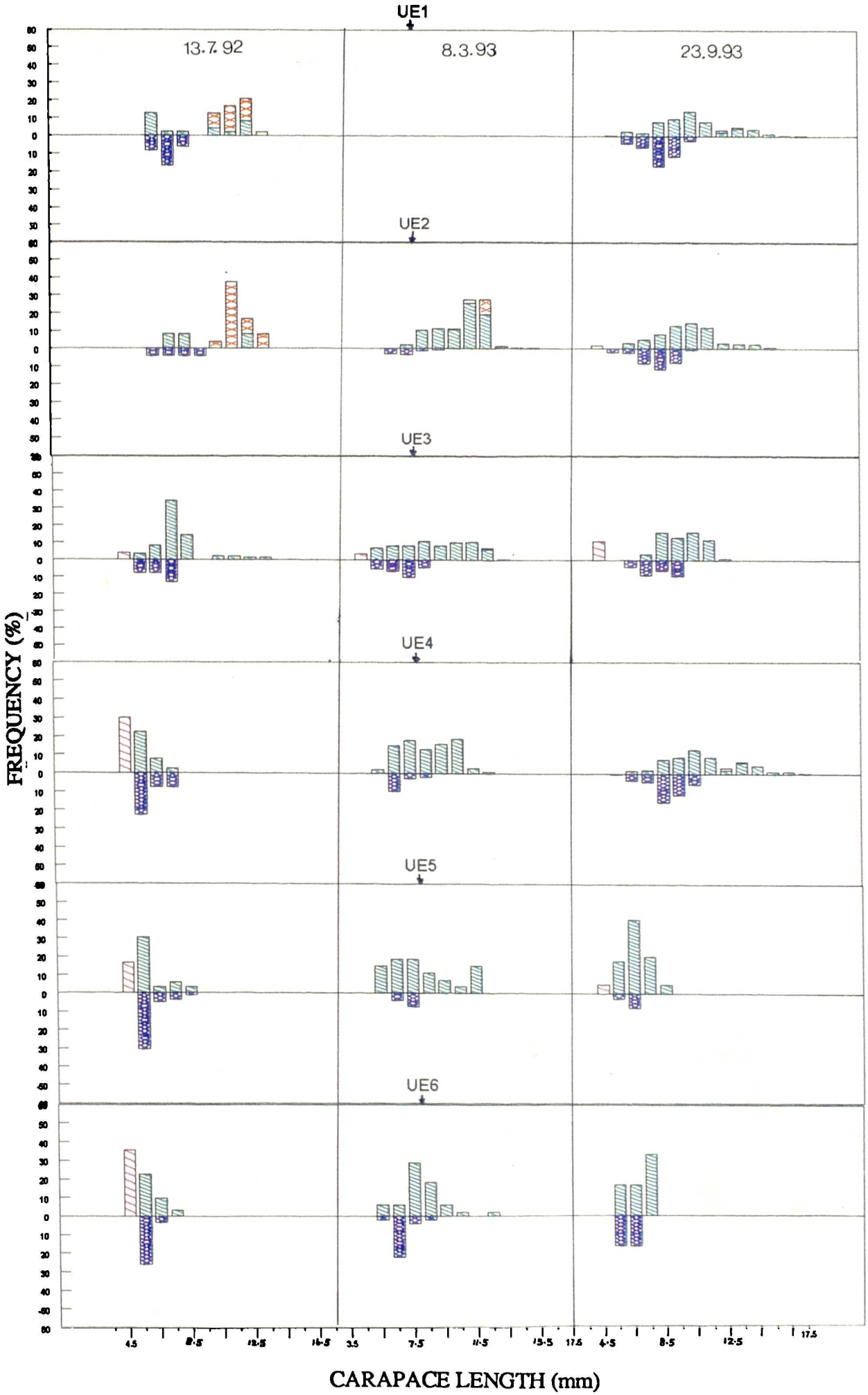


Fig. 4.12- Spatial variations in the population structure (%) of *C. crangon* in the upper Forth Estuary at three sampling occasions.

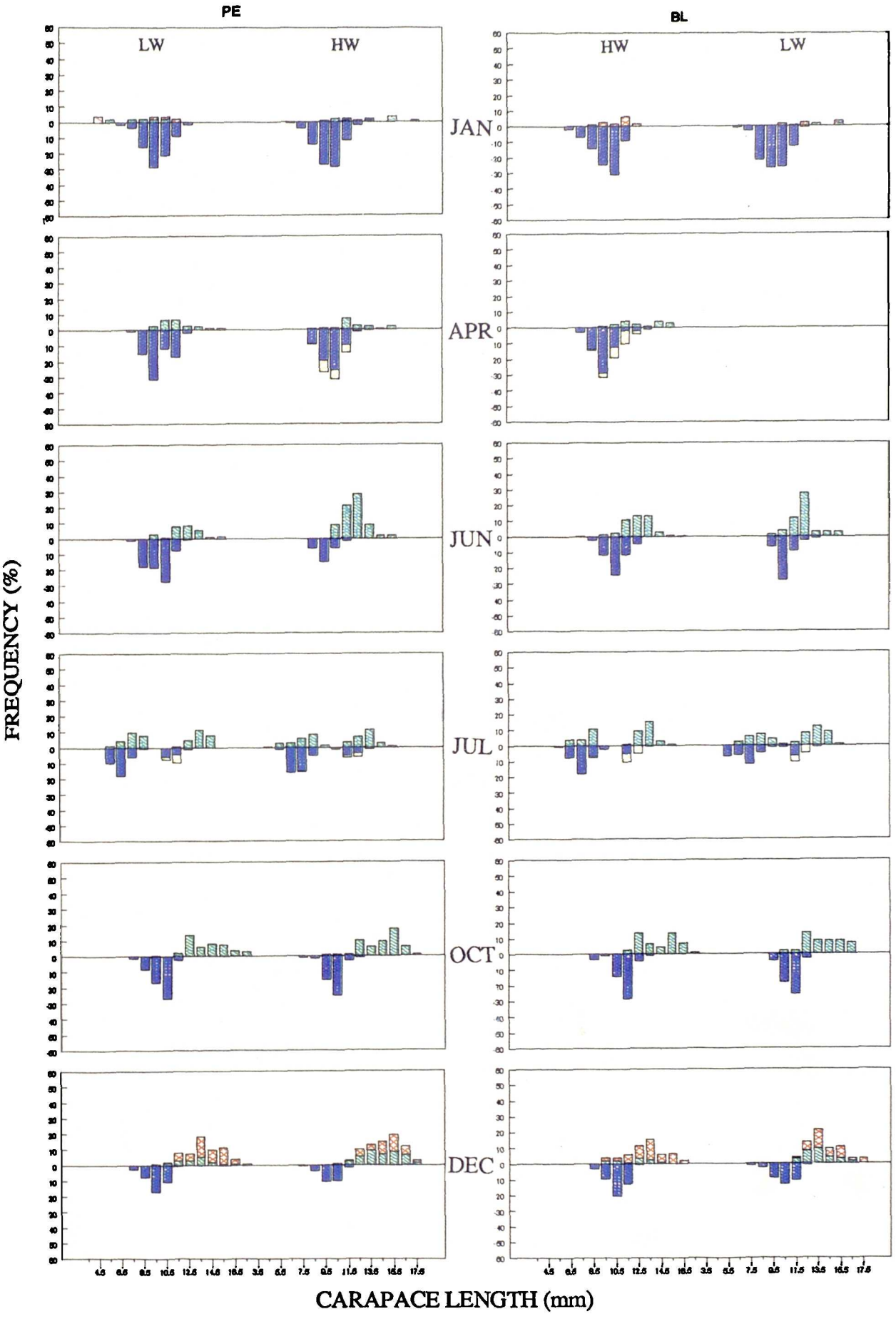


Fig.4.13 Temporal and spatial variations in the population structure (%) of *P. montagui* at Port Edgar and Blackness at high water and low water in the Forth Estuary in 1992.

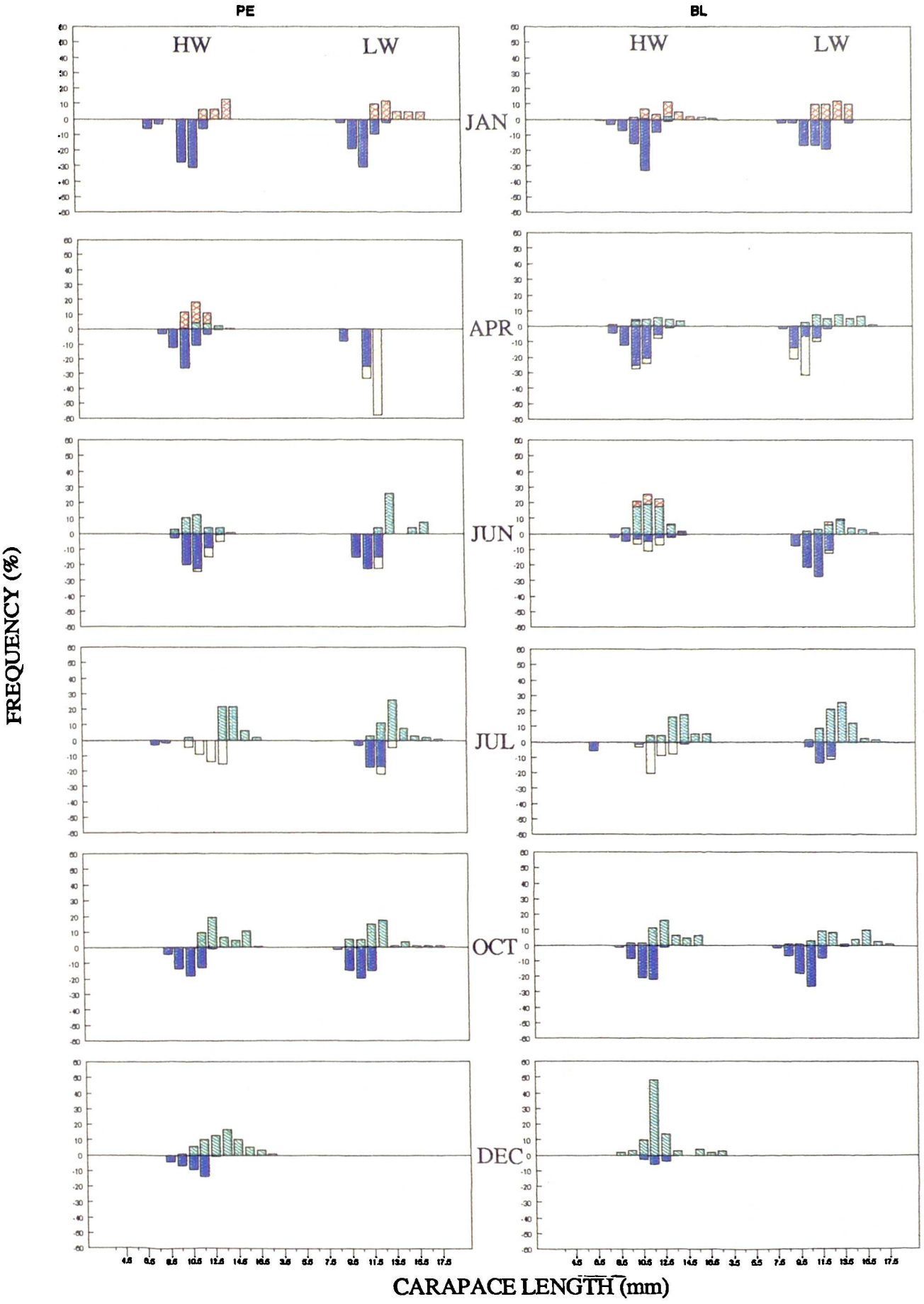


Fig.4.14 Temporal and spatial variations in population structure(%) of *P. montagui* at Port Edgar and Blackness at high water and low water in the Forth Estuary in 1993.

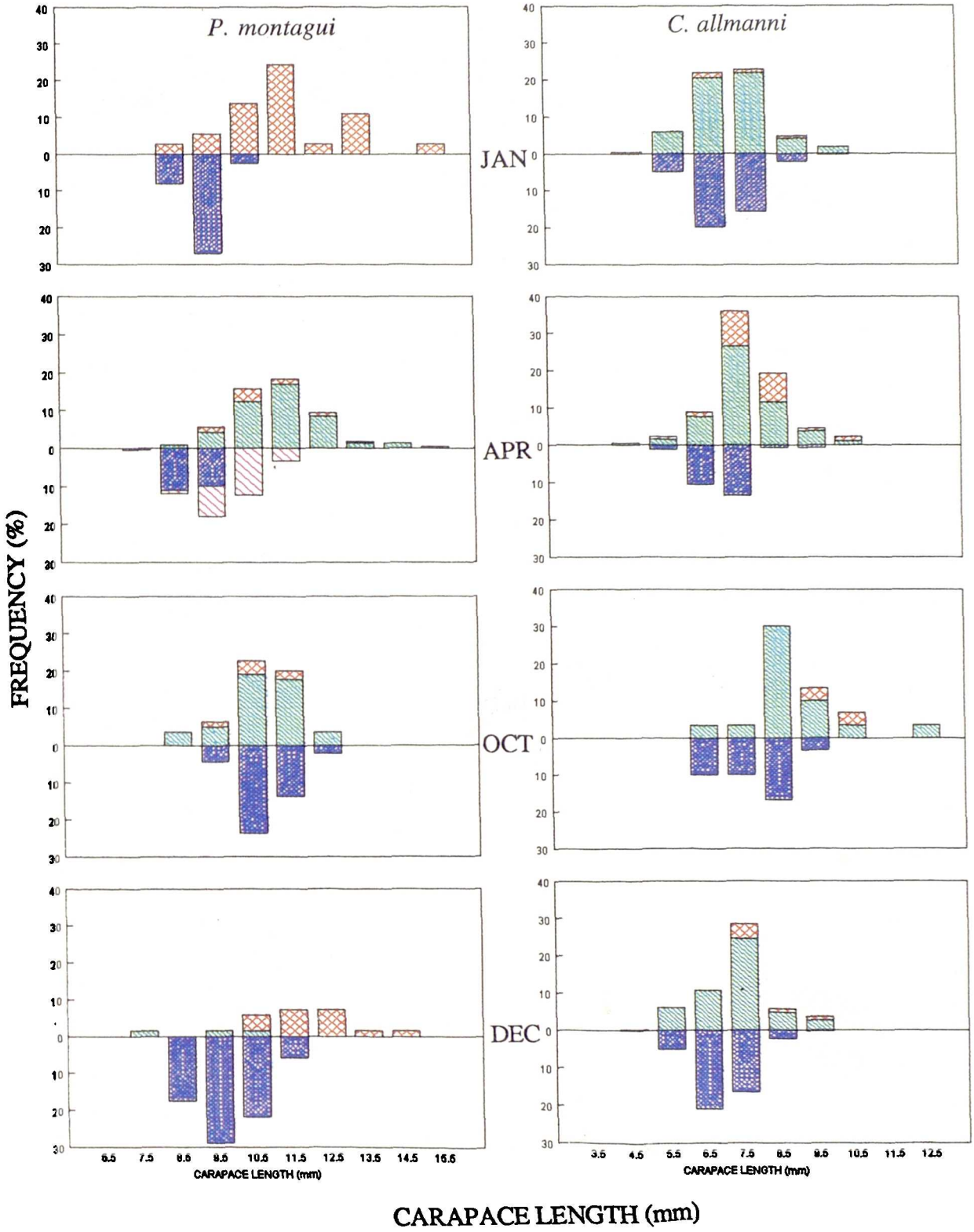


Fig.4.15 Temporal variations in the population structure of *P. montagui* and *C. allmanni* at Kingstone Hudds.

June with only two males present, but appeared again in samples in December. Smaller proportion of females were found in berry in December.

C. allmanni appeared in the estuary in October in both 1992 and 1993 (Fig.4.16 and Fig.4.17). Besides the few adult females present in October, the population clearly display one cohort which is apparently the '0'group. This is apparent from the narrow size range which included seven size classes at maximum and mostly comprised three size classes throughout the period of study. The males present in the estuary ranged from 3.5-11.5 mm in carapace length while in females it varied from 3.5-13.5 mm. Berried females were found in the catches in December and January in the size range of 8.5-13.5 mm in carapace length.

C. allmanni population in KH varied from 4.5-9.5 mm in carapace length in males and 4.5-12.5 mm in females. Berried females were found in January, April and December with a highest percentage in April. Berried females were found in the range of 5.5-10.5 mm. *C. allmanni* population was also absent in KH in June.

4.1.3.4 Mean body size

The temporal and spatial variations in the mean carapace length of male and female *C. crangon* at HW and LW are shown in Fig.4.18 and Fig.4.19 respectively. A slight decrease in the mean body size is observed at LW in the winter period in males of all stations and females at Port Edgar in 1992 but this is not marked in 1993 (Fig.4.18). A marked decrease occur in July in both years, at LW in both sexes. The differences between HW and LW, as tested by analysis of variance (oneway), were significant in July, October and December (Table 4.4). These differences seem due either to increase of mean body size of the population by immigration of large animals to the station in concern, or decrease of mean body size due to addition of new recruits to the station or emigration of large shrimps from the station. The pattern of size variation is evident showing a size decrease or increase towards the same direction in most or all the stations as indicated by the arrows in Table 4.4. In July the differences between HW and LW is due to the presence of more smaller animals at high water while in October it is due to the presence of bigger animals at high water. In December the arrows indicate the

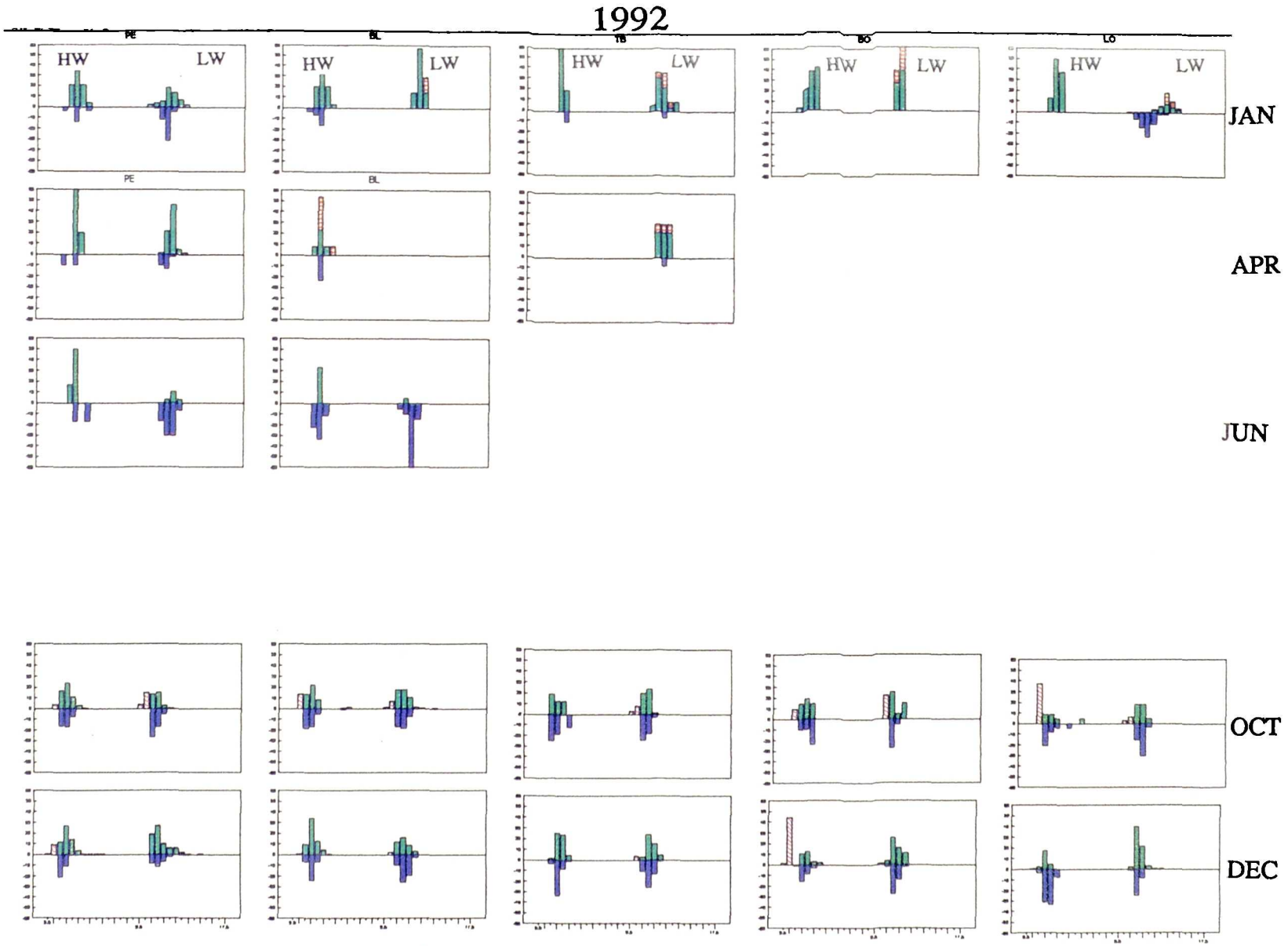


Fig.4.16 Temporal and spatial variations in population structure(%) of *C. allmanni* at five stations at high water and low water in the Forth Estuary in 1992.

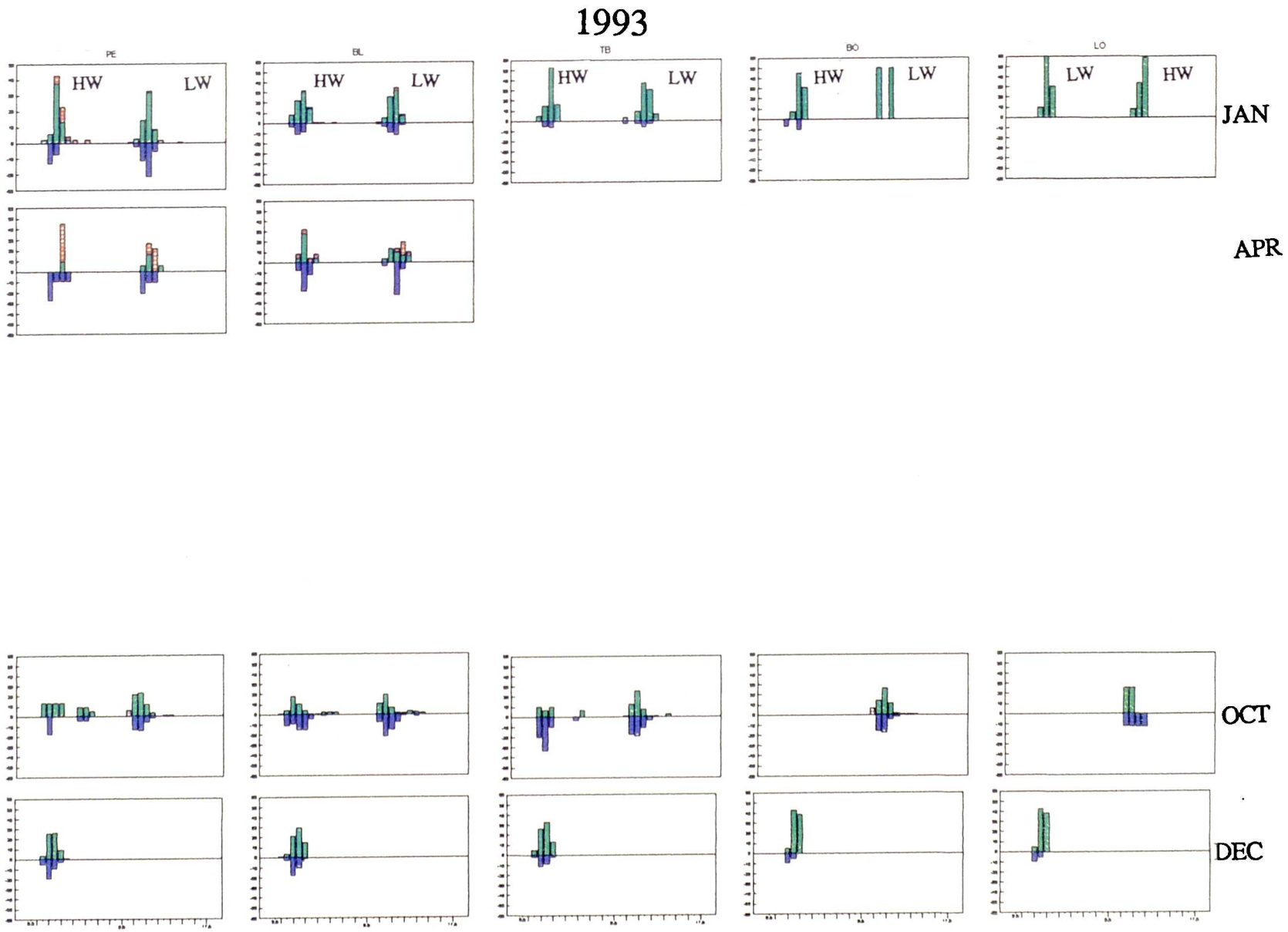


Fig.4.17 Temporal and spatial variations in population structure(%) of *C. allmanni* at five stations at high water and low water in the Forth Estuary in 1993.

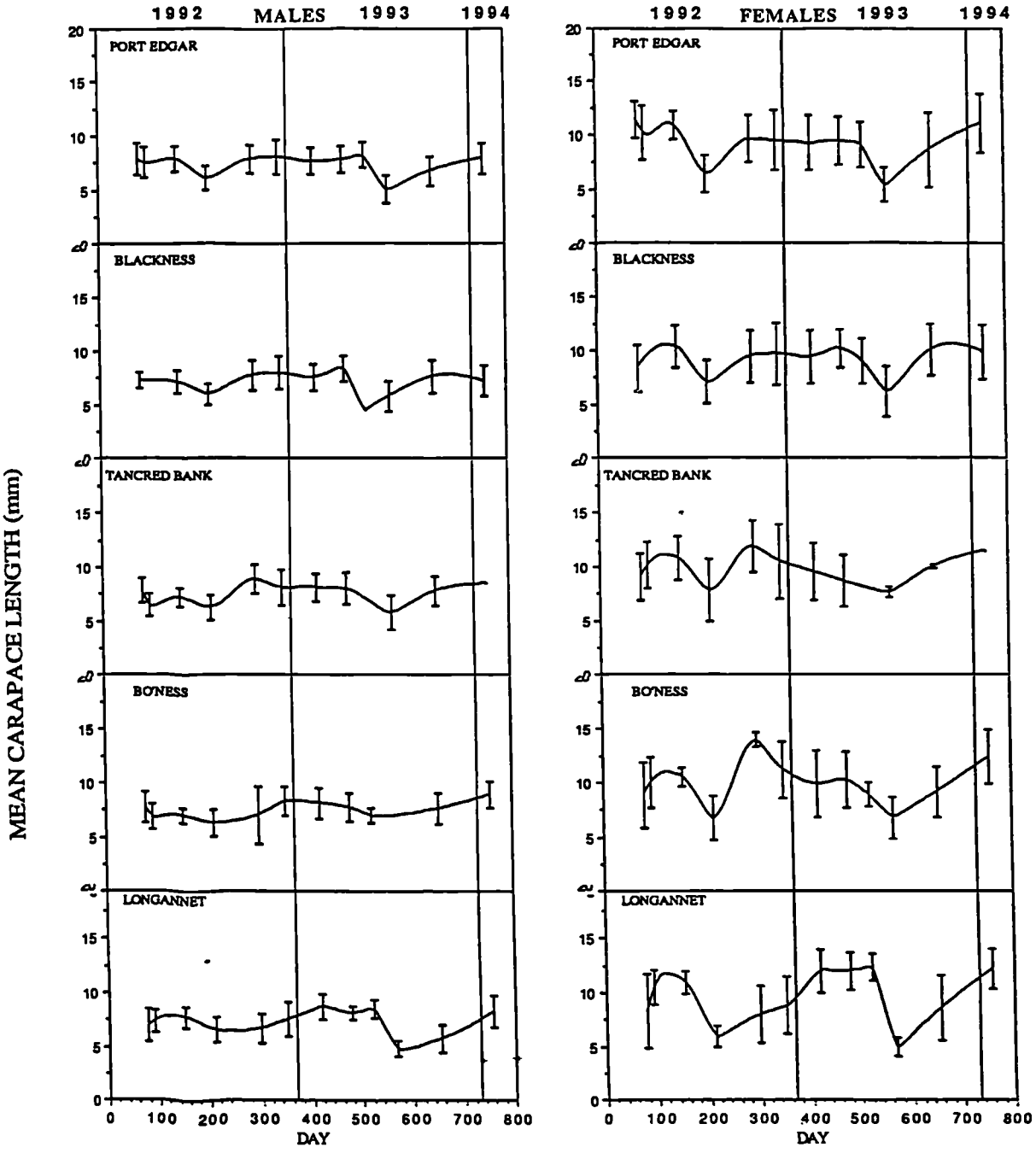


Fig. 4.18- Temporal and spatial variations in the mean carapace length ±S.E. (mm) of male and female *C. crangon* at five stations at high water in the Forth Estuary.

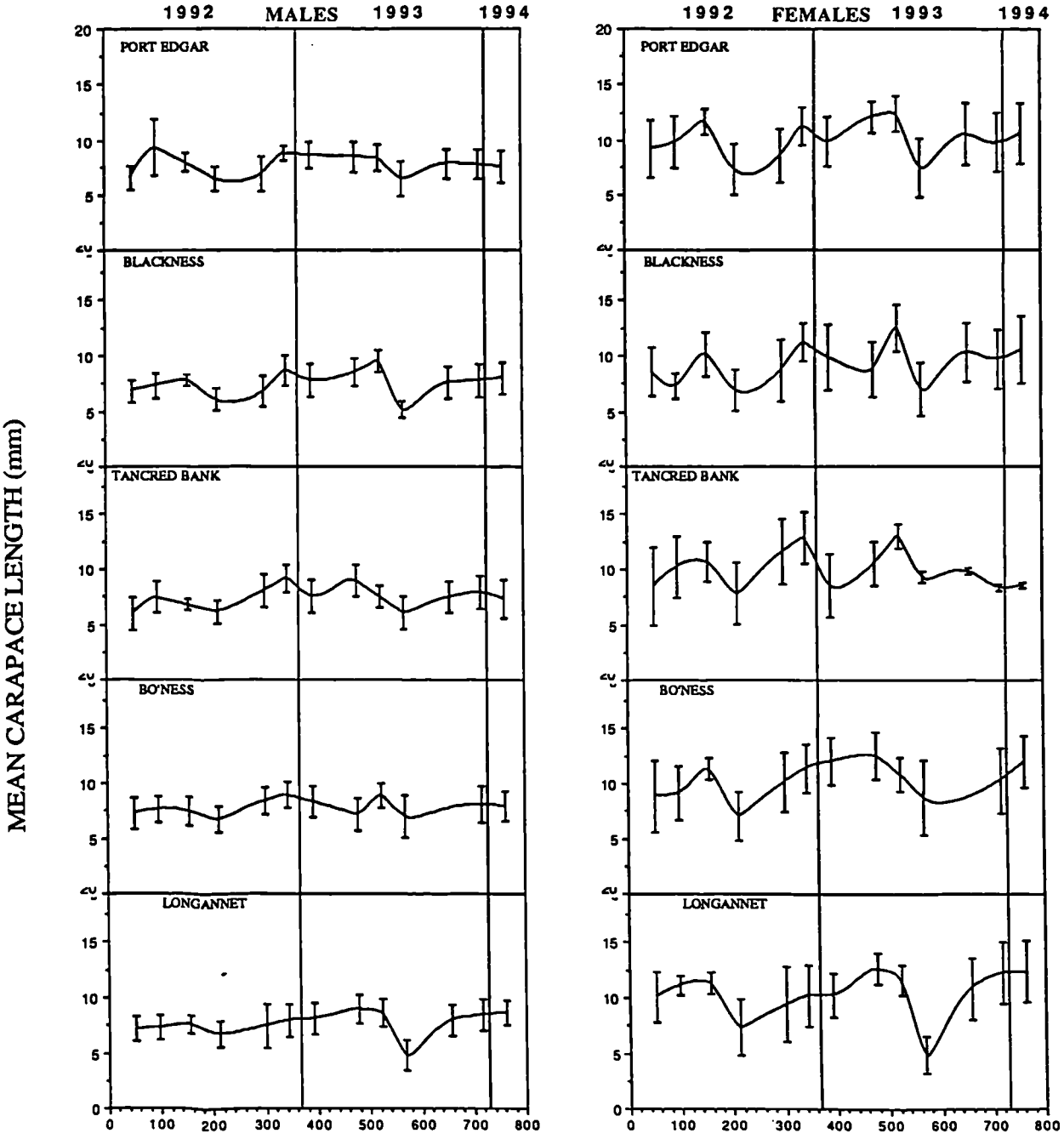


Fig. 4.19- Temporal and spatial variations in the mean carapace length ±S.E. (mm) of male and female *C. crangon* at five stations at low water in the Forth Estuary.

presence of larger animals at low water. A proportion of *C. crangon* population still stay in the uppermost stations. The differences are not significant in 1993 although lowermost stations and uppermost stations exhibit the similar trend with time. The differences in the mean carapace length is significantly different among the stations ($p<0.01$).

Mean carapace length of *P. montagui* shows a marked decrease in July in 1992 and October in 1993 (Fig.4.20). The difference between stations was not significant from April to June but significant onwards from July (Table 4.5). Again the same directional significance was found in July for males and December in both sexes indicating smaller sizes at low water in July and larger sizes in December. The direction however, varied between sexes in October showing larger males and smaller females at HW.

In *C. allmanni* an increasing trend in the mean carapace length was observed from October to April (Fig.4.20 and Fig.4.21). It is evident from the mean carapace length that a new cohort appears in the estuary each year in October. Significant difference in mean carapace length was observed only in October between HW and LW (Table 4.6).

Table 4.4 Test of significance for the mean carapace length(mm) of *C. crangon* populations between HW and LW at different sampling dates. → indicates large sizes at high water, ← indicates large sizes at low water. p = Level of significance, - indicates void trawls or inadequate numbers for test.

Month	Port Edgar		Blackness		Tancred Bank		Bo'ness		Longannet	
	M	F	M	F	M	F	M	F	M	F
January	$p<\vec{0}.001$	$p<\vec{0}.001$	$p<\vec{0}.01$	n.s.	$p<\vec{0}.001$	n.s.	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.01$
April	$p<\overleftarrow{0}.001$	n.s.	void	n.s.	$<0.\overleftarrow{001}$	n.s.	$p<\overleftarrow{0}.05$	n.s.	n.s.	$p<\overleftarrow{0}.01$
June	n.s.	n.s.	n.s.	$p<\vec{0}.05$	n.s.	n.s.	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.01$
July	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	n.s.	$p<\overleftarrow{0}.001$	n.s.	n.s.	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.01$	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$
October	$p<\vec{0}.001$	$p<\vec{0}.001$	$p<\vec{0}.001$	$p<\overleftarrow{0}.001$	$p<\vec{0}.001$	n.s.	$p<\overleftarrow{0}.01$	$p<\vec{0}.05$	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$
December	$p<\overleftarrow{0}.05$	$p<\overleftarrow{0}.05$	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	n.s.	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$
January	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.001$	$p<\vec{0}.01$	$p<\vec{0}.001$
April	n.s.	$p<\overleftarrow{0}.05$	n.s.	n.s.	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.05$	n.s.	n.s.
June	n.s.	n.s.	-	n.s.	-	-	$p<\overleftarrow{0}.05$	-	$\overleftarrow{n.s.}$	$p<\overleftarrow{0}.05$
July	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.05$	-	n.s	n.s.	n.s.
October	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	n.s.	n.s.	$p<\vec{0}.05$	n.s.	-	-	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.05$
December	n.s.	n.s.	$p<\overleftarrow{0}.05$	n.s.	-	n.s.	$p<\vec{0}.001$	n.s.	n.s.	n.s.

Table 4.5 Test of significance (one-way ANOVA) for the mean carapace length(mm) of *P. montagui* populations between HW and LW at different sampling dates. → indicates large sizes at high water, ← indicates large sizes at low water.

Month	Port Edgar		Blackness	
	Males	Females	Males	Females
January	n.s.	→ p<0.001	n.s.	→ p<0.001
April	void	void	void	void
June	n.s.	n.s.	n.s.	n.s.
July	→ p<0.001	n.s.	→ p<0.01	n.s.
October	→ p<0.001	n.s.	→ p<0.01	← p<0.05
December	← p<0.05	← p<0.001	← p<0.05	← p<0.05
January	n.s.	n.s.	n.s.	n.s.
April	→ p<0.001	n.s.	→ p<0.001	→ p<0.05
June	n.s.	→ p<0.001	n.s.	→ p<0.001
July	n.s.	← p<0.05	n.s.	← p<0.001
October	n.s.	← p<0.001	n.s.	n.s.
December	→ p<0.01	n.s.	→ p<0.05	n.s.

Table 4.6 Test of significance (one-way ANOVA) for the mean carapace length(mm) of *C. allmanni* populations between HW and LW at different sampling dates. $\rightarrow$ indicates large sizes at high water, $\leftarrow$ indicates large sizes at low water. p = level of significance and - indicates void trawls and absence of *C. allmanni*.

Month	Port Edgar		Blackness		Tancred Bank		Bo'ness		Longannet	
	M	F	M	F	M	F	M	F	M	F
January	n.s.	n.s.	-	-	$p<\vec{0}.001$	-	n.s.	-	$p<\vec{0}.001$	$p<\vec{0}.001$
April	$p<\overleftarrow{0}.05$	n.s.	void	void	-	-	-	-	-	-
June	$p<\overleftarrow{0}.05$	n.s.	n.s.	n.s.	-	-	-	-	-	-
July	-	-	n.s.	-	-	-	-	-	-	-
October	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	n.s.	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.01$	n.s.	$p<\overleftarrow{0}.001$	n.s.
December	n.s.	$p<\overleftarrow{0}.001$	n.s.	n.s.	n.s.	n.s.	$p<\overleftarrow{0}.001$	n.s.	n.s.	n.s.
January	$p<\overleftarrow{0}.001$	n.s.	n.s.	n.s.	$p<\vec{0}.01$	n.s.	n.s.	$p<\overleftarrow{0}.001$	-	-
April	n.s.	n.s.	n.s.	n.s.	-	-	n.s.	-	-	-
June	-	-	-	-	-	-	-	-	-	-
July	-	-	-	-	-	-	-	-	-	-
October	$p<\overleftarrow{0}.001$	$p<\overleftarrow{0}.001$	n.s.	n.s.	$p<\overleftarrow{0}.05$	n.s.	-	-	-	-
December	n.s.	n.s.	n.s.	n.s.	n.s.	-	$p<\overleftarrow{0}.001$	n.s.	n.s.	n.s.

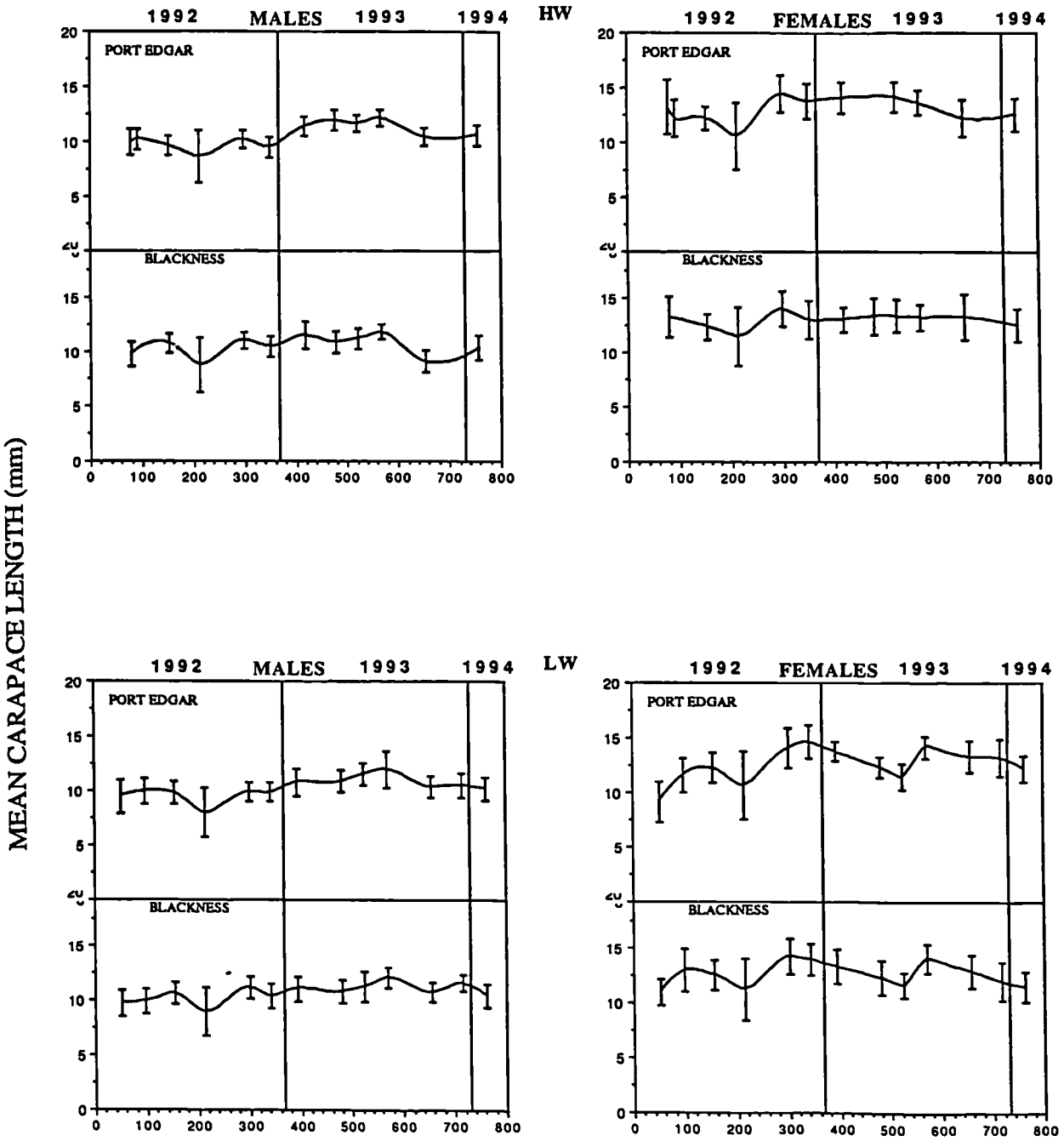


Fig. 4.20- Temporal and spatial variations in the mean carapace length ±S.E. (mm) of male and female *P. montagui* at Port Edgar and Blackness at high water and low water in the Forth Estuary.

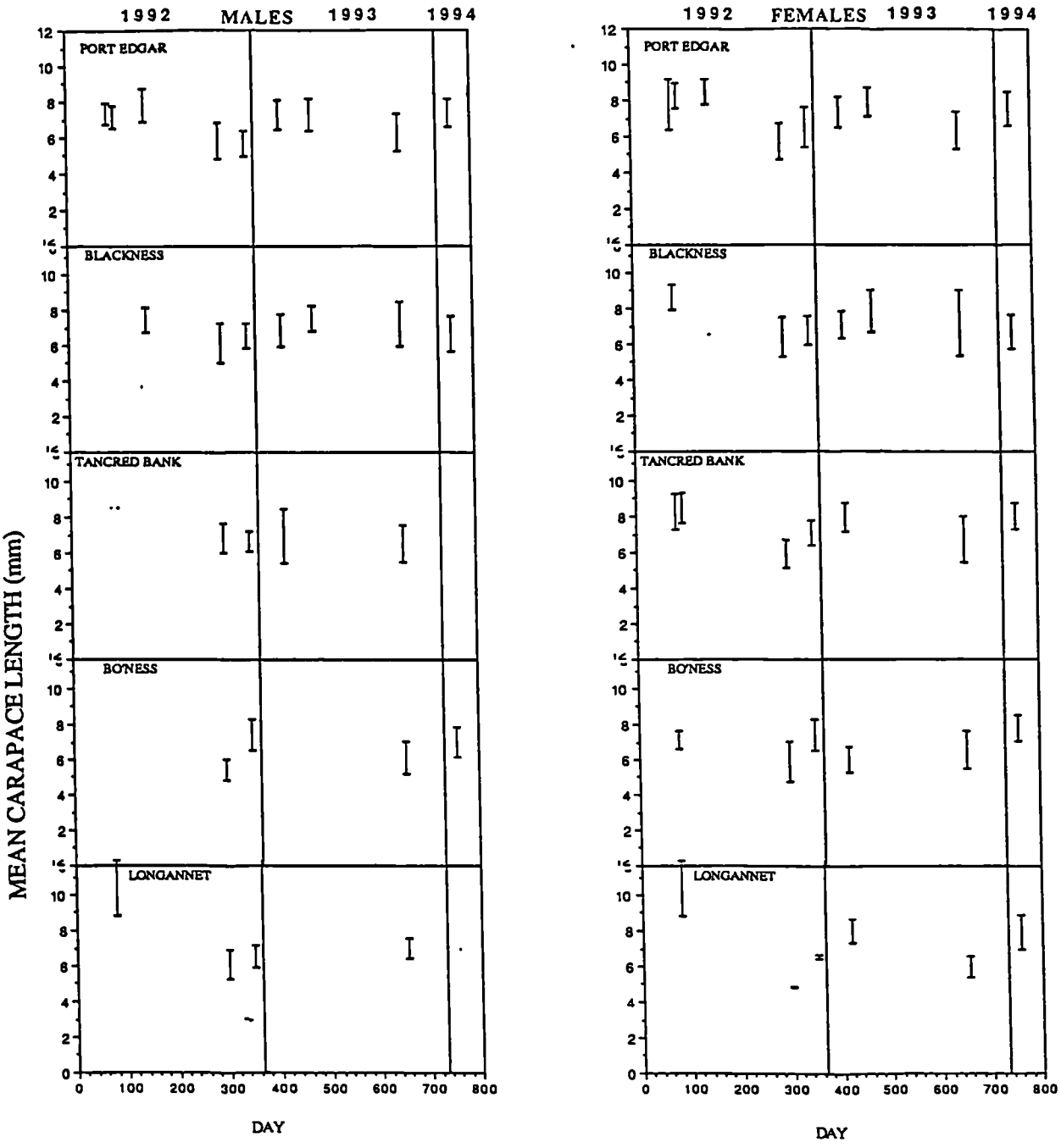


Fig. 4.21- Temporal and spatial variations in the mean carapace length ±S.E. (mm) of male and female *C. allmanni* at five stations at high water in the Forth Estuary.

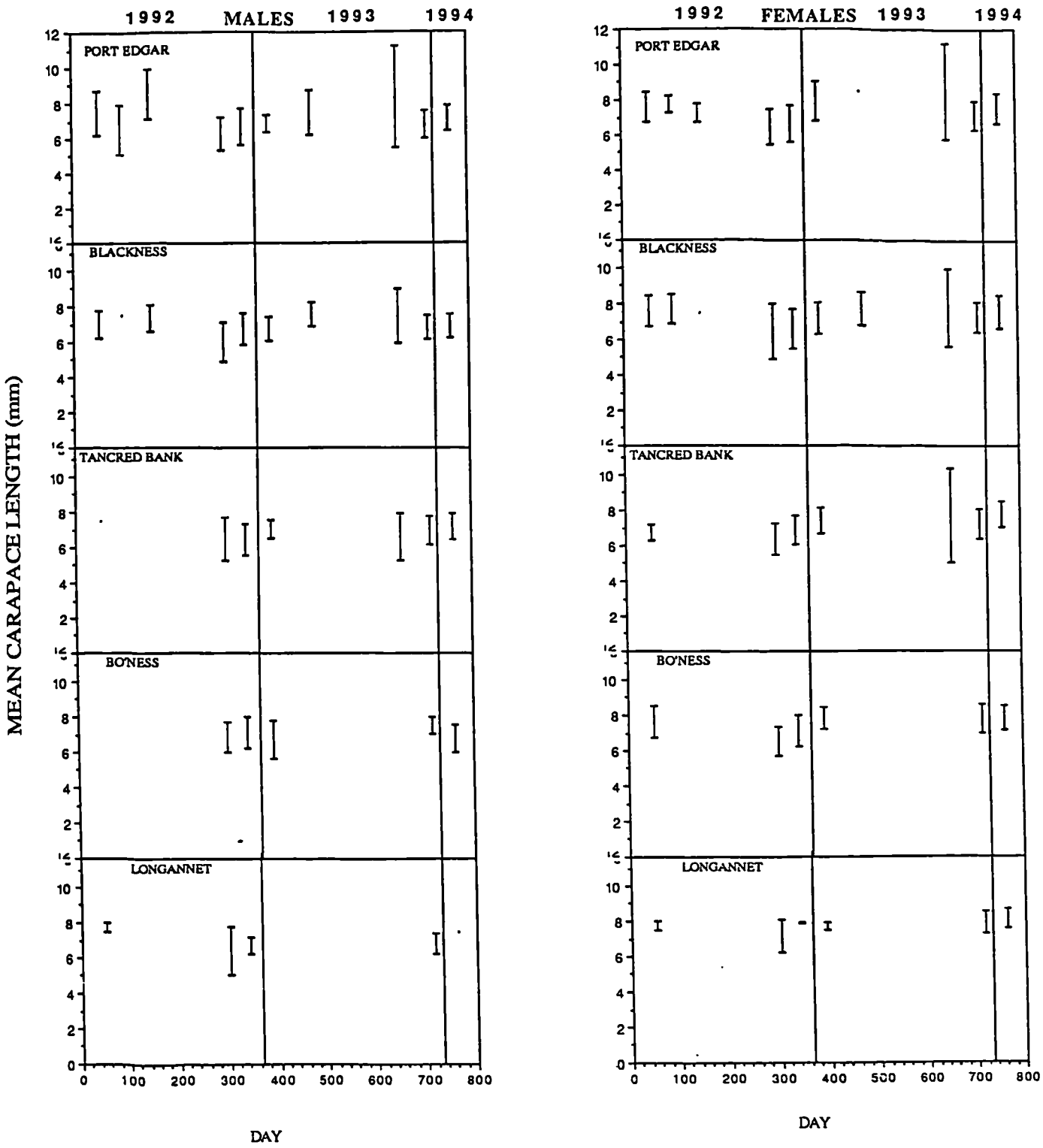


Fig.4.22 Temporal and spatial variations in the mean carapace length±S.E (mm) of male and female *C. allmanni* at five stations at low water in the Forth Estuary.

4.1.4 Discussion

Shrimps of the estuary and Firth of Forth are represented by eight species of which three were considered as important due to their relatively high abundance. It is evident that *C. crangon* inhabit the estuary all year round in varying abundance. *P. montagui* was also found in the estuary throughout the year but confined to the lowermost area. From October onwards the shrimp population is augmented by arrival of another 'periodic' species, *C. allmanni* which inhabit the estuary in autumn and winter and leave the estuary by late spring or early summer. Hunter (1981) also observed the same continuous occurrence in *C. crangon* and *P. montagui* in the Forth Estuary, but did not recognize *C. allmanni* as a different species. *C. crangon* is generally considered as a common and dominant species in Britain, and has been reported to occur in the Bristol Channel and Severn Estuary (Lloyd and Yonge, 1947; Henderson and Holmes, 1987), Solway Firth (Abbot and Perkins, 1977), Forth Estuary (Hunter, 1981), and all the estuaries and coastal areas around England (Henderson *et al.*, 1990). *P. montagui* has been recorded as one of the more common species which inhabits south east coasts of England (Mistakidis, 1957) and sublittoral areas off Nothumberland waters (Allen, 1963). Allen (1960) is the only one who has studied the biology of *C. allmanni*, and made similar observations as reported in the present study with regard to occurrence of the population in Northumberland waters and has suggested migration offshore as the possible explanation for disappearance of *C. allmanni* by early summer.

4.1.4.1 *C. crangon*

C. crangon is undoubtedly the main shrimp species in the estuary and is the most tolerant shrimp with a wide range of distribution and highest abundance thus dominating the shrimp population in the estuary. It is widely accepted as a ubiquitous member of the large mobile epibenthic fauna in the North European beaches (Pihl and Rosenberg, 1982; Evans and Tallmark, 1985; Jensen and Jensen, 1985; Pihl, 1985; Gee, 1987; Van der Veer and Bergman, 1987; Raffaelli, *et al.*, 1989). In the Forth Estuary, they were found to be distributed in all the stations in the lower estuary and in six stations in the upper estuary. Very low abundance of *C. crangon* at KH and absence of components other than females with eggs ready to hatch there, suggests that the Firth of Forth is not a regular area of inhabitance for *C. crangon*. Further, the presence of *C. crangon* at Bo'ness during the

winter suggests that *C. crangon* can dwell in the estuary even at cold environment. Moreover, they were found in the upper estuary up to UE6 (Longareach) in all three sampling occasions. Therefore, the range of distribution of *C. crangon* can be distinguished as from KH to Longareach.

The presence of berried females in higher proportions in the uppermost stations in the lower estuary and at UE1 and UE2 of the upper estuary suggests that *C. crangon* prefers the upper reaches of the estuary for egg development. Berried females were present in UE1 and UE2 on 13.7.92 but were absent even at Longannet by end of July. This is an indication of migration of berried females down the estuary, and may take place somewhere between the middle and end of July. Higher abundance of *C. crangon* in July denotes the arrival of new recruits to the population. The arrival commences in April, reaching a peak in July. Janssen and Kuipers (1980) and Kuipers and Dapper (1981) also showed that juveniles leave the tidal flat nursery areas and invade the sub-tidal area at a length of 30-35 mm in TL (i.e. 3.5-4.0 mm CL) and significant number of juveniles reach the sub-tidal stage in the beginning of July. In the present study this invasion is clearly indicated in the population in July and in agreement with Janssen and Kuipers (1980) and Kuipers and Dapper (1981). As indicated by the changes in mean carapace length between HW and LW, the whole population shows a beginning of down estuarine movement in October, which is completed in December. In Solway Firth (Abbot and Perkins, 1977) seaward migration occurred between October/November to March and shrimps migrated 40-45 km from the inner Solway to the Firth. Hunter (1981) also observed the same phenomenon in *C. crangon* in the Forth Estuary which took place in late September to October. Henderson and Holmes (1987) has made observations similar to the present study and suggested that the population in Bristol Channel and Severn Estuary is a unified population which migrates up and downstream with the season. The distribution of *C. crangon* in the Forth Estuary also exhibits the behaviour of a single population. The few animals at KH with all the size ranges, sexes and different components of the population within the estuary indicates that the migration of the population to sea is unlikely and is in disagreement with Ehrenbaum (1890), Havinga (1930), and Lloyd and Yonge (1947) who observed migration of *C. crangon* from the coastal zone to open sea in autumn and back in spring. In the Forth Estuary population,

migration of *C. crangon* down the estuary however, is evident in autumn/ winter season but there is no evidence that they leave the estuary in any large numbers and presumably few, if any, move as far as North Sea. Seasonal inshore and offshore migrations of *C. crangon*, reportedly in relation to salinity, temperature and availability of food (Ehrenbaum, 1890; Havinga, 1929, 1930; Meyer, 1935; Broekema, 1941; Lloyd and Yonge, 1947; Allen, 1966; Tiews, 1970) and in relation to reproductive behaviour (Boddeke, 1975) have been observed. Hartsuyker (1966) reported up- and downshore migrations on each tidal rise and fall in the Wadden Sea.

The mean annual abundance of *C. crangon* in the Forth Estuary varied between 1.33±2.050 ind. m^{-2} and 0.336±0.427 ind. m^{-2} at HW in 1992 and 1993 respectively, while at LW it varied between 2.203±3.900 ind. m^{-2} and 0.358±0.228 ind. m^{-2}, compared to the 30-40 ind. m^{-2} (Muus, 1967) in Niva Bay, 60-70 ind. m^{-2} (Van Lissa, 1977) in Dutch Wadden Sea, 24-37 (Evans and Tallmark (1979) in a Bay in Gullmarsfjord and 55-90 ind. m^{-2} in coastal marine waters in Sweden (Pihl and Rosenberg, 1982). It should be noted however, that these authors have reported the abundance in intertidal or shallow areas and are concerned with the juvenile population whereas the present results are based on a subtidal area and on adult populations which may be the reason for lower abundance observed. The mean annual abundance of *C. crangon* calculated using data provided in Abbott and Perkins (1977) in the Solway Firth (0.526 ind. m^{-2}) and in Hunter (1981) in the Forth Estuary (0.408 ind. m^{-2}) are close to the value of mean annual abundance of 1992 in the present study, once the numbers reported were corrected for the gear efficiency. Yearly changes in *C. crangon* abundance as seen in the present study have been also observed (Henderson and Holmes, 1989) in the Bristol Channel and the Severn Estuary. Driver (1976) relate the fluctuations in yearly landings to previous year's landings and weather conditions and states that the *C. crangon* population is a naturally fluctuating stock. According to his observations landings of shrimps correlated positively with rainfall and negatively with average air temperature, both of the previous year. In the present study the abundance of *C. crangon* is found to be significantly influenced by the water temperature (C^{o}) fluctuations in the same year, increasing with the increasing temperature.

The results suggests that the *C. crangon* population in the Forth Estuary is a unified population. The differential distribution of *C. crangon* is strongly evident from the present study, which shows that juveniles are confined to upper estuary and uppermost stations of the middle estuary, with breeding females either in uppermost or lowermost areas depending on the season. The population structure however, remains more or less the same for the whole population and follows similar trends in abundance and structure. This suggests that the population in the estuary is a single population which is differentially distributed throughout the estuary. Henderson and Holmes (1987) have found that the *C. crangon* population in the Bristol Channel and Severn estuary is likewise a unified population. Henderson *et al.*, (1990) have identified six distinct populations from the coastal waters of England and stated that each water mass in the European coastal areas hold a distinct population of *C. crangon.* As suggested by the results of the present study and previous research it is justifiable to consider the population in the Forth Estuary as a single population.

4.1.4.2 *P. montagui*

P. montagui is confined to the two lowermost stations of the estuary and to Kingstone Hudds. The down estuary limit of the distribution of *P. montagui* is uncertain due to the inadequate sampling carried out in the Firth of Forth but the upward limit can be distinguished as Blackness. This is in agreement with the findings of the Bedford (1978) and Hunter (1981) who observed the population of *P. montagui* in PE and BL. Hunter (1981) attributed the occurrence of *P. montagui* in this area to greater depth and the nature of the substratum, since *P. montagui* is known to prefer firm substratum (Mistakidis, 1957). The substratum of the lower part of the estuary is stony with broken shell fragments, and may provide ideal conditions for *P. montagui*.

The population of *P. montagui* in the two lowermost areas of the estuary was found there all year round. The female population at KH in January were represented only by berried females while the population in the estuary comprised a minor proportion of berried females. Disappearance of berried females from the estuary samples by April and the presence of berried females at KH in April support the findings of Mistakidis (1957) and Allen (1963) who observed the migration of females for spawning on the east coast of

England and Northumberland waters respectively. It is therefore, evident that the migratory component of *P. montagui* is mostly breeding females which are leaving the estuary for their spawning grounds. Although there was evidence of migration towards the sea by autumn they never disappeared completely from the estuary. The mass migration of *P. montagui* to the sea in autumn as recorded by Mistakidis (1957) was not observed in the present study. The results of the present study agrees better with Allen (1963) who observed an offshore migration of a large proportion of the population after their first breeding season in Northumberland waters. There is no evidence of later return of these shrimps. Size and sex composition of the population changed in January when few of the large groups were represented among the remaining inshore populations and the latter was predominantly males and young shrimps.

Males of *P. montagui* were smaller than females and rarely exceeded 12.5 mm in carapace length. It is evident that transition of males into females after mating remove the large animals from the male population. As shown in the present study the transition takes place during the period from April to June and is almost completed by end of July. The duration of transition found in the present study is in accordance with those reported by the previous researchers (Mistakidis, 1957; Allen, 1963; Simpson *et al.*, 1970 ; Hunter, 1981).

The mean annual abundance of *P. montagui* in the estuary (in the area between Blackness and Port Edgar) varied between 0.557±0.438 ind. m^{-2} at HW and 0.680±0.672 ind. m^{-2} at LW in 1992 and 0.257±0.283 ind. m^{-2} at HW and 0.257±0.106 ind. m^{-2} at LW in 1993. Similar abundances in HW and LW indicates that the population is resident in the Blackness and Port Edgar area. *P. montagui* did not show a strong correlation with any of the environmental parameters ($p>0.05$).

The population of *P. montagui* which occurs in the estuary also indicates a unified population, although the female part of the population is not present in the estuary during the breeding season. Hunter (1981) has reported a decrease in mean carapace length of the population in August and September due to invasion of recently metamorphosed juveniles of 5.0-9.0 mm in carapace length. Lack of samples from these months might

be the reason for the small numbers of juveniles observed in the present study. Sizes below 5.0 mm carapace length were not observed in the estuary at any time and indicates the existence of a nursery area elsewhere presumably in the Firth of Forth or North Sea.

4.1.4.3 *C. allmanni*

C. allmanni exhibits the behaviour of a true migrant species, entering the estuary in October and Leaving the estuary by April/June. The down estuary limit of *C. allmanni* is uncertain due to inadequate sampling in the Firth of Forth, but when they are present in the estuary their range of distribution extends up to Longannet. The absence of *C. allmanni* in the estuary during part of the year indicates that it is not a resident species in the estuary. Two age groups were observed only in October and in females, but disappeared by December. Both male and female groups present in the estuary exhibited clear growth uninterrupted by mixed cohorts as in *C. crangon* which indicates that *C. allmanni* present in the estuary are undoubtedly belongs to one year class. The absence of *C. allmanni* during April to May inshore which persisted throughout the summer and autumn was also observed by Allen (1960) in Northumberland waters.

C. allmanni also exhibited the same migratory behaviour as in *P. montagui*, berried females migrating seawards in January/April period. April samples from KH comprised a large proportion of berried females while the shrimps were present in very small numbers in the estuary. It is apparent that the population which visit the estuary in the following year are new recruits. Small number of females of previous year class returns to the estuary briefly in October and disappear. Lack of year II males may suggest the possibility of transition in *C. allmanni* males as in its close relative *C. crangon.*

Mean annual abundance of *C. allmanni* in 1992 and 1993 at HW, varied between 0.303±0.417 ind. m^{-2} and 0.266±0.268 ind. m^{-2}, while at LW it varied between 0.139±0.191 ind. m^{-2} and 0.114±0.768 ind. m^{-2}. High abundance observed at HW indicates that *C. allmanni* is a migrant species that moves into the estuary with HW. *C. allmanni* found to be influenced by the depth to a greater extent ($p<0.01$) and to a lesser extent by tidal amplitude ($0.05<p<0.1$).

4.1.5 Conclusion

In the present study, the abundance of *C. crangon* was found to be influenced by the water temperature and could be regarded as a good predictor for relative abundance. *P. montagui* and *C. allmanni* however, did not show any influence by the temperature. The reason perhaps is osmoregulation which has been shown to be influenced by the temperature (Broekema, 1941). According to his findings *C. crangon* requires low salinity when temperature is high for osmoregulation and high salinity when the temperature is low. This is a likely explanation for *C. crangon* because it is the only species which inhabit the low salinity areas in the estuary and hence is the only species that has to face the severe fluctuations. Findings of Gibson *et al.*, (1993), however, that crustacean numbers were correlated to salinity was not observed in this study except for *P. montagui.*

Annual fluctuations in the population were observed also in *P. montagui* and in *C. allmanni.* Gibson *et al.*, (1993) states that the changes in abundance, from a peak in most years in July/August to minimum in January/February in crustacaeans, are the result of similar processes of recruitment, mortality and offshore-inshore migrations.

The temporal variations observed in the population structure of three species are in agreement with observations of previous researchers (Lloyd and Yonge, 1947; Mistakidis, 1957; Allen, 1960, 1963; Tiews, 1970; Simpson et al., 1970 and Hunter, 1981; Boddeke, 1985; Henderson and Holmes, 1987). The disappearance of larger males in June in both *C. crangon* and *P. montagui* may indicate the transition of males to females as observed by Boddeke (1985) and Martens and Redant (1986) in *C. crangon* and Mistakidis (1957) and Allen (1963) in *P. montagui.* The aspect of reproduction will be considered in detail in the next chapter hence not discussed in here.

In conclusion it can be said that the shrimp population in the Forth Estuary are represented by three species, dominated by the species *C. crangon.* The populations can be regarded as three unified populations, as indicated by population structure and mean carapace length variations, which are distributed differentially in the estuary.

4.2 GROWTH

4.2.1 Introduction

Since the time after hatching, individuals in a brood increase in size but reduce in numbers. Thus, the size of the population, at a given time, is determined by the resultant of the forces of growth and of mortality. The growth is largely dependant on the environment, availability of food, accessability to food, inter and intra-specific competition, and the physical conditions of the environment, and is thus a good indication of the quality of the environment where animals live. Growth and mortality are also widely used as an essential instrument in the management of fisheries resources as they contribute to estimates of production, stock size, recruitment and mortality of the population concerned (Isaac, 1990). Poor growth and high natural mortality reflect the poor quality of the environment and a knowledge of growth and mortality thus provide a better understanding of the dynamics of the populations.

Growth of shrimps, cannot be studied easily. First of all, the structures such as otoliths, scales, or other hard parts which generally lead to more precise inferences on growth are lacking in shrimps (Pauly, 1987). Secondly, the growth is discontinuous due to moulting (Bergström, 1992). In temperate regions the growth is also characterized by seasonal oscillations, which are believed to be influenced chiefly by the fluctuations in the water temperature. While well conducted growth studies based on otoliths, scales or other hard parts may generate more precise estimates of growth parameters, length-based methods remain extremely important for animals such as shrimps which cannot be aged individually. The only alternative method for estimation of growth parameters in such individuals is the mark and recapture method which is time consuming, much more expensive and totally impractical in most cases. In comparison, length data can be collected cheaply, are less time consuming and are often better correlated with the biological and fisheries processes of the populations (Isaac, 1990). In the present study length-based methods were used to estimate the growth parameters.

The first technique to assess the growth on the basis of length data was developed by Petersen (1891), which triggered the development of graphical, semi-graphical (Harding, 1949; Cassie, 1954; Tanaka,1956; Bhattacharya, 1967) and computer-based methods

(Abramson, 1971; Yong and Skillman, 1971; MacDonald and Pitcher, 1979; Pauly and Caddy, 1985) for the separation of a mixture of distributions into their components. These methods basically assume that the component of the distributions investigated come from a population which are normally distributed. Schnute and Fournier (1980), Fournier and Breen (1983), Sparre (1985) and Pope (1987) presented sophisticated improvements to these techniques, but the unavailability of these computer packages worldwide and their incompatibility with cheaply available micro-computers has limited their use. Moreover, the techniques are based on a large number of assumptions and are time consuming in operation. In the present study, a software package Compleat ELEFAN version 1.11 (the latest version of the Electronic **LE**ngth **F**requency **AN**alysis) developed by ICLARM for the analysis of growth curves (Gayanilo *et al.*, 1989) was used. The programme allows for the estimation of von Bertalanffy growth parameters in animals in which age determination of individuals is not possible. It is also easy to operate and compatible with micro-computers and involves few assumptions. The method involves identification and tracing in time of cohorts which are generated by the seasonal reproduction, in a series of length distributions .

4.2.2 Materials and Methods

The carapace length (mm) data of monthly catches from all five stations at HW and LW were pooled into monthly values and subsequently grouped into 1 cm size classes. The data were analysed using Compleat ELEFAN (Gayanilo *et al.*, 1989). The programme requires the following criteria to be met for successful use of the methodology.

1. Samples are representative of the structure of the population.
2. Growth follows the von Bertalanffy model (VBGF) modified for seasonal growth.
3. Recruitment occurs in seasonal pulses.

The gear used in the present study is accepted as a standard method to obtain a representative sample from fish or invertebrate populations (Holme and McIntyre, 1984) and the recruitment in all three species occurs in seasonal pulses. Although not proven yet for *Crangon* species, Bergström (1992) showed that the growth of *Pandalus borealis* could be described best with seasonally oscillating VBGF. This justifies the assumption

that the growth of shrimps follows the VBGF model. The above requirements are therefore, reasonably met in the present study and apply for all three species.

4.2.2.1 Computation of growth curves

The growth model used in ELEFAN I is the seasonally oscillating version of the generalized von Bertalanffy Growth Function (Gayanilo *et al.*, 1989), which is regarded a very versatile one (Pauly, 1987) and is in the form of

$$L_t = L_\infty(1-e^{(-k(t-t_0)-\frac{CK}{2\pi}(\sin 2\pi(t-t_s)-\sin 2\pi(t_0-t_s)))}) \quad (4.5)$$

where L_t is the predicted standard length at age t, L_∞ is the asymptotic length, K is a growth constant, C is the amplitude of the growth oscillation, t_0 is the "age" the fish would have had at zero length if they had always grown in the manner predicted by the equation; t_s sets the beginning of sinusoidal growth oscillation with respect to t_0 (Pauly and Gaschütz, 1979). In ELEFAN I, t_s is replaced by the Winter Point (WP), which designates the period of the year (expressed as a fraction of a year) when growth is slowest.

The general procedure followed in computation of growth curves is described below.

1. Length frequency distributions were analysed with the modified Bhattacharya method (Bhattacharya, 1967, implemented in Pauly and Caddy, 1985) incorporated to ELEFAN in order to detect and separate the cohorts. The programme splits composite length frequency distributions into separate normal distributions. The modal length progression of the cohorts were then traced by linking the means of the normal distributions for all sampling dates.

2. An independent estimate of L_∞ was obtained with the Wetherall method as modified by Pauly, 1986 (ELEFAN II of Compleat ELEFAN). The Wetherall method (Wetherall, 1986; Pauly, 1986a) assumes that the population studied is stable, with constant annual recruitment, growth is described by von Bertalanffy

(1938) model and that continuous mortality occurs at a uniform instantaneous rate. This method was derived from the Beverton and Holt (1956) method of estimating Z/K (Z= instantaneous total mortality; K = growth constant) as given in the following form

$$\frac{Z}{K} = \frac{L_\infty - \bar{L}}{\bar{L} - L_c} \qquad (4.6)$$

where L_c = "Knife-edge" selection length and $\bar{L}$ = mean length of the shrimps larger than L_c.

According to Wetherall (1986), $\bar{L}$ is a linear function of the knife-edge selection length and could be expressed as

$$\bar{L} = \frac{L_\infty}{(1+\frac{Z}{K})} + \frac{L_c}{(1+\frac{Z}{K})} \qquad (4.7)$$

In the fully recruited phase of the sample (L_c), for a series of arbitrary cutoff lengths (L′), corresponding $\bar{L}$ can be calculated. A positive linear relationship occurs between L′and $\bar{L}$ ($\bar{L}$+ mL′+ C) and slope (m) and intercept (C) of the relationship are given by

$$m = \frac{L_\infty}{1+(\frac{Z}{K})}, \quad C = \frac{1}{(1+\frac{Z}{K})}$$

and L_∞ and Z/K could be derived.

Pauly (1986a) modified the Wetherall method by plotting ($\bar{L}$-L′) against L′ instead of the Wetherall plot of $\bar{L}$ Vs. L′. Then the relationship is as $\bar{L}$-L′ = a-bL′ where L_∞ = a/-b and Z/K = (1+b)/-b. This method is incorporated to Compleat ELEFAN as ELEFAN II and was used for estimating L_∞ and Z/K.

3. The data were then submitted to ELEFAN I (Pauly and David, 1981) in order to determine the cohort and sex specific growth curve parameters. The middle date between HW and LW sampling dates of each month were taken as the sampling date. For *C. crangon*, the cohorts separated by Bhattacharya method were traced to obtain the growth curve for brood 1 and 2 for both sexes. The identification of modes is obtained through 'restructuring' of the length frequency data (Brey *et al..*, 1988).

The best combination of parameters K and L_∞ were obtained by fitting the growth curve so that the Rn value lies within a reasonably high range. Rn value is calculated by ELEFAN I as $10^{ESP/ASP}$, where ESP represents the number of peaks hit by the growth curve and ASP represents the total number of available sum of peaks. Rn value lies between 0 and 1 and indicates the goodness of the fitted growth curve. The best parameter combination was estimated through the following steps.

The Rn value was determined for a wide range of parameter combinations through response surface analysis. The estimate of L_∞ obtained by the Wetherall method was used as the seed value for this purpose and the best combination for K and L_∞ was estimated. Seed values for the Winter Point and the seasonal oscillation were taken as 0.2 and 0.8 and were kept stable while estimating K and L_∞. As indicated in Pauly (1987) Winter Point in northern hemisphere lies close to 0.2 and hence this is taken as the seed value. Further, Pauly (1987) stated that the seasonal oscillation (C) is generally correlated with the difference between summer and winter temperature to which animals are exposed. The seed value used here was derived from that relationship presented in Pauly (1987). Then the best combination for C and WP were calculated. The parameters estimated were given as seed values for the automatic search routine which estimated the best fitting growth parameters.

4. Probability of capture of similar size classes was estimated via detailed analysis of the left ascending part of the catch curve by constructing a selection curve

using Z and M values estimated using preliminary estimates of L_∞ and K. Then the original data set was corrected for probability of capture (Pauly, 1986b).

5. Improved estimates for L_∞, K, C and WP were obtained by analysing the probability corrected data files. Finally the growth curve was fitted to the original data using the improved estimates of L_∞, K, C and WP.

4.2.2.2 Estimation of Total mortality (Z)

If a population follows a negative exponential decay model, the number of individuals surviving after time N_t is given by

$$N_t = N_0 \exp^{-Zt} \qquad (4.8)$$

where N_0 = initial number and Z = instantaneous total mortality rate.

The total mortality (Z) in an exploited stock is equal to the sum of instantaneous rates of natural and fishing mortalities. The stocks of shrimps in the Forth Estuary are unexploited and hence the total mortality equals to natural mortality. There are numerous methods now available to estimate total mortality (Pauly, 1984 a; Pauly and Morgan, 1987; Sparre, 1987, Sparre *et al.*, 1989) which are useful for estimating mortality in the situations where age-distribution cannot be traced. Mortality of *C. crangon*, *P. montagui* and *C. allmanni* were estimated: 1, using the 'length converted catch curve method' (Brey *et al.*, 1988); 2, using Z/K estimates of the modified Wetherall method, and 3, using the Beverton and Holt (1956) method.

1. Length-converted catch curve method

The catch curve incorporated into ELEFAN takes the form

$$Ln(\frac{N_i}{\Delta t_i}) = a - bt_i \qquad (4.9)$$

where, N_i = the number of shrimps in the length class i

Δt_i = the time needed by the shrimp to grow through the length class i,

t_i = relative age of the mid-point of length class i

and Z = -b.

The values of t_i and Δt_i are estimated from equation 4.10 and 4.11 respectively.

$$t_i = \frac{1}{K} Ln(L_\infty - L_i) + t_0 \qquad (4.10)$$

where, L_∞ , K and t_0 are von Bertalanffy growth parameters and L_i is the mid point of the length class i. By setting t_0=0 the relative age is used instead of absolute age. Pauly (1984a) showed that for estimation of Z is independent of age and a knowledge of absolute age is not necessary.

$$\Delta t_i = \frac{Ln\dfrac{(L_\infty - L_1)}{(L_\infty - L_2)}}{K} \qquad (4.11)$$

where, L_1 and L_2 are lower and upper limits of length class i .

The estimation of Z involves the assumptions that,

1. Z is constant over all size classes included in the calculations.
2. Recruitment varies little and is random.
3. All age groups are equally vulnerable to the gear used for sampling.
4. The sample used is representative of the structure of the population and covers enough age groups over the period of study (Pauly, 1984a).

The estimation of Z from the length-converted catch curve was carried out through the following steps.

1. Length frequency samples of the total period of study were pooled to simulate the steady state population.

2. The catch curve was constructed using the pooled sample and growth parameters derived in ELEFAN I.
3. Total mortality was estimated from the descending arm of the catch curve.

2. Wetherall method

Total mortality (Z) was calculated by substituting the value of growth constant (K) to the Z/K value derived in calculation of asymptotic length, in modified Wetherall method.

3. Beverton and Holt method

The Beverton and Holt (1956) formula for estimating Z is given by :

$$Z=K\frac{(L_\infty-\bar{L})}{\bar{L}-L'} \qquad (4.12)$$

Z was estimated for males and females of each species using the L_∞ and K values obtained by ELEFAN I and the mean length of shrimps ($\bar{L}$) above the fully vulnerable to the gear (L').

4.2.3. Results

4.2.3.1. Growth curves

The growth curves obtained for each species by linking the means of cohorts separated by the Bhattacharya method for the year beginning from July 1992 and ending in June 1993, are shown in Fig. 4.23. *C. crangon* exhibited two annual cohorts, the first beginning in July and the second beginning in October, whereas the other two species exhibited only one cohort. The peak recruitment to the adult population was found to occur in July in all three species.

C. crangon males recruited in July 1992 at 6.5 mm in Carapace Length (CL), grew to a size of 10.1 mm CL by following June while the females grew from 6.0 mm CL to 11.3 mm CL within the same period. The males of the October 1992 cohort which started with

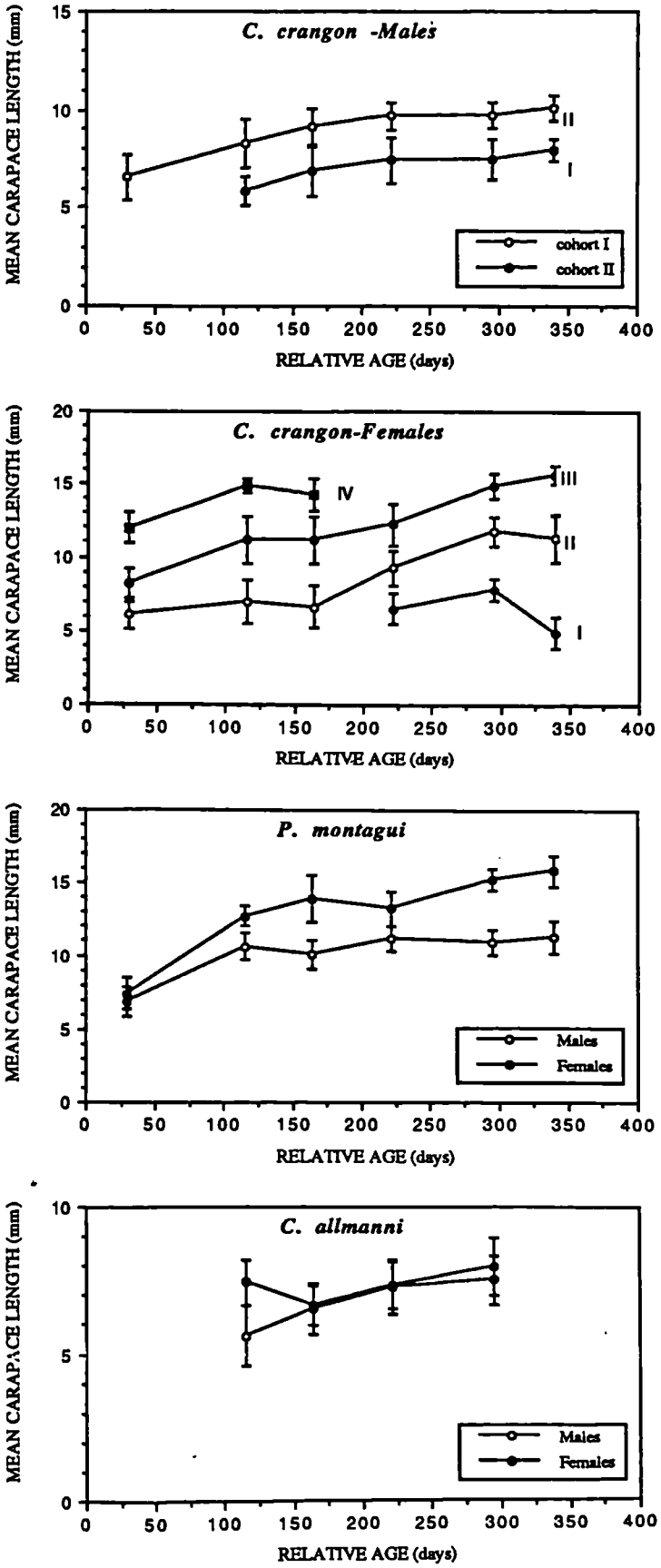


Fig.4.23 Growth curves of *C. crangon*, *P. montagui* and *C. allmanni* males and females in the Forth Estuary, drawn by linking the mean carapace lengths of the cohorts separated by Bhattacharya method. Day 1 = 1 July 1992.

a size of 5.6 mm CL grew to 8.0 mm CL by June. In females, linking the cohorts which start at a mean length of 8.2 mm in July was found difficult (cohort III in fig. 4.23) after January. In January this cohort reached the size of 12.2 mm CL, and from then either grew rapidly and reached the size of 15.6 mm CL by June or disappeared from the population for some reason. It is difficult to decide whether the large females of length classes, 14.9 mm CL in April and 15.6 mm CL in June, belonged to the cohort starting at 8.2 mm CL mean length or to the cohort starting at 12.0 mm CL in July, 1992. The former implies a higher growth rate and the latter a slower growth.

Males of *P. montagui* which were recruited in July 1992 grew from 6.8 mm CL to 11.3 mm CL by June, 1993. The growth of females showed a negative growth from January until June. The mean carapace length of the females which started at a size of 7.4 mm in July 1992 was found to be 14.0 mm by April (Fig.4.23).

Unlike in other two species, both male and female *C. allmanni* showed a steady growth pattern (Fig.4.23). Males arrived to the estuary at a size of 5.6 mm CL in October 1992, were 7.5 mm CL in size at the time of departure from the estuary in April 1993. The females grew to 8.0 mm CL within the same period. Mean carapace length of female cohort in October has obviously deviated from the size of actual new recruits as indicated by the mean size of the males. This may be due to the mixing of a few animals belonging to second year cohort, which was present in the estuary in October, with the newly arrived cohort.

The male *C. crangon* of cohort I reached 8.3 mm CL (=35.6 mm TL) by the end of October. These were apparently generated from the eggs hatched in late June/early July. By taking the date of hatching as the first of July, the average growth rate of the shrimps in the intertidal area was calculated as 0.40 mm day^{-1}. The group hatched in September reached 5.8 mm CL (=25.5 mm TL) by the end of October, thus showing a higher average growth rate, 0.52 mm day^{-1}. Likewise female *C. crangon* shows average growth rate which varied between 0.35 and 0.40 mm day^{-1} respectively for cohort I and II.

Calculation of average growth rates for *P. montagui* and *C. allmanni* was not attempted for the stages prior to entering the sub-tidal area since the exact periods for peak abundance of berried females or larvae are not known.

The average growth rate of the three species by sexes were calculated for periods where positive growth is shown. To facilitate comparisons with data recorded in previous literature where total lengths are presented instead of carapace lengths, conversion of carapace lengths to total length was performed prior to calculation of average growth, using the conversion factors derived in the preceding chapter (see Page 41). Table 4.7 presents the average growth rates (mm day^{-1}) for the three species of shrimps for the specified periods, in the sub-tidal area.

Preliminary estimates of L_∞ and Z/K obtained by modified Wetherall method for males and females of three species are given in Table 4.8 and Wetherall plots for each species by sex are shown in Fig. 4.24. The points used indicates the fully recruited phase of the shrimps.

Table. 4.8- Asymptotic length (L_∞) and Z/K derived by Wetherall method.

Species	sex	L_∞	Z/K
C. crangon	Male	12.61	3.122
	Female	18.12	2.682
P.montagui	Male	14.14	2.568
	Female	18.31	2.334
C. allmanni	Male	13.44	2.331
	Female	15.48	3.285

As indicated by the results, female shrimps grow to a larger size than males.

Table 4.7 The average growth rates (mm day^{-1}) of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary.

Species	Sex	Cohort	period	Number of days	Total Length (initial)	Total Length (final)	Growth rate (mm day^{-1})
C. crangon	Male	I	Jul 92 - Jun 93	280	28.5	43.1	0.052
		II	Oct 92 - Jun 93	230	25.6	34.7	0.040
	Female	I	Jul 92 - Jun 93	280	26.7	48.6	0.078
		II	Jul 92 - Jan 93	163	35.9	52.5	0.100
		III	Jul 92 - Dec 93	105	51.3	61.0	0.092
P. montagui	Male	I	Jul 92 - Jun 93	280	30.3	49.2	0.067
	Female	II	Jul 92 - Dec 93	105	32.8	51.2	0.066
C. allmanni	Male	I	Oct 92 - Apr 93	179	31.1	38.4	0.041
	Female	II	Dec 92 - Apr 93	131	31.3	37.4	0.047

As observed from the growth curves obtained by compleat ELEFAN method for each species for each sex (Figures 4.25, 4.26 and 4.27 and Table 4.9) only *C. crangon* females showed a lower growth rate than males. This may probably a result of ill defined cohorts due to the continuous addition of juveniles to the adult population, emigration/immigration of large females in the study area and addition of secondary females to the female population. All these factors affect the determination of growth curves and underestimate the mean size of the cohort at a certain time ultimately resulting in an underestimation of growth rate. The presence of berried females in the upper estuary proves the emigration of females to upper estuarine area during some periods. Rn values obtained in the present study are low particularly in female growth curves due to the complexity of their behaviour. Despite this fact, the growth curves obtained are logical and fit well with the data specially at the early part of the growth curve.

Table 4.9 Growth parameters (L_∞, K, C and WP) of the three species of shrimps in the Forth Estuary.

Species	Sex	Asymptotic length (L_∞)	Growth constant (K) ($year^{-1}$)	Seasonal oscillation (C)	Winter Point (WP)	Rn value ($10^{ESP/ASP}$)
C. crangon	Male-cohort	11.7	1.48	.92	.16	0.182
	Male-cohort II	10.8	1.52	.91	.14	0.347
	Female-cohort I	18.6	1.10	.92	.16	0.103
	Female-cohort II	18.6	1.10	.92	.16	0.107
P. montagui	Male	15.7	0.96	.92	.16	0.300
	Female	17.6	1.20	.94	.18	0.155
C. allmanni	Male	13.4	1.40	.98	.16	0.739
	Female	15.5	1.49	.92	.23	0.381

The length-converted catch curves for male and female *C. crangon* (Fig. 4.28) and for *P. montagui* and *C. allmanni* (Fig. 4.29) derived high mortality rates as indicated in Table 4.10 as Z_a. These values were derived by fitting straight line regressions to the right arm of each catch curve. The Z values derived by modified Wetherall method Z_b, and Beverton and Holt method Z_c (Table 4.10) were also high.

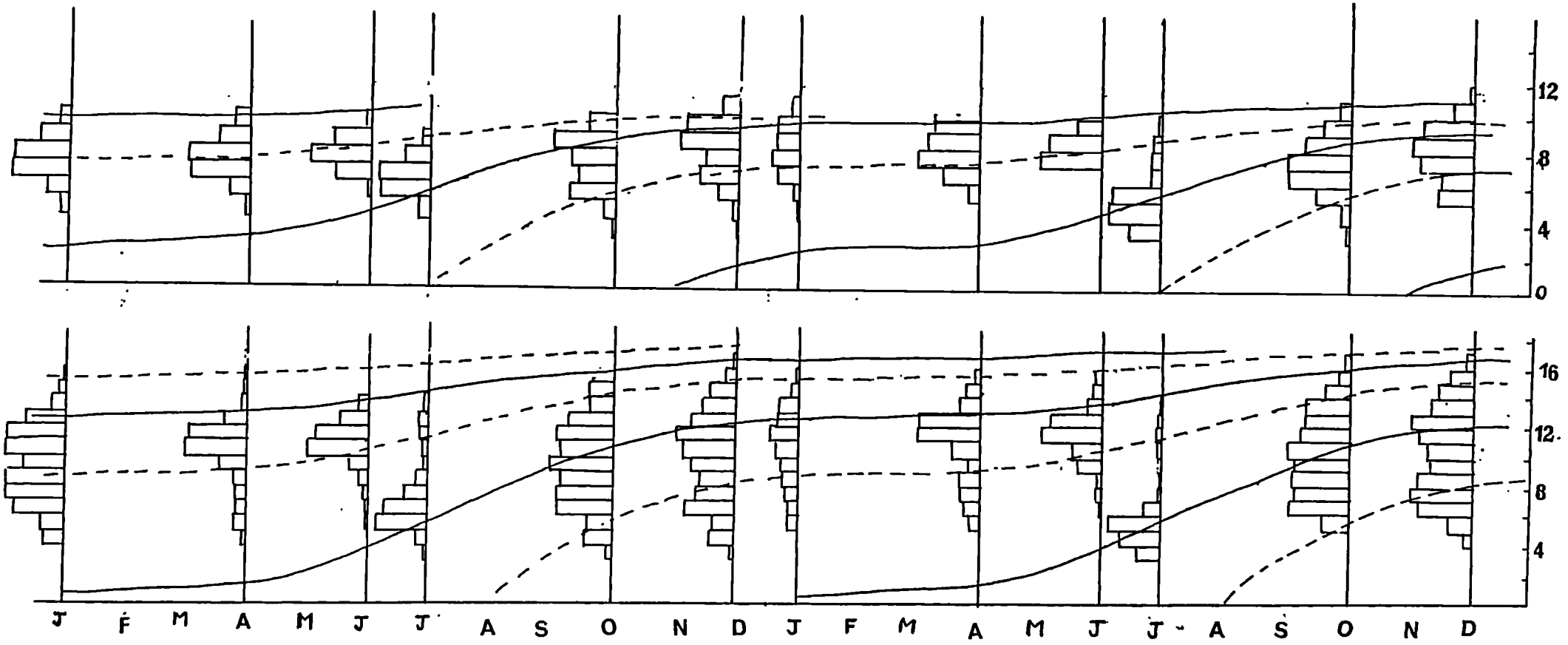


Fig.4.25- Growth curves fitted by ELEFAN I for male and female *C. crangon*. Upper series = males, lower series = females. Dotted line represents cohort II.

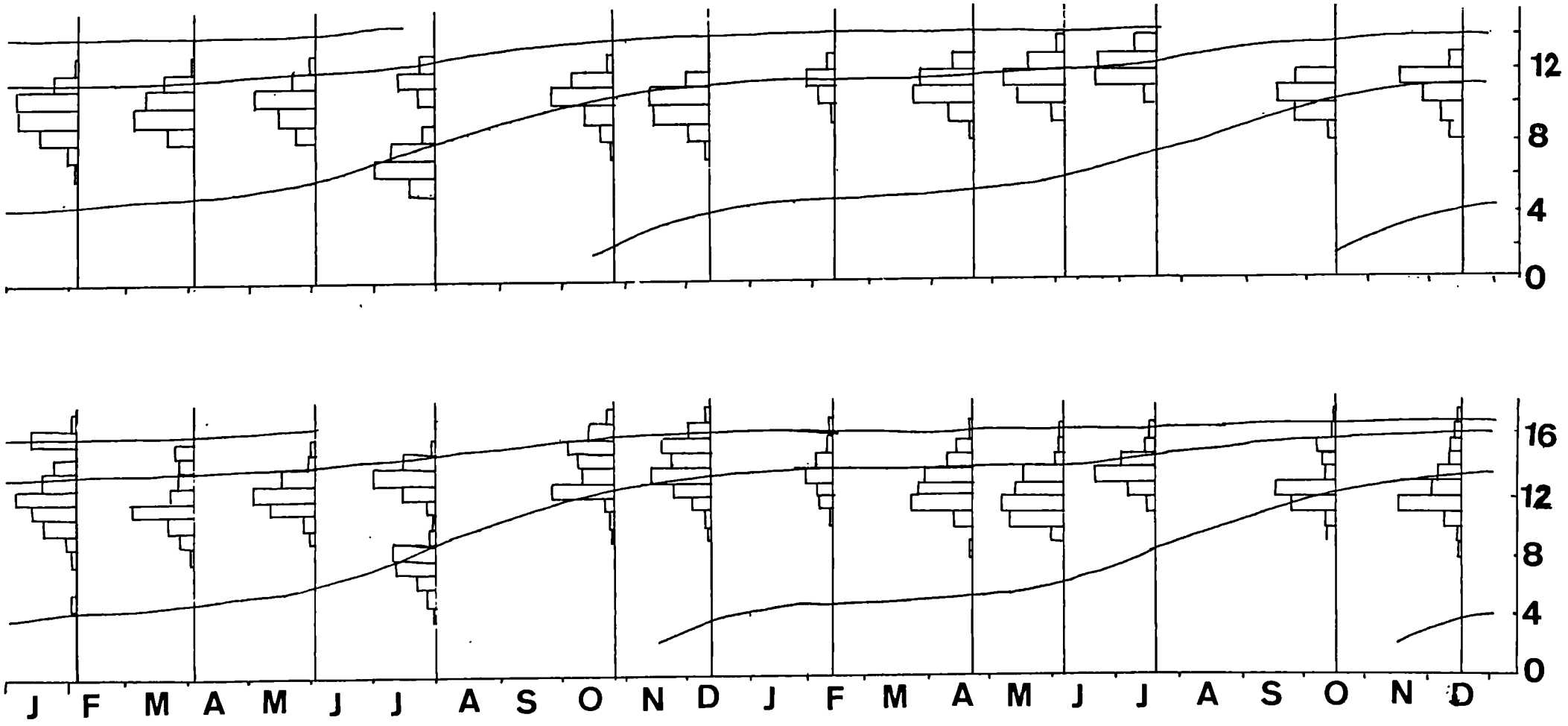


Fig.4.26- Growth curves fitted by ELEFAN I for male and female *P. montagui*. Upper series = males, lower series = females.

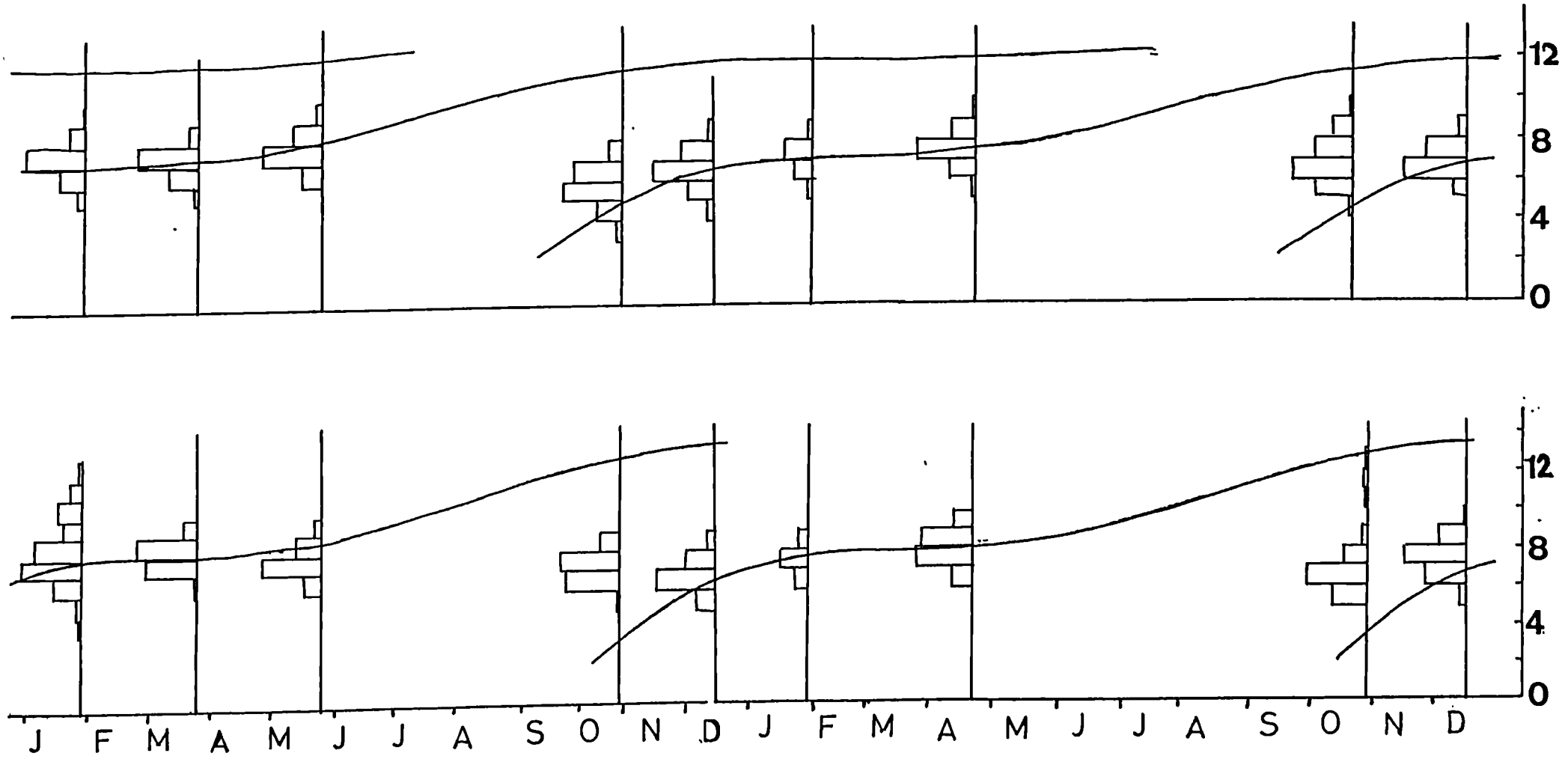


Fig.4.27- Growth curves fitted by ELEFAN I for male and female *C. allmanni*. Upper series = males, lower series = females.

Table 4.10 Instantaneous total mortality rates (Z) derived for *C. crangon*, *P. montagui*, and *C. allmanni* males and females using three methods : Z_a = Length-converted catch curve method, Z_b = modified Wetherall method and Z_c = Beverton and Holt method.

Species	Sex	Z_a	Z_b	Z_c
C. crangon	Male cohort I	3.795	4.620	3.756
	Male cohort II	3.274	4.745	3.008
	Female cohort I	5.453	2.950	4.712
	Female cohort II	5.453	2.950	4.712
P. montagui	Male	4.901	2.455	3.643
	Female	2.435	2.800	2.328
C. allmanni	Male	6.374	3.263	8.016
	Female	6.938	4.894	10.397

The mortality rates also showed a flexibility depending on the method used for estimation. Highest mortality rate was observed in *C. allmanni* by all the methods. The assumptions of length converted catch curve is not properly met with the population of *C. allmanni* since the samples in the estuary do not represent the total population and the loss by migration also may account for mortality.

4.2.4 Discussion

The growth parameter estimation of shrimps is generally considered as a difficult task due to the complexity of the biological processes involved with their life cycle. Continuous spawning and recruitment cause a great deal of confusion of growth while emigration and immigration by size classes from and to the inhabited area in relation to feeding or reproduction may underestimate the growth rate. The estimation of growth parameters by modal progression analysis is possible even under such circumstances because the bulk of the females do spawn with identifiable seasons although the presence of females carrying eggs or ripe could occur throughout the year (Qasim, 1973; Weber, 1976; Longhurst and Pauly, 1987). According to Pauly (1987) however, the separation of length groups and the attribution of ages to these lengths could be totally misleading when

additional information on recruitment pattern is not available and when two recruitment pulses occur per year. Of the three species studied here *C. crangon* exhibited two recruitment pulses while the other two species showed only one recruitment pulse per annum. By using the modified Bhattacharya method (Bhattacharya, 1967, implemented in Pauly and Caddy, 1985) cohorts generating from two recruitment pulses were separated in this study and the results are believed to give good estimates for growth and mortality of the three species. Moreover, the present study is also supported by the additional information on the recruitment, larval occurrence and occurrence of berried females of the shrimp species studied. The results obtained are discussed in the following paragraphs separately for each species.

4.2.4.1 *C. crangon*

The values of average growth rate estimated for the intertidal stages of *C. crangon* indicated moderately similar values for the males and females. The male group hatched on first of July indicated an average growth of 0.40 mm day^{-1} (male cohort I) and the group hatched in September, 0.52 mm day^{-1} (male cohort II) while females indicated an average growth of 0.35 mm day^{-1} and 0.40 mm day^{-1} respectively for cohort I and II. These growth rates which express the growth of post larvae and juvenile stages in the intertidal areas in the Forth Estuary, are comparable with the findings of previous researchers; 0.48 mm day^{-1}, Van Lissa (1977) in the Wadden Sea; 0.40 mm day^{-1},. Boddeke and Becker (1979) in coastal area in Netherlands ; 0.50 mm day^{-1}, Beukema (1992) in the Wadden Sea but are higher than that derived by Kuipers and Dapper(1981) (0.23 mm day^{-1}) in the Wadden Sea. The disparity among the values derived by Kuipers and Dapper (1981) is mostly due to the confusion regarding the birth date of the cohort which had been obtained by back calculations (Beukema, 1992) of the growth curve rather than the actual data. In the present study, the birth date was derived using the occurrence of larvae in the estuary and the occurrence of berried females in the estuary and are assumed to give valid estimates.

Growth in the subtidal areas however, was found to be much lower than those of the intertidal areas where average growth rates were 0.04-0.05 mm day^{-1} for males and 0.07-0.1 mm day^{-1} for females. This may reflect the poorer production of benthos in the

subtidal areas (Elliott and Taylor, 1989) which limit the food resources for compared to the benthos rich intertidal areas (McLusky, 1987b). The growth rate of males was faster than that of females which is contradictory to the findings of Tiews (1954) and Meixner (1966) who observed a faster growth in females based on the experiments carried out under laboratory conditions. This could be explained by several biological phenomenon involved with the females in the natural environment. The beginning of the decline in the growth of female *C. crangon* during Jan-Apr period coincides with the breeding season. This may be explained by the fact that females carrying eggs do not change size by moulting thus stagnating the growth. Further, the migration of females down the estuary for spawning as observed by Boddeke (1975) may also have an effect on the growth decline. Addition of secondary females to the population is another factor which affects the apparent growth of female cohorts. Present results indicate differences in growth seasonally and between sexual stages. The growth in *C. crangon* may best be described if the curves could be fitted separately for males, secondary females and females as demonstrated by Bergström (1992) for *Pandalus borealis*. Unfortunately, it is quite impracticable to separate the secondary females or transitionary males in the population by external features.

The *C. crangon* population in the Forth Estuary produced two cohorts per year. The males recruited in July lived approximately 1.5 years while the females lived for 2.5 years. Very few males survived longer than one year and reached the size larger than 12.5 mm in CL. There are differences in growth pattern between the sexes, males growing faster and dying quicker and females growing slower and living longer. Low Rn values obtained in the present analysis are due to the existence of two cohorts per year in which approximately half of the available sum of peaks belong to each cohort. Higher Rn values may be obtained if the growth curves were fitted to length frequencies of separated cohorts rather than to the original data. The growth parameters estimated for females are questionable due to emigration of females to spawning grounds (Boddeke, 1989) and the continuous addition of secondary females to the female population during part of the year. The asymptotic lengths derived here with ELEFAN I (males- 11.7/10.8 mm CL, females- 18.65 mm CL) and modified Wetherall method (males- 12.6 mm CL, females- 18.11) are comparable for both sexes. The growth parameter estimation by using

ELEFAN I for *C. crangon* presented here is the first of its nature and there are no estimated growth parameters to compare the present results with. The asymptotic lengths estimated in the present study for males and females (11.7 mm CL, 50.0 mm TL for males; 18.6 mm CL, 79.0 mm TL for females) are lower than the maximum lengths reported by Havinga (1930) from the German coast. The largest male *C. crangon* observed in the present study (14.5 mm CL, 61.3 mm TL) is comparable with Tiews (1954) and Boddeke (1966) who observed the maximum size of the males as 68 mm in TL and 60 mm in TL respectively. The females of 91 mm TL and 95 mm TL, reported by Havinga (1930) and Tiews (1954) respectively which correspond to the 22.5 mm CL were not observed in the present study. The lengths at age derived for *C. crangon* by tracing the unseparated cohorts by naked eye or based on the growth experiments carried out in the laboratory available from the past literature along with the present results (Table 4.11) indicated dissimilar values.

The lengths at age derived for *C. crangon* in the Forth Estuary, using the growth curve, compare well with those of the past literature specially with that reported by Tiews (1954). The estimates of Lloyd and Yonge (1947) however, are much lower than the lengths at ages derived by others. This may perhaps be due to the misidentification of the two recruitment pulses occurring in the same year as two year classes.

Table 4.11- The estimated lengths of age estimated for *C. crangon* by different researchers from different areas.

AREA	Age (years)						Reference
	0.75	1	1.5	2	3	4	
Caroliensiel, German coast	-	-	60-70 mm	-	-	-	Ehrenbaum, 1890
Zuiderzee, German coast	-		-	58 mm	74 mm	-	Havinga, 1930
Jade Bay, German coast	-	40 mm	-	72-78 mm	-	-	Meyer-Waarden, 1935
German coast	-	48 mm	-	70.5 mm	-	-	Nouvel-Van Rysselberge, 1937
Bristol Channel and Severn Estuary, UK	-	54.5 mm	-	40-45 mm-♂	50-60 mm-♀	70 mm-♂	Lloyd and Yonge, 1947
Büsum, North Sea coast (by experiment)	-	40 mm-♂ 54 mm-♀	-	55-60 mm-♂ 70-75 mm-♀	-	-	Tiews, 1954
Coast of Netherlands	52 mm	-	-	-	-	-	Boddeke, 1966
German Bight (by experiment)	-	55 mm-♂ 62 mm-♀	-	-	-	-	Meixner, 1966
Forth Estuary, Scotland	-	41.9 mm-♂ 53.5 mm-♀	-	- 66.0 mm-♀	-	-	present study

The mortality rates observed are high for both *C. crangon* males and females. Higher mortality rates are often found in the benthic invertebrates which are preferred prey of the other species. Redant (1980), Tiews and Schumaker (1969) and Boddeke (1989) observed that the predation mortality is higher than that of the fishing mortality in *C. crangon* in the French coast, German coast and Wadden Sea. In the Forth Estuary, where there is no shrimp fishery, the mortality is solely due to natural causes including predation. A higher predation mortality can be expected in the Forth estuary also since *C. crangon* has been identified as the preferred prey of six fish species inhabiting the Forth Estuary (Elliott and Taylor, 1989a; Costa and Elliott, 1992).

4.2.4.2 *P. montagui*

P. montagui in the Forth estuary produced one cohort per year. The differences between sexes were also observed in *P. montagui*, females growing at a faster rate than males. This difference between male and female growth has also been observed by Mistakidis (1957) and Allen (1963) in south east England, Northumberland waters and Stevenson and Pierce (1985) in Penobscot Bay, Maine. The plateau of the growth curve coincided with the breeding period of the shrimp implying that growth stagnation is related to breeding. The negligible growth in males during this period may be explained by the allocation of energy for testicular development and swimming activity before mating. The sex reversal which takes place after mating may also take energy resources from growth. In females growth is hampered by egg carriage, during which female is unable to moult.

The longevity of the male *P. montagui* in the Forth Estuary is estimated as one year while the females lived more than two years. These are lower than the reported longevities of *P. montagui* by Simpson *et al.*(1970) (3-4 yrs) but close to the records of Stevenson and Pierce (1985) (1-2 yrs for males and 3 yrs for females). The maximum size of the males (13.5 mm CL) observed in the present study is in agreement with the earlier records; 14 mm CL, by Allen (1963) and 10-12 mm CL by Stevenson and Pierce (1985). The maximum size of females observed by Stevenson and Pierce (1985) in Maine was not observed in the Forth Estuary.

High mortality rates were also observed in *P. montagui*. Mortality rates in males were

higher than that of the females. The mortality estimates obtained are debatable since the loss of males to female population through sex reversal and emigration of older groups of females offshore may also account for the mortality rates. The mortality rates observed may thus indicate a higher estimate.

4.2.4.3 *C. allmanni*

C. allmanni in the Forth Estuary also produces one cohort per year. Unlike *P. montagui* the second year group of *C. allmanni* is not present in the estuary. Allen (1963) observed the inshore migration of shrimps corresponding to 8 mm CL group while the other age groups remained in the offshore area. Thus there is a possibility that the *C. allmanni* population which leave the estuary in late April/early June, may remain in offshore area without returning back to the estuary.

In the estuary *C. allmanni* grew to a maximum size of 10.5 (males) and 13.5 in females. This growth is uninterrupted by the factors described above for *C. crangon* and *P. montagui* and reflects a better fitting growth curve as indicated by the higher Rn values. The Rn value is lower for females and may indicate the emigration of berried females to offshore in January.

The mortality rates obtained for *C. allmanni* is questionable since part of the population remains in the offshore area. This may include the loss of animals by emigration as well as the mortality and explains the higher mortality rates obtained.

4.2.5 Conclusion

The results obtained in the growth parameter estimation of three species of shrimps in the Forth Estuary indicates that the growth of shrimps can be explained better by the seasonally oscillating version of von Bertalanffy (Pauly and Gaschütz, 1979) curve. The complexities involved in the life cycle of the shrimps make the estimation of growth curves awkward. Thus a knowledge on the biology of the species studied is essential for estimation of the growth parameters. Despite these difficulties the estimates obtained in the present study are reasonable and compares well with the sizes at age from other European populations.

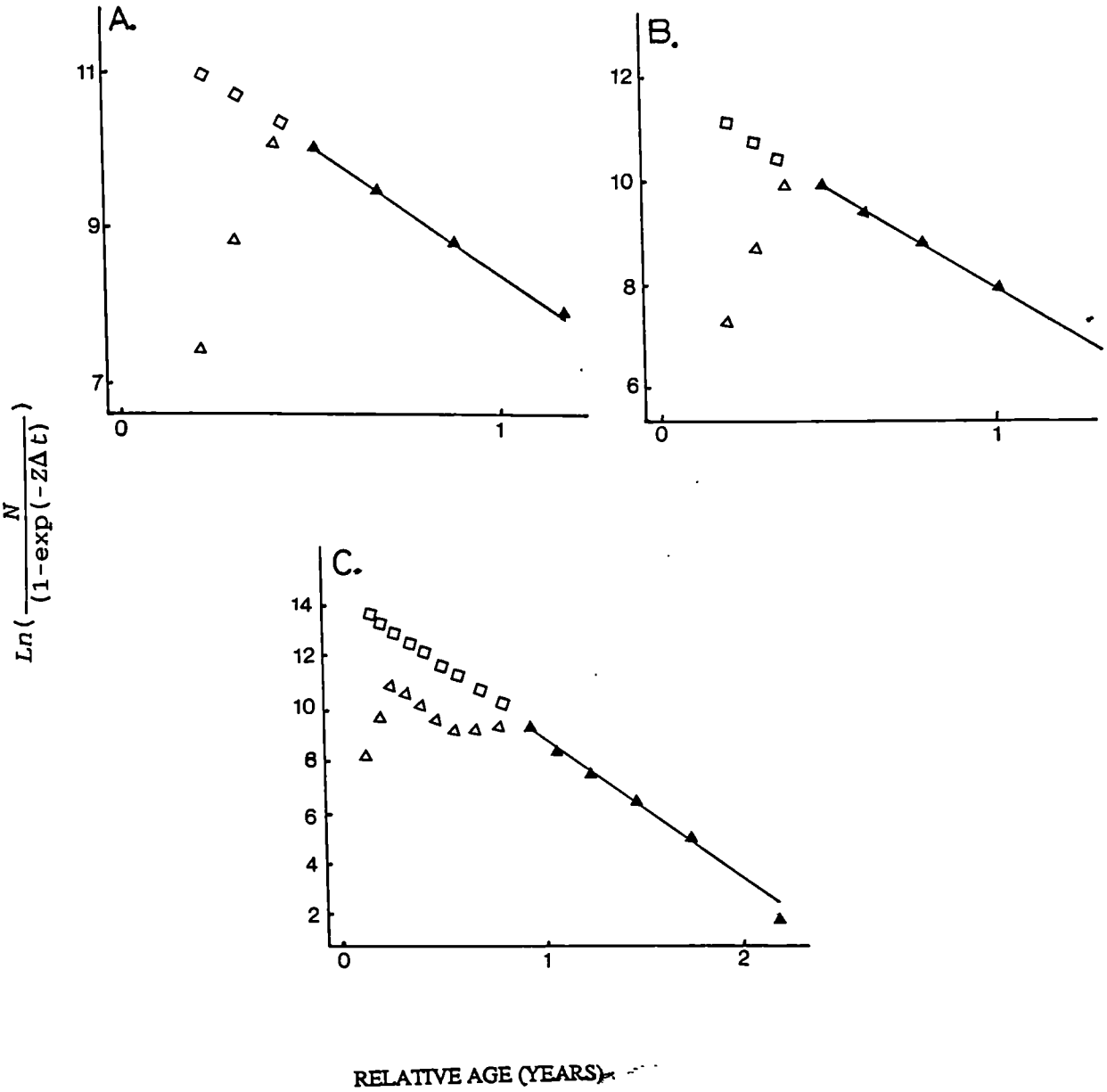


Fig.4.28 Length-converted catch curves for male (A.=cohort I, B.=cohort II) and C. female *C. crangon* as derived by ELEFAN II. ▲ - points used, △ - points not used in the regression. □ - expected numbers if fully recruited.

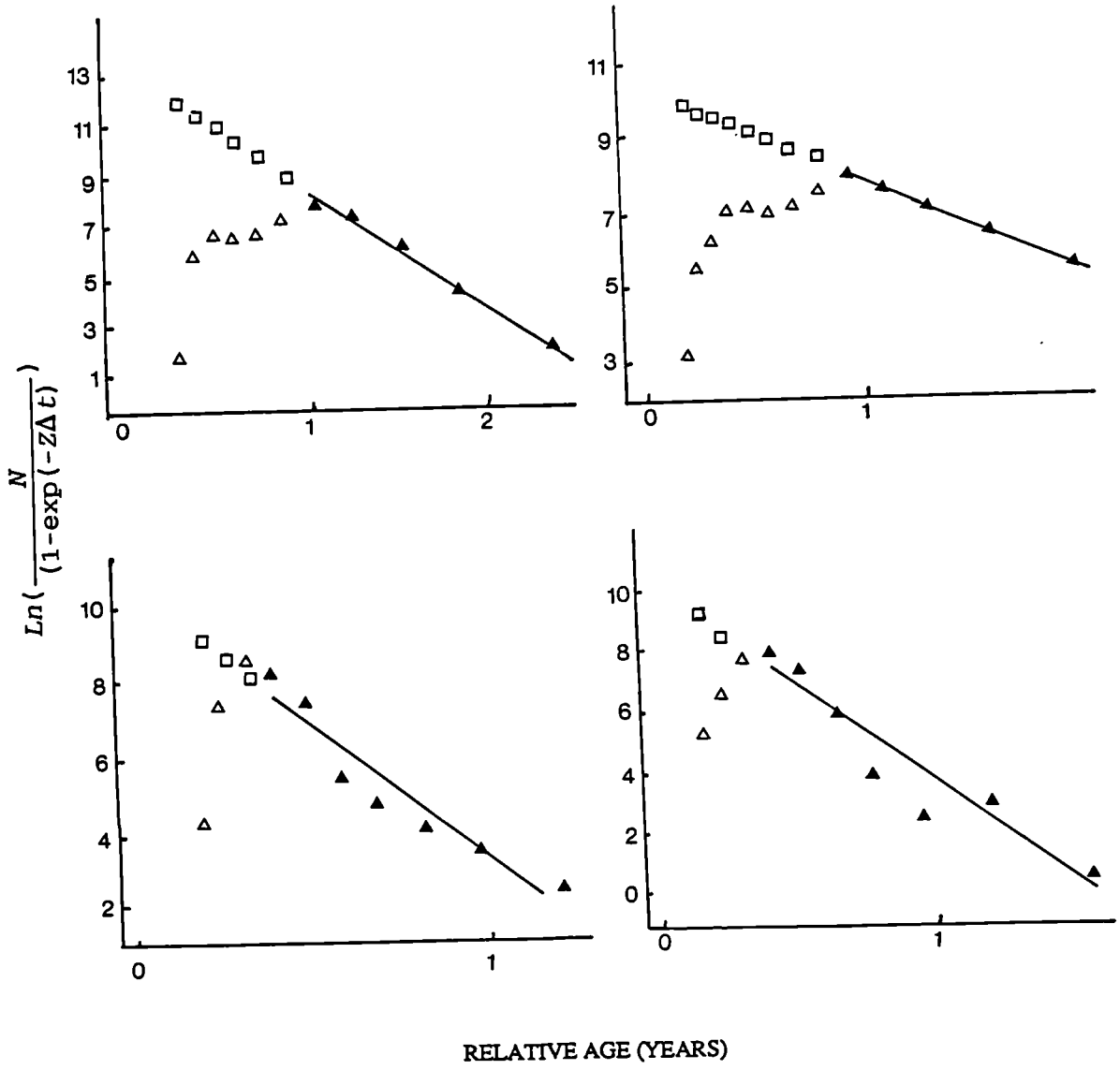


Fig.4.29 Length-converted catch curves for male and female *P. montagui* (upper series) and male and female *C. allmanni* (lower series) as derived by ELEFAN II. ▲- points used, △- points not used in the regression ◇- expected numbers if fully recruited.

4.3 BIOMASS AND PRODUCTION

The somatic production of shrimps is an important component of energy flow and organic matter cycling in many aquatic ecosystems. As Costa and Elliott (1992) indicated, the fish population of the Forth Estuary depends primarily on the production of macrobenthic fauna with *C. crangon* as the dominant prey item. The production of benthic fauna can also be considered as a method for the estimation of the health of the ecosystem concerned (Elliott *et al.*, 1986). The estimation of production of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary was carried out in order to identify the productive capacity of each species in the estuarine community and to find out their contribution to the production of the ecosystem of the Forth Estuary.

4.3.2. Materials and Methods

4.3.2.1. Estimation of biomass and production

There are numerous methods employed in estimation of production. The most popular and widely used is the growth increment summation method and removal summation method described by Crisp (1984). Some of the available methods are based on the dependence of $P/\bar{B}$ ratio on a certain aspect of the life history of an organism. Waters (1977) showed that $P/\bar{B}$ ratio increases with the increasing number of generations per year. Zaika (1970), Robertson (1979) and Warwick (1980) demonstrated a decrease of $P/\bar{B}$ ratio with increasing life span of the organisms. Banse and Mosher (1980) found that $P/\bar{B}$ ratio is inversely related to the weight of the animal at sexual maturity while Schwinghamer *et al.*(1986) showed an inverse relationship with individual body mass per size class. All these empirical findings depends on the negative exponential relation of metabolic rate to body weight in animals (Brey, 1990). Brey (1990) disregarded the methods of Robertson (1979), Warwick (1980) and Banse and Mosher (1980) due to their lack of precision and introduced an empirical relationship between P, $\bar{W}$ and $\bar{B}$ for three groups; Mollusca, Polychaetes and Crustacea. According to his model crustacean production (P) is given by the equation:

$$\log_{10}(P) = a + b_1 . \log_{10}(\bar{B}) + b_2 . \log_{10}(\bar{W})$$

where the constants a, b_1 and b_2 are given as -0.614, 1.022 and -0.360, and $\bar{B}$=mean annual biomass (g AFDW m^{-2}), $\bar{W}$= mean individual weight (g AFDW) and P=annual production (g AFDW m^{-2} yr^{-1}).

Brey (1986) also demonstrated a simple method for the estimation of production by use of total mortality rate which is found to be equivalent to $P/\bar{B}$ ratio when the population is in a steady state and the growth could be described by Von Bertalanffy Growth Function. In this method when the total mortality is derived using catch curve method the production can be calculated if the $\bar{B}$ (mean annual biomass of the population) is known.

In the present study, production estimates were obtained from the length-frequency data, and the Carapace Length-Ash Free Dry Weight regression. Since all three species exhibited recruitment in July, the annual production was calculated for the birth year, which started on 23rd July 1992 and ended on 24 June 1993. For *C. allmanni* the year began with their arrival in the estuary in October and ended at the time of their departure from the estuary in April. At each sampling date, the shrimps were pooled into 1 cm length classes. Since preliminary examination of the data (see part 4.1) revealed length and growth differences between males and females, length frequency data of the two sexes were analyzed separately. Juveniles were divided equally over the male and female data matrices. The shrimps belonging to each year classes were regarded as a separate isolated population. Cohorts were separated using the Bhattacharya method as described in the previous section (4.2).

Density of the population was calculated as the mean of five stations in the estuary at both high water and low water and was expressed as the number of individuals (N ha^{-1}), and the biomass as mg AFDW ha^{-1}. Calculations of biomass was performed using the regression between Ln CL and Ln AFDW derived in chapter 3. Seasonal differences of CL/AFDW relationship were also taken into account since the differences among the seasons were found to be significant (see Chapter 3). In order to compare the effect of seasonal differences on production, Ln CL/Ln AFDW relationships were also established for pooled data. The production of shrimps, as the material added to the population was calculated using the growth increment summation method (Crisp, 1984) for stocks with recruitment, age classes separable. This method was chosen due to the popularity of the method which makes it possible to compare the results with earlier work. In this method production (P) is calculated as the increment of biomass from one sampling to the next

throughout the cohort's life span. In mathematical terms this can be expressed as

$$P = \sum N\Delta\overline{W} \qquad (4.14)$$

where N = the number of individuals at time t, and $_{\Delta}\overline{W}$ = the increase in weight of an average individual during the time interval. The production was estimated for each species by sex using both the four seasonally varying equations and the pooled relationship of CL/AFDW.

Total production in the estuary was estimated by extrapolating the production (g AFDW ha^{-1} yr^{-1}) values to the total area of the estuary. Since the abundance represent pooled data of both high water and low water, production and biomass were estimated using both, the area covered at high water (6057 ha) and at low water (3850 ha) as the total extent of the study area. The values for area at high water and low water were estimated using the map of the Forth estuary (McLusky, 1987a) and validated by comparing with that given by Elliott and Taylor (1989b).

4.3.2.2 Estimation of the size of the population

Size of the population was estimated using the area density method, as described by Everhart *et al.* (1975) and Everhart and Youngs (1981). The total number of shrimps present at five stations at low water were used for the estimation of shrimp population in the area between Forth Bridge and Kincardine Bridge. This estimate therefore, presents an estimate for the subtidal population of the shrimps in the Forth Estuary. As described by Everhart *et al.* (1975) and Everhart and Youngs (1981) the estimator can be derived from the following formula:

$$\hat{N} = \frac{A}{a}\sum_{i=1}^{a} N_i \qquad (4.15)$$

where, $\hat{N}$ = the estimated total population, a = number of units sampled, A = number of equal units of area occupied by the total population being estimated and N_i = the

number of shrimps in the i^{th} sample.

The variance ($\hat{V}$) of the estimator is given by :

$$\hat{V}(\hat{N}) = \frac{A^2 - aA}{a} \cdot \frac{a\sum_{i=1}^{a} N_i^2 - \left(\sum_{i=1}^{a} N_i\right)^2}{a(a-1)} \qquad (4.16)$$

In estimation of populations of shrimps in the Forth Estuary, the area of each unit (a) was taken as the area swept by the trawl. Numbers corrected for gear selection were used as the numbers present at each instance. The total area of the estuary was taken as the area between Forth Railway Bridge and Kincardine Bridge and was calculated separately for high water and low water. The size of the population at high water was estimated using the total area of the estuary at high water (6057 ha) and at low water was estimated excluding intertidal area which left 3850 ha.

4.3.3 Results

4.3.3.1 Biomass and production

Production (P) as g AFDW ha^{-1} yr^{-1} and biomass ($\bar{B}$) (g AFDW ha^{-1}) and $P/\bar{B}$ ratio (yr^{-1}) of *C. crangon* computed using the CL/AFDW conversions of seasonally varying equations (P=3302.47 g AFDW ha^{-1} yr^{-1}, $\bar{B}$=1607.40 (g AFDW ha^{-1}), $P/\bar{B}$=2.05) and single equation (609.93 g AFDW ha^{-1} yr^{-1}, $\bar{B}$=241.27 g AFDW ha^{-1}, $P/\bar{B}$=2.53) varied considerably (Tables 4.12 and 4.13). Likewise, substantial variations were observed between the values of P, $\bar{B}$ and $P/\bar{B}$ ratio values for *P. montagui* derived by seasonally varying equations (Table 14) (P=1230.60 g AFDW ha^{-1} yr^{-1}, $\bar{B}$=1116.70 g AFDW ha^{-1}, $P/\bar{B}$=1.10) and those derived by using single equation (Table 15) (P=815.88 g AFDW ha^{-1} yr^{-1}, $\bar{B}$=844.41 g AFDW ha^{-1}, $P/\bar{B}$=0.96). Values of P, $\bar{B}$ and $P/\bar{B}$ ratio derived for *C. allmanni* were similar under both circumstances (Table 4.16).

The cohort of *C. crangon* born in July accounted for 90% of the male production. Production of females was higher than that of males (Table 4.12 and Table 4.13). A remarkable difference was observed between the production values obtained by four seasonally varying equations and the single equation for CL/AFDW relationship.

Table 4.12 Computation of production (g AFDW ha^{-1} yr^{-1}), mean Biomass (g AFDW ha^{-1}) and annual P/B ratio of *C. crangon* in the Forth Estuary, using AFDW values derived by seasonally varying equations of CL/AFDW relationships.

Date	Cohort	Number (ha^{-1})	Individual Weight (W_i), (g)	W_2-W_1 (g)	Mean Number (ha^{-1})	Production (g AFDW ha^{-1} yr^{-1})	Mean Biomass (g AFDW ha^{-1})	P/B Ratio
JUL		37731	0.068				2565.74	
OCT		4364	0.114	0.046	21048	968.20	497.53	
DEC	♂-I	2558	0.142	0.028	3461	96.91	363.17	
JAN		450	0.176	0.034	1504	51.12	79.13	
APR		204	0.231	0.055	327	17.98	47.17	
JUN		62	0.259	0.028	133	3.73	16.03	
					Total - cohort I	**1137.93**	**594.79**	**1.91**
JUL		3211	0.041					
OCT		2890	0.054	0.013	3050	39.66	156.04	
DEC	♂-II	1256	0.070	0.016	2073	33.17	87.93	
JAN		388	0.087	0.017	822	13.97	33.74	
APR		144	0.123	0.036	266	9.58	17.76	
					Total - cohort II	**96.37**	**73.87**	**1.30**
					Total - Males	**1234.30**	**668.66**	**1.85**
JUL		30612	0.052				1591.80	
OCT		2638	0.066	0.014	16625	232.75	174.10	
DEC	♀-I	967	0.047	-0.019	1803	-34.25	45.46	
JAN		557	.154	0.107	762	81.54	85.76	
APR		324	0.512	0.358	440	157.65	165.79	
JUN		316	0.417	-0.095	320	-30.37	131.61	
					Total - cohort I	**407.32**	**365.75**	**1.11**
JUL		5200	0.138					
OCT		*2964*	*0.276*	*0.138*	*4082*	*563.27*	*818.01*	
DEC	♀-II	1367	0.292	0.016	2166	34.65	399.28	
JAN		928	0.399	0.107	1148	122.81	370.31	
JUN		23	0.864	0.465	475	221.06	19.61	
					Total - cohort II	**941.79**	**401.80**	**2.34**
JUL		6138	0.427					
OCT	♀-III	284	0.643	0.216	3211	693.58	182.61	
DEC		204	0.688	0.045	244	10.98	140.49	
					Total - cohort III	**704.56**	**161.55**	**4.36**
APR	♀-0	326	0.051					
JUN		159	0.106	0.055	242	13.33	16.83	
JUL		21	0.119	0.013	90	1.17	2.45	
					Total - cohort 0	**14.50**	**9.64**	**1.50**
					Total - Females	**2068.17**	**938.74**	**2.20**
					Total - *C. crangon*	**3302.47**	**1607.40**	**2.05**

Table 4.13 Computation of production (g AFDW ha^{-1} yr^{-1}), mean Biomass (g AFDW ha^{-1}) and P/B ratio of *C. crangon* in the Forth Estuary, using AFDW values derived by single equation of CL/AFDW relationships.

Date	Cohort	Number (ha^{-1})	Individual Weight (W_1), (g)	W_2-W_1 (g)	Number (ha^{-1})	Production (g AFDW ha^{-1} yr^{-1})	Mean Biomass (g AFDW ha^{-1})	P/B Ratio
JUL		37731	0.010				377.31	
OCT		4364	0.019	0.009	21048	189.43	82.92	
DEC	♂-I	2558	0.025	0.006	3461	20.77	63.94	
JAN		450	0.030	0.005	1504	7.52	13.49	
APR		204	0.030	0.000	327	0.00	6.13	
JUN		62	0.033	0.003	133	0.40	2.04	
					Total - cohort I	**218.11**	**90.97**	**2.40**
JUL		3211	0.007					
OCT		2890	0.011	0.004	3050	12.20	31.79	
DEC	♂-II	1256	0.014	0.003	2073	6.22	17.59	
JAN		388	0.014	0.000	822	0.00	5.43	
APR		144	0.017	0.003	266	0.80	2.45	
					Total - cohort II	**19.22**	**14.31**	**1.34**
					Total - Males	**237.33**	**105.28**	**2.25**
JUL		30612	0.007					
OCT		2638	0.011	0.004	16625	66.50	214.28	
DEC	♀-I	967	0.011	0.000	1803	0	29.02	
JAN		557	0.027	0.016	762	12.19	10.6	
APR		324	0.053	0.026	440	11.44	15.04	
JUN		316	0.051	-0.002	320	-0.64	17.17	
					Total - cohort I	**89.49**	**50.38**	**1.77**
JUL		5200	0.019					
OCT		2964	0.044	0.025	4082	102.04	130.41	
DEC	♀-II	1367	0.044	0.000	2166	0.00	60.17	
JAN		928	0.057	0.013	1148	14.92	52.90	
JUN		23	0.098	0.041	475	19.49	2.22	
					Total - cohort II	**136.45**	**61.42**	**2.22**
JUL		6138	0.052					
OCT	♀-III	284	0.098	0.046	3211	147.71	27.83	
DEC		204	0.088	-0.010	244	-2.44	17.97	
					Total - cohort III	**145.27**	**22.90**	**6.34**
APR	♀-0	326	0.010					
JUN		159	0.015	0.005	242	1.21	2.38	
JUL		21	0.017	0.002	90	0.18	0.35	1.02
					Total - cohort 0	1.39	1.37	
					Total - Females	372.60	135.99	2.73
					Total - *C. crangon*	609.93	241.27	2.53

existence in reality by the single equation. Shrimps breed seasonally and produce more living tissues during the breeding season as indicated by the values derived by seasonal equations. Growth stagnation of animals in temperate areas is another significant factor which accounts for the seasonal changes in biomass in relation to size. The results obtained using seasonally varying equations account for these variations which exist in the life of the shrimps.

Similarly, a higher production was observed in *P. montagui* by seasonally varying equations, particularly in females (Table 4.14 and Table 4.15) in which the production is 3 order of magnitudes higher than that derived by single equation. The difference however, is not as marked as in *C. crangon* perhaps due to the emigration of breeding animals from the area of study during a part of the year. This may also account for the low production values obtained for the period from December to June.

Similar production values were obtained for *C. allmanni* by both methods (Table 4.16). This may be explained by the emigration of breeding animals from the estuary as well as the nonsignificance observed in the relationship of CL/AFDW among the seasons. (see page 47 Chapter 3).

Highest somatic production in all three species was observed in October and contributed about 75% of the total annual production. October is the beginning of the breeding season where maturation of the shrimps take place and this high production should be expected.

The production and biomass of the three species in the total area of study is given in Table 4.17. The values derived by seasonally varying equations were regarded as most valid here although the values derived using single equation are also given in the table for comparison. Highest production was observed in *C. crangon* (12.71-20.00 tons AFDW yr^{-1}) which accounted for 71.7% of the total shrimp production. *P. montagui* contributed 26.7% of the total production with a production of 4.74-7.45 tons AFDW yr^{-1} while the contribution from *C. allmanni* was negligible (1.6%) with a production of 0.28-0.45 tons AFDW yr^{-1}.

Table 4.14 Computation of production (g AFDW ha^{-1} yr^{-1}), mean Biomass (g AFDW ha^{-1}) and annual $P/\bar{B}$ ratio of *P. montagui* in the Forth Estuary, using *AFDW* values derived by seasonally varying equations of log CL/log AFDW relationships.

Date	Cohort	Number (ha^{-1})	Individual Weight (W_i), (g)	W_2-W_1 (g)	Mean Number (ha^{-1})	Production (g AFDW ha^{-1} yr^{-1})	Mean Biomass (g AFDW ha^{-1})	P/B Ratio
JUL		22.7	0.035					
OCT		2764	0.155	0.120	2485		77.24	
DEC		402	0.112	-0.043	1583	298.24	428.39	
JAN	♂-I	365	0.168	0.056	384	-68.07	45.05	
APR		672	0.175	0.007	519	21.48	61.34	
JUN		464	0.179	0.004	568	3.63	117.67	
						2.27	83.07	
				Total - cohort I (=Total Males)		257.56	135.46	1.90
JUL		1349	0.045					
OCT		1205	0.295	0.250	1277	319.18	355.33	
DEC		604	0.376	0.081	904	73.26	227.22	
JAN	♀-I	171	0.312	-0.064	388	-24.82	53.41	
APR		14	0.587	0.275	93	25.52	8.45	
JUN		41	0.543	0.231	106	24.54	22.43	
					Total - cohort I	417.68	133.37	3.13
JUL		1584	0.031					
OCT	♀-II	1215	0.698	0.397	1399	555.56	847.93	
					Total - cohort II	555.56	847.93	0.65
					Total - Females	973.24	981.30	0.99
					Total - P. montagui	1230.60	1116.70	1.10

Table 4.15 Computation of production (g AFDW ha^{-1} yr^{-1}), mean Biomass (g AFDW ha^{-1}) and $P/\bar{B}$ ratio of *P. montagui* in the Forth Estuary, using AFDW values derived by single equation of CL/AFDW relationships.

Date	Cohort	Number (ha^{-1})	Individual Weight (W_i), (g)	W_2-W_1 (g)	Mean Number (ha^{-1})	Production (g AFDW ha^{-1} yr^{-1})	Mean Biomass (g AFDW ha^{-1})	$P/\bar{B}$ Ratio
JUL		2207	0.065				143.45	
OCT		2764	0.186	0.121	2485	300.73	514.07	
DEC	♂-I	402	0.164	-0.022	1583	-34.83	65.96	
JAN		365	0.212	0.048	384	18.42	77.40	
APR		672	0.200	-0.012	519	-6.22	134.48	
JUN		464	0.216	0.016	568	9.09	100.25	
				Total - cohort I (=Total Males)		**287.18**	**172.60**	**1.66**
JUL		1349	0.079					
OCT		1205	0.288	0.209	1277	266.83	346.90	
DEC	♀-I	604	0.358	0.070	904	63.31	216.34	
JAN		171	0.317	-0.041	388	-15.90	54.27	
APR		14	0.444	0.127	93	11.79	6.39	
JUN		41	0.486	0.169	106	17.96	20.07	
					Total - cohort I	**343.98**	**128.79**	**2.67**
JUL	♀-II	1584	0.315					
OCT		1215	0.447	0.132	1399	184.72	543.02	
					Total - cohort II	**184.72**	**543.02**	**0.34**
					Total - Femalas	**528.70**	**671.81**	**0.79**
					Total - *P. montagui*	**815.88**	**844.41**	**0.96**

Table 4.16 Computation of production (g AFDW ha^{-1} yr^{-1}), mean Biomass (g AFDW ha^{-1}) and $P/\bar{B}$ ratio of *C. allmanni* in the Forth Estuary, using AFDW values derived by A, seasonally varying equations, B, single equation of CL/AFDW relationships.

Date	Cohort	Number (ha^{-1})	Individual Weight (W_1), (g)	W_2-W_1 (g)	Mean Number (ha^{-1})	Production (g AFDW ha^{-1} yr^{-1})	Mean Biomass (g AFDW ha^{-1})	$P/\bar{B}$ Ratio
A.								
OCT		3451	0.022				75.91	
DEC	♂-I	2263	0.037	0.015	2857	42.85	83.72	
JAN		598	0.054	0.017	1430	24.32	32.30	
APR		78	0.061	0.007	338	2.37	4.78	
			Total - cohort I (=Total Males)			**69.53**	**49.18**	**1.41**
OCT		2432	0.057					
DEC	♀-I	2489	0.038	-0.019	2461	-46.75	94.60	
JAN		1584	0.055	0.017	2037	34.62	87.12	
APR		85	0.075	0.020	834	16.69	6.35	
			Total cohort I (=Total females)			**4.56**	**62.69**	**0.07**
					Total - *C. allmanni*	**74.09**	**111.87**	**0.66**
B.								
OCT		3451	0.021				72.46	
DEC	♂-I	2263	0.036	0.015	2857	42.85	81.45	
JAN		598	0.053	0.017	1430	24.32	31.70	
APR		78	0.059	0.006	338	2.03	4.63	
			Total - cohort I (=Total Males)			**69.19**	**47.56**	**1.45**
OCT		2432	0.057					
DEC	♀-I	2489	0.038	-0.019	2461	-46.75	94.60	
JAN		1584	0.054	0.016	2037	32.59	85.54	
APR		85	0.074	0.020	834	16.69	6.26	
			Total - cohort I (= Total Females)			**2.52**	**62.13**	**0.04**
					Total - *C. allmanni*	**71.71**	**109.69**	**0.65**

Table 4.17 Total production (tons AFDW ha^{-1} yr^{-1}), mean biomass (g AFDW) of *C. crangon*, *P. montagui* and *C. allmanni* in the study area for the period July 1992 to June 1994, using A, values obtained by seasonally varying equations, B, values derived by single equation. Area at HW = 6057 ha and at LW = 3850 ha.

Species	Production (g AFDW ha^{-1} yr^{-1})	Biomass (g AFDW ha^{-1})	Total Production (tons AFDW)		Total Biomass (tons AFDW)	
A.			HW	LW	HW	LW
C. crangon	3302.47	1607.40	20.00	12.71	9.74	6.19
P. montagui	1230.60	1116.70	7.45	4.74	6.76	4.30
C. allmanni	74.09	111.87	0.45	0.28	0.68	0.43
	Total production of shrimps		27.90	17.73	17.18	10.92
B.						
C. crangon	609.93	241.27	3.43	2.18	1.57	1.00
P. montagui	815.88	844.41	4.94	3.14	5.11	3.25
C. allmanni	71.71	109.69	0.43	0.27	0.66	0.42
	Total production of shrimps		8.80	5.59	7.34	4.67

4.3.3.2 Size of the Population

Population size of *C. crangon*, *P. montagui* and *C allmanni* in the Forth Estuary indicates the dominance of *C. crangon* over the other two species (Table 4.18) both at high water and low water.

Table 4.18 Population size of the shrimps; *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary.

Year	Species	High Water		Low Water	
		Population (N x 10^7)	Standard Deviation x 10^7	Population (N x 10^7	Standard Deviation x 10^7
1992	*C. crangon*	8.08	2.57	7.43	2.00
1993		2.04	0.74	1.30	0.50
1992	*P. montagui*	3.33	0.96	2.62	0.71
1993		1.73	0.49	0.99	0.28
1992	*C. allmanni*	1.53	0.48	0.45	0.14
1993		1.16	0.41	0.29	0.05

Production estimated by seasonally varying equations derived values of about 5 orders of magnitudes higher for males and 4-10 order of magnitudes higher for females than that of single equation. The difference is apparently due to the omission of seasonal changes in biomass which is in Size of the population at high water and low water in *C. crangon* and *P. montagui* are comparable while the population size of *C. allmanni* was significantly less at low water. A population decline was observed in 1993 for all the species but *C. crangon* is the species affected mostly and *C. allmanni* the least.

4.4 DISCUSSION

As indicated by the results the high somatic production during the breeding season is not well represented when a single equation for whole year is used for the CL/AFDW conversion. In comparison the seasonal equations produced much more realistic estimates which account for low production in winter due to growth stagnation and high production in the breeding due to maturation. Hence the use of different equations for seasons can be regarded as the most appropriate in production calculations.

The total annual production of shrimps in the Forth Estray was estimated to be 0.84 AFDW m^{-2} yr^{-1} in which *C. crangon*, *P. montagui* and *C. allmanni* contributed 0.71, 0.12 and 0.01 g AFDW m^{-2} yr^{-1} respectively. The production of *P. montagui* and *C. allmanni* are not available from the literature and therefore only the production of *C. crangon* can be compared with the production of other areas. The production of *C. crangon* in the sub-

tidal Forth Estuary is much lower than the production estimates recorded in two bays, Gullmarswick and Sandwick in the Swedish west coast (Pihl and Rosenberg, 1982), which produced 2.20-3.08 g AFDW m^{-2} yr^{-1} and 2.25-2.64 g AFDW m^{-2} yr^{-1} respectively.

The $P/\bar{B}$ ratio was also lower at 2.05 in the Forth Estuary compared to 6.0 derived for post larval *C. crangon* in the Belgian Coastal North Sea (Redant, 1980), 7.73 - 9.31 estimated in Dutch Wadden Sea (Kuipers and Dapper, 1981). Following Elliott and (1989b) the lower $P/\bar{B}$ ratio, might indicate a more stressed population in the Forth than elsewhere.

4.5 CONCLUSION

Biomass and Production values at low water were considered as the realistic values as the adult shrimps are mostly confined to the subtidal area at low water but emigrate to intertidal areas at high water. This is further evident from the size of the population which remains fairly similar at both high and low water conditions. Thus, the area of Forth Estuary, between Forth Railway Bridges to Kincardine Bridge hold three populations of shrimps; *C. crangon*, *P. montagui* and *C. allmanni* with biomasses of 6.19 ton AFDW, 4.30 ton AFDW and 0.43 ton AFDW respectively, which produce total somatic material 17.73 ton AFDW. *C. crangon* was found to be the most important contributor, accounting for 71.7% of the total shrimp production while the contribution by *C. allmanni* was found to be negligible. The production estimates of *C. crangon*, *P. montagui* and *C. allmanni* may still be underestimated in the present study due to the following reasons.

1. The abundance of smallest fast-growing size classes was certainly underestimated due to mesh selection.

2. Only the population in the sub-tidal channel was sampled and there is evidence that the shrimps use intertidal areas, salt marsh creeks and other shallow areas.

3. The emigration of females to areas other than the study area. A part of the *C. crangon* population was observed in the upper estuary during the summer which

may be the reason for low production in the subtidal areas in June. Emigration also occurs in *P. montagui* when berried and *C. allmanni* when mature which may account for low production values.

Against this background, the production estimates presented in this study are likely to be low. Size of the population showed a high fluctuation between years although the reasons for the fluctuations are not certain. It may however, merely reflect the drastic environmental changes which may affect the survival of larval, juvenile or adult populations may reduce the size of the population in the next generation. In the Forth estuary, any drastic environmental factor which leads to an explanation of the fluctuations observed between two years are not found during the period of study.

CHAPTER 5. REPRODUCTIVE BIOLOGY

REPRODUCTIVE BIOLOGY

5.1 INTRODUCTION

Reproductive processes of caridean shrimps involve attaining maturity, mating and spawning. In addition, female shrimps have the responsibility of carrying and caring for eggs until they hatch. The eggs of caridean shrimps remain attached to the abdomen during their development and are thus vulnerable to the environmental hazards. Further, the reproductive process of *C. crangon*, *P. montagui* and *C. allmanni* is accompanied by migration (Boddeke, 1985; Mistakidis, 1957; Simpson *et al.*, 1970; Allen, 1960) and is further complicated due to the transformations of males into females after mating (Boddeke, 1961, 1975, 1982, 1989; Mistakidis, 1957). This is a particularly well known phenomenon in *P. montagui* (Mistakidis, 1957; Simpson *et al.*, 1970) in which the transformation is discernible by the external features (Fig.5.1a). There is however, disagreement regarding the transformation of *C. crangon* males (Meixner, 1966) but Boddeke (1975, 1982 and 1989) confirmed hermaphroditism in *C. crangon* by examining the histological changes which occur in the gonads after mating (Boddeke, 1989). The changes however, are not detectable from external features. Boddeke (1989) has derived linear regression equations for the relationship between the carapace length and length of the endopod separately for males and females and stated that an endopod measure which falls in between can be regarded as belonging either to a transitional or a secondary female.

In this chapter, the reproductive biology of *C. crangon*, *P. montagui* and *C. allmanni* is studied with the aim of finding out their reproductive potential, reproductive strategies and the behaviour of the reproductive components.

5.2 MATERIAL AND METHODS

Shrimps collected from all five stations in the estuary during the period of study were used for the examination of their reproductive biology. The methodology used for studying different aspects of their reproduction are described below.

5.2.1 Sex Ratio

All the shrimps in the samples were sexed using the characters described in the previous chapter (Fig.4.1) and the percentage of males in the catch was calculated by station, by size by dates and by tides. The number of males and females which occurred at each sampling station was pooled and the sex ratio (male:female) was tested using χ^2-test to find out the significant departures from 1:1 ratio. χ^2-test was performed by sampling dates and by size classes.

5.2.2 Maturity stages

Up to 25 shrimps per sex were selected at each sampling date from each station for determination of maturity stages and estimation of Fulton's condition factor as the index of maturity. The number of animals used varied depending on the availability of the shrimps and only the shrimps which are larger than the size at first maturity were used for studying these aspects. This is in particular to avoid the overestimation of immature (=inactive) stages and underestimation of condition factor by including immature animals. Since *C. crangon* females were found not "in berry" (without carrying eggs) in October and *C. allmanni* arrived in the estuary in October, this month was selected as the starting point for following the trend of maturity stages and condition factor. The maturity stages were studied therefore, for one year, from October 1992 to October 1993 for *C. crangon* and *P. montagui*. For *C. allmanni*, studies were carried out from October 1992 to June 1993.

Each shrimp was measured for carapace length and wet weighed to the nearest 0.001 g. Then the gonad was exposed by making a cut along the mid dorsal line of the carapace. Gonads of each animal was removed from the thorax and were examined microscopically in order to distinguish the maturity stage.

Gonads, in all three species, are paired organs consisting of two longitudinal tubes with closed ends. They are situated in the posterior half of the cephalothorax, ventral to the heart and dorsal to the stomach. Two lobes are connected at one fifth of the length from anterior end and so resembled 'H' shape. Testicular lobes are intricately curled, their extent depending upon the stage of development. Vasa deferentia were short and

originated from the middle of the testicular lobes and ran laterally into ejaculatory ducts. Ejaculatory ducts ended in a pore on the coxa of the each fifth periopod.

In females, characters such as the colour of the gonads and the size of ova and the position of gonads were used as the main features in determining the maturity stage and a key for the maturity stages was prepared. The key was validated by comparing the characters observed with Meredith (1952) and Abbot and Perkins (1977).

Meredith (1952) provided a key to the maturity stages based upon the embryological state of the eggs, ova diameter and size of the ovaries, and described 8 maturity stages. Abbot and Perkins (1977) made a simplified key using Meredith's (1952) key and considered only three stages of gonadal maturity; inactive, active and mature. In the present study, effort was given to establish a key which will distinguish clearcut stages of maturity thus avoiding the confusion over some intermediate stages as could be possible with Meredith's (1952) key. Once established this new key was used for all three species although small differences such as the size differences of ova and the ovary were observed among species. The criteria for the female maturity stages used in the present study are given below. For identification of maturity stages in *P. montagui* external features of the endopods of first and second pleopods described by Meredith (1952) (Fig. 5.1b) were also taken into account.

Stage of Female maturity	**Description**
1. Inactive	Ovaries small and white, ova not visible to naked eye. Two ovaries run parallel to each other and are connected by a transverse bridge. In *P. montagui* the ovaries lie parallel throughout their extent but in *C. crangon* anterior to the transverse bridge they diverge but then bend medially to meet at their tips.
2. Active	The ovaries become somewhat thicker but still white in colour. In *C. crangon* the gap between the gonads is closed and gonads start fanning out from antero-lateral sides. In *P. montagui* this stage is noted by thickening of gonads.

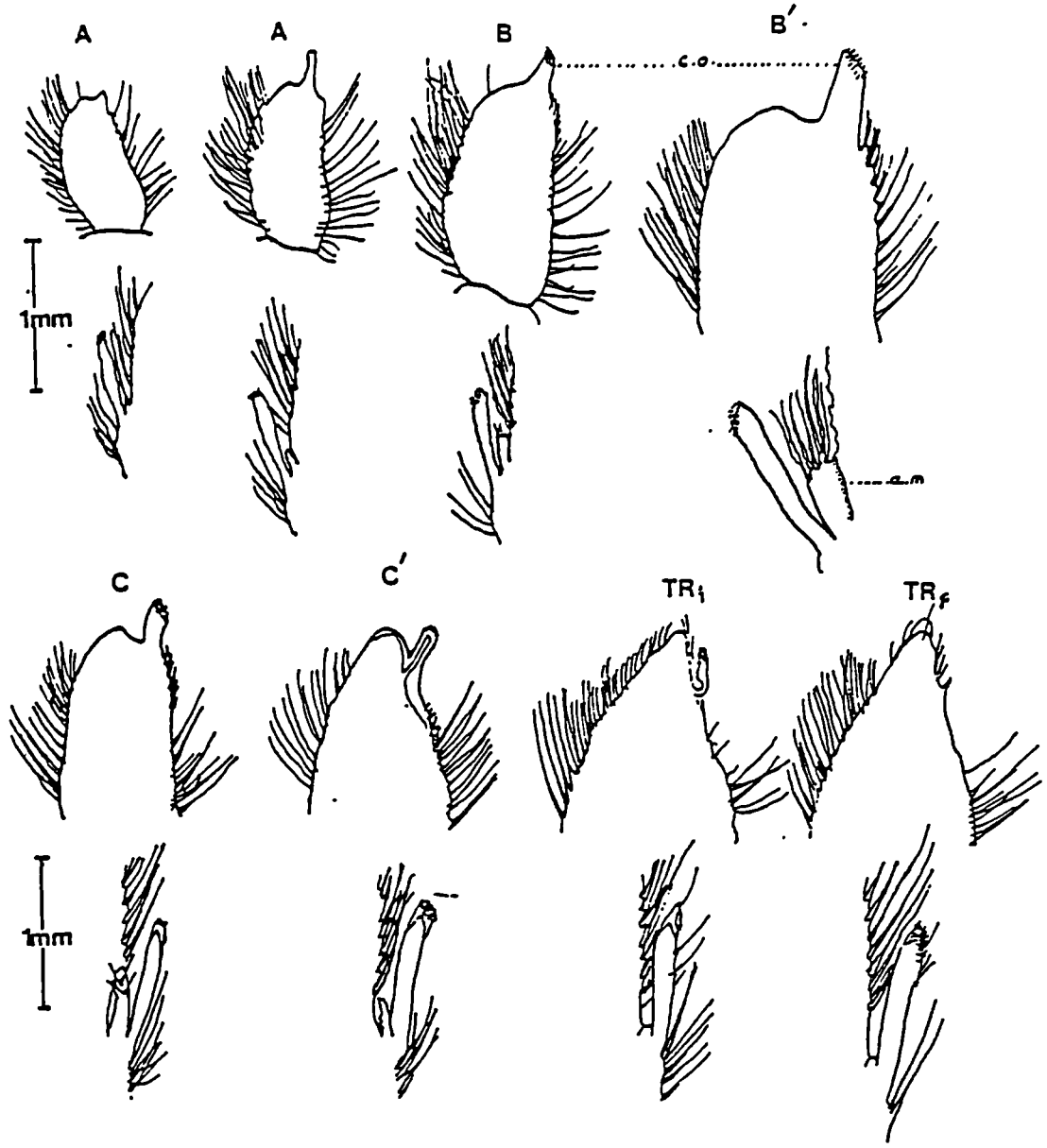


Fig.5.1a Secondary male sex characteristics of *P. montagui*. Upper series: endopodites of first pair of pleopods (c.o. - copulatory organ). Lower series: part of the endopodite of second pair of pleopods (a.m. - appendix masculina). A. immature (6.4-7.4 mm CL), B. Maturing (8.6 mm CL), B'. functional (9.8 mm CL), C. transforming (11.0 mm CL), C'. transforming (12.0 mm CL), TR_i. transitional (initial) and TR_f (final) (12.6 and 14.4 mm CL).
(After Mistakidis, 1957)

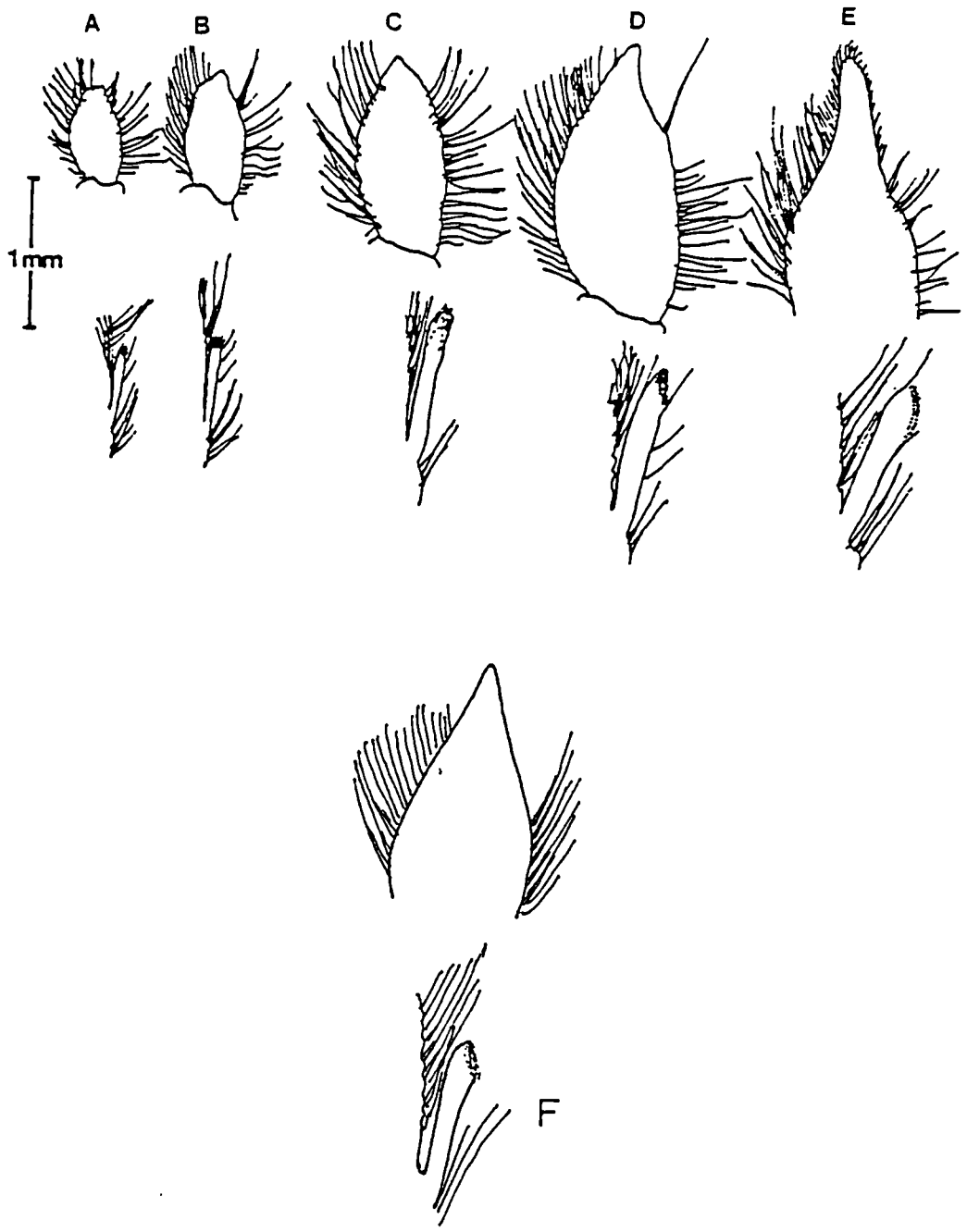


Fig.5.1b Secondary female sex characteristics of *P. montagui*. Upper series: endopodites of first pair of pleopods. Lower series: part of the endopodite of second pair of pleopods. A. and B. immature (5.6-7.2 mm CL), C. maturing (9.0 mm CL), D. mature (10.0 mm CL), E. mature (12.4 mm). F secondary female (After Mistakidis, 1957)

3. Maturing	Ovaries extend toward the anterior end of the thorax up to the posterior end of the cardiac stomach. Colour changes from cream to pale yellow. Posterior half of the cardiac stomach may be covered by the ovaries. Ova visible to naked eye. In *P. montagui* gonad extends up to the anterior end of the cardiac stomach, but not covering it fully.
4. Mature	Ovary covers the cardiac stomach completely. Ova clearly visible and brittle in nature. Colour of the ovary is orange.
5. Berried	Gonads resemble the size of inactive stage but are more wrinkled. Few large ova still remaining in the gonad. Female carrying eggs between pleopods.
6. "Hatched"	Eggs hatched and remains of connective tissues of egg attachment still present. Gonad stage varies from 1 - 4.

In males of *C. crangon* and *C. allmanni*, maturity stages were determined based on personal observations. Four maturity stages, inactive, active, mature and spent were identified. Attempts at identification of transitional stages of *C. crangon* by external features failed and the method described by Boddeke (1989) were tedious and impractical. For *P. montagui*, morphological changes in the endopod of the first pleopod and appendix masculina of the second pleopod described by Mistakidis (1957) were used to identify the different maturity stages (Fig.5.1a) in addition to changes in gonads. The transitional stages of males were also incorporated to the maturity stages as Tr_i, Tr_f and secondary females and were identified as given by Mistakidis (1957). Secondary females were identified by personal observation (Fig.5.1e). The criteria for male maturity stages are given below.

Stage of male maturity	**Description**
1. Inactive	Minute and thread-like gonads. Vasa deferentia not visible. Gonad confined to the posterior half of the carapace.

2. Active	Gonads extend up to the posterior end of the cardiac stomach. Vasa deferentia just visible. Gonads reach the posterior end of the stomach.
3. Mature	Vasa deferentia well developed. Gonads extend halfway or fullway on the cardiac stomach. Gonad full with seminal fluid.
4. Spent	Vasa deferentia flaccid and shrunken.

Fulton's condition factor [W/L^3) x 100] was calculated for each individual and monthly means were computed. Carapace length converted to total length was used as the length parameter and the weight was expressed in mg. The more popular and direct estimator, Gonado Somatic Index (GSI) was not employed due to the impossibility of separating and weighing the minute gonads, particularly of inactive and spent animals.

Spatial variations in the maturity stages for each species were tested using χ^2-test with the use of the SPSS statistical package.

5.2.3 Size at first maturity

Females

In the months of highest incidence of egg-carrying in both 1992 and 1993, samples of females were taken to estimate the size at first maturity. The months of June and July for *C. crangon*, and December and January for *P. montagui* and January and April for *C. allmanni*, emerged as the months with highest incidence of egg carrying.

The percentage of berried shrimps in each 1 mm length class was calculated and the size at maturity was estimated as the size in which 5% of the animals were in berry following Henderson and Holmes (1987).

Males

Since the maturity stages of males were not definitive in *Crangon* species, the indirect method (Somerton, 1980) was used to estimate the size at first maturity in males of those

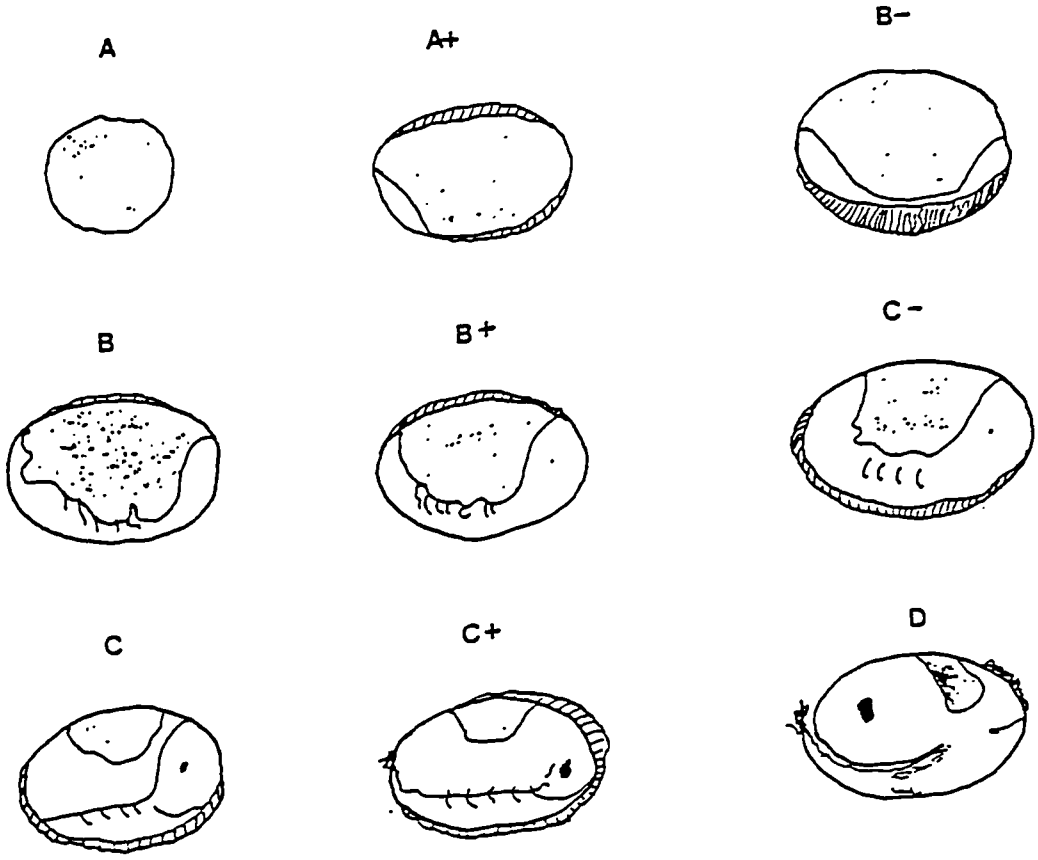
two species. A plot of carapace length versus subchela width was drawn using all the data over the total size range and the abrupt change in relative growth was sought as an indication of maturity. The size at maturity was calculated as follows:

1. Two regression lines were fitted to the data set, one for the definite adults and one for the definite juveniles using the log transformed data. Points which belonged to areas of overlap were excluded in calculations.
2. The two lines were extended to the overlapping region and the data points were assigned to the line closest to them, thus classifying them either as juveniles or adults.
3. Two regression lines were fitted again to the data set including the freshly classified data of the overlap region and the size at maturity was determined as the point where two regression lines met.

Secondly, the percentage of mature shrimps in each 1 mm length class was calculated taking the shrimps of maturity stage three and above as matured. The size at maturity was then estimated as the size in which 50% of the shrimps are matured.

5.2.4 Egg development stages in berry

Stages of egg development were studied in detail only for *C. crangon* because the later stages of egg development were not observed in the estuary in other two species. Development stages of eggs were determined using the descriptions by Meredith (1952) who described 10 egg development stages (Fig. 5.2). These stages were regrouped into 4 stages in the present study for clarity and convenience. As such the egg development stages chosen include 1. blastula stage (stage A and A+ in Meredith, 1952), 2. gastrula stage (B-, B and B+) 3. development of eye (C-, C and C+), and 4. body detached from the other parts (D). Stage 10, the post-hatching stage was not included since it refers to a stage where larvae had already hatched out. The number of berried females carrying eggs of each category was determined separately for stations. Temporal variation in each egg developmental stage was computed as the percentage of total observations throughout the year.



A A. Newly laid eggs. spherical. No development.
A+. Egg elongate in one diameter, early blastoderm visible.

B B-. Large blastoderm, onset of gastrulation.
B. Early segmentation of body.
B+. Minute eye visible, greater segmentation.

C. C-. Eye larger.
C. Eye larger; outline of carapace and abdomen discernible.
C+. Eye almost full size; abdomen increased in length.

D. D. Pre-lateral stage; eye large, abdomen long and free from head; yolk very reduced.
E. Post hatching stage (not included in this study)

Fig.5.2 Stages of egg development in *C. crangon* as described by Meredith, 1952. Bold letters refer to the stages of development used in the present study.

5.2.5 Fecundity

Up to 10 berried females of each species, per station per sampling date were randomly selected for fecundity studies. The number taken for the studies totally depended on the availability of berried females. The egg mass of each female was detached from the body by the method of rapid removal of eggs (Choy, 1985) using NaOCl solution for degenerating the connective tissues in the egg mass. The best concentration of NaOCl for egg separation was determined as 0.4 mg l^{-1} by conducting a series of trials. Swelling and bursting of eggs took about 20 - 30 minutes in this concentration while the separation of eggs took only 3-5 minutes. For the separation of eggs, shrimps were kept on petri dishes so that they lay on their ventral side with eggs dipped in the NaOCl solution. After all the eggs were separated from the egg mass (within 3-5 minutes) NaOCl was pipetted out carefully and the eggs were washed immediately, in cold water followed by 50% alcohol and preserved in 70% alcohol for later counting. The egg-development stage of each egg mass was noted and the total number of eggs was counted using the lower magnification (10 x 4.7) of the microscope. Fecundity was determined as the number of newly spawned eggs (stage A) carried by each female.

The relationship between carapace length (CL) and fecundity (F) was tested using the following models. Since CL is linearly corelated to TL, TL in Boddeke (1982) model is substituted by CL.

1. $F = a + b(CL)^3$ (Transformed from TL in Boddeke (1982) model to CL)
2. $F = a(CL)^3$ (Henderson and Holmes, 1987)

The variations between winter and summer as indicated by Boddeke (1982) and the variations in the relationship due to spatial variations of the population were also investigated.

5.2.6 Spawning season

Spawning season of the shrimps was determined by occurrence of berried females in the population. The percentage of berried females at each station was calculated as a percentage of total female catch.

5.3 RESULTS

5.3.1 Sex Ratio

5.3.1.1 Spatial, temporal and tidal variations in the sex ratio

The sex ratio of *C. crangon* showed both temporal and tidal variations although spatial variations were little (Fig.5.3). In January and April 1992, the male:female ratio was close to 1:1, but in June 1992 significant bias towards females was observed at the lower 4 stations. The male percentage dropped by about 20-30%. In July the sex ratio again showed 1:1 ratio but in October 92 - January 1993 the male fraction dominated the catch. The same temporal trend was observed in the year 1993-1994 although some irregularity among stations occurred in some instances.

The sex ratio of *C. crangon* varied little with tides in the lower three stations, but wide fluctuations were observed at Bo'ness (Fig.5.3). A higher percentage of males occurred at high water in all the stations except at Bo'ness where male percentage was higher at low water. Bo'ness showed marked variations between the tides while the variations in the other stations are little. The rise in male percentage is marked at Longannet in December and January with the percentage of males going up by 15-20% at high water. In the lower three stations, variation was marked only in June at Blackness; June, October and December at Port Edgar; and April to July and December to January at Tancred Bank. Male percentage was higher both at HW and LW from October to January.

There were little spatial variations in the sex ratio of *P. montagui*, although tidal and temporal variations are observed (Fig. 5.4). A marked drop in the male percentage was observed in December at low water, although HW carried higher percentage of males. The male percentage was generally higher from January to June.

Spatial variations in sex ratio is not marked in *C. allmanni* and the tide also had no effect on the sex ratio, indicating both males and females migrate at the same rate (Fig.5.5). In October a higher sex ratio was observed at Port Edgar and in December this was apparent only at Longannet. The percentage of males is lower generally except the period when they first arrive at the estuary.

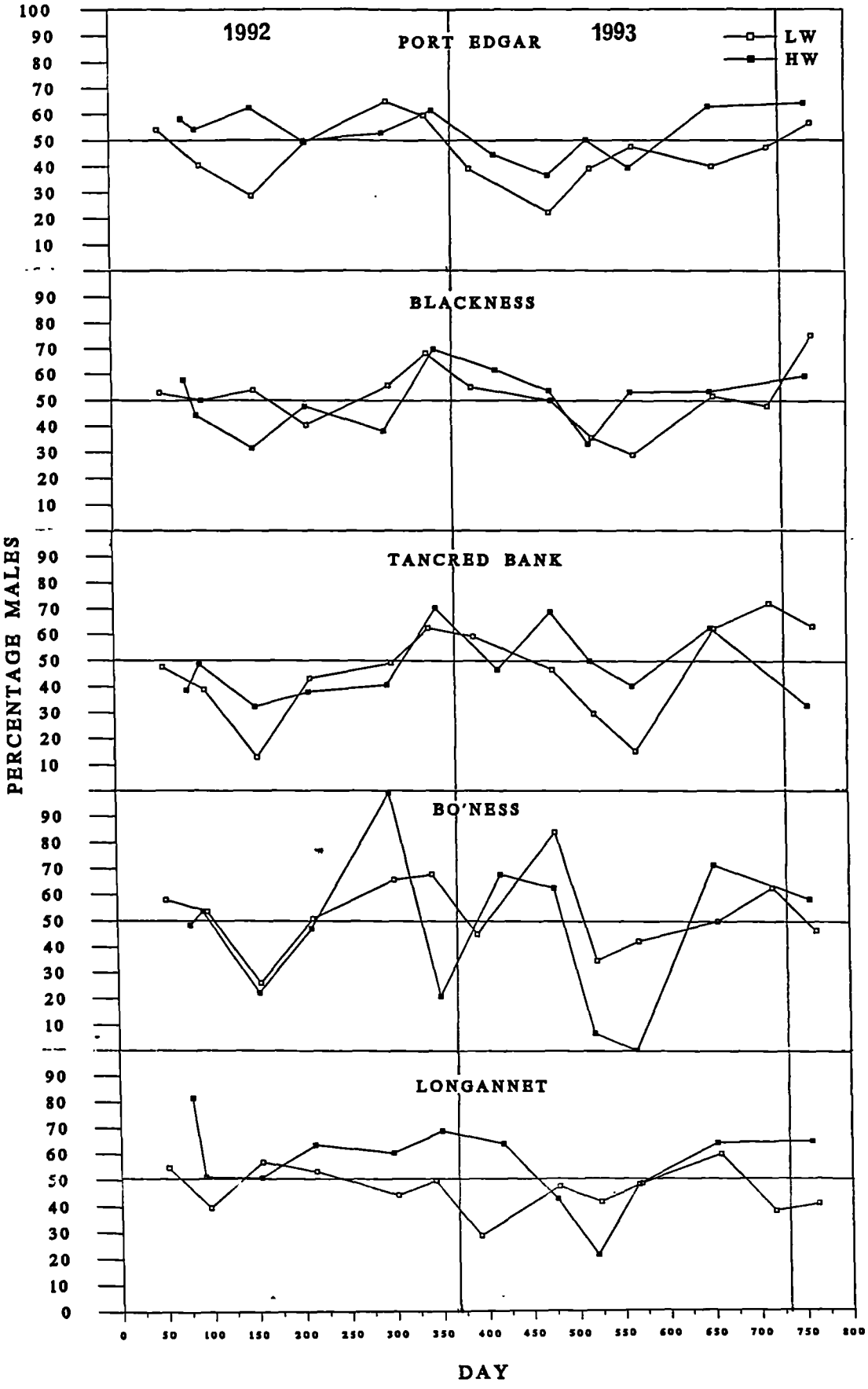


Fig.5.3 Spatial, temporal and tidal variations in the percentage of male *C. crangon* in the Forth Estuary.

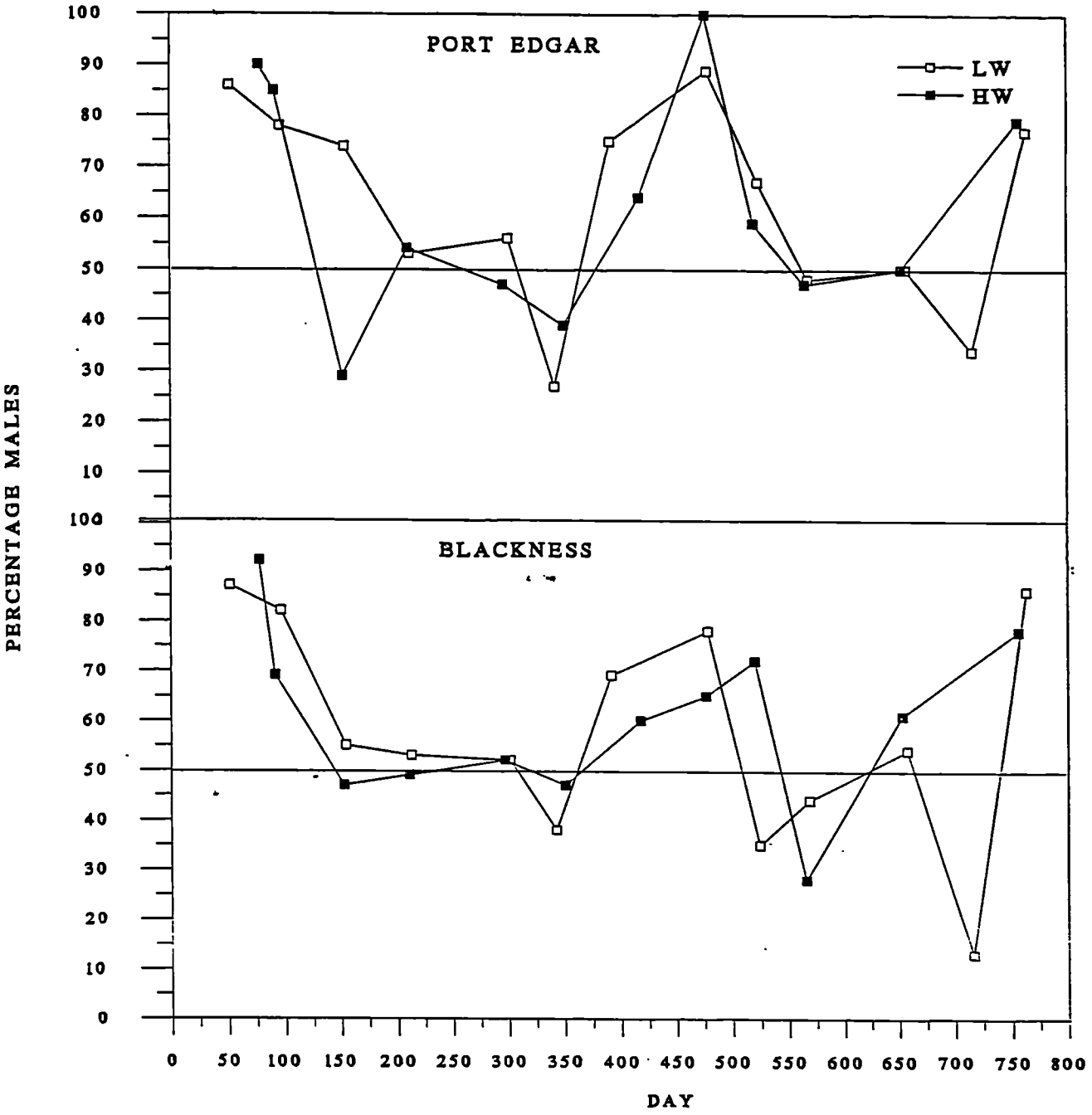


Fig.5.4 Spatial, temporal and tidal variations in the percentage of male *P. montagui* in the Forth Estuary. Day 1=1 Jan 92.

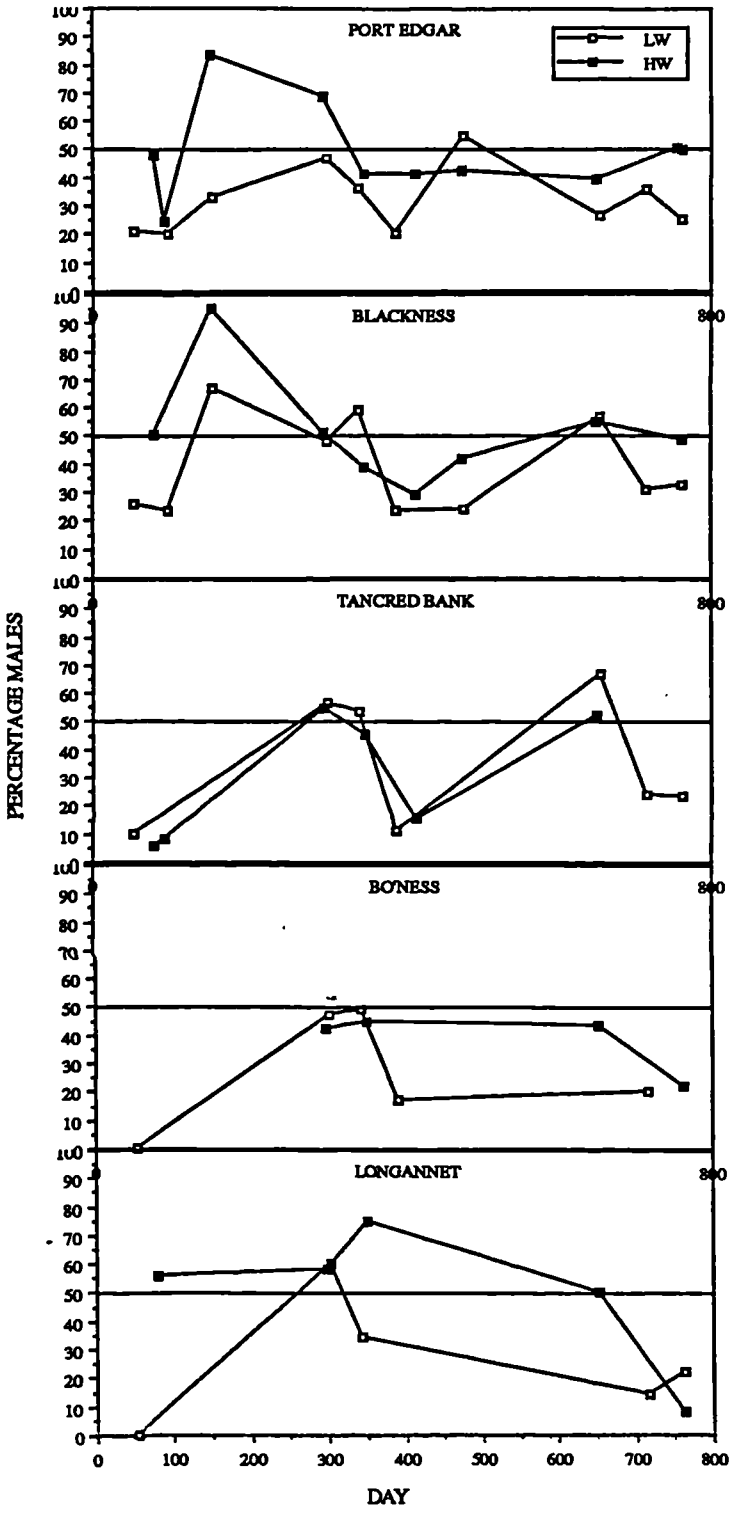


Fig.5.5 Spatial, temporal and tidal variations in the percentage of male *C. allmanni* in the Forth Estuary. Day 1=1 Jan 92.

χ^2-test revealed a significant departure from the sex ratio 1:1, for all three species (Table 5.1). 1:1 sex ratio was observed only in April in both years for *C. crangon* and June, July 1992 and December and June 1993 for *P. montagui.* Male:female ratio of *C. allmanni* did not follow the 1:1 sex ratio at any time of the year 1992, but agreed with 1:1 ratio in April 1993 and October 1993.

5.3.1.2 Sex ratio in relation to carapace length

The sex ratio of *C. crangon* and *P. montagui* showed an abrupt change at a certain size (Fig.5.6). Sex ratio remained fairly constant up to the size 9.5 CL in *C. crangon* and 11.5 in *P. montagui* but changed abruptly beyond. The change occurred in *C. crangon* at a size between 9.5 and 10.5 and in *P. montagui* at a size between 11.5 and 12.5 in carapace length. *C. allmanni* exhibited a low percentage of males at all size classes except at the smallest size (5.5 in carapace length). The change in the percentage of males decreased gradually.

Significant departure of sex ratio from 1:1 ratio was obtained for all three species in all size classes (Table 5.2). In *C. crangon* number of males were higher up to the size 9.5 and beyond the size 10.5 CL the number of males was negligible. The same applies to *P. montagui* but the male proportion becomes less at a later size, 12.5 CL. In *C. allmanni* male proportion was always found to be lower than that of females, except at the size class 5.5 CL.

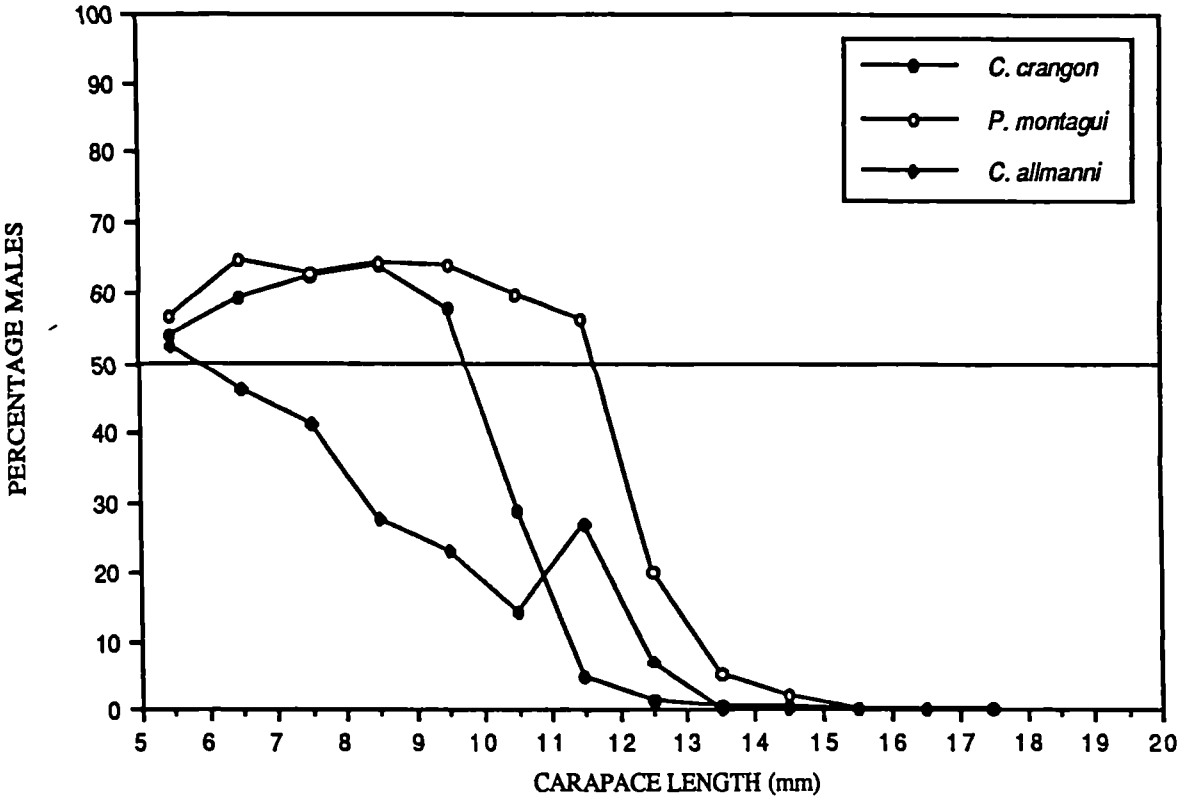


Fig. 5.6 Percentage of males of *C. crangon*, *P. montagui* and *C. allmanni* at each length class in the Forth estuary.

Table 5.1 Number of males and females of three species; *C. crangon*, *P. montagui*, and *C. allmanni* at each sampling date and the significance of the 1:1 sex ratio as indicated by χ^2-test.

	C. crangon			*P. montagui*			*C. allmanni*		
Month	N ♂	N ♀	χ^2-value	N ♂	N ♀	χ^2-value	N ♂	N ♀	χ^2-value
				1992					
JAN	616	534	5.85*	527	112	105.30***	157	266	28.09***
APR	529	556	0.67	188	124	13.133***	21	76	31.19***
JUN	273	375	16.06***	192	172	1.10	55	13	24.24***
JUL	19787	19033	14.64***	3218	3146	0.81	0	0	-
OCT	3859	2694	207.12***	258	1320	161.23***	1703	1198	87.91***
DEC	2744	1156	646.60***	238	203	2.78	1105	1353	25.02***
				1993					
JAN	839	886	1.28	190	144	6.34*	319	771	187.43***
APR	292	251	3.10	128	62	22.93***	39	47	0.74
JUN	101	176	20.31***	126	123	0.04	0	0	-
JUL	1291	651	210.92***	423	361	4.90*	0	0	-
OCT	2651	1686	214.72***	1148	922	24.67***	858	849	0.05
DEC	1018	742	43.28***	54	167	57.78***	129	304	70.73***
JAN	827	545	57.96***	393	176	82.76***	599	1089	142.24***

* - $p<0.05$
** - $p<0.01$
*** - $p<0.001$

Table 5.2 Number of males and females of three species; *C. crangon*, *P. montagui*, and *C. allmanni* by size classes and the significance of the 1:1 sex ratio as indicated by χ^2-test.

	C. crangon			*P. montagui*			*C. allmanni*		
CL (mm)	N ♂	N ♀	χ^2- value	N ♂	N ♀	χ^2- value	N ♂	N ♀	χ^2- value
5.5	8098	6905	94.86***	1581	1214	48.19***	1160	1048	5.68**
6.5	8881	6132	503.36***	1737	940	237.28***	1820	2103	20.42***
7.5	6050	3662	587.16***	1193	704	126.05***	1177	1702	95.74***
8.5	4065	2290	494.50***	869	478	113.50***	292	769	214.45***
9.5	2183	1590	93.20***	702	397	84.65***	39	130	49.00***
10.5	754	1880	481.35***	742	503	45.88***	12	72	42.86***
11.5	117	2436	2106.45***	801	625	21.72***	20	54	15.62***
12.5	30	2220	213.60***	177	708	318.60***	2	27	21.55***
13.5	3	1151	1142.03***	31	591	504.18***	0	8	8***
14.5	301	488	485.01***	6	327	309.43***	0	0	-
15.5	0	237	237***	0	234	234.00***	0	0	-
16.5	0	79	79***	0	126	126.00***	0	0	-
17.5	0	3	3***	0	12	12.00***	0	0	-

* - $p<0.05$
** - $p<0.01$
*** - $p<0.001$

5.3.2 Maturity stages

5.3.2.1 Distribution of maturity stages

In total, 1727 *C. crangon*, 1282 *P. montagui* and 663 *C. allmanni* were analysed for studies of maturity stages. The data from the same animals were used for χ^2-test excluding the stages invalid for analysis due to absence of maturity stages in some stations.

Males

More than 80% of the male *C. crangon* were in mature stage from October to April. Inactive and active stages were observed only in October (Fig.5.7). From January onwards both functional and spent males were observed but the functional males were absent in June and July. χ^2-test revealed that maturity stages are not evenly distributed both spatially (χ^2-value = 23.45, DF = 5, $p<0.001$) and tidally (χ^2-value = 8.23, DF = 5, $p<0.001$). This is in particular due to the concentration of mature males at the uppermost stations and having more mature animals at low tide.

In *P. montagui* males were always found either in mature or in transitionary stages. First indication of transition was observed in January and by April more than 50% of the males were in late transition. A significant difference was observed in spatial (χ^2-value = 8.34, DF = 2, $p<0.05$) and tidal (χ^2-value = 66.53, DF = 2, $p<0.001$) distribution and was due to higher numbers of mature animals occurring at Port Edgar. Transitional stages however, were found to be distributed equally between stations and tides.

C. allmanni comprised about 50% of inactive shrimps in October. The percentage of mature shrimps increased from December onwards while the percentage of inactive and active stages gradually decreased. Spent males were present in January but were not present in April. All the males left in the estuary in April belonged to the mature stage. The distribution of male maturity stages of *C. allmanni* also were significant both spatially (χ^2-value = 101.12, DF = 12, $p<0.001$) and tidally (χ^2-value = 30.38, DF = 3, $p<0.001$) although tidal variation in mature stages were not significant.

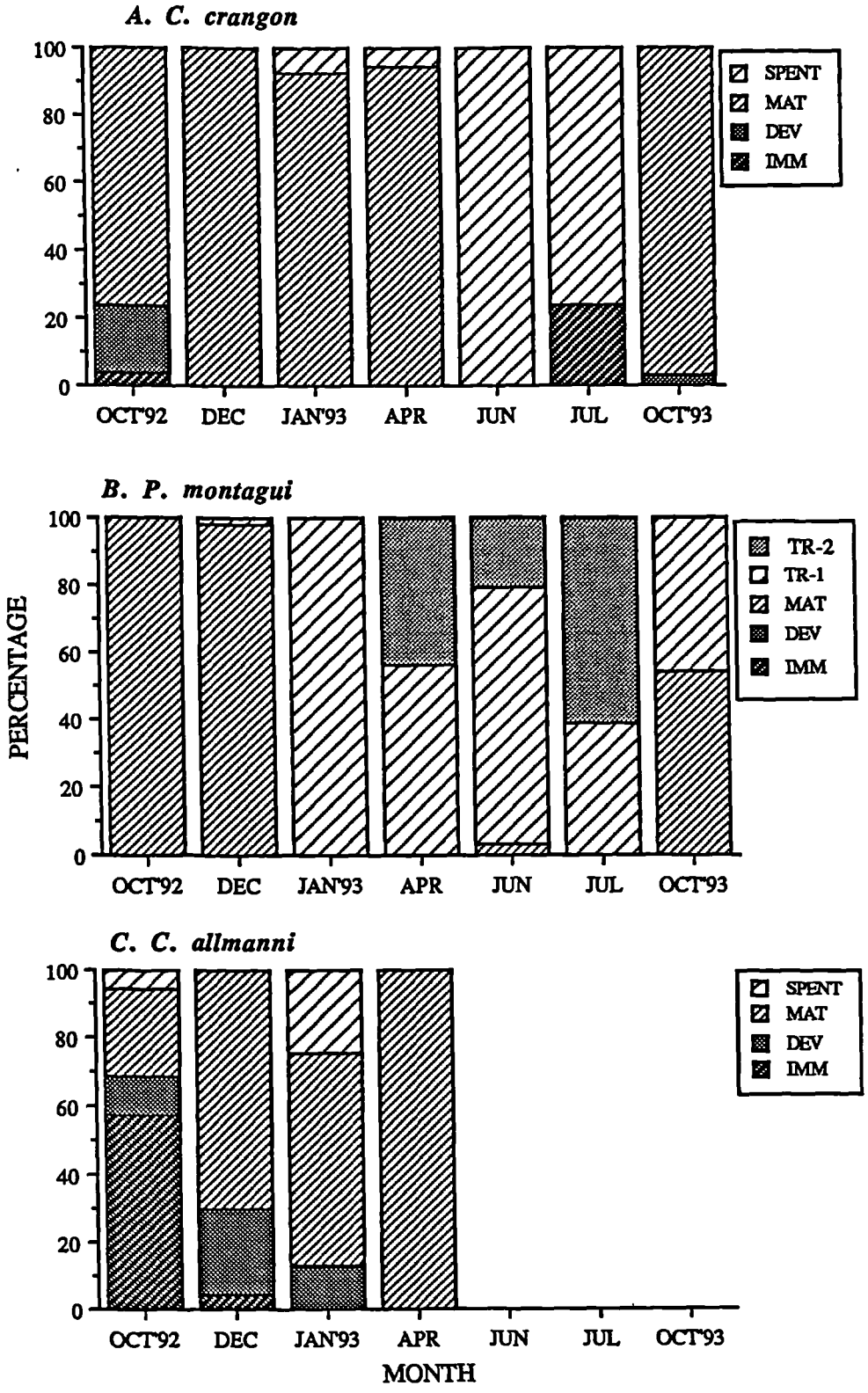


Fig.5.7 Temporal variations in the maturity stages of male A. *C. crangon*, B. *P. montagui* and C. *C. allmanni* in the Forth Estuary during the period October 1992 to October 1993.

Females

In October most of the female *C. crangon* were found to be in early maturity stages 1 and 2 (Fig. 5.8). From December to January more than 60% of the population comprised mature and berried females. Females with remnants of hatched larvae ("hatched") were first observed in April and were present in varying proportions until July. The highest percentage of females were represented by berried females during April, June and July. The distribution of female maturity stages resembled that of males varying significantly among stations (χ^2-value = 98.88, DF = 20, $p<0.001$) and tides (χ^2-value = 37.46, DF = 5, $p<0.001$). As observed in males, this is also due to the concentration of mature and berried females at uppermost stations.

In *P. montagui* mature females were found in October-December and by January all the females were in berry. Females with remnants of hatched larvae appeared in the catch in April and from June to July the females were represented by either resting or inactive shrimps. The distribution of maturity stages varied significantly between stations (χ^2-value = 18.91, DF = 5, $p<0.001$) as well as with tides (χ^2-value = 29.64, DF = 5, $p<0.001$).

C. allmanni females were in inactive stage in October. Berried females were present in January and April. The percentage of berried females was high in April and the females left the estuary in this stage. *C. allmanni* females also showed significant variation of maturity stages among stations (χ^2-value = 75.47, DF = 20, $p<0.001$) and between tides (χ^2-value = 20.43, DF = 5, $p<0.01$).

5.3.2.2 Mean condition factor

The peak mean condition factor for *C. crangon* males occurred in January and July (1.30 and 1.30), and for females in April and July, 1.32 and 1.36 respectively (Table 5.3). This indicates that males mature earlier than females. The mean condition factor of females however, remained high from December - July and dropped markedly in October. *P. montagui* males reach peak mean condition factor in October (0.92) while females were in peak condition from October to January (1.55 - 1.58). In July 1993 early maturation was observed for both sexes as indicated by an increased mean condition factor.

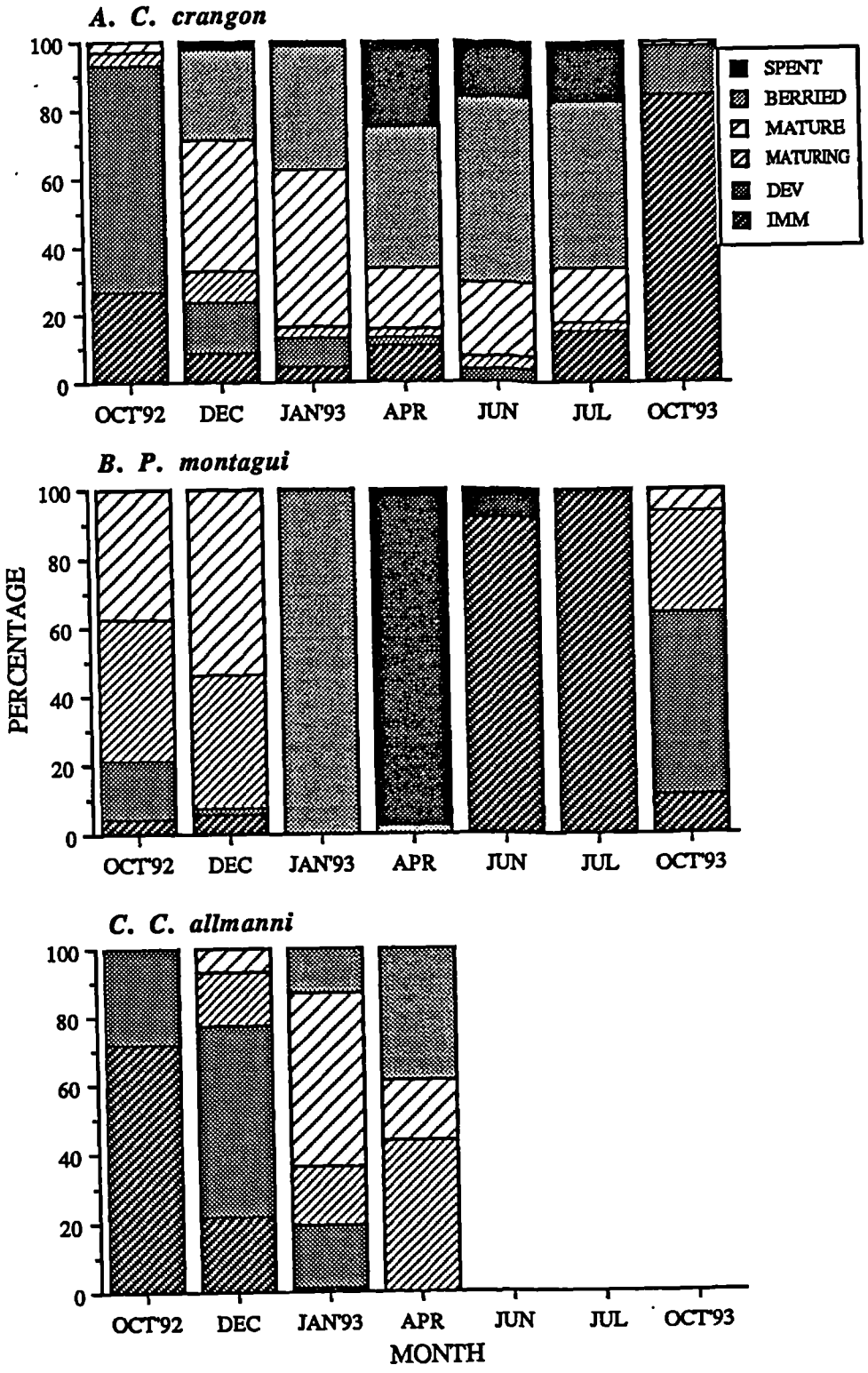


Fig.5.8 Temporal variations in the maturity stages of female A. *C. crangon*, B. *P. montagui* and C. *C. allmanni* in the Forth Estuary during the period October 1992 to October 1993.

Table 5.3 Temporal variations in mean condition factor ± std. in *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary during the period October 1992 to October 1993.

	C. crangon				*P. montagui*				*C. allmanni*			
	Male		Female		Male		Female		Male		Female	
Month	Number observed	Mean C.F.±std	Number observed	Mean C.F.±std	Number observed	Mean C.F.±std	Number observed	Mean C.F.±std	Number observed	Mean C.F.±std	Number observed	Mean C.F.±std
Oct 92	104	1.27±0.13	195	1.23±0.15	96	0.92±0.14	112	1.55±0.20	54	0.84±0.14	46	0.84±0.14
Dec 92	166	1.26±0.15	255	1.30±0.16	96	0.84±0.13	106	1.61±0.29	111	0.89±0.11	155	0.89±0.13
Jan 93	107	1.30±0.21	196	1.29±0.15	95	0.86±0.10	57	1.58±0.21	82	0.87±0.11	143	0.93±0.10
Apr 93	3871	1.24±0.13	115	1.32±0.15	85	0.85±0.12	43	1.34±0.17	29	0.85±0.10	39	0.91±0.13
Jun 93	38	1.21±0.12	79	1.34±0.20	92	0.85±0.09	87	1.43±0.24	-	-	-	-
Jul 93	50	1.30±0.10	133	1.36±0.17	116	0.92±0.09	89	1.52±0.23	-	-	-	-
Oct 93	72	1.25±0.10	146	1.23±0.16	92	0.84±0.14	109	1.40±0.19	-	-	-	-

C. allmanni males showed high mean condition factor in December (0.89) while peak condition factor for females occurred from January to April (0.93 -0.91).

5.3.2.3 Gonad maturity stages of berried females of *C. crangon*

Ovaries of female *C. crangon* were found in mature condition, while the female was still in berry with eggs at late developmental stages. These females therefore, were examined in order to find out the number of spawnings per female. More than 90% of the females examined in April and June were either in maturing or mature condition (Fig.5.9) indicating readiness for the next spawning. The majority of females of July had resting gonads indicating the cessation of spawning. A minor percentage however, still contained mature gonads.

5.3.3 Size at first mass maturity

The first massive maturity of female *C. crangon* was found to be at 8.5 mm in carapace length (Fig. 5.10) while in *P. montagui* it was 8.6 mm in Carapace length. *C. allmanni* attained its first maturity at an early size, 7.5 mm in carapace length.

The size at maturity of male *C. crangon* was determined as 8.7 mm CL (Fig.5.11) using the method of Somerton (1980) and 7.0 mm CL for *C. allmanni.* The size at maturity determined as the 50% maturity level, 8.1 mm Cl for *C. crangon* and 6.8 mm CL for *C. allmanni* (Fig. 5.12) compared well with those derived by Somerton (1980). The size at maturity of *P. montagui* was impossible to determine since all the males found in the estuary and Firth of Forth appeared to be matured. The size of the smallest matured male was 7.0 mm CL.

5.3.4 Egg developmental stages in berry

Temporal variations in the occurrence of egg development stages were similar at all stations (Fig.5.13). Peak occurrence of early stage eggs in December indicates the beginning of the breeding season. First appearance of the late stage eggs occur in April denoting April as the beginning of first larval hatching. From April onwards, the late developed eggs occur all the time until July indicating that larval hatching is a continuous process in the estuary during the summer. The second peak of the early stage varied

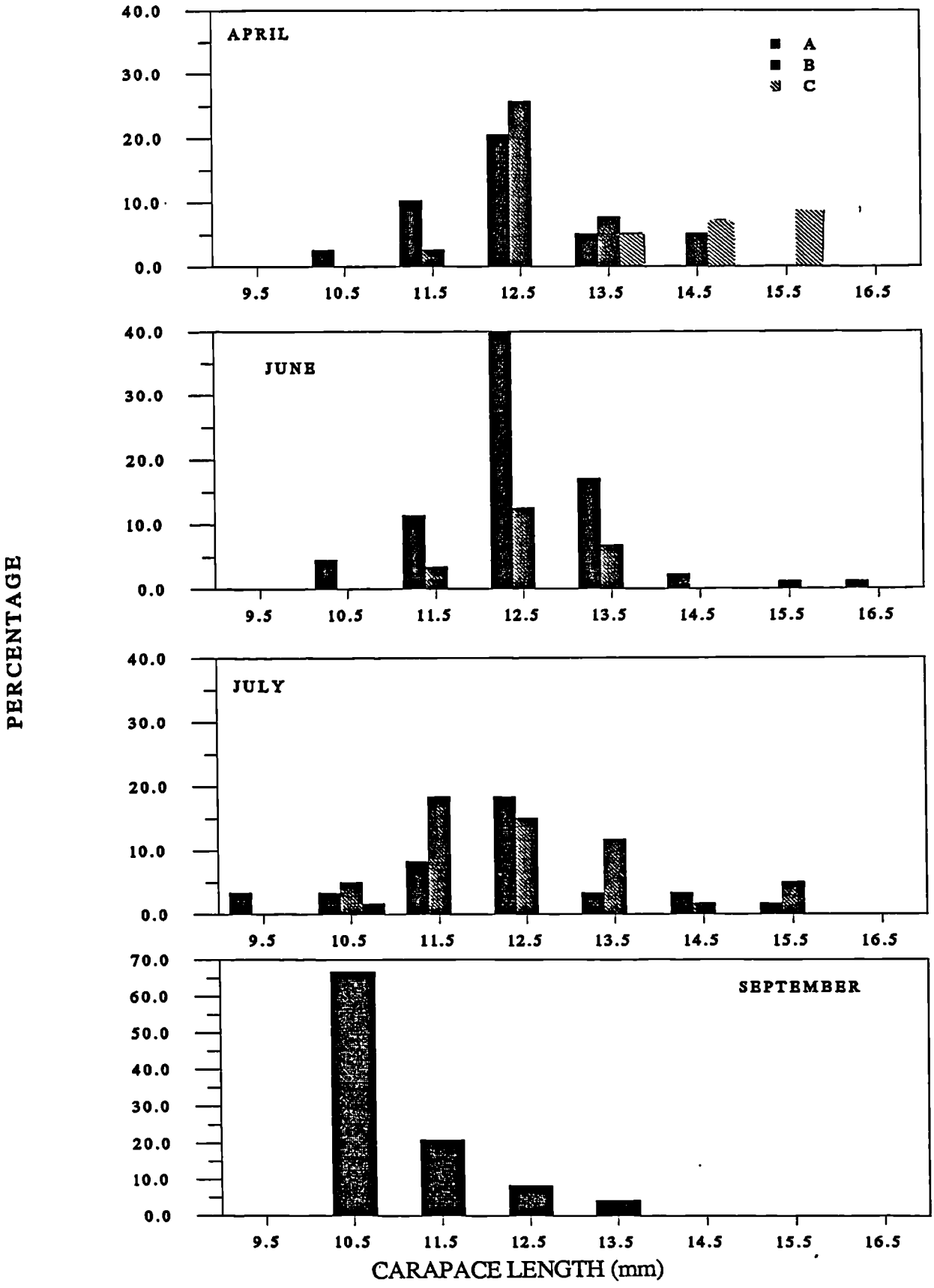


Fig.5.9 Gonad maturity stages of berried females with ripe eggs (C and D categories) and recently spawned females (remains of egg membranes still attached to pleopods).

A = females with ripe eggs / gonad mature

B = recently spawned female / gonad mature

C = recently spawned female / gonad in resting stage

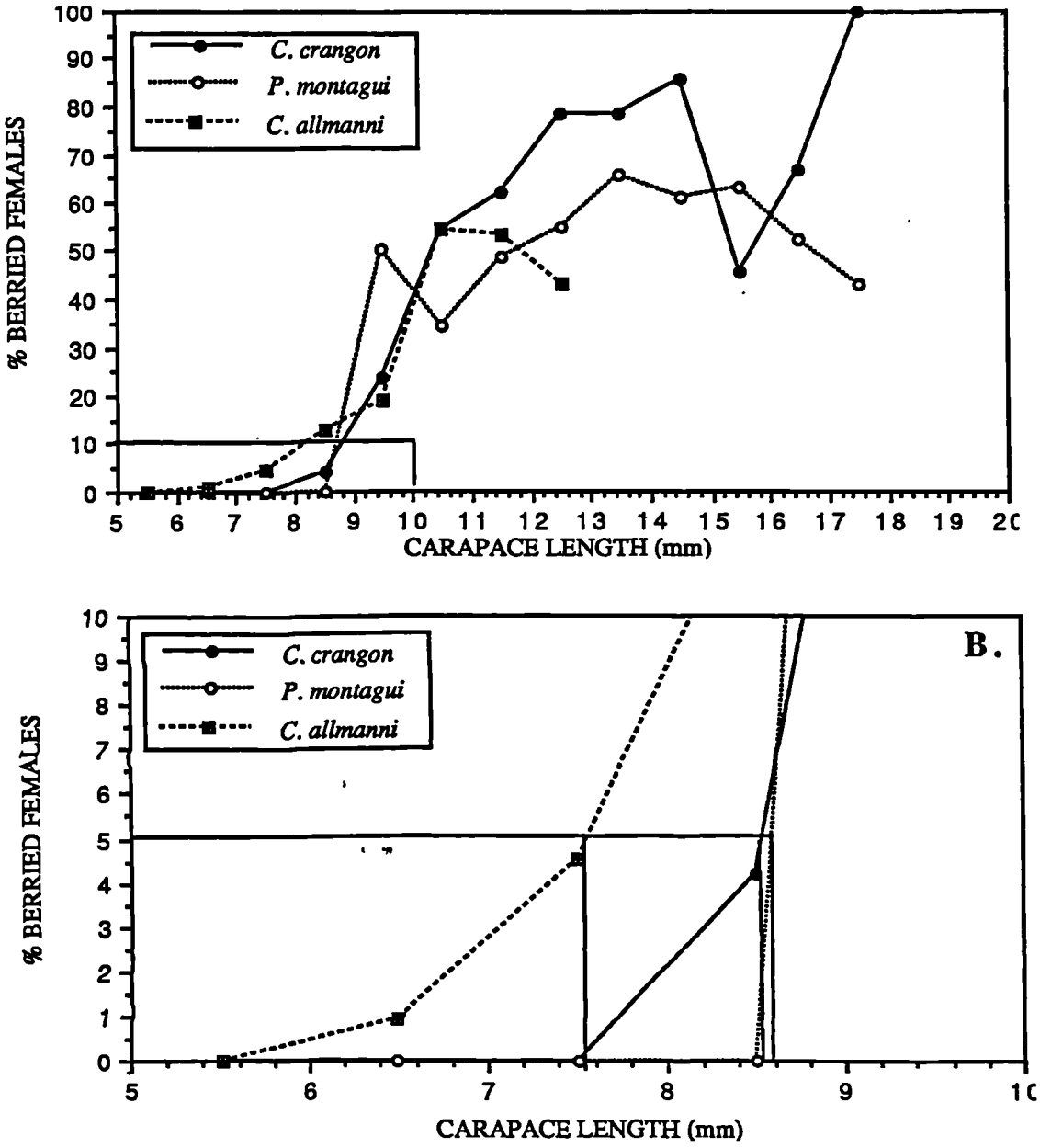


Fig.5.10 Size at first maturity in female *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary.

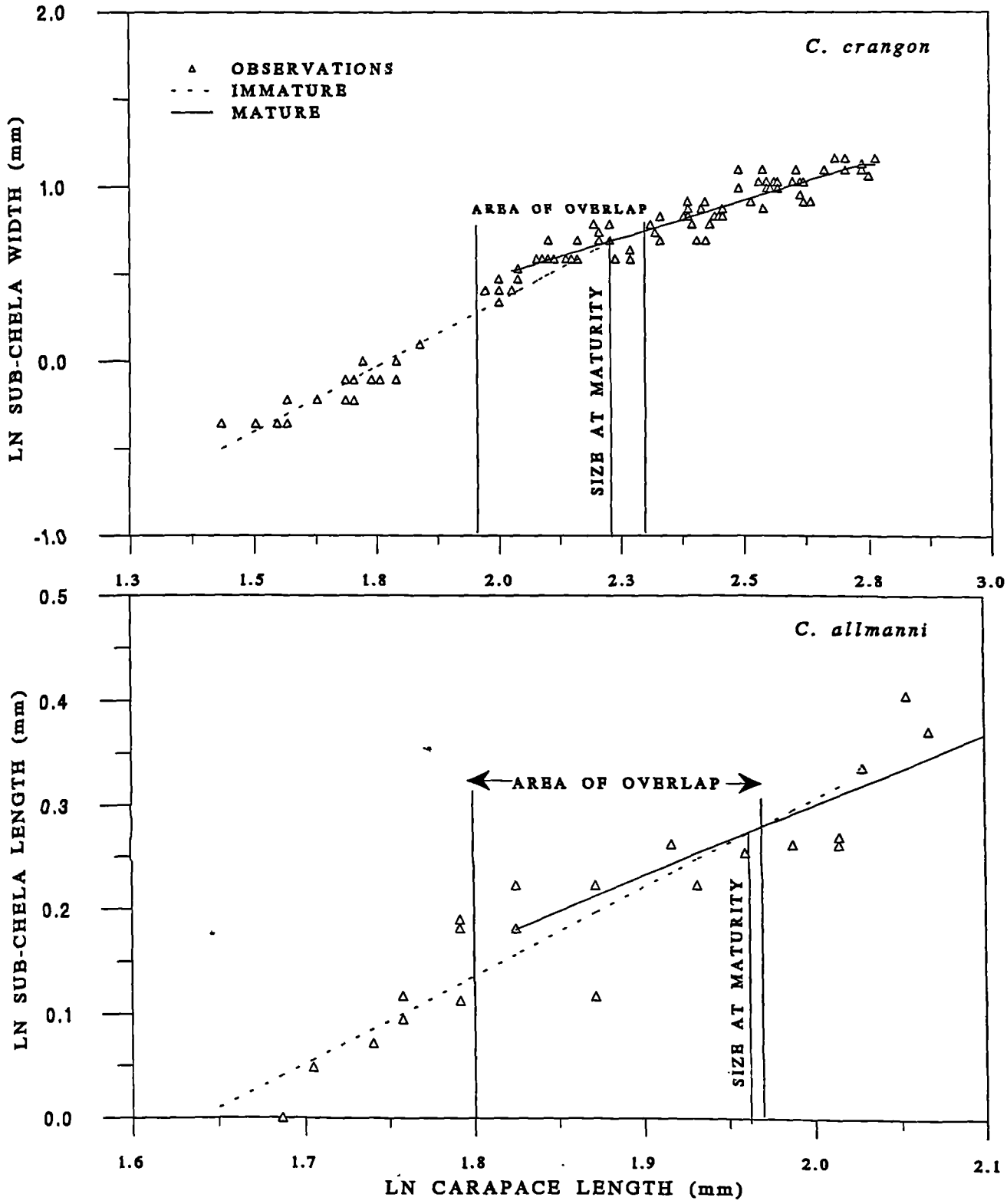


Fig.5.11 Size at first maturity in male *C. crangon* and *C. allmanni* in the Forth Estuary as derived from Somerton (1980) method.

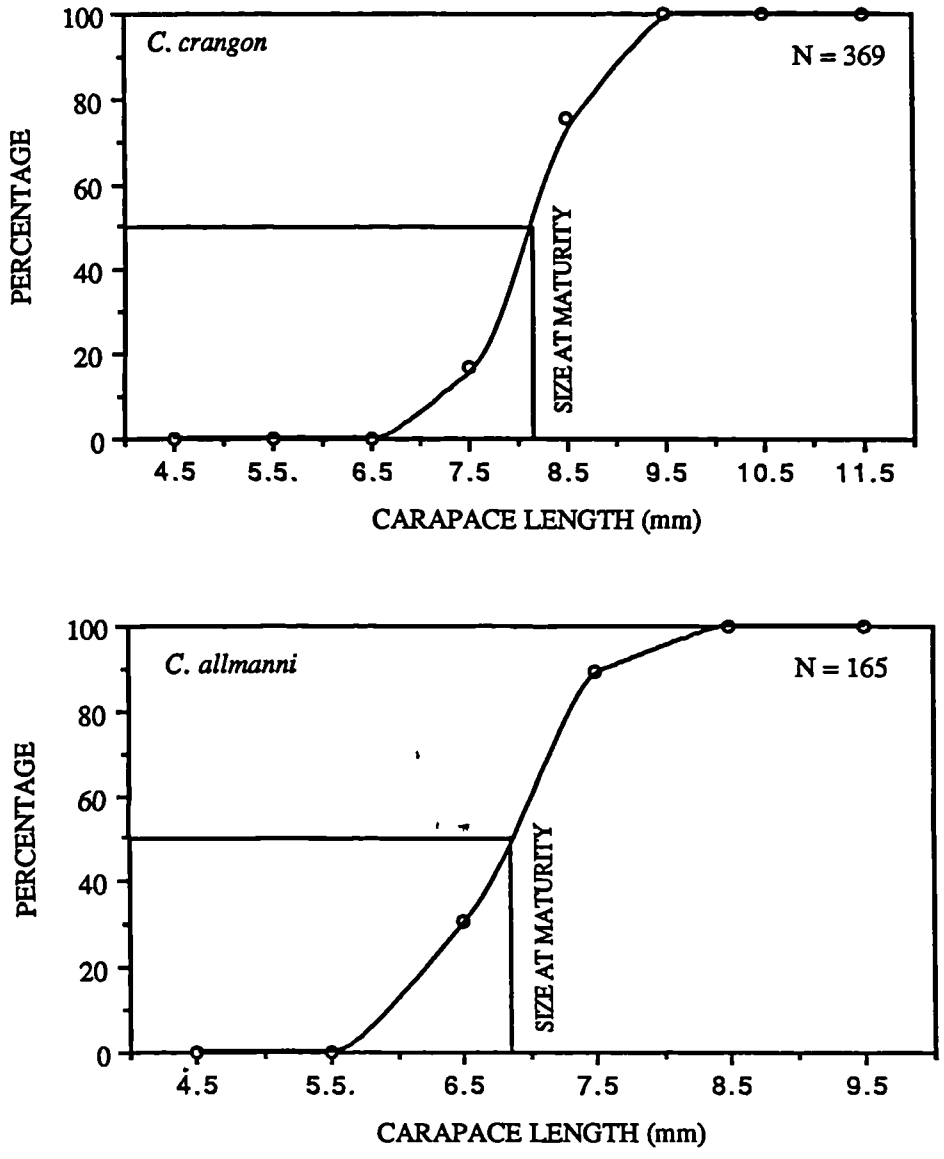


Fig.5.12 Size at first maturity in male *C. crangon* and *C. allmanni* in the Forth Estuary derived as size at 50% maturity.

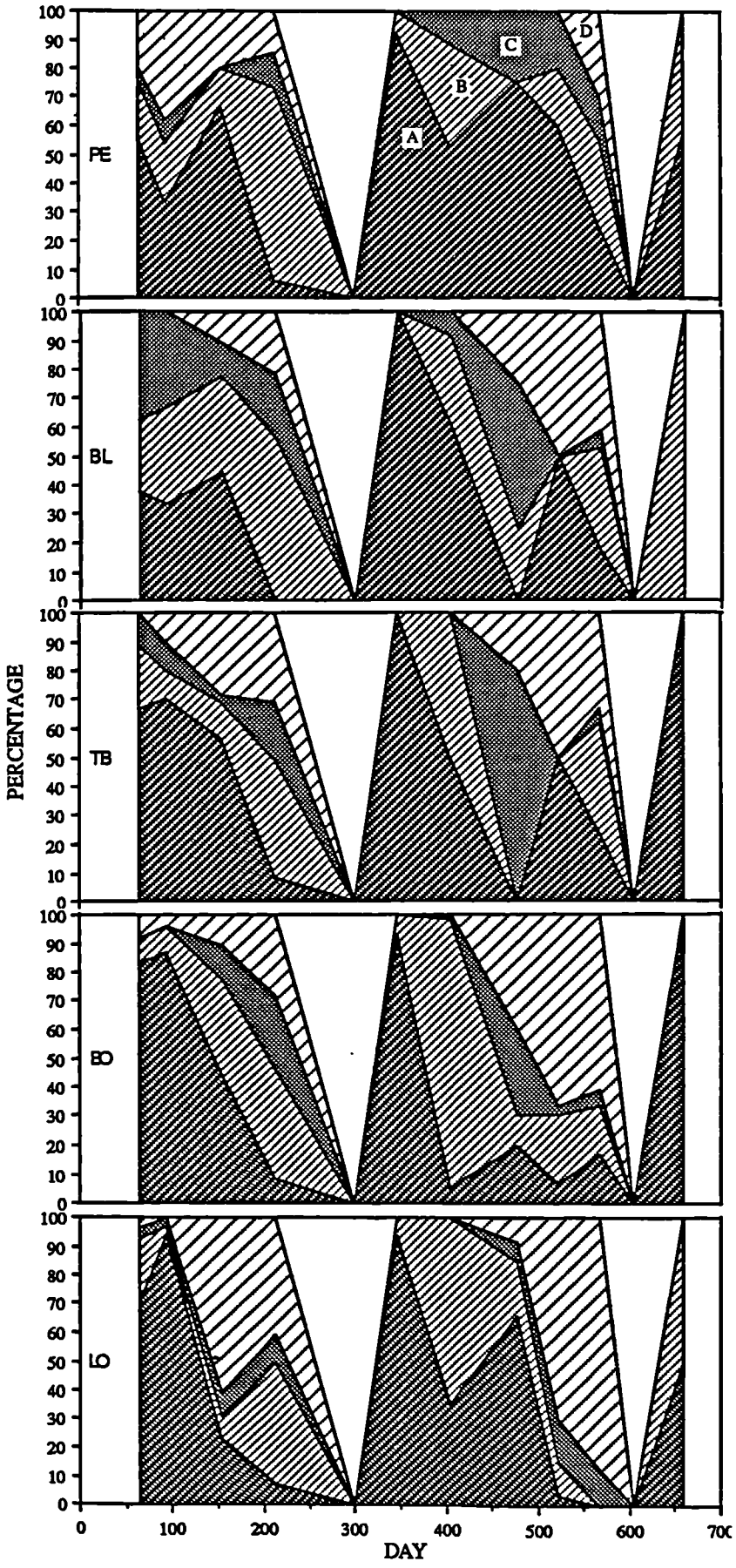


Fig.5.13 Spatial and temporal variations in the percentage of female *C. crangon* carrying eggs of different development stages (A, blastula; B, gastrula; C, with eye development; D, body detached) in the Forth Estuary.

spatially between upper and lower stations. In Longannet and Bo'ness a second peak appeared in April, earlier than in other stations. In the four lowermost stations another peak occurred in June.

The annual percentage of each egg development stage (Fig.5.14) clearly indicates two spawning peaks per year. The first occurs in April and the second in July. The pattern is similar in both years and the highest occurrence of late developed eggs marks the major hatching period as June.

The length distribution of berried females carrying eggs of developmental stages indicated two spawning groups per year(Fig. 5.15). Winter spawners (December) consisted of larger and older females; mean carapace length of 12.5±1.38 mm , range 9.5-16.5. In January a younger group , mean CL 8.5±0.37 mm, range 7.5-9.5, initiated spawning (perhaps the first spawning in their life). Summer spawning consisted entirely of younger females which spawn for the first time in their life; mean CL 11.5±1.18 mm, range 9.5-14.5.

5.3.5 Fecundity

C. crangon showed the highest fecundity producing 499 to 11,251 eggs per female per spawning of the size range 8 mm to 17.2 CL (Fig. 5.16). *P. montagui* females produced 682 to 3125 eggs for size range 10.6 to 17.5. The fecundity observed in *C. allmanni* varied between 456 to 3175 eggs in females of 6.6-11.5 CL size range.

Both models, Boddeke (1982) and Henderson and Holmes (1987) fitted with the data reasonably, deriving the equations:

1. $F = 1.57\ CL^3 + 747.34$ $(r = 0.51, n = 172, p<0.001)$
2. $F = 1.89(CL)^{2.5}$ $(r = 0.46, n = 172, p<0.001)$

for *C. crangon* (Fig. 5.17a). Boddeke's (1982) model was used for finding the winter and summer differences in the relationship for two reasons. Firstly, Boddeke's (1982) model gave a slightly higher correlation coefficient and secondly, the seasonal difference was also observed by Boddeke (1982). The equations derived for winter and summer are found to be different as illustrated in Fig. 5.17b. The equations derived for two seasons

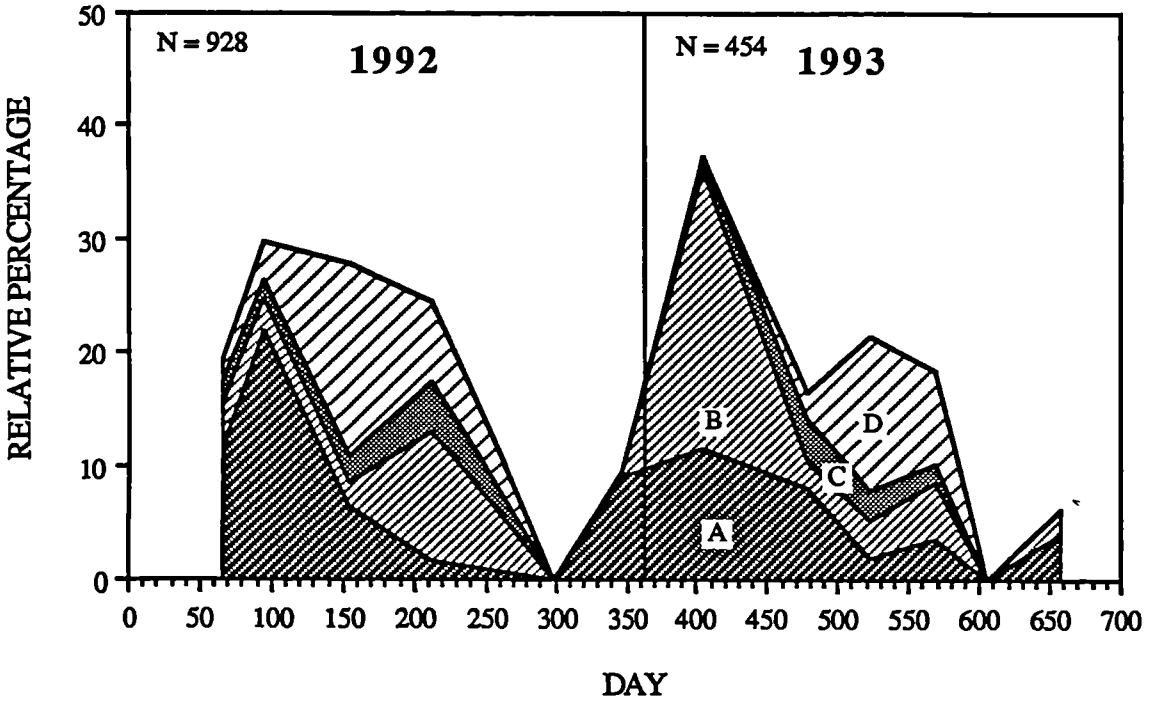


Fig.5.14 Female *C. crangon* carrying eggs of different development stages presented as a percentage of total berried females observed during the year (A, blastula; B, gastrula; C, with eye development; D, body detached).

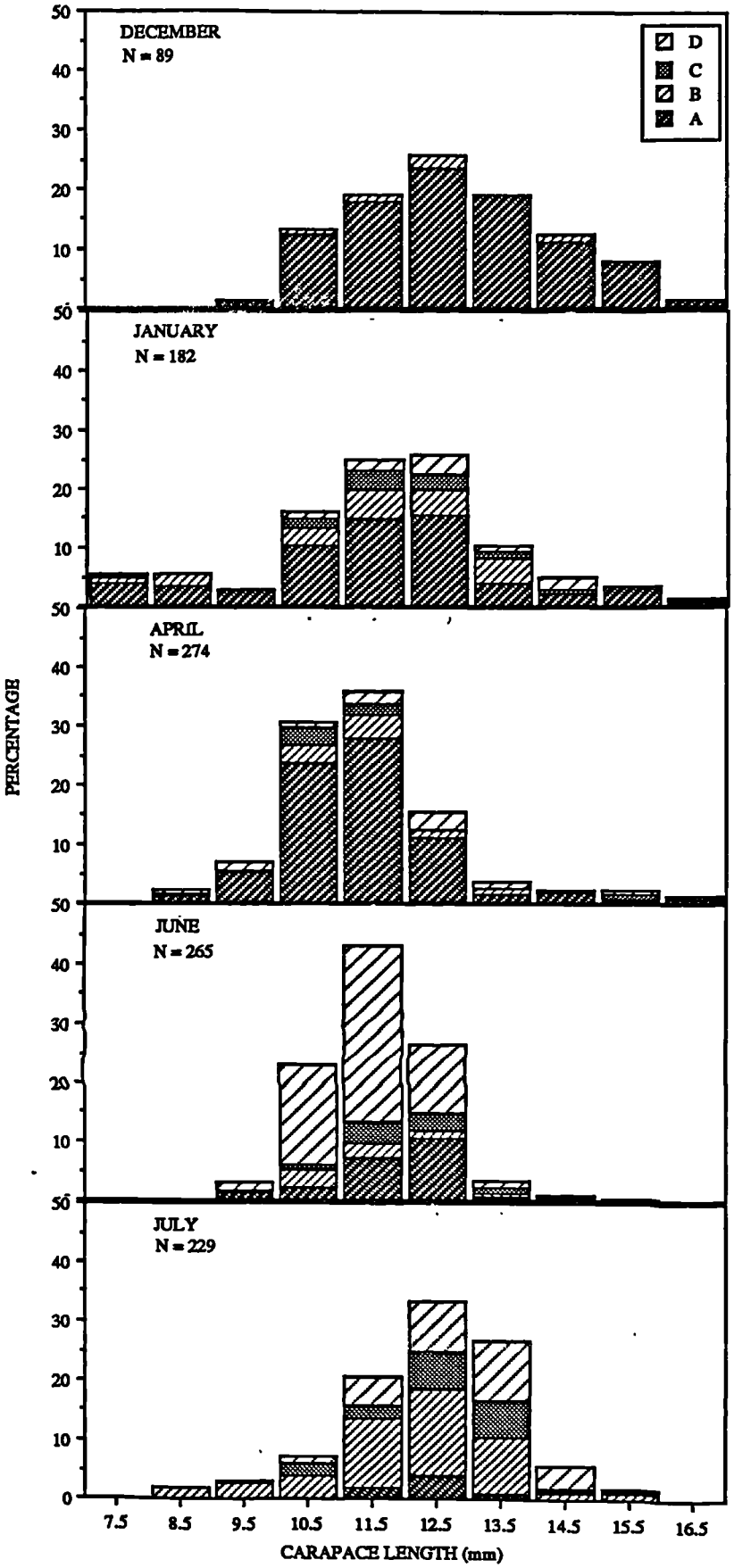


Fig.5.15 Temporal variations in the percentage length distribution of berried females of *C. crangon* in the Forth Estuary indicating the percentage of different stages of egg development (A, blastula; B, gastrula; C, with eye development; D, body detached).

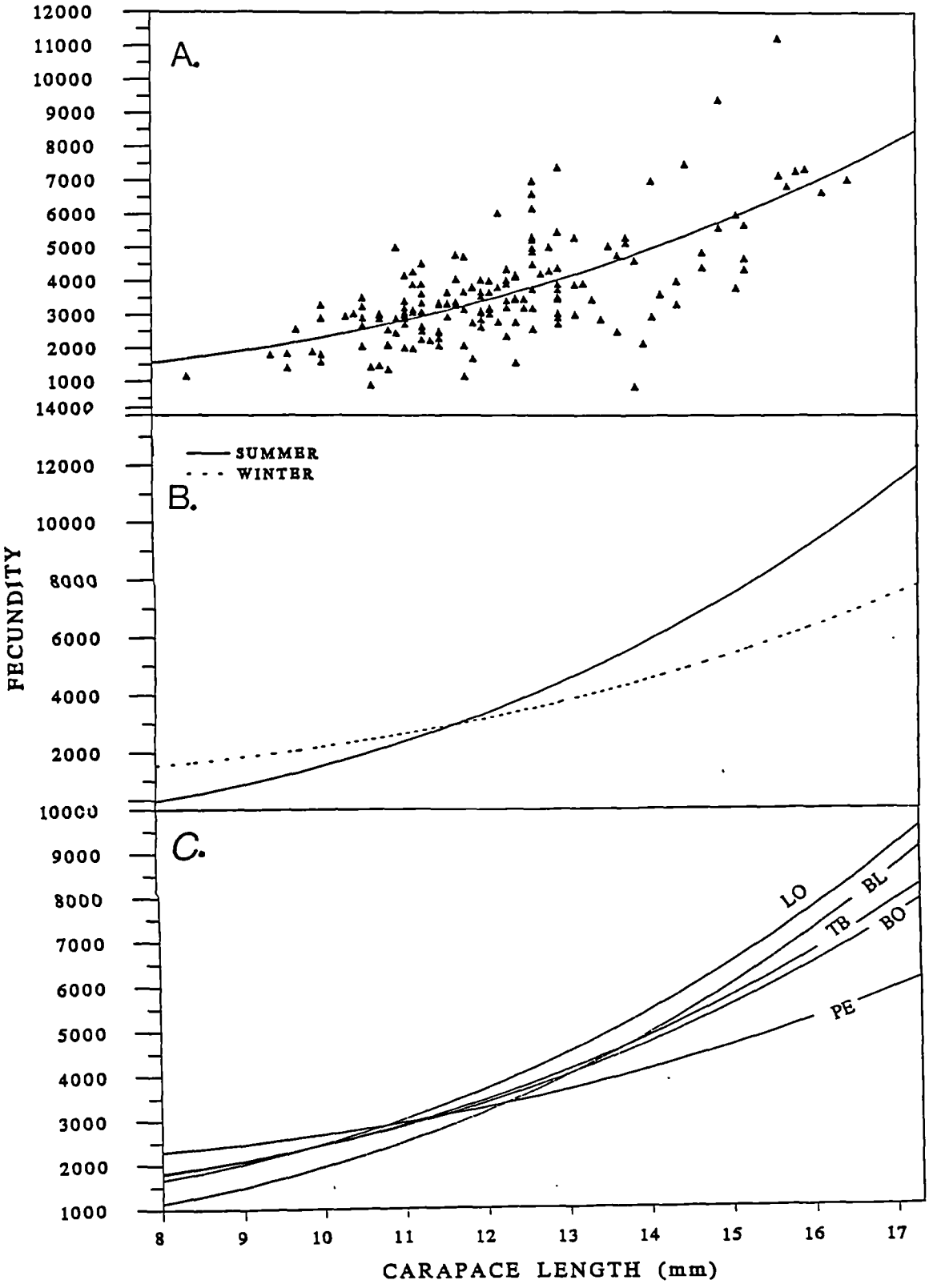


Fig.5.16 The relationship between fecundity and carapace length of *C. crangon* (Boddeke, 1982 model). A. general relationship B. summer and winter variations C. spatial variations.

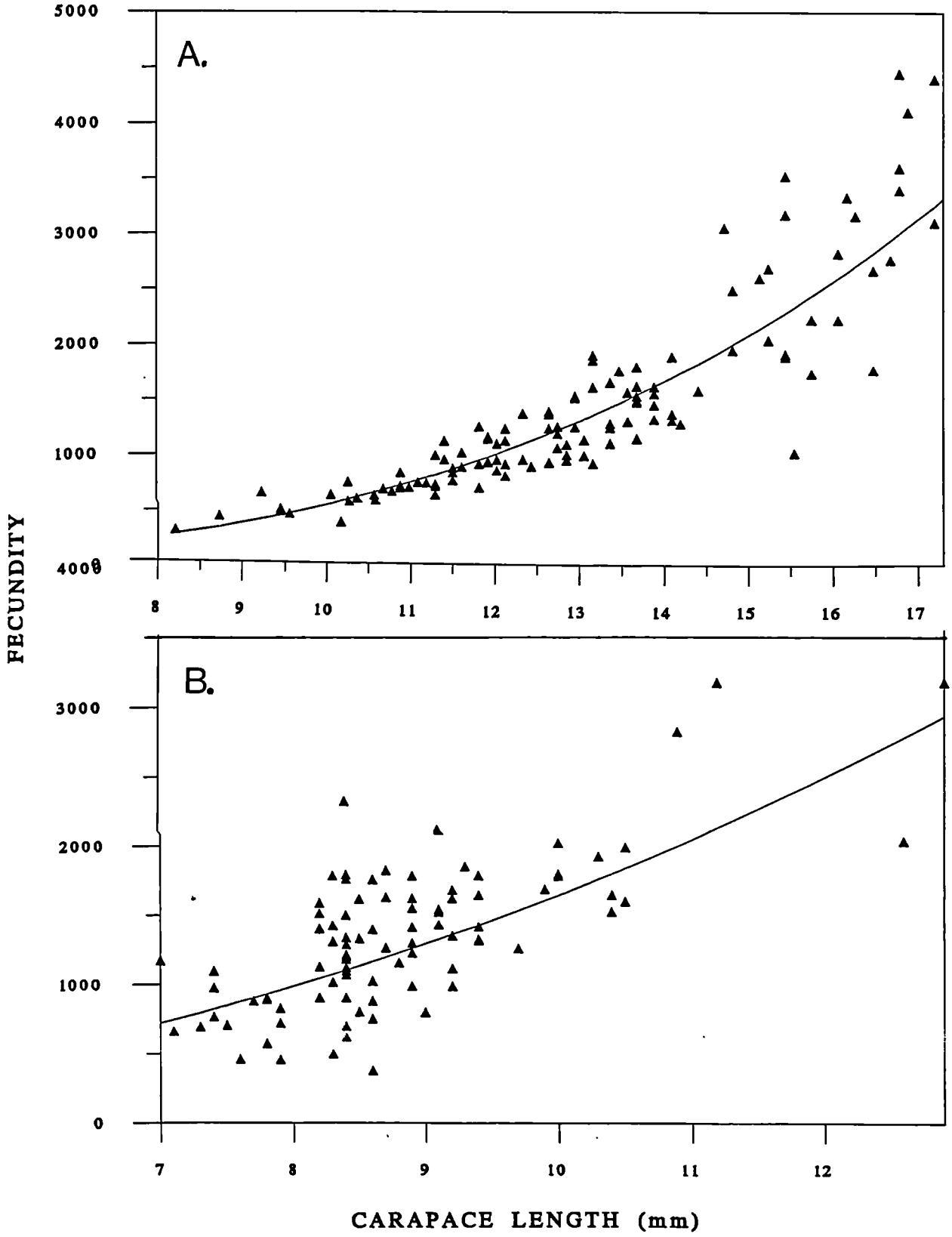


Fig.5.17 The relationship between fecundity and carapace length of A. *P. montagui* and B. *C. allmanni* fitted by Henderson and Holmes, 1987 model.

are given in below.

$F = 1.54\ CL^3 - 906.32$ ($r = 0.56$, $n = 53$, $p<0.001$) - Summer

$F = 1.41\ CL^3 - 954.74$ ($r = 0.48$, $n = 51$, $p<0.001$) - Winter

Spatial differences in the relationship between CL and fecundity were also observed (Fig. 5.17c). Among bigger females, those at Longannet produced the highest number of eggs while the females at Port Edgar produced the lowest. A clear increasing trend was observed in fecundity going upwards in the estuary from Port Edgar to Longannet in females > 11 - 12 mm carapace length. The relationship of CL/F in the lower three stations, however are poorly correlated and not significant (r=.28, .36 and .33 and p >0.1 respectively for PE , BL and TB).

$F = -0.84\ CL^3 + 1580.54$	($r = 0.28$, $n = 25$, $p<0.01$)	-	Port Edgar
$F = 1.33\ CL^3 + 1170.23$	($r = 0.36$, $n = 18$, $p<0.05$)	-	Blackness
$F = 1.41\ CL^3 + 1103.11$	($r = 0.33$, $n = 46$, $p<0.001$)	-	Tancred Bank
$F = 1.74\ CL^3 + 278.96$	($r = 0.78$, $n = 40$, $p<0.01$)	-	Bo'ness
$F = 1.73\ CL^3 - 810.44$	($r = 0.58$, $n = 42$, $p<0.01$)	-	Longannet

The same models were used to test the relationship between CL/F for *P. montagui*. The results obtain indicated good fit for both models with the data set although Henderson (1987) and model produced slightly higher correlation coefficient ($r = 0.83$). Therefore, the fecundity versus carapace length relationship of *P. montagui* was illustrated (Fig.5.15) using Henderson and Holmes (1987) model. The equations derived for the CL/F relationship using the two models are given below;

$F = 0.86\ CL^3$ ($n = 110$, $r = 0.83$, $p<0.001$) H&H model (1987)

$F = 427.24\ CL^3 - 4067.45$ ($n = 110$, $r = 0.74$, $p<0.001$) Boddeke (1982)

CL/F relationship of C. allmanni also derived the same results fitting with both models (Fig. 5.18). The equation derived by the models can be expressed as

$F = 2.43\ CL^{2.2}$ ($n = 77$, $r = 0.36$, $p<0.001$) H&H model, 1987)

$F = 1.31\ CL^3 + 506.24$ ($n = 77$, $r = 0.34$, $p<0.001$)

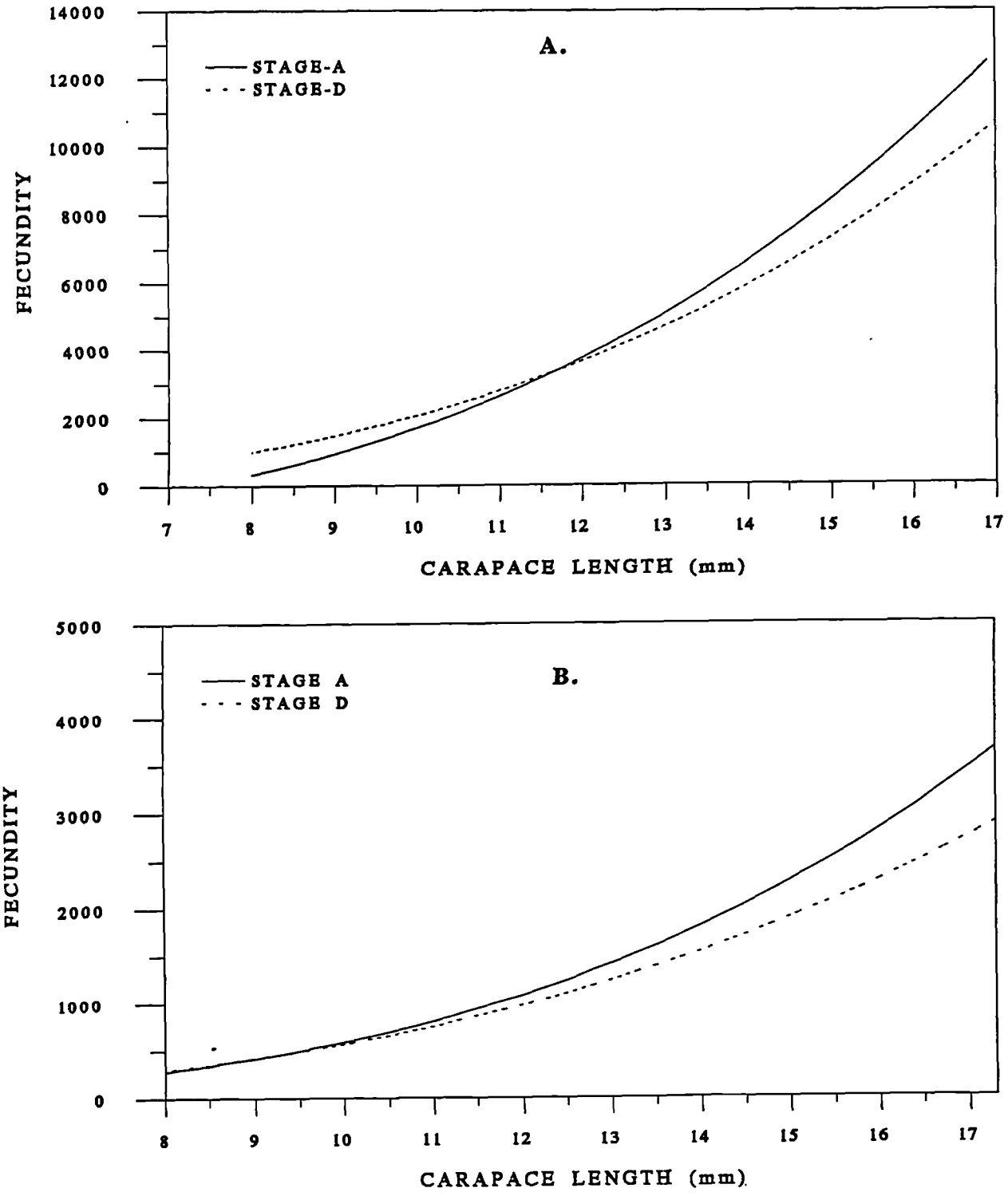


Fig.5.18 Egg loss during incubation from egg development stage A to D. A. *C. crangon*, B. *P. montagui.*

5.3.5.1 Egg loss during incubation

Egg loss during incubation was estimated using the regression equations fitted to stage A and stage D eggs. This aspect has not been studied for *C. allmanni* since adequate numbers with stage D eggs were not encountered either in the estuary or in Firth of Forth. For *P. montagui*, stage D eggs found at KH were used for the regression. Egg loss was observed only by using the stage A eggs of June and stage D eggs of July. When stage A eggs of winter and D eggs of summer or spring were analysed together the number of stage D was found to be higher. Egg loss in *C. crangon* varied from 5.1% at a length of 10.5 mm CL to 16.7% at a length of 17.5 mm CL (Table 5.4). *P. montagui* showed a loss of 1.77% eggs at 10.5 mm CL and 12.79% at 17.5 mm CL during the incubation.

5.3.6 Spawning season

Spawning season identified by the highest incidence of berried females, also indicated June as the peak spawning season for *C. crangon* (Fig. 5.19). The breeding season for *C. crangon* however appears to be long and extends from December to July.

Berried *P. montagui* were found first in January indicating it as the beginning of its breeding season (Fig. 5.20). The berried females however, left the estuary by April. The catches of KH showed females with late developed eggs from January to April. Berried females of *P. montagui* were not observed after April in any of the stations.

C. allmanni also was in berry by early January, especially at KH all the females were found to be in berry in January (Fig.5.21). Like *P. montagui* it left the estuary by April but were even absent from KH in April. The total number of berried females found was 2 in April. *C. allmanni* also exhibited only one breeding peak per year.

5.3.7 Reproductive potential

C. crangon exerts the highest reproductive potential in the estuary being highly fecund and breeding continuously (Table 5.5). The total production of eggs ha^{-1} varied from 0.80×10^7 in 1992 to 0.35×10^7 in 1993. Size classes 11.5 to 13.5 exhibited the highest potential in egg production accounting for half of the total production. The total annual egg production ha^{-1} of *P. montagui* varied from 1.09×10^6 in 1992 to 0.50×10^6 in 1993.

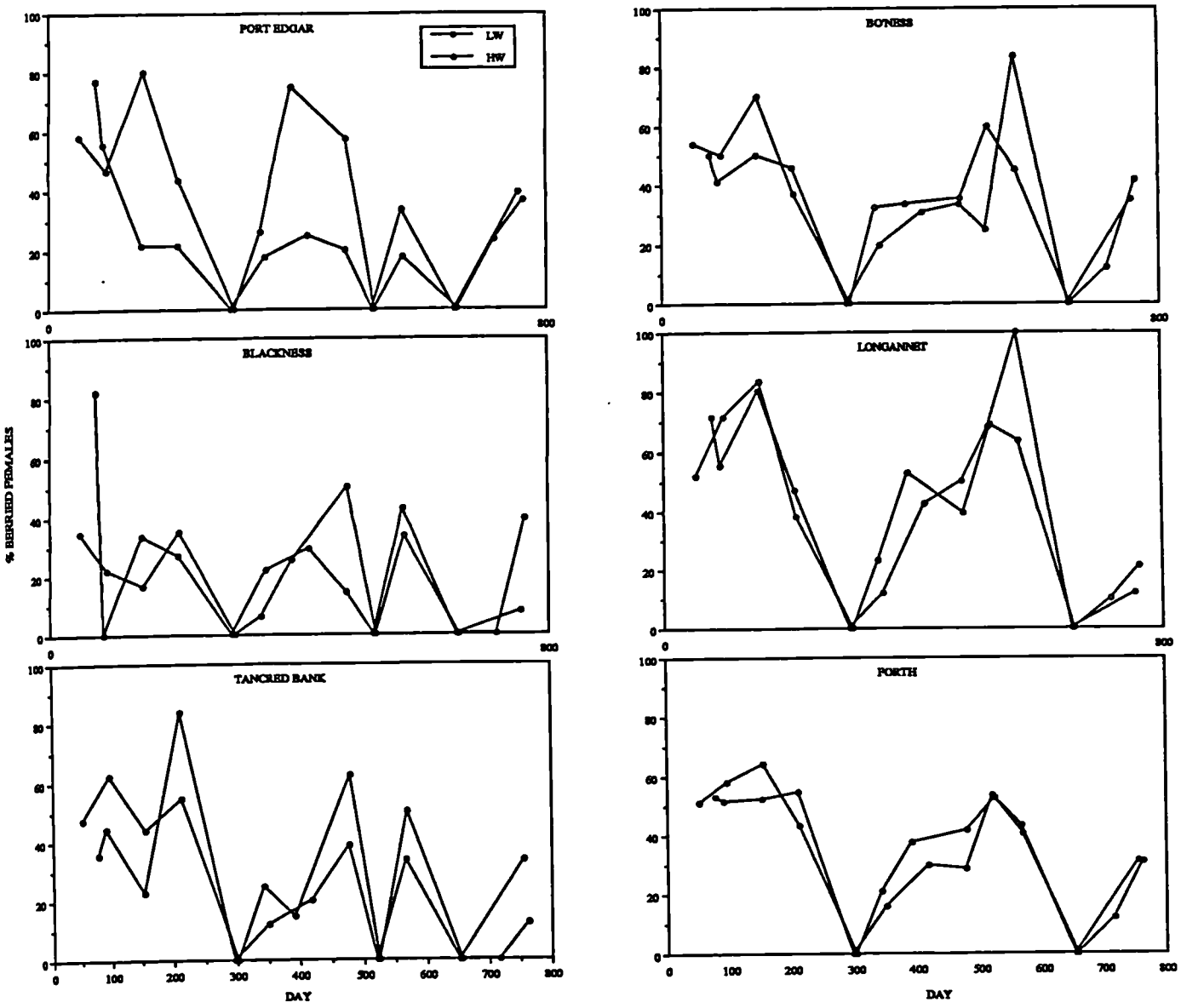


Fig.5.19 Temporal and spatial variations in the berried female *C. crangon* presented as a percentage of total females at five sites in the Forth Estuary.

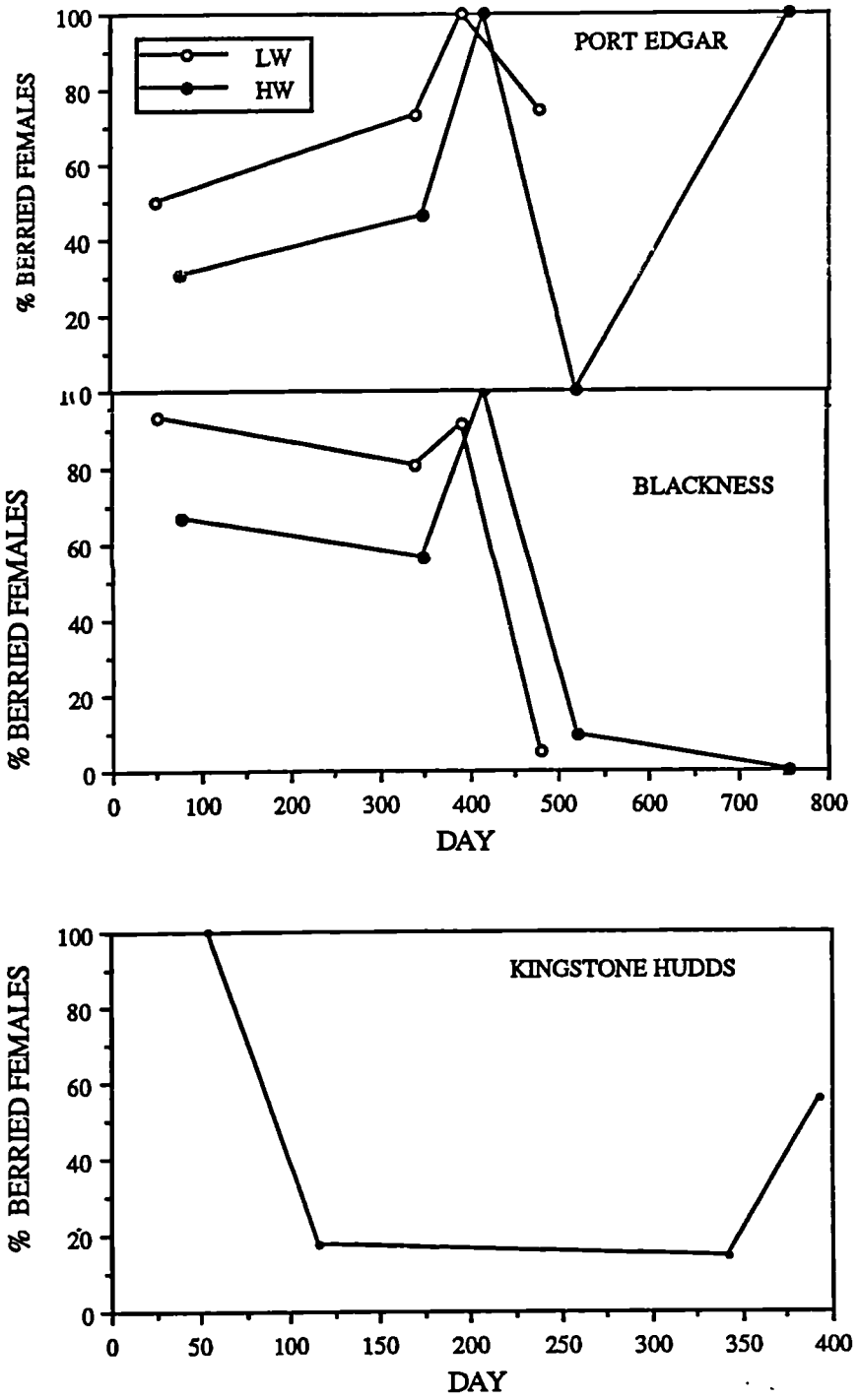


Fig.5.20 Temporal and spatial variations in the berried female *P. montagui* presented as a percentage of total females in the Forth Estuary and Kingstone Hudds.

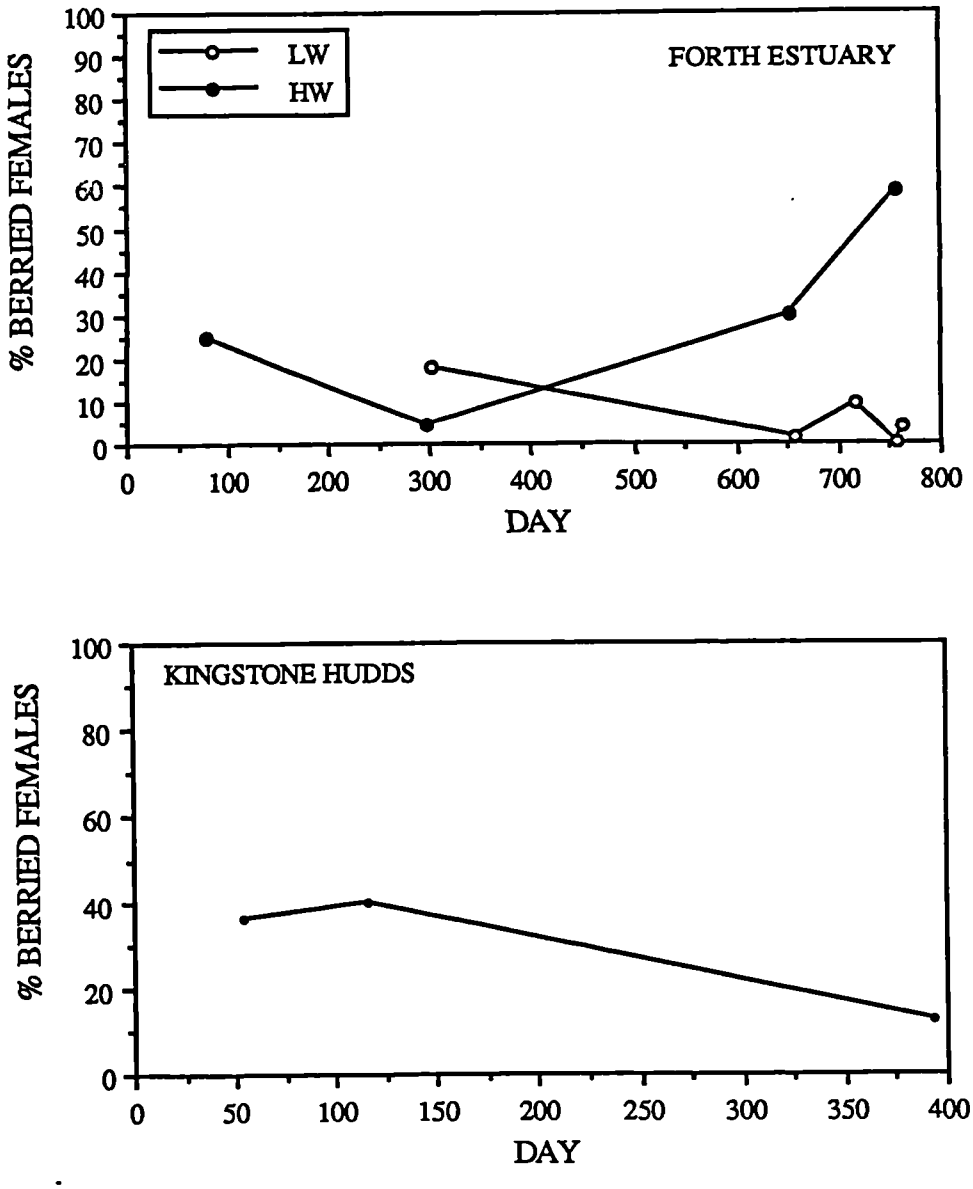


Fig.5.21 Temporal and spatial variations in the berried female *C. allmanni* presented as a percentage of total females in the Forth Estuary and Kingstone Hudds.

Table 5.4 Egg loss during incubation from egg development stage A to D in *C. crangon* and *P. montagui* in the Forth Estuary.

Carapace length (mm)	*C. crangon*			*P. montagui*		
	Number of eggs stage A	Number of eggs stage D	% egg loss	Number of eggs stage A	Number of eggs stage D	% egg loss
10.5	-	-	-	650	639	1.77
11.5	-	-	-	884	851	3.83
12.5	4369	4142	5.1	1172	1106	5.68
13.5	5794	5253	9.3	1520	1409	7.36
14.5	7447	6541	12.1	1936	1764	8.88
15.5	9344	8020	14.1	2426	2176	10.29
16.5	11503	9703	15.6	2997	2650	11.59
17.5	13940	11602	16.7	3656	3189	12.79

Table 5.5 Reproductive potential of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth estuary.

Carapace length (mm)	*C. crangon*				*P. montagui*			
	No. of mature females ha^{-1}	Fecundity	No. of spawning	Reproductive potential x 10^6	No. of mature females ha^{-1}	Fecundity	No. of spawning	Reproductive potential x 10^5
				1992				
8.5	192	1210	3	0.69	64	328	1	0.20
9.5	124	1743	3	0.64	17	466	1	0.07
10.5	143	2400	3	1.02	17	639	1	0.10
11.5	189	3196	3	1.81	62	851	1	0.52
12.5	142	4142	3	1.76	178	1106	1	1.97
13.5	75	5253	3	1.17	174	1409	1	2.45
14.5	27	6541	3	0.52	116	1764	1	2.03
15.5	11	8020	3	0.25	89	2176	1	1.94
16.5	3	9703	3	0.08	45	2650	1	1.18
17.5	0	11602	3	0	12	3189	1	0.39

Carapace length (mm)	*C. crangon*				*P. montagui*			
	No. of mature females ha^{-1}	Fecundity	No. of spawning	Reproductive potential x 10^6	No. of mature females ha^{-1}	Fecundity	No. of spawning	Reproductive potential x 10^5
				1993				
8.5	45	1210	3	0.16	1	328	1	0
9.5	45	1743	3	0.23	13	466	1	0.06
10.5	54	2400	3	0.39	36	639	1	0.23
11.5	62	3196	3	0.59	96	851	1	0.81
12.5	56	4142	3	0.69	103	1106	1	1.14
13.5	41	5253	3	0.64	66	1409	1	0.92
14.5	23	6541	3	0.44	42	1764	1	0.73
15.5	12	8020	3	0.27	30	2176	1	0.65
16.5	4	9703	3	0.12	11	2650	1	0.28
17.5	-	-	-	-	4	3189	1	0.13

The highest reproductive potential was observed in size groups 12.5 mm CL to 14.5 mm CL. The production of *C. crangon* was found to be 7-times higher than that of *P. montagui.* When considering the area of distribution in two species, reproductive potential of *C. crangon* is definitely several-fold higher than that of *P. montagui.* Reproductive potential of *C. allmanni* was not studied here due to inavailability of females carrying ripe eggs in both the estuary and Firth of Forth, and it is most unlikely for *C. allmanni* to have a higher potential than any of the other two species. *C. allmanni* is a low fecund and less abundant species and could be regarded as the species which has the lowest reproductive potential in the estuary.

5.4 DISCUSSION

Sex ratios, maturation of gonads, spawning and early development of embryos in berry were all seem to be influenced by the major variables in the estuarine environment namely, time of the year, distance up-estuary and state of tide. The pattern in relation to time of year was clear and direct with clearly marked seasonal reproductive activity. The effects of partition in the estuary and, particularly, of tides were much less clear or constatnt. The differential distribution of male and female animals in the estuary presented in chapter 4 is more emphasised by the significant variations in sex ratio both spatially and tidally. Similar observations were made by Henderson and Holmes (1987) in the Bristol Channel and Severn Estuary in *C. crangon*; by Mistakidis (1957) and Simpson *et al.* (1970) in *P. montagui* and by Allen, 1960 in *C. allmanni.* The absence of males in larger size classes was observed in *C. crangon* as well as in *P. montagui*, and supports the Boddeke's (1989) view that *C. crangon* is a hermaphrodite.

5.4.1 *C. crangon*

5.4.1.2 Spawning season

It became clear that *C. crangon* has at least two spawning seasons, one beginning in December and ending in April and the other beginning in January and continuing until July. The first group of spawners (December) consisted of old and larger females while the second group of spawners (June/July) were a younger group with mean CL of 12.5. As indicated by the gonadal maturation of the berried and/or females with remnants of hatched larvae it is most likely that another small spawning peak occurs during August

and September in the months when sampling was not carried out in this study. The occurrence of berried females in the upper estuary in September proves that the breeding is still in progress and the gonads in resting stage indicate that this is the last spawning. This was further supported by Hunter's (1981) findings in which he observed berried females as late as September. Thus, the present study agrees with the views of Havinga (1930), Ehrenbaum (1890) and Meyer-Waarden (1935) who observed three spawnings per female. Lloyd and Yonge (1947), Henderson and Holmes (1987) and Hunter (1981) shared the view that *C. crangon* spawn only twice per breeding season. Henderson and Holmes (1987) calculated the incubation time required for a female based on the equation given by Wear (1974),

$D = 20437\ (C + 3.6)^{-2.3}$ where C is the water temperature in which animal lives

and assumed that there is no sufficient time for another spawning after recovery from the June spawning. In the Forth Estuary the water temperature in July is about 12 °C which gives the incubation time as 37 days. Even if it takes one month for recovery from the last spawning which occur in June, there is still ample amount of time for another spawning which allows females to release larvae in late August or early September. This was further supported by the presence of breeding females with ripe eggs in September.

The long breeding season in *C. crangon* is a well known phenomenon and the onset and duration of spawning as recorded by the previous researchers in the area are presented in Table 5.6 which indicates the variability in the duration of breeding within the geographic range.

Table 5.6 Duration of the breeding period as indicated by presence (x) of berried females, in different areas. (*) indicates void observations, and (-) indicates the absence of berried females.

Area	J	F	M	A	M	J	J	A	S	O	N	D	Reference
Bergen, Norway	-	-	-	-	-	-	-	x	x	x	x	x	Wollebaek, 1908
German Coast	x	x	-	x	x	x	x	-	-	-	-	-	Ehrenbaum, 1890
German Coast	x	x	-	x	x	x	x	-	-	-	-	-	Meyer-Waarden, 1935
Bristol Channel and Severn Estuary	-	-	x	x	x	-	-	-	-	-	-	-	Lloyd and Yonge, 1947
German Coast	x	x	x	x	x	x	x	x	x	x	-	-	Tiews, 1970
Dutch Wadden Sea	x	x	x	x	x	x	x	x	x	-	-	-	Boddeke, 1982
Forth Estuary	*	*	*	*	x	x	x	x	x	-	-	x	Hunter, 1981
Bristol Channel and Severn Estuary	x	x	x	x	x	x	x	x	-	-	-	-	Henderson and Holmes, 1987
Forth Estuary	x	x	*	x	*	x	x	*	x	*	*	x	Present study

The peak spawning season in the Forth Estuary occurred in summer being the period with the maximum number of females carrying ripe eggs and is in agreement with Boddeke and Becker (1979) and Boddeke (1982).

The size at maturity of *C. crangon* in the Forth Estuary lies well within the range recorded by previous reseachers (Table 5.7). The values recorded by Lloyd and Yonge (1947) and Henderson and Holmes (1987) in the Bristol Channel and Severn estuary are much higher than the values found in the Forth Estuary for female *C. crangon*. The male size at maturity has been recorded so far only by Boddeke (1966) and Tiews (1954) and the present values compare well with that of Tiews (1954) but higher than that of Boddeke (1966).

Table 5.7 Comparison of size at maturity with previous records as given in Tiews (1970). * indicates the records not in Tiews (1970).

Reference	Male	Female	Locality
Wollebaek, 1908	-	45 mm	Norwegian fjords
Havinga, 1930	-	42 mm	Dutch Coast
Henking, 1958	-	30-34 mm	Pomeranian Coast
Meyer-Waarden, 1935	-	42-48 mm	outer Jade
Lloyd and Yonge, 1947	-	54	Bristol Channel and Severn
Tiews, 1954	38 mm	44-52 mm	Büsum area
Kurc, Faure and Laurent, 1965	-	50 mm	French Coast
Kurc, Faure and Laurent, 1965	-	47 mm	Gulf of Gascogne
Kurc, Faure and Laurent, 1965	-	37 mm	Bristol Channel
Boddeke, 1966	22 mm	37-42 mm	Dutch waters
Henderson and Holmes, 1987*	-	42 mm	Bristol Channel and Severn
present study*	37.3 mm	36.8 mm	Forth Estuary

The fecundity of *C. crangon* was higher (499 -11,251) than observed by Lloyd and Yonge (1947), Boddeke (1982), 1452-7951, and Henderson and Holmes (1987), 1043-6216. This may be due to the method adopted for studying fecundity or may indicate the high potential of female *C. crangon* in the Forth Estuary. Winter and summer variations observed by Boddeke (1982) were also observed in the present study. Henderson and Holmes (1987) didn't agree with this view but did not include statistical evidence to support their theory.

The reproductive strategy of *C. crangon* in the Forth Estuary involves a high fecundity and multi-spawning. The transformation of males into females provides an opportunity for the additional production of larvae and may indicate the struggle of *C. crangon* for survival in the estuary as stated by Boddeke (1989). Boddeke also found that each male mates only once and females store sperms to be used later for 2nd and third spawning. This may give the male an opportunity to take its turn in production once its duty as a male is complete.

5.4.2 *P. montagui*

5.4.2.1 Spawning season

In contrast to *C. crangon*, *P. montagui* exhibited an uncomplicated breeding cycle which is synchronous in all the animals with similar stages of gonadal or egg developmental stages. They spawn once a year in the Forth Estuary and the duration of breeding is short extending from December to April. The release of larvae takes place in deeper water in April where a higher percentage of animals were found with ripe eggs ready to hatch at Kingstone Hudds. The reproductive behaviour of *P. montagui* can be described as maturing, July to October; spawning, December-January/February; release of larvae, April. This is well in agreement with the previous records in the North Sea, where egg laying commenced in November to January/ February (Mistakidis, 1957; Allen, 1963; Stevenson and Pierce, 1985). Larger females laid eggs first, followed by females spawn for the first time (Mistakidis, 1957). This was not clearly indicated in the present study, perhaps due to lack of sampling in November which marks the initiation of breeding period. Unfortunately the November sampling is void in Hunter (1981) too. Berried females left the estuary and were found only at Kingstone Hudds in April. Mistakidis (1957) observed similar behaviour in *P. montagui* in Suffolk Coast where ovigerous females aggregated at a depth of 30-40 fm.

Females matured at a size of 8.6 mm CL and was closer to the size at maturity observed by Mistakidis (1957) and Allen (1966) (9-11 mm CL). The relationship between carapace length and fecundity was better described using the model given by Henderson and Holmes (1987) for *C. crangon* than by direct linear correlation as indicated by Mistakidis (1957). No substantial variations were found in the fecundity at different months. Each female laid one batch of eggs per season, and produced 682 (10.5 mm CL) to 3125 (17.5 mm CL) eggs. This compares well with findings of Mistakidis (1957) (492 eggs, 8.5 mm CL; 3725 eggs, 18.5 mm CL) and Allen (1963) (200 eggs, 9.5 mm CL; 3000 eggs, 19.0 mm CL).

The transition of males commenced in January-February in the Forth estuary and increased until June. June marked the peak occurrence of late transitionary period and secondary females of same size were observed in July. All the males <8.5 mm CL were

found to be in one or other transitionary stage, and the size at which the transition completed was about 12.5-13.5 mm CL. This is evident from the sex ratios as well as from the occurrence of secondary females.

The reproductive potential of *P. montagui* is lower than that of *C. crangon.* Allen (1966) stated that shallow water breeding is less important to *P. montagui* in comparison to the 9-times higher egg production in the deep water. The 0-group population in shallow water however, is 7-times higher than that of deeper waters (Allen, 1966). This may indicate that the survival for larvae is higher in shallow waters and indicate the importance of shallow water breeding. Allen (1966) attributed this particularly to the absence of *P. borealis* in shallow areas, which predate on the zoeae of *P. montagui* in deeper water. The reproductive strategy of *P. montagui* is thus, represented by synchronous breeding and deep water spawning. The transition of males into females adds more reproductive females to the population.

5.4.3 *C. allmanni*

Complete breeding cycle of *C. allmanni* was not observed either in the estuary or in Firth of Forth. Only the early part of the breeding cycle, maturing and spawning occurred in the estuary and animals left the estuary at this time. The absence of females at Kingstone Hudds in April indicated that their range of releasing larvae presumably extends further down in the Firth of Forth or in the North Sea.

The males matured at a size of 7.0 mm CL and females at a size of 7.5 mm CL. The relationship between carapace length and fecundity was as same as in *P. montagui* and the fecundity varied between 456 (6.6 mm CL) and 3175 (11.5 mm CL). Allen (1960) observed the similar size at maturity (7.0 mm CL) and fecundity (400 eggs, 7.5 mm; 7060 eggs, 17.0 mm) in Northumberland waters.

Reproductive strategy of *C. allmanni* involves a maturation period in shallow water, and egg development and spawning in deeper water. The purpose of arriving at the estuary for breeding is not clear and more studies are required in this respect.

CHAPTER 6. ABUNDANCE, DISTRIBUTION AND MIGRATION OF SHRIMP LARVAE

ABUNDANCE, DISTRIBUTION AND MIGRATION OF SHRIMP LARVAE

6.1 INTRODUCTION

Success of any population depends on the replenishment of population by new generations. As the adults are responsible for producing new broodstock, the broodstock thus produced are responsible for continuation of the population in the adult grounds. This process of arriving at new generations to the adult population which is known in population biology as the 'recruitment' (Pitcher and Hart, 1981), is a crucial factor since it ensures the continuity of the population. Recruitment in caridean shrimps, is a complex process which includes the survival through a series of developmental stages and continuously changing environment, as they possess a planktonic larval phase although the adults are benthic in habitat. The biological processes which are involved in their recruitment include: parent fertility, survival of eggs through incubation, success of parents to migrate to optimal environment to release larvae, the survival of larvae through metamorphosis, probability of arrival of larvae at nursery areas, survival in the nursery area and subsequent settlement of the juveniles in the adult feeding grounds. These processes are dependant upon various environmental factors: food availability, mortality by predation and survival through migration (Olson and Olson,1989).

Costlow and Bookhout (1970) described the larval phase of marine organisms as the 'neglected link' between generations, since most studies on population dynamics are focused mainly on the biology of adults. This is true also for shrimps. In contrast to the vast amount of literature available on the adult populations, the literature on the larval populations is meagre. Larval morphology and developmental stages of *C. crangon* (=*vulgaris*) have been described by Du Cane (1839), Ehrenbaum (1890): and Sars (1890) in the previous century, and by Webb (1921), Lebour (1931), Williamson, (1967) and Gurney (1982) in the more recent past. Records on the occurrence of larvae in different areas (Jorgensen, 1923; Lebour, 1947; Kühl and Mann, 1963), laboratory studies on the influence of ecological factors on larval survival; salinity (Broekema, 1942), temperature (Rochanaburanon and Williamson, 1976), light (Dalley, 1980) and heavy metals (Connor, 1972) and development pathways (Criales and Anger, 1986) are also documented. Studies on abundance, distribution and migration of planktonic larvae are scarce however,

(Wehrtmann, 1989; Mees *et al.*, unpublished manuscript) in comparison to morphological studies, but studies on the nursery phase in intertidal areas are well documented (Pihl, 1985; Pihl and Rosenberg, 1982; Kuipers; Dapper, 1984 and Jansen and Kuipers, 1980). Studies on the larvae and their development stages are thus important since these are responsible for the recruitment of the population, dispersal of species and colonization of new environments.

The present chapter attempts to investigate how the shrimp larvae in the Forth Estuary survive the challenges of the environment and succeed in dispersing new recruits throughout the estuary. It also focuses on the key environmental factors which may influence the migration and distribution of larvae in the estuary and Firth of Forth.

6.2 MATERIAL AND METHODS

Sampling techniques, frequency and preservation of plankton samples have been described in detail in chapter 2.

6.2.1. Identification of larvae

First and second zoea stages of *Crangon crangon* and *Pandalus montagui* were identified by hatching the larvae from eggs. The females bearing eggs which were ready to hatch (stage D^+, described in chapter 5) were reared in the laboratory at a constant temperature (10°C). Larvae were fed with egg yolk beginning from the second day after hatching and were fed with nauplii of *Artemia salina* from 5 days after hatching. Larvae survived for only 12 days under these conditions and reached stage II. Identification of the larvae found in the field zooplankton was confirmed by matching them with a reference set of larvae hatched under the laboratory conditions. Larvae of *Crangon allmanni* were not obtained in this manner due to the unavailability of females bearing eggs at suitable stages of egg development. *Crangon allmanni* larvae, however, could be easily distinguished from those of *Crangon crangon* by the presence of a dorsocentral spine on the third abdominal segment of *Crangon crangon* larvae. On the other hand *Crangon allmanni* possess two conspicuous lateral spines on the fifth abdominal segment. The descriptions of larvae given by Webb (1921), Lebour (1931), Williamson (1901) and Gurney (1982) were also consulted in confirming the identifications. The descriptions given by Criales

and Anger (1986) however, was not considered since the morphological variability in their study appears to result largely from individual differences in morphogenetic and ecdysial rates. Identification of *Pandalus montagui* larvae were carried out according to the descriptions given by Pike and Williamson (1964) and Lebour (1940).

6.2.2 Sample analysis

25 entire hauls of zooplankton were analysed using the lowest magnification (6.5 x 10) of a dissecting microscope (Leica Wild M3Z). Six stages of zoeae (zoea I - zoea VI) and one stage of post larvae were identified, isolated and counted. The identification of different larval stages was based on the key shown in Fig. 6.1a and 6.1b, which was prepared using the descriptions from Gurney (1982), Williamson (1901) and personal observations from the present study. Larvae and different larval stages of *Pandalus montagui* and *C. allmanni* were identified as described by Pike and Williamson (1964) and Williamson (1901) respectively. The size of the larvae of each stage was measured as the length between the tip of the rostrum and the posterior margin of the telson, to a precision of 0.01 mm using a micrometer scale, with an aid of a dissecting microscope. For *C. crangon* a set of ten individuals from each stage were measured whereas for *C. allmanni* all the larvae found (three) were measured.

6.2.3 Abundance of larvae

The abundance of larvae at each station at each sampling day was expressed as the number of individuals 100 m^{-3}, which was calculated by dividing the number of individuals in the sample by the volume of water filtered through the plankton net (116.36 m^3). The volume filtered was calculated using the formula:

$$V=\pi r^2 D\times C \qquad (6.1)$$

where,

V = volume filtered

r = radius of the mouth of plankton net (0.25m)

D = distance trawled (=speed of the boat x time of tow)

= (2x 1852m x 0.166h)

C = Correction for gear efficiency (96% retention) as given by

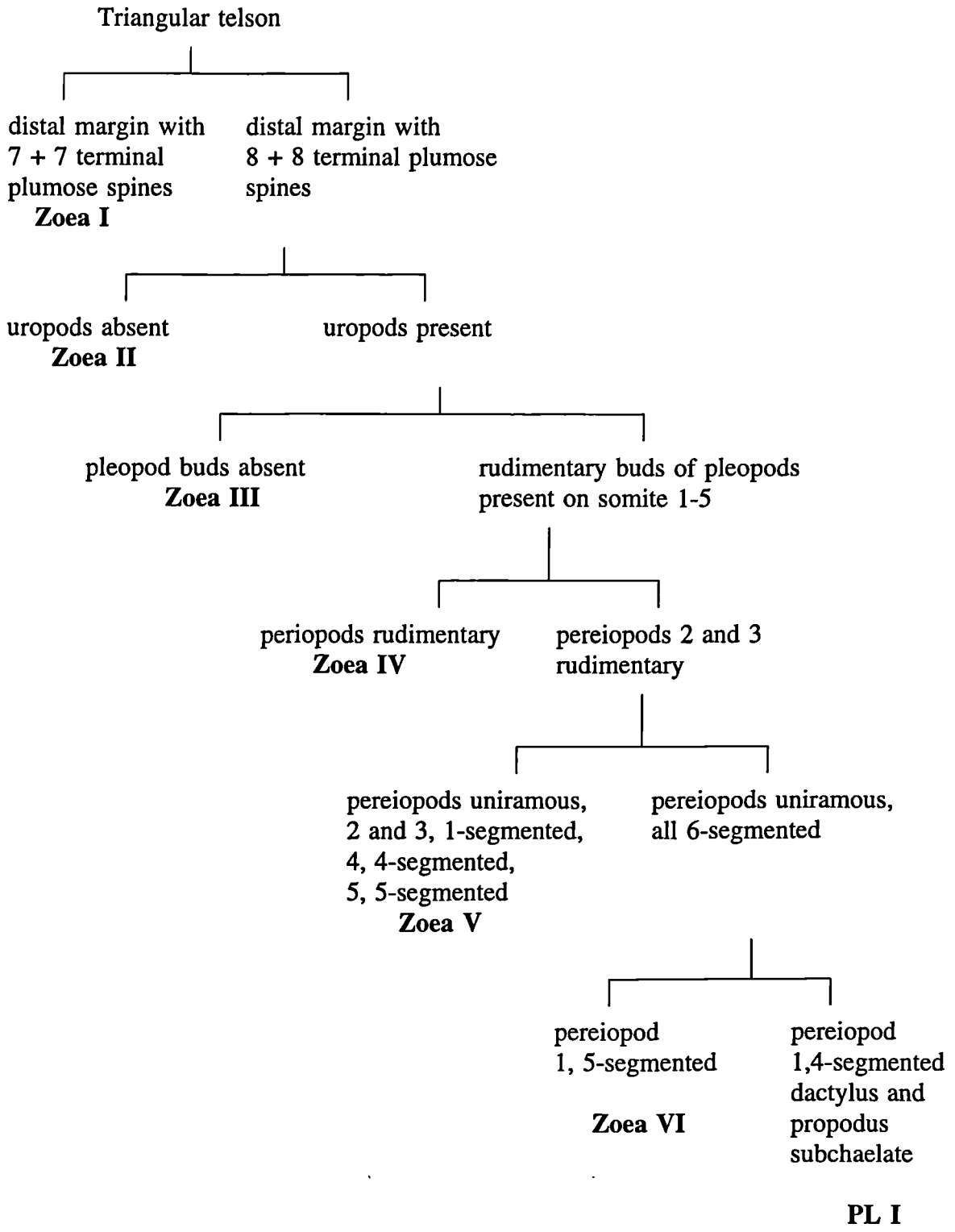


Fig. 6.1 (a)-Key to identify the different larval stages of *C. crangon* (L.) . The main morphological characters used in differentiating between stages are illustrated in Fig. 6.1 (b).

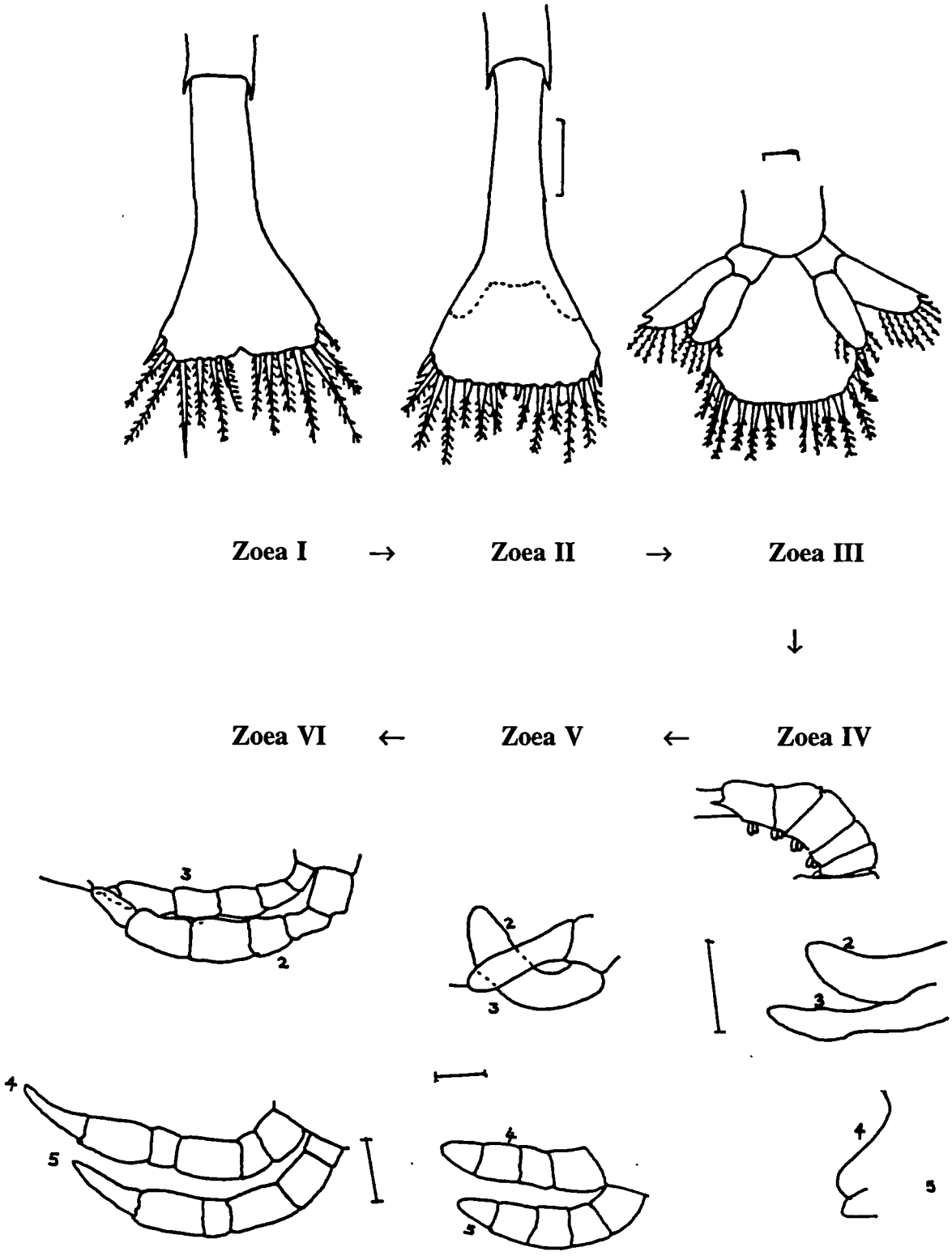


Fig. 6.1 (b) - Key used in identification of different larval stages of *Crangon crangon* (L.) (after Gurney, 1982).

Tranter (1968) and also used by Taylor (1981)

Calculation of abundance is given by the equation;

$$A=\frac{N}{V}\times 100 \qquad (6.2)$$

where,

A = abundance (100 m^{-3})

N = number found in the sample

V = volume filtered through the plankton net

Mean abundance of larvae of all stages in the estuary regardless of tidal variations was calculated as;

$$\sum_{i=1}^{5}\sum_{j=1}^{2}\frac{A_{ij}}{5\times 2} \qquad (6.3)$$

A_{ij} = abundance at station i at tide j

5 x 2 = Number of stations x number of tides

Mean abundance of different larval stages at high and low tide was calculated separately by adding the total number of larvae of a particular stage which occurred in all stations in the estuary, and expressing it as a percentage of total number of larvae present. The equation used in calculation is expressed as:

$$\frac{\sum_{i=1}^{5} X_{ij}}{\sum_{i=1}^{5}\sum_{j=1}^{7} X_{ij}}\times 100 \qquad (6.4)$$

where,

X_{ij} = Number of larvae of stage j at station i (7 stages, 5 stations)

6.2.4 Statistical analysis

The effect of various environmental parameters; temperature (C°), Salinity (ppt), suspended solids (mg l^{-1}), tidal amplitude (m), and depth at haul (m) on the abundance of larvae (number x 100 m^{-3}) was tested by multiple linear regression (stepwise) using the SPSS-X package. ANOVA was used to test the influence of group parameters; tide and stations, which could not be tested using multiple regressions.

6.3 RESULTS

6.3.1 Occurrence of larvae

All the larval stages of *C. crangon*, as described by Gurney (1982) were found in the plankton of Forth Estuary and Firth of Forth. Larvae of *C. allmanni* however, were not common and only three were found in the total of 25 hauls throughout the period of study. One zoea I was found at Port Edgar at high tide in June 1993 and the other two (zoea II) were found at Kingstone Hudds in June 1993. Larvae of *P. montagui* were not found either in the estuary or in the Firth of Forth during the present study. Five pandalid larvae which were of *Pandalina brevirostris* were found at Port Edgar at high tide in June 1993.

6.3.2 Size of larvae

The newly hatched larva (zoea I) of *C. crangon* in the Forth estuary measured 1.94±0.69 mm, and grew through 6 moults to 4.41±1.10 mm at the post larval stage (Table 6.1). Comparison of cumulative growth increment during larval development of *C. crangon* in the Forth Estuary with larvae captured in the North Sea (Ehrenbaum, 1890) and laboratory reared larvae (Gurney, 1982) are given in Fig. 6.2. Growth of zoeae follows a similar pattern with the other two areas, but growth is slower in the larvae of the Forth Estuary from stage III to VI. The larvae of stage I to IV recorded from the North Sea however, were bigger than that of Forth Estuary. Growth between zoea VI and post-larvae was positive in laboratory reared larvae (Gurney, 1982) but appeared negative in material collected from the field (Ehrenbaum, 1890 and this study Fig. 6.2).

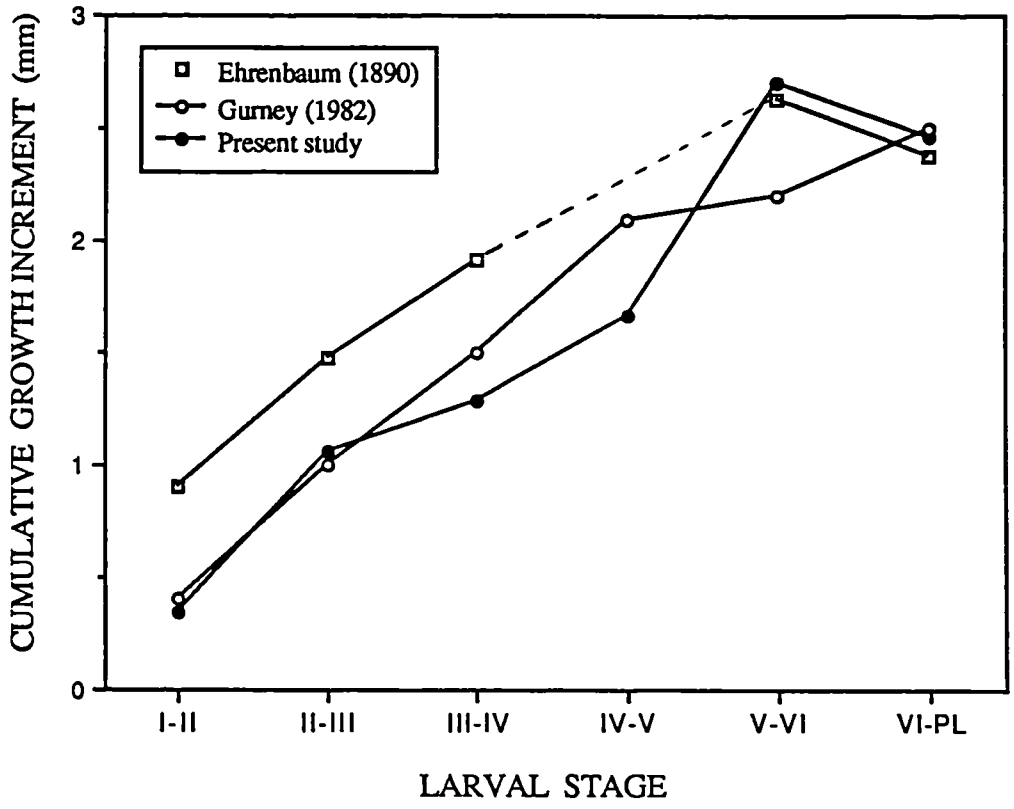


Fig. 6.2- Comparison of cumulative growth increment of the larvae of *Crangon crangon* (L.) during different developmental stages in the Forth Estuary, Scotland, with the previous records (Ehrenbaum , 1890 and Gurney, 1982). Note: stage V was not recorded by Ehrenbaum (1890).

6.3.3 General trends in abundance

Mean abundance of *C. crangon* larvae, calculated as the mean of larvae found in all the stations in the estuary varied greatly with time (Fig. 6.3). First appearance of larvae in plankton occurred in April in both 1992 and 1993. The pattern of temporal variation on abundance and occurrence of larvae was similar in both years, though the abundance of larvae was remarkably higher in July 1993. Larvae were numerous commonly 100 - 300 per 100 m^3, in plankton in June and July, and were present in small numbers in October. A few post larvae were present in Longannet in December 1992 but, in 1993, the larvae disappeared completely from the plankton by December. None were found during January -March.

6.3.4 Spatial, temporal and tidal variation in abundance and distribution

Peak abundance of larvae occurred in July in both years, at both high and low tide. At high tide, maximum number of larvae (382 x 100 m^{-3}) were found at Longannet in 1992, and at Bo'ness (715 x 100 m^{-3}) in 1993. At low tide, the maximum number (345 x 100 m^{-3}) occurred at Port Edgar in 1992 and at Tancred Bank (533 x 100 m^{-3}) in 1993 (Table 6.2). In both years, the highest number of larvae at high tide were found in the uppermost stations while the highest number of larvae at low tide were found in lowermost stations (Table 6.2 and Fig 6.4). In comparison to the estuary, the larvae were less abundant in Kingstone Hudds, and the maximum number found was 15 x 100 m^{-3} in July 1992 and 18 x 100 m^{-3} in June 1993.

Fig.6.4 shows the spatial, temporal and tidal variations in the distribution of *Crangon* larvae in the estuary from the time of first appearance to the time of disappearance. In April 1992 larvae were found only at Port Edgar and in 1993 were found at Port Edgar and Blackness. In both years they were found only at high tide in April. In 1992, larvae were present at all the stations studied, at high tide, by June and July, but were restricted to lowermost stations, Port Edgar and Blackness at low tide (Fig. 6.4). In 1993, the pattern of distribution is almost similar to that of 1992, except that in June the larvae did not penetrate as far as Longannet at high tide, and in July they were present at Tancred Bank and not found at Blackness. Additional sampling carried out at high tide in September indicates that larvae were still present in reasonable quantities at all stations.

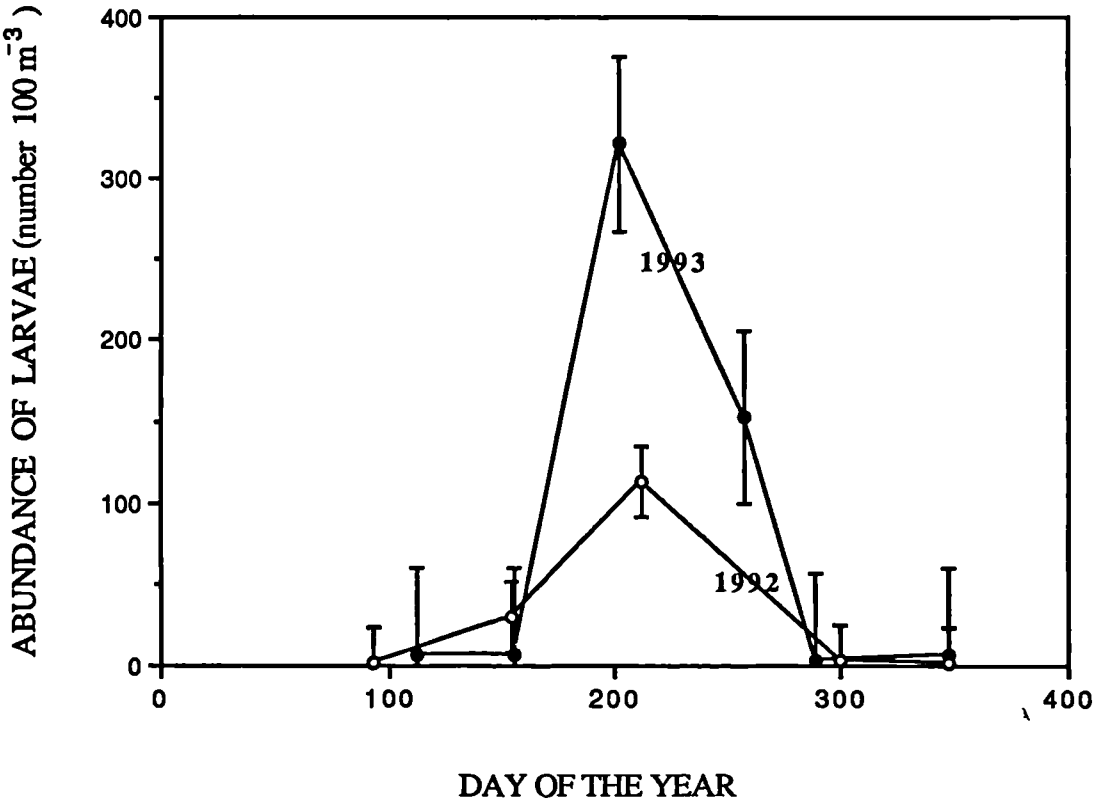


Fig. 6.3 - Mean abundance ± S.E . of *Crangon crangon* (L.) larvae in the collected from five stations; Port Edgar, Blackness, Tancred Bank, Bo'ness and Longannet in the Forth Estuary, Scotland, in 1992 and 1993.

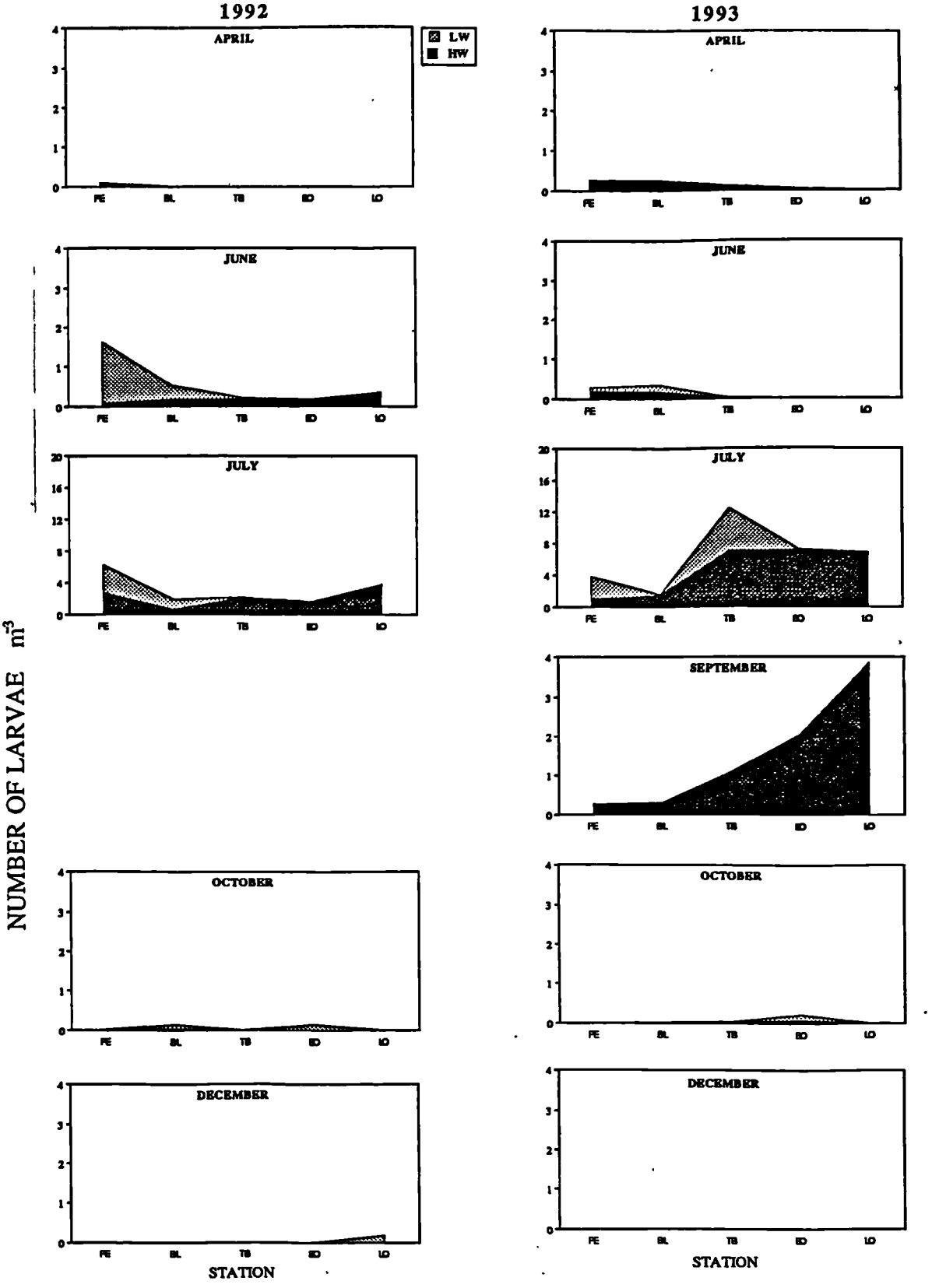


Fig. 6.4- Spatial, temporal and tidal variations in the larval distribution of C. crangon in the Forth Estuary, Scotland (categories are stacked one on top of the other. values are difference between the lines).

Table 6.1 Comparison of total length (length between tip of the rostrum and the posterior margin of telson measured in mm) of larval stages in *Crangon crangon, Crangon allmanni* and *Pandalus montagui* from different authors and in the present study.

Species	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V	Zoea VI	PL_1	References
C. crangon	1.89 - 1.22	2.82	3.40	3.84	Zoea V was not identified by these authors	4.5 - 4.7	4.25-4.30	Ehrenbaum, 1890
C. crangon	2.3	*	*	*		*	4.7[1]	Webb, 1921
C. allmanni	2.2	*	*	*		*	6.0[1]	
P. montagui	4.0	*	*	*		*	*	
C. crangon	2.0	*	*	*	*	*	4.7	Lebour, 1931
C. allmanni	2.8	3.3	4.2	4.8	*	*	6.7	Lebour, 1931
P. montagui	3.0 - 4.0	*	*	*	*	*	*	Lebour, 1940
C. crangon	2.0	2.4	3.0	3.5	4.1	4.2	4.4	Gurney, 1982
P. montagui	3.6	4.3	5.2	6.5	8.3	9.8	*	Pike & Williamson, 1964
P. montagui	3.0 - 5.0		4.5 - 7.0		7.0 - 10.0			Williamson, 1967
C. crangon	1.94 ± 0.04	2.28 ± 0.09	3.00 ± 0.05	3.23 ± 0.07	3.61 ± 0.08	4.64 ± 0.06	4.41 ± 1.10	present study
C. allmanni	2.47	3.52 ± 0.05	**	**	**	**	**	
P. montagui	**	**	**	**	**	**	**	

* - Not reported

** - larval stage not found

[1] - Webb, 1921 reported this as stage IV (mysis), which is PL_1 in the present study.

Table 6.2- Abundance of *Crangon crangon* (L.) larvae (Number/100 m^3) in the plankton at five stations in the Forth Estuary and one station in Kingstone Hudds. PE=Port Edgar, BL=Blackness, TB=Tancred Bank, BO=Bo'ness, LO=Longannet.

DAY OF THE YEAR		HW					LW				
HW	LW	PE	BL	TB	BO	LO	PE	BL	TB	BO	LO
	1992										
78	52	0	0	0	0	0	0	0	0	0	0
92	97	11	0	0	0	0	0	0	0	0	0
153	155	9	19	19	20	35	153	33	3	0	0
211	213	279	68	214	170	382	345	126	3	2	0
297	302	0	3	0	1	0	2	11	0	15	0
343	351	0	0	0	0	0	0	0	0	0	18
	1993										
53	27	0	0	0	0	0	0	0	0	0	0
112	114	22	23	9	2	1	4	3	3	2	0
155	159	18	19	0	0	0	12	16	3	0	0
201	204	108	145	710	715	687	273	15	533	15	0
258	*	27	32	112	206	386	*	*	*	*	*
288	292	0	0	3	9	0	0	3	2	14	1
*	351	*	*	*	*	*	0	0	0	0	0
	1994										
26	33	0	0	0	0	0	0	0	0	0	0

Kingstone Hudds

YEAR →	1992				1993			
Day of the year	47	97	179	294	24	*	163	*
Number of larvae	0	7	15	0	0	*	18	*

* = void

From October onwards larvae were not found in the lowermost stations and were confined to the uppermost stations both at high and low tides.

6.3.6 Abundance and distribution of different larval stages

The mean abundance of different larval stages calculated as the mean number of larvae which occurred in all the stations per sampling trip indicated high abundace of zoea I and PL stages (Fig. 6.5 and 6.6). A similar pattern of occurrence of larvae was evident in both years. The abundance of larval stages, zoea II - zoea VI were less than 5% compared to the stages; zoea I which varied between 6.2% to 38% at high water and 18% to 36% at low water and PL which varied between 12% and 22% at low water.

In April zoea I was the most abundant stage followed by a small percentage of zoea II. In June all the zoea stages were present dominated by zoea I (93% at HW and 53% at LW). Post Larvae appeared first in July, but zoea I still dominated the larval population. In September 1993, a second peak of zoea I was observed and the other stages had almost disappeared from the plankton. Subsequently, in October larval population were dominated by late larval stages and by December (1992) the only stage found was Post Larvae. Tidal transport of zoea I is apparent as the percentage was twice high as in high water (Fig. 6.5).

6.3.7 Effect of environmental factors on abundance

Tests on the effect of environmental factors; temperature (C^{o}), Salinity (ppt), suspended solids (mg l^{-1}), tidal amplitude (m), and depth at haul (m) on the abundance of larvae (number x 100 m^{-3}) showed that the abundance is influenced to a greater extent by temperature and to a lesser extent by salinity (multiple linear regression, $p<0.001$, $F=12.22$). Both these factors were positively correlated with the abundance of larvae. The data used for the test is given in Appendix 6.2. Other environmental parameters did not show a significant influence on abundance (Table 6.3).

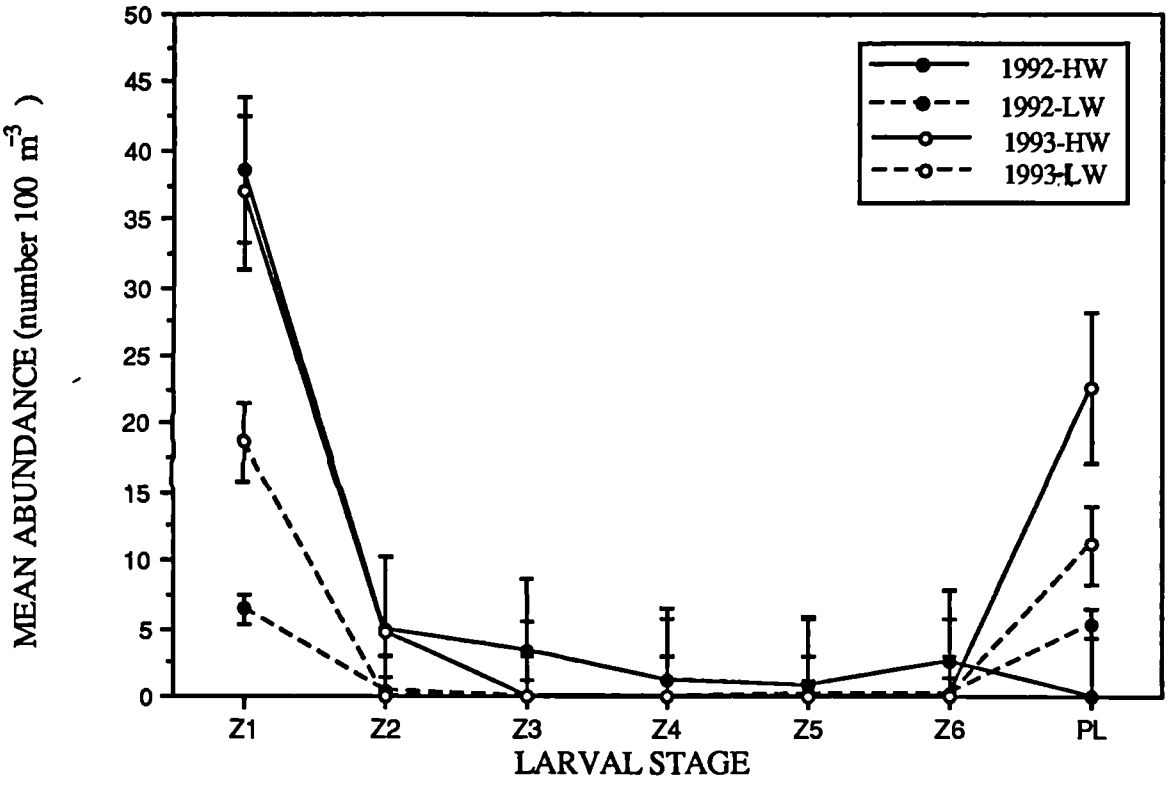


Fig. 6.5 - Mean abundance ± S.E. of different larval stages (number $100m^{-3}$) of *C.crangon* (L.) in the Forth Estuary, Scotland at high tide and low tide in 1992 and 1993.

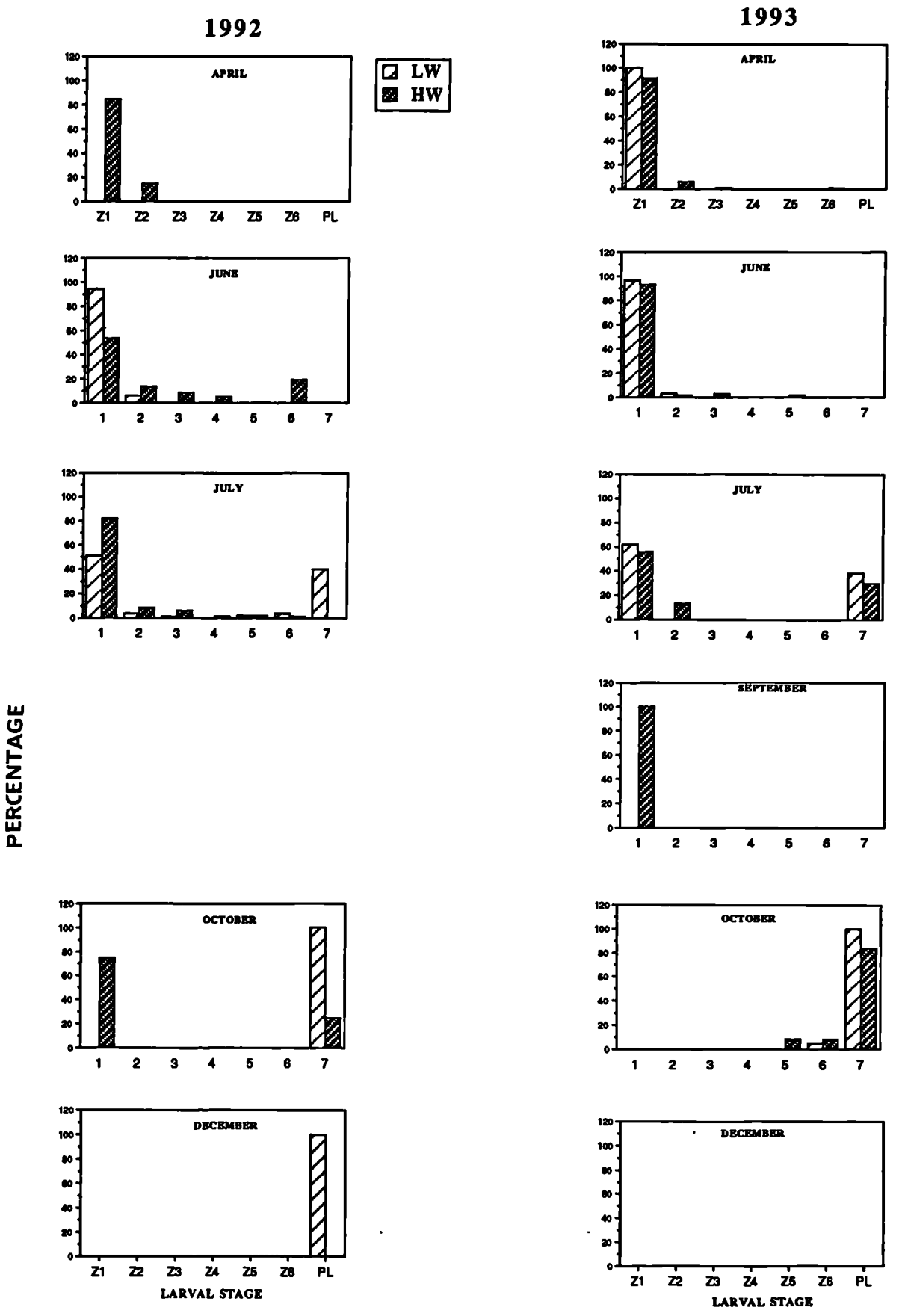


Fig. 6.6- Temporal and tidal variations in relative abundance(%) of different larval stages of *Crangon crangon* (L.) in the Forth Estuary, Scotland.

Table 6.3- Level of significance of students *t*-test on β values of the variables which are not in the equation (n=79).

Variable	β	*t*	Level of significance
Temperature(°C)	0.4157	0.0001	p<0.001
Salinity(ppt)	0.2054	0.0458	P<0.001
Suspended solids(g l^{-1})	-0.056462	0.6032	n.s.
Depth at haul(m)	-0.003227	0.9805	n.s.
Tidal amplitude(m)	0.129034	0.2361	n.s.

The abundance of larvae is described by the equation:

$$A=-401.30+19.02T+8.448S \qquad (6.5)$$

where,

T = temperature(°C)

S = *salinity(ppt)*

Tide also showed a significant influence on the abundance of larvae (ANOVA, p<0.001) though there was no influence of stations on the abundance.

6.4 DISCUSSION

During the present study, only *C. crangon* larvae were found in the Forth Estuary and Firth of Forth. Absence of *P. montagui* and *C. allmanni* larvae in the estuary and Firth of Forth suggests that the optimum conditions required for the development and survival of their larvae are not available in the estuarine environment. The earlier records from North Sea (Lebour, 1940) and Mistakidis, 1957) also indicate that *P. montagui* larvae prefer deep water and offshore areas. *C. allmanni* larvae are also recorded from offshore areas (Danish Wadden Sea, Thorson (1946); North Sea, Allen (1960); Dutch coast, Creutzberg and Leeuwen (1980) and North Sea, Lindley (1987). Lebour (1931) reported that the larvae of *C. crangon* and *C. allmanni* are seldom found together and that *C. allmanni* is a deep water offshore form while *C. crangon* is shallow water and inshore

form. It is not surprising therefore, that we haven't been able to find *C. allmanni* or *P. montagui* larvae in the Forth Estuary but it is perhaps surprising to find that Taylor (1984) who studied the zooplankton of the Forth Estuary did not record *C. crangon* larvae in his list of abundant species in the plankton.

The sizes of the larvae at each stage are in agreement with the previous records (Ehrenbaum, 1890; Williamson, 1901; Webb, 1921; Lebour, 1931; Gurney, 1982). Zoea V identified by the authors prior to Gurney, 1982 was actually the stage VI in the present study and was well in agreement with the results. The size of the post larvae which is remarkably similar to that of Ehrenbaum (1890) and Gurney (1982) may imply that there is no effect of the size of zoea at stage VI on the subsequent size of post larvae and that the size of post larva is more consistent. Zoea VI recorded by Ehrenbaum (1890) and in the present study achieve this consistent size by negative growth, while larvae reared by Gurney (1982) achieved it by positive growth.

The results of the present study concerning seasonal abundance of *C. crangon* larvae are generally in agreement with the findings of previous researchers (Table 6.4). The larvae did not occur from January to March in the Forth Estuary, which suggests that the *Crangon crangon* population in the estuary do not breed in winter. The findings of Jorgenson (1923) in the Newcastle upon Tyne estuary and Kühl and Mann (1963) in the Elbe estuary records similar results. The records from offshore areas however, suggest a winter breeding (southern North Sea, Rees (1952); British coast, Lebour (1947) and Helgoland, German Bight, Wehrtmann (1986)). It may be possible for the offshore populations to breed in winter but the inshore populations seems to have only a hatching period which starts in early spring and ends by late autumn.

The occurrence of most larvae in the lowermost stations at low tide, and in the uppermost stations at the high tide suggests a passive transport of larvae upstream with the rising tide from an estuarine source of origin. The differential occurrence of early larval stages in the lowermost stations and post larvae at uppermost stations further indicates that the larvae migrate upstream to nursery areas and settle down in the upper estuarine areas. Segregation of larval stages along the salinity gradient has also observed by Mees et al.

(unpublished manuscript) in three European estuaries (Eems, n. Netherland; Westerchelde, south west Netherland and Gironde, south west France).

The findings of the present study suggest that there are at least two hatching periods, in the Forth Estuary. The first hatching period extends from April to early or late August while the second hatching period extends probably from late August to December with a peak in September. The presence of newly hatched larvae during September and the unavailability of other larval stages supports the separation of hatching periods. This proposal is also supported by Henderson and Holmes (1987) who observed two spawning seasons per annum in the Bristol Channel and Severn Estuary. The evidence of the present study does not allow a decision concerning the exact duration of the first and second hatching since sampling was not carried out in some months.

Temperature (°C) and salinity (ppt) are found to be the most influential factors on the abundance of larval *C. crangon* in the Forth Estuary. Rochanaburanon and Williamson (1976), Rothlisberg, (1979) and Criales and Anger (1986) also observed temperature and salinity as the key factors in larval survival and development in *Crangon* species. Higher temperature increased the frequency of moulting and decreased survival under laboratory conditions (Criales and Anger, 1986). Salinity on the other hand exerts a weaker influence on larval development (Broekema, 1942; Rochanaburanon and Williamson 1976; this study).

C. crangon is generally considered as a very euryhaline species (Criales and Anger, 1986) but their larvae develop in a narrow salinity range. The results of the present study agrees with Boddeke (1976), which suggests that migration of ovigerous females downstream may transport early larvae to polyhaline areas. This may provide *C. crangon* a greater oppertunity for dispersion of its larvae with the utilisation of tides which cost minimum amount of energy. Tidal currents provide the best passive transport in estuarine areas and the larvae of *C. crangon* take full advantage of it to return upstream to their parental grounds. It is also evident that temperature has a major role to play in the life of *C. crangon* and the larvae do not take a risk of arriving at upper estuarine areas if environmental conditions are not favourable. In the present study, it is apparent that the

Table 6.4 Seasonal occurrence of *C. crangon* larvae in the North Sea and adjacent area as reported by different authors.

LOCALITY	MONTH												REFERENCE
	J	F	M	A	M	J	J	A	S	O	N	D	
Bergen Norway	-	-	-	-	-	-	-	X	X	X	X	X	Wollebaek, 1908
New Castle-upon-Tyne Estuary, UK	-	-	X	X	X	X	X	X	X	-	-	-	Jorgensen, 1923
Plymouth (inshore) UK	-	-	-	X	X	X	X	X	-	-	-	-	Lebour, 1931
Jade Bay	-	X	X	X	X	X	X	X	X	-	-	-	Meyer, 1935
Sound off Ven, Denmark	-	-	-	-	X	X	X	X	X	X	-	-	Thorson, 1946
British coast (Plymouth breakwater)	X	X	X	X	X	X	X	X	X	X	X	-	Lebour, 1947
Southern North Sea	⊗	X	X	X	X	X	X	X	X	-	-	X	Rees, 1952
Elbe Estuary, Germany?	-	-	-	X	X	⊗	X	X	X	X	-	-	Kühl and Mann, 1963
North Sea	-	-	-	X	X	X	X	X	⊗	X	X	-	Lindley, 1987
Helgoland, German Bight	X	-	X	X	X	X	X	⊗	X	X	X	X	Wehrtmann, 1989
Forth Estuary, Scotland	-	-	-	X	?	X	⊗	?	⊗	X	?	X	Present study

⊗ = peak abundance

? = Months at which sampling was not carried out

low temperature which prevailed in June, 1993 has limited the penetration of larvae upstream beyond Blackness.

It can therefore be concluded that larvae of *C. crangon* survive the challenge of estuarine environment, by 1) using the naturally available forces such as tides for their transport and dispersion and 2) delaying migration upstream until environmental conditions, principally temperature and secondarily salinity, are favourable for their development and survival.

CHAPTER 7. FEEDING BIOLOGY

FEEDING ECOLOGY

7.1 INTRODUCTION

Studies of the diet of aquatic animals based upon stomach analysis is a standard practice in ecology (Hyslop, 1980) and is a key to understanding the productivity of the environments (Henderson *et al.*, 1992). In European estuaries, shrimps, *C. crangon* in particular, are exploited as the main prey item by resident and visiting fish (Tiews, 1970; Kühl and Kuipers, 1989; Elliott *et al.*, 1990; Costa and Elliott, 1991; Henderson *et al.*, 1992). Shrimps in their turn exploit the lower benthic groups; meiofauna (Jonsson *et al.*, 1993; Nilsson *et al.*, 1993), infauna and epifauna (Allen, 1963; Simpson *et al.*, 1970; Evans, 1983; Pihl and Rosenberg, 1984; Pihl, 1985; Reise, 1985; Raffaelli *et al.*, 1989; Henderson *et al.*, 1992) thus playing the role of an important link in the food chain between lower benthic groups and fish. The use of *C. crangon* as food by resident and visiting fishes of the Forth Estuary has been studied to some extent (Ajayi,1983; Stewart, 1984; Crossan, 1985; Bell, 1990) but the food and feeding habits of *C. crangon* have been completely neglected.

The focus of this chapter, therefore, is to study the food and feeding habits of the three species of shrimps in the Forth Estuary so that their position and role in the benthic food web, and thereby their contribution to the benthic community, could be evaluated. Species composition and the spatio-temporal variations in the diet of three species are investigated and the dietary overlap among three species and predator-prey relationships are described.

7.2 MATERIALS AND METHODS

Between 15 and 25 animals per species per sample were selected randomly at each sampling date to study the diet of the shrimps. The carapace length of each shrimp was measured, sex was noted, and the stomach was exposed by cutting through the mid-dorsal line of the carapace. The stomach was removed, examined under a dissecting microscope to determine the stomach fullness and preserved individually in 70% alcohol for later examination.

7.2.1 Determination of stomach fullness

Determination of different categories of food in stomach contents by weight was found to be impractical since more than 90% of the food items were too fully digested. Due to this impossibility, subjective methods were the only possible way of determining the fullness of the stomach. Thus, the degree of fullness was determined for individual stomachs ranging from 0 (empty) to 5 (fully distended with food) by awarding fullness points to each stomach using an arbitrary scale. The fullness points were awarded to each stomach by examining under the microscope. The size of the shrimp, appearance of the stomach wall and presence of non-food components such as sand grains, coal pieces and barley husks were also taken into account when awarding the fullness points. Although this method is subjective for assessing quantitative aspects of the feeding, it is adequate for assessing variations in feeding intensity where volumetric or gravimetric methods are not practical. Fullness values were calculated by dividing the total fullness points alotted to all the shrimps in a group by the maximum possible fullness points. The results are expressed on a percentage basis to give the mean fullness of the group as

$$Mean\ \%fullness = \frac{\sum_{i=1}^{n}(X_i)}{(n\times 5)}\times 100 \qquad (7.1)$$

where X_i = fullness points of each individual, n = number of individuals in the group. Variation in the feeding intensity was assessed using % mean stomach fullness and % of empty stomachs found within the group considered for analysis. When considered for seasonal variation the data were pooled into seasonal groups: December and January = winter; April = spring; June and July = summer and October = autumn.

7.2.1.1 Statistical analysis

Season, site, sex, tide, year and stomach fullness of each individual were used for statistical analysis. Statistical analysis was performed with the use of SPSS package and the differences between years was tested using the Mann-Whitney U test. When the differences between years were significant, influence of other variables on the stomach fullness was tested separately for each year. Thus, the influence of tides, sexes, and site

and season on the stomach fullness was tested using Mann-Whitney U test (when number of variables tested (k)=2) and Kruskal-Wallis test (when k>2).

7.2.2 Identification of food items

Each stomach was opened under a dissecting microscope and the contents were emptied onto a slide and the tissues of stomach wall were removed. Identifiable items were transferred to a petri dish and the rest were spread in the slide and examined under a compound microscope. The food organisms were mostly found in a crushed and fully or half digested form. Some of the stomachs however, had undigested food. Even though they are in fully digested form some of the prey items could be identified using the undigested parts which are characteristic to the group or species. These include chaetae and jaws of polychaetes; siphons of bivalves; tails, uropods, cephalothorax, and other appendages in crustaceans (Fig.7.1). Identification of these items was carried out in the following manner.

1. Whole specimens of polychaetes, crustaceans and molluscs commonly found in the estuary, were collected from trawls and from the reference collection of FRPB, and identified to species levelusing the keys listed in Table 7.1.

2. The parts of prey which remained in the stomachs were mounted in formoglycerol and were identified by matching them with the reference slides made by using the actual animals.

Whenever possible the food items were identified to the most precise taxonomic level and counted. The items that could not be identified were catergorised as 'miscellaneous'. Percentage of non food components were also recorded.

7.2.3 Composition of the diet

The frequency of occurrence method (Hyslop, 1980) was employed for examining the dietary composition by counting the number of stomachs containing one or more individuals of each food category. The contents of the stomachs were then categorised into 4 groups ; polychaetes, crustaceans, molluscs and others. The percentage of

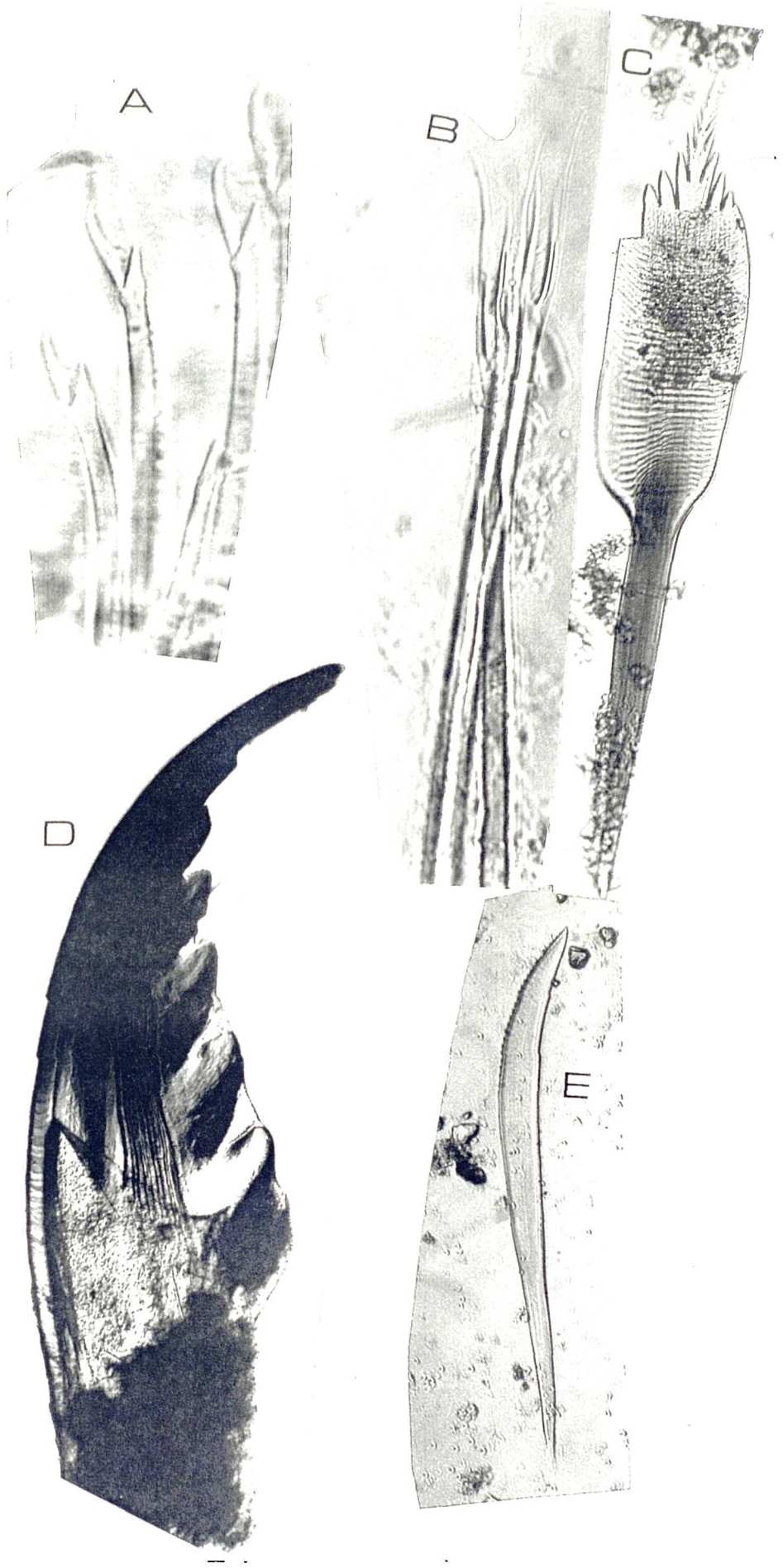
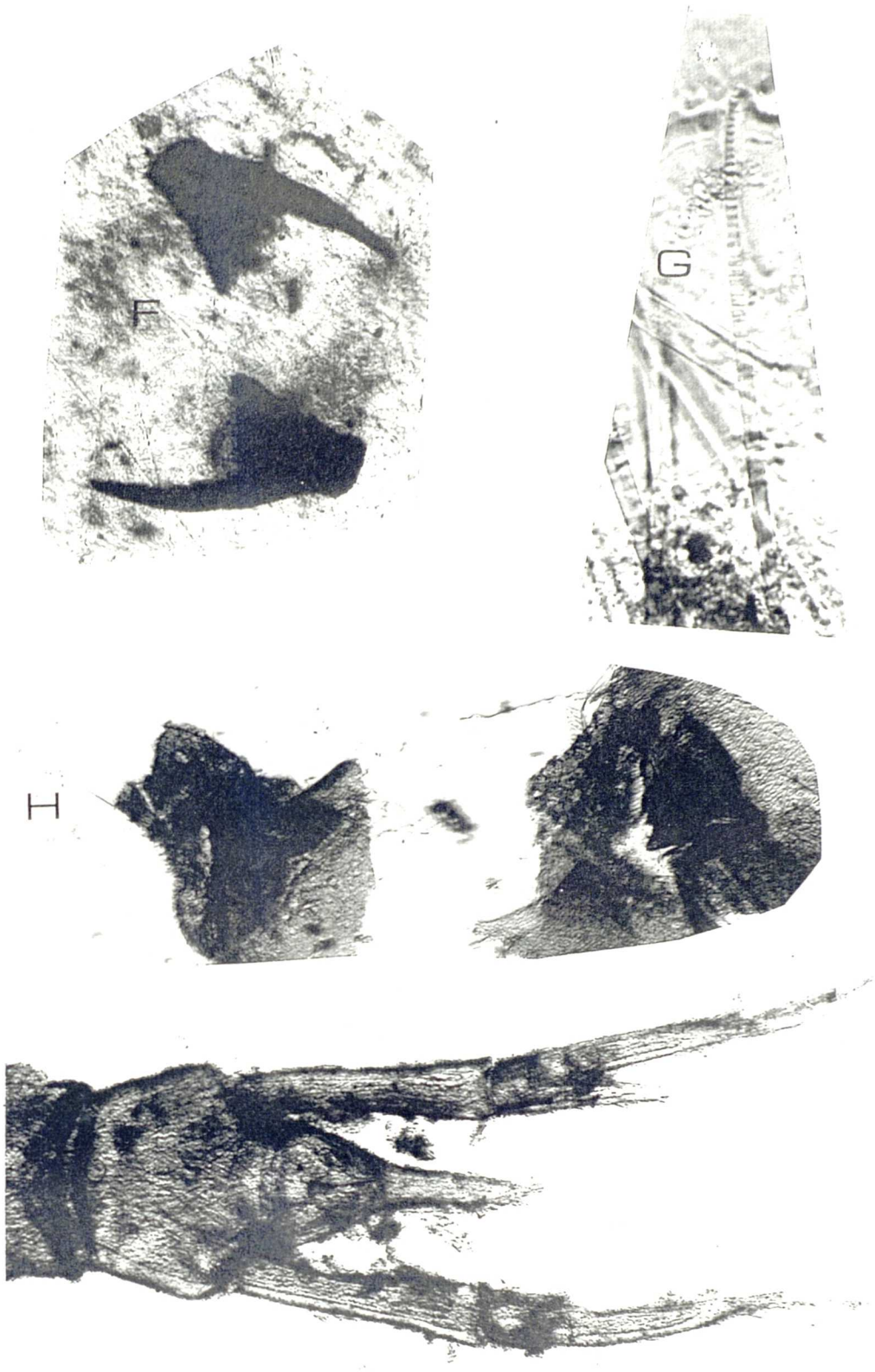


Fig.7.1 Some of the characteristic features of prey items used for identification. A. *Pholoe* (chaetae), B. scalibregmidae (chaetae) C. *Sabellaria spinulosa* D. *Nereis* (jaws) E. polynoidae (chaetae) F. Glyceridae (jaws) G. *Nephtys* (chaetae) H. *Nephtys* (jaws) I. tail part of *Diastylis*.

Contd....



Continued from Fig. 7.1.

Table 7.1 The keys and used for identification of prey items.

Group	Keys
Polychaetes	Chambers and Garwood, 1985 Chambers, 1992 Tebble and Chambers, 1982 Day, *et al.*, 1965 Day, *et al.*, Hayward and Ryland, 1990a Hayward and Ryland, 1990b
Crustaceans	Newell and Newell, 1977 Hayward and Ryland, 1990a Hayward and Ryland, 1990b
Bivalves	Hayward and Ryland, 1990a Hayward and Ryland, 1990b Tebble, 1976

stomachs with unidentifiable food items was also calculated for each species. The number was expressed as a percentage of stomachs containing each category of food. Despite the fact that this method does not indicate the relative bulk of each food category present in the stomachs it provides a somewhat crude qualitative picture of the food spectrum (Hyslop, 1980).

Variations among the food categories with respect to season, tide, area of catch, sex and size were tested using chi-square test.

7.2.4 Determination of size of the prey

The items identified to species level were used to determine the size of the prey by measuring different parts of the body which remained in the stomachs. In *Nephthys hombergi*, body girth was measured in undigested worms and the length of the animal was determined using the relationship, Length (mm) = 13.18 x 31.15 Width (mm) (Olive, 1977). In digested worms, pharyngeal jaws were removed from the animal and cleaned in NaOCl and mounted in 50:50 Formoglycerol. The longest length of the jaw (Olive, pers. comm.) was measured using the micrometer scale under the higher magnification (40 x 10) of the compound microscope. The age of *Nephthys* was also determined by counting the growth rings in the jaw as described in Olive (1977). The size of prey specimens of *Crangon crangon* found in the stomachs was determined by measuring various body parts such as sub-chela, last abdominal segment, uropod, telson, and carapace length. All these measurements were converted to carapace length using the relationships established in chapter 3. The sizes of bivalves were measured only when a whole animal was present and then the maximum body length was measured. All the measurements were taken using a micrometer scale under higher magnification (40 x10) to the nearest 0.01 mm.

7.2.5 Dietary overlap

Intra-specific and inter-specific dietary overlap was investigated following McArthur and Levins (1967) method. According to McArthur and Levins (1967) overlap of species A on species B is given by

$$\alpha_{ij} = \frac{\sum P_i P_j}{\sum P_i^2}$$

and the overlap of species B on species A is given by

$$\alpha_{ji} = \frac{\sum P_i P_j}{\sum P_j^2}$$

The value of α varies from 0 with no overlap to 1 for complete overlap. P_i and P_j represents the proportional use of a food category relative to the other categories by species A and species B.

To evaluate the dietary overlap between and within species the proportions were calculated for each category as a percentage frequency of occurrence, excluding the individuals with empty stomachs and unidentified food.

7.3 RESULTS

7.3.1 General observations on feeding behaviour

C. crangon was found to attack the prey from behind or from the middle as indicated by the position of polychaetes in the mouth and stomach. When attacked from behind the head of the polychaete was usually found hanging from the mouth of the shrimp. On some occasions polychaetes were found with both head and tail hanging from the mouth of *C. crangon* indicating that the prey was caught from the middle. *C. crangon* seemed to take the prey in without chewing it since the whole prey (mostly *C. crangon* and *N. hombergi*) were found intact inside the gut when in an undigested form. The polychaetes were usually found neatly folded and stacked in the stomach when they were not digested. In contrast to *C. crangon*, *P. montagui* crushed prey items and even when the prey items were in undigested or half digested form only crushed parts were found. *C. allmanni* seemed to follow its close relative *C. crangon* and exhibited similar feeding behaviour.

7.3.2 Stomach fullness

A total of 1015 *C. crangon* in 1992, 942 in 1993; 303 *P. montagui* in 1992 and 312 in 1993 and 466 *C. allmanni* in 1992 and 495 in 1993 were used for diet analysis. Mann-Whitney U tests revealed significant variations between two years in stomach fullness of all species (*C. crangon*, $z = -2.83$, $p<0.01$; *P. montagui*, $z = -4.005$, $p<0.001$; *C. allmanni*, $z = -3.79$, $p<0.001$), which was due to the low percentage of individuals with empty stomachs in 1992 (Appendix 7.1). The data of 1992 and 1993 for stomach fullness were hence treated separately for further analysis.

For *C. crangon*, season (Kruskal-Wallis (k-w); $\chi^2 = 30.11$, $p<0.001$ for 1992 and $\chi^2 = 6.29$, $p<0.05$ for 1993), and sex (Mann-Whitney (m-w); $z = -2.008$, $p<0.05$ for 1992 and $z = -3.195$, $p<0.01$ for 1993) indicated significant influence on the stomach fullness. Tidal influence was observed only in 1992 (m-w; $z = -2.50$, $p<0.05$) but was not observed in 1993 ($p>0.05$). Site differences (k-w; $p>0.05$) had no influence on the stomach fullness. Further analysis revealed that seasonal differences are mostly due to the higher feeding in winter, and differences between the sexes are due to higher feeding by males in winter and spring.

For *P. montagui*, both seasonal (m-w; $z = -3.815$, $p<0.05$ in 1992; $z = -2.356$, $p<0.001$ in 1993) and site (k-w; $\chi^2 = 7.83$, $p<0.05$ in 1992; $\chi^2 = 16.76$, $p<0.001$) influences on stomach fullness was observed. No influence was observed by sex (m-w; $p>0.05$) or tide (m-w; $p>0.05$). The seasonal variations were found contradictory in two years with low empty stomachs at Port Edgar in 1992 and many empty stomachs at Port Edgar in 1993.

For *C. allmanni*, site variation was the only influential factor on stomach fullness and was due to high feeding at Longannet and Bo'ness in 1992 and high feeding at Port Edgar in 1993.

Since tide showed little influence on stomach fullness of *C. crangon* and no influence on the two other species, mean stomach fullness was calculated irrespective of tidal differences. Site differences, although influential with respect to *P. montagui* and *C. allmanni*, were also disregarded due to inadequate numbers of animals found at some

stations at some occasions for *P. montagui* and *C. allmanni.* This might also be the reason for the significant differences found with regard to site in *P. montagui* and *C. allmanni. C. crangon*, which had satisfactory numbers under each circumstance, did not show significant variations with respect to stations. The % mean stomach fullness was thus calculated by year, season, and sex for each species.

No pattern of feeding intensity was apparent although low % mean stomach fullness (%MSF) of *C. crangon* and *C. allmanni* seemed to coincide with the period of maturation (Table 7.2) which is in winter for *C. crangon* and in winter/spring for *C. allmanni. P. montagui* showed generally higher %MSF than *C. crangon* and *C. allmanni* throughout the year 1992. The %MSF in 1993 however was lower and, in particular in spring and summer, very low values were obtained for *P. montagui.*

Low %MSF in winter and spring matched the higher % of animals with empty stomachs as shown in Fig. 7.2. Highest feeding intensity in females was observed in summer while winter indicated low feeding intensity. Among males, in 1992 summer indicated higher feeding intensity and spring lower intensity. In 1993, however, feeding intensity remained at a fairly constant level.

The seasonal patterns of feeding intensity as indicated by % empty stomachs were generally similar for both *P. montagui* and *C. allmanni.* The general pattern suggested that the feeding intensity declined with maturation. A gradual increasing trend of feeding intensity from winter to autumn was observed. High feeding intensities were observed in winter and spring (Fig. 7.2).

Feeding intensity in smaller size groups was higher than that in bigger size groups in *C. crangon* and *P. montagui*, but no differences were observed in *C. allmanni* (Fig.7.3). In *C. crangon* highest feeding intensity was observed in the size group 3.1-6.0 mm CL while in *P. montagui* the size group 6.1-9.0 mm CL showed the highest intensity of feeding.

Table 7.2 Variations in the mean % stomach fullness (%MSF) of *C. crangon*, *P.montagui* and *C. allmanni* by year, season and sex. N = number observed.

Season	Sex	Species					
		C. crangon		*P. montagui*		*C. allmanni*	
		N	%MSF	N	%MSF	N	%MSF
		1992					
Winter	♂	199	6.2	21	10.4	111	9.8
	♀	134	6.2	61	8.8	122	8.8
Spring	♂	79	4.0	13	9.2	20	9.0
	♀	78	8.8	45	12.4	50	10.8
Summer	♂	178	9.8	18	10.0	32	7.6
	♀	75	12.2	31	10.4	9	8.8
Autumn	♂	130	8.4	58	8.2	57	6.4
	♀	129	8.8	56	9.0	61	8.2
		1993					
Winter	♂	172	7.2	34	6.4	43	7.4
	♀	177	4.8	37	9.8	175	8.2
Spring	♂	83	9.2	30	4.0	41	5.4
	♀	84	5.4	13	7.6	49	9.4
Summer	♂	31	11.6	58	5.8	12	6.6
	♀	94	7.6	63	4.2	7	2.8
Autumn	♂	120	9.0	40	10.4	93	5.6
	♀	57	6.0	37	7.0	75	7.4

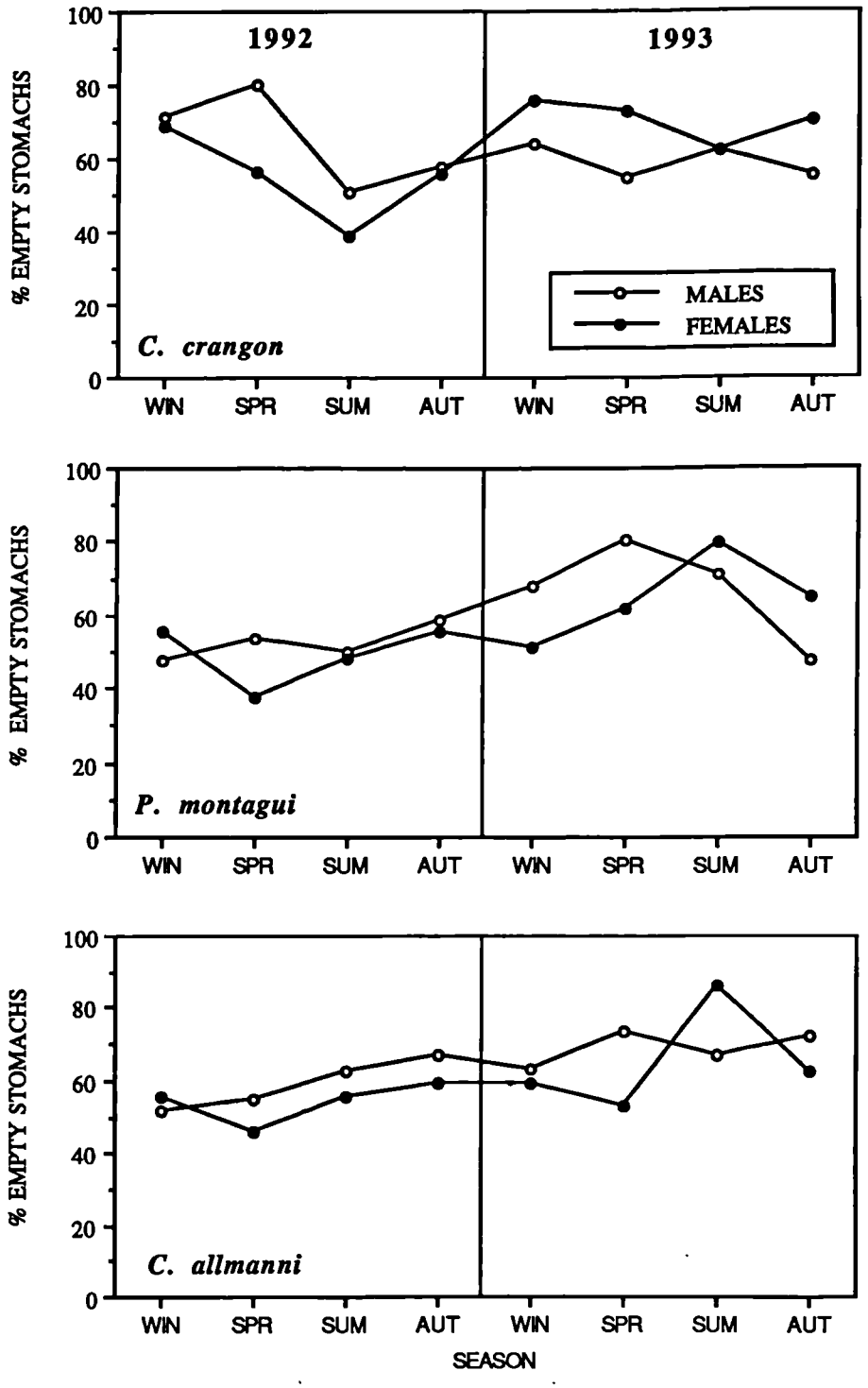


Fig.7.2 Feeding intensity of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary as indicated by % of empty stomachs.

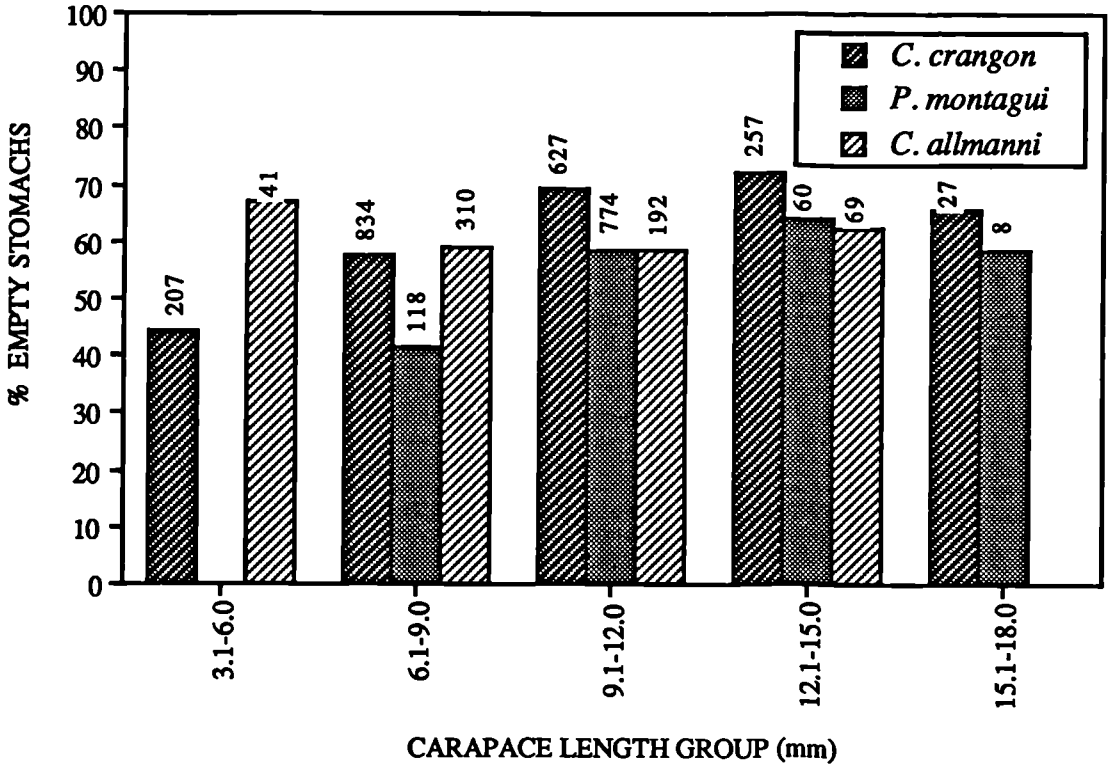


Fig.7.3 Feeding intensity of *C. crangon*, *P. montagui* and *C. allmanni* by size classes, in the Forth Estuary as indicated by % of empty stomachs.

7.3.3 Stomach contents

7.3.3.1 General trends in feeding

In terms of frequency of occurrence, the stomach contents consisted mostly of polychaetes, bivalves and crustaceans (Table 7.3). Among the species identified to the species level, *Nephtys hombergii*, *Pholoe minuta*, *Nereis diversicolor*, *Phyllodoce groenlandica*, *Gattyana cirrosa* dominated the polychaetes numerically. Identified bivalves were dominated by *Abra alba* and *Cerastoderma edule*. *Modiolus modiolus*, *Mytilus edulis*, *Mysella bidentata* were among the other bivalves identified. Crustacean prey were dominated by *C. crangon*, *Diastylis* sp., *Corophium volutator*, *Carcinus maenas*, and *Liocarcinus* sp. Less predominant prey included *Hydrobia ulvae*, the foraminiferan, *Haynesina* sp. and fish. In *C. allmanni* parts of plant matter (algae and sea weeds) were observed. The only identifiable plant was *Enteromorpha*. Detrital matter were also included in the diet, and non-food components such as sand, pieces of coal and barley husks were commonly found in the stomachs of *C. crangon* and *C. allmanni*.

7.3.3.2 Seasonal variations

No significant variations were observed between sexes in frequency of occurrence of different food categories (χ^2 test; $p>0.05$) in any of the three species, hence the data were pooled by sex for further analysis. All three species exhibited significant variations in food categories among seasons ($\chi^2 = 75.29$, DF = 9, $p<0.001$ for *C. crangon*; $\chi^2 = 56.49$, DF = 9, $p< 0.001$ for *P. montagui* and $\chi^2 = 36.11$, DF = 9, $p< 0.001$ for *C. allmanni*). Polychaetes predominated the food in winter and autumn in all species (Fig.7.4). For *P. montagui* in 1992, however, crustaceans were of similar importance. Bivalves dominated the stomach contents of *Crangon* species in spring, but were of second importance in *P. montagui* in spring, where polychaetes were the major prey group. All three major prey groups, polychaetes, bivalves and crustaceans were equally important numerically to *C. crangon* in summer. *P. montagui* predated mainly upon crustaceans and bivalves in 1992, but in 1993 crustacean prey were very low in *P. montagui* and completely absent from *C. allmanni*. Bivalve prey were also not observed in *C. allmanni*. Absence of crustaceans increased the significance of polychaetes in both *P. montagui* and *C. allmanni*.

Table 7.3 List of prey species identified from the stomachs of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary.

Prey Species	Occurrence		
	C. crangon	*P. montagui*	*C. allmanni*
A. Polychaetes			
Nephtys hombergi	+	+	+
Nereis diversicolor	+	+	+
Pholoe minuta	+	+	+
Lepidonotus squamatus	+	+	+
Gattyana cirrosa	+	+	+
Eteone longa	+	-	-
Phyllodoce groenlandica	+	+	+
Phyllodoce mucosa	-	-	+
Marenzellaria wireni	+	-	-
Prionospio malmgreni	+	-	+
Cirratulus cirratus	-	+	-
Cirriformia tentaculata	+	+	+
Capitella capitata	+	+	-
Scalibregma inflatum	-	+	+
Lagis koreni	+	-	+
Sabellaria spinulosa	+	+	+
Polydora sps.	+	-	+
Glycera alba	+	+	+
Scoloplos armiger	+	-	-
Pygospio elegans	+	-	+
Terrebelides stroemi	-	-	+
B. Crustaceans			
C. crangon	+	+	+
Carcinus maenas	+	+	-
Liocarcinus sp.	+	+	-
Diastylis bradyi	+	+	+
Corophium volutator	+	-	-
Praunus sp.	+	-	-
C. Bivalves			
Abra alba	+	+	+
Mytilus sp.	+	+	+
Cerastoderma edule	+	-	+
Macoma baltica	+	-	-
Modiolus modiolus	+	+	-
Mysella bidentata	-	-	+
Hydrobia ulvae	+	-	-
D. Other groups			
Sertularia sp. (Hydroid)	-	+	-
Haynesina sp. (Foraminiferan)	+	+	+
Golfingia sp. (Siphunculid)	-	+	-
Cephalothrix linearis (Nemertea)	-	-	+
Fish	+	-	-
Sea seeds	+	-	-

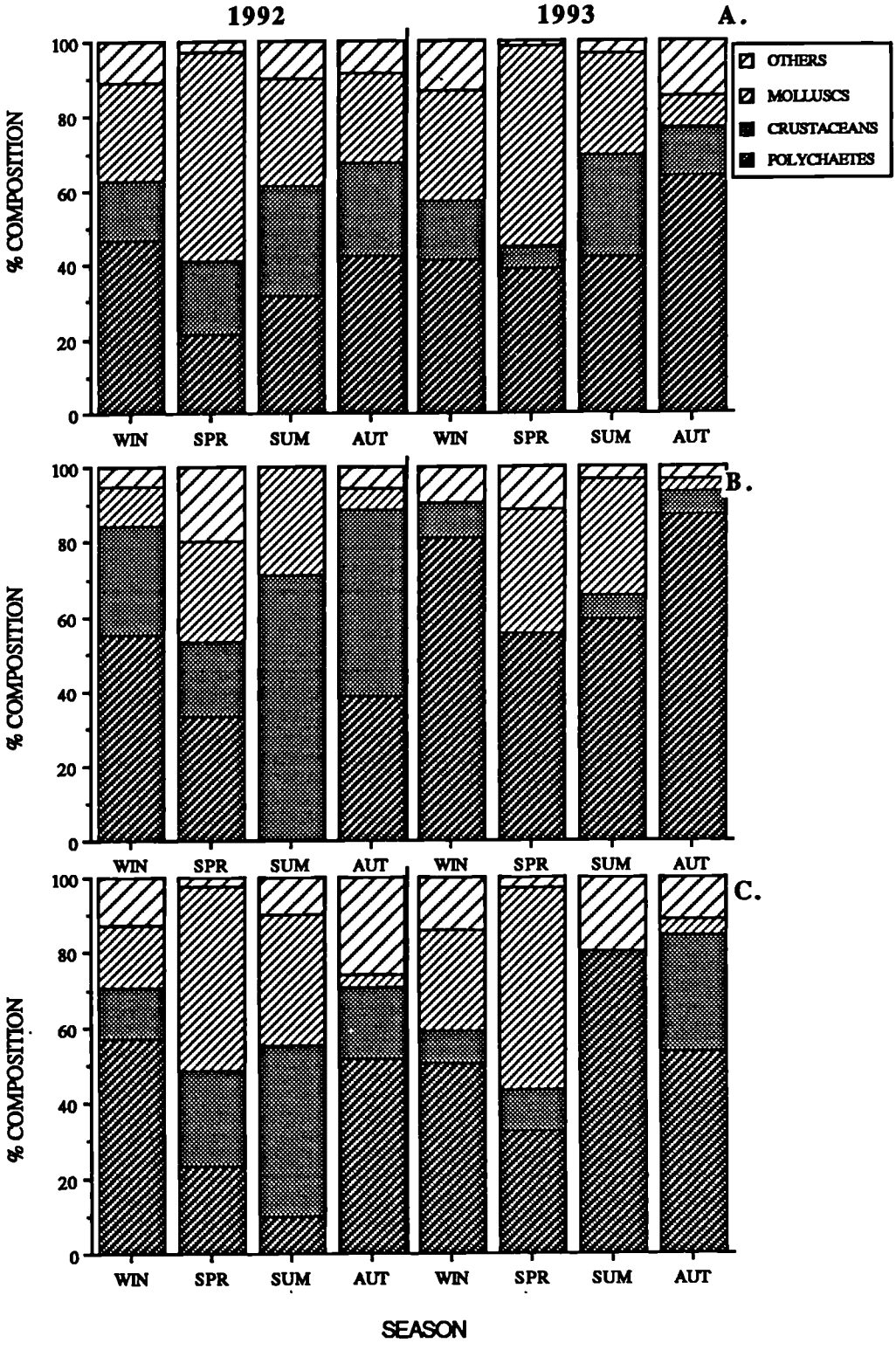


Fig.7.4 Seasonal variations in % frequency of occurrence of different food categories in A). *C. crangon* B). *P. montagui* and C). *C. allmanni.*

7.3.3.3 Spatial variation

Significant variations in the frequency of occurrence of food categories was observed in *Crangon* species $\chi^2 = 82.79$, DF = 12, $p < 0.001$ for *C. crangon*; and $\chi^2 = 71.38$, DF = 12, $p<0.001$ for *C. allmanni*), although no variation with regard to station was observed in *P. montagui* ($p>0.05$) (Table 7.4; Fig. 7.5). Further analysis showed that food categories at the lower three stations were similar in *C. crangon* ($p>0.05$) but significantly different from Bo'ness and Longannet. A significant dissimilarity was also observed between Longannet and Bo'ness ($\chi^2 = 8.45$, DF = 3, $p<0.05$). This difference was due to low predation on bivalves at uppermost stations of the estuary and higher predation on bivalves at the lowermost stations. *C. allmanni* exhibited predation on similar food categories in Port Edgar and Blackness, and again at Tancred Bank and Bo'ness, but varied from Longannet. The significant variation between Tancred Bank and the lower two stations ($\chi^2 = 22.82$, DF = 6, $p<0.001$) was due to the absence of bivalves in the food in Tancred Bank while the variations between Tancred Bank and Bo'ness against Longannet ($\chi^2 = 14.91$, DF = 6, $p<0.05$) was due to higher predation on polychaetes at Longannet and, on bivalves and other groups at Bo'ness. *P. montagui* showed similar prey groups both in Blackness and Port Edgar (χ^2 test; $p>0.05$).

Table 7.4 Frequency of occurrence of food categories in ralation to area of catch in *C. crangon* and in *C. allmanni* in the Forth Estuary.

Food category	Site				
	Port Edgar	Blackness	Tancred Bank	Bo'ness	Longannet
A. *C. crangon*					
Polychaetes	28	40	40	53	79
Crustaceans	23	15	30	15	24
Bivalves	44	39	38	15	7
Others	8	6	7	14	10
B. *C. allmanni*					
Polychaetes	37	27	23	17	27
Crustaceans	15	20	3	6	5
Bivalves	21	31	3	0	0
Others	9	4	6	11	3

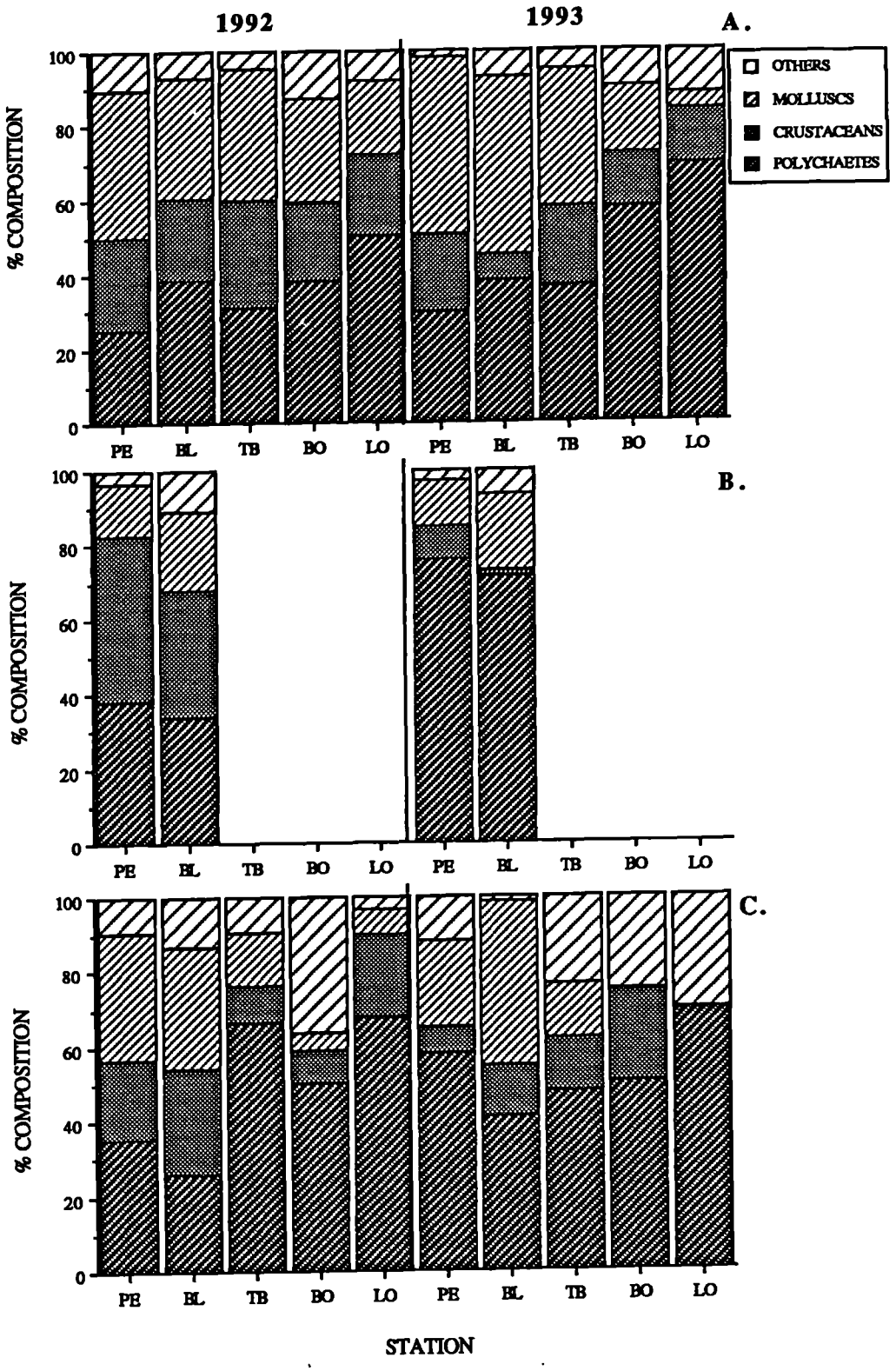


Fig.7.5 Spatial variations in % frequency of occurrence of different food categories in A). *C. crangon* B). *P. montagui* and C). *C. allmanni*.

7.3.3.4 Tidal variations

Tidal variations in food categories were evident in *Crangon* species ($\chi^2 = 9.29$, DF = 3, $p<0.05$ for *C. crangon*; and $\chi^2 = 71.38$, DF = 12, $p<0.001$ for *C. allmanni*) but had no effect on the food categories of *P. montagui* (χ^2 test; $p>0.05$). Consumption of *C. crangon* on polychaetes was higher at low water but was slightly lower on bivalves. *C. allmanni* shows the same tendency to feed on polychaetes more at low water. They fed on bivalves and crustaceans at a higher rate at high water.

7.3.4 Predator prey size relationships

Most of the prey sizes measured were from *C. crangon* while a minor proportion were from *C. allmanni.* Prey of *P. montagui* were in well crushed condition and body parts which could be measured were not encountered. *C. crangon* and *C. allmanni* exerted predation on similar prey species and the animals of similar size were found to prey on similar size groups (Fig. 7.7). Relationship between the carapace length and jaw length of *Nephtys hombergii* indicated two size groups. The absence of rings in the jaws in the first more numerous group which was more numerous indicated that they belong to age group 1 or 2 (Olive and Garwood, 1981). The other group which consisted only three individuals showed 1 growth ring each suggesting that they are in age group 3. Body girth measurements converted to length (not shown in figure 7.7) indicated that prey *Nephtys* are of the size range between 17.9 mm to 50.0 mm in length. Size of the *C. crangon* prey found in the stomachs of *C. crangon* and *C. allmanni* (Fig. 7.7 B) indicated that post larval stages and first juvenile stages are favoured as prey. Even the sizes taken by bigger *C. crangon* did not exceed this size (4 mm in CL). Most of the bivalves measured were from *C. crangon* stomachs except 4 *Abra alba* in *C. allmanni* (Fig. 7.7 C.). *A. alba* and *C. edule* were found to be the preferred bivalves in size classes from 4.0 CL to 9.0 CL while *M. modiolus* and *M. baltica* were found only in the stomachs of *C. crangon* bigger than 9.0 mm CL.

Table 7.5 Frequency of occurrence of different food categories (identified to family levels) in the stomachs of *C. crangon*, *P. montagui* and *C. allmanni*.

Prey group	*C. crangon*	*P. montagui*	*C. allmanni*
A. Polychaetes			
Spionidae	66	4	14
Nephtydae	109	7	42
Nereidae	18	5	5
Phyllodocidae	33	7	33
Sabellaridae	6	2	0
Sabellidae	1	1	2
Cirratulidae	7	2	4
Polynoidae	22	50	19
Pectinaridae	2	0	3
Glyceridae	3	2	3
Scalibregmidae	1	3	2
Terrebellidae	0	0	1
Ampharetidae	0	2	0
Maldanidae	0	1	0
B. Crustaceans			
Harpacticoid copepods	6	3	0
C. crangon	23	1	6
Diastylis sp.	3	0	6
Amphipods	2	0	4
Carcinus maenas	8	1	0
Liocarcinus	1	0	0
Corophium volutator	2	0	0
C. Bivalves			
Abra alba	4	0	5
C. edule	3	0	0
M. bidentata	0	0	0
M. baltica	5	0	0
M. modiolus	1	2	0
D. Others			
Plant matter	2	0	13
Foraminiferan	2	3	3
Fish	13	0	0
Total number of shrimps	343	98	173

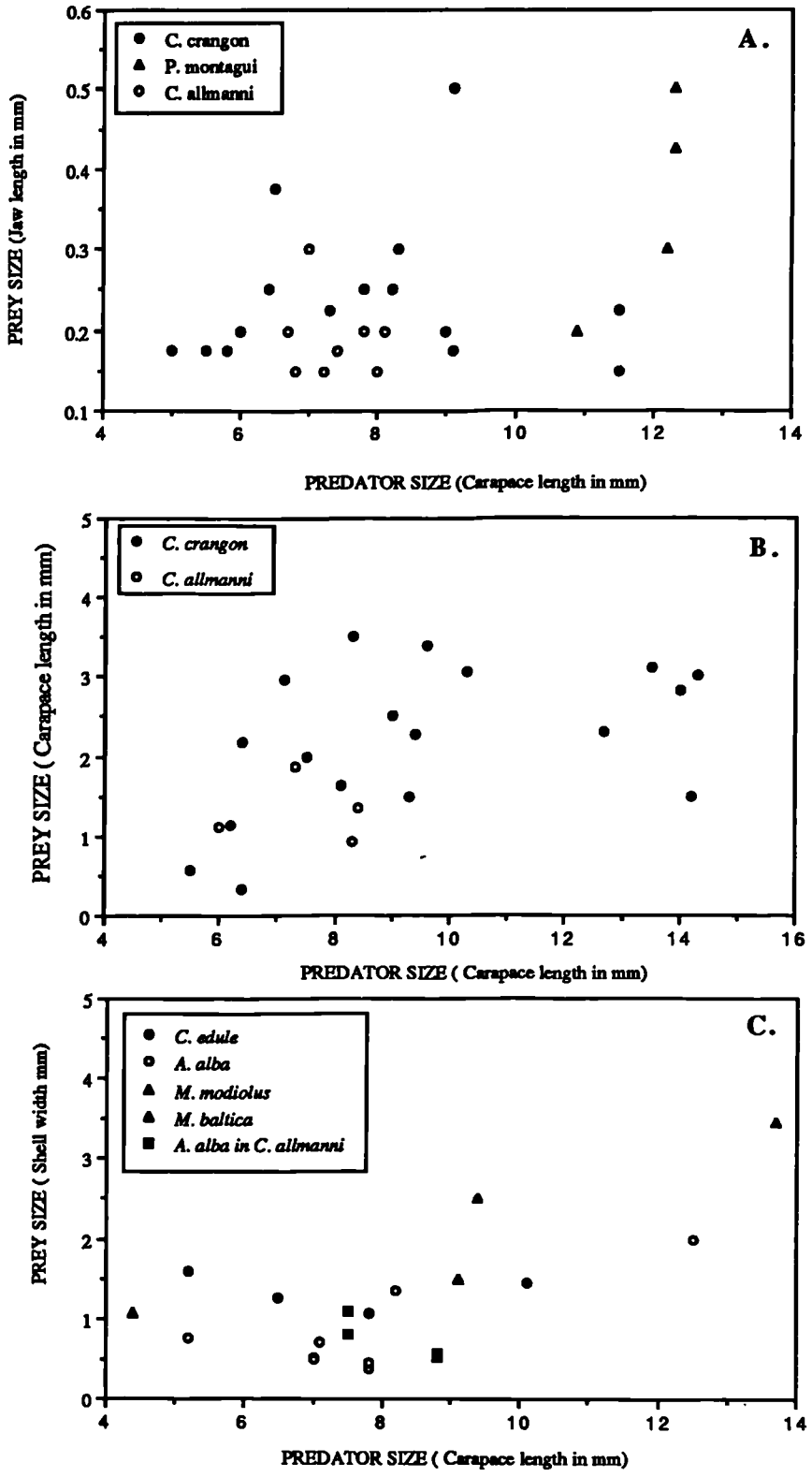
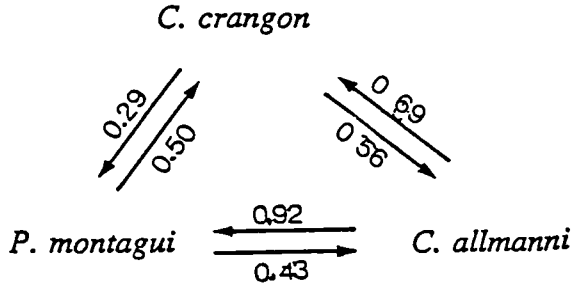


Fig.7.7 Predator-prey size relationships.
A. Predators; *C. crangon*, *P. montagui* and *C. allmanni*; Prey *N. hombergii*
B. Predators; *C. crangon* and *C. allmanni*;Prey, *C. crangon*
C. Predators; *C. crangon* and *C. allmanni*;Prey as given in the legend

7.3.5 Dietary overlap

7.3.5.1 Inter-specific overlap

As indicated by numerical occurrence of each food category (Table 7.5) there is hardly any overlap between diets of *C. crangon* and *P. montagui.* The overlap of *C. crangon* over *P. montagui* was 0.50 while overlap of *P. montagui* over *C. crangon* is very small (0.29). Spionids and nephtyds appear as the dominant prey groups of *C. crangon* while polynoids emerge as the dominant prey group of *P. montagui.* Diet overlap of *C. crangon* over *C. allmanni* was lower than that of *C. allmanni* over *C. crangon* (0.56 and 0.69 respectively). Dietary overlap of *C. allmanni* over *P. montagui* was very much closer to complete overlap (0.92) while overlap of *P. montagui* over *C. allmanni* is low (0.43). The following diagram summarises the interspecific overlap among *C. crangon, P. montagui* and *C. allmanni.*



7.3.5.2 Intra-specific overlap

C. crangon and *P. montagui* showed complete overlap of bigger size classes over smaller size classes while the overlap between adjacent size classes were higher than the remote size classes (Table 7.6). Similar overlap between two size groups of *C. allmanni* were observed (6.0 - 9.0 mm group over 9.0 - 12.0 mm size group, 0.80 and (9.0 - 12.0 group over 6.0 - 9.0 mm 0.85).

Table 7.6 Intra-specific dietary overlap. A. *C. crangon* B. *P. montagui.* The values to the left of diagonal marked by (*) shows overlap of vertically indicated sizes over horizontally indiacated sizes, those to the right of the diagonal indicates the overlap of horizontally indicated sizes over vertically indicated sizes.

A.

Size class	*C. crangon*			
	3.0-6.0 mm	6.1-9.0 mm	9.1-12.0 mm	12.0-15.0 mm
3.0-6.0 mm	*	0.76	0.62	0.62
6.1-9.0 mm	0.94	*	0.82	0.65
9.1-12.0 mm	1.0	1.0	*	0.69
12.1-15.0 mm	1.0	0.92	0.75	*

B.

Size class	*P. montagui*		
	6.1-9.0 mm	9.1-12.0 mm	12.0-15.0 mm
6.1-9.0 mm	*	0.74	0.68
9.1-12.0 mm	1.0	*	0.0.82
12.1-15.0 mm	1.0	1.0	*

7.3.6 Energy transfer by shrimps in the Forth Estuary

The published accounts of the feeding biology of fish in the Forth Estuary, Ajayi (1983), Stewart (1984), Crossan (1985), Townend (1989), Marshall (1990), Bell (1990) and Costa and Elliott (1991) were used to construct the upper part of the food web while the lower part was constructed with the observations from the present study. Energy flow from lower benthic groups to fish via shrimps was shown in Fig. 7.8. *C. crangon* is the major species which transfer energy from lower groups to upper groups being the dominant predator on different benthic groups.

7.4 DISCUSSION

All three shrimp species in the Forth estuary are benthophageous, feeding on infaunal and epifaunal invertebrates; primarily polychaetes, bivalves and crustaceans. Fish, foraminiferans, sipunculids and echinoderms are also eaten but are of minor importance

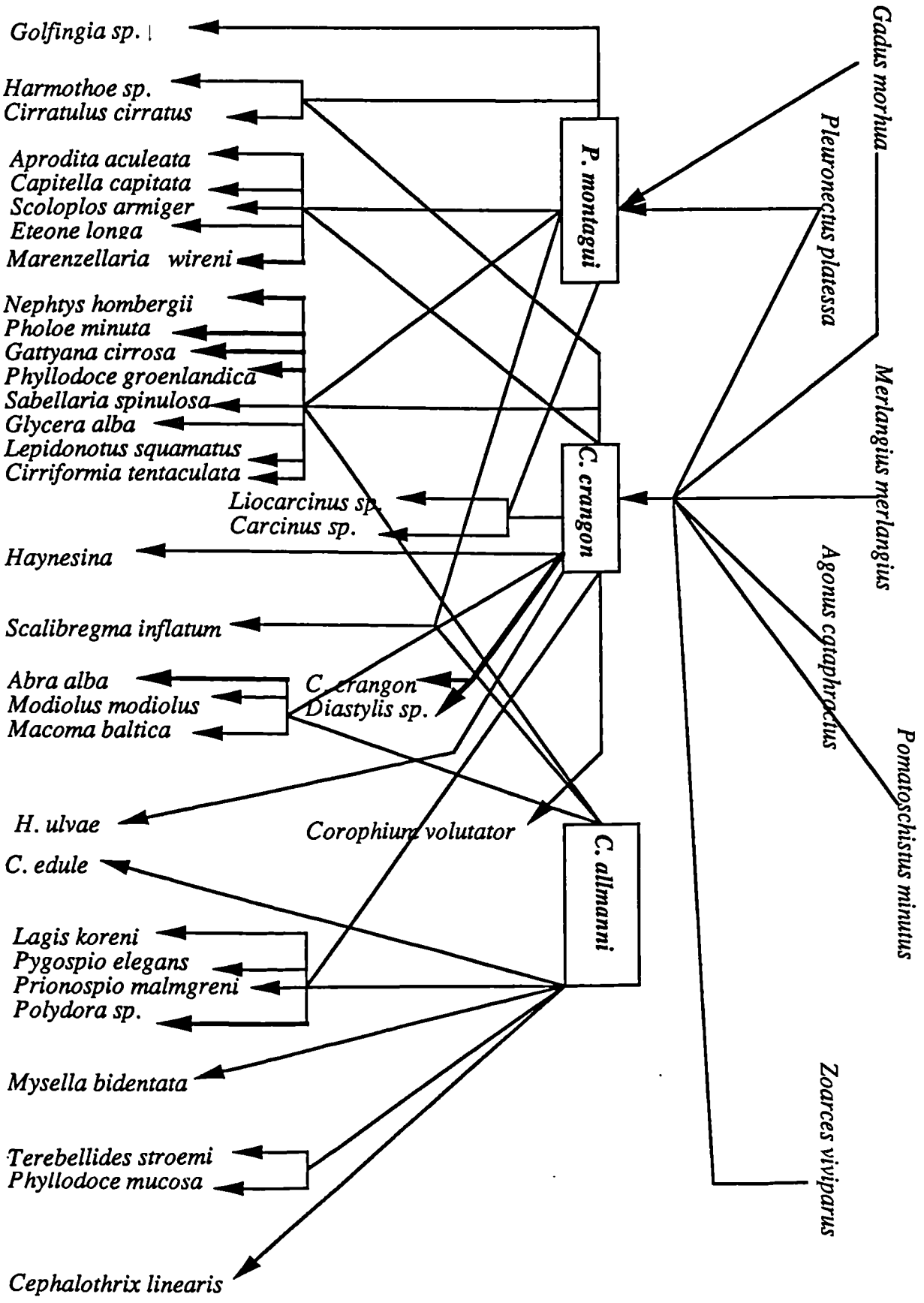


Fig.7.8 Trophic relationships of C. crangon, P. montagui and C. allmanni in the Forth estuary.

compared to the numerically dominant polychaetes and bivalves found in the stomachs. The dominance of polychaetes in the diet of *C. crangon* was also reported from other estuaries in the UK (Lloyd and Yonge, 1947; Henderson and Holmes, 1987; Henderson *et al.*, 1992), Germany (Ehrenbaum, 1890; Tiews, 1970) and Holland (Havinga, 1929) but in Swedish waters; crustaceans and bivalves dominated the food of *C. crangon* (Pihl, 1985; Pihl and Rosenberg, 1984).

In the Forth estuary the polychaetes emerged as the major prey group in all three species, but varied in terms of species selected by each shrimp species. The choice of prey species was found closely related to the natural habitat of each species. Thus, *P. montagui* which are usually found in rocky substrates fed on polynoids; *Gattyana*, *Harmothoe*, and *Pholoe* while *C. crangon* which lives in the mud and sandy substratum in the uppermost stations fed mainly on *Nephtys hombergii* and spionids, particularly *Polydora* sp. which are abundant (Elliott and Kingston, 1987) towards uppermost stations beyond Tancred Bank. The presence in the stomchs of, *N. hombergii*, *N. diversicolor*, *Corophium volutator*, *M. baltica*, *C. edule* and *M. wireni* which are abundant in intertidal flats (McLusky, 1987b) in the stomachs indicates the utilization of intertidal areas as main feeding grounds by both species of *Crangon.*

The high percentages of individuals with empty stomachs may be due to starvation, regurgitation in reaction to the stress when caught in the trawl, or rapid digestion of food. The increase in percentage of empty stomachs in autumn and winter was found due to the maturation of animals. Although not illustrated here, the females with matured gonads always had empty stomachs (personal observations).

Dietary overlap shown here, indicates similarities in the diet rather than competition among the species for food. Competition however, seems unlikely in the Forth estuary where the prey species are found in abundance. The methodology used to calculate the overlap is also questionable since frequency of occurrences were used to calculate proportions of food categories instead of proportions by weight which are commonly used. In the case of polychaetes however, this may give a fair indication of proportion of weight since on most occasions only one polychaete was found per stomach. The use of

percentage frequency for bivalves may definitely give an errorneous interpretation since the numbers present in each stomach vary from one to several and is not representative of weight. The results obtained could be largely explained simply by the distribution of the shrimps. *P. montagui* which is confined to the lower stations of the estuary have low dietary overlap over other two species while *C. crangon* and *C. allmanni* which are distributed throughout the estuary show high dietary overlap over *P. montagui.*

It is clear that *C. crangon* is the species which plays the key role in the food web of the estuary transferring energy from many lower benthic groups to fish and other higher groups. The other two species are not used by the visiting or resident fish species in the estuary as frequently as *C. crangon*, but they might transfer the energy acquired in the estuary to demersal fishes at deeper areas.

CHAPTER 8. DISCUSSION

GENERAL DISCUSSION

8.1 LIMITATIONS OF THE STUDY

The present study, which has focused on the evaluation of the shrimp resources in the Forth Estuary, and a study of their biology and significance to the estuary has suceeded in adding some knowledge to the existing information (FRPB, 1978; Hunter, 1981) on the shrimp populations in Forth. The complete success of the study, was however hindered by several limitations related to the period, frequency and methodology of sampling. Firstly, the evaluation of a resource within a short period such as two years, can not yield adequate information on the annual fluctuations of the population. Secondly, the frequency of sampling was found to be inadequate to draw conclusions on the exact boundaries to the biological activities of the shrimps. The frequency of sampling as well as the number of sampling stations at Kingstone Hudds was extremely limited and was of little use to the studies on the distribution of shrimps. Due to this drawback, the conclusions of the beginning and ending of the biological processes were sometimes based on logical assumptions rather than on direct observations. The times of beginning and ending of biological processes such as breeding and larval recruitment were thus estimated by using the other biological information from the present study as well as those reported by Hunter (1981). Thirdly, the success of collecting shrimps by Agassiz trawl was influenced by the weather conditions although it was towed to the navigational accuracy over the same area of ground at each occasion. In particular, wind velocity and tides affected the position of the trawl, and in some occasions the trawl catch was clean suggesting that it was not trawling on the bottom for long and in some occasions it was full of mud indicating that the trawl has been digging into the substratum.

In addition to these limitations, the study was also affected by the behaviour of shrimps themselves. Caridean shrimps are known to migrate to and from the estuaries in relation to feeding and breeding, and are differentially distributed. Juveniles are mostly found in intertidal areas and uppermost low salinity areas, breeding adults either in uppermost or or lowermost areas depending on the season, and non-breeding animals in subtidal areas moving up and down the estuary with the tide. Further, their biological activities are related with the environmental conditions and they respond to light penetration by burying in the mud with active swimming in the dark (Tiews, 1970). Their distribution is also

affected by the salinity and temperature variations. Broekema (1941) observed that at low temperatures *C. crangon* migrates to high salinity areas and at high temperatures to low salinity areas.

Such limitations, however are unavoidable in studies of the biology in mobile animals, and despite these limitations, the study revealed the basic biological and ecological events of the shrimps which may be useful to shrimp biologists, as well as to wider studies of the Forth estuary.

The study identified *C. crangon*, *P. montagui* and *C. allmanni* as the main three species in the estuary in order of importance. *C. crangon* is the true estuarine type, distributed throughout the estuary but not in Firth of Forth, *P. montagui* is a resident species confined to the lowermost area of the estuary but also found in the Firth of Forth and *C. allmanni* a migrant species which inhabits the estuary during winter and autumn but is not found in either at Firth of Forth or in the estuary during summer. The knowledge acquired in the present study is reviewed below separately for each species with comparisons to previous knowledge from the UK and the other areas of Europe.

8.2 *C. crangon*

C. crangon emerge as the most important shrimp species in the Forth Estuary, in terms of abundance, distribution and utilization of the estuary. Their abundance is about 10 magnitudes higher than that of other two species, and they utilize all the habitats, intertidal areas (personal observations), salt marsh creeks (Dr. Scot Mathieson, pers. comm.), upper estuary and subtidal areas of the estuary. There is little evidence for their occurrence in the Firth of Forth and the utilization of Firth of Forth by *C. crangon* is uncertain.

C. crangon in the Forth Estuary exhibits a life cycle which is quite complicated with continuous breeding and recruitment but the peak occurrences of each event are identifiable when all components of the populations are closely studied. In this regard, the study suffered since no information were available from February, May, August, September and November. The available information together with Hunter's (1981)

account on *C. crangon* identified April, June and August/September as the peak months at which the larvae were released. The months at which important events occur in the life of *C. crangon* was summarized in Table. 8.1. The events observed in this study were marked with (X) and those derived from other sources were marked (x).

Table 8.1 Monthly occurrence of different events in the life of *C. crangon.*

Event	**(X = this study, x = previous information)**											
Mature females	X	x	x	X	x	X	X	x	x	-	x	X
Berried females (stg. A eggs)	X	x	x	X	x	X	X	x	x	-	x	X
Berried females (stg. D eggs)	-	-	-	X	x	X	X	x	x	-	-	-
Larvae (zoea 1)	-	-	-	X	x	X	X	x	X	-	-	-
Post larvae	-	-	-	-	-	-	X	x	x	X	-	X
Juveniles	X	x	-	-	-	X	X	x	x	X	-	-
MONTH	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**

C. crangon showed a wide variety of food choice. Polychaetes were the most frequent prey followed by bivalves and crustaceans. Of the polychaetes, *N. hombergi* and spionids were found to be predominant. Spionids and nephtyds are abundant in the intertidal flats in the central and lower areas of the estuary (McLusky, 1987b ;FRPB, 1992), and the high frequency of their occurrence in the diet showed that the food of *C. crangon* consists mainly of locally available food items. As indicated by the food composition, *C. crangon* is the only species which utilizes the intertidal area of the estuary since intertidal species such as *M. baltica, C. volutator, C. edule* were only found in the stomachs of *C. crangon.* Utilization of such intertidal areas by *C. crangon* has also observed by previous researchers Kuipers and Dapper (1981, 1984), Pihl (1985); Pihl and Rosenberg (1984); Reise (1985) and Raffaelli *et al.* (1989).

It is evident from the present study there is a great similarity in food choice between *C. crangon* and *C. allmanni.* Competition between the two species is, however, most

unlikely since when the rich food resources occur in the spring and summer *C. allmanni* migrates from the estuary leaving all the resources for *C. crangon.* The only possible competition, if there is any, would occur in autumn and winter at the lowermost part of the estuary where all three species gather and utilize the same resources of food. The higher % of individuals with empty stomachs, and low growth rates observed during the winter period may be related to this phenomenon.

C. crangon in the Forth estuary is a prey to the most of the resident fish species; Flounder, *Platichthys flesus* (Bell, 1990); Goby, *Pomatoschistus minutus* (Stevenson, 1988); Pogge, *Agonus cataphractus* (Townsend, 1989); Eelpout, *Zoarces viviparous* (Stewart, 1984) and migrant marine species Plaice, *Pleuronectus platessa*; Dab, *Limanda limanda* (Ajayi, 1983) and Cod, *Gadus morhua* (Crossan, 1985), and the major food item in six of them (Costa and Elliott, 1991). The high fecundity and multispawning undoubtedly reflects the strategy of *C. crangon* for the survival in the estuary. They sacrifice a vast amount of larval and juvenile shrimps to the benefit of other higher invertebrates and fish. This is evident from the production of 0.80×10^7 eggs ha^{-1} which ended up in a mere 130-186 adults ha^{-1}.

8.3 *P. montagui*

P. montagui, although second in importance to *C. crangon*, is the dominant shrimp which inhabits the lowermost area of the estuary throughout the year. It's preference for a hard substratum over a soft substratum is well known (Mistakidis, 1957; Simpson et al., 1970) which may explain its confinement to PE and BL with stony substratum (Elliott and Taylor, 1986) rather than to the muddy and sandy substratum in the upper three stations.

The abundance of *P. montagui* is almost 10 times lower than that of *C. crangon.* This is not surprising because compared to *C. crangon*, *P. montagui* has a fecundity producing only 1/3 to 1/4th of egg numbers per *C. crangon* at a time per female and also spawning only once per annum. The larger females which migrate to the deeper areas for release of larvae are also a loss to the estuary since they do not return to the estuary. The mass migration reported by (Mistakidis , 1957) was not observed in the Forth where a proportion of shrimps always remained in the estuary.

From the occurrence of berried females which are ready to release larvae at KH and the absence of larvae in the estuary *P. montagui* larvae appeared to be released in the deeper areas. Observations of Lebour (1947) confirms the offshore larval stages of *P. montagui.*

It is also evident from this study, that *P. montagui* also prefers the same categories of food as *C. crangon* namely polychaetes, bivalves and crustaceans and reflects the composition of local benthic prey organisms. The polynoid species, *Gattyana cirrosa* thus became a frequent item of food in *P. montagui.* Although found in low occurrences 'ross' (*Sabellaria* sp.) did not emerge as the main item of prey in *P. montagui* of the Forth Estuary as indicated by Murie, 1903 (in Mistakidis, 1957). This may perhaps be due to the limited resources of *Sabellaria* at the PE and BL. Confinement of *P. montagui* to the lowermost stations of the estuary has limited its food spectrum to the available resources in that area and it exerts only a low overlap over the other two species. *P. montagui* has been identified as a prey for *Gadus* sp. and *Pleuronectus* sp. (Mistakidis, 1957) but not in all the fish in the Forth. Thus, it's role in energy transfer to higher level is limited and small compared to *C. crangon.* The migration of the breeding component of the *P. montagui* to deeper areas may however, transport energy to fish in marine areas. Allen (1963) observed that larvae released in 20-30 fm deep area had a better chance of survival than those released in 50 fm deep water since zoeae of *P. montagui* are eaten by *P. borealis.* He further states that *P. montagui*'s inhabitance in the shallow water is a survival strategy since no apparent predator other than adult *P. montagui* are available in shallow areas for zoeae of *P. montagui.*

8.4 *C. allmanni*

C. allmanni appeared to be the least important species of the three shrimp species present in the Forth Estuary, inhabiting the estuary for only a part of the year. The purpose of the migration of *C. allmanni* into the estuary is not very clear and according to Allen (1960) it cannot be related to either rich feeding in the estuary or to the stable conditions for breeding offshore as apply to *C. crangon* since *C. allmanni* is migrating *vice versa.* It is therefore, hard to vizualize the gain of *C. allmanni* by visiting the estuary. It may perhaps be to increase the chance of survival for the new recruits. The migratory component of *C. allmanni* consisted almost of the 0-group, the most vulnerable group to

the fish predation in marine habitat, and the migration into the estuary may give them a better chance for survival than in marine areas.

During their stay in the estuary, *C. allmanni* grow steadily, and matured by the end of their stay. Mating and spawning took place in the estuary in winter, but the females which are ready to release larvae or larval stages were absent in the estuary. It is therefore, evident that the estuary is neither a breeding ground nor a nursery ground for *C. allmanni.* The maturation and spawning periods in the estuary aresimilar to those reported by Allen (1960) in the inshore area of Northumberland waters. Thus, only the initial part of breeding cycle is spent in the estuary and larval release and metamorphosis may occur elsewhere in outer Forth or North Sea. Jorgensen's (1923) and Lebour's (1931) observations on the larvae in offshore waters may explain the absence of larval stages of *C. allmanni* in the estuary.

C. allmanni feeds on a variety of benthic invertebrates, polychaetes, bivalves and crustaceans and predominantly on phyllodocids and spionids and to a lesser extent on *Nephtys.* The bivalve, *Abra alba* is also common among the prey categories. The feeding habit is quite similar to that of *C. crangon.* When present in the estuary *C. allmanni* is distributed from PE up to LO and has an opportunity of feeding on a variety of benthic groups which inhabit there. Thus, its diet overlaps with both *C. crangon* which is more abundant in the uppermost area of the middle and lower estuary and *P. montagui,* which is confined to lowermost area from PE to BL.

The use of *C. allmanni* as a prey by fish has not been reported so far in the Forth Estuary. Since even the existence of *C. allmanni* was not known prior to this study in the Forth estuary, it cannot be totally ignored as a non-prey item to the fish of Forth. It may be interesting to see if there is any fish predation on this species since it may give a clue as to why it migrates into the estuary. In the Forth estuary where *C. crangon* as the preferred prey of almost all the species of estuarine and marine fish, is found in abundance *C. allmanni* could take refuge from the predators.

8.5 CONCLUSION

In conclusion, it can be said that the Forth estuary is being well utilized by *C. crangon, P. montagui and C. allmanni* without much competition. *C. crangon* utilizes the vast food resources in the intertidal areas which have been estimated to consist of 1200 tonnes of benthic biomass (McLusky, 1987b) and subtidal areas with a biomass of 750 tonnes (Elliott and Taylor, 1989). These support a subtidal biomass of 120-200 tonnes of *C. crangon* population which largely supports the population of 120 tonnes of fish (Costa and Elliott, 1991). The shrimp biomass in intertidal areas still remains unknown but it is certain that the biomass of these areas may be several times higher than that of subtidal area. The energy acquired by *P. montagui* supports the estuarine fish population to a lesser account, but both *P. montagui* and *C. allmanni* may be transporting much of their acquired energy resources to marine areas by migration. It is also important that three species acquire energy from different resources from different areas as seen in this study. Although the slow growth rates of *C. crangon* indicated a stressed condition in the estuary, the mean condition factor calculated by Havinga (1930), as 0.007 compared well with the present results (range 0.007-0.02) when converted to similar units, this may indicate that the population in the Forth Estuary are close to the normal conditions required for *C. crangon.*

8.6 FUTURE RESEARCH

The present study can provide the foundation for future research on the shrimp population of shrimps. Although this study revealed several aspects of the shrimp populations in the subtidal Forth Estuary more research is needed to disclose the secrets which still remain hidden. Particularly, study of the aspects indicated below may reward the biologists with absolute knowledge on these fascinating shrimps.

1. The distribution of shrimps in all habitats (intertidal, subtidal, saltmarsh creeks, Firth of Forth and upper estuary) to set the absolute limits to their distribution and to estimate the population size and migration within and between the habitats.

2. Study of reproductive biology along with histological studies of the gonads to find methods for identification of transitionary stages and secondary females of *C. crangon* to estimate the loss and gain to the population by transition.

3. Study of occurrence of post larval and juvenile stages in the intertidal areas.

4. Study of zooplankton in the Firth of Forth to find out the area of larval release and nursery area of *P. montagui* and *C. allmanni.*

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APPENDICES

Appendix 6.1 The data used for testing the influence of Environmental factors on larval abundance (by multiple regression). Stn = Station, T°C = temperature (°C), S = salinity (ppt), SS = suspended solids (g l^{-1}), D = Depth (shoot)(m), T.A. =Tidal Amplitude, and Larv. abu = Larval abundance (100 m^{-3}). (*) = missing data.

Day	Tide	Stn	T°C	S(ppt)	SS	D_s	T.A.	Larv.abu
52	1	1	*	35	0.024	*	0.7	0
78	2	1	*	35	0.012	20	6.1	0
92	2	1	5.6	31	0.058	21	5.2	11
97	1	1	6.3	31	0.032	15	0.8	0
153	2	1	14.0	32	0.010	14	5.6	9
155	1	1	14.5	32	0.028	12	0.6	153
211	2	1	13.5	34	0.012	19	5.7	279
213	1	1	13.5	33	0.024	13	0.1	345
297	2	1	10.0	33	0.016	17	5.6	0
302	1	1	8.0	31	0.064	14	0.9	2
343	2	1	6.0	28	0.016	16	5.4	0
351	1	1	6.5	28	0.018	12	1.7	0
27	1	1	4.0	27	0.008	19	1.3	0
53	2	1	6.5	33	0.020	18	5.6	0
112	2	1	8.5	31	0.020	20	5.4	22
114	1	1	8.5	30	0.032	12	0.8	4
155	2	1	11.5	30	0.022	19	5.6	18
159	1	1	12.0	30	0.048	13	0.8	12
201	2	1	15.0	32	0.020	18	5.6	108
204	1	1	14.0	31	0.042	12	0.3	273
288	1	1	11.0	30	0.026	14	5.9	0
292	2	1	8.0	30	0.074	12	0.7	0
351	1	1	5.0	24	0.096	13	1.3	0
52	1	2	*	33	0.040	*	0.7	0
78	2	2	*	33	0.024	18	6.1	0
92	2	2	*	*	*	*	5.2	0
97	1	2	6.0	30	0.040	13	0.8	0
153	2	2	14.0	32	0.012	18	5.6	19
155	1	2	14.0	31	0.032	13	0.6	34
211	2	2	13.7	33	0.014	19	5.7	68
213	1	2	14.0	31	0.036	12	0.1	127
297	2	2	9.8	31	0.020	20	5.6	3
302	1	2	7.5	31	0.054	13	0.9	11
343	2	2	6.0	27	0.022	19	5.4	0
351	1	2	6.5	27	0.022	14	1.7	0
27	1	2	4.0	24	0.018	13	1.3	0
53	2	2	6.2	33	0.022	18	5.6	0
112	2	2	8.2	30	0.004	18	5.4	23
114	1	2	8.5	25	0.032	13	0.8	3
155	2	2	11.0	30	0.020	18	5.6	19
159	1	2	12.0	29	0.032	13	0.8	16
201	2	2	14.5	32	0.020	19	5.6	145

contd.....>

Day	Tide	Stn	T°C	S(ppt)		SS	D_s	T.A.	Larv.abu
204	1	2	14.5	31	0.036	12	0.3	15
288	1	2	11.5	31	0.048	18	5.9	0
292	2	2	9.0	29	0.064	12	0.7	3
351	1	2	5.0	24	0.080	14	1.3	0
52	1	3	*	30	0.040	*	0.7	0
78	2	3	*	31	0.028	12	6.1	0
92	2	3	5.5	31	0.016	11	5.2	0
97	1	3	6.0	28	0.024	6	0.8	0
153	2	3	14.0	32	0.012	11	5.6	19
155	1	3	14.0	31	0.046	7	0.6	3
211	2	3	13.7	33	0.018	12	5.7	215
213	1	3	14.5	31	0.032	5	0.1	5
297	2	3	9.5	30	0.022	12	5.6	0
302	1	3	8.0	30	0.064	7	0.9	0
343	2	3	6.0	2	0.016	11	5.4	0
351	1	3	6.5	24	0.030	7	1.7	0
27	1	3	4.0	22	0.018	7	1.3	0
53	2	3	6.1	33	0.026	10	5.6	0
112	2	3	8.5	29	0.002	12	5.4	9
114	1	3	8.5	23	0.012	7	0.8	3
155	2	3	11.0	30	0.024	11	5.6	0
159	1	3	12.5	27	0.058	7	0.8	16
201	2	3	15.8	31	0.024	12	5.6	712
204	1	3	14.5	32	0.050	6	0.3	15
288	1	3	11.5	30	0.026	12	5.9	3
292	2	3	9.0	27	0.112	6	0.7	2
351	1	3	6.0	22	0.080	9	1.3	0
52	1	4	*	28	0.096	*	0.7	0
78	2	4	*	30	0.048	9	6.1	0
92	2	4	5.5	28	0.092	9	5.2	0
97	1	4	6.0	25	0.048	5	0.8	0
153	2	4	14.5	31	0.030	11	5.6	20
155	1	4	15.0	23	0.042	4	0.6	0
211	2	4	13.7	33	0.014	10	5.7	170
213	1	4	15.0	30	0.038	3	0.1	2
297	2	4	9.5	30	0.030	13	5.6	1
302	1	4	8.0	30	0.054	6	0.9	15
343	2	4	5.5	23	0.014	11	5.4	0
351	1	4	6.5	23	0.026	4	1.7	0
27	1	4	4.5	23	0.016	4	1.3	0
53	2	4	6.0	32	0.026	11	5.6	0
112	2	4	8.5	28	0.078	8	5.4	2
114	1	4	8.6	22	0.014	8	0.8	2
155	2	4	12.0	28	0.026	11	5.6	0
159	1	4	13.0	25	0.078	5	0.8	0
201	2	4	16.0	30	0.024	9	5.6	717
204	1	4	15.0	27	0.062	3	0.3	15
288	1	4	11.0	29	0.026	9	5.9	9
292	2	4	8.0	26	0.084	4	0.7	14
351	1	4	6.0	24	0.080	5	1.3	0
52	1	5	*	23	0.604	*	0.7	0
78	2	5	*	30	0.044	12	6.1	0
92	2	5	5.5	28	0.060	11	5.2	0
97	1	5	6.0	21	0.076	6	0.8	0

contd.....>

Day	Tide	Stn	T°C	S(ppt)		SS	D_s	T.A.	Larv.abu
153	2	5	15.5	24	0.020	9	5.6	35
155	1	5	15.5	22	0.024	6	0.6	0
211	2	5	16.5	31	0.016	10	5.7	383
213	1	5	16.0	22	0.030	5	0.1	4
297	2	5	9.5	29	0.032	11	5.6	0
302	1	5	8.0	23	0.052	7	0.9	0
343	2	5	5.5	14	0.018	10	5.4	0
351	1	5	6.5	14	0.024	7	1.7	18
27	1	5	4.0	16	0.026	6	1.3	0
53	2	5	6.0	31	0.034	10	5.6	0
112	2	5	8.2	27	0.022	10	5.4	1
114	1	5	8.8	18	0.028	6	0.8	0
155	2	5	12.0	24	0.018	10	5.6	0
159	1	5	14.0	20	0.044	4	0.8	0
201	2	5	16.0	30	0.022	11	5.6	689
204	1	5	15.0	22	0.060	5	0.3	0
288	1	5	10.0	27	0.038	10	5.9	0
292	2	5	8.0	19	0.064	6	0.7	1
351	1	5	6.0	12	0.060	7	1.3	0

APPENDIX 7.1- Number of individuals observed under each category of stomach fullness.

Species	Year	Index of stomach fullness					
		0	1	2	3	4	5
C. crangon	1992	609	66	46	86	75	133
	1993	603	65	58	87	66	62
P. montagui	1992	157	39	25	37	19	26
	1993	208	33	23	23	12	13
C. allmanni	1992	261	44	26	51	38	46
	1993	315	77	25	42	20	16

Out put of Mann-Whitney U test:

Species	Year	No. of cases	Mean rank
C. crangon	1992	1015	1008.86
	1993	941	945.00

U = 446744.5, W = 889955.5, z = -2.8328, p = 0.0046

P. montagui	1992	303	333.85
	1993	312	282.90

U = 39436.5, W = 101155.5, z = -4.0059, p = 0.0001

C. allmanni	1992	466	511.91
	1993	495	451.90

U = 100929.5, W = 238551.5, z = -3.7903, p = 0.0002