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Eco-physiology of mysids (Crustacea; Peracarida) in the River Tamar estuary.

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ECO-PHYSIOLOGY OF MYSIDS

(CRUSTACEA; PERACARIDA) IN THE RIVER TAMAR ESTUARY

By

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ECO-PHYSIOLOGY OF MYSIDS

(CRUSTACEA; PERACARIDA) IN THE RIVER TAMAR ESTUARY

ANGELA MARY MOFFAT

ABSTRACT

The mysid fauna of the River Tamar Estuary was sampled monthly between January and December 1989. The following species of mysid were found in the estuary: *Mesopodopsis slabberi*, *Neomysis integer*, *Praunus flexuosus* and *Schistomysis ornata*. The latter two species, present in low densities throughout the year, occupied the lower, more saline (>30‰) parts of the estuary, whereas *M. slabberi* and *N. integer* were abundant in the upper estuary (0.5-30‰). *Mesopodopsis slabberi* produced between two and three generations per year, and showed a pattern of alternating early and late-breeding generations. A maximum growth rate for this species was 0.24 mm d^{-1} for the fastest-growing summer cohort and annual production estimates ranged between a mean value of 50.6 mg dry weight m^{-3} y^{-1} and a maximum (based on the highest density measured on each sampling date) of 241.4 mg dry weight m^{-3} y^{-1}. This is the first time that growth and production have been estimated for *M. slabberi*. There were marked seasonal and spatial changes in abundance and distribution of *M. slabberi*. Abundance increased from a low of <50 m^{-3} in winter to a maximum of 354 m^{-3} (100 mg dry weight m^{-3}) in summer. Salinity appeared to be the major variable influencing spatial distribution and the different age-classes of *M. slabberi* had clearly identifiable and distinct salinity distributions. There was evidence of a seasonal (winter) down-estuary movement of the *M. slabberi* population. The estuarine distribution of *N. integer* overlapped with that of *M. slabberi*, but *N. integer* had a wider salinity distribution and colonised lower salinity regions of the estuary (<5‰) than *M. slabberi*. Large immature and adult *N. integer* were not sampled successfully in these surveys, suggesting that these stages exhibited a different behaviour from other life-history stages. The physiology underlying the wide salinity tolerance of *N. integer* was examined. *Neomysis integer* maintained its blood hyperosmotic to seawater in the salinity range 0.5 to 20‰ and the haemolymph responded rapidly to acute changes in salinity. This high osmoregulatory ability was correlated with changes in amino acid concentrations, and glutamine, glycine, taurine and alanine were identified as important osmoeffectors in this species.

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Publications

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CHAPTER 1

INTRODUCTION

1. INTRODUCTION

Estuaries are productive, high-energy systems characterised by rapid fluctuations in salinity, suspended sediment concentrations and temperature, caused by frequent changes in water flow, whether from the movement of the tides or from freshwater flowing down component rivers. Superimposed on these short-term, rapid diurnal variations in temperature, salinity and suspended sediment concentrations are longer-term seasonal changes. Large quantities of organic detritus are produced in estuaries or transported into them from rivers and, in some estuaries where suspended sediment concentrations are low and do not restrict light penetration, algal and phytoplankton production make a significant contribution to the nutrient budget (Dyer, 1973; Barnes, 1984).

Although the fluctuations in salinity and the highly mobile sediments result in a harsh environment for plants and animals, those species able to adapt to, or tolerate, the fluctuating conditions occur in huge numbers. The resulting high biomass and productivity allows estuaries to support large numbers of fish and birds, and makes them among the most biologically productive and fertile ecosystems in the world. Estuaries may also make a significant contribution to the pool of dissolved nutrients and particulate material in adjacent near shore waters, thus increasing the productivity of these areas (Davidson *et al.*, 1991).

Mysid shrimps (Crustacea; Peracarida) are common components of coastal and estuarine ecosystems worldwide, and form an important link between the benthic and pelagic systems of these regions (Astthorsson, 1980; Fulton, 1982a & b; Mann, 1988). Although described as detritivores, mysids also feed on phytoplankton and zooplankton, and the general mysid diet is probably better characterized as omnivorous (Lasenby and Langford, 1973; Webb and Wooldridge, 1989). Mysids have two alternative methods of feeding, they either filter feed on suspended particles, or they may utilise a raptorial feeding mechanism to feed on larger particles (Molloy, 1958, Mauchline, 1980). Mysids are thus important converters of organic detritus, living organisms and small particulates into larger food items for other species. Mysids form a major dietary item of many fish species (*e.g.* herring, mackerel, plaice, flounder, whiting, dab and bass) and may also be important in the diet of wading birds (Hartley, 1940; Tattersall and Tattersall, 1951; Mauchline, 1980, 1982; Hamerlynck *et al.*, 1990). In Japan, a number of species of mysid are harvested for human consumption (Omori, 1978).

Many species of mysid are hyperbenthic, found in the water layer immediately above the sediment surface, and are ineffectively sampled using conventional benthic or pelagic

sampling methods (Mauchline, 1980). As a result, despite their frequent occurrence and importance in the diet of fish, there is surprisingly little information available on their life history, distribution and production.

Of the *c.*765 species of mysid recorded worldwide, twenty-nine species are found around the coast of Britain in a range of habitats from estuaries and brackish-water ditches to the open sea (Makings, 1977; Mauchline and Murano, 1977; Moss, 1991). The hyperbenthic species *Mesopodopsis slabberi* (Van Beneden) and *Neomysis integer* (Leach) are two of the most common mysid species occurring in inshore coastal, estuarine and brackish waters in northern Europe (Tattersall and Tattersall, 1951; Ackefors, 1969; Hesthagen, 1973, Boysen, 1976; Parker and West, 1979). *Mesopodopsis slabberi* has a distribution covering the northeast Atlantic, western Baltic, Mediterranean, Marmara, Black and Azov Seas, and is abundant in both estuarine and marine waters in the salinity range 1.3-43‰ (Wittman, 1992). It is one of the three most abundant species occurring in the Bristol Channel where it forms an important constituent of the biomass (Williams and Collins, 1984). At the mouth of the Danube River delta, *M. slabberi* has been recorded at densities of tens of thousands per cubic metre, and has been harvested to feed livestock (Gomoiu, 1978). On the eastern Cape, South Africa, the related species *Mesopodopsis wooldridgei* (Wittman, 1992) is a common component of the surf zone where it forms a major prey item of around 33 species of fish (Wooldridge, 1983). Few quantitative or physiological data have been published for *M. slabberi*. In contrast, aspects of the life history and physiology of *Neomysis integer* have been well studied and reviewed (Ralph, 1965; Astthorsson, 1980; Astthorsson and Ralph, 1984; Mauchline 1971a; Armitage and Morris, 1982; Armitage *et al.*, 1977, 1978 & 1981; Parker and West, 1979; Mauchline, 1980; Hough and Naylor, 1992). *Neomysis integer* has seldom been reported from the open sea but is found on all the Atlantic coasts of Europe, and in brackish and coastal waters from Spain to the Marmara and White Seas (Tattersall and Tattersall, 1951). There is evidence that *N. integer* carries out seasonal migrations, overwintering in higher salinities in the lower reaches of estuaries and migrating into very low salinity regions of estuaries during the summer months (Ralph, 1965).

To exploit the relatively high quantity of organic material available in estuaries, animals must be able to maintain the concentration and volume of their body fluids in the face of fluctuating salinity. Numerous workers have investigated the ability of euryhaline invertebrates to regulate their extracellular and intracellular body fluid concentrations in response to external salinity change (Schoffeniels and Gilles, 1970a & b; Bishop, 1976; Lasserre, 1976; Lockwood, 1976; Lockwood *et al.*, 1976; Schoffeniels, 1976).

Both *M. slabberi* and *N. integer* tolerate large fluctuations in salinity and have been recorded frequently in brackish waters of low salinity. In common with many crustaceans, both *N. integer* and *M. slabberi* are hyper/hypo-osmotic regulators (Ralph, 1965). Free amino acids (FAA) have been shown to be important in controlling the intracellular osmotic concentration in osmoregulating Crustacea, and most estuarine species show changes in intracellular concentrations of these acids as they adapt to changes in sea water concentrations (Bishop, 1976; Schoffeniels, 1976). For example, in *Palaemon elegans* (Rathke), *Penaeus japonicus* (Bate) and *Crangon crangon* (L.), the amino acids glycine, proline and alanine are the main osmoeffectors after a hypo-osmotic shock, whilst hyper-osmotic shock causes increases in the concentration of most FAAs (Weber and van Marrewijk, 1972; Dalla Via, 1989). In the crayfish, *Astacus astacus*, the main osmoeffectors appear to be glutamic acid, proline and alanine (Duchâteau-Bosson and Florkin, 1961), whilst in *Neomysis integer*, increases in salinity have been shown to cause increases in the concentration of glycine, alanine, proline, glutamate and valine (Armitage and Morris, 1982).

As motile species, mysids have developed mechanisms to maintain their position in the estuary and prevent themselves from being moved into unfavourable environments or swept out to sea. Numerous studies have examined the influence of estuarine hydrodynamics and fluctuations in chemical parameters on a range of mysid species. Orsi and Knutson (1979) and Knutson and Orsi (1983) found that the spatial distribution of *Neomysis mercedis* (Holmes) in the Sacramento-San Joaquin Estuary was primarily influenced by salinity changes in response to changes in river flow and spatial separation of the life stages was observed. Similar correlations between salinity and the distribution of the mysids *Tenagomysis novaezealandiae* (Thomson) and *T. chiltoni* (Tattersall) were observed by Jones *et al.* (1989). Wooldridge and Erasmus (1980) found that *Mesopodopsis wooldridgei* was able to selectively utilize both vertical and lateral migration to maintain its position in the Sundays River Estuary whilst the larger mysid *Rhopalophthalamus terrantalis* (Tattersall) was able to maintain position using lateral migration alone. *Gastrosaccus brevifissura* (Tattersall) demonstrates differential age- and sex-specific responses to maintain its position in the Gamtoos Estuary, South Africa (Schlacher and Wooldridge, 1994).

The River Tamar Estuary, Plymouth, was chosen for this study because it is one of the best studied estuaries in the United Kingdom, and its hydrodynamics, chemistry and elements of its biology have been well researched. It is known that mysids occur in high abundance in this estuary, but little is known about their distribution in relation to environmental variables, or their contribution to productivity in the estuary. The objectives of this study were (1) to describe the geographical distribution of mysids on the River

Tamar Estuary, (2) to investigate the seasonal changes in abundance, biomass and brood characteristics of the two main species (*N. integer* and *M. slabberi*), (3) to relate these changes to a range of environmental variables and (4) to describe the changes in distribution and abundance in terms of the underlying physiology.

CHAPTER 2

STUDY SITE

2. STUDY SITE

2.1 Background

The River Tamar Estuary is situated in South-west England and extends for 66 km from its source in Cornwall to Weir Head (Fig. 2.1). At Weir Head, saline intrusion is prevented from further upstream penetration by a weir below which the river is tidal for approximately 31 km to its lower limit at Plymouth Sound. The estuary is classified as a ria (a drowned river valley formed by tectonic subsidence of the land, a rise in sea level, or a combination of both) (Davidson *et al.*, 1991). The upper parts of the estuary sit in a narrow, tree-covered valley and there is a well-defined channel with steeply sloping rocky shores. In the middle and lower reaches, the estuary is characterised by extensive intertidal mudflats backed by shale or saltmarsh. The bed of the estuary, between the River Lynher and Weir Quay, is comprised primarily of mud whilst, in the upper reaches, it consists of bedrock overlain by mud with parts of the bed made of boulders (Percival, 1929; Hiscock and Moore, 1986). The main freshwater inputs into the estuary are from the River Tamar, which drains the western slopes of Dartmoor. Additional freshwater inputs occur from the Rivers Lynher and Tavy.

The River Tamar Estuary and surrounding areas are of considerable historical importance, providing a transport route for centuries for the outputs from the main occupations in the area of farming, fishing and mining. The area of Devonport has been an important naval site since the 13th century, with a naval dockyard established in the 1690s. From around 1850-1900, the Tamar Valley was the richest producing region in Europe of copper and arsenic and the numerous quays on the estuary are testament to the volume of commercial traffic. Commercial traffic in the estuary has ceased within the last fifty years and the estuary above the Tamar Bridge is now used mainly by pleasure craft although some netting for salmon, sea trout and eels still occurs (Potts and Swaby, 1993).

There are three Sites of Special Scientific Interest (SSSI), the Tamar/Tavy and Lynher Estuary SSSIs which include most of the intertidal areas of the Tamar, Tavy and Lynher Estuaries and St John's Lake SSSI which is designated mainly for its extensive intertidal mudflats and eelgrass beds (*Zostera angustiflora* and *Z. noltii*). All three sites are important for their wintering wildfowl and waders (English Nature, 1994). The area of Plymouth Sound, together with the estuaries of the Tamar, Lynher, Tavy and Yealm, has recently been proposed as a Special Area of Conservation under the EC Habitats and Species Directive. The area is one of the finest extensive ria systems in Great Britain, and the Tamar and Lynher estuaries are outstanding British examples of changing estuarine communities with changing salinity regime.

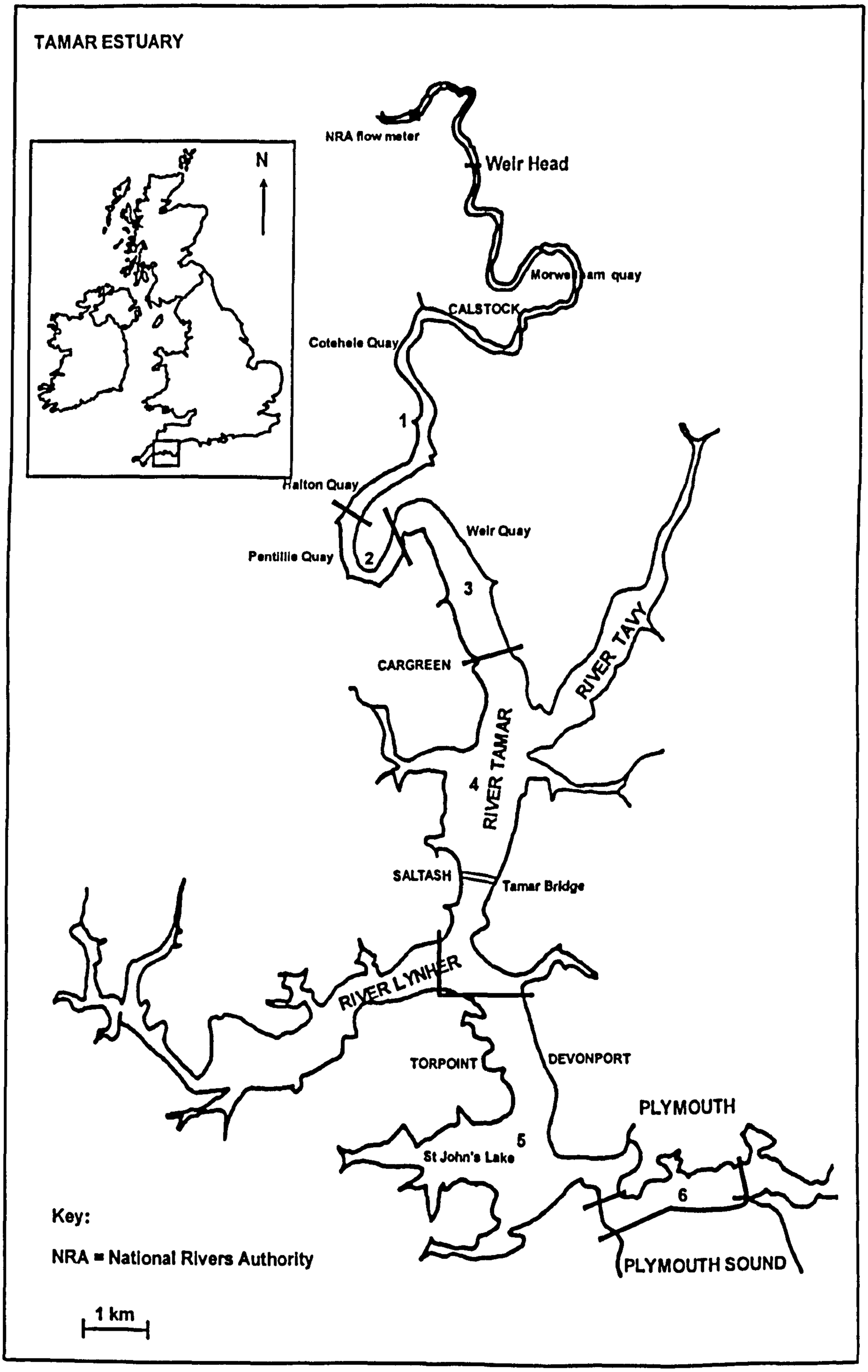


Figure 2.1 The River Tamar Estuary, South-west England, showing marine biological zones (1 upper, 2 inner, 3 transitional, 4 middle, 5 lower, 6 outer) (redrawn from Laffoley and Hiscock, 1993).

The maritime area around Plymouth has long been a centre for marine research. The Marine Biological Association of the United Kingdom was established in Plymouth in 1884 and the Institute of Marine Environmental Research in 1970 (together now Plymouth Marine Laboratory). There is considerable literature on the marine biology of the Tamar Estuary (Cooper and Milne, 1938; Hartley and Spooner, 1938; Percival, 1929; Spooner and Moore, 1940; Warwick and Gee, 1984; Warwick and Price, 1975). The *Plymouth Marine Fauna*, first published in 1904, provides species lists with notes on location, abundance and habitats obtained from the large amount of collecting which has occurred in the area, including the local estuaries (Marine Biological Association, 1904, 1931, 1957). More recent research carried out by Plymouth Marine Laboratory has concentrated on quantifying the physical and chemical dynamics of the estuary (George, 1975; Morris *et al.*, 1982a & b, 1985; Uncles *et al.*, 1983, 1985a, b & c; Uncles and Stephens, 1990).

2.2 Physical and chemical environment

The major freshwater inputs into the estuary are from the River Tamar. The mean daily flow rate, measured during 1989, varied from a maximum of $162m^3s^{-1}$ to a minimum of $1m^3s^{-1}$ (maximum instantaneous flow, $241m^3\ s^{-1}$) (data courtesy of National Rivers Authority). Under normal and high-flow conditions, the limit of salt water intrusion is located 5-15 km seaward of the weir at Weir Head, only reaching the weir when river flow is extremely low.

There are well-established gradients of salinity and suspended sediment within the Tamar Estuary which vary on both short-term (tidal) and long-term (seasonal) cycles. Tides in the estuary are semidiurnal with mean spring and neap tidal ranges of 2.2 and 4.7m, respectively. The middle reaches are generally partially-mixed, although the mixing type, and hence classification type, is variable and major changes in salinity distributions in the estuary are due mainly to runoff, rather than tidal range. During periods of medium to high run-off, the estuary becomes transitional or well mixed in the upper reaches and the saltwater-freshwater interface (FSI) is located about halfway (14 km) from Weir Head. At lower runoff, the interface location shifts to lie between 4 and 7 km from Weir Head (Uncles *et al.*, 1983, 1985a; Uncles and Stephens, 1990). Typically, the vertical salinity range is 1-2 ‰, although the estuary may become well mixed when low river flows coincide with a spring tide. Typical residence times are less than a day throughout the year in the upper 10 km of the estuary. Residence times increase in the summer to a maximum of 10-14 days for the whole estuary. During the winter when runoff is high, residence times for the whole estuary are less than five days (Uncles and Stephens, 1990). A pronounced turbidity maximum occurs in the low salinity region (<5 ‰) of the estuary and is strongly associated with the position of the freshwater-saltwater interface (Loring *et al.*, 1982;

Darbyshire and West, 1993). The geographical position of this turbidity maximum shows a large spring-neap variation due to increased tidal pumping at spring tides. Concentrations of suspended sediment at the turbidity maximum vary between 50 and >1,000ppm, and at spring tides are between one and two orders of magnitude higher than at neap tides in the upper estuary (Morris, *et al.*, 1982; Uncles *et al.*, 1985b). More detailed descriptions of the physical and chemical dynamics of the entire estuary are provided elsewhere (Milne, 1938; Butler and Tibbitts, 1972; George, 1975; Morris *et al.*, 1982, 1985; Uncles *et al.*, 1983, 1985a, b & c; Uncles and Stephens, 1990).

2.3 Biology

Hiscock and Moore (1986) and Laffoley and Hiscock (1993) identified six major ecological zones in the Tamar Estuary based on changes in the distribution of benthic communities and on salinity (Fig. 2.1). These zones are:

- Zone 1, upper estuary, salinity 0.5-5 ‰ - the uppermost limits of *Fucus vesiculosus*, *Balanus improvisus*, *Elminius modestus*, *Conopeum reticulum* and *Hediste diversicolor* occur in this zone. Percival (1929) also noted that the upper limits of the mysids *Praunus flexuosus* and *Mesopodopsis slabberi* occur at around Calstock (salinity 7.8 ‰ at high water (HW)), and of *Neomysis integer* at Morwellham Quay (salinity 0.1 ‰ at HW).

- Zone 2, the inner estuary with a salinity of 5-18 ‰ is characterised by the disappearance of *Ascophyllum nodosum* and *Pelvetia canaliculata* and the appearance of a fringe of *Phragmites*. This zone also marks the upper limit of marine plankton (Percival, 1929), although Dando (unpublished data) found *Eurytemora* over the whole of the area from Weir Quay to Weir Head.

- Zone 3 is a transitional zone and shows clearly the area of transition between characteristic marine species, and brackish-water specialists. It is characterised by impoverished shore communities with dense stands of *Ascophyllum nodosum* and *Fucus vesiculosus*. This zone represents the upper limit of intertidal mudflats which contain a sparse fauna of *Nephtys hombergi* and *Hediste diversicolor*. The upper limits of *Scrobicularia plana* and of *Nephtys hombergi*, and the lower limits of *Gammarus duebenii* and *Corophium volutator* also occur in this zone (Percival, 1929).

- Zone 4, the middle estuary, with a salinity characteristically between 8 and 18 ‰ has shores dominated by fucoids. The upper limits of *Fucus serratus*, *Polysiphonia*

lanosa and *Dynamena pumila* occur in this zone. The mudflats contain typical estuarine species (*Scrobicularia plana, Nephtys hombergii* and *Hediste diversicolor*) and large numbers of *Crangon crangon.*

- Zone 5, the lower estuary has salinities ranging between 18 and 30 ‰. The variety of algae and animals is reduced here, compared with the open sea. A few typically estuarine species occur, most notably *Clava squamata* and *Bowerbankia imbricata.*
- Zone 6, the outer estuary with salinities of >30 ‰ has communities of the intertidal and shallow subtidal areas which are typical of species found on the open coast.

Percival (1929) found four species of mysid in the Tamar estuary (*Schistomysis ornata* (Sars), *Neomysis integer, Mesopodopsis slabberi* and *Praunus flexuosus* (Müller)). He considered *S. ornata* to have the most limited range and to occur in relatively small numbers compared with the other three species. *Neomysis integer* had the widest estuarine range, from the sea to salinities of 0.1 ‰, whilst *M. slabberi* and *P. flexuosus* had more limited longitudinal and salinity ranges. Milner (1986) sampled the area from just downstream of Cargreen up to Calstock during September 1985 and also examined samples taken from the same area in 1982. He recorded the presence of two mysid species (*N. integer* and *M. slabberi*) with the bulk of the adult population of *N. integer* located upstream of adult *M. slabberi* (Milner, 1986). He also found that the distribution of juveniles and adults of both species differed. Dando (unpublished data) found three species of mysid (*N. integer, M. slabberi* and *P. flexuosus*) in the area between Weir Quay and Weir Head. The following ranges were observed: *M. slabberi* occurred in the region between Cargreen and Pentillie Quay, *P. flexuosus* between Weir and Pentillie Quays and *N. integer* from Pentillie Quay to Weir Head. No salinity data were available.

The fish fauna of the estuary has been described by Hartley (1929) and by Potts and Swaby (1993). Of the many species which use the estuary as nursery grounds, flounder, *Platichthys flesus*, was the only species found in the brackish upper reaches of the estuary. Crustaceans formed the most important component of the diet of flounder, with three species contributing more than 80 % of the total crustacean species (Hartley, 1929). *Crangon crangon* formed around 45% of the species whilst the remainder was provided by mysid shrimps (mainly *N. integer* and *S. ornata*). Dab, *Limanda limanda*, were found in the estuary, but rarely further upstream than Saltash. The diet of O-group dab was mainly crustaceans, including juvenile *N. integer* and *S. ornata.* Older dab consumed mysids mainly in the summer months, with polychaetes forming the bulk of the diet for the remainder of the year. Plaice, *Pleuronectes platessa*, were found as far upstream as the River Tavy. *Neomysis integer* and *S. ornata* were important dietary components of plaice

year round. Juvenile herring, *Clupea harengus*, also occur in the estuary. Copepods were found to be their most important food in winter, but mysids, of all four species (*M. slabberi, N. integer, P. flexuosus* and *S. ornata*) increased in importance in the summer months. The diet of the several gadoid species which occur in the estuary consists primarily of *Crangon crangon* and mysids, and the diet of gobies and bass, *Dicentrarchus labrax*, was similar.

The Tamar Estuary supports nationally important populations of wintering avocet (*Recurvirostra avosetta*), for which the Tamar Estuary is one of four main wintering sites in the UK, and black-tailed godwit (*Limosa limosa*) (comprising 14% and 2% of British populations respectively). Other species which winter in the area include spotted redshank (*Tringa erythropus)*, greenshank (*Tringa nebularia*), grey plover (*Pluvialis squatarola*), dunlin (*Calidris alpina*), curlew (*Numenius arquata*), redshank (*Tringa totanus*), green sandpiper (*Tringa ochropus*) and common sandpiper (*Tringa hypoleucos*) (English Nature, 1994). Of these species, mysid shrimps are thought to provide a significant component in the diet of avocet (P. Reay, personal communication).

CHAPTER 3

FIELD STUDIES

3. FIELD STUDIES

3.1 Introduction

Of the four species of mysid distributed horizontally along the River Tamar Estuary, *Mesopodopsis slabberi* (van Beneden) and *Neomysis integer* (Leach) are abundant in the upper estuary (Percival, 1929; Milner, 1986; Greenwood *et al.*, 1989). The life cycle of *N. integer* has been described comprehensively in the Baltic, Scotland and Ireland by Kinne (1955), Mauchline (1971), and Parker and West (1979) respectively, while that of *M. slabberi* is poorly understood. For the Tamar Estuary, there is little published information on the life history and distribution of these two species. Percival (1929) noted the distribution of these species in the Tamar Estuary in relation to salinity although his results were non-quantitative. Milner (1986) reported observations of the density and distribution of *N. integer* and *M. slabberi* on single sampling dates in 1982 and 1985. Milner (1986) recorded *M. slabberi* at densities of more than 4,500 individuals m^{-3} and *N. integer* at densities of up to 1,400 individuals m^{-3} during the summer. He found *N. integer* and *M. slabberi* confined to a relatively narrow range of salinities, with the bulk of the population of *N. integer* located in lower salinities than *M. slabberi*; there was also some evidence of spatial separation between the life stages in both species (Milner, 1986).

Greenwood *et al.* (1989) identified salinity as a major environmental factor affecting the distribution of *M. slabberi* in the Tamar Estuary. These authors examined the effect of salinity on embryo development and found that seasonal changes in salinity distribution could be a factor explaining seasonal population movements Although many studies have implicated salinity as a factor affecting the distribution of estuarine mysids, other factors such as estuarine hydraulics may also have a large influence (Orsi and Knutson, 1979; Siegfried *et al.*, 1979; Jones *et al.*, 1989). There is also some evidence that *M. slabberi* undergoes seasonal onshore/offshore migrations (Apel, 1992; Bamber and Henderson, 1993).

There is no published information available on production for *M. slabberi*. Wooldridge (1983) and Wooldridge and Bailey (1982) have estimated the standing crop of the related *Mesopodopsis wooldridgei* to be as great as 1,913 mg dry weight m^{-3} and 3,589 mg dry weight m^{-3} at some locations in the eastern Cape, South Africa at certain times of the year. Several workers have estimated production in *N. integer*, including Mees *et al.* (1994) who estimated production of *N. integer* in the Westerschelde Estuary, southwest Netherlands. Mees *et al.* (1994) obtained estimates of between 322 and 449 mg AFDW $m^{-2}yr^{-1}$, although

Bremer and Vijverberg (1982) obtained much lower estimates, in a freshwater lake in the Netherlands (10 mg DW $m^{-2}yr^{-1}$), as did Thiel (1992) in the southern Baltic (9 mg wet wt $m^{-2}yr^{-1}$).

In the subsequent 5 chapters, the life histories of *N. integer* and *M. slabberi* are examined, and the observed patterns of distribution and abundance are correlated with a number of physical and chemical variables in the upper Tamar Estuary. Estimates of growth and production are derived for *M. slabberi*. Some preliminary observations of the mysid community composition in the lower estuary are also included to aid in the understanding of distributions observed in the upper estuary.

3.2 Methods

Initial surveys along the estuary in January and February 1989 established that the bulk of the populations of *M. slabberi* and *N. integer* were located over a 17 km stretch of the estuary lying, approximately, between Cargreen and Morwellham Quay (Fig. 2.1). Some individuals of both species were present in the lower reaches of the estuary and two other species *Praunus flexuosus* and *Schistomysis ornata* were also present in these samples. Therefore, the sampling programme was divided into two parts. The first entailed quantitative sampling from a limited number of stations in the lower estuary to establish the presence (and limited data on abundance) of all four mysid species throughout the year. This element of the sampling programme did not involve measurement of physico-chemical variables. The second part was a more comprehensive survey designed to enable full descriptions of the life histories of *M. slabberi* and *N. integer* to be made, production estimates to be obtained and observed distributions correlated with a range of physico-chemical variables.

3.2.1 Lower estuary

A minimal sampling programme was carried out in the lower estuary (Fig. 3.1) to identify the occurrence of the two major species of interest in the upper estuary (*M. slabberi* and *N. integer*) and other species which may have an influence in determining their distribution. No physical or chemical measurements were taken, although data on river flow rates, obtained from the National Rivers Authority, were utilised.

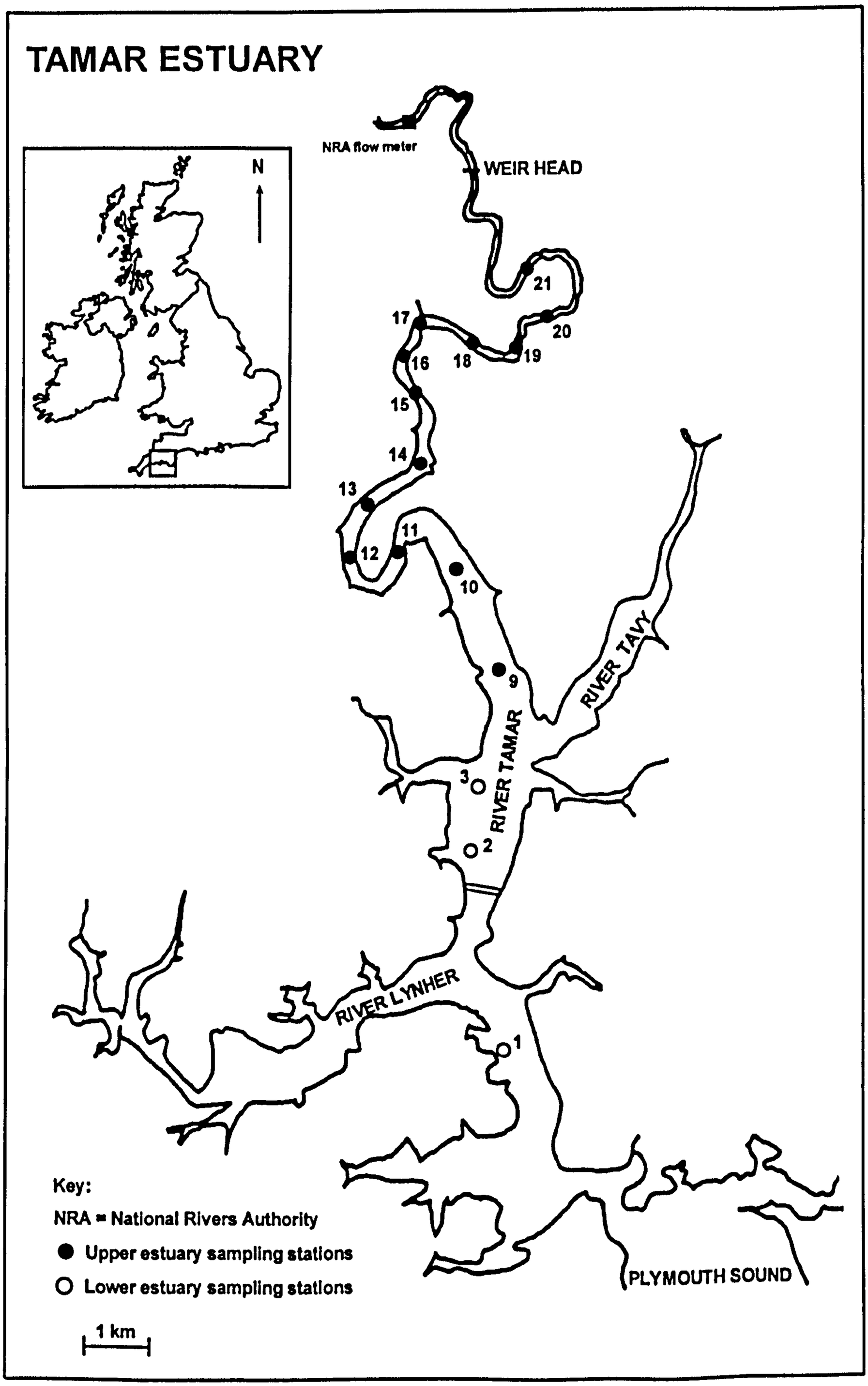


Figure 3.1 Map of the River Tamar Estuary showing upper (9-21) and lower (1-3) sampling stations.

Sampling

In January, March, April, May, June and December 1989, samples were taken from three stations in the lower estuary (Stations 1-3; Fig. 3.1). Two consecutive tows were made at each station from the *RV Sepia* using a benthic sledge fitted with a plankton net (mesh size 280 μm). The sledge was equipped with an opening/closing system which ensured that samples were taken from as near to the bottom as possible. The volume of water filtered on each tow was measured using a General Oceanics Model 2030 flowmeter. Samples were preserved immediately in a solution of buffered formalin in seawater for transport back to the laboratory. Full descriptions of the samples are included in Appendix I.

Laboratory procedures

The two samples, taken at each station, were pooled for the purposes of the analysis and were sorted to extract the mysids. The mysids were identified to species (Tattersall and Tattersall, 1951; Makings,1977), and each individual was straightened, measured (± 1 mm) from the base of the eyestalk to the posterior end of the uropods (excluding the setae) using an eyepiece graticule in a stereoscopic binocular microscope (Mauchline, 1969) and ascribed to one of six categories according to the degree of development of the secondary sexual characteristics (Mauchline, 1980):

- juvenile (secondary sexual characteristics absent);
- immature male (secondary characteristics developing, fourth pair of pleopods longer than the others);
- mature male (secondary sexual characteristics fully developed, fourth pair of pleopods extending halfway along the telson);
- immature female (marsupium developing and smaller than in the mature female, no eggs or young carried);
- mature female (marsupium fully developed, and eggs or young present in the marsupium);
- mature and empty females (marsupium fully developed, and either not yet filled with young, or young have emerged).

Data analysis

On each sampling date and for each station, individual mysids of each species were divided into 1 mm length classes and length-frequency distributions plotted. The density of each species of mysid at each sampling station was expressed as the number of individuals per m^3 (Nm^{-3}).

3.2.2 Upper estuary

Sampling

At approximately monthly intervals between February and December 1989, samples were taken from 13 stations (9-21) along the estuary (Fig. 3.1); samples were taken on two dates in February 1989 and no samples were taken in August 1989. On each sampling date, samples were taken only from those stations where the salinity was measured at between 0.2 and 25 ‰ (preliminary sampling had shown that few mysids of the species of interest occurred outside this range).

Duplicate samples were collected from the *RV Tamaris* using conical plankton nets with a mesh size of 280 μm, and mouth diameters of 0.50 and 0.45m (a net with 0.36 m diameter was used on 17 February 1989). Both nets were weighted to ensure that they sampled as close to the bottom as possible. The volume of water filtered by each net was measured using General Oceanics Model 2030 flowmeters. At each station, the nets were simultaneously towed obliquely for 5 minutes. This towing time was reduced at some stations, and at some times of the year, to reduce clogging of the nets by either suspended sediment or phytoplankton. Sampling commenced approximately 2 h before the predicted times of high water (Stevens Tide Tables for the South West based on data for the Port of Devonport, Plymouth) and always began at the sampling station furthest upstream. The nets were towed in a downstream direction and each monthly sampling series took approximately 2 h to complete (finishing at around the predicted time of high water). All samples, except those collected on 17 February 1989, were taken during daylight when it is known that hyperbenthic mysids aggregate near the bottom. Samples were preserved immediately in a solution of 4% buffered formalin in seawater. At each station, measurements were taken of surface and bottom salinity, temperature (using an *Electronics Instruments MC5* Salinity Temperature Bridge) and turbidity (using a *Partech Electronics* suspended solids monitor). The meter was calibrated by gravimetric analysis of discrete samples of surface water taken at each sampling station. Daily mean flow rates

(m^3s^{-1}) for the River Tamar (measured at Gunnislake) were supplied by the National Rivers Authority, South Western Region. The mean daily flow rate was calculated as the mean of 96 separate daily measurements of flow rate. Full descriptions of the samples are included in Appendix I; the physical and chemical data are tabulated in Appendix II.

Laboratory procedures

The turbidity meter was calibrated by filtering the surface water samples through pre-washed, pre-ashed and pre-weighed Whatman GF/C filters using a *Millipore* filtration system. Between 250 ml and 1 litre of water was filtered depending on the concentration of suspended matter. For each sampling date, one control filter was placed under one of the filters in the filtration system to assess the changes in weight in the filter as a result of the process. The filters were dried to constant weight at 100°C and stored in a desiccator. The filter was then weighed on an electronic micro-balance precise to ± 1 μg. The total suspended matter concentration (TSM) was calculated as:

$$TSM = \frac{FDW - FPW}{VOL}$$

Where, FDW = filter dry weight, FPW - filter pre-weight and VOL = volume of water filtered (l).

The filters were then placed in a furnace at 550°C for 8 h and re-weighed. The organic content of the suspended matter (OSC) was calculated as:

$$OSC = \frac{100}{TSM} \times (FDW - FAW)$$

Where, FAW = filter ash weight (mg), FDW = filter dry weight (mg), FPW = filter pre-weight (mg), OSC = organic sediment content (%), TSM = total suspended matter concentration (mgl^{-1}), VOL = volume of water filtered (l).

For each sampling date, a linear regression equation was produced showing the relationship between the surface turbidity meter readings and the calculated surface suspended matter concentrations. The resulting equations were then used to calculate suspended matter concentrations from the bottom turbidity meter readings.

Samples were sorted to extract the mysids and those containing fewer than *c.*200 mysids were examined in total. Larger samples were reduced to a sample size of approximately 200 using a Folsom plankton splitter. The mysids were identified to species using the keys of Tattersall and Tattersall (1951) and Makings (1977). Each mysid was straightened, measured (± 1 mm) from the base of the eyestalk to the posterior end of the uropods (excluding the setae) using an eyepiece graticule in a stereoscopic binocular microscope (Mauchline, 1969), and ascribed to one of six categories, according to the degree of development of the secondary sexual characteristics (Mauchline, 1980), as defined earlier for the lower estuary samples. The brood in the marsupium of each ovigerous female was classified into three stages after Mauchline (1973):

- *Stage I* (spherical eggs and developing embryos still within the egg membrane);
- *Stage II* (eyeless larvae which have hatched from the egg membrane);
- *Stage III* (eyed larvae).

The brood size of intact broods was counted in July, September and October, and a linear regression equation was produced showing the relationship between female body length (mm) and brood size (§7.1.7).

In April and September, ten individuals from each life-history class were washed in distilled water and placed onto pre-washed, pre-ashed and pre-weighed *Whatman* GF/C (glass-fibre) filters, dried for 24 h at 60°C and stored in a desiccator. The filter was then weighed on an electronic micro-balance precise to ±1 μg.

The mysid dry weight (MDW) was calculated as:

$$MDW = FDW - FPW$$

Where, FDW = filter dry weight and FPW = filter pre-weight.

A linear regression equation was produced showing the relationship between mysid body length (mm) and dry weight (mg) (§7.1.6). This equation was used in the biomass calculations.

Data analysis

For the purposes of length-frequency analysis, data from all stations were combined, and mysids of each species grouped into 1 mm size classes. The length-frequency distributions were constructed so that the sum of the height of all bars on each graph was 100% frequency. These length-frequency distributions were examined by eye to distinguish the separate cohorts. The length-frequency distribution of each cohort approximated a normal distribution. The mean size of each distribution was plotted against time to produce growth curves for each cohort.

Growth rate (G) (mm day^{-1}) of each cohort was calculated as the increase in mean length of the cohort during each sampling interval (Omori and Ikeda, 1984):

$$G=\frac{\bar{L}_{i+1}-\bar{L}_i}{t_{i+1}-t_i}$$

Where, L = mean length (mm), t = day number of sampling date and i= sample number (1-11).

Production estimates of *M. slabberi* were produced from the length-frequency data and the length-dry weight regression. Separate production estimates were produced for each cohort by the growth increment summation method which calculates production as the sum of the increase in biomass between sampling periods throughout the lifetime of each cohort (Crisp, 1984). Production (P) (mg dry weight per m^3) was calculated from the equation:

$$P=\sum_{t=0}^{t=11} \bar{N}\Delta\bar{w}$$

where $\bar{N}$ = mean number of individuals in cohort (Nm^{-3}) at time t_i and $\Delta\bar{w}$ = the increase in biomass of an average individual (mg) during the time interval $t_i - t_{i+1}$.

Two estimates of production were obtained. The first used a value of N equal to the average density of mysids over the whole sampling range each month. The second estimate used a value of N equal to the highest density recorded at a single station each month.

The estuary was divided into six 5‰ salinity bands and further frequency distributions were plotted to show the frequency of juveniles, immature and mature stages occurring in each salinity band and, for each sampling date, the length-frequency distribution of individuals in each salinity band.

The monthly distributions of the mysid populations were examined in relation to the measured physico-chemical variables (river runoff, temperature and turbidity) and in relation to salinity using Spearman's rank correlation coefficient (r_s).

CHAPTER 4

LOWER ESTUARY

4. LOWER ESTUARY

4.1 Results and Discussion

The four species of mysid found in the lower estuary were *Mesopodopsis slabberi*, *Neomysis integer*, *Praunus flexuosus* and *Schistomysis ornata*, although their densities were low throughout the year (Table 4.1).

Table 4.1 Mysid density at each sampling station and date.

Station & date	Density (Numbers m^{-3})			
	M. slabberi	*N. integer*	*P. flexuosus*	*S. ornata*
27 January 1989				
1	12.59	0	0	0.85
2	1.90	0	0	0.95
3	0.21	0	0	0.05
22 March 1989				
1	4.38	0.14	2.69	0.14
2	4.66	0	0	0.26
3	14.46	0.63	0.84	3.10
21 April 1989				
1	1.23	0.14	0.27	0
2	7.96	7.37	5.60	47.20
3	5.67	0.09	0.09	16.09
19 May 1989				
1	0	0	0.02	0.13
2	0	0	0.04	0.33
3	0.31	0.08	0.04	3.22
9 June 1989				
1	0	0	0.04	0.042
2	1.04	0.97	0.07	0
3	2.76	6.06	0.31	0.19
1 December 1989				
1	8.59	0.10	0	0
2	1.10	0	0.02	0.04
3	5.60	0.04	0	0.27

Mesopodopsis slabberi was present in the lower estuary samples on all sampling dates. In January, March and April, the population consisted of juveniles, immature and small adult stages (Fig. 4.1). The length-frequency distributions correspond to Cohort I identified in the upper estuary samples (Fig. 7.1, §7.1.1). Only in March was the density of *M. slabberi* in the lower estuary different from that in the upper estuary (14.5 m^{-3} compared with a maximum density of 0.5 m^{-3}). In May, only juvenile stages were found in the lower estuary samples and the size-frequency distribution corresponded to Cohort IIA in the upper estuary. The larger stages of Cohort I were absent from the samples and *M. slabberi* was not found lower down the estuary than Station 3. In June, the size-frequency distributions differed from those in the upper estuary in the same month. Although the bulk of the population fell into the size range of Cohort IIB, there was little evidence of the larger immature and mature stages of Cohort IIA, and the smallest two size classes were absent. Overall, densities in June were more than an order of magnitude lower than those in the upper estuary (§7.1.5) and *M. slabberi* did not appear in the Station 1 samples. The December size-frequency distribution in the lower estuary corresponded to that of the overwintering generation (Cohort I) from the upper estuary and densities were in the same range as those in the upper estuary.

The relationship between the lower and upper estuarine distributions of *M. slabberi* are discussed in Chapter 7.

Neomysis integer was present at low densities in the lower estuary on all sampling dates except January when it was absent from all samples. In most months, the few *N. integer* sampled were juvenile stages. Immature stages were present only in June, the only month for which it was possible to compare the length-frequency distribution with that from the upper estuary (Fig. 4.2, Fig. 6.1, §6.1). The comparison shows that all size classes and stages present in the upper estuary were present at Stations 2 and 3. In common with the upper estuary, few large immature or adult stages of this species were found in the samples.

The relationship between the lower and upper estuary distributions of *N. integer* are discussed in Chapter 6.

Praunus flexuosus appeared infrequently in the samples and always at very low densities. A single ovigerous female was captured in December at Station 2. Examination of the size-frequency distribution indicated that juveniles were present in the estuary on all sampling dates, except December, indicating that breeding occurs throughout the year (Fig. 4.3). Abundance was low throughout the sampling period (<3 individ. m^{-3}) (Table 4.1).

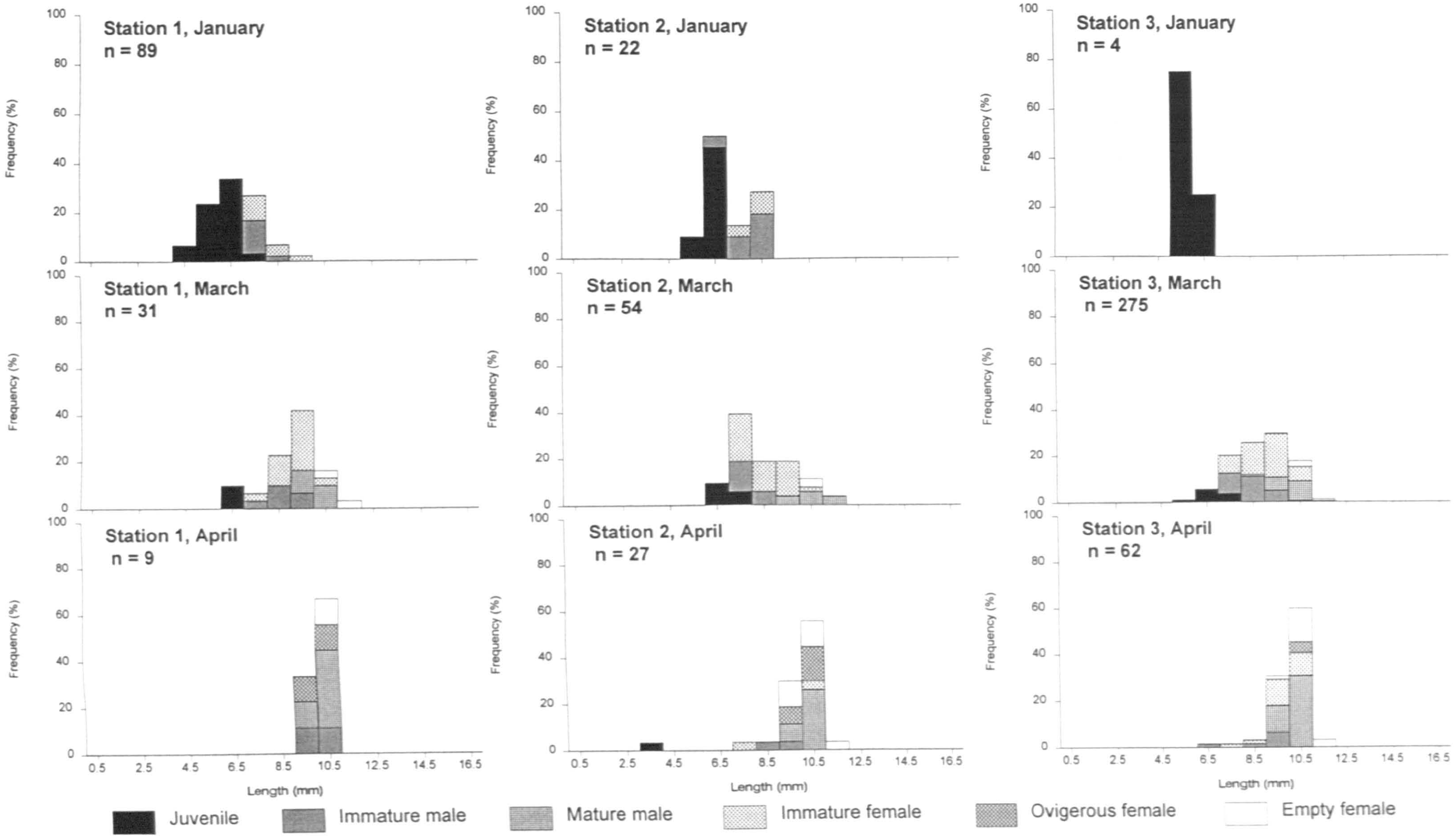


Figure 4.1 Length-frequency distribution of *Mesopodopsis slabberi* at 3 stations in the lower Tamar Estuary during 1989.

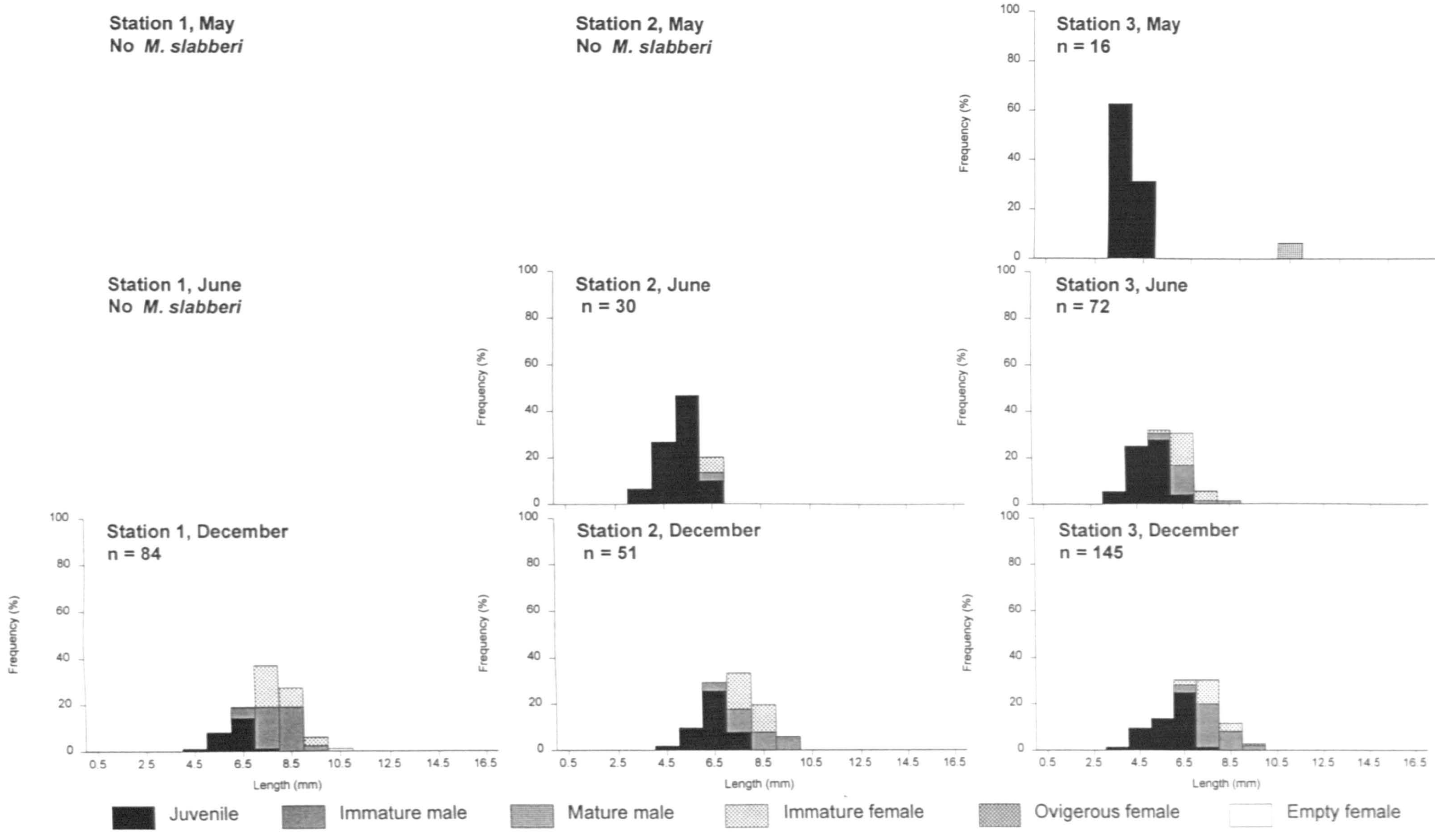


Figure 4.1 *Mesopodopsis slabberi* continued.

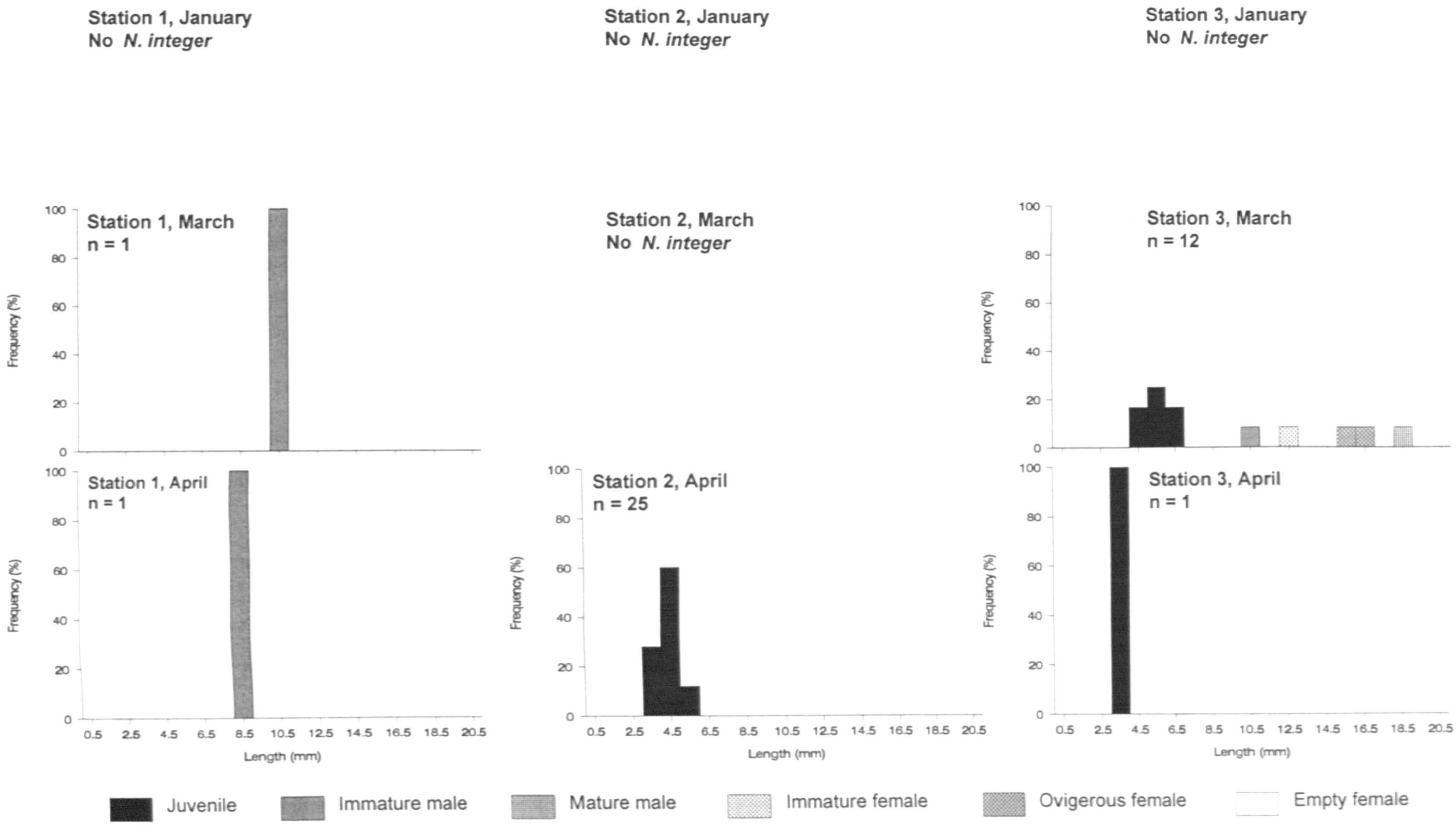


Figure 4.2 Length-frequency distribution of *Neomysis integer* at 3 stations in the lower Tamar Estuary during 1989.

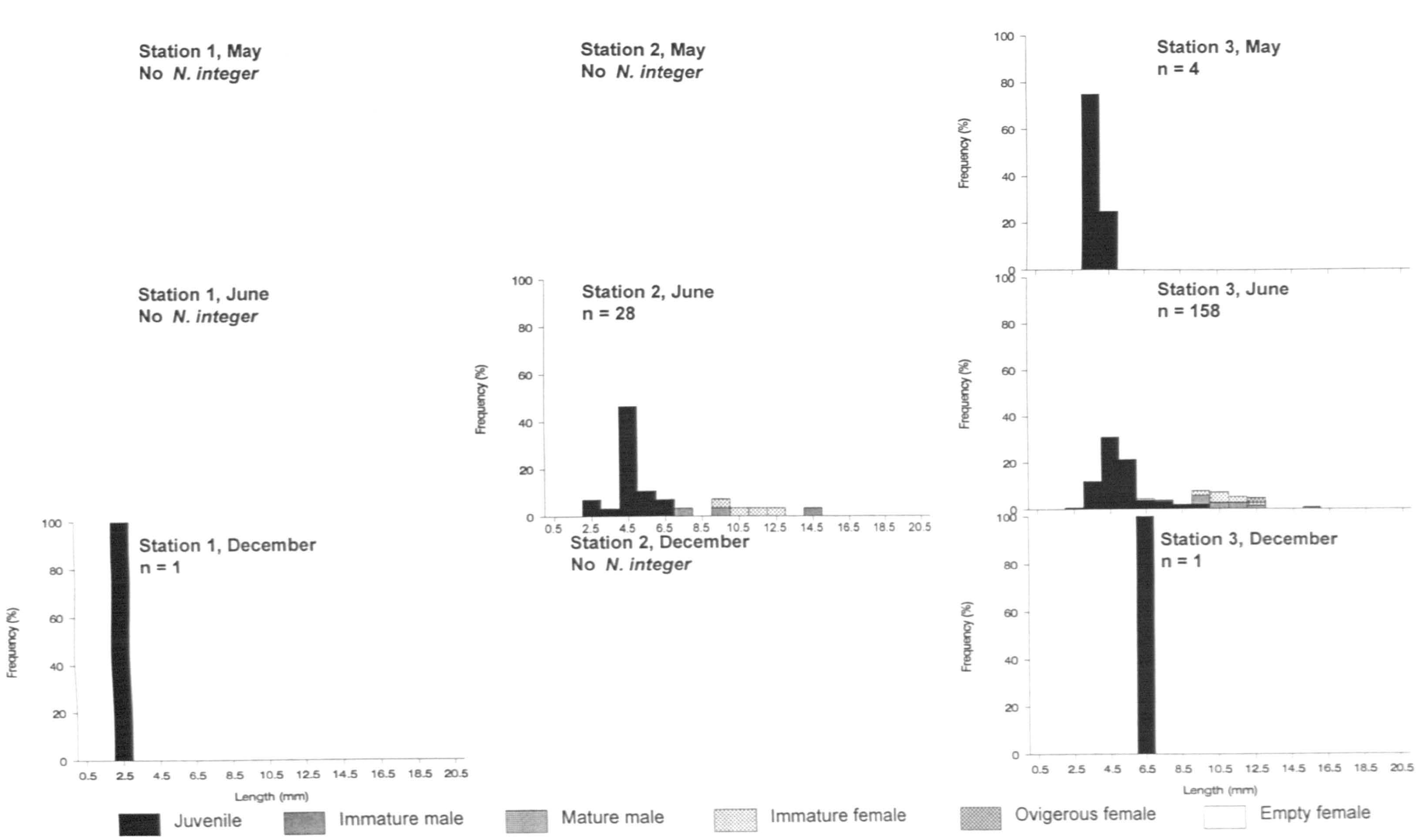


Figure 4.2 *Neomysis integer* continued.

Praunus flexuosus is one of the commonest species of mysid in British waters and is both euryhaline and eurythermal, able to tolerate salinities from full strength seawater to as low as 0.3‰ (Percival, 1929, McLusky and Heard, 1971). The habitat of *P. flexuosus* is amongst *Zostera* spp. and over sandy substrata, although, unlike other species of mysid, it does not rest on the substratum, but remains suspended in the water column (Tattersall and Tattersall, 1951). The relative scarcity of this species recorded in this study could be due to inefficient sampling by the benthic sledge, although Mauchline (1971b) successfully sampled *P. flexuosus* in Loch Etive using similar techniques. It is also a relatively large species, achieving lengths of 24.5mm, this study and in Danish waters (Tattersall, 1951), and 21mm in Loch Etive, Scotland (McLusky and Heard, 1971) and shows a powerful escape response which may have enabled it to elude capture (Tattersall and Tattersall, 1951).

Schistomysis ornata was present in the lower estuary throughout the sampling period, but only occurred in relatively high numbers at Station 2 in April (Table 4.1). The presence of juveniles on all sampling dates suggests that *S. ornata* breeds throughout the year (Fig. 4.4) which accords with the description of Tattersall and Tattersall (1951). Mauchline (1970a) found that *S. ornata* had a seasonal occurrence in the Firth of Clyde, presumably migrating offshore between June and November each year. Mauchline (1970a) also found that the main breeding period for this species was in the winter which accords with the results of this study. *Schistomysis ornata* was sampled in the upper estuary on a single occasion, Station 10 on 6 February, at a density of 1.07 indiv. m^{-3} in a salinity of 24.1‰. The sample comprised 85% juveniles, 7.3% immature males, 2.4% mature males and 4.9% immature females. It would appear that the upstream distribution of this species is limited by its salinity tolerance: *S. ornata* has not been reported from waters of less than about 20‰ salinity (Tattersall and Tattersall, 1951; Mauchline, 1970a).

The lower estuary sampling series confirms the presence of four species of mysid in the Tamar Estuary. However, whilst all sampling was quantitative, coverage of the lower estuary was insufficient to provide a detailed description of the relative distribution and abundance of the four species in this part of the estuary nor the extent to which the four species might be partitioning the environment. The lack of physico-chemical measurements also meant that it was not possible to describe the observed distributions in terms of environmental variables.

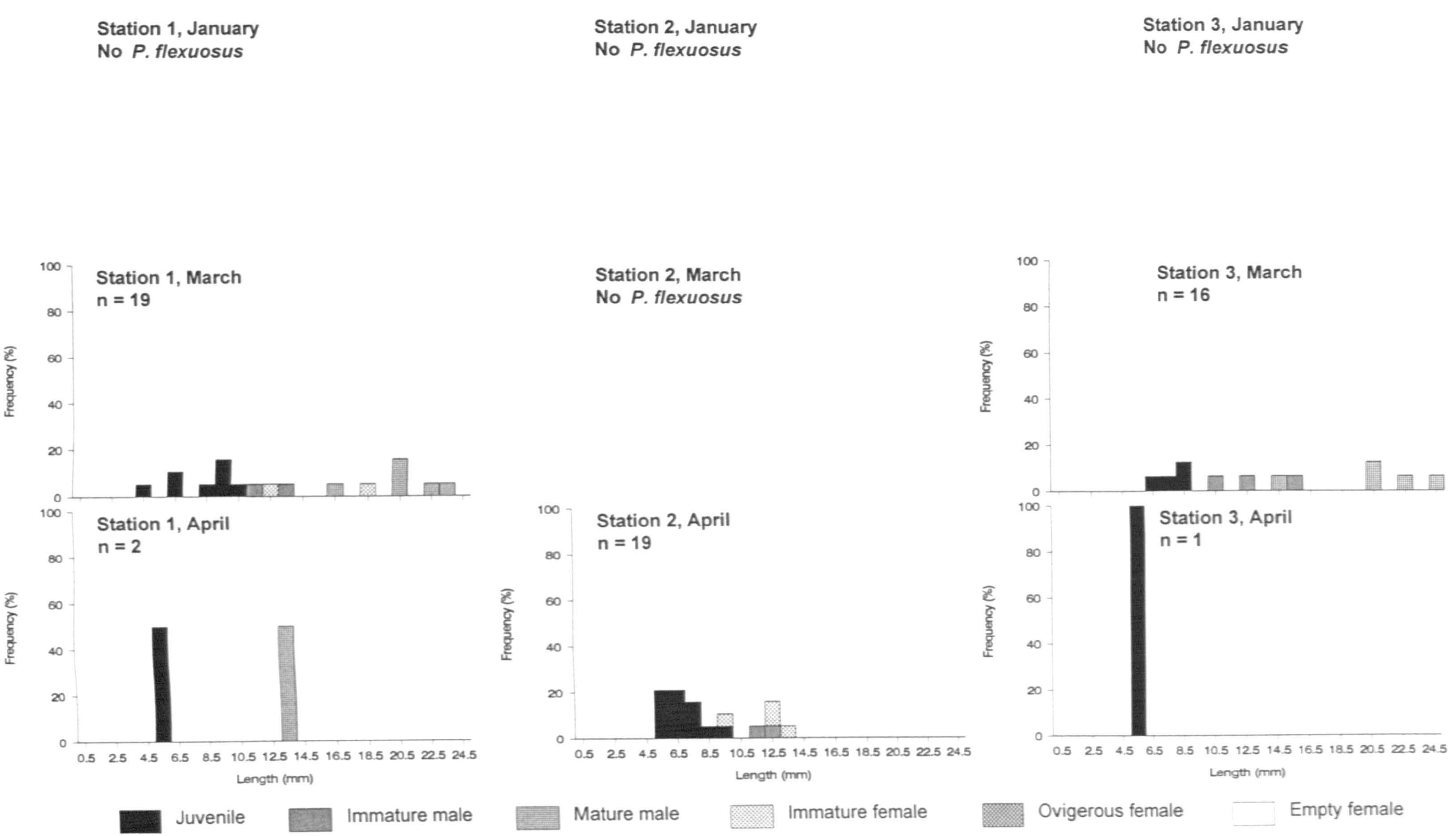


Figure 4.3 Length-frequency distribution of *Praunus flexuosus* at 3 stations in the lower Tamar Estuary during 1989.

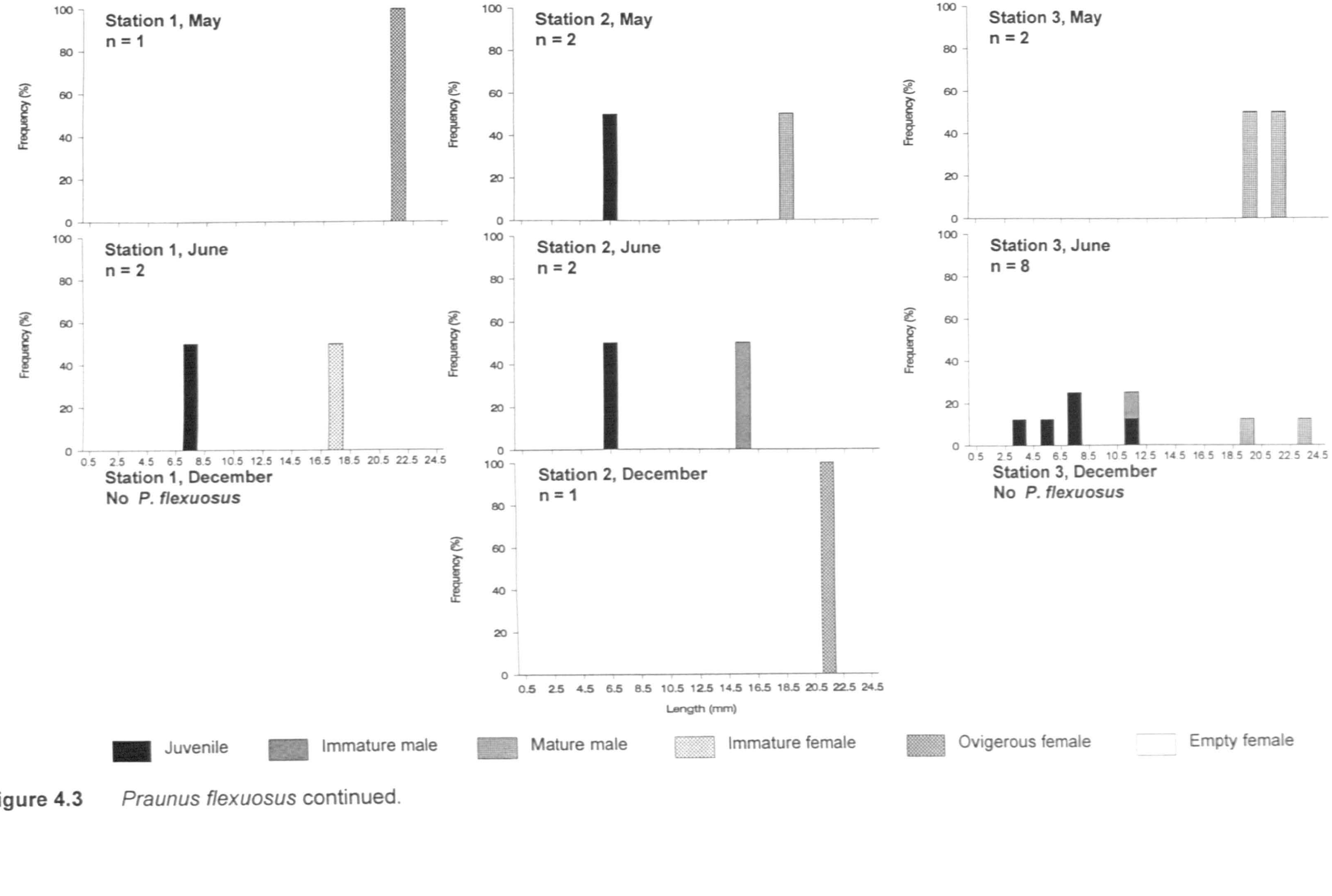


Figure 4.3 *Praunus flexuosus* continued.

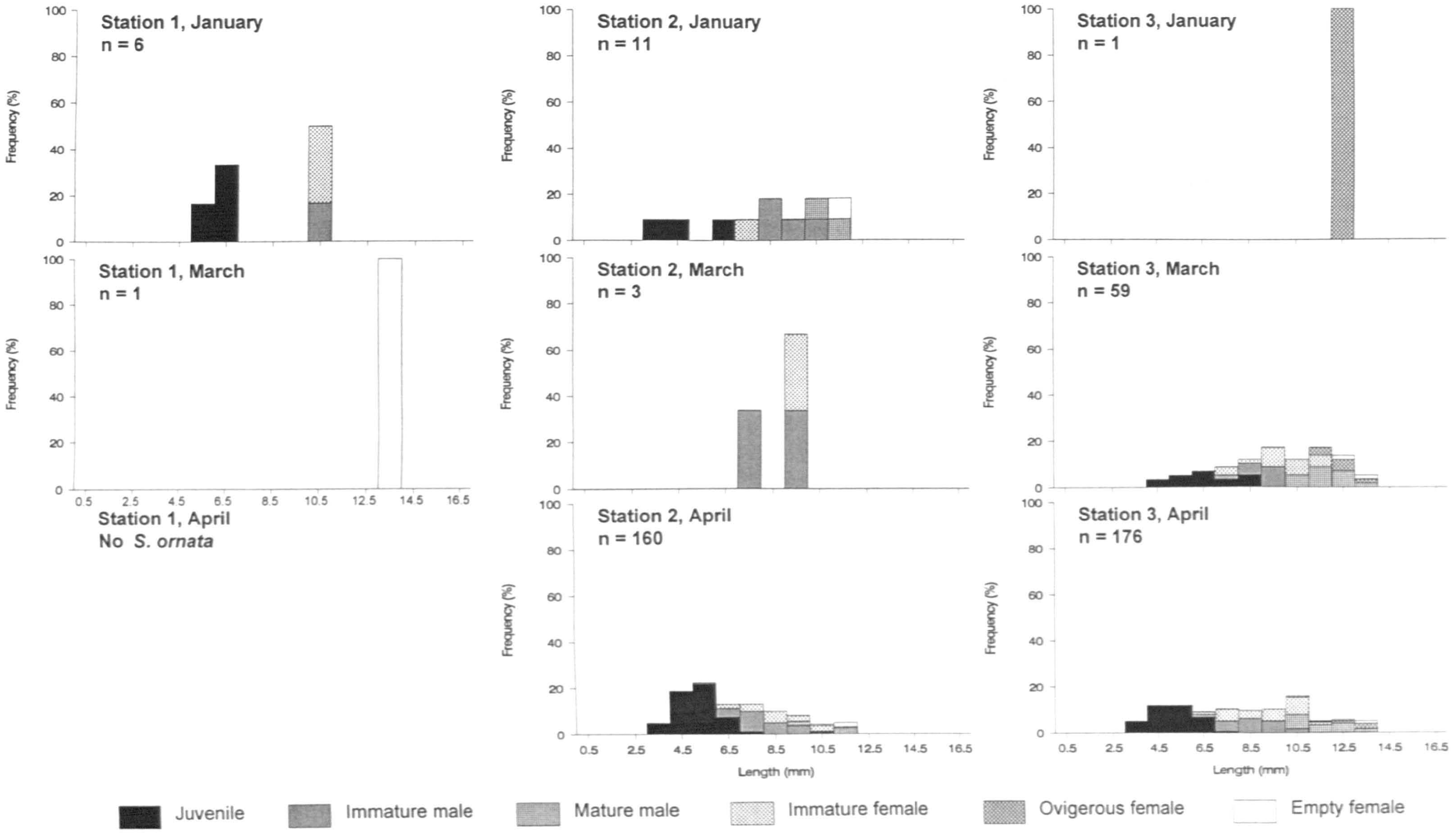


Figure 4.4 Length-frequency distribution of *Schistomysis ornata* at 3 stations in the lower Tamar Estuary during 1989.

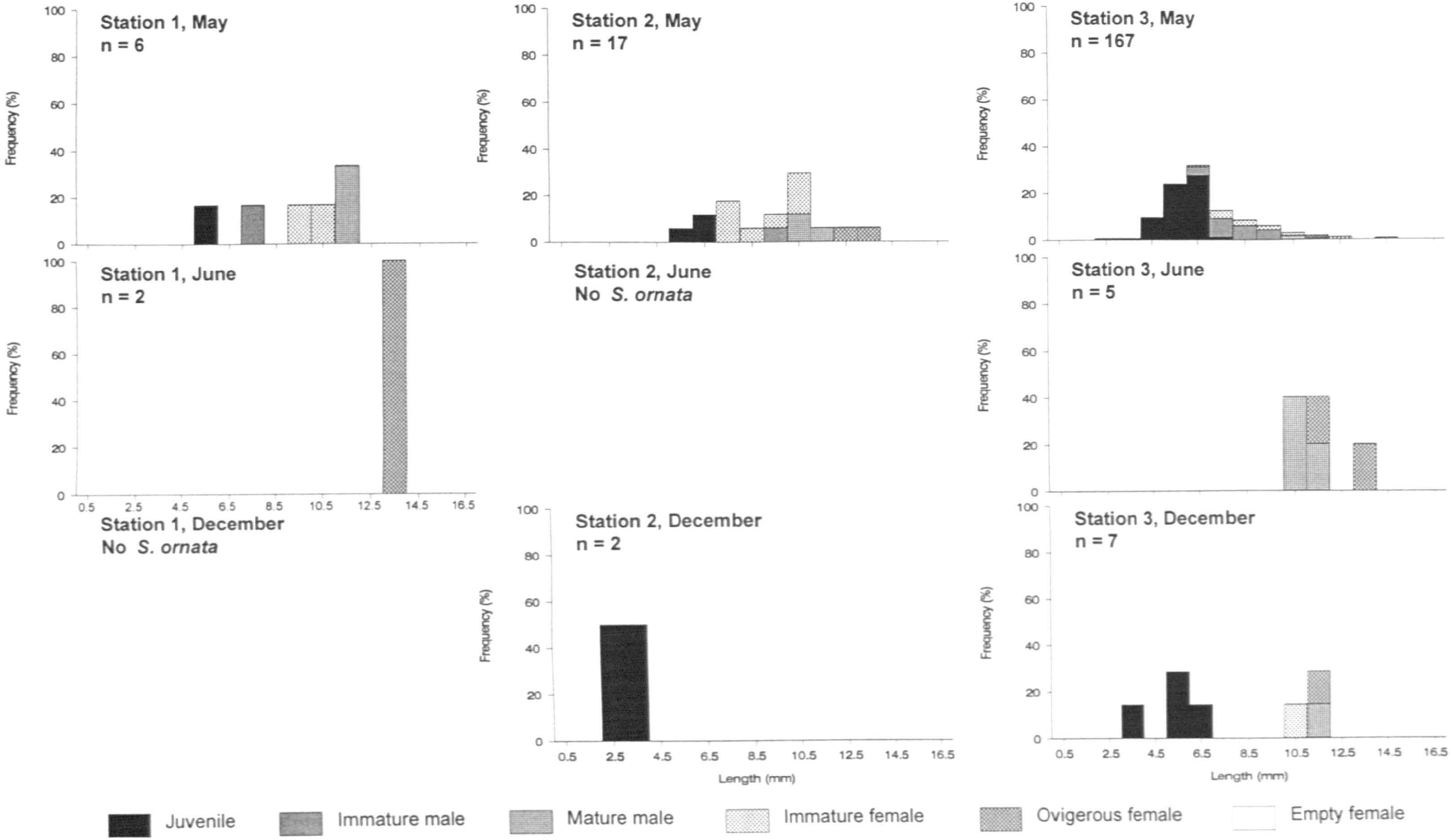


Figure 4.4 *Schistomysis ornata* continued.

CHAPTER 5

UPPER ESTUARY:

PHYSICO-CHEMICAL MEASUREMENTS

5. UPPER ESTUARY: PHYSICO-CHEMICAL MEASUREMENTS

5.1 Results and Discussion

5.1.1 Temperature

The mean annual pattern in water temperature change (all stations combined) is shown in Figure 5.1 (Appendix II). Water temperatures began to rise in February, reached a maximum (20.7°C) in July and declined to a low in December (4°C). There was no obvious temperature variation between stations on each sampling

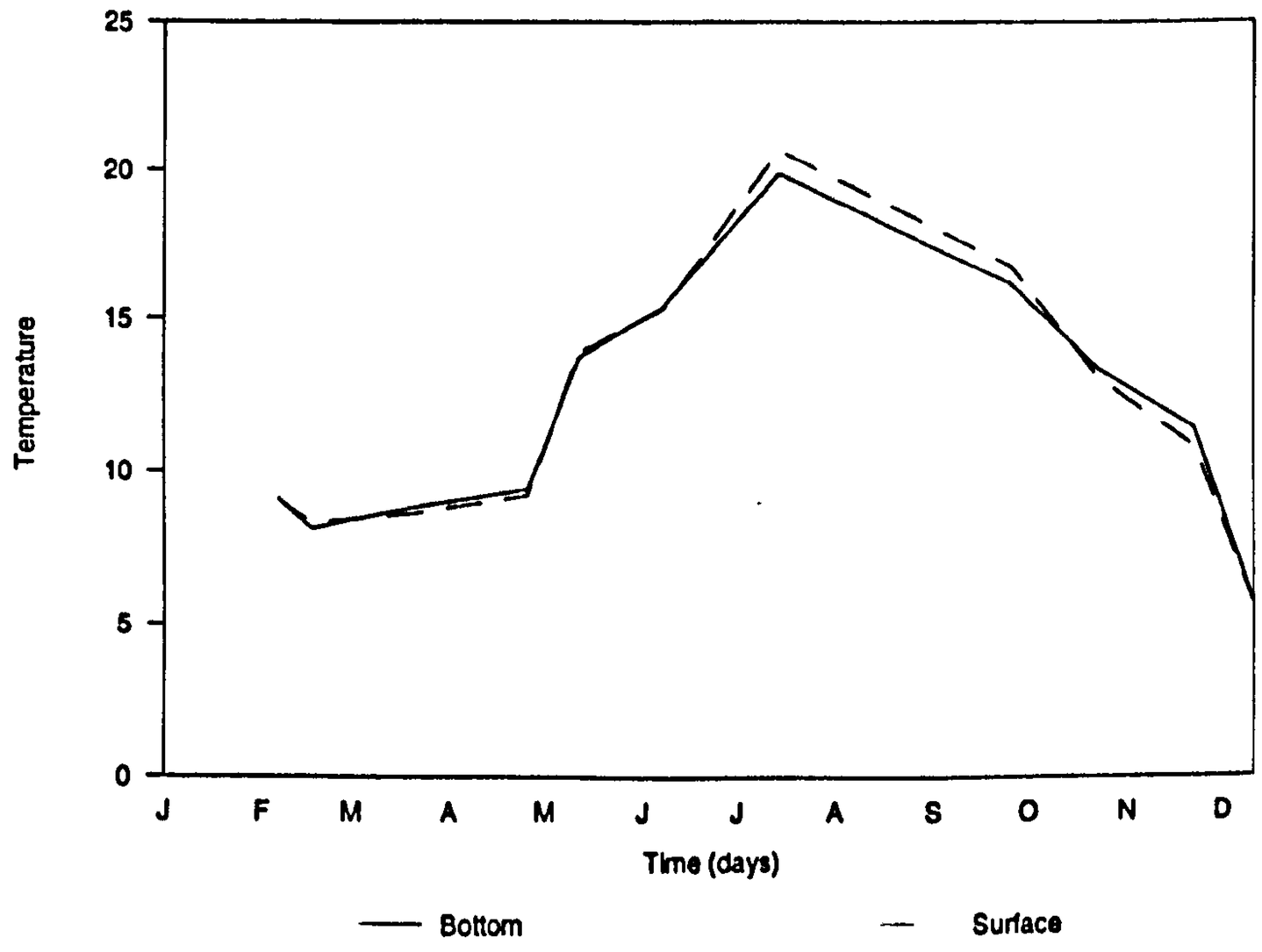


Figure 5.1 Mean monthly temperature (°C) of bottom and surface waters in the upper Tamar Estuary in 1989.

date, although there was a slight decline in temperature in the spring (February-April) and autumn (September-November) with increasing distance from Plymouth Sound (Fig. 5.2). Temperature stratification was minimal on most sampling dates, but there was some indication of stratification between July and November. In July and September, the surface waters were warmer than bottom waters, probably due to dilution of seawater with warmer freshwater from river runoff. In October and November, surface waters were cooler than the underlying layer. This reversal of the thermal stratification coincided with the period when air temperatures had started to decline and the surface freshwater layer was cooler than the underlying brackish water (Fig. 5.2) and with a period of high freshwater runoff which would have introduced greater volumes of cooler freshwater into the system (Fig. 5.3).

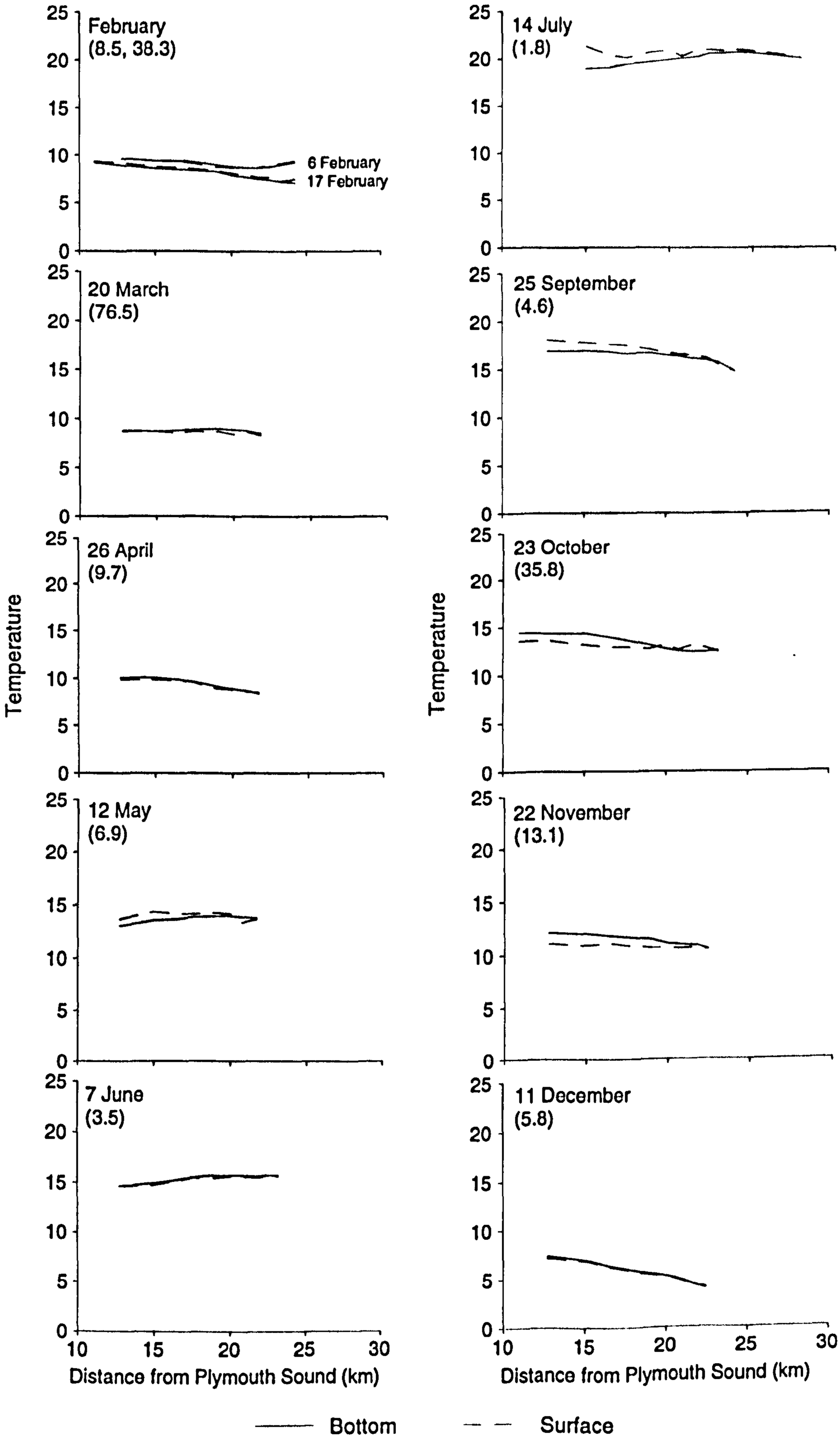


Figure 5.2 Monthly gradients in temperature along the axis of the Tamar Estuary in 1989. (Figures in brackets are runoff (m^3s^{-1}).)

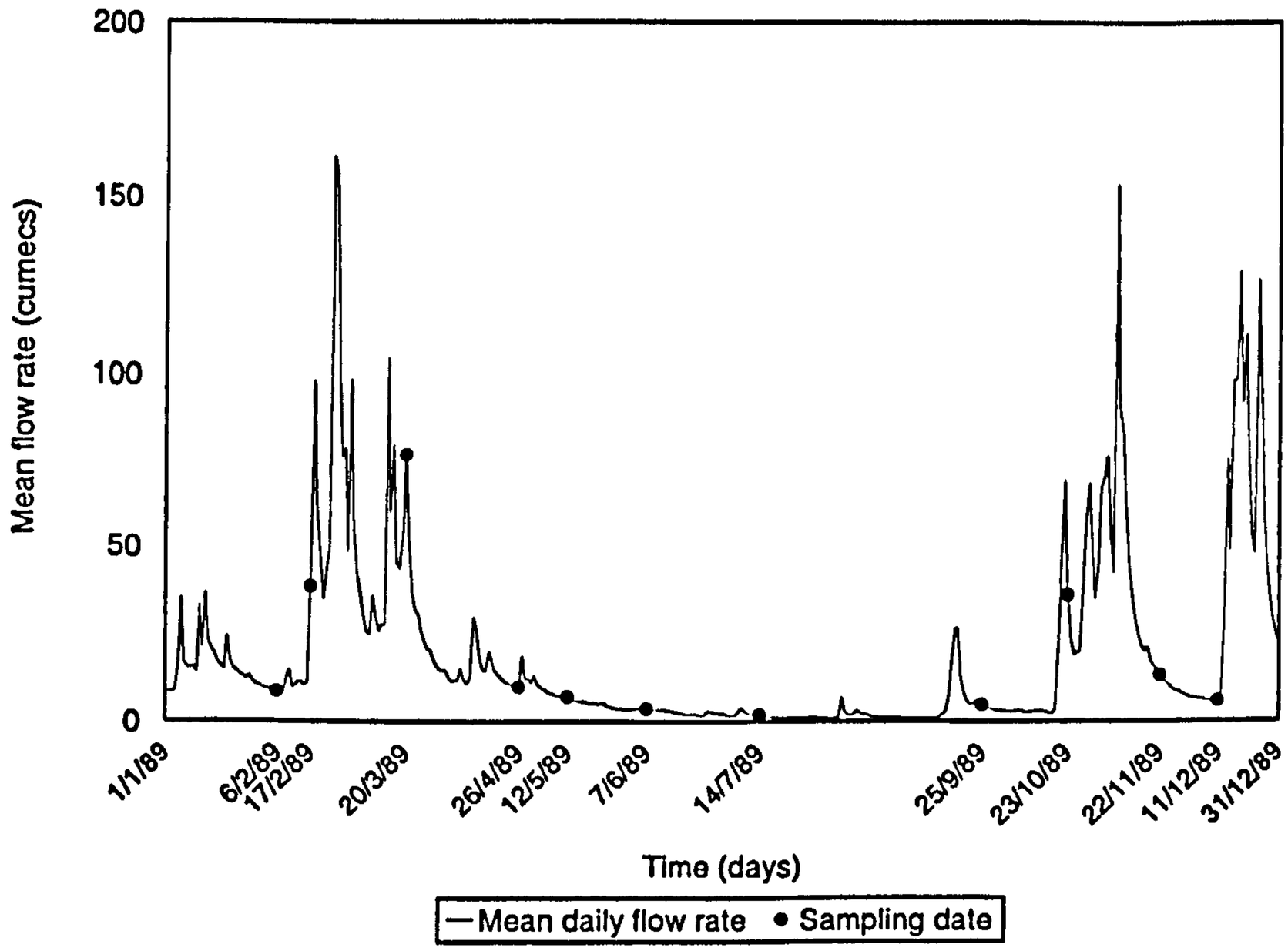


Figure 5.3 Mean daily flow rates for the Tamar Estuary during 1989 (m^3s^{-1}) showing upper estuary sampling dates. (Data supplied by the National Rivers Authority.)

5.1.2 Freshwater runoff

Figure 5.3 shows the variation in freshwater runoff from the Tamar Estuary throughout the year. The two periods of high runoff, between February and April, and between October and December, coincided with high rainfall in the river catchment. Peaks in runoff coincided with sampling dates only in early February, March and October, and river flow rate reduced within a few days following each peak.

5.1.3 Salinity

At each station, salinity was highly variable throughout the year, with lows coinciding with periods of high runoff (Fig. 5.4). Stations 10-12 were the most 'marine' stations with bottom salinities that did not fall below 8‰ throughout the year. Stations 13-16 had salinities within the range 0-25‰, and stations upstream of Station 16 did not exceed 20‰. Stations 20 and 21, which were sampled less frequently than the other stations, are not shown in Figure 5.4. At Station 20, salinity was always <6‰ and at Station 21 it was <0.5‰. It was apparent that

freshwater runoff was the primary force controlling the longitudinal salinity distribution in the estuary.

Salinity declined with distance from Plymouth Sound, on each sampling date, with the steepest salinity gradients seen during March and October, when the mean runoffs on the day of sampling were 76 and 36 m^3s^{-1} respectively (Fig. 5.5). In March and October, the freshwater-saltwater interface was situated less than 20 km from Plymouth Sound, due mainly to the high runoff. The salinity gradient in October was almost as steep as that seen in March, despite half the runoff, probably due to high runoff in combination with a neap tide. On all other sampling dates, the interface was further than 20 km from Plymouth Sound (upstream of Station 15, Fig. 3.1). The lowest runoffs recorded in June, July and September (3.5, 1.8 and 4.6 m^3s^{-1} respectively), coincided with the shallowest salinity gradients.

Marked vertical salinity stratification, of up to 23 ‰ (Fig 5.5), occurred on some dates. Salinity stratification was more apparent in the lower estuary, which has a wider profile, is deeper, and is not as well-mixed as the upper estuary (Uncles *et al*, 1985a). Salinity stratification was greatest, and was measured over the greatest area, in October and November. In October, the relatively high runoff coincided with a neap tide and created the marked stratification seen in Figure 5.5. In March, with the highest runoff, almost no salinity stratification was observed because the high river flow prevented saltwater from entering the upper estuary. The November sampling date followed a period of prolonged rainfall and also coincided with a neap tide which might account for the level of stratification in that month. In April, June, July and December, there was no apparent salinity stratification.

5.1.4 Suspended sediment concentrations

Suspended sediment concentrations were highly variable over the months for which data were collected, but generally increased with salinity (Fig. 5.6). In early February, April and June, very high levels of suspended sediment were recorded in the upper estuary (max. 1,717 mg/l). On other dates, suspended sediment concentrations remained relatively low (<300 mg/l). The highest levels of suspended sediment coincided with the position of the freshwater-saltwater interface. The organic content of the suspended matter declined with increasing salinity, except in March, perhaps reflecting the greater concentrations of

zooplankton and phytoplankton noted in the lower reaches of the sampling area.

These data are discussed in relation to mysid distribution in the next two chapters.

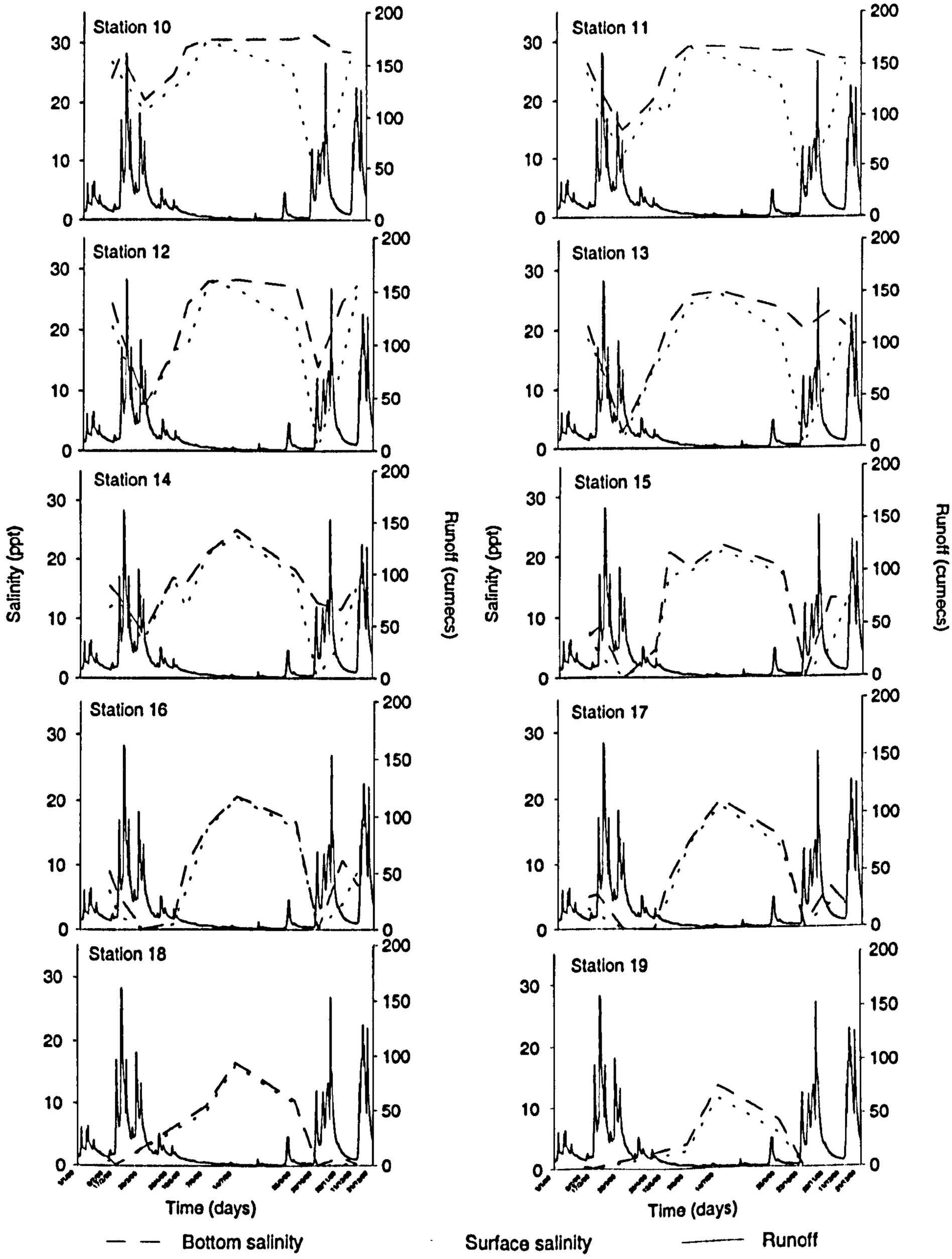


Figure 5.4 Changes in salinity (‰) at sampling stations in relation to runoff (m^3s^{-1}).

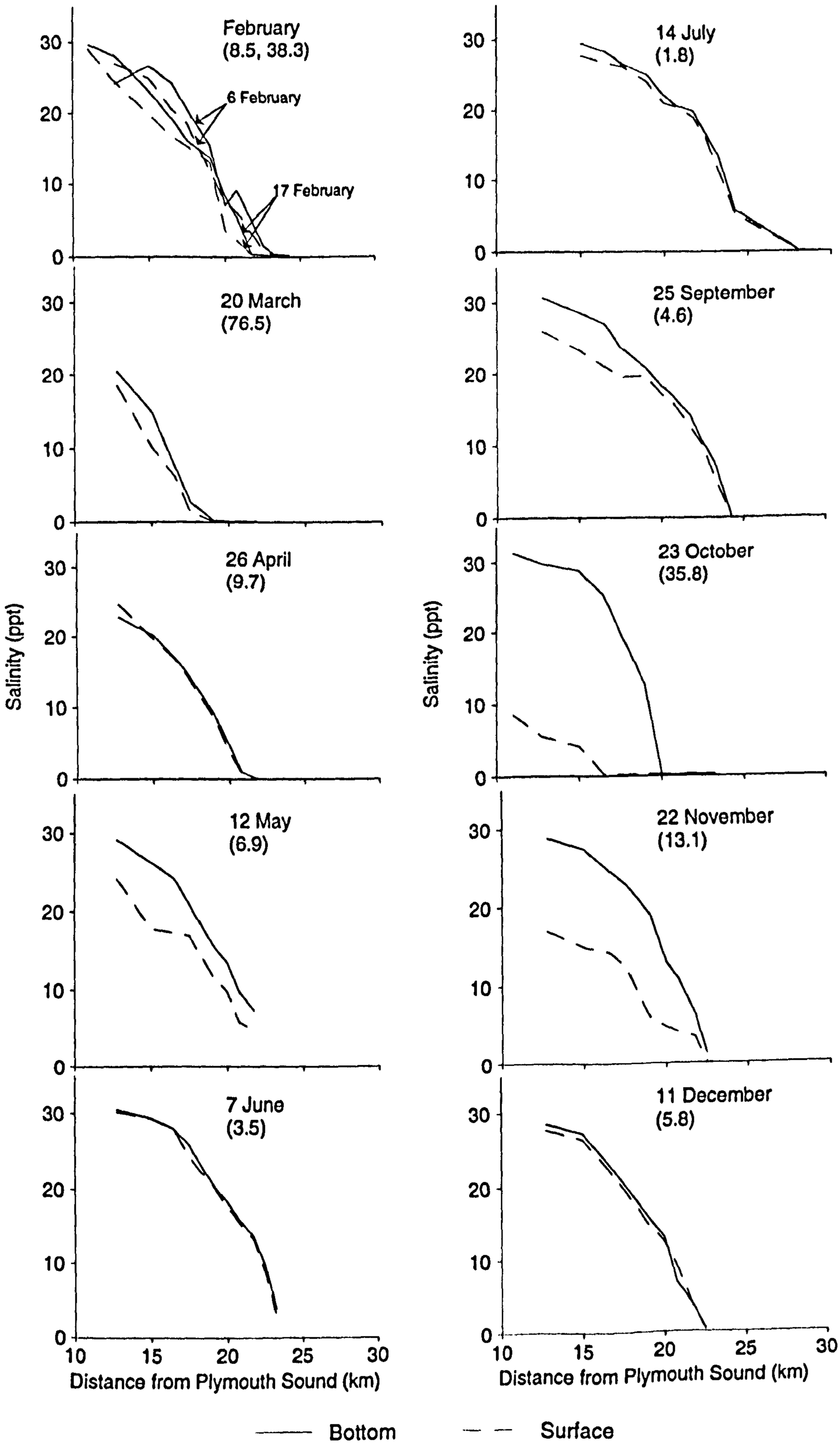


Figure 5.5 Monthly surface and bottom salinity gradients in the Tamar Estuary during 1989. (Figures in brackets are runoff (m^3s^{-1}).)

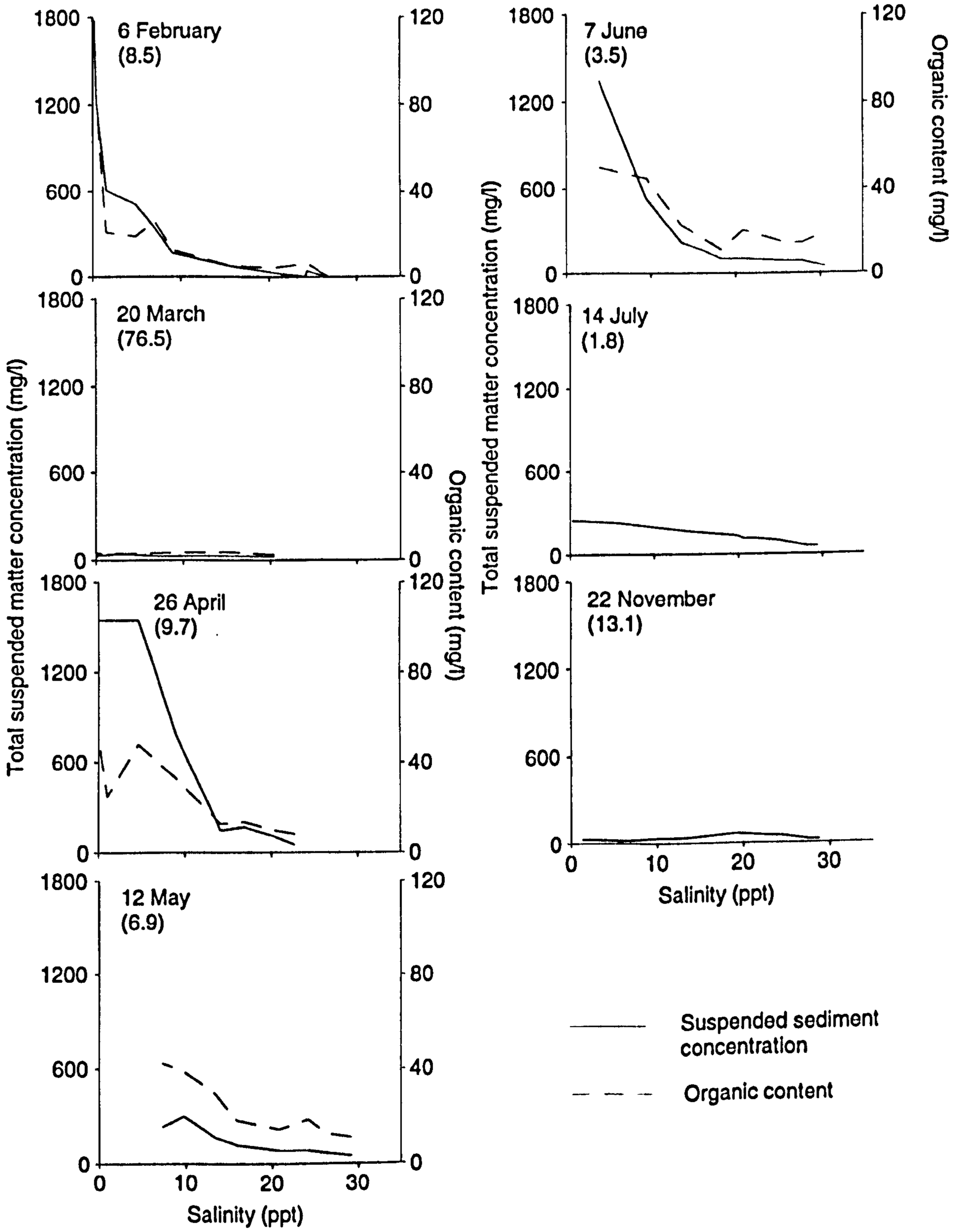


Figure 5.6 Longitudinal turbidity profiles in the Tamar Estuary during 1989. (Figures in brackets are river flow (m^3s^{-1}).)

CHAPTER 6

UPPER ESTUARY:

NEOMYSIS INTEGER

6. UPPER ESTUARY: *NEOMYSIS INTEGER*

6.1 Results

Neomysis integer was present in the estuary throughout the year (Fig. 6.1). Examination of the monthly length-frequency distributions of *Neomysis integer* shows that juveniles were the dominant life-history stage sampled each month, and relatively few immature and adult stages were sampled (Fig. 6.1). In mid-February, March (none), May, July, September and November, few *N. integer* were captured. The results were not sufficiently complete to describe fully the life history through the year.

Between February and May, the population comprised mainly juvenile stages, although a small percentage of immature males and females were present in the population. Juveniles in April were smaller than those sampled in February, suggesting a release of juveniles into the population between mid-February and April. In June, July, September and October, juvenile stages were still important, but immature individuals were identified in the population and a small proportion of mature male and female stages were found. In November, only eight *N. integer* were captured over the entire sampling range. In December, all life-history stages were again identified in the samples, although juvenile stages were present in greater proportion. Juveniles in the size class 2-3mm were present in the population in all months except May, suggesting continuous breeding throughout the year. The dominance of juveniles in the population is seen more clearly in Fig. 6.2 where the length-frequency distributions have been produced for spring, summer, autumn and winter. It is only in the summer period that immature and matures stages form a substantial proportion of the population. All other months are dominated by juveniles. The smallest juvenile found was one of 1.6mm in July, the largest male 15mm (December) and the largest female was 16.8mm (June).

Length-dry weight analysis was not carried out on *N. integer* in this study because the full size and age range of individuals was not sampled in most months. Biomass was calculated using the length-weight relationship produced by Kruijf (1977, in Bremer and Vijverberg, 1982; equation 3) for *N. integer* in the Bergumermeer, Netherlands. The relationship between length (L, mm) and weight (W, mg) (r^2=0.998m n=15) used was:

$$W=0.00391L^{2.48}$$

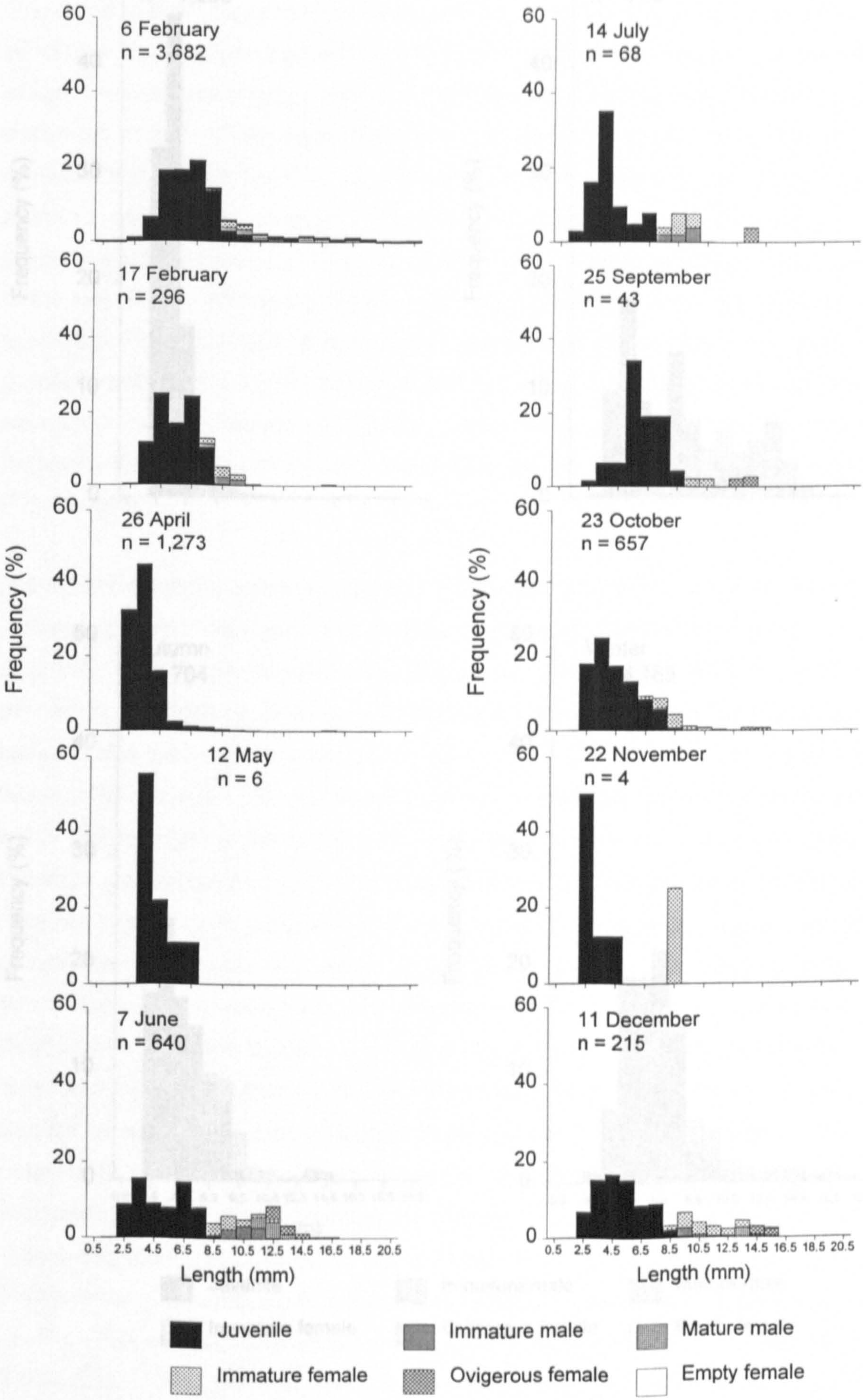


Figure 6.1 Length-frequency distribution of *Neomysis integer* in the Tamar Estuary during 1989. The data represent pooled samples for all stations.

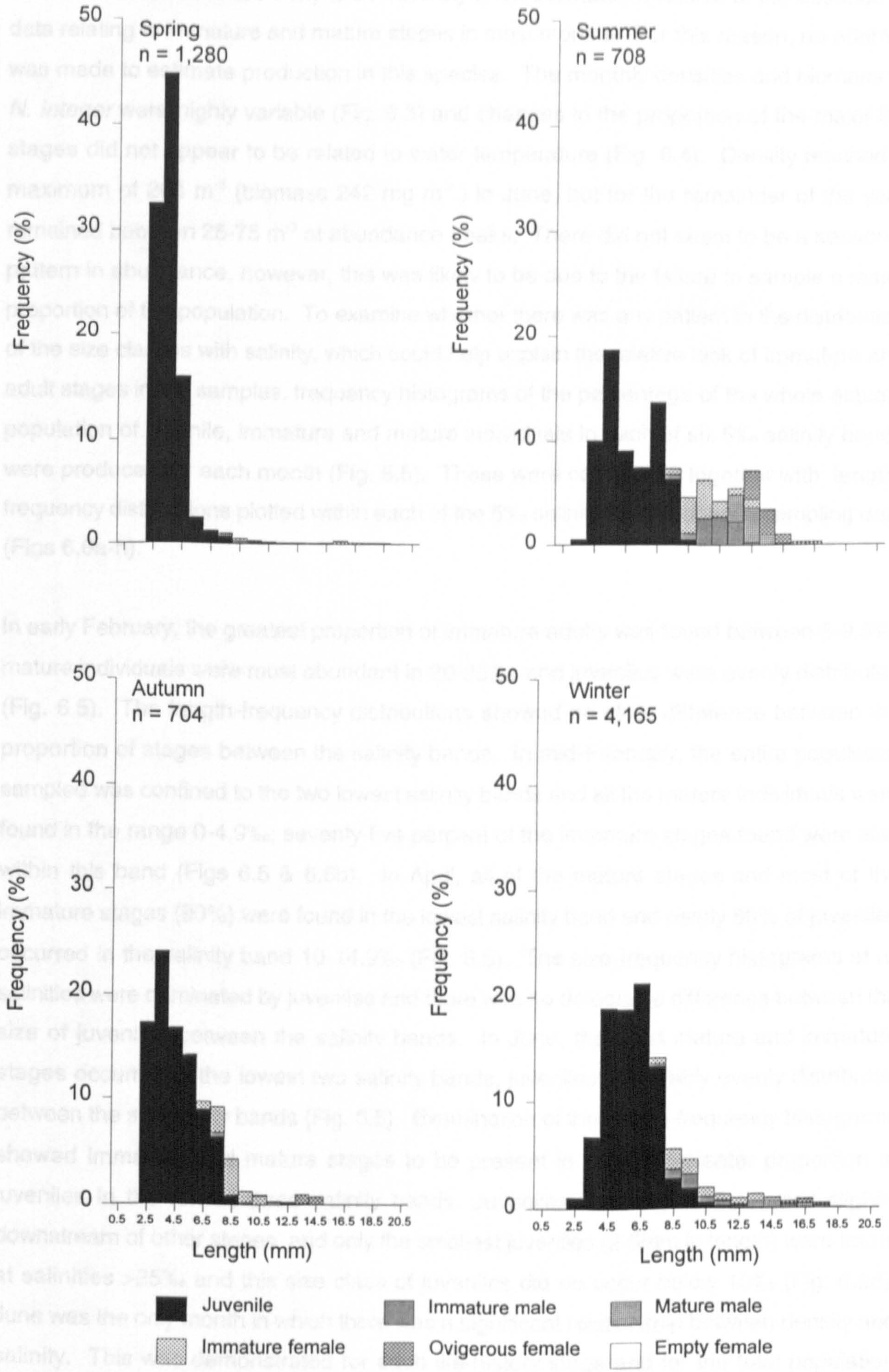


Figure 6.2 Seasonal length-frequency distributions of *Neomysis integer* in the Tamar Estuary during 1989. (Spring = March-May, summer= June-August, autumn= September-November, winter= December-February).

Estimates of biomass are likely to be severely underestimated because of the absence of data relating to immature and mature stages in most months. For this reason, no attempt was made to estimate production in this species. The monthly densities and biomass of *N. integer* were highly variable (Fig. 6.3) and changes in the proportion of the major life stages did not appear to be related to water temperature (Fig. 6.4). Density reached a maximum of 204 m^{-3} (biomass 242 mg m^{-3}) in June, but for the remainder of the year remained between 25-75 m^{-3} at abundance peaks. There did not seem to be a seasonal pattern in abundance, however, this was likely to be due to the failure to sample a major proportion of the population. To examine whether there was any pattern in the distribution of the size classes with salinity, which could help explain the relative lack of immature and adult stages in the samples, frequency histograms of the percentage of the whole estuary population of juvenile, immature and mature individuals in each of six 5‰ salinity bands were produced for each month (Fig. 6.5). These were considered together with length-frequency distributions plotted within each of the 5‰ salinity bands for each sampling date (Figs 6.6a-h).

In early February, the greatest proportion of immature adults was found between 5-9.9‰, mature individuals were most abundant in 20-25‰, and juveniles were evenly distributed (Fig. 6.5). The length-frequency distributions showed no clear difference between the proportion of stages between the salinity bands. In mid-February, the entire population sampled was confined to the two lowest salinity bands and all the mature individuals were found in the range 0-4.9‰; seventy-five percent of the immature stages found were also within this band (Figs 6.5 & 6.6b). In April, all of the mature stages and most of the immature stages (90%) were found in the lowest salinity band and nearly 80% of juveniles occurred in the salinity band 10-14.9‰ (Fig. 6.5). The size-frequency histograms at all salinities were dominated by juveniles and there was no detectable difference between the size of juveniles between the salinity bands. In June, the most mature and immature stages occurred in the lowest two salinity bands, juveniles were fairly evenly distributed between the six salinity bands (Fig. 6.5). Examination of the length-frequency histograms showed immature and mature stages to be present in equal or greater proportion to juveniles in the lowest three salinity bands. Juveniles were again distributed slightly downstream of other stages, and only the smallest juveniles (2-5mm in length) were found at salinities >25‰ and this size class of juveniles did no occur below 10‰ (Fig. 6.6d). June was the only month in which there was a significant relationship between density and salinity. This was demonstrated for each life-history stage and for the total population (Table 6.1). The pattern of distribution seen in June was repeated in July, although densities were very much lower than in June (Figs 6.3, 6.5 & 6.6e).

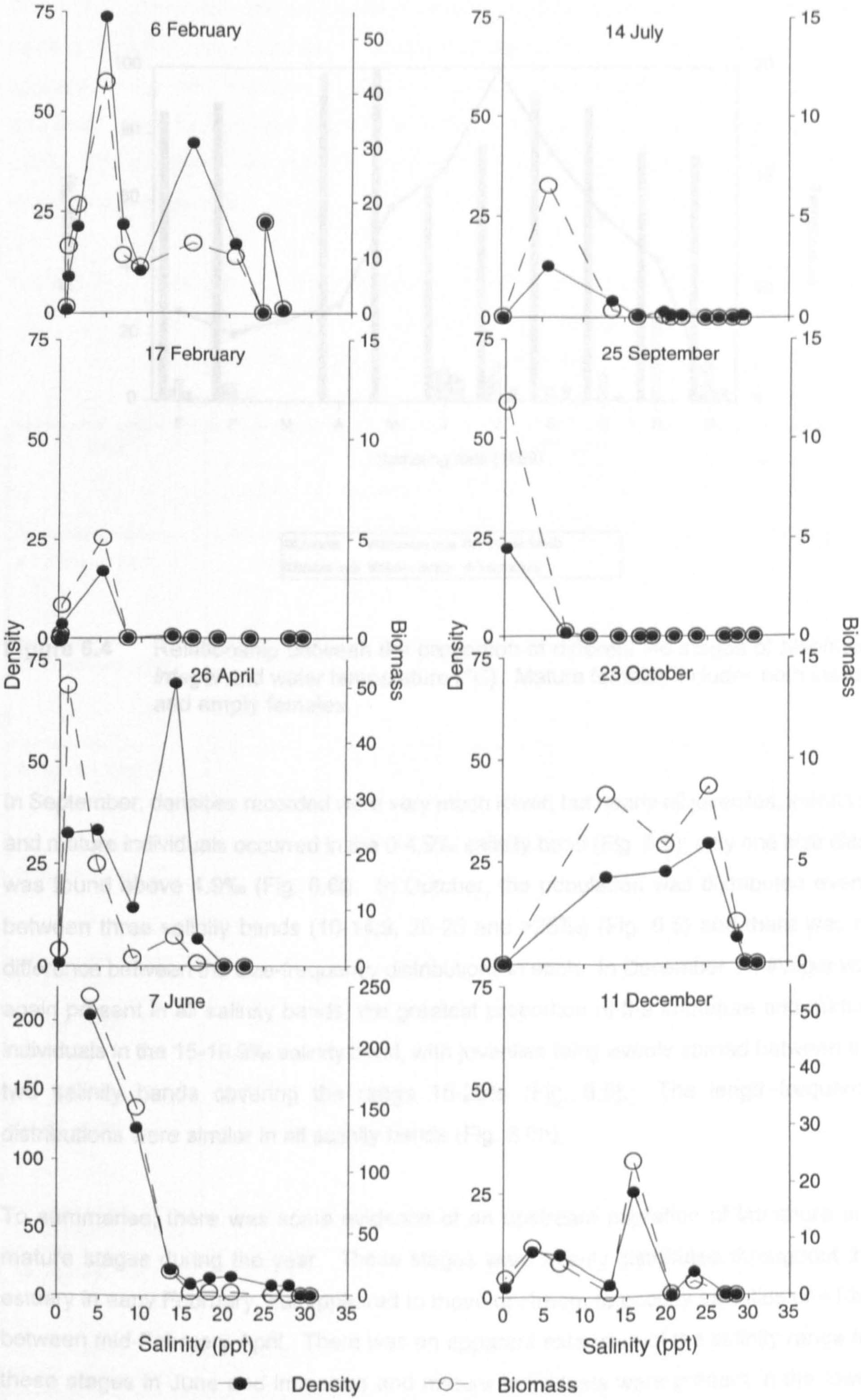


Figure 6.3 Relationship between salinity (‰), population density (Nm^{-3}) and biomass (mgm^{-3} dry weight) of *Neomysis integer* throughout the year (1989). (The density in March, May and November was < 1 individual m^{-3}).

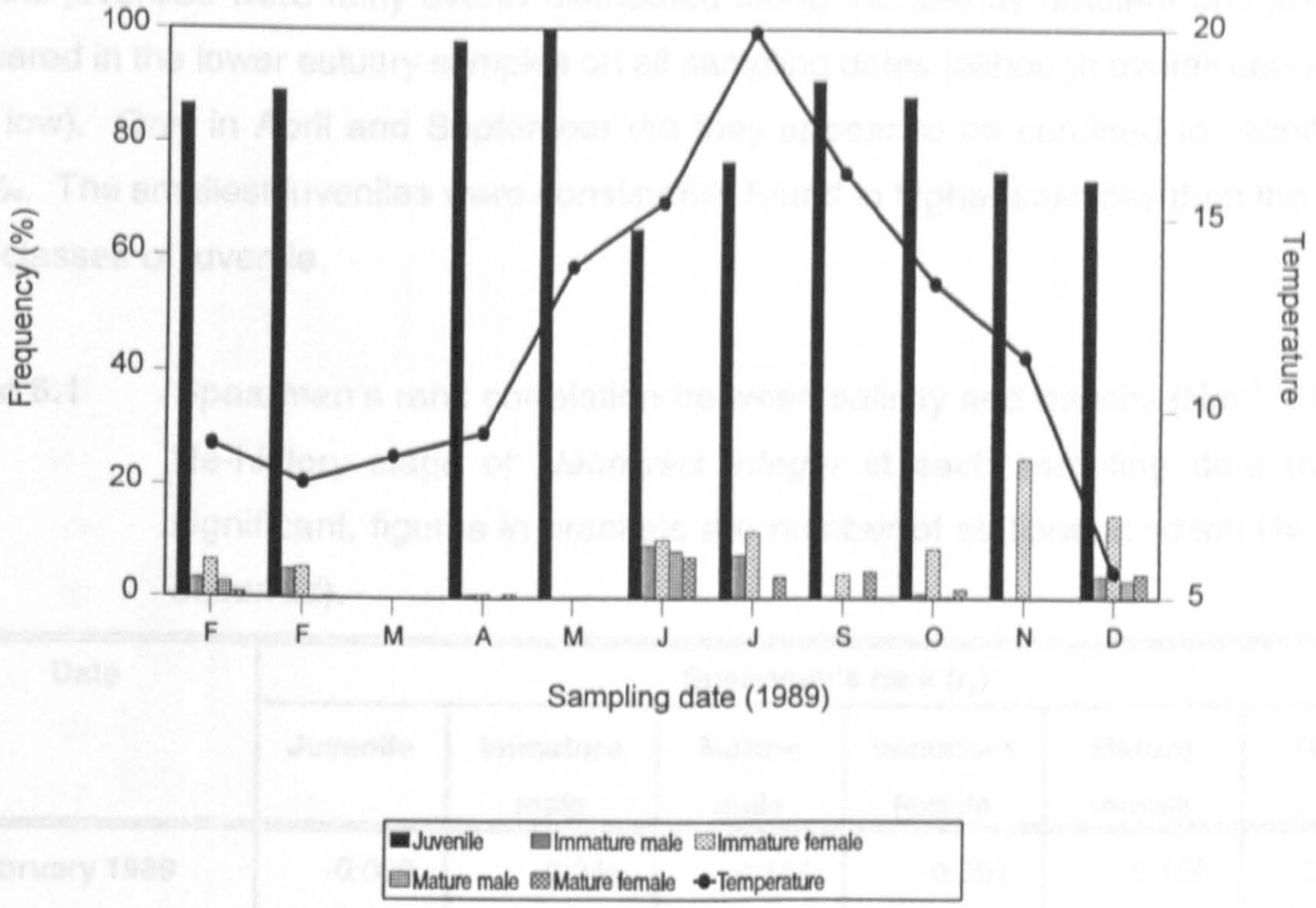


Figure 6.4 Relationship between the proportion of different life stages of *Neomysis integer* and water temperature (°C). Mature females includes both mature and empty females.

In September, densities recorded were very much lower, but nearly all juveniles, immature and mature individuals occurred in the 0-4.9‰ salinity band (Fig. 6.5); only one size class was found above 4.9‰ (Fig. 6.6f). In October, the population was distributed evenly between three salinity bands (10-14.9, 20-25 and >25‰) (Fig. 6.5) and there was no difference between the size-frequency distributions in each. In December, *N. integer* was again present in all salinity bands, the greatest proportion of the immature and mature individuals in the 15-19.9‰ salinity band, with juveniles fairly evenly spread between the two salinity bands covering the range 15-25‰ (Fig. 6.5). The length-frequency distributions were similar in all salinity bands (Fig. 6.6h).

To summarise, there was some evidence of an upstream migration of immature and mature stages during the year. These stages were evenly distributed throughout the estuary in early February, but appeared to move upstream to occupy salinities of <15‰ between mid-February April. There was an apparent extension of the salinity range for these stages in June and immature and mature individuals were present in the lower estuary in this month. The salinity distribution of immature and mature stages narrowed again in September to <5‰ before moving back into salinities >15‰ between September and October.

Distribution of juveniles did not demonstrate a clear relationship with salinity and in most months juveniles were fairly evenly distributed along the salinity gradient and juveniles appeared in the lower estuary samples on all sampling dates (although overall abundance was low). Only in April and September did they appear to be confined to salinities of <10‰. The smallest juveniles were consistently found in higher salinities than the larger size-classes of juvenile.

Table 6.1 Spearman's rank correlation between salinity and density (Nm^{-3}) of each life-history stage of *Neomysis integer* at each sampling date (ns=not significant, figures in brackets are number of stations at which life-stage occurred).

Date	Spearman's rank (r_s)					
	Juvenile	Immature male	Mature male	Immature female	Mature female	Total
6 February 1989	-0.009 (11) ns	-0.345 (10) ns	-0.164 (10) ns	-0.391 (11) ns	-0.156 (8) ns	-0.100 (11) ns
17 February 1989	0.371 (6) ns	-	-	1.000 (4) p=0.05	-	0.464 (7) ns
20 March 1989	-	0.800 (4) ns	-	0.800 (4) ns	-	0.800 (4) ns
26 April 1989	-0.643 (7) ns	-0.800 (4) ns	-	-	-	-0.452 (8) ns
12 May 1989	-	-	-	-	-	-
7 June 1989	-0.887 (10) p<0.01	-0.943 (6) p=0.01	-0.886 (6) p<0.05	-0.943 (6) p=0.01	-0.941 (6) p<0.05	-0.929 (10) p<0.01
14 July 1989	-0.424 (11) ns	-	-	-	-	-0.424 (11) ns
25 September 1989	-	-	-	-	-	-
23 October 1989	-0.600 (5) ns	-	0.738 (4) ns	-0.800 (4) ns	-0.400 (4) ns	-0.600 (5) ns
22 November 1989	-	-	-	-	-	-
11 December 1989	-0.333 (8) ns	-0.300 (5) ns	-	-0.393 (7) ns	-0.030 (6) ns	-0.381 (8) ns

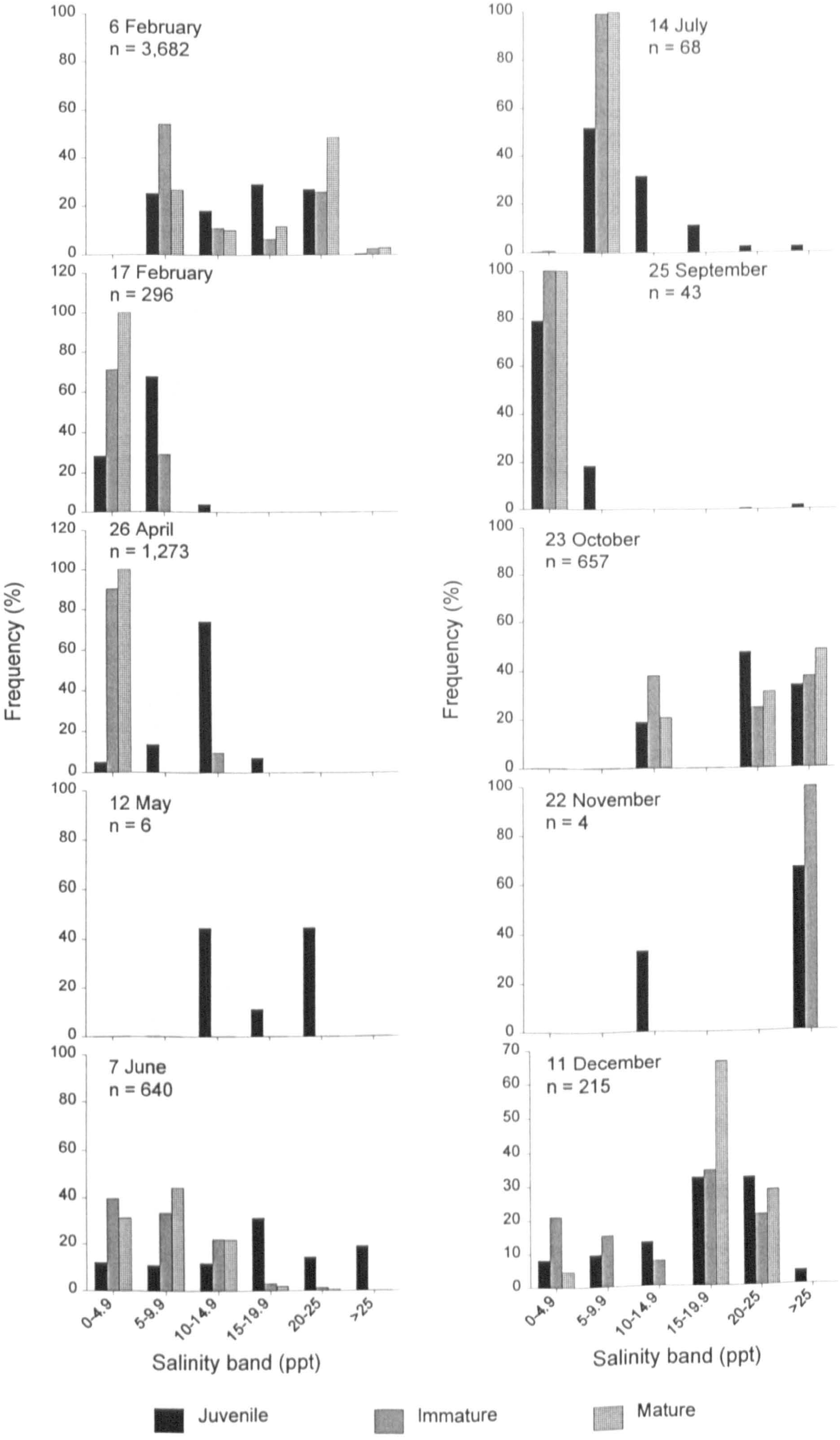


Figure 6.5 Distribution in 5 salinity bands of juvenile, immature and mature *Neomysis integer* as percentages of the whole estuary population of each life stage.

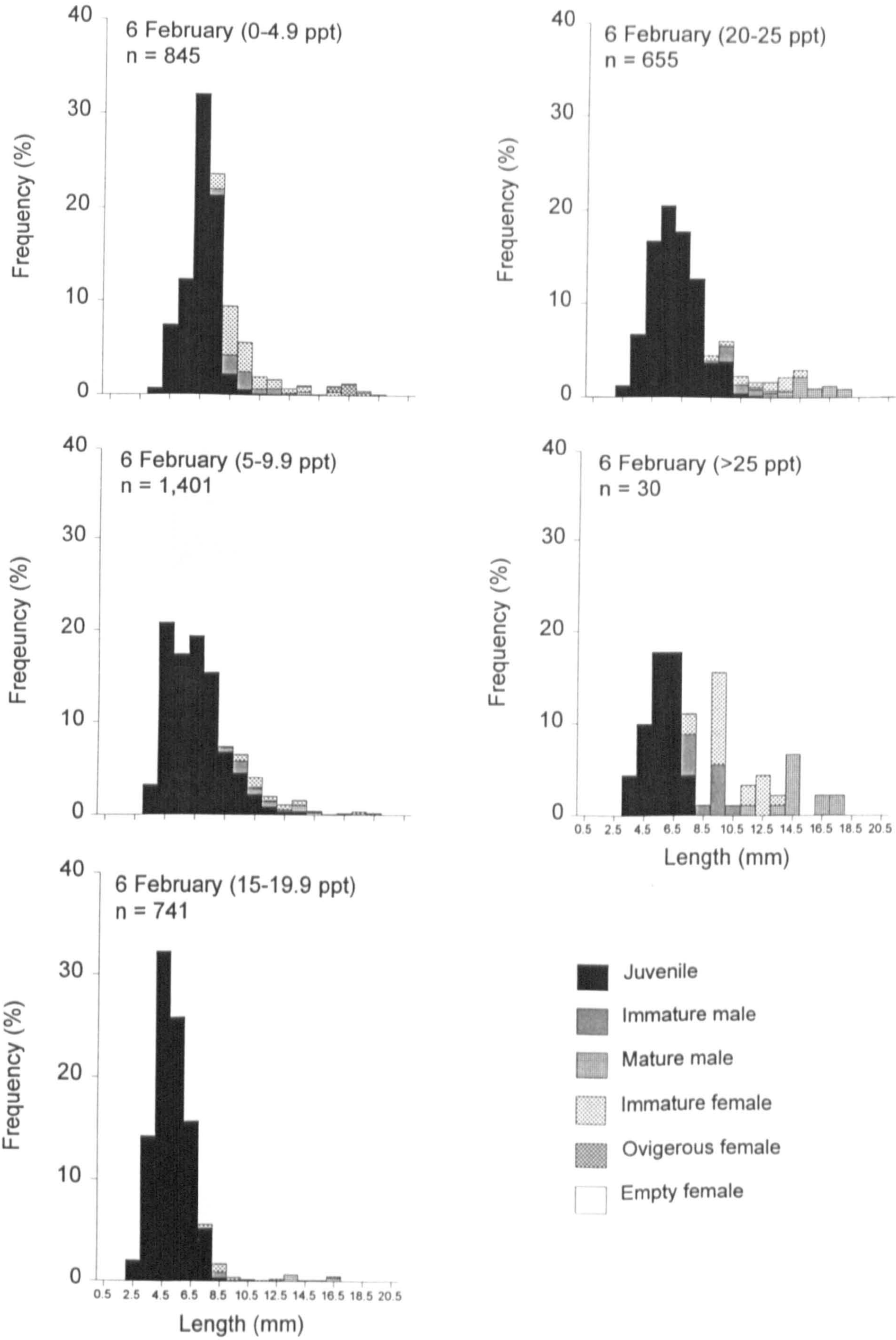


Figure 6.6a Length-frequency distribution of *Neomysis integer* in different salinity bands (6 February 1989). (Salinity bands not shown are where n < 8.)

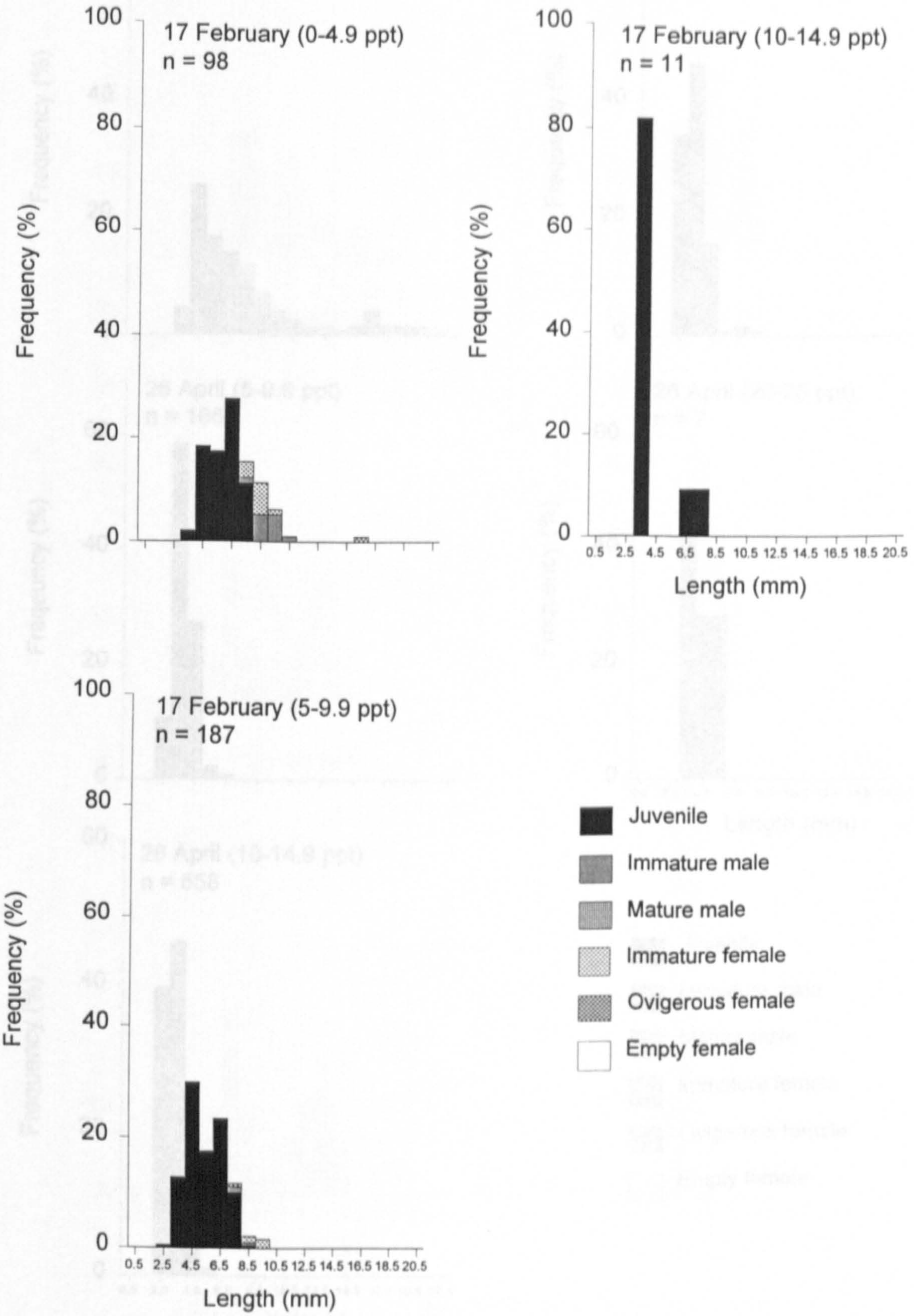


Figure 6.6b Length-frequency distribution of *Neomysis integer* in different salinity bands (17 February 1989). (Salinity bands not shown are where n < 8.)

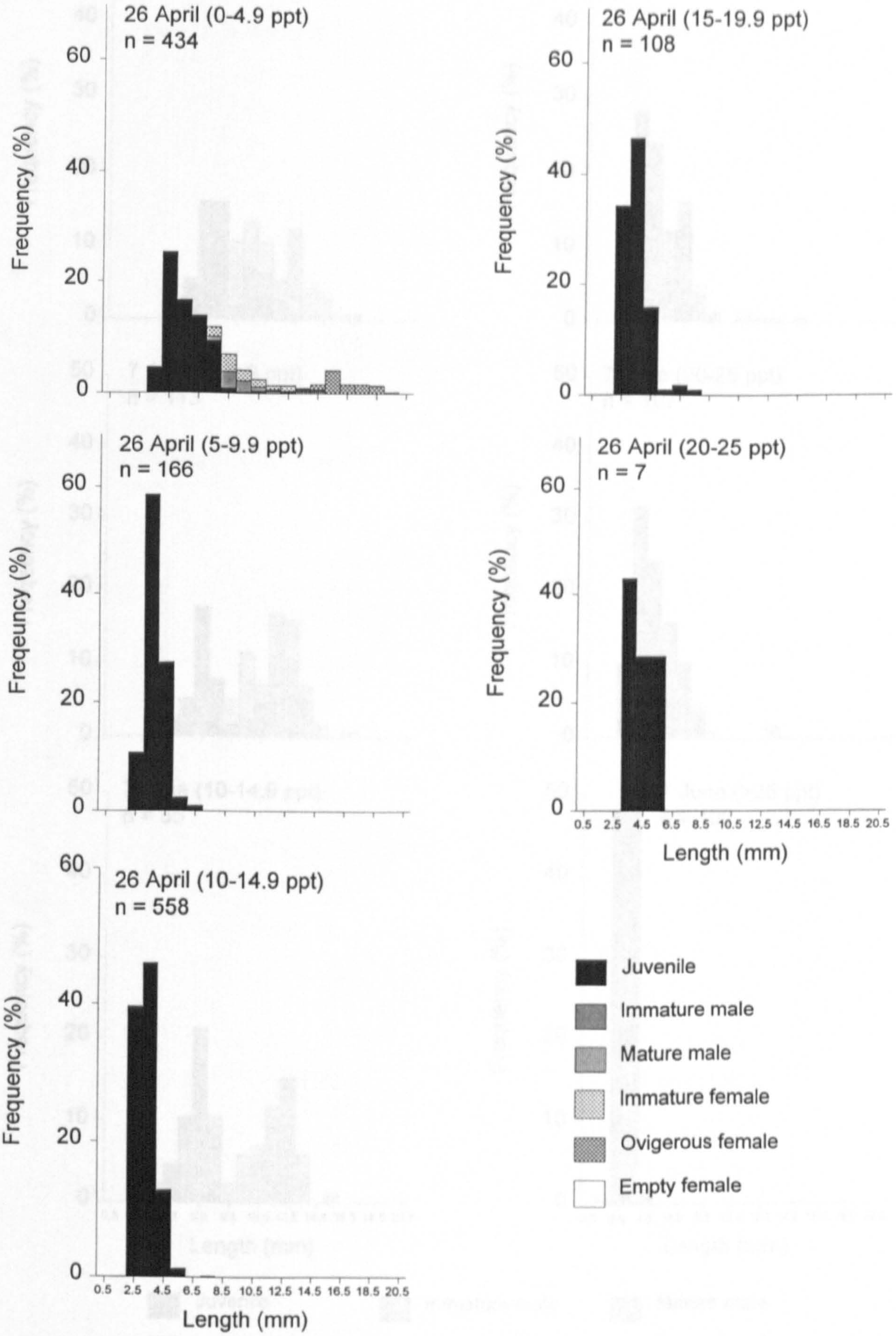


Figure 6.6c Length-frequency distribution of *Neomysis integer* in different salinity bands (April 1989). (Salinity bands not shown are where n < 8.)

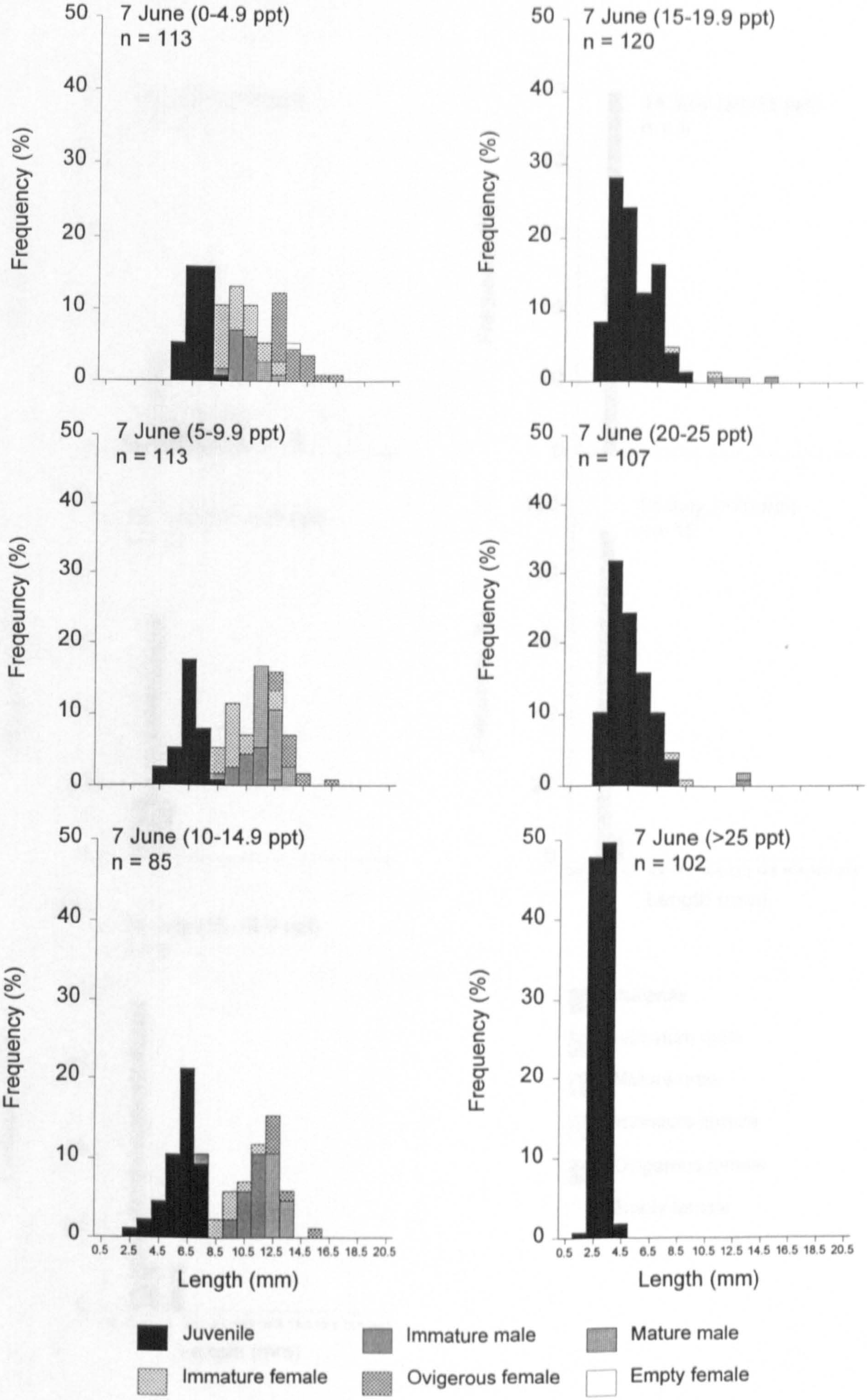


Figure 6.6d Length-frequency distribution of *Neomysis integer* in different salinity bands (June 1989). (Salinity bands not shown are where n < 8.)

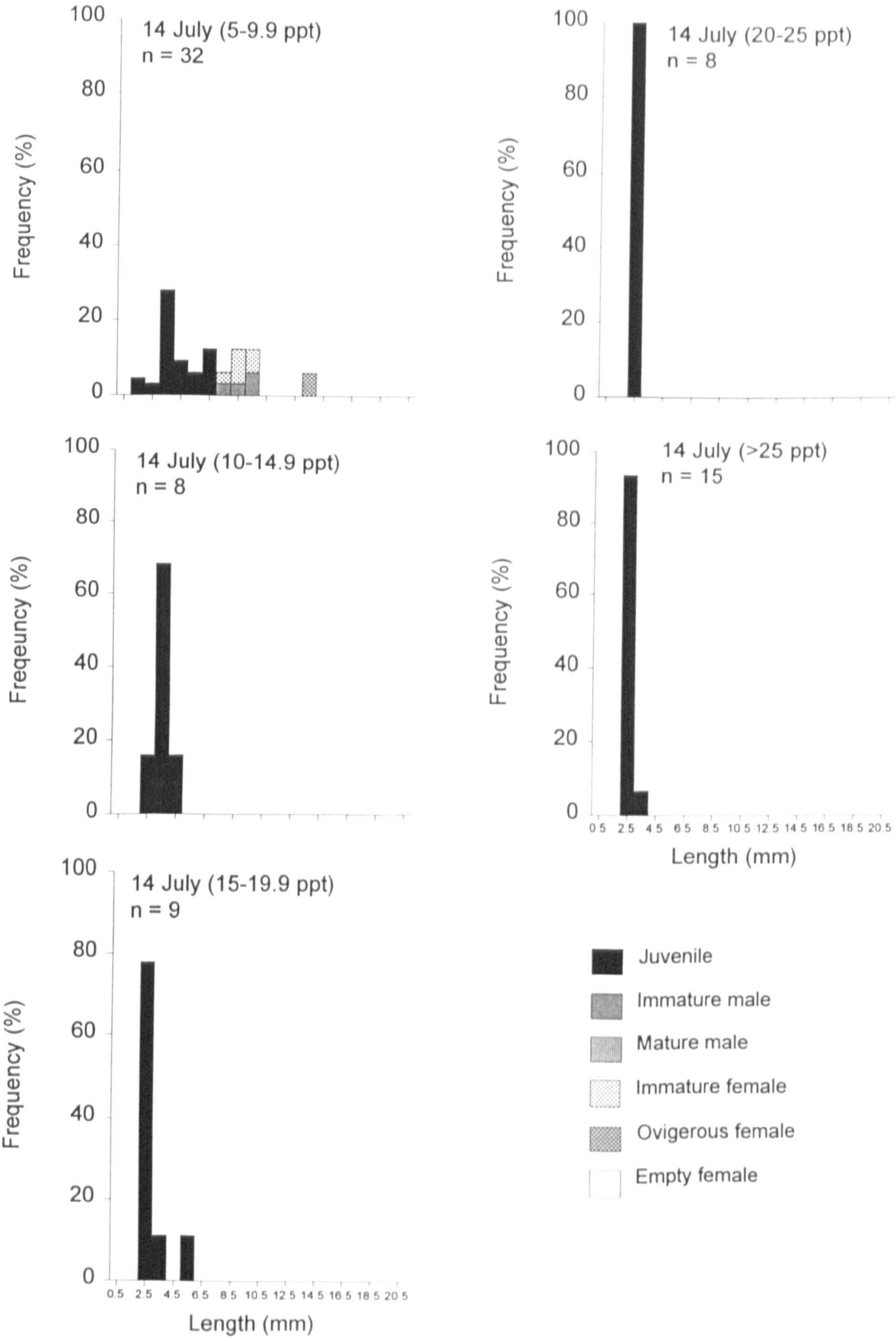


Figure 6.6e Length-frequency distribution of *Neomysis integer* in different salinity bands (July 1989). (Salinity bands not shown are where n < 8.)

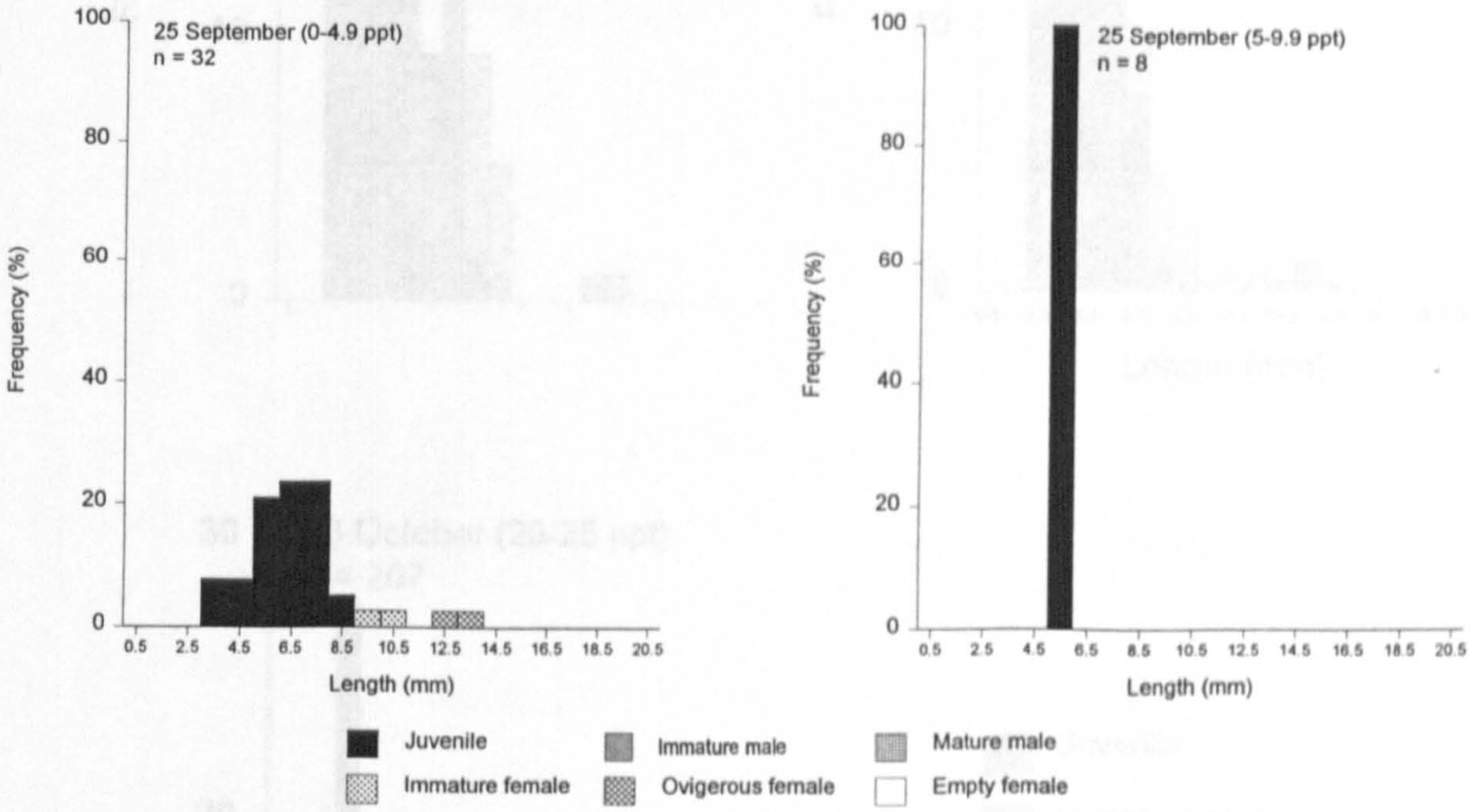


Figure 6.6f Length-frequency distribution of *Neomysis integer* in different salinity bands (September 1989). (Salinity bands not shown are where n<8.)

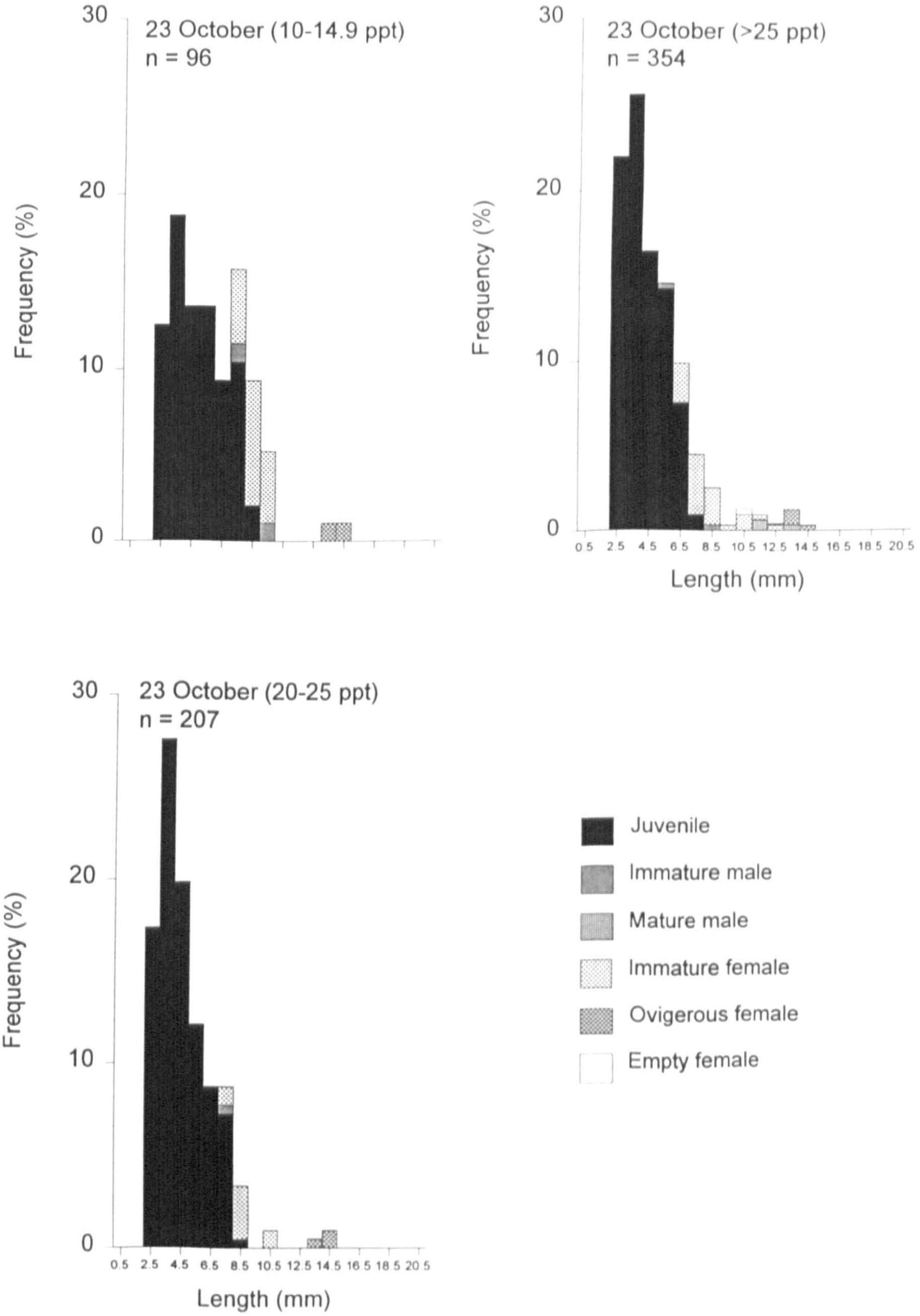


Figure 6.6g Length-frequency distribution of *Neomysis integer* in different salinity bands (October 1989). (Salinity bands not shown are where n < 8.)

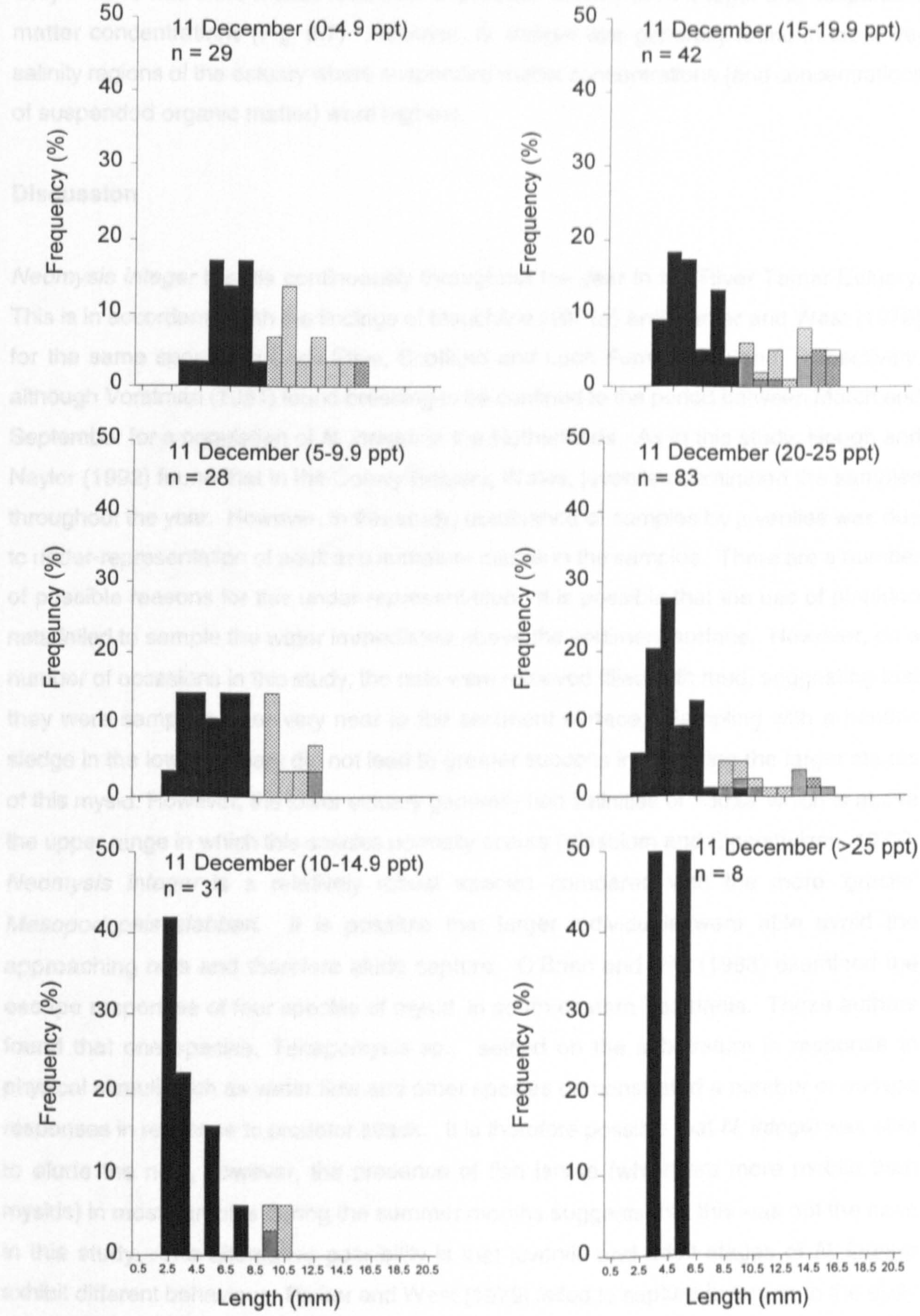


Figure 6.6h Length-frequency distribution of *Neomysis integer* in different salinity bands (December 1989). (Salinity bands not shown are where n < 8.)

Only in June was there a clear relationship between density of *N. integer* and suspended matter concentrations (Fig. 6.7). However, *N. integer* was generally found in the lower salinity regions of the estuary where suspended matter concentrations (and concentrations of suspended organic matter) were highest.

6.2 Discussion

Neomysis integer breeds continuously throughout the year in the River Tamar Estuary. This is in accordance with the findings of Mauchline (1971a) and Parker and West (1979) for the same species in Loch Etive, Scotland and Loch Furnace, Ireland, respectively, although Vorstman (1951) found breeding to be confined to the period between March and September for a population of *N. integer* in the Netherlands. As in this study, Hough and Naylor (1992) found that in the Conwy Estuary, Wales, juveniles dominated the samples throughout the year. However, in this study, dominance of samples by juveniles was due to under-representation of adult and immature stages in the samples. There are a number of possible reasons for this under-representation. It is possible that the use of plankton nets failed to sample the water immediately above the sediment surface. However, on a number of occasions in this study, the nets were retrieved filled with mud, suggesting that they were sampling at or very near to the sediment surface. Sampling with a benthic sledge in the lower estuary did not lead to greater success in capturing the larger stages of this mysid. However, the lower estuary generally had salinities of >30‰, which is above the upper range in which this species normally occurs (Vlasblom and Elgershuizen, 1977). *Neomysis integer* is a relatively robust species compared with the more 'gracile' *Mesopodopsis slabberi*. It is possible that larger individuals were able avoid the approaching nets and therefore elude capture. O'Brien and Ritz (1988) examined the escape responses of four species of mysid in south-eastern Tasmania. These authors found that one species, *Tenagomysis* sp., settled on the substratum in response to physical stimuli such as water flow and other species demonstrated a number of escape responses in response to predator attack. It is therefore possible that *N. integer* was able to elude the nets, however, the presence of fish larvae (which are more mobile than mysids) in most samples during the summer months suggests that this was not the case in this study. The alternative possibility is that juvenile and adult stages of *N. integer* exhibit different behaviour. Parker and West (1979) failed to capture juveniles in the size-class 2-4 mm in Lough Furnace, as did Kinne (1955) in the Kiel Canal, suggesting that the smallest juveniles have different habitat and/or salinity requirements than larger juveniles, immature and mature stages. Välipakka (1992) found that juvenile *N. integer* shoaled separately from, and remained in deeper waters than adults, in the western Baltic. *Neomysis integer* is known to make extensive use of creeks and saltmarsh on the margins of estuaries (Ralph, 1965; Mees, *et al.*, 1993).

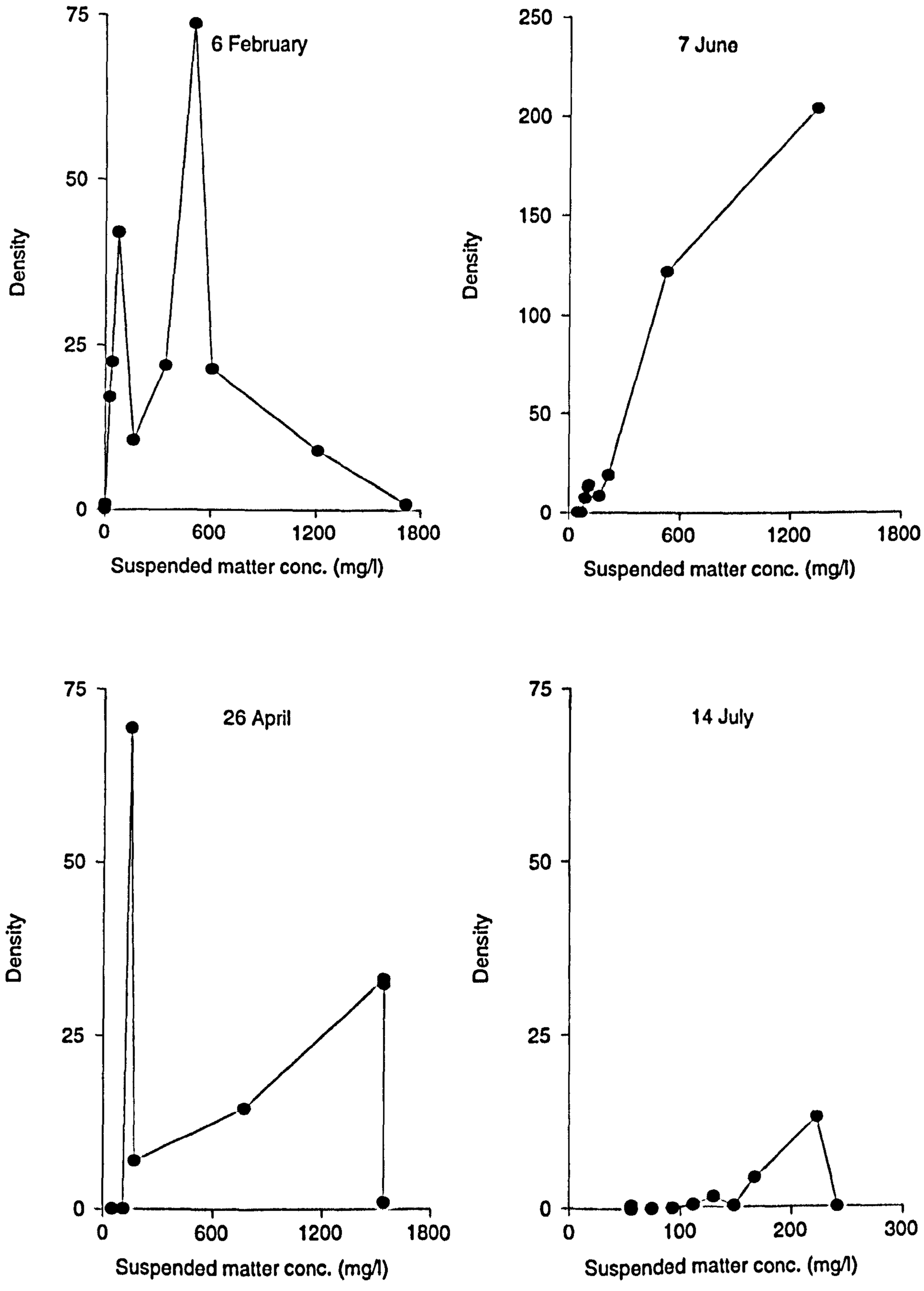


Figure 6.7 Relationship between suspended matter concentration (mg/l) and density (Nm^{-3}) of *Neomysis integer* throughout the year. (Months shown are those where turbidity readings were taken and where density exceeded 1 individual m^{-3}.)

Ralph (1965) noted that females utilised the creeks in Southampton Water whilst newly released juveniles in the smallest size class (2-3 mm) and males did not occur in the creeks where he sampled. There are numerous creeks in the upper Tamar Estuary and it is possible that some life-history stages utilised these. Hough and Naylor (1992) found the greatest concentrations of *N. integer* in mid-channel in the Conwy estuary, but they also found that *N. integer* avoided strong currents by remaining in the shallow estuary margins. These authors also found that male *N. integer* had different behaviour patterns to other life-history stages. It is possible then that juvenile *N. integer* have more of a mid-channel distribution than mature females and that males either have different habitat requirements or die soon after breeding.

Neomysis integer had a wide salinity distribution in the Tamar Estuary (most of the population occurring between 0-25‰). During the summer period, adult stages were concentrated in the low salinity (<5‰) regions of the estuary. Vlasblom and Elgershuizen (1977) found that while adult *N. integer* could tolerate salinities of between 2 and 20‰, eggs of this species developed more quickly when adapted to low salinities (3.8‰). Eggs adapted to higher salinities completed development, but over a longer timespan. The restriction of the breeding population to lower salinities in the summer months might therefore be a result of the salinity tolerance of the developing embryos rather than any particular salinity preference of the adults. Juvenile *N. integer* had a wider salinity distribution than the adults throughout the year. The interaction of *N. integer* with the other mysid (*Mesopodopsis slabberi*) occurring in the upper estuary is discussed in §7.1.9.

Neomysis integer achieved a maximum size of 15mm (male) and 16.8mm (female) in this study, smaller than the maximum lengths recorded by Vorstman (1951), but similar to lengths reported by Kinne (1955) and Tattersall and Tattersall (1951), Mauchline (1971a) and Mees *et al.* (1994).

In summary, it was not possible, even when size-frequency distribution was examined in discrete salinity bands, to discern any distinct pattern in the longitudinal density distribution of *N. integer* which might help to explain the relative lack of immature and mature stages in the samples. There was a suggestion that immature and mature stages migrated up-estuary in the spring, and spent the summer and early autumn in the lowest salinity reaches of the estuary (<5‰) and it is possible that these stages were not well sampled because they utilised the creeks and margins of the estuary at the time of sampling. This could be confirmed by carrying out additional surveys which include these shallow margins. Sampling in these shallow areas could be achieved using hand-held dip nets. However, there would be difficulties in carrying out quantitative sampling using this method.

CHAPTER 7

UPPER ESTUARY:

MESOPODOPSIS SLABBERI

7. UPPER ESTUARY: *MESOPODOPSIS SLABBERI*

7.1 Results

7.1.1 Separation of cohorts

Mesopodopsis slabberi was present in the estuary throughout the year and the monthly length-frequency distributions of the population, distinguishing the separate life-history stages, are shown in Figure 7.1. Data from 17 February 1989 were included in the following analysis although not shown in Figure 7.1. Recruitment of cohorts into the population is seen as bimodalities in the length-frequency histograms. Three cohorts were identified in the population through the year. The overwintering cohort (Cohort I) was clearly identifiable as was recruitment of Cohort IIA. Identification of cohorts between June and October was more complex and two possibilities for the succession of cohorts were identified. In early February, the population comprised around 51% juveniles with a mean length of 6.5 mm (range 4.1-9.6 mm). Less than 2% of the population were adult, the remainder being made up of immature mysids. By mid-February, juveniles contributed only 37% of the population (11% in March and 0.2% in April). This decline in the percentage of juveniles in the population was accompanied by increases in the percentage of immature individuals and adults. By April, the population was made up almost entirely of immature (30%) and mature stages (67%). This change in the relative proportion of the stages was accompanied by increases in the mean size of Cohort I (Fig. 7.2). In May, Cohort I was composed almost entirely of mature individuals and the first influx of juveniles into the population was apparent. From June-September, juveniles dominated the population only declining in numbers as water temperatures decreased.

The following two options are offered as explanations of the succession of cohorts between June and October.

Option 1

Cohort I, the overwintering generation, was identified in the population from September to May and appears to overwinter as a mixture of juveniles and immature adults, with a mean length of 6.5 mm. Individuals increased in size and matured from March to May (Fig. 7.1).

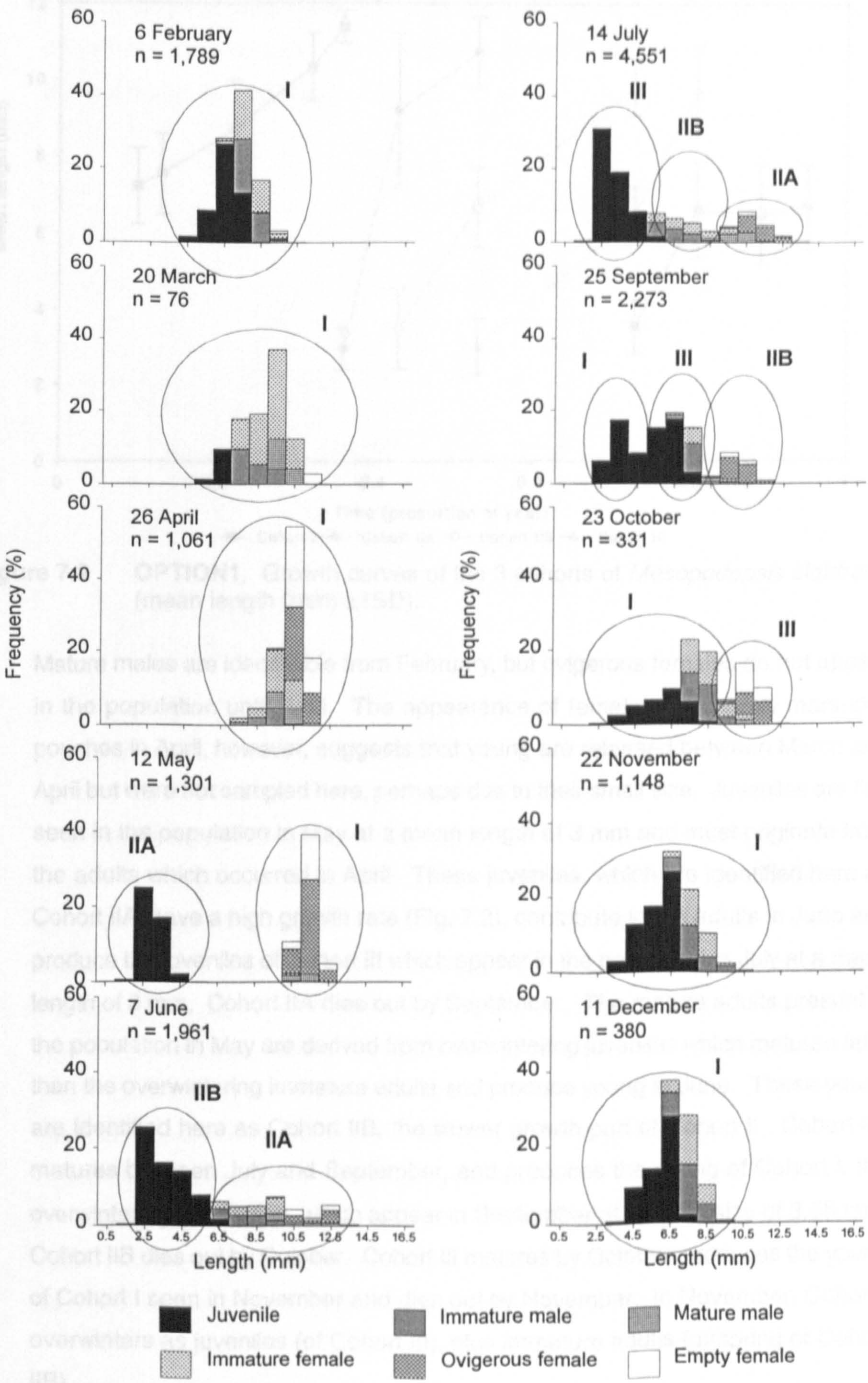


Figure 7.1 **OPTION 1**. Length-frequency distribution of *Mesopodopsis slabberi* in the Tamar Estuary identifying the 3 cohorts. (The data represent pooled samples for all stations.)

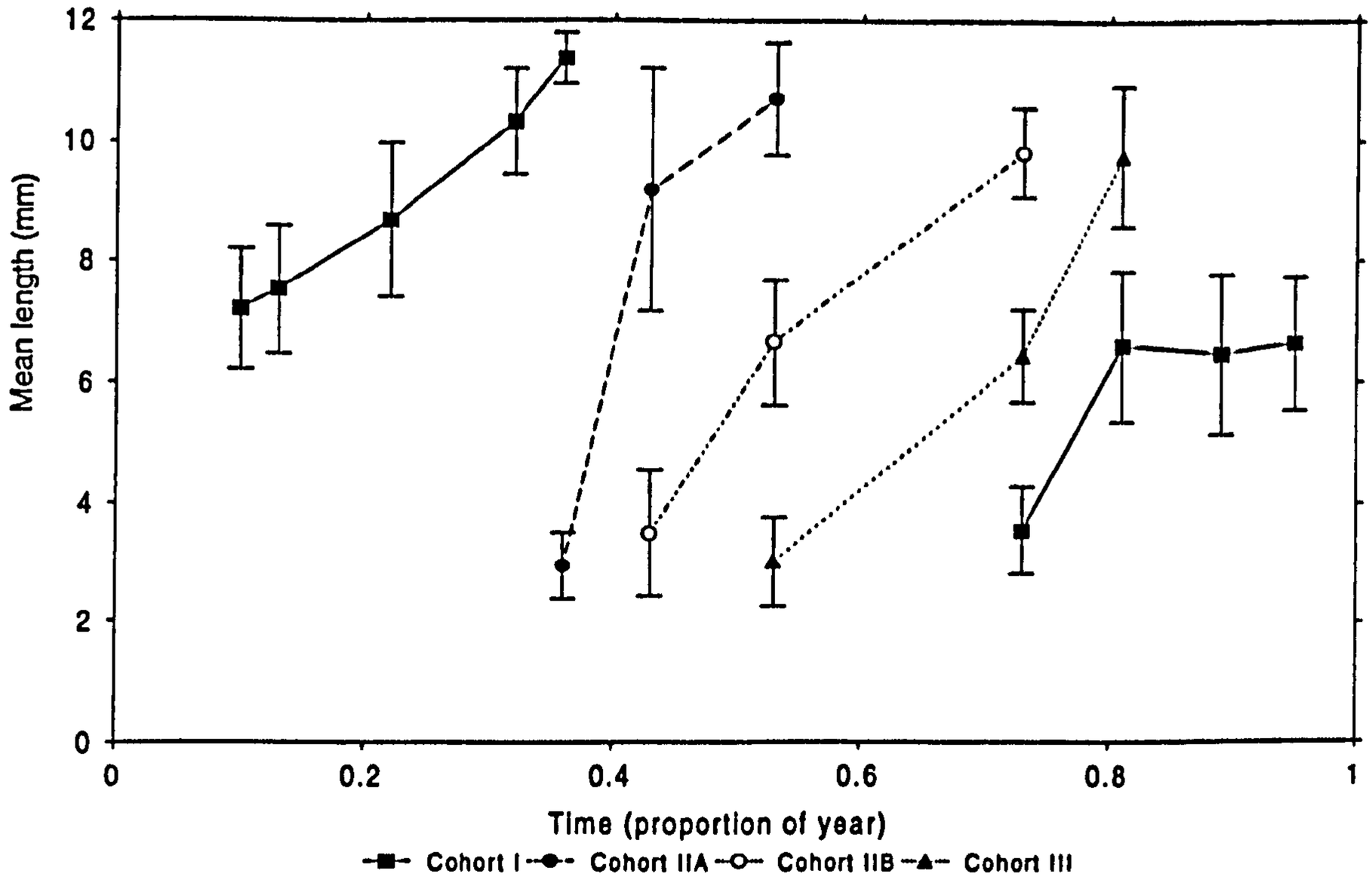


Figure 7.2 **OPTION1.** Growth curves of the 3 cohorts of *Mesopodopsis slabberi* (mean length (mm) ±1SD).

Mature males are identifiable from February, but ovigerous females do not appear in the population until April. The appearance of females with empty marsupial pouches in April, however, suggests that young are released between March and April but were not sampled here, perhaps due to their small size. Juveniles are first seen in the population in May at a mean length of 3 mm and must originate from the adults which occurred in April. These juveniles, which are identified here as Cohort IIA, have a high growth rate (Fig. 7.2), contribute to the adults in June and produce the juveniles of Cohort III which appear in the population in July at a mean length of 3 mm. Cohort IIA dies out by September. The mature adults present in the population in May are derived from overwintering juveniles which matured later than the overwintering immature adults and produce young in June. These young are identified here as Cohort IIB, the slower growth part of Cohort II. Cohort IIB matures between July and September, and produces the young of Cohort I, the overwintering generation, which appear in September at a mean size of 3.55 mm. Cohort IIB dies out by October. Cohort III matures by October, produces the young of Cohort I seen in November and dies out by November. In November, Cohort I overwinters as juveniles (of Cohort III), plus immature adults (offspring of Cohort IIB).

The above interpretation, therefore, proposes that in the Tamar Estuary *Mesopodopsis slabberi* has one 'line' with 3 generations per year (fast line) and another with 2 generations (slow line). Furthermore, the pattern of generations alternates between years with the fast line of one year overwintering as juveniles

and forming the slow line of the following year, whilst the slow line of one year overwinters as immature adults, maturing faster the following spring and forming the fast line of that year (Fig. 7.3).

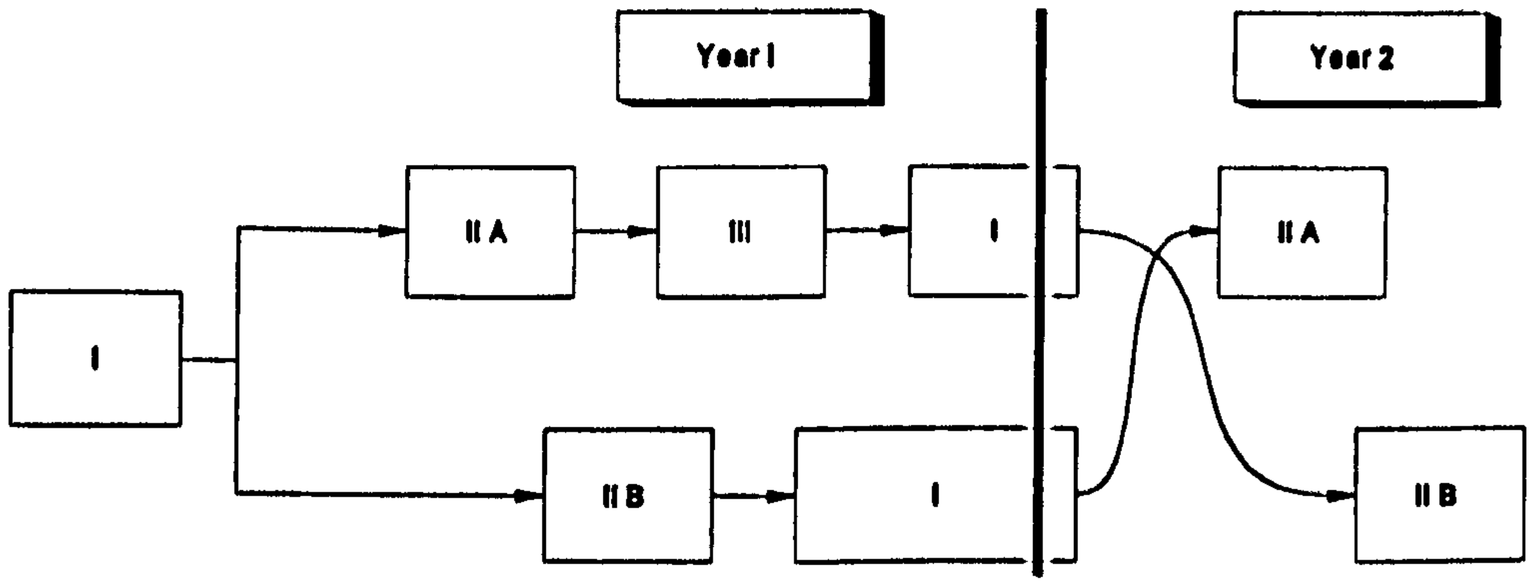


Figure 7.3 **OPTION 1.** Succession of cohorts of *Mesopodopsis slabberi* in the Tamar Estuary. (I=Cohort I, IIA= Cohort IIA fast line, IIB=Cohort IIB slow line, III= Cohort III.)

Option 2

The alternative possibility is that the mature adults in October are the remains of Cohort IIB, and the immature adults are of Cohort III which then overwinter at this stage (Fig. 7.4). In this option, Cohort III would overwinter as immature adults at a mean length of 8.23 mm. This cohort resumes growth in the spring and produces the young Cohort IIA in May. Cohort I overwinters as juveniles, matures more slowly the following year and produces the offspring, Cohort IIB, which appear in June. Examination of the growth curves (Fig. 7.5) shows that this is also feasible and indicates that *Mesopodopsis slabberi* has two 'lines' of mysids, each with two generations per year. One line would reproduce earlier in the spring, and form the immature adults of the overwintering generation and the fast line of the following year. The second line would reproduce more slowly in the spring and overwinter as juveniles, forming the slow line of the following year (Fig. 7.6).

7.1.2 Sex ratios

The sex ratio (M:F) of the population varied markedly through the year with a trend towards higher values during the summer months (Table 7.1). Females were only present in the same proportion to males in February (both dates), March, November and December (χ^2=0.06, 1.88, 4.77 and 0.01, 0.83, all $p>0.05$).

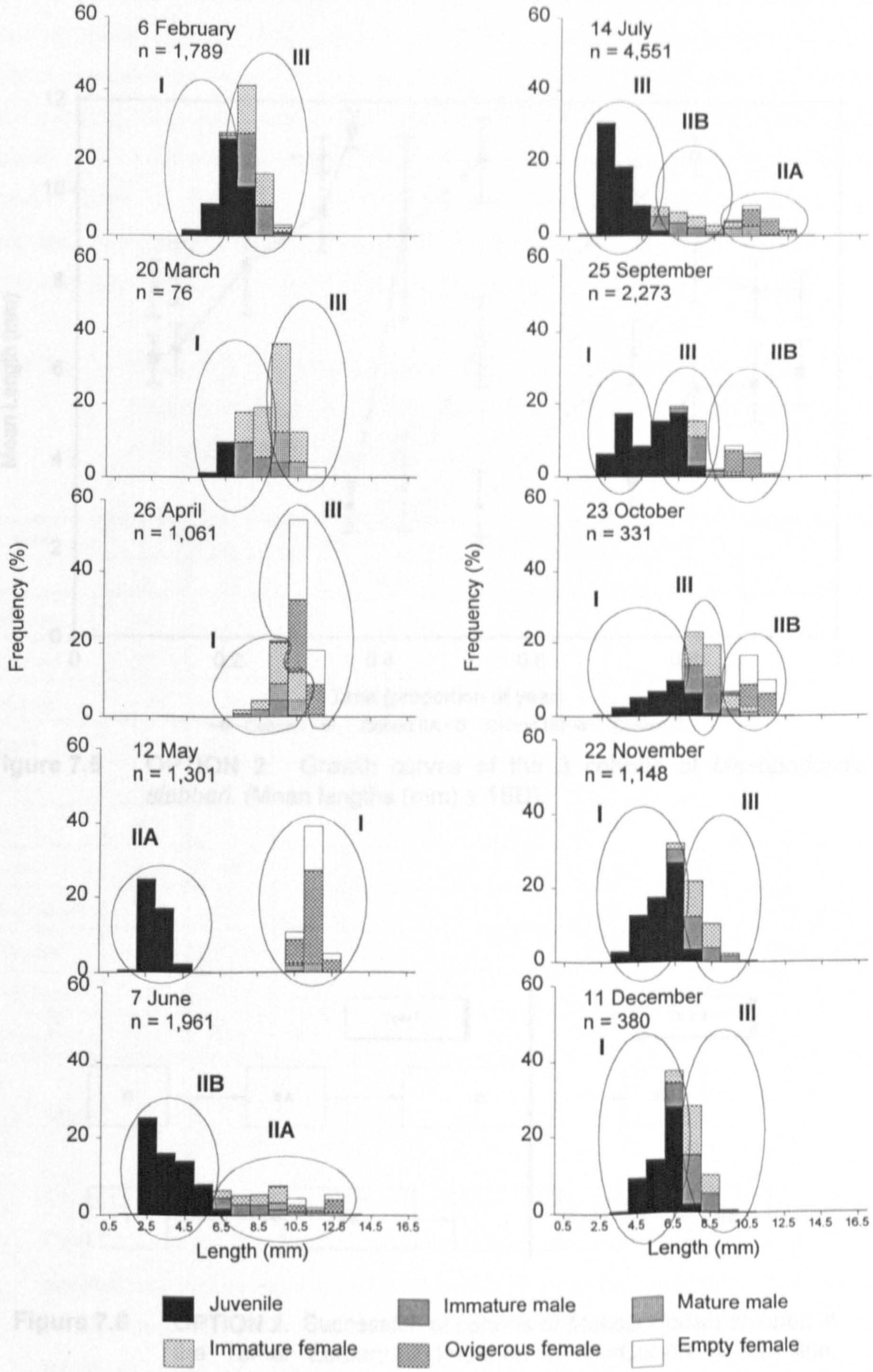


Figure 7.4 **OPTION 2**. Length-frequency distribution of *Mesopodopsis slabberi* in the Tamar Estuary showing the 3 cohorts identified. (The data represent pooled samples for all stations.)

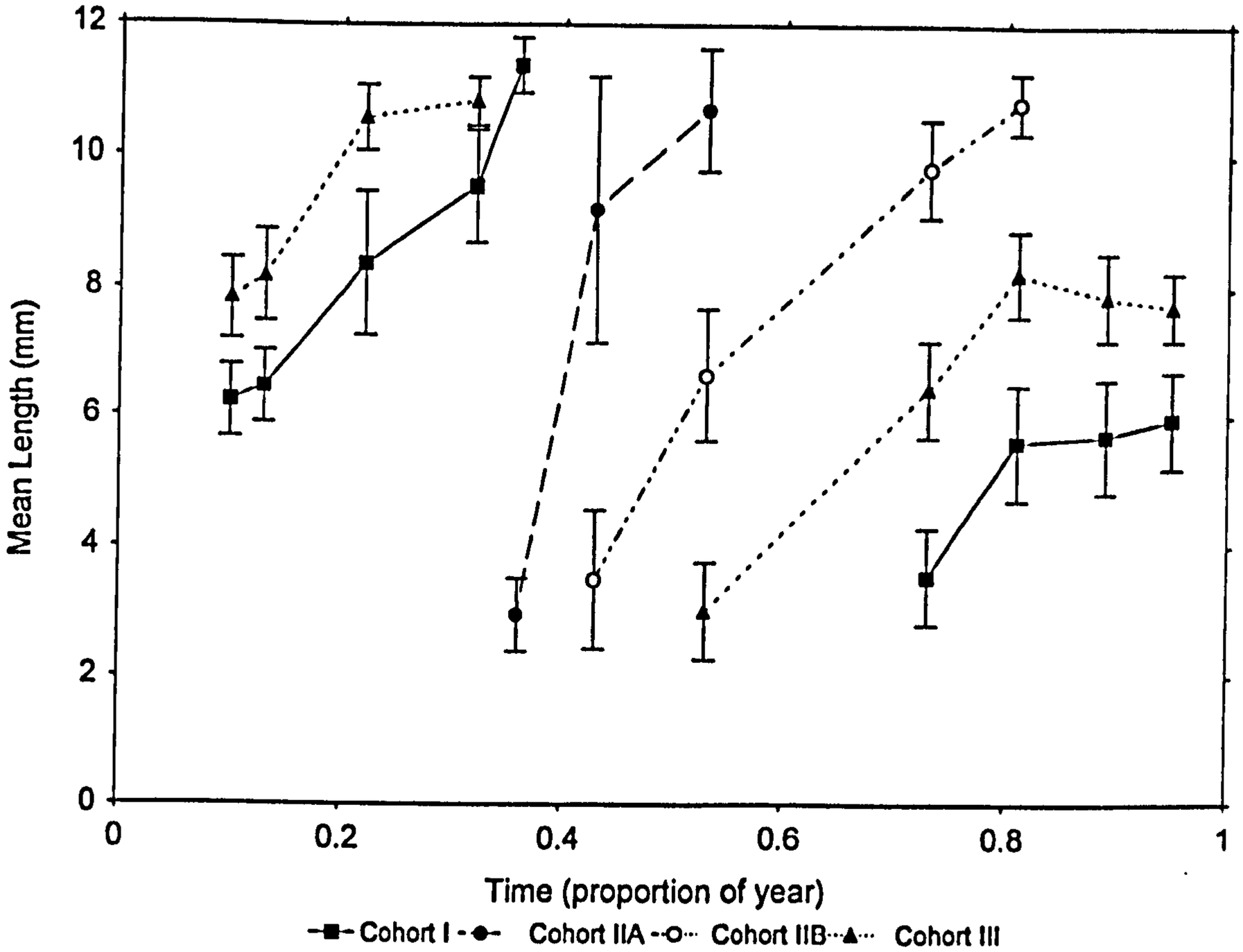


Figure 7.5 **OPTION 2.** Growth curves of the 3 cohorts of *Mesopodopsis slabberi*. (Mean lengths (mm) ± 1SD).

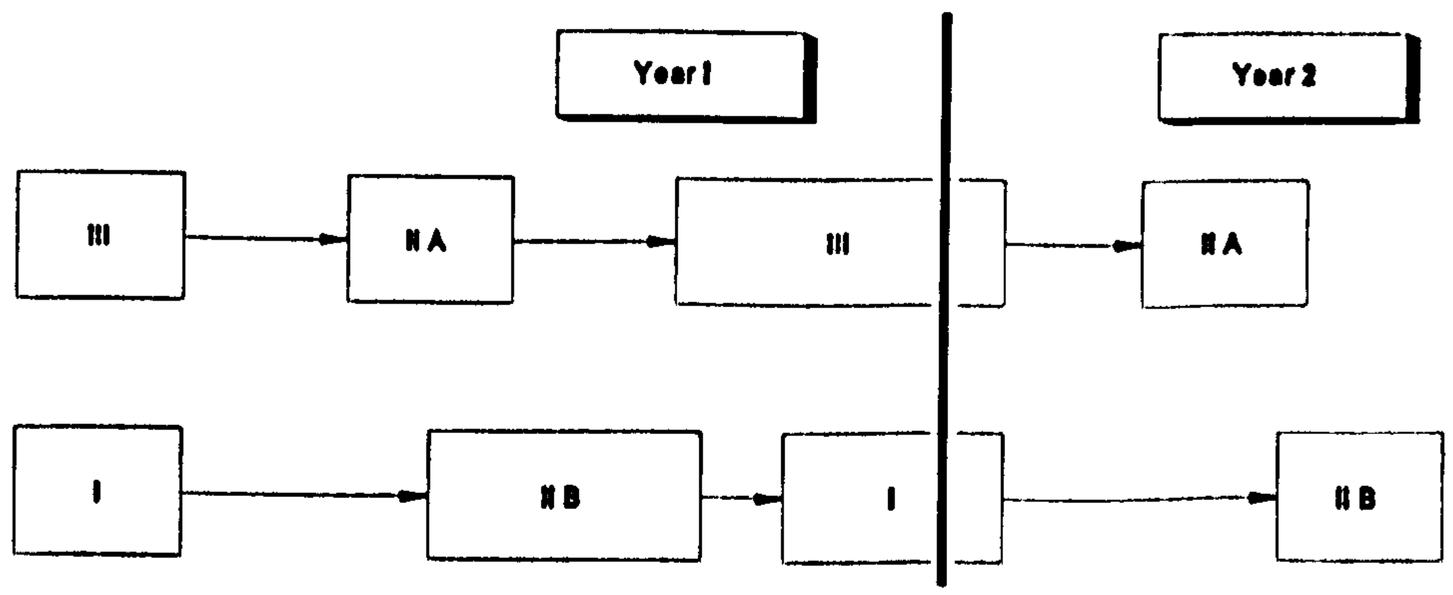


Figure 7.6 **OPTION 2.** Succession of cohorts of *Mesopodopsis slabberi* in the Tamar Estuary. (I=Cohort I, IIA=Cohort II fast line, IIB=Cohort II slow line, III=Cohort III.)

The ratio became biased towards females in the following months with the highest ratio occurring in May (13:1, χ^2=525.6, p<0.001). Mature males formed a higher proportion of the total population in March (19.8%), April (12%) and May (9%), and probably died soon after breeding. However, even in April and May, the sex ratio remained biased towards females (χ^2= 456.1 and 525.6, p<0.001). The sex ratios of the three cohorts are also shown in Table 7.1. Except for Cohort IIA in July, and Cohort III in September, which were comprised primarily of immature individuals, females predominated in the three cohorts and were up to 13.2 times more abundant than males. Only Option I was considered.

Table 7.1 Sex ratio of *Mesopodopsis slabberi* throughout the year. (M:F = male:female ratio, n = number of male and female *M. slabberi* sampled, ** = χ^2 p<0.001, * = p<0.05).

Date	Total		Cohort I		Cohort IIA		Cohort IIB		Cohort III	
	n	M:F	n	M:F	n	M:F	n	M:F	n	M:F
6 February	883	1:1	883	1:1						
17 February	651	1.1:1	651	1.1:1						
20 March	68	1.7:1	68	1.7:1						
26 April	1,059	4.8:1**	1,059	4.8:1**						
12 May	715	13:1**	715	13:1**	0	-				
7 June	672	1.5:1**			670	1.5:1**	10	9.0:1*		
14 July	1,812	1.4:1**			872	2.4:1**	940	0.9:1*	0	-
25 September	722	2:1**	0	-			485	10.8:1**	4,179	0.5:1*
23 October	262	2.7:1**	58	1.2:1					239	2.9:1*
22 November	418	1:1	418	1:1						
11 December	174	0.9:1	174	0.9:1						

7.1.3 Size

Seasonal changes in size of the different life-history stages are shown in Fig. 7.7. Only Option 1 is considered. The maximum and minimum sizes recorded for each stage are shown in Table 7.2. The smallest mature male measured was 7.95mm in December, and the smallest mature female, 9mm in early February. The mean length of all stages varied during the year with the greatest variation seen in the juveniles and immature stages. Juveniles of the overwintering generations achieved a significantly larger size than those of the summer generation (Cohort IIB) and the juveniles of Cohort III achieved the largest size. Immature stages of Cohort IIB grew to a significantly smaller size than those of the other three cohorts. There was no significant difference between the size of mature males and mature

females between the summer and winter generations (Fig. 7.7) and mature females were significantly larger than mature males only in March. The average increase in size of mature females was from about 9.5mm to 11.5mm, that of mature males from 9mm to 11mm.

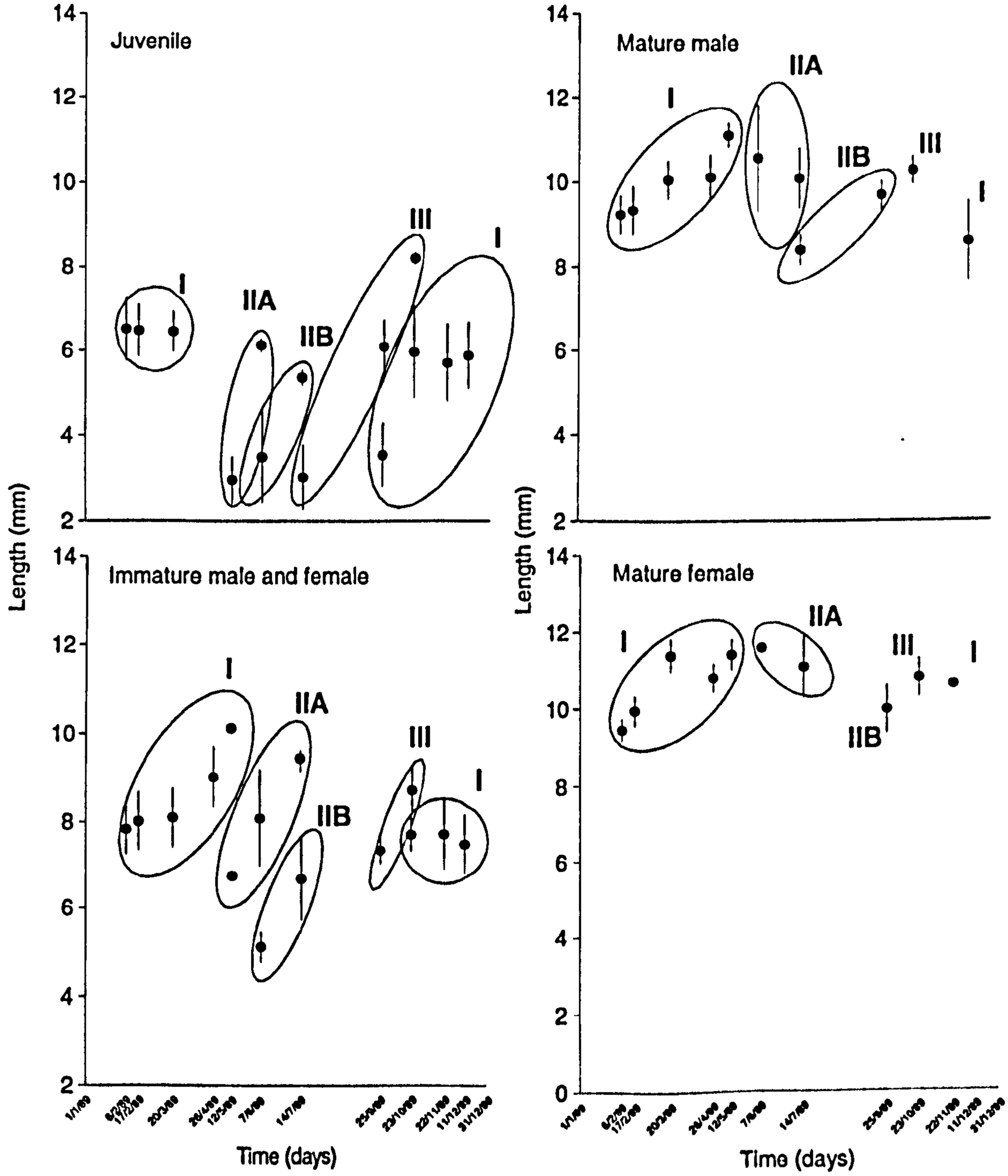


Figure 7.7 Temporal variation in mean length (±1SD) of life-history stages for each cohort of *Mesopodopsis slabberi* (Option 1 shown).

Table 7.2 Maximum and minimum sizes recorded for each life-history stage.

Life-history stage	Juvenile		Immature male		Mature male		Immature female		Mature female	
	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.
Length (mm)	1.5	8.4	5.1	10.35	7.95	13.2	4.8	10.95	9.0	13.35

7.1.4 Growth

Option 1

Growth for Option 1 is summarised in Figure 7.2 and Table 7.3. The growth rate of Cohort I was low at the beginning of February, and increased between February and April, as water temperatures started to increase (Fig. 7.8). The growth rate remained relatively low, however, probably because Cohort I overwintered at quite a large size, grew to maximum size quickly and began to reproduce in April. Cohort I reappeared in the population in September with a growth rate similar to that seen in the interval 26 April-12 May. As water temperatures declined between October and December, growth slowed down and almost ceased. Cohort IIA had the highest mean growth rate recorded, equivalent to about 7.2 mm month^{-1}, between May and June, more than double the highest rate observed in the other generations. This cohort grew rapidly, matured and began to reproduce within one month. The growth rate was slower during the following sampling interval and was consistent with a breeding population expending energy on reproduction rather than on growth. Cohort IIB had its fastest recorded growth between June and July, the period when individuals developed from juveniles into immature adults. Growth slowed between July and September, as the immature adults matured and started to breed. Cohort III had a period of high growth between September and October, as the summer juveniles matured and reproduced before disappearing from the samples.

Option 2

Growth for Option 2 is summarised in Figure 7.5 and Table 7.3. Cohort I increased in size between February and May, achieving its highest growth rate between April and May as the immature adults matured and started to reproduce. Again, Cohort

I reappeared in September and increased in size between September and October, while water temperatures were above 12 °C; growth almost ceased as water temperatures declined (Fig. 7.8). Cohort IIA had the same growth pattern as in Option 1, again, at least twice the growth rate than seen in the other generations. Cohort IIB grew as in Option I until September, but, here, it continued to grow until it died off in October, although the growth rate declined in successive months. Cohort III showed a high growth rate (3.6 mm month^{-1}) between September and October, but then declined in mean weight as water temperatures declined. Growth resumed in February and continued until March. Almost no growth occurred between March and April, the period when this cohort was reproducing.

Table 7.3 Mean growth rates of the 3 cohorts of *Mesopodopsis slabberi*.

Date	Growth rate (mm day^{-1})			
	Cohort I	Cohort IIA	Cohort IIB	Cohort III
OPTION 1				
6/2-17/2	0.03			
17/2-20/3	0.037			
20/3-26/4	0.044			
26/4-12/5	0.066			
12/5-7/6		0.24		
7/6-14/7		0.041	0.085	
14/7-25/9			0.043	0.047
25/9-23/10	0.109			0.119
23/10-22/11	-0.005			
22/11-11/12	0.009			
OPTION 2				
6/2-17/2	0.021			0.032
17/2-20/3	0.061			0.077
20/3-26/4	0.032			0.007
26/4-12/5	0.114			
12/5-7/6		0.24		
7/6-14/7		0.041	0.085	
14/7-25/9			0.043	0.047
25/9-23/10	0.074		0.036	0.064
23/10-22/11	0.003			-0.012
22/11-11/12	0.013			-0.008

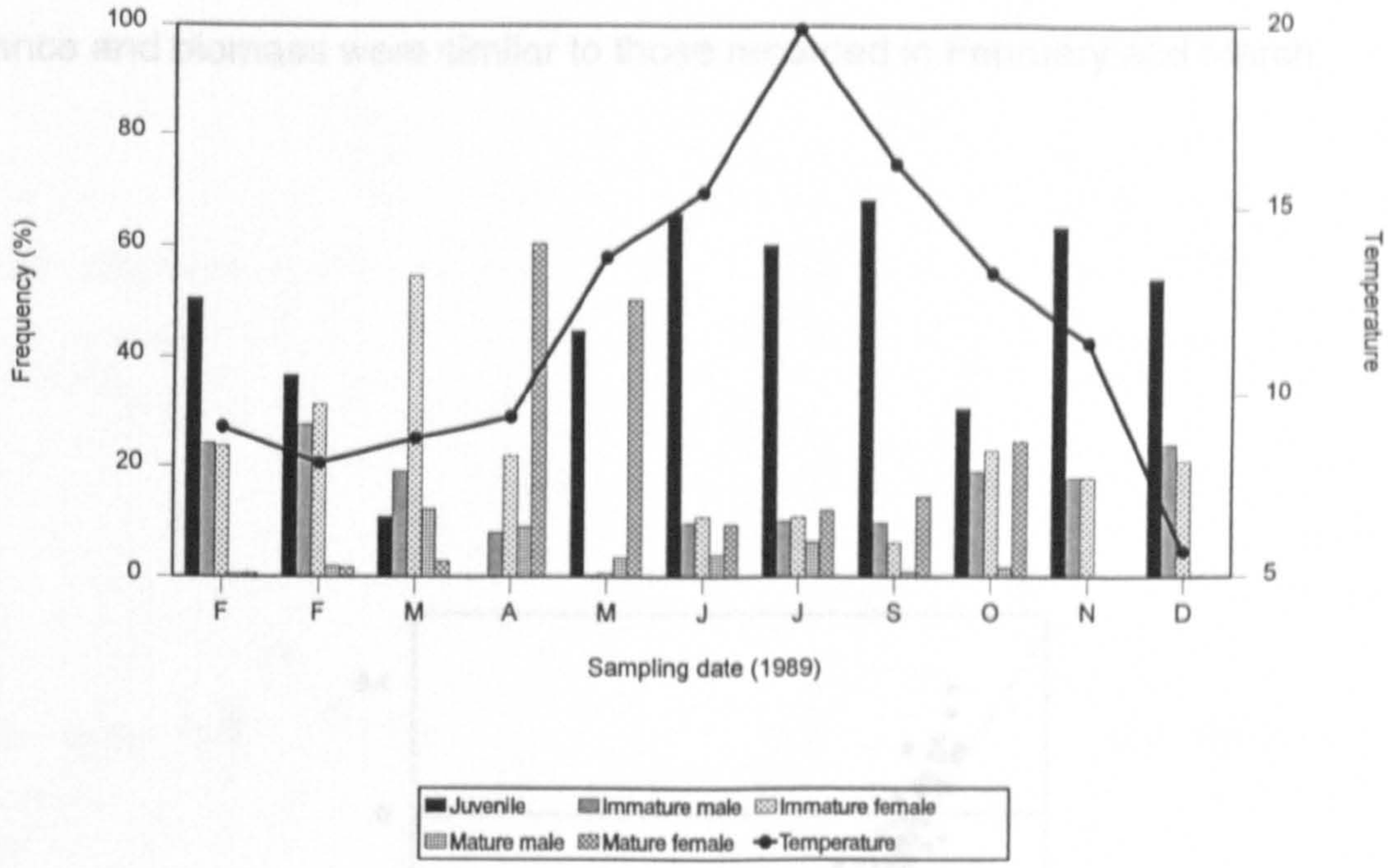


Figure 7.8 Relationship between the life stages of *Mesopodopsis slabberi* and water temperature (°C). (The mature female category includes both ovigerous females and those with empty brood pouches.)

7.1.5 Density and biomass

The relationship between length and dry weight is shown in Figure 7.9. The regression equation produced was used for the calculation of biomass. The seasonal changes in density and biomass are shown in Figure 7.10. There was a clear relationship between abundance, biomass and water temperature. All population densities remained low between February and May (<40 individuals m^{-3}), and increased between May and June. The increase coincided with water temperatures exceeding 10°C, breeding of the overwintering generation and an influx of juveniles into the population. Abundance peaked in September (354 individuals m^{-3}), decreased between September and October, and showed a secondary peak in November (118 individuals m^{-3}). In December, mysid density was at similar levels to that in the early part of the year. There was a peak in the biomass in April, presumably as a result of growth of the overwintering generation (Cohort I), which coincided with rising water temperature (Fig. 7.8). Biomass increased again in June, partly as a result of growth of Cohort II, but mainly due to an influx of juveniles of Cohort IIB into the population.

Biomass continued to rise to a maximum in September (149 mg dry weight m^{-3}). Abundance declined rapidly between September and October, but a secondary peak occurred in November as a result of a final influx of Cohort I juveniles. In December, abundance and biomass were similar to those recorded in February and March.

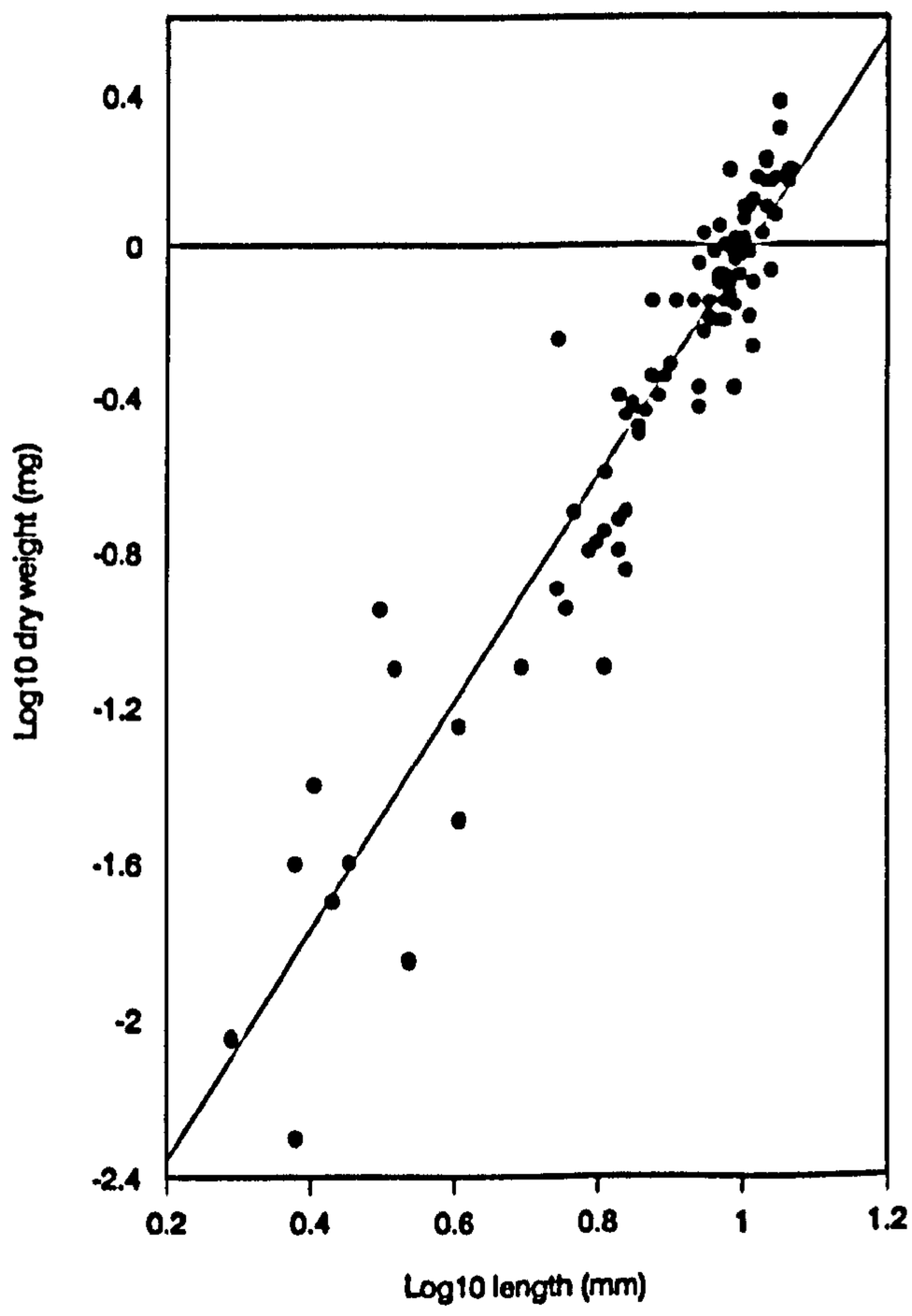


Figure 7.9 Relationship between length (mm) and dry weight (mg) of *Mesopodopsis slabberi*. (Log_{10} dry weight (mg) = 2.913 log_{10} length (mm) - 2.9403, r^2=0.89, n=115.)

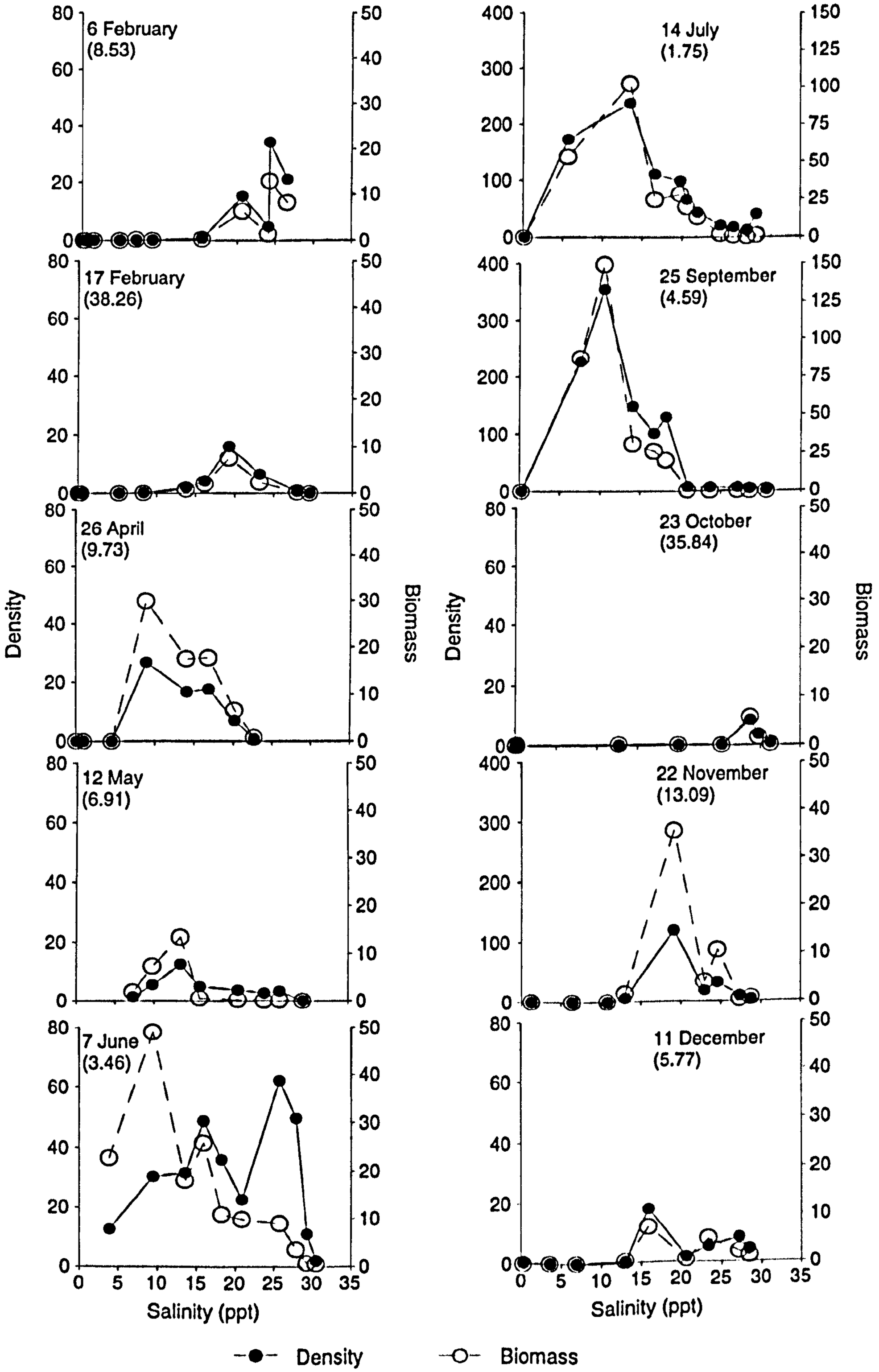


Figure 7.10 Relationship between salinity (‰), density (Nm^{-3}) and biomass (mg dry weight m^{-3}) of *Mesopodopsis slabberi* throughout the year. (The density in March was <1 individual m^{-3}.). Figures in brackets are mean runoff (m^3s^{-1}) on sampling date.

7.1.6 Production

The production estimates for *Mesopodopsis slabberi* are summarised in Table 7.4. The calculation of production was complicated by the fact that *M. slabberi* showed a very patchy distribution over the whole of its range. The estimates of production, using the mean density of all stations, are therefore likely to be an underestimate of total production for the Tamar Estuary. The production estimates for the maximum densities found on each sampling date give an indication of the range of production values over the species' range. The mean total production was 63.39 mg dry weight m^{-3} y^{-1}, although this value more than trebled at the highest densities. The highest values of production were shown by Cohorts IIB and III. These mysids reproduced during the summer and early autumn, and were present at relatively high densities. Despite its high growth rate between May and June, Cohort II had the lowest production value in Option I, and the second lowest in Option 2, mainly because it was present in much lower densities than the other cohorts. The maximum estimate of production of 114 mg dry weight m^{-3} y^{-1}, was achieved by Cohort III, and was due primarily to the very high densities of this cohort in July and September.

Table 7.4 Production (mg dry weight m^{-3} y^{-1}) estimates for *Mesopodopsis slabberi* for each cohort and both life-history options.

	Option 1 - Production		Option 2 - Production	
	Mean of all stations	Maximum	Mean of all stations	Maximum
Cohort I	11.90	31.33	5.60	18.74
Cohort IIA	11.08	32.82	11.08	32.82
Cohort IIB	14.47	63.22	15.76	70.45
Cohort III	25.94	114.08	18.16	76.74
Total	**63.39**	**241.45**	**50.60**	**198.75**

7.1.7 Brood size

Female *M. slabberi* of <9mm were not found to carry eggs. Most sexually mature females carried eggs in May, July and September (Fig. 7.1). There was a significant positive relationship ($p<0.01$) between female length and brood size, although there was considerable variation between the brood size at the same

body length (Fig. 7.11). The maximum brood size was twenty-nine stage 3 embryos retrieved from a July Cohort IIA female of 12.75mm length. Because of the low numbers of females with broods found in most months it was not possible to compare the brood size between the different generations.

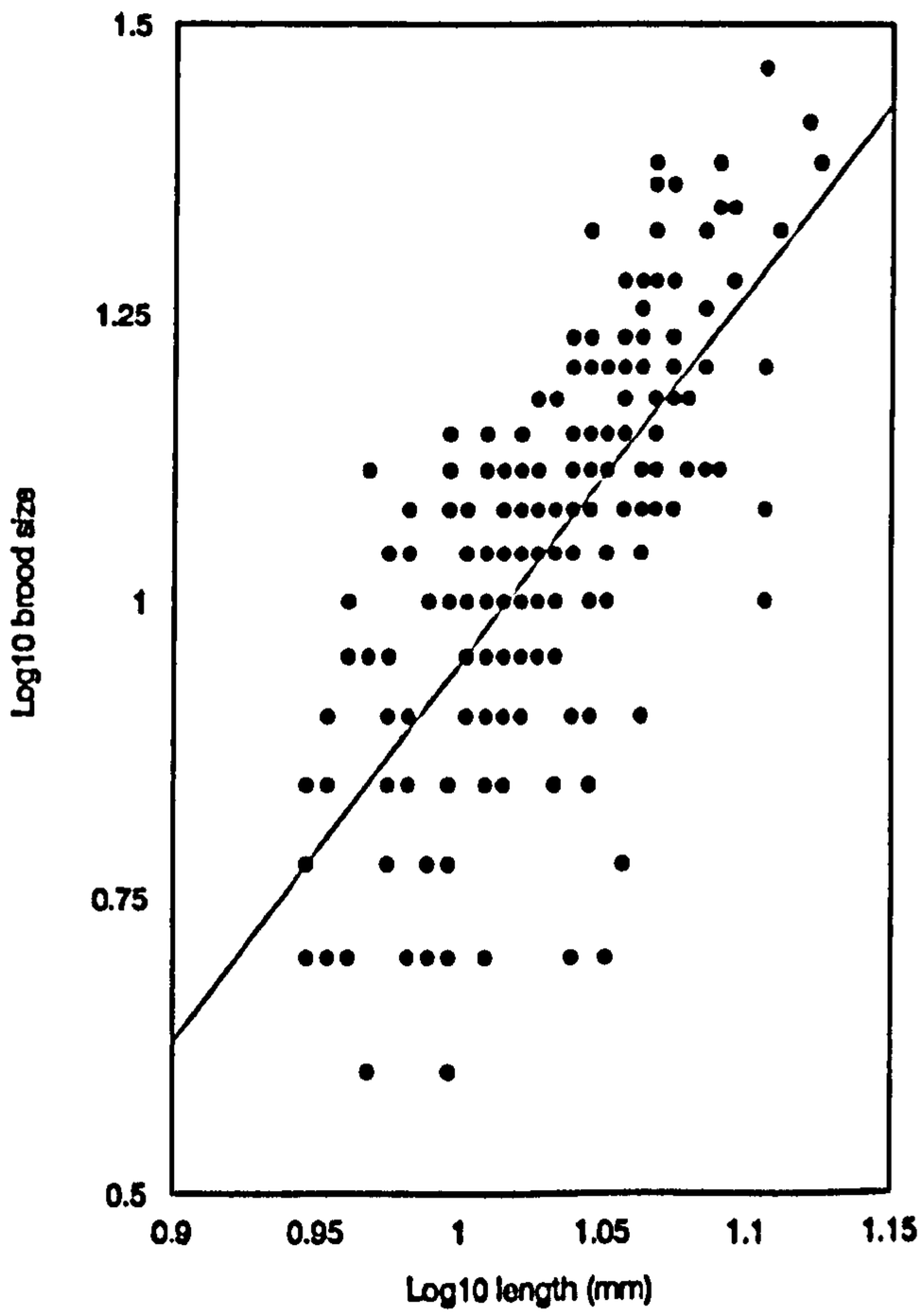


Figure 7.11 Relationship between female body length and brood size of *Mesopodopsis slabberi* (all embryological stages included). (Log_{10} brood size = 3.21 log_{10} length (mm), r^2=0.51, n=195.)

7.1.8 Distribution and correlation with physico-chemical parameters

The previous sections have described the seasonal cycles in abundance, biomass, growth, length and stage composition of *Mesopodopsis slabberi.* The life history and longitudinal distribution of the species is also influenced by a number of physical and chemical factors, including the state of the tide, freshwater runoff, salinity, temperature, suspended matter concentration and day length. The influence of temperature on growth and abundance has been described in §7.1.4 and §7.1.6. The following sections examine the influence on longitudinal distribution of those factors which show the greatest short-term and seasonal variation, namely freshwater runoff, salinity and suspended matter concentration. Salinity and freshwater runoff were considered together as the rate of freshwater runoff largely determined the longitudinal salinity distribution (§5.1.3). Physico-chemical data are described in Chapter 5 and included in Appendix II.

Salinity and runoff

The highest recorded biomass and densities occurred in June, July and September, the lowest runoff months, when *M. slabberi* had an extensive estuarine distribution (Fig. 7.10). In most months, there were several bimodalities in the distribution of *M. slabberi* along the salinity gradient. The lowest total densities and biomass of *Mesopodopsis slabberi* were recorded in mid-February and during October and March (when abundance was < 1 m^{-3}). These dates coincided with higher than average runoff and steeper salinity gradients in the upper estuary (Figs 5.3 and 5.5). Figure 7.10 shows that the main part of the population of *M. slabberi* was found between salinities of 5 and 30‰ on all sampling dates. Between February and April, there appeared to be an upstream migration of the main population into lower salinities (from 25-10 ‰). In June, and despite the low runoff in this month, the highest abundance occurred around 25 ‰; between June and September, the main abundances were again recorded in lower salinities The link between the density of *M. slabberi* and salinity was examined by plotting the distribution of the different life-history stages against salinity and by using Spearman's rank correlation (Table 7.5 and Fig. 7.12). Monthly peaks in the density distribution can be attributed to successive peaks of different life-history stages of *M. slabberi.* In early February, there were relationships between salinity and the total density, density of juveniles and of immature adults (Table 7.5). In early February, there were two peaks in the distribution of the juveniles and immature adults at 20.7 and 24.3‰. In mid-February, a peak in the total density, density of juveniles and immature adults occurred at around 20‰, and the bulk of

the population was found within a salinity range of 15-30‰. There was no significant relationship between density and salinity for any life-history stage (Table 7.5).

Table 7.5 Spearman's rank correlation between salinity and density (Nm^{-3}) of each life-history stage of *Mesopodopsis slabberi* at each sampling date (ns=not significant, figures in brackets are number of samples (n)).

Date	Spearman's Rank (r_s)					
	Juvenile	Immature male	Mature male	Immature female	Mature female	Total
6 February 1989	0.893 (7) p=0.01	0.893 (7) p=0.01	0.211 (4) ns	0.800 (5) p<0.05	-	0.893 (7) p=0.01
17 February 1989	0.371 (6) ns	-0.100 (5) ns	-	0.700 (5) ns	-0.211 (4) ns	0.371 (6) ns
20 March	-	-	-	-	-	-
26 April 1989	-	-0.100 (5) ns	-0.100 (5) ns	-0.700 (5) ns	-1.000 (5) p=0.01	-0.900 (5) p=0.05
12 May 1989	0.486 (6) ns	-	0.600 (4) ns	-	-0.821 (7) p<0.05	-0.178 (7) ns
7 June 1989	0.067 (9) ns	-0.678 (9) p<0.05	-0.762 (9) p<0.05	-0.667 (9) p<0.05	-0.890 (10) p<0.01	-0.127 (10) ns
14 July 1989	-0.818 (10) p<0.01	-0.983 (9) p<0.01	-0.709 (10) p<0.05	-0.733 (10) p<0.05	-0.960 (10) p<0.01	-0.915 (10) p<0.01
25 September 1989	-0.976 (10) p<0.01	-0.881 (8) p<0.01	-0.200 (6) ns	-0.833 (8) p=0.01	-0.964 (7) p<0.01	-0.976 (10) p<0.01
23 October 1989	0.312 (11) ns	0.740 (10) p<0.05	-	-	0.513 (10) ns	0.488 (11) ns
22 November 1989	0.143 (7) ns	-0.600 (6) ns	-	-0.371 (6) ns	-	0.143 (7) ns
11 December 1989	0.703 (9) p<0.05	0.257 (6) ns	-	0.428 (6) ns	-	0.733 (9) p<0.05

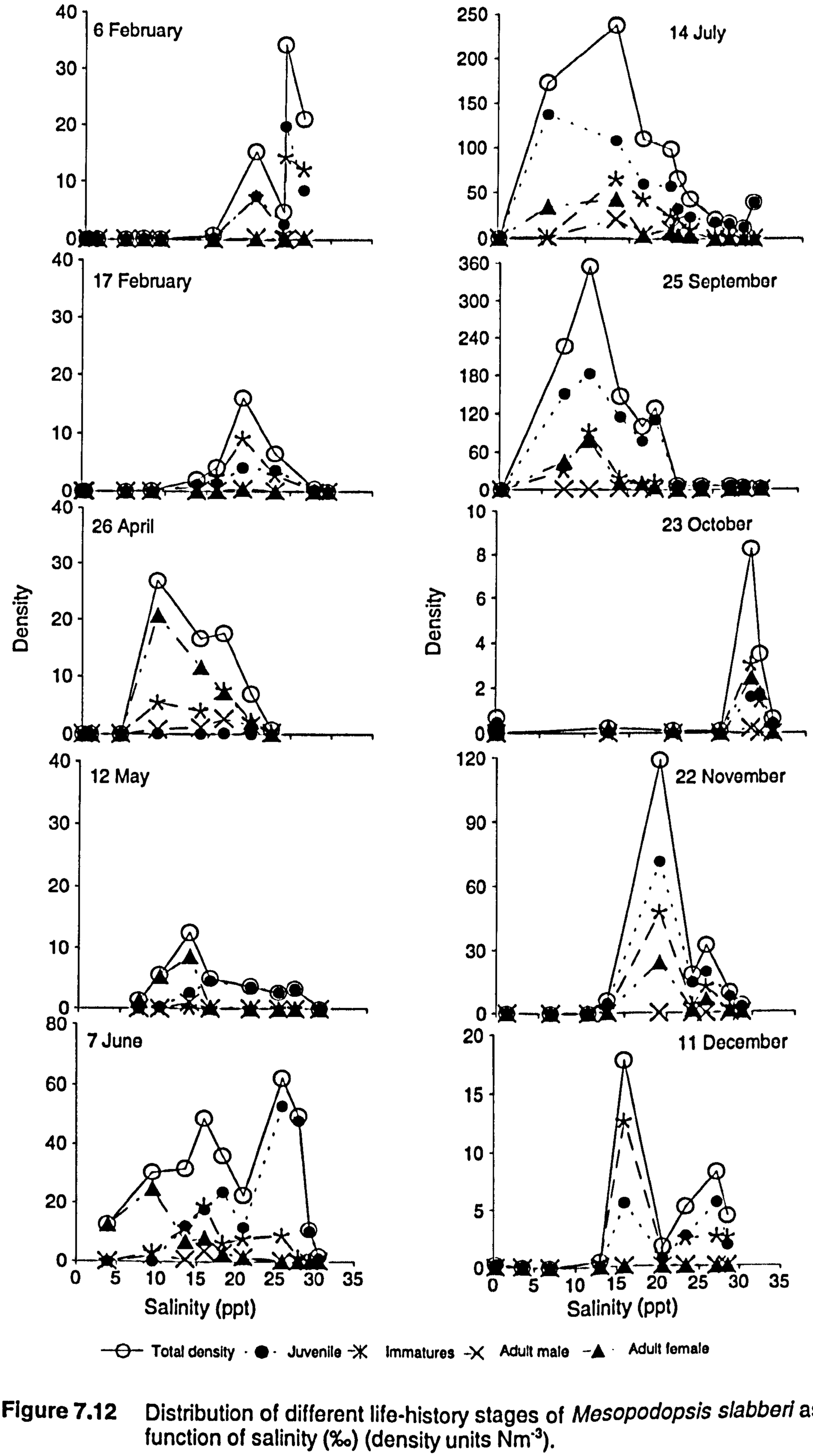


Figure 7.12 Distribution of different life-history stages of *Mesopodopsis slabberi* as a function of salinity (‰) (density units Nm^{-3}).

In March, few *M. slabberi* were captured, the majority at Stations 10 (20.4‰) and 11 (15‰). In April, two peaks in the density distribution were identified (at 9 and 16.9‰) (Fig. 7.12). Mature females accounted for most of the peak in density at 9‰, and were significantly more abundant than at other salinities (Table 7.5). At 16.9 ‰, the peak was more-or-less equally ascribed to adult females, immature stages and adult males (Fig. 7.12). In May, the density peak (13.4‰) was due to a higher abundance of mature females at this salinity (Table 7.5). In fact, in May, mature females had a very narrow distribution, between 7.3 and 13.4‰, and there was a significant negative relationship between density and salinity (Table 7.5). There were two density peaks in June. The first at 16‰ was comprised mainly of juvenile and immature stages, the second at about 25.8‰ mainly of juveniles. The maximum density of mature males coincided with the second peak. Except for juveniles, the population densities of all life-history stages were negatively correlated with salinity (Table 7.5). The distribution in July differed from that in June in that the peak densities of juveniles coincided with the peaks of the distribution of mature females and males. Densities of all life-history stages in July were negatively related to salinity. The distribution in September was similar to that in July although the salinity band occupied by the population was slightly narrower (5-25‰). There was a significant increase in the density of juveniles, immature males, immature females and mature females with decreasing salinity in September (Table 7.5). In October, there was very high runoff and low numbers of *M. slabberi* were captured. The entire population was found within a very narrow salinity range of between 25 and 30‰. In November and December, runoff was relatively low and the population was distributed over the range 15-30‰, although again, bimodal distributions of all stages present were observed in these months. Only in December was there a relationship between salinity and life-history stage for juveniles.

To examine more closely the salinity distribution of the different cohorts, frequency histograms of the percentage of the estuarine population of juvenile, immature and mature individuals were produced for each month in each of the six 5‰ salinity bands (Fig. 7.13). These were considered together with length-frequency distributions plotted within each salinity band for each sampling date (Figs 7.14a-k). Cohorts were identified according to the size-frequency distributions in Figure 7.1. Only Option 1 was considered here. It would appear from this series of figures that there was some degree of spatial separation between the three cohorts in the population. In February (Fig. 7.15 a&b), the length-frequency distribution was similar in each of the salinity bands, and corresponded to that seen for Cohort I in the same months (Fig. 7.1). Examination of Figure 7.13 showed that the bulk of the population was confined to the two highest salinity bands. An apparent up-estuary migration occurred between February and April (Figs 7.14 a-d). The whole of Cohort I was represented in all salinity bands, but the main abundance occurred in salinity bands covering the range 5-19.9‰. In May, there was a clear separation of size classes

on the basis of salinity (Fig. 7.14e). In the salinity bands covering the range 5-9.9‰, the length-frequency distribution corresponded to that of Cohort I, with individuals in the size range 10-13mm. In higher salinities, the length-frequency distribution corresponded to that of Cohort IIA and consisted almost entirely of juveniles. The situation in June was somewhat different (Fig. 7.14f). In the two lowest salinity bands, the population consisted entirely of large (>11mm) females which corresponded with the larger Cohort IIA females. In the salinity bands covering the range 10-25‰, Cohort IIB was also present and about 50% occurred in the 5-19.9‰ salinity band. The juveniles of Cohort IIB formed the greatest percentage of individuals in the upper two salinity bands, and were more abundant in salinities >25‰ (*c.* 50% of juveniles in June occurred here (Fig. 7.13)). In July *c.*65% of the immature Cohort IIB and *c.*55% of mature Cohort IIA occurred at salinities between 10-14.9‰ (Fig. 7.14g). Cohort IIB was not found in salinities <9.9‰, whilst the juvenile Cohort III was evenly distributed in terms of abundance in salinities between 5-25‰ (Fig. 7.13). Cohort IIA was not found in salinities of >19.9‰. In September, the mysid distribution was similar to that in July, with the main abundance of juvenile and mature individuals in the 10-14.9‰ salinity band (Fig. 7.14h). Juveniles (Cohort I) dominated the samples in all salinity bands, and were fairly evenly distributed between the three bands encompassing the range 5-19.9‰ (Fig. 7.13). Cohort IIB and III were not found in appreciable numbers below 19.9‰. In October, over 90% of individuals were in salinities >25‰, but few mysids were captured (Figs 7.13 & 7.14). In November and December, all the mysids were found in salinities of >15‰ (Figs 7.14 j&k).

In summary, it would appear that in May and June there is a clear division between the largest sized cohorts (Cohort I, May; Cohort IIA, June) concentrated in lower salinity regions and recently released juveniles (Cohort IIA, May; Cohort IIB, June) in higher salinities. In July and September, there was less separation between the cohorts, but larger individuals were concentrated into a narrower salinity range, at slightly lower salinities, than the smaller juveniles. In October, this pattern of distribution was broken down in the upper estuary due to the high runoff and steep salinity gradients which caused a downstream shift of all life-history stages. The juveniles and immature stages of the overwintering generation were found in higher salinities in November and December, and started to migrate into lower salinity regions in March and April as water temperatures increased and they matured and started to reproduce. Consideration of the lower estuary data suggests that while longitudinal shifts in the population occur, *M. slabberi* remains in the estuary throughout the year.

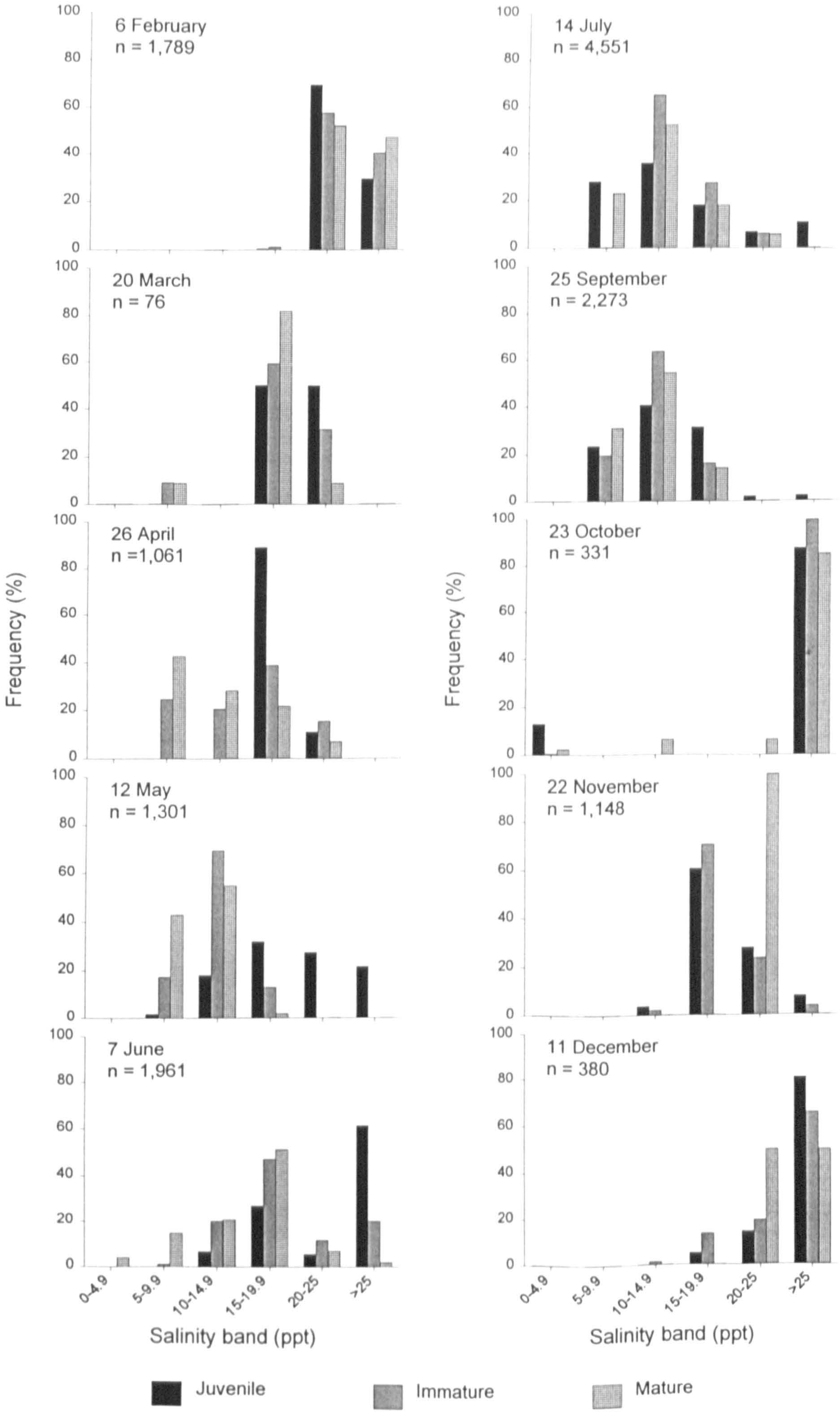
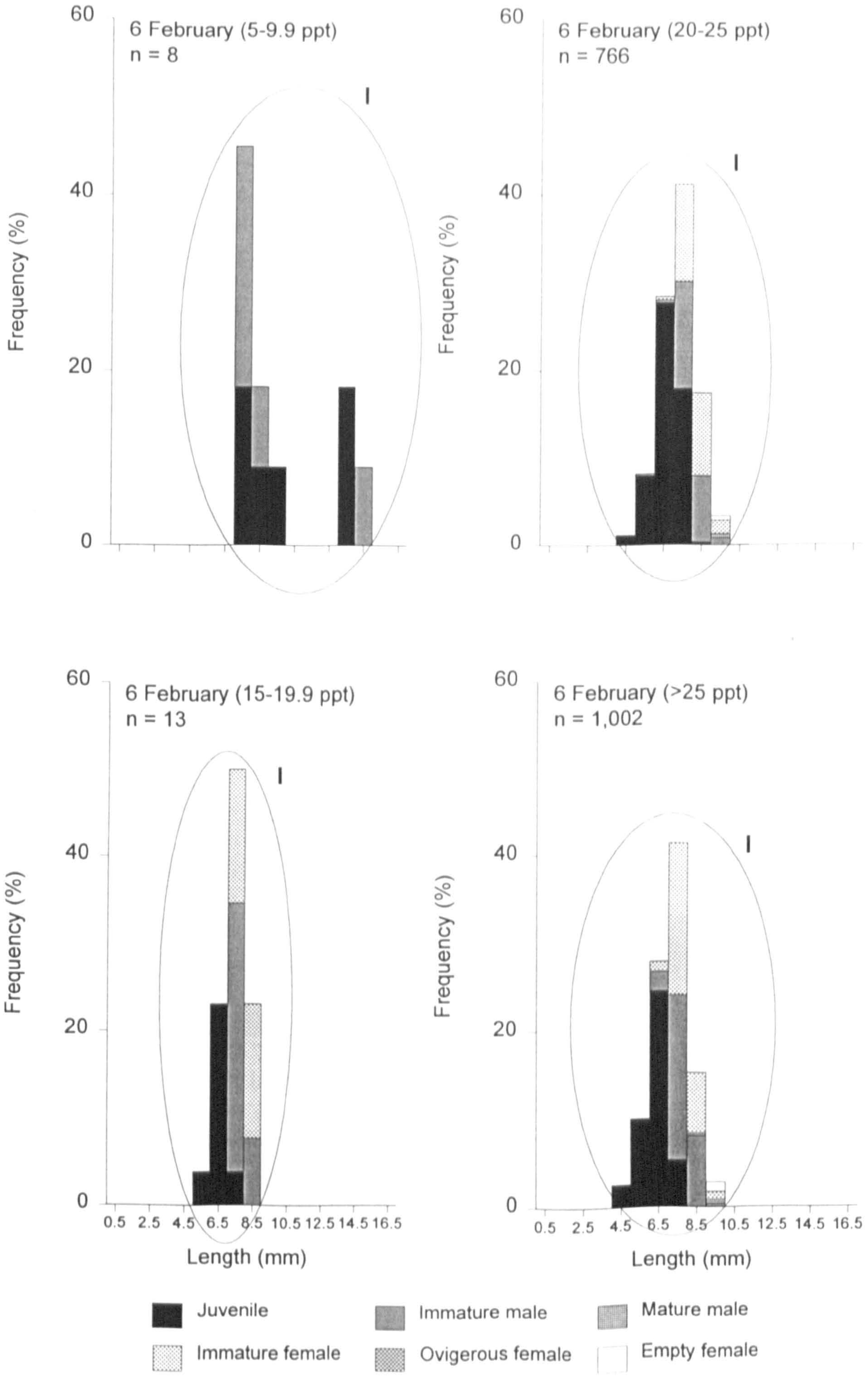


Figure 7.13 Distribution of juvenile, immature and mature *Mesopodopsis slabberi* in different salinity bands as percentages of the whole estuary population of each life stage.



Figs 7.14a Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (February 1989). (Salinity bands not shown are where n < 8.)

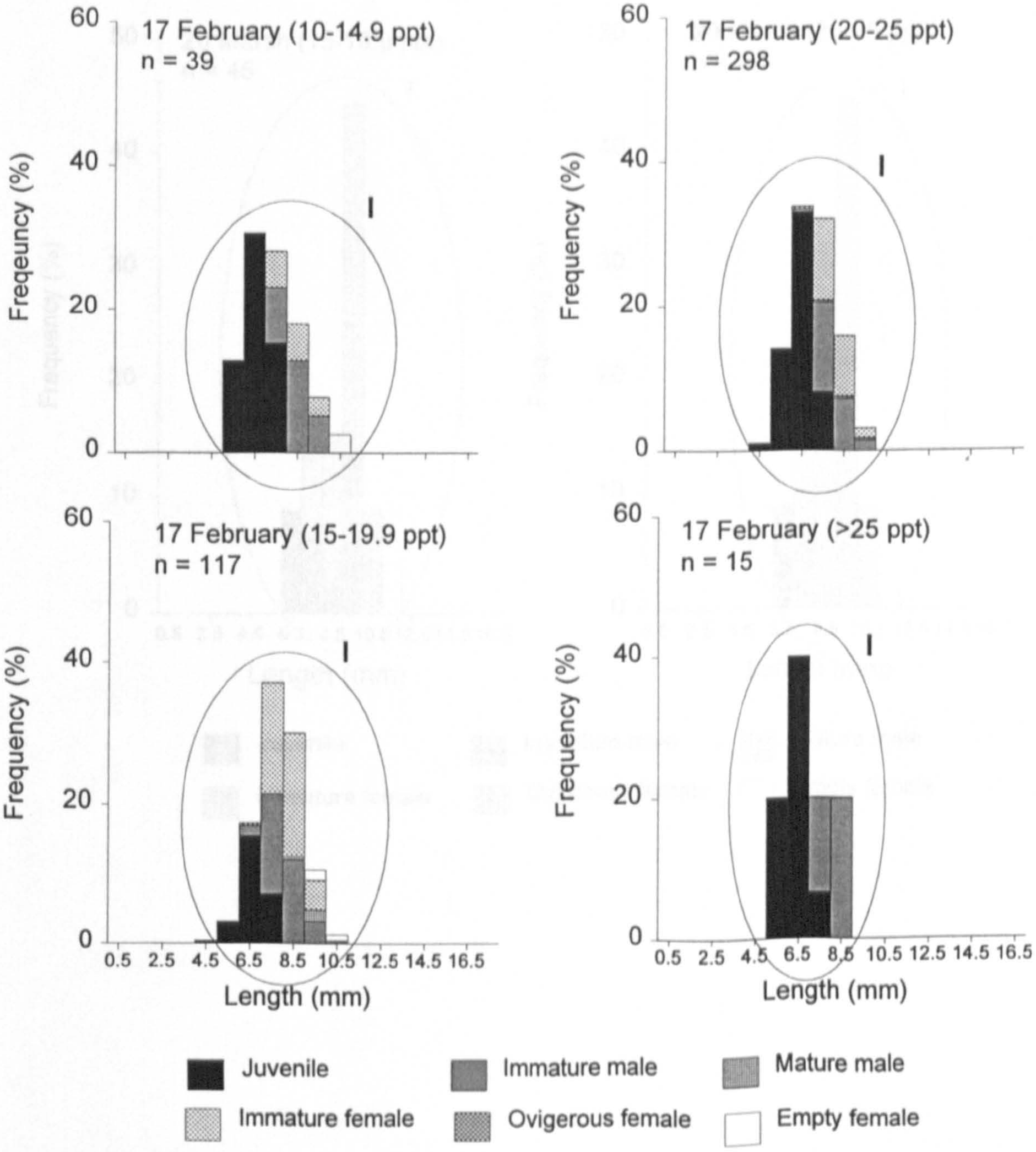


Figure 7.14b Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (February 1989). (Salinity bands not shown are where n < 8.)

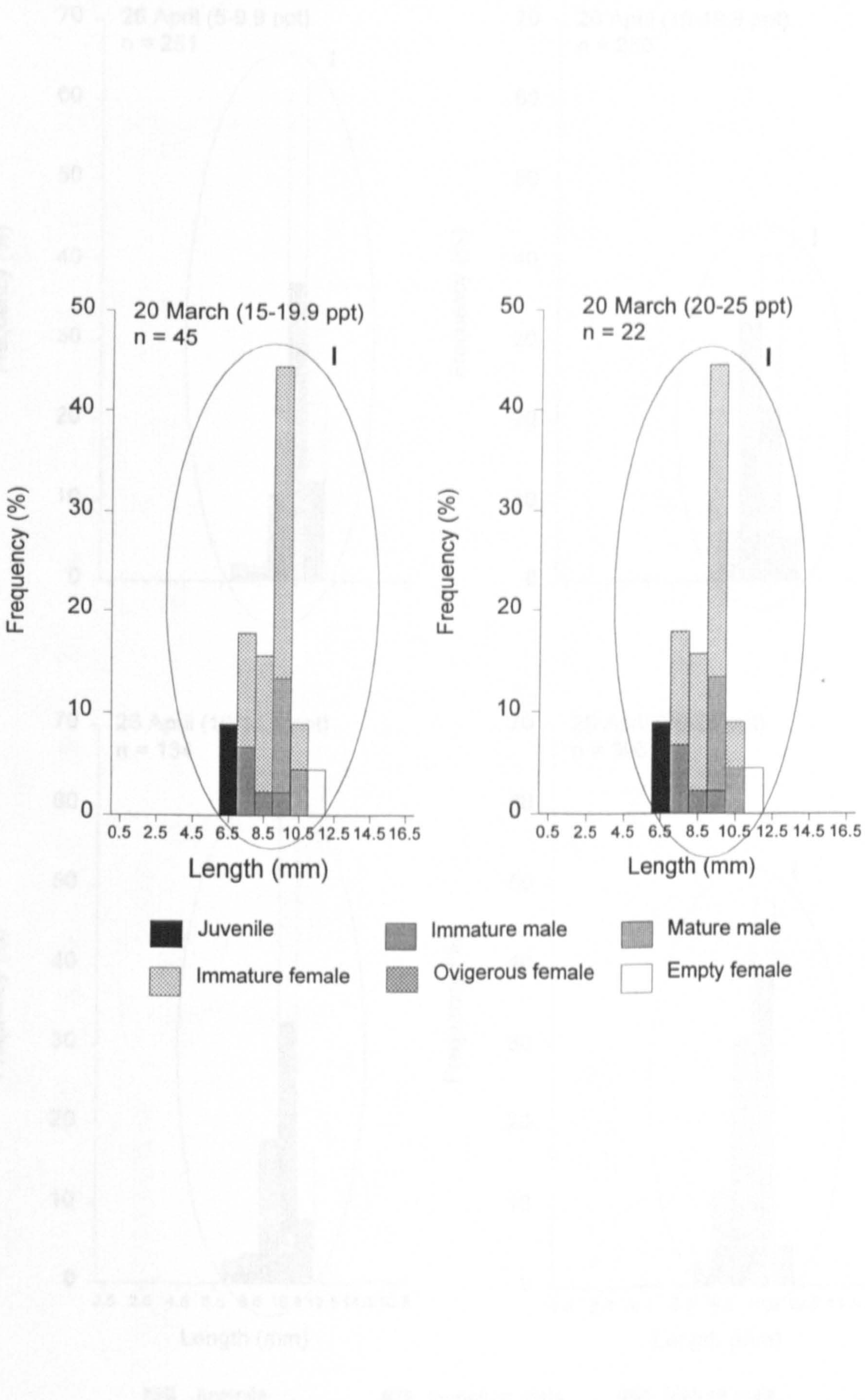


Figure 7.14c Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (March 1989). (Salinity bands not shown are where n < 8.)

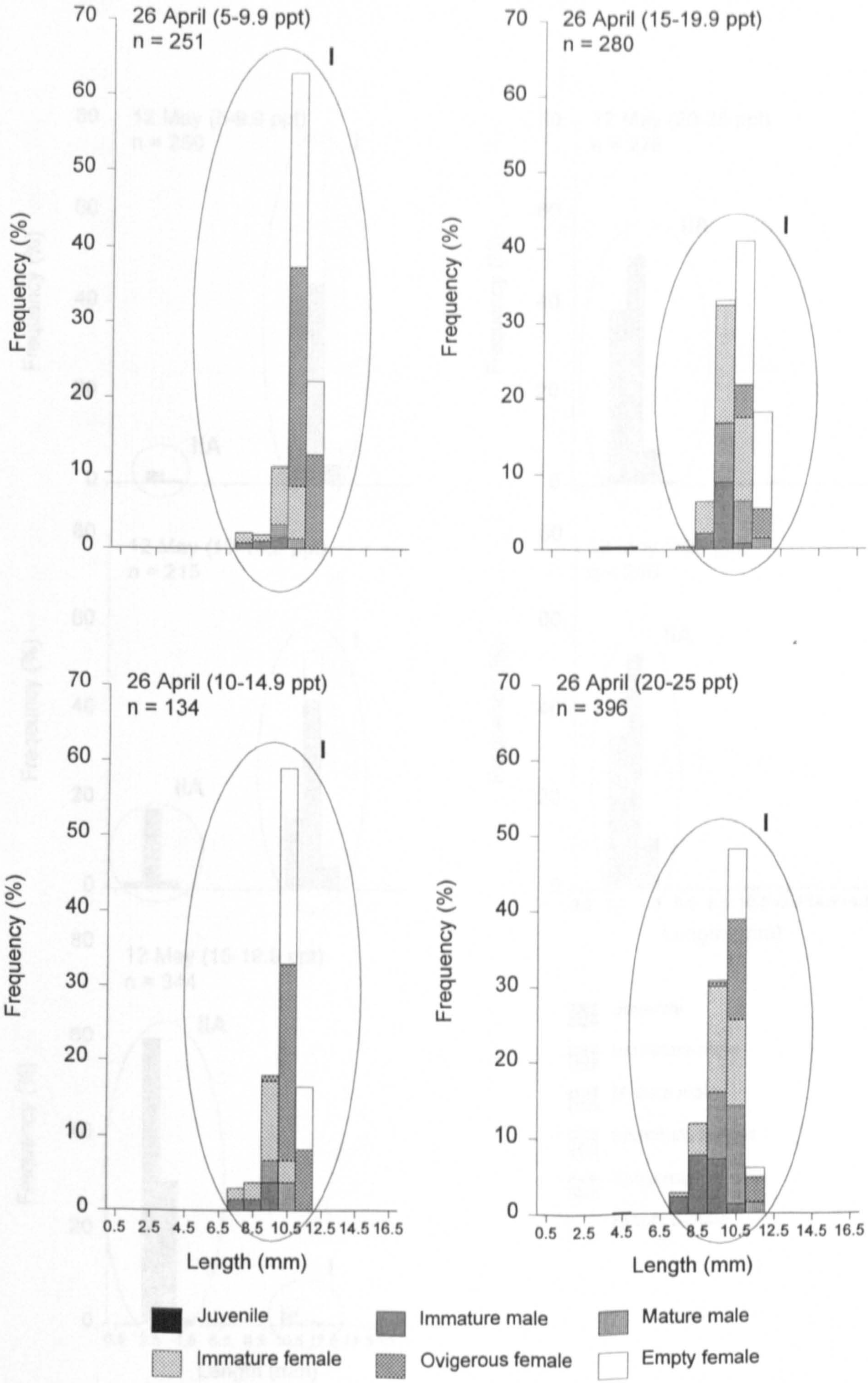


Figure 7.14d Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (April 1989). (Salinity bands not shown are where n < 8.)

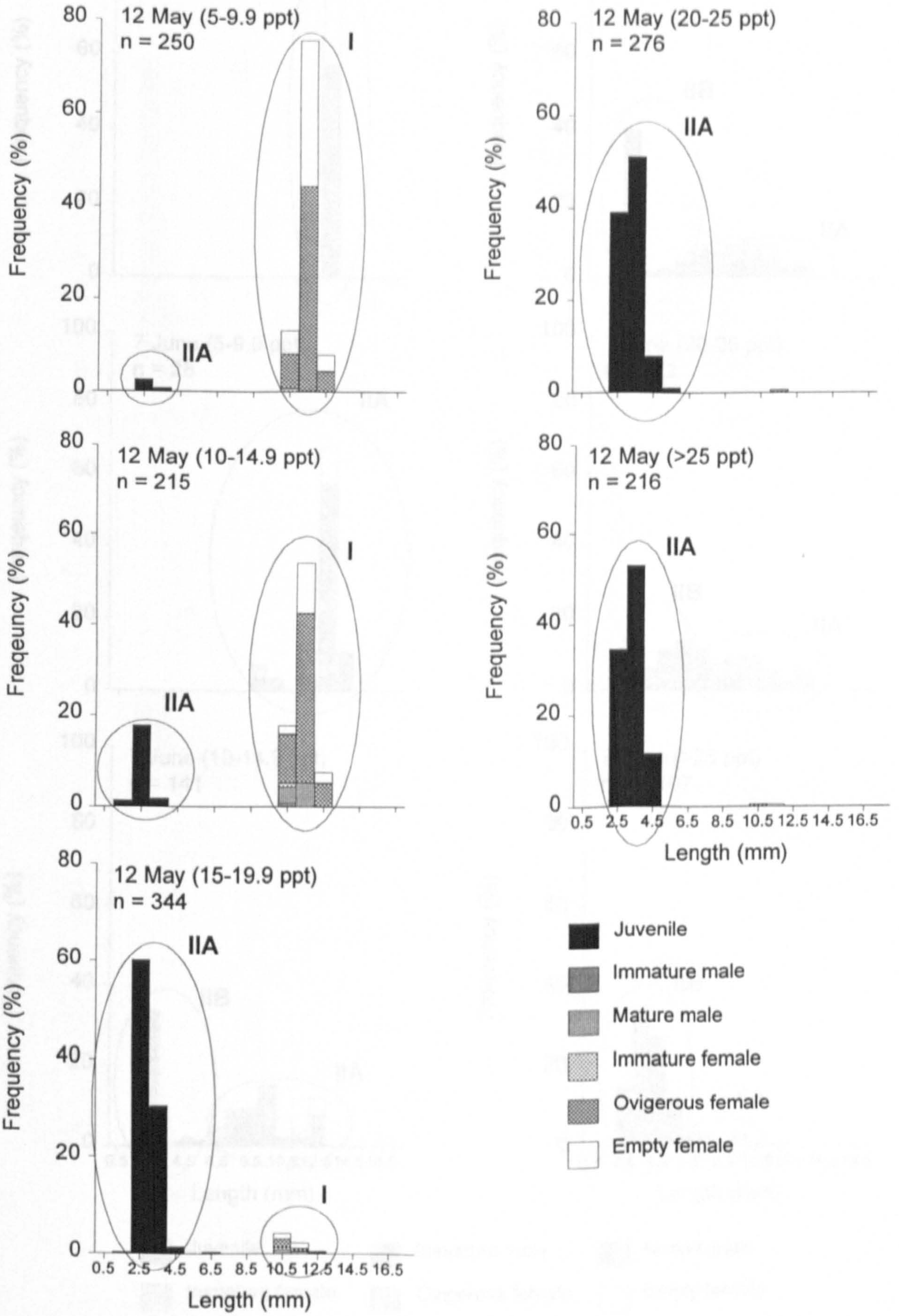


Figure 7.14e Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (May 1989). (Salinity bands not shown are where n < 8.)

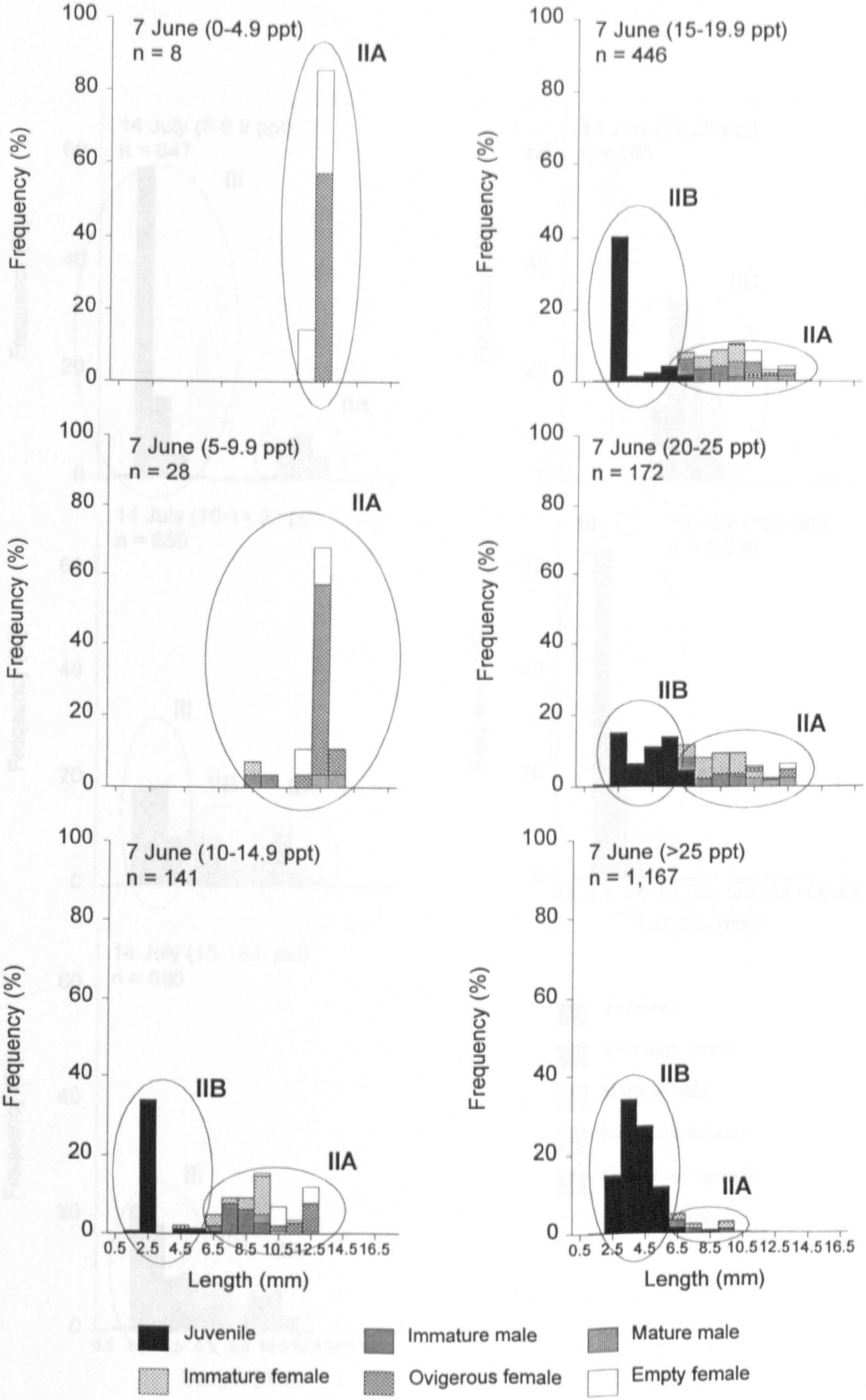


Figure 7.14f Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (June 1989). (Salinity bands not shown are where n < 8.)

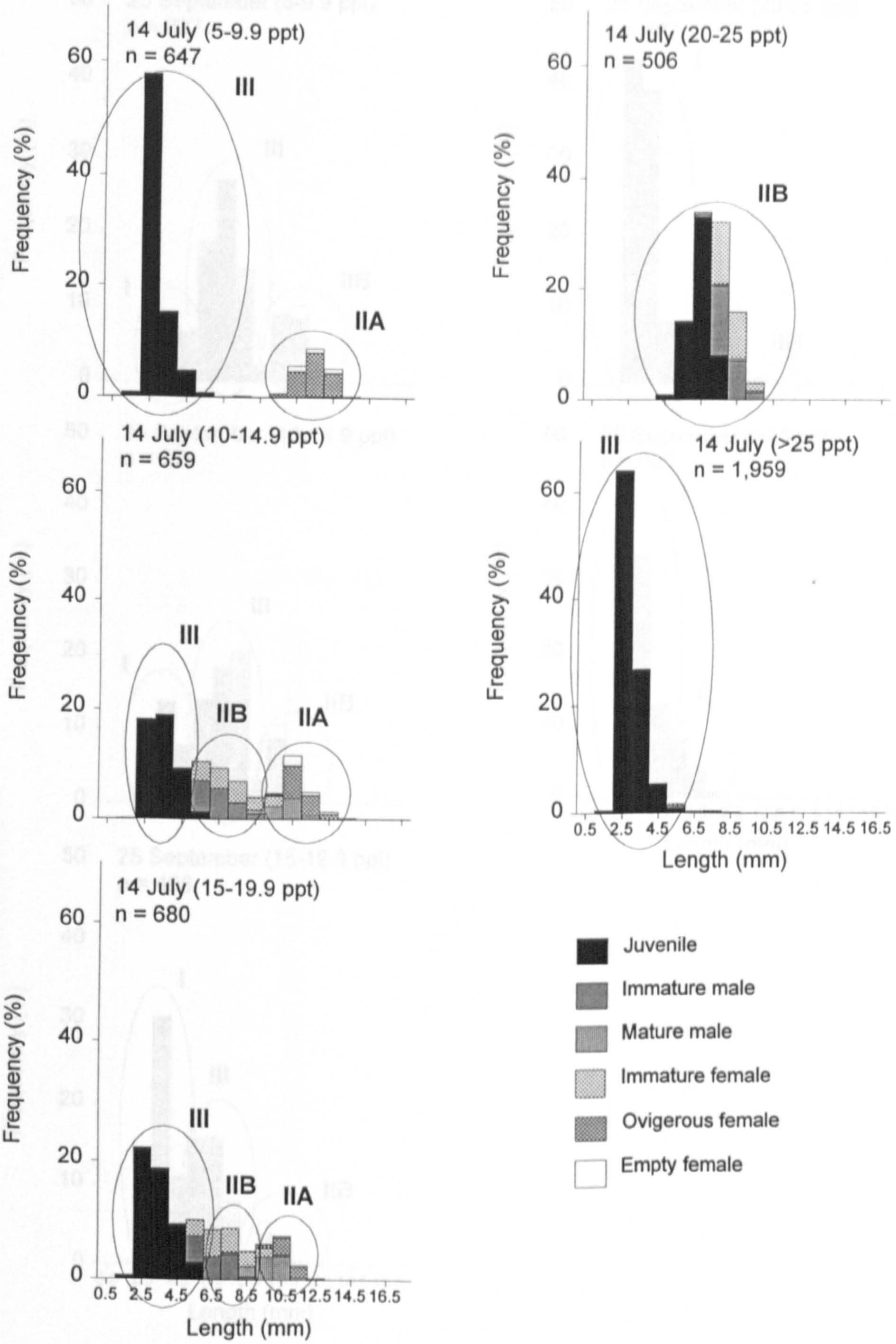


Figure 7.14g Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (July 1989). (Salinity bands not shown are where n < 8.)

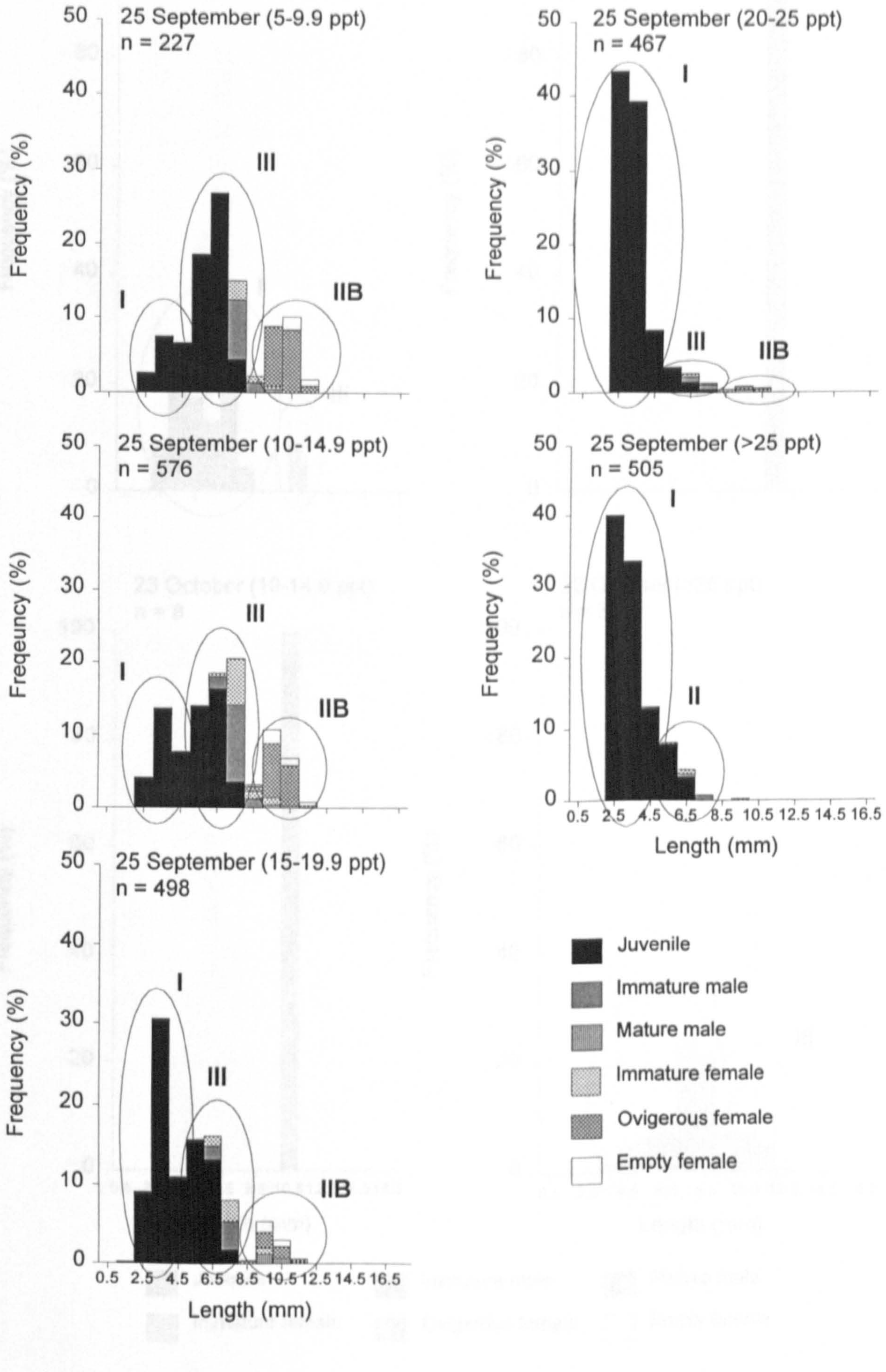


Figure 7.14h Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (September 1989). (Salinity bands not shown are where n < 8.)

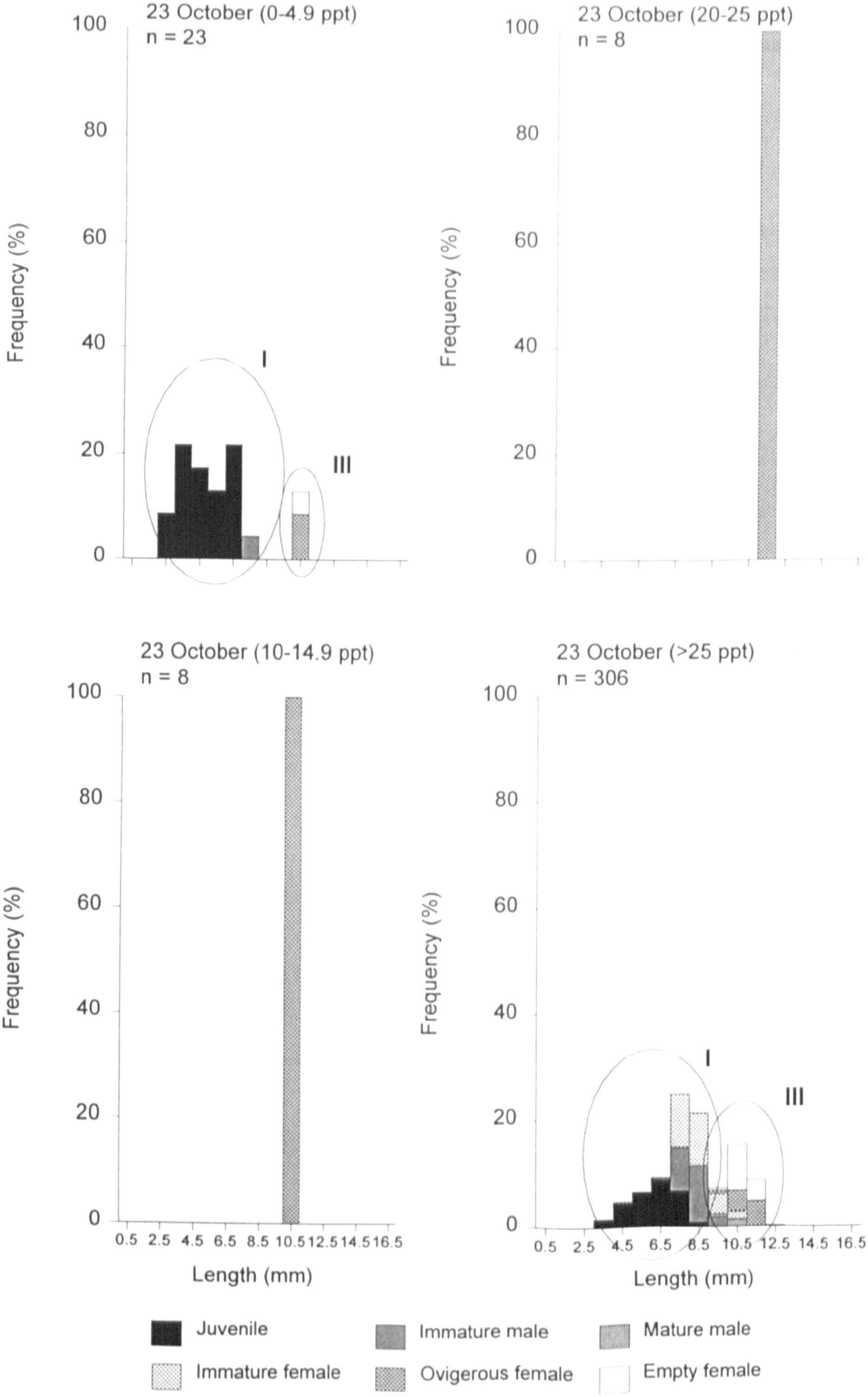


Figure 7.14i Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (October 1989). (Salinity bands not shown are where n < 8.)

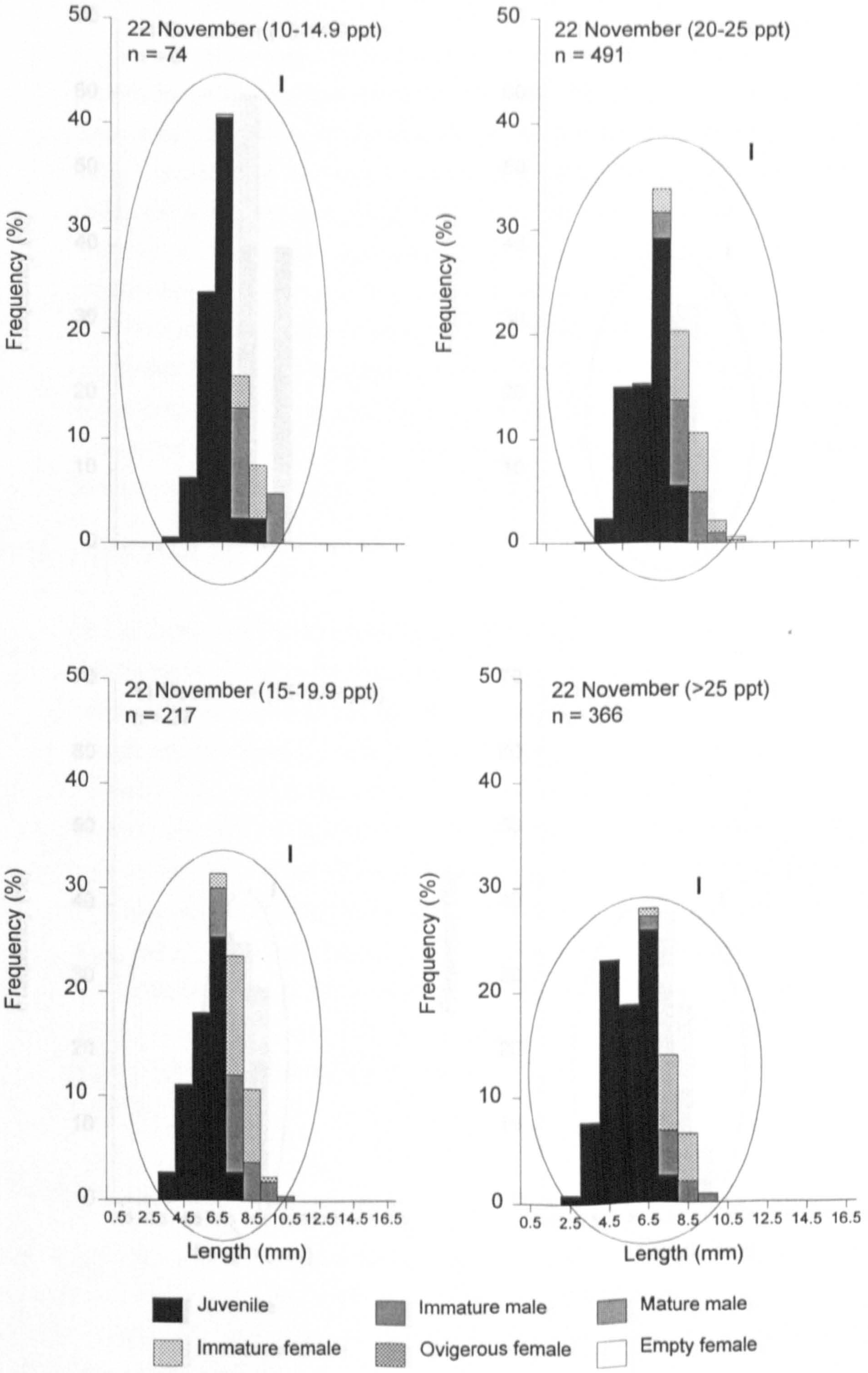


Figure 7.14j Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (November 1989). (Salinity bands not shown are where n < 8.)

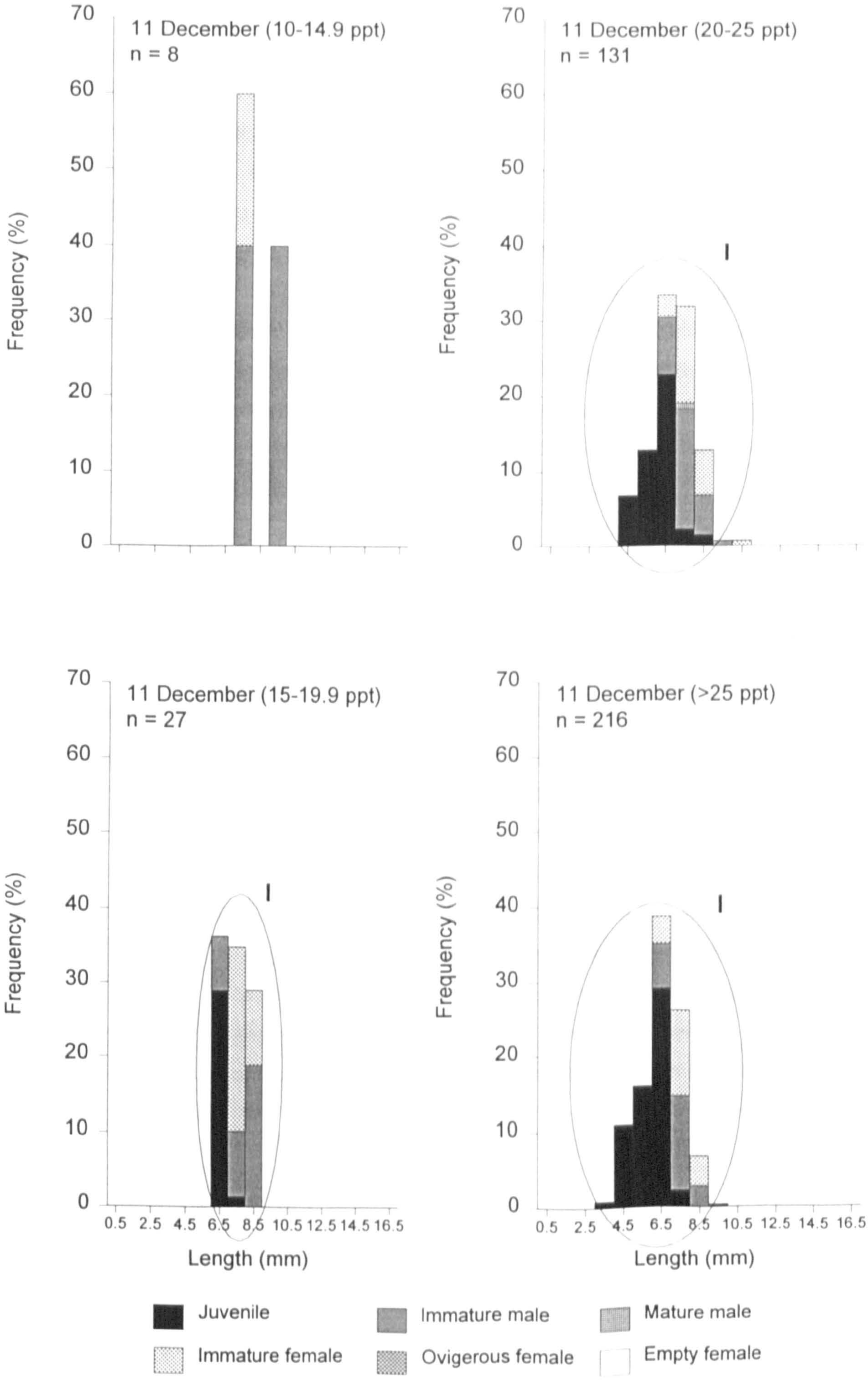


Figure 7.14k Length-frequency distribution of *Mesopodopsis slabberi* in different salinity bands (December 1989). (Salinity bands not shown are where n < 8.)

Turbidity

Suspended matter concentrations were inversely related to salinity in four of the six months for which they were measured (Fig. 5.6). Only in early February, April and June were very high levels of suspended matter concentration recorded with very steep gradients of increase in suspended matter concentrations as salinity declined. In other months, suspended matter concentrations were relatively low and did not vary much with salinity. In all months, the greatest *M. slabberi* abundances were recorded where suspended matter concentrations were <800 mg/l. However, there was no clear relationship between turbidity and abundance of *M. slabberi* (Fig. 7.15). Organic content (mgl^{-1}) was highest in the upper parts of the estuary in the region of the turbidity maximum (Fig. 5.6). A greater, more readily available, food supply was available for individuals which could remain in these zones of the estuary.

7.1.9 Biological factors

Biological factors (*eg.* competition) can also influence the distribution of species. Four species of mysid have been identified in the Tamar Estuary and possible interactions between the two major species, *Mesopodopsis slabberi* and *Neomysis integer* are examined in Figure 7.16. In February, June and October, there were marked differences in the distribution of the two species in relation to salinity. *Neomysis integer* had a wider salinity range than *M. slabberi* and was also found at substantially lower salinities than was *M. slabberi*. In April and December, there was considerable overlap in the distributions of the two species between 15 and 20‰, although the upper limit of *M. slabberi*, remained in higher salinities than that of *N. integer*. The low numbers of *N. integer* in other months made it impossible to compare distributions. The results suggest that *N. integer* had a much wider salinity distribution than *M. slabberi* in most months for which sufficient *N. integer* data were collected.

7.2 Discussion

Mesopodopsis slabberi was more successfully sampled than *Neomysis integer* in this study. On most sampling dates all life-history stages in the population were sampled, often at high abundances and, unlike the situation for *N. integer*, all size classes were also represented in the samples.

The patterns of reproduction and succession of generations are often difficult to determine in mysid species which produce more than one generation per year. Many of these

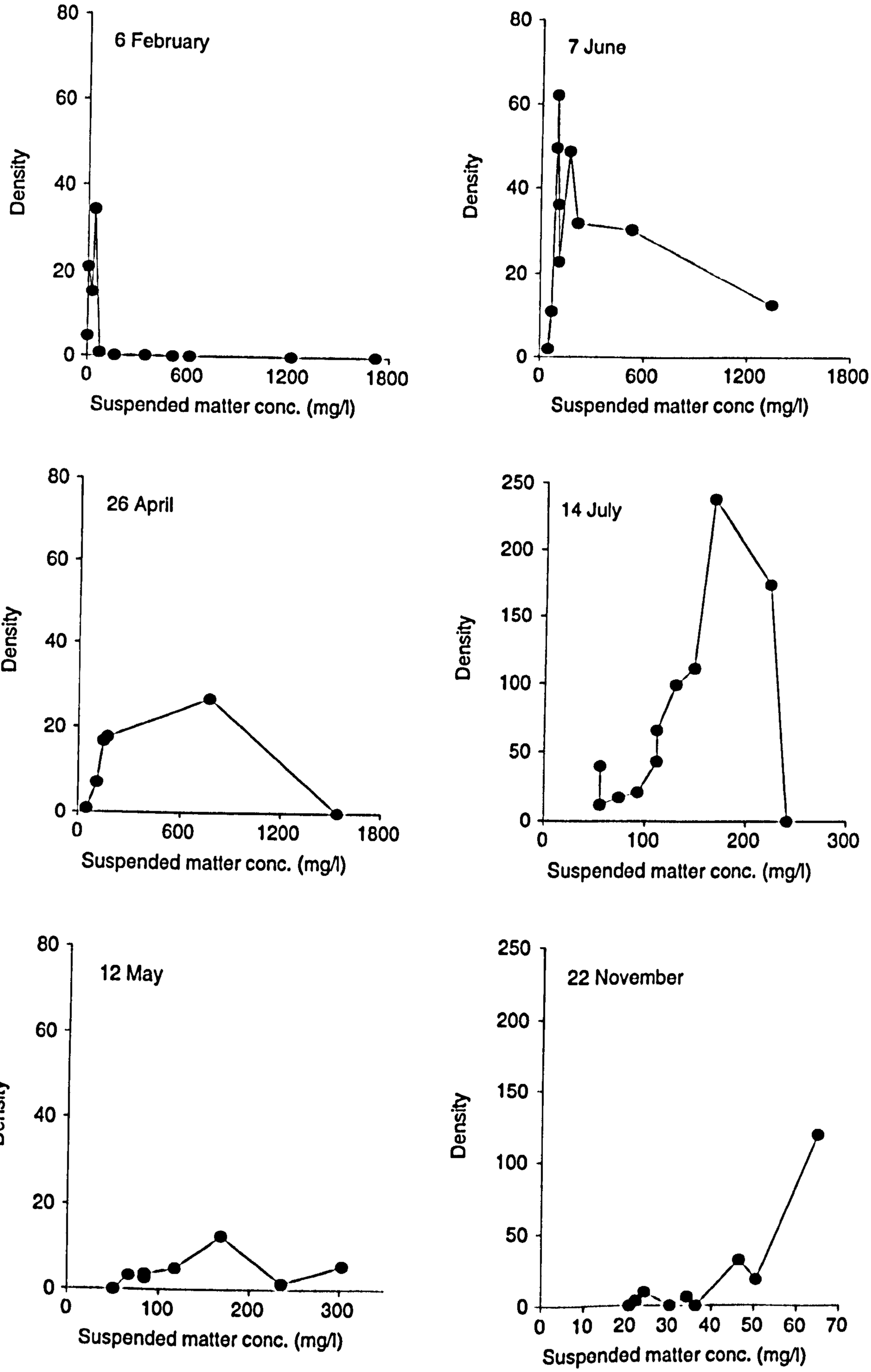


Figure 7.15 Relationship between turbidity (mg/l) and density (Nm^{-3}) of *Mesopodopsis slabberi* throughout the year (1989). (Months shown are those where the population density was > 1 individual m^{-3} and for which turbidity was recorded.)

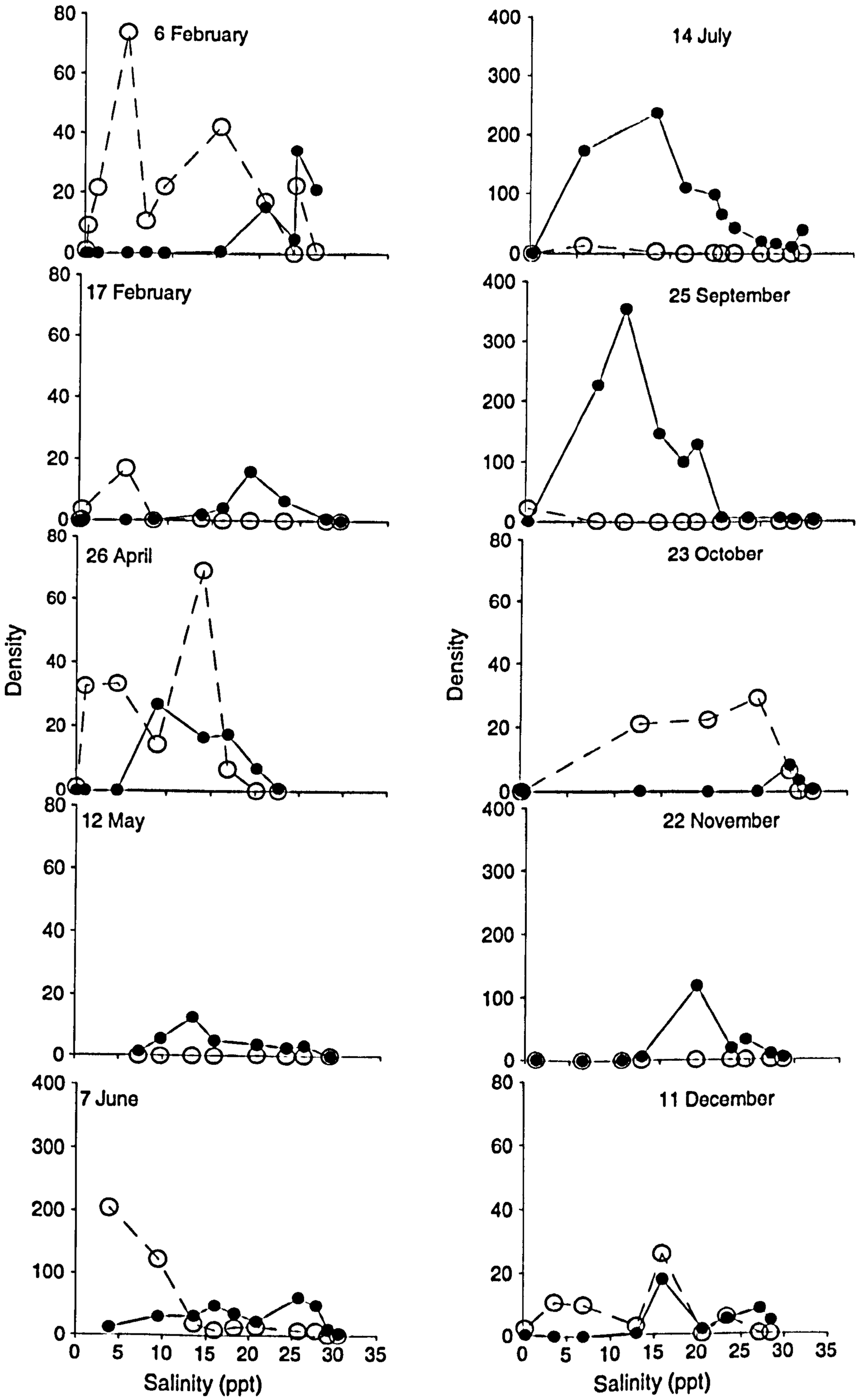


Figure 7.16 Distribution of *Mesopodopsis slabberi* and *Neomysis integer* (Nm^{-3}) in relation to salinity.

species breed continuously throughout the year and it is only when there is a degree of synchronous breeding, producing identifiable modes in the length-frequency histograms, that the brood frequency can be determined. *Neomysis americana* (Smith) in Passamaquoddy Bay, Canada, has two generations per year and the females of each generation are capable of producing two or three broods. The generation frequency is clear in *N. intermedia*, however, because there are two main peaks of recruitment during the year, one in summer and the other in autumn, which together combine to form the overwintering generation (Pezzack and Corey, 1979). There have been few studies investigating the life history of *M. slabberi* and no information on growth rate was found in the literature. Blegvad (1922) and Macquart-Moulin (1965) identified two generations per year in *M. slabberi* from Danish and French waters respectively, and Zatkutskiy (1970, in Mauchline, 1980, Table XXXIV) found the same pattern for *M. slabberi* from the Azov Sea, Russian Federation. In the Tamar Estuary, *M. slabberi* breeds from April to November and has either two or three generations a year, depending on interpretation. An overwintering generation releases young in May, to form a fast line of development which, in Option I, may produce a further two generations and overwinter to form the slow line of the following year. The overwintering generation also produces young in June to form a slow line which produces a further single generation. In Option I, this forms the fast line of the following year, while in Option II it forms the slow line of the following year. Alternating early and late-breeding generations have also been recorded for the longer-lived mysid *Mysis relicta* (Lovén) in Lake Pääjärvi, southern Finland by Hakala (1978). Greenwood *et al.* (1989) estimated the brood development time of *M. slabberi* to be *c.*16 days at 15 °C. This development time is consistent with the fast development and brood production time seen in Cohort IIA in this study. Option I identified the possibility of a fast line of development with three generations per year. A three generation life history is particularly difficult to determine although three generations have been identified for some species of mysid (*Mysidopsis gibbosa* (Sars) and *Neomysis integer*) in Scotland (Mauchline, 1970b & 1971a). The life-history pattern followed in any one year may also depend on autumnal water temperatures. The pattern of development seen in Option I could occur when water temperatures are higher in autumn allowing Cohort III to produce young late in the year, whilst in cooler years, the pattern seen in Option II could prevail. It was not possible from this study to determine which of Option I or Option II was the most likely to apply to *M. slabberi* in the Tamar Estuary. The 1 month sampling interval in this study was probably too long to confirm the presence of a third generation. A better understanding of the life-history pattern would have been obtained from more frequent (at least twice monthly) sampling.

Growth rate has not been estimated previously for *M. slabberi*, but the typical rates in this study, of up to 0.12mm day^{-1} (3.6 mm mo^{-1}), are within the range seen in other species with

similar life-history patterns. In the Westerschelde and the Ythan Estuary, Scotland *Neomysis integer* had growth rates of between 3 and 5 mm mo^{-1} for juveniles and 1-2 mm mo^{-1} for mature individuals (Astthorsson and Ralph, 1984; Mees *et al.*, 1994). The highest rates recorded here in Cohort IIA of 0.24 mm day^{1} over a single month (7.2 mm mo^{-1}) are higher than many other records of mysid growth. These growth rates contrast with the slower growth recorded in mysid species which have less than one generation a year. For example, the freshwater mysid *Mysis relicta* has a growth rate of less than 1 mm mo^{-1} in Lake Michigan, USA (Morgan and Beeton, 1978). For each cohort, as mysids matured and started to breed, males died off or left the population and growth rates declined. Each cohort, therefore, became biased towards ovigerous and empty females. This reduction in growth rate is consistent with Mauchline (1973) who has shown that adult female mysids do not moult (or grow) when young are in the marsupium.

Both the upper and lower size limit for adult individuals were lower than those reported by Tattersall and Tattersall (1951). Present ovigerous females sizes, however, were larger than those recorded by Greenwood *et al.* (1989) for *M. slabberi* in the Tamar Estuary (9.5-13.35mm as opposed to 6.01-8.51mm). The size difference may be attributed to the conversion of these author's measurements of carapace length to total length using a regression equation derived from *M. slabberi* in the Azov Sea, Russian Federation. Unlike in many other species of mysid, female *M. slabberi* did not appear to grow larger than males. The sex ratio was highly skewed towards females, except during the overwintering period and increased in favour of females as each cohort matured, suggesting that males die shortly after breeding, as is the case for *Mysis relicta* in Lake Pääjärvi (Hakala, 1978) and *N. americana* (Smith) in Passamaquoddy Bay, Canada (Pezzack and Corey, 1979). It is also possible that males occupy a different habitat to females during the day, but no evidence was found for this in this study.

In common with many species of mysid, *M. slabberi* shows a positive relationship between brood size and female length (Mauchline, 1973a). The largest brood size (29 embryos) was considerably greater than that reported previously for this species from other areas (14-20), (Tattersall and Tattersall, 1951; Macquart-Moulin, 1965), although Greenwood *et al.* (1989) recorded a brood size of 25 from a female of length 8.2mm from the Tamar Estuary. Body size of ovigerous females, however, was greater in this study than in that of either Greenwood *et al.* (1989) or Macquart-Moulin (1965) and it could be expected, therefore, that larger broods would be produced. The observed large variations in brood size at a given body length are common in other species, *eg. N. americana*, and *Tenagomysis novaezealandiae* (Pezzack and Corey, 1979; Jones *et al.*, 1989).

Mesopodopsis slabberi was abundant in the Tamar Estuary, with highest densities generally found in the salinity range 5-20 ‰. The distribution was highly aggregated and zones of maximum distribution could be distinguished for each of the life-history stages. These zones could be related to salinity gradients in the estuary, but overlaid on this pattern was a seasonal cycle of abundance which was controlled by water temperature. The effect of temperature on growth and reproduction of mysids is well documented. For example, Toda *et al.* (1983, 1984) demonstrated that increasing environmental temperature increased the brood size, brood interval and specific growth rate in *Neomysis intermedia* (Czerniavsky).

The maximum abundance of *M. slabberi* in this study of (354 m^{-3}) is of the same order of magnitude as maximum abundances recorded by Mees *et al.* (1993a & b) for the same species in the Westerschelde, Netherlands (175 m^{-2}), but an order of magnitude lower than those found by Milner (1986) in the Tamar Estuary (4,500 m^{-3}). The surf-zone mysid *M. wooldridgei* in the Sundays River Estuary, South Africa reaches densities of up to 5,950 m^{-3} and can attain a standing stock of 8,275 mgm^{-3} (Wooldridge and Bailey, 1982). The standing stock of *M. slabberi* in the Tamar Estuary is considerably lower, a maximum of 150 mgm^{-3}, and only at limited locations, but is consistent with estimates for other temperate zone mysids (Mees *et al.*, 1994).

Mesopodopsis slabberi had a longitudinal distribution in the Tamar Estuary stretching from the more saline outer estuary (salinities >30 ‰) to the low salinity (*c.*5 ‰) inner estuary. The range of salinities in which it occurred confirmed that *M. slabberi* is euryhaline (Tattersall & Tattersall, 1951). The results confirm also that salinity (which is primarily determined by runoff in this estuary) is the primary factor governing the longitudinal distribution of this species. However, under conditions of very high runoff, such as those seen in March and October, *M. slabberi* is either flushed out of the upper reaches of the estuary or actively migrates to more saline regions. The different cohorts in the population can be clearly identified along the salinity gradient, and the distribution appears to be determined by life-history stage, with the smaller juvenile and immature stages occurring in higher salinities than adult and large immature stages. The data suggest that the different life-history stages of *M. slabberi* must be able to select particular physico-chemical regimes in order to achieve this partitioning of the population. Several mysid species are known to be able to regulate their position in estuaries and coastal regions by undergoing vertical and/or lateral migrations. *Mesopodopsis wooldridgei* undergoes active vertical migration in the Sundays River Estuary. Adults migrate both laterally and vertically to maintain their position and juveniles are more frequently found in faster-flowing surface water (Wooldridge and Erasmus, 1980; Wooldridge and Bailey, 1982). *Neomysis mercedis* (Holmes) utilizes this same two-layered circulation to maintain its position in the

San Francisco Bay-Delta, with mature individuals using near-bottom tidal currents to remain above the turbidity maximum zone, while juveniles remain just below the turbidity maximum by utilizing seaward flowing surface currents (Orsi and Knutson, 1979; Siegfried *et al.*, 1979). In the Gamtoos Estuary, South Africa, the mysid *Gastrosaccus brevisfissura* has developed a number of strategies to prevent flushing out to sea. During the day, it aggregates near to the substratum on ebb-tides, is more benthic during the day and utilizes flood currents to assist up-estuary transport (Schlacher and Wooldridge, 1994). Apel (1992) found that *Mesopodopsis slabberi* in the Jade Estuary, Germany, was more abundant in catches made at night, and suggested that *M. slabberi* is able to alter its vertical and/or horizontal distribution on, at least, a diurnal basis. However, Apel (1992) found no evidence that there was a tidal influence on the changes in abundance recorded. A possible explanation for the preference of juvenile *M. slabberi* for higher salinities is given by Greenwood *et al.* (1989), who found that ovigerous *M. slabberi* were more euryhaline than mature males and that eggs of this species developed most successfully in salinities higher than 7‰. No data are available for the salinity tolerance of juvenile *M. slabberi*, however, Bhattacharya (1982) found that juvenile *Mesopodopsis orientalis* (Tattersall) survived better in 10‰ seawater than adults. The upper-estuary limit of distribution of mature females may therefore be determined by the upper limit of salinity tolerance of embryos in the brood pouch, or it may be influenced by competition with *Neomysis integer* which has a distribution which overlaps with *M. slabberi*, but which extends into lower salinity zones. Conversely, distribution of the smaller individuals (juvenile and immature stages) may be influenced by competition with the adult stages, an inability to maintain position or differing salinity preferences. Predation pressure by fish may also influence the distribution of this species; larval fish were found to be distributed throughout the salinity range between March and September. Individuals which are able to compete successfully in the upper estuary region, near to the turbidity maximum and/or maintain their position in this zone of the estuary, are likely to benefit in terms of the greater food availability in terms of greater suspended matter concentrations (and thus higher concentrations of organic matter (Fig. 5.6)). There is some evidence from the literature that *M. slabberi* undergoes seasonal onshore/offshore migrations (Baan and Holthius, 1971; Apel, 1992). However, no evidence for this was found for *M. slabberi* in the Tamar Estuary. The length-frequency distributions in the lower estuary resembled those in the upper estuary for most of the year and although there was some movement of the population into higher salinities during the overwintering period, the population remained in the estuary. Seasonal movements between the lower and upper estuary can be explained in terms of changes in salinity gradients and runoff throughout the year. The lack of mature individuals in winter samples can be accounted for by mortality of the summer breeding generations.

CHAPTER 8

LABORATORY STUDIES

8. LABORATORY STUDIES

8.1 Introduction

Neomysis integer is a hyperbenthic, euryhaline and eurythermal mysid characteristic of the estuaries of Britain and northwest Europe (Isaac *et al.*, 1990). The species is known to occur in a broad habitat range from freshwater to the open sea (Bremer and Vijverberg, 1982; Apel, 1992; Mees *et al.*, 1994). Kuhlman (1984) reported an upper salinity tolerance limit of between 25 and 30 ‰ for *N. integer* from the Kiel Canal, Germany. In the Tamar Estuary (this study), *N. integer* had a distribution encompassing the more saline lower estuary and the very low salinity (<5‰) upper reaches, but was concentrated mainly in the salinity range from 0 to 25 ‰ (§6.1-6.2). There was evidence that the larger immature and mature stages of this species migrated up-estuary in the spring, and spent the summer and early autumn in the low salinity regions of the estuary. In the Tamar Estuary, juveniles had a wider salinity distribution than adults throughout the year.

Salinity tolerance has an important role to play in determining the longitudinal distributions of mysids in estuaries and probably plays a part in influencing the spatial separation of species which would otherwise occupy similar habitats. Several studies have examined salinity tolerances and osmoregulation in *N. integer*. Vlasblom and Elgershuizen (1977) found that *N. integer* was more tolerant of salinities lower than 18‰ than *Praunus flexuosus*. *Neomysis integer* is a better osmoregulator than *P. flexuosus* (McLusky and Heard, 1971) and this may help to explain the more marine distribution of the latter species. Vlasblom and Elgershuizen (1977) examined the survival of *N. integer* at different salinity and temperature combinations, and found that adult stages survived salinities of between 2 and 20 ‰, with tolerance of low salinities increasing as temperatures increased within the range 5-20°C. These authors also found differences in the development rate of embryos at different salinities; development was faster in embryos maintained at 3.8‰ than in those kept at 12.8‰ (Vlasblom and Elgershuizen, 1977). Growth of juvenile *N. integer* was highest in salinities of between 16 to 20‰ (Kuhlmann, 1984). Ralph (1965) studied the osmoregulatory ability of *N. integer* from Southampton Water and found that it was an effective hypo-hyper-osmoregulator in salinities ranging from 5.8‰ to 40.6‰, although survival was low in salinities greater than 35‰.

There are two main types of active physiological response to changes in salinity used by marine Crustacea. Some maintain their blood at the same concentration as the medium in concentrated solution and have hyper-osmotic blood in dilute media (hyper-osmotic regulation), while others maintain their blood hyper-osmotic in diluted solutions and hypo-

osmotic to concentrated media (hypo-hyper-osmoregulation) (Schoffeniels and Gilles, 1970b). Hypo-hyper-osmoregulation is considered to be more advanced and is possessed by many estuarine invertebrates, including all marine, estuarine and brackish-water palaemonid shrimps studied to date (Campbell and Jones, 1989). A number of mechanisms are known to be involved in regulating blood osmotic concentrations including the active excretion or uptake of salt and water, and alteration of the permeability of membranes. One third to half of the osmotic concentration of cells is accounted for by inorganic ions (potassium, sodium, chloride, magnesium and calcium) whilst small organic molecules, particularly free amino acids account for the remainder (Lockwood, 1976). Amino acid concentrations are generally higher in the tissues of marine animals than in freshwater ones, and most euryhaline animals show large changes in intracellular free amino acid concentrations (DFAA) during adjustment of cellular osmotic concentrations. These findings indicate that DFAAs play an important role in the regulation of blood osmotic concentrations of crustaceans (Dûchateau-Bosson and Florkin, 1961). Numerous researchers have investigated the role of amino acids in osmoregulation (Harris, 1969; Weber and van Marrewijk, 1972; Bishop, 1976) and have identified that the most commonly used are the non-essential amino acids alanine, glycine, glutamate, proline and taurine (Gilles, 1975). More recent attention has focussed on the part played by amino acids in influencing the flavour of shrimps cultured at different salinities (McCoid, 1984; Dalla Via, 1986). The role of amino acids in the osmoregulation of estuarine mysids has yet to be determined. It was therefore of interest to examine the changes in DFAAs in *N. integer* together with the changes in blood osmotic concentrations during salinity acclimation in an attempt to explain the mechanisms involved in the wide salinity distribution of *N. integer* in the Tamar Estuary. *Neomysis integer* was chosen for the osmoregulation and amino acid analysis because it proved impossible to maintain *Mesopodopsis slabberi* in the laboratory. Individuals of this latter species when brought into the laboratory died within 24 hours for reasons that are unclear. The test salinities used in the following experiments ranged from 0.5 to 20‰ and simulated the salinity range occupied by *N. integer* in the Tamar Estuary. The test temperature of 15°C was representative of the water temperature in the Tamar Estuary in June 1989, the month when *N. integer* was recorded at the greatest abundance.

8.2 Methods

The *Neomysis integer* used for these experiments were collected from the River Looe Estuary (Cornwall), using a hand-held dip net from the shore. The mysids were transported to the laboratory in 50 l plastic containers filled with habitat water (15‰). In the laboratory, they were placed in large aquaria, with a filtered recirculating water system and seawater at either 5 ‰ or 15 ‰, at 15 (±1) °C. The mysids were held in the laboratory for

7 days, during which time they were fed twice daily on newly hatched *Artemia* sp. Due to the limitations of haemolymph sampling from small individuals, only intermoult adults (8-16 mm in length) were used in the experiments and no ovigerous females were included.

8.2.1 Experimental design

The experiments were carried out in a temperature-controlled room maintained at 15 ±1 °C, with a light intensity of 2000 Lux on a 12-h light/12-h dark cycle. The test animals were not fed during the experiments. Five mysids were placed in nine 250 ml test vessels at each of 7 salinities (0.5, 1, 2, 4, 8, 16 & 20 ‰) (*ie.* 45 mysids per salinity). Evaporation was minimised by covering each test vessel with a loosely fitting lid. At each salinity, the mysids in one vessel were sampled after 1 (amino acid experiments only), 2, 4, 8, 12, 24, 48, 72 and 96 h. This experimental design was repeated four times; twice to obtain samples for amino acid analysis (for 5 and 15 ‰ acclimated animals) and twice to obtain samples for the freezing-point analysis (with 5 and 15 ‰ acclimated animals).

To obtain haemolymph samples for the freezing-point analysis, each mysid was dried gently with tissue paper, placed under liquid paraffin (to prevent haemolymph evaporation) and the haemolymph sampled using a micro pipette made from a drawn out capillary tube. The thoracic somites underneath the posterior carapace were punctured with the tip of the micro pipette, the tip inserted into the heart and dorsal artery and samples of haemolymph, interposed with liquid paraffin, were taken into the micro pipette. The samples were then placed in capillary tubes filled with liquid paraffin which were plugged with Plasticine and stored in a deep freeze at -20 °C until analysed to determine their osmotic concentration. A sample of each of the experimental test solutions was also stored similarly.

For the amino acid analysis, the mysids were removed from the test solution, gently dried with tissue paper, wrapped in foil and frozen at -20°C until needed for analysis. They were packed in dry ice for transportation to Roscoff (France) where the analysis was carried out.

8.2.2 Analytical methods

Osmoregulation

Osmoregulation was measured with a modified Ramsay-Brown freezing-point determination apparatus (Ramsay & Brown, 1955). The frozen samples were

immersed in 70% alcohol in an insulated perspex tank. The alcohol was cooled using solid carbon dioxide (dry ice) and stirred constantly to maintain an even temperature throughout the tank. The alcohol was heated slowly using a small immersion heater. The haemolymph samples were observed through a low power binocular microscope and the temperature at which the last ice crystal in the sample melted was read from a thermometer precise to ± 0.01 °C. Three samples were analysed at each time interval and at each salinity. The significance of response of haemolymph freezing-point depression to a sudden change in salinity was examined using analysis of variance (ANOVA).

Dissolved free amino acids

The dissolved free amino acid (DFAA) analyses were carried out at the Centre National de la Recherche Scientifique, Station Biologique de Roscoff (France) over two periods (31 July to 14 August 1991 and 23-26 September 1991). Samples were analysed using the reversed-phase high-performance liquid chromatography method described by Lindroth & Mopper (1979) and adapted by Dawson *et al.* (1985) and Poulet *et al.* (1986). Analysis was carried out using a liquid chromatograph system equipped with a programmable multiple solvent delivery system (Milton Roy model CM400). Detection was achieved using a high performance fluoromonitor (Milton Roy model 1311) with a 340-380 nm excitation filter and a 418-700 nm emission filter with a 30 μl detection chamber attached to a 0-10 v chart recorder, an injection valve with a 100 μl sample loop and a CI-10B integrator. The column used was an Ultratech 250 x 4.6 mm HPLC column No. PP44411 (ultra techsphere 5 micron C18 inverted stainless steel).

8.2.3 Sample preparation

Mobile phases

A 0.05 M sodium citrate buffer was made up from tri-sodium citrate di-hydrate and Milli-Q water and adjusted to pH in the range (6.18-7.50) using 12 M hydrochloric acid. Two mobile phases were used:

Phase A - 80 % sodium citrate buffer and 20 % HPLC grade methanol.
Phase B - 80 % HPLC grade methanol and 20 % sodium citrate buffer

The mobile phases were degassed daily by placing in an ultrasonic bath for 10 minutes and then bubbling for 10 minutes with helium.

Reagent

o-phthaldialdehyde solution: 270 mg *o*-phthaldialdehyde dissolved in 5 ml methanol (stored refrigerated in the dark).

Borate buffer

Boric acid solution (0.4 M): 1.23 g boric acid made up to 500 ml in distilled water and adjusted to pH 9.5 with 1 M sodium hydroxide.

Buffered reagent solution

5 ml of *o*-phthaldialdehyde solution was made up to 50 ml with borate buffer and stored in a refrigerator in the dark.

Derivitization reagent

The derivitization reagent was made by adding 60 μl of mercapto-ethanol to 5 ml of the buffered reagent solution.

Standards

1 mM solutions of L-amino acids were prepared in Milli-Q water and stored in a refrigerator. The amino acids used were: alanine, arginine, asparagine, aspartic acid, β-alanine, γ-amino butyric acid, glutamic acid, glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, ornithine, phenylalanine, serine, taurine, threonine, tryptophan, tyrosine and, valine. Proline was not included as a standard because its secondary amine group is not detected by this analytical technique (Lindroth & Mopper 1979). The standards were prepared for injection into the HPLC by taking 200 μl of the prepared standard solution and adding 50 μl of the derivatization reagent. This solution was allowed to stand for exactly 3 minutes before injection into the HPLC.

Mysid samples

The mysids used in the analysis were removed from the freezer and allowed to reach room temperature. Between 1 and 4 individual mysids were pooled and weighed (wet weight) on a Mettler balance precise to ±0.1 mg. To extract the DFAA, the weighed mysids were ground in a tissue grinder with between 8 and

16 ml of Milli-Q water, depending on the wet weight of the tissue, and centrifuged for 10 minutes at 10,000 rpm. Fifty microlitres of the derivitization reagent was added to 200 μl of the resulting supernatant which was allowed to stand for 3 minutes before injection into the HPLC. Mysids from each time/salinity combination were prepared in this way. The preparation of the samples for injection into the HPLC is summarised in Figure 8.1.

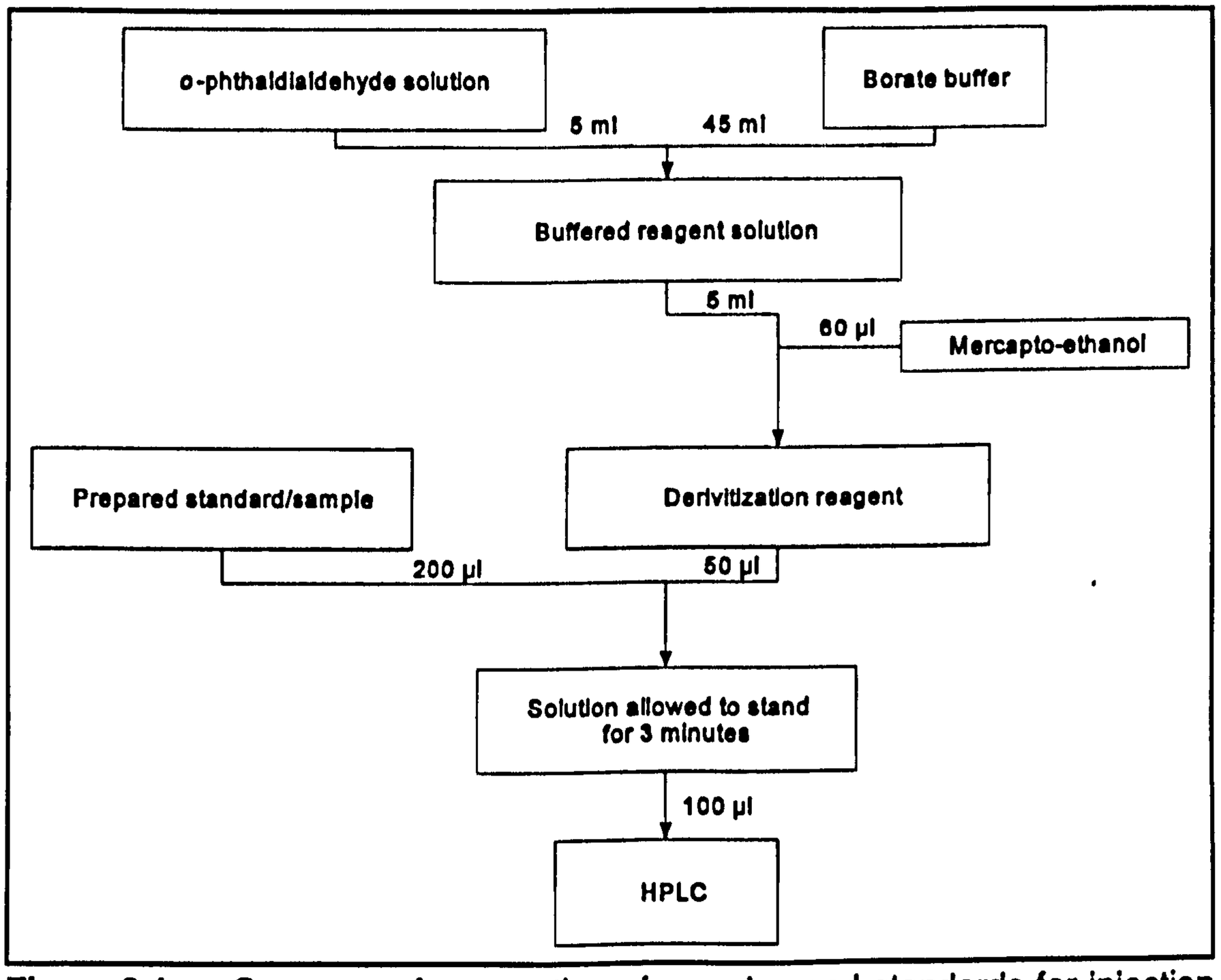


Figure 8.1 Summary of preparation of samples and standards for injection into HPLC.

To establish the variability in dissolved free amino acid concentration between individuals, single mysids sampled at time 0 h were analysed as outlined above (6 individuals in the case of the 15 ‰ acclimated experiment and 5 individuals for the 5 ‰ acclimated experiment).

To establish the order in which the amino acids were eluted and the solvent gradient which gave the best separation, a series of gradient tests was performed using mixed amino acid standards of various dilutions. The best separation of amino acids was obtained using the solvent gradients shown in Table 8.1. Gradient 1 was used for all the initial determinations of elution order using standards and for the majority of samples.

Table 8.1 Solvent gradients used for HPLC analysis.

Time (minutes)	Gradient 1		Gradient 2	
	Phase A (%)	Phase B (%)	Phase A (%)	Phase B (%)
5	100	0	100	0
10	95	5	95	5
25	95	5	95	5
45	95	5	95	5
52	70	30	70	30
61	70	30	70	30
65	65	35	65	35
70	40	60	50	50
75	35	65	45	55
80	25	75	35	65
85	10	90	20	80
90	0	100	0	100

The gradient was adjusted slightly (Gradient 2) to maintain a good separation of peaks for some samples. All the amino acids eluted within approximately 90 minutes.

The following equations were used to calculate the DFAA concentrations in each sample:

1. Concentration of DFAA in sample (ng/μl): $$X_l = \frac{C}{D_l} \times E_l$$

2. Concentration relative to wet weight (ng/mg): $$Y_l = \frac{X_l \times 1000 \times Vol}{Wwt}$$

3. Total DFAA concentration (ng/mg): $$Total = \sum_{l=1}^{l=22} Y_l$$

4. Percentage of each DFAA (%): $$P_l = \frac{X_l}{Total} \times 100$$

where:

l = amino acids 1-22 (ASP-LYS), C = Concentration of the standard ng/80µl injection, D_l = Area of each amino acid (1-22) in the standard, E_l = Area of each

amino acid (1-22) per 80µl injection, *Wwt* = Wet weight of mysids (mg) used to prepare sample and *Vol* = Volume of water (ml) used for DFAA extraction per sample.

The significance of response of haemolymph dissolved free amino acid concentration to a sudden change in salinity was examined using multivariate analysis of variance (MANOVA).

8.3 Results

8.3.1 Osmoregulation

Mean haemolymph freezing point depressions of control animals acclimated to 15‰ (freezing-point depression -0.69°C) and 5‰ (freezing-point depression -0.21°C) were -1.095°C and -0.70°C, respectively. Haemolymph responses following sudden transfer are shown in Figures 8.2a & b. It is apparent that there was considerable variability between individuals as indicated by the relatively wide standard deviations.

There was no clear time-based response to sudden change at any of the test salinities. Statistical analysis using ANOVA showed that there was no significant effect of time on haemolymph freezing-point depression (Table 8.2), although, again, there was a lot of variation between individuals. These data suggest that the response of *N. integer* to changes in salinity is very rapid (<2 h).

Table 8.2 Two-way analysis of variance of the effect of salinity (0.5, 1.0, 2.0, 4.0, 8.0, 16.0 and 20‰) and time (2, 4, 8, 12, 24, 48, 72 and 96 h) on the osmotic concentration (depression of freezing point °C) of *Neomysis integer*. (n.s. = not significant.)

Source of variation	d.f.	Sum of squares	Mean square	F-ratio	Significance level
Acclimation at 15‰					
Salinity	6	1.38	0.23	2.8	n.s.
Time	7	1.34	0.19	2.3	n.s.
Acclimation at 5‰					
Salinity	6	0.45	0.02	1.1	n.s.
Time	7	60.91	0.13	1.9	n.s.

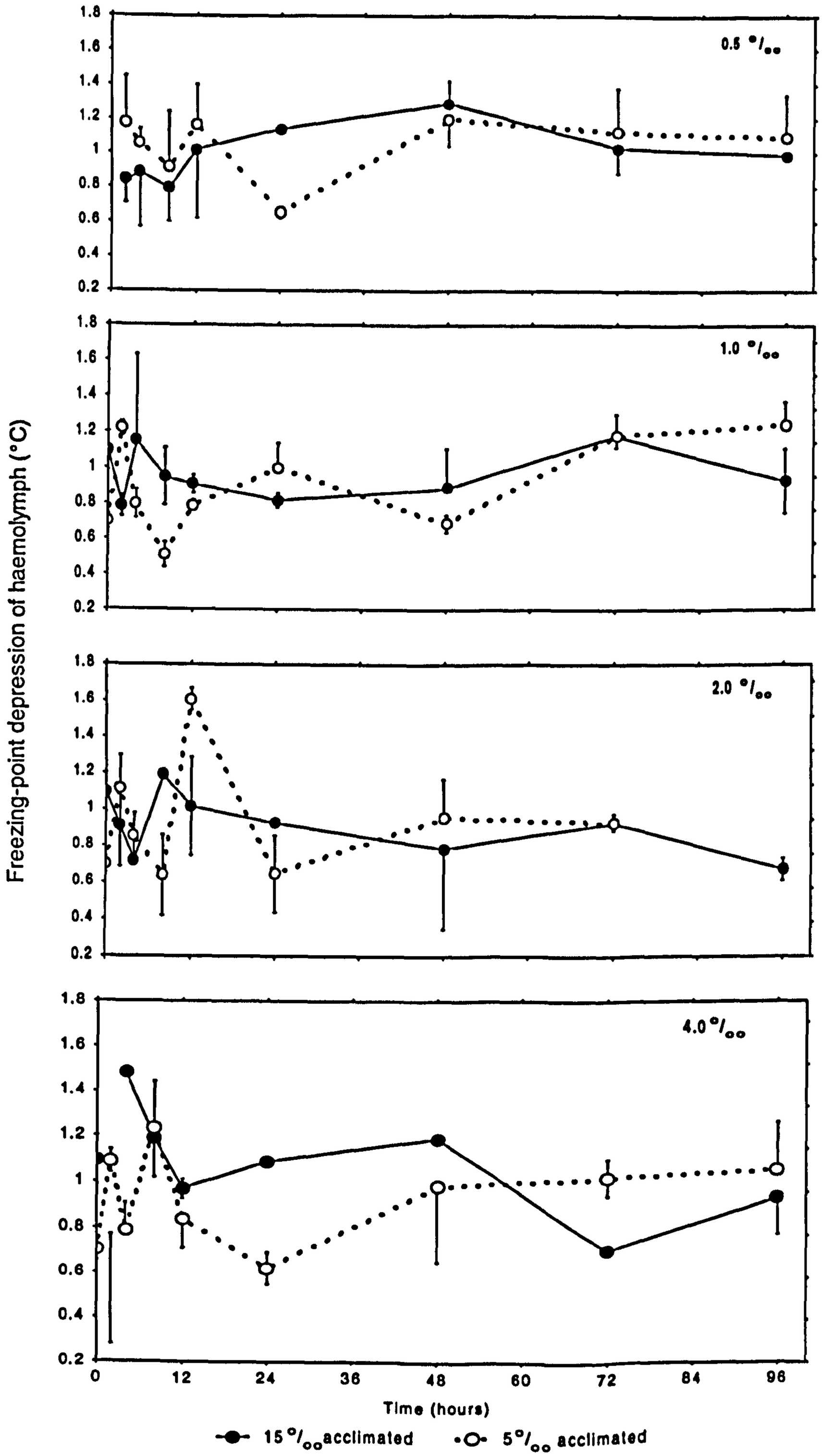


Figure 8.2a Changes in the freezing-point depression of the haemolymph (°C) of *Neomysis integer* following sudden transfer to 0.5, 1, 2 and 4 ‰ salinity after 7 days acclimation to 15 ‰ (dots) and 5 ‰ (circles). Values are means ± 1 SD.

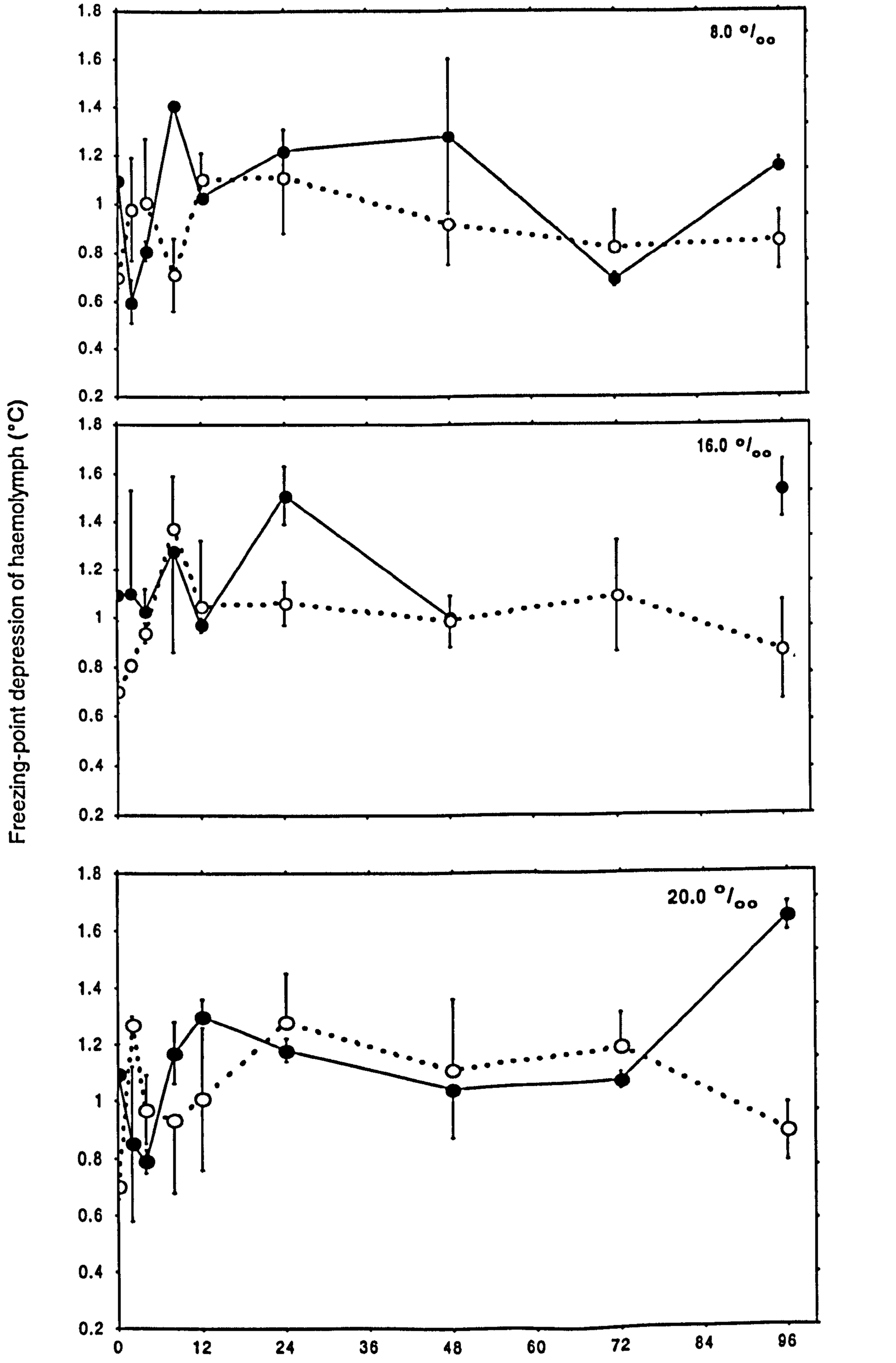


Figure 8.2b Changes in the freezing-point depression of haemolymph (°C) of *Neomysis integer* following sudden transfer to 8, 16 and 20 ‰ salinity after 7 days acclimation to 15 ‰ (dots) and 5 ‰ (circles). Values are means ±1 SD of raw pooled data.

Because ANOVA showed no effect of time on haemolymph freezing-point depression, the data from the previous figures for each salinity were combined and plotted (Fig. 8.3). Paired t-tests indicated that there was no significant difference between the freezing-point depression at the two acclimation salinities. Lack of effect of acclimation indicates that *N. integer* is an extremely efficient hyper-osmoregulator over the salinity range used in these tests.

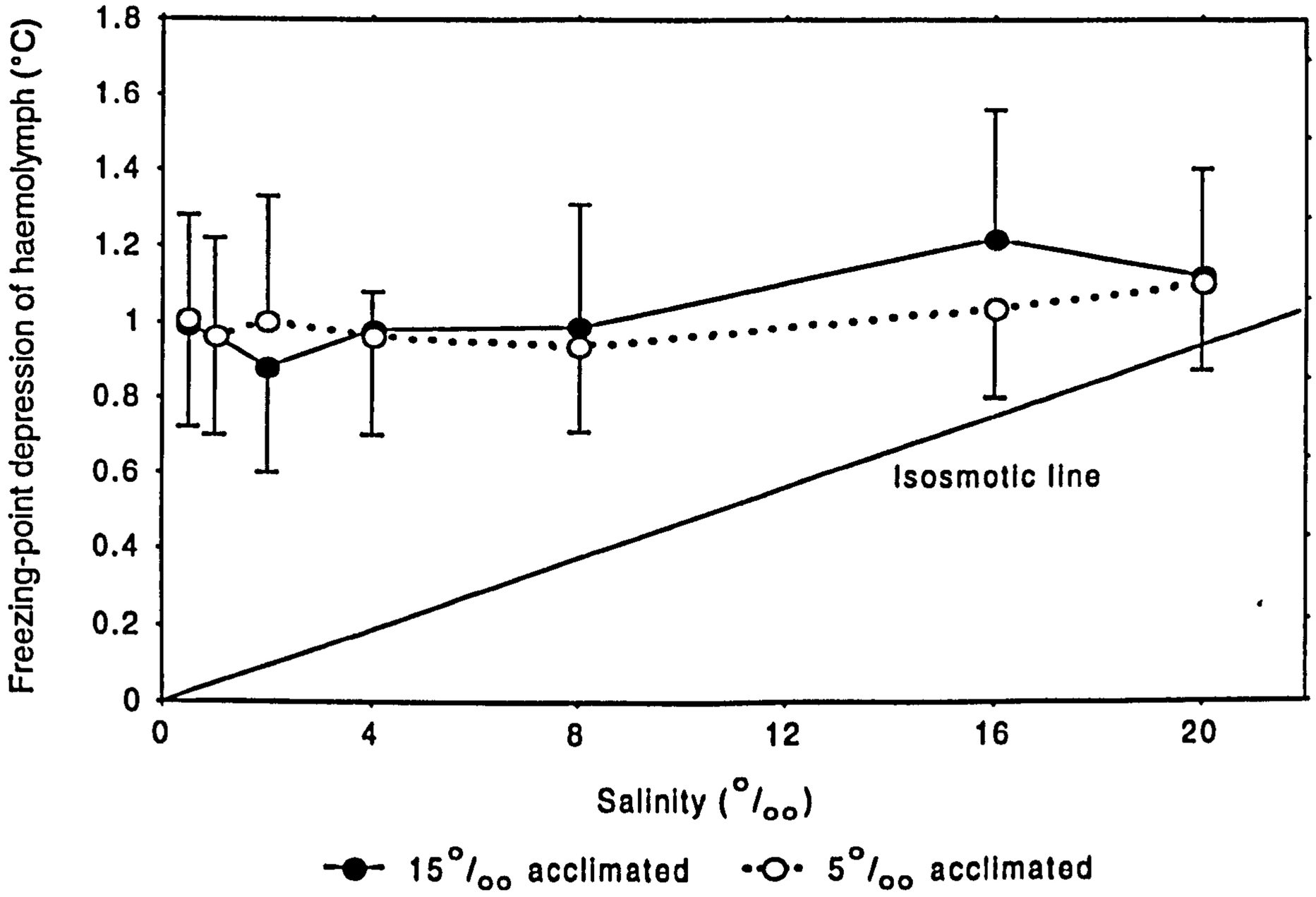


Figure 8.3 Freezing-point depression (°C) of *Neomysis integer* at a range of salinities. (Combined data for all times at each salinity.) Values are means ±1SD.

8.3.2 Amino acids

Standards and separation of amino acids

Initially, mixed standards containing all the amino acids with concentrations of 0.1 and 0.01 mM were used to determine the elution time for each amino acid, using solvent Gradient 1 shown in Table 8.3. The traces from these were compared with ones produced previously using the same technique (Poulet personal communication). From these comparisons it was possible to identify the order of elution for the majority of the 22 amino acids (Fig. 8.4, Table 8.3). There remained, however, some doubt as to the position of the peaks for glycine, arginine and threonine; β-alanine, taurine and alanine; tryptophan, methionine and valine. To establish the elution order of these amino acids, separate standards were prepared and run through the analyser as follows:

- a 0.1 mM glycine standard (Fig. 8.5).
- a 0.1 mM arginine standard (Fig. 8.6).
- a mixed standard containing β-alanine (0.1 mM), alanine (0.05 mM), tryptophan (0.025 mM), methionine (0.1 mM) and valine (0.05 mM) (Fig. 8.7).

From these standards the elution order shown in Table 8.4 was established (see also Fig. 8.4). The results for glycine/threonine and tryptophan/methionine were combined because complete separation of these peaks was not obtained.

Table 8.3 Elution order of DFAAs following initial standard run. (* = DFAAs for which the order of elution was not determined using the single mixed standard.)

Elution order	Amino acid
1	Aspartic acid (ASP)
2	Glutamic acid (GLU)
3	Asparagine (ASN)
4	Serine (SER)
5	Glutamine (GLN)
6	Histidine (HIS)
7	Arginine (ARG)*
8	Glycine (GLY)*
9	Threonine (THR)*
10	β-alanine (β-ALA)*
11	Taurine (TAU)*
12	Alanine (ALA)*
13	γ-amino butyric acid (γ-ABA)
14	Tyrosine (TYR)
15	Tryptophan (TRP)*
16	Methionine (MET)*
17	Valine (VAL)*
18	Phenylalanine (PHE)
19	Isoleucine (ILEU)
20	Leucine (LEU)
21	Ornithine (ORN)
22	Lysine (LYS)

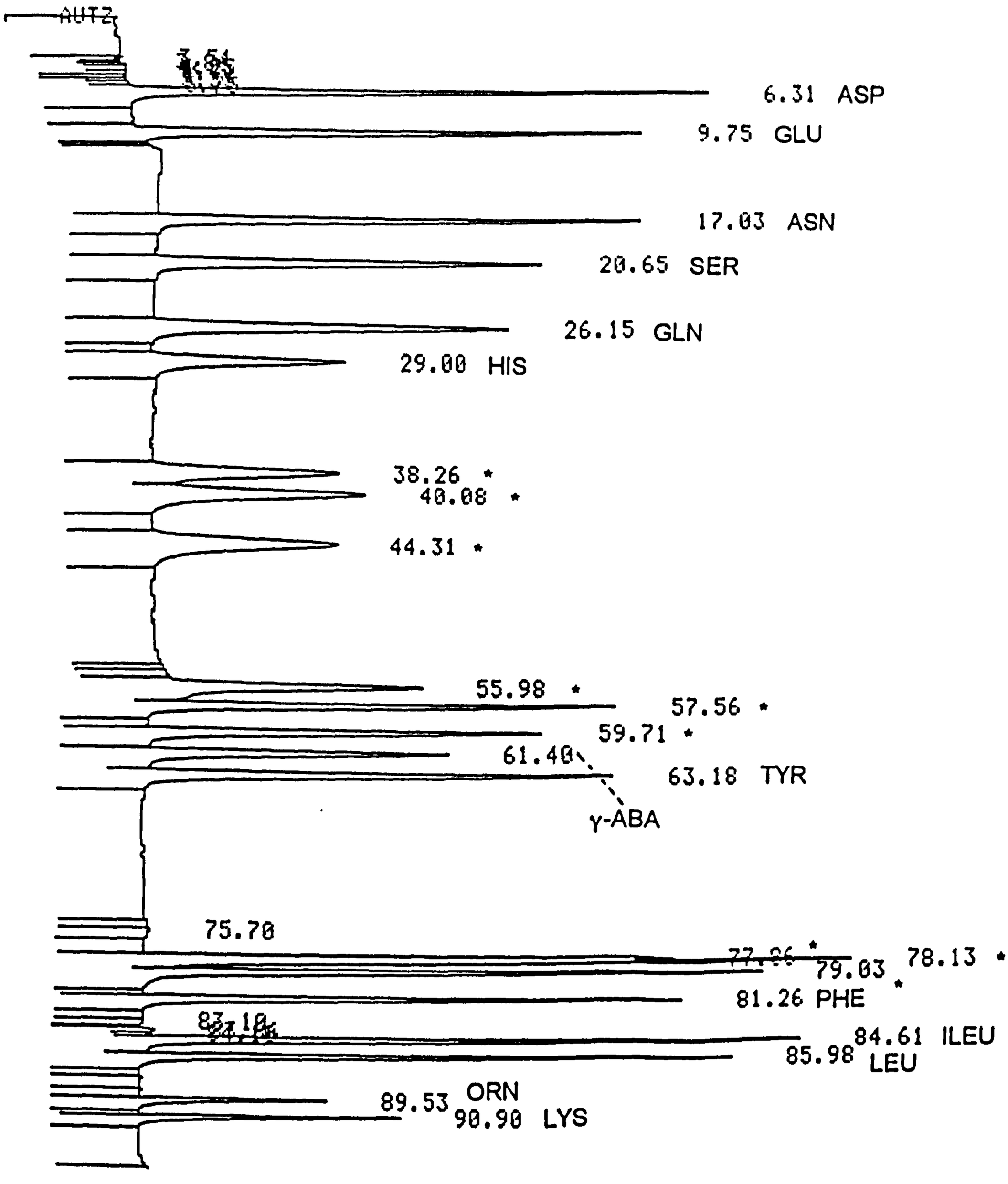


Figure 8.4 HPLC trace produced from a standard containing all 22 amino acids, each at 0.01 mM concentration. (Numbers refer to run time (minutes), full names of amino acids are listed in Table 8.3, * = peaks which were identified using separate standards, see Figs 8.5-8.7.)

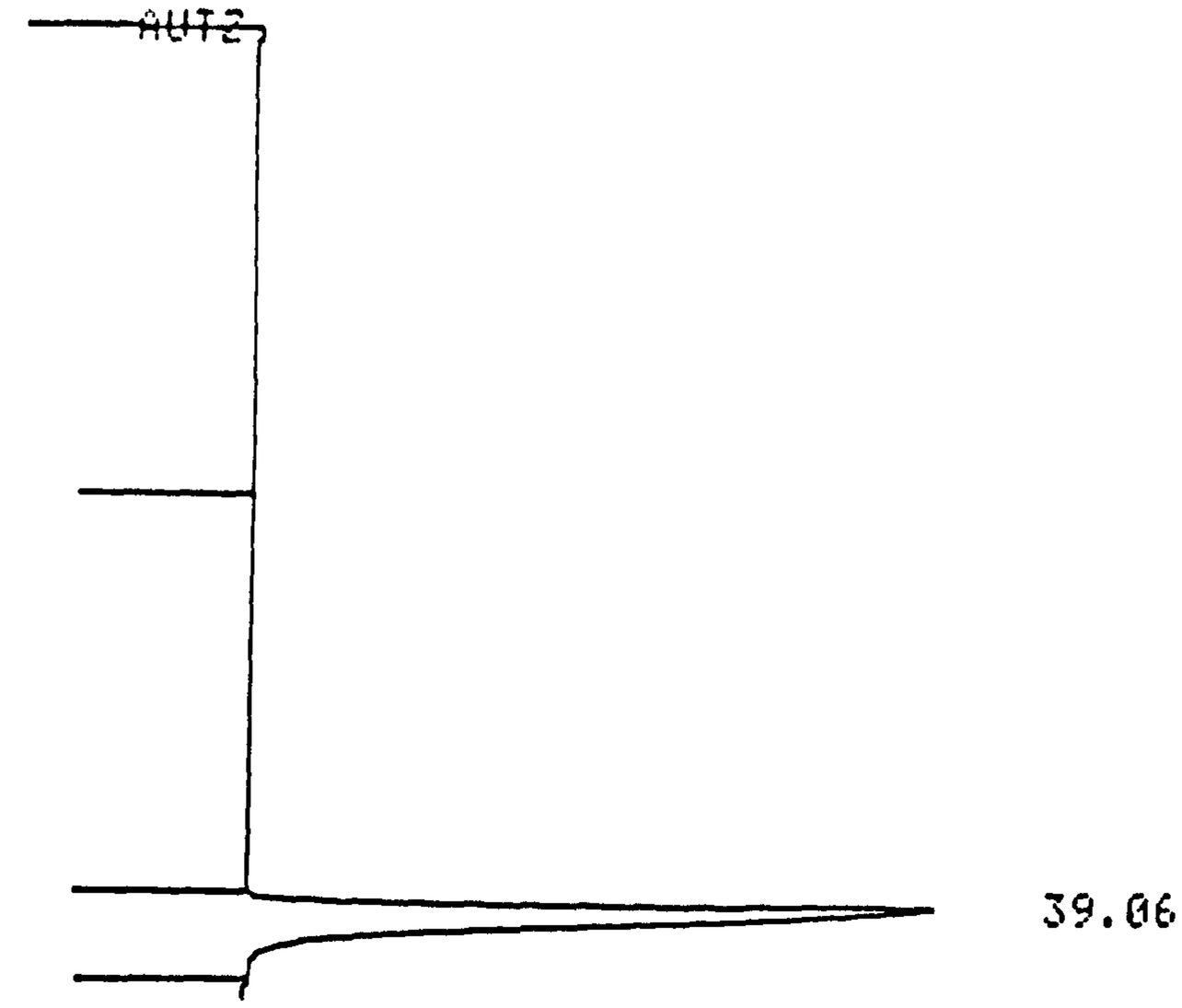


Figure 8.5 HPLC trace using a 0.1 mM glycine standard. Numbers refer to run time (minutes).

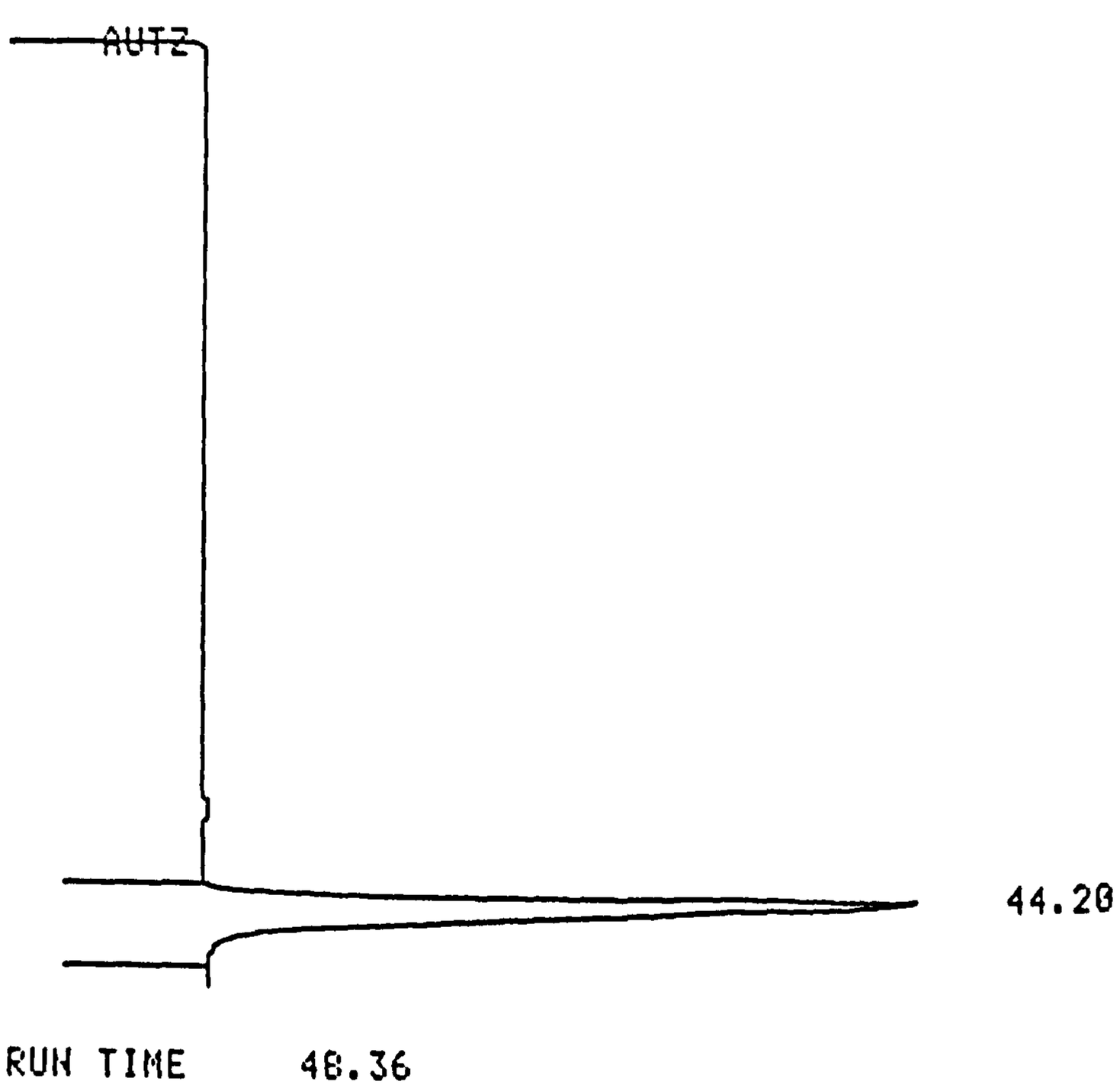


Figure 8.6 HPLC trace produced using a 0.1 mM arginine standard. Numbers refer to run time (minutes)

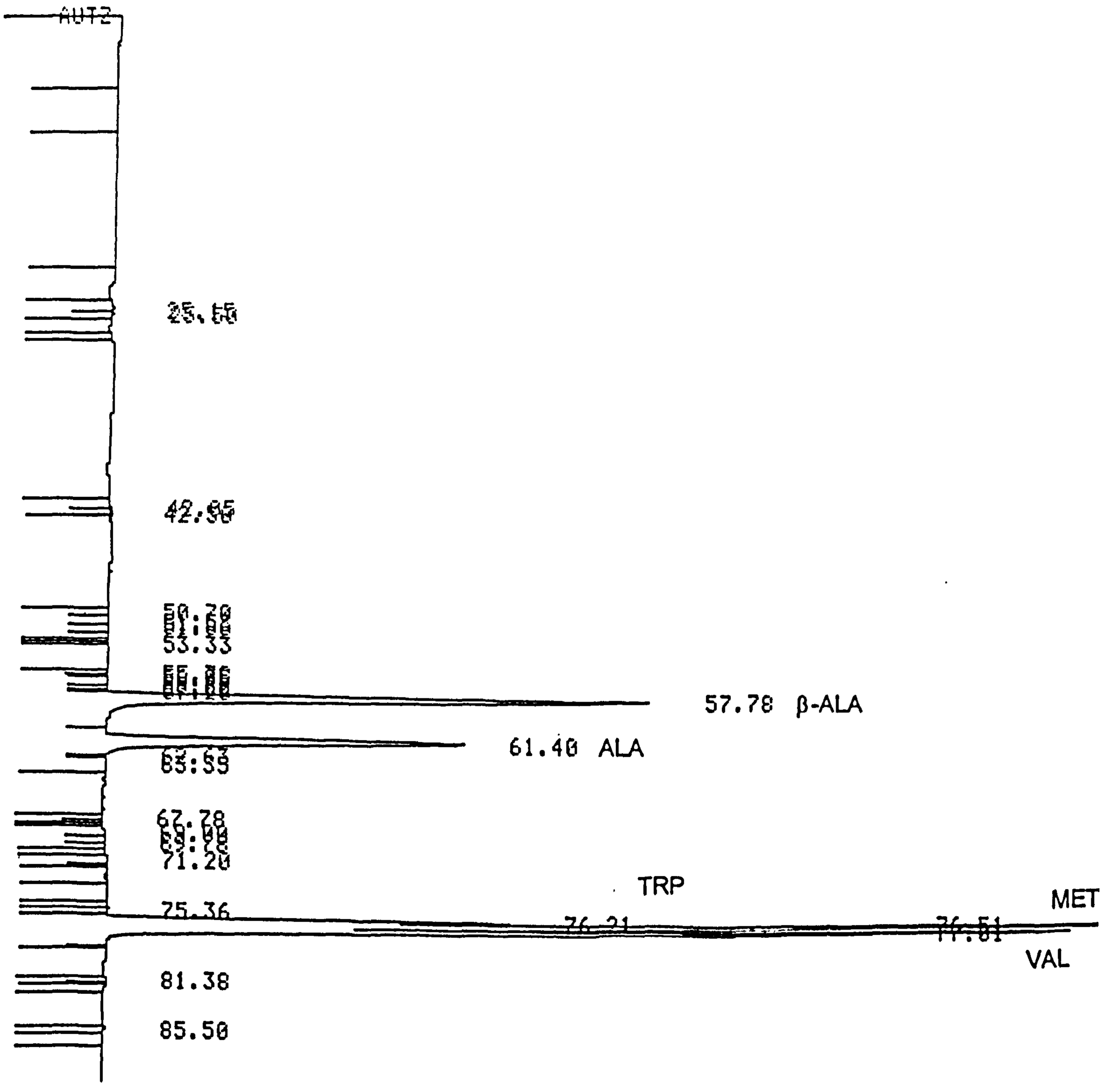


Figure 8.7 HPLC trace produced using a mixed standard containing β-alanine (0.1 mM), alanine (0.05 mM), tryptophan (0.025 mM), methionine (0.1 mM) and valine (0.05 mM). (Numbers refer to run time (minutes), full names of amino acids are listed in Table 8.3).

Table 8.4 Elution order established for the DFAAs. (*The results for glycine and threonine were pooled due to incomplete separation of peaks in many samples; ** the results for tryptophan and methionine were also pooled due to incomplete separation of peaks in many samples.)

Elution order	Amino acid
1	Aspartic acid (ASP)
2	Glutamic acid (GLU)
3	Asparagine (ASN)
4	Serine (SER)
5	Glutamine (GLN)
6	Histidine (HIS)
7	Glycine (GLY)*
8	Threonine (THR)*
9	Arginine (ARG)
10	β-alanine (β-ALA)
11	Taurine (TAU)
12	Alanine (ALA)
13	γ-amino butyric acid (γ-ABA)
14	Tyrosine (TYR)
15	Tryptophan (TRP)**
16	Methionine (MET)**
17	Valine (VAL)
18	Phenylalanine (PHE)
19	Isoleucine (ILEU)
20	Leucine (LEU)
21	Ornithine (ORN)
22	Lysine (LYS)

Variation of DFAA concentration in individuals

The results of the analysis of individual mysids acclimated to 5 ‰ and 15 ‰ are shown in Tables 8.5 and and 8.6. For animals acclimated to both 5 and 15 ‰ salinity, there was a great deal of variability in the concentration and proportion of individual DFAAs in the haemolymph. This variation is higher for animals acclimated to 15 ‰ than for individuals acclimated to 5 ‰ (Tables 8.5 and 8.6).

Table 8.5 Table showing means and standard deviations of DFAAs from samples of individual mysids (5 ‰ acclimated *Neomysis integer*, n = 5). Full names of amino acids are listed in Table 8.3.

DFAA	Mean concentration ng/mg wet weight ($x10^{-6}$)	S.d. (±)	S.d. (%)	Mean molar %	S.d. (±)	S.d. (%)
ASP	224.4	32.4	14.42	2.07	0.08	3.91
GLU	425.8	93.4	21.94	3.93	0.78	19.79
ASN	82.6	20.6	24.98	0.76	0.18	23.97
SER	202.6	32.5	16.03	1.87	0.22	11.59
GLN	156.9	50.8	32.39	1.44	0.44	30.69
HIS	39.6	23.1	58.27	0.38	0.22	57.67
GLY+THR	4,531.7	505.2	11.15	41.94	3.39	8.05
ARG	789.4	151.3	19.17	7.28	1.16	16.15
β-ALA	0.0	0.0	-	0.00	0.00	-
TAU	1,901.3	991.5	52.15	17.46	9.04	51.79
ALA	900.2	357.6	39.72	8.14	2.55	31.36
γ-ABA	21.7	4.6	21.48	0.20	0.04	18.99
TYR	116.7	27.5	23.57	1.08	0.25	20.07
TRP+MET	101.0	31.5	31.15	0.94	0.31	33.39
VAL	145.9	38.5	26.36	1.35	0.38	27.95
PHE	100.6	28.3	28.09	0.93	0.25	26.61
ILEU	123.4	25.2	20.39	1.16	0.29	25.35
LEU	226.4	54.6	24.14	2.10	0.55	26.18
ORN	369.7	40.8	11.05	3.45	0.54	15.70
LYS	378.6	70.2	18.54	3.52	0.71	20.27
TOTAL DFAA	10,838.5	1,314.2	12.12	100	-	-

Table 8.6 Table showing means and standard deviations of DFAAs from samples of individual mysids (15 ‰ acclimated *Neomysis integer*, n = 6). Full names of amino acids are listed in Table 8.3.

DFAA	Mean concentration ng/mg wet weight ($x10^{-6}$)	S.d. (±)	S.d. (%)	Mean molar %	S.d. (±)	S.d. (%)
ASP	224.9	87.5	38.90	1.64	0.56	34.08
GLU	560.6	142.4	25.40	4.11	0.95	23.06
ASN	113.8	38.6	33.92	0.83	0.24	29.42
SER	271.6	52.2	19.20	1.99	0.32	16.18
GLN	280.5	70.9	25.26	2.06	0.50	24.12
HIS	58.9	67.2	114.10	0.43	0.49	112.56
GLY+THR	4,877.8	734.9	15.07	35.98	5.95	16.55
ARG	996.4	230.6	23.15	7.36	1.80	24.48
β-ALA	30.3	17.4	57.38	0.22	0.12	55.80
TAU	2,764.4	345.4	12.50	20.33	2.00	9.85
ALA	1,488.0	147.0	9.88	11.00	1.28	11.65
γ-ABA	26.4	9.1	34.53	0.19	0.06	29.49
TYR	137.4	35.9	26.10	1.01	0.24	24.08
TRP+MET	153.0	27.2	17.81	1.12	0.17	15.05
VAL	197.2	59.1	30.00	1.45	0.44	30.51
PHE	123.7	38.9	31.42	0.91	0.28	30.39
ILEU	151.5	53.6	35.35	1.11	0.40	35.98
LEU	236.6	84.5	35.70	1.74	0.61	34.98
ORN	471.7	88.8	18.77	3.47	0.58	16.79
LYS	415.7	141.2	33.98	3.05	0.97	31.73
TOTAL DFAA	13,580.4	778.4	5.73	100	-	-

The total DFAA concentration in 15 ‰ acclimated *N. integer* was significantly higher than in 5 ‰ acclimated individuals ($p<0.01$, Table 8.7). This higher overall DFAA concentration was due, in part, to significantly higher concentrations of serine (SER), glutamine (GLN), β-alanine (β-ALA), alanine (ALA), tryptophan-methionine (TRP-MET) and ornithine (ORN), although increases were seen in the concentrations of all the DFAAs measured. Although the concentration of these individual DFAAs was higher in 15 ‰ individuals, only β-alanine significantly

increased its relative contribution to the DFAA pool ($p<0.01$, Table 8.7); β-alanine was not detected at all in 5 ‰ acclimated animals (Table 8.5).

Table 8.7 Results of 2 sample t-tests looking at the effect of pre-test acclimation to 5 and 15 ‰ salinity on the DFAA pool in individual *Neomysis integer* (n.s. = not significant). Full names of amino acids are listed in Table 8.3.

DFAA	Concentration (ng/mg wet weight) ($x10^{-4}$)			Molar %		
	d.f.	t	Significance level	d.f.	t	Significance level
ASP	7	0.015	n.s.	5	1.855	n.s.
GLU	9	1.883	n.s.	9	0.343	n.s.
ASN	8	1.711	n.s.	9	0.539	n.s.
SER	8	2.675	p<0.05	9	0.744	n.s.
GLN	6	3.360	p<0.01	9	2.173	n.s.
HIS	6	0.660	n.s.	7	0.220	n.s.
GLY+THR	9	0.922	n.s.	8	2.084	n.s.
ARG	9	0.054	n.s.	9	0.891	n.s.
β-ALA	5	4.269	p<0.01	5	4.390	p<0.01
TAU	5	1.855	n.s.	4	0.697	n.s.
ALA	5	3.441	p<0.02	6	2.271	n.s.
γ-ABA	8	1.100	n.s.	9	0.262	n.s.
TYR	9	1.085	n.s.	9	0.476	n.s.
TRP+MET	8	2.898	p<0.02	6	1.192	n.s.
VAL	9	1.729	n.s.	9	0.396	n.s.
PHE	9	1.139	n.s.	9	0.113	n.s.
ILEU	7	1.146	n.s.	9	0.196	n.s.
LEU	9	0.243	n.s.	9	1.049	n.s.
ORN	7	2.518	p<0.05	9	0.063	n.s.
LYS	8	0.565	n.s.	9	0.924	n.s.
TOTAL DFAA	6	4.104	p<0.01	-	-	-

Variation of DFAA concentration with time

Figures 8.8 a&b show how total DFAA concentrations varied with time for each test salinity for 5 and 15‰ acclimated mysids. Again, there was considerable variability

in the total DFAAs with time although most adjustment took place in the initial 12 hours of the tests. These results show that the total DFAA concentration of 5‰ acclimated *N. integer* varied significantly over the 96h test interval with significant changes recorded in the concentrations of a number of amino acids (glutamine, serine, histidine, glycine+threonine, β-alanine, taurine, alanine, γ-amino butyric acid, tryptophan+methionine, phenylalanine, ornithine and lysine) (Table 8.8).

Table 8.8 Results of MANOVA of amino acid concentration (ng/mg wet weight) against time accounting for salinity for *Neomysis integer* acclimated to 15 and 5‰. Full names of amino acids are listed in Table 8.3.

DFAA	15 ‰ acclimated mysids		5 ‰ acclimated mysids	
	F-ratio	Significance level	F-ratio	Significance level
ASP	0.54	n.s.	1.78	n.s.
GLU	0.61	n.s.	2.11	p<0.05
ASN	0.73	n.s.	0.75	n.s.
SER	1.84	n.s.	2.22	p<0.05
GLN	4.79	p<0.001	0.79	n.s.
HIS	0.87	n.s.	2.10	p<0.05
GLY+THR	1.36	n.s.	4.30	p<0.01
ARG	2.79	p<0.01	1.74	n.s.
β-ALA	0.35	n.s.	5.33	p<0.001
TAU	1.76	n.s.	2.16	p<0.05
ALA	2.26	p<0.1	2.41	p<0.05
γ-ABA	2.93	p<0.01	4.55	p<0.001
TYR	1.50	n.s.	1.21	n.s.
TRP+MET	0.68	n.s.	2.13	p<0.05
VAL	1.29	n.s.	1.29	n.s.
PHE	0.43	n.s.	2.92	p<0.01
ILEU	1.39	n.s.	1.34	n.s.
LEU	0.80	n.s.	1.55	n.s.
ORN	1.51	n.s.	5.12	p<0.001
LYS	1.32	n.s.	2.33	p<0.1
TOTAL	1.63	n.s.	4.78	p<0.001

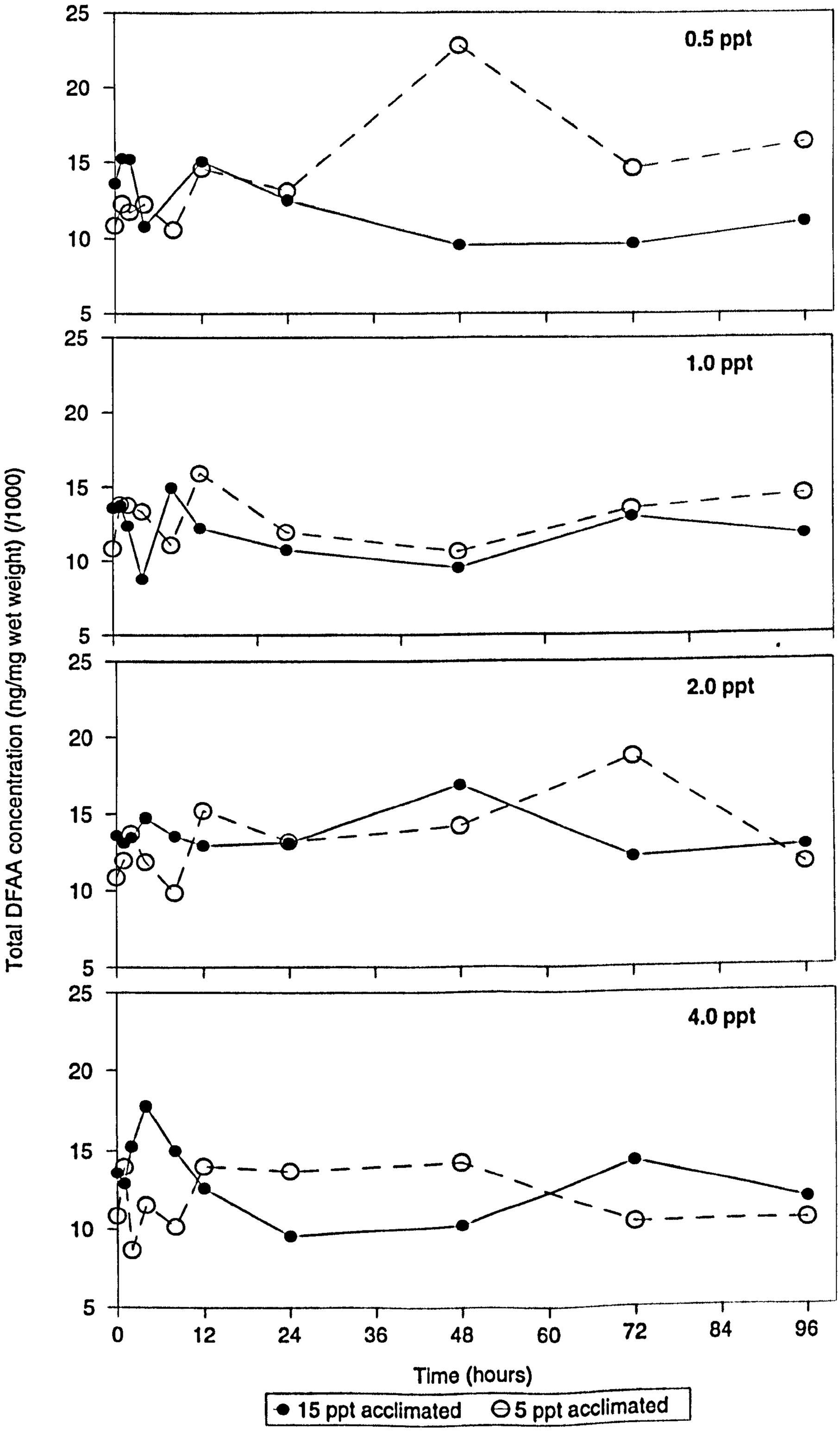


Figure 8.8a Changes in the total DFAA concentration (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 0.5, 1, 2 and 4 ‰ salinity after 7 days acclimation to 15 ‰ (dots) and 5 ‰ (circles).

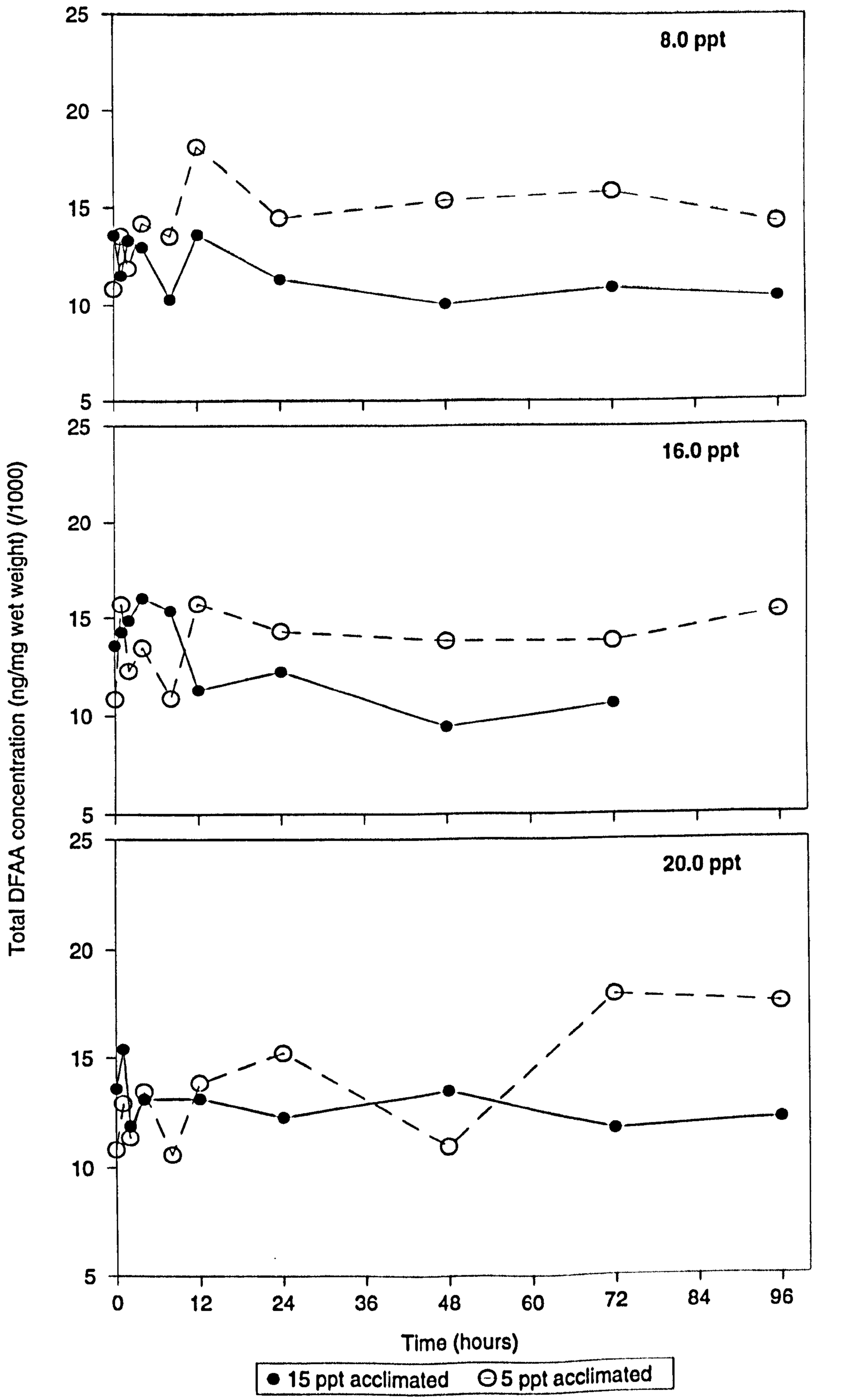


Figure 8.8b Changes in the total DFAA concentration (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 8, 16 and 20 ‰ salinity after 7 days acclimation to 15 ‰ (dots) and 5 ‰ (circles).

However, there was no significant change in the total DFAA concentration of 15‰ acclimated mysids over the test interval although significant changes were recorded in the concentrations of glutamine, arginine, alanine and γ-amino butyric acid (Table 8.8). The concentrations of the DFAAs which changed significantly with time after acclimation to 5‰ are plotted in Figures 8.9-8.11 at three time intervals. It appears from these figures that the greatest contributors to changes in total DFAA are glutamine, glycine+threonine, taurine, alanine and lysine. For *N. integer* acclimated to 15‰, the biggest contributors to changes in total DFAA were glutamine and alanine and to a lesser degree, arginine (Figs 8.12-8.14).

Variation of DFAA concentration with salinity

Test salinity did not have a significant effect on either individual amino acid concentrations or on the total DFAA concentrations in mysids acclimated to 15‰ salinity (Table 8.9). *Neomysis integer* acclimated to 5‰ did not show a significant change in total DFAA, but significant changes were observed in the concentrations of tryptophan+methionine, phenylalanine, isoleucine and leucine, (Table 8.9) which are all minor contributors to the total DFAA pool (Figs 8.15-8.17).

Relationship between haemolymph freezing-point depression and total DFAA concentrations

The relationships between haemolymph freezing-point depression and total DFAA concentrations are shown for each test salinity in Figure 8.18a&b for 15‰ acclimated *N. integer*, and in Figure 8.19 a&b for 5‰ acclimated *N. integer*. Changes in DFAA concentration are more closely mirrored by freezing-point depression in 5‰ than in 15‰ acclimated *N. integer*, despite the greater fluctuations seen in DFAA concentration in the former.

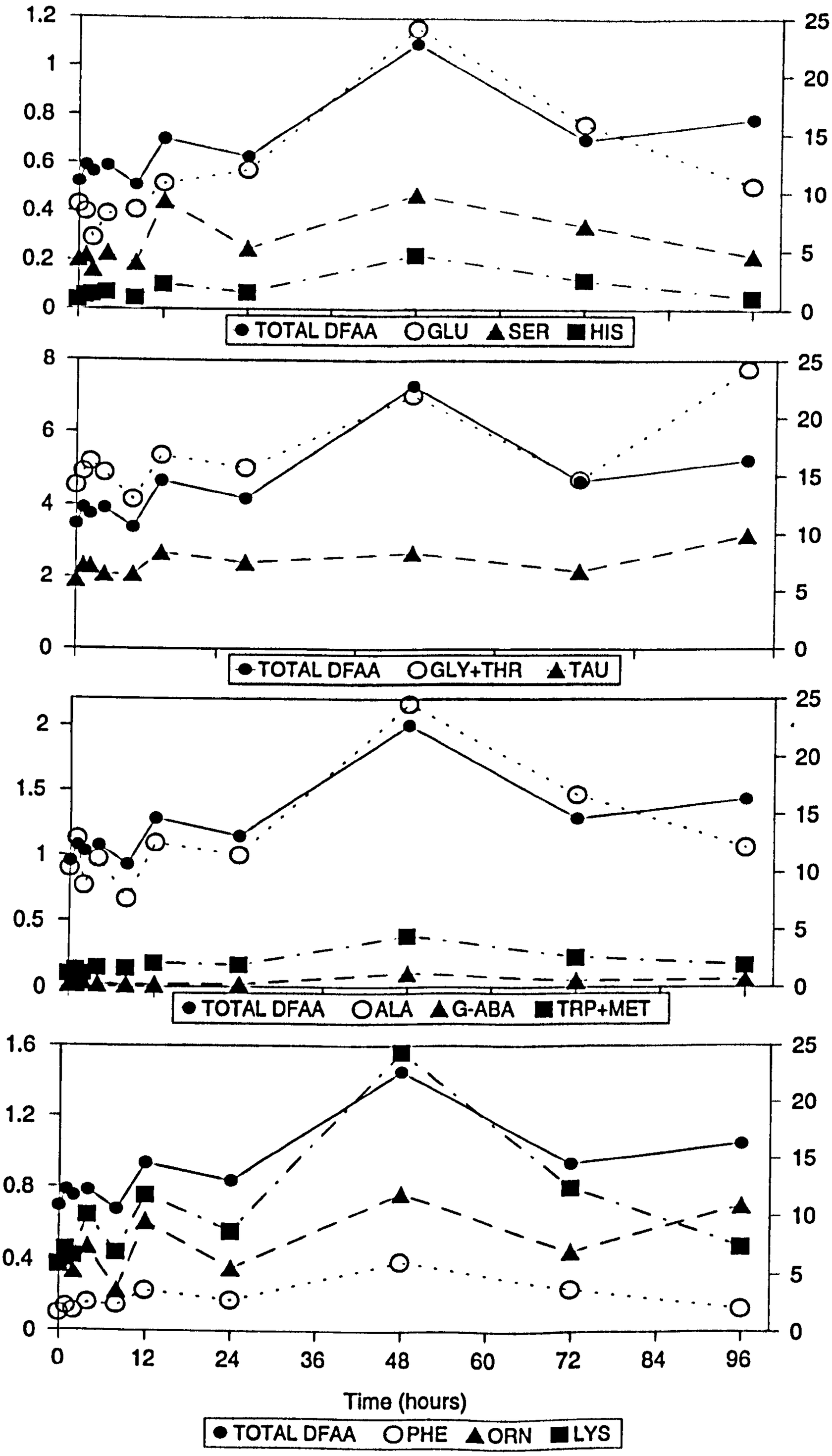


Figure 8.9 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 0.5 ‰ salinity after 7 days acclimation to 5 ‰. Full names of amino acids are listed in Table 8.3.

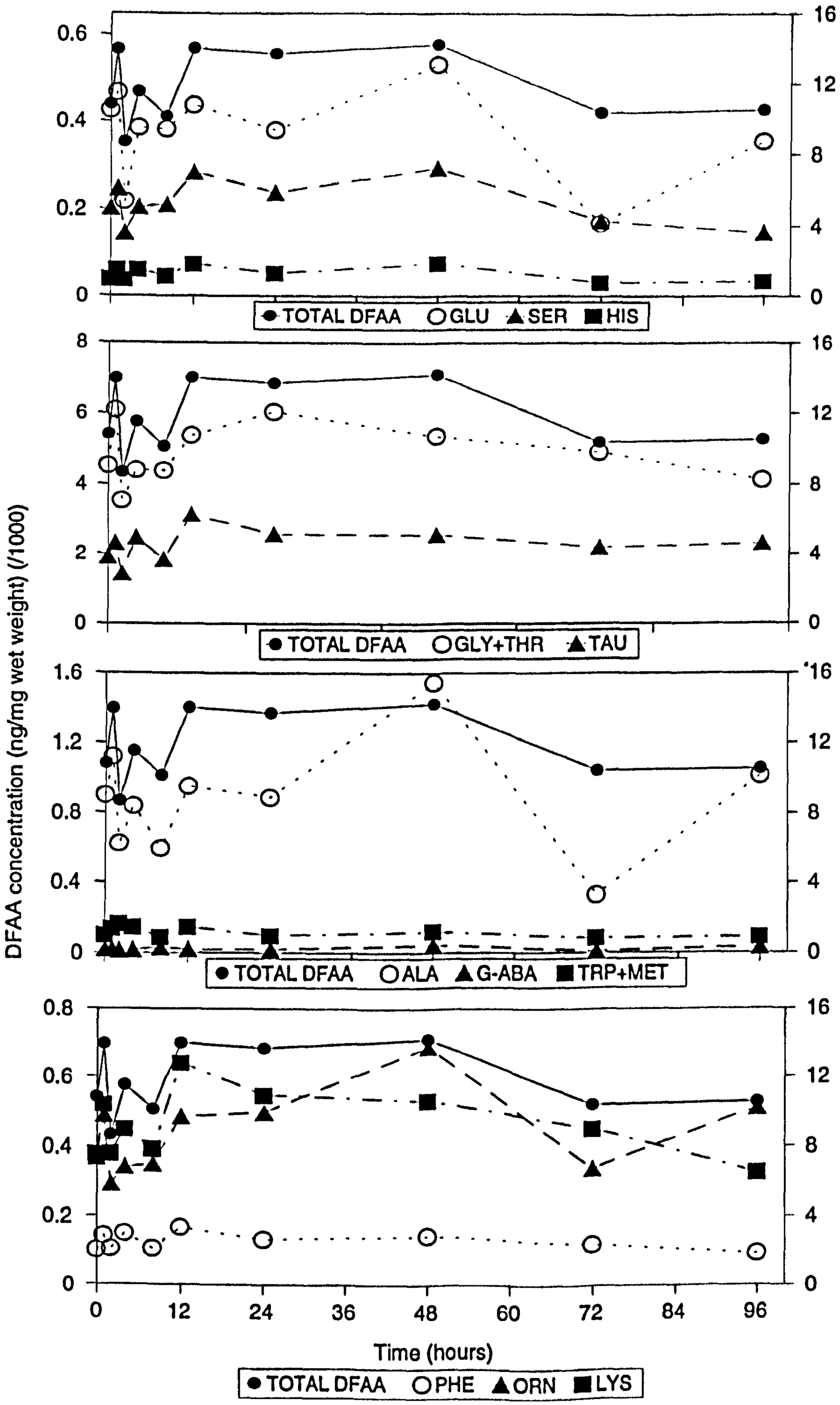


Figure 8.10 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 4‰ salinity after 7 days acclimation to 5‰. Full names of amino acids are listed in Table 8.3.

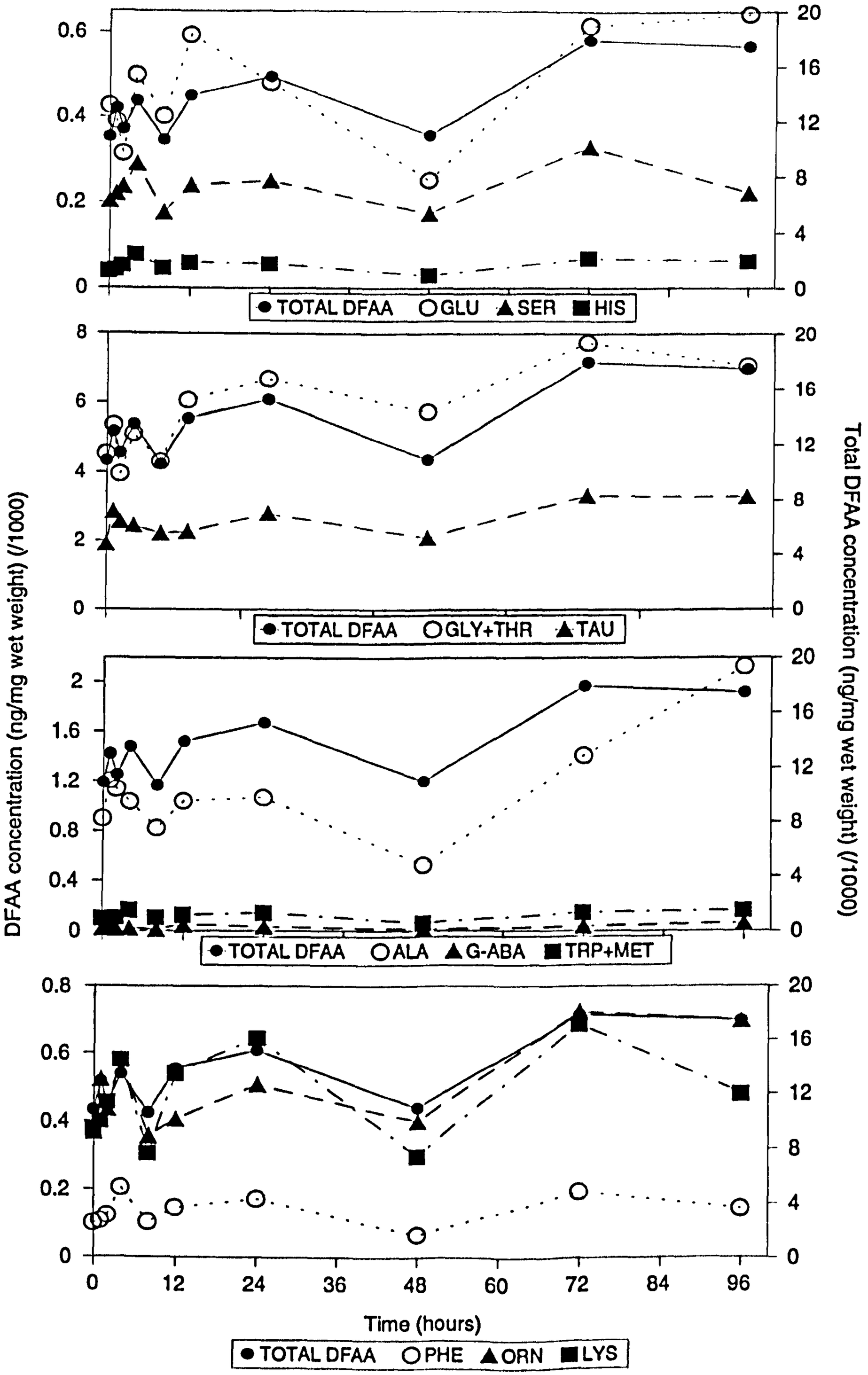


Figure 8.11 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 20‰ salinity after 7 days acclimation to 5‰. Full names of amino acids are listed in Table 8.3.

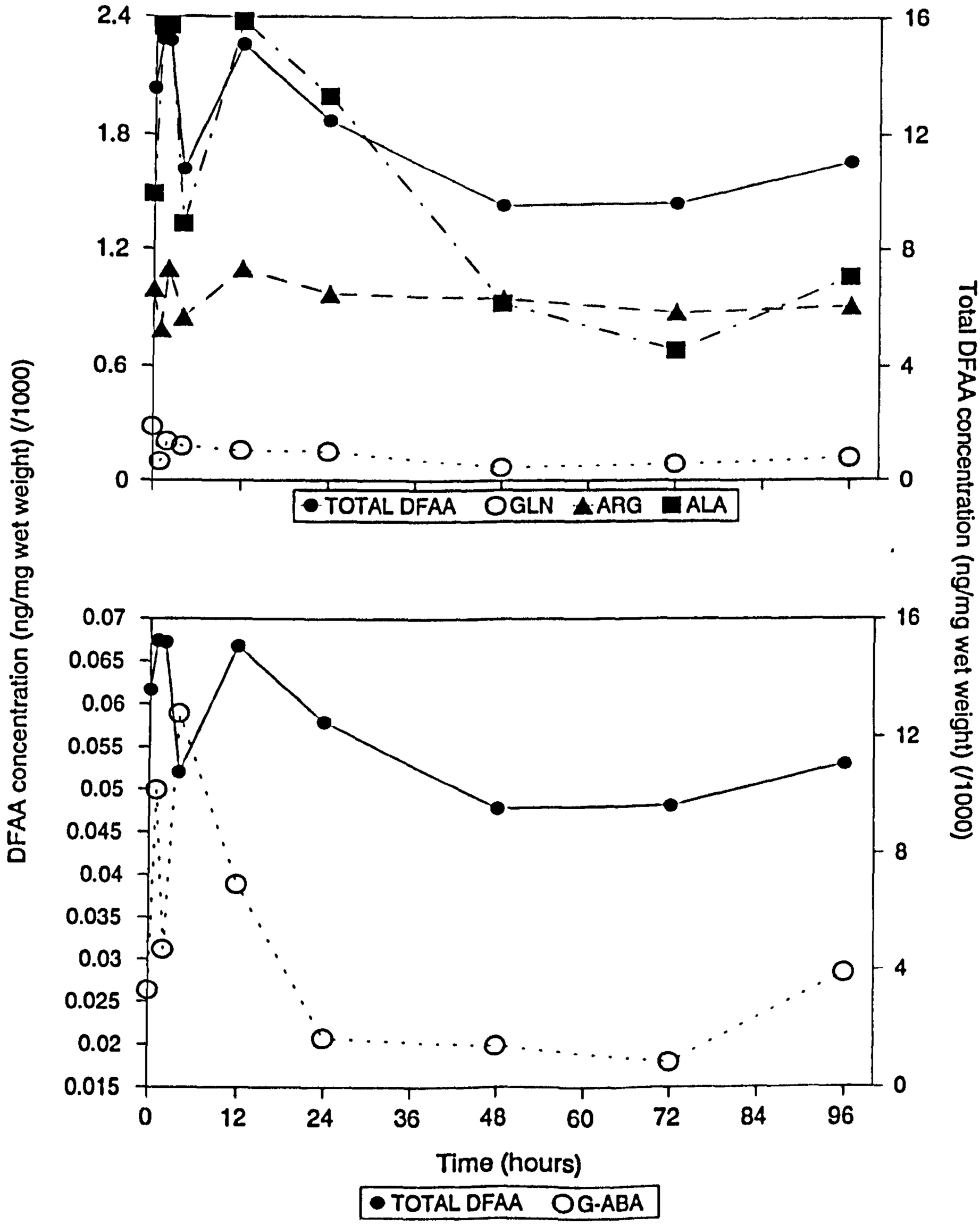


Figure 8.12 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 0.5‰ salinity after 7 days acclimation to 15‰. Full names of amino acids are listed in Table 8.3.

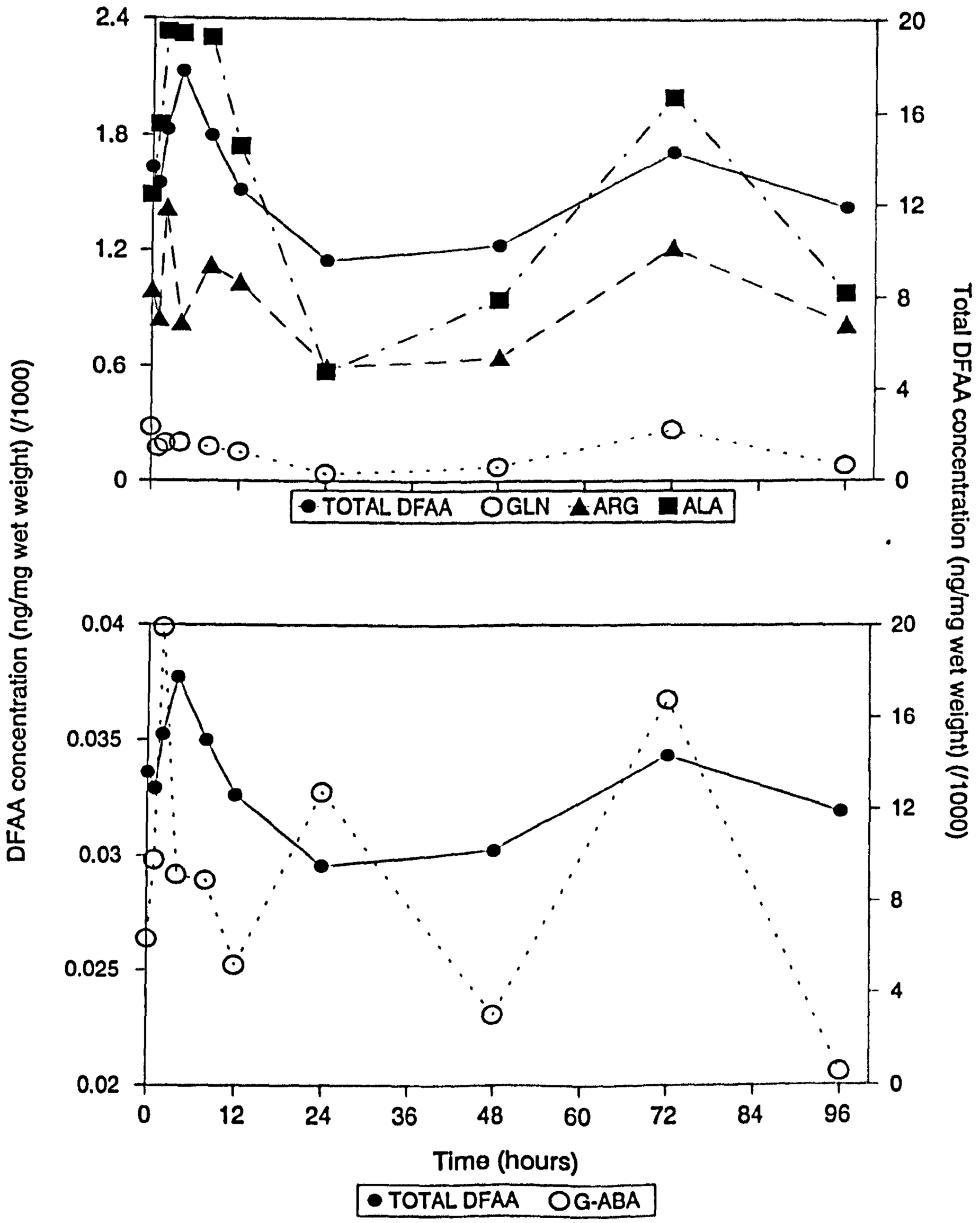


Figure 8.13 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 4 ‰ salinity after 7 days acclimation to 15‰. Full names of amino acids are listed in Table 8.3.

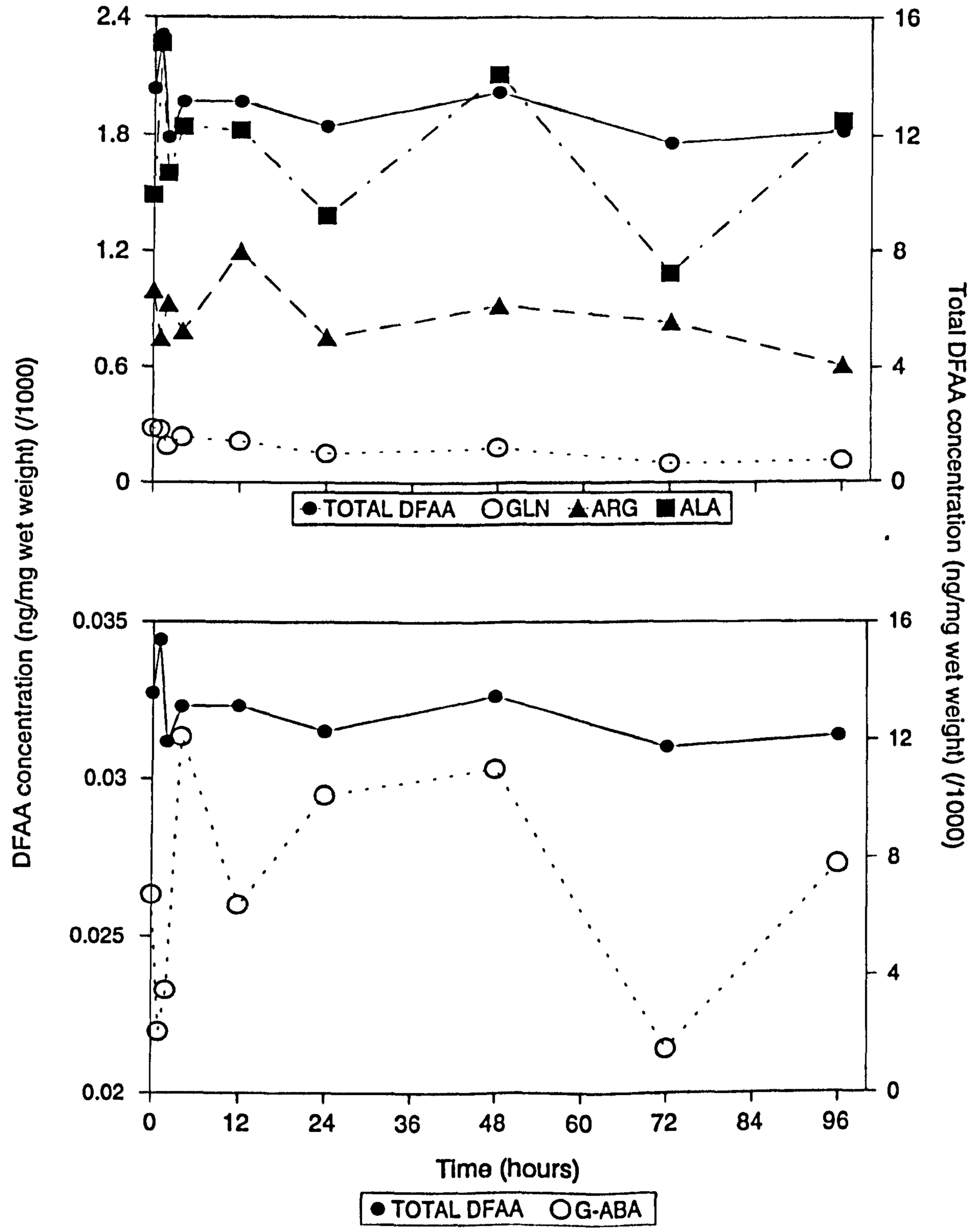


Figure 8.14 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* over time following sudden transfer to 20‰ after 7 days acclimation to 15‰. Full names of amino acids are listed in Table 8.3.

Table 8.9 Results of MANOVA of amino acid concentration (ng/mg wet weight) against test salinity (‰) accounting for time for *Neomysis integer* acclimated to 15 and 5‰. Full names of amino acids are listed in Table 8.3.

DFAA	15 ‰ acclimated mysids		5 ‰ acclimated mysids	
	F-ratio	Significance level	F-ratio	Significance level
ASP	1.19	n.s.	2.04	n.s.
GLU	0.65	n.s.	1.35	n.s.
ASN	0.86	n.s.	0.75	n.s.
SER	0.80	n.s.	1.75	n.s.
GLN	1.53	n.s.	0.99	n.s.
HIS	1.20	n.s.	1.21	n.s.
GLY+THR	0.36	n.s.	1.28	n.s.
ARG	1.54	n.s.	0.44	n.s.
β-ALA	0.52	n.s.	1.13	n.s.
TAU	0.46	n.s.	0.71	n.s.
ALA	0.69	n.s.	1.50	n.s.
γ-ABA	0.81	n.s.	1.81	n.s.
TYR	2.01	n.s.	2.17	n.s.
TRP+MET	1.08	n.s.	2.43	p<0.05
VAL	1.81	n.s.	1.95	n.s.
PHE	1.09	n.s.	2.99	p=0.01
ILEU	2.05	n.s.	2.34	p=0.05
LEU	1.47	n.s.	2.30	p=0.05
ORN	1.03	n.s.	2.10	n.s.
LYS	1.50	n.s.	1.64	n.s.
TOTAL	0.83	n.s.	1.62	n.s.

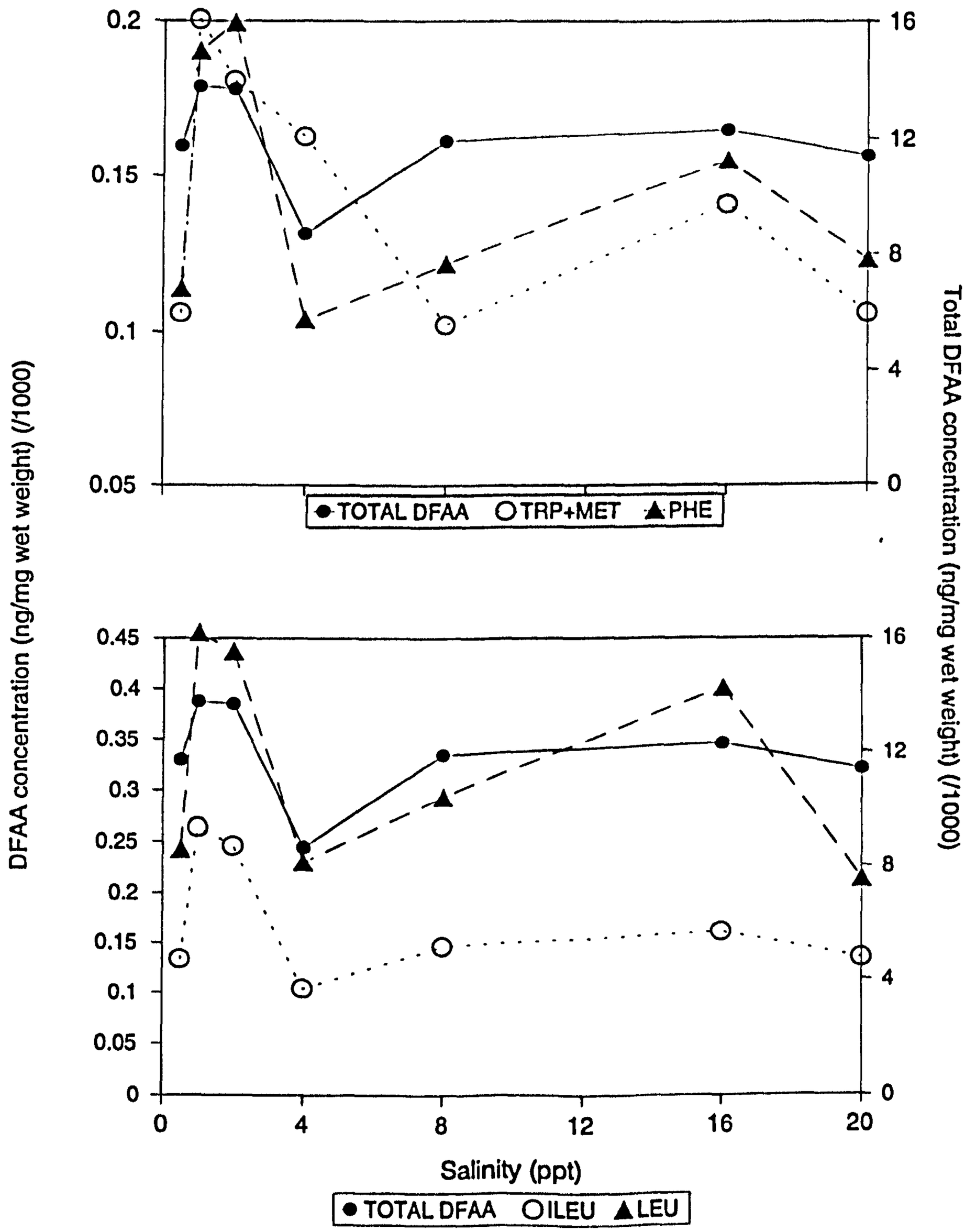


Figure 8.15 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* against test salinity after 2 hours and 7 days acclimation to 5‰. Full names of amino acids are listed in Table 8.3.

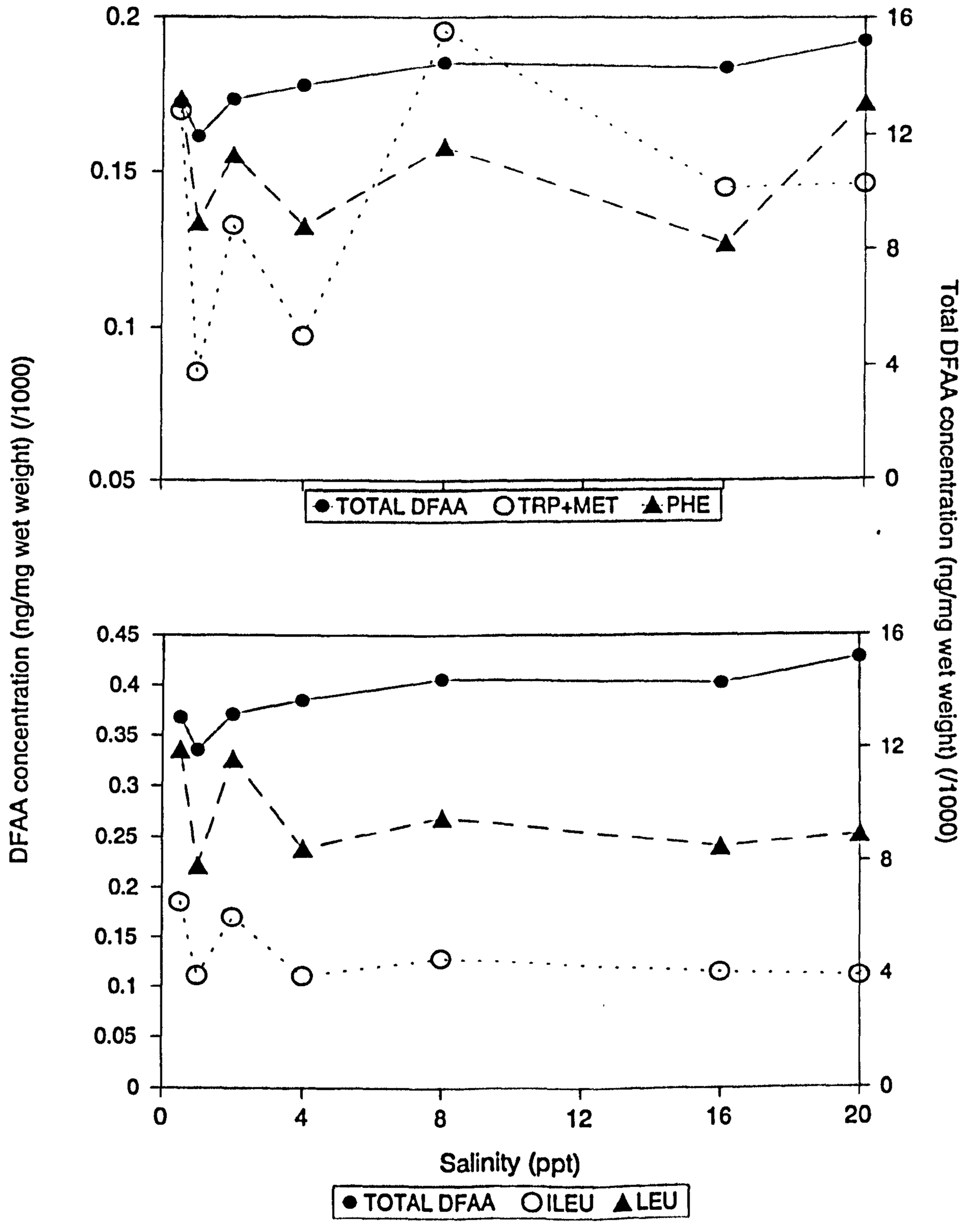


Figure 8.16 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* against test salinity after 24 hours and 7 days acclimation to 5‰. Full names of amino acids are listed in Table 8.3.

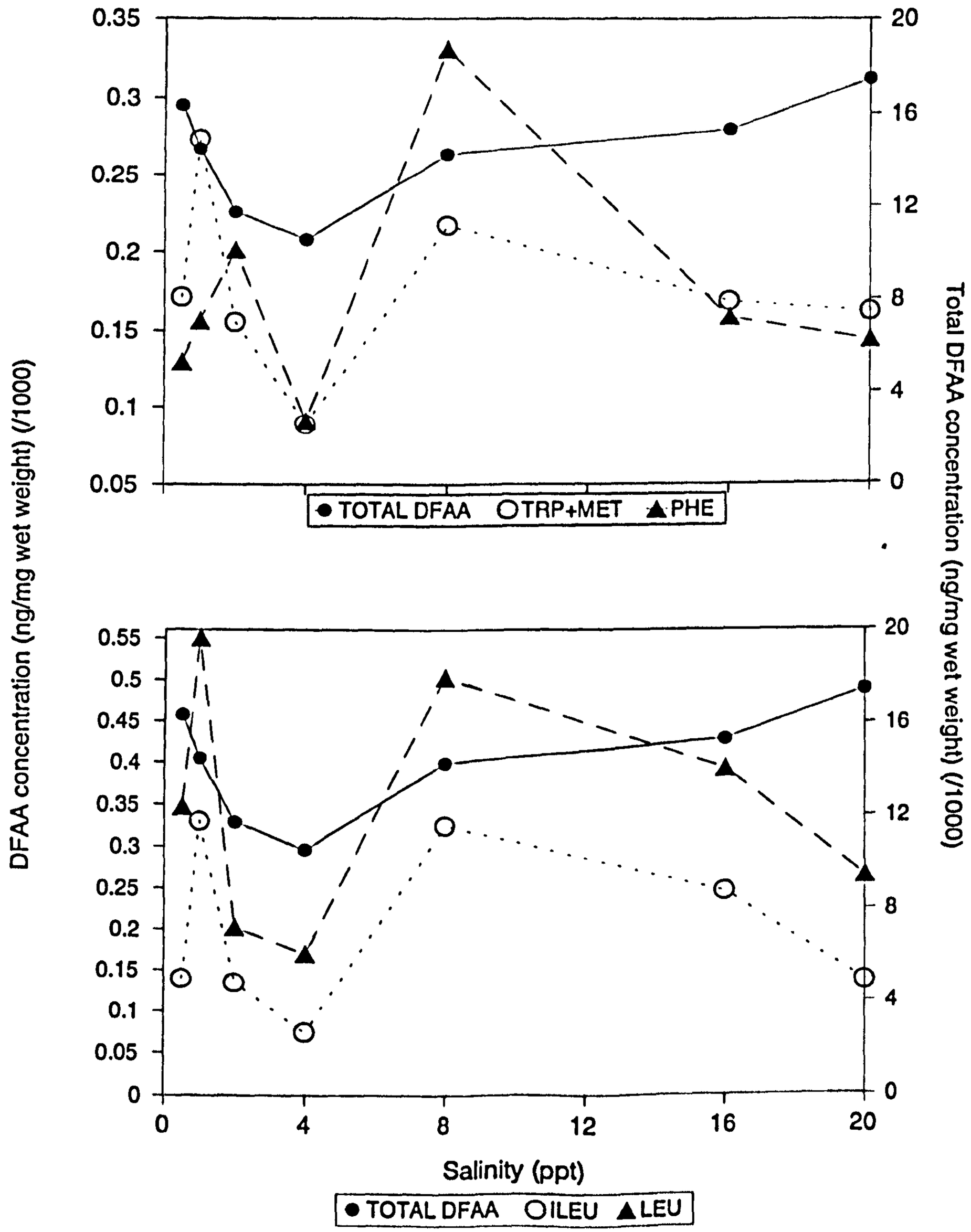


Figure 8.17 Changes in individual DFAA concentrations (ng/mg wet weight ($x10^{-3}$)) of *Neomysis integer* against test salinity after 96 hours and 7 days acclimation to 5‰. Full names of amino acids are listed in Table 8.3.

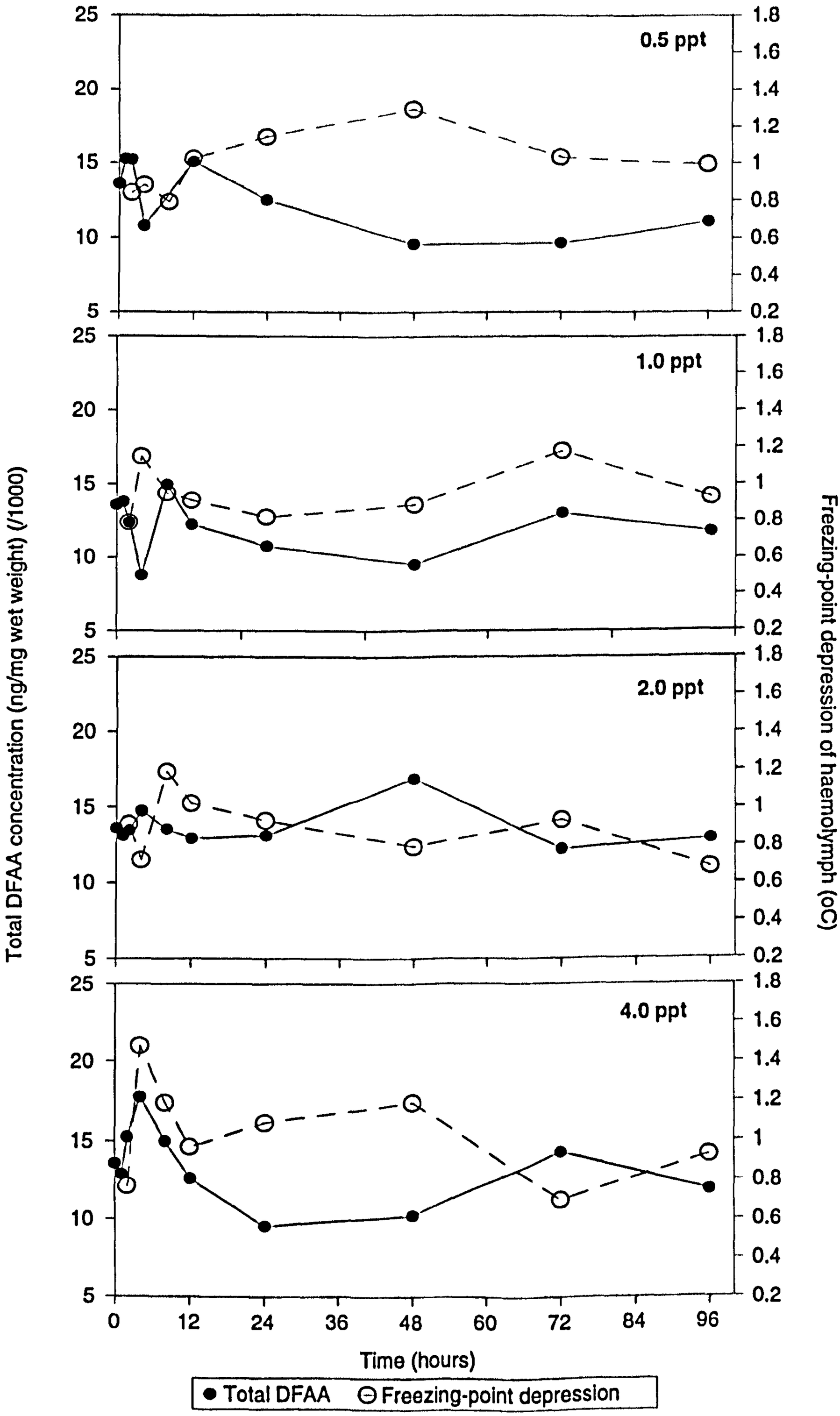


Figure 8.18a Changes in the total DFAA concentration (ng/mg wet weight ($x10^{-3}$)) (dots) and haemolymph freezing-point depression (°C) (circles) of *Neomysis integer* over time following sudden transfer to 0.5, 1, 2 and 4‰ salinity after 7 days acclimation to 15‰.

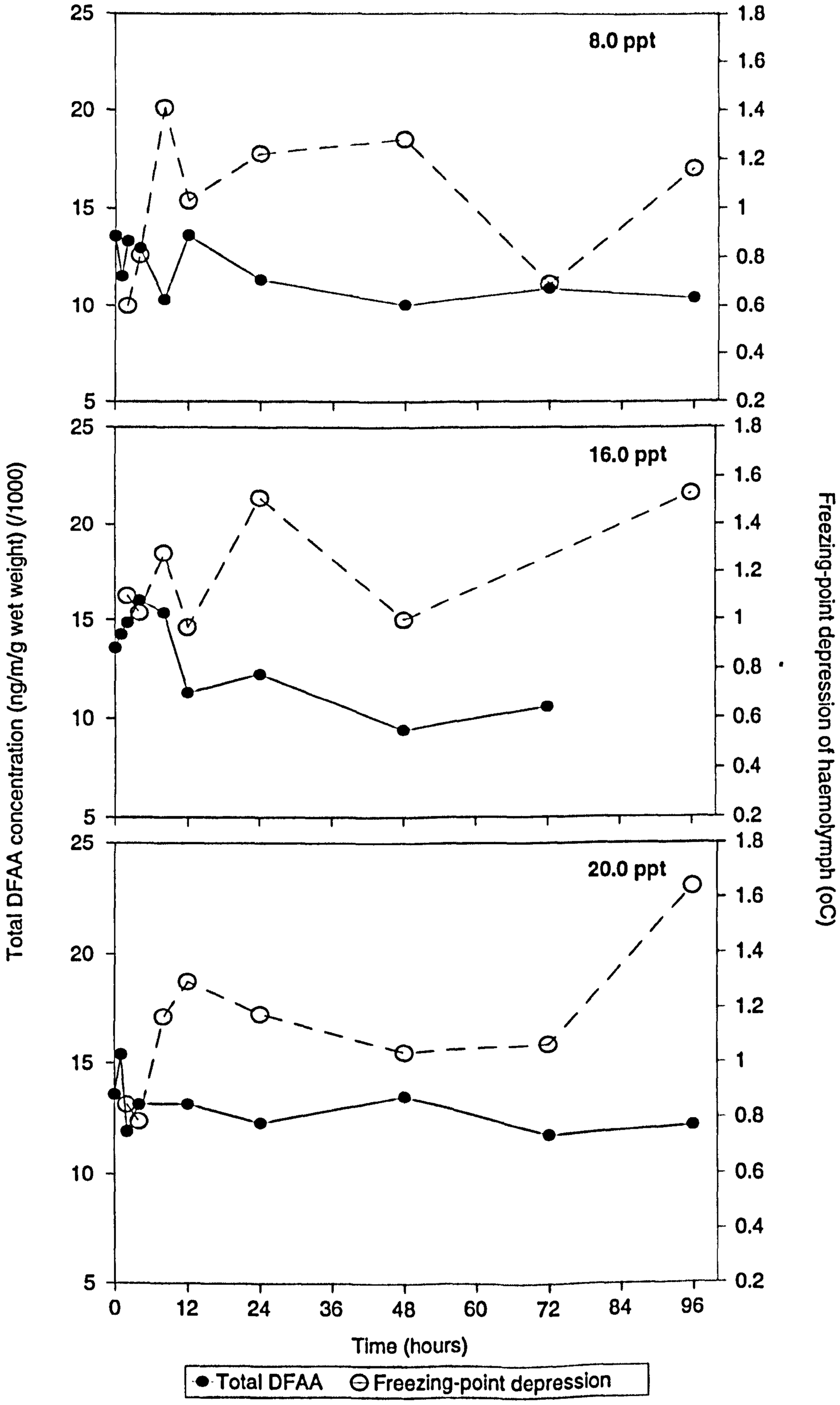


Figure 8.18b Changes in the total DFAA concentration (ng/mg wet weight ($x10^{-3}$)) (dots) and haemolymph freezing-point depression (°C) (circles) of *Neomysis integer* over time following sudden transfer to 8, 16 and 20‰ salinity after 7 days acclimation to 15‰.

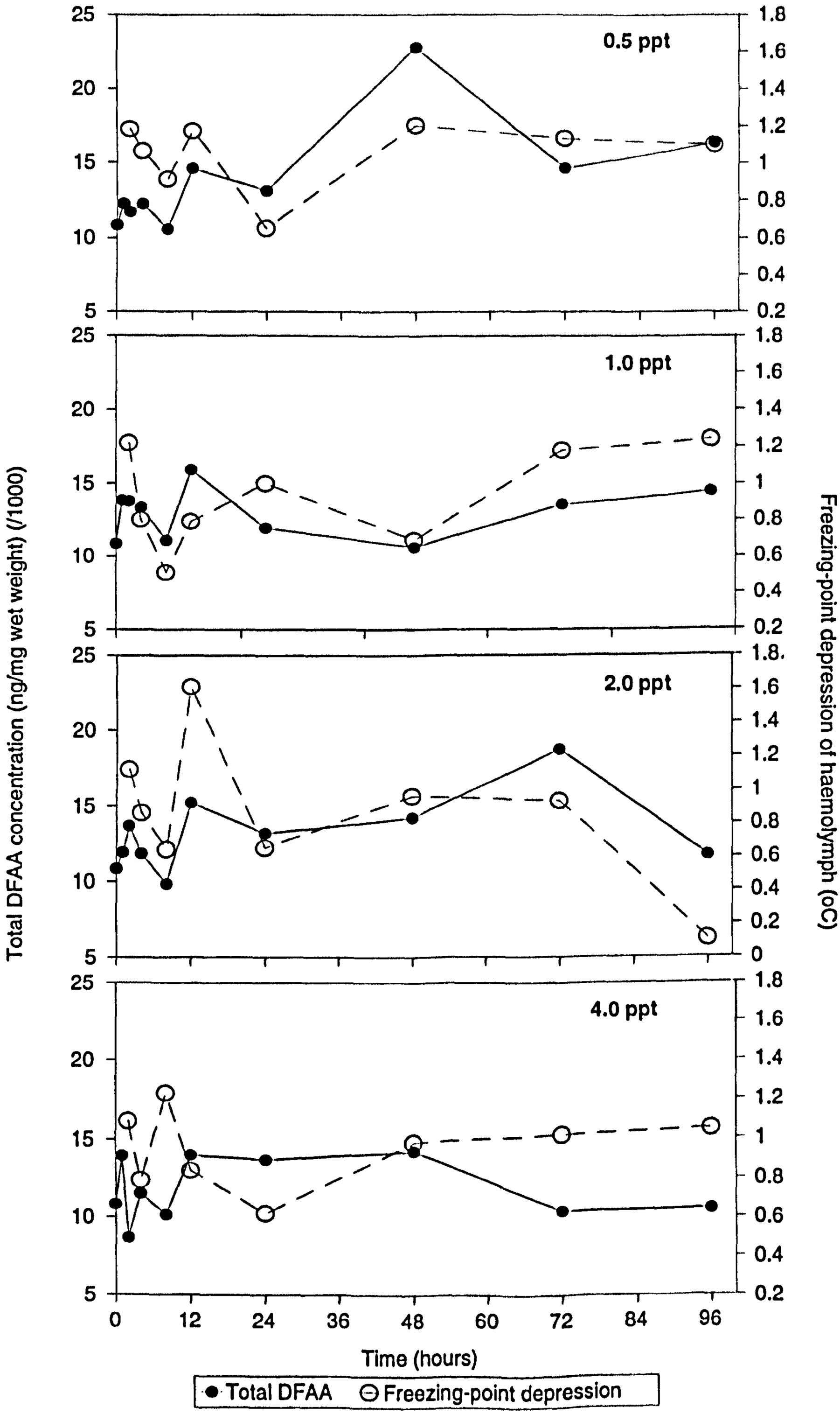


Figure 8.19a Changes in the total DFAA concentration (ng/mg wet weight ($x10^{-3}$)) (dots) and haemolymph freezing-point depression (°C) (circles) of *Neomysis integer* over time following sudden transfer to 0.5, 1, 2 and 4‰ salinity after 7 days acclimation to 5‰.

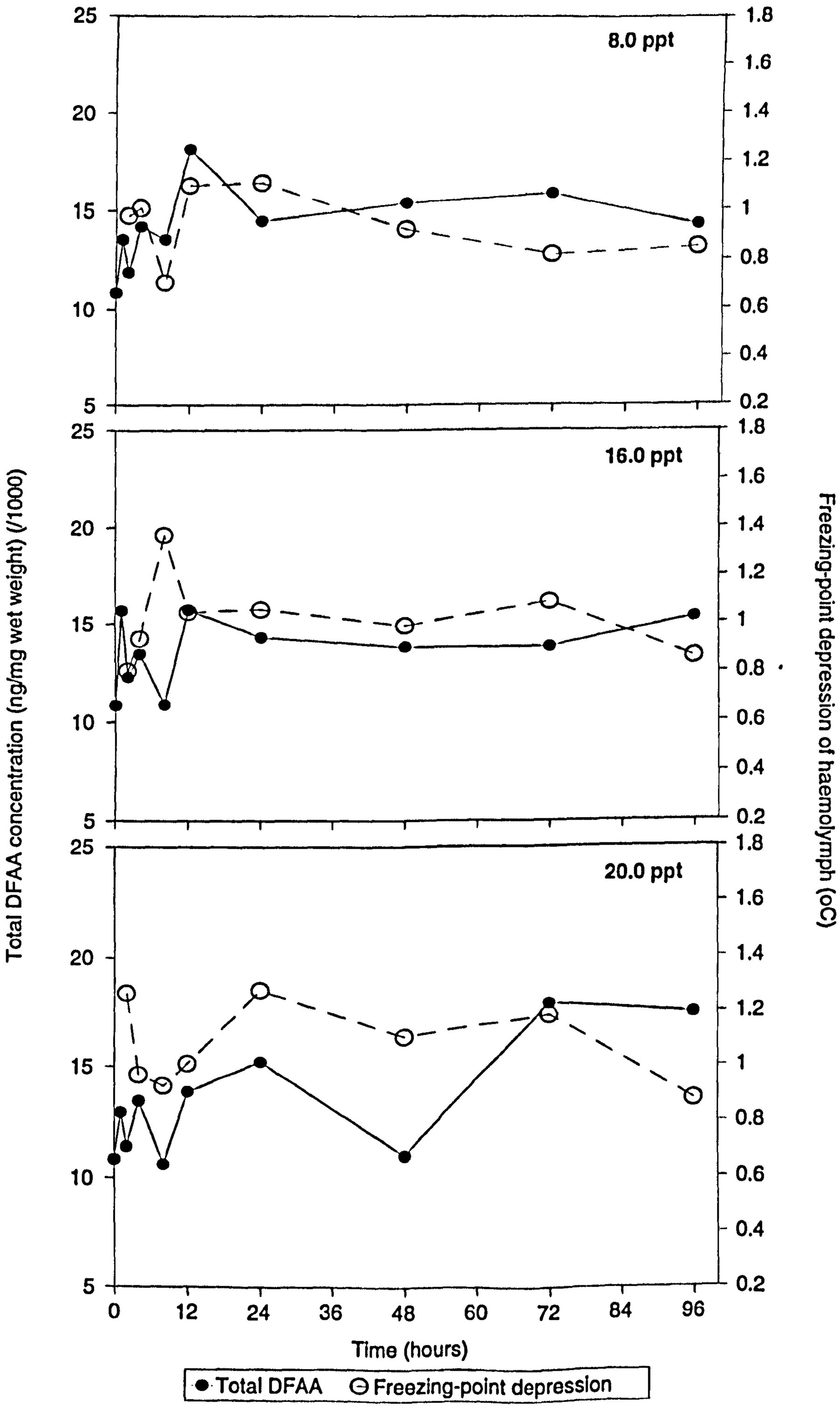


Figure 8.19b Changes in the total DFAA concentration (ng/mg wet weight ($x10^{-3}$)) (dots) and haemolymph freezing-point depression (°C) (circles) of *Neomysis integer* over time following sudden transfer to 8, 16 and 20‰ salinity after 7 days acclimation to 5‰.

8.4 Discussion

In Southampton Water, Ralph (1965) demonstrated that *N. integer* is a hypo-hyper-osmoregulator over salinities ranging from 5 to 41‰ with an isosmotic point of *c.*16‰, at 15°C and in Loch Etive, McLusky and Heard (1971) found the isosmotic point of *N. integer* haemolymph to be 19‰ at 5°C. It is not unusual for the blood osmotic concentration at a given salinity to vary between different populations of the same species. *Praunus flexuosus* from Loch Etive, Scotland maintain significantly higher blood osmotic concentrations than the same species in Isefjord, Denmark (McLusky and Heard, 1971; McLusky, 1979; McLusky *et al.*, 1982), and Theede (1969, in McLusky *et al.*, 1982) found that *Carcinus maenas* from Kiel Bay had greater blood osmotic concentrations than the same species from the North Sea when maintained at the same salinities. In this study, *N. integer* maintained its blood hyperosmotic to the test medium up to a salinity of 20‰ which is higher than previously reported for this species. The salinity at which the haemolymph becomes isosmotic with the external medium is often an indicator of the degree of adaptation of a species to its environment. In general, the isosmotic point decreases as the environmental salinity increases and this is probably an adaptation to life in conditions of reduced salinity. This has been demonstrated for palaemonid shrimps by Kirkpatrick and Jones (1985) who highlighted a general trend in reduction of isosmotic point for species which inhabit brackish water. Osmoregulation has also been examined for some other species of mysid; *Mysis relicta* (which is most commonly found in freshwater but also sometimes in brackish water, for example the Baltic) from Lake Ontario, Canada, is isosmotic at salinities ≥25‰, and *Praunus flexuosus* has an isosmotic point of 24‰ for low salinity (10‰) acclimated individuals and 21.8‰ for high salinity (35‰) acclimated individuals (Dormaar and Corey, 1978; McLusky *et al.*, 1982). No effect of acclimation salinity was found in the present study.

In relating the results from this chapter on osmoregulation and DFAA regulation in *Neomysis integer* from the Looe Estuary to the results on distribution of *N. integer* in the Tamar Estuary described in §6.1, the assumption has been that the populations of *N. integer* from both the Looe and Tamar Estuaries are physiologically similar. This assumption was not tested, and its truth should be confirmed particularly because the results of the life-history study (§6) indicate that *N. integer* in the River Tamar Estuary is more euryhaline than the isosmotic point (>20‰) of the same species from the Looe Estuary would suggest.

The percentage molar composition of individual DFAAs in *N. integer* in the present study correspond with those recorded by Srinivasagam *et al.* (1971) (Table 8.10), although

absolute concentrations vary considerably, perhaps due to differences in analytical techniques between the two studies. It would appear from Srinivasagam *et al.* (1971) that the glycine+threonine component is comprised primarily of glycine and therefore this pair of amino acids will be considered to represent glycine, for descriptive purposes. Eighty-six percent of the total DFAA in *N. integer* is accounted for by just three amino acids: glutamine, glycine+threonine and taurine.

There was a great deal of variability in concentrations of individual amino acids in animals acclimated to the different salinities. It is not uncommon to find a degree of variation between the levels of amino acids in individuals kept under similar conditions. Lockwood (1976) suggested that individual differences may be attributed either to internal or external factors such as stage in the moult cycle or oxygen tension of the medium. Lockwood (1976) also concluded that Crustacea probably do not control individual amino acids very precisely and that as far as osmotic regulation is concerned the precise component which contributes to the overall activity is immaterial.

The effect of acclimation on the salinity tolerance of Crustacea has been examined by some workers. In the mysid *Mysidopsis bahla* (Molenock), individuals acclimated to high salinities were able to tolerate a wider range of salinities than those acclimated to low salinities (De Lisle and Roberts Jr, 1986). In the present study, there was no difference in the blood osmotic concentration between *Neomysis integer* acclimated to high or low salinities. However, total DFAA concentrations were significantly higher in 15‰ acclimated *N. integer* than in 5‰ acclimated individuals mainly due to increases in alanine, glutamine, serine, β-alanine (which was not detected in 5‰ acclimated individuals), tryptophan+methionine and ornithine. This corresponds with the findings of Harris (1969) who found that the isopod *Sphaeroma rugicauda* had significantly reduced DFAA concentrations when acclimated to 2% seawater (0.7‰) than when acclimated to 100% seawater (35‰). Examination of the fluctuations in total DFAA concentrations over time following transfer to test salinities also showed an effect. Individuals acclimated to low salinity (5‰), showed greater fluctuations of total DFAAs over 96 hours with the greatest changes being seen in the concentrations of glutamine, glycine, taurine, alanine and lysine. These fluctuations in total DFAA were not significant in *N. integer* acclimated to 15‰. Glycine, alanine and taurine have been shown to be important osmoeffectors in the isopod *Sphaeroma rugicauda*, and Armitage and Morris (1982) found that glycine, alanine, proline, glutamate and valine increased in *N. integer* from Southampton Water as it adapted to increasing salinity. One of the explanations for the lack of a clear increase or decrease in individual DFAAs over time in the present study may be due to the fact that major changes in DFAA concentrations occur over a period of a few hours rather than days (similar to changes in haemolymph osmotic concentration). Large changes in DFAA concentration

were observed by Armitage and Morris (1982), in *N. integer*, and these changes occurred over a period of up to four hours rather than the longer time period examined in this study.

Table 8.10 Comparison of Molar percentage of total DFAA concentration (ng/mg wet weight) between this study and previous work.

DFAA	Mean molar % (15‰ acclimated *N. integer*, this study)	Molar % (Srinivasagam *et al.*, 1971)*
ASP	1.64	1.9
GLU	4.11	5.5
ASN	0.83	-
SER	1.99	1.4
GLN	20.6	-
HIS	0.43	1.5
GLY+THR	35.98	32.2 (30.9+1.3)
ARG	7.36	19.1
β-ALA	0.22	-
TAU	20.33	23.1
ALA	11.00	3.8
γ-ABA	0.19	-
TYR	1.01	0.6
TRP+MET	1.12	0.9 (0.7+0.2)
VAL	1.45	1.0
PHE	0.91	0.4
ILEU	1.11	0.6
LEU	1.74	0.7
ORN	3.47	0.1
LYS	3.05	1.5
Cystine+Cysteic acid	-	1.4
Proline	-	4.2
TOTAL	100	99.9

* These authors do not report the salinity of the River Test Estuary from which their *N. integer* were obtained.

These authors found that adjustment of DFAA concentrations to salinity change was time-related and occurred during either low or high water, rather than during stages of the tide when salinity was increasing or decreasing. Generally, it is the non-essential DFAAs which provide both the bulk of the free amino acid pool and the major part of any osmotic adjustment. Glutamine, glycine, taurine and alanine are non-essential amino acids in Crustacea (Bishop, 1976) and the changes of these DFAAs described in this study are likely to be in response to osmoregulatory activity. Lysine, the fourth DFAA which showed large fluctuations in the present study, is an essential amino acid in Crustacea and it is unlikely that the changes seen were related to osmotic adjustment. This is also probably the case for the other DFAAs (Tryptophan+methionine, phenylalanine, isoleucine, leucine, arginine, γ-amino butyric acid, ornithine, lysine and histidine), all essential amino acids, which showed significant changes during these experiments.

In conclusion, *Neomysis integer* from the Looe Estuary acclimated to low salinities had significantly lower total DFAA concentration than those acclimated to higher salinity. In low salinity acclimated individuals there was a greater variation of total DFAA concentration over time which could be ascribed primarily to changes in the non-essential amino acids glutamine, glycine, taurine and alanine. Changes in total DFAA concentrations parallelled changes in the haemolymph osmotic concentration confirming that DFAAs are important in determining osmoregulatory capability in this species. The isosmotic point of *N. integer* in the Looe Estuary, at >20‰, is higher than that previously reported for this species.

Mesopodopsis slabberi would have been the test species of choice in the osmoregulation experiments had it been possible to maintain it in the laboratory. Difficulty in maintaining this species in the laboratory has been experienced by other workers (M.B. Jones, personal communication). Individuals of this species, when brought into the laboratory and placed in aquaria, migrated towards the water surface and became trapped in the surface film. This occurred even when the aquaria were kept in the dark. One explanation for the lack of success in maintaining *M. slabberi* in the laboratory is light damage to the eyes during capture resulting in disorientation. *Mesopodopsis slabberi* has prominent stalked eyes and is found in the relatively high turbidity (and presumably low light) regions of the Tamar Estuary (§7.1.8). Lindström (1992) has demonstrated that the eyes of the deep water mysid *Mysis relicta* are easily damaged by light and has suggested that this damage may explain the poor success of transplanting this latter species from one lake to another (to provide a food supply for fish) in Finland. Lindström (personal communication) has suggested that success in capturing this species may be obtained by sampling and maintaining it in the dark. Further work is required to develop a method of maintaining or culturing this species in the laboratory.

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSIONS

9. GENERAL DISCUSSION AND CONCLUSIONS

Invertebrates which occur in estuarine waters may adapt to conditions in one or more ways including detection and avoidance of salinity changes, physiological and morphological adaptation to salinity and short-term tolerance of extreme conditions. These adaptations are often coupled with mechanisms to maintain the species within the estuary and may include reduction in the length of larval life and migrations, both laterally and vertically in the water column, which prevent individuals being swept out to sea. Superimposed on these adaptations, are recognisable seasonal patterns of reproduction (Lockwood, 1976).

This study has examined the geographical distribution patterns of the mysid fauna of the River Tamar Estuary and related observed distributions to a range of environmental variables (salinity, temperature, turbidity and runoff). Changes in geographical distribution have been described with reference to *Neomysis integer* and the physiology underlying its amino acid composition and osmotic regulation. Seasonal changes in abundance, biomass and brood characteristics of the most abundant species found in the estuary, *Mesopodopsis slabberi* have been described and quantified. This study represents a contribution to knowledge of the ecology of the River Tamar Estuary and, in particular, to the life-history characteristics of *M. slabberi*.

9.1 Life-history and distribution

The presence year-round of four species of mysid in the estuary has been confirmed, two (*Praunus flexuosus* and *Schistomysis ornata*) with a distribution limited to the higher salinity regions of the estuary are described in §4 and two (*M. slabberi* and *N. integer*) which are widely distributed from the high salinity regions (at low densities) to the very low salinity end of the estuary coincident with the zone of maximum turbidity are described in §6 & §7. Although no attempt was made in this study to identify or quantify other components of the community, observations of the samples from which the mysids were extracted (detailed in Appendix 1) showed that larval fish were present in the upper estuary between February and October and were found even in the low salinity (<5‰) regions of the upper estuary; these fish larvae could have exerted considerable predation pressure on the two main mysid species in the upper estuary. Fish are known to be major predators of mysid shrimps in the Tamar Estuary (Hartley, 1929).

The possible three generation life-history which has been described for *M. slabberi*, is a larger number of generations than previously reported for this species, and evidence has

been found for alternating generations between years (§7.1.1). For the first time growth, biomass and production estimates have been obtained for *M. slabberi*. Production estimates of between 50 and 241 mg dry weight y^{-1} are of the same order of magnitude as those found for other temperate mysid species (*eg. N. integer* in the Westerschelde (Mees *et al.*, 1994)) (§7.1.5), but are considerably lower than found for the related mysid *M. wooldridgei* on the eastern Cape of South Africa. It was not possible to fully describe the life-history, nor obtain production estimates for *N. integer* because of a failure to sample fully all life history stages (§6.1 & 6.2). However, *N. integer*, because of its larger size, and abundance which, at least, equals that of *M. slabberi* at some times of the year is likely to be a far greater contributor to biomass and production in the estuary. Both *N. integer* and *M. slabberi* have distributions in the estuary which can be related to salinity gradients and, in the case of *M. slabberi*, a clear separation of cohorts in the population on the basis of salinity was described (§7.1.8). There was also a suggestion that juvenile *N. integer* had a different salinity distribution to the adult stages (§6.2).

9.2 Osmoregulation and changes in amino acids

Neomysis integer in the Tamar estuary is euryhaline and able to tolerate salinities in the range 0.5-30‰ (§6.1). In the laboratory, *N. integer* acclimated to low salinities had significantly lower total dissolved free amino acid (DFAA) concentrations than the same species acclimated to higher salinity. In low salinity acclimated individuals there was a greater variation of total DFAA concentration over time which could be ascribed primarily to changes in the non-essential amino acids glutamine, glycine, taurine and alanine. Changes in total DFAA concentrations parallelled changes in the haemolymph osmotic concentration confirming that DFAAs are important in determining osmoregulatory capability in this species. The isosmotic point of *N. integer* in the Looe Estuary, at >20‰, is higher than that previously reported for this species, but remains in the range of other brackish water crustaceans (§8.4).

9.3 Comments on methodology and further work

Conical plankton nets were used in the upper estuary in this study for pragmatic reasons. However, although they proved successful in sampling the more pelagic *Mesopodopsis slabberi*, they were clearly unsuccessful in efficiently sampling *Neomysis integer*. An epibenthic sledge, as used in the lower estuary, would be the sampler of choice. However, in this study, there were practical difficulties in using the large epibenthic sledge available in the shallower upper reaches of the estuary. These difficulties related to non-availability of a vessel with sufficiently shallow draft and also equipped with a winch. An epibenthic

sledge would also have been unsuitable for sampling the shallow margins of the estuary which it is possible that the bulk of the *N. integer* population utilised. Sampling from the shore using hand-held dip nets could have been used to confirm the presence of *N. integer* in these regions of the estuary. However, samples obtained in this way are difficult to quantify.

In attempting to describe the relationship between salinity and distribution of the two upper estuary mysid species, the sampling methodology could have been improved upon. It is now clear that the choice of sampling stations in each month should have been made according to a defined salinity series, rather than the chosen method of fixed sampling stations. This would have allowed direct comparisons of monthly samples from the same salinity rather than having to group samples in salinity bands in order to compare salinity bands between months (§6.1 and §7.1.8).

The life-history characteristics of *N. integer* in the Tamar Estuary have yet to be described fully, and an estimate of production for this species in the estuary would assist in completing an ecological model for the estuary. In view of the demonstrated séparation of the different life history stages of *M. slabberi* along the salinity gradient, further laboratory work should concentrate on the salinity tolerance of the different life-history stages of this species and its osmoregulatory ability, including the contribution of amino acids. In the field, the ability of this species to undergo vertical and/or horizontal migrations on a diurnal or tidal basis should be examined to attempt to explain the mechanism by which the different life-history stages are able to maintain a spatial separation, and prevent being washed out from the estuary. More frequent sampling, at least every two weeks during the main breeding period of April to November would enable the generation frequency of *M. slabberi* to be established with more certainty. Extending any further sampling programme (into the area of Plymouth Sound around the mouth of the estuary and including both the Rivers Lynher and Tavy) and ensuring more comprehensive coverage of the lower estuary would help clarify the extent of any downstream seasonal migrations of both *N. integer* and *M. slabberi*. An extended sampling programme could also be used to assess the contribution of the two lower estuarine species *Schistomysis ornata* and *Praunus flexuosus* to the biomass available to other components of the estuarine community.

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APPENDIX I

DESCRIPTION OF SAMPLES

APPENDIX I Description of samples for all stations and dates showing presence or absence of mysids, fish larvae and zooplankton. (M=*Mesopodopsis slabberi*, N=*Neomysis integer*, P=*Praunus flexuosus*, S=*Schistomysis ornata*).

Date & station	Mysids	Fish larvae	Zooplankton
LOWER ESTUARY			
27 January 1989			
1	M, P, S	-	-
2	M, S	-	-
3	M, S	-	-
22 March 1989			
1	M, N, P, S	✗	-
2	M, S	✓	-
3	M, N, P, S	✓	-
21 April 1989			
1	M, N, P	✓	-
2	M, N, P, S	✓	-
3	M, N, P, S	✓	-
19 May 1989			
1	P, S	✓	-
2	P, S	✓	-
3	M, N, P, S	✓	-
9 June 1989			
1	P, S	✓	-
2	M, N, P	✓	-
3	M, N, P, S	✓	-
1 December 1989			
1	M, N	✗	-
2	M, P, S	✗	-
3	M, N, S	✗	-
UPPER ESTUARY			
6 February 1989			
10	M, N, P, S	✗	✗
11	M, N	✓	✗

Date & station	Mysids	Fish larvae	Zooplankton
12	M, N	✓	✗
13	M, N	✓	✗
14	M, N	✓	✗
15	M, N	✓	✗
16	M, N	✓	✗
17	N	✓	✗
18	N	✓	✗
19	N	✓	✗
20	N	✓	✗
17 February 1989			
9	✗	✗	✗
10	M	✓	✗
11	M	✗	✗
12	M	✗	✗
13	M	✗	✗
14	M, N	✗	✗
15	M, N	✗	✗
16	N	✓	✗
17	N	✗	✗
18	N	✗	✗
19	N	✗	✗
20	✗	✗	✗
20 March 1989			
10	M	✓	✓
11	M	✗	✓
12	M	✓	✓
13	M	✓	✓
14	✗	✓	✗
15	✗	✓	✗
16	N	✓	✗
17	✗	✗	✗
26 April 1989			
10	M, N	✓	✓
11	M, N	✓	✓

Date & station	Mysids	Fish larvae	Zooplankton
12	M, N	✓	✓
13	M, N	✓	✓
14	M, N	✓	✓
15	N	✓	✗
16	N	✓	✗
17	N	✓	✗
12 May 1989			
10	M	✓	✓
11	M	✓	✓
12	M	✓	✓
13	M, N	✓	✓
14	M, N	✓	✓
15	M, N	✓	✓
16	M	✓	✓
17	M	✓	✓
7 June 1989			
10	M, N	✓	✓
11	M, N	✓	✓
12	M, N	✓	✓
13	M, N	✓	✓
14	M, N	✓	✓
15	M, N	✓	✗
16	M, N	✓	✗
17	M, N	✓	✗
18	M, N	✓	✗
19	M, N	✓	✗
14 July 1989			
11	M, N	✓	✗
12	M, N	✓	✗
13	M	✓	✗
14	M	✓	✗
15	M, N	✓	✓
16	M, N	✓	✓
17	M, N	✓	✗

Date & station	Mysids	Fish larvae	Zooplankton
18	M, N	✓	✗
19	M, N	✓	✗
20	M, N	✓	✗
21	N	✓	✗
25 September 1989			
10	M	✓	✓
11	M, N	✗	✓
12	M, N	✓	✓
13	M, N	✓	✓
14	M	✗	✓
15	M	✗	✓
16	M	✗	✓
17	M	✗	✓
18	M	✗	✗
19	M, N	✓	✗
20	N	✗	✗
23 October 1989			
9	M	✓	✓
10	M, N	✓	✓
11	M, N	✓	✓
12	M, N	✗	✓
13	M, N	✓	✓
14	M, N	✓	✓
15	-	✓	✓
16	M	✗	✓
17	M	✗	✓
18	M	✗	✓
19	M	✗	✓
22 November			
10	M	✗	✓
11	M, N	✗	✓
12	M	✗	✓
13	M	✗	✓
14	M	✗	✓

Date & station	Mysids	Fish larvae	Zooplankton
15	M	✗	✓
16	M, N	✗	✓
17	✗	✗	✓
18	✗	✗	✓
11 December			
10	M	✗	✗
11	M, N	✗	✓
12	M, N	✓	✓
13	M, N	✗	✓
14	M, N	✗	✗
15	M, N	✗	✗
16	N	✗	✗
17	N	✗	✗
18	M, N	✗	✗

APPENDIX II

PHYSICAL AND CHEMICAL MEASUREMENTS

APPENDIX II Physical and chemical data for all sampling stations and dates.

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
6/2/89												
10	1905	1824	5.4	8.11	76.322	5.5	9.6	24.1	0	-	9.6	26.9
11	1848				86.932	7.0	9.4	26.6	3.37	0.56	9.4	24.9
12	1836				85.452	5.0	9.4	24.3	40.42	6.18	9.3	20.6
13	1825				70.608	4.0	9.3	20.7	26.94	4.20	9.1	18.6
14	1810				70.222	5.0	9.0	15.5	74.1	4.96	8.8	11.9
15	1756				64.719	4.5	8.8	7.0	343.53	25.76	8.7	7.6
16	1744				50.476	5.0	8.7	9.1	161.66	12.29	8.7	6.1
17	1731				33.691	7.0	8.7	4.9	505.19	18.70	8.7	3.2
18	1717				25.840	4.0	8.8	1.5	606.23	20.61	8.9	0.9
19	1703				15.384	4.0	9.0	0.4	1,212.45	80.02	9.1	0.3
20	1642				13.101	3.5	9.3	0.2	1,717.64	118.52	9.4	0.2
17/2/89												
9	1557	1605	4.5	38.26	39.527	7.0	9.2	29.6	-	-	9.3	29.0
10	1544				28.352	5.0	8.9	28.0	-	-	9.2	24.4
11	1529				45.692	5.0	8.6	23.2	-	-	8.8	19.9

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
12	1516				37.397	4.0	8.5	19.3	-	-	8.7	16.7
13	1506				18.912	4.0	8.4	16.2	-	-	8.6	15.4
14	1456				19.450	3.5	8.3	13.8	-	-	8.4	13.1
15	1442				29.011	5.0	7.9	8.4	-	-	8.2	3.6
16	1433				10.908	4.0	7.7	5.3	-	-	7.9	2.2
17	1422				23.827	5.5	7.5	0.4	-	-	7.7	0.4
18	1411				22.277	3.5	7.4	0.2	-	-	7.7	0.2
19	1400				26.991	4.0	7.2	0.15	-	-	7.2	0.2
20	1352				26.754	3.0	7.1				7.5	0.4
20/3/89												
10	1656	1715	5.0	76.47	82.825	5.0	8.8	20.4	22.0	2.55	8.7	18.5
11	1637				85.820	6.0	8.7	15.0	29.98	3.78	8.7	10.2
12	1622				77.849	5.0	8.8	7.6	26.08	3.29	8.5	6.2
13	1610				84.807	5.0	8.9	2.7	40.2	2.89	8.7	1.3
14	1554				89.959	5.0	9.0	0.2	30.0	3.12	8.7	0.1
15	1543				70.265	4.0	8.9	0.1	22.52	2.27	8.4	0.1
16	1531				54.772	6.0	8.8	0.1	25.44	3.51	8.7	0.1
17	1515				54.472	3.5	8.5	0.1	24.69	3.85	8.3	0.1

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
26/4/89												
10	1910	1816	5.3	9.73	52.683	5.0	10.1	22.7	49.36	8.14	9.9	24.6
11	1855				51.019	5.0	10.1	20.2	107.97	9.82	9.9	19.7
12	1843				63.765	4.0	9.9	16.9	169.67	13.40	9.8	16.7
13	1830				64.446	3.5	9.7	14.1	146.52	12.60	9.6	13.6
14	1817				57.174	4.0	9.2	9.0	771.21	32.39	8.9	8.4
15	1805				9.675	4.0	8.9	4.6	1,542.42	47.82	8.8	3.7
16	1750				3.167	4.0	8.7	1.0	1,542.42	24.68	8.6	0.8
17	1740				9.188	4.0	8.4	0.1	1,542.42	47.82	8.5	0.1
12/5/89												
10	1136	1052	4.2	6.91	76.117	5.0	13.0	29.2	50.43	11.30	13.6	24.2
11	1117				65.029	6.0	13.5	26.2	67.25	12.98	14.3	17.8
12	1104				73.549	5.0	13.6	24.2	84.06	18.91	14.1	17.3
13	1044				21.634	4.0	13.8	20.8	84.06	14.71	14.1	16.9
14	1031				69.280	6.0	13.9	15.9	117.68	18.59	14.2	11.9
15	1020				68.494	4.0	13.9	13.4	168.12	29.76	14.1	9.7
16	1007				80.808	5.0	13.8	9.8	302.61	38.73	13.3	5.8
17	0954				66.292	4.0	13.7	7.3	235.36	42.36	13.6	4.7

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
7/6/89												
10	1959	2026	5.2	3.46	62.204	6.0	14.6	30.5	47.55	-	14.6	30.2
11	1943				38.234	6.0	14.9	29.3	65.59	16.66	14.7	29.2
12	1932				35.047	5.0	15.2	27.9	88.55	14.34	15.1	27.9
13	1924				35.070	5.0	15.5	25.8	90.18	14.43	15.4	24.3
14	1913				30.346	6.0	15.7	20.9	106.58	20.25	15.4	20.7
15	1930				47.890	5.0	15.7	18.3	103.30	10.95	15.6	17.6
16	1854				34.704	5.0	15.7	16.0	163.97	16.56	15.6	15.6
17	1844				35.634	5.0	15.6	13.6	213.17	22.38	15.5	13.2
18	1835				7.403	4.0	15.7	9.5	524.72	44.60	15.6	8.6
19	1817				4.429	4.0	15.7	3.9	1,344.59	49.75	15.6	2.8
14/7/89												
11	1343	1342	4.4	1.75	27.372	5.0	18.9	29.4	55.98	-	21.3	27.7
12	1331				49.523	4.0	19.0	28.2	55.68	-	20.3	26.6
13	1320				34.813	4.0	19.4	26.5	74.23	-	20.1	26.1
14	1308				32.274	4.0	19.7	24.9	92.79	-	20.7	23.9
15	1257				37.199	3.5	19.9	22.0	111.35	-	20.9	20.9
16	1247				43.512	5.0	20.1	20.6	111.35	-	20.3	20.4
17	1235				39.115	5.0	20.2	19.8	129.91	-	20.9	18.9

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
18	1220				36.583	3.0	20.6	16.6	148.47	-	21.0	16.1
19	1207				46.917	3.0	20.6	13.5	167.03	-	20.9	11.5
20	1154				40.855	2.0	20.7	5.7	222.70	-	21.0	5.1
21	1136				31.315	1.5	20.0	0.2	241.26	-	20.0	0.2
25/9/89												
10	1455	1439	4.6	4.59	25.577	5.5	16.9	30.7	-	-	18.1	26.0
11	1435				42.377	5.5	16.9	28.6	-	-	17.8	23.3
12	1418				48.682	4.5	16.8	27.1	-	-	17.6	21.0
13	1405				34.870	4.0	16.6	23.7	-	-	17.5	19.5
14	1351				30.359	5.0	16.7	20.9	-	-	17.1	19.7
15	1337				31.423	4.0	16.5	18.2	-	-	16.8	17.1
16	1322				39.041	4.0	16.4	16.7	-	-	16.6	15.8
17	1311				29.114	7.0	16.1	14.1	-	-	16.5	12.5
18	1255				27.807	3.5	16.0	10.5	-	-	16.2	10.1
19	1239				32.083	3.0	15.7	7.6	-	-	15.5	5.5
20	1218				6.802	3.0	14.8	0.3	-	-	14.8	0.3
23/10/89												
9	1258	1245	4.5	35.84	31.047	8.0	14.4	31.3	-	-	13.5	8.5
10	1240				32.708	6.5	14.3	29.8	-	-	13.6	5.5

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
11	1124				34.717	6.0	14.3	28.8	-	-	13.1	4.1
12	1208				35.290	5.5	13.9	25.3	-	-	12.9	0.3
13	1155				73.759	5.0	13.6	20.0	-	-	12.9	0.2
14	1140				36.335	6.0	13.1	12.7	-	-	12.7	0.2
15	1125				33.147	4.0	12.7	0.2	-	-	13.1	0.3
16	1113				23.707	3.5	12.5	0.1	-	-	12.6	0.1
17	1100				22.375	7.5	12.4	0.2	-	-	13.1	0.3
18	1047				18.960	4.0	12.4	0.2	-	-	12.8	0.2
19	1033				22.632	4.5	12.5	0.2	-	-	12.4	0.2
22/11/89												
10	1259	1250	4.6	82.11	56.448	6.0	12.1	28.8	22.23	-	11.1	17.0
11	1239				52.462	7.5	12.0	27.4	24.25	-	10.9	15.0
12	1217				55.961	5.0	11.8	24.6	46.48	-	11.1	14.3
13	1203				57.937	4.0	11.7	23.0	50.52	-	10.9	12.6
14	1148				58.419	5.0	11.5	19.1	64.66	-	10.7	6.0
15	1135				54.290	3.5	11.1	13.0	34.35	-	10.7	4.7
16	1123				55.230	3.0	11.0	10.8	36.37	-	10.6	4.0
17	1110				40.473	8.0	10.9	6.4	20.21	-	10.7	3.4
18	1058				39.857	4.5	10.5	1.3	30.31	-	10.5	0.2

Date & station	Time (GMT)	Time of high water (GMT)	Height of tide (m)	Mean river flow (m^3s^{-1})	Total volume of water sampled (m^3)	Depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Bottom turbidity (mgl^{-1})	Organic content (mgl^{-1})	Surface temperature (°C)	Surface salinity (‰)
11/12/89												
10	1601	1637	5.4	5.77	43.675	6.0	7.4	28.5	-	-	7.2	27.7
11	1530				46.649	7.5	7.0	27.2	-	-	6.9	26.4
12	1511				13.492	5.5	6.4	23.4	-	-	6.3	22.7
13	1500				35.356	5.0	6.1	20.6	-	-	6.0	19.8
14	1446				3.880	4.5	5.6	15.9	-	-	5.5	15.0
15	1431				10.891	5.5	5.3	13.0	-	-	5.3	12.4
16	1417				2.778	4.5	5.0	6.9	-	-	4.9	9.1
17	1401				1.938	7.0	4.4	3.6	-	-	4.4	3.5
18	1344				3.580	4.0	4.0	0.3	-	-	4.1	0.5

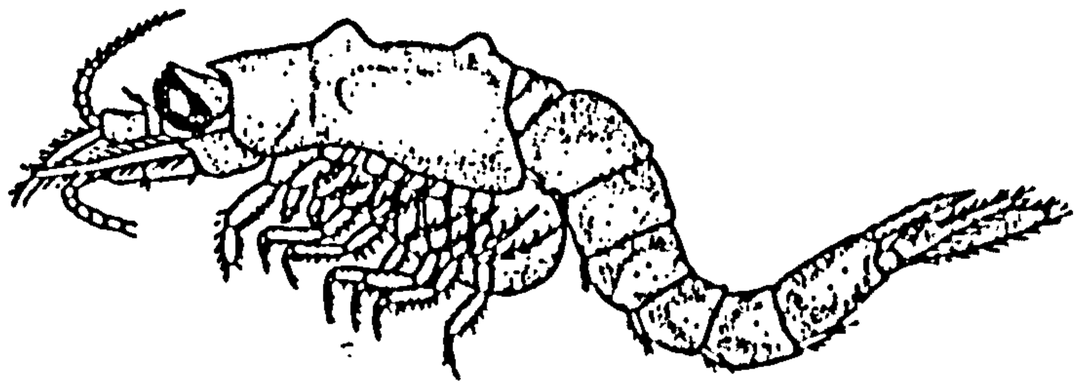
APPENDIX III

PUBLICATIONS

TAXONOMY, BIOLOGY AND ECOLOGY

OF (BALTIC) MYSIDS

(MYSIDACEA: CRUSTACEA)



Jörg Köhn, Malcolm B. Jones
&
Angela Moffat (eds.)

International Expert Conference
September 1991
Hiddensee, Germany

Rostock University
1992

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Content

BIONOMICS OF *MESOPODOPSIS SLABBERI* AND *NEOMYSIS INTEGER* (CRUSTACEA: MYSIDACEA) IN THE TAMAR ESTUARY

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ABSTRACT

Mysid shrimps occur at very high densities in the Tamar Estuary, particularly during the summer, and form a major component in the diet of some fish, thus providing an important link between the benthic and pelagic systems. However, although the dynamics of the Tamar Estuary have been well researched, the life history of the mysids is poorly understood. *Mesopodopsis slabberi* and *Neomysis integer* are the most abundant mysid species present in the estuary. There were marked seasonal changes in the abundance of the two species, and juveniles dominated both populations throughout the year. The density of *M. slabberi* increased from $<50\ m^{-3}$ in the spring to $>1000m^{-3}$ in the summer, and the increase in the population was related to the water temperature. The highest recorded density of *N. integer* was $<200m^{-3}$, this low recorded density could be accounted for by inefficient sampling of this species. *N. integer* was generally found in lower salinity water than *M. slabberi*.

INTRODUCTION

Mysid shrimps (Crustacea, Peracarida) occur in high concentrations in coastal and estuarine regions worldwide, and have been shown to form a major food source for many species of fish (e.g. herring, mackerel, plaice, flounder, whiting, dab and bass) (HARTLEY, 1940; TATTERSALL and TATTERSALL, 1951; MAUCHLINE, 1980; WOOLDRIDGE, 1983). Mysids are omnivorous, feeding on zooplankton, phytoplankton and detritus (MOLLOY, 1958; LASENBY and LANGFORD, 1973; WEBB and WOOLDRIDGE, 1989), and thus form an important link in marine and estuarine food chains (ASTTHORSSON, 1980; FULTON, 1982a, 1982b; BHATTACHARYA, 1982).

Mesopodopsis slabberi (van BENEDEN) and *Neomysis integer* (LEACH) are two of the most common mysid species occurring in inshore coastal, estuarine and brackish waters in northern Europe (TATTERSALL and TATTERSALL, 1951; ACKEFORS, 1969; HESTHAGEN, 1973; BOYSEN, 1976; PARKER and WEST, 1979). Both species tolerate large fluctuations of salinity and have been recorded frequently in brackish water of low salinity. The life cycle of *N. integer* has been described by KINNE (1955), MAUCHLINE (1971) and PARKER and WEST (1979), while that of *M. slabberi* is poorly understood. *M. slabberi* and *N. integer* are abundant in the upper reaches of the River Tamar Estuary, South-west England. Salinity has been identified as a major environmental factor affecting the longitudinal and horizontal distributions of these species in the estuary (GREENWOOD et al., 1989; MOFFAT & JONES, 1992), although other factors such as estuarine hydraulics may also have an impact. The present study investigates the life history of *M. slabberi* and *N. integer* in the upper Tamar Estuary over an annual cycle.

Taxonomy, Biology and Ecology of (Baltic) Mysids (Mysidacea: Crustacea), 1992, pp. 109-119.

International Expert Conference

Von Jörg Köhn, Malcolm B. Jones and Angela Moffat, Editors
Rostock University Press.

STUDY AREA

The River Tamar Estuary is approximately 31 km long between its boundary with Plymouth Sound and the tidal limit at Weir Head (Fig. 1). The main freshwater input comes from the River Tamar, with additional inputs from the Rivers Lynher and Tavy. There are well-established gradients of salinity and suspended sediment which vary on both short-term (tidal) and long-term (seasonal) cycles (UNCLES et al., 1983, 1985a; UNCLES & STEPHENS, 1990). A turbidity maximum occurs in the low salinity region (<5ppt) of the estuary (LORING et al., 1983), although the geographical location of this turbidity maximum shows a large spring-neap variation. Concentrations of suspended sediment at the maximum vary between 50 and >1000ppm, and at spring tides are between one and two orders of magnitude higher than at neap tides in the upper estuary (MORRIS et al., 1982; UNCLES et al., 1985b). More detailed descriptions of the physical and chemical dynamics of the entire estuary are provided elsewhere (GEORGE, 1975; MORRIS et al., 1982, 1985; UNCLES et al.,1983, 1985a,b&c; UNCLES & STEPHENS, 1990).

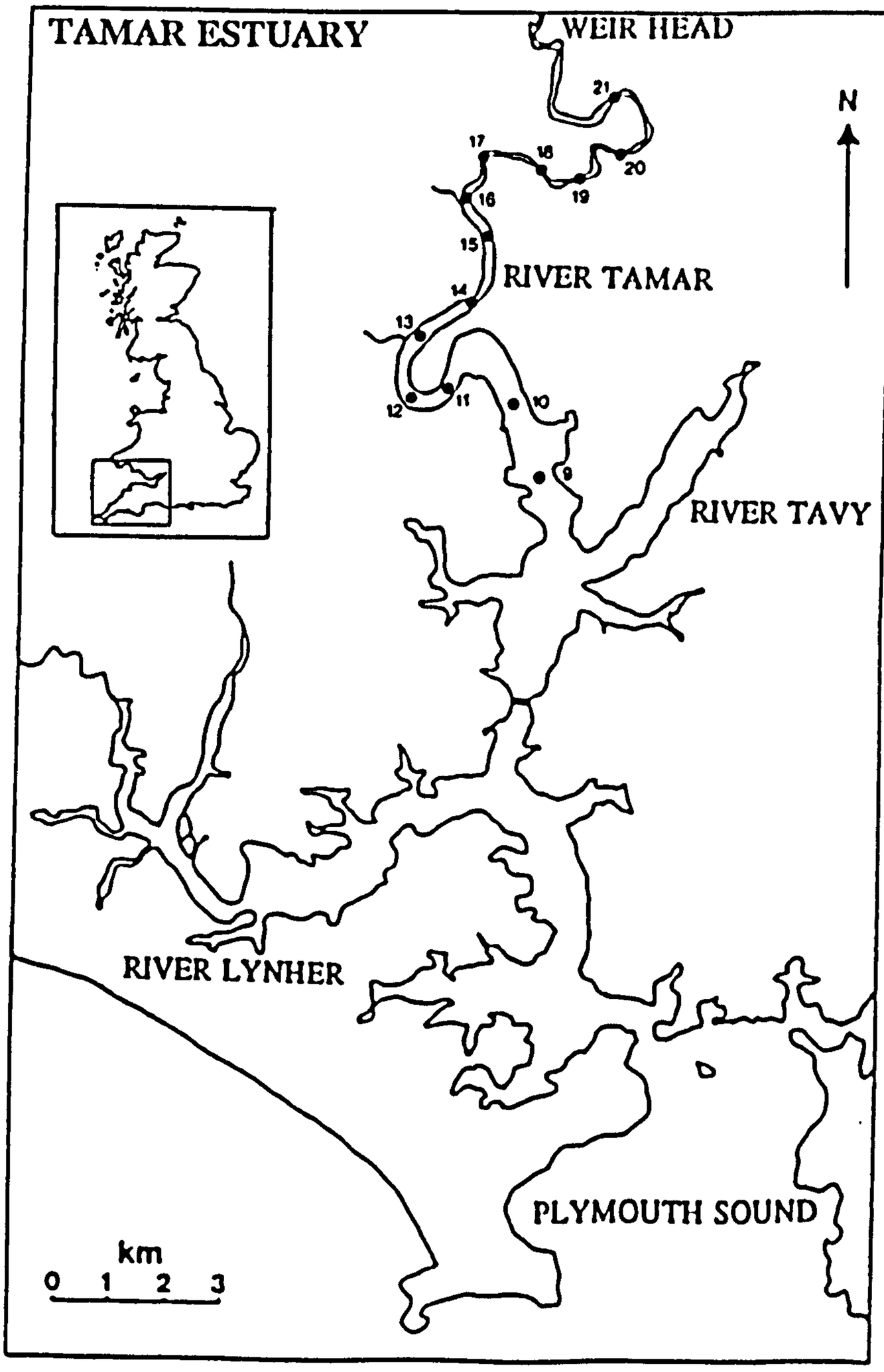

Figure 1 Map of the Tamar Estuary showing sampling stations

MATERIALS AND METHODS

At monthly intervals (February to December 1989), *Mesopodopsis slabberi* and *Neomysis integer* were sampled from a boat at fixed sampling stations in mid-estuary on the flood tide. Thirteen sampling stations, ranging from 1-8m water depth were used during the surveys (Fig. 1).

Sampling commenced 2h before the predicted times of high water and always began at the sampling station furthest upstream; each monthly series took approximately 2h to complete. The stations encompassed the salinity range 0.5 to 28ppt as preliminary sampling showed *M. slabberi*, in particular, rarely occurred outside this range. Duplicate samples were taken simultaneously at each station using conical plankton nets with a 280 μ mesh and mouth diameters of 0.45 and 0.37m. The volume of water filtered by each net was measured using General Oceanics Model 2030 flowmeters. At each station, the nets were towed obliquely for 5 min. This time was reduced at some stations, and at some times of the year, to reduce clogging of the nets by either suspended sediment or phytoplankton. All sampling was carried out during daylight hours except for samples collected on 17 February 1989. At each station, measurements of surface and bottom salinity, temperature (using an MC5 Salinity Bridge) and turbidity (using a Partech Electronics suspended sediment monitor) were made (Table 1).

Table 1: Summary of physical measurements for each station sampled during 1989.

Station	Distance from Mouth of Estuary (km)	No. of Times Station Sampled	Depth Range (m)	Salinity Range (‰)	Temperature Range (°C)	Turbidity (mg l^{-1})
9	11.00	2	7.0-8.0	29.6-31.3	9.2-14.4	0
10	12.75	10	4.0-6.5	20.4-30.7	7.4-16.9	0-19
11	15.00	11	5.0-7.5	15.0-29.4	7.0-18.9	0-30
12	16.50	11	4.0-5.5	7.6-28.2	6.4-19.0	12-55
13	17.50	11	3.5-5.0	2.7-26.5	6.1-19.4	4-42
14	19.00	11	3.5-6.0	0.2-24.9	5.6-19.7	15-238
15	20.00	11	3.5-5.5	0.1-22.0	5.3-19.9	9.6-480
16	20.75	11	3.5-6.0	0.1-20.6	5.0-20.1	15-480
17	21.75	8	3.5-8.0	0.1-19.8	4.4-20.2	14-480
18	22.50	6	3.5-4.5	0.2-16.6	4.0-20.6	44-120
19	23.25	6	3.0-4.5	0.2-13.5	7.2-20.6	50-240
20	24.25	4	2.0-3.5	0.15-5.7	9.3-14.8	67-340
21	28.00	1	1.5	0.2	20.0	83

Catches were preserved in 4% formalin immediately on collection. Those samples containing less than 200 mysids were examined in total, whereas larger samples were split using a Folsom plankton splitter until a sample size of approximately 200 mysids was obtained. Each mysid was straightened, measured ($\pm$ 1mm) from the base of the eyestalk to the posterior end of the uropods, excluding the setae, using a microscope (MAUCHLINE, 1969), and ascribed to one of six classes, according to the degree of development of the secondary sexual characteristics (after MAUCHLINE, 1980): (1) Juvenile, secondary sexual characteristics absent; (2) immature male, secondary sexual characteristics developing; (3) mature male, secondary sexual characteristics fully developed; (4) immature female,

marsupium developing and smaller than in the mature female, no young carried; (5) mature female, marsupium fully developed, and young present in the marsupium; (6) mature and empty females, marsupium fully developed, and either not yet filled with young, or young have emerged.

RESULTS AND DISCUSSION

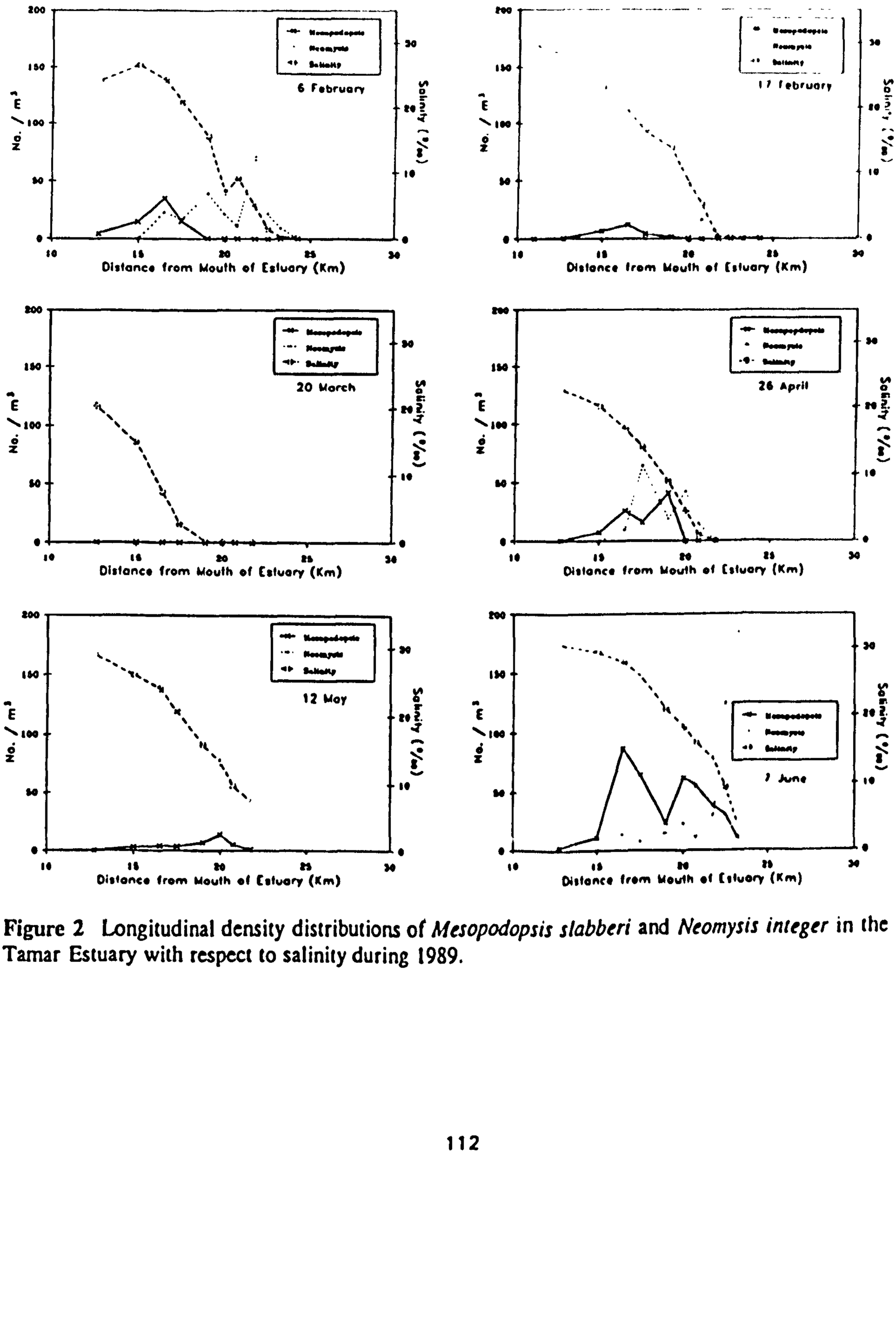

Figure 2 Longitudinal density distributions of *Mesopodopsis slabberi* and *Neomysis integer* in the Tamar Estuary with respect to salinity during 1989.

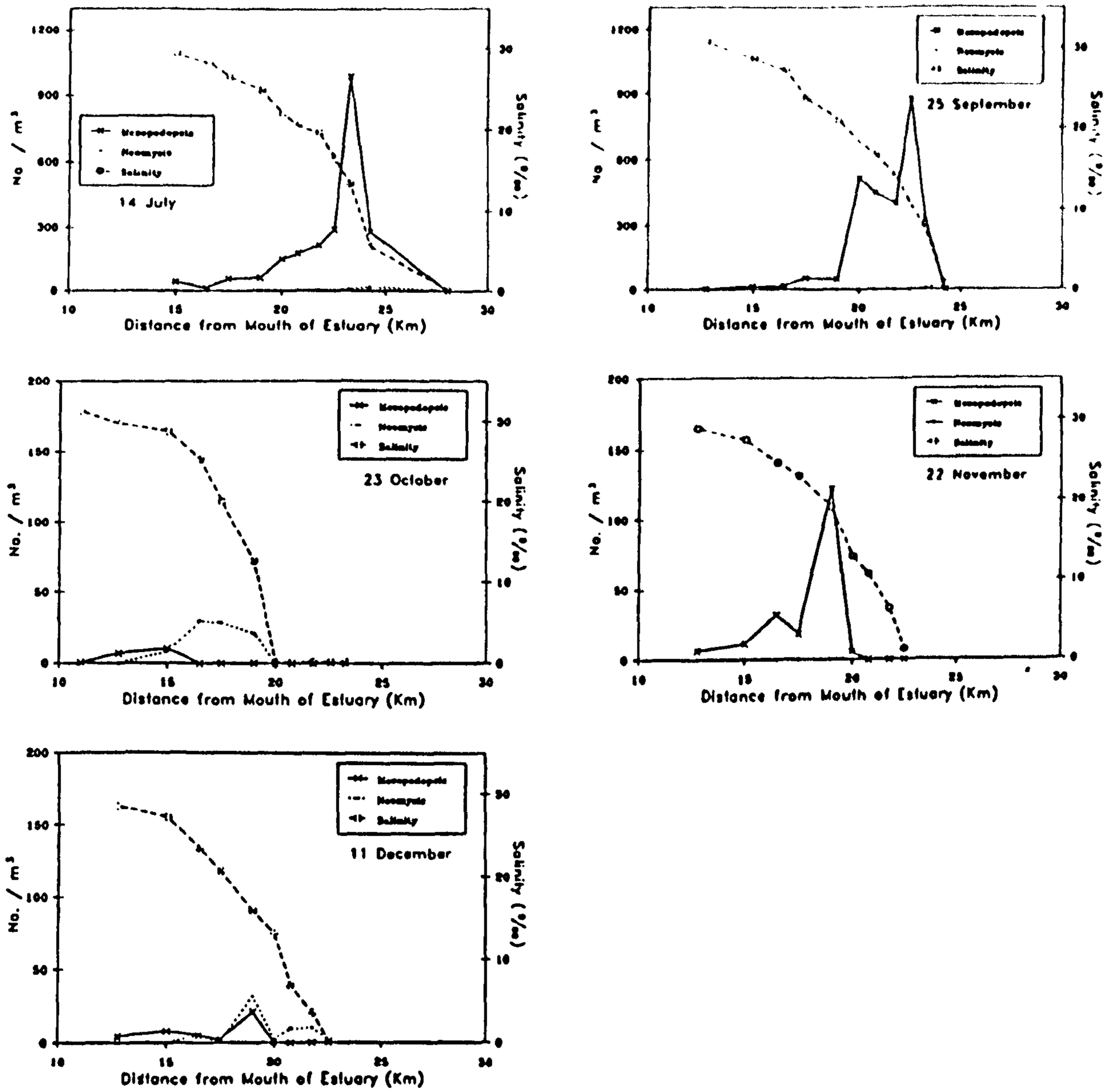

Figure 2 (cont/d) Longitudinal density distributions of *Mesopodopsis slabberi* and *Neomysis integer* in the Tamar Estuary with respect to salinity during 1989.

Both *Mesopodopsis slabberi* and *Neomysis integer* were present in the estuary throughout the year, and both populations were dominated by juveniles year round. Generally, *M. slabberi* occupied the area of the estuary with a salinity of between 5 and 25ppt, while *N. integer* was usually found further upstream (in lower salinities) (Fig. 2).

The density of *M. slabberi* remained low between February and May (<50 m^{-3}), and increased rapidly between May and June to form a peak between July and September (Fig. 2). The population density declined rapidly during autumn (October-November) to the levels recorded in the previous February. The overwintering population, consisting mainly of juveniles, immature males and females, started to mature in March, and bred in April and May; breeding appeared to be continuous from May to September (Fig. 3).

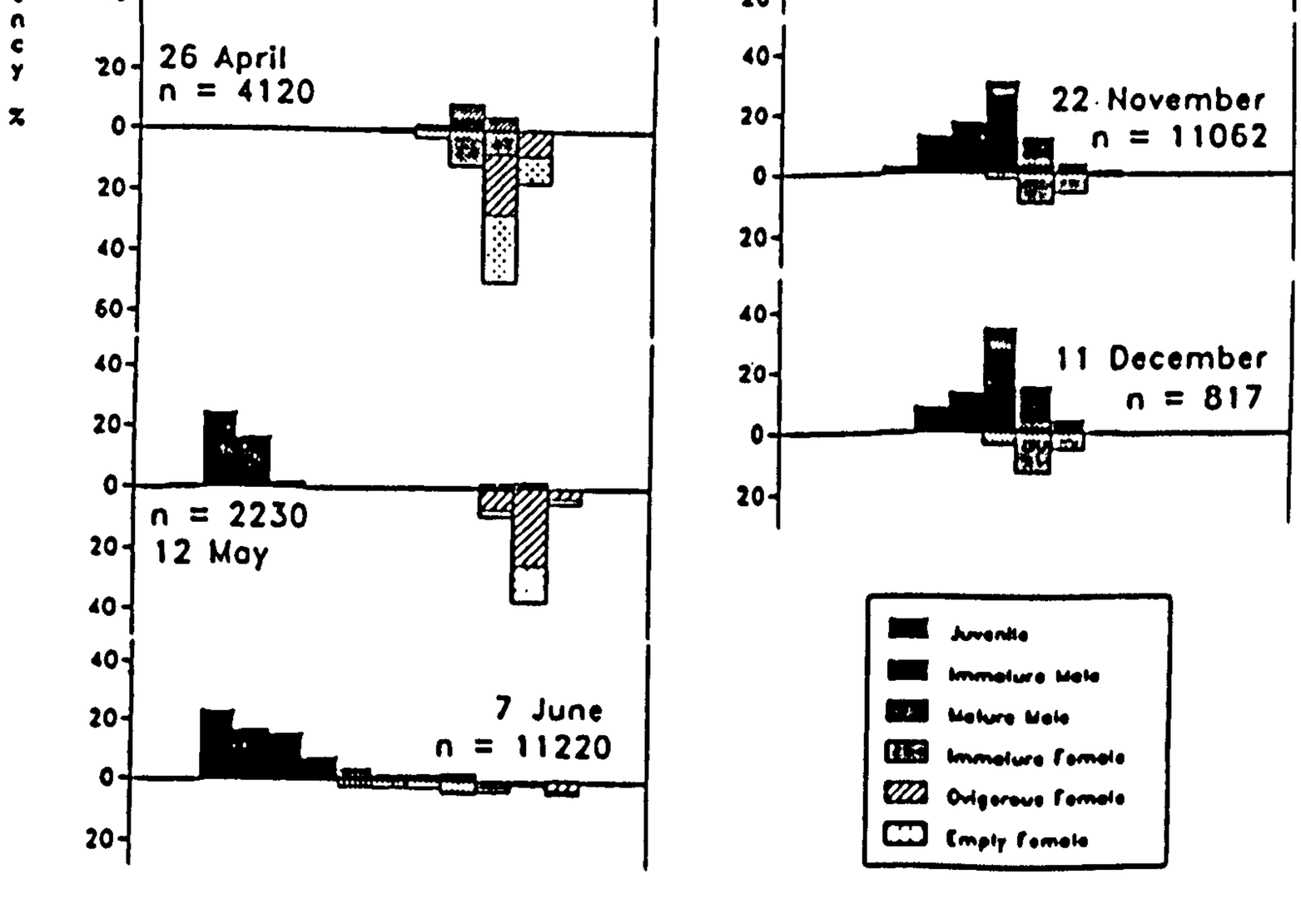

Fig. 3 Length/Frequency distribution of *Mesopodopsis slabberi* in the Tamar Estuary in 1989.

Maturation of the overwintering generation coincided with rising water temperature (Fig.4). Juveniles dominated the population until the end of the year, although their density declined as the water temperature decreased. The sex ratio of *M. slabberi* was approximately 1:1 in February, but became biased towards females in the following months with the greatest ratio occurring in May (13:1), before returning to a ratio of 1:1 by November as the breeding females of the previous years overwintering population died off.

In the Tamar Estuary, *Mesopodopsis slabberi* produces at least two generations per year, an overwintering generation, and at least one summer generation; however, it was not possible to identify statistically separate summer and autumn generations due to the continuous breeding during the summer. The interpretation of the generation frequency is in agreement with those of BLEGVAD (1922) and MACQUART-MOULIN (1965) who found that *M. slabberi* had two generations per year in Danish and French waters respectively. Several authors have suggested that the absence of adult *M. slabberi* in samples taken during the winter months is evidence of an offshore seasonal migration of part of the population (BAAN, 1971; APEL, 1992). This lack of mature individuals in winter samples in the Tamar Estuary, however, can be accounted for by mortality of the previous years overwintering generation. The seasonal abundance and breeding of *M. slabberi* appears to be controlled by seasonal changes in water temperature. This is supported by the results of TODA et al. (1983, 1984) who found that increasing environmental temperature caused an increase in brood size, brood interval and specific growth rate of the mysid *Neomysis intermedia*.

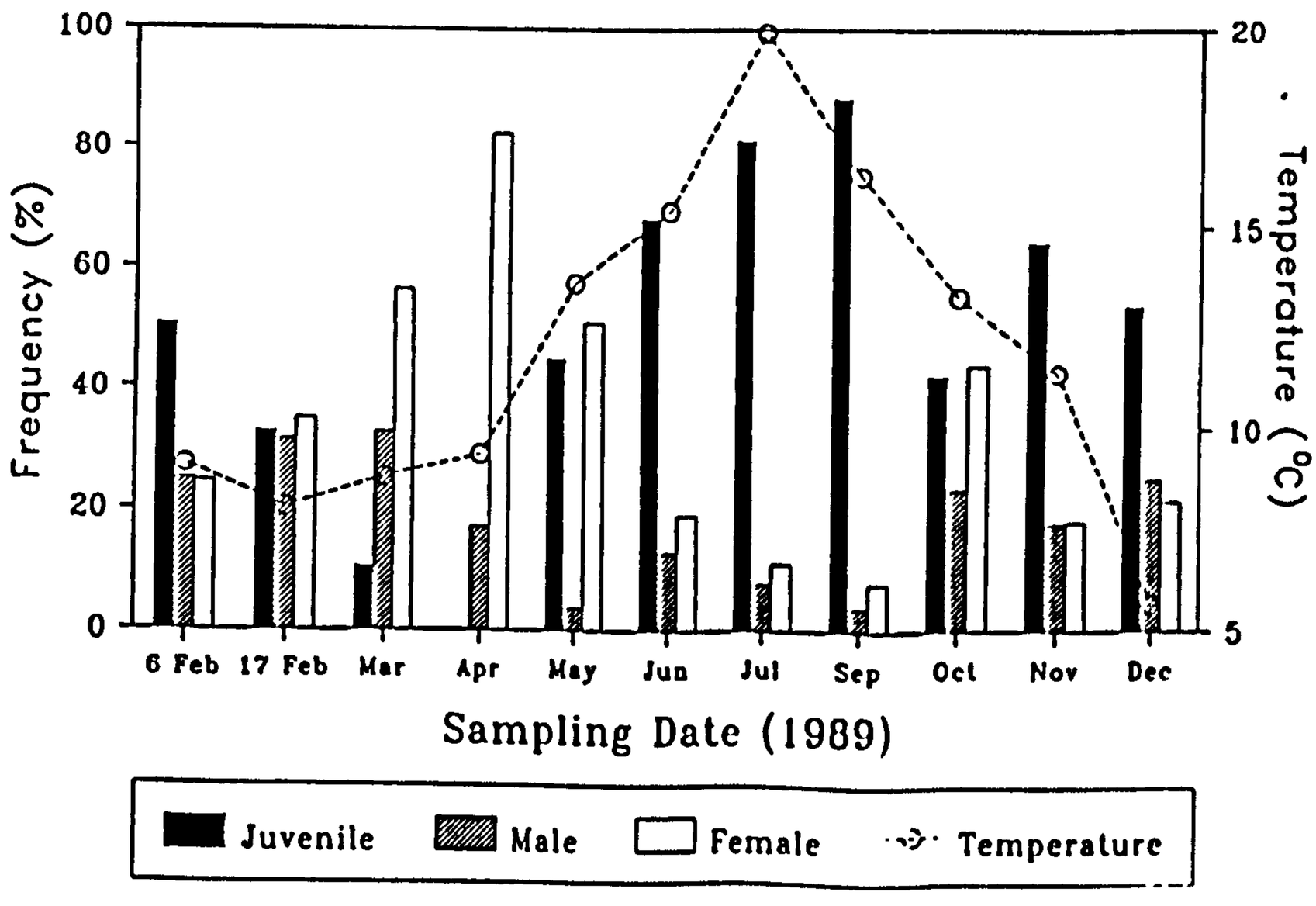

Fig. 4. Proportion of male, female and juvenile *Mesopodopsis slabberi* in the Tamar Estuary in 1989 in relation to water temperature. (From MOFFAT & JONES, 1992).

The monthly densities of *Neomysis integer* were highly variable (Fig. 2), and changes in the proportion of males, females and juveniles did not appear to be related to temperature (Fig. 5).

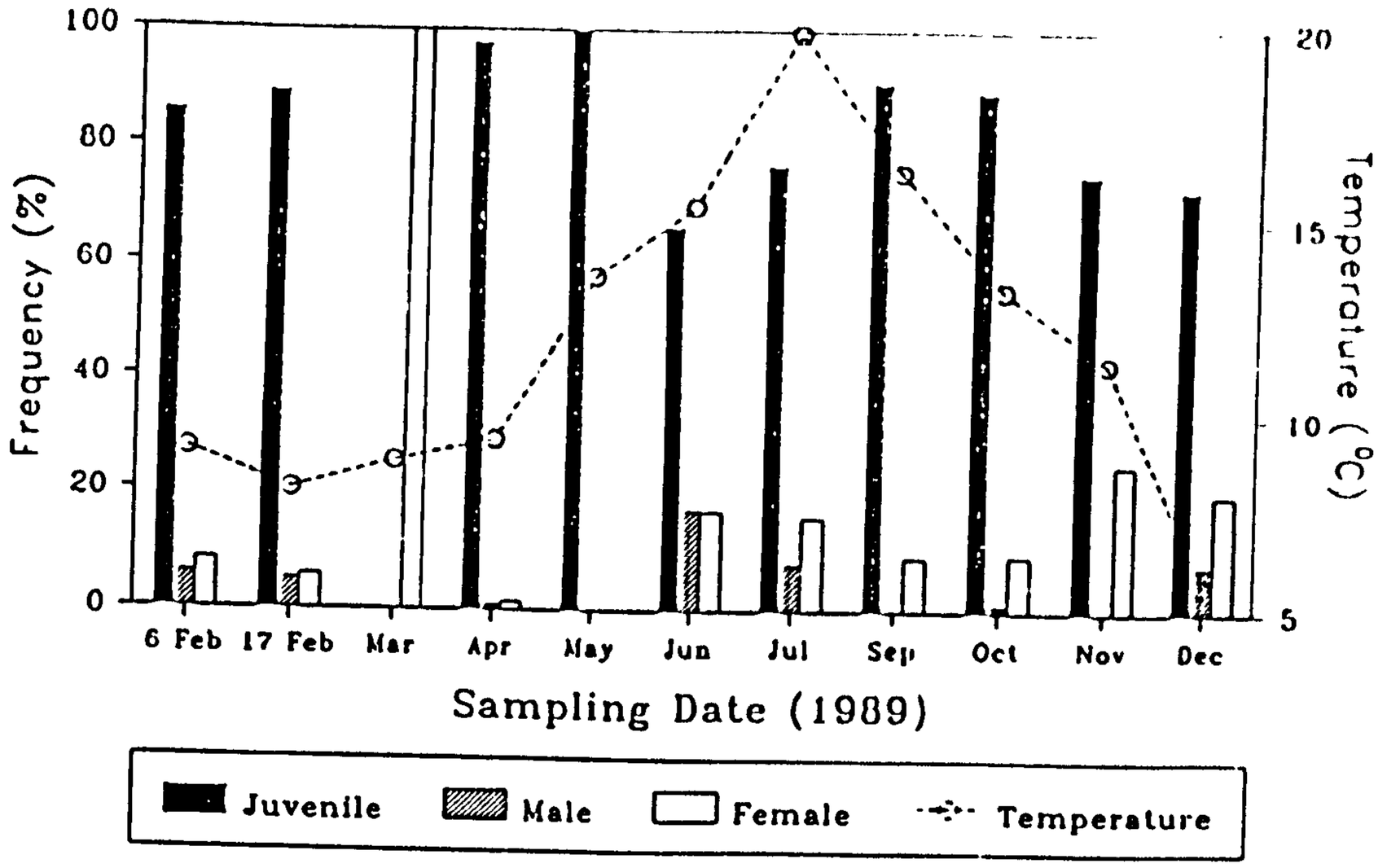

Figure 5 Proportion of male, female and juvenile *Neomysis integer* in the Tamar Estuary in 1989 in relation to water temperature.

Peaks in the population abundance occurred in early February, April and June, but densities did not exceed 200 m^{-3} during the sampling period. Mature individuals, both male and female, were poorly represented in the samples at all times of the year (Fig. 6), suggesting that all portions of the population were not sampled effectively.
The sex ratio ranged between 1:1 and 2:1 for most of the year except in October, when females outnumbered males with a ratio of 9:1.

The results of sampling *Neomysis integer* were not complete enough to describe fully the life history through the year due to a lack of mature individuals in the samples. It has often been observed that juvenile and adult stages of *N. integer* shoal separately (TATTERSALL & TATTERSALL, 1951; PARKER & WEST, 1979). Adult *N. integer* are frequently found in dense swarms near the shore margins at certain stages of the tidal cycle in estuaries, or are found in shallower water than the juveniles (SALEMAA, this volume). As the present samples were taken from the mid-channel of the estuary, any animals concentrated close to the shore would not have been sampled effectively; this may explain the lack of larger individuals in the samples.

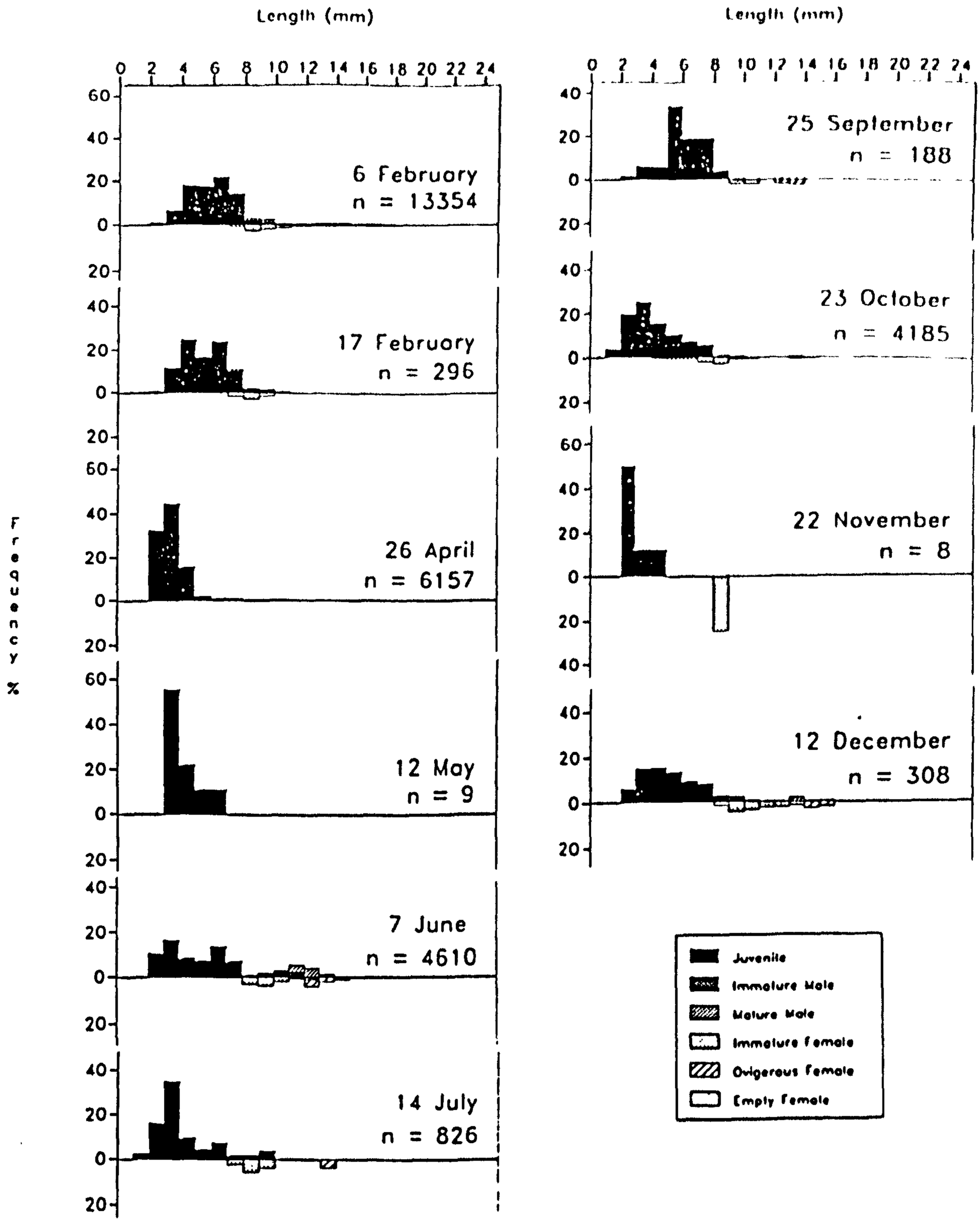

Fig. 6 Length/Frequency distribution of *Neomysis integer* in the Tamar Estuary in 1989.

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CORRELATION OF THE DISTRIBUTION OF *MESOPODOPSIS SLABBERI* (CRUSTACEA, MYSIDACEA) WITH PHYSICO-CHEMICAL GRADIENTS IN A PARTIALLY-MIXED ESTUARY (TAMAR, ENGLAND)

A.M. MOFFAT[1] and M.B. JONES

KEY WORDS: estuarine mysids; *Mesopodopsis slabberi*; distribution; Tamar Estuary.

ABSTRACT

The physical and chemical processes operating in the River Tamar Estuary (south-west England) have been comprehensively described and reported in the literature. There are well-established gradients of salinity, suspended sediment and oxygen which vary both on short-term (tidal) and long-term (seasonal) cycles. Freshwater runoff, the main factor determining salinity distribution, is also the cause of the high variability in suspended sediment concentrations. The biological processes are less well studied and information on the link between the benthic and pelagic systems is particularly lacking. Mysids, through their role as detritivores and as a major component in the diet of some fish, provide this link. Of the four species of mysid distributed longitudinally in the Tamar Estuary, the most abundant is *Mesopodopsis slabberi* which occurs between 5 and 25 km from the estuary head. Observations over an annual cycle have shown marked seasonal changes in both abundance and distribution in the estuary. During winter and spring, densities remained generally low (<50 m^{-3}) but, as water temperatures increased, the density increased and reached *ca.* 1200 individuals m^{-3} in July. There was a shift in the longitudinal distribution of *M. slabberi* in response to changes in the position of the salinity gradient. Adults comprised the majority of the population in salinities less than 10‰, whereas juveniles and immature animals were distributed over a wider area than the adults and occurred in water of higher salinity than the main adult distribution. *M. slabberi* appears to utilise the two-layered estuarine circulation to maintain its position in the estuary.

INTRODUCTION

Mysid shrimps (Crustacea, Peracarida) are common components of coastal and estuarine ecosystems worldwide, and form an important link between the benthic and pelagic systems of these regions (ASTTHORSSON, 1980; FULTON, 1982a,b). Although described as detritivores, mysids also feed on phytoplankton and zooplankton, and the general mysid diet is probably better characterized as omnivorous (LASENBY and LANGFORD, 1973; WEBB and WOOLDRIDGE, 1989). Mysids form a major dietary item of many fish species (*e.g.* herring, mackerel, plaice, flounder, whiting, dab and bass) and may also be important in the diet of wading birds (HARTLEY, 1940; TATTERSALL and TATTERSALL, 1951; MAUCHLINE, 1980).

Of the four species of mysid distributed horizontally along the length of the River Tamar Estuary, Plymouth (TATTERSALL and TATTERSALL, 1951), *Mesopodopsis slabberi* (van Beneden) is abundant in the upper reaches and reaches population densities of >4500 m^{-3} during the summer (GREENWOOD *et al.*, 1989). An earlier investigation identified salinity as a major environmental factor affecting the distribution of *M. slabberi* in the Tamar Estuary (GREENWOOD *et al.*, 1989). Many studies have implicated salinity as a factor affec-

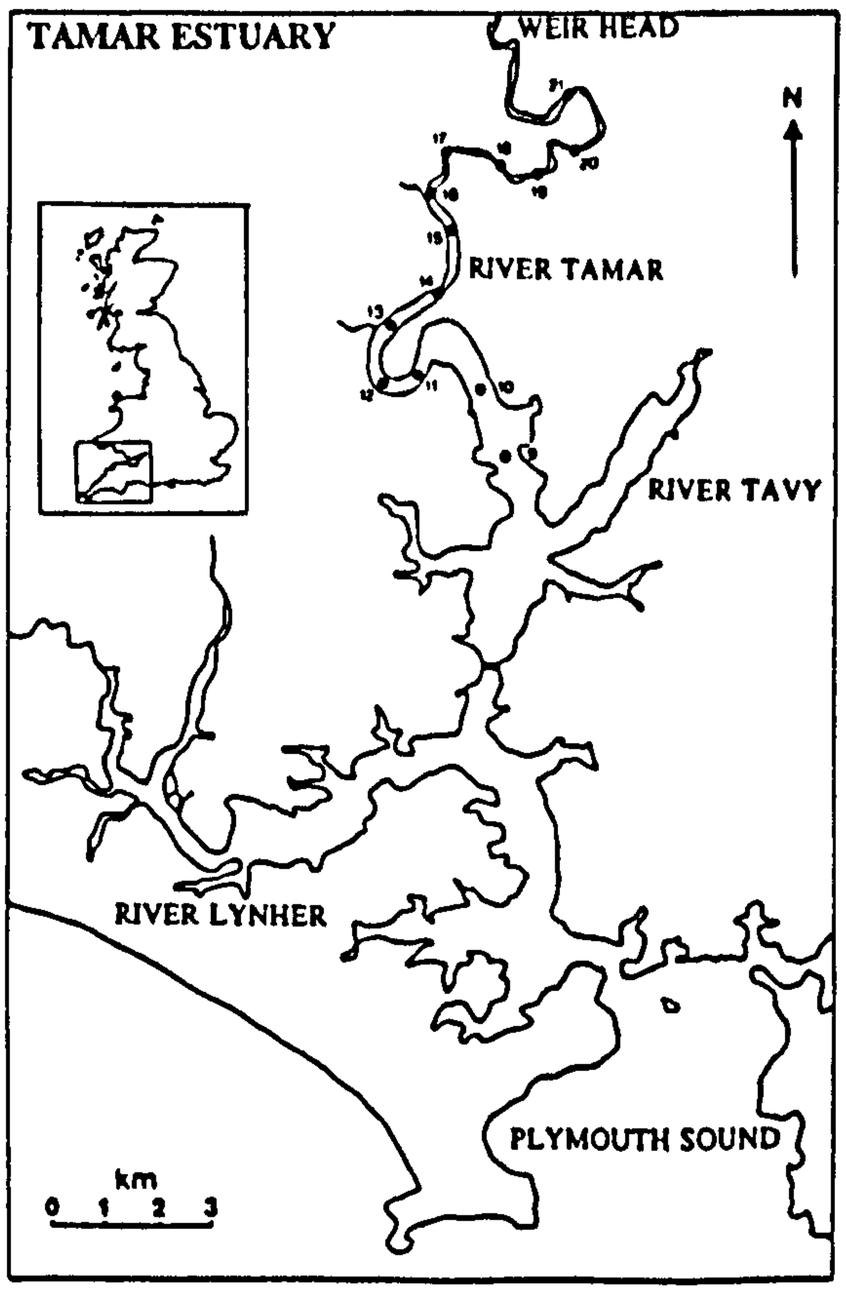

Fig. 1. Map of the Tamar Estuary showing sampling stations (9-21).

ting the distribution of estuarine mysids, however, other factors such as estuarine hydraulics may also have a large influence (ORSI and KNUTSON, 1979; SIEGFRIED *et al.*, 1979; JONES *et al.*, 1989). The present study correlates measurements of salinity, turbidity and temperature with seasonal patterns of abundance and distribution of *M. slabberi* in the upper Tamar Estuary to assess which of these environmental factors is involved in setting distributional limits of the various life-history stages.

Study area

The River Tamar Estuary is approximately 31 km long between its boundary with Plymouth Sound and the tidal limit at Weir Head (Fig. 1). The main freshwater input comes from the River Tamar, with additional inputs from the Rivers Lynher and Tavy. There are well-established gradients of salinity and suspended sediment which vary on both short-term (tidal) and long-term (seasonal) cycles.

Generally, the estuary is partially mixed (UNCLES *et al.*, 1983; UNCLES and STEPHENS, 1990), although the mixing type, and hence classification type, is variable (UNCLES *et al.*, 1985a). During average run off conditions, the Tamar Estuary is partially mixed whereas during periods of medium to high run off it becomes transitional or well mixed in the upper reaches. At times of low river flow, salinities of >5‰ may be measured 5 km downstream from Weir Head, whereas during high flow conditions, salt water may only penetrate as far as 15 km from the mouth of the estuary.

A turbidity maximum occurs in the low salinity region (<5‰) of the estuary (LORING *et al.*, 1983). The geographical position of this turbidity maximum shows a large spring-neap variation due to increased tidal pumping at spring tides. Concentrations of suspended sediment at the maximum vary between 50 and >1000 ppm, and at spring tides are between one and two orders of magnitude higher than at neap tides in the upper estuary (UNCLES *et al.*, 1985b; MORRIS *et al.*, 1982).

More detailed descriptions of the physical and chemical dynamics of the entire estuary are provided elsewhere (GEORGE, 1975; MORRIS *et al.*, 1982, 1985; UNCLES *et al.*, 1983, 1985a, b, c; UNCLES and STEPHENS, 1990).

MATERIALS AND METHODS

At monthly intervals from February to December 1989, *Mesopodopsis slabberi* was sampled on the flood tide from a boat at fixed sampling stations in mid estuary. Sampling commenced 2 h before the predicted times of high water and always started at the sampling station furthest upstream; each monthly series took approximately 2 h to complete. The stations encompassed the salinity range between 0.5 and 28‰, as preliminary sampling confirmed that *M. slabberi* rarely occurred outside this range. Thirteen sampling stations, ranging from 1-8 m water depth at the time of sampling, were used during the surveys (Fig. 1). Duplicate samples were taken simultaneously at each station using conical plankton nets with a 280 μm mesh, and mouth diameters of 0.45 and 0.37 m. The volume of water filtered by each net was measured using General Oceanics Model 2030 flowmeters. At each station each net was towed obliquely for 5 min. This time was reduced at some stations, and at some times of the year, to reduce clogging of the nets by either suspended sediment or phytoplankton. All sampling was carried out during daylight hours except for samples collected on 17 February 1989.

Table 1. Summary of physical measurements for each station sampled during 1989

Station	Distance from Mouth of Estuary (km)	No. of Times Station Sampled	Depth Range (m)	Salinity Range (‰)	Temperature Range (°C)
9	11.00	2	7 0-8 0	29 6-31 3	9 2-14 4
10	12.75	10	4 0-6 5	20 4-30 7	7 4-16 9
11	15.00	11	5 0-7 5	15 0-29 4	7 0-18 9
12	16.50	11	4 0-5 5	7 6-28 2	6 4-19 0
13	17.50	11	3 5-5.0	2 7-26 5	6 1-19 4
14	19.00	11	3 5-6 0	0 2-24 9	5 6-19 7
15	20.00	11	3 5-5 5	0 1-22 0	5 3-19 9
16	20.75	11	3 5-6 0	0 1-20 6	5 0-20 1
17	21.75	8	3 5-8.0	0 1-19 8	4 4-20 2
18	22.50	6	3 5-4.5	0 2-16 6	4 0-20 6
19	23.25	6	3.0-4.5	0.2-13.5	7 2-20 6
20	24.25	4	2.0-3.5	0 15-5 7	9.3-14 8
21	28.00	1	1 5	0 2	20 0

At each station, measurements of surface and bottom salinity, temperature (using an MC5 Salinity Bridge) and turbidity (using a Partech Electronics Suspended sediment monitor) were made (Table 1). Daily flow rates for the River Tamar during 1989 were obtained from the South West Water Authority.

Catches were preserved in 4% formalin immediately on collection. Samples containing less than 200 mysids were examined in total, whereas larger samples were reduced to a sample size of approximately 200 using a Folsom plankton splitter. Each mysid was straightened, measured (± 1 mm) from the base of the eyestalk to the posterior end of the uropods (excluding the setae) using an eyepiece graticule in a stereoscopic binocular microscope (MAUCHLINE, 1969), and ascribed to one of six classes, according to the degree of development of the secondary sexual characteristics (after MAUCHLINE, 1980): 1) juvenile, secondary sexual characteristics absent; 2) immature male, secondary characteristics developing; 3) mature male, secondary sexual characteristics fully developed; 4) immature female, marsupium developing and smaller than in the mature female, no young carried; 5) mature female, marsupium fully developed, and young present in the marsupium; 6) mature and empty females, marsupium fully developed, and either not yet filled with young, or young have emerged.

RESULTS

Mesopodopsis slabberi was present in the estuary throughout the year. Population densities were relatively low between February and May (<50 m^{-3}), and increased rapidly between May and June to form a peak between July and September (Fig.2).

Table 2. Turbidity measurements (mg l^{-1}) for each station sampled between February and June 1989 in the Tamar Estuary.

Station	Date (dd/mm) 06/02	20/03	26/04	12/05	07/06	14/07
9	0	·	·	·	·	·
10	0	19	12	·	0	·
11	0	22	30	10	5	17
12	12	20	55	14	19	17
13	4	35	42	14	15	22
14	15	26	238	10.5	21	28
15	70	19	480	9 6	19 5	33
16	32	20	480	15	45	33
17	100	22	480	15	61	38 5
18	120	·	·	·	181	44
19	240	·	·	·	493	50
20	340	·	·	·	·	67
21	·	·	·	·	·	83

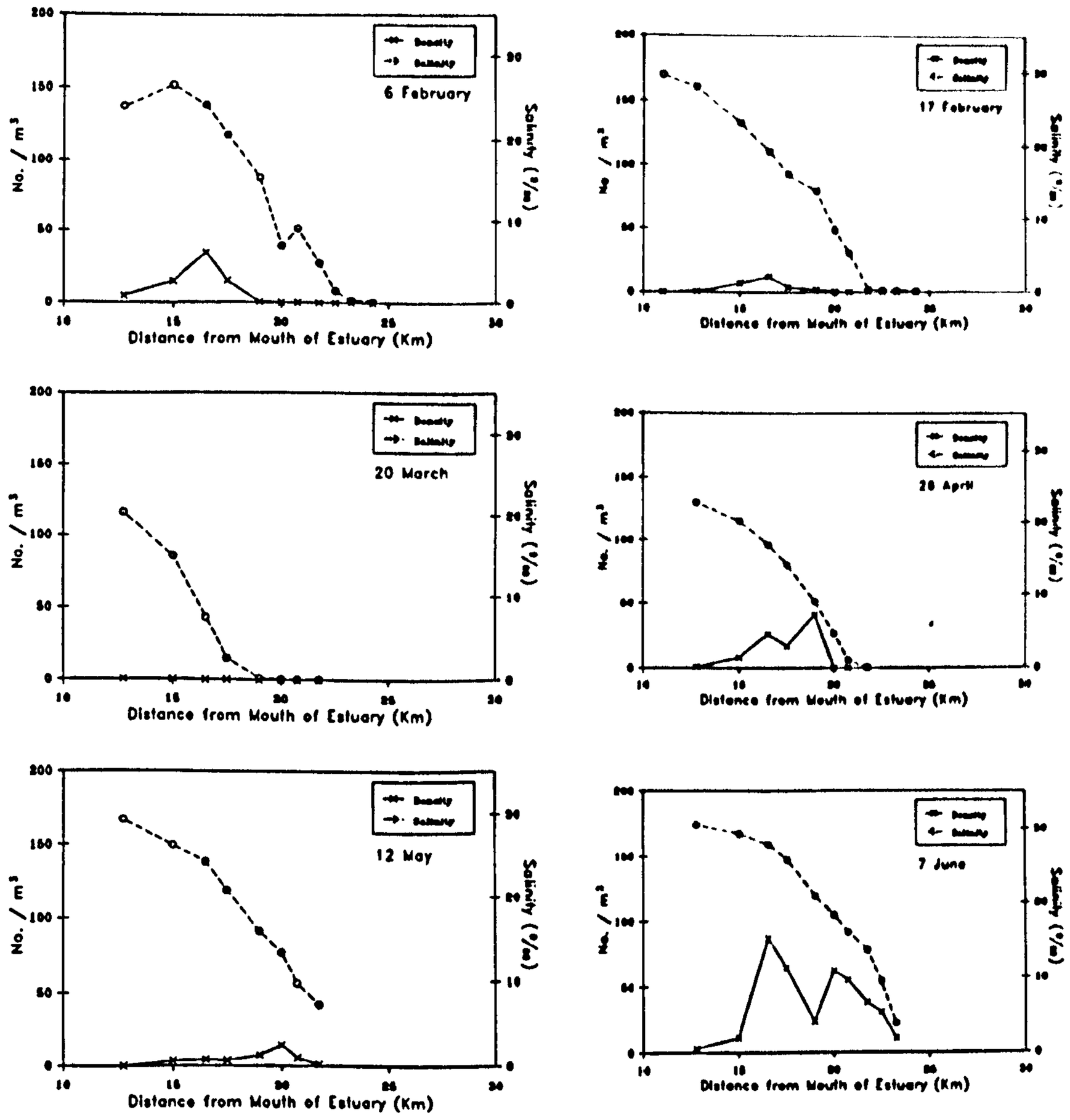

Fig. 2. Longitudinal density distributions of *Mesopodopsis slabberi* in the Tamar Estuary with respect to salinity during 1989

Mysid numbers declined rapidly during autumn (October - November) to the levels recorded in the previous February. The increase in *M. slabberi* density in spring (March - May) was due primarily to an influx of juveniles into the population and coincided with rising water temperature (Fig. 3). This increase in the relative importance of juveniles was preceded by an increase in the proportion of males and females in the population between February and April. Juveniles dominated the population until the end of the year, although their number declined as the water temperature decreased.

In March and October, few *M. slabberi* were sampled. In these months there were relatively high river discharges (76 m^{-3} s^{-1} and 46 m^{-3} s^{-1}, respectively, compared with the low record of 3.5 m^{-3} s^{-1}) causing freshwater conditions to extend to within 20 km of the mouth of the estuary. Turbidity in March was relatively low throughout the sampling area (Table 2).

M. slabberi occurred most abundantly immediately above the sediment surface (unpublished

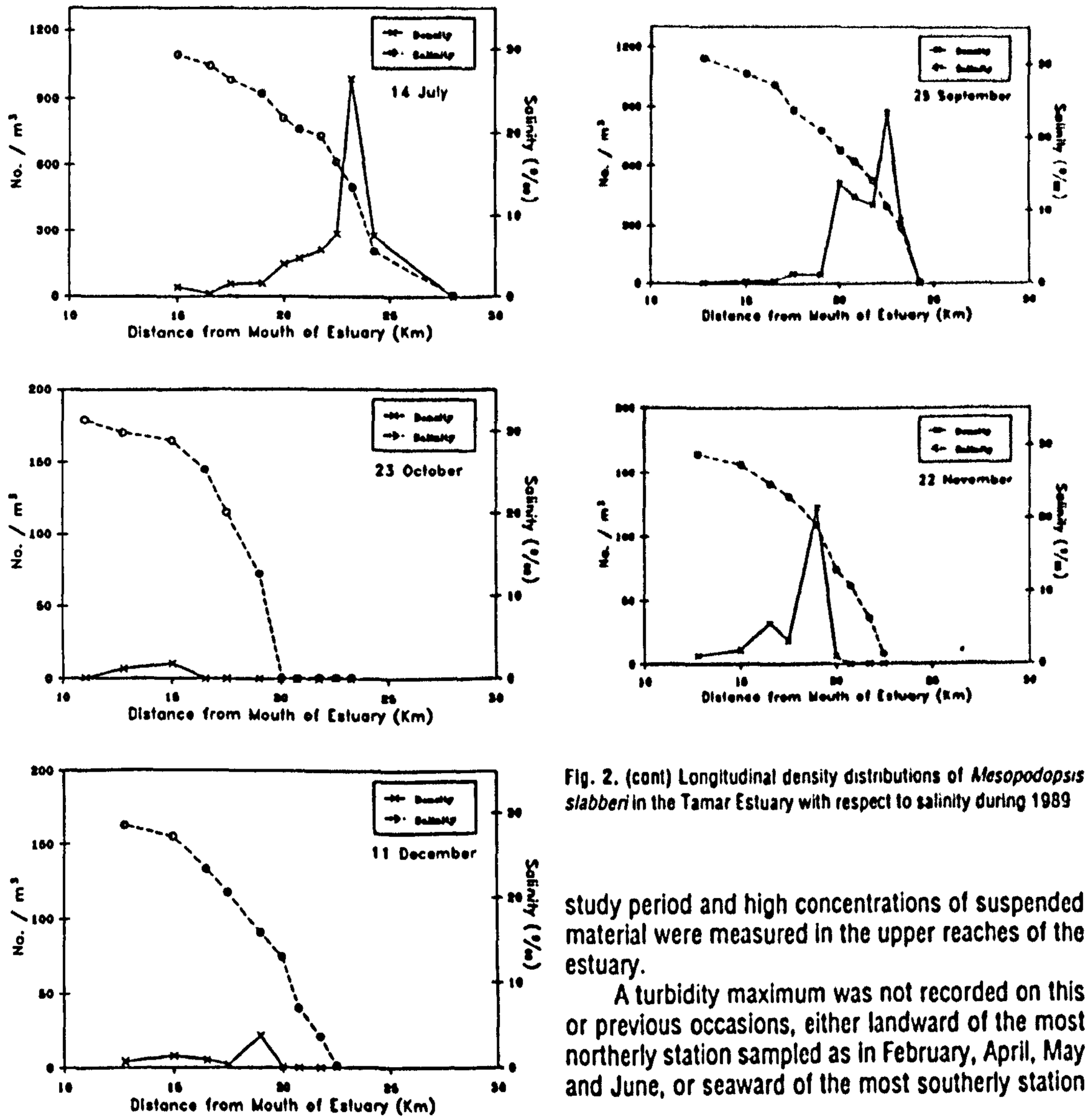

Fig. 2. (cont) Longitudinal density distributions of *Mesopodopsis slabberi* in the Tamar Estuary with respect to salinity during 1989

data), therefore only the bottom salinity measurements were used in the analysis. *M. slabberi* generally occupied the water mass with a salinty of between 5 and 25‰. Analysis of the length-frequency distribution in June (taken as a typical month in terms of mysid distribution) revealed partitioning of the adult, immature and juvenile populations along the salinity gradient (Fig. 4). The population at the highest salinity (29.3‰) consisted almost entirely of small juveniles. Immature animals and larger juveniles appeared in the mid range (21-15‰) of the salinity gradient and adults comprised almost all of the population in salinities less than 10‰. During June, the river flow was also the lowest recorded (3.5 m^{-3} s^{-1}) during the study period and high concentrations of suspended material were measured in the upper reaches of the estuary.

A turbidity maximum was not recorded on this or previous occasions, either landward of the most northerly station sampled as in February, April, May and June, or seaward of the most southerly station

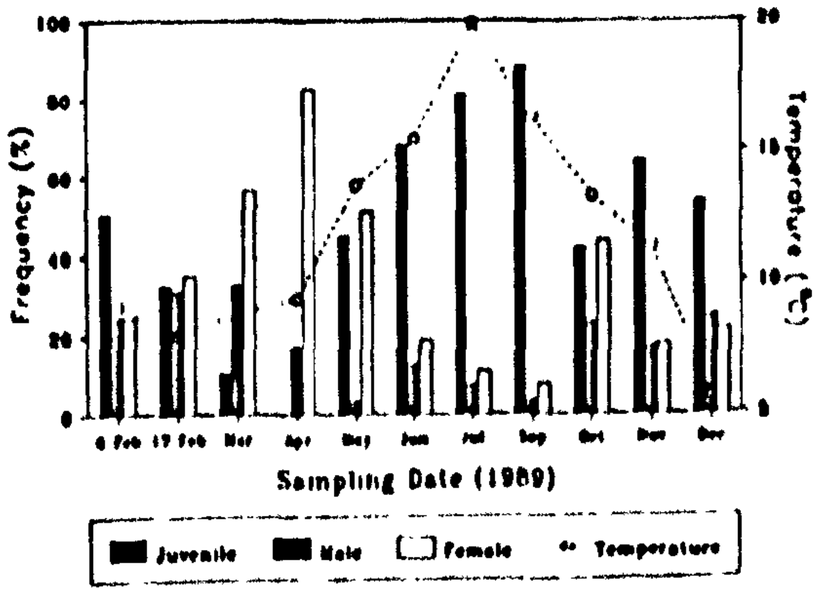

Fig. 3. Proportion of male, female and juvenile *Mesopodopsis slabberi* in the Tamar Estuary in 1989 in relation to water temperature. Refer to Fig 2 for details of density

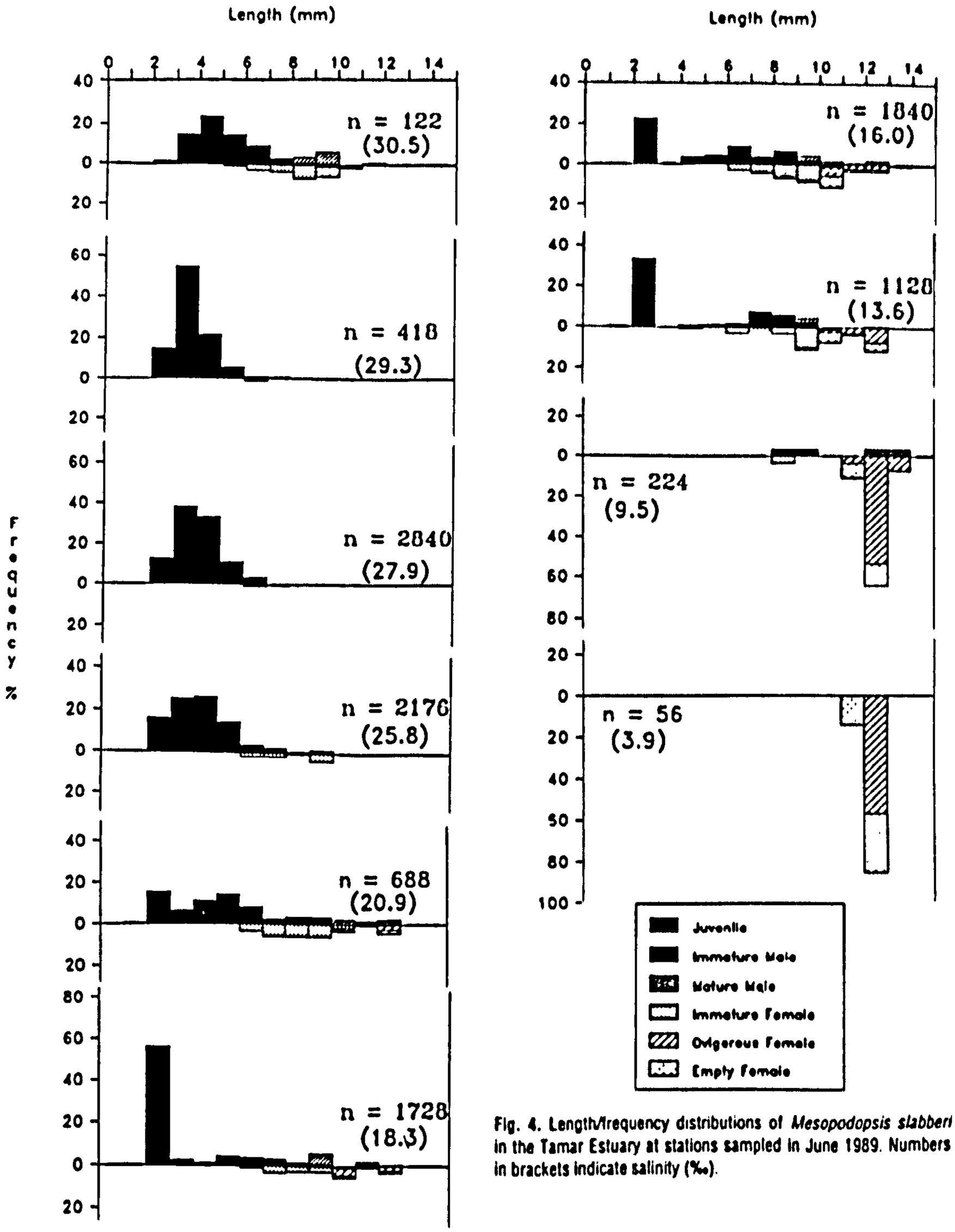

Fig. 4. Length/frequency distributions of *Mesopodopsis slabberi* in the Tamar Estuary at stations sampled in June 1989. Numbers in brackets indicate salinity (‰).

as was perhaps the case in March due to the very high run off (Table 2). Turbidity did not appear to be directly correlated with the distribution of *M. slabberi*. The entire population was found in the area of the estuary below the turbidity maximum on each sampling occasion.

DISCUSSION

The seasonal abundance of *Mesopodopsis slabberi* appears to be controlled by seasonal changes in water temperature. This agrees with the results of TODA *et al.* (1983, 1984) who found that

growth and reproduction of the mysid *Neomysis intermedia* was controlled by temperature. Increasing environmental temperature caused increases in brood size, brood interval, and specific growth rate (TODA *et al.*, 1983,1984).

The range of salinity in which *Mesopodopsis slabberi* occurred in this study confirmed that the species is euryhaline. It has been collected from salinities ranging from 1.9‰ in the mouth of the River Danube to full strength seawater in Dutch coastal waters (GOMOIU, 1978; HAMERLYNCK and MEES, 1991). However, the salinity regime in the Tamar Estuary is primarily governed by the hydrodynamics of the estuarine system and varies on both short- and long-term cycles (UNCLES *et al.*, 1985a, b, c). Under the conditions of high run off shown in the results for October and March, *Mesopodopsis slabberi* is either flushed out of the upper estuary or actively migrates to more saline regions. The results for June illustrate the distribution under conditions of low river discharge. These data suggest that the different life stages of *M. slabberi* must be able to select particular physicochemical regimes in order to achieve the partitioning seen in the population. Several mysid species are able to regulate their position in estuaries and coastal regions by undergoing vertical and/or lateral migrations. For example, *Mesopodopsis wooldrigii* (formerly *M. slabberi*; WITTMANN, 1992) undergoes active vertical migration in the Sundays River Estuary; to maintain their position, adults migrate both laterally and vertically, with juveniles more frequently found in faster-flowing surface waters (WOOLDRIDGE and ERASMUS, 1980; WOOLDRIDGE and BAILEY, 1982). *Neomysis mercedis* utilizes this same two-layered estuarine circulation to maintain its position in the San Francisco Bay-Delta, with mature individuals using near-bottom tidal currents to remain above the turbidity maximum zone while juveniles remain just below the turbidity maximum by utilizing seawards flowing surface currents (ORSI and KNUTSON, 1979; SIEGFRIED *et al.*, 1979).

In the present study, turbidity appears not to be directly important in influencing the distribution of *M. slabberi*. A possible explanation for the preference of juvenile *M. slabberi* for higher salinities is given by GREENWOOD *et al.* (1989), who found that ovigerous female *M. slabberi* were more euryhaline than mature males and eggs of this species developed most successfully in salinities higher than 7‰. No data are available for the salinity tolerance of juvenile *M. slabberi*, however, BHATTACHARYA (1982) found that juvenile *Mesopodopsis orientalis* survived better in >10‰ seawater than adults.

SUMMARY AND CONCLUSIONS

Our conclusion is that the principal factor affecting the seasonal abundance of *Mesopodopsis slabberi* is reproduction which is controlled, primarily, by environmental temperature. Abundance is greatest in the area of the estuary downstream from the maximum turbidity zone, within a salinity range of 5-25‰. The population undergoes shifts in longitudinal distribution in response to changes in the position of the salinity gradient which is in turn influenced by the rate of freshwater run-off and the state and phase of the tidal cycle. Separation of the life stages occurs along the salinity gradient, adults being confined to the low salinity (<10‰) region of the estuary. Juveniles are more widely distributed and occupy the 10-30‰ salinity range. It appears that *M. slabberi* utilises the two-layered estuarine circulation to maintain its position in the estuary.

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