

Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters

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ABSTRACT: Between 1977 and 1992, semi-quantitative samples of macroinvertebrates were taken at fortnightly intervals from the Thames Estuary (UK) utilising the cooling water intake screens of West Thurrock power station. Samples were taken for 4 h over low water, the abundances of invertebrates recorded in 30 min subsamples and related to water volume filtered. Abundances of the major estuarine species have therefore been recorded every 2 wk for a 16 yr period, together with physico-chemical parameters such as temperature, salinity and freshwater flow. Annual cycles of distribution were apparent for several species. *Carcinus maenas* exhibited a regular annual cycle, with a peak in autumn followed by a decrease in numbers over winter, relating to seasonal temperature patterns. Conversely, abundance of *Crangon crangon* was consistently lowest in summer, responding to seasonal changes in salinity, whilst *Liocarcinus holsatus*, *Aurelia aurita* and *Pleurobrachia pileus* were only present in summer samples, with *P. pileus* often in vast numbers (>100 000 per 500 million l). The estuarine prawn *Palaemon longirostris* showed no obvious sustained annual pattern, but evidence for a longer cycle of distribution was apparent. During 1989–1992 severe droughts in southeast England severely disrupted annual salinity patterns and coincided with a large increase in the Chinese mitten crab *Eriocheir sinensis* population. This included the first synchronised migration of adults in the UK. Settlement of young crabs during low-flow periods is suggested as an explanation for this population increase.

KEY WORDS: Thames · Power station · Salinity · Freshwater flow · *Crangon* · *Carcinus* · *Eriocheir* · *Palaemon* · *Aurelia* · *Pleurobrachia*

INTRODUCTION

Patterns of organism distribution along the length of an estuary are determined primarily by the longitudinal salinity profile (Remane & Schlieper 1971), a marine organism's penetration up the estuary being dependent on its tolerance to reduced salinities. The ambient salinity at any one point can also vary on a daily basis (due to tidal movement) and on a seasonal basis (due to variations in freshwater input), this variability increasing the stress organisms are subjected to and thus affecting their realized distribution (McLusky

1971). Much work has been undertaken on the diurnal rhythmic behaviour of estuarine organisms (e.g. Janssen & Kuipers 1980, McGaw & Naylor 1992, Laprise & Dodson 1994), but less is known about the effect of the seasonal variation on organism distribution. Long-term data sets with seasonal components tend to concentrate on plankton (Carter & Dadswell 1983, Castel 1993) and benthic invertebrates (Chapman & Brinkhurst 1981, Henderson 1984).

The intake of cooling water by power stations provides a convenient and comparatively efficient method of sampling estuarine organisms (Boreman et al. 1981, Summers 1989), the majority of studies focusing on fish communities entrained on intake screens (e.g. Turnpenny 1983, Robin 1988, 1991, Claridge & Potter 1994).

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Continual sampling from the intakes has provided some long-term, seasonal information on these fish communities (Van den Broek 1979, Andrews 1984, Claridge et al. 1986), together with fewer data on entrained invertebrates (Huddart & Arthur 1971a, Karas 1992, Bamber & Henderson 1994). Knowledge remains limited, however, on the consistency of cyclical seasonal patterns in estuarine populations due to the inherent difficulties of compiling such long-term data sets.

Fish populations entrained on power station intake screens were used during the 1960s and 1970s to document the recovery of the polluted Thames Estuary, UK (Huddart & Arthur 1971b, Wheeler 1979, Andrews & Rickard 1980), with a diverse fish community being present by the end of the 1970s. Huddart & Arthur (1971a, c) undertook supplementary studies on the brown shrimp *Crangon crangon* (L.) from power station intake screens, including seasonal abundance patterns and their response to the low oxygen environment present in the Thames at the time. Other studies have provided information on the benthic macrofaunal community (Birtwell & Arthur 1980, Andrews et al. 1982, Attrill et al. 1996a), with Attrill et al. (1996b) describing the response of upper estuary invertebrate communities to seasonal changes in low freshwater flow. The aims of this paper are therefore to detail the population dynamics of the most abundant invertebrates entrained on power station screens in the Thames Estuary over a period of 16 yr and, where possible, to relate these patterns to changes in the major hydrological parameters.

SITE DESCRIPTION AND SURVEY METHOD

The Thames Estuary extends 110 km from Teddington Weir (west London), the limit of tidal influence, through Greater London and out into the southern North Sea (Fig. 1). Approximately 10 million people inhabit the Thames catchment. The pressure of this large metropolitan population has resulted in periods of extremely poor water quality in the Thames Estuary (Wheeler 1979), with large anoxic stretches of the mid-estuary present during the 1950s. Recovery of the estuary since the 1960s has been documented by analysis of the fish communities entrained at power stations, particularly the coal-fired power station at West Thurrock (Fig. 1), situated on the north bank of the estuary 66.5 km seawards of Teddington Weir (National Grid Reference: TQ 590 770).

The power station extracts up to 150 million l h⁻¹ of water from the Thames estuary for cooling purposes, the intake opening being situated well below the low tide mark. Vertical slats 0.5 m apart prevent large

items of debris entering the system. The final cooling pipes leading to the power station are 2.5 cm in diameter, so all suspended solid matter and organisms >1 cm in size are filtered and removed by 6 rotating band (or Brackett) screens. At the top of the filter, the screen is washed clean by water jets, and the filtered material (including organisms) is flushed via a gutter system to a trash pit and then through a small opening back to the estuary. To collect organisms, square framed nets with mesh size of 1 mm were fitted to the end of each screen's gutter. Sampling periods started 1 h before low water and continued for a period of 4 h. The nets were emptied and repositioned every 30 min, the organisms caught in that sample being identified and enumerated. The total catch for the 4 h period can be summed for temporal comparison.

Seasonal variability in the demand for electricity dictates the amount of water needed to cool the power station's generators, and hence the number of intake pumps in operation (up to 6). Due to this variation, the number of organisms collected is expressed in terms of 500 million l to allow comparison between surveys. The number of pumps in operation can also vary during a survey as demand fluctuates, the calculation for number of individuals per 500 million l being:

$$E = \frac{100A}{(\bar{P}_1 \times L_1) + (P_2 \times L_2) + \dots + (P_n \times L_n)}$$

where E is the expected number of individuals of a species in 500 million l, A the actual number of individuals recorded in the 4 h sample, P_n is the number of pumps in operation and L_n the length of time (in hours) pumps P_n are in operation.

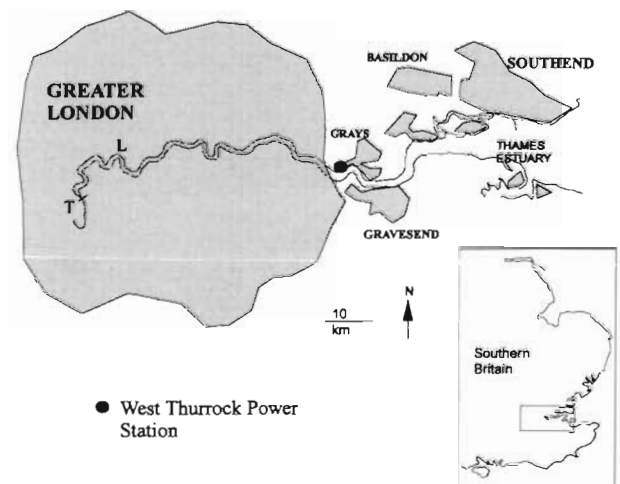


Fig. 1. Map of the Thames Estuary (UK) indicating surrounding metropolitan areas and the position of West Thurrock power station. L: Lots Road power station, Hammersmith; T: Teddington Weir

Samples of fish and invertebrates were taken by staff from the National Rivers Authority (NRA), and precursory organisations, every 2 wk at spring tide between 1977 and 1992. The power station was closed in 1993.

Daily flow rates of freshwater over Teddington Weir were measured by a NRA gauging station. Salinity and temperature measurements were obtained during weekly water analysis runs by the NRA sampling vessel along the length of the estuary, the measurements corresponding to a zone off West Thurrock power station. All salinity measurements were half-tide corrected to allow spatial and temporal comparison.

RESULTS

Physico-chemical data

As would be expected for a temperate estuary, there was a strong seasonal pattern in temperature over the 16 yr period surveyed, with summer peaks and winter troughs (Fig. 2). However, there was a distinct increase in the maximum summer temperature between 1977 and 1984, this maximum temperature being maintained above 20°C over the ensuing 8 yr. Consistently cold winters occurred between 1982 and 1988, with minimum temperature falling to around or below 5°C. In 1984 both the highest and lowest water temperatures during the survey were recorded.

Salinity followed a similar, although less predictable, pattern to temperature (Fig. 3), particularly between 1977 and 1988. Annual patterns became far more variable in the ensuing years, with high summer salinities and, at the end of the survey period, no distinguishable winter minimum. Consecutive droughts occurred in southeast England from 1989 to 1992 (Attrill et al. 1996b), thus reducing the freshwater flow over Teddington Weir (Fig. 4) and disrupting the typical salinity patterns within the estuary. High rainfall occurred at the start of 1990, which is reflected in the reduced salinities at West Thurrock, but precipitation across the catchment was minimal after this point, resulting in saline water being present all year off the power station.

Invertebrates

A wide taxonomic range of invertebrates was recorded in samples from the intake screens at West Thurrock (Appendix 1), but only 3 main groups (ctenophores, scyphozoan cnidarians and decapod crustaceans) were regularly present in large enough numbers to warrant further analysis.

Ctenophora and Cnidaria

The ctenophore *Pleurobrachia pileus* (O. F. Müller) was consistently recorded in summer (Fig. 5), in varying numbers ranging from a maximum of 10 (1985) to 100 000 (1989). During such blooms *P. pileus* was the dominant organism in catches, resulting in sampling nets rupturing under their weight in 1989. In the majority of years, peak abundances occurred during June or July. The moon jellyfish *Aurelia aurita* (L.) also formed discrete summer peaks in abundance at West Thurrock, generally being recorded in samples in July/August (Fig. 6). Large numbers of *A. aurita* were a regular occurrence during the first half of the survey, where abundances exceeded 1200 per 500 million l, but between 1985 and 1992 it was comparatively scarce, being absent during 1987.

Crustacea: Decapoda: Natantia

Six species of natant decapod were recorded in samples from West Thurrock: *Crangon crangon*, *Palaemon longirostris* Milne Edwards, *Palaemon serratus* (Pennant), *Pandalus montagui* Leach, *Palaemon elegans* Rathke and *Palaemonetes varians* (Leach), the latter 2 being rare occurrences, generally as single individuals. *P. serratus* and *P. montagui* were regularly encountered during summer months, but in low numbers. *C. crangon* was the most consistently abundant species recorded at West Thurrock (Fig. 7), and displayed a distinct cyclical distribution, regularly reaching peak abundances of 10 000 to 100 000 per 500 million l at the end of each year. A dramatic decrease in numbers was evident, generally during May and June, *C. crangon* being absent from samples in 4 years of the survey at this time. The estuarine prawn *P. longirostris* was also comparatively abundant in the Thames, regularly occurring in significant numbers (peak of 50 000 per 500 million l) on the screens at West Thurrock (Fig. 8). There is some evidence that *P. longirostris* exhibits an annual cycle of abundance, with peak numbers in summer and lower numbers during winter months, although this pattern was extremely weak, particularly over the second half of the survey. The population appears to have gone through phases of abundance in this part of the estuary, with larger scale peaks of abundance (e.g. 1982–1985, 1990–1992) followed by several years when the species was comparatively scarce (1986–1990).

Crustacea: Decapoda: Brachyura

Four species of crab were recorded at West Thurrock: *Carcinus maenas* (L.), *Liocarcinus holsatus* (Fabricus),

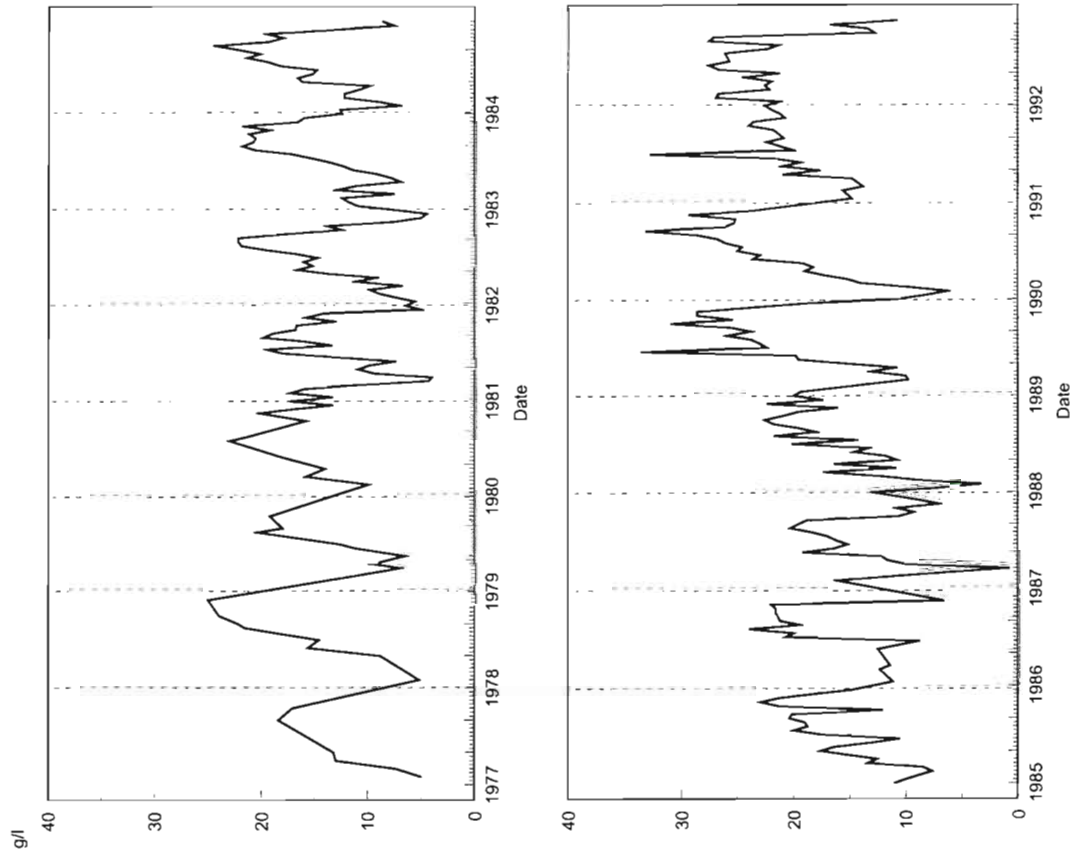


Fig. 3. Salinity of the estuarine zone off West Thurrock power station, 1977-1992

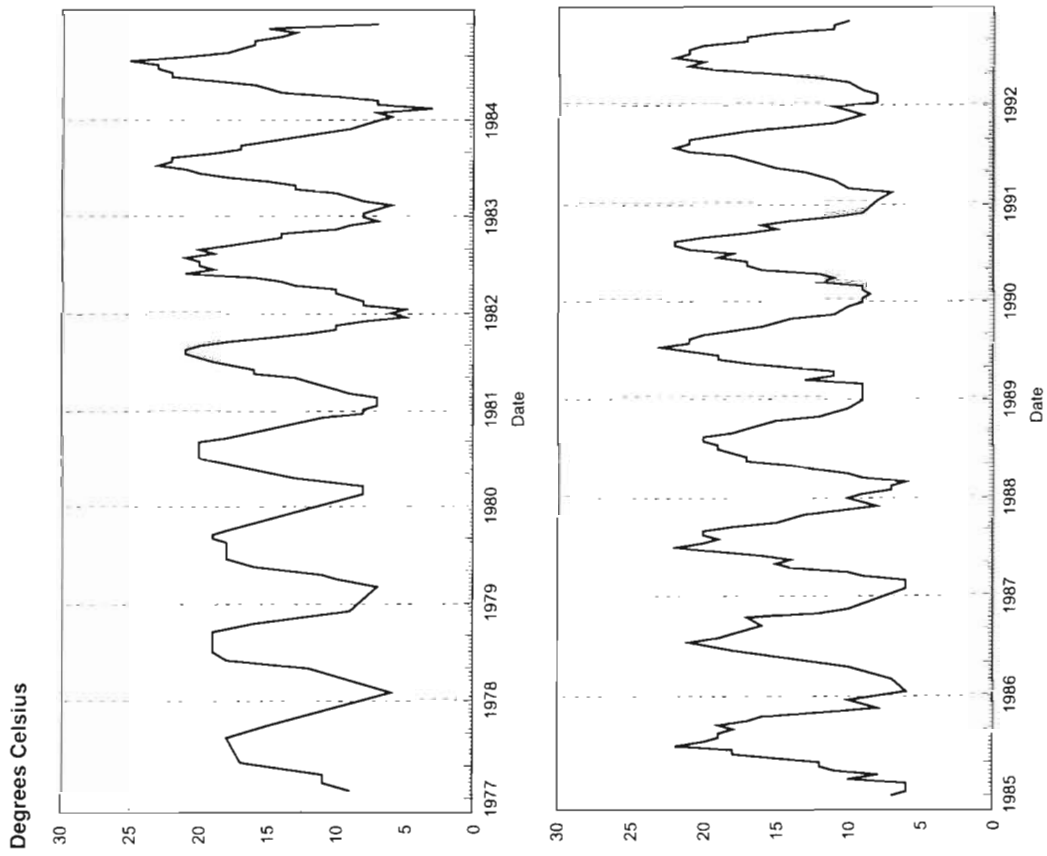


Fig. 2. Water temperature of the Thames Estuary off West Thurrock power station, 1977-1992

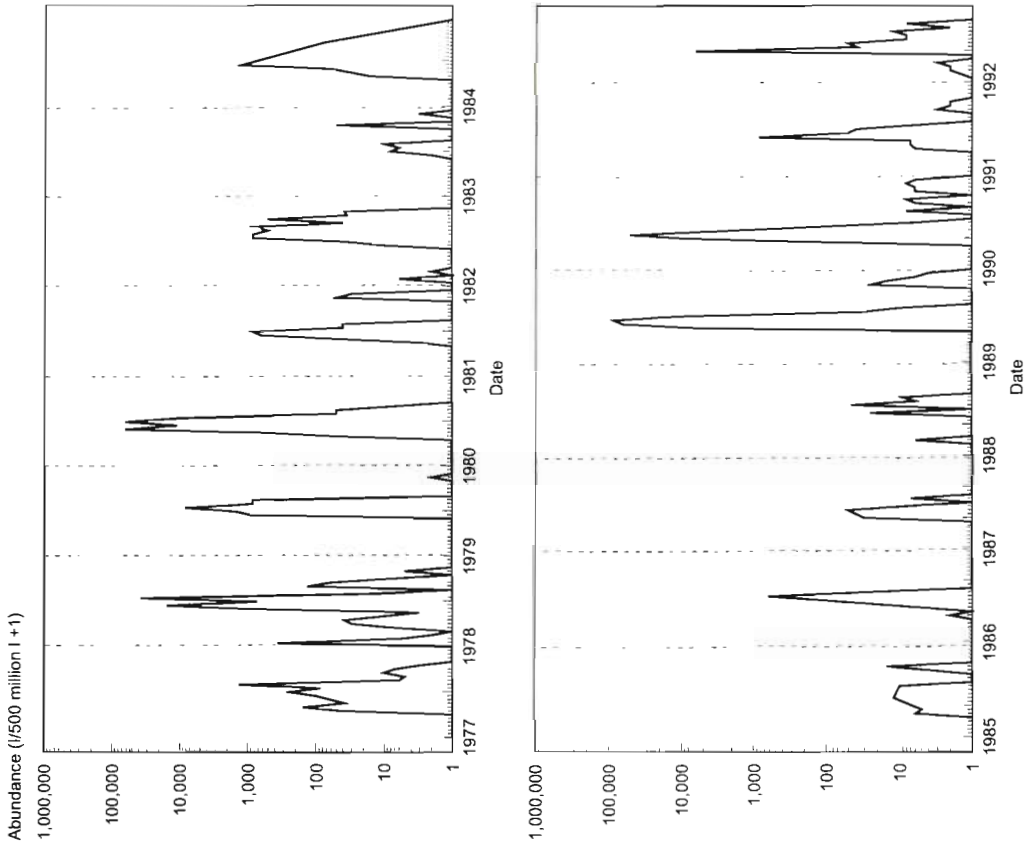


Fig. 5. Abundance of *Pleurobrachia pileus* recorded in fortnightly samples from West Thurrock power station, 1977–1992

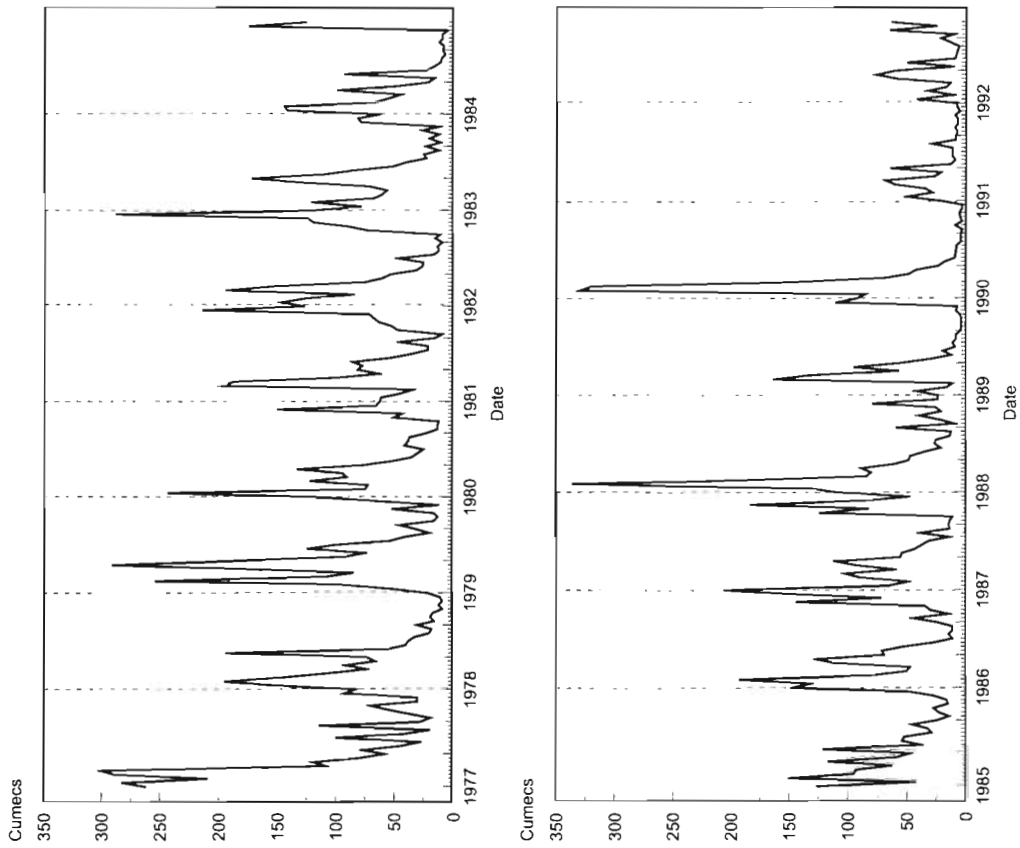


Fig. 4. Gauged freshwater flow of the River Thames over Teddington Weir, 1977–1992

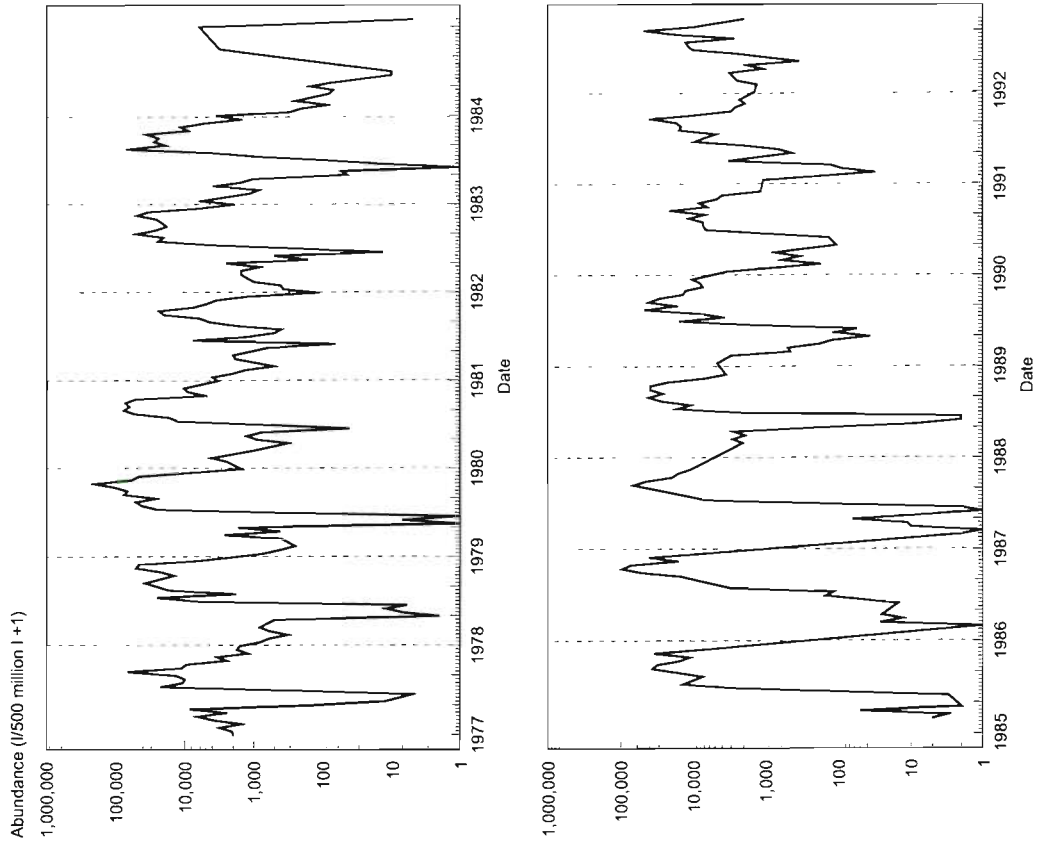


Fig. 7. Abundance of *Crangon crangon* recorded in fortnightly samples from West Thurrock power station, 1977–1992

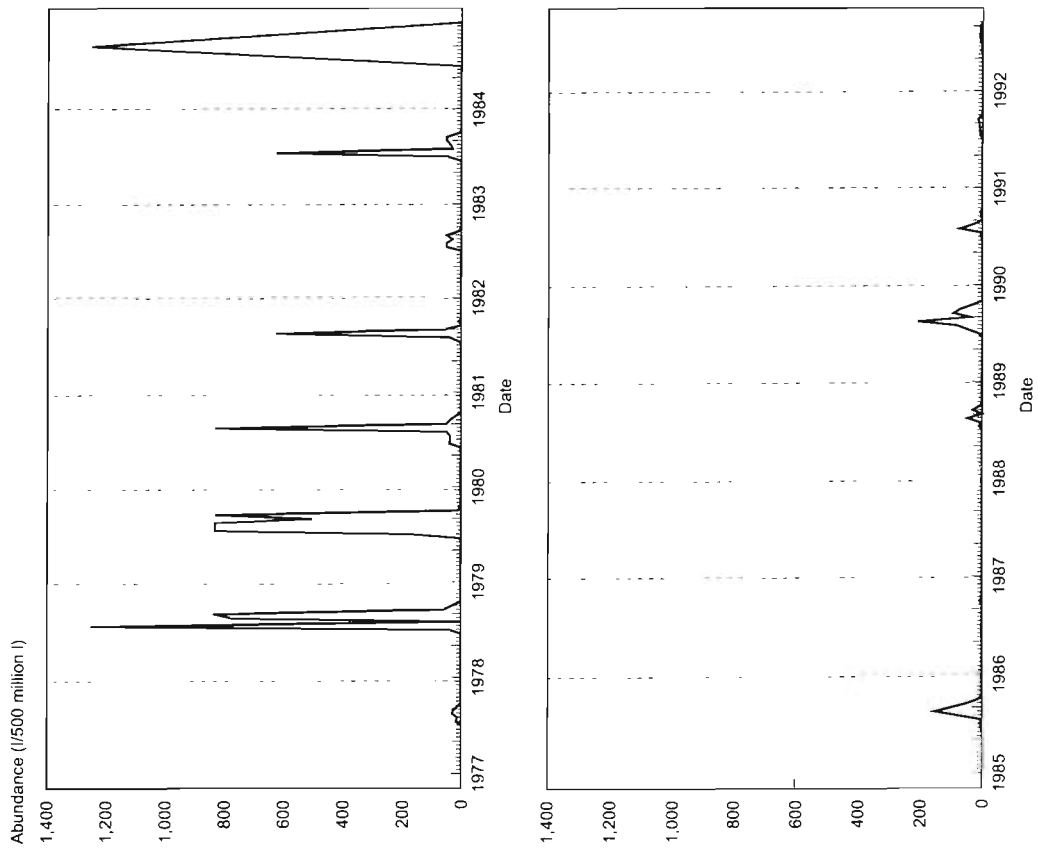


Fig. 6. Abundance of *Aurelia aurilia* recorded in fortnightly samples from West Thurrock power station, 1977–1992

Eriocheir sinensis Milne Edwards and *Macropodia rostrata* (L.). *M. rostrata* was only recorded on 1 occasion, probably associated with drifting clumps of the hydroid *Sertularia cupressina* L. The shore crab *C. maenas* exhibited a strong annual cycle (Fig. 9), with peak abundances being recorded during October or November in the majority of years, the size of this peak varying from <100 to 450 per 500 million l. This peak was generally due to a large influx of small crabs (<3 cm carapace width) and was followed by a marked decrease in the number of *C. maenas* recorded on the screens, reaching a minimum in January and February. During several years, crabs were absent from February samples. The population demonstrated a steady increase in numbers over the rest of the year. The swimming crab *L. holsatus* regularly occurred in samples taken during July and August (Fig. 10), the peak abundance for this species ranging from 300 per 500 million l in 1980 to being absent the whole year in 1987.

The Chinese mitten crab *Eriocheir sinensis* has only sporadically been recorded in the UK since 1935, mostly from the Thames (Ingle 1986), despite being present in vast numbers in European river systems (Panning 1938) following its introduction from the Far East at the start of this century. *E. sinensis* was occasionally encountered in samples taken at West Thur-

rock, but occurrences became more regular after 1988 (Fig. 11). Abundances increased during 1991–1992 culminating in 32 crabs per 500 million l being recorded in November 1992. During October 1992, hundreds of crabs were reported in the intake tanks of Lots Road power station (Hammersmith), 45 km upstream of West Thurrock (Fig. 1). All crabs recorded at West Thurrock in November 1992 were adults, with all females carrying eggs.

DISCUSSION

The distribution patterns of mobile invertebrates in the Thames Estuary can be divided into 3 categories: summer only, full annual cycles and long-term patterns. Organisms can appear in summer samples either because they are migrating up the estuary following reductions in salinity induced by reduced flow (e.g. *Lio-carcinus holsatus*) or because their population also reaches an annual peak during this season (e.g. *Pleuro-brachia pileus*, *Aurelia aurita*). *L. holsatus* generally inhabits coastal areas (Ingle 1983), the population of this swimming crab therefore increasing its spatial range within the Thames estuary during the summer period. This influx of *L. holsatus* would therefore introduce an

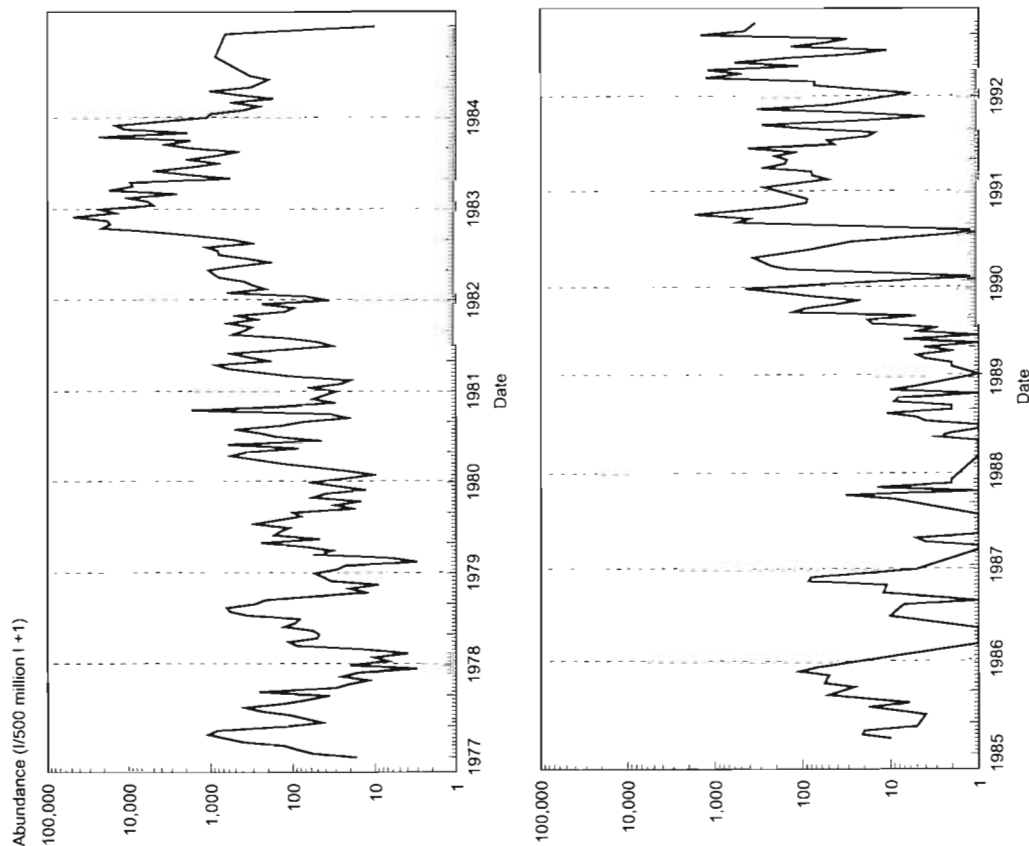


Fig. 8. Abundance of *Palaemon longirostris* recorded in fortnightly samples from West Thurrock power station, 1977–1992

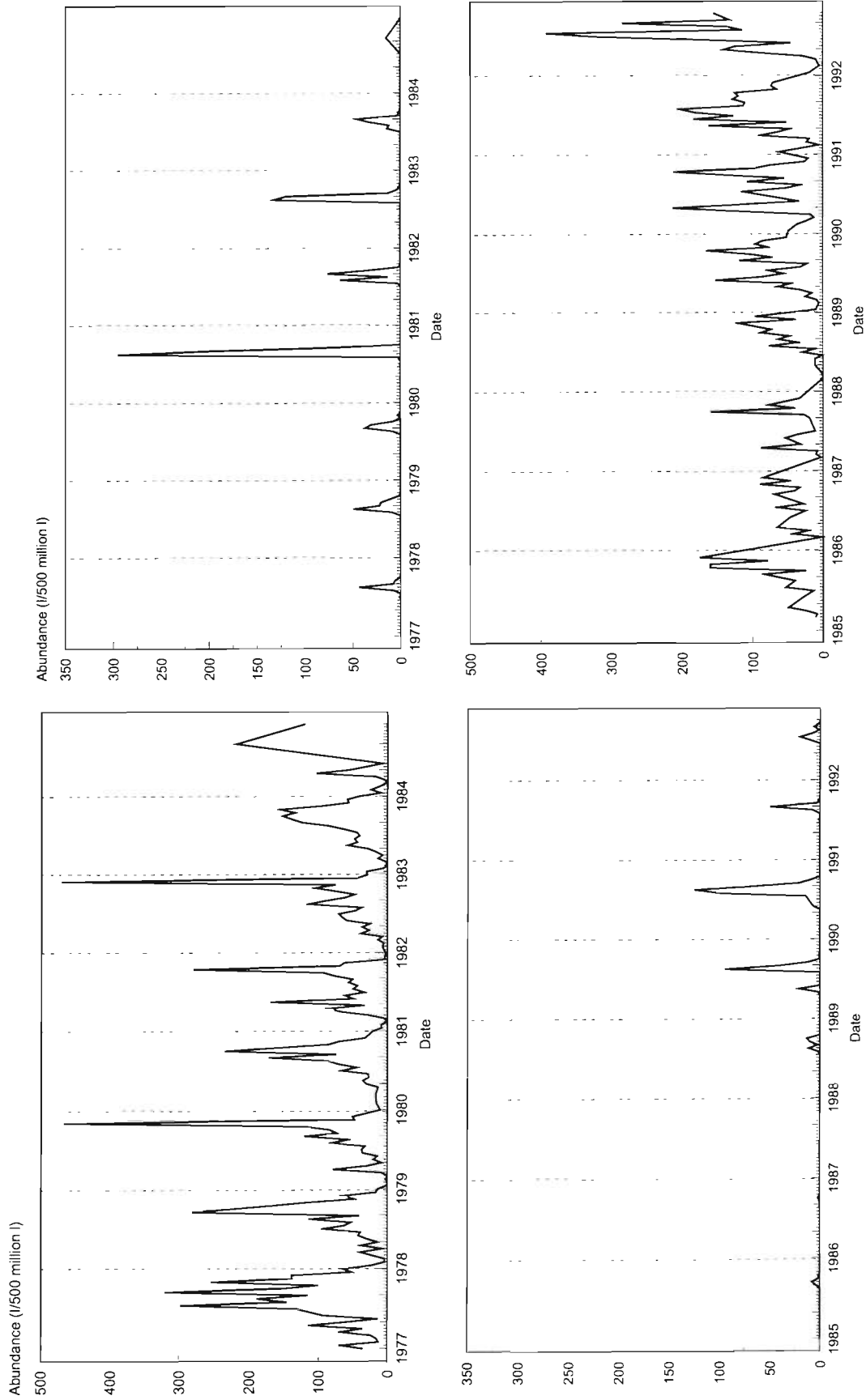


Fig. 9. Abundance of *Carcinus maenas* recorded in fortnightly samples from West Thurrock power station, 1977–1992

Fig. 10. Abundance of *Liocarcinus holtsatus* recorded in fortnightly samples from West Thurrock power station, 1977–1992

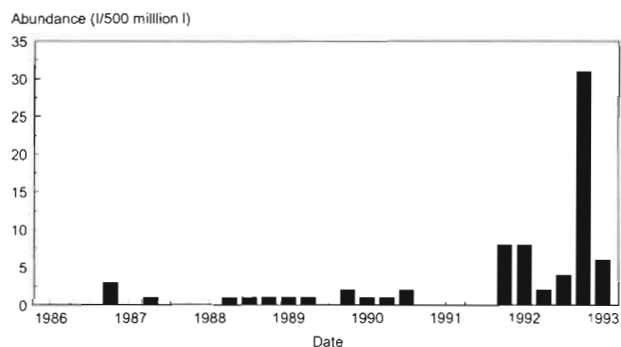


Fig. 11 Abundance of *Eriocheir sinensis* recorded in fortnightly samples from West Thurrock power station, 1977–1992. Data have been aggregated to quarters: Jan-Mar, Apr-Jun, Jul-Sep, Oct-Dec

additional competitor to resident *Carcinus maenas*, as their diets and feeding behaviour are similar (Choy 1986, Lee & Seed 1992). However, the population peak of *C. maenas* at West Thurrock occurs later in the year. Longer-term population trends are evident for *L. holtsatus*, with the species being absent, or recorded in very low numbers, between 1984 and 1989, with no associated change in the overall salinity regime for these years.

The gelatinous planktonic species also recorded peaks in abundance during the summer months, *Aurelia aurita* being present for a much shorter length of time than *Pleurobrachia pileus* and being much less common over the second half of the survey period. Annual population blooms have been widely recorded for both species (e.g. Möller 1980, Van der Veer & Sadee 1984, Frank 1986, Schneider & Behrends 1994) and have been reported to have a significant impact on the zooplankton community (Kuipers et al. 1990, Behrends & Schneider 1995). However, peak abundances as recorded at West Thurrock (Figs. 5 & 6) are later in the year for both species than in surrounding North Sea areas. Van der Veer & Sadee (1984) recorded maximum abundances of *P. pileus* in the Dutch Wadden Sea during May, whilst *A. aurita* populations generally reach a peak in late spring (Norway: Olesen et al. 1994; Southampton Water: Lucas & Williams 1994). This delayed peak in the Thames may reflect the period required for the population to move up the estuary.

Several of the crustacean species recorded at West Thurrock are present in the estuary over the majority of the year, but the abundances of 2 species on the intake screens show distinct annual, cyclical fluctuations. The brown shrimp *Crangon crangon* is perhaps the most common mobile macrofaunal species in large north European estuaries with strong tidal currents (Tiews 1970) and is present in very large numbers in the Thames. Tidal migrations have been recorded for the species (Hartsuyker 1966, Al-Adhub & Naylor 1975), although Janssen & Kuipers (1980) found no evi-

dence for this in the tidal channels of the Wadden Sea. Seasonal migrations within estuaries have also been recorded (Henderson & Holmes 1987), peak numbers occurring in the Severn Estuary (UK) between November and January with annual abundance minima during the summer. This pattern is similar to that recorded in the Thames, suggesting that populations migrate seawards during winter to avoid reduced salinities and again later in the year to reproduce (Lloyd & Yonge 1947, Henderson & Holmes 1987). At these times *C. crangon* are entrained on the screens of West Thurrock power station in large numbers, migrating further up the estuary during late spring/summer to exploit the patterns of encroaching salinity. It would therefore appear that this pattern of migration is indicative of estuarine populations of *C. crangon*; the Severn and Thames are considered to hold separate populations of this species (Henderson et al. 1990). In turn, these patterns are distinct from intertidal populations, which reach peak numbers in summer and lowest abundances during winter (Beukema 1992).

The shore crab *Carcinus maenas* also demonstrates a cyclical pattern of distribution within the Thames, with lowest abundances being recorded at West Thurrock during January-February and peak numbers during October-November. The vast majority of individuals were green type, the orange/red crabs being comparatively intolerant of reduced salinity and thus rarer in estuaries (McGaw & Naylor 1992). Aagaard et al. (1995) recorded peak numbers of *C. maenas* during August in a Danish fjord, and associated this with a peak in foraging activity rather than migrations of the population. Lowest abundances were between February and May and related to temperature-dependent activity patterns, the threshold for active foraging being 8°C (Naylor 1962, Atkinson & Parsons 1973). Water temperatures in the Thames Estuary fell below this value for only a short period during January-February in most years (Fig. 2), coincident with minimum abundances of *C. maenas* on the intake screens of the power station. It would therefore appear that reduction in catches of *C. maenas* is due to an inactive population rather than migration of adults. Peak numbers of crabs in the Thames occurred later than those recorded by Aagaard et al. (1995), but this does not necessarily suggest any differences in foraging behaviour. Peaks on the intake screens tended to be due to a large, and short-term, influx of small crabs which masked any other cycles of activity that may have been present.

Two other crustaceans, *Palaemon longirostris* and *Eriocheir sinensis*, did not show distinct annual cycles sustained throughout the length of the survey. Between 1977 and 1982, however, peak abundances of *P. longirostris* were recorded during the summer, with corresponding minima in winter. This pattern is in direct

contrast to other studies on the species in European estuaries (e.g. Marchand & Alliot 1981, Van den Brink & Van der Velde 1986, Cartaxana 1994) which have recorded movements of *P. longirostris* in response to changes in salinity. The prawns migrate up to freshwater during periods of reduced river flow and thus should have been absent at the mid-estuary site at West Thurrock during summer if this pattern was repeated in the Thames. During subsequent years this annual pattern was not so evident, the appearance of *P. longirostris* on the screens being sporadic between 1986 and 1990 when the species was absent in samples for periods of time. *P. longirostris* does, however, show evidence of longer-term population variation, with large numbers of prawns being present in the estuary between 1982–1984 and 1990–1992. During this latter period, drought conditions occurred in the Thames region, with consistent low freshwater flow (Fig. 4). If the population was following the salinity front, it would be expected that the majority of *P. longirostris* would inhabit the upper reaches of the estuary for most of the time, but this was clearly not the case.

Ever since the first Chinese mitten crab was recorded from the Thames Estuary (Harold 1935) records have been few and far between, despite the intensive sampling undertaken during the 1960s and 1970s to document the clean-up of the estuary. The intensity of sampling continued during the 1980s, with the use of the intake screens at West Thurrock power station, but the status of the mitten crab as an occasional, interesting vagrant continued. The data presented in Fig. 11 demonstrate how this pattern changed during 1991 and 1992, with adult crabs appearing more regularly at West Thurrock culminating in 32 individuals being caught in November 1992. This figure for 1 survey is greater than the combined records of *Eriocheir sinensis*

from the power station for the previous 7 yr, suggesting an aggregation of crabs, perhaps on their spawning migration. This is supported by the fact that all females were ovigerous (so must have spawned in the upper half of the estuary) and particularly by the observation of the large number of crabs at Lots Road power station during October. The estuary at West Thurrock is wider and deeper than at Lots Road, allowing the crabs to disperse. As 30 were still caught on the power station intake screens on the north bank, it would suggest that there were very large numbers of crabs in the estuary at the time. It would appear that this movement of crabs during the end of 1992 was the first large scale breeding migration of *E. sinensis* in the UK.

The question arises as to why, after 60 yr of occasional records from the UK, the Thames population of *Eriocheir sinensis* has suddenly increased in size. Vast numbers of these crabs are a familiar sight in other northern European countries, but they have never, until now, reached such large abundances in the UK. Ingle (1986) suggested that the UK rivers were much faster flowing than their northern European equivalents, so preventing any large scale settlement and development of mitten crabs. From the evidence presented in this paper it would appear that this hypothesis may be correct. The rise in the number of *E. sinensis* recorded in the Thames Estuary coincides with the overall long-term decrease in freshwater flows following the drought period since 1989 (Fig. 4). It is possible, therefore, that this decrease in flow allowed the establishment of young crabs during 1989, these crabs developing to maturity and so formed the spawning migration witnessed at the end of 1992. At this time the crabs would be approximately 3 to 4 yr old, the age of maturity suggested for the species (Ingle 1986).

Appendix 1. Taxonomic list of invertebrate species recorded from the intake screens at West Thurrock power station. Drifting colonial organisms have been excluded

Cnidaria

Aurelia aurita (L.)

Ctenophora

Pleurobrachia pileus (O.F. Müller)

Annelida: Polychaeta

Nereis diversicolor (O.F. Müller)

Nereis succinea (Frey & Leuckart)

Crustacea: Amphipoda

Corophium volutator (Pallas)

Gammarus salinus Spooner

Gammarus zaddachi Sexton

Crustacea: Isopoda

Idotea sp.

Crustacea: Mysidacea

Mesopodopsis slabberi (Van Beneden)

Neomysis integer (Leach)

Praunus flexuosus (Müller)

Schistomysis spiritus (Norman)

Sinella armata (Milne-Edwards)

Crustacea: Decapoda

Crangon crangon (L.)

Pandalus montagui Leach

Palaemon elegans Rathke

Palaemon longirostris Milne Edwards

Palaemon serratus (Pennant)

Palaemonetes varians (Leach)

Carcinus maenas (L.)

Eriocheir sinensis Milne Edwards

Liocarcinus holsatus (Fabricus)

Macropodia rostrata (L.)

Mollusca: Bivalvia

Mytilus edulis L.

Mollusca: Cephalopoda

Alloteuthis subulata (Lamarck)

Sepia officinalis L.

Sepiolo atlantica d'Orbigny

Urochordata: Ascidiacea

Molgula manhattensis (de Kay)

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Erratum

Re: Attrill MJ, Thomas RM

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- On page 32 the lower panels of Figs. 9 and 10 were accidentally exchanged. The correct layout is given below.

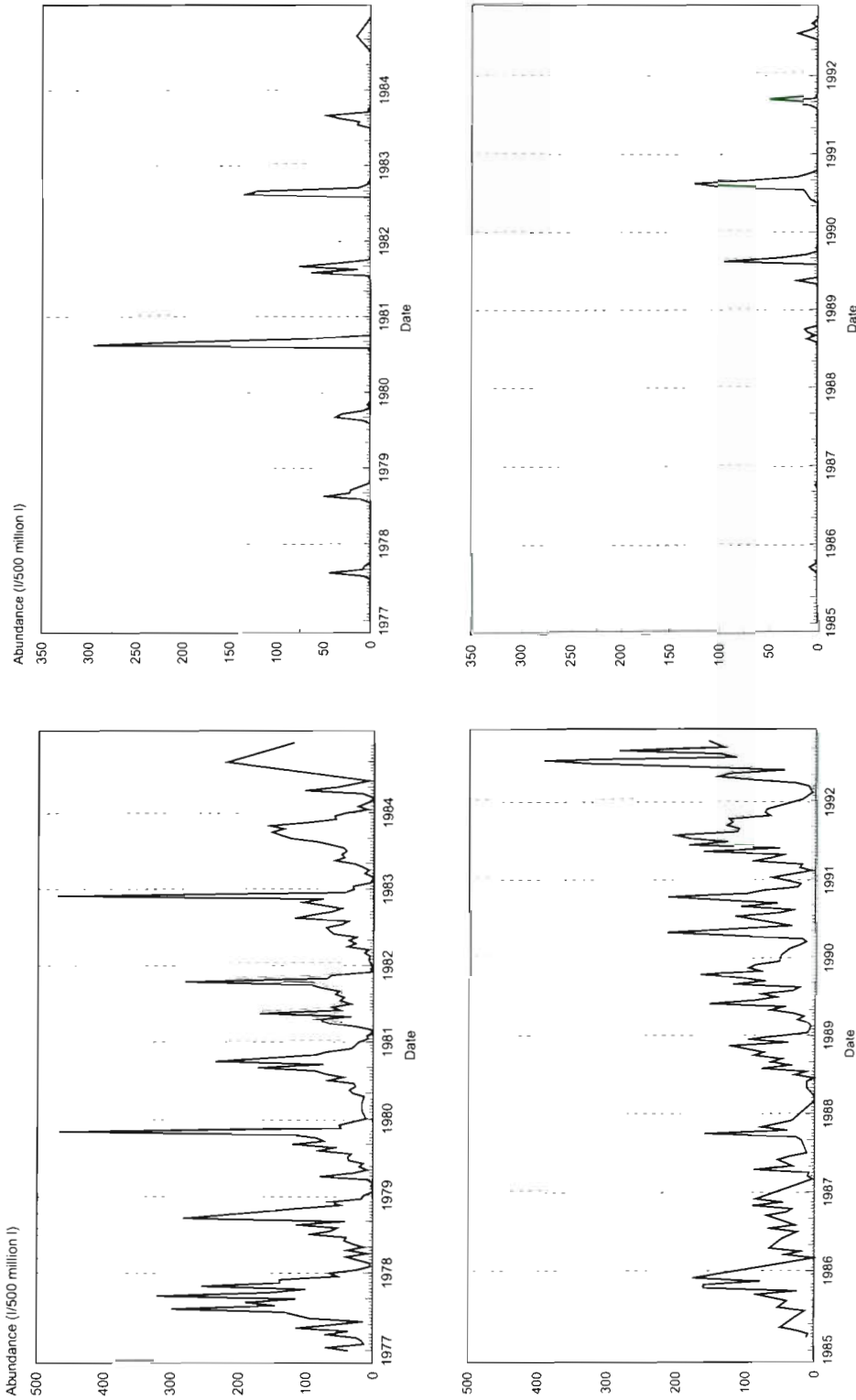


Fig. 9. Abundance of *Carcinus maenas* recorded in fortnightly samples from West Thurrock power station, 1977–1992

Fig. 10. Abundance of *Liocarcinus holtsatus* recorded in fortnightly samples from West Thurrock power station, 1977–1992