

Modelling estuarine Crustacea population fluctuations in response to physico-chemical trends

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ABSTRACT: Regular samples (generally every 2 wk) of 6 estuarine crustacean species, *Carcinus maenas*, *Liocarcinus holsatus*, *Crangon crangon*, *Palaemon longirostris*, *Palaemon serratus* and *Gammarus* spp. (mainly *G. zaddachi*), were taken over a 12 yr period from the cooling water intake screens of West Thurrock power station on the Thames estuary, UK. Additionally, comparative data sets for abiotic variables (freshwater flow, salinity, temperature, dissolved oxygen, pH, suspended solids, total nitrogen) were collected for the same time period. The comprehensive nature of the time series, and accompanying suite of variables, allowed the construction of statistical models for the trends in population abundance of the 6 species using multiple linear regression techniques. Statistically significant models were constructed for *C. maenas*, *C. crangon* and *Gammarus* spp., accurately predicting annual, and longer term, fluctuations in abundance. All models had strong seasonal components, although for *C. maenas* temperature was the only physico-chemical variable with significant explanatory power. The importance of temperature as a controlling variable for the species was reinforced by the inclusion of an instrumental variable to simulate a threshold temperature for foraging activity. The optimal value was found to be 8°C. *C. crangon* was found to be positively correlated with dissolved oxygen, but showed a slight decline in abundance over the time period. There was no significant relationship with either salinity or temperature, variables previously suggested as being important. *Gammarus* spp. abundance had 2 significant explanatory variables (temperature and salinity) but also demonstrated a large decrease in population size with time. *L. holsatus* and *P. serratus* are summer-occurring species, so were recorded too infrequently to adequately capture seasonal dynamics. Despite the long time series, no significant model was possible for *P. longirostris* abundance (non-normal residuals), which has been suggested previously as having a strong relationship with salinity. The results of the study provide the first significant multiple linear regression models that accurately predict estuarine crustacean abundance. Whilst these models are useful for helping to understand variability in the Thames, it will be interesting to determine whether populations in other estuaries demonstrate relationships with similar suites of physico-chemical parameters.

KEY WORDS: Thames · *Carcinus maenas* · *Crangon crangon* · *Gammarus* spp. · *Palaemon* spp. · Temporal trends · Models · Temperature · Salinity · Oxygen

INTRODUCTION

Continuous long-term time series of biological data (>10 yr) have been recognised as being extremely important as aids for understanding the functioning of ecosystems (Callahan 1984) and fluctuations within communities and populations (Coull 1986). They are

also required in order to estimate natural variation in undisturbed systems and interpret long-term effects on these systems (Rhoads & Germano 1986), as shorter data sets may provide misleading explanations of observed fluctuations (Gray & Christie 1983, Bourcier 1996). However, despite their value, such data sets are rare, particularly from estuarine and coastal systems (Wolfe et al. 1987), due mainly to logistical and financial constraints.

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The application of statistical techniques to the analysis of such ecological time series is even more uncommon (Jassby & Powell 1990), despite the fact that time series analysis is a well-developed branch of statistics (e.g. see Wei 1990). This is mainly due to the requirements that the observed measurements should be equally spaced with no missing values (Abraham & Ledolter 1983, Champely & Doledec 1997) and that a large number of samples are required (Jassby & Powell 1990). In addition, a suite of identically matched environmental variables are necessary if statistically significant conclusions on possible controlling factors are to be generated (Champely & Doledec 1997). The majority of long-term benthic data sets reported in the literature, whilst being of high descriptive value, are reliant on either annual (e.g. Pearson 1975, 1982), bi-annual (e.g. Buchanan & Moore 1986) or intermittent (e.g. López-Jamar et al. 1995) sampling, which provides a limited number of total samples with matching environmental variables that can be used in any time series model. Coull (1986) stated that the construction of such models, which would allow some predictive ability, should be one of the goals of long-term ecological research.

Attrill & Thomas (1996) published patterns of invertebrate abundance in the Thames estuary, UK, from >300 samples taken regularly over a 16 yr period. The trends in biota were compared with patterns of 3 physico-chemical variables (salinity, flow and temperature). However, the paper was a descriptive account of population cycles and no attempt was made to statistically relate the biotic patterns to the physico-chemical data presented, beyond inferences from visually comparing the 2 distributions. Additionally, the suite of possible abiotic controlling factors was comparatively small.

Statistical models are one of the few ways in which systematic analysis of the implications of change in complex systems can be completed (Power 1997). The aim of this paper is to apply such modelling techniques to the analysis of a comprehensive data set available for the Thames estuary as a means of investigating functional relationships between estuarine crustacean abundance and a range of abiotic variables. Rather than providing purely mechanistic explanations of trends, the analysis seeks to provide, for the first time, a set of statistically valid, multiple linear regression models that are predictive of observed trends in abundance for a set of estuarine Crustacea.

MATERIAL AND METHOD

Sampling methodology. Samples of Crustacea were taken from the Thames estuary, UK, using the cooling water intake screens of National Power's West Thurrock power station, located on the north bank of the

mid-estuary. The site was extensively used to monitor the populations of fish and invertebrates returning to the Thames following its rehabilitation (e.g. Huddart & Arthur 1971a, Andrews & Rickard 1980) until the closure of the station in 1993.

Sample methodology was outlined in Attrill & Thomas (1996) and fully described in Thomas (1998). In summary, Crustacea entering the power station through the cooling water system were removed using rotating band screens and entrapped in nets below the outflow system. These nets were emptied every 30 min and the organisms present identified and enumerated. For temporal comparison, the total catch over a 4 h survey period was pooled and data converted to number of individuals per 500 million litres of water filtered (see Attrill & Thomas [1996] for conversion equation).

Surveys were repeated every 2 wk at spring tide between 1977 and 1992 inclusive, giving a continual data set for a 16 yr period. However, the period 1989 to 1992 was atypical due to the drought conditions prevailing in the region (Attrill et al. 1996). Low freshwater flows resulting from increased water abstraction from the Thames had significant effects on the measured concentrations of heavy metals, e.g. lead, in the estuary (Power et al. 1999) and have been demonstrated to hold significant implications for invertebrate community structure (Attrill et al. 1996). As a result of the probable confounding effects of drought, analyses in this paper were restricted to the 12 yr pre-drought period from 1977 to 1988. Sample dates for the period were converted to a time index variable (weeks) measured from January 1, 1977.

Daily flow rates of freshwater into the estuary from the river Thames were measured by a fixed gauging station. Water quality parameters were obtained during water analysis runs by the National Rivers Authority (now Environment Agency) sampling vessel along the length of the estuary. Sampling was completed throughout the year at varying intervals, increasing in frequency during summer as a result of concerns about seasonal changes in water quality. The mean time between samples was 2.7 wk, with 84 % of all samples being separated by between 3.0 wk or less. Minimum and maximum times between sample dates were 0.7 and 14.9 wk respectively. The latter occurred in the winter of 1988 coincident with the reduction in winter quality sampling frequency for the period 1986 to 1988. All measurements utilised here correspond to those for the zone off West Thurrock power station. The determinants available over the time period of the study are listed in Table 1, together with the reference for the relevant analytical methodology. Salinity was mid-tide corrected to allow valid temporal comparisons. Other determinants (e.g. biochemical oxygen demand [BOD], phosphate, chlorophyll) did not have a sufficient time series to be included in models.

Table 1. List of considered model variables, together with reference for the relevant analytical method where appropriate

Parameter	Reference
Freshwater flow	n/a (gauged flow over Teddington Weir [cumecs])
Temperature	n/a (thermometer)
Salinity	EPA 600/4-79-020 Method 353.3
Dissolved oxygen	HMSO (1980a)
pH	HMSO (1979)
Suspended solids	HMSO (1980b)
Total oxidised nitrogen	EPA 600/4-79-020 Method 358.2
Weeks	n/a (Week 0 = Jan 1, 1977)
Monthly component (Jan to Dec)	n/a (instrumental variable, see text)

The data sets for 5 decapod crustacean taxa presented by Attrill & Thomas (1996) were included in this study, namely *Carcinus maenas* (L.), *Liocarcinus holsatus* (Fabricus), *Crangon crangon* (L.), *Palaemon serratus* (Pennant) and *Palaemon longirostris* Milne Edwards. These were supplemented by a further data set for *Gammarus* spp. (Amphipoda). In the field it was not possible to specify the *Gammarus* spp., although subsampling and subsequent laboratory analysis revealed them to be generally *G. zaddachi* Sexton with occasional *G. salinus* Spooner at times of high water or extreme low freshwater flow. The 2 species are regarded as siblings within the *G. zaddachi* complex and are thus genetically extremely closely related, with *G. zaddachi* preferring oligohaline and *G. salinus* mesohaline water (Bulnheim & Scholl 1981).

Modelling details. Multiple linear regression methods were used to examine the significance of associations between invertebrate abundance and available physico-chemical variables. The models postulate that abundance will be related to the physico-chemical conditions prevailing in the estuary at a given point in time, either because conditions are suited to a particular life-history stage of an organism or because conditions exceed the physiological tolerances of the organism. Accordingly, models of the form

$$Y_t = a_0 + a_1X_{1t} + a_2X_{2t} + \dots + a_kX_{kt} + \epsilon_t$$

were estimated where Y represents available invertebrate data at a given point in time (t), X_1 to X_k are the set of physico-chemical variates that explain Y and ϵ is a normally distributed error term with zero mean and unit variance (Draper & Smith 1981).

For statistical analysis, logarithmic (natural) transformations were completed on data, where necessary, to ensure conformance to an approximate normal distribution (Draper & Smith 1981). To stabilize the variation

in the *Carcinus maenas* data set for use in regression a power transformation (Draper & Smith 1981) was employed as follows:

$$W = (Y^\lambda - 1)/\lambda$$

where Y is the original data and λ is the power transformation parameter chosen to minimize the F -value connected with the extra sum of squares as recommended by Draper & Smith (1981). For the model results presented, λ was estimated to be 0.30.

To avoid problems associated with possible spurious correlation, biological rationalizations were used to select an *a priori* set of feasible variables for inclusion in the multiple regression models. This avoids the *post hoc* rationalization criticism levelled by many researchers (e.g. Walters & Collie 1988) against attempts to relate environmental variables to fluctuations in abundance. Furthermore, it requires that ecological theory and observation be used to guide model construction. For example, the use of a special trigger value for *Carcinus maenas* depends upon laboratory experimentation documenting a threshold for locomotor activity.

From amongst the feasible set of physico-chemical variables, the variables ultimately used in each of the estimated models were selected using forward stepwise regression techniques (Draper & Smith 1981, Dunn & Clark 1987). The procedure selects, from among the feasible set, the independent variable with the highest F -value and enters it in the model, provided the F -value exceeds a pre-specified F -to-enter criteria. At successive steps, previously entered regressors are retained in the equation providing their associated F -values do not subsequently fail to exceed a pre-specified threshold (F -to-remove). Here the F -to-enter and F -to-remove values used were at the upper $\alpha = 0.05$ point of the F -distribution as recommended by Draper & Smith (1981). Differing F -to-enter and F -to-remove values were used to test the effect of the choice of criteria on the subset of model variables selected and found to have no effect. Instrumental variables were used in the stepwise regression process to capture seasonal influences on fluctuations in crustacean species abundance. Variables representing each month were set equal to 1 if data were collected for that month, zero otherwise (Table 1, Koutsoyiannis 1977).

For *Carcinus maenas*, an additional instrumental variable (trigger) was defined. As has been previously suggested in the literature (Naylor 1963, Ropes 1968, Atkinson & Parsons 1973), such a variable may be used to define the temperature threshold below which locomotor activity ceases and sampled abundances may be expected to decline. Threshold values in the range 5 to 11°C were examined and an optimal value selected on the basis of r^2 and minimisation of the regression sum of squares (Draper & Smith 1981).

The statistical assumptions which allow the use of least squares estimates include normally distributed residuals, no serial correlation among the residuals and homoscedastic variances. As with any statistical procedure, if the assumptions of the methods are not met, the results of the analysis will not be valid. To ensure that the required statistical assumptions were met, a series of diagnostic tests were applied to all estimated model residuals. These included examining residuals for evidence of non-normality, heteroscedasticity and serial correlation (Draper & Smith 1981). Royston's extension of the Shapiro-Wilk W statistic (Royston 1982), applicable to sample sizes between 7 and 2000, was used to judge normality in model residuals. The Shapiro-Wilk statistic and its extensions have been recognized as amongst the most powerful omnibus tests for normality (d'Agostino 1986). Normalized versions of the Royston statistic were computed (Royston 1982) and may be compared to tabular values for the standard normal distribution to determine significance. Values <1.96 do not produce sufficient evidence to reject the assumption of normality in the residuals at the $\alpha = 0.05$ level of significance.

Serial correlation was assessed by computing the sample autocorrelations and comparing computed values to their approximate 95% confidence intervals to determine significance (Abraham & Ledolter 1983). Homoscedastic residual variances were confirmed by examining plots of the standardized residuals for evidence of characteristic patterns of increasing or decreasing variance, as recommended by Draper & Smith (1981).

RESULTS

Physico-chemical parameters

The data sets for the 7 physical and chemical parameters incorporated in the crustacean models are represented graphically in Figs. 1 & 2. Fig. 1 includes the seasonally influenced variables (flow, salinity, temperature) presented by Attrill & Thomas (1996), with the x-axis converted to the time index variable. Four new data sets have been compiled for this paper (suspended solids, pH, dissolved oxygen, total nitrogen; Fig. 2). Of these, oxygen and nitrogen (Fig. 2a,d) demonstrate winter peaks and summer troughs, whilst suspended solids and pH (Fig. 2b,c) are more erratic, responding more to random rainfall and discharge events than to seasonal influences.

Crustacean models

Of the 6 crustacean taxa included in the study, significant, statistically adequate models were con-

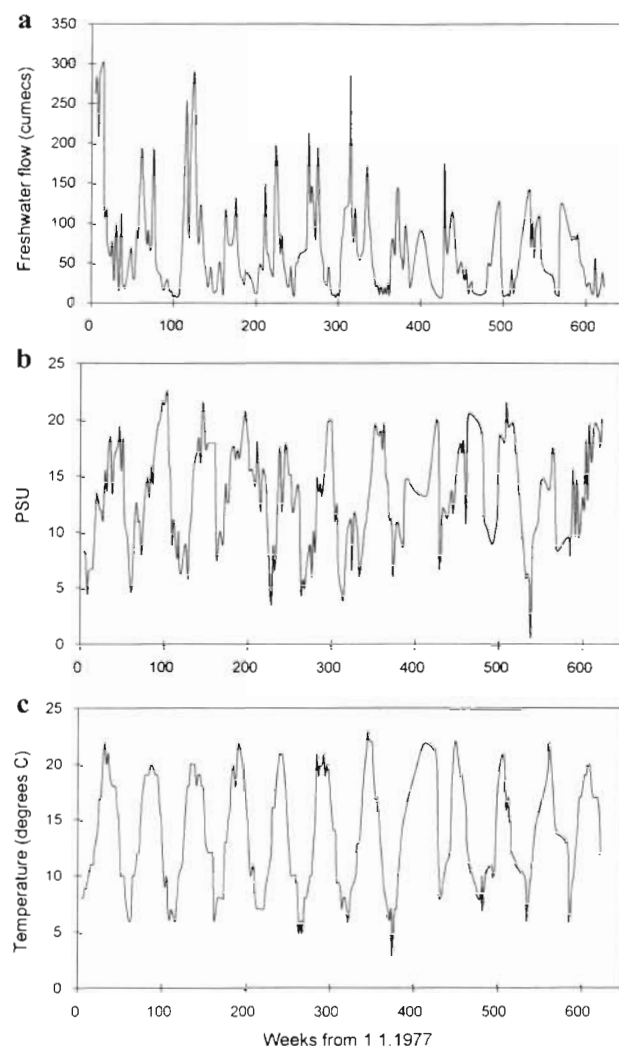


Fig. 1 Physico-chemical variables recorded over the survey period 1977 to 1988 (data from Attrill & Thomas 1996). (a) Freshwater flow into the estuary from the river Thames, (b) salinity (mid-tide corrected), and (c) water temperature. Variables (b) and (c) recorded from a zone of the Thames estuary bordering West Thurrock power station.

structed for 3 of the most abundant species (*Carcinus maenas*, *Crangon crangon*, *Gammarus* spp.). Variables contributing significantly to the explanation of observed variations in taxon abundance, parameter coefficient and standard error estimates, parameter p-values and regression diagnostics are given for each of the modelled species in Tables 2 to 4. In addition to regression r^2 and F -statistic values, the Shapiro-Wilk W statistic (SW) and its associated normalised version (NV) are reported in each of the tables. In all cases, parameter estimates are significant at the $\alpha = 0.05$ level of significance and resulting models explain greater than 54% of the observed variation in biota abundance.

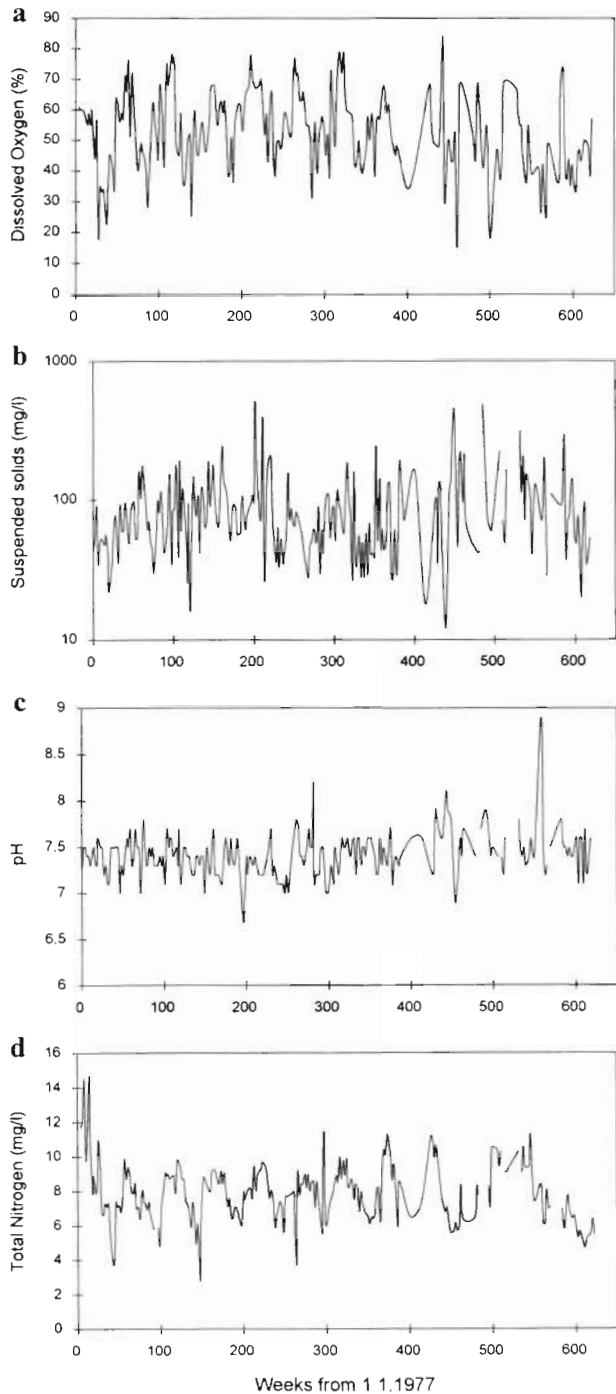


Fig. 2. Physico-chemical variables recorded over the survey period 1977 to 1988 from a zone of the Thames estuary bordering West Thurrock power station. (a) Dissolved oxygen, (b) suspended solids, (c) pH, and (d) total oxidised nitrogen

Significant models

Carcinus maenas abundance showed a strong seasonal pattern, with negative slope coefficients in late winter (February to March, Table 2) and positive coef-

Table 2. *Carcinus maenas* abundance results, where the model is in the form natural logarithm *C. maenas* abundance = $f(\text{listed variables})$ and data were first subjected to a power transformation (see text)

Variable	Coefficient	SE	p-value
Constant	3.056	0.740	<0.001
February	-2.128	0.740	0.004
March	-2.379	0.628	<0.001
August	2.010	0.624	0.002
September	3.021	0.604	<0.001
October	3.843	0.589	<0.001
November	4.326	0.594	<0.001
December	2.646	0.706	<0.001
Temperature	0.114	0.052	0.031
Trigger	2.904	0.619	<0.001
Weeks	-4.65×10^{-3}	8.70×10^{-4}	<0.001
$r^2 = 0.6152$ $F = 35.49$ $n = 233$			
Diagnostics: SW = 0.9859 NV = -0.602			

Table 3. *Crangon crangon* abundance results, where the model is in the form natural logarithm *Crangon* abundance = $f(\text{listed variables})$

Variable	Coefficient	SE	p-value
Constant	9.150	0.624	< 0.001
January	-3.407	0.492	< 0.001
February	-3.869	0.509	< 0.001
March	-4.216	0.446	< 0.001
April	-4.412	0.395	< 0.001
May	-5.308	0.455	< 0.001
June	-6.654	0.413	< 0.001
July	-1.943	0.411	< 0.001
December	-1.429	0.480	0.003
Oxygen	0.025	0.011	0.025
Weeks	-0.0016	6.32×10^{-4}	0.014
$r^2 = 0.6661$ $F = 43.19$ $n = 228$			
Diagnostics: SW = 0.9850 NV = -0.578			

Table 4. *Gammarus* spp. abundance results, where the model is in the form natural logarithm *Gammarus* spp. abundance = $f(\text{listed variables})$

Variable	Coefficient	SE	p-value
Constant	4.642	0.443	< 0.001
March	1.277	0.401	0.002
April	1.075	0.386	0.006
July	1.055	0.383	0.007
October	-1.487	0.462	0.002
Salinity	-2.589×10^{-4}	5.325×10^{-5}	< 0.001
Temperature	0.258	0.029	< 0.001
Weeks	-0.0063	6.148×10^{-4}	< 0.001
$r^2 = 0.5493$ $F = 33.78$ $n = 202$			
Diagnostics: SW = 0.9868 NV = -0.851			

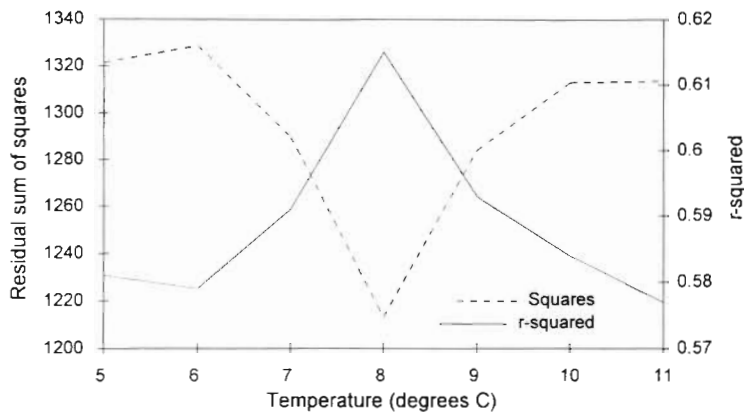


Fig. 3. Regression residual sum of squares ('squares' in figure) and r^2 value for 'trigger' instrumental variable, where regressions were repeated in 1°C increments for trigger temperatures of 5 to 11°C

ficients in late summer/autumn (August to December, Table 2). Temperature was the only physico-chemical variable with significant explanatory power ($p < 0.05$). The inclusion of an instrumental variable (trigger) indicating whether the recorded temperature exceeded a possible threshold for *C. maenas* foraging activity fur-

ther underscores the significance of temperature as an explanatory variable. Threshold temperatures in the range 7 to 9°C proved significant. An optimal value of 8°C (Fig. 3) was selected on the basis of the regression residual sum of squares and r^2 (Draper & Smith 1981); Table 2 reports the particulars of model estimation results. Model residuals showed no evidence of serial correlation or heteroscedasticity and were found to be normally distributed ($SW = 0.9859$). The predicted model for *C. maenas* abundance closely matched the fluctuations in the actual data (Fig. 4a), with only 3 datum points falling outside the 95% predictive confidence limits for the model (Fig. 4b).

The brown shrimp *Crangon crangon* model also had a strong seasonal element, with negative coefficients for the 8 mo period from December to July (Table 3), indicating a continual decrease in the population to a summer minimum. The only seasonally fluctuating physico-chemical parameter found to be significantly

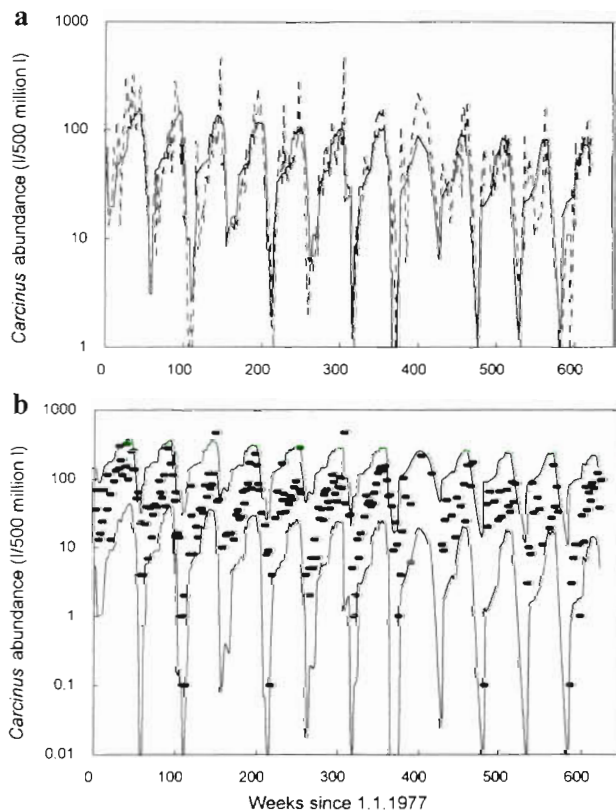


Fig. 4. *Carcinus maenas*. Plots of the model results for abundance (no. of ind. per 500 million l). (a) Predicted versus actual values for data 1977 to 1988 (solid line = model, broken line = actual values), (b) predictive 95% confidence limits of model (solid line) with actual values as individual datum points (•)

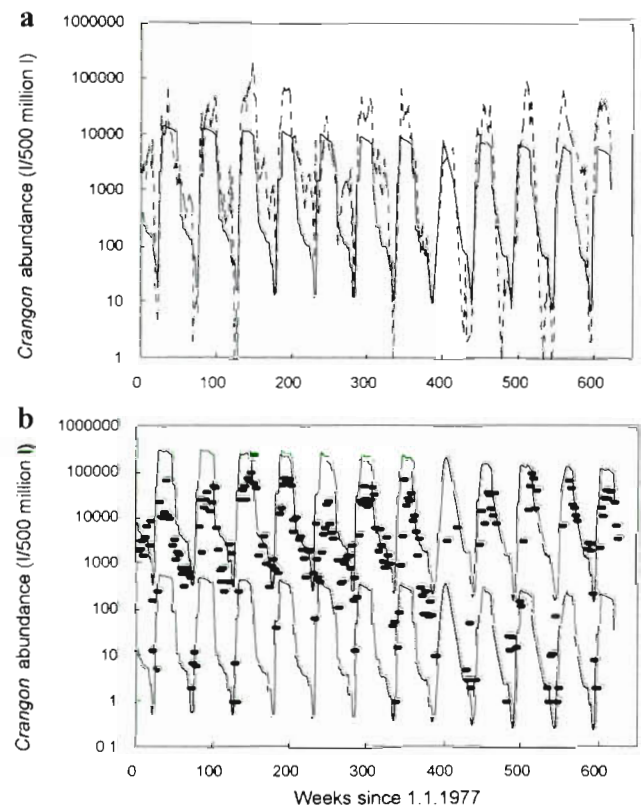


Fig. 5. *Crangon crangon*. Plots of the model results for abundance. (a) Predicted versus actual values for data 1977 to 1988 (solid line = model, broken line = actual values), (b) predictive 95% confidence limits of model (solid line) with actual values as individual datum points (•)

correlated with *C. crangon* abundance was dissolved oxygen. In addition to the positive correlation with dissolved oxygen, a slight, yet significant, temporal trend in *C. crangon* abundance over the period of the survey was found. Regression diagnostics found no evidence of serial correlation, heteroscedasticity or non-normality in model residuals, thus confirming the statistical adequacy of model estimates. As a result, the fitted model closely followed the observed pattern of annual fluctuations in *C. crangon* abundance (Fig. 5a). Although the model generally failed to accurately predict the extreme peaks and troughs, this is not an uncommon problem with data series that fluctuate through several orders of magnitude (Law & Kelton 1991). Nevertheless, the vast majority of the available datum points fell within the 95 % predictive confidence limits for the model (Fig. 5b).

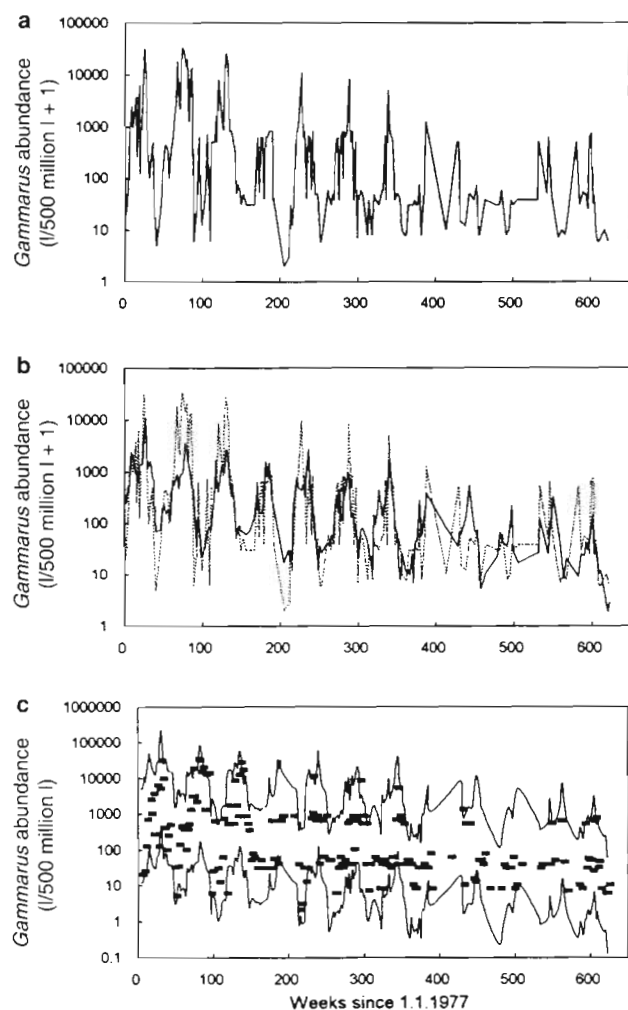


Fig. 6. *Gammarus* spp. Plots of the model results for abundance. (a) Actual values 1977 to 1988 (previously unreported) (b) predicted versus actual values (solid line = model, broken line = actual values), (c) predictive 95 % confidence limits of model (solid line) with actual values as individual datum points (•)

Gammarus spp. abundance displayed a comparatively erratic pulsed distribution over the period of the survey (Fig. 6a), yet a significant model for the data set was constructed using the available physico-chemical data. A seasonal aspect to the distribution was apparent (Table 4), with significant positive coefficients for March, April and July, and a negative coefficient for October. Two environmental variables were included in the model as a result of the strong positive correlation between temperature and *Gammarus* spp. abundance and the negative correlation between salinity and abundance. Additionally, a significant decrease in the *Gammarus* spp. population was apparent over the survey period and was reflected in the significance of the temporal trend variable (weeks). Model residuals showed no indication of serial correlation, heteroscedasticity or non-normality, thus confirming the statistical adequacy of the estimated model. The fitted model provided a good prediction of the more erratic seasonal fluctuations in the *Gammarus* spp. data set (Fig. 6b), particularly the decrease in the maximum values recorded each year. However, the model fell short of predicting zero records (Fig. 6c), although there was a better fit for these minima towards the end of the survey period. Apart from these points, the rest of the data were within the 95 % predictive confidence limits of the model.

Insignificant models

Of the 3 remaining crustacean species *Liocarcinus holsatus* and *Palaemon serratus* were recorded only during the summer months, and too infrequently to adequately capture seasonal dynamics (*L. holsatus*, $n = 47$, *P. serratus*, $n = 30$). In addition, all tested models for *P. longirostris* and *P. serratus* yielded non-normal residuals as tested with the normalised version of Royston's extension to the Shapiro-Wilk W statistic. The lack of normality in model residuals resulted in the rejection of all postulated models for describing the observed fluctuations in the abundance of either species on the basis of the statistical inadequacy of the models (Draper & Smith 1981). Furthermore, no fitted model for *P. longirostris* explained a sufficient amount of the variation in the data (maximum r^2 was 0.0431), despite an apparent long-term cycle (Attrill & Thomas 1996).

DISCUSSION

The construction of the significant models for several estuarine Crustacea provides both supplementary and supportive information on the relationship between these well studied species and their environment.

Rhythmicity in the distribution of *Carcinus maenas* has been well studied over tidal (e.g. Dare & Edwards 1981, Warman et al. 1993), and to a lesser extent seasonal (e.g. Naylor 1962, Hunter & Naylor 1993) periods. However, these investigations have tended to concentrate on the littoral zone in fully saline conditions, and far fewer studies have addressed patterns of *C. maenas* abundance in estuaries. McGaw & Naylor (1992) reported that the halokinetic response to reduced salinity previously reported for the species (e.g. Taylor & Naylor 1977) was virtually absent in estuarine forms. Whilst this conclusion was directed at tidal movement, it could be postulated that any endogenous kinetic response to low salinity would result in crabs being absent from estuarine areas during periods of high flow. This is apparent for the Thames population (negative coefficients for February to March, population displaying a spring minimum abundance), but the model for *C. maenas* did not include a significant salinity parameter, supporting the conclusions of McGaw & Naylor (1992) and suggesting other environmental cues are more important.

The *Carcinus maenas* model indicated strong, predictable seasonal components for the abundance pattern of crabs in the Thames, with significant positive coefficients for all months between August and December. Aagaard et al. (1995) recorded peak abundances during late August in a Danish fjord (although large numbers were still apparent in October), whilst very few crabs were caught in February or May, coinciding with the minimum abundance recorded in the Thames. Temperature has been evoked as a possible controlling influence for *C. maenas* population movement (e.g. Naylor et al. 1971, Attrill & Thomas 1996), and this was the only physico-chemical parameter to feature in the model. The influence of temperature has been suggested to be due mainly to a loss of rhythmic locomotor activity at low temperatures (Naylor 1962), which has resulted in proposals for a threshold temperature below which activity ceases. Ropes (1968) suggested a figure of 7°C for *C. maenas* from the eastern U.S., whilst Atkinson & Parsons (1973) concluded a common threshold of 'about 8°C'. Aagaard et al. (1995), however, noted minimal catches of *C. maenas* at a temperature of 11.7°C, but concluded that this was due to a rapid temperature rise from 8°C within a week which did not allow crabs to adapt their behaviour. The *C. maenas* model constructed for the Thames population included the instrumental variable 'trigger' to simulate temperature thresholds for activity and was found to be most significant at $T = 8^{\circ}\text{C}$, thus supporting the conclusions of Atkinson & Parsons (1973). This temperature threshold therefore appears to be consistent for a range of habitats and geographical areas where *C. maenas* is found.

The brown shrimp *Crangon crangon* has a regular, seasonal distribution in the Thames estuary which has been recorded for a range of European systems (Moore et al. 1979, Beukema 1992, Bamber & Henderson 1994), the shrimps migrating into more saline water during winter and returning up the estuary in summer months. Due to this strong seasonal migration pattern, the previous studies have inferred that *C. crangon* distribution within an estuary is governed by responses to either salinity (e.g. Lloyd & Yonge 1947, Attrill & Thomas 1996) and/or temperature (e.g. Verwey 1957, Boddeke 1968). However, these assumptions have not been statistically tested for *C. crangon* abundance, although Henderson & Holmes (1987) related the distribution of reproductive females to salinity using multiple correlation analysis. *C. crangon* distribution in the Thames, however, was not significantly related to either temperature or salinity, but did show a positive relationship with dissolved oxygen. This variable was unrecorded in most previous studies, despite the existence of work demonstrating that the shrimps display a strong avoidance behaviour to low oxygen tension (Huddart & Arthur 1971b, Dyer 1978), resulting in a low abundance of *C. crangon* being associated with conditions of reduced dissolved oxygen. Variation in dissolved oxygen in estuaries is also seasonal (Fig. 2), so it may be the case that *C. crangon* responds over a short time scale to changes in oxygen levels, particularly when hypoxia is associated with low salinity (Hagerman & Uglow 1982), with salinity being an important controlling factor during reproduction. A significant reduction in the population size of *C. crangon* also was apparent over the survey period. The reasons for this remain unclear as water quality in the Thames continued to improve over the survey period (Kinniburgh 1998) and *C. crangon* populations have been shown to positively respond to decreases in polluting inputs (Boddeke 1996). However, predation by fish can have a dramatic effect on shrimp populations (Berghahn 1996), so the consequent return of fish species to the Thames following restoration (Thomas 1998) may be having an influence that will require further investigation.

The data set for *Gammarus* spp. is additional to the species data presented by Attrill & Thomas (1996) and, like *Carcinus maenas* and *Crangon crangon*, demonstrates seasonal patterns in abundance. Although there appears to be more noise in the *Gammarus* spp. abundance pattern, significant coefficients during spring suggest a regular increase in the population at that time, with a subsequent significant regular decrease during October. *G. zaddachi*, the dominant species in the Thames estuary (Attrill 1998), has been shown to undertake seasonal reproductive migrations (Dennert et al. 1969, Girish et al. 1974, Hough & Naylor 1998).

lor 1992), the population moving seawards during spring/summer. The peak in abundance recorded at West Thurrock is therefore likely to represent *G. zaddachi* moving into this part of the estuary to reproduce, returning upstream again in autumn. Hough & Naylor (1992) reported the seaward areas of the Conway Estuary (N. Wales) were depopulated in winter; this trend is also apparent in the Thames. Previous studies have linked the seasonal migrations of *G. zaddachi* to both salinity (e.g. Hough & Naylor 1992) and temperature (Dennert & van Maren 1974), the species being able to tolerate low salinities at low temperature, but migrating downstream to reproduce during periods of higher temperature. Both of these variables were significant components within the model for the Thames population, indicating their importance as controlling factors for the species. The temporal trend for *Gammarus* spp. demonstrated a significant reduction in the size of the population. As for *C. crangon*, predation by fish may be an explanation as it is probably the single most important prey species for the majority of fish species (Wheeler 1969), but a notable upstream extension of *G. zaddachi* has been noted in the upper, freshwater part of the Thames estuary (Andrews 1977, Attrill 1998) the species replacing *G. pulex* in the tidal freshwater reaches. It is therefore possible that the whole population has demonstrated an upstream movement, the decrease in abundance at West Thurrock relating to fewer individuals in that part of the estuary rather than any reduction in total population size.

It was not possible to construct a significant model for *Palaemon longirostris*, but this negative result is interesting as previous work has suggested strong seasonal migrations related to annual patterns of salinity (e.g. Van den Brink & Van der Velde 1986, Cartaxana 1994), although such conclusions were observational and not tested statistically.

The results of this study have indicated the value of statistically relating the pattern of changes in a larger suite of estuarine environmental parameters to indices of biotic abundance. In addition, results suggest that assumptions concerning the strength of the relationships between organisms and easily measured abiotic parameters, such as salinity and temperature, may require validation. Out of the 4 large species data sets analysed for the Thames estuary, 2 demonstrated a significant relationship with temperature and 1 with salinity over the 12 yr period of study. Salinity has long been regarded as the most important controlling factor for estuarine organisms, particularly those that demonstrate strong seasonal patterns. The true case could be more subtle than this, with populations of estuarine organisms responding to other environmental cues, such as temperature and dissolved oxygen. These variables often

demonstrate seasonal patterns which may be ignored due to assumptions about relationships between species abundance and salinity. Furthermore, the prevalence of seasonality in many of the abiotic parameters raises the possibility of measures, like salinity, being correlated with abundance through a common third variable. Only when a sufficiently large suite of physico-chemical parameters are measured can a clear picture of the role of any single abiotic variable in influencing observed abundance patterns be developed. Clearly further work needs to be done and, in the meantime, researchers should treat assumptions about the influence of any single abiotic variable with care.

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