Journal of Fish Biology (2000) **56**, 1408–1426
doi:10.1006/jfbi.2000.1264, available online at http://www.idealibrary.com on IDEAL®

Temporal abundance patterns and growth of juvenile herring and sprat from the Thames estuary 1977–1992

M. Power*¶, M. J. Attrill† and R. M. Thomas‡

**Department of Biology, University of Waterloo, Waterloo, ON, N2L 3G1, Canada; †Benthic Ecology Research Group, Plymouth Environmental Research Centre, University of Plymouth, Drake Circus, Plymouth PL4 8AA, U.K. and ‡Environment Agency, Apollo Court, 2 Bishops Square Business Park, St Albans Road West, Hatfield AL10 9EX, U.K.*

(*Received 3 February 2000, Accepted 5 March 2000*)

Most herring *Clupea harengus* and sprat *Sprattus sprattus* sampled from West Thurrock power station intake screens, middle Thames estuary, between 1977 and 1992 were age-0 and followed regular patterns of seasonal occurrence. Juvenile herring entered the estuary in July, peaked in abundance November to March, and then declined. Juvenile sprat first appeared in September and peaked in abundance in January. Neither species was abundant in summer samples. While in the estuary, herring and sprat increased in length an average of 4·0 and 0·33 cm respectively. Abundance of both species was significantly affected by temperature, temporal trend, shoaling behaviour and seasonal variables, and of herring by suspended solids. Interactions between environmental variates did not influence the abundance of either species. As estuarine clupeids were influenced by a complex set of events within and outside the estuary, estuarine monitoring studies alone will not be sufficient for understanding the changes in estuarine fish communities resulting from future human activity.

Key words: Clupeidae; estuaries; Thames; juveniles; temperature; trends.

INTRODUCTION

The environment and ecology of European and British estuaries have been linked closely with the history of human activity and altered significantly by recent urban and industrial use (Clyde (Henderson & Hamilton, 1986), Mersey (Wilson *et al.*, 1988), Tyne (Pomfret *et al.*, 1988), Elbe (Thiel *et al.*, 1995) and Zeeschelde (Maes *et al.*, 1998)). The history of the Thames, in particular, provides a classic example of possible human impacts on estuarine ecosystems. From a period of anoxia in the 1950s, extensive remedial action was required to improve water quality until recovery was achieved in the 1970s (Attrill, 1998). During the recovery phase the estuary was the subject of extensive biological study (Huddart & Arthur, 1971; Wheeler, 1979, 1988; Andrews & Rickard, 1980) and much was learned about its structure and function. As a result the Thames estuary is now regarded as one of the most important draining to the North Sea (Thomas, 1998).

Since the achievement of recovery, much effort has been devoted to routine monitoring of the estuary (Attrill, 1998). Such monitoring data are important for assessing the continued recovery status of the estuary and providing baselines

---

¶Author to whom correspondence should be addressed. Tel.: 001-519-885-1211, ex. 2595; fax: 001-519-885-0534; email: m3power@sciborg.uwaterloo.ca

0022–1112/00/061408+19 $35.00/0

against which the consequences of future impacts may be gauged. Continuous long-term data sets (>10 years) have also been recognized as important for understanding the functioning of ecosystems (Callahan, 1984). They are required to estimate natural variation (Drinkwater & Myers, 1987) and interpret long-term trends properly (Walters & Collie, 1988). Nevertheless, long-term data sets are rare, particularly from estuarine and coastal systems (Wolfe *et al.*, 1987). For example, studies were conducted for 9 years in the Forth estuary (Elliott *et al.*, 1990), 6–8 years in the Severn (Claridge *et al.*, 1986; Potter *et al.*, 1986; Henderson & Holmes, 1989), 3 years is the Medway (Wharfe *et al.*, 1984) and Humber (Marshall & Elliott, 1998), and 2 years in the Clyde and Zeeschelde (Henderson & Hamilton, 1986; Maes *et al.*, 1998). In the Thames, Araujo *et al.* (1998) have presented descriptive fish community data for the 1980–1989 period.

The lack of long-term data results in multivariate statistical analyses of spatial rather than temporal dynamics, despite the existence of significant trends in the North Sea fish stocks from which estuarine fish populations originate largely (Rijnsdorp *et al.*, 1991; Heessen & Daan, 1996; Cook, 1997). Among those populations are two clupeids, herring *Clupea harengus* L., and sprat *Sprattus sprattus* (L.), for which long-term data sets from power station sampling in the tidal Thames exist. Historically, both species have been exploited heavily as adults and juveniles (Wheeler, 1979). Studies of their coastal distribution place them among the most important contributors to the British Isles inshore fish community by weight and number caught, with sprat and herring ranking as the first and third most numerous respectively (Henderson, 1988). Their presence in large numbers in estuaries is thought to have concomitant effects on the dynamics of estuaries (Henderson, 1989) which serve as critical over-wintering and nursery areas for many species (Elliott *et al.*, 1990). Nevertheless, detailed information on long-term changes in estuarine clupeid abundance and juvenile growth rates is limited (van den Broek, 1979*a*; Potter & Claridge, 1985).

Accordingly, this study uses statistical modelling techniques to analyse patterns of temporal change in data on clupeid abundances in the Thames estuary to determine the extent to which observed fluctuations in species abundance are related to physico-chemical variates and/or patterns of seasonal recruitment. A second aim of the paper is to document the current status of key clupeid populations in the Thames as a means of establishing biological baselines against which future changes in herring and sprat populations in the estuary may be interpreted.

MATERIALS AND METHODS

All fish were sampled at West Thurrock Power station, located on the north bank of the middle Thames estuary, *c.* 36 km downstream of London Bridge (Fig. 1). The station was used extensively to monitor fish and invertebrate populations returning to the Thames following its rehabilitation (Huddart & Arthur, 1971; Andrews & Rickard, 1980; Thomas, 1998) until its closure in 1993. The station extracted up to 136 000 m^3 of water h^{-1} for cooling purposes. Fish entered the cooling water intake through culverts located well below the low tide water level and all organisms and debris >1 cm in diameter were removed by rotating band screens (Thomas, 1998). Screens were washed by water jets and organisms and debris flushed *via* a gutter system to a trash pit and then back to the estuary. Fish samples were collected by fitting square framed nets (1 mm mesh size) to

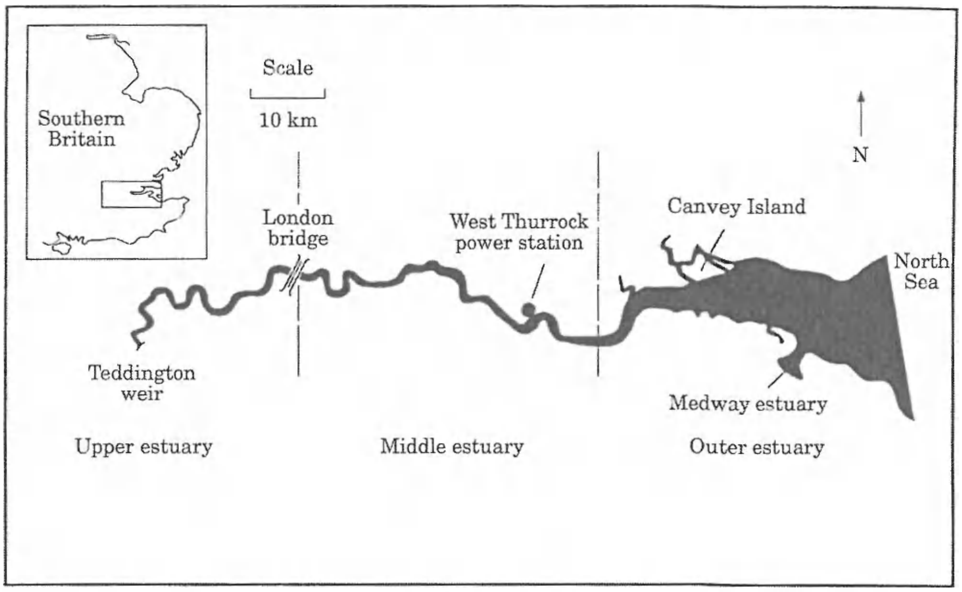

FIG. 1. A map of the Thames estuary showing the location of West Thurrock Power Station in relation to London Bridge and the outer estuary.

the end of each gutter. Sampling began 1 h before low water and continued for a 4-h period. Nets were emptied every 30 min and all fish were identified, counted and measured to the nearest cm. When extremely large samples were obtained a randomly selected sub-sample of the catch was measured.

Seasonal variation in electricity demand affected the amount of cooling water required and the number of operating intake pumps. To adjust for the effect of water volume on catch size, and facilitate temporal comparison, the total catch over a 4-h survey period was pooled and data converted to number of fish entrained per 500 000 m^3 of filtered water (Attrill & Thomas, 1996). Surveys were repeated over the 16-year period from 1977 to 1992 approximately every 2 weeks at spring tide. Minimum and maximum times between sample dates were 0·7 and 14·9 weeks, respectively. The maximum occurred in the winter of 1988 when sampling frequency was reduced. Other details of sampling methodology are described in Thomas (1998).

Coincident with fish sampling, water quality parameters and freshwater flow were measured between 1977 and 1992. Measured water quality parameters included: chlorinity (mg l^{-1}), dissolved oxygen (% saturation), pH, suspended solids (mg l^{-1}) and temperature (° C). These were obtained for the West Thurrock zone from water analysis runs by the National Rivers Authority (now Environment Agency) sampling vessel along the length of the estuary. Daily flow rates of fresh water (m^3 s^{-1}) into the estuary from the Thames were measured by a fixed gauging station at Teddington. References to the measurement methodologies used for each of the physico-chemical variables and relevant descriptive statistics are listed in Table I. Salinity was mid-tide corrected to allow valid temporal comparisons.

Length-frequency histograms for each species were based on the months of greatest estuarine abundance. For herring this was October to March and for sprat, December to March. Length-frequency keys were used to separate herring into age-0 and older age-classes (Wheeler, 1969; Potter & Claridge, 1985; Torstensen & Gjøsæter, 1995) and mean lengths were computed for all sample dates with sample sizes ≥ 10. Herring sample dates were used to compute the days (D) from 1 August, typically the month in which age-0 fish began to appear in large enough numbers to permit the computation of reliable mean lengths. Length (L) and day data were used to estimate von Bertalanffy growth

TABLE I. List of measured physico-chemical parameters (n=285) for the 1977–1992 period. Means, standard deviations (σ), coefficients of variation in % terms (CV), and reference for appropriate analytical methodologies are given

Parameter	Units	Mean	σ	CV	Reference
Chlorinity	$mg\ l^{-1}$	8369·30	3059·50	36·56	U.S. EPA (1983)
Dissolved oxygen	%	53·48	12·60	23·56	HMSO (1980*a*)
Freshweater flow	$m^3\ s^{-1}$	57·24	58·99	102·90	Gauged
pH	—	7·47	0·26	3·47	HMSO (1979)
Suspended solids	$mg\ l^{-1}$	88·88	73·05	82·19	HMSO (1980*b*)
Temperature	°C	14·07	4·88	34·69	Thermometer

models (Power & McKinley, 1997; Power & van den Heuvel, 1999) for 1980/81 and 1982/83 as follows:

$$L = L_{\max} (1{\cdot}0 - \alpha e^{-\beta D}) \qquad (1)$$

where $L_{\max}$ defines maximum attainable length, a is a parameter that reflects the position of the time origin and β is the rate of increase constant expressing the change in length as a function of the difference between maximum and present length. The short estuarine residency of sprat, and its marginal growth during that period, did not permit the separation of samples into age-classes based on length and no attempt was made to model growth. Average increases in length during estuarine residency were calculated for all individuals $\leq$9 cm in samples taken in November and March, respectively. The chosen threshold is above the 8 cm length at which the majority of Severn sprat were considered to be older than age-0 (Potter & Claridge, 1985). Torstensen & Gjøsæter (1995), however, report mean lengths for age-0 sprat taken in the littoral zone of the Norwegian Skagerrak of between 6·5 and 9·0 cm. Larger age-0 sprat have been reported also in the Medway (van den Broek, 1979*a*), a tributary of the greater Thames estuary. Accordingly, the 9 cm threshold was used to compute age-0 mean sizes for Thames sprat.

All fish captured during the survey of 13 November 1992 were retained for weight-length analysis. Fish were identified, measured, fixed in 10% formalin and transferred to 70% alcohol for later analysis. Subsequently, all fish were re-measured to the nearest mm and weighed to the nearest 0·1 g. Data were log-transformed and ordinary least squares regression methods used to estimate the standard allometric weight-length relationship.

The significance of possible interactions between estuarine physico-chemical variates were assessed using correlation analysis, with testing completed at the a=0·05 level following procedures outlined in Cox (1987). Spearman rank correlation coefficients were then used to determine the significance of measured physico-chemical variates and interactions for observed fluctuations in sample abundance. The non-parametric technique allows the relationship between parameters to be investigated individually, thus helping to determine which of the variates is likely to affect sample abundance most (Zar, 1984). Significance was determined at the a=0·05 level following procedures detailed in Conover (1980) and all significant individual and interaction variables retained for use in subsequent regression analysis.

For statistical analysis, logarithmic (ln) transformations were completed on flow and suspended solids data to ensure conformance with an approximate normal distribution. All abundance data were incremented by one (data+1) to avoid censoring zero samples from analysis, following the transformation of data to stabilize the variance. Stabilization is often required when the ratio of maximum to minimum values in the data exceeds an order of magnitude (Draper & Smith, 1981) (Fig. 2). The form of the transformation

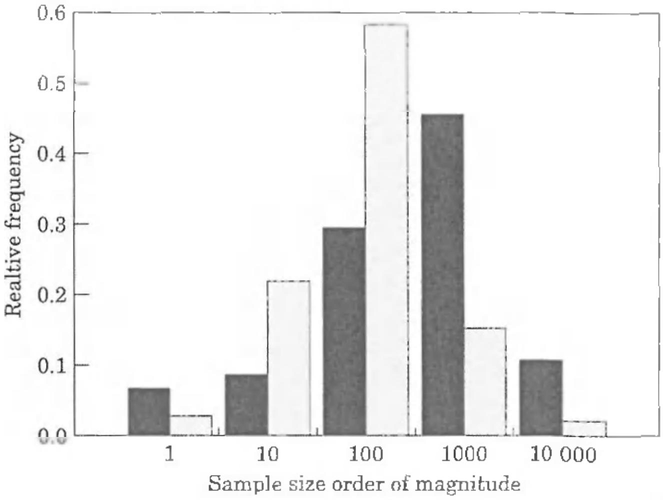

FIG. 2. Distribution of all herring (■) and sprat (□) sample sizes taken from West Thurrock Power Station intake screens 1977–1992.

used was selected from a family of possible transformations (Draper & Smith, 1981) defined by:

$$W = (Y^{\lambda} - 1)\,\lambda^{-1} \tag{2}$$

where Y was the original datum, W the transformed datum and λ the transformation parameter. The transformation parameter was chosen using maximum likelihood procedures under the assumption that the error term of the associated model was normally distributed, as recommended by Draper & Smith (1981). For herring, λ equalled 0·26 and for sprat 0·25.

Analysis of stock biomass and recruitment data from the North Sea indicates that for many species, including herring and sprat, significant temporal trends exist (Daan *et al.*, 1990; Rijnsdorp *et al.*, 1991; Heessen & Daan, 1996; Philippart *et al.*, 1996; Cook, 1997). Because trends in data can obscure the effects of physico-chemical variables likely to be correlated with patterns of variation about the trend (Brown & Rothery, 1993), a trend variable measured in numbers of weeks since the beginning of sampling in January 1977 was included in the candidate set of regression variables.

To account for the shoaling behaviour observed in both herring and sprat samples in the Thames and elsewhere (Wheeler, 1969; van der Broek, 1979*a*; Potter & Claridge, 1985), an instrumental variable was included in the possible set of regression variables. The shoaling variables for each species were set equal to one if sample size exceeded the mean plus one standard deviation, zero otherwise. To account further for the possible effects of seasonal occurrence (Potter *et al.*, 1986; Elliott *et al.*, 1990) instrumental variables for the month of capture were included also in the candidate set of regression variables. These assume a value of one for samples taken in the designated month, zero otherwise.

Then data were used to estimate multiple regression models of the form:

$$W_t = a_0 + a_1X_{1t} + a_2X_{2t} + \ldots + a_kX_{kt} + \epsilon_t \tag{3}$$

where W represents transformed abundance at time (t), a_0 to a_k are the estimated parameters, X_1 to X_k are the set of variates that explain W and $\in$ is a normally distributed error term with zero mean and unit variance (Draper & Smith, 1981).

Variables ultimately selected for inclusion in models were chosen on the basis of forward selection stepwise regression (Draper & Smith, 1981). A similar modelling approach was used to select between a limited number of environmental covariates to explain variations in freshwater fish abundance over a 2-year period in the upper Thames estuary (Araujo *et al.*, 1999). The stepwise procedure selects, from among considered independent variables, the one with the highest *F*-value and enters it in the model, provided the variable *F*-value exceeds a pre-specified *F*-to-enter criterion. At successive steps, previously entered regressors are retained only if associated *F*-values do not fail to exceed a pre-specified *F*-to-remove criterion. Here the *F*-to-enter and *F*-to-remove criteria used were the conservative upper $\alpha=0{\cdot}05$ points of the *F*-distribution as recommended by Draper & Smith (1981). Sensitivity tests on variable selection were conducted by raising and lowering the *F*-to-enter criterion to the upper $\alpha=0{\cdot}01$ and 0·10 points of the *F*-distribution respectively. Alternate backward selection was also used to confirm model variable selection. Draper & Smith (1981) note no technique is always better and there is no guarantee different procedures will converge on the same model. General agreement between procedures, however, helps establish confidence in model robustness.

As the magnitudes of regression coefficients depend on the variates included in the regression and the units of measure (Dunn & Clark, 1987), conclusions about the relative influence of an independent variable on the dependent variable should not be drawn unless coefficient estimates are standardized. Accordingly, standardized regression coefficients (β_j) measuring the amount by which the dependent variable changes in terms of units of its own standard deviation for a unit change in the standard deviation of the *j*th independent variable, when all other independent variable values are held constant, were computed following Cox (1987). The β_j coefficients allow direct comparisons to be made between variables in terms of their relative importance for explaining variations in the dependent variable and are useful for establishing which model variables have the greatest influence on species sample abundance.

All non-linear and linear models were assessed for statistical adequacy by testing residuals at the $\alpha=0{\cdot}05$ level of significance for conformance with the underlying assumptions of adopted linear or non-linear estimation methods (Dunn & Clark, 1987; Bates & Watts, 1988). This entailed establishing that model residuals were normal, independent and homoscedastic. Normalized versions of Royston's extension to the Shapiro–Wilk W statistic (Royston, 1982) were used to judge normality. Independence was assessed by examining residuals for evidence of autocorrelation using the runs test. The test is a direct assessment of the independence assumption applicable when observations are not equally spaced in time (Draper & Smith, 1981) and was computed following procedures outlined in Banks & Carson (1984). Homoscedasticity was assessed with standardized residual plots (Draper & Smith, 1981). Finally, because multicollinearity can lead to the mistaken rejection of significant explanatory variables (Dunn & Clark, 1987), multiple regression models were tested further for the presence of multicollinearity using variance inflation factors.

Incidental analyses of similarity in mean abundance between seasons and correlation between variables were completed, where necessary, at the $\alpha=0{\cdot}05$ level of significance using the non-parametric Mann-Whitney *U* or Spearman rank correlation statistics. Neither statistic necessitates assuming data are normally distributed and both have been shown to have good statistical power (Conover, 1980).

RESULTS

Herring and sprat were the most numerous clupeid species captured in the middle estuary during sampling at West Thurrock 1977–1992. A total of 117 010 herring, 37 710 sprat and 114 other Clupeidae were captured. The latter group consisted almost entirely of anchovy *Engraulis encrasicolus* (L.), although a few allis shad *Alosa alosa* (L.), pilchard *Sardina pilchardus* (Walbaum) and a single twaite shad *Alosa fallax* (Lacépède) were captured. Herring and sprat, respectively, were the second and sixth most abundant species in West Thurrock

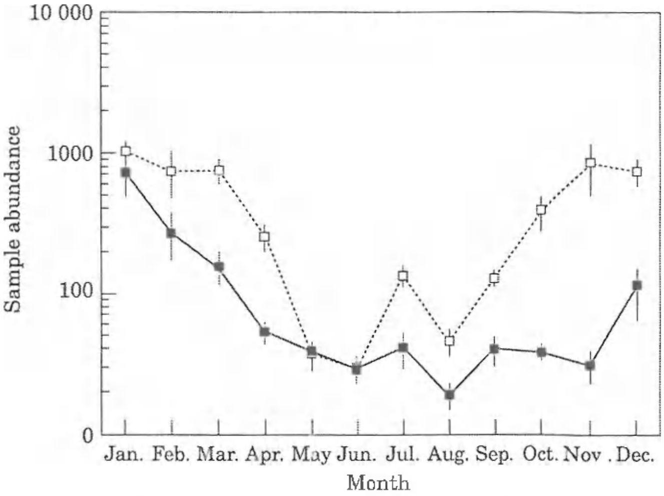

FIG. 3. Average monthly herring (– – – –) and sprat (——) sample sizes, respectively, based on West Thurrock samples showing the distinctive seasonal use of the middle estuary by each species. Error bars define ± 1 S.E. for herring and sprat samples.

samples. Herring occurred in 95% of all samples and sprat in 99%. Sample sizes ranged from 0–9534 for herring and 0–3906 for sprat. Sample mean, standard deviation and coefficient of variation (%) were 404·48, 843·61 and 208·57, respectively, for herring. For sprat the sample statistics were 113·34, 355·68 and 313·83, respectively. These suggest considerable skew in the sample sizes (Fig. 2). The tendency for shoaling behaviour contributed largely to the wide variation in numbers sampled during the study period.

Herring and sprat have been observed to co-occur throughout the year in the estuary (Huddart & Arthur, 1971). The Spearman rank correlation coefficient for herring and sprat sample size yielded a weak, though significant, association ($r=0{\cdot}383$, $P<0{\cdot}01$) for the 1977–1992 period. Correlation of winter (21 December–21 March) samples and all other sample dates indicated the strength of the association depended more on common winter use of the estuary ($r=0{\cdot}533$, $P<0{\cdot}01$) than co-occurrence at other times in the year ($r=0{\cdot}197$, $P<0{\cdot}05$).

Distinct seasonal patterns of occurrence were evident in the mean monthly catch for the years 1977–1992 (Fig. 3). Herring enter the middle estuary in large numbers in late August/early September, increase to peaks in November to March, and then decline. Peak average abundance in January was 34·8 times that of the June low. The minor increase in abundance in July was not significant ($P>0{\cdot}05$). Sprat enter the estuary in large numbers in late November and peak in January, before declining to summer lows. Average abundance in January was 38·7 times that of the August low. Although Titmus *et al.* (1978) and Potter & Claridge (1985) report bimodality in herring and sprat abundances in the Severn, the pattern was not seen in the Thames.

Length-frequency distributions for herring and sprat show (Fig. 4) that age 0+ individuals dominate in the samples of both species, but some age-1 and older individuals are evident. Modal lengths for herring and sprat, respectively, were 8 and 7 cm.

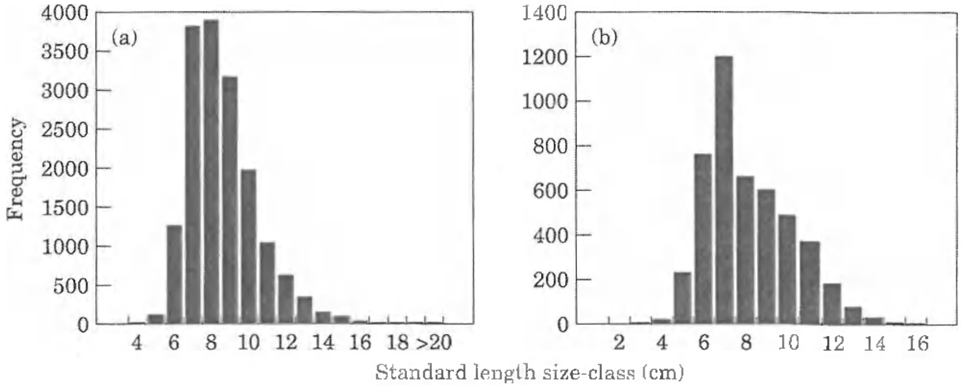

FIG. 4. Standard length (cm) frequency distributions for all measured herring and sprat sampled at West Thurrock during peak periods of estuarine occurrence. (a) Length distribution of herring October–March, (b) length distribution of sprat December–March.

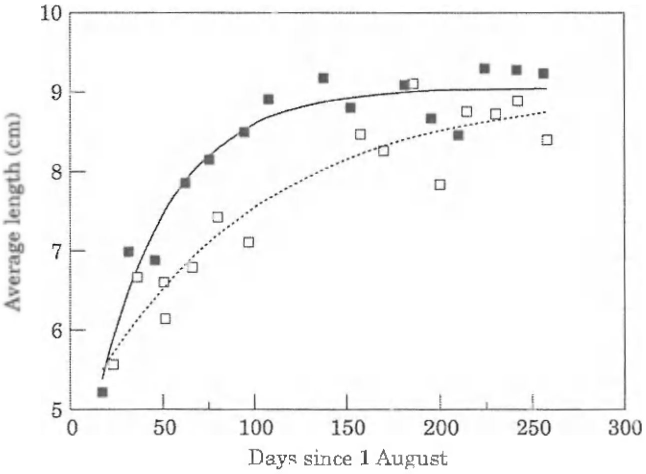

FIG. 5. Von Bertalanffy growth models for herring based on mean age-0 lengths computed for sample sizes >10 taken August through April, inclusive, for the 1981 (■) and 1982 (□) year-classes. All parameter P-values $<0{\cdot}05$ and all $r^2 \geq 0{\cdot}891$.

Length data for age-0 herring collected between 18 August and 13 April in 1981/82 and 24 August and 15 April in 1982/83 (Fig. 5) were used to estimate von Bertalanffy growth models describing first year estuarine growth as follows:

$$1981/82\colon L=9{\cdot}071\ (1{\cdot}0-0{\cdot}623\ \mathrm{e}^{-0{\cdot}0252\ D}) \tag{4}$$

$$1982/83\colon L=9{\cdot}045\ (1{\cdot}0-0{\cdot}468\ \mathrm{e}^{-0{\cdot}0105\ D}) \tag{5}$$

where D defines the number of days since 1 August. The proportion of explained variation in 1981/82 and 1982/83, respectively, equalled 0·934 and 0·891. All parameter P-values were $\leq 0{\cdot}036$. Tested residuals showed no significant autocorrelation, heteroscedasticity or non-normality. The models indicate a

c. 4 cm increase in age-0 herring length during estuarine residency. Analysis of mean lengths for sprat ≤ 9 cm in samples taken in November and March for 1979/80 through 1987/88 indicated small increases in length during estuarine residency ($0{\cdot}33 \pm 0{\cdot}22$ cm).

Herring in the range 6–12 cm ($n=98$) and sprat in the range 3–11 cm ($n=27$) were used to estimate standard allometric wet weight (w)–length (L) relationships as follows:

$$\text{Herring: } \ln w = -4{\cdot}167 + 2{\cdot}657\ L \qquad (6)$$

$$\text{Sprat: } \ln w = -5{\cdot}394 + 3{\cdot}129\ L \qquad (7)$$

Proportion of explained variation for herring and sprat equalled 0·897 and 0·902, respectively. All parameter P-values were $\leq 0{\cdot}001$ and at the $\alpha=0{\cdot}05$ level of significance residuals showed no significant autocorrelation, heteroscedasticity and were normally distributed. Non-overlapping and overlapping 95% CI, respectively, for the weight-length model intercepts and length exponents indicated initial differences in weight (Fig. 6) but comparable growth in terms of length while in the estuary, for both species.

Spearman rank correlation coefficients (Table II) yielded significant associations between herring abundance and all measured physico-chemical variables and interactions except pH and chlorinity-freshwater flow interactions. Similar correlation analysis for sprat excluded pH, suspended solids and chlorinity-freshwater flow interactions as possible determinants of sample abundance. Statistically significant models relating fluctuations in species abundance to the reduced set of significant variables in Table II and temporal trend and seasonal instrumental variables were estimated using stepwise regression. Variables contributing significantly to species abundance, model coefficient estimates, P-values, standardized regression coefficients and regression diagnostics are given in Table III. In all cases, parameter coefficient estimates were significant at the $\alpha=0{\cdot}05$ level and resulting models explained >44% of the observed variation in species sample abundance. Variation in the F-to-enter criteria to values equivalent to the upper $\alpha=0{\cdot}01$ and 0·10 points of the F-distribution did not result in the addition or elimination of model variables, thus confirming model robustness.

Fluctuations in herring abundance were related positively to the temporal trend, suspended solids and the instrumental shoaling variable and were related negatively to temperature and selected instrumental seasonal variables. Interactions had no significant affect on abundance. Standardized regression coefficients indicated that temperature was the most important physical determinant of sample abundance with suspended solids having a weaker, though important, effect. Among the instrumental and trend variables, shoaling, in particular, exerted a strong influence on measured abundance. The selected instrumental seasonal variables coincided with the timing of estuarine exit and entry (Fig. 3) and underscore the importance of juvenile migrations for changes in sample abundance. Model residuals showed no evidence of serial correlation, heteroscedasticity or non-normality when tested at the $\alpha=0{\cdot}05$ level of significance. Predicted fluctuations in sample abundance matched actual abundance

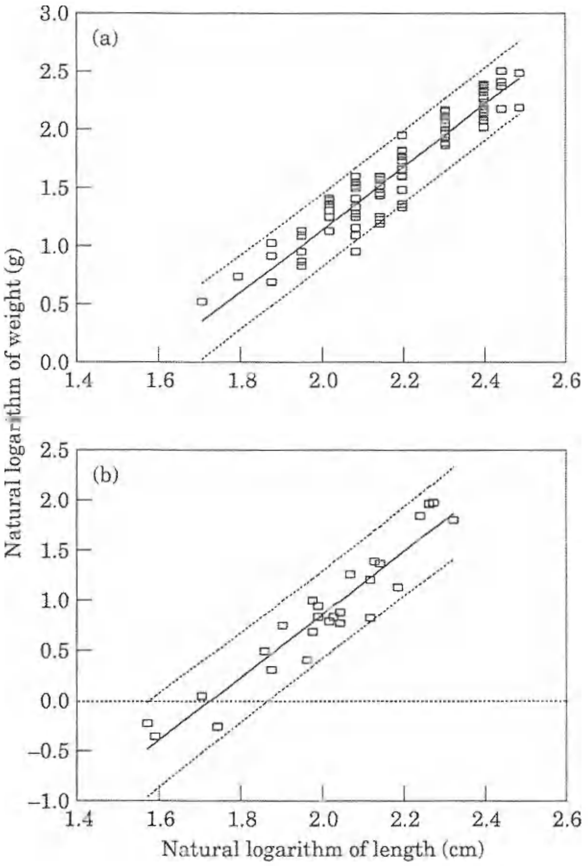

FIG. 6. Weight-length models based on fish sampled at West Thurrock in November 1992. (a) Herring; (b) Sprat. ——, Estimated weight-length relationships; – – – –, associated 95% predictive CI. All parameter P-values $<0{\cdot}01$ and all r^2 values $\geq 0{\cdot}897$.

closely [Fig. 7(a)]. Few predictions (3·16%) fell outside model predictive confidence limits and there was no evidence of statistically significant predictive bias. Changes in sprat abundance were related negatively to temperature, temporal trend and the November instrumental variables and related positively to shoaling behaviour. Interactions had no significant effect on abundance. Temperature was the only important physical determinant of sample abundance and based on standardized regression coefficients the second most important overall. As with herring, shoaling behaviour exerted a strong influence on measured fluctuations in abundance. The only significant seasonal variable coincided with the commencement of over-winter inshore migrations. Model residuals showed no evidence of serial correlation, heteroscedasticity or non-normality when tested at the $\alpha=0{\cdot}05$ level of significance. Predicted fluctuations in sample abundance matched actual abundance closely [Fig. 7(b)]. Few predictions (2·81%) fell outside model predictive confidence limits and there was no evidence of statistically significant predictive bias.

TABLE II. Spearman rank correlations ($n=285$) for herring and sprat abundances and physico-chemical parameters measured in the Thames estuary 1977–1992

Parameter	Herring	Sprat
Chlorinity	− 0·162	− 0·297
Dissolved oxygen	0·334	0·315
Freshwater flow	0·209	0·352
pH	$\underline{-0{\cdot}034}$	$\underline{-0{\cdot}051}$
Suspended solids	0·264	$\underline{0{\cdot}105}$
Temperature	− 0·561	− 0·443
Chlorinity × freshwater flow	$\underline{-0{\cdot}029}$	$\underline{-0{\cdot}014}$
Chlorinity × temperature	− 0·398	− 0·411
Freshwater flow × dissolved oxygen	0·321	0·406
Freshwater flow × pH	0·201	0·347
Freshwater flow × temperature	− 0·438	− 0·187
Temperature × dissolved oxygen	− 0·415	− 0·301

Freshwater flow and suspended solids were log-transformed for use in analysis. All other data were used as measured. Only physico-chemical interactions significant at the $\alpha=0{\cdot}05$ level are listed. Underlined coefficients indicate the tested variable did not significantly influence species abundance.

DISCUSSION

The middle Thames estuary has undergone substantial changes in the last 50 years (Tinsley, 1998). Pronounced changes in species abundances have occurred and with the influence of organic pollution reduced, patterns of seasonal usage and fluctuations in species abundance characteristic of other estuarine areas have become established. Among the most important contributors to the patterns of community structure have been the clupeids, herring and sprat. The numerical dominance of herring over sprat in the Thames reflects findings for the Medway (van den Broek, 1980), the Severn (Claridge *et al.*, 1986), and the Tyne (Pomfret *et al.*, 1991), but differs from results for the Loire (Marchand, 1980), the Forth (Elliott *et al.*, 1990), and an earlier study of the Severn (Hardisty & Huggins, 1975) where sprat were more abundant. Sampling and local factors influencing relative occurrence in coastal waters appear to explain much of the difference. For example, in the Forth, sprat and herring reflected their proportional occurrence in coastal waters (Elliott *et al.*, 1990). In the middle Thames estuary, herring, which typically are more abundant at the top of estuaries (Henderson, 1988) dominated sprat, which tend to avoid inner estuary areas except in winter when an inshore migration occurs (Henderson, 1988). Furthermore, herring spawning populations in the adjacent Blackwater estuary (Henderson *et al.*, 1984) increased the relative abundance of herring in the Thames in comparison with other sites. However, the importance of sprat in the outer Thames estuary is evidenced by the presence of a commercial fishery for them (Wheeler, 1979).

For the two year-classes studied, age-0 herring growth in the Thames was similar. End of October lengths (7·1–8·5 cm) exceeded those reported by Titmus *et al.* (1978) for the Severn estuary (6·95 cm). The 2·53 mm week^{-1} average growth rate for the Thames calculated over the August–October period for

TABLE III. Species abundance and physico-chemical regression model coefficient estimates (b_j), standardized regression coefficients (β_j), *P*-values and regression diagnostic statistics. All coefficient estimates were obtained using ordinary least squares ($n=285$)

Parameter	Herring			Sprat		
	b_j	β_j	*P*-value	b_j	β_j	*P*-value
Model variable						
Intercept	12·064		<0·001	5·257		<0·001
Ln suspended solids	1·708	0·122	0·001			
Temperature	− 0·621	− 0·331	<0·001	− 0·104	− 0·349	<0·001
Trend variable	$5{\cdot}410 \times 10^{-3}$	0·149	<0·001	$-9{\cdot}65 \times 10^{-4}$	− 0·167	<0·001
Shoal variable	15·792	0·471	<0·001	2·929	0·405	<0·001
April	− 3·590	− 0·117	0·001			
May	− 7·419	− 0·198	<0·001			
June	− 6·080	− 0·188	<0·001			
August	− 3·426	− 0·113	0·005			
November				− 0·756	− 0·151	0·001
Model diagnostics						
r^2	0·671			0·437		
Adjusted r^2	0·661			0·429		
Normalized SW	0·568			1·936		
Runs test statistic	0·808			0·569		
Maximum VIF	1·600			1·100		

Adjusted r^2 defines the proportion of explained variation when accounting for the number of model parameters estimated. Values of the normalized Shapiro–Wilk (SW) and the runs test statistics $\leq |1{\cdot}96|$ are consistent with the hypotheses of normality and independence in residuals at the 0·05 level of significance. Variance inflation factors (VIF) <10 indicate no multicollinearity.

1980/82 also exceeded the similarly calculated July–October 2·30 mm week^{-1} growth rate reported for the Severn. The 95% CI for the Thames allometric weight-length parameter (2·474–2·839) did not encompass the 2·905 parameter estimate for Severn herring >4·5 cm (Titmus *et al.*, 1978), and neither value approached the 3·75 value reported by De Silva (1973) for the Scottish west coast. This suggests herring experience lower growth in estuarine areas generally and the Thames in particular. Trade-offs between poor estuarine growth opportunities and decreased predation risk, however, may explain the preferential use of estuarine areas by the juveniles of many species (Blaber & Blaber, 1980).

Increases in sprat length during residency in the mid-estuary were small. Data from the Thames indicated increases averaged 0·33 cm over the 9 years for which sufficient length data were available. This compares with increases in size ranges from 5 to 7 cm in October to 6–7 cm in February for the Medway (1973–1975) (van den Broek, 1979*a*). Allometric weight-length parameters for the two sites also compared favourably, with the 3·129 value for the Thames approximating the mean 3·155 for the Medway (van den Broek, 1979*a*).

Seasonal usage of the Thames estuary produced abundance patterns generally, although not consistently, comparable with those reported for other estuarine studies. Medway herring displayed a January–February peak (van den Broek,

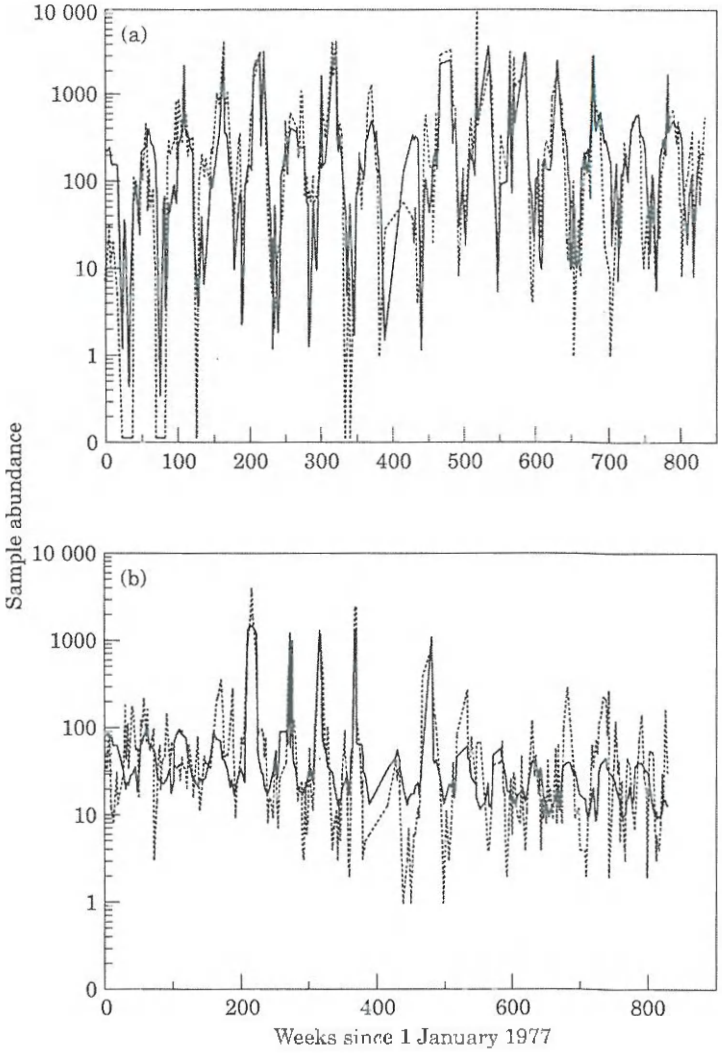

FIG. 7. Actual fluctuations of herring (a) and sprat (b) sample abundances transformed following equation (2) (– – – –) and model-predicted fluctuations in sample abundances (——).

1980) more pronounced than the November–March peak in the Thames. Sprat in the Medway were evenly distributed throughout the year (van den Broek, 1980), but peaked in January in the Thames. Hardisty & Huggins (1975), Potter & Claridge (1985) and Claridge *et al.* (1986) report distinctive August–September abundance peaks in Severn sprat and herring coincident with the in-migration of age-0 juveniles. Pomfret *et al.* (1991) report herring and sprat summer June–September abundance peaks for the Tyne similar to those in the Severn. In the Forth (Elliott *et al.*, 1990) seasonal January–March herring and sprat peaks resemble those for the Thames.

Temperature, salinity and substratum are major factors contributing to the spatial structure of estuarine fish communities (Henderson, 1989; Marshall & Elliott, 1998). Seasonal migrations further determine temporal patterns (van den

Broek, 1980; Potter *et al.*, 1986, 1997; Maes *et al.*, 1998). Turbidity (Blaber & Blaber, 1980) and interactions between physico-chemical variates, most notably dissolved oxygen and temperature (Pomfret *et al.*, 1991), are also thought to influence species abundance. Models estimated for the Thames corroborate many of these conclusions. Temperature, turbidity (as suspended solids) and seasonality influenced abundance. Interactions between environmental variables and salinity did not. Although interactions influence benthic species abundance (Pomfret *et al.*, 1991), similar reports for pelagic species do not exist. The insignificance of salinity was related to the use of fixed point sampling. This controls for the spatial gradients shown to determine species distributional patterns (Thiel *et al.*, 1995) and removed salinity from consideration as a temporal determinant of abundance.

Temperature is an important ecological resource (Magnuson *et al.*, 1979). In juveniles, temperature is a critical determinant of growth, and will affect fish distribution through differences in species' physiological tolerances. Accordingly, temperature is among the best predictors of fish abundance in estuaries (Marshall & Elliott, 1998; Thiel *et al.*, 1995). Temperature was the most important predictor of clupeid abundances in the Thames, although correlations did not necessarily agree with previously reported results. For example, temperature has been correlated positively with larval herring hatch and growth (Henderson *et al.*, 1984) and influences distributional patterns in the North Sea (Maravelias & Reis, 1995) and Humber estuary (Marshall & Elliott, 1998). Abnormally high sea surface temperatures may also be correlated with estuarine herring abundances (Holmes & Henderson, 1990). Sprat, which prefer cooler winters (Henderson, 1989), have been correlated negatively with temperature (Marshall & Elliott, 1998). In the Thames herring and sprat abundances were both correlated negatively with temperature. Herring, in particular, showed sharp declines in abundance above 10° C. Abundances above and below this threshold coincided typically with seasonal declines and tested as significantly different ($P<0{\cdot}001$). This suggests temperature may act as a cue to offshore spring migrations in juvenile herring. Sprat, however, did not display a sharp drop in abundance as a function of temperature. Abundance declined steadily as temperatures increased, suggesting sprat adjust facultatively to a preferred temperature range as the estuary warms in spring.

The existence of distinct seasonal patterns for herring and sprat are reflected in the importance of seasonal instrumental variables for explaining fluctuations in abundance. Studies of fish community structure in the Severn (Potter *et al.*, 1986, 1997) attributed changes in community structure to the sequential immigration and emigration of species from the estuary, noting that variations in flow, salinity and temperature acted only indirectly under extreme environmental conditions to influence abundance. However, standardized temperature regression coefficients in the Thames models indicated temperature was a more important determinant of abundance than was season. But significant seasonal influences suggest that variations in the seasonal timing of migrations have important modifying effects on changes in sample abundances that are independent of temperature.

Herring distribution within estuaries has been correlated negatively with turbidity measures (Marshall & Elliott, 1998). In the Thames, the analogue for turbidity, suspended solids, was correlated positively with herring abundance. Controlling for salinity had no appreciable effect on the correlation, which remained significant owing largely to an insignificant correlation between salinity and suspended solids. Turbidity has been advanced as a critical factor in reducing juvenile predation risk in estuaries (Blaber & Blaber, 1980; Maes *et al.*, 1998), which suggests a cause for the positive correlation with the largely juvenile population of Thames herring. Experiments with behavioural and feeding changes under turbid conditions have shown turbidity causes individuals to reduce, or eliminate, measurable anti-predator behaviours (Abrahams & Kattenfeld, 1997) and enhance feeding (Boehlert & Morgan, 1985), supporting further the plausibility of a positive correlation.

The significance of trend variables in the herring and sprat models compares with trends reported elsewhere for the North Sea. Heessen & Daan (1996) and Cook (1997) reported increases in North Sea herring stock biomass and strong year-classes in the early 1980s. Philippart *et al.* (1996) described a general increase in Wadden Sea herring populations over the same period. Reported biomass increases were reflected in a significant positive trend component in the West Thurrock herring model.

Sprat stock biomass in the North Sea declined sharply after 1980 and levelled after 1983 (Daan *et al.*, 1990). Declines were linked to sprat adopting a more coastal distribution. Although distributional changes might have increased relative abundance in estuarine areas, no such pattern was found in the Thames data. Reported declines in biomass were reflected directly in a significant negative trend in estuarine populations in the vicinity of West Thurrock.

The correspondence between reported North Sea biomass changes and estuarine abundance trends also occurs in the sequential 1973–1975 (van den Broek, 1979*b*) and 1981–1983 (Wharfe *et al.*, 1984) snapshots for the Medway and standardized fyke-net catches in the Oosterschelde estuary (Hamerlynck & Hostens, 1994). General agreement between trends in estuarine population abundance and reported North Sea stock trends, in this study and elsewhere, underscores the importance of complex stock dynamics for the determination of estuarine population sizes.

Differences in relative abundance, seasonal patterns and correlations with physico-chemical variates between this and other studies may have been driven by latitudinal variations in peak spawning, differences in estuarine hydrographic factors (Marchand, 1980; Rogers & Millner, 1996), regional forcing variables, such as fishing pressure or eutrophication (Heessen & Daan, 1996), or fluctuations in local environmental conditions (Philippart *et al.*, 1996). Differences may also reflect the opportunistic use of estuaries, as Potter *et al.* (1988) have suggested for whiting *Merlangius merlangus* (L.). The combination of possible influences complicates understanding of spatial and temporal patterns of change in estuarine structure and function because estuarine fish populations can reflect more widespread changes in abundance than those triggered by estuarine events alone (Elliott *et al.*, 1990). Inclusion of a trend variable in the models explaining abundance fluctuations in the Thames supports the thesis and suggests that direct comparisons between trends in estuarine abundance will need to take particular account of potentially important regional environmental influences and determinants of marine population dynamics when attempting to make inferences about the relative effects of human action on estuarine fish communities.

The authors thank the Environment Agency for permission to analyze and publish the data. Support for completion of the work was provided by an NSERC Research Grant to Power. Opinions stated in the paper are those of the authors and do not necessarily reflect those of any supporting agency or group.

References

Abrahams, M. & Kattenfeld, M. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioural Ecology and Sociobiology* **40,** 169–174.

Andrews, M. J. & Rickard, D. G. (1980). Rehabilitation of the inner Thames Estuary. *Marine Pollution Bulletin* **11,** 327–332.

Araujo, F. G., Bailey, R. G. & Williams, W. P. (1998). Seasonal and between-year variations of fish populations in the middle Thames estuary: 1980–1989. *Fisheries Management and Ecology* **5,** 1–21.

Araujo, F. G., Bailey, R. G. & Williams, W. P. (1999). Spatial and temporal variations in fish populations in the upper Thames estuary. *Journal of Fish Biology* **55,** 836–853.

Attrill, M. J. (ed.) (1998). *A Rehabilitated Estuarine Ecosystem. The Environment and Ecology of the Thames Estuary*. Dordrecht: Kluwer.

Attrill, M. J. & Thomas, R. M. (1996). Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters. *Marine Ecology Progress Series* **143,** 25–36.

Banks, J. & Carson, J. S. (1984). *Discrete-event System Simulation*. Englewood Cliffs, N.J.: Prentice-Hall.

Bates, D. M. & Watts, D. G. (1988). *Nonlinear Regression Analysis and Its Applications*. New York: John Wiley & Sons.

Blaber, S. J. M. & Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fisheries. *Journal of Fish Biology* **17,** 143–162.

Boehlert, G. W. & Morgan, J. B. (1985). Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi*. *Hydrobiologia* **123,** 161–170.

van den Broek, W. L. F. (1979*a*). Aspects of the biology of *Sprattus sprattus* (L.) in the Medway estuary. *Journal of Fish Biology* **15,** 437–447.

van den Broek, W. L. F. (1979*b*). A seasonal survey of fish populations in the lower Medway estuary, based on power station screen samples. *Estuarine, Coastal and Shelf Science* **9,** 1–15.

van den Broek, W. L. F. (1980). Aspects of the biology of estuarine fish populations from power station trash screens. *International Journal of Environmental Studies* **15,** 203–216.

Brown, D. & Rothery, P. (1993). *Models in Biology: Mathematics, Statistics and Computing*. Chichester: John Wiley & Sons.

Callahan, J. T. (1984). Long-term ecological research. *Bioscience* **34,** 363–367.

Claridge, P. N., Potter, I. C. & Hardisty, M. W. (1986). Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn estuary. *Journal of the Marine Biological Association of the United Kingdom* **66,** 229–258.

Conover, W. J. (1980). *Practical Nonparametric Statistics*. New York: John Wiley & Sons.

Cook, R. M. (1997). Stock trends in six North Sea stocks as revealed by an analysis of research vessel surveys. *ICES Journal of Marine Science* **54,** 924–933.

Cox, C. P. (1987). *A Handbook of Introductory Statistical Methods*. New York: John Wiley & Sons.

Daan, N., Bromley, P. J., Hislop, J. R. G. & Nielsen, N. A. (1990). Ecology of North Sea fish. *Netherlands Journal of Sea Research* **26,** 343–386.

De Silva, S. S. (1973). Abundance, structure, growth and origin of inshore clupeid populations of the west coast of Scotland. *Journal of Experimental Marine Biology and Ecology* **12,** 119–144.

Draper, N. R. & Smith, H. (1981). *Applied Regression Analysis*, 2nd edn. New York: John Wiley & Sons.

Drinkwater, K. F. & Myers, R. A. (1987). Testing predictions of marine fish and shellfish landings from environmental variables. *Canadian Journal of Fisheries and Aquatic Sciences* **44,** 1568–1573.

Dunn, O. J. & Clark, V. A. (1987). *Applied Statistics: Analysis of Variance and Regression*, 2nd edn. New York: John Wiley & Sons.

Elliott, M., O'Reilly, M. G. & Taylor, C. J. L. (1990). The Forth estuary: a nursery and overwintering area for North Sea fishes. *Hydrobiologia* **195,** 89–103.

Hamerlynck, O. & Hostens, K. (1994). Changes in the fish fauna of the Oosterschelde estuary—a ten-year time series of fyke catches. *Hydrobiologia* **282/283,** 497–507.

Hardisty, M. W. & Huggins, R. J. (1975). A survey of the fish populations of the middle Severn estuary based on power station sampling. *International Journal of Environmental Studies* **7,** 227–242.

Heessen, H. J. L. & Daan, N. (1996). Long-term trends in ten non-target North Sea fish species. *ICES Journal of Marine Science* **53,** 1063–1078.

Henderson, A. R. & Hamilton, J. D. (1986). The status of fish populations in the Clyde estuary. *Proceedings of the Royal Society of Edinburgh* **90B,** 157–170.

Henderson, P. A. (1988). The structure of estuarine fish communities. *Journal of Fish Biology* **33** (Suppl. A), 223–225.

Henderson, P. A. (1989). On the structure of the inshore fish community of England and Wales. *Journal of the Marine Biological Association of the United Kingdom* **69,** 145–163.

Henderson, P. A. & Holmes, R. H. A. (1989). Whiting migration in the Bristol Channel: a predator-prey relationship. *Journal of Fish Biology* **34,** 409–416.

Henderson, P. A., Whitehouse, J. W. & Cartwright, G. H. (1984). The growth and mortality of larval herring, *Clupea harengus* L., in the River Blackwater estuary, 1978–1980. *Journal of Fish Biology* **24,** 613–622.

HMSO (1979). *The Measurement of Electrical Conductivity and the Laboratory Determination of the pH Value of Natural, Treated and Waste Waters, 1978.* HMSO: London.

HMSO (1980*a*). *Dissolved Oxygen in Natural and Waste Waters, 1979 Version: Two Methods.* HMSO: London.

HMSO (1980*b*). *Suspended, Settleable and Total Dissolved Solids in Waters and Effluents.* HMSO: London.

Holmes, R. H. A. & Henderson, P. A. (1990). High recruitment in the Severn estuary: the effect of a warm year. *Journal of Fish Biology* **36,** 961–963.

Huddart, R. & Arthur, D. R. (1971). Shrimps and whitebait in the polluted Thames estuary. *International Journal of Environmental Studies* **2,** 21–34.

Maes, J., Taillieu, A., Van Damme, P. A., Cottenie, K. & Ollevier, F. (1998). Seasonal patterns in the fish and crustacean community of a turbid temperate estuary (Zeeschelde estuary, Belgium). *Estuarine, Coastal and Shelf Science* **47,** 143–151.

Magnuson, J. J., Crowder, L. B. & Medvick, P. A. (1979). Temperature as an ecological resource. *American Zoologist* **19,** 331–343.

Maravelias, C. D. & Reis, D. G. (1995). Relationship between herring (*Clupea harengus* L.) distribution and sea-surface salinity and temperature in the northern North-Sea. *Scientia Marina* **59,** 427–438.

Marchand, J. (1980). Distributions saisonnières, abondances et diversités de l'ichthyofaune de l'estuaire interne de la Loire en 1988–78. *Annales de l'Institut Océanographique* **56,** 127–137.

Marshall, S. & Elliott, M. (1998). Environmental influences on the fish assemblage of the Humber estuary, U.K. *Estuarine, Coastal and Shelf Science* **46,** 175–184.

Philippart, C. J. M., Lindeboom, H. J., van der Meer, J., van der Veer, H. W. & Witte, J. J. (1996). Long-term fluctuations in fish recruit abundance in the western

Wadden Sea in relation to variation in the marine climate. *ICES Journal of Marine Science* **53,** 1120–1129.

Pomfret, J. R., Turner, G. S. & Phillips, S. (1988). Beam trawl surveys as a monitoring tool in polluted estuaries in north-east England. *Journal of Fish Biology* **33** (Suppl. A), 71–77.

Pomfret, J. R., Elliott, M., O'Reilly, M. G. & Phillips, S. (1991). Spatial and temporal patterns in the fish communities in two U.K. North Sea estuaries. In *Estuaries and Coasts: Spatial and Temporal Intercomparisons* (Elliott, M. & Ducrotoy, J.-P., eds), pp. 277–284. Denmark: Olsen & Olsen.

Potter, I. C. & Claridge, P. N. (1985). Seasonal catches, size and meristic data for sprat, *Sprattus sprattus*, in the Severn estuary. *Journal of the Marine Biological Association of the United Kingdom* **65,** 667–675.

Potter, I. C., Claridge, P. N. & Warwick, R. M. (1986). Consistency of seasonal changes in an estuarine fish assemblage. *Marine Ecology Progress Series* **32,** 217–228.

Potter, I. C., Gardner, D. C. & Claridge, P. N. (1988). Age composition, growth, movements, meristics and parasites of the whiting, *Merlangius merlangus*, in the Severn estuary and Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom* **68,** 295–313.

Potter, I. C., Claridge, P. N., Hyndes, G. A. & Clarke, K. R. (1997). Seasonal, annual and regional variations in ichthyofaunal composition in the inner Severn estuary and inner Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom* **77,** 507–525.

Power, M. & McKinley, R. S. (1997). Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. *Transactions of the American Fisheries Society* **126,** 549–558.

Power, M. & van den Heuvel, M. R. (1999). Age-0 yellow perch growth and its relationship to temperature. *Transactions of the American Fisheries Society* **128,** 687–700.

Rijnsdorp, A. D., Daan, N., van Beek, F. A. & Heesen, H. J. L. (1991). Reproductive variability in North Sea plaice, sole and cod. *Journal du Conseil International pour l'Exploration de la Mer* **47,** 352–375.

Rogers, S. I. & Millner, R. S. (1996). Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations: 1973 to 1995. *ICES Journal of Marine Science* **53,** 1094–1112.

Royston, J. P. (1982). An extension of Shapiro and Wilk's W test for normality to large samples. *Applied Statistics* **31,** 115–124.

Thiel, R., Sepúlveda, A., Kafemann, R. & Nellen, W. (1995). Environmental factors as forces structuring the fish community of the Elbe estuary. *Journal of Fish Biology* **46,** 47–69.

Thomas, R. M. (1998). Temporal changes in the movements and abundance of Thames Estuary fish populations. In *A Rehabilitated Estuarine Ecosystem. The Environment and Ecology of the Thames Estuary* (Attrill, M. J., ed.), pp. 115–140. Dordrecht: Kluwer.

Tinsley, D. (1998). The Thames estuary: a history of the impact of humans on the environment and a description of the current approach to environmental management. In *A Rehabilitated Estuarine Ecosystem. The Environment and Ecology of the Thames Estuary* (Attrill, M. J., ed.), pp. 5–26. Dordrecht: Kluwer.

Titmus, G., Claridge, P. N. & Potter, I. C. (1978). Growth and abundance of 0-group herrings, *Clupea harengus* L., in the Severn estuary. *Zoological Journal of the Linnean Society* **64,** 251–260.

Torstensen, E. & Gjøsæter, J. (1995). Occurrence of 0-group sprat (*Sprattus sprattus*) in the littoral zone along the Norwegian Skagerrak coast 1945–1992, compared with the occurrence of 0-group herring (*Clupea harengus*). *Fisheries Research* **21,** 409–421.

U.S. EPA (1983). *Methods for Chemical Analysis of Water and Wastes.* Washington, D.C.: EPA/600/4-79-020.

Walters, C. J. & Collie, J. S. (1988). Is research on environmental factors useful to fisheries management? *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 1848–1854.

Wharfe, J. R., Wilson, S. R. & Dines, R. A. (1984). Observations on the fish populations of an east coast estuary. *Marine Pollution Bulletin* **15,** 133–136.

Wheeler, A. (1969). *The Fishes of the British Isles and North West Europe.* London: MacMillan.

Wheeler, A. (1979). *The Tidal Thames: the History of a River and Its Fishes.* London: Routledge & Kegan Paul.

Wheeler, A. (1988). Fish in estuaries: a summing up. *Journal of Fish Biology* **33** (Suppl. A), 251–254.

Wilson, K. W., D'Arcy, B. J. & Taylor, S. (1988). The return of fish to the Mersey estuary. *Journal of Fish Biology* **33** (Suppl. A), 235–238.

Wolfe, D. A., Champ, M. A., Flemer, D. A. & Mearns, A. J. (1987). Long-term biological data sets: their role in research, monitoring and management of estuarine and coastal marine systems. *Estuaries* **10,** 181–193.

Zar, J. H. (1984). *Biostatistical Analysis,* 2nd edn. Englewood Cliffs, N.J.: Prentice Hall.