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# Spatial and temporal variations in fish populations in the upper Thames estuary

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Between February 1989 and August 1990, the upper Thames estuary contained 23 species of fish. Fish numbers were higher and relatively constant in the uppermost part of the estuary. Number of species was augmented in summer from fresh water and from downstream, coinciding with high temperature, low flow and high salinity. The eight most abundant species contributed to 98·5% of the total number. Flounder *Pleuronectes flesus*, dace *Leuciscus leuciscus* and perch *Perca fluviatilis*, recruited from May to August, and common goby *Pomatoschistus microps*, roach *Rutilus rutilus* and chub *Leuciscus cephalus*, from August to November. The upper estuary (salinity 0·34–2·96 p.s.u.) formed a species transition area between the freshwater but salinity-resistant roach, chub, and gudgeon *Gobio gobio* upstream, and the estuarine eurhyhaline common goby and flounder downstream. The three-spined stickleback *Gasterosteus aculeatus* and cyprinids were more abundant at upstream while perch was more abundant at downstream sites. High abundances of gudgeon, chub and roach were associated with high transparency and dissolved oxygen and low salinity, while high abundances of perch were associated with high salinity and low transparency. Dace and three-spined stickleback were associated with high dissolved oxygen and low pH, and common goby with high pH. Flounder showed no clear preferences. 

Key words: fish community; estuaries; Thames; distribution; environmental parameters.

## INTRODUCTION

Upper limits of estuaries can be stressful for fish populations. Low salinities limit the distribution of either freshwater species downstream or marine species upstream (Haedrich, 1983). Unlike the middle reaches, characterised by high seasonal abundances of marine fishes (Araújo, 1992; Araújo *et al.*, 1998), the upper Thames estuary in south-eastern England is an area to which few marine species can adapt. The period of recovery of water quality and the return of fish to the tideway has been reported by Wheeler (1969, 1979), Huddart & Arthur (1971*a*,*b*) and Andrews (1984). Andrews *et al.* (1982) described the relation between the occurrence of fish and physico-chemical factors, focusing attention on pollution from sewage works, which continued to reduce dissolved oxygen concentration to critical levels in the middle reaches of the estuary at times. Since then, dissolved oxygen has been kept at a level above the minimum limits of tolerance for most fish. Whilst it was recognized that fish populations had

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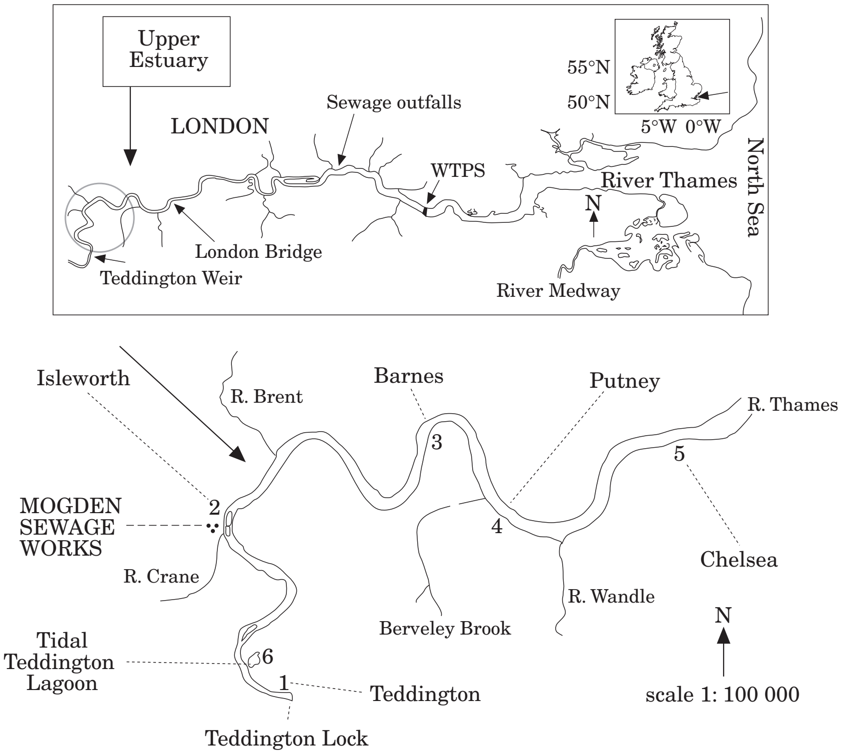


FIG. 1. Study area, showing the five sampling sites in the upper Thames estuary.

become fully established in the tidal Thames, determination of the key ecological parameters requires accumulation of more detailed basic knowledge of the complex functioning of the fish community (Thiel *et al.*, 1995); reducing pollution could lead quickly to increased populations, followed by structural changes of the fish community.

This paper aimed to determine whether spatial and temporal changes in abundance of the fish populations occur in the upper reaches of the tidal Thames, and to investigate influences of environmental factors on species distributions.

## MATERIALS AND METHODS

### AREA OF STUDY

The Thames estuary extends seaward from Teddington Weir, 30·5 km above London Bridge (LB). The study area extended from Chelsea Bridge (6 km above LB) to Teddington Weir (Fig. 1), where the influence of fresh water was likely to be greatest.

The average tidal amplitude ranged from 5 to 7 m (H.M.S.O., 1964). The bed formation was generally hard, consisting of gravel, sand, and clay with little mud. Intertidal areas consisted of walls and embankments above mud, silt and shingle or sand. Five sites were used (Fig. 1): Chelsea, Putney, Barnes, Isleworth and Teddington, at 6, 12, 17, 24 and 30·5 km upstream of LB, respectively.

### SAMPLING PROCEDURE

From February 1989 to August 1990, a small seine, 6 m long by 1 m deep with a mesh size of 1 mm, and a large seine net, 60 m long by 4 m deep with a stretched mesh size of 15 mm, were used to sample each of the five sites monthly. Starting about 1 h before low tide the sites were sampled in random sequence on the same day. At each station two hauls were made *c.* 300 m apart to avoid overlap and catches from the small and large seines were pooled. Sites were between 0·5 and 2 m deep. Overall, 87 samples were collected, from February 1989 to August 1990.

The following measurements were taken at *c.* 1 m depth, 4 m from the embankment, at each sampling: temperature and salinity, using a conductivity meter (conduktometer Model WTM LF 191) pH, using bromothymol blue indicator and a Lovibond 1000 comparator; percentage saturation of dissolved oxygen, using a pHOX system meter and probe, type 62TE; and transparency, using a standard Secchi disc. Data on water flow over Teddington Weir were provided by the National River Authority.

### DATA ANALYSIS

Logarithmic transformation (log $(x+1)$) of the raw data was performed for both environmental factors and fish abundance in order to validate assumptions for parametric analyses applied to the univariate and multivariate tests, to reduce the weighting of abundant species, and to balance the effect of different units of measurement of environmental factors.

Associations between fish abundance and environmental variables were assessed using the canonical correspondence analysis (CANOCO) proposed by Ter Braak (1986). CANOCO were performed on abundance of the eight most numerous species, which occurred in >10% of the samples and contributed, each one, >1% of the total number of fish. Including more species only affected the total variation expressed by the eigenvalues but did not change the interpretation. The Spearman rank correlation coefficient was used to determine the significance of each environmental variable to fish abundance (Zar, 1984). This univariate, non-parametric statistical technique, enables the relationship between species abundance and environmental variables to be analysed individually, thus determining the independent variables most likely to affect the distribution of each species together with the nature of the effect. To test further for relationships between fish population abundance and environmental variables, partial correlation and stepwise multiple regression analyses were applied.

## RESULTS

### FISH COMPOSITION AND RELATIVE ABUNDANCE

Twenty-three species were recorded in the upper estuary (Table I). Eight species contributed >1% of the total number of fish and, pooled, amounted to 98·5% of all fish sampled (Table I). Species abundance in decreasing order was three-spined stickleback *Gasterosteus aculeatus* L., flounder *Pleuronectes flesus* L. common goby *Pomatoschistus microps* (Kröyer), roach *Rutilus rutilus* (L.), dace *Leuciscus leuciscus* (L.), gudgeon *Gobio gobius* (L.), perch *Perca fluviatilis* L. and chub *Leuciscus cephalus* (L.). The three-spined stickleback comprised 44·7% of the overall fish catches, was by far the most abundant species and the only one present in >50% of samples [frequency of occurrence (*FO*)=50–90%] (Table I), while the other seven occurred in >10%.

Freshwater forms comprised 56·5% of the species, followed by estuarine (21·7%) and marine (17·4%). The estuarine species (three-spined stickleback and common goby) contributed 56·9% of the total number of individuals, compared

TABLE I. Number of fish species ($n$) and frequency of occurrence ($FO$) in upper Thames estuary, from February 1989 to August 1990

| Common name | Scientific name | $n$ | % $n$ | $FO$ (%) | LC |
|---|---|---|---|---|---|
| Three-spined stickleback | *Gasterosteus aculeatus* | 6024 | 44·7 | 56·5 | E |
| Flounder | *Platichthys flesus* | 1627 | 12·1 | 26·6 | M |
| Common goby | *Pomatoschistus microps* | 1583 | 11·7 | 39·0 | E |
| Roach | *Rutilus rutilus* | 1514 | 11·2 | 39·0 | F |
| Dace | *Leuciscus leuciscus* | 1280 | 9·5 | 31·6 | F |
| Gudgeon | *Gobio gobius* | 899 | 6·7 | 11·3 | F |
| Perch | *Perca fluviatilis* | 174 | 1·3 | 16·9 | F |
| Chub | *Leuciscus cephalus* | 170 | 1·3 | 10·1 | F |
| Bleak | *Alburnus alburnus* (L.) | 55 | 0·4 | 4·0 | F |
| Bass | *Dicentrarchus labrax* | 44 | 0·3 | 4·5 | M |
| Ten-spined stickleback | *Pungitius pungitius* (L.) | 36 | 0·3 | 6·2 | E |
| Eel | *Anguilla anguilla* | 22 | 0·2 | 6·8 | C |
| Bream | *Abramis brama* (L.) | 19 | 0·1 | 5·7 | F |
| Smelt | *Osmerus eperlanus* | 7 | 0·1 | 2·3 | E |
| Sand smelt | *Atherina presbyter* | 7 | 0·1 | 1·1 | E |
| Minnow | *Phoxinus phoxinus* (L.) | 5 | <0·1 | 1·7 | F |
| Pike | *Esox lucius* L. | 5 | | 0·6 | F |
| Thin-lipped grey mullet | *Liza ramada* | 4 | | 1·7 | M |
| Souffie | *Leuciscus souffia* (L.) | 4 | | 1·1 | F |
| Black goby | *Gobius niger* | 2 | | 0·6 | E |
| Common carp | *Cyprinus carpio* L. | 1 | | 0·6 | F |
| Ruffe | *Gymnocephalus cernua* (L.) | 1 | | 0·6 | F |
| Silver bream | *Blicca bjoerkna* (L.) | 1 | | 0·6 | F |
| Total | | 13 484 | | | |

C, Catadromous; E, estuarine; F, fresh water; LC, Life cycle category (according to Claridge *et al.*, 1986); M, marine.

with 30·6% freshwater (chiefly roach, dace and gudgeon), 12·5% marine (mainly flounder), and only 0·2% catadromous [eel *Anguilla anguilla* (L.)] (Table I).

## SPATIAL AND TEMPORAL CHANGES

The number of species did not show a clear trend along the sites, with the highest values recorded (17) at Putney and the lowest (13) at Chelsea (Table II). Numbers of fish per sample decreased downstream from 250 at Teddington to 11 at Chelsea,

The eight most abundant species, with the exception of gudgeon, were found at all sites (Table II). The abundant three-spined stickleback peaked at Isleworth and Teddington, contributing 52·5 and 61·2% by number, respectively, and flounder and common goby were the commonest fish at Putney and Barnes. Freshwater species were prominent at Isleworth (dace) and Teddington (roach, chub and gudgeon).

Overall mean number of species was higher from May to September than from December to April (Fig. 2). Number of fish was higher in the sites more upstream (Fig. 3).

TABLE II. Relative contribution to the total number of fish per site in the upper Thames estuary, from February 1989 to August 1990

| Species | Sites (%) | | | | |
|---|---|---|---|---|---|
| | Chelsea | Putney | Barnes | Isleworth | Teddington |
| Three-spined stickleback | 28·6 | 8·8 | 18·3 | 52·5 | 61·2 |
| Flounder | 11·0 | 44·0 | 29·8 | 10·7 | 0·4 |
| Common goby | 19·8 | 34·0 | 33·0 | 6·8 | 4·3 |
| Roach | 2·6 | 3·6 | 6·0 | 11·9 | 13·3 |
| Gudgeon | — | — | 0·2 | 0·3 | 13·6 |
| Dace | 6·6 | 5·1 | 8·5 | 15·4 | 3·4 |
| Chub | 0·4 | 0·7 | 0·3 | 0·7 | 2·0 |
| Perch | 22·9 | 1·7 | 2·4 | 0·5 | 0·4 |
| Bleak | — | 0·1 | 0·1 | 0·1 | 0·8 |
| Ten-spined stickleback | 2·2 | 0·9 | 0·4 | 0·3 | — |
| Bass | 2·6 | 0·1 | — | 0·3 | 0·2 |
| Eel | — | 0·7 | 0·6 | — | <0·1 |
| Bream | 0·4 | <0·1 | 0·3 | 0·1 | <0·1 |
| Smelt | 1·3 | 0·1 | — | — | — |
| Thin-lipped mullet | — | 0·1 | — | <0·1 | — |
| Minnow | 0·4 | — | — | 0·1 | — |
| Souffie | — | — | — | <0·1 | <0·1 |
| Pike | — | — | — | — | <0·1 |
| Sand smelt | 0·9 | — | — | <0·1 | — |
| Black goby | — | — | — | — | <0·1 |
| Common carp | — | <0·1 | — | — | — |
| Ruffe | — | — | 0·1 | — | — |
| Silver bream | — | <0·1 | — | — | — |
| Number of species | 13 | 17 | 13 | 16 | 15 |
| Number of fish | 253 | 2250 | 1026 | 2856 | 6500 |
| Number of fish/sample | 11 | 45 | 38 | 56 | 250 |
| Number of samples | 17 | 19 | 17 | 19 | 15 |

Peaks in May–June were found for flounder and dace, June–July for perch, July/August for roach, July–November for common goby, and October–November for chubb (Fig. 4). The high abundance of three-spined stickleback from April to August 1989 was not repeated in 1990, and the gudgeon peak in August 1989 was not repeated in 1990. Dace were more plentiful in summer 1989, and flounder in 1990.

Three-spined stickleback, roach, gudgeon and chub were most abundant at Teddington, while dace was more abundant at Isleworth and Teddington (Fig. 5). Flounder, common goby and perch were more widely distributed, with common goby and flounder being more abundant at Barnes and Putney, and perch at Chelsea.

Catches of the eight most abundant species (Fig. 6) consisted mainly of small young-of-the-year fish. Dace showed a wider amplitude of size (10–150 mm), with both juveniles and adults present. The high contribution of the 0+ age class indicates that most fish were from spring/summer spawning.

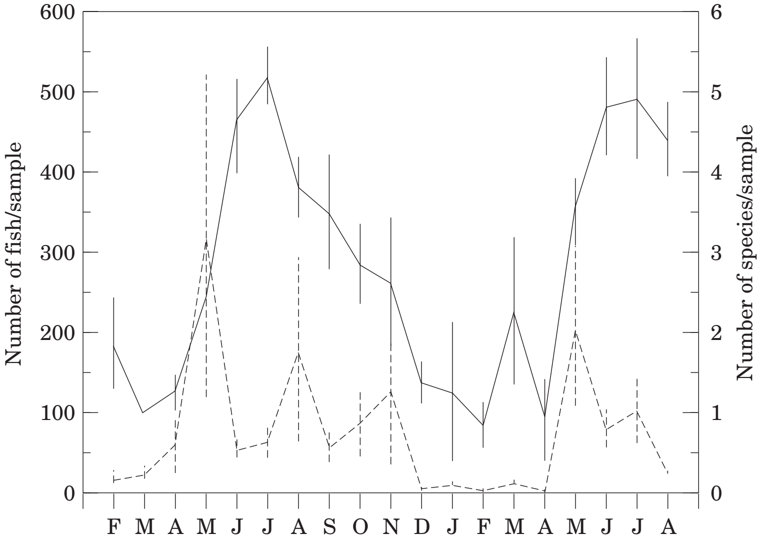


FIG. 2. Monthly means ( ± 1 S.E.) for the number of fish (– – –) and the number of species (——) in the upper Thames estuary, from February 1989 to August 1990.

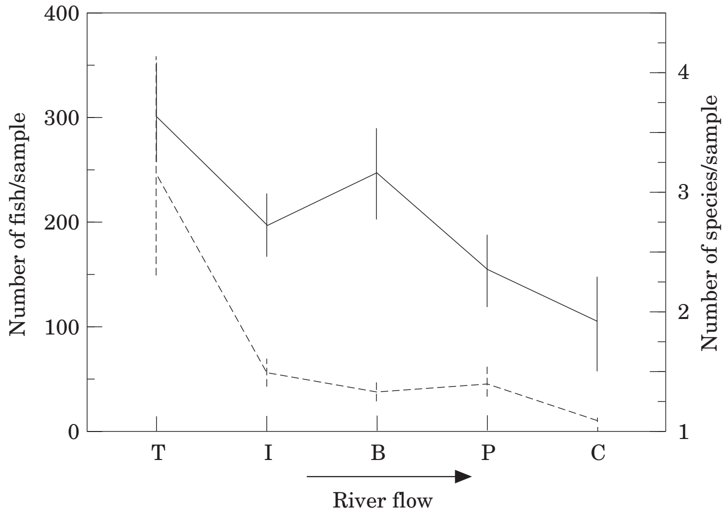


FIG. 3. Means ( ± 1 S.E.) for the number of fish (– – –) and the number of species (——) at five sampling sites in the upper Thames estuary, from February 1989 to August 1990. T, Teddington; I, Isleworth; B, Barnes; P, Putney; C, Chelsea.

## INFLUENCE OF ENVIRONMENTAL VARIABLES

Temperature and salinity were higher in summer and lower in winter, while dissolved oxygen and pH were rather stable with lower values in September and January (Fig. 7). Flow was higher in March 1989 and February 1990 while transparency was higher one month after peak flow. Dissolved oxygen, pH and

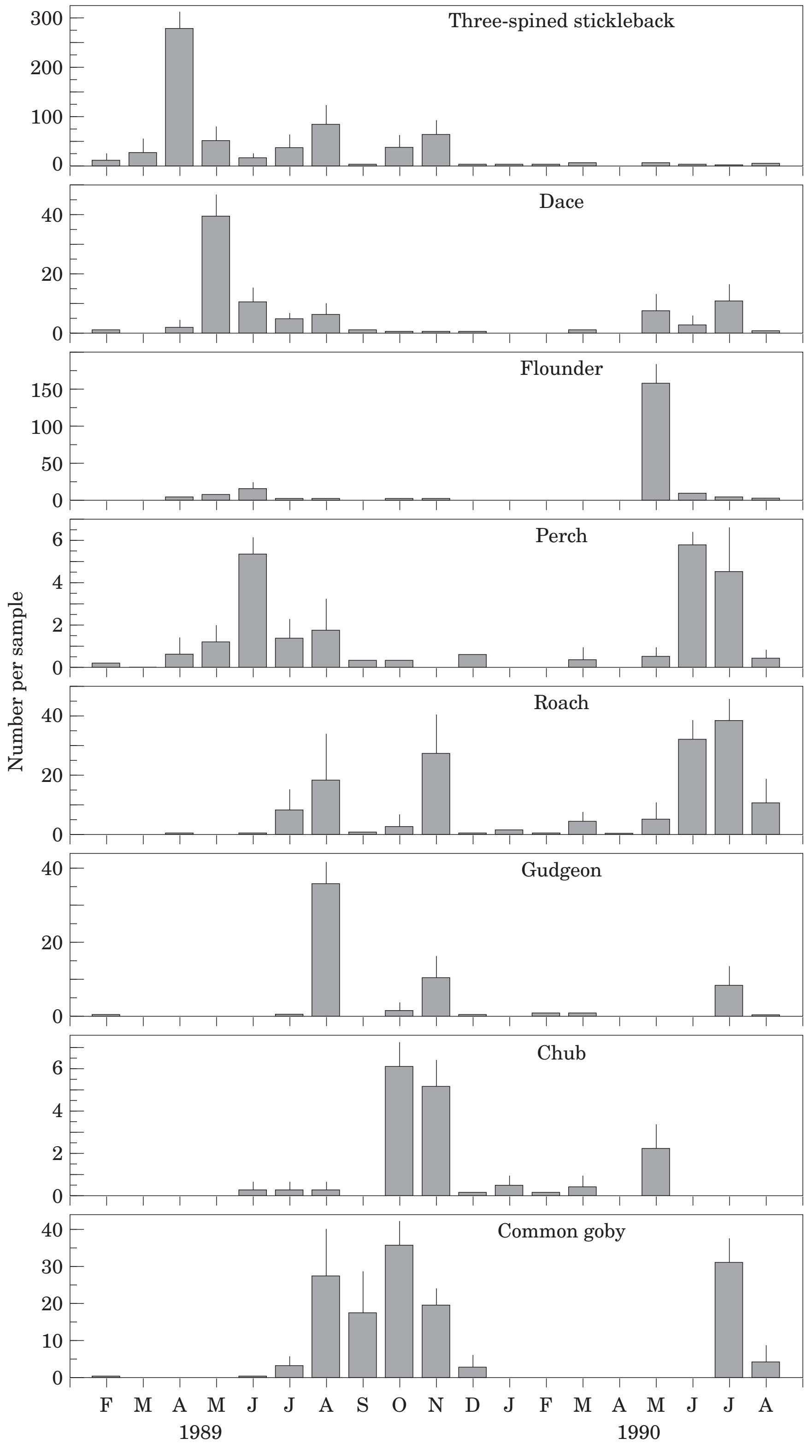


FIG. 4. Monthly means ( ± 1 S.E.) for numerical abundance of the eight most numerous fish species in the upper Thames estuary, from February 1989 to August 1990.

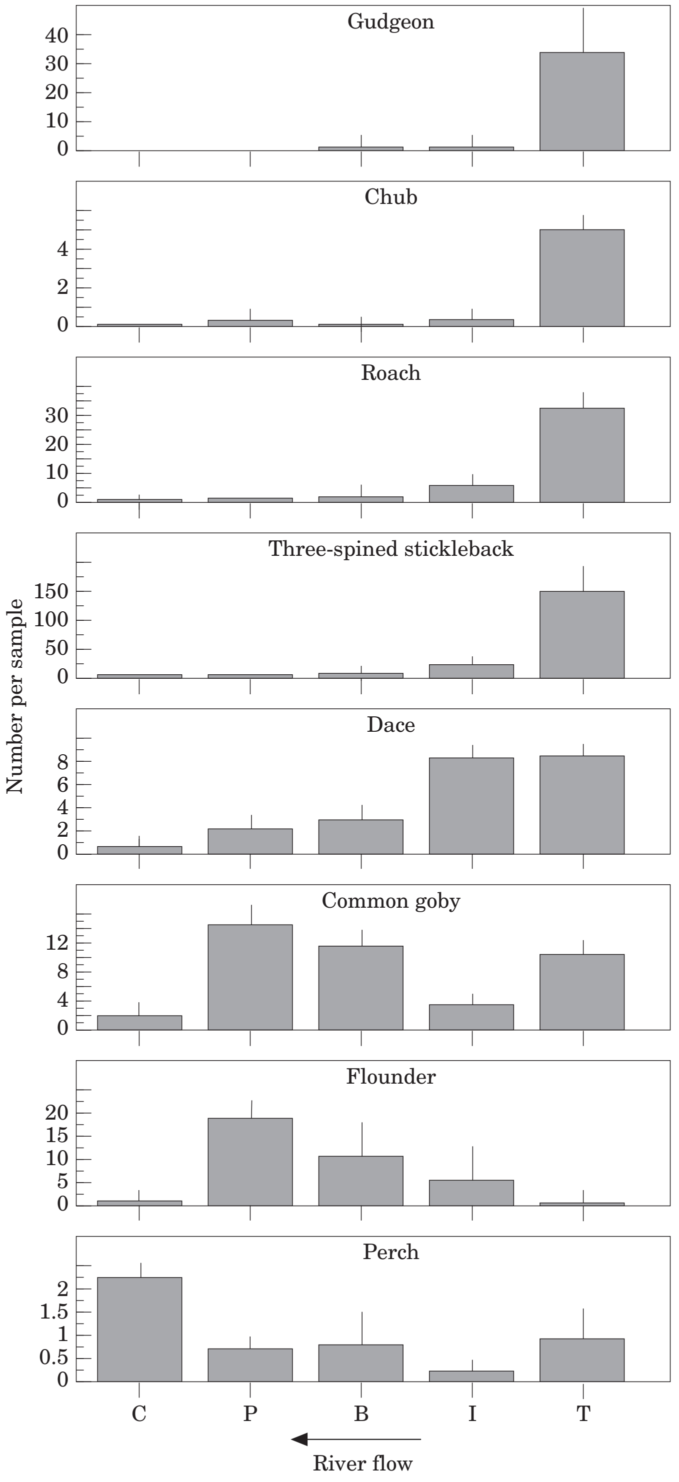


FIG. 5. Means ( ± 1 S.E.) for numerical abundance of the eight most numerous fish species at five sampling sites in the upper Thames estuary, from February 1989 to August 1990. C, Chelsea; P, Putney; B, Barnes; I, Isleworth; T, Teddington.

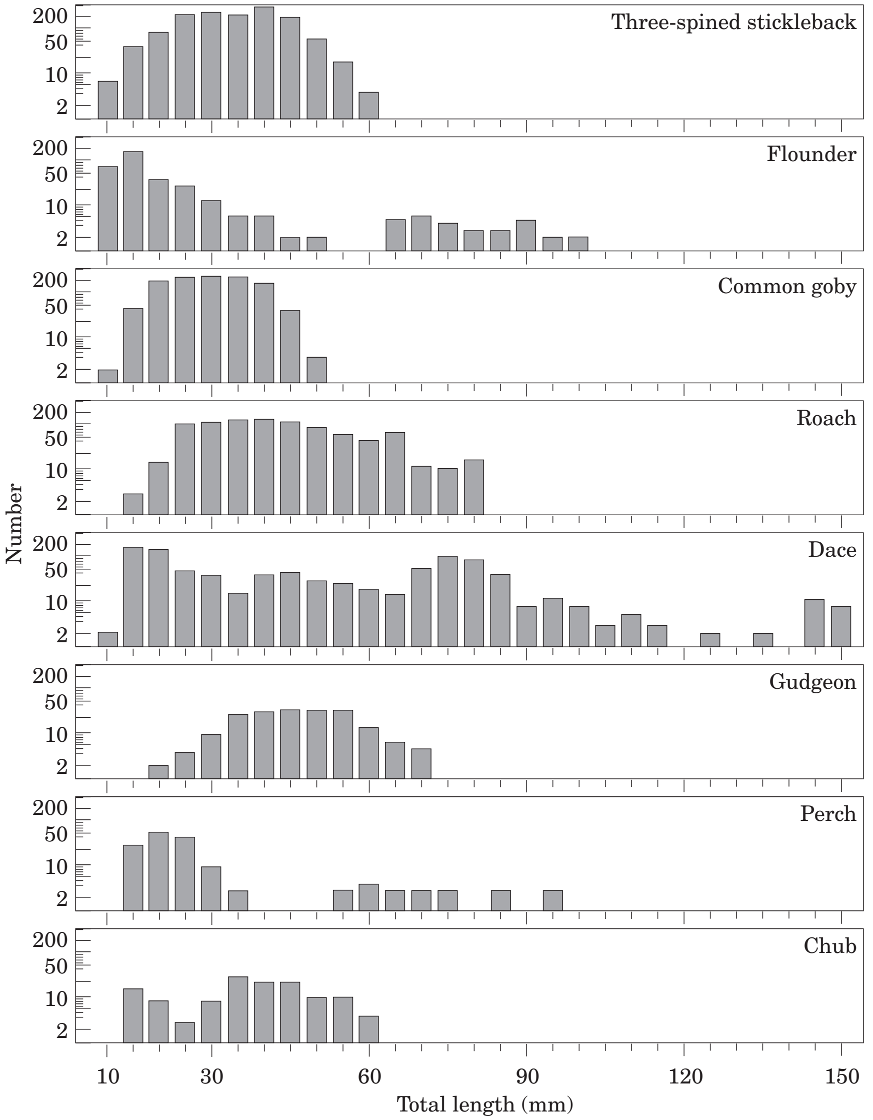


FIG. 6. Length–frequency histograms for the eight most numerous fish species in the upper Thames estuary.

transparency decreased in a downstream direction while salinity increased and temperature did not differ (Fig. 8).

Flounder, roach and dace increased in abundance with temperature (Table III) and common goby and perch with salinity and with decreasing dissolved oxygen and transparency. Gudgeon decreased with increasing salinity and decreasing transparency. Roach, gudgeon and chub increased with pH, but perch decreased. Flounder, common goby roach, dace and perch decreased as flow increased.

Stepwise multiple regression analysis showed that transparency was the principal predictor of abundance of three-spined stickleback, gudgeon and perch

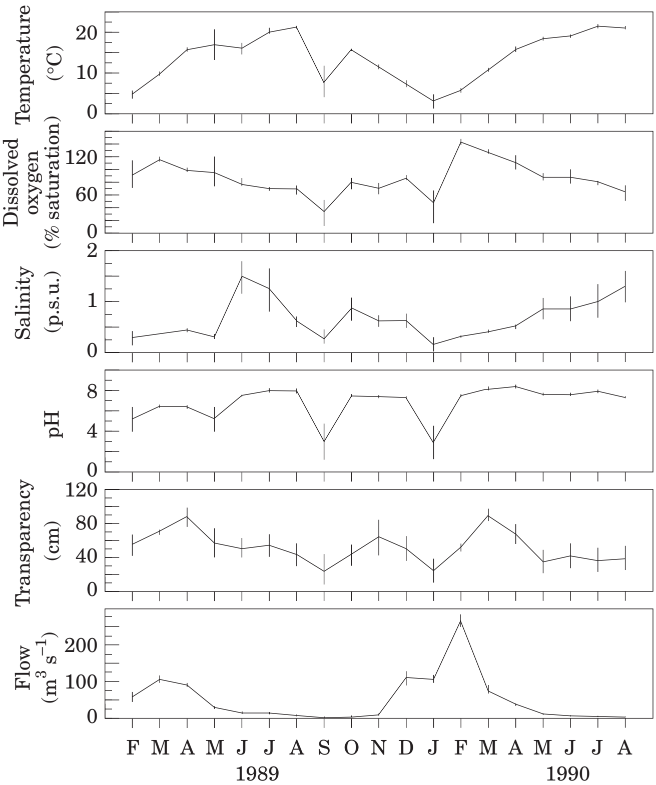


FIG. 7. Monthly means ( ± 1 S.E.) of environmental variables in the upper Thames estuary, from February 1989 to August 1990.

(Table IV). Temperature was the best predictor for abundance of flounder and dace. Low flow was best predictor for high abundance of common goby and roach, and to a lesser extent, for gudgeon. Three-spined stickleback abundance was also predicted by pH and dissolved oxygen, common goby by dissolved oxygen, salinity and temperature, roach by pH and transparency, dace by dissolved oxygen, and perch by temperature.

The canonical correspondence analysis revealed that the most significant environmental variables correlated with fish species were transparency, dissolved oxygen and salinity (Table V). Correlations between species and the four environmental axes were high for the first axis (0·824) and lower for the second (0·636) and third (0·663) axes. Finally, only 31·5% of the total inertia of the species matrix was explained by the six environmental factors included in the analysis. Although four axes were determined within the analysis, only axes 1 and 2 were plotted as they accounted for the 70·8% of the variation explained by the four axes (Fig. 9). More importantly, the two axes represented a total of 69·2% of the environmental influence on the species within the estuary. Axis 1 separated the uppermost sites of the estuary, namely Teddington and Isleworth, on the right side, in opposition to the more downstream sites of Chelsea and

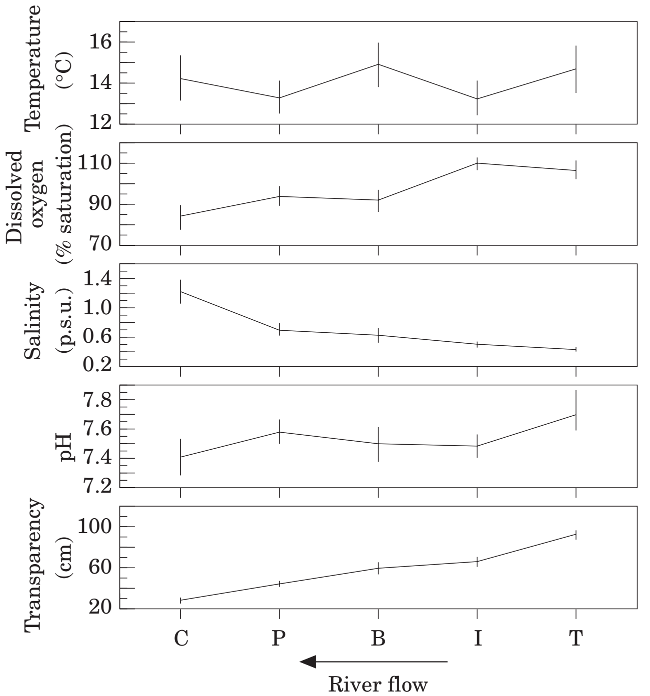


FIG. 8. Means ($\pm$ 1 S.E.) of environmental variables at five sites in the upper Thames estuary, from February 1989 to August 1990. C, Chelsea; P, Putney; B, Barnes; I, Isleworth; T, Teddington.

TABLE III. Spearman rank correlation between fish abundance and environmental variables

| | Temperature | Salinity | Dissolved oxygen | pH | Transparency | Flow |
|---|---|---|---|---|---|---|
| Three-spined stickleback | — | — | — | — | — | — |
| Flounder | 0·37** | 0·20* | − 0·25* | — | — | − 0·26* |
| Common goby | 0·32* | 0·33** | − 0·59** | — | − 0·29** | − 0·60** |
| Roach | 0·38** | — | — | 0·43** | — | − 0·44** |
| Gudgeon | — | − 0·24* | 0·20** | 0·24* | 0·40 | — |
| Dace | 0·42** | — | — | — | — | − 0·23* |
| Chub | — | — | — | 0·19* | — | — |
| Perch | 0·38* | 0·31** | − 0·33** | − 0·41** | − 0·31** | − 0·25* |

Only significant values shown: $*P<0{\cdot}05$; $**P<0{\cdot}01$.

Putney, on the left side (Fig. 9). The major source of patterned variation in the data was a marked shift in fish community structure between the upper and lower parts of the studied area, along axis 1, coincident with changes in water transparency, dissolved oxygen, pH and salinity. Gudgeon, chub and roach were associated with high transparency, dissolved oxygen and pH, and low salinity, while common goby and perch were associated with high salinity, and low transparency. Dace were found preferentially in high dissolved oxygen and low

TABLE IV. Results of the stepwise multiple regression of fish abundance on environmental variables in the upper Thames estuary, from February 1989 to August 1990 ($n$=87)

| Dependent variable | Independent variable | Partial correlation | Coefficient | S.E. | Significance | $r^2$ |
|---|---|---|---|---|---|---|
| Three-spined stickleback | Constant | | 7·82 | 7·86 | 0·0004 | 0·19 |
| | Transparency | 0·32 | 1·13 | 0·30 | 0·0004 | |
| | pH | −0·28 | −5·42 | 2·32 | 0·0221 | |
| | Dissolved $O_2$ | −0·18 | 2·06 | 0·71 | 0·0049 | |
| Flounder | Constant | | −0·81 | 0·36 | 0·0295 | 0·31 |
| | Temperature | 0·15 | 0·92 | 0·30 | 0·0034 | |
| Common goby | Constant | | 7·97 | 1·27 | 0·0000 | 0·69 |
| | Flow | −0·45 | −0·84 | 0·18 | 0·0000 | |
| | Dissolved $O_2$ | −0·34 | −2·26 | 0·59 | 0·0003 | |
| | Salinity | −0·31 | −2·24 | 0·58 | 0·0002 | |
| | Temperature | −0·31 | −1·23 | 0·46 | 0·0095 | |
| Roach | Constant | | −5·07 | 1·57 | 0·0018 | 0·62 |
| | Flow | −0·42 | −0·51 | 0·11 | 0·0000 | |
| | pH | 0·33 | 5·28 | 1·62 | 0·0016 | |
| | Transparency | 0·22 | 0·75 | 0·17 | 0·0000 | |
| Gudgeon | Constant | | −0·43 | 0·21 | 0·0405 | 0·40 |
| | Transparency | 0·29 | 0·48 | 0·13 | 0·0003 | |
| | Flow | −0·24 | −0·20 | 0·07 | 0·0092 | |
| Dace | Constant | | −4·04 | 1·05 | 0·0002 | 0·49 |
| | Temperature | 0·39 | 1·55 | 0·30 | 0·0000 | |
| | Dissolved $O_2$ | 0·18 | 1·29 | 0·42 | 0·0028 | |
| Chub | — | — | — | — | — | — |
| Perch | Constant | | 0·24 | 0·31 | 0·4533 | 0·45 |
| | Transparency | −0·27 | −0·35 | 0·11 | 0·0016 | |
| | Temperature | 0·21 | 0·44 | 0·18 | 0·0172 | |

pH. Flounder was associated with high temperature, but was likely to prefer average values or showed no clear preferences, while three-spined stickleback was associated with high dissolved oxygen and low pH.

## DISCUSSION

The fish fauna of the upper Thames estuary, composed of 23 species, was dominated by freshwater species, with a few estuarine ones and only three marine, estuarine-dependent species, which used the margins and embankments mainly during the spring/summer. Most fish were cyprinid young-of-the-year ($L_F$=10–30 mm) or short-lived species, like the three-spined stickleback or gobies, suggesting that this area was stressful and limited the distribution of most marine species. The middle estuary, on the other hand, was characterized by high seasonal abundances of marine fishes, where 44 species were recorded in 1989 at West Thurrock power station (35·5 km downstream of London Bridge) by Araújo *et al.* (1998). Overall the fish fauna of the Thames estuary is rich with 62 species (Gameson & Wheeler, 1977). Costa & Elliott (1991) reported 43 fish species for the Forth estuary, Scotland, and 45 species for the Tagus estuary,

TABLE V. Summary of the canonical corresondence analysis performed on the abundance of fish species

| | Axes | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| Correlation of environmental variables | | | | |
| Temperature | −0·28 | 0·01 | −0·58 | −0·53 |
| Salinity | −0·48 | 0·08 | −0·12 | 0·65 |
| Dissolved oxygen | 0·59 | 0·56 | −0·15 | 0·06 |
| pH | 0·22 | −0·74 | −0·53 | −0·01 |
| Transparency | 0·86 | 0·11 | 0·20 | −0·22 |
| Flow | 0·34 | 0·26 | 0·42 | 0·26 |
| Summary statistics for ordination axes | | | | |
| Eigenvalues | 0·203 | 0·132 | 0·115 | 0·024 |
| Species–environment correlations | 0·824 | 0·636 | 0·663 | 0·345 |
| Cumulative percentage of variance | | | | |
| of species data | 13·5 | 22·3 | 29·9 | 31·5 |
| of species–environment correlations | 42·0 | 69·2 | 93·0 | 97·9 |
| Sum of all unconstrained eigenvalues | | | | 1·501 |
| Sum of all canonical eigenvalues | | | | 0·483 |

Significant factors were selected by a stepwise procedure analogous to forward elimination in multiple regression analysis.

Portugal. The maximum expected number of fish species in Schelde estuary, Belgium, is close to 60 (Maes *et al.*, 1998). Comparisons between different estuaries are difficult because sampling sites may vary in their distance from the sea, resulting in obvious differences in fish composition and relative abundance. If sampling site is closer to the sea limit, the fauna sampled is more likely to be marine, and the reverse situation if the site is located in the inner in the estuary. In addition, Henderson (1989) found that the species number generally declined in estuaries with declining salinities. The National River Authority (Thames–Biology East) has a cumulative list of 112 fish species in the Thames tideway since 1964; 96 from the middle estuary and 14 upstream of West Thurrock exclusively. From the 23 species listed in this study, nine were exclusive to the upper estuary and the remaining 14 were also found in the middle estuary by Araújo (1992).

Of the marine species, flounder (in great abundance), bass *Dicentrarchus labrax* (L.) and thin-lipped grey mullet *Liza ramada* Risso (occasionally), extended their range distribution to the upper reaches of the estuary. Flounder showed a high occurrence from May to June at all sites, as new recruits migrated in from spawning grounds in the southern North Sea, suggesting the important role of the Thames as a nursery ground for this species. Among estuarine species three-spined stickleback were abundant at all sites, whereas smelt *Osmerus eperlanus* (L.), sandsmelt *Atherina presbyter* Cuvier and black goby *Gobius niger* (L.) were recorded only occasionally and in small numbers. Smelt migrating to spawn in low salinity tidal waters was an important fishery resource before the highest pollution period in the 1950s, with high abundance at Richmond (near Isleworth sampling site) in January–March, and at Greenwich (middle estuary)

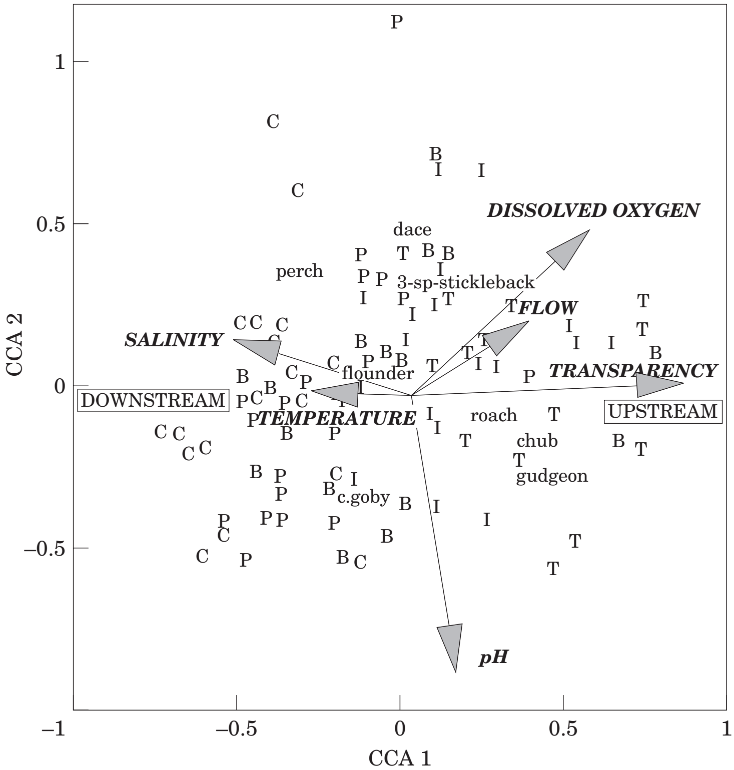


FIG. 9. Canonical correspondence analysis ordination diagram of fish abundance data, with environmental variables. B, Barnes; C, Chelsea; I, Isleworth; P, Putney; T, Teddington. Each arrow represents a factor and determines a direction in the diagram, obtained by extending the arrow in both directions.

in April–May (Wheeler, 1979; Andrews & Rickard, 1980). In other British estuaries smelt is absent or rare (Hardisty & Huggins, 1975; Claridge *et al.*, 1986; Elliott *et al.*, 1990). Recently, Thiel *et al.* (1995) reported increasing populations of smelt in the Elbe estuary, Germany, associated with improved oxygen conditions.

Current levels of dissolved oxygen are not generally a limiting factor for the occurrence of fish in the estuary, as they were in the first half of the century (Wood, 1982). In the upper estuary dissolved oxygen levels are well within acceptable conditions for the species present. The presence of flounders, elvers and smelt in the upper parts of the estuary indicates that the middle reaches are passable for those species. The dissolved oxygen decreased in the mesohaline reaches near the two biggest sewage outfalls, but remained well within the required levels for the passage of fish. Hence, the relatively low number of marine, estuarine-dependent and freshwater species in the upper estuary suggest that this region is physiologically demanding in other respects.

Water quality in the upper estuary varied according to site and influenced fish community composition and abundance. The greatest abundances of cyprinids occurred at the most upstream sites, Teddington and Isleworth, whereas estuarine and marine species like flounder and common goby occurred at the three more downstream sites. Salinity increased downstream, ranging between 0·34 and 2·96 p.s.u. suggesting that these species were close to their tolerance limits in the lower reaches of the upper estuary. Unlike cyprinids, freshwater perch was more abundant at Chelsea but present at all other sites. Spatial separation according to site of the most abundant eight species suggests that the estuary between Barnes and Isleworth is a species transition area between the freshwater but salinity-tolerant dace, roach and gudgeon, and the estuarine eurhyhaline common goby and flounder.

Changes in species composition were correlated with changes in environmental variables between sites and sampling dates, chiefly water transparency, dissolved oxygen and salinity. According to CANOCO, the most important factor was transparency. Transparency in estuaries is closely associated with resuspension of the sediment during tidal excursions leading to an increasing gradient from the more downstream sites to uppermost sites. Turbidity, normally closely inversely correlated with transparency, may provide fish with protection from visual predators or with an increased food supply (Cyrus & Blaber, 1992). In the Humber estuary the fish assemblage was not influenced by turbidity (Marshall & Elliott, 1998). In the Thames, transparencies were higher in the uppermost section at Teddington and were associated with high abundance of freshwater fishes, and with rarity of estuarine and marine-dependent species. Stepwise multiple regression confirmed that transparency is the main environmental variable associated with the abundance of three-spined stickleback, gudgeon and perch, the latter being inversely correlated with transparency.

Wheeler (1969) noted that temperature affected the seasonality and variability of migration, spawning and recruitment patterns within the area. However the number of fish per sample was not directly influenced by temperature, which seemed to affect more the number of species. Thiel *et al.* (1995) found that temperature was the best predictor of the total fish abundance in the Elbe estuary, while salinity influenced the species richness. Marshall & Elliott (1998) also found that salinity (through physiological tolerance) had a greater influence on the species composition within the Humber estuary than did temperature. Likewise, in the present study, the salinity gradient along the upper estuary was more important for fish distribution than temperature (seasonality). This latter factor showed more influence on the number of species. Temperature was the best predictor of abundance for flounder and dace and was positively correlated with abundance of flounder, common goby, roach, dace and perch.

The gradual decrease in number of fish from August to December 1989 coincided with the period of falling temperatures and low flow in the upper estuary. Flow was also the best predictor for abundance of common goby (negative association) and roach (positive). The estuarine common goby could be taking advantage of low flow to extend its upriver penetration, while increasing roach abundance could be associated with juveniles being brought down from the freshwater reaches during high flow. Higher number of species in summer coincided with higher temperatures and salinities and lower transparencies and flow, when some marine–estuarine species reach the upper part of the estuary.

Changes in peak monthly fish abundances differed slightly between summers for some species. Changes in 1989 occurred mainly in June–July compared with May–June in 1990, probably because of the short winter of 1989/1990. Higher abundances of three-spined stickleback, dace and perch in May–July 1989 compared with high occurrences of flounder in the same period for 1990 were not clearly associated with environmental variables. Higher abundances of three-spined stickleback, dace and perch in May–July 1989 coincided with higher temperatures (>18° C), lower transparency (<40 cm), lower pH (<7·7) and a sharply increasing salinity compared with the same period in 1990. Dissolved oxygen fell in both periods but remained above 50% saturation. Numbers of common goby increased from August 1989 and from July 1990, coincident with high temperature and salinity, and low transparency. Andrews (1977) reported that in years of drought, saline intrusion from the mouth of the estuary into the tidal part of the river through London allows marine and estuarine fish to extend their range of upriver penetration. In this study, despite the 1989 drought, it did not occur, with the freshwater dace and perch being even more abundant.

The disappearance of most species during winter could mean a shift with fish size in habitat from the shallow inshore area in the upper estuary to the middle reaches or, less probably, to the deeper middle channel of the river. Sampling at low water with the large seine net occurred in deeper offshore water and large fishes were not common. Potter *et al.* (1983) compared catches from an otter trawl and beach seine in a western Australian estuary. They found a tendency for smaller and larger bottom-dwelling species to inhabit regions nearer and further away from the banks respectively. Well-established cyprinid populations were found in an artificial 4·5-ha tidal lagoon connected to the river about 1 km downstream from Teddington Weir (Araújo, 1992), which reflects the residency of most freshwater species in the more stable conditions in the upper estuary.

High fish and species abundances occurred in May–October, when temperature was high and flow was low. Transparency, dissolved oxygen, salinity and pH showed a defined spatial gradient along the upper estuary, which was associated with fish distribution. Fish species associated with the more upstream sites were the cyprinids roach, gudgeon, chub and dace, and the estuarine three-spined stickleback. At the more downstream sites were the estuarine common goby, the estuarine-dependent flounder, and the freshwater perch.

The present study has suggested environmental explanations for the fish distribution patterns, but information is required on interactions between the biological variables both inter- and intraspecific to explain fully the biological characteristics of the assemblage.

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