Printed in Great Britain

SEASONAL CHANGES IN MOVEMENTS, ABUNDANCE, SIZE COMPOSITION AND DIVERSITY OF THE FISH FAUNA OF THE SEVERN ESTUARY

P. N. CLARIDGE*, I. C. POTTER[†] AND M. W. HARDISTY[‡]

* N.E.R.C. Institute for Marine Environmental Research, Prospect Place, The Hoe, Plymouth PL1 3DH
 † School of Environmental and Life Sciences, Murdoch University, Murdoch, Western Australia 6150
 ‡ School of Biological Sciences, University of Bath, Claverton Down, Bath BA2 7AY

(Figs. 1-7)

Extensive sampling of the intake screens of power stations in the Severn Estuary (Berkeley, Oldbury-upon-Severn and Uskmouth) and Bristol Channel (Hinkley Point) vielded a total of 97 species of lampreys, elasmobranchs and teleosts. Data were most comprehensive for Oldbury in the inner estuary where samples of all the fish collected over 24 h were obtained on four occasions in each month between July 1972 and June 1977. The Gadidae was the most abundant family at Oldbury, both in terms of numbers of individuals (51934) and species (13). The fifteen most abundant species at Oldbury included two anadromous (river lamprey (Lampetra fluviatilis), twaite shad (Alosa fallax)), one catadromous (European eel (Anguilla anguilla)), one estuarine (common goby (Pomatoschistus microps)) and one freshwater species (3-spined stickleback (Gasterosteus aculeatus)). The remaining ten species, which fall within the broad category of estuarine-dependent marine species, contained a large proportion of o + individuals. This group comprised a species complex consisting of two morphologically very similar sand gobies (Pomatoschistus minutus and Pomatoschistus lozanoi), which were only separated during one year of the study, and the whiting (Merlangius merlangus), flounder (Platichthys flesus), bass (Dicentrarchus labrax), sea snail (Liparis liparis), poor cod (Trisopterus minutus), thin-lipped grey mullet (Liza ramada), herring (Clupea harengus), sprat (Sprattus sprattus) and bib (Trisopterus luscus). Juveniles of the last nine species took on average between 11-15 and 38-42 weeks to enter the shallows in the middle of the inner estuary from their spawning grounds, often having previously passed further up the estuary as postlarvae. These species showed a markedly seasonal pattern of occurrence at Oldbury, with the majority of each usually being collected within distinct two month periods. The number of species, and to an even greater extent the total number of fish, underwent consistent seasonal trends, with maximum and minimum values for the latter occurring between September and January and between March and May respectively. The seasonal trends for species richness (D), Shannon-Wiener (H') and Evenness indices (\mathcal{J}) were similar, with maximum and minimum values generally occurring in the winter and summer respectively. A comparison between our data and those of earlier workers indicates that no major change has occurred in the composition of the fish fauna of the Severn Estuary during this century, except for the establishment of two 'northern' species, northern rockling (Ciliata septentrionalis) and Norway pout (Trisopterus esmarkii), during recent times.

INTRODUCTION

Estuaries perform a crucial role in the life-cycle of many fish (Cronin & Mansueti, 1971; Day, Blaber & Wallace, 1981; Dando, 1984). They provide a migratory route for anadromous and catadromous species and an environment in which the limited number of true estuarine teleosts spend the whole of their life cycle. The upper reaches are colonized by certain freshwater species while

the lower regions are penetrated by some marine fish during high tide. However, many marine teleosts enter and remain within estuaries for a period of time, often in very large numbers and particularly during the early part of life (see e.g. Gunter, 1938, 1961, 1967; Huddart & Arthur, 1971; van den Broek, 1980; Blaber & Blaber, 1980; Potter *et al.* 1983; Whitfield, 1983). The recognition that estuaries act as important nursery areas for certain teleosts by providing such features as a rich food source and protection from predation (see e.g. Pearcy & Richards, 1962; Jacquaz, Able & Leggett, 1977; Blaber & Blaber, 1980) has led to such species being referred to as estuarine-dependent (see e.g. McHugh, 1976; Beal, 1980; Fortier & Leggett, 1982). Work by McHugh (1976) in the United States and by Pollard (1976) in New South Wales, Australia, has demonstrated that approximately 70% by weight of the fisheries of these regions was based on estuarine-dependent species.

The ecological importance of the River Severn can be gauged by the fact that it has the largest drainage basin (11425 km²) of any British river system (Price, 1964). Although the Severn Estuary, and the Bristol Channel into which it opens, once contained significant commercial fisheries, their importance receded with the development of deeper water fisheries (Matthews, 1933; Lloyd, 1942). Moreover, it has been suggested that the sport fisheries of the region have also declined in recent decades through the influence of natural fluctuations, overfishing and pollution (Clark, 1971). Certainly, the shores of the Severn Estuary and Bristol Channel have become increasingly important for industrial development, and attention has been drawn to the amount of contaminants, particularly heavy metals, which are present in the environment and being accumulated by the biota (Abdullah, Royale & Morris, 1972; Butterworth, Lester & Nickless, 1972; Hardisty, Kartar & Sainsbury, 1974; Hardisty et al. 1974; Chester & Stoner, 1975; Badsha & Sainsbury, 1978a, b; Noël-Lambot et al. 1980). More recently, however, Mettam (1979) concluded that there had been no major change in the invertebrate fauna over the previous thirty years. Yet, very considerable changes would undoubtedly occur in both the invertebrate and vertebrate fauna if a proposed tidal barrage was constructed across the estuary (Department of Energy, 1981; Baker, 1984).

The use of conventional fish sampling techniques in the Severn Estuary is made difficult by the presence of extensive areas of mud and an extreme tidal range and action (Hamilton, 1980). However, analysis of data for large numbers of fish collected from the cooling water intake screens of power stations in this region, has yielded much useful information on annual variations in abundance, seasonal movements, growth, age composition and reproductive status of several species of lamprey and teleost (Hardisty & Huggins, 1973, 1975; Claridge & Gardner, 1977, 1978; Badsha & Sainsbury, 1978*a*, *b*; Gardner, 1978; Titmus, Claridge & Potter, 1978; Abou-Seedo & Potter, 1979; Claridge & Potter, 1983, 1984, 1985; Potter & Claridge, 1985; Claridge *et al.* 1985).

The present paper provides a quantitative check list of the species of fish taken over five years from four power stations in the Severn Estuary and inner Bristol

230

Channel, together with data on their size and the way in which they use the estuary. The check list is compared with that prepared over 45 years ago by Lloyd (1941) from his own data and those of earlier authors such as Day (1879) and Matthews (1933), to ascertain whether there is any evidence that the composition of the fish fauna has changed during this century. The times of year when the more abundant species typically reach peak abundance at Oldbury-upon-Severn in the inner estuary have been determined and an estimate made of the time taken for the new 0 + recruits of the more numerous marine species to appear in the shallows of this region. Data on seasonal and annual changes in total fish numbers, individual species and various diversity indices are also given for the fish community at Oldbury.

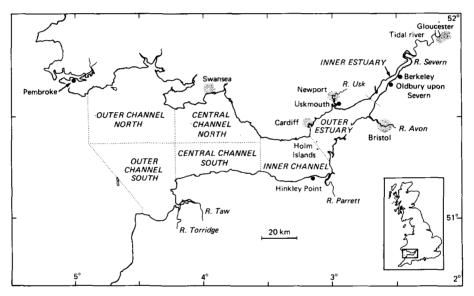


Fig. 1. Map showing the location of the power stations in the Severn Estuary (Berkeley, Oldburyupon-Severn and Uskmouth), inner Bristol Channel (Hinkley Point) and Milford Haven (Pembroke) used for the collection of fish samples.

MATERIALS AND METHODS

Sampling regime

Fish were collected from the cooling water intake screens of the Berkeley, Oldbury-upon-Severn, Uskmouth and Hinkley Point power stations (Fig. 1). These screens were of the rotating drum or band design with a mesh size of approximately 13×19 mm (for further information on power station operation and its effects on the ecology of natural ecosystems see Langford, 1983). The water at Berkeley is taken from the main deep water channel of the inner Severn Estuary, whereas at Oldbury, a further 7 km downstream, it is drawn from shallow inshore areas. The power station at Uskmouth is located on the River Usk at a point 1 km from the confluence of this river with the outer Severn Estuary, while the Hinkley Point power station lies on the southern shore of the inner Bristol Channel. (N.B. The terms inner and outer Severn Estuary and inner, central and outer Bristol Channel used in this paper and shown in Fig. 1 follow those given by Radford & Joint (1980).)

Sampling commenced in July 1972 at Oldbury, September 1974 at Berkeley and October 1975

at both Uskmouth and Hinkley Point, and in all cases was terminated in June 1977. Samples were taken from Oldbury on the same day of four different weeks of each month of the year, thus giving 48 samples per year. Sampling was also carried out weekly at Berkeley but monthly at Uskmouth and Hinkley Point. While each of the samples at the last three stations comprised material collected over variable periods of time, those at Oldbury contained all the fish entrained over 24 h. The numbers of fish at Oldbury were adjusted where necessary to correspond to an intake of $2 \cdot 2 \times 10^9$ l, the volume of water that passed through the screens daily when the station was under full load. This was the typical daily intake between the autumn and spring when the numbers of fish in the inner estuary reached a maximum.

In addition to the samples from the Estuary and Channel, five collections were taken between September 1976 and February 1977 from Pembroke power station in Milford Haven on the south-west tip of Wales (Fig. 1).

The standard length of all fish was recorded to the nearest 1 mm, except for those species whose numbers were very large in any sample, in which case the measurements were made on a subsample of at least 250.

Relative abundance and life-cycle categories

The data in Table 1 designating species as rare, regularly caught or common are based on whether the average annual catch was < 10, 10-99 or > 100 for Oldbury and Berkeley and < 5, 5-49 or > 50for Uskmouth and Hinkley Point. Most of the species fell clearly into one of the following life-cycle categories: anadromous (A), i.e. migrating from the sea into fresh water to breed; catadromous (C), i.e. migrating from fresh water to the sea to breed; estuarine (E), i.e. typically occurring and breeding in estuaries; freshwater (F), i.e. typically occurring and breeding in fresh water; marine, i.e. typically breeding in marine environments outside estuaries. The marine category was separated into three groups: species found at Hinkley Point but not in the estuary (M); species regarded as marine stragglers, occurring infrequently in the Severn Estuary and known typically not to enter estuaries in large numbers in other parts of the British Isles (MS); species found in large numbers in the Severn and/or other British estuaries and hence classified as marine estuarine-dependent (MED).

Nomenclature of Pomatoschistus and Atherina species

The catches of sand gobies at Oldbury in the Severn Estuary and Bristol Channel contained two morphologically very similar species (*P. minutus* and *P. lozanoi*) whose taxonomic validity had until recently been unclear (Webb, 1980). During the course of his taxonomic studies, C. J. Webb kindly helped us separate these two species and this enabled us to gather data on some aspects of the biology of both *P. minutus* and *P. lozanoi* (Claridge *et al.* 1985). Since such separation was restricted in duration and to samples only from Oldbury, the data in Tables 1–3 and Fig. 5 refer to the *P. minutus/P. lozanoi* complex.

Although Hardisty & Huggins (1975) recorded Atherina presbyter from Oldbury, subsequent work by Palmer, Culley & Claridge (1979) indicated that the atherinids at this locality represented an isolated and very northern population of Atherina boyeri. Yet Palmer et al. (1979) did identify the atherinids from Pembroke outside the northern boundary of the Bristol Channel as Atherina presbyter. The recent work of Bamber & Henderson (1985) has provided strong evidence, however, that A. boyeri and A. presbyter are not distinct species and that only Atherina boyeri should be recognised.

Species ranking, numbers and diversity

Values in Table 3 for relative abundance (see Warfel & Merriman, 1944) were obtained by taking the ten most abundant species in each month and awarding sequential points from 10 for the most numerous to one for the least numerous. Species were then ranked according to their total number of points in each year. Since the small number of sprat, twaite shad and herring collected in the first year of the study were not separated, estimates of their relative abundance in this year have been calculated using the proportions obtained in the last four years.

The monthly number of each species at Oldbury between 1972 and 1977 has been expressed as a percentage of the total for that species in each 12 month-period (1 July to 30 June). These percentages were transformed using angular transformation (Zar, 1974) and monthly means and 95% confidence limits calculated. The values for sprat in Fig. 2 and twaite shad in Fig. 5 are based

on data collected in the last four years. Since herring was only abundant in 1973/4 and 1975/6, the data for this species in Fig. 2 relate only to those years.

The Shannon-Wiener (H') and Evenness (\mathcal{J}) indices were calculated according to Pielou (1966) and the species richness index (D) determined using the formula employed by Margalef (1968).

Time of spawning and appearance of larvae and 0 + recruits

The spawning times in Fig. 4 are taken largely from the data compiled by Russell (1976) for studies in south-western British waters. Since sprat eggs were obtained in the Bristol Channel during April 1974 (Williams, 1984), the spawning period for this species has been extended to include this month. Since no data on breeding time are given for bib in Russell (1976), the spawning period for this species is taken from Wheeler (1978). While Russell (1976) does provide a spawning period for the sea snail, this immediately precedes the period when gonadosomatic indices were increasing rapidly in this species in the Severn Estuary (Badsha & Sainsbury, 1978b). As a result, this latter period is used in this study (Fig. 4).

The times when larval and postlarval stages of flounder, sprat, bass, poor cod, bib, whiting and sea snail were present and reached peak abundance in the Bristol Channel (Fig. 4), come from an analysis of plankton hauls carried out at regular intervals between the beginning of April and mid-September of 1974 (Russell, 1980). Since poor cod were already present in large numbers at the beginning of this sampling period, the time when their larvae and postlarvae were first found in other years was taken from Russell (1976). Larvae and postlarvae of herring and thin-lipped grey mullet were not obtained in the Bristol Channel during 1974 (Russell, 1980), a year in which few 0+ recruits of these species were taken in the estuary or channel (Titmus *et al.* 1978; Claridge & Potter, 1985). The time when yolk sac herring were taken by J. Riley (personal communication) in the Bristol Channel in April 1975 is included in Fig. 4.

The period when the 0+ recruits reached maximum abundance (see Fig. 4) was obtained from an examination of the weekly catches at Oldbury in 1974, except in the case of herring and thin-lipped grey mullet. The comparable peak abundance times for these two species were deduced from our data for 1975 and 1976 respectively when they were obtained in large numbers. The first vertical bar on the juvenile recruitment data in Fig. 4 refers to the time when 0+ fish first appeared, while the second bar denotes the time after which catches of this age class were small, i.e. rarely exceeded 10 in a single weekly sample. The arrow on the flounder data denotes sizeable catches of 0+ fish throughout the year.

RESULTS

Physico-chemical environment

Freshwater discharge rates at Gloucester in the River Severn and salinities and temperatures at Oldbury-upon-Severn, which is located a further 55 km downstream in the inner Severn Estuary (Fig. 1), have already been described for the period covered by this study (Claridge & Potter, 1984). The current account is therefore restricted to outlining the main trends. Freshwater discharge in the River Severn, which showed a close inverse correlation with the salinity at Oldbury (r = -0.954), always reached a peak between December and February. However, discharge volume showed considerable annual variation, with maximum mean monthly values ranging from a low of 94 m³ s⁻¹ in the winter of 1974/5 to a high of 420 m³ s⁻¹ in the winter of 1976/7. Salinities at Oldbury reached a maximum in either August or September and a minimum between December and February. Again, annual values varied greatly among years, with maximum monthly means ranging from 22‰ in 1973/4 to 29‰ in 1976/7, and minimum monthly means being as low as 6‰ in the wet winter of 1976/7 and as high as 18‰ in the dry winter of 1975/6.

Maximum and minimum temperatures at Oldbury occurred in July or August

and between December and March respectively. During the first three winters of this study, the mean monthly temperatures dropped to only 6 °C compared with values of approximately 4 °C in February 1976 and January 1977. Temperatures during the summers of 1975 and 1976 were higher than in previous years, reaching a maximum monthly mean of 21 °C compared with 18–19 °C in 1972, 1973 and 1974.

In general, salinities and temperatures at Berkeley were similar to those at Oldbury, except during periods of heavy freshwater discharge when the salinity declined to a lower level. The salinity at Uskmouth, which was influenced by the state of the tide and by very heavy freshwater discharge, fluctuated between 30% and freshwater levels. Compared with the estuary, the salinity at Hinkley Point was much more stable, with values rarely dropping below 30%, and the temperature did not show quite such an extreme range.

Numbers of species

A total of 97 species, representing one family of lamprey, four families of elasmobranch and 32 families of teleost, together with two cyprinid hybrids, was collected from Berkeley, Oldbury and Uskmouth in the Severn Estuary and from Hinkley Point in the Bristol Channel (Table 1). This value is only one less than the cumulative number of fish species recorded over a considerable distance in the Thames Estuary between 1964 and 1980 (Andrews, 1984).

The numbers of species at Berkeley (73) and Oldbury (78) were similar and collectively produced a total of 88 species representing 31 families (Table 1). All of the 35 species (18 families) at Uskmouth were collected at some stage from Oldbury and almost invariably also from Berkeley (Table 1). While the lower total number of species at Uskmouth can be attributed to a poorer freshwater fauna and to less frequent sampling than in the inner estuary, the same frequency of sampling at Hinkley Point yielded nearly twice as many species as at Uskmouth (66 vs. 35) (Table 1). The fish community at Hinkley, comprising 35 families, was almost entirely composed of marine species, amongst which were four elasmobranchs (nurse hound, tope, spur-dog and spotted ray) and four teleosts (pearl-side, argentine, straight-nosed pipefish and tompot blenny) which did not appear in any of the samples from the estuary. The limited number of samples from Pembroke (5) outside the Bristol Channel, yielded 37 species representing 21 families (Table 1). Apart from the bull-rout, sea scorpion and golden grey mullet, all of these species were also taken in the estuary and channel.

Life-cycle categories

The marine teleosts caught in large numbers in the inner estuary fall within the broad category of estuarine-dependent (Tables 1–3). Particularly conspicuous in this group were whiting, flounder, bass, sea snail, poor cod, thin-lipped grey mullet, herring, sprat and bib. Many of the other marine teleosts caught in the estuary were generally present only in small numbers. While their paucity may sometimes have reflected small spawning populations, most can be classified as marine stragglers which have a strong preference for marine environments at all stages in their life-cycle. Examples of this group were hake, ling, horse mackerel, ballan wrasse, rock cook, lesser weever, streaked gurnard and witch. The three species of elasmobranch collected from the inner estuary (lesser spotted dogfish, undulate ray and thornback ray), which were all taken when salinities exceeded 20%, can also be regarded as marine stragglers.

Although sea snails with large gonads were found in the inner estuary, there is good evidence to suggest that they breed outside the estuary. For example, this species was only abundant at Oldbury and Berkeley for a short period (Fig. 2) and the number of relatively mature fish was small. Moreover, larvae and postlarvae of *Liparis* sp. were taken in the Bristol Channel in 1974 (Russell, 1980). Since the common sea snail was the only liparid caught in the estuary or channel during our study, it seems likely that this was the species collected by Russell. These considerations seem to justify the designation of the sea snail as an estuarine-dependent marine species.

The checklist for the inner estuary, together with the data in Tables 2 and 3, also emphasises the role the estuary plays as a migratory route for several species. Thus, the river lamprey and twaite shad were obtained both during their downstream passage to the sea and on their migration towards freshwater spawning areas (see also Hardisty & Huggins, 1973; Potter & Huggins, 1973; Abou-Seedo & Potter, 1979; Claridge & Gardner, 1978). Less frequently caught anadromous species were the sea lamprey, allis shad, sea trout and Atlantic salmon, although smolts of the last of these were occasionally collected in considerable numbers in the autumn, spring and early summer. The catadromous eel was present throughout the year.

The high incidence of the common goby in the inner estuary, particularly in the shallows at Oldbury, and the low numbers collected from Hinkley Point, suggest that this species may breed in the Severn Estuary (see also Claridge et al. 1985). This view would be consistent with the observation that it breeds in the estuaries of the Lynher in Cornwall and the Exe in Devon (J. M. Gee, personal communication), as well as in other British estuaries (P. J. Miller, 1963; personal communication). However, since the common goby sometimes breeds in protected marine environments such as Morecambe Bay, where the salinity approaches that of full strength sea water (Jones & Miller, 1966), it may also spawn in the Bristol Channel. Although members of the Pomatoschistus minutus complex comprising P. minutus and P. lozanoi were found with large gonads at Oldbury and Berkeley (Claridge et al. 1985), considerable numbers were also obtained in samples from Hinkley Point and both species are common in other regions of the Bristol Channel (Wallis & Beardmore, 1984). Moreover, extensive plankton hauls in the Bristol Channel in 1974 produced many gobiid larvae and postlarvae (Russell, 1980), which belonged to either P. minutus or P. lozanoi (J. M. Gee, personal communication), and eggs of one of these species were collected in Plymouth Sound by Lebour (1920). Furthermore, P. minutus frequently spawns in high salinities and in marine environments (Fonds, 1973; Hesthagen, 1975;

236

found in collections from the Severn Estuary and Bristol Channel. Life-cycle categories are as follows (see also Materials and Methods), A, anadromous; * Not recorded by Lloyd (1941); +, rare; + +, regularly caught; + + +, common, \checkmark , also present at Pembroke power station, †, includes two species of the family Cottidae (Taurulus bubalis, bull rout; Myxocephalus scorpius, sea scorpion) and one of the family Mugilidae (Liza aurata, golden muller) not C, catadromous; E, estuarine; F, freshwater; M, marine and not entering estuary; MS, marine with stragglers in estuary; MED, marine estuarine-dependent species. Species totals assume both members of Pomatoschistus minutus complex present.

| Life-cycle category | Α | A | M | SW | W | W | MS | W | MS | SW | A | A | MS | MED | MED | W | A | A | W | ц | ц | ц | ц | ц | ц | н | н | ц |
|--------------------------------|--|---------------|-------------|------------------------|----------|----------|-----------------------------|---------------------------|---------------|---------------------------------|------------------------|--------------------------|----------|-------------|-------------|------------|--------|--------------------------|-----------|--------|----------------------|--------------------------------|-----------------------------------|----------|--------------------------------|--------|--------------|----------|
| Life-cycl Pembroke category | | | > | > | | | | | > | • | | | | > | > | | | > | | • | | • | • | | • | | • | • |
| Hinkley Point | + | + | + | + + | + | + | + | + | + | + | | + + + | + | + + | + + | + | • | + | + | | | | | | | • | • | + |
| Oldbury Uskmouth | • | + + | | | | | | | | | | + + | | + + | + + | | + | + | | + | | • | | | • | | • | • |
| Oldbury | + | + + + | | + | • | | | | • | + | | + + + | ÷ | + + + | + + + | • | + + | Ŧ | • | + | + | | + | + | + | | + | Ŧ |
| Berkeley | + | + + | • | + | | | + | | + | + | ÷ | + + + | + | + + + | ++++ | | + + | + | | + | | + | + | | + | + | + | |
| Standard length (mm) | 560-915 | 83-405 | 211, 229 | 118-502 | 328, 336 | 244 | 144-295 | 164 | 137-326 | 116-161 | 300, 400 | 24-357 | 64-219 | 25-140 | 25-118 | 35-52 | 83-164 | 42-400 | 179 | 48-115 | 102 | 64 | 31-73 | % | 90-294 | 67-122 | 46-352 | 57-110 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Common name | Sea lamprey | River lamprey | Nurse hound | Lesser-spotted dogfish | Tope | Spur-dog | Undulate ray | Spotted ray | Thornback ray | Anchovy | Allis shad | Twaite shad | Pilchard | Sprat | Herring | Pearl-side | Salmon | Brown trout | Argentine | Carp | Gudgeon | Tench | Crucian carp | Goldfish | Silver bream | Bleak | Bronze bream | Rudd |
| Species Common name | Petromyzontidae Petromyzon marinus Sca lamprey | | | Π | | | *Raja undulata Undulate ray | Raja montagui Spotted ray | | Engraulis encrasicholus Anchovy | Alosa alosa Allis shad | Alosa fallax Twaite shad | 57 | | | lleri | | Salmo trutta Brown trout | hyraena | rpio | *Gobio gobio Gudgeon | *Tinca tinca Contraction Tench | *Carassius carassius Crucian carp | • | *Abramis bjoerkna Silver bream | | | hthalmus |

| ццццц | ر WS | SW | MED | W | MS | MED | MED | WS | MED | MED | SW | MS | MS | MS | MED | MED | X | MED | Ľ, | WS | WS | MS | MS | MS | MS | MS | MS | MS | MS | MS | MS | MS H | IJ |
|---|-----------------------|----------------|---|-------------------------|--------------|-------------|-------------|-------------|------------------------------|------------------|---------|--------|--------------|--|-------------------|--------------------|-----------|-------------|--------------------------|----------------|------------|----------|-----------|---------------|-----------|-----------------|----------|---------------|----------|--------------|------------------|----------------|---------------|
| | > · | > . | > > | , . | | > | > | > | >` | > · | | | | | | > | | > | | | > | > | | > | | | > | | | | | . ` | > |
| | + + + + + + | + | + + | ⊦ + | + | + + + | + + + | + + | + . + . + | + + ⊣ | ⊦ + | | | + + | + + | + + + | + | + + + | | | + | | | + | | | + | + | + | + | + | | + |
| + · + · · · | + + + + | + | | | | + + + | + | + | + . + | + + | + · | | | | + + | + + | | ++++ | | | | | • | | | | + | | | | | | + + |
| + + + + · · | + + + + | + - | + + | + · | + | + + + | +++++ | + + | + . + . + | + + + | ⊦ → | - + | + | ÷ | + + | + + | • | + + + | + + | + | + + | ÷ | | + | ÷ | | + | | + | + + | + | + - - | + + + |
| + + + + + + | + + + + | + | | | + | + + + | + + | + + | + . + . + . | + - | + + | - + | + | + | + + | + + | | ++++ | + + | + | + | + | + | | + | Ŧ | + | + | + | | | • • | + + |
| 35-286 83, 320 58-230 60-243 87, 207 | 65->1000 294->1000 | 280-493 | 82-101 247 260 | 172 | 171-224 | 38321 | 33-122 | 30-212 | 31-222 | 401-10 56-561 | 74-276 | 92-192 | 87-192 | 160-424 | 47-122 | 54-270 | 80-169 | 26-480 | 41-241 | 55-300 | 42-162 | 30-120 | 83-111 | 38-165 | 55-95 | 167 | 47-141 | 57, 80 | 165-276 | 17-50 | 38-48 | 32-48 | 20-53 |
| ıybrid ybrid | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Roach Chub Dace Roach × bronze bream hybrid Bronze × silver bream hybrid | Eel Conger eel | Great pipefish | Nilsson's pipensn Snake ninefish | Straight-nosed pipefish | Blue whiting | Whiting | Bib | Norway pout | Poor cod | r ullack Cod | Hake | Ling | Tadpole fish | 3-bearded rockling | Northern rockling | 5-bearded rockling | John Dory | Bass | Perch | Horse mackerel | Red mullet | Corkwing | Goldsinny | Ballan wrasse | Rock cook | Smooth sand eel | Sand eel | Lesser weever | Mackerel | Crystal goby | Transparent goby | Jeffreys' goby | COMMUNIT GOOD |
| *Rutilus rutilus *Leuciscus cephalus *Leuciscus leuciscus *R. rutilus × A. brama *A. brama × A. bjoerkna Bronze × silver bream h | | - , | * Syngnainus rosteitatus Nilsson s pipensn Entelurus genuseus Snake ninefish | | utassou | - | | , | Trisopterus minutus Poor cod | | luccius | | . SPU | Gaidropsarus vulgaris 3-bearded rockling | | stela | | | *Perca fluviatilis Perch | | - | | 5 | | | nisquamatus | 51 | , . | | us linearis | - | 1 | |

FISH OF THE SEVERN ESTUARY

237

| Life-cycle oke category | | MED | MED | щ | SW | SW | WS | W | MS | MED | E+M | MS | SM | SW | MS | MS | SM | MED | F + E? | ц | SW | WS | WS | SW | MS | MS | MED | MS | MS | MED | WS | | |
|----------------------------|--|-------|-------------------------|-------------------------|-----------|----------------------|---------------------------|---------------|--------------------------|-------------------------|----------------------------|-------------------------------|--|-------------|-----------------------------|----------------|-------------------------------|-------------|---|-----------------------|-----------------------|--------|----------------------------|---------|-----------|---------------------|-----------------------------|------------------------------|----------------------------------|------------------|---------------------------------|-----------------------|----------------------|
| Pembroke | ` | • | • | • | > | • | > | | > | > | > | > | | | > | > | • | | • | • | > | • | • | • | | > | > | > | • | > | • | 21† | 37+ |
| Hinkley Point | + + + | • | | | • | | + | + | + | + + + | + | + | | | + | + + | + + | + + + | + | • | + | + | + | | | + + | + + + | + | | + + + | + | 35 | 66 |
| Uskmouth | + + + | - | | | | | | | • | + + | + + | • | • | | • | | | + + | + + | + | • | | + | | | + | + + + | + | | + + | | 18 | 35 |
| Oldbury | + + + | | • | + | + | | + | | + | + + + | + + | + | ÷ | + | + | + | + | + + + | + + + | + | + | Ŧ | + | + | + | + | + + + | + + | | + + | + | 29 | 78 |
| Berkeley | + + + | • | | + | + | + | + | | + | + + + | + | + | | + | + | + | + | + + + | + + | + | • | • | + | + | | + | + + + | | + | + + | | 30 | 73 |
| Standard length (mm) | | 29-73 | 19-61 | 104 | 37-75 | 6 6 | 36-168 | 104, 105 | 61–197 | 20-455 | 44-151 | 57-168 | 235 | 173, 181 | 70-180 | 39-114 | 30–380 | 40105 | 21-75 | 31-34 | 92-133 | 34-76 | 51-180 | 74-174 | 68 | 38-209 | 20-355 | 28-160 | 209 | 23-400 | 154-205 | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Common name | Sand goby | | | Black goby | Rock goby | Reticulated dragonet | Dragonet | Tompot blenny | Thick-lipped grey mullet | Thin-lipped grey mullet | Sand smelt | Grey gurnard | Streaked gurnard | Red gurnard | Tub gurnard | Armed bullhead | Lumpsucker | Sea snail | 3-spined stickleback | 10-spined stickleback | 15-spined stickleback | Turbot | Brill | Topknot | Scaldfish | Dab | Flounder | Plaice | Witch | Sole | Angler fish | | |
| Species Common name | Pomatoschistus minutus complex Sand goby | | *Pomatoschistus lozanoi | Gobius niger Black goby | iellus] | ulatus [| Callionymus lyra Dragonet | ine T | F | | Atherina boyeri Sand smelt | Eutrigla gumardus Grey gumard | Trigloporus lastoviza Streaked gurnard | ST | *Trigla lucerna Tub gurnard | ictus 1 | Cyclopterus lumpus Lumpsucker | | Gasterosteus aculeatus 3-spined stickleback | - | | - | Scophthalmus rhombus Brill | | • • | Limanda limanda Dab | Platichthys flesus Flounder | Pleuronectes platessa Plaice | Glyptocephalus cynoglossus Witch | Solea solea Sole | Lophius piscatorius Angler fish | Number of families 37 | Number of species of |

Table 1. (Cont.)

238

Lee, 1975) and has never been found breeding in estuaries during the extensive studies of British gobies by P. J. Miller (personal communication). Provisionally, therefore, the common goby is regarded as typically estuarine and at least *P. minutus* of the *P. minutus*/*P. lozanoi* complex as marine estuarine-dependent in the Severn Estuary region.

Since Atherina boyeri appears well adapted to the conditions at Oldbury (Palmer et al. 1979), and 'ripe oocytes' were found in some individuals from this region (Palmer & Culley, 1983), it seems likely that this species is estuarine. However, as A. boyeri was present in marine conditions at Pembroke outside the Bristol Channel, this atherinid might also be represented by marine populations in the south-western region of the United Kingdom.

Freshwater species, such as the perch and the members of the Cyprinidae, were widely represented at both Oldbury and Berkeley but usually not in large numbers. In contrast to the 10-spined stickleback, which was extremely rare at these two localities, the 3-spined stickleback was found in appreciable numbers in the inner estuary in most years. Moreover, since the latter was sometimes in breeding coloration, it may occasionally spawn in the upper reaches of the estuary. In this context, it is worth noting that Jones & John (1978) concluded from the condition of a fish collected from the North Atlantic and from the presence of shoals of small 3-spined stickleback in coastal waters, that *Gasterosteus aculeatus* can breed in full-strength sea water. However, while the 3-spined stickleback occurs in marine environments in northern British waters, it appears to be an essentially freshwater species in the more southern part of its range (Wheeler, 1978). The majority of the catches of 3-spined stickleback, and of freshwater teleosts in general, were obtained during those winter periods when the salinity was below 15%.

It must be recognized that it has been necessary to draw on other data such as those contained in Wheeler (1978) to provide a life-cycle category for some species whose numbers were low in the estuary and channel. Thus, for example, Nillson's pipefish is termed marine estuarine-dependent because it enters other estuaries in large numbers and the snake pipefish is referred to as a marine straggler because it is typically found in deep marine waters.

Numbers and ranking of most abundant families and species at Oldbury

The Gadidae was the most numerous of the 29 families collected from Oldbury over the study period, both with respect to numbers of individuals (51934) and species (13) (Table 1). While the Cyprinidae ranked second in terms of species (10), its total numbers (127) were far less than those of the Gobiidae (43855) which ranked second in total abundance but contained a smaller number of species (7). The numbers of the Pleuronectidae represented by three species (14590) and the Clupeidae with five species (8565) ranked these families third and sixth in total abundance respectively, while the Percichthyidae and Liparidae, which were each represented by only a single species, ranked fourth and fifth in terms of total numbers (10779 and 9900 respectively). During the period of the study, the top ten and fifteen species (treating the *P. minutus* complex as a single species) amounted to 138047 and 143727 individuals respectively, values which are equivalent to 94.0 and 97.9% of the total fish catch from Oldbury (Table 2). The numbers of gobies of the *P. minutus* complex (42859) and whiting (41471) made a far greater contribution (29.2 and 28.2%) to the catch than any other species. Since the above numbers are based on a 24-hour and once-weekly sampling regime four times a month, they need to be multiplied by a factor of just over seven to provide an estimate of the total numbers that would have been collected on the screens if the Oldbury power station had been working at full load for the whole five-year period.

In each of the five years of this study, the ten most abundant species at Oldbury contributed between $91 \cdot 0$ and $96 \cdot 9\%$ to the total catch (Table 2). The *P. minutus* complex was always one of the two most numerous taxa and the whiting, flounder, sea snail and eel always ranked amongst the top ten species. Although the bass ranked lower than tenth in both 1973/4 and 1974/5, it was the third most abundant teleost in 1976/7.

The numbers of each species showed considerable annual variation (Table 2). For example, whiting ranged from 164 in 1972/3 to 15911 in 1975/6, sea snail from 509 in 1973/4 to 5045 in 1974/5 and thin-lipped grey mullet and bass from 38 and 82 respectively in 1974/5 to 3348 and 8896 respectively in 1976/7. As can be seen from these data and those for other species listed in Table 2, no marked correspondence existed between the years when the minimum or maximum numbers of different species were recorded.

In terms of relative abundance (Warfel & Merriman, 1944), the flounder always ranked first or second and the *P. minutus* complex first, second or third (Table 3). The whiting ranked equal second in 1975/6 and the bass first in 1976/7. The contribution of the species ranked first in each year ranged from $14 \cdot 2\%$ in 1975/6 to $17 \cdot 3\%$ in 1974/5. The top three species in each year were present in every month of that year and the top three over the whole study period (sand goby, flounder and eel) were caught in every month of each year (Table 3).

Seasonal occurrence and length-frequency data for abundant marine species

The numbers of the more abundant estuarine-dependent marine teleosts in the shallow waters at Oldbury each peaked sharply at one particular time of the year (Fig. 2). Thus, on average, between 49 and 86 % of the annual numbers of sprat, bass, poor cod, bib, whiting, thin-lipped mullet and sea snail were each caught in a two month period and the same was true of the herring in 1973/4 and 1975/6. The precise time at which peak abundance was reached, however, varied among these teleosts. For example, the greatest numbers were recorded in August and September for sprat and herring, September and October for bass and poor cod, October and November for bib, whiting and thin-lipped grey mullet, and December and January for sea snail (Fig. 2). Even though flounder numbers did not show such a pronounced peak, $32 \cdot 8 \%$ of the total annual catch of this species was still taken during a two month period (July and August).

Table 2. Numbers (N), percentage contribution to the total numbers ($\sqrt[0]{0}$) and the ranking by numbers (R) for each of the 15 most abundant species at Oldbury-upon-Severn over the five years of this study, together with comparable annual data for each of these species

| N % R 2232 25:6 1 164 1.8 7 1825 19:8 3 326 3:6 6 326 3:6 6 119 1.8 7 73 0.8 10 73 0.8 10 54 0.6 13 55 0.7 12 58 0.7 12 | N 621 322 196 | | | | | | | | | | | | | | |
|---|------------------------|----------|------|-------|------|----|----------|---------|----|--------|----------|------|--------|------|----|
| 2232 25.6 1 164 1.8 7 1825 19.8 3 326 3.6 6 326 3.6 6 2131 23.1 2 500 5.4 5 13 0.8 10 73 0.8 10 73 0.8 10 73 0.8 10 54 0.6 13 35 1.8 20= | | % | R | N | % | R | N | % | æ | N | % | Я | N | % | R |
| 164 1:8 7 1825 19:8 3 326 3:6 6 2131 23:1 2 190 5:4 5 73 0:8 10 73 0:8 10 54 0:6 13 55 0:6 13 58 0:7 12 | | 37-7 | t | 11301 | 32.2 | 19 | 12 521 | 2.72 | 1 | 10 590 | 26.2 | ٦ | 42859 | 29.2 | 1 |
| 1825 19.8 3 326 3.6 6 326 3.6 6 2131 23.1 2 500 5.4 5 500 5.4 5 700 1.3 9 1.3 10 73 1.8 20= 110 54 0.6 13 35 1.8 20= tickleback 58 0.7 12 | | 19.2 | 7 | 11682 | 33.3 | 1 | 15911 | 34.6 | ٦ | 10494 | 6.52 | 1 | 41471 | 28.2 | 4 |
| 326 3.6 6 2131 23:1 2 500 5.4 5 73 0.8 10 529 5.8 4 54 0.6 13 58 0.7 12 58 0.7 12 | | 11.7 | m | 2 897 | 8:3 | 4 | 5471 | 11-9 | ŝ | 2322 | 2.2 | Ś | 14480 | 6.6 | e |
| $\begin{array}{cccccccccccccccccccccccccccccccccccc$ | | 1.5 | 11 | 82 | 0.7 | 14 | 1230 | 2.7 | 8 | 8896 | 22.0 | £ | 10779 | 7.3 | 4 |
| 500 5:4 5 119 1:3 9 73 0:8 10 529 5:8 4 53 1:8 20= 58 0:7 12 | | 3.1 | 7 | 5045 | 14.4 | ŝ | 1 627 | 3.5 | 9 | 588 | 1.5 | × | 0066 | 6.7 | Ś |
| $\begin{array}{cccccccccccccccccccccccccccccccccccc$ | | 2:3 | 8 | 477 | 1.4 | 80 | 2712 | 6.5 | 4 | 154 | 0.4 | 12 | 4228 | 2.9 | 9 |
| 73 0.8 10 529 5.8 4 54 0.6 13 35 1.8 20= 58 0.7 12 | | 1.7 | 10 | 38 | 0.1 | 25 | 115 | ė. O | 16 | 3348 | 8:3 | 4 | 3 895 | 2.7 | 7 |
| 529 5.8 4 54 0.6 13 35 1.8 20= 58 0.7 12 | | 2.3 | 6 | 94 | 6.0 | 13 | 1 790 | 6.E | Ś | 1 544 | 3.8 8 | 9 | 3879 | 2.6 | × |
| 5 5 0.6 13 35 1.8 20= d stickleback 58 0.7 12 | | 4 0 | Ś | 759 | 2.2 | Ś | 943 | 2.1 | 6 | 779 | 1-9 | 7 | 3687 | 2.5 | 6 |
| 35 1·8 20= d stickleback 58 0·7 12 | | 1.4 | 4 | 71 | 0.5 | 18 | 1 334 | 2.9 | 7 | 14 | < 0.1 | 24 | 2869 | 1.9 | 10 |
| 58 0.7 12 | | 10.6 | 9 | 484 | 1.4 | 7 | 614 | 1.3 | 10 | 120 | 6.0 | 14 = | 1 801 | 1.2 | 11 |
| | | 1.0 | 13 | 621 | 1·8 | 9 | 261 | 9.0 | 12 | 169 | 0.4 | 11 | 1 268 | 6.0 | 12 |
| lamprey 154 1.7 8 | | 0.5 | 15 | 194 | 9.0 | 10 | 381 | 0.8 | 11 | 147 | 0:4 | 13 | 956 | 0.7 | 13 |
| 98 1-1 10 | | ∧ 0.1 | 30 = | 422 | 1·2 | 6 | 105 | 0.2 | 18 | 280 | 2.0 | 10 | 911 | 9.0 | 14 |
| 37= | | 0.1 | 23 | 171 | 0.5 | 11 | 205 | 0.4 | 13 | 350 | 6.0 | 9 | 744 | o.S | 15 |
| | 1556 | 8 94·5 | | 33882 | £.96 | | 44 1 5 3 | 0.96 | | 39191 | 6.96 | | 138047 | 94.0 | |
| All fish 8740 | 16482 | 2 | | 35173 | | | 45987 | | | 40446 | | | 146828 | | |
| All species 42 | 4 | ~ | | 53 | | | 62 | | | 63 | | | 78 | | |

=, Equal ranking with at least one other species.

FISH OF THE SEVERN ESTUARY

| Table 3. Relative abundance | tance ($\%$ RA) an | d ranking (R |) for each of th | ie ten most a | bundant sj | e (% RA) and ranking (R) for each of the ten most abundant species in each of the five years of | he five years of |
|--|---------------------|---------------|------------------|---------------|------------|---|------------------|
| the study, together with pooled data for the whole period. The number of months in which each species occurred is also given | pooled data for t | he whole peri | od. The numbe | r of months i | n which e | ach species occurr | ed is also given |
| as a percentage ($\%$ O) | | | | | | | |
| | | | - | | | | |

| | | 1972/3 | | | 1973/4 | | Ŧ | 1974/5 | | | 1975/6 | | t. | 1976/7 | | | 1972/7 | |
|-------------------------|-------------|--------|------|------------|--------|------|--------|--------|------|--------|--------|------------|------|--------|-----|----------|--------|------|
| Species | % RA | R | 0 % | % RA | R | % 0 | % RA | Я | % 0 | % RA | R | 0 % | % RA | Я | 0 % | % RA | R | 0 % |
| Sand goby complex | 15.5 | 11 | 100 | 16.2 | * | 100 | | 4 | 100 | 13.3 | 2 = | 100 | | ٣ | 100 | 15.2 | -1 | 100 |
| Flounder | 16.5 | t | 100 | 15.2 2 100 | 6 | 100 | 14.7 2 | 1 | 100 | 14.2 1 | 1 | 100 | 14.8 | 0 | 100 | 14.8 | 7 | 100 |
| Eel | 13-3 | £ | 100 | 10.9 | ę | 100 | | 4 | 100 | | 4 | 100 | | 4 | | 11-0 | ŝ | 100 |
| Whiting | 3.2 | 6 | 75.0 | 8·6 | Ś | 66.7 | | £ | 100 | | 2 == | 100 | | 9 | | 8.6 | 4 | 78.3 |
| Bass | 8.7 | Ŷ | 100 | 2.2 | 13 | 75.0 | | ļ | 75.0 | | 9 | 100 | | Ļ | | 9·9 | Ś | 0.06 |
| Poor cod | 10.2 | 4 | 100 | 3.6 | 10 | 91.7 | | 9 | 100 | | S | 91.7 | | 20 | | 5.8 | 9 | 0.06 |
| Sea snail | 6.5 | 9 | 66.7 | 3.2 | 11 | 50.0 | | 7 | 2.99 | | 10 | 50.0 | | 6 | | 4.2 | 7 | 53-3 |
| Twaite shad | 1.6 | 14 | 100 | 4-9 | 7 | 75.0 | | 14 | 75.0 | | 6 | 91.7 | | 7 | | ŝ | × | 83.3 |
| 3-spined stickleback | 2.0 | 19= | 2.99 | 4.4 | × | 100 | | Ś | 100 | | 12 | 91.7 | | 15 | | 3.7 | 6 | 0.06 |
| Sprat | <0.1 | 28 | 100 | 6.5 | 9 | 91.7 | | 6 | 83.3 | | œ | 100 | | 13 | | 3.6 | 10 | 0.26 |
| Herring | 6.0 | 18 | 100 | 9.2 | 4 | 91.7 | | 15 | 6.68 | | 7 | 61.7 | | 22 = | | 3.4 | 11 | 81.7 |
| Thin-lipped grey mullet | 3.1 | 10 | 83.3 | 3·8 | 6 | 66.7 | | | 66.7 | | 21 = | 100 100 | | ٢ | | 3.2 | 12 | 83.3 |
| Sole | 3 .9 | 7 | 75.0 | 80 0 | 18 = | 58.3 | | 12 | 83-3 | | 13 | 91.7 | | 10 | | 5.7 7 | 13 | 76.7 |
| River lamprey | 2.3 | 11 | 58·3 | 0.8 | 18= | 66.7 | | 11 | 66.7 | | 11 | 66.7 | | 14 | | 2·1 | 14 | 65.0 |
| Common goby | ł | 1 | 8·3 | 0.5 | 22 | 33-3 | | × | 91.7 | | 17 | 100 | | œ | | 2.0 | 15 | 65.0 |
| Salmon | 3.4 | œ | 83·3 | 2.4 | 12 | 75.0 | | 13 | 75.0 | | 16 | 58:3 | | 18 | | 1.9 | 16 | 65.0 |
| Bib | 1.1 | 17 | 58.3 | 1 | ۱ | 16.7 | | 10 | 0.05 | | 20 | 75.0 | | 12 | | 1.5 | 17 | 56.7 |

^{=,} Equal ranking with at least one other species.

242

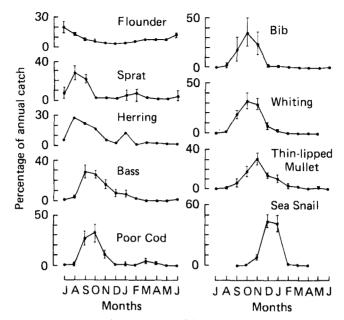


Fig. 2. The mean percentage catch $(\pm 95\%$ confidence limits) of nine of the most abundant estuarine-dependent marine teleosts collected in each month from Oldbury-upon-Severn.

The length-frequency histograms for these nine marine estuarine-dependent species during the two months when they were most abundant at Oldbury (Fig. 3), emphasize that most of the populations in this period consisted of small fish. The modal length classes ranged from 40-44 mm in flounder and sprat to 85-89 mm in whiting, with minimum lengths being less than 25 mm in the flounder, sprat and herring. Analysis of sequential monthly length-frequency histograms, often in conjunction with an examination of otolith annuli, showed that the small modal size reflects the dominance of the o + age class (Claridge & Gardner, 1977, 1978; Badsha & Sainsbury, 1978 a, b; Gardner, 1978; Claridge & Potter, 1983, 1984, 1985; Potter & Claridge, 1985). This point is illustrated by the fact that the contribution of the o+ age class to the length-frequency histograms shown in Fig. 3 was at least 75% in the case of all species except flounder. The most striking example of age class dominance was provided by whiting, where over 99.5% of the total catch was shown to belong to the 0 + age class at Oldbury in 1974/5, 1975/6 and 1976/7 (Gardner, 1978). The only species for which the histograms were markedly bimodal at the time of peak abundance was the thin-lipped grey mullet where the two modes corresponded to the o +and 1+ age classes (Claridge & Potter, 1985). Fish less than one year old dominated samples of all species shown in Fig. 3 except sprat and thin-lipped grey mullet throughout the months subsequent to the time of peak abundance. A second smaller peak in the abundance of sprat in January and February (Fig. 2), which was particularly pronounced in some years, was attributable to the immigration of numbers of larger and older fish (Potter & Claridge, 1985).

Although there was no second peak in the abundance of thin-lipped grey mullet in the winter and early spring (Fig. 2), the contribution of the 1 + age class to the samples at this time in 1976/7, when this species was most abundant (Table 2), was greater than that of the 0 + age class (Claridge & Potter, 1985).

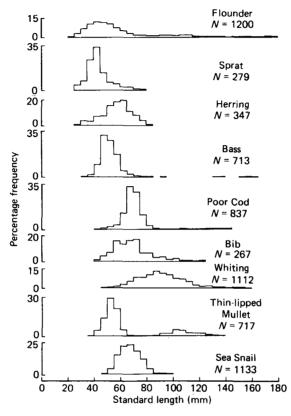


Fig. 3. Length-frequency histograms for nine of the most abundant estuarine-dependent marine teleosts caught at Oldbury-upon-Severn during the two months when each species reached maximum abundance.

Recruitment time to shallows of inner estuary

In 1974, the larvae and postlarvae of flounder were first found in plankton hauls in the Bristol Channel in mid-April (Russell, 1980), approximately nine weeks before the corresponding o + recruits were first collected from the shallows of the inner estuary at Oldbury (Fig. 4). This time interval is comparable to that between the mid-points of the periods of maximum abundance of larvae and postlarvae in the Bristol Channel (mid-May) and of o + recruits in the middle of the inner estuary (early August). Assuming that in mid-May of 1974, these larvae and postlarvae were between two and six weeks old, which would be consistent with the available information on peak spawning time, the flounder took on average 11-15 weeks to pass from the area where it had been spawned to the shallows of the middle part of the inner estuary. If spawning commenced

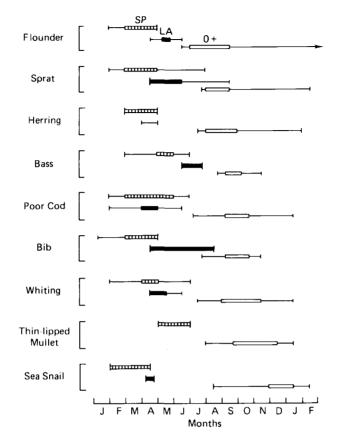


Fig. 4. The duration (single line) and peak period (rectangular area) of spawning (top-SP), and the occurrence of larvae and postlarvae in the Bristol Channel (middle-LA) and of 0+ recruits in the shallows at Oldbury-upon-Severn (bottom-0+) for nine of the most abundant estuarine-dependent marine teleosts in the Severn Estuary (see Materials and Methods).

as early as the beginning of February in 1974, the first recruits to arrive at Oldbury in this year would have been approximately 19 weeks old.

The same type of approach for estimating migration times can be applied to other species for which data on the occurrence of larvae and postlarvae are available in Russell (1980). Thus, the time between maximum occurrence of larvae and postlarvae in the channel in 1974 and of 0+ recruits in the middle of the inner estuary in the same year was 14 weeks for sprat, 12 weeks for bass, 24 weeks for poor cod, 15 weeks for bib, 23 weeks for whiting and 36 weeks for sea snail (Fig. 4). Assuming again that the larvae and postlarvae were 2–6 weeks old, the average time taken to develop and migrate to the shallows of the inner estuary at Oldbury ranged from approximately 14–18 weeks in the bass to 38–42 weeks in the sea snail.

Visual back extrapolation of the length-frequency modes of the 0+ age class for herring in 1975 when this species was relatively abundant (Titmus *et al.* 1978) suggests that the 'parental' *Clupea harengus* probably spawned in March/April of that year. This view would be consistent with the capture of yolk-sac herring on the southern tip of Wales in April 1975 (J. Riley, personal communication) and the fact that spring-spawned herring have been caught in the outer Bristol Channel (Wood, 1975). Since 0 + herring peaked at Oldbury at the end of August, they would have taken on average approximately 22 weeks to pass from their spawning grounds to the shallows of the middle of the inner estuary (Fig. 4).

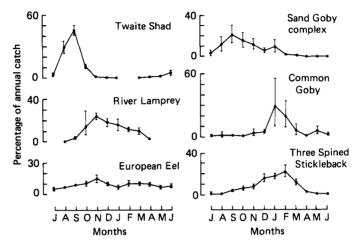


Fig. 5. The mean percentage catch $(\pm 95\%)$ confidence limits) in each month for six abundant species collected from Oldbury-upon-Severn. These comprised the anadromous twaite shad and river lamprey, the catadromous eel, the freshwater 3-spined stickleback which may spawn in the estuary, the estuarine common goby and the sand goby complex whose two members may spawn at sea.

Thin-lipped grey mullet was estimated as spawning between May and June and the 0 + recruits did not reach peak numbers at Oldbury until early November (Claridge & Potter, 1978). This species would thus have taken 23 weeks to enter the shallows in the middle of the inner estuary.

Seasonal occurrence of migratory, freshwater and goby species

As with the above marine teleosts, the sharp seasonal peak in abundance of the twaite shad was due to movement into the Oldbury area of large numbers of 0 + fish (Fig. 5). This steep rise in numbers, which took place in August and September, resulted from a downstream movement of young fish from upstream brackish or freshwater regions where they had been spawned. By contrast, the peak in the numbers of another anadromous species, the river lamprey, resulted from the capture of adults migrating towards upstream breeding areas (see also Abou-Seedo & Potter, 1979). The presence of a considerable number of river lampreys between the late summer and early spring (Fig. 5) reflects the long period when this species enters rivers, and during which the larger 'typical forms' (*ca.* 320 mm) are gradually replaced by the shorter 'praecox forms' (*ca.* 240 mm).

Although the abundance of the eel exhibited no clear seasonal trends (Fig. 5), the silver forms of this catadromous species were obtained in the late autumn and winter months when they were presumably moving through the estuary towards

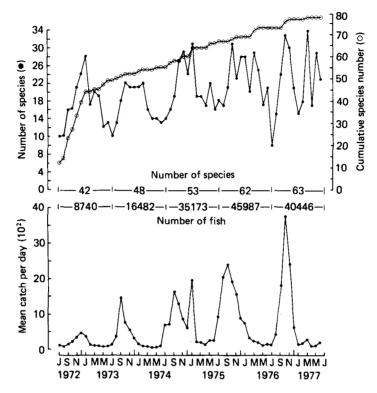


Fig. 6. The total number of species (together with the cumulative number of species) and the mean daily number of fish collected from Oldbury-upon-Severn for each month between July 1972 and June 1977. The total numbers of species and fish obtained in each year (July to June) are also given.

their oceanic spawning areas. The 3-spined stickleback was also present throughout the year, but numbers rose appreciably during the winter (Fig. 5) when freshwater discharge was high and salinities were low.

The common goby reached peak abundance at Oldbury in January and February when on average 48% of the total annual collection of this species was taken (Fig. 5). A smaller percentage of the *P. minutus* complex (36%) was taken in the two months when they were most abundant (September and October) than was the case with all other common teleosts except flounder and eel (cf. Figs. 2, 5). This less well-defined seasonal distribution may be due to the fact that the *P. minutus* complex comprises two closely related species whose biology differs in some respects (Claridge *et al.* 1985).

Seasonal and annual trends in total numbers of species and individuals

The number of species recorded each month from Oldbury showed marked seasonal variation, reaching a peak in the autumn and early winter and falling to its lowest levels in the late spring and early summer (Fig. 6). The marked drop in species number during November, December and January of 1976/7 coincided with a period of very high freshwater discharge and low salinities. The number

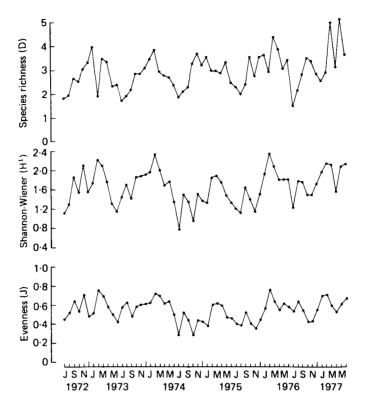


Fig. 7. Monthly values for species richness, Shannon–Wiener and Evenness indices for the collections of fish taken from Oldbury-upon-Severn between July 1972 and June 1977.

of species caught each year rose from 42 in 1972/3 to 63 in 1976/7, and the cumulative species number increased from 12 in the first month to 78 by the end of the study, 90% of which had been recorded by March 1976.

As with the number of species, the total number of fish at Oldbury each month underwent consistent seasonal changes throughout the five years of this study (Fig. 6). Thus, abundance rose rapidly in the autumn of each year, producing well-defined peaks in December of 1972, September of 1973, 1974 and 1975 and October of 1976. A second pronounced peak in January 1975 was attributable to an exceptionally large influx of sand gobies and sea snails. The numbers of fish were relatively low between February and June of each year.

The maximum mean monthly values for the total number of fish at Oldbury rose successively each year from 468 per day in 1972/3 to 3771 per day in 1976/7 (Fig. 6). While the total annual catch of fish followed the same upwards trend in each of the first four years, i.e. from 8740 in 1972/3 to 45987 in 1975/6, the numbers fell slightly to 40446 in 1976/7. This was attributable to a more rapid fall in numbers than usual in the winter of 1976/7, at a time of exceptionally high freshwater discharge and resultant low salinities in the inner estuary (<6%). The numbers of the previously very abundant whiting fell particularly sharply during this period (Claridge & Potter, 1984).

The species richness index (D) for the fish community at Oldbury tended to peak in the winter and trough in the summer (Fig. 7). Similar seasonal trends were seen with the Shannon-Wiener index (H') and also, but to a much smaller extent, with the Evenness index (\mathcal{J}) (Fig. 7).

DISCUSSION

This study has shown that large numbers of fish, representing a wide range of species, are taken on the intake screens of power stations in the Severn Estuary and inner Bristol Channel. Power station sampling has proved particularly valuable in this area where the harsh environmental conditions make conventional fishing methods relatively difficult to employ. Samples collected by this method have also been used with considerable success during recent years to obtain data on fish communities in various parts of the world (see e.g. Wheeler, 1969, 1979; Huddart & Arthur, 1971; Gallaway & Strawn, 1975; Mozzam & Rizvi, 1980; van den Broek, 1979, 1980; Maitland, East & Morris, 1980).

Contribution of abundant species to the fish community

The large contribution made by a limited number of species at Oldbury over the course of the present study (top ten species = 94.0%, top fifteen species = 97.9° (here) resembles the situation that has been reported for estuaries in various parts of the northern hemisphere using samples collected by a variety of different methods (Livingston, 1976; Hoff & Ibara, 1977; Sheridan, 1983; van den Broek, 1979, 1980; Wharfe, Wilson & Dines, 1984). The ranking of the top ten species by relative rather than total abundance, reduces the effect on the ranking of those species which were present in large numbers for only a short period of time (Warfel & Merriman, 1944), as it also did in a surf zone fish community recently investigated by Lasiak (1984). Thus, in each year of the study, the flounder and eel, which were conspicuous throughout the year but rarely in vast numbers, always ranked higher by relative than by total abundance. The reverse situation applied to the sea snail and whiting whose numbers showed a particularly sharp peak at one time of the year. Irrespective of any differences in the total and relative abundance ranking of the individual species, the top twelve species over the whole study were the same by both methods.

Since the species composition and relative numbers of individuals in samples taken from the shallow waters at Oldbury were essentially the same as those at Berkeley, such data for the former station would appear to provide a reasonable reflection of the fish community in the inner estuary. The greater incidence of elasmobranchs and the conger eel at Berkeley than at Oldbury is almost certainly related to the presence of deeper water at the former site, while the reverse situation for plaice (mostly o +), atherinids and the common goby at Oldbury presumably indicates their preference for shallow water (Wheeler, 1978; P. J. Miller, personal communication). The much lower frequency of occurrence of freshwater species at Uskmouth, where only one of the twelve cyprinids found

in the inner Severn Estuary was recorded, can be attributed to the less-rich freshwater fish fauna in the Usk compared with the Severn (A. Wheeler, personal communication) and to the close proximity of this station to the outer Severn Estuary in which the salinity is always higher than in the inner estuary. The presence of a much greater number of families and species at Hinkley Point than at Uskmouth, despite the same frequency of sampling, reflects the greater diversity of fauna typically found in marine than estuarine environments. This latter point is further emphasised by the collection of a larger number of families at Hinkley Point than in the greater number of samples taken from both Oldbury and Berkeley.

While the structure of length-frequency histograms for the major marine estuarine-dependent species at Berkeley are also similar to those from Oldbury, there was some evidence that, at the former station, the mean length of the o +age class of certain species and also the incidence of older age classes tended to be greater. This applied, for example, to thin-lipped grey mullet (Claridge & Potter, 1985), sprat (Potter & Claridge, 1985) and whiting, poor cod, bib and pollack (Claridge & Potter, 1984). Since the Berkeley Station draws water from a deeper, mid-estuary position than Oldbury, such differences presumably reflect the tendency for many species to move away from the shore and into deeper water as they increase in age and size (see e.g. Parrish & Saville, 1965; Dragesund, 1970; De Silva, 1973; Arnold, 1981; Chubb et al. 1981; Potter et al. 1983; Poxton, Eleftheriou & McIntyre, 1983; Chrystal et al. 1985). Caution must be exercised in drawing direct comparisons between the total numbers of fish in samples at Berkeley and Oldbury because of the variable periods over which they were collected at the former site. However, the views already expressed on patterns of movement would be consistent with the observation that the total numbers of each abundant marine species obtained from Berkeley during the period when the o+ age class was numerous, rarely approached the very large numbers collected from Oldbury.

Life-cycle categories of abundant species

An inspection of the types of life-cycle of the fifteen most numerous species in samples from the inner Severn Estuary shows that two of these are anadromous and that there are single examples of the catadromous, freshwater and estuarine category. While more work is clearly required to confirm whether *P. lozanoi*, like *P. minutus*, typically spawns in marine waters in this region, it is evident that the majority of the dominant species in the Severn Estuary belong to the group described as estuarine-dependent. Thus, nine estuarine-dependent marine teleosts contributed 61.5% to the total numbers of the fifteen most abundant fish at Oldbury during the five-year period. If both *P. minutus* and *P. lozanoi* are also subsequently confirmed as breeding outside the estuary, this percentage value would increase to 90.7%.

Estuarine dependent species

Since samples of each of the major estuarine-dependent marine species were

typically dominated by the 0+ age class, the shallows of the inner estuary clearly provide very important nursery habitats. It is thus noteworthy that most of these species are of commercial value in British waters (whiting, flounder, bass, poor cod, herring, sprat, bib) and that considerable interest has recently been shown in the bass fishery off south-western England. However, it must be recognized that few if any of these species are totally dependent on estuarine habitats to complete their life-cycle. Indeed, the young of several were found in considerable numbers in the Bristol Channel and are known to be capable of utilizing marine inshore areas and sea lochs in other regions (see e.g. Cooper, 1980; Gordon & De Silva, 1980; Gordon, 1981). At the same time, there would appear to be little doubt that the destruction of estuarine habitats or the construction of barriers such as the Severn Barrage (Department of Energy, 1981; Baker, 1984), would almost certainly have a detrimental effect on the more estuarine-dependent species.

Movements in the estuary

The marked seasonality in the total numbers of juvenile fish at Oldbury parallels quite closely the trends recorded for the lower Medway Estuary (van den Broek, 1979), with abundance reaching a peak during the autumn and early winter and declining to minimum levels during the summer. The data presented in our paper have demonstrated that the young of many species enter the nursery grounds in the middle of the inner Severn Estuary from three to five months after being spawned in the Bristol Channel. However, there is good indirect and direct evidence that the early stages of some species enter the inner estuary some weeks before they are caught at Oldbury. Recent work has shown, for example, that postlarval bass enter the Tamar Estuary in south-western England between mid-May and the end of June at a length of 10 mm and move quite rapidly through the estuary to the point of interface between fresh and salt water (Dando & Demir, 1985). Likewise, it is evident from the work of Aprahamian & Barr (1985) that postlarval bass appear in the upper part of the inner Severn Estuary before small juveniles are taken in the shallows at Oldbury further downstream. The movement of postlarvae of bass and other species such as eel, flounder, sprat and thin-lipped grey mullet (P. R. Dando, personal communication) through the Severn Estuary is almost certainly accomplished through selective tidal stream transport (Arnold, 1981; Norcross & Shaw, 1984) and/or passive transport (Fortier & Leggett, 1982). This view is based on the observation that elvers and the young stages of flounder, plaice and sole select the flood tides to facilitate their entry into estuaries (Creutzberg, 1961; Gibson, 1973; Creutzberg, Eltink & van Noort, 1978; De Veen, 1978), while the movement of herring less than 10 mm through the St Lawrence Estuary has been shown to correspond to the net upstream movement of passive contaminants of the environment (Fortier & Leggett, 1982). This last study did show, however, that selective tidal transport did occur in larger herring. While the absence of fish less than 15 mm in length in the samples from Oldbury could partly reflect the size of the mesh on the intake screens, it is worth noting that if such fish were present in the shallows at this

site some at least would have been expected to have been trapped on the extensive amounts of brown seaweeds collected on the screens. Moreover, no postlarvae of any species were obtained during the regular use over a two-year period of a 0.5 mm mesh plankton net to collect small crustaceans in the water inflow at Oldbury (Moore, Moore & Claridge, 1979). From the above data, it can be postulated that the postlarvae of several species are transported in the central water flow of the Severn Estuary to areas of very low salinity and are subsequently transported downstream through selective tidal stream transport. It is only then that they enter the shallows of areas such as Oldbury.

The seasonal patterns of emigration of most of the estuarine-dependent marine species suggest that they may be influenced by changes in one or more environmental variables. While there were indications that bass movements may be related to temperature (Claridge & Potter, 1983), an attempt to regress declines in the numbers of certain gadoids between successive weeks with changes in both salinity and temperature yielded no consistent interrelationship (Claridge & Potter, 1984). However, there was evidence from the latter study that the numbers of species such as the whiting were influenced markedly by exceptionally low salinities. The view that the seasonal movements of the estuarine-dependent species in the Severn are affected by temperature and salinity only under extreme conditions is borne out by a preliminary study using cluster analysis (Potter, Claridge & Warwick, unpublished data).

Species diversity indices

The presence in the Severn Estuary of similar seasonal changes in the species richness, Shannon-Wiener and Evenness indices to those recorded for the number of species and individuals, parallels the situation recorded for fish in other fish nursery areas (see e.g. Allen & Horn, 1975), and for fish communities in estuaries and embayments (McErlean et al. 1973; Gallaway & Strawn, 1975). However, this is not always the case (see e.g. Dahlberg & Odum, 1970; Hoff & Ibara, 1977; Shenker & Dean, 1979; van den Broek, 1979; Lasiak, 1984). The observation that the distinct seasonal cycles in the Severn Estuary fish fauna are related much more closely with regular migratory movements to nursery areas than with physico-chemical variations (see previous section), parallels the situation found in the Patuxent Estuary in Maryland (McErlean et al. 1973). Since the Evenness Index shows parallel trends to the Diversity Index, differences in the latter were largely due to changes in the equitability of allotment of individuals, rather than to differences in the number of species. Although the highest species-richness values were found in the last two years of the Severn study, the values for this and the Shannon-Wiener and Evenness indices did not follow the conspicuous upwards trend observed with the numbers of species and individuals. This indicates that, although the abundance of fish and species increased during the study, there was no obvious change in the structure of the community. The fact that both the minimum and maximum values for the Shannon-Wiener Index (0.8-2.3) are higher than those recorded for several other fish communities in estuaries and marine embayments (Bechtel & Copeland, 1970; Dahlberg & Odum, 1970; Haedrich & Haedrich, 1974; Allen & Horn, 1975; van den Broek, 1979), implies that the Severn Estuary has a relatively more diverse fish fauna and that the use of intake screens for fish sampling is particularly efficient.

Comparisons with past data on species composition

Our collections from Oldbury and Berkeley yielded 12 marine species, representing one family of elasmobranch and six families of teleost not shown in Llovd's (1941) total list for the Severn and Bristol Channel region (Table 1). Since Llovd referred to the common goby as *Pomatoschistus minutus* rather than P. microps, there must be some doubt concerning his identification of these common gobiids and therefore possibly also his ability to distinguish the crystal goby, Crystallogobius linearis, from the transparent goby, Aphia minuta. The only two species which were frequently collected during our study but not recorded by Lloyd (1941) were the northern rockling and Norway pout. In a recent paper on gadoids in the region, Claridge & Potter (1984) suggested that the advent of these two 'northern' species may be related to the reduction in water temperature that has occurred over recent decades, a feature which is also believed to have led to their recent appearance and that of blue whiting in other southern waters (Dando, 1975; Southward, 1980; Southward & Mattacola, 1980). Although Lloyd (1941) recorded 12 marine teleosts from the inner Severn Estuary that were not found at either Oldbury or Berkeley during the current study, all of these species were described as rare.

From the above comparisons between our data and those of Lloyd (1941), it would appear that the only evidence of a conspicuous change in the composition of the fish fauna of the Severn Estuary since the earlier decades of this century is the introduction of the northern rockling and Norway pout. Since the rise in abundance of these species can be related to climatic changes, there is no obvious indication that the introduction of contaminants or increased urbanization have had a marked effect on the composition of the fish fauna of the estuary. This parallels the situation already described for the invertebrate fauna (Mettam, 1979).

Our gratitude is expressed to R. J. Huggins, R. A. Milne, J. Knight, D. C. Gardner and M. Holtz for technical assistance and to R. J. G. Manning for drawing the figures. Helpful criticism and discussion was provided by S. J. M. Blaber, P. R. Dando, N. Loneragan, A. J. Southward and A. Wheeler. The last of these workers also kindly updated, where appropriate, the nomenclature of families and species. Financial support was provided by the Leverhulme Foundation.

REFERENCES

- ABDULLAH, M. I., ROYALE, L. G. & MORRIS, A. W., 1972. Heavy metal concentrations in coastal waters. Nature, London, 235, 158-160.
- ABOU-SEEDO, F. S. & POTTER, I. C., 1979. The estuarine phase in the spawning run of the river lamprey Lampetra fluviatilis. Journal of Zoology, 188, 5-25.
- ALLEN, L. G. & HORN, M. H., 1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. *Estuarine and Coastal Marine Science*, **3**, 371–380.

- ANDREWS, M. J., 1984. Thames Estuary: pollution and recovery. In Effects of Pollutants at the Ecosystem Level (ed. P. J. Sheehan et al.), pp. 195-227. Chichester: John Wiley.
- APRAHAMIAN, M. W. & BARR, C. D., 1985. The growth, abundance and diet of O-group sea bass, Dicentrarchus labrax, from the Severn Estuary. Journal of the Marine Biological Association of the United Kingdom, 65, 169–180.
- ARNOLD, G. P., 1981. Movements of fish in relation to water currents. In Animal Migration (ed. D. J. Aidley), pp. 55-79. Cambridge University Press.
- BADSHA, K. S. & SAINSBURY, M., 1978a. Aspects of the biology and heavy metal accumulation of Ciliata mustela. Journal of Fish Biology, 12, 213-220.
- BADSHA, K. S. & SAINSBURY, 1978b. Some aspects of the biology and heavy metal accumulation of the fish Liparis liparis in the Severn Estuary. Estuarine and Coastal Marine Science, 7, 381-391.
- BAKER, A. C., 1984. Tidal power in the United Kingdom. Interdisciplinary Science Reviews, 9, 347-357.
- BAMBER, R. N. & HENDERSON, P. A., 1985. Morphological variation in British atherinids, and the status of Atherina presbyter Cuvier (Pisces: Atherinidae). Biological Journal of the Linnean Society of London, 25, 61-76.
- BEAL, K. L., 1980. Territorial sea fisheries management and estuarine dependence. In *Estuarine Perspectives* (ed. V. S. Kennedy), pp. 67–77. London: Academic Press.
- BECHTEL, T. J. & COPELAND, B. J., 1970. Fish species diversity indices as indicators of pollution in Galveston Bay, Texas. Contributions in Marine Science, University of Texas, 15, 103-132.
- BLABER, S. J. M. & BLABER, T. G., 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology*, 17, 143-162.
- BUTTERWORTH, J., LESTER, P. & NICKLESS, G., 1972. Distribution of heavy metals in the Severn Estuary. Marine Pollution Bulletin, 3, 72-74.
- CHESTER, R. & STONER, J. H., 1975. Trace elements in sediments from the lower Severn Estuary and Bristol Channel. *Marine Pollution Bulletin*, 6, 92–96.
- CHRYSTAL, P. J., POTTER, I. C., LONERAGAN, N. R. & HOLT, C. P., 1985. Age structure, growth rates, movement patterns and feeding in an estuarine population of the cardinalfish *Apogon rueppellii*. Marine Biology, **85**, 185–197.
- CHUBB, C. F., POTTER, I. C., GRANT, C. J., LENANTON, R. C. J. & WALLACE, J., 1981. Age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon river system, Western Australia. *Australian Journal of Marine and Freshwater Research*, 32, 605–628.
- CLARIDGE, P. N. & GARDNER, D. C., 1977. The biology of the northern rockling, *Ciliata septent*rionalis, in the Severn Estuary and Bristol Channel. Journal of the Marine Biological Association of the United Kingdom, 57, 839–848.
- CLARIDGE, P. N. & GARDNER, D. C., 1978. Growth and movements of the twaite shad, Alosa fallax (Lacépède), in the Severn Estuary. *Journal of Fish Biology*, 12, 203–211.
- CLARIDGE, P. N., HARDISTY, M. W., POTTER, I. C. & WILLIAMS, C. V., 1985. Abundance, life history and ligulosis in the gobies (Teleostei) of the inner Severn Estuary. Journal of the Marine Biological Association of the United Kingdom, 65, 951–968.
- CLARIDGE, P. N. & POTTER, I. C., 1983. Movements, abundance, age composition and growth of bass, *Dicentrarchus labrax*, in the Severn Estuary and inner Bristol Channel. Journal of the Marine Biological Association of the United Kingdom, 63, 871-879.
- CLARIDGE, P. N. & POTTER, I. C., 1984. Abundance, movements and size of gadoids (Teleostei) in the Severn Estuary. Journal of the Marine Biological Association of the United Kingdom, 64, 771-790.
- CLARIDGE, P. N. & POTTER, I. C., 1985. Distribution, abundance and size composition of mullet populations in the Severn Estuary and Bristol Channel. *Journal of the Marine Biological* Association of the United Kingdom, 65, 325-335.
- CLARK, R. B., 1971. Changing success of coastal sport fishing. Marine Pollution Bulletin, 2, 153-156.
- COOPER, A., 1980. Gadoid populations of western Scottish sea lochs and their exchanges with west coast stocks. In *Fjord Oceanography* (ed. H. J. Freeland, D. M. Farmer and C. D. Levings), pp. 415-421. New York: Plenum Press.
- CREUTZBERG, F., 1961. On the orientation of migrating elvers (Anguilla vulgaris Turt.) in a tidal area. Netherlands Journal of Sea Research, 1, 257-338.

- CREUTZBERG, F., ELTINK, A. TH. G. W. & VAN NOORT, G. J., 1978. The migration of plaice larvae Pleuronectes platessa into the western Wadden Sea. In Physiology and Behaviour of Marine Organisms. Proceedings of the 12th European Symposium on Marine Biology, Stirling, Scotland, 1977 (ed. D. S. McLusky and A. J. Berry), pp. 243-251. Oxford: Pergamon Press.
- CRONIN, L. E. & MANSUETI, A. J., 1971. The biology of the estuary. In Proceedings of a Symposium on the Biological Significance of Estuaries (ed. P. A. Douglas and R. H. Stroud), pp. 14-39. Washington, D.C.: Sports Fishing Institute.
- DAHLBERG, M. D. & ODUM, E. P., 1970. Annual cycle of species occurrence, abundance, and diversity in Georgia estuarine fish populations. *American Midland Naturalist*, 83, 382-392.
- DANDO, P. R., 1975. On the northern rockling, Ciliata septentrionalis (Collett) in the Plymouth area. Journal of the Marine Biological Association of the United Kingdom, 55, 925-931.
- DANDO, P. R., 1984. Reproduction in estuarine fish. In Fish Reproduction (ed. G. W. Potts and R. J. Wootton), pp. 155-170. London: Academic Press.
- DANDO, P. R. & DEMIR, N., 1985. On the spawning and nursery grounds of bass, Dicentrarchus labrax, in the Plymouth area. Journal of the Marine Biological Association of the United Kingdom, 65, 159–168.
- DAY, F., 1879. On the fishes of Weston-super-Mare. Proceedings of the Zoological Society of London, 48, 742-763.
- DAY, J. H., BLABER, S. J. M. & WALLACE, J. H., 1981. Estuarine fishes. In Estuarine Ecology with Particular Reference to Southern Africa (ed. J. H. Day), pp. 197-221. Rotterdam: Balkema.
- DEPARTMENT OF ENERGY, UNITED KINGDOM, 1981. Tidal Power from the Severn Estuary. London: Her Majesty's Stationery Office. [Energy Paper no. 46.]
- 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.
- DE VEEN, J. F., 1978. On selective tidal transport in the migration of North Sea plaice (*Pleuronectes* platessa) and other flatfish species. Netherlands Journal of Sea Research, 12, 115-147.
- DRAGESUND, O., 1970. Distribution, abundance and mortality of young and adolescent Norwegian spring spawning herring (*Clupea harengus* Linné) in relation to subsequent year class strength. *Fiskeridirektorates skrifter* (ser. Havundersøkelser), **15**, 451–556.
- FONDS, M., 1973. Sand gobies in the Dutch Wadden Sea. Netherlands Journal of Sea Research, 6, 417-478.
- FORTIER, L. & LEGGETT, W. C., 1982. Fickian transport and the dispersal of fish larvae in estuaries. Canadian Journal of Fisheries and Aquatic Sciences, 39, 1150–1163.
- GALLAWAY, B. J. & STRAWN, K., 1975. Seasonal and areal comparisons of fish diversity indices at a hot-water discharge in Galveston Bay, Texas. *Contributions in Marine Science, University of Texas*, 19, 79-89.
- GARDNER, D. C., 1978. The Biology of the Whiting, Merlangius merlangus, in the Severn Estuary and the Bristol Channel. M.Sc. Thesis, University of Bath.
- GIBSON, R. N., 1973. Tidal and circadian activity rhythms in juvenile plaice, *Pleuronectes platessa*. Marine Biology, 22, 379-386.
- GORDON, J. D. M., 1981. The fish populations of the west of Scotland shelf. Part II. Oceanography and Marine Biology, an Annual Review, 19, 405-441.
- GORDON, J. D. M. & DE SILVA, S. S., 1980. The fish populations of the west of Scotland shelf. Part I. Oceanography and Marine Biology, an Annual Review, 18, 317-366.
- GUNTER, G., 1938. Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana with particular reference to life histories. *Ecological Monographs*, **8**, 313-346.
- GUNTER, G., 1961. Some relations of estuarine organisms to salinity. *Limnology and Oceanography*, 6, 182-190.
- GUNTER, G., 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. In *Estuaries* (ed. G. H. Lauff), pp. 621–638. Washington, D.C.: American Association for the Advancement of Science. [Publication no. 83.]
- HAEDRICH, R. L. & HAEDRICH, S. O., 1974. A seasonal survey of the fishes in the Mystic River, a polluted estuary in downtown Boston, Massachusetts. *Estuarine and Coastal Marine Science*, 2, 59-73.
- HAMILTON, D., 1980. The high energy, sand and mud regime of the Severn Estuary, S.W. Britain. In *Tidal and Estuary Management* (ed. R. T. Severn, D. Dineley and L. E. Hawker), pp. 162-172. Bristol: Scientechnica.

9

- HARDISTY, M. W. & HUGGINS, R. J., 1973. Lamprey growth and biological conditions in the Bristol Channel region. *Nature*, London, 243, 229-231.
- 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.
- HARDISTY, M. W., HUGGINS, R. J., KARTAR, S. & SAINSBURY, M., 1974. Ecological implications of heavy metal in fish from the Severn Estuary. *Marine Pollution Bulletin*, 5, 12–15.
- HARDISTY, M. W., KARTAR, S. & SAINSBURY, M., 1974. Dietary habits and heavy metal concentrations of fish from the Severn Estuary and Bristol Channel. *Marine Pollution Bulletin*, 5, 61-63.
- HESTHAGEN, I. H., 1975. Seasonal occurrence and length variation in the sand goby, *Pomatoschistus minutus* (Pallas), in the shore zone of the inner Oslofjord. Norwegian Journal of Zoology, 23, 235-242.
- HOFF, J. G. & IBARA, R. M., 1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. *Estuarine and Coastal Marine Science*, 5, 665–678.
- HUDDART, R. & ARTHUR, D. R., 1971. Lampreys and teleost fish, other than whitebait, in the polluted Thames estuary. International Journal of Environmental Studies, 2, 143-152.
- JACQUAZ, B., ABLE, K. W. & LEGGETT, W. C., 1977. Seasonal distribution, abundance and growth of larval capelin (*Mallotus villosus*) in the St. Lawrence Estuary and northwestern Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada, 34, 2015-2029.
- JONES, D. H. & JOHN, A. W. G., 1978. A three-spined stickleback, Gasterosteus aculeatus L. from the North Atlantic. Journal of Fish Biology, 13, 231-236.
- JONES, D. & MILLER, P. J., 1966. Seasonal migrations of the common goby, *Pomatoschistus microps* (Krøyer), in Morecambe Bay and elsewhere. *Hydrobiologia*, 27, 515-528.
- LANGFORD, T. E., 1983. Electricity Generation and the Ecology of Natural Waters. Liverpool University Press.
- LASIAK, T. A., 1984. Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: long-term fluctuations. *Estuarine, Coastal and Shelf Science*, 18, 459-483.
- LEBOUR, M. V., 1920. The eggs of Gobius minutus, pictus and microps. Journal of the Marine Biological Association of the United Kingdom, 12, 253-260.
- LEE, S. C., 1975. Biology of the Sand Goby, Pomatoschistus minutus (Pallas) (Teleostei, Gobioidei), in the Plymouth Area. Ph.D. Thesis, University of Bristol.
- LIVINGSTON, R. J., 1976. Diurnal and seasonal fluctuations of organisms in a north Florida estuary. Estuarine and Coastal Marine Science, 4, 373-400.
- LLOYD, A. J., 1941. Studies on the biology of the Bristol Channel. V. The marine fish fauna of the southern shores of the Bristol Channel. *Proceedings of the Bristol Naturalists' Society*, 9, 202-230.
- LLOYD, A. J., 1942. Studies on the biology of the Bristol Channel. IX. A survey of the fishing industry at Weston-super-Mare during the winter of 1940-41. Proceedings of the Bristol Naturalists' Society, 9, 316-327.
- MCERLEAN, A. J., O'CONNOR, S. G., MIHURSKY, J. A. & GIBSON, C. I., 1973. Abundance, diversity and seasonal patterns of estuarine fish populations. *Estuarine and Coastal Marine Science*, 1, 19-36.
- McHugh, J. L., 1976. Estuarine fisheries: are they doomed? In *Estuarine Processes*, vol. 1 (ed. R. F. Smith, A. H. Swartz and W. H. Massman), pp. 15–27. New York: Academic Press.
- MAITLAND, P. S., EAST, K. & MORRIS, K. H., 1980. Fish entrained in 1977 at Cockenzie power station, in the Firth of Forth. Forth Naturalist and Historian, 5, 35-45.
- MARGALEF, R., 1968. Perspectives in Ecological Theory. University of Chicago Press.
- MATTHEWS, L. H., 1933. The sea fish and fisheries of the Bristol district. Proceedings of the Bristol Naturalists' Society, 7, 442-462.
- METTAM, C., 1979. Faunal changes in the Severn Estuary over several decades. Marine Pollution Bulletin, 10, 133-136.
- MILLER, P. J., 1963. Studies on the Biology and Taxonomy of the British Gobiid Fishes. Ph.D. Thesis, University of Liverpool.
- MOORE, J. W., MOORE, I. A. & CLARIDGE, P. N., 1979. Seasonal changes in density, composition and reproductive biology of crustacean populations in the Severn estuary. *Crustaceana*, 36, 113-122.

- MOZZAM, M. & RIZVI, S. H. N., 1980. Fish entrapment in the seawater intake of a power plant at Karachi coast. Environmental Biology of Fishes, 5, 49–57.
- NOËL-LAMBOT, F., BONGUEGNEAU, J. M., FRANKENNE, F. & DISTECHE, A., 1980. Cadmium, zinc and copper accumulation in limpets (*Patella vulgata*) from the Bristol Channel, with special reference to metallothioneins. *Marine Ecology – Progress Series*, 2, 81–89.
- NORCROSS, B. L. & SHAW, R. F., 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Transactions of the American Fisheries Society, 113, 153-165.
- PALMER, C. J. & CULLEY, M. B., 1983. Aspects of the biology of the sandsmelt Atherina boyeri Risso, 1810 (Teleostei: Atherinidae) at Oldbury-upon-Severn, Gloucestershire, England. Estuarine, Coastal and Shelf Science, 16, 163-172.
- PALMER, C. J., CULLEY, M. B. & CLARIDGE, P. N., 1979. A further occurrence of Atherina boyeri Risso 1810 in North-Eastern Atlantic waters. *Environmental Biology of Fishes*, 4, 71-75.
- PARRISH, B. B. & SAVILLE, A., 1975. The biology of the north-east Atlantic herring populations. Oceanography and Marine Biology, an Annual Review, 3, 323-373.
- PEARCY, W. G. & RICHARDS, S. W., 1962. Distribution and ecology of fishes of the Mystic River estuary, Connecticut. *Ecology*, 43, 248–259.
- PIELOU, E. C., 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology, 13, 131-144.
- POLLARD, D. A., 1976. Estuaries must be protected. Australian Fisheries, 36, 6-10.
- 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. & HUGGINS, R. J., 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). Journal of Zoology, 169, 365-379.
- POTTER, I. C., LONERAGAN, N. R., LENANTON, R. C. J., CHRYSTAL, P. J. & GRANT, C. J., 1983. Abundance, distribution and age structure of fish populations in a Western Australian estuary. *Journal of Zoology*, 200, 21–50.
- POXTON, M. G., ELEFTHERIOU, A. & MCINTYRE, A. D., 1983. The food and growth of o-group flatfish on nursery grounds in the Clyde Sea area. *Estuarine, Coastal and Shelf Science*, 17, 319-337.
- PRICE, K. R., 1964. River surveys, with special reference to the River Severn. Journal and Proceedings of the Institute for Sewerage Purification, 1964, 425-433.
- RADFORD, P. J. & JOINT, I. R., 1980. The application of an ecosystem model to the Bristol Channel and Severn Estuary. *Water Pollution Control*, 78, 244-254.
- RUSSELL, F. S., 1976. The Eggs and Planktonic Stages of British Marine Fishes. London: Academic Press.
- RUSSELL, F. S., 1980. On the distribution of postlarval fish in the Bristol Channel. Bulletin of Marine Ecology, 8, 283–290.
- SHENKER, J. M. & DEAN, J. M., 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. *Estuaries*, 2, 154–163.
- SHERIDAN, P. F., 1983. Abundance and distribution of fishes in the Galveston Bay system, 1963–1964. Contributions in Marine Science, University of Texas, 26, 143–163.
- SOUTHWARD, A. J., 1980. The western English Channel an inconstant ecosystem? Nature, London, 285, 361–366.
- SOUTHWARD, A. J. & MATTACOLA, A. D., 1980. Occurrence of Norway pout, Trisopterus esmarkii (Nilsson) and blue whiting, Micromesistius poutassou (Risso), in the western English Channel off Plymouth. Journal of the Marine Biological Association of the United Kingdom, 60, 39-44.
- TITMUS, G., CLARIDGE, P. N. & POTTER, I. C., 1978. Growth and abundance of O-group herrings, Clupea harengus L., in the Severn Estuary. Zoological Journal of the Linnean Society, 64, 251-260.
- VAN DEN BROEK, W. L. F., 1979. A seasonal survey of fish populations in the lower Medway estuary, Kent, based on power station screen samples. *Estuarine and Coastal Marine Science*, 9, 1-15.
- VAN DEN BROEK, W. L. F., 1980. Aspects of the biology of estuarine fish populations sampled from power station trash screens. International Journal of Environmental Studies, 15, 203–216.
- WALLIS, G. P. & BEARDMORE, J. A., 1984. An electrophoretic study of the systematic relationships of some closely related goby species (Pisces, Gobiidae). Biological Journal of the Linnean Society of London, 22, 107–123.

- WARFEL, H. F. & MERRIMAN, D., 1944. Studies on the marine resources of southern New England.
 1. An analysis of the fish population of the shore zone. Bulletin of the Bingham Oceanographic Collection, Yale University, 9(2), 91 pp.
- WEBB, C. J., 1980. Systematics of the Pomatoschistus minutus complex (Teleostei: Gobioidei). Philosophical Transactions of the Royal Society, 291, 201–241.
- 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., 1978. Key to the Fishes of Northern Europe. London: Warne.
- WHEELER, A., 1979. The Tidal Thames. The History of a River and its Fishes. London: Routledge and Kegan Paul.
- WHITFIELD, A. K., 1983. Factors influencing the utilization of southern African estuaries by fishes. South African Journal of Science, 79, 362-365.
- WILLIAMS, R., 1984. Zooplankton of the British Channel and Severn Estuary. Marine Pollution Bulletin, 15, 66-70.
- WOOD, R. J., 1975. O-group herring on the west coast of England and Wales. Annales Biologiques 30, 150.
- ZAR, J. H., 1974. Biostatistical Analysis. New Jersey: Prentice-Hall.