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# The diet of juvenile and adult twaite shad *Alosa fallax fallax* (lacépède) from the rivers Severn and Wye (Britain)

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## Abstract

The diet of juvenile and adult twaite shad was studied at a number of freshwater and estuarine sites in the rivers Severn and Wye and in the coastal waters of Cardigan Bay (West Wales). In the Severn estuary and in the freshwater reaches of the Severn and Wye, adult twaite shad consumed little during their pre-spawning migration. In the Severn Estuary post-spawning adults were present during the summer months where they fed actively on mysids, gammarids and shrimps. Mysids dominated the diet of the adults caught in coastal waters during the autumn. The diet of one year old twaite shad was studied in the Severn Estuary. In May the one year olds from the lower estuary consumed mainly gammarids. During the summer months, this age-class moved into the inner estuary where they fed predominantly on mysids.

The larvae and juveniles (age $0^+$) fed mainly on chironomid larvae and pupae and Simuliidae larvae, while in fresh water. In the estuary copepods, cladocerans and mysids dominated the diet of the juveniles. There was some suggestion of an increase in prey size during their period of residency in the estuary. The contrasting distribution of the juveniles in two river systems is discussed in relation to the effects of channelization.

## Introduction

Comparatively little work has been carried out on the diet of the anadromous clupeid *Alosa fallax*. Studies on European stocks have dealt with the food of the adult population during their spawning migration into fresh water and/or while at sea; in most studies however, relatively few specimens were examined and only qualitative data has been presented (Bracken & Kennedy, 1967; Claridge & Gardner, 1978; Minchen, 1977; Rae & Lamont, 1961, 1962; Rae & Wilson, 1952, 1956a & b, 1961; Wheeler, 1969).

In Northern Europe populations of twaite shad, *Alosa fallax*, migrate into fresh water between April and June. Spawning takes place between the end of May and the middle of July, depending on temperature (Gallois, 1946–7; Rameye *et al.*, 1976), after which the adults migrate seaward. The $O^+$ fish remain in fresh and/or estuarine waters during the summer, migrating to sea in the autumn. A proportion of these re-enter the estuary the following spring, migrating to sea once more in late summer/early autumn.

The aim of this paper is 1) to describe the food and feeding of adult twaite shad when present in coastal and inland waters, 2) to examine the diet of the juvenile stages in fresh and estuarine waters and 3) to discuss these findings in relation to the spatial distribution of the juveniles in two river systems which differ in their physical characteristics.

## Study area

The study area is shown in Fig. 1. The River Severn, flows in a single uniform channel as far as Gloucester, where it briefly divides in two before rejoining prior to discharge into the estuary. The estuary, that part of the river system in which sea water is measurably diluted by fresh water (Pritchard, 1967), starts approximately 10 km downstream of Gloucester. Flow reversal can be detected as far as 4.5 km upstream of Tewkesbury. The bed of the river falls very slightly (0.03 p.p.t.) and by virtue of the weirs at Tewkesbury and Gloucester, a minimum water level of 3–4 m in the main channel is maintained. It is almost totally featureless the substrate ranging from thick mud to clay with only the occasional bed of gravel and outcrop of bedrock (Severn Trent Water Authority, 1979). There is little instream vegetation and the bankside growth of macrophytes is sparse. In the estuary, the intertidal substratum is composed mainly of mud with a little sand at the most upstream site (Elmore), thereafter the sand

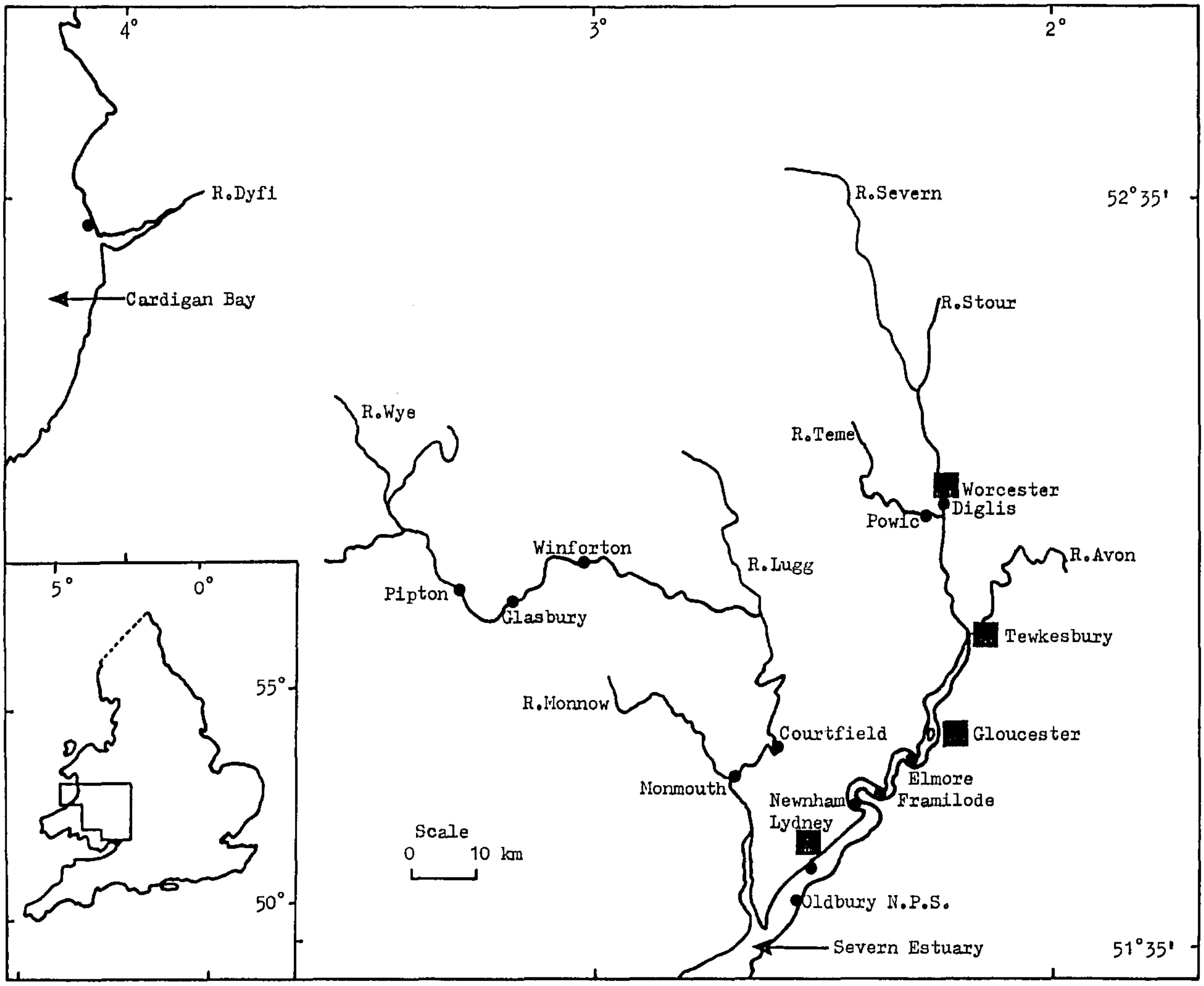


*Fig. 1.* The study area, showing the location of sampling sites ●.

component increases in proportion downstream until at Newnham, it dominates the intertidal zone. However at Oldbury mud once again covers the shore line between low and high water. In contrast the River Wye has not been subjected to the same degree of channelization for navigation purposes. The stretches of river sampled were composed of a sequence of riffles interdispersed by pools. The substratum of the riffles consists of gravels and cobbles. Macrophytes are present in considerable quantity both instream and along the margins of the river. In both rivers temperatures range from 8–11 °C in mid-April to a peak of around 20 °C during the summer. Details of the discharge pattern for the lower Severn can be found in Aprahamian (1981) and for the Wye in Edwards and Brooker (1982).

## Materials and methods

Samples of twaite shad were obtained from a number of sites in fresh, estuarine and coastal waters (Fig. 1) during 1979 and 1980. Pre- and post-spawning adults were obtained from the commercial salmon fishermen operating in the Severn Estuary during May and between June–August respectively. In fresh water pre-/partially spawned adults were sampled, using rod and line. At the end of September/early October samples of adult twaite shad were obtained from stake nets (mesh size 5 cm, knot to knot), which operate intertidally in Cardigan Bay.

Samples of the juvenile stages from all the freshwater sites and in the Severn Estuary (at Elmore, Framilode & Newnham) were caught using seine nets, except at Oldbury Nuclear Power Station where samples were obtained from the cooling water intake screens (Aprahamian & Barr, 1985). At the three upper estuarine sites sampling was carried out at low water while at Oldbury sampling commenced two hours after high water and continued for six hours. The stomach of alosids is a Y-shaped organ consisting of two parts, a terminal blind sac or gastric caecum, thin-walled and presumed to be used for storage and the pyloric region of the stomach where the muscle wall is considerably thicker enabling prey to be crushed (Harder, 1975). In all cases, except for the larvae, the composition of the diet was analysed using the contents of the blind sac, as these food items were still recognisable as opposed to those in the pyloric region of the stomach. However, in the case of the larvae, both the stomach contents and those of the hind intestine were analysed. Stomach contents were identified to order with dominant items to species. The total volume of the stomach contents was measured using a volumetric slide (Hellawell & Abel, 1971) with the exception of the larvae whose contents were too small for accurate measurement. The results were analysed using the frequency of occurrence, number and volume methods as described by Hynes (1950). For each sample the total number and volume of each food category was determined as a proportion of the total. These proportions were then summed and divided by the number of samples to produce a mean, in those cases where samples were combined.

## Results

### *Adult Alosa fallax*

The composition of the diet of pre-spawning twaite shad, collected from the Severn Estuary in May, is shown in Table 1, 48.3% of the sample

*Table 1.* The composition of the diet of pre-spawning *Alosa fallax* from the Severn Estuary at the start of the freshwater phase of their spawning migration.

| Food category | Occurrence % | Number % | Volume % |
|---|---|---|---|
| Mysidacea | 12.9 | 36.8 | 30.8 |
| Gammaridae | 80.6 | 59.7 | 50.2 |
| Idoteidae | 3.2 | 0.3 | 0.7 |
| Decapoda | 3.2 | 0.3 | 2.4 |
| Eggs (unidentified) | 19.4 | 2.9 | 0.4 |
| Detritus | 64.5 | | 15.6 |
| Mean/individual | | 5.7 | 37.6 $mm^3$ |

Number examined = 60; number empty = 29; fork length (mean ± s.d.) = 325 ± 34.1 mm.

had empty stomachs suggesting that the fish were not feeding actively. The most important food items, recorded in those fish with food in their stomachs, were *Gammarus* species followed by the Mysidacea.

At the two freshwater sites in the Severn catchment a high percentage of the fish sampled had empty stomachs; 69.4% and 60.0% (Table 2). Plastic and mainly allochthonous plant material constituted the major items in the stomachs of the remainder, with little animal matter present. In contrast, all the fish from the Wye had been feeding on animal material, mainly emergent adult Trichoptera. However the total volume of the food items per feeding fish was low, indicating, in all three rivers, that the fish were not actively feeding.

Post-spawning fish were obtained from the Upper Severn Estuary and due to the low numbers, data from two sites and for all months (June–August) were combined. The mean volume of food per post-spawned fish in the Severn estuary (Table 3) was between 100–400 times that of the pre-/partially spawned fish (Tables 1 & 2). The most important food items (Table 3) were mysids (*Neomysis integer* (Leach)) followed by gammarids (*Gammarus zaddachi* Sexton) and shrimps (*Crangon crangon* (L)). The post-spawning adults also exhibited occasional piscivory consuming typical members of the estuarine fauna; *Platichthys flesus* L, *Sprattus sprattus* (L) and members of the Gobiidae.

In Cardigan Bay at the end of September/start of October the mysid *Schistomysis spiritus* (Norman) dominated the diet, followed by fish ($O^+$ clupeids) (Table 3).

### $1^+$ *Alosa fallax*

The diet of fish caught in May, in the outer estuary (Oldbury) during their inshore migration was dominated by gammarids followed by calanoid copepods (Table 4). Eggs were the most important component numerically but constituted little in terms of volume. In contrast during the summer (June–August) $1^+$ twaite shad, present in the inner estuary (Newnham), fed mainly on the

*Table 2.* The composition of the diet of adult pre-/partially spawned) *Alosa fallax* from freshwater reaches of the Severn and Wye.

| Sample details/ Food category | Occurrence % | | | Number % | | | Volume % | | |
|---|---|---|---|---|---|---|---|---|---|
| Site | Powic | Diglis | Wye | Powic | Diglis | Wye | Powic | Diglis | Wye |
| No. examined | 62 | 15 | 25 | | | | | | |
| No. empty | 43 | 9 | 0 | | | | | | |
| Fork length mm (mean) | 316.5 | 324.3 | 294.6 | | | | | | |
| (s.d.) | ± 31.9 | ± 29.7 | ± 28.6 | | | | | | |
| Trichoptera A. | | | 26.7 | | | 77.1 | | | 43.0 |
| Trichoptera L. | | | 6.7 | | | 12.1 | | | 1.8 |
| Ephemeroptera N. | 5.2 | | 26.7 | 25.0 | | 14.6 | 0.6 | | 5.9 |
| Plecoptera N. | | | 6.7 | | | 2.1 | | | 0.7 |
| Chironomidae P. | | | 6.7 | | | 2.1 | | | 0.6 |
| Gammaridae | | | 6.7 | | | 2.1 | | | 0.6 |
| Lymnaeidae | 5.2 | | | 25.0 | | | 0.6 | | |
| *Alosa* scales | 5.2 | | | 50.0 | | | 0.2 | | |
| Eggs (unidentified) | | 66.7 | | | 100 | | | 4.6 | |
| Plastic material | 21.1 | | | | | | 16.6 | | |
| Plant material | 73.7 | 83.3 | 80.0 | | | | 82.0 | 95.4 | 47.5 |
| Mean/individual | | | | 0.06 | 0.9 | 1.9 | 14.4 | 10.1 | 21.9 $mm^2$ |

A = Adult; L = Larvae; N = Nymph: P = Pupae.

*Table 3.* The composition of the diet of post-spawning *Alosa fallax* from the upper Severn Estuary and Cardigan Bay.

| Sample details/ Food category | Occurrence % | | Number % | | Volume % | |
|---|---|---|---|---|---|---|
| | Severn Estuary | Cardigan Bay | Severn Estuary | Cardigan Bay | Severn Estuary | Cardigan Bay |
| No. examined | 36 | 13 | | | | |
| No. empty | 2 | 0 | | | | |
| Fork length mm (mean) | 346.3 | 339.3 | | | | |
| (s.d.) | ± 25.3 | ± 23.2 | | | | |
| Mysidacea | 94.1 | 100 | 94.6 | 98.6 | 84.8 | 66.6 |
| Gammaridae | 100 | 7.7 | 4.6 | 0.5 | 7.2 | < 0.1 |
| Crangonidae | 64.7 | | 1.1 | | 1.4 | |
| Idoteidae | | 7.7 | | < 0.1 | | < 0.1 |
| Ostracoda | | 7.7 | | < 0.1 | | < 0.1 |
| Decapoda | | 7.7 | | < 0.1 | | < 0.1 |
| Crustacea L. | | 7.7 | | < 0.1 | | < 0.1 |
| Mollusca | | 13.6 | | 0.1 | | < 0.1 |
| Pisces | 5.9 | 13.6 | < 0.1 | 0.9 | < 0.1 | 26.0 |
| Eggs (unidentified) | 11.8 | | < 0.1 | | < 0.1 | |
| Detritus | 79.4 | 61.5 | | | 6.6 | 7.3 |
| Mean/individual | | | 748.4 | 254.4 | 4328.8 | 2442.5 $mm^3$ |

L = Larvae.

*Table 4.* The composition of the diet of immature (age $1^+$) *Alosa fallax* from the Severn Estuary, during spring (May) and summer (June–August).

| Sample details/ Food category | Occurrence % | | Number % | | Volume % | |
|---|---|---|---|---|---|---|
| | Spring | Summer | Spring | Summer | Spring | Summer |
| No. examined | 20 | 31 | | | | |
| No empty | 0 | 2 | | | | |
| Fork length mm (mean) | 65.4 | 96.6 | | | | |
| (s.d.) | ± 0.9 | ± 15.2 | | | | |
| Mysidacea | 10.0 | 96.6 | < 0.1 | 94.2 | 0.3 | 90.6 |
| Gammaridae | 80.0 | 41.4 | 4.9 | 4.7 | 74.1 | 3.3 |
| Piscès | | 6.9 | | 0.4 | | 5.2 |
| Cladocera | | 3.4 | | 0.2 | | < 0.1 |
| Calanoidea | 50.0 | 3.4 | 10.9 | 0.2 | 2.8 | < 0.1 |
| Platyhelminthes | 30.0 | | 1.1 | | 0.9 | |
| Trichoptera N. | 5.0 | | < 0.1 | | 0.6 | |
| Terr. Insecta A. | | 3.4 | | 0.1 | | < 0.1 |
| Unid. Anim. Mat. | | 3.4 | | 0.1 | | 0.1 |
| Eggs (unidentified) | 40.0 | | 83.0 | | 0.6 | |
| Detritus | 90.0 | 10.4 | | | 20.9 | 0.7 |
| Mean/individual | | | 71.8 | 26.2 | 17.8 | 113.2 $mm^3$ |

A = Adult; N = Nymph.

mysid *N. integer* followed by gammarids and fish, mainly *S. sprattus* and members of the Gobiidae (Table 4).

### 0+ *Alosa fallax*

*i) Fresh water*

Details of the diet of larvae, all of which had absorbed their yolk sac, and of fully metamorphosed juveniles were obtained from sites on the River Wye (Pipton, Courtfield and Monmouth). The same groups of organisms characterised the diet of both larvae and juveniles, namely chironomid larvae and pupae, larvae of simuliid species and ephemeropteran nymphs (Table 5).

*ii) Estuary*

Samples of juvenile twaite shad were obtained from four sites in the Severn Estuary during the period July–October.

The diet (Table 6) was dominated by harpacticoid copepods (mainly *Tachidius discipes* Giesbrecht and a few *Microarthridion littorale* (Poppe)) and mysids *(N. integer)* followed by gammarids and calanoid copepods (*Eurytemora affinis* (Poppe)).

The smaller members of the zooplankton (harpacticoid and calanoid copepods, cladocerans (families Daphnidae and Chydoridae)) were more prominent in the diet during July and August when compared with September and October. In these latter two months the larger crustacean zooplankton (*N. integer, G. zaddachi, Gammarus salinus* Spooner, *Corophium volutator* (Pallas) and *Eurydice pulchra* leach) and fish species predominated.

## Discussion

The low level of feeding of the adult population during their upstream migration and while in fresh water agrees with the findings of Claridge and Gardner (1978) and Bracken and Kennedy (1967) for twaite shad in the Severn Estuary and River Suir (Ireland) respectively. However the fact that the freshwater samples were obtained by

*Table 5.* The composition of the diet of larvae and juvenile (age 0+) *Alosa fallax* from freshwater reaches of the River Wye in July and August.

| Sample details/ Food category | Occurrence % | | Number % | | Volume % |
|---|---|---|---|---|---|
| | Larvae | Juvenile | Larvae | Juvenile | Juvenile |
| No. examined | 53 | 46 | | | |
| No empty | 1 | 3 | | | |
| Fork length mm (mean) | 22.3 | 29.5 | | | |
| (s.d.) | ± 1.6 | ± 3.2 | | | |
| Chironomidae A. | | 13.8 | | 1.8 | 4.3 |
| Chironomidae L. | 79.3 | 88.0 | 34.3 | 30.4 | 24.4 |
| Chironomidae P. | 67.3 | 57.9 | 5.9 | 8.3 | 31.8 |
| Simuliidae L. | 98.3 | 45.7 | 48.3 | 15.6 | 18.1 |
| Ephemeroptera N. | 48.8 | 48.4 | 2.4 | 5.0 | 16.3 |
| Trichoptera L. | 2.4 | 7.2 | <0.1 | 0.9 | 1.7 |
| Molluscan Eggs | 6.5 | 6.7 | 8.9 | 38.1 | 3.0 |
| Cyclopoidae | 3.5 | | 0.2 | | |
| Ostracoda | 1.8 | | 0.1 | | |
| Detritus | | 1.8 | | | 0.4 |

A = Adults; L = Larvae; N = Nymphs; P = Pupae.

*Table 6.* The composition of the diet of juvenile (age $0^+$) *Alosa fallax* from the Severn Estuary.

| Sample details/ Food category | Occurrence % | | | | Number % | | | | Volume % | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | July | Aug. | Sept. | Oct. | July | Aug. | Sept. | Oct. | July | Aug. | Sept. | Oct. |
| No. examined | 54 | 85 | 77 | 19 | | | | | | | | |
| No. empty | 0 | 0 | 8 | 0 | | | | | | | | |
| Fk. Ln. mm (mean) | 26.4 | 36.3 | 49.7 | 52.1 | | | | | | | | |
| (s.d.) | ±4.0 | ±6.4 | ±8.8 | ±9.4 | | | | | | | | |
| Mysidacea | 75.0 | 25.4 | 81.9 | 100 | 23.7 | 2.9 | 30.6 | 59.3 | 58.5 | 19.2 | 70.5 | 77.7 |
| Gammaridae | 41.7 | 39.5 | 43.1 | 30.7 | 3.6 | 0.7 | 4.0 | 22.5 | 8.3 | 8.9 | 9.9 | 19.4 |
| Cladocera | 28.4 | 43.0 | 18.9 | | 0.8 | 2.0 | 1.5 | | 2.0 | 9.4 | 1.1 | |
| Harpacticoidea | 48.4 | 85.1 | 6.1 | | 47.1 | 82.4 | 26.4 | | 21.5 | 50.5 | 1.3 | |
| Cylopoidea | 6.7 | 29.4 | 1.0 | | 0.2 | 0.1 | 0.2 | | 0.9 | 0.9 | 0.1 | |
| Calanoidea | 61.7 | 29.4 | 33.5 | 18.2 | 24.3 | 11.8 | 15.1 | 17.9 | 6.6 | 6.9 | 6.2 | 1.2 |
| Ostracoda | | 6.7 | 6.1 | | | <0.1 | 0.2 | | | 0.1 | <0.1 | |
| Corophiidae | | | 1.0 | | | | 0.2 | | | | 0.5 | |
| Idoteidae | | | 2.3 | | | | 0.2 | | | | 0.3 | |
| Eggs (unidentified) | | | 12.0 | | | | 20.8 | | | | 0.2 | |
| Pisces | | 0.9 | 7.4 | | | <0.1 | 0.2 | | | 0.7 | 5.6 | |
| Chironomidae L. | 21.7 | 27.7 | | | 0.4 | <0.1 | | | 2.0 | 0.8 | | |
| Chironomidae P. | | 9.3 | | | | <0.1 | | | | 0.5 | | |
| Trichoptera N. | | | 3.0 | | | | <0.1 | | | | 0.2 | |
| Ephemeroptera N. | | 4.0 | 0.7 | | | <0.1 | <0.1 | | | 0.1 | <0.1 | |
| Diptera A. | 1.7 | 6.7 | 13.1 | 6.3 | <0.1 | <0.1 | 0.5 | 0.4 | 0.3 | 1.2 | 2.4 | 1.1 |
| Detritus | | 4.8 | 6.8 | 6.3 | | | | | | 0.9 | 1.5 | 0.6 |

A = Adult; L = Larvae; N = Nymph; P = Pupae.

angling, which is designed to entice prey with food, or its facsimile, may have biased the samples in favour of those fish with empty or partially filled stomachs. This assumes that the probability of catching a fish, by angling, increases with declining stomach fullness.

In the study by Claridge and Gardner (1978) stomach contents of fish sampled from the power station intakes contained only nereid jaws and small polystyrene spherules. Whereas in this study, gammarids though appearing not to have been consumed recently, occurred in 80% of the sample.

In the freshwater reaches of the Severn and the Wye the stomach contents of the adults were dominated by material of allochthonous origin, though the quality of the material constrasted markedly. This presumably reflects differing levels of productivity within the two river systems. The presence of allochthonous material in the stomachs suggests that the adults were feeding on relatively large particles in the drift or just at the waters' surface. The same conclusion may also be drawn from the study of Bracken and Kennedy (1967) where, though they found the majority of the stomachs were empty, a few contained adult stages of insects and plant material.

The reduction in feeding activity may have certain advantages. The cessation of feeding may be important for maintaining internal osmotic pressure as suggested by Nikolsky (1961). This strategy also allows a greater volume for occupation by gonad material which in females means an increase in egg number and/or size. It may however indicate that twaite shad are not morphologically and/or behaviourally adapted to feeding on benthic invertebrates (Brooks, 1968; Janssen, 1978) and would thus have to rely on drift and/or the plankton. The inference would then be that the quantity of drift and/or plankton is too low, or that the organisms are too small (Atkinson, 1951) to support active feeding.

Estuarine and coastal feeding was dominated by mysids with fish making only a small contribution to the overall diet. However the findings of Bracken and Kennedy (1967), Murie (1903), Rae and Lamont (1961 & 1962), Rae and Wilson (1952; 1956a & b; 1961) and Wheeler (1969) all indicate that in the marine environment fish and euphausiids were important components of the diet. The fact that this was not the case in the Severn Estuary or in Cardigan Bay may merely represent differences in the availability of suitable prey organisms.

Juvenile twaite shad in the fluvial environment of the Wye fed mainly on immature stages of chironomids and *Simulium* species. Similarly lotic populations of American alosids utilize immature stages of insects as well as zooplankton species (mainly copepods and cladocerans); *Simulium* larvae however did not appear to be an important constituent of their diet (Crecco & Blake, 1983; Davis & Check, 1966; Domermuth & Reed, 1980; Levesque & Reed, 1972; Mitchell & Staff, 1925; Walburg, 1956; Williams & Bruger, 1972).

Chironomid and *Simulium* larvae are generally regarded as benthic inhabitants and it is unlikely that twaite shad with their superior mouth position are morphologically adapted for feeding on the benthos. Certainly Brooks (1968) observed that *Alosa pseudoharengus* usually approach their prey from beneath which makes benthic feeding extremely difficult. Similarly Janssen (1978) found it was possible to train *A. pseudoharengus* to take food off the bottom, but only 10% of the encounters were successful. The implication therefore is that the juvenile twaite shad are feeding on the drift; in which both chironomids and *Simulium* species are abundant (Hemsworth & Brooker, 1981). The diet of juvenile twaite shad in the Severn Estuary consisted of zooplankton species, mainly copepods, cladocerans and mysids. Copepods and cladocerans were similarly found to be utilized by the American species of alosids in tidal waters (Burbridge, 1974; Davis & Cheek, 1966; Leim, 1924; Williams & Bruger, 1972). While in heavily wooded estuaries of the rivers studied by Massman (1963), juvenile *Alosa sapidissima* fed mainly on insects the majority of which were of terrestial origin (mostly Hymenoptera). Mysids were absent from the diet in the American studies which contrasts with the Severn Estuary study where they represent a major food source, perhaps again reflecting the differences in availability between various river systems. The findings also suggest that in the estuary juvenile twaite shad are well adapted to take advantage of changes in prey availibility, finding it profitable to feed on particles ranging in size from harpacticoid copepods to mysids. In the event of a tidal power barrage being constructed (Department of Energy, 1981) the juveniles should be able to cope with any changes in the planktonic food supply.

A number of studies have found an increase in the size of prey selected by alosids as they grow (Brandt, 1980; Crecco & Blake, 1983; Hutchinson, 1971; Morsell & Norden, 1968; Wells, 1970). A comparison of the diet of the $0^+$ and $1^+$ age-classes indicates a change with size; none of the $1^+$ age-class fed on the smaller members of the plankton (copepods and cladocerans) which were an important component in the diet of the $0^+$ age-class. There is obviously a morphological constraint on small fish taking large prey. It may, however, also be a tactic to reduce the risk from predation or physical stress by reducing the cost of foraging (Leviten, 1976) (density of particles declines with increasing size of the particle (Sheldon *et al.*, 1972)), that the $0^+$ age-class are less efficient at sampling their environment and/or that the energetic return of feeding on copepods and cladocerans is relatively higher when compared to the older fish (Mittlebach, 1981).

Other than physical and social factors the abundance of suitable prey items will determine the distribution of a species. In the River Severn, although twaite shad spawn as far upstream as Worcester, only a few juveniles were caught in that section of river downstream to Gloucester. The majority of the juvenile population were found in the estuary between July and October (Aprahamian, 1981). In contrast, in the River

Wye, juvenile twaite shad were found inhabiting pools well upstream of tidal influence, during July and August (Aprahamian, 1981).

The absence of juveniles from freshwater reaches of the River Severn may be due do the paucity of suitable food and/or lack of refuges from both biotic and abiotic factors (McCarthy, 1985). The majority of the bed between Worcester and Gloucester is not conducive to the establishment of a non-burrowing invertebrate population as the substratum does not provide any protection from predators or physical factors (Macan, 1961). The indications are, therefore, that the ecosystem of such rivers will be largely plant and detritus based (Weatherly, 1987). This contrasts with those freshwater reaches of the Wye, pool and riffle habitat, which are suitable for the production of non-burrowing macroinvertebrate species (Edwards and Brooker, 1982). In addition the Wye has more suitable habitat available for protection against predators and/or unfavourable flow regimes. It is thus suggested that the limited number of juveniles in the Severn between Worcester and Gloucester is due to lack of suitable prey species and/or a paucity of cover.

The strategy for juveniles in the Severn would thus appear to be to drift rapidly, either actively or passively to the estuary, an area of high productivity (McLusky, 1981), where the food organisms are both abundant and obtainable and adequate protection exists. While in the Wye, where the freshwater production of suitable prey species is greater and ample cover is available the juveniles remain feeding actively until a change in certain physical factors determines the onset of the autumn seaward migration (Claridge & Gardner, 1978; Kissil, 1974; O'Leary & Kynard, 1986; Richkus, 1975).


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