Seasonal Variation, Export Dynamics and Consumption of Freshwater Invertebrates in an Estuarine Environment

D. D. Williams[a,c] and N. E. Williams[b,c]

[a]*School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, U.K.*
[b]*Institute of Earth Studies, University of Wales, Aberystwyth, Dyfed SW23 3DB, U.K.*

In the Aber Estuary, North Wales, significant numbers of freshwater benthic invertebrates occurred in the tidal freshwater area. Distinct seasonal patterns were observed in their longitudinal zonation which appeared to be unrelated to variations in tidal inundation. The December extension downstream of freshwater taxa is hypothesized to be in response to decreasing water temperatures. In April, larvae/nymphs of the Trichoptera (caddisflies), Ephemeroptera (mayflies) and Plecoptera (stoneflies) ranged as far as a site inundated by 80·9% of all high tides, and larval Elmidae and Chironomidae (midges) occurred at the most marine site (inundated twice daily by all high tides). In July, with the exception of the Chironomidae, the range of most aquatic insects had contracted to the upper estuary. Although, in general, densities of aquatic insects decreased towards the lower estuary, significant densities persisted there. For example, maxima of 3514 chironomid larvae and 48 caddisfly larvae m^{-2} were recorded at the 80·9% inundation site. An estimated 31×10^6 freshwater invertebrates (weighing 62·6 kg), per annum, passed from fresh water into salt water across any given transect along the estuary. In comparison, the annual influx of invertebrates carried upstream by incoming tides was estimated to be $1·9 \times 10^6$ (6·2%; weighing 2·5 kg). Predominant in the downstream drift were the larvae/nymphs and/or pupae of chironomids, mayflies, stoneflies and caddisflies. The 'reverse' drift comprised mainly copepods, ostracods, amphipods and oligochaetes. Mites and the brackishwater amphipod *Gammarus zaddachi* commonly moved in both directions. Highest drift densities occurred in July, whereas the lowest densities occurred in late autumn and winter. Multiple regression analysis showed no relationship between total drift or 'reverse' drift densities and any of the measured environmental variables. Many of the freshwater invertebrates appeared not to die upon passing into tidal sections but resumed a benthic existence by virtue of varying degrees of salt tolerance. Of the three fish species common in the estuary, eel, common goby and flounder, the last two preyed measurably on freshwater taxa. Whereas gobies tended to be opportunistic feeders, depending on the section of estuary that they occupied, flounder were more restricted to the upper estuary where they fed selectively on chironomid larvae. On the latter diet, between March and September, the mean wet weight of flounders increased by more than 100 times (from 5 to 540 mg). Gobies were more numerous in the estuary from September to February, and although they ate insects their primary prey was *G. zaddachi*.

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Introduction

As rivers approach coastlines, they become influenced by salt water which periodically inundates freshwater communities and processes (tidal freshwater area, *sensu* Schuchardt *et al.*, 1993). There are varying degrees of inundation which are used, conceptually, to classify the different types of transitional environments, or estuaries. Typically this variation is predictable both in time and space. Along any estuary, there is a gradient in salinity which results in a longitudinal zonation of the biota. The classic pattern is one of

dominance of marine-derived taxa at the seaward end, occurrence of largely freshwater taxa at the landward end, and of a specialized, although somewhat depauperate, group of brackishwater-adapted taxa in between (e.g. Remane & Schlieper, 1971; Perkins, 1974; Cunha & Moreira, 1995). Whereas, there has been considerable study of the lower ends of estuaries together with their mesohaline faunas (e.g. Boesch *et al.*, 1976; Day *et al.*, 1989), in general, the freshwater invertebrate components of estuarine communities (termed 'tidal freshwater fauna' by some, e.g. Diaz, 1994) have been given short shrift by oceanographers and lotic biologists alike (Odum *et al.*, 1984; Laffoley & Hiscock, 1993; Schuchardt *et al.*, 1993).

[c]Address for correspondence: Division of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario, Canada M1C 1A4.

Further, the contribution of freshwater invertebrates (as downstream 'drift') to estuarine consumers is poorly known (Williams, 1980). Of concern is the fact that due to sewage and industrial discharges into the upper sections of estuaries, the diversity of this freshwater component is being replaced by a predominance of pollution-tolerant oligochaetes (McLusky *et al.*, 1993).

The present study aimed to provide information on the tidal freshwater fauna through a detailed, year round, qualitative and quantitative study of a river-dominated estuary in North Wales. The specific aims were: (1) to provide a description of the seasonal variation in the longitudinal distributions of the freshwater invertebrates; (2) to gather qualitative and quantitative data on the drift of these invertebrates across the freshwater seawater interface; and (3) to examine the gut contents of the predominant fishes in the estuary to determine if they feed on any of the freshwater taxa.

Study site

The Afon Aber, located in the county of Gwynedd, North Wales (54°14′N, 4°00′W), arises in the Carneddau mountain range. Its catchment is 24·5 km² and the watercourse itself comprises 82 first-order streams, 13 second-order streams, three third-order streams, and one fourth-order stream. The upper Aber Valley is composed of boulder clay, whereas the valley floor is made up largely of fluvio-glacial sand and gravel. Alluvium is present near the estuary mouth (Brown, 1960; Bassett, 1967). The upper watershed supports rough grazing for sheep, followed successively downstream by areas of coniferous plantation, the village of Aber, flat pasture and, finally, salt marsh.

Observation of water mass movements together with salinity measurements over 12 months, show the Aber Estuary to be of the freshwater-dominated, stratified, type. Freshwater flow-rates vary annually between about 30 and 110 cm s⁻¹ (discharge range=0·27 to 1·98 cumecs). The estuary is stratified on both rising and ebb tides, with a denser, bottom salt wedge that envelops the benthos. At the extreme edge of the wedge front (typically around 5–10 cm thick), salinity ranged between 8 and 17. Tides along this part of the Gwynedd shoreline are semi-diurnal with maximum annual tidal range of about 8 m on the open coast. Organisms on the estuary bed are thus subject to saltwater inundation twice daily.

Five sampling stations, each characterized by a different degree of saltwater inundation, were set up along the estuary (Figure 1). They were:
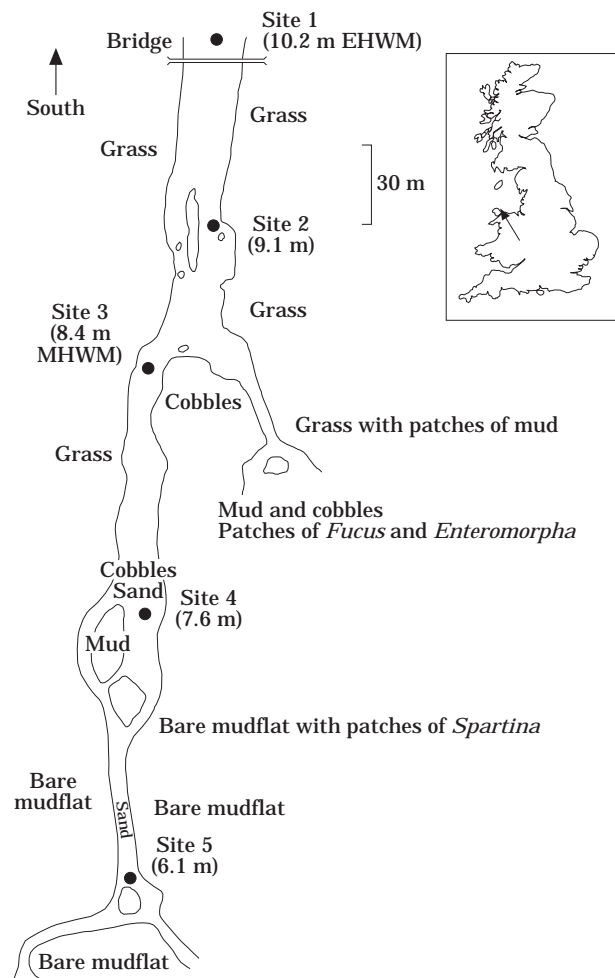

FIGURE 1. Map of the Aber Estuary showing features of the bed and channel, together with the five sampling sites located at specific tide heights (note that Site 1 is above the Extreme High Water Mark). Direction of the river flow is from top to bottom.

(1) At a point 5 m upstream of the maximum intrusion of the highest spring tide (extreme high water mark, EHWM=10·2 m); here the benthic fauna was exposed only to fresh water.

(2) At the 9·1 m mark; here the benthos was inundated by 33·7% of all high tides.

(3) At the 8·4 m mark which, in this region, represented the level of the mean high water mark (MHWM); here benthos was inundated by 50% of all high tides.

(4) At the 7·6 m mark; inundation by 80·9% of all high tides.

(5) At the 6·1 m mark; inundation by 100% of all high tides.

Percent of inundation by high tides was calculated by graphing the daily low and high tide heights at Menai Bridge over the previous year (1989–90), and

choosing a range of values for which corresponding sites along the Aber Estuary could be found. Sites were located at the appropriate times of high tide, and marker stakes were driven into the bed. Subsequent inundation measurements made during the study year (1990–91) showed some seasonal variation around the designated sites. For example, taking Site 3 (designated 50% inundation) as a reference point, 65% of all high tides inundated this site in April, compared with only 45% in June, 55% in September, and 50% in December.

At Sites 1–3, the substratum was typically riverine, comprising cobbles (up to 30 cm in diameter), stones, coarse and fine gravels, and coarse sand. At Site 4, there was much more sand, and at Site 5, the substratum was almost entirely sand. Whereas, there was evidence of occasional water-induced bed disturbance at these latter two sites, the substratum at the three uppermost sites remained largely undisturbed over the entire study period.

Materials and methods

Each site was sampled for benthic invertebrates at 3-month intervals over the period September 1990–July 1991. Samples were taken to a substratum depth of 5 cm, using a 250 µm mesh Surber Sampler (Surber, 1937) with a sampling area of 900 cm². Three, randomly positioned, replicate samples were taken from near the midline of the estuary bed at each site, starting, on each occasion, at Site 5 and working upstream. Samples were preserved in 95% ethanol in the field. In the laboratory, the samples were rinsed with tap water, floated in saturated calcium chloride solution (to help separate the animals from the inorganic substratum), and examined under a dissecting microscope. Individual animals were removed from the surrounding detritus, identified and preserved in 75% ethanol.

Drifting animals were sampled for 24 continuous hours, each month from early September to the end of July, using two nets. Each 250 µm mesh nylon net was 1 m long, with a 24 × 44 cm opening. Attached to the opening was a reversed, galvanized metal funnel which reduced the effective entry port to a narrow vertical slit measuring 5 × 20 cm. Reduction of the sampling window in this manner is standard practise in drift research as it prevents excess fine particulate material from entering the net, clogging up the mesh and causing a bow-wave effect at the net mouth with consequent loss of part of the sample. The two nets were attached to iron posts driven into the estuary bed and had their lower edges resting on the substratum

with the funnel mouths facing upstream. The nets were located 1 m apart at the 8·7 m tide level in the estuary, a point inundated by approximately 40% of all high tides. The channel width, at low tide, at this point was for example, in September, approximately 4·5 m, with a freshwater depth of 20 cm and a current speed of around 35 cm s^{-1}. Seasonal variations in freshwater flow conditions are given in Table 1. Sampling times were chosen always to coincide with a high tide that did not reach the nets and therefore 'contaminate' them. After 24 h, the contents were emptied into polyethylene bags and preserved with 95% ethanol.

'Reverse' drift, that is organisms moving up the estuary on incoming tides, was sampled, again monthly, using the same nets but positioned with the funnel entrances facing downstream. The nets were attached to stakes at the 8·4 m tide level and remained in place for 24 h, that is through two high tides. To prevent loss of collected materials due to flushing by fresh water during the intervening low tide, a baffle was inserted into each funnel. Additionally, the distal end of each net was tied to an upstream stake, to prevent collapse by the force of the fresh water.

In the laboratory, both drift and reverse drift samples were processed by separating the invertebrates from background detritus, the latter being visually assessed, dried and weighed (Table 1). The invertebrates were identified to species, wherever possible, counted and wet weighed.

Collections of the fishes living in the Aber Estuary were made both at low tide and at moderately high tides using both a 10 m seine (1 cm mesh) and, more successfully, a 45 cm wide dipnet (250 µm mesh). Collections were made on eight separate occasions throughout the year between Sites 2 and 5. Specimens were preserved immediately in 10% formalin solution. In the laboratory, they were identified, measured (body length and maximum mouth gape) and assigned to length size classes which were based on total size range rather than on specific cohorts. Subsequently, their stomach contents were removed for diet analysis. Three measures were calculated:

(1) The Index of Relative Importance (I.R.I.) of Pinkas et al. (1971). This was calculated as:

$$I.R.I. = (\%N + \%V) \times \%FO$$

where $\%N$ is the numerical percentage of a food type, $\%V$ is its volumetric percentage, and $\%FO$ is its percentage frequency of occurrence in the gut.

(2) The Food Niche Breadth Index (W) of Petraitis (1979). W incorporates an expression of potential prey availability and is approximately equal to the

TABLE 1. Environmental data associated with the times at which the drift samples were taken in the Aber Estuary

Date	Water depth (cm)	Current (cm s^{-1})	River temperature (°C)	Organic matter (g dry wt)	Total number of invertebrates		Biomass (g)
					Counts	Density[a]	
September	20	35	13·0	5·9 Green leaves	581	1816	888·3
October	30	50	12·5	56·2 Green leaves	340	500	4302·2
November	30	55	7·0	80·6 Green leaves	127	172	1454·0
December	37	90	4·0	33·5 Brown leaves	620	413	5932·8
January	32	65	2·0	51·4 Brown leaves	203	216	506·7
February	22	45	4·5	53·2 Brown leaves	540	1200	9244·6
March	28	50	5·0	13·2 Leaves+CPOM	942	150	3665·8
May	40	85	6·0	16·2 Leaves+CPOM	3234	2114	18 740·4
June	40	85	9·0	14·7 Filamentous algae/green leaves	825	539	2346·3
July	30	50	16·0	3·8 Filamentous algae/green leaves	2409	3542	2787·2

[a]Drift densities were calculated from the drift counts converted to standard river discharge and represent number m^{-3} 24 h^{-1}.

chi-square goodness-of-fit test. W ranges from a value of 0 (specialist feeder) to 1·0 (generalist feeder) and measures the likelihood that the observed proportional resource usages are the same as the proportions available. It was calculated as:

$$W=(\partial)^{1/N}$$
$$\ln \partial = \Sigma in_i \ln(a_i) - \Sigma in_i \ln(Px_i)$$

where Px_i is the proportion of food type i in species x; n_i is the amount of resource i used; a_i is the number of food type i in the environment; and N is the total number of resources used.

(3) The Niche Overlap Index (C_{xy}) of Schoener (1970). Values of C_{xy} range from 0 (no overlap) to 1 (complete overlap), with values >0·6 considered to be biologically significant. It was calculated as:

$$C_{xy}=1 - 0·5 \ (\Sigma[Px_i - Py_i])$$

where Px_i is the numerical proportion of food type i in the diet of species x and Py_i is the numerical proportion of food type i in the diet of species y. See Delbeek and Williams (1987) for further details of these protocols. Prior to statistical analyses, the data were examined for normality and homoscedasticity, and were transformed to log x where appropriate.

Results

Longitudinal zonation of the fauna and its seasonal variation

The distribution patterns of the major taxa found at the five sampling sites along the Aber Estuary can be assigned to three basic categories, illustrated by the September dataset (Figure 2). The first pattern was of a largely upstream distribution (Site 1) and was seen best in the caddisflies and mayflies. Chironomid and simuliid larvae were found as far downstream as Site 4. A few live elmid beetle larvae and stonefly nymphs were found at Site 5. The second pattern was of a largely downstream distribution and was seen in the marine-derived taxa, for example the bivalves, gastropods, polychaetes, ostracods and decapods. With the exception of some ostracods (where there were both freshwater and marine species present), none of the marine taxa was found further upstream than Site 3. The third distribution pattern was intermediate and exhibited by brackishwater taxa, for example the amphipods and isopods. Their numbers were typically greatest at Sites 2, 3 and 4. The distributions of a few taxa did not fit the above three patterns, as they were complicated by a succession of species that spread the range of their group over the five sites, for example the oligochaetes, nematodes and mites. Chironomid
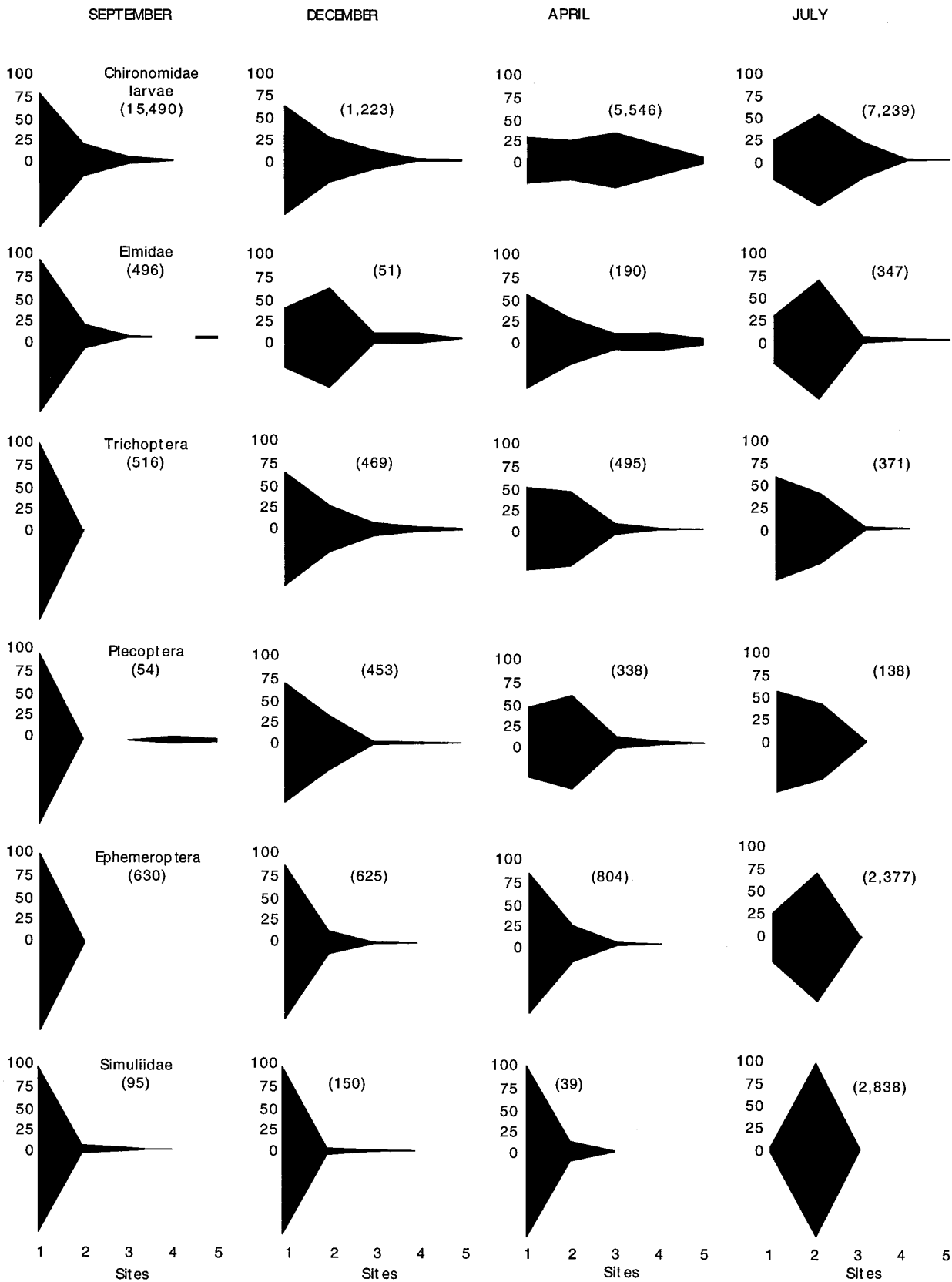
FIGURE 2. Longitudinal zonation of the major invertebrate taxa across the five sites (Site 1 being the most landward site). The kite diagrams represent percent occurrence based on the total numbers of animals found on each sampling occasion (indicated in brackets). Taxa are arranged beginning with those largely occurring in the upper estuary and ending with those occurring predominantly in the lower estuary.
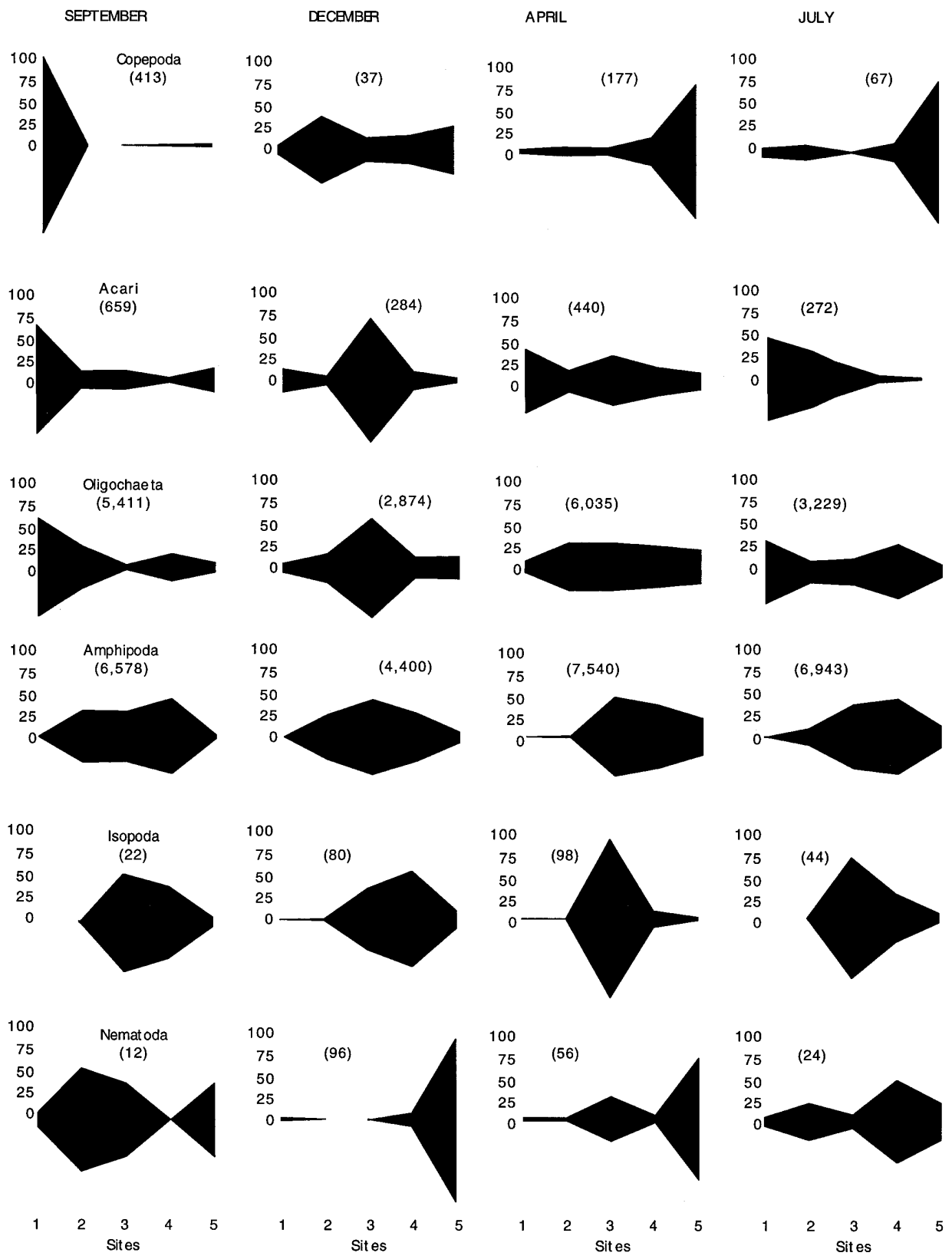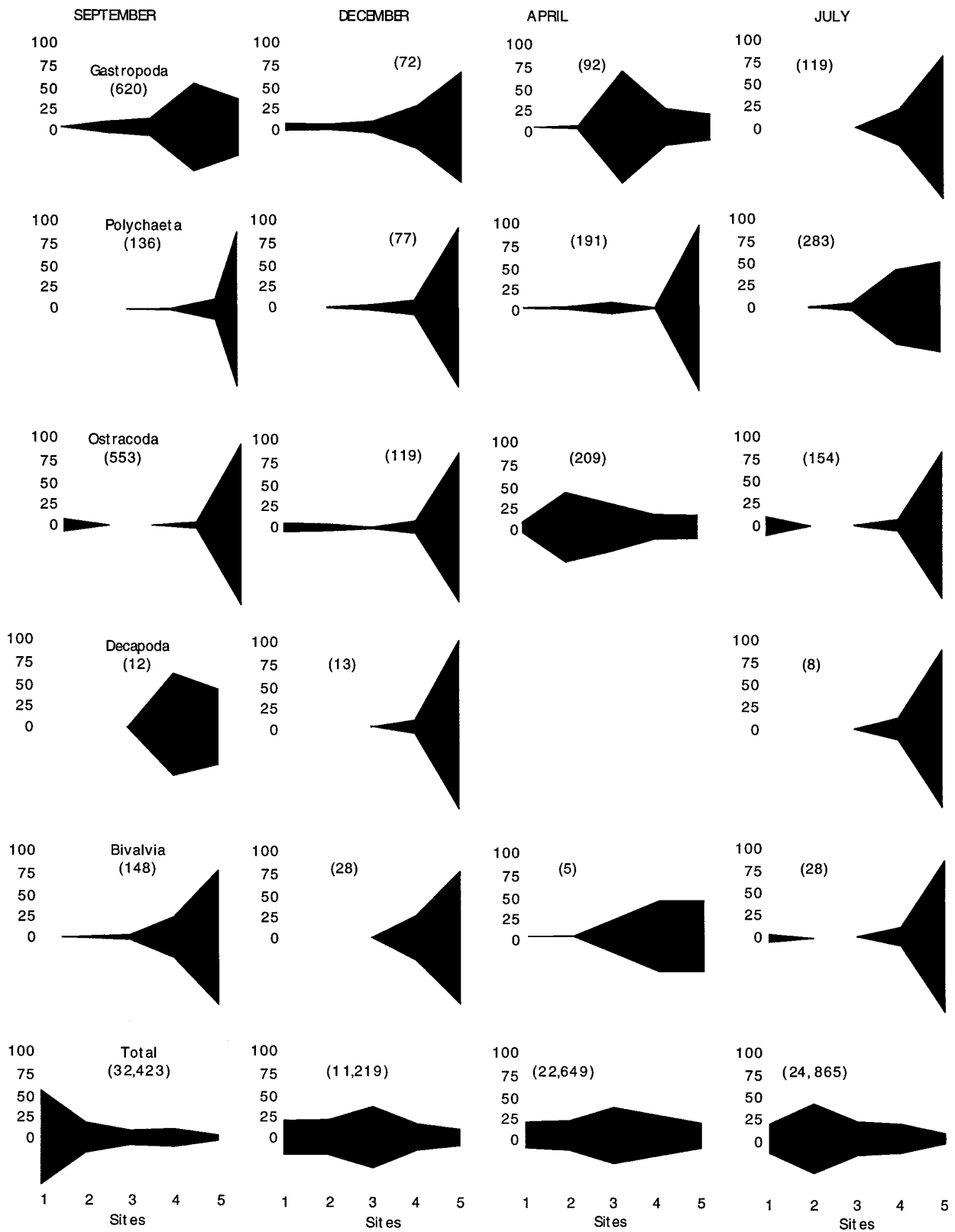
FIGURE 2. *(continued)*

FIGURE 2. *(Continued)*

pupae and adults were caught at Sites 2 and 3 in greater proportions than the larvae, and this probably reflects their increased vulnerability to being displaced by the current during these life cycle stages. In terms of the overall distribution of invertebrates in the Aber in September, the greatest numbers occurred at Site 1 and the least at Site 5, with relatively even numbers at the three intermediate sites (Figure 2).

In December, the three basic distribution patterns were still evident, however there were some notable changes. Most of the freshwater taxa showed extended ranges (e.g. the caddisflies, mayflies and chironomid larvae), and/or shifts in their proportions at down-stream sites (e.g. the elmid beetles) (Figure 2). Among the marine-derived taxa, there was an appar-ent retrenchment to the lowermost sites (e.g. as in the bivalves, decapods and fishes), sometimes accompanied by reduced densities (e.g. gastropods). The distribution of the brackishwater taxa remained the same. However, there were marked changes in the distributions of the nematodes, oligochaetes, mites and copepods. The overall distribution pattern had shifted to one where the greatest numbers occurred at Site 3.

In April, the caddisflies, mayflies and stoneflies still penetrated as far as Site 4, and the elmids and chironomids as far as Site 5 (Figure 2). Oligochaetes, mites and ostracods were more uniformly distributed among all five sites, but the amphipods were concen-trated at Sites 3–5. Some of the marine taxa, for example, the bivalves and polychaetes, were found in low numbers as far upstream as Site 2. The greatest numbers of animals again were found at Site 3.

In July, with the exception of the chironomid larvae, the range of most of the aquatic insects had contracted to Sites 1 and 2, with the bulk of the elmids, simuliids and mayflies occurring at Site 2 (Figure 2). The extended distributions of the oligochaetes, nematodes and copepods reflected the presence of more than a single species, and those of the bivalve and ostracod species were clearly disjunct. Marine-derived taxa were typically found at, and downstream from, Site 3. Highest overall densities were at Sites 1 and 2.

Whereas the densities of most insect taxa dropped substantially downstream from Site 1, there were significant numbers present further down the estuary at certain times of the year. For example, the densities of chironomid larvae at Sites 1 and 3 were not significantly different in either April or July (April: $481 \cdot 0 \pm 106 \cdot 9$ and $576 \cdot 7 \pm 49 \cdot 5$ larvae 900 cm^{-2}; July: $565 \cdot 7 \pm 128 \cdot 8$ and $507 \cdot 7 \pm 38 \cdot 4$ larvae 900 cm^{-2}; Student's $t = -0 \cdot 81$ and $0 \cdot 43$, respect-ively; $P > 0 \cdot 4$). Further, in April, at Site 4 (inundated by 81% of all high tides), a mean of $316 \cdot 3 \pm 41 \cdot 4$

larvae was recorded on only 900 cm^2 of estuary bed (3514 m^{-2}). Even at Site 5, inundated by all high tides, there were $67 \cdot 3 \pm (31 \cdot 1)$ larvae 900 cm^{-2} (747 m^{-2}). Among the larger aquatic insects, caddis-fly and elmid beetle larvae together with stonefly nymphs were consistently taken at Site 4, although their densities were lower. Nevertheless, when ex-pressed on a m^{-2} basis the numbers are unexpectedly high (e.g. a maximum of 48 caddisfly larvae m^{-2} in December and 70 elmids m^{-2} in April).

Summarizing the proportional representation of the freshwater, brackishwater and saltwater species in the classical style (*sensu* Remane & Schlieper, 1971) (Figure 3), shows a predominance of the first two categories. This confirms the earlier hydrological designation of the Aber Estuary as being of the freshwater-dominated type.

Export dynamics

Environmental conditions measured during the time the drift samples were taken are summarized in Table 1. Also shown are the total drift densities and bio-masses, together with the amounts and types of organic materials entering the estuary from upstream. The lowest drift densities consistently occurred during late autumn and winter, whereas the highest density occurred in July. Peak drift biomass occurred in late spring (April/May), a time when many lotic insects are in their largest immature stages, prior to emergence as terrestrial adults. Peak allochthonous input was dur-ing late autumn and consisted primarily of shed ripar-ian leaves. Multiple regression analysis applied to this dataset revealed no statistically significant relation-ships between either total drift density or total drift biomass and any of the measured environmental vari-ables (overall $r^2 = 0 \cdot 27$; $P > 0 \cdot 3$, and $r^2 = 0 \cdot 17$; $P > 0 \cdot 5$, respectively). Stepwise regression further revealed no significant single variable correlations.

The total invertebrates brought into the estuary on incoming tides varied between $1 \cdot 8$ and $94 \cdot 6\%$ (August and June, respectively) of the numbers brought down by the river (Tables 1 and 2). However, the taxonomic composition from the two sources was quite different. Predominant in the downstream drift were the larvae/nymphs and pupae of insects, notably midges (Chironomidae), mayflies (Ephemeroptera), stone-flies (Plecoptera) and caddisflies (Trichoptera) (Table 3). Predominant in the 'reverse' drift were copepods, ostracods, amphipods and oligochaetes. Only mites and the brackishwater amphipod *Gammarus zaddachi* were commonly caught moving in both directions. Amongst the insects, only chironomid larvae moved upstream in appreciable numbers. Peaks in 'reverse'
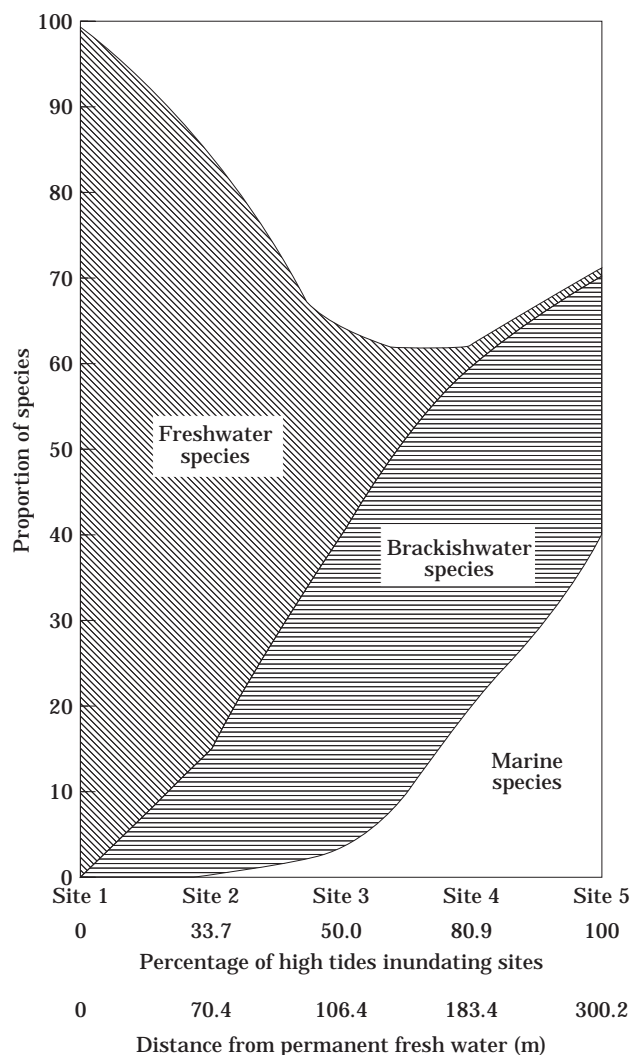
FIGURE 3. Proportional representation of the freshwater, brackishwater and saltwater species in the Aber Estuary expressed both in terms of the linear distance from permanent fresh water (Site 1) and of the percentage of high tides inundating each site with salt water. ▨, freshwater species; ▤, brackishwater species; □, marine species.

drift biomass occurred from April to June, coinciding with the times of peak ' reverse ' drift density. The amount of organic matter entering the estuary from the sea was generally small but peaked when strong onshore winds coincided with high tides (Table 2). Again, multiple and stepwise regression analysis applied to this dataset revealed no relationship between either total ' reverse ' drift density or biomass and any of the measured environmental variables (overall $r^2 = 0.12$; $P > 0.6$, and $r^2 = 0.35$; $P > 0.2$, respectively).

Among the larger aquatic insects drifting into the estuary were five species of mayfly, 13 species of stonefly, and 12 species of caddisfly, many of which exhibited different drifting profiles (Table 4). For example, whereas some entered virtually the whole year round (e.g. *Baetis rhodani*, *Chloroperla torrentium*, *Amphinemura sulcicollis*, *Hydropsyche siltalai*), others appeared to be more seasonal (e.g. *Leuctra hippopus*, *L. inermis*, *Agapetus delicatulus*). Very few of these larger insects moved back upstream into fresh water (Table 4).

Extrapolating the drift data by multiplying them by the cross-sectional area of the estuary (at the net site) and the number of 24 h periods in specific months, and then totalling the product for each month, provides an estimate of 30.9×10^6 freshwater invertebrates (weighing approximately 62·6 kg, wet weight) entering the estuary per annum. This calculation assumes that drift density was uniform across the estuary channel (which probably produces a slight overestimation) and does not take into account the distances drifted by individuals. Because it represents the numbers passing through a two-dimensional window, and there are many such possible windows along the estuary, an estimate for the total export of freshwater invertebrates into saltwater regions of the estuary is likely to be very much higher. By similar extrapolation, the annual influx of invertebrates brought by incoming tides is estimated to be 1.9×10^6 (weighing 2·5 kg), again subject to the same assumptions and errors.

Consumption of invertebrates and fish growth

Three fish species occur commonly in the Aber Estuary, eel (*Anguilla anguilla*), flounder (*Platichthys flesus*) and common goby (*Pomatoschistus microps*). Eel and flounder were most abundant between sites 2 and 3, whereas gobies extended from just below Site 2 down to Site 5. All three species exhibited growth while in the estuary. The smallest elvers (5·9–6·8 cm long) appeared between March and May, and by mid-summer had attained lengths of up to 14 cm (size class 3; Figure 4). Small (size class 1, 0–1·1 cm) flounders first appeared from March to May, and by June/August many had attained size class 3 (2·2–3·1 cm). A few specimens were more than 3·2 cm in length by September/November. The mean wet weight of the flounders when they first appeared in the estuary was $0.005 \text{ g} \pm 0.0002$ (± 1 SE), compared with $0.54 \text{ g} \pm 0.1$ when they left some 30–35 weeks later. This represents an average weight increase of 108 times. Gobies were most numerous in September–November, however their growth was more difficult to ascertain as fishes from three separate size classes had entered the estuary at this time.

The guts of all but two of the 23 eels dissected were empty (Figure 5). Of the former, one contained a

TABLE 2. Environmental data associated with the times at which the upstream samples were taken in the Aber Estuary

Date	Tide height (m)	Current/wind conditions)	Sea temperature (°C)	Organic matter[a] (g dry wt)	Total number of invertebrates[b]	Invertebrate biomass (g)
October	9·73	Strong/gale force	13·0	1·5	63	148·6
November	9·42	Strong/onshore	8·0	25·5	50	577·4
December	9·57	Strong/calm	5·0	0·08	35	438·4
January	9·12	Medium-strong/along-shore	6·0	0·11	142	130·1
February	9·15	Medium strong/strong along-shore	5·5	4·4	44	280·6
March	8·66	Weak/calm	5·5	0·23	147	96·5
May	9·63	Medium-strong/along-shore	11·0	0·96	304	124·4
June	9·45	Medium-strong/calm	13·0	3·9	510	370·8
July	8·41	Weak/calm	14·5	0·04	31	30·2
August	8·84	Weak/calm	15·5	0·0	63	147·7

[a]The small amounts of organic matter collected typically consisted of pieces of fucoid seaweeds, hydroid skeletons, filamentous algae, unidentifiable flotsam, together with terrestrial leaves in the autumn and early winter.
[b]Represents the numbers of animals caught over a 24-h period–two high tides—converted to a standardized tide height.

single large shrimp (*Crangon crangon*), the other contained several chironomid larvae. Most of the goby stomachs were at least half full, with 20% distended. Taxa prominent in the diet varied according to fish size, probably related to respective mouth gape size. Gobies in the 0–1·0 cm size class primarily ate harpacticoid copepods, oligochaetes and small amphipods (Figure 6), and this was largely true also for individuals in the 1·1–2·1 cm size class. The largest gobies, however, fed almost exclusively on larger specimens of *Gammarus zaddachi*, supplemented by chironomid and other dipteran larvae. Chironomid larvae were extremely important in the diets of all four size classes of flounder examined (Figure 7). Harpacticoid copepods, oligochaetes and small polychaetes were eaten also by flounders in size classes 1 and 2 (up to 2·1 cm long). More than 75% of the flounder guts examined were at least half full (Figure 5).

Analysis of the diet of the gobies among sites showed them to be quite opportunistic feeders. For example, at upstream Sites 2 and 3 individuals fed mostly on freshwater harpacticoids, mayflies, chironomids, small amphipods and oligochaetes (Figure 8), whereas at Site 4, *G. zaddachi* was included. At downstream Site 5, polychaetes, other oligochaetes, and marine copepods and ostracods formed the bulk of the diet.

Comparison of the diets of size classes of flounder and goby with similar gape sizes (closest comparison is $2·14 \pm 0·06$ and $3·09 \pm 0·09$ mm gape, respectively) gave a food niche overlap index value (Cxy) of 0·23, which is not considered to be biologically significant (Schoener, 1970). Further, determination of Food Niche Breadth (W; which took into account measures of potential prey availability in the estuary; Petraitis,

1979) showed both gobies and flounder to be specialists (W was close to zero for both species), although, in the case of the gobies, the prey specialized upon varied according to site.

Discussion

The limited existing faunal data indicate that tidal freshwater habitats have low species diversity, compared with brackish sections of estuaries and the non-tidal sections of rivers (Lopez, 1988), and that the major taxa present are tubificid worms and chironomids, together with molluscs, crustaceans and 'other' insects (Diaz, 1994). The fauna of the Aber Estuary confirms, to some extent, this taxonomic mix although there are important differences. Firstly, taxon richness was even along the entire length of the estuary, in that the 17 major taxonomic groups recorded (Figure 2) were present at all five sampling sites. Further, within the Trichoptera, the most diverse insect group and one which was identified to species, apart from a difference at Sites 1 and 5 (14 and 4 species, respectively), the complement of species was again even (11 species at each of Sites 2, 3 and 4). Second, whereas chironomids and oligochaetes were the numerically dominant taxa, 'other' insects (Trichoptera, Plecoptera, Ephemeroptera, Elmidae and Simuliidae) formed 10% of the total numbers of organisms collected at the tidal sites (2–5). Numerically, adding the chironomids, aquatic insects made up 32% of the Aber benthic fauna. The importance of chironomids has been shown also in the James River Estuary, Virginia, where *Coelotanypus scapularis*, along with the clam *Corbicula fluminea* and

TABLE 3. Details of the numbers of individuals caught drifting downstream and moving upstream (shown in brackets) at different times of the year in the Aber Estuary. The unit of measure was a 200 cm² area of water column, over a 24 h period, each month

Taxon	September[a]	October	November	December	January	February	March	May	June	July	August[a]
Nematoda	0	0 (0)	1 (1)	0 (2)	0 (0)	0 (1)	0 (0)	0 (1)	0 (1)	6 (0)	(0)
Polychaeta	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (7)	3 (1)	0 (0)	(0)
Oligochaeta	10	0 (6)	0 (4)	0 (1)	2 (2)	4 (0)	25 (0)	0 (4)	10 (25)	1 (1)	(0)
Ostracoda	0	0 (1)	0 (1)	0 (0)	0 (0)	0 (1)	0 (112)	9 (24)	0 (9)	0 (3)	(3)
Copepoda	1	0 (14)	0 (2)	0 (18)	0 (35)	22 (29)	3 (3)	12 (49)	1 (32)	0 (2)	(8)
Corophium sp.	0	0 (5)	0 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (27)	0 (0)	(0)
Gammarus pulex	0	0 (1)	0 (0)	4 (2)	1 (0)	2 (0)	0 (0)	6 (0)	0 (0)	1 (0)	(0)
G. zaddachi	116	84 (6)	64 (32)	78 (8)	0 (8)	196 (6)	0 (2)	18 (2)	45 (9)	79 (2)	(18)
Gammarus sp.	22	2 (3)	1 (0)	0 (0)	0 (14)	78 (2)	23 (1)	33 (8)	28 (32)	49 (0)	(4)
Crangon crangon	0	0 (0)	0 (0)	0 (0)	0 (1)	0 (1)	0 (0)	0 (0)	0 (18)	0 (0)	(10)
Decapoda (larvae)	0	0 (0)	0 (1)	0 (0)	0 (0)	2 (1)	0 (0)	0 (2)	0 (7)	0 (0)	(2)
Acari	9	12 (1)	9 (1)	24 (0)	2 (7)	14 (1)	7 (0)	78 (4)	86 (37)	74 (3)	(8)
Collembola	0	0 (1)	0 (0)	0 (0)	10 (0)	12 (0)	14 (1)	36 (1)	7 (1)	4 (0)	(0)
Plecoptera	4	4 (1)	1 (0)	74 (0)	14 (0)	22 (0)	69 (0)	81 (1)	4 (1)	13 (0)	(0)
Ephemeroptera	2	80 (2)	4 (0)	94 (1)	50 (0)	22 (0)	84 (1)	102 (3)	51 (0)	4 (0)	(0)
Trichoptera	0	8 (1)	1 (0)	92 (0)	13 (0)	56 (0)	89 (0)	123 (2)	10 (0)	5 (0)	(0)
Coleoptera	1	11 (3)	4 (1)	16 (0)	2 (0)	12 (0)	22 (1)	123 (0)	12 (0)	26 (0)	(0)
Tipulidae	1	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	4 (0)	12 (0)	5 (0)	1 (0)	(0)
Psychodidae	0	0 (0)	1 (0)	2 (0)	0 (0)	0 (0)	6 (0)	0 (0)	0 (0)	2 (0)	(0)
Dixidae	0	5 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	(0)
Simuliidae	1	8 (0)	2 (0)	136 (0)	69 (2)	8 (0)	17 (0)	72 (0)	6 (0)	38 (1)	(0)
Ceratopogonidae	0	9 (0)	4 (1)	0 (0)	0 (0)	0 (0)	0 (2)	765 (0)	3 (0)	7 (0)	(0)
Chironomidae	381	74 (12)	25 (2)	88 (2)	36 (1)	70 (1)	506 (21)	1596 (16)	415 (21)	1993 (19)	(0)
Other Diptera	1	1 (1)	0 (1)	4 (0)	1 (0)	6 (0)	14 (1)	9 (1)	2 (2)	7 (0)	(0)
Terrestrial	7	24 (2)	50 (1)	10 (2)	5 (0)	4 (0)	10 (1)	279 (1)	82 (7)	53 (3)	(1)

[a]Upstream samples were not taken in September 1990 and drift samples were not taken in August 1991.

TABLE 4. Numbers of prominent freshwater insect species drifting into, or moving upstream from (indicated in boldface), saltwater-inundated regions of the Aber Estuary

Taxon	September	October	November	December	January	February	March	May	June	July
Ephemeroptera										
Baetis rhodani	2[a]	80	2	80	45	22	61 [1]	135 [3]	10	6
Caenis sp.		[1]	1	4	1		10	18 [1]	32	
Ecdyonurus sp.			1	10			4	12		
Ephemerella sp.								3	3	
Rithrogena semicolorata				[1]	4		9	18	4	1
Plecoptera										
Adicella reducta						2				
Isoperla sp.				4	1		4	3		
Perla bipunctata							3	12		
Protonemura meyeri		[1]		6		2	4	3		
Leuctra moselyi	4	1								
L. hippopus				14	2	6	22			
L. inermis						6	3	12 [1]	[1]	
L. nigra								12		
L. fusca									1	10
Chloroperla torrentium		1	1	2	17	4	8	24	9	
C. tripunctata						2				
Amphinemura sulcicollis		1		4	28	2	16	18		2
Nemouridae (unidentified)			4							
Trichoptera										
Agapetus delicatulus		1						54 [2]	20	4
Lepidostoma hirtum				4			7	12	1	1
Silo pallipes										1
Glossosoma boltoni				8	4	2				
G. intermedium				2	1	10	12			
Hydropsyche siltalai		3		36	4	8	4	12	1	
H. instabilis				10	2	18	3			
Hydroptila sp.				4						
Philopotamus montanus		3		6						
Wormaldia sp.					1				1	
Rhyacophila dorsalis		1		14		6	8			
Polycentropodidae (unidentified)			[1]					4	19 [1]	15

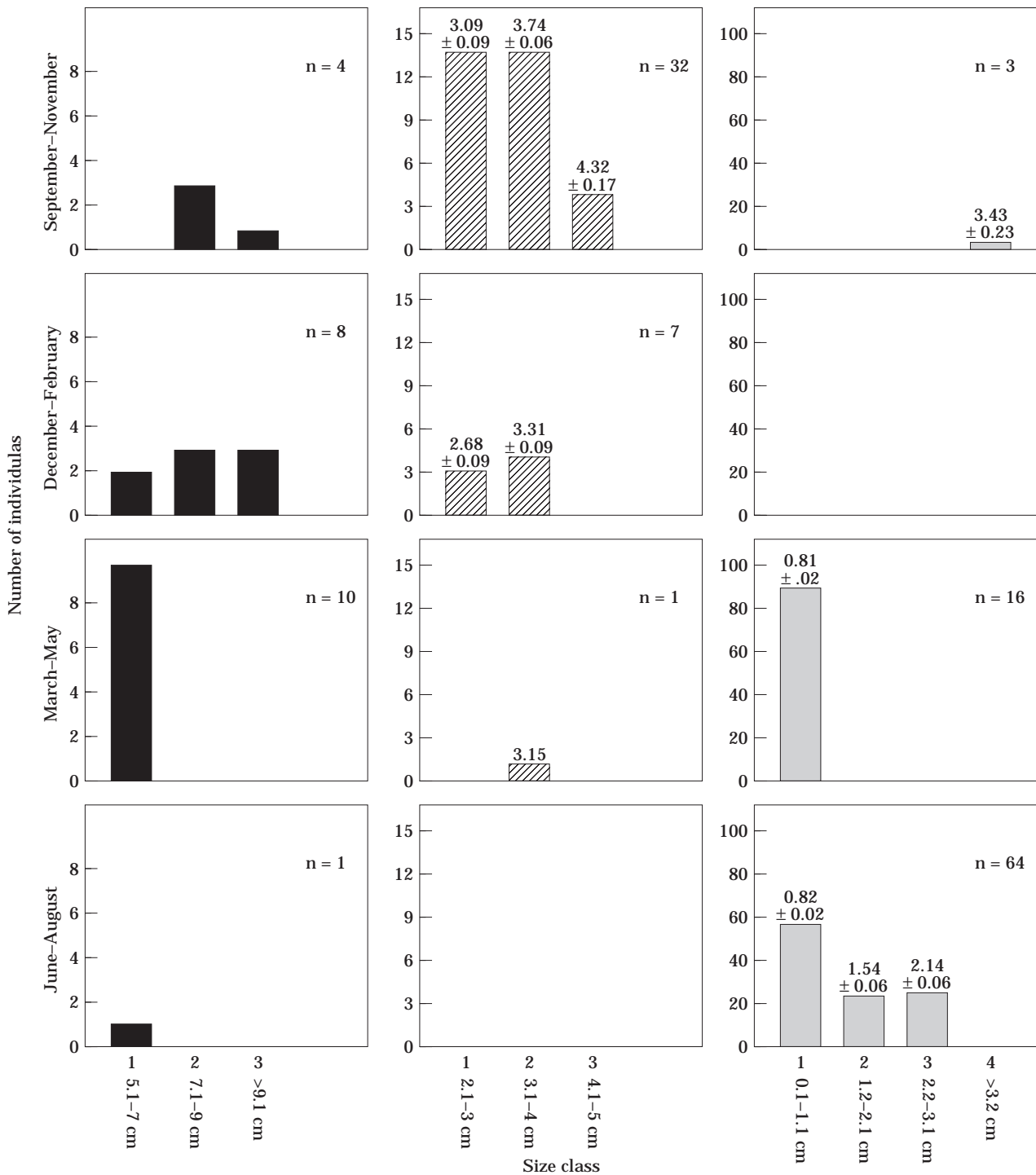[a]The numbers represent animals caught in a 200 cm^2 area of water column, over a 24 h period, each month.

FIGURE 4. Numbers of the three principal species of fish caught in the Aber Estuary throughout the period September 1990 to August 1991. Individuals of each species are assigned to body length size classes. Mean gape size (measured in mm; ± 1 SE) is also shown for each size class of goby and flounder. ■, eel; ▨, goby; ▧, flounder.

tubificid worms (*Limnodrilus*), dominated the tidal freshwater community (Diaz, 1989).

Clearly, there are differences in the longitudinal zonation patterns among the different taxa living in the Aber. Classic examples of a largely freshwater, upstream distribution (e.g. the mayflies, stoneflies and black flies), a largely marine, downstream distribution (e.g. the decapods, bivalves, gastropods and
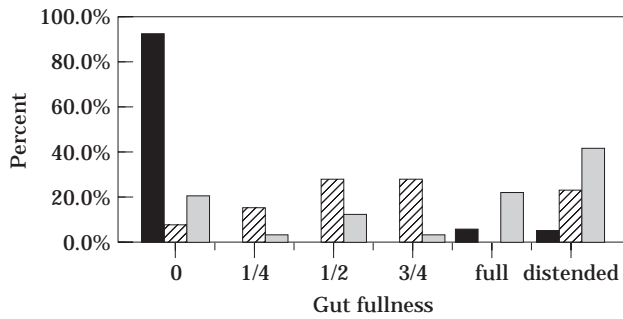
FIGURE 5. Relative fullness of the guts of the three fish species caught in the Aber Estuary. ■, eel; ▨, goby; ▢, flounder.
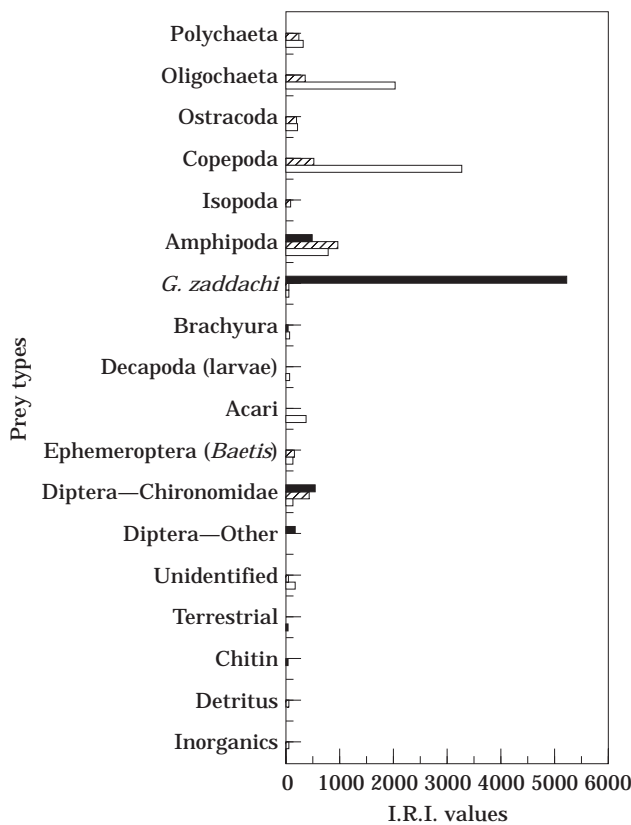

FIGURE 6. Comparison of the diets of gobies in three size classes, using the Index of Relative Importance (I.R.I.) of Pinkas et al. (1971). These classes were based on total body length range rather than on specific cohorts: Class 1=2·1–3·0 cm; Class 2=3·1–4·0 cm; Class 3=4·1–5 cm. ■, Goby class 3; ▨, goby class 2; ▢, goby class 1.

FIGURE 7. Comparison of the diets of flounder in four size classes, using the Index of Relative Importance (I.R.I.) of Pinkas et al. (1971). These classes were based on total body length range rather than on specific cohorts. Class 1=0·1–1·1 cm; Class 2=1·2–2·1 cm; Class 3=2·2–3·1 cm; Class 4=>3·2 cm. ■, Flounder class 4; ▢, flounder class 3; ▨, flounder class 2; ▢, flounder class 1.

polychaetes), and an intermediate, brackishwater, distribution (e.g. the amphipods and isopods) are evident. More interesting, perhaps, are the substantial changes in distribution according to season seen among several taxa. Compared with September, the downstream shift of chironomid larvae in December could be an artifact associated with 10-fold decrease
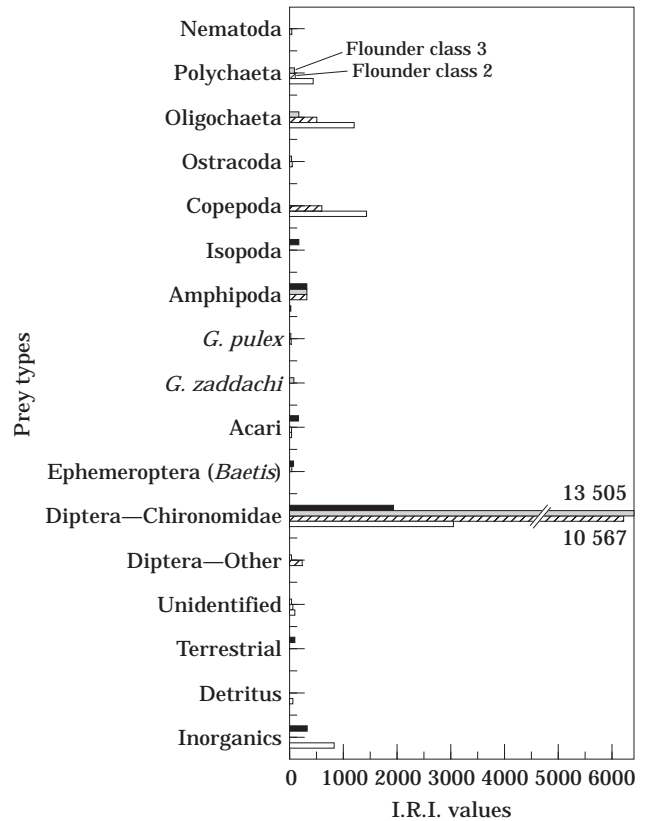
in overall numbers (Figure 2). However, the even greater extension into saltwater regions, seen in April and July, when numbers were partially restored, suggests that this phenomenon was real. An almost identical pattern was seen in the elmid beetles. The downstream extensions seen in the caddisflies, mayflies and stoneflies were under conditions of stable or increasing population densities. In the case of the black fly *Simulium variegatum*, huge numbers of larvae were concentrated at Site 2, in July. The total benthos also showed a downstream shift between September and December, and this was maintained through April and into the summer. Environmental data indicate that the September–December period in the Aber was one of decreasing riverwater temperature (monthly range from 10·0–18·0 °C down to 5·5–11·0 °C) and of increasing discharge (mean monthly discharge: September=0·32, October=0·68, November=0·74, December =1·5 m^{-3} s^{-1}). However, water temperature had increased, and discharge had decreased, prior
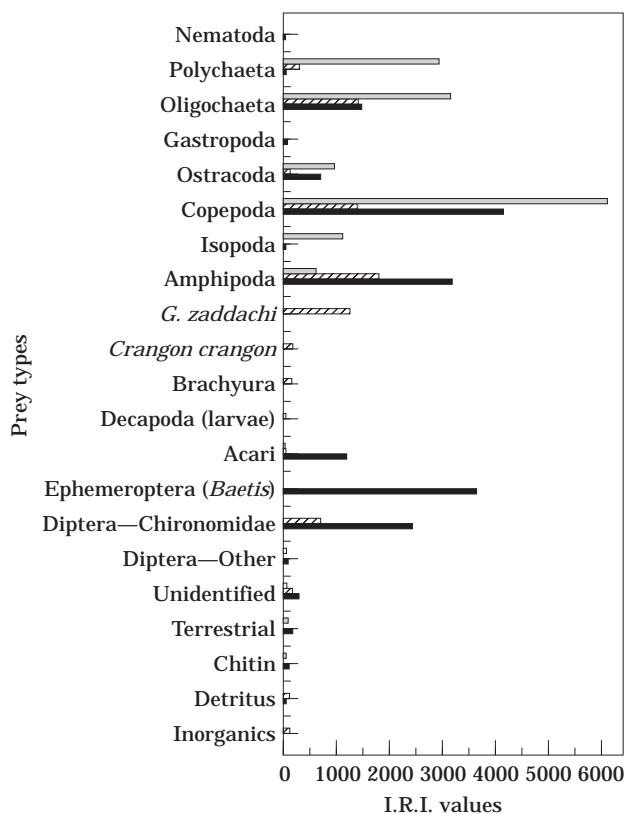
FIGURE 8. Comparison of the diets of gobies among sites along the Aber Estuary (using the Index of Relative Importance (I.R.I.) of Pinkas *et al.*, 1971). ■, Goby site 5; ▨, goby site 4; ▦, goby sites 2–3.

to April and July. Possibly, increased river discharge in the autumn and early winter promoted the observed downstream extensions which were thereafter maintained during the spring and early summer. Subsequent emergence of the adults resulted in decreased densities of immature stages in the benthos and restoration of the upstream distributions seen in September. The chain of events just described attempts to explain the observed distributions through a passive mechanism. Another passive mechanism might be related to seasonal differences in inundation by salt water, due to shifts in tidal amplitude. However, during the September–December downstream faunal shift, high tides were among the highest recorded for the year (e.g. 60% inundation of Site 3 by all high tides in October and November). Moreover, this distributional shift was maintained in April, the time of maximum saltwater intrusion into the estuary (65% inundation at Site 3). Saltwater intrusion was least in June/July, by which time the ranges of aquatic insects had contracted to sites 1 and 2. It seems unlikely, therefore, that seasonal variation in saltwater intrusion influenced the observed distributions of the

freshwater taxa. However, the upstream extension of marine bivalves and polychaetes (to Site 2) did coincide with the highest recorded saltwater intrusion, in April; juvenile polychaetes are known to be adversely affected by excessive freshwater runoff (Schiedek & Schöttler, 1991). A competing hypothesis is that the distributions of the freshwater taxa are the result of active migrations made in order to take advantage of more favourable downstream conditions, perhaps in the form of increased food supply or reduced competition. There is little doubt that the stable and large particle size nature of much of the Aber bed substratum facilitates the persistence of lotic invertebrates at downstream sites (Williams & Feltmate, 1992; McLusky, 1993).

Regardless of whether an active, passive or combined mechanism applies, it is clear that, in the Aber Estuary, large numbers of a wide variety of lotic invertebrate species move across the freshwater–saltwater interface. The qualitative and quantitative nature of this drift varies considerably with time of year although the environmental factors promoting or controlling it are unknown. This is in contrast to other drift studies, even those done on adjacent rivers where, in non-tidal sections, the numbers of animals drifting is related to current speed, water depth and water temperature (Williams & Williams, 1993; see also reviews by Waters, 1972, and Brittain & Eikeland, 1988). Among the invertebrates drifting down the Aber were considerable numbers of nymphs and larvae of lotic insects, many of which appeared not simply to die upon passing into tidal sections but resumed a benthic existence by virtue of varying degrees of salt tolerance. Drift therefore provides a mechanism by which the seasonal extensions of many of these species into the lower estuary are facilitated (see also Elliott & Corlett, 1972).

As perhaps might be expected, neither the numbers nor the taxonomic composition of the 'reverse' drift were similar to those recorded in non-tidal waters. Typically, species found moving upstream are the same as those found in the drift, and some studies have shown a positive correlation between the numbers moving downstream and upstream (Williams & Williams, 1993). Non-tidal waters, of course, do not exhibit a reversal of flow at incoming tides, the latter probable affecting the composition of the upstream-moving component. Palmer (1984), for example, has shown that the meiofauna of the North Inlet Estuary, South Carolina crawled to the bed surface only during periods of slack tide, and appearance in the drift was attributed to passive dislodgement of individuals inadvertently exposed to currents. Others (e.g. Beukema & de Vlas, 1989) have demonstrated a

definite behavioural component in drift entry (as has long been known in fresh waters; e.g. Hildrew & Townsend, 1980; Williams & Moore, 1989). However, not all taxa (e.g. nematodes) participate in such active migrations (Armonies, 1994). Composition of the reverse drift assemblage in the Aber reflects its lower estuarine/marine origin, and the presence of *Gammarus zaddachi* in both types of drift traps underlines its high level of activity within the brackish, middle reach of the estuary. It is well known that sediment-dwelling marine crustaceans, particularly amphipods and isopods, have swimming patterns strongly linked to environmental cues (e.g. Jones & Naylor, 1970; Grant, 1980; Naylor, 1985; Schlacher & Wooldridge, 1994), especially water movement and often in combination with other cues such as photoperiod. In the Aber, with the exception of the more numerous chironomids, lack of most of the larger aquatic insects in the reverse drift might be explained by their reduced downstream densities or by the weak, in comparison with the freshwater flow, saltwater currents.

The total annual drift recorded for the Aber (30 872 107 individuals) compares favourably with estimates made in other larger, British rivers, for example 374 125–10 901 820 in the River Yarty, Devon, and 16 811 900 to 147 225 670 in the River Leven, Cumbria (Bailey, 1966; Elliott & Corlett, 1972). We could find no records of comparable measurements of reverse drift elsewhere.

The fact that such large numbers of lotic invertebrates are being carried into the Aber Estuary and are becoming established in tidal sections begs the question of whether they benefit, significantly, estuarine consumers. For the two major fish species in the Aber the answer is clearly yes. In the case of the flounders, they entered the estuary as very small, post-pelagic larvae (mean weight=0·005 g, mean length=0·95 cm) in the spring and fed primarily on chironomid larvae until they migrated out to sea in the autumn. By then, individual biomass had increased more than 100-fold (mean weight=0·54 g, mean length=4·1 cm). Adult flounders were never encountered in the Aber. Larval, pupal and adult chironomids also have been shown to be important in the diets of juvenile salmonids in estuaries along the west coast of North America (Wolf *et al.*, 1983; Levings *et al.*, 1991). Interestingly, in July, chironomids were still the dominant prey type at Site 2, despite the presence of large populations of black fly (Simuliidae) larvae and *Baetis* (Ephemeroptera) nymphs, both of which occurred uncommonly in the guts. Simuliids tend to attach themselves to the upper surfaces of substratum particles, whereas chironomids typically live between and beneath stones

and gravel, where they are more accessible to the strongly benthic feeding behaviour of flounder. *Baetis* nymphs are extremely active and frequently enter the water column when approached by a predator (Williams, 1987). The absence of caddisfly larvae in the diets may be due to large size and the protection afforded by their cases in some species, and, in the abundant glossosomatids, both a strong case and an upper-substratum–surface existence.

Flounder diets have been examined in several other estuarine locations and considerable variability noted. For example, in the Tamar Estuary, Devon, the most common prey were the crustaceans *Crangon vulgaris, Neomysis vulgaris* and *Schistomysis ornata* (Hartley, 1940); in estuaries along the Danish coast, flounder around 1·0 cm in length fed primarily on harpacticoid copepods together with small annelids (Bregnballe, 1961); in the Elbe, Germany, guts contained tubificid oligochaetes and freshwater clams (*Sphaerium*) (Stadel, 1936); and in the River Tweed, Scotland, approximately 88% of the diet consisted of chironomid larvae (Radforth, 1940). However, individuals in the latter population of flounder averaged 17·6 cm in length. In the Fraser River estuary, British Columbia, Canada, the main prey of the Starry flounder (*Platichthys stellatus*) consists of oligochaetes, small crustaceans and insects (Northcote *et al.*, 1979).

Freshwater invertebrates, particularly chironomid larvae, were eaten on a regular basis also by the larger gobies, especially at upstream Sites 2 and 3. *Baetis* mayfly nymphs, small amphipods (*Gammarus pulex*), freshwater mites and copepods were consumed at these two sites as well. However, it was *G. zaddachi* that was the most important prey. As in this study, populations of the common goby, elsewhere, have demonstrated feeding differences from one part of an estuary to another. In freshwater sections of the Gwendraeth Estuary, Wales, for example, chironomid larvae, oligochaetes and harpacticoids were the major dietary items and this put the gobies into direct competition with minnows (*Phoxinus*). In pools in the surrounding salt marsh, the predominant prey consisted of harpacticoids and halacarid mites. Further seaward, guts contained mostly the broken off limbs of barnacles, together with various small crustaceans, mites and polychaetes (Green, 1968).

In the Aber, food resource partitioning appears to occur between these two fish species. The evidence for this includes: (1) differences in the predominant taxa eaten, which may be related to (2) a difference in the range of mouth gapes of the size classes present; (3) a difference in peak residency times in the estuary (gobies from September to February; flounder from March to August); and (4) some difference in their

spatial distribution in the estuary (flounder at Sites 2 and 3; gobies at Sites 2–5, but more abundantly at Sites 3–5. Any overlap with eels in the Aber could not be assessed due to the large proportion of empty guts recorded (91%) in this species.

In comparison with the research effort devoted to assessing the nature of drift in rivers and streams, that directed at tidally-influenced lotic waters is very sparse. This is despite the fact that existing studies have shown important consequences of lotic discharge. It has been shown, for example, that spring discharge from the St. Lawrence Estuary may promote the aggregation of planktonic food organisms as well as larval fishes. Indeed, it is speculated that the arrival of Atlantic mackerel in this region, to spawn, is timed to precede this annual freshet by just the time needed for their eggs to hatch and the larval egg yolks to be consumed (Coté et al., 1986). Further, freshwater inflow to the San Antonio Bay, Texas has been shown, through input of organic matter and nutrients, to stimulate microbial production, to increase the feeding rates of small, brackishwater invertebrates, and to influence meiobenthic community structure (Montagna & Yoon, 1991). Deegan et al. (1994) have hypothesized that differences in organic matter inputs among estuaries may influence the diversity and productivity of resident fish populations. The importance of estuaries in retaining allochthonous detritus and the latter's importance at the base of the estuarine food web leading to support of the immature stages of important fish species is being increasingly acknowledged (e.g. Healey, 1982; Thorpe, 1994). What needs to be appreciated more, however, is the direct and immediate input to juvenile fish diets from upstream-derived invertebrates.

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