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Phytoplankton of the Firth of Forth

R.A. Park

The Forth River Purification Board (FRPB) monitors the phytoplankton and nutrient dynamics of the Firth of Forth in accordance with the Urban Waste Water Treatment Directive (UWWTD 91/271/EC). This paper summarises FRPB's strategy for monitoring eutrophication in tidal waters, utilising a combination of boat survey and automated sampling, and describes the ecology of phytoplankton in the firth.

Phytoplankton growth is primarily controlled by sea water temperature and light conditions. The attrition of the spring bloom is probably attributed to grazing, by zooplankton and (heterotrophic) dinoflagellates, of a nutrient (silicate and inorganic nitrogen) controlled population of diatoms, dinoflagellates and *Phaeocystis*.

The effect of nutrient enrichment, from both diffuse (agricultural run-off) and point sources (industrial and urban effluent) are discussed in relation to the Forth Estuary and sewage pollution from the Edinburgh Sewage Treatment Works at Seafield.

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Introduction

In 1991 the EC adopted the Urban Waste Water Treatment Directive (UWWTD 91/271/EC) which relates to the control of sewage and some industrial discharges to tidal waters. The Directive aims, among other things, to prevent tidal waters from becoming eutrophic, namely:

"The enrichment of waters by micronutrients, especially compounds of nitrogen and/or phosphorus, causing an accelerated growth of algae or higher forms of plant life to produce an undesirable disturbance to the balance of organisms present in the water and to the quality of water concerned".

In accordance with the Directive's recommendations (UWWTD/ND 1992), FRPB has considered the status of micronutrients and phytoplankton within the Firth of Forth which has led to its designation, by the Scottish Office, as a 'High Natural Dispersive Area' (HNDA) or 'Less-Sensitive (to eutrophication) Area'.

Since 1991 FRPB has monitored the spatial and temporal variability of phytoplankton and micronutrients in the firth against a baseline of water quality data dating back to 1977. The aims of these investigations are to characterise the phytoplankton ecology of the coastal waters and to identify potential eutrophic effects, seen as abnormal phytoplankton growth. The phytoplankton are examined in relation to anthropogenic inputs of micronutrients from both diffuse (agricultural run-off) and point sources (industrial and urban effluent) of pollution.

Monitoring strategy

A bi-monthly sampling programme was used to investigate the spatial and temporal variability of phytoplankton in the firth between April and October each year.

The phytoplankton were sampled using a combination of net (63 µm mesh) and bottle (1 l), at nine stations within the firth. The location of the stations were designed to measure the phytoplankton of the inner and outer firth including stations around Edinburgh's long sea outfall at Seafield and within Largo Bay (Figure 1).

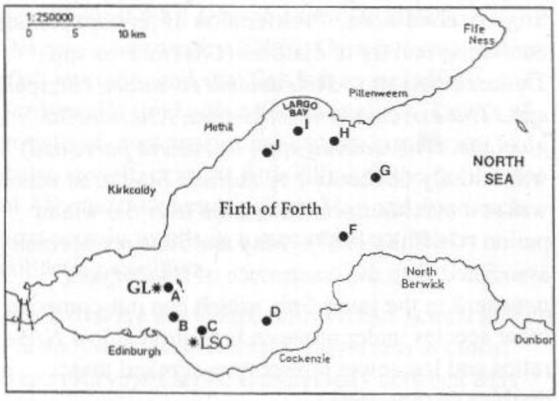

Figure 1. Map of the Firth of Forth showing the location of: the MPWQMS at Gunnet Ledge (*GL), Edinburgh's Long Sea Outfall at Seafield (*LSO) and phytoplankton and micronutrient sampling stations (A-G).

Phytoplankton community structure was determined by the identification of algae to species and a semi-quantitative estimate (scale of 1-4) made of their relative abundance (FRPB 1994b). Vertical profiles of phytoplankton chlorophyll-a and temperature were taken to provide an indication of water stability and measurements were made of nutrient concentrations (nitrite, nitrate, ammoniacal nitrogen, soluble reactive phosphate, reactive silicate), salinity and water transparency (Secchi disk depth).

In conjunction with ship-based monitoring a 'Multiparameter Water Quality Monitoring System' (MPWQMS), situated at Inchkeith (Figure 1), was used to measure the following parameters at a predetermined, variable rate: chlorophyll-a (fluorometrically), nitrate concentration, light attenuation, salinity and water temperature. These data, collected from a fixed depth of 5 m, provided detailed (semi-continuous) temporal information on bloom development and attrition in the inner firth, a region influenced by relatively nutrient-rich water originating from the lower estuary (Griffiths 1987; FRPB 1992b).

Phytoplankton ecology

Changes in phytoplankton chlorophyll-a and community structure have been evaluated in relation to environmental (light attenuation, sea water temperature), biological (zooplankton grazing), and water chemistry (salinity, micronutrients) parameters. The seasonal variation in phytoplankton chlorophyll-a in the firth during 1994 is shown in Figure 2. The onset of spring phytoplankton growth in May 1994 was probably triggered by the occurrence of stable water column conditions, which typically occur during calm weather conditions, coupled with rising sea water temperature and brighter conditions. Proliferation of phytoplankton, consisting mainly of diatoms (*Chaetoceros* spp., *Thalassiosira* spp., *Skeletonema costatum*, *Nitzschia* spp., *Thalassionema nitzschioides*, *Asterionella glacialis*, *Rhizosolenia* spp., *Bacillaria paradoxa*) was initially unchecked by nutrient limitation which was at a maximum concentration over the winter period (Griffiths 1987). May and June are normally associated with the occurrence of *Phaeocystis pouchetii* in the inner firth, which can out-compete other species under nitrogen limitation at low N/P ratios and has lower phosphorus demand than diatoms (Arhus 1991).

The spring growth of diatoms and *Phaeocystis* was characteristically followed by a proliferation of dinoflagellate species (*Protoperidinium depressum*, *P. ovatum*, *P. marielebouriae*, *P. pentagonum*) which coincided with the collapse of the spring bloom. The high densities of *Protoperidinium* species in late May is probably linked to their heterotrophic nature. Their occurrence is therefore likely to be in response to the plentiful supply of particulate food (diatoms) present in the water during this period (Dodge, pers. comm.). Grazing by zooplankton and heterotrophic dinoflagellates, on a nutrient-limited population, accounts for the annual collapse of the spring growth in late May or early June and has been a consistent feature of the phytoplankton dynamics in the firth since monitoring began in 1991 (FRPB 1991, 1993a, 1993b, 1994b). A summary of the seasonal variation in phytoplankton community structure is shown in Figure 3.

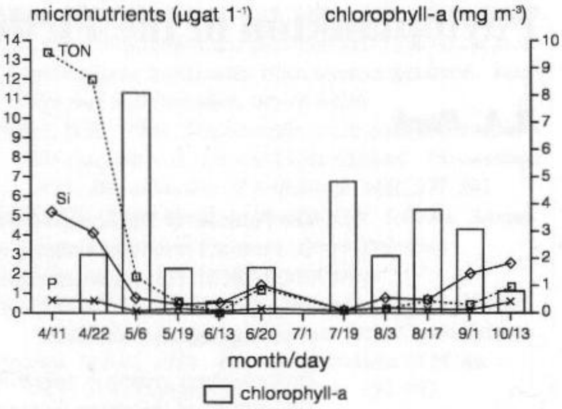

Figure 2. The temporal distribution of micronutrients (total oxidised nitrogen, reactive silicate, soluble reactive phosphate) and chlorophyll-a in the Firth of Forth, April to October 1994 (data for station G).

Following the spring blooms, the levels of nitrate and silicate occasionally fell below the concentration thought to limit phytoplankton growth, namely 1.0 µgat l⁻¹ nitrate and, for diatoms, 0.5 µgat l⁻¹ reactive silicate (Brockmann, Lane & Postma 1990). Remineralisation of micronutrients bound within dead (detrital and water-borne) phytoplankton cells may have facilitated a flourish of phytoplankton

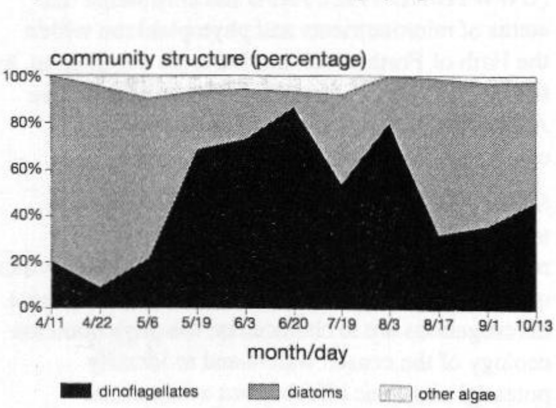

Figure 3. Temporal distribution of phytoplankton community structure as percentage composition of dinoflagellates, diatoms and other algae (e.g. *Phaeocystis*) in the Firth of Forth, 1994.

growth in August and September 1994. This also coincides with a period when warm, calm, sunny weather provided ideal conditions for phytoplankton growth. In the summer of 1994 the highest concentrations of phytoplankton chlorophyll (12 mg m^{-3}) occurred at station C in the vicinity of Edinburgh's long sea outfall (Figure 1). The bloom consisted mainly of the diatom *Chaetoceros socialis* and autotrophic dinoflagellate species: *Ceratium furca, Ceratium tripos, Ceratium lineatum, Ceratium fusus, Dinophysis acuta, Scippsiella trochoidea.*

The growth and attrition of a bloom of *Chaetoceros socialis* recorded by the MPWQMS at Inchkeith in July 1994 is shown in Figure 4. Between the 8th and 19th July chlorophyll-a was less than 1 mg m^{-3}. The increase in chlorophyll-a coincided with a rise in sea water temperature of 1.4°C (Figure 5) associated with a period of exceptionally sunny weather. On the 19th July the flooding tide brought with it a rapidly growing bloom of *Chaetoceros socialis*, shown by the tidal variation in chlorophyll-a and salinity (Figure 6). Large (0.3-6.0 mg m^{-3}) temporal variability of chlorophyll-a recorded on the 19th July diminished over the following week reflecting the spread of the bloom to the inner firth, followed by its attrition (FRPB 1995a).

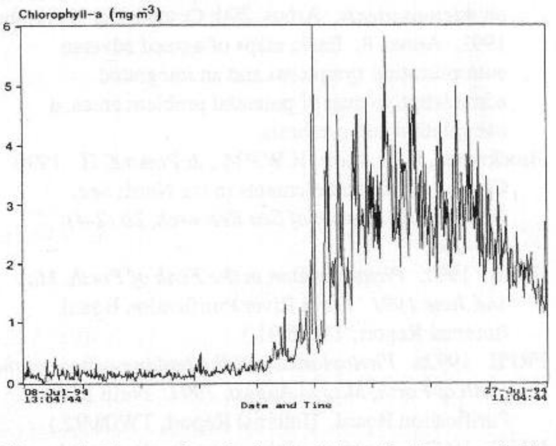

Figure 4. Temporal variation in chlorophyll-a recorded by the MPWQMS showing the growth and attrition of a phytoplankton bloom in the Firth of Forth.

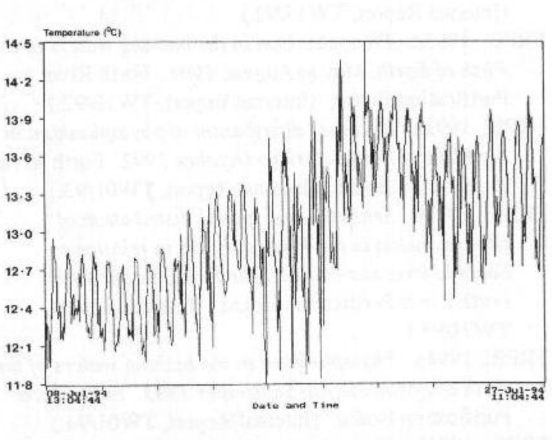

Figure 5. Temporal variation in sea water temperature recorded by the MPWQMS showing the tidal and short-term (8th-27th July) variability in temperature at Gunnet Ledge in the Firth of Forth.

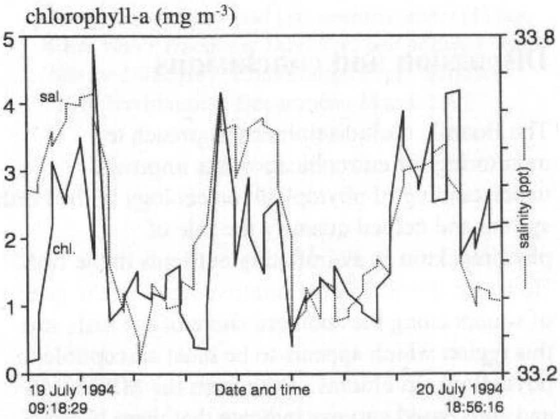

Figure 6. The relationship between phytoplankton chlorophyll-a and salinity recorded by the MPWQMS between 19th and 20th July 1994.

Nuisance algae

Some species of phytoplankton can have a significant effect on the use of the Firth of Forth for commercial fisheries and recreation, as well as causing public health problems (principally through the consumption of contaminated shellfish). The following species of potentially harmful algae have been recorded in the firth between 1991 and 1994. The ascribed potential effects are based on ICES data (ICES 1992) and have not necessarily been observed within the Firth of Forth: *Alexandrium tamarensis* (PSP, fish mortality); *Dinophysis acuminata* (DSP); *Dinophysis acuta* (DSP); *Dinophysis norvegica* (DSP); *Gyrodinium aureolum* (fish mortality and shellfish larvae mortality); *Scrippsiella trochoidea* (fish mortality). Levels of growth of most species are usually insufficient to cause any effect in the firth although the occurrence of *Alexandrium tamarensis* in May and June each year usually results in a precautionary ban on collecting shellfish.

Algae that are associated with surface scums include *Phaeocystis pouchetii* and *Chaetoceros socialis*. Beach surveys carried out annually between May and August show that these have no impact on the general amenity of bathing waters within the firth (FRPB 1992a, 1992d, 1994a, 1995b). Other potential nuisance algae include the silicoflagellate *Dictyocha speculum* (fish mortality) and the small diatom *Nitzschia pseudodelicatissima* (shellfish toxicity).

Historically, 'red tides' of phytoplankton (probably blooms of *Gyrodinium* sp.) have been observed in the Forth Estuary and in the coastal waters around Edinburgh. Although green/brown discoloration of the sea is normally associated with spring and autumn blooms in the firth, there have been no reports of 'red tides' since 1982.

Discussion and conclusions

The Board's multidisciplinary approach to monitoring for eutrophication has improved understanding of phytoplankton ecology in the Forth system and helped quantify the role of phytoplankton in assimilating nutrients in the firth. However, despite recent improvements in the quality of waters along the southern shore of the firth, it is this region which appears to be most susceptible to phytoplankton blooms. Data from the MPWQMS and ship-based surveys indicate that these blooms are greater than the natural background and can be linked to the anthropogenic input of nutrients (inorganic nitrogen) from both Edinburgh Sewage Treatment Works and nutrient-rich water originating from the Forth Estuary (FRPB 1995a).

A start (since 1994) has been made at characterising the phytoplankton in the lower Forth Estuary (FRPB 1995c) to provide a holistic view of the trophic status of the entire Forth system. Compared with the more stable marine conditions within the firth, the estuarine environment for phytoplankton is highly variable, influenced primarily by hydrodynamic variability, tides and winds (Alan & Powell 1994). Although algal blooms do sometimes give rise to public complaint, the Firth of Forth cannot be considered eutrophic. The dense algal blooms of predominantly diatoms, dinoflagellates and *Phaeocystis* are, instead, indicative of a highly productive Forth ecosystem on which the phytoplankton are the main primary producers.

In conclusion, these investigations have made a start at producing a baseline of ecological data which describe the seasonal and spatial distributions of phytoplankton growth and community structure in the firth. It is against these data that the future bloom events and perturbations of the natural phytoplankton community structure will be measured. FRPB also utilises a two-dimensional water quality model to predict the effect of current and predicted effluent discharges on phytoplankton distribution in the Firth of Forth. Collectively, eutrophication studies and water quality modelling form part of a multidisciplinary analysis of the Forth system which assist in the formation of successful management strategies. FRPB and, in due course, the Scottish Environment Protection Agency (SEPA) will continue to monitor the phytoplankton and nutrients within the Firth of Forth in accordance with National and European legislation.

Acknowledgments

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Effects of petrochemical effluent at Grangemouth on transplanted *Fucus vesiculosus* L.

T.C. Telfer & M. Wilkinson

Pollution effects on the infauna of industrial effluent discharged to Kinneil mudflats have been well documented. McLusky (1987), for macrofauna, and Moore *et al.* (1987), for meiofauna, showed distinct areas of influence along a pollution gradient away from a petrochemical input source.

Excised frond tips of *Fucus vesiculosus* L. were transplanted along this pollution gradient, to find the short-term effects of the discharges on epilithic seaweeds as indicated by measurement of growth and ion leakage. Transplants were undertaken in the winters of 1992/93 and 1993/94 and in the summer of 1993. In both winter experiments, tips transplanted to all stations, except the controls, showed a detrimental effect on growth and high levels of ion leakage, indicating stress. The controls showed no detrimental effects. None of the summer transplants showed any detrimental effects on growth and gave low levels of ion leakage.

These results suggest that there was a localised, short-term seasonal pollution effect on *Fucus vesiculosus* during the transplant period. This seasonal effect may not be shown by the infaunal communities due to sediment acting as both buffer to short-term changes and as a medium in which effluent accumulates giving little seasonal variation. The results are discussed in relation to a wider study of the use of seaweed explant techniques in the assessment of water quality in estuaries.

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Introduction

Traditionally the environmental effects of water-borne effluents can be calculated from laboratory-based toxicity tests on the constituent parts of the discharge and breakdown products. These laboratory tests are done under standard conditions using standard species and can only rank toxicity or crudely estimate environmental effects using extrapolation factors based on estimated discharge. Such tests cannot take into account the constant and unpredictable natural environmental variations. A better technique is the environmental bioassay (Calow 1989) defined as "the use of biological systems to assess the actual or potential impact of substances derived from the activity of man on the natural environment." This is a flexible technique which is used both retrospectively to monitor effluent effects and in conjunction with laboratory-derived data to validate predictive models in order to reach a realistic prediction of future effects. This work is part of the development of one particular environmental bioassay using transplanted portions of the seaweed *F. vesiculosus* (bladderwrack) in measurement of the effects of a petrochemical discharge on growth and ion leakage.

Laboratory experiments (Telfer 1995) have shown that *F. vesiculosus* gave the most consistent results, of several seaweed species, for growth and ion leakage in a variety of toxicants. These experiments also allowed the methods to measure growth and ion leakage to be refined for use with field transplants. The growth of *Fucus* occurs at the meristem which is in the few millimetres behind the tip of each frond and is initiated by the apical cell (Moss 1967). Providing the meristem and the apical cell are intact the excised tips will continue growing. Use of tips in experiments are more convenient than using the whole plant as they are easier to handle, easier to measure, and can be used in larger numbers to decrease the effects of genetic variation on the results (Burrows 1964). The ion leakage technique uses the fact that toxicants can damage the plasmalemma and therefore alter the passive efflux of ions from the free space. The toxicity of a substance can therefore be measured by calculating the amount of leakage of ions in a particular time into deionised water as indicated by increase in electrical conductivity (Axelsson & Axelsson 1987). A greater increase would be expected to occur with plants damaged by toxicants compared with control plants.

Grangemouth is a highly industrialised area of central Scotland, with a large petrochemical industry, that discharges effluent onto Kinneil mudflats and the adjacent Skinflats (see Figure 1).

The petrochemical effluent discharged onto Kinneil mudflats consists of two discharges. The first is refinery effluent, which is an aqueous mixture from ballast water, boiler and cooling tower blowdown and storm water. Discharge rates vary with weather conditions and can increase by three times in volume after heavy rain (McLusky & Bryant 1991). The second is chemical plant effluent which is formed from the production of various organic chemicals. Toxicity tests, LC_{50} 96 h, show the chemical effluent is more toxic to macrobenthic invertebrates than the refinery effluent (Smith in McLusky & Bryant 1991), but as the refinery discharges three times as much as the chemical plant it is assumed that the refinery effluent contributes more to the overall environmental effects (McLusky & Bryant 1991). Since the end of February 1994 the refinery effluent has been treated and its environmental impact is expected to be dramatically reduced (McLusky pers. comm.).

The location for transplantation was selected at Kinneil mudflats along a known pollution gradient (see Figure 2). This gradient has been defined for macrofaunal communities (McLusky 1987; McLusky & Bryant 1991) and for meiofaunal communities (Moore *et al.* 1987). The fauna showed zones of effects ranging from grossly polluted to no effect or recovering as shown in Figure 2.

Methods

Non-reproductive plants of *F. vesiculosus* were collected from South Queensferry, West Lothian. All plants used in the transplants were collected from the same vertical height on the shore in order to minimise natural inter-plant variation in growth. On arrival at the laboratory 2 cm length tips were excised and stored in filtered natural sea water (Whatman GF/C glass fibre filters) in a constant temperature room at 10°C, 80 $\mu Em^{-2} s^{-1}$ PAR (12:12 photoperiod) for 24 hours to allow recovery from cutting.

The transplant stations were placed so the station nearest the pollution source (A) was in the polluted area, the stations farther away (B, C, D) in the area of enrichment, as shown by the macrofauna, and the furthermost station (E) in the no effect zone, where there was an indigenous population of *F. vesiculosus*. Station E was considered a local control (Figure 2). In addition a control station was set up at South Queensferry (SQ). The stations were set up at very similar shore heights which were within the natural vertical range of *F. vesiculosus*. Transplant stations were set up using metal stakes to which bags could be tied. Transplanting was done in plastic mesh bags with three bags at each station. Each bag contained 20 excised tips. The mesh size of the bags was 4 mm, which was found in laboratory experiments (Telfer 1995) to allow free water transfer while containing the smaller excised tips. The duration of each transplanting time was 28 days, after which the bags were collected and allowed to recover in GF/C filtered natural sea water, overnight, in the constant temperature room.

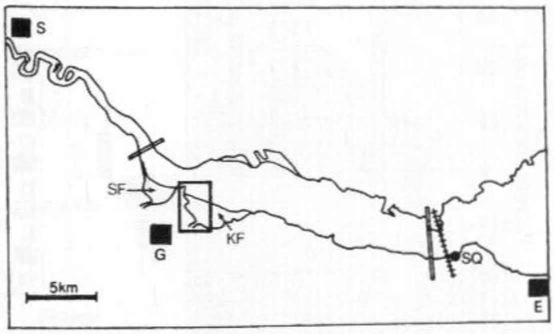

Figure 1. The Forth Estuary showing the study area (box). The letters show the relative positions of Edinburgh (E), Stirling (S), Grangemouth (G), South Queensferry (SQ), Kinneil Mudflat (KF) and Skinflats (SF).

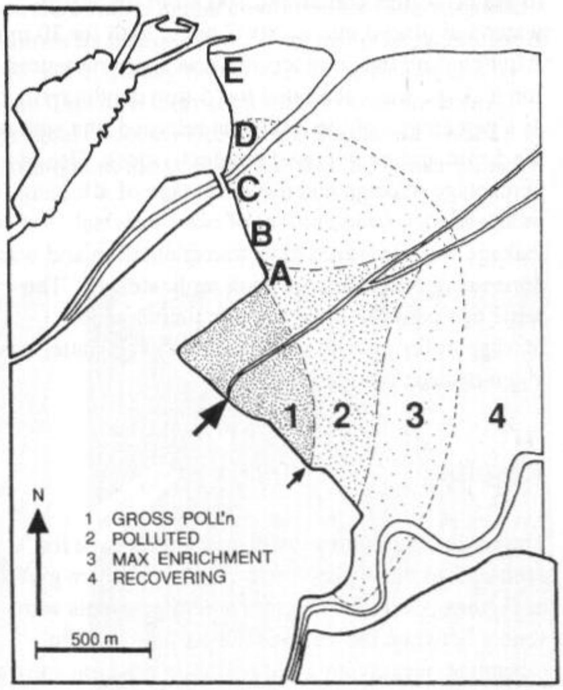

Figure 2. Detail of the study area on Kinneil mudflats in the Forth Estuary. The transplant stations are shown as letters (A to E). The annotated and shaded numbered areas correspond to the areas of pollution defined by McLusky & Bryant (1991). The large and small arrows represent the refinery outfall and the chemical plant outfall respectively.

Transplants were carried out during March 1993, August 1993 and February 1994.

Growth measurement

The growth of the excised tips was measured as percentage change in mean area over the 20 tips in each bag, thus giving three growth measurements per station. Each bag therefore represented a replicate from which the overall mean percentage change in area was calculated. Measurement of growth was achieved by photocopying the tips, which had been placed between acetate sheets, before and after transplanting. The change in mean area for the tips in each bag was measured using an image analyser in mm^2 (±0.1) on the 'before' and 'after' photocopies.

Ion leakage measurement

Ion leakage was calculated as percentage ion leakage, this is the amount of ions released after immersion in deionised water for 5 min as a percentage of the total ions released after heat treatment. The electrical conductivity of 100 ml of deionised water was measured after immersion of *Fucus* tips for exactly 5 min using a Yellow Springs Instruments model 33 Salinity-Conductivity-Temperature meter. The tips were then transferred to sealed bottles containing 100 ml of deionised water and placed into an 80°C water bath for 30 min. After cooling the conductivity was again measured. Ion leakage was calculated by '5 min conductivity' as a percentage of the total ions released (the sum of the 5 min and heat treated conductivities). Use of percentage leakage had the advantage of allowing independence from amount of plant material. Ion leakage was measured after transplantation and was done using two tips from each replicate bag. The same tips could be used for calculation of ion leakage as for growth measurement as the latter used a non-destructive method.

Results

The mean results for growth and ion leakage for each station during each transplant period are given in Figures 3 and 4 respectively. No gradients were shown between the stations during any specific transplant period along the pollution gradient shown by the infauna. However, there was an apparent seasonal effect shown by both growth and ion leakage.

Growth

The tips transplanted at stations A to D exhibited a mean decrease in size during the winter transplant periods in both March 1993 and February 1994 (see Figure 3). This indicated that the tips had probably died and were rotting. Control stations at E and SQ both grew during the winter periods. Growth was exhibited by tips transplanted to all stations during the summer transplant period (August 1993), but growth showed no specific trends away from the discharge points and there was no significant difference ($p>0.05$) between stations A to D and the control stations. Unfortunately ideal comparisons could not be made as the transplants at the control station E were lost during the winter 1994 transplant period.

Ion leakage

Transplant to show the effects on ion leakage was only undertaken during August 1993 and February 1994. This again showed a temporal effect but was less distinct than that illustrated by the growth results. An analysis of variance verified the temporal variation by showing a significant difference between the percentage leakages for the August 1993 and February 1994 transplants. The ion leakage results for the August 1993 transplant were consistently low, 17-20% (see Figure 4) and within the range expected for unstressed *Fucus* (Telfer 1995). The leakage at SQ was higher than leakages for Grangemouth but not significantly so ($p>0.05$). The results shown in February 1994 were significantly higher, up to 65%, and were characteristic of stressed or damaged *Fucus* (Telfer 1995). The control station at SQ in February 1994 showed a lower leakage than for the station at Grangemouth but did not differ significantly ($p>0.05$) from the value for August period at the same station.

Preliminary laboratory investigations had shown that for *F. vesiculosus* tips grown in filtered sea water at 10°C a consistent 'no effect' percentage leakage of

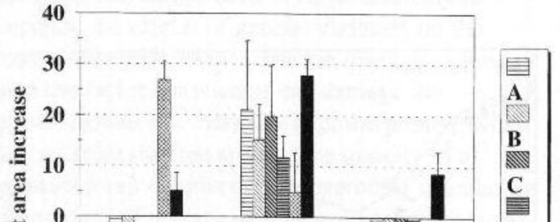

Figure 3. Percentage change in area of *Fucus vesiculosus* tips over three transplant periods. The letters correspond to the stations shown in Figure 2. Errors bars are one standard deviation.

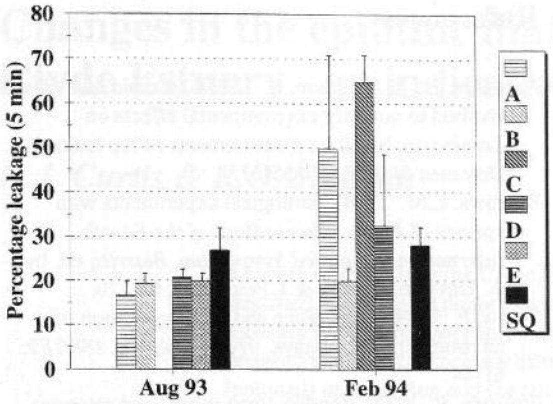

Figure 4. Percentage ion leakage of *Fucus vesiculosus* tips over two transplant periods. The letters correspond to the stations shown in Figure 2. Error bars are one standard deviation.

around 20% was obtained, even when a variety of populations was used. When stressed by a toxicant that has an effect on the integrity of the plasmalemma the percentage leakage increases to 50-80%.

Conclusions

Mills (1988) showed that at Kinneil mudflats there is little variation in salinity during the year. This is normally within the range 28-32‰, which is well within the normal growth limits of *F. vesiculosus* (Russell 1987). In addition, the continued growth of the controls throughout the year illustrated that the extreme effects on the growth and ion leakage of the transplanted tips at stations A to D were probably not due solely to natural seasonal variation. Indeed this is shown to be the case as there is a healthy population of *F. vesiculosus* at station E. Laboratory experiments (Telfer 1995) indicated that it was unlikely that the slight variation in salinity with season would have had any significant effect on the ion leakage. Therefore the effects found in this study were probably due at least partially to polluted effluent being discharged on to the mudflats. The volume of discharge from the refinery increased with higher rainfall during the winter months but the public register of the Forth River Purification Board indicated that the effluents were of fairly constant composition throughout the test period. It is possible therefore that increase in physical stress on the transplanted tips during the winter, due to lowered temperatures, light and salinity, may have combined with toxic effects of the effluent to give an acute response if a particular threshold level of effluent was present.

The gradients shown by the benthic infauna were not reflected by the results for the transplants which seemed to give an acute response only. It is reasonable to assume that this was due to the sediment acting both as a buffer against short-term toxic effects of the effluent, and as a sink allowing effluent accumulation which gave long-term effects, on the benthic faunal communities. The response shown by transplanted *Fucus* tips is an indication of the water quality rather than the sediment quality and therefore short-term toxic effects are seen. A zone of acute effect on the transplants varied throughout the year, the limit in the winter being

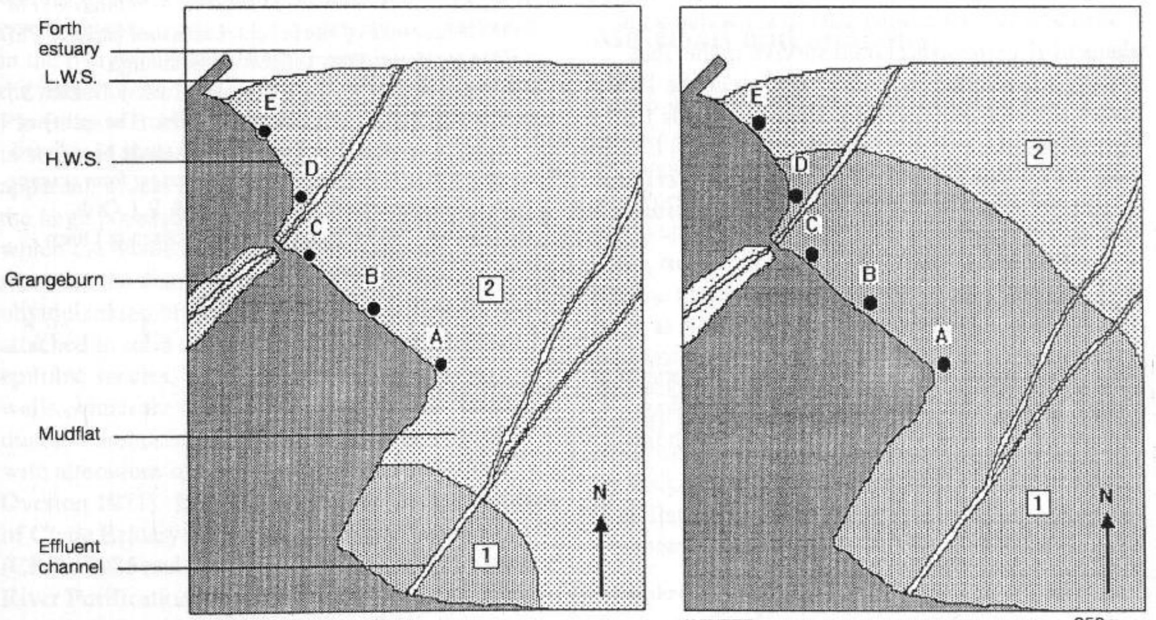

Figure 5. Suggested temporal variation in the zone of effect of the petrochemical effluents on the water quality at Kinneil mudflats. Zone 1 is an area of toxic effect whilst zone 2 is of no detectable effect.

between stations D and E and in the summer between the discharge point and station A. Even though no zone of effect was detected during the summer in this experiment it is reasonable to assume one was present, if very localised, as petrochemical effluent discharge continues throughout the year. Personal observation noted the presence of an oily sheen on the surface near to the discharge point throughout the summer, though further work would be necessary to see if this was toxic to *F. vesiculosus*. Unlike the zones shown by McLusky & Bryant (1991) for the infauna, which are stable, the zone of effect within the water column expanded and contracted throughout the year. These are illustrated diagrammatically in Figure 5. Further work would have to be undertaken to confirm this interpretation such as chemical analysis of water samples taken from each of the transplant stations at the time of transplantation.

These results illustrate how an example of an environmental bioassay using transplanted excised seaweed portions can be used to show variation in effluent effects with season. This indicates that environmental bioassays can reflect the nature of toxicants in environmental conditions, but does not give a toxicity measure as accurately as the well-defined laboratory test. It may be that the strength of this particular technique lies in validation of risk assessments derived from laboratory obtained data using transplanted seaweeds in field trials.

Seaweed transplants have also been used in solving environmental riddles (Wilkinson *et al.* 1994). The technique was used in the Esk Estuary (east coast of Scotland) to show that substrate mobility and not sewage discharge was to blame for the absence of *F. vesiculosus*. It was also used to show that adult plants of *F. vesiculosus* could survive in the Tees Estuary where none had been found since the 1930s before severe pollution was present (Edwards 1972). Recent, personal, observations from the Tees Estuary have shown that two years after the initial work was completed *Fucus* has recolonised the outer estuary.

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Changes in the epilithic diatom communities of the Clyde Estuary - an indication of improved water quality?

D.J. Curtis & R.O. McLean

A survey of sites along the Clyde Estuary between Finnieston and Ardmore Point in 1981-83 identified 307 epilithic diatom species. Of these under a third were abundant organisms with *Navicula mutica* and *Opephora martyi* being dominant, having relatively large niche breadths and demonstrating complementary distributions. The former diatom dominated the more nutrient-rich (polluted) upper region and the latter the cleaner, seaward end of the estuary. A survey in 1991 indicated that *Opephora martyi* was still dominant in the seaward end and that its distribution had extended into the upper estuarine sites. In contrast *Navicula mutica* had reduced in importance to become only the fourth most abundant diatom in the estuary. In the earlier survey the contribution of *Opephora* to diatom communities where it occurred never dropped below 40%. However, by 1993/94 its contribution never exceeded 27.1%. Overall diatom densities cm^{-2} of substrate ranged from 0.2 x 10^{6} to 3 x 10^{6} in 1981/83 but by 1993/94 these had risen to between 18 x 10^{6} and 700 x 10^{6}, indicating a much more abundant flora. All but two of the 20 most abundant species were present at all levels of the estuary in 1991 and they also showed markedly greater niche breadths. Ordination by reciprocal averaging showed clear changes in the communities along the estuary. The changes in distribution suggest that environmental conditions linked to water quality have been improving for diatom community development in the estuary.

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Introduction

The conservation importance of the Clyde Estuary is clearly apparent in terms of the relatively easily observed flocks of birds, as described for example by Curtis (1997), with some species declining as organic input to the estuary is reduced by pollution control measures. Improvements in the environmental quality of this area are also reflected in the fish populations, with dramatic events such as the return of the salmon in 1982 (Clyde River Purification Board, Annual Report). While changes in status of these obvious organisms are clearly apparent, of less immediate notice to the layman are the large populations of microscopic organisms upon which the whole estuarine system depends. Among these are the diatoms which live in the phytoplankton of the estuary, on the sediments and attached to solid structures; amongst the latter are epilithic species, living on stones, boulders and walls, which are the concern of this paper. These diatom communities may be expected to change with alterations in water quality (e.g. McIntire & Overton 1971). Improvements in the water quality of Clyde Estuary have been well documented (CRPB 1985 and Annual Reports), with the Clyde River Purification Board providing detailed information on parameters such as BOD, oxygen concentration, phosphate, nitrate, heavy metals, etc; see also Henderson (1995). Twenty years ago, the diatom flora of the Clyde Estuary was described as being dominated by *Melosira nummuloides* (Smyth *et al.* 1974) and a richer flora was evident by the early 1980s (Gow, Curtis & McLean 1984; McLean *et al.* 1986). In this paper we consider long-term variations in diatom species' abundance and distribution and their expression in terms of community parameters.

Materials and methods

A two-year survey (1981-1983) used a series of ten sample sites, shown in Figure 1, covering both north and south banks of the estuary from Ardmore Point and Port Glasgow at the seaward end to Finnieston at the upstream extremity (Gow 1985). In October 1991, to provide data comparative to the earlier survey, three sample sites were used along the north bank at Ardmore Point, Old Kilpatrick and Finnieston. These were placed so as to cover the different parts of the estuary; the 30 km length of the estuary roughly divides near the Erskine Bridge into a narrow inner part which is canalised and flanked by walls and the downstream wider expanse with tidal flats and scattered surfaces to which epilithic organisms can attach.

Samples were taken at three tidal levels: low, mid- and high. For the consideration of the autumn communities, no data were available for Ardmore high tide in 1981, so this sample station is omitted. Both surveys used 1 cm^{-2} scrapes with a clean

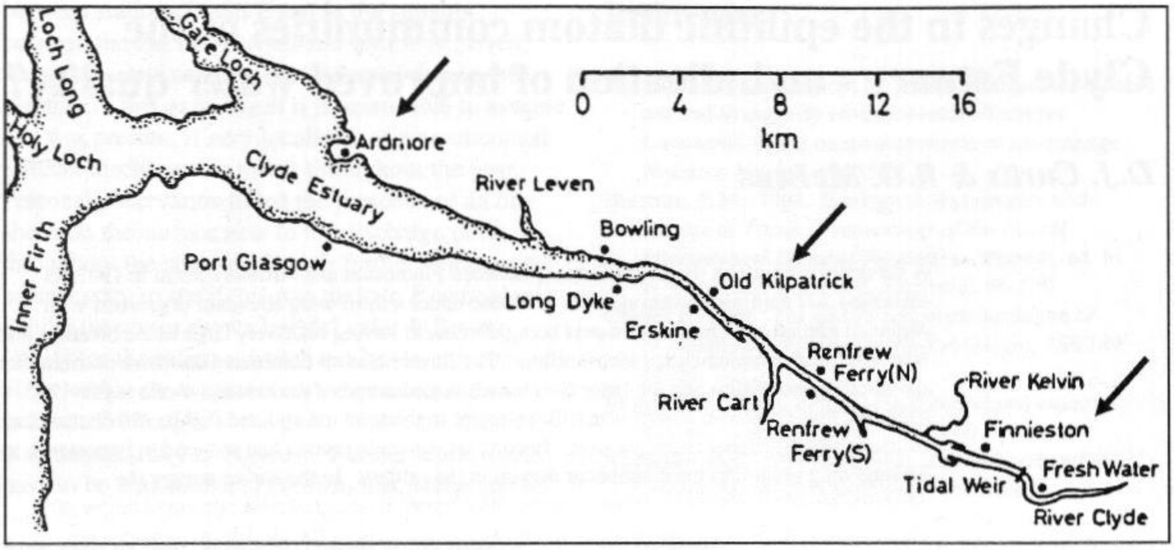


Figure 1. Map of the Clyde Estuary showing the positions of sites (•) sampled by Gow (1985), with arrows indicating the three sites re-sampled in October 1991.

scalpel blade to collect diatom cells into sterile containers; three scrapes per sample in 1981-83 and four in 1991. The mean values of these replicates are used in this account. Details of sampling are given by Gow (1985). After appropriate treatment to produce permanent mounts of the diatoms (Gow 1985), slides were examined under oil immersion with a Zeiss Universal II microscope (at x 2,500 magnification). To provide for adequate recording of species richness, at least 200 cells (= 400 values) were counted for each slide to give a value for relative abundance for each taxon (cm^{-2}); this is within the range of 150-500 values recommended by a number of workers (e.g. Moore 1976; Sullivan 1976; Colijn & Dijkma 1981; Cook & Whipple 1982).

For each sample, taxa were quantified in terms of their proportional relative abundance (% of total) and these data were used in the calculation of species diversity using Simpson's Inverse Index, calculated as $(1/\Sigma(p_i^2))$, where p_i is the proportional abundance of species *i* in the sample; this is the reciprocal of dominance and easily interpreted as the equivalent number of taxa if they were evenly represented. The transpose of this expression was used to calculate niche breadth for each taxon, i.e. $(1/\Sigma(p_j^2))$, where p_j is the proportion of the taxon's overall total in each sample *j*. Relationships between the communities were examined using ordination by means of reciprocal averaging. In these calculations, species and varieties were regarded as of equivalent taxonomic level. The main keys used for identification work were those of Van Huerck (1896), Hustedt (1930), Hendey (1964) and Patrick & Reimer (1966, 1975).

The survey of Gow (1985) covered two years 1981-83 and ten sites, only three of which were re-sampled in October 1991. The selection of the October data for the decennial comparison is justified, in spite of the phenological variations shown by many diatom species for the following reasons. For the dominant species, the pattern of their niche breadth values for October 1981 was similar to that over the full two-year period ($r = 0.829$, $p<0.001$) and only five species might be showing differences between the surveys as a result of their annual phenology patterns. These are indicated below.

Results and discussion

Overall abundances of taxa

In the 1981/83 survey, the most abundant taxon was *Navicula mutica* var. *cohnii* with a relative abundance of 31,880, but in October 1991, although its relative abundance was similar at 43,550 it had dropped to fifth in the rankings, exceeded by *Opephora martyi* (103,000, *cf.* 24,999 and second place in 1981/83), *Achnanthes linearis* (81,600, insignificant in 1981/83), *Caloneis liber* (59,190, negligible in 1981/83) and *Navicula mutica* var. *mutica* (48,660, only 3,790 in 1981/83). Other species which featured amongst the 19 most abundant listed by McLean *et al.* (1986) for the 1981/83 data also showed great changes, for example *Achnanthes hauckiana* (third in 1981/83 with 8,113, but only 15th in 1991), *Melosira nummuloides* (fifth in 1981/83 with 6,888, eighth in 1991 with 25,240), *Surirella ovata* was 19th in 1981/83 with a relative abundance of only 1,061, but ninth in 1991 with a value of 22,520.

The following species were fairly numerous in the

October 1991 samples, but not recorded in abundance in the twelve months commencing May 1981: *Achnanthes linearis, Caloneis liber, Nitzschia thermalis, Coscinodiscus perforatus, Nitzschia acuminata* and *Cocconeis scutellum* var. *parva.* Five of the 20 most abundant species might possibly have been under-sampled in October 1991 because of their phenology. *Navicula justa* was a highly stenochrone species in 1981/82 with very sharp peaks in autumn (September/October) and spring (March), so a slight shift in its seasonal occurrence might result in its absence from samples. In contrast, *Cocconeis stauroneiformis* was a eurychrone species, but with very low numbers through the year. *Navicula viridula* var. *avenacea* was also eurychrone but very abundant through the year with a peak in February 1982. Two other eurychrone species were *Synedra fasciculata* var. *truncata* which was variable in abundance with higher counts in May 1981 and February 1982, while *Surirella ovata* showed peaks in May 1981 and March 1982.

In general, there was an overall large increase in the relative abundance values. This trend was also apparent in samples taken in 1993/94, in which the contribution of *O. martyi* never exceeded 27.1% in comparison to its 40% importance in 1981/83. The much more abundant diatom flora is indicated by the observation that overall diatom densities (cm^{-2} at individual sampling stations) in 1993/94 ranged between 18 x 10^6 and 700 x 10^6, very much higher than the values of 0.2 x 10^6 to 3 x 10^6 recorded in 1981/83.

Abundance and distribution in autumn 1981 and 1991

Changes over the decade are emphasised by considering the autumn communities (September/October samples in 1981 *versus* October 1991). Table 1 lists the 20 most abundant taxa showing how their relative abundances (in percentage terms) changed markedly. Two of the dominant members of the autumn communities show marked declines, *N. mutica* var. *cohnii* and *Achnanthes subsessilis*, in contrast to the increase in *O. martyi*.

Six of the taxa featuring in the 1991 list were absent in 1981: *Achnanthes linearis*, *Caloneis liber*, *Nitzschia thermalis*, *Coscinodiscus perforatus*, *Nitzschia acuminata* and *Cocconeis scutellum* var. *parva*, while only two taxa from the 1981 list were absent in 1991: *Navicula justa* and *Navicula viridula* var. *avenacea*.

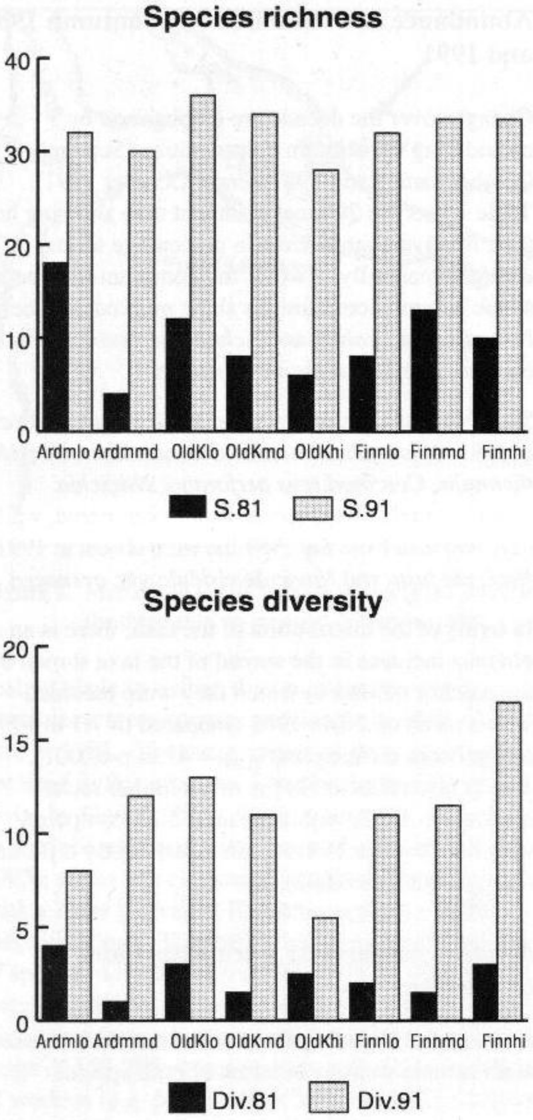
In terms of the distribution of the taxa, there is an obvious increase in the spread of the taxa shown by the number of sites in which they were recorded with a mean of 2.1 in 1981 compared to 7.1 in 1991, a significant difference ($F_{(1,39)} = 47.6$, $p<0.001$). This is also reflected in the much higher niche breadths in 1991, with a mean of 5.24 compared with only 1.46 in 1981, again significantly different ($F_{(1,39)} = 46.3$, $p<0.001$).

Autumn community parameters and ordination

As shown in Figure 2, there were marked increases at all sample stations in terms of both species

Table 1. List of the 20 most abundant diatom taxa, giving their relative abundances as percentage of the total, their spread across the sites/tidal levels and their niche breadth.

		Relative abundance (%)			*No. of sites*		*Niche breadth*	
	Taxon	*total*	*1981*	*1991*	*1981*	*1991*	*1981*	*1991*
A	*Navicula mutica* var. *cohnii*	22.6	41.4	4.8	6	8	4.5	6.0
B	*Opephora martyi*	13.1	10.3	15.7	5	8	2.5	5.6
C	*Achnanthes linearis*	7.5	-	14.6	-	8	-	7.0
D	*Achnanthes subsessilis*	6.6	12.7	0.9	1	8	1.0	6.5
E	*Navicula mutica*	5.2	1.9	8.3	3	8	2.4	5.4
F	*Navicula gregaria*	4.1	4.1	4.0	5	8	1.9	6.6
G	*Caloneis liber*	4.0	-	7.8	-	8	-	5.8
H	*Navicula justa*	3.7	7.6	-	1	-	1.0	-
I	*Melosira nummuloides*	2.6	0.8	4.3	3	8	2.7	7.0
J	*Navicula viridula* var. *avenacea*	2.6	5.4	-	3	-	2.2	-
K	*Cocconeis stauroneiformis*	2.4	0.3	4.4	1	8	1.0	5.1
L	*Nitzschia thermalis*	2.3	-	4.4	-	8	-	4.7
M	*Synedra fasciculata* var. *truncata*	2.2	0.1	4.1	1	8	1.0	6.8
N	*Surirella ovata*	1.9	0.1	3.6	1	8	1.0	4.7
O	*Achnanthes hauckiana*	1.6	1.8	1.4	6	8	3.3	5.8
P	*Coscinodiscus perforatus*	1.4	-	2.7	-	8	-	6.1
Q	*Nitzschia acuminata*	1.4	-	2.7	-	8	-	5.7
R	*Cocconeis scutellum* var. *parva*	1.1	-	2.0	-	8	-	6.5
S	*Cymbella minuta*	1.0	0.9	1.0	3	6	1.8	2.2
T	*Synedra fasciculata*	1.0	0.7	1.4	3	8	2.8	7.3



Species richness

Species diversity

Figure 2. Community parameters for the three tidal levels at the three sites in the autumn. *Ardm* = Ardmore Point; *OldK* = Old Kilpatrick; *Finn* = Finnieston; *lo, md* and *hi* = low, mid- and high tide levels respectively. High tide at Ardmore Point is omitted.

richness and species diversity. Species richness in 1981 averaged at 10.25 ± 1.53 (mean ± standard error), compared with 32.50 ± 0.91 in 1991. Similarly the average species diversity of only 2.48 ± 0.45 in 1981 compared with 10.93 ± 1.20 in 1991. These differences were very highly statistically significant with $F_{(1,14)} = 156.19$ for species richness and $F_{(1,14)} = 43.43$ for diversity, both with $p<0.001$.

The dataset covering the autumn 1981 and 1991 samples comprised 71 species and the full 16 x 71 matrix was used to generate the ordination scores plotted in Figures 3 and 4. The interpretation of the axes in terms of taxa is given in Figure 3, in which ten of the main species, including *O. martyi*, are clustered together near the centre of the plot. At a higher point on axis I is *A. haukiana* while the sequence down axis I has *S. fasciculata* and *N. mutica* very close together, then *C. minuta*, *N. mutica* var. *cohnii* and at the low extreme *N. viridula* var. *avenacea*. With respect to the occurrence of these taxa along the estuary, this corresponds to a gradient from the upstream regions (low values on axis I) to more marine conditions (high values on axis I), which is emphasised by the extremely high value of the outlier species *A. subsessilis* which was only recorded at Ardmore mid-tide in 1981, constituting 96.2% of that sample. Above the cluster of species on axis II are *M. nummuloides* and, at the top, *N. gregaria*. Both of these are particularly characteristic of the Old Kilpatrick site, the latter especially at mid-tide in 1981. They suggest that higher values on this axis might represent increasing pollution stress. Again, an outlier species with an extremely high score is present: *N. justa* which only occurred at Old Kilpatrick high tide in 1981, making up 57.9% of that sample.

The distribution of the samples relative to these axes (Figure 4) shows very strong patterns, with a clear separation of 1981 from 1991 on both axes. Two samples had extreme values and were excluded from

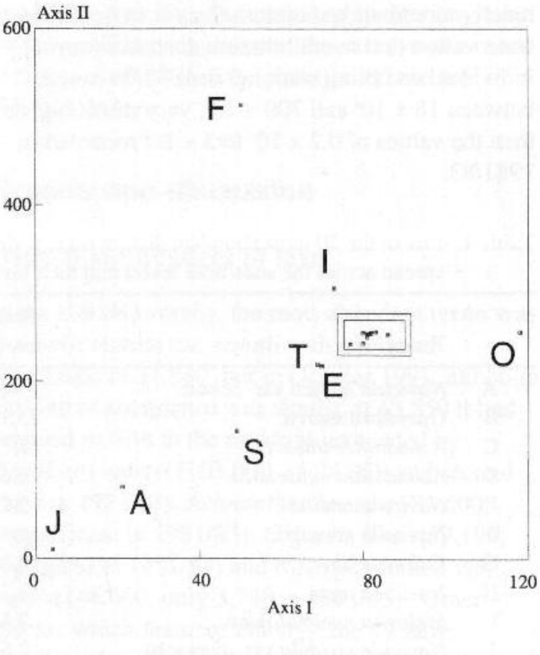


Figure 3. Ordination plot of the main species in the autumn communities, showing their relative positions on the axes I and II against which the sample stations are plotted in Figure 4. Points are labelled with letters corresponding to the taxa listed in Table 1. The box encloses the remaining ten taxa, including the numerically important *O. martyi*. Two taxa are omitted, having extreme values: *A. subsessilis* (1,324 on axis I) and *N. justa* (1,079) on axis 2.

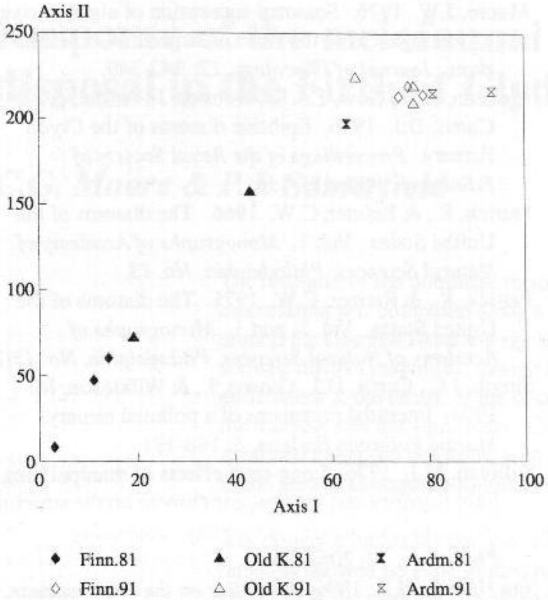


Figure 4. Ordination plot for the autumn communities. Site names are abbreviated as in Figure 2 and are also indicated by plotted symbols with an indication of the year as closed symbols for 1981 and open for 1991.

the plot and the analysis: Ardmore mid-tide in 1981 was almost pure *A. subsessilis*, the only occurrence of this species, while Old Kilpatrick high tide in 1981 was the sole locus for three species: *Fragillaria pinnata*, *Nitzschia justa* and *N. fonticola*. For the remaining 14 samples, mean scores on axis I were 29.0 in 1981 and 83.1 in 1991 ($F_{(1,12)} = 26.95$, $p<0.001$) and a similarly strong difference on axis II with means of 62.2 and 198.9 ($F_{(1,12)} = 28.36$, $p<0.001$).

For the 1981 samples, against both axes a clear gradient is expressed from Finnieston to Old Kilpatrick and then Ardmore, extending across most of the plot from the origin. The same sequence is evident for the 1991 points, but only against axis I and with a much tighter clustering. This reflects an increasing degree of similarity between the communities at the different sites, with the communities tending to become similar to that at Ardmore.

Concluding discussion

Dramatic changes are evident in the diatom communities over this time period. The higher values for species richness and diversity in 1991 compared with 1981 almost certainly relate to changes in water quality. This is substantiated by the patterns shown in the ordination analysis, in which a former long gradient, probably related to conditions of stress in the upper reaches of the estuary, has become very much shorter in 1991 compared with 1981 as conditions improve along the length of the estuary. This is in spite of a potentially damaging event in 1991 accompanying a severe oxygen sag (Henderson 1995).

These community changes are the result of (a) the much higher abundance levels of diatoms in the early 1990s compared with a decade earlier and (b) greater spread of individual taxa (species and varieties) along the estuary. The latter phenomenon could be a complex process, depending not only on the known changes in water quality but also on the potential ability of diatom species to adapt to varying conditions. Indeed, taxonomic difficulties in distinguishing varieties may ensue as the size and shape of diatom cells vary with environmental factors such as salinity (Arthur 1988), as seen in *N. mutica* and *N. mutica* var. *cohnii* (McLean *et al.* 1986) and also *O. martyi* vars (= *Martyana martyi* vars; Bell 1994). Such adaptability, manifesting as broad phenotypic plasticity, contributes to the species' abilities to exploit even slight improvements in the environment of the estuary.

The trend over the last 20 years may be summarised as: *Melosira nummuloides* dominated in the early 1970s (Smyth *et al.* 1974), to co-domination by *Navicula mutica* var. *cohnii* and *Opephora martyi* in 1981/83 (Gow *et al.* 1984), with the first of these two species declining by 1991 when *O. martyi* and *Achnanthes linearis* were the most abundant, but not greatly dominant, species in much more diverse communities.

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Response of the meiofaunal community to sewage sludge disposal in the Firth of Clyde

C.G. Moore & P.J. Somerfield

The response of the dominant meiofaunal groups (nematodes, copepods and annelids) and macrofauna was compared along a transect through the classical gradient of organic enrichment around the Garroch Head sewage sludge disposal site in the Firth of Clyde. All faunal groups showed distinct responses, though their nature differed among the groups. Despite gross organic enrichment at the centre of the disposal site, variation in the total abundance of nematodes along the transect was not significant. Copepods, annelids and macrobenthos, on the other hand, exhibited enhanced densities, with copepods and macrobenthos exhibiting clear abundance peaks in the area of strongest pollution, while annelids peaked at moderate pollution levels. All groups exhibited a clear depression in diversity in the centre of the disposal site. Macrofaunal diversity was clearly affected for the least distance and annelid diversity for the greatest distance, although annelids showed no clear graded response. Depressions in species richness and evenness also occurred at the disposal site, although the response of these measures to pollution was less clear and nematode evenness exhibited very little modification by pollution. Changes in the species composition of all faunal groups along the pollution gradient, as determined from multivariate analyses, were very marked, with the macrofaunal composition clearly modified for the least distance. Copepod species composition was clearly modified for the greatest distance, the effect on composition being more widespread than that on diversity. The patterns of response of the animal groups along the pollution gradient were very similar for identifications to specific and generic levels, but identification to family level reduced the distance of perceived impact.

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Introduction

Sewage sludge from Glasgow has been discharged into the Firth of Clyde since 1904. Before 1974 the disposal site was centred 2 km south of the Isle of Bute, where the operation was found to produce the classical macrobenthic response to organic enrichment (MacKay & Topping 1970; Mackay, Halcrow & Thornton 1972; Topping & McIntyre 1972; Halcrow, MacKay & Thornton 1973). Since 1974 the operating authority has been licenced to discharge up to 1.55 x 10^6 wet tonnes of sludge per year into a designated disposal site of 6 km^2, about 4 km south of the earlier disposal ground (Figure 1). Studies at this current disposal site have also identified a classical response by the macrobenthos to a gradient of organic enrichment (Pearson, Ansell & Robb 1986; Pearson 1987).

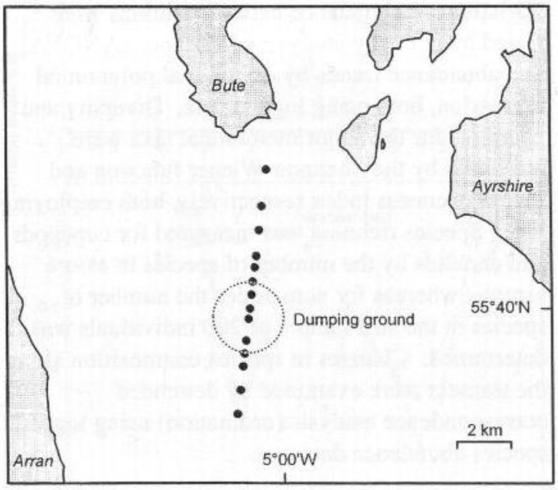

Figure 1. Location of the current sewage sludge dumping ground in the Firth of Clyde. Also shown is the position of the 14 sampling stations used in this study.

The aim of this study is to examine the changes in meiofaunal community structure along this classical gradient of organic enrichment, to compare the responses of the different meiofaunal groups, and to examine the patterns of response as revealed by various community measures, including abundance, diversity and species composition. This investigation was carried out at the same time as a survey of the macrobenthos and physico-chemical factors of sediments that included the same sampling stations (Pearson 1987), permitting comparisons of the nature and sensitivity of the responses by meiofauna and macrofauna to organic enrichment resulting from sludge disposal.

Materials and methods

Duplicate 5 cm cores of area 25.52 cm^2 were taken by Craib corer at 14 stations along a 10 km transect running through the centre of the current sludge disposal site (Figure 1) on 6th June 1981. The water depth along the transect varied between 80 and 192 m with the deeper depths occurring to the south. The sediment consisted of a fairly uniform brown silt, although a covering of sewage sludge was present at some stations near the centre of the disposal site.

Meiofauna passing through a 1,000 μm sieve but retained on a 63 μm sieve was extracted from the sediment by flotation with Ludox-TM at a specific gravity of 1.115 (McIntyre & Warwick 1984). All meiofaunal groups were enumerated in each core, with the major groups (nematodes, copepods and annelids) being identified to the species level in one replicate from each station (a sub-sample of 200 individuals was used in the case of nematodes). Macrofaunal species abundance data (counts of species retained on a 1,000 μm mesh sieve) from single van Veen grab samples from each station and physico-chemical data along the transect were taken from a contemporaneous study by Pearson (1987).

Variations in abundance between stations were tested by one-way analysis of variance (ANOVA) and abundance trends by orthogonal polynomial regression, both using logged data. Diversity and evenness for the major meiofaunal taxa were measured by the Shannon-Wiener function and Pielou evenness index respectively, both employing $\log_2$. Species richness was measured for copepods and annelids by the number of species in a core sample, whereas for nematodes the number of species in the sub-sample of 200 individuals was determined. Changes in species composition along the transect were examined by detrended correspondence analysis (ordination) using logged species abundance data.

Results

Meiofaunal abundance along the transect is strongly dominated by nematodes (mean number of individuals 961 10 cm^{-2}), annelids (157 10 cm^{-2}) and copepods (110 10 cm^{-2}), these groups together constituting at least 95% of the meiofauna at all stations. Nematode abundance varies widely along the transect but not significantly (Figure 2). ANOVA reveals no significant differences in the abundance of copepods between stations, although orthogonal polynomial regression analysis shows that there is a rise in copepod abundance towards the centre of the discharge ($p<0.05$). ANOVA reveals two significant peaks in annelid abundance occurring at intermediate distances (c. 1-2 km) either side of the discharge centre (Tukey *a posteriori* test,

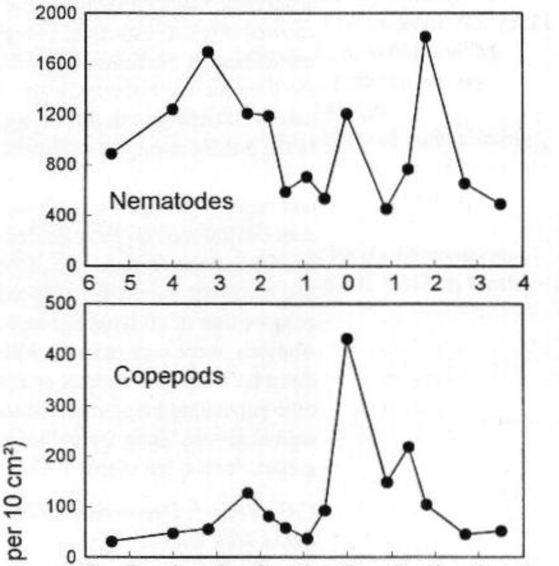

Figure 2. The abundance of the major meiofaunal groups and the total macrofauna along a transect running through the centre of the Clyde sewage sludge dumping ground. For the three meiofaunal groups abundances are based on the mean of duplicate Craib core samples, whereas macrofaunal abundance is based on single van Veen grab samples at each station.

$p<0.05$). Although replicate samples were not available for macrofauna, it is clear from Figure 2 that macrofaunal abundance is enhanced at the dump site, although the effect appears to be confined to an area extending about 1 km north and 2 km south of the dump centre.

Despite the lack of replicate measurements there are distinct patterns in diversity along the transect (Figure 3). All groups exhibit a marked depression in diversity at the centre of the dumping ground, although there are clear differences in the magnitude and horizontal extent of the depression. Nematode and copepod diversity is depressed for approximately 4 km, with the copepods showing the greater reduction. Meiofaunal annelid diversity is grossly depressed for a slightly greater distance (c. 4.5 km), although within 2 km from the dump centre there is no clear relationship between distance from the discharge and diversity. Macrofaunal diversity is clearly depressed for the shortest distance (approximately 3 km). Evenness shows broadly similar patterns to those of diversity (Figure 4) apart from in the case of nematodes, where the discharge apparently has little effect. Species richness, on the other hand, is clearly depressed in all groups (Figure 5).

Ordination of the species abundance data for all groups reveals one strong pattern in the data, clearly related to the level of pollution, and this enables the use of axis 1 scores to summarise compositional changes along the transect (Figure 6). There is a very marked difference between the response of the macrofaunal community, on the one hand, and the meiofaunal groups on the other. Macrofaunal composition is grossly modified at the dump site but the impact is largely restricted to within 1 km of the dump centre. The clear impact of the discharge on meiofaunal composition is more extensive for all groups. Of these, nematode composition appears modified for the least distance, with little change occurring beyond 2 km from the dump centre. The spatial extent of effect on copepods and annelids is clearly greater, although the lack of replicate measurements precludes statistical precision. On the southern arm of the transect there is a major change in community composition of these groups between 1.8 and 2.7 km from the dump centre and along the northern arm between 1.4 and 1.8 km from the dump centre. At 2.3 km on the northern arm the community of annelids and copepods is still clearly modified by the dumping activity, with the fauna showing high numbers of species characteristic of the grossly polluted sediments (*Ophriotrocha* sp.,

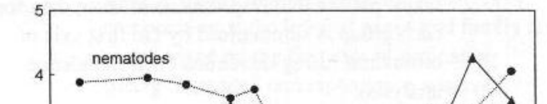

Figure 3. Shannon-Wiener diversity (using $\log_2$) of the three major meiofaunal groups and macrofauna along a transect running through the centre of the Clyde sewage sludge dumping ground. All diversity measures are based on single samples for each station.

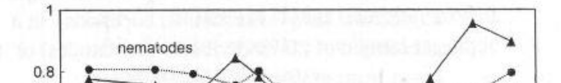

Figure 4. Pielou evenness index (using $\log_2$) for the three major meiofaunal groups and macrofauna along a transect running through the centre of the Clyde sewage sludge dumping ground. All indices are based on single samples for each station.

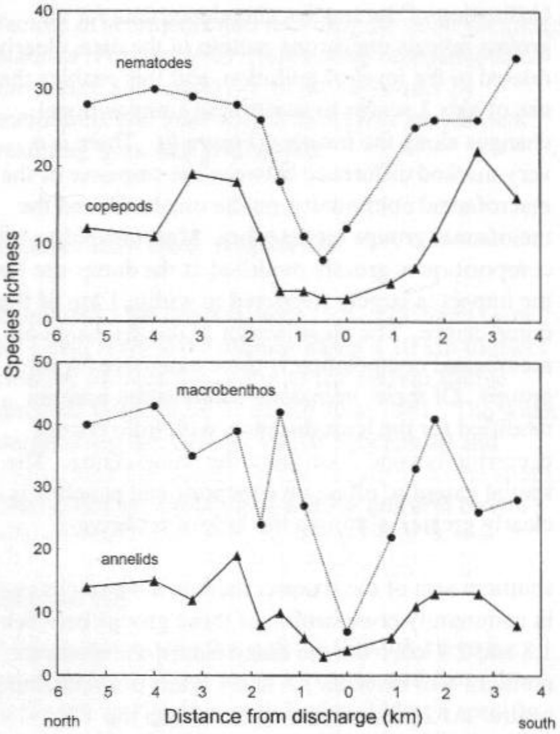

Figure 5. Species richness of the three major meiofaunal groups and macrofauna along a transect running through the centre of the Clyde sewage sludge dumping ground. Species richness is determined as the number of species in single Craib core samples (annelids, copepods), in a subsample of 200 individuals (nematodes) or in a van Veen grab sample (macrofauna).

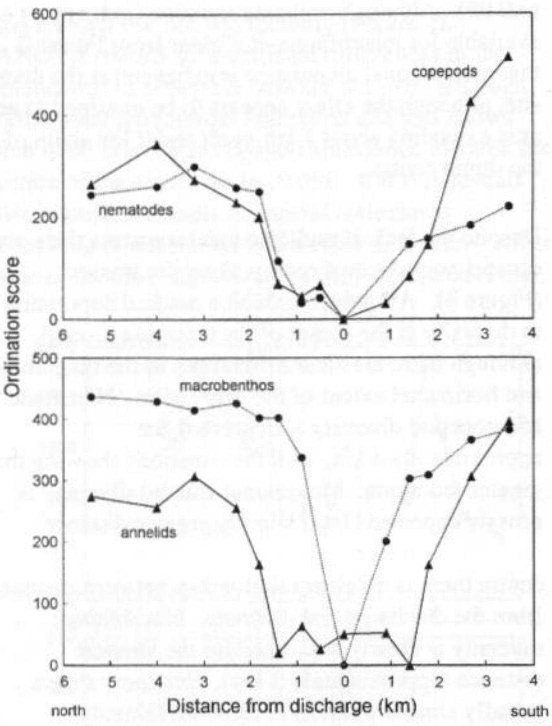

Figure 6. Variation in species composition of the three major meiofaunal groups and macrofauna along a transect running through the centre of the Clyde sewage sludge dumping ground. The major pattern in the species abundance data for each group is summarised by the first axis of ordination (using detrended correspondence analysis).

Bulbamphiascus imus). At 3.2 km on the northern arm the copepod assemblage, though not the annelid assemblage, is still exhibiting signs of perturbation, with the inclusion of several species characteristic of moderately polluted sediments around the dump centre (e.g. *Typhlamphiascus lamellifer, Paramphiascella hyperborea* (Moore & Pearson 1986)). Within 1.5 km of the dump centre the composition of the annelid assemblage fluctuates erratically and shows no relationship with the distance from the discharge centre.

Faunal identification to the levels of genus and family, rather than species, results in very similar patterns in species composition of the macrofauna along the transect (Figure 7). For the meiofaunal groups generic ordinations are little different from specific ordinations, but identification to family level reduces the perceived extent of impact, especially towards the north, where the impact is clearly discernible only up to 1.4 km from the dump centre. The pattern of diversity along the transect for all groups differs little at the specific and generic levels, this being shown for nematodes and copepods in Figure 8. The same is true for evenness and taxon richness.

Table 1 shows the relationships between biotic and abiotic parameters along the transect by means of stepwise multiple regression. In general the level of predictability of biotic parameters from abiotic parameters is very high, particularly for copepods, where at least 71% of the variation in all community parameters along the transect can be explained in terms of physico-chemical factors. By contrast, for the meiofaunal annelids only the ordination scores (reflecting taxon composition) show a relationship with abiotic factors and the variation explained is comparatively low.

There appears to be a difference between the meiofauna and the macrofauna in terms of the predictor variables. Sediment carbon content is the single best predictor for macrofaunal parameters, whereas distance from the centre of the disposal site is the strongest predictor for most of the meiofaunal parameters. It alone explains 92% of the variation in generic composition of the copepods as measured by the ordination score. This difference in relationships is principally due to the changes in macrofaunal parameters and carbon content which are very marked but are largely restricted to the central region of the disposal site. By contrast the changes in

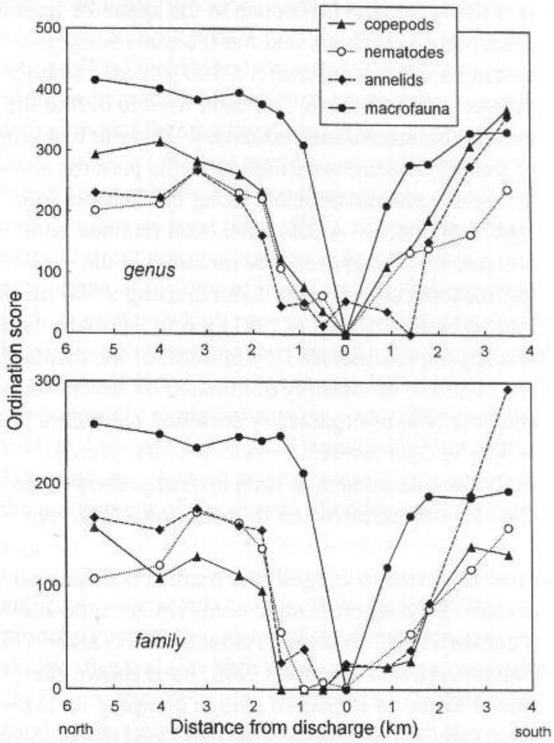

Figure 7. Variation in composition of the three major meiofaunal groups and macrofauna along a transect running through the centre of the Clyde sewage sludge dumping ground. Changes in composition at the level of genus and family are summarised by the first axis of ordination (using detrended correspondence analysis).

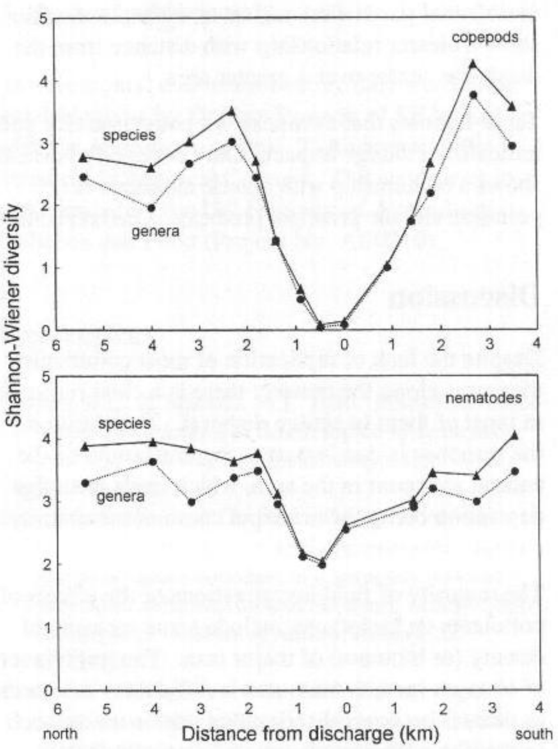

Figure 8. A comparison of the patterns in Shannon-Wiener diversity (using $\log_2$) at the specific and generic levels for copepods and nematodes along a transect running through the centre of the Clyde sewage sludge dumping ground. All diversity measures are based on single samples for each station.

Table 1. Relationships between biotic and abiotic measures along the Garroch Head transect as determined by stepwise multiple regression analysis. For each benthic animal group the predictor variables are given (in order of their importance) for each biotic (dependent) variable. The table only shows regressions significant at the 1% level. The coefficient of determination for each regression is also shown. The abiotic variables analysed include the sediment concentrations of copper, manganese, cobalt, nickel, zinc, cadmium, lead, chromium, carbon and nitrogen, the C/N ratio, the redox potential and pH at a sediment depth of 4 cm and the water depth and distance of the station from the centre of the disposal site. See text for explanation of the dependent variables.

Dependent variable	*Copepods*	*Nematodes*	*Annelids*	*Macrofauna*
Species ordination score	pH, distance (91%)	distance (79%)	distance (71%)	C (87%)
Generic ordination score	distance (92%)	distance, pH (92%)	distance (71%)	C (87%)
Family ordination score	distance (71%)	distance, N (93%)	distance (74%)	C, depth, distance (98%)
Species diversity	distance, Eh (92%)	distance (74%)		Ni, distance, C (96%)
Generic diversity	distance, Eh (92%)			Ni, distance, C (94%)
Species evenness	C, Eh (96%)			
Generic evenness	C, Eh (96%)			
Species richness	distance (82%)	distance (77%)		
Generic richness	distance (82%)			
Abundance	Cu, Zn (91%)			C (77%)

meiofaunal parameters are more widespread and show a clearer relationship with distance from the discharge centre over a greater area.

Table 1 shows that evenness is a comparatively poor indicator of sludge impact. Only copepod evenness shows a relationship with abiotic measures of pollution and the principal predictor is carbon content.

Discussion

Despite the lack of replication of most community measures along the transect there is a clear response in most of them to sludge disposal. The clarity of the response is due in part to the uniformity of the natural sediment in the area, which leads to sludge deposition being the principal cause of community change along the transect.

The majority of field investigations of the effects of pollutants on meiofauna include some measure of density (or biomass) of major taxa. The importance of changes in such measures is difficult to determine as there is no generalisation that can be made, such as that the pollution of some habitat will always result in an increase or decrease in total meiofauna, or some higher taxonomic division thereof, and no paradigm has evolved concerning meiofaunal densities and pollution (Coull & Chandler 1992). Nematode density is generally held to be relatively insensitive to pollution impact (Moore & Bett 1989), and the findings of our study support this. Similarly copepod density cannot be relied upon to change in a predictable way under the influence of various pollutants (Coull & Chandler 1992).

The majority of marine monitoring surveys concentrate on the macrobenthos (Warwick 1993). Whilst all macrofaunal community measures are strongly perturbed by sludge disposal, the spatial extent of clear impact on the macrofauna is less than that for the meiofauna. Under conditions of strong particulate organic enrichment there is evidence that the bimodal species distribution of macrofauna and meiofauna (Warwick 1984) tends to break down, with small polychaetes and large nematodes and copepods being favoured, and the two size classes tend to converge into a single mode (Warwick *et al.* 1986). Examining the macrofaunal data underlying a range of pollution studies, Warwick & Clarke (1993) suggest that it is often a general decline of truly macrobenthic species, molluscs, echinoderms and crustaceans in particular, coupled with an increase in abundance of species more typical of the meiobenthos, especially large nematodes, that discriminate polluted sites. Indeed, at this site dense aggregations of the nematode *Pontonema alaeospiculum*, of a size sufficient to be retained on a 1,000 µm mesh occur at the disposal site (Bett & Moore 1988).

It is likely that the difference in the apparent spatial extent of macrofaunal and meiofaunal responses would have been reduced if a 500 µm mesh, rather than a 1,000 µm mesh, had been used to define the meiofauna/macrofauna boundary. In particular some of the polychaetes contributing to the patterns shown by the meiofaunal annelids along the transect (e.g. *Ophriotrocha* sp.) would have been retained on a 500 µm mesh, and therefore included in the macrofaunal component. Indeed, using a 500 µum mesh Moore & Rodger (1991) found the macrofauna at a site approximately 1.5 km north of the disposal site centre to be strongly dominated by several taxa characteristic of organically enriched sediments, including *Ophriotrocha*, whereas in the present study the macrofauna at such distances showed no clear sign of perturbation by pollution. Although these surveys were separated by four years, there is some evidence to suggest that there is little annual change in the macrobenthic community at the site (Pearson 1987). Whereas Pearson (1987) and Pearson, Anwell & Robb (1986) have shown the spatial extent of impact of sludge dumping on the macrobenthos around the Garroch Head disposal site to be much greater than that described in the present study, even though sampling was carried out at the same time, it should be noted that these studies describe the results from a transect running east-west through the disposal site, rather than the north-south transect described in the present study.

The majority of studies on the effects of pollution on meiofauna have concurred with the need for identifying taxa to species (Coull & Chandler 1992). However Heip *et al.* (1988), Herman & Heip (1988), Warwick (1988a, b), Moore & Bett (1989) and Somerfield & Clarke (1995) have shown that analyses of species data give no greater refinement in assessing pollution effects than do analyses of abundance data relating to higher taxa. The results of the present study show that, in general, identifying meiofauna to species does not greatly increase the discrimination of sites in subsequent analyses. The exact level at which information becomes insufficient is not clear, but as a guideline identifying specimens to genera has had little effect on the level of discrimination in any of the analyses. Identifying specimens to families will occasionally lead to a loss of discrimination but rarely, however, will this result in a response being masked altogether (Somerfield & Clarke 1995).

There are additional reasons why meiobenthos should be monitored in pollution surveys. As an important component of the biota they contribute to the functioning of the ecosystem as a whole. In a laboratory experiment with sewage and meiofauna, Abrams & Mitchell (1980) found that metabolism (and therefore the breakdown of sewage sludge) was greater when nematodes and bacteria were present than with bacteria alone. This they attributed to nematode activity which kept the bacteria actively growing and distributed through the sediment. In addition nematode bioturbation promoted oxygen diffusion and thereby prevented a lack of oxygen from limiting bacterial metabolism and growth. Many fish are known to use components of the meiobenthos as food (Gee 1989). Copepods are of particular importance, making up a significant proportion of the diet of many smaller fish species such as gobies, which may in turn be preyed upon by larger fish of economic importance. The importance of copepods in the diet of juveniles of several commercially exploited species, especially flatfish such as *Limanda limanda*, *Platichthys flesus* and *Pleuronectes platessa* and salmonids, indicates that the assessment of the impact of anthropogenic inputs in areas where such fish occur as juveniles should include the meiobenthos. In some areas certain anthropogenic inputs may increase meiobenthic productivity. In the centre of the Clyde sewage sludge disposal site high densities of large copepods are found, and these may significantly increase the food available to fish in the area. In most cases, however, the abundance and diversity of copepods are decreased by anthropogenic inputs (Coull & Chandler 1992), and one must assume that the productivity of small fish in these areas is adversely affected.

In conclusion, the analyses of meiofaunal and macrofaunal community data from this site confirm and complement those from previous studies at this site. The response evident in macrofaunal abundance data is extreme but is limited to within 1-2 km of the centre of the disposal site and correlates with enhanced sedimentary carbon levels in this area. In analyses of meiobenthic community data the clear seriation of samples, with an obvious gradation of community change (interpretable in terms of pollution impact) from the disposal centre to stations 3-4 km to the north and south, suggest that the meiobenthos are more sensitive to different aspects of the effects of sewage sludge disposal at this site. This is supported by the strong statistical relationship between most of the measured descriptors of community structure and composition and distance from the discharge. Quite how the sludge disposal influences meiobenthic community structure has not, however, been resolved. Using genera instead of species in the analyses has little detrimental effect on the results, but aggregating data to higher taxonomic levels reduces discrimination between sites in some analyses.

Acknowledgements

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The impact of a new long sea outfall on the sublittoral benthos and sediments of the lower Clyde Estuary

M. O'Reilly, J. Boyle & B. Miller

The construction of a new long sea outfall at Ironotter Point, Greenock, provided an opportunity to monitor the initial effects of a domestic sewage discharge on the benthic fauna and sediments of a previously unimpacted area. A sediment infaunal survey was carried out in 1989, prior to commissioning of the new outfall, and again in 1992 approximately one year after commissioning.

Both species richness and faunal abundances increased throughout the area, the latter being largely attributable to an influx of indicator polychaetes associated with organic carbon enrichment. These changes, however, were not reflected in measures of faunal diversity, nor in Infaunal Trophic Index values. Classification and ordination techniques revealed subtle changes in community structure. The application of environmental quality standards recommended for coastal waters highlighted the extent of impact throughout the area.

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Introduction

The towns of Greenock, Gourock and Port Glasgow are situated in the lower Clyde Estuary and encompass a population of around 88,000. Until recently their sewage waste was disposed of, untreated, via over 30 public outfalls and numerous smaller private outfalls most of which had shoreline discharges at, or just below, low water. In 1988 Strathclyde Regional Council initiated the construction of a new comprehensive drainage scheme to serve the area with a 14 km coastal interceptor sewer eventually drawing all the sewerage waste to a headworks at Ironotter Point, Greenock. Subsequent to preliminary treatment at the headworks (coarse and fine screening, and detriting) the effluent would be diffused at the end of a new long sea outfall 1,250 m offshore at a depth of 25 m (Hunter & Scott 1991). The construction of the new long sea outfall provided the Clyde River Purification Board with an opportunity to study the initial effects of the discharge on the benthic fauna and sediments and latterly to relate these to guidance issued by the Comprehensive Studies Task Team (CSTT 1994) on the implementation of the Urban Waste Water Treatment Directive. Studies on the response of marine benthic communities to sources of organic enrichment were reviewed by Pearson & Rosenberg (1978) who detailed the effects on species richness, abundances, biomass, diversity as well as the occurrence of elevated populations of opportunist or enrichment indicator species. Monitoring procedures for benthic communities subject to enrichment were summarised by Rees *et al.* (1990) and appropriate analysis, interpretation, and derivation of environmental quality standards were discussed by MAFF (1993).

Methods

A pre-commissioning survey was carried out in May 1989, a year after the outfall pipe was laid. The outfall was commissioned in 1991 with the first part of the scheme, initially serving about 20,000 population equivalent, being phased in. The post-commissioning survey was undertaken approximately one year later in April 1992. An array of 22 seabed sampling stations was plotted consisting of eight radiating transects with inner stations approximately 100 m from the outfall and middle and outer stations at various distances up to about 1,000 m (Figure 1). The station positions were selected to be of similar depth and also to reflect the east/west current regime in this area (CRPB 1978). At each station three Day Grabs (each 0.1 m^2) were collected (except stations B1 and D2 in 1989 where only two grabs were obtained) for macrofaunal analysis and sediment sub-samples for physico-chemical analyses (% silt (material <63 µm), and % organic carbon). All the macrobenthic fauna from the grabs (retained on 0.5 mm mesh sieves) was counted and identified to species where possible. Species nomenclature follows Howson (1987) and for cirratulids Woodham & Chambers (1994a). Data from the three (or two) faunal replicates were merged prior to determination of the community parameters; species richness (total number of taxa), abundances (total number of individuals), diversity (Shannon-Weiner, H' $\log^2$) and evenness (Pielou J'). Comparison of 1989 and 1992 sedimentary and community parameters was undertaken using the non-parametric Mann Whitney Test for difference in medians. Classification (Czekanowski Average Linkage Similarity), ordination (DECORANA - Detrended Correspondence Analysis), and Spearman rank correlation (of ordination axes, % silt, % organic carbon, and community parameters), were employed as interpretative aids, all based on untransformed data.

Changes in the composition of co-dominant and organic enrichment indicator species were examined and related to sediment % organic carbon levels. Some of the recommendations of the CSTT (1994) were applied including the use of the Infaunal Trophic Index (ITI) and coastal Environmental Quality Standard criteria.

The Infaunal Trophic Index (ITI) offers a more comprehensive approach to the selection and monitoring of a limited number of indicator species by utilising functional aspects of all (or most of) the benthic species. The ITI was originally developed by Word (1978) as an aid to identifying environmental conditions in Californian coastal waters. It has recently been adapted for use in British waters by Codling & Ashley (1992) and was recommended by the CSTT (1994) as a means of achieving further insight into community changes. Although the ITI was not developed for use in estuaries the presence of a fully marine benthic community at Ironotter Point justifies its application.

At each station the benthic species representing at least 80% of the faunal abundance are allocated to one of four trophic groups depending on the type of food consumed, where the food is obtained from, and the strategy employed to capture it. In broad terms Group 1 organisms are water column detritivores, Group 2 are surface/subsurface detritivores, Group 3 are surface/subsurface deposit feeders, and Group 4 are specialised organic feeders adapted to anaerobic sediments. The groups effectively reflect increasing depositional regimes. The ITI is calculated by determining the total abundance of species belonging to each of the four groups and combining them in the following formula:

$$ITI = 100 - [33.33((0 \times Gp1 + 1 \times Gp2 + 2 \times Gp3 + 3 \times Gp4) / (Gp1 + Gp2 + Gp3 + Gp4))]$$

where Gp1, Gp2, etc. equals the total abundances of species in Group 1, and in Group 2 and so on. The coefficients in the numerator are scaling factors devised to give increasing weight to higher groups and the formula is constructed so as to produce values in the range 0 to 100. Calculation of the ITI

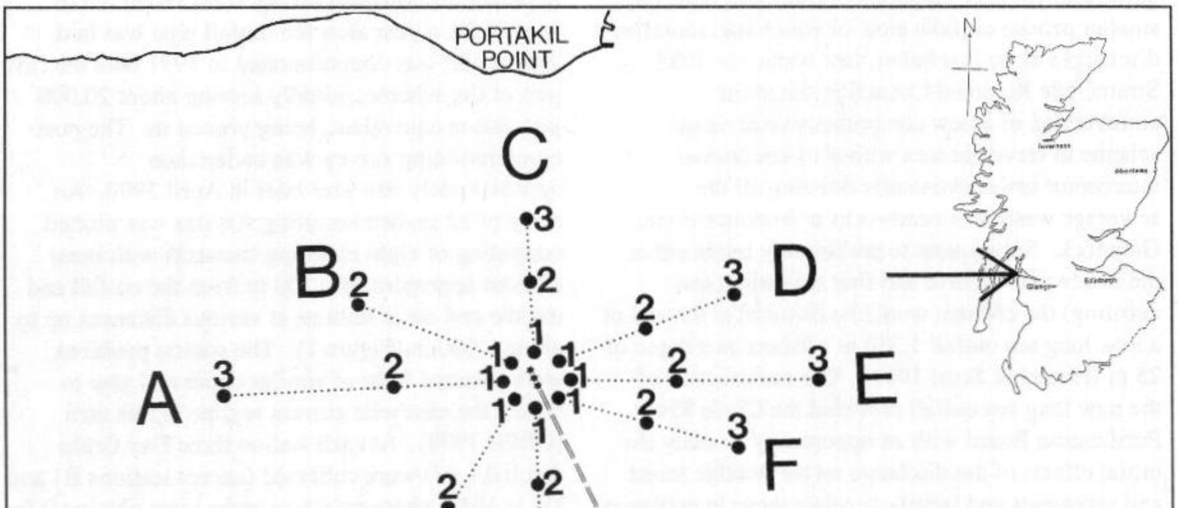


Figure 1. Location of sampling stations at Ironotter Point.

for Ironotter Point followed the methodology and classification outlined in Codling & Ashley (1992).

Results and discussion

Species richness and diversity

Although CRPB salinity data collected between 1990 and 1994 in the Ironotter Outfall area defined it as estuarine area on account of its variable surface water salinities (range 14.0-31.5 psu, mean 26.08 psu), at 20-30 m depth considerably less variation occurs with a higher mean (range 29.6-33.7 psu, mean 31.25 psu). Hence the benthic fauna at this depth is characterised by a species assemblage typical of fully marine waters. Species richness is high with totals of 190 and 200 faunal species recorded in 1989 and 1992 respectively. Species richness increased significantly in 1992 ($p<0.001$) rising at all stations except A1 and A2 (Figure 2). Faunal abundances also increased significantly in 1992 ($p<0.001$), approximately doubling throughout transects A, E, F, G and H and almost quadrupling at station E1 (Figure 3). The community diversity, however, showed no statistically significant change with all the H' values in the range 4.5 to 5.5, except F1 in 1992 which fell to 3.9. Evenness J' ranged from 0.73 to 0.91 except for a corresponding decline at F1 in 1992 to 0.64. The high diversity values contrast with those found by others using similar methods - Eleftheriou, Robinson & Murison (1986), mean H' of 2.5 at 10-11m depth in inner Irvine Bay, or a mean H' of around 3.3 found by Moore & Rodger (1991) at 'recovered' stations at 80-90 m in the old Garroch Head sludge dumping ground and by Elliott & O'Reilly (1991) at 5 m depth in the lower Forth Estuary. (However, Moore & Rodger calculated H' using a natural log base, whilst Elliott & O'Reilly employed a 1.0 mm mesh sieve for sample treatment.) The Ironotter diversities are more comparable with unimpacted stations at 30-50m depth in outer Irvine Bay (CRPB unpubl.) or between 100-130 m in the southern Irish Sea (Mackie, Oliver & Rees 1995).

Sedimentary parameters

The % silt ranged from 0.49% to 3.96% (mean 1.64%) in 1989, and from 0.74% to 4.89% (mean 2.31%) in 1992. The % organic carbon ranged from 0.54% to 2.19% (mean 1.17%) in 1989, and from 0.63% to 3.73% (mean 1.82%) in 1992. Both the % silt and the % organic carbon significantly increased in 1992 ($p<0.05$). The ranked % organic carbon was positively correlated with ranked abundance in 1989 ($r = 0.473$, $p<0.05$), but no correlations were evident between sedimentary and community parameters in 1992.

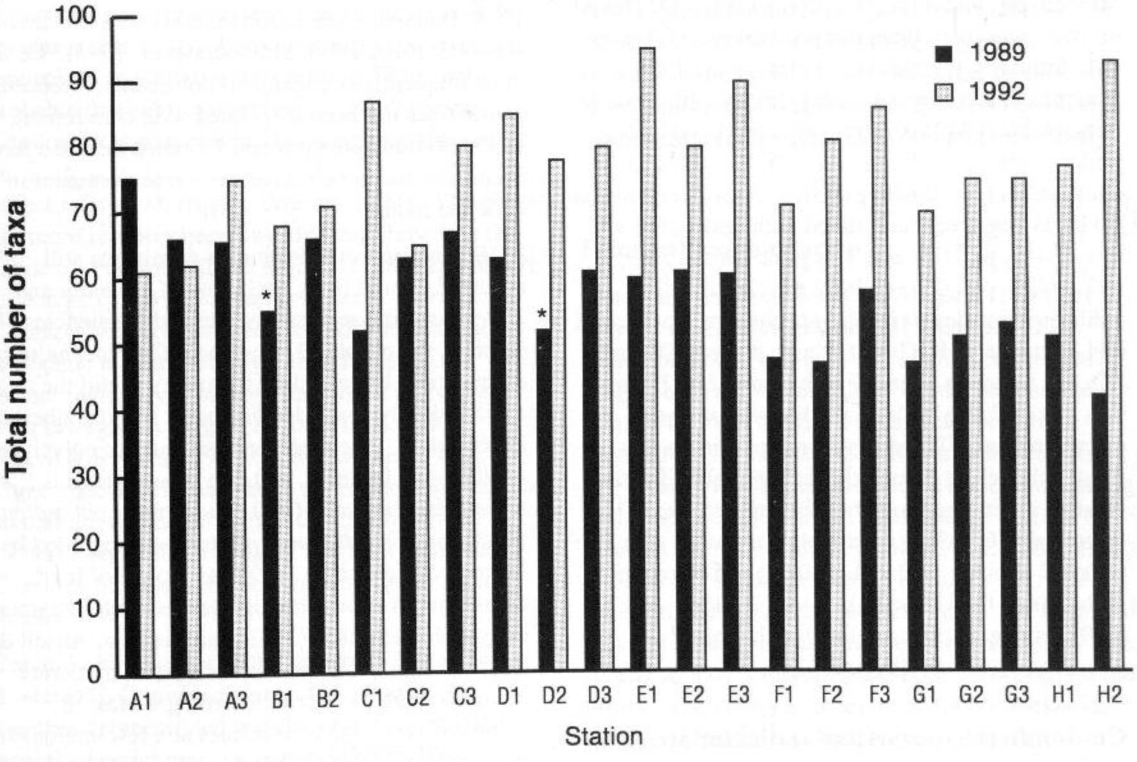


Figure 2. Species richness, 1989 versus 1992 (*denotes only two grabs obtained).

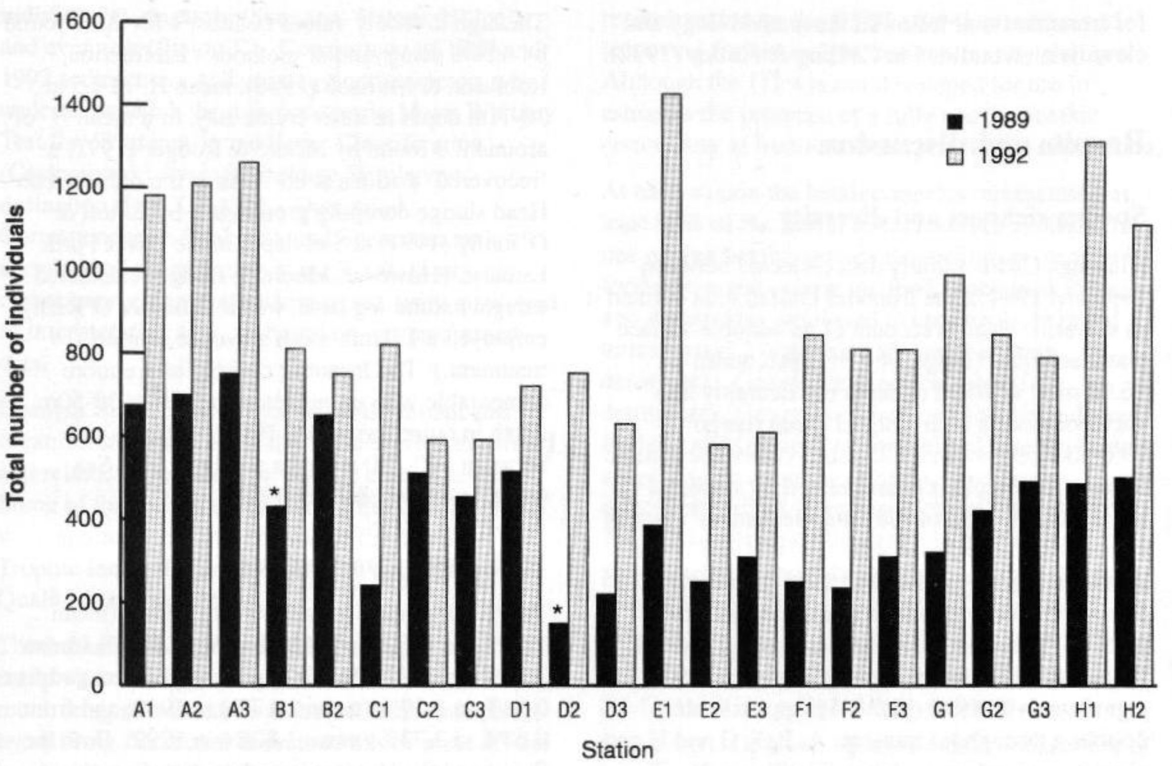


Figure 3. Faunal abundances, 1989 versus 1992 (*denotes only two grabs obtained).

Classification and ordination

Classification analysis of the surveys revealed weak clustering in 1989 - with two broad clusters more or less encompassing transects A to D and E to H respectively, and a single outlying station D2 (based on two rather than three merged replicates) (Figure 4a). Similarly the ordination plot for the 1989 stations depicts a broad scatter (Figure 4b). Axis 1 (eigenvalue 0.342) is negatively correlated with ranks of species richness ($r = -0.578$, $p<0.01$) and abundances ($r = -0.650$, $p<0.01$). Axis 2 (eigenvalue 0.111) is negatively correlated with ranks of % silt ($r = -0.449$, $p<0.05$) and % organic carbon ($r = -0.433$, $p<0.05$). In 1992 the classification analysis identifies three distinct clusters: transects A and H, transects B, C, and G with stations D1 and D2, and transects E and F with station D2 (Figure 5a), and probably reflects the known east/west current regime. The ordination plot mirrors this tighter clustering though the first two classification clusters are merged together (Figure 5b). Axis 1 (eigenvalue 0.233) is negatively correlated with ranks of % silt ($r = -0.704$, $p<0.01$) and % organic carbon ($r = -0.581$, $p<0.01$). Axis 2 (eigenvalue 0.092) is negatively correlated with rank of abundances ($r = -0.605$, $p<0.01$).

Co-dominant species and indicator species

The occurrence and frequency of co-dominant species (i.e. three most abundant species at each station) highlighted changes in the benthic community between 1989 and 1992 (Table 1). In 1989 14 taxa were represented of which 11 are cited as indicative of enrichment (Hily 1983; Moore & Rodger 1991; Pearson 1975; Pearson & Rosenberg 1978; Pearson, Gray & Johannessen 1983; Pearson, Ansell & Robb 1986; Simboura *et al.* 1995). Of the most frequently occurring co-dominants, *Anobothrus gracilis* has not been associated with enrichment, whilst *Melinna palmata* and *Thyasira flexuosa* have been recorded, albeit infrequently, as dominant in enriched muds.

In 1992 several of the same co-dominants still occurred though most, including *M. palmata* and *T. flexuosa*, at considerably reduced frequencies. In contrast, the cirratulid polychaete *Chaetozone setosa* dramatically increased its frequency as did the capitellid polychaete *Mediomastus fragilis* albeit to a lesser extent. The emergence of another polychaete, *Scalibregma inflatum*, and two new cirratulids *Aphelochaeta marioni* and *Caulleriella zetlandica* is of interest. *Scalibregma inflatum* was regarded by Pearson & Rosenberg (1978) as typical of low organic input zones although subsequently Pearson, Gray & Johannessen (1983) and Pearson, Ansell & Robb (1986) quoted it as indicative of moderate enrichment on the Garroch Head grounds. It exhibited very high abundances at a few stations in the southern Irish Sea (Mackie, Oliver & Rees 1995) but not in any association with organic enrichment. It has not featured as a dominant species in previous

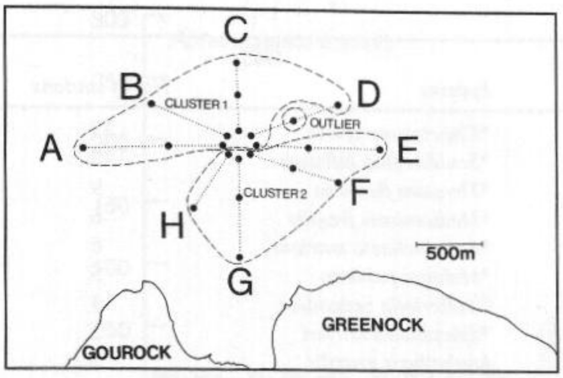


Figure 4a. Czekanowski Similarity 1989.

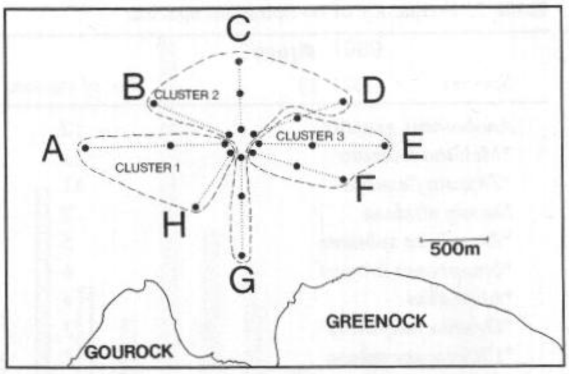
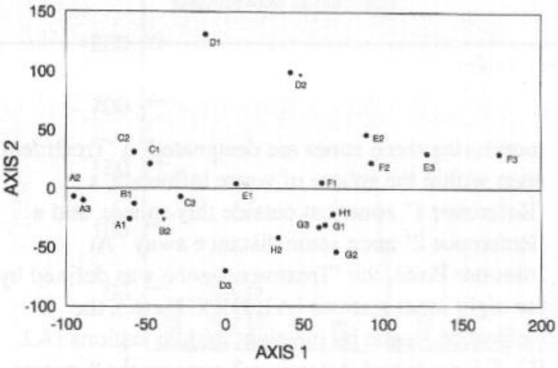


Figure 5a. Czekanowski Similarity 1992.



*ONLY 2 GRABS MERGED (REST HAVE 3)

Figure 4b. DECORANA Ordination Plot 1989.

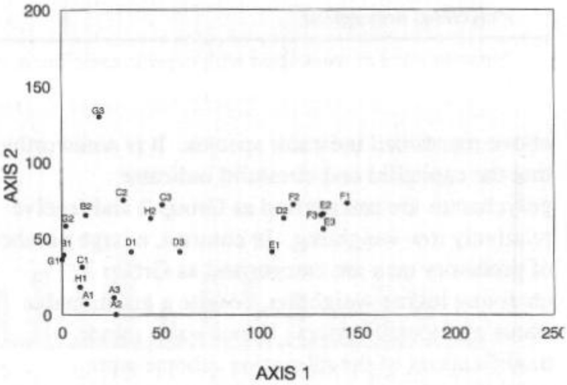


Figure 5b. DECORANA Ordination Plot 1992.

CRPB surveys around sewage outfalls in Clyde Sea waters and was not considered as an indicator species in this study. *Mediomastus fragilis* was not recognised in British waters prior to 1979, and it is probable that some earlier records of abundant *Capitomastus minimus* or *Heteromastus filiformis* in enriched areas (see Pearson & Rosenberg 1978) may in fact refer to *M. fragilis* (Warren 1979). The genus has more recently been linked to enrichment in the Clyde by Pearson, Ansell & Robb (1986) and Moore & Rodger (1991). Similarly, whilst *A. marioni* and *C. zetlandica* have not been recorded as responding to organic enrichment, high abundances of the former (as *Tharyx marioni*) have been associated with sewage discharges (Broome *et al.* 1991; Moore & Rodger 1991; Ros & Cardwell 1992). These species also have been subject to considerable taxonomic confusion (Woodham & Chambers 1994a, 1994b) and it is likely that many records of *C. setosa* include *Aphelochaeta* and *Caulleriella* species.

Certainly in previous CRPB surveys *M. fragilis*, *A. marioni*, *C. zetlandica* and *C. setosa* have together demonstrated population enhancements typical of enrichment indicators (CRPB 1993). At Ironotter Point their abundances were generally elevated in 1992 with some pronounced peaks along transects A, D, E and F (Figure 6) strengthening their validity as putative organic enrichment indicators. Although no positive correlation between abundances of these indicator species and % organic carbon was detectable, their combined % composition of the total faunal abundances clearly illustrates an escalating dominance trend (Figure 7).

Infaunal trophic index

Bascom, Mearns & Word (1978) used ITI values to classify areas of the sea bed into 'normal' (ITI values 60-100), 'changed' (ITI values 30-60) and 'degraded' (ITI values 0-30). Clyde Sea benthic infauna displays similar trends along pollution gradients in Irvine Bay and off Garroch Head with ITI values of 60-80 in unimpacted zones contrasting with values of 0-10 adjacent to sewage outfalls or disposal sites (Codling & Ashley 1992; Thom 1994). At Ironotter Point the initial ITI values for 1989 revealed that eight stations were below the threshold value of 60 suggesting that the area was already in a 'changed' (i.e. stressed) condition. However, all the initial 1992 values exceeded the ITI 60 threshold, falling within the 'normal' zone (Figure 8a).

These results appeared to be at variance with the trends of faunal abundances, particularly of the

Table 1. Frequency of co-dominant species.

1989		*1992*	
Species	*No. of stations*	*Species*	*No. of stations*
Anobothrus gracilis	12	**Chaetozone setosa*	17
**Melinna palmata*	11	**Scalibregma inflatum*	12
**Thyasia flexuosa*	11	**Thyasira flexuosa*	9
Nucula nitidosa	7	**Mediomastis fragilis*	6
**Ampelisca spinipes*	5	**Aphelochaeta marioni*	6
**Spiophanes kroyeri*	4	**Melinna palmata*	5
**Abra alba*	4	*Caulleriella zetlandica*	3
**Owenia fusiformis*	3	**Spiophanes kroyeri*	2
**Chaetozone setosa*	2	*Anobothrus gracilis*	2
**Pseudopolydora antennata*	2	*Nucula nitidosa*	2
**Nephtys kersivalensis*	1	**Abra alba*	1
**Mediamastus fragilis*	1		
**Nuculoma tenuis*	1		
Polycirrus norvegicus	1		

*species cited as associated with organic enrichment in other studies.

above mentioned indicator species. It is noteworthy that the capitellid and cirratulid indicator polychaetes are categorised as Group 2 and receive relatively low weighting. In contrast, a large number of predatory taxa are categorised as Group 3, receiving higher weighting, despite a questionable status as deposit feeders. Hence some minor modifications of the allocation scheme were undertaken in an attempt to limit any masking effect of these predatory taxa and increase the sensitivity of the ITI to the indicator species. The modified allocation details of all the species are presented in Thom (1994) but can be summarised thus:

- Nemerteans and predatory polychaetes were assigned to Group 1.
- The indicator cirratulids were retained in Group 2.
- The indicator capitellid *M. fragilis* was transferred from Group 2 to Group 4 as data from unpublished CRPB Irvine Bay studies suggests it to be tolerant of anaerobic sediments.

The modified ITI continued to imply that stations A3, B1, and D1 were already slightly 'changed' or stressed in 1989 (Figure 8b). By 1992, B1 and D1 edged back above the threshold while three previously 'normal' stations, A2, E1, and F1, slipped below. However, only station E1 displayed any noteworthy decline - a consequence of the increased weighting applied to *M. fragilis* which had its highest abundance at this site.

Environmental Quality Standards

Recommended EQSs for coastal waters, discussed by the CSTT (1994), can be applied, in part, to Ironotter Point. For the purposes of compliance monitoring three zones are designated: a 'Treatment' zone within the sphere of waste influence, a 'Reference 1' zone just outside this sphere, and a 'Reference 2' zone some distance away. At Ironotter Point, the 'Treatment' zone was defined by the eight inner stations (A1, B1, C1, etc.), the Reference 1 zone by the eight middle stations (A2, B2, C2, etc.), and Reference 2 zone by the 6 outer stations (A3, C3, D3, etc.). The community variables of Abundance (A), Species Richness or number of Taxa (T), Abundance/Taxa ratio (A/T), and Shannon-Weiner diversity (H') were utilised to produce 'EQS ratios'. Pairwise comparisons of mean values of these attributes between the different zones were expressed as percentage differences, i.e. [(Treat. zone/Ref. 1 zone) - 1] x 100. These are presented in Table 2 along with guideline values for 'status quo' of reference areas and 'acceptable change' within the sphere of waste influence.

The 1989 survey undertaken prior to commissioning can be regarded as a baseline. Inter-zone differences for the community parameters were all less than 10% indicating a broad similarity between these zones. Similar comparisons within the 1992 survey showed some notable disparities between the Treatment and Reference zones, exceeding 20% and 30% the Abundance and Abundance/Taxa values, but still within the status quo guidelines. However, a direct comparison of the same zones in 1992 and 1989 highlights significant changes in all the zones of Abundance and Taxa values. In the treatment zone the status quo guidelines are significantly exceeded for three of the variables demonstrating a clear impact in this area. In the reference zones the status quo guidelines are also exceeded indicating that the environment outside the zone of effect has not been preserved and casting doubt on the validity of these zones as unimpacted reference areas.

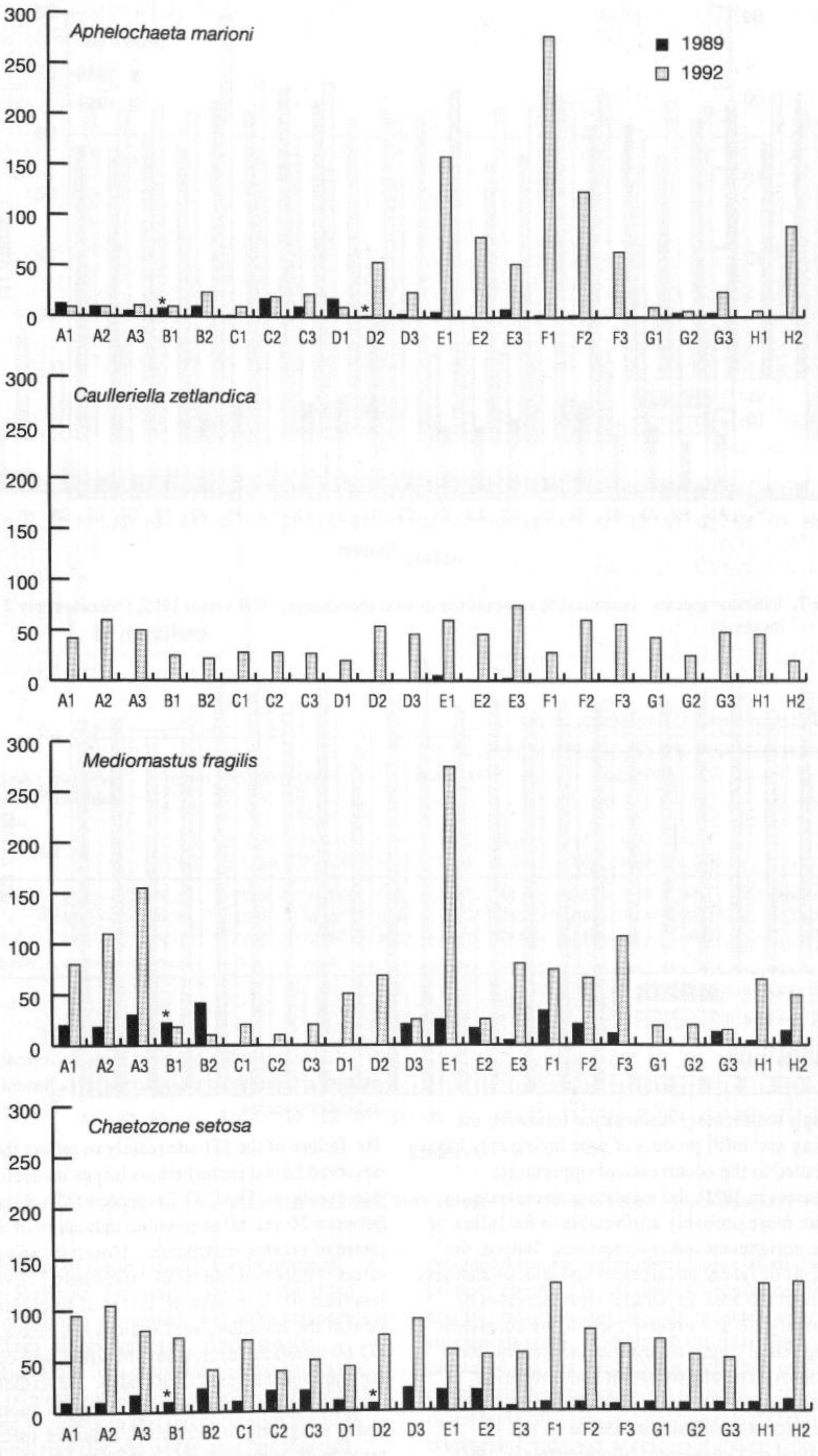


Figure 6. Abundances of four indicator species, 1989 versus 1992. (*denotes only 2 grabs obtained)

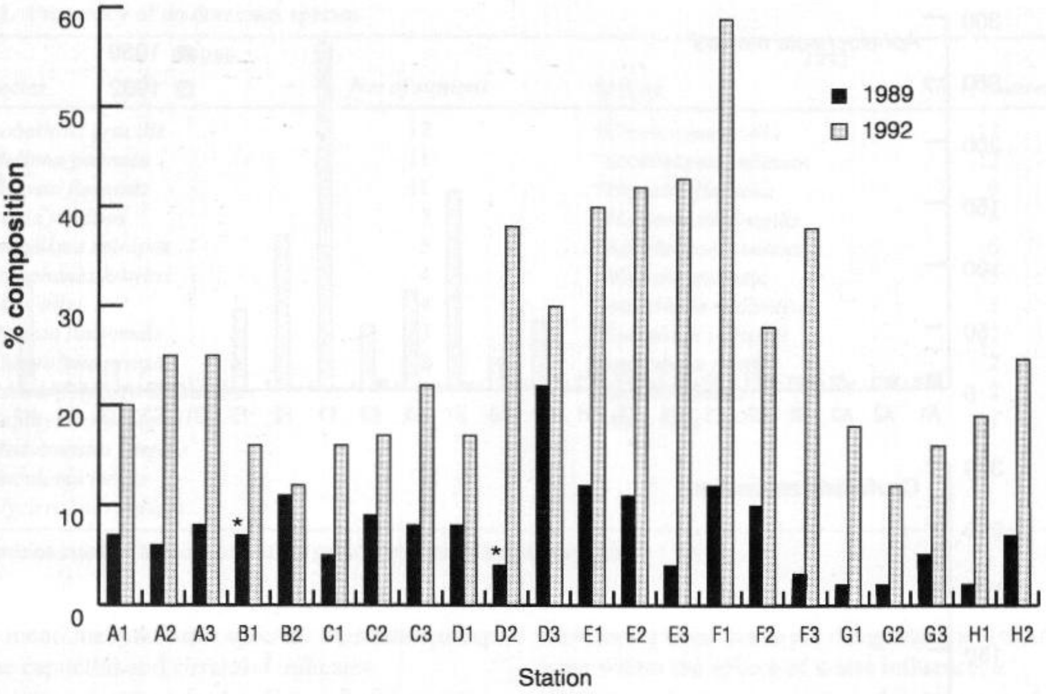


Figure 7. Indicator species - combined % composition of total abundances, 1989 versus 1992. (*denotes only 2 grabs obtained)

Table 2. Environmental Quality Standard ratios.

Pairwise comparisons of zones expressed as % differences:

	1989 values			*1992 values*			*1992 versus 1989 values*			*Status quo guidelines*	*Acceptable change guidelines*
	Treat Ref. 1	*Treat Ref. 2*	*Ref. 1 Ref. 2*	*Treat Ref. 1*	*Treat Ref. 2*	*Ref. 1 Ref. 2*	*Treat 92 Treat 89*	*Ref. 1 92 Ref. 1 89*	*Ref. 2 92 Ref.1 89*		
Abundance (A)	-1.39	0.78	2.20	21.68	28.64	5.72	137.86	92.77	86.36	+/- 50%	+ 200%
Taxa (T)	0.44	-6.20	-6.61	0.65	-5.49	-6.10	36.56	36.28	35.54	+/- 20%	+ 50%
A/T	-2.76	6.17	9.12	20.97	36.44	12.74	79.32	44.13	39.44	+/- 50%	+100%
H'	-0.63	-1.31	-0.69	-4.26	-5.36	-1.14	-1.80	1.93	2.40	+/- 20%	Not defined

Conclusions

Although sedimentary disturbance following the trenching and infill process of pipe laying may have contributed to the occurrence of opportunist polychaetes in 1989, the escalating abundances in 1992 are more probably attributable to the influx of organic enrichment indicator species. Indeed, the elevations of faunal abundances and species richness throughout the area, in parallel with increases of sedimentary silt and organic carbon, are consistent with the initial stages of organic enrichment (Rees *et al.* 1990). The classification and ordination analyses suggest that the sedimentary parameters may be exerting a greater influence on the distribution and abundance of organisms in 1992 than in 1989. It is surprising that no relationship is, as yet, demonstrable between these sediment parameters and the prevalence of enrichment indicator species.

The failure of the ITI adequately to reflect the observed faunal perturbations brings its usefulness into question. The CSTT regarded ITI values between 30 and 60 as possible indicators of an early phase of organic enrichment. However, an adverse effect is only considered to exist where ITI values of less than 30 occur outwith 100 m of an outfall. Few of the Ironotter Point stations fell below the ITI 60 threshold, even when modified, and certainly none approached the ITI 30 value. Nevertheless, the use of an index which permits the application of heavy weighting to recognised indicator species may provide an improved approach to the detection of initial community responses.

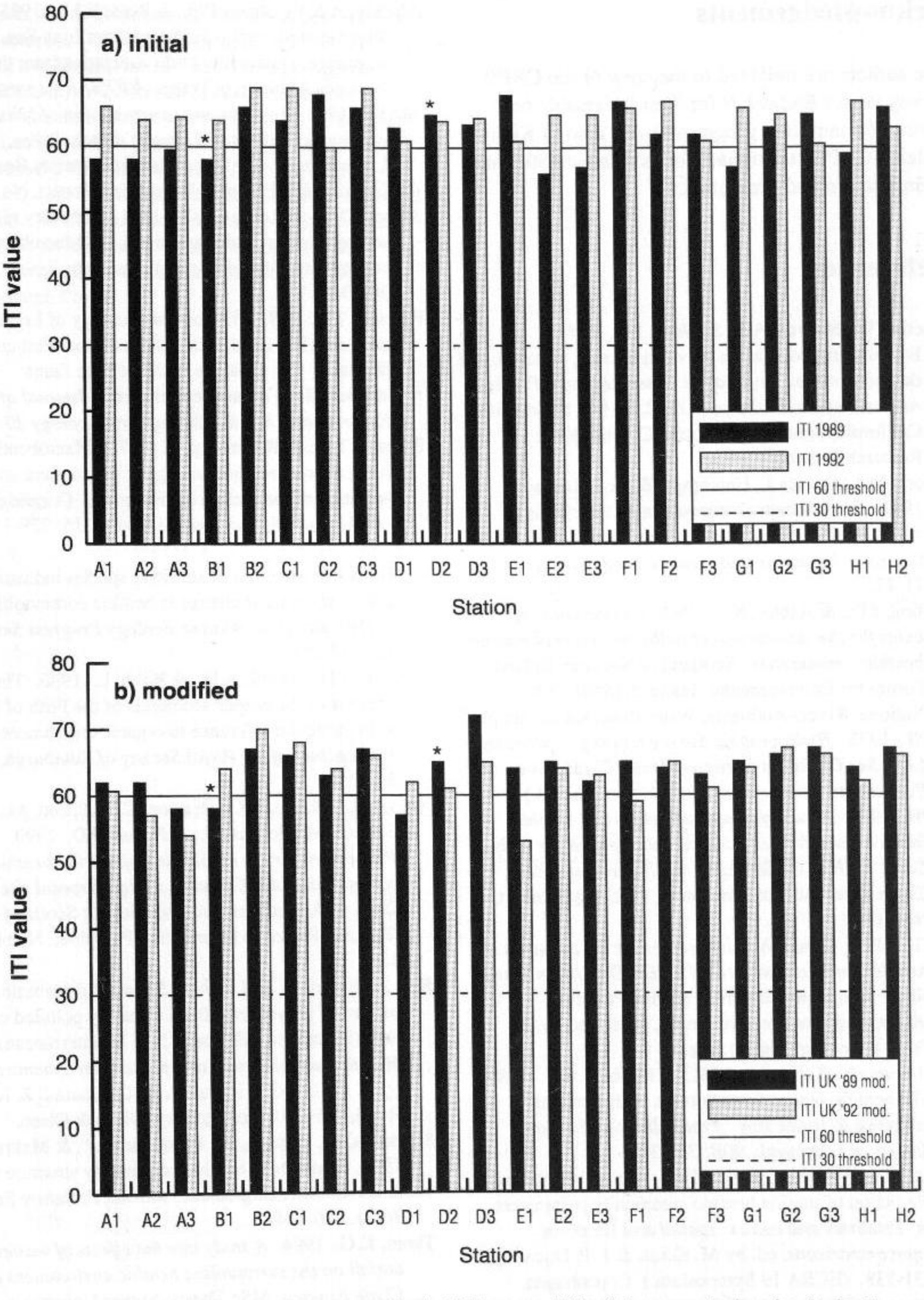


Figure 8. Infaunal Trophic Indices (initial and modified), 1989 versus 1992. (*denotes only 2 grabs obtained)

The adoption of recommended Environmental Quality Standards for coastal waters highlighted trends of primary community variables and points to the efficacy of this approach. Although the guideline values for acceptable change within the sphere of waste influence have not been breached, the trend is clearly in this direction with the EQS ratios implying that the whole area has changed between 1989 and 1992. It should be remembered, however, that 'appropriate action' is only required if the guidelines for acceptable change of all the primary community variables (Abundance, Taxa, and Biomass) are significantly breached over three successive years. It might be expected that increased loading being phased into this outfall may exacerbate the impact on the benthos. Further monitoring may reveal continuing degradation with burgeoning indicator species populations, declining diversity and ITI, and possible breaches of EQS guidelines for acceptable change.

Acknowledgements

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Coastal Zone Topics, 3: 140-145

Linked life cycles of the predatory snail *Retusa obtusa* (Montagu) and its prey *Hydrobia ulvae* (Pennant) in the Forth Estuary

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Hydrobia ulvae in the Forth Estuary produce most eggs in April-May followed by most pelagic veliger larvae in June-July, with settlement in great numbers from July-August. The newly settled young, 0.3-0.5 mm long, can just be swallowed by young *Retusa obtusa* of 1.7-2.0 mm shell length, which themselves first hatched on the intertidal flats in February-March. The only other food of *R. obtusa* is foraminiferans, which comprise the sole diet of young specimens before July. Foraminiferans become less important in the diet as *R. obtusa* grows and eats progressively more *H. ulvae* in autumn and winter. During February-April, at the height of egg-laying, *R. obtusa* consumes maximum amounts of both foraminiferans and *H. ulvae*. Post-reproductive *R. obtusa* eat only foraminiferans and die off in April-June. The timing of egg production by *R. obtusa* seemed not to be affected by manipulation of temperature or daylength. Instead it remains likely that the timing of breeding is a passive consequence of the seasonal appearance of juvenile *H. ulvae*. These prey are exploited by the smallest *R. obtusa* that can readily swallow them, thus commencing, in July-August, a programme of growth and maturation leading by winter to the onset of reproduction.

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Introduction

The opisthobranch snail *Retusa obtusa* (Montagu) occurs on British and other north European intertidal flats (McMillan 1968; Muus 1967; Thompson 1976) where salinity normally stays above 12‰ (Wolff 1973). Smith (1967) outlined the one-year life cycle with adults spawning and then dying in spring, and young hatching in a few weeks from benthic egg capsules to crawl in the substratum with no planktonic larval stage. Predation by *R. obtusa* upon foraminiferans and *Hydrobia ulvae* (Pennant) was reported by Pruvot-Fol (1954), Smith (1967) and Wolff (1973) and, in the Forth, by Elliott (1979, 1980) and McLusky & Elliott (1981). Yet little was known of this predation and even the mode of prey-ingestion was uncertain (Thompson 1976).

North European assemblages of intertidal/estuarine foraminiferans have been described by Murray (1991) including chiefly *Ammonia beccarii* and *Ammotium cassis* associations. Altenbach (1985, 1987, 1992) and others have estimated biomass and production of benthic foraminerans but not of estuarine intertidal species. Alve & Murray (1994) describe the foraminiferans of the Hamble Estuary, England, giving mean standing crops of 772 cm^{-3} in March but of only 76 10 cm^{-3} in June. Little is known of the ecology of estuarine foraminiferans and of their importance as food for benthic animals.

Hydrobia ulvae (Pennant) is one of the most abundant and conspicuous snails on estuarine intertidal flats. In the Forth, Warnes (1981) reported a maximum 94,800 m^{-2} at Torrybay, with many counts of 10,000-25,000. The annual cycle of *H. ulvae* described by Warnes (1981) in the Forth, with egg capsules mostly appearing in April-May and a sudden chief spatfall in July followed by growth for perhaps four years, largely matches patterns elsewhere in Britain (e.g. Fish & Fish 1974). Barnes (1990, 1994) in more southerly sites has recently clarified details of this life cycle and, in particular, differing reproductive strategies in response to contrasted habitats.

While predation by *R. obtusa* on *H. ulvae* was quantified in the Forth (Berry 1988; Berry & Thomson 1990), and gonads and egg-laying in *R. obtusa* were monitored (Berry, Radhakrishnan & Coward 1992), there is little understanding of factors regulating the annual life cycle of *R. obtusa*. This applies especially to any links between (a) the changing food requirements and preferences of the predator as it hatches, grows and breeds and (b) the varying availability and suitability of different species and sizes of prey. It is possible that seasonally changing environmental factors (temperature, daylength, etc.) trigger breeding activity in winter and so directly regulate the annual cycle as in, for example, some echinoderms (Pearse,

Pearse & Davis 1986, McClintock & Watts 1990). Alternatively it is possible that seasonal breeding is the passive consequence of the requirement for a particular period of growth and maturation following the appearance of a vital item of diet: a 'size-age complex' as proposed for other cases by Todd (1978). The aim of work reported here has been to record the life cycle of *R. obtusa* in the Forth Estuary, to quantify its changing pattern of predation, to learn if life cycles of predator and prey are functionally linked and, finally, to examine what factors might regulate the timing of breeding in the predator.

Materials and methods

R. obtusa and *H. ulvae* were collected from intertidal sand/mudflats at Torrybay in the Forth Estuary and examined as described by Berry (1988, 1994a). Veliger larvae of *H. ulvae* were counted in subsamples from a near-monthly series of high tide and low tide plankton hauls made in 1992 and 1993 by the Forth River Purification Board off Longannet, Bo'ness, Tancred Bank, Blackness and Port Edgar (Torrybay lies on the north shore, virtually opposite Bo'ness). Foraminiferans were monitored in the sediments and in *R. obtusa* gizzards as in Berry (1994a). Gonads were examined and egg-laying monitored in laboratory tanks at 5°C and at 10°C and in a variety of 24 hour light:dark regimes as described in Berry, Radhakrishnan & Coward (1992).

Results

A. Life cycle of R. obtusa

The benthic eggs are mostly ~260-300 μm diameter within clear jelly spheres of ~390 μm diameter adhering to sand grains in loose but discrete batches of <60. When gonads and egg-production were specifically studied (Berry, Radhakrishnann & Coward 1992), most oocytes in the ovotestis grew from 90-140 μm diameter in June-July to 200-330 μm in December-April. From December, gonads of snails >2.7 mm shell length became progressively dominated by such full-grown oocytes rather than by spermatogenic tissue. No eggs were laid in July-August. The first two batches, of 18 and four eggs, appeared in early October but through November mean egg production remained <0.3 d^{-1}. Egg-laying then increased during December-March with one batch laying a mean 5.5 each d^{-1} in late March. Spawning slowed drastically and adults died fast in April-May (Figure 1a, b, c).

In both periods of systematic population counts (August 1986-August 1987 and April 1992-March 1993) young predators were first found in the sediment at lengths of 0.5-1 mm in February-March. In each set a clear cohort grew through ~1 year to reach lengths of 3.5-5.5 mm by the following February-April. Then adults died rapidly by June without further growth (Figure 1a).

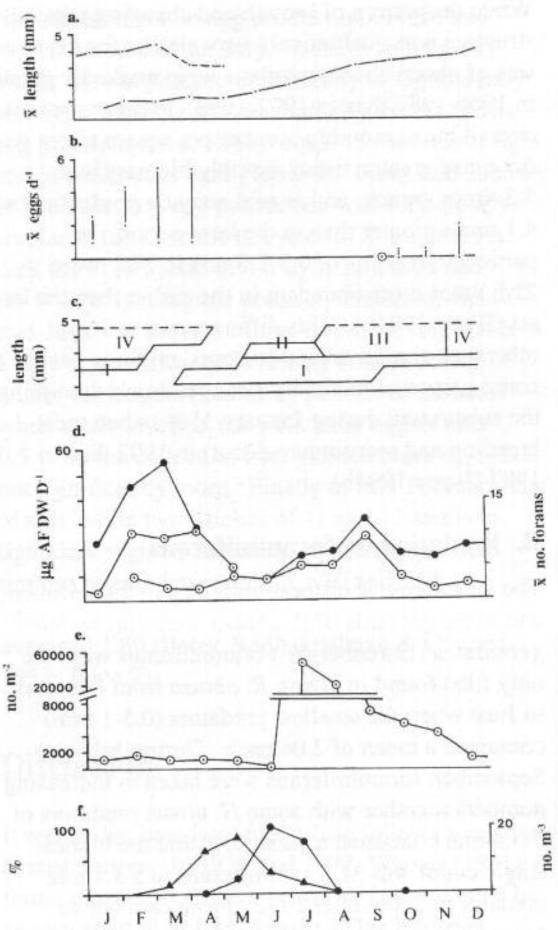

Figure 1. (a) Monthly mean cohort shell length of *R. obtusa* from first appearance in February to death (broken line) in April-May a year later.
(b) Range of daily egg production by *R. obtusa* in laboratory tanks. First eggs were observed in early October.
(c) Scheme of oocyte development in *R. obtusa* in relation to shell length and time: I = oocytes <85 μm diameter, II = many oocytes 90-140 μm, III = many oocytes 170-330 μm, IV = oocytes of 170-330 μm exceeding areas of spermatogenesis in sections.
(d) estimated daily food intake by *R. obtusa* of cohort-mean shell length: total comprises foraminiferan AFDW (●) plus *H. ulvae* AFDW (O). Note two cohorts appear in February-May as in (a).
(e) no. m^{-2} of small *H. ulvae* (<1.2 mm) in the field (note broken scale).
(f) % *H. ulvae* shells bearing *H. ulvae* egg masses at Torry Bay (▲) and mean no. m^{-3} veligers of *H. ulvae* from five sites in the Forth Estuary in 1992 and 1993 (●).

While the pattern of growth and changing population structure was qualitatively very similar for the two sets of observations, numbers were markedly greater in 1986-1987 than in 1992-1993. In the earlier set, overall mean monthly number per square metre was 6.3 times greater, mean monthly biomass was 5.3 times greater, and annual somatic production was 4.1 times greater than in the later period. In particular, recruits of 0.5-2.5 mm in May were 21.6 times more abundant in the earlier than the later set (Berry 1994b). This difference in scale, in otherwise similar annual patterns, might in part be a consequence of markedly stronger winds disrupting the substratum during January-May (when most breeding and recruitment occur) in 1992 than in 1987 (Berry 1994b).

B. Predation on foraminiferans

The vast majority of foraminiferans in the sediment and in the gizzards of *R. obtusa* were *Haynesina germanica* (Ehrenberg). Foraminiferans were the only food found in young *R. obtusa* from February to June when the smallest predators (0.5-1 mm) contained a mean of 2.06 each. During July-September, foraminiferans were taken in increasing numbers together with some *H. ulvae*: predators of 3-3.4 mm contained a mean 8.44 and the highest single count was 31 foraminiferans in a 3.1 mm predator in September 1992. From October to January, mean counts fell to 1.6 foraminiferans per gizzard as intake of *H. ulvae* rose. Foraminiferans again became abundant in full-grown *R. obtusa* of February-April (Berry 1994a).

The majority of foraminiferans ingested by *R. obtusa* were of 100-150 µm diameter with a median of 125 µm. There was only a weak increase of prey size with predator size and the more abundant foraminiferans of 200-375 µm diameter were rarely ingested (Berry 1994a).

In summary, foraminiferans were the sole food of youngest and of post-reproductive adult *R. obtusa* but were relatively less important during the onset of reproduction. They were cleared from the gizzard in ~12 hours suggesting that gizzard counts might represent about half the daily intake. If ingested foraminiferans comprise ~0.7 µg organic carbon and 1.4 µg AFDW as suggested by Altenbach (pers. comm. 1993) then the biggest *R. obtusa* take a maximum of ~30 µg AFDW d^{-1} as foraminiferans in April whereas these biggest predators may take up to 48 µg AFDW d^{-1} as *H. ulvae* in February-March (Figure 1d; Berry 1988).

C. Predation on *H. ulvae*

All prey are swallowed entire into a voluminous gizzard where calcareous shells are dissolved over 1-7 d depending on size of prey and of predator. Trials with empty shells showed that the biggest prey shell that could easily be inserted into a predator's shell is described as follows:

$$\frac{\textit{H. ulvae}}{\text{shell (mm)}} = 0.582 \times \frac{\textit{R. obtusa}}{\text{length (mm)}} - 0.22$$

($r^2 = 98.7\%$).

Thus the newly settled *H. ulvae* at 0.3-0.4 mm long should be available to predators of 0.9-1.1 mm shell length. Yet *H. ulvae*, even of only 0.3 mm shell length, were never found in gizzards of *R. obtusa* of <1.7 mm shell length. The two largest prey ever found in field *R. obtusa* were 2.1 mm in a 4.1 mm predator (which might have taken prey up to 2.17 mm long) and 1.9 mm in a 3.9 mm predator (which might have taken *H. ulvae* up to 2.05 mm long). Bigger *R. obtusa* did not eat bigger *H. ulvae* even though a 5 mm predator should be able to eat 2.7 mm prey. Generally, the ingested *H. ulvae* were conspicuously smaller than the biggest available prey which could have been swallowed.

In March-June, virtually all *H. ulvae* were too big to be eaten by a new cohort of young *R. obtusa*. *Hydrobia ulvae* first appeared in gizzards when large numbers of young *H. ulvae* first settled in July and August by which time *R. obtusa* had mostly grown to 1-2.5 mm (July) with most at 2-3 mm in August (Figure 1).

In the two sets of one-year observations (Berry 1988, 1994a), only 1.33% and 2.8 % of *R. obtusa* contained *H. ulvae* in July. This proportion rose to 11-41 % in August and then progressively to ~90 % in January. In February-March 1987, 96-100% of *R. obtusa* (virtually all full-grown) contained *H. ulvae* while, in the same months of 1993 by contrast, proportions fell to 56% and 26%. Only 6% and 11% of gizzards bore *H. ulvae* in April and none, not even the few big ones, bore them in May.

Mean shell length of ingested *H. ulvae* increased from 0.5 and 0.6 mm in August 1986 and 1987 to 1.38 mm in November 1986 when most gizzards still contained a single *H. ulvae* but a few gizzards contained two. From December till March, however, in the biggest breeding *R. obtusa*, sizes of *H. ulvae* prey paradoxically decreased to a mean of 0.74 mm in January 1987 while numbers in the gizzards increased to a mean of 3.17 in February, when one gizzard contained 11 shells of 0.5-0.9 mm and none lacked *H. ulvae* (Berry 1988). This shifting size-preference for *H. ulvae* was confirmed in the laboratory where *R. obtusa* of all sizes at most times of year selected *H. ulvae* of 0.6-1.0 mm rather than those of 1.4-2.2 mm. Only in late November-early December did big predators briefly choose more large than small prey (Berry & Thomson 1990).

Laboratory consumption of *H. ulvae* rose from ~3-4 µg AFDW d^{-1} in *R. obtusa* of 2-2.5 mm (August) to 42-48 µg AFDW d^{-1} in predators of ~5 mm shell length in February according to the equation:

$$\begin{array}{c}\log_e\\ \text{consumption}\\ (\mu\text{g AFDW d}^{-1})\end{array} = 0.934 \times \begin{array}{c}R.\ obtusa\\ \text{length (mm)}\end{array} - 0.787$$

(n = 76 *R. obtusa*; R^2 = 62.2%; Berry 1988).

Throughout growth of a predator of mean monthly shell length, foraminiferan AFDW exceeded *H. ulvae* AFDW in the diet during February-September but thereafter foraminiferans were largely replaced by *H. ulvae* as the predators grew to full size and became reproductive. Then, at the height of reproductive activity in February and March, both items of diet occurred in gizzards at near-maximum frequencies. Lastly, post-reproductive adults ate only foraminiferans (Figure 1d). It is estimated that such a typical predator consumes some 2,747 foraminiferans (~3,845 µg AFDW) in a year from February to February and, in the same period, eats ~2,396 µg AFDW as *H. ulvae* (Berry 1994a).

D. Regulation of breeding

Field records of the *R. obtusa* population together with laboratory observations (above) confirm that ovotestes mature in autumn, leading to spawning mostly in December-March (Figure 1b, c). While there is a wide range of sizes in a cohort at any one time, snails of 3-5.2 mm laid virtually no eggs before December yet those of identical sizes commonly laid 2-4 eggs d^{-1} over sustained periods in January-March.

Laboratory cooling, crudely simulating autumn-winter changes, did not speed egg production. Eggs were not produced faster during mid-October-mid-December by 70 snails held at 5°C than by 68 held at 10°C (Table 1). Very few eggs were produced at these times (<0.2 d^{-1}) and, in two matched sets, 25 warmer snails produced on average eight times as many eggs as 27 cooler ones, but still only 0.08 d^{-1}. At 15°C, laboratory survival was markedly reduced and virtually no eggs were produced.

Varying light:dark regimes at 7-10°C had no significant effect on egg production. From mid-November to mid-January, 42 snails in long-day cycles did not produce consistently or significantly less eggs than 40 snails in short-day cycles. Also, egg production was almost equal in continuous light and in continuous dark (Table 2). From mid-January to late February, egg production was very closely similar in (a) 12 snails in cycles of 8 h light:16 h dark (b) 11 in cycles of 4 h light:20 h dark and (c) 11 in a light regime precisely matching that of mid-June. At the same time, five surviving snails in a light regime closely following contemporary winter daylengths (including periods of darkness when water levels in the field were higher than 0.5 m on the collection site) yielded more eggs, but not significantly more. Finally in mid-February-late March, while two batches of 11 and 12 snails in light/dark regimes matching contemporary field timings released averages of 1.70 and 1.96 eggs d^{-1} $snail^{-1}$, 11 snails in continuous dark also averaged 1.80 (Berry, Radhakrishnan & Coward 1992; Table 2).

Table 1. Mean no. eggs d^{-1} $snail^{-1}$ produced by 138 *R. obtusa* during a total of 71 days observation at 5°C or 10°C.

dates	*n*	*T°C*	*mean no. eggs*
23 October-21 November	43	05	0.19
	43	10	0.14
24 October-5 December	27	05	0.01
	25	10	0.05

Discussion

It seems that breeding in *H. ulvae* follows a regular annual pattern. In 1976 and 1977, Warnes (1981) found most egg capsules in April-May followed by sudden spatfall in July-August. This has been confirmed by informal observations of egg capsules and counts of small *H. ulvae* between 1987 and 1992 (Berry 1988, 1994a). This was again confirmed by the appearance in Forth Estuary plankton of most larvae during June and July of 1992 and 1993 (Berry, unpublished; Figure 1e, f). The annual cycles of Forth *R. obtusa* and *H. ulvae* are linked in that a cohort of predators grows to 1.5-3.0 mm by July-August and is, therefore, big enough to exploit the sudden appearance at that time of abundant young prey of 0.3-0.6 mm (Figure 1). Growing prey are then eaten through autumn by growing predators. Earlier breeding by *R. obtusa* would bring them to a competent size before the first appearance of settling *H. ulvae* and, hence, growth would be impeded and losses increased. Later breeding would leave predators too small in July-August to ingest the young, rapidly growing *H. ulvae*.

Natural selection might be expected to favour mechanisms which fix the time of spawning so that young *R. obtusa* grow to 1-1.5 mm long when *H. ulvae* spat first appear, as in cases reported by DeWitt (1967), Usuki (1970), Pearse, Pearse & Davis (1986), and McClintock & Watts (1990). Yet preliminary manipulation of temperature and daylength did not alter spawning rates. It remains possible that specific signals do trigger maturation of oocytes or spawning, and that this might be revealed

Table 2. Mean no. eggs d^{-1} snail^{-1} produced by 174 *R. obtusa* during a total of 156 days observation in different light:dark (L:D) regimes. Where months are specified (January, February, March, June), laboratory L:D regimes closely followed contemporary timings in the field including darkness when the collection site was under >0.5 m water at high tides.

dates	*n*	*L:D(h)*	*Mean no. eggs*	*sd*
15 November-3 December	30	16:08	0.30	0.114
	30	08:16	0.29	0.087
12 December-15 January	12	16:08	0.50	0.541
	10	08:16	1.09	0.400
17 December-12 January	10	LL	0.80	0.478
	8	DD	0.93	0.706
16 January-24 February	12	08:16	1.34	0.432
	11	04:20	1.16	0.662
	5	January/February	2.34	0.729
	11	June	1.47	0.963
15 February-26 March	12	February/March	1.96	0.610
	11	February/March	1.70	0.817
	11	DD	1.80	0.410

by longer observation than the 3-6 week periods feasible here, or with further combinations of temperature, daylength and perhaps other factors, such as salinity.

However, the present information suggests that rapid spawning starts when animals have simply grown to a threshold length (~2.7 mm) and had time to accumulate sufficient stocks of full-grown oocytes. Even if no environmental trigger regulates breeding and if *R. obtusa* can potentially breed at any time of year, the regular and sudden provision of an essential food item at a specific time will strongly disfavour predators that hatch too early or too late to exploit the food at the earliest competent size. The annual cycle of *R. obtusa* might well be the passive consequence of the breeding cycle of its prey, *H. ulvae*. This might be tested on shores where *R. obtusa* eats prey with different settlement times.

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Some aspects of the sublittoral benthic macrofauna of the Clyde Estuary in relation to sediment and water quality (summary)

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Data on the sublittoral benthos of the upper Clyde Estuary have been collected at varying levels of intensity since 1967. Changes in stability, density, species composition and distribution have been recorded. An area at the head of the estuary remains colonised and dominated by oligochaete species including *Paranais littoralis* and an ephemeral freshwater drift population. Farther downstream, species composition has altered more significantly in recent years with a marked change in species composition. Oligochaetes and *Capitella capitata* have given way to a greater variety of polychaetes, crustacean and molluscan species. Although estuarine water quality has improved with improvements in waste disposal, the fauna is still subject to extreme stress, and severe oxygen sags still occur in dry seasons. Although seasonal fluctuations in invertebrate populations are regularly recorded, an unexpected total crash was detected in 1991. Dissolved oxygen data highlighted an unusually prolonged and extensive sag, which coincided with increased BOD discharge from Dalmuir Sewage Treatment Works. This effectively had either a direct impact on the benthos or possibly caused sediment changes hostile to the fauna, the mechanisms of which were unknown. Sediments in the Clyde Estuary are routinely examined in terms of metals, OC, Eh and sulphide but there was insufficient evidence to explain this event. Since equivalent sags have been previously recorded with no such faunal crash, it is proposed that some toxic event took place under extreme conditions of low DO. Poor sediment quality in the Clyde clearly affects water quality and its importance to recolonising fauna should not be underestimated.

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Biology of the shrimps in the Forth Estuary

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From February 1992 the populations of shrimps from five stations in the Forth Estuary were sampled for two years, to investigate their population dynamics, reproductive biology and feeding ecology. Two residents, *Crangon crangon* and *Pandalus montagui,* and a migrant species, *Crangon allmanni,* were identified as the main species. *Crangon crangon* was found throughout while *P. montagui* was confined to the lower reaches of the estuary; *C. allmanni* appeared in October and left by June.

For all species the breeding cycle commenced in October, and berried females were found by December/January. Berried female *P. montagui,* and male and female *C. allmanni,* migrated from the estuary to deeper areas, never to return. *Crangon crangon* females with eggs ready to hatch, spent females and larvae all occurred in the estuary *(C. crangon* larvae from April to October). Larvae of the other two species were not found in the estuary.

All species fed mainly on polychaetes, followed by bivalves and crustaceans, indicating a benthophagous feeding habit. The choice of food depended on the local availability of prey items and the range of the particular shrimp species within the area; shrimps fed on prey which was abundant in their area of residence rather than moving elsewhere. The Forth Estuary is well utilised by the three species. Although a slow growth rate was observed in *C. crangon,* the mean condition factors were close to those reported elsewhere for shrimps.

The Forth Estuary shrimp populations varied between 1.6-7.7 x 10^7 for *C. crangon,* 1.6-2.5 x 10^7 for *P. montagui* and 0.7-1.0 x 10^7 for *C. allmanni.* These three species contributed to the total annual shrimp production of 17.73-27.90 tonnes dry weight, in the ratio 40:14:1. Both resident and migratory fish species benefit from this production because shrimps play a key role in the food web, forming the major link between the benthic invertebrates and predatory fish.

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Introduction

Shrimps (Decapoda, Natantia) form an important component of the fauna of estuarine and coastal waters. In European temperate regions they are represented mainly by carideans (Allen 1966) which are found in almost all the estuaries, coastal waters and deep marine areas. British caridean shrimp fauna includes 41 species of which *Crangon crangon* Linnaeus (= *Crangon vulgaris*) and *Pandalus montagui* Leach are the most common (Smaldon 1993). These two species have been recorded previously in the Forth Estuary on the east coast of Scotland (FRPB 1987; Hunter 1981) where the present study was based. The present study added a third common species, *C. allmanni* Kinahan, as well as several other rarer species to the estuary list. Although the importance of *C. crangon* as the central organism in supporting estuarine nekton within the Forth Estuary has been recognised (Costa & Elliott 1991), little information exists on the biology of any of the shrimps. An evaluation of the shrimp resources is completely lacking. This study attempts to examine the biology of the shrimps and to identify the production in the estuary and contribution of each species to the estuarine community.

Materials and methods

The lower Forth Estuary was sampled by an Agassiz trawl at five stations: Port Edgar, Blackness, Tancred Bank, Bo'ness and Longannet (Figure 1) at both high and low water from February 1992 to January 1994 six times a year (January, April, June, July, October and December). The Agassiz trawl used had a 2 m wide mouth with a 1.3 cm stretched-mesh net and was towed at 2.5 knots over 0.8 km by S.V. *Forth Ranger.* The entire catch of shrimps was analysed on each occasion, except in July and October 1992 when the catch was particularly large and a random sub-sample was taken after sorting all the shrimps from the catch. Shrimps were preserved immediately in 5% formosaline for further analysis. In the laboratory, the shrimps were identified, sexed (from pleopod characteristics) and counted. The numbers of berried females in the catch were noted and the development stage of the egg mass was determined according to Tiews (1970). The carapace length of each shrimp was measured from the base of the eye to the posterior margin of the carapace and the shrimps were pooled into 1 mm size classes. Since preliminary examination of the data revealed length and growth differences between males and females (Jayamanne 1995), length-frequency data of the two sexes were analysed separately. Juveniles were divided equally over the male and female data matrices.

Production estimates were obtained from the length-frequency data and the Carapace Length-Ash Free Dry Weight (CL-AFDW) regression. As all three species recruited in July, the annual production was calculated for the birth year (24 July 1992 to 23 July 1993). For *C. allmanni* the year began with their arrival in the estuary in October and ended at the time of their departure from the estuary in April. The shrimps belonging to each year class were regarded as a separate isolated population, with cohorts separated using the Bhattacharya method as described in Jayamanne (1995).

Density was calculated as the mean of the five stations in the estuary at both high water and low water, and was expressed as the number of individuals (N ha^{-1}), the biomass was presented as g AFDW ha^{-1}. Calculations of biomass were performed using the seasonally-varying regression between Ln CL and Ln AFDW as derived by Jayamanne (1995). To compare the effect of season on production, Ln CL/Ln AFDW relationships were also established for pooled data. The production of shrimps, as the material added to the population, was calculated using the growth increment summation method (Crisp 1984, for stocks with recruitment, age classes separable). This method was chosen owing to the popularity of the method which makes it possible to compare the results with earlier work. In this method production (P) is calculated as the increment of biomass from one sampling to the next throughout the cohort's life span. The production was estimated for each species by sex using both four seasonally varying equations and the pooled relationship of CL/AFDW.

Total production in the estuary was estimated by extrapolating the production (g AFDW ha^{-1} yr^{-1}) values to the total area of the estuary, and assuming a homogeneous distribution. Since the abundance represents pooled data of both high water and low water, production and biomass were estimated using both the area covered at high water and at low water as the total extent of the study area. The total area of the estuary was taken as the area between the Forth Railway Bridge and Kincardine Bridge, and was calculated separately for high water and low water. The total area of the estuary at high water was calculated as 6,057 ha and, by excluding the intertidal area (McLusky 1987; Elliott & Taylor 1989), at low water as 3,850 ha.

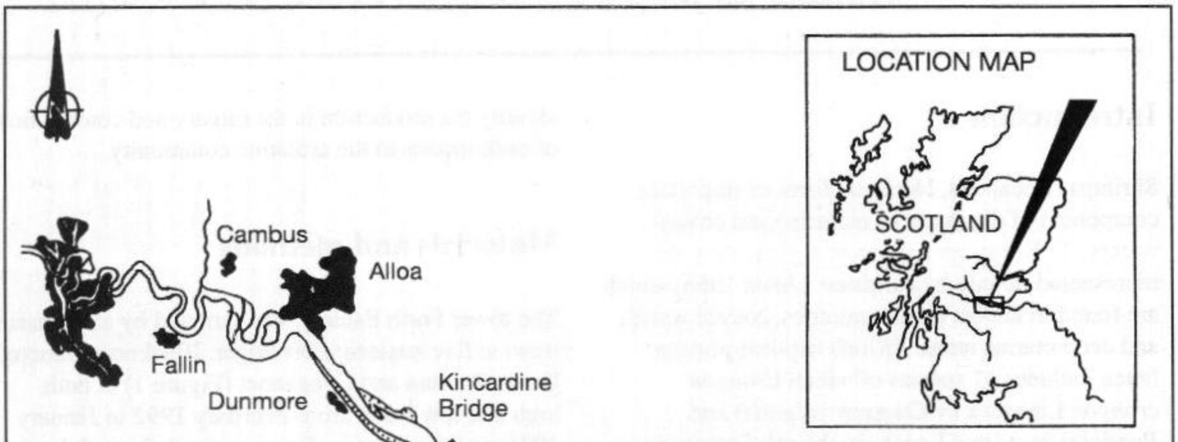

Figure 1. The Forth estuary showing water and shrimp sampling stations.

The size of the population was estimated using the area density method. The total number of shrimps present at five stations at high and low water were calculated for the estimation of shrimp population in the area between Forth Bridge and Kincardine Bridge. This estimate therefore, presents an estimate for the subtidal population of the shrimps in the mid- and lower Forth Estuary, calculated from the area swept by the trawl. Numbers corrected for gear selection (33%) were used as the numbers present at each instance.

To study the feeding biology of the shrimps, each stomach of a randomly selected sub-sample of 25 animals was opened under a dissecting microscope and the contents were emptied onto a slide and the tissues of stomach wall were removed. Identifiable items were transferred to a petri dish and the rest were spread on the slide and examined under a compound microscope. The food organisms were mostly found in a crushed and fully or half-digested form. Some of the stomachs, however, had undigested food. Whenever possible the food items were identified to the most precise taxonomic level and counted. The items that could not be identified were categorised as 'miscellaneous'.

Results

The complete results of this study are presented in Jayamanne (1995), and only selected summary results are presented here.

The study identified *C. crangon*, *P. montagui* and *C. allmanni* as the three principal species in the estuary (Figure 2). *Crangon crangon* is a true estuarine species, distributed throughout the estuary, while *P. montagui* is a resident species confined to the lowermost areas of the estuary. *Crangon allmanni* is a migrant species which inhabits the estuary during winter and autumn but is not found in either the Firth of Forth or the estuary during summer.

Breeding and egg development

The breeding cycle commenced in October and berried females were found by December/January for all species. Berried female *P. montagui*, and both male and female *C. allmanni*, migrated from the estuary to deeper areas, never to return.

Crangon crangon females with eggs ready to hatch, spent females and larvae all occurred in the estuary. Temporal variations in the occurrence of egg development stages of *C. crangon* were similar at all stations (Figure 3). Peak occurrence of early stage eggs in December indicates the beginning of the breeding season. First appearance of the late stage eggs occur in April, denoting April as the beginning of first larval hatching. From April onwards, the late developed eggs occur all the time until July, indicating that larval hatching is a continuous process in the estuary during the summer. The second peak of the early stage varied spatially between upper and lower stations. In Longannet and Bo'ness a second peak appeared in April, earlier than in other stations. In the four lowermost stations another peak occurred in June.

Crangon crangon larvae were present in the estuary from April to October. Larvae of the other two species were not found in the estuary.

Production and biomass

The production and biomass of the three species in the total area of study is given in Table 1. The

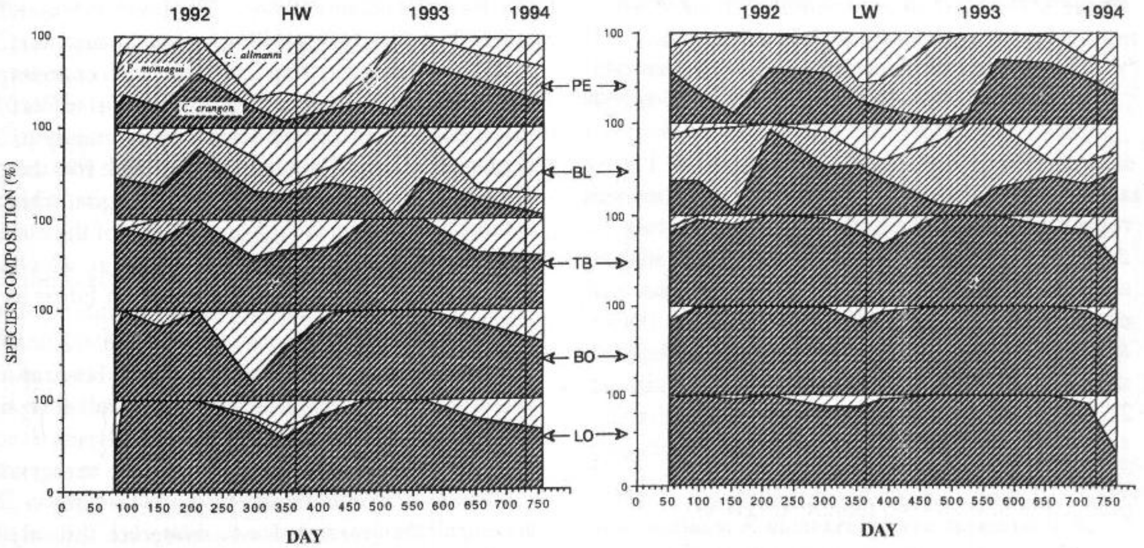

Figure 2. Species composition (%) of shrimps; *C. crangon, P. montagui* and *C. allmanni* at five stations: Port Edgar, Blackness, Tancred Bank, Bo'ness and Longannet in the Forth Estuary. Day 1 = 1 January 1992.

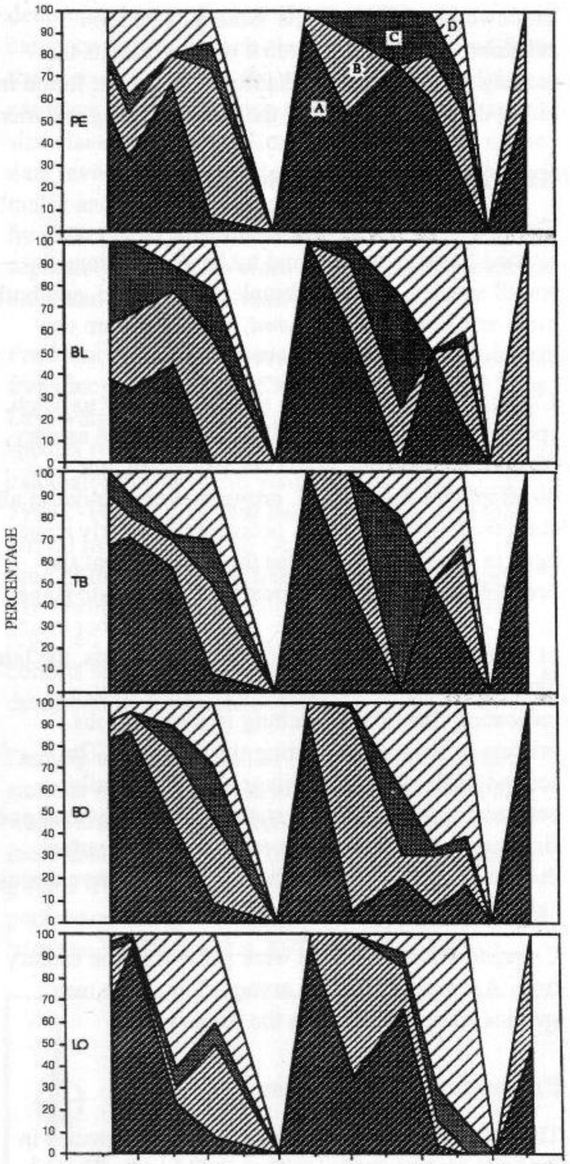

Figure 3. Female *C. crangon* carrying eggs of different development stages (A-D) presented as a percentage of total berried females observed during the year, at five different locations in the Forth Estuary. (Locations as Figure 2.).

values derived by seasonally varying equations were regarded as most valid here, although the values derived using single equation are also given in the table for comparison. Highest production was observed in *C. crangon* (12.71-20.00 tonnes AFDW yr^{-1}) which accounted for 71.7% of the total shrimp production. *Pandalus montagui* contributed 26.7% of the total production with a production of 4.74-7.45 tonnes AFDW yr^{-1} while the contribution from *C. allmanni* was negligible (1.6%) with a production of 0.28-0.45 tonnes AFDW yr^{-1}.

Size of the population

Population size of *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary indicates the dominance of *C. crangon* over the other two species (Table 2) both at high water and low water.

Feeding by shrimps in the Forth Estuary

Crangon crangon showed a wide variety of food choice (Table 3, Figure 4). Polychaetes were the most frequent prey followed by bivalves and crustaceans. Of the polychaetes, *N. hombergi* and spionids were found to be predominant. Spionids and nephtyds are abundant in the intertidal flats in the central and lower areas of the estuary (McLusky 1987; FRPB 1992), and the high frequency of their occurrence in the diet showed that the food of *C. crangon* consists mainly of locally available food items. As indicated by the food composition, *C. crangon* is the only species which utilises the intertidal area of the estuary since intertidal species such as *Macoma baltica*, *Corophium volutator* and *Cerastoderma edule* were found in the stomachs of only *C. crangon*. Utilisation of such intertidal areas by *C. crangon* has also been observed by previous researchers Kuipers & Dapper (1981, 1984); Pihl (1985); Pihl & Rosenberg (1984); Reise (1985) and Raffaelli *et al.* (1989).

Pandalus montagui also prefers the same categories of food as *C. crangon*, namely polychaetes, bivalves and crustaceans and reflects the composition of local benthic prey organisms. The polynoid species, *Gattyana cirrosa*, was a frequent item of food in *P. montagui*. Confinement of *P. montagui* to the lowermost stations of the estuary has limited its food spectrum to the available resources in that area and it exerts only a low overlap with the other two species.

Crangon allmanni feeds on a variety of benthic invertebrates, polychaetes, bivalves and crustaceans, and predominantly on phyllodocids and spionids and to a lesser extent on *Nephtys*. The bivalve *Abra alba* is also common amongst the prey categories. The feeding habit is quite similar to that of *C. crangon*. In the estuary *C. allmanni* is distributed from Port Edgar up to Longannet and has the opportunity to feed on a variety of benthic groups which live there. Thus, its diet overlaps with both *C. crangon*, which is more abundant in the uppermost area of the middle and lower estuary, and *P. montagui*, which is confined to the lowermost area from Port Edgar to Blackness.

There is a great similarity in food choice between *C. crangon* and *C. allmanni*. Competition between the two species is, however, most unlikely since when the rich food resources occur in the spring and summer *C. allmanni* migrates from the estuary leaving all the resources for *C. crangon*. The only possible competition, if there is any, would occur in autumn and winter at the lowermost part of the estuary where all three species gather and utilise the

Table 1. Total production (tonnes AFDW ha^{-1} yr^{-1}), mean biomass (g AFDW) of *C. crangon*, *P. montagui* and *C. allmanni* in the study area for the period July 1992 to June 1994, using A, values obtained by seasonally varying equations, B, values derived by single equation. Area at HW = 6,057 ha and at LW = 3,850 ha.

Species	*Production (g AFDW ha^{-1} yr^{-1})*	*Biomass (g AFDW ha^{-1})*	*Total production (tons AFDW)*		*Total biomass (tons AFDW)*	
			HW	*LW*	*HW*	*LW*
A.						
C. crangon	3,302.47	1,607.40	20.00	12.71	9.74	6.19
P. montagui	1,230.60	1,116.70	7.45	4.74	6.76	4.30
C. allmanni	74.09	111.87	0.45	0.28	0.68	0.43
	Total production of shrimps		*27.90*	*17.73*	*17.18*	*10.92*
B.						
C. crangon	609.93	241.27	3.43	2.18	1.57	1.00
P. montagui	815.88	844.41	4.94	3.14	5.11	3.25
C. allmanni	71.71	109.69	0.43	0.27	0.66	0.42
	Total production of shrimps		*8.80*	*5.59*	*7.34*	*4.67*

Table 2. Population size of the shrimps *C. crangon*, *P. montagui* and *C. allmanni* in the Forth Estuary.

Year	*Species*	*High Water*		*Low Water*	
		Population (N x 10^7)	*Standard Deviation x 10^7*	*Population (N x 10^7)*	*Standard Deviation x 10^7*
1992	*C. crangon*	8.08	2.57	7.43	2.00
1993		2.04	0.74	1.30	0.50
1992	*P. montagui*	3.33	0.96	2.62	0.71
1993		1.73	0.49	0.99	0.28
1992	*C. allmanni*	1.53	0.48	0.45	0.14
1993		1.16	0.41	0.29	0.05

same food resources. The higher percentage of individuals with empty stomachs, and low growth rates observed during the winter period, may be related to this phenomenon.

Discussion

Crangon crangon

In terms of abundance, distribution and utilisation, *C. crangon* emerges as the most important shrimp species in the Forth Estuary. Its abundance is about 10 times higher than that of other two species, and *C. crangon* utilises all the habitats, intertidal areas (pers. obs.), saltmarsh creeks (S. Mathieson, pers. comm.), upper estuary and subtidal areas of the estuary.

In the Forth Estuary *C. crangon* exhibits a life cycle with continuous breeding and recruitment but with identifiable peak occurrences. The present information, together with Hunter (1981), has identified April, June and August/September as the peak months at which larvae are released. The months at which important events occur in the life of *C. crangon* is summarised in Table 4. High fecundity and multispawning undoubtedly reflect a strategy for survival in the estuary. This is evident from the production of 0.80 x 10^7 eggs ha^{-1} which resulted in a mere 130-186 adults ha^{-1}.

Pandalus montagui

Pandalus montagui, although second in importance to *C. crangon*, is the dominant shrimp which inhabits the lowermost area of the estuary throughout the year. Its preference for a hard substratum over a soft substratum is well-known (Mistakidis 1957; Simpson *et al.* 1970) which may explain its confinement to Port Edgar and Blackness with stony substratum (Elliott & Taylor 1989) rather than to the muddy and sandy substratum in the upper three stations. The abundance of *P. montagui* is almost 10 times lower than that of *C. crangon.* Compared with *C. crangon*, *P. montagui* is less fecund: it produces only one-quarter to one-third the number of eggs at a time per female and also spawns only once per year. The larger females, which migrate to deeper areas to release larvae, are also a loss to the estuary since they do not return to the estuary. The mass migration reported by Mistakidis (1957) was not observed in the Forth where a proportion of shrimps always remained in the estuary.

From the occurrence of berried females at Kingstone Hudds in the Firth of Forth and the absence of larvae in the estuary, *P. montagui* larvae appeared to be released in the deeper areas. Observations of Lebour (1947) confirm the offshore larval stages of *P. montagui*.

Table 3. List of prey species identified from the stomachs of *C. crangon, P. montagui* and *C. allmanni* in the Forth Estuary.

Prey species	*Occurrence*		
	C. crangon	*P. montagui*	*C. allmanni*
A. Polychaetes			
Nephtys hombergi	+	+	+
Nereis diversicolor	+	+	+
Pholoe minuta	+	+	+
Lepidonotus squamatus	+	+	+
Gattyana cirrosa	+	+	+
Eteone longa	+	-	-
Phyllodoce groenlandica	+	+	+
Phyllodoce mucosa	-	-	+
Marenzellaria wireni	+	-	-
Prionospio malmgreni	+	-	+
Cirratulus cirratus	-	+	-
Cirriformia tentaculata	+	+	+
Capitella capitata	+	+	-
Scalibregma inflatum	-	+	+
Lagis koreni	+	-	+
Sabellaria spinulosa	+	+	+
Polydora sp.	+	-	+
Glycera alba	+	+	+
Scoloplos armiger	+	-	-
Pygospio elegans	+	-	+
Terrebelides stroemi	-	-	+
B. Crustaceans			
C. crangon	+	+	+
Carcinus maenas	+	+	-
Liocarcinus sp.	+	+	-
Diastylis bradyi	+	+	+
Corophium volutator	+	-	-
Praunus sp.	+	-	-
C. Bivalves			
Abra alba	+	+	+
Mytilus sp.	+	+	+
Cerastoderma edule	+	-	+
Macoma baltica	+	-	-
Modiolus modiolus	+	+	-
Mysella bidentata	-	-	+
Hydrobia ulvae	+	-	-
D. Other groups			
Sertularia sp. (Hydroid)	-	+	-
Haynesina sp. (Foraminiferan)	+	+	+
Golfingia sp. (Siphunculid)	-	+	-
Cephalothrix linearis (Nemertea)	-	-	+
Fish	+	-	-
Sea seeds	+	-	-

Crangon allmanni

Crangon allmanni appeared to be the least important of the three shrimp species present in the Forth Estuary, inhabiting the estuary for only a part of the year. The purpose of the migration of *C. allmanni* into the estuary is not very clear and according to Allen (1960) it cannot be related to either rich feeding in the estuary or to the stable conditions for breeding offshore as apply to *C. crangon,* since *C. allmanni* is migrating *vice versa*. It is therefore, hard to visualise what *C. allmanni* gains by visiting the estuary.

During their time in the estuary, *C. allmanni* grow steadily, and have matured by the end of their stay. Mating and spawning take place in the estuary in winter, but the females ready to release larvae, and larval stages, were absent in the estuary. It is therefore, evident that the estuary is neither a breeding ground nor a nursery ground for *C. allmanni*. The maturation and spawning periods

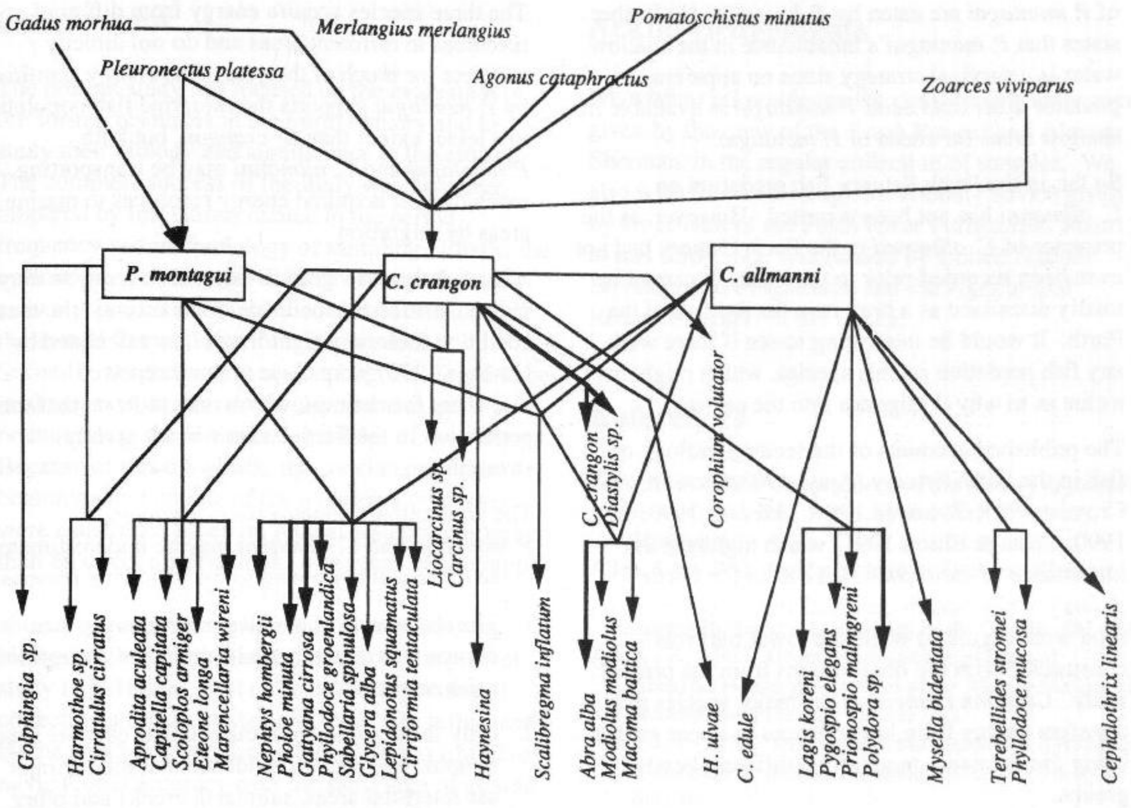

Figure 4. Feeding relationships involving shrimps in the Forth Estuary. Upper names are fish which prey upon the three shrimp species *(P. montagui, C. crangon & C. allmanni).* Lower names are the food items consumed by the shrimps.

in the estuary are similar to those reported by Allen (1960) in the inshore area of Northumberland waters. Thus, only the initial part of the breeding cycle is spent in the estuary, and larval release and metamorphosis may occur elsewhere in the outer Forth or North Sea. Jorgensen's (1923) and Lebour's (1931) observations on the larvae in offshore waters may explain the absence of larval stages of *C. allmanni* in the estuary.

Feeding by fish on shrimps in the Forth Estuary

In the Forth Estuary *C. crangon* is prey to most of the resident fish species: flounder *Platichthys flesus* (Bell 1990); goby *Pomatoschistus minutus* (Stevenson 1988); pogge *Agonus cataphractus* (Townend 1989); eelpout *Zoarces viviparous* (Stewart 1984) and migrant marine species including plaice *Pleuronectus platessa*; dab *Limanda limanda* (Ajayi 1983) and cod *Gadus morhua* (Crossan 1985), and is the major food item for six of them (Costa & Elliott 1991).

Pandalus montagui has been identified as a prey for *Gadus* sp. and *Pleuronectus* sp. (Mistakidis 1957) but not in all the fish in the Forth. Thus, its role in energy transfer to higher levels is limited and small compared with *C. crangon*. The migration of the breeding component of *P. montagui* to deeper areas may however transport energy to fish in marine areas. Allen (1963) observed that larvae released in 20-30 fm deep area had a better chance of survival than those released in 50 fm deep water since zoeae

Table 4. Monthly occurrence of different events in the life of *C. crangon*.

Event												
Mature females	X	x	x	X	x	X	X	x	x	-	x	X
Berried females (stg. A eggs)	X	x	x	X	x	X	X	x	x	-	x	X
Berried females (stg. D eggs)	-	-	-	X	x	X	X	x	x	-	-	-
Larvae (zoea 1)	-	-	-	X	x	X	X	x	X	-	-	-
Post larvae	-	-	-	-	-	-	X	x	x	X	-	X
Juveniles	X	x	-	-	-	X	X	x	x	X	-	-
MONTH	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**

(X = this study, x = previous information) of *P. montagui* are eaten by *P. borealis*. He further states that *P. montagui*'s inhabitance in the shallow water is a survival strategy since no apparent predator other than adult *P. montagui* is available in shallow areas for zoeae of *P. montagui*.

So far, in the Forth Estuary fish predation on *C. allmanni* has not been reported. However, as the presence of *C. allmanni* in the Forth Estuary had not even been recorded prior to this study, it cannot be totally dismissed as a prey item for the fish of the Forth. It would be interesting to see if there were any fish predation on this species, which might give a clue as to why it migrates into the estuary.

The published accounts of the feeding biology of fish in the Forth Estuary (Ajayi 1983; Stewart 1984; Crossan 1985; Townend 1989; Marshall 1990; Bell 1990; Costa & Elliott 1991) which highlight the importance of shrimps in fish diet in the Forth Estuary, were used to construct the upper part of the food web (Figure 4) while the lower part was constructed with the observations from the present study. *Crangon crangon* is the major species that transfers energy from lower groups to upper groups, being the dominant predator on different benthic groups.

Energy transfer in the Forth Estuary

The Forth Estuary is being well utilised by *C. crangon*, *P. montagui* and *C. allmanni* without much apparent competition among species. The shrimps utilise the vast food resources in the intertidal areas which have been estimated to consist of 2,010 tonnes wet weight of benthic biomass and subtidal areas with a biomass of 1,450 tonnes wet weight (Table 5). These support a subtidal biomass of 110-170 tonnes wet weight of shrimp population which largely supports the population of 120 tonnes wet weight of fish (Costa & Elliott 1991). The shrimp biomass in intertidal areas still remains unknown but it is certain that the biomass of these areas may be considerably higher than that of the subtidal areas.

The three species acquire energy from different resources in different areas and do not directly compete for much of the year. The energy acquired by *P. montagui* supports the estuarine fish population to a lesser extent than *C. crangon*, but both *P. montagui* and *C. allmanni* may be transporting much of their acquired energy resources to marine areas by migration.

Although the slow growth rates of *C. crangon* may indicate a stressed condition in the estuary, the mean condition factors (weight/length^3, as calculated by Havinga 1930) were close to those reported elsewhere for shrimps, which may indicate that the population in the Forth Estuary is not unduly stressed.

The production estimates for *C. crangon*, *P. montagui* and *C. allmanni* may be underestimated in the present study owing to the following reasons:

1. The abundance of smallest fast-growing size classes was certainly underestimated owing to mesh selection.
2. Only the population in the subtidal channel was sampled and there is evidence that the shrimps use intertidal areas, saltmarsh creeks and other shallow areas.
3. The emigration of females to areas other than the study area. Part of the *C. crangon* population was observed in the upper estuary during the summer which may be the reason for low production in the subtidal areas in June. Emigration also occurs in *P. montagui*, when berried, and in *C. allmanni*, when mature, which may account for low production values.

Against this background, the production estimates presented in this study are likely to be low. The size of the population showed a high fluctuation between years, although the reasons for the fluctuations are not certain, and no environmental factor which could lead to an explanation of the fluctuations was found during the period of study.

Table 5. Total biomass and production of benthos, shrimps and fish in the Forth Estuary.

	Biomass production tonnes dry-weight		*Biomass production tonnes wet-weight*	
Fish	(12*	33.5*)	120	335
Shrimps	10.92-17.18	17.73-27.90	(110-70*	180-300*)
Benthos				
intertidal	201	256		
subtidal	142	289		
total	343	545	(3,430*	5,450*)

Data presented as ash-free dry weight and as wet weight, all as tonnes for the Forth Estuary, between Kincardine and Queensferry bridges. Information from present study, McLusky (1987) and Elliott and Taylor (1989). Where indicated by *, assumes dry weight as 10% of wet weight.

Conclusions

The present study has focused on the evaluation of the shrimp resources in the Forth Estuary and to study their biology and significance to the estuary. The complete success of the study was, however, hindered by limitations related to the period, frequency and methodology of sampling. Firstly, the evaluation of a resource within a short period such as two years, cannot yield adequate information on the annual fluctuations of the population.
Secondly, the frequency of sampling was found to be inadequate to draw conclusions on the exact boundaries to the biological activities of the shrimps. Because of this drawback, the conclusions of the beginning and ending of the biological processes were sometimes based on logical assumptions rather than on direct observations. The times of beginning and ending of biological processes such as breeding and larval recruitment were thus estimated using biological information other than from the present study (e.g. Hunter 1981). Thirdly, the success of collecting shrimps by Agassiz trawl was influenced by the weather conditions although it was towed to navigational accuracy over the same area of ground at each occasion. In particular, wind velocity and tides affected the position of the trawl. At times the trawl catch was clean, suggesting that it was not trawling on the bottom for long and at other times it was full of mud indicating that the trawl had been digging into the substratum.

In addition to these limitations, the study was also affected by the behaviour of shrimps themselves. Caridean shrimps are known to migrate to and from the estuaries in relation to feeding and breeding, and are differentially distributed. Juveniles are mostly found in intertidal areas and uppermost low salinity areas, breeding adults in either uppermost or lowermost areas depending on the season, and non-breeding animals in subtidal areas moving up and down the estuary with the tide. Furthermore, their biological activities are related to the environmental conditions and they respond to light penetration by burying in the mud, with active swimming in the dark (Tiews 1970). Their distribution is also affected by salinity and temperature variations, for example, Broekema (1941) observed that at low temperatures *C. crangon* migrates to areas of high salinity, and at high temperatures to areas of low salinity. These behavioural variables are, however, unavoidable in studies of the biology of mobile animals, and despite these limitations, the study revealed the basic biological and ecological events of the shrimps which may be useful to shrimp biologists, as well as to wider studies of the Forth Estuary.

Acknowledgements

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Long-term changes in intertidal invertebrates and birds in the Clyde Estuary

D.J. Curtis

The Clyde Estuary has long been recognised as an important feeding area for wintering shorebirds. A comparison between two winter surveys for invertebrates, 1976/77 and 1990/91, shows mean densities for *Nereis diversicolor* of 1,038 m^{-2} in 1976/77 and 1,752 m^{-2} in 1990/91, with corresponding maxima of 5,220 m^{-2} and 6,341 m^{-2} and for *Hydrobia ulvae* means of 2,141 m^{-2} and 2,499 m^{-2}, maxima of 29,600 m^{-2} and 28,746 m^{-2}. In contrast, *Corophium volutator* densities showed a marked decline (means of 1,544 m^{-2} and 1,195 m^{-2}), especially in terms of the maxima (13,320 m^{-2} and 6,552 m^{-2}). There were corresponding changes in the degree of patchiness of these species.

For the same two periods, attention is focused on seven species of shorebirds: black-headed gull, curlew, dunlin, greenshank, lapwing, oystercatcher and redshank (which is of international importance). While there were marked variations between months, in terms of overall total values of feeding density, only two species showed similar numbers in 1976/77 and 1990/91: black-headed gull (107% in 90/91 cf. 76/77) and oystercatcher (95%). In contrast, curlew numbers were much higher in 1990/91 (209% cf. 1976/77). The remaining species all declined: lapwing (72%), dunlin (57%), greenshank (36%) and redshank (32%).

This decline in redshank numbers on the Clyde Estuary is also evident in peak counts over the period 1973-1991, in contrast to relatively steady values for the UK index. This is shown to relate to *Corophium* densities and especially with the degree of patchiness or clumping, expressed as the maximum:mean ratio (RKnos = 941.Cvpatch, $p<0.001$).

The birds' distributions over feeding areas changed markedly and this must be taken into account when considering development proposals for the estuary.

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Introduction

Ever since the earliest records of Gray (1871) and those of McWilliam (1936) and Gibson (1958), the Clyde Estuary has been recognised as an important resort for wintering shorebirds. Those authors pointed to high numbers of lapwing, oystercatcher, dunlin, redshank and curlew using the flats as feeding areas in the winter months, during the period of heavy pollution late in the nineteenth century and in the first half of the twentieth. During the second half of the twentieth century there has been much effort, spearheaded by the activities of the Clyde River Purification Board (CRPB), to 'clean up' the estuary and reduce its pollution load. One of the significant events was the commissioning by Strathclyde Regional Council of the new sewage treatment works at Shieldhall on 1st June 1985. This is the largest sewage works in Scotland (cost £57 million), designed to meet the stringent standards of the CRPB, and in fact producing an effluent of even better quality. The environmental conditions in the estuary and, consequently on the tidal flats, have changed much over this period, as can be seen from the Annual Reviews of the CRPB. Much of this pollution was in the form of organic matter, supplying a nutrient input to the ecosystem of the intertidal mudflats, which support the benthic invertebrate populations upon which the shorebirds feed (Smyth *et al.* 1974, 1977).

Even before the commissioning of the Shieldhall sewage works, trends were evident in the Clyde Estuary of declining bird populations, as a suspected response to lower prey densities, evident in a series of studies (e.g. Smyth *et al.* 1977; Curtis 1978; Curtis & Smyth 1982). The patterns of relationships between birds and their prey over the course of a single year (1976/77) were described by Thompson, Curtis & Smyth (1986), highlighting the complex interactions that occur. Since then, an additional full survey of feeding birds has been carried out (Curtis & Figures 1992), extending the time-series of data available. In this paper emphasis is placed on long-term changes in the overall distribution patterns over two decades, in terms of fluctuations in numbers of seven key bird species, together with the density of their main prey species.

Data sources and species considered

Data have been taken from survey results held at Paisley for the invertebrates and birds. In the statistical analysis of these, each variable was tested for conformity with normal data prior to the application of parametric tests (analysis of variance and regression analysis). Where appropriate a log(n+1) transformation was applied.

Bird data

The bird data are provided by the only two major surveys of feeding birds conducted in 1976/77 and 1990/91. The 1976/77 survey was designed to evaluate the conservation status of the estuarine flats in terms of feeding birds and their prey (Curtis 1978; Halliday 1978; Halliday *et al.* 1982). It comprised six two-monthly sample periods over a full year, with birds being allocated to 200 x 200 m quadrats over the tidal flats. A team of five ornithologists, led by J.B. Halliday, was used to cover the entire mudflats during each two-month period. Feeding and non-feeding birds were counted for 30-minute slots over a full tidal cycle.

The greater part of the Clyde Estuary intertidal flats have protected status in conservation terms (Ramsar site, Site of Special Scientific Interest, RSPB reserve). In response to a proposal to claim land in a bay at Woodhall/Parklea, within the Enterprise Zone at the eastern edge of the Port Glasgow urban area, Inverclyde District Council commissioned an environmental impact assessment because of the potential effects on the statutorily protected shore over the rest of the estuary. The 1990/91 survey was conducted under the auspices of this environmental impact assessment (Curtis & Figures 1992). Counts were made at monthly intervals over the whole of the estuary (with the exception of Pillar and Cockle Banks) for most of the tidal period, recording disaggregated data for separate tidal hours. The flats were divided into 37 sample stations within 12 sample areas, each area being designed so that one observer could easily cover it with a good telescope from a suitable vantage point. Teams of ornithologists with good local knowledge were coordinated to provide for simultaneous coverage of these areas and so minimise problems with over- or under-counting. Counts were also made at high tide at the main roosts for the birds, in a manner similar to the methodology of the Birds of Estuaries Enquiry.

The 12 areas, with their extent in hectares, were as follows: on the north bank, Ardmore 113.21, Cardross 482.11, Ardoch 167.78, Havoc 83.27, West Ferry (N) 97.25, Milton (N) 57.41; on the south bank, Woodhall 64.90, Langbank 100.73, West Ferry (S) 165.52, Milton (S) 205.52, Longhaugh 44.84, Erskine 33.31 (see Figure 1).

The data of the 1976/77 survey were recorded with reference to contiguous 200 x 200 m quadrats and

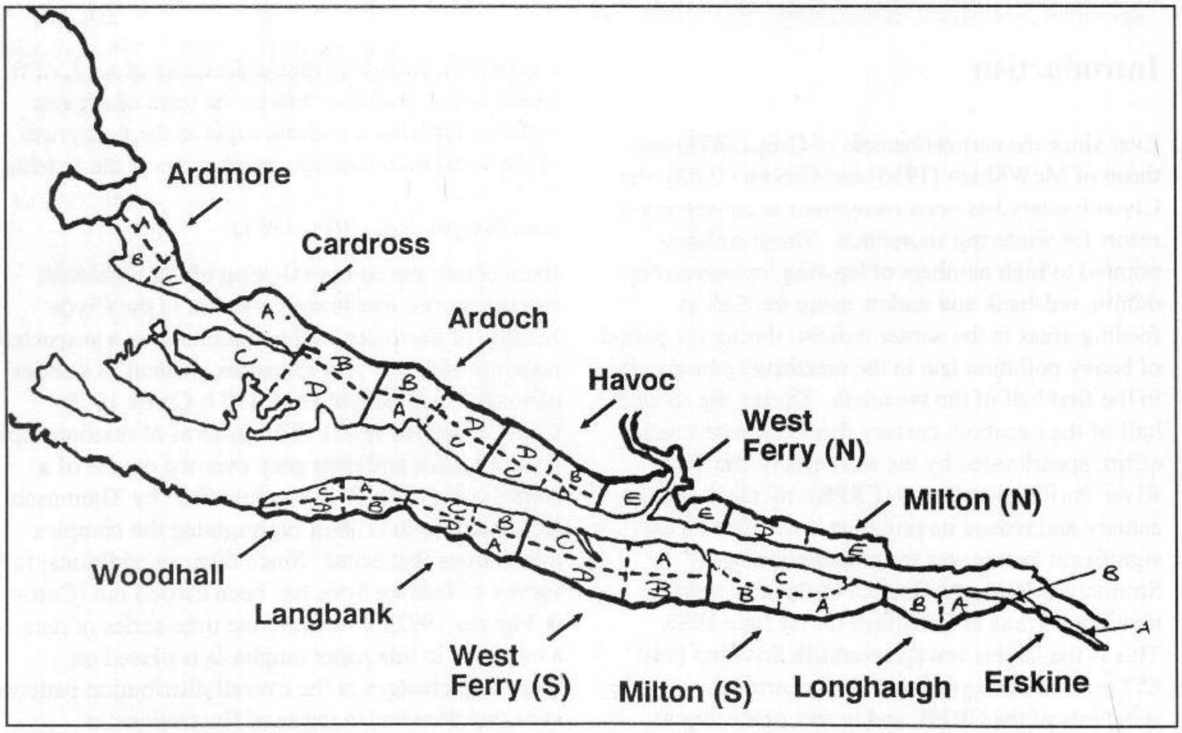

Figure 1. The locations of the 12 areas (and their sub-areas) into which the mudflats were divided for the 1990/91 survey. These areas were delimited with respect to coverage from suitable vantage points for the feeding bird counts.

the coordinates of these were used to allocate data into the 12 areas of the 1990/91 environmental impact assessment. Comparisons between these two sets of data are considered here, using data for early and late winter counts (November and February), with concentration on the latter which coincides with most maximal peak counts. As well as total numbers, the distribution of these birds over the 12 areas of the estuarine shores is described. The birds show much movement over the estuary at different stages of the tide; to take account of this, feeding densities have been calculated as the sum of peak counts for ebb, low and flow tides divided by the area (ha).

Attention is focused on seven species of shorebirds: black-headed gull *Larus ridibundus* and six waders - curlew *Numenius arquata*, dunlin *Calidris alpina*, greenshank *Tringa nebularia*, lapwing *Vanellus vanellus*, oystercatcher *Haematopus ostralegus* and redshank *Tringa totanus*. Of these, the last species is most significant, regularly occurring in numbers of international importance. Greenshank occur only in very small numbers, but nevertheless amount to about 30% of the Scottish population (Gibson 1978) and so are included amongst the key species. With the exception of lapwing (which occurs in large flocks), the other species were indicated as of national importance by Halliday *et al.* (1982). Some species of ducks are also of importance on the Clyde Estuary. Shelduck is of international importance, while goldeneye and eider often exceed 1% of the British total and mallard have been recorded in large numbers.

The estuary is very rich in bird species, as shown by the list of 55 species recorded during the survey work for the environmental impact assessment. These included 16 wildfowl, 19 waders and eight gulls; they are listed in Appendix 1. Some of these species have been recorded in only very low numbers and represent occasional visitors to the estuary. However, for the seven key species (especially the waders) the estuary forms an important resort in the winter, particularly from the point of view of providing food, with suitable shelter for roost sites nearby.

Dietary characteristics of the birds

Oystercatcher feed in small groups or solitarily and their diet consists primarily of bivalve molluscs especially cockles, mussels and baltic tellin, as well as limpets, periwinkles, dog whelks and small crabs. The method of feeding varies considerably with experience, hour of the tidal cycle and position on the shore. The strong beak is used in two main methods: hammering and stabbing, on mussels (Heppleston 1971). Interstitial molluscs such as cockles are obtained by probing the sediment and some prey items may be swallowed whole, particularly small cockles, mussels and crabs.

Curlew feed almost entirely during the day by both touch and sight (Burton 1974), in autumn taking small shore crabs and in winter marine worms, predominantly *Nereis diversicolor* (Goss-Custard, Kay & Blindell 1977a, b), and small bivalve molluscs. The birds make use of the curvature of the bill in three types of feeding behaviour (Streefkeerk 1960): pecks capturing small crabs, and shallow or deep probes for interstitial prey, usually worms.

Redshank on estuaries are mainly visual feeders during the day, although feeding also occurs at night. Feeding territories may be established and defended. They have a preference for muddy river channels and upper shores and also feed inland in fields where they may take beetles and dipteran larvae and adults (Burton 1974). Their diet varies with the seasons and a wide variety of prey species is taken on estuaries including *Corophium volutator, Carcinus maenus, Crangon vulgaris, Hybrobia ulvae, Macoma balthica, N. diversicolor* and *Nephtys hombergi* (Goss-Custard 1969, Burton 1974), with the birds employing various feeding behaviours with movements classed as pecks, jabs, probes and sieving or 'mowing' (Burton 1974). Generally, pecks are the most frequent behaviour and *H. ulvae* and *C. volutator* appear to be obtained using this method, whereas probing obtains bivalves and larger worms. *C. vulgaris* and *C. maenas* are captured using the mowing method. Feeding by touch is usually used at night to detect shrimps, *H. ulvae* and winkles (Goss-Custard 1969). Goss-Custard, Kay & Blindell (1977a) found that *N. diversicolor* and *C. volutator* were the most important constituents of the diet, although other studies have suggested that *H. ulvae* can be of greater importance in some areas (Burton 1974). Diet has been shown to vary with season and weather on the Ythan Estuary (Goss-Custard 1969) and elsewhere, e.g. the Wash (Goss-Custard *et al.* 1977b). Goss-Custard (1977a, b, c) found the density of feeding redshanks to be correlated with the density of *C. volutator*, and that birds preferred *C. volutator* to *N. diversicolor*, with fewer worms being taken as the density of the amphipod increased Goss-Custard (1977a). Goss-Custard (1969) and Goss-Custard, Kay & Blindell (1977a) have shown that particular size classes of prey are usually selected, with a preference for large *C. volutator* (4-9 mm) and *H. ulvae* (2-6 mm).

Greenshank employ a variety of feeding methods: probing, mowing and active hunting, sometimes performing a 'dance' through shallow water in the search for food (Nethersole-Thompson & Nethersole-Thompson 1979). Their prey include small fish (goby), *Crangon* sp. and *C. volutator*, *H. ulvae* and *C. maenas*.

Dunlin locate their prey day and night using both sight and touch, using three types of feeding method: pecks, jabs and 'stitching', involving a very rapid series of shallow probes whilst walking forward on a straight or zigzag course. Most prey is swallowed as the bill is extracted from the mud and includes *H. ulvae*, amphipods and *N. diversicolor* (Burton 1974).

Lapwing feed mainly by sight but can also locate prey by hearing. They walk or make a short run, then pause and probe, with their body tilted forward. Foot trembling or paddling is used to flush inconspicuous prey. Prey include molluscs and small fish.

Black-headed gulls take a very wide range of prey items in a wide diversity of habitats used. Feeding methods and diet vary with locality, season, food availability and individuals. In estuaries, methods of feeding on wet sand or mud and in pools include: foot paddling; crouch feeding while moving slowly; upright feeding; and a rapid pace interrupted by frequent surface pecks. Methods for feeding, while in or above water, include: dips to surface; surface plunging to take floating food; becoming fully submerged; surface feeding while swimming either with the head and neck immersed; or upending (Vernon 1970, 1972). Feeding behaviour varies with flock density (Curtis & Thompson 1985) and with time of year probably as a result of seasonal differences in prey, as well as variations over the tidal cycle (Curtis *et al.* 1985). The crouch technique is most frequently used in summer, whereas upright feeding (capturing *C. volutator* and *N. diversicolor*) and paddling, which captures *C. volutator* only, occurs mainly in winter.

Invertebrates

Over the period from 1973 to 1991, data from nine survey periods of the intertidal invertebrate benthos are used for the three invertebrate prey species: *Corophium volutator, Nereis diversicolor* and *Hydrobia ulvae*. All of these studies utilised the same methodology, taking cylindrical cores (10 cm diameter x 10-15 cm deep) and sieving through 0.5 mm mesh for small worms or 1 mm mesh for the macrofaunal species considered here. In particular, invertebrate surveys were conducted to coincide with the bird surveys indicated below. The surveys are listed in Table 1, including an indication of their seasonal coverage. No data are available on size classes of these invertebrates.

Although concentration is placed here on the main prey species, the invertebrate community of the estuary is rich with many other species, as listed in Appendix 1. Some of these are found in relatively small numbers and do not constitute important prey items, while others are of very small size and can form part of the diet of specialised feeders such as shelduck and dunlin. The surveys have all concentrated on the interstitial fauna and as a consequence the numbers have probably been underestimated of species such as *Mytilus edulis* which have a very clumped distribution concentrated in mussel beds towards the seaward end of the estuary, and of sessile species attached to rocks, pilings, etc.

Table 1. List of surveys of intertidal invertebrate benthos. N = number of stations at which samples (two cores) were taken. The 1979 and 1985 surveys concentrated on eastern areas of the mudflats to check on densities of *C. volutator* and *N. diversicolor* as food for birds. The remaining surveys covered all of the flats.

Year (season) N	*Sample period*	*For further information*
1973 (summer) 39	July - September	Minto *et al.* (1974); Smyth *et al.* (1974).
1974 (winter) 38	October 74 - March 75	Stobie *et al.* (1976).
1975 (summer) 38	April - September	Stobie *et al.* (1976).
1976 (summer) 66	May - November	Halliday (1978); Curtis (1978); Halliday *et al.* (1982); Thompson *et al.* (1986).
1977 (winter) 66	November 76 - May 77	Halliday (1978); Curtis (1978); Halliday *et al.* (1982); Thompson *et al.* (1986).
1979 (winter) 19	March	Curtis & Smyth (1982).
1985 (winter) 25	October - December	A. Brand (unpublished).
1990 (winter) 36	December 90 - January 91	Curtis & Figures (1992).
1991 (summer) 36	September	Curtis & Figures (1992).

Distribution of birds and invertebrates

Bird feeding numbers

There have been marked changes in the peak numbers of birds on the estuary. While black-headed gull showed a noticeable increase in 1991 compared with 1976/77 (August 1977: 10,000+, January 1991: 24,041, cf. 32,390 in September 1972), as did curlew (September 1976: 746, February 1991: 1,974), peak counts for dunlin were fairly constant (November 1976: 8,700, December 1991: 8,975, cf. 9,380 in February 1976), as were those for greenshank (September 1976: 41, February 1991: 47) and lapwing (November 1976: 6,300, November 1991: 4,653, cf. 6,648 in February 1973). Oystercatcher showed an increase from 1976/77 to 1991 (November 1976 and February 1977: 2,500, February 1991: 5,040), representing a return to former higher numbers (5,250 in February 1973). Of greatest significance was the decline in peak counts for redshank (November 1976: 9,700, February 1991: 3,486, cf. 10,800 in October 1974).

Among the ducks, mallard showed fairly similar peak numbers between the two surveys (340 in November 1976, 485 in October 1991). In sharp contrast, the peak counts for shelduck dropped markedly from 1,200 in February 1977 to only 443 in March 1991 (516 in June 1991).

In terms of overall total values of the summed tidal peaks as a measure of feeding utilisation of the flats, only two species showed similar numbers in 1976/77 and 1990/91: black-headed gull (107% in the later survey compared with 1976/77) and oystercatcher (95%). In contrast, curlew numbers were much higher in 1990/91 (209% cf. 1976/77). The remaining species all showed declines: lapwing (72%), dunlin (57%), greenshank (36%); the most marked decline was for redshank with the 1990/91 total being only 32% of the 1976/77 value. These figures are based on a combination of November and February counts' data. Figure 2 shows the summed tidal peaks for the seven species in February 1977 and 1991, in which relatively higher 1977 counts for black-headed gull and curlew contrast sharply with declines for dunlin, lapwing, oystercatcher and redshank.

Over the sampling period for the environmental impact assessment, counts at high tide were also taken at the five main roosts of the birds (Ardmore, Cardross, Woodhall-Newark Castle, West Ferry-Finlaystone and Milton Island-Longhaugh). These counts yielded the following numbers (with feeding birds count in parentheses) for the seven key species in February 1991: black-headed gull 1,867 (7,948), curlew 1,522 (1,974), dunlin 1,184 (5,687), greenshank 11 (47), lapwing 1,862 (4,583), oystercatcher 4,135 (5,040) and redshank 2,221 (3,486). Discrepancies between these roost counts and the corresponding numbers of feeding birds reflect, not only differences resulting from counting technique (especially in the case of dunlin), but also the fact that some of these roosting birds may feed outwith the estuary on farmland, e.g. lapwing, or that birds from more distant roosts may visit the estuary to feed, e.g. black-headed gulls. These discrepancies also point to problems in using roost counts to describe feeding usage of the estuary by these birds.

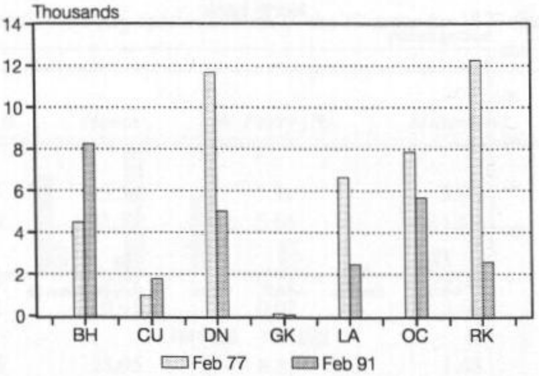

Figure 2. Feeding utilisation by the key species of the estuarine flats in February 1977 and 1991 expressed as the sum of the peak counts for ebb, low and flow tides.

Bird feeding distribution

In terms of all seven key species and their summed feeding densities, there are marked variations between north and south banks of the estuary and between the different areas along these banks, as shown in Figure 3 (February 1977 and 1991 data).

On both banks there are higher densities of feeding birds in the eastern half of the estuary - Havoc, West Ferry (N and S), Milton (N and S), Longhaugh and Erskine. On the northern shores, between 1977 and 1991, there appears to be an eastward shift with Milton (N) becoming relatively more important while Havoc and West Ferry (N) densities decline markedly. The southern areas all show a drop in feeding densities. In both surveys, feeding densities were much higher on the south bank. The total figures for the north and south banks dropped significantly from their respective values of 17,478 and 27,742 in 1977 to 7,712 and 19,296 in 1991; the north bank figure in 1991 was only 44% of the 1977 value, with the south bank showing a reduction to 70%.

The different changes for the various key species are evident in Table 2 which lists the feeding densities of these species for the 12 areas. Some species show

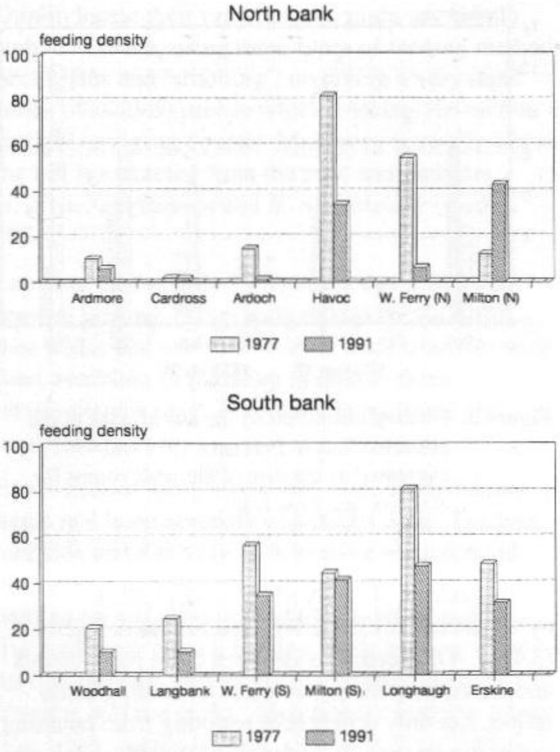

Figure 3. Feeding densities summed for the key species, i.e. feeding utilisation per hectare, in February 1977 and 1991, for the 12 sample areas. Note the continuing importance of Milton (S) and the increased importance of Milton (N) in 1991, in contrast to declines in other areas.

opposing trends, e.g. oystercatcher, curlew and black-headed gull densities increase at Longhaugh and Erskine, whereas dunlin, lapwing and, to a lesser degree, redshank decline. When the 1991 densities are expressed as a percentage of the 1977 values, particular contrasts are evident for the Havoc area, where black-headed gull densities in 1991 were 645% of the 1977 value in contrast to marked drops for dunlin (8.5%), oystercatcher (26.6%) and redshank (13%). These latter figures emphasise the impression of a withdrawal of the birds from the north bank. Another significant area of decrease for redshank is at Milton (S), where the 1991 density is only 29% of the 1977 figure and even more so at West Ferry (S) with a fall to only 5.4% of the 1977 density. To some extent these declines are compensated by a rise at Woodhall where the 1991 density was 223% of the 1977 level.

The distribution over the 12 areas was similar between 1977 and 1991 for black-headed gull ($r = 0.570$, p approximately 0.05), dunlin ($r = 0.848$, $p<0.001$), greenshank ($r = 0.675$, $p<0.02$, though numbers very low) and lapwing ($r = 0.730$, $p<0.01$). Curlew distribution patterns did not correlate between the two surveys ($r = -0.002$) and to a lesser extent the distributions of oystercatcher ($r = 0.344$, n.s.) and redshank ($r = 0.308$, n.s.) did not show correlated patterns comparing 1991 with 1977.

Invertebrate densities

A comparison between the winter surveys for invertebrates of 1976/77 and 1991 suggests similar or even slightly higher densities in the latter for *N. diversicolor* (means of 1,038 m^{-2} in 1976/77 and 1,752 m^{-2} in 1990, with corresponding maxima of 5,220 m^{-2} and 6,341 m^{-2}). The observed densities in the two surveys were very similar for *H. ulvae* (means of 2,141 m^{-2} and 2,499 m^{-2}, maxima of 29,600 m^{-2} and 28,746 m^{-2}). In contrast, *C. volutator* densities showed a marked decline from 1976 to 1990 (means of 1,544 m^{-2} and 1,195 m^{-2}), especially in terms of the maxima (13,320 m^{-2} and 6,552 m^{-2}). These are illustrated in Figure 4.

Details of the levels in the 12 areas are listed in Table 3 and it is interesting to note significant differences between the two surveys. Even in terms of their mean densities in the 12 areas, the pattern of correlations between the three species is robust, with significant positive correlation between *N. diversicolor* and *C. volutator* ($r = 0.761$, $p<0.01$) and significant negative correlations with *H. ulvae* of *N. diversicolor* ($r = -0.779$, $p<0.01$) and *C. volutator* ($r = -0.607$, $p<0.05$). In 1991, the negative correlation between *N. diversicolor* and *C. volutator* with *H. ulvae* had weakened with respective correlations of -0.336 and -0.452, both not significant. Even the strong correlation between *N. diversicolor* and *C. volutator* had become non-significant at $r = 0.556$. The main contributing factor to this was a change in the distribution of *C. volutator* with a low correlation of only 0.385 (n.s.) between the 1977 and 1991 densities in the 12 areas. Both *N. diversicolor* ($r = 0.890$, $p<0.001$) and *H. ulvae* ($r = 0.584$, $p<0.05$) distributions showed significant agreement between the two surveys.

For all three species their mean densities varied significantly between the 12 areas, according to analysis of variance on log transformed data. Their overall mean densities in the estuary did not differ significantly between the years, in comparison to the differences between areas. From Table 3, the marked differences between the eastern and western halves of the estuary are apparent, with the general trends described in earlier reports being maintained in the 1991 values. The main difference is the lower degree of clumping (patchiness) shown by all three species and especially by *C. volutator*, i.e. lower occurrence of high density patches of the prey species.

Table 2. Feeding densities (summed tidal peak counts per hectare) of the key species in each of the 12 areas for 1977 and 1991 February surveys. Zero densities are indicated by -.

North bank *Year*	*Ardmore*	*Cardross*	*Ardoch*	*Havoc*	*W. Ferry (N)*	*Milton (N)*
Black-headed gull:						
1977	1.24	0.13	2.75	3.34	7.91	3.8
1991	0.78	0.16	0.39	21.57	5.66	21.5
Curlew:						
1977	0.33	0.19	0.61	0.67	0.11	0.03
1991	1.47	0.85	0.41	0.91	0.02	3.66
Dunlin:						
1977	0.01	0.49	1.35	23.95	8.37	1.43
1991	-	-	-	2.04	-	2.56
Greenshank:						
1977	0.01	0.02	0.01	0.01	0.04	-
1991	0.01	-	-	-	-	-
Lapwing:						
1977	2.52	0.09	1.75	2.01	2.40	3.03
1991	1.01	-	-	0.01	-	5.78
Oystercatcher:						
1977	5.34	0.13	3.22	23.19	14.16	0.64
1991	1.87	0.54	0.57	6.16	0.77	9.39
Redshank:						
1977	1.02	0.80	5.16	29.09	21.97	3.48
1991	0.99	0.13	-	3.78	-	0.24

South Bank *Year*	*Woodhall*	*Langbank*	*W. Ferry (S)*	*Milton (S)*	*Longhaugh*	*Erskine*
Black-headed gull:						
1977	3.17	1.65	4.17	7.15	3.01	4.32
1991	1.17	3.83	9.21	8.53	11.82	10.45
Curlew:						
1977	1.59	2.80	1.49	0.43	-	-
1991	0.66	0.63	0.81	2.61	2.92	0.54
Dunlin:						
1977	3.81	8.09	19.56	12.52	30.51	9.85
1991	1.71	-	15.87		10.43	1.08
Greenshank:						
1977	0.12	0.12	0.02	-	-	-
1991	0.09	0.17	-	-	-	-
Lapwing:						
1977	7.35	4.47	11.10	8.24	11.75	23.66
1991	-	0.02	2.82	8.51	1.74	1.23
Oystercatcher:						
1977	1.82	1.83	10.46	5.26	6.38	1.17
1991	0.34	3.80	5.70	8.44	14.43	10.51
Redshank:						
1977	2.90	6.00	9.91	11.26	29.75	9.73
1991	6.47	1.95	0.54	3.28	16.82	7.78

Inter-relationships between bird and invertebrate species

Detailed consideration of the relationships between the birds and their prey requires incorporation of the detailed variations between tidal states and finer scale analysis than that used here to describe long-term changes. However, it is possible to point to some of the salient features, based on the densities in the 12 areas. The patterns for 1977 appear different from those described by Thompson, Curtis & Smyth (1986) as a result of this difference in scale of description. In considering the correlations described here, it must be remembered that correlation does not necessarily imply causation and interpretation should take account of the dietary characteristics of the birds, especially in the case of curlew.

Black-headed gulls in 1977 showed a significant correlation with *N. diversicolor* (r = 0.794, $p<0.01$) and *C. volutator* (r = 0.749, $p<0.01$) and a corresponding negative correlation with *H. ulvae* (r = -0.590, $p<0.05$); similar patterns were shown

Table 3. Invertebrate densities (number metre^{-1}, mean and maximal values) in the 12 areas for the two sampling periods winter 1976/77 and 1990/91, corresponding with the bird data presented in Table 2.

North Bank *Year*	*Ardmore*	*Cardross*	*Ardoch*	*Havoc*	*W. Ferry (N)*	*Milton (N)*
C. volutator:						
1977 mean	0	20	1,490	4,660	5,700	4,548
1991 mean	18	405	13	40	1,480	2,827
1977 max.	0	120	4,140	5,340	10,200	13,320
1991 max.	53	634	53	106	1,480	5,390
N. diversicolor:						
1977 mean	0	93	1,110	1,240	3,060	2,532
1991 mean	18	36	1,506	2,074	6,024	3,831
1977 max.	0	240	3,000	1,800	4,200	4,440
1991 max.	53	71	3,752	6,341	6,024	4,333
H. ulvae:						
1977 mean	1,590	5,142	1,770	1,320	390	96
1991 mean	951	2,149	5,377	2,113	1,480	265
1977 max.	2,160	29,600	3,120	2,340	600	240
1991 max.	2,272	3,699	10,410	3,118	1,480	423
South Bank *Year*	*Woodhall*	*Langbank*	*W. Ferry (S)*	*Milton (S)*	*Longhaugh*	*Erskine*
C. volutator:						
1977 mean	90	228	2,220	4,300	1,680	270
1991 mean	502	726	1,545	5,416	5,337	705
1977 max.	360	660	5,880	7,380	2,520	360
1991 max.	1,321	2,272	2,801	6,130	6,552	1,163
N. diversicolor:						
1977 mean	165	288	2,280	2,240	2,430	1,720
1991 mean	740	1,228	1,968	4,544	2,589	2,431
1977 max.	600	600	5,220	4,860	2,640	2,580
1991 max.	1,268	2,219	2,378	4,650	2,642	3,347
H. ulvae:						
1977 mean	4,320	4,272	2,250	110	210	30
1991 mean	2,074	8,164	1,229	344	0	0
1977 max.	7,440	7,680	5,340	600	420	60
1991 max.	4,333	28,746	4,597	423	0	0

with the maximal densities of these prey species. In contrast, the 1991 black-headed gull distribution did not correlate with any of the prey mean densities, but only with maximal values for *N. diversicolor* ($r = 0.638$, $p<0.05$).

Curlew showed a remarkable change between 1977 and 1991, being significantly correlated with *H. ulvae* mean densities ($r = 0.628$, $p<0.05$) in the first survey and with *C. volutator* mean ($r = 0.751$, $p<0.01$) and maximal ($r = 0.821$, $p<0.01$) densities in the second. Greenshank showed significant correlation with *H. ulvae* in both surveys, although their numbers are too low to ascribe statistical meaning.

Lapwing were not correlated with any prey species in 1977, but did correlate with *C. volutator* in the 1991 set, with $r = 0.743$ ($p<0.01$) for mean and $r = 0.763$ ($p<0.01$) with maximal densities of this prey.

Oystercatcher correlated with mean densities of *C. volutator* in both years ($r = 0.618$, $p<0.05$, in 1977 and 0.707, $p<0.02$ in 1991) but with maximal densities only in 1991 ($r = 0.734$, $p<0.01$).

Redshank showed no significant correlations at all with prey densities, although the highest correlations were with *C. volutator* ($r = 0.546$, n.s.) and *N. diversicolor* ($r = 0.556$, n.s.) in 1977 and with *C. volutator* in 1991 ($r = 0.500$, n.s.). The correlation between this bird and *N. diversicolor* in 1991 was $r = 0.000$, i.e. no correlation at all.

Patterns of association between bird species changed between the years. In 1977, there were significant positive correlations of greenshank with curlew ($r = 0.822$, $p<0.01$) and redshank with oystercatcher ($r = 0.752$, $p<0.01$). In addition, dunlin were positively correlated with both oystercatcher (0.590, $p<0.05$) and redshank (0.860, $p<0.001$). The redshank with oystercatcher ($r = 0.681$, $p<0.02$)

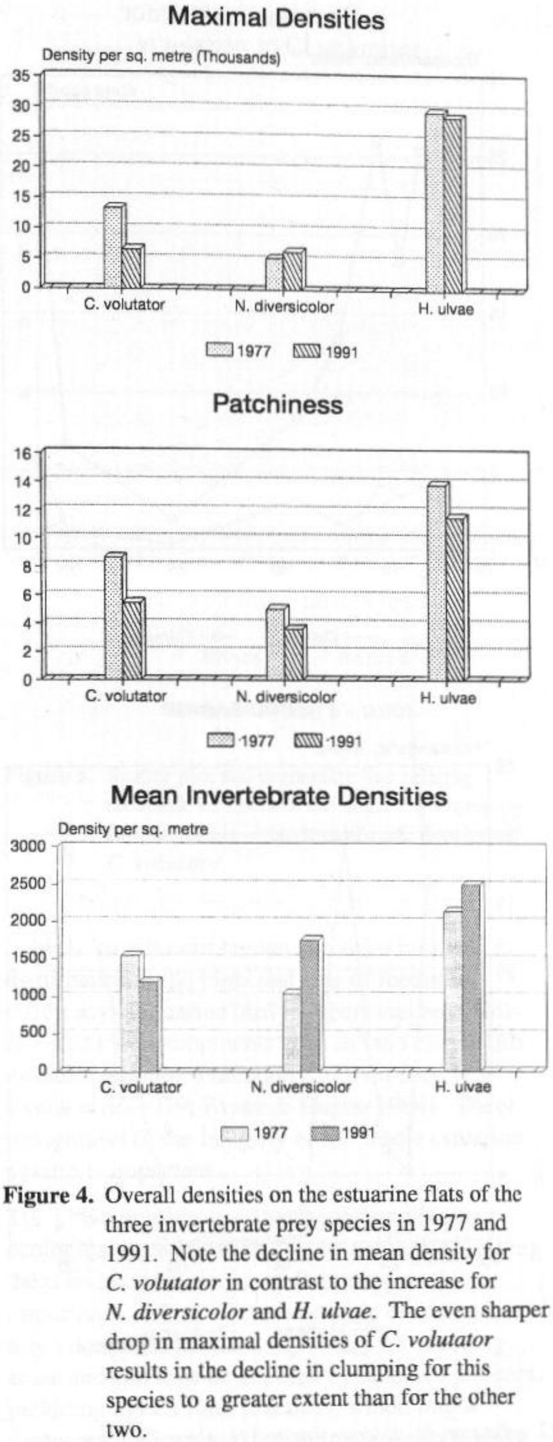

Figure 4. Overall densities on the estuarine flats of the three invertebrate prey species in 1977 and 1991. Note the decline in mean density for *C. volutator* in contrast to the increase for *N. diversicolor* and *H. ulvae*. The even sharper drop in maximal densities of *C. volutator* results in the decline in clumping for this species to a greater extent than for the other two.

correlation was the only one of these to reappear in the 1991 data. Other 1991 correlations were of black-headed gull with oystercatcher ($r = 0.679$, $p<0.02$), dunlin with lapwing ($r = 0.595$, $p<0.05$) and curlew with both lapwing ($r = 0.746$, $p<0.01$) and oystercatcher ($r = 0.675$, $p<0.02$).

These correlations only describe the general distributions of these birds relative to the 12 areas of the estuary, but they do emphasise the changes in the birds' distributions between the two survey periods.

Redshank over the years

This species of international importance clearly shows marked diminution in overall numbers between the two feeding bird surveys and this decline is also evident in data for peak counts taken from the Clyde Bird Reports (e.g. Gibson 1991) and Birds of Estuaries Enquiry data (e.g. Cranswick, Kirby & Waters 1992). These data, compiled from roost counts, provide estimates of the total peak populations using the estuary and exhibit the marked decline shown in Figure 5. This decline is in marked contrast to the relatively steady values for the UK index for this species which has only oscillated from a value of around 100% at the start of this period down to about 70% in 1986, up to 110% in 1989 and 1990 and 85% in 1991. Thus, the decline in Clyde redshank numbers was not mirrored on other estuaries around Britain.

Figure 5 also shows the corresponding variation in the densities of the three invertebrate species. Both *N. diversicolor* and *H. ulvae* show wide oscillations over the period from 1973 to 1991, in contrast to a steady decline, especially evident in maximal densities recorded, from 1973-1975 to 1985 in *C. volutator* with a suggestion of an increase at the end of the period. These changes are consistent with reported changes for the sublittoral macrofauna of the estuary channel (Henderson 1995); the rise in *C. volutator* in 1991 even mirrors an oxygen sag reported for the estuary at that time with a remarkable crash in the invertebrate fauna of the channel benthos. Taking into consideration just those invertebrate surveys coincident with redshank counts, redshank numbers showed no significant correlations with prey densities. Using the maximum:mean ratio as a measure of clumping of the prey in a simple regression model, however, reveals a relationship between this bird and its prey. Figure 6 shows a plot of redshank numbers (RKnos) against the clumping of *C. volutator* (Cvpatch), to which a straight line may be fitted,

RKnos = 941.Cvpatch, which is statistically significant (p 0.001).

This simple model, easily interpreted in terms of the feeding ecology of this species, supports the view that the decline in redshank numbers is related to the availability of their food, as it is the presence of high density patches of prey indicated by the degree of clumping which influences the birds, rather than just the general prey levels.

Conclusion: conservation implications

This analysis has concentrated upon the seven key species and particularly on the main species of international importance which winters on this

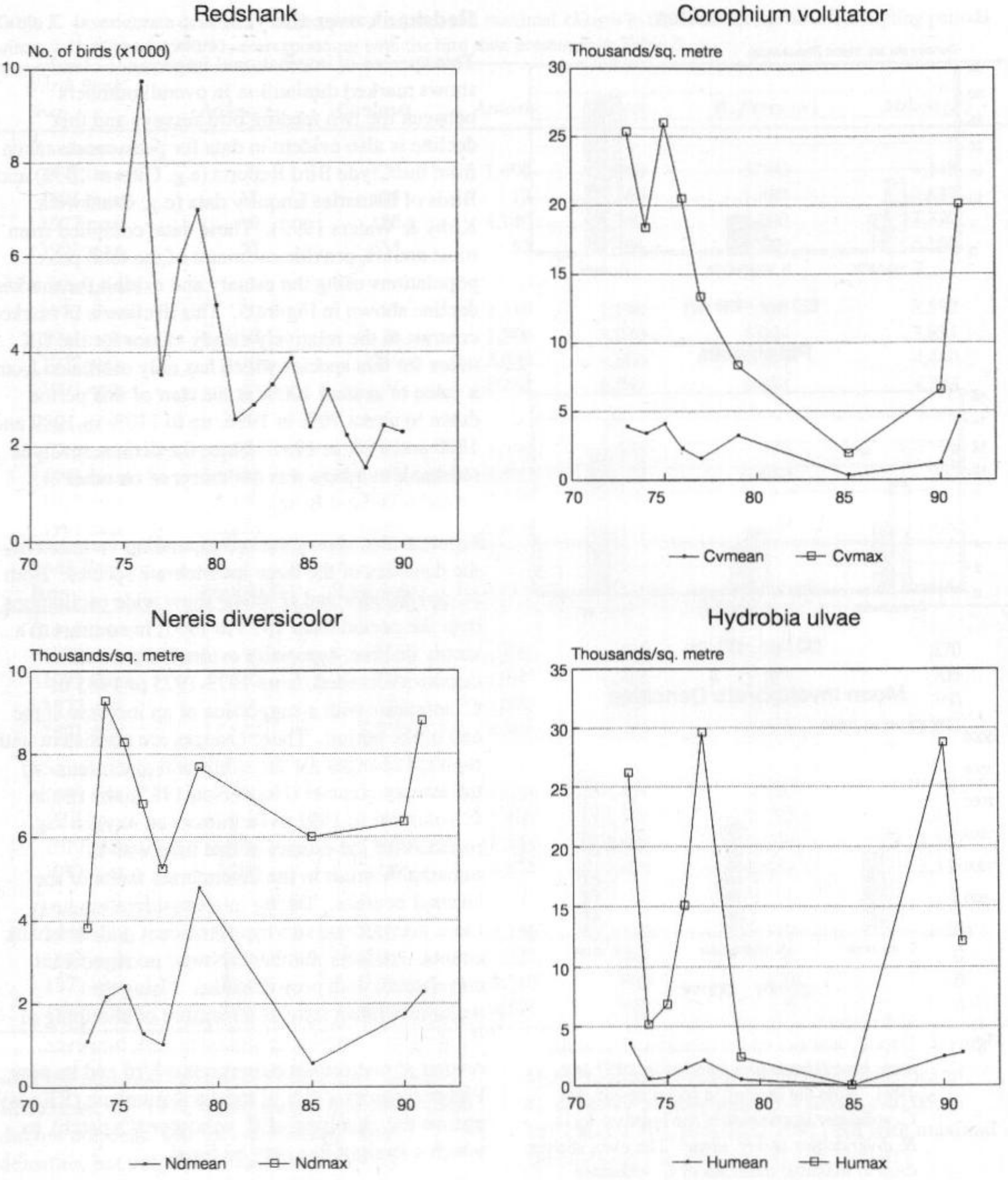

Figure 5. Variations in redshank peak counts and densities of *C. volutator*, *N. diversicolor* and *H. ulvae* for the whole estuary over the period 1973-1991.

estuary. The species richness of the estuary also contributes to its conservation importance. In a broad study of 109 British estuaries, Hill *et al.* (1993) placed the Clyde with 23 other estuaries in their Group 4, a set characterised by more diverse wader communities than their other three groups. The Clyde Estuary has long been recognised for its ornithological importance and features as one of 38 British estuaries of conservation importance that are presently threatened by reclamation proposals; as such it is also protected by Special Protection Area and Ramsar status (Stroud, Mudge & Pienkowski 1990). However, within the current planning system in Scotland, it is not impossible that relatively small proposals (but with disproportionately large impacts) in different parts of the estuary might be considered by separate authorities and important feeding grounds might thus be lost. This loss could occur in quite subtle ways, such as changes in sediment properties affecting the availability of invertebrates

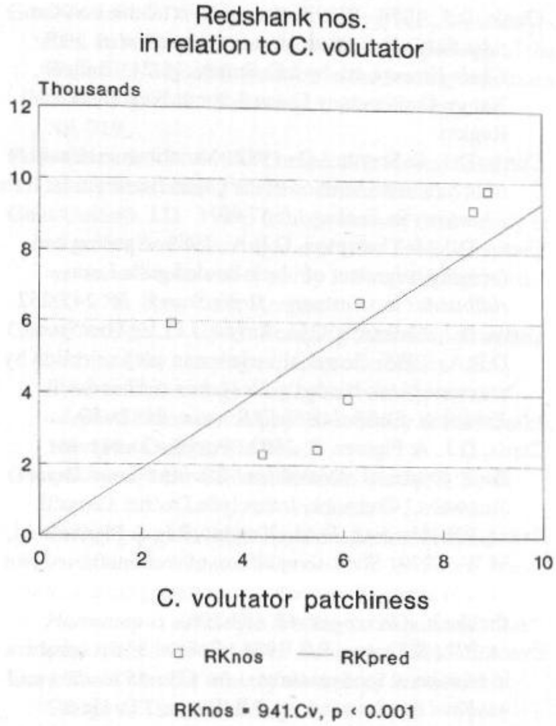

Figure 6. Scatter plot and regression line relating redshank numbers to the degree of clumping (or patchiness = maximum/mean density) of *C. volutator*.

to birds, or adjacent human activities resulting in disturbance of the birds and loss of feeding efficiency. Estuarine bird numbers can be rapidly affected by developments such as land claims that interfere with the availability of their food (e.g. Evans *et al.* 1979; Evans & Dugan 1984). The recognition of the integrity of the whole estuarine system is important.

The position of these estuarine flats within an ecological network must also be recognised, giving them an international as well as a national importance. Many of the wintering estuarine species rely upon other habitats, especially for breeding areas and can thus be affected by land-use patterns, including agricultural practices, which might determine their survival rates in quite subtle ways (e.g. Beintema 1991a). Some species of waders, such as redshank, might be harmed by the increasing use of intensive agriculture, while others, e.g. oystercatcher and lapwing, may even benefit by being able to exploit intensively-farmed grasslands (Beintema 1991b). Although much of the decline in waders might be ascribed to impacts on their reproductive characteristics (Visser & Beintema 1991), the combined impacts of breeding habitat disturbance and loss of estuarine feeding grounds clearly interact with each other. The birds' reproductive success will be influenced by their health as they move from estuarine winter resorts to their breeding ground. This, in turn, would influence the size of the population subsequently returning to winter on the estuary. Related to this is the fact that many of the birds roosting by the estuary might not use only the intertidal flats but also feed in other habitats, such as adjacent sea lochs (Halliday 1979) and farmland (especially lapwing and oystercatcher; M.L.P. Thompson, unpubl.). Evidence regarding the movements of individual birds is, however, extremely limited, e.g. the study of marked birds by Furness *et al.* (1986).

Although there have been relatively few experimental investigations (e.g. Raffaelli & Hall 1992), there have been many studies on the complexity of factors which influence the patterns of feeding distribution of these estuarine birds, e.g. influence of tides and seasons on feeding behaviour of black-headed gulls (Curtis & Thompson 1985; Curtis *et al.* 1985), effects of age-dependent risk of predation in relation to feeding location of redshank (Cresswell 1994), application of game theory models to oystercatcher feeding distributions (Goss-Custard *et al.* 1995), the influence of weather on survival rates of lapwings (Peach, Thompson & Coulson 1994). Additionally, as bird densities change, perhaps as a consequence of loss of feeding areas and possible concentration into smaller areas, interference and interactions between birds might affect their feeding success (e.g. Goss-Custard 1977d, 1980; Selman & Goss-Custard 1988). On the Clyde Estuary at Longhaugh Bay in winter 1985/86, M.L.P. Thompson (unpubl.) in fact found that the overall rate of encounters between birds was low and that the majority were intraspecific. Thompson, Curtis & Smyth (1986) discuss the various factors and summarise literature relating to components of pattern in estuarine bird-prey associations. In this present concentration on long-term changes, these detailed interactions are taken for granted as the underlying mechanisms determining the birds' numbers and distributions. They are likely to differ according to species; further analyses are being conducted to reveal the patterns of variation at a finer scale related to season and tidal state.

The finding of a clear relationship between the numbers of redshank on the estuary and the degree of clumping of their main prey species confirms long-held suspicions concerning the cause of this bird's decline on the Clyde. Furness *et al.* (1986) considered a number of factors which might be influential, including national (or international) trends, weather, changes in breeding areas, availability and quality of roost sites, and food. The evidence presented here indicates that food is certainly a major influence, though it may possibly not be the only one. The detailed pattern of distribution of the birds over the estuarine flats might be influenced by factors other than those responsible for the long-term decline. The proximity of roost sites to prey-rich areas of flat is important; as the invertebrate distributions change, even though their overall mean densities are maintained, the energetics of foraging may have an impact (see, e.g. Goss-Custard 1984, 1985; Thompson, Curtis & Smyth 1986).

In conclusion, differences in the relative utilisation of different areas of the mudflats are clearly evident when comparing the two bird surveys. The birds' preferences for feeding areas changed markedly and this variation is an important aspect which must be taken into account when considering development proposals for the estuary which might involve reclamation or other forms of disturbance excluding or displacing the birds from their feeding areas.

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Appendix 1.

(a) List of bird species recorded during the two surveys, 1976/77 and 1990/91, indicated by *a* and *b* respectively.

Red-throated diver *Gavia stellata*[a,b], great crested grebe *Podiceps cristatus*[a,b], Slavonian grebe *P. auritus*[a,b], little grebe *Tachybaptus ruficollis*[a], gannet *Sula bassana*[a,b], cormorant *Phalacrocorax carbo*[a,b], shag *P. aristotelis*[a,b], grey heron *Ardea cinerea*[a,b], mute swan *Cygnus olor*[a,b], whooper swan *Cygnus cygnus*[b], shelduck *Tadorna tadorna*[a,b], teal *Anas crecca*[a,b], wigeon *A. penelope*[a,b], mallard *A. platyrhynchos*[a,b], pintail *A. acuta*[a,b], shoveler *A. clypeata*[b], scaup *Aythya marila*[a,b], tufted duck *A. fuligula*[a,b], pochard *A. ferina*[a], goldeneye *Bucephala clangula*[a,b], long-tailed duck *Clangula hyemalis*[a,b], eider *Somateria mollissima*[a,b], king eider *S. spectabilis*[a], red-breasted merganser *Mergus serrator*[a,b], goosander *M. merganser*[b], greylag goose *Anser anser*[a], barnacle goose *Branta leucopsis*[a], Canada goose *B. canadensis*[a], pink-footed goose *A. brachyrhynchus*[b], coot *Fulica atra*[a,b], oystercatcher *Haematopus ostralegus*[a,b], ringed plover *Charadrius hiaticula*[a,b], golden plover *Pluvialis apricaria*[a,b], grey plover *P. squatarola*[a,b], lapwing *Vanellus vanellus*[a,b], knot *Calidris canutus*[a,b], curlew sandpiper *C. ferruginea*[a,b], dunlin *C. alpina*[a,b], little stint *C. minuta*[a], pectoral sandpiper *C. melanotos*[a], sanderling *C. alba*[a], ruff *Philomachus pugnax*[a,b], snipe *Gallinago gallinago*[a,b], jack snipe *Lymnocryptes minimus*[a], black-tailed godwit *Limosa limosa*[a,b], bar-tailed godwit *L. lapponica*[a,b], curlew *Numenius arquata*[a,b], whimbrel *N. phaeopus*[a], spotted redshank *Tringa erythropus*[a,b], redshank *T. totanus*[a,b], greenshank *T. nebularia*[a,b], common sandpiper *Actitis hypoleucos*[a,b], turnstone *Arenaria interpres*[a,b], Mediterranean gull *Larus melanocephalus*[b], black-headed gull *L. ridibundus*[a,b], common gull *L. canus*[b], lesser black-backed gull *L. fuscus*[b], herring gull *L. argentatus*[b], Iceland gull *L. glaucoides*[b], great black-backed gull *L. marinus*[b], kittiwake *Rissa tridactyla*[b], Sandwich tern *Sterna sandvicensis*[b], common tern *S. hirundo*[b], Arctic tern *S. paradisaea*[b], Arctic skua *Stercorarius parasiticus*[a], razorbill *Alca torda*[a], guillemot *Uria aalge*[a,b], black guillemot *Cepphus grylle*[a,b].

(b) Other invertebrate species recorded from the Clyde Estuary mudflats, with an indication of peak mean and maximal densities for most species and the years in which these were recorded.

Annelida: *Nepthys hombergi* (8; 296 in 1973), *Arenicola marina* (14; 222 in 1973), *Eteone longa* (61; 423 in 1991), *Phyllodoce maculata* (27; 419 in 1974 and 1973 respectively), *Scoloplos ciliata* (2; 74 in 1974), *Scoloplos armiger* (28; 888 in 1974), *Cirratulus cirratus* (8; 296 in 1973), *Polydora ciliata* (95; 793 in 1991), *Capitella capitata, Fabricia sabella, Lanice conchilega, Manayunkia aestuarina, Tubificoides benedeni, Tubifex costatus.*

Crustacea: *Carcinus maenas* (29; 197 in 1973, 1974), *Balanus balanoides* (452; 15,384 in 1974), *Crangon crangon* (1; 25 in 1974), *Idotea chelipes* (14; 370 in 1974), *Jaera albifrons* (12; 395 in 1974), *Sphaeroma rugicauda* (26; 345 in 1973), *Bathyporeia pelagica, Melita palmata* (22; 524 in 1974).

Mollusca: *Macoma balthica* (103; 528 in 1991), *Mytilus edulis* (147; 2,294 in 1974), *Cerastoderma edule* (31; 1,110 in 1973), *Littorina littorea* (56; 987 in 1974), *Tellina tenuis* (1; 49 in 1974), *Acmaea tessulata* (4; 49 in 1973), *Littorina saxatilis* (53; 1,209 in 1974), *Littorina littoralis* (10; 370 in 1974), *Retusa alba* (3; 99 in 1974).

Long-term population changes amongst wintering waders (Charadrii) on the Forth Estuary: effects of changing food densities

D.M. Bryant & D.S. McLusky

Annual changes in the numbers of waders (Charadrii) wintering on the Forth Estuary over 22 years are reviewed. Population changes on the estuary as a whole largely reflected those at the two largest mudflats, Kinneil and Skinflats. Of seven common species mainly dependent on intertidal invertebrates, knot *Calidris canutus* declined at both Kinneil and Skinflats, curlew *Numenius arquata* showed no persistent changes, while the remainder increased or decreased at only one site. Changes in wader numbers wintering in the UK, as indicated by the national indices of winter abundance, explained some of the population fluctuations on the Forth, particularly amongst redshank *Tringa totanus* and black-tailed godwit *Limosa limosa* at Kinneil and dunlin *Calidris alpina* and curlew at Skinflats. There was no strong evidence of density-dependent usage of the two study sites by any species and a 'winter cold' index for Scotland revealed no marked effects of local climate on waders. Foreshore engineering at Kinneil in the 1970s, which resulted in substantial losses of intertidal mudflats and alteration to the tidal regime, apparently affected knot and dunlin populations adversely. Little evidence was found for interspecific competition amongst shorebirds, and human disturbance and avian predators were considered unimportant for long-term population trends.

The main focus of the study was on the effects of changing food densities, using data on intertidal invertebrates and waders obtained over 18 years. Correlations between food supplies and wader abundances, controlling for changes in national populations and coastal engineering operations at Kinneil, as appropriate, showed that four species responded positively to recorded food variations. At Kinneil, redshank increased in association with *Corophium volutator* and bar-tailed godwit *Limosa lapponica* with polychaete worms, particularly *Eteone longa* and *Nephthys hombergi*. Numbers of knot and oystercatcher *Haematopus ostralegus* at Skinflats rose in response to *Hydrobia ulvae* and *Cardium edule* densities respectively. While the behavioural mechanisms underlying these responses remain unclear, the study showed that wintering wader populations of several species were related to changes in the abundance, and by implication the carrying capacity, of a favoured prey.

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Introduction

Populations of wintering shorebirds change from year to year across spatial scales ranging from beaches to Flyways. These fluctuations may or may not be synchronised across sites, and have causes which extend from the local to the global (Dolman & Sutherland 1994; Goss-Custard *et al.* 1994). The reasons for population changes in winter on any estuary, therefore, may include factors which operate remotely, on the breeding grounds or migration routes. Weather conditions and predators, for example, have important effects on breeding success among waders breeding in the high arctic (Summers & Underhill 1987; Ebbinge 1989; Boyd 1992). Also, high mortality rates on migration can depress wintering populations (Ebbinge 1991).

In spite of their greater accessibility for study, the causes of population changes on wintering grounds are incompletely known (Evans & Pienkowski 1984). Deteriorating weather is often considered to encourage onward movements at northerly wintering sites, leading fewer waders to remain during cold winters (Townshend 1982; Evans & Pienkowski 1984). Harsh winter weather may induce severe mortality at wintering sites (Boyd 1964; Swennen & Duiven 1983) but its most extreme effects are irregular and cannot explain all year to year changes or sustained increases or decreases. Predation can also depress wader numbers locally (Page & Whitacre 1975; Whitfield 1985), and could regulate non-breeding populations, but again there is no evidence that changing predation pressure underlies often substantial yearly changes. Relaxation of local hunting pressure has been implicated in population increases amongst a few wader species (Tubbs 1992) and disturbance by humans in some local population declines (Davidson & Rothwell 1993).

Factors which determine spatial variation in population density, such as sediment characteristics (Goss-Custard *et al.* 1985) and food supplies (Bryant 1979) are obvious candidates for driving population changes, because they show marked annual changes themselves (McLusky & McCrory 1989). Also, seasonal movements of waterbirds commonly follow depletion of food supplies (Van Eerden 1984), further suggesting a close link between food supplies and bird numbers. A striking example of population decline following loss of feeding is provided by the disappearance of a flock of scaup *Aythya marina* from the Firth of Forth once a supply of waste grain was curtailed (Campbell 1984). Progressive changes in shorebird communities related to the effects of pollution have been described from several estuaries (Hill *et al.* 1993), including the Scheldt and Clyde (Van Impe 1985; Furness *et al.* 1986), and demonstrate a potential for the quality, abundance, availability, or perhaps palatability, of food supplies to affect shorebird populations. Studies of annual changes in wader populations in relation to food sources, whether natural or derived from man, are scarce. Oystercatchers *Haematopus ostralegus* respond to fluctuations in cockles *Cardium edule*, particularly the two-year age class (Sutherland 1982; Meire 1993). Knot *Calidris canutus* numbers reflect changes in *Macoma balthica* abundance in autumn (Zwarts, Bloment & Wanink 1992). Yet few other waders have been shown to respond to annual differences in food supplies. The scarcity of evidence could simply arise from a lack of suitable data for testing purposes or, although less likely, may reflect a genuine absence of effect. Further, the longevity of most waders and a tendency towards residency are likely to have a damping effect on population responses to changing conditions, making it correspondingly difficult to detect an interaction.

The aim of this study was to identify changes in wader populations which were related to food supplies. External factors are likely to affect the overall size of UK wader populations and hence those occurring on estuaries such as the Forth. The effects of wider population changes can be allowed for by comparing observed populations with winter population indices (Prys-Jones, Underhill & Waters 1994). In addition, regional weather factors, which might operate independently of conditions along the Flyway or across the UK as a whole, were considered. These may affect local food supplies between sampling and exploitation by shorebirds in early winter, influence availability of food, or encourage onward movements or mortality among waders. They may also be responsible for reducing food supplies in the year following. Disturbance may originate from shooting, recreation, agriculture, industry or predators (Furness 1973; Davidson & Rothwell 1993; Burger 1994), but since none was considered to have had a substantial effect on shorebird feeding throughout the estuary (Bryant 1979), as on other estuaries (Owen 1993; Kirby, Clee & Seager 1993), the matter is not considered in detail. Species may also interact, so population changes in one species could affect others (Myers 1984). Distinguishing between interspecific competition and contrasting but independent responses to changing conditions is often impossible. We nevertheless briefly explore this possibility but accept that competition could occur but go undetected. Competition between fish populations and estuarine birds is a particularly intractable example of competition for estuarine resources which defies simple analysis (Summers 1980; Furness *et al.* 1986). When wintering shorebird populations increase, areas previously avoided may be used. Density dependency of site-usage of this type (Zwarts 1981) means that less favoured sites can show changes in numbers when populations rise, while numbers on preferred sites remain stable (Moser 1988). Analysis of changes at any site, therefore, could merely reflect changes due to remote causes among the wider population and lack a local component. It is therefore necessary to show the extent to which Kinneil and Skinflats, the two sites considered here in detail, show evidence of proportionate changes in use as a result of population fluctuations on the Forth as a whole. This assumes that the scale at which wader densities are relevant is that of the estuary as a whole. Land claim can leave food densities largely unaffected on remaining mudflats, but will normally influence the total supply, and so could influence wader populations (McLusky *et al.* 1992). Effects of changes in water quality or effluent discharges, however, were not considered, since it is known that these were reflected in changes in food supply (McLusky & McCrory 1989). Palatability of food items is assumed to remain unchanged.

Finally, a familiar caution is offered; that experimental confirmation of cause and effect is desirable, even though immensely difficult to engineer at the scale of the estuarine mudflat. Nevertheless, the application of fertiliser to Forth mudflat plots led to short-term local increases of both invertebrates and waders relative to controls (Gillon 1992), so we can be sure that on the timescale of a single winter birds are indeed able to respond locally to changes in food density. It therefore follows that the changes in food supplies detected in autumn, prior to the arrival of wintering populations, could lead to changes in wader numbers.

Methods

Invertebrate abundance

The study area is described by McLusky (1987) and Bryant (1989). It lies to the west of the Forth Bridges at Queensferry within the Forth Estuary. Detailed studies of invertebrates and waders were focused at two intertidal mudflats, Kinneil (6.5 km^2) and Skinflats (3.7 km^2), lying respectively to the east and NW of Grangemouth Docks. Invertebrate sampling methods at Kinneil are described by McLusky & McCrory (1989). In brief, they consisted of collecting 25 cm^2 mud samples to a depth of 5 cm (n = 100 per annum) in August along 10 transects covering the entire mudflat area during 1976-94. All mud samples were passed through a 0.25 mm sieve to obtain invertebrates for counting. Sampling at Skinflats was also carried out each autumn, during 1975-92 (July-September, once in early October), along 4-5 transects spread evenly across the mudflats. Mud samples were collected (n = 18-31 per annum) in 625 cm^2 quadrats to a depth of 15 cm and sieved through a 1 mm sieve (N. Shillabeer unpubl.). The results presented here refer to the mean density of invertebrate species across all samples from each site. The differences in sieve mesh and sample size between Kinneil and Skinflats makes detailed comparisons inappropriate but allow assessments of mean annual changes within each site.

Wader populations

Co-ordinated counts of wildfowl and waders have been carried out on the Forth Estuary since the winter of 1969/70 in association with the Wetlands Bird Survey (WeBS; formerly Birds of Estuaries Enquiry, BOEE, Prater 1981). Over the early years of the survey, however, counts were sometimes incomplete, especially for species which were dispersed across many roost sites. Accordingly, this analysis is based on counts from the winter of 1973/74 (hereafter called 1974) onwards, by which time full and regular coverage was established, which continues to the present. Specifically, wader population estimates were compiled from counts to the west of a line from Rosyth Dockyard to Blackness Castle. Counts began on the rising tide and finished around high water. They therefore included birds present during the later flow-tide feeding period, the majority of which are known from other studies (Bryant 1979) to feed within each site during the low-tide period. Previous studies of shorebirds at Kinneil and Skinflats in particular, as well as on the Forth more generally, have recorded various measures of feeding effort on a site by site basis: mean bird-feeding hours per tide cycle, mean number of birds per tide cycle, mean and peak winter counts, and bird-months per annum (Bryant 1979). Since they were significantly intercorrelated, the peak winter count was adopted as a measure of population size because it was available for both main sites and for all years and species, yet at the same time was correlated with more comprehensive measures of feeding usage. Most wintering wader populations reached their peaks during mid-winter; between December and February (Bryant 1979); these months were therefore used in this study to obtain the peak winter count for each species. Detailed analysis is restricted to the seven commonest species, all of which depend largely on the intertidal habitat. Species which occurred in small numbers, or which fed extensively inland, are considered only briefly.

Environmental factors

Weather conditions during winter were summarised using an 'coldness' index for the Scottish mainland (Harrison & Harrison 1991). Land claim occurred at Kinneil but not at Skinflats. Small-scale losses of inshore mudflats to waste dumping was continuous at Kinneil throughout the early years of the study (Bryant, Hudson & Newton 1990). In 1978 a bund partially enclosing an area of mudflats was extended, greatly restricting tidal access. It led to the drying out of a particularly large intertidal area. Losses to land claim before 1979 comprised about 9% of the intertidal area available at Kinneil during the early 1970s (Bryant, Hudson & Newton 1990). For the purpose of this analysis, therefore, 1979 is treated as the start of a period when the impact of land claim might be evident. Hence 1974-78 is taken as 'pre' land claim and 1979-94 as 'post' land claim. An index of abundance of wintering waders is described by Prys-Jones, Underhill & Waters (1994). Competition between species was inferred from negative correlations between counts. To minimise the risk of associations arising by chance a probability threshold of $p<0.01$ was adopted. No formal data on human disturbance levels were available. Several activities which impinge on shorebirds were nevertheless evident. Shooting occurred at both study sites, but was generally at a low level and was not known to change in intensity during the study. Movements of people and machinery associated with land claim and waste disposal affected Kinneil, and to a much lesser extent, Skinflats, but were remote from both the feeding birds on the extensive mudflats and from the roosts and did not have obvious effects. Shipping moved nearby, but was ignored by birds. Overall, therefore, disturbance was considered to have no substantial effect on the numbers of birds visiting the estuary, although it could have affected local distributions of roosting birds (Bryant 1979).

Wader diets

The diets of most species included in this study, and for all those considered in detail, have been established using a range of methods, including direct observation, and pellet and gut analysis. These results have been summarised by Bryant (1979) and are reported in detail by Warnes (1981) and Warnes, Bryant & Waugh (1982). Correlations between food abundance and wader numbers imply interdependence only if the invertebrate is known from these studies, or occasionally other studies when local data are not available, to be likely to occur in the diet.

Results

Numbers of waders on the Forth Estuary

The peak number of wintering waders (all species combined) on the Forth Estuary declined soon after the start of the study in 1974. The decline continued until the mid-1980s; after which numbers started to increase (Figure 1). Kinneil and Skinflats, the largest mudflats on the estuary, usually held the bulk of the waders and experienced similar changes.

Knot and dunlin *Calidris alpina* declined over the study period (Table 1). Their numbers fell at both Kinneil and Skinflats and, since they were the commonest wader species, this largely explained the decline in overall wader numbers on the Forth. A recent partial recovery by these two species (Figure 2) has led to a corresponding rise in overall numbers on the estuary (Figure 1). Oystercatcher, grey plover *Pluvialis squatarola* and turnstone *Arenaria interpres* have shown continuing declines (Table 1) but since all occur at relatively low densities their impact on overall numbers was small. Black-tailed godwit *Limosa limosa* is the only species to show a significant increase on the Forth throughout the study period, mainly owing to the increase at Kinneil, where numbers of bar-tailed godwit *Limosa lapponica* and redshank also rose (Table 1). Lapwing showed a significant increase at Kinneil (Table 1) but since they are heavily dependent on conditions inland, and no increase was found at Skinflats, they are not examined further.

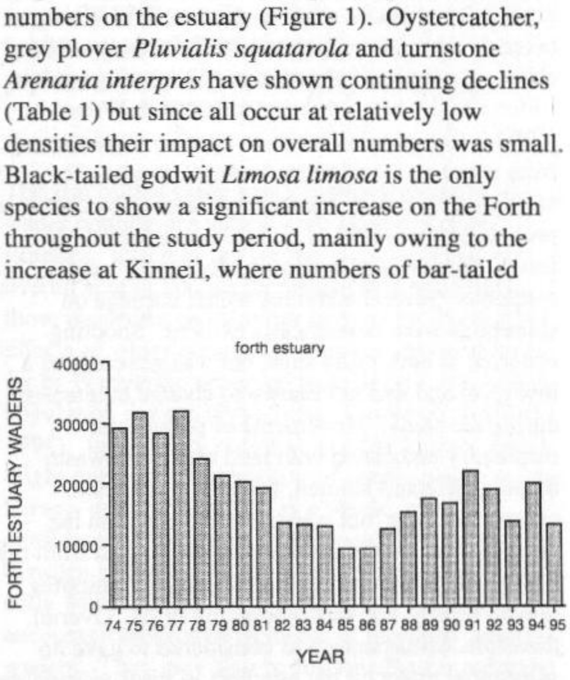

Figure 1. Peak numbers of wintering waders on the Forth Estuary during the period 1973/74 (74) to 1994/95 (95).

Forth waders in relation to national wader population indices

Three wader species on the estuary as a whole showed highly significant positive correlations ($p<0.01$) with national winter abundance indices: curlew *Numenius arquata*, dunlin and redshank (Table 2). Similar results emerged for Kinneil alone, again with three species involved (Table 2), although black-tailed godwit replaced curlew. The dunlin, however, was apparently also affected by land claim at Kinneil, hence if the data are split into 'before' and 'after' land claim (see below), the significance of the population index is lost. In contrast, similar treatment for the black-tailed godwit, confirmed the index as the only significant factor (Figure 3). The third species apparently related to the indices, redshank, was also influenced by local food supplies, and potentially by land claim and so is considered further below. Of the waders wintering at Kinneil, therefore, only the black-tailed godwit appeared to be predominantly influenced by changes in the UK population.

Positive correlations ($p<0.01$) between wader numbers at Skinflats and the national indices

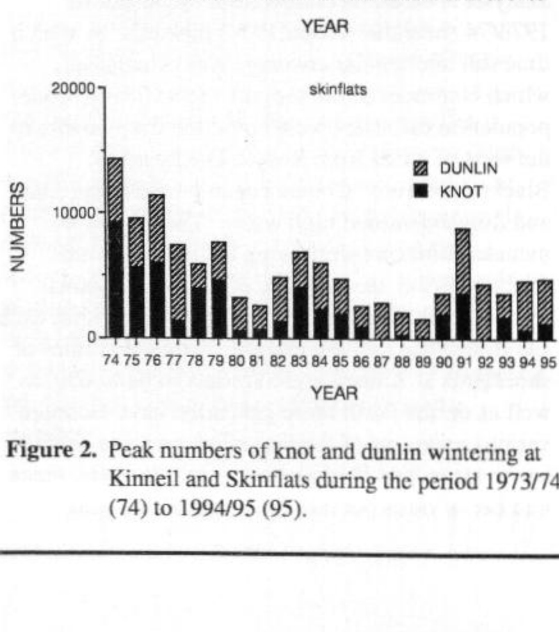

Figure 2. Peak numbers of knot and dunlin wintering at Kinneil and Skinflats during the period 1973/74 (74) to 1994/95 (95).

Table 1. Mean and maximum numbers of wintering waders on the Forth Estuary during 1973/74 to 1993/94. Correlation coefficients are given for annual peak numbers in relation to year (n = 21). Peak (all) includes all species, peak (estuary) excludes lapwing and golden plover. p<0.05 *, p<0.01 **.

	Forth Estuary				*Kinneil*				*Skinflats*			
	Mean n	*Max n*	*r*	*p*	*Mean n*	*Max n*	*r*	*p*	*Mean n*	*Max n*	*r*	*p*
Peak (all)	19,172	31,890	-.60	**	8,095	16,707	-.48	*	7,847	17,028	-.57	**
Peak (estuary)	15,102	26,353	-.62	**	7,484	15,084	-.49	*	6,943	15,698	-.59	**
Oystercatcher	935	1,709	-.47	*	105	415	.08	NS	42	95	.50	*
Ringed plover	61	108	-.20	NS	5	23	-.18	NS	4	21	.23	NS
Golden plover	1,115	4,027	-.38	NS	211	1,500	-.52	*	222	700	-.04	NS
Grey plover	28	87	-.65	**	7	27	-.50	*	17	55	-.55	*
Lapwing	2,945	5,624	-.18	NS	377	1,006	.54	**	698	2,250	.04	NS
Knot	4,986	10,880	-.57	**	3,385	7,050	-.48	*	2,468	9,300	-.64	**
Dunlin	5,374	10,707	-.65	**	2,464	6,490	-.58	**	3,203	6,100	-.34	NS
Black-tailed godwit	10	68	.57	**	10	68	.67	**	1	6	-.42	NS
Bar-tailed godwit	335	493	-.16	NS	197	392	.62	**	10	42	.02	NS
Curlew	1,086	1,844	-.11	NS	322	532	.01	NS	250	512	-.01	NS
Redshank	2,170	3,039	.02	NS	906	1,406	.62	**	984	1,550	-.25	NS
Turnstone	116	198	-.80	**	9	47	.10	NS	7	24	-.20	NS

Table 2. Pearson product moment correlation coefficients for wintering wader populations (peak winter counts, n = 20) in relation to national abundance indices. p<0.05 *, p<0.01 **.

	Forth Estuary	*Kinneil*	*Skinflats*
Oystercatcher	NS	NS	NS
Ringed plover	NS	NS	0.48*
Golden plover	No abundance indices available		
Grey plover	-0.53**	NS	-0.52*
Lapwing	No abundance indices available		
Knot	NS	NS	NS
Dunlin	0.85**	0.75**	0.76**
Black-tailed godwit	0.52*	0.60**	NS
Bar-tailed godwit	NS	NS	NS
Curlew	0.69**	NS	0.61**
Redshank	0.74**	0.67**	NS
Turnstone	-0.55*	NS	NS

involved dunlin and curlew, with ringed plover *Charadrius hiaticula* significant at p<0.05. Too few ringed plovers were present to provide a robust test (Table 1), however, and are therefore discussed no further. Numbers of dunlin and curlew reflected the national indices but no other factors, suggesting that conditions away from the Forth affected wintering populations and were mainly responsible for the observed changes at Skinflats (Figure 4).

The rise in national populations of grey plovers *Pluvialis squatarola* has been accompanied by a decline on the Forth, particularly at Skinflats where most usually occur (Table 1). Since numbers wintering on the Forth were relatively few, however, and the trend achieved significance at only the 5% level. This anomalous pattern, also seen among turnstone on the Forth as a whole (Table 2), is considered no further.

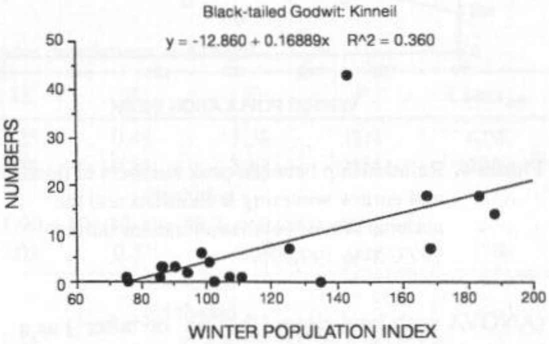

Figure 3. Relationship between peak numbers of black-tailed godwit wintering at Kinneil and the national winter population indices during 1973/74 to 1992/93.

Winter coldness: effects on waders

The winter coldness index during the same or previous winter was not significantly correlated (p<0.01) with wader numbers, either for the Forth Estuary as a whole, or for Kinneil or Skinflats individually.

Land claim at Kinneil: effects on waders

Four species differed significantly in numbers before and after the land claim and engineering works at Kinneil in 1978. Both knot (ANOVA F = 12.0, p = 0.002, df = 20) and dunlin declined while black-tailed godwit and redshank increased. To investigate the independent effect of land claim, however, it was necessary to allow for wider population changes of species showing significant changes during the study period by using the national indices of wader abundance (Table 2). This confirmed that dunlin populations fell at Kinneil following land claim, even allowing for national abundance changes

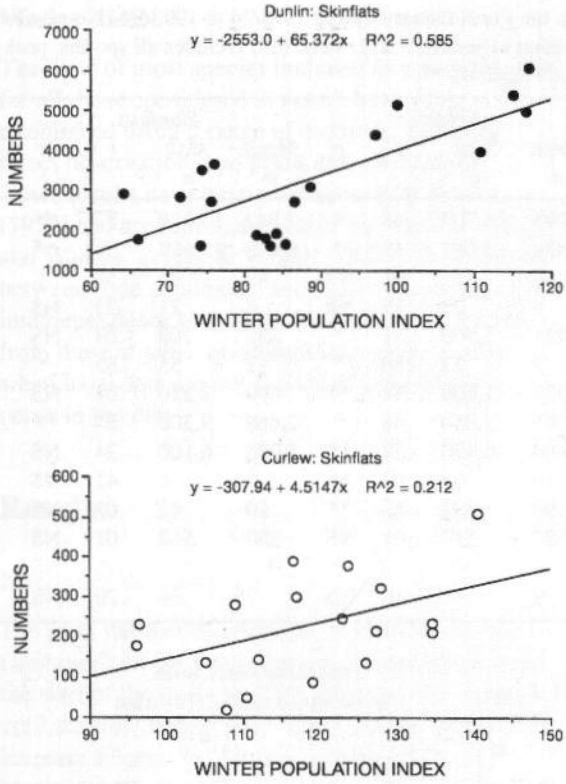

Figure 4. Relationship between peak numbers of dunlin and curlew wintering at Skinflats and the national winter population indices during 1973/74 to 1992/93.

(ANOVA with land claim ('before' or 'after') as a factor and the dunlin index entered as a covariate: Year effect F = 35.6, $p<0.001$, df = 17). On the other hand, black-tailed godwit and redshank showed no significant effect due to land claim, with numbers being related to national changes (Table 2). This analysis suggests that of the four species, only knot and dunlin may have been affected negatively by the loss of mudflats in an area they used extensively for feeding.

Other factors: effects on waders

Wader densities on mudflats may be subject to density-dependent effects. Typically, waders might use less-preferred sites more when estuary populations increase, while densities on preferred sites remain constant. Hence, the proportions of each species occurring at Kinneil and Skinflats were examined in relation to overall estuary populations. Neither at Kinneil or Skinflats, however, did the proportion of any wader population change significantly with overall population size.

Correlations amongst shorebird species revealed a wide variety of possible interactions. While positive associations are most simply interpreted as a common response to other factors, negative associations could imply an effect of one species on another. In no case, however, did highly significant negative correlations ($p<0.01$) emerge between two wader species, suggesting that such relationships, even if present, were at most weak.

Data on avian predators have been gathered on a casual basis throughout the study period. Five species were observed in small numbers in every year (sparrowhawk *Accipiter nisus*, peregrine *Falco peregrinus*, merlin *Falco columbarius*, kestrel *Falco tinnunculus*, short-eared owl *Asio flammea*). Since the number of predators fluctuated within narrow limits (0-2 of each species observed per visit), however, they seem unlikely to have caused the major changes among waders observed here.

Wader populations and invertebrate densities at Kinneil

Invertebrate samples from Kinneil were dominated numerically by annelids, particularly *Manayunkia aestuarina* and oligochaetes. *Hydrobia* and *Corophium* were recorded at the highest densities at Skinflats (Table 3), where coarser sieves were used. Correlation coefficients, considering only those cases where $p<0.01$, showed *Nepthys hombergi*, *Corophium*, *Eteone* and *Mytilus edulis* to be related to wader abundances at Kinneil. Bar-tailed godwit was positively correlated with both *Nepthys* ($r = 0.61$, $p<0.01$) and *Eteone* ($r = 0.71$, $p<0.01$). Numbers of redshank ($r = 0.70$, $p<0.01$) and black-tailed godwit ($r = 0.66$, $p<0.01$) were correlated with *Corophium*, and black-tailed godwit with *Mytilus* ($r = 0.80$, $p<0.01$). Controlling for the effect of population size using the wader index in a multiple regression analysis, however, left only two significant correlations, that between redshank and *Corophium* (Figure 5) and for bar-tailed godwits with two polychaete species (see above, Figure 5) and 'worms' (Table 4). For the black-tailed godwit, therefore, it is assumed that the correlations with *Mytilus* and *Corophium* did not signify cause and effect; which was anyway unlikely since neither is usual in the godwit's diet. An effect of land claim on redshank did not appear to be important (see above). For Kinneil, therefore, it appears that the increase in *Corophium* over the past two decades, in combination with the rising national index, has encouraged the marked increase in redshank at the site (Table 4).

Wader populations and invertebrate densities at Skinflats

Knot and dunlin showed highly significant ($p<0.01$) correlations with the density of *Hydrobia* (knot $r = 0.62$, $p<0.01$, Figure 6; dunlin $r = 0.65$, $p<0.01$). Dunlin were also positively correlated with

Table 3. Densities of invertebrates (n m^{-2}) in the Forth Estuary study area. Different sampling methods were used at each site (see text).

	Kinneil		Skinflats	
	x	*± SD*	*x*	*± SD*
Hydrobia ulvae	6,052	3,303	2,377	1,272
Littorina littorea	8	19	0	-
Macoma balthica	340	180	303	202
Cardium edule	141	151	39	86
Mytilus edulis	20	46	0	-
Mya arenaria	0	-	8	6
Nereis diversicolor	611	275	131	71
Nephthys hombergi	262	372	22	13
Eteone longa	257	234	20	24
Manayunkia aestuarina	36,461	29,503	19	54
Oligochaetes	26,046	9,516	455	371
Spionids	1,466	1,780	0	-
Corophium volutator	842	924	891	562
All invertebrates	72,508	38,767	4,465	1,363
All worms	1,131	583	173	81
All molluscs	501	276	550	241
n	18		18	

Table 4. Stepwise multiple regression analysis of wintering wader populations at Kinneil.

	Variable	$b_{partial}$	*± SE*	*β*	*T*	*P*	$Cum.r_{adj}$
Redshank	Index	10.98	3.25	0.49	3.38	.008	61%
	Corophium	0.17	0.05	0.51	3.51	.004	78%
	Year				Excluded		
	Constant		-311.90 ± 304.40, F = 29.2, p<0.0001, df_2 = 14				
Bar-tailed godwit	Worms	0.15	0.03	0.77	4.67	.003	57%
	Index				Excluded		
	Year				Excluded		
	Constant	27.71	42.18		F = 21.8, p<0.003, df_2 = 15		

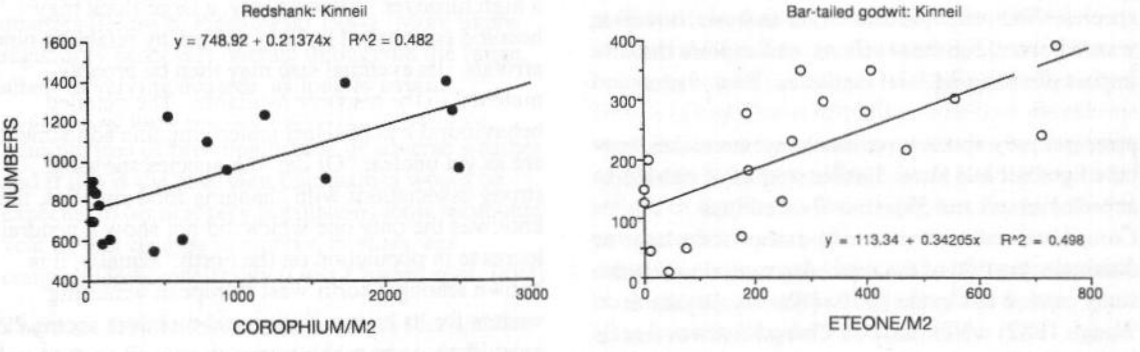

Figure 5. Relationship between (a) peak numbers of wintering redshank and *Corophium* density and (b) peak numbers of wintering bar-tailed godwit and *Eteone* density at Kinneil during 1976/67 to 1994/95.

'worm' density (r = 0.69, p<0.01). In addition, oystercatchers were correlated with *Cardium* density, although they showed a marked curvilinearity in their response (Figure 6). When these correlations were explored further, using multiple regression analysis and entering national abundance indices, knot continued to demonstrate a significant response to *Hydrobia*, whereas among dunlin, only the national index remained as significant. This suggests that use of Skinflats by knot and oystercatcher depended on the abundance of one of their principal foods (Figure 6), but that changes in dunlin numbers largely reflected changes in the national population (Figure 4).

Discussion

The study showed that wintering wader populations on the Forth Estuary fluctuated in association with a

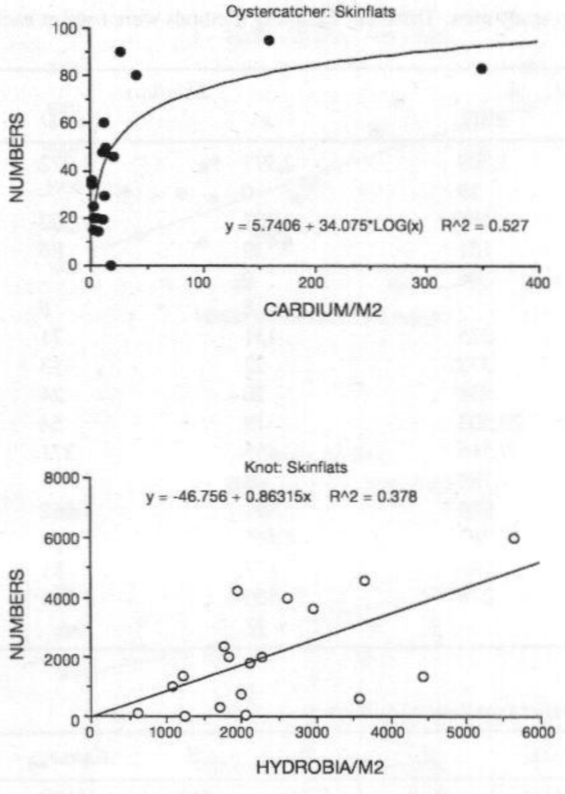

Figure 6. Relationship between (a) peak numbers of wintering oystercatcher and *Cardium* density and (b) peak numbers of wintering knot and *Hydrobia* density at Skinflats during 1975/76 to 1992/93.

variety of factors. National population sizes and land claim had significant effects on one or more species. The principal aim of the analysis, however, was to control for these effects, and explore the impact of changing food densities. Four wader species showed annual fluctuations linked to a principal prey species: redshank, oystercatcher, bar-tailed godwit and knot. Earlier studies of redshank at both Kinneil and Skinflats showed that *Corophium volutator* generally comprised a large or dominant fraction of the diet. An exception was a study carried out in the 1970s (Warnes, Bryant & Waugh 1982) which showed *Corophium* was scarce in diets at Kinneil, and so it seems likely that the increase in redshank at Kinneil was facilitated by, and increasingly dependent on, increases in *Corophium* since the 1970s. Support for this view also comes from a shift in the areas where redshank fed, away from the centre of Kinneil mudflats (Bryant 1979) to the areas where *Corophium* are now commonest in the vicinity of freshwater inflows (McLusky 1994). Bar-tailed godwits generally rely on burrowing annelids (Smith & Evans 1973). The rise in numbers at Kinneil was particularly associated with the spread of *Eteone* on the outer mudflats (McLusky 1994), where the godwits mainly fed (Bryant 1979).

The response of oystercatchers at Skinflats to a rise in the density of cockles, the main prey in the study area (Warnes 1981), closely mirrored results from other studies, which involved bivalves *Cardium*, *Mytilus* or *Macoma* as prey (Sutherland 1982; Meire 1993; Bryant 1979). In all cases, oystercatcher numbers rose sharply when their prey showed moderate increases but reached an asymptote at higher prey densities, probably because of interference between feeding oystercatchers (Goss-Custard *et al.* 1994). In contrast, knot did not show such a decelerating response to changing prey numbers. *Hydrobia*, along with *Macoma*, form the dominant prey of knot at Skinflats and elsewhere on the Forth (Warnes 1981). Knot visited Skinflats in increasing numbers at higher *Hydrobia* densities. This pattern is analogous to Zwarts, Blomert & Wanink (1992) observations on knot feeding on *Macoma* on the Waddensee, although they interpreted the response as sigmoidal and not linear. Neither dataset, however, was adequate for specifying a definitive response model, although a sigmoidal form would be consistent with spatial distribution patterns of knot in response to food supplies, both on the Forth (Bryant 1979) and the Waddensee (Zwarts, Blomert & Wanink 1992).

Winter movements of knot up the east coast of Britain perhaps reflect changing prey availabilities (Evans 1981; Davidson 1991), with accumulations occurring where harvestable prey (Zwarts, Blomert & Wanink 1992) are densest. Hence in years with few *Hydrobia* at Skinflats birds may pass through quickly, leading to peak numbers being depressed by a high turnover. Alternatively, a large flock may become established in early winter, by retaining new arrivals. Its eventual size may then be broadly matched to the resource available. The detailed behavioural mechanisms underlying this adjustment are as yet unclear. Of the four species showing strong associations with changing food supplies, the knot was the only one which did not show a general increase in population on the Forth. Equally, it is known amongst north-west European wintering waders for its high mobility, and therefore seems the most likely to be making annual, as well as seasonal and daily (Symonds, Langstow & Pienkowski 1984; Piersma 1994) choices of feeding site which reflect the abundance of favoured prey. This perhaps suggests there is likely to be a closer association between knot and their food supplies than would be found for species with greater site fidelity or residency during winter. Less vagile species would more often show time lags, both in upward and downward adjustments to changing food supplies, so loosening associations with food supplies.

While four waders showed correlations with food supply, the other species examined did not. In some cases an effect of food supply may have been overridden by land claim, national population changes or the undetected effects of other factors. Dunlin and the small population of black-tailed godwits, both experiencing large changes in abundance at the national level, may fall into this category. Redshank and bar-tailed godwits relied on 'annual' invertebrates, respectively *Corophium* and polychaetes, especially *Eteone* and *Nephthys*; the ages and therefore sizes of which will remain relatively constant from year to year. In contrast, some other waders depend more heavily on molluscs, which generally persist from year to year. For bivalves, sampling procedures were inadequate for closely monitoring changes in the abundance of the 'harvestable' component of food stocks (Zwarts, Blomert & Wanink 1992). Species which depended on these may therefore have failed to reveal a correlation because prey densities refer predominantly to young age classes. In the case of *Hydrobia*, however, size distributions are relatively constant from year to year (Warnes 1981), so variation in this respect should not bias sampled densities as measures of prey availability. The lack of an effect on oystercatchers at Kinneil in this study may have been because two-year-old cockles were infrequent in samples at the site (McLusky unpubl.). It is quite possible, however, that the more general scarcity of comparable results from other studies indicates that food effects are sometimes irrelevant to annual changes in wader numbers. oOne view is that breeding success determines numbers and that conditions in winter are non-regulatory; another is that drastic weather periodically depresses populations, and that no regulation occurs on winter quarters (Evans & Pienkowski 1984). More likely, regulatory processes operate throughout the range, albeit to varying degrees, as long as overall populations have not been severely reduced by hunting, loss of breeding habitat or adverse weather, and if this is the case then fluctuations would be expected to occur if prey populations show substantial year to year changes in number, biomass, age composition or availability (Goss-Custard *et al.* 1994).

There are further reasons why some wader species could fluctuate independently of changes in their measured food supply, even when external factors are eliminated:

1. Food may not decline sufficiently to depress feeding rates.
2. Numerical changes in food density may be compensated by increases in prey size or energy density.
3. Waders may respond to more than one prey, either by being non-discriminatory, having a broad dietary niche, or by prey-switching in response to a decline.
4. Sampling, particularly of scarcer prey, may not reflect true abundance changes.
5. Mortality or dispersal in response to food changes may occur after the winter peak, and so pass undetected.
6. Wader populations may have been too small in some cases for the techniques used here to identify non-random events.
7. Adverse weather may have, by chance, caused onward movements in the same years as food increased, or *vice versa*.
8. Differences in weather between sampling and midwinter may have caused prey to vary in availability or quality, but not density.

Earlier studies have shown a negative effect of land claim on some waders at Torry Bay, also on the Forth (McLusky *et al.* 1990). This analysis, covering a longer period, provides further support for this view; with populations of knot and dunlin being significantly lower at Kinneil after engineering works than expected from changes in the national indices of abundance or food supplies. The negative effect is likely to have resulted from the reduction in area of mudflat, which since it was the last to flood may have been particularly valuable as a food source.

Long-term changes in wader populations in some cases tracked those of national populations. In particular, dunlin declined and rose again at both Kinneil and Skinflats in line with national trends. *Spartina* had only a trivial presence (a single record at Kinneil) in the study area and cannot have affected dunlin directly. In contrast, *Spartina* has been implicated in declines of dunlin elsewhere in Britain (Goss-Custard & Moser 1988). If dunlin were displaced from southern estuaries by the spread of *Spartina*, therefore, they clearly did not seek refuge on the Forth. This might anyway have been anticipated from indications that dunlin find estuaries on the north-east coast of Britain exposed, necessitating correspondingly large fat stores (Pienkowski, Lloyd & Minton 1979).

Boyd (1992) suggested that the numbers of knot wintering in Britain may be influenced by changes in weather on their breeding grounds, which particularly affected breeding success. The changes in the index of wintering abundance therefore reflect, at least in part, poor arctic summers. Is this compatible with the finding of this study, that wintering knot populations responded to food supply? The observations are easily reconciled, since there was no correspondence between the winter index and numbers on the Forth as a whole or at the two study sites. Hence, Forth wintering populations of knot are variable, and are largely dependent on the abundance of *Hydrobia* (Piersma 1994). This factor, rather than the changes in the Flyway population, appears to be the main influence on numbers using Skinflats, and maybe the Forth Estuary more generally.

It is useful to question why national population changes may have affected waders at one of the study sites but not the other. Indeed, only dunlin showed evidence of an effect at all levels: the estuary, Kinneil and Skinflats (Table 1). Two explanations are available: in the case of black-tailed godwits, for example, only at Kinneil was an adequate population available for comparison with national indices. Of the species abundant on the Forth, redshank showed no relation to the national index at Skinflats, but did at Kinneil, perhaps because Skinflats is its preferred site on the Forth. Hence, wider population increases do not affect sites already close to capacity, but cause secondary sites to be used more intensively. While density-dependent site usage was not demonstrated in this study, such processes may be complex and require a more detailed analysis to reveal them.

This study of wader numbers at two large mudflats on the Forth Estuary has given evidence of annual changes in wader populations in winter being dependent on changes in food supply. While this result is not unexpected, there are currently very few studies, restricted to a handful of species, which demonstrate similar patterns. This may be explained by reasons which are both ecological (see above) and logistic. Sustaining long-term studies of food supplies is difficult, especially in maintaining constancy of methodology. This was achieved in this study through funding devoted to monitoring programmes which had pollution effects as their main focus. Long-term studies of birds are commoner, perhaps because the fieldwork is often carried out or assisted by amateurs, and therefore funding has only to be found for co-ordination purposes. It is to be hoped that a similar conjunction has led to comparable datasets being gathered elsewhere, since the annual trends identified here, while consistent with earlier studies of spatial distributions on the Forth, would benefit from replication at other study sites.

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Bird preferred areas in relation to proposed land claim in the Clyde Estuary

D.J. Curtis, J. Figures, J. Matthews & P. Tatner

Environmental impact studies are increasingly being made following proposals for changing the land use of an area. Estuarine habitats today are lost from a combination of large-scale industrial development of the upper shore and continual loss from many small land claims. Each removal of any area, no matter what size, reduces the total area available to the birds as feeding ground. Infilling of intertidal areas entirely destroys an area for shorebirds with new flats rarely being created elsewhere. Disturbance can reduce the attractiveness of a site to waders even though the habitat remains intact.

This work places land claim, or 'reclamation', within the context of the ecosystem of the Clyde Estuary and examines the potential impact of a proposed infill on populations of shorebirds, particularly redshank *Tringa totanus* and greenshank *Tringa nebularia*. A direct approach to predicting the potential re-distribution of birds following a proposed reclamation is presented, based on utilisation and preference indices. The latter provide a description of the estuarine mudflats in terms of areas preferred by the birds for feeding. Only a relatively small proportion of the estuarine flats on the Clyde are preferred for feeding by redshank, thus highlighting the relative sensitivity of sites in conservation terms.

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Estuarine mudflats - an important resource for conservation

Mudflats form the major part of the estuarine ecosystem supporting sometimes complex ecosystems with communities comprising crustaceans, worms and molluscs on which fish and many of the nationally and internationally important shorebirds feed (Smyth *et al.* 1974, 1977). Davidson *et al.* (1991) emphasise this in their review of British estuaries in which they give a good account of the richness and diversity of these systems and their conservation importance. Unfortunately, there are many human pressures on these resources: "tidal flats are vulnerable to progressive land claim, bait and shellfish collecting and the impacts of waste discharge and pollution" (Davidson *et al.* 1991). Estuarine birds can be highly mobile and depend on a network of sites or parts of sites during their annual cycles and their use of a particular estuary varies from bird to bird, species to species and from year to year. However there is accumulating evidence that individual birds appear to follow the same movement patterns year after year resulting in strong wintering site fidelity (see Davidson *et al.* 1991).

There are many factors that influence shorebirds in their competition for food in places to which they regularly return (e.g. Table 1 in Thompson, Curtis & Smyth 1986; Goss-Custard 1984, 1985; Goss-Custard *et al.* 1995) and it is possible that for some species many preferred wintering sites are at their capacity to support birds. Data on the total population sizes for British estuaries are available from the work of the Birds of Estuaries Enquiry (BoEE) in particular (Moser 1987). Loss of habitat at any one site in a network may threaten the survival of the birds using it since these birds will then be forced to try to find alternative feeding areas where they may possibly be at a competitive disadvantage with birds already regularly using and familiar with a site.

The loss and degradation of estuarine habitat tends to be piecemeal and cumulative. Migratory birds do not recognise our boundaries and all estuaries are part of a total, finite resource. Damaging one part can therefore jeopardise the functioning of much more. The Clyde Estuary is no different from many other estuaries in being impacted by a variety of human activities, among which is the threat of 'reclamation' of intertidal areas. Cumulative loss of small parts of the Clyde mudflats would eventually reduce its suitability as a winter resort for shorebirds and impair and eventually destroy its significant contribution to the ecological network of sites used by these migratory birds.

Environmental impact assessment procedures taking account of available background information for the Clyde Estuary (e.g. Curtis & Smyth 1982; Curtis 1997) should provide an objective approach for the consideration of this local situation. Scientists with a fundamental knowledge of estuarine processes plus detailed local knowledge have an important contribution to make for the future survival and management of estuaries. Provided that we adhere to sound scientific practices (Rosenberg *et al.* 1981), through the vehicle of environmental impact assessment (EIA) we can provide valuable guidance on the effects of estuarine development proposals at a local level. It is to be hoped that ultimately this type of work can influence government policy and lead to the implementation of appropriate national legislation which will safeguard 'sustainable development' of estuaries for the future benefit of all.

EIA methodology on the Clyde Estuary - birds know best?

An environmental impact assessment was commissioned by Inverclyde District Council, in accordance with the Environmental Assessment (Scotland) Regulations 1988, because of the juxtaposition of proposed land claim and development in an Enterprise Zone at Port Glasgow and the ornithologically important mudflats with statutorily protected status. This area is located at the western end of the Clyde intertidal flats (Figure 1(a)), of which large areas are designated in various ways: RSPB reserve, Site of Special Scientific Interest, proposed Ramsar Site, Proposed Special Protection Area under the EC Wild Birds Directive 79/409 (Stroud, Mudge & Pienkowski 1990). This EIA was based on intensive survey work carried out in 1990/1991, with some additional data from 1992 (Curtis & Figures 1992).

The proposed development involved reclamation of a bay at Woodhall, at the eastern end of the Port Glasgow urban area and adjacent to an existing promontory formed by an earlier reclamation. As part of the overall assessment by Inverclyde, we were required to report on likely impacts on the feeding of shorebirds, with particular reference to redshank *Tringa totanus*. Some attention was also given to numbers of greenshank *Tringa nebularia*, which is of importance locally. Redshank numbers, although having declined over the past two decades, were still high enough at around 2,000 birds for the whole estuary in winter to qualify as internationally important flocks, comprising more than 1% of the total international population of 109,000; the British population is of the order of 75,000 so that 69% of the international population use British sites (Stroud, Mudge & Pienkowski 1990). Greenshank numbers were very much lower, only of the order of 25, but this is out of a total British population of only 400 (Stroud, Mudge & Pienkowski 1990). Five other key species were also considered: black-headed gull *Larus ridibundus*, curlew *Numenius arquata*, dunlin *Calidris alpina*, lapwing *Vanellus vanellus* and oystercatcher *Haematopus ostralegus*, as well as all other species observed being noted (a total of 55). This necessitated survey work over the whole of the estuary, in order to address the question of displacement of the birds to other areas of estuarine mudflats. To account for seasonal variation detailed sampling was conducted over a full 12 months and the range of tides over which the birds fed were covered so that comparisons could be made of ebb, low and flow conditions.

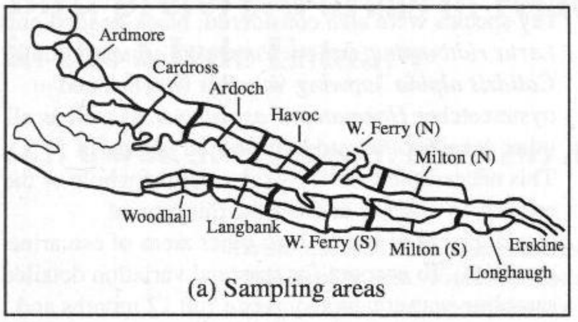
The estuarine flats were divided into ten areas, comprising 37 sample sites. The boundaries of these areas were delineated so that, on each survey occasion, sufficient observers were employed to count over all of these areas simultaneously. From west to east along the south shore, these areas were designated Woodhall, Langbank, West Ferry, Milton, Longhaugh and Erskine; the north shore areas were Ardmore, Cardross, Ardoch, Havoc, West Ferry and Milton, the last two areas including flats on both north and south shores. The remote parts of Pillar Bank and Cockle Bank were not included in the survey because of difficulties with making accurate visual observations.

The location of sampling sites is shown in Figure 1(a), while in Figures 1(b, c) an indication is given of the relative use made of the different sites by birds, in terms of the peak numbers recorded at any one time regardless of tidal hour, for all species combined. For the species of particular conservation interest, redshank, the relative feeding densities in terms of maximum numbers at any one time are shown in Figures 1(d, e).

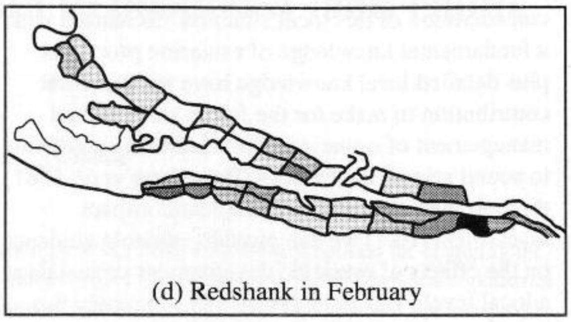
Predicting impacts using utilisation index values

Data were gathered for sediment conditions and the densities of invertebrate prey species (see Curtis 1997). However, rather than utilise relatively complex statistical predictive models, such as the multiple regressions used by Thompson *et al.* (1986) to describe patterns of association between birds and invertebrates, we employed a more direct approach based on Duncan's (1983) utilisation and preference indices (cf. used by Bignal, Curtis & Matthew (1988) for birds on Islay).

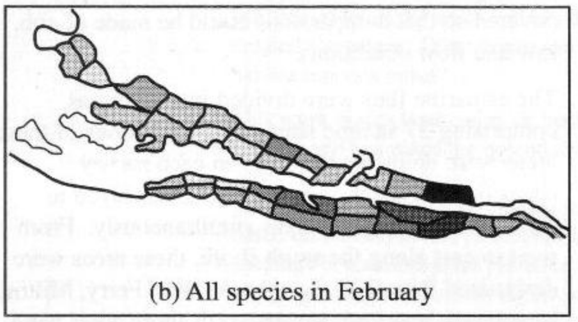
The un-normalised index of Duncan (1983) effectively represents a utilisation index (Ui) describing the proportional use of each site *i* on the flats for feeding by the birds. It is calculated as the number of birds feeding in a site divided by the total number of feeding birds recorded over the whole



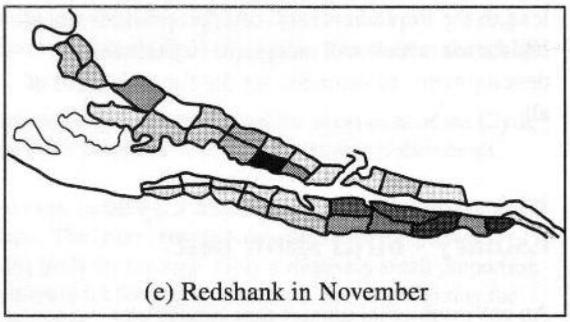
(a) Sampling areas



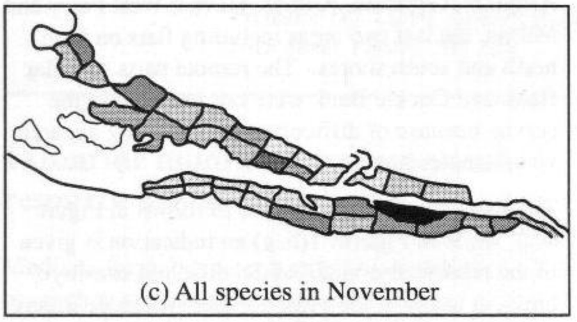
(d) Redshank in February



(b) All species in February



(e) Redshank in November



(c) All species in November

Figure 1. (a) Map of the Clyde Estuary showing the division of the mudflats into ten sampling areas and their subdivision into sites. The location of the proposed land claim is filled solid black, with the adjacent areas at Woodhall stippled dark grey. (b and c) Relative numbers of birds, in terms of the maximum recorded at any one time, with the highest count in solid black and other areas in relative shades of grey, for February (b) and November (c). (d and e) Relative numbers of redshank, in terms of the maximum recorded at any one time, with the highest count in solid black and other areas in relative shades of grey, for February (d) and November (e).

estuary at that time. While overall density of birds may be useful when comparing between estuaries, values of U_i facilitate the description of potential re-distributions of birds as well as comparative evaluations of sites within the estuary.

This index was used to describe the likely re-distribution of birds displaced from the proposed development site. The observed number of birds at the land claim site were allocated to the remaining areas in proportion to their U_i values, so that the more preferred areas are treated as attracting more of the displaced birds. The resulting bird feeding densities, derived by dividing the bird numbers by the sites' areas, could then be compared with previously described levels, including estimates based on roost counts (distributed over the estuarine sites according to their U_i values). In this way, a simple direct displacement model is used to describe the potential impact of loss of these feeding grounds to the birds; an example of the impact diagrams produced using redshank data, at low tide in February 1991, is shown in Figure 2. In the impact diagram, the observed distribution of the birds is represented in the form of a bar chart. On the assumption that birds displaced from an area could re-distribute themselves over the flats in accordance with the U_i values, and depending on whether a limited displacement (from the land claim site only, Woodhall D) is considered or a more diffuse disturbance of the birds (including areas adjacent to the land claim, i.e. Woodhall A, B, C and D), the resultant numbers are displayed as additional bars adjacent to the observed counts. For comparison, these bars are superimposed over a line plot showing the resultant of distributing roost counts over the estuarine flats according to U_i values. This provides a graphical illustration of the potential effect of displacing the birds by the land claim; there are marked increases at Erskine, Longhaugh and Milton.

Distribution patterns and preference index

The majority of the key species did not show random distribution over the 37 sites. Their

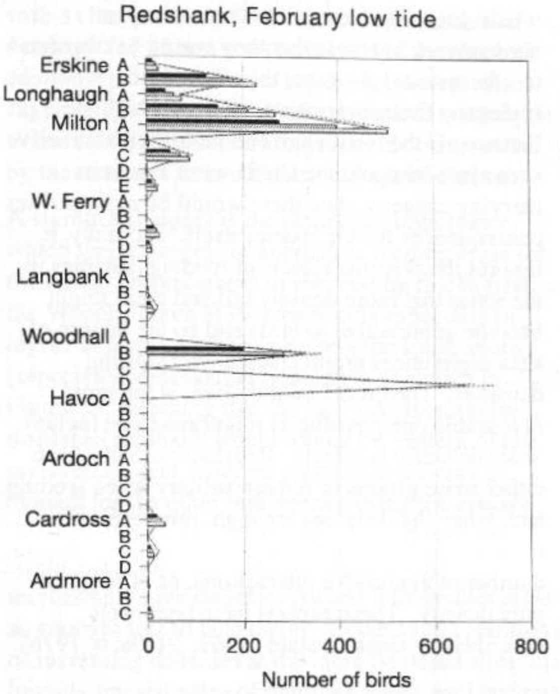


Figure 2. Impact diagram constructed using redshank data. For each site three bars are drawn: shortest (black) shows the observed number of birds, the intermediate (striped) shows the resultant number by the addition of birds displaced from the immediate reclamation site, and the longest (light stippled) shows the result of birds displaced additionally from areas adjacent to the reclamation site. These effects are calculated using the U_i values for each site to give appropriate weighting reflecting the birds' distribution according to their initial preference for the different sites. Note the marked increase in birds at Erskine, Longhaugh and Milton. If these sites were also reclaimed, the overall impact on the birds would be very damaging. Solid and dashed lines show the pattern for distributing the number of birds counted on roosts by BoEE and the EIA respectively.

distributions varied over the tidal cycle and between months, but for all three tidal phases (ebb, low and flow) in both the February and November samples considered here, oystercatcher, redshank, dunlin, lapwing and black-headed gull were all significantly clumped according to the variance/mean ratio used as an index of dispersion and associated 2 values (all with $p<0.001$). Greenshank numbers were too low to permit this test, but were necessarily restricted in distribution, being mostly at Langbank, but also at Woodhall and a few occurrences on the north bank opposite. Only curlew failed to reach significance for the index of dispersion in November and the ebb tide in February, but were clumped during the low and flow tides in that month's sample ($p<0.001$).

An alternative approach is to quantify the birds' preference for sites. For each site *i*, the normalised preference index (P_i) of Duncan (1983) was calculated as: $P_i = \log_{10}((U_i / A_i) + 1)$, where A_i is the proportional area of site *i* relative to that of the total intertidal flats. If the use of a site by feeding birds is simply in direct ratio to its relative area, the value in brackets equates to 2 and so $P_i = 0.303$. Any value of P_i greater than 0.303 indicates that the birds were showing a positive preference for the site, higher values indicating greater attractiveness. Values below 0.303 suggest less than expected use of a site, i.e. possible avoidance or at least non-attractiveness. If all sites were equally attractive, the birds would distribute themselves randomly over the flats and the sites' P_i values would all vary randomly around the value of 0.303; if they were uniformly distributed, all P_i values would equal 0.303. Thus, we used P_i to describe the importance of the different areas of the flats for feeding birds. The results could then be represented graphically as bar charts. An example using redshank data is illustrated in Figure 3.

Translation of these P_i values for the different sites to their spatial distribution over the estuary gives a clear indication of those areas of the flats which are of importance to the birds, but it must be borne in mind that their distributions change with tide and

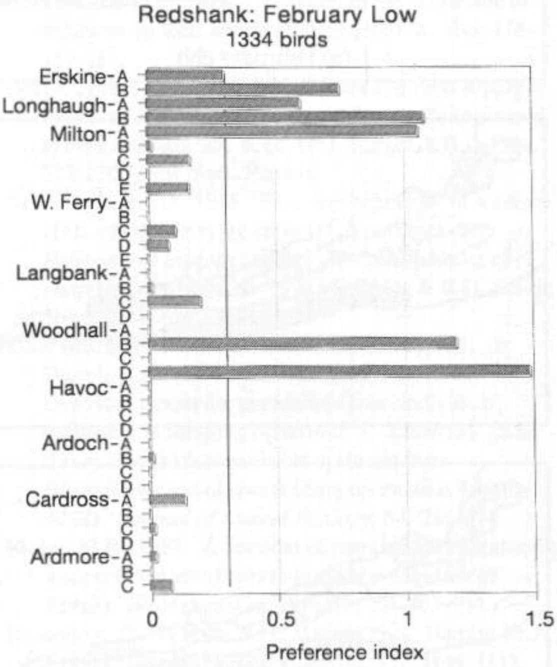
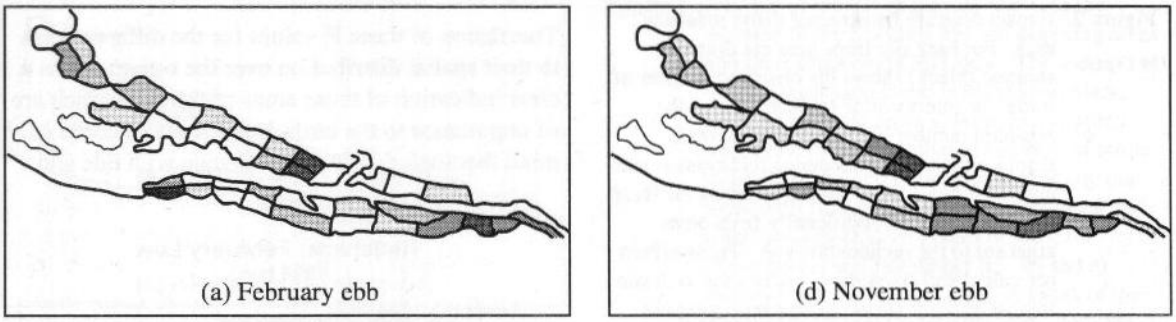


Figure 3. Bar chart showing preference index (Pi) values for redshank at the sampling sites over the Clyde Estuary mudflats in February 1991. Values of P_i greater than 0.303 (marked by the line on the bar chart) may be interpreted as indicative of preferential selection of that particular site by the species.

season. For redshank in 1991, these are shown in Figure 4, giving maps for the three tidal states (ebb, low and flow) and for two months (February and November). Inspection of these maps shows clearly how these patterns change between tides and between months, emphasising the importance of considering the whole estuary as an integrated system as the birds move around to use the food resources available to them to different degrees as availability of prey changes with tidal cover/exposure, weather conditions, proximity to roosts, seasonal variations, etc.

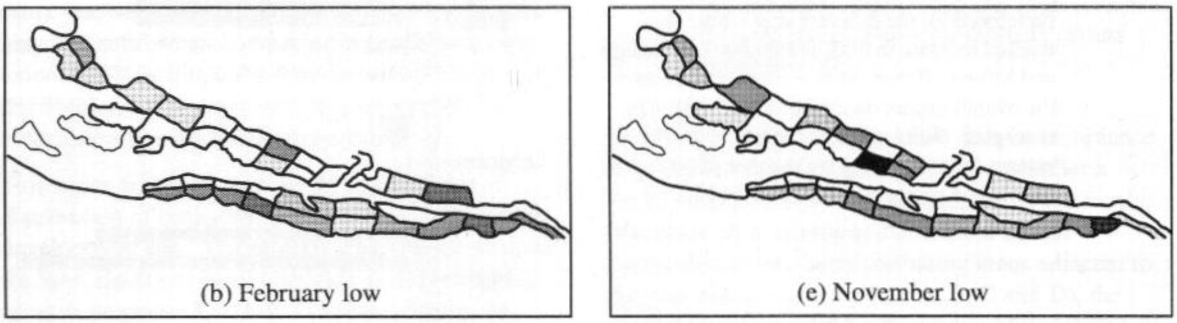
Conclusion

This approach gave a clear indication of the feeding distribution which could result from displacement of the birds if the proposed development were carried out, albeit subject to certain assumptions. Firstly, the model assumes that all of the displaced birds would pack themselves into this estuary; an alternative scenario is that they would be displaced to other coastal sites, but the effect of this would be to destroy the conservation value of the Clyde Estuary. If the birds were unable to find alternative sites elsewhere and the Clyde were also at its carrying capacity, then there would be more serious consequences for the species itself. Secondly, it ignores the possible effects of feeding densities in the sense that more densely utilised areas might become unattractive to birds and so the pattern of sites preferences might change with shifting densities. The model output, then, is the most favourable one possible as it ignores these higher-order deleterious effects. Redshank usually form either loose groups or remain solitary when feeding, and, when the densities are high, interference between birds may occur as a result of an increasing number of aggressive interactions, or of reduced prey density. These aspects have been well described by Goss-Custard (1969, 1970a, b, 1976)



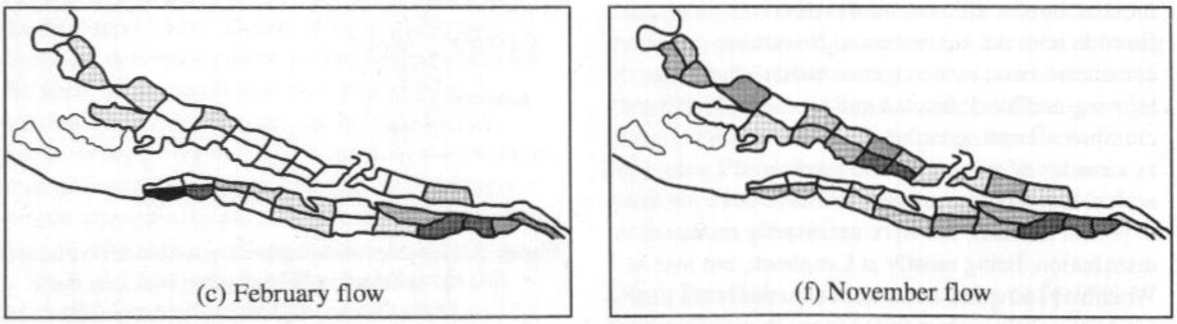
(a) February ebb

(d) November ebb



(b) February low

(e) November low



(c) February flow

(f) November flow

Figure 4. Maps showing the preferred sites for redshank feeding on the estuary in February and November 1991. Darker shading indicates higher preference, with the solid black area being most preferred and white areas unused by the birds. Note how the pattern varies between tides and between months.

with a clear indication that a greater proportion of redshank fed on less preferred areas of the shore as the density of birds on the estuary increased. This suggests that the tendency of redshank to congregate in the most profitable feeding areas is counteracted by the tendency to avoid areas of high bird density.

A significant aspect is the increasing importance which then emerges for alternative feeding areas for the birds. Displacement of the feeding flocks from the Woodhall area at Parklea results especially in higher densities farther east along the south shore (especially Milton and Longhaugh, as shown in Figure 2), assuming that the likely destination for displaced redshank would follow the pattern of site preferences, and different preference patterns are evident for the other bird species using the estuary. The behaviour of the birds, and their consequent feeding success, may well be impaired by increasingly high densities packed into smaller areas as sites are lost to land claim. Under such conditions of increasing densities at the more favoured sites, the initially unused areas of mudflats might well become used as alternative feeding areas by the birds and so land claims there could also have a deleterious effect. Similar arguments would apply to proposals for development at any site in the estuary used by birds. Such proposals might well be considered separately in isolation by different local authorities with their responsibilities for different areas of the estuary. A co-ordinated approach to the consideration of development proposals would be much better in conservation terms and help save the important bird feeding grounds of this estuary from the threat of a gradual erosion of its environmental quality and wildlife.

Acknowledgements

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The Eden Estuary: a review of its ecological and conservation interest, with particular reference to water quality

B.E. Clelland

Situated on the Fife coast, just north of St Andrews, Scotland, the Eden Estuary is a small but important coastal feature. It is one of a series of east coast sites which provide roosting and feeding areas for nationally important numbers of waders and wildfowl. The estuary is a Site of Special Scientific Interest and has been managed as a Local Nature Reserve since 1978. It continues to be used for wildfowling.

The principal features of the estuary are discussed together with the more significant external influences on its ecology. Reference is made to a number of published and unpublished works and this paper draws particularly on those which contribute to our understanding of major ecological influences, such as water quality, and of key communities, such as benthic invertebrates. Recent improvements in effluent treatment and the consequent reduction in pollution are discussed in this context.

At a time when estuaries generally are under threat from so many forms of human impact the Eden Estuary appears to suffer relatively little. Its protected status, sound management and fortuitous geography are helping it to retain its integrity as well as its interest.

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Introduction

The estuary of the River Eden is found on the north coast of Fife, Scotland, between St Andrews and the Firth of Tay (Figure 1). Despite its relatively small size (10 km^2) the estuary is of recognised significance for nature conservation. This paper draws on a number of published and unpublished works relating to the estuary, particularly those which contribute to our understanding of major ecological influences, such as water quality, and of key communities, such as benthic invertebrates. In doing so it is hoped to draw attention to some points of interest of the estuary and to its value as a natural resource.

Physical characteristics

Low tide exposes most of the Eden Estuary as mudflats (7.9 km^2) with the river occupying a single narrow channel, easily waded in many places. Intertidal sediments vary in texture from coarse sand near the estuary mouth to glutinous mud in some inner areas. Sediment movements within the estuary are mainly caused by tidal currents. The effect of wave action is limited owing to the sheltered form of the estuary and to its small size (McManus & Green 1977). Sediments are also stabilised by the entrapping effects of mussel beds and mats of filamentous algae (Eastwood 1977).

Under average flow conditions in the River Eden and the Motray Water the mixing index (the ratio of the volume of freshwater to the total volume of water entering the estuary during the period of flood tide) is 0.009. In river flood conditions the increased discharge of freshwater raises the mixing index to 0.12 (N.E.F.D.C. 1992). This contribution of freshwater is relatively low and at high tide the estuary is well mixed with a uniform salinity of 28‰. At low tide there is a gradient ranging from around 10‰ at Guardbridge to around 26‰ at the estuary mouth. The limit of tidal influence is found at Nydie Mill, some 3 km upstream of Guardbridge.

The sand spit at Out Head dominates the mouth of the estuary and intertidal sediments to seaward are also sandy. Sediment transport in this area has been studied in some detail (Jarvis & Riley 1987; Jarvis 1989). An important process is shown to be the formation of transverse sand bars or mega-ripples at the mouth, which disperse wave energy and shelter the estuary. Coble House Point and Coble Shore provide further protection for the inner mudflats.

Extensive dune systems flank both northern and southern shores of the estuary mouth and contribute significantly to its character. There is some concern over the erosion of the dunes at Out Head and subsequent collapse of the gabions which protect the margin of the golf course. Erosion of the saltmarsh to the south of the inner estuary may also be occurring. It is suspected that around 1 m of

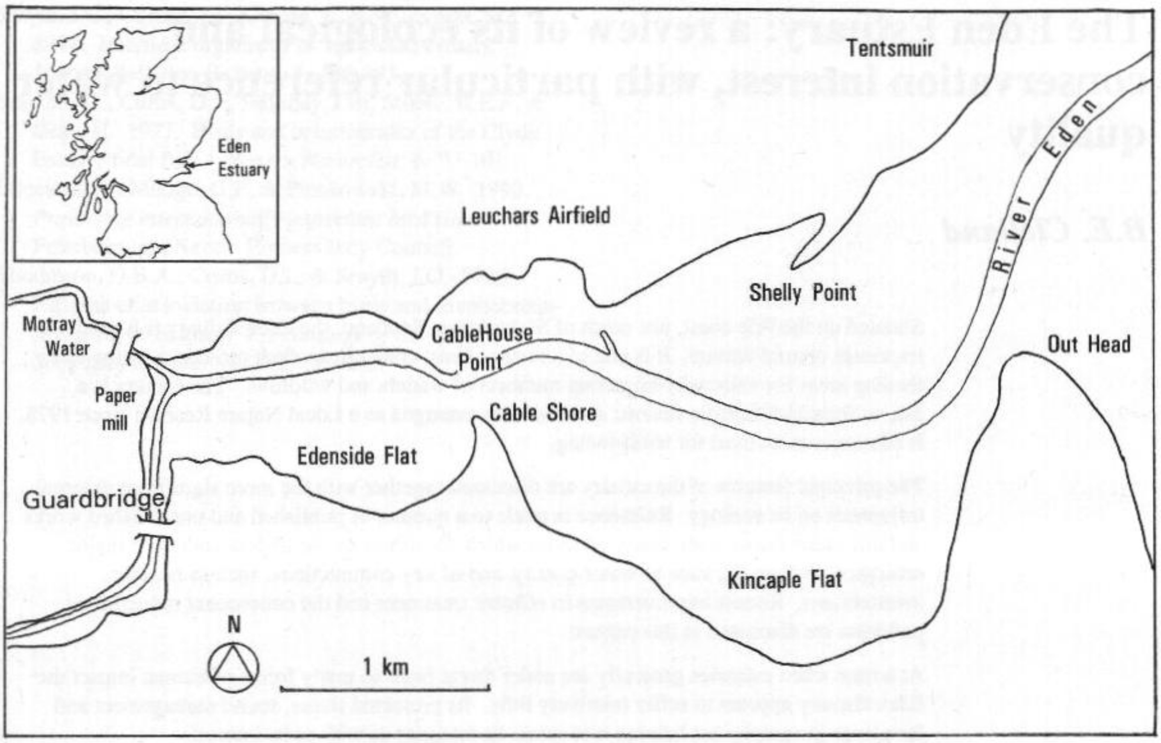

Figure 1. Location and major features of the Eden Estuary.

saltmarsh has been lost since 1976 (L. Hatton pers. comm.).

Water chemistry and pollution

Improved waste water treatment facilities in the River Eden catchment have resulted in a generally high quality of river water being discharged to the estuary. Using the water quality classification scheme based on chemistry and adopted by the Scottish Office Environment Department (1990) for National Water Quality Surveys, the river is considered by the Tay River Purification Board to be Class 1 - "unpolluted or recovered from pollution" (Tay RPB Annual Reports). However, there remains some concern over pollution from diffuse agricultural sources, notably the elevated concentrations of nitrogen in both surface and groundwaters, which are approaching the 50 mg l^{-1} EC limit at a borehole supply at Balmalcolm, Fife (Tay River Purification Board 1994). Nitrogen loading to the estuary comes principally from agricultural run-off. Tay RPB data for concentrations of total oxidised nitrogen at Kemback, just 2 km upstream of the tidal limit, suggest an upward trend over the past 15 years (Figure 2). MacDonald *et al.* (in press) report similar results for the Ythan catchment and relate their findings to the increased use of nitrogenous fertilisers for winter cereal crops.

A urea-based de-icing compound is sometimes used at Leuchars airfield. The contribution from this source to nitrogen loading of the estuary is not known but given its seasonality it is unlikely to be significant.

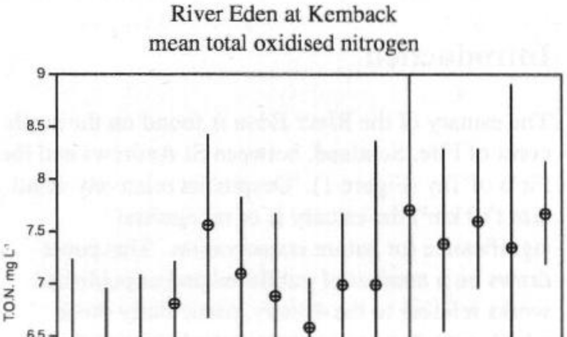

Figure 2. Annual mean concentrations of total oxidised nitrogen in the River Eden at Kemback (vertical bars show standard deviations, n = 10-15 each year).

A conspicuous and major source of pollution to the estuary has been the paper mill at Guardbridge owned by GB Papers. Pressure from the Tay RPB resulted in the construction of a £2.5 million treatment plant, completed in 1992, which has dramatically improved the quality of the mill's

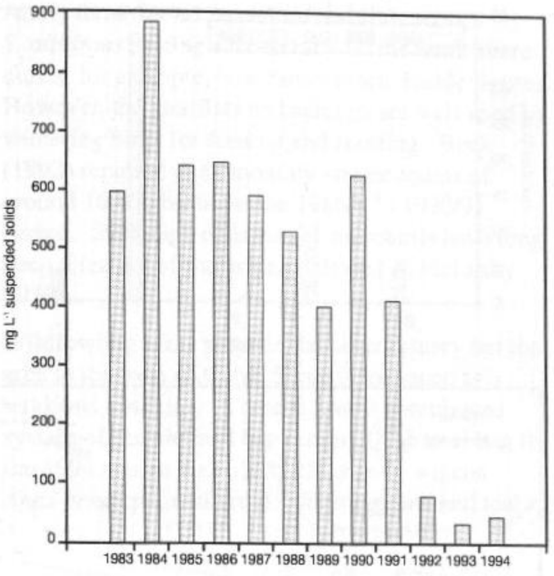

Figure 3. Annual mean concentrations of suspended solids in the effluent from Guardbridge paper mill.

effluent. Recovery of paper fibre has been particularly helpful in producing a reduction in discharges of suspended solids (Figure 3).

Treated sewage from Leuchars, Guardbridge and neighbouring villages is discharged to the inner estuary close to the paper mill and has aggravated the pollution problems there. Conditions are expected to improve, however, since a newly constructed sewage treatment works to serve Balmullo, Leuchars and Guardbridge was commissioned early in 1995 at a cost of around £1.5 million. This provides full biological treatment and is designed to better the standards set by the EC Urban Wastewater Treatment Directive (91/271/EEC) of 25 mg l^{-1} biochemical oxygen demand and 35 mg l^{-1} suspended solids.

As a consequence of sewage discharges, mussels in the estuary are contaminated with faecal coliform bacteria to the extent that in December 1992 they were classified under the terms of the EC Shellfish Hygiene Directive (91/492/EEC) as unfit to market for human consumption. This brought to an end the small-scale mussel harvesting which had taken place. It is not known if the recent improvements to sewage treatment facilities mentioned above have significantly reduced levels of contamination in mussel tissues. If so, a reclassification of the estuary as a shellfish harvesting area may follow.

There has clearly been substantial local investment in pollution control which was at least partly driven by the Tay RPB's objective of improving water quality in the Eden Estuary. Previously considered by Tay RPB to be a Class B estuary ('fair') using the estuary classification scheme adopted for National Water Quality Surveys (Scottish Office Environment Department 1990) the Eden Estuary is expected to rate as Class A - 'good' - in 1995. There is considerable interest in the consequences of these improvements, particularly for the estuarine flora and fauna.

Intertidal flora and fauna

The sheltered mudflats to the east of Coble Shore and Coble House Point typically develop extensive growths of green algae in summer. Further, less extensive areas to the west of Coble House Point are also affected. The algal mats are composed principally of *Enteromorpha intestinalis* with lesser amounts of *Ulva lactuca*. These green algae and the less conspicuous diatom populations which impart a yellow tinge to some areas of the Edenside mudflats have an important effect on sediment stability, greatly increasing its resistance to erosive stress (Paterson 1994). In contrast, the distribution of bladder wrack *Fucus vesiculosus* in the estuary appears to be severely restricted by the lack of anchorage points.

Patches of eelgrass *Zostera angustifolia* and *Z. noltii* are a notable botanical feature of the mudflats and there is concern over the possible smothering of these by mats of green algae. A baseline study by Caudwell & Jones (1994) found the maximum density of algal cover to be around 60%, to the east of Coble Shore, with a peak mean wet weight of 712 g m^{-2} (38.9 g m^{-2} dry wt). Their study indicated that algal biomass was around one third of that found in the Ythan Estuary, where similar mats have been shown to reduce population densities of mudshrimps *Corophium* spp. (Raffaelli *et al. 1*991). The Eden study also compared 1994 observations with 1988 aerial photographs and earlier descriptions, concluding that there was no evidence to suggest that the algal mats were a new phenomenon or that they have become significantly more extensive.

Enteromorpha growths have been shown to accumulate nitrogen from the waters which flow into the estuary. As the algae decay each winter heterotrophic and denitrifying bacteria proliferate and make the nitrogen available to other parts of the ecosystem (Christofi *et al.* 1979).

Saltmarsh vegetation communities are present along the shores of the estuary, notably at Edenside. There is a transition to freshwater plant communities in the inner reaches, to the west of Guardbridge. Cord grass *Spartina anglica* was introduced into the Eden Estuary in 1947 and is regarded as an invasive threat to the estuarine ecosystem. Despite a vigorous control campaign it has not proved possible to eradicate the species.

Ragworm *Nereis diversicolor* and mudshrimp *Corophium volutator* are abundant on the mudflats of the inner estuary with densities of around 1,000 m^{-2} and 8,000 m^{-2} respectively in some areas (Tay RPB 1992). Also significant are oligochaete worms with *Tubificoides benedeni* densities of several thousand per m^2. The laver spire snail *Hydrobia ulvae* is common and was found by Johnston, Cobb & Bell (1979) to exceed densities of 1,000 m^{-2} at some upper shore sites.

East of Coble House Point the more varied habitat and narrower salinity fluctuations accommodate a more diverse fauna. Common bivalves are the Baltic tellin *Macoma baltica*, cockle *Cerastoderma edule* and peppery furrow shell *Scrobicularia plana*. Commonly found polychaete worms are *Capitella capitata*, *N. diversicolor* and lugworm *Arenicola marina*. Lugworm densities of up to 59 per m^2 were recorded by Caudwell & Jones (1994). The mussel beds are particularly rich in invertebrate species.

Blewer (1993) surveyed the invertebrate fauna of Kincaple Flat to the east of Coble Shore and related his results to the earlier work of Johnston, Bell & Cobb (1978). The population density and range of *Corophium* were apparently reduced while *C. capitata* and *H. ulva* were more abundant. The limitations of the survey are acknowledged but a number of potentially fruitful lines of research are evident.

A Tay RPB survey of the inner mudflats in 1989 indicated that polluting discharges of sewage and paper mill effluent were responsible for a zone of largely anoxic mud along the north bank of the inner river channel (Tay RPB 1992). Invertebrate fauna was scarce or absent from a number of the sites sampled, with these indications of impoverished fauna extending for some 500 m seaward of the discharges. Follow-up surveys of the area in 1992, when paper mill effluent treatment improved and in 1994 indicated a recent influx of several species of invertebrates. The mudshrimp *C. volutator*, for example, is now common at sites where no invertebrates were recorded in 1989. Numbers per 10 cm diameter core (to 20 cm depth) are shown in Figure 4. This improvement is associated with the decreased evidence of anoxia and solid waste, and attributable to more effective waste water treatment.

Waders and wildfowl

The Eden Estuary is internationally important for its populations of wintering shelduck *Tadorna tadorna* and nationally important for several species of wintering wildfowl and waders, including black-tailed godwit *Limosa limosa*, grey plover *Pluvialis squatarola*, bar-tailed godwit *Limosa lapponica*, oystercatcher *Haematopus ostralegus* and redshank *Tringa totanus* (N.E.F.D.C. 1992). Roosts of pink-footed geese *Anser brachyrhynchus* and greylag geese *A. anser* in the estuary currently peak at around 4,000-5,000 birds each winter.

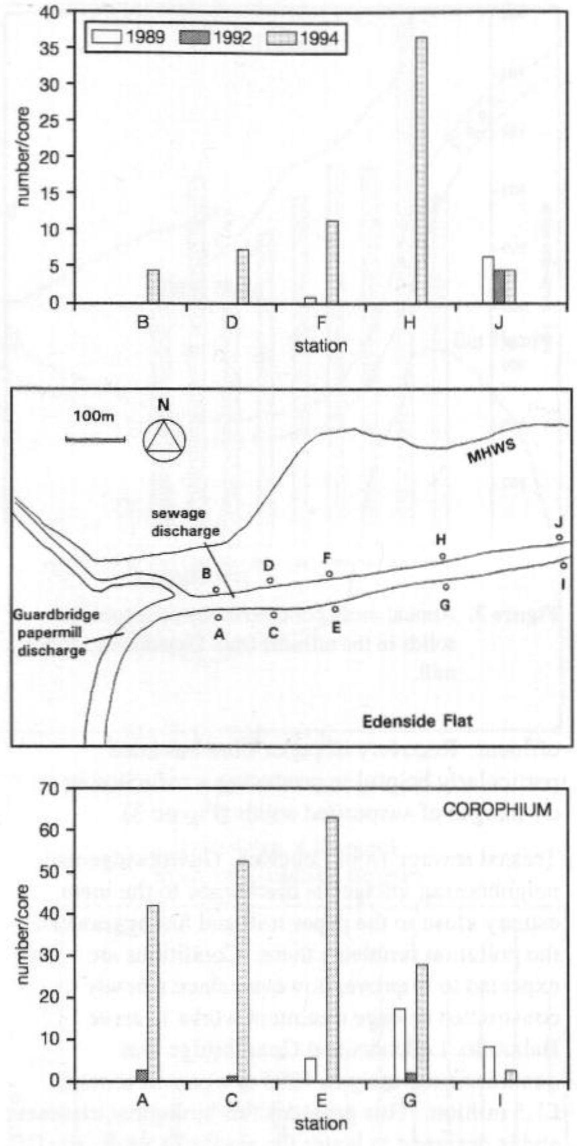

Figure 4. Survey records of *Corophium volutator* for the inner Eden Estuary.

Johnston, Cobb & Bell (1979) made detailed observations of shorebirds over one year with particular reference to feeding behaviour and the distribution of invertebrate food species. Complex patterns were apparent which showed how different species were able to optimise their feeding activities according to tidal state and available prey. Clear preferences were apparent implying that a change in invertebrate community would affect bird populations.

Suitable nesting areas are scarce around the estuary and suffer from human disturbance. The numbers of

Arctic terns *Sterna paradisea* and little terns *S. albifrons* nesting successfully on the north shore dunes, for example, now rarely reach double figures. However, the mudflats and saltings are well-used by wintering birds for feeding and roosting. Buck (1992) reported peak monthly winter counts of around 16,000 birds for the 1986/87 - 1990/91 period. Such high densities of shorebirds have long been a feature of the estuary (Bryant & McLusky 1976).

Wildfowling takes place in the outer estuary but the area to the west of Coble Shore is managed as a wildfowl sanctuary. There is a well coordinated system of permits and bag returns. The total bag for the 1994 season was 656 birds, mostly wigeon *Anas penelope*, mallard *A. platyrhynchos* and teal *A. crecca* (N.E.F.D.C. Annual Report 1994).

Conservation

The estuary was declared a Site of Special Scientific Interest in 1971 by the then Nature Conservancy Council, primarily in recognition of its ornithological importance. Key features of the site and its conservation interest are summarised by Buck (1992). In 1978 North East Fife District Council designated the Eden Estuary as a Local Nature Reserve (LNR) under the National Parks and Access to the Countryside Act 1949. The LNR management plan for the estuary (N.E.F.D.C. 1992) provides an excellent review of its history and natural history as well as a working document for those responsible for the reserve.

The estuary forms part of the Eden Estuary, Tentsmuir Point and Abertay Sands proposed Ramsar site under the Convention on wetlands of international importance, especially as waterfowl habitat. It is also a proposed Special Protection Area under the EC Directive on the Conservation of Wild Birds (79/409/EEC). This is an indication of its high national and international conservation status.

The landscape is visually less attractive than that of many other estuaries, dominated as it is by the Guardbridge paper mill and Leuchars airfield. Large numbers of ornithologists visit the estuary nonetheless and are rewarded by the variety and large numbers of passing and wintering waders and wildfowl.

Much of the impetus for original designation of the estuary as a reserve came from local wildfowlers and it has since proved possible to sustain traditional wildfowling activities without serious conflict with other interests. Wildfowlers continue to play an active part in reserve management and co-operate closely with the ranger service.

Access to the estuary is easiest from the West Sands at Out Head to the south and this helps to reduce disturbance in the inner mudflats. So too does the presence of the paper mill and Leuchars airfield, which together form an effective barrier along the northern shore. However, nesting areas to the north of the outer estuary are particularly vulnerable to mountain-bike and motorcycle riders who gain access at Kinshaldy, 3 km away. Co-operation with landowners and foresters is helping to restrict and control these sources of disturbance.

Discussion

Despite its small size the Eden Estuary is of great interest. The gradients of salinity and exposure produce a typically complex estuarine ecosystem with a mosaic of habitats. Its mudflats and mussel-beds support a rich and diverse benthic invertebrate fauna which in turn attracts significant wintering bird populations.

In addition to these obvious features there are other noteworthy processes in evidence. Pollution control of point source discharges is having a discernible effect on areas of the inner mudflats which were previously damaged. More subtle changes may be occurring in the outer mudflats. Here, as in many such estuaries, the sheltered mudflats and nutrient-rich waters appear to encourage the development of green algal mats. The ecological consequences of this and its implications for management of the estuary are both interesting and important. Experience in, for example, the Ythan Estuary suggests that excessive growths can be detrimental to populations of some invertebrates, notably *Corophium* (Raffaelli, Hull & Milne 1989, 1991). Lower densities of important prey species can be expected to reduce the numbers of birds which the estuary can sustain. Management of this problem appears to hinge on controlling the use of nitrate fertilisers in the arable farmland of the catchment (Pugh 1993). There is no obvious mechanism for achieving this unless, as proposed for the Ythan catchment, a Nitrate Sensitive Area were to be designated under the EC Nitrates Directive (91/676/EEC). This could not easily be justified for the Eden Estuary on present evidence, but there is clearly good reason to establish effective surveillance of both nutrient levels and algal productivity.

It is of interest that some of the apparently unfavourable features of the estuary work to its advantage. The low scenic value of the inner reaches which are dominated by the paper mill and military airfield undoubtedly helps to restrict numbers of visitors to those with a genuine interest for the estuary. Similarly, the high mudflats and narrow river channel are not conducive to potentially damaging water-based recreation. Sewage contamination of shellfish has curbed the disturbance and damage once caused by harvesting. Wildfowling at a modest and sustainable level has involved a group who use the estuary and can actively contribute to its management.

The educational role of the Eden Estuary is important and its proximity to Universities at Dundee and St Andrews has provided many opportunities for student projects and surveys. Co-operative reserve management has made available a valuable resource for ecological study, the results of which may in turn be of value to the managers.

In general the Eden Estuary now appears to be under no serious pressure from potentially damaging influences. Continuing sound management and its enhanced status as a Special Protection Area should ensure its ecological integrity for the foreseeable future.

Acknowledgements

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The use and appropriateness of contingent valuation in the context of the strategic management of the Forth Estuary (summary)

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This study was initiated to determine the use and appropriateness of environmental valuation techniques in the context of a strategic estuarine management initiative: Forth Estuary Forum, with a view to assessing the potential role of such techniques in increasing community participation. Attention was focused on contingent valuation, which is a technique for placing monetary values on those aspects of the environment for which it is not possible to establish a direct market value, such as aesthetic appreciation value, the value associated with simply knowing that natural areas exist and the values associated with potential uses of the environment, by this and future generations. It is argued that if such 'indirect' or 'non-use' values can be established and monetarised, they can be included in environmental cost-benefit analyses, which may otherwise be out of balance or biased towards the economic development value of natural areas.

Contingent valuation is a survey-based approach whereby respondents are asked to specify their willingness to pay for an environmental 'good', based on a description of a hypothetical scenario, in which they may be asked to pay to protect, preserve or improve a specific natural asset. There are many arguments for and against the use of such approaches, based on the extension of market economics to environmental management, underlying ethical issues and the methodological accuracy of the contingent valuation technique. These arguments have essentially become 'deadlocked', though many regulatory agencies are adopting the approach of environmental valuation and cost-benefit analysis in their policies.

The focus of this study was therefore to apply contingent valuation in a range of scenarios in order to explore the circumstances in which the technique may or may not be appropriate in the specific context of a strategic estuarine management initiative. People in the immediate vicinity of Torry Bay, on the Fife coast, were surveyed and asked to state their willingness to pay under one of the following scenarios:

- to prevent the construction of a tidal barrage at the mouth of the Forth which would result in the loss of 90% of all the mudflats on the Firth;
- to establish a Local Nature Reserve to assist in the preservation of Torry Bay;
- to purchase Torry Bay in order to improve its long-term preservation prospects;
- to upgrade the sewage treatment system flowing into Torry Bay.

These scenarios thus range from a critical, widespread habitat degradation context to a local marginal environmental improvement context. A total of 315 surveys were carried out, the results of which indicate the following:

- that most people understood and did not object to the approach, regardless of the scenario, and that they were willing to participate appropriately in the survey;
- that the willingness to pay of those people surveyed would more than justify expenditure on the conservation project in question.

The validity and applicability of the survey results to strategic coastal management decisions is discussed with specific reference to the following issues:

- the effect on people's willingness to pay of the locality of the natural area in question;
- the relationship between the scale of the natural area and people's willingness to pay;
- the extent to which the hypothetical willingness to pay stated in the survey relates to people's actual willingness to pay to protect, preserve or improve the natural area in question (this aspect is identified as a key area for further research).

Though the above factors may be of significance in certain circumstances, the following overall conclusions were made:

- that contingent valuations could be an important justification for conservation expenditure and that the technique is, as such, a mechanism for increasing community accountability rather than community participation;

- that estimates of people's indirect values for natural areas are important in achieving a balance with economic development values in environmental cost-benefit analyses;
- that contingent valuation might be particularly appropriate for determining the publics' willingness to pay for wider scale strategic initiatives, though scale effects may still be significant;
- that the technique may not be appropriate for determining the detailed allocation of expenditure between specific sites;
- that extreme caution should be exercised in transferring the results of such surveys from one site to another, or scaling-up/scaling-down the results in terms of the number and area of such sites.

Overall, it might be concluded that while there are arguably grounds for fundamentally objecting to environmental valuation and cost-benefit analysis, such approaches are increasingly being incorporated in many aspects of public policy decisions; therefore they should not be dismissed. This study identifies scenarios in which contingent valuation results might be a potent factor in influencing decisions in the context of the activities of the Forth Estuary Forum, though it must, however, also be recognised that there are limits to the appropriateness of such approaches.

As such, this study concludes that further research efforts might be best focused on formulating guidelines and criteria concerning the appropriateness of contingent valuation under different circumstances in order to avoid the tactical and, arguably, inappropriate use of such techniques. This will enable the debate to move on from the present impasse and efforts to be concentrated on the search for potential middle ground in which environmental valuation might be appropriately applied.

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Firth management in Scotland: the Forth Estuary Forum

M. Jennison & S.M. Atkins

Scotland's Firths are recognised as being of vital cultural, economic and natural heritage importance. Integrated coastal zone management (ICZM) is increasingly promoted and used world-wide as a tool to obtain an integrated approach to overcoming complex and interacting pressures on the environment. A major project currently being undertaken on several firths around the Scottish coastline adopts this approach and applies techniques that are unique and sympathetic to the constraints associated with ICZM on the scale and complexity of such areas.

The Scottish Natural Heritage 'Focus on Firths' project has two main objectives: (1) to increase understanding and awareness of the vital importance of estuaries as natural ecosystems and (2) to promote integrated management by stimulating understanding and co-operation among the range of users and statutory authorities. The project has four themes which are being developed by project officers on three firths. These are: (1) integrated management through broad-based partnerships; (2) information collation and review; (3) promoting awareness through education and interpretation, and (4) promoting community involvement in the firth management process. The range of activities being undertaken under these four themes is described.

The origins and progress of 'Focus on Firths' are discussed together with the application of a range of management techniques which are emerging for different sites. Work undertaken on the Firth of Forth is examined in detail, particularly the development of a voluntary partnership of organisations known as the Forth Estuary Forum. The structure, operation and work programme of this group are explained together with its long-term objectives, terms of reference and the development of topic groups.

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Introduction

Integrated coastal zone management (ICZM) is increasingly used world-wide as a tool to obtain an integrated approach to the sustainable use and development of multi-use coastal areas. King & Bridge (1994) identified 90 ICZM initiatives in England alone in May 1994. There are well-established systems of ICZM in Australia, New Zealand and the Far East as well as the USA where legislation for coastal and marine management is in place (Wilcox 1994).

The concepts of ICZM are increasingly being incorporated into international and national policy statements. Agenda 21 from the Rio Conference (UN Conference on Environment and Development) promotes new approaches to marine and coastal management which are integrated and precautionary. Under the EC programme of sustainable development 'Towards Sustainability' (Commission of the EC 1992) the 5th Action Plan advocates integrated management of coasts in the objective of "Sustainable development of coastal zones and their resources in accordance with the carrying capacity of coastal environments". A European Workshop on CZM in April 1991 defined the coastal zone as an area requiring increased care and protection and emphasised the importance of natural processes in determining management objectives. The European Coastal Conservation conference in Holland, November 1991, issued a final resolution recognising the urgent need to adopt and implement a European strategy for integrated management of coastal zones.

The SNH Firths Initiative (Focus on Firths) is included in the UK Biodiversity Action Plan (DoE 1994), as "aimed at securing integrated management plans for the Moray Firth, Solway Firth and Firth of Forth and, in due course, other significant estuaries in Scotland". The timescale for completion of these management plans or frameworks of 1998 is stated as a target.

Most recent Government policy is set out in two papers published in 1993 relating to coastal policy in England and Wales (DoE/Welsh Office 1993a, b). These documents restate Government policy that CZM in general is supported in principle through the mechanism of voluntary partnership agreements without overarching new institutions or legislation. This policy has resulted in the establishment of a National Coastal Forum for England. Coastal policy in Scotland is due to be set out in detail with the publication of a Scottish Office paper in the near future.

Focus on Firths

Focus on Firths was developed by SNH in response to a growing awareness of the need for integrated management of the wide range of human activities and the extensive natural heritage interest of the coastal and marine areas of firths and estuaries. The planning of development and ongoing activities around most firths is regulated by a diverse array of statutory bodies with a poor overview of the extent to which resources are utilised or exploited across the whole firth. The various activities in the marine areas are controlled by a wide range of legislation and authorities acting within sectoral and/or local constraints. This renders co-ordinated and integrated decision-making a difficult process. Consequently development of all types and the increase in activities such as agriculture, fisheries, aquaculture, aggregate extraction, power generation and recreational pursuits tend to occur in a piecemeal fashion with no co-ordination of developments, planning or integrated management across the whole firth. Proposals are assessed on an individual basis as they arise and there are no overall guidelines and no overall forward planning to take account of their cumulative effect. This has resulted, for example, in the loss of 50% of the intertidal area in the Forth Estuary over the last two centuries and equivalent destruction in some other firths (McLusky, Bryant & Elliott 1992). Focus on Firths seeks to address the problem of activities taking place outside an integrated management or planning framework causing unnecessary or great excess environmental damage and loss.

The project is founded on the premise that integrated management is the most effective method of delivering the potential benefits and opportunities provided by the resources of the Scottish firths. Focus on Firths is more than a reactive solution to problems as they are presently perceived. It is a precautionary approach which may be required in relatively undeveloped areas where interactions and conflicts between activities and user groups are likely to arise in the future. Firth management is designed to be an ongoing process, not a time-limited task. It will not only aim to assess and propose management options for the present range of activities and issues, but also create a mechanism and approach for future developments which may occur by setting up partnerships with an ongoing remit. Focus on Firths is new to Scotland where the scale and complexity of firths creates major challenges to such an approach. It is integrated in that it will address all issues and the agendas of all partners. Finally, it is precautionary since it will instigate a management mechanism which will accommodate both present environmental problems and future issues which arise.

Scope of Focus on Firths

In Scotland, common usage identifies firths as large coastal areas of sea, generally widening out from estuaries to the open sea. Estuaries are the area of interface between rivers and sea, characterised by a salinity gradient from freshwater to fully saline water. For the purposes of this project, the sites referred to are the five major firths of Scotland, namely the Solway, Clyde, Forth, Tay and Moray, including the inner Moray, Cromarty and Dornoch Firths. The boundaries of the firth project are nominally the upper tidal limits, lines between headlands at the mouths and the surrounding coastal hinterlands. These boundaries are intended to remain flexible according to the range of each issue, but the focus of interest of the project will be the inshore waters and adjacent maritime lands as appropriate.

Project definition, aims and themes

Focus on Firths is designed to facilitate the wise and sustainable management of the marine areas of Scottish firths and related coastal areas. It is derived from the concept of Integrated Coastal Zone Management, stresses the environmental importance of firths and addresses the pressures which are concentrated in them. In the absence of statutory mechanisms to protect marine areas it is dependent for success on negotiation and voluntary agreement among all the interest groups.

Focus on Firths has two broad aims as follows:

1. To secure integrated management strategies for the Solway, Forth and Moray Firths and other significant firths by facilitating consensus and co-operation among all users and statutory authorities, having regard to the UK Biodiversity Action Plan.

2. To increase appreciation and understanding of the vital importance of the natural heritage significance of Scotland's firths, through information collation and dissemination, the production of educational and interpretative materials, promoting community involvement and local ownership.

These aims are interpreted in terms of work programmes and actions under four themes which will be developed in parallel, centrally and locally.

1. Integrated management

The primary approach will be the establishment of local management partnerships for each firth. These Firth Fora will attempt to bring together representation from the widest possible range of statutory authorities, users and interest groups, providing maximum opportunity for greater dialogue, exchange of views, and mutual understanding. The increase in understanding and awareness of the roles, remits, responsibilities and aims of members will be crucial in providing the right environment for the development of integrated management. If successful, fora will develop and implement management objectives policies and proposals in consultation with all interests, identify and resolve issues and conflicts, and implement management through negotiation and voluntary agreement, to promote the wise use of the firth.

Through the identification of joint areas of interest, duplication of activity, shared aims and information requirements, fora will exploit potential synergy between different interest groups and find ways of completing tasks through partnerships to generate efficiency and added value benefits. For example, they may undertake large- or small-scale review, research, educational and community projects using joint resources (financial or in kind) which may not be possible for a single organisation.

The partnerships exemplify the 'voluntary approach' promoted by government policy for the management of marine areas. Any management proposals will be non-statutory and must be implemented by consensus. However there will be issues which cannot be resolved through this means where legislation will be required. The projects will have a role in the identification of issues where changes or additions to legislation are required.

2. Information review, analysis and research

A full analysis of existing data and information for each firth is required to develop fully integrated management proposals. Information review is therefore being conducted for each firth to collate all current data. This review will be used to identify gaps in knowledge and future research needs. The data will be analysed to identify interactions between activities, trends and changes taking place over time and develop management proposals.

Two contrasting approaches have been adopted by firth projects in Scotland:

1. The completion and publication of an information review largely or entirely in advance of the development of a partnership, as for the Moray Firth Review (Harding-Hill 1993). The Minch Review (Bryan 1994) is a similar example.
2. Undertaking the information review, data collation, and analysis of issues as a single exercise in partnership with outside agencies. This involves the establishment of a forum structure with subgroups (topic groups) with a remit to investigate, analyse and report on specific issues or topics. The collation of these reports contributes to the development of a targeted and specific review which addresses the needs of the forum. This method is being used in the Forth, Solway and Clyde projects.

Effective data management is essential to the success of the Focus on Firths projects. In order to achieve fully integrated management there is a need for an information system to analyse fully and compare all the data and information that exist for the site. There should also be facilities to overlay different datasets, update and reanalyse as new information becomes available and interrogate the data with a range of possible future scenarios.

A Geographical Information System (GIS) will generate and promote valuable links with partner organisations such as RPBs, Regional and District Councils and voluntary organisations, all of whom want an overview or integrated approach to environmental management. Data sharing and exchange will promote mutually beneficial relationships and co-operation.

It is a key aim of Focus on Firths to generate an ongoing management system which will be maintained in the future and will be inclusive of future issues and environmental problems and conflicts which will arise. A GIS will provide an easily-updated source of information which could readily be adapted to include new datasets and information relating to issues as they arise. This aspect of the future continuation and development of coastal zone management projects is an important consideration which is addressed through the GIS approach.

3. Education and awareness

The education programme is designed to disseminate environmental information about the natural heritage importance of the firths, and the suite of activities which take place within them. The programme is aimed at all age groups and sections of the community. Examples of materials which have already been published from the project include leaflets (all firths), newsletters (Forth, Solway), slide packs (Moray, Forth), site directory of the natural heritage resources for the area

(Moray), museum display 'Under the Sea' (Moray), and posters (Moray, Forth).

4. Community involvement

A basic principle of Focus on Firths is that there should be wide-ranging and well-informed commitment to the management process from the whole community of users and occupiers of the firth. This will be obtained through the partnership process outlined above as well as projects designed to promote community involvement.

The community involvement programme aims to find new and more effective ways of determining the views of local people, and involving the whole of society in the decision-making process. A number of techniques and approaches have been or are being trialled. Their success and value is being assessed and recommendations on future use will be made.

The Forth Estuary Forum example

In November 1992, ICI, (now Zeneca), hosted a seminar at Grangemouth considering the importance of the Firth of Forth and the threats posed to its long-term future. It was concluded that in-line with national thinking there was a need to work towards a more co-ordinated system of planning and management for the whole of the Forth and to create a vision for its future. In response, in November 1993, the Forth Estuary Forum was launched (Burbridge & Burbridge 1994).

The Forth Estuary Forum is a voluntary partnership of representatives from a diverse range of organisations and agencies, including industry, commerce, local authorities, conservation groups and recreational bodies. At present there are over 150 participants. The Forum has an interest in the tidal waters of the Forth from the tidal limit at Stirling to a line drawn from Fifeness on the north coast and Dunbar on the south coast. The Forum also has an interest in the surrounding landward area of the Firth where there is potential for impacts and activities that may affect the Firth itself.

The Forum's aim is to promote the wise and sustainable use of the tidal waters of the Forth by pursuing various objectives. These are:

1. to improve communication and exchange of information between users, fostering greater understanding and encouraging more effective ways of handling matters in the future;
2. to encourage the exchange of information and opinions about the Forth;
3. to promote environmental education opportunities to extend awareness and understanding of issues related to the area;
4. to create links with national and international estuarine groups to promote good practice and integrated action; and
5. to develop a management strategy that will identify and assess issues and opportunities and reconcile any problems.

Given the scale and complexity of the Forth, and the number and diversity of organisations involved, the Forum has produced a constitution, a set of functions, a set of principles and a set of terms of reference under which the Forum operates.

The Forum is based on a simple structure, having a core management group to co-ordinate and manage the work programme and a series of topic groups, formed as and when required, to undertake the bulk of the work. The management group consists of 16 individual members who together represent a balanced range of interests and user groups from around the Forth. The secretariat is provided by a project officer funded under the SNH Focus on Firths Initiative. The topic groups have one or both of two functions, either to address specific issues and formulate recommendations for their resolution, or to progress initiatives and projects funded by the Forum's partners.

Topic groups

The work programme of the Forum began by identifying and prioritising issues and opportunities for the Firth of Forth through a consultation exercise with the entire Forum membership. This allowed the grouping together of similar issues and opportunities into distinct categories and subsequently the formation of specific topic groups. For the Firth of Forth the following topic groups have now been formed as a result of this issue identification process:

- Marine and coastal pollution
- Tourism and recreation
- Coastal defence
- Nature conservation
- Landscape and amenity
- Built and archaeological heritage
- Economic development

These topic groups comprise representatives of different organisations, specific interest groups, and/or individuals with specialist expertise and knowledge of the topic in question. The groups will identify opportunities, e.g. environmental improvements, and issues, e.g. conflicts of interest, and will then formulate management recommendations to address and resolve these. The representatives, under the auspices of the topic group, can best address specific issues which otherwise would not be addressed by the management group. The support they provide for the management group will help set targets and priorities, aid future management decisions, and inform partners to a variety of viewpoints (Kennedy 1994).

Topic papers

The topic groups will publish their deliberations in the form of a series of topic papers. The aim of the topic papers are to provide the management group, in a concise and readily usable form, with information about specific uses, issues and opportunities, and to highlight potential or actual conflicts of interest and the implications for future management options. They will fill current gaps in information and inform decision- and policy-making. It is not anticipated that topic papers will include or generate large quantities of data, however, they will review data availability and draw conclusions in relation to trends in estuary use (Kennedy 1994).

Topic groups consist of three or four key members who are responsible for progressing the production of the topic paper. However, this core group can co-opt additional members, as required, from a range of different backgrounds to provide expert opinions and advice. Consultation with the entire Forum membership will occur during the production of the topic paper and at the end of its work schedule the topic group will be dissolved. The first topic papers are expected ready for consultation in the summer of 1995, with other papers at regular intervals over the following year and a half.

Support groups

It is felt that the role of an estuarine Forum extends beyond the specific remit of developing management and policy recommendations. Improved communications, education opportunities and information sharing are just a few benefits achieved through the formation of such a voluntary partnership. To exploit the full potential of the Forth Estuary Forum two additional sub-groups have also been formed. These are:

- Awareness and education
- Information and research

The Awareness and education group is helping to disseminate the knowledge gained from the topic groups. This group is looking at methods of producing and financing educational and publicity material with the object of raising awareness of the various aspects of the Firth and of keeping interested parties informed of the Forum's progress. Products currently under production by this group include a Firth of Forth Users Directory, a brochure, a map, a newsletter and poster.

The Information and research group is intended to support the work of the topic groups in the production of the topic papers by providing a service where necessary information and data can be supplied as and when required. This will prevent duplication of effort and resources especially as the same datasets will be required by several topic groups. Key to the provision of this service is the development of a Forth Information System based on a GIS. This group is also compiling a register of research undertaken on the Forth and is producing a data directory outlining the major suppliers of relevant data.

Firth of Forth management strategy

The production of comprehensive topic papers is seen as the first step in the development of a widely accepted management strategy for the Firth of Forth. However, given the size, scale and complexity of the Forth, it is felt that the development of the process of issue resolution is of highest priority and therefore, at the moment, the Forth Estuary Forum aims to demonstrate its credibility and ability to resolve local concerns by successfully resolving one or two key issues and promoting agreed action. Once this has been achieved the Forum's timetable can then concentrate on achieving the 1998 target laid down in the UK's Biodiversity Action Plan.

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Costs of improving water quality in the Forth Estuary

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As part of a project on tradable pollution permits, information was collected on hydrology and water quality, and on the costs of pollution abatement, in the Forth Estuary. Two computer models, of estuarial water quality and of the economic behaviour of firms responsible for polluting discharges, were used in conjunction to estimate the overall costs associated with improving water quality. The scope for such improvement turns out not to be great, though it is perhaps sufficient to eliminate what are presently significant obstacles to migrating fish.

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As part of a research project to investigate the scope for using tradable pollution permits to control pollution (see Note 1), information was collected on the hydrology of, and water quality in the Forth Estuary (Project Report No. 1) and on the costs of reducing polluting discharges to it (Project Report No. 2). (The project is entitled Market Mechanisms for the Control of Water Pollution and is funded by the UK Economic and Social Research Council.) The hydrological and water quality information was a matter of public record, held by the Forth River Purification Board (except for tidal data obtained from HM Dockyard, Rosyth, and topological data from Admiralty charts), while the cost information was obtained by means of questionnaires sent to, and interviews with, representatives of the firms and municipal authorities responsible for the major discharges of biological oxygen demand (BOD).

Following consideration of current water quality issues in the estuary, it was decided to focus on levels of dissolved oxygen (DO), and the effect on them of BOD. (BOD is primarily due to the decay of organic material and is commonly measured and thought of as a unitary component, in terms of the amount of oxygen that would be consumed under certain conditions.) Fish migration is known to be affected at certain times of year (mainly May to August) by low levels of DO associated with low freshwater flow and high temperatures.

Using software developed by the Danish Hydrological Institute (MIKE 11) with the hydrological and water quality data, a computer model of water quality in the estuary was constructed (see Figure 1, showing predicted and observed levels of DO at a point 21 km downstream from Stirling). This enabled the likely effects of reducing discharged BOD on DO levels to be determined. A transfer coefficient matrix was derived, with each coefficient representing the effect on DO at one of several points on the estuary of BOD from one of the major discharges being reduced by a certain amount (i.e. an m*n matrix of m discharge points and n monitoring points). Owing to various limitations, a period of only a few weeks during the crucial time of year in 1992 was modelled, and so only short-run variability in the transfer coefficients is covered and changes (mainly in discharges) that have occurred since then are not accounted for. Short-run variability is due mainly to the spring-neap fortnightly tidal cycle, as spring tides resuspend significantly more sediment, thus causing higher ambient levels of BOD. Long-run variability is mainly due to the factors already mentioned as causing low levels of DO, on a yearly cycle. (Anthropogenic discharges may be assumed to contribute to both short- and long-run variability.)

An economic computer model was also constructed, using linear programming techniques, and was used first to determine the most economically efficient

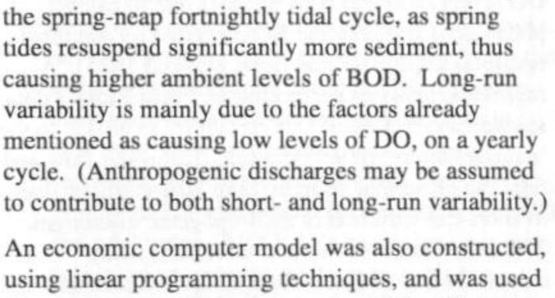

Figure 1. Predicted versus observed DO levels at km 21, May to August (inclusive) 1992.

distribution of BOD cuts across discharges to obtain various levels of aggregate BOD reduction (Project Report No. 2). A new constraint set, incorporating the transfer coefficient data, was then substituted for the constraint concerning aggregate reduction, so that the model could now calculate the most efficient distribution of reductions to achieve a certain water quality goal, i.e. a given increase in the mean DO level at a certain point in the estuary.

The potential for improving water quality in this way turns out to be relatively limited. The largest increase in DO obtained was less than 1 mg l^{-1}, i.e. less than 10% of saturation, while fish migration is considered to be inhibited at less than 60% and prevented at less than 40% (Priede *et al.* 1988), and observed levels at the crucial time of year are often less than 40%. Also, of the six points on the estuary for which calculations were made, at only three were increases of 0.1 mg l^{-1} or more found to be possible.

However, because a number of estimates used in calibrating the water quality model were believed to be rather conservative regarding the effects of anthropogenic discharges, the economic model was re-run with the transfer coefficients doubled, i.e. assuming twice the calculated increase in DO at a given point on the estuary to result from a given reduction in BOD from a given discharge. This seems a reasonable upper limit, giving a maximum increase in DO of a little under 2 mg l^{-1} or 20% saturation, as similar estuaries without anthropogenic discharges have been found to have DO levels as low as 60% at times due to natural phenomena (notably the BOD exerted by sediment resuspended due to tidal flow; Maskell 1985). A regression analysis performed on Forth Estuary data showed about 80% of DO variability to be due to the 'natural factors' of temperature, freshwater flow and tidal range, so that no more than 20% could be due to short-run variation in anthropogenic discharges. There are therefore two sets of results, using calculated and doubled transfer coefficients, and these are considered to represent between them a relatively realistic range of outcomes.

Figure 2 shows the total costs of improvements in DO at three points on the estuary: 18 km, 24 km and 30 km downstream from Stirling (which is generally considered the upper limit of the estuary). Figure 3 indicates the corresponding costs with doubled transfer coefficients, i.e. twice the effect on DO of a given cut in discharged BOD. Note the logarithmic vertical scale in these and the following figures.

Figures 4 and 5 show the marginal costs of the given improvements in DO levels, for calculated and doubled transfer coefficients, respectively.

It will be noted that the curves generally tend to rise to the right. This is in line with the expectation that greater improvements in DO levels, requiring greater reductions in BOD discharged, will be increasingly difficult to achieve. On the other hand, the curves are not smooth; for instance, there is an obvious dip in the marginal cost curve for the 24 km point at 0.4 mg l^{-1} (calculated coefficients) and 0.8 mg l^{-1} (doubled coefficients). This is due to the fact that one of the largest discharges, untypically, has decreasing marginal costs. Different levels of reduction for this discharge, and generally, imply the use of different technologies, so allowing decreasing marginal costs in this case, and, generally, discharge reduction cost functions being stepped rather than continuous. The dips in the 18 km and 30 km curves at 0.4 mg l^{-1} (doubled coefficients) have the same cause: the reduction required of this particular discharge at this level has a lower unit cost than that of the next lower level of DO improvement.

We reach this step at 0.4 mg l^{-1} for 18 km and 30 km, as opposed to 0.8 mg l^{-1} for 24 km, indicating that improvements in DO are more difficult to achieve at the former than the latter points. This is no doubt due to many factors, but among the more significant would seem to be the locations of the major discharges, largely downstream of these points, the

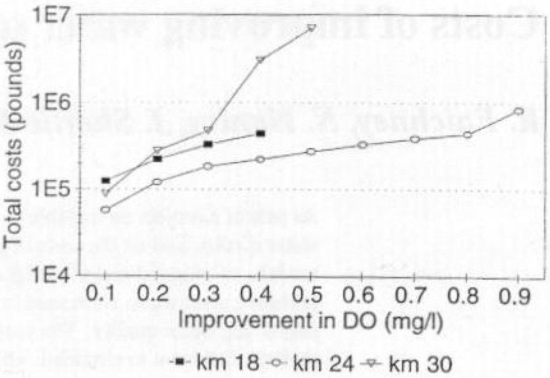

Figure 2. Costs of improving DO levels at three points on the estuary (calculated transfer coefficients).

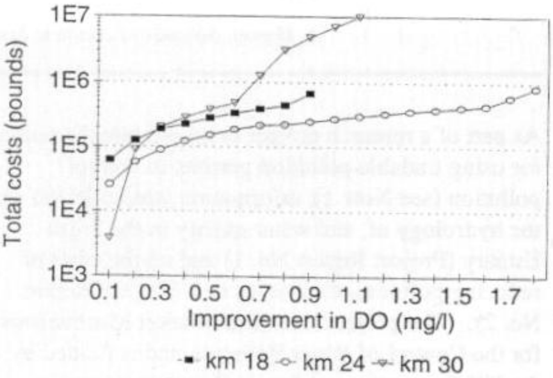

Figure 3. Costs of improving DO levels at three points on the estuary (doubled transfer coefficients).

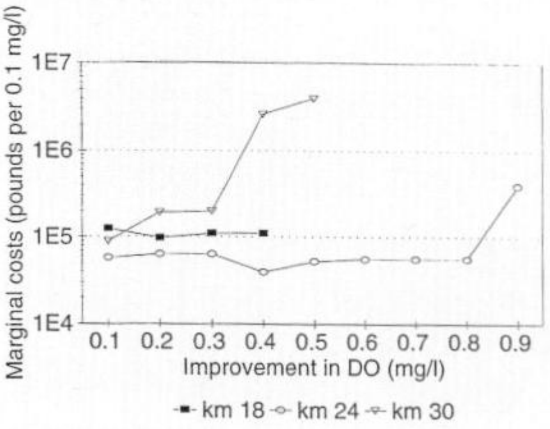

Figure 4. Marginal costs of improving DO levels (calculated coefficients).

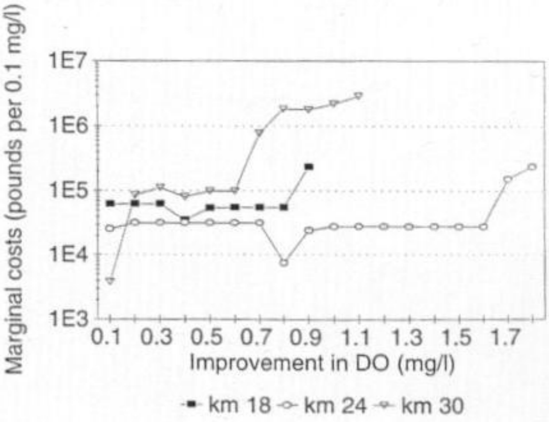

Figure 5. Marginal costs of improving DO levels (doubled coefficients).

fact that discharge reductions generally seem to have more effect downstream than upstream of the discharge point (despite the symmetrical nature of tidal flow, there is a net flow downstream owing to freshwater inflow, though it is at a minimum at the season with which we are currently concerned), and the topography of the estuary. At 30 km, the cross-sectional area of the estuary and therefore the volume of water affected has increased considerably, so any factor that is to have an effect on its quality has to be correspondingly large. While transfer coefficients are small at 30 km, a relatively large number of discharges affect water quality at this point, so there is great potential for discharge reduction, but improving water quality is relatively expensive. On the other hand, largely as a result of the topography, the problems with low DO levels tend to occur upstream.

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Notes

1. We have also investigated barriers to trade in such markets; see Discussion Papers in *Ecological Economics* No. 95/2, Impediments to trade in markets for pollution permits, Munro *et al.*, February 1995. Copies available from the address in note 2.
2. For copies of Project Reports contact the Environmental Economics Research Group, Economics Department, University of Stirling, Stirling, FK9 4LA, UK.
3. Mike 11 has the capacity to take into account the effect of resuspension of sediment on DO levels, but due to certain problems experienced with the software, that capacity could not be utilised in this case. Resuspension being mainly due to tidal flow, with which tidal range is closely correlated, regression analysis was used to determine the relationship between observed DO and tidal range. MIKE 11's output was not post-processed to factor in tidal range using the regression analysis figures for all results reported in this paper.