



Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland

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Abstract

The community structure of Dublin Bay, Ireland was analysed using trophic guilds of the benthic macrofauna. This approach afforded stronger demarcation than a previous multivariate analysis on a taxonomic basis of the pattern of communities, in which tidal height and sediment type appeared to be the two most important abiotic factors for the distribution of the benthos. Graphical dominance analysis (abundance/biomass comparison and partial dominance curves) detected disturbance effects, but did not distinguish between natural and anthropogenic (pollution) stress in this intertidal system. Derived numerical values (*W*-scores) provided greater discrimination, particularly used in conjunction with the trophic analysis, but must be interpreted with caution. However, the methods were useful for evaluating structural dynamics and changes in the trophic communities. © 1998 Elsevier Science B.V.

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1. Introduction

The factors governing the distribution of animals in the intertidal are commonly considered to follow the classical model of Connell (1961), in which the upper limits are set by physical variables, for example temperature or desiccation, and the lower limits by the biological interactions of competition and predation. Although Connell (1961) was describing epifaunal communities on a rocky shore, many workers have suggested that similar mechanisms operate for infauna in sedimentary environments (e.g. Wilson, 1978; Ansell et al., 1980; Thrush et al., 1991).

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However, competition and predation appear to result in different outcomes in rocky and in sedimentary environments. Brown and McLachlan (1990) (p. 40) point out that the evidence available (e.g., Reise, 1985) suggests that firstly exclusion of predators in soft substrates increases diversity and secondly that competition in sediments is far less important than on rocky shores, suggestions reinforced by Wilson (1991). Gray (1981) has discussed at some length the various ideas on controlling factors that have been put forward, notable those of Sanders (1968); Rhoads and Young (1970); Levinton (1972) and Woodin (1976), and has extended the discussion into *r*- and *k*-selection and into the impacts of disturbance and pollution. Analysis of the interaction between the infaunal composition of benthic communities and sediment grain size (reviewed by Snelgrove and Butman, 1994) suggests that a mechanism by which grain size per se controls benthic community composition has not been conclusively demonstrated, but that there were a complex of factors, some of which co-vary with grain size, including the mode of feeding or feeding type.

Central to these ideas is the link between control or type of control and feeding type, but there is considerable disagreement as to the link between feeding type and either diversity or stability. The importance of the functional approach in an exploratory analysis of benthic communities has been emphasised by several authors (Gray, 1981; Warwick, 1982; Gagnon and Haedrich, 1991). The factors which control the distribution of trophic groups set the structure of the community (e.g. Anger, 1975; Committo and Ambrose, 1985), and the distribution and abundance of functional groups are correlated with physical factors of the environment. Numbers of the deposit feeders *Hydrobia ulvae* and *Arenicola marina* for instance are higher in silty sediments, which have higher organic matter and nitrogen contents, than in sandy sediments (Longbottom, 1970), and in turn the sediment particle size is controlled by wave energy.

There are currently a variety of multivariate methods including principal components analysis (PCA), principal co-ordinates analysis (PCOORD) and multi-dimensional scaling (MDS) being used to discriminate communities from species lists (Wilson and Jeffrey, 1994). Shillabeer (1991) tested with the same data set a number of these approaches employed in different laboratories and found that they all gave much the same results. A common feature of all approaches tested was that relatively little of the total variation in the abundance data can be explained, but this could be improved by transformation of the data or the omission of rare species (Shillabeer, 1991). Burd et al. (1990) have summarised the uses of a variety of techniques, while Warwick and Clarke (1991) have evaluated a number of univariate, graphical and multivariate techniques. Warwick and Clarke (1991), (1993) considered multivariate methods the most sensitive for detecting community change.

Warwick (1986) used the ABC-method (short for abundance biomass comparison) and Clarke (1990) developed a statistical treatment of this method to describe stability and also pollution status of marine benthic communities. The distribution of numbers of individuals among species and the distribution of the biomass among species are different in disturbed and undisturbed systems (Pearson and Rosenberg, 1978; Gray, 1979). Such a difference is due to the dominance of *r*-selected or opportunistic species in disturbed systems and a dominance of *k*-selected or conservative species in undisturbed systems. In disturbed areas a numerical dominance of one or few small-

sized species can be expected which contribute little to total biomass. In contrast, in more stable (undisturbed) areas one or a few species would dominate in biomass but contribute little to the total numbers. A graphical description using curves of k -dominance in which the species are ranked in order of dominance (separately for biomass and abundance) on the x -axis with cumulative percentage dominance on the y -axis can be drawn (Lamshead et al., 1983). Warwick's (1986) hypothesis predicts that the abundance curve will fall above the biomass in a disturbed system, and vice versa for a stable system. Whereas the data presented for subtidal areas appears quite convincing, Beukema (1988) concluded after an evaluation of the method on tidal flats that it showed "artificial" evidence for pollution in low biomass and low diversity communities with high densities of small animals (e.g., *Hydrobia ulvae*) or juveniles.

Since then, the ABC method has been widely used and Warwick and Clarke (1994) have not only summarised the results of these analyses, but also investigated more fully the mechanisms of the ABC curves with a number of sublittoral data sets. They identified taxonomic shifts between phyla and within the Polychaeta as the major contributors to ABC changes and thus warned against erroneous conclusions when ABC changes could be attributed to non-annelid species (e.g., Beukema, 1988).

Using a cumulative scale of percentages the shape of the ABC curve strongly depends on the initial value of numbers or biomass of the first ranked species (Beukema, 1988). Clarke (1990) therefore improved the classical ABC method by recalculating the relative dominance of each successively ranked species resulting in a non-cumulative graph.

The configuration of the two plots can be condensed into a single value by subtracting percentage biomass from percentage abundance for each rank and summing the differences. These values (termed W values) indicate either disturbed ($W < 0$) or undisturbed ($W > 0$) areas (Beukema, 1988). A more sophisticated description of this approach and its statistical treatment is given by Clarke (1990).

The objectives of the present study were:

- (1) to categorise the biological communities based on trophic guilds;
- (2) to examine community structure by means of ABC curves as a means of characterising stability and
- (3) to evaluate the W values as disturbance (e.g., pollution) detectors in littoral infaunal communities.

2. Materials and methods

Dublin Bay lies immediately to the east of the city of Dublin and is about 10 km from north to south. The intertidal region extends in a broad arc round most of the Bay, giving a total intertidal area of some 20 km². Descriptions of Dublin Bay and its intertidal environment are given in earlier papers by several authors (Crisp, 1976; Jeffrey et al., 1978; West et al., 1979; Wilson, 1982, 1983), and the latter has characterised the benthic community using distribution and biomass of the species and the Shannon–Weiner index. Wilson (1983) recognised four main biotopes with regard to the macrobenthic

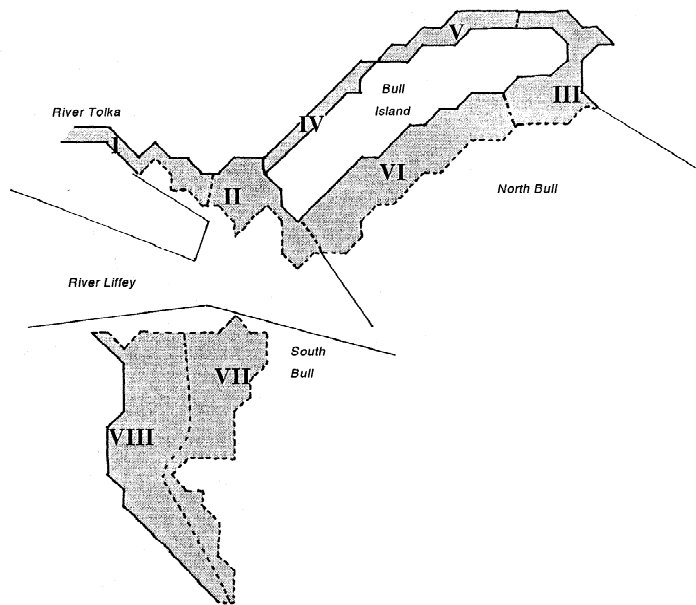


Fig. 1. Dublin Bay — Extent of the intertidal zone (shaded area) and distribution of the 8 subareas (I–VIII). For further explanation see text.

fauna: (1) the lower shore exposed sand; (2) the mid/upper shore rather siltier sand; (3) the muddy lagoons and (4) the basin of the river Tolka (see Fig. 1).

A total of 313 sites were sampled throughout the Bay intertidal. At each site a 0.25m² sample was sieved through a 1 mm mesh sieve, and the animals identified, counted and weighed (wet weight, shell-free for molluscs) in the laboratory (Wilson, 1982, 1983). The results of multivariate analysis (unpublished data) carried out on the 313 macrobenthic samples indicated that the Bay could be subdivided into 8 subareas (see Fig. 1) corresponding well with the few areas defined on environmental factors by Wilson (1983).

Although there is still considerable uncertainty about exact feeding habits and diets of many species (Walker and Rees, 1979; Gray, 1981), each of the 74 sampled species was assigned to a trophic guild (after e.g., Fauchald and Jumars (1979) for polychaetes) to group the sample data into functional communities. The following feeding pattern classes were used: carnivore, omnivore, commensal, deposit feeders, substratum ingestors, suspension feeders, suspension/deposit feeders, suspension/carnivore and herbivore (grazer). Species with a flexible feeding pattern were assigned to the predominant feeding mechanism. The feeding types of the 16 most abundant species (those occurring in at least 10% of the samples) are presented in Table 1.

Abundance and biomass values of each species with the same feeding type were summed for each of the 313 sample sites such that the single species data were summarised to abundance and biomass figures for trophic guilds. From this the principal trophic structure was determined for each site. Stepwise discriminant analysis on the

Table 1
Feeding type of the most abundant species

Species	Feeding type
<i>Phyllodoce</i> spp.	Carnivore
<i>Nereis virens</i>	Carnivore
<i>Nereis diversicolor</i>	Omnivore
<i>Nephtys caeca</i>	Carnivore
<i>Nephtys hombergi</i>	Carnivore
<i>Arenicola marina</i>	Sediment ingester
<i>Lanice conchilega</i>	Suspension feeder
<i>Hydrobia ulvae</i>	Deposit feeder
<i>Mytilus edulis</i>	Suspension feeder
<i>Cerastoderma edule</i>	Suspension feeder
<i>Angulus tenuis</i>	Suspension feeder
<i>Macoma baltica</i>	Deposit feeder
<i>Scrobicularia plana</i>	Deposit feeder
<i>Crangon crangon</i>	Omnivore
<i>Carcinus maenas</i>	Omnivore
<i>Corophium volutator</i>	Deposit feeder

log-transformed data was used to group sites with similar trophic structure, that is based on the biomass and abundance distribution of the trophic groups. The significance of the community groupings was tested by using jack-knifing of the Mahalanobis distances and *a posteriori* probabilities. The Mahalanobis distance from each group mean to each case was computed and the probability of being in any group was tested for each case. The results are expressed as correctness of grouping using a percentage value (see Dixon, 1991).

Spatial distribution, variability and proportion of feeding type communities (functional communities) are shown for the total area sampled. Mean and standard deviation of the representation of each single feeding type were counted for each class of community.

2.1. Dominance curve analysis

ABC (abundance biomass comparison) curves (Warwick, 1986; Warwick et al., 1987) which use the *k*-dominance curves of Lambshead et al. (1983) were plotted for abundance and biomass data for the samples. Graphical results of the ABC method plot were condensed to a single figure (*W*) using the following formula (Clarke, 1990):

$$W = S_{i=1}^s (B_i - A_i) / (50(S - 1))$$

where B_i = biomass of species *i*, A_i = abundance of species *i* and S = number of species. The *W* values display range from -1 to $+1$, with $W \geq +1$ for equal abundance across species, but biomass dominated by a single species and $W \geq -1$ for the converse. Negative values indicate disturbance and positive values stability. *W* values were computed for all the sample sites in Dublin Bay and spatial variability was tested using

non-parametric statistics (Mann–Whitney Test) because the distribution of the individual data was far from normal. W values were also calculated for each functional community and again used to evaluate disturbance or stability.

Partial dominance curves were used to show the importance of single species in the functional community dominance curve and its calculated W value. Partial dominance of species was computed (using the PRIMER package) according to Clarke (1990) as follows:

$$p_1 = 100a_1/(S_{j=1}^s a_j), p_2 = 100a_2/(S_{j=2}^s a_j), \dots p_{s-1} = 100a_{s-1}/(a_{s-1} + a_s), p_s = 100a_s/a_s = 100.$$

where a_j is the abundance of the j th species when ranked in decreasing order and p_i ($i=1, 2, 3, \dots n$) is the partial dominance of the single species.

3. Results

3.1. Spatial variation of the W value

The 313 calculated values for W ranged from -0.544 to 0.912 , with a mean of 0.199 and a standard deviation of 0.216 . Of the 313 values, 89 were negative and the bulk ($n=259$) were between -0.2328 and 0.3896 . The W values have been grouped into percentage classes ($<10\%$, $10\text{--}30\%$, $31\text{--}50\%$, $51\text{--}70\%$, $71\text{--}90\%$ and $>90\%$) to emphasise the trend of the distribution of values (Fig. 2).

Spatial variation of the W values were compared among the 8 subareas as defined above (Fig. 1), and the range, mean and standard deviation of the W values are shown in Table 2. Differences of W values were tested using a sample comparison between all subareas (Table 3).

3.2. Trophic structure of the benthic communities

The percentage proportions of the individual feeding type are expressed with respect to the total 313 sites sampled and to the total biomass within the Bay (Table 4).

The stepwise discriminant analysis grouped the samples with regard to biomass and abundance of the different feeding types into the following trophic communities:

- (A) Both high biomass (70–90% of the total site biomass) and high abundance (60–90% of the total numbers) of suspension feeders;
- (B) high biomass (70–90%) but lower abundance ($<50\%$) of suspension feeders;
- (C) high biomass and high abundance (both 60–90%) of sediment ingestors;
- (D) biomass and abundance shared in similar proportions among three or more feeding types, none of which account for more than 30–50% of total biomass;
- (E) deposit feeders dominate both biomass ($>65\%$) and abundance (never $<90\%$);
- (F) sediment ingestors and suspension feeders account for about the same biomass (30–60%) but abundance values can differ more widely;

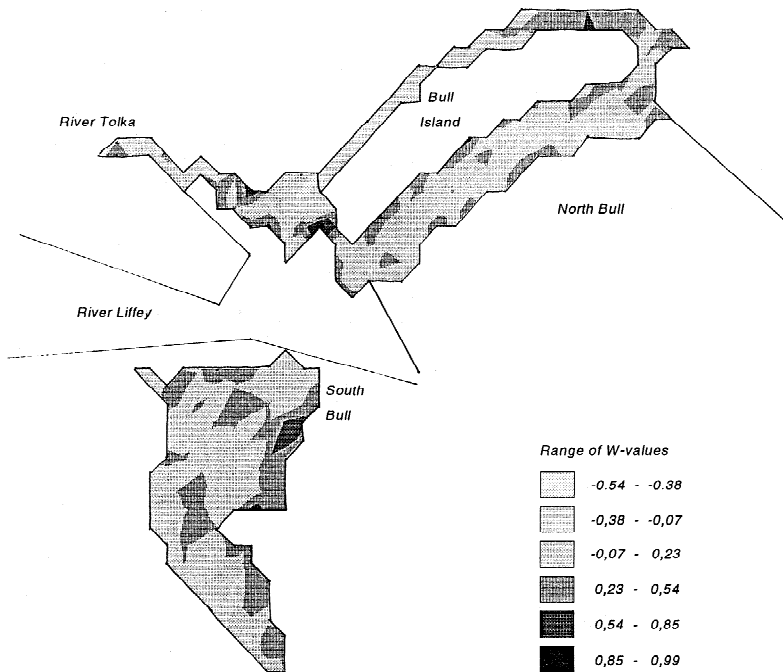


Fig. 2. Dublin Bay: distribution of W values.

(G) community is dominated by carnivores both in terms of biomass (>60%) and abundance (>50%);

(H) sites with high biomass and high abundance (both 30–60%) of carnivores and lower levels of suspension feeders, sediment ingestors or deposit feeders; and finally a grouping of mixed trophic habits

(I) sites with other patterns, i.e. suspension feeder and deposit feeder communities (4 sites), deposit feeder and omnivore communities (3 sites) and omnivore dominated communities (4 sites).

Table 2
Descriptive statistics of W -values for all subareas of Dublin Bay (see Fig. 1)

Subarea	No. of samples	Average of W	SD of W	Min. of W	Max. of W
I	34	0.134	0.261	-0.361	0.912
II	13	-0.108	0.259	-0.544	0.345
III	49	0.198	0.186	-0.219	0.568
IV	11	-0.161	0.117	-0.429	0.008
V	13	-0.033	0.184	-0.287	0.252
VI	47	0.145	0.151	-0.095	0.557
VII	47	0.231	0.231	-0.465	0.715
VIII	83	0.072	0.169	-0.416	0.521

Table 3
Comparisons of *W* values between subareas of Dublin Bay using Mann–Whitney test

	II	III	IV	V	VI	VII	VIII
I	−0.164	−1.18	−2.13*	−1.64	−0.52	−2.46*	−0.641
II	–	−2.84*	−0.88	−0.83	−2.29*	−2.90*	−2.55*
III	–	–	−2.84**	−2.55*	−1.24	−0.79*	−3.09**
IV	–	–	–	−1.68	−2.93*	−2.84**	−2.93**
V	–	–	–	–	−2.20*	−2.34*	−1.64
VI	–	–	–	–	–	−2.49*	−1.85
VII	–	–	–	–	–	–	−3.52**

* and ** indicate significant at $P=0.05$ and $=0.01$ respectively.

Table 4
Percentage occurrence and percentage biomass distribution of feeding types

Feeding type	Occurrence in %	Biomass distribution in %
Carnivore	94.3	13.8
Omnivore	47.1	4.7
Deposit feeders	58.9	11.1
Sediment ingesters	78.7	18.3
Suspension feeders	86.6	49.3
Suspension/deposit feeders	9.1	0.3
Herbivores	5.1	0.3
All other	<3.0	2.2

These community groups account for 87.9% of all sites, with the remainder belonging to other feeding types (e.g., herbivores) or sites with an irregular pattern. The occurrence of trophic communities and the correctness (see Dixon, 1991) of the classification into trophic groups is given in Table 5.

Fig. 3(a–c) show the spatial distribution pattern of functional communities in the Bay. The Tolka basin communities are dominated partially or completely by macrofaunal carnivores (groups G and I), with the dominance decreasing toward the outer part of the

Table 5
Occurrence and percentage correctness of functional communities (see text for explanation)

Functional community	Number and percentage occurrence of sites	Correctness in %
A	82 (26.1%)	73.2
B	55 (17.5%)	47.7 ^a
C	33 (10.5%)	100
D	11 (3.5%)	45.0
E	30 (9.5%)	96.4
F	40 (12.7%)	94.4
G	24 (7.6%)	90.5
H	27 (8.6%)	70.0
I	11 (3.5%)	66.7

^a Feeding type-communities were mainly grouped on basis of the biomass data in the discriminant analysis, but the splitting between A and B was based on the abundance figures only (see text).

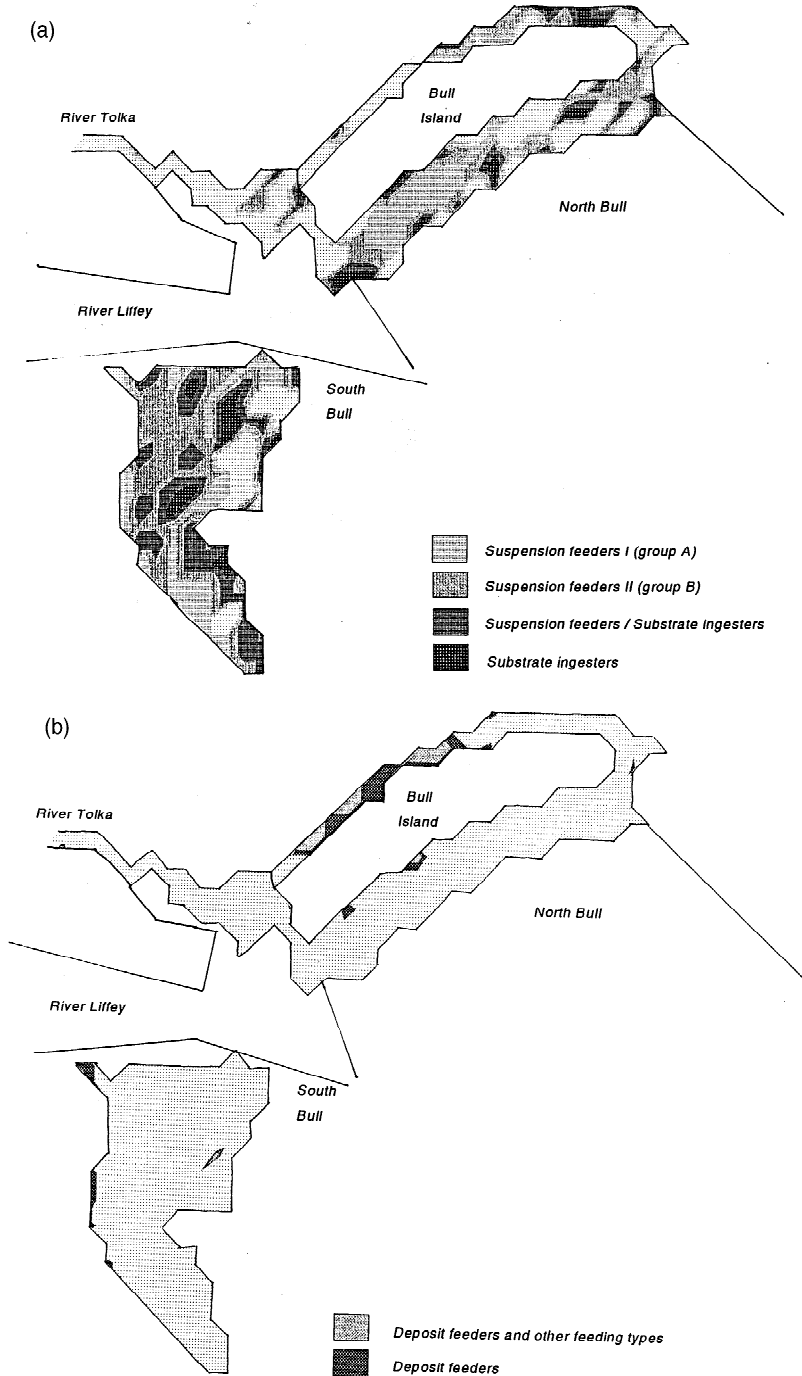


Fig. 3. (a) Dublin Bay: distribution of suspension feeders and sediment ingesters. (b) Dublin Bay: distribution of deposit feeders. (c) Dublin Bay: distribution of omnivores, mixed communities and carnivores.

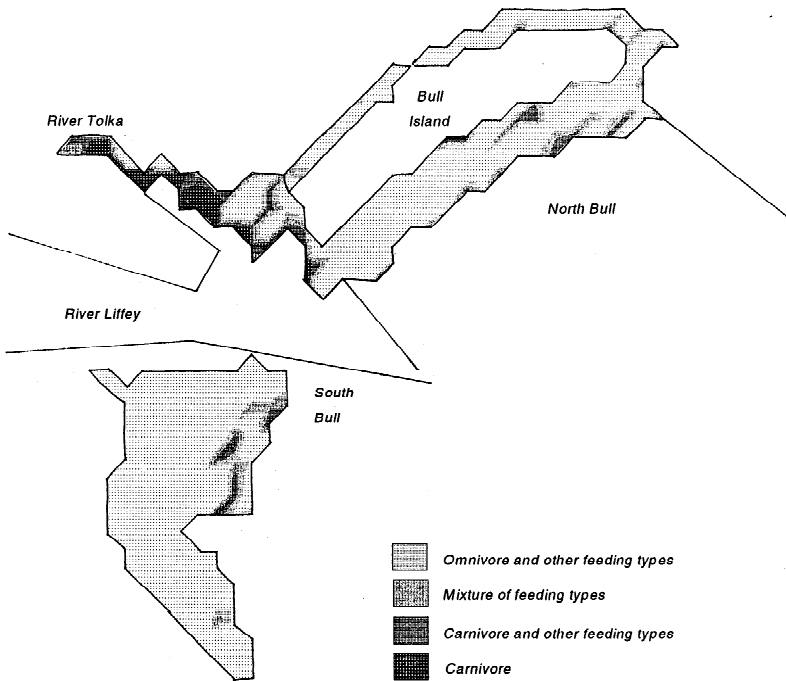


Fig. 3. (continued)

basin. The north lagoon shows an interesting mixture of deposit feeding communities and suspension feeding communities lying along the gradient of tidal influence and connection to the open sea (Fig. 3(a)). There are differences between the suspension feeding communities in the north and the south of the Bay. In the south Bay, the more protected areas are colonised by suspension feeding communities with high biomass and low abundance (group B) while in the outer parts of the south Bay and in the north Bay the community is one of high biomass and high abundance (group A). Moving from the upper shore to the sea, the suspension feeding communities (groups A, B) were replaced successively by suspension feeders/sediment ingestors (group F) and sediment ingestors (group C).

3.3. Dominance curves and W values of functional communities

While the discriminant analysis provides good clustering, the contribution of single species to communities can be better explored through dominance curves. The ABC curves and the partial dominance curves have been plotted for communities A to H, respectively, and examples of these plots are shown in Figs. 4; 5; 6; 7; 8; 9.

In contrast to the comparison of subareas, there is much lower correspondence between the graphical plots and the W values (Table 6), and the reason is a higher overlap between the functional communities as expressed in the statistical test (Table 7).

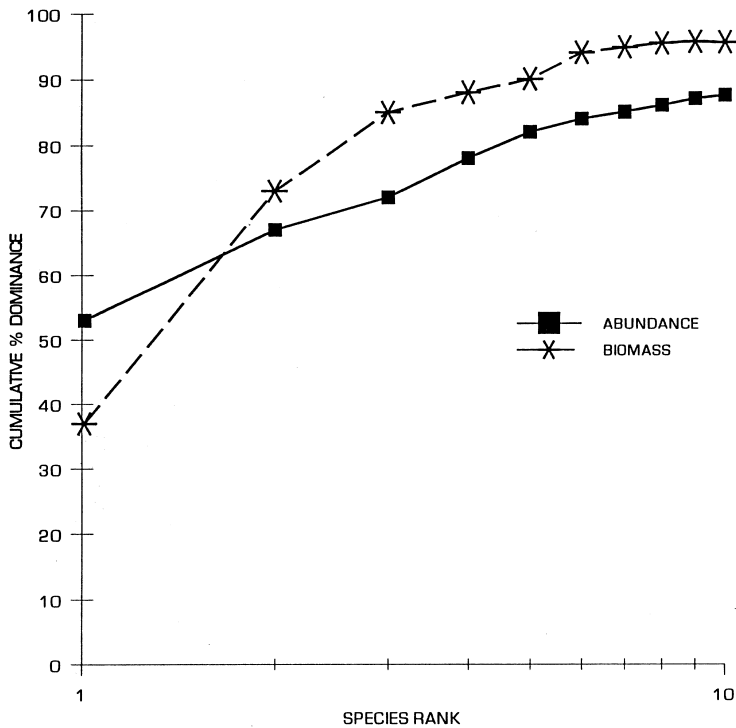


Fig. 4. ABC-curves of functional community A (suspension feeders 1).

The ABC method and the partial dominance curves agree only in certain cases in their evaluation of disturbance or stability of the functional communities. The partial dominance curves of communities B, C and G indicate slight disturbance whereas the ABC curves do not (see as examples, Fig. 7 and Fig. 8). In fact the partial dominance curves indicate a slight tendency toward disturbance for all community types with the exception of type F, in which there are equal biomasses of sediment ingestors and suspension feeders.

Detailed investigation of the deposit feeding community (group E) reveals an interaction between feeding type and the dominance curve. In Dublin Bay, community E had the following rankings:

Species Rank	Abundance	Biomass
1	<i>Hydrobia ulvae</i>	<i>Hydrobia ulvae</i>
2	<i>C. volutator</i>	<i>C. volutator</i>
3	<i>S. plana</i>	<i>S. plana</i>
4	<i>N. diversicolor</i>	<i>C. edule</i>
5	<i>S. armiger</i>	<i>N. diversicolor</i>

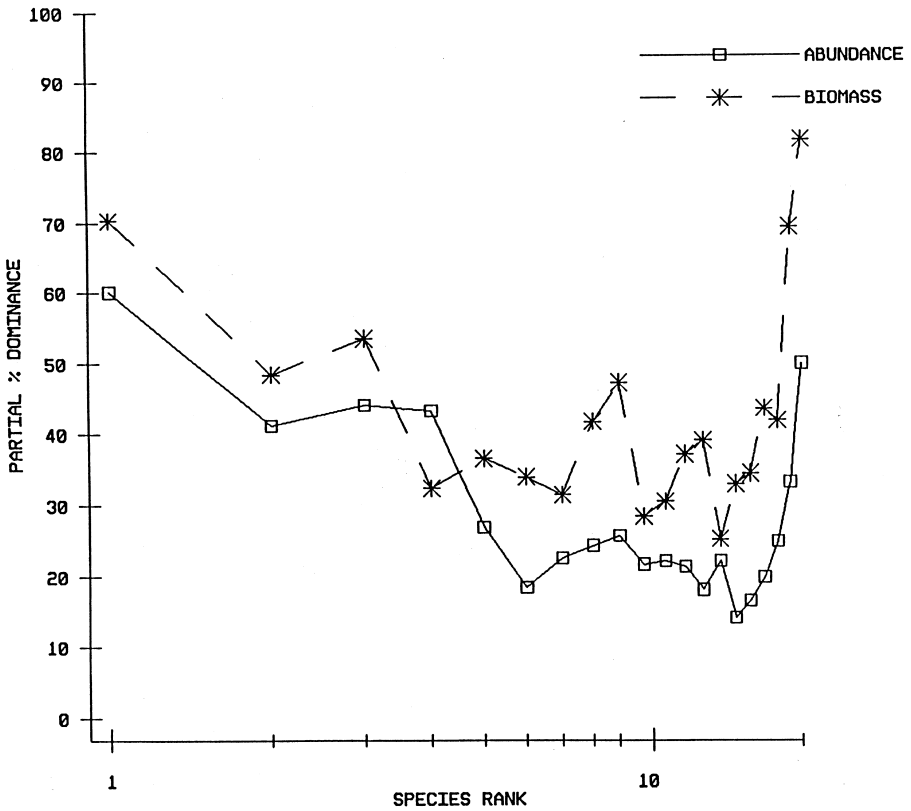


Fig. 5. Partial dominance curves of functional community A (suspension feeders 1).

The first three ranks in both scales are held by deposit feeders, but rank 4 shows a switch in both feeding type and constituent species, from *N. diversicolor* (an omnivore) to *C. edule* (a suspension feeder). This switch coincides with the cross-over in the partial dominance pattern (Fig. 9), which with the abundance surmounting biomass in the initial stages of the curve, agrees with Clarke's (1990) predictions for disturbed communities.

The deposit feeder dominated community (community E) also had *W* scores that were significantly different (Clarke, 1990) from all other functional communities except group I, which in itself was rather a heterogeneous assemblage. The other distinct grouping was the suspension feeder assemblage (group A), which was significantly different from group B, the other suspension feeding dominated assemblage, and from group C (Table 7).

Inspection of the ABC plots and the partial dominance curves for the suspension feeding dominated communities (groups A and B, Figs. 4–6, respectively) show slight disturbance in group A but little or none in group B. In group B *C. edule* accounted for over 70% of the total biomass, but accounted for about the same proportion of abundance as another suspension feeder, *Angulus (Tellina) tenuis* (16% and 11%

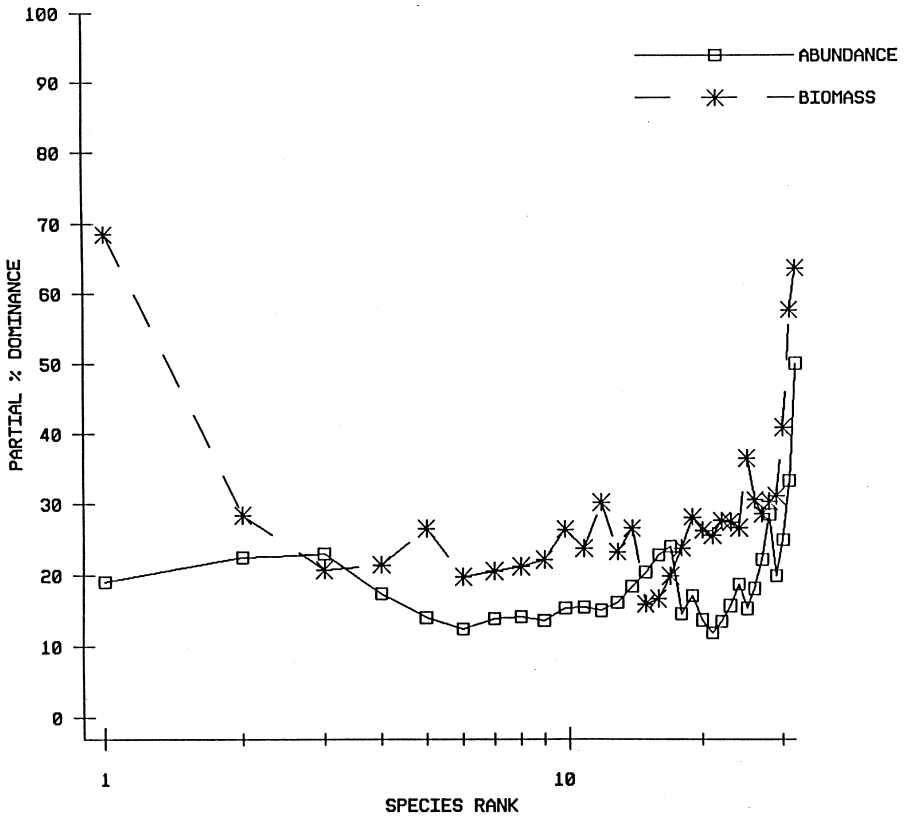


Fig. 6. Partial dominance curves of functional community B (suspension feeders 2).

respectively), while the most abundant species was the sediment ingesting polychaete, *S. armiger*. Thus in group B *C. edule* is the competitive dominant, having a high biomass and few individuals. In group A almost three quarters of the biomass is shared between *C. edule* and *M. edulis* (36.5% each). The next ranked species on biomass is *A. tenuis*, which accounts however for 53.5% of the individuals, followed by *C. edule* (12.4%) and *Scoloplos armiger* (6.2%), while *M. edulis* accounts for only 3.9% of the abundance in group A. The low abundance of *M. edulis* in group A was due to the low number of sites at which it was present, albeit at very high biomasses in mussel beds in the north lagoon (Wilson, 1982). That these mussel bed sites align in group A with the open, sandy *C. edule* sites is evidence of the robustness of the technique, in that the functional discrimination of community type was not affected by a change in species composition even in the dominant species.

For the carnivore communities, crossovers are evident in both plots, that is for group G and in the partial dominance curve for group H indicating some disturbance, although it should be noted that some sites were excluded because only one species occurred and that at low abundance (<5 individuals). Inspection of the data suggests a succession of

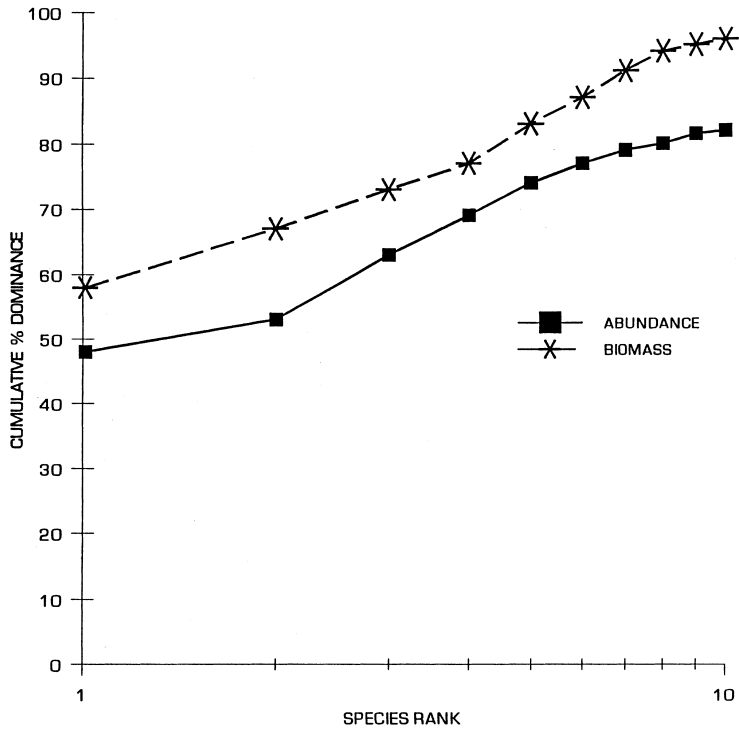


Fig. 7. ABC-curves of functional community C (substratum ingesters).

carnivore communities, beginning with a one species system of mobile carnivores or omnivores which grades into a carnivore dominated system (group G) and ends with a system shared between carnivores and other groups (group H). In group G, *N. virens* was the most abundant (49.4% of all individuals) but *N. caeca* and *N. hombergii* had the highest biomass (37.6 and 35.4%, respectively). The intersection in Fig. 10 is due to *N. virens*, which may in this situation be acting as an opportunistic species. In group H, where the carnivores are more evenly represented with other feeding types, the sediment ingester *S. armiger* accounts for 41.0% of the abundance and the suspension feeders *C. edule* and *M. edulis* represent 23.6 and 10.4% of the biomass respectively, in comparison to *N. virens* which accounts for 44.9% of the biomass but only 31.5% of the abundance.

4. Discussion

The ability of marine benthic animals to establish and maintain themselves under certain environmental conditions is mostly determined by physiological requirements, one of which is the food intake, which in turn is influenced by the feeding pattern and the ability to make use of the food potentially available to them. Suspension feeders tend

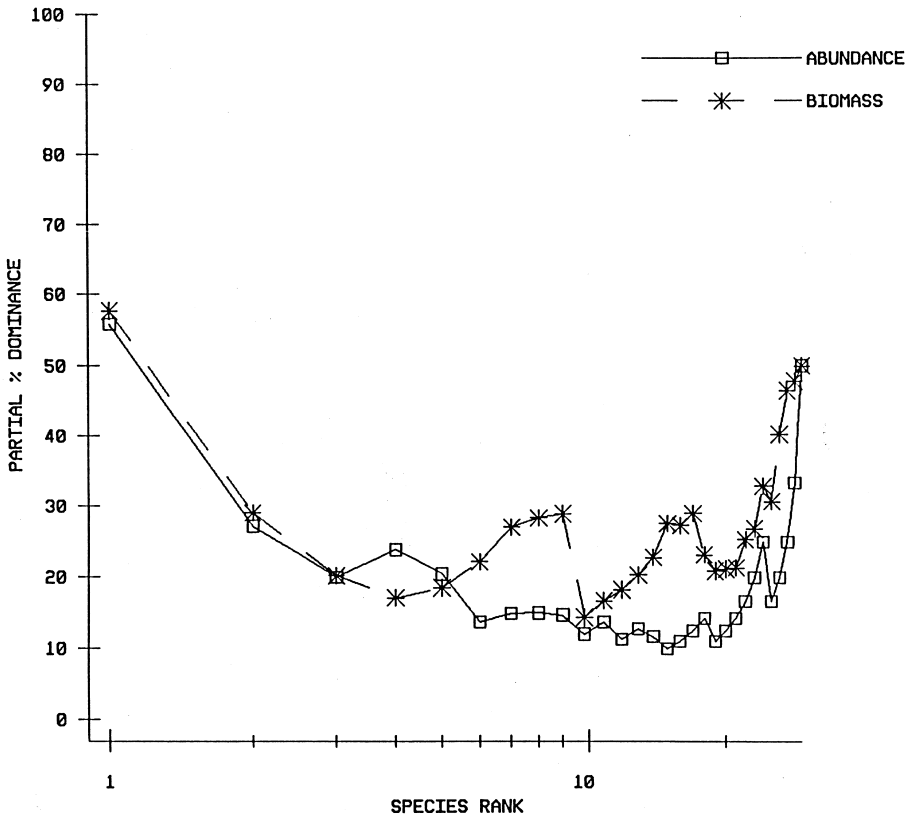


Fig. 8. Partial dominance curves of functional community C (sediment ingesters).

to an overlap in their food selection (e.g., Foster-Smith, 1975), whereas sympatric deposit feeders have the capacity to partition the resource (e.g., Fenchel et al., 1975) so that both niche width and niche overlap can vary. Different feeding strategies are influenced by environmental factors and consequently so is the distribution of trophic groups among communities (e.g., Rhoads, 1974; reviewed by Snelgrove and Butman, 1994).

Factors such as stability, water and organic content, oxygen content, particle size and microbiomass of sediment have all been shown to be significantly correlated with trophic composition of benthic communities (Gaston, 1987). No such quantitative data were available for this present study, but there is information on parts of the Bay about sediment characterisation (Jeffrey et al., 1978; Wilson, 1983), tidal height (Wilson, 1993) and pollution status (Wilson et al., 1986; Jeffrey et al., 1991).

Wilson (1982), (1983) concluded that tidal height and sediment type, which to some extent were correlated, were the dominant factors for macrobenthos distribution in Dublin Bay, but noted that axes 1 and 2 of his principal coordinates analysis (PCOORD) accounted for only 18% of the total variation. A similar influence of tidal height and

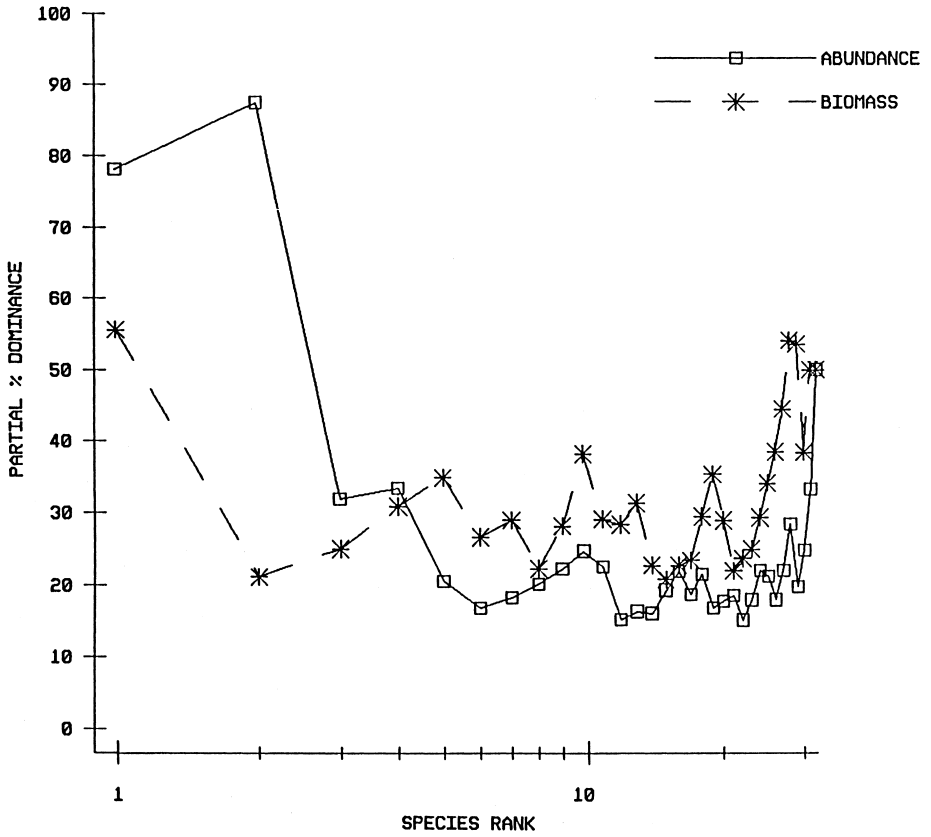


Fig. 9. Partial dominance curves of functional community E (deposit feeders).

Table 6
Descriptive statistics of W values of functional communities

Functional community	No. of samples	Average of W	SD of W	Min. of W	Max. of W
A	70	0.074	0.147	-0.273	0.476
B	65	0.177	0.188	-0.301	0.715
C	30	0.226	0.209	-0.204	0.568
D	11	0.109	0.202	-0.429	0.478
E	25	-0.096	0.130	-0.287	0.324
F	36	0.144	0.220	-0.416	0.458
G	16	0.238	0.233	-0.067	0.604
H	14	0.298	0.054	-0.544	0.912
I	9	0.079	0.292	-0.222	0.521

All samples with only one species (W=1) are omitted. Therefore the number of samples of functional communities is reduced compared to Table 5.

Table 7
Comparisons of *W* values between functional communities using Mann–Whitney test

	B	C	D	E	F	G	H	I
A	-3.55**	-2.43*	-0.76	-4.21***	-0.99	-1.16	-0.58	0.82
B	-	-0.79	-2.12*	-4.04***	-2.07*	-0.07	-1.92	-0.88
C	-	-	-1.23	-4.02***	-1.29	-0.20	-2.22*	-1.59
D	-	-	-	-2.83**	-0.44	-1.80	-0.03	-0.59
E	-	-	-	-	-4.60***	-3.15**	-3.01**	-1.24
F	-	-	-	-	-	-1.44	-0.80	-0.17
G	-	-	-	-	-	-	-0.87	-0.77
H	-	-	-	-	-	-	-	-0.65

*,** and *** indicate significant at $p=0.05$, $=0.01$ and $=0.001$ respectively.

sediment type can be seen in the distribution of the groups in Fig. 1, especially on the South Bull. Burd et al. (1990) consider that PCOORD is simply a more generalised form of multidimensional scaling (MDS), the method recommended by Warwick and Clarke (1991), (1994) as the most sensitive in detecting community change. Grouping by

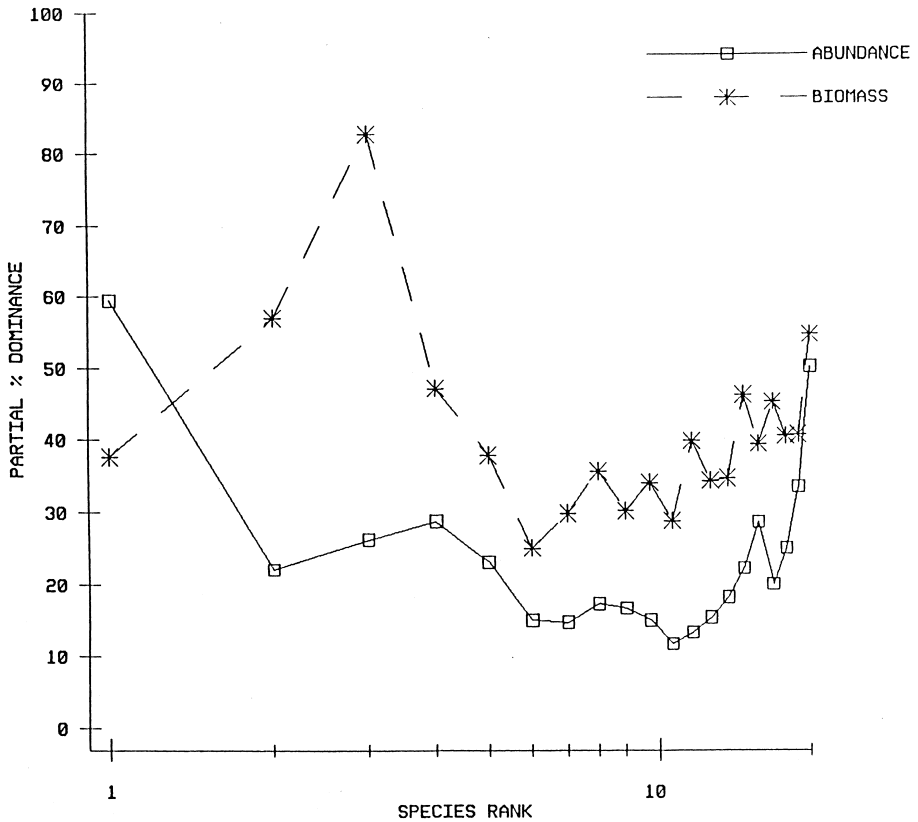


Fig. 10. Partial dominance curves of functional community G (carnivores 1).

trophic preferences produced a much stronger separation, with correctness typically being over 70% (Table 5). Evidence of better discrimination is also shown by the trophic groupings (Fig. 3(a–c)) which suggest different assemblages in the north and south Bays, a difference which Wilson (1983) had been unable to detect. The correctness of the groupings and the robustness, in that the re-classification of species whose trophic mode was uncertain or mixed did not materially change the zonations, of the approach suggests that it has potential as a powerful tool to investigate system function and organisation.

The different trophic groups are associated with different biotopes, although the strength of the groupings was rather surprising given that their boundaries will inevitably lie across environmental gradients which, while strong in the inner parts of the Bay, were certainly much more diffuse on the north and south Bays. This suggests that another factor, based on the trophic differences which were the basis for the groups, was operating.

Deposit feeders were restricted to the muddy lagoons and to some upper shore sites, although there was a gradient in deposit feeder dominance and evidence of coexistence with other feeding types (Fig. 3(b)). Deposit feeders, when present at high densities, can prevent the establishment of other feeding types (Rhoads and Young, 1970; Levinton, 1972; Gray, 1981). Coexistence between deposit feeders and suspension feeders should therefore be limited either to areas with a substrate sufficiently stable to allow suspension feeders to colonise (which implies limited reworking of the sediment) or areas with high densities of tube-dwelling polychaetes (Rhoads and Young, 1970; Young and Rhoads, 1971). In the Dublin Bay intertidal, sediment-stabilising large polychaetes have a relatively restricted distribution and occur mostly in low numbers along the low water mark (Wilson, 1983). Sediment ingesters such as the polychaete *S. armiger*, which only occurred in low densities in sites with mixed communities of suspension feeders and deposit feeders, and the much larger *Arenicola marina* were much more widespread (Wilson, 1983). However, it must be stated that the data used here are based on a single survey and can only present this type of mixed community, but cannot demonstrate or explain the development and establishment of coexistence of deposit feeders with other feeding types over time. A similar caution should be entered as regards spatial variability and patchiness in relation to the scale of sampling.

The structure of the suspension feeder community changes along the gradient from the top of the shore to low water (Fig. 3(a)), with varying degrees of dominance by *C. edule*, even if the actual species composition does not. Wilson (1993) in Dublin Bay and Dankers and Beukema (1975) in the Wadden Sea have shown that *C. edule* reaches its maximum density at a tidal height around mean sea level or just above. However, in the community (Group B) at this level *C. edule* represented <50% of abundance even if it did dominate the biomass. Group A, which was found both higher and lower on the shore than group B, was representative of another type of *C. edule* community, in which a decline in the density, that is in the numbers of individuals, was combined with an increase in proportional abundance of *C. edule*, suggesting that this species is either more robust or can occupy a wider niche, than some of its sympatriots.

The Tolka basin is that part of the area studied in Dublin Bay with the highest stress factors, both in terms of the freshwater input and anthropogenic pollution (Jeffrey et al.,

1985). Wilson (1983) reported low biomass but both high and low diversity from sites close together within the Tolka basin. In the analysis presented here, the carnivore communities (groups G, H) were the most common (Fig. 3(c)), although there were other functional communities represented (Fig. 3(a,b)). This coexistence can be interpreted as the result of a rather arbitrary development following pollution or environmental disturbance. While the presence of the predators may simply indicate their mobility, they may also be responding to the abundances of opportunistic small polychaetes and oligochaetes which were not sampled by the 1.0 mm mesh (Wilson, 1983).

In the Tolka basin, many sites had either no benthic macrofauna or at most a one species system of *N. virens* or *N. diversicolor*, both at very low abundance. *N. diversicolor* in particular has been shown to be markedly resistant to pollution (e.g., Bryan and Hummerstone, 1971), and both species are mobile enough to migrate into unoccupied niches, from which under normal conditions they might be displaced over time by a more complex system dominated by the carnivores (groups G, H). Colonisation by suspension feeders such as *C. edule* or *M. edulis* and their coexistence with carnivores might be the final stage in the succession in the Tolka basin. These changes in species composition and community structure can be considered as evidence of resilience of the benthic system as a whole.

Because all these stages of community succession occur together in an irregular pattern in the Tolka basin, it must be assumed that the extinction of biota at the single sites happens irregularly and randomly. Therefore the starting points of resilience of the benthic community are distributed randomly and all stages of the process occur together in a mosaic of patches. This would lead to the high variability (standard deviation) of *W*-values noted in the Tolka basin (subareas I, II; see Table 2).

High variability of the *W* values were observed both for the subareas (Table 2) and for the functional communities (Table 6). However, despite this variability some pattern can be discerned. The lowest *W* values are associated with deposit feeders, both in terms of the spatial groupings (areas IV and V, Table 2) and the functional groups (groups E, Table 6). This supports Beukema's (1988) criticism that the ABC-curve could not be used to detect pollution disturbance in deposit feeding controlled areas without an exact knowledge of the species composition. Thus, in communities with high numbers of small species or of juveniles, the value of partial dominance curves (Fig. 9) from which the successive contributions of each species to community structure may be identified, becomes evident. What was shown in the Beukema (1988) study was disturbance and since pollution is merely a subset of this, it cannot be detected by the ABC method which cannot distinguish between physical and chemical effects.

This study reveals the need to include data on functional community structure in the assessment of the influence of disturbance on intertidal benthic fauna through dominance curves or related methods. A summary of sites with different functional communities can be misinterpreted or reveal an irregular pattern. Undoubtedly also, the paucity of species at some sites can result in misleading results, for example in the one- or two-species system in the Tolka which yielded *W* values, ABC curves and partial dominance curves indicative of an undisturbed area (subarea I; see Table 2), yet which had been evaluated by other methods, including chemical analyses, as being under severe pollution stress

(Jeffrey et al., 1985). It is interesting to speculate to what extent the use of a smaller mesh (e.g., 0.5 mm as opposed to 1.0 mm), which would have retained many more small worms, would have changed this particular conclusion.

The high number of subareas and of functional communities that were assessed as disturbed by ABC curves and by partial dominance curves indicate a general fluctuation and instability in environmental conditions in the intertidal. These environmental disturbances impact in the same manner as pollution disturbances, and thus methods which have been used with success in the subtidal, where environmental fluctuations are less severe, have to be employed and interpreted with caution in the intertidal. A similar caution exists for estuaries (Wilson and Jeffrey, 1994). In terms of discrimination, that is the power to detect disturbance, the partial dominance curves indicate more disturbed systems and thus seem to be more sensitive, as reported by Clarke (1990).

But can a comparison of W values, based on functional pattern data, be used to detect disturbance status of the subarea? After excluding all sites which are either controlled by deposit feeders (subareas IV, V) or colonised by very few species (subarea I), the outer Tolka basin is picked out as the most disturbed area because it has the lowest W values (subarea II; see Table 2).

The W values are also connected to the stability of the environment when the suspension feeder communities are considered. W values increase from high shore to low shore as the community changes from one dominated by suspension feeders of a large body size, to one again dominated by suspension feeders but typically with many more smaller *C. edule* and finally to one with a range of species and feeding types (Figs. 2 and 3(a–c)). Physical stresses decrease from high to low shore, and physical control is replaced by biological, linking in with the increased stability in the low shore region. It has been suggested (Wilson, 1991, 1984; Wilson and Elkaim, 1991) that *C. edule* is more tolerant of emersion and its consequences than some other benthic bivalves (e.g., *A. tenuis*, *M. balthica*) found in the Bay, and thus survives better on the inner parts of the south Bay which dry out for long periods. The north Bay is more exposed, with a narrower intertidal area and was found to be equivalent to the middle part of the south Bay in regard to W values and its functional communities (Figs. 2 and 3(a–c)).

Beukema (1988) used the difference between biomass and abundance to condense the plots into a single value, for which zero was seen as the indicator threshold for disturbance. This present study, by using W values instead of Beukema (1988) summed figures, reveals that zero is not a threshold value, but rather that trends in W values can be used to detect disturbance, provided that this is taken in conjunction with a knowledge of functional structure in the benthic community.

In summary, the ABC method and related treatments have little or no power to detect pollution effects in intertidal systems like Dublin Bay. However, the methods employed, especially the partial dominance curves, picked out the dynamics and changes in the functional communities. Therefore the importance of functional groups such as suspension feeders can be understood through the details of the spatial and temporal development of the benthic fauna (see e.g., Herman and Scholten, 1990). Further testing would seem to be indicated to see if the methods might help to distinguish pollution and naturally caused disturbance in long term surveys (e.g., Clarke and Green, 1988).

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