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Sources of mortality and associated life-cycle traits of selected benthic species: a review

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FOREWORD

This review was prepared as a working document for an ICES Study Group on the Ecosystem Effects of Fishing Activities which met for the second time in April 1992*. Its aim was to provide an assessment of the relative importance of a variety of sources of mortality of selected benthic species, amongst which the action of commercial trawling and dredging at the seabed were of particular interest. Because such an appraisal necessitated a consideration of the influence of a wide range of factors (natural and anthropogenic) in attempting to place fishing effects in context, the account was felt to have a wider interest, notably because it crossed traditional boundaries for applied assessments. While several of the species will be familiar to fisheries or environmental scientists, synopses of relevant information along the lines of the following account have not hitherto been readily available.

There is clearly scope for widening the approach to other named species or species-groups for which integrated assessments of the implications of man-induced changes are likely to be helpful. It is hoped that this account will provide a stimulus for future activity.

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1. INTRODUCTION

Depending on the objectives of investigation, studies of the benthos may vary from assessments of the functional properties of whole communities e.g. standing stock and production (which may be particularly important in relation to fish-feeding), to evaluations of individual benthic species of commercial value (of which there are several examples) and, finally, to determinations of the densities, distribution or well-being of individual species or species-groups which are valued strictly on aesthetic or scientific criteria (e.g. environmental indicator status). However, there is frequently common ground between these various interests.

The purpose of this review is to summarise the available information on the responses of selected benthic species to natural and anthropogenic influences, amongst which the effects of fishing activities are of particular current interest, in relation to assessments of the quality status of the North Sea.

Nine species were selected, representing four major invertebrate groups (Polychaeta, Crustacea, Mollusca and Echinodermata). They were considered to provide a reasonable spread across the 'r/K' continuum (see Pianka, 1970 and Annex), and - in combination - cover a wide range of habitats, geographical areas and 'sensitivities' to natural and anthropogenic factors. Although at least three of the species are valued commercially, all were examined in similar fashion under the following pre-defined headings:

(i) species characteristics: life-style, habitat/distribution, densities, biomass/production, life-cycle strategy, recruitment, longevity, annual mortality rate;

(ii) sources of mortality: burial/wash-out, temperature, predation, plankton blooms/eutrophication, trawl/dredge effects, pollution and 'other'.

This was to avoid any pre-disposition to rank them according to, for example, their 'nutritive', 'conservation' or 'nuisance' status. Inevitably, however, there was some tendency for published studies to reflect such different viewpoints, whether in terms of their quantity or content.

Regarding anthropogenic effects, it is known that diffuse inputs of nutrients, such as those arising from agricultural land run-off, may contribute to eutrophication and related consequences (e.g. Rosenberg, 1985). However, it is often very difficult to separate natural from man-made influences, and so events associated with the latter (if and where present) were considered alongside those such as the collapse of algal blooms in 'pristine' areas, which appear to be entirely natural in origin.

The consequences of other anthropogenic inputs are separately dealt with under 'pollution', and assessment is confined to the outcome of field studies, rather than inferences from laboratory-based toxicity tests. Serious oil spills are excluded from consideration under this item, on the basis that it is extremely difficult to predict where such events might occur in the future, if at all. For the same reason, 'chance' natural events, such as failure of recruitment due to abnormal weather conditions, cannot be accounted for, even though they may have significant longer-term consequences for the survival of local populations (e.g. Lewis, 1980).

The review begins with a synopsis of the available literature along the above lines, and is followed by an assessment of the relative importance of a range of factors governing the survival of populations which, as will be seen, necessarily involved a subjective element. The merits and limitations of such an approach to sea-wide assessments of anthropogenic influences are
considered and, finally, a summary is given of the main conclusions arising from the exercise.

2. SYNOPSIS OF PUBLISHED INFORMATION

2.1 *Pectinaria (Lagis) koreni* (trumpet worm)

Life-style: infaunal, tubicolous, deposit-feeder; motile while feeding within surface layer of sediments (see e.g. Schafer, 1972); often co-occurring with high densities of *Abra alba* (e.g. Eagle, 1975; Caspers, 1987).

Habitat/distribution: typically muddy sands or sandy muds, reaching highest densities in inshore regions; widely distributed in the North Sea/English Channel.

Densities: adult densities may exceed 1000 m^{-2} (e.g. Eagle, 1975; Nichols, 1977; Rees *et al.*, 1992); numbers characteristically fluctuate widely from year to year, due to variations in recruitment success/mortality.

Biomass/production: annual production P = 18.3 g AFDW m^{-2} y^{-1}; average annual biomass B = 2.5 g AFDW m^{-2}; P:B = 7.3 off the North Wales coast, UK (Nicolaidou, 1983, converted to AFDW after Brey, 1990); B (September only) = 5.8-51.4 g AFDW m^{-2} in Liverpool Bay, UK (Rees *et al.*, in prep.); P:B = 3 off the French coast (Elkaim and Irlinger, 1987); P = 3-10.4 g AFDW m^{-2} y^{-1}; B = 0.6-3 g AFDW m^{-2}; P:B = 3.2-5.4, for the related species *Pectinaria californiensis* off the US coastline (Brey, 1990, after Nichols, 1975).

Life-cycle strategy: 'r'; rapid growth following settlement, reaching sexual maturity within one year (e.g. Nicolaidou, 1983); these attributes, accompanied by flexibility in other life-cycle traits, are commonly associated with species that thrive in unstable environments. (Similar population characteristics were found in the related species *P. australis*: Estcourt, 1974).

Recruitment: via pelagic larvae: numbers settling are typically erratic from year to year, but may reach several thousand m^{-2} (e.g. Macer, 1967; Basimi and Grove, 1985); Nichols (1977) noted an early and late summer recruitment in Kiel Bay, but with additional sporadic recruitment occurring through most of the year. Comparable events were recorded by Elkaim and Irlinger (1987) in Seine Bay, France, with one or two main recruitment periods, depending on year and location. Nicolaidou (1983) observed only one recruitment (in June) off the North Wales coast, UK. Colonisation of any new or disturbed substrata may also occur through re-distribution of adults (e.g. Eagle, 1975; Rees *et al.*, 1977).

Longevity: probably rarely exceeding one year in nature, though animals survived for 2.5 years in laboratory conditions (Nicolaidou, 1983).

Annual mortality rate: typically approaching 100%.

Sources of mortality:

(i) ***Burial/wash-out***: dense populations characteristically occur in organically-rich inshore sediments, e.g. off estuary mouths, and hence are often vulnerable to storm-induced sediment disturbance; Rees *et al.* (1977) recorded strandings following storms on the North Wales coast; feeding activities of the animals themselves may contribute to sediment instability (Eagle, 1975; Rees *et al.*, 1975); sediment re-working rates of up to 83 mg $worm^{-1}$ h^{-1} were observed by Dobbs and Scholly (1986). Animals have the capacity to upwardly migrate if lightly buried (Schafer, 1972).

(ii) ***Temperature***: Arntz and Rumohr (1986) report sensitivity to extremely low bottom temperatures for Baltic populations; feeding rate appears to be temperature-related (Nicolaidou, 1983; 1988).

(iii) ***Predation***: a significant food-source for commercially-important demersal fish, especially dab and plaice, e.g. Macer (1967), Lockwood (1980), Basimi and Grove (1985): seasonally-averaged contribution by weight to diet amounted to some 35%, Carter *et al.* (1991); Peer (1970) estimated that about 80% of mortality of the related species *Pectinaria hyperborea* was due to predation, in Canadian waters.

(iv) ***Plankton blooms/eutrophication***: high mortality associated with periodic oxygen-deficiency of bottom waters of Kiel Bay (e.g. Nichols, 1977), but capable of rapid re-colonisation through larval recruitment following such events, reaching former densities within a year (e.g. Arntz and Rumohr, 1986); mortality at some (but not all) stations in the German Bight, following a period of low oxygen concentrations (Niermann *et al.*, 1990).

(v) ***Trawl/dredge effects***: Schafer (1972) notes that adults are incapable of re-constructing (delicate) sand-tubes once removed from them, and hence mortality following any damage from trawl/tickler chain disturbance must be very high; this is also true for animals retained in nets (e.g. de Groot and Apeldoorn, 1971).

(vi) ***Pollution***: may favour moderate organic enrichment, but displaced in anoxic sediments (e.g. Pearson and Rosenberg, 1978); preferentially recolonise perturbed habitats such as dredged material disposal sites (Rees *et al.*, 1992 and in prep.).

(vii) ***Other***: feeding activities of dense adult populations may inhibit survival of new recruits (e.g. Eagle, 1975).

2.2 *Sabellaria spinulosa* (Ross worm)

Life-style: sedentary, epifaunal, tubicolous suspension-feeder; in favourable conditions, colonies consisting of fused sand-tubes develop, which can form extensive reefs, commonly known as 'Ross' (see e.g. Schafer, 1972).

Habitat/distribution: typically on shell (especially oyster valves), sandy gravel or rocky substrates with moderate to strong tidal flow, from the low intertidal to offshore; widespread in North Sea/English Channel.

Densities: colonies may support large numbers of adult individuals, e.g. over 6000 m^{-2} in the Bristol Channel, UK (George and Warwick, 1985).

Biomass/production: P = 0.76 g AFDW $m^{-2} y^{-1}$; mean annual biomass B = 4.56 g AFDW m^{-2}; P:B = 0.2 (George and Warwick, 1985).

Life-cycle strategy: 'K'; colonies are often persistent, individuals are slow-growing and may live for several years (George and Warwick, 1985).

Recruitment: via planktonic larvae; in low numbers in March and November for a Bristol Channel population (George and Warwick, 1985); Wilson (1970) found planktonic larvae in the Plymouth area from January to April; annual intensity of settlement of the related species *Sabellaria alveolata* was very variable at an intertidal location, ranging from zero to high densities (Wilson, 1976); larvae preferentially settle on existing colonies (Schafer, 1972).

Longevity: no precise information, but some individuals of *S. alveolata* may live for at least 10 years (Wilson, 1971; 1974); Schafer (1972) notes that some reefs of *S. spinulosa* survive for one or two years only, unless re-inforced by new settlement, suggesting a shorter life-span.

Annual mortality rate: little information, but appears to be very low in Bristol Channel populations (George and Warwick, 1985).

Sources of mortality:

(i) ***Burial/wash-out***: colonies of *S. alveolata* dominated by old individuals become increasingly prone to fragmentation unless re-inforced by a new recruitment; killed by prolonged burial under sand, but may survive for several weeks beforehand (Wilson, 1971; Schafer, 1972).

(ii) ***Temperature***: mortality of intertidal *S. alveolata* noted at a number of UK locations, but colonies of *S. spinulosa* were unaffected, following the severe winter of 1962/63 (Crisp, ed, 1964).

(iii) ***Predation***: other polychaetes e.g. *Lepidonotus* (Schafer, 1972); an association between the pink shrimp *Pandalus* and *Sabellaria* reefs has long been appreciated, and laboratory observations on feeding have demonstrated a predatory capability (Warren, 1973); however, the association may be as much a function of the often prolific nature of the benthic food supply associated with Ross colonies, as of the presence of the worms themselves.

(iv) ***Plankton blooms/eutrophication***: no information

(v) ***Trawl/dredge effects***: although healthy colonies are robust to all but the most severe weather, their vulnerability to damage by bottom-fishing gear has long been recognised; furthermore, they are apparently unable to re-build tubes once dislodged from them (Schafer, 1972). Riesen and Riese (1982) ascribed the disappearance of *Sabellaria* reefs at a location in the German Wadden Sea to destruction by shrimp-fishing trawls. Mussel beds have now extended over parts of a nearby area subject to similar change (Riese and Schubert, 1987). The same explanation has been offered for reduction in reefs off parts of the UK coast (Mistakidis, 1956; Warren, 1973; see also Graham, 1955; Rees, 1982).

(vi) ***Pollution***: no information.

(vii) ***Other***: no information.

2.3 *Cancer pagurus* (edible crab)

Life-style: motile epifaunal predator/scavenger.

Habitat/distribution: on substrates ranging from sand/gravel to rock, at depths from 0-200 m; widely distributed in the North Sea/English Channel; juveniles tend to be found inshore, and adults offshore.

Densities: clearly varies according to the suitability of the habitat; sampling is done mainly with baited traps, so densities per unit area are not available.

Biomass/production: no information; (commercial landings presently amount to some 10 000 tonnes y^{-1} for England and Wales).

Life-cycle strategy: 'K'; high fecundity, wide larval dispersal and relatively long-lived. Reach maturity (first breeding) at about five years old; growth (moult frequency) reduces with age, more so for females; maximum size c. 270 mm carapace width (4 kg live wt) for males, c. 240 mm (2 kg) for females (Bennett, in press).

Recruitment: planktonic larvae found over several months (April-November), and widely distributed; adult females make extensive directed movements, probably to spawning/ hatching grounds, compensating for larval drift; ovigerous females overwinter without feeding (Bennett, in press).

Longevity: c. 10-20 years.

Annual mortality rate: natural mortality of adults c. 10%; fishing mortality up to 60% (D. B. Bennett, Ministry of Agriculture, Fisheries and Food: pers. comm.).

Sources of mortality:

(i) ***Burial/wash-out***: occasional reports of mass strandings on beaches following storms (e.g. north-east coast of England: D. B. Bennett, pers. comm.).

(ii) ***Temperature***: reasonably temperature-tolerant, though several observations of dead specimens in the southern North Sea during the severe winter of 1962/63 (Crisp, ed, 1964).

(iii) ***Predation***: fish eat juveniles; Schafer (1972) notes predation by catfish, which are well adapted for crushing shells; *Cancer* are noted as a component of the diet of US *Asterias* populations (Menge, 1979). Vulnerable to predation when soft (i.e. recently moulted) at which stage they usually seek shelter; adult females in this state are accompanied by hard males for mating and protection (D. B. Bennett, pers. comm.).

(iv) ***Plankton blooms/eutrophication***: dead *Cancer* observed at some rocky localities in response to a *Chrysochromulina* bloom along the Norwegian coast (Bokn *et al*., 1990); occasional dead specimens noted following a plankton bloom off the Cornish coast, UK (Griffiths *et al*., 1979).

(v) ***Trawl/dredge effects***: mortality arising from damage or retention for commercial sale will be associated with an unquantified 'bycatch' from bottom trawls and dredges, along with probable unseen damage and mortality at the seabed; in experimental beam-trawling off the Dutch coast, mortality among trawl-caught specimens amounted to some 40% of large crabs during daylight, but rarely at night, possibly due to their nocturnal activity at the sediment surface which resulted in their being caught undamaged (Bergman *et al*., 1990).

(vi) ***Pollution***: some evidence to suggest mortality of adults of the related species *Cancer irroratus* during summer offshore migration across a sewage-sludge disposal site in the New York Bight; similarly for settling larvae in the vicinity of sewage-sludge and dredgings disposal sites (Pearce, 1972); higher prevalence of shell disease noted in sewage-contaminated areas (Sawyer, 1991). Destruction of habitat through e.g. infilling of rock crevices in the vicinity of inshore solid-waste disposal sites along the north-east coast of England has been cited as a cause of locally-reduced commercial catches (Shelton, 1973).

(vii) ***Other***: a commercially-fished species (see Edwards, 1979): widely exploited, mainly using pots; some tangle-netting (e.g. off south-west Britain). Schafer (1972) notes that colonies of *Sabellaria* settling on the carapace can eventually render the animal top-heavy, usually resulting in death through starvation or predation; however, this is unlikely to be a significant source of mortality in population terms.

2.4. *Abra alba* (white furrow shell)

Life-style: thin-shelled surface deposit feeder, typically found in the top 1-2 cm layer of sediments.

Habitat/distribution: a characteristic inhabitant of inshore muddy sand or mud substrates in north-west European waters; typically from the shallow sublittoral to 70 m, but especially abundant in depths to 20 m (Tebble, 1966).

Densities: adult densities may exceed 1000 m^{-2} in favourable conditions (e.g. Caspers, 1987; Rees *et al*., in prep.); abundances typically fluctuate widely from year to year due to variation in recruitment success or adult mortality (e.g. Muus, 1973; Eagle, 1975; Rees and Walker, 1983; Rainer, 1985; Arntz and Rumohr, 1986; Caspers, 1987; Dauvin and Gentil, 1989).

Biomass/production: in Kiel Bay, mean annual biomass varied markedly between sites and between years: B = 0.1-3 g AFDW m^{-2}; long-term average P:B = c. 2.2 (Rainer, 1985); B = 0.1-2 g AFDW m^{-2} and P:B = 1.7-2.9 from 5 years of sampling at a location off the French coast (Dauvin, 1986); B = 0.3 g AFDW m^{-2} and P:B = 1.4 in the Bristol Channel, UK (Warwick and George, 1985); B (September only) = 0.3-111.7 g AFDW m^{-2} in Liverpool Bay, UK (Rees *et al*., in prep.).

Life-cycle strategy: 'r'; capable of rapidly exploiting any new or disturbed substratum suitable for colonisation through larval recruitment, secondary settlement of post-metamorphosis juveniles or re-distribution of adults following storms (e.g. Eagle, 1975; Rees *et al*., 1977; Bosselmann, 1991(a)). Off the French coast, juveniles settling in Autumn reached sexual maturity in about 6 months; most lived only one year, reaching modal lengths of 1.2-1.4 cm (Dauvin, 1986); typically 1.3-1.6 cm after 2 years in Kiel Bay (Rainer, 1985); maximum length c. 2-2.5 cm (e.g. Ansell, 1974; Eagle, 1975; Hily and Le Bris, 1984).

Recruitment: varies between localities, e.g. peak in recruitment usually in August, sometimes with a second peak between December and February in Kiel Bay (Rainer, 1985); Dauvin and Gentil (1989) found three recruitments (in February-March, April-June and August-October) in response to eutrophic conditions following the Amoco Cadiz oil-spill in the Bay of Morlaix, France. This was considered to be an adaptive response over the normally-occurring twice-yearly recruitment. Two peaks (in July and Sept-Oct) were noted in the Limfjord (Jensen, 1988), with densities in excess of 20 000 m^{-2} being recorded; Warwick and George (1980) inferred that settlement in Swansea Bay, UK could occur over a period of several months (July-November). Similarly, Glemarec and Menesguen (1980) identified overlapping cohorts in populations from the Bay of Concarneau, France, which indicated pulses of recruitment occurring throughout the year (see also Hily and Le Bris, 1984).

Longevity: 1-2.5 years (Kiel Bay: Rainer, 1985); c. 1.5 years (French coast: Dauvin, 1986); 3+ years in deeper water off the Scottish coast (Ansell, 1974).

Annual mortality rate: typically approaching 100%, as would be expected; mortality occurred mainly between January-June, and by weight approximately equalled production over a 3-year period (Kiel Bay: Rainer, 1985); 98.5% for juveniles of the related intertidal species *Abra tenuis* (Bachelet, 1989).

Sources of mortality:

(i) Burial/wash-out: vulnerable to wave-induced bottom disturbance, but those not damaged or predated as a consequence are capable of re-colonising new substrates if conditions are favourable (see Rees *et al*., 1977); animals may also have the ability to excavate themselves if lightly buried. Feeding activities of the animals themselves may contribute to destabilisation of sediments (Eagle, 1975).

(ii) Temperature: Arntz and Rumohr (1986) noted sensitivity to extreme low temperatures in Kiel Bay, recovery to former densities taking some 2 years; high mortality of Wadden Sea populations of the related intertidal species *Abra tenuis* following a severe winter (Beukema, 1979).

(iii) Predation: a common food item for (*inter alia*) *Asterias rubens* and demersal fish (e.g. Rees *et al*., 1977); *Abra* constituted some 20% by weight (annual average) of the important food species of plaice in Kiel Bay (Arntz, 1980; see also Rainer, 1985) and some 40% by weight (seasonal average) off the North Wales coast, UK (Basimi and Grove, 1985; see also Carter *et al*., 1991). Production in Kiel Bay appears to substantially exceed consumption by commercially-sized species, but *Abra* may also be an important food source for juvenile fish and 'intermediate-level' predators (Rainer, 1985). Significant effect of the predatory gastropod *Lunatia* (*Natica)* on mortality of an offshore population of the related species *Abra nitida* (Josefson, 1982).

(iv) Plankton blooms/eutrophication: reported to be sensitive to lowered oxygen concentrations arising from eutrophication off the Swedish west coast (Rosenberg and Loo, 1988); lethal effects of low oxygen concentrations also noted by Weigelt and Rumohr (1986) and Arntz and Rumohr (1986) for the western Baltic, recovery to former densities taking some 1.5 years. (See also review of mortality/recolonisation of benthos following oxygen depletion events in this area by Weigelt, 1991).

***(v) Trawl/dredge effect*s**: delicate shells vulnerable to physical damage (e.g. by otter boards: Rumohr and Krost, 1991), but small size relative to meshes of commercial trawls may ensure survival of at least a moderate proportion of disturbed individuals which pass through.

(vi) Pollution: high abundances in moderately-enriched environments (e.g. Caspers, 1987).

(vii) Other: competition for space/food seems a likely source of mortality at some locations where very high densities at settlement occur (e.g. Caspers, 1987).

2.5 *Arctica* (*Cyprina*) *islandica* (ocean quahog/clam)

Life-style: infaunal sedentary filter-feeder.

Habitat/distribution: widespread in the North Sea and English Channel; on firm bottoms of sand and muddy sand, from low intertidal zone to considerable depths (Tebble, 1966); more common in the deeper muddy areas of the central and northern North Sea, where it is less prone to sediment perturbations, according to Schafer (1972); (see also Lutz *et al*., 1982). In coarse sand (USA); c. 4-256 m in the north-west Atlantic (Merrill and Roper, 1969; Lutz *et al*., 1982).

Densities: small (0.1 m^2) grab samplers are unlikely to provide accurate density estimates, at least for adult populations in the North Sea; c. 50 m^{-2} in Kiel Bay (Brey *et al*., 1990).

Biomass/production: no information for North Sea; on major fishery areas of the north-west Atlantic, standing stock expressed as wet meat weight over 119 000 km^2 averaged 10 g m^{-2}, with a maximum (over 19 000 km^2) of 16 g m^{-2} (Murawski and Serchuk, 1989(a); note that total live wt. shell/flesh wt. ratio is not stated, but is presumed to be 2:1 or 3:1). For Kiel Bay, annual P = 15 g AFDW m^{-2} y^{-1}; B = 44.4 g AFDW m^{-2}; P:B = 0.34 (Brey *et al*., 1990: *Arctica* accounted for some 40% of total benthic community production).

Life-cycle strategy: 'K'; characteristically stable, long-lived populations with very slow growth; growth rates (for the first 20 years) of Atlantic and Baltic populations were very similar (Brey *et al*., 1990).

Recruitment: via planktonic larvae: settlement may occur over several months (see Thompson *et al*., 1980(a)); very low recruitment to adult populations off the US coast (over a 21-year study period), and delayed maturity: at a mean age of 12-13 years for Canadian populations (Rowell *et al*., 1990); comparable evidence for delayed maturity from the mid-Atlantic Bight (Thompson *et al*., 1980(b)).

Longevity: exceptionally long-lived: populations off north-east USA dominated by animals of 40-80 years old, with a substantial proportion over 100 years old; Ropes (1984) estimated the age of one individual to be 225 years old; modal age of 65-105 years, with specimens up to about 150 years, in a study of mid-Atlantic Bight populations (Thompson *et al*., 1980(a)); c. 20 years in Kiel Bay (Brey *et al*., 1990).

Annual mortality rate: 1-3% assumed, for consistency with observed longevity (Murawski and Serchuk, 1989(a)); mortality was higher for younger and older specimens, than for intermediate ones, in Kiel Bay: this may be explained by opposing trends of decreased vulnerability to predation of whole specimens with age, against increased vulnerability to trawl damage with age (Brey *et al*., 1990; see also below).

Sources of mortality:

(i) Burial/wash-out: sudden sedimentation (e.g. during abnormal weather) is likely to be a source of mortality for inshore populations (Schafer, 1972); small numbers noted on North Wales coast following storms (Rees *et al*., 1977). Clearly, the extensive deep-water populations are not prone to such effects.

(ii) Temperature: no abnormal mortalities of subtidal populations reported during the severe winter of 1962/63 (Crisp, ed, 1964).

(iii) Predation: crabs, including *Cancer*, on juveniles (USA); catfish (Schafer, 1972); asteroids, e.g. *Asterias* (Anger *et al*., 1977; Hunt, 1925 in Vevers, 1949). Cod and dab are important predators in the Baltic (e.g. Arntz, 1980): Brey *et al*. (1990) estimated that some 40% of annual cod production depended on *Arctica*, in the period 1970-85; also noted in stomachs of North Sea cod (Cramer and Daan, 1986), though its role as a food source evidently bears no comparison with the Baltic.

(iv) Plankton blooms/eutrophication: adults generally considered to be tolerant of prolonged oxygen deficiency (see e.g. Rosenberg and Loo, 1988), though (exceptionally) Weigelt (1991) noted high mortality of a Baltic population following an anoxic event in 1985; similarly for parts of the New York Bight in 1976 (Murawski *et al*., 1989). *Arctica* has a capacity to respire anaerobically (Taylor, 1976).

(v) Trawl/dredge effects: hydraulic dredges cause significant non-harvest mortality (Murawski and Serchuk, 1989(b)); Medcof and Caddy (1971) estimated that some 80% of uncaught specimens, and some 20% of those caught, were damaged. Damage to older specimens caused by otter-trawls may release a significant amount of hitherto unavailable biomass for predatory fish in the Baltic (see Brey *et al*., 1990 and Rumohr and Krost, 1991); c. 90% damage of specimens noted in the 'by-catch' of beam trawl hauls off the Dutch coast (Bergman *et al*., 1990).

(vi) Pollution: no information.

(vii) Other: a commercially-fished species mainly in US waters, using dredges.

2.6 *Pecten maximus* (scallop)

Life-style: epibenthic filter-feeder; effectively sedentary, but with limited mobility e.g. as an escape-reaction.

Habitat/distribution: generally found on a range of gravelly and stony bottoms, but will also occur on sandier and rockier substrates; at depths from c. 20-100 m in the English Channel, where it is widespread and often common; scarce and very localised in the western North Sea and off the Norwegian coast.

Densities: rarely 1 m^{-2}; more typically 0.1-0.01 m^{-2} on (even unfished) good fishing grounds.

Biomass/production: rough estimates from French coast as follows: (i) St Brieuc Bay (1991): 8 000 tonnes of 2+ year-old animals on 600 km^2 (= c. 15g m^{-2} live weight, i.e. including shells); (*NB*. an exceptionally dense fishable stock; P. Berthou: pers. comm.); (ii) Baie de Seine (September, 1990): 1.3-5.7g m^{-2} live weight of 2+ year-old animals on main fishing areas (re-calculated after Vigneau and Morin, 1991); (iii) ICES Sector 7d (offshore, July 1990): 0.3-1.9 g m^{-2} live weight of 2+ year-old animals (re-calculated after Vigneau and Morin, 1991).

Life-cycle strategy: 'K'; reach first maturity at 2 years, and full maturity at 3-5 years; generally low population turnover.

Recruitment: via planktonic larvae; variable in time and space due to different spawning patterns; usually annual and of low-moderate intensity, with few large fluctuations.

Longevity: generally 15-20 years (exceptionally c. 25 years) in unfished stocks.

Annual mortality rate: c. 10-15% for adults.

Sources of mortality:

(i) ***Burial/wash-out***: small numbers washed up on the North Wales coast following storms (Rees *et al*., 1977); clearly, populations inhabiting deeper (50 m+) locations are not subject to such effects.

(ii) ***Temperature***: examples of mortalities due to severe cold include the Baie de Seine during the winter of 1985/6, and southern Ireland and St Brieuc Bay (North Brittany) in early 1963; also, widespread mortalities of coastal populations along the English south coast during the severe winter of 1962/63 (Crisp, ed, 1964).

(iii) ***Predation***: starfish (*Asterias*, *Marthasterias*) and crabs (especially *Cancer*) take juveniles and some adults (Sloan, 1980; Lake *et al*., 1987); spat are probably also taken by some fish, e.g. dragonets.

(iv) ***Plankton blooms/eutrophication***: no reports of significant mortalities, though Forster (1979) noted apparently moribund specimens in response to a plankton bloom off the UK coast.

(v) ***Trawl/dredge effects***: dredges cause mortality among uncaught animals left in tracks; possible trawl damage (slight).

(vi) ***Pollution***: no reports of significant mortalities; very unlikely in near-oceanic habitats.

(vii) ***Other***: a commercially-fished species (see Mason, 1983): widely exploited using dredges.

2.7 *Asterias rubens* (common starfish)

Life-style: epifaunal; motile; feeds on a wide range of benthic species (living or dead) but especially noted for predation of commercially-important bivalve molluscs e.g. *Pecten*, *Chlamys*, *Mytilus* (Mortensen, 1927; Vevers, 1949; Hancock, 1955; Dare, 1982). Anger *et al*. (1977) consider that *Asterias* on soft bottoms in the Western Baltic consume more macrofaunal biomass than commercially-important fish.

Habitat/distribution: widely distributed on hard and soft ground in the North Sea/English Channel from the littoral zone to >100 m.

Densities: up to 100 m^{-2} in aggregations (noted in Barker and Nichols, 1983); 2-31 m^{-2} on fine sand and 324-809 m^{-2} on algal carpets (Baltic: Anger *et al*., 1977); for two related species *A. vulgaris* and *A. forbesi* along the eastern US coast, average densities (where present) at a variety of inter- and shallow sub-tidal locations ranged from about 2-60 m^{-2} in the period May-October; some evidence of migration to deeper waters in winter (Menge, 1979); 300-400 m^{-2} on mussel beds during swarming (Dare, 1982; see also review by Sloan, 1980).

Biomass/production: size varies markedly with food availability and hence is not necessarily a good indicator of age; size may reduce in the absence of food (e.g. Hancock, 1958; Menge, 1979); may survive for many months in the virtual absence of food (Vevers, 1949); 0.3-2.1 g AFDW m^{-2} on sands and 11.7-23.5 g AFDW m^{-2} on algal mats (Baltic: Anger *et al*., 1977). Individual weights of related US species may range up to about 400 g wet weight (Menge, 1979; = 45 g AFDW using conversion factors in Rumohr *et al*., 1987).

Life-cycle strategy: 'r/K'; flexible in terms of growth and feeding (e.g. Vevers, 1949; Anger *et al*., 1977; see also Sloan, 1980); may grow to a radius of 8-9 cm and become sexually mature within one year in favourable conditions (Mortensen, 1927; Vevers, 1949); in Baltic populations, Nauen (1978) refers to a 'waiting stage' of varying duration for post-metamorphosed juveniles, prior to the onset of rapid growth, which would have adaptive value.

Recruitment: spawning from February to July depending on location (Nichols and Barker, 1984); planktonic larval phase of c. 90 days; settle on a wide range of substrates, followed by initial fast growth (Barker and Nichols, 1983); migration of adults to/from a locality notably in response to food supply probably very common (Sloan, 1980).

Longevity: no recognised means of ageing individuals from measurement of hard parts; 7-8 years according to Schafer (1972), which is in agreement with interpretation of size-frequency histograms for French populations (Guillou, 1983).

Annual mortality rate: little information; Hancock (1958) records 98% mortality of juveniles over 2 years, following a heavy settlement in the River Crouch, UK, which he ascribed to competition for limited food, cannibalism and predation by *Crossaster.*

Sources of mortality:

(i) Burial/wash-out: wave-induced transport, especially of juveniles, on soft sediments is probably a regular occurrence (e.g. Anger *et al*., 1977); burial following storm-induced sediment disturbance in shallower areas considered to be a significant source of mortality by Schafer (1972); beach strandings following storms have been noted (e.g. Rees *et al*., 1977); storm effects were considered by Menge (1979) to be a potentially important source of mortality for shallow-water populations of related US species of *Asterias*.

(ii) Temperature: autotomy (arm-shedding) then death in response to prolonged exposure to unusually high temperatures (Schafer, 1972).

(iii) Predation: predators include the starfishes *Crossaster* and *Luidia*; cannibalism also occurs (e.g. Mortensen, 1927; Hancock, 1958; see also Sloan, 1980); predated by a wide variety of demersal fish (Schafer, 1972); also crabs/lobsters, though the quantitative significance of this source of mortality is unclear (see comments in Menge, 1979 for related US species); birds, during swarming on intertidal mussel beds (Dare, 1982).

(iv) Plankton blooms/eutrophication: autotomy and then death in conditions of prolonged hypoxia (Schafer, 1972) e.g. as may occur following collapse of a plankton bloom; mass mortalities have been recorded in response to low oxygen conditions in the Kattegat (Laholm Bay, West Sweden: Rosenberg and Loo, 1988); extensive mortality of rocky-bottom populations in response to a toxic algal bloom along the Norwegian coast (*Chrysochromulina*: Bokn *et al*., 1990).

(v) ***Trawl/dredge effects***: readily caught in commercial trawls/dredges, but survival on return to sea may approach 100% according to Bergman *et al.* (1990); de Groot and Apeldoorn (1971) recorded damage to some 3% of trawl-caught *Asterias* and *Astropecten*; comparable figures were noted by Houghton *et al.* (1971); about 13% of animals retained in a sample dredge towed immediately behind an otter board were damaged (Rumohr and Krost, 1991); Rauck (1988) also refers to fishing-induced mortality of *Asterias*. The frequency of occurrence of *Asterias* with regenerating arms has been linked to damage caused by bottom trawls (de Graaf and de Veen, 1973).

(vi) ***Pollution***: no information.

(vii) ***Other:*** has been commercially fished for fertiliser (Mortensen, 1927; Schafer, 1972); not a popular animal in areas of commercial bivalve fisheries (see e.g. Hancock, 1958); parasitism of testes by a ciliate was observed in up to 30% of males in a population off Plymouth, UK, rendering most infertile (Vevers, 1951) :conse-quences for recruitment in subsequent years remain speculative, but could be significant if infestation was sufficiently widespread. Menge (1979) observed disease-related mass mortality in a population of the related US species *Asterias vulgaris*, though the causative agent was not identified. Reliable report (to P. Dare) from the Wash, UK of a low-intertidal swarm being killed by a summer rainstorm in 1988.

2.8 *Echinocardium cordatum* (heart urchin or sea potato)

Life-style: motile infaunal surface/sub-surface deposit feeder; found to c. 20 cm depth in sediments, but - according to Beukema (1985) - is mainly found in the upper 5 cm, penetrating deeper in winter than in summer; Bergman *et al.* (1990) recorded a peak in densities of larger specimens at 10-12 cm in sandy sediments at a location in the southern North Sea in August; 2 cm or less in offshore silty sand (Buchanan, 1966). Plays an important role in sediment bioturbation, through its feeding activities (e.g. Bromley, 1990).

Habitat/distribution: occurs littorally, but mainly associated with coastal and offshore sediments in the southern North Sea (e.g. Ursin, 1960; Kunitzer *et al.*, 1992) and coastal sediments of the English Channel (Holme, 1966); widely distributed, typically in sands or muddy sands. Sandy substrates may be favoured due to increased ability to pass large amounts of sediment through the gut (Buchanan, 1966; 0.38 g sediment animal^{-1} hour^{-1}: de Ridder and Jangoux, 1985). Tends to be replaced by lower densities of *Echinocardium flavescens*, *Spatangus purpureus* and *Brissopsis lyrifera* north of the Dogger Bank.

Densities: 5-10 m^{-2} in littoral sediments, and c. 40 m^{-2} offshore (Buchanan, 1966); about 12 m^{-2} on average, for central North Sea; maximum densities occur at c. 40 m, according to Ursin (1960); 15-20 m^{-2} (frequently 60-80 m^{-2}) in sands off the Dutch coast (in Schafer, 1972); >250 m^{-2} at times of juvenile settlement on the Dogger Bank (Davis, 1925, quoted in Ursin, 1960).

Biomass/production: in central/southern North Sea, accounted for 50% of benthic biomass at sandy sites, and 5% at muddy sites (Duineveld and Jenness, 1984). P = -0.012 g AFDW m^{-2} y^{-1}; B = 5.138 g AFDW m^{-2}; P:B = -0.002 (Carmarthen Bay, UK: Warwick *et al.*, 1978).

Life-cycle strategy: 'K'; growth rates vary with location, e.g. faster in shallow-water sands than deeper-water muddy sands; possibly temperature-mediated (Duineveld and Jenness, 1984; Buchanan, 1966), though transient settlements of suspended organic matter over each tidal cycle may ensure that those animals capable of surviving regular sediment disturbance in shallower sandy areas have a rich food supply (Jenness and Duineveld, 1985). Some evidence for aggregation of adults for breeding (June-August: Buchanan, 1966). Fast growth for first three years; slower thereafter (Beukema, 1985).

Recruitment: infrequently successful, even though initial settlement in high densities may be a regular feature in some areas (e.g. Bosselmann, 1991(b)); recruitment success may depend on temperatures of preceding winter in some areas (Beukema, 1985); an offshore silty sand population was never sexually mature (Buchanan, 1966). Successful recruitment years may be synchronised over wide areas (see Beukema, 1985).

Longevity: 10-20 years (Buchanan, 1966; Ursin, 1960); probably <10 years in southern North Sea (Beukema, 1985).

Annual mortality rate: 15-30% (Buchanan, 1966; Beukema, 1985) but prone to 'catastrophic' storm-induced mortality. No evidence for migration or density-dependence (Beukema, 1985).

Sources of mortality:

(i) Burial/wash-out: probably significant in most exposed shallow-water environments (see Beukema, 1985); mortality on wash-out may occur through transport to unfavourable environments or destruction/predation at sediment surface; mass strandings have been observed on shore-lines following storms (see e.g. Schafer, 1972; Rees *et al*., 1977).

(ii) Temperature: significant mortality of coastal populations of parts of the UK coast and German Bight during the severe winter of 1962/63 (Crisp, 1964; Ziegelmeier, 1978).

(iii) Predation: asteroids, notably *Astropecten* (see Sloan, 1980); a component of the diet of a number of demersal fish, e.g. plaice (Carter *et al*., 1991).

(iv) Plankton blooms/eutrophication: mass emergence/mortality frequently observed following collapse of algal blooms, as a result of lowered oxygen concentrations in bottom water/sediments (release of biotoxins may also be important in some cases), e.g. eastern Irish Sea (Ballantine and Smith, 1973; Helm *et al*., 1974); Danish coast (Dyer *et al.*, 1983); German Bight (Westernhagen *et al*., 1986; Niermann *et al*., 1990: populations of this and other species rapidly became re-established following recruitment in the following year); English Channel (Forster, 1979; Griffiths *et al*., 1979). Rainer (1982) notes the sensitivity of this species to prolonged deoxygenation. Rachor (1990) ascribed reduced abundances or absence of *Echinocardium* at a number of muddy inshore locations in the German Bight to effects of eutrophication; reduction in mean size (=age) of *Echinocardium* in the Kattegat, compared with an early survey at the turn of the century, may be explained by recent mortality of an older stock following an hypoxic event some two years prior to the repeated survey (Pearson *et al*., 1985; Rosenberg and Loo, 1988), though a contributory effect of intensive fishing could not be dismissed. Sublethal effects (partial loss of spines) noted in response to a toxic algal bloom (*Chrysochromulina*: Bokn *et al*., 1990). Kvavig (1975) refers to large numbers of dead specimens being washed up onto a Norwegian shoreline, though the cause was unclear.

(v) Trawl/dredge effects: immediate effects are clearly dependant on the depth of penetration of gear, relative to the distribution of animals in sediments; significant (c. 60%) reduction in densities of small individuals following beam trawling; reduction in larger individuals was not statistically significant; c. 100% damage to larger individuals retained in trawl net (Bergman *et al.*, 1990). Houghton *et al.* (1971) recorded 70% damage in trawl nets; Graham (1955), de Groot and Apeldoorn (1971) and Rauck (1988) also refer to significant trawl-induced mortality of *Echinocardium*.

(vi) Pollution: displaced in response to a build-up of anoxia in sediments in organically-enriched areas (e.g. Pearson and Rosenberg, 1978), though may respond positively to moderate inputs, e.g. Oslofjord (Rosenberg *et al.*, 1987).

(vii) Other: high frequency of parasitism noted by de Ridder and Jangoux (1984), but no evidence of adverse effects on health of individuals.

2.9 *Echinus esculentus* (European or edible sea urchin)

Life-style: epifaunal browser, commonly associated with kelp zones of rocky subtidal; important role as algal grazers demonstrated by Jones and Kain (1967) and Forster (1959), but may also graze on encrusting bryozoa, barnacles and tunicates (Bonsdorff and Vahl, 1982; Nichols *et al.*, 1985(a); Gubbay, 1988).

Habitat/distribution: rock or coarse gravel, from c.5 to >100 m; North Sea from northern Norway as far south as the Wash/Helgoland; English Channel; western and northern UK coasts; as far south as Portugal but only sporadically in the southern North Sea, largely due to the absence of suitable coarse deposits. Their occurrence on wrecks in this area indicates their potential for survival here (Gubbay, 1988; see also Ursin, 1960; Cranmer, 1985).

Densities: typically <1 to 5 m^{-2} in coastal localities (e.g. Forster, 1959; Comely and Ansell, 1988; Nichols *et al.*, 1985(a)).

Biomass/production: no information.

Life-cycle strategy: ‘K’; slow growth for first 2-3 years, exponential growth to sexual maturity, tailing off thereafter (Sime and Cranmer, 1985; but see also Gage, 1992(a)); may grow thicker tests in more exposed conditions (Moore, 1935; Sime, 1982; see also Menge, 1979); there may be a significant genetic component to growth variability between individuals, which would have survival value (Gage, 1992(a)). Reaches up to 15 cm diameter.

Recruitment: little information, but apparently a slow trickle of surviving juveniles maintains populations. Limited evidence for maintenance of shallower stocks by in-migration of deeper stocks; spawns February-April/May with additional later (summer) spawnings in some populations (e.g. Nichols *et al.*, 1985(a); Comely and Ansell, 1989); duration of planktonic larval phase: 45-60 days for spring spawners (Nichols, 1979).

Longevity: 10+ years (up to 12 years off Plymouth: Nichols *et al.*, 1985(b); 16+ years for Scottish coast: Gage, 1992(b)).

Annual mortality rate: Ebert (1975) quotes an instantaneous mortality rate of 0.52 (= c.40% mortality per year) for an Irish Sea population sampled by Moore (1935); however, it would seem reasonable to assume that mortality rate would generally be relatively low beyond a critical size. Ebert and Russell (1992) found a mortality rate of about 10% for US intertidal populations of the red sea urchin *Strongylocentrotus franciscanus*.

Sources of mortality:

- *(i)* ***Burial/wash-out***: little information, but may be dislodged in severe storms or crushed by pebbles during such events (Schafer, 1972).

- *(ii)* ***Temperature***: no evidence for temperature as a constraint on distribution in the North Sea (Ursin, 1960); for the echinoderm *Strongylocentrotus*, disease prevalence in littoral populations inhabiting Canadian waters has been linked to the occurrence of exceptionally high water temperatures (Scheibling, 1984).

- *(iii)* ***Predation***: catfish (also called 'wolf-fish'), especially *Anarhichas lupus*; also a predator of the related offshore species *Echinus acutus* (Wheeler, 1969; Sime and Cranmer, 1985); crabs/lobsters are probably significant predators, especially of smaller specimens (this is certainly true for *Strongylocentrotus*: e.g. Lang and Mann, 1976; this species is also predated by US populations of *Asterias*: Menge, 1979); otters: Scottish coast (Comely and Ansell, 1988); *E. acutus* fed on by mature haddock but quantitative importance to diet is uncertain (Sime and Cranmer, 1985).

- *(iv)* ***Plankton blooms/eutrophication***: extensive mortality noted on a shallow sublittoral reef, following collapse of a dinoflagellate bloom (south-west England: Griffiths *et al.*, 1979); similarly for populations along the Norwegian coast in response to a toxic algal bloom (*Chrysochromulina*; Bokn *et al.*, 1990).

- *(v)* ***Trawl/dredge effects***: probably relatively high as a consequence of commercial dredging, e.g. for scallops; also some crushing of specimens likely to occur in animals caught in commercial trawl nets, and during processing of catches. Because of thicker tests, animals are less prone to breakage than e.g. the burrowing urchin *Echinocardium*, but some observations on intact trawl-caught specimens held in laboratory tanks showed high subsequent mortality: those that did not die often shed their spines after 1-2 days, and the tests became reddened, as a result of red cells migrating to damaged areas as a host-defence response; furthermore, the normally sterile coelomic fluid of trawl-caught specimens was frequently heavily contaminated by bacteria (M. Service, Dept. of Agriculture, Northern Ireland pers. comm.).

- *(vi)* ***Pollution***: no information. Jangoux (1984) reviews examples of the sensitivity of related species to inputs of heavy metals, oil and sewage. Populations may be enhanced by moderate organic enrichment.

- *(vii)* ***Other***: collected by pleasure divers for souvenirs or for sale (e.g. tests used as lamp shades); concern has been expressed over possible over-exploitation in some areas of southern Britain; gonads regarded as a delicacy especially in Portugal (e.g. Southward and Southward, 1975; Comely and Ansell, 1988; Gubbay, 1988). About 5% of diver returns from a UK survey of the species in 1986 noted 'bald, sickly or blackened' sea urchins, which may be disease-related (Gubbay, 1988; M. Service, Dept. of Agriculture, Northern Ireland: pers. comm.) or, conceivably, an indication of senescence (see e.g. Schafer, 1972); Maes and Jangoux (1984) report cases of 'bald-sea-urchin' disease off the French coast, though the causative agent was not identified. Quantitative significance as a source of mortality is unclear, but mass mortalities of the related echinoderm

Paracentrotus from the Mediterranean and Californian coasts have been reported. Pearse *et al.* (1977) report on localised mass mortality of Californian populations of *Strongylocentrotus*, disease symptoms being characterised by spine loss and reddish-brown discoloration of affected parts, the latter possibly indicating antimicrobial activity (see Service and Wardlaw, 1984). Mass mortalities of *Strongylocentrotus* along the Canadian coast have been tentatively ascribed to the action of an amoeboid protist; predation of moribund specimens may contribute to mortality (Scheibling, 1984).

3. SYNTHESIS OF LIFE-CYCLE TRAITS AND MORTALITY SOURCES

An arbitrary system of scoring (on a scale of 1-4) was employed, in order to summarise the available information on life-cycle traits for each species (Table 1). This approach was adopted because there were insufficient data to compile absolute estimates in all cases. In addition, species were scored according to their perceived position on an 'r/K' continuum (see Pianka, 1970; Krebs, 1978 and Annex), and according to their perceived 'resistance' and 'resilience'. Boesch and Rosenberg (1981) have used the latter terms to describe, respectively, the buffering capacity of a community in response to a perturbation, and the capacity of a community to recover, following such an event. While none is considered to be exceptionally resistant to environmental stressors (such as fishing activity), there is greater variability in resilience and — as might have been anticipated — scores conform closely with the 'r/K' scale.

The data are expressed in Figure 1 as the combined output from cluster analyses by species and by attribute (using the Bray-Curtis similarity measure: Bray and Curtis, 1957, and average- linkage sorting: Lance and Williams, 1967). The three species groups are considered to provide a reasonable summary of the available life-cycle information.

Sources of mortality are scored in Table 2(a), again on a 4-point scale. Each source was then weighted according to its perceived importance relative to others, and the outcome is shown in Table 2(b) and Figure 2, the latter giving the combined output from cluster analyses by species and by attribute. While it is accepted that there are inherent difficulties in attempting to generalise from the often patchy information on the susceptibility of <u>local</u> populations to a range of adverse influences (see below), nevertheless the three species groups from cluster analysis appear to adequately reflect the outcome of the preceding literature reviews. Thus populations of *Pectinaria*, *Abra* and *Echinocardium* are identified as being particularly susceptible to storm-induced burial or wash-out (at least in shallower areas) and — where such events occur — to reduced oxygen concentrations of bottom waters. Inshore populations of *Echinus* and, to a lesser extent, *Cancer* and *Asterias* are also identified as being potentially vulnerable to the consequences of exceptional algal blooms.

Trawl-induced mortality may be locally — or even regionally — significant for a number of species, especially in intensively-fished areas. The logical expectation for a locality with a per-sistently high frequency of trawl disturbance would be the favouring of r- over K-selected species, as noted by de Groot (1984), among others. In this respect, intermittent effects on populations of 'resilient' species such as *Pectinaria* and *Abra* might be considered intrinsically less significant than for *Sabellaria* and *Arctica*. In the former case, the re-development of reefs may take several years, while the re-establishment of mature populations of the latter would similarly be an extended process, by virtue of its long life-span. In both cases, variability in recruitment success adds a further element of unpredictability to recovery rates. One rider to this is the, apparent benefit accruing to local fisheries from the enhanced turnover of 'younger' specimens of *Arctica* in the Baltic, which may be partly due to trawl-induced disturbance (Brey *et al*., 1990).

The quantitative importance of predation as a source of local mortality is difficult to assess from the available information, though it may be assumed to be significant for *Pectinaria* and *Abra* in areas favoured by flatfish populations.

Assessment of the significance of pollution also presents some problems: evidence from field surveys points to the localisation of gross effects around discharge points, at least in coastal and offshore areas (e.g. Rees and Eleftheriou, 1989). It does not follow that the biota at distance from discharges are entirely immune from influence, but recent wide-scale surveys of the North Sea (e.g. Eleftheriou and Basford, 1989; Kunitzer *et al*., 1992) and historical comparisons (e.g. Pearson *et al*., 1985; Rosenberg *et al*., 1987) provide no indication that pollution-related mortality has resulted in wholesale changes in species occurrences or community structure. (Note that effects of eutrophication are considered separately).

The influence of temperature and other identified factors are, in general, considered to be relatively unimportant, though notable exceptions periodically occur, e.g. severe winters.

There is clearly scope for inclusion of additional 'representative' taxa in order to provide more comprehensive coverage of this topic. Among those identified for future attention were the hermit crab *Pagurus*, the horse-mussel *Modiolus*, the infaunal brittle-star *Amphiura*, and selected hydroids and bryozoans.

4. DISCUSSION

Insufficient data were available over the distributional range of selected species to permit a fully quantitative assessment of life-cycle traits and mortality sources on a North Sea-wide scale. However, with the possible exception of the consequences of climatic change, it is probably more relevant to conduct evaluations on local - or, at most, regional - scales, because of the expectation of marked habitat-related differences.

A notable example of this is the frequent occurrence of hypoxic events in more quiescent areas of the Baltic compared with, for example, the western seaboard of the North Sea and English Channel. Bottom trawling and dredging have the potential for a more 'global' influence on some of the widely-distributed species, though spatial differences in fishing effort, along with the nature and size of gear deployed, are to be anticipated (e.g. Daan, 1991; Rijnsdorp *et al*., 1991).

Benthic communities inhabiting soft sediments in exposed coastal areas are prone to periodic storm-induced disturbance; as a result, many of the component species can be characterised by an opportunistic life-style (high fecundity and wide larval dispersal; fast growth-rate and high population turnover) which ensures their long-term survival. It is also evident that a proportion of individuals may survive redistribution or light burial. The effects of man-made disturbances at the sea bed in such environments may (depending on frequency) simply mimic these events. Another parallel which may be drawn is that both may temporarily promote the availability of benthic species as food for demersal fish: for example, there is much anecdotal evidence of increased fish abundances in the vicinity of recently-trawled areas.

However, there may also be some undesirable consequences. For example, the re-establishment of some types of food organisms (e.g. *Sabellaria*) may be severely inhibited by persistent trawl disturbance. Also, contaminants may be re-mobilised from underlying sediments in areas of enrichment, e.g. near to estuaries. In this case, recent increases in the size and weight of some types of fishing gear could create new problems even in historically intensively-fished areas. Finally, Jangoux (1984) has suggested that, as some diseases of invertebrates (especially those caused by trematodes and nematodes) may be communicable to fish, excessive trawl-induced damage to benthos might increase the potential for disease-transmission, though direct evidence for this is lacking.

On current evidence, the most severe consequence of anthropogenic activity that might be anticipated is that of local extinction of populations: there is no indication that the above (or any other) benthic species are at wider risk in the North Sea/English Channel. Further, such a consequence is unlikely to be permanent, unless the habitat has been materially altered. Noting that vacant spaces in nature will be filled, Krebs (1978) poses the questions: by what, and how long will it take? Many studies have been made of the sequence of recolonisation, and ‘recovery’ time, following gross disturbance of a habitat, and useful insights regarding the benthos can be gained from the pollution literature (e.g. Pearson and Rosenberg, 1978; Clark, 1989).

Boesch and Rosenberg (1981) predicted that, in general, recovery times for the macrobenthos of temperate regions would be less than five years for shallow waters (including estuaries) and less than ten years for coastal areas of moderate depth. Clearly, the recovery of communities characterised by the presence of long-lived species with low recruitment (exemplified by the bivalve *Arctica*) would be much longer.

5. CONCLUSIONS

Appraisals of the literature for nine selected species provided useful insights into life-cycle traits and the significance of various sources of mortality, though, as was to be expected, there was wide disparity in the availability of quantitative data across their distributional ranges. There is scope for future coverage of a range of other species or species-groups along these lines.

Inshore species and communities are vulnerable to a wide range of natural and anthropogenic sources of mortality but, for those inhabiting soft substrates in exposed areas, they are generally the most resilient. The consequences of anthropogenic influences for the fauna of stable deposits (inshore and offshore) may be considered to be more significant, because of prolonged rates of recovery due to the longer life-spans and intermittent recruitment success of a number of the characterising species.

Species occurrences, or community types, are largely determined by the nature of the physical habitat; criteria by which to judge the significance of anthropogenic influences should therefore take account of locality- and habitat-specific factors.

6. REFERENCES

ANGER, K., ROGAL, U., SCHRIEVER, G. AND VALENTIN, C., 1977. *In-situ* investigations on the echinoderm *Asterias rubens* as a predator of soft-bottom communities in the western Baltic Sea. Helgolander wiss. Meeresunters., ***29***:439-459.

ANSELL, A. D., 1974. Seasonal changes in biochemical composition of the bivalve *Abra alba* from the Clyde Sea area. Mar. Biol., ***25***:13-20.

ARNTZ, W. E., 1980. Predation by demersal fish and its impact on the dynamics of macrobenthos. pp. 121-149 *In*: Tenore, K. R. and Coull, B. C. (Eds), Marine Benthic Dynamics. Columbia: University of South Carolina Press.

ARNTZ, W. E. AND RUMOHR, H., 1986. Fluctuations of benthic macrofauna during succession and in an established community. Meeresforsch., ***31***:97-114.

BACHELET, G., 1989. Recruitment in *Abra tenuis* (Montagu) (Bivalvia, Semelidae), a species with direct development and a protracted meiobenthic phase. pp. 23-30 *In*: Ryland, J. S. and Tyler, P. A. (Eds), Reproduction, genetics and distributions of marine organisms. Fredensborg: Olsen and Olsen.

BALLANTINE, D. AND SMITH, F. M ., 1973. Observations on blooms of the dinoflagellate *Gyrodinium aureolum* Hulburt in the River Conway and its occurrence along the North Wales coast. Brit. Phycol. J., ***8***:233-238.

BARKER, M. F. AND NICHOLS, D., 1983. Reproduction, recruitment and juvenile ecology of the starfish *Asterias rubens* and *Marthasterias glacialis*. J. Mar. Biol. Ass. UK., ***63***:745-765.

BASIMI, R. A. AND GROVE, D. J., 1985. Estimates of daily food intake by an inshore population of *Pleuronectes platessa* L. off eastern Anglesey, North Wales. J. Fish. Biol., ***27***:505-520.

BENNETT, D. B. (in press). Factors in the life-history of the edible crab which influence modelling and management. Rapp. P.-v. Reun. Cons. int. Explor. Mer.

BERGMAN, M. J. N., FONDS, M., HUP., M., LEWIS, W., VAN DER PUYL, P., STAM, A. AND DEN UYL, D., 1990. Direct effects of beamtrawl fishing on benthic fauna in the North Sea. pp. 33-57. *In*: BEON Report No. 8. (Published by the Netherlands Institute for Sea Research).

BEUKEMA, J. J., 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. Neth. J. Sea Res., ***13***:203-223.

BEUKEMA, J. J., 1985. Growth and dynamics in populations of *Echinocardium cordatum* living in the North Sea off the Dutch north coast. Neth. J. Sea Res., ***19***:129-134.

BOESCH, D. F. AND ROSENBERG, R., 1981. Response to stress in marine benthic communities. pp. 179-200. *In*: Barrett, G. W. and Rosenberg, R. (Eds), Stress Effects on Natural Ecosystems. London and New York: J Wiley and Sons.

BOKN, T., BERGE, J. A., GREEN, N. AND RYGG, B., 1990. Invasion of the planktonic alga *Chrysochromulina polylepis* along south Norway in May-June 1988. Acute effects on biological communities along the coast. pp. 183-193. *In*: Lancelot, C., Billen, G. and Barth, H. (Eds), Eutrophication and Algal Blooms in the North Sea Coastal Zones, and Adjacent Areas: Prediction and Assessment of Preventive Actions. Brussels: Commission of the European Communities.

BONSDORFF, E. AND VAHL, O., 1982. Food preference of the sea urchins *Echinus acutus* and *E. esculentus*. Mar. Behav. Physiol., ***8***:243-248.

BOSSELMANN, A., 1991(a). Recruitment and postlarval growth of some macrozoobenthos species in the German Bight. Meeresforsch., ***33***:141-158.

BOSSELMANN, A., 1991(b). Larval plankton and recruitment of macrofauna in a subtidal area in the German Bight. pp. 43-54. *In*: Elliott, M. and Ducrotoy, J.-P. (Eds), Estuaries and coasts: Spatial and Temporal Intercomparisons. Fredensborg: Olsen and Olsen.

BRAY, J. R. AND CURTIS, J. T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr., ***27***:325-349.

BREY, T., 1990. Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. Meeresforsch., ***32***:329-343.

BREY, T., ARNTZ, W. E., PAULY, D. AND RUMOHR, H., 1990. *Arctica* (*Cyprina*) *islandica* in Kiel Bay (western Baltic): growth, production and ecological significance. J. Exp. Mar. Biol. Ecol., ***136***:217-235.

BROMLEY, R. G., 1990. Trace fossils: biology and taphonomy. London: Unwin Hyman Ltd., 280 pp.

BUCHANAN, J. B., 1966. The biology of *Echinocardium cordatum* (Echinodermata: Spatangoidea) from different habitats. J. Mar. Biol. Ass. UK., ***46***:97-114.

CARTER, C. G., GROVE, D. J. AND CARTER, D. M., 1991. Trophic resource partitioning between two co-existing flatfish species off the North coast of Anglesey, North Wales. Neth. J. Sea Res., ***27***:325-335.

CASPERS, H., 1987. Changes in the benthos at a sewage-sludge dumpsite in the Elbe estuary. pp. 201-230. *In*: Capuzzo, J. M. and Kester, D. R. (*Eds*), Oceanic Processes in Marine Pollution. ***1***. Biological Processes and Wastes in the Ocean. Florida: R.E. Krieger.

CLARK, R. B., 1989. Marine Pollution. (2nd edition). Oxford: Clarendon Press, 220 pp.

COMELY, C. A. AND ANSELL, A. D., 1988. Population density and growth of *Echinus esculentus* L. on the Scottish west coast. Est. Cstl Shelf Sci., ***27***:311-334.

COMELY, C. A. AND ANSELL, A. D., 1989. The reproductive cycle of *Echinus esculentus* L. on the Scottish west coast. Est. Cstl Shelf Sci., ***29***:385-407.

CRAMER, S. AND DAAN, N., 1986. Consumption of benthos by North Sea cod and haddock in 1981. ICES CM 1986/G:56, 14 pp. (mimeo).

CRANMER, G. J., 1985. Recent investigations into the distribution of regular echinoids in the North Sea. J. Mar. Biol. Ass. UK., ***65***:351-357.

CRISP, D. J., 1964. The effects of the winter of 1962/1963, on the British marine fauna. Helgolander wiss. Meeresunters., ***10***:313-327.

CRISP, D. J. (Ed), 1964. The effects of the severe winter of 1962-63 on marine life in Britain. J. Anim. Ecol., ***33***:165-210.

DAAN, N., 1991. A theoretical approach to the evaluation of the ecosystem effects of fishing in respect of North Sea benthos. ICES CM 1991/L:27, 6 pp. (mimeo).

DARE, P. J., 1982. Notes on the swarming behaviour and population density of *Asterias rubens* L. (Echinodermata: Asteroidea) feeding on the mussel, *Mytilus edulis* L. J. Cons. int. Explor. Mer, ***40***:112-118.

DAUVIN, J.-C., 1986. Biologie, dynamique et production d'une population d'*Abra alba* (Wood) (mollusque-bivalve) de la baie de Morlaix (Manche occidentale). J. Exp. Mar. Biol. Ecol., ***97***:151-180.

DAUVIN, J.-C. AND GENTIL, F., 1989. Long-term changes in populations of subtidal bivalves (*Abra alba* and *A. prismatica*) from the Bay of Morlaix (western English Channel). Mar. Biol., ***103***:63-73.

DAVIS, F. M., 1925. Quantitative studies on the fauna of the sea bottom. No.2. Results of the investigations in the southern North Sea, 1921-24. Min. Agric. Fish., Fish. Invest., Ser. 2, ***8***:(4), 1-50.

DOBBS, F. C. AND SCHOLLY, T. A., 1986. Sediment processing and selective feeding by *Pectinaria koreni* (Polychaeta: Pectinariidae). Mar. Ecol. Prog. Ser., ***29***:165-176.

DUINEVELD, G. C. A. AND JENNESS, M. I., 1984. Differences in growth rates of the sea urchin *Echinocardium cordatum* as estimated by the parameter *w* of the von Bertalanffy equation applied to skeletal rings. Mar. Ecol. Prog. Ser., ***19***:65-72.

DYER, M. F., POPE, J. G., FRY, P. D., LAW, R. J. AND PORTMANN, J. E., 1983. Changes in fish and benthos catches off the Danish coast in September 1981. J. Mar. Biol. Ass. UK., ***63***:767-775.

EAGLE, R. A., 1975. Natural fluctuations in a soft bottom benthic community. J. Mar. Biol. Ass. UK., ***55***:865-878.

EBERT, T. A., 1975. Growth and mortality of post-larval echinoids. Amer. Zool., **15**:755-775.

EBERT, T. A. AND RUSSELL, M. P., 1992. Growth and mortality estimates for red sea urchin *Strongylocentrotus franciscanus* from San Nicolas Island, California. Mar. Ecol. Prog. Ser., ***81***:31-41.

EDWARDS, E., 1979. The edible crab and its fishery in British waters. Farnham, England: Fishing News Books Ltd., 142pp.

ELEFTHERIOU, A. AND BASFORD, D. J., 1989. The macrobenthic infauna of the offshore northern North Sea. J. Mar. Biol. Ass. UK., ***69***:23-143.

ELKAIM, B. AND IRLINGER, J. P., 1987. Contribution a l'etude de la dynamique des populations de *Pectinaria koreni* Malmgren (Polychete) en Baie de Seine Orientale. J. Exp. Mar. Biol. Ecol., ***107***:171-197.

ESTCOURT, I. N., 1974. Population study of *Pectinaria australis* (Polychaeta) in Tasman Bay. N.Z. J. Mar. Freshw. Res., ***8***:283-290.

FORSTER, G. R., 1959. The ecology of *Echinus esculentus* L. Quantitative distribution and rate of feeding. J. Mar. Biol. Ass. UK., ***38***:361-367.

FORSTER, G. R., 1979. Mortality of the bottom fauna and fish in St Austell Bay and neighbouring areas. J. Mar. Biol. Ass. UK., ***59***:517-520.

GAGE, J. D., 1992(a). Natural growth bands and growth variability in the sea urchin *Echinus esculentus*: results from tetracycline tagging. Mar. Biol., ***114***:607-616.

GAGE, J. D., 1992(b). Growth bands in the sea urchin *Echinus esculentus*: results from tetracycline-mark/recapture. J. Mar. Biol. Ass. UK., ***72***:257-260.

GEORGE, C. L. AND WARWICK, R. M., 1985. Annual production in a hard-bottom reef community. J. Mar. Biol. Ass. UK., ***65***:713-735.

GLEMAREC, M. AND MENESGUEN, A., 1980. Functioning of a muddy sand ecosystem: seasonal fluctuations of different trophic levels and difficulties in estimating production of the dominant macrofauna species. pp. 49-68. *In*: Tenore, K. R. and Coull, B. C. (Eds), Marine Benthic Dynamics. Columbia: University of South Carolina Press.

GRAAF, U. H. DE AND VEEN, J. F. DE, 1973. *Asterias rubens* and the influence of the beam trawl fishery on the bottom fauna. ICES CM 1973/K:37, 5pp. (mimeo).

GRAHAM, M., 1955. Effect of trawling on animals of the sea bed. Deep-Sea Res., ***3***:(Suppl.), 1-6.

GRIFFITHS, A. B., DENNIS, R. AND POTTS, G. W., 1979. Mortality associated with a phytoplankton bloom off Penzance in Mounts Bay. J. Mar. Biol. Ass. UK., ***59***:520 -521.

GROOT, S. J. DE, 1984. The impact of bottom trawling on benthic fauna of the North Sea. Ocean Manag., ***9***:177-190.

GROOT, S. J. DE AND APELDOORN, J., 1971. Some experiments on the influence of the beam trawl on the bottom fauna. ICES CM 1971/B:2, 5 pp. (mimeo).

GUBBAY, S., 1988. A coastal directory for marine nature conservation. Ross-on-Wye: Marine Conservation Society, 319 pp.

GUILLOU, M., 1983. La croissance d'*Asterias rubens* L. (Echinodermata Asteroidea) en baie de Douarnenez (Finistere). Ann. Inst. Oceanogr., Paris, ***59***:141-154.

HANCOCK, D. A., 1955. The feeding behaviour of starfish on Essex oyster beds. J. Mar. Biol. Ass. UK., ***34***:313-331.

HANCOCK, D. A., 1958. Notes on starfish on an Essex oyster bed. J. Mar. Biol. Ass. UK., ***37***:565-589.

HELM, M. M., HEPPER, B. T., SPENCER, B. E. AND WALNE, P. R., 1974. Lugworm mortalities and a bloom of *Gyrodinium aureolum* Hurlburt in the eastern Irish Sea, Autumn 1971. J. Mar. Biol. Ass. UK., ***54***:857-869.

HILY, C. AND LE BRIS, H., 1984. Dynamics of an *Abra alba* population (bivalve-scrobiculariidae) in the Bay of Brest. Est. Cstl Shelf Sci., ***19***:463-475.

HOLME, N. A., 1966. The bottom fauna of the English Channel. Part II. J. Mar. Biol. Ass. UK., ***46***:401-493.

HOUGHTON, R. G., WILLIAMS, T. AND BLACKER, R. W., 1971. Some effects of double beam trawling. ICES CM 1971/B:5, 12 pp. (mimeo).

HUNT, O. D., 1925. The food of the bottom fauna of the Plymouth fishing grounds. J. Mar. Biol. Ass. UK., ***13***:560-598.

JANGOUX, M., 1984. Diseases of echinoderms. Helgolander Meeresunters., ***37***:207-216.

JENNESS, M. I. AND DUINEVELD, G. C. A., 1985. Effects of tidal currents on chlorophyll *a* content of sandy sediments in the southern North Sea. Mar. Ecol. Prog. Ser., ***21***:283-287.

JENSEN, J. J., 1988. Recruitment, growth and mortality of juvenile *Corbula gibba* and *Abra alba* in the Limfjord, Denmark. Kieler Meeresforsch., ***6***:357-365.

JONES, N. S. AND KAIN, J. M., 1967. Subtidal algal colonisation following the removal of *Echinus*. Helgolander wiss. Meeresunters., ***15***:460-466.

JOSEFSON, A. B., 1982. Regulation of population size, growth and production of a deposit-feeding bivalve: a long-term field study of three deep-water populations off the Swedish west coast. J. Exp. Mar. Biol. Ecol., ***59***:125-150.

KREBS, C. J., 1978. Ecology: the experimental analysis of distribution and abundance. (2nd edition). New York: Harper and Row, 678 pp.

KUNITZER, A., BASFORD, D., CRAEYMEERSCH, J. A., DEWARUMEZ, J. M., DORJES, J., DUINEVELD, G. C. A., ELEFTHERIOU, A., HEIP, C., HERMAN, P., KINGSTON, P., NIERMANN, U., RACHOR, E., RUMOHR, H. AND DE WILDE, P. A. J., 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES J. Mar. Sci., ***49***:127-143.

KVAVIG, K. J., 1975. Mass mortality of *Echinocardium cordatum*. Fauna, ***28***:97-98.

LAKE, N.C.H., JONES, M.B. AND PAUL, J.D., 1987. Crab predation of scallop (*Pecten maximus*) and its implication for scallop cultivation. J. Mar. Biol. Ass. UK., ***67***: 55-64.

LANCE, G. N. AND WILLIAMS, W. T., 1967. A general theory of classificatory sorting strategies. 1. Hierarchical systems. Computer Journal, ***9***:373-380.

LANG, C. AND MANN, K. H., 1976. Changes in sea urchin populations after the destruction of kelp beds. Mar. Biol., ***36***:321-326.

LEWIS, J. R., 1980. Options and problems in environmental management and evaluation. Helgolander Meeresunters., ***33***:452-466.

LOCKWOOD, S. J., 1980. The daily food intake of 0-group plaice (*Pleuronectes platessa* L.) under natural conditions. J. Cons. int. Explor. Mer, ***39***:154-159.

LUTZ, R. A., MANN, R., GOODSELL, J. G. AND CASTAGNA, M., 1982. Larval and post-larval development of *Arctica islandica*. J. Mar. Biol. Ass. UK., ***62***:745-769.

MACER, C. T., 1967. The food web in Red Wharf Bay (North Wales) with particular reference to young plaice (*Pleuronectes platessa*). Helgolander wiss. Meeresunters., ***15***:560-573.

MAES, P. AND JANGOUX, M., 1984. The bald-sea-urchin disease: a biopathological response. Helgolander Meeresunters., ***37***:217-224.

MASON, J., 1983. Scallop and queen fisheries in the British Isles. Farnham, England: Fishing News Books Ltd., 144pp.

MEDCOF, J. C. AND CADDY, J. F., 1971. Underwater observations on performance of clam dredges of three types. ICES CM 1971/B:10 7pp. (mimeo).

MENGE, B. A., 1979. Coexistence between the sea-stars *Asterias vulgaris* and *Asterias forbesi* in a heterogeneous environment: a non-equilibrium explanation. Oecologia, ***41***:245-272.

MERRILL, A. S. AND ROPER, J. W., 1969. The general distribution of the surf clam and ocean quahog. Proc. Nat. Shellfish. Assoc., ***59***:40-45.

MISTAKIDIS, M. N., 1956. Survey of the pink shrimp fishery in Morecambe Bay. Lancashire and Western Sea Fisheries Joint Committee, 14 pp.

MOORE, H. B., 1935. A comparison of the biology of *Echinus esculentus* in different habitats. Part II. J. Mar. Biol. Ass. UK., ***20***:109-128.

MORTENSEN, T., 1927. Handbook of the echinoderms of the British Isles. London: Oxford University Press, 471 pp.

MURAWSKI, S. A. AND SERCHUK, F. M., 1989(a). Mechanical shellfish harvesting and its management: the offshore clam fishery of the eastern United States. pp. 479-506. *In*: Caddy, J. F. (Ed), Marine Invertebrate Fisheries: Their Assessment and Management. J. Wiley and Sons.

MURAWSKI, S. A. AND SERCHUK, F. M., 1989(b). Environmental effects of offshore dredge fisheries for bivalves. ICES CM 1989/K:27, 12 pp. (mimeo).

MURAWSKI, S. A., AZAROVITZ, T. R. AND RADOSH, D. J., 1989. Long-term biological effects of hypoxic water conditions off New Jersey, USA 1976-1989. ICES CM 1989/E:11, 22 pp. (mimeo).

MUUS, K., 1973. Settling, growth and mortality of young bivalves in the Oresund. Ophelia, ***12***:79-116.

NAUEN, C. E., 1978. The growth of the sea star, *Asterias rubens*, and its role as benthic predator in Kiel Bay. Kieler Meeresforsch., ***4***:68-81.

NICHOLS, D., 1979. A nationwide survey of the British sea-urchin *Echinus esculentus*. Prog. Underwat. Sci., ***4***:161-176.

NICHOLS, D. AND BARKER, M. F., 1984. A comparative study of reproductive and nutritional periodicities in two populations of *Asterias rubens* (Echinodermata: Asteroidea) from the English Channel. J. Mar. Biol. Ass. UK., ***64***:471-484.

NICHOLS, D., BISHOP, G. M. AND SIME, A. A. T., 1985(a). Reproductive and nutritional periodicities in populations of the European sea-urchin, *Echinus esculentus* (Echinodermata: Echinoidea) from the English Channel. J. Mar. Biol. Ass. UK., ***65***:203-220.

NICHOLS, D., SIME, A. A. T. AND BISHOP, G. M., 1985(b). Growth in populations of the sea-urchin *Echinus esculentus* L. (Echinodermata: Echinoidea) from the English Channel and Firth of Clyde. J. Exp. Mar. Biol. Ecol., ***86***:219-228.

NICHOLS, F. H., 1975. Dynamics and energetics of three deposit-feeding benthic invertebrate populations in Puget Sound, Washington. Ecol. Monogr., ***45***:57-82.

NICHOLS, F. H., 1977. Dynamics and production of *Pectinaria koreni* (Malmgren) in Kiel Bay, West Germany. pp. 453-463 *In*: Keegan, B. F., O'Ceidigh, P. and Boaden, P. J. S. (Eds), Biology of benthic organisms. Oxford: Pergamon Press.

NICOLAIDOU, A., 1983. Life history and productivity of *Pectinaria koreni* Malmgren (Polychaeta). Est. Cstl Shelf Sci., ***17***:31-43.

NICOLAIDOU, A., 1988. Notes on the behaviour of *Pectinaria koreni*. J. Mar. Biol. Ass. UK., ***68***:55-59.

NIERMANN, U., BAUERFEIND, E., HICKEL, W. AND WESTERNHAGEN, H. V., 1990. The recovery of benthos following the impact of low oxygen content in the German Bight. Neth. J. Sea Res., ***2***:215-226.

PEARCE, J. B., 1972. The effects of solid waste disposal on benthic communities in the New York Bight. pp. 404-411. *In*: Ruivo, M. (Ed), Marine Pollution and Sea Life. West Byfleet: Fishing News (Books) Ltd.

PEARL, R., 1928. The rate of living. New York: Knopf.

PEARSE, J. S., COSTA, D. P., YELLIN, M. B. AND AGEGIAN, C. R., 1977. Localized mass mortality of red sea urchin, *Strongylocentrotus franciscanus*, near Santa Cruz, California. Fish. Bull., ***53***:645-648.

PEARSON, T. H. AND ROSENBERG, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev., ***16***:229-311.

PEARSON, T. H., JOSEFSON, A. B. AND ROSENBERG, R., 1985. Petersen's benthic stations revisited. I. Is the Kattegat becoming eutrophic? J. Exp. Mar. Biol. Ecol., ***92***:157-206.

PEER, D. L., 1970. Relation between biomass, productivity and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperborea*. J. Fish. Res. Bd. Can., ***27***:2143-53.

PIANKA, E. R., 1970. On *r*- and *K*-selection. Amer. Nat., ***104***:592-597.

RACHOR, E., 1990. Changes in sublittoral zoobenthos in the German Bight with regard to eutrophication. Neth. J. Sea Res., ***25***:209-214.

RAINER, S. F., 1982. Trophic structure and production in the macrobenthos of a temperate Australian estuary. Est. Cstl Shelf Sci., ***15***:423-441.

RAINER, S. F., 1985. Population dynamics and production of the bivalve *Abra alba* and implications for fisheries production. Mar. Biol., ***85***:253-262.

RAUCK, G., 1988. What influence have bottom trawls on the seafloor and bottom fauna? Inf. Fischwirtsch., ***35***:104-106.

REES, E. I. S. AND WALKER, A. J. M., 1983. Annual and spatial variation in the *Abra* community in Liverpool Bay. Oceanol. Acta, Proc. 17th Europ. Mar. Biol. Symp., 165-169.

REES, E. I. S., EAGLE, R. A. AND WALKER, A. J. M., 1975. Trophic and other influences on macrobenthos population fluctuations in Liverpool Bay. pp. 589-599 *In*: Persoone, G. and Jaspers, E. (Eds), Proc. 10th Europ. Symp. Mar. Biol. Belgium: Universa Press, ***2***.

REES, E. I. S., NICOLAIDOU, A. AND LASKARIDOU, P., 1977. The effects of storms on the dynamics of shallow water benthic associations. pp. 465-474. *In*: Keegan, B. F., O'Ceidigh, P. O. and Boaden, P. J. S.(Eds), Biology of Benthic Organisms. Oxford: Pergamon Press.

REES, H. L., 1982. Fisheries. pp. 52-59 *In*: Gameson, A. L. H. (Ed), The Quality of the Humber Estuary. Leeds: Yorkshire Water Authority.

REES, H. L. AND ELEFTHERIOU, A., 1989. North Sea benthos: a review of field investigations into the biological effects of man's activities. J. Cons. int. Explor. Mer, ***45***:284-305.

REES, H. L., ROWLATT, S. M., LIMPENNY, D. S., REES, E. I. S. AND ROLFE, M. S., 1992. Benthic studies at dredged material disposal sites in Liverpool Bay. Aquat. Environ. Monit. Rep., MAFF Direct. Fish. Res., Lowestoft, (***28***):21 pp.

REES, H. L., ROWLATT, S. M., LIMPENNY, D. S., LAMBERT, M. A., LEES, R. G. AND JONES, B. R., (in prep.). Effects of dredged material disposal on the benthos of Liverpool Bay, United Kingdom. Mar. Environ. Res.

REISE, K. AND SCHUBERT, A., 1987. Macrobenthic turnover in the subtidal Wadden Sea: the Norderaue revisited after 60 years. Helgolander Meeresunters., ***41***:69-82.

RIDDER, C. DE, AND JANGOUX, M., 1984. Intracoelomic parasitic Sporozoa in the burrowing spatangoid echinoid *Echinocardium cordatum*: coelomocyte reaction and formation of brown bodies. Helgolander Meeresunters., ***37***:225-231.

RIDDER, C. DE AND JANGOUX, M., 1985. Origin and turnover rate of ingested sediment in the spatangoid echinoid, *Echinocardium cordatum* (Pennant) (Echinodermata). Ann. Inst. Oceanogr., Paris (Nouv. Ser.), ***61***:51-58.

RIESEN, W. AND REISE, K., 1982. Macrobenthos of the subtidal Wadden Sea: revisited after 55 years. Helgolander Meeresunters., ***35***:409-423.

RIJNSDORP, A. D., GROOT, P. J. AND BEEK, F. A. VAN, 1991. The microdistribution of beam-trawl effort in the southern North Sea. ICES CM 1991/G:49, 20 pp. (mimeo).

ROPES, J. W., 1984. Procedures for preparing acetate peels and evidence validating the annual periodicity of growth lines formed in the shells of ocean quahogs, *Arctica islandica*. Mar. Fish. Rev., ***46***:27-35.

ROSENBERG, R., 1985. Eutrophication - the future marine coastal nuisance? Mar. Pollut. Bull., ***16***:227-231.

ROSENBERG, R. AND LOO, L.-O., 1988. Marine eutrophication-induced oxygen deficiency effects on soft bottom fauna, western Sweden. Ophelia, ***29***:213-226.

ROSENBERG, R., GRAY, J. S., JOSEFSON, A. B. AND PEARSON, T. H., 1987. Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skaggerak enriched? J. Exp. Mar. Biol. Ecol., ***105***:219-251.

ROWELL, T. W., CHAISSON, D. R. AND MCLANE, J. T., 1990. Size and age of sexual maturity and annual gametogenic cycle in the ocean quahog, *Arctica islandica* (Linnaeus, 1767), from coastal waters in Nova Scotia, Canada. J. Shellfish Res., ***9***:195-203.

RUMOHR, H., BREY, T. AND ANKAR, S., 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. Baltic Marine Biologists, Publ. **9**:56 pp.

RUMOHR, H. AND KROST, P., 1991. Experimental evidence of damage to benthos by bottom trawling with special reference to *Arctica islandica*. Meeresforsch., ***33***: 340-345.

SAWYER, T. K., 1991. Shell disease in the Atlantic rock crab, *Cancer irroratus* Say, 1817, from the northeastern United States. J. Shellfish Res., ***10***:495-497.

SCHAFER, W., 1972. Ecology and palaeoecology of marine environments. Chicago: University of Chicago Press, 568 pp.

SCHEIBLING, R. E., 1984. Predation by rock crabs (*Cancer irroratus*) on diseased sea urchins (*Strongylocentrotus droebachiensis*) in Nova Scotia. Can. J. Fish. Aquat. Sci., ***41***:1847-1851.

SERVICE, M. AND WARDLAW, A. C., 1984. Echinochrome-A as a bactericidal substance in the coelomic fluid of *Echinus esculentus* (L.). Comp. Biochem. Physiol., ***79***b:161-165.

SHELTON, R. G. J., 1973. Some effects of dumped, solid wastes on marine life and fisheries. pp. 415-436 *In*: Goldberg, E. D. (Ed), North Sea Science. Cambridge, Massachusetts: MIT Press .

SIME, A. A. T., 1982. Growth ring analysis in regular echinoids. Prog. Underwat. Sci., **7**:7-14.

SIME, A. A. T. AND CRANMER, G. J., 1985. Age and growth of North Sea echinoids. J. Mar. Biol. Ass. UK., ***65***:583-588.

SLOAN, N. A., 1980. Aspects of the feeding biology of asteroids. Oceanogr. Mar. Biol. Ann. Rev., ***18***:57-124.

SOUTHWARD, A. AND SOUTHWARD, E., 1975. Endangered urchins. New Scientist, **66**:70-72.

TAYLOR, A. C., 1976. Burrowing behaviour and anaerobiosis in the bivalve *Arctica islandica* (L.). J. Mar. Biol. Ass. UK., ***56***:95-109.

TEBBLE, N., 1966. British bivalve seashells. Edinburgh: Her Majesty's Stationery Office, 212 pp.

THOMPSON, I., JONES, D. S. AND DREIBELBIS, D., 1980(a). Annual internal growth banding and life history of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). Mar. Biol., ***57***:25-34.

THOMPSON, I., JONES, D. S. AND ROPES, J. W., 1980(b). Advanced age for sexual maturity in the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). Mar. Biol., ***57***:35-39.

URSIN, E., 1960. A quantitative investigation of the echinoderm fauna of the central North Sea. Medd. fra Danm. Fiskeri-og Havunders., **2**:204 pp.

VEVERS, H. G., 1949. The biology of *Asterias rubens* L.: growth and reproduction. J. Mar. Biol. Ass. UK., ***28***:165-187.

VEVERS, H. G., 1951. The biology of *Asterias rubens*. II. Parasitization of the gonads by the ciliate *Orchitophyra stellarum* Cepede. J. Mar. Biol. Ass. UK., ***29***:619-624.

VIGNEAU, J. AND MORIN, J., 1991. Evaluation du stock de coquilles Saint-Jacques de la Manche-est et application d'une nouvelle methodologie. Rapport Technique IFREMER (Ouistreham), France, 33 pp.

WARREN, P. J., 1973. The fishery for the pink shrimp *Pandalus montagui* in the Wash. Ministry of Agriculture, Fisheries and Food, Lowestoft, Laboratory Leaflet (New Series), ***28***:46pp.

WARWICK, R. M. AND GEORGE, C. L., 1980. Annual production in an *Abra* community. pp. 517-538. *In*: Collins, M. B., Banner, F. T., Tyler, P. A., Wakefield, S. J. and James, A. E. (Eds), Industrial Embayments and Their Environmental Problems. A case study of Swansea Bay. Oxford and New York: Pergamon Press.

WARWICK, R. M., GEORGE, C. L. AND DAVIES, J. R., 1978. Annual macrofauna production in a *Venus* community. Est. Cstl Mar. Sci., *7*:215-241.

WEIGELT, M., 1991. Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (western Baltic) due to oxygen depletion and eutrophication. Meeresforsch., ***33***:197-224.

WEIGELT, M. AND RUMOHR, H., 1986. Effects of wide-range oxygen depletion on benthic fauna and demersal fish in Kiel Bay 1981-1983. Meeresforsch., ***31***:124-136.

WESTERNHAGEN, H., HICKEL, W., BAUERNFEIND, E., NIERMANN, U. AND KRONCKE, I., 1986. Sources and effects of oxygen deficiencies in the south-eastern North Sea. Ophelia, ***26***:457-473.

WHEELER, A., 1969. The Fishes of the British Isles and North-west Europe. London: Macmillan, 613 pp.

WILSON, D. P., 1970. The larvae of *Sabellaria spinulosa* and their settlement behaviour. J. Mar. Biol. Ass. UK., ***50***:33-52.

WILSON, D. P., 1971. *Sabellaria* colonies at Duckpool, north Cornwall, 1961-70. J. Mar. Biol. Ass. UK., ***51***:509-580.

WILSON, D. P., 1974. *Sabellaria* colonies at Duckpool, north Cornwall, 1971-1972, with a note for May 1973. J. Mar. Biol. Ass. UK., ***54***:393-436.

WILSON, D. P., 1976. *Sabellaria alveolata* (L.) at Duckpool, north Cornwall, 1975. J. Mar. Biol. Ass. UK., ***56***:305-310.

ZIEGELMEIER, E., 1978. Macrobenthos investigations in the eastern part of the German Bight from 1950 to 1974. Rapp. P.-v. Reun. Cons. int. Explor. Mer, ***172***:432-444.

Table 1. Life-cycle traits scored for optimal conditions: North Sea/English Channel (1 = low; 4 = high)

Species	Density m^{-2}	B m^{-2}	P m^{-2} y^{-1}	Recruitment	Longevity	Mortality y^{-1}	K(1)- ->r(4)	Resilience	Resistance
Polychaeta									
Pectinaria koreni	4	3	4	4	1	4	4	4	2
Sabellaria spinulosa	4	3	2	1	2	2	2	2	1
Crustacea									
Cancer pagurus	1	1	1	2	3	2	2	2	2
Mollusca									
Abra alba	4	3	3	4	1	3	4	4	3
Arctica islandica	1	3	1	1	4	1	1	1	2
Pecten maximus	1	2	1	2	3	2	1	1	2
Echinodermata									
Asterias rubens	3	3	3	3	2	2	3	4	3
Echinocardium cordatum	2	3	1	2	2	2	2	3	2
Echinus esculentus	1	2	1	1	3	2	1	1	2

Table 2(a). Assessment of risk of local extinctions through various natural and anthropogenic factors (1 = low; 4 = high)

Species	Burial/wash-out	Temperature	Predation	Plankton blooms /eutrophication	Trawl/dredge effects	Pollution	Other (excl. fishing)
Polychaeta							
Pectinaria koreni	4	2	3	2	3	1	1
Sabellaria spinulosa	1	1	2	1	4	2	1
Crustacea							
Cancer pagurus	1	2	1	2	2	2	2
Mollusca							
Abra alba	4	2	3	3	2	1	1
Arctica islandica	1	1	1	1	3	2	1
Pecten maximus	1	2	2	1	2	2	1
Echinodermata							
Asterias rubens	2	1	2	2	1	1	1
Echinocardium cordatum	3	2	1	4	3	2	1
Echinus esculentus	2	1	1	3	2	2	2
Weighting (1 = low; 4 = high)	3	1	2	4	3	2	1

Table 2(b). As Table 2(a), but with weighting factors applied

Species	Burial/wash-out	Temperature	Predation	Plankton blooms /eutrophication	Trawl/dredge effects	Pollution	Other (excl. fishing)
Polychaeta							
Pectinaria koreni	12	2	6	8	9	2	1
Sabellaria spinulosa	3	1	4	4	12	4	1
Crustacea							
Cancer pagurus	3	2	2	8	6	4	2
Mollusca							
Abra alba	12	2	6	12	6	2	1
Arctica islandica	3	1	2	4	9	4	1
Pecten maximus	3	2	4	4	6	4	1
Echinodermata							
Asterias rubens	6	1	4	8	3	2	1
Echinocardium cordatum	9	2	2	16	9	4	1
Echinus esculentus	6	1	2	12	6	4	2

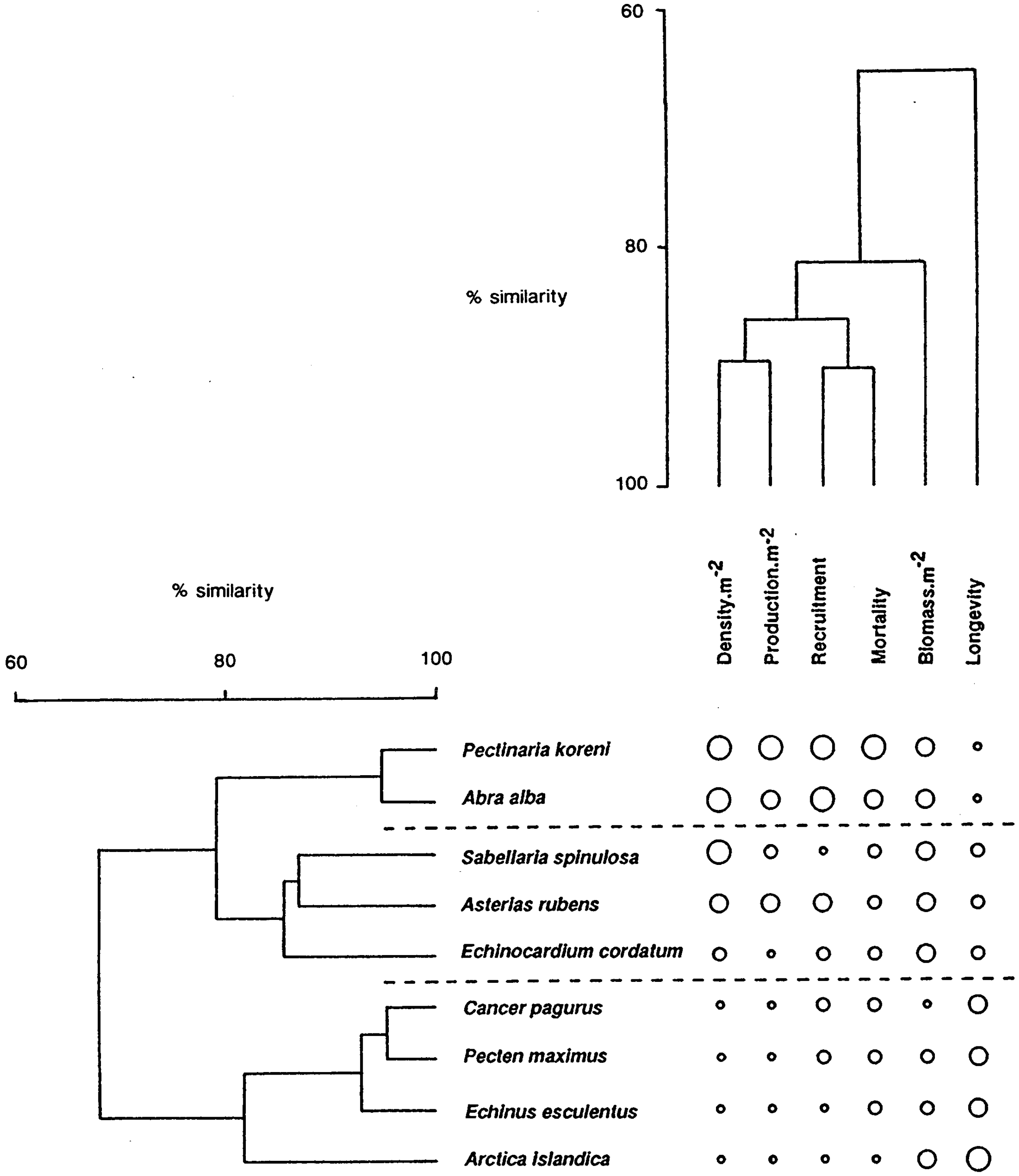

Figure 1. Combined output from cluster analyses by species and by life-cycle trait. Sizes of circles correspond with sources in Table 1

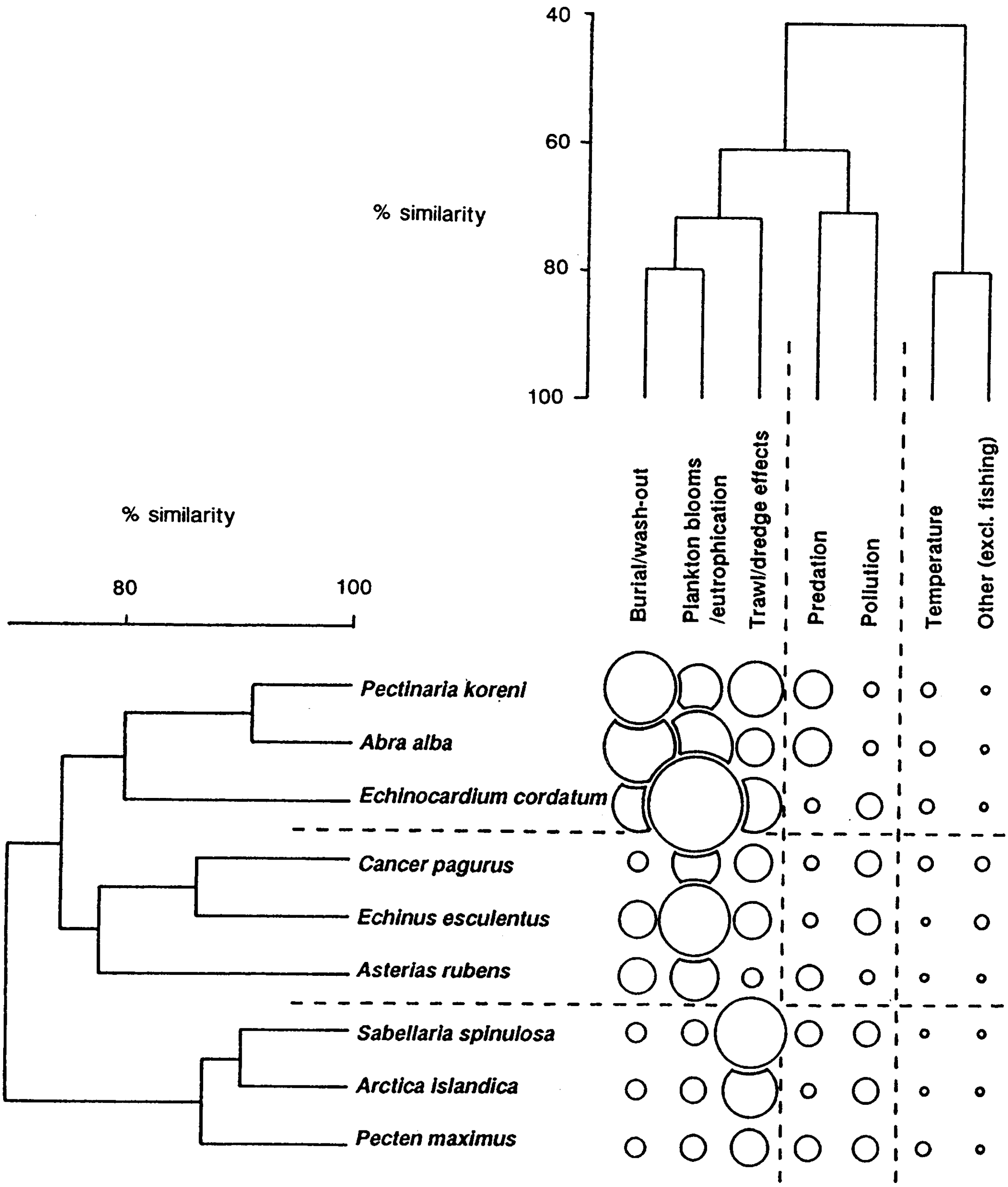

Figure 2. *Combined output from cluster analyses by species and by mortality source. Sizes of circles correspond with weighted scores in Table 2(b)*

ANNEX. POPULATION TRAITS ASSOCIATED WITH *r*- AND *K*-SELECTED SPECIES (from Krebs, 1978 after Pianka, 1970)

	r SELECTION	*K* SELECTION
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic, nondirected, density independent	More directed, density dependent
Survivorship	Often type III (see Figure A1)	Usually types I and II (see Figure A1)
Population size	Variable in time, non equilibrium: usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecological vacuums; recolonisation each year	Fairly constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; no recolonisation necessary
Intra- and interspecific competition	Variable, often lax	Usually keen
Selection favours	1. Rapid development 2. High r_m (=innate capacity for increase) 3. Early reproduction 4. Small body size 5. Single reproduction	1. Slower development 2. Greater competitive ability 3. Delayed reproduction 4. Larger body size 5. Repeated reproductions
Length of life	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to	Productivity	Efficiency

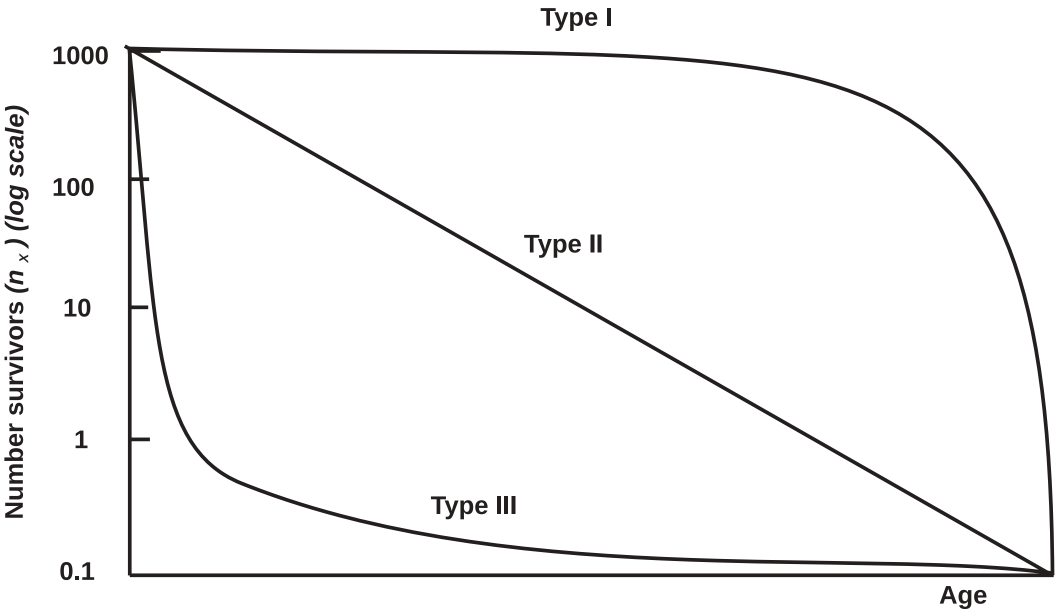

Figure A1. Hypothetical survivorship curves (from Krebs, 1978 after Pearl, 1928)

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