THE INTERTIDAL SYSTEM: SUSTAINABILITY AND LONG-TERM INDICATORS OF SYSTEM STATUS

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ABSTRACT

The intertidal system provides the classic control paradigm of physical control at the landward extreme to biological control at the seaward. Consequently, stability is an unlikely property, yet many intertidal systems display remarkable consistency in character and community type or biotope, if not in individual species' abundances or biomass.

There are several barriers to sustainability, as outlined by the OECD. Principal among these are sea level rise under climate change, habitat loss, habitat degradation (including over-exploitation) and pollution.

Selection of long-term indicators of intertidal system status is limited both by the characteristics of the system, and in particular its susceptibility to physical disturbance, and by the lack of long-term data by which the noise of natural variation can be distinguished from that of anthopogenically-induced change. Community measures such as H' or SAB curves, which again have reference conditions, can be used to assess status, although they operate under the restrictions of both species' impoverishment and variability in community structure. However these approaches can yield false positives, in that departures from reference condition are the norm rather than the exception.

The final approach is long-term monitoring of selected 'key' species such as *Tellina tenuis*, *Cerastoderma edule* or *Macoma balthica*. Results suggest that several species are needed for an overall picture.

INTRODUCTION

Accessibility has been a major factor in our knowledge of the intertidal ecosystem. Mathieson and Nienhuis (1991) acknowledged this influence, in terms both of the geographical coverage and of the type of shore, where they pointed out that studies on

sedimentary shores were later and fewer than those on rocky shores and lacked an overall synthesis of ecosystem functioning.

Work on interactions between organisms on the rocky shore has in fact provided two major ecological paradigms. The first, chronologically speaking was Connell's (1961) work on the barnacles *Balanus* (now *Semibalanus*) *balanoides* and *Chthamalus stellatus* while the second was Paine's (1974) experiments with the mussels *Mytilus californianus* and the starfish *Pisaster ochraceus*. The first (Connell 1961) demonstrated that the upper limit of distribution on the shore was set by physical tolerance limits, while the lower limit was a function of biological factors, in this case competition. The second (Paine 1974) advanced the concept of 'keystone' species, in which the structuring of the community, both physical and biological, is determined by the control (usually top-down) of species which might be numerically insignificant, but whose interactions (in this case predation of the mussels by the starfish) determine the current status. Other work has yielded valuable insights into the functioning of the wider marine system, ranging from the mechanisms of habitat selection by larvae (e.g. Crisp, 1961) to the pressures of and responses to evolutionary driving forces (e.g. McMahon, 2001), and a useful review of community function is given in this volume by Crowe.

In contrast, work on sedimentary shores has tended to be dominated by the habitat itself, in that many of the factors which apply directly on the rocky shore are buffered or mediated by the sediments. One aspect of the buffering is that sedimentary environments display a spatial homogeneity (Wilson 1977, Thrush *et al.* 1989) and this in turn has made it a lot easier to put together budgets and derive metrics for the system (e.g. Baird and Milne 1981).

There have been many studies since Baird and Milne's (1981) first energy budget, but the majority have tended to focus on estuaries and other, mainly sedimentary, locations (e.g. Brown and McLachlan 1990, Wilson 2002). These investigations have been extended into consideration of the systems' reaction to anthropogenic and other pressures such as resource exploitation or pollution (Baird *et al.* 1991, Wilson and Parkes 1999). However, the number of systems for which sufficient information exists for ecological modelling is still extremely limited (e.g. Soetart and Herman 1995). Energy budgets have also been used to investigate system properties through network analysis (Baird and Ulanowicz 1993, Wilson and Parkes 1999), from which metrics can be derived quantifying properties such as system throughput, capacity and stability (Wulff *et al.* 1989).

McArthur (1955) was one of the first to articulate the view that system stability was linked to diversity through the provision of parallel, often redundant, functions. Sanders (1968) 'stability-time' hypothesis developed this and thus would predict low stability for littoral systems. This view has also been supported by other studies, for example those of Roth and Wilson (1998) who calculated system metrics signifying low stability in the littoral communities of Dublin Bay. Nevertheless, palaeontological records and archaeological records show some constancy in the general species' associations at particular coastal locations (e.g. Wilson 1993b), while workers such as May (1973), McNaughton (1977) and Tilman (1996) have teased out the diversity/stability relationship and emphasised the distinction between the responses at population and at community level.

The OECD provide regular updates on the current international development goals (e.g. OECD 2002), but these are seriously deficient as regards the marine environment even if 'marine quality' is listed as one of the localised environmental issues under consideration by the DAC Working Party on Environment and Development. The Bruntland Commission in 1987 defined a sustainable society as one that meets the needs of the present without compromising the ability of future generations to meet their own needs and this is generally accepted as the starting point for most discussions. However, Meadows *et al.* (1992) drew a sharp distinction between growth and development. Quantitative growth must inevitably reach its limit in a finite system, while qualitative development, which they argued follows different laws, should result in something better or at least different (Meadows *et al.* 1992). Other workers such as Goodland (1995) have distinguished environmental sustainability from social and economic stability and pointed out that the environment has now become a major constraint on human progress.

In the littoral zone, there a number of barriers to sustainability. These include climate change, habitat loss and degradation and pollution. Climate change incorporates a range of possible impacts, including wholesale and fundamental alterations of physical, chemical and biological characteristics, but arguably the most important and certainly the most predictable is that of sea level rise (Wilson 2002). The IPCC Second Assessment Report in 1997 estimated a rise of between 15–95 cm in mean sea level by 2100 (IPCC 2001). The immediate consequence will be accelerated erosion of unprotected coastlines, along with an increased risk of flooding of the hinterland. It is entirely possible that the intertidal systems could adjust, as they have in the past, to the new regime, but there will be difficulties where managed retreat is not possible. In these circumstances, the intertidal area may be further squeezed between reclaimed land and the rising sea level.

Loss of intertidal habitat is fortunately becoming rarer, partly as a result of increased awareness of the many vital functions performed by these zones and partly also because a lot of the more accessible intertidal land has already been reclaimed. On the other hand, habitat degradation is increasing as a result particularly of population pressure, and the loss of mangroves is one of the few 'marine quality' issues specifically cited by the OECD (OECD 2002). GESAMP's (1990) report on the *State of the Marine Environment*, differentiated strongly between the threats in the open sea and those inshore. For the latter, the report that considered habitat loss, along with fishery pressures, were at least as important as pollution.

Many shores, particularly estuaries, in the industrialised nations still suffer from high levels of contamination, but it would be fair to say that the past thirty years has seen a considerable effort on the part of many nations to remove the worst of the persistent contaminants from the system. A growing body of international legislation now limits what may and may not be discharged and under what conditions and this, coupled with the decline of much of the heavy industry in Europe and the USA has resulted in at least partial recovery. TBT, which first came to prominence in the 1970's for its commercial impacts on intertidal oyster culture and for its environmental impacts on intertidal gastropod populations, was reviewed over ten years ago by Bryan and Gibbs (1991), and provides an excellent example of how the focus of pollution concerns have changed. In 1967 the wreck

of the *Torrey Canyon* provided a spectacular example of impacts on the shore some of which may still be detected tens of years later (Hawkins and Southward 1992). Now, although it is fair to say that the capacity for spectacular oil spills is still with us, the focus has shifted from the acute to the more subtle sub-lethal effects, such as shown by the TBT imposex response, itself paralleled by the impacts of oestrogen mimics, and to more subtle ecosystem disruptions like eutrophication and harmful algal blooms (HABs). The latter are now being tackled under a regulatory framework which covers all inputs, including diffuse sources from river catchments (e.g the co-called Framework Directive 60/2000/EC dealt with in detail in this seminar) and mandatory treatment standards for point sources (e.g. Wastewater Treatment Directive 96/1995/EC). However, there still remain considerable difficulties in extrapolating measurable changes even up to population level to community impacts *in situ*, even for the best-studied substances (Hawkins *et al.* 1994).

Investigation of ecosystem disruption of necessity entails consideration of long-term changes and this calls into consideration the natural cycles and variability of the system, and the partitioning of impacts between natural variation, anthropogenic variation and inevitably now, climate change variation.

In this study it is proposed to set out the controls on the sedimentary intertidal ecosystem, to examine what properties of the system may be used to quantify the stability of the system, and to look at long-term changes in the system and in some of its more prominent components.

MATERIALS AND METHODS

Details of the physico-chemical characteristics of the selected sites in Dublin Bay have been published in Desprez *et al.* (1991) and Ducrotoy *et al.* (1991), while the mapping of the topography of the South Bull (Figure 1) is set out in Wilson (1993b).
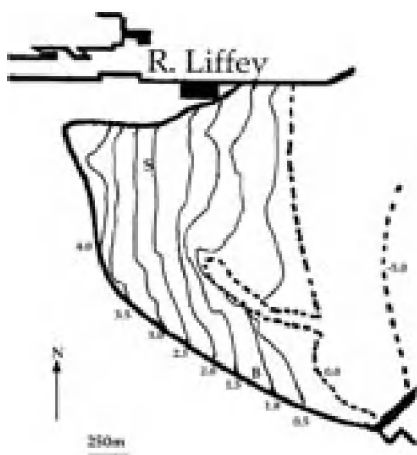

Figure 1. South Bull, Dublin Bay showing shore heights relative to Chart datum (CD) along with position of long-term sample sites Blackrock (B) and Sandymount (S): dotted lines indicate low water mark (0.0 m CD) and the five metre contour (−5.0 m CD).

Unless otherwise specified, the calculations of parameters including density (individuals m^{-2}) and biomass (g wet flesh weight^{-2}) related to height on shore are based on samples of 0.25 m^2 (Wilson 1982). Those for the long-term monitoring (after 1985) are based on multiple cores of 0.03 m^2 (Wilson 1993b, 1997, Wilson and Emblow, 2002). Productivity was calculated using Schwinghamer *et al.*s (1986) relationship for macrofauna

P:B = 0.525*W$^{-0.304}$

where W = individual body size (kcal).

RESULTS

Figure 1 shows the map of Dublin Bay with height contours and sample sites/transect across the South Bull (Sandymount strand). The height contours indicate a fairly gentle and consistent slope toward low water mark, but also emphasise how the upper margins of the shore have been truncated and squeezed by urbanisation. Within these contours, there are also smaller features which vary in size from irregular small channels and runnels to patterned ripples.

Figure 2 shows the metrics for a transect from the landward edge of Sandymount Strand down to the low water mark. Densities (individuals m^{-2}) increase from low to high shore, but the peak of biomass is clearly around mid-shore (Figure 2a: note the log scale on the y-axis). The Shannon-Weiner index (H') and evenness (J = H'/H$_{max}$) were both highest at low shore, reasonably consistent over the bulk of the mid shore, but declined precipitously at the topmost sites (Figure 2b). The different pattern of response in abundance and biomass up the shore is clearly demonstrated in Figure 2c, not only simply in terms of the individual body size (biomass) but also in terms of the Shannon-Weiner Evenness Proportion (SEP = H'$_{biomass}$/H'$_{abundance}$, McManus and Pauly, 1990). The latter indicates clearly that partitioning of biomass among the species at high shore is much more equitable than the partitioning of abundance. Productivity (Figure 2d) is low at both high and low shore, but the overall pattern seems to suggest that it is the higher levels (> +2m) which contribute most to littoral productivity.

The Species Abundance Biomass (SAB) curves (Warwick 1986, Warwick and Clarke 1994) suggest that the greatest difference is between the low shore (Figure 3a), where the curve for biomass is well above that of numbers, and the mid shore (Figure 3b) with high shore (Figure 3c) somewhat in-between. This ranking implies a gradient of stability low>high>mid shore.

Clarke (1990) has recommended using partial dominance curves, in which the dominance of each species is calculated successively. This avoids the problem, particularly prevalent where there are random fluctuations of small, numerically dominant species, that the shape of the curve is essentially decided by the characteristics of the first-ranked species. The partial dominance curves, shown also in Figure 3 essentially confirm the patterns and the rankings of the full ABC curves and support the hypothesis that the influence of shore height pervades the whole community and is not simply being expressed through a single dominant species.
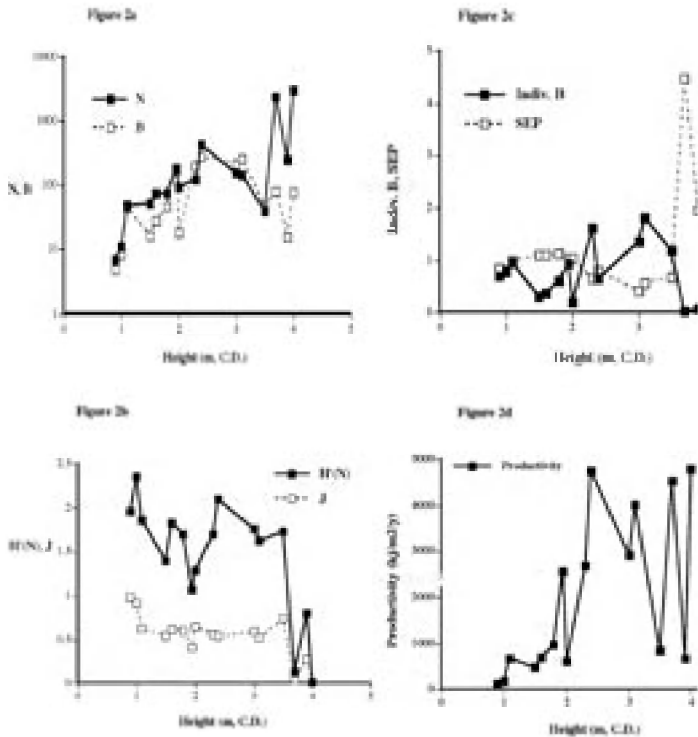
Figure 2. Upshore transect showing community metrics with height (m CD) on shore: a) numbers of individuals (N, 0.25m^{-2}) and biomass (B, 0.25m^{-2}); b) Shannon-Weiner Index (H') and evenness (J); c) individual biomass (B, g) and Shannon-Weiner Evenness Proportion (SEP); and d) productivity (kj.m^{-2}.y^{-1}).

Figure 4 shows the long-term changes in numbers of species (Figure 4a) and in H' (Figure 4b) at the Sandymount site (mid shore) and the Blackrock site (low shore) in Dublin Bay. The two measures of diversity show radically different patterns. The numbers of species at the two sites has essentially remained unchanged over the sampling period, albeit with considerable inter-annual variation. There is perhaps some slight suggestion of higher numbers of species at the mid shore (Sandymount) site in the last five years or so, but this period also contains very high and very low numbers (Figure 4a).

A marked contrast is shown in the pattern of diversity, H' (Figure 4b). Although both sites follow much the same trends, until recently anyway, there seems very much more variability in H' at mid shore, which can change from extremely low values (<1.0) to relatively respectable values (>2.0) within the same year. For most of the period of monitoring, the inter-annual trends followed the same pattern suggesting that perhaps the controlling factors were operating at the level of the Bay, whereas the recent divergence may imply a much more localised influence. Note that the influence can cover also the removal of a restriction, such that a species' numbers may suddenly increase not because of the sudden increase in one parameter, but a decrease in another, perhaps limiting or controlling factor. This is discussed further in relation to the numbers of *T. tenuis*.
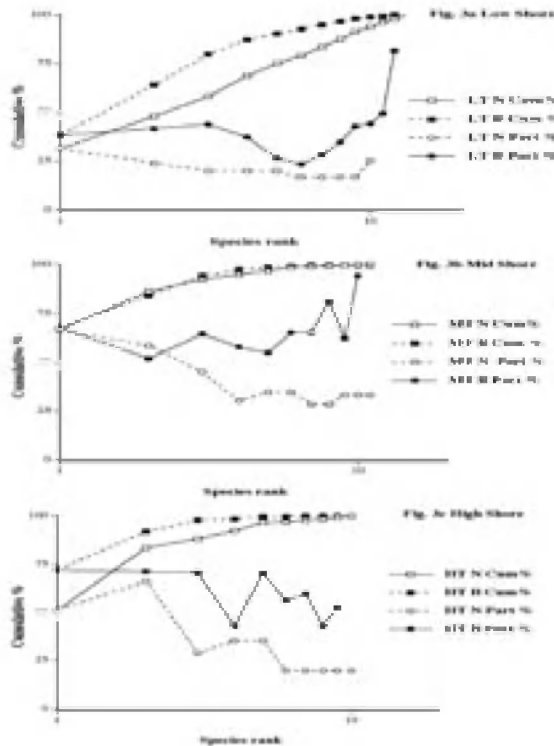
Figure 3. Abundance Biomass Comparison (ABC) curves (squares) and partial dominance curves (circles) showing ranked species' contribution to numbers (N, open symbols) and biomass (B, filled symbols) for a) Low shore (LT); b) Mid shore (MT); and c) High shore (HT).

The decline in H' at low shore (Figure 4b) coincides with the remarkable increase in the numbers of one species, the bivalve *Tellina tenuis* (Figure 5a) whose density increased almost ten-fold from 1996 to 1998. In contrast, cockle (*Cerastoderma edule*) densities (Figure 5b) have declined from a peak in the mid 1980s, with a slight resurgence after 1995, to the levels recorded by West *et al.* (1978) in the early 1970s. In addition, the cockle densities show much greater variability, both between years and within years, than do those of *Tellina*. The decline in the cockle populations is mirrored in the decline of *Macoma balthica* (Figure 5c), again at mid-shore, to the extent that the population has almost disappeared. As with *C. edule*, there was considerable variability in the *M. balthica* density from one sampling interval to the next.

There were few indications that the benthic populations in Dublin Bay are responding directly to climatic or other large scale variables. Figure 6 shows the winter average NAO Index and the annual first year's growth in *C. edule* and the two were significantly correlated ($r = 0.49$, $0.05 > p > 0.01$). A similar, though slightly less strong correlation was obtained for the annual average NAO index and *C. edule* first year's growth ($r = 0.45$, $0.05 > p > 0.01$). However, neither growth in subsequent *C. edule* age-classes nor in any age-class of *T. tenuis* (Figure 6) was correlated with the NAO index.
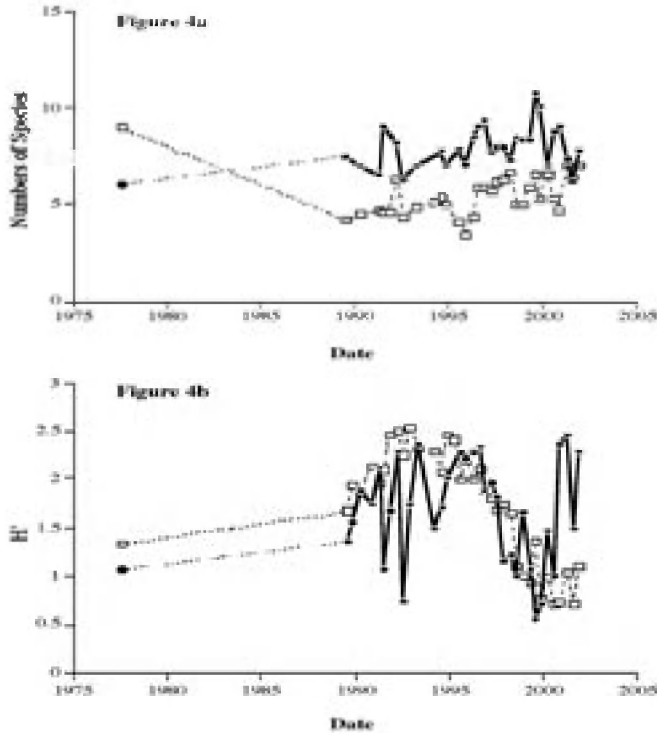
Figure 4. Long-term monitoring of Blackrock (squares) and Sandymount (circles), showing a) Numbers of species; and b) Shannon-Weiner Index (H'): 1977 data from Wilson (1982)

DISCUSSION

The sustainability of the Dublin Bay littoral system will depend on the system's responses to external forcing factors such as sea level rise, climate change or increase in mean temperatures and on the varying pattern of response of the component species.

Sea level rise will be a major factor in the future of the Bay, since the landward extension of the intertidal zone is curtailed by development and hard defences. Wilson (1993b) modelled a scenario in which the sole consequence was loss of area, but there are complications. High, mid, and low shore communities display differing properties and any change in their proportions may result in a disproportionate change in the Bay system. The various metrics presented here suggest that mid and high shore communities may be less stable and resilient than those of low shore, yet these contributed most to the benthic productivity, which in turn provides food for the overwintering waders in Dublin Bay. The results presented here support some, but not all of the concepts embedded in Sanders (1958) 'stability-time' hypothesis and developed by others such as Odum (1969) and McCann (2000). Currently, the disturbance-diversity-productivity model incorporates the intermediate disturbance and other hypotheses, and while evidence broadly supports this theory, there is still considerable debate as to the nature of the relationship(s) (e.g. Liebold 1999).
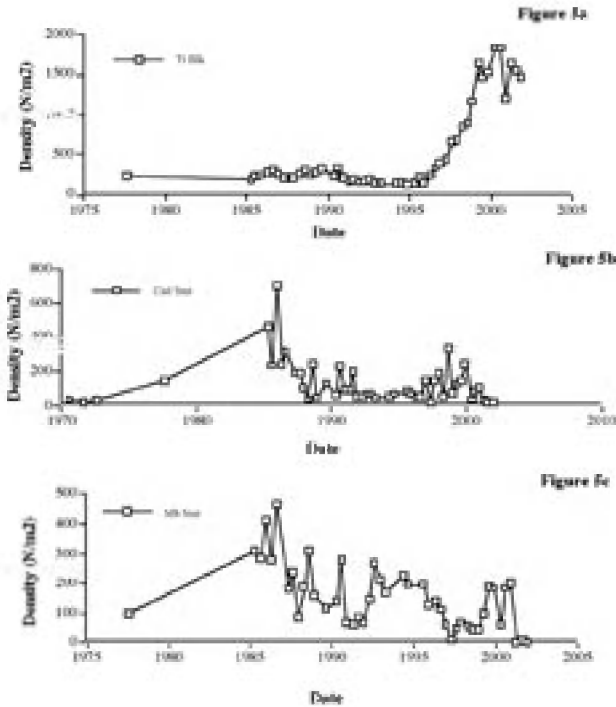
Figure 5. Long-term monitoring of selected bivalve species: a) *T. tenuis***, Blackrock; b)** *C. edule***, Sandymount (1971–1973 data from West** *et al.* **1978); c)** *M. balthica***, Sandymount.**

Firstly, the gradients of change in system properties down the shore are not linear. As the physical gradient, in terms of shore height, does change in a fairly regular fashion, then the conclusion must be either that there are processes operating at a smaller spatial scale than mapped here or that change proceeds on a version of punctuated equilibria.

Thrush *et al.* (1989) have identified patterns and patches of heterogeneity of the distribution of species on sandflats at a variety of scales from some tens to some thousands of m². Aronson (1994) has even suggested that scale independence is a property only of large, interactive systems, clearly implying that some effect of scale should not be expected in the organisation of intertidal systems. However, both Thrush *et al.* (1989) and Aronson (1994) emphasised the random nature of the majority of species' distributions.

As the gradient of physical control increases up the shore, then clearly the probability of disturbance increases. Does the shore then confirm to the 'intermediate disturbance' model? The answer would appear to be, yes, to some extent, in that the zone of potentially highest disturbance (high shore) was consistently lowest in terms of species numbers and diversity (H', J), but not SEP. However, the low shore/mid shore transition was less clear and it was the mid-shore sites which showed the least stable ABC pattern.

The long-term results also point to radical differences in interpretation according to which of the metrics are examined. The numbers of species has remained fairly constant, even perhaps increasing over time, yet the Shannon-Weiner diversity (H') showed a clear and consistent decline over much of the same period. To what extent the decline, which
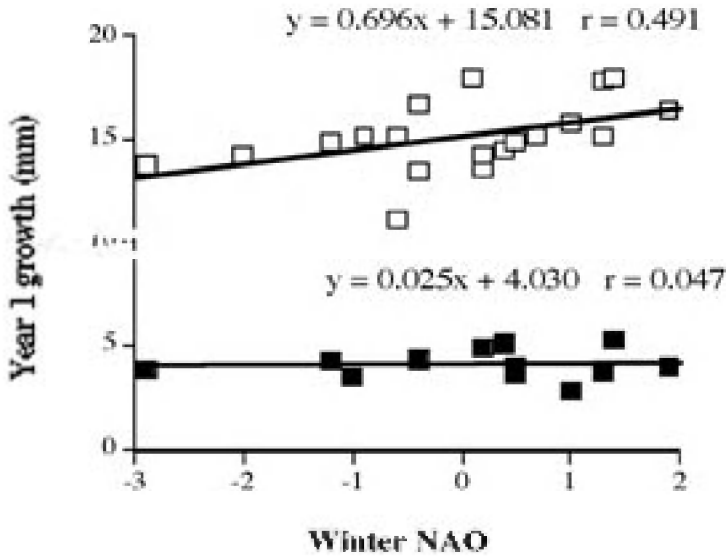
$$y = 0.696x + 15.081 \quad r = 0.491$$

$$y = 0.025x + 4.030 \quad r = 0.047$$

Figure 6. First year's growth (shell length (mm) at 1-y-o) of *C. edule* **(open symbols) and** *T. tenuis* **(closed symbols) with average winter NAO Index 1981–1999.**

was mirrored at both low and mid shore, was symptomatic of larger changes in the Bay as a whole, is still questionable, especially as the two zones dramatically diverged following the recruitment success of a single species (*T. tenuis*) at low shore.

In terms of sustainability, the results present certain contradictions. The metrics for low, mid and high shore zones suggest that while the low shore presented the most consistently stable values, there was nevertheless a long-term decline in H' over the middle ten years or so of the monitoring period. However, since low shore showed low biomass and low productivity, perhaps changes here are less important in terms of system function than changes at mid or high shore. Wilson (1993b, 2001) has demonstrated that species such as *C. edule* and *M. balthica* have declined on the whole in Dublin Bay, but reported that these changes showed no correlation with changes in bird numbers, even with those species for whom they are a primary food source. In fact the evidence that bird numbers have been high, indeed with densities as high as anywhere in Europe, for many years seems to imply that the system overall is extremely resilient and has shown considerable resilience in the face of the many natural and anthropogenic stressors to which it has been subjected. It has even been suggested that the essential character of the Bay, and its prominent species have remained largely unaltered over the centuries (Wilson 1993b, 1997).

Ducrotoy *et al.* (1989) proposed *C. edule* as a 'key' species, whose fluctuations reflect short term changes in environmental variables or pollution, whereas *M. balthica* should be considered more of a 'target' species for large-scale (temporal or spatial) monitoring. While this suggestion is somewhat borne out by Beukema's long-term data from the Wadden Sea (Beukema 1988; Dekker and Beukema 1999) and by a pan-European comparison of the two species (Desprez *et al.* 1991, Ducrotoy *et al.* 1991), the

driving forces on the continent were climate extremes, which, moderated by Ireland's Atlantic influence, are much dampened down in the Dublin Bay populations. This point was further considered by Wilson (Wilson 1993a, Wilson and Elkaim 1992) who noted moreover that many estuarine species, including the supposedly stable *M. balthica* did in fact display the characteristics of opportunist or r-strategist species associated with disturbed environments. There was however support for the suggestion of *M. balthica* as a candidate for long-term monitoring, but with the eurytolerant *M. edulis* as a stress indicator (Wilson 1993a, Wilson and Elkaim 1992). Overall, it is probably worth persevering with the larger shore bivalves as indicator species, partly on the grounds of ease of collection and identification, but mostly because they are major contributors to biomass and productivity especially in Dublin Bay (Wilson 1982).

Prediction of future changes to the system is still largely guesswork, although the extent of changes to the driving forces (sea level rise, climate (temperature) change, sewage input) are well documented. Thus, the sustainability of current usages is also uncertain. As shown here, there are already forces which are shaping the Dublin Bay system and there have been speculations, discussed above, as to the nature and causes of these changes. It may be therefore that present incompatibilities within the system usages (e.g. sewage disposal and bathing water) may be replaced by other causes of conflict (less organic input leading to fewer birds) and that an essential component of sustainable management is an understanding of how the ecological system operates.

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