

Long-term changes in density, population structure and growth rate of *Tellina tenuis* from Dublin Bay, Ireland

Tellina tenuis
Long-term
Population
Growth
Ireland

Tellina tenuis
Long terme
Population
Croissance
Irlande

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ABSTRACT

Changes in the *Tellina tenuis* population in Dublin Bay, Ireland since 1977 are described. Population density at the monitoring site increased from 260 m⁻² (although a maximum density of 548 m⁻² was found nearby) in 1977 to a peak of 434 m⁻² in 1989. Densities recently have been the lowest recorded, around 170 m⁻². These changes do not seem to have been associated with any change in elevation of the site.

The population structure has changed considerably, from one dominated by larger, older animals in 1977, when there did not seem to have been any significant recruitment for the previous two years, to one in which recruitment, if not in any great numbers, has at least been more or less regular, with the last two years (1993 and 1994) showing the highest densities of young (<10 mm) recruits despite having the lowest overall population densities. However there was no direct correlation between population density and recruits, but there is some indication that the level of recruitment into the population was higher following milder winters.

The larger sizes seen in the 1977 population appear to be due to the longevity of the population, as the L_{∞} value (derived from Ford-Walford plots) was not noticeably higher than for other years. There were differences from year to year in both the L_{∞} and the coefficient of catabolism k , but as the growth parameter $w (= L_{\infty} \cdot k)$ stayed relatively constant with a ten year mean of 6.15, it is suggested that the different rates of growth could be due to better feeding conditions and reallocation of resources.

RÉSUMÉ

Variations à long terme de la densité, de la structure et de la croissance d'une population de *Tellina tenuis* dans la baie de Dublin.

Les variations d'une population de *Tellina tenuis* ont été suivies dans la baie de Dublin (Irlande) depuis 1977. Sur le site d'étude, la densité a augmenté de 260 m⁻² en 1977 jusqu'à un maximum de 434 m⁻² en 1989. Les valeurs les plus faibles, voisines de 170 m⁻² ont été enregistrées récemment; ces variations ne semblent pas liées à quelque changement du niveau du site.

La structure de la population a évolué considérablement, d'abord dominée en 1977 par des individus âgés et de grande taille, sans recrutement significatif pendant les deux années précédentes, pour arriver à une structure où le recrutement, bien que peu important, est assez régulier. Le plus fort recrutement de juvéniles (<10 mm) s'est produit pendant les deux dernières années (1993, 1994) avec, globalement, les densités les plus faibles. En revanche, il n'y a pas de corrélation directe entre la densité de la population et le recrutement, mais celui-ci est plus important après les hivers doux.

Les grandes tailles observées en 1977 dans la population sont liées à la longévité de la population, car la valeur de L_{∞} (méthode graphique Ford-Walford) n'est pas plus élevée que les autres années. Le L_{∞} et le coefficient de catabolisme k varient d'une année à l'autre, mais le paramètre de croissance $w (= L_{\infty} \cdot k)$ relativement constant, est en moyenne de 6,15 sur une dizaine d'années. Les différences affectant la croissance seraient liées à l'amélioration des conditions nutritives et à une redistribution des ressources énergétiques.

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INTRODUCTION

Tellina tenuis is found throughout Europe from the Atlantic, where it is often the dominant (and occasionally the only) macrofauna on sandy beaches, to the Mediterranean, where the sediment preference is the same, but the centre of the distribution has shifted to the shallow sublittoral (Tebble, 1966; Massé, 1972; Atkins *et al.*, 1985; Wilson, 1990).

The classical work of Stephen (1928, 1932) in and around Kames Bay in Scotland, described in detail the biology of *T. tenuis*, and, besides data on the density and distribution, included measurements of both seasonal and annual growth. Small sizes predominated below low water mark (LWM), with larger ones becoming progressively more common above low tide. In this investigation, Stephen (1928) noted that, although populations attained densities of up to 4,000 m⁻², recruitment could still be sporadic with some year classes barely represented. In a later paper, Stephen (1938) showed that unusually good recruitment (of *T. tenuis* but also of other species) coincided with high environmental temperatures and suggested that this was due to an overall improvement in conditions and particularly the food available.

Detailed studies by Trevallion and her co-workers (Ansell and Trevallion, 1967; Trevallion, 1971; Trevallion and Ansell, 1967; Trevallion *et al.*, 1973) set out in more detail the energy partitioning in *T. tenuis* during the growth cycle, and again emphasised the link between environmental conditions and growth. In these studies (Ansell and Trevallion, 1967; Trevallion, 1971; Trevallion and Ansell, 1967; Trevallion *et al.*, 1973) it was calculated that a major drain on the population was the cropping of the siphons by juvenile plaice, which might account, in some years, for the failure of reproduction. McIntyre (1971) in his study of several populations of *T. tenuis*, again pointed out the irregular recruitment of many populations, and suggested that the more regular recruitment into populations such as those studied by Stephen in the Clyde could be due to the richer environment in the latter, which allowed the animals to withstand cropping and achieve reproduction.

Stephen's (1928, 1932, 1938) studies include observations from 1897 (when the density was over 7500 m⁻²) through the 1930s and up to his final observations in 1951 (Stephen, 1953), although his major systematic sampling programme was concentrated into the ten years or so from 1926 onward. More recently, the regular monitoring of Hunterston sands, a sublittoral site across from Kames

Bay in the Clyde where the area is subjected to the warm water outflow from the power stations, has yielded a wealth of data on long-term population changes of (among others) *T. tenuis* (Barnett and Watson, 1986). Like Stephen (1938), Barnett and Watson (1986) found higher settlement following years with higher summer temperatures, but the picture concerning growth was less clear. The Hunterston animals did not grow as large as those from Kames Bay except in one year for which it was suggested that an unusually good phytoplankton bloom had allowed the animals to take advantage of both the higher temperatures at Hunterston and the abundant food supply.

In Dublin Bay, *T. tenuis* is found from around mid-tide level to just below LWM, with the highest population densities of just over 500 m⁻² just above the LWM (Wilson, 1982, 1983). The metabolic responses of *T. tenuis* to temperature show that environmental temperatures at Dublin rarely reach those at which direct stress would be imposed (McMahon and Wilson, 1981; Wilson, 1981; Wilson and Elkaim, 1991) and studies on the thermal tolerance show they are capable of acclimatising to and withstanding temperatures very much higher again (Wilson, 1978; Ansell *et al.*, 1980). Studies on other species in the COST 647 programme have shown that while species in Dublin Bay seem not to attain the densities found elsewhere neither do their populations undergo fluctuations of the same magnitude, an observation which is attributed to the mildness of the climate compared to continental Europe (Desprez *et al.*, 1991; Ducrotoy *et al.*, 1991). Nevertheless, recent work on *Cerastoderma edule* and *Macoma balthica* in Dublin Bay has shown that some populations of both these bivalves have declined sharply in recent years (Wilson, 1993; unpublished data), which may be a indication of a recent environmental change.

This paper investigates the changes in a population of *T. tenuis* in Dublin Bay, with particular reference to growth and recruitment.

METHODS

The sample site was just off Blackrock, in Dublin Bay, at a tidal height of about 1.2 m, at which height they are uncovered at all but the smallest neap tides. The core size for the 1977 survey was 0.25 m², and from 1985 onwards multiple cores of 0.04 m² were taken. The sieve mesh size was 1.0 mm, and shell sizes and growth rings were

measured with vernier callipers to the nearest 0.02 mm. For growth rings, around 15 specimens were selected at random from the sample.

Temperatures refer to air temperatures at Dublin Airport, which is the nearest recording station.

RESULTS AND DISCUSSION

The population densities at the sample site of *T. tenuis* and the closely related *Tellina fabula* from 1977 to 1995 are shown in Figure 2.

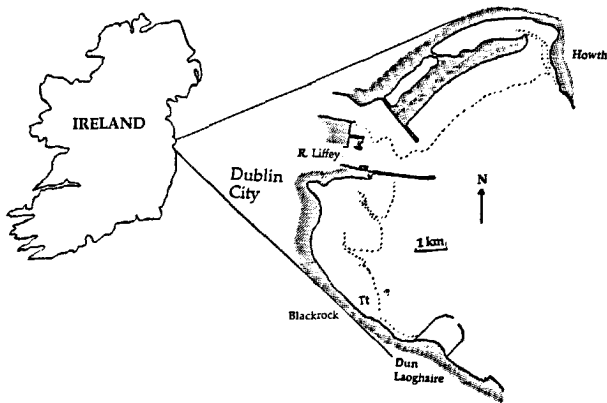


Figure 1

Dublin Bay, showing position of sample site ("Tr").

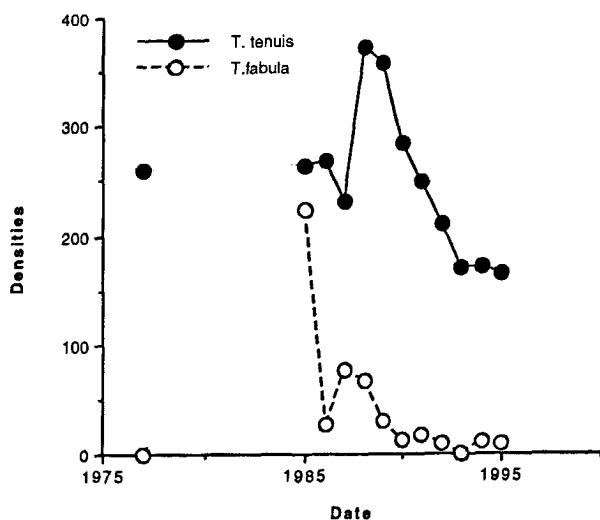


Figure 2

Densities (Nos. m⁻²) of *T. tenuis* and *T. fabula* at Blackrock.

The highest densities of *T. tenuis* were found toward the end of the 1980s since when there has been a consistent decline. *T. fabula* densities have likewise declined since the start of regular sampling in 1985 and for the last six years or so, they have been represented by only the occasional individual in the samples. However, they were not found in the 1977 survey, and Figure 2 may indicate no more

than unusually good conditions for *T. fabula* leading up to 1985 followed by a return to "normal" conditions.

A second possibility may be a change in the environmental conditions at the site, although neither sediment type nor species composition in general shows much evidence of marked change since 1977 (Wilson, unpublished data). The latter argument seems also to discount the possibility of a change in the elevation of the site, in that *T. fabula* is largely a species of the Dublin Bay sublittoral (Wilson, 1976, 1981), and this point will be returned to later.

Figure 3, which shows mean (average of samples over the year) annual *T. tenuis* densities along with mean annual temperatures for the same years, shows some evidence of a relationship between the two, especially since 1987. However, correlation (measured with Spearman rank correlation r_s) between density and temperature, although positive, was not statistically significant ($r_s = 0.39$, $p > 0.05$), and there was little correlation at all between density and the temperature of the previous year ($r_s = 0.25$, $p > 0.05$).

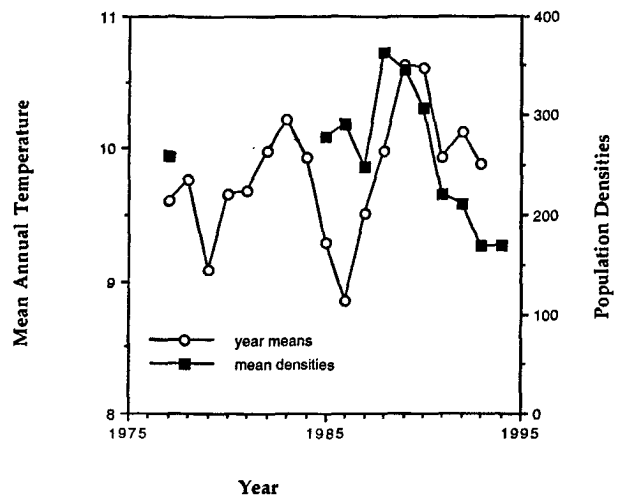


Figure 3

Mean annual population densities (Nos. m⁻²) of *T. tenuis* with mean annual temperatures (°C).

The *T. tenuis* population at the sample site over the years has been largely composed of older individuals (Fig. 4). In 1977, for which the length frequency histogram represents the entire South Bull comprising the 77 sites at which *T. tenuis* was found there were almost no small (<10.00 mm) specimens present. This trend is repeated from 1985 until 1993 and 1994, when for practically the first time, substantial numbers of smaller animals appeared in the population.

Sporadic recruitment into *T. tenuis* populations seems to be the rule rather than the exception, even for abundant populations (Stephen, 1928, 1938; Barnett and Watson, 1986) and is even more pronounced in sparse populations on more exposed beaches (McIntyre, 1971; Atkins *et al.*, 1985). In Dublin Bay, as in other locations, there are differences in population structure with shore height, with smaller individuals found at greater densities near

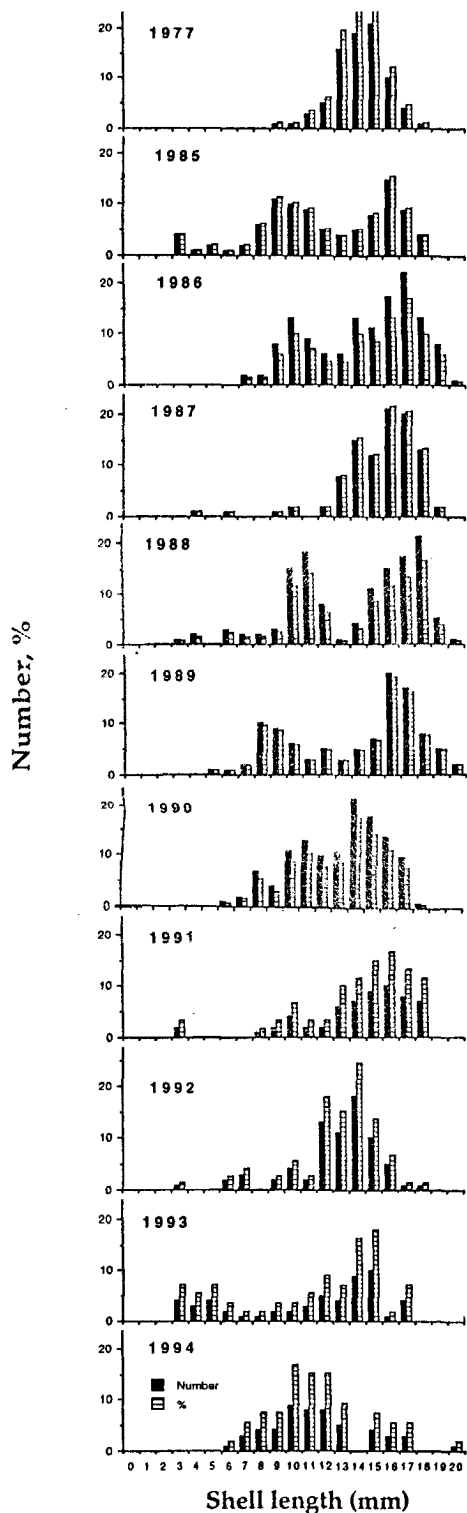


Figure 4
 Length-frequency histograms for *T. tenuis* from 1977 and 1985-1994. The scale on the y-axis refers to both the numbers of individuals and to percentage.

LWM, and the reasons for, and the mechanisms behind this phenomenon have been considered at length by Stephen (1926, 1928). Although no quantitative data are available, observations at the site do not suggest the large-scale sediment movements that might exhume settled and burrowed adults, especially as they are commonly found at depths of 10 cm and more (Wilson, 1979) and might

transport them around. Wilson (1976) found no evidence of any migration of adults up or down the shore in Kames Bay, and there is no reason to suppose that the Dublin population would behave any differently. However, the paucity of smaller individuals (Fig. 4) in the population over such a length of time does therefore seem to imply some degree of immigration of larger animals into the population.

Previous work (Stephen, 1938; Barnett and Watson, 1986) has linked recruitment to environmental temperature and Figure 3 does show some relation between population density and temperature. Figure 5 shows the relationship between the number of small (<10 mm shell length) animals and mean temperature of the previous winter months, December, January and February.

As with the population densities, there appears to be some link between recruitment (in this broad sense) and temperature. The strongest, but not statistically significant correlation (Spearman $r_s = 0.46$, $p > 0.05$) was with previous winter temperature (Fig. 5), although the relation with mean annual temperature of the previous year was nowhere near as strong ($r_s = 0.20$, $p > 0.05$).

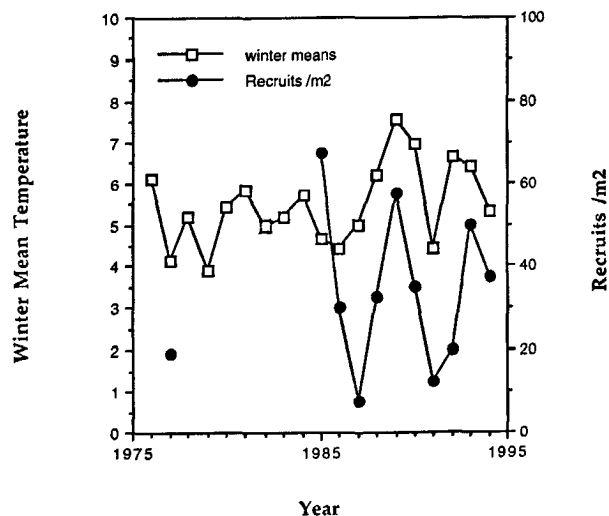


Figure 5
 Density (Nos. m⁻²) of recruits (<10 mm shell length) of *T. tenuis* versus temperature (°C) the previous winter.

There is clearly some link with temperature, although the evidence presented here is inconclusive. The link may be direct, through survival, which Beukema (1979) found to be lessened after severe winters in the Wadden Sea, or indirect, through the improvement in feeding conditions suggested by a number of authors (Stephen, 1938, 1953; McIntyre, 1971; Barnett and Watson, 1986). Barnett (1985) has shown that growth of *T. tenuis* larvae, whose numbers will obviously impact on subsequent adult densities, in the laboratory where food supply was not limiting was greatest at temperatures between 10°C and 15°C, which corresponded to the range of July sea temperatures in cool years and warm years respectively.

Stephen's (1928) study included an analysis of the age structure of the population, and his measurements have

been largely supported by the subsequent studies at other locations around Scotland (McIntyre, 1971). However, Barnett and Watson (1986) who used a smaller mesh size (0.5 mm as opposed to 1.0 mm) suggested that the initial growth ring was laid down at a shell length of <2.0 mm and that Stephen's (1928) first ring at around 3 mm-4 mm was indicative of the 1+ year group. In this study, the year classes will follow Barnett and Watson (1986) such that year 1 refers to the first full year of growth *i.e.* the 1+ age group.

The average growth curve over the period of study 1985-1994 is shown in Figure 6, and the shell lengths of each year class in Table 1.

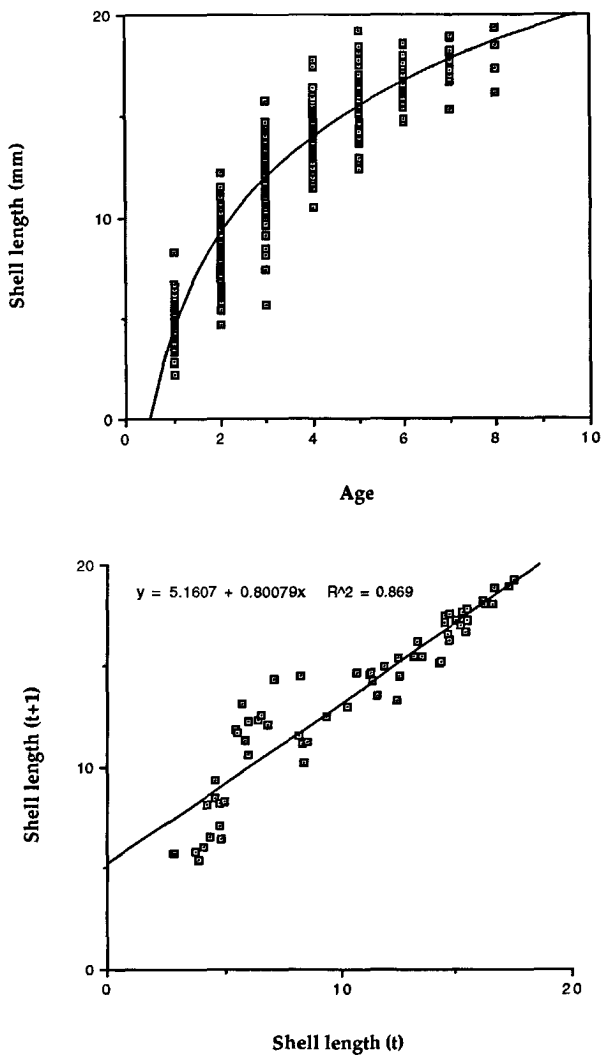


Figure 6
(a) Von Bertalanffy curve and b) Ford-Walford plot of mean year-class size: *T. tenuis*, 1985-94.

Compared to Scottish animals, growth in Dublin Bay appears to be somewhat better, and it is tempting to ascribe that to the milder climate as suggested by Barnett and Watson (1986) whose data seem to indicate that Hunterston animals grew faster than those at Kames Bay due to the higher temperature environment of the thermal effluent even if they did not grow as large.

Table 1

Shell lengths (mm, mean and standard deviation (s.d.)) of *T. tenuis* year classes 1985-94, and comparison with a) Stephen (1928, 1953) and Barnett and Watson (1986) from b) Kames Bay and c) Hunterston.

| Year Class | N | Mean SL | s.d. | a | b | c |
|------------|-----|---------|------|----|---------|-------|
| 0 | - | - | - | 3 | 1-1.25 | 1.5-2 |
| 1 | 91 | 4.87 | 0.94 | 7 | 3.5-4.0 | 5-6 |
| 2 | 115 | 8.29 | 1.68 | 9 | 7.5-9 | ? |
| 3 | 112 | 11.99 | 1.54 | 11 | ? | ? |
| 4 | 102 | 14.25 | 1.29 | - | ? | ? |
| 5 | 78 | 15.68 | 1.28 | | | |
| 6 | 34 | 16.57 | 0.90 | | | |
| 7 | 12 | 17.57 | 1.01 | | | |
| 8 | 4 | 17.84 | 1.38 | | | |

It can be seen from Figure 6 that there was considerable variation in annual growth, and the growth parameters L_{∞} and k of the von Bertalanffy equation along with $w (= L_{\infty} \cdot k)$, which is considered to be a more robust measure of growth (Gallucci and Quinn, 1979; Duineveld and Jenness, 1984), for each year class are shown in Table 2.

Table 2

Growth parameters L_{∞} and k of the von Bertalanffy equation along with $w (= L_{\infty} \cdot k)$ for *T. tenuis*. See also text for explanation and discussion.

| Year | L | k | w |
|---------|-------|-------|------|
| 1889-93 | 18.94 | 0.361 | 6.84 |
| 1905-6 | 21.84 | 0.318 | 6.95 |
| 1977 | 19.98 | 0.261 | 5.22 |
| 1985 | 26.34 | 0.220 | 5.80 |
| 1986 | 22.85 | 0.318 | 7.27 |
| 1987 | 19.20 | 0.366 | 7.03 |
| 1988 | 19.22 | 0.405 | 7.77 |
| 1989 | 21.90 | 0.248 | 5.44 |
| 1990 | 20.16 | 0.344 | 6.93 |
| 1991 | 20.57 | 0.321 | 6.59 |
| 1992 | 19.97 | 0.321 | 6.40 |
| 1993 | 18.72 | 0.357 | 6.68 |
| 1994 | 18.88 | 0.373 | 7.03 |
| 1985-94 | 19.65 | 0.313 | 6.15 |

Table 2 also shows the growth parameters for specimens deposited in the National Museum Ireland around the turn of the century. Unfortunately, apart from approximate location, details on the actual collection, or even if the animals were alive, are missing. Those from 1889-93 came from Portmarnock, about 30 km north of Dublin Bay, while those from 1905-6 came from the north Bull in Dublin Bay, whose *T. tenuis* populations, in 1977 at least, showed no discernible difference to those of the south Bull used in Figure 4 (Wilson, unpublished data).

In Table 2, the year 1985 stands out because of a very high calculated L_{∞} . On inspection of the Ford-Walford plot for this year, this appears due to a low coefficient of catabolism (k) with suggestions of small size at year 1,

Table 3

Annual mean temperature (°C) and yearly growth (mm) from 1979 to 1993 and cumulative growth of all five year classes.

| Year | Temp. | year 1 | year 2 | year 3 | year 4 | year 5 | years 1-5 |
|------|--------|--------|--------|--------|--------|--------|-----------|
| 1979 | 9.090 | 3.960 | - | - | - | - | - |
| 1980 | 9.660 | 3.320 | 3.440 | - | - | - | - |
| 1981 | 9.680 | 2.700 | 3.970 | 2.000 | - | - | - |
| 1982 | 9.980 | 3.720 | 5.800 | 2.620 | 1.920 | - | - |
| 1983 | 10.220 | 4.190 | 4.270 | 2.190 | 1.798 | 1.820 | 14.268 |
| 1984 | 9.930 | 4.300 | 3.480 | 2.204 | 2.104 | 1.638 | 13.726 |
| 1985 | 9.290 | 4.790 | 3.230 | 2.012 | 1.536 | 0.480 | 12.048 |
| 1986 | 8.850 | 3.800 | 2.700 | 2.380 | 1.333 | 1.527 | 11.740 |
| 1987 | 9.510 | 4.240 | 3.300 | 2.430 | 1.544 | 1.220 | 12.734 |
| 1988 | 9.980 | 3.880 | 2.910 | 1.848 | 1.668 | 1.293 | 11.599 |
| 1989 | 10.630 | 3.750 | 3.530 | 2.302 | 1.546 | 1.370 | 12.498 |
| 1990 | 10.610 | 3.580 | 3.190 | 1.989 | 1.597 | 1.260 | 11.416 |
| 1991 | 9.930 | 5.020 | 2.980 | 1.742 | 1.708 | 1.610 | 13.060 |
| 1992 | 10.120 | 5.230 | 2.750 | 1.634 | 1.320 | 1.280 | 12.214 |
| 1993 | 9.880 | - | 2.100 | 1.873 | 1.820 | 1.250 | - |

although by year 2 the animals had made up most of the lost ground. Of the other years, 1986-1988 had high *w* values, as did 1994. The year 1977 showed a slightly lower *k* value than average, but was otherwise unremarkable, nor was there any indication that conditions have changed markedly, as far as growth of *T. tenuis* is concerned since the last century.

None of the changes in the growth parameters (of which for clarity only *w* is shown in Figure 7) seemed to correlate with temperature. This is not perhaps surprising, as the overall parameter *w* is a function of the performance over a number of years, and a "good" year can just as easily be cancelled by a "bad" one. The data in Figure 7 suggest, if anything, a negative relationship between the two, although the correlation (Spearman $r_s = 0.18, p > 0.05$) was not significant.

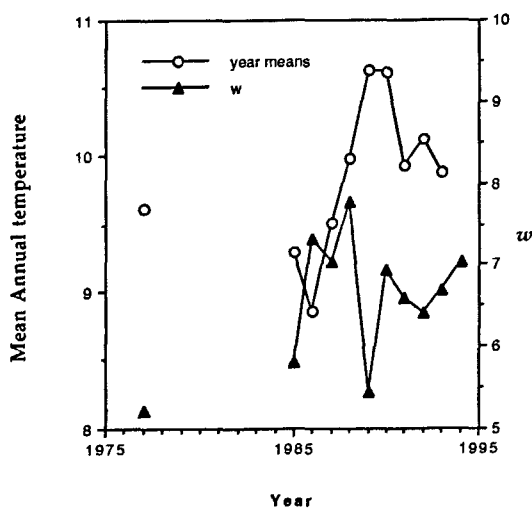


Figure 7

Growth parameter *w* (see text) of *T. tenuis* with yearly mean temperature (°C).

To investigate annual growth, the data was divided by year and by year class and the mean increments with year and class are shown in Table 3.

As can be seen in Table 3, there were considerable differences in growth of a year class from year to year. These differences were significant for year classes 1 and 2 but not for the older groups (Table 4).

Table 4

One-way ANOVA (AOVONEWAY by MINITAB (1991)) of individual growth increments by year classes over the period 1980-1993, showing *F*s value (degrees of freedom for factor and error respectively) and probability (*p*).

| Year Class | <i>F</i> s value | <i>p</i> |
|------------|---------------------|----------|
| 1 | $F_{12,106} = 1.90$ | 0.042 |
| 2 | $F_{12,102} = 2.54$ | 0.006 |
| 3 | $F_{11,88} = 1.31$ | 0.232 |
| 4 | $F_{9,58} = 1.10$ | 0.377 |
| 5 | $F_{7,21} = 0.49$ | 0.830 |

The size at which the animals in Dublin Bay mature is around 10 mm (Wilson, unpublished data), which corresponds to year 3. Year 2 is therefore the last year of growth in which the resources are undividedly allocated to somatic growth. One might thus expect a relationship between growth and temperature for the first two years, but not perhaps thereafter as the excess energy is diverted to gonad output.

The relationship between year class growth and annual temperature is shown graphically in Figure 8, which clearly shows that there was little direct link between environmental temperature and growth. The relationship was mostly positive, with the exception of year 3, but neither the individual yearly growth nor the summed growth of years 1-5 were significantly ($p > 0.05$) correlated with temperature. There are perhaps some suggestions that the maximum growth coincided with the middle of the temperature range, declining toward both relatively high and low temperatures (Fig. 8), but this would seem to imply that populations from higher temperature locations and from lower temperature locations should have smaller individuals than those from Dublin Bay, which does not seem to be the case (Wilson, 1990). However, the

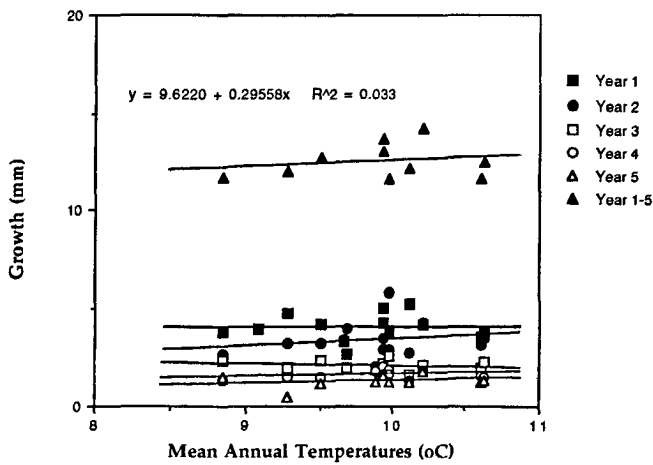


Figure 8

Yearly growth (mm) of *T. tenuis* versus mean annual temperature ($^{\circ}\text{C}$), with regression equation of summed growth up to age 5 (Year 1-5) versus mean annual temperature.

distribution of the data may be suggesting that there is in fact an optimum, which in this case appears to be just over 10°C , but that there other factors can intervene to prevent its expression.

Temperature therefore has some influence on the population and the evidence presented here suggests that this influence is exerted via recruitment or immigration into the population.

The other major influence highlighted by Stephen (1938, 1953) and alluded to by subsequent workers (McIntyre, 1971; Barnett and Watson, 1986) which would play a part would of course be food supply. Unfortunately, data on primary production in Dublin Bay is extremely scanty, and there is no equivalent time series. There are, however, interesting observations over a number of years since 1977 on the growth of *Enteromorpha* in the bay (Jeffrey *et al.*, 1990; Brennan *et al.*, 1994). From these observations, it appears that some years were substantially better than others for algal growth and they may be ranked thus: 1987 > 1990 > 1989 > 1985 > 1993 > 1980 > 1977 and this increasing trend has been noted (Jeffrey *et al.*, 1989). If a similar trend in the growth parameter w (Table 2) is compared, the following sequence is seen 1987 > 1990 > 1993 > 1985 > 1989 > 1977 (no data for 1980), while for summed growth (years 1-5, Table 3) the sequence (for those years available) is 1989 > 1987 > 1985 > 1990. There are differences in the two sequences, but some similarities can be seen and is tempting to conclude that a good year for primary production (*e.g.* 1987) is similarly a good year for *T. tenuis* growth.

That good conditions are not automatically registered as somatic growth could be explained by the partitioning

of energy between soma and gonad, such that excess over a certain baseline is automatically diverted to gamete production. Since primary production is dependent on light, which is usually more available in fine (hot) summers, then this provides link between temperature and recruitment and temperature of course directly controls time of spawning in many bivalves through the number of "degree days" needed. However, it must be remembered that the "young" individuals coming into the population have already spent at least two years elsewhere, and in that case recruitment (or more properly immigration) may be simply a function of stochastic events such as storms.

A final point to consider is the predation pressure on the population. The work by Trevallion and her co-workers (Ansell and Trevallion, 1967; Trevallion, 1971; Trevallion and Ansell, 1967; Trevallion *et al.*, 1973) demonstrated the drain of energy on a population of siphon cropping by flatfish. This would affect larger animals, while the juveniles, which may not be so deeply buried as adults, would be more likely to be taken whole by fish or by crabs or by wading birds. No quantitative data on predation pressure are available, but bird populations have been increasing, with species such as the oystercatcher (*Haematopus ostralegus*) being 50% more abundant than in the early 1980s, and these have been implicated in the decline of another bivalve in Dublin Bay, namely the cockle (*C. edule*) (Wilson, 1993).

CONCLUSIONS

1. Over the last ten years, the population of *T. tenuis* has been largely dominated by older (>3-y-o) animals.
2. Recruitment (immigration) into the population was linked to temperature, but shell (somatic) growth was not.
3. Recently the population has declined, but no significant trends were noted in environmental factors.
4. The population may therefore depend for long-term balance on stochastic events such as storms.

Acknowledgements

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