Environmental variables and their influence on growth of the great scallop
(Pecten maximus) in the English Channel

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Abstract

Recent and historic surveys of the great scallop (Pecten maximus) in the English Channel have shown that most scallops at a specific location exhibit similar growth characteristics, but that groups more than a few tens of kilometres apart may show different growth characteristics. These characteristics and differences appear to be relatively stable through time. Many studies of scallop species have linked growth with a wide range of environmental factors. The stability through time of characteristic growth patterns for scallops implies that the particular environmental conditions responsible for specific growth characteristics are relatively persistent and are more influential than very fine scale micro-environmental conditions that might affect an individual scallop. We estimated von Bertalanffy growth parameters for scallops at survey stations in the English Channel and also extracted environmental variables from available datasets for these locations. Regression analyses carried out to explore the relationships between growth parameters and environmental variables suggested that temperature, seabed stress and chlorophyll concentration were influential for maximum size ($H_\infty$), growth rate parameter $k$ and the combined growth parameter, phi prime ($\phi'$). A sediment size index was non-significant for $H_\infty$, while $k$ and $\phi'$ were sometimes influenced by catch rate (a proxy for abundance). Depth was a significant parameter for unweighted fits to both $H_\infty$ and $k$, but depth was considered to be more a descriptor of location than an environmental variable. Single effect models suggested that increasing seabed stress and temperature both had a positive relationship with $H_\infty$, while increases in chlorophyll a concentration had a negative effect. However, chlorophyll a concentration was positively related with $k$ and all of these three environmental variables were positively related to $\phi'$. As in many studies of this kind, strong correlations both between environmental signals and between the growth parameters themselves complicated interpretation.

Keywords: scallop, Pecten maximus, growth, environmental variables, English Channel, chlorophyll, temperature, seabed stress, depth, sediment type, catch rate

Introduction
The fisheries for scallops (*Pecten maximus*) in the English Channel are among the most valuable fisheries in UK, with annual landings in the region of 9000 tonnes and an annual first sale value of around £14 million (€20 million). Within the English Channel the UK scallop fleets operate in a number of different areas and the exact nature of relationships between these (sub-) stocks remains unclear. However, there are clear differences in scallop growth and spawning cycles between some of these areas.

Between 2004 and 2006 three annual scallop surveys were carried out in an area of the western English Channel supporting important scallop fisheries and spanning a sufficiently wide geographical area that populations with different growth and life cycle characteristics were encountered. An additional short survey was carried out in the eastern English Channel as part of a separate habitat mapping project. These four surveys yielded information regarding the spatial structure of catch rates, as well as providing a considerable resource in terms of length and age data available from retained scallop shells.

During historic scallop surveys as well as these recent surveys, it has been apparent that whilst most scallops at a specific location exhibit similar growth characteristics, groups more than a few tens of kilometres apart may show quite different growth characteristics. This suggests that at a particular location most scallops are experiencing a similar environmental regime and that wide variation in growth due to differences in micro-habitat is not a major factor. It has also been noted that the growth characteristics for a particular location appear to be relatively stable through time, which suggests that the particular environmental conditions responsible for these specific growth characteristics are also relatively persistent through time. These observations provide a rationale for investigating the influence of environmental conditions on scallop growth by comparing environmental variables and scallop growth parameters at different locations in the English Channel.

There is an extensive literature regarding scallop growth, covering a wide number of scallop species and based on studies of scallops in cultured and experimental systems as well as under wild conditions. Culture systems have the advantage that more controlled experimental approaches can be applied to study growth. However, scallop hard parts (shells), which are usually discarded during processing, provide a history of both age and size and this facilitates studies of growth for wild scallop stocks.

Many environmental variables have been cited as influencing growth, but within the literature there are many conflicting results. This may be because in studies correlating environmental conditions with growth, it is usually difficult to identify the causative factor(s) among many environmental signals that are often highly co-varying amongst themselves.

Temperature is the environmental variable most frequently cited as influencing scallop growth for many scallop species and over a very wide geographical range (Table 1). A number of authors have noted the importance of temperature for *Pecten maximus* and clearly the influence of temperature on metabolic rates provides a mechanism to explain its impact on growth rates.
Table 1. References linking temperature with scallop growth rates

<table>
<thead>
<tr>
<th>Species</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aequipecten opercularis</td>
<td>Roman et al., 1999</td>
</tr>
<tr>
<td>Argopecten irradians</td>
<td>Barber &amp; Davis, 1997</td>
</tr>
<tr>
<td>Argopecten ventricosus</td>
<td>Sicard, et al., 1999</td>
</tr>
<tr>
<td>Chlamys farreri</td>
<td>Wang et al., 1999; Yang et al., 1999</td>
</tr>
<tr>
<td>Chlamys islandica</td>
<td>Reinsnes, 1984</td>
</tr>
<tr>
<td>Chlamys varia</td>
<td>Shafee, 1980</td>
</tr>
<tr>
<td>Euvola ziczac</td>
<td>Lodeiros &amp; Himmelman, 1994</td>
</tr>
<tr>
<td>Hinnites multirugosus</td>
<td>Leighton, 1979</td>
</tr>
<tr>
<td>Nodipecten subnodosus</td>
<td>Barrios-Ruiz et al., 2003; Koch et al., 2005; Rupp et al., 2005b; Maeda-Martinez et al., 2006; Taylor et al., 2006</td>
</tr>
<tr>
<td>Patinopecten yessoensis</td>
<td>Maru &amp; Obara, 1967; Yoo et al., 1981; Shimada et al., 2000</td>
</tr>
<tr>
<td>Pinctada maxima</td>
<td>Mills, 2000</td>
</tr>
<tr>
<td>Placopecten magellanicus</td>
<td>MacDonald &amp; Thompson, 1985; 1986; Cote et al., 1993; Emerson et al., 1994; Pozdnyakova, 1995; Claereboudt &amp; Himmelman, 1996; Kleinman et al., 1996; Cranford &amp; Hill, 1999; Pilditch &amp; Grant 1999; Grecian et al., 2003</td>
</tr>
<tr>
<td>Pecten maximus</td>
<td>Wilson, 1987; Andersen &amp; Emil Naas, 1993; Allison, 1994; Chauvaud et al.1998; Laing, 2000; Robert &amp; Nicolas, 2000; Christophersen &amp; Strand, 2003</td>
</tr>
</tbody>
</table>

Other environmental variables cited as influencing scallop growth include food or variables that may be related to food abundance including particulate organic matter, turbidity, phytoplankton, chlorophyll concentration and seston. The relevance of food availability with growth rate is also clear. Examples of references linking these and other environmental factors with scallop growth are listed in Table 2.

Energy expenditure on feeding processes provides a mechanism that could justify the importance of flow rates, which are also frequently implicated. Stock density may be related to food or oxygen limitation and has been related to scallop growth by many studies in cultured systems as well as some in the wild.

Depth has also been widely correlated with scallop growth because it has been recognised as having a strong influence on most aspects of scallop growth and biology (Smith et al., 2001). However, in reality depth may be a descriptor of location rather than an environmental variable and as such represents a particular combination of environmental variables.

A wide variety of other variables have also been linked with growth rates including culture method, fishing intensity, genetics, salinity, wave action, latitude, silting and pollution and many more. Other authors have commented generally that growth is related to site specific environmental factors such as such as salinity, water temperature and water depth (Frenette et al., 2001) or that differences between growth characteristics of populations at different latitudes could be due to density-dependence, different biological interactions and food availability (Lomovasky, 2006).
Table 2. References linking other environmental factors with scallop growth rates

<table>
<thead>
<tr>
<th>Factor</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>Shafee, 1980; Claereboudt &amp; Himmelman, 1996; Pilditch &amp; Grant 1999</td>
</tr>
<tr>
<td>Particulate organic matter</td>
<td>Leighton, 1979; Reinsnes, 1984; Wallace &amp; Reinsnes, 1985; Wilson, 1987;</td>
</tr>
<tr>
<td></td>
<td>Andersen &amp; Emil Naas, 1993; Yang et al., 1999; Grecian et al., 2003</td>
</tr>
<tr>
<td>Turbidity</td>
<td>Rupp et al., 2005a</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>Lodeiros &amp; Himmelman, 1994; 2000; Reitan et al., 1999; Mills, 2000</td>
</tr>
<tr>
<td>Chlorophyll concentration</td>
<td>Cote et al., 1993; Lodeiros et al., 1995; Kleinman et al., 1996;</td>
</tr>
<tr>
<td></td>
<td>Rheault &amp; Rice, 1996; McLoughlin et al., 1998; Roman et al., 1999;</td>
</tr>
<tr>
<td></td>
<td>Lodeiros &amp; Himmelman, 2000; Shimada et al., 2000; Grecian et al., 2003</td>
</tr>
<tr>
<td>Seston</td>
<td>Wilson, 1987; Borrero &amp; Bricelj, 1993; Emerson et al., 1994</td>
</tr>
<tr>
<td>Flow rates</td>
<td>Wilson, 1987; Borrero &amp; Bricelj, 1993; Rheault &amp; Rice, 1996; Robert &amp;</td>
</tr>
<tr>
<td></td>
<td>Nicolas, 2000; Bacher et al., 2003</td>
</tr>
<tr>
<td>Stock density (cultured)</td>
<td>Duggan, 1973; Kingzett &amp; Bourne, 1991; Freites et al., 1995; Hernandez-</td>
</tr>
<tr>
<td></td>
<td>Llamas &amp; Gomez-Munoz, 1996; Acosta et al., 2000; Cano et al., 2000;</td>
</tr>
<tr>
<td></td>
<td>Grecian et al., 2000; Davidson, 2001; Frechette &amp; Daigle, 2002; Roman</td>
</tr>
<tr>
<td></td>
<td>et al., 2003; Louro et al., 2005</td>
</tr>
<tr>
<td>Stock density (wild)</td>
<td>Gwyther &amp; McShane, 1988; Kurata, 1999; Harris &amp; Stokesbury, 2006</td>
</tr>
<tr>
<td>Depth</td>
<td>Monical, 1979; Reinsnes, 1984; Wallace &amp; Reinsnes, 1984; Schick et al.,</td>
</tr>
<tr>
<td></td>
<td>1988; Garcia-Dominguez et al., 1992; Grecian et al., 2000</td>
</tr>
<tr>
<td>Culture method</td>
<td>Sun et al., 1996; Gonzalez et al., 1999; Grant et al., 2003</td>
</tr>
<tr>
<td>Fishing intensity</td>
<td>Beukers-Stewart et al., 2005; Harris &amp; Stokesbury, 2006</td>
</tr>
<tr>
<td>Genetics</td>
<td>Cruz et al., 1998</td>
</tr>
<tr>
<td>Salinity</td>
<td>Chauvaud et al.1998; Laing, 2002; Christophersen &amp; Strand, 2003</td>
</tr>
<tr>
<td>Wave action</td>
<td>Belogrudov, 1974; Kingzett &amp; Bourne, 1991; Freites et al., 1999</td>
</tr>
<tr>
<td>Latitude</td>
<td>Defeo &amp; Gutierrez, 2003; Lomovasky, 2006</td>
</tr>
<tr>
<td>Pollution</td>
<td>Silina, 2003</td>
</tr>
</tbody>
</table>

In this study we describe the growth of the great scallop (*Pecten maximus*) using data from recent surveys in the English Channel and explore the relationships between spatially structured differences in growth rates and a limited set of variables reflecting different long-term environmental conditions.

Methods
Scallop data

Scallops were sampled from 3 surveys (each of 11-14 days duration) in the western English Channel in June 2004 and October 2005 and 2006. In addition, a short survey (2 days) in the eastern English Channel that took place in November 2005, as part of a separate habitat mapping project. Scallops were aged for a subset of the stations of the 2004 survey, but for all scallops, where ageing was possible, in the 2005 and 2006 surveys.

The scallop survey stations were a grid design with stations approximately 13 km (7 nm) apart and typically around 2 km average length. Scallop survey station positions had been adjusted *a priori* to avoid known foul ground and static gear zones, as well as during the surveys to avoid *in situ* static gear, which can be widespread in the western English Channel.

Scallops were aged using optical microscopy to identify growth patterns from the structure of microstriae of the left (flat) shell valve. Comparison of ages derived from oxygen isotope analysis with age estimates from macroscopical examination of the shell has suggested that the use of macroscopically identified external growth checks was not reliable and was prone to subjective error and bias when applied to scallops in British waters (Dare & Deith, 1991). However microscopic analysis of the microstriae structure performed considerably better (Dare, 1995). Stable oxygen isotope analysis has been used to investigate external growth checks for *Pecten maximus* in the UK (Dare & Deith, 1991; Dare, 1995). The oxygen isotope (\(^{18}O\)) method itself was previously verified by the use of tagged scallops exposed in the sea for a known length of time. Stable oxygen isotope analyses have also been used to verify external shell annuli in a number of other species including *Placopecten magellanicus* (Cai et al., 1990; Krantz, et al., 1984a; b), *Adamussium colbecki* (Heilmayer et al., 2003) and *Aequipecten opercularis* (Heilmayer et al., 2004). Verification has also been carried out using marking for *Equichlamys bifrons* (Wolf & White, 1995) and magnesium concentration (or calcium/magnesium ratio) for *Chlamys albidus* (Silina & Pozdnyakova, 1986).

Environmental data

Environmental data for the English Channel were extracted from a number of datasets available as interpolated point estimates at around 3.7 km separation, i.e. finer resolution than the scallop survey. Values for environmental variables corresponding to each scallop survey station were obtained by searching for the point in the environmental dataset that was nearest to the station mid-point and accepting this value. It is acknowledged that micro-habitats and environmental signals may change at considerably smaller scales, below the resolution of both the dredge sample and the interpolated environmental data, but the generally similar growth characteristics of scallops from a particular location suggests this is not extreme.

Seabed stress

Raw seabed stress data were available at a scale of around 8km and subsequently interpolated.
Depth

Depth data were available from the survey data, but the hydrographic dataset was used as this was standardised for tidal variations. The hydrographic dataset was derived from point estimations and contours that were converted to points at 500m intervals.

Temperature

Temperature data were derived from bottom temperatures over the period 1997 to 2003. It was noted that off the south coast of the UK data were very detailed and reasonably varied.

Sediment type

A data set based on BGS sediment classification was similarly allocated to each station position. Sediment classification data were transformed into a continuous variable (BGS Phi) representative of approximate average particle size for each sediment type (Table 3). BGS Phi scores were obtained using the Folk (1954) classification chart to approximate the proportions of sand, mud and gravel in each sediment type, and calculating a weighted average particle size for the proportion of each of these sediment types using approximations taken from the BGS grain size scheme (McMillan & Powell, 1999). This was then transformed by taking the negative of base 2 logarithms. Information regarding dredge contents was in broad accord with the overall trends observed in the sediment dataset. Acoustic seabed discrimination data were collected during the surveys, but were not fully processed at the time of this analysis and were therefore not used.

Table 3. BGS sediment types and approximated BGS Phi used

<table>
<thead>
<tr>
<th>BGS sediment type</th>
<th>BGS Phi</th>
</tr>
</thead>
<tbody>
<tr>
<td>MUDDY SAND</td>
<td>1.8881</td>
</tr>
<tr>
<td>SAND</td>
<td>1.5000</td>
</tr>
<tr>
<td>SLIGHTLY GRAVELY MUDDY SAND</td>
<td>-1.7058</td>
</tr>
<tr>
<td>SLIGHTLY GRAVELY SAND</td>
<td>-1.7411</td>
</tr>
<tr>
<td>GRAVELLY MUDDY SAND</td>
<td>-4.1475</td>
</tr>
<tr>
<td>GRAVELLY SAND</td>
<td>-4.1531</td>
</tr>
<tr>
<td>MUDDY SANDY GRAVEL</td>
<td>-5.7845</td>
</tr>
<tr>
<td>SANDY GRAVEL</td>
<td>-5.7855</td>
</tr>
<tr>
<td>GRAVEL</td>
<td>-6.6439</td>
</tr>
<tr>
<td>UNDIFFERENTIATED BEDROCK LITHOLOGY</td>
<td>-13.0000</td>
</tr>
</tbody>
</table>

Chlorophyll a

Chlorophyll a generally correlates well with other measures of phytoplankton abundance such as cell counts, and can be measured in a number of ways, including by satellite remote sensing. Surface chlorophyll a concentrations for the years 2002-2006 were extracted from a database of remote sensing images in ArcGIS, using the latitudes and longitudes of scallop survey stations to identify the relevant pixels and averaged over the time series.

Scallop density
Survey catch rates of scallops were used as a proxy for scallop density. Catch rates are generally transformed for regression analyses and plots of variances and standard deviations on means indicated that the variance was not homoscedastic. Box Cox likelihood profiles (Box & Cox, 1964; Venables & Ripley, 2002) of survey catch rates indicated a log transformation with an offset of 4 was suitable for regression analyses of these data and this transformation was therefore used throughout this analysis.

Growth model

Scallop growth has been shown to vary seasonally (Allison, 1994), but seasonal data were not available from the annual series of surveys and because length at age was taken from shell microstructure the season of the length measurement was approximately equal for all shells. Therefore, the annual form of the von Bertalanffy growth function (Bertalanffy, 1934; 1957) was used to model growth with scallops measured in terms of dorso-ventral height ($H$) rather than length.

$$H_t = H_\infty (1 - e^{-k(t-t_0)})$$

Growth curves were estimated by non-linear least squares minimisation for reference stations where the number of length at age measurements was at least 12. Outputs included the parameters, variance estimates for each parameter, covariance estimates and confidence intervals obtained by likelihood profile. The parameter values and their variance estimates formed inputs to subsequent generalised linear modelling of the growth parameters and environmental data.

Growth performance indices

Growth performance was compared using the von Bertalanffy growth parameters ($k$ and $H_\infty$) and Munro’s phi prime ($\varphi'$) index derived from them. Phi prime was calculated using natural logarithms (Sparre et al., 1989) rather than base 10 logarithms as used by the original authors (Munro & Pauly, 1983; Pauly & Munro, 1984)

$$\varphi' = 2 \ln H_\infty + \ln k$$

Phi prime is generally considered preferable because it is more robust than the von Bertalanffy growth parameters, which are highly negatively correlated. A difference in $\varphi'$ is likely to represent a change in growth rate whereas an increase in $H_\infty$ may be offset by a lower $k$ and may not actually reflect a genuine change in growth performance. We did not use the $\omega$ index ($\omega = H_\infty k$), although it has previously been computed for scallops in the English Channel, because phi prime has been shown to perform better than four other alternative growth performance indices, including $\omega$ (Moreau et al., 1986).

To estimate the variance for phi prime we used the ‘deltamethod’ function in the R package ‘msm’. The delta method (Oehlert, 1992) can be used to approximate variances of functions of random variables using a first-order Taylor expansion. The variance of $f(X)$ is approximated by $\sigma^2(f'[\mu])^2$, where $\mu$ and $\sigma^2$ are the mean and variance of $X$ and $f'(x)$ is the derivative of $f(x)$ with respect to $x$. The ‘deltamethod’
function returns the approximate standard error of a function $g(X)$. Multiplying by the square root of the number of observations and then squaring, back-transformed this to the variance of phi prime.

Linear modelling

Growth parameters ($H_\infty$, $k$ and $\phi'$) were modelled as linear functions of the environmental variables for each reference station. Models were fitted to the growth parameters both without weighting and using an inverse variance weighting. The latter provides a means of weighting that takes account of the fit quality for each parameter estimate.

Initially each growth parameter was fitted against each environmental variable separately. Subsequently generalised linear models were used to explore the relationships between growth and the combined effects of the environmental factors. As with the single effect models both un-weighted and inverse variance weighted models were applied. Stepwise regression using the Akaike Information Criterion (AIC) to select the most parsimonious model was carried out using the MASS library (Venables & Ritchie, 2002) in the statistical modelling environment R (R Development Core Team, 2006). The basic model included terms for each environmental effect and an interaction term for log catch rate and sediment type as dredge efficiency and hence catch rate is known to vary with sediment type.

Results

Place names used in the text are shown in Figure 1.

Environmental data

The major features of highest catch rates on the inshore Cornish grounds and lower densities in Lyme Bay were relatively stable through the time series of scallop surveys (Figure 2). High catch rates were also achieved at some stations in the eastern English Channel and some of the offshore stations south of west Cornwall.

The spatial distribution of ground types indicated finer sediments inshore of south Devon and Cornwall and in the eastern part of the eastern English Channel survey coverage (Figure 3). Coarser sediments exist offshore in most areas and one or two areas of rock were suggested off south and west Cornwall and Devon, sometimes associated with major headlands (Lizard Point and Start Point). The sediment types are generally consistent with observations of dredge contents.

Near bottom temperature showed a general reduction from east to west and from inshore to offshore that might well be associated with increasing depth (Figure 4). Within this general pattern there were exceptions and in general the contrast in the dataset was quite low.

Seabed stress was very low in close inshore areas of Lyme Bay and inshore south of Cornwall (Figure 5). Moderate values were found to the south and west of the Lizard Point, offshore south of Cornwall and in the east of the eastern English Channel. High
values were present offshore from Lyme Bay and on the eastern English Channel grounds, where some very high values are also present.

The distribution of Chlorophyll a showed high values in inshore areas of Lyme Bay, south Cornwall and the eastern English Channel (Figure 6). These may reflect intense blooming due to higher nutrient availability, but could be artefacts if the satellite sensor was actually viewing the seabed. There was a general trend of increasing chlorophyll from west to east. Aside from the very high values to the south of Devon chlorophyll concentration increased from inshore to offshore, but further west declined from inshore to offshore.

Depth shows a general increase from east to west and from inshore to offshore (Figure 7). The eastern English Channel and inshore Lyme Bay are shallower than inshore areas further west.

Bivariate plots of the environmental datasets suggested a number of correlations between the environmental signals (Figure 8). Four were significant; bedstress with temperature, depth and sediment and temperature with depth. The latter three of these can be explained directly, but no obvious causal relationship exists between bedstress and temperature and it may be that this correlation reflects the relationship of each variable with depth. Substantial correlations between the environmental datasets that are considered as independent variables in subsequent analyses make interpretation more difficult.

Growth

Growth curves were fitted by reference station to maximise the available data and because the stable long-term environmental effects of environment on growth were being considered. One station (ECS22) in the eastern English Channel had implausible results and investigation revealed it consisted of 27 shells all of which were aged 1 or two with one exception aged 3. The single point representing height at age 3 had very high leverage due to its isolation and the truncated age distribution at this reference station. Removal of this point resulted in a growth curve with values inside the range of the remaining stations and this action was therefore taken.

Examination of the parameter $t_0$ revealed that for most stations this was estimated close to one, but for 6 stations it was nearer to zero. These stations were not particularly poorly sampled and were split evenly between minimum ages with a length check of 1 and 2, the latter being the minimum age with a length check for most stations. They also all had significant numbers of records for length at older ages and so were considered valid and retained in the analysis.

Graphical examination of the estimated parameters and their likelihood profiled 95% confidence intervals shows that for most stations the parameters were well estimated with relatively low variance (Figure 9). However, the likelihood profile failed for five stations with relatively low sample numbers, although it also worked satisfactorily for other stations with similar low sample numbers.

Growth curves were generally typical of those seen for *Pecten maximus* with relatively fast initial growth, which slows rapidly once the scallops begin spawning.
The recent surveys confirmed historic findings that growth is slow in the inshore Cornish grounds, where the scallops tend not to reach large size, and very fast in the eastern English Channel where they grow quickly and attain large maximum size. Growth in Lyme Bay tends to be fast and to a moderate maximum size as does that for some stations south east of Start Point and some intermediate grounds south of Cornwall. Scallop growth in the area offshore to the south of the Scilly Isles tended to be slow, but to a moderately high maximum size (Figure 10).

Plots of the growth parameters did not suggest any transformation was necessary for $H_\infty$, or $\phi'$, but that $k$ might be log normally distributed. A plot of variance against mean for parameter $k$ indicated two outlying points with mean and variance, but no strong relationship in the remaining data. It was therefore decided that a transformation for $k$ was not required.

Single effect linear regression of $H_\infty$, $k$ and $\phi'$ against the each of the environmental variables (Table 4; Figures 11 to 13) suggested that $H_\infty$ may be positively influenced by seabed stress and temperature and decreases with increasing depth and chlorophyll concentration (weighted fit only). However, the negative correlation of both temperature and seabed stress with depth should be borne in mind. Un-weighted fits for $k$ showed a significant and positive relationship only with chlorophyll concentration, but using an inverse variance weighting resulted in positive relationships with catch rate and depth as well as with chlorophyll concentration. $\phi'$ was positively related to seabed stress, temperature and chlorophyll concentration, with log catch rate also significant when using a weighted fit.

Table 4. Significance and direction of single effect linear regression models

<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>Weighted Log Catch rate</th>
<th>Seabed stress</th>
<th>Temperature</th>
<th>Depth</th>
<th>Sediment size Phi</th>
<th>Chlorophyll Chlorophyll exc. high</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H_\infty$</td>
<td>No</td>
<td>n/s</td>
<td>+</td>
<td>++</td>
<td>---</td>
<td>n/s n/s n/s</td>
</tr>
<tr>
<td>$H_\infty$</td>
<td>Yes</td>
<td>- n/s (p=0.0535)</td>
<td>++</td>
<td>+</td>
<td>n/s</td>
<td>--- -</td>
</tr>
<tr>
<td>$k$</td>
<td>No</td>
<td>n/s</td>
<td>n/s</td>
<td>n/s</td>
<td>n/s</td>
<td>++ +++</td>
</tr>
<tr>
<td>$k$</td>
<td>Yes</td>
<td>+++</td>
<td>n/s</td>
<td>+</td>
<td>- n/s (p=0.0511)</td>
<td>+++ +++</td>
</tr>
<tr>
<td>$\phi'$</td>
<td>No</td>
<td>n/s</td>
<td>+</td>
<td>+</td>
<td>n/s</td>
<td>++ +++</td>
</tr>
<tr>
<td>$\phi'$</td>
<td>Yes</td>
<td>++</td>
<td>+++</td>
<td>++</td>
<td>n/s</td>
<td>+++ +++</td>
</tr>
</tbody>
</table>

Positive relationships: +: p<0.05 ++: p<0.01 +++: p<0.001
Negative relationships: -: p<0.05 --: p<0.01 ---: p<0.001
n/s: not significant

Results of GLMs selected by stepwise AIC (Table 5) indicate that the best un-weighted generalised linear model for $H_\infty$ included seabed stress and depth, with additional non-significant terms for sediment size and chlorophyll. However, depth may be considered as more representative of location rather than as a causative environmental factor so a stepwise AIC was run with all the variables except depth included in the model. This resulted in a model including seabed stress, temperature, sediment size and chlorophyll, but with all terms being non-significant.
Using an inverse variance weighting, the best fitting GLM for $H_\infty$ was a model including seabed stress, temperature, sediment size and chlorophyll concentration, all of which were significant.

Table 5. Summary of best fitting GLMs

<table>
<thead>
<tr>
<th>Model</th>
<th>Significance</th>
<th>Weighted AIC</th>
<th>Catch rate</th>
<th>Seabed stress</th>
<th>Temperature</th>
<th>Depth</th>
<th>Sediment size</th>
<th>Chlorophyll</th>
<th>Sediment code*Catch rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H_\infty$ ~ Seabed stress + Depth + Sediment size + Chlorophyll</td>
<td>No</td>
<td>400.8</td>
<td>0.025</td>
<td>0.018</td>
<td>0.082</td>
<td>0.150</td>
<td>(1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$H_\infty$ ~ Seabed stress + Temperature + Sediment size + Chlorophyll</td>
<td>No</td>
<td>403.5</td>
<td>0.103</td>
<td>0.080</td>
<td>EXC</td>
<td>0.077</td>
<td>0.153</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>$H_\infty$ ~ Seabed stress + Temperature + Sediment size + Chlorophyll</td>
<td>Yes</td>
<td>293.7</td>
<td>0.007</td>
<td>0.011</td>
<td>0.063</td>
<td>6.8e-7</td>
<td>(3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k$ ~ Chlorophyll</td>
<td>No</td>
<td>327.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.001</td>
<td>(4)</td>
<td></td>
</tr>
<tr>
<td>$k$ ~ Temperature + Depth + Catch rate + Chlorophyll</td>
<td>Yes</td>
<td>188.8</td>
<td>0.067</td>
<td>0.074</td>
<td>0.013</td>
<td>6.9e-5</td>
<td>(5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k$ ~ Catch rate + Chlorophyll</td>
<td>Yes</td>
<td>191.3</td>
<td>0.036</td>
<td>EXC</td>
<td></td>
<td></td>
<td>1.1e-5</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>$\phi'$ ~ Seabed stress + Chlorophyll</td>
<td>No</td>
<td>-283.9</td>
<td>0.013</td>
<td></td>
<td></td>
<td></td>
<td>0.002</td>
<td>(6)</td>
<td></td>
</tr>
<tr>
<td>$\phi'$ ~ Seabed stress + Temperature + Catch rate + Chlorophyll</td>
<td>Yes</td>
<td>-226.0</td>
<td>0.016</td>
<td>0.033</td>
<td>0.119</td>
<td></td>
<td>0.002</td>
<td>(3)</td>
<td></td>
</tr>
</tbody>
</table>

(1) Unsuccessful  
(2) Not run  
(3) Same parameters  
(4) Chlorophyll and sediment size  
(5) Chlorophyll (significant) and sediment size * log catch rate interaction (non-significant)  
(6) Seabed stress and chlorophyll (significant) but also depth and sediment size * log catch rate interaction (non-significant).

The un-weighted GLM with the lowest AIC score for $k$ included chlorophyll concentration only and this was highly significant. When fitted using an inverse variance weighting the lowest AIC score was for a model including temperature, depth and log catch rate as well as chlorophyll. In this model temperature and log catch rate terms were marginally non-significant. Removing depth on the rationale that it is a descriptor rather than causative lead to the same model for the un-weighted fit and a model including significant catch rate and chlorophyll concentration terms when using an inverse variance weighting.

For $\phi'$ the best fitting un-weighted GLM model included chlorophyll concentration and seabed stress and both terms were significant, while using an inverse variance weighting resulted in a model including chlorophyll concentration, seabed stress and catch rate as significant terms as well as temperature which was insignificant.

Models fitted using the chlorophyll series with the 5 highest values removed were also investigated. An un-weighted fit to $H_\infty$ encountered problems with the stepwise
regression due to changes in the number of data points available when the removal of the chlorophyll concentration series was evaluated. However, the chlorophyll series was significant in all other fits and in most cases the stepwise regression procedure resulted in very similar fits to those when the complete chlorophyll series was used (Table 5 superscripts and footnotes).

Discussion

This analysis utilised a substantial dataset of scallop age and length information, obtained from recent surveys in the English Channel, in conjunction with historic datasets for environmental variables from the area. The rationale behind the analysis was that within patches of scallops variation in growth characteristics is low, implying that all scallops in a patch are exposed to similar environmental conditions. However, between patches variation in growth characteristics can be high, suggesting that environmental conditions may vary significantly at the scale of some tens of kilometres. The growth characteristics of scallops from different areas in the English Channel appear consistent over long time periods, which suggests that environmental conditions and their spatial variations have also been relatively stable through time.

However, for the context of the analysis, it is important to consider the uncertainties associated with the datasets used in the analysis. Microscopic interpretation of striae was found to be considerably more accurate than macroscopic determination of growth checks and particularly so in the western English Channel, because true winter zones could be distinguished from spurious disturbance marks (Dare, 1995). However, there are problems with scallop ageing using this method including; the inability to reliably locate the first winter ring and sometimes other early rings and the tendency for observers to overestimate size at age in the first 1-2 winters and underestimate size at age after the fifth winter for some stocks (Dare & Deith, 1991). The south Cornwall population (one of the areas in our surveys) was noted as particularly difficult to age. Poor definition of the first ring continues to present a fundamental problem for ageing scallops and we therefore acknowledge that there may be errors in the exact ages. This is also true for very old scallops where growth is minimal and many checks may be present near the shell edge. In both these cases the specification of exact age and therefore the cohort may include error. Nonetheless, even if a systematic bias (resulting from not identifying the first ring) is present significant trends in growth rates between areas can be identified and plausibly related to environmental conditions in these areas.

A second problem with analysis of growth is the negative correlation between the von Bertalanffy parameters. This may be influential where the results of the regression analysis give opposing relationships for a variable, for example in the case of chlorophyll concentration which was positively related with \( k \) and negatively with \( H_\infty \). The use of phi prime as a ‘general’ growth parameter may to some extent overcome this problem and in this case chlorophyll concentration was found to be positively correlated with phi prime. The use of an inverse variance weighting should also help to reduce the influence of growth parameters that were less well estimated.

Environmental data used in the analysis were based on interpolated datasets and assumed to be representative of long-term environmental conditions. Although the basic data were at a higher resolution than our survey data, there may be variations
and anomalies in these datasets that render them not fully representative. For example, the very high chlorophyll concentrations in some inshore stations were a cause for concern. Unfortunately, these also coincided with some of the more influential survey stations, for example the inshore Cornwall stations which had a small $H_\infty$ that also tended to be very well estimated because these stations had high catch rates. A further complication relates to the correlation between environmental variables. We have commented that depth is really a location descriptor rather than a feature of environment, but many of the environmental variables are strongly related to depth and also amongst themselves. Our preliminary analyses highlighted positive correlations for seabed stress with temperature and sediment size and negative correlations for both seabed stress and temperature with depth.

Taking account of the frailties in both growth rate and environmental data it is clear that results from this analysis should only be used in a broad way to highlight environmental variables that may be influential to scallop growth and to possibly indicate the likely direction of the effect within the range of current values.

Our single effect analysis for phi prime suggested that seabed stress, temperature and chlorophyll concentration were important and that catch rate (a proxy for abundance) might also have an influence. Plausible mechanisms explaining how these environmental conditions might influence growth are available for these variables, but the positive relationship with catch rate is counter-intuitive, as we would generally expect lower growth rates at higher densities. It was driven largely by a strong positive relationship between $k$ and catch rate, which may reflect negative correlation between von Bertalanffy parameters and the influence of the heavily sampled inshore Cornwall stations where small old scallops are prevalent.

Our multiple regression results tended to be dominated by chlorophyll concentration, which was highly significant, but they also included seabed stress as a significant variable. Temperature and catch rate only featured in the weighted model and even then temperature was non-significant. In previous analyses that we carried out before the chlorophyll data were available, temperature had a very significant influence on phi prime.

Previous work in the UK noted that through the English Channel there was strong evidence for an east to west gradient of declining growth performance as shown by $\omega$ and $\phi'$ growth indices. Best growth performance is that of Sussex populations, the poorest occurs near the Shelf Edge. This trend probably not only reflects the effect of decreasing summer temperatures with increasing water depth, but also lower food (detritus) resources for scallops in the western English Channel and especially shelf waters (Dare & Palmer, unpublished). Estimates of $H_\infty$ for French scallop stocks increased from low values in the west (north Brittany) to higher in the east (Dieppe-Boulogne) and notable high values in the shallow Baie de Seine (Antoine, 1978; Antoine et al., 1979; Lubet, 1992). Estimates of the growth performance index $\omega$ were high throughout.

Although our work has been conducted over a smaller spatial scale than these previous studies it confirms a general trend of reducing growth performance from east to west, but identifies local variations that do not follow the general trend. Even with the reduced spatial coverage of our surveys indicated that growth rates as represented
by the phi prime parameter tended to be lower on the grounds close inshore to the
south of Cornwall and offshore south of Cornwall and the Scilly Isles and higher in
the eastern English Channel, Lyme Bay and offshore south east of Start Point (Figure
14). However, this work goes further in highlighting chlorophyll concentration and
seabed stress, in addition to temperature, as environmental variables that appear to
influence scallop growth in this area.

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References

juveniles of Lyropecten (Nodipecten) nodosus (Pteroida: Pectinidae) at off-bottom

Allison, E.H., 1994. Seasonal growth models for great scallops (Pecten maximus (L.)
and queen scallops (Aequipecten opercularis (L.)). J. Shellfish Res. 13:555-564.

Andersen, S. & Emil Naas, K., 1993. Shell growth and survival of scallop (Pecten
maximus L.) in a fertilized, shallow seawater pond. Aquaculture. 110:71-86.

Antoine, L., 1978. La croissance journaliere chez Pecten maximus (L.), (Pectinidae,

175.

Bacher, C., Grant, J., Hawkins, A.J.S., Jianguang, Fang & Mingyuan, Zhu, &

Barber, B.J. & Davis, C.V., 1997. Growth and mortality of cultured bay scallops in
the Damariscotta River, Maine (USA). Aquacult. Int. 5:451-460.

Nodipecten subnodosus (Bivalvia: Pectinidae) in La Paz Bay, Mexico. Aquacult.
Res. 34:633-639.

Belogrudov, E.A., 1974. Growth of the sea scallop Mizuhopecten yessoensis in


Figure 1. Map of the study area indicating place names used
Figure 2. Spatial distribution of scallop catch rates from all four surveys

Figure 3. Spatial distribution of sediment type
Figure 4. Spatial distribution of near seabed temperature

Figure 5. Spatial distribution of bedstress
Figure 6. Spatial distribution of chlorophyll a concentration

Figure 7. Spatial distribution of depth
Figure 8. Correlations between environmental data

Significant relationships:
Seabed stress with temperature (positive)
Seabed stress with depth (negative)
Seabed stress with sediment size index (negative, implies sediment particle size increases with seabed stress)
Temperature with depth (negative)
Figure 9. Von Bertalanffy growth parameter estimates and 95% confidence intervals

Figure 10. A selection of von Bertalanffy growth curves from clusters of stations in the English Channel
Figure 11. Relationships between $H_\infty$ and environmental variables
Point size represents the inverse variance weighting
Dashed line inverse variance weighted fit
Figure 12. Relationships between $k$ and environmental variables
Point size represents the inverse variance weighting
Dashed line inverse variance weighted fit
Figure 13. Relationships between $\phi'$ and environmental variables
Point size represents the inverse variance weighting
Dashed line inverse variance weighted fit
Figure 14. Spatial distribution of deviations from the mean of phi prime estimates