A re-examination of the relationship between cod recruitment and *Calanus finmarchicus* in the North Sea

K. Brander

Introduction

The total catch of four large gadoid species (cod, haddock, saithe, and whiting) in the North Sea increased from 200–300 Ktonnes during the period 1948–1963 to 1500 Ktonnes in 1969 and has since declined fairly steadily to about 400 Ktonnes in 1990 (Fig. 1). The increase in catch was due to increased biomass, in particular the outstanding 1967 haddock year class and also higher levels of cod recruitment than in previous decades. The subsequent slow decline (although catches...
remain higher than during the earlier period) is due to reduced biomass and increased fishing mortality (Daan et al., 1990). Attempts have been made to look for general explanations for the so-called "gadoid outburst" and to associate it with long-term changes in the physical and biological environment. Cushing (1984) suggested that: "The upsurge of cod-like fishes from 1962 onwards is then attributed to the delay in Calanus production in the northeastern North Sea by about a month." He reported a correlation between the spring timing and abundance of the copepod Calanus finmarchicus in the NE North Sea over the period 1954–1977 and the subsequent recruitment of cod.

The annual catch of cod in the North Sea rose from around 100 Ktonnes during the period 1948–1962 to over 300 Ktonnes in 1971 and 1972 due to the large 1969 and 1970 year classes and declined throughout the 1980s to just over 100 Ktonnes in 1989 (Fig. 2). The average recruitment (number of one-year-old fish estimated by VPA; Anon., 1991) was 20–30% higher during the 1970s than during the 1960s or 1980s, but the interdecadal differences are not significant because of the annual variability (Fig. 3). Trends in the catch of cod depend largely on the level of recruitment (Fig. 4), so we need to understand the causes of variability in early life, probably during the pelagic phase, in order to account for the observed changes in catch. Surveys of juvenile cod shortly after they settle from the plankton to the seabed give an indication of recruitment, but the degree to which year-class strength is determined by feeding and survival during the first four months is not known.

Recent studies (Ellertsen et al., 1989) support Cushing’s hypothesis that the growth and survival of cod larvae depend on both the timing and abundance of Calanus finmarchicus. The correlation which Cushing reported can be investigated in terms of component processes rather than being purely phenomenological.

The aim of this paper is to review the evidence relating cod recruitment to Calanus abundance in the North Sea over the period 1960–1989 and to discuss the component processes. This leads inevitably to spatial and temporal disaggregation, because the distribution of cod larvae and their prey in space and time varies from year to year. The information from the CPR surveys is evaluated to see whether it may provide the spatial and temporal coverage and resolution of copepod populations required to model their dynamics.

Materials, methods and results

The CPR data used by Cushing (1984) were the numerical abundance of Calanus finmarchicus plus helgolandicus for the northeastern North Sea (area B1, 58–63°N and east of 3°E) for the months April–June for the period up to 1978. The original counts were transformed (log(1 + x)) and backtransformed using an empirical relationship described by Colebrook (1975). The time series has been updated (Table 1), but years with missing data (i.e. not all months sampled) have been excluded. The average abundance of Calanus helgolandicus is less than 5% of Calanus finmarchicus in the northeastern North Sea area at this time of year.
In order to provide a more complete picture of distribu­tional and secular changes in *Calanus* spp. over the whole of the North Sea, CPR data for each ICES rectangle (1° longitude × 1/2° latitude) for every month between 1958 and 1990 were included in the analysis. Details of the CPR sampling are given by the Oceanographic Laboratory, Edinburgh (1973). The number of monthly samples in each rectangle over the 30-year period (1960–1989) is given in Figure 5 and the annual mean number of *Calanus* (copepodite stages V + VI m⁻³) in Figure 6. Sampling was most frequent along the regular routes, but some of these have changed over time. In order to simplify analysis and interpretation and to ensure adequate numbers of samples in each area and time period, the North Sea was divided into four quadrants (see Fig. 5). The mean number of *Calanus* in each
of these four areas in each month (Fig. 7) gives an indication of the variability between years, between areas, and seasonally. The monthly abundances for the four areas are all significantly positively correlated, but the closeness of the relationship varies considerably and it must be noted that the seasonal signal is included in the analysis.

Coefficient of determination ($r^2 > 358$ deg. of freedom) of monthly rectangle values for four quadrants in the North Sea.

<table>
<thead>
<tr>
<th></th>
<th>NE</th>
<th>NW</th>
<th>SW</th>
<th>SE</th>
</tr>
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<tbody>
<tr>
<td>NE AREA</td>
<td>0.22</td>
<td>0.07</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>NW AREA</td>
<td>0.23</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SW AREA</td>
<td></td>
<td></td>
<td>0.31</td>
<td></td>
</tr>
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</table>

The mean annual abundance of *Calanus* fluctuated without evident trend over the 30-year period (Fig. 8). The mean abundance during spring (February to May) may have declined slightly until the end of the 1970s and then increased again (Fig. 9). The timing of *Calanus* abundance during the first six months of the year was calculated by weighting the date (in months) by the abundance in each month and dividing by the total abundance. There was no evident trend in timing in the two northern areas, but in the southern area the timing advanced by about two weeks over the 30-year period (Fig. 10).

Cushing (1984) applied his multiple regression model to data for the years 1954 to 1977 and found a correlation coefficient of 0.559 for 21 d.f. ($p < 0.05$). The same model was applied to the *Calanus* data for area B1 and

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**Figure 5.** Number of months in which each rectangle was sampled during the period 1960–1989. The four quadrants into which the whole area has been divided for analysis are marked.
the most recent estimates of cod recruitment (Anon., 1991) for the year classes 1962–1986. The year classes from 1954 to 1961 were not included because they are not part of the VPA time series.

Cod recruitment

\[ \text{Cod recruitment} = F_n \text{(Delay in } \text{Calanus} \text{ timing, } \text{Calanus} \text{ abundance)} \]

Analysis of variance for the multiple regression of cod recruitment on Calanus timing and abundance. Data used are given in Table 1.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delay</td>
<td>99 366</td>
<td>1</td>
<td>113</td>
<td>0.0</td>
</tr>
<tr>
<td>Calanus</td>
<td>11 369</td>
<td>1</td>
<td>83 180</td>
<td>1</td>
</tr>
<tr>
<td>Del*Cal</td>
<td>118 761</td>
<td>1</td>
<td>126 901</td>
<td>2.7</td>
</tr>
<tr>
<td>Residual</td>
<td>849 742</td>
<td>17</td>
<td>47 511</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1 079 237</td>
<td>20</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Neither of the main covariates (abundance and timing of Calanus) nor their interaction accounted for a significant part of the variance in recruitment. This is also the case if the tests are carried out stepwise. In spite of the failure of this simple model, it is probably premature to abandon investigation of the relationship between cod recruitment and copepod abundance. The model is incomplete in several respects, since it treats the whole North Sea stock as one unit which is dependent on the abundance of one species of copepod in one area. The relationship between cod recruitment and Calanus abundance, if it exists, is not strong enough to emerge from this simple analysis.

Cushing (1984) also suggested that variability in Atlantic inflow into the North Sea might be responsible for observed fluctuations in Calanus finmarchicus, since the distribution of this species is principally oceanic. Svendsen and Magnusson (this symposium) provide an index of the influx of Atlantic water into the northern North Sea for the period 1968–1990. This is the percentge of the North Sea north of 57°N over which the salinity at a depth of 50–200 m is greater than 35.1 psu (see Table 1). The measurement is made in June/July, but they regard it as a good index of the integrated flux during the previous months. The correlation between this index and the abundance of Calanus in area B1 in April–June is not significant.

A more complete model of larval population processes should include more detail of the distribution of spawning and consequent larval distribution of cod. This distribution has been well described for the southern North Sea (Daan, 1978), but information for the rest of the North Sea is scant. From the ICES pelagic 0 group
Figure 7. Mean number m$^{-3}$ of *Calanus* in each quadrant (a) NW, (b) NE, (c) SW, (d) SE of the North Sea in each month for the period 1960-1989.

surveys over the period 1974–1983 it appears that the main area of occurrence of cod larvae is in a wide arc, west and south of the Norwegian Trench, extending north of 61°N (Fig. 11). This differs considerably from the distribution of cod larvae given by the CPR for 1948–1956 (Fig. 12), when the largest numbers occurred in the German Bight and NW area of the North Sea, but not north of 59°N. Coombs (1980) noted that cod larvae were absent from CPR samples in the German Bight between 1958 and 1972 and there may have been a northerly shift in the distribution of spawning since 1950.

Discussion

The rationale behind the multiple regression model relating cod recruitment to *Calanus* abundance and timing is the match-mismatch hypothesis (Cushing, 1990). There are a number of difficulties in applying it to a stock such as North Sea cod, in which spawning occurs over a wide area and over several months. The hypothesis postulates a relationship between production of suitable food and survival of larvae. Although cod feed principally on copepods throughout the larval stage...
(Ellertsen et al., 1989), the size composition of their prey increases and they feed on different species in different areas.

For most of their larval life cod feed on stages of *Calanus* which are smaller than those whose distribution is described here (the adult stages V + VI). The CPR, with mesh size of $285 \times 315$ microns, does not sample small stages of *Calanus* adequately (Nichols and Thompson, 1991). However, the production of eggs and nauplii of *Calanus* in spring is a function of the number of adult copepods, as well as of temperature and primary production; therefore adult abundance may be used to estimate food available for fish larvae.

A more detailed model relating cod recruitment to copepod dynamics for the North Sea should include four main components:

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**Figure 8.** Mean annual abundance of *Calanus* stages V + VI.

**Figure 9.** Mean spring (Feb-May) abundance of *Calanus* stages V + VI.
1. Distribution of larvae in space and time.
2. Distribution of major copepod food species.
3. A model of copepod egg and nauplius production as a function of temperature, advection, adult copepod abundance, and phytoplankton production.
4. A model of the relationship between copepod abundance and larval survival.

The first of these would be extremely costly in survey time for an area as large as the North Sea. Dispersion and advection of larvae could be modelled after the initial distribution had been determined by survey, but resulting population distributions also require assump-

Figure 10. Mean timing of Calanus occurrence during the first six months of the year.

Figure 11. Mean distribution of pelagic zero-group cod in June/July for the period 1974-1983.

Figure 12. Mean distribution of cod larvae from the CPR for the period 1948-1956 (from Henderson, 1961). Cod larvae occur in all months from February to August, with greatest numbers in April.
tions about mortality rates. Modelled distributions may be validated using CPR data, although the volumes sampled by the CPR are small in relation to concentrations of fish larvae.

For copepods the CPR sampling is clearly of great value in showing distribution patterns. Its usefulness for cohort-based population analysis is more limited, because it does not sample all sizes of copepods.

A geographic array of one-dimensional models of copepod production as a function of temperature, primary production, and adult population could be constructed for the North Sea in order to resolve time and space scales which affect the overall population dynamics of fish larvae. If transport of overwintering adult populations is a major cause of year-to-year variability then it may be necessary to include horizontal processes. The CPR provides geographic coverage of adult population levels; however, it is not obvious that the data allow rates of horizontal transport to be estimated. Indicator species provide qualitative information on major circulation changes. Cushing’s multiple regression model resolves the time scale by including the timing of peak abundance of *Calanus*, but it ignores spatial heterogeneity.

References


