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Match/mismatch predictions of spawning duration versus recruitment variability

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ABSTRACT

According to the match/mismatch hypothesis, larval fish survival and eventual recruitment is dependent on the offset time between the peaks of abundance of larvae and their planktonic prey. A rudimentary larval food supply model is developed to determine the dependence of food availability on the mismatch between peaks. The model predicts that recruitment variability should increase as spawning duration decreases, a result which is moderately supported by an analysis of Atlantic cod (*Gadus morhua*) data.

Key words: Atlantic cod, larvae, recruitment, match/mismatch hypothesis

INTRODUCTION

The match/mismatch hypothesis of Cushing (1969, 1982, 1990) has proved to be an influential guide to thinking about year class success and its variability in marine fish populations. Cushing posits that the closeness of the temporal match between the abundance peaks of larvae and their planktonic prey controls larval mortality, either because of the vulnerability of first-feeding larvae to starvation or due to the fact that poorly fed larvae grow slowly and are more susceptible to predation. Since larval mortality is thought to be very high, the larval stage may be the principal determinant of year class strength. This picture seems very plausible, and it enjoys some empirical support (review: Cushing, 1990).

Cushing (1990) has noted that the effect of variable and unpredictable timing of the plankton peak will be mitigated if a fish stock spreads its spawning effort over a broad temporal window. In order to evaluate how effective this measure might be in reducing the variability of plankton available to the larval fish, we will develop a rudimentary food supply model. This corollary of the match/mismatch hypothesis also suggests that there might exist a relationship between the width of the spawning window (the standard deviation of the estimated egg production versus time curve), for a given stock, and its recruitment variability.

Following a discussion of the data required for our study, the food supply model will be developed. Next we will apply the model to assessing the likely significance of stock-to-stock variations in the width of the spawning window. We will also empirically test for a relationship between recruitment variability and the width of the spawning window. Crude model-based estimates of the variability of larval stage cumulative mortality will be compared with corresponding estimates derived from research surveys. In the final section the results will be summarized.

DATA AND ANALYSIS

For the applications of the model which follow in a later section, we will require information on the temporal widths of the curves of plankton abundance and spawning intensity and estimates of the interannual variability in the timing of the peaks of these curves. We will limit our study to fish stocks and plankton species of the North Atlantic and environs. Many of the standard fishing zones referred to below are shown in Fig. 1; these are NAFO (Northwest Atlantic Fisheries Organization) zones. (The region shown has been selected to identify the less familiar fishing zones.) The methods for extracting the required quantities are described in this section.

Spawning data

Here, we will assume that the temporal width of the larval production curve can be represented by the width of the egg production curve. (The dates of the egg and larval peaks may jointly vary from year to year, perhaps under the influence of temperature, an effect which will inflate the width estimate; this factor is discussed at the end of this subsection.) Proxy egg production as a function of time will be estimated from maturity data or from planktonic egg surveys. We will exclusively exam-

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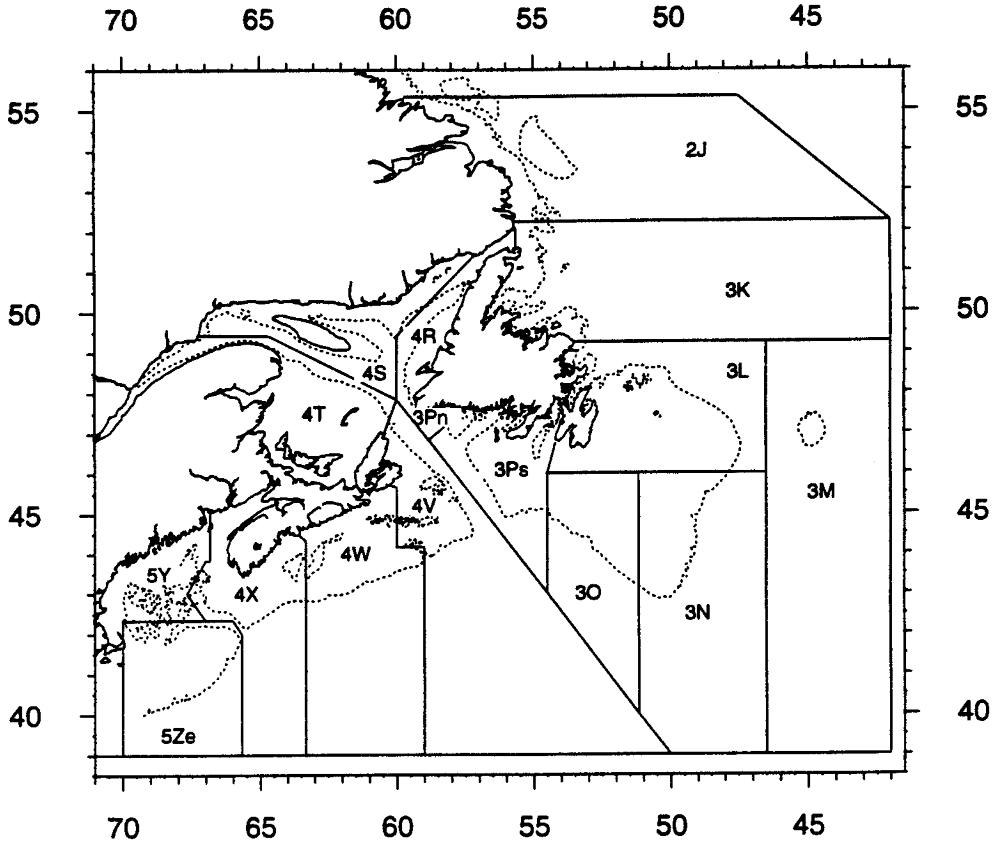
Figure 1. Map of selected NAFO zones. The 200 m depth contour (– – –) as shown.



ine data from Atlantic cod (*Gadus morhua*) stocks, since there is a wealth of reliable data available for this species and since cod is a spring spawner and is thus an appropriate subject for study of the match/mismatch hypothesis.

The maturity curves were calculated from the assessed spawning condition of samples of fish taken in trawl surveys. These surveys are designed to take close to a random sample of the population, and thus should be more representative of the population than estimates taken from present commercial samples. Only data for female fish were examined. The fish were divided into two categories: (1) those that were in prespawning or spawning condition and (2) those that were spent or in postspawning condition. (The maturity stages are described in Table 1 of Templeman *et al.*, 1978.) We then used a maximum likelihood probit analysis to estimate the mean and standard deviation of the normal distribution that best described the distribution of spawning (McCullagh and Nelder, 1989; Hutchings and Myers, 1993; Myers *et al.*, 1993). The logistic and Gompertz distributions were also fitted to the maturity data. We found that the Gaussian cumulative distribution provided an adequate model of the data; no other distribution consistently provided a superior fit to the data. These model fits can also provide some information on the year-to-year variability of peak spawning times (Hutchings and Myers, 1994).

Department of Fisheries (Canada) trawl survey data were utilized for the following NAFO regions: 2J3KL, 3M, 3NO, 3Ps, 3Pn4RS, 4TVn, 4X. For Iceland, research trawl survey data were available from Jonsson (1982) for the years 1953–1974.

We used planktonic egg and larval surveys for the other regions. The mean and standard deviation of the stage 1 egg abundance versus time curve for Browns Bank (NAFO region 4X) were calculated for years 1983–1985 from data presented in Campana *et al* (1989). Similar, unpublished data from the MARMAP (Sherman *et al.*, 1984) surveys of Georges Bank (region 5Z) were kindly provided by P. Perrien and M. Forgarty of the National Marine Fisheries Service for 1978 to 1987, a total of 66 cruises. For the NE Arctic cod populations, planktonic egg surveys were carried out from 1976 to 1982 in the Lofoten fiord (Pedersen, 1984). Data from nine cruises, in the Southern Bight of the North Sea, in the winter and spring of 1971, were used to calculate the spawning distribution for the North Sea (Harding *et al.*, 1978).

The timing of spawning of cod varies among subpopulations (Myers *et al.*, 1993; Brander, 1994) and among years (Hutchings and Myers, 1994). The timing and duration of spawning also increases with age (Hutchings and Myers, 1993). Each of these factors will increase the estimated spawning duration from that one would observe for an individual fish. The factor most likely to bias our results is the inflation caused by averaging over many years in some stocks, e.g. 3Ps, while using only one year's data in others, e.g. the North Sea. To address this factor we estimated a separate mean date of spawning for each year and a common variation within a year for 3Ps, 3NO, and 3L using the methods described by Hutchings and Myers (1994). This will overestimate the proportion of the variance attributable to the among-years variation because some of the sampling variability among years will be included in the year effects. We found that the duration of spawning was reduced by an average of 22% if we eliminated all the year effects. This is not enough to greatly affect our results in Figs. 4 and 5, and we conclude that our results are robust to this source of bias.

Recruitment variability index

Recruitment variability can be estimated from analyses of commercial catch-at-age data, e.g. virtual population analysis (VPA) (Gulland, 1965). We will use the coefficient of variation (CV) of recruitment as an index of its variability. The sources for the recruitment estimates obtained from virtual population analysis are described in Myers *et al.* (1990).

Variability of larval mortality

We are chiefly interested in the variability of mortality during the larval stage. Recruitment estimates provide an imperfect index for the variability of larval mortality because density-dependent juvenile mortality may strongly attenuate the variability of survival in the larval stage (Myers and Cadigan, 1993a,b), so that the CV for recruitment is smaller than the CV for the abundance of age 0 fish. This deficiency can be ameliorated through utilization of the Myers and Cadigan (1993a,b) methodology which, in effect, corrects the abundance of age 0 fish for estimation error, allowing reliable assessment of the true year-to-year variability in the numbers of age 0 fish. This permits the calculation of a CV representing variability before density-dependent juvenile mortality; this CV is an estimate of the CV for larval mortality.

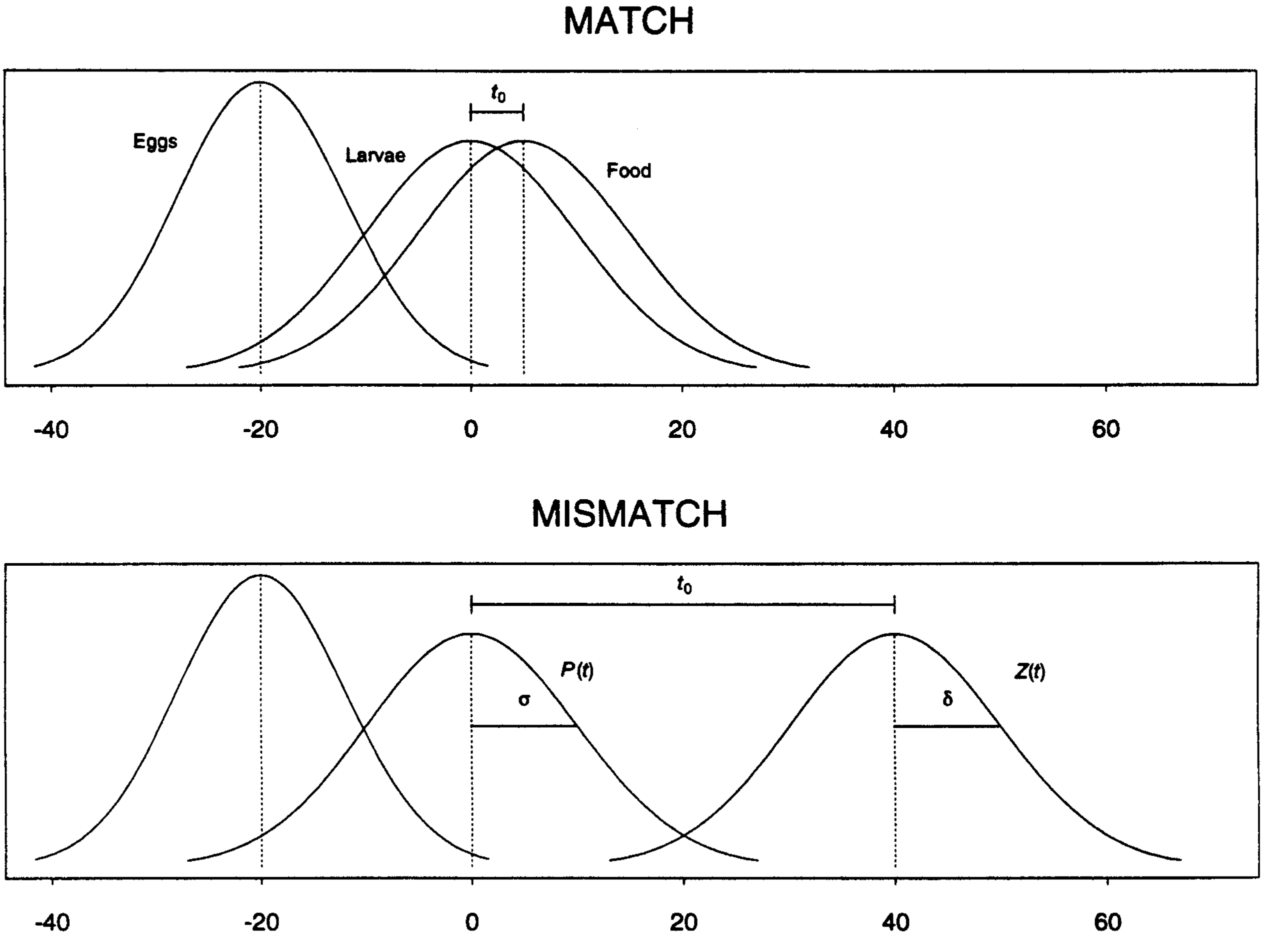
The estimation of population abundance during the larval or juvenile stages requires research surveys and entails considerable estimation error. It is difficult to separate true variation from estimation error. However, multiple surveys of juvenile fish permit separation of the true variation of juvenile abundance from estimation error, and this separation in turn enables one to calculate larval mortality and its variability. Myers and Cadigan (1993a) were able to perform this separation by examining stocks for which there are time series of tandem survey estimates of abundance (as may occur when two nations have joint jurisdiction over a stock). The procedure may be understood from the following example: consider a population in which there are two simultaneous surveys to estimate the abundance at age 0 and two more a year later for the age 1 fish. Assume, in this idealization only, that the variance of estimated abundance is the same for all surveys. If there is no interannual variability in survival between ages 0 and 1, then the correlations between the survey estimates should be the same at the same age as between ages. However, if there is large interannual variability in survival from 0 to 1, then there should be higher correlations in the surveys at the same age than between ages. The Myers and Cadigan model formalizes these ideas.

The CVs for variability before density-dependent mortality from the Myers and Cadigan analysis are available for a sufficient number of stocks to warrant comparison with the spawning window widths, and this will be presented in Fig. 5. These CVs, for the North Sea, 3NO and 5Z stocks, were calculated in Myers and Cadigan (1993a), while the 3Ps estimate is from Myers and Cadigan (1993b). For 3M cod we applied the same method to estimate the variability before density-dependent mortality using data for the 1961 to 1983 cohorts from Russian surveys (Konstaninov, 1981) for ages 1 to 3. Similarly, we used data from the Canadian fall surveys for ages 0 to 3 for cohorts from 1967 to 1990 for 4X (Campana and Hamel, 1991). There were no other regions for which we could obtain research surveys that caught juvenile fish sufficiently well over a long time period (at least 12 years) for us to obtain reliable estimates.

A LARVAL FOOD SUPPLY MODEL

Figure 2, adapted from Cushing (1982), illustrates the match/mismatch hypothesis. It is clear that larval food supply must depend on the synchrony of the abundance peaks for larvae and zooplankton. It is equally clear that

Figure 2. Illustration of a match and a mismatch of larval fish to their planktonic prey. (The time units (horizontal axis) are arbitrary.) Production of larvae $P(t)$ follows egg release and in a match situation (top panel) the larval production peak closely coincides with the peak of palatable zooplankton (the curve designated $Z(t)$). The match condition is characterized by $t_0 \approx 0$. The representative widths of the larval production and zooplankton peaks are σ and δ respectively.



the importance of a mismatch in these two peaks must be judged in relation to the widths, δ (zooplankton) and σ (larvae), characterizing the temporal distributions. (Strictly speaking, σ and δ are half-widths.) For example, if the spawning window has a width of 2 months, a mismatch of peaks equal to 2 weeks may be inconsequential. The model developed below is intended to quantify this idea.

We envision first-feeding larvae being produced at a rate $P(t)$ (numbers per unit time) (Fig. 2) and foraging from t to $t + t_f$, where t_f is the foraging duration (the larval phase ends after t_f days). The number of larvae produced between times t and $t + dt$ is $P(t)dt$. At a later time, t', where $t \leq t' \leq t_f$ (t' is a dummy variable which will be integrated out in subsequent calculations), these larvae have diminished in number to $P(t)dt \exp[-M(t' - t)]$, where M is the larval mortality rate. The entire number of larvae produced (the number in the cohort) is simply $\int_{-\infty}^{\infty} P(t)dt$. The integration limits are intended to indicate that the integration extends from well before the peak of $P(t)$ to well after it.

If $Z(t)$ is the abundance of zooplankton palatable to the larvae, then the food consumed by the larvae first appearing in the interval t to $t + dt$ is proportional to

$$\int_t^{t+t_f} P(t)dt\, e^{-M(t'-t)}Z(t')dt' = P(t)dt \int_t^{t+t_f} e^{-M(t'-t)}Z(t')dt'. \quad (1)$$

Thus, the food consumed (F) by the entire cohort is just

$$F = \text{const} \times \int_{-\infty}^{\infty} P(t) \left[\int_t^{t+t_f} e^{-M(t'-t)}Z(t')dt' \right] dt \quad (2)$$

where const is a constant.

Larval mortality rates (especially early larval mortality rates; Bradford, 1992) tend to be high, generally about 10% per day (Pepin, 1991; Bradford, 1992). This rate corresponds to an e-folding time (the time required for change by a factor of e) of $M^{-1} = 9.5$ days, or equivalently a half-life of 6.6 days, for a batch of larvae. We can argue that the square-bracketed integral in eqn 2 can be approximated by

$$\int_{t}^{t+(1/M)} e^{-M(t'-t)} Z(t')dt', \qquad (3)$$

because of the rapid attrition implicit in the exponential term. (We are also assuming that $t_f > M^{-1}$, which is certainly reasonable; e.g. Bradford, 1992.) Furthermore, since the interval M^{-1} is only 9.5 days, we argue that it is permissible to treat $Z(t')$ as a constant over the integration interval in eqn 3; explicitly $Z(t') \approx Z(t)$ for $t \leq t' \leq t + M^{-1}$. With this approximation, eqn 3 is approximately equal to $Z(t)/M$, or more precisely it is given by

$$\frac{Z(t)}{M}(1 - e^{-1}), \qquad (4)$$

and eqn 2 becomes

$$F = \text{const}' \times \int_{-\infty}^{\infty} P(t)Z(t)dt, \qquad (5)$$

where const′ is a constant and we have absorbed the term $(1 - e^{-1})/M$ appearing in eqn 4 into this constant.

We now specify functional forms for Z and P: $Z = Z_0 \exp[-(t - t_0)^2/\delta^2]$; $P = P_0 \exp(-t^2/\sigma^2)$, where t_0 (Fig. 2) is the offset time between the peaks of Z and P. These forms are flexible enough for our needs in that the zooplankton and larval production curves can be made to appear either smooth or spiky by adjusting δ and σ. With these forms, eqn 5 becomes

$$F = \text{const}'' \times P_0 Z_0 \exp\left(-\frac{t_0^2}{\delta^2 + \sigma^2}\right), \qquad (6)$$

where const″ is a constant. This equation sensibly predicts that the food supply for the cohort, F, is maximum when $t_0 = 0$, that is, when there is a match between the peak of production of first-feeding larvae and the zooplankton peak.

From eqn 6 we can calculate how year-to-year changes in F are related to those in t_0. Since F is a maximum for $t_0 = 0$, we expect that the average value of t_0 is zero. We will expand t_0 about its mean, by writing $t_0 = 0 + \Delta t_0 = \Delta t_0$, where Δt_0 represents the year-to-year departures of t_0 from its mean value. The changes in F corresponding to the fluctuations in t_0 may be obtained from the Taylor expansion of F about its maximum at $t_0 = 0$;

$$\Delta F \approx \left(\frac{dF}{dt_0}\right)_{t_0=0} \Delta t_0 + \frac{1}{2}\left(\frac{d^2F}{dt_0^2}\right)_{t_0=0} (\Delta t_0)^2. \qquad (7)$$

This second-order expansion is necessary because the first derivative vanishes when $t_0 = 0$. The constant (const″) can be eliminated by expressing ΔF as a relative change: from equations 6 and 7 we find that

$$\frac{\Delta F}{F} \approx -\frac{(\Delta t_0)^2}{\delta^2 + \sigma^2}. \qquad (8)$$

This form is particularly useful in that the absolute value of $\Delta F/F$ is closely analogous to a CV.

Alternatively, eqn 8 can be heuristically derived with the aid of dimensional analysis. On the basis of dimensional consistency it can be argued that

$$\frac{\Delta F}{F} = \text{func}[(\Delta t_0/\delta), (\Delta t_0/\sigma)],$$

where func is a function to be determined. This function must even in Δt_0 (invariant under a change of sign in Δt_0) since both positive and negative values of Δt_0 must reduce F. We expect that the influence of δ and σ are in a sense additive. This leaves eqn 8 as the simplest, dimensionally consistent, form which meets the requirements of our picture.

Implied lags

In the simple model presented above the production of larvae is in phase with the zooplankton abundance. Given the envisioned high mortality rate, the larvae are perishing almost as fast as they are produced, so that the number of larvae present ($N(t) \approx P(t)/M$) closely mirrors the production rate, and thus larval abundance is in phase with zooplankton abundance. To be more explicit, the peak in the numbers of first-feeding larvae will coincide with the peak in the numbers of zooplankton nauplii (assuming nauplii are targeted by the first-feeding larvae). The small numbers of larvae that survive for times considerably greater than M^{-1} will presumably consume the post-naupliar zooplankton which are growing in parallel with them (e.g. Jones and Henderson, 1988).

If we consider the opposite case (to which the model presented above does not apply) of low mortality (specifically $M^{-1} \gg t_f$), then, to maximize food supply, the peak of larval production should produce a batch which feeds over a period symmetrically straddling the zooplankton peak, from $t_0 - t_f/2$ to $t_0 + t_f/2$ (this assumes that the zooplankton peak is symmetric about its maximum). Thus the peak of larval production would lead the zooplankton peak by a time of $-t_f/2$. However, in this low-mortality case, larvae accumulate as they are produced, and thus the abundance peak will lag the production peak by about an interval of t_f. It follows that the peak of abundance will lag the zooplankton peak by a span of about $(-t_f/2) + t_f = t_f/2$.

Only in the high-mortality case is it clear that the maximum of larval abundance should coincide with the zooplankton peak.

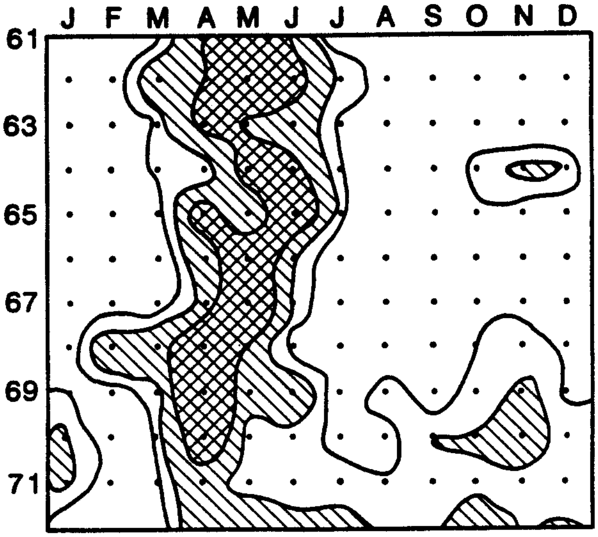
APPLICATIONS

Our first test of the match/mismatch hypothesis, based on our model, simply involves utilizing the data described earlier ('Data and analysis') to assign values to the quantities in eqn 8, in order to discern the expected magnitude of the variations in the larval food supply. Specifically, we wish to determine if the $|\Delta F/F|$ from eqn 8 is 'not small', whether it is order one (or greater). Jumping ahead somewhat, it is apparent from Table 1 (covering all major cod stocks in the North Atlantic sector) that a typical spawning window width is about 1 month, indicating from eqn 8 that Δt_0 must be of the order of 1 month if the CV for F is to be order one. Thus, for a typical cod stock, a mismatch of about a month is significant. In the next few paragraphs we will refine these considerations.

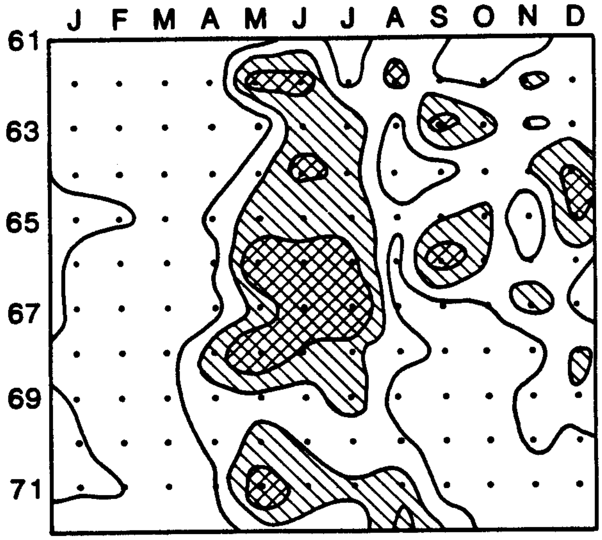
The focus will be on *Calanus finmarchicus* since this is a dominant species among the net-captured plankton of the North Atlantic (Runge, 1988) and since *Calanus* eggs and nauplii are important prey items for the larvae of a number of fish species (Cushing, 1982; Runge, 1988). Figure 3, redrawn from Robinson et al. (1975), shows year–month contours of the continuous plankton recorder (CPR) catch of *Calanus* I–IV for NAFO regions 3L, 3M, 3NO, 3Ps. For reference, the greenness index is also displayed to indicate the timing of the phytoplankton peak. It is reasonable to assign a width (δ) of about 2 weeks to the *Calanus* peak. The peaks for total *Calanus* in many regions of the North Atlantic sector (Colebrook, 1982) have a width of about 1 month; it is reasonable that total *Calanus* should exhibit a broader peak than I–IV. Perhaps more relevant is the temporal width of the *Calanus* naupliar abundance curve; this appears to be 5–10 days (for the Lofoten area, off Norway) (Ellertsen et al., 1989). This latter value will underestimate width of the food window for larval fish if they also prey on early *Calanus* stages. These considerations suggest a representative value of $\delta = 2$ weeks.

Figure 3 provides estimates of the variability in timing of the *Calanus* peak (Δt_0). The peak occurs as early as May and as late as August, but for most years it occurs close to June, so that the variability in timing can be characterized by $|\Delta t_0| = 2$ weeks to 1 month. Brander (1992) has examined the timing of the *Calanus* V–VI peak in three regions of the North Sea. Figure 10 of Brander (1992) shows that timing of the peak can

Figure 3. Month–year contours, for region 3 (3L, 3M, 3NO, 3Ps of Fig. 1), of the abundance of phytoplankton (greenness index, contours at 2, 4, 6) and *Calanus finmarchicus* I–IV (number per CPR sample, contours at 42, 83, 155). Adapted from Robinson *et al.* (1975).



Phytoplankton – Colour



Calanus finmarchicus I–IV

Table 1. Means (Julian days) and standard deviations (days) of the spawning distributions of a number of North Atlantic cod stocks.

Stock	Mean	SD
2J3KL	128	32
3M	77	11
3NO	135	34
3Ps	141	52
3Pn4RS	154	41
4TVn	115	51
4X	90	21
5Z	67	36
Iceland	125	12
North Sea	67	22
NE Arctic	91	10

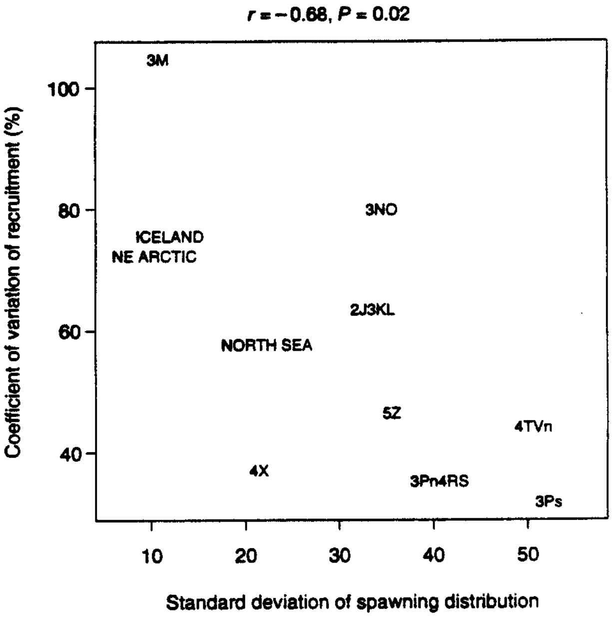
deviate by up to 2 months from the mean, and the typical fluctuations in timing of the peak can be characterized by an amplitude of about 2 weeks to 1 month.

The factor $(\Delta t_0)^2$ includes a contribution from year-to-year variability in spawning time. If we assume that the variations in spawning time are uncorrelated with those in timing of the plankton peak, then $(\Delta t_0)^2 = (\Delta t_{\text{plank}})^2 + (\Delta t_{\text{spawn}})^2$. Earlier, under the heading 'spawning data', we noted that the magnitude of Δt_{spawn} is about 20% of the spawning window width, which is typically 1 month, implying that the representative magnitude of $(\Delta t_{\text{spawn}})$ is about 1 week. Thus, $(\Delta t_0)^2 \approx (0.5 \text{ to } 1 \text{ month})^2 + (0.25 \text{ month})^2 = 0.3 \text{ to } 1.1 \text{ (month)}^2$, where we have set $(\Delta t_{\text{plank}}) = 0.5$ to 1 month based on the information in the preceding paragraph.

We can now consolidate the information from the previous three paragraphs and utilize it in eqn 8. From Table 1, $0.3 \leq \sigma \leq 2$ month, so that, with $\delta = 0.5$ month, $0.34 \leq \delta^2 + \sigma^2 \leq 4.25 \text{ (month)}^2$. Thus, with this information, $0.1 \leq |\Delta F/F| \leq 3.2$. Only for two or three stocks in Table 1 (4TVn, 3Ps and 3Pn4RS) is the predicted $|\Delta F/F|$ clearly small (<0.5). This provides some corroboration for the match/mismatch hypothesis in showing that, for a typical North Atlantic cod stock, the variability of plankton peak timing is sufficient to produce an order-one CV for F.

We can consider the sole effect of stock-to-stock differences in spawning window width on $\Delta F/F$. With a typical $(\Delta t_0)^2$ of 0.7 (month)^2 (and again $\delta = 0.5$ month), $|\Delta F/F|$ varies from 0.2, for maximum σ (= 2 months), to 2.1, for minimum σ (= 0.3 month). Thus, the width of the spawning window strongly affects $|\Delta F/F|$. This result supports the contention that fish stocks can reduce their recruitment variability by spawning over a protracted period, a hypothesis which can also be empirically tested (see next paragraph).

Figure 4. The coefficient of variation (given as a percentage) of recruitment versus standard deviation (in days) of the spawning intensity versus time curve (width of the spawning window) for North Atlantic cod stocks.



A direct test for a relation between recruitment variability and width of the spawning window is possible. Using the data listed in Table 1 and the recruitment CVs described above ('Data and analysis'), we have constructed Fig. 4. This plot shows a significant relationship between recruitment variability and the width of the spawning window. Figure 4 lends some credence to the match/mismatch hypothesis, which predicts that such a relationship should hold (Cushing, 1990).

It is possible that the width of the spawning window is correlated with the magnitude of the interannual fluctuations in the timing of the plankton peak. Such a tendency would undermine the argument that there should be a relationship between recruitment variability and the width of the spawning window. Ideally, one would like to complement Fig. 4 with a corresponding plot of spawning window width versus an index of variability of the timing of the zooplankton peak. However, this latter quantity cannot be estimated with sufficient areal resolution from the plankton data available.

Mortality estimates

The CVs for variability before density-dependent juvenile mortality, discussed earlier ('Data and analysis'), are estimates of the variability of larval mortality. Thus it is worthwhile to sketch how our food supply might be used to predict the variability of cumulative larval mortality (C).

It is common to picture larval mortality as dependent on predation (e.g. Cushing, 1990) and thus being mitigated by rapid growth; "Hence one would expect growth and mortality to be inversely related" (Cushing, 1990). Food supply will determine the rate of growth of weight, and this allows some surmises about the dependence of C on F.

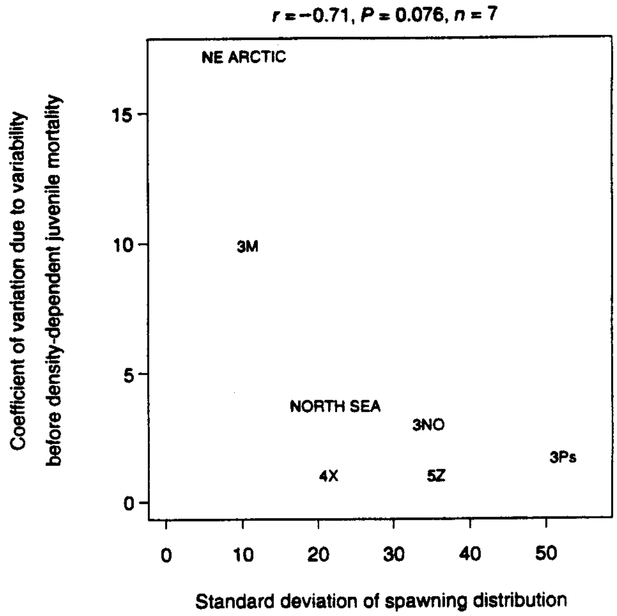
If one assumes that the ability of larvae to avoid predators is proportional to their length, then, since food supply determines the weight increment, mortality will be inversely proportional to the one-third power of F (length being approximately proportional to the one-third power of weight). On the other hand, survival might be proportional to weight itself, assuming that the ability of larvae to withstand food deprivation (in a patchy environment) depends on gross reserves (perhaps proportional to weight). We have no knowledge of the constant putatively relating survival (or mortality) and weight (to some power); therefore, we will once again standardize, by expressing the variability of mortality in fractional form. Allowing for these uncertainties in how mortality scales with weight (and thus food supply) we write

$$\frac{\Delta C}{C} \approx -\left(\tfrac{1}{3} \text{ to } 1\right)\frac{\Delta F}{F} \approx \left(\tfrac{1}{3} \text{ to } 1\right)\frac{(\Delta t_0)^2}{\delta^2 + \sigma^2}. \qquad (9)$$

As noted earlier, stock-to-stock differences in σ have an appreciable effect on the magnitude of $|\Delta F/F|$, implying, through eqn 9, that stock-to-stock variations in σ will also influence $\Delta C/C$. Specifically, if we adopt the largest likely value for the coefficient in eqn 9, then $\Delta C/C \approx |\Delta F/F|$; then if we again set $(\Delta t_0)^2 = 0.7$ $(\text{month})^2$, we find that $\Delta C/C$ ranges from 0.2 ($\sigma = 2$ months) to 2.1 ($\sigma = 0.3$ month). Equation 9 predicts that spawning window width does affect the CV for larval mortality.

In Fig. 5 we have plotted the Myers and Cadigan (1993a,b) estimates of the CVs for larval mortality versus the estimated width of the spawning window for the stock. Clearly there is a great range in the plotted CVs; the maximum observed CV is much larger than the maximum predicted by eqn 9. However, there is, in agreement with eqn 9, an apparent relationship (which is almost significant at the $P = 0.05$ level) between the CV for larval mortality and the spawning window width. Given the quantitative inadequacies of the model underlying eqn 9, we feel that it is appropriate to emphasize the qualitative agreement between the trend predicted by eqn 9 and the trend evident in Fig. 5.

Figure 5. The coefficient of variation (note that this is not given as a percentage) for larval mortality (Myers and Cadigan, 1993a,b) versus estimates of the spawning window width.



SUMMARY

To test the match/mismatch hypothesis we have developed perhaps the simplest possible model for larval food supply which can incorporate the match/mismatch mechanism. The model provides a measure of substantiation for the match/mismatch hypothesis by demonstrating that significant variations (an order-one CV) in the larval food supply are implied by the observed fluctuations in timing of the plankton peak. The model also indicates that the width of the spawning window appreciably influences the variability of larval food supply.

We have compiled estimates of the spawning window width for the major cod stocks of the North Atlantic. By correlating these widths with the recruitment variability for each stock, we have shown that there is a significant relationship between these quantities, providing a degree of support for the match/mismatch hypothesis.

We have also found that research-survey-based estimates of the variability of larval mortality appear to be correlated with the width of the spawning window. This is in qualitative agreement with the predictions of our model. The existence of a relationship between the variability of larval mortality and the spawning window width provides additional confirmation of the match/mismatch hypothesis. We believe that it would be profitable to assemble a larger set of spawning window widths, and corresponding recruitment variability indices, in the hope of providing a more stringent test of the match/mismatch hypothesis.

It is, of course, true that much has been omitted from this study. There is a multitude of potential biotic and abiotic sources of recruitment variability. Perhaps the most thoroughly explicated alternative to match/mismatch is the member/vagrant hypothesis (e.g. Sinclair, 1988) which holds, *inter alia*, that recruitment fluctuations correspond to variations in the advective losses of eggs and larvae from the waters providing their haven. Sinclair (1988) has consolidated considerable evidence for the importance of advective effects. However, all-inclusive modelling efforts are simply intractable, suggesting the continued relevance of rudimentary single-process-oriented studies such as the one presented here.

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