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The effect of spatial and temporal variation in zooplankton concentrations on larval cod growth and survival on Georges Bank: a sensitivity analysis based on modelling and observations

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Abstract

The U.S. GLOBEC Georges Bank/NW Atlantic program has generated an unprecedented body of data on vital rates, abundance and distribution of zooplankton and ichthyoplankton on Georges Bank. Concurrent with the data-gathering activity has been the development and refinement of a coupled physical-trophodynamic model describing growth, survival and distribution of larval cod and haddock. Using the trophodynamic model and zooplankton data from the Georges Bank broadscale cruises in 1995 and 1998, we investigate the sensitivity of growth rates of larval cod to observed spatial/temporal variation in abundance of larval prey. Here we examine the potential role of *Calanus finmarchicus*. The results are consistent with the hypothesis that interannual variations in the copepod production on the northeast peak and southern flank are sufficient to make the difference between weak and strong growth of larvae on the Bank. .

Introduction

Using a larval fish trophodynamic model and observed copepod prey field concentrations acquired during the U.S. GLOBEC NW Atlantic/Georges Bank 1995 broadscale surveys,

Werner et al. (2000) calculated the bank-wide variability in growth rates of cod larvae developing on the bank between March and May. These results advance previous model studies of larval fish growth on the Bank, in which the prey field was represented by depth-independent and temporally constant concentrations of copepod nauplii inferred from averaged, sparse literature data (e.g., Werner et al. 1996; in press) or mean abundances of adult stages from decadal averaged 1977-1987 MARMAP surveys (Lynch et al. 2000). Lynch et al. (2000) concluded that the average distributions of the planktonic copepod, *Calanus finmarchicus*, were better matched with the zone of cod larval feeding than *Pseudocalanus* spp., another very dominant copepod species group. Their analysis indicated that *Pseudocalanus* alone could on average not sustain growth of 10-12mm cod larvae during the observed spawning period on Georges Bank, but was sufficient to sustain growth of smaller 4-6mm cod larvae. *Calanus finmarchicus* was found to provide good growth for the larger, 10-12mm cod larvae. Here, in this companion paper to Werner et al. (2000), we use the trophodynamic model and the Georges Bank broadscale survey data from 1995 and 1998 to develop the hypothesis that the observed variability in production of the planktonic copepod, *Calanus finmarchicus*, has potentially significant impact on the growth rates of larvae retained on the bank.

The hypothesis is developed from a study of relationships among climate-induced variation in winter-spring runoff from the St. Lawrence watershed, zooplankton biomass and recruitment into the stock of Atlantic mackerel in the southern Gulf of St. Lawrence (Runge et al. 1999). The observed covariation is consistent with the hypothesis of a strong trophic link between production of copepod nauplii and strength of the year class of mackerel in this region. Analysis of the copepod species composition suggests that the abundance of *Calanus* females producing naupliar prey was a primary factor determining the exceptional mackerel year class that occurred in 1982. According to the hypothesis, in some years *C. finmarchicus* females would be much more abundant in the southern Gulf of St. Lawrence. Because of its great capacity for egg production, a high abundance of *C. finmarchicus* females relative to other copepod producers would have a disproportionate impact on the availability of prey for larvae; nauplii hatching from the *Calanus* eggs would overwhelm the local prey field, resulting in exceptional potential for high survival of mackerel larvae. We suggest a similar role for *Calanus* in the Georges Bank system. Interannual variation in the spatial-temporal pattern of *Calanus* female abundance and local processes determining its egg production may make the difference between weak and strong larval cod growth rates.

Using the Georges Bank trophodynamic model, we explore the sensitivity of larval cod growth rates to the observed variation in *Calanus* prey concentrations observed on the Bank in spring of 1995 and 1998. This study represents a preliminary model analysis of the broadscale survey data. The survey year 1995 was selected because of the completeness of the sample analysis and existence of ancillary data from process cruises, such as measurements of in situ growth rates (Werner et al. 2000). The survey year 1998 was selected first for comparison because of indications that *Calanus* abundance was greater than in other survey years (E. Durbin, unpubl. observations). This year also supported a strong year class of haddock. We reasoned that focus on 1998 would provide

guiding insight into the reasons for differences in recruitment success in these two fish species.

Methods

To estimate spatial and seasonal variation in growth rate of cod larvae, we use the same trophodynamic model, with extensions to include the influence of temperature on metabolism discussed in Buckley et al. (2000), and simplifying assumptions described in Werner et al. (2000). The physical environment was fixed at a representative temperature, light and turbulence field for Mar-Apr. and May. The 1995 distribution of biomass of early life stages of the dominant planktonic copepods, *C. finmarchicus*, *Pseudocalanus* spp. and *Oithona* spp. was based on the 10-station, broadscale pump survey samples collected during missions EN263, EN265 and AL9505 to Georges Bank in 1995. The 1998 distribution of biomass of *C. finmarchicus* nauplii was calculated from pump samples collected during missions EN319, EN322 and AL9806. The 1998 biomass of the other prey species has not yet been objectively analyzed. The prey field was assumed to comprise *Pseudocalanus* spp. stages N1-C6, *Oithona* stages N1-C6 and *Calanus* stages N1-N6, without selectivity among species or stages. Satiation was defined by constraining a maximum limit of prey biomass in gut. The zooplankton data were objectively analyzed into a three-dimensional finite element grid, as described in Werner et al. (2000).

The abundance of *Calanus* females was determined from analysis of depth stratified MOCNESS samples (158 μ m mesh) taken at the broadscale survey stations. Female specific egg production rates were estimated from an empirically determined relationship between an index of reproduction of preserved *C. finmarchicus* females and their corresponding in situ egg production rate, measured at sea during process cruises (Runge 1987; Niehoff and Runge, in prep.). The reproductive index of *C. finmarchicus* in preserved broadscale samples was measured by estimating the proportion of females carrying mature oocytes, based on methods described in Runge (1987), Niehoff and Hirche (1996) and Niehoff and Runge, (in prep).

Results

Fig. 1 summarizes the distribution of the copepod prey biomass in March, April and May on Georges Bank. The biomasses are the depth-averaged values of the objectively analyzed prey concentrations over the upper 60m of the finite element grid (Werner et al. 2000). In 1995, *Pseudocalanus* and *Oithona* prey concentrations were highest in April on the northeast peak and southern flank, which are considered to be the principal areas of cod spawning and development on the bank. The prey biomass of these two species was 2-4 times lower in the same areas in March and May. *Calanus* naupliar concentrations in 1995 were highest on the crest of the bank in April and very low in May. Concentrations on the northeast peak and southern flank in April, 1995 were 2-8 times lower than *Pseudocalanus* and *Oithona* in the same region. In contrast, *Calanus* prey biomass was greater in 1998 in March and May on the southern flank and particularly in April on the northeast peak and southern flank, where concentrations were on the order of 3-10 times higher than observed in 1995.

Growth rates of cod larvae in these prey fields were calculated with the trophodynamic model. Werner et al. (2000) present 1995 growth rates calculated at specific depths for each prey species separately and combined; Fig. 2 summarizes these results, showing 60m integrated (i.e. depth averaged) growth rates for cod larvae of selected size feeding in the 1995 *Pseudocalanus* and *Oithona* prey field (top row) and the combined 1995 *Pseudocalanus*, *Oithona* and *Calanus* prey fields (middle row). In March, the estimated depth averaged growth rates were positive only in the crest region of the bank, due possibly in large part to the enhancement of feeding success by the increased turbulence. In May, the trophodynamic model estimated negative depth-averaged growth rates in all regions except for limited areas on crest and extreme southwest of the bank. In April, positive growth rates are estimated over a large portion of the bank in the combined prey field (middle graph of middle row). These depth-averaged growth rates were nevertheless low, typically on the order of 0-5% d⁻¹ particularly on the northeast peak and eastern southern flank. In the presence of the 1998 *Calanus* prey field, however, estimates of depth averaged larval cod growth rates in April increase substantially in these regions, to 5-10% d⁻¹. Note that depth-averaging includes areas where there is very little (even negative) growth due to absence of prey, light inhibition or limitation, etc. Thus the positive growth measure provided by depth averaging is a strong statement to the potentially favorable feeding environment in April 1998 resulting from the abundance of *Calanus* nauplii.

We consider this result to reflect the potential for interannual variation in *Calanus* egg production to influence larval fish growth rates. The source of variation is both female abundance (Fig. 3) and the female-specific egg production rate (Fig. 4). In April, female abundance is two to three times larger in 1998 than in 1995 on the northeast peak and southern flank. (Fig. 3). At the same time, the reproductive index, an estimator of the female-specific egg production rate, was also higher in the same region of the bank. The two variables combined estimate the daily input of *Calanus* eggs into the water column, shown on the right hand panels of Fig. 4. The results indicate that *C. finmarchicus* egg production rates in April were 2-10 times higher on the southern flank and northeast peak in 1998, consistent with the pattern of *Calanus* naupliar concentrations observed in the pump samples.

Discussion

This preliminary sensitivity analysis is consistent with the initial hypothesis that spatial-temporal variation in *C. finmarchicus* production can have significant impacts on growth of fish larvae on Georges Bank. In this particular example, the significant impact arose from the interannual variation in April in the abundance of *Calanus* naupliar stages on the northeast peak and southern flank. In March and May, the slightly higher biomass of *Calanus* nauplii on, respectively, the southwestern and southern edges of the Bank was not sufficient to substantially influence larval cod growth rates. However, in April, which is a prime period of production of larvae on the Bank, the difference between 1995 and 1998 in *Calanus* prey concentrations is considerable in the areas where cod larvae hatch and grow; this is reflected in model estimates of growth rates that would be conducive to higher survival.

In our analysis, we have assumed that the changes in biomass of the other dominant prey are independent of variation in *Calanus* production, in other words, that the physical/biological processes influencing population dynamics are not necessarily the same for the three prey species. We have, for purposes of the sensitivity analysis here, assumed that the *Pseudocalanus* and *Oithona* prey field for cod larvae was invariant between the two years under study. Work is underway to objectively analyze broadscale data of *Pseudocalanus* and *Oithona* abundance in order to investigate the validity of this assumption. If either or both prey abundances are significantly different in 1998, our estimates of larval cod growth rate would of course be altered. It is possible, for example, that growth rates in April would be enhanced or reduced, depending on the direction of change in the other prey species. Growth rates in March or May may also be different. The important result of the sensitivity analysis is that the variation in *Calanus* prey abundance that is actually observed to occur on the Bank is sufficient to have a substantial impact on cod growth rates. If our assumption of independence in variation among prey species is correct, the potential exists for a situation in which fluctuations in *Calanus* production would make the difference between weak and strong growth rates.

This conclusion is founded on other assumptions. Underlying our analysis is the assumption that the growth of fish larvae on the Bank is indeed food limited, in other words, that the trophodynamic model and prey fields described in Werner et al. (2000) represents with reasonable accuracy the ingestion and growth rates of larvae on the peak and flank of the bank. We postulate as well that *C. finmarchicus* nauplii are indeed available as prey for cod larvae. This implies that the vertical distribution of *Calanus* nauplii and cod larvae coincides, so that larvae would indeed encounter *Calanus* prey as represented by our 2-D portrayal of *Calanus* prey biomass. We assume that cod larvae are capable of capturing and ingesting *Calanus* prey with the same efficiency as the other prey species. Studies of arctonorwegian cod diets (e.g. Skreslet 1989; Fossum and Ellertsen 1994) as well as earlier studies of dietary composition of cod larvae on Georges Bank (Kane 1984) indicate that cod larvae are capable of feeding on *Calanus* nauplii. However, studies of the diet of larval cod on Georges Bank in 1981 and 1983 indicate that *Pseudocalanus* and *Oithona* are predominant in the diet of cod larvae captured in April and May on the southern flank (Lough and Mountain 1996). At this time, it is not clear whether this is a consequence of the simple absence of *Calanus* from the southern flank in these years, or that *Calanus* nauplii present on the southern flank were unavailable to the larvae, either by differences in vertical distribution or by some behavioural mechanism discouraging capture upon encounter.

Successful recruitment is determined by a number of physical and biological processes, not just those that influence prey availability and feeding success. In 1998, the higher growth rates for cod larvae we have calculated here apparently were not sufficient to produce an above average year class in cod. (Anon. 2000) The quantity of cod eggs spawned on the Bank, the temporal/spatial variation in circulation relative to the initial distribution of cod early life stages and variation in the field of larval fish predators act to enhance, moderate or negate potential survival advantages due to increased prey availability and growth rates. The value of the coupled physical- trophodynamic model is that these factors can be taken into account; as such the model approach is a powerful

tool for understanding mechanisms controlling survival of fish larvae in the Georges Bank system.

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References

- Anon. 2000. Assessment of 11 Northeast Groundfish Stocks through 1999: A Report to the New England Fishery Management Council's Multi-Species Monitoring Committee. Northern Demersal Working Group, Northeast Regional Stock Assessment Workshop. Northeast Fisheries Science Center Reference Document 00-05. NOAA, NMFS. Woods Hole, Massachusetts. 175 pp.
- Buckley, L.J., R.G. Lough, M.A. Peck and F.E. Werner (2000a) Comment: Larval Atlantic cod and haddock growth models, metabolism, ingestion, and temperature. *Can. J. Aquat. Sci.*, **57**:1957-1960.
- Fossum, P., and Ellertsen, B. 1994. Gut content analysis of first-feeding cod larvae (*Gadus morhua* L.) sampled at Lofoten, Norway, 1979-1986. *ICES marine Science Symposium*. **198**: 430-437.
- Kane, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Marine Ecology Progress Series*. **16**: 9-20.
- Lough, R.G. and D.G. Mountain. 1996. Effect of small-scale turbulence on feeding rates of larval cod and haddock in stratified water on Georges Bank. *Deep-Sea Res. II*. **43**: 1745-1772.
- Lynch, D.R., C.V.W. Lewis and F.E. Werner (2001) Can Georges Bank larval cod survive on a calanoid diet? *Deep Sea Research II*, **48**:609-630
- Niehoff, B., and Hirche, H.-J. 1996. Oogenesis and gonad maturation in the copepod *Calanus finmarchicus* and prediction of egg production from preserved samples. *Polar biol.* **16**: 601-612.
- Niehoff, B. and J. A. Runge. In prep. A revised methodology for prediction of egg production of the marine planktonic copepod, *Calanus finmarchicus*, from preserved samples.
- Runge, J. A. 1987. Measurement of egg production rates of *Calanus finmarchicus* from preserved samples. *Canadian Journal of Fisheries and Aquatic Science*. **44**: 2009-2112.

Runge, J.A., M. Castonguay, Y. de Lafontaine, M. Ringuette, and J.-L. Beaulieu. 1999. Covariation in climate, zooplankton biomass and mackerel recruitment in the southern Gulf of St. Lawrence. *Fish Oceanogr.* **8**: 139-149.

Skreslet, S. 1989. Spatial match and mismatch between larvae of cod (*Gadus morhua* L.) and their principal prey, nauplii of *Calanus finmarchicus* (Gunnerus). *Rapp. P.-v. Réun. Cons. int. Explor. Mer.* **191**: 258-263.

Werner, F.E., R.G. Lough, J.A. Quinlan, L.J. Buckley, E. Durbin, L.S. Incze, and J.A. Runge. 2000. Modeling growth of larval cod and haddock on Georges Bank: a synthesis of observations and model results for spring, 1995. ICES C.M. 2000/M:24.

Werner, F.E., B.R. MacKenzie, R.I. Perry, R.G. Lough, C.E. Naimie, B.O. Blanton and J.A. Quinlan. In press. Larval trophodynamics, turbulence, and drift on Georges Bank: a sensitivity analysis of cod and haddock. *Scientia Marina*.

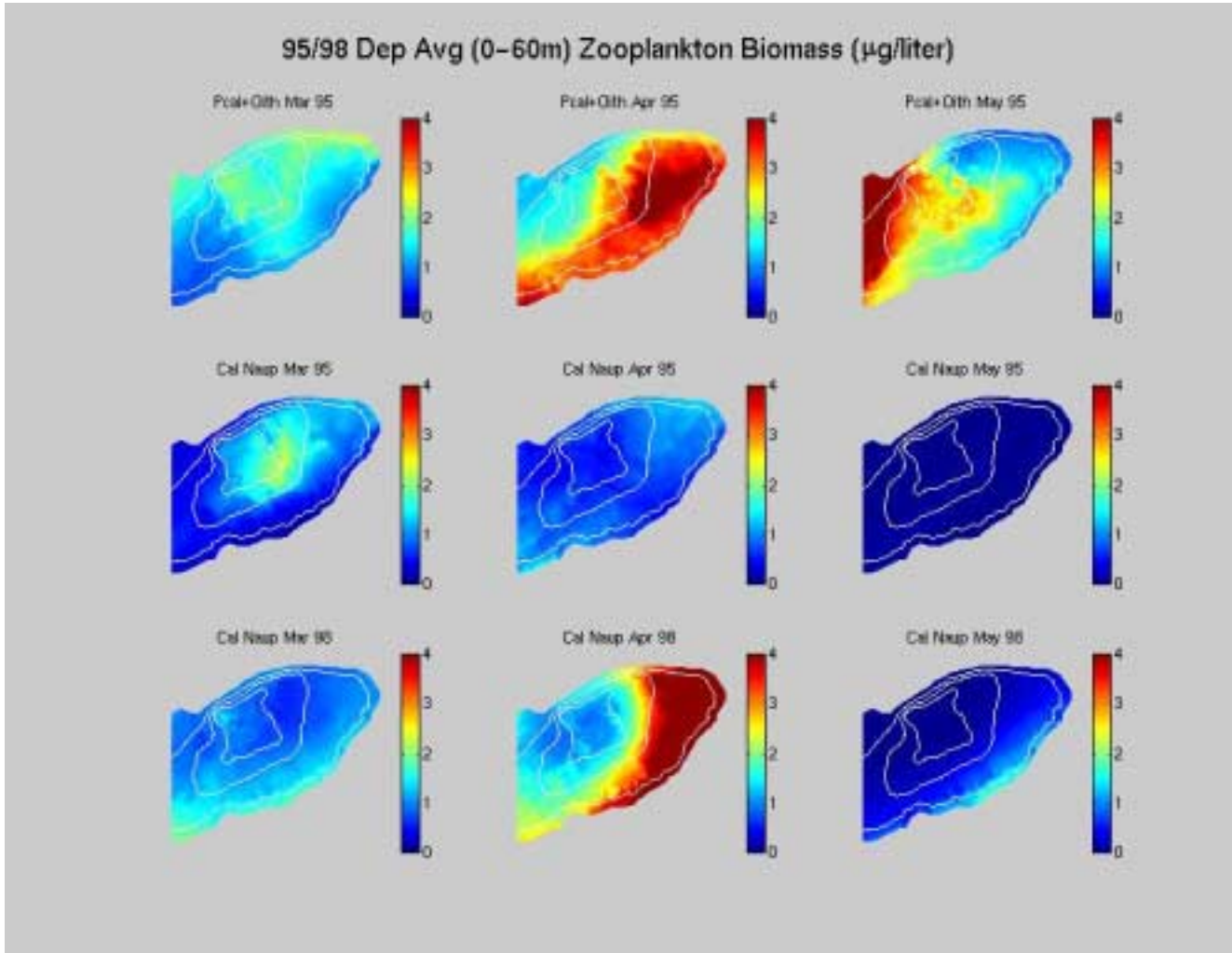


Fig. 1. Vertically averaged (0-60m) biomass of zooplankton prey (*Pseudocalanus* and *Oithona* N1-CVI, *C. finmarchicus* N1-N6) in March, April and May for 6mm, 8mm and 10 mm larvae, respectively.

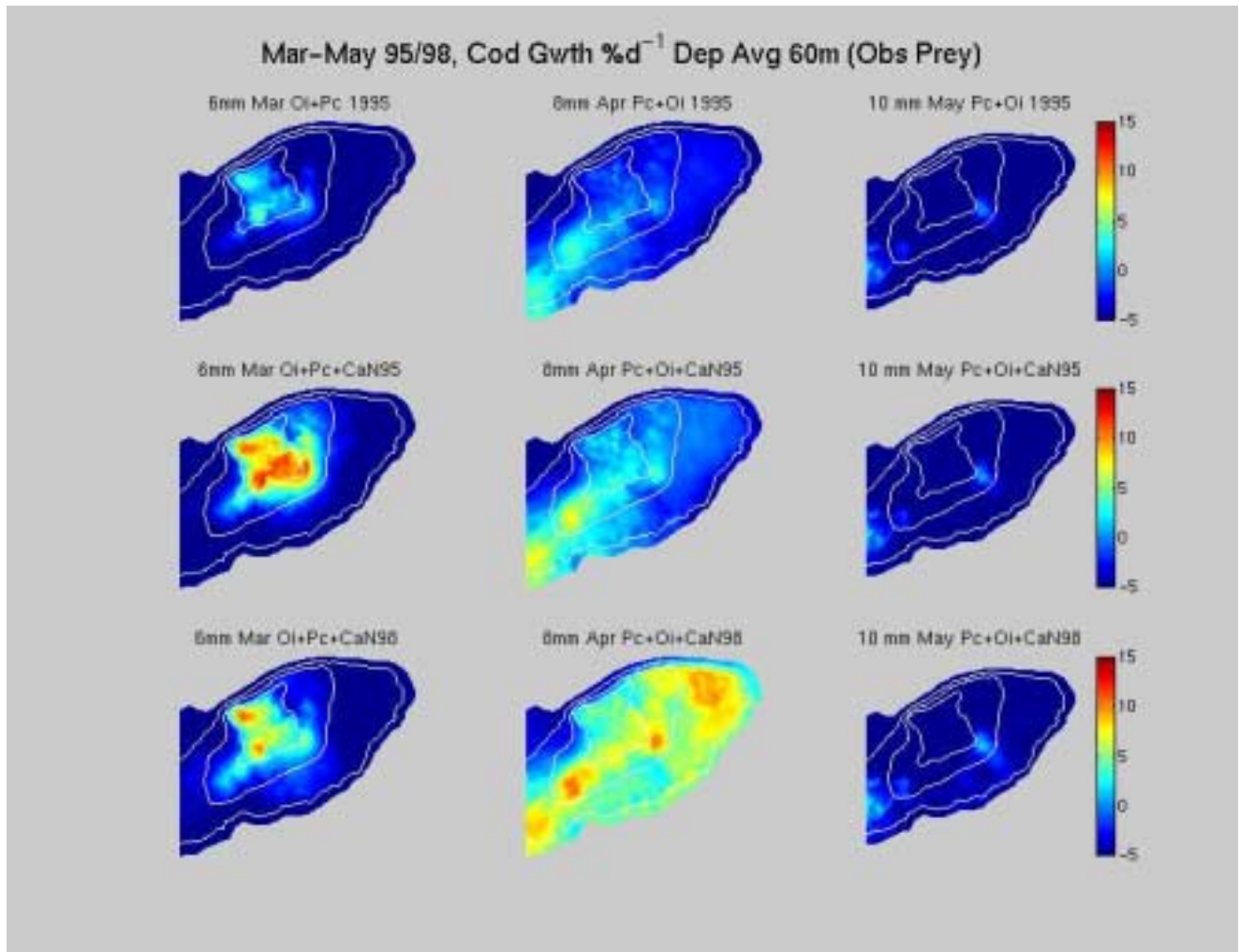


Fig. 2. Model calculation of depth-averaged larval cod growth rates (over the top 60m of the water column) based on observed prey concentrations from broadscale pump surveys, presented in Fig. 1. Top row: growth rates for 6, 8 and 10 mm larvae for Mar, Apr. and May, respectively, for larvae feeding only on 1995 concentrations of *Pseudocalanus* and *Oithona* prey. Middle row: growth rates for larvae feeding in 1995 on *Pseudocalanus*, *Oithona*, and *Calanus* prey combined. Bottom row: growth rate as in middle row, except for substitution of *Calanus* 1998 naupliar concentrations for the *Calanus* 1995 observations

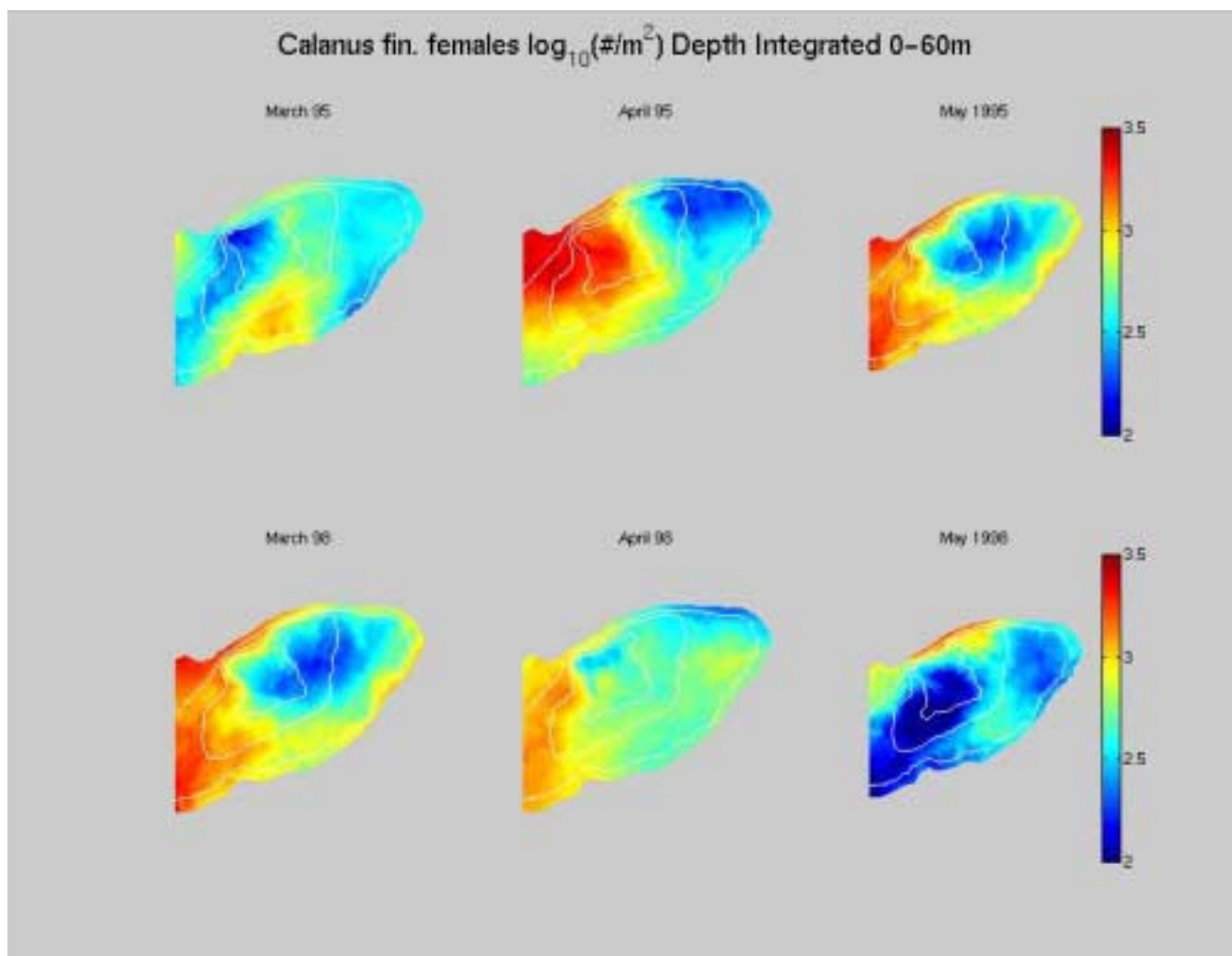
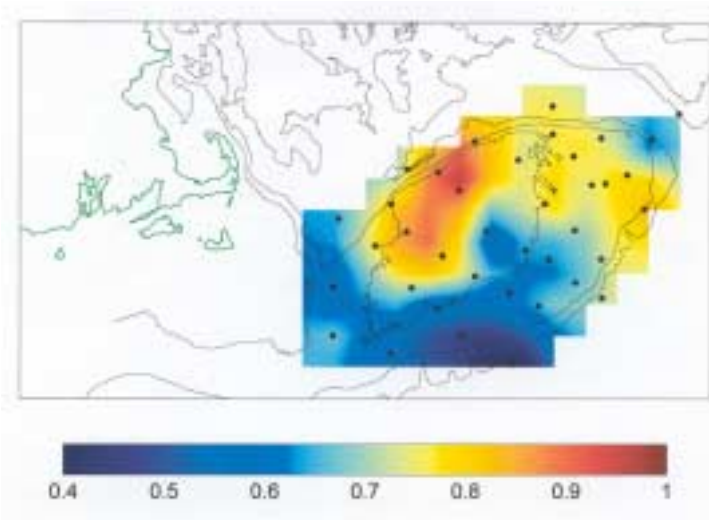


Fig. 3. The abundance of *Calanus* females (no. m⁻²) from broadscale survey MOCNESS samples, integrated over the upper 60 m of the water column.

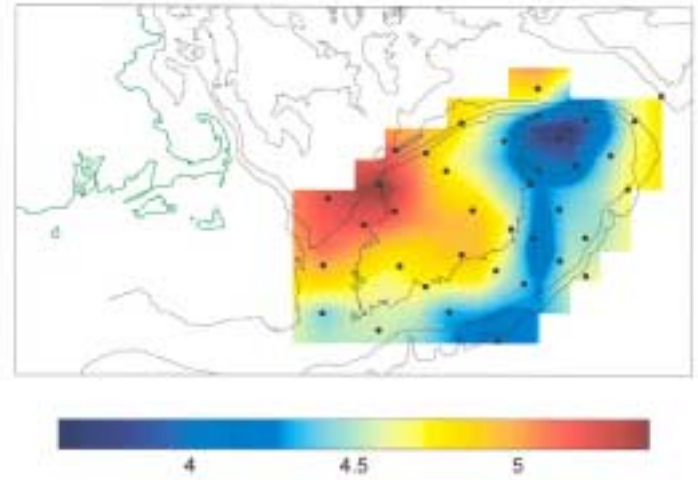
Calanus finmarchicus

Reproductive Index

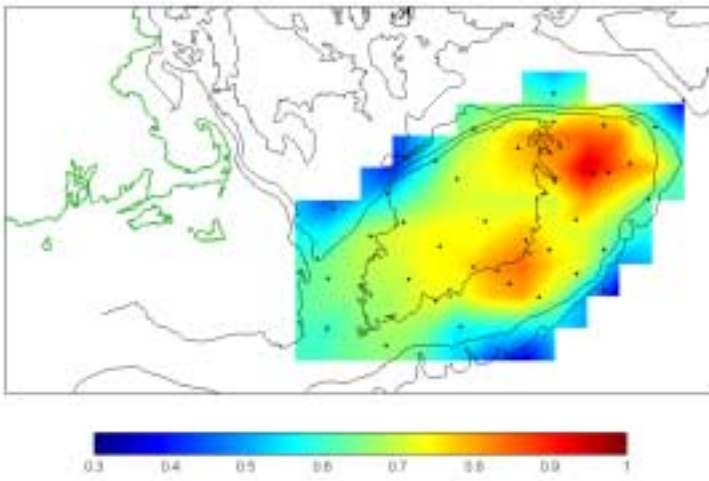
Egg Production Rate



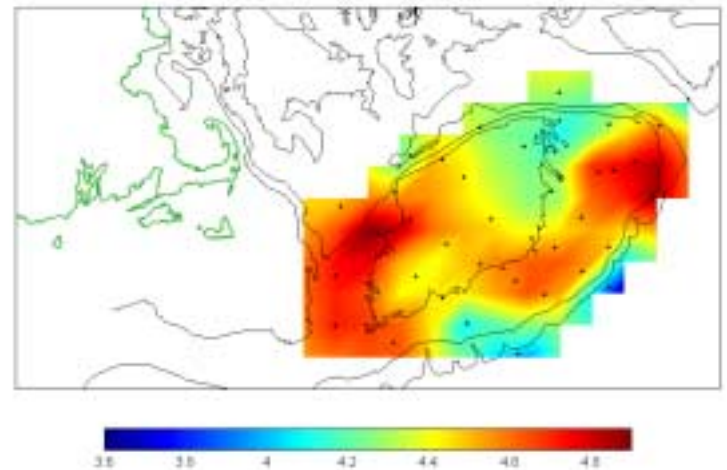
1995



1995



1998



1998

Fig. 4. Reproductive Index (left, linear scale), an estimate of female-specific egg production derived from evaluation of maturation state of preserved females in broadscale survey samples and egg production rate (right, log scale, eggs $\text{m}^{-2}\text{d}^{-1}$), the product of female abundance (females m^{-2}) and the estimated female-specific egg production rate (eggs $\text{female}^{-1}\text{d}^{-1}$), for *Calanus finmarchicus* in 1995 and 1998.