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Spatial and temporal variation in egg production of *Calanus finmarchicus* on Georges Bank: implications for the productivity of prey of cod and haddock larvae

Jeffrey Runge, E. Durbin, S. Plourde and Y. Gratton.

ABSTRACT

As part of the US-GLOBEC Georges Bank program, egg production rates of *Calanus finmarchicus* and of other common copepod species were estimated between January and June, 1995. Female *C. finmarchicus* spawned continuously during this period. The monthly, median wt-specific rate measured by shipboard incubation was highest in February-March (10.5% d-1); at other times it varied between 5.5% d-1 in January to 8% d-1 in June. *C. finmarchicus* was capable of sustaining egg production under most environmental conditions in the Georges Bank region. Measurements of egg production rate by shipboard incubation during process cruises were used to calibrate a reproductive index based on the proportion of females in preserved samples carrying oocytes in advanced stages of vitellogenesis. The product of the female-specific egg production rate determined from this relationship and the female abundance estimated from net tows yielded the depth-integrated rate of egg production during the broadscale cruises, which sampled a grid of ~40 stations monthly during the same January-June period. In April and May, the period of highest abundance of fish larvae on the southern flank of Georges Bank, the daily input of *Calanus* eggs into the water column (eggs m^{-2} d^{-1}) varied by almost two orders of magnitude. The total copepod egg (naupliar) production on the southern flank during this period varied from 1- 80 mgC m^{-2} d^{-1}, of which the proportion contributed by *Calanus* ranged between 25-80%. This variability in prey field production may have a significant impact on the growth rates of fish larvae as they are transported along the southern flank corridor.

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INTRODUCTION

The U.S. GLOBEC Northwest Atlantic/Georges Bank program recently sponsored a series of research cruises investigating physical and biological processes that govern productivity of the Georges Bank ecosystem. In June, 1994 and between January-June, 1995, six process-oriented cruises investigated zooplankton vital rates, with focus on a target zooplankton species, the planktonic copepod *Calanus finmarchicus*, but also including other copepod and predator species. In addition, a hydrographic and zooplankton/ ichthyoplankton broad-scale survey of the bank was conducted at approx. 4 week intervals between Feb. and July, 1995. One of the goals of the program is to understand factors controlling variability in the productivity and abundance of zooplankton and how this variability may affect the growth and survival of larvae of cod and haddock stocks that spawn on the bank.

We investigate here the spatial-temporal variation in egg production rate of planktonic copepods on Georges Bank in 1995. Particular emphasis is placed on the productivity of *C. finmarchicus*, a GLOBEC target species prominent in the zooplankton of the bank and surrounding region in spring and early summer. Egg production rates of *C. finmarchicus* have been previously studied in Canadian waters (e.g. Runge, 1985; Runge and Plourde 1996; Cabal et al. 1997), but not with the same comprehensive, spatial-temporal coverage offered by the Georges Bank program. We apply to the April and May broad-scale surveys a method for determination of *Calanus* egg production rates from preserved samples, yielding for the first time 2-D spatial maps of depth-integrated production over the entire bank. To evaluate the role of *Calanus* production, egg production of other dominant copepod species during broadscale surveys was also estimated.

The egg production rate (eggs $m^{-2}d^{-1}$) not only contributes fundamentally to the establishment of recruitment into copepod populations but also represents an index of the productivity of the prey field for fish larvae, which eat mostly copepod early life stages (eggs, nauplii and early copepodites). We argue here that spatial/temporal change in depth-integrated total production is a significant source of variability that influences growth and ultimately survival of fish larvae, and that variation in *Calanus* production may determine the magnitude of the interannual variation in total copepod production. Years of high survival of larvae may correspond to years of unusually higher abundance and subsequent reproduction of *C. finmarchicus* females.

METHODS

Copepod egg production rates were measured by direct observation (Runge 1985) during process cruises. Zooplankton was typically captured in the early afternoon with a 1-m diameter ring net towed at low speed either vertically or obliquely from near bottom to the surface. The catch was diluted into gallon jars containing filtered seawater maintained at a temperature close to ambient at 10 m. Female copepods for egg laying observations were immediately sorted (within 1 h. of capture for *C. finmarchicus* and within 2-3 h. for other species) under a binocular microscope. Forty *C. finmarchicus* females were placed individually into polystyrene petri dishes (50 ml capacity) containing filtered sea water. The dishes were kept in a 12h dark:12 h dim light, controlled temperature incubator at a temperature approximating ambient at 10 m. They were inspected at approx. 8 h intervals for the presence of eggs, which were counted and removed. Daily egg production rate was calculated from the total number of eggs produced in 24 h divided by the total number of incubated females. A more variable number (20-60) of females of other broadcast copepod species (*Temora longicornis*, *Centropages typicus*, *C. hamatus*) were incubated individually for 24 h in 45 ml tissue culture flasks filled with ambient, 73-µm screened seawater collected at the chlorophyll maximum. Eggs of these species were counted either immediately after incubation or were preserved in the flasks with 4% formaldehyde and counted later in the laboratory. Egg production of *Pseudocalanus* spp, which lay eggs in clutches attached to females until hatching, were estimated from the number of eggs produced during the incubation of 6-12 females in 4-6 replicate 45-ml flasks filled with ambient, screened seawater from the chl. max.

The female abundance of these copepod species were estimated from preserved samples taken during broadscale cruises. Tows of the water column at each broadscale station (Fig. 1) were usually made in three depth intervals with a 1-meter MOCNESS fitted with 150 µm mesh nets. Female concentrations were determined for depth interval, then integrated to obtain the density per m^2. At some stations, due to weather or equipment problems, an oblique bongo tow was substituted. Because of their small size, *Oithona* females were counted only at the higher level priority stations. The maximum observed density of *Oithona* females during each broadscale survey was used to estimate their abundance at the lower priority stations.

An index of *C. finmarchicus* egg production (the reproductive index) was determined at each broadscale station for each survey and for each direct observation of egg laying conducted during process cruises. The reproductive index is the frequency of females in the population containing oocytes that have commenced secondary vitellogenesis. Females in a subsample (n = 30) from the preserved net tow catch (either broadscale survey samples or a preserved portion of the catch from live tows during process cruises) were staged using criteria used for identification of stages of oocyte maturity described in Runge (1987).

For estimates of dry and carbon mass, individual *Calanus* females (n = 12-24) were sorted from a live tow at each station, measured for prosome length, rinsed in distilled water and stored on preweighed tin boats in a dessicator on ship. Upon return to shore, the samples were dried at 70° C for 36-48 h and measured for dry weight on a Cahn microbalance. These same females were then combusted in a Perkin Elmer CHN Elemental Analyser for carbon mass. Diameters of formaldehyde-preserved, *Calanus* eggs obtained from direct observations were measured under a light microscope. Egg carbon mass was calculated from the relationship between egg volume and carbon described in Kiorboe et al. (1985).

RESULTS

Egg production of *C. finmarchicus*

Direct observations during process cruises indicate that *C. finmarchicus* released eggs throughout the winter-spring period. Excluding two measurements in the Great South Channel (west of Georges Bank) in June which likely represent a different population in diapause, egg production rates varied between 11-77 eggs female^{-1} d^{-1}. Egg production in terms of daily percentage of body carbon per day, which takes into account seasonal changes in body carbon (90-200 µg C female^{-1}) and slight changes in egg carbon (0.20 - 0.24 µgC egg^{-1}) mass, varied between 1.3 and 12.3 % d^{-1} (Fig. 2). The monthly (i.e. per process cruise) median rate varied by a factor of two, from 5.5% d-1 in January to 8% d-1 in June. The overall median, weight-specific rate was 7.2 % d^{-1} (n = 66).

The direct observations of C. *finmarchicus* egg production rate were used to calibrate its reproductive index, determined from females sorted and preserved at the start of 60 of the 68 shipboard incubations. The relationship is highly significant ($p < 0.01$), with a correlation coefficient (r^2) of 0.74 (Fig. 3). This provides a means for estimation of C. *finmarchicus* egg production rate from the preserved samples obtained during the broadscale cruises. At each broadscale station, the reproductive index is determined from a subsample of C. *finmarchicus* females (typically 30). Female carbon mass is estimated from a relationship between prosome length (mm) and carbon (µg): $\ln(\text{body C}) = 3.04 \ln(\text{prosome length}) + 1.97$ ($r^2 = 0.60$) and egg mass is assumed to be constant at 0.23 µg C. With this information, it is possible to map both the spatial variation in female-specific egg production across the bank and the depth-integrated daily input of C. *finmarchicus* eggs into the water column (eggs $m^{-2} d^{-1}$), as described below.

Egg production rates of other copepod species

In addition to C. *finmarchicus*, six copepod species (or species groups) were predominant on Georges Bank (Table 1). The egg production rate of four species was measured at a variable number of stations during process cruises. Presented here are the median rate and range for each of these species during the April-early June cruises (Table 1). Median rates varied from 4 (*Pseudocalanus* in early April) to 100 (C. *typicus* in early June) eggs (nauplii) female^{-1} d^{-1}. The carbon mass of an individual egg (from data summarized by Kiorboe and Sabatini, 1995) varies with species from approx. 8% (*Oithona*) to 80% (*Metridia*) of the mass of a *Calanus* egg .

Daily production of copepod eggs on the southern flank

The daily total production (TP, in terms of mg C $m^{-2}d^{-1}$) of copepod eggs is determined from:

$$TP = \sum F_i \, Ep_i \, c_i / 1000$$

where F_i is the abundance of females of species i (females m^{-2}), Ep is the female-specific egg production rate (eggs female^{-1} d^{-1}) and c is the carbon mass of an egg of species i (µg C egg^{-1}). The TP was calculated for each station in broadscale surveys in April and May. The Ep of C. *finmarchicus* was obtained from the reproductive index measured at each station. For the other species, egg production was estimated from process cruises or from other regions (Table 1) and was assumed constant across the bank.

From the TP data, geostatistical analysis (Kriging Toolbox for MATLAB, Y.Gratton, INRS) was used to generate spatial maps (not shown here) of copepod production in April and May. In both months, total production varied by 2 orders of magnitude across the bank. In April, production estimates ranged from 1 (Sta. 14: see Fig. 1) to 88 (Sta. 35), with a median of 18 mg C $m^{-2}d^{-1}$. In May, estimates ranges from 1 (Sta. 16) to 220 (Sta. 34), with a median of 21 mg C $m^{-2}d^{-1}$. Very low values (the TP "hole") were observed on the crest and interior of the northeast peak with an extension onto the southern flank. The highest values occurred in the west and northwest of the region surveyed. Hence there was a gradient in TP from west to east and from north to south on the bank. The total production at representative stations on the southern flank is shown in Fig. 4

Overall, C. *finmarchicus* contributed approx. 50% to the total daily egg production in April and May. On the southern flank, C. *finmarchicus* production made up between 20% and 80% of the total (Fig.4). Spatial mapping shows a strong resemblance between the patterns of *Calanus* and total production across the bank, particularly the zone of low production on the crest and northeast peak and the zone of high production on the bank's northwest margin.

DISCUSSION

These results show the potential for substantial spatial variation in total copepod egg production on Georges Bank. In April-May, TP varied by approx. two orders of magnitude. The variation was structured in clearly demarcated zones of high (Western Bank/Franklin Basin) and low (Crest/NE Peak/SE Flank) production. The range of values (1-200 mg C $m^{-2}d^{-1}$) is similar to total production observed in May on Dogger Bank, a productive fishing ground in the southern North Sea (Nielsen and Sabatini 1996) and the only other location where TP has been similarly determined.

The egg production of *Calanus finmarchicus* was a dominant component, contributing about 50% to the overall total production. In general, the spatial pattern of *Calanus* production, showing a northwest to southeast gradient and prominent hole on the bank crest, was also reflected in the spatial pattern of total production. This dominance derives in part from the tremendous capacity of *C. finmarchicus* to produce and sustain egg production, given sufficient nutrition relative to other copepod species (Runge 1988). On the southern flank, the impact of low *Calanus* production was moderated somewhat by the production of other species, particularly *Pseudocalanus*.

We expect a relationship between variation in population egg production and spatial/temporal patterns of recruitment into *Calanus* population(s) on the Bank. Pulses and patches of young *Calanus* may derive from the zones of high and low production. In 1995, the northern and western parts of the bank, notably Georges Basin and the Fundian Channel were potential sources of recruitment. The central crest region of the bank as well as the Great South Channel in late spring/early summer were clearly zones of low recruitment. The Great South Channel contains large numbers of *Calanus* in early summer, but females were not feeding or reproducing and appeared to be in diapause.

The nauplii that hatch from copepod eggs constitute primary prey items for fish larvae. Hence, the same factors that influence *Calanus* recruitment also have potentially important implications for the growth and survival of fish larvae. Spawning of cod and haddock normally occurs on the northeast peak between Feb. and April The eggs drift and hatch along the southern flank corridor and larvae attain highest concentrations along the southern flank in April and May (Lough and Potter 1993). Our observations show that total egg production in 1995 was relatively low along this portion of the Bank There was a gradient in TP on the southern flank, showing low prey production on the east but increasing toward the western end of the bank, indicating that food conditions for larvae improved as the larvae drifted to the southwest.

There is very little knowledge about interannual variation in both the magnitude and spatial structure of total and *Calanus* egg production. Are there large interannual differences in mean depth-integrated production? Are the gradient in production from the northwest to the southeast bank and the TP hole on the northeast peak persistent interannual features in April-May on Georges Bank? We suggest here that they are not;

and that the pattern and magnitude of total egg production on Georges Bank is highly variable from year to year. If a high abundance and sufficient nutrition for *Calanus* females is set up in some years on the northeast peak and southern flank, food conditions for fish larvae could increase by an order of magnitude or more, with consequent dramatic improvement in their growth and survival.

The methods we have presented here for estimation of TP require further development and refinement. The potential for spatial variation in egg production of copepod species other than *Calanus* needs investigation. A study of spatial variation in the abundance of *Oithona* females is needed to confirm that this species is not a major contributor to TP, similar to findings of Nielsen and Sabatini (1996) in the North Sea. Finally, some females release eggs into the water column where they develop and hatch (e.g. *Calanus, Centropages, Temora*) whereas others (e.g. *Pseudocalanus, Oithona*) carry eggs until hatching. The mortality regime for each of the two egg laying strategies is potentially very different. These mortality differences may alter the patterns of copepod recruitment and prey availability to fish larvae in ways not predictable by measurement of the egg production rate alone.

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Table 1. Median egg production rate (eggs female^{-1}d^{-1}) of four predominant copepod species (excluding *C. finmarchicus*) on Georges Bank in 1995, measured by shipboard incubation during process cruises EN264 (26Mar-7 April), EN266 (26 Apr- 9 May) and EN267 (22 May-5 Jun). Range of values (n = 1-15, depending on species and cruise) in parentheses. Estimated egg production rate (eggs female^{-1}d^{-1}) for broadscale survey stations EN265 (11-22 Apr) and AL9505 (9-18 May). *Metridia* rate from unpublished data, Gulf of St. Lawrence : *Oithona* rate from Nielsen and Sabatini 1996). Egg mass from Kiorboe and Santini (1995).

Species	**EN264**	**EN265**	**EN266**	**AL9505**	**EN267**	**Egg mass (µg C)**
Pseudocalanus sp.	8 (6-10)	7	4 (3-7)	7	6 (2- 9)	0.14
Temora longicornis	46	59	58 (20-72)	67	83 (80-87)	0.04
Centropages typicus	32 (24-33)	60	61 (60-62)	90	101 (73-128)	0.04
Centropages hamatus	-	67	67 (65-68)	60	51 (46-68)	0.04
Metridia sp.	-	50	-	50	-	0.18
Oithona spp.	-	2.3	-	2.3	-	0.02

FIGURES

Fig. 1. Georges Bank, showing location of broadscale survey stations. Priority indicates level of zooplankton sampling and analysis. Copepod female abundance was estimated at all stations. Solid line shows coastline of Massachusetts (USA).

Fig. 2. Egg production rate (% of female body carbon d^{-1}) of *Calanus finmarchicus* on Georges Bank, 1994-1995 process cruises. Crest is region within 60 m isobath (refer to Fig. 1). Georges Basin is region north of the bank, near broadscale Sta. 29. Great South Channel refers to channel west of the bank, near broadscale Sta. 1. Northeast Peak is the northeast region of bank in water depth of 60-100 m., near Sta. 20-23. Southern flank refers to 60-100 m water along the southern corridor of the bank, near Sta. 3, 6, 8 and 9.

Fig. 3. The relationship between *C. finmarchicus* egg production rate measured by shipboard incubation during process cruises and the reproductive index (Stages 4-7, according to criteria described in Runge, 1987) determined from females preserved from the same live catch. Filled circles show results from Great South Channel.

Fig. 4. The relative contribution of the dominant copepod species to total egg (nauplii) production (mg C $m^{-2}d^{-1}$: number in panel) on the southern flank of Georges Bank during broadscale cruises in April (EN265) and May (AL9505), 1995. See Fig. 1 for station locations.

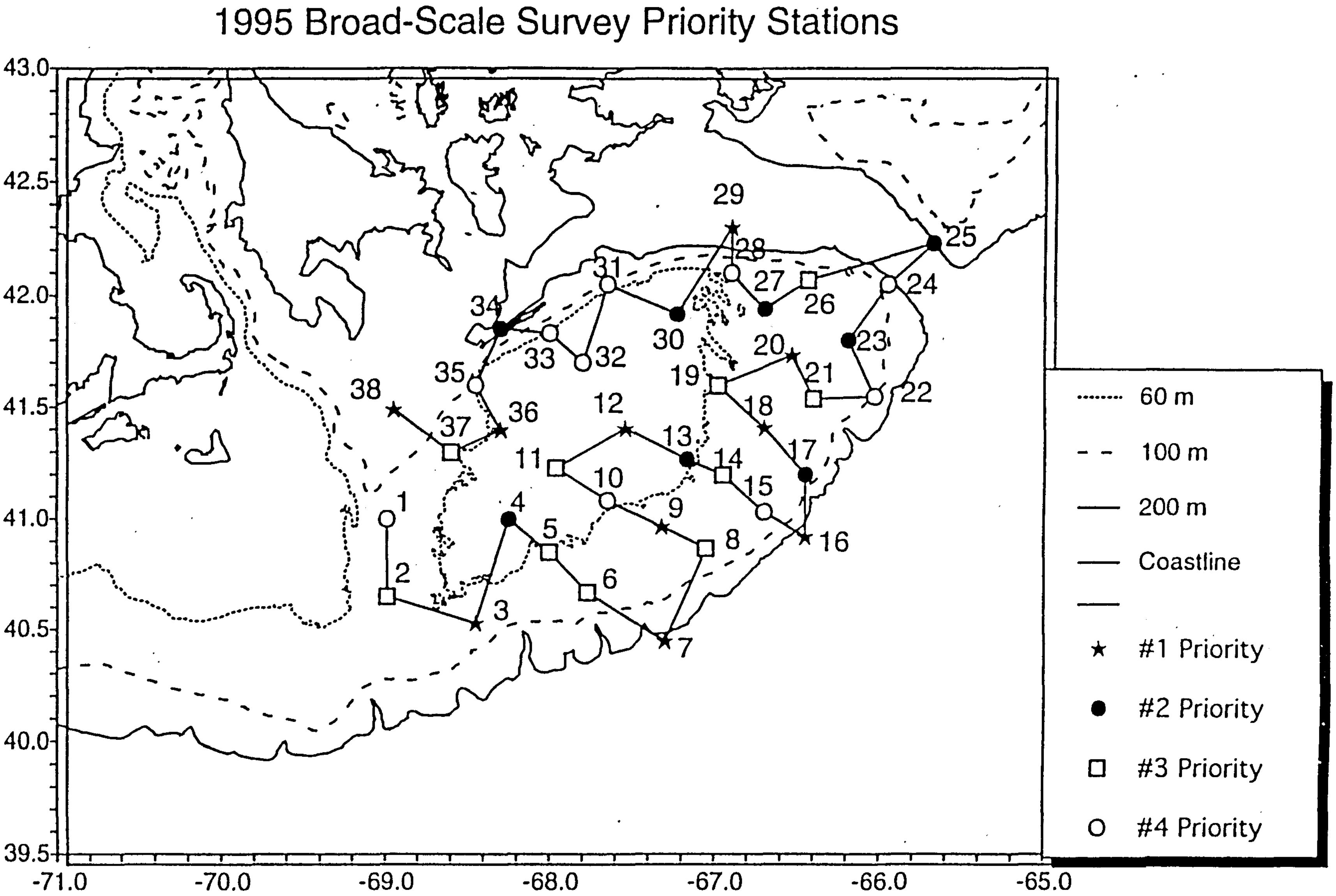
1995 Broad-Scale Survey Priority Stations
43.0
42.5
42.0
41.5
41.0
40.5
40.0
39.5
-71.0
-70.0
-69.0
-68.0
-67.0
-66.0
-65.0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
60 m
100 m
200 m
Coastline
#1 Priority
#2 Priority
#3 Priority
#4 Priority

Fig. 1

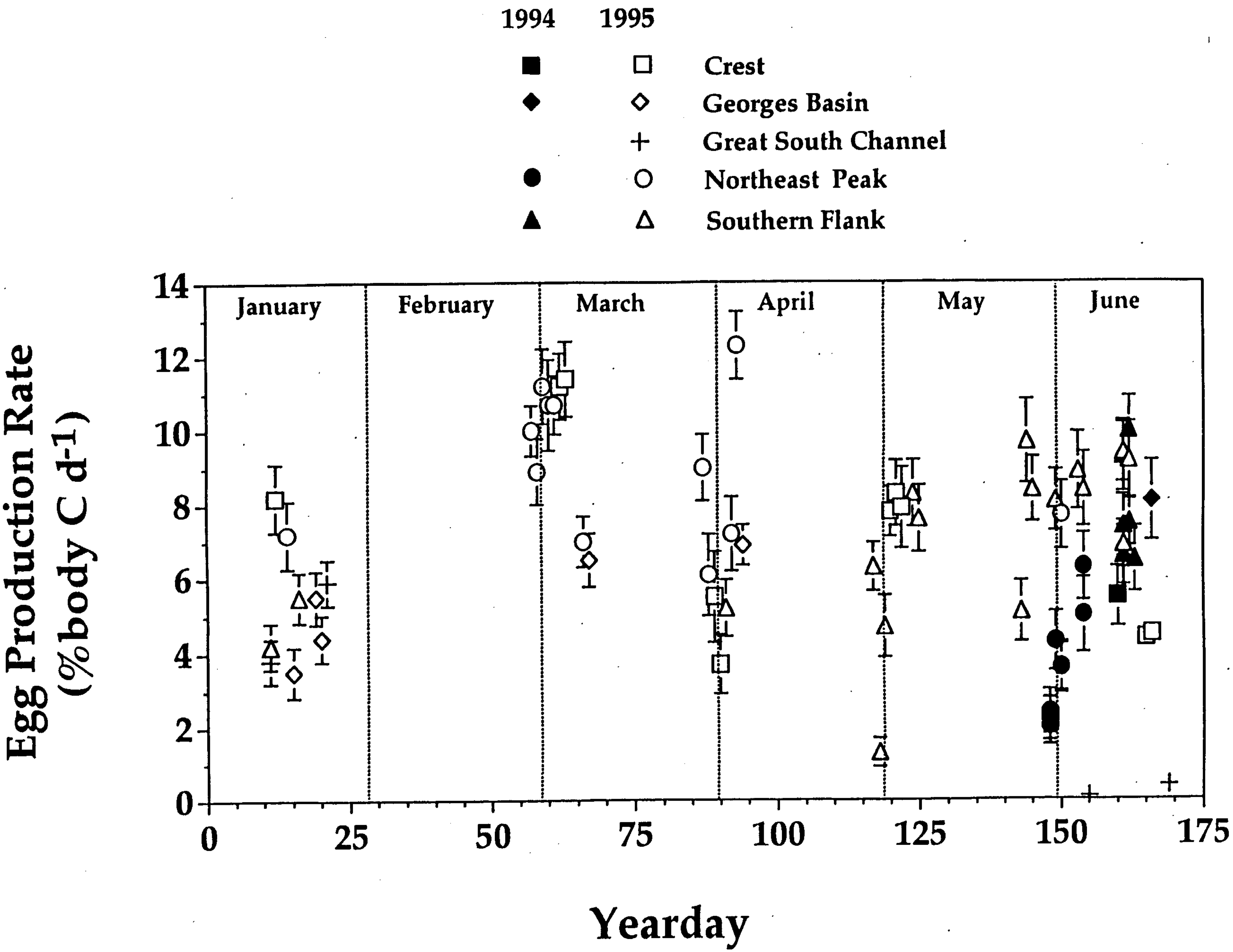
1994 1995
■ □ Crest
◆ ◇ Georges Basin
+ Great South Channel
● ○ Northeast Peak
▲ △ Southern Flank
January
February
March
April
May
June
Egg Production Rate (%body C d-1)
0
2
4
6
8
10
12
14
0
25
50
75
100
125
150
175
Yearday

Fig. 2

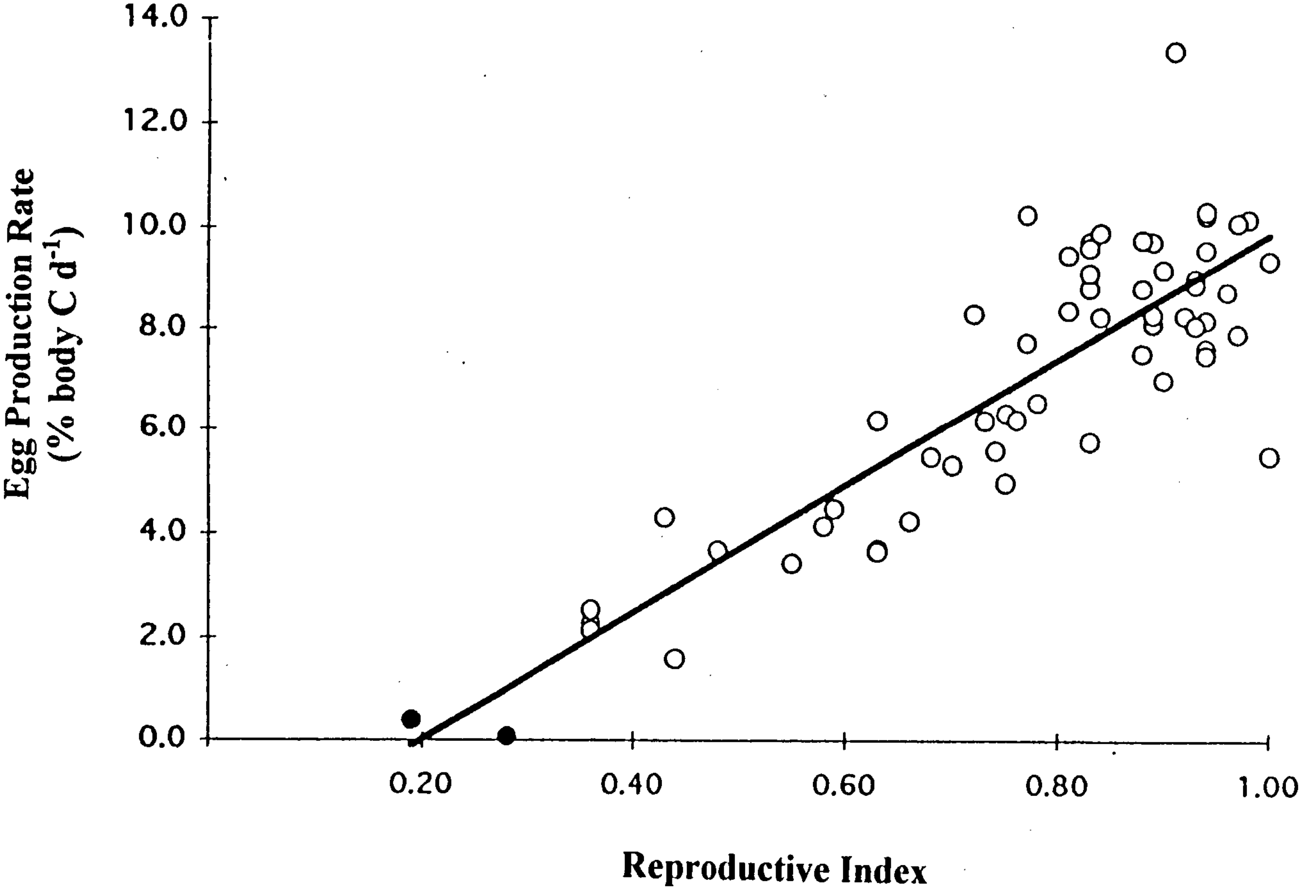
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Egg Production Rate
(% body C d^{-1})
0.20
0.40
0.60
0.80
1.00
Reproductive Index

Fig. 3

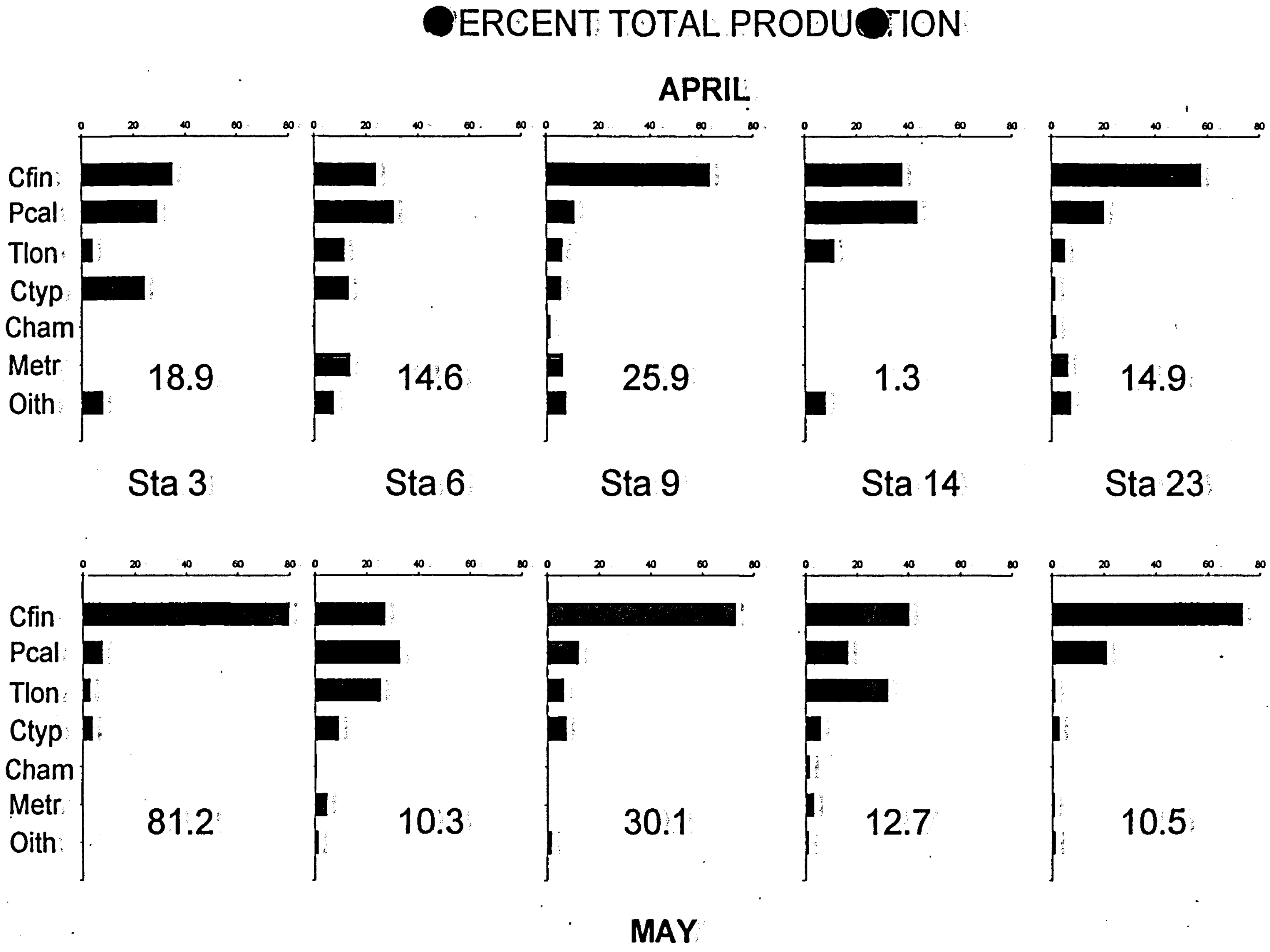
PERCENT TOTAL PRODUCTION
APRIL
0
20
40
60
80
Cfin
Pcal
Tlon
Ctyp
Cham
Metr
Oith
18.9
14.6
25.9
1.3
14.9
Sta 3
Sta 6
Sta 9
Sta 14
Sta 23
81.2
10.3
30.1
12.7
10.5
MAY

Fig. 4