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Copepod production drives recruitment in a marine fish

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Abstract

Predicting fluctuations in recruitment of marine fish remains the Holy Grail of fisheries science[1-4]. In previous studies, we identified statistical relationships linking Atlantic mackerel recruitment to regional climate, zooplankton biomass and the production of copepod nauplii over a decade that included the exceptionally strong year class of 1982 [5,6]. Here we tested the validity of these relationships by adding a second decade of observations that includes another exceptional year class in 1999. We provide the first field-based evidence linking the availability of plankton prey[6-8] in the sea to early growth of larval fish and ultimately to year-class strength in a commercially exploited marine fish. Recruitment can be anticipated three years in advance based on prey availability during larval stage. We predict a strong mackerel year class in 2006.

Hjort's[9] seminal hypothesis that the abundance of fish cohorts (i.e., year classes) is determined during early larval life in the plankton still prevails[1,10,11]. Availability of adequate prey in the weeks after hatching is considered necessary for a strong year class to emerge[12-14]. However, empirical evidence of the role of prey availability in driving fluctuations in year-class strength has remained elusive[15]. Most studies that attempted to link recruitment to environmental conditions focused on abiotic factors such as temperature or salinity[2,16,17]. Statistical links between prey availability and recruitment success[5,12,18] remain few and often fail when re-tested with longer time series[2]. The impacts of feeding conditions in the plankton on recruitment are particularly difficult to elucidate due to (1) an often low spatial and temporal sampling resolution; (2) imprecision in the identification of the actual prey of the larvae; and (3) relatively little contrast between the weakest and strongest year classes in some fish stocks/species. Atlantic mackerel (*Scomber scombrus*) represents an ideal model to study the effect of prey availability during larval life on recruitment because it exhibits high interannual variability in year-class strength and completes spawning over a short time interval (<1 month) in a well-defined area (southern Gulf of St. Lawrence), facilitating sampling of the larvae and their prey[19].

The exceptionally strong mackerel recruitment of 1982 occurred during a year of atypical abiotic and biotic conditions in the southern Gulf of St. Lawrence. Winter–spring freshwater discharge from the St. Lawrence River into the Gulf, an index of climate variability in eastern Canada termed RIVSUM[20], was particularly low, while the biomass of large (>1000 μm) zooplankton was the highest of the decade[5]. The latter was considered a proxy of the abundance of *C. finmarchicus* females with the underlying assumption that the abundance of eggs and nauplii of this species dictate larval mackerel survival[5,21]. The abundance of *C. finmarchicus* females in 1982 was the greatest of the 1982-1991 period, and stomach contents of mackerel larvae during that year were significantly heavier largely due to a greater ingestion of *C. finmarchicus* nauplii[6].

The following decade of data (1992-2003) included a second year of exceptional mackerel recruitment in 1999. As in the strong year class of 1982, low RIVSUM and high zooplankton biomass prevailed in the southern Gulf of St. Lawrence in 1999. Despite these similarities between the two years of extreme recruitment, only two of the three relationships linking year class strength to climate and zooplankton identified by Runge *et al.*[5] for the decade 1982-1991 remained significant with the addition of new data for 1992-2003 (Fig. 1). The relationship between recruitment strength and RIVSUM became non significant (Fig. 1d), while the once strong relationship between recruitment and zooplankton biomass >1000 μm weakened, explaining only 21% of the variance of the expanded data set (Fig. 1f). Statistical relationships linking recruitment to broad indices of the environment such as temperature, salinity or total zooplankton biomass often subside when re-tested with longer time series[2]. In this study, the weakening of the recruitment−zooplankton biomass relationship is likely attributable to changes in the relative abundance of large copepods between the two decades (Fig. 2). From the 1980s to the 1990s, the contribution of the large arctic calanoid *Calanus hyperboreus* to zooplankton biomass doubled. *C. hyperboreus* typically reproduces from mid December to March in the Gulf of St. Lawrence and therefore does not contribute to the production of nauplius prey during the period of mackerel larval growth in summer[22]. Hence inter-decadal shifts in the relative abundance of this large copepod will seriously bias total zooplankton biomass as a proxy for the availability of nauplius prey to mackerel larvae.

The above emphasizes the importance of focusing on the actual zooplankton prey of larvae in trying to link recruitment variability to fluctuations in ecosystem productivity. In the Gulf of St. Lawrence, mackerel larvae prey selectively on the nauplii of the copepods *Calanus finmarchicus*, *Pseudocalanus* spp. and *Temora longicornis*[6-8], the availability of which is approximated by the number of eggs spawned by females (Fig. 3a). A strong linear relationship linked year-class strength to the combined egg production of the three species (Fig. 3b). The exceptional recruitment of 1982 and 1999 corresponded to the highest egg production, ~1 $\mu g\ C\ L^{-1}\ d^{-1}$, by the three preferred copepods.

High prey availability is assumed to promote early survival and recruitment through the optimization of food intake and growth during larval life in the plankton[12,14]. In the southern Gulf of St. Lawrence, feeding success and recent growth of young mackerel larvae increased hyperbolically as a function of the density of their preferred nauplius prey (Fig. 4). Optimal feeding (Fig. 4a) and growth (Fig. 4b) were achieved above a threshold concentration of preferred nauplius prey of ~1 μg C L^{-1}. Taken altogether, these results provide the first field-based evidence linking the availability of actual plankton prey to early growth and, ultimately, to year-class strength in a commercially exploited fish.

Our results provide support for a strong dependence of year-class strength on food production during the larval stage, as postulated by prevailing hypotheses on recruitment determination in marine fish[9,12-14]. In contrast with many previous studies including ours, this dependence was revealed by measuring the production *in situ* of the actual prey species selected by the young fish (rather than bulk zooplankton standing biomass). On the basis of the measured high production of copepod eggs (> 1 μg C L^{-1}), we dare predict exceptional mackerel recruitment in 2006.

Methods

Since 1982, Atlantic mackerel reproductive biomass in Canada has been estimated annually (except 1994 and 1997) by measuring egg abundance on the main spawning site during peak spawning in late June[19]. A Bongo net (61 cm diameter) fitted with 333 μm mesh and flow meters is deployed at 65 stations over a fixed grid covering the southern Gulf of St. Lawrence. Double-oblique tows are conducted between 0 and 50 m to sample fish eggs and larvae, and zooplankton. Zooplankton biomass is measured for the size fractions <1000 μm (mainly small copepods) and >1000 μm (mainly late copepodites of *Calanus* spp.). The relationships between recruitment success and zooplankton biomass for 1982-1991, the mackerel recruitment index MACREC and details of methods are presented in Runge *et al.*[5]. Data on zooplankton stage abundance and egg production are from Ringuette *et al.*[6] for 1982, 1985, 1987 and 1990 and from new analyses for 1988, 1993, 1996, 1999, 2000, and 2003. Years were selected to span the two decades evenly while including the strong year classes of 1982 and 1999.

The sampling of mackerel larvae and their prey in the northeastern part of the spawning ground for feeding selectivity and otolith microstructure analyses is detailed in previous studies[8,23]. First-feeding larvae were defined as individuals with standard lengths of 3-5 mm (ages 3-7 days). Young larvae in this area selected *Pseudocalanus* spp. nauplii almost exclusively. Feeding success was defined as the residual value of the regression of *Pseudocalanus* spp. nauplius prey carbon in larval stomachs on larval mackerel length to compare feeding among larvae of different sizes. A detrended recent growth index (last 3 days prior to capture) was computed following Pepin *et al.*[24] to compare growth among larvae of different ages. Feeding success and recent growth were averaged by net tow to avoid inflating degrees of freedom.

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Figure legends

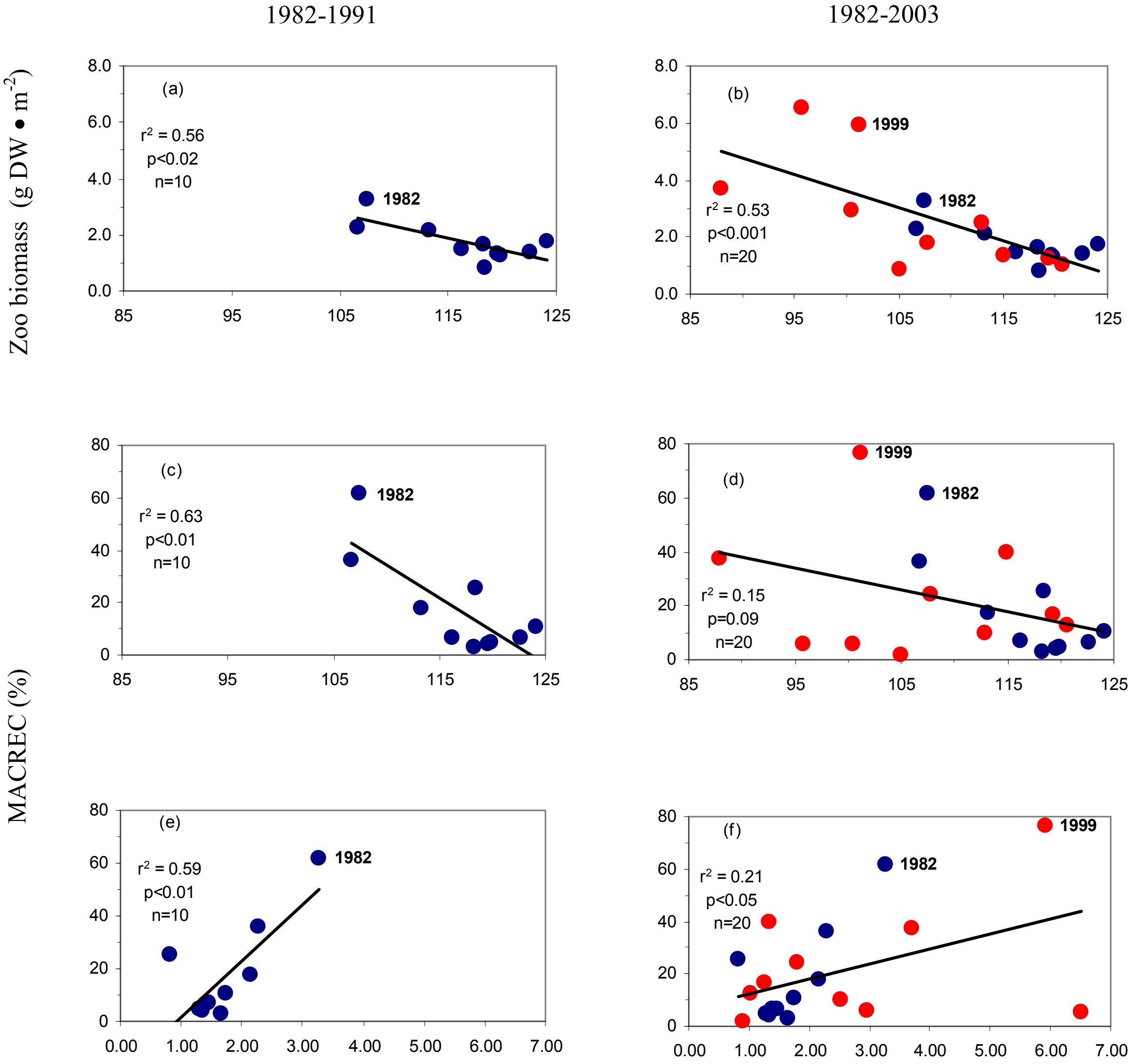
Figure 1. Environmental relationships, zooplankton, and mackerel recruitment for 1982-1991 (left) and 1982-2003 (right). Regressions of zooplankton biomass >1000 µm (g dry weight m^{-2}) (a, b), and of mackerel recruitment index (MACREC, i.e., % of age 3 fish in Canadian catch-at-age) (c, d), versus an index of climate variability (RIVSUM, i.e., January-May freshwater discharge from the St. Lawrence River into the Gulf of St. Lawrence). Lower panels (e, f) show regressions of MACREC against zooplankton biomass >1000 µm. Blue circles represent 1982-1991 data while red ones show 1992-2003 data (1995 and 1997 missing); 1982 and 1999 are highlighted. Coefficient of determination (R^2), level of significance and sample size are reported.

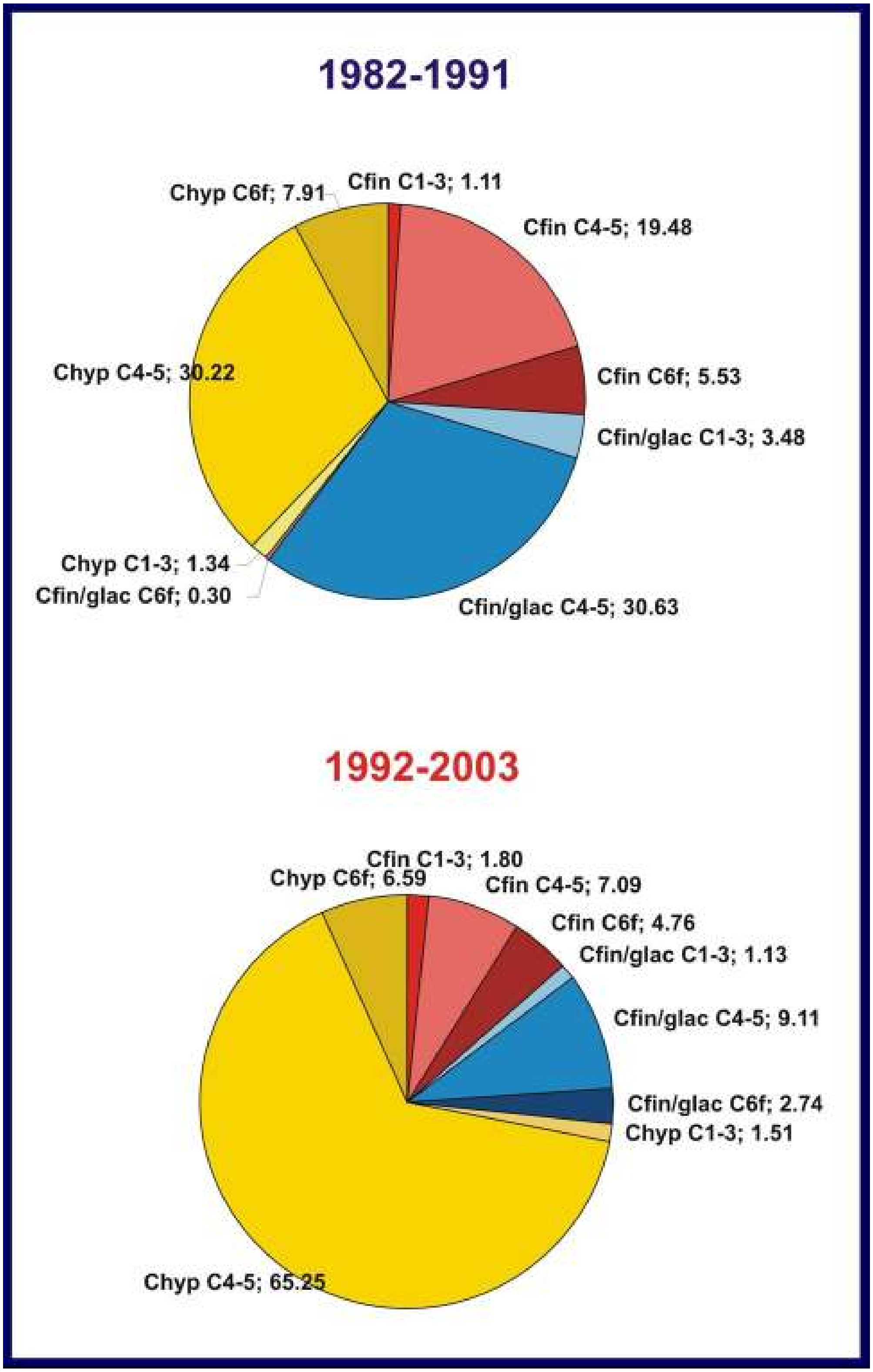
Figure 2. Composition (%) of zooplankton biomass in the >1000 µm fraction in the southern Gulf of St. Lawrence for two time periods. Chyp=*Calanus hyperboreus;* Cfin/glac=*Calanus finmarchicus/glacialis;* C1-3=copepodite stages 1 to 3; C4-5=copepodite stages 4-5; C6f=copepodite stage 6 and females. *C. glacialis* was grouped with *C. finmarchicus* because these species were not differentiated in the 1982-1991 samples. However, *C. glacialis* abundance typically represents < 5% of the *C. finmarchicus* abundance in the region.

Figure 3. (a) Daily egg production rates for the copepods *Calanus finmarchicus*, *Pseudocalanus* spp. and *Temora longicornis* in the southern Gulf of St. Lawrence for

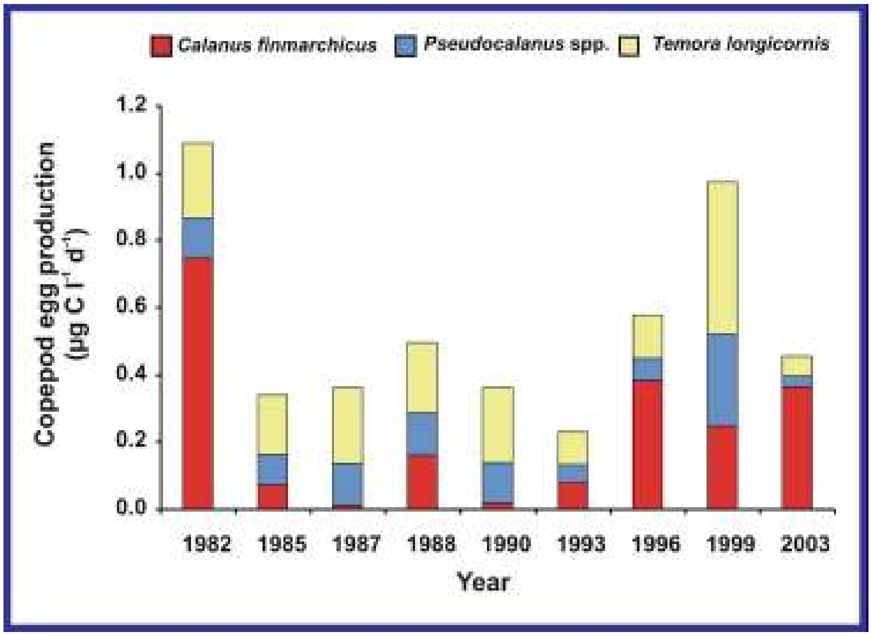
selected years. Rates were calculated as the product of mean female abundance and specific egg production rates to obtain an estimate of prey production[6]. (b) Regression of mackerel recruitment (MACREC) as a function of copepod egg production as presented in (a). Blue circles: 1982-1991; red circles: 1992-2003. Years of exceptional recruitment in 1982 and 1999 are highlighted. Coefficient of determination (R^2), level of significance, and sample size are reported.

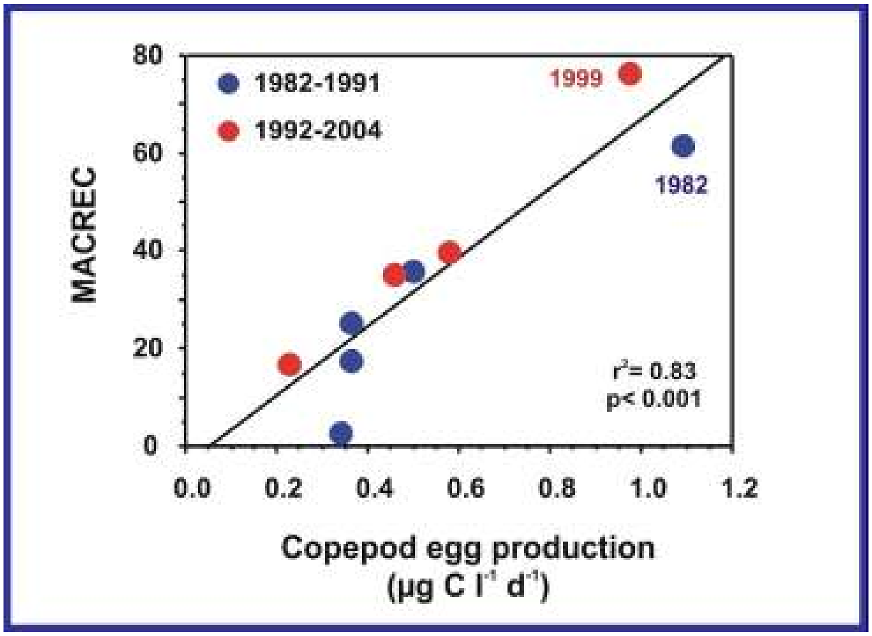
Figure 4. (a) Feeding success and (b) recent 3-day mean growth rate of mackerel larvae in relation to the density of the preferred prey *Pseudocalanus* spp. nauplii. Individual feeding success and growth were averaged per net tow. Ivlev functions[25] were fitted with a statistical weight corresponding to the inverse standard deviation. Measurements were made between 1997 and 2000. Equations of Ivlev functions are (a) $y = 1.099 (1-e^{-0.0015x}) - 0.585$, and (b) $y = 1.909 (1-e^{-0.0018x}) - 1.38$.

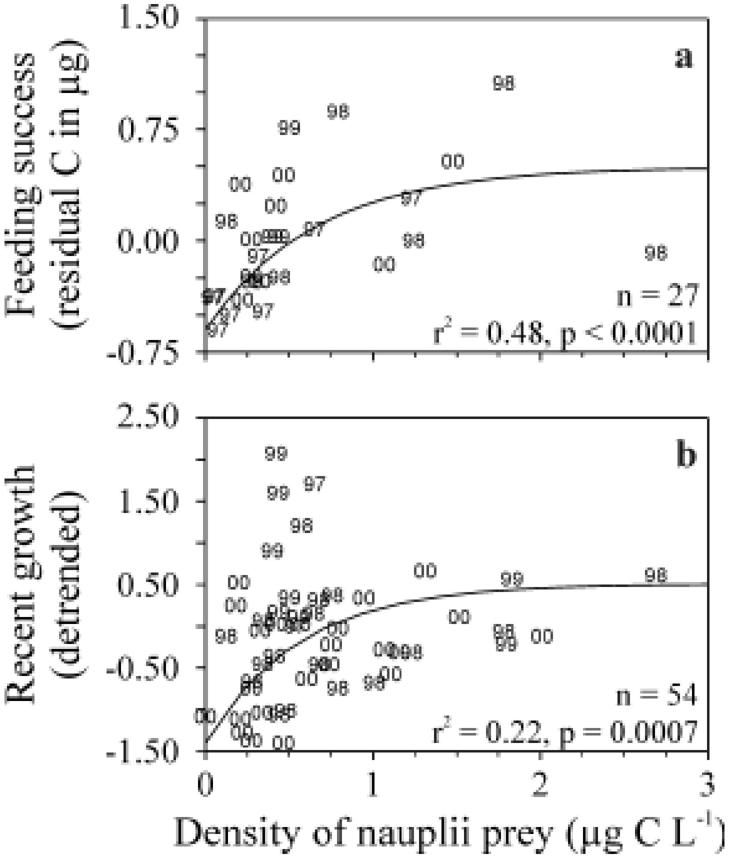

1982-1991
1982-2003
Zoo biomass (g DW • m-2)
MACREC (%)
(a)
r2 = 0.56
p<0.02
n=10
1982
8.0
6.0
4.0
2.0
0.0
85
95
105
115
125
(b)
1999
1982
r2 = 0.53
p<0.001
n=20
(c)
r2 = 0.63
p<0.01
n=10
1982
80
60
40
20
0
(d)
1999
1982
r2 = 0.15
p=0.09
n=20
(e)
r2 = 0.59
p<0.01
n=10
1982
0.00
1.00
2.00
3.00
4.00
5.00
6.00
7.00
(f)
1999
1982
r2 = 0.21
p<0.05
n=20


1982-1991
Chyp C6f; 7.91
Cfin C1-3; 1.11
Cfin C4-5; 19.48
Chyp C4-5; 30.22
Cfin C6f; 5.53
Cfin/glac C1-3; 3.48
Chyp C1-3; 1.34
Cfin/glac C6f; 0.30
Cfin/glac C4-5; 30.63
1992-2003
Cfin C1-3; 1.80
Chyp C6f; 6.59
Cfin C4-5; 7.09
Cfin C6f; 4.76
Cfin/glac C1-3; 1.13
Cfin/glac C4-5; 9.11
Cfin/glac C6f; 2.74
Chyp C1-3; 1.51
Chyp C4-5; 65.25

213


Calanus finmarchicus
Pseudocalanus spp.
Temora longicornis
Copepod egg production
(μg C l⁻¹ d⁻¹)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1982
1985
1987
1988
1990
1993
1996
1999
2003
Year


MACREC
80
60
40
20
0
1982-1991
1992-2004
1999
1982
r² = 0.83
p< 0.001
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Copepod egg production
(μg C l⁻¹ d⁻¹)


a
Feeding success (residual C in µg)
1.50
0.75
0.00
-0.75
n = 27
r² = 0.48, p < 0.0001
b
Recent growth (detrended)
2.50
1.50
0.50
-0.50
-1.50
n = 54
r² = 0.22, p = 0.0007
0
1
2
3
Density of nauplii prey (µg C L⁻¹)