

1 **Interannual differences in larval haddock survival: hypothesis testing**  
2 **with a 3D biophysical model of Georges Bank**

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24 **ABSTRACT**

25 The ultimate goal of early life studies of fish over the past century has been to better  
26 understand recruitment variability. As evident in the Georges Bank haddock  
27 (*Melanogrammus aeglefinus*) population, there is a strong relationship between  
28 recruitment success and processes occurring during the planktonic larval stage. This  
29 research sought new insights into the mechanisms controlling the recruitment process in  
30 fish populations by using biological-physical modeling methods together with laboratory  
31 and field data sets. We created the first three-dimensional model of larval haddock on  
32 Georges Bank by coupling models of hydrodynamics, lower trophic levels, a single  
33 copepod species, and larval haddock. Interactions between feeding, metabolism, growth,  
34 vertical behavior, advection, predation, and the physical environment of larval haddock  
35 were quantitatively investigated using the coupled models. Particularly, the model was  
36 used to compare survival over the larval period and the sources of mortality in 1995 and  
37 1998, two years of disparate haddock recruitment. The results of model simulations  
38 suggest that the increased egg hatching rates and higher food availability, which reduced  
39 starvation and predation, in 1998 contributed to its larger year-class. Additionally, the  
40 inclusion of temperature-dependent predation rates produced model results that better  
41 agreed with observations of the mean hatch date of survivors. The results from this  
42 biophysical model imply that food-limitation and its related losses to starvation and  
43 predation, especially from hatch to 7 mm, may be responsible for interannual variability  
44 in recruitment and larval survival outside of the years studied.

45

46 *Keywords:* larval fish, individual-based model, recruitment, GLOBEC

47 **INTRODUCTION**

48 The annual variation in year-class size of a fish population can greatly influence the  
49 biomass of the population that can be fished (Trippel & Chambers, 1997). Despite its  
50 importance, the causes of recruitment variability are not clear, and understanding  
51 recruitment variability has long been a goal to aid in the management of fisheries. Since  
52 Hjort's (1914) hypothesis that the size of a year-class is determined during the early life  
53 stage of fish, much emphasis has been placed on survival from the egg to the early  
54 juvenile stage. The haddock, *Melanogrammus aeglefinus*, population on Georges Bank  
55 (Fig. 1) has the classic dependence on intense but sparse recruitment years and also is  
56 known to have a strong relationship between recruitment and processes occurring during  
57 the larval stage (Mountain *et al.*, 2008).

58 Larval haddock had greater survival when mismatched (phase-shifted) to the  
59 copepod populations for the years 1995-1999 (Buckley & Durbin, 2006). By hatching  
60 before the spring bloom, haddock maximized size at time of year rather than size at age  
61 (Lapolla & Buckley, 2005; Buckley & Durbin, 2006; Buckley *et al.*, 2010). Though  
62 hatching early results in slower growth from lower temperatures, less food, and less light  
63 available for visual feeding compared to later in the year, it leads to less predation as well  
64 (Lapolla & Buckley, 2005; Buckley & Durbin, 2006; Buckley *et al.*, 2010). These  
65 findings appear to contradict the larval fish paradigms about size and survival,  
66 specifically that individuals with higher growth rates will spend less time as vulnerable  
67 larvae, particularly small larvae, with high mortality rates (Leggett & DeBlois, 1994).  
68 However, if changing climate conditions lead to higher prey availability earlier in the  
69 year (Ji *et al.*, 2008), survival of early-spawned larvae could be further enhanced. In

70 addition to seasonal prey availability and predation risk, advection could be important in  
71 regulating the recruitment of haddock. Advective loss of larvae or their planktonic  
72 copepod prey could occur early in the spawning period before the gyre has strengthened  
73 with seasonal stratification (Butman & Beardsley, 1987), as well as from Gulf Stream  
74 rings (Butman *et al.*, 1982; Flierl & Wroblewski, 1985), and strong wind events (Chase,  
75 1955; Lewis *et al.*, 1994, 2001).

76         Spatially-explicit coupled biological-physical individual-based models (IBMs) are  
77 ideal for studying the processes of feeding, growth, predation, and advection during the  
78 larval stage. Such models act as laboratories where simulation experiments can be  
79 conducted to disentangle these factors, determine their relative importance, and reveal  
80 how they are affected by environmental variability. We seek to gain insights into the  
81 recruitment variability of Georges Bank haddock by using a spatially-explicit coupled  
82 biological-physical IBM to examine two disparate years sampled during the U.S.  
83 GLOBEC Northwest Atlantic/Georges Bank (GLOBEC GB) program during 1995-1999  
84 (GLOBEC, 1992; Wiebe *et al.*, 2002). The 1998 haddock year-class was the largest of the  
85 study period and the largest since 1978, until the record 2003 year-class (Brodziak &  
86 Traver, 2006) that outsized the previous record 1963 year-class. The 1998 year-class had  
87 a broad spawning period, low egg production, and the highest egg and larval survival  
88 rates of the five GLOBEC study years (Buckley & Durbin, 2006; Mountain *et al.*, 2008).  
89 On the other hand, 1995 was a year of low recruitment with low prey biomasses (Buckley  
90 & Durbin, 2006) resulting in food-limited growth and the condition of some first feeding  
91 haddock larvae indicative of starvation (Buckley *et al.*, 2006). In addition to recruitment,

92 both recruitment per hatched egg (Mountain & Kane, 2010) and larval abundance at 15  
93 days post hatch (Mountain *et al.*, 2008) were higher in 1998 than 1995.

94         We coupled a hydrodynamics model, a nutrient-phytoplankton-zooplankton-  
95 detritus (NPZD) model, a stage-based copepod population model, and a larval haddock  
96 IBM to simulate the processes on Georges Bank during the larval period of haddock. The  
97 model was used to compare survival over the larval period and the sources of mortality in  
98 1995 and 1998. As stated above, there are generally three hypothesized sources of larval  
99 mortality: advection, predation, and starvation. These hypotheses were tested to see if any  
100 accounted for the observed differences between 1995 and 1998. Specifically, we tested  
101 the role of hatch location and abundance, the physical environment, prey density, vertical  
102 swimming behavior, seasonal predation, spatial predation, and interannually-varying  
103 predation.

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115 **METHODS**

116 *Physical model*

117 The hydrodynamics were provided by the Finite Volume Coastal Ocean Model  
118 (FVCOM). FVCOM is a prognostic, unstructured-grid, finite-volume, free-surface, three-  
119 dimensional (3D), primitive equation coastal ocean circulation model (Chen *et al.*, 2003).  
120 FVCOM receives input from an atmospheric model (Fifth-Generation Penn State/NCAR  
121 Mesoscale Model, MM5), is driven by realistic surface and boundary forcing, and  
122 assimilates satellite and buoy data. There is a Lagrangian particle-tracking routine for  
123 FVCOM, which can be used to couple individual-based biological models (Chen *et al.*,  
124 2006; Ji *et al.*, 2012). The particle-tracking routine was run offline with FVCOM output  
125 saved every hour as the physical forcing. Preliminary tests demonstrated that daily output  
126 was too coarse and resulted in different trajectories compared to hourly, which captured  
127 the important tidal circulation on Georges Bank. Chen (1992) estimated the auto-  
128 correlation time scale of currents on Georges Bank as one hour, using 5 min ADCP data  
129 recorded in the Great South Channel. Thus, velocities at time scales shorter than one hour  
130 are coherent, and there was no need to use FVCOM flow output at a higher temporal  
131 resolution than hourly. Additionally, hourly output of FVCOM results have been applied  
132 to the Gulf of Maine and Georges Bank region (Huret *et al.*, 2007; Churchill *et al.*, 2011)  
133 and the resulting trajectories captured the general transport patterns well.

134         The saved velocities were used to calculate Lagrangian pathways by linear  
135 interpolation in space and time, with an explicit fourth order Runge-Kutta scheme and a  
136 time step of 30 s. A random walk model was applied to simulate vertical diffusion by  
137 applying the method of Visser (1997) using the FVCOM-saved vertical velocity and

138 vertical eddy diffusivity that was calculated with the Mellor and Yamada (1982) level 2.5  
139 turbulence closure model. This random walk model is sensitive to the time step, thus a  
140 smaller time step of 0.2 s was necessary for the random walk process to prevent specious  
141 particle accumulation in areas of low diffusivity. In addition to velocity and diffusivity,  
142 temperature, light, and bottom depth from FVCOM were also stored and used in the  
143 biological submodels.

144

#### 145 *Prey field*

146 Many IBMs use size-based feeding models, however it has been shown that larval fish  
147 prey selection is not purely size-based (Petrik *et al.*, 2009). Copepod prey of similar size  
148 are ingested in amounts disproportionate to their abundance in the environment (Kane,  
149 1984; Heath & Lough, 2007). In addition to its size, the behavioral properties of the  
150 copepod *Pseudocalanus* spp. make it the most preferred prey item of larval haddock  
151 (Petrik *et al.*, 2009). It is the majority of the prey biomass consumed (Kane, 1984, Lough  
152 *et al.*, 2005; Heath & Lough, 2007) and its biomass is highly correlated to larval haddock  
153 growth rate (Buckley & Durbin, 2006). As a simplification, *Pseudocalanus* spp. was used  
154 as the sole prey source to larval haddock in the coupled model. The *Pseudocalanus* spp.  
155 density was modeled with a 4-stage (eggs-nauplii-copepodite-adult) concentration-based  
156 population model (Hu *et al.*, 2008; Ji *et al.*, 2009), excluding the eggs as a prey source.  
157 The FVCOM hydrodynamics model was coupled to a NPZD model, with the flow fields,  
158 temperature, and phytoplankton serving as inputs to the copepod population model (Ji *et*  
159 *al.*, 2009). These runs were completed prior to the haddock IBM simulations, with the

160 resulting *Pseudocalanus* spp. concentrations stored every hour and used as offline prey  
161 inputs.

162

### 163 *Larval haddock IBM*

164 The following descriptions are all components in the IBM of larval haddock within the  
165 offline FVCOM particle tracking routine. These processes occurred with a time step of 15  
166 min. For complete equations and parameterizations, see the Appendix.

167

#### 168 Super-individuals

169 To simulate realistic numbers of individuals and prevent significant variation  
170 from being lost from the population, super-individuals (Scheffer *et al.*, 1995) were used  
171 to represent larvae. The number of individuals,  $n$ , within each super-individual was  
172 determined from estimated egg hatching rates calculated for the years 1995 and 1998 on  
173 Georges Bank (Mountain *et al.*, 2003, 2008). Daily estimates of egg hatching rates were  
174 spatially interpolated to a regular grid covering the sampling area (Mountain *et al.*, 2003,  
175 2008), with roughly 1955 grid nodes within the 200 m isobath used to define Georges  
176 Bank in this study. Egg hatching rates in units of  $\text{no. } 10 \text{ m}^{-2} \text{ d}^{-1}$  were converted to total  
177 number of individuals hatched per month by multiplying the rate by the area covered by  
178 that grid box and the total number of days in that month. Depending on cohort and year,  
179 this method resulted in hatching at 890-1874 of the grid cells with various numbers of  
180 individuals. The center of each grid box was the location each super-individual was  
181 released at hatch. The number of super-individuals necessary to produce stable results  
182 was tested by releasing 1, 2, or 3 super-individuals at each grid node with estimated egg

183 hatching. For each test case, the reference model (see *Simulations* section below) was run  
184 and summary metrics (see *Analyses* section below) were calculated. Data for untested  
185 numbers of particles was added to these graphs by randomly subsampling the model  
186 output with 3 super-individuals per node 100 times for each number that was not  
187 simulated. The minimum number of particles needed was equivalent to the asymptotes of  
188 the graphs of metric as a function of particle number. Asymptotes were defined as when  
189 the mean of 100 subsamples fell within one standard deviation of the results with the  
190 greatest number of particles subsampled. The simulated results and the mean results of  
191 random subsamples converged when particles  $>2250$ . The final numbers used in all  
192 simulations were  $2.67 \times 10^3 - 5.63 \times 10^3$  super-individuals with  $6.43 \times 10^5 - 2.42 \times 10^{10}$   
193 individuals per super-individual (Table 1). These amounts are similar to the numbers of  
194 particles simulated by Huret *et al.* (2007) with FVCOM in the Gulf of Maine, who  
195 independently performed a stability analysis.

196

#### 197 Foraging submodel

198 The foraging submodel (Appendix eqs. 1-16) was based on the larval fish feeding  
199 models of Caparroy *et al.* (2000) and Fiksen and MacKenzie (2002), adapted for cod by  
200 Kristiansen *et al.* (2007) and parameterized for larval haddock and *Pseudocalanus* spp.  
201 by Petrik *et al.* (2009). Ingestion was the product of encounter rate and the probability of  
202 successful capture. Encounter rate was a function of prey density, prey swimming speed,  
203 turbulent velocity, larval fish pause duration and frequency, and larval perception  
204 distance (dependent on light and larval size). The probability of successful capture was an  
205 empirical function of copepod species (*Pseudocalanus* spp.) and developmental stage

206 length parameterized from mechanistic simulations of species-specific copepod escape  
207 behaviors, including the deformation rate threshold, escape jump speed, and escape jump  
208 angle. The species-specific prey characteristics were also size-specific, however size was  
209 not a state variable in the copepod population model. As a first approach, the length,  
210 width, and biomass of a grouped developmental stage (e.g. nauplii) was set as the mean  
211 of all stages within that group (e.g. mean of NI-NVI) using the lengths, widths, and  
212 biomasses in Davis (1984, 1987). This empirical function was used to reduce computing  
213 time instead of simulating  $10^2$ - $10^5$  iterations of each larva trying to capture each prey item  
214 at each time step to calculate the probability of successful capture as was done in Petrik *et*  
215 *al.* (2009).

216

#### 217 Bioenergetics submodel

218 The bioenergetics submodel (Appendix eqs. 17-33) was the same as that used in  
219 Petrik *et al.* (2009) for larval haddock, which was based on Kristiansen *et al.* (2007) for  
220 larval cod. The energy derived from the amount of biomass ingested in the foraging  
221 submodel was apportioned to metabolism and growth, both of which were temperature-  
222 and larval size-dependent. Metabolism was increased a constant amount during light  
223 hours to account for the swimming activity of feeding fish. The light threshold was  
224 updated to reflect the findings of Vollset *et al.* (2011) of active feeding at low light  
225 intensities. The light threshold changed from  $1.0 \times 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$  for all sizes, to  
226  $5.0 \times 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$  for larvae  $< 7.5 \text{ mm}$  and  $5.0 \times 10^{-4} \mu\text{mol m}^{-2} \text{s}^{-1}$  for larvae  $\geq 7.5 \text{ mm}$ .

227

#### 228 Predation submodel

229 Interactions with individual predators were not modeled, but both visual and  
230 nonvisual predators were represented by predation rates (Appendix eqs. 34-39).  
231 Nonvisual predation, representative of ambush or tactile invertebrate predators, was  
232 assumed to be a decreasing function of larval fish (their prey) size. The nonvisual  
233 predation rate was found using a size-dependent model adapted from Peterson and  
234 Wroblewski (1984) and was constant spatially and temporally for a given size.

235 Visual predators were simulated by following the visual predation models of  
236 Aksnes and Giske (1993), Aksnes and Utne (1997), and Fiksen & Jørgensen (2011).  
237 Visual predator density was assumed to decrease with increasing larval size since the size  
238 of the predator must increase, and larger animals tend to have lower densities than  
239 smaller ones (Sheldon *et al.*, 1972; Jennings & Mackinson, 2003). The visual predation  
240 rate decreased with larval size and depth, but was constant horizontally and in time.

241 The total base predation rate was the sum of nonvisual and visual predation rates.  
242 The visual predation rate was parameterized such that the total base predation rate was  
243 approximately  $0.1 \text{ d}^{-1}$  for a 5 mm larva (Bailey & Houde, 1989). Similar to the visual  
244 predation rate, the total predation rate decreased with larval size and depth, and was  
245 constant horizontally and in time.

246

#### 247 Mortality

248 Mortality of larvae resulted from starvation, advection, or predation. Entire super-  
249 individuals were removed from the population if they starved or were lost to advection. A  
250 larva was considered to have starved to death if its mass fell below 70% of the mass that  
251 it would have at that length under unlimited food conditions (Kristiansen *et al.*, 2009;

252 Appendix eq. 33). Since all individuals within a super-individual were identical  
253 biologically, starvation of a super-individual resulted in loss of all of its individuals.  
254 Similarly, if a super-individual was lost to advection, then all of its individuals were lost  
255 because they all have the same location in time and space. Super-individuals were  
256 deemed lost by advection when they crossed the 200 m isobath (Fig. 1). The 200 m  
257 isobath has been used to define the edge of Georges Bank in other studies that estimated  
258 bank residence times (Colton & Anderson, 1983; Page *et al.*, 1999) and retention of  
259 larval fish (Lough *et al.*, 2006). Advective loss served as a proxy for the combination of  
260 starvation that would occur as the larvae left the rich prey environment of the bank,  
261 predation by mesopelagic fishes off the slope of the bank, and the inability to find  
262 suitable juvenile settlement habitat.

263 As argued by Scheffer *et al.* (1995), losses of individuals within a super-  
264 individual via predation were modeled by drawing a random number from a binomial  
265 distribution (Appendix eqs. 51-55). The probability of predation,  $p$ , for a super-individual  
266 was calculated from an exponential probability distribution from the total predation rate.  
267 This probability was used with an exact binomial probability density function when  
268  $n \leq 20$ . To reduce computation time, approximations for the binomial distribution were  
269 used when  $n > 20$ . When  $n > 20$  and  $np \leq 50$ , the Poisson approximation for a binomial  
270 distribution with small  $p$  was used. The Poisson distribution was further approximated by  
271 a normal distribution when  $n > 20$  and  $np > 50$ . At each time step,  $n$  was reduced by the  
272 number drawn from the binomial or binomial approximated probability distribution.

273

274 *Simulations*

275 Two contrasting years in haddock recruitment, 1995 and 1998, as observed during the  
276 GLOBEC GB field study, were chosen for this modeling study. Super-individuals were  
277 initialized as newly-hatched 5 mm larvae in the number and location specified from the  
278 egg hatching rate estimates of each year. Hatch locations were determined from  
279 observations of egg abundance (Sibunka *et al.*, 2006) projected forward using estimated  
280 egg mortality rates and spatially integrated using kriging as described in Mountain *et al.*  
281 (2003, 2008). Initial depth was random from surface to bottom to approximate the  
282 uniform distribution of eggs from wind and tidal mixing (R. G. Lough, NOAA NMFS  
283 NEFSC, USA, pers. comm.). Three different cohorts were simulated each year, which  
284 hatched on the midpoint of February, March, and April. Simulations were run until mid-  
285 June, the last month sampled by the GLOBEC GB surveys in 1995. Thus, the run time of  
286 the April cohort was 55 d. For equality, each cohort was analyzed until 55 days post  
287 hatch (dph). Analyses were made at 55 dph or at the time when larvae reached 12 mm,  
288 the average length at the transition to pelagic juveniles, if that occurred before 55 dph. It  
289 was assumed that the model no longer applied to juveniles because they have different  
290 metabolisms, are less vulnerable to predation, and have greater swimming abilities. The  
291 model timespan of 55 dph was deemed an adequate representation of the larval period  
292 since the time of transition from pelagic juveniles to demersal juveniles (which occurs  
293 after the transition from larvae to pelagic juveniles) has been estimated as 2 months (Page  
294 *et al.*, 1999; Mountain *et al.*, 2003). Because the mortality calculations include  
295 individuals that survived the first 55 dph, but did not reach 12 mm, the analyses represent  
296 the processes acting during the majority of the larval period, and not up until the exact  
297 time of juvenile transition.

298 A total of 19 different simulations were run, 9 for 1995 and 10 for 1998 (Table 2).  
299 The reference case used the model in its simplest form to contrast larval survival in 1995  
300 and 1998. The additional simulations can be considered as hypothesis tests or sensitivity  
301 analyses. They were performed to test whether additional information was necessary to  
302 replicate the hatch dates of survivors and the survival differences between 1995 and  
303 1998.

304

305 Reference case (R)

306 As a reference case, super-individuals were modeled as passive (neutrally  
307 buoyant) particles. All other model components were as described above.

308

309 Opposite environment (O)

310 To distinguish the effect of the environment during transport from that of hatch  
311 locations and abundance, the locations and numbers of one year were used in conjunction  
312 with the physical (velocity, temperature, light) and biological (prey density) environment  
313 of the other year.

314

315 Low prey (L)

316 The spatial and temporal patterns in *Pseudocalanus* spp. abundance from the  
317 population model match climatological observations (Ji *et al.*, 2009). The tempo-spatial  
318 patterns from a preliminary model run for *Pseudocalanus* from 1995-1999 also agreed  
319 with yearly observations, but the absolute abundances for 1998 were lower than  
320 observed. The observed abundance of *Pseudocalanus* in 1998 was 2-3 times higher than

321 that in 1995 (Ji *et al.*, 2012). To account for this, the 1998 copepod model concentration  
322 was increased by a factor of 5 to result in mean abundances 2-3 times higher than the  
323 1995 output from the copepod model in the reference case and all other cases. In the  
324 “low-prey” simulation the 1998 densities were only increased by a factor of 2.5 to  
325 approximate the 1995 prey densities and to test if prey density was the cause of  
326 differential survival.

327

### 328 Swimming behavior (DVM)

329         Since the mechanism responsible for larval haddock depth selection has not been  
330 resolved, a simple vertical behavior was simulated to test its effect on survival. Lough  
331 and Potter (1993) observed a diel difference in vertical distribution of larvae 9 mm and  
332 larger. The diel vertical migration (DVM) behavior simulations imposed preferred  
333 daytime and nighttime depths of 40 m and 20 m, respectively, for larvae >9 mm  
334 following observations. Daytime was regarded as when surface light (from the physical  
335 model) was  $>1.0 \times 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$ . Vertical swimming velocity was implemented as a  
336 tangential function that directed larvae towards the preferred depth (Appendix eqs. 56-  
337 57). The swimming speed was symmetric about the preferred depth. Above it the velocity  
338 was negative so that larvae swam down; below it the velocity was positive so that larvae  
339 swam up. Speed decreased as a super-individual neared the preferred depth.

340

### 341 Temperature-dependent predation (TP)

342         Following Houde (1989), the temperature-dependent predation rate increased 0.01  
343  $\text{d}^{-1}$  per  $1^\circ\text{C}$  increase in temperature (Appendix eqs. 40-42). The base temperature was set

344 as 6.5°C, the temperature associated with the predation rate of 0.1 d<sup>-1</sup> for a 5 mm larva  
345 (Jones, 1973; Bailey & Houde, 1989; Houde, 1989). A second temperature-dependent  
346 predation simulation was run with a lower base temperature (5.5°C), which caused even  
347 greater predation rates during warmer months. Both forms were used to test if higher  
348 predation rates in the late spring would result in more survivors from the early hatch  
349 dates as observed.

350

351 Spatially-dependent predation (CP, FP)

352         The distribution of potential predators of larval haddock on Georges Bank (e.g.  
353 chaetognaths, predatory copepods, amphipods, mysid shrimps, decapod shrimps,  
354 euphausiids, hydroids, hydromedusae, scyphomedusae, siphonophores, herring,  
355 mackerel) falls into two groups, those that are more abundant on the shallow, well-mixed  
356 crest region (shoalward of the 60 m isobath; C in Fig. 1), and those that are more  
357 abundant on the seasonally stratified flanks that are in waters deeper than 60 m (e.g. NF  
358 and SF in Fig. 1). The predators are more diverse and abundant on the crest (Sullivan &  
359 Meise, 1996), however this does not necessarily equate to higher predation rates because  
360 of possible differences in consumption rates. Two different simulations were run to test  
361 the effect of spatially-dependent predation, one where predation was three times as high  
362 on the crest compared to the flanks, and a second where predation was higher on the  
363 flanks (Appendix eqs. 43-46). Predation rates were offset from the base predation rate by  
364 ±50% to keep predation losses comparable to simulations that did not have spatially-  
365 dependent rates.

366

367 Interannually varying predation (95P+, 95P-)

368 We varied the predation rates in 1995 and 1998 to investigate the hypothesis of  
369 dissimilar rates from any combination of different predator communities, abundances,  
370 and consumption rates between the two years. The base predation rate was altered by  
371  $\pm 10\%$  in one year and by  $\pm 10\%$  in the opposite direction in the other (Appendix eqs. 47-  
372 50). The results presented are as the variation made to the 1995 simulations (e.g. 95P+ or  
373 P+ is 10% higher in 1995 and 10% lower in 1998).

374

375 *Analyses*

376 Starvation, predation, and advection fatalities were calculated as the fraction of  
377 individuals hatched in each cohort that were lost to that source of mortality before 55 dph  
378 or upon reaching 12 mm. Similarly, percent survival was assessed as the number of  
379 individuals hatched in each cohort that were alive at 55 dph or upon reaching 12 mm. To  
380 better discriminate the sources of mortality affecting larval survival in the model  
381 simulations, percent loss to different sources was analyzed in a systematic way to isolate  
382 the impact of each. This approach allowed distinguishing between whether loss to one  
383 source of mortality was reduced/increased because of its driving factors (i.e. prey  
384 abundance, predation rate, etc.) or because the other sources of mortality were  
385 increased/reduced.

386 In addition to the fractions of each cohort that survived or were lost to different  
387 sources of mortality, hatch distributions, cohort contributions, and survival per hatch  
388 were also calculated from model results. The hatch distribution of each year was the  
389 fraction of individuals hatched in each month out of the total hatched that year. The

390 contribution of each cohort to survivors represented the percent of survivors from each  
391 hatch date out of the total number of survivors from all hatch dates in one year combined.  
392 Hatch distribution and cohort contribution analyses were repeated for larvae that hatched  
393 on the western and eastern sides of Georges Bank separately. Cohort contributions were  
394 compared to the estimated hatch dates of juvenile survivors collected in the field (Lapolla  
395 & Buckley, 2005; Mountain *et al.*, 2008). The total annual percent survival was the total  
396 number of survivors from all hatch dates out of the total number of individuals hatched in  
397 that year, and is termed “survival per hatch.” The survival per hatch ratio compared the  
398 survival per hatch value of 1998 to that of 1995 for each simulation. Model survival per  
399 hatch was compared to recruits per hatch estimated from observations (Mountain &  
400 Kane, 2010).

401 Cohort and year means were calculated for each simulation for the following  
402 properties: time to 12 mm, specific growth rate, depth, temperature experienced, and prey  
403 concentration experienced. Mean depth was calculated for all individuals and those that  
404 survived to 12 mm, whereas means of time to 12 mm, specific growth rate, temperature,  
405 and prey concentration were only calculated for individuals that survived to 12 mm.  
406 Means of growth rate, temperature, and prey concentration accounted for the time from  
407 hatch until each individual reached 12 mm. All results were analyzed at the level of  
408 individuals within the super-individuals. A weighted mean, the mean of the super-  
409 individuals weighted by the number of live individuals within each super-individual, was  
410 used since these properties were shared by all individuals within a super-individual.

411

412

413 **RESULTS**

414 *Reference case*

415 Larval distributions

416 Distributions of larvae at hatch differed between months and years in the passive,  
417 reference simulations (Fig. 2a-c, 3a-c). In February of 1995, larvae hatched on both the  
418 eastern and western sides of the bank, with none in the middle (Fig. 2a). In March 1995,  
419 larvae were missing from the very center crest and center Southern Flank (SF; Fig. 2b),  
420 whereas hatching in April was restricted to the east side and along the SF (Fig. 2c). The  
421 majority of larvae hatched in February 1998 were on the eastern side of the bank, with  
422 some on the NW side (Fig. 3a). March 1998 hatch distributions surrounded the perimeter  
423 of the bank, but were not in the very center of the bank (Fig. 3b), while in April, larvae  
424 hatched all over the bank (Fig. 3c).

425 The final distributions of all individuals, dead or alive, at the mean time that  
426 cohort reached 12 mm (Table 3) varied between months and years because of disparities  
427 in initial locations and advection (Fig. 2d-f, 3d-f). In 1995, larvae of all cohorts were  
428 absent from the Northern Flank (NF; Fig. 2d-f). In contrast, larvae in 1998 were more  
429 abundant and widespread in the Mid-Atlantic Bight (MAB), demonstrative of stronger  
430 advection (Fig. 3d-f). This advection to the southwest through the Great South Channel  
431 (GSC) increased with hatch date in both years (Fig. 2d-f, 3d-f).

432 The distributions of 12 mm survivors (Fig. 2g-i, 3g-i) indicated the final locations  
433 of individuals that were transported through favorable environments, and were small  
434 fractions of the areas covered by the final distributions of all larvae. In 1995, survivors of  
435 all cohorts were confined to the bank crest, and the area occupied increased with hatch

436 date (Fig. 2g-i). The February and March 1998 cohorts followed this pattern, but the  
437 April cohort was located in the MAB and in most areas on the bank except the SF (Fig.  
438 3g-i). The area spanned by survivors from the 1998 cohorts exceeded that of the  
439 corresponding 1995 cohorts (Fig. 2g-i, 3g-i).

440

#### 441 Mortality

442       When only advective loss was considered (no starvation, no predation), advection  
443 resulted in 3-13% of losses in 1995 and 6-27% in 1998 (Table 4). Losses to advection  
444 were greatest for the March cohort in 1995 and the April cohort 1998, but the  
445 contribution of these cohorts to total survival in each year was still the highest (Table 4)  
446 because of their large numbers of larvae (Table 1). Survival per hatch was higher in 1995  
447 than 1998 (Table 4).

448       When larvae were allowed to starve to death, the fraction of larvae lost to  
449 advection did not change for any cohort or year (Table 4). Starvation greatly affected  
450 survival, reducing it from 87-97% to 8-45% in 1995, and from 73-94% to 12-41% in  
451 1998 (Table 4). Adding starvation resulted in a positive relationship between percent  
452 survival and hatch date, and altered the contribution of each cohort to total survivors such  
453 that later hatch dates contributed more (Table 4). Starvation losses reversed the survival  
454 per hatch pattern between years to be greater in 1998 than in 1995 (Table 4).

455       When predation mortality was taken into account, percent survived, advected, and  
456 starved all decreased (Table 4). In general, predation was a greater source of mortality to  
457 larvae that would have starved than to larvae that would have been lost to advection. The  
458 patterns of the greater survival per hatch in 1998 and of increasing cohort contribution

459 with hatch date in both years remained unchanged, and the contributions of the April  
460 cohorts were intensified (Table 4). Survival per hatch decreased from 23-29% due to  
461 advection and starvation only, to 1-2% with the addition of predation mortality (Table 4).

462

#### 463 Cohort survival

464 A greater number of larvae hatched in all months of 1998 compared to 1995  
465 (Table 1). In 1998, the April cohort made up the largest proportion of larvae hatching and  
466 surviving, and the February cohort the least (Fig. 4 right). Conversely, the majority of  
467 larvae hatching in 1995 came from the March cohort, but the proportion of survivors that  
468 originated in the April cohort was greater than the proportion of all hatched larvae  
469 derived from that cohort (Fig. 4 left).

470 Percent survival increased with cohort hatch date in both 1995 and 1998 (Table  
471 4). Percent survival of all the 1995 cohorts was lower than the respective 1998 cohorts  
472 (Table 4). The 1998 April cohort had the highest percent survival (Table 4) and the  
473 greatest number of surviving individuals (Table 5). Starvation losses decreased with  
474 hatch date for both years, while advection losses increased (Table 4). In 1995, predation  
475 losses were highest and equal for the March and April hatch dates, whereas loss to  
476 predation increased with hatch date in 1998 (Table 4).

477

#### 478 Growth rates

479 The weighted mean time to 12 mm (d) decreased with increasing cohort hatch  
480 date for both years, however weighted mean specific growth rates ( $d^{-1}$ ) of 12 mm  
481 survivors did not increase with hatch date (Table 3). Mean time included individuals that

482 reached 12 mm after the 55 d larval period, but mean growth did not. The March cohort  
483 had the fastest growth rates in 1995 and the slowest in 1998, when the April cohort had  
484 the highest (Table 3). The mean time was shorter and mean growth rate faster for the  
485 February and April cohorts in 1998 compared to the corresponding cohorts from 1995,  
486 but the March cohorts had equivalent mean times and growth rates (Table 3). Since the  
487 mean temperatures experienced by the surviving larvae of the February and April cohorts  
488 in 1998 were similar to those experienced in 1995 (Table 6), the faster growth rates in  
489 1998 can be attributed to higher prey concentrations experienced by these larvae (Table  
490 7). The mean temperatures experienced by the April cohorts were near the optimal  
491 temperature for larval haddock growth under food-limited conditions (7°C; Buckley *et*  
492 *al.*, 2004), while the other cohorts were below optimal (Table 6). Despite the lower  
493 temperatures (Table 6) and prey concentrations (Table 7) experienced by the March 1995  
494 cohort, the mean growth rate was higher than that of the April cohort, suggesting  
495 selection pressure from predation, possibly from the shallower distribution of the cohort  
496 in the water column (discussed in *Alternate hypotheses*-Mean depth section below).

497

#### 498 *Alternate hypotheses*

##### 499 Mean depth

500 Weighted mean depths were used to compare depth distributions between passive  
501 (reference case, R) and vertically migrating (DVM case) larvae, between years, and  
502 between all individuals and only those that survived to 12 mm. The weighted mean depth  
503 of the largest fraction of all larvae was between 30 and 40 m, regardless of passive or diel  
504 vertical behavior, for all hatch dates and years (Fig. 5a,c,e,g). The depth distributions of

505 all passive larvae and all larvae with behavior were very similar with slight differences by  
506 cohort (Fig. 5a,c,e,g). Of the larvae that survived to 12 mm, the weighted mean depth of  
507 the largest fraction, either 20 or 30 m, was higher in the water column than all larvae. The  
508 passive and DVM surviving larvae from 1995 showed similar depth distributions for the  
509 April cohorts, but the February and March cohorts differed (Fig. 5b,d). The passive  
510 larvae from February and March 1995 had sharp maxima at 30 m while the larvae with  
511 DVM had broader maxima between 20 and 30 m (Fig. 5b,d). Regardless of passive or  
512 DVM, the 1995 February and March cohorts had greater fractions higher in the water  
513 column than the April cohort. In 1998, survivors of the March and April cohorts had  
514 similar depth distributions with or without DVM (Fig. 5f,h), and in contrast to the 1995  
515 population, the passive February cohort was slightly more broadly distributed than the  
516 individuals from February with DVM (Fig. 5f,h). The proportion of surviving individuals  
517 at depth gradually increased with hatch date with or without vertical swimming behavior  
518 in 1998 (Fig. 5f,h).

519 Comparing between years, the 1995 February and March cohorts had greater  
520 proportions of all larvae with and without DVM around 30 m compared to 1998, while  
521 the 1995 April cohort had fewer proportions near this depth than in 1998 (Fig. 5a,c,e,g).  
522 The passive and behaving larvae that survived to 12 mm from the February cohort were  
523 in higher proportion at 30 m in 1995, whereas there was a higher proportion at 20 m in  
524 1998 (Fig. 5b,d,f,h). The DVM larvae that survived to 12 mm from the March cohort  
525 were in greater abundance higher in the water column in 1995 compared to 1998 (Fig.  
526 5d,h). Conversely, the April cohort survivors from 1995 were deeper than the 1998  
527 cohort, both passive and with behavior (Fig. 5b,d,f,h).

528           The greatest differences in depth distributions were between all larvae and only  
529 those that survived to 12 mm. The 12 mm survivors from all cohorts were generally more  
530 abundant above 50 m (Fig. 5b,d,f,h), while all larvae had greater fractions below 50 m  
531 (Fig. 5a,c,e,g). In all comparisons, there was a steep decrease in survivors below 50 m  
532 that contrasted with the more gradual decrease of all individuals (Fig. 5). Copepod prey  
533 concentrations were highest in the surface layer with maximum concentrations generally  
534 between 0 to 35 m in 1995 and 0 to 65 m in 1998. Thus the majority of larvae in all cases  
535 were at depths with high prey availability. There was a sharp decline in prey density  
536 between 50 and 100 m coincident with the decreased abundance of surviving larvae (Fig.  
537 5b,d,f,h).

538

539 Hatch distribution effect on survival and sources of mortality

540           The cross-initialization case demonstrated that both hatch locations and the  
541 environment affected survival. The environment had the greatest influence on starvation,  
542 with increased starvation in the 1995 environment, whereas advection losses depended  
543 more strongly on hatch location, which were greater with the 1998 hatch locations (Table  
544 8, Fig. 6). Larvae hatched in the 1995 February and March locations had greater percent  
545 survival than those hatched in the 1998 locations under both environments. Cohorts  
546 hatched in the 1995 locations experienced increased survival when in the 1998  
547 environment (Table 8, Fig. 6a,b), while cohorts hatched in the 1998 locations experienced  
548 a decrease in survival when in the 1995 environment (Table 8, Fig. 6c,d). With the  
549 exception of the February cohorts in the 1995 environment, predation caused the plurality  
550 of losses in all simulations (Table 8, Fig. 6).

551            Since hatch location and time influenced survival patterns, the fractions of  
552 individuals hatched west or east of 67.5°W (midpoint of GB) that survived or were lost to  
553 different sources of mortality were calculated for each cohort and year (Fig. 7). The  
554 greatest differences in mortality occurred in 1995. The dominant source of mortality of  
555 larvae hatched in February 1995 was predation for those hatched west of 67.5°W (Fig.  
556 7a) and starvation for those hatched to the east (Fig. 7b). The fate of larvae hatched to the  
557 east in April 1995 (Fig. 7b) mimicked the pattern of all larvae (Fig. 6a). In contrast,  
558 larvae hatched in April 1995 west of 67.5°W were predominantly lost to advection (Fig.  
559 7a). Total advection losses were greater for cohorts hatched to the west of 67.5°W (66%  
560 vs. 31%; Fig. 7a,b) in 1995 and to the east of 67.5°W in 1998 (35% vs. 15%; Fig. 7c,d).

561            As a result of all losses, the greatest fraction of survivors in 1995 were from  
562 individuals hatched east of 67.5°W in the April cohort, followed by the eastern March  
563 cohort, and then the western March cohort (Fig. 8 top left). The 1998 April cohort  
564 hatched east of 67.5°W also contributed the most to the total number of survivors, but  
565 was followed by the western April and the eastern March cohorts (Fig. 8 top right). Of all  
566 the larvae in 1995, roughly 90% of those hatched and those that survived were hatched  
567 east of 67.5°W (Fig. 8 bottom left). A greater fraction of larvae hatched on the western  
568 side of the bank in 1998 (Fig. 8 bottom right). In both years, larvae hatched to the west  
569 contributed more to survivors than to the total numbers hatched. In 1995 6.3% hatched to  
570 the west, but 11.1% of survivors came from the west, with particular increases in the  
571 February and March cohorts (Fig. 8 left). The amount hatched to the west of 67.5°W in  
572 1998 was 27% of all larvae hatched and 34% of the survivors, mainly due to the April  
573 cohort (Fig. 8 right).

574

575 Survival in the alternate hypotheses simulations

576         The fraction of individuals that survived out of those that hatched was greater in  
577 1998 than 1995 for all cases (Fig. 9a). Temperature-dependent predation with a base  
578 temperature of 5.5°C (TP5) resulted in the lowest survival per hatch in both years, while  
579 DVM and temperature-dependent predation with a base temperature of 6.5°C (TP6) also  
580 decreased survival from the reference for both years (Fig. 9a). Spatially-dependent  
581 predation with increased rates on the crest and decreased rates on the flanks (CP) resulted  
582 in the highest survival in both years, while increased flank predation (FP) also increased  
583 survival rates (Fig. 9a). Though this seems counterintuitive, there was an asymmetry in  
584 the losses to predation, advection, and starvation in these two cases such that the number  
585 of survivors from reduced predation losses (CP; Fig. 10b) and reduced advection and  
586 starvation losses (FP; Fig. 10a,c) outweighed the increased losses from the other  
587 mortality sources in those simulations. Surprisingly, both increasing (95P+) and  
588 decreasing (95P-) the total predation by 10% resulted in a greater number of survivors in  
589 1995 (Fig. 9a). Again this was the result of an asymmetry in mortality where the  
590 increased losses to predation and advection with 95P+ (Fig. 10a,c) were  
591 overcompensated by decreased starvation (Fig. 10b). 1998 produced the expected  
592 response of a 10% predation reduction (95P+) improving survival and a 10% increase  
593 (95P-) lessening it (Fig 9a). In addition to the increases and decreases mentioned above,  
594 the opposite environment (O) enhanced survival in 1995 but reduced it in 1998, which  
595 also experienced survival decreases with the low prey (L) case (Fig. 9a).

596           The greater survival per hatch of all 1998 cases resulted in a ratio of survivors per  
597 hatch in 1998 to 1995 greater than one (Fig. 9b). Mountain and Kane (2010) calculated  
598 the number of recruits per hatched larva for the GLOBEC GB years. Comparing the  
599 number of recruits per hatch in 1998 to 1995 yields a ratio of 1.17 (dashed line in Fig.  
600 9b). The opposite environment simulation (O) produced the survivor per hatch ratio  
601 (1.24) most similar to the recruits per hatch ratio of Mountain and Kane (2010). Of the  
602 cases that simulated processes that could have realistically affected those years, the next  
603 closest ratio of 1.32 occurred with interannually-varying predation that was greater in  
604 1995 (95P+; Fig. 9b). Other comparable ratios were a result of reduced predation in 1995  
605 (95P-), and spatially-varying flank predation (FP; Fig. 9b). All simulations lowered the  
606 ratio below that of the reference case (2.45), which was most dissimilar from the  
607 Mountain and Kane ratio (Fig. 9b).

608

609   The effect of alternate hypotheses on the sources of mortality

610           The fraction of larvae lost to advection was low compared to other mortality  
611 sources, with greater loss in 1998 than 1995 for all cases (Fig. 10a). DVM, CP, and 95P+  
612 increased advection losses in both years, with 95P- additionally increasing advection  
613 losses in 1995 (Fig. 10a). Alternatively, FP, TP6, and TP5 lessened advective losses in  
614 both years, with 95P- and L also reducing advective loss in 1998 (Fig. 10a). As noted  
615 previously, 1995 hatch locations in the opposite environment suffered lower advection  
616 losses, while 1998 hatch locations underwent the reverse effect (Fig. 10a). Percentages of  
617 hatched larvae lost to predation were greater in 1995 than 1998 for all cases (Fig. 10b).  
618 Starvation mortality in 1995 exceeded that in 1998 for 6 of the 10 cases. The 1995

619 cohorts suffered fewer starvation losses with the O, FP, 95P+, and L simulations (Fig.  
620 10c). For both years, FP resulted in the greatest predation losses while CP led to the least  
621 (Fig. 10b). These cases had the contrasting effect on starvation losses, the most from CP  
622 and the least from FP (Fig. 10c). In all cases and years, the plurality of larvae (>0.4) were  
623 lost to predation (Fig. 10).

624

625 Changes in cohort contribution from the reference

626 In 1995, the percent of total survivors from the February cohort was low across all  
627 simulations. The contribution of this cohort was increased from the reference case by all  
628 cases except DVM and CP (Fig. 11a). The results of the February 1998 cohort were  
629 similar, except that O reduced the contribution and CP increased it (Fig. 11d). The  
630 contributions of the March and April cohorts to all the surviving larvae in 1995 and 1998  
631 tended to vary reciprocally (Fig. 11b,c,e,f). In 1995, all cases increased the contribution  
632 of the March cohort and diminished that of the April cohort (Fig. 11b,c). In 1998, the CP,  
633 FP, 95P+, TP6, and TP5 cases all increased the contribution of the March cohort and  
634 decreased that of the April cohort (Fig. 11e,f). The variations in the contribution to  
635 survivors by the different cohorts were smaller in 1998 with the largest changes occurring  
636 for the 1995 March and April cohorts.

637

638 Growth rate

639 In comparison to 1995, the 1998 simulations had survivors with faster mean  
640 specific growth rates ( $d^{-1}$ ) from hatch until survival to 12 mm in all cases (Fig. 12).

641 Relative to the reference, 1995 growth rates were amplified by all cases except TP6 and

642 TP5 (Fig. 12). Both of these cases reduced growth rates in 1998, with the addition of  
643 cases O, DVM, 95P-, and L (Fig. 12). In the O, DVM, and L simulations, the fraction of  
644 larvae in 1998 lost to starvation was higher than the reference case (Fig. 10c), suggesting  
645 that poor feeding gave rise to slower growth rates. Despite experiencing lower prey  
646 concentrations than the reference with the O and L cases, growth rates of the 1998  
647 simulations still exceeded those of 1995. With the exception of the February cohort, L  
648 prey densities were greater than those experienced in 1995, even though they were  
649 lowered to be comparable (Table 7). Mean prey availability was less for 1998 compared  
650 to 1995 in the O case, thus the higher mean growth rates of 1998 must be accounted for  
651 by spatially-dependent differences of the larvae with 1998 hatch locations, perhaps in  
652 predation selecting for faster growth rates. Larvae in the 95P- case had a deeper weighted  
653 mean depth than the reference case, thus lower temperatures, irradiance, and prey  
654 densities could have reduced growth rates.

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665 **DISCUSSION**

666 Coupled biological-physical modeling simulations revealed disparities in the processes  
667 occurring during the larval period of haddock on Georges Bank between the years of  
668 differing recruitment, 1995 and 1998. The overall model results suggest that increased  
669 initial numbers of hatched larvae and higher food availability (which reduced starvation  
670 and predation) in 1998 contributed to its larger year-class.

671

672 *Vertical behavior*

673 Diel vertical migration (DVM) of larvae greater than 9 mm reduced survival per hatch in  
674 both years and the mean growth rate in 1998. In general, lower survival stemmed from  
675 increased advection in both years and starvation in 1998. The increased starvation and  
676 lower growth rates can be attributed to the greater proportions of larvae deeper in the  
677 water column where temperatures, prey densities, and light intensities were lower. By  
678 comparing all larvae to those that survived to 12 mm, regardless of vertical behavior, it  
679 can be seen that depths above 30 m benefitted the February cohort, likely from higher  
680 prey concentrations and more light for feeding. On the other hand, more survivors from  
681 the March and April cohorts were found deeper than the February survivors. These  
682 cohorts experienced higher depth-integrated prey concentrations compared to larvae  
683 hatched in February, so did not need to be as shallow in the water column. These cohorts  
684 benefitted from deeper depths where visual predation rates were reduced. Though these  
685 larvae survived by avoiding predation, their growth rates were lower in 1998 than if they  
686 had been shallower. Moreover, the 20 m nighttime depth could have been detrimental to  
687 all cohorts by increasing near-surface advection loss.

688           The vertical behavior used in the DVM simulation was an inadequate  
689 representation for larval haddock on Georges Bank, as behavior should not decrease  
690 survival. Observations of the vertical distribution of larval haddock and their prey  
691 (Lough, 1984; Buckley & Lough, 1987; Lough & Potter, 1993) suggest that the larvae  
692 have a prey-seeking vertical migration behavior. Conversely, larvae may have a preferred  
693 depth unrelated to prey that prevents advection off the bank. The modeling results of  
694 Werner *et al.* (1993, 1996) suggest that larvae must stay below 30 m to remain on the  
695 bank, despite observations of larvae above this depth. Regardless of whether the vertical  
696 behavior of larval haddock is aimed at finding prey, avoiding predation, or avoiding  
697 advection, the mechanism governing the behavior has not been determined and is an  
698 important area for future research.

699

#### 700 *Hatch date of survivors*

701 Lapolla and Buckley (2005) back-calculated the hatch date of young-of-year juvenile  
702 haddock and found that the hatch date frequency of the surviving juveniles peaked  
703 between February and mid-March, with 1998 having a significantly later peak hatch date  
704 than 1995. More larvae hatched in April and May of 1998 survived than the 1995-1999  
705 average, but the highest survival was still from the early hatch dates (Lapolla & Buckley,  
706 2005). Mountain *et al.* (2008) also found that the peak contribution of each cohort  
707 occurred in March of 1995 and 1998 by back calculating hatch dates from larval  
708 abundances and estimated mortality rates. The contributions to total survival from the  
709 modeled February and March cohorts were low in the reference simulation, but both  
710 temperature-dependent predation cases increased their contributions in both years.

711           The temperature-dependent predation rate was used to test the hypothesis that  
712 early-hatched haddock are the dominant survivors because they reach an invulnerable  
713 size before their predators become abundant (Lapolla & Buckley, 2005; Buckley &  
714 Durbin, 2006; Buckley *et al.*, 2010). Temperature-dependent predation increased the  
715 February and March cohort contributions while decreasing that of the April cohort even  
716 though it failed to increase the fraction of survivors above that from April. Part of the  
717 discrepancy between our results and theirs could be that we measured survival at the end  
718 of the larval period rather than during the juvenile stage. Nevertheless, a different  
719 parameterization of temperature-dependent predation may result in cohort contributions  
720 that agree better with observations of the mean hatch date of survivors. The predation rate  
721 could be further improved by representing temperature-related increases in consumption  
722 rates and seasonal increases in predator abundances.

723           Observations from 1976-1987 (Lough *et al.*, 2006) and 1995-1999 (Mountain *et*  
724 *al.*, 2008) show peak haddock spawning between March and April. Evolutionarily, the  
725 peak in spawning and subsequent hatching should be timed to result in the highest  
726 survival of eggs and larvae. During the 1976-1987 period, the large and moderate year-  
727 classes of haddock were spawned in April and benefitted from high hatching rates, high  
728 physical retention, high prey concentrations in May, and a late seasonal temperature-  
729 dependent growth optimum (Lough *et al.*, 2006). In contrast, observations from the 1995-  
730 1999 GLOBEC GB study period demonstrate a mismatch between the time of peak  
731 hatching and time when most survivors hatched (Lapolla & Buckley, 2005; Mountain *et*  
732 *al.*, 2008). For example, 1998 peak spawning occurred between February and March

733 (days 45-85) followed by peak hatching in April (day 115), but the peak hatch time of  
734 survivors was in early March (day 65; Mountain *et al.*, 2008).

735         Following the seasonal predation hypothesis (Lapolla & Buckley, 2005; Buckley  
736 & Durbin, 2006; Buckley *et al.*, 2010), there could have been a decadal shift in the  
737 predator community on Georges Bank that resulted in higher predation rates in April and  
738 May for 1995-1999 compared to 1976-1987 and thus the earlier hatch dates of survivors.  
739 This shift in the predator community could be related to the increased zooplankton  
740 abundance on Georges Bank that occurred in the 1990s (Mountain & Kane, 2010).  
741 Similarly, bottom-up biological processes in 1995-1999 could have caused prey  
742 concentrations in February and March that were high enough to support growth to a size  
743 invulnerable to predators. A potential mechanism responsible for this hypothesis is  
744 increased stratification from the input of low salinity water into the Gulf of Maine and  
745 Georges Bank from the Arctic, which could produce an earlier spring bloom and earlier  
746 development of larval haddock prey populations (Ji *et al.*, 2008). Regardless of the cause  
747 of the mismatch in peak hatching time of all eggs and just those that survived, if this state  
748 persists, one might expect the adult haddock population to shift its peak spawning time to  
749 coincide with the ideal conditions.

750         Alternatively, the time of peak spawning may be controlled by the age structure of  
751 the adult population. Age-2 females of the North Sea haddock population spawned 27-36  
752 days later than older females in 1994, 1996, and 1999 (Wright & Gibb, 2005). Similar to  
753 the 1995-1999 observations from the Georges Bank population, the timing of peak spawn  
754 date of surviving North Sea juveniles was earlier than the peak in egg production in 1996  
755 and 1999 (Wright & Gibb, 2005). Wright and Gibb (2005) suggested that the negative

756 selection on late spawning dates was the result of less viable eggs and larvae produced by  
757 the age-2 females. This hypothesis is supported by the fact that older haddock females  
758 produce larger eggs (Hislop 1988) from which larger larvae hatch (Rideout *et al.*, 2005).  
759 Larger larvae have more advanced morphological characteristics that could confer  
760 survival advantages during the first few days after hatch (Rideout *et al.*, 2005). In  
761 addition, haddock are batch spawners and egg size decreases with each batch spawned  
762 (Rideout *et al.*, 2005). Thus, the early hatch date of surviving haddock in the Georges  
763 Bank population could be the product of high mortality of the many small eggs spawned  
764 late in the year as last batches and/or from young females, and it merits further study.

765

#### 766 *Advection*

767 Larvae followed the general clockwise circulation pattern of Georges Bank. Advection  
768 only losses of 3-24% of a cohort were congruent with Georges Bank studies of modeled  
769 retention rates between 20 and 65% (Lewis *et al.*, 2001; Lough *et al.*, 2006), and  
770 residence times of <10 d to 70 d estimated from drogued drifters (Colton & Anderson,  
771 1983) and a particle-tracking model (Page *et al.*, 1999). The 1998 egg hatching patterns  
772 resulted in larvae developing all over the bank, while the 1995 cohorts were absent from  
773 the Northern Flank. Advective losses were greater in 1998 despite this year having lower  
774 off-bank wind stress (Mountain *et al.*, 2008). In general, these higher losses in the 1998  
775 model runs were due to hatch locations that made larvae more susceptible to advective  
776 loss, and not the result of between-year differences in the physical circulation. If  
777 advection had been the only source of mortality for larvae, haddock in 1995 would have  
778 had higher survival per hatch than in 1998.

779 Chase (1955) examined haddock recruitment from 1928 to 1951 in relation to  
780 wind-driven advection on Georges Bank. Weighted “damage units” to recruitment were  
781 assigned to the number of days with a continuous pressure difference between Nantucket,  
782 Massachusetts and Yarmouth, Nova Scotia, a proxy for the component of geostrophic  
783 wind that drives current perpendicular to the southern edge of Georges Bank. Chase  
784 (1955) found a significant correlation between year-class strength and the damage total  
785 from spawning (defined as when the rate of change of surface temperature lessens) until  
786 May 1. Similarly, Mountain *et al.* (2008) found a strong correlation between recruitment  
787 of haddock during the GLOBEC GB period of 1995-1999 and the estimated number of  
788 hatched eggs, with interannual variability in egg mortality related to wind-driven  
789 transport off the Southern Flank of Georges Bank. The correlation between recruitment  
790 and the number of larvae reaching 15 dph was almost as high as the recruitment  
791 correlation with egg hatching, however, there was no relationship between larval  
792 mortality rates and wind-driven transport (Mountain *et al.*, 2008). Combined, their results  
793 and ours suggest that the influence of advection losses on recruitment spanned the entire  
794 early life period (spawn to May 1) for 1928-1951, and shifted to only during the egg  
795 stage for 1995-1999.

796 As mentioned in the *Methods* section, advection past the 200 m isobath was a  
797 proxy for starvation from leaving the rich prey environment of Georges Bank, heavy  
798 predation off the slope of the bank, and the inability to find suitable juvenile settlement  
799 habitat. Alternatively, each of these processes could be modeled. Super-individuals and  
800 individuals were followed for the entire duration of the simulation, such that information  
801 on starvation, predation, and location were available after a larva left the region denoted

802 by the 200 m isobath as long as it remained in the model domain. Many of these  
803 individuals starved and/or were eaten after advective loss in the model simulations.  
804 Though potential prey would be advected off the bank in the same mass of water that  
805 contained the larvae being advected, starvation would occur from spatial and temporal  
806 mismatch of the larvae and prey. If larvae swam out of the layer of water that was  
807 advected, they would immediately experience the lower prey densities off the continental  
808 slope. Also, prey concentration would decrease as both the prey and their resources were  
809 diluted in the deep-ocean environment and as the prey were eaten by many of the same  
810 slope-water predators that would consume the larval fish. As with all predation, it is  
811 difficult to determine how to parameterize the off-bank predation rates to simulate the  
812 losses to mesopelagic fish and other predators. Finally, it is possible for larvae to be  
813 advected back onto the bank before experiencing either starvation or predation, thus true  
814 advective loss should be determined from individuals that are not near the favorable  
815 pebble-gravel settlement habitats on Georges Bank (Lough *et al.*, 1989) at the time of the  
816 demersal transition. As this transition from a pelagic to demersal lifestyle happens during  
817 the juvenile stage, it could not be simulated in the present study because the physiological  
818 and behavioral models do not hold for juvenile haddock.

819

#### 820 *Predation*

821 Predation accounted for the most losses in all simulations. Percent loss to predation  
822 increased with hatch date, which is contrary to the hypothesis that larvae with faster  
823 growth rates (March 1995, April 1998) would be exposed to predation for less. However,  
824 like the larval fish, the visual predators benefited from longer photoperiods and greater

825 light intensities later in the season, which increased predation rates. Furthermore,  
826 starvation losses decreased with hatch date, which left more live larvae available for  
827 predators to eat. Total predation losses were higher in 1995, suggesting that the smaller,  
828 slower growing larvae were more susceptible to predation. This conclusion is further  
829 supported by the systematic addition of mortality sources. When predation was added as  
830 a source in addition to advection and starvation, it claimed a greater fraction of larvae that  
831 would have eventually starved.

832         Altering the predation rate was the only way to increase the contributions of early  
833 hatch dates to the surviving juveniles as observed. All temperature-dependent predation  
834 and some spatially dependent predation cases increased the contributions of the February  
835 and March cohorts and decreased those of April. It can be inferred that a predation rate  
836 that increased with temperature most likely contributed to the observations of early hatch  
837 dates of survivors, while a spatial predation component may have also played a role.

838         There are many types of potential invertebrate predators of fish larvae such as  
839 chaetognaths (Kuhlmann, 1977), copepods (e.g. *Euchaeta norvegica*; Bailey, 1984; Yen,  
840 1987), amphipods (e.g. *Parathemisto* spp.; Shearer & Evans, 1975; Yamashita *et al.*,  
841 1985), mysids (Bailey, 1984), decapod shrimps (e.g. *Crangon septemspinosa*; Wilcox &  
842 Jeffries, 1974), euphausiids (Bailey, 1984), hydroids (Madin *et al.*, 1996), medusae  
843 (Bailey, 1984; Purcell, 1985), and siphonophores (Purcell, 1985), as well as vertebrate  
844 predators like Atlantic herring (*Clupea harengus*) and mackerel (*Scomber scombrus*;  
845 Garrison *et al.*, 2000). Most of these predators are opportunistic such that the prey items  
846 found in their guts reflect the natural abundances of the plankton. Since fish larvae are  
847 rather dilute (0-2.5 m<sup>-3</sup>; Lough, 1984), it is doubtful that they make up a significant

848 portion of any opportunistic predator's diet. Even though predation of fish larvae may be  
849 incidental, there may be considerable loss of larvae if predator abundances and  
850 consumption rates are high.

851 Chaetognaths are probably not significant predators on larval haddock since they  
852 can only eat larvae within a narrow time period after hatch (4 dph) because of size  
853 limitations (Kuhlmann, 1977). Similarly, the copepod *E. norvegica* cannot consume  
854 larvae >7 mm (Bailey, 1984). In addition, its consumption rate of larval fish is low in  
855 comparison to medusae and euphausiids (Bailey, 1984) and it is the least abundant of all  
856 potential invertebrate predators on Georges Bank (Sullivan & Meise, 1996), thus  
857 negating it as a dominant predator. Though the filtering rates of mackerel could lead to  
858 high predation losses, their lack of spatial and temporal overlap on Georges Bank with  
859 haddock larvae discounts them as important predators (Garrison *et al.*, 2000). Suspended  
860 hydroid colonies can be another significant predator of fish larvae on the crest of Georges  
861 Bank (Madin *et al.*, 1996), unfortunately, these and other gelatinous predators are  
862 difficult to sample.

863 Consequently, we examined the potentially significant predators for which there  
864 was abundance data from the GLOBEC GB cruises (amphipods, mysids, *C.*  
865 *septemspinosa*, euphausiids, siphonophores, and herring). We assessed these data for  
866 interannual differences that could substantiate the survivor per hatch ratios of the  
867 simulations with interannually varying predation and higher flank predation, and for  
868 seasonal differences that increased the contributions of the February and March cohorts  
869 in several simulations. Herring stock estimates indicate that the population was greater in  
870 1998 (DFO, 2003), while some invertebrate predators were more abundant in 1995 (Fig.

871 13). Neither the presence of euphausiids ( $p=0.71$ ), mysids ( $p=0.50$ ), and *C.*  
872 *septemspinosa* ( $p=1.00$ ), nor their abundance when found ( $p=0.13$ ,  $p=0.38$ ,  $p=0.81$ ,  
873 respectively) was significantly different in 1995 and 1998. In contrast, there was a greater  
874 chance of collecting siphonophores ( $p<0.01$ ) and hyperiid amphipods ( $p=0.02$ ) in 1995,  
875 and the abundances of these predators were significantly higher in 1995 ( $p<0.01$  and  $p=0$ ,  
876 respectively; Fig. 13).

877         It is very possible that the greater abundances of siphonophores and hyperiid  
878 amphipods in 1995 compared to 1998 resulted in greater predation rates in 1995 and the  
879 observed differences in survival rate. Unlike the other invertebrate predators that eat fish  
880 larvae incidentally, larvae can comprise 90-100% of the diets of cystonect siphonophores  
881 and are frequently consumed by physonect siphonophores (Purcell, 1981; 1985). The many  
882 gastrozooids of siphonophores allow them to ingest more than one larva at a time  
883 (Purcell, 1985). Hyperiid amphipods can also have a detrimental effect on larval fish  
884 populations depending on densities of predator and prey, and on their spatial and  
885 temporal overlap. For example, predation by the hyperiid amphipod *Parathemisto*  
886 *japonica* resulted in daily predation losses up to 45.2% of sand-eel larvae (Yamashita *et*  
887 *al.*, 1985).

888         The importance of siphonophores and hyperiid amphipods as predators on  
889 haddock larvae is further supported by their lowest abundances occurring in March (Fig.  
890 13), which could lead to an increase in the contribution of larvae hatched during this  
891 month as observed (Lapolla & Buckley, 2005; Mountain *et al.*, 2008). The  
892 climatological distributions of siphonophores and hyperiids indicate greater abundances  
893 outside the 60 m isobath (Sullivan & Meise, 1996), which lends credence to model

894 predictions of a survival per hatch ratio similar to the Mountain and Kane (2010) ratio  
895 and increased contributions of the February and March cohorts with the higher flank  
896 predation simulation.

897         Conversely, mysids and *C. septemspinosa* are more abundant on the crest region  
898 inside 60m (Davis, 1987; Sullivan & Meise, 1996). The mysid abundance was also  
899 lowest in March (Fig. 13). An increase in crest predation rates raised early cohort  
900 contributions for 3 of the 4 February and March cohorts, but not as much as increased  
901 flank predation rates. Similarly, high crest predation reduced the survivor per hatch ratio,  
902 but the ratio of the high flank predation case was more similar to the Mountain & Kane  
903 (2010) ratio. Thus, the fact that mysids and *C. septemspinosa* were not significantly more  
904 abundant in 1995 might be irrelevant if predation in this region is not important in driving  
905 interannual variability in larval survival. Additionally, the warm water intrusions in 1995  
906 could have advected slope water predators onto Georges Bank (Brown *et al.*, 2005),  
907 thereby increasing overall predation rates, as well as rates on the flank.

908         Neither the interannual nor the spatial pattern in predation rates on Georges Bank  
909 is fully resolved, and neither can be used to reject or accept the simulations of increased  
910 predation rates in 1995, decreased predation in 1995, and increased flank predation that  
911 each produced modeled survival per hatch ratios approximating the recruits per hatch  
912 ratio of Mountain and Kane (2010), and in the case of flank predation, enhanced the  
913 contribution of the February and March cohort contributions to survivors. However, the  
914 high larval fish ingestion rates and the seasonal abundance pattern of mysids,  
915 siphonophores, and hyperiid amphipods suggest these taxa are important predators of  
916 larval haddock. This analysis was a small effort to understand the spatially and

917 temporally dependent predation rates on Georges Bank. Further work is required in the  
918 form of horizontal and vertical distributions of predators and consumption rates on larval  
919 fish since predation mortality is the most uncertain component in larval fish models, and  
920 one that can have substantial effects.

921

#### 922 *Starvation and growth*

923 Though starvation was not responsible for the largest fraction of larval mortality, food-  
924 limitation determined the interannual variability in survival of haddock larvae in 1995  
925 and 1998. When advection was considered the only source of loss, survival per hatch was  
926 greater in 1995 than 1998. By adding starvation as a mortality source, percent survival  
927 became greater in 1998 compared to 1995. The high survival rates of 1998 ought to have  
928 been a direct result of higher growth rates and lower starvation losses from the greater  
929 *Pseudocalanus* spp. concentrations. Buckley *et al.* (2006) report very low incidence of  
930 starvation in 5-12 mm larvae of haddock, however direct starvation of larvae is difficult  
931 to observe since malnourished larvae are smaller and have higher predation rates. This  
932 likely explains why modeled losses to predation were higher in 1995 and lower in 1998.  
933 Not only did fewer larvae in 1998 starve to death, but faster growth from higher prey in  
934 1998 could have led to larvae that were vulnerable to predation for less time (Davis *et al.*,  
935 1991). Slow growing larvae in 1995 would have been exposed to predators for a longer  
936 amount of time, and would have experienced higher predation rates by being smaller at a  
937 given time and less able to avoid capture.

938         Starvation decreased with hatch date because as the season progressed, both  
939 photoperiod and copepod prey concentrations increased, allowing for the consumption of

940 more biomass. These seasonal increases were somewhat reflected in the modeled growth  
941 rates and mean times to 12 mm. The growth rate of the 1998 April cohort was high from  
942 the dramatic increase in the copepod population later in the season such that food was not  
943 limiting. The higher growth rates later in the season may have skewed the mean growth  
944 rates of all cohorts and mitigated the effect of prey availability on total survivorship.

945         The growth rate of haddock larvae is strongly correlated with the *Pseudocalanus*  
946 spp. biomass with a Michaelis-Menten type response (Buckley & Durbin, 2006). The  
947 modeled weighted mean growth rates of surviving 5-7 mm larvae were much lower than  
948 the curve derived from RNA:DNA measurements (Buckley and Durbin 2006; Fig. 14a),  
949 potentially indicating a higher half-saturation biomass concentration, lower maximum  
950 growth rate, and/or a non-zero concentration needed for positive growth. The  
951 disagreement between the 5-7 mm model results and the empirical curve could be  
952 accounted for by differing temperatures that larvae were exposed to in the model and in  
953 1992-1994 when Buckley and Durbin (2006) sampled. If temperature was not the cause,  
954 then either the model did not correctly represent some aspect of the growth of 5-7 mm  
955 larvae, or the model failed to kill slower growing larvae that died in the ocean and were  
956 not sampled by Buckley and Durbin (2006). Potential sources of error in the growth  
957 model include modeled *Pseudocalanus* spp. concentrations without sufficient resolution  
958 in the vertical dimension, possibly by not representing micropatchiness (Davis *et al.*,  
959 1991), and mischaracterization of consumption rates from aggregating the copepod stages  
960 and using mean parameter values across the stages. Alternatively, the starvation threshold  
961 in the model may be too low, which could account for the divergent growth rates if  
962 slower growing larvae die in the ocean but not in the model. Despite the discrepancy for

963 5-7 mm larvae, the simulated 7-12 mm survivors had growth rates that correspond well  
964 with the maximum growth rate calculated by Buckley and Durbin (2006; Fig. 14b). Since  
965 these growth rates were at the maximum, it must have been growth and starvation during  
966 the early larval period (hatch to 7 mm) that was most important to interannual variability  
967 in survival.

968

#### 969 *Survival*

970 The percent of hatched larvae that survived was greater in 1998, in agreement with  
971 estimates of percent of hatched larvae that survived to 15 dph (Mountain *et al.*, 2008) and  
972 that recruited (Mountain & Kane, 2010). The overestimation of the modeled survivor per  
973 hatch ratio compared to the recruit per hatch ratio of Mountain and Kane (2010) could be  
974 for several reasons. One, the modeled *Pseudocalanus* spp. prey concentrations do not  
975 capture important spatial and/or temporal differences between the two years. This source  
976 of error could be examined with a more detailed copepod population model. Two,  
977 inclusion of copepod eggs and other copepod species as prey could reduce starvation in  
978 1995 and compensate for the difference between the two ratios. Though the four  
979 dominant prey taxa were more abundant in 1998 than 1995 (Buckley & Durbin, 2006),  
980 the gut contents of haddock larvae indicated positive feeding preferences for other  
981 copepod species in 1995; unfortunately preferences from 1998 were unavailable  
982 (Broughton & Lough, 2010). Three, the magnitude of the predation rate, its relationship  
983 with larval fish size, and its variability vertically, horizontally, seasonally, and/or  
984 interannually are uncertain. The base predation rate was parameterized as best as possible  
985 to agree with mortality estimates for larval fish, and the inverse relationship with larval

986 size agrees with calculations of decreased mortality with increasing larval age from the  
987 GLOBEC GB study period (Mountain *et al.*, 2008). Fourth and finally, the processes  
988 responsible for the discrepancy between the modeled survivor per hatch ratio and the  
989 recruit per hatch ratio could occur during the juvenile stage, which was not included in  
990 this model.

991         The higher total numbers of surviving larvae in the reference simulations of 1998  
992 compared to 1995 appear to be related to the greater number of larvae hatched in 1998.  
993 Since the number surviving was only a small percentage of the initial number of larvae,  
994 changes in predation, advection, and growth were expected to be important causes of  
995 changes in numbers of surviving larvae between years. However, the initial abundance  
996 and distribution of hatched larvae was critically important, as can clearly be seen in the  
997 run with opposite environment, i.e., the larvae hatched at the 1998 locations but subjected  
998 to the 1995 environmental conditions still had a greater number of survivors even though  
999 percent survival was lower. The largest proportion of larvae that hatched and that  
1000 survived were hatched east of 67.5°W in both 1995 and 1998. However, larvae that  
1001 originated west of 67.5°W composed a greater fraction of the total survivors than the total  
1002 number hatched. Depending on temperature, the egg stage ranges from 10 to 20 d (mean  
1003 16 d; Page & Frank, 1989). Based on the circulation of Georges Bank, it is likely that the  
1004 larvae that hatched west of 67.5°W were also spawned on that side of the bank, and the  
1005 modeled proportions of 6% and 27% of larvae hatched in 1995 and 1998 compare  
1006 favorably with observed proportions of 4% and 30% of the eggs spawned in those  
1007 locations in those years (Mountain *et al.*, 2008). Though spawning predominantly occurs  
1008 on the Northeast Peak (NEP), spawning on western Georges Bank can contribute

1009 survivors in the winter when advective loss from the surface waters of the NEP is highest  
1010 (Lough *et al.*, 2006). Notably, hatching success, which contributed to the higher survival  
1011 in 1998 simulations, is significantly correlated to the fraction of eggs spawned west of  
1012 67.5°W, and not to the total number of eggs spawned (Mountain *et al.*, 2008).

1013

#### 1014 *Conclusions*

1015 From the model results, we conclude that the survival of larval haddock on Georges Bank  
1016 is dominated by food-limitation, particularly from hatch to 7 mm, with both starvation  
1017 and slower growth leading to higher predation and longer exposure to predation acting as  
1018 important sources of mortality. Both starvation and predation losses were greater in  
1019 simulations of larval haddock in 1995, thus it must have been the higher prey  
1020 concentrations in 1998 that resulted in observations of higher survival and recruitment  
1021 per hatched larvae in 1998 compared to 1995 (Mountain *et al.*, 2008; Mountain & Kane,  
1022 2010). Temperature-dependent predation rates resulted in cohort contributions that better  
1023 agreed with observations of the mean hatch date of survivors, further supporting the  
1024 hypothesis that seasonal increases in predation rate favor survival of larvae from earlier  
1025 hatch dates (Lapolla & Buckley, 2005; Mountain *et al.*, 2008). The importance of  
1026 advection during the larval period was negated by the fact that modeled advective losses  
1027 were small in general, and higher in 1998 despite lower wind stress that year, due to  
1028 hatch location. This conclusion is corroborated by Mountain *et al.* (2008), who did not  
1029 find a relationship between modeled wind-driven transport and early larval mortality  
1030 rates.

1031           In addition to higher prey concentrations leading to increased growth rates and  
1032 decreased starvation, the greater total number of survivors in 1998 was related to the  
1033 greater number of eggs that hatched in that year. The better hatching success of 1998 was  
1034 a result of weaker southeastern wind stress and a larger proportion of eggs spawned on  
1035 the western part of Georges Bank (Mountain *et al.*, 2008). The number of haddock eggs  
1036 spawned is not significantly correlated to recruitment, whereas egg hatching and larval  
1037 survival are correlated to recruitment (Mountain *et al.*, 2008). Mountain *et al.* (2008)  
1038 found that the contributions of egg and larval mortalities to overall haddock survivorship  
1039 were comparable. In light of their results and the modeling work presented here, we  
1040 conclude that interannual differences in haddock recruitment during the 1995-1999  
1041 GLOBEC GB study period were dominated by advection during the embryonic period  
1042 and food-limitation during the larval stage. Our results suggest that food-limitation and  
1043 its related losses to starvation and predation may be responsible for interannual variability  
1044 in recruitment and larval survival outside of the years studied. Further research is needed  
1045 to assess whether these patterns hold for other years.

1046

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1055

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1302 **TABLES**

1303 **Table 1.** Statistics on the number of individuals ( $n$ ) per super-individual (super) at time

1304 of hatch.

	1995			1998		
	Feb	Mar	Apr	Feb	Mar	Apr
Min.( $n$ )	$6.50 \times 10^5$	$7.10 \times 10^5$	$6.96 \times 10^5$	$6.43 \times 10^5$	$7.14 \times 10^5$	$1.37 \times 10^6$
Max.( $n$ )	$2.37 \times 10^9$	$2.42 \times 10^{10}$	$6.24 \times 10^9$	$1.99 \times 10^{10}$	$2.31 \times 10^{10}$	$2.11 \times 10^{10}$
Mean( $n$ )	$1.62 \times 10^8$	$1.06 \times 10^9$	$6.74 \times 10^8$	$1.09 \times 10^9$	$2.22 \times 10^9$	$2.52 \times 10^9$
Std. Dev.( $n$ )	$3.22 \times 10^8$	$2.22 \times 10^9$	$1.02 \times 10^9$	$2.04 \times 10^9$	$3.87 \times 10^9$	$3.35 \times 10^9$
Total( $n$ )	$4.81 \times 10^{11}$	$4.47 \times 10^{12}$	$1.80 \times 10^{12}$	$3.90 \times 10^{12}$	$3.47 \times 10^{12}$	$1.42 \times 10^{13}$
Annual total( $n$ )		$6.75 \times 10^{12}$			$2.85 \times 10^{13}$	
Total(super)	$2.97 \times 10^3$	$4.22 \times 10^3$	$2.67 \times 10^3$	$3.59 \times 10^3$	$4.69 \times 10^3$	$5.63 \times 10^3$
Annual total(super)		$9.86 \times 10^3$			$1.39 \times 10^4$	

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1319 **Table 2.** The different simulations, their notation, the variable or process changed, and  
 1320 the hypothesis tested with each.

Case name	Notation	Changed	Hypothesis tested
Reference	R	--	Interannual recruitment variability; hatch date of survivors
Cross initialization	O	Physical environment	Hatch location vs. physical environment during transport
Low prey	L	1998 prey densities	Food-limitation
Swimming behavior	DVM	Vertical swimming	Effect of vertical distribution
Temperature-dependent predation	TP6 TP5	Total predation rate $T_{base}=6.5^{\circ}C$ $T_{base}=5.5^{\circ}C$	Seasonal increases in predation rate
Spatially-dependent predation	CP FP	Total predation rate C+50%, F-50% C-50%, F+50%	Spatially distinct predator communities
Interannually varying predation	95P+ 95P-	Total predation rate 95+10%, 98-10% 95-10%, 98+10%	Interannually different predation rates

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1331 **Table 3.** Weighted mean time (d) to 12 mm and weighted mean specific growth rate ( $d^{-1}$ )  
1332 of individuals from hatch until survival to 12 mm in the reference case. Mean time  
1333 calculations include individuals that reached 12 mm after the 55 d larval period, but the  
1334 mean growth rates do not.

	Feb		Mar		Apr	
1995	51	0.041	46	0.051	46	0.042
1998	48	0.054	47	0.049	38	0.062

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1353 **Table 4.** Fate, contribution of each cohort, and annual survival of individuals (as fraction  
 1354 of total individuals hatched) at 55 dph or 12 mm in the reference case with systematic  
 1355 addition of mortality sources.

		1995			1998		
		F	M	A	F	M	A
	Advection	0.03	0.13	0.11	0.06	0.24	0.27
	Survival	0.97	0.87	0.89	0.94	0.76	0.73
Advection only	Cohort contribution	0.08	0.65	0.27	0.17	0.36	0.47
	Survival per hatch		0.88			0.77	
Advection and starvation only	Advection	0.03	0.13	0.11	0.06	0.24	0.27
	Starvation	0.89	0.71	0.44	0.82	0.57	0.32
	Survival	0.08	0.16	0.45	0.12	0.19	0.41
	Cohort contribution	0.03	0.46	0.52	0.06	0.24	0.71
	Survival per hatch		0.23			0.29	
All sources	Advection	0.01	0.07	0.09	0.04	0.15	0.16
	Starvation	0.49	0.24	0.20	0.39	0.21	0.12
	Predation	0.49	0.69	0.69	0.57	0.63	0.68
	Survival	0.003	0.003	0.022	0.005	0.006	0.036
	Cohort contribution	0.02	0.27	0.71	0.03	0.11	0.86
	Survival per hatch		0.01			0.02	

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1362 **Table 5.** Total number of surviving larvae ( $\times 10^{10}$ ) by cohort in the reference case.

	Feb	Mar	Apr	Total
1995	0.14	1.51	4.01	5.66
1998	1.91	6.23	50.47	58.61

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1383 **Table 6.** Weighted mean temperature (°C) experienced by individuals from hatch until  
1384 survival to 12 mm for each cohort in the reference case.

	Feb	Mar	Apr
1995	6.5	6.4	7.0
1998	6.4	6.4	7.4

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1403 **Table 7.** Weighted mean *Pseudocalanus* spp. concentration (no. m<sup>-3</sup>) of the grouped  
 1404 developmental stages experienced by individuals from hatch until survival to 12 mm for  
 1405 each cohort and year in the reference case.

	1995 reference			1998 reference			1998 low prey		
	Feb	Mar	Apr	Feb	Mar	Apr	Feb	Mar	Apr
Nauplii	472	983	2085	692	1815	4552	357	1035	2333
Copepodites	231	315	416	490	594	1471	300	354	761
Adults	22	62	93	41	108	222	22	69	111
Total	726	1360	2594	1223	2517	6245	679	1458	3204

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1423 **Table 8.** Fate of all individuals, as fraction of total individuals hatched, at 55 dph or 12  
 1424 mm in the reference and cross-initialization cases.

		1995 environment			1998 environment		
		Feb	Mar	Apr	Feb	Mar	Apr
1995 hatch	Advection	0.01	0.07	0.09	0.01	0.03	0.11
	Starvation	0.49	0.24	0.20	0.38	0.20	0.13
	Predation	0.49	0.69	0.69	0.61	0.76	0.73
	Survived	0.003	0.003	0.022	0.006	0.009	0.028
1998 hatch	Advection	0.08	0.24	0.12	0.04	0.15	0.16
	Starvation	0.46	0.24	0.21	0.39	0.21	0.12
	Predation	0.47	0.51	0.64	0.57	0.63	0.68
	Survived	0.001	0.003	0.032	0.005	0.006	0.036

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1441 **FIGURE CAPTIONS**

1442 **Fig. 1.** Map of the Gulf of Maine (GOM) and Georges Bank with the subregions: Crest  
1443 (C), Great South Channel (GSC), Mid-Atlantic Bight (MAB), Northeast Peak (NEP),  
1444 Northern Flank (NF), and Southern Flank (SF). The 60, 100, and 200 m isobaths are  
1445 shown and labeled.

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1447 **Fig. 2.** 1995 reference case distributions of individuals at hatch (a-c), of all individuals,  
1448 dead or alive, at the weighted mean time to 12 mm (d-f), and of individuals that survived  
1449 to 12 mm at the weighted mean time to 12 mm (g-i). The gray lines are the 60, 100, and  
1450 200 m isobaths. Hatch locations were determined from observations of egg abundance  
1451 (Sibunka *et al.*, 2006) projected forward using estimated egg mortality rates and spatially  
1452 integrated kriging as described in Mountain *et al.* (2003, 2008). Contours are presented  
1453 for the log of the fraction of individuals.

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1455 **Fig. 3.** 1998 reference case distributions of individuals at hatch (a-c), of all individuals,  
1456 dead or alive, at the weighted mean time to 12 mm (d-f), and of individuals that survived  
1457 to 12 mm at the weighted mean time to 12 mm (g-i). The gray lines are the 60, 100, and  
1458 200 m isobaths. Hatch locations were determined from observations of egg abundance  
1459 (Sibunka *et al.*, 2006) projected forward using estimated egg mortality rates and spatially  
1460 integrated kriging as described in Mountain *et al.* (2003, 2008). Contours are presented  
1461 for the log of the fraction of individuals.

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1463 **Fig. 4.** Percent contributed by each cohort to the total number of individuals (top) hatched  
1464 and (bottom) survived to 55 dph or 12 mm in the reference case. F: February (black), M:  
1465 March (gray), A: April (white).

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1467 **Fig. 5.** Weighted mean depth of larvae from 1995 (a-d) and 1998 (e-h) hatch until 55 dph  
1468 or 12 mm in 10 m depth bins. Passive: reference, DVM: diel vertical migration, All: all  
1469 larvae, 12 mm: only those that survived to 12 mm.

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1471 **Fig. 6.** Fate of all individuals, as percent of total individuals hatched, at 55 dph or 12 mm  
1472 in the reference and cross-initialization cases. A: advection, P: predation, St: starvation,  
1473 Su: survived.

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1475 **Fig. 7.** Fate of all individuals, as percent of total individuals hatched west or east of  
1476 67.5°W, at 55 dph or 12 mm in the reference case. A: advection, P: predation, St:  
1477 starvation, Su: survived.

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1479 **Fig. 8.** Percent contributed by each cohort to the total number of individuals (top) hatched  
1480 west or east of 67.5°W and (bottom) survived to 55 dph or 12 mm in the reference case.  
1481 F: February, M: March, A: April, W: west, E: east.

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1483 **Fig. 9.** (a) Survival per hatch (fraction of individuals that survived to 55 dph or 12 mm  
1484 out of all those hatched) in 1995 and 1998 for all ten cases. The dashed lines are the 1995  
1485 and 1998 reference case values. (b) 1998:1995 ratio of the number of survivors per

1486 hatched larva. The dashed line at 1.17 represents the calculated 1998:1995 ratio of the  
1487 number of recruits per hatch from Mountain and Kane (2010). R: reference, O: opposite  
1488 environment, DVM: diel vertical migration behavior, CP: spatially-dependent high crest  
1489 predation, FP: spatially-dependent high flank predation, 95P+: higher 1995 predation,  
1490 95P-: lower 1995 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}\text{C}$ , TP5:  
1491 temperature-dependent predation  $T_{base}=5.5^{\circ}\text{C}$ , L: low prey.

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1493 **Fig. 10.** The fraction of individuals hatched that were lost to (a) advection, (b) predation,  
1494 and (c) starvation in 1995 and 1998. Note differences in y-axis scales. The dashed lines  
1495 are the 1995 and 1998 reference case values. R: reference, O: opposite environment,  
1496 DVM: diel vertical migration behavior, CP: spatially-dependent high crest predation, FP:  
1497 spatially-dependent high flank predation, 95P+: higher 1995 predation, 95P-: lower 1995  
1498 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}\text{C}$ , TP5: temperature-  
1499 dependent predation  $T_{base}=5.5^{\circ}\text{C}$ , L: low prey.

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1501 **Fig. 11.** Fraction of surviving individuals from each cohort (cohort contribution) is  
1502 presented as the difference from the reference case for 1995 (a-c) and 1998 (d-f). O:  
1503 opposite environment, D: diel vertical migration behavior, C: spatially-dependent high  
1504 crest predation, F: spatially-dependent high flank predation, P+: higher 1995 predation,  
1505 P-: lower 1995 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}\text{C}$ , TP5:  
1506 temperature-dependent predation  $T_{base}=5.5^{\circ}\text{C}$ , L: low prey.

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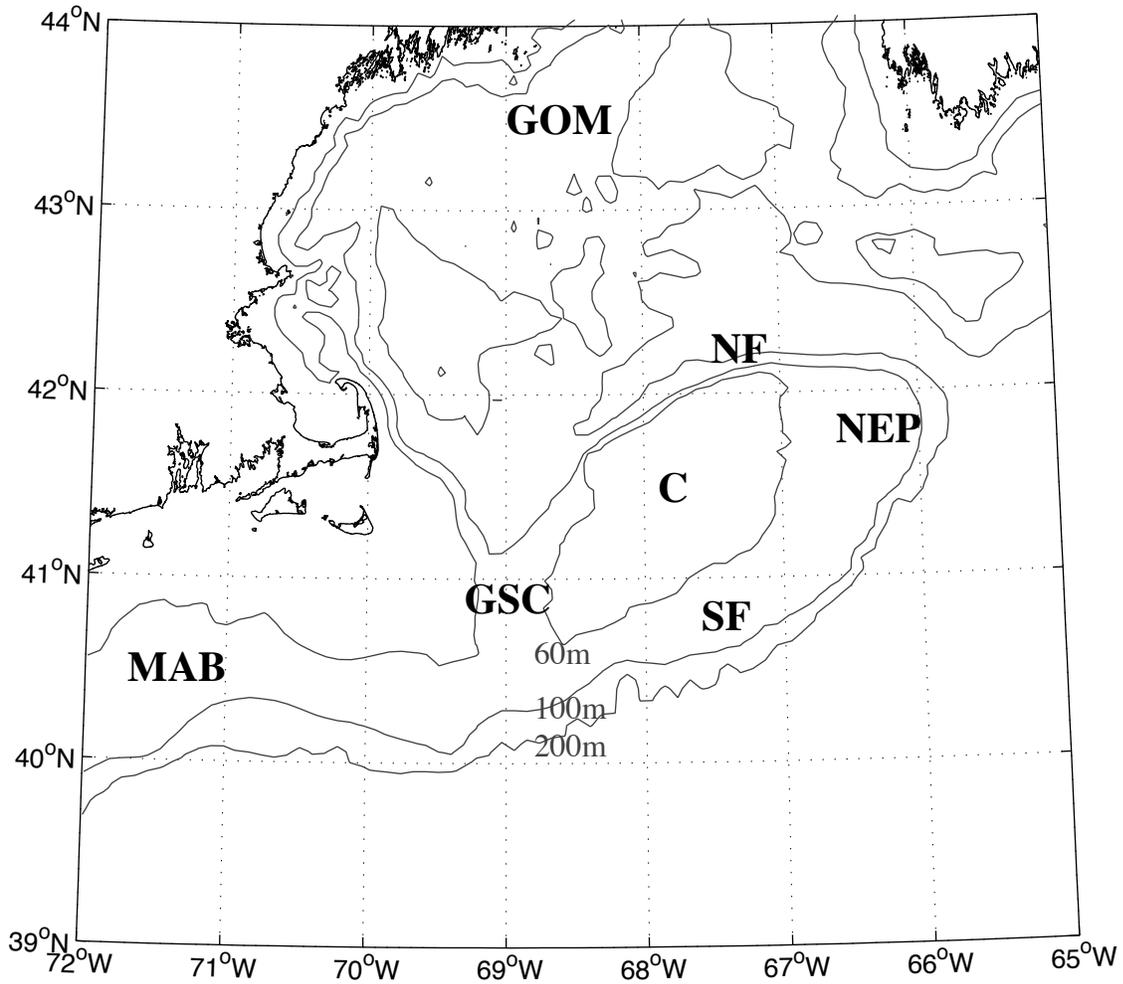
1508 **Fig. 12.** Weighted mean specific growth rate ( $d^{-1}$ ) of surviving 12 mm individuals from  
1509 all cohorts in 1995 and 1998. The dashed lines are the 1995 and 1998 reference case  
1510 values. R: reference, O: opposite environment, DVM: diel vertical migration behavior,  
1511 CP: spatially-dependent high crest predation, FP: spatially-dependent high flank  
1512 predation, 95P+: higher 1995 predation, 95P-: lower 1995 predation, TP6: temperature-  
1513 dependent predation  $T_{base}=6.5^{\circ}C$ , TP5: temperature-dependent predation  $T_{base}=5.5^{\circ}C$ , L:  
1514 low prey.

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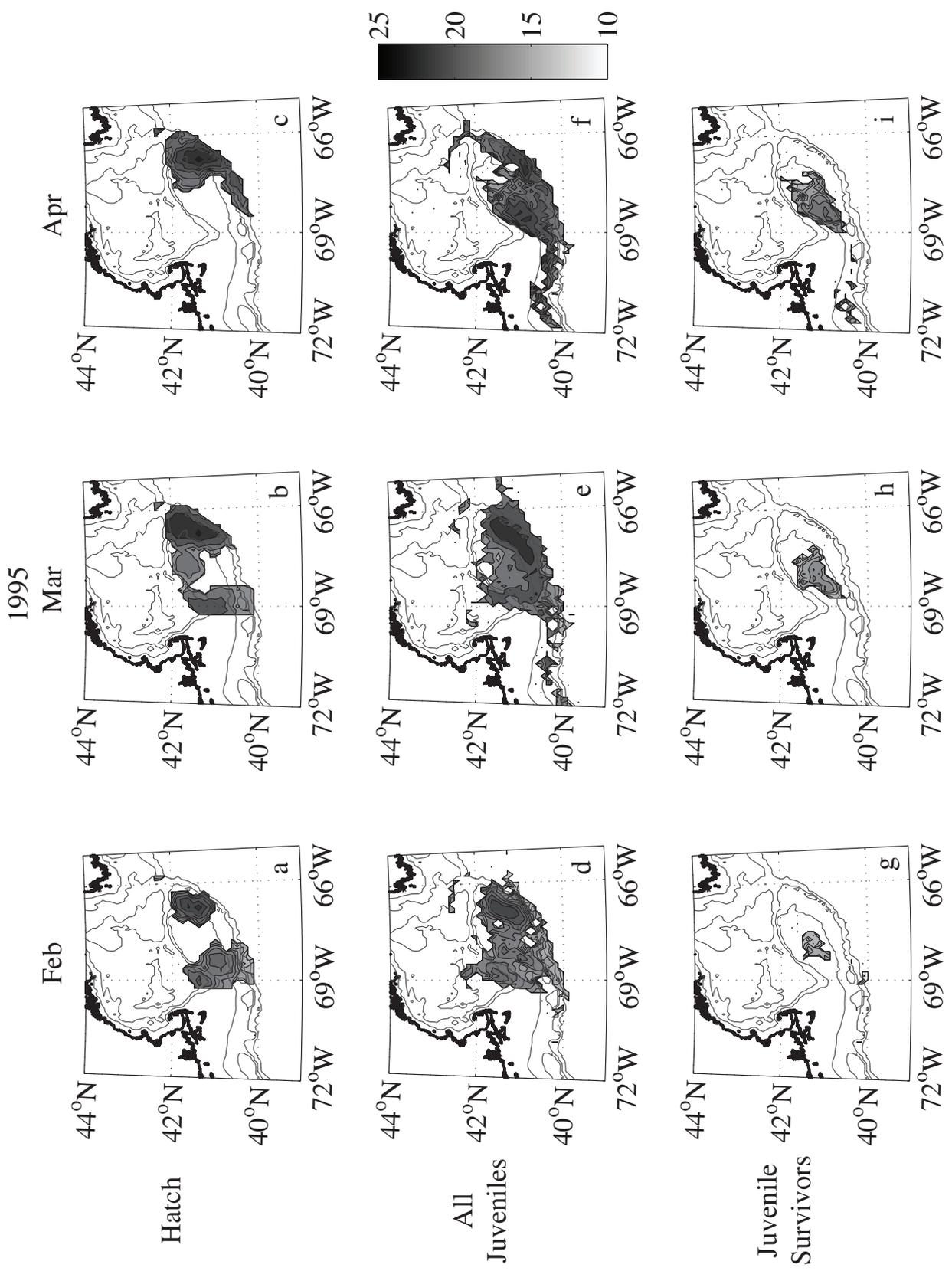
1516 **Fig. 13.** Mean log abundance and standard errors ( $m^{-3}$ ) of the potential predators (a)  
1517 mysid shrimps, (b) siphonophores, and (c) hyperiid amphipods on Georges Bank in 1995  
1518 (solid line) and 1998 (dashed line).

1519

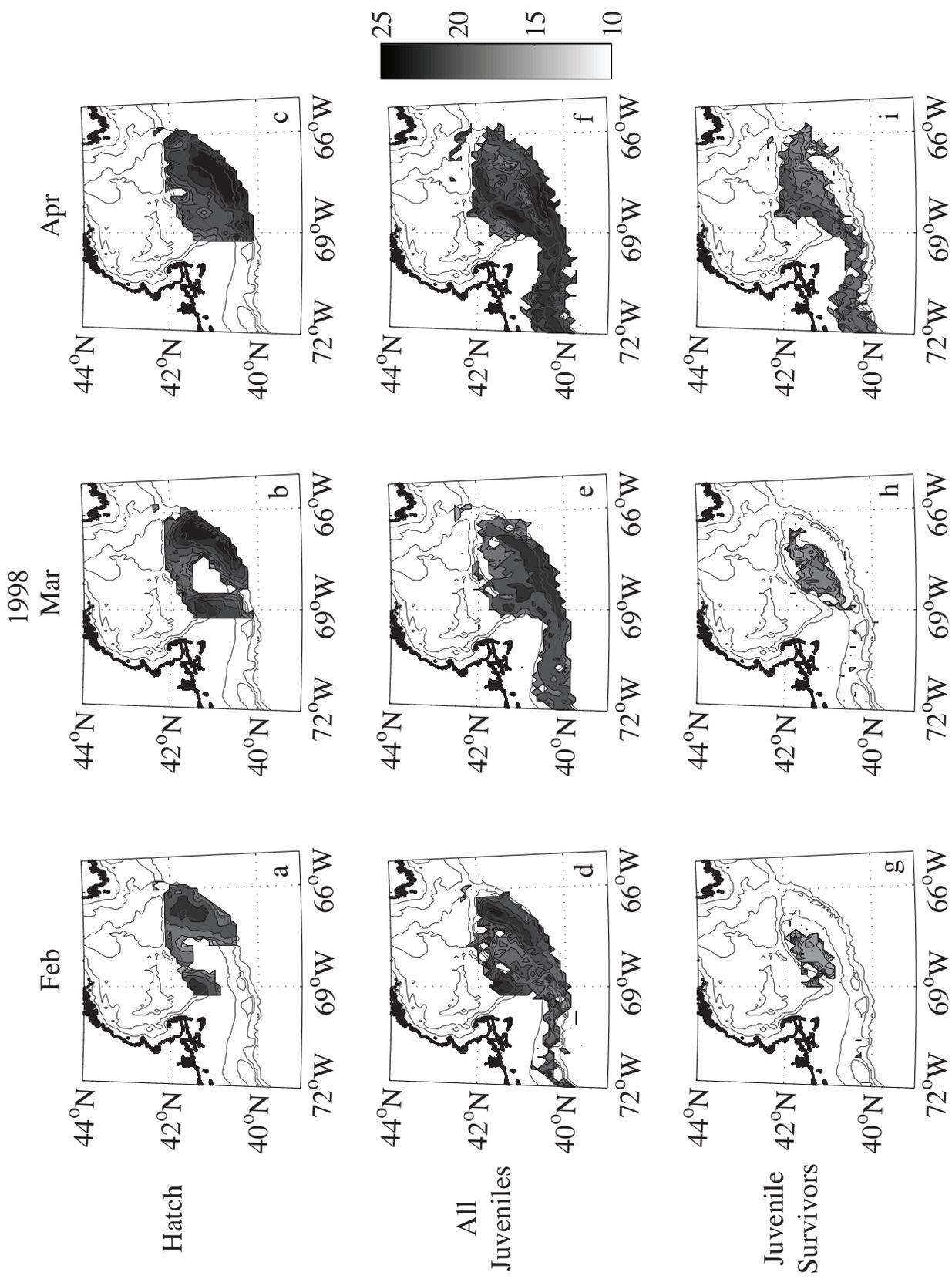
1520 **Fig. 14.** Comparison of Buckley and Durbin (2006) derived curves (lines) to model  
1521 weighted mean specific growth rates ( $d^{-1}$ ) of 12 mm survivors and the weighted mean  
1522 prey concentrations they experienced for (a) 5-7 mm and (b) 7-12 mm larvae. 1995  
1523 reference (circle), 1998 reference (diamond), 1998 low prey (plus). Note the differences  
1524 in x- and y-axis scales in (a) and (b).



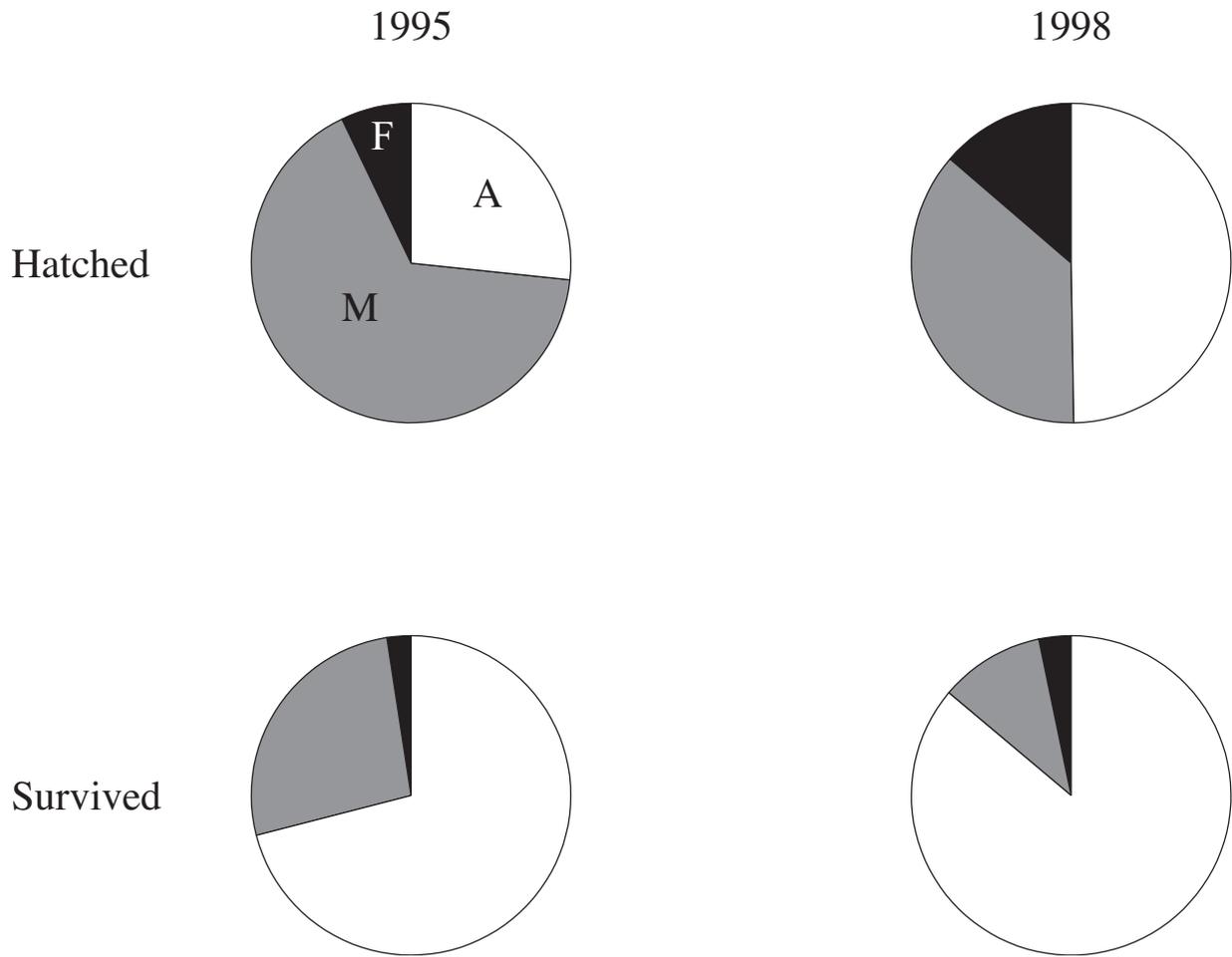
**Fig. 1.** Map of the Gulf of Maine (GOM) and Georges Bank with the subregions: Crest (C), Great South Channel (GSC), Mid-Atlantic Bight (MAB), Northeast Peak (NEP), Northern Flank (NF), and Southern Flank (SF). The 60, 100, and 200 m isobaths are shown and labeled.



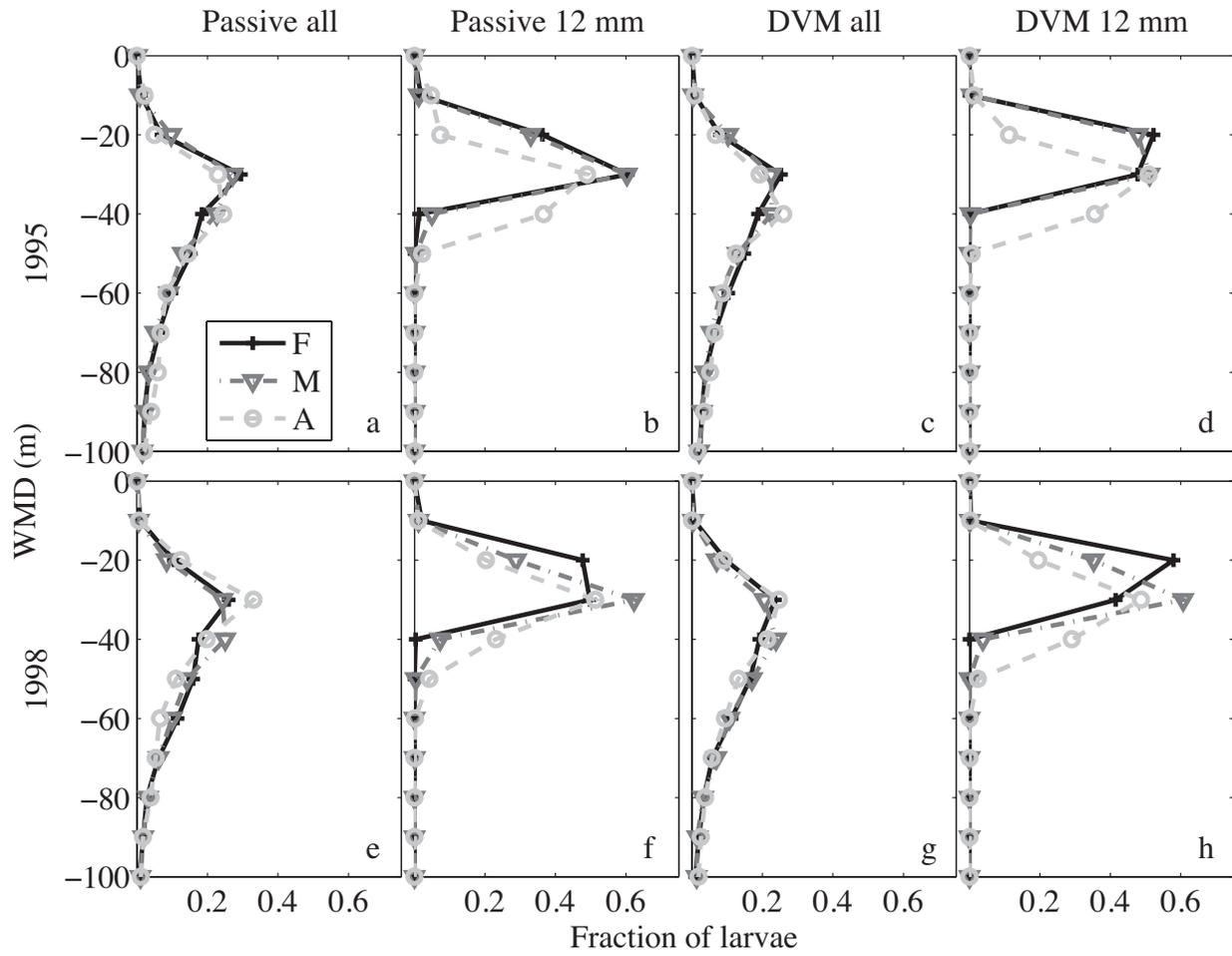
**Fig. 2.** 1995 reference case distributions of individuals at hatch (a-c), of all individuals, dead or alive, at the weighted mean time to 12 mm (d-f), and of individuals that survived to 12 mm at the weighted mean time to 12 mm (g-i). The gray lines are the 60, 100, and 200 m isobaths. Hatch locations were determined from observations of egg abundance (Sibunka *et al.*, 2006) projected forward using estimated egg mortality rates and spatially integrated kriging as described in Mountain *et al.* (2003, 2008). Contours are presented for the log of the fraction of individuals.



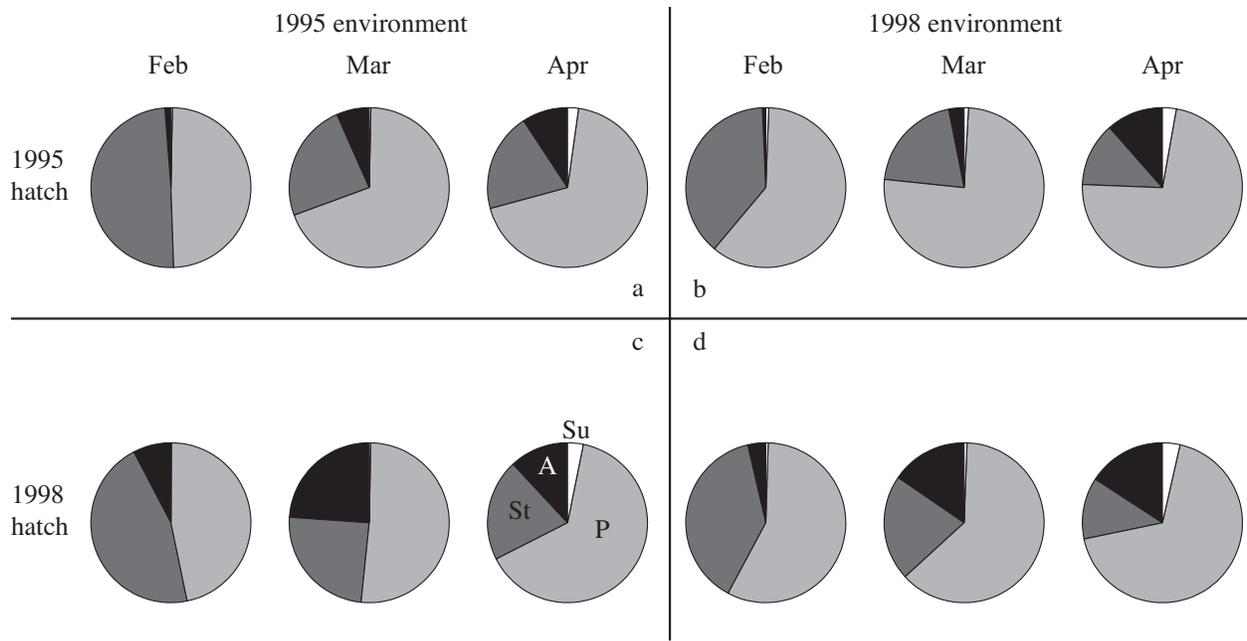
**Fig. 3.** 1998 reference case distributions of individuals at hatch (a-c), of all individuals, dead or alive, at the weighted mean time to 12 mm (d-f), and of individuals that survived to 12 mm at the weighted mean time to 12 mm (g-i). The gray lines are the 60, 100, and 200 m isobaths. Hatch locations were determined from observations of egg abundance (Sibunka *et al.*, 2006) projected forward using estimated egg mortality rates and spatially integrated kriging as described in Mountain *et al.* (2003, 2008). Contours are presented for the log of the fraction of individuals.



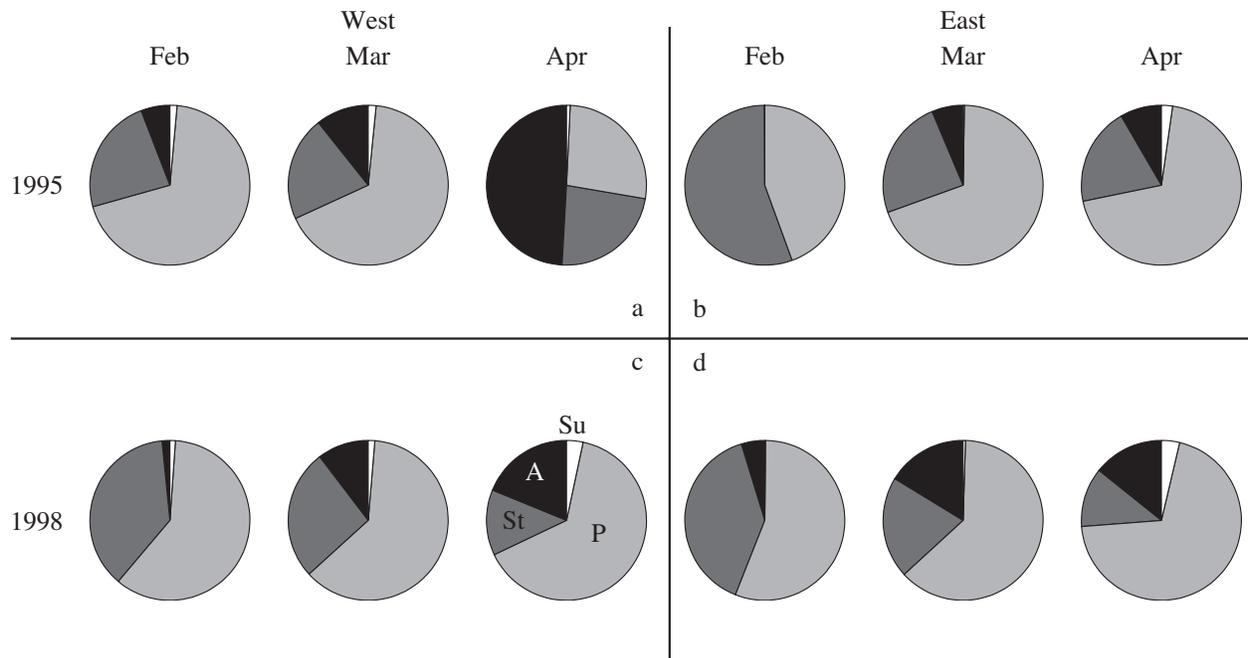
**Fig. 4.** Percent contributed by each cohort to the total number of individuals (top) hatched and (bottom) survived to 55 dph or 12 mm in the reference case. F: February (black), M: March (gray), A: April (white).



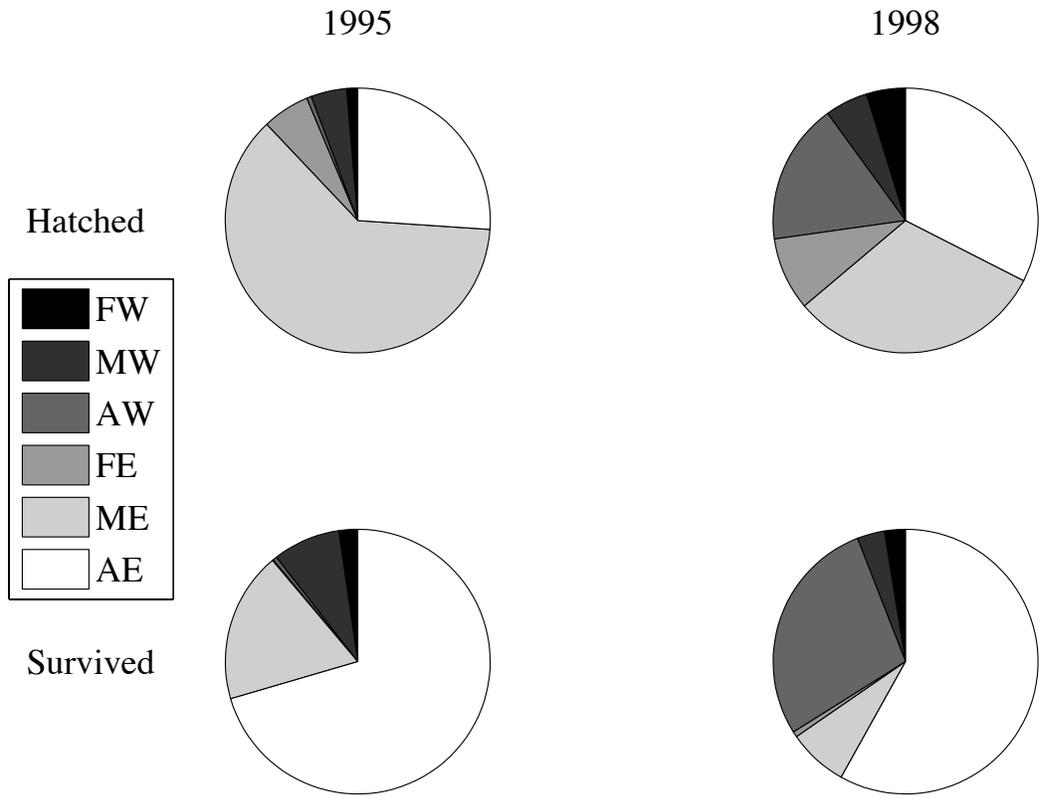
**Fig. 5.** Weighted mean depth of larvae from 1995 (a-d) and 1998 (e-h) hatch until 55 dph or 12 mm in 10 m depth bins. Passive: reference, DVM: diel vertical migration, All: all larvae, 12 mm: only those that survived to 12 mm.



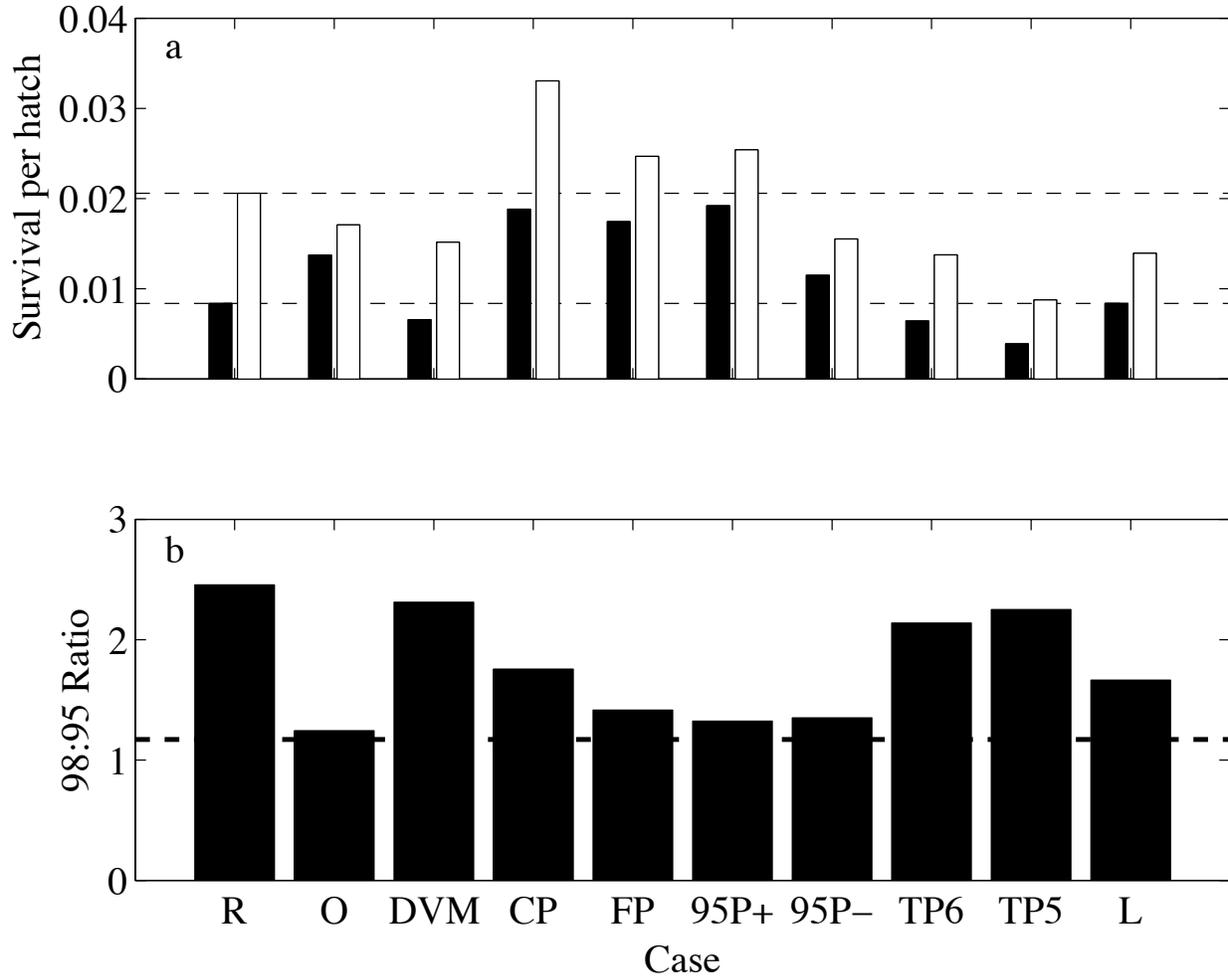
**Fig. 6.** Fate of all individuals, as percent of total individuals hatched, at 55 dph or 12 mm in the reference and cross-initialization cases. A: advection, P: predation, St: starvation, Su: survived.



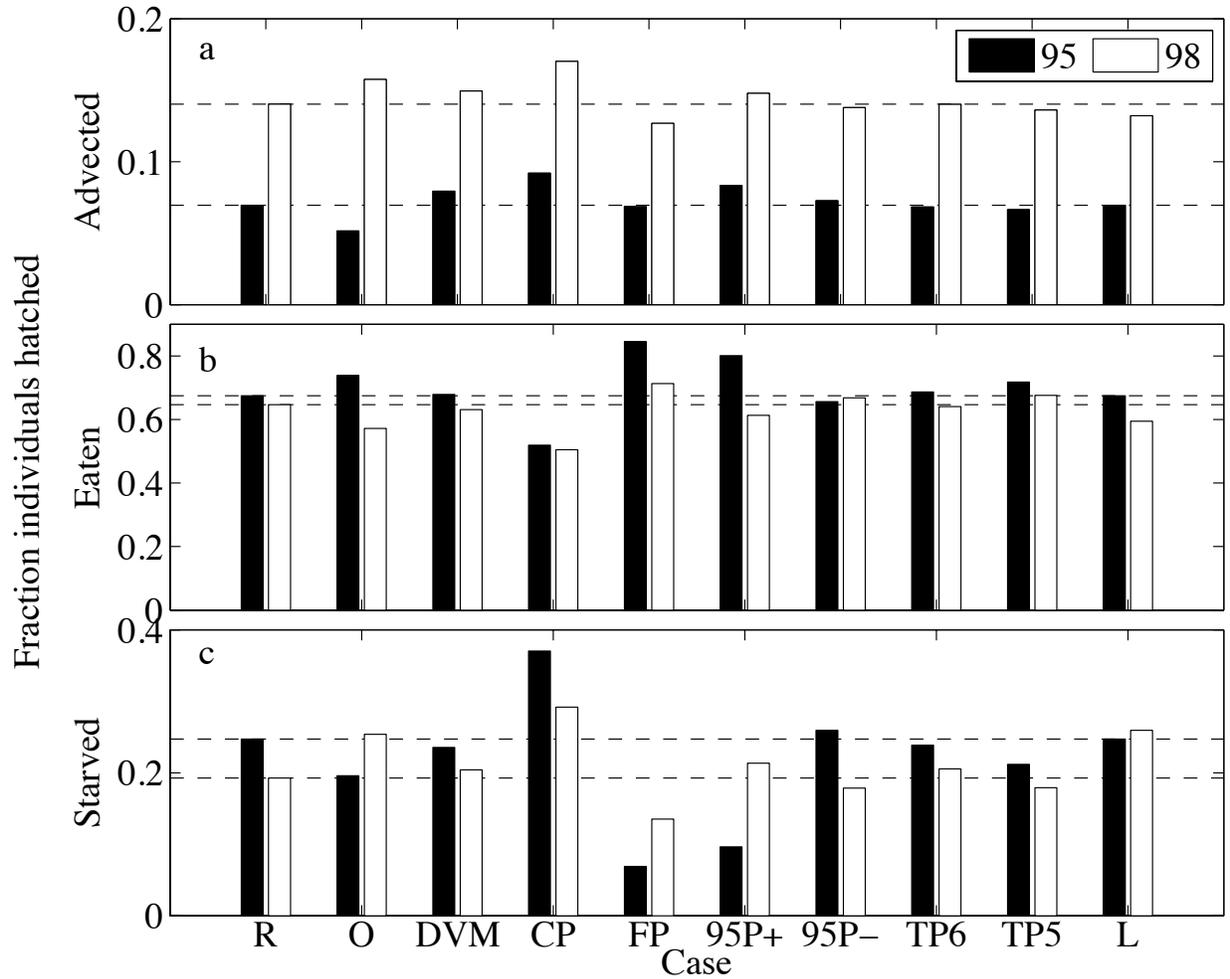
**Fig. 7.** Fate of all individuals, as percent of total individuals hatched west or east of  $67.5^{\circ}\text{W}$ , at 55 dph or 12 mm in the reference case. A: advection, P: predation, St: starvation, Su: survived.



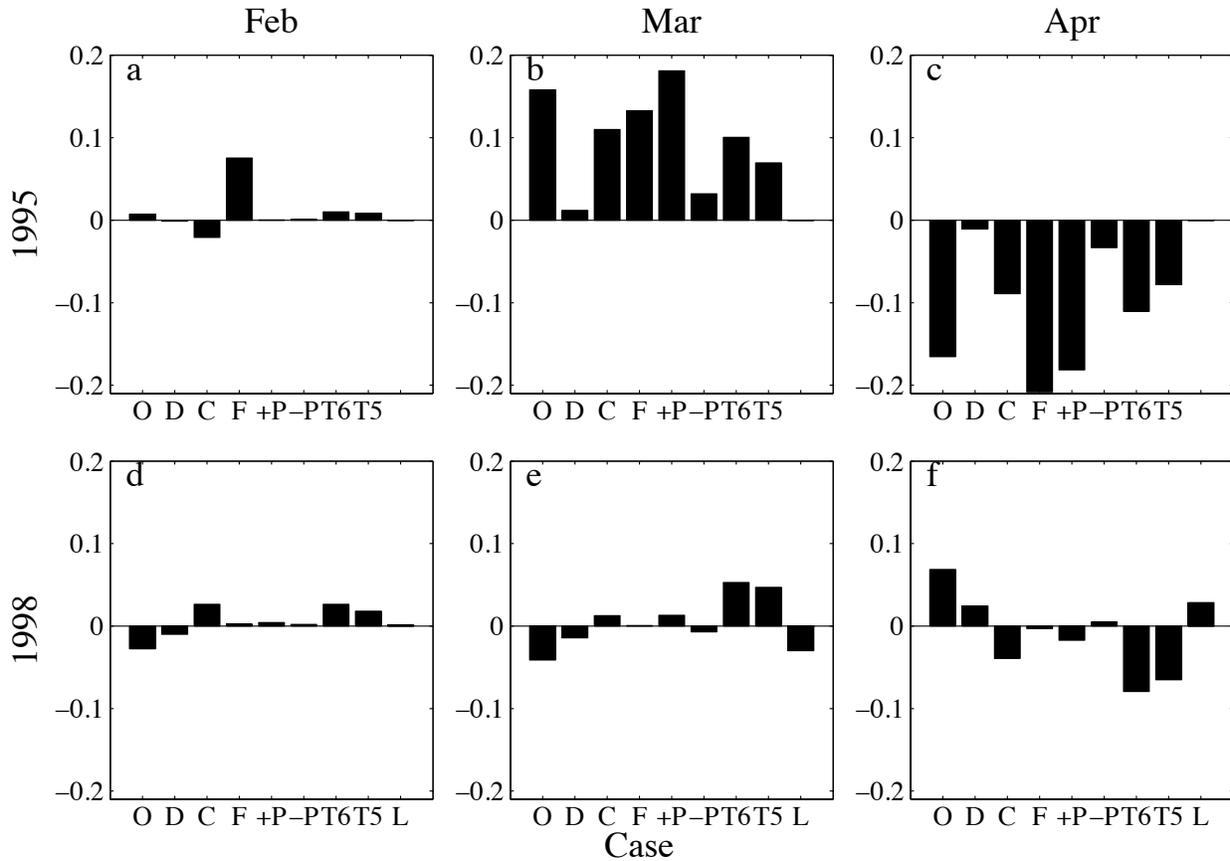
**Fig. 8.** Percent contributed by each cohort to the total number of individuals (top) hatched west or east of 67.5°W and (bottom) survived to 55 dph or 12 mm in the reference case. F: February, M: March, A: April, W: west, E: east.



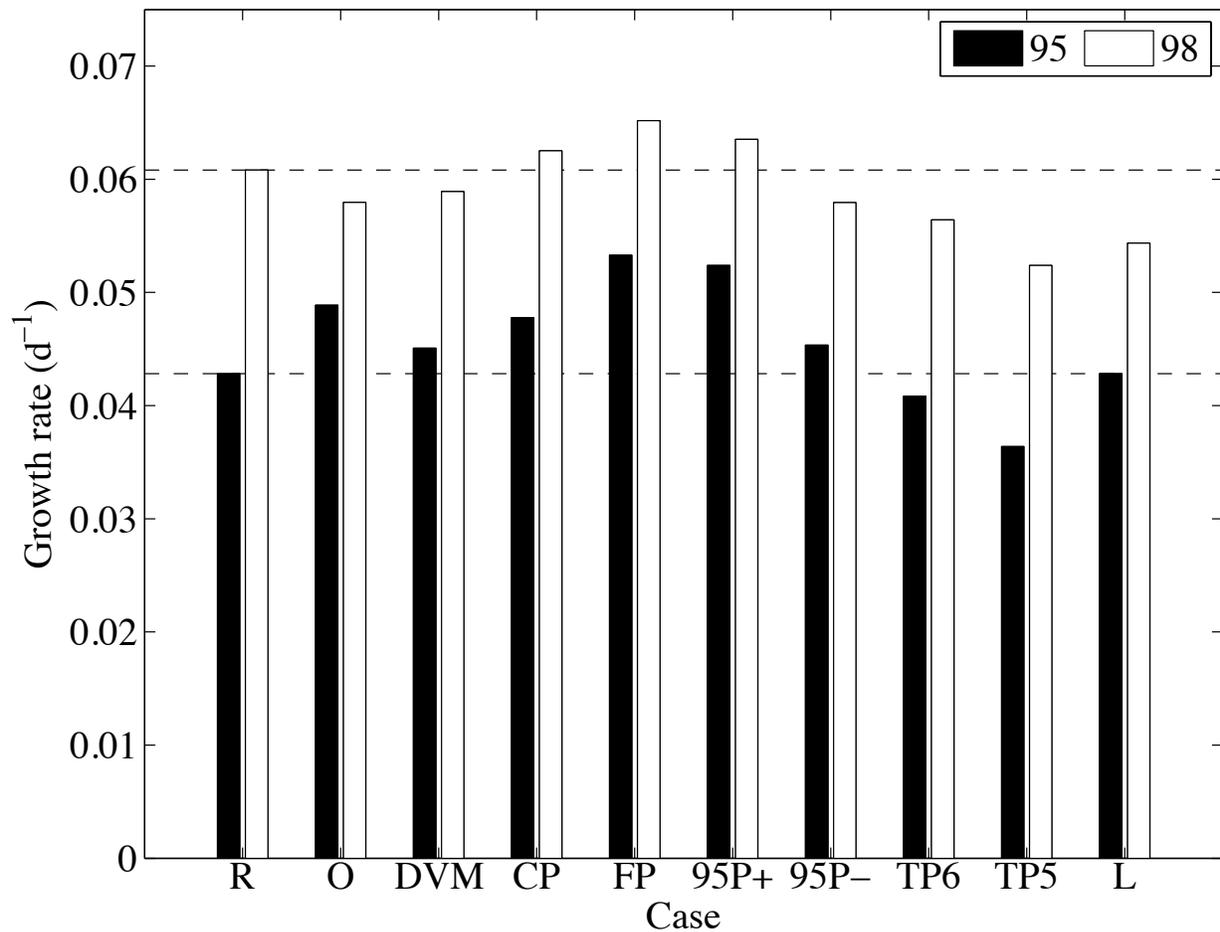
**Fig. 9.** (a) Survival per hatch (fraction of individuals that survived to 55 dph or 12 mm out of all those hatched) in 1995 and 1998 for all ten cases. The dashed lines are the 1995 and 1998 reference case values. (b) 1998:1995 ratio of the number of survivors per hatched larva. The dashed line at 1.17 represents the calculated 1998:1995 ratio of the number of recruits per hatch from Mountain and Kane (2010). R: reference, O: opposite environment, DVM: diel vertical migration behavior, CP: spatially-dependent high crest predation, FP: spatially-dependent high flank predation, 95P+: higher 1995 predation, 95P-: lower 1995 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}\text{C}$ , TP5: temperature-dependent predation  $T_{base}=5.5^{\circ}\text{C}$ , L: low prey.



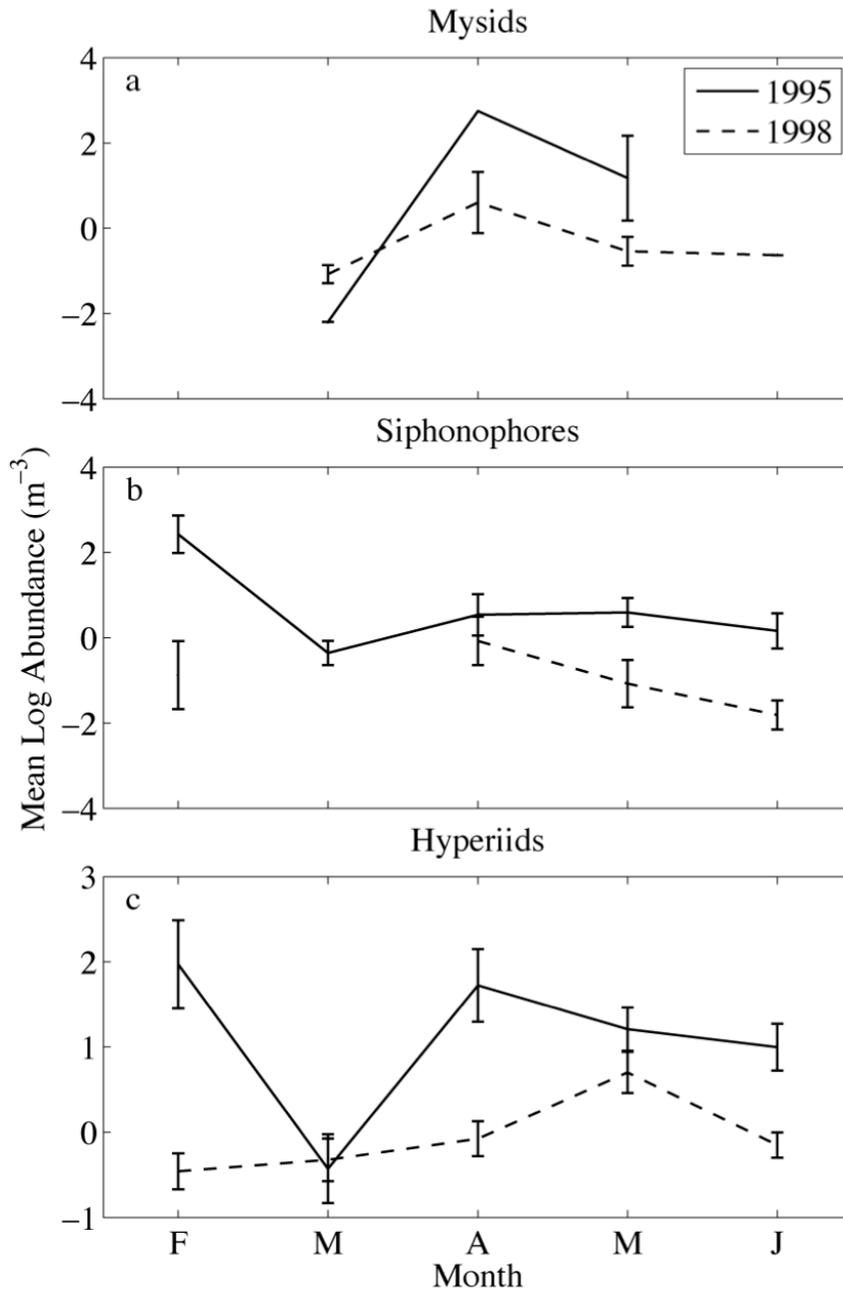
**Fig. 10.** The fraction of individuals hatched that were lost to (a) advection, (b) predation, and (c) starvation in 1995 and 1998. Note differences in y-axis scales. The dashed lines are the 1995 and 1998 reference case values. R: reference, O: opposite environment, DVM: diel vertical migration behavior, CP: spatially-dependent high crest predation, FP: spatially-dependent high flank predation, 95P+: higher 1995 predation, 95P-: lower 1995 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}\text{C}$ , TP5: temperature-dependent predation  $T_{base}=5.5^{\circ}\text{C}$ , L: low prey.



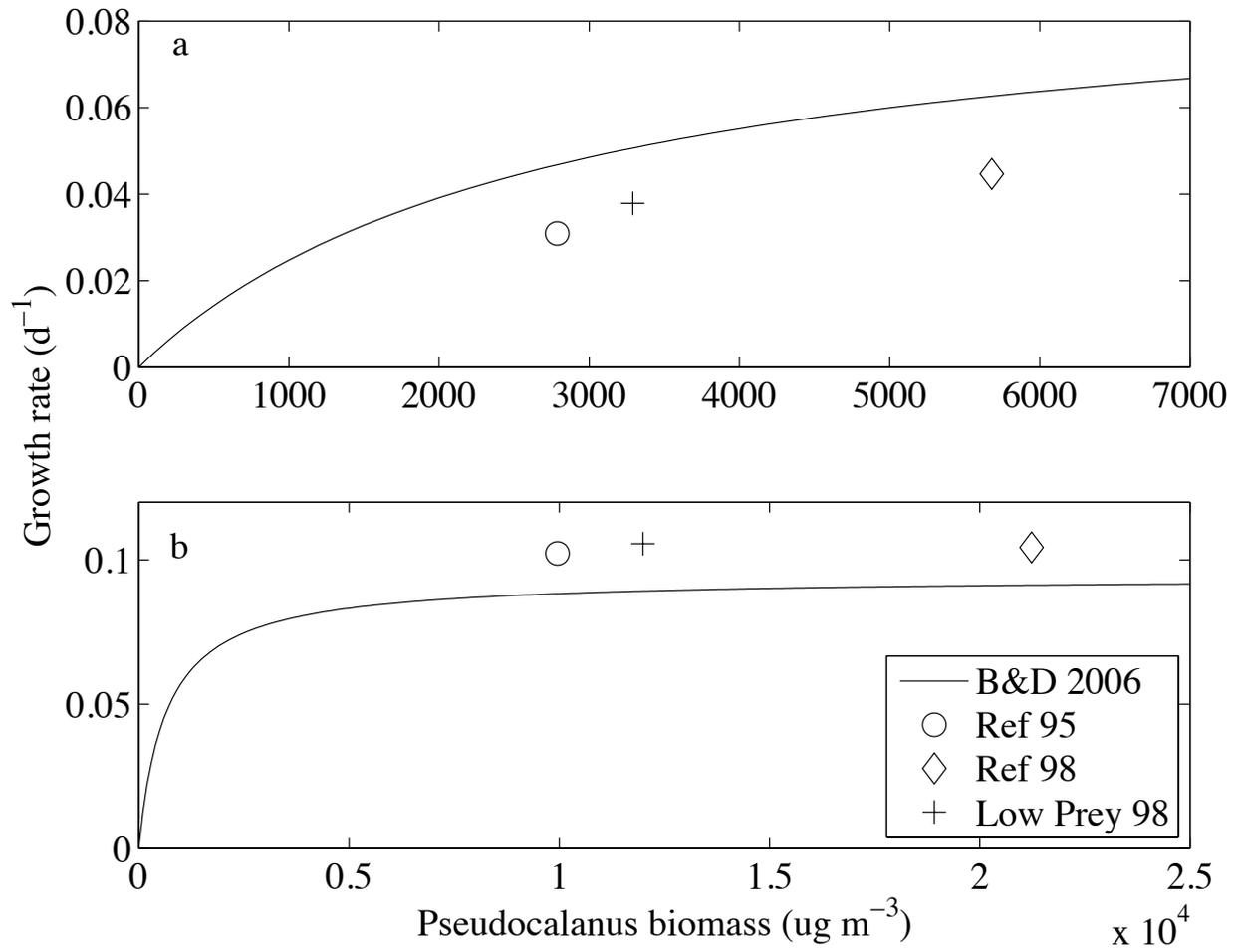
**Fig. 11.** Fraction of surviving individuals from each cohort (cohort contribution) is presented as the difference from the reference case for 1995 (a-c) and 1998 (d-f). O: opposite environment, D: diel vertical migration behavior, C: spatially-dependent high crest predation, F: spatially-dependent high flank predation, P+: higher 1995 predation, P-: lower 1995 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}\text{C}$ , TP5: temperature-dependent predation  $T_{base}=5.5^{\circ}\text{C}$ , L: low prey.



**Fig. 12.** Weighted mean specific growth rate ( $d^{-1}$ ) of surviving 12 mm individuals from all cohorts in 1995 and 1998. The dashed lines are the 1995 and 1998 reference case values. R: reference, O: opposite environment, DVM: diel vertical migration behavior, CP: spatially-dependent high crest predation, FP: spatially-dependent high flank predation, 95P+: higher 1995 predation, 95P-: lower 1995 predation, TP6: temperature-dependent predation  $T_{base}=6.5^{\circ}C$ , TP5: temperature-dependent predation  $T_{base}=5.5^{\circ}C$ , L: low prey.



**Fig. 13.** Mean log abundance and standard errors (m<sup>-3</sup>) of the potential predators (a) mysid shrimps, (b) siphonophores, and (c) hyperiid amphipods on Georges Bank in 1995 (solid line) and 1998 (dashed line).



**Fig. 14.** Comparison of Buckley and Durbin (2006) derived curves (lines) to model weighted mean specific growth rates ( $\text{d}^{-1}$ ) of 12 mm survivors and the weighted mean prey concentrations they experienced for (a) 5-7 mm and (b) 7-12 mm larvae. 1995 reference (circle), 1998 reference (diamond), 1998 low prey (plus). Note the differences in x- and y-axis scales in (a) and (b).

## 1 APPENDIX: Model equations

2 All parameters and variables are defined in Table A1.

3

### 4 *Prey density*

5 The *Pseudocalanus* spp. density was modeled with a 4-stage (eggs-nauplii-  
6 copepodite-adult) concentration-based population model (Hu *et al.*, 2008; Ji *et al.*, 2009),  
7 excluding the eggs as a prey source. Individual-based model copepod density,  $prey_{dens,i}$   
8 ( $\text{mm}^{-3}$ ), was calculated from the *Pseudocalanus* spp. population model density,  $ENCA_i$   
9 ( $\text{m}^{-3}$ ), for each developmental stage  $i$  (N, C, A) according to the following.

10 For all 1995 simulations,

$$11 \quad prey_{dens,i} = 10^{-9} \cdot ENCA_i. \quad [1]$$

12 For the 1998 low prey simulation,

$$13 \quad prey_{dens,i} = 2.5 \cdot 10^{-9} \cdot ENCA_i. \quad [2]$$

14 For all other 1998 simulations,

$$15 \quad prey_{dens,i} = 5.0 \cdot 10^{-9} \cdot ENCA_i. \quad [3]$$

16

### 17 *Copepod characteristics*

18 The length, width, and biomass of a grouped developmental stage was set as the  
19 mean of all stages within that group using the stage-specific lengths,  $l_{cope}$  (mm), widths,  
20  $width$  (mm), and biomasses,  $biom$  ( $\mu\text{g}$ ), in Davis (1984, 1987) (Table A2). The copepod  
21 image area,  $A_{cope}$  ( $\text{mm}^2$ ), was

$$22 \quad A_{cope} = 0.75 \cdot l_{cope} \cdot width, \quad [4]$$

23 and the *Pseudocalanus* spp. specific swimming speed,  $u$  ( $\text{mm s}^{-1}$ ), was

24  $u = 0.859 \cdot l_{cope}$ . [5]

25

26 *Light*

27 Visible surface light, PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), was estimated from the physical model  
28 output of shortwave radiation, *swrad* ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),

29  $\text{PAR} = 0.45 \cdot \text{swrad}$  [6]

30 A ratio of PAR to shortwave radiation of 0.45 is representative of field measurements  
31 (c.f. Papaioannou *et al.*, 1993). In situ light,  $E(z)$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), decayed with depth;

32  $E(z) = \text{PAR} \cdot e^{-z \cdot \text{att}}$ , [7]

33 with an attenuation coefficient, *att* ( $\text{m}^{-1}$ ), characteristic of the Gulf of Maine/Georges  
34 Bank region.

35

36 *Larval visual range*

37 Larval eye sensitivity,  $E_l$ , was a function of its length,

38  $E_l = \frac{l^2}{0.015}$ . [8]

39 and was used in the calculation of visual range,  $R_{larva}$  (mm),

40  $R_{larva}^2 = C \cdot A_{cope} \cdot E_l \cdot \exp(-c \cdot R) \cdot \frac{E(z)}{K_e + E(z)}$ , [9]

41 also a function of prey contrast,  $C$ , copepod image area, the scattering of image-forming  
42 light,  $c$ , in situ light, and the larval light half saturation value,  $K_e$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

43

44 *Turbulence*

45 Turbulent kinetic energy, *tkc* ( $\text{m}^2 \text{s}^{-3}$ ), was related to the vertical diffusivity, *kh* ( $\text{m}^2 \text{s}^{-1}$ ),  
46 from the physical model,

47  $tke = 1.6 \cdot 10^{-5} \cdot kh,$  [10]

48 and was used to calculate the turbulent velocity,  $\omega$  (mm s<sup>-1</sup>),

49  $\omega = 10^{-3} \cdot \sqrt{3.615 \cdot (tke \cdot (R_{larva} \cdot 10^{-3}))^{2/3}}.$  [11]

50

51 *Probability of successful capture*

52 The probability of successful capture,  $p_{cap}$ , was an empirical function of prey  
 53 species (*Pseudocalanus* spp.) and stage length fit to the results of mechanistic simulations  
 54 of species-specific prey escape behaviors, which included the deformation rate threshold,  
 55 escape jump speed, and escape jump angle, such that

56 
$$p_{cap} = \frac{\exp(d_1 \cdot r^3 + d_2 \cdot r^2 + d_3 \cdot r + d_4)}{1 + \exp(d_1 \cdot r^3 + d_2 \cdot r^2 + d_3 \cdot r + d_4)},$$
 [12]

57 where  $d$ 's are species-specific constants, and  $r$  is the copepod prey to larval fish length  
 58 ratio.

59

60 *Encounter rate*

61 If  $p_{cap} < 0.05$ , then the number of prey encountered,  $enc$  (mm<sup>-3</sup>), was zero.

62 Otherwise, the number of prey encountered per time step,  $dt$ , was a function of prey  
 63 density, larval pause frequency,  $f$  (s<sup>-1</sup>), larval pause duration,  $\tau$  (s), larval visual range,  
 64 copepod swimming speed, and turbulent velocity,

65 
$$enc = prey_{dens} \cdot \left( \frac{2}{3} \pi \cdot f \cdot R_{larva}^3 + \pi \cdot f \cdot \tau \cdot R_{larva}^2 \cdot \sqrt{u^2 + \omega^2} \right) \cdot dt.$$
 [13]

66

67 *Ingestion*

68 Each copepod developmental stage was encountered and captured separately. The  
 69 number of each stage captured,  $cap$ , and the biomass of each stage ingested,  $ingest_i$  ( $\mu\text{g}$ ),  
 70 for each stage were

$$71 \quad cap = enc \cdot p_{cap}, \quad [14]$$

$$72 \quad ingest_i = cap \cdot biom. \quad [15]$$

73 Total ingestion,  $ingest_{tot}$  ( $\mu\text{g}$ ), was the sum of the biomass ingested of each copepod  
 74 developmental stage;

$$75 \quad ingest_{tot} = \sum_i^{N,C,A} ingest_i. \quad [16]$$

76 A fraction of the ingested biomass was assimilated using a size-dependent assimilation  
 77 efficiency,  $assim$ ,

$$78 \quad assim = 0.8 \cdot (1.0 - 0.4 \cdot \exp(-0.002 \cdot (m_{\mu g} - 50.0))) \cdot dt/3600. \quad [17]$$

79 The assimilated biomass moved into the stomach, but was limited by the amount of room  
 80 available in the stomach from the previous time step. The new gut contents,  $gut$  ( $\mu\text{g}$ ),  
 81 became

$$82 \quad gut_t = gut_{t-dt} + assim \cdot ingest_{tot} \quad [18]$$

83 if they were less than the size of the larval gut. Otherwise, they were the size of the gut,  
 84 which was 6% of the larval mass.

85

### 86 *Metabolism*

87 The routine respiration rate,  $metab$  ( $\mu\text{g}$ ), of haddock was set as

$$88 \quad metab_r = 1.021 \cdot m_{m.g}^{0.979} \cdot e^{0.092 \cdot T} \cdot dt/3600, \quad [19]$$

89 where  $T$  is temperature in  $^{\circ}\text{C}$ . Metabolism was increased a constant amount during light  
 90 hours to account for the swimming activity of feeding fish. The light threshold was

91 updated to reflect the recent findings of active feeding at low light intensities. The light  
 92 threshold was  $5.0 \times 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$  for larvae  $< 7.5 \text{ mm}$  and  $5.0 \times 10^{-4} \mu\text{mol m}^{-2} \text{s}^{-1}$  for  
 93 larvae  $\geq 7.5 \text{ mm}$ . Active metabolism,  $metab_a$  ( $\mu\text{g}$ ), was

$$94 \quad metab_a = 1.4 \cdot metab_r \quad [20]$$

95 for larvae  $\leq 5.5 \text{ mm}$  and

$$96 \quad metab_a = 2.5 \cdot metab_r \quad [21]$$

97 for larvae  $> 5.5 \text{ mm}$ .

98

### 99 *Maximum growth*

100 If the gut contents were enough for maximum growth ( $gut \geq D$ ), then the mass  
 101 specific growth rate ( $\% \text{ d}^{-1}$ ) was a temperature-dependent rate,

$$102 \quad sgr_{\max} = s_1 + s_2 \cdot T - s_3 \cdot T \cdot \ln(m_{mg}) - s_4 \cdot T \cdot \ln(m_{mg})^2 + s_5 \cdot T \cdot \ln(m_{mg})^3 \quad [22]$$

103 where  $s$ 's are constants. The maximum instantaneous growth rate  $g_{\max}$  ( $\text{dt}^{-1}$ ) was  
 104 calculated from the specific growth rate,

$$105 \quad g_{\max} = \ln\left(\left(\frac{sgr_{\max}}{100}\right) + 1\right) \cdot dt / (24 \cdot 3600). \quad [23]$$

106 The biomass required to grow at the maximum rate,  $D$  ( $\mu\text{g}$ ), was

$$107 \quad D = (\exp(g_{\max}) - 1) \cdot m_{\mu\text{g}} + metab_a. \quad [24]$$

108 If  $gut \geq D$ , then the gut contents were reduced by  $D$ ,

$$109 \quad gut = gut - D, \quad [25]$$

110 the weight gain,  $gain$  ( $\mu\text{g}$ ), was

$$111 \quad gain = (\exp(g_{\max}) - 1) \cdot m_{\mu\text{g}}, \quad [26]$$

112 and growth,  $g$  ( $\text{dt}^{-1}$ ), was set as

113  $g = g_{\max} \cdot$  [27]

114

115 *Food-limited growth*

116 If the gut contents were lower than required ( $gut < D$ ) by the maximum growth,  
117 then growth was determined by the biomass available in the stomach. The weight gain  
118 equaled

119  $gain = gut - metab_a,$  [28]

120 and the gut contents were reduced by this amount

121  $gut = gut - gain.$  [29]

122 Instantaneous growth was calculated as

123  $g = \ln(m_{\mu g} + gain) - \ln(m_{\mu g}).$  [30]

124

125 *Size increase*

126 The larval weight was updated by the mass gained,

127  $m_{\mu g} = m_{\mu g} + gain.$  [31]

128 Length was calculated from weight as

129  $l = \frac{m_{\mu g}^{1/3.768}}{0.194}$  [32]

130 if this length was greater than or equal to the old length, otherwise the length from the  
131 previous time step was used since shrinking in length is not possible.

132

133 *Starvation*

134 A larva was considered to have starved to death if its mass fell below 70% of the  
 135 reference mass,  $m_{ref}$  ( $\mu\text{g}$ ), the mass that it would have at that length from an empirical  
 136 length-weight relationship of haddock larvae;

$$137 \quad m_{ref} = 0.194 \cdot l^{3.768}. \quad [33]$$

138

### 139 *Predation submodel*

140 The nonvisual predation rate,  $pred_{nv}$  ( $\text{dt}^{-1}$ ), was found using a size-dependent  
 141 model adapted from Peterson and Wroblewski (1984)

$$142 \quad pred_{nv} = 2.63 \cdot 10^{-4} \cdot m_g^{-0.25} \cdot dt/3600, \quad [34]$$

143 with larval mass,  $m_g$ , in g.

144 Visual predators were simulated by following the visual predation models of  
 145 Aksnes and Giske (1993), Aksnes and Utne (1997), and Fiksen & Jørgensen (2011).  
 146 Similar to larval vision, predator vision was a function of prey contrast, larval prey image  
 147 area,  $A_l$  ( $\text{m}^2$ ), predator eye sensitivity,  $E_p$ , the scattering of image-forming light, in situ  
 148 light, and the light half saturation of the predator,  $K_e$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Prey (larval fish)  
 149 width was assumed to be a constant 20% of its length such that the equation for image  
 150 area simplified to

$$151 \quad A_{larva} = 0.75 \cdot l \cdot 0.2 \cdot l = 0.15 \cdot l^2. \quad [35]$$

152 The perception radius of a predator,  $R_{pred}$  (mm), increased with larval fish size as

$$153 \quad R_{pred}^2 = C \cdot A_{larva} \cdot E_p \cdot \exp(-cR_{pred}) \cdot \frac{E(z)}{K_e + E(z)}. \quad [36]$$

154 Visual predator density  $N_{vis}$  ( $\text{m}^{-3}$ ) was assumed to decrease with increasing larval size;

$$155 \quad N_{vis} = 1.36 \cdot 10^{-2} \cdot m_{\mu\text{g}}^{-1}. \quad [37]$$

156 The visual predation rate,  $pred_{vis}$  ( $\text{dt}^{-1}$ ), took the form of that for a cruising fish predator,

157 
$$pred_{vis} = 1800 \cdot \pi \cdot v \cdot R_{pred}^2 \cdot N_{vis} \cdot dt , \quad [38]$$

158 where  $v$  ( $m s^{-1}$ ) was a constant that accounted for predator velocity, converting perception  
 159 radius from mm to m, and a parameterization such that the total base predation rate was  
 160 approximately  $0.1 d^{-1}$  for a 5 mm larva (Bailey & Houde, 1989). The visual predation rate  
 161 decreased with larval size and depth.

162 The total base predation rate,  $pred_{base}$  ( $dt^{-1}$ ), was the sum of nonvisual and visual  
 163 predation rates,

164 
$$pred_{base} = pred_{vis} + pred_{nv} . \quad [39]$$

165

166 *Temperature dependent predation*

167 In the alternate simulations, temperature-dependent predation,  $pred_{temp}$  ( $dt^{-1}$ ), was  
 168 modeled as a  $0.01 d^{-1}$  per  $1^\circ C$  increase in temperature following Houde (1989). The base  
 169 predation rate was the constant rate used in the reference simulations.

170 
$$pred_{temp} = pred_{base} + 0.01 \cdot (T - T_{base}) \quad [40]$$

171 In the T6 simulation, the base temperature,  $T_{base}$  ( $^\circ C$ ), was set as  $6.5^\circ C$ , the temperature  
 172 associated with the predation rate of  $0.1 d^{-1}$  for a 5 mm larva (Jones, 1973; Bailey &  
 173 Houde, 1989; Houde, 1989);

174 
$$pred_{temp} = pred_{base} + 0.01 \cdot (T - 6.5). \quad [41]$$

175 In the T5 simulation,  $T_{base}$  was lowered to  $5.5^\circ C$  to cause greater predation rates during  
 176 warmer months,

177 
$$pred_{temp} = pred_{base} + 0.01 \cdot (T - 5.5). \quad [42]$$

178

179 *Spatially-dependent predation*

180 Two different simulations were run with spatially-dependent predation. In each, the base  
 181 predation rate was increased 50% in one location and decreased 50% in the other,  
 182 resulting in a predation rate that was three times greater in one area than the other. In the  
 183 higher crest predation simulation (CP), predation shoalward of the 60 m isobath,  $pred_{crest}$   
 184 ( $dt^{-1}$ ), and predation in waters deeper than 60 m,  $pred_{flanks}$  ( $dt^{-1}$ ), were

$$185 \quad pred_{crest} = 1.5 \cdot pred_{base} , \quad [43]$$

$$186 \quad pred_{flanks} = 0.5 \cdot pred_{base} . \quad [44]$$

187 In the opposite simulation with higher predation on the flanks (FP) the rates were

$$188 \quad pred_{crest} = 0.5 \cdot pred_{base} , \quad [45]$$

$$189 \quad pred_{flanks} = 1.5 \cdot pred_{base} . \quad [46]$$

190

### 191 *Interannually varying predation*

192 Another set of simulations varied the predation rates between years. The base predation  
 193 rate was altered by  $\pm 10\%$  in one year and by  $\pm 10\%$  in the opposite direction in the other.

194 10% higher in 1995, 10% lower in 1998 (95+ or P+),

$$195 \quad pred_{95} = 1.1 \cdot pred_{base} , \quad [47]$$

$$196 \quad pred_{98} = 0.9 \cdot pred_{base} , \quad [48]$$

197 10% lower in 1995, 10% higher in 1998 (95- or P-),

$$198 \quad pred_{95} = 0.9 \cdot pred_{base} , \quad [49]$$

$$199 \quad pred_{98} = 1.1 \cdot pred_{base} , \quad [50]$$

200

### 201 *Predation mortality losses*

202 Losses of individuals within a super-individual via predation,  $n_{pred}$ , were modeled  
203 for each super-individual by drawing a random number from a binomial distribution of  
204 the current number of individuals,  $n$ , with the probability of predation,  $p$ .

$$205 \quad n_{pred} \sim \text{binomial}(n, p). \quad [51]$$

206 The probability was calculated from an exponential probability distribution from the total  
207 predation rate,

$$208 \quad p = 1 - \exp(-pred_{base}). \quad [52]$$

209 This probability was used with an exact binomial probability density function when  
210  $n \leq 20$ . When  $n > 20$  and  $np \leq 50$ , the Poisson approximation for a binomial distribution with  
211 small  $p$  was used,

$$212 \quad n_{pred} \sim \text{Poisson}(n \cdot p). \quad [53]$$

213 The Poisson distribution was further approximated by a normal distribution when  $n > 20$   
214 and  $np > 50$ ,

$$215 \quad n_{pred} \sim \text{normal}(n \cdot p, n \cdot p). \quad [54]$$

216 At each time step, the number of individuals was reduced by the number drawn from the  
217 binomial or binomial approximated probability distribution,

$$218 \quad n_t = n_{t-dt} - n_{pred}. \quad [55]$$

219

## 220 *Swimming behavior*

221 The diel vertical behavior simulations imposed preferred daytime and nighttime  
222 depths of 40 m and 20 m, respectively, for larvae  $>9$  mm following observations. Vertical  
223 swimming velocity,  $w$  ( $\text{m s}^{-1}$ ), was implemented as a tangential function that directed  
224 larvae towards the preferred depth,  $z_{pref}$  (m);

225  $w = w_{max} + \tanh (z - z_{pref}) ,$  [56]

226 where  $w_{max}$  ( $\text{m s}^{-1}$ ) was 1.5 times the routine swimming speed of larval cod,

227  $w_{max} = 1.5 \cdot 10^{-3} \cdot (0.261 \cdot l^{1.552} \cdot l^{-0.08} - \frac{5.289}{l}).$  [57]

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248 **Table A1.** Descriptions, units, values, and sources of symbols used in model equations.

Symbol	Description	Units	Value	Source
$A_{cope}$	copepod image area	mm <sup>2</sup>	eq. 4	Kristiansen <i>et al.</i> (2007)
$A_{larva}$	larval image area	mm <sup>2</sup>	eq. 35	Fiksen & Jørgensen (2011)
$assim$	assimilation efficiency	-	eq. 17	Lough <i>et al.</i> (2005)
$att$	light attenuation coefficient	m <sup>-1</sup>	0.18	Kristiansen <i>et al.</i> (2007)
$biom$	copepod biomass	µg	Table A2	Davis (1984, 1987)
$C$	prey contrast	-	0.3	Aksnes & Utne (1997)
$c$	image-forming light attenuation	mm <sup>-1</sup>	$5.4 \cdot 10^{-4}$	Aksnes & Giske (1993)
$cap$	number of each copepod stage captured	-	eq. 14	
$D$	biomass needed for maximum growth	µg	eq. 24	Kristiansen <i>et al.</i> (2007)
$d_1$	capture fit constant	-	$-1.06 \cdot 10^3$	
$d_2$	capture fit constant	-	$3.86 \cdot 10^3$	
$d_3$	capture fit constant	-	$-4.96 \cdot 10^2$	
$d_4$	capture fit constant	-	20.2	
$dt$	biological model time step	s	3600	
$E_l$	larval eye sensitivity	-	eq. 8	Fiksen & MacKenzie (2002)
$E_p$	predator eye sensitivity	-	$5 \cdot 10^4$	Fiksen & Jørgensen (2011)
$E(z)$	light	µmol m <sup>-2</sup> s <sup>-1</sup>	eq. 7	
ENCA	population model copepod density	m <sup>-3</sup>	ENCA output	Ji <i>et al.</i> (2009)
$enc$	number encountered	-	eq. 13	MacKenzie & Kiørboe (1995)
$f$	pause frequency	s <sup>-1</sup>	0.53	MacKenzie & Kiørboe (1995)
$g$	instantaneous growth rate	dt <sup>-1</sup>	eqs. 27, 30	
$g_{max}$	maximum instantaneous growth rate	dt <sup>-1</sup>	eq. 23	
$gain$	weight gain from growth	µg	eqs. 26, 28	Kristiansen <i>et al.</i> (2007)

<i>gut</i>	larval gut contents	$\mu\text{g}$	eqs. 18, 25, 29	Kristiansen <i>et al.</i> (2007)
<i>i</i>	copepod developmental stage	-	N, C, A	
<i>ingest<sub>i</sub></i>	biomass ingested of each stage	$\mu\text{g}$	eq. 15	
<i>ingest<sub>tot</sub></i>	total copepod biomass ingested	$\mu\text{g}$	eq. 16	
<i>K<sub>e</sub></i>	light half saturation	$\mu\text{mol m}^{-2} \text{s}^{-1}$	1.0	Aksnes & Utne (1997)
<i>kh</i>	vertical diffusivity	$\text{m}^2 \text{s}^{-1}$	FVCOM output	
<i>l</i>	larval length	mm	eq. 32	Lankin <i>et al.</i> (2008)
<i>l<sub>cope</sub></i>	copepod length	mm	Table A2	Davis (1984, 1987)
<i>m<sub>g</sub></i>	larval mass	g	$m_{\mu\text{g}} \cdot 10^{-6}$	
<i>m<sub>ref</sub></i>	larval reference mass	$\mu\text{g}$	eq. 33	Lankin <i>et al.</i> (2008)
<i>m<sub><math>\mu\text{g}</math></sub></i>	larval mass	$\mu\text{g}$	eq. 31	
<i>m<sub>mg</sub></i>	larval mass	mg	$m_{\mu\text{g}} \cdot 10^{-3}$	
<i>metab<sub>a</sub></i>	active metabolism	$\mu\text{g}$	eqs. 20, 21	Lough <i>et al.</i> (2005)
<i>metab<sub>r</sub></i>	routine metabolism	$\mu\text{g}$	eq. 19	Lankin <i>et al.</i> (2008)
<i>N<sub>vis</sub></i>	visual predator density	$\text{m}^{-3}$	eq. 37	
<i>n</i>	number of individuals per super-individual	-	eq. 55	
<i>n<sub>pred</sub></i>	number of individuals lost to predation	-	eqs. 51, 53, 54	Scheffer <i>et al.</i> (1995)
<i><math>\omega</math></i>	turbulent velocity	$\text{mm s}^{-1}$	eq. 11	MacKenzie & Leggett (1993)
PAR	surface light	$\mu\text{mol m}^{-2} \text{s}^{-1}$	eq. 6	
<i>p</i>	predation probability	-	eq. 52	
<i>p<sub>cap</sub></i>	capture success probability	-	eq. 12	
<i>pred<sub>95</sub></i>	predation rate specific to 1995	$\text{dt}^{-1}$	eqs. 47, 49	
<i>pred<sub>98</sub></i>	predation rate specific to 1998	$\text{dt}^{-1}$	eqs. 48, 50	
<i>pred<sub>base</sub></i>	reference predation mortality rate	$\text{dt}^{-1}$	eq. 39	
<i>pred<sub>crest</sub></i>	predation mortality rate on crest	$\text{dt}^{-1}$	eqs. 43, 45	
<i>pred<sub>flanks</sub></i>	predation mortality rate on flanks	$\text{dt}^{-1}$	eqs. 44, 46	

$pred_{nv}$	nonvisual predation mortality rate	$dt^{-1}$	eq. 34	Peterson & Wroblewski (1984)
$pred_{temp}$	temperature-dependent predation mortality rate	$dt^{-1}$	eqs. 40, 41, 42	
$pred_{vis}$	visual predation mortality rate	$dt^{-1}$	eq. 38	Fiksen & Jørgensen (2011)
$prey_{dens}$	copepod density	$mm^{-3}$	eqs. 1, 2, 3	
$R_{larva}$	larval perception distance	mm	eq. 9	Aksnes & Utne (1997)
$R_{pred}$	predator perception distance	mm	eq. 36	Aksnes & Utne (1997)
$r$	prey:larva length ratio	-	$l_{cope}:l$	
$s_1$	maximum growth constant	$\% d^{-1}$	1.08	Folkvord (2005)
$s_2$	maximum growth constant	$\% d^{-1} \text{ } ^\circ C^{-1}$	1.79	Folkvord (2005)
$s_3$	maximum growth constant	$\% d^{-1} \text{ } ^\circ C^{-1} \text{ } mm^{-1}$	0.074	Folkvord (2005)
$s_4$	maximum growth constant	$\% d^{-1} \text{ } ^\circ C^{-1} \text{ } mm^{-2}$	0.0965	Folkvord (2005)
$s_5$	maximum growth constant	$\% d^{-1} \text{ } ^\circ C^{-1} \text{ } mm^{-3}$	0.0112	Folkvord (2005)
$sgr_{max}$	maximum specific growth rate	$\% d^{-1}$	eq. 22	Folkvord (2005)
$swrad$	short wave radiation	$\mu mol \text{ } m^{-2} \text{ } s^{-1}$	FVCOM output	
$\tau$	pause duration	s	1.4	MacKenzie & Kiørboe (1995)
$T$	temperature	$^\circ C$	FVCOM output	
$T_{base}$	base temperature	$^\circ C$	T6:6.5, T5:5.5	
$tke$	turbulent kinetic energy	$m^2 \text{ } s^{-3}$	eq. 10	Davis <i>et al.</i> (1991)
$u$	copepod swimming speed	$mm \text{ } s^{-1}$	eq. 5	Petrik <i>et al.</i> (2009)
$v$	visual predator constant	$m \text{ } s^{-1}$	0.05	
$w$	larval swimming speed	$m \text{ } s^{-1}$	eq. 56	
$w_{max}$	maximum larval swimming speed	$m \text{ } s^{-1}$	eq. 57	Peck <i>et al.</i> (2006)
$width$	copepod width	mm	Table A2	Davis (1984, 1987)
$z$	larval depth	m		
$z_{pref}$	preferred depth for vertical behavior	m	day:40 m, night:20 m	Lough & Potter (1993)

250 **Table A2.** Mean copepod properties (Davis 1984, 1987).

	Developmental stage		
	N	C	A
<i>l<sub>cope</sub></i> (mm)	0.2850	0.6340	1.000
<i>width</i> (mm)	0.1483	0.3040	0.4000
<i>biom</i> (μg)	0.5767	4.040	16.67

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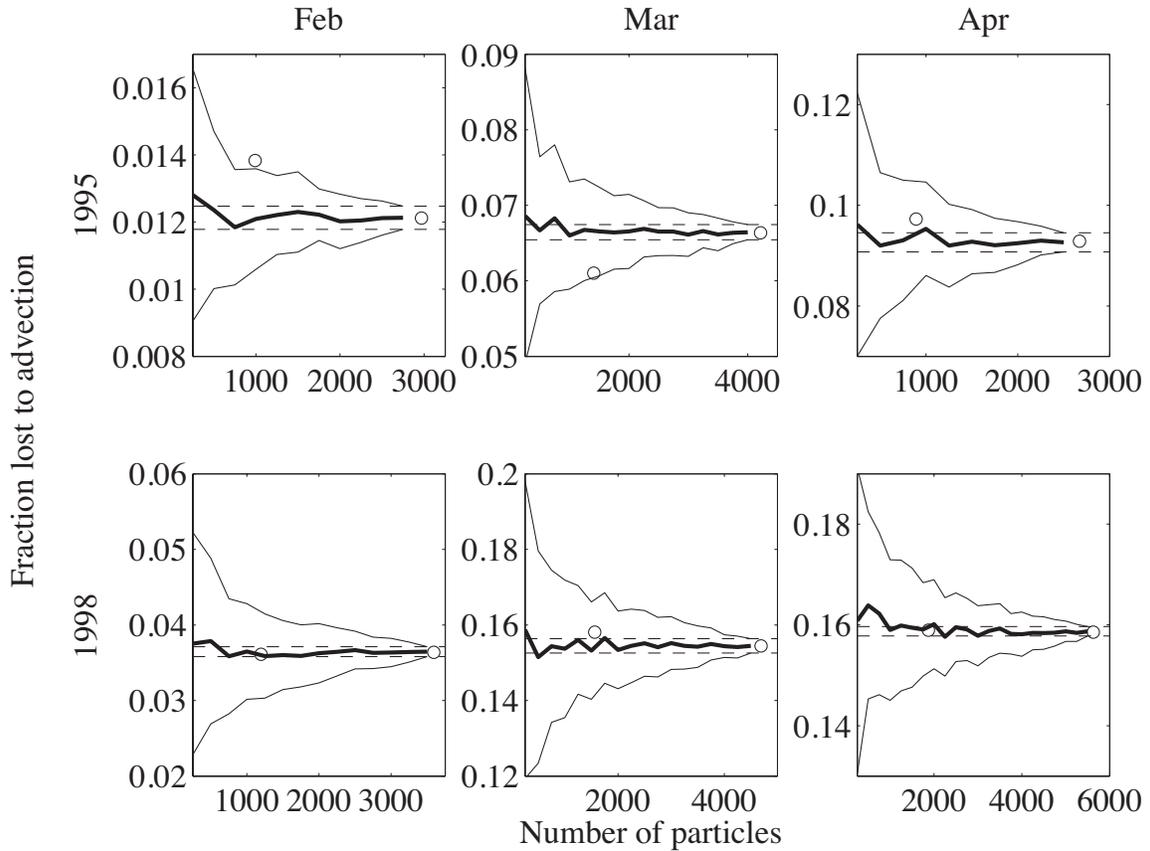
## **APPENDIX 2: Particle number sensitivity analysis**

### **METHODS**

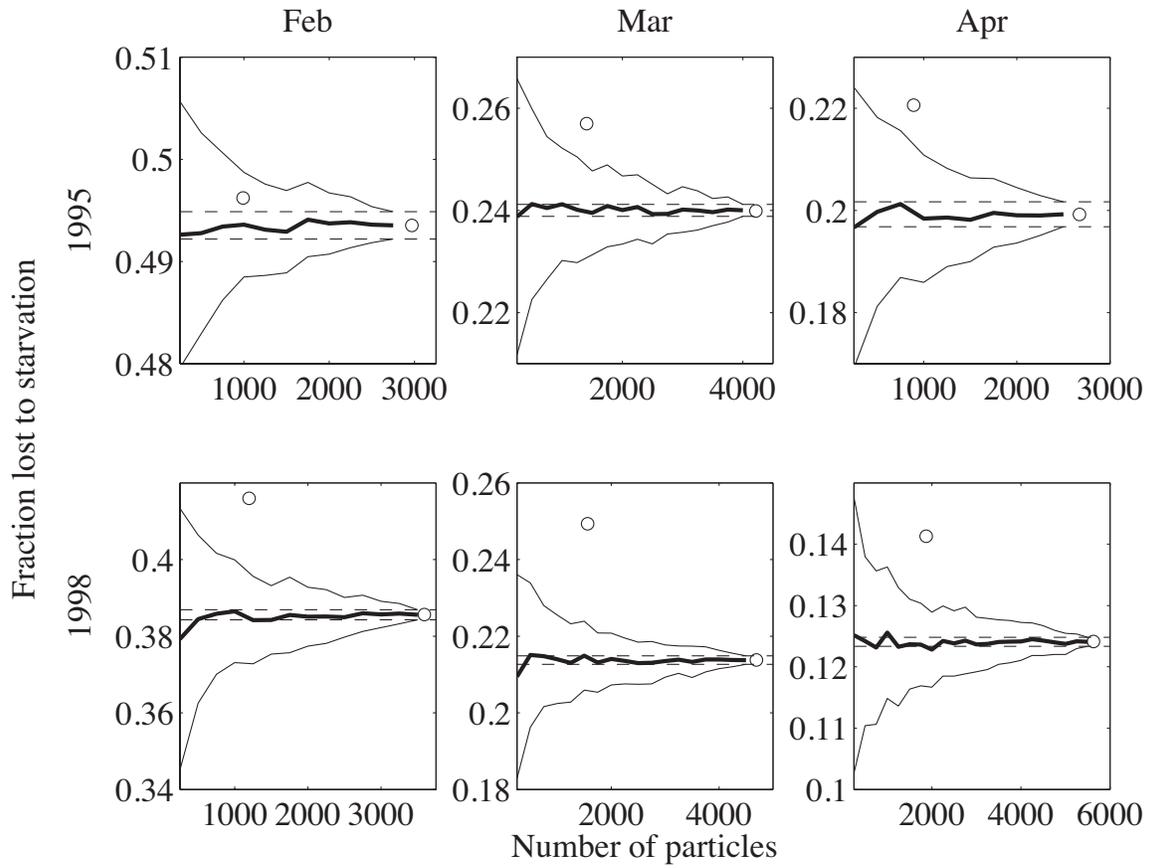
We randomly subsampled the model output with 3x particles to mean values and standard deviations for numbers of particles not simulated, and to see how modeled results compared to these. The reference cases for 1995 and 1998 were used as the model output. This output was randomly subsampled 100 times for each number of particles. We tested from 250 to the maximum number of particles of each cohort at intervals of 250. Model simulation results, subsampling mean  $\pm 1$  s.d., and  $\pm 1$  s.d. of the maximum number of particles subsampled were plotted against the number of particles. We defined convergence as when the mean fraction fell within  $\pm 1$  s.d. of the maximum number of particles subsampled.

### **RESULTS**

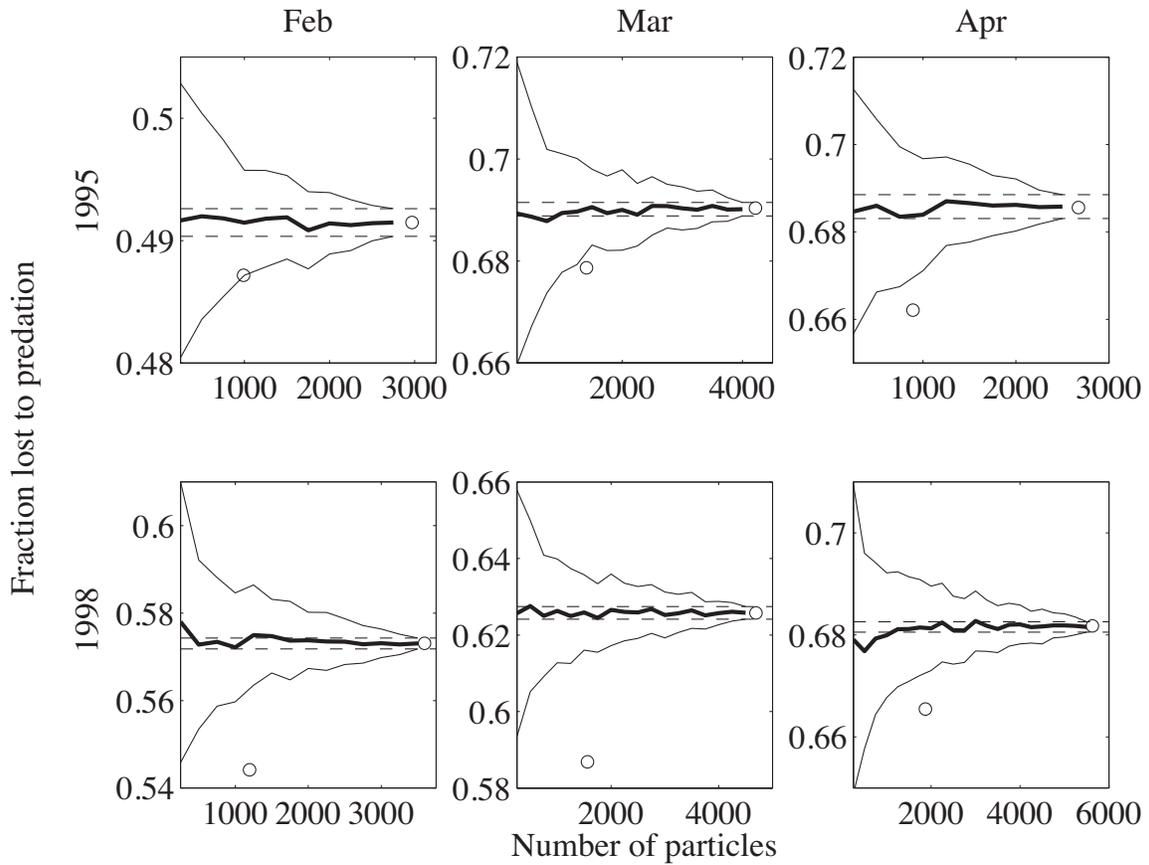
The mean fractions lost to the different sources of mortality and fractions survived appeared robust for particles  $\geq 1000$  in all cohorts of both years (Fig. A1-A4). However, model results with the original number of particles often fell outside of  $\pm 1$  s.d. of the subsampled results (14/24 times). The subsample means were always within  $\pm 1$  s.d. of the maximum number of particles subsampled for particle numbers  $\geq 2250$ . Simulations with 3x the original number of particles always fell within  $\pm 1$  s.d. of the maximum number of particles subsampled.



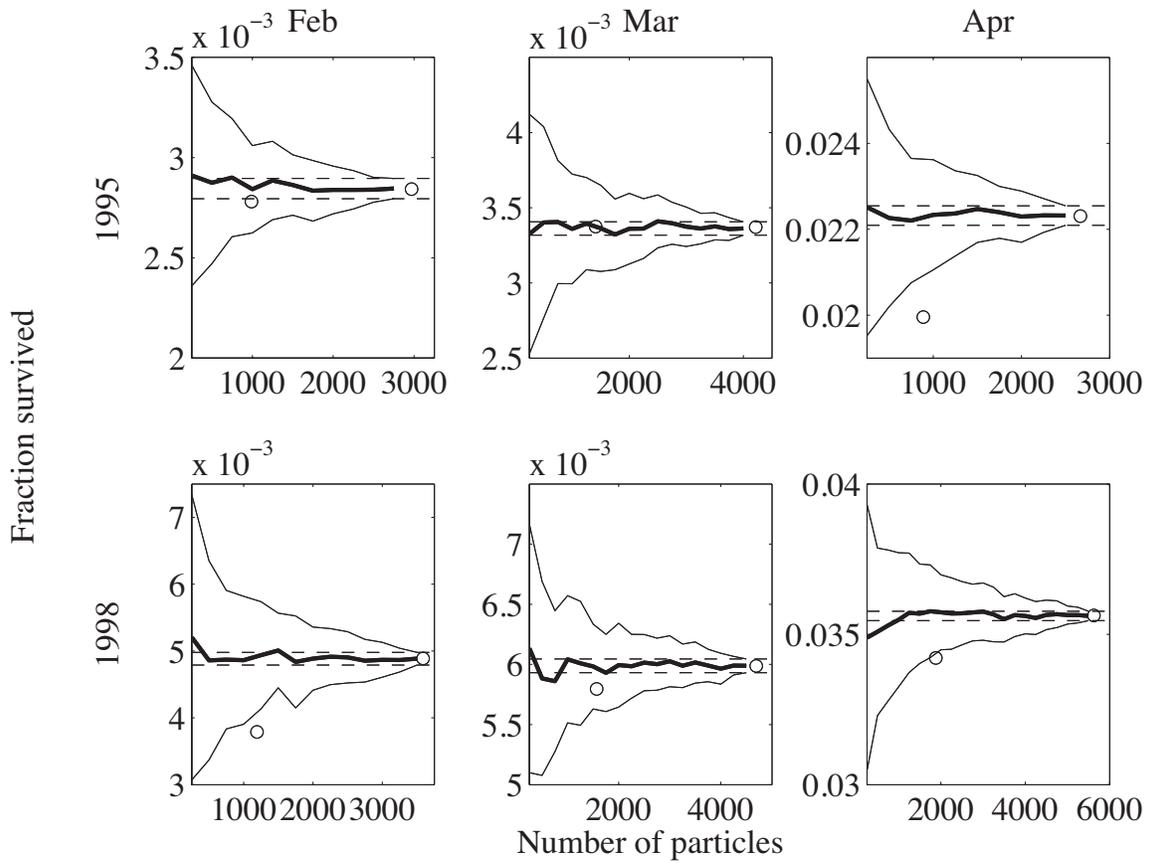
**Fig. A1.** Fraction of individuals lost to advection as a function of the number of particles simulated or subsampled. Heavy line: mean of 100 subsamples, thin line:  $\pm 1$  s.d. of 100 subsamples, dashed line:  $\pm 1$  s.d. of maximum number of particles subsampled for that cohort, circles: model simulations with 1x and 3x the original number of particles.



**Fig. A2.** Fraction of individuals lost to starvation as a function of the number of particles simulated or subsampled. Heavy line: mean of 100 subsamples, thin line:  $\pm 1$  s.d. of 100 subsamples, dashed line:  $\pm 1$  s.d. of maximum number of particles subsampled for that cohort, circles: model simulations with 1x and 3x the original number of particles.



**Fig. A3.** Fraction of individuals lost to predation as a function of the number of particles simulated or subsampled. Heavy line: mean of 100 subsamples, thin line:  $\pm 1$  s.d. of 100 subsamples, dashed line:  $\pm 1$  s.d. of maximum number of particles subsampled for that cohort, circles: model simulations with 1x and 3x the original number of particles.



**Fig. A4.** Fraction of individuals that survived as a function of the number of particles simulated or subsampled. Heavy line: mean of 100 subsamples, thin line:  $\pm 1$  s.d. of 100 subsamples, dashed line:  $\pm 1$  s.d. of maximum number of particles subsampled for that cohort, circles: model simulations with 1x and 3x the original number of particles.