

1 Species-specific abundance of bivalve larvae in relation to biological and physical conditions in
2 a Cape Cod estuary: Waquoit Bay, Massachusetts (USA)

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12 **RUNNING HEAD:** Species-specific abundance of bivalve larvae

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32 **ABSTRACT**

33
34 Physical and biological conditions impact recruitment and adult population structure of
35 marine invertebrates by affecting early life history processes from spawning to post-settlement.
36 We investigated how temperature, salinity and phytoplankton influenced larval abundance and
37 larval size structure for three species of bivalves over two non-consecutive years in Waquoit
38 Bay, MA. Abundance and size of *Mercenaria mercenaria* (quahog), *Anomia simplex* (jingle
39 clam), and *Geukensia demissa* (ribbed mussel) larvae were compared between locations in the
40 bay and with environmental conditions. Shell birefringence patterns using polarized light
41 microscopy were used to distinguish species. Larval abundances for all three species were higher
42 in 2009 than in 2007 and were positively correlated with temperature in both years. Differences
43 in larval abundance and size structure between bay sites were attributed to salinity tolerances and
44 potential source locations. Higher survival in 2009 than in 2007, as determined by number of
45 pediveligers, was likely due to higher temperatures and greater food availability during the peak
46 abundance months of July and August in 2009. Yearly differences in larval growth and survival
47 can have a large impact on recruitment. Knowing the optimal periods and locations for larval
48 abundance and survival can be useful for isolating species-specific patterns in larval dispersal
49 and to aid resource managers in enhancing or restoring depleted populations.

50

51 **INTRODUCTION**

52 The dispersal and supply of planktonic invertebrate larvae has important consequences
53 for benthic adult population structure (Roughgarden 1988). The strength of larval flux to a given
54 habitat or area can vary from year to year because of environmental conditions (Thorson 1950,
55 Shirley and Shirley 1989, Gaines and Bertness 1992). Larval supply can be influenced by many
56 factors including the timing of larval release or spawning, local hydrographic effects, larval
57 behavior, and quality of larvae (Scheltema 1986, Todd 1998). Mean densities of bivalve larvae
58 can vary greatly between consecutive years (Carriker 1961, Fegley 2001). Particularly for areas
59 where commercial adult populations are managed, larval supply can be a link in the relationship
60 between reproductive output and population growth (Botsford et al. 1998).

61 Understanding bivalve larval supply is essential to understanding the relationship
62 between larval abundance and the population structure at later stages (Pineda et al. 2007, Cowen
63 and Sponaugle 2009). Many bivalve species are harvested commercially, and natural population
64 stocks are typically managed by studying adult survivorship and fecundity without accounting
65 for the larval period (Orensanz et al. 1991). When measurements of adult reproductive effort do
66 not support their subsequent recruitment, it could be due to larval success which is rarely
67 measured. It is difficult to study pelagic larvae because of their microscopic size, short larval
68 period compared to the adult lifespan, high mortality, and ability to disperse long distances
69 (Levin 2006). A need for more in-depth studies of bivalve larvae has been expressed for years
70 (Carriker 1988, Mann 1988), but progress has lagged behind that of other invertebrate larvae
71 because of a lack of usable techniques to identify bivalve larvae at the species level (Garland and
72 Zimmer 2002).

73 Many of the biological and physical controls on bivalve larval abundance are subject to
74 seasonal and annual variation that can affect yearly recruitment dynamics (Botsford et al. 1994).
75 Wind speed and direction can affect estuarine retention time (Geyer 1997), leading to
76 fluctuations in larval import and export from an estuary (Boicourt 1988, Gaines and Bertness
77 1992, Belgrano et al. 1995). Adult spawning can be affected by water temperature and adult
78 fecundity (Keck et al. 1975, Kassner and Malouf 1982), which can affect larval survival, growth
79 and recruitment (Loosanoff et al. 1951, Davis and Calabrese 1964, Brousseau 1977, Gallagher et
80 al. 1986, Pechenik et al. 1990, Dekshenieks et al. 1993). Areas of low salinity can be intolerable
81 to certain species of bivalves (Loosanoff and Davis 1963). Furthermore, environmental factors
82 such as food availability and water temperature will affect the length of the larval period in the
83 plankton (Bayne 1965, Hodgson and Bourne 1988) which can affect survival and dispersal
84 distance (Loosanoff et al. 1951, Jorgensen 1981, Raby et al. 1994, Wilson and Meekan 2001).
85 Timing of phytoplankton blooms has been shown to affect timing of larval abundance in
86 barnacles, mussels and urchins (Starr et al. 1991), fish larvae (Townsend and Cammen 1988) and
87 crab larvae (Shirley and Shirely 1989), but under estuarine conditions typical bloom patterns do
88 not always occur (Litaker et al. 1987, Tomasky-Holmes 2008). These factors can vary spatially
89 with certain areas being more favorable for survival or retention than others. Although it is
90 challenging to isolate the effects of one particular environmental variable on larval abundance
91 and survival in the field, by concentrating on a few environmental variables over a long time
92 series we may be able to discern which factors have a greater effect on larval abundance on a
93 seasonal and bay-wide scale.

94 A majority of studies on larval bivalve growth and feeding have been performed in
95 laboratories (e.g. Loosanoff and Davis 1963), demonstrating growth and survival responses to

96 temperature, salinity, and food availability (Loosanoff et al. 1951, Davis and Calabrese 1964,
97 Bayne 1965, Gallagher et al. 1986, Dekshenieks et al. 1993). Effects of these factors on larval
98 growth rates in the field is not well documented due to challenges with larval sampling, as well
99 as confounding factors such as advection and mortality due to predation. A few studies have
100 attempted to follow growth and survival of larval cohorts from estimates of their size frequency
101 distributions (Jorgensen 1981, Chicharo and Chicharo 2001, Rigal et al. 2010), but this is most
102 applicable for closed systems with high retention.

103 The purpose of our study was to investigate the biological and physical factors affecting
104 larval abundance and survival of three bivalve species for 2007 and 2009 in Waquoit Bay, an
105 embayment on Cape Cod, MA. *Mercenaria mercenaria* (quahog), is a commercially important
106 shellfish resource for the bay and is found in open waters with sandy bottoms; *Guekensia*
107 *demissa* (ribbed mussel) grows along the banks in marsh channels and plays an ecologically
108 important role by filtering particles and removing nitrogen (Jordan and Valiela 1982) and
109 stabilizing shorelines and fertilizing marsh plants (Bertness 1984). *Anomia simplex* is a
110 widespread fouling organism around Cape Cod often found attached to rocks and shells (Eckman
111 1987). We compared time series of abundance and size of these three species of bivalve larvae
112 from four sites in Waquoit Bay from May through mid-October (when water temperatures
113 exceeded 15°C) and applied a state-of-the-art image-analysis method using shell birefringence
114 patterns to distinguish larval species (Twari and Gallagher 2003a,b, Thompson et al. *in press*).
115 Environmental conditions prevailing during two non-consecutive years of data collection
116 allowed us to compare a warm, dry year (2007) to an initially cooler, wet year (2009). We
117 hypothesized that better food quality in 2009 would result in more growth and show better
118 survival of larvae. We used abundance of pediveliger larvae as a proxy for larval survival to

119 competency as we were unable to estimate growth rates. We addressed the following questions:
120 (1) Does larval abundance and survival differ spatially and temporally? and (2) How do
121 environmental variables at each site and between years influence larval supply? This study
122 presents a novel effort to address species-specific questions in bivalve larval supply in Waquoit
123 Bay and relate them to population dynamics and management.

124 **METHODS**

125 **Study Site and Sampling Locations.** Waquoit Bay is a 16 km² estuary on the south
126 shore of Cape Cod, Massachusetts. The average depth in the bay is 2.5 m with an average tidal
127 range of about 0.5 m (Howes et al. 2004). Waquoit Bay exchanges water with outer Nantucket
128 Sound through two inlets with a residence time of 2-3 days and is subject to occasional
129 enhancement or reduction of exchange via wind forcing (Geyer 1997). The main freshwater
130 input to Waquoit Bay is through groundwater, but several sub-embayments exchange water with
131 the main bay and vary with freshwater and nutrient inputs (Howes et al. 2004). Residence times
132 in the sub-embayments are longer than the main bay on the order of several days to weeks
133 (Howes et al. 2004, Tomasky-Holmes 2008). We sampled at four sites representing different
134 areas of the bay (Fig. 1). The Menauhant site (MN) is the western inlet to the bay, Little River
135 (LR) is a well-mixed sub-embayment on the eastern side, Waquoit Bay – Metoxit Point site
136 (WB) is located in the middle of the bay proper, and the Childs River site (CR) is a sub-
137 embayment upstream of the western inlet and has the lowest salinities and high nitrogen
138 concentrations. In 2007 weekly samples were taken from 23 May – 26 October and in 2009
139 samples were taken weekly from 7 May – 14 October. These periods correspond to temperatures
140 exceeding 15°C, which cause spawning of most local bivalves.

141 **Larval Sampling Procedure.** On each sampling date, all four sites were sampled within
142 3-5 hours. The Waquoit Bay – Metoxit Point samples were taken from a boat both years. At each
143 other site, 2007 samples were taken from a boat and 2009 samples were taken from the same
144 dock the boat samples were taken from to save time. A bilge pump (West Marine BilgePro 2200)
145 attached to a hose and powered either from the boat console or a portable 12V battery was used
146 to collect samples with a flow rate of at 18-24 L/min. Samples were taken by slowly moving the
147 pump through the surface to 20 cm above the bottom in order to get a depth-integrated sample of
148 100-200 L. Water was filtered through a 53 μm nylon mesh PVC screen with a pre-screen of 333
149 μm mesh which was discarded. The pre-screen may have removed some large pediveliger larvae
150 but none were ever found in select 333 μm fractions that were collected. All filtered samples
151 from the 53 μm fraction were immediately preserved in 4% buffered formalin.

152 **Sample Processing and Larval Identification.** Plankton samples were first counted in
153 full or by volumetric sub-sampling for denser samples (to ensure at least 300 individuals were
154 counted per sample) under a dissection microscope. Volumes were standardized to one cubic
155 meter. One-hundred larvae were then subsampled from the total sample (or the total sample was
156 used if it contained fewer than 100 individuals) and individually imaged using a Zeiss IM35
157 microscope fitted with Moticam 1000 digital camera, polarization filter, and full wave
158 compensation plate. Motic Images Plus (version 2.0; Motic China Group, Ltd.) was used to
159 capture each polarized image.

160 Several criteria for identification were used to ensure accuracy. Field identification
161 guides of Chanley and Andrews (1971) and Loosanoff et al. (1966) were used for morphology
162 and size criteria. A polarized image library of confirmed hatchery reared and molecularly
163 identified field collected larvae was used to confirm birefringence patterns for each species.

164 These patterns have been shown to be species-specific and can aid in larval identification (Tiwari
165 and Gallagher 2003a,b, Thompson et al. *in press*). Based on these criteria, we visually sorted
166 images into fourteen species categories. Only the larval images that were identified as *Anomia*
167 *simplex*, *Geukensia demissa*, or *Mercenaria mercenaria*, composing about one-third of the total
168 images, were used in further analysis as library images of these species were identified using
169 PCR methods (Hare et al. 2001). These sorted larvae were used to test an automated image-
170 analysis method. Accuracies from control tests using these criteria to visually sort four species of
171 known larvae ranged from 85-100% and were not significant between size classes (Thompson et
172 al. *in press*), however, accuracies for both visual and automated methods are expected to
173 decrease with increasing numbers of species categories. Agreements with manually classified
174 larvae (this study) and computer classified larvae using a six-species training set ranged from 72-
175 82% for the three species studied here, which provides some estimate of the accuracies of the
176 classifications in this study.

177 Measurements of each larval shell were made by masking each larval image from its
178 background and cropping it to only the region of the larval shell. An edge-detection image
179 analysis routine in MATLAB (version R2009a; Mathworks, Inc.) was used to obtain major and
180 minor axes in pixels, which were converted to microns by calibration with a stage micrometer.
181 To assess abundance of pediveliger larvae, we used larvae greater than 200 μm as a cutoff for
182 *Mercenaria mercenaria* and *Geukensia demissa*, and greater than 175 μm for *Anomia simplex*
183 based on literature estimates (Chanley and Andrews 1971).

184 **Phytoplankton Counts.** Alongside each larval sample, 100 mL of unfiltered water was
185 sampled from the water column. Phytoplankton were identified and counted on a hemacytometer
186 slide with a light microscope a few hours after collection. Cell sizes were measured with an

187 optical micrometer. Subsamples of 10^{-3} to 10^{-1} ml were counted depending on phytoplankton
188 density. The larger volumes were examined by counting multiple chambers per sample.

189 **Environmental Data.** Measurements of temperature, salinity, pressure (depth),
190 chlorophyll a fluorescence, and other parameters were recorded in 15 minute intervals from
191 moored units (YSI 6600 sonde, YSI Inc.) at each sampling location (Fig. 1). Three sites (MN,
192 WB, and CR) were maintained by the Waquoit Bay National Estuarine Research Reserve's
193 (WBNERR) seawater quality monitoring program (SWMP), and the Little River instrument was
194 maintained by the Mashpee Shellfish Constable. Wind speed and direction were recorded from a
195 weather station at the WBNERR facility on the north end of Waquoit Bay. Data from these
196 instruments were averaged daily during the sampling period.

197 A handheld instrument (YSI 650 MDS, YSI Inc.) recorded instantaneous temperature,
198 and salinity at the time and location of plankton collection. Measurements were taken at the
199 surface, middle, and bottom of the water column. Values at these depths were averaged for each
200 sample. If salinity and/or temperature differed between by one unit or more between the surface
201 and bottom the water column was considered stratified.

202 **Time series Analysis.** Autocorrelation analysis on time series of each species'
203 concentration and mean size at each site was performed to determine the scale of independence
204 for the samples and if there was periodicity. Series means were initially subtracted from each
205 value to detrend the data prior to analysis. Only autocorrelations at lags of 1-2 weeks were
206 considered meaningful based on the total length of our time series (less than 20%, Emery and
207 Thomson 1997). To determine if larval abundance and size structure were coherent between
208 sites, cross-correlation analyses were performed between pairs of sites for species concentrations
209 and mean sizes. Data were lagged in both directions by weekly time steps. In the few cases of

210 missing data points due to a lost sample or instrument failure (no more than two per series), the
211 missing data point was interpolated using a quadratic spline to ensure continuity of the time
212 series for analysis. The time scale for independent samples for each time series was determined
213 by the time point where the autocorrelation was no longer significantly different from zero (α
214 = 0.05). Degrees of freedom were calculated by dividing the total length of the time series by the
215 time scale for independent realizations. Although this is a less conservative approach than using
216 decorrelation times (the time point when the autocorrelation function crosses the x-axis), we
217 chose this method because the time series was only 24 points and most of the time series' were
218 not autocorrelated.

219 We explored possible associations between larval concentrations and physical
220 measurements of temperature, salinity and chlorophyll using the autocorrelation and cross-
221 correlation methods described above. For these cross-correlations, the log of larval concentration
222 was used to normalize the variance of larval time series with respect to the physical variables.
223 Temperature and salinity values were recorded simultaneously with each larval sample, and
224 chlorophyll fluorescence from the continuous records were averaged for the tidal period when
225 the sample was taken. We only regarded correlations with salinities at no time lags to be
226 biologically relevant, as the salinity time series oscillates predominately at a tidal frequency,
227 much shorter than our weekly sampling interval. All statistical tests were performed using
228 MATLAB and SYSTAT (version 12.0; SPSS, Inc) software.

229 **RESULTS**

230 **Environmental Setting.** Records from water quality monitoring instruments from the
231 main bay site (WB) indicate that bay water temperatures in spring and early summer in 2007
232 were warmer and had lower chlorophyll concentrations than in 2009 (Fig. 2a, c). Initial spawning

233 temperatures over 16°C occurred in May at all sites, ideal spawning temperatures over 20°C
234 were reached by late May in 2007, but not until late June in 2009. Temperatures warmed earlier
235 at the Little River site (Thompson 2011). During August, water temperatures and chlorophyll
236 concentrations were higher in 2009 than in 2007. Salinities were similar between the two years.
237 Salinity oscillated around 27-32 PSU with slightly fresher bay water in 2009 (Fig. 2b).

238 We grouped phytoplankton into flagellate and diatom categories to represent available
239 food sources for larvae (Fig. 3). Flagellates included dinoflagellates and represent the
240 background available food source for larvae in the bay, and diatoms found were both pennate
241 (such as *Nitzschia sp.*) and centric forms (*Chaetoceros sp.*, *Thalassiosira sp.*, *Skeletonema sp.*)
242 and represent a more nutritious source when available. Food was extremely low in Little River,
243 Menauhant, and the main bay (Fig. 3a,b,d) in May and June 2007. The higher chlorophyll
244 observed in 2009 was a result of diatom blooms starting in mid-June.

245 The typical summer prevalent southwest wind pattern for southern Cape Cod was
246 observed for both years (Fig. 4), with average onshore wind speeds around 0.5-1 m/s. This would
247 lead to increased freshwater buildup and stratification within the bay (Geyer 1997). In spring and
248 fall of 2009 there were sporadic storm events changing wind speed and direction, leading to
249 more mixing and flushing of bay water during these periods.

250 **Species-specific Concentration and Size Distribution.** Concentrations of all three
251 species were higher in 2009 than in 2007 (Fig. 5-7). For both years, peak abundance occurred in
252 July and August. For *Anomia simplex*, larvae were present from late June through August in
253 2007 and from June through September with a few individuals into October in 2009 (Fig. 5).
254 This species appeared to spawn weekly throughout its period of abundance with large portions of
255 smaller larvae and pediveligers appearing simultaneously. *A. simplex* was observed first in the

256 inlet site (MN) in 2007, but in 2009 the inner bay sites, Waquoit Bay and Little River, had the
257 highest early concentrations. Few *A. simplex* were observed at Childs River. Pediveliger larvae
258 were present throughout July and August of 2009 for all sites except Childs River, indicating
259 more survival. Pediveligers only appeared 1-2 times any site in 2007.

260 Larvae of the ribbed mussel, *Geukensia demissa*, were mostly observed July through
261 October both years, with some spawning in late June in 2007 (Fig. 6). Two distinct and equal
262 spawning events were observed in 2007, while in 2009 there was a mass spawn in July and a
263 smaller spawn afterwards (with the exception of Childs River which had three large peaks).
264 Abundances were greatest at Little River and Childs River where marshes are prevalent. In 2009,
265 *G. demissa* larvae were first observed from the Menauhant inlet site, far from the upper marsh
266 regions where adults are more abundant. Pediveligers were present in August in 2007 and July
267 through September in 2009, but in lower abundance compared to the other species.

268 *Mercenaria mercenaria* larvae appeared the earliest (May-June) of all the species
269 suggesting a lower spawning temperature threshold (Fig. 7). Little River and Waquoit Bay had
270 the highest concentrations of larvae in 2009, but in 2007 the highest concentrations were
271 observed at the inlet and less from the bay sites. *M. mercenaria* concentrations had bi-weekly
272 peaks in 2007 and 2009 with modes in July and August. Pediveliger larvae were prevalent in
273 2009 at all sites with highest concentrations in August and lasting through October, but only
274 occurred at the bay site in 2007.

275 **Spatial Patterns in Concentration and Mean Size.** Correlations were performed as a
276 way to assess the consistency, or coherence, of larval abundance and size with space and time.
277 There was no significant autocorrelation beyond a one week lag for either year for both the
278 abundance and mean size time series for all species with the exception of *Geukensia demissa*

279 abundance at Childs River in 2009, which was correlated for three weeks. We subtracted degrees
280 of freedom by two or three for the autocorrelated time series in the cross-correlations. Significant
281 correlations between sites (no lags) are depicted in Fig. 8. All correlation coefficients and
282 significant lag times are reported in supplementary material (Figs. S1-S2).

283 Comparing locations, there were significant correlations in abundance between the sites
284 on the eastern sides of the bay (Little River and Waquoit Bay site) and the western channels
285 (Menauhant inlet and Childs River), though these relationships were not consistent for all species
286 or for both years. *Anomia simplex* was the least well-mixed species in the bay showing consistent
287 separation between sites. In 2007, *A. simplex* concentrations at both Menauhant and Waquoit
288 Bay lagged behind Little River for 1-2 weeks ($r = 0.73$ and 0.52 , respectively) and no sites were
289 correlated with Childs River. Mean sizes were significantly correlated for the three lower sites
290 (Fig. 8a), and also lagged two weeks behind Little River ($r = 0.73$ for MN and $r = 0.91$ for WB).
291 In 2009, Little River and Waquoit Bay were significantly cross-correlated for *A. simplex*
292 abundance ($r = 0.79$), as were Menauhant and Childs River ($r = 0.66$), and there was a two week
293 lag in cross-correlations between the two sides of the bay (Fig. 8b).

294 *Geukensia demissa* was more well-mixed between sites in 2009, but in 2007 there was
295 some spatial separation between east and west sites. *G. demissa* concentrations at Waquoit Bay
296 were correlated with both Little River and Menauhant (Fig. 8c, $r = 0.62$ and $r = 0.73$,
297 respectively), and Menauhant was correlated to Childs River ($r = 0.76$). Waquoit Bay and Little
298 River concentrations had significant one-week lags behind Menauhant and Childs River
299 (WB:MN $r = 0.67$, LR:MN $r = 0.71$, LR:CR $r = 0.51$). Only Menauhant and Childs River had
300 correlations with sizes in 2007 ($r = 0.65$), and all sites were lagged to Little River. In 2009,
301 positive and significant correlations were observed between Little River, Waquoit Bay, and

302 Menauhant (LR:WB $r = 0.94$, LR:MN $r = 0.75$, MN:WB $r = 0.74$) and between Childs River and
303 Waquoit Bay ($r = 0.58$) in 2009 (Fig. 8d). All mean sizes were strongly correlated in 2009
304 indicating strong coherence in population structure throughout the bay (LR:MN $r = 0.59$, LR:CR
305 $r = 0.66$, LR:WB $r = 0.66$, MN:CR $r = 0.71$, MN:WB $r = 0.80$).

306 *Mercenaria mercenaria* had little population coherence in 2007, but high coherence
307 among the more downstream sites in 2009. In 2007, abundances at Menauhant and Waquoit Bay
308 had a significant correlation ($p = 0.69$) and Little River abundances lagged all other sites by 1-2
309 weeks (Fig. 8e). All sites lagged Childs River. In 2009, Little River abundances and sizes were
310 significantly correlated with the Menauhant and Waquoit Bay sites (LR:MN $r = 0.71/0.52$,
311 LR:WB $r = 0.76/0.79$) and Childs River lagged Little River by one week ($r = 0.63$). Similar to
312 the other species, *M. mercenaria* time series' at Childs River were not correlated with many
313 other sites.

314 **Relationship to Environmental Factors.** Cross-correlations between environmental
315 conditions and individual species suggested that temperature was most influential at predicting
316 larval abundance for each species on a temporal scale, but salinity was more important on a
317 spatial scale. We compared the abundance and distributions of each species in relation to average
318 water column temperature and salinity by plotting larval concentration (on a log scale) as a
319 function of both these variables (Fig. 9). Childs River was almost always stratified when samples
320 were taken, while Menauhant and Wauquoit Bay - Metoxit Point were occasionally stratified.

321 Bivalve larvae were commonly found in samples taken during high temperature and
322 salinity conditions. Temperature and salinity trends were similar for both years, though 2009 had
323 a wider range of salinities, due to lower Childs River salinities (Fig. 9, squares). Little River
324 (Fig. 9, circles) had the highest ranges of observed temperatures in 2007, and Little River and

325 Menauhant (Fig. 9, triangles) had the highest ranges of temperatures in 2009. Results from both
326 years show that larval concentrations peak above 20°C indicating that these three species are
327 warm-water spawners. Salinity ranges were broader for *Geukensia demissa* with abundant
328 samples through mid-salinity ranges, but *Anomia simplex* and *Mercenaria mercenaria* favored
329 higher salinities (Fig. 9).

330 Temperature was the environmental variable that had the most significant correlations
331 with larval concentration time series (Fig. 10). Cross-correlations were significant between
332 temperature and *Anomia simplex* and *Geukensia demissa* concentration both years with the
333 exception of *A. simplex* at Childs River in 2007. In 2009, all species and sites were positively and
334 significantly correlated with temperature with the exception of *Mercenaria mercenaria* at Little
335 River. The only significant correlation with salinity was negative for *A. simplex* at Menauhant in
336 2007 ($r = -0.615$).

337 There were a few significant correlations with chlorophyll in 2007, but they were low and
338 possibly not biologically relevant. Waquoit Bay chlorophyll was negatively cross-correlated with
339 *Geukensia demissa* larvae ($r = -0.44$), and Childs River chlorophyll was positively cross-
340 correlated with *Anomia simplex* (0.47). We used phytoplankton counts for a better estimate of
341 larval food abundance. Comparing larval abundances to the presence of phytoplankton from the
342 counts (Fig. 3), higher survival in the later months of 2009 may be attributed to the diatom
343 bloom at many of the sites, which was absent in 2007. See supplementary material for all
344 correlation coefficients (Fig. S3-S4).

345 **Synthesis.** Based on the information in this study, the proposed mechanism for higher
346 concentrations and sizes in 2009 compared to 2007 is that initially cooler temperatures delayed
347 mass spawning but wetter conditions encouraged phytoplankton growth. Once species spawned

348 temperatures increased and diatoms were abundant encouraging rapid growth and better survival
349 of larvae. Higher wind speeds let to more circulation in the bay causing larvae to be transported
350 further upstream and retained.

351 **DISCUSSION**

352 The purpose of this study was to investigate environmental factors that could influence
353 larval abundances on a weekly scale. We were able to document two very different years in
354 terms of biological and physical characteristics, and we propose this had a pronounced affect on
355 larval concentrations and survival. Larval growth depends mainly on nutritional factors and
356 larval survival depends on predation, advection, and initial density (Fegley 2001). We used
357 density of veliger and pediveliger larvae to interpret larval survival which also may imply
358 successful growth, however, growth rates were not calculated as we would have to successfully
359 isolate cohorts and assume no larval loss. This study suggests annual patterns in water
360 temperature and food availability can lead to yearly fluctuations in larval abundance. These
361 differences can affect potential settling of adults, emphasizing the importance of recognizing
362 larval stages to explain population dynamics in management applications. Because enhancement
363 efforts can rely heavily on spat collection to measure recruitment, knowing optimal times and
364 locations to place collectors is valuable to maximizing returns.

365 **Species-Specific Concentration and Size.** We compared species-specific yearly
366 differences in larval abundance and survival, which is rare for studies of bivalve larvae. The few
367 field studies that have been performed on *Mercenaria mercenaria* reported large differences in
368 abundance between years (Carriker 1961, Fegley 2001). Despite its commercial importance to
369 the area, there is little documentation of *M. mercenaria* spawning for Cape Cod. Spawning
370 temperatures for *M. mercenaria* near New Bedford, Massachusetts have been reported at 21°C

371 and can occur as low as 18-19°C in more northern areas (Eversole 2001). Spawning of *M.*
372 *mercenaria* has been documented for areas south of Long Island from June – November
373 (Loosanoff et al. 1951, Keck et al. 1975). Our study showed that *M. mercenaria* larvae were
374 present in low concentrations as early as mid-May in both 2007 and 2009 at water temperatures
375 above 16°C. A Rhode Island study performed in 1954 found larvae appearing by the end of May
376 with highest abundances of *M. mercenaria* larvae in mid to late June, however late July and
377 August had the highest concentrations in our study (Fegley 2001). Carriker (1961) found larvae
378 appearing in late May with highest densities in July when sampling from 1948-1951 in Little
379 Egg Harbor, NJ. The differences between our study and older studies of *M. mercenaria* could
380 reflect differences in regional populations as well as possible adaptations to climate change.

381 *Mercenaria mercenaria* had a coherent population structure within Waquoit Bay in 2009
382 as both abundance and sizes were correlated between sites indicating the population was well-
383 dispersed and uniform throughout the bay. There was less coherence in 2007. Results indicated
384 that Little River and Waquoit Bay could be source or spawning locations as larvae were more
385 abundant and initially appeared there. A major biomass and high density source of spawning
386 quahogs was located in a ten hectare shellfish aquaculture farm in the Seapit River that flows
387 tidally between Waquoit Bay and Childs River. The tidal direction during a major spawning
388 period would determine the concentration of larvae from the spawn transported to the main bay.
389 Tides flowing in the Childs River direction during a big spawn in 2007 might explain the high
390 concentrations observed there and at Menauhant with other sites lagging behind, with larvae
391 ultimately succumbing to low salinities or export. In 2009, a tide flowing in the opposite
392 direction might explain the high concentrations and retention of *M. mercenaria* in the main bay.
393 The highest abundance of *M. mercenaria* pediveligers was in August 2009 at all sites, with

394 Childs River in particular having a high proportion of pediveliger larvae. This may be due to
395 lower salinities in Childs River discouraging pediveliger larvae from settling and causing them to
396 remain in the water column. *M. mercenaria* spawned again later in the season and may have
397 settled at Little River and the main bay, despite not growing as fast as in mid-summer. In 2011,
398 two-year old *M. mercenaria* made up a large portion of adults and most of the seed in the
399 Waquoit Bay population (R. York, unpublished result). This can now be traced to the favorable
400 conditions and high larval supply in mid-summer 2009.

401 For the jingle clam, *Anomia simplex*, different conclusions can be made. Abundance and
402 population structure were separated between sides of the bay, and no correlations between
403 abundances and sites were observed in 2007 when overall concentrations were low. Little River
404 was a likely source population, and early 2007 data indicated a possible source of *A. simplex*
405 larvae from the inlet. However, *A. simplex* did not seem to stay in Little River, as more
406 pediveligers were found in Menauhant and the main bay. There was some evidence for this
407 species to be found in bay waters on ebb tides, supporting an estuarine source and export for *A.*
408 *simplex*. More upstream transport from the inlet may have caused *A. simplex* abundance in
409 Childs River to be correlated with Menauhant in 2009. As the adult lifespan for *A. simplex* is
410 only 1-2 years (Chanley and Andrews 1971), year-to-year differences in larval abundance would
411 depend on the previous year's recruitment and might explain the patchiness and inconsistencies
412 observed between years. The multitude of peaks in the time series suggest *A. simplex* spawns
413 continuously, and our data suggest these spawns may come from different locations. Larval
414 periods of 3-4 weeks are typical for this species (Chanely and Andrews 1971), so retention in the
415 bay system may be difficult.

416 Despite both *Mercenaria mercenaria* and *Anomia simplex* achieving sizes that could lead
417 to settlement in Waquoit Bay, *Geukensia demissa* larvae showed little evidence of survival to
418 pediveligers or retention in 2009 despite maintaining stable concentrations in the bay with well-
419 mixed populations. It is likely that marsh areas in the bay and channels like Little River were
420 sources of larvae for *G. demissa*, though some larvae were found in the inlet site early in 2009.
421 *G. demissa* spawned with 2-3 distinct cohorts, but the middle cohort that had the highest
422 concentrations did not result in many pediveligers observed later. It remains uncertain why *G.*
423 *demissa* had reduced survival compared to the other species when all were present concurrently.
424 Food availability was better in the early and later periods, and *G. demissa* may have been more
425 vulnerable to export. Rigal et al. (2010) found that tidal efflux resulted in a lack of settlement-
426 stage gastropod larvae in an embayment. For instance, larvae spawned in marsh channels on an
427 outgoing tide could be instantly flushed out of the bay and not retained as well as *M. mercenaria*
428 larvae spawned in the middle of the bay and caught in a gyre or transported to a channel with
429 higher retention times.

430 **Spatial Patterns in Concentration.** Time series of abundances at different sites can
431 allow for predictions of dispersal. Larval abundance at most sites was autocorrelated for a
432 maximum of two weeks, which is on the order of water residence times and the larval
433 development period. Each species had different trends: *Anomia simplex* was the least dispersed,
434 but *Geukensia demissa* and *Mercenaria mercenaria* were well dispersed at times, particularly
435 during 2009. This suggests that there are both periods of limited dispersal and homogeneity
436 throughout a spawning season for different species. Other studies have failed to show temporal
437 correlations between sites with younger *M. mercenaria* larvae, but older larvae were found to be
438 more dispersed, although these studies were performed over a greater spatial range (Fegley

439 2001). Childs River often showed distinct abundance patterns from the other sites, which could
440 be a result of its upstream location, lower salinities, higher nutrients, and longer retention times
441 (Tomasky-Holmes 2008).

442 There are several physical factors that may have contributed to the observed differences
443 in larval abundance. All sites were separated by only 1-2 km, thus the sometimes large
444 differences in concentrations between sites emphasize the patchiness within the system. Flow
445 dynamics through an inlet are different than flow through estuarine channels and open water. In
446 Waquoit Bay, the inlets have the strongest flows and exchange water rapidly with the main bay.
447 Flows through sub-embayments vary, exchanging waters over 1-3 days with the bay proper, but
448 have much longer residence times within the whole bay system due to marsh storage areas
449 (Howes et al. 2004). In addition, sporadic wind forcing from the north can disrupt stratification
450 and lead to increased flushing of the bay (Geyer 1997), which may be responsible for occasional
451 decreases in concentration. Increased wind speeds in 2009 could have led to increased mixing
452 and transport in the bay and could account for the larger presence of larvae, particularly *Anomia*
453 *simplex* and large *Mercenaria mercenaria* larvae, upstream at Childs River.

454 **Relationships with Environmental Conditions.** We looked at larval abundance over
455 two years when environmental conditions within the bay differed with respect to temperature,
456 chlorophyll and food quality. We chose these conditions based on environmental influences that
457 may operate on our weekly sampling scale. Other factors, such as tidal flow and wind stress need
458 to be investigated at higher frequencies (i.e. Roegner et al. 2007). If we use total abundance as a
459 proxy for spawning activity, spawning was less in 2007 despite higher temperatures. In 2009,
460 bivalve larval concentrations for the Waquoit Bay site were as large as 90/L with individual
461 species' concentrations ranging from 8.5-22/L. This is extremely high, even for an estuary, and

462 may indicate multiple mass spawnings. Typical reported peaks range from a few hundred to
463 thousand bivalves per m³ (Wood and Hargis 1971, Andrews 1983, Garland 2000), although
464 reported densities from Carriker (1961) were up to 70/L. This suggests Waquoit Bay is an
465 abundant pool of bivalve larvae when conditions are right.

466 Temperature was revealed to be important in predicting larval abundance. Abundances of
467 each species indicated that 20°C and above are optimal temperatures for larval abundance, most
468 likely due to peak spawning. In 2009, spawning for *Geukensia demissa* occurred later than in
469 2007 because temperatures warmed up later in 2009. This delayed spawn could have led to the
470 higher larval concentrations observed if adult gonads were allowed to ripen longer. Correlations
471 with temperature were seen at all sites both years, but they were highest in 2009. *Mercenaria*
472 *mercenaria* was the only species found consistently present below 20°C. Temperature has been
473 shown to have significant correlations with other bivalve and reef fish larval abundance in other
474 studies (Chicharo and Chicharo 2001, Wilson and Meekan 2001), most likely due to the role it
475 plays in increasing metabolic and growth rates as well as the growth of algae, which can be good
476 for survivorship if enough food is present.

477 Salinity and chlorophyll showed weaker correlations with larval abundance. Salinity did
478 not vary much temporally, but showed variations between sites. Negative cross-correlations with
479 *Anomia simplex* and salinity at Menauhant in 2007 suggest that there could have been tidal effect
480 with more larvae present on outgoing tides, but this pattern is not necessarily causation and
481 merits further investigation on a tidal scale (Thompson 2011). Site-specific differences in
482 salinities highlight potential larval tolerances for each species, and low salinities can reduce
483 survivorship of sensitive species. *G. demissa* had the highest abundance during low salinity
484 periods in Childs River, and *Anomia simplex* was the least tolerant of low salinity conditions.

485 However, this relationship could also be explained by proximity to sources or different patterns
486 in dispersal between species. Although we did see some significant correlations to chlorophyll,
487 these were weak and suggest that larvae are not necessarily associated with areas of high or low
488 chlorophyll. It is possible that the extremely high concentrations of larvae associated with these
489 samples were effective at grazing the phytoplankton down to the lower levels observed,
490 particularly for 2009. In 2007, blooms of large dinoflagellates at Childs River created a lot of
491 turbidity and could be a deterrent to larvae. Overall, relationships to chlorophyll were
492 inconsistent, and it may be necessary to investigate this question with higher frequency sampling
493 to see any patterns (Domingues et al. 2011). Other field studies of bivalve larvae have also failed
494 to find associations with chlorophyll (Tremblay and Sinclair 1990, Raby et al. 1994).

495 **Food Quality.** We compared the abundance of diatoms, a quality larval food source, and
496 flagellates, usually a mediocre food source, for both years. There was very little available
497 phytoplankton that would be suitable for larval ingestion and growth in May and June of 2007.
498 Together with higher temperatures, this would have led to more starvation for these cohorts.
499 Diatom blooms coinciding with higher temperatures in July and August 2009 could have led to
500 their increased survival.

501 In 2007, lower numbers of pediveligers could suggest that low food quality may have
502 limited larval survival and growth, although other food sources may have been present. Bivalve
503 larvae typically consume food particles in the pico- to nano- plankton size range of 0.5–12 μm ,
504 occasionally ingesting large particles up to 30 μm if abundant (Baldwin and Newell 1995).
505 However, it is well documented that bivalve larvae are capable of ingesting bacteria (Douillet
506 1993, Gallagher et al. 1994, Tomaru et al. 2000), although it mostly supplements growth on a
507 phytoplankton-based diet (Baldwin and Newell 1991). Larvae can grow in estuarine conditions

508 with low natural phytoplankton abundances, although growth patterns are species-specific (Crisp
509 et al. 1985), and diets are likely supplemented with bacteria or detritus (Fritz et al. 1984). Larvae
510 can continue shell growth without food by depleting tissue for energy (Crisp et al. 1985).

511 More predation could explain the observed low abundance of pediveliger larvae in 2007
512 if food was not limiting. Although predation may be relatively low for larvae overall, certain
513 predators, if abundant, are capable of reducing a bivalve larval population by upwards of 80%
514 (Johnson and Shanks 2003). In 2007 the ctenophore *Mnemiopsis leidyi* was more abundant than
515 in 2009 (C.M. Thompson, pers. obs.) and could have reduced larval abundance through top-
516 down control.

517 **Conclusions.** By performing a species-specific study using a new method to identify
518 bivalve larvae, we were able to depict spatial and temporal trends and uncover environmental
519 factors that may regulate larval supply for each species. We observed general patterns affecting
520 larval abundance, such as seasonal temperature and site-specific salinity differences, which are
521 likely to have the greatest effect on survivability. Species-specific patterns suggested that for a
522 commercial species like *Mercenaria mercenaria*, higher recruitment based on larval supply alone
523 would likely be achieved in a year where high temperatures are coupled with abundant quality
524 food. For an ecologically important species like *Geukensia demissa*, our study suggests that
525 larval survival was low, and that larval supply may be subsidized from other marshes or limited
526 to the few individuals retained in high-retention areas of the bay. We used cross-correlation
527 analyses to determine whether such characteristics had a relationship with larval abundance,
528 however these results are correlative but not necessarily causation. There could be many other
529 mechanisms leading to the observed patterns in larval abundance and survival that were not
530 investigated in this study, such as tidal flow, wind-driven transport, or environmental conditions

531 and spawning rates from nearby populations. Furthermore, we did not test correlations separately
532 for size classes which can sometimes lead to different patterns (Fegely 2001). Because Waquoit
533 Bay has abundant shellfish resources for both recreational and commercial fisheries and such a
534 high abundance of larvae, a study such as ours is necessary to understand the factors regulating
535 these valuable resources and to managing future populations and biodiversity.

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537
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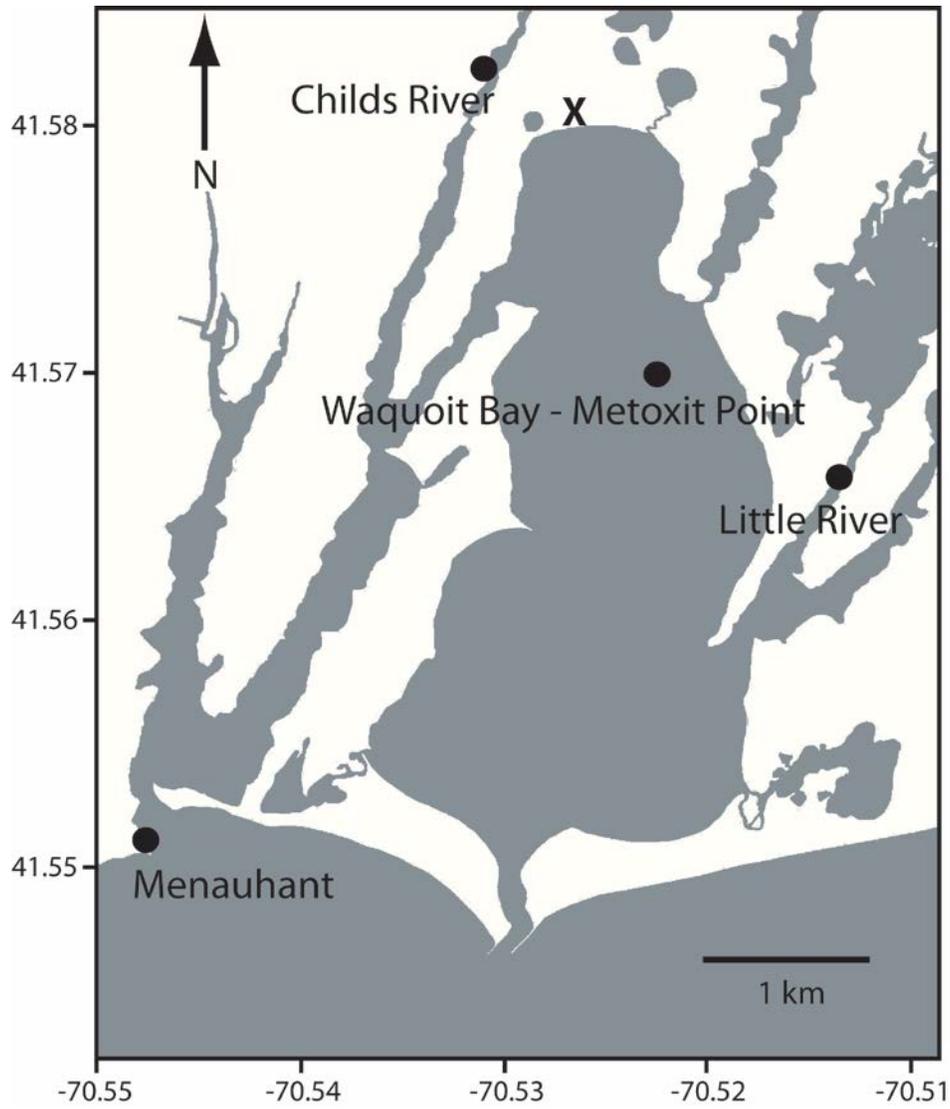
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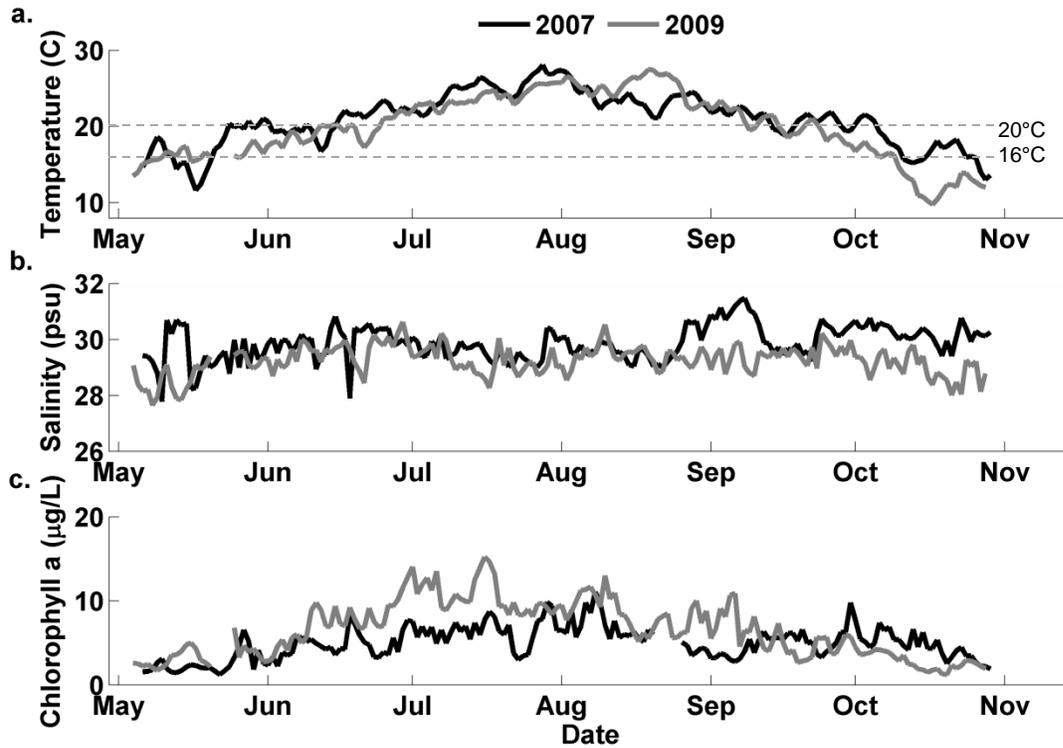
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712

713 Figure 1. Map of Waquoit Bay showing the four larval sampling sites (black dots). The 'X'
714 marks the location of the Waquoit Bay National Estuarine Research Reserve and weather station
715 where wind data was collected.

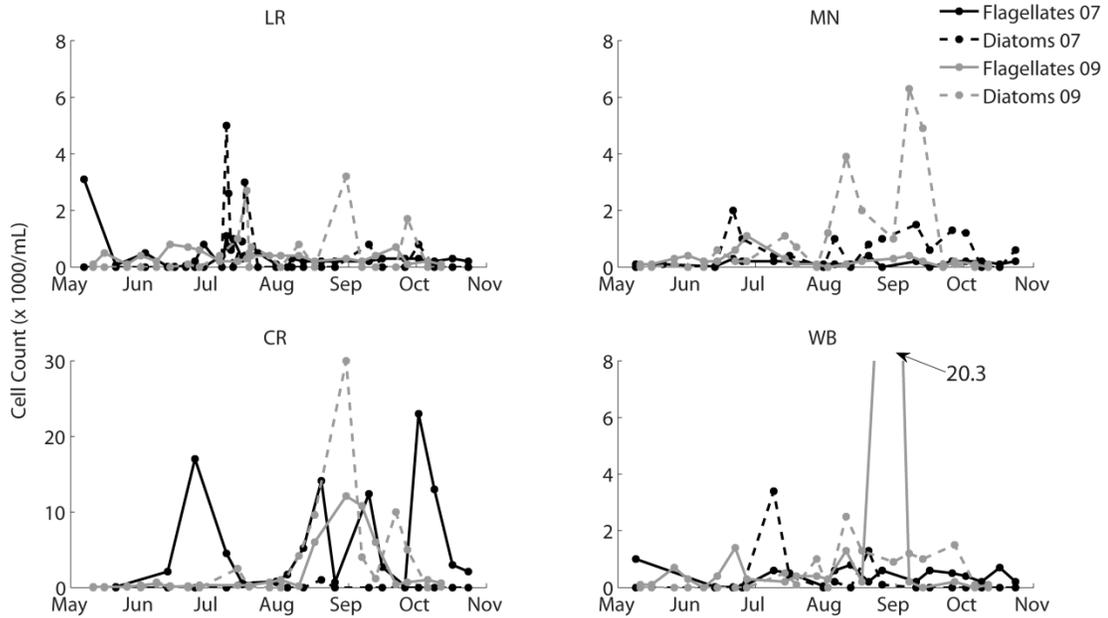


716

717 Figure 2. Daily averaged (a) temperature (b) salinity and (c) chlorophyll a for Waquoit Bay –
 718 Metoxit Point. All recorded data were averaged daily from moored loggers for the sampling
 719 periods of May through October in 2007 and 2009. Dashed lines in (a) represent lower and
 720 higher threshold spawning times of 16°C and 20°C, respectively.

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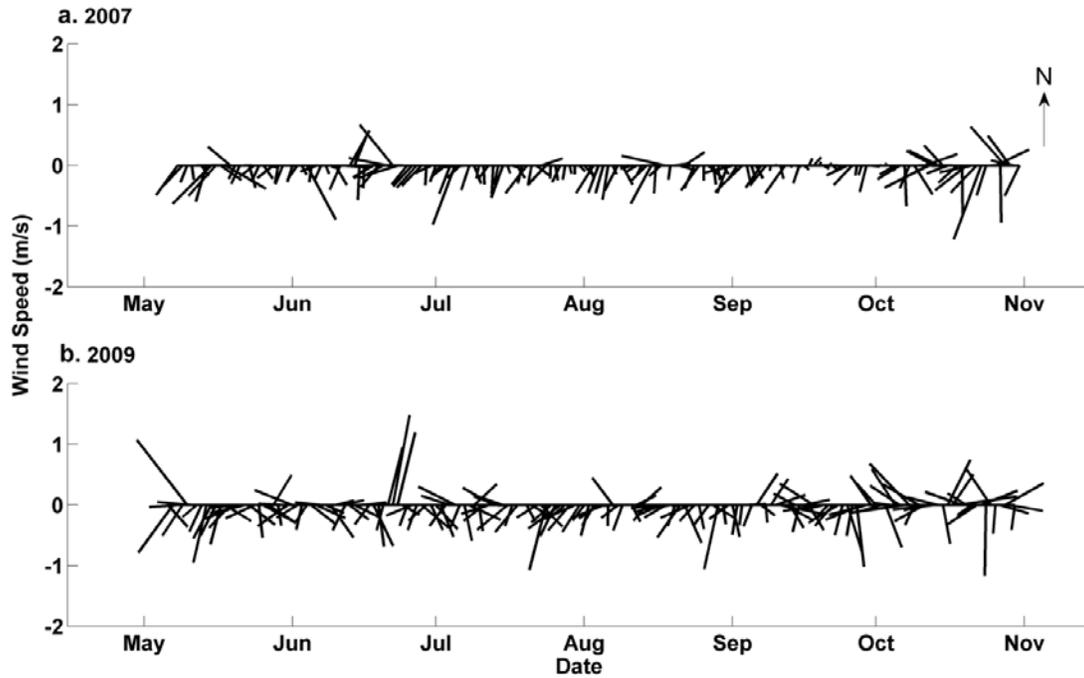
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724 Figure 3. Phytoplankton counts for all sites in 2007 (black) and 2009 (gray). Total counts of
 725 flagellates (solid line) and diatoms (dashed lines) from water samples on each sampling date are
 726 plotted for each site. Flagellates included counts for flagellates and dinoflagellates and diatoms
 727 consisted of centric, pennate, *Chaetoceros sp.*, *Skeletonema sp.*, *Thalassiora sp.*, and *Nitzchia sp.*
 728 Note the different axis scale for (c) and outlier value for (d). Site abbreviations: LR = Little
 729 River; CR = Childs River; MN = Menauhant; WB = Waquoit Bay – Metoxit Point.

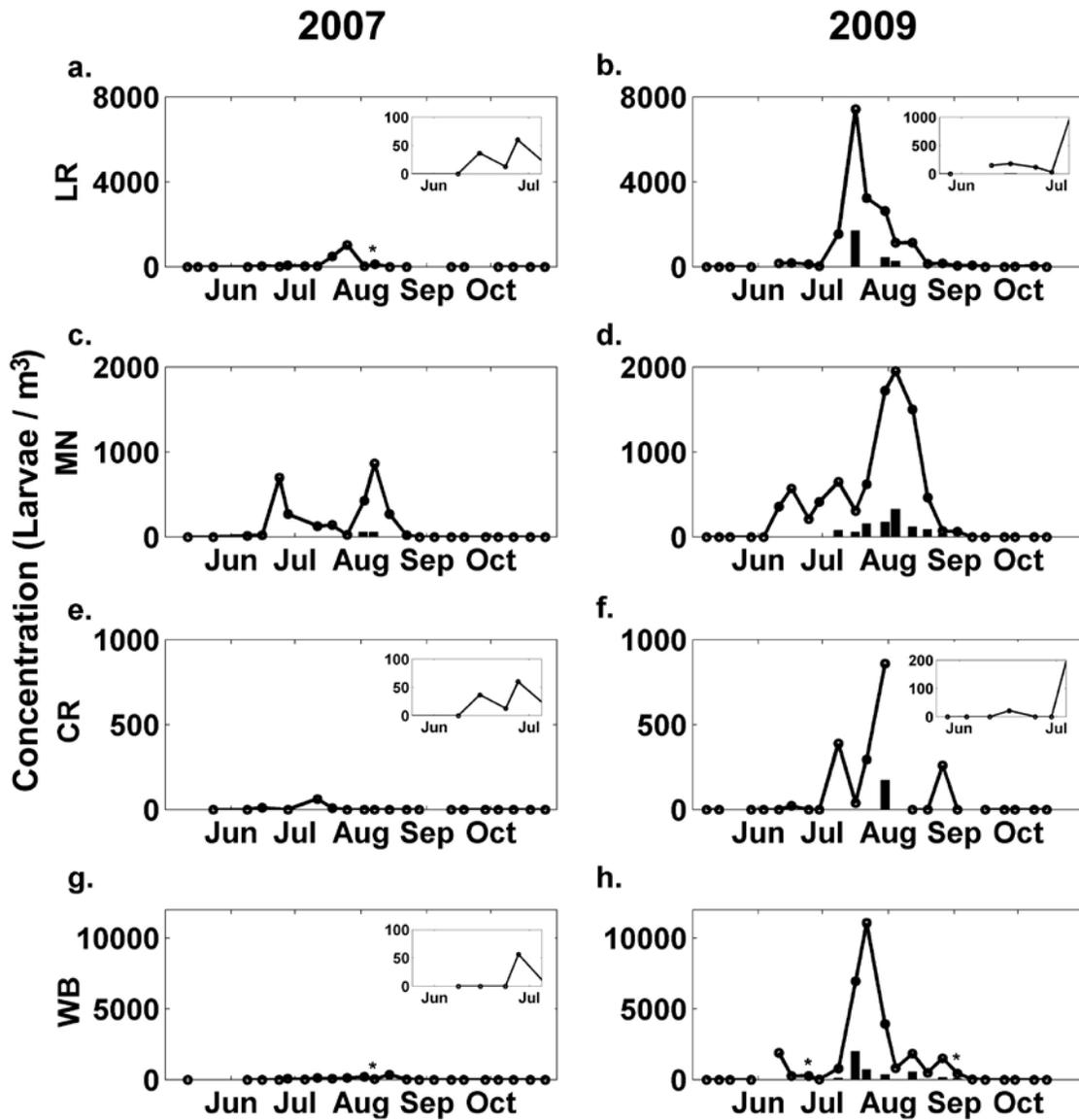
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732 Figure 4. Time series of wind vectors for Waquoit Bay for (a) 2007 and (b) 2009. Wind speed
 733 (m/s) and direction were averaged daily from May through October for both years. The weather
 734 station was located at the north tip of the bay at the Waquoit Bay National Estuarine Research
 735 Reserve.

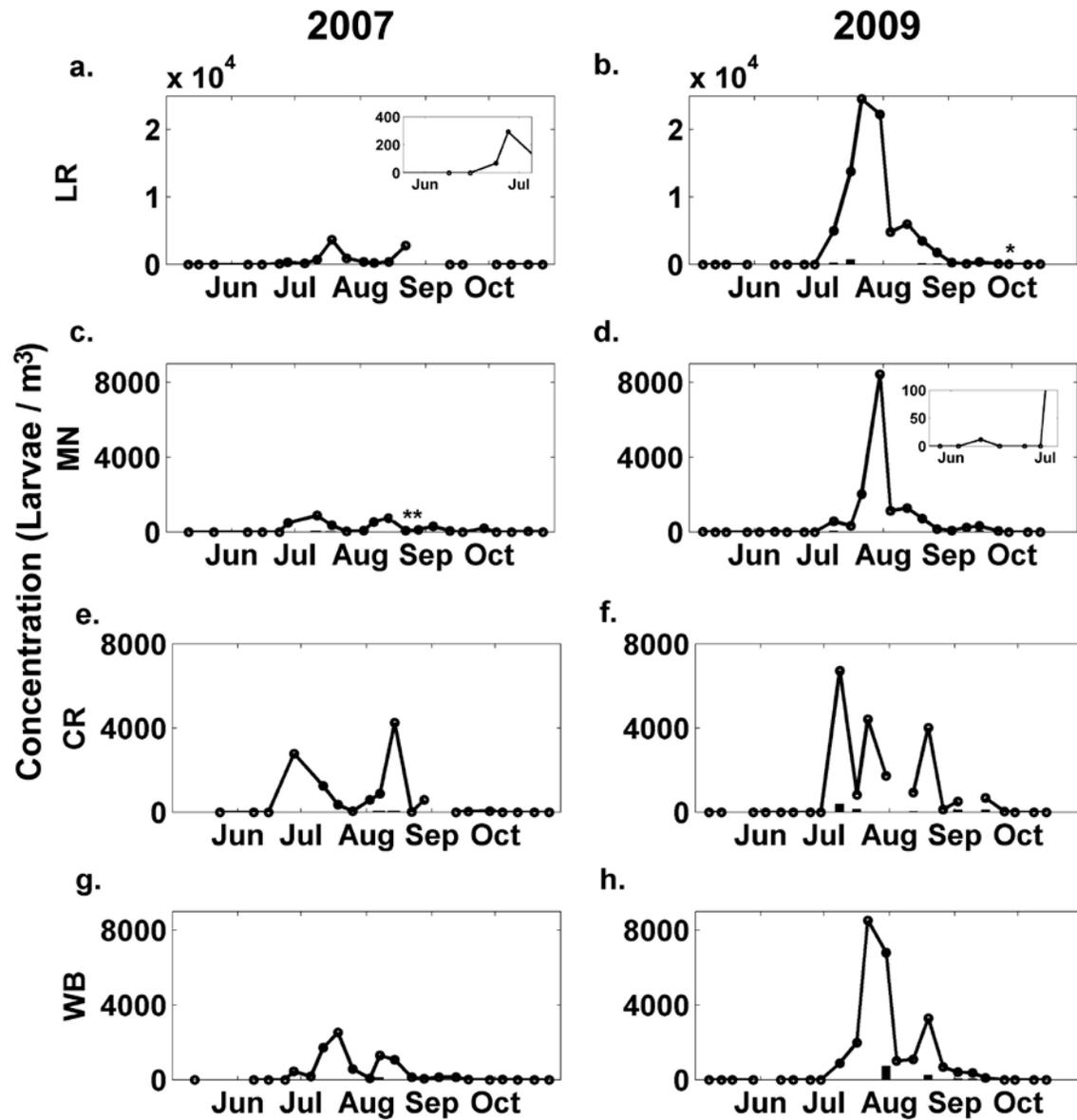
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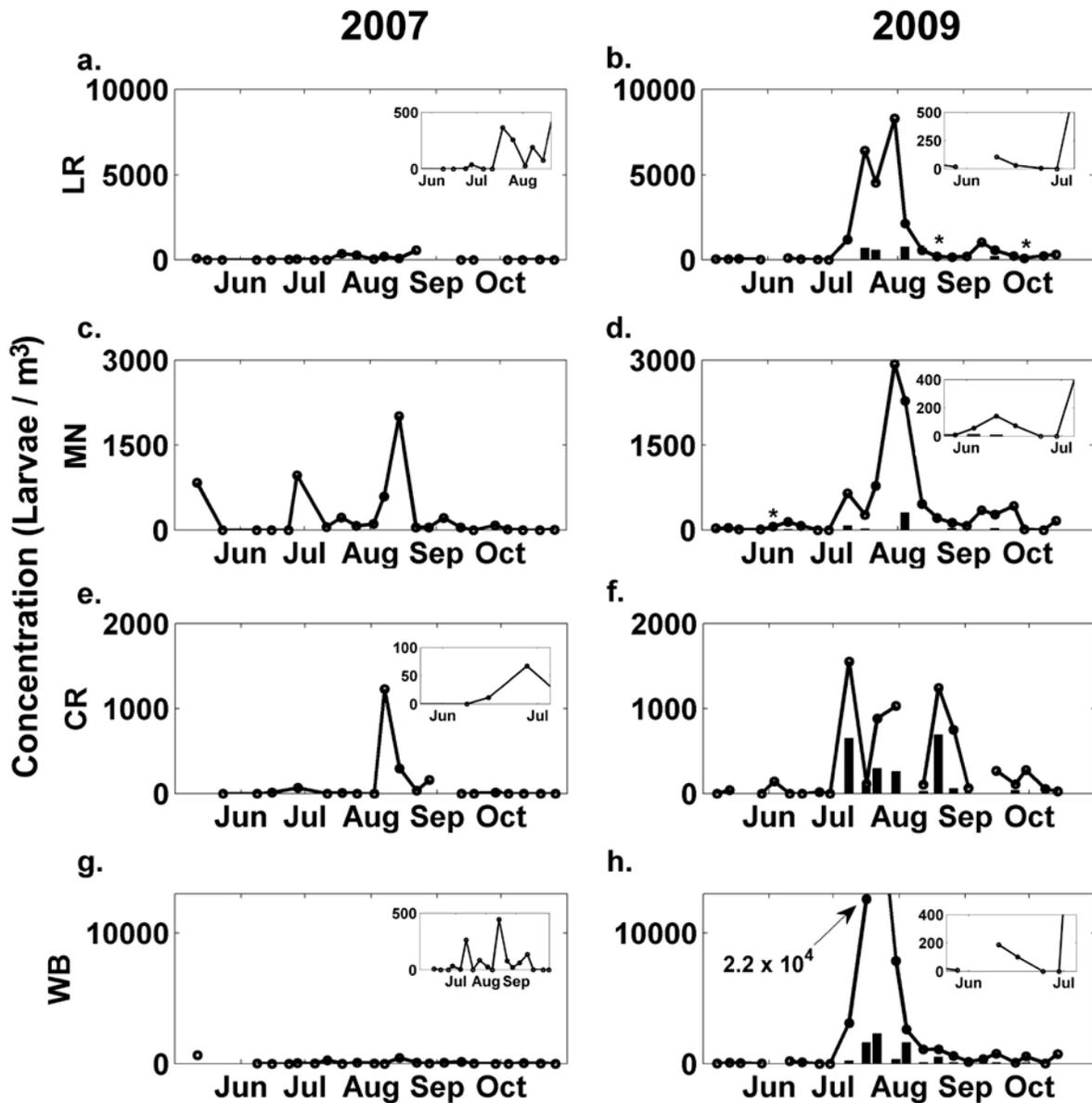
739 Figure 5. Time series of *Anomia simplex* larvae at each sampling site for 2007 and 2009. Black
 740 lines show total concentration and bars underneath represent concentration of pediveliger (> 175
 741 µm) larvae. Inserts show a zoomed in area to depict trends if not visible on full graph. Asterisks
 742 represent samples where pediveliger larvae were present but concentrations were too small to
 743 appear on figure. Site abbreviations: LR = Little River; CR = Childs River; MN = Menauhant;
 744 WB = Waquoit Bay – Metoxit Point

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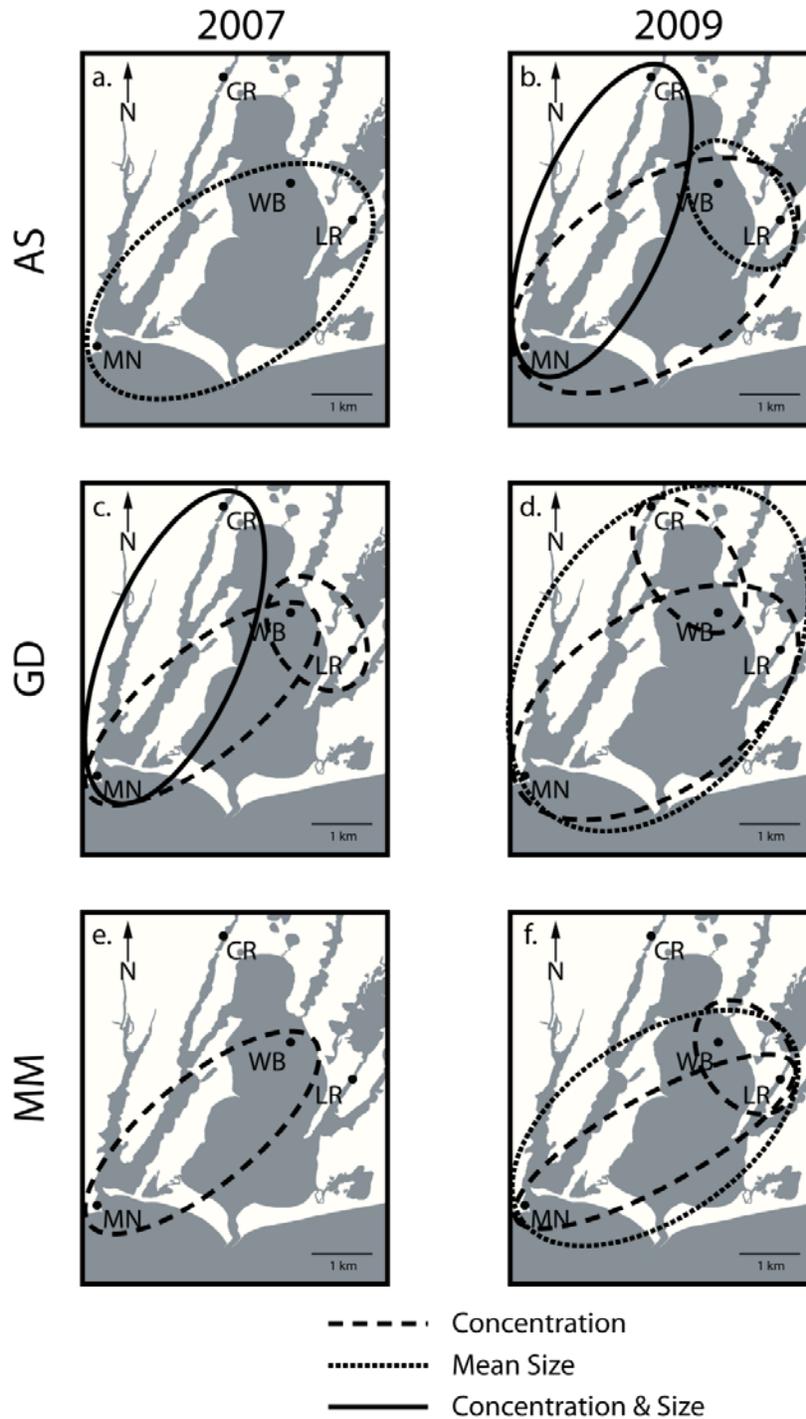


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Figure 6. Time series of *Geukensia demissa* larvae at each sampling site for 2007 and 2009. Black lines show total concentration and bars underneath represent concentration of pederiveliger (> 200 μm) larvae. Inserts show a zoomed in area to depict trends if not visible on full graph. Asterisks represent samples where pederiveliger larvae were present but concentrations were too small to appear on figure. Site abbreviations: LR = Little River; CR = Childs River; MN = Menauhant; WB = Waquoit Bay – Metoxit Point

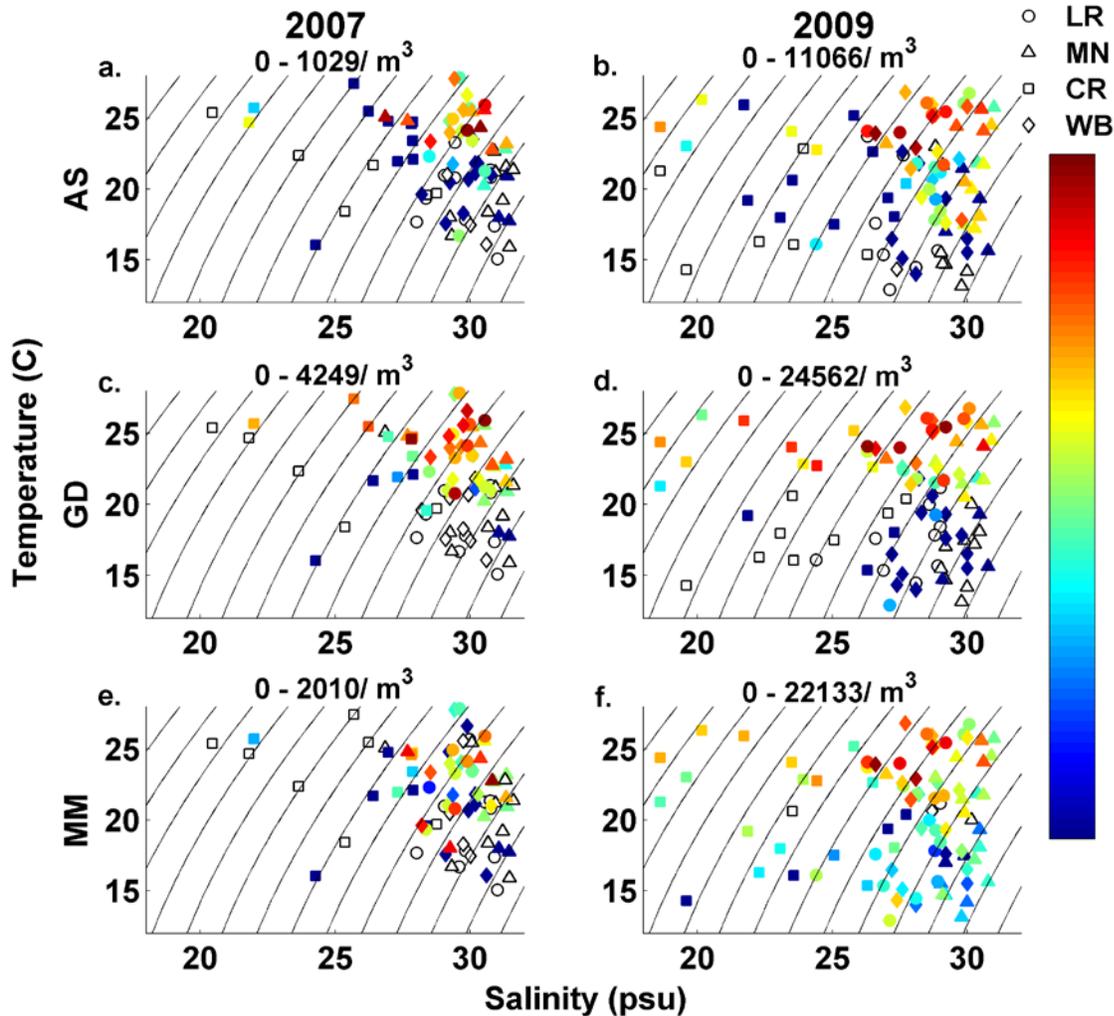


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 756 Figure 7. Time series of *Mercenaria mercenaria* larvae at each sampling site for 2007 and 2009.
 757 Black lines show total concentration and bars underneath represent concentration of pederivelger
 758 (> 200 µm) larvae. Inserts show a zoomed in area to depict trends if not visible on full graph.
 759 Asterisks represent samples where pederivelger larvae were present but concentrations were too
 760 small to appear on figure. Site abbreviations: LR = Little River; CR = Childs River; MN =
 761 Menauhant; WB = Waquoit Bay – Metoxit Point
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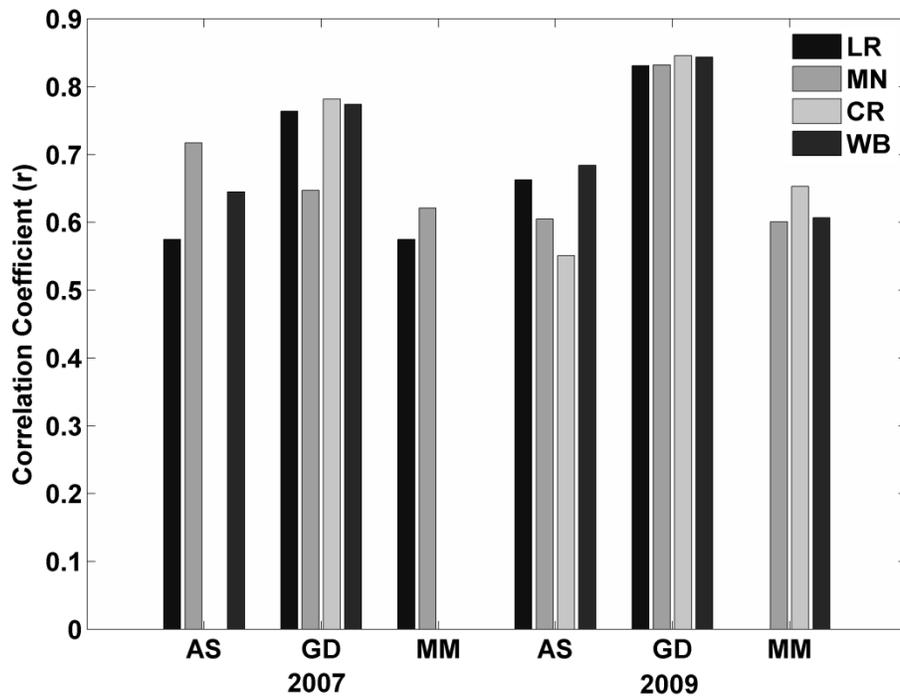
764 Figure 8. Correlations between time series of concentrations and mean size of bivalve larvae.
 765 Ellipses represent positive and significant cross-correlations ($p > 0.05$) between sampling sites.
 766 Solid lines represent significant correlations for both concentration and mean size. Species
 767 abbreviations: AS = *Anomia simplex*; GD = *Geukensia demissa*; MM = *Mercenaria mercenaria*.
 768 Site abbreviations: LR = Little River; CR = Childs River; MN = Menauhant; WB = Waquoit Bay
 769 – Metoxit Point



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771 Figure 9. Temperature-salinity-plankton plots of three species of bivalve larvae at all four sites
 772 in 2007 (a,c,e) and 2009 (b,d,f). The location of each data point represents the temperature and
 773 salinity as recorded during each sample. The color of each point represents the concentration of
 774 each species as determined from the percentage observed in each subsample and total
 775 concentration. Numbers at the top of each figure are the range of concentrations for each species
 776 that correspond to the colorbar. Concentrations are on a log scale. Each site is depicted with its
 777 own symbol. Unfilled symbols represent zero larvae. Black lines represent constant density at
 778 one sigma-t unit. Species abbreviations: AS = *Anomia simplex*; GD = *Geukensia demissa*; MM =
 779 *Mercenaria mercenaria*. Site abbreviations: LR = Little River; CR = Childs River; MN =
 780 Menauhant; WB = Waquoit Bay – Metoxit Point.

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Figure 10 Correlation coefficients for each larval concentration time series and water temperature during sample collection. Correlation coefficients are Pearson's r and significant for $\alpha = 0.05$. Species abbreviations: AS = *Anomia simplex*, GD = *Geukensia demissa*, MM = *Mercenaria mercenaria*. Site abbreviations: LR = Little River; CR = Childs River; MN = Menauhant; WB = Waquoit Bay – Metoxit Point

790 **Supplementary Figures**

791 Table S1. Matrix of cross-correlation coefficients (r) for concentration and shell length data
 792 between sites for each species in 2007. All reported correlation coefficients were significant ($p <$
 793 0.05) and adjusted for autocorrelation of the lowest frequency. Bold values were significant for
 794 the decorrelation time of the series. Integers in parentheses represent if there was a significant lag
 795 between the sites in the columns and the rows. A positive lag means the sites in the columns
 796 lagged the sites in the rows by the factor, and a negative lag means the sites in the rows lagged
 797 behind the sites in the columns. ns = not significant

	---- Little River ----		---- Menauhant ----		---- Childs River ----	
	Conc.	Size	Conc.	Size	Conc.	Size
<i>Anomia simplex</i>						
Menauhant	0.73 (-3)	0.73 (-2) 0.67 (-1) 0.61 (0)				
Childs River	ns	ns				
Waquoit Bay	0.52 (-1)	0.65 (-3) 0.91 (-2) 0.78 (-1) 0.58 (0)				
<i>Geukensia demissa</i>						
Menauhant	0.71 (1)	0.58 (-3)				
Childs River	0.51 (1)	0.68 (-1)				
Waquoit Bay	0.62 (0)	0.63 (-1)	0.53 (-1) 0.76 (-1)	0.65 (0)	ns	ns
<i>Mercenaria mercenaria</i>						
Menauhant	0.54 (1)	ns				
Childs River	0.66 (2)	ns				
Waquoit Bay	0.73 (1)	ns				

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806 Table S2. Matrix of cross-correlation coefficients (r) for concentration and shell length data
 807 between sites for each species in 2009. All reported correlation coefficients were significant (p <
 808 0.05) and adjusted for autocorrelation of the lowest frequency. Bold values were significant for
 809 the decorrelation time of the series. Integers represent if there was a significant lag between the
 810 sites in the columns and the rows. See Table S1 caption for description of lags. ns = not
 811 significant

	---- Little River ----		---- Menauhant ----		---- Childs River ----	
	Conc.	Size	Conc.	Size	Conc.	Size
<i>Anomia simplex</i>						
Menauhant	0.84 (-2)	0.65 (-1) 0.81 (0) 0.75 (1) 0.54 (2)				
Childs River	0.83 (-2)	ns				
Waquoit Bay	0.79 (0)	0.67 (-1) 0.88 (0) 0.63 (1)	0.66 (0) 0.67 (1)	0.59 (0)	0.55 (1)	ns
			0.67 (1)	0.67 (-2) 0.85 (-1) 0.88 (0) 0.73 (1)	0.89 (2)	
<i>Geukensia demissa</i>						
Menauhant	0.79 (-1) 0.75 (0)	0.59 (0) 0.61 (1)				
Childs River	0.56 (1)	0.67 (0) 0.71 (1)				
Waquoit Bay	0.73 (-1) 0.94 (0) 0.60 (1)	0.66 (0) 0.64 (1) 0.68 (2)	0.47 (-1) 0.45 (1)	0.71 (0) 0.54 (1)	0.62 (-2) 0.56 (0)	0.71 (0) 0.69 (1)
			0.74 (0) 0.80 (1)	0.57 (-1) 0.80 (0) 0.81 (1) 0.61 (2)		
<i>Mercenaria mercenaria</i>						
Menauhant	0.67 (-2) 0.79 (-1) 0.71 (0)	0.52 (0) 0.49 (1)				
Childs River	0.63 (-1)	ns				
Waquoit Bay	0.61 (-1) 0.76 (0) 0.85 (1)	0.79 (0)	ns	ns	ns	ns
			0.87 (1) 0.85 (2)	0.41 (-1) 0.56 (0)		

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814 Table S3 Significant Pearson correlation coefficients (r) from cross-correlations of larval
 815 concentrations to temperature, salinity and chlorophyll time series for each species in 2007.
 816 Correlations were performed between full time series as well as independent samples only when
 817 larvae were present. All reported correlations were significant at $p < 0.05$. Numbers in front of
 818 cross-correlations represent the lag of the larval time series with respect to the physical series
 819 (i.e., a lag of -1 would mean larval concentration lagged the physical time series by one week).
 820 No correlations were significant when accounting for full decorrelation time of each time series.

	<i>Anomia simplex</i>	<i>Geukensia demissa</i>	<i>Mercenaria mercenaria</i>
Temperature			
Little River	0.58 (0)	0.76 (0)	0.48 (-1)
		0.60 (1)	0.58 (0)
		0.60 (2)	
Menauhant	0.72 (0)	0.65 (0)	0.62 (0)
Childs River		0.78 (0)	
Waquoit Bay	0.63 (-1)	0.58 (-1)	
	0.65 (0)	0.77 (0)	
Salinity			
Menauhant	-0.62 (0)		
Chlorophyll			
Childs River	0.47 (0)		
Waquoit Bay		-0.44 (0)	

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832 Table S4 Significant Pearson correlation coefficients (r) from cross-correlations of larval
 833 concentrations to temperature and chlorophyll for each species in 2009. No significant
 834 correlations were observed with salinity. Correlations were performed between full time series as
 835 well as independent samples only when larvae were present. All reported correlations were
 836 significant at $p < 0.05$. See table S3 for description of lags. Time-series were adjusted for
 837 autocorrelation of the lowest frequency for both time-series. Bold values indicate significant
 838 correlations accounting for full decorrelation time.

	<i>Anomia simplex</i>	<i>Geukensia demissa</i>	<i>Mercenaria mercenaria</i>
Temperature			
Little River	0.66 (0)	0.54 (-2)	
		0.72 (-1)	
		0.83 (0)	
		0.79 (1)	
		0.62 (2)	
Menauhant	0.61 (0)	0.73 (-1)	0.60 (0)
	0.64 (1)	0.83 (0)	0.62 (1)
	0.68 (2)	0.80 (1)	
	0.69 (3)	0.64 (2)	
	0.63 (4)		
Childs River	0.55 (0)	0.57 (-2)	0.55 (-3)
		0.74 (-1)	0.54 (-2)
		0.85 (0)	0.57 (-1)
		0.77 (1)	0.65 (0)
		0.61 (2)	0.54 (1)
Waquoit Bay	0.68 (0)	0.58 (-2)	0.61 (0)
	0.71 (1)	0.73 (-1)	0.59 (1)
	0.73 (2)	0.84 (0)	
	0.69 (3)	0.83 (1)	
		0.73 (2)	
Chlorophyll			
Little River			-0.66 (1)
Childs River			-0.44 (-2)
			-0.51 (-1)

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