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3 Fishing and Bottom Water Temperature as Drivers of Change in Maximum Shell Length in
4 Atlantic Surfclams (*Spisula solidissima*)
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Abstract

Maximum shell length of Atlantic surfclams (*Spisula solidissima*) on the Middle Atlantic Bight (MAB) continental shelf, obtained from federal fishery survey data from 1982-present, has decreased by 15-20 mm. Two potential causes of this decreasing trend, fishery removal of large animals and stress due to warming bottom temperatures, were investigated using an individual-based model for post-settlement surfclams and a fifty-year hindcast of bottom water temperatures on the MAB. Simulations showed that fishing and/or warming bottom water temperature can cause decreases in maximum surfclam shell length (body size) equivalent to those observed in the fished stock. Independently, either localized fishing rates of 20% or sustained bottom temperatures that are 2°C warmer than average conditions generate the observed decrease in maximum shell length. However, these independent conditions represent extremes and are not sustained in the MAB. The combined effects of fishing and warmer temperatures can generate simulated length decreases that are similar to observed decreases. Interannual variability in bottom water temperatures can also generate fluctuations in simulated shell length of up to 20 mm over a period of 10 to 15 years. If the change in maximum size is not genotypic, simulations also suggest that shell size composition of surfclam populations can recover if conditions change; however, that recovery could take a decade to become evident.

Keywords

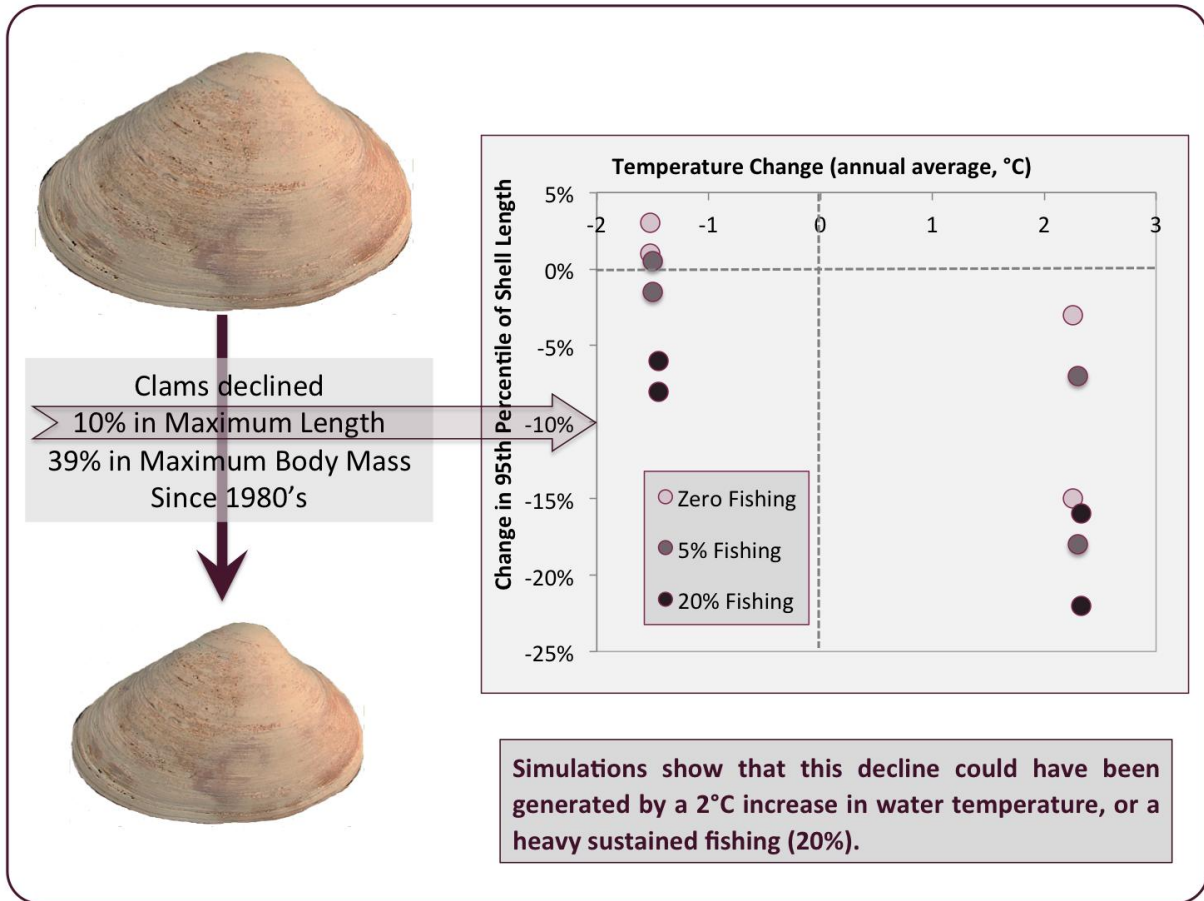
Shellfish fisheries, *Spisula solidissima*, Length-at-age, Temperature, Surfclam, Population model

58 **Graphical Abstract**

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64 **Introduction**

65

66 Human-induced changes in life history traits of fished populations (Law, 2007; Hutchings and
67 Fraser, 2008; Enberg et al., 2012) have been associated with genetic changes, and thus evolution
68 of exploited populations (reviews: Allendorf et al., 2008; Hard *et al.*, 2008; Hutchings and
69 Fraser, 2008; Dunlop *et al.*, 2009). Examples of fisheries-induced evolution include changes in
70 maturation timing (Barot *et al.*, 2004; Olsen *et al.*, 2004; Gårdmark and Dieckmann, 2006,
71 Kendall and Quinn, 2012), fecundity (Yoneda and Wright, 2004; Walsh *et al.*, 2006), and growth
72 (Ricker, 1981; Conover and Munch, 2002; Swain *et al.*, 2007; Nusslé *et al.*, 2009; Enberg et al.,
73 2012). In some cases, observed shifts in life history traits are not associated with genetic shifts.
74 Instead, changes in a fished population can be a result of fishery truncation of size distributions
75 (Kraeuter et al. 2007; Fenberg and Roy, 2008), or phenotypic plasticity driven by environmental
76 variability such as change in temperature (Thresher et al., 2007; Sheridan and Bickford, 2011;
77 Irie et al., 2013; Teplitsky and Millien, 2014).

78

79 In many fisheries, the largest animals in the stock are targeted (size-selective harvest), or a lower
80 size limit is applied to prevent harvest of the smallest animals (Baskett et al., 2005; Coggins et
81 al., 2007; Fenberg and Roy, 2008). In other fisheries, both lower and upper limits are used so
82 that medium sizes are selected and the largest animals are spared (Crowder et al., 2008), a
83 strategy intended to minimize the impacts of selective fishing (Conover and Munch, 2002). In
84 fisheries that target the largest animals, the continued removal of large animals from a stock
85 truncates the population size distribution and effectively reduces the average and maximum body
86 size in that population (Heino and Godø, 2002; Hsieh et al., 2010; Rouyer et al., 2011). Over

87 time, size-selective harvest can impact the fecundity (Carver et al., 2005; Chiba et al., 2013) or
88 genetics of the stock (Fenberg and Roy, 2008) and have wider ecological consequences for
89 species other than those targeted by the fishery (Jørgensen et al., 2007; Allendorf et al., 2008).

90

91 Environmental changes, such as shifts in temperature or food availability, can constrain the
92 physiology of some species and lead to shifts in the distribution of body sizes within a population
93 (Witbaard et al., 2005; Sheridan and Bickford, 2011). Many species exhibit temperature
94 regulated growth rates such that, in warmer temperatures, they reach a smaller adult body size,
95 whilst in cooler conditions they may grow larger (*sensu* Bergmann's Rule, Teplitsky and Millien,
96 2014). In addition, changing temperature distributions, such as those from climate change, can
97 cause size-selective mortality in some species (Peck et al., 2009; Pörtner, 2010). Regardless of
98 the cause, shifts in life history traits, such as a decrease in maturation size or maximum body size
99 can translate to an overall reduction in stock productivity, or a change in the ecological role of
100 the population (Shin et al., 2005).

101

102 Atlantic surfclams (*Spisula solidissima*) are a large-bodied, long-lived (maximum age >30 years,
103 Jones et al., 1978, 1983) species that are found along the continental shelf in the northwestern
104 Atlantic Ocean from the Chesapeake Bay mouth to Georges Bank (Figure 1) where they form
105 dense aggregations (Jacobsen and Weinberg, 2006; NEFSC, 2013). Surfclams support a major
106 commercial fishery in the western North Atlantic Ocean that harvests using a hydraulic dredge
107 (i.e., wet dredge) to extract surfclams from the sandy bottom (Serchuck and Murawski, 1997;
108 Wallace and Hoff, 2005; NEFSC, 2013) with high pressure hydraulic jets that fluidize the
109 sediment and reduce breakage of clams (Medcof and Caddy, 1974; Ropes, 1980). Like many

110 dredges, surfclam dredges are size-selective and surfclams less than 80 mm shell length
111 generally pass easily through the dredge and are not caught, whilst those larger than 80 mm are
112 retained at increasing efficiency up to a maximum efficiency at 125 mm shell length and larger
113 (NEFSC, 2010). Selective fishing for the largest clams in this fishery has the potential to truncate
114 the size distribution in the fished population.

115
116 Surfclams have a small optimal temperature range (16–22 °C) (Loosanoff and Davis, 1963;
117 Savage, 1976; Snelgrove et al., 1998; Munroe et al., 2013), with temperatures in excess of 23°C
118 causing impaired physiological functioning or mortality (Woodin et al., 2013), especially in
119 larger (older) surfclams (Saila and Pratt, 1973; Goldberg and Walker, 1990; Marzec et al., 2010).

120 Analysis of annual surfclam shell growth increments shows a negative relationship between
121 average annual water temperature and growth, such that warm years yield smaller growth
122 increments (Jones, 1981). Likewise, body size comparisons among inshore (warmer) and
123 offshore (cooler) populations show that clams from cooler locations grow faster and attain a
124 larger overall size (Jones et al, 1978; Cerrato and Keith, 1992). Recent declines in abundance of
125 surfclams in the most southern portion of their range on the Middle Atlantic Bight (MAB)
126 continental shelf has been attributed to warming bottom waters (Kim et al., 2004; Weinberg,
127 2005) and increased frequency of conditions that result in episodic warming events of bottom
128 waters (Narváez et al., 2015), ultimately causing starvation and thermal-induced mortality
129 (Munroe et al., 2013; Narváez et al., 2015). Thus, increasing bottom water temperature also has
130 the potential to shift the size distribution in surfclams.

131

132 Federal stock assessment surveys of Atlantic surfclams on the MAB continental shelf (Figure 1)
133 show a trend of decreasing maximum shell length over time (Figure 2). This trend could be
134 driven by fishery truncation (size selection), increasing bottom water temperature (Bergmann's
135 Rule) or some combination of the two. In this study an individual-based population dynamics
136 model (IBM) that simulates the growth of post-settlement surfclams (Munroe et al., 2013;
137 Narváez et al., 2015) is used to evaluate the influence of various levels of fishing pressure and
138 environmental temperature changes, independently, on the size structure of surfclam populations
139 in the MAB. The simulation results are assessed using observed surfclam sizes obtained from
140 federal survey data.

141

142 **Materials and Methods**

143

144 *Survey Trend Analysis*

145 Surfclams were collected from the federal United States (U.S.) surfclam stock during stock
146 assessment surveys beginning in 1982 and continuing approximately every 3 years through 2012.
147 The fishery operates in the U.S. Exclusive Economic Zone in approximately 20 to 60 m depth,
148 from off the mouth of the Chesapeake Bay, to Georges Bank (Figure 1). This study focused on
149 an area identified in the assessment as stratum 21 off New Jersey (Figure 1) because this location
150 has been the most intensely sampled and provides sufficient replicate observations for reliable
151 calculation of length-at-age over time. On average, 125 surfclams were collected from stratum
152 21 in each survey year using 21 hydraulic dredge tows (sample sizes in each year vary, details
153 are provided in Table 1). A representative subset of surfclams collected in each tow, including as
154 wide a range of sizes as possible, were retained for estimation of length-at-age. Shells from

155 these surfclams were measured (length, mm), then later used to evaluate age by counting annular
156 rings in the shell following standard shell sectioning and aging methods (Jacobsen et al., 2006).

157

158 The individual shell length and age measurements were used to calculate the growth curve and
159 estimate the population's asymptotic shell length over time. In each survey year, the group of
160 surfclams collected includes a mix of sizes and ages (cohorts) and therefore integrates growth
161 conditions over time for that population. The shell length change over time (*shell length_t*) was
162 obtained by fitting von Bertalanffy growth curves (von Bertalanffy, 1938):

$$163 \quad \textit{shell length}_t = L_\infty(1 - e^{-k(t-t_0)}) \quad (1)$$

164 to the length-at-age data. Values for the asymptotic shell length (L_∞) and growth rate constant
165 (k) and their associated uncertainty were obtained using likelihood methods following Kimura
166 (1980) (calculations performed using R libraries fishmethods, FSA, NCStats, and nlstools; R
167 Development Team, 2007). The change over time in L_∞ was analyzed by fitting a regression
168 weighted by the inverse standard error to the maximum shell lengths over time. The analysis of
169 the shell length trend provided the evaluation criteria for the simulations conducted with the
170 individual-based post-settlement growth model.

171

172 *Modeling Surfclam Populations*

173 An individual-based model (IBM) has been developed and implemented for the Atlantic
174 surfclam (Munroe et al., 2013; Narváez et al., 2015). In this study, the IBM was used to simulate
175 the growth of post-settlement (>20mm shell length) surfclams in response to varying bottom
176 water temperatures. The model includes parameterizations for feeding, respiration, somatic and
177 shell growth, and spawning. A summary of the equations and parameterizations used in the

178 surfclam model are given in Narváez et al. (2015) and Munroe et al. (2013). Details of the model
179 components that are relevant to this study and which differ from those described previously are
180 given below.

181
182 A range of general relationships covering the physiological capabilities of most bivalves were
183 used to parameterize growth and reproduction, including respiration (Powell and Stanton, 1985)
184 with a Q_{10} temperature response of 2 (Rueda and Small, 2004), and filtration rate (Powell *et al.*,
185 1992), with a modal temperature relationship well-described for bivalves (Hofmann *et al.*, 2006;
186 Flye-St.Marie *et al.*, 2007; Fulford *et al.*, 2010) that has a temperature optimum at 18°C and
187 cessation near 0°C and 24°C, consistent with observed physiological responses (Marzec *et al.*,
188 2010). Collectively, this allows for temperature to affect the physiological functions of surfclams
189 such that food assimilation increases linearly with shell length (body size) and temperature up to
190 a thermal limit of 25°C (Powell *et al.*, 1992), but respiration increases exponentially with
191 biomass (Møhlenberg and Kiørboe, 1981) resulting in a thermal limit, or transient event margin
192 (*sensu* Woodin *et al.*, 2013) at which respiration will exceed assimilation and the surfclam will
193 begin to lose somatic tissue (a full description of model equations for individual clam growth are
194 provided in Munroe *et al.*, 2013).

195
196 The total population mortality (M) is a sum of natural mortality, fishing mortality and deficit
197 stress mortality (Table 2). At each model time step ($dt = 0.2$ day) the number of surfclams
198 (clams m^{-2}) is reduced by a factor of $I - e^{-Mdt}$. Natural mortality (M_n) is set to a constant rate of
199 $4 \times 10^{-4} d^{-1}$ based on observations reported in Weinberg (1999) and NEFSC (2013). In the
200 calculation of fishing mortality (M_f), L_1 (120 mm) is the shell length at which the hydraulic

201 dredge is 100% efficient (catches all clams this size and larger), L_2 (25 mm), is the length at
202 which the hydraulic dredge is 0% efficient (does not catch any of this size class and smaller).
203 The size-selective fishing mortality parameters (L_1 and L_2) are derived from the selectivity
204 function previously fit to data obtained for a commercial hydraulic dredge by NEFSC (2013).

205
206 Deficit stress mortality (Getz, 2011) (M_v , Table 2) occurs when environmental conditions cause
207 surfclams to lose somatic tissue (e.g. high temperature or low food concentration), which in
208 terms of bivalves results in a decrease in condition index. A deficit stress (v_i) in an individual
209 surfclam is accumulated (Getz, 2011) any time somatic tissue declines. Specifically, if the
210 somatic tissue declines in a given time step by an amount dS (g), then v_i is increased by $dS \times dt$,
211 which has units of g•d (gram-day). Surfclams recover slowly from deficit stress, so v_i is reduced
212 each time step by a factor, $1 - e^{-Rdt}$, where R is 0.004 d^{-1} . The functional form of deficit stress
213 mortality (Table 2) allows the mortality to remain low until stress reaches a value near $1.45 \text{ g}\cdot\text{d}$
214 and then switches rapidly to high mortality when the stress exceeds $1.8 \text{ g}\cdot\text{d}$. Larger and older
215 surfclams have a smaller scope-for-growth than smaller and younger surfclams (Munroe et al.
216 2013). The deficit stress formulation allows older surfclams to accrue stress more rapidly and
217 therefore older clams are subject to higher mortality during stressful periods.

218

219 *Simulations*

220 The surfclam model was implemented at two locations on the MAB continental shelf (Figure 1).
221 The northern location (NJ) is offshore of New Jersey and is centrally located within stratum 21.
222 The southern location is located off the Delaware-Maryland-Virginia (DMV) coast in the same
223 depth as the NJ location, and is approximately the southern extent of the commercial fishery for

224 this species over the period covered by the stock assessment surveys. The simulations were
225 forced with a 50-year time series (1958-2007) of bottom water temperatures obtained from an
226 implementation of the Regional Ocean Model System (ROMS) for the Northwest Atlantic (Kang
227 and Curchitser, 2013).

228

229 Each simulation at the two sites was initialized with a stable multi-cohort surfclam population
230 that was generated using an annual bottom water climatology. The annual climatology (Figure
231 3a) was constructed from the 50-year time series by averaging the simulated bottom water
232 temperatures for each day of the year. Simulations were then run for an additional 50 years using
233 different bottom temperature and fishing rates (Table 3 and Figure 3 B, C). The food supply time
234 series used for the simulations (Munroe et al., 2013) was invariant from one year to the next,
235 thereby removing variability in food supply as a factor influencing surfclam growth.

236

237 The 95th percentile of shell length of the population was calculated each year for all simulations.
238 This metric is known exactly from the shell lengths of each individual in the simulated
239 population and was used to compare the simulated and observed asymptotic shell lengths. The
240 empirically derived linear relationship between the 95th percentile of shell length and the
241 asymptotic shell length (L_{∞}) has a slope close to 1 ($R^2=0.39$, unpublished data) and therefore can
242 be used as comparable representations of the largest body sizes in a given population.

243

244 The influence of temperature on shell length in surfclam populations at the two locations on the
245 MAB continental shelf was simulated using different temperature scenarios, which were applied
246 for the second 50 years. At the southern location (DMV), bottom temperature ranged seasonally

247 from $\sim 7^{\circ}\text{C}$ in March to $\sim 16^{\circ}\text{C}$ in October (Figure 3A); the pattern of temperature variation at the
248 northern location (NJ) was similar but about $\sim 1.7^{\circ}\text{C}$ lower overall (Fig. 3a). These site-specific
249 climatologies, which were constructed from the 50-year bottom water temperature simulation,
250 were used to develop a reference case (normal years) for each location. The effect of an annual
251 temperature cycle that is colder by 1.5°C on average relative to the 50-year climatology was also
252 simulated for each site (Fig. 3b). The colder temperature time series was an individual year
253 selected from the 50-year simulation. As a comparison, a warm year (2.3°C on average) was
254 also selected from the 50-year hindcast (Figure 3C) for each site. The percent change in
255 maximum surfclam shell length in simulations obtained for the cold and warm years was
256 calculated relative to the normal year simulations.

257

258 Simulations were also used to assess the influence of fishing on maximum shell length in
259 surfclam populations. All three temperature scenarios for each location were simulated under
260 conditions of zero, 5%, or 20% fishing pressure (Table 3). Additionally, simulations were
261 conducted that used levels of fishing pressure that vary in intensity over time (Table 3); these
262 used the bottom water climatology calculated for both locations that was repeated for the second
263 50 years, thereby removing temperature effects and focusing on the effects of varying fishing
264 only. The combined effect of annually varying bottom water temperature and fishing pressure
265 was also simulated for each site. These simulations used a 5% fishing effort and the 50-year
266 hindcast of bottom water temperatures.

267

268 **Results**

269

270 *Survey Shell Length Trend*

271 Observed surfclam maximum shell length decreased from approximately 180mm in the early
272 1980s, to less than 160 mm three decades later (Figure 2) in the region of stratum 21 off New
273 Jersey; a 10% decrease in shell length over time. Results of a weighted (by inverse standard
274 error) regression fit to the maximum shell lengths over time showed a significantly ($p=0.004$,
275 $F=12.4$, $DF =13$) negative trend in maximum shell length (Figure 2). This 20 mm decrease in
276 shell length scales to a biomass decline of approximately 70 g or a 39% lower biomass of the
277 largest size class in the population over time (biomass (g) = aL^b , $a= 8.3 \times 10^{-5} \text{g mm}^{-1}$, L =length,
278 mm, $b=2.85$; from Marzec et al.,2010).

279

280 *Temperature and Fishing Simulations*

281 Temperature affects the physiological functions of simulated surfclams such that larger clams
282 tend to be more heavily impacted by warm temperatures than small clams (Figure 4A), and
283 average temperature of about 8°C generates the largest clams, with maximum size decreasing as
284 temperature increases or decreases (Figure 4B, 5). At location DMV (Figure 5A), the 95th
285 percentile of shell length decreases from 177 mm (climatology base case) to 150 mm (15%
286 decrease) in the warm simulation, and increases to 183 mm (3% increase) in the cool simulation
287 (Figure 5A). Likewise at location NJ (Figure 5D), the 95th percentile of shell length decreases
288 from 182 mm (climatology base case) to 176 mm (a 3% decrease) in the warm temperature
289 simulation, but increases to 184 mm (1% increase) in the cool temperature simulation (Figure
290 5D). The influence of temperature and fishing are additive in the model such that warm
291 conditions and highest fishing (20%) generate the greatest decrease in the 95th percentile of shell

292 length; a 22% and 16% decrease relative to the no fishing climatology base case at DMV and NJ,
293 respectively (Figure 5C, F).

294

295 Fishing decreases the simulated maximum shell length, with higher fishing generating a larger
296 decrease in length (Figure 4B, 6). At DMV (Figure 6A), a 5% increase in fishing decreases the
297 95th percentile of shell length from 177 mm to 172 mm (a 3% length decrease at 5% fishing). A
298 20% increase in fishing decreases the 95th percentile of shell length to 157 mm (an 11% decrease
299 at 20% fishing). At the NJ location (Figure 6B), the slightly cooler conditions allow surfclams to
300 have a larger non-fishing shell length compared to DMV surfclams. At NJ, a 5% increase in
301 fishing decreases the 95th percentile shell length by 3%, from 182 mm (zero fishing) to 177 mm
302 (5% fishing), whilst 20% fishing decreases the 95th percentile of shell length by 8% (Figure 6B).
303 At both locations and for both fishing pressures, the reverse occurs when fishing pressure is
304 removed.

305

306 At both locations, it takes 10 years (10 years represents 10 new cohorts, one per year) from the
307 time fishing starts until the change in the 95th percentile of length is evident, and stability of the
308 95th percentile of length is reached in 15 years at 5% fishing, but takes longer (25 years) at the
309 higher fishing rate (Figure 6). Likewise, when fishing is removed (e.g. simulations High-None
310 and Low-None in Figure 6), the response in the 95th percentile of shell length is not evident for
311 10 years, and stability of the 95th percentile of length is not reached until 15 years later at 5%
312 fishing and 25 years later at 20% fishing (Figure 6).

313

314 Allowing temperature to vary from one year to the next creates temporal variation in the 95th
315 percentile of length (Figure 7). At DMV, the 95th percentile of shell length fluctuated by 20 mm
316 over a period of approximately 10 years; whereas, at NJ, fluctuations of the 95th percentile of
317 shell length were much smaller, approximately 5 mm.

318

319 **Discussion**

320

321 Surfclam survey length-at-age data show that the maximum body size in the U.S. surfclam stock
322 off New Jersey has declined by approximately 10% over 30 years of observations (NEFSC,
323 2013). This difference in length is important; it scales to a biomass decline of approximately 70 g
324 or 39% lower biomass over time. Smaller surfclams could lead to decreased fishery yields and
325 lower secondary production within the shelf ecosystem (Munroe et al., 2013). The simulations
326 that include temperature and size-selective fishing effects on population size structure
327 demonstrate that changing bottom water temperature and/or fishing can cause changes in
328 maximum shell length of this magnitude. Independently, either sustained elevated temperatures
329 of 1 to 2°C on average, or continuous localized fishing at high rates (20%), generate the observed
330 decrease in maximum shell length (Figure 4B); however, these conditions may occur rarely.
331 More realistically, when occurring in concert, a 5% increase in fishing along with an average
332 temperature increase above 8°C can lead to a decline in maximum shell length in excess of that
333 observed (Figure 4B). Narváez et al. (2015) noted no strong or sustained warming trend in
334 hindcast bottom water temperature anomalies, and fisheries management has maintained annual
335 fishing rates of 1 to 5% of the fully selected stock (NEFSC, 2013) during the time this change in
336 maximum size was observed. Given that neither of the independent conditions (sustained high

337 temperature, nor continuous high fishing) has occurred, it is likely that temperature and fishing
338 have acted synergistically to affect population shell lengths (Hidalgo et al., 2011; Rouyer et al.,
339 2011).

340

341 Distinguishing the contribution of environment versus fishing in producing the observed
342 maximum body size is difficult. Dredge fisheries have been shown to cause a decrease in
343 maximum shell sizes in other clam populations. Both Moura et al. (2013) and Dalgiç et al.
344 (2010) documented differences in growth and body size between fished and non-fished clam
345 populations; however, the differences documented in Moura et al. (2013) were confounded with
346 a latitudinal gradient in growth conditions such that the unfished population came from warmer
347 locations that were more conducive to faster growth and larger asymptotic size in the species
348 (*Dosinia exoleta*) they were studying. This demonstrates the difficulty in distinguishing the
349 relative influence of environment versus fishing in the absence of manipulation or controlled
350 experiments. In this study, simulations that vary temperature and fishing independently allowed
351 the relative role of the two effects to be evaluated and suggested that the two factors can each
352 independently affect maximum shell length, but acting together generate the greatest decrease in
353 maximum shell length.

354

355 Population dynamics near the geographic limits of a species range are known to be sensitive to
356 environmental fluctuations (Caddy and Gulland 1983; Parsons 1991), suggesting that the biggest
357 changes in surfclam maximum size should be evident in the most southerly portion of the stock.
358 This was the case for the simulated populations, where the largest changes in simulated shell
359 length were indeed obtained for the southern location, under warm temperature and high fishing

360 conditions. Simulations with a sustained fishing rate of 20% produced the observed change in
361 population shell length (about 10%) at the southern location (DMV), but this fishing rate was
362 insufficient to produce the observed changes at the northern (NJ) location.

363

364 Bergmann's rule predicts that in general, animal size decreases with increasing temperature
365 (Teplitsky and Millien, 2014). This trend has been documented in other clam species (Beukema
366 et al., 2009) and fisheries in general (Pörtner and Peck, 2010). Temperature affects the
367 physiological functions of surfclams such that food assimilation increases linearly with shell
368 length (body size) and temperature up to a thermal limit of 25°C (Powell et al., 1992), but
369 respiration increases exponentially with biomass (Møhlenberg and Kiørboe, 1981) resulting in a
370 thermal limit at which respiration will exceed assimilation and the surfclam will begin to lose
371 somatic tissue (starve) (Munroe et al., 2013). Ingestion and respiration functions for the
372 simulated surfclams both depend on body size; therefore, the thermal limit or transient event
373 margin (Woodin et al., 2013) changes with surfclam size such that larger clams tend to be more
374 heavily impacted by warm temperatures than small clams because of the large clam's elevated
375 metabolic demands relative to lower assimilation and ingestion rates (Figure 4A). Thus, a
376 reduced scope for growth assures that larger surfclams will be more sensitive to increased
377 temperatures. It is possible that temperature could constrain surfclam growth in other indirect
378 ways, for example through changes in the timing of phytoplankton blooms and hence food
379 availability, shifts in spawning time, or changes in predation or competition relationships with
380 other species. Those other indirect effects are not explored in this model.

381

382 Density-dependent growth has been suggested for surfclams (Weinberg 1998). An unusually
383 high recruitment event, followed by a local fishery closure, resulted in sustained high surfclam
384 densities, reduced growth rates and smaller sizes in MAB populations (Weinberg 1998).
385 However, more recently the occurrence of smaller surfclams has been attributed to warming in
386 the southern Mid-Atlantic (Kim et al., 2004; Weinberg, 2005) and increased frequency of
387 anomalous oceanographic events (Narváez et al., 2015), rather than density dependency.
388 Moreover, the time series of maximum size used in this study (Figure 2) is unlikely to be
389 influenced by density dependence because fishing effort in Stratum 21 over the period of interest
390 would have thinned the population and alleviated density-dependent competition.

391
392 Rapid rates of change in the average physiology of a population could derive from phenotypic
393 plasticity rather than genetic selection. Distinguishing between phenotypic changes in a
394 population over time (response to environment) versus genotypic changes (responses of a
395 population to selective pressure) based on physiology alone can be difficult (Law 2000). Both a
396 phenotypic and genotypic change in a population can manifest as the same response (e.g. change
397 in size over time), yet could be the result of differing mechanisms. The simulation design used
398 in this study focuses only on phenotypic changes and suggests that the observed changes could
399 occur without a genetic change.

400

401 Increases in water temperature have been associated with fish stock redistributions in other
402 species within the MAB region (Nye et al., 2009; Overholtz et al., 2011; Pinsky et al., 2013).
403 Surface and bottom water temperatures are forecast to increase by more than 2°C (up to 8°C in
404 some emission scenarios) over the next 50 to 100 years in this region (Frumhoff et al., 2007).

405 Potential ongoing and projected temperature changes over the bulk of the fished stock have the
406 potential to cause changes in the physiology and stock distribution of surfclams (Figure 4B). An
407 approximate 10% change in the maximum shell length, which corresponds to a 39% decline in
408 maximum biomass, has been observed in the surfclam stock from the MAB continental shelf
409 from approximately 1980 until today. Model simulations suggest that this change could be the
410 result of warmer summer bottom water and size-selective fishing. Importantly, when
411 interannually varying bottom temperatures are used to simulate surfclam population size
412 dynamics over time, the interannual variability in bottom water alone generates fluctuations in
413 the maximum size that are on the order of 10% over 10 to 15 years. This fluctuation is consistent
414 with the observed change in the stock. Therefore, it is possible that the observations are simply a
415 result of natural fluctuations driven by temporally varying temperatures. These results also
416 suggest that populations can recover if this change is not the product of a corresponding
417 genotypic change; however, that response could take a decade to become evident, and much
418 longer before full size recovery is achieved. Observations over a longer period will be necessary
419 to determine if the trend observed is due to natural fluctuations in the environment, or is
420 sustained over time as a function of directional trends in temperature or sustained fishing.

421

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751

752 Table Captions

753

754 Table 1: Summary of samples taken during stock surveys (NFSC, 2013) that were used to
755 determine age at length curves.

756

757 Table 2: Variables, equations and parameterizations used in individual-based model population
758 mortality calculations. Additional details for model equations and parameterizations are
759 given in (Munroe et al., 2013; Narváez et al., 2015).

760

761 Table 3: Temperature and fishing conditions used in each simulation for both DMV and NJ
762 locations. The climatology (Figure 3) was an average of the simulated bottom water
763 temperatures for each day of the year using a 50-year time series of bottom water
764 temperature (1958-2007); the cool and warm conditions were repeated cooler and warmer
765 (respectively) than average years from the 50 year hindcast. Fishing percentages shown are
766 calculated as a percentage of the stock removed annually.

767

768

769

770 Figure Captions

771

772 Figure 1:

773 Locations of stratum 21 (outlined region) and the New Jersey (NJ) and Delmarva (DMV)

774 simulation sites (x) on the Middle Atlantic Bight continental shelf. Dashed grey lines show

775 depth contours every 50 m.

776

777 Figure 2:

778 Surfclam asymptotic length (L_{max}) over time derived from growth curves fit to fishery survey

779 observations made within stratum 21 using a von Bertalanffy growth relationship. Error bars

780 show the standard error. A weighted (by inverse standard error) regression fit to the maximum

781 shell lengths over time showed a significantly negative slope (slope = -0.7, adjusted $R^2 = 0.45$, F

782 statistic=12.4, degrees of freedom = 13, p-value=0.004).

783

784 Figure 3:

785 Annual bottom water temperature times series used with the surfclam individual-based model for

786 simulations at the New Jersey (NJ, grey) and Delmarva (DMV, black) sites for the A) base case,

787 constructed from 50-year simulation, B) cold year, and C) warm year.

788

789 Figure 4:

790 Panel A: influence of temperature and shell length on simulated annual average net productivity

791 (d^{-1}) (assimilation -respiration/body mass) for an individual surfclam for a range of sizes (y axis)

792 and temperatures (x axis). The zero net productivity contour is shown (dotted white line); values
793 below are positive and above are negative. Panel B: influence of temperature and fishing on the
794 asymptotic length (95th percentile) of simulated surfclam populations.

795

796 Figure 5:

797 Asymptotic length (95th percentile) of simulated surfclam populations obtained from the different
798 temperature simulations for the Delmarva (DMV, top panels) and New Jersey (NJ, bottom
799 panels) for no fishing (A,D), 5% fishing (B,E) and 20% fishing (C,F).

800

801 Figure 6:

802 Asymptotic length (95th percentile) of simulated surfclam populations obtained from the fishing
803 effort simulations.

804

805 Figure 7:

806 Asymptotic length (95th percentile) of simulated surfclam populations obtained using bottom
807 water temperatures from the 50-year hindcast simulation for the sites off New Jersey (NJ, black
808 line) and Delmarva (DMV, grey line).

809

810

811

812 Tables

813

814 Table 1: Summary of the stock assessment surveys (NFSC, 2013) that provided the surfclam
815 samples and the number that were aged to obtain the age-at-length growth curves.

816

Survey Year	Dredge Tows (Number)	Clam Samples (Number)
1978	29	100
1980	15	44
1981	20	103
1982	18	161
1983	18	140
1986	19	159
1989	20	111
1992	20	58
1994	20	190
1997	20	119
1999	33	188
2002	27	207
2005	20	152
2008	28	196
2011	15	38

817

818

819

820 Table 2: Variables, equations and parameterizations used in individual-based model population
 821 mortality calculations. Additional details for model equations and parameterizations are
 822 given in (Munroe et al., 2013; Narváez et al., 2015).
 823

Variable	Governing Equations	Parameter Definitions (Units)
Total Mortality (M)	$M = Mn + Mf + Mv$	Mn = natural mortality, Mf = fishing mortality, Mv = deficit stress mortality
Fishing Mortality (M_f)	$M_f = 0.5M_{f_0} \left(1 + \tanh \frac{L_t - L_1}{L_2} \right)$	M_{f_0} = maximum fishing mortality rate L_1 (120 mm) = clam size at which the hydraulic dredge is 100% efficient L_2 (25 mm) = clam size at which the hydraulic dredge is 0% efficient L_t = clam length at the current time step
Deficit Stress Mortality (M_v)	$M_v = 0.5M_{v_0} \left(1 + \tanh \frac{v_i - M_{v_1}}{M_{v_2}} \right)$	M_{v_0} (0.0055 d) = maximum deficit stress mortality rate M_{v_1} (1.5 g•d) = stress at which the mortality rate is half of M_{v_0} M_{v_2} (0.2 g•d) = controls the range stress over which mortality changes from zero M_{v_0} .

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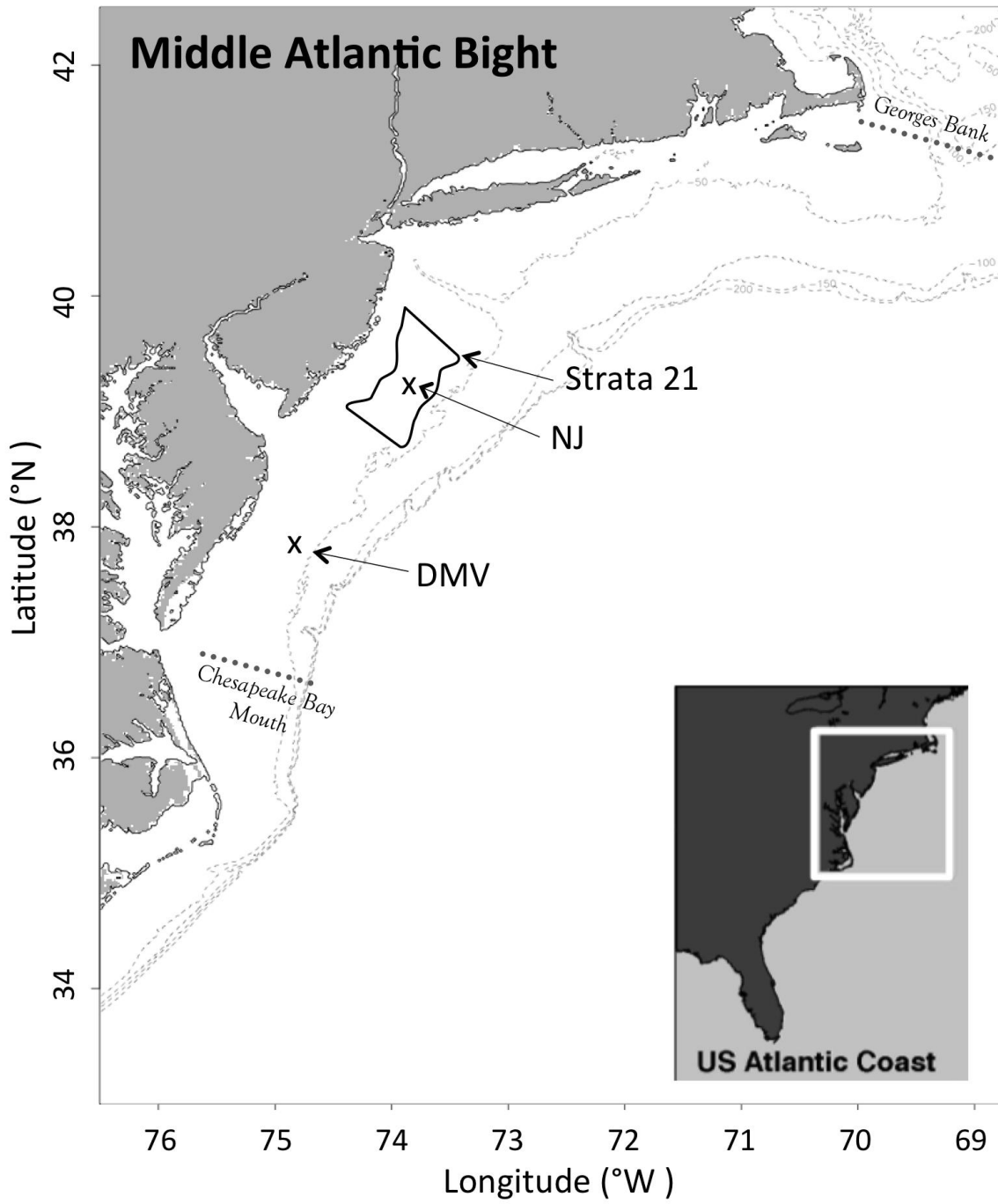
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Table 3: Temperature and fishing conditions used for the individual simulations implemented at the DMV and NJ locations. The temperature climatology (Figure 3) was constructed from the daily average of the bottom water temperatures for each year of the 50-year bottom water temperature (1958-2007) simulation; the cool and warm temperature simulations represent conditions that are approximately 1.5°C cooler and 2.3°C warmer relative to the average climatology, respectively. Fishing percentages were calculated as a percentage of the stock removed annually.

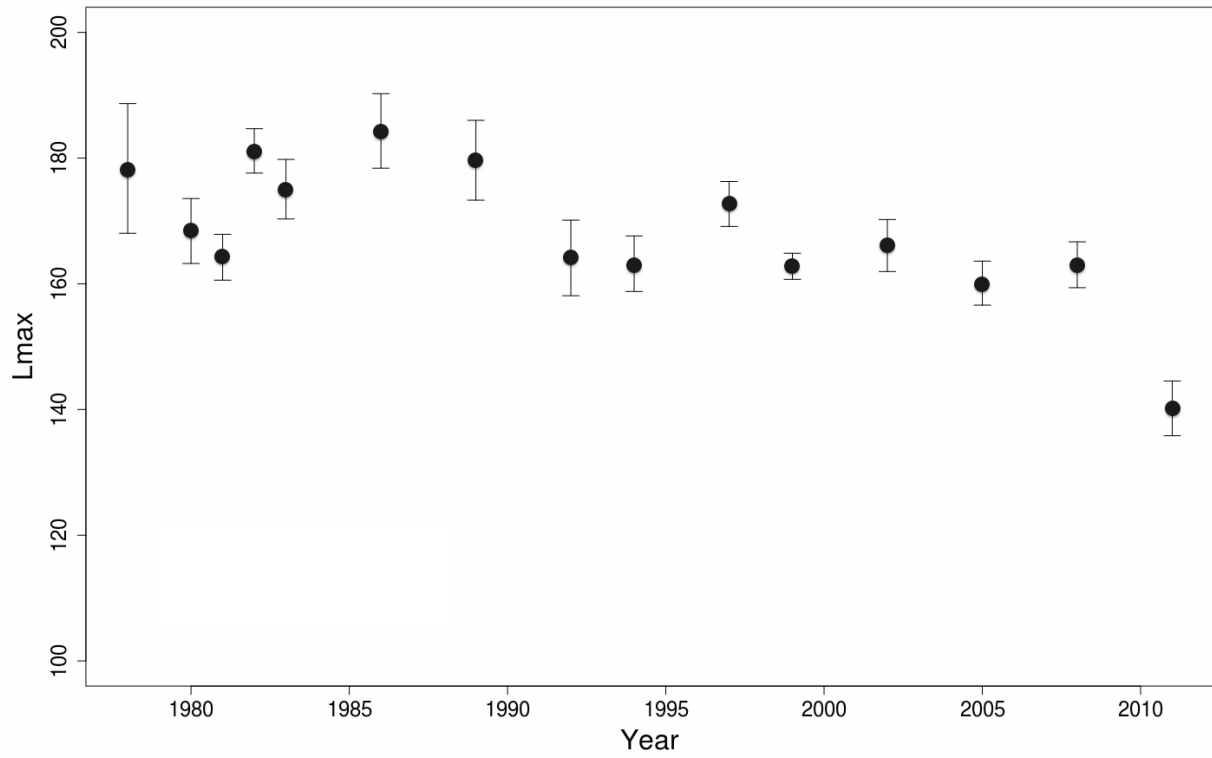
	Temperature Conditions	Fishing Conditions
Fishing Simulations		
Fish_0-5	Climatology	0% 1958-1982; 5% 1982-2008
Fish_0-20	Climatology	0% 1958-1982; 20% 1982-2008
Fish_0-5-20	Climatology	0% 1958-1962; 5% 1962-1987; 20% 1987-2008
Fish_0-5	Climatology	5% 1958-1982; 0% 1982-2008
Fish_20-0	Climatology	20% 1958-1982; 0% 1982-2008
Fish_20-5-0	Climatology	20% 1958-1962; 5% 1962-1987; 0% 1987-2008
Temperature Simulations		
Clim_0	Climatology	0%
Clim_5	Climatology	5%
Clim_20	Climatology	20%
Cool_0	Cool	0%
Cool_5	Cool	5%
Cool_20	Cool	20%
Warm_0	Warm	0%
Warm_5	Warm	5%
Warm_20	Warm	20%
Annually Varying Temperature Simulations		
Hind	50-year Hindcast	5%

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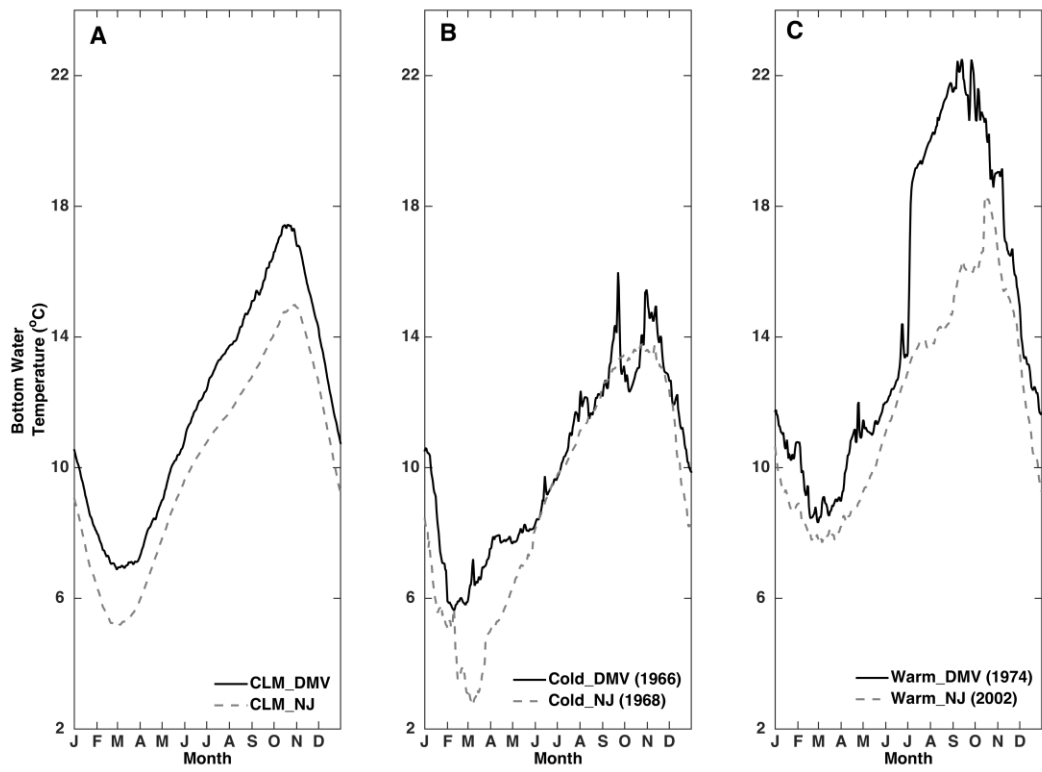
841 Figures
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844 Figure 1
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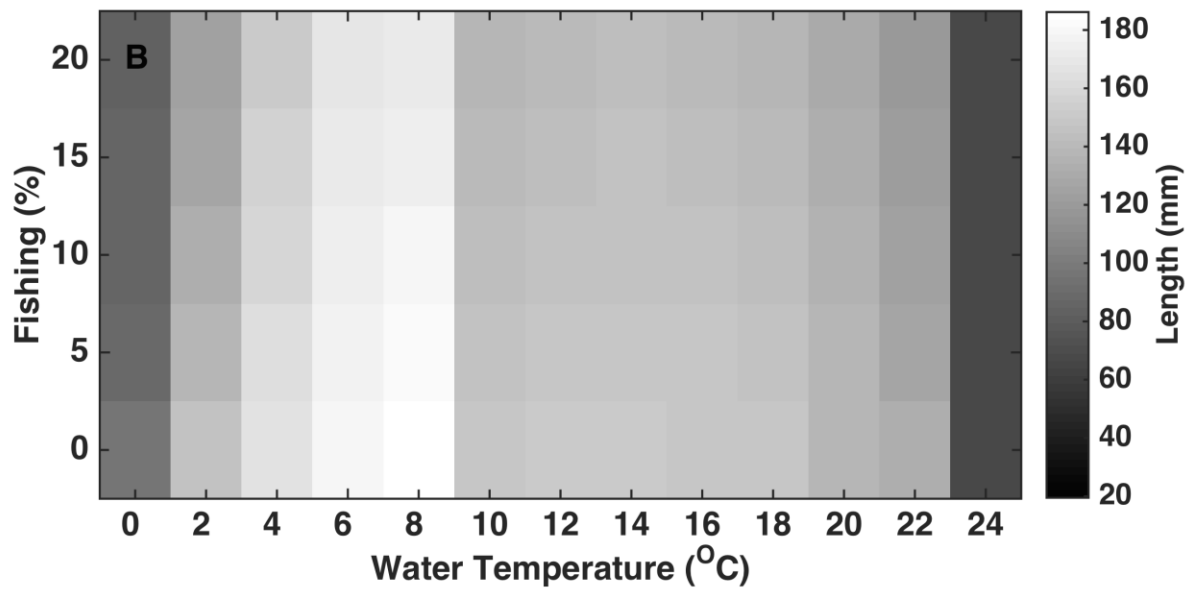
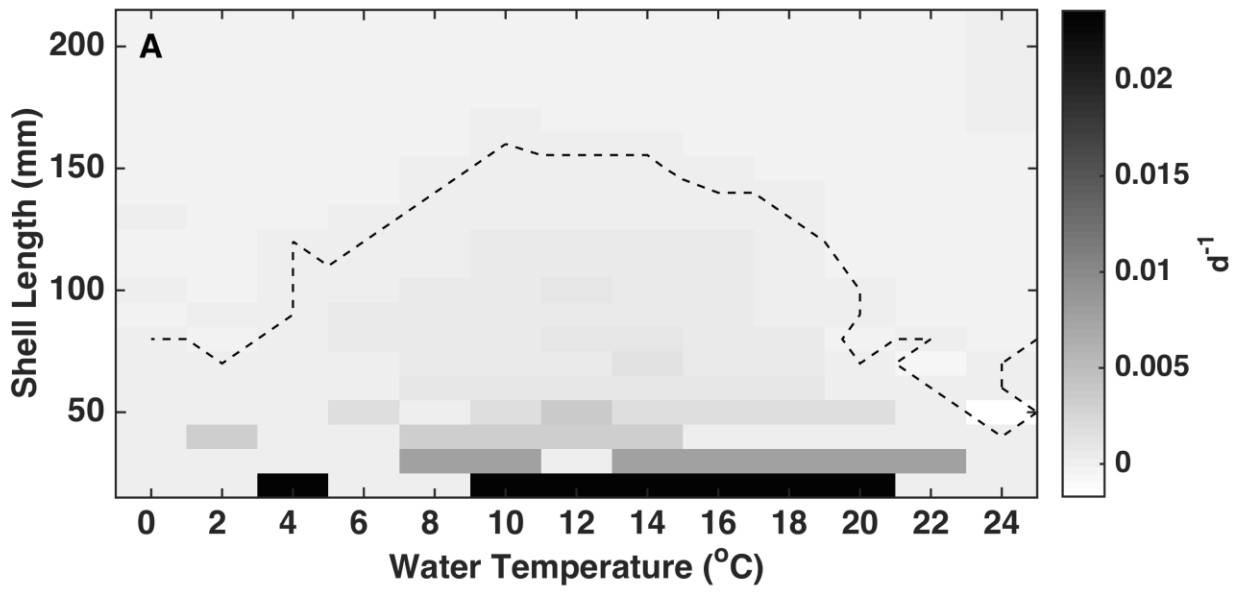


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847 Figure 2
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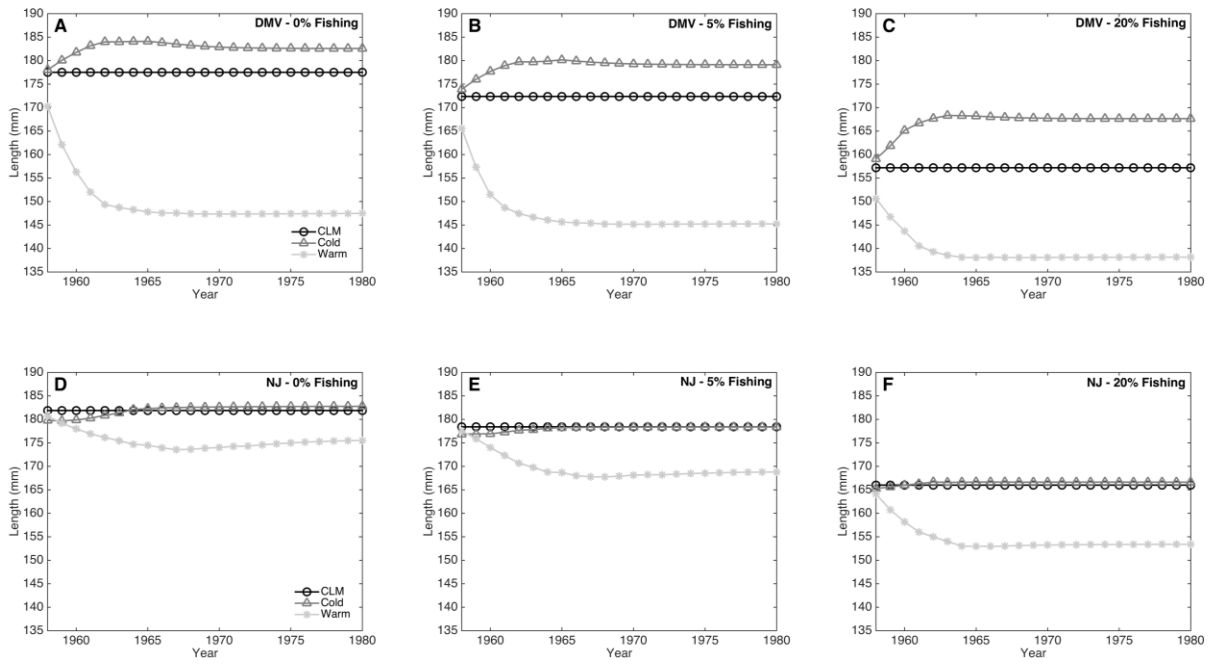


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Figure 3

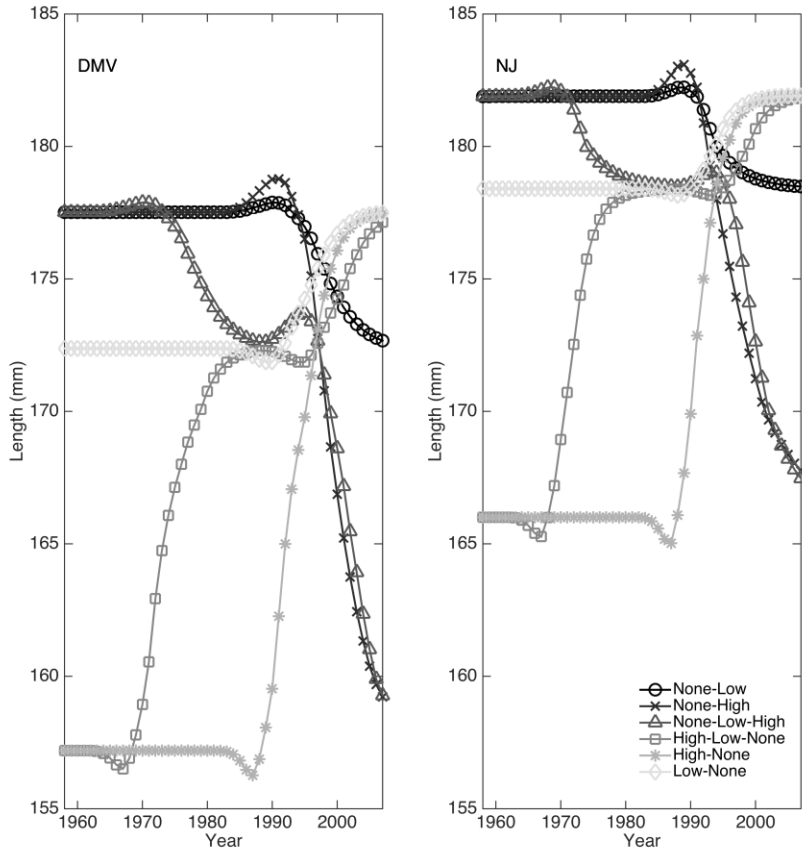


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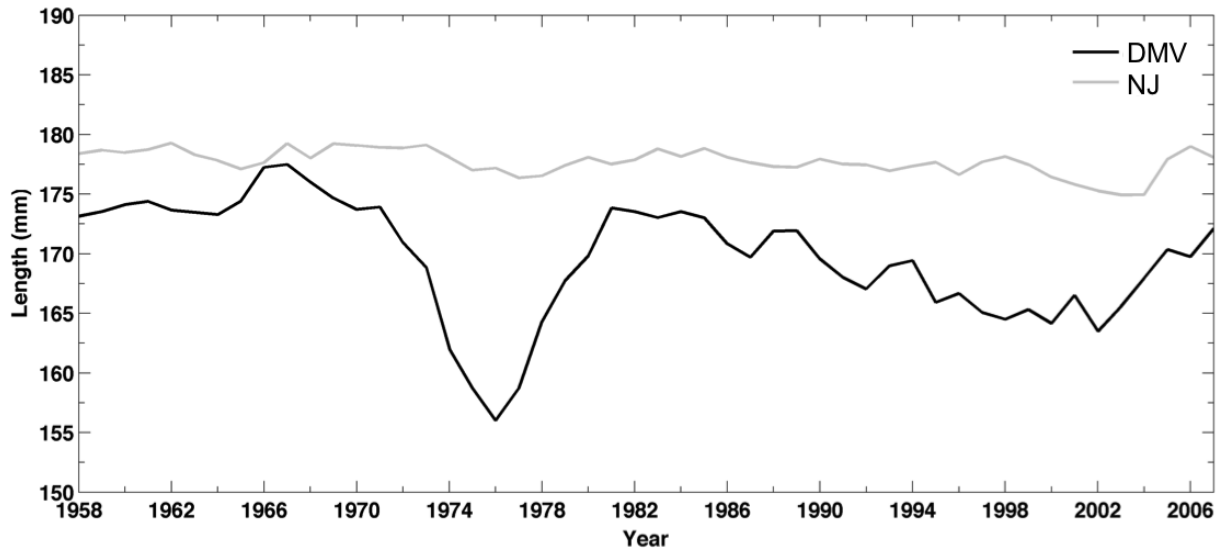
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862 Figure 5
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869 Figure 6
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Figure 7