Warming increases the top-down effects and metabolism of a subtidal herbivore

Ecological theory and experiments indicate that warming can increase the relative strength of top-down effects via alterations to metabolic rates in several different systems, thereby resulting in decreased plant biomass at higher temperatures. However, the general influence of increased environmental temperature on top-down effects is not well understood in systems where organisms experience relatively large variation in temperature. Rapid ocean temperature changes are pervasive throughout the Galápagos Islands due to upwelling and downwelling of internal waves, ENSO events and seasonality. We measured the effect of large, but not uncommon, water temperature variation on the metabolism and grazing rate of a common subtidal herbivore and on photosynthesis of their algal prey in the Galápagos Islands in July 2012. We found that green urchin consumption and metabolism were greater at the higher temperature treatment (28 °C), resulting in significantly less algal biomass. Our result that warming increased green urchin metabolic rates, even in a highly dynamic system, provides further support for a mechanistic link between environmental temperature and feeding rates. And further, our findings suggest individual response to temperature results in changes in top-down effects. And if this response is maintained over longer-time scales of days to weeks, this could translate to alterations of larger-scale ecological patterns, such as primary producer community composition and structure.

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Introduction

The strength of herbivore-plant interactions determines the composition and distribution of primary producers in many marine communities (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Paine 1992, Duffy & Hay 2000, Burkepile & Hay 2006). Several studies have found that this interaction is influenced by sublethal changes in environmental temperature, via alterations to metabolic rates (O'Connor 2009, Kratina et al. 2012). For example, higher temperatures often cause increases in both primary production and consumption rates; however, due to differential temperature scaling of photosynthesis and respiration, consumption is predicted to increase relative to production at warmer temperatures (Allen et al. 2005, O'Connor 2009, O'Connor et al. 2009). In some circumstances, this could lead to lower standing plant biomass due to stronger top-down effects.

A growing body of literature demonstrates that in a warming world the relative strength of top-down effects increases (within a non-lethal or non-stressful thermal environment), in freshwater, marine and terrestrial systems (O'Connor 2009, Barton et al. 2009, O'Connor et al. 2009, Yvon-Durocher et al. 2010, Hoekman 2010, Kratina et al. 2012). To date, these experimental studies were conducted with relatively small but relevant changes in temperature (from ambient to +6°C). It is unclear to what degree temperature influences species interactions in systems where organisms experience higher temperature variation. For example, it is possible that high natural temperature variability selects for physiological tolerance of temperature change (i.e., plasticity). Hoekman (2010) used the wide range of temperatures (10°C - 35°C) experienced by the inquiline community in pitcher plants to determine how temperature influences the top-down effects of mosquito larvae on protozoa. He found mosquito larvae developed faster at the warmer temperatures, and consequently, had higher energy demands and

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33 fed on protozoa at a faster rate relative to slowly developing mosquito larvae. Yet there are few

34 other studies that quantified the effect temperature has on top-down control in environments with

35 highly dynamic temperature regimes.

36   We used the nearshore system in the Galápagos Islands to determine how temperature

37 affects the metabolism and the strength of top-down effects of a common subtidal grazer, the

38 green sea urchin (*Lytechinus semituberculatus*). Ocean temperature in the Galápagos is highly

39 variable in space and time, ranging from 11°C - 31°C due to upwelling and downwelling of

40 internal waves, El Niño-Southern Oscillation (ENSO) events and seasonality. Sea urchins are a

41 key grazer on macroalgae in marine systems and can regulate the benthic algal community

42 productivity and structure (Paine 1980, Witman 1985, Hereu et al. 2005, Brandt et al. 2012).

43 They are the most significant invertebrate grazer guild in the Galápagos Islands (Irving &

44 Witman 2009, Brandt et al. 2012), and at high densities can convert macroalgal assemblages to

45 urchin barrens or pavements of encrusting algae (Ruttenberg 2001, Edgar et al. 2009).

46 Therefore, if urchins exert strong top-down control in a system with large spatial and temporal

47 variation in environmental temperature, warmer temperatures should strengthen the top-down

48 effect of urchins on macroalgal assemblages and possibly result in increased urchin barrens.

49   We manipulated temperature in outdoor mesocosms and measured the effects on urchin

50 grazing rate and metabolism, as well as plant photosynthesis. Our findings suggest warming

51 strengthens the top-down effects of urchins and results in lower algal standing biomass.

52 **Methods**

53 *Study System*

54   The Galápagos Islands are located 965 km off the coast of Ecuador and are centered at

55 the confluence of several oceanographic currents leading to a high degree of variability in ocean

56 temperature and phytoplankton biomass. The Equatorial Undercurrent runs from west to east

57 across the Pacific Basin and drives major upwelling as it collides with the western islands,

58 resulting in cold and nutrient-rich waters around these islands (Houvenaghel 1978, 1984). The

59 cool Humbolt Current delivers nutrient-rich water to the southern edge of the archipelago

60 (Kessler 2006). The northeast region of the archipelago is strongly influenced by the warm,

61 nutrient-poor waters of the North Equatorial Countercurrent (NECC, or the Panama current)

62 (Kessler 2006). Both of these currents contribute to the South Equatorial Current (SEC), a

63 westward flowing current that strongly influences the central region of the archipelago

64 (Houvenaghel 1984) (Fig. 1).

65   The dominant influence of the SEC changes seasonally, depending on the location of the

66 Intertropical Convergence Zone (ITCZ) (Houvenaghel 1984). The ITCZ is north of the equator

67 during the *Garùa* (fine mist) season (May to December), and the Humbolt Current is the major

68 contributor to the SEC. During the wet season (December to May) the ITCZ shifts towards the

69 south and the dominant influence to the SEC is the NECC. This results in fluctuating gradients

70 of temperature and resource availability throughout the central archipelago.

71   The maximum average SST across the archipelago occurs in February and March, with

72 the minimum usually occurring in August or September (Houvenaghel 1978, Schaeffer et al.

73 2008) (Fig. 2). Temperature data were collected from two sites on San Cristobal (the

74 easternmost island in the archipelago). During 2011, there was a cold season low of 13°C in

75 November 2011 and a high of 25°C in July 2011. In 2012, there was a warm season high of

76 30°C in February 2012 and a low of 20°C in May 2012 (Fig. 2 and Supplemental Data File #1).

77 This annual cycle is interrupted during ENSO events (Barber & Chavez 1983, Chavez et al.

78 1999).

4   4

79   During the warm ENSO phase (El Niño), the easterly trade winds weaken resulting in a

80   deeper EUC thermocline, warmer waters and decreased upwelling. This results in low standing

81   stock of primary producers in the euphotic zone (Pennington et al. 2006); and, ultimately marine

82   consumer populations, such as seabirds, marine iguanas, and sea lions, decrease in abundance

83   (Valle et al. 1987, Laurie & Brown 1990). In contrast, the cold ENSO phase (La Niña) occurs as

84   the easterly trade winds strengthen, sea surface temperatures decrease, and upwelling intensifies

85   resulting in higher standing stock of primary producers (Izumo et al. 2002). During La Niña,

86   ocean temperature in the western islands can be as low as 11°C (Wellington et al. 2001).

87   In addition to regional-scale spatiotemporal variability in temperature and resource

88   availability, the upwelling and downwelling of internal waves result in extreme and rapid

89   temperature changes over smaller spatial and temporal scales (Witman & Smith 2003). For

90   example, over a 53-week period on a rocky subtidal wall in the central archipelago at depths

91   between 3-12m, 20 cold water events were recorded where temperature dropped by 3-9ºC over a

92   25 hr period (Witman & Smith 2003).

93   *Study organisms*

94   We tested the effect of temperature on the common subtidal herbivore *Lytechinus*

95   *semituberculatus* (green sea urchin) and the green macroalga *Ulva* sp. *Lytechinus*, *Tripneustes*

96   *depressus* (white sea urchin), and *Eucidaris galapagensis* (slate pencil urchin) are the three most

97   common urchin species in the Galápagos Islands and together comprise 91% of urchin biomass

98   (Brandt & Guarderas 2002, Brandt et al. 2012). In rocky subtidal habitats throughout the

99   archipelago at depths between 1-5m, *Lytechinus* and *Eucidaris* are the two most common

100   urchins, while *Tripneustes* is rare (Table 1). Further, *Lytechinus* is a strong interactor and

101   capable of converting algal turfs (brown filamentous turf, order Ectocarpales: *Giffordia* sp.,

5   5

102 *Ectocarpus* sp.) to urchin barrens in relatively short time periods, while *Eucidaris* does not have

103 any detectable effect on the abundance of algal turfs (Irving & Witman 2009).

104   *Ulva* sp. was chosen as a food item for *Lytechinus* for several reasons: 1) *Ulva* sp. are one

105 of the most abundant macroalgal species, along with turf, crustose coralline algae, and

106 *Sargassum*, in the Galápagos nearshore habitats (Vinueza et al. 2006, Vinueza 2009); 2)

107 ephemeral species, like *Ulva*, are highly palatable for herbivores (Carpenter 1986); and 3) sea

108 urchin fronts in the Galápagos appear to consume all macroalgal species except for brown

109 species (e.g., *Padina*) (L. Carr *personal observation*) and damselfish turfs (Irving & Witman

110 2009).

111   Urchins and *Ulva* were haphazardly collected from the southern part of San Cristobal

112 Island (89°36'41.85"W, 0°55'39.36"S), and were immediately transported to the laboratory in

113 buckets filled with seawater. All urchins were collected from a depth of ~1.5 m. Study

114 organisms were maintained in culture tanks indoors at 23ºC (ambient sea water temperature) for

115 two days prior to beginning water temperature adjustments. Assays were conducted in a shaded,

116 outdoor facility at the joint UNC/USFQ Galápagos Science Center (San Cristobal Island,

117 Galápagos).

118 *Herbivore feeding rate*

119   We conducted feeding rate assays in July 2012 to test the effect of two different

120 temperatures (14ºC or 28ºC) on green urchin grazing rates on *Ulva*. Water temperature in the

121 culture tanks was adjusted from ambient (23ºC) to either 14ºC or 28ºC over a four-day period.

122 This is within the time period of shallow subtidal temperature changes of this magnitude in the

123 Galápagos (Witman & Smith 2003).

6   6

124   *Ulva* and urchins were placed in 4-L plastic container mesocosms and received a fresh

125   supply of temperature-conditioned seawater every 12 hours. Temperature treatments were

126   maintained with either Visi-Therm submersible individual heaters (Marineland, Blacksburg,

127   Virginia, USA) or ice baths. Feeding assays were replicated twice ($n = 5$ replicates for each

128   trial). Herbivore presence and absence treatments were randomly assigned in water tables. Each

129   mesocosm was equipped with an iButton Thermochron datalogger (Dallas semiconductor,

130   Dallas, Texas, USA) and water temperature was recorded every 5 minutes. Eight mesocosms

131   were equipped with a HOBO Pendant temperature/light sensor (HOBO, Bourne, Massachusetts,

132   USA) and relative light intensity was measured every 5 minutes.

133   Starting conditions for each mesocosm were 2.50 ± 0.004 g of wet mass *Ulva* tissue and

134   either three urchins or no urchins (control to test for autogenic loss). The average test size for the

135   urchins in the mesocosms was 3.55 ± 0.08 cm, which is representative of the green sea urchin

136   populations in southern San Cristobal ($n = 120$ from two sites measured in May and June 2011:

137   minimum 2.75 cm, maximum 5.8 cm. Mean $\pm$ 1 SE of 3.79 ± 0.61 cm).

138   Assays were terminated and final algal biomass was measured after 48 hrs (when ~ 50%

139   of algal tissue was consumed (Tomas et al. 2011)). Biomass consumption was estimated as ([H_i

140     $\times C_f/C_i] - H_f$), where H_i and H_f were the initial and final wet weights of algal tissue in the

141   presence of herbivores, and C_i and C_f were initial and final wet weights of the controls. Relative

142   light intensity levels did not vary between mesocosms and was 326.06 ± 19.7 lumens/ft^2. These

143   light levels are less than the average relative light levels at 1.5 m depth in the field ($886.86 \pm$

144   74.07 lumens/ ft^2), but are within the range of light conditions experienced throughout the tidal

145   cycle at the southern sites of San Cristobal Island during the month of June (Table 1).

7   7

146   Feeding rate assays were initially analyzed using a mixed model ANCOVA with one level

147   of nesting. The analysis tested for one fixed effect (temperature treatment), covariate (urchin test

148   size), and one random effect (temporal block). Consumption data were log transformed to meet

149   the assumption of homogeneity of variances. The random effect was not significant (p = 0.183).

150   Therefore, results were pooled and the random effect was dropped, for final analysis of treatment

151   effects. All statistical analyses were performed in R (v. 2.15.2).

152   *Respiration and Photosynthesis*

153   To estimate the temperature response of metabolic pathways (net photosynthesis and

154   respiration), we measured oxygen production and consumption rates for *Ulva* and green urchins

155   in 0.6L containers under conditions identical to the feeding rate assays. Initial and final oxygen

156   concentrations were measured for *Ulva* (5 ± 0.08 g of leaf tissue) and paired blanks (seawater

157   only) (n = 20 replicates) using a YSI-200 oxygen sensor (Yellow Springs Instruments, Yellow

158   Springs, Ohio, USA). Samples of *Ulva* tissue (5 ± 0.08 g) were obtained by using three *Ulva*

159   "rosettes" plucked from the substrate by the holdfast. Rosettes used were similar sizes and no

160   cutting or tearing was necessary. After the initial measurement, aquaria were covered with

161   plastic to minimize oxygen exchange with the air and left for 2 hrs. Net photosynthesis rates

162   were estimated by subtracting measurements of dark oxygen consumption from light oxygen

163   production.

164   *Lytechinus* oxygen consumption rates were measured according to methods described in

165   Siikavuopio et al. (2008). Urchins were held at 23°C prior to oxygen consumption trials. One

166   randomly selected urchin was placed into an airtight, closed-system respirometry chamber (0.6L)

167   and water temperature was gradually adjusted over a 10 hour period to 14°C and then back up to

168   28°C over a 30 hour period. Within the chamber was a mounted YSI 200 dissolved oxygen

8   8

169 probe to measure oxygen concentrations (mg/L) and a pump for water circulation to prevent the

170 development of strong oxygen and temperature gradients. The chamber was placed into a water

171 bath to maintain temperature treatments. An individual urchin was then placed into the chamber

172 and oxygen concentrations were measured every five minutes for one hour at each temperature

173 treatment (14°C and 28°C). Trials were repeated for 11 urchins. The mean weight specific

174 oxygen consumption rate (Q, mg O_2 kg^{-1} h^{-1}) was calculated with the equation of Karamushko

175 and Christiansen (2002):

176

177 $Q = (C_0 – C_t)V/WT$

178

179 C_0 and C_t are the initial and final oxygen concentration (mg O_2 l^{-1}), respectively. V is the volume

180 (l) of the chamber minus the test urchin volume (test urchin volume was estimated from their

181 biomass). W is the biomass of the urchin in kg. T is the measurement time in hours.

182   Oxygen consumption and production test were analyzed with a t test on change in O_2. All

183 statistical analyses were conducted using R (version 2.15.2).

184 **Results**

185 *Herbivore feeding rate*

186   Temperatures in the cold mesocosms were maintained at 14.01 ± 0.08°C and 14.03 ±

187 0.07°C for trials 1 and 2, respectively. Warm mesocosms for trials 1 and 2 were 28.06 ± 0.09°C

188 and 28.00 ± 0.04°C, respectively. The range of temperatures maintained across both trials was

189 13.54 – 14.47°C for the cold treatment and 27.56 – 28.5°C for the warm treatment (Fig. 3).

190 Green urchin consumption was 46% higher at the warmer temperature ($p < 0.0001$) (Fig. 4A).

191 Urchin test size was not a significant covariate ($p = 0.87$).

192 *Respiration and Photosynthesis*

193   Green urchin metabolism was significantly higher at 28ºC than at 14ºC ($p < 0.001$, Fig

194 4B). *Ulva* oxygen consumption was greater at 28ºC (at 14ºC, 2.55 ± 0.11 g O_2•g tissue^{-1}•hr^{-1}; at

195 28ºC, 3.24 ± 0.13 g O_2•g tissue^{-1}•hr^{-1}; $p = 0.004$). Oxygen production was also greater at 28ºC (at

196 14ºC, 3.88 ± 0.09 g O_2•g tissue^{-1}•hr^{-1}; at 28ºC, 4.74 ± 0.15 g O_2•g tissue^{-1}•hr^{-1}; $p = 0.01$).

197 However, net photosynthesis rates did not vary with temperature ($p = 0.45$, Fig 4C).

198 **Discussion**

199   Consistent with the predictions based on metabolic theory and a growing body of

200 literature, our results indicated that sublethal warming significantly increases the strength of

201 top-down effects. Specifically, we found a 14°C increase in temperature resulted in a 46%

202 increase in grazing rate and lower standing plant biomass. Similar results have been found in

203 other marine systems (O'Connor 2009: with herbivores there was a nearly 100% decrease in

204 algal net growth at high temperatures compared to growth at low temperatures with or without

205 herbivores) and grasslands (Barton et al. 2009: warming of 1°C increased the strength of

206 top-down indirect effects on grasses and forbs by 30-40%).

207   One limitation of our study was that the urchins and algae might have acclimated to the

208 ~5°C temperature change had we warmed the treatment tanks more slowly or maintained the

209 experiment for longer. Thus, it is difficult to extrapolate to how slower or longer-term changes in

210 temperature will affect urchin-algal interactions and, consequently, larger spatial scale changes in

211 ecological patterns. However, the rate of temperature change during the acclimation period and

212 experiment is similar to temporal patterns of temperature fluctuation experienced by urchins

213 around San Cristobal and the Galápagos Archipelago in general (Palacios 2004, Vinueza 2009,

214 Witman et al. 2010). In this dynamic system, urchins rarely spend more than several days to a

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215 few weeks at the same temperature, suggesting that our experimental treatments were

216 representative of the natural temperature regime.

217   While there was a significant temperature effect on consumer metabolism and feeding

218 rates, there was not a significant temperature effect on algal photosynthesis rates following the

219 4-day acclimation period in this study. It is possible that this was because light, nutrients, carbon

220 dioxide, or some other resource was limiting and thus warming could not stimulate

221 photosynthesis. Further, the positive effect of increased temperature on algal photosynthetic rate

222 can be reduced or reversed at sub-saturating light levels because warming can increase the light

223 level needed to reach the compensation point (Davison 1991). Light conditions in the

224 experiment were within the range of light levels in the nearshore habitats in the Galápagos (Table

225 1) and further, most populations of subtidal algae are subject to subsaturating light conditions

226 (Davison 1991); therefore the experimental conditions likely reflect algal performance in the

227 field. Our results are consistent with O'Connor (2009) which found no temperature effect for

228 *Sargassum* with a 4°C temperature change.

229   Organisms throughout the nearshore habitats of the Galápagos Islands experience large

230 and frequent temperature fluctuations (Witman & Smith 2003, Palacios 2004, Vinueza et al.

231 2006, Schaeffer et al. 2008, Vinueza 2009, Witman et al. 2010, Vinueza 2010). Therefore,

232 populations in this environment could be less metabolically sensitive to extreme temperature

233 changes due to adaptation, resulting in metabolic responses that deviate from the predicted

234 outcomes of metabolic theory. For example, in the rocky intertidal, adaptive regulation results in

235 reduced snail metabolic rates at warmer temperatures (Marshall & McQuaid 2011). However,

236 our results provide evidence that in a dynamic system where organisms experience relatively

237 large variation in environmental temperature, metabolism and consumption still scale with

11   11

238 temperature, which is consistent with metabolic theory (Allen et al. 2005, O'Connor 2009,

239 O'Connor et al. 2009).

240   At the upper range of species' thermal tolerances metabolism and consumption are

241 predicted to scale differently and metabolic demands should outpace increased grazing intensity

242 (Rall et al. 2010). Lemoine and Burkepile (2012) found *Lytechinus variegatus* consumption and

243 metabolism scaled differently at temperatures beyond 29°C, a 9°C increase from the starting

244 temperature treatment (20°C). Ultimately, urchin ingestion efficiency was decreased at the

245 higher temperature, resulting in possible reduced consumer fitness. Because shallow subtidal

246 temperatures around San Cristobal reach 30°C, future work should focus on understanding

247 *Lytechinus* metabolism/consumption ratios at the highest temperatures in the Galápagos and the

248 implications for species interactions and the strength of top-down effects under these conditions.

249   Our finding that warming increased urchin metabolism, even in a thermally variable

250 system, provides further support for a mechanistic link between environmental temperature and

251 feeding rates. Additionally, our findings indicate warming increases grazing intensity, which

252 could in turn affect ecological patterns, such as primary producer community composition and

253 biomass. For example, if these grazing rates are maintained over longer time-scales (i.e., days to

254 weeks), warmer temperatures may increase the prevalence of urchin barrens in areas of the

255 Galápagos with high densities of sea urchins because of the increased relative strength of

256 top-down effects. This study focused on one algal species and thus we cannot extrapolate to how

257 temperature would affect other algal-urchin interactions. Furthermore, macroalgal primary

258 production is highly seasonal in the Galapagos nearshore habitats (Vinueza et al. 2006, Vinueza

259 2009) and it is unclear what effect this could have on urchin-plant interaction strength. We also

260 recognize that other factors influence urchin-plant interactions and primary production. Future

12   12

261 work should focus on elucidating the stability of this interaction under larger temporal and

262 spatial scales, and various environmental conditions (i.e., different seasons, ENSO cycles,

263 varying light intensities, etc.) and with different algal species.

264   The absence of macroalgae in intertidal and shallow subtidal habitats during warm

265 periods (e.g., El Niño) in the Galápagos Islands is generally attributed to the decreased strength

266 of bottom-up forcing (i.e., upwelling) and subsequent lack of nutrients (Vinueza et al. 2006).

267 However, temperature stress (i.e., desiccation) does play a minor role in regulating intertidal

268 algal biomass in the Galápagos (Vinueza 2009). Therefore, future work should focus on

269 understanding the constraints of physical stress on macroalgal growth in the Galápagos Islands,

270 as stress is known to alter the relative importance of bottom-up and top-down effects (Thompson

271 et al. 2004).

272   Low macroalgal biomass in warm seasons and years could also be due in part to

273 increased grazing intensity due to higher temperature (e.g., O'Connor et al. 2009). Both

274 mechanisms could be operating (i.e., changes in top-down and bottom-up control), although the

275 relative strength of these mechanisms in influencing large-scale ecological patterns in upwelling

276 systems is unknown. In freshwater pond systems, Kratina et al. (2012) found a negative

277 interaction between warming and nutrient input on total phytoplankton biomass in freshwater

278 systems, suggesting a shift toward stronger top-down and weaker bottom-up effects with

279 warming regardless of nutrient availability. However, the mechanism behind this shift is not

280 known. Therefore, future warming could result in stronger consumer control in systems where

281 nutrients are plentiful (i.e., upwelling or well-mixed aquatic systems) that could lead to short-

282 and /or long-term changes in community structure and function.

283

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Figure 1

Map of Galápagos Archipelago and the surrounding currents

Colored triangles relate to curves in Fig. 2. Map courtesy of A. Valdivia and modified from Schaeffer et al. 2008.
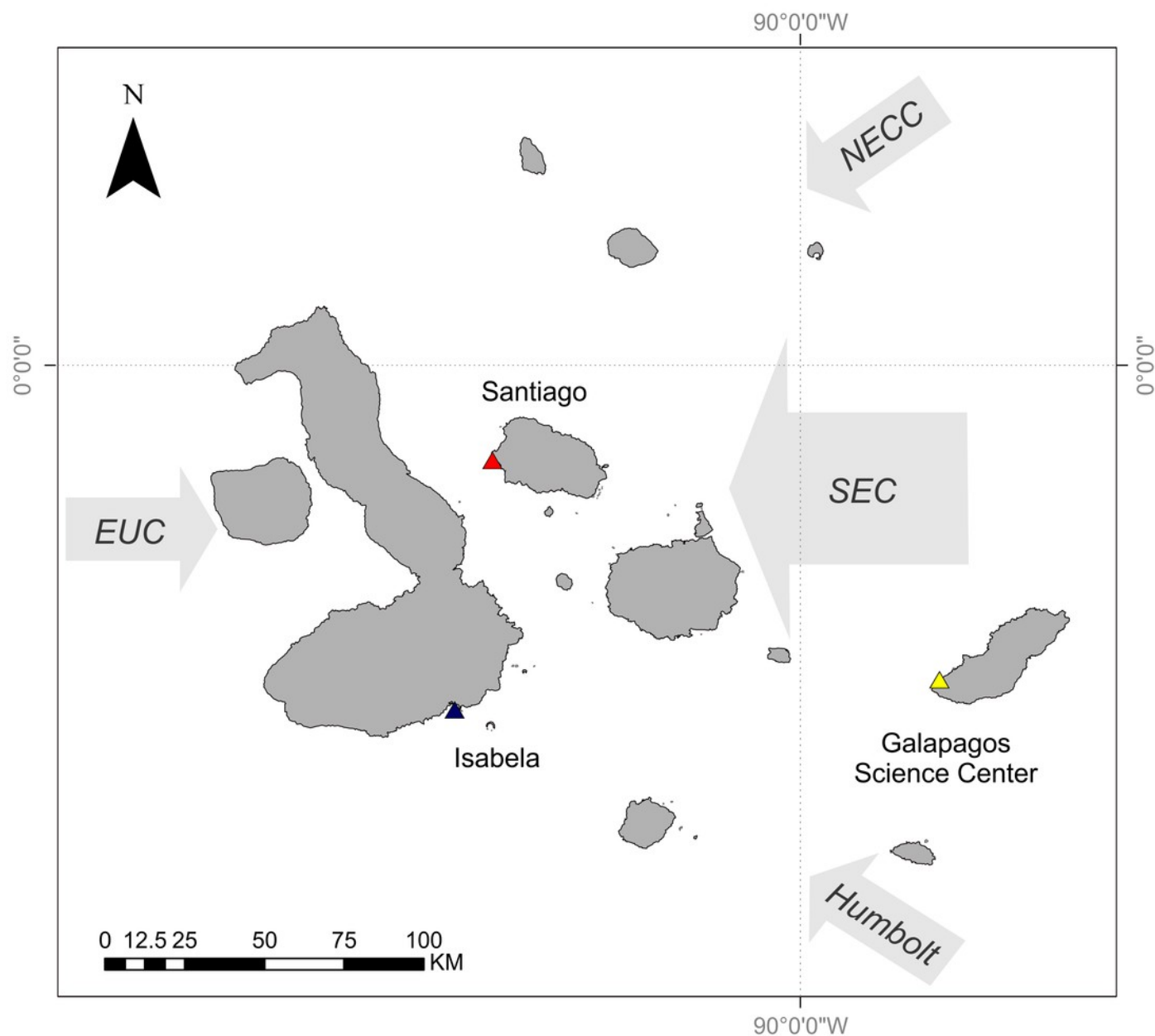
Figure 2

Daily water temperature (mean) measured in the shallow subtidal (< 5m) at Santiago, Isabela and San Cristobal.

The Galapagos Science Center is on San Cristobal. Water temperature measurements were recorded every 30 mins with a HOBO temp logger. The smoothing curve was done in Kaleidagraph (v. 4.1.). A Stineman function was applied to the data. The output of this function has a geometric weight that is applied to the data points and ± 10% of the data range to generate the smoothed curve.
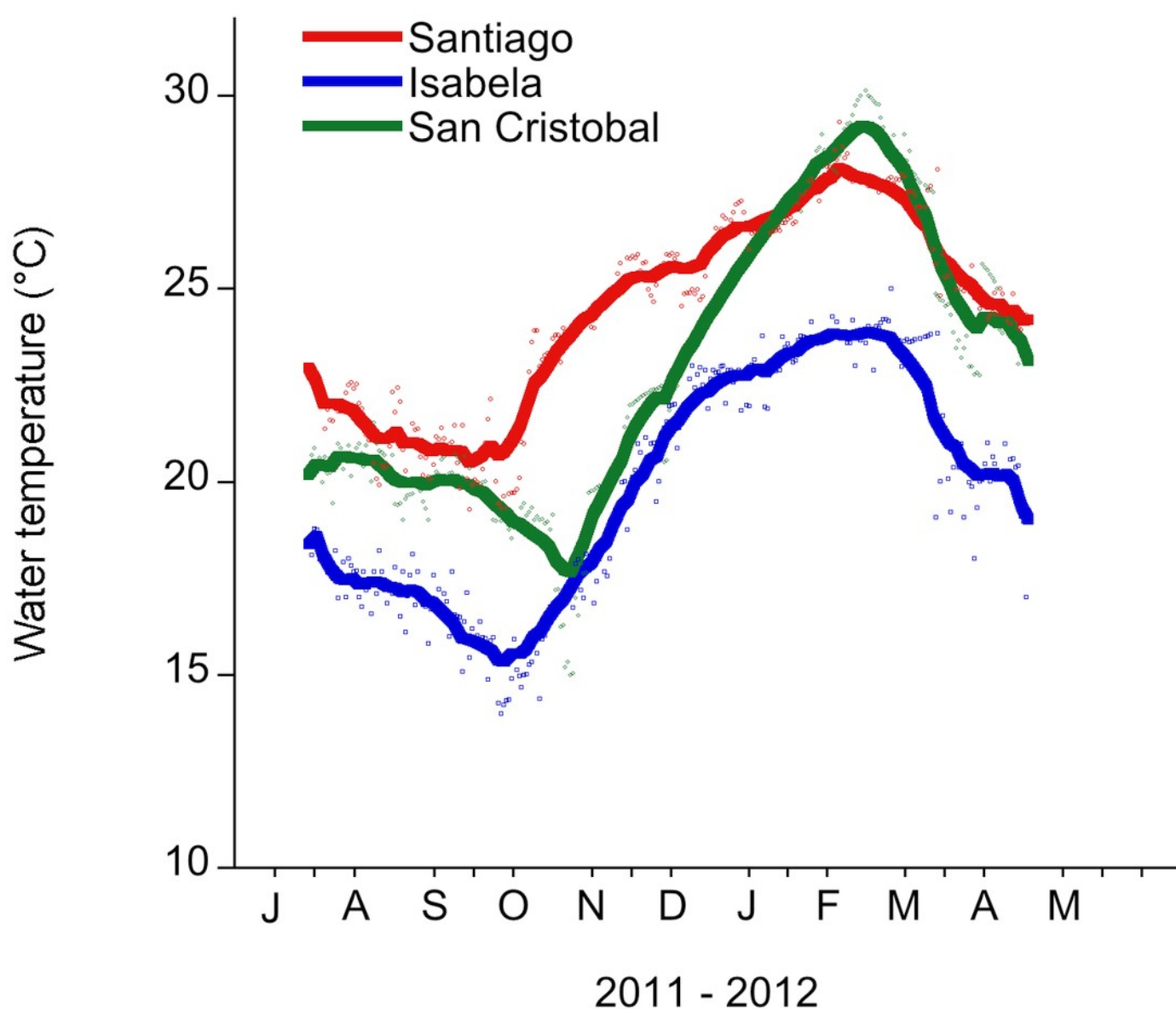
Table 1_(on next page)

Natural variation in algal cover, temperature and urchin density in shallow subtidal habitats in the Galápagos Islands.

Sites were surveyed in June 2010 and July 2012. Site codes: LL = La Loberia (San Cristobal, SC), LT = Las Tijeretas (SC), PP = Punta Pitt (SC), CD = Cabo Douglas (Fernandina, FE), PE = Punta Espinosa (FE). Values represent means ± SE (n = 25 quadrats for urchin density and algal cover). Any other urchin species (e.g., *Tripneustes*) were present at densities less than 0.3 m^{-2} in all quadrats. Temperature was estimated with both *in situ* temperature loggers and satellite data (AQUA Modis) for the 30-day period prior to sampling, SE < 0.07 for all sampling points. Light intensity was measured using HOBO Light/Temperature Pendants before and during the experimental duration.

Site	2010				2012		
	LL	LT	PP	CD	LL	LT	PE
Ulva cover (%)	9.7 ± 3.3	58.4 ± 3.5	2.9 ± 0.4	36.3 ± 5.1	7.8 ± 2.1	28.9 ± 2.7	23.4 ± 1.5
Eucidaris density (m^{-2})	4.8 ± 1.3	1.6 ± 0.7	1.6 ± 0.2	8.4 ± 2.4	6 ± 1.9	2.1 ± 0.4	3.2 ± 1.3
Lytechinus density (m^{-2})	10.2 ± 2.6	11.8 ± 1.8	11.2 ± 1.9	1.2 ± 0.7	14.9 ± 2	13.2 ± 1.6	17.6 ± 4.5
Temperature (°C)	24.8	23.7	20.8	11.4	25.3	23.2	17.8
Light Intensity Range (lumens ft^{-2})	N/A	N/A	N/A	N/A	0-3102	0-2968	N/A

Figure 3

Mesocosm temperature values during both experiments

Temperature in each mesocosm (n = 20 per temperature) was recorded every 5 mins. with an iButton Thermochron datalogger (Dallas semiconductor, Dallas, Texas, USA). The box corresponds to the 25th and 75th percentiles and the dark line inside the box represents the median consumption value. Error bars are the minimum and maximum.
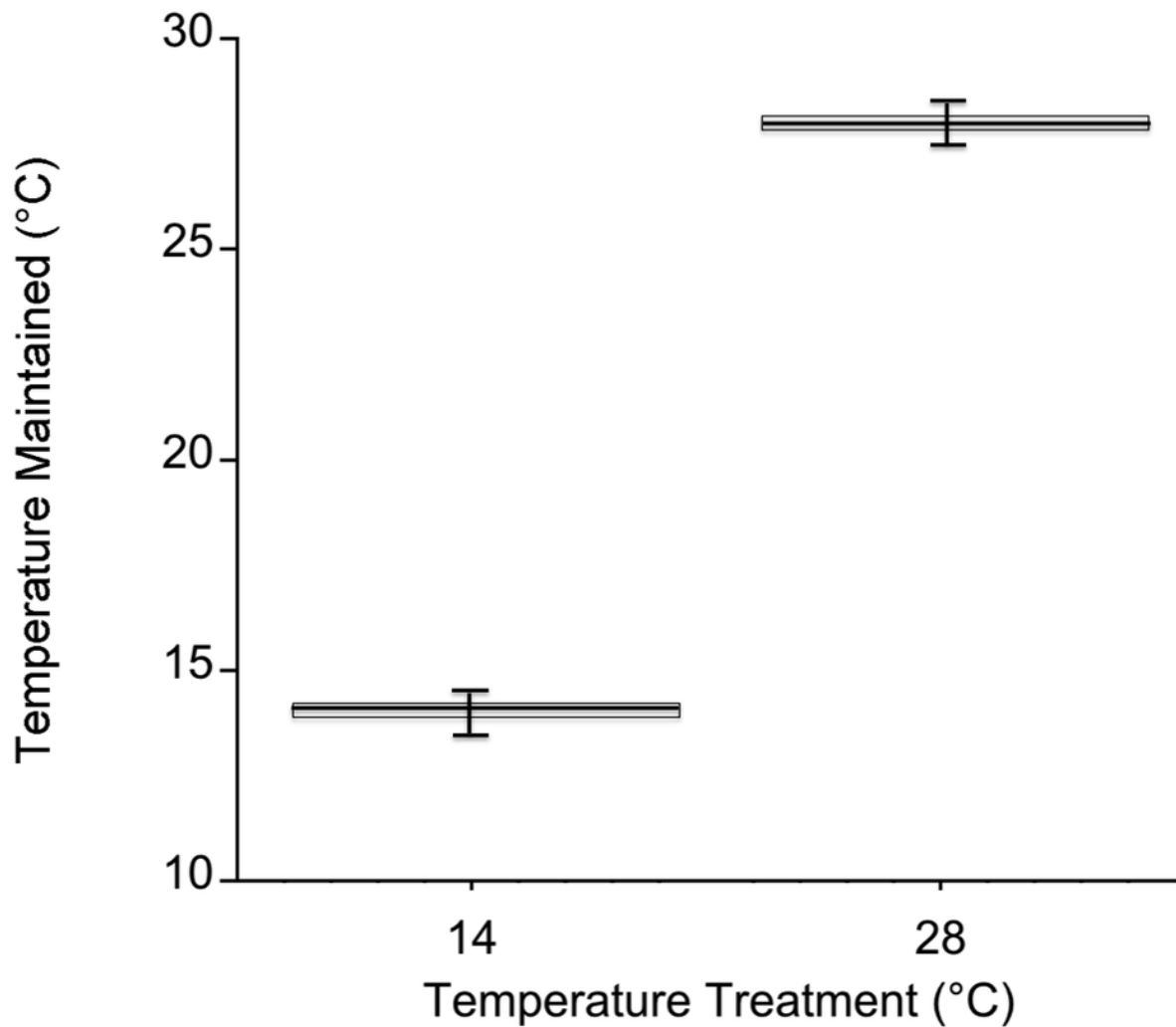
Figure 4

Temperature effects on urchin grazing rates, metabolism and algal photosynthesis

Temperature effects on A) urchin consumption of *Ulva*, B) urchin oxygen consumption, and C) on *Ulva* net photosynthesis. Values are means ± SE; n = 10.