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GROWTH AND TISSUE BIOCHEMICAL COMPOSITION OF *HALIOTIS FULGENS* AT ELEVATED TEMPERATURES IN BAJA CALIFORNIA UNDER TWO DRIED BROWN ALGAL DIETS

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ABSTRACT Growth, survival, and tissue biochemical composition of juvenile green abalone *Haliotis fulgens* were recorded for two temperature regimes simulating the contrasting marine conditions, one as a normal year and the other as an El Niño 1997 to 1998 event during 120 days in the laboratory. Abalones were fed *Macrocystis pyrifera* or *Eisenia arborea*. During the experiment, juveniles were sampled for biochemical analysis at the maximum temperature, which occurred at 60 days and at 120 days. Significant differences in growth of shell length and wet body weight among treatments were recorded. The highest growth (39 $\mu m \cdot day^{-1}$and 16.0 $mg \cdot day^{-1}$) occurred in juvenile abalone within the El Niño temperature pattern and fed *M. pyrifera*. Survival rates were approximately 95% without significant differences between treatments. At maximum temperature, juveniles within the El Niño pattern had higher levels of protein in the hepatopancreas, regardless of diet. A significant interaction between temperature regimen and food was observed for glycogen in muscle, with the highest levels in juveniles fed *M. pyrifera* within the El Niño pattern. At the end of the experiment, juveniles in the normal year pattern had higher levels of lipids in the hepatopancreas. Increased levels of protein, total carbohydrates, and glycogen in muscle were present in juveniles in the El Niño pattern, regardless of diet. Juveniles fed *M. pyrifera* had higher levels of protein and lipids in the hepatopancreas and increased levels of protein, carbohydrates, and glycogen in muscle tissue, regardless of temperature regimen. The influence of diet and temperature regimen on several biochemical components closely matched their effects on growth.

KEY WORDS: biochemical composition, carbohydrates, El Niño, glycogen, green abalone, *Haliotis fulgens*

INTRODUCTION

Long-term temperature series have shown that, during El Niño oceanographic conditions, the appearance of unusually warm surface waters in the eastern tropical Pacific Ocean is one of the most prominent aspects of El Niño (ENSO) phenomenon (Philander 1990). There is an anomalous increase of sea surface temperature and a coincident drop in nutrient concentration (Jackson 1977, Zimmerman & Kremer 1984, Hernández-Carmona et al. 2001). Along the Baja California Peninsula, the maximum sea surface temperatures recorded during an El Niño was in 1997 to 1998, around 28°C (Ponce-Díaz et al. 2003b). It has been considered the most intense of the 20th century (McPhaden 1999).

The effect of temperature on the physiology of abalone includes gonadal maturation, larval development, feed consumption, ammonia excretion, oxygen consumption, growth rate, and survival (Britz et al. 1997). Thermal tolerance limits are more restrictive in larvae and recently settled individuals, but temperature affects abalone species differently. In *Haliotis fulgens* Philippi, 1845, the upper lethal limit for juveniles (1–2 cm) is 31.5°C (LT_{50}, 48 h) (Leighton et al. 1981). This suggests that there was little or no direct effect of temperature during the strong El Niño event of 1997 to 1998 on survival of green abalone juveniles along the Baja California Peninsula coast, Mexico. Nevertheless, environmental fluctuations may favor the development of some diseases, as in California (USA); high temperatures may increase the mortality rate of black abalone (*H. cracherodii* Leach, 1814) affected by withering syndrome (WS) (Friedman et al. 1997). Mass mortality of black abalone was recorded after the occurrence of the 1984 El Niño (Haaker et al. 1992). Friedman et al. (2002) found an intracellular bacterium (order Rickettsiales) as the etiologic agent for that die off.

Availability of a major food of abalone, the brown alga *Macrocystis pyrifera* (L.) C. Ag., becomes limited during El Niño events. Warm-water events lead to large-scale declines of surface canopy fronds in *Macrocystis* due to thermal stress and reduced nutrients in local nearshore areas (North 1957, North 1971, Hernández-Carmona 1987, Dayton & Tegner 1990, Ladah et al.1999, Hernández-Carmona et al. 2001, Guzmán del Próo et al. 2003). Feed availability may be a significant factor to be considered regarding how abalone stocks may be affected during future El Niños and global warming. Along the Baja California coast, juvenile green abalone showed high variability in size, which may be an indirect effect of the 1997 to 1998 El Niño on their food supply (Guzmán del Próo et al. 2003). This study was designed to assess the survival, growth, and biochemical composition of the tissue of juvenile green abalone (*Haliotis fulgens*) under two temperature regimes that simulate the contrasting summer marine conditions during a normal year and a severe El Niño (1997–1998) while being fed the two dried brown algal diets *M. pyrifera* and *Eisenia arborea* Aresch.

MATERIAL AND METHODS

Temperature Patterns and Natural Diet

Two elevated temperature regimes (July to November), one for a normal year (18°C to 21°C) and the other El Niño 1997 to 1998 (20°C to 28°C), were simulated in tanks following the daily measurements of sea surface temperature at Bahía Asunción, Baja California Sur. The normal year data was obtained from an average

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of 1992 to 1996, and the El Niño year from data obtained during 1997 (Fig. 1a) (Ponce-Díaz et al. 2003a). Controlled temperatures in laboratory tanks varied ±2°C, which was related to the precision of the equipment used to control the seawater temperature (Fig. 1b).

In each temperature regimen, 2 brown algae, *M. pyrifera* and *E. arborea*, were used as food. *M. pyrifera* is considered a major food of abalone. Most fronds are lost during intense El Niño events (Hernández-Carmona et al. 2001). *E. arborea* is also believed to be an important species as a potential food for abalone along Baja California (Guzmán del Próo et al. 1972, Serviere-Zaragoza et al. 1998). Its populations decrease during El Niño events, but do not disappear (Hernández-Carmona et al. 2001). *M. pyrifera* and *E. arborea* (blades excluding pneumatocysts) were collected from the central coast of Baja California peninsula, Mexico. Blades were air dried and stored in cardboard boxes at 20°C to preclude deterioration. Diets were rehydrated before administration.

Experimental Procedure

Growth and survival of 312 hatchery-produced, green abalone *Haliotis fulgens* (average starting size 29.0 mm ± 4.3 [sd] shell length and average starting wet body 2.37 g ± 1.1 [sd] weight) were recorded for a 120 d experiment. Experimental animals were held in 16-L fiberglass rearing tanks (50 × 30 × 35 cm, LWH). Abalone were marked with plastic tags glued to the shell. Rehydrated diets were given *ad libitum* in the afternoon at intervals of 2 days. Three replicate tanks were used for each of 4 treatment conditions: El Niño-*M. pyrifera*; El Niño-*E. arborea*; Normal-*M. pyrifera*, and Normal-*E. arborea*. Each tank contained 26 abalone (12 tanks). Treatments were randomized among tanks. Every second morning, uneaten food and feces were removed. Micro algae growing on the inner walls of tanks were removed twice a week with a brush. Filtered (10 μm) seawater was supplied at a flow-through rate of 70 mL/min giving about 6 water exchanges/day. The water was vigorously aerated. Seawater temperatures lower than 24°C were maintained with a flow trough in a chiller. Higher temperatures were maintained with 100-W heaters immersed in each tank (VISI-THERM).

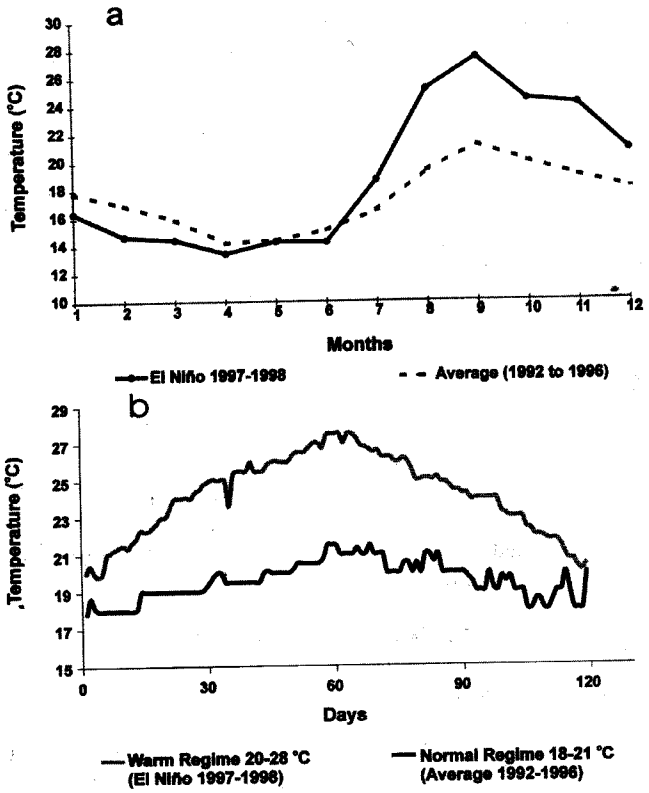

Figure 1. a. Monthly average seawater surface temperature in Bahía Asunción, measured from 1992 to 1996 and during El Niño 1997 to 1998. b. Daily average seawater temperature simulated in laboratory aquaria to represent a normal year and an El Niño year (1997 to 1998).

Growth

Shell length was measured with a vernier caliper, and wet body weight with an electronic balance (nearest 0.001 g) at 0, 30, 58, 97, and 120 days. Dead animals were removed and replaced to maintain the standard density, although data from these animals were not used in the analysis. Daily growth rates for shell length ($GR_{SL} = (SL_f - SL_i)/T$) and wet body weight ($GR_{BW} = (BW_f - BW_i)/T$) were calculated. SL_f = mean final shell length, SL_i = mean initial shell length, BW_f = mean final wet weight, BW_i = mean initial wet weight, and T = time in days.

Biochemical Analysis

At both temperature regimes, specimens were sacrificed for composition samples twice, once at the maximum temperature (60 days after the beginning of the experiment) and the other at the end of the study (120 days after the beginning of the experiment). On each date, fifteen animals from each treatment were sampled at random. The hepatopancreas and shell muscle were dissected, weighed (wet wt), and stored at −70°C for biochemical analysis.

Hepatopancreas was homogenized with 0.5 mL of 35‰ saline solution and muscle with 5 mL of 10% trichloroacetic acid (TCA) with a mechanical homogenizer (Vir- Tis). Protein was determined after digestion with 0.1 N NaOH (hepatopancreas) and 5NNaOH (muscle) (Bradford 1976) and total carbohydrates by the anthrone method (Roe 1955). In hepatopancreas, total lipids were determined by the sulphophosphovanillin method (Barnes & Blackstock 1973). In muscle, glycogen was extracted with absolute ethanol and the anthrone method (Van Handel 1965). Levels of all fractions are reported as $mg \cdot g^{-1}$ of tissue (wet weight). The water content in hepatopancreas was 69% ± 4% (sd) and in muscle 76% ± 3% (sd) (n = 50).

STATISTICAL ANALYSES

At the beginning of the assay, statistical differences in shell length and wet body weight among replicates were not detected ($P < 0.05$). At 60 and 120 days, two-way ANOVA was performed to assess significant differences in growth variables and in biochemical composition of hepatopancreas and muscle, using temperature regimen (normal year or El Niño) and diet (*M. pyrifera* or *E. arborea*) as independent variables (Sokal & Rohlf 1995). Mean comparisons were done by Tukey test only when there was a significant effect of the interactions ($P < 0.05$). Statistical analysis was done with STATISTICA 6.0 software.

RESULTS

Growth

Shell length (SL) and wet body weight (BW) growth ($P < 0.01$) was greater in juveniles fed *M. pyrifera* than juveniles fed *E. arborea*, regardless of temperature regimen. Nevertheless, both SL and BW growth were affected by diet in relation to the temperature

regimen (interaction: $P < 0.05$). At the end of the study period, the greatest mean SL and BW (34.94 mm ± 0.60, sd and 4.61 g ± 0.24, sd) occurred in juveniles under El Niño-*M. pyrifera* treatment, whereas the least mean (30.12 mm ± 0.91, sd and 2.83 g ± 0.33, sd) was observed in juveniles fed *E. arborea* under El Niño-*E. arborea* treatment (Fig. 2a, 2b).

Daily growth rate of SL and BW (main effect: $P < 0.01$) were higher in juveniles fed *M. pyrifera* than juveniles fed *E. arborea*, regardless of temperature regimen, although they were affected by diet in relation to the temperature regimen (interaction: $P < 0.05$). The highest daily growth rates of SL and BW (39 $\mu m \cdot day^{-1}$ ± 3 and 16 $mg \cdot day^{-1}$ ± 1) occurred in juveniles under El Niño-*M. pyrifera* treatment, and were statistically different from juveniles fed *E. arborea*; Normal-*E. arborea*, or El Niño-*E. arborea*. The lowest daily growth rates (11 $\mu m \cdot day^{-1}$ ± 3 and 4 $mg \cdot day^{-1}$ ± 1) was in juveniles fed *E. arborea* under El Niño-*E. arborea*, and were statistically different from juveniles fed *M. pyrifera*; Normal-*M. pyrifera*, and El Niño-*M. pyrifera* (Fig. 3a, 3b). The mean percent (± sd) of survival was 96% ± 4% in Normal-*M. pyrifera*, 95% ± 5% in El Niño-*M. pyrifera*, 94% ± 6% in Normal-*E. arborea*, and 93% ± 2% in El Niño-*E. arborea*, without significant differences between treatments (not shown).

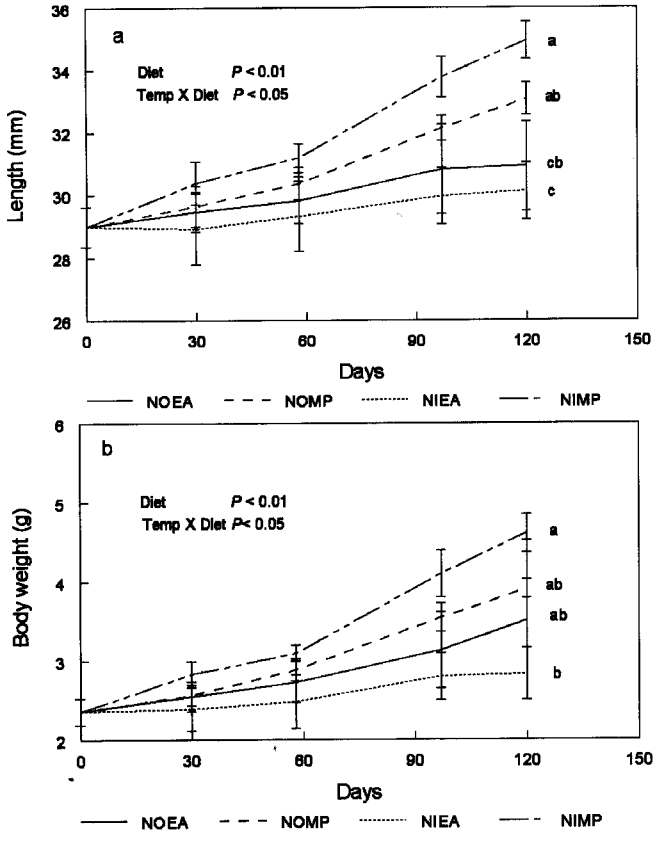

Figure 2. Mean ± SD for triplicate groups of $n \leq 26$ of: (a) shell length and (b) body weight of juvenile green abalone *H. fulgens*. To each date, the results of bifactorial ANOVA are inserted in the figure. Factors considered for the analysis were temperature regimen (NO = normal or NI = El Niño) and diet (MP = *M. pyrifera* or EA = *E. arborea*). The main effects and interactions are shown only when significant. Mean comparisons were done by Tukey test only when there was a significant effect of the interactions. Lines not sharing the same letter are significantly different ($P < 0.05$).

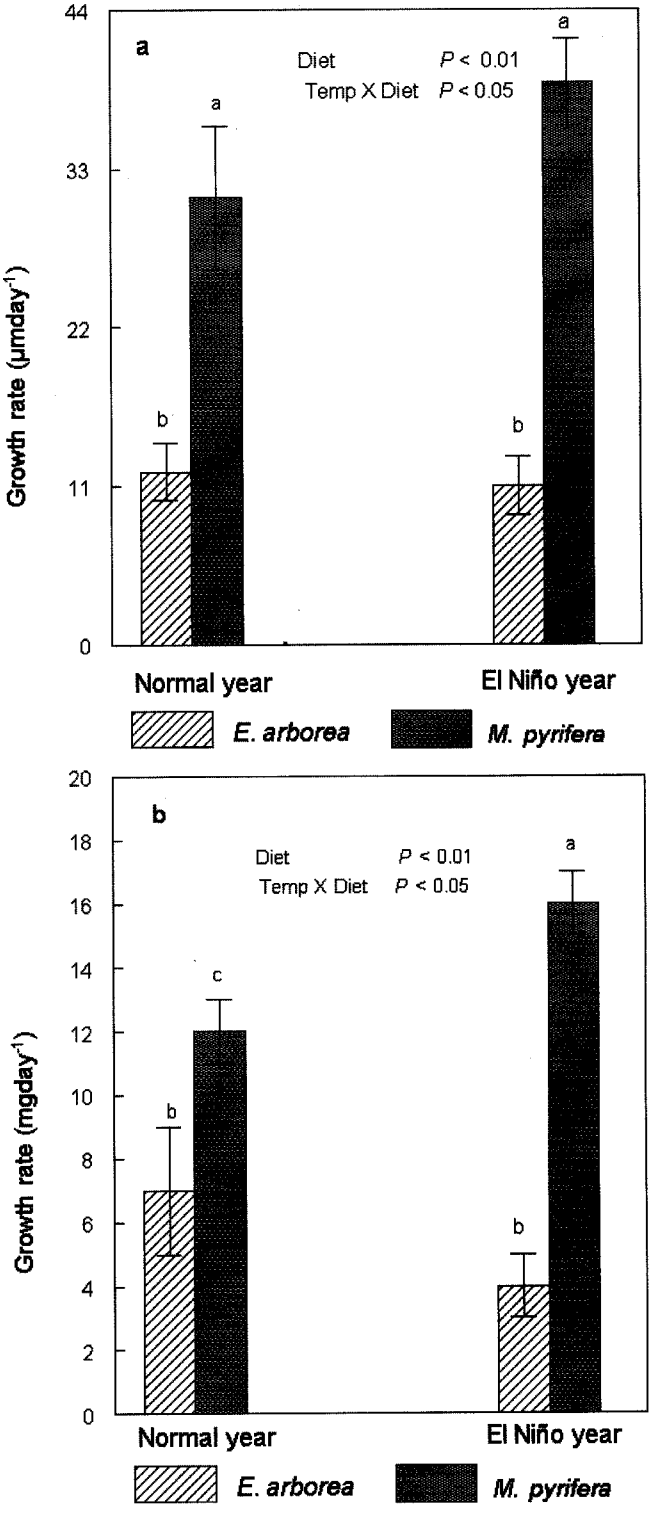

Figure 3. Mean ± SD for triplicate groups of $n \leq 26$ for daily growth in: (a) shell length and for (b) body weight in triplicate groups of juvenile green abalone *H. fulgens*. See Figure 2 for statistical analysis.

Biochemical Variables

Hepatopancreas

At maximum temperature (60 days), the protein levels of juveniles within the El Niño pattern (global mean, 121.8 mg/g) were

higher than within the normal pattern (global mean, 99.6 mg/g) (main effect: $P < 0.01$), regardless of diet. At 120 days, juveniles fed *M. pyrifera* had higher levels of protein (global means, 107.2 mg/g vs. 88.7 mg/g) (main effect: $P < 0.05$), regardless of temperature regimen (Fig. 4a). During the assay, no significantly different effect was observed in carbohydrate levels in relation to temperature or diet (Fig. 4b). At 60 days, no significant effect in lipid levels in relation to temperature or diet was observed. At 120 days, juveniles within the Normal pattern had higher levels of lipids (global means, 9.6 mg/g vs. 6.2 mg/g) (main effect: $P < 0.01$), regardless of diet. Juveniles fed *M. pyrifera* had higher levels of lipids (global means, 10.3 mg/g vs. 5.5 mg/g) (main effect: $P < 0.01$), regardless of temperature regimen (Fig. 4c).

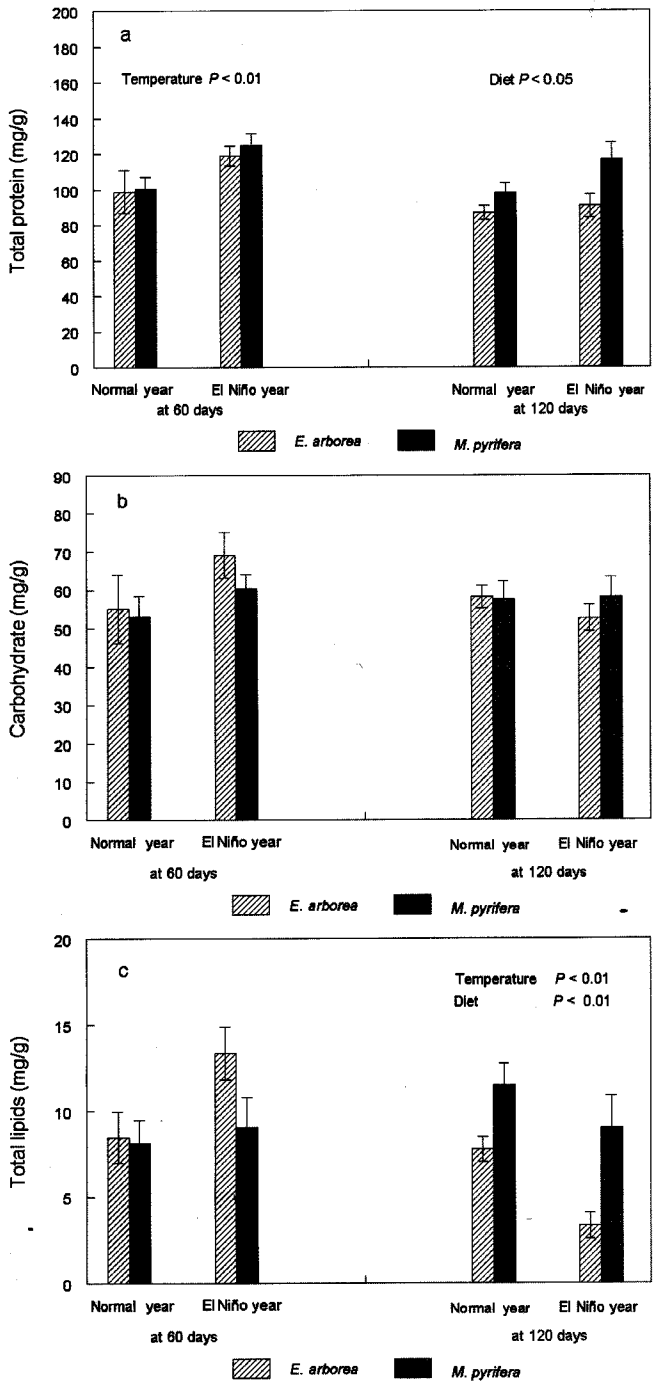

Figure 4. Mean ± SE of hepatopancreas levels (mg·g^{-1} hepatopancreas tissue wet weight) of total protein (a), carbohydrate (b), and total lipids (c) in juvenile green abalone *H. fulgens*. See Figure 2 for statistical analysis at 60 and 120 days.

Muscle

At 60 days, no significant differences were observed in protein levels in relation to temperature or diet, but at 120 days, increased levels of protein (main effect: $P < 0.01$) were present in juveniles within the El Niño pattern (global means, 164.1 mg/g vs. 141.1 mg/g), regardless of diet. Juveniles fed *M. pyrifera* had higher levels of protein (158.8 mg/g vs. 146.4 mg/g) (main effect: $P < 0.05$), regardless of temperature regimen (Fig. 5a). For carbohydrates at 60 days, no significant effect was observed in relation to temperature or diet. At 120 days, increased levels of carbohydrates (main effect: $P < 0.01$) were present in juveniles within the El Niño pattern (4.6 mg/g vs. 2.9 mg/g), regardless of diet. Juveniles fed *M. pyrifera* had higher levels of carbohydrates (4.5 mg/g vs. 3.0 mg/g) (main effect: $P < 0.05$), regardless of temperature regimen (Fig. 5b). At 60 days, glycogen levels of juveniles within the El Niño pattern (1.9 mg/g) were higher than within the Normal pattern (1.3 mg/g) (main effect: $P < 0.05$), regardless of diet. A significant interaction between temperature regimen and food was observed for the carbohydrate glycogen in muscle, with the highest levels in juveniles fed *M. pyrifera* within the El Niño pattern (interaction: $P < 0.05$). At 120 days, increased glycogen (main effect: $P < 0.01$) was present in juveniles within the El Niño pattern (3.5 mg/g vs. 1.6 mg/g), regardless of diet. Juveniles fed *M. pyrifera* had more glycogen (3.3 mg/g) than those fed *E. arborea* (1.8 mg/g) (main effect: $P < 0.05$), regardless of temperature regimen (Fig. 5c).

DISCUSSION

Higher growth obtained in juveniles fed *M. pyrifera* within the two temperature regimes may be related to the relative dietary value of the common alga species along the coast of Baja California Sur. The dietary value of species, such as *E. arborea*, *Gelidium robustum* (Gardn.) Hollenb. & Abb., and the sea grass *Phyllospadix torreyi* Watson were inferior to that of the dominant algal species of southern California, *M. pyrifera* (Serviere-Zaragoza et al. 2001). In California mariculture, *M. pyrifera* is a valuable food for young red abalone, but relatively poor diet for green abalone (Leighton 1989). Growth rates for juveniles fed rehydrated *E. arborea* and *M. pyrifera* were in the range reported by other authors in animals fed fresh or rehydrated macroalgae. Growth rates of 12 and 16 μm·day^{-1} have been reported for juveniles fed fresh kelp, *M. pyrifera* (Viana et al. 1993, Viana et al. 1996), whereas values of 19 μm·day^{-1}, and 46 μm·day^{-1}, were obtained for juveniles fed rehydrated *E. arborea* and *M. pyrifera*, respectively (Serviere-Zaragoza et al. 2001). Difference in rates of growth among juveniles fed the same diet in different studies may be related to differences in the chemical composition of the algae used in each assay.

Biochemical composition of tissues is affected by macroalgal diets. Although most elements of the diet are nutritionally important for growth, including carbohydrate and protein components, lipid class and content may be especially vital to abalone nutrition (Nelson et al. 2002a). Foot muscle and hepatic and gonadal tissue serve as storage depots for carbohydrates and lipids, respectively (Mercer et al. 1993). In our study, juveniles fed *M. pyrifera* had

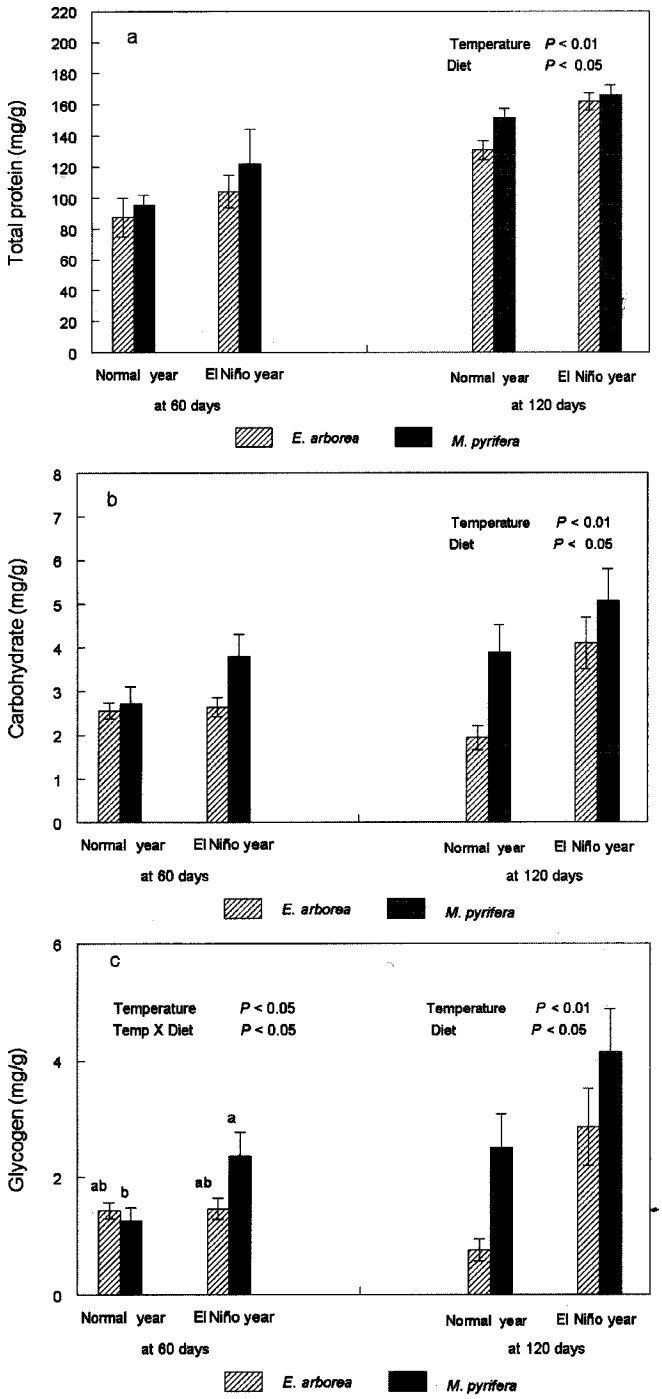

Figure 5. Mean ± SE of muscle levels (mg·g^{-1} shell muscle tissue wet weight) of total protein (a), carbohydrate (b), and glycogen (c) in juvenile green abalone *H. fulgens*. See Figure 2 for statistical analysis at 60 and 120 days.

higher levels of all components in muscle than juveniles fed *E. arborea* in both temperature regimens. Muscle protein was, by far, the major component and its higher levels reflect muscle growth in accordance with the high overall growth observed in juveniles fed *M. pyrifera*. Polysaccharides stored in the foot muscle may be mainly glycogen as in many gastropods including abalone *H. discus hannai* Ino, 1953 and *H. tuberculata* Linnaeus, 1758 (Mercer et al. 1993). At the end of the assay, higher lipid levels in the hepatopancreas of juveniles fed *M. pyrifera* were obtained, regardless of temperature. Macroalgae have lipid profiles that differ between taxa, and vary geographically and seasonally (Nelson et al. 2002b). In Baja California Sur, *E. arborea* and *M. pyrifera* have low lipid levels, ranging from 0.4% to 1.0%, without significant differences (Serviere-Zaragoza et al. 2002). Nevertheless, according to Mercer et al. (1993), lipid levels in the viscera reflect the combination of lipid levels in the diet and their bioavailability to the animals in addition to possible lipid synthesis by the abalone. This suggests differences in lipid bioavailability for these macroalgae to juvenile *H. fulgens*. Nelson et al. (2002a) found that diet and temperature influenced seasonal changes in lipid profiles, where diet most strongly affects body mass and temperature to shell length.

High survival observed in the assay (~90%) suggests that the maximum temperatures reached during El Niño 1997 to 1998 did not directly cause mortality in coastal juvenile green abalone populations. In culture, juvenile green abalone is tolerant of extremes in water temperature, and shows the best growth at 20°C to 28°C (Leighton 1974, Leighton et al. 1981). Low temperature reduces growth, at least in part, by affecting feeding rates and feeding duration (Uki 1981). In natural populations, high variability in size in green abalone (Guzmán del Próo et al. 2003) and reduction of growth rate in red abalone (Haaker et al. 1998) were reported during El Niños, suggesting variations in growth rate from changes in environmental conditions. This will be discussed later because it may also reflect low availability of food. In California, Friedman et al. (1997) and others suggested that high temperatures during El Niños may increase mortality of black abalone affected by the withering syndrome bacterial agent.

At the end of the experiment, hepatopancreas of juveniles within the El Niño pattern had lower levels of lipids than juveniles within the Normal pattern, regardless of diet. This suggests that during an El Niño, juveniles may use more lipid reserves than during normal years, which may in turn affect development. For macroalgae, Nelson et al. (2002b) reported that temperature induced changes in specific fatty acids, especially polyunsaturated eicosopentaenoic fatty acids, which may be important factors in gonadogenesis, and consequently, affect larval production and recruitment.

In this study, the best growth was obtained under the El Niño regimen (20°C to 28°C), providing abalone was fed *M. pyrifera*. The combined effect of high temperature and optimal food must be discussed together, because better growth was associated with higher levels of protein, carbohydrates, and glycogen in muscle. However, southern nutrient-poor water accompanies El Niño events, causing local or large-scale disappearance of the *M. pyrifera* kelp forests (North 1971, Gerard 1984, Hernández-Carmona et al. 2001). Our results suggest that higher temperatures associated with El Niño events may promote the growth of green abalone, but only if the phenomenon is not sufficiently strong to cause widespread destruction of *M. pyrifera* and other temperature-sensitive macroalgae. If El Niño events are too severe, abalone lose a main food source in Baja California Sur and must shift to other inferior algae, resulting in lower growth rates. In southern Baja California in September 1997, water temperature was high (25.3°C, anomaly + 5.7°C) and nutrients were presumably low (<1 μM), causing large-scale disappearances of all kelp forests at the southern end of their distribution (Hernández-Carmona et al. 2001). The effects of high temperatures in the Pacific waters of the Baja California Peninsula during El Niño years have been evident

in *M. pyrifera* harvests recorded in 1958, 1983, and 1998 (Casas-Valdez et al. 2003). During El Niño 1997 to 1998, *E. arborea* populations did not disappear, but its biochemical composition changed with the increase in temperature. In *E. arborea*, tissue nitrogen content decreased from 1.95% to 0.88% between July 1997 and October 1998 monitored at Isla Asunción, in Baja California (Hernández-Carmona et al. 2001).

Although the collapse of abalone populations has been ascribed to overfishing (Prince & Guzmán del Próo 1993, Shepherd et al. 1998), impacts of El Niño events on kelp forest communities suggest that these periodic environmental influences also have contributed to these declines (Lluch-Cota et al. 1999, Guzmán del Próo et al. 2003). In this study, high temperatures (simulating El Niño) enhance growth and associated biochemical indices, if optimal food availability is maintained. Data suggest that algal species, as the main diet, may be a more important factor controlling abalone growth than temperature or the interaction between them. The effects of climate-ocean extremes, like El Niño and La Niña conditions, should be incorporated into our understanding of changes in abalone stocks, related to each species, and its age class. Further laboratory studies will be useful to increasing our understanding of the ecologic values of these influences.

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