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Experimental effect of cold, La Niña temperatures on the survival of reef fishes from Gorgona Island (eastern Pacific Ocean)

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Abstract The eastern tropical Pacific (ETP) reefs are affected at irregular times by extremely cold temperatures that occur principally during La Niña events. The effects of these low temperatures on the survival of reef fishes were experimentally assessed by determining the critical thermal minimum (CTM) of 15 reef fish species from Gorgona Island (ETP), and comparing these CTMs with the records of temperature during past La Niña events. Among species, mean CTMs ranged from 10.8°C to 16.3°C, which were lower than the coldest temperature recorded during the last La Niña event (18°C during La Niña 1998–1999). However, the observed ranges of CTM for two species (*Thalassoma lucassanum* and *Eucinostomus gracilis*) extended above 18°C. These results suggest that most of the reef fishes we studied are physiologically tolerant to the cold temperatures encountered during La Niña, though decreases in at least two populations may be expected as a result of the mortality of less tolerant individuals. Although tolerant to cold temperatures, reef fish populations may still experience negative changes during La Niña, because other determinants in population maintenance (e.g. reproduction and recruitment) are more temperature sensitive. The effects of other cold phenomena on reef fish survival are also discussed herein.

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Introduction

Temperature can have major effects on natural processes, operating from from cell to community levels (Smith and Smith 2000). In the eastern tropical Pacific Ocean (ETP), temperature is perhaps the most variable environmental factor. This region is affected at irregular times (3–7 years on average) by extreme temperatures that occur during El Niño–Southern Oscillation (ENSO) events. This phenomenon is characterized by increases in water temperature, but also usually by an abnormal temperature drop during a post-El Niño phenomenon called La Niña. During El Niño, sea surface temperature in the ETP has risen to 32°C (4–5°C above normal levels). These thermal anomalies have been associated with negative changes in marine organisms such as mammals, birds, fishes and invertebrates (Barber and Chávez 1983; Grove 1985; Glynn and D'Croz 1990; Glynn 1991; Urban 1994; Arntz and Fahrbach 1996); extinction has even been reported for corals (Glynn and de Weerdt 1991). Although changes in temperature during La Niña can be of equal or higher magnitude than those during El Niño, the effects of La Niña on marine populations are unknown. The negative effects of cold-water events of lesser intensity than La Niña (e.g. currents or upwellings) on the composition and abundance of marine organisms from the ETP (Hubbs and Rosenblatt 1961; Glynn and Stewart 1973; Glynn and Leyte Morales 1997) suggest that the effects of cold, La Niña temperatures on reef fishes may be significant.

The present study deals with the effects of cold, La Niña temperatures on the survival of reef fishes. These animals can be particularly susceptible to the effects of thermal phenomena, because they are sedentary after settlement and therefore unable to move to areas with better conditions as pelagic species might do. In this research we experimentally assessed the effects of the cold temperatures of La Niña by determining a measurement of thermal tolerance (critical thermal minimum) in 15 reef fish species from Gorgona Island (ETP) and comparing these values with the records of temperature during past La Niña events.

Materials and methods

Study area and species

This study was done in Gorgona Island national park (2°58′N; 78°11′W). Gorgona is a continental island located 35 km off the Colombian coast. It is a typical locality from the ETP; its sea surface temperature and salinity are representative of a broad portion of this region (Glynn et al. 1982; Cortés 1997). Annual water temperature typically ranges between 25°C and 27°C, with occasionally low (< 19°C) and high (32°C) temperatures recorded mainly during La Niña and El Niño events, respectively (Glynn et al. 1982; Vargas et al. 2002). Below 15 m depth, Gorgona has also been influenced at times by a cold-water current, when temperature has reached 13°C (authors' unpublished data).

A total of 15 species, belonging to 11 families, were studied: *Halichoeres dispilus*, *Thalassoma lucasanum* (Labridae), *Lutjanus guttatus* (Lutjanidae), *Apogon dovii*, *A. pacifici* (Apogonidae), *Coryphopterus urospilus*, *Bathygobius ramosus* (Gobiidae), *Mugil curema* (Mugilidae), *Malacotenus zonifer* (Labrisomidae), *Eucinostomus gracilis* (Gerreidae), *Stegastes acapulcoensis*, *Chromis atrilobata* (Pomacentridae), *Haemulon steindachneri* (Haemulidae), *Plagiotremus azaleus* (Blenniidae) and *Cirrhitichthys oxycephalus* (Cirrhitidae). The focal species are common on rocky and coral reefs, and are widely distributed in the eastern Pacific, from the Gulf of California to the northern coast of Peru (Allen and Robertson 1994).

Determination of thermal tolerance

The critical thermal minimum (CTM) was used as a measure of the thermal tolerance of these species. The CTM is determined under laboratory conditions by exposing a group of fish to a constant rate of water temperature decrease until a non-lethal endpoint (e.g. loss of equilibrium or muscle spasms) is reached. Although this endpoint may be non-lethal in the laboratory, it represents a physiological disorganization that leads to death if the condition persists (Bennett and Judd 1992; Bennett and Beitinger 1997). It can also be considered the temperature of ecological death, because it disables the fish from escaping unfavorable conditions (Hutchison 1976; Bennett and Judd 1992; Bennett and Beitinger 1997).

Fish were collected with hand nets from Gorgona reefs, and then transported to the laboratory during a period of no longer than 20 min. Collected fish (number and sizes are shown in parentheses in Fig. 1) were randomly placed into six 100 l aquaria, where they remained for 24 h before the experiment commenced (each species was tested separately). During this 24 h period, water in the aquaria was kept at a temperature similar to that at the capture site (26.5 ± 0.5°C) and was constantly aerated to maintain high levels of oxygen and homogeneous water temperature. The aquaria were covered with plastic lids to prevent evaporation and subsequent changes in salinity. Aquaria were 50% flushed with fresh salt water before each experiment to minimize contamination due to fish excrement.

The experiment was conducted by reducing water temperature, in three randomly selected aquaria, at a rate of 1°C h^{-1} (using electronic refrigerators, accuracy of ± 0.1°C). The other three aquaria were maintained at the constant original temperature and were used as controls. Fishes were continually monitored to record the temperature at which individual fish reached the endpoint. The CTM of each species was calculated as the mean of these endpoints.

To assess the effect of the cold, La Niña temperatures on the survival of reef fishes, we compared the CTMs of these species with temperature records from past La Niña events at Gorgona Island. Field records of temperature for this island were only available for the most recent La Niña event (1998–1999). However, given that this event is recognized as one of the strongest in the last half-century (see "Results"), these records provide a good indicator of the extreme thermal conditions during this phenomenon.

Results

No evidence of stress was observed in any fish during the acclimation period or in any fish in control aquaria

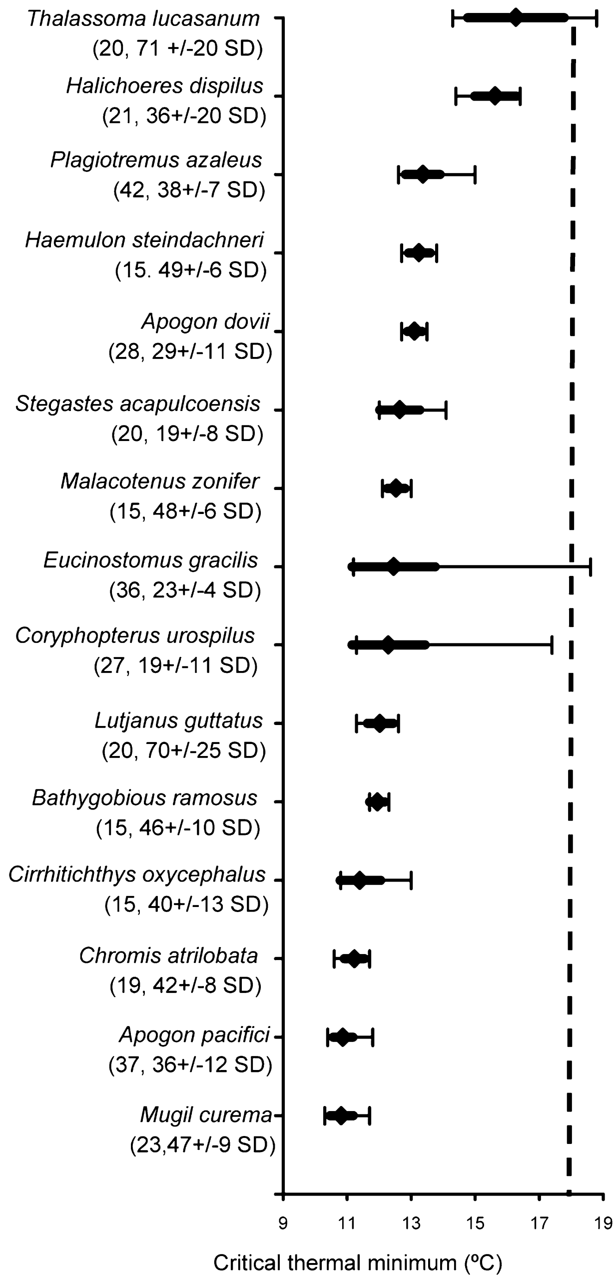

Fig. 1. Critical thermal minima (*CTM*) of 15 reef fish species from Gorgona Island, and their comparison with one of the coldest records of temperature during La Niña at Gorgona Island in the past half century (*dotted line*). Number of individuals and mean length (± SD, mm) are shown in *parentheses*. For each species, the variation in CTM is expressed as ± SD (*thick horizontal line*) and range (*thin horizonal line*)

during the experiment, suggesting that responses of fish in experimental aquaria resulted from the influence of temperature and not to other factors.

Muscular spasm was the endpoint observed in almost all species. In non-vagile and bottom-associated species, such as *Coryphopterus urospilus*, *Bathygobius ramosus*, *Malacotenus zonifer* and *Cirrhitichthys oxycephalus*, erratic swimming after being stimulated with a ruler was selected as the endpoint. The CTMs of the studied species are shown in Fig. 1; mean CTMs ranged from 10.8°C in *Mugil curema* to 16.3°C in *Thalassoma lucasanum*. The intraspecific range in CTM was low (1°C in most species); only *T. lucasanum* and *Eucinostomus gracilis* presented ranges over 4°C. The CTM in *T. lucasanum* ranged from 14.3°C to 18.8°C and from 11.2°C to18.6°C in *E. gracilis*.

La Niña has occurred at least ten times in the last 50 years (Fig. 2a). Although its intensity has been quite variable, La Niña 1998–1999 was among the strongest events in the past half-century (Fig. 2a, b.). This event started in June 1998 and extended throughout 1999 (Fig. 2b), with a peak in November 1998, when water temperature dropped below 20°C in the equatorial eastern Pacific (Fig. 2c). At Gorgona the coldest temperature (18°C) was recorded in January 1999. We consider this record as part of La Niña because of it being coincident with the time of La Niña occurrence (Fig. 2b, c). All reef fish species we studied presented mean CTM values below this record (Fig. 1); although some individuals of *T. lucasanum* and *E. gracilis* showed CTMs above 18°C (Fig. 1).

We reiterate that records of temperature below 19°C at Gorgona could be related to a narrow, northward-flowing coastal current that is sometimes observed in this area from April to June (Glynn et al. 1982). This current might not be independent of La Niña, because the northwestward winds along the coast of Peru during La Niña increases the northward flow of the relatively cool Peru Current. When coincident in time, both phenomena can probably yield cooler temperatures at Gorgona. Very likely La Niña does not act independently of other thermal phenomena, and particular interactions may have different consequences. For instance, Thompson and Lehner (1976), during the winter of 1970–1971, which matches the time of one of the strongest La Niña events (Fig. 2a, b), reported temperatures for northern California as low as 8.9°C. Such low temperatures were not reported in previous winters at that location (Thompson and Lehner 1976).

Discussion

The thermal tolerance of fish can be experimentally quantified by using dynamic or static methods, which yield estimates useful for different purposes (Bennett and Judd 1992). Therefore, a wrong selection in the thermal tolerance method can bias data interpretation. We briefly describe both methods in order to justify our choice. The critical thermal minimum is obtained using the dynamic method, and represents the mean temperatures at which individual fish reach a point of thermal stress after being exposed to gradually decreasing temperatures. In contrast, the static method gives the lethal temperature of 50% of a population (LT_{50}), which is a value extrapolated from a regression of percent of

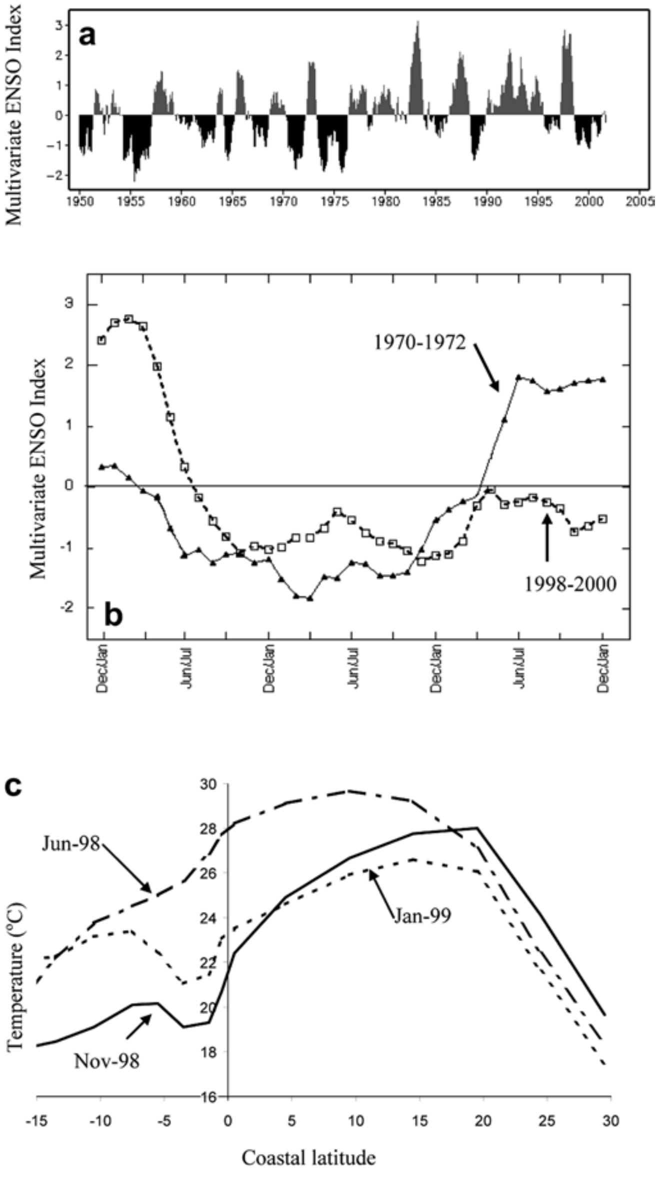

Fig. 2a–c. La Niña events in the eastern tropical Pacific. **a** La Niña occurrences during the last 50 years. The multivariate ENSO index is based on several variables such as sea level, winds, sea surface temperature, air surface temperature and cloudiness, which vary during ENSO and therefore help to identify it (after NOAA Climate Prediction Center http://www.cpc.noaa.gov/~kew/MEI/). Positive values of this index correspond to El Niño and negative ones to La Niña. **b** Temporal variation of two of the strongest La Niña events (data from http://www.cpc.noaa.gov/~kew/MEI/). **c** Temperature variations along the tropical Pacific coast of America during La Niña 1998–1999 (data of temperature for each latitude and date was obtained from http://www.ferret.noaa.gov/nopp/main.pl/, Reynolds SST data set)

mortality on static temperatures near the low lethal limit (Hutchison 1976; Bennett and Judd 1992; Bennett and Beitinger 1997). Given differences in methods and endpoints, the CTM and LT_{50} of a species are not equal (Bennett and Judd 1992; Bennett and Beitinger 1997). It is argued that the LT_{50} provides useful standards for physiological comparisons between species, while the CTM more closely approximates natural conditions (Bennett and Judd 1992; Bennett and Beitinger 1997). On the one hand, the gradual change of temperature in the CTM method reflects changes of temperature as they occur in nature. On the other hand, fish have been observed under natural temperatures that are lethal according to LT_{50} but tolerant according to CTM. Since our aim was to assess the effect of cold temperatures that occur naturally during La Niña on the survival of reef fishes, we chose CTM as our criteria of thermal tolerance.

The CTMs of a given species may vary depending on the rate of temperature change, because of the different levels of fish acclimation at different rates. Therefore, it might be argued that CTMs determined at a rate of 1°C h^{-1} are not comparable to the levels of fish tolerance during natural phenomena such as La Niña, when temperature changes over weeks and months. Recent studies have demonstrated, however, that CTM values do not change significantly when using rates slower than 1°C h^{-1} (Elliott and Elliott 1995; Mora and Ospina, unpublished data). This could be because at such a slow rate fish have enough time to reacclimatize during the trials. Since CTM values do not change with rates slower than 1°C h^{-1}, our results represent a real indication of the levels of tolerance that fish may have to changes in temperature during La Niña (for an extended discussion about the incidence of other factors on thermal tolerance and the applicability of CTM values to natural conditions see Mora and Ospina 2001).

Many reefs around the world are exposed to the effects of thermal phenomena such as global warming, El Niño and La Niña. Given the increasing intensity of these disturbances and the ecological and economic importance of coral reefs, understanding the effects of these phenomena on reef populations is critically important. Information about the effects of thermal phenomena on reef fishes is largely lacking. In this study, we experimentally addressed the effect of cold, La Niña temperatures on the survival of reef fishes. Overall, the study species presented mean CTM values lower than temperatures occurring during La Niña, suggesting that reef fishes can tolerate the thermal conditions of this phenomenon. However, in two species (*Thalassoma lucasanum* and *Eucinostomus gracilis*), the CTM ranges spanned water temperatures observed during the last La Niña event in Gorgona. Therefore, one might expect reductions in the size of these populations as a result of the mortality of less tolerant individuals.

Although physiologically tolerant to La Niña thermal conditions, the possibility of negative effects of this phenomenon on reef fish populations cannot be rule out. Most marine species reproduce over a narrower range of temperatures than the range that permits individual survival (Hutchison 1976). Therefore, it is likely that some reef fish populations may decrease as consequence of cold, La Niña temperatures on reproduction. Temperature can also affect growth and condition of reef fish larvae (Fukuhara 1990; McCormick and Molony 1995), both of which have been shown to influence post-settlement survival (McCormick 1998; Mora and Zapata 2002). Thus, changes in temperature during La Niña might affect larval growth and condition and subsequently the dynamics of reef fish populations. Persistence of some fish species may also hinge on feeding behavior when temperature is close to levels of tolerance (Bennett et al. 1997). This highlights another way in which species with thermal tolerances close to the temperatures observed during La Niña may be affected. Possible effects of La Niña on migration are low, because of the sedentary nature of reef fishes.

The temperature of tolerance represents the thermal conditions within which individuals of a species can operate. Therefore, studies quantifying thermal tolerance are particularly important in regions such as the ETP, where thermal anomalies are more extreme than in other places of the world (Cortés 1997). This study provides for the first time indices of low thermal tolerance in reef fishes from the ETP. These data are particularly useful in assessing the effects of different cold-water phenomena in this region. For instance, periods of intense seawater cooling, when temperature drops below 18°C (or lower) for several days or weeks, occur fairly commonly in the major upwelling centers of the ETP (Glynn 1989). Our results show that this temperature can be nearly lethal for individuals of some species. Thermal tolerance might, therefore, be an important factor driving geographic changes in population size, as well as the exclusion of some species from particularly cold localities. As a second example, temperatures around 13°C have been recorded below 15 m depth in Gorgona (authors' personal observations). Our results show how this exposure can be lethal for at least five species and nearly lethal for the others. Thus, thermal tolerance may be the factor limiting the bathymetric distribution of fishes on reefs below this depth at Gorgona. Thermal tolerance may also explain the massive mortality of deep-water fishes (e.g. ballistids, serranids, lutjanids, among others) observed at Gorgona when this temperature was recorded in February–March 1999. Comparable mass mortalities of reef fishes have been observed in northern California when water temperature dropped below 10°C (Thompson and Lehner 1976). Overall, phenomena reducing water temperature in the ETP seem to be diverse and have a high potential for affecting the dynamics of reef fish populations. However, an accurate explanation of these thermal phenomena on reef fishes will only be possible after further experimental studies and long-term monitoring.

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References

Allen G, Robertson R (1994) Fishes of the tropical eastern Pacific. University of Hawaii Press, Honolulu

Arntz W, Fahrbach E (1996) El Niño, experimento climático de la naturaleza. Fondo de la cultura económica, Mexico City

Barber R, Chávez F (1983) Biological consequences of El Niño. Science 222:1203–1210

Bennett W, Beitinger T (1997) Temperature tolerance of the sheepshead minnow, *Cyprinodon variegatus*. Copeia 1997:77–87

Bennett W, Judd F (1992) Comparison of methods for determining low temperature tolerance: experiments with pinfish, *Lagodon rhomboides*. Copeia 1992:1059–1065

Bennett W, Currie RJ, Wagner PF, Beitinger TL (1997) Cold tolerance and potential overwintering of red-bellied piranha, *Pygocentrus nattereri*, in the United States. Trans Am Fish Soc 126:841–849

Cortés J (1997) Biology and geology of eastern Pacific coral reefs. Coral Reefs 16[Suppl]:39–46

Elliott J, Elliott J (1995) The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. J Fish Biol 47:917–919

Fukuhara O (1990) Effects of temperature on yolk utilization, initial growth, and behavior of unfed marine fish-larvae. Mar Biol 106:169–174

Glynn P (1989) Coral morality and disturbances to coral reef in the tropical eastern Pacific. In: Glynn P (ed) Global ecological consequences of El 1982–83 El Niño southern oscillation. Elsevier, New York, pp 55–126

Glynn P (1991) Coral reef bleaching in the 1980s and possible connection with global warming. Trends Ecol Evol 6:175–179

Glynn P, D'Croz L (1990) Experimental evidence for high temperature stress: the cause of El Niño-coincident coral mortality. Coral Reefs 8:181–191

Glynn P, de Weerdt W (1991) Elimination of two reef building hydrocorals following the 1982–83 El Niño warming event. Science 253:69–71

Glynn P, Leyte Morales G (1997) Coral reefs of Huatulco, West Mexico: reef development in upwelling Gulf of Tehuantepec. Rev Biol Trop 45:1033–1047

Glynn P, Stewart R (1973) Distribution of coral reef in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol Oceanogr 18:367–379

Glynn P, Prahl von H, Guhl F (1982) Coral reefs of Gorgona Island, Colombia, with special reference to corallivores and their influence on community structure and reef development. An Inst Invest Mar Punta Betín 12:185–214

Grove J (1985) Influence of the 1982–1983 El Niño event upon the icthyofauna of the Galapagos archipelago. In: El Niño en la Islas Galapagos: el evento de 1982–1983. Fundación Charles Darwin, Quito, Ecuador, pp 191–198

Hubbs C, Rosenblatt R (1961) Effects of equatorial currents on the Pacific distribution of fishes and other marine animals (abstract). In: Symposium papers of the 10th Pacific science congress, pp 340–341

Hutchison V (1976) Factors influencing thermal tolerance of individual organisms. In: Esch GW, McFarlane R (eds) Symposium Series of the National Technical Information Service, Springfield, Va., pp 10–26

McCormick M (1998) Condition and growth of reef fishes at settlement: is it important? Aust J Ecol 23:258–264

McCormick M, Molony B (1995) Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. Mar Ecol Prog Ser 118:59–68

Mora C, Ospina A (2001) Tolerance to high temperatures and the potential impact of sea warming phenomena on reef fishes from Gorgona Island (tropical eastern Pacific). Mar Biol 139:765–769

Mora C, Zapata F (2002) Effects of a predatory site-attached fish on abundance and body size of early post-settled reef fishes from Gorgona Island, Colombia. In: Proc 9th Int Coral Reef Symp. Bali, Indonesia (in press)

Smith LR, Smith TM (2000) Elements of ecology. Cummings Science, San Francisco

Thompson DA, Lehner CE (1976) Resilience of a rocky intertidal fish community in physically unstable environment. J Exp Mar Biol Ecol 22:1–29

Urban J (1994) Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño. Mar Ecol Prog Ser 107:139–145

Vargas B, Zapata F, Hernandez H, Jimenez J (2002) Coral and coral reef responses to the 1997–98 El Niño event on the Pacific coast of Colombia. Bull Mar Sci (in press)