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Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical eastern Pacific)

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Abstract Knowledge of upper thermal-tolerance limits of marine organisms in the tropical eastern Pacific (TEP) is important because of the influence of phenomena such as El Niño and global warming, which increase sea temperature. Laboratory experiments were conducted to determine the critical thermal maximum (CTM) of reef fishes from the TEP. In 15 reef fishes of Gorgona Island (TEP) the CTM was between 34.7°C and 40.8°C. None of these CTMs was exceeded by sea temperature in the TEP during any of the strongest El Niño events in this century (32°C during El Niño 1982–1983 and 1997–1998), which indicates that all species studied here may tolerate El Niño maximum temperatures. In addition, the CTM of the least-tolerant species was 8°C above the current mean sea temperature in a wide range of latitudes in the TEP. This suggests that fishes live far from their upper thermal tolerance limits and that the current global-warming trend is still unlikely to be dangerous for these species. If sea temperature continues to increase at the current rate, in about a century sea temperature could exceed the thermal tolerance of some reef fishes and threaten them with extinction. Such risk, however, might occur sooner if the sea temperature during El Niño also increased in step with the global warming, but also because other processes involved in maintaining population, such as reproduction, can be affected at lower temperatures. The possible ability of reef fishes to adapt to increases in sea temperature is discussed.

Introduction

Temperature is one of the most important environmental factors affecting marine organisms. It can affect the function of cell molecules (Somero 1969), mortality, growth and reproductive rates of individuals (Brey 1995), size and distribution (local and geographical) of populations (Moore 1975; Wilson 1981; Grove 1985; Arntz and Fahrbach 1996) and structure of communities and ecosystems (Glynn 1988).

In the tropical eastern Pacific (TEP), El Niño and global warming are recognised as the principal causes of increasing sea temperature (Barber and Chavez 1983; Jokiel and Coles 1990; Roemmich 1992; Urban 1994; Cortés 1997; Strong et al. 2000). During El Niño, sea-surface temperature in the TEP has briefly (days to months) reached 30–32°C (4–5°C above normal high levels). On the other hand, as a consequence of the global warming, increments of 0.5–1°C per decade in sea temperature in the TEP have been reported (Jokiel and Coles 1990; Roemmich 1992; Strong et al. 2000). The knowledge of upper temperature-tolerance limits of marine organisms in the TEP becomes important, since sea warming related either to global warming or to El Niño has been associated with negative changes in several marine populations, such as those of certain mammals, birds, fishes and invertebrates (Barber and Chavez 1983; Grove 1985; Glynn 1988, 1991; Arntz and Fahrbach 1996; Veit et al. 1996; Urban and Tarazona 1996). High-temperature-tolerance studies in the TEP, however, are scarce and generally limited to invertebrates and especially corals (Coles et al. 1976; Glynn and DCroz 1990; Urban 1994; Mate 1997). These studies indicate that most of the coral-reef species live near their upper thermal limits, which threatens them, considering the current global-warming trend (Jokiel and Coles 1990; Glynn 1991, 1993). On the other hand, high temperatures during El Niño have exceeded the upper thermal-tolerance limits of corals; therefore, temperature has been considered as responsible for massive

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bleaching and death in corals in the TEP during this phenomenon (Glynn and DCroz 1990). In contrast, populations of bivalves from Peru, although decreasing their density during El Niño events (Urban and Taranza 1996), seem to be tolerant of high El Niño temperatures (Urban 1994). Thus, the importance of high El Niño temperatures may not be relevant to all organisms in the TEP.

Because reef fishes have a juvenile and adult benthic phase, high temperatures may particularly affect them; they cannot escape from thermal conditions by moving to other areas, as pelagic species might do. In fact, some reef-fish populations have decreased, and have even locally disappeared during El Niño events (Grove 1985); however, the cause of these changes remains unknown. Changes in reef-fish populations related to global warming have not been reported, perhaps because of the lack of long-term monitoring. In populations of birds and corals monitored for a long time, decreasing trends in density have been related to global warming (Glynn 1991, 1993; Veit et al. 1996). In this paper we determine the critical thermal maximum (CTM) of 15 reef fishes of Gorgona Island in the TEP, in order to identify reef-fish tolerance of high El Niño temperatures and the possible impact of global warming on these species.

Materials and methods

This research was carried out in Gorgona Island national park (2°58'N, 78°11'W). Gorgona is a typical locality of the TEP; its sea-surface temperature and salinity are representative of a broad portion of this region (Glynn et al. 1982; Cortés 1997). Within-year water temperature remains between 25°C and 27°C, but occasionally low (<19°C) and high (32°C) temperatures are recorded during, respectively, upwelling and El Niño events (Glynn et al. 1982; Vargas et al., in press). Salinity varies between 24‰ and 30‰. As in other localities in the TEP, the reefs of Gorgona are small and less diverse than central and Indo-Pacific reefs (Cortés 1997).

The reef-fish species studied were *Thalassoma lucasanum*, *Halichoeres dispilus* (Labridae), *Lutjanus guttatus* (Lutjanidae), *Apogon pacifici*, *A. dovii* (Apogonidae), *Coryphopterus urosphilus*, *Bathygobius ramosus* (Gobiidae), *Mugil curema* (Mugilidae), *Malacotenus zonifer* (Labrisomidae), *Eucinostomus gracilis* (Gerreidae), *Stegastes acapulcoensis*, *Chromis atrilobata* (Pomacentridae), *Haemulon steindachneri* (Haemulidae), *Plagiotremus azaleus* (Blenniidae), and *Cirrhichthys oxycephalus* (Cirrhichthidae). All species are common on reefs, and *M. curema*, *M. zonifer* and *B. ramosus* are typically present in intertidal ponds also. The 15 species are widely distributed in the TEP, from the Gulf of California to the northern coast of Perú; moreover, *C. oxycephalus* is trans-Pacific and *M. curema* is cosmopolitan.

Description of temperature-tolerance methods

Thermal tolerance of fishes can be quantified in the laboratory using either static or dynamic methods. Although we used a dynamic method, a brief synopsis of both methods is provided here in order to justify our choice. More details of the approaches and assumptions of the methods can be found in Hutchison (1976), Bennett and Judd (1992) and Bennett and Beitinger (1997).

The static method quantifies time-dependent mortality of fishes suddenly plunged into high static temperatures near their upper

lethal limits. The static high lethal temperature (SHLT) for 50% of the sample is then interpolated from a regression of percentage mortality on static temperature. Dynamic trials estimate the CTM by exposing fishes to a constant rate of water-temperature increase, until a non-lethal end-point (e.g. loss of equilibrium or onset of muscular spasm) is reached. The CTM is calculated as the arithmetic mean of the collective thermal points at which the end-point is reached. Because techniques and end-points differ between both methods, they do not yield similar values (Bennett and Judd 1992). Normally, in a given species, the SHLT is lower than the CTM (Bennett and Judd 1992; Bennett and Beitinger 1997). Thermal shock and handling stress are additional factors that reduce thermal tolerance in the static trials (Bennett and Judd 1992). Although dynamic methods do not have these problems, the CTM of one species may vary depending on the temperature-change rate chosen (Hutchison 1976; Elliott and Elliott 1995). However, recent studies have demonstrated that using rates slower than 1°C/h controls this problem because, above this rate, the CTM does not change significantly (Elliott and Elliott 1995; Mora and Ospina, unpublished data). Different authors argue that the static method provides useful standards for physiological comparison between species, while dynamic trials are more accurate predictors of responses of fishes to natural thermal conditions (Bennett and Judd 1992; Bennett and Beitinger 1997). Dynamic trials are better at simulating temperature changes as they occur in nature than are static methods; furthermore, fishes have been found in natural environments at temperatures that are lethal according to static indices but tolerable according to dynamic indices. Therefore, since our purpose was to determine the thermal tolerance of some reef fishes and assess the impact of sea warming on them, we preferred the dynamic method at a rate of 1°C/h. An additional advantage of the CTM is that, considering a sublethal, rather than a lethal, temperature as a reference of tolerance, it takes into account possible chronic or delayed lethal effects of temperature, which leads to a conservative measurement of thermal tolerance.

Fishes were collected with hand nets on the reefs of Gorgona Island and then transported to the laboratory within 20 min. Fishes, principally juveniles (number and sizes by species are shown in Fig. 1), were randomly separated and placed into six 100-l aquaria (each species was tested separately). After handling, fishes were left 24 h to acclimate to the experimental conditions. Aquaria were 50% flushed with fresh salt water before each experiment. Water was maintained at a temperature equal to that of the sampling site (26.5 ± 0.5°C). Adequate aeration of the aquaria permits a high oxygen concentration and a continuous mix of water. Additionally, aquaria were covered with lids to prevent evaporation and consequent salinity changes. At the end of the acclimation period, in each of three aquaria randomly selected, temperature was gradually increased by 1°C/h with electronic heaters (±0.1°C precision). The other three aquaria were kept at a stable temperature and were used as experimental controls. Aquaria were monitored all the time in order to record the temperature at which fishes reached their end-points. CTM was calculated as the arithmetic mean of these collective thermal points.

Results

There was no evidence of stress in fishes, either in all aquaria during the acclimation period or in the controls during the experiment. Therefore, the response of fishes to these experiments likely resulted from the influence of temperature and not of other factors.

Loss of equilibrium was the principal end-point found in all the reef-fish species studied. Non-vagile and demersal fishes, such as *Cirrhichthys oxycephalus*, *Coryphopterus urosphilus*, *Bathygobius ramosus* and *Malacotenus zonifer*, were stimulated with a ruler to

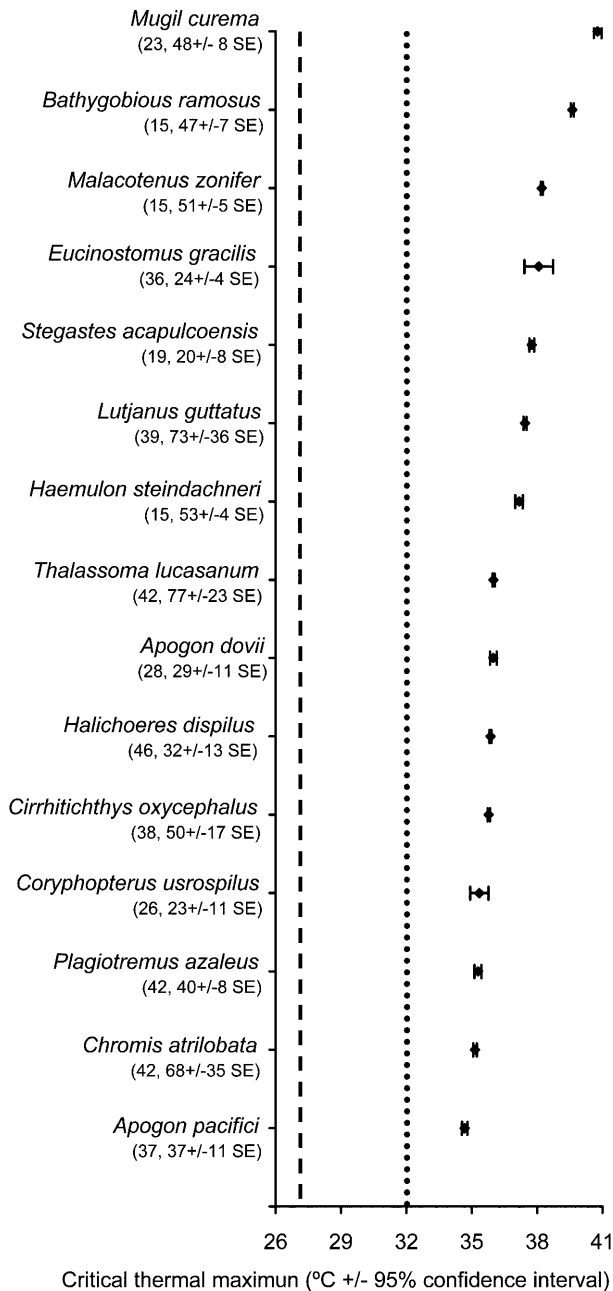


Fig. 1 Critical thermal maxima of 15 reef fishes of Gorgona Island and their comparison with mean sea-surface temperature in several localities in the tropical eastern Pacific (*dashed line*) and the highest temperature recorded during past El Niño events (*dotted line*). Number of individuals and average standard length in millimetres are shown in parentheses

force them to swim and thus allow us to identify equilibrium loss. The CTMs, together with their 95% confidence interval for all species, are shown in Fig. 1. In the reef fishes studied here, the CTMs ranged from 34.7°C for *Apogon pacifici* to 40.8°C for *Mugil curema* (Fig. 1). The CTM tended to be variable among species (6.1°C), whereas intraspecific variability in the CTM was generally low (Fig. 1). Within species, CTM usually varied no more than 0.5°C.

Discussion

Temperature of acclimation, time of acclimation and body size are among the most important factors that may affect the thermal tolerance of fishes (Hutchison 1976). Implications of the CTMs can be biased if one of these factors is not controlled in experimental designs. Therefore, we consider it important to discuss each of these factors and their effects on CTM:

1. The thermal-tolerance limit of a given species depends on the acclimation temperature; normally, fishes acclimated to low temperatures can tolerate lower temperatures than fishes acclimated to higher temperatures and vice versa (Hutchison 1976; Bennett and Judd 1992). In this study, temperature was increased from a single acclimation temperature. However, when using the dynamic method at a low rate of temperature increase (e.g. 1°C/h), the temperature of acclimation does not have a significant effect on CTMs, because fishes are able to acclimate to temperature changes at slow rates (Elliott and Elliott 1995).
2. The acclimation period at the lab was 24 h, which might be considered as a short time of acclimation. However, similar temperature between sampling site and aquaria avoided the need for thermal acclimation. On the other hand, it is recognised that the concentration of stress hormones increases with time in captivity after capture (Pankhurst and Sharples 1992); therefore, testing fishes within a few hours of capture provides a means of minimising stress levels.
3. Body size may affect CTM values, owing to a slower rate of heat penetration in larger organisms, and to differences due to age, sexual maturity, and other physiological factors associated with age (Hutchison 1976). In this study, principally individuals of small size (juveniles) were tested. This selection was made because of the insufficient number of larger fishes on the reefs and previous research (Ospina and Mora, in preparation) that did not find a correlation between CTM and body size among conspecifics of seven reef-fish species of Gorgona Island. In that study, Ospina and Mora concluded that the small body size that characterises most of the reef-fish species in general reduces the effects of body size on CTM.

Critical thermal maxima

Compared with other marine animals of the TEP, such as corals and bivalves, reef fishes can be less susceptible to the effects of thermal phenomena. Overall, reef fishes are more tolerant to high temperatures than are corals and bivalves (Glynn and D'Croze 1990; Urban 1994; Mate 1997). Among reef-fish species, differences in CTM may confer different abilities to colonise warmer habitats. For

instance, intertidal ponds on Gorgona Island are habitats that can reach 36°C during very sunny days (Mora, personal data). In these habitats, three of the most tolerant species (*Mugil curema*, *Bathygobius ramosus* and *Malacotenus zonifer*) are common, whereas the other less-tolerant species are infrequent or absent. In fact, for some species, such as *Apogon pacifici*, *Chromis atrilobata* and *Plagiotremus azaleus*, the water temperature in this habitat can reach lethal limits (Fig. 1).

Effects of sea warming on reef-fish populations

Temperature can reduce population abundance by affecting survival of benthic individuals or by affecting somehow reproduction and recruitment (effects on migration or immigration are rather slight, because of the sedentary nature of reef fishes). Because we assessed the lethal effects of temperature on benthic individuals, our data are relevant to the effect of sea warming on post-recruitment mortality.

El Niño is the principal phenomenon associated with short-term warming in the TEP. Its intensity has been variable, but El Niño 1982–1983 and 1997–1998 are recognised as the strongest events in the last century (Quinn et al. 1987; NOAA 2001). During these particular warm events, sea temperature reached 32°C in a broad range of latitudes in the TEP (Wellington and Victor 1985; Vargas et al., *in press*). According to our results, all the studied reef-fish species are tolerant to temperatures occurring during the most extreme El Niño events (Fig. 1). Hence, mortality due to high El Niño temperatures is unlikely the reason for reef-fish population decreases during this phenomenon. Other factors implicated in population changes during El Niño are discussed below.

In recent years, it has been reported that sea temperature in the TEP has increased by almost 1°C per decade (Jokiel and Coles 1990; Roemmich 1992; Strong et al. 2000). In our results it is noted that the least-tolerant species has a thermal tolerance 8°C above the current mean sea-surface temperature in the TEP (Fig. 1). This indicates that reef fishes live far from their upper thermal-tolerance limits and that, on a short time scale, the current global-warming trend is unlikely to be dangerous for these species. If sea temperature continues to increase at the current rate (1°C per decade), in about a century from now sea temperature could exceed the thermal tolerance of some reef fishes and threaten them with extinction. This risk, however, could occur sooner if temperature during El Niño also increased in step with that global-warming trend. Moreover, it is important to mention that other processes involved in maintaining population (e.g. reproduction) can be affected at lower temperatures; hence the effect of sea warming on reef fishes might be not necessarily too far off if sea temperature continues to increase.

Perhaps the most interesting question is what will happen to reef fishes if sea temperature reaches lethal limits? In spite of our present limited understanding of

the genetic structure of reef-fish populations and the mechanisms and rates of speciation, some available information may provide clues to the ability of reef fishes to adapt to increases in sea temperature. Firstly, we need to differentiate between short-term temperature increases (STI) during phenomena such as El Niño and long-term temperature increases (LTI) related to phenomena such as global sea warming. During STI, fishes require rapid adaptation to altered thermal conditions, whereas in LTI the adaptation can be slower. The magnitude of adaptation to either STI or LTI depends on genetic variability and life-history characteristics, such as generation time. In an STI situation, some reef fishes may be seriously threatened with extinction, not only by the low intraspecific variability in thermal tolerance (Fig. 1), but also because generation time in reef fishes is slower than the time in which sea temperature reaches high levels. Although in an LTI situation reef fishes may be equally threatened with extinction, they have more chance of adaptation because more generations may increase genetic variability.

Effects of El Niño on reef-fish populations

As we already pointed out above, temperature by itself is unlikely to be responsible for reef-fish population decreases during El Niño. This phenomenon, besides promoting a temperature increase, is linked to a decrease of planktonic primary production (Barber and Chavez 1983; Arntz and Fahrbach 1996). Probably, during El Niño, fishes are subject to starvation. Starvation can affect population size by increasing mortality or indirectly by reducing thermal tolerance (Hutchison 1976) or reproductive effort (Hirshfield 1980). The effects of starvation during El Niño, however, could be different among reef-fish species. Unlike planktivores for herbivores, food availability during El Niño increases, owing to algal overgrowth resulting from the massive coral mortality.

Fish larvae are much more sensitive to increasing temperature than are adults (Hutchison 1976) and are pelagic in reef fishes. This implies that, during El Niño, larvae are subject to high temperatures, starvation and interaction between starvation and thermal tolerance. Therefore, El Niño can affect the survival of larvae and thus reduce recruitment. The lack of larvae in the plankton (L. Zapata, personal communication) and low recruitment (Wellington and Victor 1985) of reef fishes during El Niño events might support the idea of larval mortality during this phenomenon, but alternatively, might be due to a low reproduction of reef fishes during El Niño. In fact, changes in the reproductive cycles of some bivalves and commercial fishes have been reported during El Niño (Urban and Tarazona 1996; L. Zapata, personal communication). The El Niño conditions might affect reproduction through physiological mechanisms (e.g. inducing hormonal upset or decreasing energy available for reproduction because of the effect of starvation in some reef-fish species). Alternatively, reef

fishes could change their reproductive strategy by decreasing reproductive effort during El Niño, which would avoid loss of energy in gamete production when unfavourable conditions are present for the survival of postbreeding individuals. This kind of change in the reproductive strategy during El Niño has been reported for bivalves from Peru (Urban and Tarazona 1996). In summary, El Niño may affect the reproduction and the survival of benthic and pelagic individuals depending on the living and reproductive strategies of reef fishes. However, a more accurate explanation of the effects of El Niño on reef fishes can be possible only with more experimental studies and long-term monitoring.

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