THE EFFECT OF THE EL NIÑO–SOUTHERN OSCILLATION EVENT ON THE DISTRIBUTION OF REEF-ASSOCIATED LABRID FISHES IN THE EASTERN PACIFIC OCEAN

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ABSTRACT

We surveyed the labrid fishes of the eastern Pacific ocean at multiple sites before, during, and after the 1997–98 ENSO event. Our observations showed that reef fish communities in general did not appear to change markedly as a result of the ENSO. Recruitment of labrids at the Galápagos Islands, Clipperton Atoll and Baja California was generally high near the end of the ENSO, indicating no negative effect on populations. Two labrid species did extend their known range during the ENSO: *Stethojulis bandanensis* settled onto the tip of Baja California and to the Galápagos Islands, while *Thalassoma virens* recruited heavily to sites along the southern Sea of Cortez in Baja California. We discuss the oceanographic conditions during the ENSO that may have promoted the range extensions. Adults of these species were present in Baja California and Galápagos 2 yrs after the end of the ENSO. Our observations raise the question why these species do not colonize these sites in normal years, given the potential for long larval durations (up to a maximum of 104 d in *T. virens*) and rapid long-distance transport between islands in the region (recruits of *S. bandanensis* spent only about 32 d in the plankton).

The recent El Niño–Southern Oscillation (ENSO) event of 1997–98 is considered to be one of the most intense of the past few centuries and has had a profound effect on the marine environment of the eastern Pacific Ocean (Glynn et al., this issue). The most significant and lasting result has been widespread mortality of reef-building corals throughout the region. The effect on reef-associated fishes is less dramatic and less well-documented, yet may be important to explaining the biogeography of fishes in the eastern Pacific Ocean. The epicenter of the temperature anomalies during the ENSO is near the Galápagos Islands, where the normal cool annual upwelling cycle disappears, the thermocline deepens, and a vast region of exceptionally warm surface water develops and persists for many months (reviewed in Enfield, this issue). In addition, the eastward flowing North Equatorial Countercurrent (NECC) speeds up considerably, and warm tropical water builds up in the eastern Pacific and flows towards more temperate regions (Wyrtki, 1985; Lea and Rosenblatt, 2000).

The eastern Pacific region is particularly well-suited to an analysis of how oceanographic anomalies such as the ENSO affect reef fish biogeography. The distribution of habitats is simple: a long north-south stretch of thin continental shelf with several isolated island groups at varying distances from the coast (Fig. 1). There are marked temperature variations, both seasonal and latitudinal, distinct regions of upwelling, and clearly delineated areas of rocky coastline, coral reefs, and soft sediment (Glynn and Ault, 2000). Furthermore, the whole region is separated from the complex biogeographical regions of the central and western Pacific by a vast ocean expanse, the East Pacific Barrier, over 5000 km without island stepping stones (Leis, 1984; Grigg and Hey, 1992). As a result, the vast majority of reef fish species in the area are endemic to the eastern Pacific and, furthermore, exhibit a great variety of patterns of distribution within the region (Briggs, 1974; Allen and Robertson, 1994; Victor and Wellington, 2000).

The effects of unanticipated events such as the ENSO are difficult to study due to the lack of appropriate pre-event data. There have been some reports during and after prior ENSO events focusing on specific localities (e.g., Grove, 1984 for Galápagos) or particular species (e.g., Wellington and Victor, 1985 for a Panamanian damselfish), however, no broad-scale regional studies have been made. We were fortunate to have surveyed populations of labrid fishes at multiple sites within the eastern Pacific Ocean in the years preceding, during, and after the 1997–98 ENSO. Our surveys included the extreme limits of the warm tropical fauna at the tip of the Baja California peninsula in the north and the Galápagos Islands in the south as well as the offshore islands of Clipperton Atoll and Cocos. The Galápagos Archipelago is notable for containing an often abrupt transition from a tropical warm water fauna in the central and northern islands to a cool Peruvian province fauna in the western and southern islands (Rosenblatt and Walker, 1963; McCosker and Rosenblatt, 1984). Although much of the data presented here is qualitative and some is anecdotal, an overview of the effect of the 1997–98 ENSO on labrid and some other reef fishes can be assembled from our observations.

METHODS

We surveyed the labrid fauna at multiple sites in the tropical eastern Pacific before, during, and after the 1997–98 ENSO event (see details in Wellington and Victor, 1992; Robertson and Allen, 1996; Victor and Wellington, 2000). Methods of survey, collecting effort, ocean conditions, and personnel involved differed substantially between sites and dates, precluding a globally rigorous quantitative assessment of the regional effect of the ENSO. Two sets of data were collected consistently: quantitative collections of tidepool recruits in Baja California and qualitative estimates of abundances in the Galápagos (discussed below). Other data included species lists from various sites, general observations by local fish biologists, periodic quantitative fish counts, collections of labrid juveniles for other studies, and full-scale ichthyocide collections. Collections and surveys were made by various authors at Clipperton Atoll in April 1994 and May 1998, Cocos Island in November 1990 and November 1997, the Revillagigedo Archipelago in June 1990, Galápagos Islands in April 1990, January 1995, May–August 1998, and June–August 2000 and the tip of Baja California in October 1989, January 1997, February, March, May and September 1998, July 1999, April, July, and August 2000 (Fig. 1).

In conjunction with a study on the pelagic larval duration and the biogeography of eastern Pacific labrid and pomacentrid fishes (Victor et al., 2000), we examined the otoliths of some of the fishes we collected. We were interested in examining individuals that settled during the ENSO and belonged to species that were not resident in the area prior to the ENSO. These individuals could therefore represent long distance migrants delivered by ENSO-induced currents (i.e., *Stethojulis bandanensis* to Galápagos and Baja California and *Thalassoma virens* to Baja California). The otoliths of these fishes were processed and the daily increments counted as described in Victor (1991). We determined the pelagic larval duration for 10 individuals of *S. bandanensis* settling in the Galápagos Islands and 10 *T. virens* and seven *S. bandanensis* settling in Baja California.

We did few quantitative surveys, but in Baja California we collected labrids in a set of tidepools just south of Punta Pescadero on the east Cape of the tip of the Baja Peninsula, south of La Paz (Fig. 1). This site consisted of an area of about 100 m² of shallow tidepools and on our visits to Baja California we collected all of the juvenile labrids present in the pools at low tide (typically only *Thalassoma* spp.). Seven collections were made between January 1997 and August 2000 (Fig. 2).

In the Galápagos Islands we did a more qualitative survey of the labrids. The abundance of each labrid species was recorded for each dive at each location in 1990, 1995, and 1998. On each expedition, we visited Santa Cruz, Santiago, Isabela, Fernandina, and Genovesa and included Marchena in 1990 and 1995, Floreana in 1995 and Wolf in 1998. The surveys are comparable because about 20 dives were made on each trip, most of the dive sites were the same (commonly visited locations),
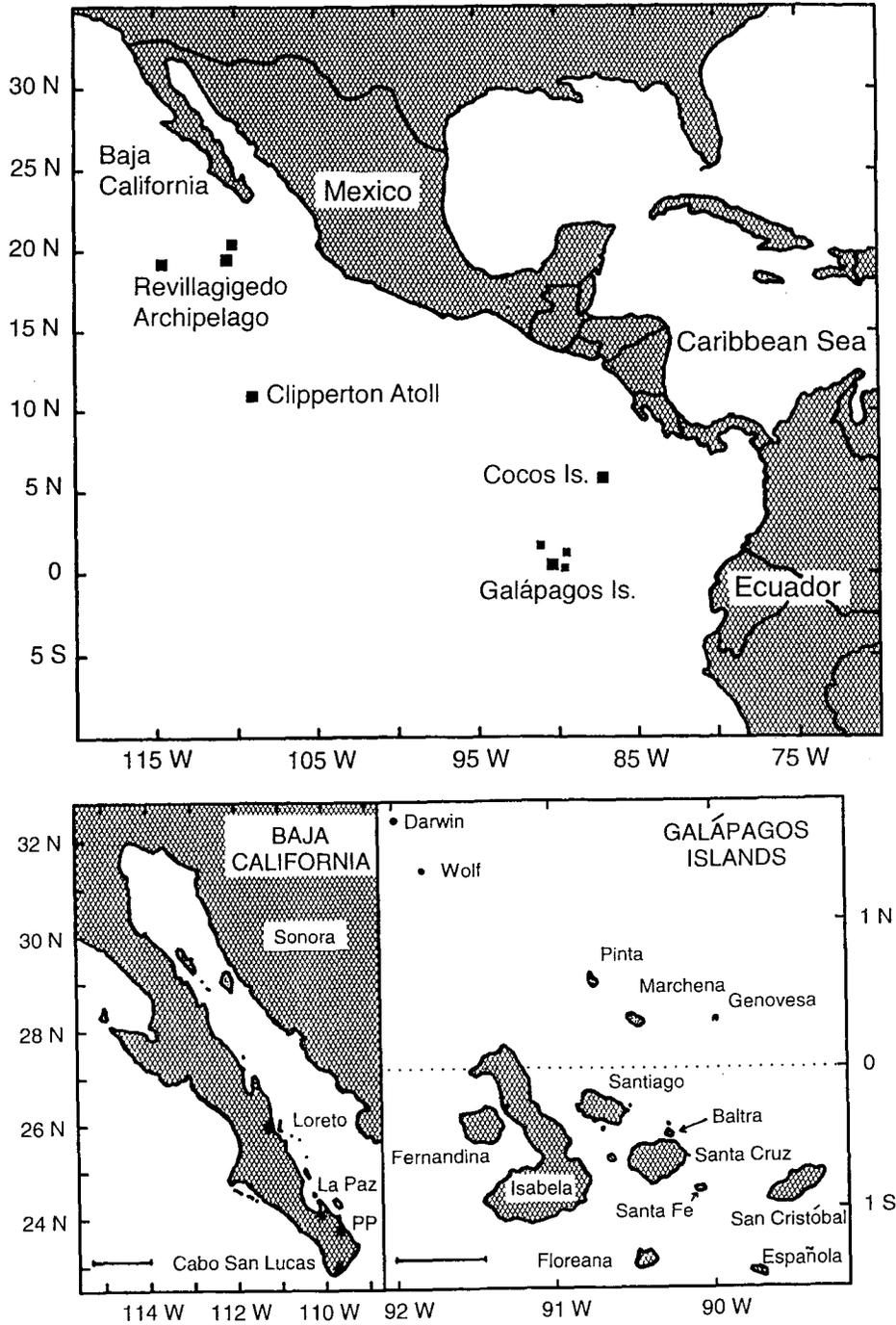
Figure 1: Map of the eastern Pacific region (upper) and detailed maps of Baja California and the Galápagos Islands (lower). Scale bars represent 200 km for the Baja California map and 60 km for the Galápagos Islands map. PP = Punta Pescadero.

the surveys were done by a single experienced observer (B.C.V.), and conditions were good at all times. Abundance for each year (overall, not per site) was categorized as none, rare (one sighting of one or two individuals), uncommon (one or two sightings of fewer than three individuals), occasional (more than two sightings of a few individuals), common (present at most sites), and abundant (abundant at most sites).

RESULTS

The most notable finding of our surveys was the range extension of two species of common labrids to the northern edge of the range of tropical fauna in the eastern Pacific Ocean. Both *S. bandanensis* and *T. virens* settled onto Baja California where they were previously unrecorded (Thomson et al., 2000). *T. virens* is common and *S. bandanensis* is present at the Revillagigedo Archipelago, about 400 km south-west of the tip of Baja California. *S. bandanensis* is common and *T. virens* is present at Clipperton Atoll, 1300 km south of the Baja peninsula (Allen and Robertson, 1994; Robertson and Allen, 1996).

T. virens settled onto Baja California in such numbers that it was the most common labrid recruit in the tidepool region of the east Cape in the collection of April 1998, during the ENSO (Fig. 2). No juveniles of this species were collected at the site before the ENSO or in subsequent years. We collected an adult *T. virens* in the same area 2 yrs later, on 1 August, 2000: the fish measured 159 mm SL and was 838 d old by otolith count (photograph in FishBase; Froese and Pauly, 2001), indicating that this species can persist in the area during cold La Niña conditions. Similarly, some *S. bandanensis* recruits were collected from the Cabo San Lucas region and near La Paz during the ENSO, and a few adults have been sighted in the La Paz area as well as north of Loreto at San Sebastián, up to 3 yrs after the end of the ENSO (B. Victor, pers. observ. and E. Sala, O. Aburto-Oropeza and G. Paredes, pers. comm.).

Few conspicuous changes in labrid numbers were noted on our repeated surveys in the Galápagos Islands (Table 1). The one exception was *S. bandanensis*, which settled in

Table 1. Abundances of labrid species in the Galápagos Islands before and during the 1997–98 ENSO. 0 = absent, + = rare, ++ = uncommon. +++ = occasional. ++++ = common, +++++ = abundant (see methods for definitions).

| Species	April 1990	January 1995	May–June 1998
Bodianus diplotaenia	+++++	+++++	+++++
Bodianus eclancheri	++	++	++
Halichoeres chierchiae	0	+	++
Halichoeres dispilus	+++++	+++++	+++++
Halichoeres nicholsi	++++	++++	+++++.
Halichoeres notospilus	++++	++++	++++
Novaculichthys taeniourus	++	++	+++
Semicossyphus darwini	++	++	++
Stethojulis bandanensis	+	0	++++
Thalassoma grammaticum	++++	++++	++++
Thalassoma lucasanum	+++++	+++++	+++++
Thalassoma purpureum	++	+	+++
Xyrichtys pavo	++	++	+++
Xyrichtys sp. n. G	+	+	+
Xyrichtys victori	+++	+++	+++
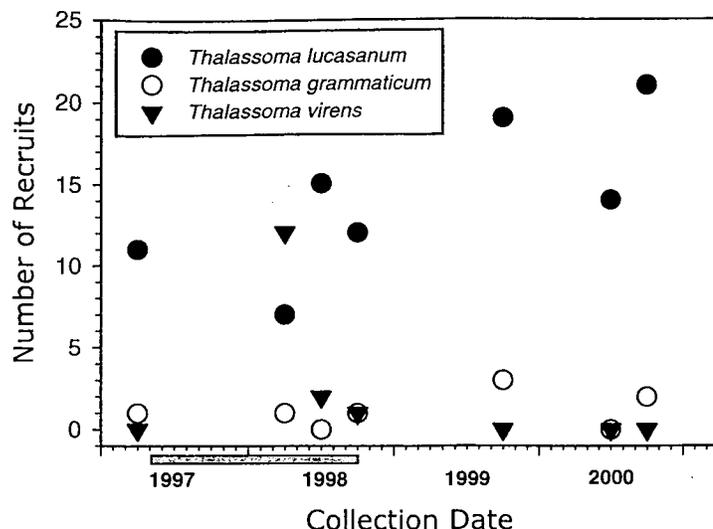
Figure 2: The abundance of *Thalassoma* spp. at a tidepool site (100 m²) at Punta Pescadero, Baja California before, during and after the 1997–98 ENSO. Numbers represent the total population at the site. Shaded bar indicates approximate duration of the ENSO.

large numbers to the central islands of the Galápagos Archipelago where they were previously rare or absent. According to Grove (1984), *S. bandanensis* was not known in the Galápagos prior to 1982. Grove and Lavenberg (1997) document only three specimens of this species collected from the Galápagos and only a few other reported sightings. We observed a single adult at Genovesa in 1990 and saw none in 1995. This species is common at Clipperton Atoll and Cocos Island, but has been previously noted as present or rare on mainland Costa Rica (Bussing, 1985) and Colombia (Zapata and Morales, 1997) and not uncommon in the Gulf of Chiriquí, Panama in 1990 and 1998 (D. R. Robertson, pers. observ.). As in Baja California, some adults of *S. bandanensis* have persisted through the subsequent La Niña and have been recorded at Española, Santa Fe, and Bartolomé (on the island of Santiago) as late as March 2001 (B. Ruttenberg, pers. observ. and F. Rivera and G. Edgar, pers. comm.).

The surveys in the Galápagos showed no other major changes in labrid abundances. Relative abundances of many species may have changed to a degree that would not show up against the typical background of marked recruitment variability and surveys at different times of year. We observed heavy recruitment of many labrids during the ENSO at Baja California, Clipperton Atoll, Cocos Island, and the Galápagos Islands, and new recruits of all warm-water species were collected in the Galápagos in May and June 1998, even the uncommon and rare labrid residents, such as *Novaculichthys taeniourus*, *Thalassoma purpureum*, *Xyrichtys pavo*, and an undescribed species, *Xyrichtys* n. sp. G (Victor et al., 2001). The two cold-water labrids of the Galápagos, *Bodianus eclancheri* and *Semicossyphus darwini*, were occasionally seen in deeper water and in the western-most sites and we have insufficient data to assess the effect of the warm water on their populations.

Analysis of daily otolith increments revealed markedly different pelagic larval durations (PLD) for *S. bandanensis* and *T. virens*. *S. bandanensis* from the two sites had the same PLD, a mean of 32.3 d (SD = 3.2, range of 28–38 d, n = 10) for Galápagos and a mean of 32 d (SD = 2.4, range of 28–35 d, n = 7) for Baja California. In contrast, *T. virens*

had an extremely long and variable PLD in Baja California, with a mean of 78.6 d and a maximum of 104 d in our small sample (SD = 14.2, range of 61 to 104 d, n = 10).

DISCUSSION

The most notable finding in our surveys is that despite the fact that the 1997–98 ENSO was one of the largest in recent history, there was not a great impact on the reef fish fauna at the sites we surveyed in the eastern Pacific region, certainly nothing like the impact on corals. While there are few quantitative abundance data for reef fishes in the eastern Pacific before and after the ENSO (with the exception of Ruttenberg, 2000), no profound changes in reef fish communities were noted by regular observers. A few reef fish species, particularly those that have limited distributions within the region, were noticeably affected by ENSO conditions.

Among the labrids, observed settlement rates by the end of the ENSO (at Galápagos, Clipperton Atoll, and Baja California) were relatively high, especially for the more 'tropical' species and the widespread Indo-Pacific species. In addition, two labrid species extended their known range in the region. *S. bandanensis*, a widespread Indo-Pacific species, had a heavy recruitment to the Galápagos Islands in the south and to the Sea of Cortez in the north. In addition, *T. virens*, a species previously known only from the Revillagigedo Archipelago and Clipperton Atoll, settled in Baja California in large numbers.

This expansion of range during the ENSO can be explained by altered current flows in the region (summarized in Glynn and Ault, 2000). The normal pattern of currents is westward-flowing currents north of 10°N (the North Equatorial Current, NEC) and south of the equator (the South Equatorial Current, SEC), with a strong eastward flowing current occupying the central portion of the region (the North Equatorial Countercurrent, NECC). In addition there is a deep current flowing eastward beneath the SEC called the Equatorial Undercurrent (EUC). A shift of a few degrees north or south in any one of these currents can expose any of the offshore island groups to strong flow in either direction. During the ENSO, the NECC eastward flow is markedly increased in speed and volume, making it much easier for larvae to cross from the central Pacific (Richmond, 1990). Furthermore, the massive buildup of water in the ocean basin forces currents northward along the central American coast (the Costa Rican Coastal Current, CRCC) toward Baja California and up to Southern California. The cold California Current is pushed away and transport of tropical fishes to Southern California is enhanced (Lea and Rosenblatt, 2000). There is also increased flow southward from the Central American coast (the Panama Current, PC), which could bring warm water to the Galápagos Islands from the east.

The enhanced delivery of tropical species to Baja California can be explained by the increased flow of the CRCC. In the case of *S. bandanensis* and *T. virens*, larvae could be picked up at Clipperton Atoll and transported eastward with the NECC and then north with the CRCC. Other hypothetical scenarios could be proposed, but resolution awaits detailed genetic studies of these species that could elucidate the origin of propagules. Similarly, *S. bandanensis* larvae could be transported from Panama, Clipperton Atoll or Cocos Island to the Galápagos Islands via the enhanced NECC and then south-east with the PC.

The extension of the range of *S. bandanensis* and *T. virens* during the ENSO raises some intriguing questions about eastern Pacific fish biogeography. These settlers were not vagrants, i.e., a few stray individuals, but massive settlements that lasted for weeks. Furthermore, the larval durations of the new recruits were no different from those from other sites and years,

and in one species were very short (about 32 d in *S. bandanensis*). Clearly, long-distance transport of substantial numbers of larvae is quite feasible. So why don't these species colonize and therefore become regular residents during non-ENSO periods? ENSO events are known to produce rapid currents that could play a role in dispersing short-lived reef-fish larvae, yet *T. virens* has a very long larval duration (up to 104 d) and still does not settle during normal years and colonize the Baja Peninsula. Perhaps something unique about the ENSO promotes long-distance transport of reef fish larvae, but, equally relevant, something about normal years and the La Niña period prevents colonization.

The fact that the range extensions are at the northern and southern limits of the species' distributions suggests that temperature may be the limiting factor. Indeed, we observed mortalities of warm-water fauna near the end of the ENSO at Fernandina in the Galápagos Islands. On May 28, 1998, there was sudden cold upwelling near Punta Espinosa, dropping the temperature substantially over a matter of hours. After our survey dive, we noticed dead and moribund fishes floating by the boat, including an adult *Stegastes leucorus beebei* and a large *Holacanthus passer*. However, if temperature were simply the limiting factor on warm-water species' distributions, then we would expect to see summer settlements and winter disappearances. This would be analogous to some temperate region dynamics, such as in California, where juveniles of more tropical species show up each summer or during ENSO periods and disappear each winter or during non-ENSO periods when the water is either too cold or the upstream source is from cold-water regions (e.g., Cowen, 1985; Lea and Rosenblatt, 2000). But, normal summer water temperatures in Baja California and Galápagos are similar to temperatures at Clipperton Atoll and Cocos Island and quite suitable for recruitment of most other tropical reef fishes, yet for some reason these two species do not settle during normal warm seasons at these sites. This raises the question of whether there is something else about ENSO years that is required for successful transport and survival of larvae of some species.

In addition, the fact that adults can persist through La Niña cold years (as observed both in Baja California and Galápagos) indicates that they are capable of surviving the full range of variation in conditions. Of course, whether they are reproductively active or suffer high enough mortalities to extinguish the population during non-ENSO periods has yet to be discovered. Indeed, the reef itself may be quite suitable for survival, growth and reproduction, but some requirement for their larvae may be absent during non-ENSO periods ('larval habitat requirements' sensu Leis, 1991). Clearly, there is a more complex and elusive explanation for the curious patterns of ENSO effects on reef fishes in this region.

Despite the magnitude of this ENSO, we noted no conspicuous arrivals from the central Pacific region to the Galápagos, Clipperton Atoll, or Baja California (all three sites were surveyed in April–June 1998, near the end of the ENSO). As of November 1997, surveys at Cocos Island also showed no trans-Pacific vagrants. In the past, a few vagrants have been recorded crossing the East Pacific Barrier to the Galápagos, especially to the northernmost Galápagos Islands, Wolf and Darwin (Grove, 1988; Merlen, 1988; McCosker and Humann, 1996). Our surveys at Wolf at the end of the ENSO found no labroid vagrants, however, we observed some adult central Pacific chaetodontids that have been recorded in the area before (Merlen, 1988) and could have been resident since the previous ENSO. Interestingly, the *S. bandanensis* that arrived in the central islands during this ENSO were not seen at Wolf. Since *S. bandanensis* is common at Cocos Island and Clipperton Atoll, it is likely that they did not cross from the Central Pacific, but arrived

from Cocos Island, Panama, or Clipperton Atoll to the north and north-east. Furthermore, the one-month larval duration of these ENSO settlers makes a crossing of the Eastern Pacific Barrier very unlikely; Richmond (1990) has calculated that even with markedly enhanced eastward flow during the ENSO, it would still take a minimum of about 50 to 80 d to cross the barrier.

While it is clear that a number of widespread Indo-Pacific species have crossed to the eastern Pacific biogeographic region since the Pleistocene (Rosenblatt et al., 1972), it is not at all certain to what degree this crossing occurs regularly during ENSO events. The recent discovery of additional trans-Pacific species has been ascribed to vagrants crossing the barrier during recent ENSO events (Merlen, 1988; McCosker and Humann, 1996; Grove and Lavenberg, 1997). However, with more complete surveying of reef fishes in the region, some of these species have proven to be widespread residents of the region, occupying offshore islands as well as the continental margins and successfully recruiting during non-ENSO periods. Among the labrids, all trans-Pacific species (*N. taeniourus*, *S. bandanensis*, *T. purpureum*, and *X. pavo*) have well-established populations in the region. The degree of recent gene flow across the barrier among trans-Pacific fishes is presently unknown and awaits a genetic study similar to that of Lessios et al. (1996, 1998). In those studies, mitochondrial DNA sequences were used to show some evidence of recent gene flow across the East Pacific Barrier among reef-associated sea urchins.

Some non-labrid reef fish species also increased in abundance in Galápagos during the ENSO. Ruttenberg (2000) conducted transect surveys on reef fishes in the Galápagos before and after the 1997–98 ENSO and recorded a significant increase in abundance of bumphead parrotfish (*Scarus perrico*) and the Mexican goatfish (*Mulloidichthys dentatus*). However, most reef fishes counted in his surveys did not show major changes. Perhaps the best known of the ENSO effects on reef fishes in Galápagos is the influx of the Acapulco damselfish, *Stegastes acapulcoensis*, previously found along the mainland and not on the offshore islands of the eastern Pacific (Allen and Robertson, 1994). This influx has been noted for past ENSOs (Grove and Lavenberg, 1997; Meekan et al., 2001) and certainly recurred in full force during this ENSO (B. Victor, G. Wellington, and B. Ruttenberg, pers. observ.). Interestingly, the recruitment of this species has continued strongly since 1998 through at least 2000 (B. Ruttenberg and G. Edgar, unpubl. data), indicating a possible true colonization of the islands. Prior to 1982, the species was considered rare in the Galápagos Islands (Grove, 1984). Perhaps the low Southern Oscillation index anomaly and corresponding high sea-surface temperatures over the past two decades have permitted a critical mass of adults to finally accumulate and successfully reproduce during non-ENSO years.

Some reef fishes may suffer from the excessively warm waters (up to 30°C at the surface) and deep thermocline that develop during the ENSO. Unlike corals that are sedentary, however, fishes can often escape these warm temperatures by moving deeper, and thus few reef fish populations appear to be severely harmed by the ENSO. The entire cool-water fauna of the south-western Galápagos Islands was less abundant, at least in shallow waters, following the ENSO of 1982–83 (Grove, 1984). The Galápagos endemic tube blenny, *Acanthemblemaria castroi*, was noted to have almost disappeared during the most recent ENSO, but has rapidly recovered (B. Ruttenberg, pers. observ.). The pattern of a drastic reduction followed by recovery of this species was observed after the 1982–83 ENSO in the Galápagos Islands (Grove and Lavenberg, 1997). The tube blenny lives primarily in barnacle shells in very shallow water, and thus would be particularly suscep-

tible to warming surface waters. There are, however, deep water refuge populations in the Galápagos that certainly escaped the effects and permitted a recovery (Grove and Lavenberg, 1997). Whether other inconspicuous fishes experienced declines during the ENSO is unknown.

The marked reduction in productivity during the ENSO certainly reduces the availability of food for planktivorous and herbivorous reef fishes and their numbers were reported to decrease during past ENSOs (Grove, 1984; Grove and Lavenberg, 1997). In fact, the blackspot chromis, *Azurina eupalama*, recorded only in the Galápagos Islands and Cocos Island, is presumed to have disappeared completely since the ENSO of 1982–83 (Grove and Lavenberg, 1997). The species is, however, easily confused with another mid-water damselfish, *Chromis atrilobata*, and found further from the reef and therefore less likely to be noticed. Furthermore, it is a more temperate species and may well eventually be found offshore of Ecuador and Peru. At present, it appears to be unique among recent marine fishes as a case of true natural extinction (Roberts and Hawkins, 1999). Whether it is extinct or just reduced in numbers and remains in an unsurveyed area or depth is still unanswered.

ACKNOWLEDGMENTS

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