

GIANT KELP (*MACROCYSTIS PYRIFERA*, PHAEOPHYCEAE) RECRUITMENT NEAR ITS SOUTHERN LIMIT IN BAJA CALIFORNIA AFTER MASS DISAPPEARANCE DURING ENSO 1997–1998¹

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During the ENSO event of 1997–1998, density and population structure were evaluated in a *Macrocystis pyrifera* forest located in Bahía Tortugas, Baja California, Mexico, near the southern limit of the species' distribution in the Northern Hemisphere. Observations in Bahía Tortugas were made quarterly from January 1997 to September 1998 using SCUBA diving surveys. No macroscopic plants were found in the Bahía Tortugas area from October 1997 to April 1998, a local absence of at least 7 months. Aerial surveys further suggest regional disappearance along most of the Baja California coast during the event. Unexpectedly, plants were found in Bahía Tortugas again in July 1998, in spite of the widespread disappearance of the species less than a year earlier. Long-distance spore dispersal was an unlikely cause of the recruitment because: 1) the nearest spore source was more than 100 km away; 2) recruitment appeared to be simultaneous at many sites and occurred rapidly after the cessation of the ENSO event; and 3) the recruits occurred in the same areas as before disappearance. We suggest that a microscopic stage that was not visible during dive surveys survived the stressful conditions of ENSO and caused the recruitment event, supporting the hypothesis that a bank of microscopic forms can survive conditions stressful to macroscopic algae.

Key index words: Baja California; disturbance; El Niño; ENSO; extinction; giant kelp; *Macrocystis pyrifera*; Mexico; microscopic stages; population dynamics

During ENSO events, high temperatures and low nutrient concentrations commonly result in widespread mortality of giant kelp forests (*Macrocystis pyrifera* (L.) C. Ag) (Dayton and Tegner 1984, Gerard 1984, Dayton 1985, Zimmerman and Robertson 1985, Tegner and Dayton 1987, 1991, Tegner et al.

1996). Recolonization is a common occurrence following local or large-scale disappearance of kelp forests (Dayton 1985, Ebeling et al. 1985, Tegner and Dayton 1991, North et al. 1993). The current controversy surrounding the strategy whereby colonization occurs after disappearance revolves around whether long-distance spore dispersal (Reed et al. 1988, 1997) or dormant microscopic stages (Dayton 1985, Foster and Schiel 1985, tom Dieck 1993) are responsible.

Large-scale disappearances and subsequent recolonizations of *M. pyrifera* have occurred repeatedly in Baja California, Mexico, during ENSO events (North 1957, 1971, Hernández-Carmona 1988), particularly at the southernmost range of the species. Unfortunately, recovery following disappearance at the southern limit has not been the subject of any study and has been documented only by occasional aerial surveys (North 1959, Hernández-Carmona et al. 1991). There is no information available on population structure or demography during the recolonization period after an ENSO-caused disappearance at the southern limit of distribution. Because local and regional extinctions may be common at the southern limit, the study of recolonization thereafter would provide insight into the strategies for recovery.

The Baja California *M. pyrifera* populations in the southern area are separated from those in the north by a disjuncture in the species' distribution along the Bahía Sebastián Vizcaíno with an absence of plants for approximately 300 km of coastline. In this area, hard substrate is rare and a tongue of warm offshore water moves shoreward (Dawson 1951, 1952). The southern limit of *M. pyrifera* was once reported as far south as Bahía Magdalena (Setchell and Gardner 1925). In 1971, the southern limit was reported in Punta San Hipolito (Guzmán-del-Prío et al. 1971). After the 1982–1983 ENSO event, *Macrocystis* disappeared from and never returned to Punta San Hipolito (Hernández-Carmona 1988). The southern limit, though variable, has since been documented further north in the Bahía Tortugas/

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Punta San Roque area (Hernández-Carmona et al. 1991). The populations at the southern limit raise numerous questions. The plants at the southern limit have an apparent high temperature tolerance (North 1971, 1972), they show morphological and physiological anomalies (Clendenning and Sargent 1957, 1958, Clendenning 1971, North 1972), and they form intertidal beds (North 1971, pers. observ.). Using demographic surveys, a forest of *M. pyrifera* in Bahía Tortugas near the southern limit of distribution was studied to determine the impact of and recovery after the ENSO event of 1997–1998. The unique situation at the southern limit, where all local (Bahía Tortugas) and regional (south of B. Sebastián Vizcaíno) plants were wiped out during the ENSO of 1997–1998, presented us with the opportunity to speculate about mechanisms of recolonization following incidents of massive disappearance. We considered the hypothesis that a bank of microscopic forms survived the disturbance and resulted in subsequent recruitment in the absence of spore-producing adults. A bank of microscopic forms in algae has been suggested to play an important ecological role similar to the role of a seed bank in land plants (Hoffman and Santelices 1991).

MATERIALS AND METHODS

Study site description. The Los Morros study site in Bahía Tortugas ($27^{\circ}39.97' N$, $114^{\circ}54.18' W$) (Fig. 1) was chosen because of its accessibility and representation of the southern limit of distribution of *M. pyrifera* in Baja California (Hernandez-Carmona et al. 1991). The Los Morros study site consists of plants distributed at the southern extension of the bay in a southerly and westerly exposed area. The plants occur at depths between 8 and 15 m (MLLW). The outer edge is apparently delimited by sand and the inner edge by wave action. The forest grows on a fairly homogeneous shelf of hard substrate interlaced with patches of sand. Minimal variation in depth occurs along the shelf where hard substrate does occur.

Size class and species distinctions. For purposes of this study, plants with fewer than four fronds were considered juveniles (because they often do not produce viable spores), and those with four or more fronds were considered adults (Neushul 1963, Dayton et al. 1992). Blade-stage *M. pyrifera* recruits were distinguished from other brown algae recruits (particularly *Eisenia*) by basal cleft presence and basal spine absence. Also *M. pyrifera* recruits tend to be thinner and lighter in color than *Eisenia* recruits.

Oceanographic conditions. Mean monthly sea surface temperatures were extracted from NOAA COADS (Comprehensive Ocean and Atmospheric Data Set) for the Bahía Tortugas area. Recording thermographs (Hobo Temp loggers) were located at the surface and at the bottom of the Los Morros study site; however, they could not be recovered.

Sampling methodology. The Los Morros study site was monitored quarterly using SCUBA diving beginning in January 1997. During each evaluation, dives were conducted in both the Los Morros study site and the surrounding areas. A permanent buoy was set at the inshore edge of the Los Morros study site as a reference point. April 1997 and January 1998 were not evaluated due to unfavorable weather conditions. The absence of *M. pyrifera* plants and recruits at the study site was determined in winter 1997 by M. Graham and colleagues (pers. commun.). July 1997 entailed only observational data.

In Los Morros, density of plants taller than 1 m was determined with 10×2 -m transects. The density transects were placed approximately every 20 m along a haphazard transect through the center of the forest. Density transects were always placed along

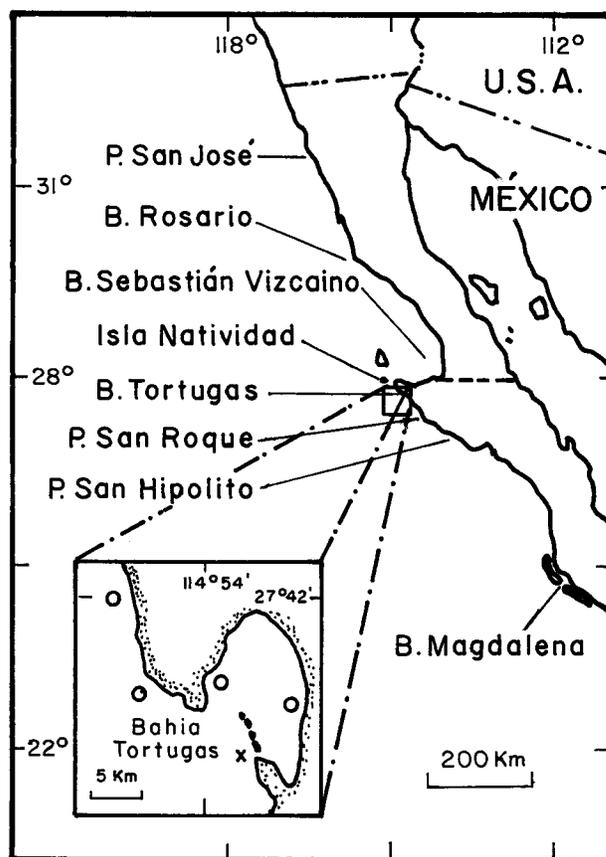


FIG. 1. Map of Baja California, Mexico. Inset shows Bahía Tortugas with the Los Morros study site (X), and alternate dive sites (O's) marked.

the same depth. A minimum of nine density transects were performed during each evaluation. Frond counts were taken 1 m above the holdfasts on plants encountered along a haphazard transect through the center of the forest. Between 15 and 30 plants were counted for frond evaluations.

All data in text and graphs is reported as means \pm one standard deviation.

Determination of distribution limits along the coast. Distribution limits of *M. pyrifera* forests were determined by searching for plant extension to the north and south with land vehicles, boats, and SCUBA diving surveys, in addition to information provided by aerial surveys (courtesy Dale Glantz, Kelco Biopolymers, San Diego, California) and personal communications.

When no plants were found in the Los Morros area, observational survey dives were made in other sites where forests were known to exist previously. The alternative dive sites were in the northern part of Bahía Tortugas and outside of the bay between Bahía Tortugas and Punta Eugenia (Fig. 1). These alternative surveys were performed to determine whether extinction was only in the Los Morros area or the whole region. For this same reason, two observational dives, one in April and one in July 1998, were also made at Isla Natividad.

RESULTS

Oceanographic conditions. Sea surface temperatures in Bahía Tortugas during ENSO 1997–1998 were warmer than normal (Fig. 2a) and showed a positive anomaly when compared to normal years. Temperature anomalies greater than $1^{\circ} C$ persisted continuously for 8 months. Anomalies from August 1997

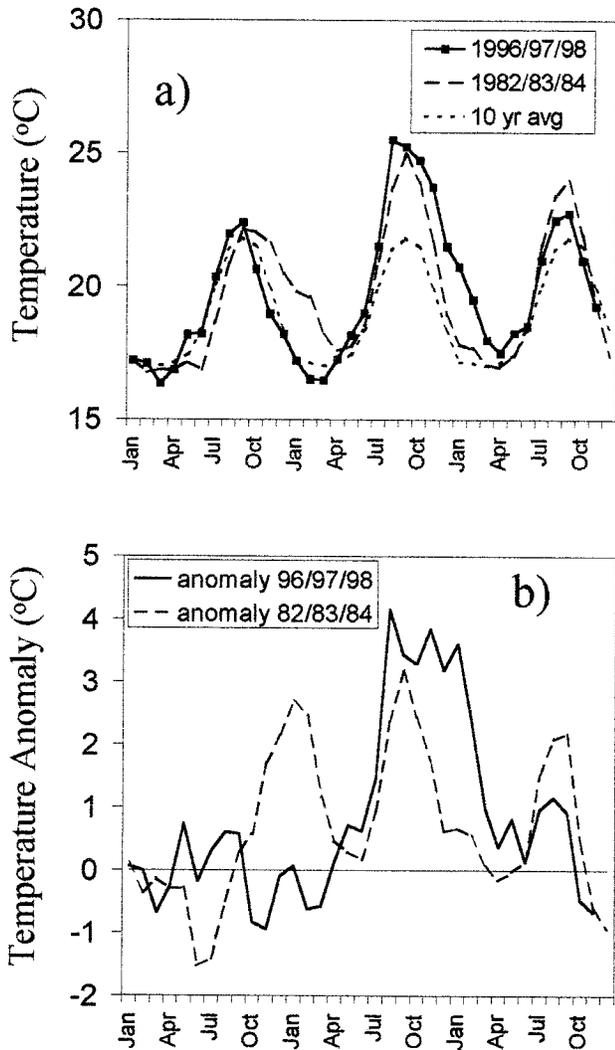


FIG. 2. (a) Mean monthly sea surface temperatures for Bahía Tortugas and (b) temperature anomalies compared to previous 10-year average for the area.

to January 1998 (a 6-month period) were greater than +3° C when compared to the previous 10-year average. From March to July 1998, temperature anomalies remained below +1° C. By October and November 1998, temperatures had dropped below the 10-year average, showing about a -0.5° C anomaly (Fig. 2b).

Kelp dynamics. In winter 1996 and spring 1997, extensive *M. pyrifera* forests were present along the coast between Punta Eugenia and Bahía Tortugas. In Bahía Tortugas, the forests were distributed on both the northern and southern edges of the bay, with many intertidal plants present within the bay. In winter 1996, the Los Morros plants had 10.26 ± 5.78 fronds per plant ($n = 15$ plants) (Fig. 3b). The plants had up to 21 fronds; 6% of the plants were juveniles and 94% were adults (Fig. 3c). Plants reached the surface and a thick surface canopy was present. Density was not evaluated. Until summer

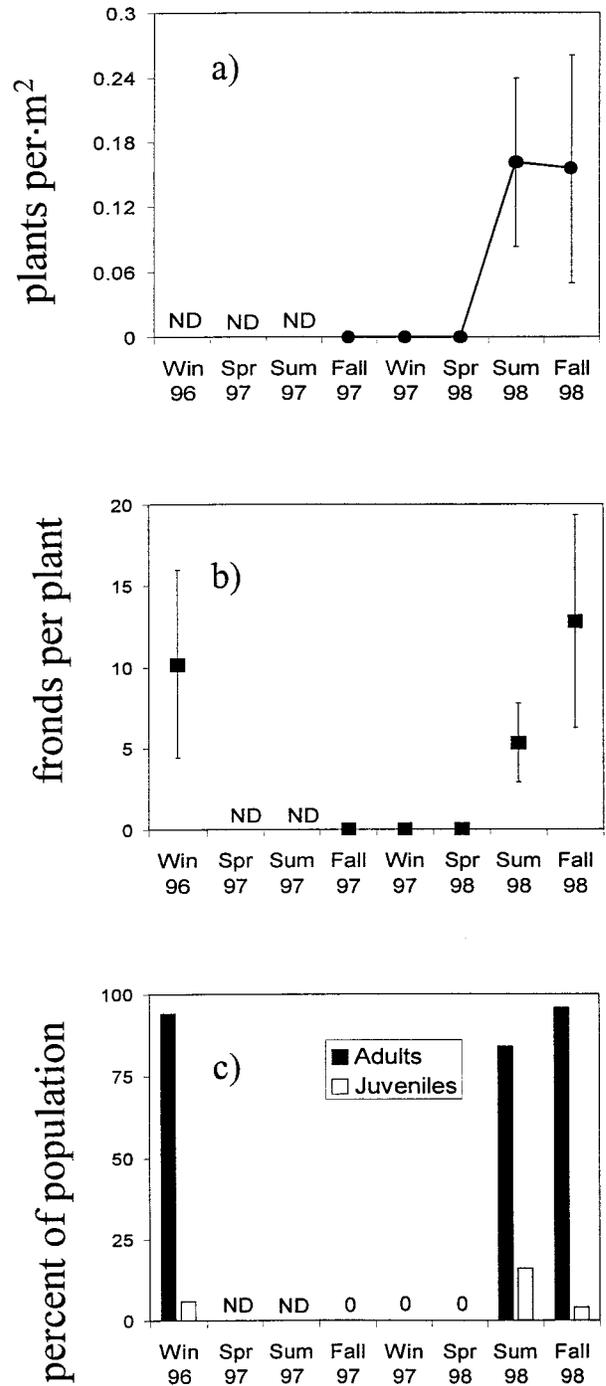


FIG. 3. (a) *Macrocystis pyrifera* plant density, (b) fronds per plant, and (c) percentage of population as juveniles and adults at the Los Morros site, Bahía Tortugas, during ENSO 1997-1998. ND, no data; 0, no visible plants.

1997, plants were present in Bahía Tortugas and to the north between Bahía Tortugas and Punta Eugenia.

From fall 1997 to spring 1998, there were no macroscopic *M. pyrifera* plants found in Los Morros or in any of the alternative dive sites, nor were any *M. pyrifera* recruits observed. Only decaying holdfasts of

M. pyrifera were found. In spring 1998 there was extensive recruitment of *Eisenia* in Los Morros and a few sickly *M. pyrifera* blade-stage recruits were observed at Isla Natividad.

By summer 1998, plants were again present in Bahía Tortugas. Plant density at Los Morros was $0.161 \pm 0.078 \cdot \text{m}^{-2}$ ($n = 9$ transects) (Fig. 3a). Plants had 5.32 ± 2.41 fronds per plant ($n = 31$ plants) (Fig. 3b). All plants had 10 fronds or fewer; 16% of the plants were juveniles and 84% were already adults (Fig. 3c). Some plants had reached the surface in 10 m of water. Neither old holdfasts nor recruits of *M. pyrifera* were found. The Bahía Tortugas forests were distributed in many different areas, both inside and outside of the bay. In general, plants appeared in about the same areas where they had been prior to their disappearance.

In fall 1998, plant density was about the same as in summer 1998 (Fig. 3a). However, the number of fronds per plant increased, reaching about the same as during the pre-ENSO winter 1996 (Fig. 3b). Plant density in Los Morros was $0.155 \pm 0.105 \cdot \text{m}^{-2}$ ($n = 19$ transects) (Fig. 3a). A maximum of 25 fronds per plant was found. Plants had 12.79 ± 6.55 fronds per plant ($n = 24$ plants) (Fig. 3b); only 4% of the plants were juveniles and 96% were adults (Fig. 3c). No *M. pyrifera* recruits were found.

Distributional limits. *M. pyrifera* plants were documented by land and by free diving in Punta San Roque in January 1997. In April 1997, the plants were still present in Punta San Roque and Bahía Tortugas, as documented by SCUBA. In October 1997, the southern limit of *M. pyrifera* plants was somewhere north of Punta Eugenia (absence between Punta Eugenia and Bahía Tortugas and in Bahía Tortugas determined using SCUBA). In February 1998, plants were only found as far south as Punta San José by aerial survey (Dale Glantz, pers. commun.). In April 1998, plants were documented by SCUBA in the southern region, again as far south as Isla Natividad, yet were still absent from Bahía Tortugas, as determined by SCUBA. In July 1998, the southern limit had reached Bahía Tortugas, again determined by SCUBA.

DISCUSSION

The large-scale disappearance of *M. pyrifera* in Baja California and the local disappearance in Bahía Tortugas during ENSO 1997–1998 were not surprising. Warmer than normal temperatures prevailed along the Baja California coast. It is well established that prolonged high temperatures and the associated low nutrients adversely affect the plants (Zimmerman 1983; Zimmerman and Robertson 1985). Two strong hurricanes, Linda and Nora, passed through the region and caused adverse survival conditions for plants, as well. Yet, in spite of the widespread disappearance, plants were documented in Bahía Tortugas as early as 8 months after their disappearance. This rapid recruitment was most cer-

tainly not expected in light of the local absence of reproductive *M. pyrifera* plants in the southern region and the massive disappearance along the coast. From laboratory cultures, it is known that microscopic stages require between 1 and 3 months to grow to a visible blade-stage plant. Although recruits were never observed and only surface temperatures were available, whereas recruitment occurs on the bottom, it is possible to estimate when microscopic growth began. The temperature drop from March to July 1998, combined with the timing of blade stages reported in May 1998 (Bahía Tortugas Cooperative and S. Guzmán del Proó, pers. commun.) and the size of plants in July 1998, suggests that microscopic growth began around March or April 1998. Compared with other studies, the ability to grow from a microscopic stage that was not visible in April 1998 to plants with up to 10 fronds (some at least 10 m long) in July 1998 is relatively expeditious (North 1994, Tegner et al. 1996). This may be an adaptation of the southern limit plants to short growing seasons, and needs further investigation. Because all the plants appeared at the same time and had the same age structure and because new recruits were not observed after the recruitment event, it appears all the new plants in Los Morros came from the same cohort.

The disappearance in Bahía Tortugas during ENSO 1997–1998 is not unprecedented. During the 1982–1983 ENSO, most plants disappeared at the southern limit in Baja California following intense storms in fall 1982 when temperatures approached a $+2^\circ \text{C}$ anomaly. Temperatures remained high through spring 1984 (Fig. 2a,b), and plants did not return until fall 1984 (Hernández-Carmona 1988). Anomalies for the 1982–1984 ENSO were $+3^\circ \text{C}$ or more for approximately 1 month. Yet during the 1997–1998 ENSO, temperatures were $+3^\circ \text{C}$ or more for at least a 6-month period (Fig. 2b), suggesting a more intense event. However, post-ENSO temperatures during 1984 remained high (still 2°C warmer than average) more than 2 years after the event began, whereas during 1998, temperatures dropped below the 10-year average 8 months sooner than in 1984 (Fig. 2a, b). ENSO-induced mortality in *M. pyrifera* populations is a function of not only the extremity of the stress imposed on the plants, but also the duration of the stress. ENSO 1997–1998 resulted in more extreme temperatures in the southern area, but for a shorter period of time than ENSO 1982–1983. This possibly explains the recruitment in Bahía Tortugas in less than a year after the event, whereas in 1982–1984, it appeared to have taken at least 2 years (Hernández-Carmona 1988).

Recolonization after extinction is not always successful. It is not uncommon for *M. pyrifera* forests to disappear and never return (North 1959, 1971, 1994, North et al. 1986), as occurred during ENSO 1982–1983 in Punta San Hipólito (Hernández-Carmona 1988). Physical factors such as temperature

and light are important in regulating recruitment (Deysher and Dean 1986). However, competition may also play an important role during recolonization after a disturbance because kelp canopy absence would result in greater abundance of understory and turf competitors (Dayton et al. 1984, 1992; Reed and Foster 1984; Kennelly 1987; Graham 1997; Edwards 1998). Competition with *Eisenia* and coralline algae during recolonization may have contributed to the recession of the southern limit. Changes in hydrographic conditions, such as gradually increasing temperatures (McGowan et al. 1998), may also play an important role in defining the southern distribution. Sea surface temperatures are warmer now than two decades ago and the thermocline is deeper (Miller 1996). This may explain the southern limit recession over the past two decades, because forests of giant kelp depend on the upwelling of nutrient-rich water and the nutrient pulses associated with internal wave activity. A depressed thermocline would have reduced the frequency of both these occurrences (Zimmerman and Robertson 1985).

In *M. pyrifera*, recovery after disturbance is often explained by spore dispersal (Reed et al. 1988, 1997; Santelices 1990). However, recruitment from attached plants seems to only occur over short distances, restricted to within 5–40 m from spore-bearing adults (Anderson and North 1966; Dayton et al. 1984; Reed et al. 1988). Drifting adult plants or fertile fragments may also disperse spores; however, they often leave a defined line of recruitment (Dayton et al. 1984). Gamete fertilization experiments in the laboratory suggest a density of at least 1 spore·mm⁻² is necessary for successful recruitment (Reed 1990; Reed et al. 1991); therefore, the dilution of spores after extended periods of time in the ocean would, in all likelihood, limit long-distance recruitment. Although long-distance dispersal may still occur episodically (Reed et al. 1992), the possibility that this mechanism established the forests at their southern limit after the disturbance is unlikely for the following reasons: 1) the nearest spore source was greater than 100 km away; 2) recruitment appeared to be simultaneous at many sites and occurred rapidly after the cessation of the ENSO event; and 3) the recruits occurred in the same areas as before disappearance. Although the recolonization event did occur after intense storms, which have been suggested to aid in the dispersal of spores (Reed et al. 1988), long-distance dispersal still remains unlikely due to the great distance. The possibility that local spore-producing plants could have survived the extreme oceanographic conditions is also unlikely in light of the high temperatures, low nutrients, and dive survey results.

The mass disappearance of macroscopic plants encountered during this ENSO and the subsequent recolonization provide grounds for speculation as to the ecological role of microscopic stages and the po-

tential for their survival in a dormant state during unfavorable conditions. The microscopic life stages of *M. pyrifera* include several distinct processes, all of which are difficult to study in the field because of their small size (Deysher and Dean 1986; Schiel and Foster 1986). Laboratory work suggests that microscopic stages can tolerate more stressful conditions than macroscopic plants by surviving in a semi-dormant state, therefore providing a seed bank of sorts (tom Dieck 1993). This may be important in the ecological success and survival of the species, particularly in light of the increasing frequency of warm events over the past two decades (McGowan et al. 1998) and the apparent corresponding rise in frequency of local extinctions.

Microscopic dormant stages have been shown to play an important role in the recruitment of kelp. Atlantic *Laminaria* spp. gametophytes have a greater ability to withstand higher temperatures than sporophyte stages (Bolton and Luning 1982). *Laminaria saccharina*, near its southern limit, oversummers in the microscopic gametophyte stage, appearing as an annual plant (Lee and Brinkhuis 1986). It has been suggested that gametophytes of *M. pyrifera* can survive approximately 45 days in the wild (Deysher and Dean 1986). Yet, there is evidence of long-term survival (16 months) in dark conditions (tom Dieck 1993), suggesting that microscopic stages may subsist in nature under low light intensities in a semi-dormant state until conditions become favorable. The fact that minimal sediment scour is detrimental to microscopic stages (Devinnny and Vorse 1978) does not rule out the possibility of survival in areas protected from scour, such as in dark rock crevices (Dayton 1985).

It has been suggested recently that microscopic stages have little capacity for dormancy (Reed et al. 1997). Yet experiments suggesting this were not designed to evaluate whether microscopic stages have the capacity for dormancy, but rather, were designed to determine the contribution to recruitment of preexisting microscopic recruits versus new recruits within a healthy forest. It cannot be assumed that the bottom always contains microscopic stages, because of the many variables that can affect microscopic recruit survival. Also, it is possible that recruitment would occur from healthy settled spores and not from assumed dormant stages if new spores were available. The microscopic dormant stage recolonization strategy may provide a stabilizing storage tactic, as does a seed bank (Dayton 1985; Hoffman and Santelices 1991; Santelices et al. 1995), and may only repopulate areas outside the typical range of spore dispersal. The mechanism that recolonized Bahía Tortugas may or may not be a common occurrence in healthy kelp forests where healthy spores are readily available but may, nonetheless, be critical to the recovery of forests after large-scale disturbance or at their distributional limits.

The above observations suggest that an alternative

mechanism to spore dispersal caused the recolonization of *M. pyrifera* in Bahía Tortugas after the massive disappearance during ENSO 1997–1998. We suggest the hypothesis that a microscopic stage of *M. pyrifera* survived the stressful conditions during this ENSO, possibly in a dormant state, and caused the documented recruitment. This may or may not be a common occurrence but could be critical at the southern limit, where disappearance of plants is fairly common. This hypothesis would explain the rapid recruitment following the mass disappearance as documented herein. Laboratory experiments are presently underway to clarify which microscopic stage is most tolerant to ENSO-type stresses and the stress exposure times that can be tolerated; field experiments are also underway to determine if the plants have particular adaptations for recovery.

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