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Population dynamics of *Caulerpa sertularioides* (Chlorophyta: Bryopsidales) from Baja California, Mexico, during El Niño and La Niña years

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This study monitored the abundance of the tropical/subtropical seaweed *Caulerpa sertularioides* (Chlorophyta: Bryopsidales) from a sandy beach from Balandra Cove, on the south-eastern coast of the Baja California Peninsula, Mexico, between April 1998 and April 2000, including consecutive El Niño and La Niña events. El Niño conditions, indicated by relatively high seawater temperatures, were associated with a high population abundance (April–June 1998), whereas La Niña conditions, indicated by relatively low temperatures, were associated with the absence of *C. sertularioides* (April–June 1999 and April 2000). *Caulerpa sertularioides* was present during other times of the year during the study period, but never with the high abundance reached during El Niño conditions. Seaweeds of temperate affinity occurring in Baja California, such as *Gelidium robustum* (Rhodophyta: Gelidiales) and *Macrocystis pyrifera* (Phaeophyceae: Laminariales), decreased sharply in abundance during El Niño conditions. Therefore, the biogeographic affinity of seaweeds from Baja California might be helpful in predicting the effects of El Niño and La Niña on their abundance, with implications for resource management and for the prediction of the effects of long-term oceanographic changes on seaweed distribution.

INTRODUCTION

One of the main goals of population ecology is to predict the dynamics of populations under a varying set of environmental conditions. To achieve this, the first step is usually to measure population abundance for a given site periodically. If done over a relatively long period covering an extensive range of environmental variation, inferences about the main environmental factors that drive population dynamics can be made (Ricklefs & Miller, 1999). For seaweeds, studies of population dynamics have been done most frequently for periods of one year or less, and are limited predictors of the effects of interannual environmental variability on population abundance. This is particularly true for tropical and subtropical species; those from temperate areas have been relatively more investigated.

The clonal seaweed *Caulerpa sertularioides* (S.G. Gmelin) M. Howe (Chlorophyta: Bryopsidales) occurs in several tropical and subtropical coasts worldwide (Meinesz et al., 1981; Meñez & Calumpong, 1982; Lawson & John, 1987; Adams, 1994; González-González et al., 1996; Silva et al., 1996; Benzie et al., 1997; Larned, 1998; Littler & Littler, 2000; see photographs of thalli in Littler & Littler, 2000). Thus, population ecological studies for this species could serve as a basis for making ecological and evolutionary comparisons between geographically distant regions. However, its population ecology has rarely been studied, significantly less than for other species of the genus, such as *Caulerpa prolifera* (Forsskål) Lamouroux and *Caulerpa taxifolia* (Vahl) C. Agardh (Meinesz, 1979; Meinesz et al., 1995; Ceccherelli & Cinelli, 1998; Smith & Walters, 1999, and references therein). Then, it is important to undertake ecological research specifically on *C. sertularioides* populations. This paper analyses interannual differences of the population abundance of *C. sertularioides* from south-eastern Baja California, Mexico, where this species is frequent (Casas Valdez et al., 1997; Cruz-Ayala et al., 1998, 2001; Paul-Chávez & Riosmena-Rodríguez, 2000).

The studied period (spring 1998 to spring 2000) included consecutive El Niño and La Niña events in the tropical Pacific (Kousky & Bell, 2000; Climate Prediction Center's web site: www.cpc.ncep.noaa.gov). El Niño events are known to dramatically affect the population dynamics of other seaweeds from Baja California dramatically, such as the giant kelp, *Macrocystis pyrifera* (Linnaeus) C. Agardh (Phaeophyceae: Laminariales; Ladah et al., 1999), and the agarophyte *Gelidium robustum* (Gardner) Hollenberg & Abbott (Rhodophyta: Gelidiales; Hernández-Guerrero et al., 2000). This could also lead to the prediction of great interannual variability for the population dynamics of *C. sertularioides* undergoing an El Niño event. However, there are apparently no published studies on the population dynamics for any seaweed from the study area (described below) and research on the physiological response of local *C. sertularioides* to abiotic conditions is lacking. Thus, it was difficult to predict whether the studied population was going to differ between years and, if so, how much. This paper addresses this issue as a baseline (Underwood et al., 2000) for further ecological research on the comparative population ecology of *C. sertularioides* from different geographic regions.

MATERIALS AND METHODS

The population of *Caulerpa sertularioides* described here occurred in a sandy subtidal area from Balandra Cove (24°20′N 110°19′W), located within La Paz Bay, on the south-eastern coast of the Baja California Peninsula, Mexico (Figure 1). The identification to species level was done according to Littler & Littler (2000). The main oceanographic characteristics of the Gulf of California, in which La Paz Bay is located, are described in Álvarez-Borrego (1983). Balandra Cove is a pristine area, ~20 km away from the city of La Paz, which is the closest site of major human activities. The beach where this study was carried out (Figure 2) is of intermediate type in the dissipative–reflective continuum (Little, 2000; Mann, 2000). Wave action is generally very low and particle size is also small (mostly sand); subsurface sandbars occur in the cove and can be observed during the lowest tides. The studied population of *C. sertularioides* was close to the shoreline, located in an area of ~300 m^2 at ~0.3–0.6 m below the level of mean lower low water. The population was never seen directly exposed to the air, even during the lowest tides. Thalli of *C. sertularioides* were anchored to the sandy bottom mainly through several colourless rhizoids, which would also serve as structures for the uptake of nutrients, as shown for other species of *Caulerpa* (Williams, 1984; Chisholm et al., 1996). In the study area, there were no other benthic sessile organisms similar in size to *C. sertularioides*. In neighbouring areas, the substrate was a mixture of sand, small rocks, and sea shells, which apparently allowed for the existence of a more diverse benthic community. In rocky subtidal areas of Balandra Cove, *C. sertularioides* occurred directly attached to the rocks.

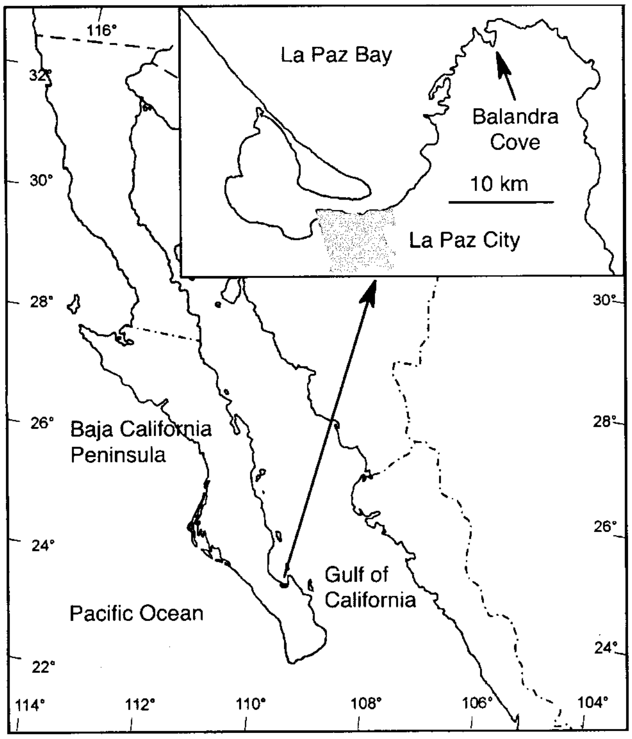

Figure 1. Maps showing the location of Balandra Cove.

Figure 2. View of the studied beach. *, place where *Caulerpa* was found, covering a band parallel to the shore line. Photograph taken 11 April 2000 by Ricardo Scrosati.

For the study site, the population abundance of *C. sertularioides* was described by stand wet biomass and by frond density, which were determined at approximately bimonthly intervals between the spring seasons of 1998 and 2000. Sampling dates were 29 April 1998, 29 June 1998, 27 August 1998, 29 October 1998, 27 December 1998, 28 February 1999, 27 April 1999, 30 June 1999, 26 August 1999, 31 October 1999, 29 December 1999, 28 February 2000 and 11 April 2000. On each sampling date, all of the algal material occurring in ten 400-cm^2 areas, randomly located across the bed, was collected and taken to the laboratory in plastic bags inside a cooler. In the laboratory, thalli were cleaned from other benthic materials (sand, pieces of sea shells, and worm tubes), blotted dry, and weighed to the nearest milligram. All of the fronds present in each quadrat were counted. Monthly means of stand biomass and frond density were compared using a one-way Kruskal–Wallis analysis of variance (Howell, 1992) for each variable using SYSTAT 5.2.1 for Macintosh (Wilkinson et al., 1992).

Seawater temperature is one of the main factors that affect seaweed growth rates (Graham & Wilcox, 2000). Sea surface temperature (SST) was determined at the study site on each sampling date (except for the first one, because SST was determined on 12 April 1998) with a mercury thermometer to the nearest 1°C. Point SST data may not represent well monthly SST trends, as day-to-day variations are not recorded. Therefore, a second set of SST data was used, which included monthly SST means determined for a quadrant between 24°N and 25°N and between 110°W and 111°W between January 1982 and April 2000. This set was gathered from Lluch-Cota et al. (2000). The long-term nature of this second data set allowed comparison of monthly SST means for the study period with monthly SST means for the 1982–1997 period (16 y) using SST anomalies. The importance of the first SST data set was to describe on-site SST conditions at the time of sampling, whereas the second SST data set allowed estimation of possible regional cumulative

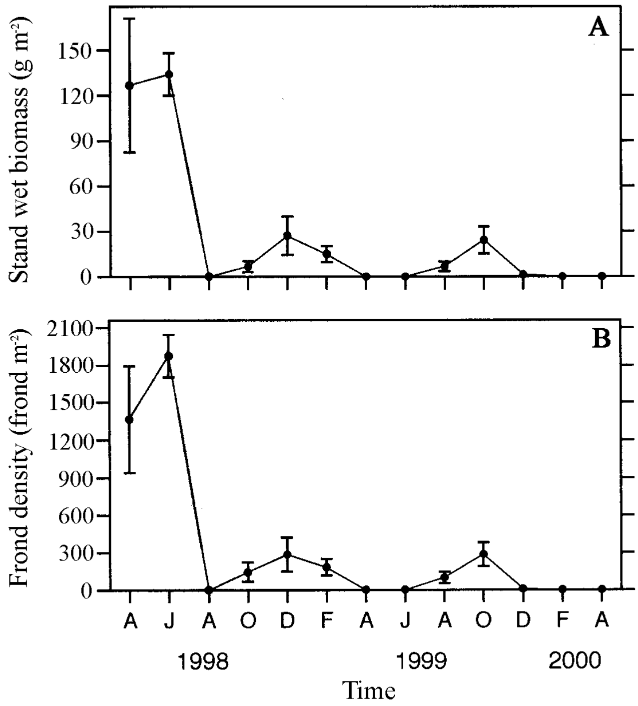

Figure 3. Temporal variation of: (A) stand wet biomass (mean ±SE; N=10); and (B) frond density (mean ±SE; N=10) of *Caulerpa sertularioides* from Balandra Cove.

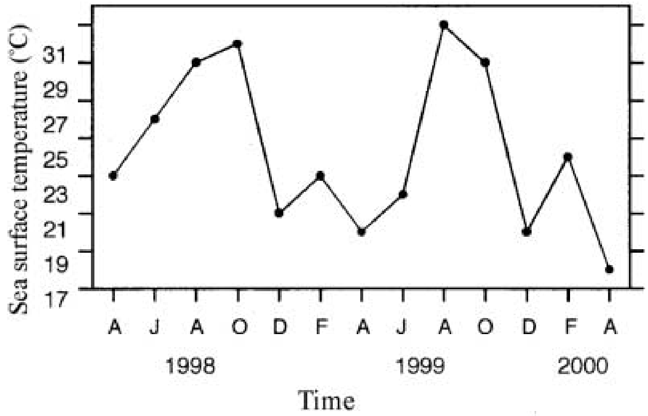

Figure 4. Temporal variation of sea surface temperature at Balandra Cove.

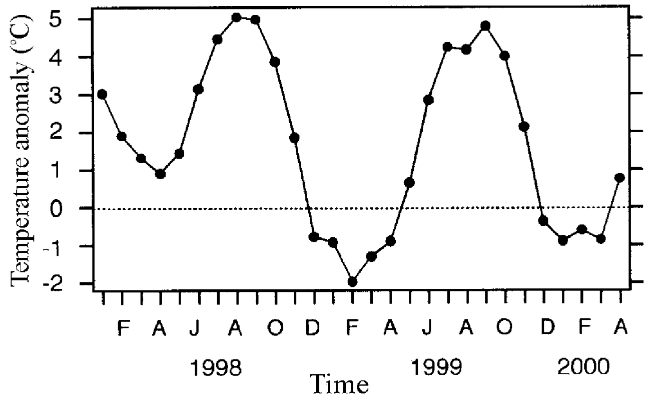

Figure 5. Temporal variation of the anomalies of mean monthly sea surface temperature close to Balandra Cove (see text for details).

effects of SST on abundance a few months before a specific abundance was recorded.

RESULTS

Caulerpa sertularioides was not always present at the subtidal sandy area studied at Balandra Cove between April 1998 and April 2000. Stand wet biomass varied between monthly means of 0 ±0 g m^{-2} (mean ±SE, N=10) and of 134 ±14 g m^{-2} (Figure 3A). A Kruskal–Wallis analysis of variance indicated that there were significant differences between months (H=84.2, P<0.001). Between August 1998 and April 2000, stand biomass fluctuated following seasonal trends that were relatively common for both years. In April and June 1998, however, stand biomass was unusually high, whereas there was no biomass recorded for those months in 1999 and 2000.

Frond density varied between monthly means of 0 ±0 fronds m^{-2} and of 1875 ±172 fronds m^{-2} during the study period (Figure 3B). A Kruskal–Wallis analysis of variance indicated that there were significant differences between months (H=81.6, P<0.001). The temporal fluctuation of frond density during the study period was basically the same as that described for stand biomass. A final observation carried out at the study site in August 2000 indicated that *C. sertularioides* had recolonized the area after its absence recorded at the last formal sampling date (April 2000). Its abundance, however, was relatively low, and did not reach the high levels shown in April and June 1998. During the entire study period, the highest frond length recorded was 5.4 cm (October 1999), although high values were infrequent.

Sea surface temperature recorded at the study site varied between 18 and 31°C during the study period, with high values in summer and autumn and low values in winter and spring (Figure 4). As with stand biomass and frond density, the fluctuations of SST also followed similar seasonal trends between August 1998 and April 2000. In April and June 1998, however, SST was between 3 and 5°C higher than for the same months of 1999 and of 2000. The regional SST anomalies fluctuated following similar seasonal trends between May 1998 and April 2000 (Figure 5). However, the anomaly for the first four months of 1998 was on average ~3 and 2°C higher than for the same period of 1999 and of 2000, respectively.

DISCUSSION

Temperature is one of the most important abiotic factors that affect seaweed growth rates (Graham & Wilcox, 2000). The unusually high abundance of *Caulerpa sertularioides* noted in April and June 1998, relative to the same months of 1999 and of 2000, might have resulted from the interannual differences in SST observed during or shortly before those months. The relatively high SST values observed at the beginning of 1998 represented the last part of the 1997–1998 El Niño event, while the relatively low SST values registered for the same period of 1999 and of 2000 reflected the La Niña events described for the tropical Pacific for those periods (Kousky & Bell, 2000; Climate Prediction Center's web site: www.cpc.ncep.noaa.gov). A meaningful statistical analysis of the correlation between abundance and SST during spring and early summer of 1998, 1999, and 2000 was not possible due to the low number of sampling dates (five) when abundance was measured.

A number of studies have measured growth rates and photosynthetic parameters for *C. sertularioides* from other parts of the world (Mishra & Kefford, 1969; Williams et al., 1985a,b; Gacia et al., 1996; Larned, 1998). However, they have not specifically investigated how growth rates vary with changes in seawater temperature. Therefore, their information could not be used to predict interannual population differences for Balandra Cove. Even if those studies had included research on the relationship between growth rates and seawater temperature, direct extrapolations to Balandra Cove would have been risky given the phenotypic and environmental differences that are normally expected between geographically distant sites (Foster, 1990). Studies on the effects of seawater temperature on the rate of photosynthesis and growth have been carried out for other species of *Caulerpa* (O'Neal & Prince, 1988; Terrados & Ros, 1992; Komatsu et al., 1997; Chisholm et al., 2000), but their potential relevance for predicting the interannual variability of *C. sertularioides* from Balandra Cove was even more limited, given the differences at the species level in addition to those at the site level.

To establish that seawater temperature was the main factor that determined the interannual differences in abundance of *C. sertularioides* from Balandra Cove, additional information would be required. For example, nutrient concentration, irradiance, water motion, and biotic interactions also affect seaweed growth rates (Graham & Wilcox, 2000). However, data on these variables are not available for Balandra Cove for the study period. Field observations suggest that irradiance during spring and early summer did not vary much between 1998, 1999, and 2000, as weather was usually sunny during these periods. Water motion was generally low during sampling, but there was evidence of occasional sand movement between sampling dates (indicated by the changing amount of sand covering coastal rocks), which could have affected the abundance of *C. sertularioides*. However, sand movement would not explain the great differences in abundance between April 1998 and April 1999. In April 1999, *C. sertularioides* was also absent from a nearby area with rocky substrate, where the species had been observed the year before, but sand never covered this rocky area during the study period, so this factor would not explain the interannual differences in abundance observed at the study site. Competition with other macroscopic organisms should not have affected *C. sertularioides* abundance, as this was the only relatively large benthic species occurring on the sand during the periods for which the interannual differences were observed. Diatoms and filamentous blue-green algae (possible competitors for light and nutrients) occurred as epiphytes on fronds of *C. sertularioides*, but they were only abundant in December 1998.

It is important to note that when *C. sertularioides* became absent at the study site in August 1998, it still occurred in nearby areas where the substratum was more firm. These areas may have served as a source of thallus fragments which may have recolonized the study site through clonal growth after being brought by water movement. This mechanism of recolonization has been observed for other species of *Caulerpa* (Ceccherelli & Cinelli, 1999; Smith & Walters, 1999; Ceccherelli & Piazzi, 2001). However, when *C. sertularioides* became absent at the study site in April 1999, it was not found even in those nearby areas. Studies of sexual reproduction, rarely done for *C. sertularioides* (Goldstein & Morrall, 1970; Clifton, 1997), and of dispersal of clonal fragments between sites will be necessary to understand patterns of recovery of local populations.

The only other papers that described the seasonality of *C. sertularioides* from south-eastern Baja California (Casas Valdez et al., 1997; Cruz-Ayala et al., 1998, 2001) were based on seasonal surveys done in La Paz Bay in 1993. However, those papers described such annual cycle in conflicting ways, which prevents any useful comparison with this study.

El Niño seems to affect the abundance of seaweeds from Baja California differently, depending on their biogeographic affinity. For example, *Macrocystis pyrifera*, a kelp with a temperate affinity, has its southern distribution limit for the Pacific coast of North America in central Baja California and the 1997–1998 El Niño event resulted in the complete disappearance of macroscopic thalli from such area (Ladah et al., 1999). The red seaweed *Gelidium robustum* also has a temperate affinity and its southern limit of distribution for Pacific North America is also Baja California (Stewart, 1976). Similarly, populations from central Baja California were negatively affected by the 1982–1984 El Niño event (Hernández-Guerrero et al., 2000). On the contrary, *C. sertularioides* is primarily of tropical affinity and Baja California represents its northern distribution limit for the Pacific coast of America (Abbott & Hollenberg, 1976; González-González et al., 1996; Aguilar-Rosas et al., 2000). The last part of the 1997–1998 El Niño event was associated with an unusually high population abundance of this species at Balandra Cove. Therefore, the biogeographic affinity of seaweeds might be used to predict the effects of El Niño (and possibly of La Niña) events on their abundance in Baja California, although, obviously, this would have to be investigated for more species. This type of information, together with the knowledge of temperature effects on the intensity of biotic interactions (Sagarin et al., 1999; Leonard, 2000), could be ultimately useful in predicting latitudinal changes of the abundance of seaweed species as affected by long-term changes of seawater temperature.

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REFERENCES

Abbott, I.A. & Hollenberg, G.J., 1976. *Marine algae of California*. Stanford: Stanford University Press.

Adams, N.M., 1994. *Seaweeds of New Zealand*. Christchurch: Canterbury University Press.

Aguilar-Rosas, L.E., Aguilar-Rosas, R., Mendoza-González, A.C. & Mateo-Cid, L., 2000. Marine algae from the northeast coast of Baja California, Mexico. *Botanica Marina*, **43**, 127–139.

Álvarez-Borrego, S., 1983. Gulf of California. In *Ecosystems of the world. 26. Estuaries and enclosed seas* (ed. B.H. Ketchum), pp. 427–449. Amsterdam: Elsevier.

Benzie, J.A.H., Price, I.R. & Ballment, E., 1997. Population genetics and taxonomy of *Caulerpa* (Chlorophyta) from the Great Barrier Reef, Australia. *Journal of Phycology*, **33**, 491–504.

Casas Valdez, M.M., Cruz Ayala, M.B. & López, G.E., 1997. Algas marinas bentónicas más abundantes en la bahía de La Paz, B.C.S. In *La bahía de La Paz, investigación y conservación* (ed. J. Urbán Ramírez and M. Ramírez Rodríguez), pp. 83–92. La Paz: UABCS—CICIMAR—Scripps.

Ceccherelli, G. & Cinelli, F., 1998. Habitat effect on spatio-temporal variability in size and density of the introduced alga *Caulerpa taxifolia*. *Marine Ecology Progress Series*, **163**, 289–294.

Ceccherelli, G. & Cinelli, F., 1999. The role of vegetative fragmentation in dispersal of the invasive alga *Caulerpa taxifolia* in the Mediterranean. *Marine Ecology Progress Series*, **182**, 299–303.

Ceccherelli, G. & Piazzi, L., 2001. Dispersal of *Caulerpa racemosa* fragments in the Mediterranean: lack of detachment time effect on establishment. *Botanica Marina*, **44**, 209–213.

Chisholm, J.R.M., Dauga, C., Ageron, E., Grimont, P.A.D. & Jaubert, J.M., 1996. 'Roots' in mixotrophic algae. *Nature, London*, **381**, 382.

Chisholm, J.R.M., Marchioretti, M. & Jaubert, J.M., 2000. Effect of low water temperature on metabolism and growth of a subtropical strain of *Caulerpa taxifolia* (Chlorophyta). *Marine Ecology Progress Series*, **201**, 189–198.

Clifton, K.E., 1997. Mass spawning by green algae on coral reefs. *Science, New York*, **275**, 1116–1118.

Cruz-Ayala, M.B., Casas-Valdez, M.M. & Ortega-García, S., 1998. Temporal and spatial variation of frondose benthic seaweeds in La Paz Bay, B.C.S., Mexico. *Botanica Marina*, **41**, 191–198.

Cruz-Ayala, M.B., Núñez-López, R.A. & López, G.E., 2001. Seaweeds in the southern Gulf of California. *Botanica Marina*, **44**, 187–197.

Foster, M.S., 1990. Organization of macroalgal assemblages in the northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia*, **192**, 21–33.

Gacia, E., Littler, M.M. & Littler, D.S., 1996. The relationships between morphology and photosynthetic parameters within the polymorphic genus *Caulerpa*. *Journal of Experimental Marine Biology and Ecology*, **204**, 209–224.

Goldstein, M. & Morrall, S., 1970. Gametogenesis and fertilization in *Caulerpa*. *Annals of the New York Academy of Sciences*, **175**, 660–672.

González-González, J., Gold-Morgan, M., León-Tejera, H., Candelaria-Silva, C., León-Álvarez, D., Servière-Zaragoza, E. & Fragoso, D., 1996. Catálogo onomástico (nomenclátor) y bibliografía indexada de las algas bentónicas marinas de México. *Cuadernos del Instituto de Biología*, **29**, 1–422.

Graham, L.E. & Wilcox, L.W., 2000. *Algae*. Upper Saddle River: Prentice Hall.

Hernández-Guerrero, C.J., Casas-Valdez, M., Ortega-García, S. & Hernández-Vázquez, S., 2000. Effect of climatic variation on the relative abundance of the red alga *Gelidium robustum* in Baja California Sur, Mexico. *Journal of Applied Phycology*, **12**, 177–183.

Howell, D.C., 1992. *Statistical methods for psychology*, 3rd ed. Belmont: Duxbury Press.

Komatsu, T., Meinesz, A. & Buckles, D., 1997. Temperature and light responses of alga *Caulerpa taxifolia* introduced into the Mediterranean Sea. *Marine Ecology Progress Series*, **146**, 145–153.

Kousky, V.E. & Bell, G.D., 2000. Causes, predictions, and outcomes of El Niño 1997–1998. In *El Niño 1997–1998. The climate event of the century* (ed. S.A. Changnon), pp. 28–48. Oxford: Oxford University Press.

Ladah, L.B., Zertuche-González, J.A. & Hernández-Carmona, G., 1999. Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. *Journal of Phycology*, **35**, 1106–1112.

Larned, S.T., 1998. Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology*, **132**, 409–421.

Lawson, G.W. & John, D.M., 1987. *The marine algae and coastal environment of tropical West Africa*, 2nd ed. Berlin: Gebrüder Borntraeger.

Leonard, G.H., 2000. Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology*, **81**, 1015–1030.

Little, C., 2000. *The biology of soft shores and estuaries*. Oxford: Oxford University Press.

Littler, D.S. & Littler, M.M., 2000. *Caribbean reef plants*. Washington, DC: Offshore Graphics.

Lluch-Cota, S.E., Pacheco-Ayub, C.A., Bautista-Romero, J.J., Hernández-Vázquez, S. & Lluch-Cota, D.B., 2000. *Colección de información ambiental para el Pacífico mexicano*. CD-ROM available from the Centro de Investigaciones Biológicas del Noroeste (CIBNOR), AP 128, La Paz, 23000 Baja California Sur, Mexico.

Mann, K.H., 2000. *Ecology of coastal waters, with implications for management*. Malden: Blackwell Science.

Meinesz, A., 1979. Contribution à l'étude de *Caulerpa prolifera* (Forsskål) Lamoroux (Chlorophycée—Caulerpale). III. Biomasse et productivité primaire dans une station des côtes continentales françaises de la Mediterranée. *Botanica Marina*, **22**, 123–127.

Meinesz, A., Benichou, L., Blachier, J., Komatsu, T., Lemée, R., Molenaar, H. & Mari, X., 1995. Variations in the structure, morphology, and biomass of *Caulerpa taxifolia* in the Mediterranean Sea. *Botanica Marina*, **38**, 499–508.

Meinesz, A., Jaubert, J. & Denizot, M., 1981. Distribution of the algae belonging to the genus *Caulerpa* in French Polynesia (atoll of Takapoto and island of Moorea). *Proceedings of the Fourth International Coral Reef Symposium*, **2**, 431–437.

Meñez, E.G. & Calumpong, H.P., 1982. The genus *Caulerpa* from central Visayas, Philippines. *Smithsonian Contributions in Marine Science*, **17**, 1–21.

Mishra, A.K. & Kefford, N.P., 1969. Developmental studies on the coenocytic alga, *Caulerpa sertularioides*. *Journal of Phycology*, **5**, 103–109.

O'Neal, S.W. & Prince, J.S., 1988. Seasonal effects of light, temperature, nutrient concentration, and salinity on the physiology and growth of *Caulerpa paspaloides* (Chlorophyceae). *Marine Biology*, **97**, 17–24.

Paul-Chávez, L. & Riosmena-Rodríguez, R., 2000. Floristic and biogeographical trends in seaweed assemblages from a subtropical insular island complex in the Gulf of California. *Pacific Science*, **54**, 137–147.

Ricklefs, R.E. & Miller, G.L., 1999. *Ecology*, 4th ed. New York: W.H. Freeman & Co.

Sagarin, R.D., Barry, J.P., Gilman, S.E. & Baxter, C.H., 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, **69**, 465–490.

Silva, P.C., Basson, P.W. & Moe, R.L., 1996. *Catalogue of the benthic marine algae of the Indian Ocean*. Berkeley: University of California Press.

Smith, C.M. & Walters, L.J., 1999. Fragmentation as a strategy for *Caulerpa* species: fates of fragments and implications for management of an invasive weed. *P.S.Z.N.I. Marine Ecology*, **20**, 307–319.

Stewart, J.G., 1976. Family Gelidiaceae. In *Marine algae of California* (ed. I.A. Abbott and G.J. Hollenberg), pp. 340–352. Stanford: Stanford University Press.

Terrados, J. & Ros, J.D., 1992. The influence of temperature on seasonal variation of *Caulerpa prolifera* (Forsskål) Lamouroux photosynthesis and respiration. *Journal of Experimental Marine Biology and Ecology*, **162**, 199–212.

Underwood, A.J., Chapman, M.G. & Connell, S.D., 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*, **250**, 97–115.

Wilkinson, L., Hill, M.A. & Vang, E., 1992. *SYSTAT: statistics, version 5.2 edition*. Evanston: SYSTAT.

Williams, S.L., 1984. Uptake of sediment ammonium and translocation in a marine green macroalga *Caulerpa cupressoides*. *Limnology and Oceanography*, **29**, 374–379.

Williams, S.L., Breda, V.A., Anderson, T.W. & Nyden, B.B., 1985a. Growth and sediment disturbances of *Caulerpa* spp. (Chlorophyta) in a submarine canyon. *Marine Ecology Progress Series*, **21**, 275–281.

Williams, S.L., Gill, I.P. & Yarish, S.M., 1985b. Nitrogen cycling in backreef sediments (St Croix, US Virgin Islands). *Proceedings of the Fifth International Coral Reef Congress*, **3**, 389–394.

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