The discovery of kelp forests in deep-water habitats of tropical regions

Bernabé Santelices*

Department of Ecology and Center for Advanced Studies in Ecology and Biodiversity, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Tracing large-scale patterns of ecosystem distribution in land and marine environments is a fundamental task of field biology. The resulting patterns often have important implications in ecology, biogeography, and evolution as well as applied consequences in resource management and utilization. Classically, studies of marine ecosystems found at the sea edge, on hard substratum at levels down to 30–40 m, have distinguished three main ecological systems that replace each other at different latitudes. Coral reefs characterize lower latitudes and tropical waters (1), kelp forests replace coral reefs in most cold and temperate waters in both hemispheres (2, 3), whereas thickets of other large brown algae occupy the cold waters around Antarctica (4). Work by Graham *et al.* (5) included in a recent issue of PNAS changes dramatically this well accepted latitudinal pattern of marine ecosystem distribution. Using a diversity of data, Graham *et al.* first predicted the widespread occurrence of unexplored, submerged (30- to 200-m depth) kelp habitats in regions between the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S). Then, using deep-water SCUBA diving, they documented the presence of extensive kelp forests in eight localities within one of the predicted tropical regions. The emerging picture (Fig. 1*A*) is one of widespread occurrence of kelp forest formations in both surface and deep waters along most continents.

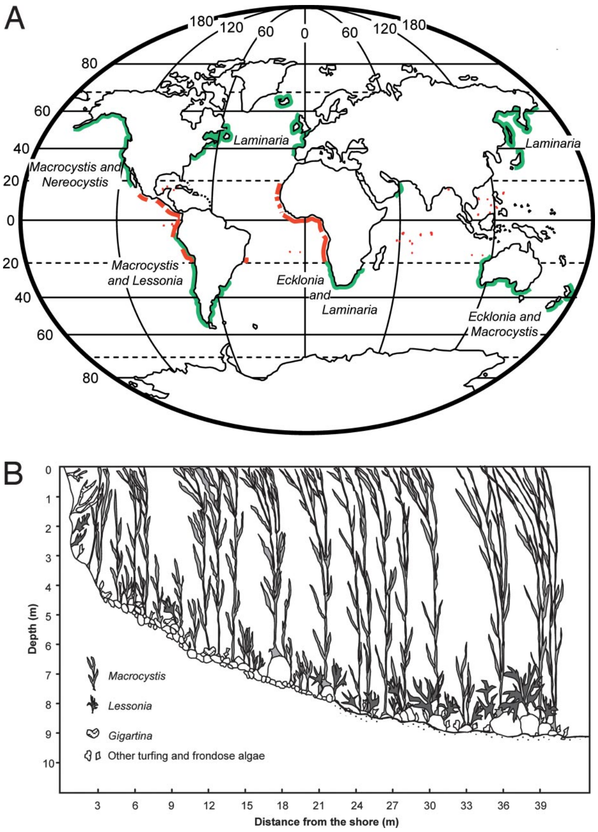

Fig. 1. World distribution and example of structure of kelp forests. (*A*) Geographic distribution of kelp forests in surface (green lines) and deep (red lines) waters. The figure was redrawn from refs. 2, 5, and 6. (*B*) Diagrammatic profile of a kelp forest in southern Chile with *Macrocystis* forming an upper canopy and *Lessonia* forming a second canopy. The illustration was prepared by Jorge Alvarado (Pontificia Universidad Católica de Chile).

The term "kelp" is presently used to designate large (up to 30 m long) seaweeds attached by holdfasts to the rocky bottom, with stems and fronds extending upward into the water column. Depending on the size of the dominant species, dense aggregations may result in kelp forests with floating canopies (Fig. 1*B*). Individuals of kelp species of smaller sizes may form canopies at intermediate and lower heights in the water column (6, 7), while low kelp fronds and prostrate kelp species may constitute additional vegetational layers. Similar to land forests, kelps provide vertical structure and habitat complexity to these subtidal forests. Also, they alter the physical environment by modifying wave strength, and therefore, influencing water flow and associated processes of sedimentation, recruitment, and production. Kelps also provide shelter, food, and nursery grounds for many pelagic and benthic organisms. Because the canopies reduce light, they also create understory conditions favorable for groups of species adapted to low light intensity, affecting competitive interactions among algae (8, 9). In addition, kelps are substratum for numerous sessile animals and algae and provide habitat for mobile organisms specialized to lie and feed directly on the kelp or its associated assemblages (6). Different species of kelp may differ in the quality or quantity of the food or habitat that they provide, but kelp forests in general are regarded as highly productive and highly diverse marine ecosystems, with hundreds of associated species. Quantifications performed in some of these forests in California indicate (7, 9) that up to 35% of 275 common taxa (flora and fauna) found in a given forest were associated with the kelp (*Macrocystis pyrifera* in this case). Approximately 25% of these organisms were obligate associates and >90% of the taxa were more common in forested than deforested areas.

Technically, true kelps belong to a single order (Laminariales) in the brown algae (traditionally known as *Phaeophyta*). The order includes 30–35 genera and 100–120 species (10). Although molecular data suggest a polyphyletic origin for the Laminariales (10, 11), several of the

---

Author contributions: B.S. wrote the paper.

The author declares no conflict of interest.

See companion article on page 16576 in issue 42 of volume 104.

*E-mail: bsantelices@bio.puc.cl.

www.pnas.org/cgi/doi/10.1073/pnas.0708963104

ecologically dominant genera, at different latitudes, exhibit somewhat similar ecophysiological responses. Kelps require a minimum annual penetration of sunlight to support photosynthesis (irradiance dose) above 50 $E\cdot m^{-2}$ (E, einstein, is 1 mol of photons) (12), and their growth can be severely limited by the availability of dissolved nitrogen, especially nitrate. In fact, surface kelp canopies may deteriorate in summer, when surface nitrate reaches levels below 1 μM (9). Nitrate concentrations in coastal waters are inversely related to temperature, with negligible amounts of available nitrates for temperatures above 15°C (12). Therefore, warmer water conditions will affect kelp growth through nutrient depletion more than through temperature itself. If adequate nutrient concentrations are available in the water, kelps can survive up to temperatures near 23°C.

Because of these ecophysiological patterns, warm water temperatures and low nutrient concentrations were classically regarded as factors preventing the development of kelp forests in surface waters of tropical and subtropical regions (13, 14), with exceptions explained by the occurrence of cool oceanic currents flowing toward the equator and extending into the Tropics [e.g., along the coast of Chile and southern Peru (15)] or by the presence of nutrient-rich waters from upwelling areas that could allow for the occurrence of kelps in tropical and subtropical regions (16, 17). In fact, when the kelps *Laminaria brasiliensis* and *Laminaria abyssalis* were first described from Macaé (18), 103 km away from Rio de Janeiro State, Brazil, they were collected in deep (70-m), temperate (15°C) waters, whereas the surface habitats with temperatures between 22°C and 23°C lacked kelps.

The above and similar cases (e.g., kelp species found in deep waters around Morocco, Qatar, and the Philippines) were regarded (19) as relicts of shallow-water populations that existed during the glacial periods when the oceanographic climate was cooler. However, this explanation did not convince Graham *et al*. (5). They thought that deep-water areas (down to 200 m) in upwelling zones of tropical regions might have adequate temperatures and enough nutrient supply to support kelp growth. Meanwhile, the surface water of tropical regions would allow for high water clarity in deep zones because tropical surface waters are frequently nutrient-poor and lack abundant planktonic biota that filter out incident radiation. Thus, the deep-water zones in tropical regions would be euphotic, with adequate temperature and nutrient supply for kelp growth.

To test this change of paradigm, Graham *et al*. (5) first built an ecophysiological model for kelps, incorporating light, temperature, and nutrient requirements. This model was coupled with a global surface-to-seafloor model of oceanographic conditions that considered active photosynthetic radiation, global bathymetry, surface-to-seafloor temperature profiles, and substrate availability. Results not only supported the proposed paradigm shift, they also revealed that kelp forests at deep water levels of tropical regions were widespread, abundant, and extensive, occupying an estimated total area of some 23,504 km^2 when all oceans were considered (5). In addition, they predicted that the kelp species found in deep-water habitats in tropical regions would not be relictual remains but rather examples of foundation species of modern kelp forests, occurring in habitable deep-water environments below uninhabitable surface tropical waters.

The study performed by Graham *et al.* (5) is an excellent example of the progress that has been made possible in macroecology and biogeography by the development of technical tools yielding large quantities of computerized data on distribution at local to global scales of abiotic and environmental variables, by the provision of comparable data on diversity, abundance, and distribution of taxonomic and functional groups of organisms, and by the utilization of analytical tools (global positioning systems, new statistics, dynamic models, and others) for compiling, interpreting, and analyzing relationships between the organisms and the environment. These advances allowed Graham *et al*. to characterize the niches or climate space of the kelps, hypothesize where still-undiscovered kelp forests may be found, and evaluate scenarios of how these patterns may shift under various directions and magnitudes of changes in different environmental variables.

Besides the methodological importance of this study, the findings are very relevant to marine biology, ecology, and related fields. Comparative studies of temperate kelp forests over the last 20 years have resulted in significant advances of our understanding in many biological fields including, among others, ecological organization and regulation of complex marine communities, factors originating and maintaining biodiversity in the sea, processes favoring coupling between the benthic and the pelagic environments and the important consequences of this coupling on larval dispersal and food supply, new demographic models and understanding of complex life-history strategies, physiological models, and new examples of ecophysiological regulation of several ecologically important members of these communities. Research in these forests has also been important to delineate new approaches to the study of scales, stability, and conservation. Now that kelp forests have been discovered in deep-water habitats of tropical regions, it is likely that a new series of studies will test the generality of the above principles in these newly discovered grounds. Similarly, it is anticipated that future comparative studies searching for new general patterns in kelp forests will have to be extended to include shallow as well as deep-water systems.

In addition, the discovery of kelp forests in deep-water habitats of tropical regions should have a profound and varied scientific impact, stimulating many new studies in oceanography, marine biology, and related fields. One can anticipate a whole series of studies whose purpose will be to characterize the new forests, the taxonomy and phylogeography of their members (including algae, invertebrates, and fishes), the climate of the new habitats, and their oceanographic and trophic relations with habitats and systems occurring at the more superficial waters above them. Kelp forests have been a source of fascination and inspiration since Darwin's (20) explorations of *Macrocystis* beds in southern Chile, and it seems highly probable that they will continue to be so for decades to come.

This work was supported by Fondo Nacional de Desarrollo Científico y Tecnológico, Grant 1060474, and Fondo de Investigación Avanzada en Areas Prioritarias Grant 1501-0001, Program 7.

1. Connell JH (1978) *Science* 199:1302–1310.
2. Mann KH (1973) *Science* 182:975–981.
3. North WJ (1971) *Beih Nova Hedwigia* 32:1–650.
4. Moe RL, Silva PC (1973) *Science* 196:1206–1208.
5. Graham MH, Kinlan BP, Druehl LD, Garske LE, Banks S (2007) *Proc Natl Acad Sci USA* 104:16576–16580.
6. Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) *Environ Conserv* 29:436–459.
7. Graham MH (2004) *Ecosystems* 7:341–357.
8. Santelices B, Ojeda PO (1984) *Mar Ecol Prog Ser* 14:175–183.
9. Graham MH, Vásquez JA, Buschmann AH (2007) *Oceanogr Mar Biol Annu Rev* 45:39–88.
10. Lane CE, Mayes C, Druehl LD, Saunders GW (2006) *J Phycol* 42:493–512.
11. De Reviers B, Rousseau F (1999) *Prog Phycol Res* 13:109–201.
12. Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) *Ecol Monogr* 69:219–250.
13. Bolton JJ, Anderson RJ (1987) *Mar Biol* 96:293–297.
14. Gerard VA (1997) *J Phycol* 33:800–810.
15. Santelices B (1991) in *Intertidal and Littoral Ecosystems, Ecosystems of the World*, eds Mathieson AC, Nienhuis PH (Elsevier, New York), Vol 24, pp 347–369.
16. Hatcher BG, Kirkman H, Word WF (1987) *Mar Biol* 95:63–73.
17. Santelices B, Bolton JJ, Meneses I (2008) in *Marine Macroecology*, eds Witman J, Kaustov R (Univ of Chicago Press, Chicago), in press.
18. Joly AB, Oliveira EC (1967) *Inst Pesq Marin* 4:1–7.
19. Lünning K (1960) *Seaweeds: Their Environment, Biogeography and Ecophysiology* (Wiley, New York).
20. Darwin C (1839) *The Voyage of the Beagle*, reprinted (1909) in Harvard Classics (Collier, New York), Vol 29.