

RESEARCH NOTE

Morphological plasticity and apparent loss of apical dominance following the natural loss of the main apex in *Pterocliadiella capillacea* (Rhodophyta, Gelidiales) fronds

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In an intertidal population of *Pterocliadiella capillacea* from southern Baja California, Mexico, fronds that lacked their main apex were bushier than intact fronds. A multivariate statistical analysis showed that the absence of the main apex was associated with higher frond biomass, a higher degree of branching, higher frond width, and longer main branches. The variation in frond form when the main apex is absent might be a response to the loss of apical dominance. The potential relevance of this morphological plasticity for the survival of thalli in the intertidal zone is discussed.

Pterocliadiella capillacea (S.G. Gmelin) Santelices & Hommersand (Rhodophyta, Gelidiales) occurs on several warm-temperate and tropical coasts around the world (Felicini & Perrone 1994; Santelices & Hommersand 1997). Its thallus is composed of branched horizontal or prostrate stolons, which maintain the thallus attachment to the substratum, and of several upright fronds, which are highly branched (Fig. 1). Each frond, together with the basal portion that keeps it attached to the substratum, can be considered as a ramet for this clonal seaweed (*sensu* de Kroon & van Groenendael 1997; Scrosati 2001). Fronds grow in length primarily through the activity of an apical cell (Dixon 1958; Hommersand & Fredericq 1996). During an ecological survey of a population of this species from southern Baja California, Mexico, it was noticed that the form of the fronds was different when the main apex was lacking because of physical damage: the absence of the main apex was generally associated with a higher development of branches. The objective of this note is to provide a quantitative comparison between damaged and intact fronds, in order to increase our understanding of the significance of the main apex for the morphological development of *P. capillacea* fronds.

The population of *P. capillacea* studied is located at Lobos Point (23°25'N, 110°14'W), on the Pacific coast of southern Baja California, Mexico. The highest tidal amplitude is about 2 m at this site, and *P. capillacea* is the dominant species between about 0.3 and 1.5 m above mean lower low water on vertical rocky walls exposed to direct wave action, although its upper limit may be higher in some places, owing to topography and wave action. Between March 1998 and March 1999, the highest stand biomass and frond density of *P. capillacea* occurred in spring and in summer, and the lowest val-

ues occurred in winter (Scrosati & Servièrre-Zaragoza 2000). Surface seawater temperature in this area varied between 18°C (winter) and 29°C (summer) (R. Scrosati, unpublished observations). A recent taxonomic analysis based on *rbcL* gene sequences compared samples of *P. capillacea* from Lobos Point with samples of *P. capillacea* from other sites of the world, which has confirmed the identity of the Lobos Point entity (D.W. Freshwater, personal communication).

On 1 and 18 January 1999, 50 fronds with intact main axes and 50 fronds with broken main axes were collected at random during low tide among fronds of medium and large size. The fronds were taken to the laboratory in plastic bags inside a cooler. Once in the laboratory and while still alive, the fronds were placed in seawater until they had rehydrated completely. The variables measured for each frond were wet biomass (to the nearest milligram), main axis length (to the nearest millimetre), maximum frond width (to the nearest millimetre), the number of orders of branching, and length of the longest first-order branch (to the nearest millimetre). Maximum frond width was considered to be the longest distance between the apices of opposite branches measured perpendicular to the frond axis. To measure maximum frond width, fronds were set flat on a table while keeping the natural angles between the axis and its branches. The first order of branching was the set of branches directly attached to the frond axis. Only a few of the collected fronds with broken axes showed visible signs of regeneration (*sensu* Felicini & Perrone 1994) from the broken end of the main axis.

To determine if this set of variables could distinguish between fronds with intact axes and those with broken axes, a Hotelling's T^2 test (Manly 1986; Morrison 1990) was done with SYSTAT 5.2.1 for Macintosh (Wilkinson *et al.* 1992). For this test to be valid, the two samples being compared are assumed to come from multivariate normal distributions with equal covariance matrices. The assumption of normality of

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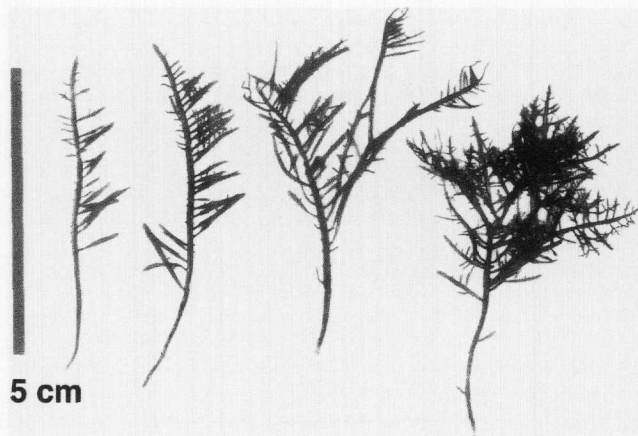


Fig. 1. Fronds with main apex (the two fronds to the left) and without it (the two fronds to the right), showing the different degree of branch development. Scale bar = 5 cm.

scores for each variable was assessed with normal probability plots and accepted, although some deviation from multivariate normality is not serious (Manly 1986). In relation to the second assumption, if sample sizes are equal and large ($n_1 = n_2 = 50$, for our case), possible unequal covariance matrices have no effect on the type I error rate or on the power function (Morrison 1990), so the assumption was not tested. Roy–Bose simultaneous confidence intervals (Morrison 1990) were calculated for each variable to determine which variables were significantly different between the two groups of fronds. The alternative – testing for significant differences with separate univariate *t*-tests for each variable – is inappropriate, because protection against the effects of possible positive correlations between variables would be lacking and because of the inflated familywise type I error rates that would result if each *t*-test were done at the same significance level as the T^2 test (Manly 1986; Morrison 1990).

Fronds with intact main axes were significantly different from fronds with broken main axes, based on frond wet biomass, main axis length, maximum frond width, the number of orders of branching, and the length of the longest first-order branch, all considered together (Hotelling's T^2 test, $F_{5,94} = 47.81$, $P < 0.001$). Roy–Bose simultaneous confidence intervals for each variable indicated significant differences between the two groups of fronds for all the variables, as no interval

included zero. For fronds with intact axes, axis length was generally higher, whereas wet biomass, maximum frond width, the number of orders of branching, and the length of the longest first-order branch were generally lower (Fig. 1). Summary statistics for the morphological variables are in Table 1.

The greater development of branches in fronds with broken main axes, compared to fronds with intact main axes, may have resulted from the loss of apical dominance. This phenomenon has mostly been studied in terrestrial plants and refers to the inhibitory effects that the growing apical bud imposes on the growth of lateral buds. If the shoot apex is removed, one or more of the lateral buds usually grows out as a result (Taiz & Zeiger 1998). Although seaweeds are morphologically simpler than terrestrial plants, apical dominance also occurs in some species (Buggeln 1981; Lobban & Harrison 1994). For *P. capillacea*, the occurrence of apical dominance has been suggested previously, based on qualitative morphological observations (Felicini & Perrone 1994); the present study provides the first quantitative morphological evidence that indicates its existence. An alternative explanation for the differences reported here could be that the higher branch development in fronds with broken main axes occurred simply because these fronds were older than fronds with intact axes. However, the Lobos Point population was sampled periodically for one year between 1998 and 1999 to study its dynamics (Scrosati & Servièrre-Zaragoza 2000) and fronds with intact main axes were never observed with the high morphological development shown by fronds with broken main axes.

The occurrence and causes of apical dominance have been investigated in greater depth for terrestrial plants than for seaweeds. For terrestrial plants, phytohormones or growth substances, such as auxins and cytokinins, play an important role in the development of lateral buds, although the physiological processes involved are not completely understood (Taiz & Zeiger 1998; Cline 2000; Wilson 2000). Auxins and cytokinins have been identified in some seaweeds, but their site of origin and whether they function as regulators of apical dominance are much less clear than for terrestrial plants; even the universality of phytohormones in algae is in doubt (Chamberlain *et al.* 1979; Bradley 1991; Evans & Trewavas 1991; Zhang *et al.* 1991; Jacobs 1993; Yokoya & Handro 1996; Ashen *et al.* 1999; Chapman 1999).

Understanding the variation of frond form is important beyond the study of apical dominance itself. For example, the

Table 1. Summary statistics for morphological variables for fronds with intact main axes (I) and with broken main axes (B); $n = 50$ for each case. Roy–Bose confidence limits apply to the difference between I and B means for each variable.

Variable	Axis condition	\bar{x}	s_x	Range	Roy–Bose confidence limits	<i>P</i>
Frond wet biomass (mg)	I	23.6	1.6	4–49	1.6–36.7	<0.005
	B	42.8	3.7	10–113		
Axis length (mm)	I	46.7	1.9	15–67	12.8–35.5	<0.005
	B	22.6	1.8	4–65		
Maximum frond width (mm)	I	10.7	0.7	4–27	0.1–9.7	<0.01
	B	15.6	0.9	3–31		
Orders of branching	I	2.0	0.1	1–3	0.3–1.5	<0.005
	B	2.9	0.1	2–5		
Length of the longest first-order branch (mm)	I	9.3	0.9	3–28	12.2–28.1	<0.005
	B	29.4	1.6	13–68		

morphological plasticity of fronds of *P. capillacea* might be ecologically relevant. In the intertidal zone, wave action, desiccation, irradiance, and temperature can all cause loss of tissues or death under extreme conditions: increasing the aggregation of individuals or of fronds generally mitigates the negative effects of these factors (Hay 1981; Padilla 1984; Taylor & Hay 1984; Denny *et al.* 1985; Santelices 1988; Wheeler 1988; Carrington 1990; Kain & Norton 1990; Norton 1991; Scrosati & DeWreede 1998). For example, the main apices of medium and large fronds of *P. capillacea* are lost after becoming bleached at Lobos Point, but bleaching does not occur in the understory, where crowding is higher than in the canopy. The stimulated development of branches in fronds with lost main apices might therefore constitute a mechanism by which thalli could increase crowding and achieve a higher protection against physical stress. This mechanism would not occur in populations of other clonal red seaweeds, such as *Mazzaella* G. De Toni (Gigartinales), whose fronds do not exhibit apical growth and which probably depends more on the production of new fronds to increase crowding. This is a research area where the interaction between morphologists and ecologists could be fruitful.

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REFERENCES

- ASHEN J.B., COHEN J.D. & GOFF L.J. 1999. GC-SIM-MS detection and quantification of free indole-3-acetic acid in bacterial galls on the marine alga *Prionitis lanceolata* (Rhodophyta). *Journal of Phycology* 35: 493–500.
- BADLEY P.M. 1991. Plant hormones do have a role in controlling growth and development of algae. *Journal of Phycology* 27: 317–321.
- BUGGELN R.G. 1981. Morphogenesis and growth regulators. In: *The biology of seaweeds* (Ed. by C.S. Lobban & M.J. Wynne), pp. 627–660. University of California Press, Berkeley.
- CARRINGTON E. 1990. Drag and dislodgment of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützinger. *Journal of Experimental Marine Biology and Ecology* 139: 185–200.
- CHAMBERLAIN A.H.L., GORHAM J., KANE D.F. & LEWEY S.A. 1979. Laboratory growth studies on *Sargassum muticum* (Yendo) Fensholt. II. Apical dominance. *Botanica Marina* 22: 11–19.
- CHAPMAN D.J. 1999. Auxins and algal galls: a new perspective on phytohormones in algae. *Journal of Phycology* 35: 445–446.
- CLINE M.G. 2000. Execution of the auxin replacement apical dominance experiment in temperate woody species. *American Journal of Botany* 87: 182–190.
- DE KROON H. & VAN GROENENDAEL J. 1997. *The ecology and evolution of clonal plants*. Backhuys, Leiden. 453 pp.
- DENNY M.W., DANIEL T.L. & KOEHL M.A.R. 1985. Mechanical limits to size in wave-swept organisms. *Ecological Monographs* 55: 69–102.
- DIXON P.S. 1958. The structure and development of the thallus in the British species of *Gelidium* and *Pterocladia*. *Annals of Botany* 22: 353–368.
- EVANS L.V. & TREWAVAS A.J. 1991. Is algal development controlled by plant growth substances? *Journal of Phycology* 27: 322–326.
- FELICINI G.P. & PERRONE C. 1994. *Pterocladia*. In: *Biology of economic algae* (Ed. by I. Akatsuka), pp. 283–344. SPB Academic Publishing, The Hague.
- HAY M.E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62: 739–750.
- HOMMERSAND M.H. & FREDERICQ S. 1996. Vegetative and reproductive development of *Pterocladia capillacea* (Gelidiales, Rhodophyta) from La Jolla, California. *Nova Hedwigia* 112: 147–160.
- JACOBS W.P. 1993. A search for some angiosperm hormones and their metabolites in *Caulerpa paspaloides* (Chlorophyta). *Journal of Phycology* 29: 595–600.
- KAIN J.M. & NORTON T.A. 1990. Marine ecology. In: *Biology of the red algae* (Ed. by K.M. Cole & R.G. Sheath), pp. 377–422. Cambridge University Press, Cambridge.
- LOBBAN C.S. & HARRISON P.J. 1994. *Seaweed ecology and physiology*. Cambridge University Press, Cambridge. 366 pp.
- MANLY B.F.J. 1986. *Multivariate statistical methods. A primer*. Chapman & Hall, London. 159 pp.
- MORRISON D.F. 1990. *Multivariate statistical methods*, ed. 3. McGraw-Hill, New York. 495 pp.
- NORTON T.A. 1991. Conflicting constraints on the form of intertidal algae. *British Phycological Journal* 26: 203–218.
- PADILLA D.K. 1984. The importance of form: differences in competitive ability, resistance to consumers, and environmental stress in an assemblage of coralline algae. *Journal of Experimental Marine Biology and Ecology* 79: 105–127.
- SANTELICES B. 1988. Synopsis of biological data on the seaweed genera *Gelidium* and *Pterocladia* (Rhodophyta). *FAO Fisheries Synopsis* 145: 1–55.
- SANTELICES B. & HOMMERSAND M. 1997. *Pterocladia*, a new genus in the Gelidiales (Gelidiales, Rhodophyta). *Phycologia* 36: 114–119.
- SCROSATI R. 2001. Demographic studies on genets of clonal red seaweeds: current limitations and proposed solutions using genetic markers from experimental populations. *Hidrobiológica* 11: in press.
- SCROSATI R. & DEWREDE R.E. 1998. The impact of frond crowding on frond bleaching in the clonal intertidal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinales) from British Columbia, Canada. *Journal of Phycology* 34: 228–232.
- SCROSATI R. & SERVIÈRE-ZARAGOZA E. 2000. Ramet dynamics for the clonal seaweed *Pterocladia capillacea* (Rhodophyta, Gelidiales): a comparison with *Chondrus crispus* and with *Mazzaella cornucopiae* (Gigartinales). *Journal of Phycology* 36: 1061–1068.
- TAIZ L. & ZEIGER E. 1998. *Plant physiology*, ed. 2. Sinauer, Sunderland. 792 pp.
- TAYLOR P.R. & HAY M.E. 1984. Functional morphology of intertidal seaweeds: adaptive significance of aggregate vs. solitary forms. *Marine Ecology Progress Series* 18: 295–302.
- WHEELER W.N. 1988. Algal productivity and hydrodynamics – a synthesis. *Progress in Phycological Research* 6: 23–58.
- WILKINSON L., HILL M.A. & VANG E. 1992. *SYSTAT: Statistics, Version 5.2 Edition*. SYSTAT, Evanston. 724 pp.
- WILSON B.F. 2000. Apical control of branch growth and angle in woody plants. *American Journal of Botany* 87: 601–607.
- YOKOYA N.S. & HANDRO W. 1996. Effects of auxins and cytokinins on tissue culture of *Grateloupia dichotoma* (Gigartinales, Rhodophyta). *Hydrobiologia* 326/327: 393–400.
- ZHANG W., CHAPMAN D.J., PHINNEY B.O., SPRAY C.R., YAMANE H. & TAKAHASHI N. 1991. Identification of cytokinins in *Sargassum muticum* (Phaeophyta) and *Porphyrta perforata* (Rhodophyta). *Journal of Phycology* 27: 87–91.

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