# Review of studies on biomass-density relationships (including self-thinning lines) in seaweeds: Main contributions and persisting misconceptions

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## SUMMARY

Ecological models relating biomass and density are relatively simple to calculate and offer information on, for example, the interactions among organisms and size constraints. Biomass-density relationships have mostly been studied for terrestrial plants, but recently they have also been increasingly investigated for seaweeds. Unfortunately, a number of misconceptions have limited the overall contribution of algal studies to biomass-density theory in general. Aiming to improve this situation, the present paper first summarizes the current knowledge on biomass-density theory, particularly focusing on the main concepts that, with varying degrees of validity, exist in the published literature: the self-thinning rule (in its boundary and dynamic interpretations), the interspecific biomass-density relationship, and the ultimate biomass-density line. Afterwards, the present paper provides a critical review of past biomass-density studies on seaweeds. The main contributions of studies on clonal and unitary species are discussed, while the misconceptions that persist to these days are identified in order to help future studies to be based on solid grounds.

Key words: clonal, interspecific biomass-density relationship, self-thinning rule, ultimate biomass-density line, unitary.

# INTRODUCTION

Ecological models are important tools used to understand natural patterns and to make predictions. Models are developed using a combination of field and/or laboratory observations and of mathematical and statistical work. Accuracy in data gathering is, therefore, essential, but so is the careful consideration of the existing knowledge in order to produce meaningful contributions. For plants and animals in general, the relationship between biomass and density has been studied and modelled for many years. Biomass and density are usually not very difficult to measure in field conditions, and the simple functions that relate

both variables (Weller 1987a, 1989; Enguist et al. 1998) give information on basic ecological properties such as competition intensity or size constraints. Although less frequently, biomass-density relationships have also been investigated for seaweeds, primarily during the last few decades. Algal studies have generally been based on those for vascular plants, because theory was traditionally developed first for vascular plants. However, the existing theory was not always considered adequately in algal studies, which has resulted in several misconceptions persisting in phycology. As a consequence, the contributions from this discipline to biomass-density theory have been relatively limited. In an effort to improve this situation, the present review summarizes the current knowledge on biomass-density relationships for vascular plants and then provides a critical analysis of past seaweed biomass-density studies, identifying their main contributions and clarifying the persisting misconceptions.

# SELF-THINNING LINES

Self-thinning is the process by which small individuals in even-aged, crowded plant stands progressively die as a result of competition with larger plants (mainly for light) during active growth (Weller 1987a). Self-thinning also occurs in animal populations (Guiñez & Castilla 2001; Rincón & Lobón-Cerviá 2002), but such studies are not the focus of the present review. On a bilogarithmic scale, stand biomass and plant density co-vary along a straight line with a negative slope during self-thinning (Weller 1987a). In the past, studies on this topic usually referred to the 'self-thinning rule' (STR) as a general principle, so it might be useful to explain first what the STR was. The original published literature on this matter (see Osawa & Sugita 1989, for a list of the original references) referred to a straight line with a negative slope in a bilogarithmic biomass-

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density plot above which no biomass-density combinations could exist. It was postulated that, once an evenaged stand with a given initial density approaches this boundary line during growth, the only way in which stand biomass can keep increasing is through the death of some plants, that is, through self-thinning (this concept is graphically shown in fig. 1 in Weller 1990). Therefore, this boundary line would never be surpassed. The mathematical formulation of this line is:

$$\log B = \log K + \beta \log N, \tag{1}$$

where *B* is stand dry biomass, *N* is plant density, and K and  $\beta$  are constants. Originally, it was thought that a slope ( $\beta$ ) of -0.5 (-1/2) applied to all of the species within the plant kingdom (the intercept value, log K, was less clear). Over the years, subsequent researchers switched to considering the self-thinning line as the line fitting biomass-density combinations during self-thinning (the 'dynamic thinning line', *sensu* Weller 1990; this concept is graphically shown also in fig. 1 in Weller 1990), rather than representing the boundary line that could not be surpassed. A slope of -0.5 was also thought to be universal among plants for this second concept of the STR.

Regardless of which of the two concepts was preferred to define the STR, a major development occurred when a re-analysis of an extensive data set on many plant species showed that the self-thinning slope actually varies among species and among stands of the same species (Weller 1987a). In fact, modelling studies showed that the self-thinning slope is systematically related to the geometry of space occupation by plants during growth (Weller 1987b). In the end, this determines the variety of 'species boundary lines' (sensu Weller 1990), which are species-specific boundaries, and 'dynamic thinning lines', which vary intraspecifically according to abiotic conditions. On theoretical grounds, the old prediction of a universal slope of -0.5 was based on the assumption that plants maintain the same shape (isometric growth) during self-thinning, which is now known to be unrealistic (Weller 1987b). A few years later, Sackville Hamilton et al. (1995) claimed that the evidence against a universal STR, in its boundary meaning, was still weak. However, their arguments were similar to those previously expressed by Osawa and Sugita (1989) on the same issue, and they had been logically refuted by Weller (1990). Therefore, as already indicated for seaweed studies (Scrosati 1997), there is little point in making more comparisons with a unique, universal STR that has been discarded as a quantitative rule. Studies on self-thinning are more productive when, for example, they investigate intraspecific changes in the self-thinning slope as affected by abiotic conditions (Morris 2003; Steen & Scrosati 2004) or when

they investigate the interspecific variation in boundary lines.

A side comment applies to the variables used to calculate self-thinning lines. In the past, most studies on vascular plants used mean plant biomass instead of stand biomass (the now-discarded universal selfthinning slope therefore becoming -1.5, or -3/2 (Yoda et al. 1963)). Ecological models based on mean plant biomass are not wrong as long as they are calculated properly. In fact, some modern allometric models in ecology are based on mean biomass (Enguist et al. 1998, 2000; Belgrano et al. 2002). Additionally, models based on mean biomass and on stand biomass can be easily interconverted mathematically. However, variable selection becomes particularly important when self-thinning lines are to be calculated. Using mean plant biomass might result in the wrong estimation of the true self-thinning slope and intercept because of the ratio nature of mean biomass (obtained by dividing stand biomass by plant density), which creates problems of interpretation in dynamic relationships (Weller 1987a; Scrosati 1997). Therefore, stand biomass should be preferred over mean biomass for the calculation of self-thinning lines.

Another relevant comment to make is that dynamic biomass-density relationships should be calculated (when in the linearized, log-log form) through a Model II regression technique (such as principal components analysis or reduced major axis), because both variables are random and subject to measurement error. The common technique of least squares linear regression should not be used for this purpose, because this Model I regression technique assumes that the *X* variable (*N*, in this case) should be fixed (Weller 1987a; Sokal & Rohlf 1995).

Recently, a way to determine the self-thinning slope separately for consecutive time intervals during the development of a plant stand has been presented (Roderick & Barnes 2004). However, the study by Roderick and Barnes considers some time intervals that are not consistent with self-thinning (again, defined broadly as a simultaneous biomass increase and density decrease). More importantly, different consecutive pairs of values might yield rather different slopes simply because of a combination of sampling error and low sample size (n = 2). Ensuring that only self-thinning data are considered (Weller 1987a) and using several consecutive data points simultaneously, as traditionally done, seems the most informative method to compare self-thinning dynamics among populations and species. It is worth noting that other recent developments in the study of self-thinning involve the inclusion of other variables (such as soil fertility) in the equation relating biomass and density (Bi 2004), but multivariate relationships are not the focus of the present review.

# INTERSPECIFIC BIOMASS-DENSITY RELATIONSHIP

For crowded stands of a wide variety of plants (from mosses to trees) plotted together, there is a linear, negative relationship between stand biomass and plant density on a bilogarithmic scale (this relationship is graphically shown in fig. 3 in Weller 1989). This interspecific biomass-density relationship (IBDR) is of a static nature because it describes biomass-density combinations across species within the plant kingdom. It must not be confused with (dynamic) self-thinning lines, which describe the temporal variation of biomassdensity combinations for single plant stands. Therefore, any reference to the IBDR as a 'static self-thinning rule' or 'law' is inappropriate (Weller 1989). Originally, the slope of the IBDR was also thought to be -0.5 (mathematically equivalent to -1.5 if based on mean plant biomass). Moreover, the IBDR and the universal selfthinning line were originally thought to be simply facets of the same law. However, a re-analysis of an extensive data set on many plant species (Weller 1989) showed empirically that the interspecific slope is -0.33 (the intercept being close to 4.0). The shallower (than -0.5) nature of the interspecific biomass-density slope is independently supported by a theoretical model based on trends in plant geometry across the plant kingdom (Weller 1989). More recent theoretical models based on morphological and physiological considerations specifically predict a slope of -1/3 for the IBDR (Enquist et al. 1998; Franco & Kelly 1998), in coincidence with Weller's (1989) empiric findings.

# ULTIMATE BIOMASS-DENSITY LINE

The data points used to calculate the IBDR form a band that extends above and below this function (Weller 1989). The ultimate biomass-density line (UBDL) is simply the upper boundary of this band, that is, the line parallel to the IBDR above which no biomassdensity combinations have been found for the plant kingdom (Weller 1989). Therefore, the UBDL qualitatively represents the concept that the old STR implied in its boundary interpretation, that is, a boundary line for all plants. The current mathematical expression of the UBDL is:

$$\log B = 4.87 - 0.33 \log N,$$
 (2)

with *B* and *N* defined as above. Its slope (-0.33) is the same as the IBDR's because the UBDL is the upper boundary of the interspecific biomass-density band. The intercept (4.87) of the UBDL, however, has no theoretical basis for the moment; it was simply calculated empirically by Scrosati (2000) using the large data set that Weller (1989) used to calculate the interspecific relationship. If future research finds biomass

values surpassing the boundary indicated by the current UBDL, its intercept will need to be adjusted accordingly.

# INITIAL BIOMASS-DENSITY STUDIES ON SEAWEEDS

Both dynamic and static biomass-density relationships have been measured for seaweeds. The following paragraphs offer a historical account and a critical review of such studies.

One of the first investigations on dynamic biomassdensity relationships for seaweeds was done by Black (1974), who detected self-thinning for the kelp Egregia menziesii (Turner) J. E. Areschoug during its growth season, although self-thinning lines were actually not calculated. Schiel and Choat (1980) investigated the compliance of stands of the kelp Ecklonia radiata (C. Agardh) J. Agardh and the fucoid species Sargas*sum sinclairii* J. D. Hooker & Harvey with the (dynamic) STR, which was considered valid at that time. Based on the data that Schiel and Choat (1980) presented in their figure 1, they concluded that these seaweeds do not conform to the STR. However, Schiel and Choat (1980) followed a static sampling program to produce their figure 1, that is, they measured biomass and density for different stands at single points in time (Cousens & Hutchings 1983; Schiel 1985), therefore preventing the adequate assessment of self-thinning to be done. Schiel and Choat (1980) also monitored the survivorship of *S. sinclairii* individuals throughout time in several artificially seeded plates. They did observe mortality of individuals over time, but they gave no data on biomass changes for those plates, so the occurrence of self-thinning cannot be assessed either. Schiel and Choat (1980) also measured survivorship for naturally occurring *E. radiata* stands after 1 year, but the observed temporal decreases in density were not compared explicitly with temporal changes in biomass, which prevents the occurrence of self-thinning to be assessed. Therefore, the study by Schiel and Choat (1980) remains inconclusive.

The next study that investigated the compliance of seaweed stands with the old STR, still considered valid at that time, was done by Cousens and Hutchings (1983). They considered the boundary interpretation of the STR and used mean plant (or frond) biomass instead of stand biomass, so the universal slope for this version of the STR was -1.5. Basically, Cousens and Hutchings (1983) found transgressions to the universal biomass-density boundary for four seaweed species (marginally for three cases and strongly for one), which shows what was realized years later, that is, that different plant species actually have different boundary lines (*sensu* Weller 1990). Cousens and Hutchings (1983), however, erroneously concluded that the old 'universal'

self-thinning line constrained the biomass of seaweed stands. In their study, Cousens and Hutchings (1983) also included data for biomass-density trajectories for *Chordaria flagelliformis* (O. F. Müller) C. Agardh. However, even though its biomass-density trajectory could be described by a (dynamic) negative relationship, therefore indicating the occurrence of self-thinning, they erroneously concluded that self-thinning was unlikely to have occurred for this species. The fact that the self-thinning line for *C. flagelliformis* (graphed, but not mathematically expressed in their study) was different than the old universal thinning line simply illustrates what was found years later, that is, that dynamic self-thinning lines (*sensu* Weller 1990) differ among plant species.

Another early study on dynamic biomass-density relationships in seaweeds was one on the brown species Leathesia difformis (Linnaeus) Areschoug (Chapman & Goudey 1983). As thalli grew in size during the growth season (resulting in the progressive increase of crowding levels), mortality rates also increased, suggesting that self-thinning might have occurred. However, figure 3 in Chapman and Goudey (1983) does not show any time interval in which stand biomass increased involving a decrease in thallus density, a condition that characterizes self-thinning (Weller 1987a). This apparent contradiction is difficult to explain at this point. Nonetheless, a manipulative experiment, done separately, showed that the experimental thinning of L. difformis stands resulted in a decrease in mortality rates, which is consistent with self-thinning expectations.

A few years later, Robertson (1987) calculated the dynamic biomass-density relationship for *Fucus spiralis* Linnaeus for a short period of 2 months mainly during the autumn. Biomass and density were negatively related throughout time. However, this negative relationship was not a result of self-thinning, because stand biomass actually decreased (mainly as a result of biomass losses in large size classes) and frond density increased (as a result of recruitment) during this period. Therefore, the study by Robertson cannot be analyzed in terms of self-thinning theory, as this would have required data on the period of active growth (Weller 1987a).

One year later, Cheshire and Hallam (1988) compared biomass-density data for the bull kelp *Durvillaea potatorum* (Labillardière) Areschoug with the STR in its boundary interpretation. However, they used data on wet biomass only, which prevents adequate comparisons to be done, as the old biomass-density boundary was defined based on dry biomass. Wet biomass is, by definition, higher than dry biomass for any organism, so the transgressions to the old biomass-density boundary reported for *D. potatorum* by Cheshire and Hallam (1988) are irrelevant in terms of biomassdensity theory. Basically, the above analysis of the initial studies on seaweed biomass-density relationships indicates that evidence of self-thinning occurring in seaweed populations was accumulating, but that important misconceptions also affected most studies substantially, therefore preventing such studies from contributing much to biomass-density theory.

# RECENT BIOMASS-DENSITY STUDIES ON UNITARY AND CLONAL SEAWEEDS

The period between 1987 and 1989 represents a major breakthrough for the understanding of plant biomass-density relationships in general, mainly because of the work of Weller (1987a,b, 1989), as discussed above. Minor clarifications were published a few years later (Weller 1990, 1991). Although published in the best ecological journals, these findings were not always considered properly in the seaweed biomass-density studies that followed, which is analyzed in detail below.

Before discussing the latest algal biomass-density studies, it might be useful to make the distinction between clonal and unitary (also called non-clonal or aclonal) seaweeds. A clonal seaweed is that in which its holdfast produces a number of fronds vegetatively, each frond having the potential capacity for autonomous life if it becomes physically isolated from the rest while remaining attached to the substrate by an original portion of holdfast. The basal part (holdfast tissue) of such an isolated frond has the potential capacity for generating new holdfast tissue horizontally, which subsequently may produce new fronds. Therefore, fronds of clonal seaweeds can be referred to as ramets, a term originally developed for shoots of clonal vascular plants (de Kroon & van Groenendael 1997). The entire thallus of clonal algae (including the holdfast and the associated fronds) that develops from one spore, zygote, or parthenogenetic gamete is referred to as the genet (Scrosati 2002). In some groups of clonal seaweeds (e.g. Gigartinales, Rhodophyta; Figs 1,2,4), neighboring genets may coalesce once their holdfasts make contact during growth (Santelices et al. 1999, 2003, 2004), which results in chimeric thalli (that is, thalli each composed of two or more original genotypes). Other groups of clonal seaweeds (e.g. Gelidiales, Rhodophyta; Fig. 3) do not exhibit coalescence among genets (Santelices et al. 1999). Unitary seaweeds (e.g. some species of the Fucales, Durvillaeales, and Laminariales, Phaeophyta; Figs 5,6) only produce one frond or axis from the holdfast, and therefore lack ramets. More examples of these groups are given in Collado-Vides (2002) and Santelices (2004). Following several differences in population dynamics between clonal and unitary vascular plants (de Kroon & van Groenendael 1997), seaweed biomass-density studies were progres-



**Figs 1–6.** Coalescing clonal (1,2,4) and non-coalescing clonal (3) seaweeds, and unitary (5,6) seaweeds. 1. *Mazzaella parksii* (Gigartinales, Rhodophyta) from British Columbia, Canada; note the numerous foliose fronds (ramets), which arise from crustose holdfasts. 2. *Sarcothalia crispata* (Gigartinales, Rhodophyta) from Patagonia, Argentina; several foliose fronds arise from a crustose holdfast. 3. *Pterocladiella capillacea* (Gelidiales, Rhodophyta) from Baja California, Mexico; the branched fronds arise from stoloniferous holdfasts. 4. *Chondrus crispus* (Gigartinales, Rhodophyta) from Nova Scotia, Canada; the foliose fronds arise from crustose holdfasts. 5. *Durvillaea antarctica* (Durvillaeales, Phaeophyta) from the Tenth Region, Chile; note the discoid holdfast and unique stipe. 6. *Laminaria saccharina* (Laminariales, Phaeophyta) from British Columbia, Canada; each holdfast is composed of several haptera and gives rise to only one stipe (the arrow indicates an individual that is simply growing attached to another individual's holdfast). Photographs by R. Scrosati.

sively being focused separately on clonal and unitary species.

The recent studies on dynamic biomass-density relationships for unitary seaweeds have generally found that self-thinning occurs at one point or another during population growth. These studies have been done on brown algae, such as Fucus gardneri P. C. Silva (Ang & DeWreede 1992), Himanthalia elongata (Linnaeus) S. F. Gray (Creed 1995), Phyllariopsis purpurascens (C. Agardh) E. C. Henry & G. R. South (Flores-Moya et al. 1997), Laminaria digitata (Hudson) J. V. Lamouroux and Fucus serratus Linnaeus (Creed et al. 1998), Sargassum muticum (Yendo) Fensholt (Arenas & Fernández 2000), and F. serratus and Fucus evanescens C. Agardh (Steen & Scrosati 2004). Examples of the intraspecific variability in the self-thinning slope (which gives information on the intensity of competition) are becoming available (Steen & Scrosati 2004). As mentioned above, however, algal biomass-density studies not always considered adequately the existing knowledge on biomass-density theory. For example, the original calculations for the kelp *P. purpurascens* (Flores-Moya et al. 1996) were based on mean thallus biomass (which biased the estimation of its true selfthinning slope) and were compared with the old STR in its dynamic interpretation (which had been discarded years before). However, a re-analysis based on updated theory provided an adequate estimation of self-thinning for this species (Flores-Moya et al. 1997). Creed (1995) and Creed et al. (1998) calculated self-thinning lines for H. elongata, L. digitata, and F. serratus properly, but they compared them with the old (dynamic) STR, curiously stating in their methodology that the support for the rule was given by Weller (1987a), who in fact had shown that the STR should be discarded. The most recent example of the persisting misconceptions in phycology is a study (Karez 2003) on three Fucus species. Self-thinning was claimed to have occurred in Fucus stands, but no negative biomass-density relationships are evident in Karez's (2003) figure 1. Instead, his figure 1 shows that biomass was uncorrelated to density for one species and positively correlated to density for the other two species. A number of interpretations were offered in the discussion to explain such an apparent contradiction. However, the data sets shown in that figure cannot be used to describe dynamic biomass-density relationships, as they are of a static nature (data correspond to replicate experimental units at the last sampling date only), so there is no evident contradiction to analyze. Static biomass-density data sets might look several ways and might or might not resemble the dynamic biomass-density relationships where they come from. By measuring biomass and density throughout time, the classic negative relationship between biomass and density that characterizes selfthinning can, indeed, be observed in crowded stands of *Fucus* (Steen & Scrosati 2004).

Regarding clonal seaweeds, among the first studies investigating their biomass-density relationships are those by Pybus (1977), on Chondrus crispus Stackhouse and Mastocarpus stellatus (Stackhouse) Guiry, and Martínez and Santelices (1992), on Mazzaella laminarioides (Bory de Saint-Vincent) Fredericg. Both studies measured frond density, not genet density, which has basically been the norm for studies on clonal seaweeds up to these days. Genets of clonal seaweeds are generally difficult, if not impossible, to identify in the field visually due to the high frond densities in mature stands, to the possible coalescence of neighboring genets (Santelices et al. 1999, 2003, 2004), and to the possible break-up of one original genet into two or more clonal fragments (sensu Angevine & Handel 1986). The study by Pybus (1977) presented static biomassdensity data, but for purposes other than to test biomass-density theory, and only included large fronds in the calculations. The study by Martínez and Santelices (1992) was done to test the validity of the old boundary STR, which had in fact been discarded years before. In any case, that study also concluded that M. laminarioides fronds do not undergo self-thinning, but this conclusion was based on a static biomassdensity data set (measurements corresponded to different stands at single points in time), which cannot be used to infer dynamic biomass-density relationships unequivocally (Weller 1989). Later studies on clonal seaweeds did measure frond density and stand biomass repeatedly for the same stands over time, therefore allowing for proper tests of self-thinning to be done. For Gelidium sesquipedale (Clemente) Thuret (Santos 1995), Mazzaella parksii (Setchell & N. L. Gardner) Hughey, P. C. Silva & Hommersand (Scrosati & DeWreede 1997), Pterocladiella capillacea (S. G. Gmelin) Santelices & Hommersand and C. crispus (Scrosati & Servière-Zaragoza 2000), stand biomass was found to increase during the growth season without involving self-thinning among fronds. Actually, frond density also increased during the growth season, as a result of their continuous vegetative production by established holdfasts. The dynamic biomass-density relationship for these clonal species was, therefore, found to have a positive slope.

The reasons for the observed lack of self-thinning among fronds of these clonal algae are unclear, but the published literature on clonal vascular plants (reviewed by de Kroon 1993 and Suzuki & Hutchings 1997) offers clues. Particularly in algal stands where fronds are mainly produced every year by perennating holdfasts (as opposed to by recruitment from spores), the combination of density-dependent production of new fronds and the seasonality of the environment might be important factors. For example, field experiments have shown that fronds of *M. parksii* from mature stands are mostly produced vegetatively by perennating holdfasts (Scrosati 1998), in a density-dependent manner (Scrosati & DeWreede 1997; see Viejo & Åberg 2001 for an example with another clonal seaweed). This regulation of frond production might result in stands not reaching critical biomass-density levels (beyond which selfthinning would occur) even when biomass accumulation peaks, just before external stresses (such as bleaching, Scrosati & DeWreede 1998, and herbivory, Heaven & Scrosati 2004) start to cause significant biomass losses (summer) that reduce crowding levels until the next growth season. Physiological integration among ramets (see Gonen et al. 1996, for evidence of intrathallus translocation in clonal red algae) was once thought to be another possible explanation for the lack of self-thinning among ramets observed in many clonal vascular plants, but a re-analysis of the available evidence later questioned its real importance (de Kroon 1993). Coalescence among thalli has also been mentioned as a possible explanation for the observed lack of self-thinning among fronds of (coalescing) clonal algae (Santelices 2004), but this seems unlikely. Coalescence might result in the avoidance of genet mortality when the crustose holdfasts of neighboring genets make contact during growth (e.g. Santelices et al. 2004), but this does not explain why the continuous production of new fronds by established holdfasts does not result in self-thinning among fronds as they grow in biomass, which progressively increases crowding levels during the growth season. On the other hand, the common pattern of biomass-density dynamics found for coalescing (M. parksii and C. crispus) and noncoalescing (G. sesquipedale and P. capillacea) clonal species (Santos 1995; Scrosati & DeWreede 1997; Scrosati & Servière-Zaragoza 2000) suggests that factors other than coalescence (such as the density-dependent production of new fronds and the seasonality of the environment) might be more important in explaining the lack of self-thinning among fronds observed for these clonal algae.

The coalescence of neighboring genets that make contact during growth might explain, again, a possible lack of self-thinning among genets, as they would avoid competitive exclusion. Non-coalescing clonal seaweeds might avoid self-thinning among genets by, for example, intermingling their stoloniferous holdfasts as neighboring genets make contact and continue to grow. The demography of genets of clonal algae growing at high densities has not been quantified as yet, however. Nonetheless, the observations done at the frond level (Santos 1995; Scrosati & DeWreede 1997; Scrosati & Servière-Zaragoza 2000) suggest that self-thinning probably does not occur among genets either. This might be so because studies on clonal vascular plants have found that, when self-thinning among genets occurs, which is expressed as a negative relationship between stand biomass and genet density over time, a negative biomass-density relationship also results at the shoot (ramet) level (Kays & Harper 1974; Lonsdale & Watkinson 1982; Makita 1996).

It is important to note, however, that self-thinning was reported for one species of clonal red alga, Asparagopsis armata Harvey (Flores-Moya et al. 1997). That study did not specify whether self-thinning occurred among fronds within genets, among genets, or at both levels of organization. In theory, it is possible that neighboring genets that produce relatively long fronds, have relatively small holdfasts, and do not experience coalescence (the Bonnemaisoniales, to which A. armata belongs, do not coalesce; Santelices et al. 1999) might undergo self-thinning in crowded conditions, therefore resembling the dynamics of a stand of unitary seaweeds. Although it is not always evident whether at the genet or ramet level, self-thinning is known to occur at the end of the growth season in some stands of clonal herbs from seasonal habitats (Hutchings 1979; Mook & van der Toorn 1982). Clonal plants with larger ramets that can grow for several years (such as woody species) may display self-thinning for longer periods after a number of years of continuous growth (de Kroon & Kalliola 1995; Peterson & Jones 1997). The study on *A. armata* by Flores-Moya *et al.* (1997) might indicate that self-thinning might occur for groups of clonal seaweeds other than the Gelidiaceae (including Gelidium and Pterocladiella) and Gigartinaceae (including Chondrus and Mazzaella). This points out the need of documenting biomass-density dynamics for groups of clonal seaweeds differing in clonal traits such as frond size, holdfast size, and coalescence potential. Westoby (1984) and de Kroon and Kalliola (1995) discuss possible biomass-density trajectories for clonal vascular plants and how they might end up selfthinning or not, depending on clonal attributes and initial density. Their analyses might be useful for the needed research on clonal seaweeds.

Studies aimed to compare seaweeds with the IBDR and the UBDL have been less frequent. Data for M. parksii were compared with the UBDL (Scrosati & DeWreede 1997), but erroneously considering the old boundary line with -1.5 as its slope (when based on mean biomass) and 5.0 as its intercept (White 1985). In addition, to build figure 3 (the figure used to make the comparison with the UBDL) in Scrosati and DeWreede (1997), frond density was calculated by dividing the number of fronds found in clumps by holdfast area. This resulted in an overestimation of frond density, because fronds (including their canopy) in discrete clumps actually cover a larger area than holdfast area. Also, wet biomass, instead of dry biomass, was considered for those calculations. These factors prevented a valid comparison with the UBDL to be

achieved. A similar problem of overestimation of frond density occurred in the study done by Martínez and Santelices (1992) on M. laminarioides thalli (E. Martínez, pers. comm. 2004), therefore rendering those data also invalid for comparisons. The problems mentioned above for *M. parksii* were solved when a different (and correctly measured) data set for this species was compared with the most current version of the UBDL (Scrosati 2000). This new study on M. parksii, which also included Pterocladiella capillacea data, showed that the highest (frond) density observed for these clonal species are among the highest density values found for autotrophic macro-organisms in general, from mosses to trees. This study also showed that the highest values of stand biomass for these algae are higher than the mean trend predicted by the IBDR for the appropriate densities. A number of hypotheses, based on physiological considerations and differences between marine and terrestrial habitats, were offered as possible explanations, aiming to stimulate future research. Finally, that study showed that even the highest biomass-density combinations for M. parksii and P. capillacea are also constrained by the UBDL (Scrosati 2000). Regarding other recent studies on this, Karez (2003) attempted to test whether Fucus stands surpass the biomass-density boundary known for vascular plants. However, Karez (2003) considered a 'conventional self-thinning line' with a slope of -0.5(based on stand biomass) and an intercept of 5.0 as a baseline against which his Fucus data were compared. In other words, he based his study on the old STR in its boundary interpretation, which had been discarded 16 years before. With this approach, Karez (2003) claimed that Fucus stands transgress the biomassdensity boundary known for terrestrial plants. However, such a conclusion is erroneous, because, by manually plotting the current UBDL (Scrosati 2000) in Karez's (2003) figure 1, it can be seen that all of his Fucus data points lay below this line. Therefore, Fucus stands are actually also constrained by the biomass-density boundary as currently known for plants.

## CONCLUDING REMARKS

In sum, studies on static and dynamic biomass-density relationships in seaweeds have been increasing in frequency during the last few decades. As a result, a number of contributions have been made by phycology to biomass-density theory in general. However, a number of misconceptions still persist in the phycological community, which have limited the value of several investigations. To produce significant advances along this research line in phycology, it will be essential to consider the current knowledge on biomass-density theory. Hopefully, this review will contribute towards such an objective.

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