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MINIREVIEW

Grow with the flow: Is phenotypic plasticity across hydrodynamic gradients common in seaweeds?

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Abstract

Seaweeds are widely assumed to be phenotypically plastic across hydrodynamic gradients, yet while many marine macroalgae exhibit intraspecific phenotypic variation that correlates with flow, researchers often fail to test whether such variation is due to plasticity or another mechanism, such as local adaptation. In this minireview, we considered mechanisms for sensing flow in seaweeds that could facilitate adaptive phenotypic plasticity across hydrodynamic gradients. We then reviewed the literature from 1900 to 2024 to see how often phenotypic variation and plasticity across hydrodynamic gradients had been observed and demonstrated in different groups of seaweeds. In the last 124 years, phenotypic variation and plasticity in response to flow have been well documented in brown algae but scarcely documented in red and green algae. This could suggest that brown algae are better able to sense and respond to flow than red and green algae, perhaps due to the intercalary meristem of many brown algae, including most kelps. However, this skewed distribution could also be the result of publication bias, as most studies involving flow have been conducted on brown algae. Only 30% of 141 papers specifically investigated if observations of phenotypic variation along hydrodynamic gradients were due to plasticity. To date, phenotypic plasticity in response to flow has been demonstrated in 20 brown algal species, five red algal species, and two green algal species. Thus, the assumption that phenotypic plasticity to flow is common across seaweeds is not particularly well supported by the literature. Mechanisms underlying plasticity to flow are poorly understood and remain a critical avenue for future research.

KEYWORDS
adaptation, algae, boundary layers, drag, growth, intraspecific variation, morphology

INTRODUCTION

Seaweeds are widely assumed to exhibit phenotypic plasticity across a range of environmental gradients (e.g., Blanchette et al., 2002; Díaz-Tapia et al., 2020; Duggins et al., 2003; Kalvas & Kautsky, 1993; Miller et al., 2011), including those of hydrodynamic forcing. Indeed, many marine macroalgae show conspicuous patterns of intraspecific phenotypic variability across gradients of water motion. Patterns commonly associated with increased wave or current exposure include the adoption of narrower, "streamlined" morphologies (Armstrong, 1989; Blanchette et al., 2002; Buck & Buchholz, 2005; Duggins et al., 2003; Koehl & Alberte, 1988), reduction in thallus size (e.g., Blanchette, 1997; Wolcott, 2007), fortification of support

Abbreviations: DBL, diffusion boundary layer; DIC, dissolved inorganic carbon.

tissues (Armstrong, 1987; Blanchette et al., 2002; Johnson & Koehl, 1994; Kitzes & Denny, 2005), and increasing attachment strength (Jackelman & Bolton, 1990; Kawamata, 2001). These patterns have been largely interpreted as adaptive phenomena facilitating increased endurance of seaweeds to increasing water motion through either drag reduction or increased resistance to breakage or detachment (Armstrong, 1987; Blanchette et al., 2002; Koehl & Alberte, 1988; Starko & Martone, 2016; Wolcott, 2007). However, such variation is not necessarily indicative of phenotypic plasticity.

Phenotypic plasticity refers to trait variation induced by the environment (Stearns, 1989). It may be adaptive or not (Ghalambor et al., 2007; Padilla & Adolph, 1996; Smith-Gill, 1983; Stearns, 1989), and it may result from either active facilitation by the organism (i.e., a developmental pathway triggered by an environmental cue that the organism senses and responds to physiologically; Harvell, 1984; Krueger & Dodson, 1981; Smith-Gill, 1983) or passive environmental impact (i.e., physical damage caused by external factors; Blanchette, 1997; Smith-Gill, 1983; Wolcott, 2007). Developmental plasticity resulting from active facilitation is most likely to be adaptive, as the evolution of a targeted response to the environment and a complex developmental pathway likely reflect some form of selection (Smith-Gill, 1983). Conversely, plasticity resulting from mechanical damage is presumably not under organismal control, instead reflecting a passive response to environmental factors. Although damage ultimately depends upon organismal morphology or biomechanical properties that might be products of selection (e.g., Demes et al., 2013; Stewart, 2006), mechanical failure of predetermined weak points does not require active physiological response to the physical environment, and such passive phenotypic changes cannot be assumed to be adaptive (Smith-Gill, 1983). Phenotypic plasticity should be contrasted with genetic differentiation, which refers to genetically fixed differences between individuals or populations that do not change with the environment (Alpert & Simms, 2002). When genetic differences have a positive effect on organismal fitness in a specific environment, it can be termed local adaptation (Kawecki & Ebert, 2004). Both adaptive plasticity and local adaptation are evolutionary strategies for dealing with environmental heterogeneity and can increase organismal fitness in certain conditions; however, the adoption of flexible versus fixed phenotypes is thought to be differentially favored depending on selective circumstances (Alpert & Simms, 2002; Ghalambor et al., 2007). Local adaptation, for instance, is hypothesized to be most advantageous when immediate environmental conditions are relatively stable, whereas plasticity is thought to be most advantageous when organisms are subject to greater temporal or spatial heterogeneity (Cook & Johnson, 1968). Ultimately, seaweeds that are phenotypically plastic to flow conditions, adjusting morphology or material properties in response to the hydrodynamic environment, may be better able to survive and grow when flow conditions change, produce offspring that can adjust and thrive in many different flow environments, and inhabit a wider range of current or wave exposures.

Although many studies have observed intraspecific variation in seaweeds across hydrodynamic gradients, most have not investigated whether variation is due to plasticity or genetic differentiation (Armstrong, 1989; Duggins et al., 2003; Jackelman & Bolton, 1990; Kitzes & Denny, 2005). So, can it really be assumed that plasticity induced by water motion is common in seaweeds? In this minireview, we first consider cue sensing and response mechanisms that might underlie phenotypic plasticity across hydrodynamic gradients in seaweeds. We then review the literature to quantify the frequency of published observations of intraspecific phenotypic variation and verified phenotypic plasticity across hydrodynamic gradients in different groups of seaweeds. Differentiating between phenotypic plasticity and genetic differentiation can lend insight into species ecology and raise new research questions. Because these two phenomena arise through unique selective conditions (Alpert & Simms, 2002; Ghalambor et al., 2007), determining whether phenotypic variation reflects one or the other can provide insight into trait evolution (e.g., Demes & Pruitt, 2019; Fowler-Walker et al., 2006; Roberson & Coyer, 2004). Moreover, differentiating between plastic and genetically fixed phenotypes is essential for taxonomic studies, as mistaking one for the other can lead to incorrect species designations (e.g., Belton et al., 2014; Demes et al., 2009; Garbary et al., 1978; Hind et al., 2014). A clear understanding of macroalgal responses to environmental variation can also help researchers predict how organisms may fare in a changing climate (e.g., Richter et al., 2012; Sheth & Angert, 2014; Supratya et al., 2020).

MECHANISMS FOR SENSING FLOW

Reliable environmental cues are critical for the evolution of adaptive plasticity (DeWitt, 1998; Ghalambor et al., 2007; Levins, 1963; Reed et al., 2010), and such cues are only valuable if organisms can sense them (Getty, 1996; Schlichting & Smith, 2002; Smith, 1990). Therefore, in order for seaweeds to evolve adaptive plasticity across hydrodynamic gradients, there would need to be (1) chemical or mechanical cues indicative of flow speed and (2) biological mechanisms for sensing and responding to those cues. Unfortunately, we know very little about the mechanisms underlying observed phenotypic plasticity across hydrodynamic gradients in seaweeds. Here, we consider several different environmental cues, detection mechanisms, and organismal responses that might facilitate phenotypic plasticity in seaweeds.

The only environmental cue that has been explicitly demonstrated to mediate plasticity across flow gradients in seaweeds is mechanical loading imposed by drag. This phenomenon was first observed in the kelp *Saccharina latissima* by Gerard (1987), who observed that longitudinal tension continuously applied to kelp blades caused them to grow narrower and longer. These morphological changes were consistent with those observed in several kelp species following field transplants between areas of differing wave exposure (e.g., Gerard & Mann, 1979; Norton, 1969; Pace, 1972; Sundene, 1964), so researchers widely concluded that drag was likely the cue being sensed by kelps to initiate flow-induced plasticity. Associations between mechanical forces and plasticity have since been demonstrated in the kelp *Nereocystis luetkeana* (Coleman & Martone, 2020; Koehl et al., 2008; Koehl & Silk, 2021; Supratya et al., 2020).

One way for drag-induced mechanical loading to be an effective indicator of flow speed would be for thalli to have tissue distal to meristems that could act as a drag element tugging on actively dividing cells (Figure 1a). This condition would be best met in seaweed thalli exhibiting intercalary or diffuse growth. Coleman and Martone (2020) observed that *Nereocystis luetkeana* thalli would only adjust blade morphology when tension was applied directly to intercalary meristems at the base of blades, suggesting that cue sensing and plasticity were spatially confined to meristematic cells. This result raises questions about the ability of seaweeds with apical growth, such as most red algae and fucoid brown algae (Figure 1b; Graham et al., 2017), to sense drag and exhibit adaptive plasticity to flow. Perhaps, unlike *Nereocystis*, other seaweeds sense mechanical cues in proximal non-growing regions of their thalli and communicate those cues to meristem regions via long-distance signaling mechanisms, such as hormones. Although we know hormones contribute to growth and development in marine macroalgae (Basu et al., 2002; Coleman, 2021; de Nys et al., 1990; Hart, 1982; Kai et al., 2006; Tarakhovskaya et al., 2007), hormone activity in algae remains largely mysterious, and no research to date has connected mechanical cues to hormone activity. Alternatively, cell-to-cell communication of mechanical cues could be facilitated by electrical signaling. Touch stimuli in the freshwater green alga *Chara* can trigger a cascade of action potentials in adjacent algal cells (e.g., Iwabuchi et al., 2007; Kaneko et al., 2009), suggesting that drag sensed by proximal tissue could conceivably be communicated by electrical signals to an apical meristem. However, this kind of electrophysiological phenomenon is unknown in seaweeds.

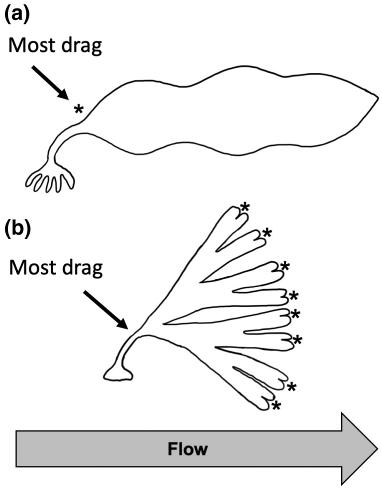

FIGURE 1 Spatial distribution of drag experienced by two seaweeds with different meristem types. (a) *Saccharina latissima* has an intercalary meristem that would experience drag imposed on the entire distal blade, while (b) *Fucus distichus* has apical meristems with no distal tissue. Meristems are indicated by *.

Phenotypic plasticity across flow gradients could also be regulated through chemical cues. One way for such cues to be an effective indicator of flow speed would be through the effects of the diffusion boundary layer (DBL), a concentration gradient that forms within the viscous layer of fluid along the surface of all aquatic organisms, including seaweeds (Hurd, 2000). When flow speeds are relatively slow, the DBL around macroalgal thalli becomes thick, which can reduce mass transfer, that is, diffusion rates of nutrients, gases, and other chemicals in and out of algal tissue (reviewed in Hurd, 2000). However, as flow speed increases, DBL thickness decreases, which increases rates of mass transfer (Gerard, 1982; Hurd et al., 1996; Wheeler, 1980). Such flow-induced variation in chemical diffusion is utilized by fucoid brown algae for sensing water motion during reproduction. The brown algae *Fucus distichus* and *Pelvetia compressa* use dissolved inorganic carbon (DIC) depletion within the DBL as a trigger for gamete release, which allows these seaweeds to coordinate reproductive output during low tides and avoid turbulent water motion that would negatively impact settlement (Levitan et al., 1992; Pearson et al., 1998; Pennington, 1985). A similar DBL-mediated chemical cue could potentially regulate phenotypic plasticity in response to water motion. However, once flow reaches approximately $20\,\mathrm{cm} \cdot \mathrm{s}^{-1}$, the DBL is effectively minimized and mass transfer becomes saturated (Hurd, 2000). Therefore, a DBL-mediated mechanism would be most useful at flow velocities less than $20\,\mathrm{cm} \cdot \mathrm{s}^{-1}$, as algae may not be able to sense changes in flow directly if mass transfer were saturated. Given that intertidal water velocities routinely exceed $200\,\mathrm{cm} \cdot \mathrm{s}^{-1}$ along wave-sheltered coastlines and $2000\,\mathrm{cm} \cdot \mathrm{s}^{-1}$ at wave-exposed coastlines (Denny et al., 2003; Denny and Gaylord, 2002), it is difficult to imagine that DBL-mediated variation in diffusion rates could explain phenotypic variation among wave exposures. Nevertheless, at faster flow speeds, seaweeds may be able to sense changes in flow using chemicals that exist at very low concentrations in the water. As flow velocity increases, rare chemicals could be delivered at higher rates, which could theoretically allow seaweeds to detect and respond to changes in water motion. More research is needed on the involvement of chemical cues in mediating phenotypic plasticity across hydrodynamic gradients.

PREVALENCE OF PHENOTYPIC PLASTICITY ACROSS HYDRODYNAMIC GRADIENTS IN SEAWEEDS

We reviewed over 100 years of phycological literature (1900–2024) to investigate the general assumption that phenotypic plasticity across hydrodynamic gradients is common in seaweeds. We quantified (1) observations of intraspecific variation across hydrodynamic gradients, (2) experiments specifically testing for phenotypic plasticity in response to flow, and (3) demonstrations of phenotypic plasticity across hydrodynamic gradients. We considered plasticity to be demonstrated if manipulating flow conditions (actual or simulated) had a statistically significant effect on an observed phenotype. Demonstrations of phenotypic plasticity that resulted solely from damage were noted; all other documented cases of plasticity were considered to be possible instances of developmental plasticity. See Appendix S1 in the Supporting Information for details of review methods.

Despite broad claims that phenotypic plasticity to flow is common in seaweeds, there was mixed evidence for its prevalence in the phycological literature. We found 141 papers documenting intraspecific phenotypic variation across hydrodynamic gradients in 60 species of seaweed (Table 1). These included 43 species of brown algae, 12 species of red algae, and five species of green algae. The origin of observed phenotypic variation was investigated in 30 species (50% of the total; Table 2) across 42 papers (30% of the total). Most studies that demonstrated phenotypic plasticity used field-based manipulative experiments, including transplantations. Phenotypic plasticity was identified in 27 species, including 20 species of brown algae, five species of red algae, and two species of green algae. Of these species, plasticity was attributed to mechanical damage (i.e., not development) in two brown algal species, one red algal species, and one green algal species. Plasticity was tested for but not found in four brown algal species, one red algal species, and no green algae.

Our review uncovered inconsistent evidence for widespread phenotypic plasticity across hydrodynamic gradients in seaweeds. Although we did find an abundance of papers documenting both intraspecific trait variation and plasticity in brown algae, particularly in kelps, we uncovered fewer examples of such variation and plasticity in red and green algae. Only five species of red algae were observed to be phenotypically plastic, with one of those species observed to be passively plastic from mechanical damage (Steneck & Adey, 1976). Furthermore, only two species of green macroalgae, *Codium fragile* and *Caulerpa okamurae*, were observed to be plastic across flow gradients, and the plasticity observed in *Codium* was attributed by the authors to passive mechanical damage (Bégin & Scheibling, 2003; D'Amours & Scheibling, 2007; Fralick & Mathieson, 1972; Kang et al., 2024). That more observations of phenotypic plasticity were made in brown algae than in red and green algae is supported by a previous systematic review on plasticity (Padilla & Savedo, 2013), which covered a wider range of plasticity in algae and did not specifically consider responses to flow. Overall, the evidence of phenotypic plasticity in response to water motion occurring in red and green algae is limited, calling into question the assumption that this phenomenon is widespread. Could plasticity in response to water motion be common in brown algae but rare in red and green algae, perhaps due to differences in thallus construction that may facilitate or complicate sensing and responding to flow? For example, as discussed above, intercalary meristems could make kelps better able to detect changes in flow velocity than other seaweeds. Unfortunately, at the present time, it is not possible to determine whether the numerous examples of brown algal plasticity reflect brown algae being more plastic or simply being studied more frequently. Ultimately, to clarify whether plasticity across flow gradients is more common in brown algae than in other macroalgal groups, additional manipulative experiments testing the ability of red and green algae to respond to flow are needed.

TABLE 1 Summary of literature on phenotypic plasticity in seaweeds across hydrodynamic gradients (January 1900 to June 2024).

Group	Total papers	Total species	Species where plasticity tested	Species where plasticity found	Species where plasticity due to damage	Species where plasticity not found
Brown algae	118	43	22	20	2	4
Red algae	16	12	6	5	1	1
Green algae	7	5	2	2	1	0
Total	141	60	30	27	4	5

TABLE 2 Summary of macroalgal species in which plasticity to flow has been experimentally tested.

Group	Species	Publication	Phenotype	Plasticity
Brown algae	*Dictyoneurum californicum*	Ramsay (2019)	Morphology	Yes
	Dictyoneurum reticulatum	Ramsay (2019)	Morphology	Yes
	Dictyopteris undulata	Stewart and Carpenter (2003)	Morphology	Yes
	Ecklonia radiata	Fowler-Walker et al. (2006)	Morphology	Yes
	Egregia menziesii	Blanchette et al. (2002)	Morphology	No
		Hackney et al. (1994)	Cellular	Yes
		Kraemer and Chapman (1991a)	Cellular	Yes
		Kraemer and Chapman (1991b)	Cellular, biomechanical	Yes
	Eisenia arborea	Roberson and Coyer (2004)	Morphology	No
	Fucus distichus	Blanchette (1997)	Morphology	Damage only
		Sideman and Mathieson (1985)	Morphology	No
	Fucus vesiculosus	Molis et al. (2015)	Biomechanical	Yes
	Laminaria digitata	Sundene (1961)	Morphology	Yes
		Sundene (1964)	Morphology	Yes
	Laminaria hyperborea	Svendsen and Kain (1971)	Morphology	Yes
	Lessonia trabeculata	Venegas et al. (1993)	Cellular	Yes
	Macrocystis pyrifera	Druehl (1978)	Morphology	Yes
		Druehl and Kemp (1982)	Morphology	Yes
		Pace (1972)	Morphology	Yes
	Nereocystis luetkeana	Coleman and Martone (2020)	Morphology	Yes
		Koehl and Silk (2021)	Morphology	Yes
		Koehl et al. (2008)	Morphology	Yes
		Supratya et al. (2020)	Morphology	Yes
	Saccharina japonica	Kawamata (2001)	Morphology, biomechanical	Yes
		Sato et al. (2017)	Morphology	Yes
	Saccharina latissima	Buck and Buchholz (2005)	Morphology	Yes
		Gerard (1987)	Morphology	Yes
		Kregting et al. (2023)	Morphology	Yes
		Peteiro and Freire (2011a)	Morphology	Yes
		Peteiro and Freire (2013)	Morphology	Yes
	Saccharina longicruris	Gerard and Mann (1979)	Morphology	Yes
	Saccorhiza polyschides	Norton (1969)	Morphology	Yes
	Sargassum cymosum	De Paula and De Oliveira (1982)	Morphology	No
	Sargassum muticum	Andrew and Viejo (1998)	Morphology	Damage only
	Turbinaria ornata	Stewart (2006)	Morphology	Yes
	Undaria pinnatifida	Nanba et al. (2011)	Morphology	Yes
		Peteiro and Freire (2011b)	Morphology	Yes
	Zonaria farlowii	Stewart and Carpenter (2003)	Morphology	Yes
Green algae	*Caulerpa okamurae*	Kang et al. (2024)	Morphology	Yes
	Codium fragile	Bégin and Scheibling (2003)	Morphology	Damage only
		D'Amours and Scheibling (2007)	Morphology	Damage only
		Fralick and Mathieson (1972)	Morphology	Damage only
Red algae	*Chondrus crispus*	Chen and Taylor (1980)	Morphology	No
		Floc'h (1969)	Morphology	No
	Devaleraea ramentacea	Munda (1977)	Morphology	Yes
	Lithophyllum kaiseri	Steneck and Adey (1976)	Morphology	Damage only
	Mazzaella linearis	Shaughnessy (2004)	Morphology	Yes
	Mazzaella splendens	Shaughnessy (2004)	Morphology	Yes
	Pyropia abbottiae	Hannach and Waaland (1989)	Morphology	Yes

Note: Studies that found plasticity ("yes") are considered possible examples of developmental plasticity, unless solely determined to be the result of passive mechanical damage ("damage only"). Studies that found no evidence of plasticity are also indicated ("no").

Our literature review yields a new perspective on the putative importance of an intercalary meristem in brown algae for sensing and responding to flow. Although many species of brown algae have demonstrated plasticity in blade morphology when flow is manipulated (e.g., Buck & Buchholz, 2005; Druehl & Kemp, 1982; Fowler-Walker et al., 2006; Gerard & Mann, 1979; Koehl et al., 2008), a few species have not. One of these is the feather boa kelp, *Egregia menziesii*. Although this alga develops smaller bladelets and thicker rachi in wavier environments (Abbott & Hollenberg, 1976; Blanchette et al., 2002; Henkel et al., 2007), transplantation experiments have failed to attribute this variation to plasticity (Blanchette et al., 2002). Interestingly, unlike other kelps, *Egregia* has an unusual intercalary meristem that moves distally as thalli mature (Burnett & Koehl, 2020). This thallus construction may interfere with the ability of the intercalary meristem of *Egregia* to sense flow, similar to an apical meristem, which could explain the lack of observed plasticity. It should be noted, however, that this species does show plasticity in material properties and cytological characteristics in response to mechanical stimulation (Hackney et al., 1994; Kraemer & Chapman, 1991a, 1991b). In addition, very few studies have demonstrated plasticity in non-kelp brown algae, which mostly exhibit apical growth. For example, species in the genus *Fucus* have been the subject of numerous studies documenting phenotypic variation across hydrodynamic gradients worldwide (e.g., Coleman & Muhlin, 2008; Jordan & Vadas, 1972; Kalvas & Kautsky, 1993; Knight & Parke, 1950; Rice et al., 1985), yet zero studies, including multiple transplant experiments (Blanchette, 1997; Sideman & Mathieson, 1985), have demonstrated that morphological variation is due to plasticity (although tissue properties can be plastic; Molis et al., 2015). Instead, morphological variation in this genus is more likely due to widespread, fine-scale genetic differentiation, which can be detected among seaweeds within several meters of each other (Coyer et al., 2003; Tatarenkov et al., 2007). Interestingly, the only non-kelp brown alga that exhibits morphological plasticity similar to that of many kelps in fast flow conditions is *Saccorhiza polyschides* (Norton, 1969), which possesses an intercalary meristem (Norton, 1970).

Although our data show more evidence of phenotypic plasticity across hydrodynamic gradients in brown algae with intercalary meristems than in other seaweeds, it must be reiterated that we also uncovered evidence of phenotypic plasticity in four species of red algae and one species of green algae. One of the four red algal species exhibits diffuse growth (Munda, 1977) and is likely capable of utilizing drag as a cue for mediating plasticity like seaweeds with intercalary meristems. However, three red algal species and one green algal species demonstrated plasticity to flow despite having apical meristems; how they accomplish this is unclear. Could these seaweeds detect drag in proximal tissue and communicate signals to distal meristems to direct development? Or could apical meristems sense a chemical cue associated with water motion as opposed to a mechanical cue? More research is needed to determine if plasticity to flow is more common in red and green algae than currently documented and also to illuminate physiological mechanisms that might permit apical meristems to respond to flow.

Across all papers we reviewed, the origin of phenotypic variation was investigated less than one-third of the time. This indicates that few studies on intraspecific trait variation have deduced whether phenotypic plasticity or some other mechanism, such as genetic differentiation, is involved. Failure to distinguish between these two processes can result in incorrect taxonomic designations (Belton et al., 2014; Garbary et al., 1978) as well as incomplete understanding of species ecology and evolutionary history. For example, a case of intraspecific phenotypic variation incorrectly attributed to plasticity could actually represent undetected genetic divergence between populations—perhaps even a nascent speciation event (Demes & Pruitt, 2019; Roberson & Coyer, 2004).

Several seaweed species have had plasticity explicitly tested, but not observed. Such an outcome has several possible explanations, and further study will likely be needed to clarify the lack of plasticity (Mathieson et al., 1981). One possible explanation is that the species are truly not plastic in response to water motion, and observed phenotypic variation is due to genetic differentiation between different groups of individuals. This may suggest the presence of selection favoring distinct genotypes in different environmental conditions. Roberson and Coyer (2004) proposed genetic differentiation as the underlying mechanism for the lack of morphological plasticity observed across a wave exposure gradient in the kelp *Eisenia arborea*, and they supported this conclusion with genetic data. This is an interesting conclusion, raising questions about why one kelp species might not evolve to be plastic in response to flow while other closely related kelp species are incredibly plastic. It also serves as a reminder to researchers studying intraspecific trait variation in seaweeds not to overlook the possibility of genetic differentiation as a driver of phenotypic differences between populations. An alternative mechanistic explanation for the lack of plasticity to flow is developmental canalization. In some forms of phenotypic plasticity, the organism can only undergo phenotypic changes for a limited time during development, after which its relevant phenotype becomes fixed or “canalized” (e.g., Blanchette et al., 2002). In this situation, a mature seaweed transplanted across a flow gradient may not show plasticity that it might otherwise have shown if it had been transplanted earlier in development. Developmental canalization could be relevant to some seaweed species that failed to exhibit phenotypic plasticity across a flow gradient but were perhaps tested too late in development. However, developmental canalization and its effect on phenotypic plasticity has not been studied in seaweeds and deserves further scrutiny.

CONCLUSIONS

Phenotypic plasticity across flow gradients has been well documented in brown seaweeds, but not well documented in green and red seaweeds. This discrepancy may be the result of publication bias or it could reflect fundamental differences in the ability of different groups of seaweeds to detect and respond to flow. Although flow sensing in many brown seaweeds, particularly kelps, likely relies upon the presence of intercalary meristems, flow sensing in red and green seaweeds, which often possess apical meristems, remains a mystery. Additional studies are needed to clarify physiological mechanisms underlying phenotypic plasticity across flow gradients. The assumption that phenotypic plasticity in response to flow is common in seaweeds is not particularly well supported by the literature. Researchers are advised to consider other mechanisms, such as genetic differentiation, before assuming that observed variation in seaweed traits along a hydrodynamic gradient is due to plasticity.

AUTHOR CONTRIBUTIONS

Liam J. M. Coleman: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); writing – original draft (lead); writing – review and editing (equal). **Patrick T. Martone:** Conceptualization (equal); data curation (supporting); funding acquisition (lead); investigation (supporting); methodology (supporting); project administration (lead); supervision (lead); writing – original draft (supporting); writing – review and editing (equal).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Methods for reviewing seaweed plasticity literature.

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