It takes two to stay afloat: interplay of morphology and physiological acclimation ensures long-term floating dispersal of the bladderwrack *Fucus vesiculosus* (Phaeophyceae, Fucales)

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Abstract

Floating algae can be found in high abundances at mid and high latitudes, their prolonged positive buoyancy allowing long-distance dispersal. However, despite their importance to dispersal and ecological and evolutionary meta-population dynamics, little is known about the buoyancy responses of high latitude algae to the conditions at the sea surface. Indeed, even at 60°N environmental conditions during spring/summer can be challenging, and may cause the demise and sinking of floating algae. The bladderwrack, *Fucus vesiculosus*, from the Northern Baltic Sea floats on the sea surface when detached from the benthic substratum. We conducted a field experiment with tethered individuals during their reproductive period to measure variation in floating time and how that is related to morphological traits such as occurrence of vesicles and/or receptacles and to measure growth and photosynthesis while afloat.

Algal individuals with receptacles tended to sink quickly, whereas the longest floating time was evident for individuals carrying vesicles but lacking receptacles. While afloat, all individuals grew in size, showed photosynthetic acclimation to sea surface conditions, and had a few invertebrates associated with them. Our results showed that rafts of *F. vesiculosus* were physiologically viable until their day of sinking and that morphological traits such as the occurrence of vesicles and receptacles modified their floating time. Accordingly, floating algae with a similar morphological set-up and thus also reproductive phenology as *F. vesiculosus* can have a high floating persistence but, depending on their reproductive structures, they may mostly serve as long-range dispersal vehicles for associated organisms.

Key words: Acclimation; floating algae; floating time; *Fucus vesiculosus*; high latitude; morphology; receptacles; vesicles

Introduction

Macroalgae with positively buoyant features such as gas-filled vesicles or honeycomb structures (Rothäusler *et al.*, 2015 for *Fucus vesiculosus* L., Tala *et al.*, 2013 for *Durvillaea antarctica*, respectively) can float on the sea surface when they become detached from the benthic substratum and remain buoyant for weeks or even months (Hobday 2000a; Vandendriessche *et al.,* 2007; Yatsuya 2008; Graiff *et al.*, 2013, 2016; Tala *et al.*, 2019). Prolonged buoyancy provides potential to float for long distances (e.g. Fraser *et al.*, 2009; Rothäusler *et al.*, 2015; van Hees *et al.,* 2018) and these long distance dispersers can contribute to population connectivity and to the (re-) colonization of new habitats (Muhlin *et al.*, 2008; Coyer *et al.*, 2011). Dispersal ability and range therefore primarily depend on the abundance of floating individuals and their persistence time on the sea surface. There is also evidence that these algae are travelling considerable distances at the mercy of currents and winds, having the potential to release gametes or spores at one or more new and suitable sites, such as has been shown for the subantarctic regions, where populations of *D. antarctica* and *Macrocystis pyrifera* are connected between distant islands or land masses driven by the West Wind Drift (Macaya & Zuccarello, 2010; Fraser *et al.*, 2009; 2010).

At high latitudes in the Baltic Sea, *Fucus vesiculosus* is the principal foundation species covering large areas of the shallow rocky subtidal. Consequently, floating thalli of *F. vesiculosus* are highly abundant between the Finnish and the Swedish Archipelagoes (Rothäusler *et al.*, 2015) and most likely around the whole Baltic Sea. Rafts of *F. vesiculosus* have also been described from the North Atlantic and adjacent seas (Tully & Ó Céidigh, 1986; Ingólfsson 1998; Ólafsson *et al.*, 2001;Vandendriessche *et al.*, 2006; Khalaman & Berger, 2006; Muhlin *et al.*, 2008; Thiel *et al.*, 2011).

Fucus vesiculosus is known for its gas-filled vesicles, which are found in pairs on the algae. When algae get older they break and leave the vesicles without gas, therefore after a couple of years adult algae have only vesicles towards their younger end (Rothäusler, personal observation). At these ends, also known as the vegetative apical tips, the meristem is located, which either transform to receptacles or they stay vegetative. Only the vegetative tips keep forming vesicles.

In the Baltic, in addition to gas-filled vesicles, *F. vesiculosus* possess enlarged air pockets in their reproductive apices (hereafter receptacles). These may provide additional buoyancy during the reproductive season in spring/summer in comparison to Atlantic *F. vesiculosus* that lack such air-filled receptacles (Bäck *et al.*, 1993). After releasing gametes, receptacles disintegrate (Rothäusler, personal observation) and thus the algal rafts may lose their buoyancy if that is based solely on receptacles. Thus it seems likely that different morphological traits such as the occurrence of receptacles and vesicles can influence the floating time of detached *F. vesiculosus*.

Once dislodged, algae begin their journey via surface winds and currents and have to withstand the prevailing higher solar radiation and temperature at the sea surface, which requires an efficient physiological acclimation (Graiff *et al.*, 2016 for *Durvillaea antarctica*; Rothäusler *et al.*, 2009 for *Macrocystis pyrifera;* van Hees *et al.*, 2018 for *Sargassum spinuligerum*). Acclimatization processes, such as pigment adjustment, dynamic photoinhibition and/or repair mechanisms, enable floating individuals to retain growth and reproductive ability, as well as to persist and disperse before sinking (Rothäusler *et al.*, 2011a, 2018a; Graiff *et al.*, 2013; Tala *et al.,* 2013; Graiff *et al.,* 2016; van Hees *et al.,* 2018). Photosynthetic performance that largely determines the ability to these acclimation processes has been found to be highly variable among individuals in benthic fucoid species (Johannesson *et al.,* 2012; Rothäusler *et al.,* 2016). This implies that floating duration may vary because some individuals are better adapted to the conditions on the sea-surface than others and thus persist afloat for longer.

While the persistence of floating algae in terms of physiology and growth has been relatively well studied at mid latitudes on both hemispheres (Hobday 2000a; Yatsuya 2008; Rothäusler *et al.*, 2009, 2011a, b, c, 2018a ; Graiff *et al.*, 2013; Tala *et al.*, 2013; Graiff *et al.*, 2016), corresponding data at high latitudes are scarce (Tala *et al.*, 2016; 2019). At high latitudes, the overall modest surface conditions in spring/summer (low irradiance, temperature and epibiosis) in comparison to mid and low latitudes may favour the survival of floating algae (Ingólfsson, 1998; Tala *et al.*, 2016; Rothäusler *et al.*, 2009, 2011b, 2018a; Graiff *et al.*, 2013, 2016). Several studies document successful dispersal of macroalgae (e.g. Fraser *et al.*, 2009; Olsen *et al.*, 2010; Macaya & Zuccarello, 2010), thus, attesting facilitation of long-distance dispersal under benign climate conditions. However, these studies provide little information about the functional traits of the algae such as morphology and photosynthetic acclimation potential that allow persistent buoyancy.

Rafting, whereby other organisms hitchhike on buoyant objects, such as algae, can affect their floating persistence (Vandendriessche *et al.*, 2007; Rothäusler *et al.*, 2009, 2011b) and hence reduce their dispersal distances. The herbivorous hitchhikers (e.g., amphipods and isopods) actively feed on their rafts, which at increasing temperatures and densities can reduce photosynthetic thalli (Vandendriessche *et al.*, 2007; Rothäusler *et al.*, 2009). At the same time epibionts (e.g. non-buoyant algae, bryozoans, and barnacles) can successively cover their floating host, which may suppress algal photosynthesis (Oswald *et al.*, 1984; Rothäusler *et al.*, 2011c), decrease buoyancy and ultimately cause sinking (Graiff *et al.*, 2016).

Although the potential to persist at the sea surface is a key factor for the dispersal of macroalgae, our understanding of the factors behind variation in the floating duration of algal individuals is in its infancy. Furthermore, climate change with increasing sea surface temperatures (Lehmann *et al.*, 2011) and intensifying solar radiation (Wild 2005), may further challenge the floating dispersal ability of high-latitude macroalgae calling for the understanding of their functional traits such as morphology (vesicles and receptacles) and photosynthetic acclimation potential. Therefore, we conducted a field experiment with detached *F. vesiculosus* during the species reproductive season. We hypothesized that (i) the floating time differs among individuals, depending on morphological traits, such as the presence of air-filled vesicles and receptacles, and (ii) the individuals able to maintain their photosynthetic performance and growth while floating will persist afloat for longer than those less able to acclimate to sea surface conditions. Further, we quantified the accumulation of invertebrates on macroalgae with the floating duration.

Materials and Methods

Collection of algal material

We collected adult individuals of *F. vesiculosus* on the 2nd of June 2014 by snorkeling within a continuous algal belt in the southwestern Archipelago Sea (60° 08 'N, 22° 17 'E), Finland. A total of 14 mature individuals with their disc-shaped holdfast were detached at 5 m intervals at ~ 1.5 m depth. Algae were then stored in buckets filled with seawater and brought to the Archipelago Research Institute of the University of Turku at the island of Seili (60°14’N, 21° 57’ E). They were kept overnight in flow-through seawater tanks before being measured and tethered in the field. Algae were prepared for experimentation by rinsing them carefully with seawater in order to remove associated grazers and epiphytes.

The 14 adult individuals varied in shape and biomass (mean ± SD, 175 ± 76 g) thus representing the natural morphological variation of the sampled population. However, all individuals were reproductive (mean ± SD, 166 ± 14) and presented vegetative meristems (109 ± 18) but four individuals did not carry vesicles (N = 10, 32 ± 6). We split each individual in three approximately equal sized thalli without a holdfast (mean ± SD, largest thallus 97 ± 13 g; smallest thallus 23 ± 5 g). Hence, after cutting each of the replicated thalli consisted of several apical tips with meristems but not all of them had receptacles and/or vesicles. Hereafter, the mean of the three thalli from the same individual represents one genetic individual. Throughout the manuscript, when referring to one thallus it represents one replicate of the genetic individual. During the course of our experiment, no new receptacles were formed.

Experimental design

The experiment was set-up close by the island of Seili, approximately 300 m from the shore of the nearest island. This region is characterized by skerry landscapes, consisting of many small islands that inhabit benthic *F. vesiculosus* from ~ 1 to 4 m depth. Via snorkeling we built up side by side a total of three buoyant long lines (25 m in length) with approximately 5 m distance to the sea bottom. At their ends, we anchored theses long lines to the sea bottom.

Each of the 42 thalli received a unique identification tag attached to the base of the stipe and a floating cord of 50 cm length. In order to avoid physical damage to the stipe, we surrounded it with a rubber hose that was fixed with cable ties to the cord. Then we distributed the thalli over the three experimental lines, so that one thallus from each genetic individual (N = 14) was represented on each line and spaced 1.5 m apart, allowing them to float freely on the sea surface.

We checked the 42 thalli every third day to monitor their date of sinking. For logistical reasons, after six weeks of experimentation, floating thalli were checked only once a week. We considered the thalli as sunken when they were completely submerged and no part remained above the sea surface. Four thalli were lost from the experimental lines during our experiment.

Sea surface conditions: Solar radiation, UV, and temperature

Sea surface light intensity (µmol photons m^{-2} s^{-1}) and water temperature (˚C) were monitored every 20 min during the course of experimentation using HOBO (Pendant temp/light Onset, USA) light and temperature loggers. A total of six loggers, two of each to one of the buoyant experimental lines were attached at 30 cm below the sea surface. In addition UV-index data were measured by the Seili weather station. Light intensity and UV-index were presented as average monthly midday values, ranging from 11:00 to 14:00, while water temperature was calculated as monthly average over the duration of the experiment (Table 1).

During experimentation (June to September) we found a progression in sea surface temperature, with a lowest value at the start of the experiment in June (mean ± SD, 14.4 ± 1.3 °C), reaching a peak in August (21.0 ± 1.9) and a decline in September (18.1 ± 0.4). Our irradiance data such as solar radiation and UV-index showed highest values in June and July (Table 1).

Measures of Fucus vesiculosus

Photosynthetic performance such as ETR_{max}, E_k, and alpha (α_{ETR}) were determined from all 14 genetic individuals at the beginning of experimentation (day 0, initial) before each of them were split, and again at their observed day of sinking (final) from each replicated thallus. Morphological features such as the initial number of vesicles, number of receptacles, number of meristems, length of thalli (mm) as well as their wet biomass (g) were measured after their splitting in the beginning and at their day of sinking. We calculated growth rate while floating in terms of biomass, meristems, and length as follows: (final size - initial size) / floating time (d).

We measured the ETR_{max}, E_k, and alpha from apical meristematic tips via photosynthetic versus light intensity (P-I) curves. This was done *in vivo* using a computeraided portable pulse amplitude-modulated fluorometer (PAM 2000, Walz, Effeltrich, Germany). Three samples of the respective tissue were put separately in test tubes that were wrapped with aluminium foil and irradiated individually with increasing intensities of photosynthetic active radiation (PAR: 0-500 µmol photons m^{-2} s^{-1}), which was provided by a light-emitting-diode lamp of the PAM device (Schreiber *et al.*, 1995). The ETR was estimated by relating the effective quantum yield (PSII) and the intensity of the radiation as described in (Rothäusler *et al.,* 2011b). The hyperbolic tangent model of Jassby and Platt (1976) was fitted to each data set as follows:

$$ETR = ETR_{max} * \tan h * (\alpha_{ETR} * I / ETR_{max})$$

where ETR_{max} (µmol $e^{-}\cdot m^{-2}\cdot s^{-1}$) is the maximal electron transport rate; tan h is the hyperbolic tangent function; α_{ETR} (µmol $e^{-}\cdot m^{-2}\cdot s^{-1}$ [µmol·photons·$m^{-2}\cdot s^{-1}$]) is the initial slope of the P-I curve and stands for the electron transport efficiency, and I is the photon fluence rate of PAR. The saturation irradiance for electron transport E_k (µmol·$m^{-2}\cdot s^{-1}$) was also calculated as the intercept between α, and the ETR_{max} values (ETR_{max} / α_{ETR}). The mean value of the three replicated measurements represented the photosynthetic parameter of one thallus, while the grand mean of the three thalli represented one genetic individual.

Associated organisms

Before each sunken algal thallus was taken up, we enclosed it carefully in a mesh bag (1 mm mesh size) in order to retain the mobile invertebrates that colonized it while afloat. The mesh bags were brought to the laboratory at Seili and the associated invertebrates dislodged from each individual thallus as well as those clinging to the thallus were counted and identified.

Statistical analysis

To test whether different genetic individuals of *F. vesiculosus* (random factor) had different growth rates (measured as number of meristem, length, and biomass in respect to their days afloat) and varied among experimental lines (random factor), we applied Generalized Linear Mixed Models (GLMM) implemented with the R package “lme4” (Bates *et al.*, 2015). The same models were used for the physiological responses of ETR_{max}, E_k, and α_{ETR} at the end of their floating time.

Within all GLMM analyses, we calculated the amount of variation due to random factors and tested the significance of them and their interactions with the likelihood-ratio test between the models with and without the random factors with the R package “lmtest” (Zeileis & Hothorn 2002), and then simplified the model by excluding the non-significant effects, with the aid of the Akaike Information Criterion (AIC). The error variance distribution of the response variables was Gaussian, which was checked by visual inspection of the residual plot. We derived the individual estimates for each independent variable from the model as a best linear unbiased predictor (BLUP, Littell *et al.,* 2006). In addition, we tested whether being afloat affected the physiological responses of the same genetic individual with repeated-measures ANOVA (Proc GLM). We included in this analysis the initial and the final photosynthetic measurements. This last analysis was done using SAS 9.4 (SAS Institute Inc 2014).

We conducted structural equation modeling (SEM) to construct three plausible models to determine whether morphological (initial wet biomass, initial number of receptacles, initial presence of vesicles) and physiological traits (initial ETR_{max}, growth rate in terms of biomass) were significant predictors of floating time (dependent variable). In model I all observed variables were included, and initial biomass and ETR_{max} were found not significant. In model II, initial biomass was excluded and ETR_{max} was still not significant. By deleting the two non-significant observed variables (initial biomass and ETR_{max}) we found the best model fit in model III (Table 2), which was guided by the goodness of fit as suggested by Kline (2005). Further, we fed the model I allowing all possible correlations among all observed variables and in the final model III we kept only the significant correlations between initial number of receptacles and initial presence of vesicles. For all models, we estimated standardized path coefficients using a maximum likelihood method. Goodness of fit was evaluated through Root Mean Square Error of Approximation (RMSEA), Comparative Fit Index (CFI) and Akaike Information Criterion (AIC). Genetic individuals and experimental lines were not included because they were not significant in the previous analyses. The Structural Equation Modeling, SEM, was analyzed by using the R package Lavaan (Rosseel 2012).

In order to visualize the variation of observed floating duration with the predicted values by the factors found important in SEM, we further conducted a multiple regression analysis of floating duration on the number of receptacles, number of vesicles and growth rate. The SEM and multiple regression approaches gave very similar results. We show the result as a SEM path diagram because SEM allows explicit hypotheses about causalities and covariance structures.

To test whether there is a relationship between the floating time of *F. vesiculosus* and its associated hitchhikers, we performed Pearson correlations between floating time and the total number of invertebrates and then separately between each group of invertebrates (amphipods, isopods, and mytilids) and floating time. These analyses were run with the R-package stats v3.5.1 (R core team, 2013).

Results

Fucus floating time

Genetic individuals significantly differed in their floating time at the sea surface during spring/summer (variance component due to individual 61.4 %, $X^2 = 14.8$, $p < 0.001$), ranging from 23 ± 9 d to 88 ± 9 d (mean ± SE) (Fig. 1). The shortest floating time of a single thallus was 12 d while the longest was 96 d. Floating time did not vary among the experimental lines (variance component due to line 0 %).

Fucus growth and photosynthesis

While afloat, all genetic individuals grew new meristems (mean ± SE, 1.2 ± 0.4), and gained in length (5.4 ± 1.6 mm) and in wet biomass (0.4 ± 0.2 g). None of the three measured growth rates differed among genetic individuals (variance component due to individuals (%); meristems: 17.2 %, $X^2 = 2.07$, $p = 0.07$; length: 3 %, $X^2 = 2.32$, $p = 0.13$; biomass: 3 %, $X^2 = 1.98$, $p = 0.16$,) or experimental lines (variance component due to lines (%); meristems: 9.5 %, $X^2 = 1.88$, $p = 0.09$; length: 0 %; biomass: 0 %).

Both ETR_{max} (start: 98.7 ± 3.2; end: 72.0 ± 5.4) and α_{ETR} (start: 0.59 ± 0.01; end: 0.38 ± 0.01) of genetic individuals declined (repeated-measures ANOVA, $F_{(1, 36)} = 15.8$, $p < 0.001$, $F_{(1, 36)} = 83.9$, $p < 0.001$, respectively) by 27 % and 36 %, respectively, from the start to the end of floating. No such changes were evident for E_k (start: 172.0 ± 7.2; end: 165.7 ± 6.9: $F_{(1, 36)} = 0.43$; $p = 0.51$).

ETR_{max} and E_k at the end of floating did not vary among genetic individuals (mean ± SE, 73.1 ± 6.0 and 134.2 ± 24.9 µmol photons m^{-2} s^{-1}, respectively) or experimental lines (Table 2, Fig. 2A and 2B, respectively). Only final α_{ETR} significantly varied among genetic individuals with values ranging from 0.3 ± 0.06 to 0.5 ± 0.05 (Table 2, Fig. 2C).

Morphological and physiological traits as predictors of floating time

The SEM analysis for model III, which is the best-fitting model, suggested that the floating duration of *F. vesiculosus* is strongly affected by morphological traits (Fig. 3A, 3B, Table 3). The strongest negative effect on floating time was caused by the number of receptacles, which was followed by growth rate (biomass), both significantly reduced algal floating times. On the contrary, the presence of gas-filled vesicles had a positive effect on floating time. Finally, genetic individuals with more receptacles carried less vesicles (SEM correlation coefficient = -0.35, $p < 0.05$).

Associated invertebrates

Mobile invertebrates colonized floating *F. vesiculosus* during experimentation (Fig. 4). In total, 24 thalli carried invertebrates at their date of sinking. There was no relationship between floating time and the total number of invertebrates (r = 0.2, df = 22, p = 0.3) nor for each invertebrate group such as amphipods (r = 0.20, df = 22, p = 0.23), isopods (r = 0.22, df = 22, p = 0.29), and mytilid mussels (r = -0.33, df = 22, p = 0.12). No correlation was run for the decapods, because only one thallus that stayed afloat for 88 d carried a juvenile *Rhithropanopeus harrisii.* There is a general trend that with floating time the hitchhiking invertebrate community became more variable and diverse, with several thalli having abundant amphipods (Fig. 4).

Discussion

The floating time of *F. vesiculosus* under spring/summer field conditions ranged on average from 3 weeks to 3 months, and varied among genetic individuals. This variation in buoyancy appears to be largely explained by morphological traits such as the number of receptacles and the presence of vesicles, because all individuals acclimated well to the new surface conditions. Hence our study provides evidence that the composition of buoyancy devices and reproductive structures within an algal individual determine their floating time and thus dispersal potential.

Floating time and morphological traits

Here, we showed evidence that both the number of vesicles (enhance buoyancy) and receptacles (reduce buoyancy when degrading) played a role in determining the floating time of *F. vesiculosus*. First, the SEM path coefficients as well as the multiple regression coefficients indicated that when one of them is kept constant the other one has a significant effect. Second, when thalli had only vesicles the floating duration was almost always longer (75 to 90 d) than when they carried both vesicles and receptacles (20 to 75 d), and always longer than when they carried only receptacles (20 to 50 d). Similar high floating times have been reported for the Chilean *Durvillaea antarctica* floating at 50ºS in summer (Tala *et al.,* 2019) and for fragments of North Sea *F. vesiculosus* (50ºN) when kept in an indoor microcosm (Vandendriessche *et al.,* 2007). While the buoyancy of *D. antarctica* decreased as soon as their honeycomb structure inside their thalli started to disintegrate (Graiff *et al.,* 2013; Tala *et al.,* 2016), we showed that for *F. vesiculosus* the amounts of receptacles and vesicles jointly determined their floating time.

Genetic individuals with more receptacles carried fewer vesicles and sank earlier. This is because reproductive branches of *F. vesiculosus* stop growing, and thus also stop with the formation of vesicles. Although all genetic individuals were collected at the same site and at the same time, variation in the receptacle maturation phenology probably influenced the floating time. In fact, some receptacles may already have started the release of gametes when collected in June, while others carried immature receptacles. For several *Sargassum* species, floating ability decreases with the progressing reproductive stage because thalli increased their water content due to degradation processes (Yatsuya 2008). Similarly, after *F. vesiculosus* releases its gametes, receptacles start to disintegrate and become filled with water (Rothäusler, personal observation), causing an increase in biomass. Thus receptacle maturation and subsequent disintegration during the experiment decreased buoyancy, and the more the genetic individuals carried receptacles the more prone for sinking they were, despite the presence of vesicles.

Using a biophysical particle tracking model with flow fields from an ocean circulation model, we showed in a former study that Baltic Sea *F. vesiculosus* with a floating time of 20 d had a mean floating distance of 50 km whereas a floating time of 100 d increased the mean floating distance to > 200 km (Rothäusler *et al.*, 2015). This implies that genetic individuals with receptacles and/or few vesicles (20 to 50 d afloat) disperse over more limited distances than those without receptacles (> 75 d afloat) but on the other hand their chance to release viable gametes when arriving at a new and suitable site might be higher and thus also their fertilization success with a resident bladderwrack. We did not check for the viability of gametes from our floating algae but rafted fucoid seaweeds from New Zealand and Australia released viable propagules for up to 60 d (Hawes 2008; McKenzie & Bellgrove, 2008).

Aggregations of macroalgae as a consequence of entanglement can increase the size of algal patches significantly (e.g. Hinojosa *et al.*, 2010) and may disperse low persistent thalli over larger distances, which could be the case here. However, higher frequencies of bigger sized *F. vesiculosus* items have been only observed in summer but aggregations were very small (60 to 150 cm) (Rothäusler *et al.*, 2015) compared to patches of *M. pyrifera* and *D. antarctica* (1 to 4 m in diameter) (Hinojosa *et al.*, 2010). Hence, these small aggregations with a high load of mature receptacles in summer rather enhance their sinking than provide extra buoyancy.

Our findings imply that the floating time of *F. vesiculosus* and thus the probability of long distance dispersal is likely much higher in seasons when floating individuals are without mature receptacles, which is either in early spring or autumn/winter. During spring, when receptacles are still growing, a long floating time may provide the opportunity for long-range gamete dispersal, but only when receptacle maturation takes place at the new site of arrival e.g. when rafted thalli entangle with benthic conspecifics. In autumn/winter, a higher floating persistence may instead facilitate the dispersal of algal-associated organisms. Considering the presence of strong seasonal variation in weather conditions in the north-eastern Baltic Sea regions with higher storm probabilities in April/May and again in August/September (Soomere & Räämet, 2011), it supports the idea of larger travel distances in spring and autumn due to storm induced winds that can improve floating dispersal.

Physiological performance and associated organisms

On their days of sinking, all genetic individuals responded with lower ETR_{max} and α_{ETR} than in the beginning of their floating (decreased by 27 % and 36 %, respectively), implying acclimation to new surface conditions while afloat instead of declining physiological functioning. This down-regulation of PSII from the benthic to the floating state is known to protect the photosynthetic apparatus against the prevailing irradiance conditions and has been observed previously for *M. pyrifera* and *D. antarctica* (Rothäusler *et al.,* 2011a, b, c; Graiff *et al.,* 2013; Tala *et al.,* 2019). Also the fact that similar low ETR_{max} values were detected for benthic *F. vesiculosus* during spring/summer (Ekelund *et al.*, 2008; Rothäusler *et al.*, 2016), supports our idea of a high acclimation potential and does not indicate deterioration. Moreover, *F. vesiculosus* continued to grow, similar as shown for floating *M. pyrifera* (Rothäusler *et al.*, 2009; 2011a, b, c), underscoring the fact that algae stayed physiologically viable.

Rafted genetic individuals responded with varying photosynthetic efficiencies (α_{ETR}), implying that they converted the received surface radiation to a different degree into chemical energy. Possibly, these varying responses were generated because some genetic individuals possess different Chl *a* contents, light harvesting complexes, or their rate of carbon fixation by Rubisco differed.

In the Northern Baltic Sea, benthic *F. vesiculosus* experience considerable seasonal variations in temperature and light climates (e.g. Lehvo *et al.*, 2001), with ice and darkness in autumn/winter and warm water temperatures and high irradiances in spring/summer, which are accompanied by an extension of daylight hours. Therefore, we suggest that the experienced surface conditions were within the tolerance range of the species because algae adjusted their photosynthesis and even continued to grow until sinking. Additionally, we did not observe tissue softness, breakage or fragmentation of thalli, which would indicate deterioration.

Over time, floating macroalgae often become successively inhabited by mesograzers (e.g. isopods and amphipods) (e.g. Ingólfsson 1998; Hobday 2000b; Vandendriessche *et al.*, 2006), which at high densities can contribute via grazing to the loss of photosynthetic tissues, thereby suppressing algal growth (Rothäusler *et al.*, 2011c; 2018a). Until sinking, our experimental thalli were colonized by few organisms such as amphipods, isopods, bivalves, and decapods. The reason for this could be that at high latitudes in the Baltic Sea, benthic *F. vesiculosus* individuals are inhabited by relatively low abundances of mobile invertebrates during spring (e.g. Jormalainen *et al.*, 2016). Mobile invertebrates are also the ones that easily leave the floating thallus (Miranda & Thiel, 2008; Gutow *et al.*, 2009). Thus, it is unlikely that the mobile invertebrates found herein affected the floating time. Similarly, *Ascophyllum nodosum* fronds tethered at 64ºN were colonized by benthic and pelagic organisms but they did not cause their sinking (Ingólfsson 1998).

During the course of our experiment, we observed natural floating *F. vesiculosus* rafts entangled in our experimental thalli. In case these natural rafts were carrying organisms, they probably contributed to the colonization of our thalli. Overall, at high latitudes, the acclimation to spring/summer surface-water conditions together with the morphological traits enhancing buoyancy indicates that floating *F. vesiculosus* individuals serve to disperse associated organisms.

Implications

Fucus vesiculosus is one of the dominant floating macroalgae in the world's oceans (Thiel & Gutow 2005, Rothäusler *et al.*, 2012) and is common to find floating in the northern N-Atlantic > 45 °N (Tully & Ó Céidigh, 1986; Ingólfsson 1998; Vandendriessche *et al.*, 2006) but also in the Baltic Sea > 57 °N (Pereyra *et al.*, 2013; Rothäusler *et al.*, 2015). Their non-receptacle carrying thalli with an extended floating time > 75 d can travel > 200 km as compared to reproductive ones (20 to 50 d, travel distance of 50 km) (Rothäusler *et al.*, 2015), and therefore feature a particularly good potential for long-distance dispersal. This suggests that the floating dispersal prior (autumn/winter) or at the start (spring) of the reproduction period is likely to be most effective for *F. vesiculosus* gene flow over long distances.

In the face of global change, understanding the physiology and the reproductive phenology of floating macroalgae is important in order to predict their floating time, long-distance dispersal, and thus potential population connectivity over vast distances. Recently it was shown for benthic *F. vesiculosus* that ongoing climate change such as the combined effect of warming and hyposalinity (Meier & Eilola, 2011) hampered receptacle formation (Rothäusler et *al.*, 2018b) and that hyposalinity strongly affected sperm viability and thus also the subsequent fertilization success (Rothäusler *et al.*, 2019). This negative effect on the reproductive phenology of benthic populations also influences indirectly the supply of floating individuals.

Certainly, global change is already compromising the persistence and reproduction of floating macroalgae, and consequently reducing their distances and frequencies of dispersal. Thereby affecting not only the dispersal processes of the macroalgae themselves but also of their associated hitchhikers (Macreadie *et al.*, 2011). Future studies are needed in order to determine if different species and individuals of rafted macroalgae vary in their floating persistence and if they can release viable propagules under climate change. This will help to evaluate their rafting implications in a changing world.

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Author contributions

E. Rothäusler, V. Jormalainen: original concept, drafting and editing manuscript, set-up of experiment and sampling; L. Rugiu: statistical analyses, set-up of experiment and sampling; Tiina Tiihonen: set-up of experiment and sampling.

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Table 1. Environmental conditions of surface water temperature, solar radiation, and UV-index during the course of experimentation in 2014. Solar radiation and water temperature were extracted from HOBO data loggers tied to the main lines in the field. UV-index data were obtained from the Seili weather station (http://seili.utu.fi/projects/saa/NOAA.php), with irradiance sensors (Davis Instruments, CA, USA) detecting UV-radiation at wavelengths of 290 to 390 nm. Irradiance data were extracted between 11 am and 14 pm, and were transformed from lux to µmol photons m^{-2} s^{-1} with the conversion factor 0.085 (https://www.apogeeinstruments.com/conversion-ppfd-to-lux/).

	June	July	August	September
Temperature (°C)				
mean ± SD	14.4 ±1.3	19.6 ± 3.4	21.0 ± 1.9	18.1 ± 0.4
max	22.3	26.1	24.8	19.0
min	11.8	13.4	17.7	17.5
Solar radiation (µmol photons m^{-2} s^{-1})				
mean ± SD	410 ± 280	400 ± 275	390 ± 280	350 ± 260
max	1640	1640	1375	1170
min	120	135	105	100
UV-index				
mean ± SD	1.8 ± 0.7	2.2 ± 0.5	1.3 ± 0.5	0.8 ± 0.4
max	3.6	3.8	3.5	3.2
min	0.9	1.5	0.9	0.6

Table 2: Variance components (%) due to the random effects of genetic individual and experimental line with their statistical significance in physiological responses (ETR_{max}, E_k, and α_{ETR}) of *F. vesiculosus* at the end of the floating period.

Source of variation	ETR_{max}			E_k			α_{ETR}		
	Var. (%)	χ^2	P	Var. (%)	χ^2	P	Var. (%)	χ^2	P
Random Factors									
genetic individual	0	0.0	0.99	22.1	1.65	0.19	45	5.8	**0.015**
experimental line	0	0.03	0.98	0	0.0	1	2.6	0.23	0.63

Table 3. Results from the structural equation models. Model I includes the variables: initial biomass, initial number of vesicles, initial number of receptacles, growth rate (wet biomass), and ETR$_{max}$. Model II does not include initial biomass but all the rest of the variables such as initial number of vesicles, initial number of receptacles, growth rate (wet biomass), and ETR$_{max}$. Model III does not include initial biomass and ETR$_{max}$ but it includes initial number of vesicles, initial number of receptacles, and growth rate (wet biomass). Goodness of fit of the three tested models was evaluated through Root Mean Square Error of Approximation (RMSEA), Comparative Fit Index (CFI) and Akaike Information Criterion (AIC). Degrees of freedom (df) and p-value for the chi-square are provided. The R^2 refers to the response variable floating time.

Model	χ^2	df	P-value	AIC	RMSEA	CFI	R^2
I	2.1	1	0.14	1866	0.17	0.99	0.69
II	2.2	2	0.3	1570	0.05	0.99	0.67
III	2.1	1	0.3	1228	0.05	0.99	0.64

Figures:

Figure 1: Floating time (d) of different genetic individuals of *Fucus vesiculosus* (N = 14) tethered in their native habitat. Data are showing genetic individual estimates (mean ± SE, based on N = 3 thalli). Due to the loss of four thalli, the mean of the genetic individual 1, 7, 8, and 10 is based on N = 2 thalli.

Figure 2: Scatter plots showing the relationship between floating time and final ETR_{max} (A) as well as floating time and final E_k (B) of all tethered thalli that have been recovered at the end of experimentation (N = 38, four were lost). Different symbols are showing the N = 38 thalli with different morphologies. Dots = receptacle and vesicle carriers, triangles = only vesicle carriers, and squares = only receptacle carriers. R^2 values for the fit of the polynomial regressions are displayed. Bar plot (C) shows the genetic individual estimates (mean of the N = 3 thalli ± SE, N = 14) for the final α_{ETR}.

Figure 3: Path model III (see Table 2) showing the best fit (A). Standardized path coefficients are provided for each one-headed arrow, and correlation coefficient for the two-headed one. The asterisk indicates significant regression weights. The curved arrow indicates significant correlation among the observed variables. Multiple regression scatterplot (B), where the floating time is plotted against the predicted values. The latter ones are generated by a multiple regression model including the three independent variables: # of receptacles (β ± SE: -0.26 ± 0.8, $p < 0.01$), # of vesicles (1.21 ± 0.32, $p < 0.001$), and growth rate (-1.74 ± 0.84, $p < 0.05$), with the R^2 of 0.53. The grey area surrounding the regression line represents the confidence interval.

Figure 4: Colonization of invertebrates with floating time (d). Results are from N = 24 *F. vesiculosus* thalli.

Figure 1

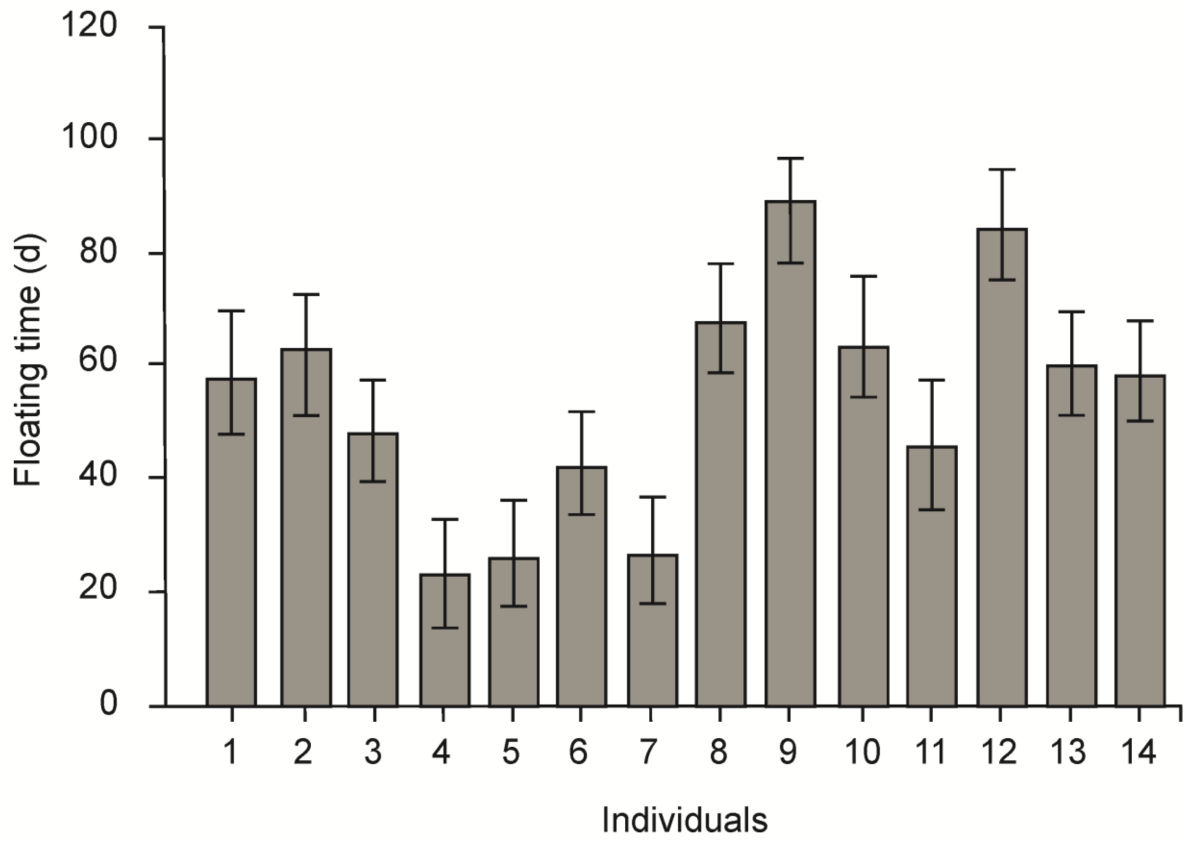

Floating time (d)
0
20
40
60
80
100
120
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Individuals

Figure 2

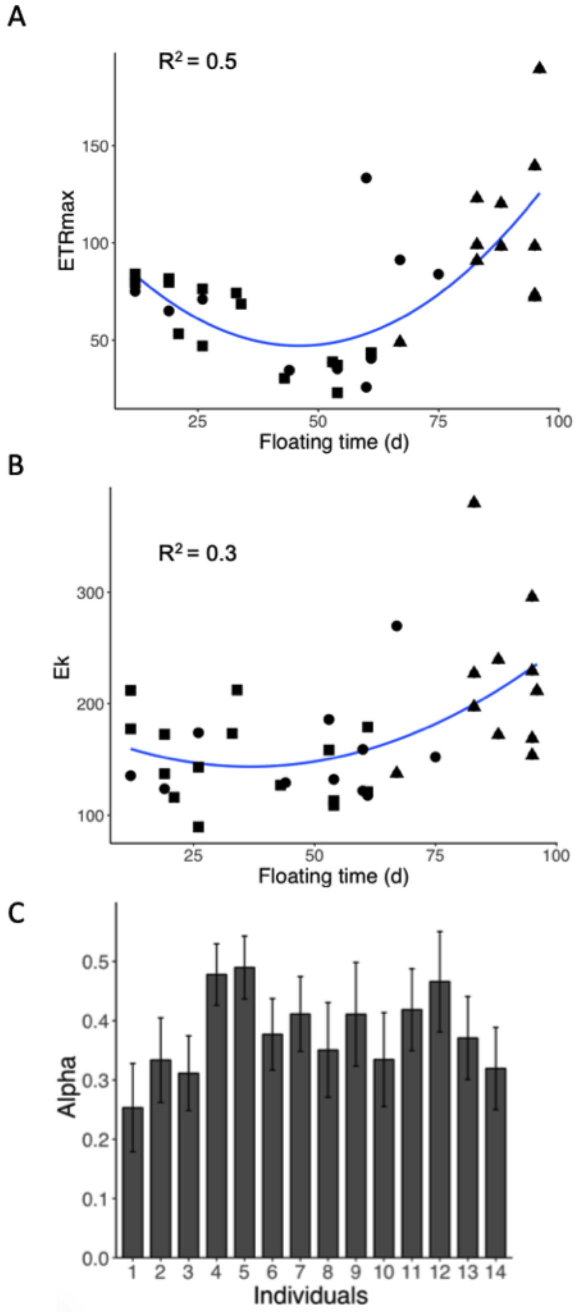

A
R² = 0.5
ETRmax
150
100
50
25
50
75
100
Floating time (d)
B
R² = 0.3
Ek
300
200
100
25
50
75
100
Floating time (d)
C
Alpha
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Individuals

Figure 3

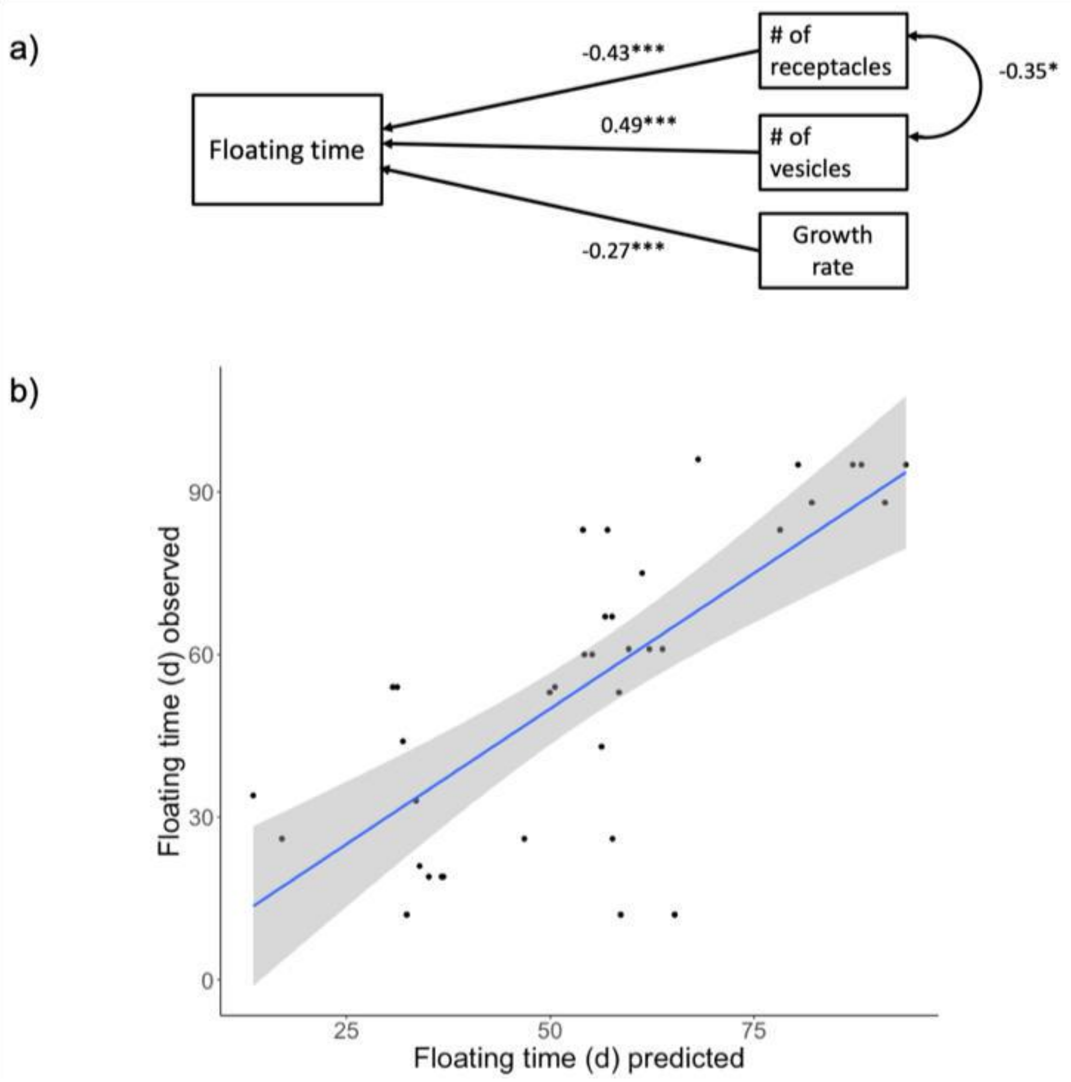
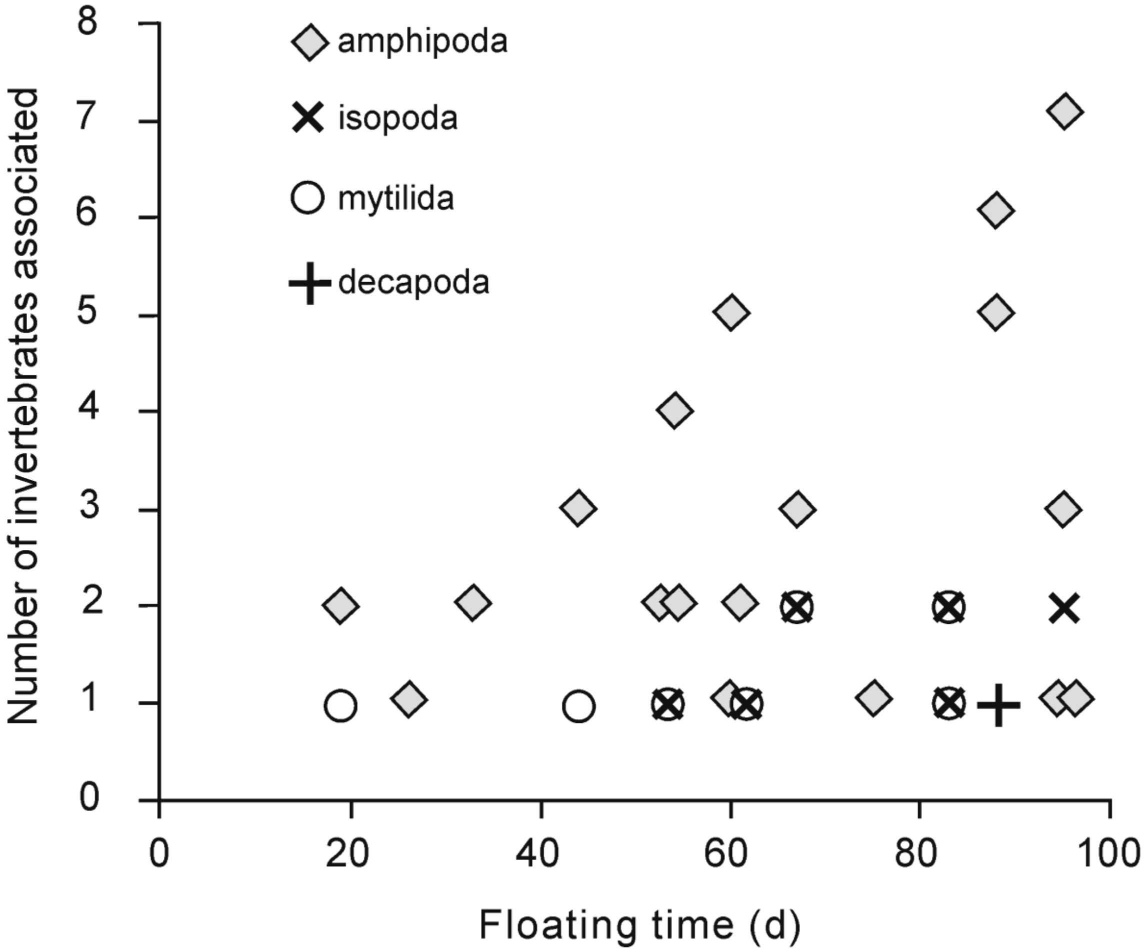

a)
Floating time
# of receptacles
# of vesicles
Growth rate
-0.43***
0.49***
-0.27***
-0.35*
b)
Floating time (d) observed
Floating time (d) predicted
0
30
60
90
25
50
75

Figure 4


◇ amphipoda
✕ isopoda
○ mytilida
+ decapoda
Number of invertebrates associated
0
1
2
3
4
5
6
7
8
0
20
40
60
80
100
Floating time (d)