

The role of buoyancy in mitigating reduced light in macroalgal aggregations

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Abstract

Many organisms live in aggregations. For marine organisms attached to the substratum, the presence of neighbors may reduce both the water flow and light encountered by an individual within a group. We used the marine macroalga *Turbinaria ornata* to investigate how water velocity and photon flux density were affected by aggregations under natural flow and light conditions in the field, and to explore how the ability to stand upright due to buoyancy impacted light interception by individuals in aggregations. We found that the flow experienced by thalli in the middle of a group in a backreef habitat was only about half the speed of the water flow they encountered after their neighbors were removed. This suggests that aggregated algae are subjected to lower hydrodynamic forces than are solitary thalli, but may also experience reduced rates of transport of dissolved nutrients and gases. Light sensors placed along the length of thalli positioned within and outside of clumps of *T. ornata* showed that the tops of buoyant upright thalli experienced similar light levels to solitary thalli, but that neighbors shaded the lower portions of thalli in aggregations. Individuals that were rendered non-buoyant (by filling their airbladders with water) could not support their own weight and those in aggregations experienced lower light at all points along their lengths than did upright buoyant individuals. Using *in situ* determinations of the rate of photosynthesis of *T. ornata* as a function of irradiance, we converted our field measurements of light interception to mg carbon fixed over the course of a day for whole fronds. Such estimates indicated that carbon fixation was higher for solitary buoyant and non-buoyant *T. ornata* than for buoyant individuals in aggregations, all of which were greater than for non-buoyant thalli in those clumps. Our results indicate that living in aggregations reduces the productivity of *T. ornata*, but this effect is mitigated by the buoyancy of thalli.

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1. Introduction

In benthic marine communities, individuals in aggregations may be exposed to lower light and water

flow than are solitary individuals. For photosynthetic organisms, high densities of individuals can lead to light limitation (Reed, 1990; Holbrook et al., 1991), as shading by overhead individuals can reduce light penetration into assemblages, thereby affecting light interception on lower parts of organisms and smaller individuals. The photic regime within aggregations of flexible organisms may also be highly variable as movement of individuals by turbulent water flow

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changes the gaps through which light can penetrate (Gerard, 1984; Wing and Patterson, 1993). Resistance to water flow by densely-packed individuals and shunting of water around aggregations can lead to reduced water velocities within the group (Fonseca et al., 1982; Jackson and Winant, 1983; Heiss et al., 2000), and correspondingly reduced nutrient (Jackson, 1977; Thomas et al., 2000), gas and particle delivery (Buss and Jackson, 1981; Eckman et al., 1989; Pullen and LaBarbera, 1991) within assemblages, and potentially lower productivity for individuals within aggregations (Okamura, 1986; Dalby, 1995).

However, organisms for which an aggregate lifestyle is common may have mechanisms to mitigate such consequences. Physiological adaptations of algae to low and fluctuating light environments include increases in number and size of photosynthetic units (Fietz and Nicklisch, 2002), changes to chlorophyll content (Walsh and Legendre, 1982), altered photosynthetic efficiency (Walsh and Legendre, 1982; Wing and Patterson, 1993), and increased growth rates under fluctuating light relative to constant light (Greene and Gerard, 1990).

Morphological responses of algae to low light levels include increases in the ratio of surface area to volume (Hay, 1986) as well as changes in morphology that lead to decreased self-shading, such as thinning of cell walls, decreases in branch frequency, and increases in the ratio of photosynthetic to structural tissues (Rigalov et al., 1988; Skriptsova and Yakovleva, 2002). When in aggregations where they compete for light with closely-packed neighbors, the palm algae, *Postelsia palmaeformis*, develop longer stipes that hold their crowns of fronds higher above the substratum than do solitary individuals (Holbrook et al., 1991). Terrestrial trees in dense stands face similar light interception issues, and photosynthesis in lower portions of trees can be limited by poor light penetration into a stand (Tang et al., 2003). Some species of light-demanding trees attain a position in the canopy by producing tall, slender trunks made of low density wood, thereby rapidly reaching reproductive size at a low cost of construction and support. However, the architecture of these trees is ultimately a balance between height extension and the ability to support the weight of the crown. In many terrestrial trees the proportion of total biomass allocated to foliage decreases as tree height becomes greater, reflecting the disproportionate increase in structural material required to maintain mechanical stability with height (Givnish, 1988).

In marine systems, buoyancy provides an additional strategy for maintaining an upright posture without the trade-off of investing in expensive structural support. This study was conducted to examine the effect of

buoyancy on light interception by algae in aggregations. The tropical macroalga *Turbinaria ornata* (Div. Phaeophyta) is a common macroalga on the reefs around the islands of French Polynesia (Payri and N'Yeurt, 1997). *T. ornata* occurs in aggregations or as solitary individuals, depending on the availability of hard substratum for attachment. In forereef habitats, *T. ornata* is a dominant organism on solid dead coral pavement from 1–10 m depth under breaking waves. Here there is ample hard substratum for settlement and growth and thalli are spread across the substratum, and flow is wave-driven and bi-directional. In backreef habitats, the substratum consists of coral heads separated by sand and dense aggregations of *T. ornata* form on dead patches of coral throughout the backreef, where they are exposed to primarily unidirectional flow. Aggregated adult thalli of *T. ornata* at backreef sites differ morphologically from isolated individuals from forereef sites in a number of ways (Payri, 1984; Stewart, 2006a), the most striking of which is the presence of air bladders in their blades, which makes them buoyant (Stewart, 2004). Adult fronds from forereef habitats do not possess air bladders and are not buoyant (Stewart, 2004), but thalli from the forereef develop bladders when transplanted to calm backreef habitats (2006a). Given that buoyancy is a phenotypically plastic trait expressed in backreef habitats where *T. ornata* forms dense aggregations, we used this system to investigate potential performance consequences of buoyancy of macroalgae in aggregations.

This study addressed the following questions: 1) How much are flow and light reduced within aggregations of *T. ornata*? 2) How does buoyancy affect light interception and carbon fixation for thalli outside and within aggregations?

2. Methods

2.1. Study sites

This research was conducted from the Richard B. Gump Research Station, University of California at Berkeley, on the island of Moorea, French Polynesia. Experiments were conducted in aggregations of *T. ornata* in the backreef of the barrier reef between Cook's Bay and Opunahu Bay on the north shore of Moorea (S 17° 28.699' W 149° 50.215').

2.2. Aggregations of *T. ornata*

The density of individuals of *T. ornata* in aggregations was determined by counting all individuals within

a 0.25 m² quadrat placed in twenty aggregations throughout the backreef. Aggregations were randomly chosen along 30-m transects using a random number table. If no aggregation was present at the selected random number (due to the patchiness of coral heads within the backreef), subsequent numbers were selected until the designated transect site fell on an aggregation.

2.3. Flow measurements

Measurements of flow velocities inside and outside twenty randomly-selected aggregations of *T. ornata* were made using a Marsh–McBirney electromagnetic water current meter (Model 511) over several days during July and August 2003. The probe of the meter was situated at the average height of adult thalli in the aggregations. For each aggregation, water velocity was recorded for five-minute periods with a sampling rate of 1 Hz. Then, without moving the probe, all thalli of the aggregation were manually removed and the flow recorded at the same position for 5 min. We then calculated the percentage of the mean ambient flow experienced in each aggregation. All measurements within a day were made within 1 h of each other. By alternating measurements in and out of aggregations, and conducting measurements within a relatively short time period (1 h), any changes in the ambient flow over this period did not affect results, which are presented as reduction of flow in aggregations as percentage of ambient flow. Flow regime was not observed to vary perceptibly during these measurements.

2.4. Light in aggregations

A LiCor 1400 4- π sensor was used to measure ambient photon flux density (PFD) of photosynthetically active radiation outside and inside aggregations of *T. ornata* on both sunny and overcast days in July and August 2003. All measurements within a day were conducted under the same type of sky conditions (i.e. all measurements on a sunny day were conducted in the absence of clouds). The cable of the sensor was attached to the base of an adjacent thallus so that the sensor was held at the mid-height of the aggregation. The height of the tip of the sensor was measured with a ruler with a precision of 0.5 cm. The sensor's cable held the sensor upright but was flexible and allowed it to sway like the adjacent algae with the ambient flow. Ambient light was measured in an open area adjacent to the aggregation by placing the sensor at the same height above the substratum as it was measured in the aggregation. The sensor was held in place with a dive weight. Light was

recorded at 1-second intervals for 5 min alternately inside and outside an aggregation over a period of 30 min, for 20 aggregations between 10:00–14:00 on days in June–August, 2003.

2.5. Light intercepted along length of buoyant and non-buoyant fronds in and out of aggregations

To compare light interception along the length of solitary buoyant and non-buoyant thalli, and buoyant and non-buoyant thalli in aggregations, twenty fronds equipped with photodiodes (described below) were placed either into the center ($n=5$ aggregate buoyant, $n=5$ aggregate non-buoyant), or well away from aggregations ($n=5$ solitary buoyant, $n=5$ solitary non-buoyant) in the backreef before dawn. Healthy adult thalli of *T. ornata* for use in the light experiments were haphazardly collected from the backreef, held in tanks with running seawater and used within one day. Adult thalli are defined as in Stewart (2006b) as thalli with reproductive tissue, but with less than 50% of their surfaces covered with epiphytes.

Photodiodes were created for underwater use by waterproofing galinium sulfide diffusion-type photodiodes (Hamamatsu Corporation) used in terrestrial ecology (Percy, 1989). Onset[®] Hobo[®] 4-channel external dataloggers were housed in waterproof boxes (Otterbox[®] 2000 series) and connections were waterproofed using Heat-shrinkable tubing (Digi-Key[®]) and Devcon[®] Flexane two-part epoxy. Photodiodes were attached with small cable ties to thalli in similar orientation as blades in each part of the thallus (Fig. 1). The top diode faced upward, toward the apex of the thallus, and the lower three diodes were positioned to face laterally, away from the stipe. Orientation of diodes was similar for all thalli in all treatments and diodes maintained their orientation throughout the sampling period.

Calibration of voltage to PFD of photodiodes was conducted by correlating the voltage recorded by each photodiode over the course of a day in June 2003 to photon flux density measured simultaneously from an adjacent LiCor PAR 4- π sensor ($r^2 > 0.80$ for all diodes). Diodes were attached face up next to one another on a metal grid situated at 1-meter depth in the backreef. Signals from the photodiodes were recorded every 5 s with a precision of 0.1 $\mu\text{mol photons}/(\text{m}^2\cdot\text{s})$. High frequency noise from the voltage signal from the photodiodes was later filtered using a low pass Butterworth filter in Matlab software at a cut-off frequency as determined using the method of Biewener and Full (1992).

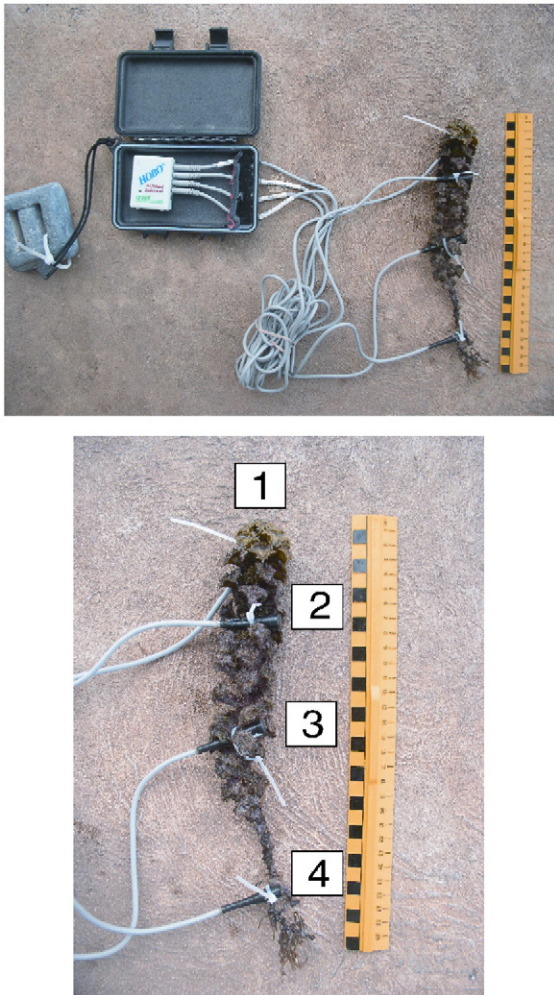


Fig. 1. Set up of datalogger in waterproof housing and placement of photodiodes on a backreef thallus of *Turbinaria ornata*.

For the non-buoyant treatment, thalli were used that had the gas in their airbladders replaced with water, rendering them non-buoyant, but not altering their shape. To remove the air, a small hole was cut into the end of the airbladder and the air within the bladder was shaken out. Buoyancy was only altered for non-buoyant test thalli. Aggregations were haphazardly selected based on size and accessibility from the lab for early morning and dusk sampling. Only aggregations greater than 0.5 m \times 0.5 m were used. Thalli placed in aggregations were attached by their holdfasts with cable ties to the bases of adjacent thalli in the aggregation so that their tips were at the same height as neighbors within the group. Thalli placed outside of aggregations were attached with cable ties to protuberances and holes in bare substratum. Housings containing dataloggers were weighted with 5 lb dive weights and

placed nearby so that there was sufficient slack in the cables that the movements of the thalli were not impeded and experimental fronds moved to and fro with ambient water motion in a similar way as adjacent fronds. Voltages registered by the photodiodes were recorded every 5 s from dawn until late afternoon over five days in July 2003.

Due to logistical limitations, ambient PFD measurements with the LiCor PAR 4- π sensor were recorded only during short portions (12:00–14:00) of the periods for which the photodiodes were deployed. To compare light intercepted by photodiodes across days that varied in ambient light (e.g. sunny and cloudy days), PFD recorded by photodiodes were normalized by dividing them by the ambient PFD recorded simultaneously.

2.6. Estimates of photosynthesis

Photosynthesis and respiration were estimated from whole thalli of *T. ornata*, incubated in 3-L. glass jars. Thalli were collected just prior to the experiments in the reef nearby the experimental area. Selected specimens did not have epiphytes and were about 18 cm in height, which represents approximately 0.8 g of dry mass. The ratio between the algal mass, the jar volume and the incubation duration was previously calculated according to Littler's (1979) recommendation in order to avoid any bottle effect (e.g., oxygen over-saturation in the jar during the incubation). Measurements were made during 24-h cycles in the field under natural light conditions; the jars were immersed at 1 m deep in the reef flat. Following a 30-minute incubation period, photosynthesis was measured every hour during daylight while respiration was recorded every hour and half at night after a 60-minute incubation. Between two incubation times, the jars were opened and the water was completely renewed before starting the following

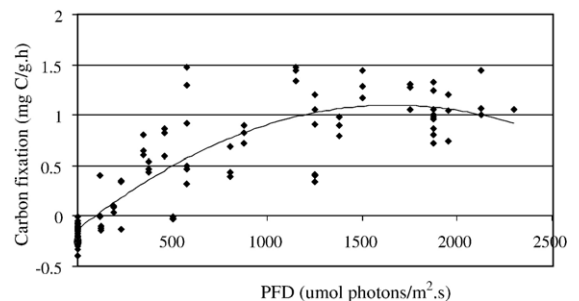


Fig. 2. Photon flux density PFD ($\mu\text{mol photons/m}^2\cdot\text{s}$) vs. carbon fixation ($\text{mg C fixed/g dry mass}\cdot\text{h}$) for *T. ornata*. Relationship is characterized by a second order polynomial fit of $y = -4E - 07x^2 + 0.0015x - 0.133$, $r^2 = 0.80$ (Matlab v.7).

incubation period. During incubations jars were frequently gently shaken in order to reduce the affects of diffusion limitation on photosynthesis. The experiment was conducted on six independent replicates, during Austral winter (July) and summer (December) in order to consider seasonal variation of photosynthesis. Dissolved oxygen was determined (± 0.01 ppm) using a Yellow Spring Instrument Model 57 oxygen meter equipped with a self-stirring polarographic probe. The oxygen rates were calculated as in Payri (1987) and expressed for each sample in mg C fixed/h·g dry mass assuming a metabolic quotient equal unity. Dry mass was obtained over 48 h at 60 °C in a drying oven. Irradiance was measured with a LI-COR LI-192SA quantum irradiance sensor (cosine collector), interfaced with a LI1000 datalogger. We assume that the incubation condition did not have strong effects on photosynthesis because the photosynthetic rates after

24 h were in the same range as at the beginning of the experiment.

2.7. Carbon fixation

Using the photosynthetic estimates, a calibration equation was established to convert PFD to rates of photosynthesis (mg C fixed/h·g dry mass) for buoyant and non-buoyant thalli in and out of aggregations (Fig. 2). The amount of carbon fixed over the course of a day was then calculated for thalli using photodiodes positioned at the top, middle and bottom of the bladed section and at the base of the stipe of each thallus ($n=5$) (Fig. 1). The dry mass of each section (top, middle, bottom, base) was calculated from the mean of each section of all test thalli. Thalli were rinsed in freshwater, cut into the four sections and dried at 60 °C on a drying oven for 48 h. The photosynthetic rate (mg C fixed/h·g dry mass) over the

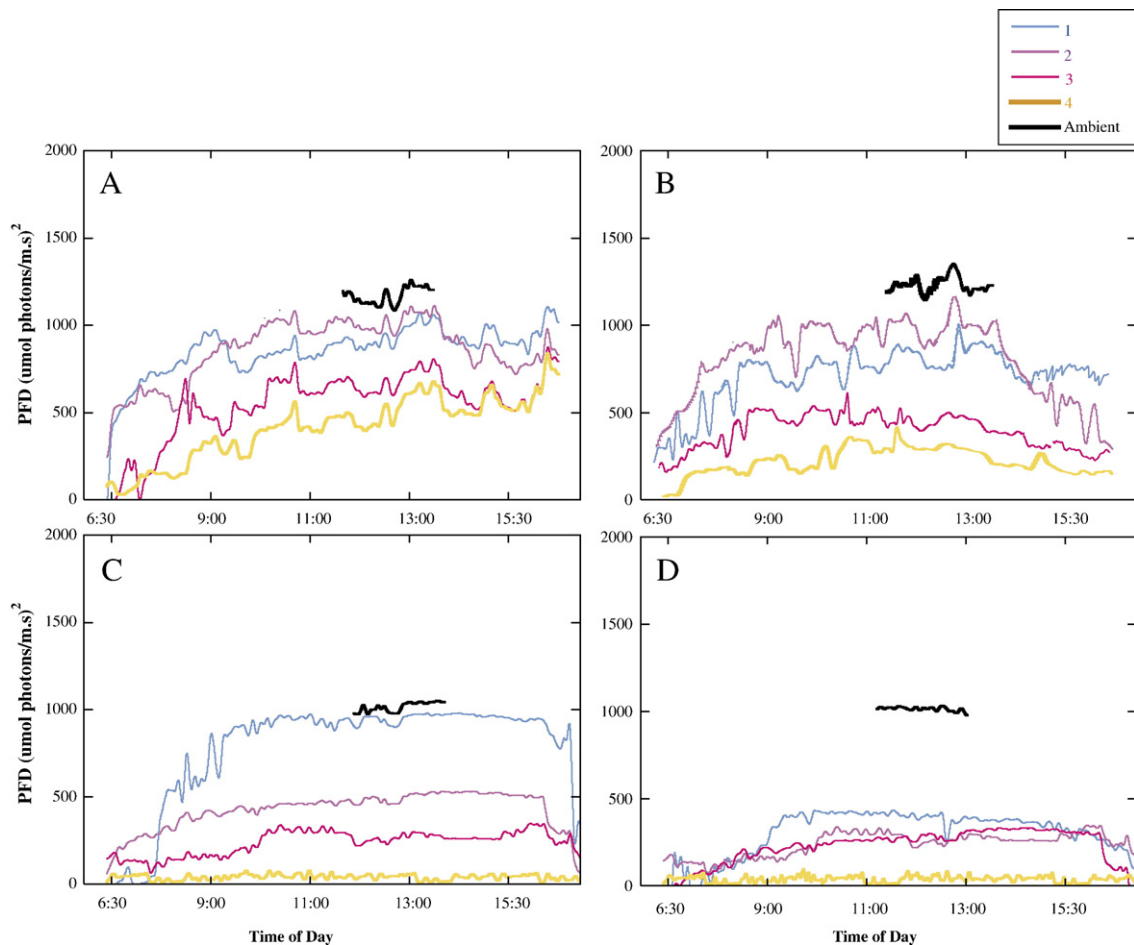


Fig. 3. Examples of PFD data collected by photodiodes 1, 2, 3, and 4 on A) solitary buoyant, B) solitary non-buoyant, C) aggregate buoyant and D) aggregate non-buoyant thalli from dawn until late afternoon on overcast days in Moorea in July, 2003. Ambient PFD from 12:00–14:00 is indicated.

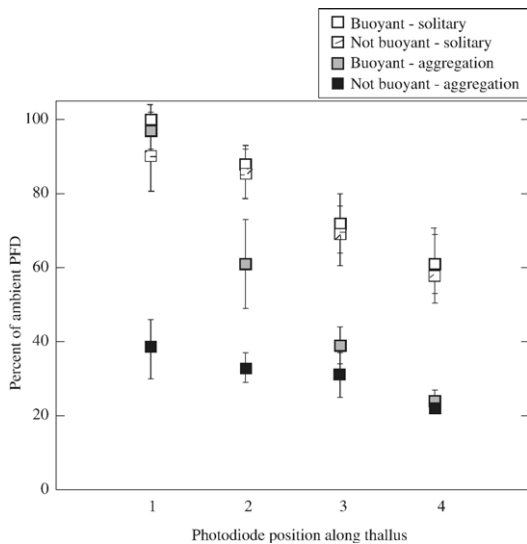


Fig. 4. Percent of ambient PFD intercepted by photodiodes at four heights on solitary and aggregate, buoyant and non-buoyant thalli of *T. ornata* (mean \pm standard deviation, $n=5$). Position 1 is at the top of thalli, position 2 is from 7–10 cm from the top, position 3 is from 13–15 cm from the top, and position 4 is just above the holdfast at the bottom of the stipe.

course of the day for each photodiode was then multiplied by the appropriate mean dry mass for that section and by 0.0014 (the number of times an hour divides into the 5-second sampling interval) to yield the amount of C fixed for each section of a thallus in each treatment during daylight hours. The C fixed by each section was summed to yield an estimate of the total daily C fixed by a whole adult thallus in each treatment.

2.8. Statistical analysis

All statistical analyses were conducted using Matlab software (v. 7, The Mathworks, Inc.) and significance determined by $p < 0.05$.

3. Results

3.1. Aggregations

The density of fronds of *T. ornata* in aggregations on coral heads in the backreef ranged from 64 to 140 individuals per 1 m² (96.4 ± 3.66 mean \pm S.E., $n=20$ quadrats).

3.2. Reduction of ambient flow speed in aggregations

Mean flow speed inside aggregations of *T. ornata* was only $52 \pm 2.7\%$ of ambient flow measured in the

same location after the removal of the aggregation ($n=20$ aggregations, paired t -test on arcsine square-root transformed proportions $t=7.352$, $df=38$, $p < 0.001$).

3.3. Reduction of ambient light within aggregations

Light was reduced within aggregations. The mean PFD measured with the LiCor PAR 4- π sensor light meter inside of aggregations was only $35 \pm 7.9\%$ of ambient light at the same depth outside aggregations ($n=20$ aggregations, paired t -test on arcsine square-root transformed proportions $t=21.247$, $df=38$, $p < 0.001$).

3.4. Photosynthesis vs. irradiance

Carbon fixation increased with increasing irradiance to 1600 PFD. Higher PFD resulted in photoinhibition (Fig. 2).

3.5. Effect of buoyancy on light interception and productivity in aggregations

Fig. 3 shows examples of light interception by photodiodes on buoyant and non-buoyant thalli in and out of aggregations over the course of a day. These data indicate that solitary thalli intercepted more light per thallus whether or not they were buoyant, and within aggregations buoyant thalli intercepted more light than non-buoyant thalli (Fig. 4). A three-way analysis of variance on PFD intercepted by photodiodes on thalli in each treatment indicated a significant interaction between the three factors (buoyant or not buoyant, solitary or aggregate, and photodiode position) (Table 1). In general, the percentage of ambient PFD intercepted by the tops of buoyant thalli inside and outside of aggregations was similar, but the proportion of ambient PFD reaching lower positions (i.e. toward the holdfast) on thalli in aggregations was less than that

Table 1

Results of a three-way ANOVA testing effects of aggregate vs. solitary distribution ('aggregate'), positive vs. negative buoyancy ('buoyancy'), and four levels of photodiode height ('height') on percentage of ambient PFD intercepted by algal thalli

Source	df	MS	F	p
Aggregate	1	2.187	279.94	<0.001
Buoyancy	1	1.276	163.29	<0.001
Photodiode height	3	0.752	96.29	<0.001
Aggregate \times buoyancy	1	0.100	12.91	<0.001
Aggregate \times height	3	0.048	6.18	<0.001
Buoyancy \times height	3	0.297	38.08	<0.001
Aggregate \times buoyancy \times height	3	0.038	4.87	<0.001
Error	64	0.007		



Fig. 5. Estimated carbon fixation per thallus over the course of a day for buoyant solitary, non-buoyant solitary, buoyant aggregate and non-buoyant aggregate thalli (mean \pm standard error, $n=5$). Carbon fixation values are based on PFD intercepted by photodiodes on thalli in each treatment converted to photosynthetic estimates using the photosynthesis vs. irradiance curve in Fig. 2. The horizontal line indicates means that were not significantly different as compared by Tukey–Kramer multiple comparisons (Matlab v.7).

reaching corresponding locations on solitary thalli (Fig. 4). Non-buoyant solitary thalli were not shaded by neighbors and the reduction of light intercepted by photodiodes lower on thalli was not as severe. Both buoyant and non-buoyant solitary thalli intercepted higher PFD than thalli in aggregations. In aggregations, buoyant fronds intercepted higher PFD along their lengths than non-buoyant thalli (Fig. 4). The percentage of ambient light reaching all photodiodes on buoyant thalli that maintained upright positions within the aggregation was higher than for non-buoyant thalli that bent under their own weight to positions below other buoyant thalli in the aggregation.

Estimates of carbon fixation indicate that buoyant thalli in aggregate distributions do experience a cost to productivity as a result of reduced light interception, but the reduction is not as much as if they were not buoyant. Outside of aggregations, carbon fixation of non-buoyant thalli was similar to buoyant thalli. Estimates of daily carbon fixation for whole thalli indicate that carbon fixation was significantly lower for non-buoyant aggregate thalli than buoyant aggregate, buoyant and non-buoyant solitary thalli (ANOVA $F=8.72$, $df=3$, $p=0.0012$). Whole non-buoyant thalli in aggregations were estimated to fix only 54–58% of the carbon that buoyant thalli fixed in aggregations, 45–50% of carbon fixed by non-buoyant solitary thalli, and roughly 40% of fixation by buoyant solitary thalli. Buoyant thalli of *T. ornata* in aggregations produced approximately 80% of the carbon produced by solitary buoyant fronds receiving

full ambient light (Fig. 5). Much of the difference in carbon fixation between buoyant solitary and buoyant aggregate thalli was due to reduced rates of productivity by the middle and lower sections of the bladed region of fronds, where light was reduced to 60% and 35% of ambient levels, respectively (Fig. 4). However, in aggregations higher values of carbon fixation in buoyant than in non-buoyant thalli were additionally the result of differences in light interception by the top section of the bladed region. The top sections of non-buoyant fronds in aggregations were estimated to produce only 40% of the carbon produced by the top section of buoyant fronds.

4. Discussion

4.1. Effect of buoyancy on light interception in and out of aggregations

Non-buoyant thalli experienced decreased light interception and carbon fixation compared to buoyant fronds. However, this effect was more pronounced for thalli in aggregations. Solitary, buoyant thalli intercepted the most light, followed by non-buoyant solitary thalli and buoyant aggregate thalli, although calculations of carbon fixation based on light interception and photosynthetic estimates indicated that these differences in carbon fixation were not significant. Non-buoyant thalli in aggregations intercepted significantly less light than any other treatment, and this was due to shading by neighbors. Non-buoyant thalli could not support their own weight and bent toward the substratum. Without neighbors, the amount of light non-buoyant thalli received was similar to upright, buoyant solitary thalli. The main difference between the solitary treatments was that light interception was generally reduced in the top diode of non-buoyant thalli, as the top was no longer pointed upwards but to one side as the non-buoyant thallus slumped under its weight. The result on light interception was minimized due to the clarity of the tropical water and the short height of thalli of adult *T. ornata* (~18 cm). For large kelps in temperate water, the effect of non-buoyancy in solitary thalli would be expected to be substantial given the high extinction coefficients experienced over 10–20 m, a typical length of temperate *Macrocystis* or *Nereocystis* kelp fronds (Abbott and Hollenberg, 2001). Loss of buoyancy for these large macroalgae might well result in drastically reduced light availability and subsequent productivity (e.g. King and Schramm, 1976; Stewart and Carpenter, 2003; Wernberg et al., 2005). The results of this study indicate that for *T. ornata* in tropical locations the effect of non-buoyancy on light interception and subsequent carbon fixation of solitary thalli likely is not very important.

In aggregations, however, loss of buoyancy in *T. ornata* substantially decreased light interception due to shading by neighbors. Non-buoyant thalli that slumped to the substrate no longer occupied a place in the top of the aggregation where most light interception occurred (Fig. 4). The degree to which non-buoyant thalli are affected by shading is a function of the density of neighbors and the degree to which they move in the ambient water motion and create gaps that allow light to penetrate into the group (Wing et al., 1993). However, the pinecone-like shape of *T. ornata* and its buoyancy maintains spacing in the aggregation allowing light penetration into the stand and ensures that at least the tissue at the top of the thallus, which is the youngest and may support the highest photosynthetic rates (Kilar et al., 1989; Stengel and Dring, 1998) is exposed to maximal light. Buoyancy also ensures that thalli do not stack up on top of one another as might occur in an aggregation of non-buoyant thalli.

4.2. Effects of aggregations on water flow

Reduced water flow velocity within aggregations of macroalgae may result in decreased delivery of nutrients and dissolved gases to algae within the clump, affecting photosynthetic rates that can be flow-dependent (Wheeler, 1981; Koehl, 1986; Koehl and Alberte, 1988; Stewart and Carpenter, 2003). Reduction of flow speeds to 5–7 cm/s, as occurred in aggregations of *T. ornata* when ambient flow velocity was 14 ± 0.6 cm/s, is within or below reported saturation velocities for other macroalgae that fall between 0.05 and 0.18 m/s (Boynton et al., 1981), 0.02–0.06 m/s (Wheeler, 1980, 1981) and 0.08–0.17 m/s (Stewart and Carpenter, 2003), and may limit photosynthesis for *T. ornata*. However, during severe winter storms, flow speeds in the backreef of the north shore of Moorea may reach up to 1.5–2.0 m/s (J. Henchn, pers com.), which can exert hydrodynamic forces strong enough to break stipes of *T. ornata* (Stewart, 2006a,b). In these instances, reduction of flow velocities and corresponding hydrodynamic forces (which are proportional to the velocity² and the acceleration of water motion) in aggregations may protect fronds within aggregations from dislodgement, as has been found for other aggregated algae (Johnson, 2001; Pratt and Johnson, 2002).

4.3. Effects of aggregations on light interception and photosynthesis

Crowding of individuals in dense assemblages can reduce productivity due to competition for resources

(e.g. Okamura, 1986; Scrosati and DeWreede, 1998). Light within aggregations of *T. ornata* was reduced to 35% of ambient levels compared to ambient levels at the base of bladed regions of solitary thalli. Light levels measured within aggregations of the bull kelp, *Nereocystis luetkeana*, range from 29% to 84% of ambient levels, depending on blade morphology and fluttering in ambient currents (Koehl and Alberte, 1988), whereas irradiance within aggregations of the intertidal sea palm *Postelsia palmaeformis* drop to 10% of ambient levels at mid-height of an aggregation (Holbrook et al., 1991). The consequences to light interception and photosynthesis of this decrease depend on the arrangement of blades (the main photosynthetic organs). Blades of *P. palmaeformis* are confined to a crown at the top of the stipe where light levels are ~75% of ambient and only experience shading on the ends of their blades that hang into the aggregation or are shaded by adjacent blades. Blades of *T. ornata* grow at least halfway down the length of its stipe and therefore light reduction within aggregations affects many of the blades and can substantially reduce whole frond productivity.

Estimates of carbon fixation in this experiment were determined directly from light interception measured in the field, and laboratory measurements of photosynthesis at a range of constant PFDs at a fixed water motion level. They therefore do not incorporate effects to photosynthesis due to slow or variable water velocities inside of aggregations or physiological adaptations to low light by thalli or tissues experiencing reduced irradiance inside of aggregations. Many seaweeds can adjust physiologically to low and inconsistent light levels, and may actually experience higher photosynthetic rates under light flecking conditions than under steady light of the same mean value (Walsh and Legendre, 1983; Queguiner and Legendre, 1986; Greene and Gerard, 1990; Wing and Patterson, 1993). However, the effect of light fluctuations on photosynthesis can depend on the spectral quality, the intensity of light, the number of flecks per time, and can be species specific (Queguiner and Legendre, 1986; Dromgoole, 1988; Litchman, 1998, 2003). Thus, it is difficult to predict the effect or even the direction of the effect of natural light fluctuations to the metabolism of *T. ornata*.

However, if all backreef fronds of *T. ornata* respond in a similar fashion to reduced and variable light levels, as well as decreased flow rates then the patterns presented in this study should be applicable for comparison between fronds of *T. ornata* in and out of aggregations. In addition, by removing the effect of physiological response to low light or flow this study provides the opportunity to isolate the effect of one

factor, buoyancy, on carbon fixation for seaweeds in aggregations.

Carbon fixation calculations were made from values from whole thalli, and therefore do not incorporate age-specific photosynthetic rates of tissue at different locations on thalli. We suspect that whole thallus photosynthetic rates average the differences between young and old tissue, but this was not specifically tested. Elevated carbon fixation rates in young tissue may accentuate the trend depicted in Fig. 5 if the contribution to whole thallus photosynthesis and carbon fixation from tissue lower on fronds is minimal and young tissue at the tips of *T. ornata* thalli is able to maintain overall thallus photosynthetic rate. In this case, the reduction to productivity from shading by neighbors is less than if photosynthetic rate were similar along the entire thallus. This possibility highlights the potential for additional value of buoyancy for productivity of *T. ornata* in aggregations.

5. Conclusions

Buoyancy is a mechanism by which algae maintain upright postures in the water column. In aggregations buoyancy can reduce shading by neighbors by keeping portions of algae at or near the top of the canopy where they intercept more light (and thus may show higher productivity) than if they were not buoyant and were prostrate along the bottom. Thus, in marine systems buoyancy provides an alternative mechanism to stiffness for maintaining an upright posture in the water column, and this can be particularly important for photosynthetic organisms living in dense aggregations.

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