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The Ecology Of Drift Algae In The Indian River Lagoon, Florida

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THE ECOLOGY OF DRIFT ALGAE
IN THE INDIAN RIVER LAGOON, FLORIDA

by

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B.S. University of Tampa, 2000

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
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ABSTRACT

To gain an understanding of the ecology of drift algae in the Indian River Lagoon system along the east coast of central Florida, four questions were addressed: 1) What is the composition and rate of accumulation of drift? 2) How much movement and turnover occurs within drift accumulations? 3) Do growth rates differ for drift versus attached algae? 4) Is there a difference in photosynthetic performance in drift versus attached algal species? Manipulative field and laboratory experiments were conducted to address these questions with the green macroalga *Codium decorticatum* and the red macroalga *Gracilaria tikvahiae*. Changes in pigment concentration and biomass were used as indicators of acclimation from an attached to drift state in *Gracilaria tikvahiae* and *Codium decorticatum*. Short-term physiological changes as demonstrated by electron transport rate (ETR) were also used as indications of acclimation from an attached to drift state in *C. decorticatum*. Composition and rate of accumulation of drift varied by season. While both transport and turnover of drift occurred, turnover within drift accumulations occurred at low rates and was significantly lower in the spring during decreased flow rates. There were no significant differences in growth or pigment concentrations in drift versus attached *G. tikvahiae or C. decorticatum.* In addition, there were no apparent physiological acclimations to a drift state in *C. decorticatum*.

To my family, friends and Mr. Step Aside Butch,

thank you for everything! “1,4,3”.

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CHAPTER ONE: INTRODUCTION

A marine alga may exist attached to a substrate, fixed in sediment, unattached on the benthos, or as a free-floating individual (Norton and Mathieson 1983, Dawes 1998). These last two groups are classified as drift algae. Drift algae originate when attached algae are removed from their substrate through physical processes such as storms, tidal surge, wave action, abrasion, or feeding by fish and invertebrates (Norton and Mathieson 1983). Reattachment of drift is uncommon (Norton and Mathieson 1983), but does occur in some species (Walters *et. al*. 2002, Herren, *et. al*. in press). Communities of drift algae are common and found throughout the world's fjords, oceans, salt marshes, bays, and estuaries (e.g. Norton and Mathieson 1983, Virnstein and Carbonara 1985, Lobban and Harrison 1994, Dawes 1998). As freely moving organisms, drift algae passively disperse with currents (Lobban *et al.* 1983, Norton and Mathieson 1983, Virnstein and Carbonara 1985). The suite of physical factors that drift algae encounter may significantly impact their physiology (Norton and Mathieson 1983, Lobban and Harrison 1994). Responses of attached benthic macroalgae to environmental factors are widely studied and are common in the literature. Unattached algae may encounter more frequent changes in temperature, water motion, light and nutrient availability than their attached counterparts. The dispersal and potentially unique responses in physiology of drift individuals to these factors are addressed in this study.

1.1 Biology of Unattached Algae

Most macroalgae, unlike terrestrial plants, do not possess vascular tissue and therefore do not need to be anchored to absorb nutrients (Norton and Mathieson 1983). The site of nutrient uptake in macroalgae is the entire thallus, with rhizoid structures used only for attachment purposes (Norton and Mathieson 1983, Lobban and Harrison 1994, Dawes 1998). All unattached algae are derived from individuals that were originally attached to substrates via rhizoids (Norton and Mathieson 1983). Attached individuals originate from settlement of algal spores, zygotes, or vegetative fragments whose rhizoids affix to the substrate and mature. The establishment of an attached population is dependent on adhesive rhizoid development and contact with a suitable substrate. These rhizoids attach to whatever they contact, whether or not that substrate is suitable for long-term retention. For example, an oyster shell may provide sufficient substrate for initial attachment, but further growth of the alga may dislodge the shell and send both adrift (Burrows 1958).

Rhizoid contact with a substrate does not guarantee attachment. Moss *et al.* (1973) and Norton (1978) found that silt covering a substrate will deter rhizoids from securely attaching to a substrate, as the rhizoids adhere to the sediment particles instead of the substrate. Viability of rhizoids is also a factor to consider for successful attachment. In some species, zygotes have been found to have adhesive rhizoids for a limited time (Norton 1978, Deysher and Norton 1982). Individuals suspended in the water column after that time will not attach thereafter even if it comes into contact with a viable substrate (Deysher and Norton 1982). For example, zygotes of *Sargassum muticum* have viable rhizoids for approximately one month (Deysher and Norton 1982). Either of these scenarios would render an alga part of the drifting community very early in its life-history.

Macroalgae that do successfully attach face many post-settlement challenges. Although their rhizoids initially prevent them from being dislodged, abiotic and biotic factors can dislodge macrophytes from their substrate. Abiotic factors include water motion, light availability, and nutrient availability, while biotic factors include competition and herbivory (Norton and

Mathieson 1983). Wave action and water motion can increase until the alga can no longer withstand the resulting drag on the thallus. This may result in abrasion against the substratum or other organisms (Lobban and Harrison 1994). Reduced light availability and nutrients can cause tissue atrophy and death in portions of an individual, leading to pieces of the thallus breaking off (Peckol and Rivers 1996, Menéndez and Comín 2000). Competition between algal species for space can result in shading or overgrowth of individuals that, in turn, causes breakage via tissue atrophy (Lobban and Harrison 1994). Fishes and invertebrates feeding on macroalgae or using fragments for camouflage can also contribute to mechanical stress on the thallus (Norton and Mathieson 1983, Lobban and Harrison 1994, Dawes 1998, Norkko 1998, Macía 2000, Walters *et al.* 2002, Herren *et al.* in press). These factors all have the potential to remove macroalgae from their substrate or create fragments.

Individuals with no rhizoids or viable holdfast are considered drift algae (Collins 1914, Norton and Mathieson 1983). Norton and Mathieson (1983) identified five major categories of drift: entangled, loose-lying, aegagropilous, embedded, and floating. Entangled algae are found intertwined around other macrophytes or invertebrates. Common entangled examples include *Hypnea musciformis* and several species of the genus *Gracilaria* (Norton and Mathieson 1983). Loose-lying individuals are simply found on the benthos, sometimes forming large matted accumulations. Examples of common loose-lying species include *Codium decorticatum* and *Dasya baillouviana* (Phillips 1961). Aegagropilous forms resemble a spherical ball composed of one or several species. Members of the genus *Cladophora* are examples of aegagropilous forms (Norton and Mathieson 1983). Embedded algae lack holdfasts but have their bases buried in sediment. They are therefore fixed in place, but are not technically attached. For these individuals to survive, they must rely on a faster upwards growth rate than the sedimentation rate. This is the rarest form of unattached algae. Members of the genus *Fucus* are commonly found embedded (Den Hartog 1972). Pelagic, floating algae are found at various levels in the water column, depending on their buoyancy. The best example of floating drift algae are members of the genus *Sargassum* (Norton and Mathieson 1983).

After detachment, drift algae may be dispersed from its original location or remain nearby. Dispersal mechanisms include abiotic and biotic vectors (Collins 1914, Conover 1964, Norton and Mathieson 1983, Dawes 1998). Abiotic vectors include wind and water motion (Collins 1914, Conover 1964, Virnstein and Carbonara 1985, Dawes 1998). Biotic vectors include transport by herbivores. If the individual disperses from its point of origin, it is susceptible to varying environmental conditions that can be a radical departure from the original habitat. Light levels, nutrient availability, temperature, pH, flow rates, and herbivory rates may change. Whether or not the individual can acclimatize to these new conditions will determine survival.

Morphological acclimation to abiotic factors has been noted for many drift macrophytes, although the mechanisms behind these changes are not well understood (Norton and Mathieson 1983). Known morphological changes in drift individuals versus their attached counterparts include flattening or thickening of the thallus, curving of apical tips, differences in pigmentation, and overall shape of the individuals (Collins 1914, Norton and Mathieson 1983). Attached and unattached individuals from the same species can also exhibit altered branching patterns (Naylor 1928, Norton and Mathieson 1983). For example, *Fucus serratus* had an increased number of closely packed branches in drift forms compared to attached forms (Naylor 1928). The most common physiological acclimation to a drift state across all taxonomic groups of algae is the loss of reproductive capacity (Norton and Mathieson 1983, Lobban and Harrison 1994). The literature of drift studies describes the inability of many drift species to reproduce sexually. Drift macrophytes instead rely solely on vegetative fragmentation as a means of propagation (Lobban *et al.* 1983, Norton and Mathieson 1983, Dawes 1998). In a few studies, reproductive drift individuals were collected, but it was determined that the individuals were reproductive prior to entering the drift (Gibb 1957, Chock and Mathieson 1976, Oliveira and Fletcher 1980). Womersley and Norris (1959) reported collection of reproductive individuals from the drift, but later found that there was a low frequency of viable reproductive structures on those individuals. Gibb (1957) also reported low viability of gametes in drift individuals.

Induction of reproductive growth in macrophytes is triggered by environmental cues and natural circadian rhythms (Lobban and Harrison 1994, Dawes 1998). Environmental cues include temperature, light quality, day length (photoperiod), and salinity fluctuations. Photoperiod is considered to be the most important environmental cue for production of reproductive tissues (Norton and Mathieson 1983, Lobban and Harrison, 1994). These factors may change constantly when an individual enters a drift state. It has been hypothesized that lack of normal cues and photoperiods can result in a constant vegetative state (Norton and Mathieson 1983).

Vegetative growth is not as energetically expensive to an individual as reproductive growth, and therefore may be favored when energy reserves are low (Lobban and Harrison 1994). However, asexual reproduction has the disadvantage of not producing any genetic variation (Lobban and Harrison 1994). Therefore, fragmented individuals may survive, but by not reproducing sexually they are not adding variation to the population. Teasing apart the effects of photoperiod from other environmental factors and natural algal circadian rhythms is difficult. To date, no one has determined why unattached algae are unable to sexually reproduce.

1.2 Ecology of Drift Communities

Drift algae can be beneficial to marine communities (Norton and Mathieson 1983). Larval forms of many species of fish and invertebrates inhabit drift algae until they are large enough to survive threats of predation in the open water (e.g. Sand-Jensen and Borum 1991, Bonsdorff 1992, Valiela *et al*. 1997, Dawes 1998, Raffaelli 2000). Rafting of organisms within assemblages of algae has been well documented and has implications for transport to new habitats (e.g. Bell and Hall 1997, Dawes 1998, Abgrall and Walters 2003). Rafting can lead to increased geographic ranges and rates of dispersal of animals associated with drift (Bonsdorff 1992, Bell and Hall 1997). Drift algal mats can also result in local increases in species richness and composition through provision of additional resources (Shaffer *et al.* 1995). For example, drift algae provide space on their thalli for mud tubes for several species of amphipods (Shaffer *et al.* 1995, Norkko 1998).

Rafting has the potential to bring invertebrates and larval fish to otherwise unvegetated soft-bottom habitats that they would normally not inhabit, altering community structure (Norton and Mathieson 1983, Bonsdorff 1992, Lobban and Harrison 1994). Bonsdorff (1992) found that drifting mats of algae impacted a sandy-bottom benthic community. Settlement of the bivalve *Macoma balthica* was reduced by over 70% by drift algae in the Baltic Sea (Bonsdorff 1992). In addition, the locally dominant polychaete *Manayunkia aestuarina* was not found under drift mats, while the amphipod *Corophium volutator* increased in abundance under the algae (Bonsdorff 1992). Differences in invertebrate abundances during this two-year study were positively correlated with the presence of drift, but not correlated with changes in organic content of the sediment or oxygen levels in the water due to the algae (Bonsdorff 1992).

One potential negative effect of dispersal of drift algae is the ability for exotic species to invade new habitats (Cole and Sheath 1990, Dawes 1998). Transport of marine organisms on drift algae or the drift algae itself can contribute to species invasions (Norton and Mathieson 1983, Cole and Sheath 1990, Bonsdorff 1992, Shaffer *et al.* 1995, Dawes 1998). If, after entering a new habitat, these organisms find their new surroundings suitable for growth and propagation, established breeding populations can result. Once established, invasive species can often be hard to remove and may result in lowered species richness and diversity (Cole and Sheath 1990, Dawes 1998).

Dispersal of drift algae not only affects faunal diversity, but that of other macrophytes as well. As macroalgae disperses, wind and water flow may bring individuals into contact with each other, forming drifting mats (Norton and Mathieson 1983). These drift assemblages are usually species rich and may have both positive and negative effects on macrophytes beneath them (shading) or that they contact (allelopathy) (Philips 1961). Algae within these assemblages often have reduced fitness due to shading from canopy individuals and therefore decreased photosynthetic activity and growth (Norton and Mathieson 1983, Lobban and Harrison 1994, Dawes 1998). Peckol and Rivers (1996) investigated the effects of hypoxia, anoxia, elevated ammonium, and reduced light on the physiological responses of the macroalgae *Cladophora vagabunda* and *G. tikvahiae* in Waquoit Bay, Massachusetts. These two species merged and accumulated in drifting mats in summer months. Within these mats, Peckol and Rivers (1996) found elevated ammonium levels, rapid light attenuation, hypoxic, and anoxic conditions. Photon flux density (PFD) decreased to 10% of surface irradiance within 2 to 4 cm in mats of *C. vagabunda* and *G. tikvahiae* (Peckol and Rivers 1996). Oxygen profiles within algal mats of both species were positively correlated with mat depth and fell to anoxic levels within 3 cm

(Peckol and Rivers, 1996). Both species were found to have reduced respiration rates, depressed growth and nutrient uptake rates when associated with these mats (Peckol and Rivers 1996). In addition, they found that only *C. vagabunda* was able to fully recover from long-term burial within a drift mat. Under optimum light and oxygen levels, blackened fronds of *C. vagabunda* showed normal photosynthetic and nutrient uptake rates after only two days of recovery (Peckol and Rivers 1995, 1996). Peckol and Rivers (1995) concluded that reduced ammonium uptake and respiration rates were a necessary acclimation to drift conditions and rapid light attenuation within macroalgal mats.

Light attenuation within algal mats is not only important in the physiological aspect of algae in the drift assemblage itself, but to the organisms inhabiting the zone beneath the mat. Benthic algae and seagrasses can be shaded by drift, potentially affecting their fitness (Virnstein and Carbonara 1985, Lobban and Harrison1994, Dawes 1998). Algae that do not receive enough light to bring them to their minimum photosynthetic capacity will respire and consume oxygen from the surrounding water (Lobban and Harrison 1994). If the algal oxygen demand outstrips oxygen availability, oxygen levels drop to extremely low (hypoxic) or zero (anoxic) levels (Lobban and Harrison 1994). Eventually, individuals not able to compensate for reduced irradiance and low oxygen levels will begin to decompose. Although decomposition of drift algae has been shown to be an important source of nutrients in some ecosystems (Sassi *et al.* 1988), decomposition in an anoxic habitat can drive oxygen levels even lower (Lobban and Harrison 1994, Valiela *et al.* 1997, Dawes 1998). Coupled with reduced flow through dense aggregations of drift algae, the lack of oxygen may be fatal to infaunal and epibenthic organisms such as shrimp, tube-building worms, and crabs (Lobban *et al.* 1983, Norkko and Bonsdorff 1996a, b, Norkko 1998).

1.3 Physiology of Macroalgae

Photosynthesis is a metabolic process occurring in all oxygen-producing plants (Lobban and Harrison 1994). The incorporation of carbon from the environment into organic compounds is primary productivity, which is the purpose of photosynthesis. All photosynthetic organisms utilize energy from light as the power source behind photochemistry (Ramus *et al.* 1976, Lobban and Harrison 1994).

Light traveling in packets (photons) are absorbed by pigment molecules in the thylakoid membrane of the chloroplast. Chlorophylls, carotenoids and phycobiliproteins are three types of algal pigments used in light harvesting (Lobban and Harrison 1994). Chlorophyll *a* is found in all photosynthetic plants and is the most important light harvesting pigment (Lobban and Harrison 1994). Light-harvesting molecules are arranged into two photosystems within the thylakoid membrane; Photosystem I (PS-I) and photosystem II (PS-II). These two systems have pigment complexes that funnel light energy to reaction centers (RCs), where electrons are passed on to eventually produce ATP (Ramus *et al.* 1976, Lobban and Harrison 1994, Dawes 1998).

The number, size, and distribution of light harvesting pigments, photosystems, and chloroplasts help determine the efficiency at which light is harvested (Lobban *et al.* 1983, Dawes 1998). Photosynthetic rate depends on the amount of light absorbed. This relationship is mathematically represented as a photosynthesis vs. irradiance curve (P vs. I) (Platt 1980). The upward initial slope of a curve is called alpha (α) and is an indicator of quantum yield (Krause and Weis 1991, Lobban and Harrison 1994). The maximum photosynthetic rate (P_{max}) is the height of the curve where photosynthesis is saturated. The irradiance level at which P_{max} occurs is called saturating irradiance or I_k (Lobban and Harrison 1994). These parameters, when measured and compared can give insight into the overall efficiency of the light harvesting and photochemical pathways of photosynthesis (Krause and Weis 1991).

In the present study, accurate estimates of photosynthetic performance were made based on fluorescence of chlorophyll *a* rather than more traditional carbon fixation or oxygen evolution methods. The reaction center of PS II houses a molecule of chlorophyll *a*. As electrons are passed out of the reaction center, an acceptor molecule must be available to that electron. In the absence of an open electron acceptor, excess light hitting the reaction center is re-emitted at a higher state (Lobban and Harrison 1994). This photon re-emittance is called fluorescence (Krause and Weis 1991). Measurements of chlorophyll *a* fluorescence against known irradiance levels provide a reliable estimate of electron transport rate (ETR) through PS II (Beach *et al.* 2003). Resulting graphs of ETR versus irradiance (ETR vs. I curves) can then be used to compare physiological performance in photosynthetic organisms (Krause and Weis 1991, Beach *et al.* 2003).

1.4 Drift Algae in the Indian River Lagoon

In Florida, The Indian River Lagoon (IRL) system is a shallow (average depth: 1.5 m), wind-driven system with wide annual ranges of temperature (9 to 35ºC) and salinity (15 to 45 ppt) (Walters *et al.* 2002). Despite high abundances of drift algae present in this system, little is known about the ecology and physiology of these macrophytes (Virnstein and Carbonara 1985, Walters *et al.* 2002, Abgrall and Walters 2003).

Drift algal accumulations in the IRL vary in frequency and size over both short (24 hours) and long (weeks) time periods (Virnstein and Carbonara 1985, Abgrall and Walters 2003). Movement of drift is dynamic and was found to be affected by seagrass canopy height, wind velocity, and water depth (Virnstein and Carbonara 1985). A study done in Tampa Bay under conditions similar to those in the IRL found that transport of drift algae was greatest in high wind (>8.5 m/s) and shallow water (<1.0 m) conditions (Madley and Bell 1996). Information on drift communities in the IRL has been limited to percent cover at the division level (i.e. Rhodophytes) when drift assemblages were retained in seagrass beds (Virnstein and Carbonara 1985). Snelson and Johnson (1995) found that the presence of drift algae in the IRL altered fish community structure by increasing the number of juveniles of the pinfish *Lagodon rhomboides*, possibly due to increased habitat and refuge provided by drift accumulations.

1.5 Biology of Gracilaria tikvahiae

With approximately 4,000 identified species (98% marine), red algae are classified in Division Rhodophyta, Kingdom Protista (Dawes 1998). Members of the genus *Gracilaria* (Gracilariaceae, Gigartinales) are a major component of drift in the IRL (Phillips 1961, Virnstein and Carbonara 1985, Virnstein and Howard 1987). Part of this study focuses on *Gracilaria tikvahiae* (McLachlan). *Gracilaria tikvahiae* (Fig. 1A) is commonly found in calm waters of estuaries and bays to depths of 10 m (Littler and Littler 2000). This genus is found in all oceans except the Arctic; *G. tikvahiae* has been reported in temperate to tropical waters (McLachlan and Bird 1984). The appearance of the species can vary between individuals, ranging from 10 to 37 cm in length and from deep green to yellow, red, or brown in color, depending on the concentrations of chlorophyll and phycobilin pigments (Littler and Littler 2000). *Gracilaria tikvahiae* can be found growing free in drift or attached to small rocks or coral fragments in subtropical waters (Littler and Littler 2000) or on other available hard substrates, such as shells of the eastern oyster *Crassostrea virginica* in Mosquito Lagoon.

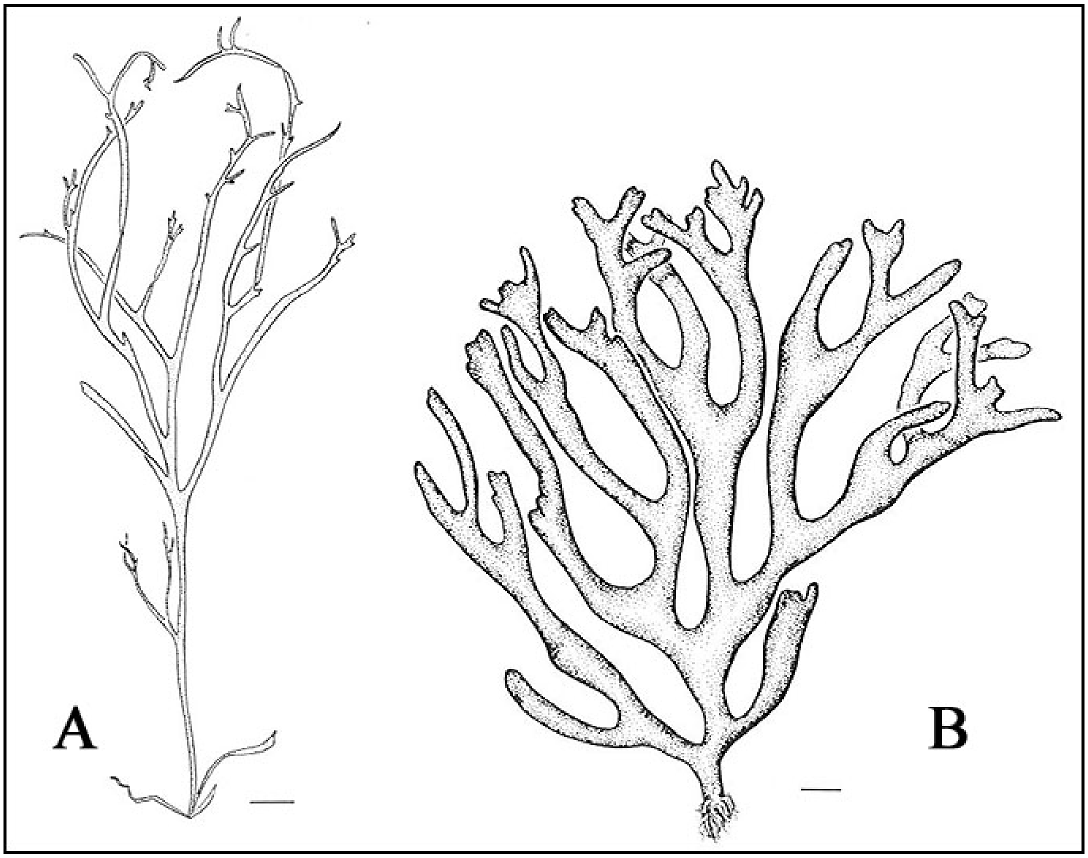

Figure 1: A) Thallus of Gracilaria tikvahiae. B) Thallus of Codium decorticatum (Schneider and Searles 1991).

1.6 Biology of Codium decorticatum

Another important component of drift in the IRL is *Codium decorticatum* (Codiaceae, Bryopsidales) in Division Chlorophyta, Kingdom Protista (Dawes 1998). *Codium decorticatum* (Howe) is a large unicellular alga with spongy, dichotomously branched thalli reaching 25-100 cm in height (Fig. 1B) (Littler and Littler 2000). This species is found in low-flow, temperate and subtropical estuaries and bays to depths of 15 m. It can also be found on intertidal and subtidal high-energy coastlines to depths of 15 m (Littler and Littler 2000). In the IRL, *C. decorticatum* can be found growing on shells of the eastern oyster *Crassostrea virginica* or shells of the clam *Mercenaria mercenaria* and *M. campechiensis*.

CHAPTER TWO: RESEARCH METHODS

2.1 Study Sites

Research was conducted at two sites in the Indian River Lagoon (IRL) along the east coast of central Florida between March 2002 and June 2003 (Fig. 2). One site was in waters adjacent to Fellers House Field Station (28º 54’ N; 80º 49’ W) in Mosquito Lagoon, in the northern region of Canaveral National Seashore. The second site was in Titusville (28º 33’ N; 80º 48’ W) on the Indian River. Major components of drift algal assemblages at both locations were the red macroalgae *Hypnea spinella, Gracilaria tikvahiae, Dasya baillouviana, Agardhiella subulata* and *Acanthophora spicifera*, and the green algae *Enteromorpha intestinalis, Enteromorpha flexuosa,* and *Codium decorticatum* (Virnstein and Carbonara 1985, Abgrall and Walters 2003). Species found as both attached and unattached individuals varied over the course of a year (Abgrall and Walters 2003). *Gracilaria tikvahiae* (Rhodophyta) and *Codium decorticatum* (Chlorophyta) are two of the most abundant drift species in the IRL and were therefore chosen for manipulative experiments during this study. Experiments on *G. tikvahiae* were conducted in the summer and winter of 2002. *Codium decorticatum* experiments were run in the spring of 2003.

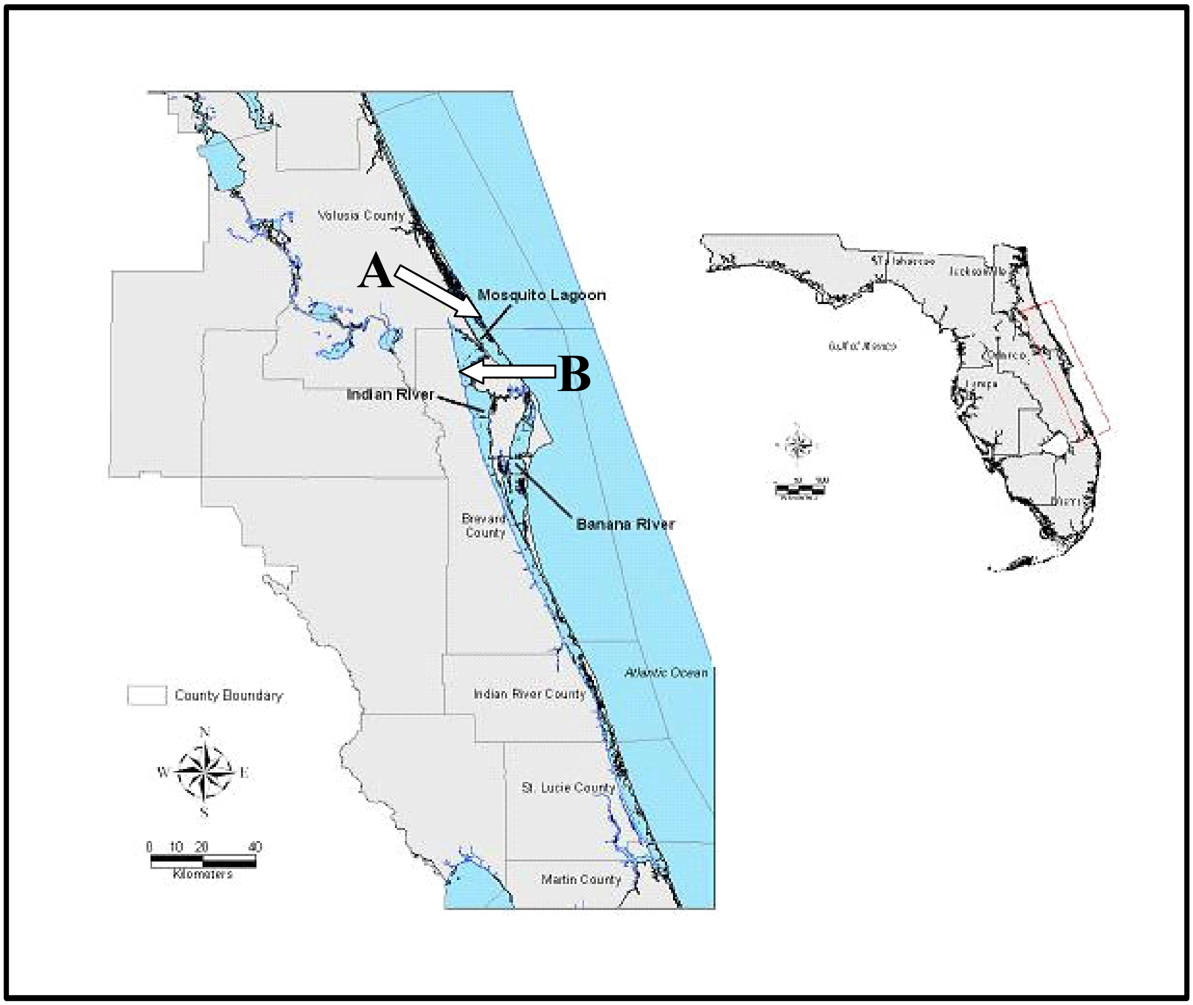

Figure 2: Map of two research sites. A) Fellers House Field Station in Mosquito Lagoon, and B) near Titusville in the Indian River.

2.2 Composition and Rate of Accumulation of Drift

Ten drift collections were made on haphazardly chosen days at randomly determined times during three sampling seasons: Summer 2002 (June-July), winter 2002 (December-January), and spring 2003 (March-April). On each collection date, drift composition, algal biomass, water motion, and wind speed were recorded. Drift was collected using two 3.0 L x 1.0 W meter seine nets with a mesh size of 3 mm. At each site, one net was placed 6 m and one was placed 21 m from the shoreline. Both were held in place by two 2.0 m long PVC pipes (2.5 cm diameter) that were embedded 20 cm into the sediment. The nets were always oriented to face into the direction of flow and extended from the benthos to 0.5 m above the surface of the water. Floats at the top and weights at the bottom of the nets kept them perpendicular to the benthos and allowed for the collection of drift throughout the entire water column.

Nets were checked every 10 minutes for one hour. At each 10-minute interval, the contents of each net was collected and placed in a labeled plastic bag. Later, in the laboratory, all collected material was separated to the species level and blotted-dry wet weights for each species were obtained using an Ohaus Scout II digital top-loading balance.

Pre-weighed Plaster-of-Paris spheres (4.5 cm in diameter) were placed in the middle of each upright PVC pipe with a cable tie to measure water motion via plaster dissolution (Muus 1968). Plaster-of-Paris balls were made using Botanical Science brand plaster and spherical ice cube molds (Ice Shapes) modified to allow a cable tie to be embedded in the plaster. At the end of every hour, plaster spheres were retrieved and placed in a drying oven at 60ºC for 4 days. Water motion was calculated based on plaster weight changes and a linear regression was obtained from calibration in a flow tank. Wind speed (m/s) was collected at 10-minute intervals using a Kestrel 2000 handheld wind gauge.

2.3 Transport of Drift Rhodophytes

For each replicate (n = 10/season/site), naturally occurring drift individuals were located in shallow (< 1.0 m) beds of the seagrass *Halodule wrightii* southwest of the Fellers House Field Station dock. Seasonal availability of species in the drift determined the species used in trials. Species observed during all seasons included *C. decorticatum*, *G. tikvahiae*, *S. filamentosa*, *Chondria* spp., *Hypnea musciformis*, *H. spinella*, *D. baillouviana*, *Chaetomorpha linum*, and *Enteromorpha intestinalis.* These species were present in the drift in different proportions and the number of individuals of each species used in trials therefore varied accordingly. On each trial date, 30 drift individuals were located within a seagrass bed. Specimens were positioned 1.0 m from any other individual. Algae were marked with numbered orange construction flags within 5.0 cm of each individual. Flags were composed of a 45 cm long wire embedded 10 cm in the sediment with an 8 x 8 cm vinyl tag partially visible at the surface of the water. Each flag was then revisited after 12 hours and 24 hours. Movement was recorded by noting the presence or absence of algal individuals within a 0.5 m diameter circle of their corresponding flag. Water motion was also recorded at 12 and 24 hours as described above. Transport was expressed as the number of individuals that dispersed within 12 and 24 hours.

2.4 Turnover Within Drift Accumulations

Vertical migration or mixing within drift algal assemblages was determined by observing the movement of tagged individuals. Again, the availability of species in the drift determined the species used in trials and species observed during all seasons included *C. decorticatum*, *G.*

tikvahiae, *S. filamentosa*, *Chondria* spp., *Hypnea musciformis*, *H. spinella*, *D. baillouviana*, *Chaetomorpha linum*, and *Enteromorpha intestinalis.* Tested species included *C. decorticatum*, *G. tikvahiae*, *H. musciformis*, *H. spinella*, and *D. baillouviana.* *Aghardiella subulata* and *A. spicifera* were not collected in our experimental nets, but were present in the drift during summer and were also used in these trials. For each replicate (n =10/season/site), a consistent volume of mixed natural drift species was collected in a 38 L bucket and placed in a 0.25 m^2 quadrat over bare sediment in shallow (< 1.0 m) water. Fifteen individuals randomly chosen from the drift were tagged with a small piece of flagging tape (0.5 x 2.0 cm) and placed on the surface of each quadrat. Trials were run on haphazardly chosen days and times. Accumulations were checked every 15 minutes for 2 hours. At each interval, the number of visible, tagged individuals was recorded. Water motion and average wind speed were also recorded as described above. Turnover is expressed as the number of individuals that moved vertically per hour.

2.5 Growth of Drift vs. Attached Algae

Spring and summer trials were conducted with *G. tikvahiae*; a winter trial was run with *C. decorticatum*. Three treatments (drift, manipulated drift, and attached) were used in each trial (Table 1). The drift treatment (n=20) included individuals collected from natural drift, the manipulated drift treatment (n=20) included individuals removed from a hard substrate immediately before the start of the trial, and the attached treatment (n=20) included individuals attached to a hard substrate. Substrates included disarticulated shells of the eastern oyster *Crassostrea virginica*, the clam *Mercenaria campechiensis* or *M. mercenaria* and brick, cement, wood, glass, and fiberglass.

Table 1: Descriptions of treatments and water depths for each of the seasonal growth experiments.

Treatment	*Depth*	*Description*	*N*
Drift (D)	Surface (S)	Naturally occurring drift individuals placed 2.0 cm below the surface of the water	10
	Bottom (B)	Naturally occurring drift individuals placed 2.0 cm above the sediment surface	10
Attached (A)	Surface (S)	Individuals placed 2.0 cm below the surface of the water attached to their natural substrate	10
	Bottom (B)	Individuals placed 2.0 cm above the sediment surface attached to their natural substrate	10
Manipulated Drift (MD)	Surface (S)	Individuals removed from their natural substrate and placed 2.0 cm below the surface of the water	10
	Bottom (B)	Individuals removed from their natural substrate and placed 2.0 cm above the sediment surface	10

All macroalgal individuals were collected, rinsed with fresh water, and then cleaned of all epiphytes. Debris was also removed from the substrates of all attached individuals. Individuals were blotted with paper towels and blotted-dry wet weights were recorded using a calibrated top-loading balance (Ohaus Scout II). Each individual was then labeled with a 12.0 cm x 3.0 cm piece of flagging tape. Individuals were then placed in separate 10.0 cm x 20.0 cm plastic mesh bags (mesh diameter: 4.0 mm). These bags were large enough to allow individuals to move with flow and continue growing. Using a randomized design, each bagged individual was tethered by a cable tie to one of sixty 1.5 m PVC poles (2.5 cm diameter) placed 1.0 m apart and embedded 0.5 m in the sediment (Fig. 3). This array was located 10 m northwest of the Fellers House Field Station dock. Individuals were tethered either 2.0 cm below the water line or 2.0 cm above the benthos at the base of the pole (Figure 3). At no time were surface individuals exposed to the air. Surface and bottom water temperatures were recorded every thirty minutes for the duration of each trial using two StowAway TidbiT temperature sensors (Onset Computer Corporation), one at each depth. Subsurface irradiance levels were also recorded at 2.0 cm below the surface and 2.0 cm above the benthos every hour using two HOBO light intensity data loggers housed in clear submersible polycarbonate cases (Onset Computer Corporation) for the duration of each trial.

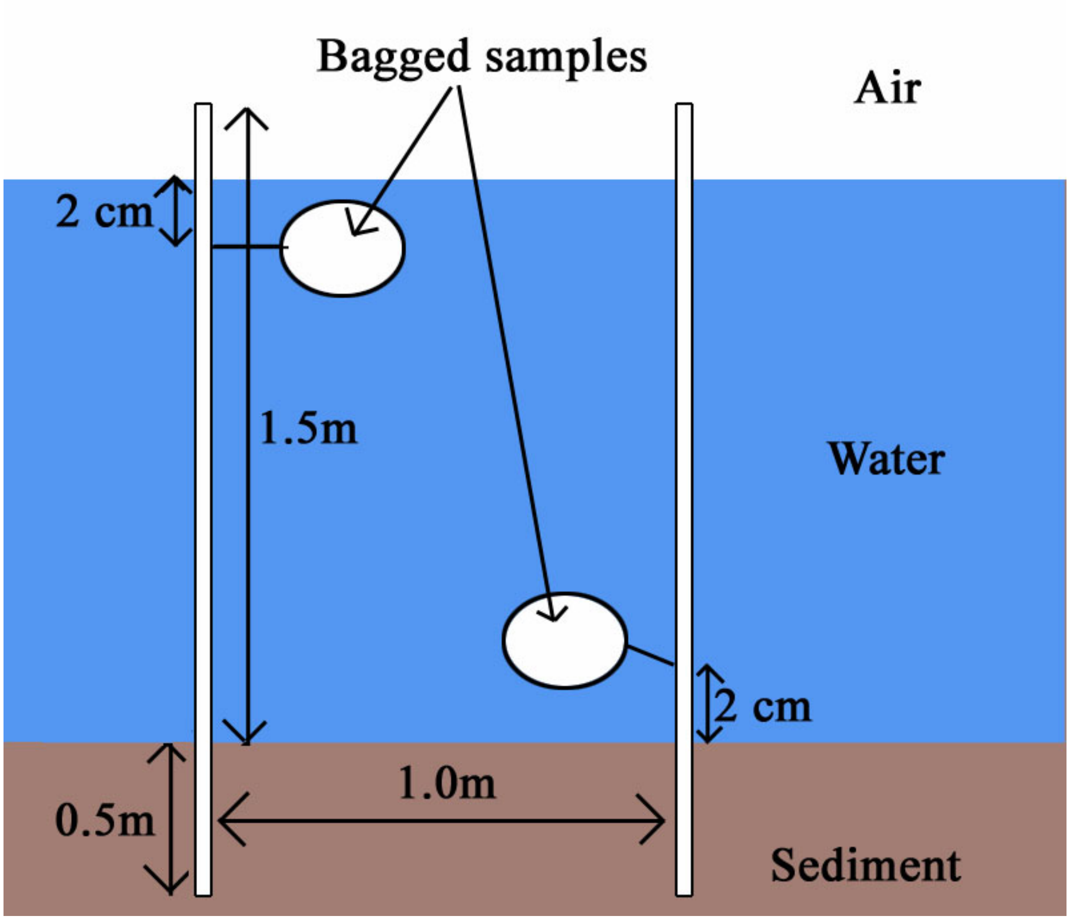

Figure 3: Schematic of field array for growth and photosynthetic performance experiments. One bagged individual was attached to each upright PVC pole either 2 cm above the sediment or 2 cm below the air-water interface.

Individuals were monitored weekly for 45 days. At each visit, all debris in the array was removed and any damage to bags was repaired. After 45 days, all individuals were brought into the laboratory. Individuals were rinsed with fresh water, all epiphytes were removed, and the weights of all substrates of attached individuals were determined. The weight of the cleaned substrate was subtracted from the starting weight of the algae and its substrate to yield the starting weight of each individual.

Since both growth and photosynthetic rates are related to light harvesting efficiency and therefore pigment levels, pigment concentrations were monitored in the experimental individuals. A small amount of algal tissue (0.02 - 0.25 g) from each sample was placed in 5.0ml of N,N dimethyl-formamide (DMF) for photosynthetic pigment extraction (Inskeep and Bloom 1985, Porra et.al. 2002). Pigment samples were labeled and evaluated 8-10 days after collection using a Cary 3 Bio UV-Vis Spectrophotometer and CaryWinUV software. Absorbances were recorded at standard wavelengths of 480, 510, 630, 646 and 664 nm (Inskeep and Bloom 1985). Pigment concentrations were calculated using standard equations for extraction in DMF (Inskeep and Bloom 1985, Porra et.al. 2002) and expressed in μg/g dry weight.

2.6 Photosynthetic Performance of Attached vs. Drift *C. decorticatum*

A diving (D) pulse-amplitude modulated (PAM) fluorometer (WALZ, Germany) was used to measure chlorophyll fluorescence in *C. decorticatum*. This instrument gives accurate measurements of photosynthetic performance *in situ*, greatly reducing stress on sampled individuals and reducing the amount of time required per replicate (WALZ, Germany). Laboratory measurements of photosynthesis versus irradiance (P vs. I) not only require destructive sampling, but also take from one to two hours per sample (WALZ, Germany). This is reduced to 90 seconds using the D-PAM fluorometer. PAM fluorometry gives an estimate of the health and light-harvesting efficiency of photosynthetic organisms. In this experiment, rapid light curves were used to compare short-term changes in physiology in individuals. Rapid light curves apply gradually increasing amounts of light to photosynthetic tissue at assigned intervals and record the fluorescence yield (*Y*) at each interval. Electron transport rate (ETR) is estimated by the D-PAM and is plotted versus the irradiance levels applied to the tissue. The resulting curve is then statistically compared to known models of photosynthetic peformance (Platt et al. 1980). Mean values of saturation irradiance (I_k), quantum efficiency or alpha (α) and ETR_{max} can be compared statistically using pairwise comparisons or an analysis of variance (ANOVA). In this case, two-way ANOVAs were used to determine if changes in photosynthetic efficiency occurred between treatments.

During spring 2003, photosynthetic performance of *C. decorticatum* was evaluated using a D-PAM fluorometer. Measurements were obtained on all *C. decorticatum* individuals used in the growth experiment (Section 2.5). ETR vs. I curves were not obtained for *G. tikvahiae* during growth experiments due to extremely low fluorescence yields. Measurements were made twice for each individual of *C. decorticatum*, once at the beginning and once at the end of each growth trial. Immediately before collection from the field, 15-minute dark-acclimated rapid light curves were obtained using a D-PAM, mini-fiberoptic cable, and dark leaf clips (WALZ, Germany 1998). Light curve settings were set to 15-second intervals at a light intensity of 20 and remained constant throughout the sampling process. These settings were determined during preliminary research on natural drift and attached individuals of *C. decorticatum* collected from a range of depths (30 cm to 1.5 m) and ensured saturating ETR curves for each independent sample. The samples were then treated for the growth experiment as described above (Section

2.5) and allowed to grow for 45 days. After this period, the samples were again measured with D-PAM in the field using the same initial settings and time of day as the first set of light curves.

2.7 Laboratory Controls

To control for any bag effects (Section 2.5), nine individuals of *C. decorticatum* and nine of *G. tikvahiae* were collected from Mosquito Lagoon and brought to the laboratory. Each was rinsed with fresh water and cut into two pieces with a razor blade. Each half of the individual was labeled and blotted wet weights were recorded. Samples ranged in weight from 9.2 to 37.0 g for each half of *C. decorticatum* and from 1.1 to 3.7 g for each half of *G. tikvahiae.* Using a D-PAM fluorometer, dark acclimated ETR vs. I curves were recorded for each half prior to manipulation (Section 2.6) for *C. decorticatum*.

Each "A" labeled half was placed in a 4 mm plastic mesh bag, identical to the ones used in the field studies. The bag was then tied shut and tethered to the side of a 13.5 x 13.5 x 5.0 mm plastic dish with a 4.0 mm long piece of flagging tape. Each "B" labeled half was placed in an identical dish without a bag or a tether. All dishes were then filled with 250 ml of filtered sea water and arranged in a haphazard array under a light bank on a 12 hr light/ 12 hr dark timer. Each dish was separately aerated and covered with clear plastic wrap to reduce evaporation. Dishes were placed on a 84.0 x 42.0 x 6.0 cm lexan platform that was modified to create an x-y plane shaker table. The flat platform moved 10 cm in a horizontal motion from side to side at a rate of nine revolutions per minute. After 45 days, dark acclimated ETR vs. I curves were obtained (in the *C. decorticatum* trial only) and the blotted wet weights of all individuals were recorded. In addition, a small amount of tissue (0.02-0.25g) from each sample was placed in 5.0 ml of DMF for photosynthetic pigment extraction.

2.8 Data Analysis

Data analysis was conducted using SPSS 11.0 statistical software. Tests for homogeneity (Levene's test) and normality (Kolmogorov-Smirnov and Shapiro-Wilk tests) were run on all data to assure ANOVA assumptions were met (Fry 1993). For heterogeneous data sets, data were transformed using a natural log transform in SPSS and then rechecked for homogeneity. Two-Way ANOVAs were used to detect significant differences between treatment groups with subsequent Tukey HSD Post-Hoc tests where appropriate.

Analysis of photosynthetic data was more complex. Two rapid light curves were obtained for each sample in the laboratory and field experiments. Each light curve was imported into Sigma Plot and compared via linear regression for fit to one of two accepted photosynthesis versus irradiance models. Data showing photoinhibition at the end of a curve were compared to Platt's photoinhibition model (Platt *et al.* 1980). Data not showing a photoinhibitory effect at the end of a curve were compared to the hyberbolic tangent model. In either case, correlations producing R^2 values ≥ 0.90 were accepted as reliable data. Eighteen separate curves showed deviant points in the ETR vs. I curves and returned R^2 values < 0.90. These deviations from the normal values in the curves were likely a result of human error or shifting of the tissue under the fiber-optic sensor due to environmental conditions during sampling. For these curves, one to four aberrant data points were removed and the data re-checked for correlation with accepted models.

Of the 60 sets of curves from the field experiment, 10 were unusable due to sample mortality or errors during sampling and 6 were thrown out due to unacceptable R^2 values. Of the 18 sets of curves from the laboratory experiment, 4 were unusable due to sample mortality or errors during sampling and one was thrown out due to an unacceptable R^2 value. Therefore, a total of 44 acceptable sets of curves were obtained for the field experiment and 13 for the laboratory experiment. For each acceptable curve, ETR_{max}, alpha and I_k were recorded. Mean ETR_{max}, alpha, and I_k were then compared in SPSS using two-way ANOVAs (fixed factors: treatment and location) as described above (Fry 1993).

CHAPTER THREE: RESULTS

3.1 Composition and rate of accumulation of drift

At the Mosquito Lagoon site, nine species were collected during all three seasons with *C. decorticatum* dominating the drift in spring (Fig. 4). In summer, both *C. decorticatum* and *G. tikvahiae* were the dominant species collected. *Gracilaria tikvahiae* was the dominant species in winter. At the Indian River site, 11 algal species were collected during spring and summer, while ten species were collected during the winter sampling (Fig. 5). Two genera collected were composed of species that were hard to distinguish and were therefore identified only to their generic taxon. *Chondria* species included *C. capillaris* and *C. littoralis*. *Dasya* species included *D. baillouviana* and *D. crouaniana. Halodule wrightii* was the most abundant species in the drift in spring and summer and *G. tikvahiae* dominated in winter. Accumulation rates in the Indian River ranged from 0.15 - 20.15 g/hr compared to 0.40 - 26.35 g/hr in Mosquito Lagoon. There were no significant differences in accumulation rates in any season at either study site or between sites (Table 2).

Flow rates during net trials as measured by dissolution of plaster spheres ranged from 5.38 – 11.45 cm/s in Mosquito Lagoon and 8.22 – 9.58 cm/s in the Indian River (Fig. 6). Flow rates were examined using two-way ANOVA with season (spring, summer, winter) and location (shore, offshore) as fixed factors. There were no significant differences in flow rates between shore and offshore locations in Mosquito Lagoon (p=0.979) or the Indian River (p=0.970) (Tables 3, 4). Data for shore and offshore nets were therefore combined and considered as replicates at each site for each of the three sampling seasons. Flow rates in Mosquito Lagoon were significantly different between seasons (p=0.032) (Table 3). A Tukey HSD post-hoc test shows the lowest mean flow rates occurred in winter with similar rates in spring and summer (Table 5). Wind speeds during net trials ranged from 5.01 – 7.64 m/s in Mosquito Lagoon and 5.68 – 8.05 m/s in the Indian River (Fig. 7). Wind speeds were examined using two-way ANOVA with season and location as fixed factors. There were no significant differences in wind speeds in any season or at either site (Table 6).

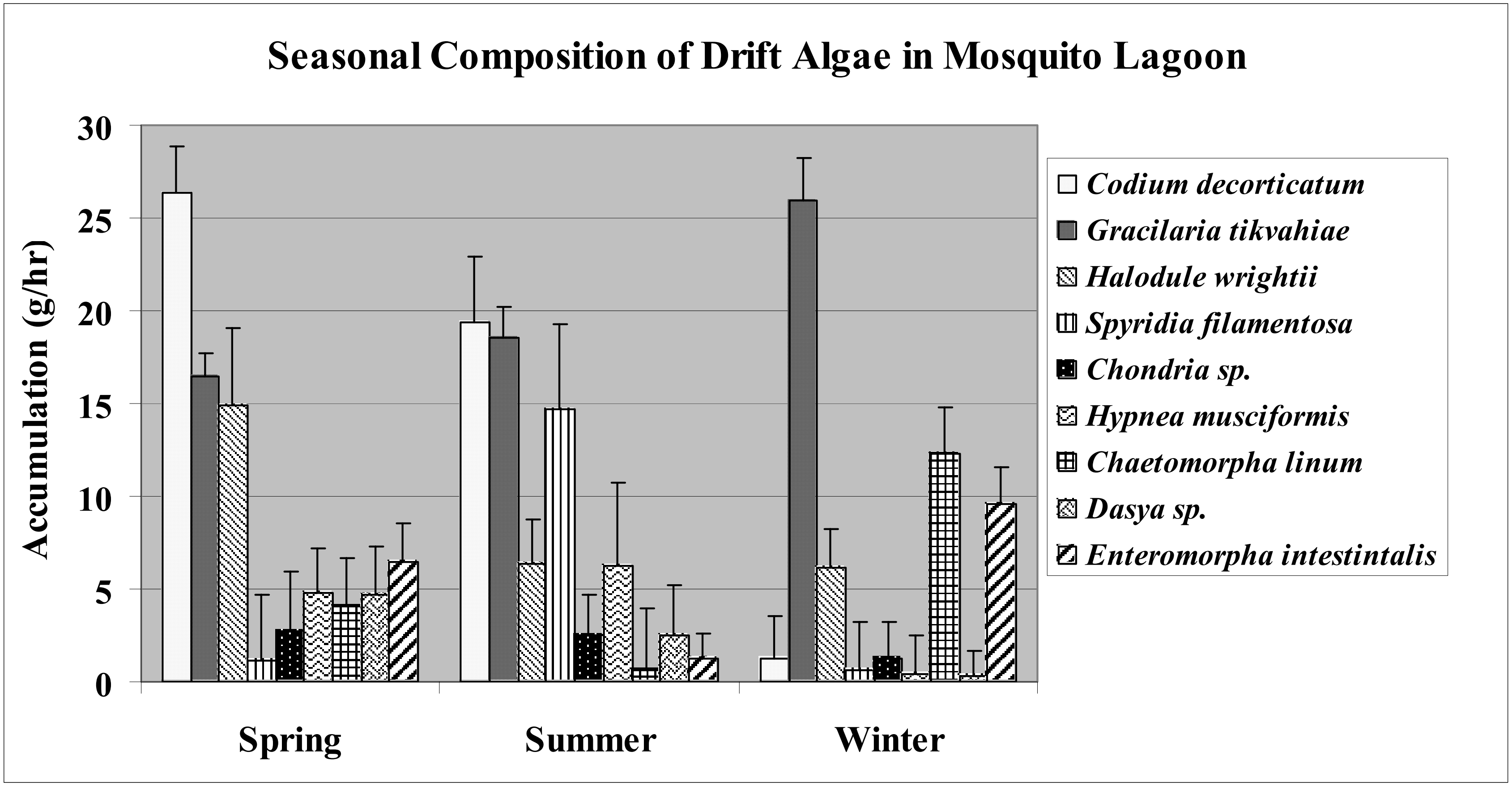

Figure 4: Seasonal composition of drift algae (mean ± standard error) across three sampling seasons in Mosquito Lagoon, Florida (n = 20).

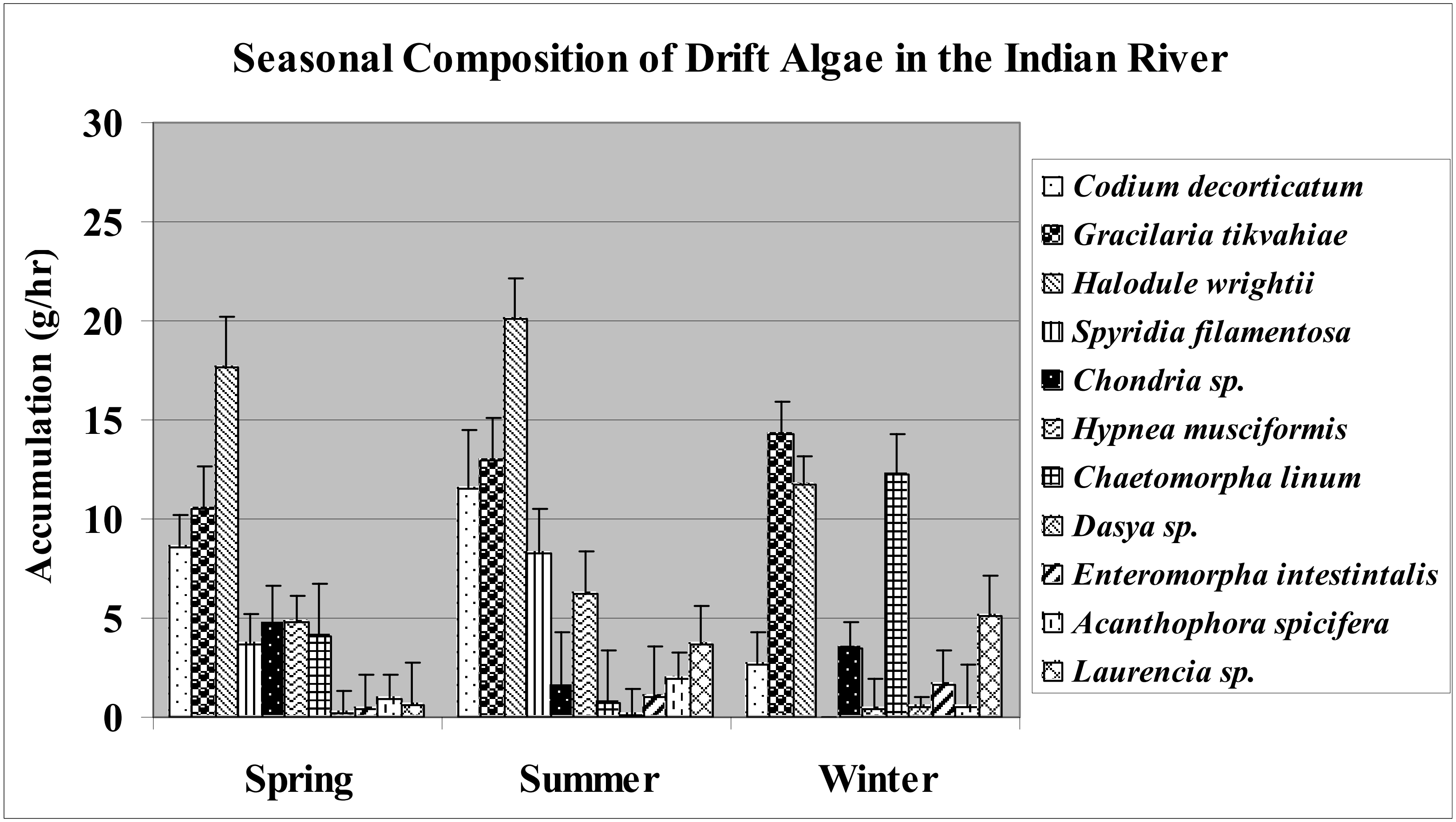

Figure 5: Seasonal composition of drift algae (mean ± standard error) across three sampling seasons in the Indian River, Florida (n = 20).

Table 2: Two-way ANOVA results comparing drift algal accumulation rates with season (summer, winter, spring) and site (Mosquito Lagoon, Indian River) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	90.420	1	90.420	1.892	0.175
Season	29.441	2	14.720	0.308	0.736
Site*Season	16.499	2	8.249	0.173	0.842
Error	2581.272	54	47.801		
Total	5227.537	60			

Table 3: Two-way ANOVA results for Mosquito Lagoon flow rates during net trials with season (summer, winter, spring) and location (shore, offshore) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Season	150.954	2	75.477	4.279	0.032
Location	1.300×10^{-2}	1	1.300×10^{-2}	0.001	0.979
Season*Location	0.530	2	0.0265	0.015	0.985
Error	282.191	16	17.637		
Total	2484.428	22			

Table 4: Two-way ANOVA results for Indian River flow rates during net trials with season (summer, winter, spring) and location (shore, offshore) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Season	58.083	2	29.041	1.218	0.330
Location	3.629×10^{-2}	1	3.629×10^{-2}	0.002	0.970
Season*Location	0.163	2	8.158×10^{-2}	0.003	0.997
Error	286.078	12	23.840		
Total	2184.972	18			

Table 5: Tukey HSD Post-Hoc results for flow rates in Mosquito Lagoon compared by season (Winter < Spring = Summer).

(I) Season	**(J) Season**	**Mean Difference (I-J)**	**Std. Error**	**P value**	**95% Confidence Interval**	
					Lower Bound	**Upper Bound**
summer	winter	5.6774	2.2680	0.058	-0.1750	11.5297
	spring	-0.3854	2.0998	0.982	-5.8036	5.0328
winter	summer	-5.6774	2.26806	0.058	-11.5297	0.1750
	spring	-6.0627	2.26806	0.042	-11.9151	-0.2104
spring	summer	0.3854	2.09982	0.982	-5.0328	5.8036
	winter	6.0627	2.26806	0.042	0.2104	11.9151

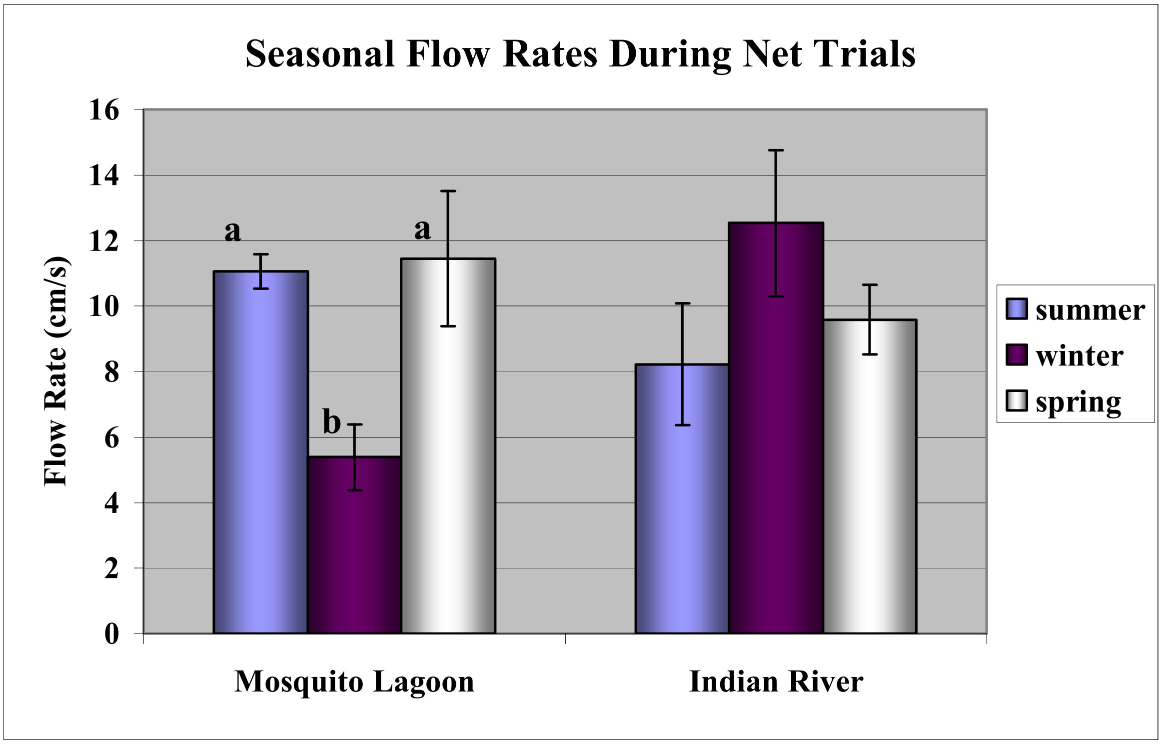

Figure 6: Flow rates during net trials in Mosquito Lagoon and the Indian River (mean ± standard error). Letters designate significance differences between seasons in Mosquito Lagoon at alpha = 0.05. There was no significant difference between seasonal flow rates in the Indian River (n = 40).

Table 6: Two-way ANOVA results comparing wind speeds during net trials with season (summer, winter, spring) and site (Mosquito Lagoon, Indian River) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	85.674	1	81.654	1.874	0.252
Season	30.547	2	13.452	0.247	0.654
Site*Season	17.542	2	7.263	0.223	0.724
Error	2154.334	52	45.671		
Total	5886.024	61			

3.2 Transport of drift rhodophytes

Differences in rates of drift transport were analyzed using a 2-way ANOVA (factors: season, site). Drift transport occurred at both sites and in all three sampling seasons with an average of 9 drift individuals (30%) moving after 12 hours (Fig. 8). After 24 hours, the highest number moved at both sites was 16 individuals (53%) in Mosquito Lagoon (Fig. 9). At both 12 and 24 hour intervals, transport was not significantly affected by season ($p=0.165$, $p=0.340$, respectively) or site ($p=0.621$, $p=0.770$, respectively) (Tables 7, 8). Flow rates during transport trials were examined using a 2-way ANOVA (factors: season, site). Flow rates were not found to be significantly different during any season or between sites (Fig. 10, Table 9). Wind speeds during transport trials ranged from 5.22 - 7.04 m/s in Mosquito Lagoon and 6.01 - 6.97 m/s in the Indian River (Fig. 11). Wind speeds during transport trials were examined using two-way ANOVA (factors: season, site). Wind speeds were not found to be significantly different during any season or between sites (Table 10).

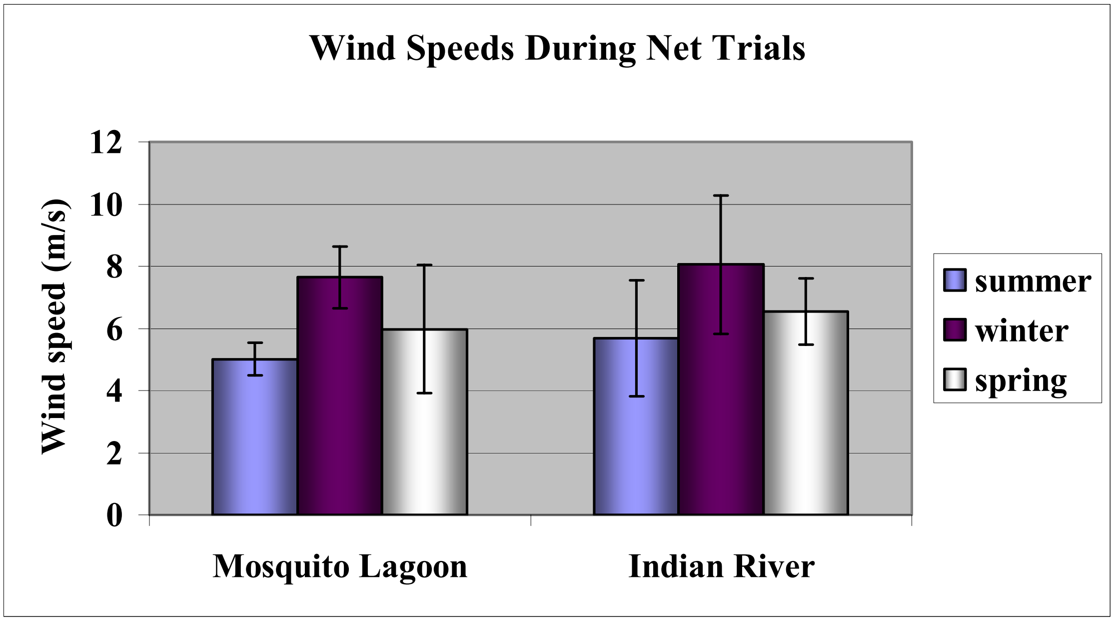

Figure 7: Mean wind speeds (± standard error) during net trials (n = 60).

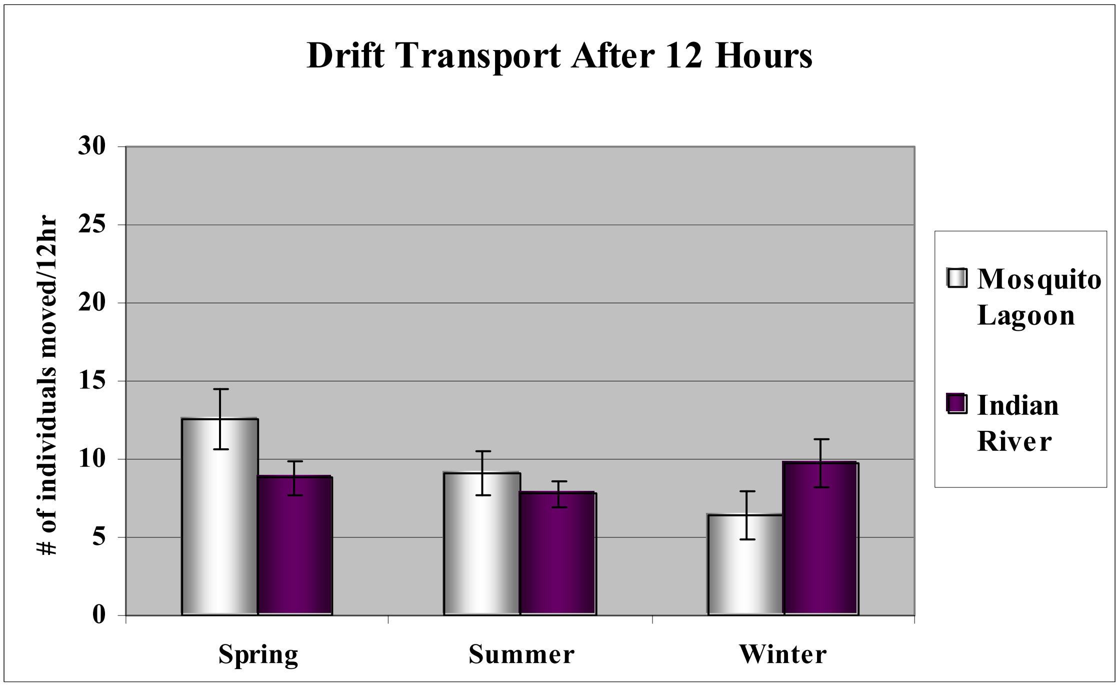

Figure 8: Transport of drift algae (mean ± standard error) after 12 hours at two sites (n = 10).

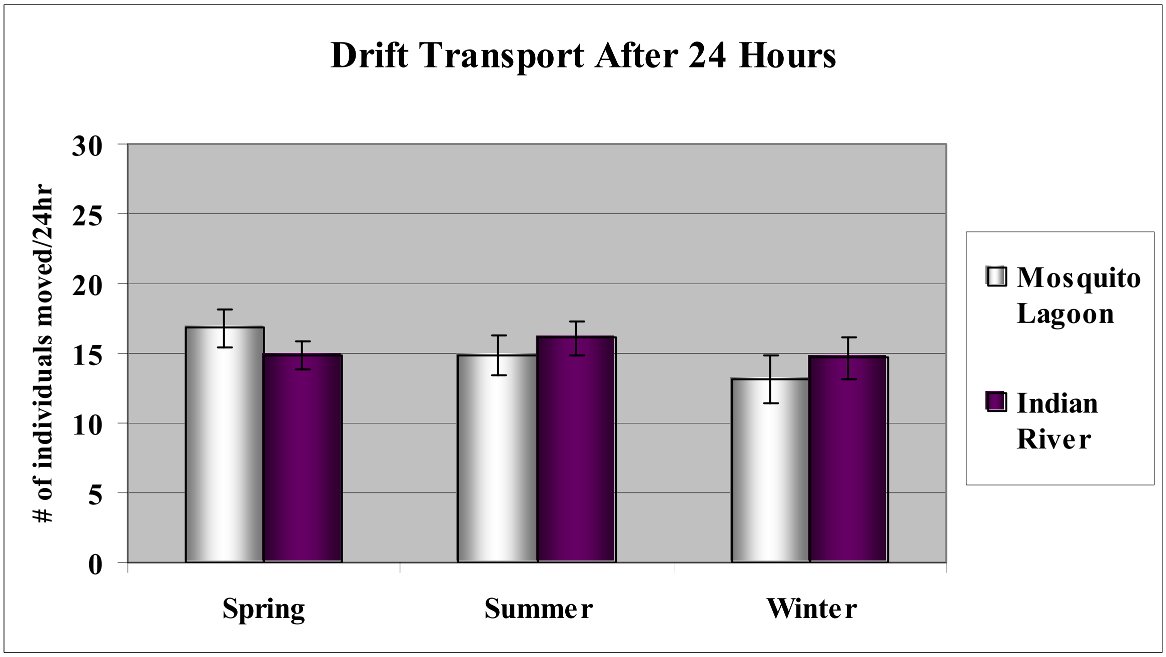

Figure 9: Transport of drift algae (mean ± standard error) after 24 hours at two sites (n = 10).

Table 7: Two-way ANOVA results comparing seasonal transport of drift algae over 12 hours with season (summer, winter, spring) and site (Mosquito Lagoon, Indian River) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	5.400	1	5.400	0.247	0.621
Season	81.633	2	40.817	1.866	0.165
Site*Season	129.700	2	64.850	2.965	0.060
Error	1181.000	54	21.870		
Total	6330.000	60			

Table 8: Two-way ANOVA results comparing seasonal transport of drift algae over 24 hours with season (summer, winter, spring) and site (Mosquito Lagoon, Indian River) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	1.667	1	1.667	0.087	0.770
Season	42.433	2	21.217	1.102	0.340
Site*Season	37.633	2	18.817	0.977	0.383
Error	1040.000	54	19.259		
Total	14742.000	59			

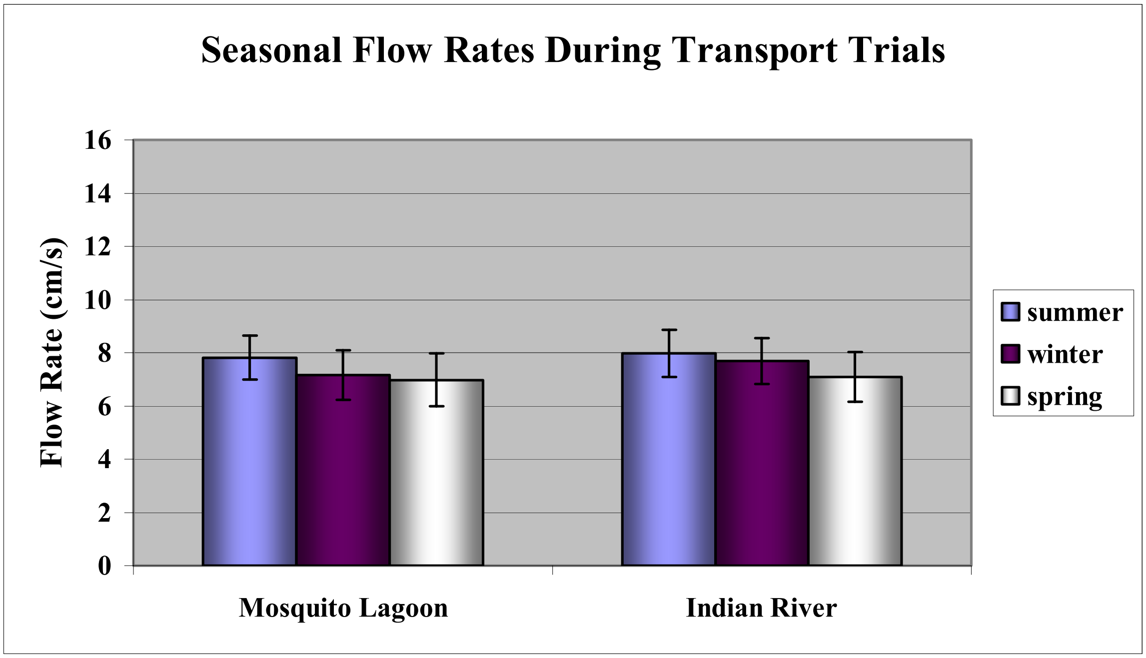

Figure 10: Flow rates during transport trials (mean ± standard error) (n = 60).

Table 9: Two-way ANOVA results comparing flow rates during transport trials with season and site as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	1.051	1	1.051	0.128	0.722
Season	7.509	2	3.754	0.457	0.636
Site*Season	0.516	2	0.258	0.031	0.969
Error	443.707	54	8.217		
Total	3784.989	60			

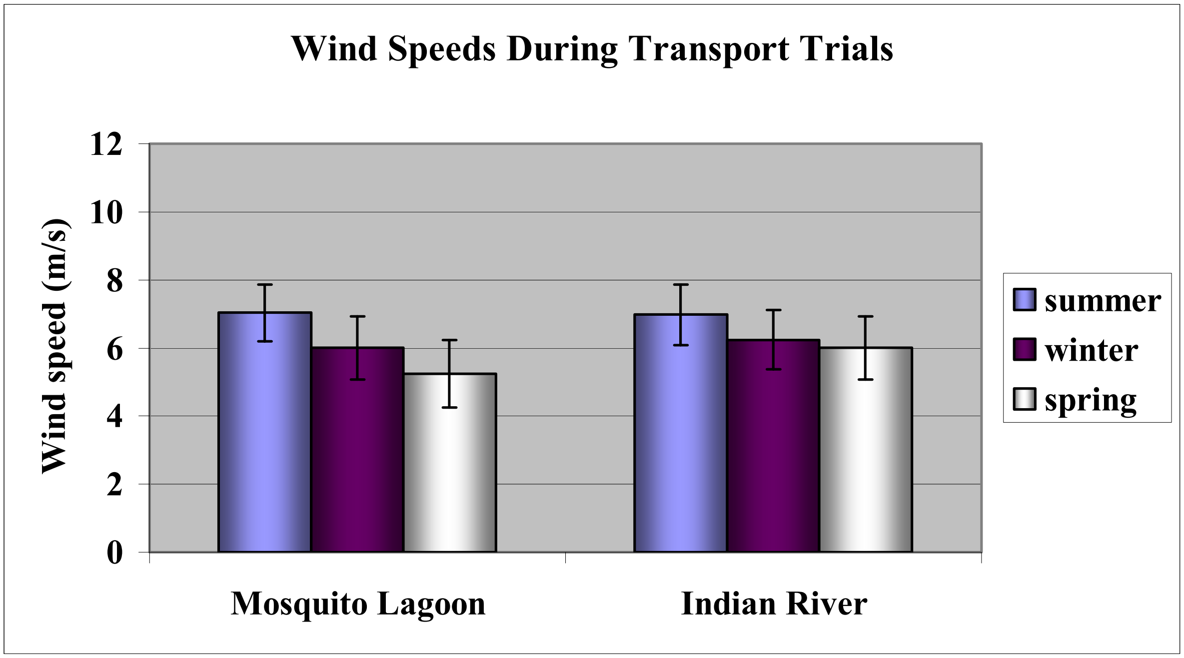

Figure 11: Mean wind speeds (± standard error) during transport trials (n = 30).

Table 10: Two-way ANOVA results comparing wind speeds during transport trials with season and site as fixed factors.

Source	Type III Sum of Squares	df	Mean Square	F	P value
Site	2.024	1	2.024	0.142	0.634
Season	6.574	2	3.221	0.654	0.521
Site*Season	0.467	2	0.229	0.0291	0.942
Error	442.112	50	7.965		
Total	2574.151	59			

3.3 Turnover within drift accumulations

Turnover of individuals within experimental accumulations did occur, but at low rates (Fig. 12). Turnover rates ranged from 0.95 – 2.25 individuals per hour in Mosquito Lagoon and 0.96 – 2.75 individuals per hour in the Indian River. The lowest turnover rates occurred in spring at both sites with less than one individual moved per hour (2-way ANOVA and subsequent Tukey post-hoc test) (Tables 11, 12). Flow rates ranged from 2.88 – 8.84 cm/s in Mosquito Lagoon, and 2.52 – 8.69 cm/s in the Indian River (Fig. 13). Flow rates during transport trials were examined using a 2-way ANOVA (factors: season, site). Flow rates were not significantly different between sites (p=0.936), however they were significantly different between seasons (p=0.001) (Table 13). A Tukey HSD post-hoc test showed significantly lower flow rates during spring sampling at both sites while flow rates were similar during summer and winter (Table 14). Wind speeds during trials ranged from 4.66 – 6.99 m/s in Mosquito Lagoon and 5.00 – 6.88 m/s in the Indian River (Fig. 14). Wind speed data were examined using two-way ANOVA (factors: season, site). No significant differences were found between wind speeds by either season or location (Table 15).

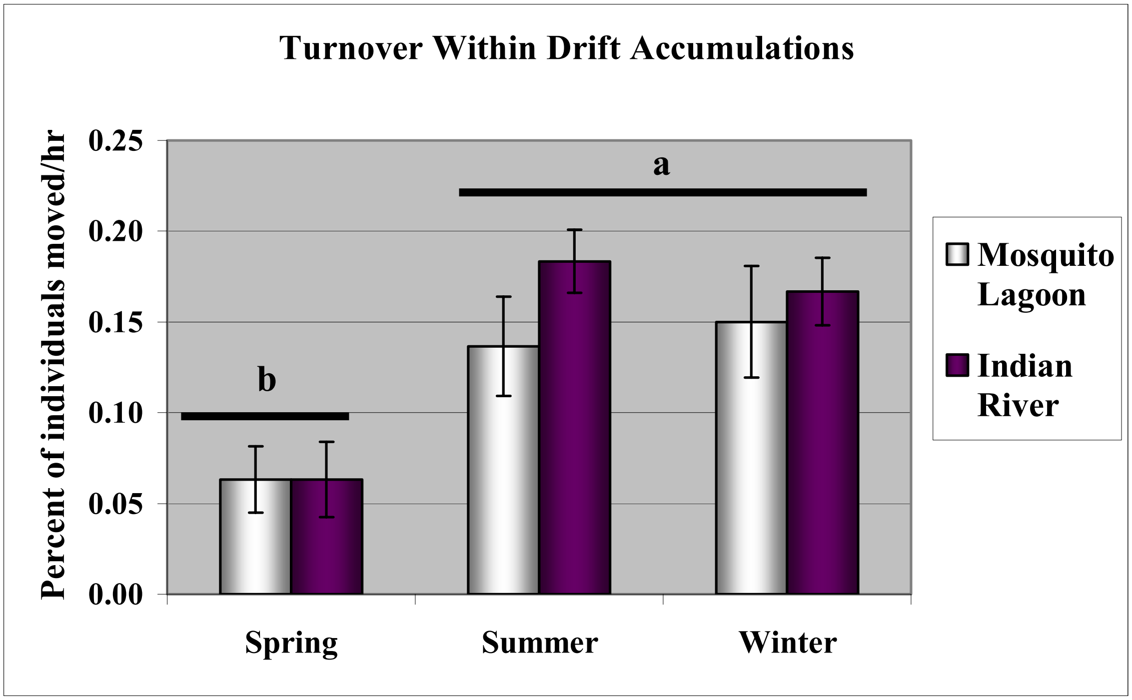

Figure 12: Turnover within drift accumulations (mean ± standard error) in Mosquito Lagoon and Indian River. Letters designate significance levels between seasons at both sites at alpha = 0.05 (ANOVA, Tukey HSD Post-Hoc test) (n = 10).

Table 11: Two-way ANOVA results comparing seasonal turnover of drift algae with season and site as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	1.504	1	1.504	1.291	0.261
Season	24.558	2	13.779	11.825	<0.0001
Site*Season	1.258	2	0.629	0.540	0.586
Error	62.925	54	1.165		
Total	311.750	60			

Table 12: Tukey HSD Post-Hoc results for turnover rates compared by season.

(I) Season	**(J) Season**	**Mean Difference (I-J)**	**Std. Error**	**P value**	**95% Confidence Interval**	
					Lower Bound	**Upper Bound**
summer	winter	-1.450	0.341	<0.0001	-2.273	-0.627
	spring	-1.425	0.341	<0.0001	-2.248	-0.602
winter	summer	1.450	0.341	<0.0001	0.627	2.273
	spring	0.025	0.341	0.997	-0.798	0.848
spring	summer	1.425	0.341	<0.0001	0.602	2.248
	winter	-0.025	0.341	0.997	-0.848	0.798

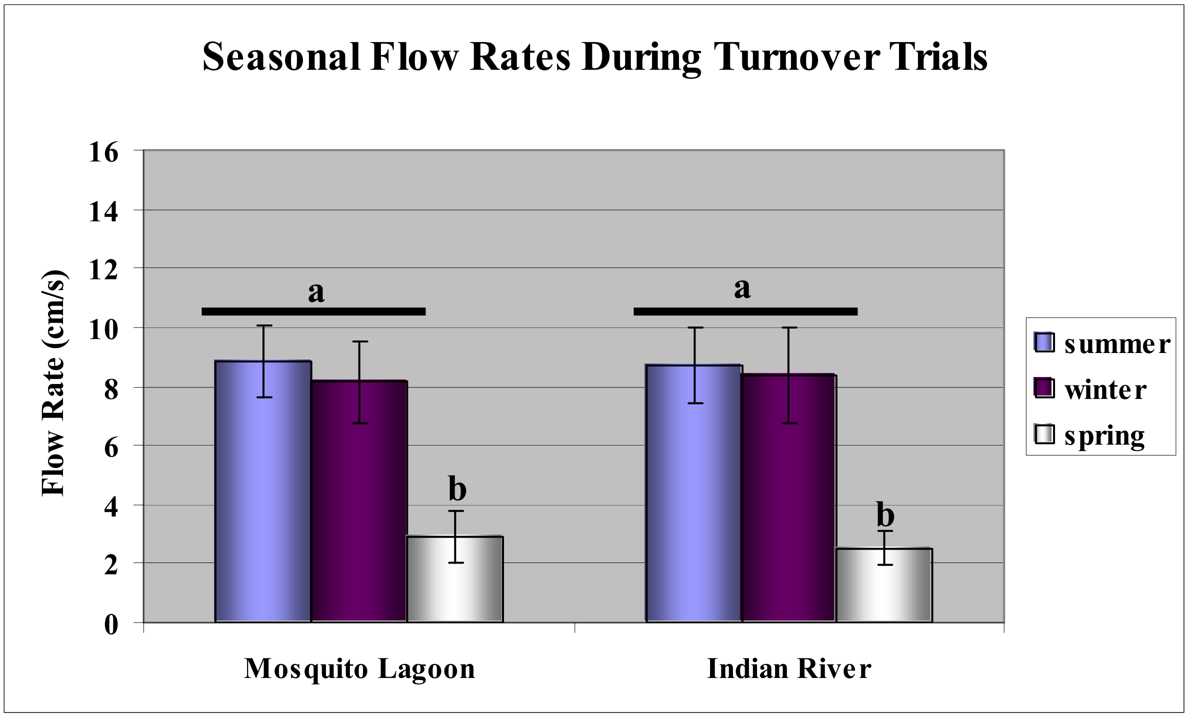

Figure 13: Flow rates at both sites during turnover trials in Mosquito Lagoon and the Indian River (mean ± standard error). Letters designate significance levels between seasons at both sites at alpha = 0.05. There was no significant difference in flow rates between sites (ANOVA, Tukey HSD Post-Hoc test) (n = 30).

Table 13: Two-way ANOVA results comparing flow rates during turnover trials with season (summer, winter, spring) and site (Mosquito Lagoon, Indian River) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	4.013×10^{-2}	1	4.013×10^{-2}	0.007	0.936
Season	151.725	2	75.862	12.658	0.001
Site*Season	0.266	2	0.133	0.022	0.978
Error	95.891	16	5.993		
Total	1318.445	22			

Table 14: Tukey HSD Post-Hoc results for flow rates during turnover trials compared by season.

(I) Season	**(J) Season**	**Mean Difference (I-J)**	**Std. Error**	**P value**	**95% Confidence Interval**	
					Lower Bound	**Upper Bound**
summer	winter	0.5041	1.2642	0.917	-2.7579	3.7662
	spring	6.0671	1.2642	0.001	2.8051	9.3292
winter	summer	-.05041	1.2642	0.917	-.37662	2.7579
	spring	5.5630	1.4134	0.003	1.9159	9.2101
spring	summer	-6.0671	1.2642	0.001	-9.3292	-2.8051
	winter	-5.5630	1.41341	0.003	-9.2101	-1.9159

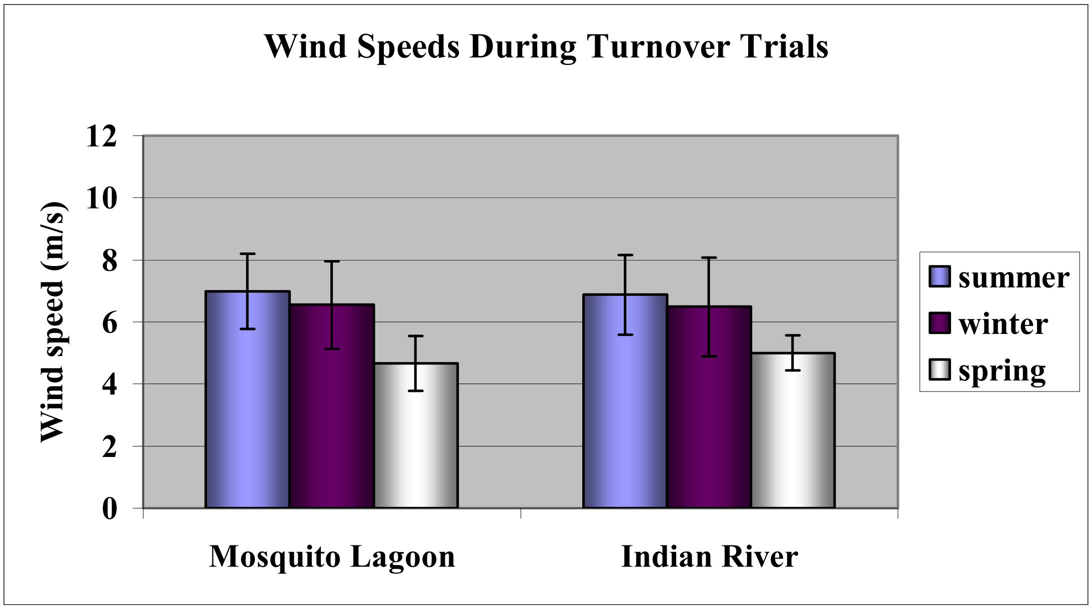

Figure 14: Mean wind speeds (± standard error) during turnover trials (n = 30).

Table 15: Two-way ANOVA results comparing wind speeds during turnover trials with season (summer, winter, spring) and site (Mosquito Lagoon, Indian River) as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Site	3.021×10^{-2}	1	3.021×10^{-2}	1.647	0.124
Season	167.35	2	66.251	13.749	0.071
Site*Season	0.425	2	0.278	0.054	0.991
Error	96.332	15	4.227		
Total	1244.010	22			

3.4 Growth of drift vs. attached algae

Weight data for growth samples were normalized by the initial weights of individuals and percent growth per day was calculated by treatment in each sampling season. Heterogeneity of errors was found for growth data in all three seasons and for chlorophyll ratio data in Spring (Levene's tests). Natural logarithmic transformations of data were required to restore homogeneity and assured ANOVA assumptions were upheld (Fry 1993).

During spring, growth of *C. decorticatum* was not significantly different between treatments ($p=0.436$) or locations ($p=0.905$) in the water column (Fig. 15, Table 16). Growth rates ranged from 0.74% - 1.11% per day. Chlorophyll *a* concentrations ranged from 0.301 to 0.777 mg/g dry weight of tissue (dwt) (Fig. 16). There were no significant differences in chlorophyll *a* concentrations in any treatments or at either locations (Table 17). Chlorophyll *b* concentrations ranged from 0.011 to 0.192 mg/g dwt (Fig. 17). Bottom locations had significantly higher concentrations of chlorophyll *b* as compared to surface individuals (Table 18). Ratios of chlorophyll *a* to *b* ranged from 3.061 to 132.846 mg/g dwt but there were no significant differences between treatments or locations (Fig. 18, Table 19). Total carotenoid concentrations ranged from 2.349 to 3.105 mg/g dwt (Fig. 19). No significant differences in total carotenoid concentrations were found in any treatments or at either location (Table 20). Temperatures during spring ranged from 16.6 - 30.9ºC and light intensities from 0.01 to 3.9×10^3 lum/m^2.

During summer, growth in *G. tikvahiae* was not significantly different between treatments ($p=0.238$), but was significantly lower in individuals grown at bottom locations ($p<0.001$) (Fig. 20, Table 21). Growth rates ranged from 0.42% – 1.09% per day. We found no

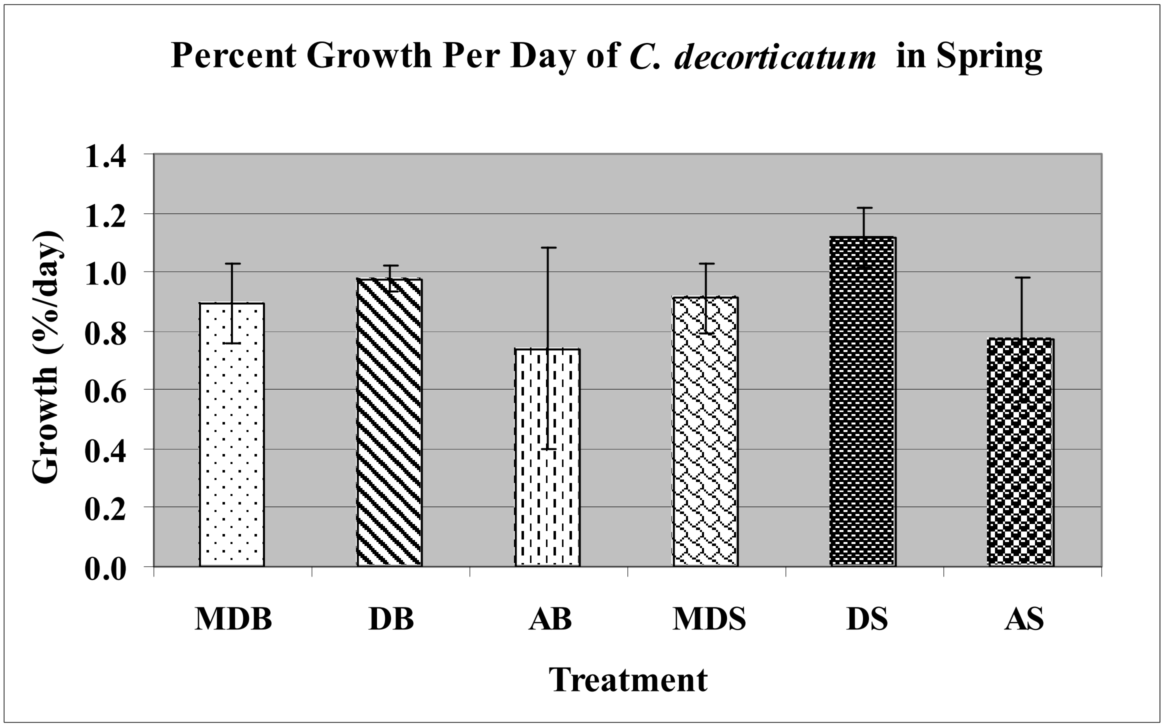

Figure 15: Growth in percent per day for *C. decorticatum* during spring (mean ± standard error). Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 16: Two-way ANOVA results comparing growth of *C. decorticatum* in spring. Analysis was conducted on natural-log transformed data with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	2.288×10^{-2}	2	1.44×10^{-2}	0.854	0.436
Location	1.950×10^{-4}	1	1.950×10^{-4}	0.015	0.905
Treatment*Location	2.064×10^{-2}	2	1.032×10^{-2}	0.770	0.472
Error	0.415	31	1.340×10^{-2}		
Total	4.223	37			

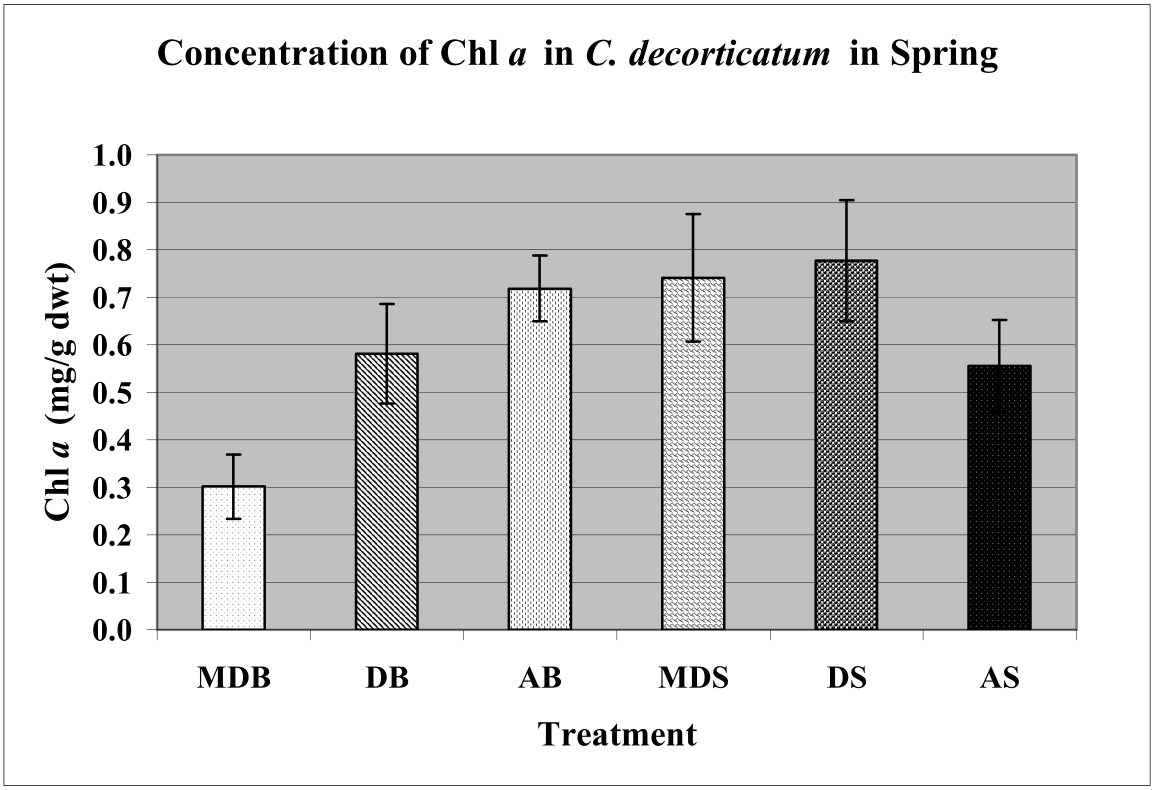

Figure 16: Chlorophyll *a* concentrations for *C. decorticatum* in mg/g dry weight of tissue during spring (mean ± standard error). Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 17: Two-way ANOVA results comparing chlorophyll *a* content of *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	0.181	2	9.05×10^{-2}	1.119	0.339
Location	0.207	1	0.207	2.565	0.119
Treatment*Location	0.464	2	0.232	2.865	0.072
Error	2.507	31	8.089×10^{-2}		
Total	17.252	36			

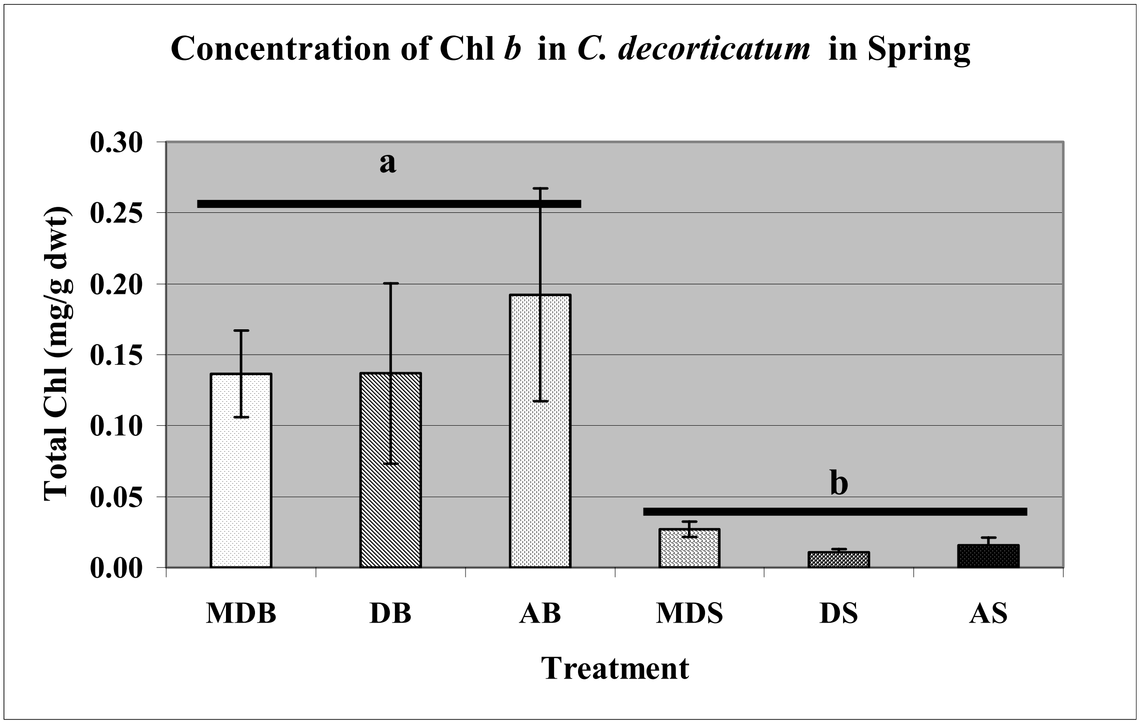

Figure 17: Chlorophyll *b* concentrations for *C. decorticatum* in mg/g dry weight of tissue during spring (mean ± standard error). Letters designate significant differences at p=0.05 level. Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached Surface (n = 10).

Table 18: Two-way ANOVA results comparing chlorophyll *b* content of *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	4.724×10^{-3}	2	2.362×10^{-3}	0.211	0.811
Location	0.158	1	0.158	14.128	0.001
Treatment*Location	5.81×10^{-3}	2	2.906×10^{-3}	0.260	0.773
Error	0.346	31	1.117×10^{-2}		
Total	0.708	37			

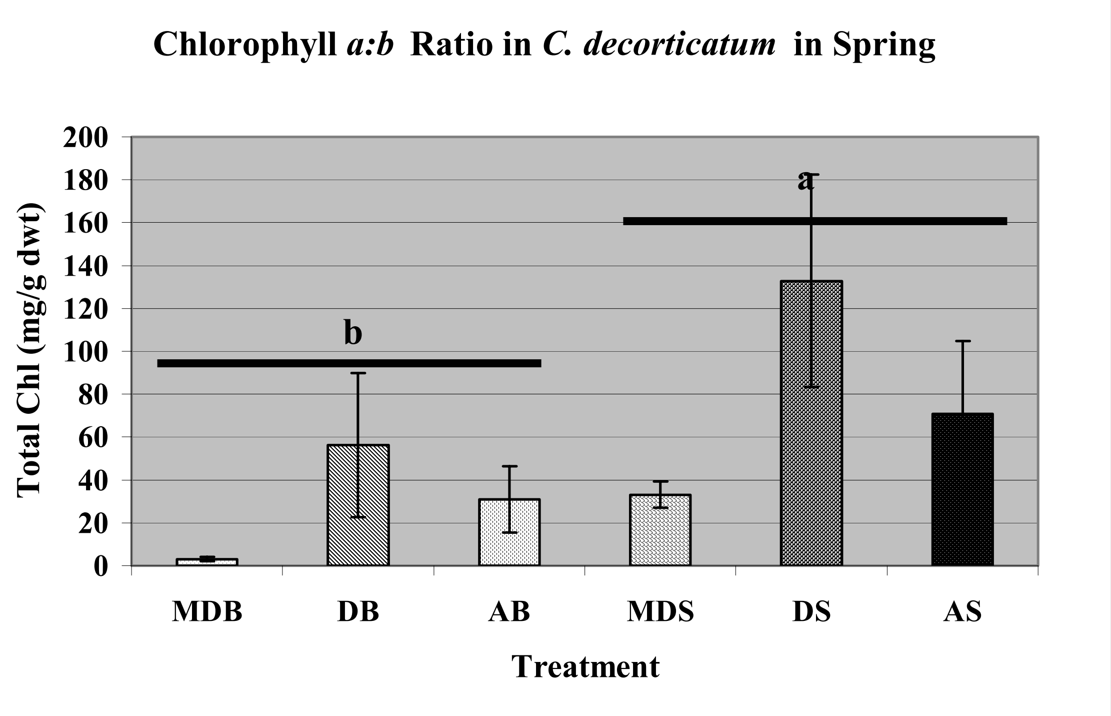

Figure 18: Chlorophyll *a:b* ratios for *C. decorticatum* in mg/g dry weight of tissue during spring (mean ± standard error). Letters designate significant differences at p=0.05 level. Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 19: Two-way ANOVA results comparing chlorophyll *a*:*b* ratios of *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	2.022	2	1.011	3.233	0.054
Location	4.505	1	4.505	14.408	0.001
Treatment*Location	0.552	2	0.276	0.883	0.424
Error	9.068	29	0.313		
Total	68.745	35			

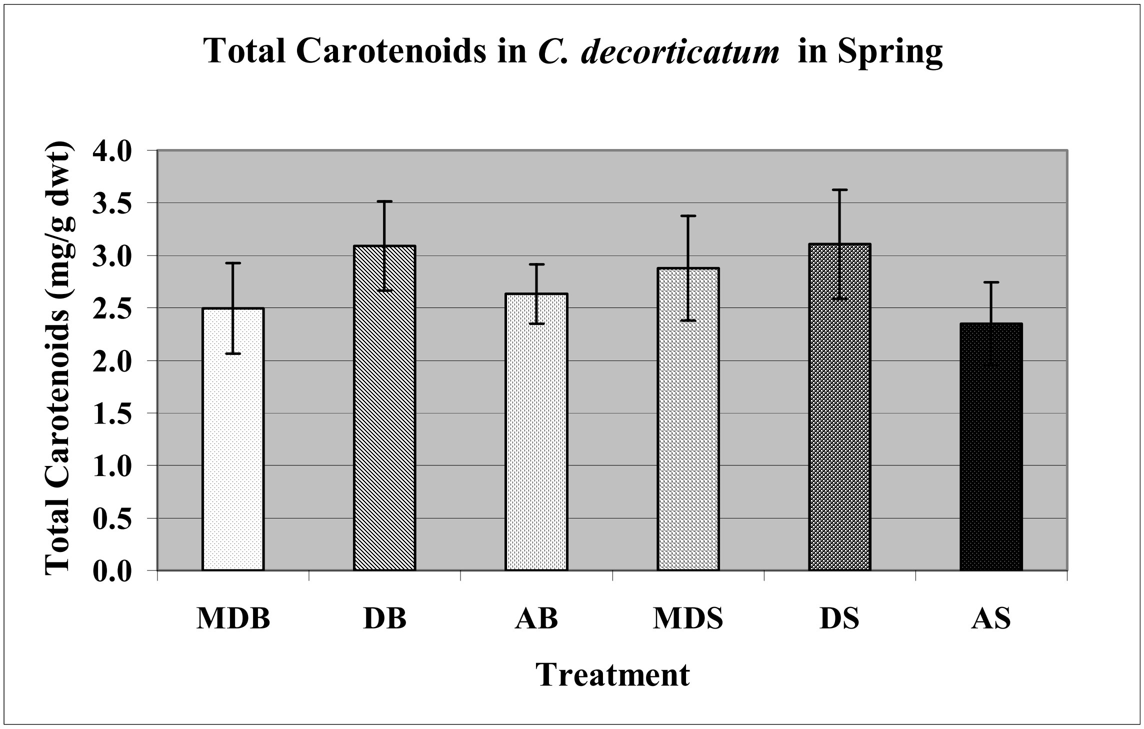

Figure 19: Total carotenoids content for *C. decorticatum* in mg/g dry weight of tissue during spring (mean ± standard error). Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 20: Two-way ANOVA results comparing total carotenoid content of *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	2.156	2	1.078	0.763	0.475
Location	1.284×10^{-2}	1	1.28×10^{-2}	0.009	0.925
Treatment*Location	0.600	2	0.300	0.212	0.810
Error	43.793	31	1.413		
Total	333.460	35			

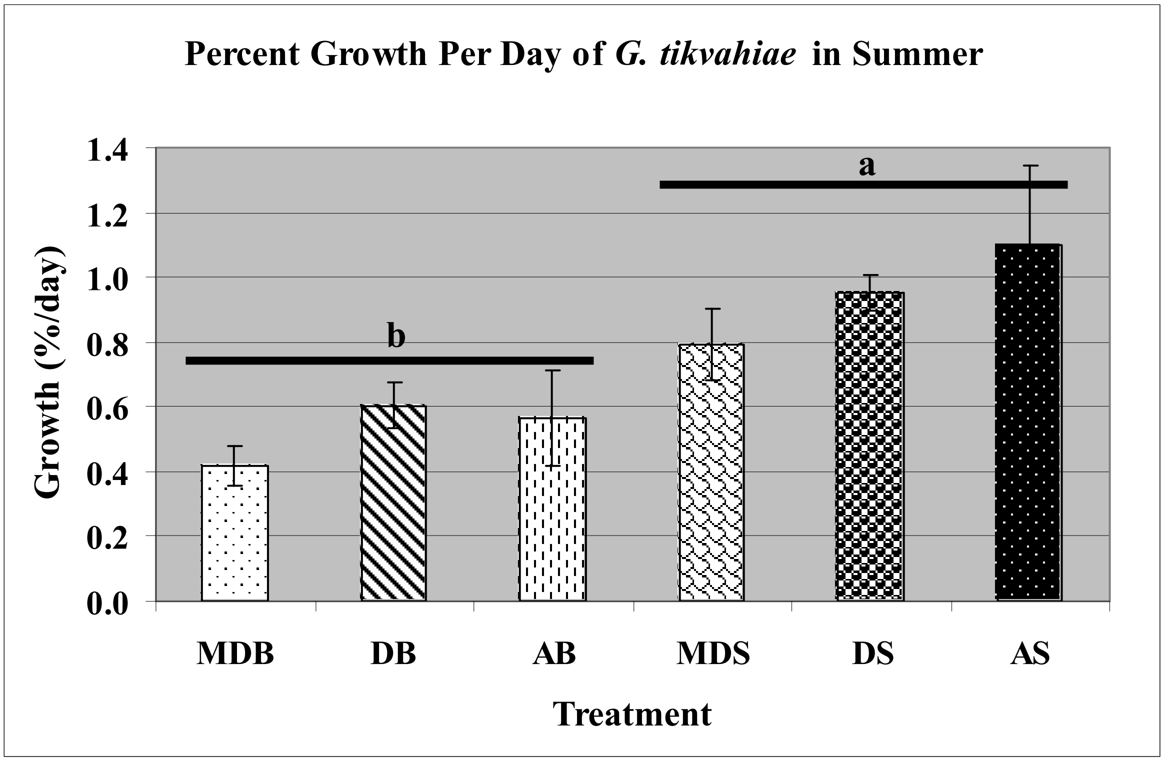

Figure 20: Growth in percent per day for *G. tikvahiae* during summer (mean ± standard error). Letters designate significant differences at p=0.05 level. Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 21: Two-way ANOVA results comparing growth of *G. tikvahiae* in summer. Analysis was conducted on natural-log transformed data with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	3.697	2	1.848	1.485	0.238
Location	30.052	1	30.052	24.141	<0.0001
Treatment*Location	1.746	2	0.873	0.701	0.501
Error	53.529	43	1.245		
Total	95.910	49			

significant differences in chlorophyll *a* content between either locations (p=0.919) or treatments (p=0.432) (Fig 21, Table 22). Chlorophyll *a* concentrations ranged from 3.62 – 4.14 mg/g dwt. Temperatures during summer ranged from 21.1 - 32.8ºC and light intensities from 0.01 to 6.3 x 10^3 lum/m^2.

During winter, growth in *G. tikvahiae* was not significantly different between treatments (p=0.177), but was significantly higher for individuals grown at surface locations (p<0.001) (Fig. 22, Table 23). Growth rates ranged from 0.96% - 5.26% per day. Chlorophyll *a* concentrations were significantly higher in individuals grown at bottom locations (p=0.004), no significant differences between treatments were found (p=0.785) (Fig. 23, Table 24). Chlorophyll *a* concentrations ranged from 1.9 – 3.35 mg/g dwt. Temperatures during winter ranged from 15.2 - 22.8ºC and light intensities from 0.01 to 5.0 x 10^3 lum/m^2.

3.5 Photosynthetic performance of attached vs. drift *C. decorticatum*

Photosynthetic performances ($ETR_{max,}$ α) of bagged *C. decorticatum* grown in the laboratory were not significantly different from unbagged individuals grown under the same conditions (Paired T-tests: p=0.521 for α, p=0.142 for ETR_{max}, respectively). Therefore, the bags used in the field experiment had no detectable effect on photosynthetic capacity. *Codium decorticatum* used in field experiments showed no significant differences between drift and attached algae by ETR_{max}, alpha or I_k in any treatment group either pre or post-manipulation (Figs. 24 - 26; Tables 25 - 27). Attached and drift individuals had similar measurements of α and ETR_{max}, which translates to similar light harvesting and quantum efficiency before and after entering a drift state.

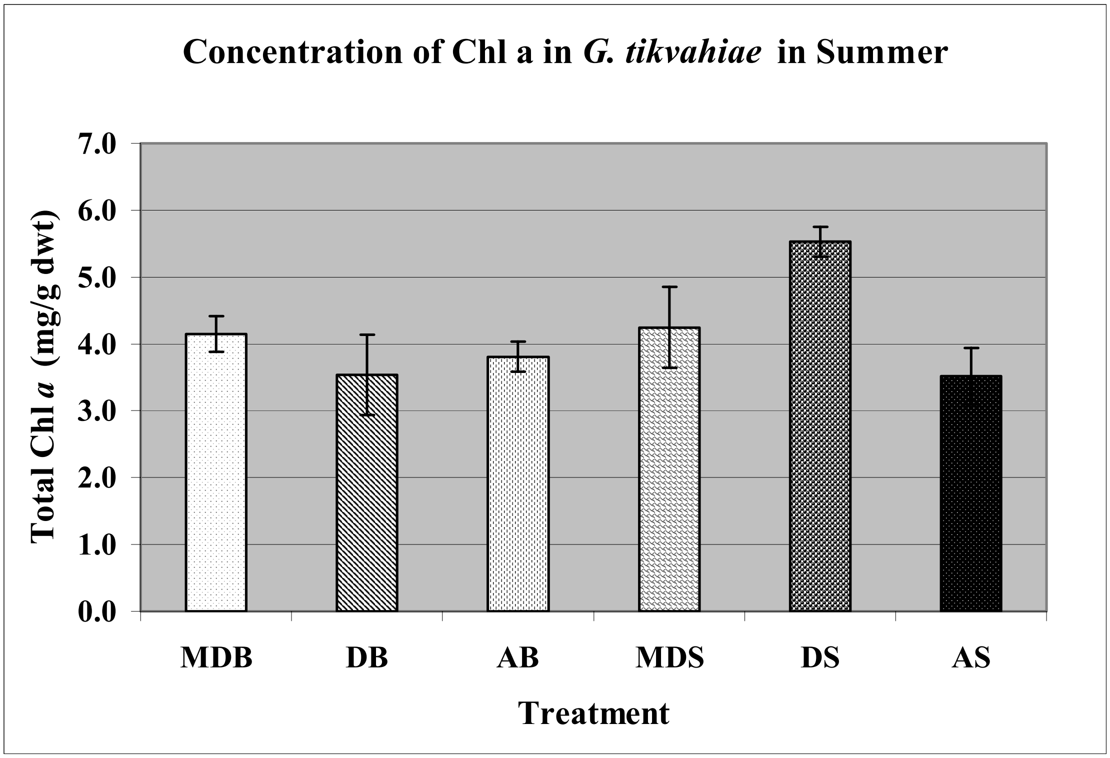

Figure 21: Chlorophyll *a* concentrations for *G. tikvahiae* in mg/g dry weight of tissue during summer (mean ± standard error). Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 22: Two-way ANOVA results comparing chlorophyll *a* content of *G. tikvahiae* in summer with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	6.192×10^{-2}	2	3.096×10^{-2}	0.085	0.919
Location	0.231	1	0.231	0.631	0.432
Treatment*Location	$1.341\ 10^{-2}$	2	6.703×10^{-3}	0.018	0.982
Error	12.821	35	0.366		
Total	196.175	41			

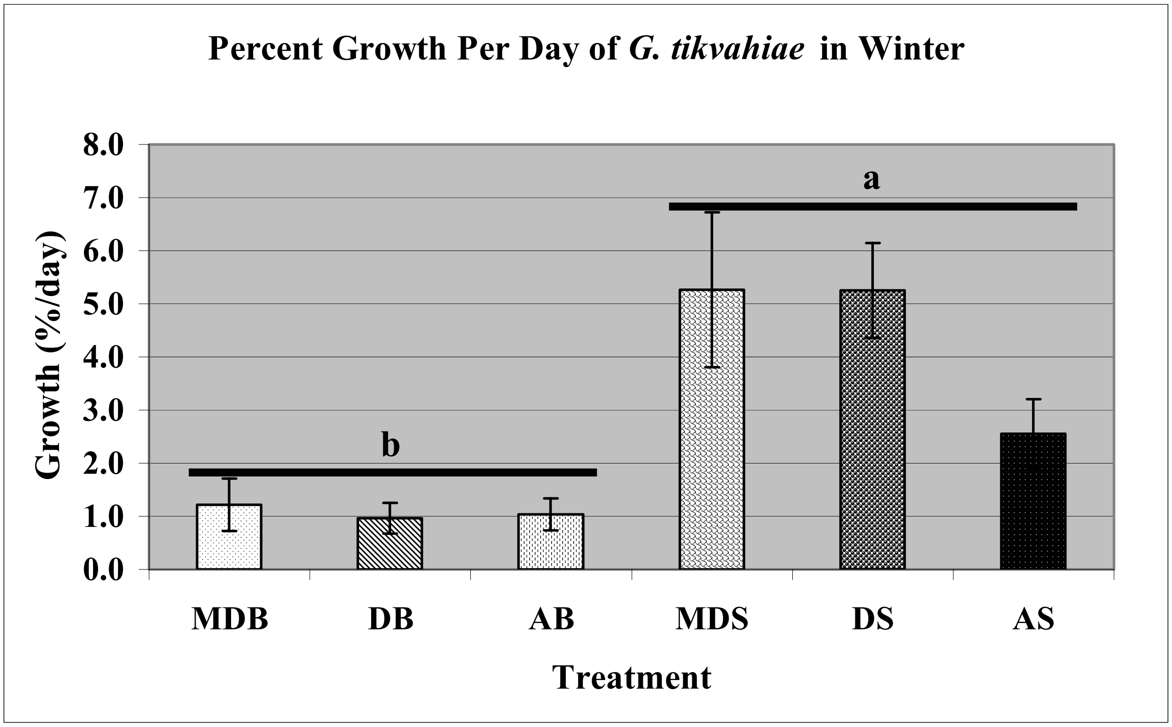

Figure 22: Growth in percent per day for *G. tikvahiae* during winter (mean ± standard error). Letters designate significant differences at p=0.05 level. Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 23: Two-way ANOVA results comparing growth of *G. tikvahiae* in winter. Analysis was conducted on natural-log transformed data with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	20.229	2	10.115	1.806	0.177
Location	129.029	1	129.029	23.037	<0.0001
Treatment*Location	19.058	2	9.529	1.701	0.195
Error	240.843	43	5.601		
Total	789.708	49			

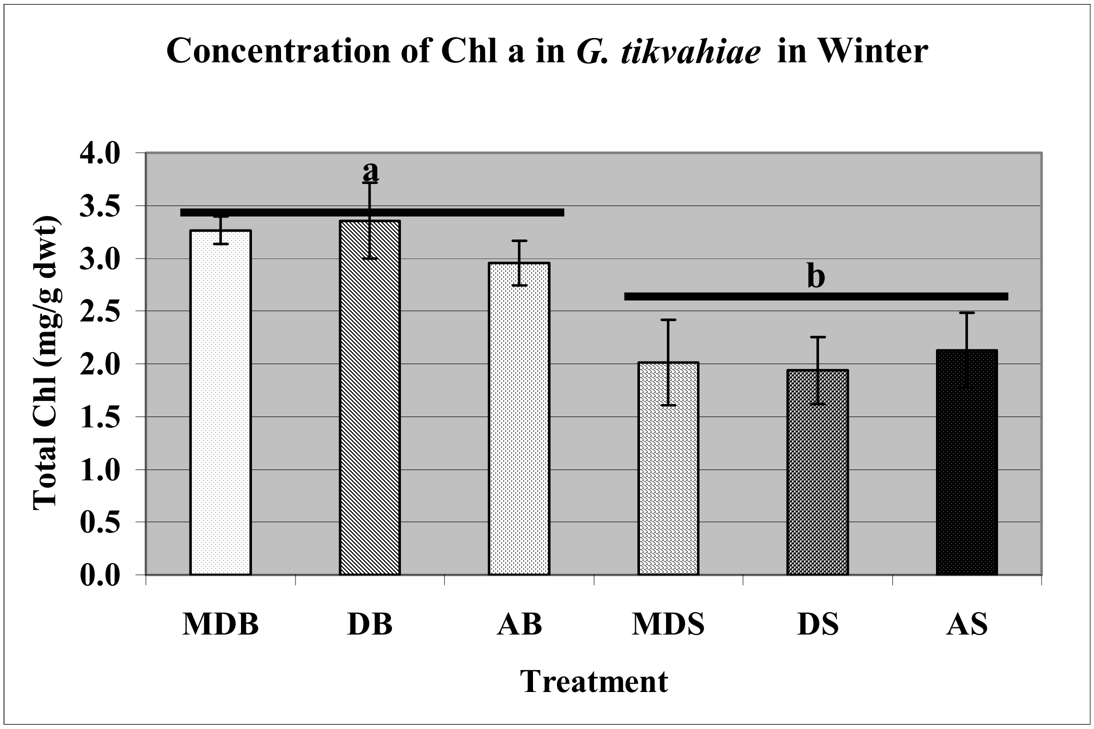

Figure 23: Chlorophyll *a* concentrations for *G. tikvahiae* in mg chl /g dry weight of tissue during winter (mean ± standard error). Letters designate significant differences at p=0.05 level. Treatment abbreviations are as follows: MDB= Manipulated Drift, Bottom; DB=Drift, Bottom; AB=Attached, Bottom; MDS=Manipulated Drift, Surface; DS=Drift, Surface; AS=Attached, Surface (n = 10).

Table 24: Two-way ANOVA results comparing chlorophyll *a* content of *G. tikvahiae* in winter with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	6.192×10^{-2}	2	3.251×10^{-2}	0.090	0.785
Location	0.663	1	0.663	0.842	0.004
Treatment*Location	$1.267\ 10^{-2}$	2	6.944×10^{-3}	0.025	0.364
Error	11.621	34	0.366		
Total	111.142	40			

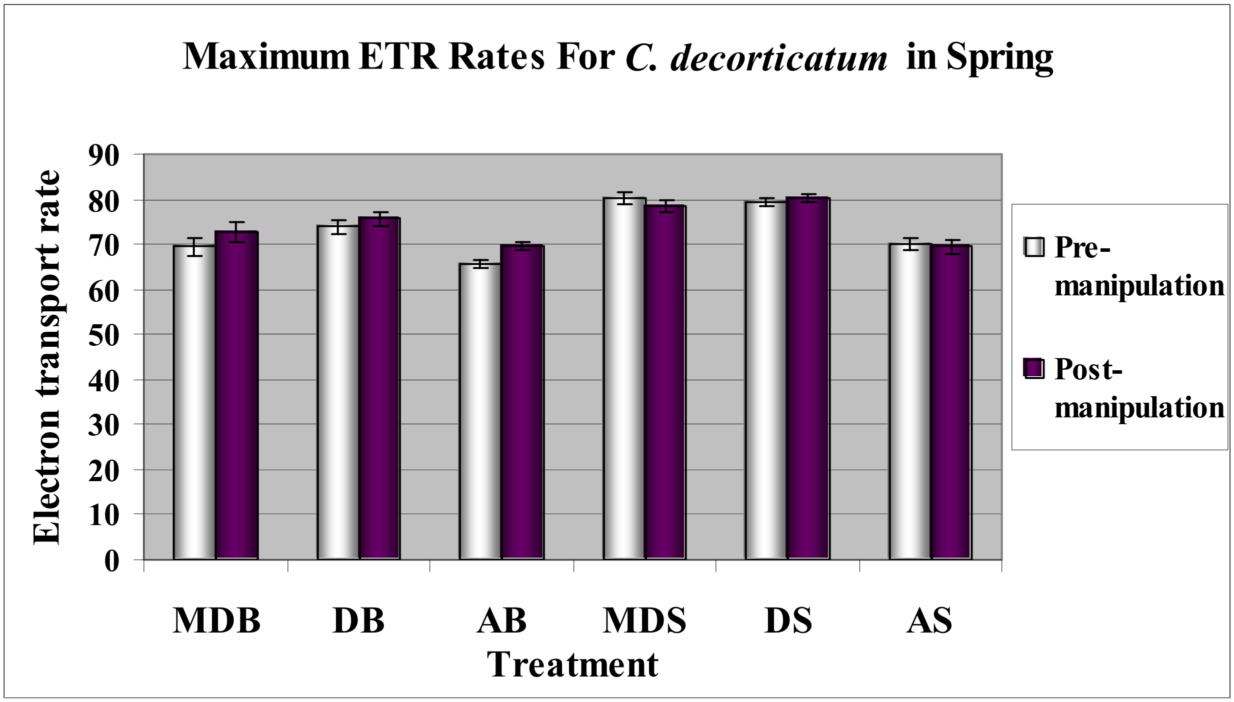

Figure 24: Maximum electron transport rates (ETR_{max}) for field *C. decorticatum* before and after manipulation (mean ± standard error). Treatment abbreviations are as follows: AB=Attached, Bottom; AS=Attached, Surface; DB=Drift, Bottom; DS=Drift, Surface, MDB=Manipulated Drift, Bottom, MDS=Manipulated Drift, Surface (n = 10).

Table 25: Two-way ANOVA results comparing pre-manipulation ETR_{max} values for *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	6.142×10^{-2}	2	2.351×10^{-2}	0.057	0.067
Location	0.288	1	0.417	0.547	0.274
Treatment*Location	$1.541\ 10^{-2}$	2	6.724×10^{-3}	0.127	0.622
Error	18.556	32	0.487		
Total	124.021	39			

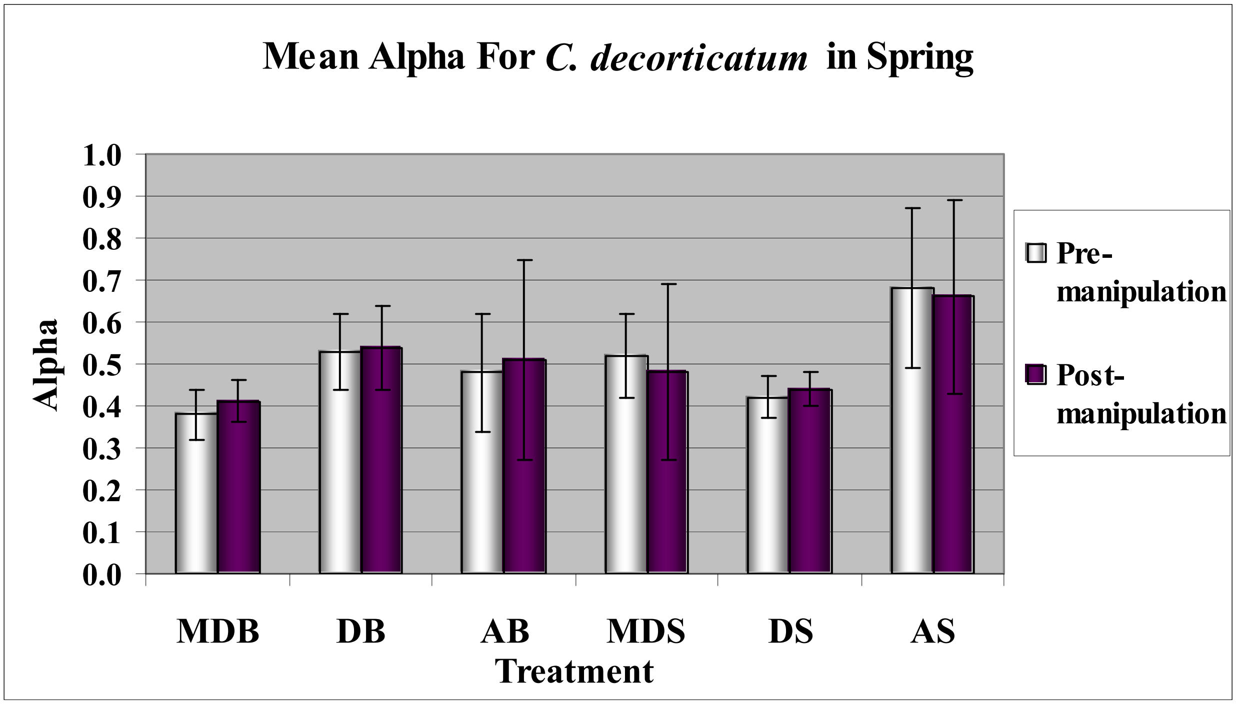

Figure 25: Mean quantum efficiency (α) for field *C. decorticatum* before and after experimental manipulation by treatments (mean ± standard error). Treatment abbreviations are as follows: MDS=Manipulated Drift, Surface; MDB=Manipulated Drift, Bottom; DS=Drift, Surface DB=Drift, Bottom; AS=Attached, Surface; AB=Attached, Bottom (n = 10).

Table 26: Two-way ANOVA results comparing pre-manipulation quantum efficiency (α) values for *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	6.324×10^{-2}	2	1.654×10^{-2}	0.124	0.219
Location	0.925	1	0.687	0.688	0.925
Treatment*Location	1.642×10^{-2}	2	8.724×10^{-3}	0.222	0.061
Error	22.604	32	0.324		
Total	187.31	39			

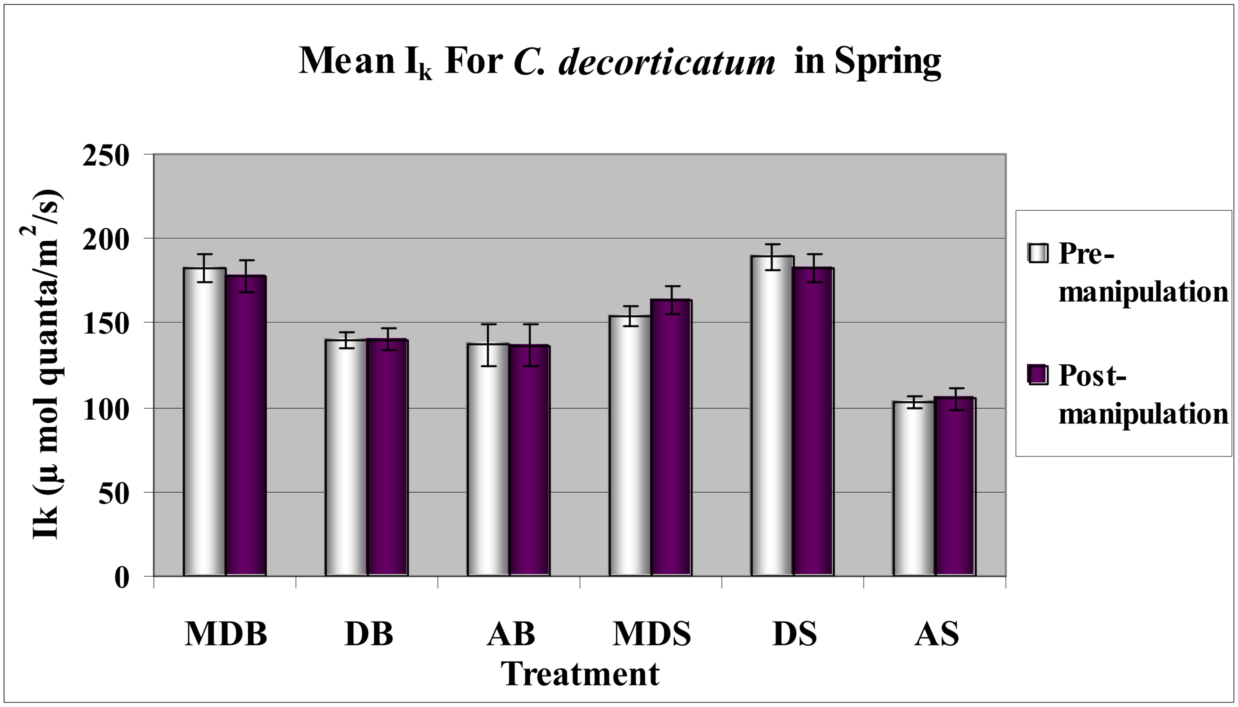

Figure 26 Mean light compensation (I_k) for field *C. decorticatum* before and after experimental manipulation by treatments (mean ± standard error). Treatment abbreviations are as follows: MDS=Manipulated Drift, Surface; MDB=Manipulated Drift, Bottom; DS=Drift, Surface DB=Drift, Bottom; AS=Attached, Surface; AB=Attached, Bottom (n = 10).

Table 27 Two-way ANOVA results comparing pre-manipulation light compensation I_k values for *C. decorticatum* in spring with treatment and location as fixed factors.

Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Treatment	5.314×10^{-2}	2	2.004×10^{-2}	0.827	0.492
Location	0.8885	1	0.687	0.724	0.081
Treatment*Location	1.331×10^{-2}	2	8.724×10^{-3}	0.275	0.054
Error	36.615	32	0.324		
Total	190.11	39			

CHAPTER FOUR: DISCUSSION

4.1 Summary

From June 2002 to April 2003, I investigated the ecology and physiology of drift algae in the Indian River Lagoon. During this period, drift accumulation did not vary seasonally or spatially at the Mosquito Lagoon site or the Indian River site, but species richness was higher at the Indian River site(Figs. 4, 5). Within drift assemblages, processes such as vertical mixing and transport occurred at the IRL site. Turnover occurred at relatively low rates (<1%), while transport of drift after 12 and 24 hours was high (>50%) (Figs. 7, 8, 9). In addition, there is a lack of physiological change in individuals of *G. tikvahiae* and *C. decorticatum* to a drift state by both growth (both species) and photosynthetic performance (*C. decorticatum*). This suggests that individuals have other acclimations to entering a drift state or that no acclimation occurs in these species.

4.2 Drift Accumulation and Composition

Over the course of this study, drift accumulation did not vary between seasons at either sites in Mosquito Lagoon or the Indian River (Table 2). Accumulation rates at both sites were similar and no significant differences were found (Table 2). Composition of the drift remained constant at both sites, suggesting a similar species composition in both the Mosquito Lagoon and the Indian River sites over the course of the sampling period. However, two more species (*A. spicifera* and *Laurencia* sp.) were found in the Indian River as compared to Mosquito Lagoon. These two species were never found in Mosquito Lagoon in the drift, although they are commonly seen growing attached at that study site. Dominant species in the drift at both locations were the same species that dominated as attached individuals at these two sites. For example, blades of *H. wrightii* dominated in the drift in spring and summer at the Indian River site. This location had a large number of seagrass beds nearby, which may have been a source of the drifting blades. The Mosquito Lagoon site also had beds of *H. wrightii*, although there were fewer of them near the sampling site and blades of *H. wrightii* were not as prevalent in the drift (Figs. 4, 5).

In comparison to other studies for this area of the IRL, this data complements some previous research and differs from others. The earliest study on drift algae in the IRL was done by R.C. Phillips between 1957 and 1959. Phillips (1961) reported 59 drift species from quarterly collections over two years in the St. Lucie Inlet vicinity, approximately 150 km south of the Indian River site and 172 km south of the Mosquito Lagoon site in this study. Philips (1961) did not quantify relative abundance and only biomass estimates were provided. He found the highest amounts of unattached algae during autumn and lowest amounts in the spring with yearly variations in biomass (Phillips 1961).

In 1975-1976, the Harbor Branch Foundation conducted a study on the standing crop of drift algae in a seagrass bed near the Fort Pierce Inlet in the Indian River, 110 km south of the Indian River site in this study. In contrast to the 11 total species representing two algal divisions (Chlorophyta, Rhodophyta) and one species of seagrass in this study, Benz *et al.* (1979) identified 63 species with 5% Cyanophyta, 19% Chlorophyta, 14% Phaeophyta, and 62% Rhodophyta (Benz *et al.* 1979). Two of most common species found during Benz's study were *Dictyota dichotoma* and *Rosenvingea intricata* (Phaeophyta); neither were found at the sites in this study. Benz *et al.* (1979) also found the highest drift biomass occurred in spring with numbers decreasing in mid-fall to its lowest level in winter. High temperatures and irradiance during the summer in their study may have caused decreases in biomass from the spring peak

(Benz *et al.* 1979). The validity of these two studies was questioned later due to their methodology and the influence of oceanic water and macrophytes from the nearby Fort Pierce Inlet, which is not representative of the IRL (Virnstein and Carbonara 1985).

From 1982-1983, Virnstein and Carbonara (1985) provided the first quantitative data for seasonal drift algal abundance north of Fort Pierce Inlet, 97 km south of our Indian River site. Maximum drift algal biomass varied seasonally with the spring peak biomass at more than three times the attached above-ground seagrass biomass (Virnstein and Carbonara 1985). Drift algal abundance also varied yearly during their study, suggesting that patterns in drift accumulations vary over larger temporal scales than could be observed during the current study period (Virnstein and Carbonara 1985). The primary taxa present in the drift was of the genus *Gracilaria* spp. (Virnstein and Carbonara 1985). Other common species in the drift were *Jania adhaerens* (Rhodophyta)*, Rosenvingea intricata* and *Dictyota dichotoma* (Phaeophyta); none of these taxa were found during this study (Virnstein and Carbonara 1985).

Abgrall and Walters (2003) reported the abundance and diversity of macrophytes in Mosquito Lagoon in the northernmost section of the IRL between 1998-2000. During their two-year study at the same Mosquito Lagoon site, they reported 26 species of drift macrophytes, of which *Gracilaria* spp. and *H. wrightii* were the dominant species collected (Abgrall and Walters 2003). No consistent seasonal patterns of drift abundance or accumulation rates were found and there were no correlations between macrophyte abundance and wind speed or flow rate (Abgrall and Walters 2003).

The aforementioned studies all used different techniques to capture drift. Two studies from this region used quadrat sampling of benthic drift macrophytes (Benz *et al.* 1979, Virnstein and Carbonara 1985) while Phillips 1961 and Abgrall and Walters 2003 used various collection techniques to sample drift macrophytes directly from the water column. Benz et al. (1979) collected seagrass and associated drift using 15 x 15 x 20 cm cores as well as hand collection of drifting macrophytes. Virnstein and Carbonara (1985) also used aerial surveys and stratified quadrat sampling to directly quantify drift biomass. Philips (1961) used hand collection techniques in sampling drift biomass. Abgrall and Walters (2003) used an array of drift collectors that collected only surface floating drift from the water column. The current findings support the lack of seasonal patterns in drift abundance or accumulation rates for the Mosquito Lagoon and the Indian River sites (Figs. 4, 5). Compared to these other studies however, this study reports much lower species diversity at both sites. Eleven total species were found during this study while other studies collected 59, 63, and 26 species (Philips 1961, Benz *et al.* 1979, Abgrall and Walters 2003), respectively.

During this research, drift individuals were observed in the vicinity of the sampling apparatus, but did not encounter the nets. It is possible that in areas where large stationary drift accumulations are common, quadrat sampling methods would more accurately reflect the diversity of the drift. Flow rates during my net trials ranged from 5.38 – 11.45 cm/s in Mosquito Lagoon and 8.22 – 9.58 cm/s in the Indian River. During low flow, drift accumulations remained nearly stationary and may not have drifted into nets or other collectors meant to sample moving drift from the water column. At these study sites, large stationary accumulations of drift individuals were rare, and when present were found in less than 30 cm of water on the shoreline prior to the start of drift trials. Drift macrophytes seen at both study sites during sampling periods were actively drifting, therefore sampling moving drift from the water column should be an accurate collection technique. While the apparatus used here did collect drift from the entire vertical water column, the data only represent the surface areas of the nets, which is considerably less than the area of the water column near shore at both sites.

Although low flow and wind speeds could explain lower amounts of drift, these data do not suggest a direct relationship between flow rates, wind speeds, and drift accumulation. Flow rates during net trials were lowest at the Mosquito Lagoon site in winter and highest in spring. At the Indian River site, flow rates were lowest in summer and highest in winter. Wind data during net trials show lowest rates during summer at both sites. These data do not correspond with previous data gathered from spring of 1998 to spring of 2000, suggesting yearly fluctuations in wind speed and water motion (Abgrall, 2002). While drift accumulation rates were not statistically significant between seasons, lowest rates occurred in spring at the Mosquito Lagoon site and in winter for the Indian River site (Figs. 4, 5). Low replication or small collection areas may account for the lower species diversity and accumulation rates seen during this study. An alternative is that for the duration of this study, species diversity was simply lower and there was less drift in the water column than in previous years.

4.3 Transport of Drift Rhodophytes

Virnstein and Carbonara (1985) were the first to suggest that dramatic increases in biomass of drift macrophytes could not be solely attributed to growth of individuals present in drift accumuations. Observed ten-fold increases in drift algal biomass over short time periods (24 hours) during studies (e.g. Kulczycki *et al.* 1981) are unlikely based on growth alone. Virnstein and Carbonara (1985) hypothesized that the import of additional drift biomass from nearby areas may have been involved in these increases in local biomass. They tracked the movement of marked drift individuals over time and concluded that drift movement occurred when current velocities exceeded 15 cm/s (Virnstein and Carbonara 1985). Marked individuals were not found within a 30 m radius of their starting points after 24 hours, although drift placed in seagrass beds remained stationary for weeks (Virnstein and Carbonara 1985).

Transport trials in this study were conducted on haphazardly chosen days. Research sites for these trials in Mosquito Lagoon were accessible only by canoe and therefore inclement weather occasionally prevented visitation of these sites. Inclement weather was defined as thunderstorms, with wind gusts or flow rates that made crossing the lagoon in a canoe dangerous. Thus, the data presented here covered a variety of weather conditions and ranges of flow for both sites. Weather during these trials ranged from calm days with wind speeds of < 1 m/s and flow rates of < 3 cm/s to mild storm conditions with rain, with wind speeds > 8 m/s and flow rates > 12 cm/s. The inability to conduct transport trials during periods of more intense flow and storm conditions does underestimate transport rates at both sites. However, it is also possible that a single trial conducted under adverse weather conditions could have skewed the data towards higher transport rates. Further research in this area is needed to determine the full extent of the impact of physical parameters (flow, wind, temperature, rainfall, light availability) on transport of drift macrophytes.

Individuals used for transport trials were selected based on their availability in the drift. Although *G. tikvahiae* was present during all seasons at both sites during the accumulation trials, transport trials were not always conducted on the same days as accumulation trials. Therefore, there were many occasions where there was so little drift at these sites that multiple species were needed to conduct the transport trials. Of the species observed at both sites, individuals of *G. tikvahiae, S. filamentosa, Chondria* spp., *H. musciformis,* and *H. spinella* were used in the transport trials. Although these species have slightly varying morphologies, all are present in natural drift accumulations and it did not appear that any one species drifted more efficiently than another. Species with obvious morphological characteristics that could possibly affect drift movement were not used in transport trials. For example, *C. decorticatum* (Chlorophyta) was not used because it holds air within its thallus and floats more than other species, and *Acanthophora spicifera* (Rhodophyta) was not included because it has a spiky thallus that may help with entanglement in other marine macrophytes.

4.4 Turnover Within Drift Accumulations

In this study multi-species drift assemblages were created based on the availability of species during the sampling season. Resulting experimental accumulations closely resembled naturally occurring drift assemblages observed in other areas of the IRL and are believed to be accurate representations of natural accumulations. In both Mosquito Lagoon and the Indian River, flow rates were found to be significantly lower in spring during transport trials (Table 9, Fig. 10). This trend is reflected in the turnover data, as the lowest turnover rates were reported during the spring trials (Tables 11, 12, Fig. 12). Turnover did occur within my experimental accumulations with less than 1% of experimental individuals moving per hour. However, with a minimum of 1 individual moving per hour, it is possible for complete turnover within these experimental groups within 15 hours. While these numbers are low per hour, extrapolation for time shows that turnover is occurring over longer periods of time. Increased replication during low and high flow rates and for extended time periods may be necessary to fully understand the impact of flow on turnover within algal accumulations.

4.5 Growth of Drift vs. Attached Algae

There were no acclimations in growth rates in *C. decorticatum* and *G. tikvahiae* in response to entering a drift state. Unattached macroalgae at the Mosquito Lagoon site can remain close to their original substrate or move via currents to other locations. Mosquito Lagoon varies in depth and in water quality seasonally and spatially (Walters *et al.* 2001). Individuals entering the drift may be exposed to varying light, salinity and temperature levels different from their prior habitat. For example, an attached individual of *C. decorticatum* growing in 4 m of water is detached from its substrate. The individual is moved towards shore and remains adrift at the surface of the water column in 1 m of water for several months. Light quality and quantity has increased substantially and effects from storm activity in the form of rain and wave action are now environmental factors to which this individual must acclimate. If these data showed differences between treatments, this would suggest acclimation to these new factors. This is not the case here.

Acclimation is defined as a changing of physiological pathways to accommodate changes in environment, including the factors discussed here. Previous studies involving drift collection have noted morphological and pigmentation differences as well as the lack of reproductive structures in drift individuals when compared to their attached counterparts (Collins 1914, Norton and Mathieson 1983). However, these are observations only and are not reinforced by hard data; actual experimentation showing acclimation to a drift state is rare (Norton and Mathieson 1983). According to these data, there were no significant changes to individuals of these two species to entering the drift in either growth rate or chlorophyll content. There is value in documenting a lack of acclimation to a drift state. Individuals of these two species are able to enter the drift without changing physiological pathways associated with growth or chlorophyll content, regardless of changes in environmental factors. The ability to survive this change in life-history without the metabolic expense of altering photochemical pathways can be of great importance to drift individuals.

4.6 Photosynthetic Performance of Attached vs. Drift *C. decorticatum*

PAM-fluorometry has been proven as a useful tool in estimating the light harvesting capabilities of photosynthetic organisms, ranging from seagrasses (Ralph et al. 1998, Ralph 2000, Durako and Kunzelman 2002, Campbell *et al.* 2003) to corals (Lesser and Gorbunov 2001, Ralph *et al.* 2002) to arctic algae (Kuehl *et al.* 2001, Michler *et al.* 2002). Studies on macroalgae are numerous (Haeder and Figureoa 1997, Gorbunov *et al.* 2000, Beer *et al.* 2000, Beach *et al*. 2003); the application here is not common in the literature. Measurements of quantum efficiency (α), saturating irradiance (I_k) and ETR_{max} were used as an indication of acclimation from an attached to a drift state. The treatment groups used naturally occurring attached and drift individuals remaining in these states in our experimental field array. There should have been no significant differences in $ETR_{max,}$ I_k and α from ETR vs. I curves of experimental individuals. This would be due to the fact that they did not undergo a physical transformation from attached to drift as demonstrated by the growth and pigment data. This is indeed true for these experimental individuals from all treatments.

Manipulated drift (MD) treatment individuals were predicted to show differences in ETR_{max}, I_k, and α pre-and post- manipulation; this would show acclimation from their prior (attached) state. Some physiological changes were expected to be necessary for these individuals to maximize their light harvesting potential following detachment. However, no significant difference between pre- and post- manipulation ETR vs. I curves for ETR_{max}, I_k or α parameters were found. This suggests that there is no photosynthetic acclimation in *C. decorticatum* to becoming drift by the parameters measured or that the acclimation, if present, was not detectable by the methods used here.

While this analysis does not find indications of acclimation to a drift state in *C. decorticatum*, the parameters measured do provide insight into the photosynthetic processes of these individuals. In an ETR vs. I curve, the initial slope of the curve or α is used as an indication of the light harvesting efficiency of the individual measured (Krause and Weis 1991; R. Gademann, pers. com.). As α nears a value of 1.0, the closer the relationship between ETR and light absorbed approaches a 1:1 ratio. The ETR_{max} parameter estimates the maximum rate that the sampled individual is able to move light energy through its photochemical pathways (Maxwell and Johnson 2000, Beach *et al.* 2003, R. Gademann pers. com.). Comparing the results for α for *C. decorticatum,* similar α values were seen in most cases for surface locations than bottom (Fig. 25). Individuals in these trials were similarly efficient at using light in their photochemical.pathways regardless of treatment or location. Surface individuals were exposed to slightly higher light levels than bottom individuals, so they should be receiving light faster than bottom individuals and therefore would have a higher quantum efficiency (α). The data for ETR_{max} between treatments shows similar ETR across both treatments and locations (Fig. 24) This experiment may have benefited from replication with repeated rapid light (ETR vs. I) curves taken at numerous intervals during the experimental period, perhaps for a longer duration. It is possible that the adaptation to a drift state does occur within the photochemical pathways, but that my measurements were not taken at times and durations that may have revealed these changes. Conversely, it is also possible that a longer period of acclimation may be necessary, but unlikely due to known rapid changes in light harvesting efficiency in marine macrophytes (Karsten *et al.* 2001, Aguilera *et al.* 2002, Bischof *et al.* 2002).

4.7 Conclusions

Past studies on drift macrophytes in the Indian River Lagoon have been limited to quantification of drift (Phillips 1961, Benz *et al.* 1979, Virnstein and Carbonara, 1985, Abgrall and Walters 2003), effects of drift accumulations on seagrasses (Virnstein and Carbonara 1985), and relationships with benthic invertebrates or larval vertebrates (Kulczycki *et al.* 1981, Virnstein and Howard 1987, Snelson and Johnson 1995, Abgrall, 2002). The current study is the first to address the physiological aspects of drifting macroalgae in the IRL and further explore the ecology of drift. Transport of drift algal individuals does occur in both Mosquito Lagoon and the Indian River with no seasonal trends at either site. Turnover within drift accumulations occurs at low rates at both sites and was lowest in spring. Longer periods of study of accumulations may reveal higher turnover rates. The data presented here show no indications of adaptation to a drift state by growth, photosynthetic performance, or chlorophyll content in *C. decorticatum* or *G. tikvahiae*. The lack of acclimation shown here raises questions about drift macrophytes. Are drift individuals any different from their attached counterparts? I only sampled two species during this study; is it possible that acclimations to drift are species-specific? At present, there are more questions about drift macrophytes and drift accumulations than literature providing insight into drift ecology and physiology. Further investigations into the processes allowing attached individuals to survive upon entering a drift state are required to better understand the ecophysiology behind this important community in the IRL.

Drift algal accumulations are natural features of many estuaries and other marine communities throughout the world. Studies involving aspects of larval settlement, community structure, seagrass interactions, and invertebrate interactions may benefit from literature exploring the ecology and physiology of the drift macrophyte communities. These studies rely upon basic physiological data to provide an understanding of relationships between experimental organisms. If indeed drift macrophytes are physiologically dissimilar from attached communities, it is conceivable then that studies involving drift or interactions with drift may be lacking basic data that could prove useful in explaining these processes. It is beneficial to the scientific community to explore this aspect of marine ecology in the pursuit of a better understanding of drift ecology and physiology.

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