The role of spatial and ontogenetic morphological variation in the expansion of the geographic range of the tropical brown alga, *Turbinaria ornata*

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Synopsis
Like many reefs worldwide, reefs in French Polynesia are experiencing a shift from coral-dominated to algal-dominated systems. The macroalgae *Turbinaria ornata* comprises the majority of the increasing algal biomass on the barrier reefs surrounding these islands, and its distribution is increasing throughout this region. Aspects of the ecomorphology of *Turbinaria* make it ideally suited to thrive under the physical conditions found across barrier reefs throughout French Polynesia. Spatial morphological variation allows *Turbinaria* to produce morphotypes that are suited either to the calm, unidirectional, slowly flowing water in the backreef or to the high-energy wave-driven flow of the forereef. Backreef plants are flexible and produce airbladders that make them buoyant, whereas forereef plants are not buoyant, but strong and stiff. Production of bladders and resulting buoyancy has been found to be a phenotypically plastic trait in response to movement of water and confers advantages to backreef plants and plays an important role in dispersal. Ontogenetic variation of buoyancy, material properties, and reproductive capacity is part of a dispersal strategy whereby fertile, buoyant fronds drift between oceanic islands and form new populations, thereby contributing to the recent expansion of range of *T. ornata* across French Polynesia.

Introduction
In any habitat, interactions between individuals and the physical environment determine organismal performance, which forms the foundation of species distributions, and ultimately population and community structure. Examinations of physical-biological interactions at the organismal level provide a mechanistic understanding of strategies that organisms have evolved to contend with physical conditions across their geographic range. Identifying such mechanisms (1) provides insight into the processes responsible for current community structure, (2) can help predict how that structure may change across physical gradients or temporally as conditions change within a habitat, and (3) can guide decisions about conservation and management under specific, changing physical scenarios.

Coral reefs are a system in which organismal response to physical factors are increasingly responsible for the dramatic phase shift from coral-dominated to algal-dominated systems worldwide. Much effort has been paid to the response of physiological parameters of reef-forming corals to predicted physical changes (e.g. Goreau and Goreau 1959; Gates & Edmunds 1999, Fitt et al. 2001) and how reef algae can benefit from altered nutrient regimes and reduced pressure of herbivory due to overfishing (e.g. Szmant 2002; Lapointe et al. 2005; Smith et al. 2005). Additionally, the ecomorphology of successful reef algae is also an important driver of algal success on reefs, but has received relatively little attention (but see Collado-Vides et al. 1998; Walters et al. 2002; Anderson et al. 2006).

On the barrier reefs in French Polynesia, the tropical macroalga, *Turbinaria ornata* is becoming increasingly abundant (Payri and Naim 1982; Payri 1987; Done et al. 1991). Although native to parts of the region (the Society Islands and the Austral Islands), since 1980, it has expanded its range to include many of the islands in the Tuamotu archipelago (Stiger and Payri 2005), and its abundance is increasing dramatically to the point that it is functioning as an invasive species (Stiger and Payri 1999a; Andrefouet et al. 2004). This increase in *Turbinaria* is both a symptom of, and contributor to, the phase shift from coral-dominated to algal-dominated reefs in many places in the South Pacific Ocean.

Many factors contribute to the increase of this alga. Reefs in French Polynesia are experiencing...
similar stresses as are many other coral reefs (Hoegh-Guldberg et al. 2007), including episodes of coral bleaching and outbreaks of the Crown of Thorns starfish, *Acanthaster planci*, both of which result in dead coral suitable for settlement of *Turbinaria*. Additionally, increased nutrient input from agriculture and development on islands, as well as decrease of herbivorous fishes and urchins due to overfishing, are contributing to degradation of coral health (Hutchings et al. 1994). This background of altered nutrient input and coral degradation create a situation in French Polynesia that *T. ornata* is able to exploit through a combination of life-history strategy and spatial and ontogenetic morphological variability. This article provides an overview of the role of the ecomorphology of *Turbinaria* in its recent expansion of range in French Polynesia.

**Natural history of Turbinaria**

*Turbinaria ornata* is a perennial macroalga of the class *Phaeophyceae*, order *Fucales*, family *Sargassaceae*. It is widely distributed in tropical and subtropical areas of the Indian Ocean and throughout the western and southern Pacific Ocean (Wynne 2002, Rohfritsch et al. 2007). Thalli of *Turbinaria* consist of a holdfast from which grow one to several unbranched or dichotomously branched fronds that can reach lengths of 30 cm. New fronds can grow from a viable holdfast if all fronds are removed. *Turbinaria* is sometimes described as upright leathery seaweed and has the common name of “spiny-leaf seaweed” due to the double row of sharp spines on the margins of its pyramid-shaped blades. *Turbinaria* is well protected from herbivores, both by phenolic compounds (Stiger et al. 2004), spines, and a hard, tough texture. It is reproductive year-round, although fertility rates vary seasonally (Stiger & Payri 1999a, 2005). Reproductive receptacles form at the base of each blade on mature fronds. Thalli can be monoecious or dioecious, and gametes consist of motile sperm and large nonmotile eggs that are fertilized inside the female receptacle. Male gametes are released once a month in response to the lunar cycle (Stiger and Payri 1999b).

**How morphological variation maintains distribution across a barrier reef**

Available habitat for *Turbinaria* in French Polynesia is on barrier reefs that form close to shore around the many high volcanic islands in the region. Barrier reefs create an extreme hydrodynamic gradient over relatively short spatial scales, where high-energy bi-directional wave-driven flow on the forereef and calm, relatively slow unidirectional flow in the backreef can occur within several hundred meters of each other. Many organisms are specialized to cope with one type of flow or the other, but *Turbinaria* is abundant in both types (Stewart 2006b), producing different morphologies that are suited to either backreef or forereef conditions (Payri 1984; Stewart 2006b) (Fig. 1). Forereef thalli have shorter, more compact shapes with stronger and stiffer stipes, enabling them to remain attached on the forereef in the face of velocities of flow that can exceed 4 m/s (Stewart 2006b). Very few organisms can withstand these forces and this ability enables *Turbinaria* to exist on the forereef where competition for space is reduced. Thalli on the backreef are longer than those on the forereef, have more widely spaced blades, and flexible weak stipes (Stewart 2004) that cannot withstand the forces imposed by flows on the forereef, as demonstrated by transplant experiments whereby backreef thalli transplanted to the forereef all broke at their stipes (Stewart 2006b). Calculations of ESF (Johnson and Koehl 1994), or the potential for detachment of fronds in their natural habitats, revealed that detachment of backreef and forereef fronds may be similar, considering the different hydrodynamic conditions they experience (Stewart 2006b). Flow velocities under the largest waves on the forereef (height of breaking waves 4–15 m) may be as high as 4.7 m/s. Velocities in the backreef during such storms may reach 1–2 m/s. Under these conditions all forereef and backreef fronds are predicted to break. Under typical nonstorm conditions, however, ESF calculations predict that neither backreef nor forereef fronds will break (Stewart 2006b).

Backreef thalli also differ morphologically from forereef thalli in that they have air bladders in their blades that impart buoyancy to the thallus (Fig. 2). Adult backreef thalli have as much as 85% of their blades containing pneumatocysts, which impart buoyant forces of \( \sim 0.023 \pm 0.007 \text{ N} \), while forereef thalli that lack air bladders experience negative buoyant forces of \( -0.01 \pm 0.005 \text{ N} \) (mean ± SE). Eight-week transplants of thalli from the forereef to the backreef resulted in development of air bladders in forereef blades and increases in buoyancy over the negative buoyancy of forereef controls, indicating that production of air bladders and the resulting buoyancy are phenotypically plastic traits in *T. ornata* (Stewart 2006b).

A flexible, buoyant morphology is well suited to the habitat available for *Turbinaria* in the backreef, which is primarily on the tops of coral bommies (Fig. 3) where low tides have exposed and killed the
coral tissue. This morphotype enables *Turbinaria* on the tops of bommies to track the surface of the water, its buoyancy keeping it in the most upright position possible without sticking out of the water where it would suffer desiccation. Maximizing the height in the water column increases the speed of flow experienced by thalli as it positions them higher in the benthic boundary layer where flow is faster, thereby increasing rates of mass transfer of nutrient and gases (Stewart 2004, 2006a). This is an important consideration in unidirectional, slow, low-nutrient water in the backreef. A flexible, buoyant morphology also allows backreef *Turbinaria* to “duck out” of high flow when waves do come over the reef during storms. Flexibility allows thalli to be reconfigured and pushed over, into slower flow near the substratum, reducing the force they experience,
and then buoyancy passively returns the thallus to an upright position when the flow slows (Stewart 2006a). Measurements of drag force experienced by backreef and forereef thalli indicate that the production of airbladders in *Turbinaria* increases drag (Stewart 2006b), but because backreef thalli generally experience relatively slow flow, damage by hydrodynamic force is likely less to occur. Thus, the spatial variation in morphology allows *Turbinaria* to cope with the extreme hydrodynamic gradient that exists across the barrier reefs of French Polynesia.

An upright position also increases interception of light in the dense aggregations of *Turbinaria* that form on the tops of bommies (Stewart et al. 2007) (Fig. 3). Field experiments that measured the amount of light intercepted along the length of thalli over the course of a day indicated that more light was intercepted by buoyant thalli in aggregations than by nonbuoyant thalli in aggregations. Additionally, nonbuoyant thalli in the open intercepted similar amounts and intensities of light as buoyant thalli in aggregations, indicating that shading by neighbors is the main contributor to reduction of light when thalli are rendered nonbuoyant. Using photosynthesis versus light relationships established for *T. ornata* in the field under ambient conditions, interception of light was translated into fixation of carbon for buoyant and nonbuoyant thalli both in aggregations and in the open. Nonbuoyant thalli in aggregations fix significantly less carbon than did nonbuoyant thalli in the open, and less than buoyant thalli either in aggregations or in the open. The fact that backreef fronds are maintained in upright positions decreases shading of fronds by their neighbors, and maximizes overall interception of light in aggregations of *Turbinaria*. The unique columnar shape of *Turbinaria* fronds means that in aggregations light is still able to penetrate into the gaps between adjacent fronds (Stewart, unpublished data) (Fig. 4), relative to bladed kelp that form thick overlapping canopies that block light and can reduce ambient light by 90% (Gerard 1984; Stewart et al. in review).

**How ontogenetic morphological variation contributes to dispersal between islands**

In addition to morphological variation between habitats, changes in morphology through the lifetime of *Turbinaria* (Fig. 5) contribute to its dispersal among islands. The buoyancy of backreef thalli enables them, when detached, to float at the water’s surface, and this is an important component of interisland dispersal. Material properties reveal that the breaking stress and extension ratio of stipes (where they break naturally) of *Turbinaria* decrease...
with ontogeny, and the net buoyant force experienced by thalli increases (Stewart 2006c). Therefore, as backreef thalli age, they become reproductively mature, longer, more buoyant, and their stipes become weaker and less extensible (Stewart 2006c). Drag on thalli also increases as thalli age and become longer. Drag on old fronds in flow speeds \( \sim 75 \text{ cm/s} \) [a reasonable estimate of high flow in the backreef (Stewart 2006c)] was 3 \( \times \) higher than that experienced by juveniles and 1.5 \( \times \) the drag experienced by young adults. Estimates of the potential for breakage (ESF) of thalli are higher for older fronds under realistic scenarios of flow for reefs in Moorea. In rafts found floating in the backreef after storms, 79% were characterized as “old” thalli, 21% as younger adults and less than 1% were juveniles. This contrasts to age composition of thalli still attached on the reef, where 70% were juveniles, 26% were young adults and 5% were old (Stewart 2006c). Phenolic content also increases as thalli age (Stiger et al. 2004), thereby decreasing palatability with reproductive maturity and providing chemical defense for mature floating thalli.

After storms, detached thalli are congregated by surface winds and currents, and can form large mats (up to 2500 m\(^2\)) (Andrefouet et al. 2004) of floating, old fertile thalli (Stewart 2006c). Fertility is maintained in detached thalli for up to 3 months, during which time male thalli experience multiple spawning cycles, triggered by lunar phases (Stiger and Payri 1999b). Fertilization occurs in the receptacle of the female thallus. Germlings released from female receptacles disperse only up to 1 m from the parent plant (Stiger and Payri 1999b). Dispersal by floating adult thalli of \( T. \ ornata \) has been attributed as the cause of the expansion of its range from the Society and Austral Islands to the Tuamotu, a minimum distance of \( \sim 200 \text{ km} \) (Martinez et al. 2006). Given the morphological variability and plasticity of \( T. \ ornata \), it is likely that germlings have the ability to develop into morphotypes well adapted to conditions in either backreef or forereef habitats, depending on where they are released and settle (Fig. 6).

**Summary**

The spatial and temporal morphological variability of \( T. \ ornata \) plays an important role in the success of this alga on barrier reefs of islands across French Polynesia. Small, stiff, and strong forereef thalli survive under high-energy waves, and weaker, longer, flexible, buoyant backreef fronds thrive on tops of bommies in the backreef where flow is slow and
unidirectional. Ontogenetic increases in buoyancy correlate with increases in reproductive potential, and with decreases in tissue strength and extensibility that create differential detachment of buoyant, fertile fronds. As the abundance of *T. ornata* increases, larger mats of drifting fronds travel to more distant islands, where populations may be established. Thus, *T. ornata* can capitalize on declining health of corals through its ability to disperse to new areas and create morphotypes appropriate to the physical conditions of the substratum that becomes available. Once established, its anti-herbivory properties help ensure its establishment. Recognizing the role of ecomorphology in the success of this alga is important in understanding the mechanisms contributing to the shifts from domination by corals to algal domination of reefs.

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