

Turbinaria ornata as an herbivory refuge for associate algae

Sarah Joy Bittick · Nicholas D. Bilotti ·
Heather A. Peterson · Hannah L. Stewart

Received: 18 May 2009 / Accepted: 1 October 2009 / Published online: 24 October 2009
© Springer-Verlag 2009

Abstract Habitat associations are an integral part of coral reef community structure. Commonly, one organism lives in such close association within or near another that a spatial refuge occurs, whereby one of the organisms provides protection to the other. This is often the result of defenses of the host deterring an associate organism's consumers. In Moorea, French Polynesia, the range and abundance of the brown macroalga, *Turbinaria ornata*, have increased drastically since 1980 such that dense aggregations of this macroalga are a dominant component of the backreef habitat. *Turbinaria ornata* is both mechanically and chemically defended from herbivores. Other species of macroalgae grow within aggregations of *Turbinaria* and may benefit from these defenses. This study investigates whether aggregations of *Turbinaria* create a refuge from herbivory for associate macroalgae. When *Turbinaria* aggregations were removed experimentally, there was a significant increase in the number of associate algal species. Moreover, an herbivory assay using the palatable local alga *Acanthophora spicifera* identified herbivory as the mechanism for lower diversity on bommies lacking *Turbinaria* aggregations. The local increase in algal richness due to the refuge from herbivory afforded by *Turbinaria* may be an important

contribution to macroalgal and community dynamics on reefs in Moorea, French Polynesia.

Introduction

An associational refuge is one in which a host species provides protection that enhances the survival of associate species. Such interactions affect community structure directly by increasing local species richness (Dayton 1975; Stachowicz 2001a) and indirectly via positive effects that influence higher trophic levels (Hacker and Bertness 1996) and may have community wide ramifications (Levenbach 2008a, b). Positive interactions such as associational defense and refuge are increasingly recognized as important drivers of ecosystem function (Bertness and Callaway 1994; Bruno et al. 2003).

Many tropical seaweeds use chemicals to protect themselves from fishes and large invertebrates, an adaptation that provides the opportunity for small organisms to be protected from their predators by associating with these defended hosts (Hay 1997). A diverse assortment of invertebrates, including crustaceans, gastropods, polychaete worms and urchins has been found to take refuge in chemically defended algae (Stachowicz 2001b). For example, the amphipod *Ampithoe longimana* seeks refuge from fishes in species of unpalatable seaweeds from the genus *Dictyota* (Sotka et al. 2003; Duffy and Hay 1994) and the snail *Littornia fabalis* uses furoid seaweeds as a refuge from crab predation (Kemppainen et al. 2005). Macroalgae may also benefit from spatial refuges within unpalatable host algae (Pfister and Hay 1988). Increased local diversity of invertebrates and macroalgae resulting from spatial refuges can have important implications for marine ecosystem structure (Stachowicz 2001b; Hay 1986).

Communicated by S. D. Connell.

S. J. Bittick · N. D. Bilotti · H. A. Peterson · H. L. Stewart
Department of Ecology and Evolutionary Biology,
University of California, Los Angeles, CA, USA

H. L. Stewart (✉)
UMS 2978 EPHE-CNRS,
Centre de Recherche Insulaire et Observatoire de l'Environnement
(CRIOBE), BP 1013, Papetoai 98729, Moorea,
French Polynesia
e-mail: hannahcriobe@gmail.com

As macroalgae are important components on many coral reefs worldwide, and may be increasing in some areas (e.g., Done 1992; Smith et al. 2001, but see Bruno et al. 2009), it becomes important to understand the implications of changing amounts of macroalgae to reef community structure. The possibility of an increase in local algal diversity due to an associational herbivory refuge provided by another alga may have increasingly important ramifications in coral reef ecosystems. Examining the mechanisms underlying these local associational interactions with dominant macroalgae provides insight into the processes structuring these systems. This study was motivated by the observation that a rich abundance of seaweed species occurs within aggregations of *Turbinaria ornata* (Turner) J. Agardh (Fucales, Phaeophyceae), an increasingly dominant brown alga in Moorea, French Polynesia. The range of *Turbinaria* throughout French Polynesia has increased markedly since the 1980s (Payri and Stiger 2001; Stiger and Payri 2005) at which time it was found only in the Austral and Society Islands (Payri and Naim 1982). *Turbinaria ornata* has been recorded in islands in the north and south regions of the Tuamotu Archipelago (Montaggioni et al. 1985; Payri and Stiger 2001; Stiger and Payri 2005; Martinez et al. 2007) and in Mangareva in the Gambier Archipelago (H. L. Stewart, personal observation 2009). The abundance of *Turbinaria* in this region has increased as well, especially in Tahiti and Moorea (Payri 1987; Martinez et al. 2007). In Moorea, *Turbinaria* is a dominant organism found in the backreef (Stiger and Payri 1999; Stewart 2006a). *Turbinaria ornata* attaches to areas of dead coral and is prominent on coral bommies where it forms dense aggregations, usually between 15 and 35 thalli per 0.25 m² (Stewart 2006b).

Turbinaria ornata has a number of characteristics that make it unpalatable to herbivores including the following: (1) hard, rough texture, (2) double row of sharp spines on the blade margins (Littler and Littler 2003; Payri et al. 2004) and (3) high phenolic content (Deslandes et al. 1997; Stiger et al. 2004), which provides an effective chemical defense against herbivores (Norris and Fenical 1982; Hay and Fenical 1988; Harlin 1996; Hay 1996; Martinez 1996; Amsler et al. 1998; Targett and Arnold 1998). Grazing by herbivorous fishes (parrotfish (*Chlorurus sordidus*) and lined bristletooth surgeonfish (*Ctenochaetus striatus*)) is low on *Turbinaria* aggregations and high on adjacent patches dominated by crustose algae in Moorea (Gleason 1996).

We investigated the mechanism by which *Turbinaria*, a mechanically and chemically defended host species, provides an associational refuge for other seaweed species. Specifically, we asked: (1) Is seaweed diversity higher within *Turbinaria* aggregations than on comparable patches of dead coral? (2) Does removal of *Turbinaria* reduce diversity of associate macroalgae? (3) Do aggregations of

Turbinaria prevent herbivory on associated palatable algae?

Materials and methods

Study site

This study was conducted on the backreef northwest of Cook's Bay on the north shore of the island of Moorea, French Polynesia (17°30'S, 149°50'W). Research was based at the University of California's Gump South Pacific Research Station in Cook's Bay.

Field survey

This research was motivated by the observation that bommies with aggregations of *Turbinaria ornata* appeared to harbor higher abundances and diversity of other macroalgal species than bommies lacking *Turbinaria*. Surveys of algal diversity on 22 randomly selected coral bommies (11 with and 11 without *Turbinaria*) were conducted to quantify this observation. All suitable bommies were covered by at least 50% live coral to ensure that all sites had a similar community structure and the bommies with *Turbinaria* had a minimum of 10 *Turbinaria* thalli per 20 × 20 cm² area. To quantify algal diversity, thalli of *Turbinaria* were cut and removed just above the holdfast and the underlying algae were collected for identification. All material was scraped from the coral heads and placed in watertight collection bags in order to prevent the loss of small algal pieces. Samples were then taken back to the lab, examined using a Leica compound dissecting microscope and identified to species. The number of species was totaled for each sample, and the difference in diversity between bommies with and without *Turbinaria* was statistically analyzed using a paired *t*-test.

Effects of *Turbinaria ornata* on algal species richness

To determine whether the presence or absence of *Turbinaria ornata* on bommies was responsible for differences in understory algal diversity, we conducted a field experiment whereby *Turbinaria* densities were manipulated and the number of species of associated algae was counted after 14 days. Twenty random bommies were selected using 20 random compass headings. We swam in the direction of each compass heading until we came to a suitable bommie. Again suitable bommies were those with at least 50% live coral and at least 10 thalli per 20 × 20 cm² area. Each bommie was tagged with a numbered label.

Our experimental design consisted of two factors, presence or absence of *Turbinaria*, and caged/uncaged

bommies. Cages prevented herbivory by fishes, important herbivores in this system (Hay 1986; Carpenter 1986; Ogden and Lobel 1978). Urchins, another important herbivore (Pfister and Hay 1988), were also removed from the cage area. On ten randomly selected bommies, *Turbinaria* were cut off approximately 3 cm above the holdfast, at the point where plants naturally break (Stewart 2006a), leaving algal species that occur in and around the holdfast undisturbed. Five of these bommies and five of the bommies from which the *Turbinaria* was not removed were randomly selected to be caged.

Cages were constructed from metal caging material with a mesh size of 1.69 cm². They were 20 × 20 cm² at the base and 25 cm high. Strips of caging material of area 5 × 20 cm² were attached loosely to each side of the base using zip-ties to form a skirt that later was fit to the topography so that the cage would be flush with the bommie in order to effectively exclude herbivorous fishes and urchins.

At each bommie receiving the cage treatment, the area of highest *Turbinaria* density was selected as the location of the cage. The cage was secured to the bommie using one to two nails that were hammered into the skirt on each side. If necessary, the skirt was also zip-tied to the nails for added stability. Sites without cages were measured using our 20 × 20 cm² quadrat and marked with nails at each of the four corners to outline the study area. Once each site was marked by nails or a cage, the *Turbinaria* was cut from the ten bommies selected for the no *Turbinaria* treatment. All cages and plots were set out on May 14, 2008.

On May 27, 2008, 14 days later, the study area of each bommie was scraped with a paint scraper into individually labeled collection bags. Algal species were identified using a Leica compound dissecting microscope for all samples, and species diversity was analyzed using a two-factor ANOVA (*Turbinaria*/No *Turbinaria*; Cage/No Cage).

Herbivory assay

In order to determine the relative efficacy of aggregations of *Turbinaria ornata* in providing a refuge from herbivory, we conducted an herbivory assay for our treatments using the experimental setup mentioned earlier. Five grams of the palatable alga *Acanthophora spicifera* were weighed and zip-tied to a 0.5 m piece of string. Twenty of these strings were prepared, one for each of our study bommies. At each bommie, the rope with 5 g of *A. spicifera* was tied to two nails so that it laid flush with the dead coral substrate and crossed diagonally through the plot. On the *Turbinaria* bommies, the *A. spicifera* was placed underneath the *Turbinaria* canopy and the rope tied accordingly. Extra *Turbinaria* thalli were attached to the rope if necessary to ensure that the palatable algae were within an aggregation of *Turbinaria*. The herbivory assay ran for 2 days, from

May 23 to May 25, 2008, at which point the remaining *A. spicifera* was weighed. A two-factor ANOVA was performed on percent change in wet weight of *A. spicifera* (*Turbinaria*/No *Turbinaria*; Cage/No Cage).

Statistical analyses were conducted using JMP (v6.0.3, SAS Institute).

Results

Effects of *Turbinaria ornata* on algal diversity

Our study shows that aggregations of *Turbinaria ornata* provide a refuge for other seaweed species. Surveys demonstrated that there was a significantly higher number of associate algal species within aggregations of *Turbinaria* than on otherwise similar bommies that lacked *Turbinaria* (*t*-test $t_{10} = 11.7$, $P < 0.001$). We were not able to always identify to species, but abundant algae in *Turbinaria* aggregations included these fleshy species: *Caulerpa serrulata*, *Dictyota bartayresiana*, *Sargassum mangarevense*, *Valonia utricularis*, *Ventricaria ventricosa*. Bommies without *Turbinaria* lacked fleshy, palatable algae and were dominated by crustose coralline algae, filamentous algal turfs and cyanobacteria. For bommies with *Turbinaria*, there were 14.5 ± 1.0 (mean \pm SE, $n = 11$) algal species in a 20 × 20 cm² area, whereas on bommies without *Turbinaria*, the same area contained 2.8 ± 0.3 species (mean \pm SE, $n = 11$) (Fig. 1).

Our field experiment indicated that aggregations of *Turbinaria* were effective for enhancing species richness. Treatments with aggregations of *Turbinaria* had similar algal richness as the two caged treatments, and when

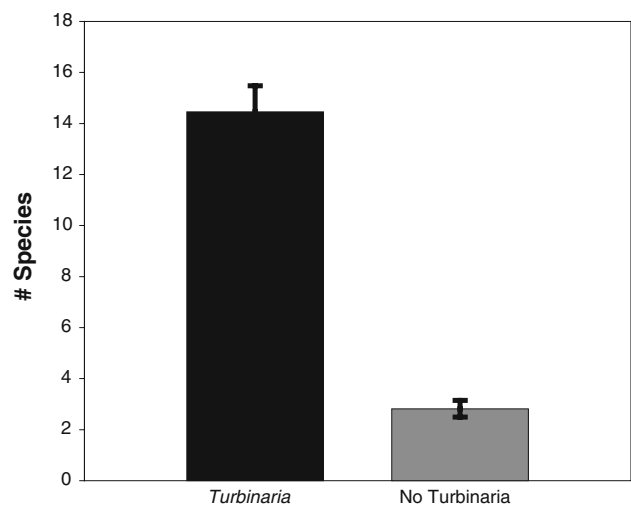


Fig. 1 The mean number of algal species on coral bommies with and without aggregations of *Turbinaria* (*t*-test, $t = 11.714$, $df = 10$, $P < 0.001$, mean \pm SE, $n = 11$)

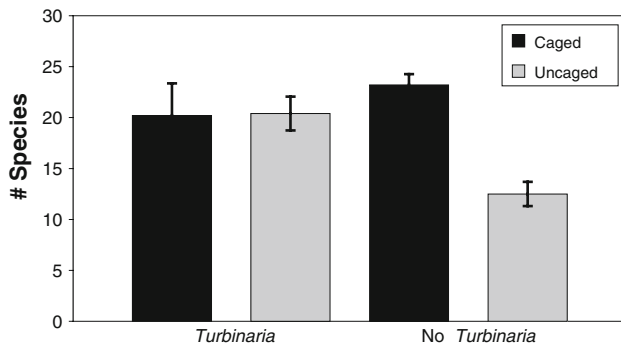


Fig. 2 The mean number of algal species on bommies with and without cages and with *Turbinaria* intact or removed (ANOVA $F_{1,15} = 7.136$, $P < 0.05$, mean \pm SE, $n = 5$)

Table 1 Results of a two-way fixed factor ANOVA testing the effects of the presence of *Turbinaria ornata* and the presence of a cage on number of algal species present

Source	df	MS	F	P
<i>Turbinaria</i>	1	28.247	1.442	0.2484
Cage	1	129.706	6.622	0.0212
<i>Turbinaria</i> \times Cage	1	139.776	7.136	0.0174
Error	15	19.587		

Turbinaria was cleared and the bommies were left uncaged, richness was reduced to almost half that of the other three treatments. Caged treatments had 20.2 ± 3.2 (mean \pm SE, $n = 5$) and 23.2 ± 1.1 (mean \pm SE, $n = 5$) algal species for bommies with and without *Turbinaria*, respectively. Similarly, *Turbinaria*/No cage bommies had 20.4 ± 1.7 (mean \pm SE, $n = 5$) algal species. The No *Turbinaria*/No cage treatment had a lower species diversity of 12.5 ± 1.2 (mean \pm SE, $n = 4$) (Fig. 2). There was a significant interaction between caging and the presence or absence of *Turbinaria* (ANOVA $F_{1,15} = 7.136$, $P < 0.05$, $n = 5$; Table 1).

Herbivory assay

The herbivory experiment showed that rates of herbivory (as measured by loss of *Acanthophora* biomass) were highest on bommies lacking both cages and *Turbinaria* (Fig. 3). *Acanthophora* biomass was unchanged solely in the no *Turbinaria*/cage treatment. This suggests that the cages were effective for preventing herbivory, and is congruent with the species richness results (Fig. 2). Although herbivory rates were twice as high in uncaged vs. caged *Turbinaria* treatments, the presence of uncaged *Turbinaria* reduced herbivory by more than half compared to treatments with no cage and no *Turbinaria* (Fig. 3). The effect of caging, presence or absence of *Turbinaria* and the interaction between them were significantly different from one another (ANOVA $F_{1,16} = 27.251$, $P < 0.01$, $n = 5$; Table 2).

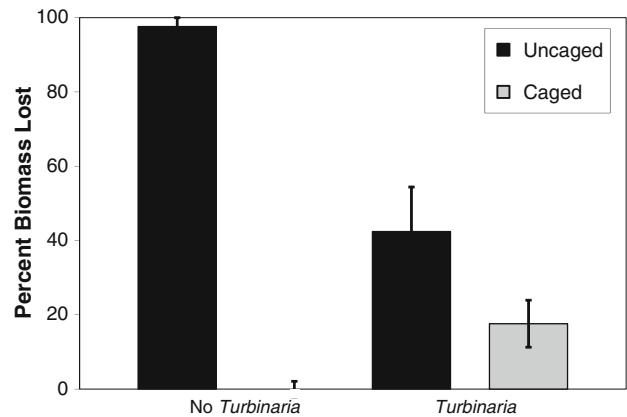


Fig. 3 Percent change in wet weight of *Acanthophora spicifera* in response to herbivory by macrograzers in experimental plots (ANOVA $F_{1,16} = 27.251$, $P < 0.01$, mean \pm SE, $n = 5$)

Table 2 Results of a two-way fixed factor ANOVA testing the effects of the presence of *Turbinaria ornata* and the presence of a cage on percent wet weight change of *Acanthophora spicifera* after a two-day herbivory assay

Source	df	MS	F	P
<i>Turbinaria</i>	1	1,767.2	7.269	0.0159
Cage	1	18,727.2	77.035	<0.0001
<i>Turbinaria</i> \times Cage	1	6,624.8	27.251	<0.0001
Error	16	243.1		

Conclusions

This work identifies the spatial refuge from herbivory provided by *Turbinaria ornata* to other algal species on coral reefs in Moorea, French Polynesia. Associate macroalgal species richness was higher on bommies with *Turbinaria* aggregations, and removing *Turbinaria* from bommies caused a significant decrease in macroalgal species richness. As such, *Turbinaria* may be increasing local overall algal species richness by sheltering species that would otherwise be excluded by their consumers, an effect that has been shown to result from associational refuges in other systems (Hay 1986; Pfister and Hay 1988; Kerr and Paul 1995; Stachowicz 2001b). Certainly, this interaction extends the range of the associated algal species from protected cracks and crevices in the reef to the exposed tops of coral bommies where grazing rates are generally high.

This work did not specifically investigate recruitment into *Turbinaria* stands, but the higher number of species within the aggregation indicates that the protection provided during the processes of settlement and survival of newly recruited algae in these aggregations was likely important, particularly as chemical defense is generally low

in young algal tissue (Stiger et al. 2004). At the other end of the life cycle, associate algae may thrive and reach sexual maturity within a host aggregation (Hay 1986), despite conditions of general reduced light (e.g., Gerard 1984; Stewart et al. 2009), and flow in macroalgal stands (e.g., Jackson and Winant 1983; Stewart et al. 2007; Fram et al. 2008) that can have physiological (e.g., Parker 1981; Stewart and Carpenter 2003) and growth implications for macrophytes (e.g., Reed and Foster 1984; Stewart et al. 2009). In this way, aggregations of *Turbinaria* on coral bommies may be acting as sources of propagule supply that could increase algal recruitment to other areas on the reef where herbivory pressure is low enough for settlement.

Protection afforded by *Turbinaria* to associated organisms is both mechanical and chemical. In addition to the high phenolic content of adult thalli that deters herbivores from consuming it (Stiger et al. 2004), *Turbinaria* is an exceptionally tough (Stewart 2006a) and spiny alga, and a dense aggregation presents a formidable physical barrier to potential consumers. *Turbinaria* was an effective herbivore deterrent particularly for major mobile herbivores [e.g., urchins (*Echinometra* sp.), parrotfish (*Chlorurus sordidus*) and lined bristletooth surgeonfish (*Ctenochaetus striatus*)]. This mechanical refuge from herbivory is similar to the refuge created for fish by the spines of urchins (Townsend and Bologna 2007) and the crown of thorns seastar *Acanthaster planci* (Stier et al. 2008). Similarly, the morphology of the soft coral *Sinluaria* sp. protects the green alga *Halimeda* from herbivory around its base (Kerr and Paul 1995). *Turbinaria* aggregations also serve a similar functional role to the associational defense (implying an active behavioral mechanism) of some invertebrates that creates a refuge for associated organisms. This kind of refuge is also provided by cnidarians whose own defenses against predation (stinging nematocysts) provide refuge for associated species in the Caribbean (Littler et al. 1986) and southern California (Levenbach 2008a, b).

In North Carolina, USA, consumption of the red alga, *Gracilaria*, in the presence of chemically defended species was 35% less compared to *Gracilaria* alone (Pfister and Hay 1988). Our results were more dramatic, with nearly 50% loss of *Acanthophora* biomass in treatments lacking *Turbinaria* and cages (open to herbivores) versus treatments with *Turbinaria* but without cages. Although the two caged treatments (with and without *Turbinaria*) had lower rates of herbivory than *Turbinaria* alone (Fig. 3), indicating that cages are more effective than *Turbinaria* for reducing herbivory, our results show that the number of associated species is maintained in treatments with *Turbinaria* alone (Fig. 2), underlining the effectiveness of *Turbinaria* as a refuge. It is interesting that bommies with both *Turbinaria* and cages exhibited higher rates of herbivory than those without *Turbinaria* and with cages. One explanation may

be the presence of small herbivorous invertebrates, which have also been found to take refuge in unpalatable algae (Hay 1997; Stachowicz 2001b), and in *Turbinaria* (Amirhamzeh, McKnight and Briley, unpublished data), and would not have been excluded by the cages.

Turbinaria ornata is rapidly becoming an important functional reef component and in some areas, stands of *Turbinaria* are replacing coral heads as the dominant structural features. The implications of *Turbinaria* as a refuge for an associational community are large. In addition to the algal community discussed here, a diverse community of invertebrates (Amirhamzeh, McKnight and Briley, unpublished data), including coral recruits (Bittick, Bilotti and Peterson, unpublished data), is harbored by *Turbinaria*. In the 1980s, the range of *Turbinaria* increased (Payri and Stiger 2001; Stiger and Payri 2005), at least partly due to its ability to form floating, reproductive mats (Stewart 2006a) capable of dispersing several hundred kilometers (Stiger and Payri 1999, 2005; Martinez et al. 2007). As a result, *Turbinaria* is a relatively recent foundational species in this region. It is still to be determined whether associated species are moved with *Turbinaria* mats to new sites, or whether native species, formerly limited to crevices, find refuge in new aggregations. Both situations may occur. In any case, the consequences of increased density of *Turbinaria* and its associational community clearly have the potential to influence the structure and dynamics of coral ecosystems in French Polynesia.

Overall, this study has demonstrated an important functional role of aggregations of *Turbinaria* on nearshore coral reefs. By providing a refuge from herbivory for macroalgae on exposed bommies, *Turbinaria* creates habitat for macroalgal species that would otherwise be excluded and plays a role in maintaining algal diversity in the backreef community. This associational refuge plays an important role in structuring the natural pattern of algal distribution on the reef and is becoming more important as the distribution and the abundance of *Turbinaria* increase across French Polynesia.

Acknowledgments We would like to thank the University of California, Los Angeles Marine Biology Quarter 2008 teaching staff for their support throughout the project. Thanks to Peggy Fong for her inspiration and sharing her knowledge of macroalgae and David Jacobs for the encouragement to explore Moorea as this gave us many ideas. Many thanks to Ryan Ellingson, Ranjan Muthukrishnan, Sandy Trautwein and Rachel Clausen for helping us fine tune our methodology, and Briana Fodor, Jessica Pringle and Miles Hogan for help in the field and the rest of our fellow UCLA MBQ 2008 students. We would especially like to thank the University of California's Gump Research Station staff and researchers for their hospitality and scientific support. Finally, we would like to thank the UCLA Ecology and Evolutionary Biology Department for giving us the opportunity to study in Moorea, French Polynesia. This is contribution #180 of the University of California Berkeley's Gump South Pacific Research Station. All

experiments were conducted in accordance with the laws of the United States of America and French Polynesia.

References

- Amsler CD, Mc Clintock JB, Baker BJ (1998) Chemical defense against herbivory in the antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). *J Phycol* 34:53–59
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90(6):1478–1484
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56:345–363
- Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol Monogr* 45:137–159
- Deslandes E, Payri C, Stiger V (1997) Chemical defenses (as antifeedant) of two invasive brown seaweeds on a Polynesian barrier reef. *Phycologia* 36(4):25
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132
- Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology* 75:1304–1319
- Fram JP, Stewart HL, Brzezinski MA, Gaylord B, Reed DC, Williams SL, MacIntyre S (2008) Physical pathways and utilization of nitrate supply to the giant kelp, *Macrocystis pyrifera*. *Limnol Oceanogr* 53(4):1589–1603
- Gerard VA (1984) The light environment in a giant kelp forest—influence of *Macrocystis pyrifera* on spatial and temporal variability. *Mar Biol* 66:27–35
- Gleason MG (1996) Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. *J Exp Mar Biol Ecol* 207:79–101
- Hacker SD, Bertness MD (1996) Trophic consequences of a positive plant interaction. *Am Nat* 148(3):559–575
- Harlin MM (1996) Allelochemistry in marine macroalgae. *CRC Crit Rev Plant Sci* 5:237–249
- Hay ME (1986) Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am Nat* 128:617–641
- Hay ME (1996) Marine chemical ecology: what's known and what's next? *J Exp Mar Biol Ecol* 200:103–134
- Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs* 16(Suppl):67–76
- Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. *Ann Rev Ecol Syst* 19:111–145
- Jackson GA, Winant CD (1983) Effect of a kelp forest on coastal currents. *Cont Shelf Res* 2:75–80
- Kemppainen P, van Nes S, Ceder C, Johannesson K (2005) Refuge function of marine algae complicates selection in an intertidal snail. *Oecologia* 43(3):402–411
- Kerr JN, Paul VJ (1995) Animal-plant defense association: the soft coral *Sinularia* sp. (Cnidaria, Alcyonacea) protects *Halimeda* spp. from herbivory. *J Exp Mar Biol Ecol* 186(2):183–205
- Levenbach S (2008a) Community-wide ramifications of an associational refuge on shallow rocky reefs. *Ecology* 89(10):2819–2828
- Levenbach S (2008b) Behavioral mechanism for an associational refuge for macroalgae on temperate reefs. *Mar Ecol Prog Ser* 370:45–52
- Littler DS, Littler MM (2003) South Pacific reef plants: a divers' guide to the plant life of South Pacific coral reef. Offshore Graphics, New York
- Littler MM, Taylor PR, Littler DS (1986) Plant defense associations in the marine environment. *Coral Reefs* 5:63–71
- Martinez EA (1996) Micropopulation differentiation in phenol content and susceptibility to herbivory in the Chilean kelp *Lessonia nigrescens* (Phaeophyta, Laminariales). *Hydrobiologia* 326(327):205–211
- Martinez E, Maamaatuaiahutapu K, Payri CE, Ganachaud A (2007) *Turbinaria ornata* invasion in the Tuatmotu Archipelago, French Polynesia: ocean drift connectivity. *Coral Reefs* 26:79–86
- Montaggioni L, Richard G, Bourrouilh-Le Jan Gabriele' C, Humbert L, Monteforte M, Naim O, Payri CE, Salvat B (1985) Geology and marine biology of Makatea, an uplifted atoll, Tuamotu archipelago, French Polynesia. *J Coastal Res* 1(2):165–171
- Norris JN, Fenical W (1982) Chemical defenses in tropical marine algae. In: Rutzler K, MacIntyre IG (eds) Atlantic barrier reef ecosystems at Carrie Bow Cay, Belize I: structure and communities. *Smithsonian Contrib Mar Sci* 12:417–431
- Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. *Evol Biol Fish* 3:19–63
- Parker HS (1981) Influence of relative water motion on the growth, ammonia uptake and carbon and nitrogen composition of *Ulva lactuca* (Chlorophyta). *Mar Biol* 63:309–318
- Payri CE (1987) Zonation and seasonal variation of the commonest algae on Tiahura Reef (Moorea Island, French Polynesia). *Bot Mar* 18:141–149
- Payri CE, Naim O (1982) Variations entre 1971 et 1980 de la biomasse et de la composition des populations de macroalgues sur le récif corallien de Tiahura (île de Moorea, Polynésie Française). *Cryptogam Algol* 3(3):229–240
- Payri CE, Stiger V (2001) Macroalgal community changes on French Polynesian reefs, 1980–2000. *Phycologia* 40(4):111
- Payri CE, N'Yeurt ADR, Orempuller J (2004) Algues de Polynésie française (Algae of French Polynesia). Au Vent des Iles Editions, Tahiti
- Pfister CA, Hay ME (1988) Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* 77:118–129
- Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937–948
- Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332–342
- Sotka EE, Wares JP, Hay ME (2003) Geographic and genetic variation in feeding preference for chemically defended seaweeds. *Evolution* 57(10):2262–2276
- Stachowicz JJ (2001a) Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51:235–246
- Stachowicz JJ (2001b) The other side of the coin: positive effects of algal chemicals on animals. *J Phycol* 37(Suppl 1):45–46
- Stewart HL, Carpenter RC (2003) The effects of morphology and water flow on photosynthesis among and within functional form groups of marine macroalgae. *Ecology* 84(11):2999–3012
- Stewart HL (2006a) Ontogenetic changes in buoyancy, breaking strength, extensibility, and reproductive investment in a drifting macroalga *Turbinaria ornata* (Phaeophyta). *J Phycol* 42:43–50
- Stewart HL (2006b) Morphological variation and phenotypic plasticity of buoyancy in the macroalga *Turbinaria ornata* across a barrier reef. *Mar Biol* 149:721–730
- Stewart HL, Payri CE, Koehl MAR (2007) The role of buoyancy in mitigating reduced light in macroalgal aggregations. *J Exp Mar Biol Ecol* 342:11–20
- Stewart HL, Fram JP, Reed DC, Williams SL, Brzezinski M, MacIntyre S, Gaylord B (2009) Differences in growth, morphology and

- tissue C and N of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. *Mar Ecol Prog Ser* 375:101–112
- Stier AC, Steele MA, Brooks AJ (2008) Coral reef fishes use crown-of-thorns seastar as habitat. *Coral Reefs* 28(1):227
- Stiger V, Payri CE (1999) Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangarevense* in a coral reef on Tahiti. *Mar Ecol Prog Ser* 191:91–100
- Stiger V, Payri CE (2005) Natural settlement dynamics of a young population of *Turbinaria ornata* and phonological comparisons with older populations. *Aquat Bot* 81:225–243
- Stiger V, Deslandes E, Payri CE (2004) Phenolic contents of two brown algae, *Turbinaria ornata* and *Sargassum mangarevense* on Tahiti (French Polynesia): interspecific, ontogenetic and spatio-temporal variations. *Botanica Marina* 47(5):402–409
- Targett NM, Arnold TM (1998) Predicting the effects of brown algal phlorotannins on marine herbivores in tropical and temperate oceans. *J Phycol* 34:195–205
- Townsend T, Bologna PAX (2007) Use of *Diadema antillarum* spines by juvenile fish and mysid shrimp. *Gulf Caribb Res* 19:55–58