

Consumption by herbivorous fishes of macroalgae exported from coral reef flat refuges to the reef slope

John Stimson*

Department of Zoology, University of Hawai'i, Honolulu, Hawaii 96822, USA

ABSTRACT: Much of the production by macroalgae on the broad, sandy reef-flat of the fringing reef of Moku o Loe in Kāne'ohe Bay, Oahu, Hawai'i, is transported to the leeward outer reef flat and reef slope areas by wind-driven currents. The export of algae from the inner reef flat can amount to an average delivery rate over a year of $163 \text{ g wet weight d}^{-1} \text{ m}^{-1}$ of leeward reef crest ($2.45 \text{ g C d}^{-1} \text{ m}^{-1}$). This export is equivalent to estimates of the production of fixed carbon by grazed turf algae on the hard substratum at the outer edge of the reef. Grazing by herbivorous fishes resident on the reef slope and outer reef flat area can prevent the development of accumulations of this transported macroalgae in these habitats or gradually eliminate accumulations; however, when rates of delivery are high, long-lasting accumulations of macroalgae can develop between and on top of living corals. Broad sandy reef-flats have often been reported to have stands of macroalgae which are not utilized by herbivorous fishes, and the production of these stands may often be transported to other leeward habitats. The reason for the development of herbivore-free refuges for algae could be the relatively low preference herbivores have for macroalgae in comparison with the more nutrient-rich filamentous algal turfs available on the hard surfaces of the outer reef flat and reef slope.

KEY WORDS: Reef zone · Introduced macroalgae · Algal refuge · Production · Transport · Accumulation · Herbivory

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

A number of instances have been reported in which benthic algae are transported by water movements between habitats of coral reefs. This process is of interest because it represents transfers of fixed energy or nutrients. Wiebe et al. (1975) reported the transport of blue-green algae from outer reef flats to more lagoon-ward sites, thus enriching those sites with nitrogen which had been fixed by the blue-green algae. Carpenter (1990) reported the export of macroalgae, which had bloomed as a result of the die-off of *Diadema antillarum*, to back-reef and lagoonal habitats. Several studies have reported transport of algae from reef flats to reef slopes (Morrissey 1985, Kilar & Norris 1988, Tyler & Fitzhardinge 1989). In some of these cases, the result of this transport has been the accumulation of transported algae in coral-

rich habitats. In the temperate zone, transport of macroalgae from limestone reefs to seagrass beds has been described by Wernberg et al. (2006) and Vanderklift & Wernberg (2008); Wernberg et al. (2006) reported that, once delivered to the seagrass bed, the algae were consumed by urchins and fishes. Those cases in which transported algae accumulate in a habitat represent the most obvious examples of transport. In other instances, where there is no accumulation, transport may not be detected, yet could be adding to the fixed-carbon supply in the receiving community. Morrissey (1985) and Tyler & Fitzhardinge (1989), identified the source of the transported macroalgae as the high standing stocks on the interior of sandy reef flats. Such high standing stocks of macroalgae on sandy reef flats or sandy terraces have also been reported by Hay (1981), Hay et al. (1983), Lewis (1986), and Reinthal & Macintyre (1994).

*Email: jstimson@hawaii.edu

Herbivorous fishes apparently do not use this resource, and such areas have been referred to as refuges for macroalgae (Lewis 1986). Such refuges occur on the interior of many reef flats in Kāneʻohe Bay, Oahu, Hawaiʻi, and include both native and non-native algae (Stimson et al. 2001).

In contrast to reef flats, reef slopes are generally characterized by coral cover and little or no macroalgae (Hay et al. 1983) so it was unusual to observe a high percent cover of macroalgae on reef slopes in Kāneʻohe Bay (Hunter & Evans 1995). The high algal cover on the lee slope of a fringing reef raised the possibility that the algae had been transported by currents tens or hundreds of meters from the extensive upwind stands of macroalgae on the reef flat (Rodgers & Cox 1999, Conklin & Smith 2005, Conklin 2007). An alternative explanation for the high cover of algae on the slope is that overfishing or anthropogenically-enhanced nutrient concentrations have stimulated algal growth in the Bay and resulted in the colonization of this habitat by these algae.

This study was carried out to test the idea that current-driven transport of macroalgae is responsible for the presence of macroalgae on the leeward reef slope of the fringing reef of Moku o Loe, an island in Kāneʻohe Bay, and if so, to determine the magnitude and timing of the transport of algal biomass from the reef flat, the fate of transported algae once it is deposited on the slope, and why such a large biomass of macroalgae develops in the source area on the reef flat. This study of transport and herbivory on reefs differs from most other studies of processes on reefs in its emphasis on inter-habitat exchange, rather than on comparisons of processes among sometimes distant study sites or processes occurring within habitats.

MATERIALS AND METHODS

Study site

The studies described below were almost entirely conducted on the leeward reef flat and reef slope of the fringing reef of Moku o Loe (Coconut Island, 21° 26.172' N, 156° 47.478' W) in Kāneʻohe Bay, Oahu, Hawaiʻi (Fig. 1), the site of the Hawaiʻi Institute of Marine Biology (HIMB). The biota of this and other reefs in the Bay are described in Smith et al. (1981), Stimson et al. (2001) and Stimson & Conklin (2008). The leeward fringing reef flat of Moku o Loe is the area bounded by the shore, seaward by the reef crest (i.e. the line of intersection of the reef flat and reef

slope), and by an abandoned sewer line and a mangrove-covered peninsula which extends from the shore to the 1250 m marker on the reef crest (Fig. 1). For the purpose of this paper, the leeward fringing reef flat is subdivided into the inner reef flat, >40 m from the reef crest, and the outer reef flat. The outer 2 to 5 m of the outer reef flat is a band composed primarily of hard substratum: corals, coralline algae and limestone covered with filamentous algae, with occasional sand-pockets or channels. This structure is referred to here as the reef platform (Fig. 2). Its shoreward margin is the region where the platform gives way abruptly (Fig. 2) to a narrow band of scattered coral heads on a sandy substratum, and this in turn gives way to the broad sand and rubble inner reef flat which extends 150 to 250 m to the shoreline

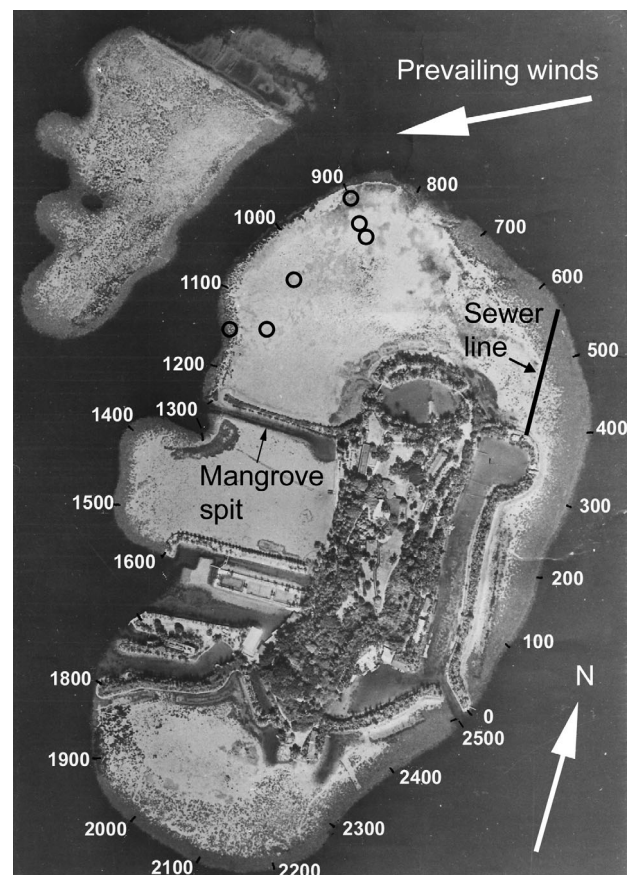


Fig. 1. Aerial photograph of Moku o Loe reef, Kāneʻohe Bay, Hawaiʻi, showing the positions of reef reference markers on reef crest (only positions of markers at 100 m intervals are shown), positions of crescent-shaped traps (O), position of sewer line and mangrove spit, and the direction of trade winds. *Gracilaria salicornia* accumulations develop primarily on the sections of reef slope from 900 to 1200 m and from 1800 to 2000 m. The dark outer perimeter of the reef flat is the reef platform



Fig. 2. Moku o Loe reef: view of the outer leeward reef flat looking SW with the reef platform in the center. The reef platform is narrowest (~2–3 m) at this point and becomes wider in the distance. The reef crest is the right edge of the platform. Almost all coral constituting the platform is *Porites compressa*; its living tissue is primarily restricted to the sides of colonies. Photo taken during a low tide in the spring, when no accumulations of macroalgae were present

of the island. The top of the platform is ~10 cm above the lowest tide level; the level of the sand and rubble which constitutes most of the substratum of the outer reef flat is ~30 cm deeper than the top of the platform and is not exposed at low tides. The maximum tidal range in the Bay is ~100 cm. The seaward margin of the platform, i.e. the reef crest, is marked at 50 m intervals with short numbered PVC marker posts (positions of 100 m markers are shown in Fig. 1) to facilitate the location of field studies and censuses. These markers were used to identify the position of sampling sites used to estimate the cover and distribution of macroalgae found on the reef slope. This leeward reef of Moku o Loe is largely free of human disturbances such as net fishing, spear fishing or trap fishing, foot traffic or boating because it is part of a scientific preserve.

The upper 4 m of the leeward reef slope (western exposure, 800 to 1250 m, Fig. 1) is steep, abruptly extending down at an angle of ~45° from the reef flat. Coral cover is high on the upper 3 m of the slope (~65%) and decreases rapidly to almost 0% by a depth of 5 m (Hunter & Evans 1995).

Algal cover and biomass on the inner reef flat

Two introduced red algal species, *Acanthophora spicifera* and *Gracilaria salicornia*, have become widespread and abundant on reef flats throughout

the bay since their introductions in the 1950s and 1970s, respectively (Russell 1992, Rodgers & Cox 1999, Smith et al. 2002). On many reef flats in the bay they are the dominant algal species (Stimson et al. 2001). Native algae still occur in this habitat, including *Dictyosphaeria verschluysii*, *Hydroclathrus clathratus*, *Padina sanctae-crucis* and *Ceramium* sp.

The biomass per unit area of *Acanthophora spicifera* and *Gracilaria salicornia* on the leeward reef flat of Moku o Loe was estimated by determining their percent cover and the biomass per unit area of thallus. An estimate of percent cover was made in February of 2008 utilizing a grid of 160 equally spaced sampling points (~20 m apart) established on the leeward reef flat in the area bounded by the sewer line, the shoreline, the mangrove spit, and the inner margin of the reef platform (Fig. 1), an area of ~7.5 ha. At each sampling point the percent cover of *A. spicifera* and *G. salicornia* was visually estimated to the nearest 5% in a 2 × 2 m quadrat which had been divided into 20 × 20 cm subdivisions. *A. spicifera* frequently grows as an epiphyte on *G. salicornia*. The cover of each species was estimated independently, thus the sum of percent cover values would lead to an overestimate of the total area covered of these algae on the reef flat. The biomass of *G. salicornia* and *A. spicifera* per unit area of cover of these algae was estimated in summer 2006 using a PVC cylinder, 30 cm tall and 30 cm diameter, with a chisel-like lower edge. The cylinder was pushed into a mat composed of multiple thalli and all algal material within the cylinder was collected, cleaned of invertebrates and attached rubble, drained of water by inverting the container for 15 s, and then wet-weighed to the nearest 10 g.

The pattern of distribution of macroalgae, filamentous algae and substratum types in the outer 40 m of the reef flat and upper 3 m of the reef slope were estimated using point-intercept transects. These point-intercept transects were set perpendicular to the reef crest.

Cross-reef algal transport rate assessment

Data on wind direction and speed were obtained from a weather station at HIMB on Moku o Loe. Small drogues made of 4 l plastic bottles, weighted so that only their caps were visible at the surface, were used to assess the direction and speed of movement of water across the leeward reef flat. Drogues were only 30 cm deep to prevent them from encountering benthic obstructions, so their rate of movement probably overestimates the rate of movement near the

bottom of the water column where transport of the algae was occurring and flow probably encounters more resistance. In addition, a set of 10 individually marked 15 cm diameter *Gracilaria salicornia* thalli were used to estimate the rate of transport of thalli across the reef flat. The thalli were detached from the substratum and marked by threading lengths of pink surveying tape through the center of each thallus. These thalli were set out on the sand, leeward of the center of the old sewer line on the leeward reef flat (Fig. 1). The windward side of the leeward reef platform was then monitored daily for 10 d to determine how long it took for these thalli to be transported to this habitat and to determine where they lodged along the leeward platform.

Traps were set up on the outer margin of the leeward reef flat in October 2005 to intercept any drift algae and to estimate the rate of transport of this material across the reef flat. The traps consisted of fences, constructed from 30 cm tall × 5 m long strips of 2.5 cm mesh chicken wire. These were erected as crescents with an opening 3.5 m wide facing the prevailing NE (~50°) trade winds. Six of these traps were deployed near the leeward perimeter of the leeward reef flat (Fig. 1). Four were located 40 m windward of the reef crest, 2 of these, 20 m apart, shoreward of the 900 m marker, and one each shoreward of the 1050 m and 1150 m markers. The 4 traps at 40 m were designed to catch drift algae at a distance great enough from the reef crest to ensure that the weight of the catch was not reduced by the feeding of herbivorous fishes, because virtually no herbivorous fishes are seen over the generally sandy substratum which dominates the reef flat at distances >10 m from the reef crest (Conklin 2007). Two other traps were set up at 10 m from the reef crest, just windward of the platform, shoreward of the 900 and 1150 m markers. These 10 m traps were set up to estimate the rate of delivery of algal material to the platform and slope.

All the traps were checked at weekly intervals over most of a 2 yr period, and any macroalgal thalli or fragments which had accumulated against the fences were removed, sorted by species, drained of water by inverting their container for 15 s, and wet-weighed to the nearest 100 g. Many thalli caught in the traps were still attached to the rubble pieces which had been their anchorage; these pieces were removed prior to weighing the algae. The rate of delivery of macroalgae to the traps was expressed as kilograms wet weight of algae per meter of trap-mouth width per week. The delivery rates to the four 40 m traps were averaged, as were the values for the two 10 m traps.

The catches underestimated the quantity of drift algae in a number of ways. The traps were designed to catch large thalli (10 to 30 cm diameter), such as those seen in accumulations on the reef platform and reef slope, and not small fragments of algae. When wind and currents were strong the traps filled, and some thalli were evidently pushed over the accumulated thalli and over the top of the trap. During low tides some dense mats of algae, especially those with attached mats of filamentous algae, developed air pockets during the period of their exposure, as the tide level rose, the trapped air caused the thalli to lift off the substratum, and float over the traps. The algae held by the traps, particularly the traps located 10 m from the crest, was subject to herbivory during the 1 wk intervals between removal of the algae. Finally, because of the fixed orientation of the openings of the traps, they underestimated transport when winds came from directions other than the prevailing trade wind direction.

Timing and duration of drift macroalgae accumulations on the reef slope

The extent, magnitude and seasonality of the accumulations of *Gracilaria salicornia* and *Acanthophora spicifera* on the leeward reef slopes of Moku o Loe were estimated on 44 dates over a 2.5 yr period from 2007 to 2009. The number of square meters of cover of *G. salicornia* and *A. spicifera* on the upper slope was visually estimated between the crest and a depth of 3 m within each of the nine 50 m intervals between the permanent marker posts on the leeward reef (from 800 m to 1250 m, Fig. 1), then these 9 estimates were averaged. This method of estimation was sufficiently sensitive to detect the magnitude and spatial extent of an accumulation on the slopes, and the time it takes for an accumulation to disappear. Because *A. spicifera* is greatly preferred by herbivorous fishes (Stimson et al. 2001), it generally does not remain on the reef slope as long as *G. salicornia* does, so the frequency and duration of accumulations of *A. spicifera* are probably underestimated.

Growth rates and grazing rates of *Gracilaria salicornia* on the reef slope

Caged and uncaged preweighed thalli of *Gracilaria salicornia* were placed on the leeward reef slope of Moku o Loe to determine if *G. salicornia* can grow on the reef slope and the degree to which it is grazed.

If caged thalli can grow in this habitat, then the percent cover values and the length of time accumulations persist could be due to the sum of 4 factors: the rate of transportation of the algae to the slope, and the rates of growth, grazing, and decomposition while on the slope. Pre-weighed thalli were attached to vinyl-covered wire mesh platforms as described in Stimson et al. (2001). The platforms were placed on the reef slope at a depth of 1 to 3 m below the reef crest and left in place for 5 d, a period short enough to ensure that fouling of the cage mesh was minimal. These assays were conducted in January and September of 2008. After 5 d, the platforms were collected and the algal thalli reweighed. The weights of the algae at the start and end of the exposure period were obtained by spinning the thalli briefly in a salad spinner to remove excess water and then weighing them to the nearest 0.1 g. The changes in wet weight of both the caged and uncaged thalli on each platform were calculated and expressed as a specific rate (g g^{-1} initial weight d^{-1}). The change in weight of the caged thallus was used as a measure of the ability of the algae to grow in this habitat. The difference in the rates of growth of the caged and uncaged thallus on a platform was used as a measure of grazing intensity. The use of cages may have reduced flow and thus have reduced both the estimate of growth and grazing intensity. However, measurements made with an irradiance meter and spherical sensor at the end of a run indicated that the cages reduced irradiance by ~5%, and growth rates of caged and uncaged *G. salicornia* measured in a flume (velocity 2 cm s^{-1}) were not significantly different by a paired *t*-test ($t = 0.475$, SE 0.003, number of pairs = 35).

Pattern of grazing intensity across the outer reef flat

To test the influence of grazing fishes on the distribution and biomass of macroalgae on the outer reef flat, assays were performed in which pairs of pre-weighed caged and uncaged algal thalli were placed on the outer reef flat at 10 m intervals along 40 m transects which extended from the reef crest shoreward, perpendicular to the reef crest. These transects were located in the area between the 900 m crest marker and the 1000 m marker. Both *Acanthophora spicifera* and *Gracilaria salicornia* were used in the assays. Thalli were attached to the vinyl-coated wire-mesh platforms as described above. After 1 wk in the field, the platforms with *G. salicornia* were collected and the algal thalli reweighed. Platforms with *A. spicifera* were collected after 2 d because of the greater

preference herbivorous fishes have for this species (Stimson et al. 2001). The platforms located at 0 or 5 m from the crest were placed in shallow depressions on the reef platform; cages at 10 m or more from the crest were on the sand at the same depth.

Biomass distribution of herbivorous fishes

The biomass per unit area of herbivorous fishes on the reef slope and at 5 distances onto the reef flat was estimated in strip-transects oriented parallel to the reef crest and conducted in January, February, and March 2010. The transects were located between the 850 m and 1250 m markers. Transects on the slope were 50 m long and 4 m wide and surveyed the upper 4 m of the slope. On the platform and sandy reef flat, transects were 50 m long and 2 m wide, and were conducted at 1, 10, 20, 30 and 40 m from the crest. The fishes included in the survey were parrotfishes and surgeonfishes (both generally less than 15 cm in length). The parrotfishes included in the survey were predominantly juvenile *Scarus psittacus*; the acanthurids included *Acanthurus triostegus*, *Zebbrasoma flavissimus*, *Z. veliferum*, *A. blochii* and *Ctenochaetus strigosus*. The biomass per unit area of herbivorous fishes on each transect was calculated from the counts and estimated lengths of individuals using length-weight relationships obtained from R. Brock, University of Hawai'i (pers. comm.). Herbivorous pomacentrids, kyphosids and urchins were very rare and not included in the surveys.

These estimates of herbivorous fish biomass on the reef flat at various distances from the reef crest were compared to similar estimates made on Reef 30 ($21^{\circ}28.265' \text{ N}$, $157^{\circ}49.415' \text{ W}$) in central Kāne'ohe Bay (numbering system of Roy 1970; map in Stimson et al. 2001). Reef 30 differs from Moku o Loe in that it has a solid limestone reef flat across its 110 m width. Biomass was estimated as above, at 1, 10, 20, 30, and 40 m from the crest on the leeward reef flats of Reef 30. These estimates were performed in the fall of 2008 and in the summer of 2009 and 2010.

RESULTS

Biomass and distribution of macroalgae on the reef flat source region

Gracilaria salicornia and *Acanthophora spicifera* were the most abundant macroalgae on the reef flat of Moku o Loe year round. *Kappaphycus alvarezii*,

Padina sanctae-crucis, *Dictyosphaeria cavernosa*, *D. verschluisii*, *Hydroclathrus clathratus*, and *Ceramium* sp. were also present, but far less abundant. Algal thalli of *G. salicornia* can be 5 to 6 cm thick when attached to the substratum, and can develop into mats which have a biomass of ~ 10 kg wet weight m^{-2} of thalli. *A. spicifera* has a less compact thallus with thinner branches which can reach a length of 20 cm; mats of this species can have a biomass of ~ 2 kg wet weight m^{-2} . The cover of *G. salicornia* on the entire leeward reef flat (7.5 ha) was $\sim 1.5\%$ (SE 0.12%, sample size 163), the cover of *A. spicifera* was higher, $\sim 3.5\%$ (SE 0.45%, sample size 163). The cover of these macroalgae on the sandy leeward reef flat was largely a function of the availability of limestone rubble to which most thalli are attached. The combined biomass of these 2 species of algae was 220 g wet weight m^{-2} of reef flat.

The cover of these algae on the reef flat increased with distance from the reef crest (Fig. 3a) as measured by point intercept transects. When the rates of transport were high (discussed in more detail below), *Gracilaria salicornia*, and occasionally *Acanthophora spicifera*, became lodged against the windward edge of the platform or in depressions in the platform, causing cover of these algae to be high between the reef crest and the windward edge of the platform (Fig. 3b).

The outermost edge of the reef flat, or platform consisted of limestone supporting an algal turf assemblage (57%, 95% binomial confidence interval [CI] 50 to 64%; data from May 2010); the corresponding value for the upper 3 m of the leeward slope was 25% limestone/turf (CI 19 to 31%), the balance of the area on both the platform and upper slope was soft sediments and living coral.

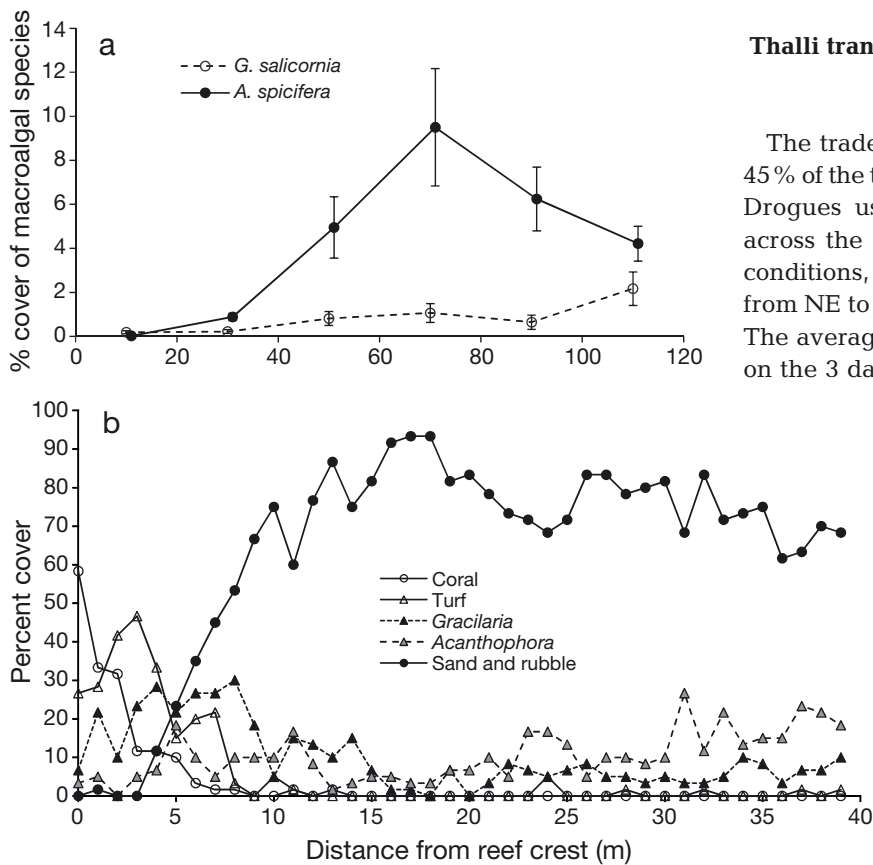


Fig. 3. Algal cover on the leeward flat of Moku o Loe reef as a function of the distance shoreward from the reef crest (0 m). (a) Percent cover of macroalgal species *Gracilaria salicornia* and *Acanthophora spicifera* in winter (February 2008); (b) percent cover of macroalgal categories in summer (August to September 2008). Note that in (b), the category 'turf' is almost entirely restricted to the platform. In both cases, the 10 m point is the greatest shoreward extent of the platform and the percent cover shown is the average of cover values from 5 transects

Thalli transport rate across the reef flat and timing and extent of accumulations

The trade winds blew from the NE (22.5° to 67.5°) 45% of the time and at an average speed of ~ 17 $km\ h^{-1}$. Drogues used to simulate the movement of water across the reef flat, and released under trade wind conditions, moved toward the leeward reef slope from NE to SW, parallel to the direction of the trades. The average speeds of the drogues over the reef flat on the 3 days were 12, 14 and 16 $cm\ s^{-1}$. Four of the tagged thalli released near the sewer line (Fig. 1) were found at positions on the leeward reef platform and slope within 3 d of their release. They were transported ~ 400 m in the direction of the travel of the drogues.

The 2 yr record of the rate of capture of *Gracilaria salicornia* at the 40 m traps showed a seasonal pattern, with higher rates of recapture in the fall and winter (Fig. 4a). Maximum wind speed and water temperature both had high values in the fall. *G. salicornia* and *Acanthophora spicifera* constituted 97% of the weight of macroalgae caught in the traps.

The average capture rate of *Gracilaria salicornia* in the 4 traps at 40 m locations over the whole study period (3.56 kg wet weight $trap^{-1}\ wk^{-1}$) was about 7 times greater than for *Acanthophora spicifera* (0.53 kg $trap^{-1}$

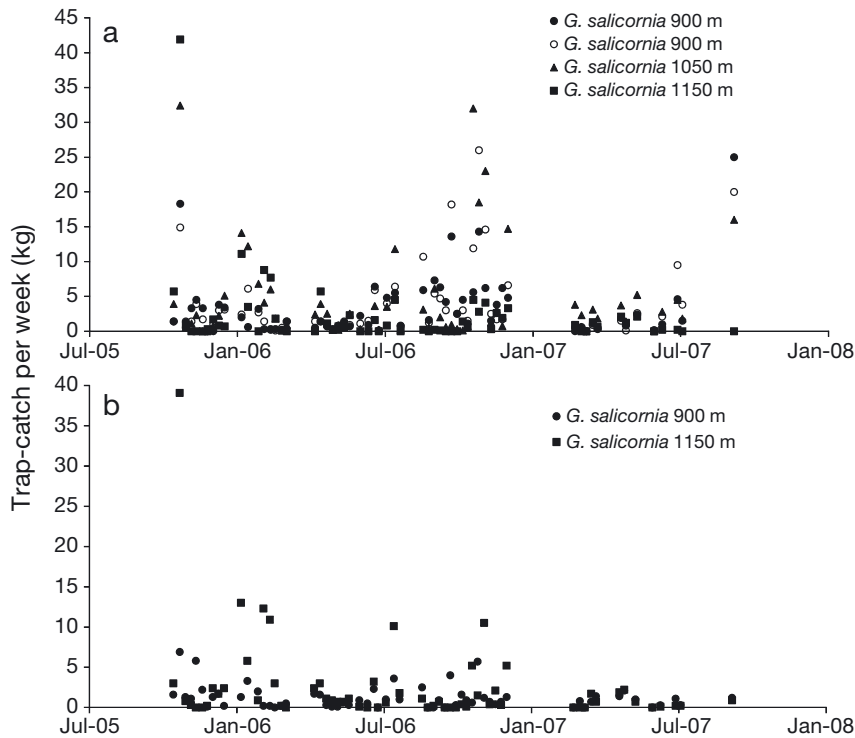


Fig. 4. *Gracilaria salicornia*. Weekly catches (kg wet weight) in traps located at (a) 40 m (4 traps) and (b) 10 m (2 traps) windward of the reef crest. Traps were located shoreward of the 900, 1050 and 1150 m markers (see Fig. 1)

wk⁻¹) (Table 1). The average catch of macroalgae in the 40 m traps can be thought of as a delivery rate of macroalgae to the populations of herbivorous fishes on the leeward reef of Moku o Loe, because most herbivorous fishes do not venture 40 m onto the reef flat of Moku o Loe (see below). If the catches above are converted to delivery rates per meter of reef crest (by dividing by the width of the trap, i.e. 3.5 m) they produce rates of ~1 and 0.14 kg m⁻¹ wk⁻¹ for *G. salicornia* and *A. spicifera*, respectively.

Table 1. *Gracilaria salicornia* and *Acanthophora spicifera*. Comparison of weekly capture rates (mean \pm SD) over the 2 yr period from October 2005 to September 2007 at 2 distances from the reef platform on Moku o Loe in Kāne'ohe Bay, Hawai'i. Sample sizes were 59 trap weeks for each species and distance

Distance from platform (m)	Capture rate (kg wet wt wk ⁻¹)	Paired <i>t</i>	df	<i>p</i>
<i>G. salicornia</i>				
10	1.97 \pm 3.29	4.04	58	<0.001
40	3.56 \pm 4.71			
<i>A. spicifera</i>				
10	0.07 \pm 0.20	4.33	58	<0.001
40	0.53 \pm 0.85			

The capture rates for both species were significantly less at 10 m than at 40 m, i.e. 1.97 and 0.07 kg wet weight trap⁻¹ wk⁻¹ for *Gracilaria salicornia* and *Acanthophora spicifera*, respectively (Table 1, Fig. 4b). The difference between the capture rates at the 2 distances from the reef crest presumably reflects the fact that much of the transported algae was consumed as the thalli got closer to the reef crest and were more subject to grazing by the fish which venture onto the outer reef flat. The fact that there was a greater proportional drop in the weight of *A. spicifera* reflects the fact that it is preferred to *G. salicornia* by some herbivorous fishes. The wet weight of algae delivered to the leeward platform and reef slope can be estimated, from these catches in the 10 m traps, as 0.56 and 0.02 kg m⁻¹ wk⁻¹ for *G. salicornia* and *A. spicifera*, respectively. Macroalgae which are transported across the leeward reef platform, drop down the slope and accumulate on corals, in pockets, channels, or on relatively flat areas. Accumulations of macroalgae in low places can become a meter deep. Accumulations can extend down-slope to a depth of 10 m, but most of the accumulations are at depths less than 3 to 4 m.

The highest cover of *Gracilaria salicornia* on the reef slope occurred in fall and winter corresponding with the timing of the high rates of transport as measured by the traps (Fig. 5). These accumulations of *G. salicornia* persisted for as long as half a year. The accumulations of *Acanthophora spicifera* seemed to develop throughout the year with perhaps a low point in summer. All these accumulations disappeared naturally, presumably because of a combination of grazing, as suggested by the results in Table 2, and decomposition of thalli at the bottom of the accumulations. Grey anoxic sediments could be found on the slope at the sites where accumulations of *G. salicornia* had recently disappeared. As much as 130 m² of algal cover was estimated on the upper 3 m of the slope within an individual 50 m sampling interval.

The highest cover of *Gracilaria salicornia* on the reef slope occurred in fall and winter corresponding with the timing of the high rates of transport as measured by the traps (Fig. 5). These accumulations of *G. salicornia* persisted for as long as half a year. The accumulations of *Acanthophora spicifera* seemed to develop throughout the year with perhaps a low point in summer. All these accumulations disappeared naturally, presumably because of a combination of grazing, as suggested by the results in Table 2, and decomposition of thalli at the bottom of the accumulations. Grey anoxic sediments could be found on the slope at the sites where accumulations of *G. salicornia* had recently disappeared. As much as 130 m² of algal cover was estimated on the upper 3 m of the slope within an individual 50 m sampling interval.

Growth of *Gracilaria salicornia* on reef slopes

Thalli in the accumulations of the upper 1 to 3 m of the reef slope are capable of growing, as indicated by

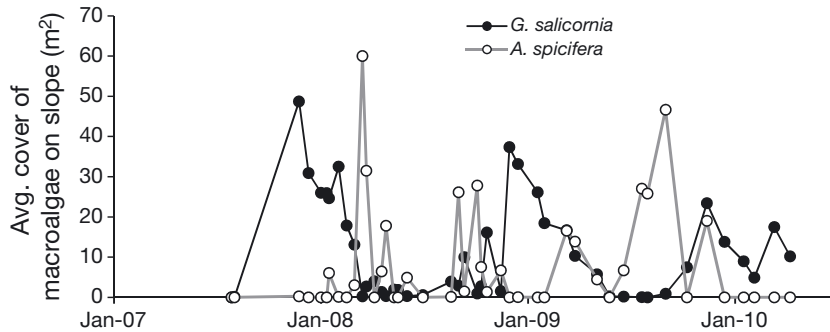


Fig. 5. *Gracilaria salicornia* and *Acanthophora spicifera*. Cover (m^2) on the lee slope between 800 and 1250 m markers (see Fig. 1), based on visual estimations of cover between the reef crest and a depth of 3 m within each of the nine 50 m sections demarcated by the marker posts

the growth of the caged thalli (Table 2). Caged thalli showed growth on the reef slope in 2 of the 3 time periods (1-tailed t test of hypothesis that growth > 0); uncaged thalli lost weight in all 3 time periods (1-tailed t -test of hypothesis that growth < 0), presumably because of grazing. The September values were obtained during a period when there was some *Acanthophora spicifera* and an abundance of *G. salicornia* on the leeward reef slope in the area of the test, yet consumption of the uncaged experimental *G. salicornia* could still be detected.

Distribution of herbivorous reef fishes and grazing

The biomass of herbivorous reef fishes (g m^{-2}) was significantly greater on the leeward platform of Moku o Loe than on the adjacent sand rubble reef flat 10 to 40 m from the crest (Table 3). No herbivo-

Table 2. *Gracilaria salicornia*. Daily growth rates (mean \pm SD) over a 5 d period of caged and uncaged macroalgae placed on the windward and leeward reef slopes of Moku o Loe, showing the results of 1-sample t -tests of the hypotheses that growth rates of caged thalli > 0 and that growth rates of uncaged thalli < 0 . ns: not significant

Location and date	Growth rate (g g^{-1} initial wt d^{-1})	Sample size (n)	t	p
Leeward slope: January 2008				
Caged	0.010 ± 0.039	13	0.92	ns
Uncaged	-0.057 ± 0.0325	13	6.32	< 0.001
Leeward slope: September 2008				
Caged	0.027 ± 0.013	18	8.80	< 0.001
Uncaged	-0.018 ± 0.019	16	3.79	< 0.005
Windward slope: September 2008				
Caged	0.023 ± 0.026	20	3.96	< 0.001
Uncaged	-0.245 ± 0.159	14	5.77	< 0.001

rous fishes were found on the transects 20, 30 and 40 m from the reef crest. The parrotfishes and acanthurids on the leeward platform and reef slope were generally small (< 12 cm total length), although schools of large acanthurids (35 to 40 cm total length) were also found. In contrast to this pattern on the leeward reef of Moku o Loe, transect studies of the distribution and abundance of herbivorous fishes on the leeward side of Reef 30, whose 110 m diameter reef flat consisted entirely of hard substratum, showed that herbivorous fishes have as high a

biomass 40 m in from the crest as they do on the outer reef flat (Table 4). Values of biomass per square meter are higher on the reefs of Moku o Loe because of the protection from fishing they receive as the Hawai'i Marine Laboratory Refuge.

The intensity of grazing was found to decrease with distance from the reef crest onto the reef flat (Fig. 6). Pre-weighed thalli outside cages lost more weight at sites near the reef crest, i.e. on the platform or on the sand just windward of the platform, than if placed 20 to 40 m from the reef crest on the reef flat, regardless of whether greatly preferred algae such

Table 3. Biomass of herbivorous reef fishes (mean \pm SD, 7 transects per zone) on the leeward reef slope and in platform and sand habitats on the outer reef flat at Moku o Loe. No herbivorous fishes were found in transects on the reef flat over sand/rubble at 20, 30 and 40 m from the reef slope. Data are from January, February and May of 2010. Different superscript letters indicate significant differences between zones (Mann-Whitney test, $p < 0.01$)

Zone	Distance from slope (m)	Biomass (g m^{-2})
Slope	0	39.7 ± 22.3^a
Platform	1	47.8 ± 18.4^a
Sand	10	0.6 ± 1.2^b
Sand	20–40	0.0

Table 4. Biomass of grazing fishes (mean \pm SD, 9 transects per distance) on Reef 30, a reef with hard substratum across its 110 m width, at different distances from the reef crest

Distance from crest (m)	Fish biomass (g m^{-2})
1	9.9 ± 7.6
10	14.7 ± 3.6
20	12.3 ± 5.3
30	15.0 ± 6.2
40	10.3 ± 2.2

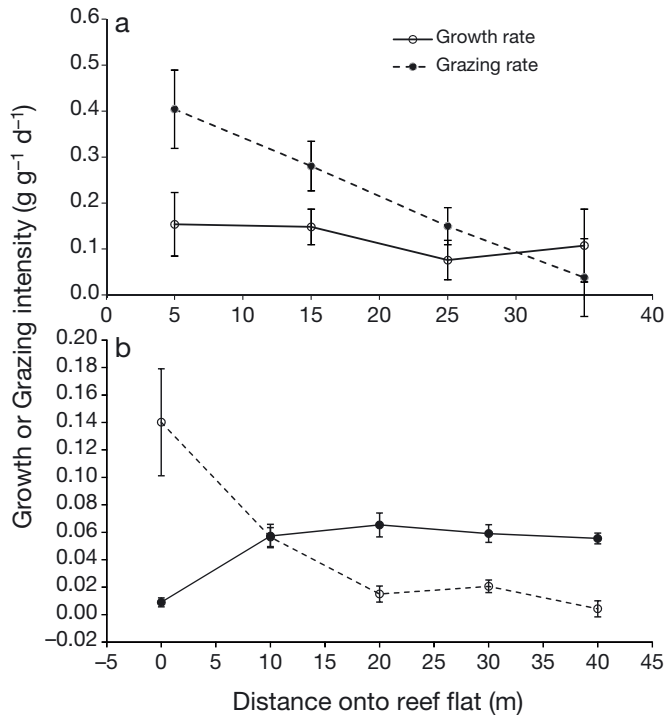


Fig. 6. *Gracilaria salicornia* and *Acanthophora spicifera*. Growth rate (mean \pm 1 SE) of caged thalli and grazing intensity (calculated as the difference between weight gain per day of caged thalli and weight loss of uncaged thalli) at a range of distances from the reef crest at 2 sites on the leeward reef flat, for (a) the greatly preferred alga *A. spicifera* in August 2005 and (b) the less preferred alga *G. salicornia* in January 2010

as *Acanthophora spicifera* (Fig. 6b) or less preferred algae such as *Gracilaria salicornia* (Fig. 6a) were used. Caged thalli at all these locations tended to gain weight.

DISCUSSION

The catches of macroalgae in the traps demonstrated that there is transport of macroalgae from the inner reef flat habitat toward the reef slope habitat and that the accumulations on the slope are probably due to this transport. The temporal record of the extent of the accumulations demonstrated that they do not persist, and the results from the comparison of weight changes of experimental algal thalli inside and outside cages demonstrated that this transported algae is fed upon by the herbivorous fishes (Table 2; Stimson et al. 2001) which probably contribute to the disappearance of the accumulations. Taken together, these results indicate that these algal species have not colonized or established in this slope habitat.

A number of factors are thought to be responsible for this transfer of production between reef habitats. First, the reef flats of the Bay offer a suitable environment for the 2 introduced species of red macroalgae which make up 97% of the weight of transported algae. Second, these introduced species have high growth rates. *Acanthophora spicifera*, in particular has a growth rate of $>10\%$ (wet weight) d^{-1} in this (Fig. 6a) and similar environments (Stimson & Conklin 2008, Vermeij et al. 2009). *Gracilaria salicornia* can achieve a growth rate of 6% d^{-1} in this environment (Fig. 6b). Third, the physical conditions of the inner reef flat, such as high water flow and irradiance, are suitable for the macroalgae to grow fast and for thalli to reach large size (Glenn & Doty 1992). Fourth, trade winds, but particularly strong winds, can break off thalli or parts of thalli, move them across the sand and ultimately deposit them on the reef slope.

Probably the most important factor in this transport process is the fact that there is a high biomass of macroalgae growing on the inner reef flat and that little of their production is consumed *in situ*. The presence of macroalgae in the sand-dominated inner reef flat, their refuge, is reminiscent of the pattern reported in other studies (Hay 1981, 1984, Hay et al. 1983, Lewis 1986, Reinthal & Macintyre 1994, Rogers 1997). The pattern is evidently due to the distribution of herbivorous fishes (Lewis 1986, McCook 1996, 1997, Conklin 2007, Fox & Bellwood 2007, Friedlander et al. 2007), whose abundance declines with increasing distance onto the reef flats of many reefs (Klumpp & Polunin 1990, Reinthal & Macintyre 1994, Russ 2003, Fox & Bellwood 2007, Hoey & Bellwood 2008). On the fringing reef of Moku o Loe, and on large patch reefs in the bay, surgeonfishes and parrotfishes evidently make very little use of the algal resources of the sandy inner reef flat (Table 3), even though they evidently feed sufficiently on the transported algae to reduce its abundance by the time it reaches the 10 m traps (Table 1, Fig. 4). These fish will also feed on the macroalgae from the inner reef flat if it is brought to them experimentally (Table 2; Stimson et al. 2001). It is unclear why these herbivores do not use macroalgal resources on sandy inner reef flats or sandy plains, which would preclude the development of this refuge.

Part of the answer to this question may lie in the fact that those patch reefs in the bay which have a solid limestone surface across their widths apparently do not provide the algal refuge seen on the sandy inner reef flat of Moku o Loe and most other patch reefs. On Patch Reef 30, which has an almost

continuous hard substratum across the 110 m width of its reef flat, herbivorous fishes ventured 40 m or more onto the reef flat (Table 4). Their use of the full width of the reef flat occurs despite its low rugosity, although the platform does contain holes, crevices and depressions which are used by fish for shelter. Their grazing activity on the inner reef flat evidently precludes the development of macroalgae in this habitat. Other studies performed on broad limestone reef flats also indicate there is very limited development of macroscopic algae on the hard substratum far from the reef crest, and that schools of herbivorous fishes will venture far onto reef flats with solid substratum. Russ (1984) described reef flat habitats on 6 reefs where turf algae predominated 75 to 150 m from the crest. Klumpp & McKinnon (1989) described a ~500 m wide reef flat on Davies Reef in the Great Barrier Reef as being without erect macroalgae. Klumpp & McKinnon (1992) reported similar results from cross-reef transects on 7 reefs. Bouchon-Navarro & Harmelin-Vivien (1981) reported substantial numbers of herbivorous fishes at 60 m onto a reef flat with solid substratum. Miller (1982) reported abundant herbivorous fishes 60 m or more from the reef crest on a windward limestone reef flat at Enewetak Atoll, Marshall Islands. Lewis & Wainwright (1985) reported high grazer densities 100 to 200 m from a reef crest in Belize. So, herbivorous fishes will move large distances onto solid reef flat areas, while they are apparently unwilling to move equivalent distances onto sandy areas of similarly low relief. Chapman & Kramer (2000) reported that reef fishes tended not to move across sandy inter-reef areas wider than 20 m.

An explanation for the failure of herbivorous fishes to graze macroalgae within the refuge on the inner reef flat is suggested by 4 observations on the grazing of filamentous algae. First, filamentous algae or algal turfs are a principal food of small herbivorous fish (Scott & Russ 1987, Bruggemann et al. 1994, McAfee & Morgan 1996, Kopp et al. 2010). Second, Russ (2003) re-

ported that the biomass of herbivorous fishes in 3 habitats (slope, crest and flat) corresponded to the rate of production by filamentous algae in these 3 habitats; the biomass of herbivorous fishes and production rate by filamentous algae were highest in the reef crest habitat. Third, filamentous algae are characteristic of hard substrata, not of sand, thus would be more readily available on the outer reef flat platform and reef slope described in this study, which have 57 and 25% hard substratum respectively. Fourth, filamentous algae have a higher nitrogen content than macroalgae, potentially making them more attractive to herbivorous fishes. The C:N ratios of macroscopic algae in offshore and inshore environments in Hawai'i range between 17 and 34 (Atkinson & Smith 1983, Smith 1994, Larned 1997) (Table 5), and in *Sargassum* spp. in Australia the ratio varies seasonally from 22 to 36 (Lefèvre & Bellwood 2010). C:N ratios for filamentous algae from reef environments in Hawai'i and Australia, are lower (6.8 to 20), indicating higher percent nitrogen content (Table 5). Experimental elevation of nutrient concentrations of macroalgae increases the rate of herbivory (Boyer et al. 2004), and fish eating macroalgae with different concentrations of protein prefer the species with the higher protein concentrations (Horn & Neighbors 1984). The macroscopic algae on the inner reef flat may not be as attractive to herbiv-

Table 5. Comparison of published C:N values for filamentous and macroalgae. nd: no data given

Location	Algal type	Mean	SE	Sample size	Source
Macroscopic algae					
Hawai'i Inshore	Rhodophyta	17	2.31	12	Smith (1994)
	Chlorophyta	26	1.42	18	"
	Phaeophyta	22	2.12	8	"
Hawai'i Offshore	Rhodophyta	34	5.71	14	"
	Chlorophyta	21	1.89	7	"
	Phaeophyta	26	1.66	13	"
Kāne'ohe Bay	<i>Dictyosphaeria cavernosa</i>	24.6	nd	6	Larned (1997)
Hawai'i	14 species	23.5	12.9	17	Atkins & Smith (1983)
N. Queensland	15 species	23.4	7.0	17	Atkins & Smith (1983)
Central Great Barrier Reef (GBR)	<i>Sargassum</i> sp.	32	nd	nd	McCook (1996)
	<i>Sargassum</i> sp.	39	nd	nd	McCook (1996)
	<i>Sargassum</i> sp.	22–36	nd	72	Lefèvre & Bellwood (2010)
Filamentous algae					
Hawai'i		11.1–15.1	nd	nd	R. Carpenter (pers. comm.)
N., Cent, and S. GBR		20	1.8	8	Wilson (2000)
N. GBR		6.8	0.8	7	Wilson & Bellwood (1997)
N. GBR		9.3	nd	nd	Purcell & Bellwood (2001)
N. GBR		9.1	0.6	7	Wilson & Bellwood (1997)

orous fishes because they offer a lower nitrogen availability than filamentous algae, thus fishes in the Bay primarily concentrate their feeding on the filamentous algae of the outer reef flat and slope.

Transport of macroalgae between habitats, and sometimes accumulation of algal material, have been reported in other studies. Wiebe et al. (1975) reported the transport of blue-green algae from an outer reef flat habitat to leeward zones of the reef flat and considered this a significant source of fixed nitrogen for the communities in the latter zones. Kilar & Norris (1988) reported cross-reef transport of macroalgae at Galeta Point, Panama. The transport of algal propagules (branch segments) has been reported by Smith & Walters (1999) and by Smith et al. (2002). Morrissey (1985) reported the transport of *Acanthophora spicifera* and the native *Sargassum echinocarpum* on a nearby patch reef (Reef 8, per Roy 1970) in Kāne'ohe Bay, with a peak capture rate in the fall, as found in the present study. The trap mesh used in Morrissey's (1985) study was smaller than that used in this study, which may partly explain why her traps caught more material, i.e. 491 g wet weight m^{-1} trap width d^{-1} . Tyler & Fitzhardinge (1989) reported a storm-induced transport of native *Padina* sp. onto the leeward reef slope of Moku o Loe. The transported material was deposited on a 40 m long section of reef slope, persisted there for 2 mo and caused coral mortality. Usually this species is almost entirely restricted to inner reef flat sites because of the strong preference parrotfishes have for it. *Padina* sp. was a minor component of the accumulations reported here. Finally, Polunin & Klumpp (1992) proposed that algal production which was not accounted for by grazing may have been exported to other reef zones.

The amount of macroalgae transported to the leeward reef platform and reef slope rivals production by turfs in these zones. The amount of algae transported to the leeward reef was converted to grams of carbon for comparison with published values on the productivity per unit area of the turfs in various reef zones (Paddack et al. 2006). The wet weight of transported *Gracilaria salicornia* and *Acanthophora spicifera* was converted to dry weight by multiplying by 0.08 (Larned 1997) and dry weight was converted to grams of carbon using conversion factors from Atkinson & Smith (1983), i.e. 33% for *A. spicifera* and 21% for *G. salicornia*. These conversions were applied to the average annual catches of the 10 m traps and give estimates of 1.42 g C m^{-1} reef crest d^{-1} for *G. salicornia* and *A. spicifera* combined. Trap catches at 10 m are substantially lower than those at 40 m, particularly for *A. spicifera* which is greatly preferred by herbivorous fishes

(Stimson et al. 2001), and this decline is presumably the result of consumption of transported algae by herbivorous fishes as the algae is carried closer to the reef crest. If the catches at 40 m are used to estimate the carbon subsidy supplied by the transport process, this gives a value of ~ 2.45 g C m^{-1} d^{-1} for the 2 algae.

This daily fixed carbon input supplied by the transport process can be compared to estimates of the fixed carbon generated by the growth of turf algae growing on the platform and upper reef slope, but to do this the area on the platform and slope which can support turf has to be estimated. The leeward reef flat platform is narrow, from 2 to 5 m in width, and $\sim 57\%$ of the area is limestone supporting a turf algal community; the upper 4 m of the leeward slope is $\sim 25\%$ limestone supporting a turf community. For each meter of leeward reef perimeter, there are then ~ 3 m^2 of limestone substratum on the platform and slope which could support a turf community capable of producing fixed carbon. If this area is multiplied by the estimates of the rate of production of fixed carbon by turf communities, i.e. ~ 1 g C m^{-2} d^{-1} (Hatcher & Rimmer 1985, Klumpp & McKinnon 1989, 1992, Paddack et al. 2006), or more (Klumpp & Polunin 1990), the product is ~ 3 g C d^{-1} . Compared to the carbon content of the transported macroalgae as estimated above, transported macroalgae provides about as much fixed carbon to the platform and upper slope habitats per day as is produced in these habitats by filamentous algae. While this source of fixed carbon is possibly less preferred by herbivorous fishes, compared to filamentous algae, they do consume some (perhaps most) of it; but at the present levels of biomass of herbivorous fishes per square meter they are only capable of contributing to the gradual elimination of accumulations and keeping the slope free of macroalgae for part of the year (Fig. 6).

In general, this study shows that the production of fixed carbon and nutrients within the leeward platform and slope may not constitute the whole supply of fixed carbon and nutrients available to herbivores in these habitats, and that materials transported from other, inaccessible or less accessible habitats may provide a substantial fraction of the fixed carbon or nutrients consumed. In this case the rate of transport reaches such high levels in some seasons that the transported material accumulates on the reef slope, and the presence of the accumulations revealed that transport was taking place. In other instances of transport, the rate may not be as high and accumulations may not develop; there may nonetheless be a fixed carbon subsidy supplied to the grazers of one habitat or zone by cross-reef transport from a second habitat or zone.

Acknowledgements. I thank HIMB for the use of lab space at Moku o Loe, for access to weather data and for access to the reefs. I acknowledge the field assistance of E. Conklin, L. Iwahara and J. Wilson, and thank E. Conklin and L. Iwahara for discussions of the manuscript.

LITERATURE CITED

- Atkinson MJ, Smith SV (1983) C:N:P ratios of benthic marine plants. *Limnol Oceanogr* 28:568–574
- Bouchon-Navaro Y, Harmelin-Vivien ML (1981) Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Mar Biol* 63:79–86
- Boyer KE, Fong P, Armitage AR, Cohen RA (2004) Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass and mangrove habitats. *Coral Reefs* 23:530–538
- Bruggemann JH, van Oppen MJH, Breeman AM (1994) Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Mar Ecol Prog Ser* 106:41–55
- Carpenter RC (1990) Mass mortality of *Diadema antillarum*. *Mar Biol* 104:67–77
- Chapman MR, Cramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. *Environ Biol Fishes* 57:11–24
- Conklin EJ (2007) The influence of preferential foraging, alien algal species and predation risk on the interaction between herbivorous fishes and reef macroalgae. PhD dissertation, University of Hawai'i, Honolulu, HI
- Conklin EJ, Smith JE (2005) Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kāne'ohe Bay, Hawai'i and an experimental assessment of management options. *Biol Invasions* 7:1029–1039
- Fox RJ, Bellwood DR (2007) Quantifying herbivory across a coral reef depth gradient. *Mar Ecol Prog Ser* 339:49–59
- Friedlander AM, Brown E, Monaco ME (2007) Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Mar Ecol Prog Ser* 351:221–223
- Glenn EP, Doty MS (1992) Water motion affects the growth rates of *Kappaphycus alvarezii* and related red seaweeds. *Aquaculture* 108:233–246
- Hatcher BG, Rimmer DW (1985) The role of grazing in controlling benthic community structure on a high latitude coral reef: measurements of grazing intensity. *Proc 5th Int Coral Reef Congr, Tahiti* 6:229–236
- Hay ME (1981) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am Nat* 118:520–540
- Hay ME (1984) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64:396–407
- Hay ME, Colbourn T, Downing D (1983) Spatial and temporal patterns in herbivore on a Caribbean fringing reef: the effects of plant distribution. *Oecologia* 58:299–308
- Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27:37–47
- Horn MH, Neighbors MA (1984) Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. *Trans Am Fish Soc* 113:388–396
- Hunter CL, Evans CW (1995) Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. *Bull Mar Sci* 57:501–515
- Kilar JA, Norris L (1988) Composition, export, and import of drift vegetation on a tropical, plant dominated, fringing-reef platform (Caribbean Panama). *Coral Reefs* 7:93–103
- Klumpp DW, McKinnon AD (1989) Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. *J Exp Mar Biol Ecol* 131:1–22
- Klumpp DW, McKinnon AD (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Mar Ecol Prog Ser* 86:77–89
- Klumpp DW, Polunin NVC (1990) Algal production, grazers and habitat partitioning on a coral reef: positive correlation between grazing rate and food availability. In: Barnes M, Gibson RN (eds) *Trophic relationships in the marine environment*. Proc 24th Eur Mar Biol Symp. Aberdeen University Press, Aberdeen, p 372–388
- Kopp D, Bouchon-Navaro Y, Cordonnier S, Haouisée A, Louis M, Bouchon C (2010) Evaluation of algal regulation by herbivorous fishes on Caribbean coral reefs. *Helgol Mar Res* 64:181–190
- Larned SL (1997) Nutrient limited growth and sources of nutrients for coral reef macroalgae. PhD dissertation, University of Hawai'i, Honolulu, HI
- Lefèvre CD, Bellwood DR (2010) Seasonality and dynamics in coral reef macroalgae: variation in condition and susceptibility to herbivory. *Mar Biol* 157:955–965
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56:183–200
- Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. *J Exp Mar Biol Ecol* 87:215–228
- McAfee ST, Morgan SG (1996) Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Mar Biol* 125:427–437
- McCook LJ (1996) Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: cross-shelf transplants. *Mar Ecol Prog Ser* 139:179–192
- McCook LJ (1997) Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Mar Biol* 129:713–722
- Miller AC (1982) Effects of differential fish grazing on the community structure of an intertidal reef flat at Enewetak Atoll, Marshall Islands. *Pac Sci* 36:467–482
- Morrissey J (1985) Carbon flow through fleshy macroalgae on coral reefs. PhD dissertation, University of Hawai'i, Honolulu, HI
- Paddack MJ, Cowen RK, Sponaugle S (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25:461–472
- Polunin NVC, Klumpp DW (1992) Algal food supply and grazer demand in a very productive coral-reef zone. *J Exp Mar Biol Ecol* 164:1–15
- Purcell S, Bellwood D (2001) Spatial patterns of epilithic algal and detrital resources on a windward coral reef. *Coral Reefs* 20:117–125
- Reinthal PN, Macintyre IG (1994) Spatial and temporal variations in grazing pressure by herbivorous fishes: Tobacco Reef, Belize. *Atoll Res Bull* 425:1–14
- Rodgers SK, Cox EF (1999) Rate of spread of introduced rhodophytes *Kappaphycus alvarezii*, *Kappaphycus striatum* and *Gracilaria salicornia* and their current distributions in Kāne'ohe Bay, O'ahu, Hawai'i. *Pac Sci* 53:232–241

- Rogers RW (1997) Brown algae on Heron Reef Flat, Great Barrier Reef, Australia: spatial, seasonal and secular variation in cover. *Bot Mar* 40:113–117
- Roy KJ (1970) Changes in bathymetric configuration, Kaneohe Bay, 1889–1969. Sea Grant Report TR 70-6, University of Hawai'i, Honolulu, HI
- Russ G (1984) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar Ecol Prog Ser* 20:23–34
- Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* 22:63–67
- Russell DJ (1992) The ecological invasion of Hawaiian reefs by two marine red algae *Acanthophora spicifera* (Vahl) Boerg, and *Hypnea musciformis* (Wulfen) J.Ag., and their association with two native species, *Laurencia nidi-fica* J.Ag. and *Hypnea cervicornis* J.Ag. *ICES Mar Sci Symp* 194:110–125
- Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. *Mar Ecol Prog Ser* 39: 293–304
- Smith AAC (1994) The effects of nutrient loading on C:N:P ratios of marine macroalgae in Kaneohe Bay, Hawaii. MSc thesis, University of Hawai'i, Honolulu, HI
- Smith CM, Walters LJ (1999) Fragmentation as a strategy for species: fates of fragments and implications for management of an invasive weed. *PSZN I: Mar Ecol* 20:307–319
- Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac Sci* 35:279–395
- Smith JE, Hunter CL, Smith CM (2002) Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. *Pac Sci* 56: 299–315
- Stimson J, Conklin EJ (2008) Potential reversal of a phase shift: the rapid decrease in the cover of the invasive green macroalga *Dictyosphaeria cavernosa* Forsskål on the coral reefs in Kane'ohe Bay, Oahu, Hawai'i. *Coral Reefs* 27:717–726
- Stimson J, Larned ST, Conklin EJ (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19:343–357
- Tyler WA III, Fitzhardinge R (1989) Comparison of impact of two disturbances on coral assemblages. *Pac Sci* 43: 204–205
- Vanderklift MA, Wernberg T (2008) Detached kelps from distant sources are a food subsidy for sea urchins. *Oecologia* 157:327–335
- Vermeij MJA, Smith TB, Dailer ML, Smith CM (2009) Release from native herbivores facilitates the persistence of invasive marine algae: a biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success. *Biol Invasions* 11:1463–1474
- Wernberg T, Vanderklift MA, How J, Lavery PS (2006) Export of detached macroalgae from reefs to adjacent seagrass beds. *Oecologia* 147:692–701
- Wiebe WJ, Johannes RE, Webb KL (1975) Nitrogen fixation in a coral reef community. *Science* 188:257–259
- Wilson SK (2000) Trophic status and feeding selectivity of blennies (Blenniidae: Salariini). *Mar Biol* 136:431–437
- Wilson S, Bellwood DR (1997) Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). *Mar Ecol Prog Ser* 153:299–310

*Editorial responsibility: Charles Peterson,
Morehead City, North Carolina, USA*

*Submitted: February 17, 2012; Accepted: August 14, 2012
Proofs received from author(s): December 12, 2012*