

DEEP SUBTIDAL MARINE PLANTS FROM THE NORTHWESTERN HAWAIIAN ISLANDS: NEW PERSPECTIVES ON BIOGEOGRAPHY

BY

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ABSTRACT

In the past 15 years, scientific focus on the marine flora of the Northwestern Hawaiian Islands (NWHI) has intensified, resulting in a doubling of the total number of known species. In 1989, 205 species were recorded; as of January 2005, 353 species have been published for the NWHI. Over 5,100 specimens collected from Midway Atoll and other atolls, reefs, islands, and deep-water sites in the NWHI have shown a marine flora with geographic distribution patterns different from any known similar-sized area in the Pacific. Several new species of macroalgae have been described, including *Dudresnaya babbittiana* (Rhodophyta), *Kallymenia thompsonii* (Rhodophyta), *Hydroclathrus tumulis* (Phaeophyta), *Padina moffittiana* (Phaeophyta), and *Codium hawaiiense* (Chlorophyta). Since 1989, numerous macroalgal and two seagrass species have been documented as records of species new to the NWHI, including *Kallymenia sessilis*, *Desmarestia ligulata*, *Nereia intricata*, *Sporochnus moorei*, *Caulerpa antoensis*, *C. cupressoides*, *C. elongata*, *C. microphysa*, *Halophila decipiens*, and *H. hawaiiiana*. Although the Hawaiian Archipelago is considered part of the Tropical Indo-West Pacific phytogeographic region, the NWHI's mixture of tropical species, cold-temperate species, species with disjunct distributions, and endemic species suggests alternative biogeographic patterns and dispersal routes.

INTRODUCTION

While the bulk of the Hawaiian marine flora contains species that are found throughout the tropical Pacific, as is true of the marine floras of other warm Pacific areas (i.e., Fiji and Tahiti), the occurrence of subtropical and cool water entities marks the Hawaiian marine flora as different from most other locations. Collections of marine plants in the Northwestern Hawaiian Islands (NWHI) since 1978 have yielded numerous new species; some appear to be NWHI endemics, and others are new records from these atolls, islands and reefs north of the main Hawaiian Islands (MHI) (Brostoff, 1984; Abbott, 1989; Abbott, 1999; DeFelice, 1999; Abbott and McDermid, 2001; McDermid et al., 2001; Abbott and McDermid, 2002; Abbott and Huisman, 2003; Kraft and Abbott,

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2003; Abbott and Huisman, 2004; Vroom and Abbott, 2004 a, b). In the last 4 years, deep subtidal (10 - 100 m in depth) collections from the National Oceanic and Atmospheric Administration (NOAA) cruises to the NWHI in connection with National Marine Fisheries Service (NMFS) lobster monitoring, and recent National Ocean Service (NOS) and NMFS biological surveys conducted by the Northwestern Hawaiian Islands Rapid Ecological Assessment and Monitoring Program (NOWRAMP, 2000 and 2002), have shown a marine flora with geographic distribution patterns different from any known similar-sized area in the Pacific. For instance, some recently discovered species in the NWHI previously were known only from Japan (i.e., *Kallymenia sessilis* Okamura and *Nereia intricata* Yamada), or Australia (i.e., *Distromium flabellatum* Womersley and *Sporochmus moorei* Harvey), or only from cool temperate to polar regions (*Desmarestia ligulata* (Lightfoot) Lamouroux) (Abbott and Huisman, 2004). The geographic isolation of the Hawaiian Archipelago, whose nearest neighbor is Johnston Atoll over 600 km to the southwest, and whose closest continental land mass is over 5,000 km away, makes species with disjunct distributions of special significance to our understanding of biogeography. The purpose of this paper is to take stock of the many new species of deep subtidal marine plants recently recorded from the NWHI, and for the first time to evaluate their biogeographic affinities, and examine possible oceanographic explanations for these patterns.

METHODS AND MATERIALS

Pressed herbarium specimens and microscope slides of marine plants, preserved according to methods outlined by Tsuda and Abbott (1985), that had been hand-collected using SCUBA or recovered from lobster traps from the NWHI during various NOS and NMFS research expeditions (1978-2002), were examined. Distribution records of previously reported genera and specific species were compared (Abbott, 1999; Guiry and Nic Dhonncha, 2002; Abbott and Huisman, 2004).

RESULTS

Approximately 300 species of marine macroalgae and 2 species of seagrasses are known from the NWHI (Abbott, 1999; McDermid et al., 2001, 2003; Abbott and Huisman, 2004). Many species, either new to science or newly reported for the area, have been discovered in recent NWHI collections (Table 1). Many of the macroalgal and both seagrass species belong to characteristically tropical genera known from the warm Indo-West Pacific, such as *Caulerpa*, *Dictyota*, *Dudresnaya*, *Halophila*, *Hydroclathrus*, and *Padina*. The calcified green seaweed genus, *Halimeda*, also has a warm tropical distribution, but several species found in the NWHI (*H. copiosa* Goreau et Graham, *H. macroloba* Decaisne, and *H. velasquezii* Taylor) have no published records in the MHI.

Some NWHI species have unusually disjunct distributions. Species with Japanese affinities include *Crouania mageshimensis* Itono collected from a depth of 10-70 m in the NWHI (Abbott, 1989), *Nereia intricata* from 32-94 m Maro Reef (Abbott and Huisman 2003), and *Kallymenia sessilis* found subtidally in the NWHI and the Island of Hawai'i

Table 1. New species** and new records* from NWHI, 1984 to 2004.

Name	Distribution	Reference
CHLOROPHYTA		
* <i>Caulerpa antoensis</i>	NWHI (Gardner, Necker), Ant Atoll, Bikini Atoll, Tanzania	Abbott & Huisman (2004)
* <i>Caulerpa cupressoides</i>	NWHI (FFS), circumtropical	Abbott & Huisman (2004)
* <i>Caulerpa elongata</i>	NWHI (Lisianski), Indo-West Pacific	Abbott & Huisman (2004)
* <i>Caulerpa microphysa</i>	NWHI (Midway), Indian Ocean, Fiji	Abbott & Huisman (2004)
** <i>Codium campanulatum</i>	NWHI & MHI endemic	Silva & Chacana in Abbott & Huisman (2004)
** <i>Codium desultorum</i>	NWHI & MHI endemic	Silva & Chacana in Abbott & Huisman (2004)
** <i>Codium hawaiiense</i>	NWHI endemic	Silva & Chacana in Abbott & Huisman (2004)
** <i>Codium intermedium</i>	NWHI endemic	Silva & Chacana in Abbott & Huisman (2004)
* <i>Codium subtubulosum</i>	NWHI, MHI, Japan, Pakistan	Abbott & Huisman (2004)
* <i>Halimeda copiosa</i>	NWHI, Caribbean, Australia, Micronesia	Abbott (1989)
* <i>Halimeda macroloba</i>	NWHI (Midway), Indo-West Pacific	Abbott & Huisman (2004)
* <i>Halimeda velasquezii</i>	NWHI, Philippines, China, Japan, Indian Ocean	Abbott (1989)
PHAEOPHYTA		
* <i>Desmarestia ligulata</i>	NWHI (Necker), Alaska, California, Chile, Australia, Antarctica, Scotland	Abbott & Huisman (2003)
* <i>Dictyota stolonifera</i>	NWHI, MHI, Nicaragua, Kenya	Abbott & Huisman (2003)
* <i>Distromium flabellatum</i>	NWHI, MHI, southern Australia, New Caledonia	Abbott & Huisman (2003)
** <i>Hydroclathrus tumulis</i>	NWHI endemic	Kraft & Abbott (2003)
* <i>Nemacystus decipiens</i>	NWHI, MHI, Japan, Indian Ocean, Arabian Sea	Abbott (1989)
* <i>Nereia intricata</i>	NWHI (Maro), Japan	Abbott & Huisman (2003)
** <i>Padina moffittiana</i>	NWHI endemic	Abbott & Huisman (2003)
* <i>Sporochnus dotyi</i>	NWHI & MHI endemic	Brostoff (1984), Abbott & Huisman (2004)
* <i>Sporochnus moorei</i>	NWHI, southern Australia, New Zealand	Abbott & Huisman (2003)

Table 1. Continued.

RHODOPHYTA

** <i>Acrosymphyton brainardii</i>	NWHI (FFS) endemic	Vroom & Abbott (2004a)
* <i>Crouania mageshimensis</i>	NWHI, Japan, Caroline Is.	Abbott (1989)
** <i>Dudresnaya babbittiana</i>	NWHI (Midway) endemic	Abbott & McDermid (2001)
* <i>Kallymenia sessilis</i>	NWHI, MHI, Japan	Abbott & McDermid (2002)
** <i>Kallymenia thompsonii</i>	NWHI endemic	Abbott & McDermid (2002)
** <i>Scinaia huismanii</i>	NWHI endemic	Vroom & Abbott (2004b)

MAGNOLIOPHYTA

* <i>Halophila decipiens</i>	NWHI (Midway), MHI, circumtropical	McDermid et al. (2001)
* <i>Halophila hawaiiiana</i>	NWHI (Pearl & Hermes, Midway) & MHI endemic	DeFelice (1999) McDermid et al. 2003)

(Abbott and McDermid, 2002). Taxa with Australian affinities include *Acrosymphyton*, *Distromium*, and *Sporochnus*. *Distromium flabellatum* is found only in southern Australia, the NWHI, and the MHI, and all other species in this genus are restricted to Japan and the Juan Fernandez Islands off Chile. *Sporochnus moorei* is known only from southern Australia, New Zealand, and Necker Island at 38-72 m (Abbott and Huisman, 2003), and Midway Atoll at 20 m (collected Sept. 23, 2002, specimen number KM7992).

Other members of the NWHI marine flora have cold-temperate water biogeographic affinities, including *Desmarestia*, *Sporochnus* and *Kallymenia*. *Desmarestia ligulata*, a species frequently occurring with kelps from Alaska to Antarctica, and often in California, was found alive on Necker Island at a depth of 30-56 m (Abbott and Huisman, 2003). Most members of *Sporochnus*, except the Hawaiian endemic, *S. dotyi* Brostoff, are cool water species from Japan, China, Australia, Scandinavia, California, and the Galapagos Islands. *Kallymenia* species "are unusual occurrences in the tropics" (Abbott, 1999), since most species in this genus are cool-temperate water species of North and South America and Japan.

In addition, several recently reported new species probably are endemic to the NWHI, including *Acrosymphyton brainardii* Vroom et Abbott, *Codium hawaiiense* Silva et Chacana, *Codium intermedium* Silva et Chacana, *Dudresnaya babbittiana* Abbott et McDermid, *Hydroclathrus tumulis* Kraft et Abbott, *Kallymenia thompsonii* Abbott et McDermid, *Padina moffittiana* Abbott et Huisman, and *Scinaia huismanii* Vroom et Abbott.

Often in the NWHI, cold-temperate species are collected sympatrically with tropical species; for instance, *Sporochnus* (Phaeophyta) entangled on the same lobster trap as *Caulerpa* (Chlorophyta), and *Kallymenia* (Rhodophyta) found within the same 0.25 m² quadrat as *Halimeda* (Chlorophyta). Such observations call for investigation of species' actual temperature requirements, as well as measurement of localized thermal fluxes that might allow these species to co-exist.

DISCUSSION

The geographic distributions of marine plants are attributed primarily to water temperature and the temperature thresholds governing growth, reproduction, and survival of each species (Breeman, 1988; Lüning, 1990; Bolton, 1994; Lobban and Harrison, 1994). The large-scale phytogeographic regions for benthic marine plants are based on water temperature according to van den Hoek (1984). The marine floras of oceanic Pacific islands, including the Hawaiian Archipelago, have been lumped within a huge phytogeographic region: the Tropical Indo-West Pacific Region, which stretches 22,000 km from East Africa to the Tuamotus in French Polynesia. Warm water is the defining character used to unite this vast region of diverse landmasses and complex oceanographic conditions. Adey and Steneck (2001) proposed a temperature/space/time integrated model for marine biogeographic regions, which compiles rocky, sublittoral, photic zone temperature regimens and coastal area over time since the last glacial period 18,000 years before present (BP). The model defines 20 thermogeographic regions, including an Indo-Pacific region to which the Hawaiian Islands are assigned. However, the use of temperature alone as the critical factor in distribution or in delineating phytogeographic regions is debatable.

It has been assumed that "in general, the stock of seaweed species of central Pacific oceanic islands is relatively small and consists mainly of immigrated, widely distributed species accompanied by few endemics" (Lüning, 1990, p. 232). This assumption does not hold true for the Hawaiian Islands, which are home to over 500 species of marine macroalgae, perhaps because of the Archipelago's extreme isolation, geologic time frame, and variety of habitats. Even within the island chain, the NWHI differ from the MHI in terms of substratum, habitat variety, age, size, intertidal area, water temperature, current patterns, day length, and exposure to short-term climate events (e.g. El Niño Southern Oscillations) (Abbott, 1989; Silva, 1992).

With another theory, known as vicariance biogeography, scientists explain the geographic distribution of marine algae based primarily on patterns of dispersal and barriers to dispersal (Hommersand, 2001). Barriers to dispersal to the Hawaiian Islands include open-ocean distance, ocean depth, current patterns, and open-ocean sea temperatures. The sea surface temperatures in the north Pacific in the vicinity of the Hawaiian-Emperor Chain were above 20°C in the early Tertiary, about 65 to 40 million years ago (mya), then ranged between 16°C and 20°C during the Oligocene and Early Miocene (40-15 mya), then rose above 20°C again, and have remained nearly stable in the central gyres of the subtropical north Pacific since the last glacial period (18,000 years BP) (Grigg, 1988). In addition, cores from the Emperor Seamounts contain tropical, shallow, marine fossils (Grigg, 1988). However, Grigg (1988) hypothesized that prior to 34 mya, the Hawaiian Archipelago was isolated from the Indo-West Pacific because of the dominant equatorial circulation patterns before the closure of the Tethys Sea. The ancient marine flora of the Hawaiian-Emperor Chain may have been very different from today. Subsequent to the Tethys Sea closure, north-south circulation patterns (gyres) were enhanced, and currents in the north Pacific may have been strengthened sufficiently to transport organisms from the Indo-West Pacific to the Hawaiian Archipelago.

Xie et al. (2001) suggested the existence of a subsurface, eastward ocean current, the Hawaiian Lee Counter Current located at 19° N latitude and driven by the wind wake that trails westward behind the Hawaiian Islands. The Hawaiian Lee Counter Current draws warm water at nearly 0.2 m/s from the Asian coast 8,000 km from the Hawaiian Archipelago. At this rate it would take approximately 400 days for a propagule to travel from the Philippines to Hawai'i in this current. The role of this current in spore dispersal and vegetative fragment transport is unknown.

The deployment and tracking of 6 floats and 22 drifters in the NWHI from 2001-2003 (Firing et al., 2004) have shown various patterns of surface-water (0-35 m) movement, including "lingering" of drifters around the northernmost atolls, long distance travel of drifters among central atolls, limited connections between southern NWHI and northern MHI, movement of two floats from the NWHI westward to Johnston and Wake Atolls, and even a round-trip voyage by one drifter from the NWHI to the coast of Japan and back. These circulation patterns suggest several possible dispersal routes for algal spores, seagrass seeds, and marine plant fragments to and from the NWHI, and may provide a mechanism for the retention of endemic species within the NWHI.

Kuroshio Current eddies and meanders, and the Kuroshio Extension in the north Pacific may be responsible for the presence of macroalgae in the Hawaiian Islands with Japanese affinities. *Desmarestia ligulata* populations in the NWHI may be the result of microscopic gametophytes (whose gametes fuse to form macroscopic sporophytes) rafting in the California Current as it turns southwest (Abbott and Huisman, 2004). Species shared by southern Australia and the Hawaiian Islands perhaps traveled via a long route in the West Wind Drift to South America and northward. While many studies have tracked the movement of large fishes, such as tuna, or macroalgae floating in the Sargasso Sea, in connection with oceanographic currents, no Pacific studies, to our knowledge, have used marine plants of *Sargassum*-size or smaller to test hypotheses that might explain their occurrences in isolated locations.

Our present concepts about large-scale phytogeographic regions are focused on water temperature. Other factors also may be responsible for marine plant distributions in the Pacific, such as circulation patterns, seasonal, localized, deep subtidal temperature fluxes or upwellings, short-term climate events, and the presence of suitable substrata for hitchhiking epiphytes, e.g. logs, nets, or other floating plant material. Although the Hawaiian Archipelago is considered part of the Tropical Indo-West Pacific phytogeographic region, the NWHI's mixture of tropical species, cold-temperate species, species with disjunct distributions, and endemic species confounds current biogeographic regional boundaries, and suggests alternate patterns and dispersal routes. In the future, molecular methods, in combination with phylogenetic systematics and paleo- and modern oceanographic data, may help identify ancestral taxa, ancestral areas, and dispersal pathways.

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