Observations on the Genus *Rhodymenia* Grev. (Rhodophyta, Rhodymeniales) in the California Islands

Kathy Ann Miller[1]
University Herbarium, University of California, Berkeley, CA 94720

Abstract – The natural history of four sympatric species of red seaweeds in the genus *Rhodymenia* Greville (*R. californica* Kylin, *R. pacifica* Kylin, *R. callophyllidoides* Hollenberg & Abbott and *R. arborescens* Dawson) was investigated in the course of subtidal surveys at 68 sites in the eight California Islands. Despite their broad latitudinal range, these cool-temperate species are ecologically specialized, being restricted to deep-water or habitats characterized by upwelling, currents or oceanic swell in southerly latitudes.

The four species can be distinguished by their local distributions and phenological patterns. *Rhodymenia californica* and *R. pacifica* have the broadest latitudinal and vertical ranges. Fertile plants occur most frequently in the subtidal, with tetrasporophytes more common than fertile gametophytes. While *R. californica* is fertile throughout the year, *R. pacifica* is probably winter fertile. *Rhodymenia callophyllidoides* is strictly subtidal, has a narrower latitudinal distribution and a very different pattern of reproduction, with fertile plants common and abundant throughout the year. *Rhodymenia arborescens*, also subtidal, has the most limited distribution and has been collected the least. It is at the northern end of its range in California and may be more common in deeper waters to the south.

Introduction

Although the intertidal seaweeds of the eight California Islands have been studied in detail (*e.g.*, Apt *et al.* 1988; Murray & Littler 1981; Murray *et al.* 1980, 1989), the subtidal seaweeds are less well-known. During the years I was conducting reconnaissance surveys of subtidal seaweeds with the Channel Islands Research Program, I was studying the morphology and systematics of the California species in the genus *Rhodymenia* Greville (Rhodophyta, Rhodymeniales). As I became familiar with the diversity of habitats around the islands, I decided to focus on the distribution of *Rhodymenia* species, which occur frequently, though rarely in great abundance, in the southern and northern Channel Islands. I hypothesized that fine-scale ecological and phenological characters would be useful for delineating these four species that share similar (and phenotypically plastic) morphological features (Sparling 1957; Miller 1986).

Although eight species are recorded in the algal flora of California (Abbott & Hollenberg 1976), I recognize four species, all of which occur sympatrically in the California Islands: *Rhodymenia californica* Kylin, *R. pacifica* Kylin, *R. callophyllidoides* Hollenberg & Abbott and *R. arborescens* Dawson. Previous studies (Sparling 1957; Dawson 1941, 1963; Hollenberg & Abbott 1965) have described the form and reproductive structures of these species, but little is known about their natural history. Although I had to sacrifice rigorous quantitative methods for coverage of a large number of sites around the eight California Islands, I was able to make observations on the distribution and relative abundance, habitats, morphology, and reproductive states of these four species. In this paper, I present these observations, a summary of the literature on each species and inferred phenological patterns from these new

[1]**Current Address:** Biology Department, University of Puget Sound
Tacoma, WA 98416

collections and herbarium records, discussed in terms of latitudinal and vertical distribution and seasonality.

Materials and Methods

Sites: From 1983-1986, specimens of *Rhodymenia* were collected during three SCUBA dives (usually 3-5 hours duration) at 68 sites in the eight California Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa, San Nicolas, Santa Barbara, Santa Catalina, and San Clemente; see Appendix 1). Collections were limited to times of clement weather, from May through November. Specimens were collected haphazardly at depths of 6-18 m. The relative abundance of each of four species was rated as follows: 1 = rare (1-3 plants encountered); 2 = occasional, infrequent (5-10 plants

Table 1. Relative abundances of four *Rhodymenia* species at 64 sites in the California Islands. Sites are organized by biogeographic affinity (cold, cold-mixed, warm-mixed, warm) and exposure to water motion (very exposed to very sheltered). The collections at these sites were made chiefly at depths of 6-18 m. (Sites listed by island in Appendix 1.)

Number	Site	RCA	RPAC	RCALLO	RARB	Affinity	Exposure
4	Wilson's Rock	3	2	2		C	*****
5	Castle Rock	2				C	*****
7	Wyckoff Ledge		2	2		C	*****
8	Talcott Shoals	2				C	*****
14	Bee Rock	2	2	1	2	C	*****
15	Rodes Reef	2	2			C	*****
16	Chickashaw	3	3	2		C	*****
37	Begg Rock	2	1			C	*****
1	Nifty Rock	2	2			C	****
3	Bay Point	2		2		C	****
6	Crook Point	2	4	4		C	****
10	Carrington Point	2				C	****
2	Cuyler's Harbor	2	4	1		C	**
18	Fraser's Cove	2	2	2		C-M	*****
38	Area Alpha	3	2	1	2	C-M	****
39	Daytona Beach	3	2	1	3	C-M	****
40	Dutch Harbor	3	3		2	C-M	****
19	Hazard Cove	2	2	2		C-M	****
20	Lady's Cove	3	2	3	1	C-M	****
21	Orizaba Cove	3		2	3	C-M	****
22	Diablo Rock	2	2	2		C-M	****
11	East Point	3	3	2		C-M	***
12	Ford Point	2	2			C-M	**
13	Johnson's Lee	3	2	2	2	C-M	**
9	Beecher's Bay	1				C-M	**
17	Forney's Cove	2	2			C-M	*
65	Seal Cove	2	2	1		W-M	*****
24	Potato Rock	2		3	4	W-M	****
27	Gull Island			1		W-M	****
28	San Pedro Point	2	1	2	2	W-M	****
30	Albert's/Valley	3	2	2	1	W-M	****
31	Yellow Banks	2		2	3	W-M	****
36	Admiral's Reef	2	2		2	W-M	****
41	Shag Rock	3	3		3	W-M	****
46	SW side reef	2				W-M	****
60	Castle Rock	2			2	W-M	****
25	Little Scorpion Cove	3	2	3	4	W-M	***
26	Big Scorpion Bay	3	1	3	2	W-M	***

encountered); 3 = common, frequent (up to 5% cover); 4 = conspicuously abundant (up to 10% cover) (Table 1). This quasi-quantitative approach was adopted because of time constraints imposed by SCUBA diving and because the patchy local distribution, and often cryptic habitats of these species (in crevices, under other algae, on walls), precluded quantitative methods.

By observing floristic and faunal assemblages (see Appendix 2 for further explanation of this method) and referring to hydrographic patterns around the islands described by Hendricks (1977) and Pelaez & McGowan (1986), each site was characterized as having overall affinities with: 1) the warm temperate biogeographic province (W); 2) the cool temperate province (C) or 3) a mixture (M) of

Table 1 (cont.)

Number	Site	RCA	RPAC	RCALLO	RARB	Affinity	Exposure
29	Albert's Anchorage	1				W-M	***
34	Bat Ray Cove	2		2		W-M	***
42	Arch Point	2	2			W-M	***
44	Cat Canyon	3	2		2	W-M	***
45	Sutil Island	3	3	2	3	W-M	***
23	Prisoners Harbor		2		2	W-M	**
32	Willows Cove		2		2	W-M	**
33	East Fish Camp	1		1	3	W-M	**
35	Cathedral Cove	2	1		1	W-M	**
61	Northwest Harbor	1				W-M	**
43	Landing Cove	1				W-M	*
64	Pyramid Cove				1	W-M	*
47	West End	2				W	****
59	Ironbound Bay	3				W	****
48	Starlight Reef	1				W	***
49	Parson's Landing	2	2			W	***
50	Arrow Point	3	2			W	***
58	Kelp Point	2	2			W	***
66	Dune Point	2		2		W	***
51	Bird Rock	2				W	**
52	Intake Pipe(CMSC)	2				W	**
53	Blue Cavern	2				W	**
54	Goat Harbor	1				W	**
63	NW of White Rock					W	**
67	Wash Gully	1				W	**
68	Two Trees	1				W	**
55	Hen Rock					W	*
56	Willow/Pinnacle	1				W	*
57	Catalina Head					W	*
62	Wilson's Cove	1				W	*

1 = rare		*	sheltered
2 = present, infrequent		**	moderately sheltered
3 = common, frequent		***	moderately exposed
4 = conspicuous, abundant		****	exposed
		*****	very exposed

M (mixed): elements of both cool and warm temperate biotas
W-M: predominantly warm with some cool species
C-M: predominantly cool with some warm species

the two (C-M or W-M) (Table 1). Exposure to water motion at each site also was estimated qualitatively. Five relative categories were recognized (from very exposed to very sheltered) based on visits to sites in the summer and autumn months. Exposed sites are subject to waves, current and swell; sheltered sites are typically protected coves or embayments (Table 1, Appendix 1). Because estimates of abundance, exposure and biogeographic affinities are non-quantitative, patterns are offered as qualitative correlations.

During each dive, reproductive plants encountered haphazardly in an area 100-200 m^2 were collected for phenological information. On shipboard, voucher specimens were either pressed on herbarium paper and air-dried, or liquid preserved in 4% Formalin/seawater. Pressed specimens are deposited in the Herbarium of the University of California at Berkeley.

More than 600 specimens from the following California herbaria were examined: University Herbarium, University of California at Berkeley (UC); Allan Hancock Foundation Herbarium, Los Angeles (AHF); Catalina Marine Science Center Herbarium, Santa Catalina Island (CAT); the residue of the Gilbert Morgan Smith Herbarium, Hopkins Marine Station, Pacific Grove (GMS). Information obtained from each sheet was organized with the dBASE II (Ashton-Tate) data base management program. Specimens were sorted by geographic location, site, phase and depth for distributional and phenological analyses. Additional distributional information from the algal collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), mostly collections made by E.Y. Dawson and G.J. Hollenberg, were incorporated. Distributions were mapped based on recent California Islands specimens, herbarium collections and the literature (Doty 1947; Johansen 1965; Kjeldsen 1974; Sparling 1977).

Each specimen was examined for reproductive structures (cystocarps, spermatangia, tetrasporangia). Presence/absence data were tallied by month for five latitudinal regions and organized by depth (Table 2), latitude (Table 3) and season (Table 4).

There are limitations in these data because of the various and unknown sources of bias that influence herbarium collections, especially constraints involving convenience of site and season. The absence of a datum, therefore, is not always significant, and phenological patterns are, at best, inferred.

Results and Discussion

Rhodymenia californica Kylin

References: Kylin 1931:21, pl. 9(fig. 21); Dawson 1941:135-136, pl. 20(fig. 15); 1963:457, pl. 89(figs. 3-4); Sparling 1957:361, fig. 12c, e, f; Abbott & Hollenberg 1976:554, fig. 499.

Latitudinal Distribution: The Mazarredo Islands (54° N), Queen Charlotte Islands, northern British Columbia (Hawkes *et al.* 1979) to Cabeza Ballena (23° N), Baja California del Sur (Dawson 1963) [note: the southern North American limit of Nayarit, Mexico of Taylor (1945) and Abbott & Hollenberg (1976) was considered doubtful by Dawson (1963)], including South Farallon Island (UC), the California Islands (this study); Pucusana (12° S), Peru (Dawson *et al.* 1964, USNM), and the Galapagos Islands (Taylor 1945, Dawson 1961, USNM).

Vertical Distribution: Although *Rhodymenia californica* is predominantly subtidal, it is not uncommon in the low intertidal, where collectors specified that it was found under other algae, on vertical or undercut faces of rocks, or in shaded niches. It can occur at higher levels in the presence of strong surge and wave action, *e.g.*, Lady's Cove [site 20], where it grows in association with *Mytilus californianus* on sheer rock faces.

Rhodymenia californica has been collected by dredge at depths to 55 m (Arrecifo de Sacramento Reef, Baja California del Norte, Mexico, AHF 70993), and by SCUBA diving in depths exceeding 30 m at Farnsworth Bank and Isthmus Reef, off Santa Catalina Island (AHF

Table 2. Intertidal and subtidal phenological patterns of two species of *Rhodymenia* collected in the California Islands.

Species	Phase	*n*I	(%T)	*n*S	(% T)	Total
R. californica	Fertile	49	(17%)	75	(26%)	
	Tetra	39	(14%)	42	(15%)	
	Female	6	(2%)	25	(9%)	
	Male	4	(1%)	8	(3%)	
	TOTAL	125	(43%)	163	(57%)	288
R. pacifica	Fertile	23	(10%)	43	(19%)	
	Tetra	17	(7%)	24	(10%)	
	Female	5	(2%)	13	(6%)	
	Male	1	(.5%)	6	(3%)	
	TOTAL	107	(46%)	125	(54%)	232

I: intertidal
S: subtidal
T: total number of fertile plus sterile collections examined

Fertile: total number of specimens bearing tetrasporangial sori, cystocarps, or spermatangial sori.
Tetra: bearing tetrasporangial sori (sporophyte)
Female: bearing cystocarps (carposporophytes on fertilized female gametophyte)
Male: bearing spermatangial sori (male gametophyte)

Table 3. Latitudinal phenological patterns for four species of *Rhodymenia*.

Species	Phase	BAJA	SCA	CI	CCA	ORE	Total
R. californica	Fertile	10(31%)	14(54%)	64(41%)	39(51%)	4(67%)	
	Tetra	8(26%)	9(35%)	45(29%)	27(36%)	3(50%)	
	Female	1(4%)	3(12%)	15(10%)	10(13%)	1(17%)	
	Male	1(4%)	2(8%)	7(4%)	2(3%)		
	TOTAL	32	26	158	76	6	298
R. pacifica	Fertile	2(29%)	14(21%)	16(21%)	34(36%)		
	Tetra	2(29%)	14(18%)	11(15%)	14(15%)		
	Female		3(4%)	2(3%)	13(14%)		
	Male				7(7%)		
	TOTAL	7	68	76	95	5	251
R. callo-phyllidoides	Fertile	2		17(52%)	29(91%)		
	Tetra			14(42%)	9(28%)		
	Female	1		6(18%)	18(56%)		
	Male				2(6%)		
	TOTAL	2	1	33	32		68
R. arborescens	Fertile	2(20%)	1(14%)	10(37%)			
	Tetra	2(20%)	1(14%)	6(22%)			
	Female	0	0	3(11%)			
	Male	0	0	1(4%)			
	TOTAL	10	7	27			44

BAJA: Baja California, Mexico
SCA: southern California mainland
CI: California Islands
CCA: central California (most records from Monterey area)
ORE: Oregon

Fertile: total number of specimens bearing tetrasporangial sori, cystocarps, or spermatangial sori.
Tetra: bearing tetrasporangial sori (sporophyte)
Female: bearing cystocarps (carposporophytes on fertilized female gametophyte)
Male: bearing spermatangial sori (male gametophyte)
TOTAL: total number of fertile plus sterile collections examined

Table 4. Seasonal phenological patterns for four species of *Rhodymenia*.

	J	F	M	A	M	J	J	A	S	O	N	D
R. californica												
Baja California, Mexico												
Tetrasporophyte		1		3		1		1		1		1
Female				1								
Male												1
Southern California												
Tetrasporophyte	1	1			2	1	1			1		2
Female					1	1						1
Male												2
California Islands												
Tetrasporophyte	1	3	7		2	1	5	3	9	11		2
Female			1			1	2	3	5	3		
Male			2	1					1	1	1	1
Central California												
Tetrasporophyte			1	1	1	6	7	3	2	2	3	1
Female					1	1	3	1	1	1	2	1
Male								1			1	
Oregon												
Tetrasporophyte							1	2				
Female								1				
R. pacifica												
Baja California, Mexico												
Tetrasporophyte	1							1				
Southern California												
Tetrasporophyte	2	1								2	2	4
Female											3	
California Islands												
Tetrasporophyte			1	1		1	1		1	6		3
Female			1									1
Central California												
Tetrasporophyte	1	1			1	1		2	1		3	4
Female	1	1	1					1	2	2	3	2
Male					1	1	1		1	1	2	
R. callophyllidoides												
Baja California, Mexico												
Tetrasporophyte								1	1			
Islands												
Tetrasporophyte			2				2	1	3	3	3	
Female							1	1		2	2	
Central California												
Tetrasporophyte			1	1		1	1	2		2		1
Female	1	2	1	1	1	4	2	3	2	1	1	1
Male							2					
R. arborescens												
Baja California, Mexico												
Tetrasporophyte				1				2				
Southern California												
Tetrasporophyte											1	
California Islands												
Tetrasporophyte			1	1					2	1		
Female								2	1			

Numbers indicate number of sites where fertile specimens have been collected or reported in each month.

77136, AHF 77478) and at Cortes and Tanner banks (Lewbel *et al.* 1981). It is reported to occur at shallower depths (less than 13 m) in northern Washington and British Columbia (Hawkes & Scagel 1986).

Habitats: In the California Islands, *Rhodymenia californica* is widely distributed, occurring at 61 out of 68 sites (90%), though it is not conspicuously abundant at any site (Table 1). Most of these sites have affinities with cool or mixed biogeographic provinces.

At Santa Catalina, Santa Barbara, Santa Cruz and San Clemente Islands, *Rhodymenia californica* was not collected at sheltered habitats, but was found at sites that are exposed to water motion due to currents or oceanic swell. It tolerates the extreme, exposed oceanic conditions prevalent at offshore rocks (Begg Rock [site 37], Bee Rock [14], Wilson's Rock [4], Castle Rock [5], Seal Cove [65]).

Rhodymenia californica grows most luxuriantly at depths between 6-18 m (pers. obs.). A well-documented component of the understory flora of *Macrocystis pyrifera* forests (Dawson *et al.* 1960a; North 1971; Foster & Schiel 1985), it becomes infrequent under a very thick canopy (*e.g.*, Shag Rock [site 41] in June 1985; Nifty Rock [1] in September 1983) though it may be common on nearby boulders and walls at the same site (see also Foster & Schiel 1985). It is found only occasionally in the drift, even where it is subtidally abundant, probably due to the tenacity of its stolons.

Habit and Morphology: *Rhodymenia californica* is perennial, growing on the sides and tops of boulders, in crevices and on outcrops of bedrock reefs, on the vertical faces and horizontal ledges of walls and pinnacles, on kelp holdfasts and on invertebrates (*Hinnites gigantea*, *Astraea undosa*, *Haliotis* spp., *Loxorhynchus crispatus*, *Diopatra ornata*, *Phragmatopoma californica*, various sponges). It is commonly associated with other species in the Rhodymeniales, including other species of *Rhodymenia*, *Fauchea laciniata* J. Agardh, *Fryeella gardneri* (Setchell) Kylin, *Botryocladia pseudodichotoma* (Farl.) Kylin and *Sciadophycus stellatus* Dawson.

The variation in size and the morphological plasticity of the blades are notable; several morphs are illustrated in (Figs. 1A - D). High intertidal plants are small and sparingly branched (Figs. 1A) as are plants from very exposed sites. Plants from moderately exposed sites tend to be relatively large, with palmate lamina and several orders of branching and rounder apices (Fig. 1D). Deep-water plants and those from shaded habitats have narrow lamina segments with acute apices (Fig. 1C). Stolons are common in plants growing in soft substrata (*e.g.*, sponges) or on heterogeneous substrata such as walls or ledges.

Older blades often become encrusted with coralline algae (*e.g.*, *Melobesia marginata*) and bryozoans. New blades are generated from stipes, holdfasts and stolons throughout the year. Lamina tips that are injured, grazed or are the site of dehisced fertile sori often regenerate new blades or small proliferations. In the southern part of its range, *Rhodymenia californica* bears distinctive white stripes on its blades due to accumulations of starch granules in the medullary tissue (Fig. 1B).

Phenological Patterns: Almost half (43%) of the 288 collections examined for phenological data were intertidal (Table 2). Unfortunately, very few subtidal collections from Baja California, southern California and Oregon were available in herbaria. While the representation of tetrasporophytes was similar in both habitats, gametophytes, although rare, were far more common in the subtidal.

The distribution of fertile plants is apparently independent of latitude, although the data for Oregon and the mainland south of Point Conception are regrettably sparse (Table 3). Tetrasporophytes are generally more common than gametophytes and occur throughout the year (Table 4). The apparent preponderance of subtidal tetrasporophytes in the fall, especially from the northern Channel Islands, and intertidal tetrasporophytes in the winter, especially from the southern islands, probably reflects collecting biases rather than seasonality. Cystocarpic plants are infrequent in the winter and early spring at all latitudes.

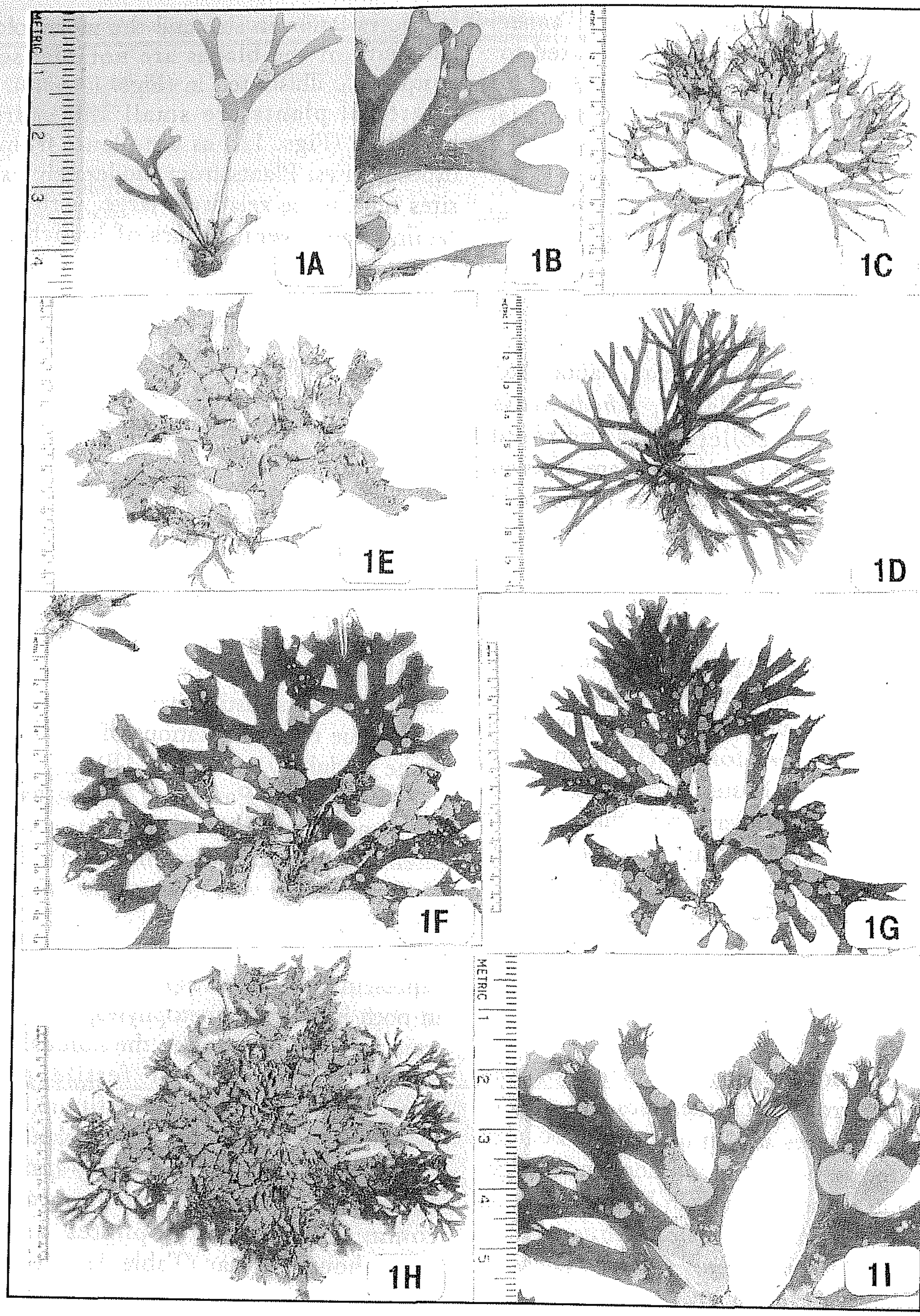

Figure 1. Pressed specimens of *Rhodymenia* from the California Islands; note variations in habit and blade form. All specimens are deposited in the Herbarium of the University of California, Berkeley. A - D: *R. californica*; E - I: *R. pacifica*. A: Sutil Island, Santa Barbara Island. B: Close-up of starch stripes. C: Ironbound Bay, Santa Catalina Island. D: Ford Point, Santa Rosa Island. E: Cuyler's Harbor, San Miguel Island (heavily encrusted blades). F: Parson's Landing, Santa Catalina Island. G: Dutch Harbor, San Nicolas Island. H: Scorpion Anchorage, Santa Cruz Island. I: Johnson's Lee, Santa Rosa Island (proliferations).

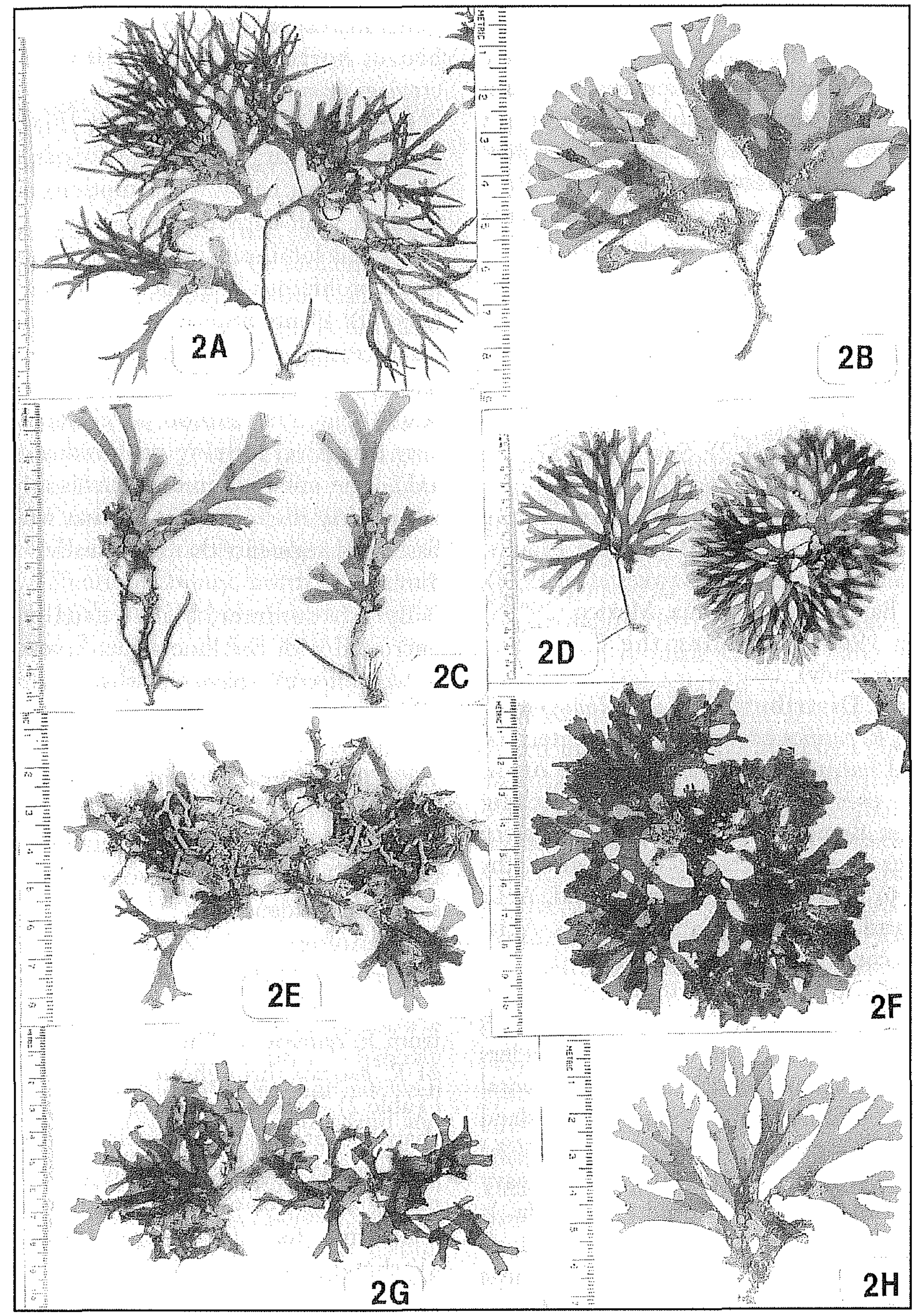

Figure 2. Pressed specimens of *Rhodymenia* from the California Islands; note variations in habit and blade form. All specimens are deposited in the Herbarium of the University of California, Berkeley. A - D: *R. callophyllidoides*; E-H: *R. arborescens*. A: Potato Harbor, Santa Cruz Island. B: Area Alpha, San Nicolas Island. C: Orizaba Cove, Santa Cruz Island. D: Daytona Beach, San Nicolas Island. E. Sutil Rock, Santa Barbara Island. F. Bee Rock, Santa Rosa Island. G. Yellow Banks, Santa Cruz Island. H. Wyckoff Ledge, San Miguel Island.

Males are recognizable in the winter and spring, preceding the appearance of cystocarpic females. Gametophytes are apparently absent in Washington and British Columbia, but tetrasporophytes have been reported from July through December (Hawkes & Scagel 1986).

My conception of *Rhodymenia californica* includes *R. californica* var. *attenuata* (Dawson) Dawson.

Rhodymenia pacifica Kylin

References: Kylin 1931:21, pl. 9(fig. 21); Dawson 1941:142, pl. 20(fig. 14); Dawson 1963:461, pl. 90(figs. 1-2); Sparling 1957:359; Abbott & Hollenberg 1976:557, fig. 504.

Latitudinal Distribution: From the Mazarredo Islands, Queen Charlotte Islands, British Columbia (54° N) (Hawkes *et al.* 1978), to Punta Baja, Baja California, Mexico (29° N) (Dawson 1963), including the California Islands (this study).

Vertical Distribution: Like *Rhodymenia californica*, *R. pacifica* occurs in the low intertidal in shaded habitats under other algae or on vertical or overhanging rock surfaces, reaching its greatest abundance subtidally, to depths of 25 m. It has been collected by dredge at depths reported to be 42 m (Santa Cruz Island, AHF 71048) and 64-74 m (Tanner Bank, AHF 71050), according to herbarium labels.

Habitats: *Rhodymenia pacifica* occurs at 36 (53%) of 68 sites (Table 1), and was conspicuously abundant on the tops of boulders in Cuyler's Harbor [site 2] and on horizontal slabs at Crook Point [6] on San Miguel Island (Table 1). It is rare or infrequent at 29 (43%) of the sites, most of which are exposed to heavy water motion or are sheltered and sandy. It occurred at 4 sites on Santa Catalina Island, all of which are moderately exposed to oceanic swell, currents or upwelling.

Habit and Morphology: *Rhodymenia pacifica* is perennial, growing as isolated plants or occasionally in dense stands. It is chiefly saxicolous and often found in association with *Gigartina corymbifera* (Kütz.) J. Agardh on the tops of boulders or reefs. Perhaps because of its generally larger size, it frequently grows on broad, horizontal surfaces, rather than in crevices or vertical surfaces.

Blade form is highly variable (Figs. 1E - I); plants from marginal habitats (upper intertidal, lower depths, heavy water motion) tend to be smaller, with narrower and more extensively branched lamina. Reproductive plants have more proliferous branchlets than sterile plants (Fig. 1I). Plants from northerly waters (central California, San Miguel Island) tend to be larger and broader (Fig. 1F) than specimens from the south (Fig. 1H). Stolon development can be very extensive, forming proliferous mats (Fig. 1H). The most common form is a rosette of irregularly dichotomous lamina with obtuse bases and segments that are usually wider than 5 mm.

By late summer, blades usually become encrusted with coralline algae, bryozoans (*e.g.*, *Membranipora*), spirorbid worm tubes, and/or hydrozoans (*e.g.*, *Obelia*) (Fig. 1E; Breda 1982). At the same time, lamina become injured, abraded and grazed, and tend to regenerate new blades and proliferations (Figs. 1H,I). *Rhodymenia pacifica* is moderately represented in the drift, though not proportionate to its subtidal abundance.

Phenological Patterns: The reproductive patterns of *Rhodymenia pacifica*, as well as its fine-scale substratum preferences, distinguish it from *R. californica*. The majority of collections of *R. pacifica* throughout its range are sterile (Table 2). Tetrasporophytes are more common than gametophytes, especially in southerly latitudes. Whereas cystocarpic plants comprise nearly a quarter of the collections in central California, its apparent sterility in northern Washington and British Columbia implies that it is not boreal (Table 3). It is clearly winter-fertile in the south, but reproduces in a broader season (earlier in the fall and through the winter) in central California (Table 4).

My conception of *Rhodymenia pacifica* includes *R. lobata* Dawson and *R. rhizoides* Dawson.

Rhodymenia callophyllidoides Hollenberg & Abbott

References: Sparling 1957:359, pl. 51(fig. 12a, b, g, j) [as *R. pacifica*]; Hollenberg & Abbott 1965:1184, fig. 4; Abbott & Hollenberg 1976:555, fig. 501.

Latitudinal Distribution: *Rhodymenia callophyllidoides* was described by Hollenberg & Abbott from Monterey Bay, central California, and has not been widely collected. It has been found in: Humboldt County, Point Cabrillo, (UC); Monterey County, south and west end of Monterey Bay (Del Monte, Coast Guard Breakwater, Monterey Yacht Harbor, Mussel Point); Moss Beach, Pescadero Point, Pebble Beach and Carmel Beach (GMS; USNM); the California Islands (Abbott & Hollenberg 1976; this study); Ventura County, north of Ventura (AHF 78364); Santa Barbara County, Signal Oil Ellwood Pier, Ellwood (USNM 85926); Bahia Papalote, Baja California del Norte, Mexico (GMS 12516, now USNM).

The majority of herbarium specimens of *Rhodymenia callophyllidoides* was collected near its type locality in Monterey Bay (Hollenberg & Abbott 1965). The few specimens from the northern portion of its known latitudinal range (Humboldt County, California) are robust and fertile, suggesting the probability of range extensions in this direction with more subtidal collections.

Vertical Distribution: *Rhodymenia callophyllidoides* is strictly subtidal, usually occurring at a depth of 5-18 m, but has been collected from 27 m off Santa Cruz Island and at Bahia Papalote in Mexico at 27 m.

Habitats: *Rhodymenia callophyllidoides* occurred at 29 (43%) of the 68 sites (Table 1), though with conspicuous abundance only at Crook Point [site 6] where it grew on the surfaces and sides of large, flat boulders with *R. pacifica*, *Fauchea laciniata*, *Fryeella gardneri*, *Weeksia reticulata* Setchell, *Polyneura latissima* (Harvey) Kylin and *Phycodrys setchellii* Skottsberg, a distinctly cool-temperate assemblage. It was common at sites with moderately exposed walls and mixed floristic affinities, but was absent from sheltered, sand-influenced sites with low relief. It has been collected at Santa Catalina Island only once (Farnsworth Bank, 24 m, AHF 78109), and infrequently at San Clemente Island, either below the thermocline (Dune Point [site 66]) or on vertical surfaces at exposed sites (Seal Cove [65]).

Habit and Morphology: *Rhodymenia callophylloides* is perennial, growing in clumps from a primary crust or mat of prostrate blades, usually on walls or the sides of rocks. It frequently ramifies through sponges, especially those growing on vertical rock surfaces. It is often associated with *R. californica*, *R. pacifica*, *Fryeella gardneri* and *Fauchea laciniata*.

At shallower depths (6-10 m), plants tend to grow on vertical surfaces and their blades are narrow and repent (resembling the prostrate form of *Fryeella gardneri*) (Figs. 2E,G); at greater depths (15-18 m) on horizontal surfaces of boulders or shale reef, the habit is upright with large, fan-shaped lamina (Figs. 2F,H). Blades tend to be narrow at sites with warm-mixed biogeographical affinities. Stolons are absent in both prostrate and upright forms.

Phenological Patterns: The abundance of fertile plants in this species contrasts with their scarcity in *Rhodymenia californica*, *R. pacifica* and *R. arborescens* (Table 2). Collections south of Point Conception are infrequently fertile. In the California Islands, tetrasporophytes are twice as common as females, which dominate the central California collections. The latter may reflect a bias in collecting because cystocarp position is a hallmark character of this species; sterile and tetrasporangial specimens are probably overlooked, and more likely to be confused with *R. pacifica*. Seasonal patterns in reproduction are unclear because of the paucity of collections from December through May in the California Islands (Table 4). Nevertheless, tetrasporophytes are evidently more common in the summer and fall in the islands than in central California. Females occur throughout the year, but especially in the summer in central California.

When more specimens are collected, especially from farther north, *Rhodymenia* *callophyllidoides* may prove to have a wider range. The common occurrence of females, as well as the anatomy of the tertasporangial sori (Sparling 1957 [as *R. pacifica*; Abbott & Hollenberg 1976; Miller 1986) distinguish *R. callophylloides* from other *Rhodymenia* species, including the British species (Guiry 1977), that resemble *R. californica* and *R. pacifica* in their paucity and subtidal occurrence of cystocarpic specimens.

Rhodymenia arborescens Dawson

References: Dawson 1941:149, pl. 20(fig. 19), pl. 30(fig. 43); 1963:456, pl. 87; Abbott & Hollenberg 1976:553, fig. 498.

Latitudinal Distribution: From southern California (Laguna Beach), Anacapa Island (Abbott & Hollenberg 1976; this study) and Santa Cruz Island (this study), to near Isla Isabel, Sinaloa, Mexico (Dawson 1963). It is apparently absent from San Miguel and Santa Catalina Islands, though its distribution is poorly documented. I have collected it 23 times, examined 18 herbarium sheets (UC) (AHF), and obtained data from 13 sheets (USNM). It is more frequently collected in the upwelling regions of Baja California del Norte than in California (Dawson *et al.* 1960a & b; Dawson 1963; USNM, AHF).

Rhodymenia arborescens has the most restricted California distribution of the four species considered here. While it does not extend farther north than the north side of Santa Cruz Island, it is commonly found in cool habitats, often associated with kelp beds, as are *R. californica* and *R. pacifica*.

Vertical Distribution: Strictly subtidal, it occurs as shallow as 8 m, but is usually found at greater depths. It was collected by SCUBA at 40 m at Isla Navidad, Mexico (Dawson *et al.* 1960b; Dawson 1963) and was dredged from a reputed depth of 46 m off West Anacapa and San Nicolas Islands (AHF 26776, AHF 26802), and 51 m off San Nicolas Island (AHF 26802). These depths may be inaccurate because the plants were probably growing on pinnacles or uplifted ridges above a deeper bottom (see Lewbel *et al.* 1981).

Habitats: The local distribution of *Rhodymenia arborescens* is extremely patchy, and it rarely is found in large numbers. It occurs at 22 (32%) out of the 68 sites (Table 1), and is conspicuously abundant at Little Scorpion [site 25] on exposed vertical walls and at Potato Rock [24] under *Eisenia arborea* Areschoug on ledges at the exposed mouth of the cove.

Rhodymenia arborescens occurs at sites with mixed floras, with the exception of Bee Rock [site 14], which sustains a predominantly cool flora due to its oceanic exposure. It was not seen in the sheltered sites on San Clemente Island. It is apparently less common at San Clemente than at Santa Barbara and San Nicolas Islands and has not been collected at Santa Catalina Island.

Habit and Morphology: *Rhodymenia arborescens* is perennial, and tends to grow on vertical surfaces, including walls and the sides of boulders or reefs. It is often in the midst of other algae (*e.g.*, *R. pacifica*, *Gelidium nudifrons* Gardner and *G. robustum* (Gardner) Hollenberg & Abbott in or adjacent to *Macrocystis* beds.

Its conspicuous, terete stipes and conical crustose holdfast usually are encrusted with coralline algae, bryozoa and sponges (Dawson *et al.* 1960a), as are the older lamina (Figs. 2A-D). The stipes, of variable length, are capable of initiating new blades (Fig. 2C). Stolons, if present, are terete and sparingly branched. Lamina shape ranges from cuneate (Figs. 2A-C) to pseudo-peltate or nearly circular (Figs. 2B-D). Apices may be blunt (Fig. 2B) or pointed (Fig. 2A).

Phenological Patterns: In 44 collections, only 13 were fertile: 9 tetrasporophytes, 3 females and 1 male (Table 3). In California, this species appears to be at the northern endpoint of its latitudinal distribution, with patchy populations, a tendency to occur deep, and infrequent sporic reproduction. These characterisitics do not enhance recruitment and increased abundance, or greater frequency. It is possible that *Rhodymenia arborescens* is more common and fertile in deeper water in California, so that specimens at hand represent fringe populations.

Factors involved in the rather abrupt northern limit of this species at Santa Cruz Island cannot be determined, but its presence corroborates the suggestion (*e.g.*, Valentine 1966; Murray *et al.* 1980; Murray & Littler 1981) that Point Conception is a more formidable barrier to the northern spread of southern species than to the southern spread of northern species (*e.g.*, *Rhodymenia californica*, *R. callophyllidoides* and *R. pacifica*).

My conception of *Rhodymenia arborescens* includes *R. hancockii* Dawson.

Conclusions

Temperature has been considered a determining factor in the geographic distribution of marine algae since the work of Setchell (1893, 1920) and more recently by Druehl (1981) and Druehl & Foottit (1985). Recent studies (Murray *et al.* 1980; Murray & Littler 1981) have correlated surface circulation patterns and temperature with the distribution of intertidal seaweeds in southern California, including the California Islands. Rather than following a strictly latitudinal gradient, the biogeographical affinities of the California Islands reflect hydrographic and site-specific features in the Southern California Bight, as suggested by statistical comparisons of intertidal floras and faunas at various sites (Seapy & Littler 1980; Murray & Littler 1981, 1989).

The pattern of relative abundance of the four species (Figs. 1-2) reflects the variety of habitats found in the islands. In general, their geographic distribution is similar to that of *Macrocystis pyrifera*. All four species are most common at sites with moderate water motion, high relief substrates (such as boulders, pinnacles and walls), and mixed biogeographic affinities, regardless of island. They are least frequently encountered at Anacapa, Santa Catalina and San Clemente Islands, sites with the greatest percentage of warm-temperate habitats. Sand-influenced areas with low relief, are not suitable habitats, and *Rhodymenia* species, if present, occur infrequently (see also Breda 1982). Pinnacles or walls rising above sand provide a refuge from abrasion and burial.

In areas with cool or cool-mixed affinities, very heavy water motion (especially at precipitous offshore rocks) excludes many algal species and diminishes populations. At Begg Rock [site 37], mussels (*Mytilus californianus*) and sea anemones (*Anthopleura elegantissima*, *Mytridium senile*) dominate down to 25 m; at Castle Rock [5], encrusting and dendritic bryozoa occupy most of the surfaces, and sponges and tunicates dominate at Wilson's Rock [4] (pers. obs.). *Rhodymenia* species are present at sites with some protection from prevailing oceanic swells (e.g., Cuyler's Harbor [2], Daytona Beach [39]) or with horizontal surfaces (e.g., Crook Point [6], Rodes Reef [15]) or heterogeneous, rather than sheer, vertical walls (e.g., Wyckoff Ledge [7], Fraser's Cove [18]).

Deep-water sites and those exposed to oceanic waters or upwelling provide a relatively cool-temperate environment even in the southern part of the range of these species (e.g., Shag Rock [41], Sutile Island [45], Lady's Cove [20], Seal Cove [65], Little Scorpion [25], Arrow Point [50], Kelp Point [58], Ironbound Bay [59]) (Stewart 1984). Habitat specificities within a wide range of subtidal climates indicate that these species, including the commonly distributed *Rhodymenia californica*, are not as broadly tolerant as has been supposed (*e.g.*, Abbott & North 1972 included *R. californica* and *R. pacifica* as "warm-tolerant" species whereas Widdowson, 1971, classified the distribution of *R. californica* as southern). *Rhodymenia callophyllidoides*, with its rarity at Anacapa, Santa Catalina and San Clemente Islands, shows a pattern of distribution that probably is restricted more by temperature than the other species. However, the high degree of morphological variation characteristic of all four species indicates a flexibility in phenotypic expression within the limits of physiological (*e.g.*, temperature) tolerances.

The degree of exposure, mediated by the orientation of the substrate, and the absence of sand abrasion and sediment accumulation, may be primarily responsible for the successful establishment and maintenance of populations throughout the geographic ranges of these species (see Murray & Littler 1989). Herbivory, plant-animal and plant-plant interactions are also likely to be important, but are largely unexplored. For example, the ability of *Rhodymenia californica* to tolerate low light levels may allow it to avoid competition with other plants (M. Foster, pers. comm.).

The frequent occurrence of *Rhodymenia californica*, *R. pacifica* and *R. callophyllidoides* throughout the islands suggests that these species possess efficient dispersal mechanisms that may be enhanced by current patterns, particularly from the north. The first two species are able to hold space, compete in exposed environments and perennate by means of stolons (Foster 1975), which augment or replace sporic reproduction, resulting in stable clonal mats that resist invasion by ephemeral species.

The *Rhodymenia* species investigated in this study overlap in large regions of their latitudinal ranges, supporting the hypothesis that congeneric species overlap each other frequently, with the implication that geographic ranges are not affected by interspecific competition (Pielou 1977). These species show differences in their fine-scale habitat affinities and broad-scale phenological patterns.

The overlapping distributions of these species do not imply sympatric speciation events. *Rhodymenia callophyllidoides* is probably not congeneric with the other species treated here (Miller 1986). *Rhodymenia californica* may be closely related to, or possibly conspecific with, other species such as *R. intricata* (Okam.) Okam. from Japan and Korea (Lee 1978) and *R. pseudopalmata* (Lamour.) Silva from the North Atlantic and South Africa (Sparling 1957). *Rhodymenia arborescens* has morphological similarities with the South American genus *Dendrymenia* (Miller 1986). The evolutionary history of these species cannot be predicted from their current distribution.

Environmental factors which determine the endpoints of latitudinal distribution of a species (reviewed by Druehl 1980) are both physical (*e.g.*, seawater temperature and salinity, light levels and quality, water motion, availability of nutrients and gases, appropriate substrates) and biological (*e.g.*, physiological tolerances, efficiency and distance of propagule dissemination, herbivory, competition). Attempts to tighten the correlations between biogeography and environmental factors experimentally (*e.g.*, Cambridge *et al.* 1984; Edwards 1979; van den Hoek 1984; McLachlan & Bird 1984) are necessary for an analysis of the causes of observed biogeographic trends, but are difficult to interpret or extrapolate because of the complexity and dynamics of natural environments and the offshore hydrography that shape them. Such studies must be preceded by field studies of individual species and assemblages on both local and global scales.

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Appendix 1.

California Island collection sites and dates: 1983-1986.

CIRP: Tatman Foundation's Channel Islands Research Program
NPS: National Park Service Kelp Forest Monitoring cruise
UREP: University Research Expedition sponsored cruise (in collaboration with CIRP)

San Miguel Island
1. Nifty Rock
   17 IX 83 CIRP (exposed)
2. Cuyler's Harbor
   1 IX 85 jetty site CIRP (moderately sheltered)
3. Bay Point (SE)
   26 X 86 CIRP (moderately exposed)
4. Wilson's Rock
   24 X 86 north side CIRP (very exposed)
5. Castle Rock
   25 X 86 SW side (very exposed)
6. Crook Point (east)
   30 VIII 85 CIRP (exposed)
7. Wyckoff Ledge
   27 X 86 CIRP (very exposed)

Santa Rosa Island
8. Talcott Shoals
   18 IX 83 SRIII CIRP (very exposed)
9. Beecher's Bay
   22 IX 84 CIRP (moderately sheltered)
10. Carrington Point
   22 IX 84 CIRP (exposed)
11. East Point
   19 IX 84 CIRP (moderately exposed)
12. Ford Point
   15 IX 83 CIRP (moderately sheltered)
13. Johnson's Lee
   21 IX 84 CIRP (moderately sheltered)
   29 VIII 85 (1.2 m. E) CIRP
   11 IX 86 NPS
14. Bee Rock
   16 IX 83 CIRP (very exposed)
   23 X 86 CIRP
15. Rodes Reef
   11 IX 86 NPS (very exposed)
16. Wreck of the Chickashaw (E)
   22 X 86 CIRP (very exposed)

Santa Cruz Island
17. Forney's Cove
   26 VIII 84 CIRP (sheltered)
18. Fraser's Cove
   26 VII 85 UREP (very exposed)
19. Hazard Cove
   25 VIII 84 CIRP (gradient)
20. Lady's Cove
   25 VII 85 UREP (exposed)
21. Orizaba Cove
   25 VII 85 UREP (gradient)
22. Diablo Rock & Harbor
   24 VIII 84 CIRP (gradient)
23. Prisoners Harbor
   23 VIII 84 CIRP (sheltered)
24. Potato Rock
   23 VIII 84 CIRP (gradient)
25. Little Scorpion Cove
   23 VII 85 UREP (gradient)
26. Big Scorpion Bay
   22 VIII 84 CIRP (gradient)
   23 VII 85 UREP
27. Gull Island
   10 IX 86 NPS (west side)
   26 IX 86 CIRP (inshore)
28. San Pedro Point
   23 IX 86 CIRP (exposed)
29. Albert's Anchorage
   24 IX 86 CIRP (sheltered)
30. Albert's/Valley (midway)
   25 IX 86 CIRP (moderately exposed)
31. Yellow Banks (west)
   8-9 IX 86 NPS (exposed)
32. Willows Cove (outer rocks, east)
   26 IX 86 CIRP (moderately protected)

Anacapa Island
33. East Fish Camp
   22 VII 84 UREP (moderately sheltered)
34. Bat Ray Cove
   27 VII 85 UREP (moderately exposed)
35. Cathedral Cove
   12 IX 86 NPS (sheltered)
36. Admiral's Reef
   12 IX 86 NPS (exposed)
   27 IX 86 CIRP

San Nicolas Island
37. Begg Rock
   27 IX 85 CIRP (very exposed)
38. Area Alpha
   26 IX 85 CIRP (exposed)
39. Daytona Beach
   28 IX 85 CIRP (exposed)
40. Dutch Harbor (33 13' 03" X 119 29' 20")
   29 IX 85 CIRP (exposed)

Santa Barbara Island
41. Shag Rock
   20 VI 85 UREP (exposed)
42. Arch Point
   30 VII 84 NPS (moderately exposed)
   16 X 84 SBI CIRP
43. Landing Cove
   23 IX 83 CIRP (sheltered)
44. Cat Canyon
   30 IX 85 CIRP (moderately exposed)
45. Sutil Island
   21 VI 85 UREP (moderately exposed)
46. SW end, between the Arch and Sutil Island
   24 IX 83 CIRP (exposed)

Santa Catalina Island
47. West End (lee)
21 V 84 CIRP (exposed)
48. Starlight Reef
19 V 84 CIRP (moderately exposed)
49. Parson's Landing
18 VI 85 UREP (moderately exposed)
50. Arrow Point
21 V 84 CIRP (moderately exposed)
51. Bird Rock
19 IX 84 (moderately sheltered)
52. Intake Pipes: Catalina Marine Science Center
26 V 84 (moderately sheltered)
53. Blue Cavern Cove
21 IX 84 (moderately sheltered)
54. Goat Harbor
17 VI 85 UREP (moderately sheltered)
55. Hen Rock
22 V 84 CIRP (sheltered)
56. Willow Cove/Pinnacle Point
22 V 84 CIRP (sheltered)
57. Catalina Head and Harbor
20 V 84 CIRP (gradient)
58. Between Kelp Point and Whale Rock
20 V 84 CIRP (moderately exposed)
59. Ironbound Bay
19 V 84 CATII CIRP (exposed)

San Clemente Island
60. Castle Rock
10 X 83 CIRP (exposed)
61. Northwest Harbor
11 X 83 CIRP (moderately sheltered)
62. Wilson's Cove
12 X 83 CIRP (sheltered)
63. NW of White Rock
13 X 83 CIRP (moderately sheltered)
64. Pyramid Cove
14 IX 83 CIRP (sheltered)
65. Seal Cove
27 VIII 86 CIRP (exposed)
66. Dune Point
28 VIII 86 CIRP (moderately sheltered)
67. Wash Gully
29 VIII 86 CIRP (moderately sheltered)
68. Two Trees
30 VIII 86 CIRP (moderately sheltered)

Appendix 2

This appendix is not intended to be a comprehensive list of organisms characteristic of areas with cold and warm biogeographic affinities in the California Islands. However, because temperature is difficult to measure, especially on meaningful scales, I offer this synopsis (based on my experience and that of J.M. Engle, Channel Islands Research Program) as an indication of my method for designating biogeographic affinities, based not on temperature, but on floristic and faunal assemblages. These assemblages result from an integration of long-term environmental influences and are thus biotic indicators of temperature-related regimes (for a similar approach to intertidal assemblages see Murray & Littler 1989).

Warm Temperate Biota (W)

1. Dominant Plant Species (characterized by low profile cover, turf associations)
   A. Intertidal
      - Turfs composed of *Corallina* spp., *Gelidium* spp., *Laurencia* spp.
   B. Subtidal
      - Coralline turfs composed of *Amphiroa zonata*, *Halyptilon gracile*, *Lithothrix aspergillum*.
      - *Macrocystis pyrifera* forests with dictyotalean understory: *Dictyopteris undulata*, *Dictyota flabellata*, *D. binghamiae*, *Pachydictyon coriaceum*, *Taonia lennebackerae*, *Zonaria farlowii*.
      - Gelidiales: *Gelidium nudifrons*, *G. purpurascens*, *G. robustum*, *Pterocladia capillacea*.
2. Other Plant Species
   - *Acrosorium uncinatum*, *Carpopeltis bushiae*, *Chondria* spp., *Codium cuneatum*, *Colpomenia sinuosa*, *Cutleria cylindrica*, *Cystoseira neglecta*, *Eisenia arborea*, *Hydroclathrus clathratus*, *Hypnea* spp., *Laurencia spectabilis* var. *diegoensis*, *L. snyderae*, *L. subopposita*, *Liagora californica*, *Pelagophycus porra*, *Sargassum palmeri*, *Sporochnus pedunculatus*, *Tinocladia crassa*, *Ulva californica*.
3. Animal Species
   A. Fishes
      - *Girella nigricans* (opaleye), *Heterodontus francisci* (horn shark), *Hypsopops rubicunda* (garibaldi), *Lythrypnus dalli* (blue spot goby), *Semicossyphus pulcher* (sheephead).
   B. Invertebrates
      - *Cypraea spadicea* (chestnut cowry), *Hemisquilla ensigera* (mantis shrimp), *Panulirus interruptus* (spiny lobster), *Parastichopus californicus* (cucumber), *Tegula regina* (queen turban).

Cool Temperate Biota (C)

1. Dominant Plant Species (characterized by lush and distinctly stratified communities)
   A. Intertidal
      - Distinct zonation dominated by fucoids: *Pelvetia compressa*, *Hesperophycus californica*.
   B. Subtidal
      - Lush, stratified communities dominated by *Macrocystis pyrifera* and other large phaeophytes: *Cystoseira osmundacea*, *Laminaria setchellii*, *Pterygophora californica*.
      - Large Delesseriaceae: *Cryptopleura ruprechtiana*, *Hymenena flabelligera*, *Phycodrys setchellii*, *Polyneura latissima*.
      - Foliose reds: *Halymenia* spp., *Callophyllis* spp., *Schizymenia* spp.
      - Articulated corallines: *Bossiella* spp., *Calliarthron cheilosporioides*, *C. tuberculata*.
2. Other Plant Species
   - *Callithamnion pikeanum*, *Callophyllis violacea*, *Cladophora graminea*, *Costaria costata*, *Gigartina corymbifera*, *Gymnogongrus chiton*, *Iridaea splendens*, *Laurencia spectabilis*, *Microcladia borealis*, *Neorhodomela larix*, *Opuntiella californica*, *Phycodrys setchellii*, *Rhodoptilum plumosum*, *Weeksia reticulata*.
3. Animal Species
   A. Fishes
      - *Embiotica lateralis* (striped surfperch), *Hypsurus careyi* (rainbow surfperch), *Sebastes mystinus* (blue rockfish), *Sebastes* spp.
   B. Invertebrates
      - *Acarnus* spp. (red encrusting sponges), *Calliostoma* spp. (striped turban snails), *Cancer* spp. (rock crabs), *Cryptochiton stelleri* (gumboot chiton), *Hopkinsia rosacea* (Hopkin's rose nudibranch), *Pycnopodia helianthoides* (sunstar),