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**LIFE HISTORY AND FEEDING ECOLOGY OF A SPECIALIZED
NUDIBRANCH PREDATOR (*PHYLLODESMIUM POINDIMIEI*)
WITH IMPLICATIONS FOR BIOCONTROL OF AN INVASIVE
OCTOCORAL (*CARIJOA RIISEI*) IN HAWAI'I**

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By
Daniel Wagner

Thesis Committee:

Robert J. Toonen, Chairperson
Jeffrey C. Drazen
Matthew J. Church

We certify that we have read this thesis and that, in our opinion, it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Oceanography (Marine Biology).

THESIS COMMITTEE

Chairperson

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Daniel Wagner**

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CHAPTER 1. INTRODUCTION

With approximately 3000 species, the Nudibranchia is the largest order within the Opisthobranchia (Thompson 1976; Todd 1981; Waegele and Klussmann-Kolb 2005). Nudibranchs are all carnivorous, feeding on an array of sessile, benthic animals, such as sponges, tunicates, bryozoans, hydroids, anemones or corals, which are not exploited heavily by other invertebrate taxa (Thompson 1976; Todd 1981, 1983; Bertsch and Johnson 1981; Waegele and Klussmann-Kolb 2005). The genus *Phyllodesmium* Ehrenberg 1831 (Suborder Aeolidoidae, Family Facelinidae) includes 19 currently described species (see Baba 1949, 1991, 1991b; Rudman 1981, 1991; Avila et al. 1998, Ortiz and Gosliner 2003; Burghardt and Waegele 2004; Burghardt and Gosliner 2006) (Table 1). The different species of *Phyllodesmium* are similar in that they (1) prey exclusively on alcyonarian corals, (2) exclusively occur in the Indo-Pacific, (3) lack oral glands, (4) possess salivary glands, (5) have cerata that autotomize readily when disturbed, (6) lack defensive nematocysts in their cnidosacs, (7) have sparse epidermal ceratal glands, (8) possess nearly identical reproductive systems, and (9) possess a unique tooth shape among aeolids (Rudman 1981, 1991; Avila et al. 1998; Burghardt and Waegele 2004; Burghardt and Gosliner 2006). This genus is also quite unique in that most of its member species house symbiotic zooxanthellae within their digestive gland cells (Rudman 1981, 1991) (Table 1). Additionally, most *Phyllodesmium* species are relatively stenophagous, relying on one or a few species of alcyonarians as their food source (Rudman 1981, 1991; Waegele 2004). Stenophagy is common among the Nudibranchia (Todd 1981, 1983), however, alcyonarian prey is unusual among aeolid nudibranchs which feed most commonly on hydroids or sea anemones (Edmunds 1975; Rudman 1981). The individual species of *Phyllodesmium* are distinguished based on

differences in the external color pattern, shape and arrangement of the cerata, digestive gland branching pattern, radular morphology and anal position (Rudman 1981, 1991; Burghardt and Gosliner 2006).

Most of the published literature on the genus *Phyllodesmium* has centered on taxonomic descriptions, with scarce information available on the ecology and life history of these animals. As specialized predators, *Phyllodesmium* species have intimate ecological relationships with their alcyonarian prey (Rudman 1981, 1991); however, such relationships have thus far not been investigated thoroughly. I became interested in this question after finding *Phyllodesmium poindimiei* (Risbec 1928) apparently feeding on *Carijoa riisei* (Duchassaing and Michelotti 1860) in Hawaii (Wagner et al. 2007).

C. riisei is an azooxanthellate, shallow-water octocoral (Order Alcyonacea, Family Clavulariidae) originally described from the Caribbean and tropical Atlantic (as *Telesto riisei*) (Bayer 1961). *C. riisei* was first seen in Hawaii in 1966 (Kahng 2006; Kahng et al. 2008) and the first published record was in 1972, when it was discovered within the fouling community of Pearl Harbor (Evans et al. 1974). Prior to this, *C. riisei* had not been seen in Hawaii, despite several surveys of invertebrate fauna in areas that now form habitat for *C. riisei* (Edmonson 1944; Edmonson & Ingram 1939). Since these initial discoveries, *C. riisei* has spread throughout the Main Hawaiian Islands where it has become common in habitats with hard substrata, low light and moderate current flow (Devaney and Eldredge 1977; Thomas 1979; Coles and Eldredge 2002; Kahng 2006). At depths below 70 m it has been found overgrowing large fields of black corals *Antipathes cf. dichotoma* and *A. grandis*, as well as scleractinian plate corals *Leptoseris* spp. (Kahng and Kelley 2007; Kahng and Grigg 2005; Grigg 2004; Grigg 2003). Similarly, in favorable shallow-water habitats (shallower

than 70 m), *C. riisei* commonly overgrows cup corals and bivalves and attains high densities thereby saturating the substrata to the exclusion of native benthic fauna (Kahng 2006).

However, recent molecular work has revealed the presence of at least 2 different species of *Carijoa* in Hawaii, and exposed that this genus is in need of taxonomic revision (Concepcion et al. in press). Pending such taxonomic revision I continue to use the accepted name of *Carijoa riisei* here.

Management strategies to address biological invasions include: (1) prevention of the spread of the potentially invasive species in the first place; (2) eradication of the invasive populations when these are small; (3) use of mechanical or chemical methods when invasive populations are established; or (4) the use of biocontrol agents (Secord 2003; Sax et al. 2005). Given the large spread and abundance of *C. riisei* in Hawaii (Kahng & Grigg 2005; Kahng 2006; Kahng et al. 2008), there is interest in identifying potential biocontrol agents against *C. riisei*. The basic premise of biological control is the use of a pest organism's natural enemies, such as parasites, parasitoids, pathogens or predators, to reduce the abundance of the pest organism (Lafferty & Lafferty 1996; Kareiva 1996; Murdoch & Briggs 1996; Simbeloff & Stiling 1996; Secord 2003; Sax et al 2005). There are three fundamentally different strategies within biocontrol (Secord 2003): (1) classical biocontrol where the natural enemy from the pest's native range is introduced into the pest's new range; (2) neoclassical biocontrol where a non-indigenous species is introduced to control a native pest; and (3) augmentative biocontrol where the already established natural enemy populations of a pest are enhanced.

Biocontrol has been used successfully in terrestrial agricultural systems for a long time (Funasaki et al. 1988; Murdoch & Briggs 1996; Simbeloff & Stiling 1996; Secord

2003), however, in marine systems biocontrol is still in its infancy (Simbeloff & Stiling 1996; Secord 2003). In estuary and marine systems only few proposals to identify and test potential biocontrol agents have been put forward (reviewed by Secord 2003). These include: (1) pathogenic microorganisms (viruses, bacteria and protozoa) against harmful algal blooms; (2) the predatory butterfish *Peprilus triacanthus* and the parasitic larval sea anemone *Edwardsia lineata* against the ctenophore *Mnemiopsis leidyi* in the Black Sea; (3) the castrating barnacle *Sacculina carcini* against the crab *Carcinus maenas*; (4) the spermiphagous ciliate *Orchitophyra stellarum* against the starfish *Asterias amurensis*; (5) sacoglossan opisthobranchs against the green alga *Caulerpa taxifolia* in the Mediterranean Sea; and (6) the planthopper *Prokelesia marginata* against the saltmarsh cordgrass *Spartina alterniflora*.

Besides the shorter history of marine biological control, as opposed to terrestrial biocontrol, there are several fundamental differences between terrestrial and marine ecosystems that directly influence organismal biology. These differences include life histories, taxonomic relationships and biodiversity, larval and adult dispersal strategies, biomechanics of the medium and relative system openness (Strathmann 1990; Lafferty and Kuris 1996; Kareiva 1996; Secord 2003). Together, the uncertainty in predicting marine systems is much greater, making it harder to identify and test potential biocontrol agents (Lafferty and Briggs; Secord 2003).

Decisions on the identification of potential biocontrol agents are guided by host specificity and seek to maximize damage to the pest populations, with both of these factors being important (Murdoch and Briggs 1996; Secord 2003; Sax et al. 2005). For instance, studies with sacoglossan opisthobranchs as potential biocontrol agents against the alga

Caulerpa taxifolia in the Mediterranean Sea revealed that several slug species are specialized feeders of *C. taxifolia*; however slugs were ineffective biocontrol agents due to low feeding rates (Williams and Walker 1999; Coquillard et al. 2000; Thibaut et al. 2001). Ideally, a biocontrol agent should maximize damage to a specific pest without affecting non-target species. Additionally, the life histories of potential biocontrol agents need to be considered (Simberloff and Stiling 1996; Secord 2003). For example, the sacoglossans *Oxynoe olivacea* and *Lobiger seradiflaci* are unsuitable biocontrol agents against *Caulerpa* because of low feeding rates and planktotropic larval development, which typically leads to dispersal away from the biocontrol's local target pest (Lafferty and Kuris 1996; Secord 2003).

The only reported predators of *Carijoa* outside of Hawaii are ovullids in Indonesia (Calcinaï et al. 2004), and an endemic tritoniid nudibranch *Tritonia* sp. (Kahng 2006), the aeolid nudibranchs *Phyllodesmium serratum* and *P. poindimiei*, all from southern Australia (Rudman 1981, 1991). In Hawaii, studies on the associated microcommunity of *C. riisei* conducted in the 1970's failed to identify any predators of *C. riisei* (Thomas 1979). In 1995, the dendronotid nudibranch *Tritoniopsis elegans* (Audoin 1826) and the aeolid nudibranch *Phyllodesmium poindimiei* (Risbec 1928), were first seen in Hawaii apparently feeding on *C. riisei* (Wagner et al. 2007). Laboratory assays with the native Hawaiian octocorals *Sinularia densa* (Whitelegge 1897) and *Sarcothelia edmonsoni* (Verrill 1928) in the presence and absence of *C. riisei*, demonstrated that *T. elegans* is a generalist octocoral predator which preys readily on *C. riisei*, but also feeds on *S. edmonsoni* and *S. densa* when *C. riisei* is absent (Wagner et al. 2007). The generalist nature of *T. elegans* feeding makes it an undesirable biocontrol agent against *C. riisei* in Hawaii. In contrast, *P. poindimiei* quickly starved in the absence of *C. riisei* even when offered alternative octocoral prey (Wagner et al.

2007; current study). Prior to these studies, *P. poindimiei* had only been observed from a variety of Western Pacific locations from New Caledonia to southern Australia (Rudman 1981, 1991; Burn 2006; Slack-Smith & Bryce 2004) in close association with *Carijoa* (Rudman 1991).

Given the rapid proliferation and ecological impact of *C. riisei* in Hawaii (Kahng and Grigg 2005), there is interest in the potential use of *P. poindimiei* as a biocontrol agent. However, little is known about the basic biology of this nudibranch species. The purpose of this study was to: (1) confirm the specialized nature of *P. poindimiei* feeding; (2) quantify the impacts of *P. poindimiei* on *C. riisei*; and (3) answer basic life history questions of *P. poindimiei* including adult longevity, fecundity and larval type, by using both laboratory cultures and time-series observations of field sites.

Species	Authority	Previous names	Length (mm)	Food	Zoox.	Known distribution	References
<i>P. briareum</i>	(Bergh, 1896)	<i>Ennoia briareus</i>	7-25	Briaridae	Yes	Indo-Pacific, Australia	Avila et al. 1998, Burghardt et al. 2005, Rudman 1991, Waegele & Johnsen 2001
<i>P. colemani</i>	Rudman, 1991		9-18	<i>Tubipora musica</i>	Yes	Coral Sea	Avila et al. 1998, Rudman 1991
<i>P. crypticum</i>	Rudman, 1981	<i>Phylloidesmium cryptica</i>	45-60	<i>Xenia</i>	Yes	Australia	Avila et al. 1998, Burghardt & Waegele 2004, Rudman 1981, Rudman 1981
<i>P. guamensis</i>	Avila, Ballesteros, Slattery, Starmer & Paul 1998		8-48	<i>Sinularia polydactyla</i> , <i>S. maxima</i> , <i>S. sp.</i>	Yes	Guam	Avila et al. 1998, Carlson & Hoff 2003, Slattery et al. 1998
<i>P. horridum</i>	(Macnae, 1954)	<i>Favorinus horridus</i> , <i>Phylloidesmiopsis horridus</i> , <i>P. horridus</i>	8-27	<i>Melitodes</i>	No	S. Africa, Australia	Avila et al. 1998, Rudman 1981, Rudman 1991, Burghardt & Gosliner 2006
<i>P. hyalinum</i>	Ehrenberg, 1831	<i>P. xeniae</i> , <i>Favorinus horridus brevitentaculatus</i>	14-45	<i>Xenia</i> , <i>Xenia umbellata</i> , <i>Heteroxenia fuscens</i>	Yes	Pacific, Red Sea, Tanzania, Australia, Japan, Philippines, Marshall Islands	Avila et al. 1998, Gohar & Aboul-Ela 1957, Rudman 1981, Rudman 1991
<i>P. iriomotense</i>	Baba, 1991		20	Found on thread like alcyonarian	No	Japan	Baba 1991b, Burghardt & Gosliner 2006
<i>P. jakobsenae</i>	Burghardt & Waegele, 2004		≤30	<i>Xenia</i>	Yes	N. Sulawesi	Burghardt & Waegele 2004
<i>P. kabiranum</i>	Baba, 1991		38	?	Yes	Japan	Baba 1991b
<i>P. longicirum</i>	(Bergh, 1905)	<i>Myrthine longicirra</i>	33-140	<i>Sarcophyton tracheliophorum</i>	Yes	Australia, Indonesia	Avila et al. 1998, Coll et al. 1985, Burghardt & Gosliner 2006
<i>P. macphersonae</i>	(Burn, 1962)	<i>Cratena macphersonae</i>	4-35	unknown	Yes	Australia, Tanzania, Japan	Avila et al. 1998, Rudman 1981, Rudman 1991, Baba 1991
<i>P. magnum</i>	Rudman, 1991		12-130	<i>Sinularia sp.</i>	Yes	Australia, New Caledonia, Marshall Is., Hong Kong, N. Kermadec, Guam	Avila et al. 1998, Brook 1998, Carlson & Hoff 2003, Rudman 1991
<i>P. opalescens</i>	Rudman, 1991		8-19	?	No	Hong Kong	Avila et al. 1998, Rudman 1991
<i>P. orientale</i>	Baba, 1991	<i>P. hyalinum</i>	25	Found on <i>Xenia</i>	Yes	Japan	Baba 1991b
<i>P. parangatum</i>	Ortiz & Gosliner, 2003		8-20	?	Yes	N. Philippines	Ortiz & Gosliner 2003, Burghardt & Gosliner 2006
<i>P. pecten</i>	Rudman, 1981		4-22	<i>Xenia</i>	Yes	Tanzania	Avila et al. 1998, Rudman 1981
<i>P. poindimiei</i>	(Risbec, 1928)	<i>Aeolidia poindimiei</i> , <i>Phestilla poindimiei</i> , (?) <i>Phidiana tenuis</i>	12-50	<i>Carijoa sp.</i>	No	Australia, New Caledonia	Avila et al. 1998, Burn 2006, Rudman 1981, Burghardt & Gosliner 2006
<i>P. rudmani</i>	Burghardt & Gosliner 2006		≤45	<i>Xenia</i>	Yes	N. Sulawesi, Phillipines	Burghardt & Gosliner 2006
<i>P. serratum</i>	(Baba, 1949)	<i>Hervia serrata</i> , <i>Cratena serrata</i> , <i>Babaiella serrata</i> , <i>P. serrata</i>	7-40	<i>Comularia sp.</i> , <i>Clavularia sp.</i> , <i>Carijoa sp.</i> , <i>Steronephthia sp.</i>	No	Australia, Japan, Tanzania	Avila et al. 1998, Baba 1991, Burn 2006, Rudman 1991, Burghardt & Gosliner 2006

Table 1. Summary of published ecological information for the 19 described *Phylloidesmium* species.

CHAPTER 2. MATERIALS AND METHODS

2.1 Nudibranch collections

In Hawaii, we found *Phyllodesmium poindimiei* living in close association with *Carijoa riisei* on the islands of Oahu, Kauai and Maui. During the day, nudibranchs were very cryptic tending to hide at the bases of colonies, whereas at night they were observed actively crawling over the entire colony, and aggregating near the tips of polyps (Figure 1). Three sites on the island of Oahu were chosen as the primary study sites due to their contrasting environments and their large populations of *C. riisei* (Figure 2). The Hawaii Kai site (N 21° 17.108' W 157° 43.120') is located under a bridge in a sheltered, lagoon channel, in which *C. riisei* colonies grow on a variety of hard substrata shaded from direct sunlight in 0.5-3 m of water and are exposed to diurnal tidal currents. The YO-257 site (N 21° 15.633' W 157° 50.217') is a sunken ship in 24-30 m of water on which *C. riisei* grow on shaded metal surfaces. In the Shark's Cove site (N 21° 39.305' W 158° 03.807'), *C. riisei* grows in 9-15 m of water on the undersides of caves and shaded rocks. At each of these three sites the biomass of *C. riisei* to displace 2.0 liters of water, was collected in roughly monthly intervals for one year and the number of *P. poindimiei* individuals found within the coral were counted. Density measurements were made as point estimates, as no data on the variability of density at a given sample date was recorded. The body length of individual nudibranchs was measured to the nearest 5 mm while actively crawling as described by Folino (1993). For the Shark's Cove site, *P. poindimiei* densities across time were plotted against wave height and sea surface temperature data collected by the Waimea Bay Buoy (N 21° 39.970' W 158° 07.340') maintained by the University of Hawaii. Cross correlation analyses were performed using nudibranch density vs. average wave height on the date of nudibranch collection, and

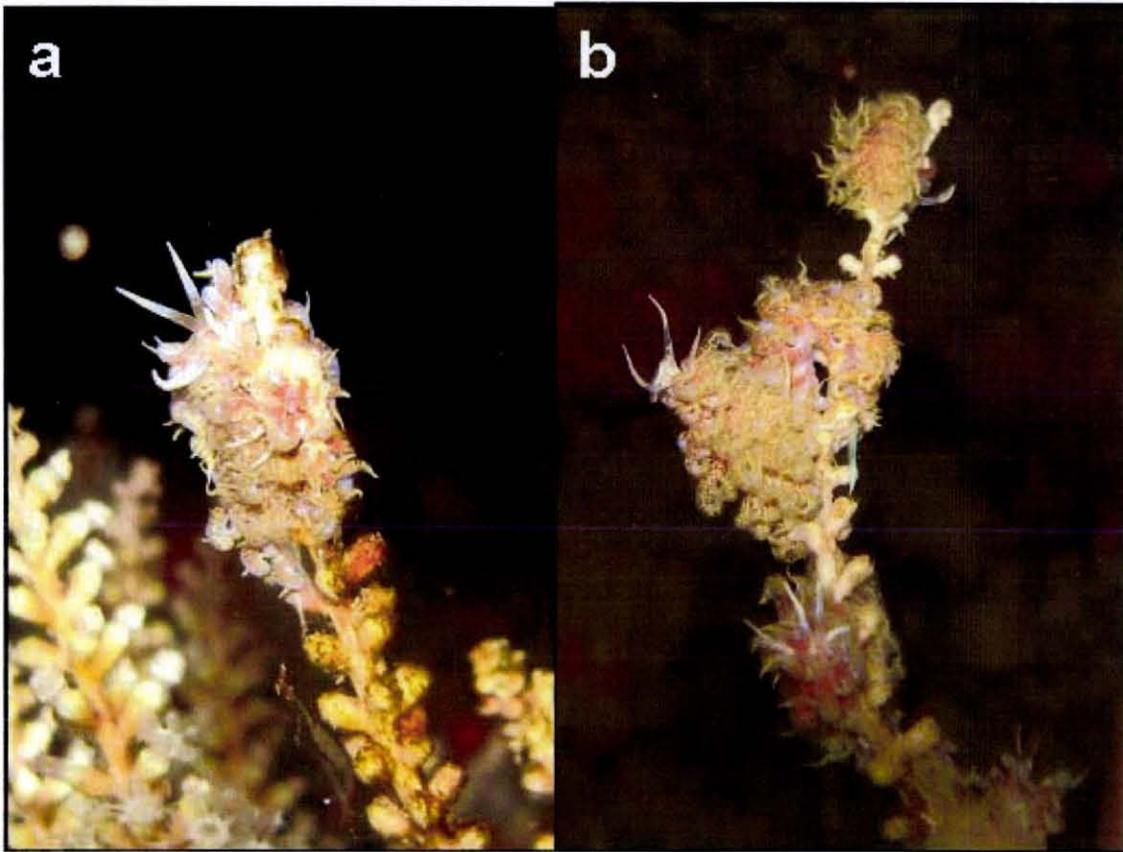


Figure 1a. *P. poindimiei* near tip of *C. riisei* polyp at night; **b.** *P. poindimiei* aggregation near tip of *C. riisei* polyp at night.

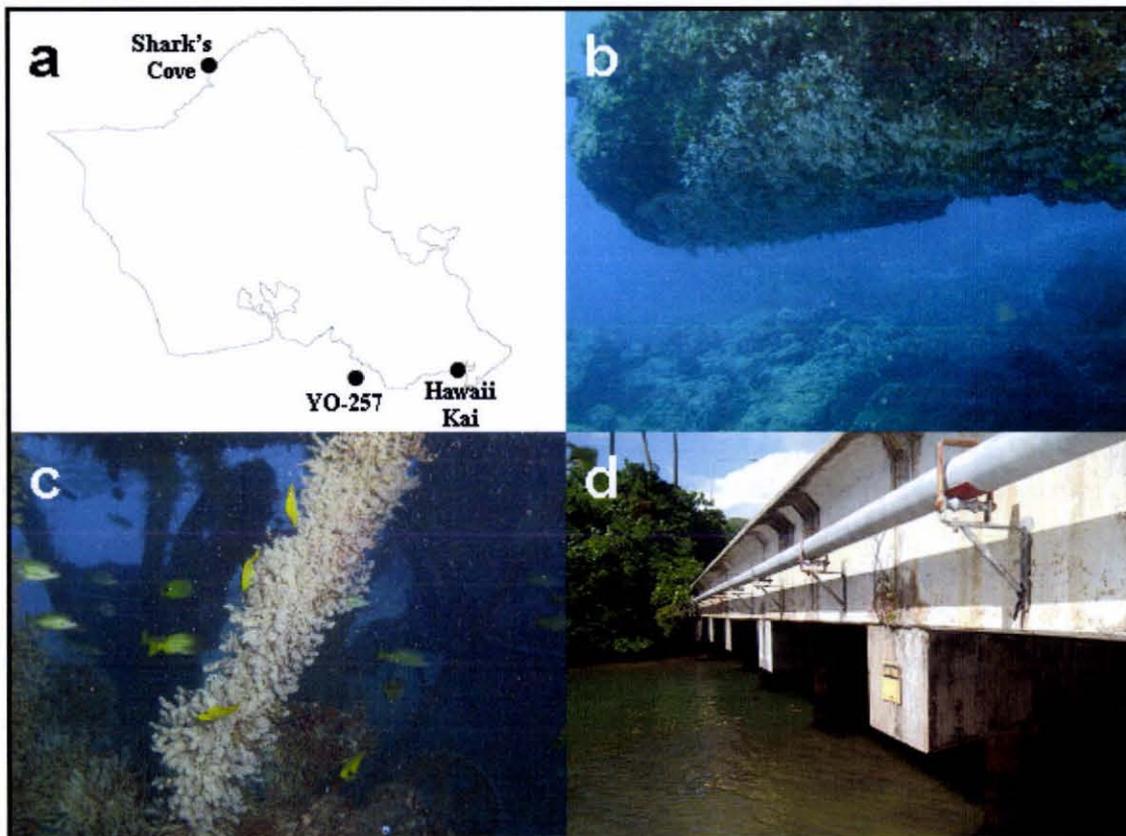


Figure 2a. Map of time-series study sites on Oahu, Hawaii; **b.** *C. riisei* growing on undersides of caves at Shark's Cove site; **c.** *C. riisei* growing on shaded metal surfaces at YO-257 site; **d.** Hawaii Kai site.

nudibranch density vs. average sea surface temperature on the date of nudibranch collection. For the YO-257 site, *P. poindimiei* densities across time were plotted against sea surface temperature data collected by the Kailua Buoy (21° 25.020' W 157° 40.630') maintained by the University of Hawaii. Cross correlation analyses were performed using nudibranch density vs. average sea surface temperature on the date of nudibranch collection. The collected nudibranchs were brought back to the Hawaii Institute of Marine Biology and used for a variety of experiments as described below.

2.2 Life history

10 pairs of *Phyllodesmium poindimiei* individuals of approximately similar size were isolated into aerated 9-liter aquaria and observed over time (Table 2). At roughly weekly intervals, the body length of individuals was measured as described above, and the number of egg masses found in each aquarium was recorded. The approximate number of egg masses laid per individual was calculated by dividing the number of egg masses found in each tank by the number of live individuals of that tank. Spawning was analyzed for lunar periodicity by converting each observation date to the nearest full moon (-14 to +14) and plotting the data against the lunar period as described by Kahng et al. (2008). Some of the egg masses were removed from aquaria using a pipette and observed under a Nikon SMZ-U binocular microscope to count the number of eggs per mass. Freshly laid egg masses were removed from aquaria using a pipette and placed into aerated 800mL beakers with filtered seawater (50 µm). In these, 100% water changes were performed daily and eggs were inspected using a Nikon SMZ-U binocular microscope. Once larvae hatched, these were daily fed Shellfish Diet 1800® (Instant Algae®, Reed Mariculture, 25% *Isochrysis*, 20% *Pavlova*, 20% *Tetraselmis*, 30% *Thalassiosira weissflogii*, 5% *Nannochloropsis*) at concentrations of

10,000cells/L, and daily water changes were performed. Larvae were kept in both the presence and absence of *C. riisei* fragments to see whether larvae would settle.

2.3 Feeding assays

2.3.1 Prey species preference

Species within the genus *Phyllodesmium* are specialized on feeding on octocorals (Rudman 1991, 1981). In Hawaii, only six octocoral species are reported in shallow-water: *Carijoa riisei*, *Sarcothelia edmonsoni* (Whitelegge 1897), *Simularia densa* (Verrill 1928), *S. molokaiensis* (Verseveldt 1983), *Acabaria bicolor* (Nutting 1908) and an undescribed brown soft coral from Maui (P. Alderslade and C. Pittman pers comm.); of these only *C. riisei*, *S. edmonsoni* and *S. densa* are relatively common (Hoover 2005; Fenner 2005). Due to difficulty obtaining source colonies of the rarer octocoral species (*S. molokaiensis* and *A. bicolor*), feeding assays were only performed with the more common ones (*C. riisei*, *S. edmonsoni* and *S. densa*). For each octocoral species, colonies were placed in both the presence (treatment) and absence (control) of adult *P. poindimiei* individuals and observed for any signs of coral tissue damage. For each experimental treatment 5 *P. poindimiei* individuals (30-35mm) were placed in an aerated 9-liter aquarium with an octocoral colony (25cm²). Control aquaria without the nudibranchs were set-up in the same manner. Every two days coral colonies were photographed, tissue damage was noted, and the nudibranchs were measured and inspected for reduction in size or autotomy of cerata (i.e. signs of starvation). Experiments lasted for a total of four weeks and were repeated in the same manner above described on a second occasion.

2.3.2 Feeding rates on *Carijoa riisei*

Phyllodesmium poindimiei suctorially feeds on *Carijoa riisei*, meaning that it sucks the tissue out of polyps without destroying the body wall (Figure 3). This mode of feeding allows for assessment of feeding rates by counting individual polyps based on their level of disintegration (Pratt and Garson 2007). After exposure to nudibranchs, polyps were scored as either preyed upon (intact body wall but missing polyp tissue) or intact (polyp full). Feeding rates of *P. poindimiei* on *C. riisei* were quantified as the number of polyps preyed upon over time and were then standardized to nudibranch size as described above. Individual nudibranchs were placed into separate aerated 800 mL beakers with a 6 cm fragment of *C. riisei* selected to have similar number and size of lateral polyps. The number of polyps preyed upon was recorded every two days, at which time *C. riisei* fragments were replaced with fresh specimens.

2.3.3 Feeding rates on sponge overgrown *Carijoa riisei*

A number of sponges are frequently observed overgrowing *Carijoa riisei* in Hawaii. Feeding rates of *Phyllodesmium poindimiei* (30-35mm) were measured as described above, but with sponge overgrown fragments of *C. riisei*. Four different sponges that are frequently observed on Oahu were used during the trials (Figure 4). For these assays *C. riisei* fragments were chosen in which live polyps were almost completely surrounded by overgrowing sponge.

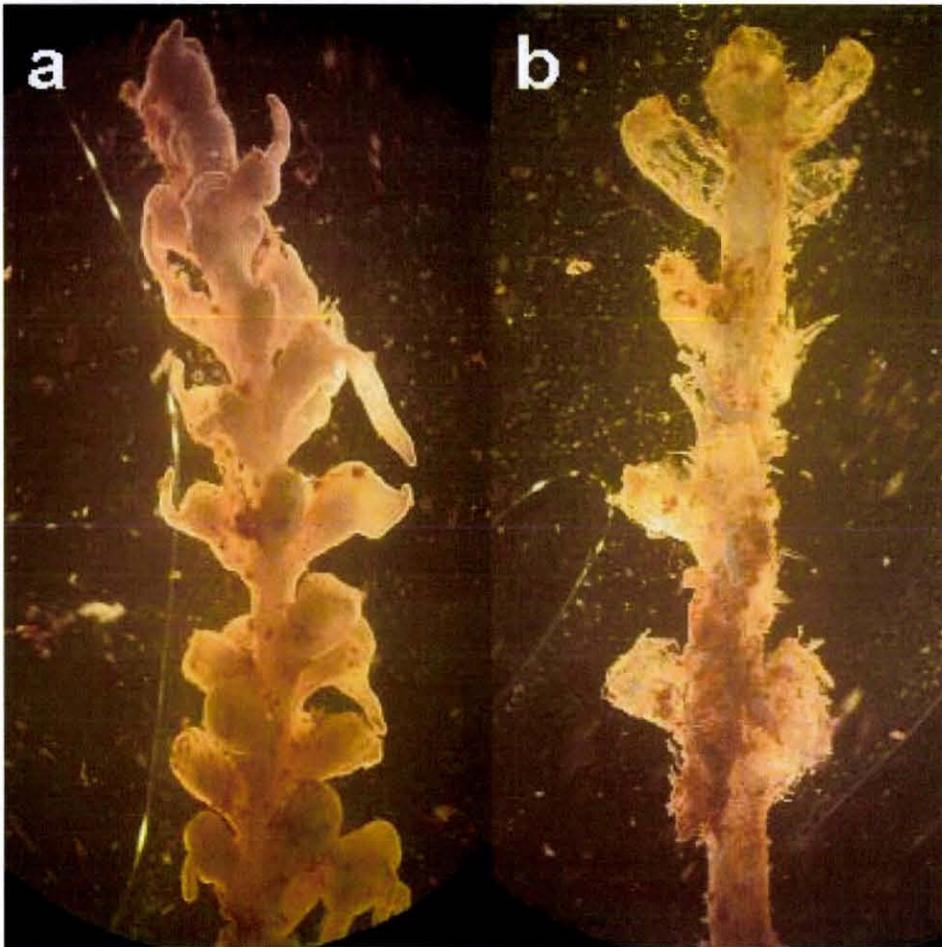


Figure 3a. *C. riisei* fragment before being exposed to *P. poindimiei* predation; **b.** *C. riisei* fragment 48 hours after exposure to *P. poindimiei* predation.

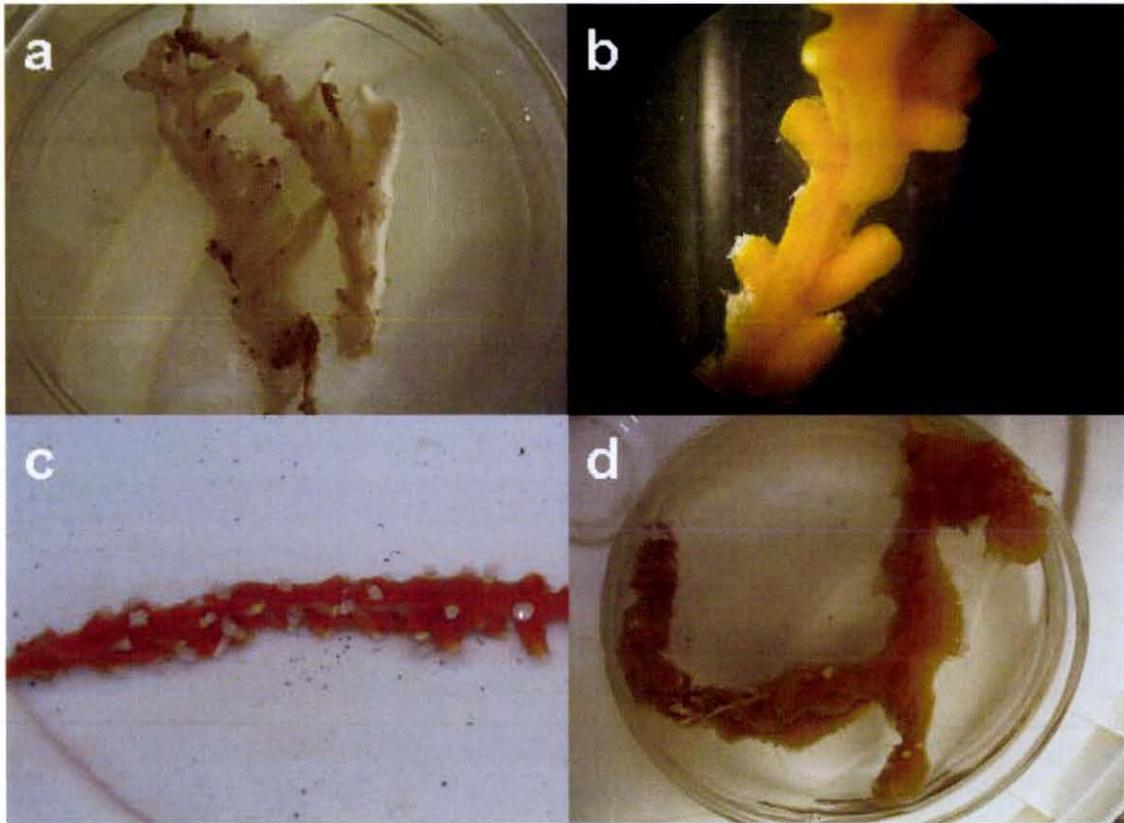


Figure 4. *C. riisei* epizoic sponges; **a.** white sponge; **b.** yellow sponge; **c.** red sponge; **d.** grey sponge.

2.4 Predators

Fish fauna commonly found near *Carrizoa riisei* colonies in the field were tested as potential predators of *Phyllodesmium poindimiei*. Assays were performed at the YO-257 field site. Fish were attracted using pieces of bread and then offered live *P. poindimiei*. Fish species that mouthed *P. poindimiei* were noted and observed for regurgitation of the nudibranchs. Based on initial observations, laboratory assays were subsequently performed with the butterflyfish *Forcipiger longirostris* (Broussonet 1782) and *F. flavissimus* (Jordan and McGregor 1898), which are the dominant browsers among large *C. riisei* aggregations; and the portunid crab *Thalamita integra* Dana 1852, which is commonly found within *C. riisei* colonies. Three adults of each of the two butterflyfish species and the crab species were kept in separate tanks and fed frozen clams once a day. While feeding, pieces of *P. poindimiei* (cerata, mantle and viscera) were mixed in with slices of clams. The animals were observed for consumption or uptake and regurgitation of *P. poindimiei* pieces. Additionally live individuals of *P. poindimiei* were placed in tanks with *F. longirostris*, *F. flavissimus*, and *T. integra* and the nudibranchs were observed daily for any signs of attacks (i.e. missing body parts or nudibranchs).

CHAPTER 3. RESULTS

3.1 Nudibranch densities across time

The densities of *Phyllodesmium poindimiei* were significantly different among the three sites (Kruskal Wallis: $H = 6.71$, $p = 0.035$). However, measurements represent point estimates as no data on the variability of density within a sample site was recorded for a given date. At the Hawaii Kai site, densities were continuously low and did not appear to follow any patterns (Figure 5). At the YO-257 site, densities fluctuated more, but these fluctuations did not coincide temporally to seasonal fluctuations in sea surface temperature (Figure 6). No statistically significant cross correlations were recorded at any lag phase between sea surface temperature and nudibranch density (highest correlation at lag phase 5= 0.612). However, cross correlation analysis assumes that data is collected in uniform time intervals, which was not done at the YO-257 site. Therefore results of the analysis should be interpreted with caution. For the Shark's Cove site, densities were highest in the summer (May-September) and lowest during the winter. The high nudibranch densities in the summer roughly coincided with periods of reduced wave height, elevated sea surface temperature (Figure 7a and 7b), and increases in *C. riisei* biomass. The low nudibranch densities in the winter roughly coincided with periods of elevated wave height, reduced sea surface temperature (Figure 7a and 7b), and decreases in *C. riisei* biomass. No statistically significant cross correlations were recorded at any lag phase between sea surface temperature and nudibranch density (highest correlation at lag phase 2= 0.637), or wave height and nudibranch density (highest correlation at lag phase 2= -0.652). The cross correlation assumption of equal periods between data points was violated at the Shark's Cove site, and hence results of the analysis should be interpreted with caution.

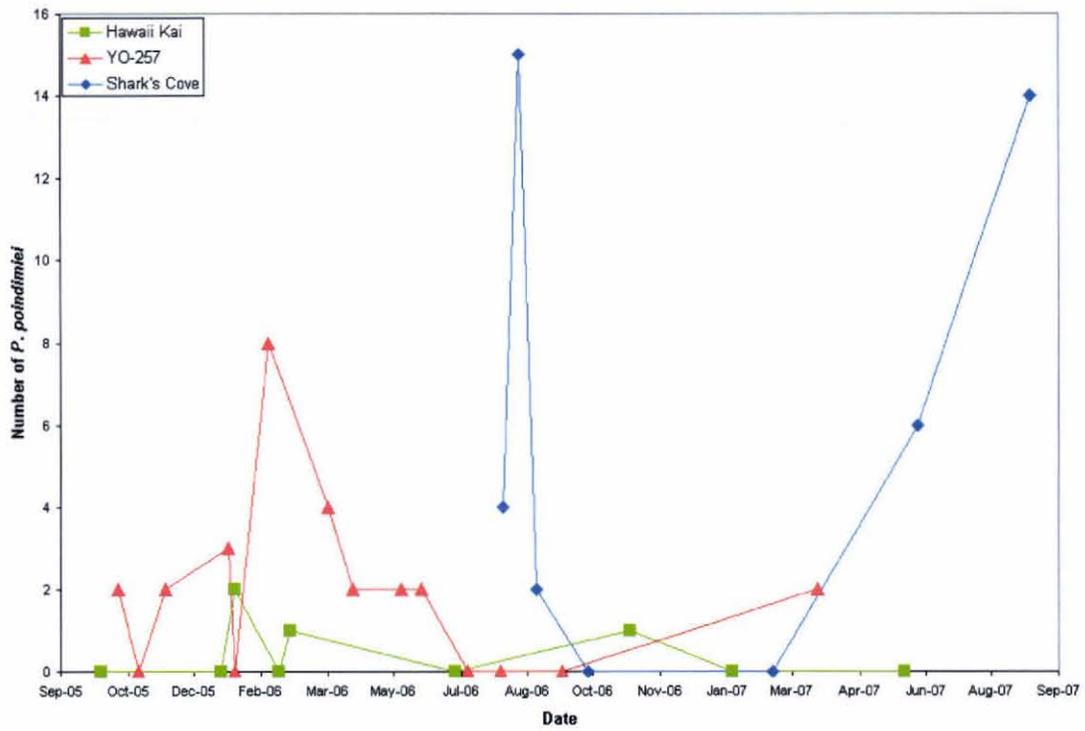


Figure 5. Time-series *P. poindimiei* densities at study sites. *P. poindimiei* densities were recorded by counting number of individuals found within *C. riisei* biomass to displace 2.0 liters of water.

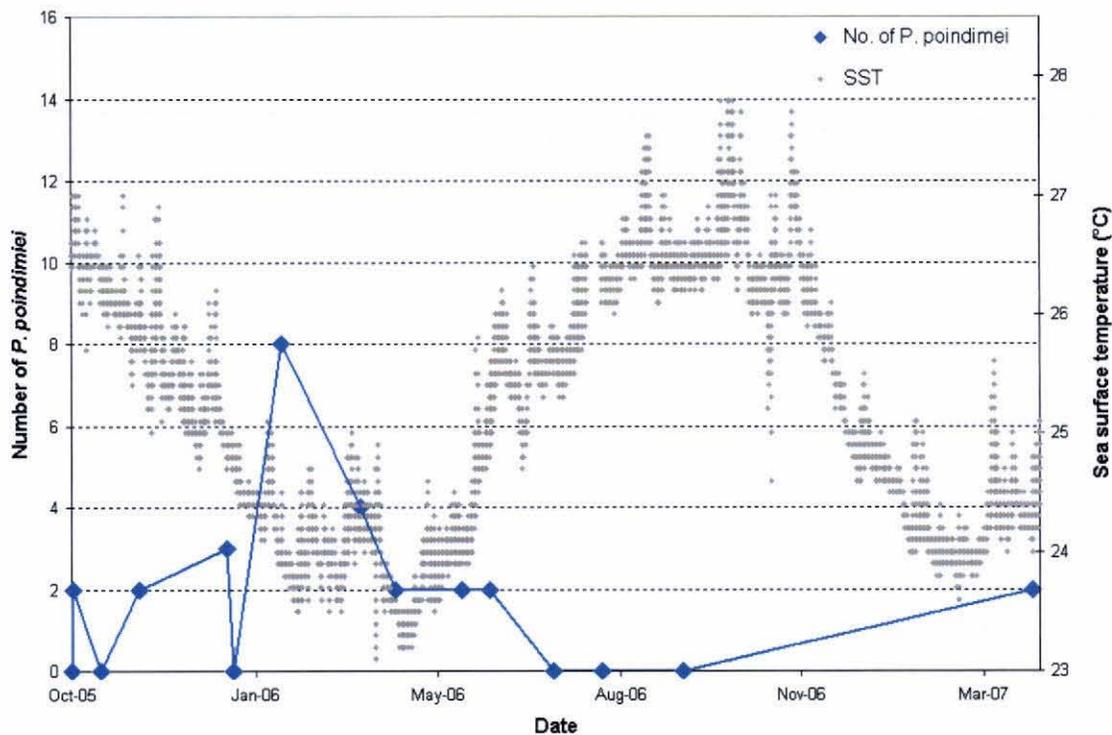


Figure 6. Time-series *P. poindimiei* density at YO-257 site and sea surface temperature at Kailua buoy. *P. poindimiei* densities were recorded by counting number of individuals found within *C. riisei* biomass to displace 2.0 liters of water.

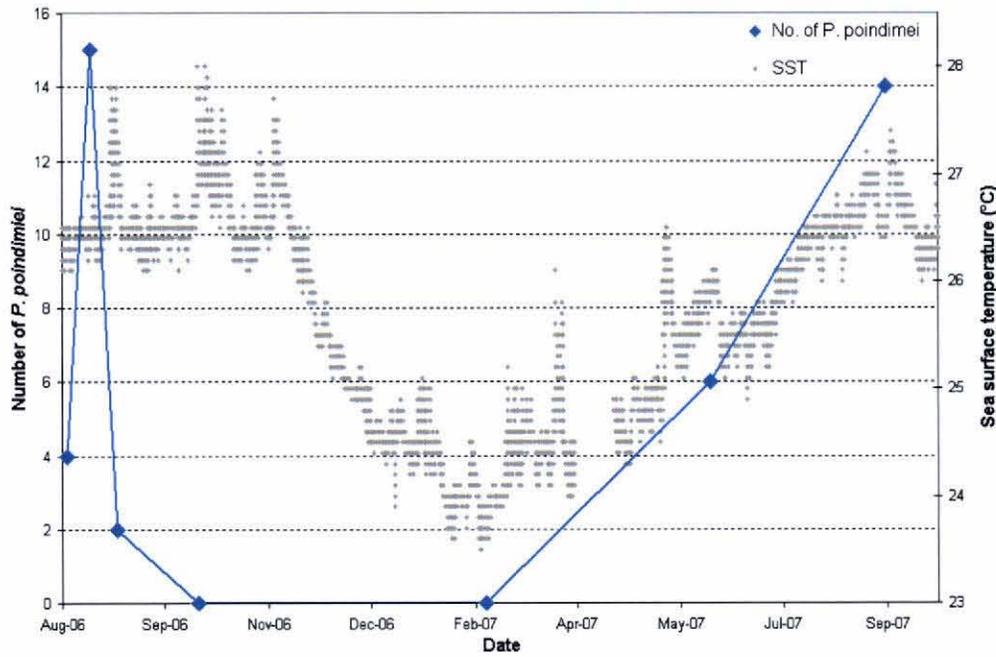
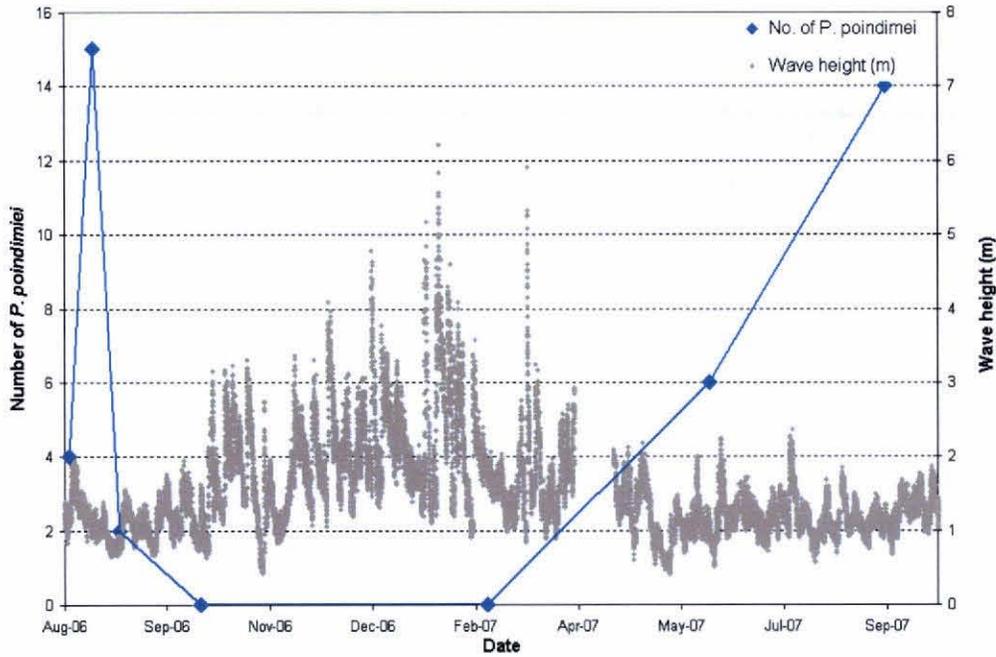


Figure 7a. Time-series *P. poindimiei* density at Shark’s Cove site and wave height at Waimea buoy; **b.** Time-series *P. poindimiei* density at Shark’s Cove and sea surface temperature at Waimea buoy. *P. poindimiei* densities were recorded by counting number of individuals found within *C. riisei* biomass to displace 2.0 liters of water.

3.2 Life history

In the laboratory *Phyllodesmium poindimiei* deposited egg masses on the glass of aquaria (Figure 8a and 8b) or on the surface of *Carijoa riisei* colonies (Figure 8c).

Oviposition was observed only after animals reached a minimum body length of 15 mm. The maximum number of egg masses laid by one individual was 16 with a mean of 6 (\pm 5.3 SD) (Table 2). Egg masses were found continuously throughout the study with no evidence of any lunar periodicity (one-way ANOVA $p=0.873$). In no case did death of individuals immediately follow oviposition, and individuals lived for up to 79 days after the last egg mass was laid.

Egg masses were white to opaque, and eggs were deposited in single sheets (Figure 8b). Individual egg capsules were \sim 100 μ m at oviposition. The number of eggs per egg mass ranged from 6,750-11,260. Eggs hatched 5-6 days after oviposition, giving rise to free-swimming veligers (Figure 8d and 8e), which were observed ingesting individual phytoplankton cells on multiple occasions under the microscope. The free-swimming larvae remained in motion for up to 13 days after hatching, at which time the veligers measured \sim 150-156 μ m. In no case did larvae settle or metamorphose. *P. poindimiei* remained alive in the laboratory for up to 318 days with a mean of 122 days (\pm 77.3 days SD) (Table 2). Note that *P. poindimiei* were collected from the field as post juveniles of unknown age, and therefore total nudibranch longevity is higher than the above values. Most of the animals showed reductions of body length (shrinking from 5-15 mm over 3 weeks) and autotomy of cerata prior to death.

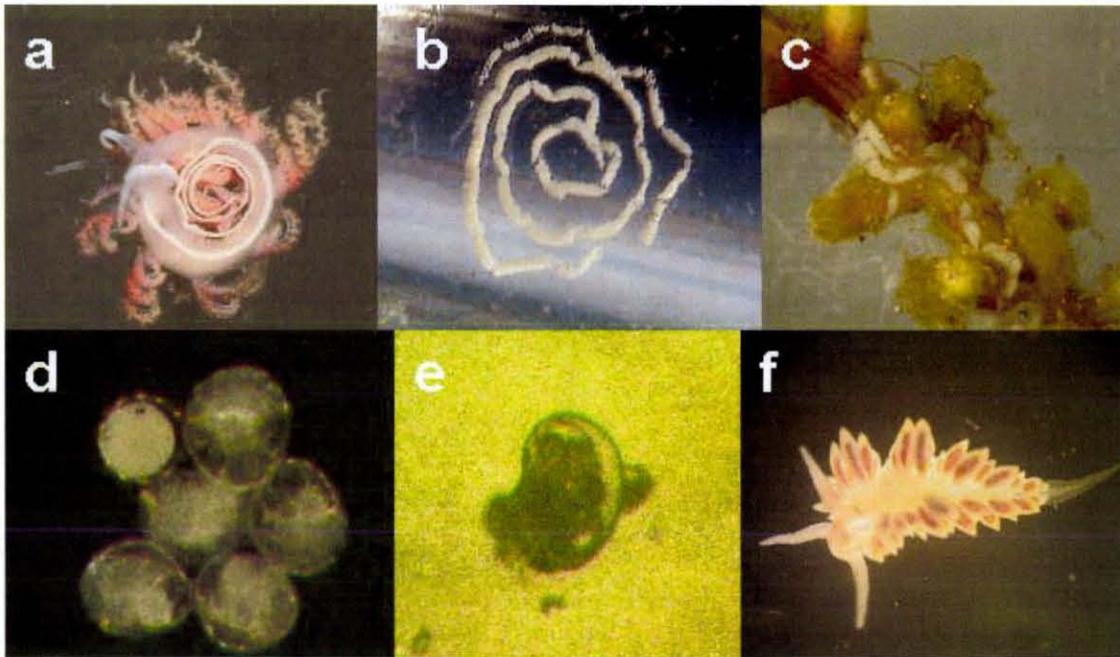


Figure 8a. *P. poindimiei* adult (35mm) laying eggs in tank; **b.** *P. poindimiei* egg mass on glass of tank (d=15mm); **c.** *P. poindimiei* egg mass on *C. riisei* **d.** *P. poindimiei* larvae 6 days after oviposition (115-122 μm); **e.** *P. poindimiei* larvae 7 days after oviposition (122 μm); **f.** *P. poindimiei* juvenile (5 mm).

Tank ID	Initial size (mm)	Final size (mm)	Longevity (days)	Egg masses laid
1	5	10	209	0
	5	5	18	0
2	5	5	6	0
	10	10	110	0
3	10	15	272	12
	10	15	134	11
4	10	30	318	12
	10	5	100	11
5	10	40	201	6
	10	15	152	6
6	15	20	114	2
	15	10	93	2
7	15	10	114	2
	20	20	65	2
8	20	5	100	8
	20	10	93	8
9	25	15	114	16
	25	10	93	16
10	30	20	65	5.5
	30	20	65	5.5

Table 2. Longevity and fecundity for 10 pairs of *P. poindimiei* kept in separate tanks.

3.3 Feeding assays

3.3.1 Prey species preference

In both experimental trials with *Carijoa riisei* all 5 *Phyllodesmium poindimiei* adults survived. Abundant tissue damage was recorded on polyps of the experimental *C. riisei* colony, whereas none was ever observed in the control colony. Tissue damage was noted exclusively on polyps of *C. riisei*, whereas the body wall and stolons remained intact. In contrast, no signs of *P. poindimiei* predation were observed in trials with *Simularia densa* and *Sarcothelia edmonsoni*, and the nudibranchs showed progressive signs of starvation including reduction in body size, autotomy of cerata and eventually death. For assays with *S. densa* and *S. edmonsoni*, all *P. poindimiei* apparently starved after 20-28 days and 14-20 days respectively.

3.3.2 Feeding rates on *Carijoa riisei*

Phyllodesmium poindimiei individuals exhibited an initial positive relationship between body length and feeding rate on *Carijoa riisei* that eventually reached an asymptote at ~35mm (Figure 9). In no case was *C. riisei* tissue damage observed for *P. poindimiei* individuals of the smallest size class (5mm), however only few observations were made for this class (n=4).

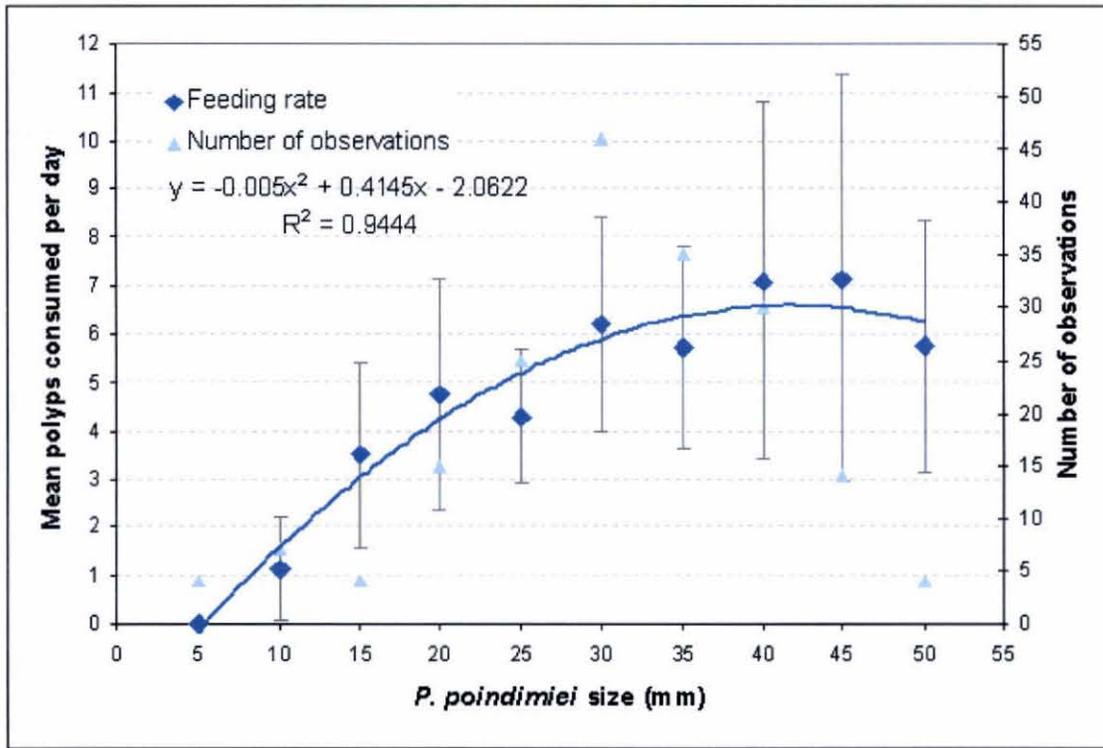


Figure 9. Feeding rate vs. size of *P. poindimiei*. Error bars represent standard deviations. Feeding rates were measured in the laboratory.

3.3.3 Feeding rates on sponge overgrown *Carijoa riisei*

The feeding rates of *Phyllodesmium poindimiei* adults on *Carijoa riisei* fragments overgrown by the different sponges were all significantly lower than on sponge-free *C. riisei* (all t-tests with overall Bonferroni error rate of 0.05: $p < 0.001$) (Figure 10). However, sponge cover did not completely suppress *P. poindimiei* predation, because feeding was still observed but at much lower rates. In general predation occurred on portions of *C. riisei* polyps with lowest sponge cover. These assay results were consistent with observations in the field, where *P. poindimiei* individuals were only observed on sponge free *C. riisei* and never on colonies that had substantial sponge overgrowth.

3.4 Predators

No fish species were observed to consume *Phyllodesmium poindimiei* in field assays. *Chaetodon miliaris* (Quoy and Gaimard 1825), *Lutjanus kasmira* (Forsskål 1775), *Thalassoma duperrey* (Quoy and Gaimard 1824), *Forciper longirostris* and *F. flavissimus* all mouthed but did not consume the nudibranchs. In the laboratory assays with *F. longirostris* and *F. flavissimus*, these fish species bit on nudibranchs on several occasions but quickly spat them back out and then avoided other pieces of food. Additionally there was no evidence of attacks when *F. longirostris* and *F. flavissimus* were left in tanks with *P. poindimiei*. In contrast, *Thalamita integra* did consume pieces and whole *P. poindimiei* individuals. These crabs readily attacked *P. poindimiei* in tanks and were never observed regurgitating after consuming the nudibranchs.

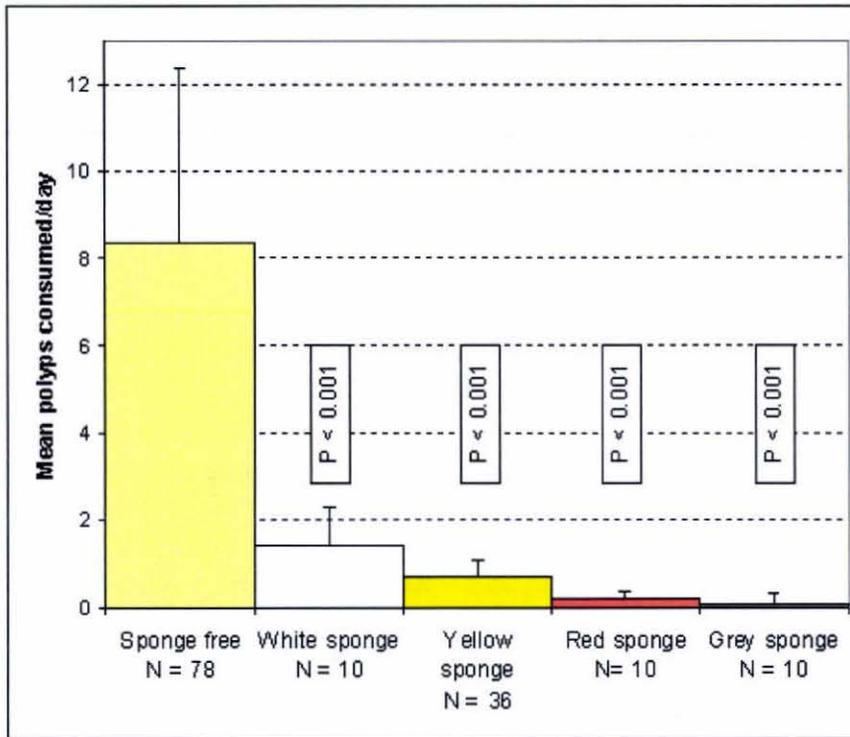


Figure 10. Feeding rate of *P. poindimiei* on *C. riisei* overgrown by various epizoic sponges. Error bars represent standard deviations. Feeding rates were measured in the laboratory. All feeding rates on sponge overgrown *C. riisei* were significantly different from sponge free *C. riisei* (all 2 sample t-tests $p < 0.001$).

CHAPTER 4. DISCUSSION

The presented data provide evidence that *Phyllodesmium poindimiei* is a specialized predator on *Carijoa riisei*, because individuals perished in the absence of *C. riisei* even when offered alternative prey. These results are consistent with previous reports of *P. poindimiei* in southern Australia, which associate exclusively with *Carijoa* sp. (Rudman 1981, 1991). Furthermore, the obligate association between *P. poindimiei* and *C. riisei* suggest that *P. poindimiei* likely followed its octocoral prey in colonizing Hawaii. Interestingly, *C. riisei* predation was not observed for the smallest *P. poindimiei* (5 mm) individuals (Figure 9), even though these were found in association with *C. riisei* both in the field and in the laboratory. These results suggest that the feeding rates of small juveniles is either so minimal that it remained undetected with the above described methodology, or that juveniles subsist on an alternate food source before switching to *C. riisei* at a larger size. Ontogenetic prey switching is common among many marine animals including the Nudibranchia (Perron and Turner 1977; Nybakken and McDonald 1981; Bickell and Kempf 1983; Chia and Koss 1988). Prey switching makes sense from a mechanical perspective, because small juveniles often lack the full development of the feeding structures required to prey on the adult prey (Hadfield 1963; Nybakken and McDonald 1981), as well as from an evolutionary perspective, because it reduces intraspecific competition among different sized conspecifics.

Observations of *P. poindimiei* larvae are consistent with planktotrophic development. The diameter of individual eggs at the time of oviposition (~100 μm) is similar to those observed for other nudibranch species with planktotrophic development (e.g. Todd and Doyle 1981; Todd 1983). Additionally, developing larvae were observed ingesting individual phytoplankton on several occasions under the microscope. Veligers remained in the free

swimming stage for up to 13 days, which is roughly comparable to 20 days reported for the congeneric *P. hyalinum* (= *P. xenidae*) (Gohar and Aboul-Ela 1959; Hadfield 1963; Soliman 1987). Unfortunately, as in studies with *P. hyalinum* (Gohar and Aboul-Ela 1959), settlement and metamorphosis was not observed during this study. The lack of settlement and metamorphosis in the laboratory might have been caused by absence of necessary settlement cues. Larvae were raised in both the presence and absence of *C. riisei* fragments without successful settlement. The adult food source has been reported as a settlement cue for a number of nudibranch larvae (Bonar and Hadfield 1974; Harris 1975; Perron and Turner 1977; Chia and Koss 1978; Arkett et al. 1989). However, it has also been argued that metamorphic induction by the adult prey organism would be detrimental in cases where larvae are so small that they run the risk of being ingested by the animals which will eventually become their prey, because this would mean that larvae are chemically attracted to their predators (Hadfield 1963). In this latter case, alternative intermediate settlement substrates have been proposed (Hadfield 1963). The size of *P. poindimiei* larvae is consistent with the size range of zooplankton found in gut content analyses of *C. riisei* (Kahng 2006). Therefore if *P. poindimiei* larvae were indeed chemically attracted to *C. riisei* for settlement cues, the larvae would run the risk of being ingested by *C. riisei* prior to settlement and metamorphosis. *P. poindimiei* juveniles were not observed to actively feed on *C. riisei* (Figure 9), suggesting that juveniles subsist on an alternate food source before switching to *C. riisei* at a larger size. If juveniles have an alternative prey to *C. riisei*, such results would be consistent with settlement on an alternate substrate.

There does not appear to be any lunar pattern in spawning periodicity of *P. poindimiei* (one-way ANOVA $p=0.873$). Furthermore, egg masses were found both in the

laboratory and in the field throughout the year indicating that spawning occurs year round for this species. Egg masses analyzed in this study contained between 6,750-11,260 eggs that hatched 5-6 days after oviposition. Gohar and Aboul-Ela (1959) report between 8,600-11,200 individual eggs in egg masses of *P. hyalinum* (= *P. xeniae*), which hatched 4 days after oviposition. An egg hatching time of 5-6 days is also reported for *P. jakobsenae* (Burghardt and Waegele 2004).

The life cycles of several nudibranch species are related to the availability of their prey (Miller 1962; Thompson 1976; Eyster 1981; Todd 1981). In Hawaii, the octocoral *C. riisei* has been described as being abundant year-round and forming part of the climax community that dominates favorable habitat after succession of other fouling organisms (Thomas 1979). However, significant fluctuations in biomass have been observed in shallow water populations due to large rainfall events or seasonal changes in wave energy (Kahng 2006). After collection from the field, *P. poindimiei* individuals survived between one and more than 10 months, suggesting that this species is capable of having an annual life cycle. The field density measurements of *P. poindimiei* indicate different population cycles among the sites (Figure 5). No data was collected on the density variability at a given sample date, and hence density differences might represent differences in the patchiness of nudibranchs among sites or sampling periods. At the YO-257 and Hawaii Kai study sites *P. poindimiei* densities were relatively low throughout the year. In contrast, at the Shark's Cove site nudibranch densities were highest in the summer and lowest in the winter. These trends coincided temporally with variability of sea surface temperature and wave height. Consistent with observations made during this study, previous research at the site indicates that *C. riisei* biomass fluctuates seasonally, with highest biomass observed in the summer and lowest

biomass in the winter when large swells remove *C. riisei* from the substrata (Kahng 2006). Thus, *P. poindimiei* densities and *C. riisei* biomass appear to be related at the Shark's Cove site, suggesting a relationship between nudibranch densities and the biomass of their prey. The site is located in relatively shallow water (9-15m) and therefore is impacted by the large differences in wave energy between summer and winter months. In contrast, the Hawaii Kai site is located in a sheltered lagoon with very low wave energy throughout the year. While previous research at the Hawaii Kai site has revealed reductions of *C. riisei* biomass after large rainfall events (Kahng 2006), these were not observed in the time period of this study. *C. riisei* biomass was relatively constant throughout the study. Consistent with this, *P. poindimiei* densities did not show any large temporal fluctuations (Figure 5). The YO-257 site is located deeper than the other sites (24-30m), and benthic communities are therefore less likely impacted by seasonal fluctuations of wave height or rainfall events. Consistent with this, no large fluctuations of *C. riisei* biomass was observed at the site as part of this study.

Nudibranchs possess elaborate defensive strategies including aposematic coloration, autotomy, camouflage, mimicry, crypsis and nocturnal activity (Thompson 1976; Todd 1981; Behrens 2005). These elaborate defensive mechanisms suggest that visual predation has been an important factor in the evolution of nudibranch defensive strategies (Harris 1987). Morphological and/or behavioral adaptations that are discussed in the published literature as possible defensive mechanisms of *Phyllodesmium* include autotomy, camouflage, crypsis and nocturnal activity (Gohar and Aboul-Ela 1957; Slattery et al. 1998; Burghardt and Gosliner 2006), which were all observed for *P. poindimiei* during this study. However, such

discussions of defense mechanisms of *Phyllodesmium* are mostly hypothetical for there are very few observations of animals preying on these nudibranchs (Rudman 1981). The few exceptions are feeding experiments with *P. guamensis*, which suggest that different fish species prey on or avoid this nudibranch species (Slattery et al. 1998), and a sole observation of *P. serratum* being ingested by *Octopus vulgaris* in False Bay, South Africa (Smith 2003). The results of this study exposed at least one potential predator of *P. poindimiei*, the portunid crab *Thalamita integra*. The crab was observed ingesting both pieces and whole individuals of *P. poindimiei* in laboratory studies. This crab was frequently observed living directly within *C. riisei* colonies in the field, particularly at the Hawaii Kai site, perhaps helping to explain the lower nudibranch densities observed at the site (Figure 5). In Hawaii, fish and crustacean predators have been identified for the corallivorous aeolid nudibranch *Phestilla sibogae*, and proposed as factors explaining the lack of strong impacts of the nudibranch on its coral prey in the field (Gochfeld and Aeby 1997). The fish species *Thalassoma duperrey*, *T. ballieui* and *Chaetodon auriga*, the crab species *Pilodius aerolatus*, *Phymodius monticulosus* and *Thalamita* sp., and the stomatopod *Gonodactylus falcatus* are reported as predators of the nudibranch *P. sibogae* (Gochfeld and Aeby 1997). Gochfeld and Aeby propose that nudibranch predation by fish outside coral colonies, in combination with crustacean predation inside coral colonies, may control populations of *P. sibogae* (1997).

The fish species *Chaetodon miliaris*, *Lutjanus kasmira*, *Thalassoma duperrey*, *F. longirostris* and *F. flavissimus* all mouthed *P. poindimiei* individuals, then quickly proceeded to spitting them out, suggesting that *P. poindimiei* is distasteful or defended. The incorporation of diet derived secondary metabolites for defensive purposes has been reported for *P. longicirra* (Coll et al. 1985; Sammarco and Coll 1992; McClintock et al. 1994,

Gavagnin and Fontana 2000) and *P. guamensis*. (Slattery et al. 1998; Gavagnin and Fontana 2000). Both of these *Phylloidesmium* species possess highest concentrations of the secondary metabolites in the cerata, as opposed to other body parts, which indicates potential defensive uses, as cerata are more exposed to predation.

While the results of this study only exposed one predator of *P. poindimiei* in Hawaii, predation may be an important factor in controlling the abundance of these nudibranchs. In August of 2006, high *P. poindimiei* densities (16) were recorded at the Shark's Cove site (Figure 5), and evidence of predation was noted on *C. riisei* colonies. The site was revisited 10 days after, and a much lower *P. poindimiei* density (2) was recorded. While movement of individuals away from the site cannot be ruled out, the reduction in densities may have been caused in part by nudibranch predation.

Species of the octocoral genus *Carijoa* (= *Telesto*) have frequently been observed associated with a number of sponges (Calcinai et al. 2004). Sponges are well known to deter predation by a number of marine predators (Chanas et al. 1996; Becerro et al. 2004). Previous studies of the relationship between *C. riisei* and the demosponge *Desmapsamma anchorata* in Indonesia revealed that sponge covering protected *C. riisei* from predation by ovulids and nudibranchs (Calcinai et al. 2004). Both of these predators were sometimes observed on *C. riisei* colonies that were not covered by *D. anchorata*, but not on *C. riisei* overgrown by the sponge. The nudibranchs observed during that study were not described; however they were not *P. poindimiei* (B. Calcinai pers. comm.). In Hawaii a number of different sponges are associated with *C. riisei* and sponge overgrowth can occur in large portions of *C. riisei* biomass, especially in shallow-water (Kahng 2006). The presented data

provide evidence that various sponges protect *C. riisei* from *P. poindimiei* predation, because the feeding rates of *P. poindimiei* on sponge overgrown *C. riisei* were significantly lower than those on sponge free *C. riisei* (all t-tests with overall Bonferroni error rate of 0.05, $p < 0.001$). Thus sponge overgrowth provides *C. riisei* a refuge from nudibranch predation. This has important implications for the potential use of *P. poindimiei* as a biocontrol agent against *C. riisei*, as biocontrol is most efficient when there is little refuge of the target species (Hawkins et al. 1993; Murdoch and Briggs 1996).

Another form of predation refuge arises from the fact that *P. poindimiei* adults were only observed preying on fleshy polyps of *C. riisei* and not on stolons or the body wall of the octocoral (see above). When *C. riisei* colonies were kept in aquaria with high *P. poindimiei* densities, most of the *C. riisei* polyps disappeared fairly rapidly, eventually leading to the starvation of *P. poindimiei* individuals. Stolons were always left behind in aquaria even after large predation events, which eventually regenerated giving rise to new polyps and colonies. These observations are consistent with studies of other aeolid nudibranchs that suggest that these are often partial predators (see Harris 1987).

CHAPTER 5. CONCLUSION

Since its initial discovery in 1966, *Carijoa riisei* has rapidly spread and proliferated throughout the Main Hawaiian Islands (Kahng and Grigg 2005; Kahng and Kelley 2007; Kahng et al. 2008). The specialized association between *P. poindimiei* and *C. riisei* (Rudman 1981, 1991), and the fact that *P. poindimiei* populations are already established in Hawaii (Wagner et al. 2007), make this nudibranch a logical candidate for an augmentative biocontrol agent of *C. riisei* in Hawaii. Ideally biocontrol agents should be host specific in order to minimize impact on non-target species, and maximize damage to the target pest species (Murdoch and Briggs 1996; Secord 2003; Sax et al. 2005). The results of this study indicate that *P. poindimiei* is a specialized *C. riisei* predator. However, several factors appear to limit the effectiveness of *P. poindimiei* at controlling *C. riisei* and hence its applicability as a biocontrol agent: (1) *P. poindimiei* has a planktotrophic larval phase, which might disperse larvae away from their parents, and hence away from local *C. riisei* populations; (2) there is at least one natural predator of *P. poindimiei* in Hawaii, and hence artificial augmentation of *P. poindimiei* populations can be counteracted by predation on this nudibranch; (3) epizoic sponges provide *C. riisei* with an effective predation refuge, and consequently portions of *C. riisei* populations that are sponge overgrown, which are typically abundant in shallow water (Kahng 2006), cannot be controlled through nudibranch predation; (4) *P. poindimiei* predation on *C. riisei* is incomplete as portions of *C. riisei* colonies (i.e. stolons) are left unharmed after nudibranch predation. Thus *C. riisei* is able to regenerate even after large predation events. These factors taken together indicate that *P. poindimiei* would be a poor biocontrol agent, and hence biocontrol of *C. riisei* using *P. poindimiei* should not be pursued.

REFERENCES

- Arkett SA, Chia FS, Goldberg JI & Koss R (1989). Identified settlement receptor cells in nudibranch veligers respond to specific cue. *Biological Bulletin* 176: 155-160.
- Avila C, Ballesteros M, Slattery M, Starmer J & Paul VJ (1998). *Phyllodesmium guamensis* (Nudibranchia: Aeolidioidea), a new species from Guam (Micronesia). *Journal of Molluscan Studies* 64: 147-160.
- Baba K (1991). The anatomy of *Phyllodesmium serratum* (Baba, 1949) from Japan (Nudibranchia: Facelinidae). *Venus* 50(2): 101-108.
- Baba K (1991b). Taxonomical study of some species of the genus *Phyllodesmium* from Cape Muroto-misaki, Shikoku, and Okinawa Province, Southern Japan (Nudibranchia: Facelinidae). *Venus* 50(2): 109-124.
- Bayer FM (1961). The shallow-water Octocorallia of the West Indian Region. A manual for marine biologists. In *Studies on the fauna of Curacao and other Caribbean Islands* (eds. PW Hummenlinck and LJ van der Steen), pp. 1-373. Uitgaven van de Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen , no. 23. The Hague: Martinus Nijhoff.
- Becerro MA, Thacker RW, Turon X, Uriz MJ & Paul VJ (2004). Biogeography of sponge ecology: comparisons of tropical and temperate defenses. *Oecologia* 135(1): 91-101.
- Behrens DW (2005). Nudibranch behavior. New World Publications, Inc. Jacksonville, FL, 176pp.
- Bertsch H & Johnson S (1981). Hawaiian nudibranchs. Oriental Publishing Company, Honolulu, HI, 112pp.
- Bickell LR & Kempf SC (1983). Larval and metamorphic morphogenesis in the nudibranch *Melibe leonine* (Mollusca: Opisthobranchia). *Biological Bulletin* 165: 119-138.
- Bonar DB & Hadfield MG (1974). Metamorphosis of the marine gastropod *Phestilla sibogae* Bergh (Nudibranchia: Aeolidacea). I. Light and electron microscope analysis of larval and metamorphic stages. *Journal of Experimental Marine Biology and Ecology* 16: 227-255.
- Burghardt I & Wägele H (2004). A new solar powered species of the genus *Phyllodesmium* Ehrenberg, 1831 (Mollusca: Nudibranchia: Aeolidioidea) from Indonesia with analysis of its photosynthetic activity and notes on biology. *Zootaxa* 596: 1-18.
- Burghardt I & Gosliner TM (2006). *Phyllodesmium rudmani* (Mollusca: Nudibranchia: Aeolidioidea), a new solar powered species from the Indo-West Pacific with data on its symbiosis with zooxanthellae. *Zootaxa* 1308: 31-47.

Burn R (2006). A checklist and bibliography of the Opisthobranchia (Mollusca: Gastropoda) of Victoria and the Bass Strait area, south-eastern Australia. *Museum Victoria Science Reports* 10: 1-42.

Calcinai B, Bavestrello G & Cerrano C (2004). Dispersal and association of two alien species in the Indonesian coral reefs: the octocoral *Carijoa riisei* and the demosponge *Desmapsamma anchorata*. *Journal of the Marine Biological Association of the United Kingdom* 84: 937-941.

Chanas B, Pawlik JR, Lindel T & Fenical W (1996). Chemical defense of the Caribbean sponge *Agelas clathrodes* (Schmidt). *Journal of Experimental Marine Biology and Ecology* 208: 185-196.

Chia FS & Koss R (1978). Development and metamorphosis of the planktotrophic larvae of *Rostanga pulchra* (Mollusca: Nudibranchia). *Marine Biology* 46: 109-119.

Chia FS & Koss R (1988). Induction of settlement and metamorphosis of the veliger larvae of the nudibranch, *Onchidoris bilamellata*. *International Journal of Invertebrate Reproduction and Development* 14: 53-70.

Coles S, & Eldredge L (2002). Nonindigenous species introductions on coral reefs: a need for information. *Pacific Science* 56:191-209.

Coll JC, Bowden BF, Tapiolas DM, Willis RH & Djura P (1985). Studies of Australian soft corals – XXXV: the terpenoid chemistry of soft corals and implications. *Tetrahedron* 41(6): 1085-1092.

Concepcion GT, Crepeau MW, Wagner D, Kahng SE & Toonen RJ (in press). An alternative to ITS, a hypervariable, single-copy nuclear intron in corals, and its use in detecting cryptic species within the octocoral genus *Carijoa*. *Coral Reefs*.

Coquillard P, Thibaut T, Hill DRC, Gueugnot J, Mazel C & Coquillard Y (2000). Simulation of the mollusc *Ascoglossa Elysia subornata* population dynamics: application to the potential biocontrol of *Caulerpa taxifolia* growth in the Mediterranean Sea. *Ecological Modelling* 135: 1-16.

Devaney D & Eldredge L (1977). Reef and shore fauna of Hawaii Section 1: Protozoa through Ctenophora. Bishop Museum, Honolulu.

Edmonson C & Ingram W (1939). Fouling organisms in Hawaii. Occasional Papers of Bernice P. Bishop Museum. Bernice P. Bishop Museum, Honolulu, pp. 251-300.

Edmonson C (1944). Incidence of fouling in Pearl Harbor. Occasional Papers of Bernice P. Bishop Museum. Bernice P. Bishop Museum, Honolulu, pp. 1-34.

Edmunds M (1975). An eolid nudibranch feeding on bryozoa. *The Veliger* 17(3)269-270.

- Eyster LS (1981). Observations on the growth, reproduction and feeding of the nudibranch *Armina tigrina*. *Journal of Molluscan Studies* 47: 171-181.
- Evans EC, Buske NL, Grovhoug JG, Guinther EB, Jokiel PL, Kam DT, Kay EA, Peeling TJ & Smith SV (1974). Pearl Harbor biological survey – final report. Rep NUC TN 128, Naval Undersea Center, San Diego.
- Fenner D (2005). *Corals of Hawai'i. A field guide to the hard, black, and soft corals of Hawai'i and the Northwest Hawaiian Islands, including Midway*. Mutual Publishing, Honolulu, 144pp.
- Folino NC (1993). Feeding and growth of the aeolid nudibranch *Cuthona nana* (Alder and Hancock, 1842). *Journal of Molluscan Studies* 59: 15-22.
- Funasaki GY, Lai PY, Nakahara LM, Beardsley JW & Ota AK (1988). A review of biological control introductions in Hawaii: 1890 to 1985. *Proceedings of the Hawaiian Entomological Society* 28: 105-160.
- Gavagnin M & Fontana A (2000). Diterpenes from marine opisthobranch molluscs. *Current Organic Chemistry* 4: 1201-1248.
- Gochfeld DJ & Aeby GS (1997). Control of populations of the coral-feeding nudibranch *Phestilla sibogae* by fish and crustacean predators. *Marine Biology* 130: 63-69.
- Gohar HAF & Aboul-Ela A (1957). On a new nudibranch *Phyllodesmium xeniae*. *Publications of Marine Biological Station Al-Ghardaqa* 9: 131-144.
- Grigg RW (2003). Invasion of a deep black coral bed by an alien species, *Carijoa riisei*, off Maui, Hawaii. *Coral Reefs* 22: 121-122.
- Grigg RW (2004). Harvesting Impacts and Invasion by an Alien Species Decrease Estimates of Black Coral Yield off Maui, Hawai'i. *Pacific Science* 58 (1): 1-6.
- Hadfield MG (1963). The biology of nudibranch larvae. *Oikos* 14(1): 85-95.
- Harris LG (1975). Studies on the life history of two coral-eating nudibranchs of the genus *Phestilla*. *Biological Bulletin* 149: 539-550.
- Harris LG (1987). Aeolid nudibranchs as predators and prey. *American Malacological Bulletin* 5 (2): 287-292.
- Hawkins BA, Thomas MB & Hochberg ME (1993). Refuge theory and biological control. *Science* 262: 1429-1432.
- Hoover JP (2005). *Hawai'i's Sea Creatures. A guide to Hawai'i's marine invertebrates*. Revised edition. Mutual Publishing, Honolulu, 366pp.

- Kahng SE & Grigg RW (2005). Impact of an alien octocoral (*Carijoa riisei*) on black corals in Hawaii. *Coral Reefs* 24 (4): 556-562.
- Kahng SE (2006). Ecology and ecological impact of an alien octocoral, *Carijoa riisei*, in Hawaii. Dissertation in Oceanography. University of Hawaii at Manoa, Honolulu, 284pp.
- Kahng SE, Benayahu Y, Wagner D & Rothe N (2008). Sexual reproduction in the invasive octocoral, *Carijoa riisei* (Duchassing & Michelotti, 1860) in Hawaii. *Bulletin of Marine Science* 82(1):1-17.
- Kahng SE & Kelley C (2007). Vertical zonation of megabenthic taxa on a deep photosynthetic reef (40-140 m) in the Au'au Channel, Hawaii. *Coral Reefs* 26(3): 679-687.
- Kareiva P (1996). Special feature: contributions of ecology to biological control. *Ecology* 77(7): 1963-1964.
- Lafferty KD & Kuris AM (1996). Biological control of marine pests. *Ecology* 77(7): 1989-2000.
- McClintock JB, Baker BJ, Slattery M, Heine JN, Bryan PJ, Yoshida W, Davies-Coleman MT & Faulkner DJ (1994). Chemical defense of common Antarctic shallow-water nudibranch *Tritoniella belli* Eliot (Mollusca: Tritonidae) and its prey, *Clavularia frankliniana* Rouel (Cnidaria: Octocorallia). *Journal of Chemical Ecology* 20(12): 3361-3372.
- Miller MC (1962). Annual cycles of some Manx nudibranchs with a discussion of the problem of migration. *The Journal of Animal Ecology* 31(3): 545-569.
- Murdoch WW & Briggs CJ (1996). Theory of biological control: recent developments. *Ecology* 77(7): 2001-2013.
- Nybakken J & McDonald G (1981). Feeding mechanisms of West American nudibranchs feeding on bryozoa, cnidaria and ascidiacea, with special respect to the radula. *Malacologia* 20(2): 439-449.
- Ortiz DM & Gosliner TM (2003). A new species of *Phyllodesmium* Ehenberg, 1831 (Mollusca, Nudibranchia) from the Tropical Indo-Pacific. *Proceedings of the California Academy of Sciences* 54(9): 161-168.
- Perron FE & Turner RD (1977). Development, metamorphosis, and natural history of the nudibranch *Doridella obscura* Verril (Corambidae: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology* 27: 171-185.
- Risbec J (1928). Contribution à l'étude des nudibranches Néo-Calédoniens. *Faune des Colonies Françaises* 2: 1-328.

- Rudman WB (1981). The anatomy and biology of alconarian feeding aeolid opisthobranch molluscs and their development of symbiosis with zooxanthellae. *Zoological Journal of the Linnean Society* 73: 219-262.
- Rudman WB (1990). *Protaeolidiella atra* Baba, 1955 and *Pleurolidia juliae* Burn, 1966; one species, two families (Nudibranchia). *Journal of Molluscan Studies* 56: 505-514.
- Rudman WB (1991). Further studies on the taxonomy and biology of the octocoral-feeding genus *Phyllodesmium* Ehrenberg, 1831 (Nudibranchia: Aeolidioidea). *Journal of Molluscan Studies* 57: 167-203.
- Sammarco PW & Coll JC (1992). Chemical adaptations in the Octocorallia: evolutionary considerations. *Marine Ecology Progress Series* 88: 93-104.
- Secord D (2003). Biological control of marine invasive species: cautionary tales and land-based lessons. *Biological Invasions* 5: 117-131.
- Simberloff D & Stiling P (1996). How risky is biological control. *Ecology* 77(7): 1965-1974.
- Slack-Smith SM & Bryce CW (2004). A survey of the benthic molluscs of the Dampier Archipelago, Western Australia. *Records of the Western Australian Museum Supplement* 66: 221-245.
- Slattery M, Avila C, Starmer J & Paul VJ (1998). A sequestered soft coral diterpene in the aeolid nudibranch *Phyllodesmium guamensis* Avila, Ballesteros, Slattery, Starmer and Paul. *Journal of Experimental Marine Biology and Ecology* 226: 33-49.
- Smith CD (2003). Diet of *Octopus vulgaris* in False Bay, South Africa. *Marine Biology* 143: 1127-1133.
- Soliman GN (1987). A scheme for classifying gastropod egg masses with special reference to those from the Northwestern Red Sea. *Journal of Molluscan Studies* 53: 1-12.
- Thibaut T, Meinesz A, Amade P, Charrier S, De Angelis K, Ierardi S, Mangialajo L, Melnick J & Vidal V (2001). *Elysia subornata* (Mollusca) a potential control agent of the alga *Caulerpa taxifolia* (Chlorophyta) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* 81: 497-504.
- Thomas WJ (1979). Aspects of the microcommunity associated with *Telesto riisei*, an introduced alcyonarian species. M.S. Thesis in Zoology, University of Hawaii at Manoa, 88 pp.
- Thompson TE (1976). Nudibranchs. T.F.H. Publications, Inc., Ltd., Neptune City, NJ, 96pp.
- Todd CD (1981). The ecology of nudibranch mollusks. *Oceanography and Marine Biology, Annual Review* 19: 141-234.

Todd CD & Doyle RW (1981). Reproductive strategies of benthic marine invertebrates: a settlement-timing hypothesis. *Marine Ecology Progress Series* 4: 75-83.

Todd CD (1981). The ecology of nudibranch mollusks. *Annual Review of Oceanography and Marine Biology* 19: 141-234.

Todd CD (1983). Reproductive and trophic ecology of nudibranch mollusks. In: *The Mollusca, Vol. 6* (WD Russell-Hunter, ed.) 6: 225-259. Academic Press, New York, NY.

Waegele H (2004). Potential key characteristics in Opisthobranchia (Gastropoda, Mollusca) enhancing adaptive radiation. *Organisms Diversity & Evolution* 4: 175-188.

Waegele H & Klussmann-Kolb A (2005). Opisthobranchia (Mollusca, Gastropoda) – more than just slimy slugs. Shell reduction and its implications on defence and foraging. *Frontiers in Zoology* 2:1-18.

Wagner D, Kahng SE & Toonen RJ (2007). New report of nudibranch predators of the invasive octocoral *Carijoa riisei* in the Main Hawaiian Islands. *Coral Reefs* 26(2): 411.