The feeding ecology of a common temperate mesoherbivore, the oligophagous sea slug *Placida dendritica* (Gastropoda: Opisthobranchia: Ascoglossa), was examined from April 1985 to June 1989. Along the central coast of Oregon, *Placida* consumed three host species: the low intertidal green algae *Codium setchellii*, *C. fragile*, and *Bryopsis corticulans*. Individual slugs tended to specialize on a single algal host species with limited capacity to change host species. In laboratory experiments, many individuals died in the presence of unfamiliar host species that sympatric conspecifics consumed. This rigid diet specificity was not modifiable.
through hunger level, algal condition, or intraspecific interaction. *Placida* populations, therefore, were functionally subdivided into sympatric subpopulations.

*Placida* formed feeding congregations on *Codium* spp. Members of groups composed of similar-sized slugs grew significantly faster than solitary individuals. In mixed-sized congregations, however, trophic benefits were not shared equally among all members. Small slugs always benefited from the presence of conspecifics; large slugs, however, benefited only if conspecifics were large. The mechanisms of intraspecific facilitation involved both behavioral stimulation of feeding and modification of algal food quality.

*Placida* was numerically and functionally the major herbivore of *C. setchellii*. The alga had a partial refuge from the slug in high sand or wave disturbance habitats. *Placida*'s attack was concentrated on algal thalli whose anti-herbivore defenses were probably compromised by stress: thalli in desiccation-prone microhabitats and thalli with existing grazing damage. Field transplant experiments indicated that *Placida*'s herbivory may restrict the between-habitat distribution of *C. setchellii* along the central coast of Oregon.
Marine Herbivore - Plant Interactions:
The Feeding Ecology of the Sea Slug *Placida dendritica*

by

Cynthia D. Trowbridge

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Chapter I

HERBIVORE - PLANT INTERACTIONS

INTRODUCTION


The defensive and offensive interactions between terrestrial plants and herbivores may involve a form of coevolutionary arms-race (Ehrlich and Raven 1964, Rhoades 1985), diffuse coevolution (Fox 1981, 1988), or asymmetrical interaction (e.g., not co-evolution). The defensive adaptations of plants include pre-formed...
constitutive defenses (e.g., deterents or toxins), inducible chemical and structural defenses, possibly acquired immunity to and recognition of specific herbivores, and communication among plants (Rhoades 1985 and references therein). Whether these "defenses" evolved in direct response to intense herbivory by (1) specific herbivores, (2) the diverse assemblage of local herbivores, or (3) no herbivores is an open question (Barbosa 1988, Bernays and Graham 1988, Courtney 1988, Fox 1988, Janzen 1988, Jermy 1988, Rausher 1988, Thompson 1988a, and references therein).

Rhoades (1985) suggests that the complementary offensive tactics of herbivores form two general attack strategies. One hand, "stealthy" herbivores may detoxify the constitutive defenses of their food plants, suppress any induced defenses, possibly suppress plant recognition of herbivores, and suppress communication among plants (Rhoades 1985). On the other hand, "opportunistic" herbivores may avoid plants defended with constitutive defenses, overwhelm induced defenses (e.g., by mass attack), possibly "surprise" plants by spatially or temporally unpredictable attack, and emit countersignals that "misinform" plants (sensu Rhoades 1985). Stealthy herbivores display adaptations minimizing their grazing impact on plant fitness whereas opportunistic herbivores do not. The two types of
herbivores differ in population dynamics, life history attributes, intraspecific interactions, and hence food plant use (Table I.1).

Hay and Fenical (1988) suggest that the potential for strong, consistent associations and, hence, coevolution between herbivores and plants may be lower in marine communities than in terrestrial ones. Two apparent barriers to coevolution in marine herbivore-plant associations are (1) long generation time of and (2) inefficient host location by herbivores. If the life span of the herbivore is shorter than that of the plants, then the herbivores may adapt to plant defenses faster than plants can respond to the new feeding abilities of the herbivores (Steneck 1982, Steneck and Watling 1982, Hay and Fenical 1988). Many of the marine macroherbivores (e.g., fishes, urchins, large gastropods), however, are long-lived with generation times significantly longer than their algal food species.

Furthermore, Hay and Fenical (1988) suggest that the high mobility and sensory acuity of terrestrial insects enable adults to select specific hosts, including nonapparent plants, thus enhancing the potential for coevolution between herbivore and host plant. In contrast, many marine macroherbivores have
Table I.1. Proposed attributes of stealthy and opportunistic herbivores (Rhoades 1985).

<table>
<thead>
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<th>Attributes</th>
<th>Stealthy Herbivores</th>
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<td>Growth &amp; Fecundity</td>
<td>Low &amp; Constant</td>
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<td>Nonmigratory</td>
<td>Migratory &amp; Nonmigratory</td>
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<td>Intraspecific Interactions</td>
<td>Competition</td>
<td>Facilitation</td>
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<td>Use of Hosts</td>
<td>&quot;Conservative&quot; e.g., low value tissues</td>
<td>&quot;Profligate&quot; e.g., high value tissues</td>
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planktonic larvae which may have limited capacity to select specific host plants due to their limited mobility and sensory acuity (Hay and Fenical 1988). The constraints, however, imposed by planktonic dispersal may affect effectiveness of food plant location more than species-specific differences in mobility and sensory acuity. For example, although planktonic larvae are widely dispersed, their host selection is constrained by (1) the movement of water currents and near-shore wave action, (2) the short competency period during which larvae must select a substrate for settlement, and (3) the inability to make sequential settlement choices. Furthermore, regardless of the sensory acuity of larvae, the constraints of viscous and often turbid water may limit the effectiveness of long distance visual or chemosensory food location. Long herbivore generation time and planktonic larval host plant selection may limit the potential for strong and consistent associations between herbivores and marine plants. These predictions are supported by the observation that specialist herbivores are less common in marine habitats than in terrestrial ones (Lubchenco and Gaines 1981, Steneck 1982, Hay et al. 1987, 1988a,b, Hay and Fenical 1988).

The effect of predation on herbivore food selection and diet breadth is not well known. Bernays and Graham
(1988) suggest that predation on herbivorous insects may be a strong selective force restricting the host range used by the herbivores. Hay et al. (1987) made a similar argument for the apparent restricted host use of some marine herbivores with direct larval development (i.e., no planktonic phase). In contrast, Hay et al. (1988a) suggest that intense predation may select for generalized host plant use by settling larval herbivores. This discrepancy is difficult to evaluate because of the paucity of quantitative evidence.

The marine equivalents of terrestrial phytophagous insects are not macroherbivores, but the smaller mesoherbivores (Brawley and Fei 1987, Hay et al. 1987, 1988a,b). The short life spans, often direct larval development, and low vagility make small herbivores such as some species of amphipods, isopods, tanaids, small prosobranch snails, and small sea slugs candidates for coevolved herbivores (Steneck 1982, Steneck and Watling 1982, Hay and Fenical 1988, Hay et al. 1988a).

Reports on mesoherbivore grazing on marine plants in situ suggest that their effect may be small relative, especially to that of sympatric macroherbivores (e.g., Carpenter 1986). The apparently small effect may reflect, in part, that intense predation limits mesoherbivore abundance (Hay 1985, Nelson 1979a,b, 1981, Stoner 1980). There is little evidence supporting or
refuting the hypothesis that grazing by crustacean or polychaete mesoherbivores has ecologically or evolutionarily important consequences to the algal hosts (but see Coen 1988a,b) or that the algae have developed mechanisms to reduce such herbivory. For example, Carpenter (1986) found that the grazing by tropical crustacean mesoherbivores had limited effect on algae, even when the fish predators were removed and mesoherbivore abundances increased. Thus, although several mesoherbivore species have evolved mechanisms to tolerate chemically defended algae (Paul et al. 1987, Hay et al. 1988a,b,), the herbivore-algal interaction is asymmetrical.

In contrast, another group of mesoherbivores, the ascoglossan [=sacoglossan (Marcus 1982, Gascoigne 1985)] sea slugs, have a well-adapted and possibly coevolved association with their algal hosts (Jensen 1980, Clark and DeFreese 1987). Ascoglossans are suctoridal herbivores that feed on coenocytic and siphonous green algae. Ascoglossan diversity and abundance can be substantial. Estimates of species richness on regional scales (Table I.2) range from 3-4 species in arctic to boreal waters to 11-76+ species in subtropical and tropical localities. Species richness on a local scale, however, may be lower than reported for the whole geographic region. For example, of the 37 species
Table I.2. Estimates of ascoglossan species richness (S) on a regional scale from 22 species lists. In many areas, these values are conservative underestimates due to limited examination of the ascoglossan fauna and limited taxonomic treatment. For example, the richness values for Japan (Baba 1959) were based primarily on one family in the order Ascoglossa.

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<th>Region</th>
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<td>N.E. Atlantic</td>
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<td>Sars 1878, Odhner 1939</td>
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<td>N.E. Atlantic</td>
<td>5-10</td>
<td>Miller 1962, Thompson 1976, Platts 1985</td>
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<td>N.W. Atlantic</td>
<td>11</td>
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<td>N.E. Pacific</td>
<td>7</td>
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<td>N.W. Pacific</td>
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<td>Baba 1959, Habe &amp; Kikuchi 1960</td>
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<td>So. Africa</td>
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<td>Guam</td>
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collected by Clark and DeFreese (1987) in four Caribbean regions, at most 14 species occurred in any single habitat. Peak slug densities range from 70 to 700 slugs g⁻¹ dry weight of algae though many species are much less abundant (Clark and DeFreese 1987). Although the potential effect of ascoglossan herbivory is difficult to estimate from such density values because of lack of information on the spatial distribution of algal biomass, temperate ascoglossans often have a "major seasonal impact on algal populations, commonly overgrazing the food supply to the point of destruction" (Clark 1975, Clark and DeFreese 1987). The question of whether herbivory by mesoherbivores, particularly the specialist sea slugs, is ecologically important to marine plants merits further attention.

The objective of this dissertation is to describe in detail the association between the common ascoglossan mesoherbivore Placida dendritica A. & H. (Gastropoda: Opisthobranchia: Ascoglossa) and its green algal host species (Codium setchellii, C. fragile, and Bryopsis corticulans). I demonstrate that the sea slug displays characteristics of an opportunistic herbivore (Table I.1, Rhoades 1985) that may significantly restrict the abundance and distribution of at least one of its green algal host species along the central coast of Oregon.
OVERVIEW

In Chapter II, I describe the phenology of the oligophagous sea slug *Placida dendritica* at several sites along the central coast of Oregon. I demonstrate that (1) *Placida* was a short-lived herbivore, with less than one month elapsing from larval settlement to adult sexual maturity; (2) *Placida*'s larval recruitment to the algal hosts was continuous during the spring and summer; and (3) *Placida*'s movement among conspecific algal hosts in the field was rapid. Because two of the three local host species, namely *C. setchellii* and *C. fragile*, are long-lived perennials, *Placida* has the potential to adapt to *Codium* defenses faster than the algae can respond to changes in the slugs' feeding abilities.

*Placida* exhibited extremely rigid feeding specificity: individuals tended to specialize on a single algal host species with limited capacity to change host species (Chapter III). The diet specificity was not modifiable through hunger level, algal condition, or intraspecific interaction. The basis of this inflexible behavior was either developmental or genetic. *Placida* populations, therefore, were functionally divided into sympatric subpopulations analogous to those of phytophagous insects, particularly of parthenogenetic species (Alstad and Edmunds 1983, Weber 1986). My results are contrary to the predictions
that mesoherbivores with planktonic larvae should be generalists (Hay and Fenical 1988). The lack of parthenogenetic reproduction in Placida and the extended planktonic larval phase, however, may prevent greater feeding specialization (e.g., monophagous species).

Placida formed feeding groups analogous to those of terrestrial suctorial herbivores (e.g., aphids). In Chapter IV, I describe the patterns and consequences of Placida's gregarious behavior. Group members grew significantly faster than solitary conspecifics on two of the three algal host species. Placida's gregarious feeding (1) stimulated conspecifics to feed and (2) enhanced food quality, herbivore effectiveness, or both. Gregarious feeding enabled Placida to feed on Codium spp.

Finally, Placida's herbivory may limit the between-habitat distribution and abundance of its Codium hosts (Chapter V). The slugs attacked 14.5% of the C. setchellii and 71.5% of the C. fragile examined during the spring and summer. C. setchellii had no low-density, temporal, or morphological escapes from Placida's herbivory though the alga did have a partial refuge in high disturbance habitats. The slugs opportunistically attacked algal hosts in desiccation-prone microhabitats. Placida's effective attack strategy and Codium's apparent absence of effective
constitutive or inducible defenses suggest that the slug's herbivory may restrict the between-habitat distribution of Codium along the central coast of Oregon.
Chapter II

PHENOLOGY OF THE MARINE SPECIALIST HERBIVORE

PLACIDA DENDRITICA ON THE CENTRAL COAST OF OREGON

ABSTRACT

The phenology of the common ascoglossan sea slug Placida dendritica A. & H. was documented at several sites along the central coast of Oregon from 1985 to 1989. Placida was found on the low intertidal green algae Codium setchellii, C. fragile, and Bryopsis corticulans during the spring and summer. Larval recruitment of Placida to the algal hosts was continuous during the spring and summer. Placida's growth was rapid, with less than one month elapsing from larval settlement to adult sexual maturity. Slug populations, therefore, were composed of many overlapping generations. Movement of adult slugs among C. setchellii thalli was rapid. Continuous larval recruitment and adult immigration not only enabled Placida to locate and colonize its algal hosts rapidly, but also made the slug's herbivory a chronic influence on the algae throughout the spring and summer.
INTRODUCTION

Terrestrial and marine plants are attacked by a diverse array of invertebrate herbivores. In terrestrial communities, these herbivores include both generalist and specialist feeders, and representatives of both categories are common. Marine herbivores, in contrast, are primarily generalist feeders (Lubchenco and Gaines 1981, Hay and Fenical 1988). Diet specificity may be associated with small herbivore size and short herbivore life span (Lubchenco and Gaines 1981, Steneck 1982, Steneck and Watling 1982, Hay et al. 1987, Hay and Fenical 1988). Because most ecological work on marine herbivores has focused on the larger, more obvious taxa such as fishes, urchins, and large gastropods, little detailed information is known about the smaller, often short-lived mesoherbivores.

Diet specificity in marine invertebrates may be correlated with feeding mode. Only a few scraping marine herbivores are known to be specialists: the lined chiton Tonicella lineata (Barnes 1972, Barnes and Gonor 1973, Demopulos 1975) and several species of acmaeid limpets (Carlton 1976, Steneck 1982, and references therein). Furthermore, while many of the chewing herbivores (e.g., idoteid isopods, cranefly larvae, and chironomid larvae) are often associated with one or a few plant species (Morris et al. 1980), none
have been shown to be oligophagous. Suctorional herbivores, however, are primarily oligophagous, being well represented by members of the molluscan order Ascoglossa [= Sacoglossa (Marcus 1982, Gascoigne 1985)]. The order is composed of about 200 species (Jensen 1983) of small sea slugs that might be considered marine counterparts to terrestrial suctorional insects (e.g., aphids and leaf hoppers). They share a number of features including small size, short life span, piercing mouth parts, suctorional feeding, and diet specificity.

If more were known about the patterns of distribution, abundance, recruitment, and mobility of ascoglossan sea slugs, then ecological studies on the slugs could provide more valuable insight on whether herbivory by marine specialists is a strong selective pressure on marine plants. This information would complement existing information for marine generalist herbivores and terrestrial specialist phytophagous insects. For example, it would be interesting to know the conditions under which marine specialist herbivores are abundant. Quantitative information on ascoglossan abundance, population turnover, and grazing for individual species is scarce, and most of the past studies are characterized by sample sizes, short project durations, and unspecified spatial scales (Warmke and Almodovar 1972, Clark 1975, Jensen 1975b, Brandley 1984,
Clark and DeFreese 1987, DeFreese 1987). Some ascoglossan species, particularly temperate stiligerids, have highly eruptive populations that may locally deplete algal hosts (Clark 1975, Clark and DeFreese 1987), but the effect on algal fitness has not been quantified.

One of the major gaps in our understanding of the population ecology of the oligophagous ascoglossans--and of most marine herbivores--is the spatial and temporal variation in larval recruitment, growth, adult immigration, and hence grazing pressure. In this paper, I describe the phenology of the common ascoglossan sea slug Placida dendritica A. & H. (= Hermaea dendritica A. & H., see Long 1969, Bleakney 1989) on the central coast of Oregon. I demonstrate that (1) Placida larvae recruited to the green algal hosts continuously throughout the spring and summer, (2) Placida grew and matured rapidly, and (3) Placida adults moved among conspecific algal hosts. Therefore, although short-lived Placida individuals may exert little effect on their algal hosts, local populations of Placida exert a chronic grazing pressure.
**BACKGROUND**

*Placida dendritica* is common in warm-temperate to boreal coastal waters throughout the world (Schmekel and Portmann 1982) and is one of seven species of herbivorous ascoglossans in the northeastern Pacific (MacFarland 1966, Williams and Gosliner 1973, Lambert 1976, Behrens 1980, Millen 1980). *Placida* has a complex life cycle with planktotrophic larvae and benthic adults (Clark 1975). Benthic eggs are laid on algal hosts in the spring and summer and mature in 7-10 days (Alder and Hancock 1844-1845, Evans and Evans 1917, Greene 1968), releasing veliger larvae which live and feed in the plankton for an extended period (Clark 1975). Larvae settle and metamorphose; post-metamorphic individuals feed, grow, mate, and spawn on their algal hosts.

Throughout its geographic range, *Placida* feeds on the green algae *Codium* spp. and *Bryopsis* spp. At certain localities, the ascoglossan also consumes other green algae: *Cladophora* spp. (Oakes 1979), *Derbesia* spp. (Bleakney 1989), and *Halimeda cuneata* (Macnae 1954). Along the central coast of Oregon, the algal hosts are the crustose perennial *Codium setchellii*, the upright, dichotomously branching perennial *C. fragile*, and the delicate filamentous-like ephemeral *Bryopsis corticulans* (Fig. II.1). Although *Placida* retains chloroplasts from these algal hosts in digestive
Figure II.1. Schematic diagrams of the algal host species of *Placida dendritica* along the central coast of Oregon. *Bryopsis* thalli, 5-10 cm tall, are tubular with no internal crosswalls (Abbott and Hollenberg 1976). *Codium* thalli are composed of tightly interwoven tubes called utricles. The upright *C. fragile* thalli grow to 10-30 cm in height; the crustose *C. setchellii* thalli grow to 25 cm in diameter or more by coalescence (Abbott and Hollenberg 1976). Close-up of *Codium* surface illustrates utricle tips and relative size of a recently settled *Placida* recruit. *Placida* punctures the algal tubes with a single radular tooth and sucks out the algal protoplasm.
diverticula, the herbivore does not obtain photosynthetic benefit from the "endosymbiotic" organelles (McLean 1976, Santisi 1985), in contrast to many other species of ascoglossans (Hinde and Smith 1974, Clark and Busacca 1978).
METHODS

Seasonality and Spawning

Placida was monitored on C. setchellii from April 1985 to September 1987 at three sites along the central coast of Oregon, USA. These sites from north to south were Yaquina Head, Seal Rock, and Strawberry Hill (Fig. II.2). Each month, I systematically censused C. setchellii thalli at each site and noted the presence of Placida and associated egg masses.

From April 1987 to September 1988, I monitored Placida's presence on C. fragile from Boiler Bay, OR (Fig. II.2). Each month I collected specimens of the alga at 1-m intervals along each of two 10-m transects through an extensive C. fragile bed. I quantified the presence of Placida and egg masses on each thallus, using a dissecting microscope. I also noted Placida's presence or absence on Bryopsis clumps at Boiler Bay during the same period.

Population Structure

Placida was collected approximately monthly from C. setchellii at Strawberry Hill in the spring and summer of 1986 and 1987. In April and May 1987, ascoglossans were also collected from Seal Rock to examine whether population size-structure varied between sites. In 1988 the entire low intertidal at Strawberry Hill was buried
Figure II.2. Location of the study sites along the central coast of Oregon, USA. Yaquina Head was directly north of the Yaquina Head National Monument; Seal Rock was at Seal Rock State Park; Strawberry Hill was directly south of Neptune State Park at the Strawberry Hill parking area; and Boiler Bay was at the north end of Boiler Bay State Park. Upwelling data were from Cascade Head and sea surface temperature data from Charleston.
by sand, so monthly Placida collections were made at Seal Rock. Algal thalli were systematically censused along a transect. Entire groups of Placida were scraped into a plastic bag with seawater and brought back to the laboratory. In addition, animals from the monthly C. fragile collections in 1987 were removed for measurement. Individual slugs were blotted on a paper towel and weighed to the nearest 0.01 milligram. The data, however, are presented in 0.5-mg weight classes. The precision of blotting and weighing Placida (2.7%) was calculated as the mean percent difference in weight of 25 individuals weighed twice.

Environmental Correlates

Because Placida has planktotrophic larvae, the physical conditions of nearshore waters may influence the extent of larval settlement and possibly post-metamorphic growth. I used stepwise regression analysis to elucidate the relative importance of upwelling and sea surface temperature (current and preceding month) on Placida recruitment and growth. Upwelling and temperature data were obtained from the Oregon Department of Fisheries and Wildlife. Upwelling data were monthly mean Bakun Index values (metric tons of water/100 m coastline/s) measured at Cascade Head, OR; temperature data were monthly mean sea surface values
(°C) at Charleston, OR (Fig. II.2). The recruitment and growth data examined were (1) the percentage of slugs that were recent recruits (<0.5 mg) or recruits plus juveniles (<1.0 mg) and (2) the maximum body weight of Placida. For each analysis, I used stepwise regression analysis to determine which factors accounted for the most variation ($R^2$) in Placida's recruitment and maximum size. All statistical analyses were done on a microcomputer with Systat (version 4.0, Evanston, IL).

Recruitment and Growth Rates

Four field experiments were conducted to estimate the recruitment and growth rates of Placida on C. setchellii transplanted to Boiler Bay (Fig. II.2). Because of the location and timing of the experiments and the diet specificity of the ascoglossans, Placida recruitment to C. setchellii transplants was primarily from settlement of planktonic larvae. The Boiler Bay site was selected because C. setchellii occurred in extremely low densities, rendering movement of adult slugs from established C. setchellii to the transplants unlikely. Because three of the four experiments were conducted several months after Placida seasonally appeared on its hosts, immigration of any overwintering slugs from surrounding vegetation should be minimal. Placida had not burrowed into the C. setchellii thalli
(pers. obs.) prior to my transplanting the algae in the field. Finally, while the slugs theoretically may move from *C. fragile* or *Bryopsis* at Boiler Bay to transplanted *C. setchellii* samples, individual slugs have limited capacity to switch algal host species (Chapter III). For example, in laboratory experiments, *Placida* collected from *Bryopsis* died, rather than switched to *C. setchellii*, even in the presence of "experienced" feeding conspecifics. Hence, ascoglossan recruitment to *C. setchellii* transplants in the field was primarily from larval settlement.

The field experiments were designed to determine whether (1) *Placida* recruited continuously all summer, (2) *Placida* recruitment and population structure varied at different wave exposures, (3) *Placida* matured rapidly, and (4) *Placida* recruited equally to *C. setchellii* and *C. fragile*. In June 1988, I transplanted *C. setchellii* to a cove fairly protected from wave force. In July, I transplanted *C. setchellii* to eight locations of varying exposure to wave force: three wave-protected, two intermediate, and three exposed areas of Boiler Bay. In August, I transplanted *C. setchellii* to one of the three exposed areas to compare temporal changes in *Placida* recruitment and growth. In April 1989, I transplanted *C. setchellii* and *C. fragile* to a wave-protected area to compare *Placida*'s
recruitment and early growth on the two host species. For all four experiments, at each location I transplanted 5-25 replicate samples.

The transplant technique involved collecting *C. setchellii* from Seal Rock or *C. fragile* from Boiler Bay, placing ca. 30-g amounts of algae in 25 cm x 10 cm plastic mesh bags (mesh opening 6-8 mm; ©Protex, Norplex Inc., Kent, WA), and attaching them with monofilament line to stainless steel screws cemented into the rocky substrate. The location of the experiments in the lower end of the low intertidal zone (ca. -0.5 to -0.8 m) and the timing of the experiments were chosen to minimize desiccation stress to the transplants. The algal samples were collected after about 4 weeks and placed in 70% ethanol. Using a dissecting microscope with an ocular micrometer, I categorized the preserved *Placida* into four size classes, corresponding to recent recruits (< 0.5 mg), juveniles (0.5-0.9 mg), adults (1-3 mg), and large adults (>3 mg) (pers. obs. and results below).

**Minimum Size of Reproduction**

Estimates of *Placida's* minimum size of reproduction were calculated in the laboratory. I placed individual ascoglossans in small plastic petri dishes (60 mm diameter x 15 mm deep) with seawater and held them at 11°C, comparable to the seawater temperature in the
field. I checked the dishes for egg masses and changed the seawater every 2-4 days until the cumulative total of individuals spawning either stabilized or approached 100%.

Adult Immigration

To evaluate whether adult ascoglossans moved among algal thalli in a local area, I quantified (1) whether Placida immigrated to C. setchellii cleared of conspecifics and (2) whether local dense groups of Placida enhanced their local immigration. In May 1989, I randomly selected six C. setchellii thalli along a 20-m transect line on an east-facing wall in the low intertidal zone at Strawberry Hill. I removed all the Placida on C. setchellii thalli within a 1-m radius of the randomly selected central thallus. In three of the six areas, I placed 100 large adult Placida on the central thallus; in the other three areas, I added no Placida. After one day, I counted the number of Placida immigrants on each C. setchellii thallus in the 1-m radius areas. The experiment was repeated the following day on a west-facing wall that was less buffered from wave force than the east-facing wall.
RESULTS

Seasonality

Placida was found on algal hosts from March or April to September or October along the central coast of Oregon. This pattern was identical on C. setchellii from April 1985 to September 1987 and on C. fragile and Bryopsis from April 1987 to September 1988. Thus, the ascoglossans were on all the algal host species simultaneously.

Placida's arrival on and departure from algal thalli usually corresponded to the low tide series nearest to the spring and fall equinoxes. In the spring and summer (when Placida was present), the low tides exposing Codium along the Oregon coast were in the early to mid-morning hours when daily temperatures and light levels were high and, hence, algal desiccation was high. The duration of aerial exposure time (number of days per month and hours per day) also peaked in these months.

Population Size-Structure

Temporal Variation

Placida's population size-structure on C. setchellii varied widely among months and years (Fig. II.3). The ascoglossans sampled in April 1986, shortly after their appearance on the algae, had a wide range of body sizes. By June, a few individuals were extremely
Figure II.3. Size-structure of *Placida dendritica* collected from *Codium setchelli* at Strawberry Hill, OR in 1986 and 1987 and at Seal Rock, OR in 1988. The number of ascoglossans weighed each month is indicated.
large: up to 5.5 mg wet weight. In July, the large Placida were no longer present on the algae, and small to medium-sized ascoglossans (0.5-2.0 mg) dominated. By August a wide range of ascoglossan sizes were represented. Throughout 1987, the size-frequency distribution was strongly skewed to the smallest size classes (<1.0 mg), reflecting heavy larval settlement, slow juvenile growth, or high adult mortality. In April 1988, Placida's size-structure resembled that seen in April 1986. From May to August 1988, however, very small Placida predominated, as in 1987. The size-structure of Placida on C. fragile in 1987 (Fig. II.4) was strongly skewed to the smallest size class (<0.50 mg), closely resembling that of animals on C. setchellii during the same time.

Placida size-structure was related to sea surface temperature but not to upwelling (Table II.1). The percentage of Placida less than 0.5 mg (recent recruits) on C. setchellii was inversely related to sea surface temperature of the preceding month (P=0.027), when veliger larvae were presumably in the plankton. On C. fragile, the percentages of recent recruits (<0.5 mg) and recruits plus juveniles (<1.0 mg) were inversely related to temperature of the current month, rather than the preceding month. Placida may either settle more rapidly or grow more slowly on C. fragile than on C.
Figure II.4. Size-structure of *Placida dendritica* collected in 1987 from *Codium fragile* at Boiler Bay, OR. The number of ascoglossans weighed each month is indicated.
Table II.1. Results of stepwise regression analysis on the relation between (1) monthly mean upwelling (Upwell) and sea surface temperature (SST) for the current month and preceding month (Lag) and (2) three aspects of Placida dendritica size-structure: the percentage of individuals that were recruits (<0.5 mg wet weight) and recruits plus juveniles (<1.0 mg) and the maximum body size (mg wet weight). Data for Placida on C. setchellii were based on monthly values from April 1985 to August 1987; data for Placida on C. fragile were based on monthly values from April 1987 to May 1988. P-values of significant variables are indicated. The alpha-value for variables to enter and exit the model was 0.150. $R^2$ denotes the amount of variation explained.

<table>
<thead>
<tr>
<th>Significant Variables</th>
<th>Codium setchellii</th>
<th>Codium fragile</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Recruits</td>
<td>Recruits &amp; Recruits</td>
</tr>
<tr>
<td></td>
<td>&lt;0.5 mg</td>
<td>&lt;1.0 mg</td>
</tr>
<tr>
<td>SST/Lag</td>
<td>7.0</td>
<td>2.6</td>
</tr>
<tr>
<td>F-ratio</td>
<td>0.027</td>
<td>0.143</td>
</tr>
<tr>
<td>P-value</td>
<td>0.374</td>
<td>0.136</td>
</tr>
<tr>
<td>n</td>
<td>11</td>
<td>11</td>
</tr>
</tbody>
</table>
setchellii, thus making the more recent temperature estimate more applicable. Maximum Placida size was not correlated with temperature or upwelling. The fact that the correlations are stronger for the younger than for the larger slugs suggests that temperature or temperature-related factors may be associated with recruitment.

**Spatial Variation**

Placida population structure varied on large and small spatial scales. For example, Placida size-structure was significantly different at Seal Rock and Strawberry Hill in April (Chi-square test, $X^2=25.5$, 6 df, $n=594$, $P<0.001$) and May 1987 ($X^2=41.1$, 4 df, $n=290$, $P<0.001$). On smaller spatial scales in Boiler Bay, Placida size-structure varied, both with degree of exposure to waves and among sites of high wave exposure (Table II.2). Placida size-structure at the exposed sites differed from those at the intermediate and protected sites ($P<0.001$) with proportionally fewer recruits and more juveniles. Furthermore, the percentage of individuals in each size-class varied among replicate exposed areas ($P=0.018$, Table II.2B): 45-58% of the individuals were recent recruits and 30-35% were juveniles. Placida size-structure exhibited little variation within the protected and intermediate
Table II.2. A. Size-structure of *Placida dendritica* on *Codium setchellii* transplanted in July 1988 to eight localities in Boiler Bay: 3 wave-protected areas, 2 intermediate, and 3 exposed areas. Data are the overall percentage of *Placida* for the 2-3 areas at each wave exposure. B. Results of Chi-square analyses are based on categorical size-structure data from areas of different and similar wave exposures.

A. Size-Structure Results

<table>
<thead>
<tr>
<th>Location</th>
<th>Recruits</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Large Adults</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protected</td>
<td>68%</td>
<td>17%</td>
<td>9%</td>
<td>6%</td>
<td>1069</td>
</tr>
<tr>
<td>Intermediate</td>
<td>63%</td>
<td>21%</td>
<td>9%</td>
<td>7%</td>
<td>535</td>
</tr>
<tr>
<td>Exposed</td>
<td>52%</td>
<td>35%</td>
<td>8%</td>
<td>5%</td>
<td>408</td>
</tr>
</tbody>
</table>

B. Chi-Square Analyses

<table>
<thead>
<tr>
<th>Comparison</th>
<th>$X^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among Different Exposures</td>
<td>56.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Within Similar Exposures</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protected</td>
<td>9.0</td>
<td>0.176</td>
</tr>
<tr>
<td>Intermediate</td>
<td>1.1</td>
<td>0.783</td>
</tr>
<tr>
<td>Exposed</td>
<td>15.3</td>
<td>0.018</td>
</tr>
</tbody>
</table>
wave-exposure localities: 63-68% of the ascoglossans were recent recruits and 17-21% were juveniles.

Reproduction

Placida spawned on C. setchellii in the field in all months that it was present, except April 1985. Between 9% and 61% of the Placida groups were associated with egg masses, and these masses were laid primarily in surface depressions of the rugose, crustose thalli. On C. fragile, egg masses were not common. Only 6-10% of the Placida groups were associated with egg masses, and these masses were located primarily in the axillary region of algal branches. In 1988, egg masses were noted on C. fragile only from May to July rather than during all months that the slugs were present.

The minimum size of egg mass production of Placida was between 0.5 and 1.0 mg on all three algal host species: 0.53 mg on C. setchellii, 0.96 mg on C. fragile, and 0.84 mg on Bryopsis. This size, however, did not represent a threshold response: some of the larger individuals spawned but others did not (Fig. II.5). Ascoglossans collected from the three algal host species differed in the size-specific egg mass production (Chi-square test, $X^2=19.3$, 4 df, $P=0.001$). Egg mass production, therefore, may be age-specific, rather than size-specific. Alternatively, Placida on
Figure II.5. Size-specific egg mass production of *Placida dendritica* from the three algal host species.

The number of ascoglossans examined is indicated.
Bryopsis may frequently delay egg mass production until attaining greater weight.

Recruitment and Growth

Placida arrived on its algal hosts in the spring, but larval recruitment continued throughout the summer. In June 1988, an average of 193.1 Placida (SE=19.2, n=25 algal thalli) had recruited to each transplanted C. setchellii thallus after one month. In July, Placida recruitment ranged from 384.4 individuals per alga (SE=3.8, n=5 thalli) at the protected area to 24.6 (SE=87.9, n=5) at the exposed area. Finally, in August, mean Placida abundance was 11.0 individuals per alga (SE=2.3, n=21 thalli) at the exposed locality.

On C. setchellii transplants at Boiler Bay, Placida's growth was extremely rapid. In July 1988, 15% of the Placida that had recruited to the algal transplants had grown to sexual maturity. At one of the exposed points in Boiler Bay, 10% of the Placida recruiting in July and 58% of those recruiting in August had grown to sexual maturity within one month (Table II.3). Even if age-specific mortality or emigration of Placida occurred, clearly many individuals grew to sexual maturity in less than 4 weeks. These growth estimates are supported by the animals' rapid growth in the laboratory (Chapters III-IV). Placida populations,
Table II.3. Size-structure of *Placida dendritica* after one month on *Codium setchellii* transplanted to an exposed point at Boiler Bay in July and August 1988.

<table>
<thead>
<tr>
<th>Month</th>
<th>Recruits</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Large Adults</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td>58%</td>
<td>32%</td>
<td>5%</td>
<td>5%</td>
<td>103</td>
</tr>
<tr>
<td>August</td>
<td>10%</td>
<td>32%</td>
<td>45%</td>
<td>13%</td>
<td>232</td>
</tr>
</tbody>
</table>
therefore, were composed of a large number of overlapping generations.

*Placida* recruited to transplants of the two *Codium* spp. at similar rates (Student's t-test, \( t = -1.4, P = 0.190 \)) (*C. setchellii*: \( \bar{X} = 2.0 \) slugs/g algae, SE = 0.4, n = 7; *C. fragile*: \( \bar{X} = 1.2, SE = 0.4, n = 7 \)). The size-structure of these colonists, however, differed significantly with algal species (Table II.4, \( P < 0.001 \)). After one month, 64% of the slugs on *C. setchellii* and 42% of the slugs on *C. fragile* were adults. Growth rates of *Placida*, then, were greater on *C. setchellii* than on *C. fragile* transplants in the field.

**Adult Immigration**

Adult *Placida* moved among *C. setchellii* thalli. After one day, I observed *Placida* about 30-35% of the defaunated thalli in the two experiments (Fig. II.6).

Although this result may reflect experimental error (e.g., inadequate removal of *Placida* at the start of the experiments), the relatively small size of *C. setchellii* thalli (2-29 cm diameter), the large size of adult *Placida* (ca. 3-6 mm long), and the large number of *Placida* appearing on some thalli (maximum 20) suggest that experimental error was not sufficient to explain the results. Whether *Placida* movements among algal hosts were due to dislodgment or active emigration from
Table II.4. Size-structure of *Placida dendritica* after one month on *Codium setchellii* and *C. fragile* transplanted to a wave-protected area at Boiler Bay in April 1989. Chi-square analysis based on categorical size-structure data.

<table>
<thead>
<tr>
<th>Algae</th>
<th>Recruits</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Large Adults</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. setchellii</em></td>
<td>15%</td>
<td>21%</td>
<td>46%</td>
<td>18%</td>
<td>259</td>
</tr>
<tr>
<td><em>C. fragile</em></td>
<td>36%</td>
<td>21%</td>
<td>36%</td>
<td>7%</td>
<td>137</td>
</tr>
</tbody>
</table>

Chi-square test, $X^2=28.3$, $P<0.001$
Figure II.6. Immigration of adult *Placida dendritica* to *Codium setchellii* one day after experimental removal of conspecifics. Results are in the percentage of *C. setchellii* thalli with *Placida* and the number of *Placida* per attacked thallus in the presence or absence of a local point source (+ and 0, respectively). The experiment was conducted twice in May 1989: A. on a wave-protected, east-facing wall and B. on a wave-exposed, west-facing wall at Strawberry Hill, OR. The number of *Codium* thalli examined in each treatment is indicated. The P-values are based on Fisher Exact tests in the upper panels and Student's t-tests in the lower panels.
Figure II.6.
host thalli is not known. *Placida*'s rapid appearance on *Codium* (1 day) excludes the possibility that the adult *Placida* occurred after growth from larval settlement.

Local point sources of *Placida* enhanced adult immigration in some but not all cases. In the first experiment on the wave-protected east-facing wall (Fig. II.6A), *Placida* moved more frequently to *C. setchellii* thalli within 1 m of the *Placida* point source than to thalli not near a source (Fisher Exact Test, $P=0.031$). In the second experiment on the west-facing wall (Fig. II.6B), the frequency of *Placida*'s immigration did not vary with proximity to a point source of adults (Fisher Exact Test, $P=0.501$). Furthermore, in both experiments, the number of immigrants per attacked algal thallus did not vary with presence or absence of point source (Student's t-tests: A. $t=0.1$, $P=0.908$; B. $t=0.4$, $P=0.663$). These results indicate that *Placida* adults move among conspecific hosts, but the spatial scale of such movements may be greater than the 1-m radius areas examined.
DISCUSSION

Seasonality

The seasonality of *Placida dendritica* is associated with water temperature. For example, *Placida*'s occurrence is similar on different algal hosts (*Codium* and *Bryopsis* spp.), at different tidal heights (intertidal and subtidal) on temperate shores in the northern hemisphere. Collections from the northeast Atlantic (Alder and Hancock 1844-1845, Garstang 1890, Hecht 1895, Evans and Evans 1917, Miller 1958 cited by Thompson 1976), the northwest Atlantic (Clark and Franz 1969, Clark 1975), and the northeastern Pacific (MacFarland 1966, Long 1969, Williams and Gosliner 1973, Lambert 1976, Millen 1980) indicate that *Placida* occurs on its algal host species during the spring and summer. Fewer reports from temperate localities in the southern hemisphere are available, but they indicate that *Placida* occurs on its algal hosts primarily during the austral summer in South Africa (Macnae 1954) and Australia (Thompson 1973, S. Bleakney, pers. comm.). In warmer waters such as the southeastern United States (Marcus 1961, Clark 1975), the Lesser Antilles (Marcus and Marcus 1963, 1970), and the Mediterranean coast of France (Vayssière 1888, Haefelfinger 1960) and Italy (Schmekel 1968), *Placida* has been seen primarily in winter and early spring when water temperature was at an
annual low. The cold-temperate results may reflect a minimum temperature threshold for *Placida* (Clark 1975); similarly, the warm temperate and subtropical results may indicate a maximum temperature threshold, above which the larvae or slugs cannot survive.

**Environmental Correlates**

While the association between temperature and *Placida*'s occurrence is clear, its effect on *Placida*'s population dynamics is not as straightforward as suggested by Clark (1975). For example, *Placida* exhibits similar timing of recruitment and peak population density in the North Atlantic and Pacific Oceans, which are characterized by different seasonal temperature regimes. Clark (1975) reported *Placida*'s arrival on *C. fragile* in Connecticut occurred at about 5°C in March, and ascoglossan density peaked at about 15°C in June. In contrast, during the present study, the mean monthly water temperature ranged from 9.1°C (December 1985) to 12.5°C (June 1988), and the March/April arrival and the May/June peak density of *Placida* in Oregon did not coincide with temperature transitions.

The synchrony of *Placida* populations in different years and at different geographic locations (e.g., Connecticut and Oregon) indicates that water temperature
cannot be the sole proximate factor unless different *Placida* populations respond differently to temperature. Photoperiod would be a more reliable cue to the slugs. For example, a minimum threshold photoperiod may signal *Placida* to move onto the algae in the spring and summer and off in the fall. Alternatively, increasing light levels, temperature, or both may trigger blooms of phytoplankton on which larval *Placida* feed. At high temperatures, plankton abundances and, hence, *Placida*’s larval survival may decline. Probably, *Placida*’s population dynamics were influenced by a variety of factors including water temperature and light.

**Immigration**

The movement of *Placida* among algal hosts in a local area may result from active emigration or passive dislodgment and subsequent host location. *Placida* frequently switches among conspecific algal hosts in the laboratory, rejecting some and selecting others. Whether this behavior occurs in the field, however, is difficult to verify. The dislodgment of sea slugs by waves has been directly observed (Potts 1970) or surmised (Crozier 1917, Nybakken 1978, DeFreese 1987). *Placida* is quite tenacious despite its elongate shape: its mucus is so adhesive that individuals are difficult to dislodge manually (Garstang 1890). Furthermore, the
animals congregate in the surface depressions on *C. setchellii* thalli and among the branches of *C. fragile* thalli (pers. obs.), presumably reducing the probability of dislodgment. Yet moving *Placida*, especially solitary individuals, are periodically dislodged by waves at my study sites (pers. obs.). Miller (1974) demonstrated that moving shelled gastropods have lower tenacity than stationary conspecifics.

Whether emigrating or dislodged opisthobranchs can relocate prey species is controversial (Crozier 1917, Costello 1938, Miller 1962, Potts 1970, Nybakken 1974 1978) but has not been tested experimentally. Results of my field experiments demonstrate that local movements of adult slugs could be rapid. The absence of an effect of local *Placida* source in the wave-exposed experiment (Fig. II.6B) supports the interpretation of wave-dispersal rather than slugs crawling among hosts. *Placida* emigration or dislodgment from algal hosts resulted in local dispersal of the herbivores similar to that reported for the generalist snail *Lacuna* (Martel 1988). The continuous dispersal and initial feeding attacks by adult slugs may catalyze group formation by settling larvae.

**Overwintering**

One aspect of *Placida*’s life history that is not known is the life stage (adults, eggs, or larvae) and
location in which the animals overwinter. Based on the
wide range of body size and sexual maturity of the
spring colonists (Fig. II.3-4), some adults may
overwinter, returning to the algae in the spring.
Placida does not overwinter on intertidal or subtidal
Codium spp. (Clark 1975, this study, pers. obs.), and
the ephemeral Bryopsis corticulans is not present in theall and winter. Placida may overwinter apart from its
algal hosts, but the probability of locating the slugs
is low because of their small size and cryptic
coloration. Placida can survive extended periods
without food (> 3 months in the laboratory, pers. obs.).

Placida probably does not overwinter as eggs or
planktonic larvae. The rapid development of
encapsulated larvae (7-10 days: Alder and Hancock 1844-
1845, Evans and Evans 1917, Greene 1968) indicates that
eggs probably are not the overwintering stage
hypothesized by Evans and Evans (1917), unless fall eggs
differ fundamentally from spring and summer ones.
Overwintering of eggs, however, has been demonstrated
for other ascoglossan species (Jensen 1975b). Placida
larvae probably do not remain in the plankton during the
fall and winter because 6-7 months would be an extremely
long planktonic period. Planktotrophic larval periods
usually range from about 9 to 35 days, based on data for
23 species of opisthobranchs (Hadfield and Switzer-
Dunlap 1984). Larval period of opisthobranchs, however, can be significantly extended under conditions of low food availability (R. Strathmann, pers. comm.).

Implications

In Oregon, Placida's occurrence coincides with seasonal desiccation stress in the low intertidal zone. In fact, Placida's attack was concentrated on thalli in desiccation-prone microhabitats: at the upper edge of the alga's tidal range and on sunny south and east-facing surfaces (Chapter V). Thus, ascoglossan herbivory is focused on Codium already partially stressed. Desiccation is not necessary for the slugs to attack Codium spp., based on reports of shallow subtidal populations (Haefelfinger 1960, Schmekel 1968, Clark 1975). Yet, desiccation stress may increase the apparentcy of the algal hosts to the herbivore (e.g., chemical exudation by damaged algal hosts). Alternatively, water stress may reduce algal defenses, rendering Placida's feeding more effective. While the importance of algal desiccation to Placida performance has not been examined, these types of water stress mechanisms do influence vascular plant-insect associations (White 1969, 1974, 1976, Louda et al. 1987a,b) and marine algae-herbivore associations (Santelices et al. 1981, A. Olson, pers. comm.).
Placida's life history may influence the importance of the ascoglossan as an herbivore. On one hand, Placida's short life span indicates that individuals may have only a transitory effect on algal "prey" as Nybakken (1974, 1978) suggested for short-lived nudibranch predators. On the other hand, Placida's high, though variable, recruitment throughout the spring and summer enables Placida to have a more persistent, even chronic, association with the hosts. Continuous larval recruitment and adult immigration enables Placida to track changes in algal host abundance or accessibility. For example, ascoglossans were able to locate and colonize the perennial Codium spp., even at the low densities used in my transplant experiments. Yoshioka (1982) reported a similar example with high recruitment of short-lived specialist nudibranch predators. High nudibranch abundances significantly reduced the larval production of the bryozoans on kelp fronds.

Many attributes, other than life span, may influence the effectiveness of an herbivore species as a consumer (Lubchenco and Gaines 1981, Dirzo 1984). The high probability of Placida encountering and consuming Codium coupled with the species' gregarious feeding (Alder and Hancock 1844-1845, Macnae 1954, Clark 1975) and the timing and thallus location of the grazing,
indicate that the ascoglossan may reduce algal host biomass. Herbivory by other marine specialists (Steneck 1982, Clark 1975, Clark and DeFreese 1987) may also strongly influence algal hosts. Whether such effects will influence local community structure depends on the role of the host plants. If the hosts are competitive dominants in marine benthic communities, such as *C. dimorphum* in Chile (Santelices et al. 1981) and *C. fragile* subsp. *tomentosoides* in the northwestern Atlantic, herbivory by marine specialists may have far-reaching community effects.
Chapter III

DIET SPECIALIZATION LIMITS HERBIVOROUS SEA SLUGS' CAPACITY TO SWITCH AMONG ALTERNATE FOOD SPECIES

ABSTRACT

Resource use among sympatric, conspecific individuals can vary from (1) the generalized activity of each individual to (2) the collective activity of different types of specialist individuals. The oligophagous sea slug Placida dendritica (Gastropoda: Opisthobranchia: Ascoglossa) exhibited the latter pattern: individuals specialized on a single green algal host species with different individuals specializing on different algal hosts. The capacity of Placida individuals to feed and grow on alternate host species was unusually limited: a large percentage of the slugs died in the presence of alternate host species that sympatric conspecifics consumed. In this study of Placida's feeding specificity, three crucial results were found. First, individuals from different host species exhibited different rank preferences of host species. These differential preferences did not change through time and were independent of Placida size. Second, the pattern of Placida's exploration and use of alternate host species was not strictly a function of food quality or taxonomic affinity of algal hosts alone,
but may be a combination of the two attributes. Third, Placida's highly rigid feeding specificity was not modified through hunger level, algal condition, or social facilitation. Placida's extreme trophic specialization indicates that the physiological or behavioral costs to switching hosts may be extremely high in short-lived foragers.
INTRODUCTION

Resource use of sympatric, conspecific individuals can vary from (1) the generalized activity of each individual (e.g., polyphagous individuals) to (2) the collective activity of different types of specialist individuals (e.g., oligophagous individuals) (Van Valen 1965, Roughgarden 1974, Singer 1982, Werner and Sherry 1987). Because natural selection acts on individuals, understanding the foraging and feeding behavior of individuals is essential to understanding the ecological and evolutionary implications of resource use (Singer 1982, West 1986, 1988, Thompson 1988b). Interindividual variation in foraging preferences, specificity, and methods occurs in different types of foragers (consumers, pollinators, and ovipositors) in a range of taxa (insects, rotifers, gastropods, fishes, reptiles, and birds) (Table III.1). Such variation has both ecological and evolutionary implications.

Interindividual variation in foraging may influence how foraging effort is distributed among and with prey species (Selander 1966, West 1988). If the behavioral variation is genetically based, it may lead to sympatric race formation of the foragers.

Three general types of mechanisms may select for increased interindividual variation in foraging: intense predation, intense intraspecific competition,
Table III.1. Reports of interindividual variation in foraging preferences, specificity, and methods in different types of foragers and different taxa.

<table>
<thead>
<tr>
<th>TYPES OF FORAGERS &amp; TAXA</th>
<th>REFERENCES</th>
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<tbody>
<tr>
<td><strong>CONSUMERS</strong></td>
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<tr>
<td>Insects</td>
<td></td>
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<tr>
<td>aphids</td>
<td></td>
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<tr>
<td>Gastropods</td>
<td></td>
</tr>
<tr>
<td>snails</td>
<td>West 1986, 1988</td>
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<tr>
<td>slugs</td>
<td>Jensen 1989, this study</td>
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<tr>
<td>Fishes</td>
<td></td>
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<tr>
<td>trout</td>
<td>Bryan &amp; Larkin 1972</td>
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<tr>
<td>Reptiles</td>
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<tr>
<td>snakes</td>
<td>Arnold 1981</td>
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<tr>
<td>Birds</td>
<td></td>
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<tr>
<td>oyster-catchers</td>
<td>Norton-Griffiths 1967</td>
</tr>
<tr>
<td>tits</td>
<td>Partridge 1976</td>
</tr>
<tr>
<td>finches</td>
<td>Grant 1981, Grant et al. 1976, Werner &amp; Sherry 1987</td>
</tr>
<tr>
<td>woodpeckers</td>
<td>Selander 1966</td>
</tr>
<tr>
<td><strong>POLLINATORS</strong></td>
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<tr>
<td>Insects</td>
<td></td>
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<tr>
<td>butterflies</td>
<td>A.C. Lewis 1986, 1989</td>
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<tr>
<td><strong>OVIPOSITORS</strong></td>
<td></td>
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<tr>
<td>Insects</td>
<td></td>
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<tr>
<td>fruit flies</td>
<td>Jaenike &amp; Grimaldi 1983</td>
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<tr>
<td>Rotifers</td>
<td>L. Walsh (pers. comm.)</td>
</tr>
</tbody>
</table>
and differential fitness on abundant, temporally predictable, and diverse resources (Van Valen 1965, Roughgarden 1972, 1974, Wiklund 1974, Partridge 1976, Futuyma and Moreno 1988, West 1988). The proposed benefit to a forager of within-population trophic specialization is reduced predation, reduced competition, or increased foraging efficiency; the ecological cost is reduced efficiency, or even reduced capacity, to use alternate prey (Grant 1950, Alstad and Edmunds 1983, Rausher 1983, A.C. Lewis 1986, 1989, Moran 1988). The evolutionary cost may be limited capacity to use newly available superior hosts (Moran 1988).

In species with interindividual variation in foraging, individual foragers often exhibit a high degree of foraging consistency in preferences, specificity, or methods through time (Norton-Griffiths 1967, Bryan and Larkin 1972, Heinrich 1976, 1979, Rissing 1981, West 1986, 1988, Werner and Sherry 1987, Lewis 1989). Yet, for many of the long-lived species examined, the foraging consistency relative to the foragers' life span or oviposition stage is not known. When the life span of the animal is shorter than the availability of the resource (e.g., worker honeybees, Heinrich 1976), individuals may exhibit relatively inflexible foraging preferences or methods. Animals with life spans longer than the availability of the
resource (e.g., queen honeybees, Heinrich 1976, 1979; ants, Rissing 1981), however, may exhibit short-term trophic specializations that change with resource availability.

Foraging consistency may also be associated with social foraging, though pertinent information is sparse. Social foragers that recruit conspecifics (e.g., honeybees, ants) often display greater host-consistency than either social solitary foragers (e.g., bumblebees) or non-social foragers (Heinrich 1976, 1979). Past studies, however, on foraging specialization of social insects are complicated by several variables. First, while individuals are specialist collectors, they often share food resources in the colony (Heinrich 1976, 1979). Individual fitness, therefore, is not directly coupled with individual foraging performance. Second, in social insects, the workers are often non-reproductive. The effect of foraging specializations on individual survival and fitness are thus difficult to assess. Third, the effect of social foraging among unrelated conspecifics on trophic specialization is not known.

A major gap in our understanding of prey or host consistency in short-lived animals, social or non-social, is whether the rigid behavior can be modified by satiation level, prey condition, or conspecific
behavior. For many oligophagous species, eventually any host becomes acceptable (Singer 1982, Rausher 1983). In this study, I investigate the highly rigid feeding behavior of the herbivorous sea slug Placida dendritica (Gastropoda: Opisthobranchia: Ascoglossa): individuals specialize on different green algal species with limited capacity to switch to algal host species that sympatric conspecifics consume. I address three central questions. First, do different individuals exhibit the same preference rankings of host species? Second, what are the behavioral "rules" of sea slug diet choice and capacity to switch? What do the rules indicate about the types of trophic constraints? Third, is the sea slug's rigid feeding behavior modifiable either through extrinsic factors (e.g., food quality or quantity) or intrinsic factors (e.g., satiation level or learning)?
BACKGROUND

Placida is a common sea slug in warm-temperate to boreal coastal waters throughout the world (Schmekel and Portmann 1982). The herbivore has a complex life cycle with planktotrophic larvae (Clark 1975) and benthic adults. Larvae settle, metamorphose, recruit to the algal hosts throughout the spring and summer (Millen 1980, Chapter II); individuals grow to maturity in less than one month (Clark 1975, Chapter II). Macroalgal host utilization, therefore, is determined by the settling larvae and mobile adults (Chapter II).

Because of the wide geographic distribution of Placida, the ascoglossan's diet appears fairly broad. The benthic juvenile and adult Placida feed on the green algae Codium spp. and Bryopsis spp. throughout their range. In certain localities, the ascoglossan also feeds on other green algae: Derbesia spp. (Bleakney 1989), Halimeda cuneata (Macnae 1954), and Cladophora sp. (Colgan 1911, Oakes 1979; but not seen by Evans and Evans 1917 or Trowbridge, pers. obs.). Along the central coast of Oregon, the algal hosts are the perennial Codium setchellii and C. fragile as well as the spring-summer ephemeral Bryopsis corticulans. Because Placida occur on all these hosts from April to September (Chapter II), the slugs' host specificity does not reflect differential host phenology as suggested for
some insects (Holdren and Ehrlich 1982, Mitter and Futuyma 1983, Williams and Bowers 1987). Furthermore, because the three algal species are often sympatric in the low intertidal zone, Placida's differential host specificity does not reflect microhabitat specialization.
MODELS

A forager's prey choice and capacity to switch may range from fully constrained (monophagous individuals) to unconstrained (polyphagous individuals). In the latter case, individuals may switch freely among all prey types used by conspecifics. Most foragers, however, exhibit intermediate patterns such that behavioral, morphological, or physiological constraints prevent individuals from switching among all prey types. These constraints may be associated with differential food quality or taxonomic similarity of prey.

Food Quality Model

Based on food quality alone, Placida should prefer the highest quality host available; the slugs should switch readily to high quality food but resist switching to a low quality food (Fig. III.1A). For example, Placida from C. setchellii (Cs) should switch readily both to C. fragile (Cf) and Bryopsis (Bc) (solid arrows). In contrast, slugs from Bryopsis should resist switching to either Codium species (dashed arrows), at least in the short-term.

I have four à priori reasons to consider Bryopsis the highest quality food, C. fragile intermediate, and C. setchellii the lowest of Placida's local host species (Table III.2). I hypothesize that Bryopsis is a high
Algal Quality Model

Bc

\[ \text{Taxonomic Model} \]

Cf

Cs

Hybrid Model

Bc

Cs \rightarrow Cf

Bc

\[ \text{Figure III.1. Predictions of three partial constraint models on how Placida dendritica selects among its three algal host species: Bryopsis corticulans (Bc), Codium fragile (Cf), and C. setchellii (Cs). Arrows indicate the relative number of Placida individuals that switch readily between hosts: solid arrow denotes most or all, dashed arrow indicates some, dotted arrow indicates few, and no arrow between two host species indicates no individuals.} \]
Table III.2. A priori reasons to rank the food quality of the algal hosts of Placida dendritica as follows:

*Bryopsis corticulans* (highest) > *Codium fragile* > *C. setchellii* (lowest).

<table>
<thead>
<tr>
<th>Attributes</th>
<th><em>Bryopsis corticulans</em></th>
<th><em>Codium fragile</em></th>
<th><em>Codium setchellii</em></th>
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<tr>
<td>Macrostructure a</td>
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<tr>
<td>Upright</td>
<td>Upright</td>
<td>Crustose</td>
<td></td>
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<tr>
<td>Finely branched</td>
<td>Coarsely branched</td>
<td>Unbranched</td>
<td></td>
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<tr>
<td>Herbivores Grasp Algae</td>
<td>easily</td>
<td>moderately</td>
<td>laboriously</td>
</tr>
<tr>
<td>Herbivores Remove Tissue</td>
<td>easily</td>
<td>moderately</td>
<td>laboriously</td>
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<tr>
<td>Microstructure b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single large tube</td>
<td>interwoven siphons</td>
<td>interwoven siphons</td>
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<tr>
<td>Cell Sap Volume Per Puncture (benefit)</td>
<td>high</td>
<td>moderate</td>
<td>low</td>
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<tr>
<td>Wall Penetration Resistance (cost)</td>
<td>low</td>
<td>moderate</td>
<td>high</td>
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<td>Life History c</td>
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<tr>
<td>Ephemeral</td>
<td>Perennial</td>
<td>Long-lived</td>
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<tr>
<td>Apparentance to Herbivores</td>
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<td>Moderate to high</td>
<td>High</td>
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<td>Herbivore Response d</td>
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<tr>
<td>Placida's Max. Size Field</td>
<td>135 mg</td>
<td>7 mg</td>
<td>5 mg</td>
</tr>
<tr>
<td>Laboratory</td>
<td>similar</td>
<td>30 mg</td>
<td>similar</td>
</tr>
</tbody>
</table>


*b* Silva (1951), Jensen (1983), Trowbridge (pers. obs.)

*c* Feeny (1976), Jensen (1983), Trowbridge (pers. obs.)

*d* Trowbridge (unpubl. data)
quality food because the ease with which herbivores can grasp the thallus and remove tissue relative to Codium spp. For a suctorial feeder such as Placida, the amount of "cell sap" food available per puncture is greater in Bryopsis than in Codium due to the algal microstructure (Silva 1951). Furthermore, the cost of puncturing walls to feed is less for Bryopsis than for Codium spp. (Jensen 1983, Trowbridge, pers. obs.). Because Bryopsis is an ephemeral alga, it may be less apparent to herbivores than the perennial Codium spp. (Feeny 1976). Finally, Placida maximum weight is almost 20-fold greater on Bryopsis than on Codium spp. in the field. A similar comparison of the two Codium species suggests that C. fragile is higher in quality than C. setchellii.

Taxonomic Model

Oligophagous insects generally feed on hosts in the same family rather than different families because of chemical and structural similarities of the plants (Dethier 1954, Ehrlich and Raven 1964, Cruden 1972). Similarly, within algal divisions, the production of secondary metabolites occurs in specific families, and the green algae consumed by ascoglossan species typically belong to "chemically rich families" (Hay and Fenical 1988). Algal structural attributes are also often family and order-level characters. Because Bryopsis and Codium
belong not only to different families but also to
different orders, Placida may switch more readily between
Codium species than between Codium and Bryopsis (Fig.
III.1B).

A hybrid model of food quality and taxonomic
similarity of algal food is possible as well (Fig.
III.1C). The prey species may be ranked by absolute food
quality, but barriers exist between prey that are
taxonomically dissimilar (e.g., structurally or
chemically). In some cases, these taxonomic constraints
may prevent some or all individuals from consuming
readily available, high quality foods (Moran 1988).
METHODS

General Experimental Procedures

Feeding experiments were conducted in the laboratory in 1987 and 1988 to examine intraspecific variation in *Placida*'s feeding preferences, growth, and survival on the three algal host species. I collected circular plugs of *C. setchellii* (1.6 cm diameter), the top 2.5-5.0 cm of *C. fragile* branch tips, and clumps of *Bryopsis*. Algae were kept in running seawater for at least two days prior to use. Algae and ascoglossans were placed in separate 0.5-liter containers with fresh seawater. The containers were placed within a shallow, running-seawater table to maintain the temperature close to that in the field.

Preference Experiments

In the feeding preference experiments, individual *Placida* were offered the choice of the three algal species. The number of *Placida* on each algal species was counted periodically for two days. The algal species with the highest number of ascoglossans per census was considered to be preferred. Distinct preferences were exhibited within 5-10 hours and maintained for several days.

Growth Rates and Survival

In the short-term growth experiments, individual
Placida were weighed to the nearest 0.01 milligram and placed on restricted single-species diets. At the end of each experiment (usually 2.5 to 5 days), the Placida were reweighed and the daily percent weight change calculated. The precision of blotting and weighing was 2.7%, based on the mean percent difference in weight of 25 individuals weighed twice. To examine whether diet switching would occur over a longer period of time, I weighed individual ascoglossans, placed them on restricted single-species diets, and monitored their fate and behavior for 2 to 3 weeks. The duration of these experiments, thus, spanned over half of the slugs' post-metamorphic life: the animals grow to sexual maturity in less than a month after larval settlement (Chapter II).

To determine whether Placida's capacity to switch diets was related to slug size, I placed individual preweighed Placida from Bryopsis on C. fragile, and monitored the slugs for nine days. These test animals ranged in size from 0.8 to 26.1 mg. The mean size of (1) survivors and fatalities, (2) feeders and non-feeders, and (3) effective and ineffective feeders was compared in separate Student's t-tests.

Starvation Tolerance

Placida may differ in the quality or quantity of food reserves obtained from different diets, and such
differences may influence the time individuals survive while learning to feed on novel hosts. To test this hypothesis, I compared the starvation tolerances of Placida from each algal species. I placed groups of 10 individuals from each algal species in separate containers with seawater and monitored Placida's survivorship in 10 replicate groups per algal source for 11 days. Next, I investigated whether starvation tolerance was size-specific. I placed 96 individually weighed Placida from C. fragile and 40 from C. setchellii in petri dishes with seawater in a 11°C constant temperature room. The seawater was changed every 2-4 days. After 2.5 weeks I quantified which Placida had died. The categorical data of survivors and fatalities were analyzed, using a Chi-square test.

Modification of Behavior

Placida's rigid feeding specificity may relax if the "unfamiliar" host species are damaged by feeding conspecifics. To test this hypothesis, I placed 0 or 5 large Placida from C. fragile on individual pieces of C. fragile tissue. After two days, the experimental algal tissue was extensively damaged by Placida's grazing; control tissue was undamaged. I removed the ascoglossans and used the algae to test whether Placida from Bryopsis and C. setchellii exhibit differential growth on
undamaged and damaged "unfamiliar" algae; Placida from C. fragile were used as a control.

Many animal species learn to feed on new prey species by observing experienced individuals. To test whether inexperienced Placida individuals had the capacity to learn to feed on "unfamiliar" host species, I placed individual inexperienced Placida from Bryopsis on C. fragile in the presence or absence of experienced C. fragile-slugs. I also placed inexperienced Placida from C. setchellii on Bryopsis in the presence or absence of experienced Bryopsis-slugs. For both experiments, I quantified the percent daily weight change of the inexperienced Placida individuals over 2-5 days.
RESULTS

Recent Feeding History

Preference

In algal choice experiments, Placida from different host species exhibited different preference rankings. Placida from C. fragile and Bryopsis strongly preferred the algal species from which they had been collected in the field (Fig. III.2B,C). In contrast, while individuals from C. setchellii preferred Codium over Bryopsis, they exhibited no preference between the two species of Codium (Fig. III.2A). These preferences were not size-specific: they were consistent for a wide range of body sizes of Placida from each algal species.

The extent of variation in preferences of slugs from each algal species differed. Placida from C. setchellii exhibited more variation in algal preference than conspecifics from C. fragile and Bryopsis (Fig. III.2A). Diet consistency of individuals during the two-day experiment also varied significantly with algal source: 24% of the slugs from C. setchellii, 54% of those from C. fragile, and 88% of those from Bryopsis were observed on only their original diet (Chi-square test, $X^2=21.5, 2$ df, $P<0.001$).

Performance

Placida from different algal sources grew differently on the three algal host species (highly
Figure III.2. Algal preferences of individual *Placida dendritica* collected from: (A) *Codium setchellii* (Cs), (B) *C. fragile* (Cf), and (C) *Bryopsis corticulans* (Bc). The symbol denotes the algal source. The number of *Placida* tested from each algal host is indicated.
significant interaction \( P<0.001 \), Table III.3). Placida from Bryopsis grew well on that alga but lost weight at starvation rates on both Codium spp. None of the ten animals from Bryopsis raised on Codium spp. ever switched their rigid feeding behaviors. In contrast, slugs from C. fragile exhibited no difference in relative growth rates on Bryopsis and C. fragile but performed worse on C. setchellii. Furthermore, one of the five individuals from C. fragile did eventually feed on Bryopsis and grew at an astronomical rate (104% per day). Finally, Placida from C. setchellii exhibited the highest relative growth rate on C. fragile, not on C. setchellii; no slugs switched successfully switched to Bryopsis. The time and ability for slugs to learn to feed on unfamiliar algal hosts varied.

**Survival**

Results of the long-term feeding experiments indicated that Placida's rigid feeding specificity did not change through time (Fig. III.3). Ascoglossans from C. setchellii held on the two Codium species had similar high survival (Chi-square test, \( X^2=0.1, P=0.734 \)) but had low survival on Bryopsis (Fig. III.3A). In fact, survival on Bryopsis was comparable to that of slugs in the starvation control (\( X^2=2.0, P=0.159 \)). Placida's survival on the Codium spp. restricted diets was greater
Table III.3. A. Treatment sum of ranks of the relative growth rate of *Placida dendritica* collected from the three algal hosts (source) when maintained on restricted diets of each host (restricted diet) for five days. Algal host species were *Codium setchellii* (Cs), *C. fragile* (Cf), and *Bryopsis corticulans* (Bc). Five replicate individuals were examined per treatment. Note that low sum of rank values denote high relative growth rates and high values denote low growth rates. B. Results of a nonparametric two-way analysis of variance (extension of Kruskal-Wallis test, Zar 1984).

A. SUM OF RANKS OF RELATIVE GROWTH

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>Cs</th>
<th>Cf</th>
<th>Bc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cs</td>
<td>105</td>
<td>81</td>
<td>193</td>
</tr>
<tr>
<td>Cf</td>
<td>129</td>
<td>78</td>
<td>78.5</td>
</tr>
<tr>
<td>Bc</td>
<td>174</td>
<td>165.5</td>
<td>31</td>
</tr>
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</table>

B. NONPARAMETRIC 2-WAY ANOVA

<table>
<thead>
<tr>
<th>Factors</th>
<th>df</th>
<th>SS</th>
<th>H</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cells</td>
<td>8</td>
<td>4664.9</td>
<td>-</td>
<td>&lt;0.050</td>
</tr>
<tr>
<td>Source</td>
<td>2</td>
<td>356.4</td>
<td>2.1</td>
<td>&gt;0.050</td>
</tr>
<tr>
<td>Diet</td>
<td>2</td>
<td>413.0</td>
<td>2.4</td>
<td>&gt;0.050</td>
</tr>
<tr>
<td>Source x Diet</td>
<td>4</td>
<td>3895.5</td>
<td>22.6</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
than on the **Bryopsis** and starvation control diets 
\(X^2=37.0, P<0.001\). A similar response was seen for the 
ascoglossans from **C. fragile**. Animals held on the two 
**Codium** spp. had similar high survival \(X^2=0.1, P=0.717\) 
and those on the **Bryopsis** and starvation control diet had 
similar low survival \(X^2=1.7, P=0.197\). Furthermore, the 
slugs' survival on the **Codium** spp. diets was 
significantly greater than on the **Bryopsis** and starvation 
control diets \(X^2=11.6, P=0.001\).

**Placida** collected from **Bryopsis** responded 
differently (Fig. III.3B): individuals had low 
indistinguishable survival on the **C. setchellii** and the 
starvation control diets (Chi-square test, \(X^2=0.1, 
P=0.722\)). Individuals held on **C. fragile** survived 
significantly better on **C. fragile** than on **C. setchellii** 
\(X^2=10.9, P=0.001\). **Placida** from **Bryopsis** were not held 
on that alga in this experiment because it was 
logistically not feasible to provide sufficient food to 
the voracious **Bryopsis**-feeders during a long-term 
experiment. The slugs' survival in comparable 
experiments, however, was close to 100% (pers. obs.).

The results of this set of three long-term 
experiments illustrate two crucial points. First, some 
of the animals have the capacity to switch ("switchers"); 
others do not ("non-switchers") and die in the presence
Figure III.3. Survivorship curves of *Placida dendritica* from (A) *Codium setchellii* and (B) *Bryopsis corticulans* when maintained on different restricted laboratory diets. Algal diets are abbreviated as follows: *C. setchellii* (Cs), *C. fragile* (Cf), and *Bryopsis* (Bc). In (B) the *Bryopsis*-diet control was not conducted for logistical reasons.
Figure III.3.
of algal food. Second, the capacity to switch appears to be a function of the source and target alga. For example, slugs from *C. setchellii* were more willing than those from *Bryopsis* to switch to *C. fragile* (Fig. III.2, Table III.3). Slugs, however, would not switch between *C. setchellii* and *Bryopsis* (Fig. III.3, Table III.3).

**Starvation Tolerance**

Over half the slugs from all three host species survived the 2-week starvation tolerance experiment, suggesting that the animals in groups have sufficient energy reserves to survive a moderate period of learning to feed on unfamiliar host species. The starvation tolerance of *Placida* from different host species, however, did vary significantly after 5 and 11 days of food deprivation ($P=0.047$ and $P=0.004$, Table III.4A) but not after 14 days ($P=0.960$). Slugs collected from *C. setchellii* had higher survivorship than slugs from the other two host species.

Starvation tolerance was not size-specific for *Placida* from *C. fragile* ($P=0.439$) or from *C. setchellii* ($P=0.763$) (Table III.4B). After extended deprivation, the slugs lost the ability to cling to surfaces, presumably due to a lack of mucus, and were easily dislodged. They then became immobile and unresponsive -- even to food. *Placida* may not have sufficient energy reserves to survive extended periods of learning to feed
Table III.4. A. Starvation tolerance of Placida dendritica from the three algal host species. Survivorship data in percentage of slugs alive at the start of each time interval. B. Size-specific starvation tolerance of Placida from the two Codium spp. Data in percentage of individuals in each size class (mg wet weight) that survived 2.5 weeks.

A. HOST-SPECIFIC SURVIVAL

<table>
<thead>
<tr>
<th>Host Species</th>
<th>Day 5</th>
<th>Day 11</th>
<th>Day 14</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bryopsis corticulans</td>
<td>77%</td>
<td>87%</td>
<td>85%</td>
</tr>
<tr>
<td>Codium fragile</td>
<td>82%</td>
<td>73%</td>
<td>87%</td>
</tr>
<tr>
<td>C. setchellii</td>
<td>90%</td>
<td>91%</td>
<td>85%</td>
</tr>
</tbody>
</table>

Chi-square tests:
\[ X^2 = 6.1, \quad X^2 = 10.9, \quad X^2 = 0.1 \]
\[ P = 0.047, \quad P = 0.004, \quad P = 0.960 \]

B. SIZE-SPECIFIC SURVIVAL

<table>
<thead>
<tr>
<th>Placida from Codium fragile</th>
<th>Weight Classes (mg)</th>
<th>Placida from C. setchellii</th>
<th>Weight Classes (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;0.5</td>
<td>&lt;1.0</td>
<td>&lt;1.0</td>
</tr>
<tr>
<td></td>
<td>&gt;1.5</td>
<td>&gt;2.0</td>
<td>&gt;2.0</td>
</tr>
<tr>
<td>%</td>
<td>76.3</td>
<td>88.2</td>
<td>64.0</td>
</tr>
<tr>
<td>%</td>
<td>73.3</td>
<td>66.7</td>
<td>53.9</td>
</tr>
<tr>
<td>n</td>
<td>38</td>
<td>17</td>
<td>25</td>
</tr>
<tr>
<td>n</td>
<td>15</td>
<td>13</td>
<td>18</td>
</tr>
</tbody>
</table>

Chi-square test:
\[ X^2 = 2.7, \quad P = 0.439 \]
\[ X^2 = 0.5, \quad P = 0.763 \]
on unfamiliar algal hosts. Alternatively, the herbivores may be morphologically or physiologically incapable of switching.

Behavioral Modification

Effect of Algal Damage

Individual Placida from C. fragile grew significantly faster (ANCOVA: $F=10.1, P=0.004$) on C. fragile damaged by conspecifics (Fig. III.4B). Placida from the other two host species exhibited different responses. Placida from C. setchellii (Fig. III.4C), on average, grew faster on damaged C. fragile though not significantly so (ANCOVA: $F=1.9, P=0.185$). Placida from Bryopsis lost weight at comparable rates (ANCOVA, $F=1.1$, $P=0.299$) on damaged and undamaged C. fragile (Fig. III.4A). Algal condition, therefore, did not modify Placida's highly rigid feeding specificity though it did influence growth of experienced individuals that did feed (e.g., Placida from C. fragile).

Effect of Experienced Conspecifics

Placida's feeding specificity was also not modifiable through exposure to "experienced" conspecifics (Table III.5). After 2.5 days (early), Placida from Bryopsis had, on average, lost less weight on C. fragile in the presence of experienced conspecifics than in the other three treatments. This difference, however, was
Figure III.4. Mean percent daily weight change of Placida from (A) Bryopsis corticulans, (B) Codium fragile, and (C) C. setchellii when maintained on restricted diets of C. fragile undamaged (Undam) or damaged (Dam) by Placida grazing. Vertical bars denote ± 1 SE. The number of replicates per treatment is indicated. Results were analyzed using analyses of covariance with initial Placida weight as the covariate. Data for C. setchellii animals were transformed prior to analysis to reduce the heterogeneity of variances.
Figure III.4.
Table III.5. Mean percent daily weight change (A, B) and survivorship (B) of inexperienced *Placida dendritica* in the presence or absence of algal food and experienced conspecifics. Inexperienced individuals were from (A) *Bryopsis corticulans* and (B) *Codium setchellii*; experienced *Placida* were from (A) *C. fragile* and (B) *Bryopsis*. "Early" denotes the initial 2.5-day period; "late" denotes the subsequent 2.5-day period.

### A. INEXPERIENCED *BRYOPSIS* SLUGS

<table>
<thead>
<tr>
<th></th>
<th>EARLY</th>
<th>LATE</th>
<th>2-way ANOVAS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ø C. fragile Ø C. fragile</td>
<td>diet</td>
<td>conspecifics</td>
</tr>
<tr>
<td># OF EXPERIENCED CODIUM-FEEDERS</td>
<td></td>
<td></td>
<td>F=1.8 P=0.203</td>
</tr>
<tr>
<td>Ø</td>
<td>-14.8</td>
<td>-13.6</td>
<td>-12.4 -12.0</td>
</tr>
<tr>
<td>5</td>
<td>-13.6</td>
<td>-5.6</td>
<td>-12.8 -12.8</td>
</tr>
</tbody>
</table>

### B. INEXPERIENCED *CODIUM* SLUGS

<table>
<thead>
<tr>
<th></th>
<th>% DAILY WEIGHT CHANGE</th>
<th>SURVIVORSHIP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ø SE n</td>
<td>% n</td>
</tr>
<tr>
<td># OF EXPERIENCED BRYOPSIS-FEEDER</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ø</td>
<td>-7.8 1.0 10</td>
<td>58.8% 17</td>
</tr>
<tr>
<td>1</td>
<td>-5.9 1.6 7</td>
<td>41.2% 17</td>
</tr>
</tbody>
</table>

Student’s t-test
t=-1.0, P=0.314

Chi-square test
X²=1.1, P=0.303
not statistically significant and disappeared by day five. In fact, the rate of weight loss in all treatments was indistinguishable from that in the starvation control. When I repeated this experiment, I again detected no significant growth response due to the presence of the experienced feeders, even when the rate of weight loss was corrected for initial body size (ANCOVA: F=0.6, P=0.436). Experienced Codium-feeders, therefore, did not induce, stimulate, or teach Bryopsis-feeders to eat Codium in short-term experiments.

Placida from C. setchellii that were fed Bryopsis performed similarly in the presence and absence of experienced Bryopsis-feeders. After five days, there was no significant difference in survival of the inexperienced individuals in the two treatments (Chi-square test, $X^2=1.1$, $P=0.303$) or the percent weight change of the survivors (Student's t-test, $t=-1.0$, $P=0.314$). The rigid feeding specificity of Placida from C. setchellii was not modifiable through exposure to the feeding activities of conspecifics.

Size-Specific Capacity To Switch Algal Species

Placida's capacity to switch host species was not a function of body size (Table III.6). For slugs from Bryopsis that were held on C. fragile, the mean size of the survivors did not differ from that of the fatalities.
Table III.6. Mean initial sizes (mg wet weight) of *Placida dendritica* from *Bryopsis corticulans* with respect to survival and feeding behavior on *Codium fragile*.

*Placida* ranged in size from 0.8 to 26.1 mg. Half of the data sets were transformed prior to analysis to make the variances homogeneous. Mean values were compared, using Student's t-tests.

<table>
<thead>
<tr>
<th></th>
<th>DAY 2</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SD</td>
<td>n</td>
<td>$\bar{X}$</td>
<td>SD</td>
<td>n</td>
</tr>
<tr>
<td><strong>SURVIVORSHIP</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survivors</td>
<td>6.2</td>
<td>6.1</td>
<td>44</td>
<td>5.6</td>
<td>6.4</td>
<td>35</td>
</tr>
<tr>
<td>Fatalities</td>
<td>5.6</td>
<td>4.6</td>
<td>14</td>
<td>6.6</td>
<td>4.7</td>
<td>23</td>
</tr>
<tr>
<td>t=0.3</td>
<td>t=0.6</td>
<td>t=0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P=0.737</td>
<td>P=0.561</td>
<td>P=0.584</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>BEHAVIOR</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeders</td>
<td>3.8</td>
<td>3.4</td>
<td>11</td>
<td>5.6</td>
<td>7.4</td>
<td>19</td>
</tr>
<tr>
<td>Non-Feeders</td>
<td>6.9</td>
<td>6.7</td>
<td>33</td>
<td>5.7</td>
<td>5.3</td>
<td>16</td>
</tr>
<tr>
<td>t=1.4</td>
<td>t=0.02</td>
<td>t=1.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P=0.161</td>
<td>P=0.985</td>
<td>P=0.300</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Furthermore, the mean size of feeders did not differ from that of the non-feeders. Finally, the "effective feeders" (created extensive structural damage to the algae) did not differ in size from those that were "ineffective" (no observable damage) (Student's t-test, t=0.6, P=0.586). The capacity of *Placida* to switch algal host species, therefore, did not vary with ascoglossan size.
DISCUSSION
Host Species Ranking

A puzzling question is why not all individuals in a consumer population feed on the most profitable prey available. Based on food quality or taxonomic relatedness of prey species alone, all individuals should exhibit the same rank order of prey preferences but a different number of prey selected, depending on the degree of choosiness or specificity (Singer 1982, Thompson 1988b). Several studies provide such evidence (Wiklund 1981, Singer 1971, 1982, Thompson 1988b). If the preferred prey is not available or if the consumer has imperfect information about the available prey, the consumer should use the most preferred prey it can locate (Heinrich 1976, Singer 1982, 1983). For example, if Placida larvae that are competent to settle can locate only C. setchellii, they may select the inferior host rather than no host. Preference, therefore, may not always result in differential host use (Singer 1983). Yet, theoretically, the individuals should exhibit the same preference rankings when exposed to all the hosts in choice experiments.

Many studies, however, have documented inter-individual variation in the rank order of consumer preference of prey species (Tabashnik et al. 1981, Jaenike and Grimaldi 1983, Singer 1983, West 1986, Ng
1988, this study). Possible explanations for this pattern are three-fold. First, heterogeneity in food quality within prey species will generate overlap in prey acceptability to an individual forager (Alstad and Edmunds 1983, Singer 1983). This mechanism may occur in consumers (1) with low mobility or (2) in environments with low plant density; the consumers, thus, have limited opportunity to sample plants. Second, foragers' limitations in modifying behaviors may prevent foragers from using the "best" prey after they initially specialize on an inferior host. For example, the cost of switching prey species may exceed the cost of bypassing acceptable prey. Alternatively, foragers' genotypes may restrict host use (Alstad and Edmunds 1983). Third, some foragers may not be continuously sensitive to prey quality: they may have a discrimination phase during development in which they assess the quality of the available prey, and then focus their search for the selected prey (Singer 1983).

Although the prey heterogeneity hypothesis was not explicitly tested, it does not adequately explain the variation in Placida's host rankings because of Placida's strong source effect (Fig. III.2, Table III.3). The forager limitation hypothesis has been used to explain difficulties of consumers to modify "stereotyped" feeding methods (Laverty 1980, Jensen 1989). While this
explanation is plausible for Placida, it is difficult to test because of the low incidence of successful switches. The discrimination phase hypothesis (Singer 1983) has no unequivocal support and seems maladaptive for animals in changing environments.

Behavioral Rules

Because of the variation in Placida's preference rankings and survival (Fig. III.2, Table III.3), the observed results do not strongly support the hypothesized taxonomic or food quality models. Placida from C. setchellii exhibited preferences consistent with the taxonomic and hybrid models: no preference between Codium spp. but a slight preference for and better survival on Codium spp. relative to on Bryopsis. Furthermore, although these animals did not exhibit a preference between Codium species, they did grow faster on C. fragile, the hypothesized superior Codium species. Slugs from Bryopsis exhibited food preference rankings and relative performance consistent with the food quality and hybrid models. Finally, the behavior of slugs from C. fragile were consistent with the hybrid model: the animals resisted using the inferior C. setchellii in preference experiments but eventually consumed it in the restricted diet survivorship experiments. Furthermore, they appeared unable to use the superior Bryopsis.
A simple answer, therefore, to which alga represents the "best" food is not possible because algal source or recent dietary history affects an individual's performance on a given algal food. The evidence tends to support the hybrid model such that the slugs grow better on superior algal species that are closely related to the animals' original diet. Most individuals have limited capacity to consume taxonomically dissimilar, superior host species.

Diet Flexibility

Slugs may vary in the extent of their choosiness or discrimination: the least choosy or discriminating individuals consuming a broad diet and the most choosy or discriminating ones consuming only the most preferred food (Singer 1982, 1983, Ng 1988). This variation in choosiness or discrimination may reflect variation in the fitness of foragers on different prey: "discriminators" may have higher fitness on preferred hosts whereas conspecific "non-discriminators" may have similar fitness values on all hosts (Ng 1988). This hypothesis may partially explain my results. Placida "non-switchers" (the choosiest consumers) have the highest fitness on their preferred hosts and the lowest on their least preferred hosts. For example, Bryopsis slugs grow well on Bryopsis but not on Codium spp. In contrast,
"switchers" (the least choosy individuals) have less discrepancy in their survival and growth on original and alternate hosts. For example, C. setchellii slugs readily consumed C. fragile.

**Characteristics That May Vary**

Whether or not foraging behavior is modifiable depends on both (1) the specific attributes that determine the behavior and (2) the ultimate basis of the behavior. For example, interindividual variation in foraging is often, but not always, associated with behavioral, morphological, or physiological variation (Van Valen 1965, Selander 1966, Roughgarden 1974, Grant et al. 1976, Grant 1981, Werner and Sherry 1987). Do Placida individuals from different algal hosts species differ? Placida exhibited host-specific differences in gregariousness, forming feeding groups on Codium spp. but not on Bryopsis (Chapter IV). Whether such differences reflect differing algal stimuli or innate ascoglossan behavior is not known because few Placida successfully switch between algal genera.

The morphology of Placida's soft-parts and radular teeth exhibits little variation throughout the species' geographic range (Bleakney 1989) or with algal diet (Gosliner, pers. comm.). Bleakney (pers. comm.), however, found evidence of host-specific variation in (1)
the number and relative size of slug teeth relative to body length and (2) the number of discarded teeth stored in the sac-like ascus. This type of variation in scaling may reflect the different growth rates of Placida's teeth and body as suggested by Raymond and Bleakney (1987). Variation in relative tooth size may influence the size-specific capacity of slugs to switch algal species. Several workers have stressed the importance of tooth size vs algal filament size or siphon-like utricle size (Macnae 1954, Usuki 1977, Jensen 1980, 1981a). My results from individuals from Bryopsis, however, indicated that Placida's diet capacity to switch algal host species was not size-specific over the wide range of slug and algal sizes tested (Table III.6).

Interindvidual variation in diet choice may reflect physiological differences, either (1) in the composition of digestive or salivary enzymes (e.g., ingestive conditioning, Wood 1968) or (2) in the capacity of the herbivores to detoxify secondary metabolites. Differences in digestive enzymes or detoxification mechanisms, however, are probably not the limiting constraint to Placida's feeding. Non-switchers do not ingest unfamiliar food: because Placida's body wall is translucent, any ingested food can readily be seen. The limiting step is ingestion, not digestion. Variation in suction pressure, salivary enzymes, or feeding methods
are potential mechanisms that may limit ingestion and, hence, Placida's host use.

Basis of Variation in Behavior

Prey or host selection in foragers (consumers, pollinators, and ovipositors) may be learned or determined developmentally or genetically. When the costs of switching prey or host species are relatively low (e.g., transient reduction in foraging efficiency), diet or host selection usually is modifiable through learning -- either (1) trial and error or (2) observation (Bryan and Larkin 1972, Heinrich 1976, Partridge 1976, Laverty 1980). When the costs of switching are high, such as in many short-lived insects, foraging behavior is often under developmental or genetic control. Irreversible switches during developmental may be triggered during the egg or larval stage. Eggs may be labeled by maternal diet (e.g., energy reserve in eggs) or by vegetation at the oviposition site. Larvae may imprint upon contact with the first appropriate host encountered, or larval feeding behavior may be modified by early diet. Finally, prey selection and subsequent growth may reflect the genotype of the forager. Evidence exists for each of these mechanisms of interindividual variation in resource use (Arnold 1981, Jaenike and Grimaldi 1983, Mitter and Futuyma 1983, Futuyma and

Placida's diet was not modified by adult experience, and was, therefore, either developmentally or genetically determined. Substrate labeling of eggs may occur. One possible advantage of this mechanism is that although planktonic larvae have a low probability of remaining in the parental habitat, they have a fairly high probability of locating a comparable habitat because of the wide geographic distributions of the algal hosts (Silva 1951). There are, however, two pieces of evidence that do not support this mechanism. First, egg masses were common on C. setchellii but not on C. fragile in the field; yet both species were attacked by high densities of adults. Second, errors in Placida oviposition should result in rapid shifts to use of introduced species of Codium or Bryopsis. Yet, in the northwestern Atlantic, Placida has not rapidly shifted from Bryopsis and Derbesia to the introduced Codium fragile subsp. tomentosoides (Marcus 1961, Clark and Franz 1969, Clark 1975, Bleakney 1989).

Larval imprinting on or conditioning by the first appropriate host encountered seems the most plausible, though untested, explanation for Placida's diet specificity. If Placida larvae cannot discriminate host quality or if their selection is limited by a short competency period, the slugs may occur on low quality
hosts such as *C. setchellii* when superior hosts are locally abundant. This mechanism, however, should also result in rapid use of introduced species of *Codium* and *Bryopsis*, a shift that has not been observed.

Finally, Placida's preferences may be genetically determined. Genetically determined resource use, however, typically occurs in species in which offspring remain in the parental habitat, such as parthenogenetic species (Mitter and Futuyma 1983) or direct developers. For Placida, the major constraint to a genetic basis of diet selection is the slugs' high dispersal. Because the planktonic larvae probably settle in geographically distant habitats, geographic variation in algal attractiveness or defenses may reduce the effectiveness of genetically determined food choice. Genetically determined diet preferences theoretically would be associated with some variation of Placida's morphology on different host species, especially because the slugs mate with conspecifics on the algal hosts (i.e., assortative mating). Such morphological variation, however, apparently does not occur (Bleakney 1989).

Implications of Variation In Resource Use

The implications of variation in resource use among conspecific, sympatric individuals depends in part on the (1) type of forager (consumer, pollinator, ovipositor),
(2) temporal persistence of the specializations, (3) basis of such specializations, and (4) life history attributes (life span, reproductive mode, recruitment) of the foragers. Variation in foraging behavior among sympatric conspecifics theoretically should influence how foraging effort of a species is distributed among and within prey species (Selander 1966, West 1988). In a population of polyphagous individuals, foraging may be concentrated on the prey highest in quality or quantity; in populations of oligophagous individuals, foraging is spread among the available prey species or even prey genotypes (Alstad and Edmunds 1983, Weber 1986, Karban 1989).

If the trophic specialization is temporally persistent, the local forager population may be functionally divided into subpopulations (Alstad and Edmunds 1983, Weber 1986). Although subdivided populations are exhibited by Placida and other short-lived sexually breeding consumers, such subdivisions are particularly pronounced in species with low mobility, short life spans, and parthenogenetic reproduction (Weber 1986). If variation in resource use is genetically based, then differential host use may play an important role not only in shifts to newly available host species (Tabashnik et al. 1981) but also in sympatric race formation and incipient speciation of the foragers.
For pollinators, foraging specificity may ultimately enhance race formation and eventually speciation not only in the foragers but also in the host plants. Cruden (1972) reviews evidence that flower and location specificity of bees results in inbreeding of plants. Plant species pollinated by "consistent" insects may vary geographically substantially more than plants pollinated by "promiscuous" species (Cruden 1972).

To understand the ecological and evolutionary implications of resource use, we need to investigate different types of foragers -- varying in taxonomy, life history, social behavior, prey consistency, and basis of resource specialization -- and quantify the effect of variation in resource use on the foragers as well as the prey.
Chapter IV

GROUP MEMBERSHIP FACILITATES FEEDING

OF THE HERBIVOROUS SEA SLUG PLACIDA DENDRITICA

ON ITS GREEN ALGAL HOSTS CODIUM SPP.

ABSTRACT

The herbivorous sea slug Placida dendritica A. & H. (Gastropoda: Opisthobranchia: Ascoglossa) forms feeding groups on the coenocytic green algae Codium setchellii and C. fragile but not on the related green alga Bryopsis corticulans. The trophic implications of Placida congregation were examined in a series of laboratory experiments. The effect of group membership on Placida growth depends on the number and relative sizes of individuals in the group. Members of Placida congregations composed of similar-sized individuals grow significantly faster than single individuals. In mixed-sized congregations, however, trophic benefits are not shared equally among all members. Small slugs always benefit from the presence of conspecifics, small or large; large slugs, however, benefit only if conspecifics are the same size. Small Placida tend to reduce, rather than enhance, the performance of large conspecifics. Although the mechanisms of intraspecific facilitation and competition among group members are only partially elucidated, Placida's feeding not only stimulates other
group members to feed but also modifies algal condition, enhancing the quality of the food to other conspecifics.
INTRODUCTION

Among the diverse advantages of group membership (Wilson 1975, Bertram 1978, Wittenberger 1981, Pulliam and Caraco 1984), a major one is direct trophic benefit. Groups may enhance different stages of food procurement: (1) searching for and locating food, (2) capturing, collecting, or gaining access to food, and (3) consuming food. Differential prey distribution, size, defense mechanisms, and mobility may select for different types of cooperative effort among consumers (Table IV.1).

When food is patchily distributed in time or space, group searching may facilitate food location (Table IV.1, case 1). Mobile animals such as many insects, birds, and fishes often search in groups for small, patchily distributed prey (Wilson 1962 a,b, 1971, Hölldobler 1971, Krebs et al. 1972, Andersson et al. 1981, Baker et al. 1981, Pitcher et al. 1982, Street and Hart 1985, Ekman and Hake 1988). Prey detection may be short-range and chemosensory or long-range and visual. The extent of cooperation, however, among individuals varies. Individuals searching for food may find it by watching the behavior of conspecifics (Andersson et al. 1981, Pitcher et al. 1982, Pitcher and Magurran 1983, Street and Hart 1985) or by capitalizing on intentionally shared information (Wilson 1962a,b, Evans 1982). Group members may (1) stimulate other conspecifics to forage (social
Table IV.1. Attributes of prey that may select for coordinated or cooperative effort among foraging and feeding consumers.

<table>
<thead>
<tr>
<th>CASE</th>
<th>RELATIVE PREY SIZE</th>
<th>PREY DEFENSE</th>
<th>RELATIVE PREY MOBILITY</th>
<th>TROPHIC BENEFIT TO CONGREGATING CONSUMERS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Small to Large</td>
<td>Spatial or Temporal Patchiness</td>
<td>High or Low</td>
<td>Locate Food</td>
</tr>
<tr>
<td>2</td>
<td>Moderate to Large</td>
<td>Fleeing or Fighting</td>
<td>High or Low</td>
<td>Capture Food</td>
</tr>
<tr>
<td>3</td>
<td>Small to Large</td>
<td>Parents or Territory Holder</td>
<td>Low or No</td>
<td>Gain Access To Food</td>
</tr>
<tr>
<td>4</td>
<td>Large</td>
<td>Structural Chemical</td>
<td>Low or No</td>
<td>Consume Food</td>
</tr>
</tbody>
</table>
facilitation), (2) direct their feeding to a specific location (local enhancement), or (3) make them responsive to changes in food patch profitability. Group foraging may also increase effective food density as searchers flush prey from hiding (Morse 1970).

Cooperative capture of prey occurs when the prey are moderately large relative to the consumers and the prey are well defended (Table IV.1, cases 2-3). Coordinated food acquisition enables consumers to obtain food resources that are not available to individuals, for example, (1) large, mobile, and often dangerous prey (Estes and Goddard 1967, Mech 1970, Kruuk 1972, Schaller 1972, Bowen 1981, Blankley and Branch 1984) or (2) defended prey (Kruuk 1972, Robertson et al. 1976, Foster 1985, 1987). This type of social behavior occurs in a diversity of species though the extent of cooperation varies: mammalian hunters and social insects are often highly cooperative, exhibiting temporary restraint and often division of labor (Wilson 1975), whereas invertebrate predators (e.g., seastars, Blankley and Branch 1984) are not. Prey defense may be extrinsic, rather than intrinsic, to the prey individuals (Table IV.1, case 3). For example, parents guard vulnerable offspring (Kruuk 1972, Foster 1987) or territorial consumers defend sessile resources (Robertson et al. 1976, Foster 1985).
The consequences of group membership on feeding per se have been reported for small consumers, typically insects, feeding on large, sessile prey (Table IV.1, case 4). Behavioral stimulation of feeding (Ibbotson and Kennedy 1951), overcoming the structural defenses of prey (Ghent 1960, Berryman 1969, Raffa and Berryman 1983), and local enhancement of food quality (Way and Cammell 1970, Dixon and Wratten 1971, Forrest 1971, Shearer 1976, Hargreaves and Llewellyn 1978) occur. The generality of these mechanisms in non-insect taxa is not known.

The majority of studies on gregarious trophic behavior are complicated by several variables. The extent of communication, cooperation, dominance hierarchies, relatedness, and non-trophic interactions among group members may influence the conditions under which gregarious trophic behavior occurs and the manner in which trophic benefits are distributed. Furthermore, the allocation of food among group members has generally not been examined experimentally (but see Baker at al. 1981).

In this paper, I investigate the gregarious feeding behavior (Table IV.1, case 4) of herbivorous sea slugs (Gastropoda: Opisthobranchia: Ascoglossa) in which the effects of the complicating variables above are minimized. Specifically, I demonstrate that gregarious feeding enables small consumers, such as herbivorous sea
slugs, to overcome prey defenses. The ascoglossan sea slug *Placida dendritica* A. & H. (= *Hermaea dendritica* A. & H., see Long 1969, Bleakney 1989) is common in warm-temperate to boreal coastal waters throughout the world (Schmekel and Portmann 1982). *Placida* forms discrete feeding groups on its coenocytic green algal hosts *Codium setchellii* and *C. fragile* but not on the related green alga *Bryopsis corticulans* (Fig. II.1). *Placida* has a complex life cycle with planktotrophic larvae and benthic adults. The eggs laid on the algal hosts mature, releasing veliger larvae. Because the larvae move into the plankton to feed for an extended period (Clark 1975), rather than joining the parental group, group members are probably not closely related. Larvae settle, metamorphose, and grow to maturity on *Codium* and *Bryopsis*. I demonstrate herein that (1) the sea slug congregated on *Codium* spp. but not on *Bryopsis*, (2) trophic benefits were not shared equally among group members, and (3) growth facilitation resulted from complex mechanisms.
METHODS

Field Patterns

Group Size

The spatial and temporal patterns of *Placida* distribution on *Codium* spp. and *Bryopsis corticulans* were quantified in the field. *Placida* distribution on *C. setchellii* was monitored from April 1985 to September 1987 at five sites along the central coast of Oregon, USA. These sites from north to south were Yaquina Head North, Seal Rock North, Seal Rock South, Strawberry Hill North, and Strawberry Hill South (Fig. II.2). Each month, I systematically censused *C. setchellii* thalli at each site. *Placida* typically clustered such that individuals were either in direct physical contact with conspecifics or, less frequently, within a body length of conspecifics. These discrete groups were typically separated by at least 1 cm on the algae. The number of *Placida* per group and number of groups per thallus were quantified for each attacked thallus. In addition, for each group, I noted the presence of egg masses and grazing damage.

*Placida* congregations on *C. fragile* from Boiler Bay (Fig. II.2) were monitored from April 1987 to September 1988. Ten thalli were systematically collected along each of two 10-m transect lines through an extensive *Codium* bed. The number of groups and number of
ascoglossans per group were quantified in the laboratory. Placida's distribution on *Bryopsis* clumps from Boiler Bay was quantified from April to September 1987 and qualitatively observed in May 1988.

**Group Composition**

To quantify within-group composition, I collected 65 Placida groups from *C. setchellii* from Seal Rock South and Strawberry Hill South in April 1987. I weighed all the individuals and calculated the range of body weights represented within each group. For each monthly sample of *C. fragile*, I calculated within-group size composition based on visual estimates of Placida size: very small (<0.5 mg), small (0.5-0.9 mg), medium (1.0-3.0 mg), and large (>3.0 mg). These size categories correspond roughly to recent recruits, juveniles, adults, and large adults.

**Laboratory Feeding Experiments**

**General Procedures**

Feeding experiments were conducted in the laboratory to examine (1) the effect of group size and composition on Placida growth and (2) the mechanisms of feeding and growth facilitation. I collected circular plugs of *C. setchellii* tissue (1.6 cm diameter), the top 2.5-5.0 cm of *C. fragile* branch tips, and clumps of *Bryopsis*. Algae were placed in running seawater for at least two days.
prior to use in experiments. Algae and ascoglossans were then placed in individual 0.5-liter containers with fresh seawater. The containers were placed within a shallow, running-seawater table to maintain the temperature close to that in the field, and the seawater in the containers was replaced with fresh seawater at least twice a day.

The wet weight of *Placida* was determined at the beginning and end of each growth experiment. The animals were weighed as a group because the identities of individuals could not be determined. Thus, I was not able to quantify whether a change in group weight was due to a change in all the members or a few members, though my observations supported the former. Depending upon the nature of the experiment, different numbers (i.e., group sizes) of individuals were weighed. Furthermore, in experiments involving large and small *Placida*, the ascoglossans were weighed by size class. Animals were gently blotted on paper towel and weighed to the nearest 0.01 milligram. The precision of blotting and weighing *Placida* (2.7%) was calculated as the mean percent difference in weight of 25 individuals weighed twice. In the feeding experiments, changes in *Placida*’s body weight were (1) positive due to ingestion and growth or (2) negative due to starvation-induced tissue shrinkage, characteristic of many invertebrates.
Group Size

I examined the effect of group size on Placida growth in a series of short-term experiments. First, I calculated the daily percent weight change for small groups of Placida on Codium spp. and Bryopsis for 2-5 days. Second, I quantified the effect of group size (1, 5) and Placida body size (small, medium, large) on Placida growth for two days. Third, I conducted another two-way factorial experiment with group size (1, 5) and time (1, 2, 3 days) as factors. I started the experiments with 9-10 replicates per treatment. Replicates in which individuals died were excluded from analysis.

Group Composition

Because many of the groups in the field were composed of individuals of different body sizes, I examined the trophic interactions between large and small ascoglossans. To determine whether Placida growth was affected by the body size composition of other group members, I held group size constant at four individuals and varied group composition. I established three types of groups: (1) four large Placida, (2) two large & two small Placida, and (3) four small Placida per container. If competition was occurring, then all individuals should perform better with small conspecifics than large ones. Specifically, large slugs should grow better in treatment
(2) than (1), small slugs should grow better in treatment (3) than (2). If interactions were asymmetrical, however, one size class should grow faster and the other size-class slower with dissimilar-sized conspecifics.

Mechanisms of Facilitation

Facilitation of feeding and growth in gregarious consumers may reflect behavioral stimulation of the consumers, changes in quality or quantity of food, or both. Thus, I conducted a series of feeding experiments to determine the mechanisms contributing to enhanced growth of Placida group members. I tested whether the feeding activities of the animals stimulated conspecifics to feed on one of the algal foods, C. fragile, or whether the presence of non-feeding conspecifics was sufficient. To control the feeding behavior of the treatment ascoglossans, I used Placida from different algal host species. Placida from Bryopsis will not switch to Codium and, hence, were "non-feeders"; ascoglossans from Codium fed on the alga in the experiment and, hence, were "feeders".

Did Placida's enhanced growth in groups reflect algal modification (e.g., structural, chemical) or ascoglossan communication (e.g., pheromones)? I tested whether slugs exhibited differential growth on, or preference for, Codium that had been (1) damaged by conspecifics or undamaged controls and (2) experimentally
damaged or undamaged controls. For the natural damage experiments, I placed 5 or 0 large Placida on each of the C. fragile samples. After two days, I removed the ascoglossans and used the algae for slug growth or preference experiments. For the experimental damage trials, I simulated Placida's suctorial feeding by puncturing Codium utricles on half the samples with a dissecting needle. Because the dissecting needle was much larger than Placida's radular tooth, the extent of algal leakage was greater than that produced by Placida attack.

Growth trials followed the protocol outlined above. For the feeding preference experiments, 5 Placida were added to each replicate container, and the number of Placida on each piece of algae was counted periodically for two days. Algae with more animals per census were considered to be preferred. Distinct preferences were exhibited within 5-10 hours and maintained for several days. Student's t-tests were used to determine if significant differences in preference existed after one day.
RESULTS

Field Patterns

Group Size

Placida were not observed to cluster on naturally occurring Bryopsis in 1987 (Fig. IV.1A). In May 1988 after an intense larval settlement of Placida, I saw many recent recruits clumped on Bryopsis axes and branches. When ascoglossan abundance declined, I observed no signs of gregariousness. Thus, while gregarious larval settlement may occur on Bryopsis, feeding groups composed of adults were not common.

In contrast, Placida typically congregated as recent recruits and adults on Codium spp. in the field (Fig. IV.1B,C). Groups were located in different positions, according to the morphology of the host species: in the surface depressions of the rugose C. setchellii thalli and at the axillary region of branches of C. fragile. Maximum group size in 1987 was 72 slugs on C. setchellii and 15 on C. fragile. In 1987 when Placida was collected from both Codium species, 14.9% of the slug groups on C. setchellii and 66.7% of the groups on C. fragile were single individuals. The majority of individuals, however, belonged to groups > 2 individuals: 97.4% of the Placida on C. setchellii and 60.3% of the Placida on C. fragile. Group size was positively correlated with grazing damage to C. setchellii (r=0.604,
Figure IV.1. Congregation patterns of **Placida dendritica** in 1987 on its three algal host species. (A) *Bryopsis* and (B) *C. fragile* data were from Boiler Bay; (C) *C. setchellii* data were from Strawberry Hill South. The sample sizes indicate the number of groups examined from April to September 1987. For the two species of *Codium*, the right tail of the size-frequency distribution was truncated for clarity. Maximum group sizes were 15 for *C. fragile* and 72 for *C. setchellii*. 
Figure IV.1.

A. Bryopsis corticulans  B. Codium fragile  C. Codium setchellii
n=611, P<0.001); comparable estimates were not made for C. fragile.

Placida group size on C. setchellii varied significantly with site, month, and year (multiple regression analysis, Table IV.2), but these three factors accounted for little of the variation in group size ($r^2=0.038$). On C. fragile, Placida group size did vary significantly between months ($P=0.013$) though, again, little of the variation was accounted for by month ($r^2=0.010$). This variation in group size may reflect variable recruitment, growth, and senescence of the short-lived herbivore. These processes are strongly correlated with several physical factors, namely sea surface temperature, wave action, and sand scour (Trowbridge, unpubl. data).

The number of ascoglossan groups per attacked C. setchellii thallus ranged from 1 to 10 with mean values for the different sites varying between 1.0 and 2.8. The number of groups per thallus did not differ significantly between the five sites ($P=0.147$) though there was significant monthly variation ($P=0.006$) (multiple regression analysis, Table IV.2). Furthermore, large thalli had significantly more groups than small thalli ($P<0.001$). On C. fragile, the number of groups ranged from 1 to 27, and monthly means ranged from 1.0 to 9.1. The number of groups did not vary with month ($P=0.678$).
Table IV.2. Results of multiple regression analysis on Placida dendritica group size and number of groups per attacked thallus. (A) Codium setchellii group size data were from five sites and number of groups per attack thallus data were from four sites from April to September 1985, 1986, and 1987. (B) C. fragile data were from one site from April 1987 to August 1988.

A. Codium setchellii

<table>
<thead>
<tr>
<th>Factors</th>
<th>Group Size</th>
<th>Number of Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factors</td>
<td>Coef.</td>
<td>t</td>
</tr>
<tr>
<td>Constant</td>
<td>0.194</td>
<td>3.822</td>
</tr>
<tr>
<td>Site</td>
<td>0.032</td>
<td>4.159</td>
</tr>
<tr>
<td>Month</td>
<td>0.039</td>
<td>4.552</td>
</tr>
<tr>
<td>Year</td>
<td>0.047</td>
<td>2.714</td>
</tr>
<tr>
<td>Algal Diameter</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

n=1432, $r^2=0.038$  
Regression ANOVA  
Regression 3 df  
Residual 1428 df  
F=18.9, P<0.001

B. Codium fragile

<table>
<thead>
<tr>
<th>Factors</th>
<th>Group Size</th>
<th>Number of Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factors</td>
<td>Coef.</td>
<td>t</td>
</tr>
<tr>
<td>Constant</td>
<td>1.506</td>
<td>6.909</td>
</tr>
<tr>
<td>Month</td>
<td>-0.057</td>
<td>2.503</td>
</tr>
<tr>
<td>Year</td>
<td>0.342</td>
<td>-1.436</td>
</tr>
</tbody>
</table>

n=730, $r^2=0.010$  
Regression 2 df  
Residual 727 df  
P=3.8, P=0.022

n=172, $r^2=0.028$  
Regression 2 df  
Residual 169 df  
P=2.4, P=0.090
but varied significantly between years (P=0.030).

**Group Composition**

The size range of individuals at each site was quite broad throughout the spring and summer. Individual groups also varied widely in size structure. Non-reproductive recruits and juveniles (<1 mg) and reproductive adults (>1 mg) frequently occurred together (Fig. IV.2). Of the 65 *Placida* congregations examined from *C. setchellii*, 72% were composed of individuals ranging widely in weight; for example, the largest and smallest individuals varied by at least 1 mg. Of the 256 *C. fragile* congregations examined, 51% were composed of comparably sized animals, 38% were composed of animals from adjacent size classes (e.g., recruits and juveniles), and the remaining 11% were composed of animals from non-adjacent size classes (e.g., recruits and adults).

**Laboratory Experiments**

**Group Size**

Group members did not grow at significantly different rates than single individuals on *Bryopsis* (Fig. IV.3A), based on ANOVA (P=0.206) and ANCOVA with *Placida* size as a covariate (P=0.475). *Bryopsis* feeders did not exhibit feeding facilitation in groups though the animals did occasionally aggregate. In contrast, members of
Figure IV.2. Within-group size structure of *Placida dendritica* on *Codium setchellii* from Seal Rock South and Strawberry Hill South in April 1987. All the *Placida* in each group were individually weighed, and the range of body weight within each of the 65 groups was calculated.
Figure IV.3. Effect of group size on *Placida dendritica*'s growth rate (mean percent daily weight change) on the three algal host species: A. *Bryopsis corticulans*, B. *Codium fragile*, and C. C. *setchellii*. Error bars denote one standard error of the mean. The number of replicates in each of the three experiments is indicated. Data were analyzed with one-way analyses of variance.
Figure IV.3.
Placida groups on Codium spp. grew significantly faster than did single individuals (Fig. IV.3B,C): C. fragile (P=0.046) and C. setchellii (P=0.006). This growth advantage was exhibited by all sizes of Placida (Table IV.3) though small animals grew disproportionately faster in the presence of conspecifics than did larger ascoglossans (highly significant group size x body size interaction effect, P=0.005). Effective feeding appeared to be the major problem for solitary individuals on Codium. Only 11% of the solitary individuals were growing after one day and only 44% after three days (Fig. IV.4). Significantly more group members than solitary individuals were growing by the second and third day (Fisher Exact Tests: P=0.020 and P=0.029, respectively).

Group Composition

Placida had asymmetrical trophic interactions with different sized conspecifics. When group size was held constant at four animals on C. fragile (Fig. IV.5), small slugs grew at the same rate in the presence of large and small conspecifics (Mann-Whitney test, U=60.0, P=0.450). In contrast, large Placida grew faster in the presence of other large ascoglossans than in the presence of small conspecifics (Mann-Whitney test, U=22.0, P=0.0343).

Pairs of large Placida tended to perform better in the absence than in the presence of pairs of small
Table IV.3. Effect of group size and body size on *Placida dendritica*’s growth rate on *Codium fragile* after two days. Data are in percent daily weight change. Initial replication was 9; some replicates were lost due to *Placida* mortality. Results of a two-way analysis of variance are indicated.

<table>
<thead>
<tr>
<th>Group Size</th>
<th>Placida Body Size</th>
<th>Data</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>1</td>
<td>2.9%</td>
<td>4.4%</td>
<td>7</td>
</tr>
<tr>
<td>5</td>
<td>32.1%</td>
<td>5.2%</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td></td>
<td>1.4%</td>
<td>2.1%</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>9.6%</td>
<td>4.9%</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Large</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td></td>
<td>-2.4%</td>
<td>3.8%</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>1.2%</td>
<td>2.7%</td>
<td>9</td>
</tr>
</tbody>
</table>

Results of a two-way analysis of variance are indicated:

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group Size</td>
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<td>P&lt;0.001</td>
</tr>
<tr>
<td>Body Size</td>
<td>1</td>
<td>18.1</td>
<td>P&lt;0.001</td>
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<tr>
<td>Interaction</td>
<td>2</td>
<td>5.9</td>
<td>P=0.005</td>
</tr>
</tbody>
</table>
Figure IV.4. Effect of group size on *Placida dendritica*'s growth in early stages of attack on *Codium setchellii*. Data are in percentage of groups that grew. The number of replicate groups examined is indicated. P-values are based on Fisher Exact Tests.
Figure IV.5. Effect of group composition on growth rate of different-sized *Placida dendritica* on *Codium fragile*. Group size was held constant at four animals; group composition treatments were similar sized slugs (4 small or 4 large) and dissimilar sized slugs (2 small & 2 large). Data are in percent daily weight change. Horizontal bars denote median values; box edges indicate first and third quartiles; vertical bars indicate range of outer values; stars denote statistical outliers. Results were analyzed with Mann-Whitney U tests.
Figure IV.5.
Figure IV.6. Mean percent daily weight change of pairs of large Placida dendritica on Codium fragile in the presence of 0 or 2 small conspecifics. Error bars denote one standard error of the mean. The number of replicates used is indicated. Data were analyzed with a Student's t-test.
con specifics (Fig. IV.6) though this difference was not statistically significant (Student's t-test, t=1.973, P=0.064). Sixty percent of the pairs of large Placida grew in the absence of small conspecifics whereas only 10% of the pairs grew in the presence of small conspecifics (Fisher Exact Test, P=0.057). The number of large Placida on C. fragile, presumably trying to feed, did not differ in the two treatments. These results indicate that small Placida tend to reduce the growth of larger conspecifics, probably by interfering with the effectiveness of large animals feeding rather than by reducing foraging time.

**Mechanisms of Facilitation**

Placida's feeding stimulated other conspecifics to feed (Table IV.4). Significantly more of the slugs which were held with feeding conspecifics fed than those which were held with non-feeding conspecifics (Chi-square test, $X^2=6.67$, P=0.010). Thus, feeding, rather than simply the presence of conspecifics, was the major stimulus enhancing slug feeding and presumably growth.

Placida did not preferentially select damaged tissue. In the laboratory grazing-damage trials (Fig. IV.7), slugs did not exhibit a statistically significant preference between algae damaged and undamaged by conspecifics though there was a tendency in three of the four experiments for Placida to prefer grazed to ungrazed
Table IV.4. Effect of *Placida dendritica*’s feeding on the behavior of conspecifics (test individuals) on *Codium fragile*. Treatment "feeder" slugs were collected from *Codium* and "non-feeder" slugs from *Bryopsis*.

<table>
<thead>
<tr>
<th>Treatment Animals</th>
<th>Feeders</th>
<th>Non-Feeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test Individuals</td>
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<td>12</td>
</tr>
<tr>
<td></td>
<td>Not Feeding</td>
<td>8</td>
</tr>
</tbody>
</table>

Chi-square test, $X^2=6.67$, $P=0.010$
Figure IV.7. Preferences of groups of five Placida dendritica for naturally grazed (G) and ungrazed (U) Codium setchellii and C. fragile. Data were analyzed with Student's t-tests to determine if significant differences in preference existed after one day. The number of replicate groups used in each of the four experiments is indicated.
algae. Simulated grazing damage did not significantly affect the slugs: they exhibited no detectable preference between Codium punctured with a dissecting needle and undamaged controls (C. setchellii: Student's t-test, t=-0.084, p=0.933; C. fragile: t=1.094, p=0.281). Chemosensory cues (e.g., protoplasm leakage from wounded algae), thus, did not account for enhanced feeding of group members. Furthermore, because ascoglossans frequently moved between algal treatments, tactile cues or short-range chemosensory cues (e.g., macromolecular feeding stimulants) were probably not involved.

Although Placida exhibited no preference between damaged and undamaged Codium spp., Placida's feeding modified the alga, making it easier for conspecifics to consume. Hence, the herbivore grew significantly faster on Codium damaged by conspecifics than on undamaged control algae (Table IV.5A). Placida growth differed significantly on damaged and undamaged algae when differences in growth were adjusted for the animals' body size (ANCOVA, P=0.002, Table IV.5A). Furthermore, algal source was also significant: Placida from C. fragile grew faster than conspecifics from C. setchellii.

On experimentally damaged C. fragile (utricles punctured with a dissecting needle), however, the growth rate of large slugs did not differ from that on undamaged control algae (P=0.924, Table IV.5B), even when
Table IV.5. Growth rate of Placida dendritica on Codium fragil (A) naturally and (B) experimentally damaged and undamaged controls. Data are in daily percent weight change. Two separate collections of Placida, varying in algal source and slug body size, were used in the first experiment; one collection of Placida from C. fragile and ranging widely in slug body sizes was used in the second experiment. The data were analyzed after transformations to make variances homogeneous.

A. Natural Damage

<table>
<thead>
<tr>
<th>Algal Treatment</th>
<th>Small Placida from C. setchellii</th>
<th>Large Placida from C. fragile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undamaged</td>
<td>$-1.4%$</td>
<td>$4.6%$</td>
</tr>
<tr>
<td>Damaged</td>
<td>$5.6%$</td>
<td>$14.7%$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Factor</th>
<th>ANOVA</th>
<th>ANCOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Source &amp; Size</td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Interaction</td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Initial Size</td>
<td>df</td>
<td>F</td>
</tr>
</tbody>
</table>

B. Experimental Damage

<table>
<thead>
<tr>
<th>Algal Treatment</th>
<th>Large Placida from C. fragile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undamaged</td>
<td>$11.0$</td>
</tr>
<tr>
<td>Damaged</td>
<td>$11.6$</td>
</tr>
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<th>Factor</th>
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<td>Initial Size</td>
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</tbody>
</table>
differences in growth were adjusted for animals' body size (ANCOVA, P=0.909). Because Placida grew significantly faster on naturally but not on experimentally damaged algae than on undamaged control algae, animal effects (e.g., mucus, pheromones, salivary injections) may partially account for Placida's feeding and growth facilitation. While algal effects cannot be discounted, animal effects appear to prevail.
DISCUSSION

Feeding Advantages of Congregation

Gregarious feeding is one way in which small consumers can successfully feed on large, sedentary prey. Group feeding enabled Placida to eat Codium spp. The most difficult aspect of Placida feeding was the initial attack. Many solitary individuals were never able to feed effectively enough to survive and grow (Fig. IV.4). They rarely produced observable signs of grazing damage on Codium in the field or laboratory. Group members, however, performed significantly better than solitary individuals.

The patterns of Placida congregation on the two species of Codium differed. Placida formed a few groups, often quite large, on C. setchellii and a large number of small groups on C. fragile. These results may indicate that (1) group size was less constrained on C. setchellii than on C. fragile, (2) Placida groups of a given size were less effective on C. setchellii than on C. fragile, or (3) both. Although the maximum group size on C. fragile in the field was 15 (n=484 groups examined), groups in the laboratory often exceeded 50 individuals. In fact, Clark (1975) reported groups of ca. 50 Placida on C. fragile, ssp. tomentosoides in protected subtidal areas in Connecticut. Along the Oregon coast, Placida's group size may be limited by unpredictable wave action,
Placida's group feeding may be more necessary on C. setchellii than on C. fragile: only 3% of the Placida on C. setchellii occurred as solitary individuals compared to 40% on C. fragile. C. setchellii was more difficult for Placida to consume: the utricles were smaller and the walls typically thicker in C. setchellii than in C. fragile (Silva 1951). The elongate shape of C. setchellii utricles may also create greater resistance to suctorial feeding than the globose C. fragile utricles. The group feeding response of Placida on the two species of Codium, however, was qualitatively similar.

Why do Placida on Bryopsis not benefit from group feeding and why do such groups rarely form? Individual Placida, even small ones, can feed effectively on the alga, sucking all the protoplasm out of axes (pers. obs.). When several Placida occur in the same Bryopsis clump, they typically are on separate axes. Perhaps the rate at which individuals locate the ephemeral Bryopsis and deplete the patches effectively eliminates the chance that many other individuals will join them.

Mechanisms of Trophic Facilitation

Although the mechanisms of facilitation for Placida are not completely clear, the basis of trophic facilitation appeared three-fold. First, the presence of
conspecifics, feeding or not, was important in determining Placida's survival. Single individuals, particularly small ones, often wandered away from algal food (pers. obs.), comparable to the behavior of gregarious lepidopteran larvae (Long 1955) and sawfly larvae (Kalin and Knerer 1977). Second, feeding Placida stimulated other conspecifics to feed as reported for aphids (Ibbotson and Kennedy 1951). Third, Placida groups damaged Codium, probably rendering the alga easier to consume. Several different aspects of feeding may have been affected: penetration through the algal wall, suctorial removal of the algal protoplasm, or detoxification and digestion of the protoplasm.

If the probability of an individual penetrating the plant is extremely low and group members share damaged hosts (Ghent 1960), gregarious behavior will enhance the probability of individuals successfully feeding. Alternatively, consumers may overwhelm the defenses of their hosts (Berryman 1969, Raffa and Berryman 1983). For Placida, however, the physical effect of puncturing utricles was not the limiting step for feeding and growth based on the utricle-puncturing experiment.

For suctorial consumers, such as Placida, the viscosity of the prey fluid may limit food uptake (Daniel and Kingsolver 1983, Kingsolver 1987). The use of salivary enzymes or anticoagulants to reduce prey fluid
viscosity has evolved in various suctorial consumers, including phytophagous insects (Miles 1968a,b, 1972, 1978, Hori 1976) and blood-sucking insects (Edman et al. 1985, Kingsolver 1987). While the existence of ascoglossan anticoagulants has not been demonstrated, observations by Jensen (1981b) support their existence. Many species, including Placida, feed by alternate sucking and "buccal regurgitation", which may enable the ascoglossans to mix salivary enzymes or anticoagulants with algal protoplasm; the viscosity of algal protoplasm appears lower after regurgitation than before the process (Jensen 1981b). Salivary secretions injected by feeding Placida into Codium may either stimulate Placida to feed or facilitate food uptake.

Biochemical changes of host plants, such as mobilization of bound nitrogen or production of secondary compounds, may influence consumers' feeding and growth. Ascoglossans, such as Placida, feed primarily on green algae in "chemically rich families" (Hay and Fenical 1988), and some ascoglossan species are attracted to rather than repelled from plant parts with high concentrations of secondary compounds (Paul and Van Alstyne 1988), comparable to many oligophagous insects (Rhoades 1985). The effect of Placida's feeding on the biochemistry of its algal hosts and the effect of any biochemical changes on subsequent Placida feeding is not
known.

Asymmetrical Interactions

Small *Placida* individuals always benefited from group membership whereas large *Placida* benefited only from association with other large conspecifics. In many species of animals, trophic benefits are often not shared equally when group members vary substantially in size, age, sex, or experience. Specifically, the costs of food location and acquisition and the benefits of feeding may not be equally shared (Mech 1970, Murton et al. 1971, Krebs et al. 1972, Kruuk 1972, Schaller 1972, Baker 1978, Krebs 1980, Baker et al. 1981, Street and Hart 1985).

Do certain individuals consistently initiate food procurement or are the costs shared through time among conspecifics? Kruuk (1972) reported that certain hyenas were consistently involved in hunting whereas others joined the group after the prey was killed. For wild dogs, Estes and Goddard (1967) observed a single leader initiating attacks though Schaller (1972) observed some sharing of effort. *Placida* groups were composed of "producers" and "scroungers" (sensu Barnard and Sibly 1981), such that large individuals usually initiated feeding and small conspecifics congregated around them (pers. obs.). Individuals initiating food capture often experience a disproportionate share of the risks. Major
costs of feeding for \textit{Placida} are tooth damage (Bleakney 1989) and energy expenditure. The risks of slugs feeding on algae, however, are undoubtedly small compared to consumers capturing mobile, often dangerous, prey.

An intriguing question is why individuals that have expended energy to locate or to acquire food should share food or information intentionally with others (Evans 1982). Food sharing may be based on genetic relatedness as demonstrated for wolves (Mech 1970), wild dogs (Kruuk 1971), and lions (Schaller 1972). For species that congregate in part to reduce predation, food or information sharing may be a cost of group living. Yet, \textit{Placida} group members were presumably unrelated due to their long planktonic larval phase and predation appeared relatively unimportant (pers. obs.). If successful large \textit{Placida} cannot prevent unsuccessful conspecifics from joining them, the "sharing" may be inadvertent.

The size-specific variation in trophic benefit that \textit{Placida} exhibited differs markedly from the rank-specific variation of many other species: small slugs benefited more than large ones in mixed-sized assemblages. Why did large \textit{Placida} congregate with small conspecifics, given that the animals were probably not related? On one hand, large slugs may not be able to prevent recruits from joining them, given the high recruitment rates of larvae (Chapter II). On the other hand, the cost for a large
Placida to leave its group and survive as an individual or to join an alternate group may be greater than the cost of remaining with the original group (Murton et al. 1971). The asymmetry in trophic benefits was transitory because small Placida rapidly grew and, hence, became increasingly more valuable to other group members. Finally, the relative proportion of large and small individuals in a group may influence the degree of inequality of benefits. For example, a large number of small individuals may enhance the growth of a large conspecific, particularly if the amount of salivary enzymes each individual injected into the plant was proportional to body size.

Most studies on the trophic consequences of social behavior focus on the effect of group size on food location and acquisition, but not on feeding. Group feeding is one mechanism by which small consumers can overcome the constitutive and inducible defenses of their prey (Rhoades 1985). To understand the conditions under which gregarious behavior occurs, we need to quantify the trophic consequences of varying group size and composition at all stages in the general foraging and feeding processes and in a variety of vertebrate and invertebrate species.
Chapter V

PATTERNS OF SEA SLUG ATTACK, SEAWEED REFUGES, AND CONSEQUENCES OF HERBIVORY

ABSTRACT

The patterns and consequences of food plant use by marine mesoherbivores, particularly specialist herbivores, are not known. From 1985 to 1989, I examined patterns of algal host use by the oligophagous, gregarious sea slug Placida dendritica (Gastropoda: Opisthobranchia: Ascoglossa). During the spring and summer, Placida occurred on 14.5% of the C. setchellii and 71.5% of the C. fragile thalli at several low intertidal sites on the central coast of Oregon. Both species of Codium had a small-size refuge from Placida: C. setchellii less than 20 mm in diameter were not attacked at all and C. fragile less than 20 g in wet weight were attacked less frequently than larger thalli. In field transplant experiments, Codium density did not influence the abundance of Placida recruits. Codium, therefore, had no low-density escape from Placida. Codium also had a partial refuge in areas affected by high sand movement or wave force. Placida attacked disproportionately thalli stressed by desiccation or damaged by prior slug grazing. In a 7-week field transplant experiment, C. setchellii lost 40-80% of its
initial weight in wave-protected areas with high *Placida* recruitment and 15-20% of its weight in moderately wave-exposed areas with low slug recruitment. The slugs were a major and often dominant component of the mesoherbivore fauna on the low intertidal green algae *Codium setchellii* and *C. fragile*. Furthermore, the slugs were associated with grazing damage five times more frequently than the other herbivores. The high incidence of *Placida*’s attack, coupled with the slugs' effective feeding, indicate that the sea slug may restrict the abundance and distribution of its *Codium* hosts along the central coast of Oregon.
INTRODUCTION

Herbivory structures many plant populations and communities (McNaughton 1976, 1979, 1985, Lubchenco 1978, 1983, Lubchenco and Gaines 1981, Menge and Lubchenco 1981, Gaines and Lubchenco 1982, Crawley 1983, Hawkins and Hartnoll 1983, Hixon and Brostoff 1983, Hay 1985, Carpenter 1986, S.M. Lewis 1986, Menge et al. 1986, Schiel and Foster 1986, and references therein). Studies on marine herbivory typically focus either (1) on plant strategies to escape, tolerate, and deter herbivory or (2) on herbivore strategies to overcome plant defenses. The effect of herbivore grazing damage, however, depends on attributes of the plants, herbivores, and environment collectively (Lubchenco and Gaines 1981). Herbivore grazing damage is a function of three components: the probability that individual plants will be encountered by herbivores \( P(En) \), the probability that the plants will be eaten once encountered \( P(Ea|En) \), and the reduction in plant fitness due to grazing damage \( E(1-W_{\text{given } En \text{ and } Ea}) \) (Lubchenco and Gaines 1981). For herbivory to significantly affect plants, all three components must be high (Lubchenco and Gaines 1981).

The diversity of plants and herbivores makes a number of different plant "escapes" possible. Individual plants can have "non-coexistence escapes" \( P(En)=0 \) such that the plants and herbivores do not come in contact.
with one another. The relative size and shape of host plants, their spatial dispersion, and the texture of surrounding vegetation influences the apparency of plants to herbivores and, hence, the probability that the plants will be encountered by herbivores (Tahvanainen and Root 1972, Root 1973, Feeny 1976, Smith 1976, Rhoades and Cates 1979, Bach 1980, Lubchenco and Gaines 1981, Risch 1981, Kareiva 1983, Risch et al. 1983, Stanton 1983, Sheehan 1986, and references therein). For example, plants may have escapes from herbivory in small-size, cryptic morphology, low-density, or association with unattractive or even repellent neighbors (McNaughton 1978, Lubchenco and Gaines 1981, Hay 1986). Herbivores with high sensory acuity and high mobility may be extremely effective at locating host plants, even non-apparent ones. Physical disturbance, however, may restrict the foraging or even abundance of consumers (Menge 1978, Lubchenco and Gaines 1981), thus providing spatial and temporal refuges for plants.

Plants may also have different types of "coexistence escapes" [low P(Ea|En)]. For example, such plants may have effective chemical, physiological, and structural defenses to reduce or prevent herbivory. Alternatively, plants may have a low probability being consumed by herbivores by associating with plant species that are more attractive or palatable to herbivores (Lubchenco and
Gaines 1981). Finally, plants may tolerate herbivory [low $E(1-W \text{ given } E_n \text{ and } E_a)$] by having expendable parts or rapid regeneration following tissue loss.

One of the major gaps in our understanding of marine herbivore-plant interactions is the consequence to plants of herbivory, particularly the effect of timing and location of damage (Lubchenco and Gaines 1981). Depending on the timing and location of herbivore attack, construction of the plants, and location of growth meristems and reproductive structures, small herbivores may reduce the survival, growth, or reproduction of their food plants. Detailed information, however, on fine-scale patterns of food plant use by mesoherbivores is sparse.

In this study, I examine how attributes of algae, herbivores, and environment influence sea slug abundance on and grazing damage to the low intertidal green algae Codium setchellii and C. fragile along the central coast of Oregon. In particular, I focus on the types of refuges for the algae, the ways in which the oligophagous sea slug Placida dendritica (Gastropoda: Opisthobranchia: Ascoglossa) is particularly effective as an herbivore, and the consequences of Placida's herbivory to C. setchellii's between and within-habitat distribution.
BACKGROUND

**Oligophagous Slugs**

The ascoglossan sea slug *Placida dendritic* is common in warm-temperate to boreal coastal waters throughout the world (Schmekel and Portmann 1982) and is one of seven species of herbivorous ascoglossans in the northeastern Pacific (MacFarland 1966, Williams and Gosliner 1973, Lambert 1976, Behrens 1980, Millen 1980). *Placida* has a complex life cycle with planktotrophic larvae and benthic adults (Clark 1975). Benthic eggs are laid on algal hosts in the spring and summer and mature in 7-10 days (Alder and Hancock 1844-1845, Evans and Evans 1917, Greene 1968), releasing veliger larvae which live and feed in the plankton for an extended period (Clark 1975). Larvae settle and metamorphose; post-metamorphic individuals feed, grow, mate, and spawn on their algal hosts. The slugs are short-lived, with less than one month elapsing from larval settlement to adult sexual maturity (Chapter II).

Throughout its geographic range, *Placida* feeds on the green algae *Codium* spp. and *Bryopsis* spp. Along the central coast of Oregon, the algal hosts are the crustose perennial *Codium setchellii*, the upright, dichotomously branching perennial *C. fragile*, and the delicate filamentous-like ephemeral *Bryopsis corticulans* (Fig. II.1). Although *Placida* retains chloroplasts from these
algal hosts in digestive diverticula, the herbivore does not obtain photosynthetic benefit from the "endosymbiotic" organelles (McLean 1976, Santisi 1985), in contrast to many other species of ascoglossans (Hinde and Smith 1974, Clark and Busacca 1978).

Algal Hosts

C. setchellii ranges from Alaska to southern California (Silva 1951). Throughout its range, the alga predictably occurs in specific types of microhabitats: primarily shaded, vertical rock surfaces in low intertidal areas strongly influenced by sand scour and burial (Silva 1951). Even within these specific areas, the alga was patchily distributed: natural densities ranged from 0 to 10 established thalli (>1 cm diameter) per 0.25 m². Mean C. setchellii abundance was 3.3 thalli per m² and 1.8% primary cover at sand-influenced sites along the central coast of Oregon; the alga was 100-fold less abundant at non-sandy sites (Trowbridge, unpubl. data).

C. fragile, in contrast, is widely distributed in temperate waters: it occurs in the Pacific, Atlantic, and Indian Oceans (Silva 1951). The low intertidal alga inhabits sandy and non-sandy sites ranging widely in wave exposure (Silva 1951). Along the central coast of Oregon, C. fragile was patchily distributed, growing as individual thalli, small clumps, or dense beds.
METHODS

Timing of Attack

Placida dendritica was monitored on the low intertidal crustose C. setchellii from April 1985 to September 1987 at five sand-influenced sites along the central coast of Oregon, USA. These sites from north to south were Yaquina Head North, Seal Rock North and South, and Strawberry Hill North and South (Fig. II.2). The low intertidal zone was frequently, though unpredictably, buried by sand (cm to m in depth). The relative sand level at each site was estimated depending on the degree of exposure of the Codium thalli: most to all exposed, partially buried by sand, and totally buried.

Each month, I systematically censused C. setchellii thalli at each site. Placida's abundance and grazing damage were noted. Damage was categorized based on percentage of algal thallus area affected. Placida's feeding was distinctive because the slugs sucked the chloroplast-rich algal protoplasm from the algal cortex: grazed tissue, therefore, was pale green compared to the dark green coloration of ungrazed tissue.

I monitored Placida on Codium fragile at Boiler Bay, Oregon. Each month from April 1987 to September 1988, I collected specimens of the alga at 1-m intervals along each of two 10-m transects through an extensive C. fragile bed. I quantified the abundance of the slugs on
each thallus, using a dissecting microscope.

To determine how **Placida**'s abundance was correlated with environmental stress, I quantified the temporal variation in aerial exposure of the low intertidal zone. First, using a local tide table, I estimated the predicted number of days per month that low intertidal **Codium** were exposed each month: (1) total number of exposures and (2) exposures during midday hours (10 a.m.-2 p.m.). Next, I calculated a step function of estimated aerial exposure with respect to tidal height, based on personal observations at Strawberry Hill North in the summer of 1985. From this function and a local tide table, I estimated the (1) total number of hours and (2) number of midday hours that the low intertidal **Codium** thalli were emergent each month throughout the year.

**Desiccation Gradients**

The pattern of **Placida** attack on **C. setchellii** at individual sites was examined along two desiccation gradients: substrate aspect and tidal height. From March to July 1986, I quantified **Placida**'s abundance and grazing damage on **C. setchellii** attached to the walls of two low-intertidal surge channels at Strawberry Hill North. In the first surge channel, the east-facing wall was in direct sunlight and the west-facing wall, cast in deep shade during low tide. In the second channel, the
north-facing wall was shaded and the south-facing wall, exposed to direct light during the spring and summer.

Each month from April to July 1987, I quantified the pattern of Placida abundance on C. setchellii at Yaquina Head North along 25-m transects at the upper and lower end of the alga's tidal range (ca. +0.4 m and -0.8 m, respectively). The substrate was relatively homogeneous, with a gently sloping western exposure. The algae along the upper transect were exposed longer than conspecific thalli along the lower transect: the upper thalli were exposed earlier as the tide ebbed and submerged later as the tide rose. On days with calm seas, the difference in exposure time was frequently 30 to 45 minutes (pers. obs.).

Laboratory Feeding Experiments

Did Placida's pattern of attack reflect the slugs' preference for Codium from desiccation-prone microhabitats? If algal desiccation stress enhanced the attractiveness of C. setchellii to the slugs, I would expect the animals to prefer thalli collected from sunny microhabitats to those from shady surfaces due to differential exposure to direct sunlight during low tide. Furthermore, I would expect slugs to prefer hosts collected from the upper edge of the alga's tidal range to those from the lower edge due to differential exposure
times during low tide. To test this hypothesis, in July 1987 I conducted slug feeding-preference experiments with *C. setchellii* collected from different substrate aspects and tidal heights. I collected the algae from Strawberry Hill South along each of four transects: east- and west-facing substrata and upper and lower ends of the alga's tidal range. Individual *Placida* were placed in individual 0.5-liter containers with fresh seawater and offered pairwise-choices of algae (east vs. west; high vs. low). The containers were placed within a shallow, running-seawater table to maintain the temperature close to that in the field. The number of *Placida* on each piece of algae was counted after one and two days. The categorical data were analyzed with Chi-Square tests separately for each day.

**Algal Transplant Experiments**

**General Procedures**

Field experiments were conducted in the summer of 1988 to examine the effect of algal spatial arrangement and wave exposure on the abundance of *Placida* recruits. Because of the location of the experiments and the diet specificity of the ascoglossans, slug recruitment to *C. setchellii* transplants was primarily from settlement of planktonic larvae. The Boiler Bay site was selected for two reasons. First, the alga occurred at extremely low
densities, rendering movement of adult slugs from established *C. setchellii* to the transplants unlikely. Second, summer sand scour and sand burial at the sites were negligible. Although the slugs theoretically may move from *C. fragile* or *Bryopsis* in situ to transplanted *C. setchellii* samples, individual *Placida* have limited capacity to switch host species (Chapter III). For example, in laboratory experiments, slugs collected from *Bryopsis* died, rather than feeding on *C. setchellii*, even in the presence of "experienced" feeding conspecifics. Hence, *Placida* recruitment to *C. setchellii* transplants in the field was presumed to be primarily from larval settlement.

Approximately 30-g of *C. setchellii*, collected from Seal Rock South, was placed in individual plastic mesh bags (25 cm x 10 cm bags; mesh opening 6-8 mm; Protex, Norplex Inc., Kent, WA). The bags were attached with monofilament line to stainless steel screws cemented in the low intertidal rocky substrate at Boiler Bay (Fig. II.2). The location of the experiments in the lower end of the low intertidal zone (ca. −0.5 m to −0.8 m) and the timing of the experiments were chosen to minimize desiccation stress to the transplants. The transplants were collected after 2-4 weeks, weighed, and preserved in 70% ethanol.
Experimental Designs

To test whether *Codium* had a low-density escape from *Placida*, I transplanted *C. setchellii* in two spatial arrangements: 1 and 4 thalli per 0.25 m² quadrat with five replicates per treatment. Patch size and algal density, therefore, were varied together. The treatments were distributed at randomly selected points, at least 2 m apart, across the surface of a gently sloping low intertidal bench. Because of the spatial arrangement of treatments, the functional algal densities ranged from (1) 1 and 4 thalli per 0.25 m² to (2) <0.25 and <1.0 thalli per m². Both treatments, therefore, represented low host densities. The transplant experiment was conducted twice at Boiler Bay: once under high *Placida* recruitment conditions (June 1988 in a protected area) and once under low recruitment conditions (August 1988 in an exposed area).

To test whether *Codium* had a partial escape from *Placida* at high wave force, I transplanted *Codium* to eight low intertidal locations of varying wave exposure at Boiler Bay: three wave-protected areas, two moderately exposed areas, and three highly exposed areas. At each location, I attached five bags at randomly selected points along a 20-m transect placed horizontally along the shore. Bags were at least 2 m apart from one another to ensure independence of samples.
Weight Loss of *C. setchellii*

Did *Placida*'s herbivory result in tissue loss to *C. setchellii*? Because of the small size and high mobility of the slugs (Chapter II), inclusion and exclusion techniques were not feasible for long-term field experiments. Therefore, to assess the importance of *Placida*'s herbivory, in May 1989 I transplanted *C. setchellii* to areas characterized by either high or low slug recruitment, namely three wave-protected and three moderately wave-exposed areas at Boiler Bay. I transplanted 3-4 defaunated, preweighed thalli at each of the six localities. After 7 weeks, I collected the samples, counted and weighed the remaining algal fragments. The weight loss (% of initial weight) of algae in wave-protected and wave-exposed areas was compared, using analysis of variance for the nested design.

Slug Recruitment To Damaged Hosts

To test how the presence and absence of *Placida* grazing damage on *Codium* influenced subsequent slug attack, I conducted two grazing-damage experiments. *C. setchellii* was collected from Seal Rock South, and ca. 25-g amounts placed in 0.5-liter containers with seawater in a running seawater table. I added 50 *Placida* to each experimental thallus and none to control thalli. *Codium*
tissue exposed to Placida's feeding became extensively damaged; control thalli were not damaged. After a 2-week pretreatment period, I removed all the Placida, and transplanted the algae to Boiler Bay. After 2-4 weeks, I collected the algal transplants and counted the number of Placida recruits. I conducted this experiment twice: once under conditions of low Placida recruitment (August 1988 at an exposed locality) and once under conditions of high recruitment (June 1989 at a protected locality).
RESULTS

Opportunistic Timing of Attack

Placida was on its algal host plants during the spring and summer when desiccation stress during daytime low tides was at an annual high. Furthermore, Placida's abundance on C. setchellii and C. fragile typically peaked in May or June (Fig. V.1) simultaneously with the peak in aerial exposure time during midday hours (Fig. V.2). Irrespective of whether this relation was causal, clearly Placida attacked Codium that were experiencing desiccation stress during low tide.

Partial Low-Desiccation Refuges

Placida attack was concentrated on C. setchellii in two types of desiccation-prone microhabitats. From May to July 1986, the slugs attacked a disproportionately large number of Codium thalli on the sunny east-facing surface of a surge channel at Strawberry Hill North (Fig. V.3A) compared to on the west-facing surface (Chi-square test, $X^2=16.0, P=0.001$). This effect, however, was not manifest in the second surge channel (Fig. V.3B) with sunny south-facing and shaded north-facing substrate surfaces (Chi-square test, $X^2=1.9, P=0.166$). The mean number of Placida per attacked thallus was significantly greater on east- than west-facing substrata (Student's t-test, $t=2.5, P=0.017$) and greater on south- than north-
Figure V.1. Temporal abundance of Placida dendritica on Codium setchellii at three sites (A, B) and C. fragile at one site on the central coast of Oregon. Data are in the number of slugs per 100 algal thalli examined each month.
Figure V.1.
Figure V.2. Temporal pattern of predicted aerial exposure of the low intertidal zone along the central coast of Oregon: (A) number of days with exposure per month and (B) number of hours of exposure per month. For both indices of exposure, the total number of days or hours (stippled) are compared with the number occurring during the midday hours (10 a.m.-2 p.m.; not stippled) when desiccation stress may be high. Data were calculated, in part, from a local tide table (see text for details). These two indices of predicted exposure exhibit little inter-annual variation.
Figure V.3. Percentage of *Codium setchellii* thalli attacked by *Placida dendritica* in two surge channels at Strawberry Hill North in 1986. In A, the surge channel had a sunny east-facing (E) and west-facing (W) wall. In B, the surge channel had a sunny south-facing (S) and a shady north-facing (N) wall. The number of thalli examined on each surface each month is indicated.
Figure V.3.

A.

Sunny (E,S) –
Shady (W,N) –

B.

1986
facing substrata (t=3.0, P=0.005). The proportion of *C. setchellii* thallus area damaged by Placida's grazing was, on average, greater on the sunny surfaces than the shaded ones though this trend was not statistically significant due to the small sample sizes and large variances (Student's t-test, t=-1.8, P=0.077 in the first surge channel; t=-1.0, P=0.319 in the second).

In 1986 at Yaquina Head North (Fig. V.4), Placida's attack was concentrated on *C. setchellii* thalli at the upper end of the alga's tidal range (Chi-square test, $X^2=10.8$, P=0.001 in May; $X^2=9.6$, P=0.002 in June). In July the upper end of the Codium zone became buried by sand; by August, the lower area was buried as well. *C. setchellii* appeared to have a partial refuge from Placida's attack in low desiccation-prone microhabitats: shaded surfaces and the lower end of the low intertidal zone.

In laboratory preference experiments, however, individual adult Placida exhibited no preference between *C. setchellii* collected (1) from east- and west-facing substrata (P=0.100 on day 1; P=0.379 on day 2) and (2) from the upper and lower end of the alga's tidal range (P=0.217 on day 1; P=0.597 on day 2). Possible explanations for these results are that (1) adult Placida did not prefer stressed algae though larvae may, (2) algae collected from the desiccation-prone habitats
Figure V.4. Percentage of *Codium setchellii* thalli attacked by *Placida dendritica* at the upper and lower edge of the alga's tidal range at Yaquina Head North (ca. +0.4 m and -0.8 m, respectively). In July the upper end of the *Codium* zone became buried by sand; in August, the lower end was buried as well. The number of thalli examined at each tidal level each month is indicated.
rapidly improved in condition upon continual submergence in the laboratory, or (3) Placida responded to microhabitat cues rather than algal cues. Regardless of the causal mechanism, Placida attack was concentrated on thalli desiccation-prone habitats.

Partial Small-Size Refuge

During the spring and summer of 1985, 1986, and 1987, Placida occurred on 14.5% of the 5260 C. setchellii thalli examined at Yaquina Head North, Seal Rock North and South, and Strawberry Hill North and South. During the spring and summer of 1987 and 1988, the slugs attacked 71.5% of the 175 C. fragile thalli examined at Boiler Bay. Both species of Codium had a partial small-size refuge from Placida (Table V.1). C. setchellii less than 20 mm in diameter were not attacked at all, and the percentage of thalli attacked increased with thallus size. C. fragile less than 20 g in wet weight were attacked less frequently than larger thalli.

No Low-Density Refuge

The results of the algal-density experiments indicated that small scale differences in C. setchellii density and patch size did not significantly affect Placida recruitment (Table V.2). Placida abundance did not differ significantly between the high and low density
Table V.1. Size-specific differences in the percentage of *Codium* thalli attacked by *Placida dendritica*. Data are in percentage of thalli attacked. *Codium setchellii* data (A) were from April 1985 pooled from all study sites. *C. fragile* data (B) were from May 1988 from Boiler Bay. The results indicate a partial small-size escape for both *Codium* species from *Placida*.

A. *Codium setchellii* (mm diameter)

<table>
<thead>
<tr>
<th>Diameter</th>
<th>%</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-20</td>
<td>0%</td>
<td>159</td>
</tr>
<tr>
<td>20-40</td>
<td>8%</td>
<td>108</td>
</tr>
<tr>
<td>40-60</td>
<td>9%</td>
<td>47</td>
</tr>
<tr>
<td>60-80</td>
<td>19%</td>
<td>42</td>
</tr>
<tr>
<td>80-100</td>
<td>47%</td>
<td>30</td>
</tr>
<tr>
<td>100+</td>
<td>65%</td>
<td>43</td>
</tr>
</tbody>
</table>

Chi-square test

\[ X^2 = 144.7, \text{ 5 df, } P < 0.001 \]

B. *Codium fragile* (g)

<table>
<thead>
<tr>
<th>Diameter</th>
<th>%</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-20</td>
<td>25%</td>
<td>12</td>
</tr>
<tr>
<td>20-40</td>
<td>73%</td>
<td>22</td>
</tr>
<tr>
<td>40+</td>
<td>64%</td>
<td>11</td>
</tr>
</tbody>
</table>

Chi-square test

\[ X^2 = 7.5, \text{ 2 df, } P = 0.024 \]
Table V.2. Frequency of attack by *Placida dendritica* on *Codium setchellii* at high and low densities in two transplant experiments. The first experiment (July 1988) was conducted in a protected area with known high *Placida* abundance; the second experiment (August 1988) was conducted in an exposed area of low *Placida* abundance. Values in brackets represent the number of replicates per treatment.

<table>
<thead>
<tr>
<th>ALGAL DENSITY</th>
<th>HIGH RECRUITMENT</th>
<th>LOW RECRUITMENT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PROTECTED AREA</td>
<td>EXPOSED AREA</td>
</tr>
<tr>
<td>% thalli attacked</td>
<td>100% (5)</td>
<td>100% (5)</td>
</tr>
<tr>
<td></td>
<td>100% (5)</td>
<td>100% (4)</td>
</tr>
<tr>
<td>$#$ Placida per attacked thallus$^a$</td>
<td>195 (5)</td>
<td>185 (5)</td>
</tr>
</tbody>
</table>

$^a$ Student's t-test, $t=0.20$, $P=0.842$ $t=-0.83$, $P=0.433$
Codium treatments under conditions of high recruitment (Student's t-test, t=0.20, P=0.842) or low recruitment (t=-0.83, P=0.433). Codium, therefore, did not have an effective low-density escape from Placida, even at low algal and slug densities. The herbivores were extremely effective at locating the algal transplants.

Partial High-Disturbance Refuge

Two types of physical disturbance provide C. setchellii thalli with a partial refuge from Placida's attack: (1) sand scour and sand burial and (2) wave action or force. Because of unpredictability in the frequency or severity of sand disturbance along the central coast of Oregon (Trowbridge, unpubl. data), field experiments evaluating the effect of sand on slug abundance were not feasible. Slug abundance (Table V.3A), therefore, was based on long-term monitoring of three sites that experienced different degrees of sand disturbance: one site that experienced frequent, severe sand inundations, one site with moderate disturbance, and one site with low sand movement. Both the percentage of the C. setchellii attacked by Placida and the mean number of slugs per attacked thallus decreased with increased sand disturbance, suggesting that Codium may have a partial refuge from Placida's herbivory in areas of high sand movement. Results of the wave-exposure experiment
Table V.3. *Placida dendritica* abundance on (A) *Codium setchellii* in situ at three sites characterized by differential frequency and severity of sand disturbance and (B) *C. setchellii* transplanted to eight sites of varying wave force at Boiler Bay: three wave-protected areas, two intermediate areas, and three exposed areas. Data in (A) were pooled for all spring and summer censuses at each site. Data in (B) were based on a one-month transplant experiment conducted in July 1988 at Boiler Bay. Values in brackets represent the number of replicate thalli.

A. Sand Disturbance (frequency and severity of movement)

<table>
<thead>
<tr>
<th></th>
<th>Low</th>
<th>Moderate</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>% thalli</td>
<td>32% (1321)</td>
<td>19% (770)</td>
<td>6% (1161)</td>
</tr>
<tr>
<td>attacked</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td># Placida per</td>
<td>12.2 (340)</td>
<td>9.5 (144)</td>
<td>6.8 (74)</td>
</tr>
<tr>
<td>attacked thallus</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Chi-square test, \(X^2=264.7, P<0.001\)

B. Wave Force

<table>
<thead>
<tr>
<th></th>
<th>Low</th>
<th>Moderate</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>% thalli</td>
<td>100% (15)</td>
<td>100% (10)</td>
<td>100% (15)</td>
</tr>
<tr>
<td>attacked</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td># Placida per</td>
<td>203 (15)</td>
<td>67 (10)</td>
<td>30 (15)</td>
</tr>
<tr>
<td>attacked thallus(^a)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) ANOVA, \(F=40.6, P<0.001\)
indicate that Codium may also have a partial refuge from Placida in areas of high wave force (Table V.3B). Although slugs attacked all the transplants at the non-sandy Boiler Bay site, the number of individuals per attacked thallus was significantly greater at wave-protected than wave-exposed areas.

Low Grazing Damage In Refuges

Moderate ascoglossan grazing damage (<25% of the thallus area affected) of C. setchellii in situ at sandy sites was present in most spring and summer months during all three years. Severe damage (>25%) was observed from June to August 1985 on about 5-10% of the algal thalli. In 1986 and 1987, grazing damage never exceeded 2% of the thalli examined. Extensively damaged and fragmented thalli rapidly disappeared (pers. obs.), however, so the reported values underestimate the actual frequency of damage. Variation in Placida abundance explained 36.5% of the variation in grazing damage: high slug abundance resulted in high levels of thallus damage ($r=0.604$, $n=611$, $P<0.001$). Comparable estimates were not made for C. fragile.

High Algal Tissue Loss Outside Refuges

The spatial pattern of C. setchellii's weight loss at Boiler Bay (Fig. V.5) paralleled the gradient of
Figure V.5. Mean weight loss of *C. setchellii* transplanted to three wave-protected and three wave-exposed areas at Boiler Bay. Weight loss values (% of initial wet weight) after seven weeks in May and June 1989. The number of transplants at each site is indicated.
Placida's abundance (Table V.3) and, hence, grazing intensity. At three wave-protected areas, C. setchellii transplants lost, on average, about 40% to 80% of their weight in the 7-week experiment; at three areas of intermediate wave exposures, transplants lost, on average, between 15% and 20% of their weight. These differences were significantly different (nested ANOVA, F=24.0, P<0.001) even when the most wave-protected area was excluded from the analysis (F=6.8, P=0.025).

Three lines of indirect evidence indicated that this pattern of C. setchellii's weight loss was probably produced by Placida's herbivory. First, the slugs composed over 90% of the herbivores on the transplants both in this experiment and the previous wave exposure experiment (Trowbridge, unpubl. data). Second, based on field observations, the slug was the only herbivore that produced appreciable grazing damage to Codium (Table V.4). Third, the observed pattern of weight loss was the opposite that would be expected if wave action was the causal mechanism. Placida's herbivory, therefore, may be extremely effective in eliminating Codium from low disturbance areas such as the non-sandy wave-protected Boiler Bay sites.

Damaged Algal Thalli Often Reattacked

The effect of slug grazing damage on subsequent slug
Table V.4. Frequency with which different mesoherbivores were associated with grazing damage on *Codium setchellii*. Data are from Yaquina Head North, Seal Rock North, Seal Rock South, and Strawberry Hill North in 1985 and 1986. Number of cases examined for each herbivore taxon is indicated.

<table>
<thead>
<tr>
<th>Taxa</th>
<th># of Cases</th>
<th># of Cases</th>
<th>% of Cases</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Examined</td>
<td>With Damage</td>
<td>With Damage</td>
</tr>
<tr>
<td>Placida</td>
<td>376</td>
<td>78</td>
<td>20.7%</td>
</tr>
<tr>
<td>Lacuna (Snails)</td>
<td>158</td>
<td>5</td>
<td>3.2%</td>
</tr>
<tr>
<td>Limpets</td>
<td>50</td>
<td>2</td>
<td>4.0%</td>
</tr>
<tr>
<td>Chitons</td>
<td>23</td>
<td>1</td>
<td>4.3%</td>
</tr>
<tr>
<td>Amphipods</td>
<td>8</td>
<td>0</td>
<td>0.0%</td>
</tr>
<tr>
<td>Isopods</td>
<td>34</td>
<td>1</td>
<td>2.9%</td>
</tr>
</tbody>
</table>
attack of algal hosts varied. In the first experiment, the abundance of **Placida** recruits was significantly greater on **C. setchellii** experimentally damaged by slugs than on undamaged control algae (Fig. V.6A, P=0.010). **C. setchellii**, therefore, did not have an inducible defense effective against recruiting **Placida**: damaged thalli were reattacked in a positive feedback fashion, thus leading to extensive damage and possible algal mortality. In contrast, under conditions of high larval recruitment, the abundance of slug recruits was similar on damaged and undamaged thalli (Fig. V.6B, P=0.750). These results may reflect that (1) the damaged algae became comparatively less attractive, possibly due to partially induced defenses or (2) the high attack and subsequent grazing damage swamped out the treatment effect.
Figure V.6. The mean abundance of *Placida dendritica* recruits on *Codium setchellii* that was experimentally damaged (Dam) and undamaged (Undam) by the feeding activities of conspecifics. Error bars are ±1 SE. The number of algal replicates is indicated. The low slug recruitment experiment (A) was conducted in August 1988 at a wave-exposed area of Boiler Bay; the high recruitment experiment (B) was conducted in June 1989 at a protected area.
DISCUSSION

Incidence of Slug Attack

The effect of an herbivore on its plant prey is a function of the frequency and severity of attack and the consequences of grazing damage (Lubchenco and Gaines 1981, Dirzo 1984). During the spring and summer, 14.5% of the C. setchellii thalli examined at sand-influenced sites and 71.5% of the C. fragile thalli examined at a wave-protected, non-sandy site were attacked by Placida. The incidence of Placida attack on C. setchellii was higher at low-disturbance localities compared to high-disturbance ones. The probability that an individual Codium thallus was attacked and partially consumed by Placida was high.

Quantitative data for other ascoglossan species on the incidence of attack are sparse (but see Clark and DeFreese 1987 and references therein). The majority of ascoglossan population studies report the data as number of slugs per gram algae. These data are difficult to interpret from the alga's perspective because algal thalli vary widely in biomass. Yet, to understand the effect of ascoglossan grazing on algal survival and growth, we need to know how ascoglossans are distributed within and among algal thalli in a single habitat. Jensen and Clark (1983) report ascoglossan occurrence in microhabitats varying in wave exposure, solar exposure,
and nutrient level. Such descriptive observations, however, may reflect variation in ascoglossan microhabitat preferences, algal distribution, or both. Experimental manipulations of algal distributions are necessary to distinguish among these alternatives.

**Slug Dispersal**

The capacity of ascoglossans to disperse within or among communities will influence the probability that algae can have an effective low-density or associational escape from the herbivores. Most ascoglossan species have a planktonic larval phase (Table V.5), theoretically enabling them to locate different algal thalli or even populations. Species with limited planktonic development (lecithotrophic larvae) may recruit into a locality close to the adults whereas species with extended planktonic development (planktotrophic larvae) may be dispersed great distances by prevailing water currents. Areas with low densities of adult slugs may be recruitment-limited due to a paucity of allochthonous sources of larvae. For example, Clark (1984) found that Bermuda ascoglossans with lecithotrophic development had denser populations than did species with extended planktotrophic development. Furthermore, areas with moderate densities of ascoglossans may occur due to larval transport rather than through local larval production (Clark 1989).
Table V.5. Life history patterns of ascoglossan sea slugs in temperate and tropical coastal areas.

<table>
<thead>
<tr>
<th></th>
<th>TEMPERATE</th>
<th>TROPICAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N.W. Atlantic</td>
<td>N.E. Pacific</td>
</tr>
<tr>
<td>Planktotrophic</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>Lecithotrophic</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Direct Developing</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Number of Species</td>
<td>4</td>
<td>5</td>
</tr>
</tbody>
</table>

- Clark 1975
- Strathmann 1987
- Clark 1984
- Jensen and Clark 1983 and references therein
- 3 of the 24 described species exhibited more than one type of life history, Jensen and Clark 1983 includes 2 undescribed species.
- Florida includes 2 undescribed species.
Consequences of Herbivory

Timing of Attack

Placida's occurrence coincided with seasonal desiccation stress in the Oregon low intertidal zone rather than herbivory and desiccation occurring at different parts of the year (e.g., in the Mediterranean, Vayssiere 1888, Haefelfinger 1960, Schmekel 1968). Slug herbivory was directed at stressed thalli whose defenses may be reduced. Specifically Placida's attack was concentrated on thalli in desiccation-prone microhabitats: on sunny south and east-facing surfaces and at the upper edge of the alga's tidal range. Stressed algal hosts may be more attractive than unstressed hosts to settling larvae and, hence, function as initial settling centers. This mechanism may occur in Placida because adult slugs exhibited no significant preference between unstressed and desiccation-stressed thalli, but larval settlement was often greater on stressed than unstressed thalli.

Plant Stage

The consequences of an herbivore's feeding depends on a variety of plant attributes: plant stage, structural organization, and quality and quantity of tissue damaged (Lubchenco and Gaines 1981, Dirzo 1984). Size-specific vulnerability of algae to ascoglossan attack has been frequently implied for slug species that
exhibit size-specific preferences among algal filaments (Gonor 1961b, Jensen 1975a, 1981a) or filamentous-like siphons called utricles (Macnae 1954). The importance of overall thallus size, however, has not been previously reported. Whether Codium's small-size refuge was related to size, per se, or to size-related attributes is not known. C. setchellii did have subtle size-specific differences in morphology: small thalli were typically flat whereas large thalli were highly rugose with numerous depressions in which Placida congregated. In addition, small C. fragile had less epiphytic growth than larger conspecifics. In either case, the size-related morphology or extent of epiphytic growth may influence Placida attack rather than thallus size, per se.

**Structure of Plant and Location of Attack**

The structural organization of plants may influence the extent of tissue damage. For example, if herbivore attack is concentrated on structurally vital plant parts, such as the bases of C. fragile branches (Clark 1975, Trowbridge, unpubl. data), algal tissue loss may be substantially greater than the amount actually consumed. Damage to lower parts of uniseriate algal filaments (e.g., Chaetomorpha) may result in total filament loss (Clark 1975, Trowbridge, pers. obs.). Similarly, grazing by urchins at the base of kelp stipes may detach the entire thallus (Dayton 1985).
How common is this type of attack in ascoglossans? Although the descriptive notes on slugs are difficult to evaluate, most of the reports are on non-strategic parts of thalli: branch tips (Hecht 1895, Jensen 1983), external surfaces of robust algae or seagrasses (Clark 1975, Jensen 1981b), medullary areas of robust algae (Jensen and Clark 1983, Clark 1984), and stolons and rhizoids (Gascoigne and Sartory 1974, Jensen 1981b, Gosliner 1987).

*Placida*'s grazing fragmented *C. setchellii* in situ and in transplant experiments (pers. obs.). Quantitative estimates, however, of the reduction in survival or growth for *C. setchellii* in situ were not feasible because of the unpredictability of sand burial that hindered monitoring individual thalli. The high rate of *C. setchellii* weight loss in the 7-week field transplant experiment indicated that *Placida*’s herbivory may eliminate the algae from wave- and sand-protected areas on the central coast of Oregon. Even at sandy sites, *Placida*’s herbivory may reduce the alga's abundance on south- and east-facing rocky substrata and may determine the upper limit of the alga's tidal range.

**Quality of Tissue Lost**

If grazing is focused on high-quality tissue, even small amounts of grazing may significantly reduce the fitness of the plant. Little work has quantified the
location of grazing relative to the location of the algal meristem or reproductive structures though some work suggests that mesoherbivores prefer reproductive plants to non-reproductive ones (Gaines 1985, Waugh and Clark 1986).

Algal tissue quality may also vary in (1) nutrient levels and (2) secondary chemical composition (Carlson et al. 1989). Although the effect of plant nitrogen status has not been examined in sea slug - algal associations, nitrogen availability does influence insect herbivore attack (White 1969, 1974, 1976). The effect of secondary chemicals on ascoglossan attack appears to parallel results from terrestrial systems (Hay and Fenical 1988, Paul and Van Alstyne 1988). Specifically, the specialist ascoglossans frequently attack algal species or parts of algae high in secondary metabolites. Sea slugs not only tolerate the compounds but also apparently sequester them (Doty and Anguilar-Santos 1970, Norris and Fenical 1982, Jensen 1984, Paul and Van Alstyne 1988). Thus, individual thalli or parts of thalli with high secondary metabolites may not be protected from herbivore attack.

**Herbivore Effectiveness**

*Codium* thalli damaged by *Placida* were attacked more frequently than undamaged thalli. Subsequent attack, therefore, often occurred in a positive feedback manner. The causal mechanism, however, is not known. Larval
Placida may settle on Codium marked with adult-derived cues (e.g., from mucus) or on Codium leaking protoplasm. While the latter did not influence adult Placida (Chapter IV), leaking protoplasm may be a chemical attractant to settling larvae.

Adult ascoglossan chemosensory food detection has been demonstrated for two slug species eating siphonaceous algae (Caulerpa and Vaucheria: Hartog 1959, Jensen 1982) and two species eating uniseriate, septate filaments (Cladophora: Gonor 1961b, Jensen 1975). Evidence showing the lack of slug chemosensory food detection is exclusively from the uniseriate, septate filaments (Hartog 1959, Gonor 1961a,b Jensen 1975, Usuki 1977). For ascoglossan slugs with planktotrophic or lecithotrophic larvae, however, chemosensory food detection would be expected during the larval stage, but not necessarily during the adult stage. The mechanisms of food detection by larvae has received little attention.

In conclusion, grazing by the mesoherbivore Placida may be ecologically important to its host plants. The slug's grazing effectiveness results from attributes of both the algae and herbivores. First, individual C. setchellii thalli have a high probability of being encountered by the slugs because of the (1) high apparency of the thalli in low intertidal habitats and
high density, mobility, and possibly sensory acuity of the herbivores. Second, thalli encountered by slugs have a high probability of being consumed because of the lack of effective defenses against the specialist herbivores and (2) extreme diet specificity of the slugs. Third, the consequences of grazing damage are probably severe to *C. setchellii* because of the (1) lack of expendable parts (entire thallus becomes reproductive) and rapid regrowth of damaged thalli (pers. obs.) and (2) intraspecific feeding facilitation of slugs.

High density, mobility, sensory acuity, diet specificity, intraspecific feeding facilitation, and "profligate" host use are all mechanisms by which small, short-lived herbivores may effectively locate and attack large plants (Rhoades 1985 and references therein). This study demonstrates that these mechanisms do occur in marine herbivore - plant associations, thus complementing past work on terrestrial associations. Additional parallels between marine and terrestrial herbivore - plant associations probably exist. To discover these similarities, we need to examine the fine-scale patterns of food plant use by other mesoherbivores. Temperate species of ascoglossan sea slugs offer significant, though often overlooked, potential for future comparative work.
Chapter VI

CONCLUSIONS:
COMPARISONS OF HERBIVOROUS SEA SLUGS
AND TERRESTRIAL PHYTOPHAGOUS INSECTS

The associations between small terrestrial herbivores and their plant foods have been extensively examined; complementary information on marine mesoherbivore - seaweed associations, however, is extremely limited. In many cases, the ecological effect of grazing by small marine herbivores on marine plants is not known. Two intriguing unresolved questions are whether small consumers (terrestrial or marine) exert a strong selective pressure on their food plants and whether the plants develop reciprocal defenses to prevent or reduce subsequent herbivory.

In this dissertation, I focused primarily on the ecological implications of the trophic interactions between an oligophagous sea slug and its green algal host species. Specifically, I documented the life history attributes, diet specificity, intraspecific interactions, and algal host use patterns of the sea slugs. I found several interesting parallels between terrestrial insect-plant interactions and the sea slug-seaweed associations studied here.
Life History Attributes

Placida was a short-lived herbivore, with less than one month elapsing from larval settlement to adult sexual maturity. Larval recruitment was continuous, though variable, throughout the spring and summer. Adult slugs moved extensively among local conspecific hosts. Thus, Placida tracked temporal and spatial changes in the abundance and accessibility of its algal hosts through (1) dispersal and settlement of its planktonic larval phase in successive generations during the year and (2) high mobility of adults.

Many of these attributes are comparable to those of terrestrial phytophagous insects. The ascoglossans and insects, however, do differ in several important ways. First, the slugs are simultaneous hermaphrodites with an obligate sexual life cycle. Insects, in contrast, are typically dioecious with sexual and, in some species, parthenogenetic reproduction. Second, in Placida, dispersal occurs during the planktonic larval phase and the benthic adult phase. In insects, the dispersal phase is the mobile adults. Third, individual slugs probably do not spend their entire lives on individual host plants, particularly in areas of high action where water as well as wave-borne sediment and debris may frequently dislodge the animals. Many species of insects, however, are associated with individual hosts for many generations.
(e.g., Karban 1989).

Diet Specificity

Placida individuals had limited capacity to switch to algal hosts consumed by sympatric conspecifics. The ecological significance of the slugs' behavior in the field is that local slug populations are divided into fairly discrete subpopulations with assortative mating. This phenomenon is strikingly similar to the behavior of many terrestrial insects, especially crop pests (Weber 1986 and references therein), with three important differences. First, Placida always reproduced sexually whereas many phytophagous insect species reproduce parthenogenetically. Thus, even if the slugs' diet selection was genetically based, the fitness of successful genotypes is not amplified through clonal increase as it is in parthenogenetic species. Local fine-scale adaptation of mesoherbivores to single host species or host individuals probably does not occur, in contrast to that suggested for some terrestrial insect species (Edmunds and Alstad 1978, Karban 1989).

Second, because of the duration of Placida's larval phase and the movement of the ocean currents, offspring probably did not recruit to the parental habitat. Larvae may have behavioral adaptations to remain close to the parental habitat. The results of my transplant
experiments, however, support the idea that larvae are widely dispersed because of the rapid recruitment to *C. setchellii* at Boiler Bay where the alga was uncommon. Slug abundance, therefore, was strongly dependent on recruitment processes rather than reproduction. Furthermore, larvae dispersed to distant habitats in which selection pressures on the slugs and algal hosts probably differed. Third, because of the wave forces exerted on marine mesoherbivores, fidelity of animals with individual host plants probably is quite low. Terrestrial insects, however, frequently are able to remain with an individual tree or shrub through many generations.

These differences between terrestrial insect and marine invertebrate herbivores in (1) mode of reproduction, (2) spatial scale of dispersal, and (3) host fidelity may influence the extent to which small herbivores can specialize on their host plants and possibly coevolve with them. For example, why did *Placida* specialize at the individual level, but not at the population or species level (Fox and Morrow 1981). The dispersal larval phase may constrain the species from specializing on one algal species. Because of the spatial patchiness of the algal hosts, slug larvae may not be able to locate the appropriate algal host during the time they are competent to settle. Furthermore,
because the slugs have a much greater geographic range than their algal hosts, gene flow from slug populations using different host species may prevent specialization on a single host species. Mesoherbivores with shorter planktonic larval phases (e.g., lecithotrophic development; Table V.6) or direct development may have a greater potential to specialize than herbivores with longer, planktotrophic development.

Intraspecific Interactions

Placida formed feeding congregations on Codium that were comparable to the feeding groups of suctorial insects (Ibbotson and Kennedy 1951, Way and Cammell 1971, Dixon and Wratten 1971, Forrest 1971, Shearer 1976, Hargreaves and Llewellyn 1978). Gregarious feeding not only stimulated the suctorial slugs and insects to feed but also enhanced their feeding effectiveness. For the insects, the mechanism of facilitation is modification of the vascular fluid (e.g., enhanced nutritional quality or reduced mechanical resistance). I speculate that a comparable mechanism occurs during Placida's feeding.

Should we expect group attack of other mesoherbivore species? Gregarious feeding by other species of herbivorous sea slugs is common (T. Gosliner, pers. comm.) though not well documented. Gregarious feeding may be particularly advantageous in suctorial herbivores
because of the plant construction. Coenocytic green algae such as *Codium* and siphonous species such as *Bryopsis* have large thalli with few internal cross-walls. Herbivores puncturing the external thallus walls, therefore, gain access to a large volume of algal protoplasm, analogous to the xylem and phloem of vascular plants.

Mass attack may be one mechanism for small herbivores, mesoherbivores and insects, to breech the structural cortical defense of plants. Mass attacks of mesoherbivores on parenchymatous marine plants, comparable to the attack of bark beetles and sawflies on conifers (Ghent 1960, Berryman 1969, Kalin and Knerer 1977, Raffa and Berryman 1983), apparently are not common. Swarms of feeding amphipods on intertidal algae (pers. obs.) and large fluxes of small snails on kelp (Fralick et al. 1974), however, do periodically occur. Perhaps the constraints of aquatic life (e.g., the need for gas exchange on all surfaces) have necessitated the use of chemical defenses in marine plants relatively more than structural defenses against small herbivores.

**Patterns of Host Use**

For plants to persist, they can escape, deter, or tolerate herbivory. *C. setchellii* appeared to inhabit high disturbance areas that offer a partial refuge from
Placida's herbivory. The alga had no effective defenses against the specialist during the spring and summer. The slugs attacked algae when the algal hosts were experiencing prolonged aerial exposure during daytime low tides. In addition, Placida's attack was concentrated on plants in desiccation-prone habitats such as the sunny east- and south-facing surfaces and the upper edge of the alga's tidal range. Whether these plants were more apparent to recruiting Placida or more vulnerable to their attack is not known.

The macro- and microstructure of Codium and probably other attributes effectively reduced the number and effectiveness of generalist herbivores. Thus, although Codium was apparent to low intertidal herbivores, Placida dominated the fauna on the algae (numerically and functionally). Whether the paucity of generalist herbivores reflected effective past defensive investments is not known. Placida's herbivory, however, exerted a strong ecological pressure on Codium.

Whether feeding by mesoherbivores will select for defensive mechanisms in marine plants will depend on (1) the diversity and abundance of other herbivores (i.e., diffuse vs non-diffuse selection) and (2) the genetic potential of the plants to evolve defenses. Our understanding of these processes is at the incipient stages, even for terrestrial herbivore-plant
associations. To evaluate these ecological and evolutionary issues in marine benthic communities, we must examine all components of the herbivore fauna including the small, elusive mesoherbivores.
BIBLIOGRAPHY


Bach, C.E. 1980. Effects of plant density and diversity on the population dynamics of a specialist herbivore,
the striped cucumber beetle, *Acalymma vittata* (Fab.) Ecology 61: 1515-1530.


Berenbaum, M. 1981. Patterns of furanocoumarin distribution and insect herbivory in the


Dethier, V.G. 1988. Induction and aversion-learning in
polyphagous arctiid larvae (Lepidoptera) in an ecological setting. Canadian Entomologist 120: 125-131.


Garstang, W. 1890. A complete list of the opisthobranchiate mollusca found at Plymouth; with further observations on their morphology, colours, and natural history. Journal of the Marine Biological
Association of the United Kingdom 1: 399-457.


Grant, P.R., B.R. Grant, J.M.N. Smith, I.J. Abbott, and


Hartog, C. den. 1959. Distribution and ecology of the


comparative notes on radular and buccal anatomy.


Bishop Museum Special Publication 64: 1-653.


Lubchenco, J.L. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant
escapes during succession. Ecology 64: 1116-1123.


Martel, A. 1988. Drifting as an important dispersal and recruitment mechanism in small intertidal


Nybakken, J. 1978. Abundance, diversity and temporal variability in a California intertidal nudibranch


Ecology and Sociobiology 10: 149-151.


Naturalist 106: 683-718.
Schmekel, L., and A. Portmann. 1982. Opisthobranchia des Mittelmeers Nudibranchia und Sacoglossa. Springer-


Vayssière, M.A. 1888. Recherches zoologiques et anatomiques sur les mollusques opisthobranches du


West, L. 1986. Interindividual variation in prey
selection by the snail Nucella (=Thais) emarginata.
Ecology 67: 798-809.

West, L. 1988. Prey selection by the tropical snail
*Thais melones*: a study of interindividual variation.

White, T.C.R. 1969. An index to measure weather-induced
stress of trees associated with outbreaks of psyllids

White, T.C.R. 1974. A hypothesis to explain outbreaks of
looper caterpillars, with special reference to
populations of *Selidosema suavis* in a plantation of

White, T.C.R. 1976. Weather, food and plagues of

Wiklund, C. 1974. The concept of oligophagy and the
natural habitats and host plants of *Papilio machaon*
L. in Fennoscandia. Entomologica Scandinavica 5: 151-
160.

Wiklund, C. 1981. Generalist vs. specialist oviposition
behaviour in *Papilio machaon* (Lepidoptera) and
functional aspects on the hierarchy of oviposition

host-plant use by the montane butterfly *Euphydryas
gillettii* (Nymphalidae). American Midland Naturalist
118: 153-161.


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