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Local and Regional Abundance Patterns of the Ascoglossan (= Sacoglossan) Opisthobranch *Alderia modesta* (Lovén, 1844) in the Northeastern Pacific

by

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Abstract. The ascoglossan (= sacoglossan) opisthobranch *Alderia modesta* (Lovén, 1844) associates with the high intertidal, mat-forming, yellow-green alga *Vaucheria* (Chrysophyta: Xanthophyceae) in temperate estuaries throughout much of the Northern Hemisphere. Although *A. modesta* has been extensively studied on N.E. and N.W. Atlantic shores, complementary information for N.E. Pacific estuaries is sparse. The opisthobranch was common on *Vaucheria* mats in Yaquina Bay and Coos Bay, Oregon, USA with mean densities ranging from tens to hundreds per square meter of algal mat. In Oregon, *A. modesta* was present throughout the entire year. During winter, the ascoglossan persisted on *Vaucheria* within gaps of salt marsh vegetation and in sunny microhabitats with a southern exposure. The opisthobranch numerically dominated the epifaunal invertebrate assemblage associated with *Vaucheria* mats. In northern California, USA, *A. modesta* was sparse in Humboldt Bay and apparently absent from Arcata Bay and Eel River Slough. The species was patchily distributed within Bodega, Tomales, and Drakes bays in California with mean densities $<20/m^2$. High densities of predators, particularly shorebirds and the mud-flat crab *Hemigrapsus oregonensis,* may reduce ascoglossan densities in California though other factors may contribute as well.

INTRODUCTION

Estuaries are complex ecosystems composed of several biologically important intertidal habitats including salt marshes, mud flats, and eelgrass beds. One habitat often overlooked is high intertidal algal mats: the yellow-green alga *Vaucheria* (Chrysophyta: Xanthophyceae) forms extensive mats within the lower marsh, in tidal creeks, and on mud flats, downshore from salt marshes. Although *Vaucheria* inhabits and often dominates this habitat in many temperate and boreal estuaries in the Northern Hemisphere (NIENHUIS & SIMONS, 1971; SIMONS, 1974a, b, 1975a, b; JONGE, 1976; POLDERMAN & POLDERMAN-HALL, 1980; GARBARY & FITCH, 1984), basic ecological information on *Vaucheria* and its associated invertebrate fauna is meager (but see HARTOG & SWENNEN, 1952; HARTOG, 1959).

The alga is the primary, or even sole, food of three species of ascoglossan (= sacoglossan) opisthobranchs. In temperate and boreal estuaries throughout the Northern Hemisphere, *Alderia modesta* (Lovén, 1844) associates with *Vaucheria* mats (HARTOG, 1959; BLEAKNEY & BAILEY, 1967; THOMPSON, 1976; BLEAKNEY & MEYER, 1979; MILLEN, 1980; ROGINSKAJA, 1984; BLEAKNEY, 1988). In the N.E. Atlantic Ocean, White Sea, and Barents Sea, the ascoglossan *Limapontia depressa* Alder & Hancock, 1862, coexists with *A. modesta* (THOMPSON, 1976; ROGINSKAJA, 1984). Finally, *Elysia chlorotica* Gould, 1870, is an estuarine species endemic to the N.W. Atlantic that associates with *Vaucheria* and the filamentous green alga *Cladophora* (BAILEY & BLEAKNEY, 1967; CLARK, 1975; BLEAKNEY & MEYER, 1979; BROMLEY & BLEAKNEY, 1979; GRAVES *et al.,* 1979).

Although the ascoglossans have been examined in many

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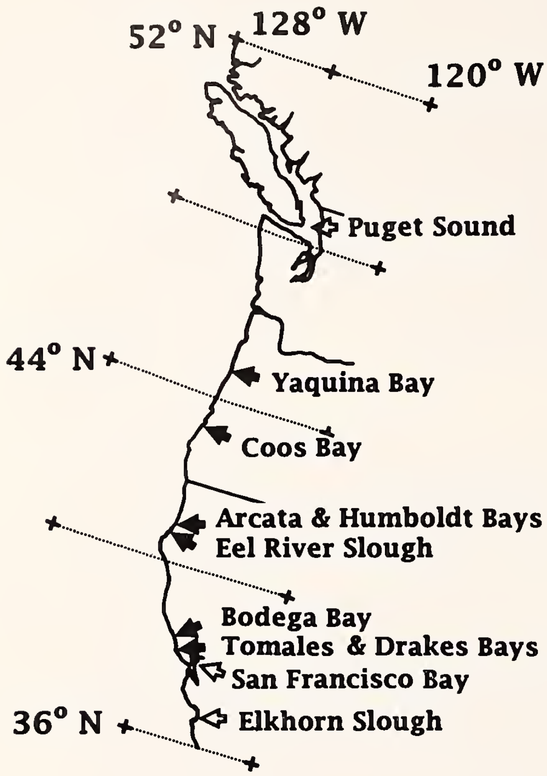

Figure 1

Location of N.E. Pacific estuaries surveyed in this study (solid arrows) and several previous studies (hollow arrows; HAND, 1955; HAND & STEINBERG, 1955; STEINBERG, 1963). Latitudes and longitudes are indicated.

areas of their geographic ranges, information on *Alderia modesta* in the N.E. Pacific is limited (HAND, 1955; HAND & STEINBERG, 1955; STEINBERG, 1963; MILLEN, 1980; TROWBRIDGE, 1993). The species occurs from Vancouver Island, British Columbia (MILLEN, 1980) to Elkhorn Slough, California (STEINBERG, 1963). Within this regional range, *A. modesta* is reportedly common in at least three localities (hollow arrows, Figure 1): Bay Farm Islands in San Francisco Bay and Elkhorn Slough, California, and San Juan Island in Puget Sound, Washington (HAND, 1955; HAND & STEINBERG, 1955; STEINBERG, 1963). Yet, quantitative density estimates are lacking, and the ascoglossan is not included in most other opisthobranch surveys that encompass northern California or Oregon shores. Therefore, this study addresses whether *A. modesta* is widely distributed and abundant in N.E. Pacific estuaries.

NATURAL HISTORY

Alderia modesta has planktotrophic larvae and benthic adults. Larvae settle, metamorphose, and recruit to the algal hosts during spring, summer, and fall in Atlantic localities (HARTOG, 1959; VADER, 1981), and large adults overwinter in marsh ponds (BLEAKNEY & BAILEY, 1967; BLEAKNEY & MEYER, 1979; BROMLEY & BLEAKNEY, 1979). The ascoglossan grows to sexual maturity about 10 days after metamorphosis (SEELEMANN, 1967). Maximum slug size ranges from 5 to 16 mm, depending on locality (ENGEL *et al.*, 1940; HARTOG, 1959; BLEAKNEY & BAILEY, 1967). In the N.E. Pacific, the reported maximum size of *A. modesta* ranges from 6 to 8 mm (HAND & STEINBERG, 1955; BLEAKNEY, 1988; TROWBRIDGE, 1993). The species apparently manifests no endemism or local morphological variation despite its wide geographic distribution (BLEAKNEY, 1988).

Although HARTOG (1959) noted that *Alderia modesta* associated with some, but not all, estuarine species of *Vaucheria,* little is known about specific algal-host associations. At least four species of *Vaucheria* occur in the N.E. Pacific (GARBARY & FITCH, 1984; SCAGEL *et al.*, 1986): *V. intermedia* and *V. thuretii* are summer to fall species whereas *V. litorea* and *V. longicaulis* are fall to spring species (CONOVER, 1958; NIENHUIS & SIMONS, 1971; SIMONS, 1975a; POLDERMAN & POLDERMAN-HALL, 1980). Because the coenocytic algal filaments interweave (JONGE, 1976), species identification is difficult. Thus, in this study, I did not identify the species composing the *Vaucheria* mats examined.

METHODS AND MATERIALS

Local Patterns

Because the alga *Vaucheria* and ascoglossan *Alderia modesta* are not widely recognized as common estuarine species in the N.E. Pacific and because the herbivore occurs almost exclusively on or around *Vaucheria* mats, I collected information on the distribution of the alga in Yaquina and Coos bays on the central coast of Oregon, USA (Figure 1). During the summers of 1990 and 1991, I walked the shoreline for several hundred meters at every access point on the bays, searching for the alga.

I selected two well-developed regions of algal mats in Yaquina Bay for monitoring of *Alderia modesta.* At each of the two sites, I marked 50-m transects directly downshore from the salt marsh. From May 1990 to January 1992, I surveyed these regions at periodic intervals. During each survey, I examined 10 to 52 randomly selected 0.25-m^2 quadrats along each transect line. I counted the number of epifaunal *A. modesta* within each quadrat. Because the density of epifaunal ascoglossans declined with increased exposure time, I started counting immediately upon aerial exposure on ebbing tides. To determine whether *A. modesta* was the major invertebrate associated with the algal mats, I also quantified all other taxa encountered in the quadrats. Furthermore, in November 1990, I measured the percent cover of the *Vaucheria* beds, width of beds downshore from the salt marsh, and height of beds above the adjacent mud flat.

Regional Patterns

To evaluate whether the algal-ascoglossan patterns observed in Oregon were typical of other estuaries in the N.E. Pacific, I surveyed Arcata and Humboldt bays and Eel River Slough in Humboldt County, California (Figure 1) in May 1992. Furthermore, I visited Bodega Bay in Sonoma County and Tomales and Drakes bays in Marin County, California (Figure 1) in July 1990 and May 1992. I looked for *Vaucheria* and *Alderia modesta* at most of the public access points around each bay (based on CALIFORNIA COASTAL COMMISSION, 1991).

In areas that I found the alga, I quantified ascoglossan density in 8 to 15 haphazardly selected quadrats (each 625 cm^2) of the lushest, greenest sections of the algal mat, where ascoglossans were typically abundant. These values provided estimates of peak ascoglossan densities. Next, I stretched a 15-m transect line along the *Vaucheria* zone and examined 10 to 15 randomly selected 0.25-m^2 quadrats along each transect. I counted the ascoglossans in each quadrat and calculated mean population densities. To facilitate comparisons of values from different studies using a variety of quadrat sizes (1 dm^2 to 1 m^2), I present all densities of *Alderia modesta* as numbers per square meter. In May 1992, I also measured the maximum size of *A. modesta* at each site to determine the extent to which ascoglossan size varied regionally.

Between-site variation in ascoglossan populations may be due to differences in predator assemblages: shorebirds appeared to consume *Alderia modesta* in Norway (VADER, 1981), and estuarine fishes and shore crabs readily consumed the ascoglossan in Oregon (Trowbridge, unpublished data). Therefore, in July 1990 and May 1992, I noted the presence or absence of shorebirds and shore crabs at each census location.

RESULTS

Local Patterns

Algal distribution: In Yaquina Bay, the alga *Vaucheria* occurred in two areas. On the south shore (Figure 2), the alga covered 70–80% of the area along two transects (SE and SW) directly below the salt marsh and formed extensive mats about 150 cm broad and 1.5 to 3 cm tall (above the mud flat). On the north shore (N), the *Vaucheria* bed covered only about 10% of the substrate sampled and was relatively narrow (about 20 cm) and thin (<1 cm) (Figure 2). The alga formed discrete "patch islands" below the marsh.

In Coos Bay (Figure 3), the alga was extremely sparse (1) near the mouth of the bay where the beaches were muddy sand and (2) in many of the sloughs that had pebbly to rocky substrate. Much of Coos Bay was highly channelized due to logging: the alga occurred only in trace amounts within the marsh in these areas. *Vaucheria* was not common where low marsh vegetation (*e.g.*, the pickleweed *Salicornia virginica*) was missing.

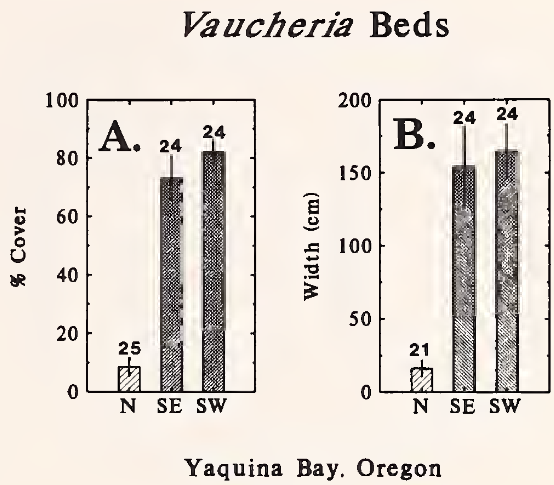

Figure 2

Description of the *Vaucheria* beds in Yaquina Bay, Oregon. Data were collected in November 1990. Error bars denote ±1 SE. Values above each bar indicate the number of replicate 0.25-m^2 quadrats examined.

In South Slough of Coos Bay (Figure 3), however, *Vaucheria* formed extremely thick, lush mats during the summer. At the mouth of the slough, the alga formed mats fringing the marshes and "patch islands." The latter were

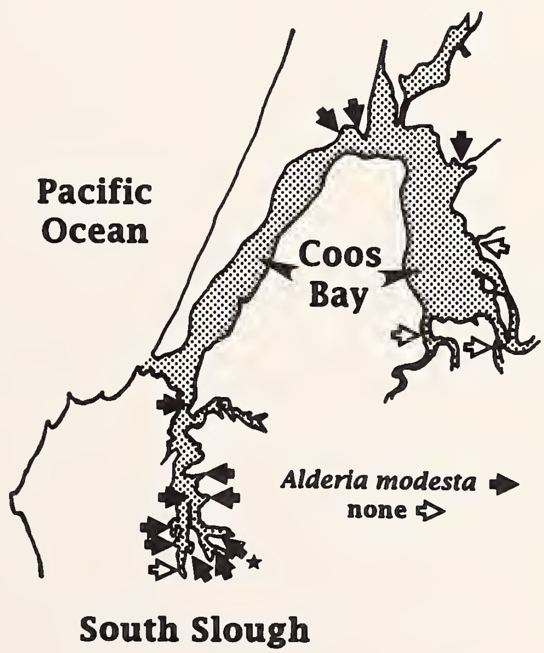

Figure 3

Distribution of *Alderia modesta* in Coos Bay, Oregon, during the summer of 1991. Solid arrows denote areas with *A. modesta*; hollow arrows denote areas without the ascoglossan. The star denotes the site with peak ascoglossan density (about 5000/m^2 in September 1991).

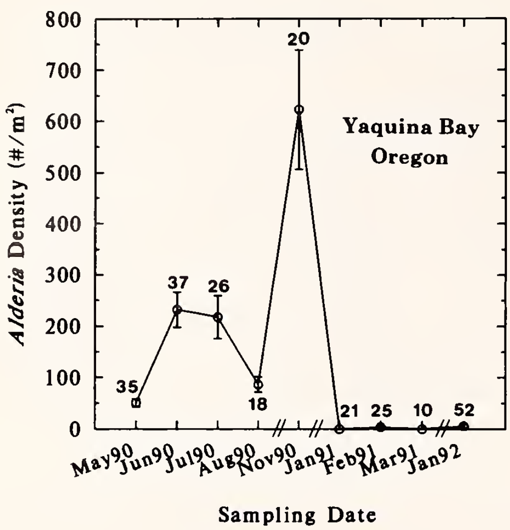

Figure 4

Temporal abundance pattern of *Alderia modesta* on the south side of Yaquina Bay (Idaho Point Road), Oregon. Error bars denote ± 1 SE. Values above each circle indicate the number of replicate 0.25-m^2 quadrats examined.

stable structures, 15 to 30 m in length, that persisted throughout the year. Although the alga was extremely sparse on the extensive mud flat flanking the main channel of the slough, *Vaucheria* dominated the substrate directly downshore of the marsh vegetation in many of the side tributaries. These regions historically had been diked pastures but subsequently reverted to salt-marsh and mud-flat communities. This historical change is typical of many estuaries in Oregon and northern California.

Ascoglossan abundance: *Alderia modesta* occurred on most of the well-developed *Vaucheria* mats in Yaquina Bay and South Slough of Coos Bay. Mean ascoglossan density ranged from tens to hundreds per square meter of algal mat. Peak densities in individual quadrats were 2152/m^2 in November 1990 in Yaquina Bay and about 5000/m^2 in September 1991 in the upper reaches of South Slough (star symbol in Figure 3).

Alderia modesta was present during the entire year (Figure 4) except following an abnormally cold storm in December 1990 when the temperature dropped below freezing for a week, and extensive mortalities of intertidal invertebrates occurred. In February and March 1991, *A. modesta* populations in Yaquina Bay had not yet recovered: no ascoglossans were observed despite extensive searching. In South Slough of Coos Bay, however, low densities of *A. modesta* were found on *Vaucheria* in gaps within the marsh vegetation. For example, based on 19 quadrats examined (each 625 cm^2), mean ascoglossan density was 290/m^2 (SD = 368). No ascoglossans were found on exposed *Vaucheria* mats below the South Slough marsh.

During the following winter, freezing weather did not occur, and *Alderia modesta* persisted, although the species' distribution was extremely patchy. For example, in January 1992, few ascoglossans persisted on the *Vaucheria* bed below the marsh on the south side of Yaquina Bay (Figure 4) although adults did occur in gaps in the marsh vegetation. On the north side of the bay (with a southern exposure), however, the algal mats were extremely lush, and ascoglossans were abundant: >800/m^2 based on 10 haphazardly selected 0.25-m^2 quadrats. Thus, the seasonal persistence of *A. modesta* in Oregon was associated with local variation in microhabitats.

Invertebrate assemblage: *Alderia modesta* numerically dominated the invertebrate assemblage associated with *Vaucheria* mats. Based on nine pooled censuses from May 1990 to January 1992 in Yaquina Bay, the ascoglossan composed 99% of the epifaunal community (n = 5708 invertebrates). Insects, particularly larval and adult chironomids, were often present on *Vaucheria* mats, though in extremely low densities.

Regional Patterns

Distribution: In May 1992, I found little *Vaucheria* and no *Alderia modesta* at access points of Arcata Bay or the nearby Eel River Slough. Both drainage basins were primarily high-energy environments with marsh banks severely undercut by erosion. The South Jetty region of Humboldt Bay, however, was a low-energy environment with trace amounts of *Vaucheria* and some *A. modesta* in the muddy sand region. The south bay area within the U.S. Fish & Wildlife refuge appeared, from a distance, to be ideal for the alga and ascoglossan—a muddy, low-energy environment with well-developed marsh vegetation. The area, unfortunately, could not be feasibly sampled due to limited safe access. Most of the areas visited in Sonoma and Marin counties, however, had well-developed *Vaucheria* mats.

Abundance: When I haphazardly selected lush portions of the algal mats, the density of *Alderia modesta* (Figure 5) was moderately high at two sites in California: >100/m^2 at Bodega Marine Laboratory Research Reserve in Bodega Bay and at Inverness in Tomales Bay. These values represent peak abundances calculated from small spatial scales (625-cm^2 quadrats). When I counted ascoglossans in randomly selected quadrats (each 0.25 m^2), mean *A. modesta* densities ranged from 2 to 20 slugs per square meter (Figure 5). Therefore, even though small patches of *Vaucheria* in California had moderate densities of *A. modesta,* randomly determined densities were quite low: about 1 to 2 orders of magnitude lower than in Oregon.

Ascoglossan size: The maximum length of *Alderia modesta* varied little among sites in California and other areas in the N.E. Pacific (Table 1). Peak ascoglossan size was 9 mm in May 1992 at Doran Beach in Bodega Bay, California. Although size-frequency data were not collected for *A. modesta* in California, few small individuals were observed. Qualitatively, average ascoglossan size was greater in California than in Oregon.

Potential predators: Small, migrating shorebirds (*e.g.*, plovers, sanderlings) were common at many sites in California in July 1990 and May 1992 but generally not observed in Oregon estuaries (Table 2). Furthermore, the density of shore crabs, particularly the mud-flat crab *Hemigrapsus oregonensis*, was much higher in California than in Oregon. I found up to 10 crabs in every quadrat surveyed in California and no crabs in quadrats in Oregon.

DISCUSSION

Distribution and Abundance

Local patterns: *Alderia modesta* was patchily distributed on a local scale. Part of this variation was associated with the relative abundance of places for the ascoglossans to hide during emergence. Hartog (1959) noted that slug densities were low when the *Vaucheria* bed was closed (*i.e.*, tightly interwoven algal filaments) because of the difficulty for slugs to burrow and hide. Most *A. modesta* occurred along the margins of cover, around the open spaces in vegetation, and in shrinking rents in the substrate during emergence (Hartog, 1959; C. D. Trowbridge, personal observations). Furthermore, I observed that the ascoglossans hid in surface depressions of the *Vaucheria* mats, invertebrate burrows (crabs, clams, polychaetes), and in holes produced by feeding shorebirds. It is not known whether *Vaucheria* mats differing in surface texture represent different algal species or a single species under different environmental conditions.

Predation by shorebirds and crabs presumably contributed to the patchy distribution of ascoglossans. Vader (1981) reported that Little Stints (*Calidris minuta*) regularly occupied the *Vaucheria* zone in Norway, and he observed that the birds consumed *Alderia modesta* and/or their egg capsules. Furthermore, Trowbridge (unpub-

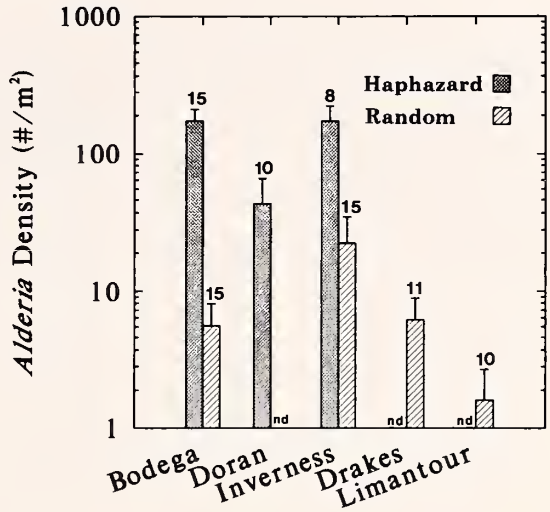

Figure 5

Density of *Alderia modesta* in haphazardly placed and randomly selected quadrats. Bodega Marine Laboratory Research Reserve and Doran Beach are in Bodega Bay; Inverness is in Tomales Bay; Drakes and Limantour esteros are in Drakes Bay, California. The symbol "nd" denotes no data collected. Error bars denote ±1 SE. Values above each bar indicate the number of replicate quadrats examined.

Table 1

Maximum reported length of *Alderia modesta* in the N.E. Pacific. Sample sizes (*n*) denote number of ascoglossans examined. The symbol "na" indicates that sample size was not provided by authors.

Locations	Body length (mm) Maximum	*n*	References
British Columbia			
Bamfield Marine Station	6	12	Bleakney, 1988*
Washington			
Friday Harbor Labs	7	10	Bleakney, 1988*
Oregon			
Yaquina Bay	6	148	Trowbridge, 1993
California			
Doran Beach	9	27	this study†
Bodega Marine Lab Reserve	7	184	this study†
Inverness	5	171	this study†
Drakes Estero	4	18	this study†
Limantour Estero	3	4	this study†
Elkhorn Slough	8	na	Hand & Steinberg, 1955

* Data not collected for specific purpose of determining maximum length of local population.
† Data collected during the May 1992 survey.

Table 2

Visual assessment of the abundance of shorebirds and mud-flat crabs (*Hemigrapsus oregonensis*) on *Vaucheria* in several N.E. Pacific estuaries. Data for Oregon sites were based on several months of observations whereas data for California sites were based on two surveys (July 1990 and May 1992).

Locations	Shorebirds	Mud-flat crabs
Yaquina Bay, Oregon		
Bay Road	absent	absent*
Idaho Point Road	absent	absent*
Coos Bay, Oregon		
Main Branch†	absent	absent
Charleston Bridge	absent	absent*
South Slough†	absent	absent
Bodega Bay, California		
Doran Beach	abundant	abundant
Research Reserve	abundant	abundant
Tomales Bay, California		
Walker Creek	absent	absent
Alan Sieroty Beach	absent	abundant
Millerton Point	absent	abundant
Inverness	abundant	abundant
Drakes Bay, California		
Drakes Estero	absent	abundant
Limantour Estero	absent	very abundant

* Low densities of crab burrows observed at site but not in quadrats.

† Many locations pooled (see Figure 3).

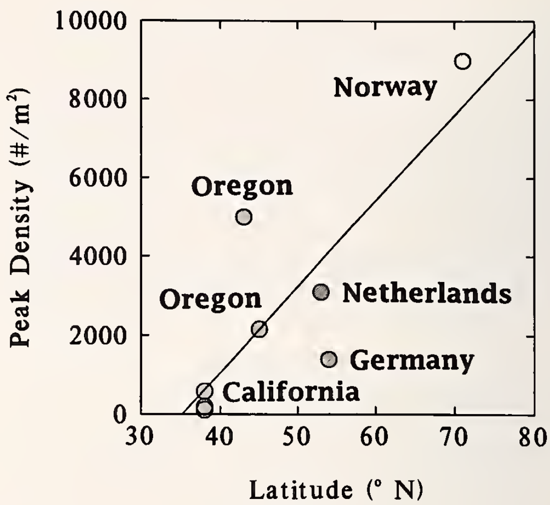

Figure 6

Relationship between peak ascoglossan density and latitude. Data are from this study (Oregon, California) and previous studies (Hartog, 1959; Seelemann, 1967; Vader, 1981).

lished data) found that predators (probably fishes and crabs but not birds) significantly reduced populations of *A. modesta* in Yaquina Bay, Oregon. Yet, although predation may reduce ascoglossan densities, the burrowing behavior and small size of *A. modesta* presumably would offer some protection from predators: total exclusion of ascoglossans seems unlikely.

Another potentially important source of variability in slug density was the recruitment rate of larval ascoglossans. Information on patterns of water circulation and larval transport within N.E. Pacific estuaries is limited. Water masses containing larvae may not penetrate all the tributaries of the estuaries (*e.g.,* Walker Creek near the mouth of Tomales Bay), thus explaining the absence of *Alderia modesta.* Alternatively, abiotic factors such as salinity fluctuations may exclude ascoglossans from some locations. Engel *et al.* (1940) reported that *A. modesta* can survive at salinities from about 2 to ≥37‰ though the effects of low salinity on ascoglossan growth and fecundity are not known.

Regional patterns: *Alderia modesta* was often abundant, ranging from tens to thousands of animals per square meter throughout its geographic range. For example, Hartog (1959) reported 20 to 56 individuals per square meter in the Netherlands with a peak density of 3100/m². Seelemann (1967) observed 1400/m² on the German Baltic coast. Vader (1981) reported that densities of 500 to 1500 ascoglossans/m² were typical of most sites in Norway; at Klubbukt, however, the mean density was 4820/m² with a peak value of 9000/m². Density values for Oregon and California were, therefore, comparable to values from N.E. Atlantic localities.

Clark & De Freese (1987) reported an increase in multispecies ascoglossan density from low to high latitudes. A similar pattern was seen for a single species (*Alderia modesta,* Figure 6). The correlation was highly significant ($r = 0.825$, $P = 0.012$, $n = 8$ sites) even though the data were from different locations, years, and seasons as well as based on different sample and quadrat sizes. At least three factors may account for the latitudinal trends in population density: (1) decrease in predation intensity, (2) increase in algal productivity (Clark & De Freese, 1987), or (3) increase in larval recruitment with increased latitude. This study provides some evidence supporting (1), but predation was not the sole factor. Although *Vaucheria* beds were generally lusher in Oregon than California, algal productivity probably did not constrain ascoglossan populations in California for two reasons. First, the alga was not a limiting resource for the ascoglossans. Second, maximum body length did not differ much for populations throughout the N.E. Pacific (Table 1). The paucity of juvenile ascoglossans in California and abundance of small individuals in Oregon (Trowbridge, 1993) support the recruitment hypothesis (3). The relative importance of predation intensity, algal quality (as food and substratum), and larval recruitment need to be further elucidated for us to understand regional differences in ascoglossan populations.

Ecological Effects

As the numerically dominant invertebrate associated with *Vaucheria* mats, *Alderia modesta* has two ecological roles within the estuarine food web: (1) as a stenophagous consumer and major herbivore of the algal mats and (2) as prey for estuarine predators. Ascoglossan herbivory may be important to algal hosts under conditions of high feeding rates and/or high population densities (CLARK, 1975; TROWBRIDGE, 1992). Information on feeding rates of *A. modesta* are meager. EVANS (1953) commented on the rapid feeding rate of the ascoglossan: 10 *Vaucheria* filaments per minute. This value, however, is difficult to evaluate because filament size was not given. Because herbivory may be important to algal hosts when ascoglossan density is high, ascoglossan herbivory in Oregon estuaries may contribute to the periodic fragmentation of *Vaucheria* mats.

High densities of *Alderia modesta* in Oregon estuaries suggest that ascoglossans may represent an important food source to estuarine fishes, crabs, and perhaps birds. Although predators rapidly reduced densities of *A. modesta* in August 1990 in Yaquina Bay (Trowbridge, unpublished data), feeding preferences of predators may change ontogenetically or seasonally. For example, small (<10 cm) staghorn sculpins (*Leptocottus armatus*) voraciously consumed *A. modesta* whereas larger conspecific fish (>15 cm) ignored the small opisthobranchs (Trowbridge, unpublished data). Thus, the ascoglossan may be either (1) an important food base within high intertidal, estuarine habitats or (2) a minor prey base sampled by a diverse array of inexperienced juvenile predators. In summary, the ecological role of *A. modesta* merits further attention, particularly at high latitudes where ascoglossan densities are high.

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