



Padilla Bay

National Estuarine Research Reserve

Technical Report No. 22

**GREEN MACROALGAE IN ESTUARIES OF
PUGET SOUND AND THE STRAIT OF GEORGIA:
A COMPARISON OF SPECIES ASSEMBLAGES**

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and

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1999

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TABLE OF CONTENTS

ABSTRACT	iii
INTRODUCTION	1
OBJECTIVES	2
STUDY AREAS	2
METHODS	4
RESULTS	6
DISCUSSION	13
CONCLUSIONS	19
APPENDIX	20
ACKNOWLEDGMENTS	21
LITERATURE CITED	22

Abstract

In northeast Pacific estuaries, macroalgae form multispecies assemblages which often include species of the Ulvaceae (Chlorophyta), commonly known as “ulvoids”. The green macroalgae of the Padilla Bay Estuarine Research Reserve was mapped by Bulthuis (1991) and studied further Hayden and Waaland in 1996-1997 (in press). The goals of the current study were to determine whether the assemblage of green macroalgae in Padilla Bay is similar to that of other Puget Sound/Strait of Georgia estuaries and if there is a diagnostic assemblage found in these northeast Pacific habitats. Two estuaries in Washington state were chosen for comparison: Drayton Harbor and Ellisport/Tramp Harbor. Chlorophytic macroalgae were collected on three days at four or five sites in each estuary from 26 April to 21 August 1998. The Sørensen coefficient (S_s) was used to assess the similarity of macroalgal assemblages. This study indicates that green macroalgal species diversity in Padilla Bay is similar to that in similar habitats in Puget Sound and the Strait of Georgia. Additionally, a diagnostic assemblage of green macroalgae in northeast Pacific mixed-fines estuaries includes a relatively short list of species.

Introduction

Estuaries are highly productive habitats providing spawning grounds and nurseries for fish and invertebrates and food for resident and migrating shorebirds and other fauna. The great diversity of organisms in estuaries and the overall health of these biological systems depend on the community's primary producers (seagrasses, benthic algae and phytoplankton) which provide food, shelter and camouflage for many species. Without these autotrophs, estuaries cannot support such diversity and abundance. In northeast Pacific estuaries, seagrass meadows are typically composed of native *Zostera marina* L. and/or introduced *Z. japonica* Aschers. & Graebn. (Thom 1989). Unlike these rooted seagrass stands, macroalgae usually form multispecies assemblages (Lindstrom & Foreman 1978). These assemblages often include species of the Ulvaceae (Chlorophyta), commonly known as "ulvoids" (e.g., Dethier 1990). These green macroalgae take the form of flat blades or thin tubes and grow attached to seagrass, rocks and shells, or unattached and free-floating. Members of this group are morphologically similar and are often difficult to distinguish (van den Hoek et al. 1995). As a result, few estuarine studies detail ulvoid species composition, and green algal diversity in these habitats is poorly understood (e.g., Dethier 1990, Bulthuis 1991).

In 1996 and 1997, we identified and mapped the green macroalgae of the Padilla Bay National Estuarine Research Reserve (PBNERR) at six sites in the estuary (Hayden & Waaland, in press). The current study places findings from that initial research in a larger context by comparing green macroalgal species diversity in Padilla Bay to that at two other Puget Sound/Strait of Georgia mixed-fines estuaries. The goals of this study were to determine whether Padilla Bay has an assemblage of green macroalgae similar to that of other Puget Sound/Strait of Georgia estuaries and if there is a diagnostic assemblage found in these northeast Pacific habitats. Following Dethier (1990), the term "diagnostic" describes the species characteristic of a given habitat type (e.g., most abundant, obvious, functionally-important, or restricted to one habitat type). Usually no one species by itself is diagnostic of a habitat, but the correlated occurrence of several species can be characteristic. Two estuaries were chosen for comparison: Drayton Harbor, near the city of Blaine, Washington, and Ellisport/Tramp Harbor on Vashon Island, Washington.

Objectives

The objectives of this study were to: 1) compare green macroalgal species assemblages at Padilla Bay, Drayton Harbor and Ellisport/Tramp Harbor, Vashon Island; 2) establish whether the green macroalgal species assemblage of Padilla Bay is similar to that in other northeast Pacific estuaries; and 3) determine if there is a diagnostic assemblage of green macroalgae in mixed-fines estuaries of Puget Sound/Strait of Georgia.

Study Areas

Major environmental factors affecting global and local distributions of macroalgae include temperature, substratum, light, nutrients, salinity and exposure. In a study of seaweed community composition in the Strait of Georgia, Lindstrom & Foreman (1978) reported local macroalgal distribution to be determined mainly by three environmental factors. The primary factor was substratum, followed by desiccation intensity and light climate. Given these results, study estuaries to compare with Padilla Bay were chosen based on substratum type. Dethier (1990) classified estuarine habitat types in Washington according to depth, substratum and energy level. Padilla Bay is classified as a partially enclosed, mixed-fines intertidal type. This classification includes backwaters or deltas away from large distributary channels consisting of mixed sand and mud with small amounts of gravel or some clay and peat. The substratum is generally stable, firm and organic-rich, and productivity is high due to seagrasses, micro- and macroalgae, and salt marsh vegetation. Drayton Harbor and Ellisport/Tramp Harbor, Vashon Island have substratum traits similar to Padilla Bay and are accessible areas included in this habitat type (Figure 1):

- Drayton Harbor, located in southern Strait of Georgia, is approximately 10 km², 67% of which is intertidal and shallow subtidal. Seagrass meadow (*Z. marina* and *Z. japonica*) occupies 33% of the harbor with the rest comprised of mudflats (Thom et al. 1988).
- Padilla Bay, located in northern Puget Sound, is approximately 45 km², 90% is intertidal. Seagrasses cover 3,500 hectares of the Bay with the rest comprised of sand and mud with small patches of gravel (Thom 1989).
- Ellisport, located on Vashon Island in the East Passage, comprises an area with the adjacent Tramp Harbor of approximately 1.5 km². Seagrasses form dense stands at low intertidal and shallow subtidal depths with the nearshore area comprised of mud and sand (Thom et al. 1984).

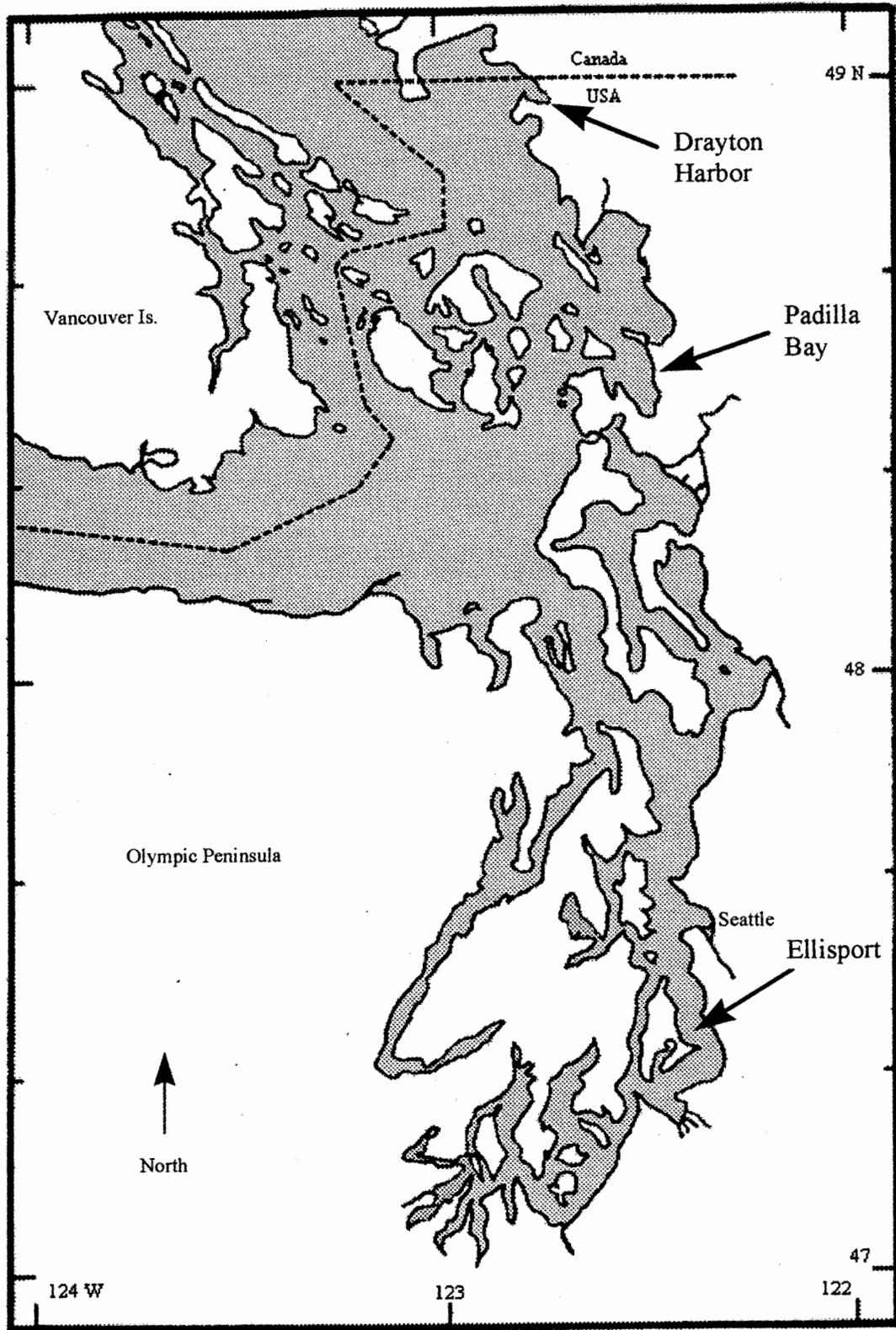


Figure 1. Location of three study estuaries in Puget Sound and the Strait of Georgia (Base map source: Thom et al. 1988)

Methods

Chlorophytic macroalgae were collected on three days in each estuary, a total of 9 visits, from 26 April to 21 August 1998. Each estuary was visited in spring/early summer (April, May or June), July, and August. Collections were made during low tide at four or five sites within each estuary. Tables 1, 2 and 3 include approximate geographical coordinates taken with a hand-held GPS unit (Garmin 45) and habitat information (Dethier 1990) for these collection sites.

Table 1. Collection sites in Drayton Harbor.

Site	Coordinates	Substrate	Exposure	Vegetation
DH 1 Blaine Marina	48° 59.72' N 122° 45.41' W	mud, loose cobbles	protected	macroalgae
DH 2 Drayton Harbor Rd bridge	48° 57.72' N 122° 45.41' W	mud, sand, isolated boulders	moderate	macroalgae, salt marsh vegetation
DH 3 Beach along road to Semiahmoo	48° 58.74' N 122° 47.46' W	mud, sand, loose cobble	moderate	<i>Z. marina</i> , <i>Z. japonica</i> , macroalgae
DH 4 Semiahmoo marina	48° 59.27' N 122° 46.39' W	riprap	protected	macroalgae

Table 2. Collection sites in Ellisport/Tramp Harbor.

Site	Coordinates	Substrate	Exposure	Vegetation
EP 1 Beach at Portage Way SE & Dockton Rd SW	47° 24.44' N 122° 26.24' W	loose cobbles, sand, mud, isolated boulders	moderate	macroalgae
EP 2 Tramp Harbor Dock	47° 24.81' N 122° 26.29' W	riprap, loose cobble, sand, shell debris, piling, muds	moderate	macroalgae
EP 3 Beach at Tramp Harbor Rd SW & Dockton Rd SW	47° 25.02' N 122° 26.40' W	mud, sand	moderate	macroalgae, <i>Z. marina</i>
EP 4 Beach at Heyer Point	47° 25.29' N 122° 25.90' W	loose cobbles, sand, mud	moderate	macroalgae, <i>Z. marina</i>

Table 3. Collection sites in Padilla Bay.

Site	Coordinates	Substrate	Exposure	Vegetation
PB 1 Hat Island	48° 31.40' N 122° 32.56' W	stable rocks, loose cobble, outcrops of consolidated boulders	moderate	macroalgae
PB 2 Bay View Channel	48° 29.18' N 122° 30.41' W	mud, sand, scattered shell debris	protected	<i>Z. marina</i>
PB 3 Swinomish Channel	48° 28.71' N 122° 30.20' W	mud, sand	protected	macroalgae, salt marsh vegetation
PB 4 Joe Hammel Beach	48° 29.36' N 122° 28.78' W	mud, sand, riprap, loose cobbles	protected	<i>Z. japonica</i>
PB 5 South Bay	48° 28.11' N 122° 28.32' W	riprap, sand, mud, pilings	protected	macroalgae, salt marsh vegetation

Collection trips in Padilla Bay during 1996 - 1997 indicated that algal distribution is patchy in the estuary (Hayden & Waaland, in press). Patchy distribution also was observed in Drayton Harbor and Ellisport/Tramp Harbor. To maximize species detection effort within patches, a temporary 50 m transect was established across algal patches and macroalgae were examined along the length of the transect. Multiple temporary transects were used at a given site when patches of different species assemblages were observed. In addition to transects, an area of 50 x 50 meters was surveyed visually for small patches of isolated species.

Several specimens of each field-identified chlorophytic macroalgal species were collected at each site during each visit. A large number of blade thalli were collected at each site due to the difficulty in field identification and the potential for multiple coexisting species. Algal specimens were rinsed in coarse-filtered seawater in the laboratory and identified using morphological and ecological characters: thallus shape, length, width and branching pattern; number of cell layers; cell shape, length, width and arrangement in surface view; cell height and width in cross-sectioned thalli; pyrenoid number; structure of attachment cells; and ecology (Bliding 1963, 1968; Scagel et al. 1990; Tanner 1979; Kornmann & Sahling 1977). Nomenclature follows Scagel et al.

(1993). Voucher specimens were made of each species from each estuary and were deposited in the Herbarium of the University of Washington and the Padilla Bay Reserve.

The Sørensen coefficient (S_s) (Sørensen 1948), also referred to as the coefficient of community, was used to assess the similarity of macroalgal assemblages. The S_s measures the degree to which the species composition of two samples are alike giving weight to the species that are common to both samples rather than those that only occur in either sample. The formula is:

$$S_s = 2a/2a + b + c$$

where S_s = Sørensen coefficient

a = number of species in common to both samples

b = number of species in sample 1

c = number of species in sample 2

The S_s ranges from 0 (no species common to two samples) to 0.5 (all species common to both samples). For example, if ten species exist in sample 1 and the same ten species exist in sample 2, $S_s = 2(10)/2(10) + 10 + 10 = 0.5$.

The S_s was used to assess the similarity of species assemblages among the three study estuaries. It also was used to assess the similarity of species assemblages among all collection sites within each estuary.

Results

Twelve chlorophytic macroalgal species were found in the study estuaries (Table 4). The majority of these species belong to a group commonly referred to as the "ulvoids." Ulvoids are seaweeds that belong to several genera, including *Blidingia*, *Enteromorpha*, *Monostroma*, *Ulva* and *Ulvaria*. With the exception of *Monostroma*, each of these genera is represented in these mixed-fines estuaries. *Blidingia minima* var. *minima*, *Enteromorpha intestinalis*, *E. linza* and *Ulva fenestrata* were found in all three estuaries. *E. compressa*, *E. flexuosa*, *E. prolifera* and *Ulvaria obscura* var. *blyttii* were found at two of the estuaries. *E. clathrata*, *Prasiola meridionalis*, *U. californica* and *Urospora penicilliformis* were found in only one estuary. Different numbers and combinations of chlorophytic macroalgal species were found in each estuary. Seven species were found at Drayton Harbor, nine at Ellisport, and eight at Padilla Bay.

Using the presence/absence data in Table 4, the Sørensen coefficient can be calculated to assess similarity in macroalgal species assemblages among the three estuaries (Table 5).

Table 4. Chlorophytic macroalgal species collected in Drayton Harbor, Ellisport and Padilla Bay from April to August 1998. A "1" indicates species presence and "0" indicates species absence in the estuaries.

Species	Drayton Harbor	Ellisport	Padilla Bay
<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin var. <i>minima</i>	1	1	1
<i>Enteromorpha clathrata</i> (Roth) Greville	1	0	0
<i>Enteromorpha compressa</i> (Linnaeus) Greville	1	1	0
<i>Enteromorpha flexuosa</i> (Roth) J. Agardh	0	1	1
<i>Enteromorpha intestinalis</i> (Linnaeus) Link in Nees von Esenbeck	1	1	1
<i>Enteromorpha linza</i> (Linnaeus) J. Agardh	1	1	1
<i>Enteromorpha prolifera</i> (Müller) J. Agardh	0	1	1
<i>Prasiola meridionalis</i> Setchell et Gardner	1	0	0
<i>Ulva californica</i> Wille in Collins, Holden et Setchell	0	0	1
<i>Ulva fenestrata</i> Postels et Ruprecht	1	1	1
<i>Ulvaria obscura</i> (Kützing) Gayral var. <i>blyttii</i> (Areschoug) Bliding	0	1	1
<i>Urospora penicilliformis</i> (Roth) Areschoug	0	1	0
Number of ulvoid taxa	7	9	8

Table 5. Similarity of macroalgal assemblages among estuaries using pairwise comparisons for the Sørensen coefficient.

Estuaries	Sørensen coefficient
Padilla Bay vs. Drayton Harbor	0.35
Drayton Harbor vs. Ellisport	0.38
Padilla Bay vs. Ellisport	0.45

Within each estuary different species assemblages were found at collection sites (Figures 2-4). Species presence/absence was recorded at all collection sites. These data were used to calculate the Sørensen coefficient to assess similarity of macroalgal assemblages among collection sites within each estuary (Appendix).

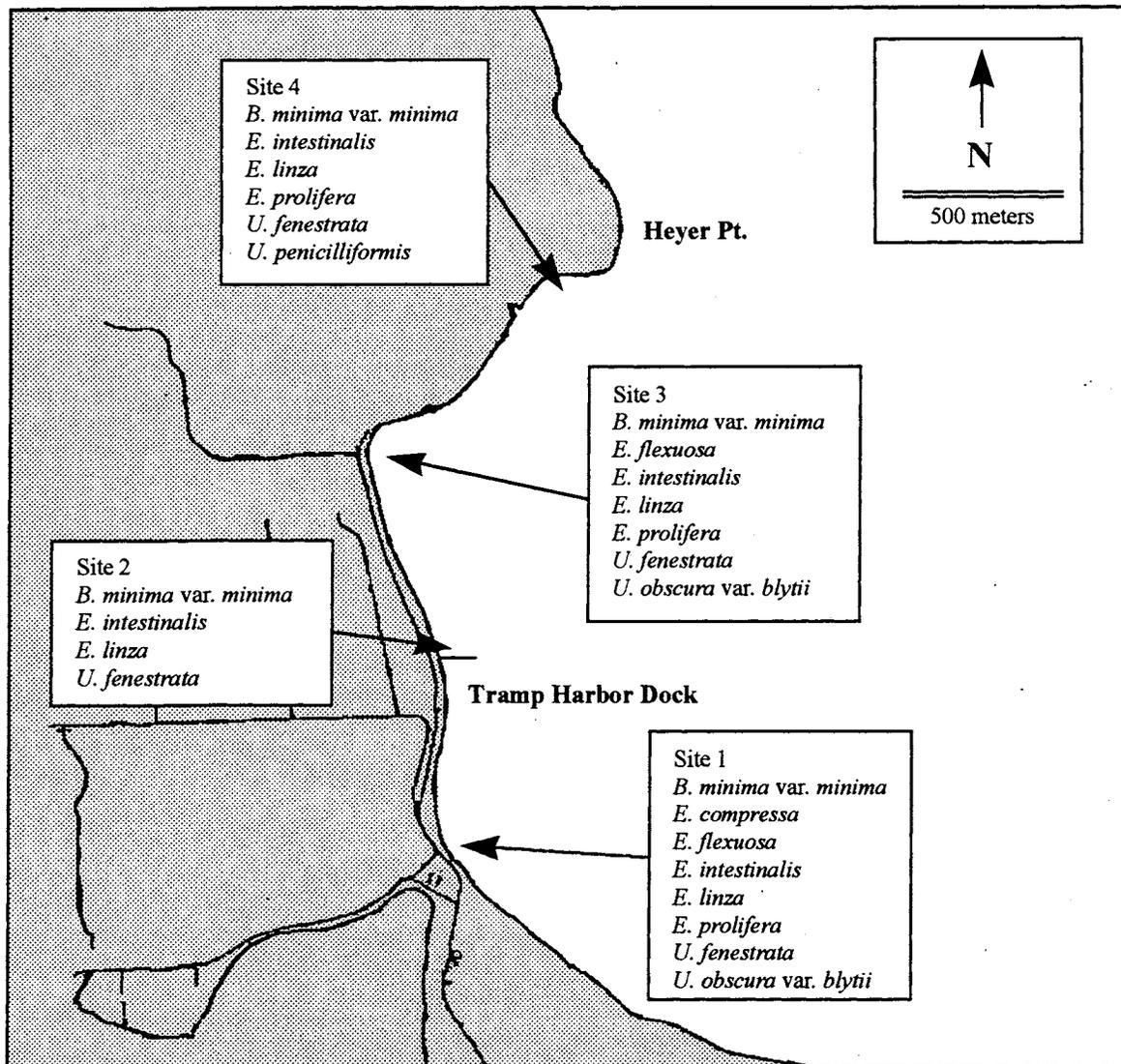


Figure 2: Species of green macroalgae collected at study sites in Ellisport/Tramp Harbor June through August 1998. (Base map source: King Co. Thomas Guide 1982)

The composition of species assemblages at collection sites within all estuaries changed from April to August 1998 (Tables 5-7). Species were considered common (c), abundant (a), or relatively rare (r) based on qualitative observations. Species were considered abundant when relatively large amounts of biomass were observed (i.e., 75 - 100% cover). They were considered rare when found only at one or a few sites and in each case with very low biomass. At Drayton Harbor, *E. clathrata*, a highly branched filamentous green alga, was pervasive at collection sites with the exception of site 4 when it was found in August as drift material. Late in the summer this alga was found in patches several meters in diameter with over 100% cover on the mudflats at site

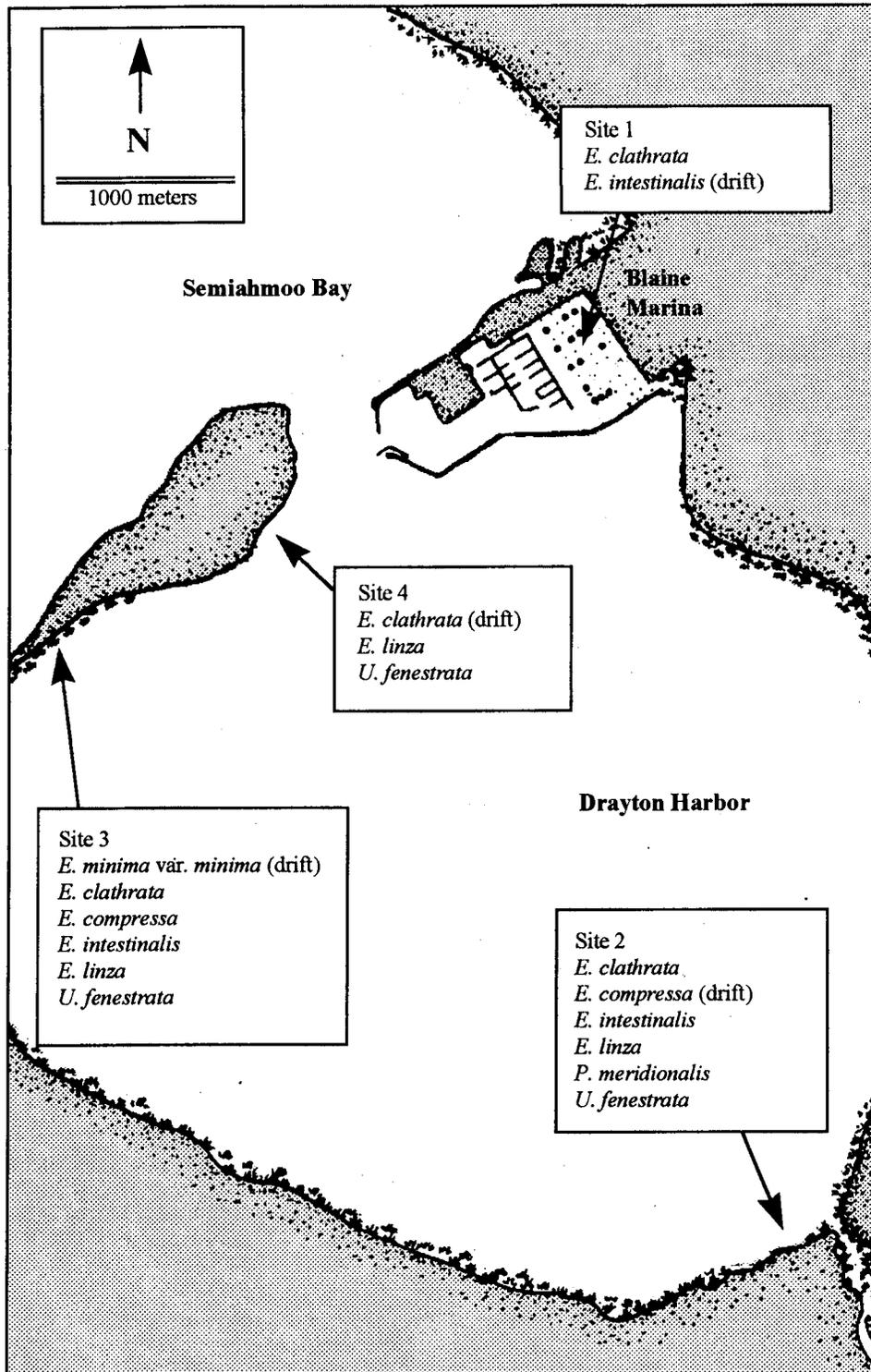


Figure 3: Species of green macroalgae collected at study sites in Drayton Harbor May through August 1998. (Base map source: Thom et al. 1988)

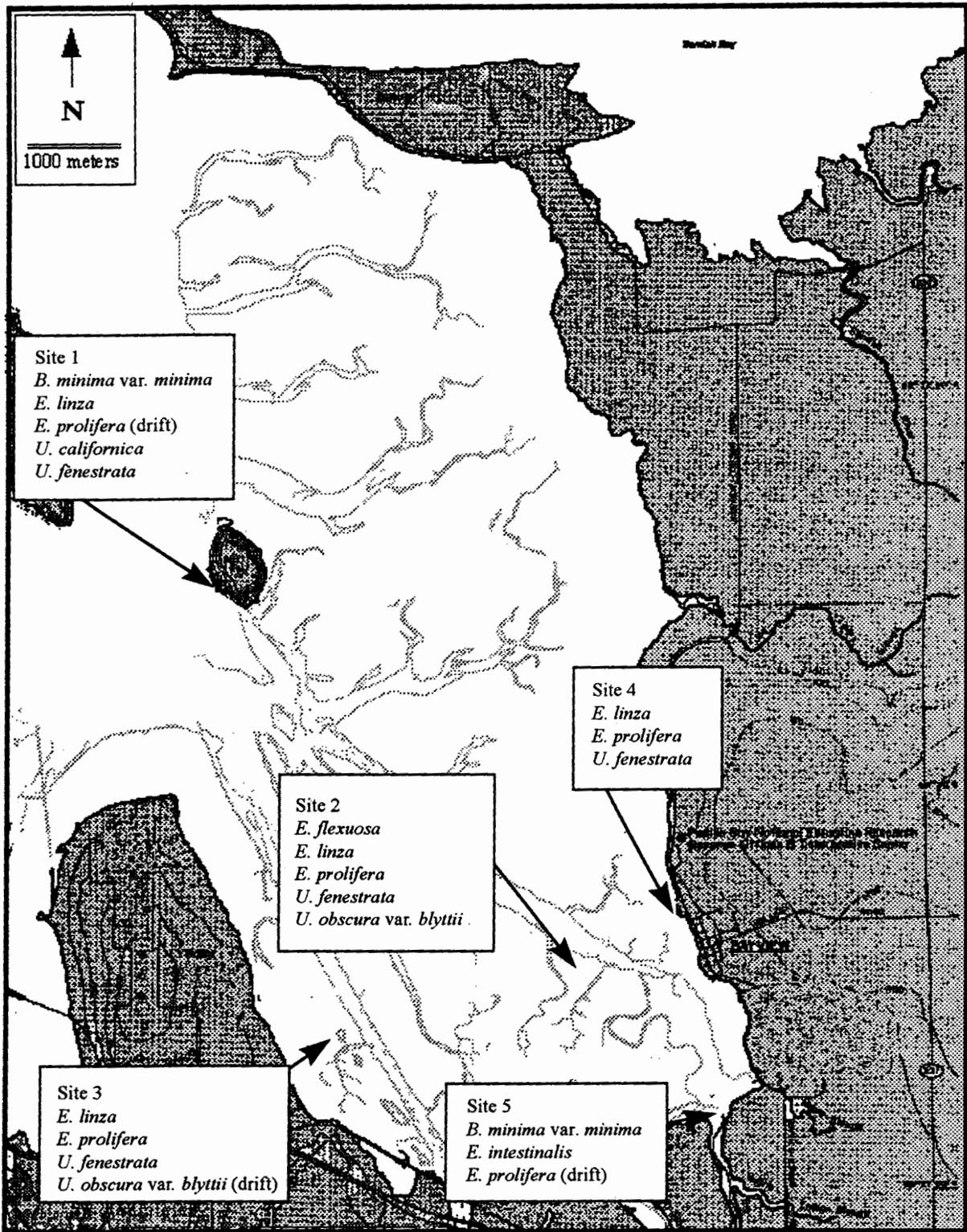


Figure 4: Species of green macroalgae collected at study sites in the Padilla Bay National Estuarine Research Reserve April through August 1998. (Base map source: Bulthuis 1991)

2 and in *Z. marina* beds at site 3 and other areas of the harbor as seen from Drayton Harbor Rd. *U. fenestrata*, *E. intestinalis* and *E. linza* though found at several sites had relatively low abundance in the harbor across collection visits. Small individuals of these taxa (< 5 cm tall) were found attached to riprap at site 4 and cobbles at site 3. Moderate-sized *U. fenestrata* individuals (6 - 40 cm tall) were found attached to isolated boulders at site 2. No drift *U. fenestrata* was encountered. *E. compressa* only was found during the spring collection at site 2 as drift material and at site 3 attached to cobbles. *B. minima* var. *minima* only was found at site 3 and a single patch of *P. meridionalis* was found only in July atop an isolated boulder at site 2.

Table 5. Species assemblages at four collection sites at Drayton Harbor from May to August 1998. Species are noted as common (c), rare (r), abundant (a) or as drift material.

Drayton Harbor	May	July	August
DH 1	<i>E. clathrata</i> (c) <i>E. intestinalis</i> (drift)	<i>E. clathrata</i> (c)	<i>E. clathrata</i> (c)
DH 2	<i>E. clathrata</i> (c) <i>E. compressa</i> (drift) <i>E. intestinalis</i> (r) <i>E. linza</i> (r) <i>U. fenestrata</i> (r)	<i>E. clathrata</i> (c) <i>P. meridionalis</i> (r)	<i>E. clathrata</i> (a)
DH 3	<i>B. minima</i> var. <i>minima</i> (r) <i>E. compressa</i> (r) <i>E. intestinalis</i> (r) <i>E. linza</i> (drift)	<i>B. minima</i> var. <i>minima</i> (r) <i>E. clathrata</i> (c) <i>E. intestinalis</i> (r) <i>E. linza</i> (r)	<i>B. minima</i> var. <i>minima</i> (r) <i>E. clathrata</i> (a) <i>E. intestinalis</i> (r) <i>E. linza</i> (r) <i>U. fenestrata</i> (r)
DH 4	<i>E. linza</i> (r) <i>U. fenestrata</i> (r)	<i>E. linza</i> (r) <i>U. fenestrata</i> (r)	<i>E. clathrata</i> (drift) <i>E. linza</i> (r) <i>U. fenestrata</i> (r)

At Ellisport species assemblages were relatively consistent across collection visits. The same set of taxa was found at site 2 during each visit while only two or three changes in taxa were observed at the remaining collection sites from April to August. Relative abundance of taxa, however, was variable based on qualitative observations. Large amounts of *U. obscura* var. *blytii* were observed at sites 1 and 3 during the spring collection. Large blades (> 30 cm tall) were found attached to cobbles, free-floating in masses and caught among eelgrass leaves. This alga was not found during summer collections. In April small to moderate-sized individuals of *U.*

fenestrata were found attached at sites 1, 2 and 3. In July large amounts of attached and drift *U. fenestrata* were observed at all sites and in August mats of decaying *U. fenestrata* were observed at sites 2 and 3 and small individuals were found again at site 1. *E. flexuosa* was found at two sites during the August collection but was absent from all sites in spring and early summer. In August this alga along with *E. compressa* and *E. intestinalis* was relatively abundant at site 1. *E. prolifera* was found sporadically and never in great abundance in this estuary. *U. penicilliformis* was observed in small amounts at site 4.

Table 6. Species assemblages at four collection sites at Ellisport from June to August 1998. Species are noted as common (c), rare (r), abundant (a) or as drift material.

Ellisport	June	July	August
EP 1	<i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>E. prolifera</i> (r) <i>U. fenestrata</i> (c) <i>U. obscura</i> var. <i>blytii</i> (a)	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>U. fenestrata</i> (a)	<i>E. compressa</i> (a) <i>E. flexuosa</i> (a) <i>E. intestinalis</i> (a) <i>E. linza</i> (c) <i>U. fenestrata</i> (c)
EP 2	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>U. fenestrata</i> (c)	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>U. fenestrata</i> (a)	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>U. fenestrata</i> (a)
EP 3	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>U. fenestrata</i> (c) <i>U. obscura</i> var. <i>blytii</i> (a)	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>E. prolifera</i> (r) <i>U. fenestrata</i> (a)	<i>E. intestinalis</i> (c) <i>E. flexuosa</i> (c) <i>E. linza</i> (c) <i>U. fenestrata</i> (a)
EP 4	no collection	<i>B. minima</i> var. <i>minima</i> (c) <i>E. intestinalis</i> (c) <i>E. linza</i> (c) <i>E. prolifera</i> (r) <i>U. fenestrata</i> (a) <i>U. penicilliformis</i> (r)	<i>E. linza</i> (c) <i>U. fenestrata</i> (c) <i>U. penicilliformis</i> (c)

Species assemblages at Padilla Bay were moderately consistent across collection visits. The same set of taxa was found at site 1 from June to August; however, at sites 2 - 5 species composition was variable with one or two changes in taxa. Relative abundance of green macroalgae was variable in the estuary. In June and July *U. obscura* var. *blytii* was abundant at site 2 but in August was absent and only was found as drift material at site 3 throughout spring

and summer. *E. prolifera* was present across collection visits but was noticeably most abundant in July. In August this alga was found senescing on mudflats and among fringe drift material at sites 1, 2, 3 and 5. *E. flexuosa* and *E. intestinalis* only were found in August at sites 2 and 5 respectively. No green macroalgae were observed in August at site 4; however, new growth of *U. fenestrata* and *E. linza* was observed at site 1 that month.

Table 7. Species assemblages at four collection sites at Padilla Bay from April to August 1998. Species are noted as common (c), rare (r), abundant (a) or as drift material.

Padilla Bay	June	July	August
PB 1	<i>U. californica</i> (c) <i>E. linza</i> (a) <i>U. fenestrata</i> (a)	<i>U. californica</i> (c) <i>E. linza</i> (a) <i>U. fenestrata</i> (a)	<i>U. californica</i> (c) <i>E. linza</i> (a) <i>E. prolifera</i> (drift) <i>U. fenestrata</i> (a)
PB 2	<i>E. linza</i> (c) <i>E. prolifera</i> (c) <i>U. fenestrata</i> (c) <i>U. obscura</i> var. <i>blytii</i> (a)	<i>E. linza</i> (c) <i>E. prolifera</i> (a) <i>U. fenestrata</i> (c) <i>U. obscura</i> var. <i>blytii</i> (c)	<i>E. flexuosa</i> (r) <i>E. linza</i> (c) <i>E. prolifera</i> (c) <i>U. fenestrata</i> (drift)
PB 3	<i>E. linza</i> (c) <i>E. prolifera</i> (c) <i>U. obscura</i> var. <i>blytii</i> (drift)	<i>E. linza</i> (c) <i>E. prolifera</i> (a) <i>U. fenestrata</i> (c) <i>U. obscura</i> var. <i>blytii</i> (drift)	<i>E. prolifera</i> (c) <i>U. obscura</i> var. <i>blytii</i> (drift)
PB 4	<i>E. linza</i> (c) <i>E. prolifera</i> (c) <i>U. fenestrata</i> (c)	<i>E. prolifera</i> (drift) <i>U. fenestrata</i> (c)	no green macroalgae
PB 5	<i>B. minima</i> var. <i>minima</i> (c) <i>E. prolifera</i> (drift)	<i>B. minima</i> var. <i>minima</i> (c)	<i>E. intestinalis</i> (r) <i>E. prolifera</i> (drift)

Discussion

Objective #1: To compare green macroalgal species assemblages at Padilla Bay, Drayton Harbor and Ellisport.

Padilla Bay, Drayton Harbor and Ellisport/Tramp Harbor share a number of macroalgal species in common. In all three estuaries *B. minima* var. *minima*, *U. fenestrata* and several species of *Enteromorpha* were observed (Table 4). When all species are considered, the Sørensen coefficient values suggest that the similarity of species assemblages among the three study estuaries is relatively high (Table 5). In particular, the assemblages at Padilla Bay and

Ellisport/Tramp Harbor are quite similar ($S_s = 0.45$, or 90% similarity). Though the S_s value for the comparison of Padilla Bay and Drayton Harbor is lower, it suggests there is 70% similarity among these two assemblages. These relatively high similarity values may result from the fact that macroalgal species distribution is determined primarily by substratum (Lindstrom & Foreman 1978) and these estuaries share substratum attributes on a large scale, as mixed-fines estuaries, as well as on a small scale (Tables 1, 2, and 3). Other factors, such as salinity, water transparency, nutrient concentrations, and seasonal and temperature ranges also have been shown to influence species distribution (Middelboe et al. 1998, and as noted above). Differences in species composition in these estuaries may be due to differences in these factors, as well as differences in the availability of hard substratum. For example, the substratum at three of four sites at Ellisport was dominated by cobbles, boulders and riprap whereas the substratum at most sites in Drayton Harbor and Padilla Bay was dominated by mud and sand. Ellisport had the largest number of taxa and the greatest biomass contribution from blade species such as *U. fenestrata* and *U. obscura* var. *blytii*. The greatest contribution of biomass at Drayton Harbor and Padilla Bay came from tubular species of *Enteromorpha*, *E. clathrata* in the former and *E. prolifera* in the latter. Although the blade species can survive and even thrive unattached, generally they have been observed attached to hard substratum, especially at early stages in their growth cycle; however, these *Enteromorpha* species are most often found free-floating or partially buried in mud without obvious attachment to solid substratum (pers obs., see also Abbott & Hollenberg 1976).

Within each estuary differences in species assemblages at collection sites are likely due to differences in substratum and exposure to wind and water currents that characterize each site (Lindstrom & Foreman 1978). The Sørensen coefficient values among collection sites are highest for two sites with similar physical attributes. For example, S_s values range from 0.40 to 0.48 for pairwise comparisons of sites within Ellisport/Tramp Harbor (Appendix I). As noted previously, collection sites at this estuary were more homogeneous than those at Drayton Harbor or Padilla Bay, all having some combination of hard (cobbles, boulders) and soft (sand, mud) substratum (Table 2). Conversely, S_s values are lowest for pairwise comparisons of sites with differing physical attributes. For example, at Drayton Harbor the S_s value for the comparison of site 1 (mud flat) and site 4 (riprap) is zero, as is the S_s value for three site comparisons at Padilla Bay.

Changes in species assemblages at collection sites from April to August 1998 may be the result of several factors. These estuaries are dynamic environments and macroalgae may be moved throughout the area via water currents at high tide or wind at low tide. For example, at Padilla Bay *U. obscura* var. *blytii* was observed attached at site 2 in June and July but was found only as drift material at site 3 during visits these months. Seasonality of algal species would also appear to play a role in changing species composition. *E. flexuosa* was found in Ellisport and Padilla Bay, but at both these locations it was observed only in August. Conversely, *U. obscura* var. *blytii* thrives earlier in the growing season and is only found as drift material in the late summer. This is a similar pattern to that observed in Padilla Bay in summer 1997.

Grazers may also influence algal species assemblages. In July 1997, large numbers of the non-native snail *Battilaria attramentaria* were observed on algal blades at site 4 in Padilla Bay and biomass was noticeably diminished at that site in August. In 1998, these snails were observed again at site 4 in July. In August 1998, no macroalgae was observed at this site. Although herbivore preference studies were not conducted, snails and other herbivores may have the ability to render a species inconspicuous or absent.

As in the 1997 study, every effort was made to detect all green macroalgal species present at each site, and it is possible that some species were simply absent during a particular collection visit. Four species found in Padilla Bay in 1997 were not observed in 1998. *Urospora penicilliformis* and *Rhizoclonium riparium* are green, uniseriate filaments that relatively common in Puget Sound and the San Juan Islands. These algae were neither conspicuous nor abundant in Padilla Bay in 1997 and may have been absent at sites in 1998. *Acrosiphonia coalita*, an alga having the appearance of a frayed green rope, was conspicuous on Hat Island in 1997. Its absence in 1998 is curious and as yet unexplained. *Ulva stenophylla*, a simple, lanceolate alga that was present in July and August 1997 may have been present in Padilla Bay during parts of these months not visited in 1998. It is also plausible that an unusually lanceolate-shaped blade of *U. fenestrata* was mis-identified as *U. stenophylla* in 1997 as these species have few diverging morphological characters and exhibit much morphological plasticity (Tanner 1979). This possibility points to the need for a more definitive way to identify these algae, such as use of diagnostic molecular markers.

Finally, observed differences in assemblages in Padilla Bay from year to year, and among collection sites within each estuary in a given year, may depend on frequency of observations. Many ulvoid species are fast growing, respond rapidly to environmental changes, and thrive unattached which makes them readily transported by wind and water currents (Littler & Littler 1980, Valiela et al. 1997). It is plausible that certain species grow rapidly and senesce or get flushed out of an estuary in very short time periods.

Objective #2: To establish whether the green macroalgal species composition of Padilla Bay is similar of that in other Pacific Northeast estuaries.

Data provided by this study and others suggest that the assemblage of green macroalgal species in Padilla Bay is generally representative of that in other Northeast Pacific estuaries. As discussed under Objective #1, species composition in Padilla Bay is quite similar to that in Drayton Harbor and Ellisport/Tramp Harbor. Additionally, there are several studies addressing macroalgal assemblages in estuaries in the literature (Neushul 1967, Washington; Pomeroy & Stockner 1976, British Columbia; Orris 1980, Maryland; Thom 1980, 1984, Washington; Zedler 1980, California; Davis & McIntire 1981, Oregon; Rao 1987, India; Thom & Albright 1990, Washington; Hardy et al. 1993, England; Valiela et al. 1997, general review). With few exceptions, reported green macroalgal assemblages include at least one variety of *Blidingia minima*, several species of *Enteromorpha*, and a minimum of one *Ulva* species, such as *U. fenestrata* or *U. lactuca*, a species with similar morphology. Taxa from several additional green macroalgal genera, such as *Acrosiphonia*, *Chaetomorpha*, *Cladophora*, *Monostroma*, *Rhizoclonium*, *Ulothrix* and *Urospora*, are also frequently collected in estuaries. Representatives of these genera have been reported in Padilla Bay; however, they have been observed as only a small number of individuals or biomass (Thom 1989, Riggs 1997, Hayden & Waaland in press).

Several studies were conducted in Northeast Pacific mixed-fines estuaries. In their study of benthic vegetation standing-stock in central Puget Sound, Thom and Albright (1990) reported eight green macroalgal species in cobble/boulder-dominated intertidal study sites. Four of these species, *Enteromorpha intestinalis*, *E. linza*, *Ulva fenestrata* and *Ulvaria obscura*, were conspicuous and relatively abundant on the six collection days between July 1982 and November 1983. The four other species reported, *Acrosiphonia saxatilis*, *Chaetomorpha cannabina*,

Cladophora sericea and *Monostroma grevillei*, had relatively low biomass throughout the study period, and some were absent on several collection days. In his study of macroalgae in Grays Harbor Estuary, Thom (1984) reported thirteen green macroalgal species, though four of these later were synonymized (Scagel et al. 1993) with other taxa yielding a total of nine species. Five taxa found in Padilla Bay, *B. minima*, *E. flexuosa*, *E. intestinalis*, *E. linza* and *U. fenestrata*, and one species found in Drayton Harbor and Ellisport, *E. clathrata*, were found in the Grays Harbor Estuary. The three remaining species reported in Grays Harbor were *Gayralia oxyspermum*, *Rhizoclonium riparium* and *Ulothrix flacca*. The most abundant and conspicuous algae in the Grays Harbor Estuary were *E. clathrata*, *E. intestinalis* and *E. linza*. Interestingly, *E. clathrata*, was abundant in Drayton Harbor, and a morphologically similar species, *E. prolifera*, was abundant in Padilla Bay. All three of these estuaries have extensive intertidal sand and mudflats which may provide large amounts of habitat for these often free-floating species. Finally, in their study of benthic algae in the Squamish River Estuary, Pomeroy and Stockner (1976) reported six green macroalgal species: *B. minima* var. *minima* (as *E. minima*), *E. prolifera*, *R. riparium*, *Spirogyra* sp., *U. flacca* and *U. fenestrata* (as *U. lactuca*). The most abundant species were *B. minima* var. *minima* and *U. fenestrata*.

While the green macroalgal species assemblage in Padilla Bay reported here is unique, it does appear to be generally representative for other Northeast Pacific estuaries. Many species found in Padilla Bay are also found in other estuaries and past studies reported in the literature suggest that the absence of certain genera in the current Padilla Bay study may be due to their low abundance overall.

These findings may help to address a related question of whether green macroalgae in Padilla Bay are native or introduced. This question was raised in the 1996-1997 Padilla Bay study as a result of a macroalgal bloom reported in the Bay in 1989. It was asked whether the bloom was a native species reacting to an environmental change (e.g., nutrient loading or water temperature) in the Bay, or was an introduced species which suddenly thrived in the Bay. Non-native macroalgae may be introduced via shipping, aquaculture, or commercial shellfish transport (Olson et al., submitted). The data presented here suggest that green macroalgal species in Padilla Bay are native; however, it is possible that 1) there is cryptic diversity among green macroalgae (i.e., taxa are morphologically similar, but genetically divergent), 2) certain taxa were introduced

in the past, thrived and spread throughout the region resulting in the historical impression that they are native, and 3) non-native green macroalgae exist in areas of Padilla Bay not sampled in this study. There is evidence for both cryptic diversity (e.g., Stiller & Waaland 1993, van Oppen et al. 1996) and invasiveness among macroalgae (Trowbridge 1995, Gillespie et al. 1997, Rico & Fernandez 1997). Phylogenetic analysis using molecular characters is necessary to address the possibility of either cryptic diversity or a past introduction. Additional collections and analyses are required to resolve the third possibility.

Objective #3: To determine if there is a diagnostic assemblage of green macroalgae in mixed-fine estuaries of Puget Sound and the Strait of Georgia.

Based on two years of study during spring and summer in Pacific Northeast estuaries, there does appear to be a diagnostic assemblage of green macroalgae in mixed-fines estuaries of Puget Sound and the Strait of Georgia. As noted above, such estuaries that have been studied in the Northeast Pacific (as well as estuaries in other parts of the world) have green macroalgal assemblages during these seasons which generally include at least one variety of *Blidingia minima*, several species of *Enteromorpha*, and a minimum of one *Ulva* species. Without exception *E. clathrata* or *E. prolifera*, and *U. fenestrata* or *U. lactuca* are listed as present, and often these taxa are abundant. In the vast majority of studies, *E. intestinalis* and *E. linza* are conspicuous as well. Other taxa commonly found in mixed-fines estuaries include species of *Acrosiphonia*, *Chaetomorpha*, *Cladophora*, *Monostroma*, *Rhizoclonium*, *Ulothrix* and *Urospora*. These taxa may or may not be abundant. A most narrowly defined diagnostic assemblage would therefore include the pervasive *Enteromorpha* and *Ulva* species. A more expanded diagnostic assemblage could include other “common” taxa.

While it is clear that only certain green macroalgae are present in mixed-fines estuaries, it is not recommended that diagnosis of these habitats be based on their presence alone. There are many other organisms, including higher plants and invertebrates, that characterize mixed-fines estuaries, and they should be included in any diagnosis of habitats or biotic diversity.

Conclusions

This study indicates that green macroalgal species diversity in Padilla Bay is representative of that in similar habitats in Puget Sound and the Strait of Georgia. Species lists from this study provide a baseline for resource managers to monitor changes in diversity in the estuaries over time. A diagnostic assemblage of green macroalgae in Northeast Pacific mixed-fines estuaries includes a relatively short list of species. Combined with diagnostic higher plants and invertebrates, this list may be useful for identifying estuarine areas in the region for conservation and other management purposes.

APPENDIX

Table Ia. Ellisport/Tramp Harbor data matrix. Species are represented by the first letter of the genus followed by the first one or two letters of the specific epithet.

Quadrats	Bm	Ecl	Eco	Ef	Ei	El	Ep	Pm	Uc	Uf	Uo	Up	Total
EP1	1	0	1	1	1	1	1	0	0	1	1	0	8
EP2	1	0	0	0	1	1	0	0	0	1	0	0	4
EP3	1	0	0	1	1	1	1	0	0	1	1	0	7
EP4	1	0	0	0	1	1	1	0	0	1	0	1	6

Table Ib. Similarity of macroalgal assemblages among collection sites within Ellisport/Tramp Harbor using pairwise comparisons for the Sørensen coefficient (S_s).

Quadrats	a	b	c	S_s
1 x 2	4	8	4	.40
1 x 3	7	8	7	.48
1 x 4	5	8	6	.42
2 x 3	4	4	7	.42
2 x 4	4	4	6	.44
3 x 4	5	7	8	.40

Table Ic. Drayton Harbor data matrix.

Quadrats	Bm	Ecl	Eco	Ef	Ei	El	Ep	Pm	Uc	Uf	Uo	Up	Total
1	0	1	0	0	0	0	0	0	0	0	0	0	1
2	0	1	0	0	1	1	0	1	0	1	0	0	5
3	1	1	1	0	1	1	0	0	0	1	0	0	6
4	0	0	0	0	0	1	0	0	0	1	0	0	2

Table Id. Similarity of macroalgal assemblages among collection sites within Drayton Harbor using pairwise comparisons for the Sørensen coefficient (S_s).

Quadrats	a	b	c	S_s
1 x 2	1	1	5	.25
1 x 3	1	1	6	.22
1 x 4	0	1	2	0
2 x 3	4	5	6	.42
2 x 4	2	5	2	.36
3 x 4	2	6	2	.33

Table Ie. Padilla Bay data matrix.

Quadrats	Bm	Ecl	Eco	Ef	Ei	El	Ep	Pm	Uc	Uf	Uo	Up	Total
1	1	0	0	0	0	1	0	0	1	1	0	0	4
2	0	0	0	1	0	1	1	0	0	1	1	0	5
3	0	0	0	0	0	1	1	0	0	0	1	0	3
4	0	0	0	0	0	1	1	0	0	1	0	0	3
5	1	0	0	0	1	0	0	0	0	0	0	0	2

Table If. Similarity of macroalgal assemblages among collection sites within Padilla Bay using pairwise comparisons for the Sørensen coefficient (S_s).

Quadrats	a	b	c	S_s
1 x 2	2	4	5	.31
1 x 3	1	4	3	.22
1 x 4	2	4	3	.36
1 x 5	1	4	2	.25
2 x 3	3	5	3	.43
2 x 4	3	5	3	.43
2 x 5	0	5	2	0
3 x 4	2	3	3	.40
3 x 5	0	3	2	0
4 x 5	0	3	2	0

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LITERATURE CITED

- Abbott, I.A. and G.J. Hollenberg. 1976. *Marine algae of California*. Stanford Univ. Press, CA. 827 pp.
- Bliding, C. 1963. A critical survey of European taxa in Ulvales, Part I: *Capsosiphon*, *Percursaria*, *Blidingia*, *Enteromorpha*. *Bot. Notiser*, 8: 3-160.
- Bliding, C. 1968. A critical survey of European taxa in Ulvales, Part II: *Ulva*, *Ulvaria*, *Monostroma*, *Kornmannia*. *Bot. Notiser*, 121: 535-629.
- Bulthuis, D.A. 1991. Distribution of habitats and summer standing crop of seagrasses and macroalgae in Padilla Bay, Washington. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve Tech. Report No. 2, Mount Vernon, WA, 35 pp.
- Bulthuis, D.A. 1995. Distribution of seagrasses in a North Puget Sound estuary: Padilla Bay, Washington, USA. *Aquat. Bot.*, 50: 99-105.
- Davis, M.W. and McIntire, C.D. 1981. Production dynamics of sediment-associated algae in two Oregon estuaries. *Estuaries* 4: 301.
- Dethier, M.N. 1990. A marine and estuaries habitat classification system for Washington State. Washington Natural Heritage Program, Department of Natural Resources, Olympia, WA, 56 pp.
- Gillespie, R.D., Meinesz, A. and Critchley, A.T. 1997. Growth response of *Caulerpa taxifolia* (Ulvophyceae, Chlorophyta) from South African aquarist trade. A potential invasive of South African coastal waters. *S. African J. Bot.* 63: 480-483.
- Hardy, F.G., Evans, S.M. and Tremayne, M.A. Long-term changes in the marine macroalgae of three polluted estuaries in north-east England. *J. Exp. Biol. Ecol.* 172: 81-92.
- Hayden, H.S. and Waaland, J.R. (in press). Green tide algae of the Padilla Bay Estuary, Washington. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve Tech. Report, Mount Vernon, WA, 15 pp.
- Kornmann, P. and Sahling, P.H. 1977. Marine algae of Helgoland. Benthic green, brown and red algae. *Helgo. Wiss. Meeresunters.*, 29: 1-289.
- Lindstrom, S.C. and Foreman, R.E. 1978. Seaweed associations of the Flat Top Islands, British Columbia: a comparison of community methods. *Syesis*, 11: 171-185.
- Littler, M.M. & Littler, D.S. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.*, 116: 25-44.

- Middelboe, A.L., Sand-Jensen, K. and Krause-Jensen, D. 1998. Patterns of macroalgal species diversity in Danish Estuaries. *J. Phycol.* 34: 457-466.
- Neushul, M. 1967. Studies of subtidal marine vegetation in western Washington. *Ecology* 48: 83-93.
- Olson, A.M, Linen, E.H. and Waaland, J.R. (submitted). The global spread of marine macroalgae: The nature of invasiveness. Submitted to *Conservation Biology* (and currently in review).
- Orris, P.K. 1980. A revised species list and commentary on the macroalgae of the Chesapeake Bay in Maryland. *Estuaries* 3: 200-206.
- Pomeroy, W.M. and Stockner, J.G. 1976. Effects of environmental disturbance on the distribution and primary production of benthic algae on a British Columbia estuary. *J. Fish. Res. Board Can.* 33: 1175-1187.
- Rao, M.U. 1987. Algae of Indian estuaries. *J. Mar. Biol. Ass. India.* 29: 1-9.
- Rico, J.M. & Fernandez, C. 1997. Ecology of *Sargassum muticum* on the North Coast of Spain: II. Physiological differences between *Sargassum muticum* and *Cystoseira nodicaulis*. *Bot. Mar.* 40: 405-410.
- Riggs, S. 1997. Padilla Bay National Estuarine Research Reserve Natural Resource Stewardship and Management Report. Washington State Department of Ecology, Olympia, WA, 111 pp.
- Scagel, R.F., Gabrielson, P.W., Garbary, D.J., Golden, L., Hawkes, M.W., Lindstrom, S.C., Oliveira, J.C. & Widdowson, T.B. 1990. *Keys to the benthic marine algae and seagrasses of British Columbia, Southeast Alaska, Washington and Oregon*. Phycological Contribution No. 4, Department of Botany, University of British Columbia, Vancouver, B.C., 187 pp.
- Scagel, R.F., Gabrielson, P.W., Garbary, D.J., Golden, L., Hawkes, M.W., Lindstrom, S.C., Oliveira, J.C. & Widdowson, T.B. 1993. *A synopsis of the benthic marine algae of British Columbia, Southeast Alaska, Washington and Oregon*. Phycological Contribution No. 3, Department of Botany, University of British Columbia, Vancouver, B.C., 535 pp.
- Stiller, J.W. and Waaland, J.R. 1993. Molecular analysis reveals cryptic diversity in *Porphyra* (Rhodophyta). *J. Phycol.* 29: 506-517.
- Tanner, C.E. 1979. The taxonomy and morphological variation of distromatic ulvaceous algae (Chlorophyta) from the Northeast Pacific. Ph.D. Thesis, University of British Columbia, Vancouver, B.C., 249 pp.

- Thom, R.M. 1980. Seasonality in low intertidal marine algal communities in central Puget Sound, Washington, USA. *Bot. Mar.* 23: 7-11.
- Thom, R.M. 1984. Composition, habitats, seasonal changes and productivity of macroalgae in Grays Harbor Estuary, Washington. *Estuaries* 7: 51-60.
- Thom, R. M., Albright, R., Simenstad, C., Hampel, J., Cordell, J.R. & Chew, K. 1984. Renton Sewage Treatment Plant Project: Seahurst baseline study. Fisheries Research Institute, University of Washington School of Fisheries. Final report to METRO, vol. IV, section 5. 177 pages.
- Thom, R. M., Simenstad, C. A., Cordell J.R. & Salo E. O. 1988. Fisheries mitigation plan for expansion of moorage at Blaine Marina, Blaine, Washington. Fisheries Research Institute, University of Washington School of Fisheries. Final Report to the Port of Bellingham. 24 pages.
- Thom, R.M. 1989. Plant standing stock and productivity on the tidal flats in Padilla Bay, Washington: a temperate North Pacific estuarine embayment. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve Reprint Series No. 13, Mount Vernon, WA, 37 pp.
- Thom, R.M. and Albright, R.G. 1990. Dynamics of benthic vegetation standing-stock, irradiance and water properties in central Puget Sound. *Mar. Biol.*, 104: 129-141.
- Thom, R.M., Miller, B. and Kennedy, M. 1991. Temporal pattern of grazers and vegetation in a temperate seagrass system. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve Reprint Series No. 15, Mount Vernon, WA, 28 pp.
- Trowbridge, C. D. 1995. Establishment of green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: Current distribution and invertebrate grazers. *J. Ecology* 83: 949-965.
- Valiela, I., McClelland, J., Hauxwell, J. Behr, P.J., Hersh, D. and Foreman, K. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42: 1105-1118.
- van den Hoek, C., Mann, D. G. & Jahns H. M. 1995. Algae: an introduction to phycology. Cambridge University Press. 623 pages.
- van Oppen, M.J.H., Klerk, H., Olsen J.L. and Stam, W.T. 1996. Hidden diversity in marine algae: Some examples of genetic variation below the species level. *J. Mar. Biol. Ass. UK* 76: 239-242.
- Zedler, J.B. 1980. Algal mat productivity: comparisons in a salt marsh. *Estuaries* 3: 122-131.

