THE TAXONOMY AND MORPHOLOGICAL VARIATION OF DISTROMATIC ULVACEOUS ALGAE (CHLOROPHYTA) FROM THE NORTHEAST PACIFIC by

CHRISTOPHER EUGENE TANNER
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We accept this thesis as conforming to the required standard

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Department of Botany

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date October 18, 1979
Carl Linnaeus: father of plant systematics and of Ulva.
ABSTRACT


A large degree of morphological and anatomical variation was observed in herbarium specimens and in field populations of *Ulva*. Some of this variation is related to differences in environmental parameters. Dentation in *U. taeniata* is reduced or eliminated with an increase of water temperature, while blade thickness increases with an increase of water temperature. As a result specimens from the southern part of its range are often incorrectly identified. The size, shape and thickness of thalli in populations of *U. fenestrata* from the west coast of Vancouver Island and from Vancouver vary significantly with vertical position in the intertidal zone and with wave exposure. Most species of *Ulva* show some seasonal variation in size and thickness. Morphology is generally more conservative than blade thickness or cell dimensions. Pyrenoid number is useful for separating *U. californica* from other species; however, in species with more than one pyrenoid per cell, the number is not consistent and cannot be used as a taxonomic criterion.
Studies of reproduction, development and interspecific hybridization potential confirmed observations made in the field. In culture *U. taeniata* does not produce marginal dentation above 16° C. Development and morphology in *U. californica* varies with temperature. At relatively low temperatures (7°-11° C) upright filaments develop before the basal systems and result in plants similar to *U. scagelii* from British Columbia. At higher temperatures (13°-19° C) the basal system is initiated first and develops into an extensive basal system that produces numerous upright germlings. The resulting tufted plants are similar to *U. californica* from southern California. These two species also form viable zygotes when crossed, supporting the synonymy of *U. scagelii* with *U. californica*. As living specimens of *U. fasciata* were not encountered in the northeast Pacific, an isolate from Hawaii was used for the culture study of the reproduction and development of this species. This Hawaiian isolate demonstrated an unusual form of reproduction. Marginal vegetative cells round up and develop into aplanospores that divide into a floating multicellular globose stage. The cells of the globose stage eventually release biflagellated swarmers that develop into normal appearing germlings.

A cytological study was undertaken to determine if species of *Ulva* from the northeast Pacific differed in their chromosome numbers. All of the species of *Ulva* studied have a similar haploid chromosome number of around 8 or 9. Following parthenogenetic development of gametes, haploid, diploid and dikaryotic cells are occasionally observed in the same germling. The dikaryotic cells may represent a transitional stage in the doubling of the chromosome number. In a few of these parthenogenetic germlings some of the cells become enlarged and multinucleate. These cells may have lost the capacity for cytokinesis.

A diminutive distromatic ulvaceous alga was encountered in southern
California. This alga resembles Ulva morphologically; however, its developmental pattern is distinctly different from Ulva and other ulvaceous algae. In Ulva the distromatic blade develops by the collapse of a monostromatic tubular germling. In this alga the distromatic blade forms by longitudinal divisions parallel to the surface of the germling. A new genus and species, Chloropelta caespitosa, are proposed and described for this alga.
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I. GENERAL INTRODUCTION

The ulvaceous green algae are an assemblage of genera united primarily by the presence of a monostromatic or distromatic, parenchymatous thallus in at least part of their life histories. Except for basal rhizoidal cells, which may be multinucleate, the cells of the parenchymatous thallus are uninucleate and generally have single parietal chloroplasts with one or more pyrenoids. Reproduction is by quadriflagellated (occasionally biflagellated) zoospores and isogamous or anisogamous, biflagellated gametes. The delimitation of genera and species in this group has always been an enigma to phycologists because of the lack of good taxonomic criteria and the large degree of morphological and anatomical plasticity encountered. Classically, species were separated on easily observable characteristics such as thallus size, shape, thickness, cell dimensions and pyrenoid numbers. Many of these criteria were found to vary greatly (Setchell and Gardner, 1903; van den Hoek, 1964), in some instances in response to environmental factors (Vingogradova, 1974; Titlyanov, et al., 1975; Steffensen, 1976a).

Recently, researchers have recognized the value of using relatively stable criteria, such as reproductive details, germling ontogeny and hybridization potential, along with morphological and anatomical characteristics to delimit species. Using these criteria, Bliding (1963, 1968) effectively delimited the European members of the Ulvales. In similar but less extensive studies several French researchers worked on the ulvaceous algae from France and Morocco (Cauro, 1958; Dangeard, 1958a, 1959), and Kapraun (1970) investigated species of *Enteromorpha* and *Ulva* from Port Aransas, Texas. Numerous studies have been made on individual species.

The northeast Pacific, defined for this study as the coast from the Aleutian Islands, Alaska, to the southern tip of Baja California, Mexico, is second only to New Zealand in the number of species of *Ulva* reported in the
literature. All but one (Chihara, 1968) of the 12 species reported for the northeast Pacific were described entirely on morphological and anatomical characteristics. Little is known about the life histories and development of these species, and, although a large amount of morphological variation has been noted (Setchell and Gardner, 1903), no studies on morphological or anatomical variation have been published for the northeast Pacific.

This thesis is the result of an extensive investigation of the species of _Ulva_ from the northeast Pacific with the goal of re-evaluating the taxonomic criteria on which they were based. Four approaches were taken during the course of the study. First, morphological and anatomical characteristics of living and herbarium specimens from the northeast Pacific as well as from other areas of the world were studied and compared. This included the study of all pertinent type material that could be located. Next, life histories, reproductive details and germling development were studied in culture for the various morphological types collected in the field. Germlings were grown under different temperatures and salinities to determine if these factors could influence developmental patterns and morphology. From the information gained from herbarium, field and culture studies, several species could be delimited with confidence. In a few instances hybridization experiments were used to check species. Third, several transects were established to determine the relationship between taxonomic characteristics and some environmental factors such as position in the intertidal or subtidal zones and wave exposure. Last, cytological studies were made for most of the species in an attempt to determine the value of chromosome number in delimiting species.

During the study, a diminutive, distromatic alga previously referred to as _Ulva_ was collected and studied. The morphology and initial stages of development of this alga were similar to _Ulva_, but the later stages of development followed a pattern to my knowledge undescribed for the green
algae. This alga is tentatively given the name of Chloropelta caespitosa. To determine the affinities of Chloropelta with other algae, the literature on the ulvaceous algae was surveyed (Section II).
II. REVIEW OF THE CLASSIFICATION OF ULVACEOUS GREEN ALGAE

A. GENERIC CONCEPTS

_Ulva_ is an ancient name, having been used frequently by the Latin poets to refer to marsh plants (Greville, 1830; Setchell and Gardner, 1920b). The name apparently originated from the Celtic _ul_, which means water (Greville, 1830). In Ray’s third edition of _Synopsis Methodica_ (1724) _Ulva_ was listed as a leafy moss and included aquatic plants of any color that were thin, flat and "quandoque tubulosis" (at some time or other tubular). Twelve polynomial species were listed, seven of which were added by Dillenius, a contemporary of Linnaeus, who revised the third edition of the Synopsis (Stearn, 1973). Linnaeus, who borrowed heavily from Ray and Dillenius, included as binomials five of their species in his _Species Plantarum_ (1753), a sixth that Ray had placed under _Fucus_ and three that had been described in previous publications (Table 1).

Modern botanical nomenclature starts with Linnaeus, and, hence, his work is important for determining the generic concept of _Ulva_. Unfortunately, _Ulva_ included a variety of unrelated algae. Of the nine species listed in the _Species Plantarum_, eight have since been removed to other genera (Silva, 1952; Papenfuss, 1960; Table 1). Linnaeus (1754), as did Ray, at first considered the genus _Ulva_ to be characterized by hollow plants and probably used _Enteromorpha intestinalis_ (Linnaeus) Link as the basis of his description (Papenfuss, 1960). However, later in his _Systema Vegetabilium_ he changed his description of _Ulva_ as a hollow membrane to simply a membrane (Lamouroux, 1813).

Lamouroux (1813) removed most of the non-chlorophycean algae with the exception of some modern _Porphyra_ species and split _Ulva_ species into two sections depending on whether they were planular (_Ulva Foliis planis_) or tubular (_Ulva Foliis fistulosus_). Three of the nine taxa listed in the
Table 1. Development of the generic concept of Ulva.

<table>
<thead>
<tr>
<th>Ray (1724)</th>
<th>Linnaeus (1753)</th>
<th>Modern Interpretation</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ulva lactuca</strong></td>
<td>Ulva lactuca L.?</td>
<td>Papenfuss (1960); Bliding (1968).</td>
<td></td>
</tr>
<tr>
<td><strong>U. umbilicalis</strong></td>
<td><em>Porphyra umbilicalis</em></td>
<td>C. agardh (1824) as <em>P. laciniata f. umbilicalis</em></td>
<td></td>
</tr>
<tr>
<td><strong>U. linza</strong></td>
<td>U. linza L. or <em>Enteromorpha linza</em></td>
<td>J. Agardh (1883)</td>
<td></td>
</tr>
<tr>
<td><strong>U. intestinalis</strong></td>
<td><em>Enteromorpha intestinalis</em></td>
<td>Link (1820)</td>
<td></td>
</tr>
<tr>
<td><strong>U. compressa</strong></td>
<td><em>E. compressa</em></td>
<td>Greville (1830)</td>
<td></td>
</tr>
<tr>
<td><strong>U. confervoides</strong></td>
<td><em>Ceramium rubrum</em></td>
<td>C. Agardh (1828); Silva (1952)</td>
<td></td>
</tr>
<tr>
<td><strong>U. granulata</strong></td>
<td><em>Botrydium granulatum</em></td>
<td>Greville (1830); Silva (1952)</td>
<td></td>
</tr>
<tr>
<td><strong>U. latissima</strong></td>
<td><em>Laminaria saccharina</em></td>
<td>Setchell and Gardner (1920b); Silva (1952); Papenfuss (1960)</td>
<td></td>
</tr>
<tr>
<td><strong>U. pruniformis</strong></td>
<td><em>Nostoc pruniforme</em></td>
<td>C. Agardh (1824); Silva (1952)</td>
<td></td>
</tr>
</tbody>
</table>

1Papenfuss (1960) and Bliding (1968) disagree as to whether the type specimen of Ulva lactuca L. fits the modern interpretation of that species.
section U. Foliis planis are presently considered valid species of Ulva. Later C. Agardh (1824) established the genus Porphyra, removing the last of the red algae from Ulva.

In the 1800's Ulva was split into several genera on morphological and anatomical characteristics. A number of different generic names were proposed for hollow species, but Enteromorpha Link (1820) was the first to become firmly established (Greville, 1830; Silva, 1952). In 1823 Bory described the genus Percursaria for unbranched filaments composed of two longitudinal rows of cells (Kornmann, 1956). Areschoug in 1851 separated the genus Letterstedtia on the presence of lateral, more or less pinnate leaflets (Papenfuss, 1960). Letterstedtia as in the modern concept of Ulva is distromatic. Monostromatic species were placed in Ulvaria by Ruprecht (1851) and in Monostroma by Thuret (1854). Though Monostroma is antedated by Ulvaria the wide use of Monostroma for monostromatic ulvaceous algae led Papenfuss (1960) to propose that it be conserved against Ulvaria. Capsosiphon was established by Gobi in 1879 for a tubular plant that differed from Enteromorpha by lacking rhizoidal cells (Bliding, 1968) and by having cells in groups of two's and four's embedded in a mucilaginous matrix material (Papenfuss, 1960).

More recently cytological and reproductive details were used to establish genera. Chadefaud (1957) described Feldmannodora on the shape of the chloroplast, and Chapman (1952) described Gemina and Lobata separating from Enteromorpha and Ulva on the presence of reproductive cells along the central axis.

As many of the ulvaceous algae were cultured, reproductive, developmental and life history differences became apparent and were used to establish new genera. Blidingia was separated from Enteromorpha by Kylin (1947) on the type of initial development and on the relatively small dimensions of vegetative cells. Enteromorpha develops directly into an upright filament attached by rhizoidal protuberances from the basal cells. Blidingia germinates by a germination tube and develops an extensive prostrate disk before the formation of
the upright germling (Dangeard, 1961). Dangeard (1952) separated Rhizenteron from Enteromorpha also on developmental criteria. Rhizenteron forms a thick tubercular growth at the base composed of coalesced rhizoids. Eventually, tubular fronds that resemble Enteromorpha grow out of the upper surface of the tubercular base. A variety of reproductive details, life histories and developmental patterns were found in the monostromatic species (Suneson, 1947; Gayral, 1962, 1965; Kornmann, 1962, 1964; Kornmann and Sahling, 1962; Hirose and Yoshida, 1964; Kida, 1966; Dube, 1967; Bliding, 1968; Tatewaki, 1972). This variation caused some confusion and disagreement about characteristics to be used to separate genera and regarding nomenclature. The species originally placed in Ulvaria by Ruprecht (1851), U. fusca (Postels et Ruprecht) Ruprecht and U. splendens Ruprecht, were found to have life histories consisting of an alternation of isomorphic sporophytic and gametophytic phases (Dube, 1967). Reproductive details and developmental patterns of Ulvaria closely resemble those of Ulva and Enteromorpha. On the other hand, Thuret (1854) based Monostroma on two species, one with a heteromorphic life history, M. bullosum (Roth) Thuret, and the other, M. oxycocum (Kützing) Thuret = M. oxyspernum (Kützing) Doty, that lacked an alternation of generations. Neither was designated the type (Bliding, 1968). Monostroma bullosum and M. oxyspernum also differ from each other and the species placed in Ulvaria in their developmental patterns and the manner in which swarmers are released (Tatewaki, 1972). Gayral (1965) proposed that Monostroma be typified by M. oxyspernum, that Ulvaria be revived for the isomorphic species and that the heteromorphic species be placed in a new genus, Ulvopsis Gayral. Kornmann (1964), Bliding (1968) and Vinogradova (1974) proposed M. bullosum as the lectotype of Monostroma, and Bliding (1968) placed M. oxyspernum in Ulvaria as U. oxysperma (Kützing) Bliding, noting the similarity in developmental patterns. He also described the genus Kornmannia for a monostromatic species, M. leptodermum Kjellman, that
resembled Blidingia in cell size and development. Kornmannia lacks pyrenoids and differs in life history from M. bullosum (Bliding, 1968; Tatewaki, 1972). Vinogradova (1969, 1974) accepted most of Bliding's generic concepts but differentiated M. oxyspermum from Monostroma and Ulvaria by placing it in the new genus, Gayralia Vinogradova based on the method by which swarmers were released. In Ulvaria, as well as in Ulva and Enteromorpha, swarmers are released one at a time through a small pore in the outer wall of the parental cell. In Monostroma species swarmers are released all at once through an irregular hole (Tatewaki, 1972). In Gayralia swarmers are released by disintegration of the parental cell wall. Ulvaria and Gayralia also differ in the manner in which the vesicular stage opens (Tatewaki, 1972). Vinogradova (1969) also created the new genus Protomonostroma Vinogradova for M. undulatum Wittrock. This species has a heteromorphic life history but differs from other genera in the type of development and method of swarmer release (Tatewaki, 1972).

There is still considerable disagreement regarding the criteria used to delimit genera of ulvaceous algae, particularly as noted previously for the monostromatic species. Several workers have kept all the monostromatic species in Monostroma (Scagel, 1966; Abbott and Hollenberg, 1976). The differences between Ulva and Enteromorpha have been questioned (LeJolis, see Anderson, 1891; Silva, 1972; Bonneau, 1977). These two genera have similar life histories and developmental patterns, and their separation is complicated by the presence of intermediate morphological forms such as E. linza (Linnaeus) J. Agardh. Some feel that Letterstedtia is not distinct enough from Ulva to warrant generic status (Papenfuss, 1960), whereas others accept this genus (Pocock, 1959; Chapman, 1964). Papenfuss (1960) also questioned the validity of Gemina and Lobata, suggesting that the special reproductive cells produced along the axis were actually rhizoidal cells filled with starch granules. Chapman (1964) maintained that these cells were reproductive structures. The separation of
Blidingia from Enteromorpha has also been questioned. Some isolates of Blidingia show a life history similar to that of Enteromorpha (Prange, 1976), and some species of Enteromorpha and Ulva produce extensive basal systems under some culture conditions (Cauro, 1958; Baudrimont, 1961).

Even the typification of Ulva Linnaeus (1753) has been questioned. Though Linnaeus apparently had a hollow plant in mind when describing Ulva, this genus was subsequently narrowed to contain only the distromatic, bladed green algae. Only one of the original species, U. lactuca Linnaeus actually fits the modern concept of Ulva (Table 1). Papenfuss (1960) examined the type of U. lactuca and found that it differed from the modern concept of this species. He proposed that, because of the uncertainty of Linnaeus' concept of Ulva, the genus be conserved in the sense of Thuret (1854), and that it be typified by U. rigida (C. Agardh) Thuret. Bliding (1968) stated that the type of U. lactuca fits the modern concept and that it be retained as the type of Ulva.

Despite the disagreement over generic concepts, certain patterns in morphology, life history and development are becoming clearer for this group. Supportive evidence such as Hori's (1972) study of pyrenoid structure is helping to clarify relationships between genera. However, because of the ubiquitous distribution and large degree of morphological plasticity in this group, it is likely that more genera will be proposed in the future on the basis of development and life histories.

B. FAMILY, ORDER AND CLASS CLASSIFICATION

Lamouroux in 1813 established the family Ulvacees for uniform herbaceous plants of green color. In this he placed the genera Ulva, Asperococcus, Bryopsis and Caulerpa. Dumortier in 1822 latinized the spelling to Ulvaceae (Rhyne, 1973). Whereas Greville (1830) and Harvey (1858) included in the
Ulvaceae a variety of unrelated genera, Thuret (1854) defined it as containing the ulvaceous genera Ulva, Enteromorpha and Monostroma.

In 1934 Kunieda proposed that Monostroma be placed in the separate family Monostromaceae (Suneson, 1947; Papenfuss, 1960; according to Bliding (1968) and Vinogradova (1974) the spelling is Monostromataceae Kunieda ex Suneson) on the basis of life history. Chapman (1952) proposed the new family Capsosiphonaceae for Capsosiphon because of the lack of motile reproductive cells. However, Bliding (1968) and Chihara (1967) found that Capsosiphon produced flagellated swarmers, though in both instances the isolates did not show an alternation of generations. These swarmers were released through an aperture in the parental cell wall as a mass enclosed in an envelope (Chihara, 1967). This type of swarmer release is also found in Monostroma (Tatewaki, 1972).

Papenfuss (1960) and Chihara (1967) suggested that there were insufficient differences between Capsosiphon and other genera in the Ulvaceae to justify separating it into a new family. Iwamoto (Bliding, 1968) considered Capsosiphon to be more closely related to Monostroma than to Enteromorpha, whereas Gayral (1964), Bliding (1968) and Vinogradova (1974) thought that there were sufficient differences to justify a separate family. Gayral (1971) suggested that Capsosiphon was related to Monostroma oxyspermum (= Gayralia oxysperma) and that after further studies they may be placed in the same family.

In 1968 Bliding proposed that Percursaria be transferred from the Ulvaceae to the new family Percursariaceae. He suggested that Percursaria was sufficiently different from other ulvaceous algae to justify transfer of it because of: 1, the lack of a hollow stage during development of the upright thallus; 2, the lack of rhizoidal cells; 3, germination of reproductive cells into prostrate disks. He has not been followed by more recent authors (Gayral, 1971; Vinogradova, 1974; Abbott and Hollenberg, 1976; Table 2).

Vinogradova in 1969 established the family Gayraliaceae to contain
Table 2. Various classification schemes for the ulvaceous algae.

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<td>Chlorophyceae</td>
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<td>Capsosiphon</td>
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<td>Percursaria</td>
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<td>Enteromorpha</td>
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<td>Ulva</td>
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<td>Rhizenteron</td>
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<td>Feldmannodora</td>
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<td>Blidingia</td>
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<td>Monostromatales</td>
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<td>(including Ulvaria)</td>
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<td>Monostromataceae</td>
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<td>Ulvopsis</td>
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<td>Kornmannia</td>
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<td>Codiolophyceae</td>
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<td>Monostromatales</td>
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<td>Monostromataceae</td>
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<td>Gayraliaceae</td>
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<td>Gomontia</td>
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<td>Protomonostroma</td>
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the genera, *Gayralia* and *Protonostroma* (Gayral, 1971; Vinogradova, 1974). These two genera are held together by a similar method of swarmer release, though they differ in developmental patterns (Tatwaki, 1972).

Borzi in 1895 transferred the Ulvaceae to the new order Ulotrichales (Rhyne, 1973). Blackman and Tansley (1902) removed the Ulvaceae from the Ulotrichales and placed them in the new order Ulvales on the basis of their parenchymatous construction in contrast with the filamentous construction of most ulotrichalean algae. Further support for this separation came when life history studies demonstrated an alternation of isomorphic generations for *Ulva* and *Enteromorpha* (Hartmann, 1929; Föyn, 1929, 1934) and an alternation of heteromorphic generations for *Ulothrix* (Grosse, 1931). However, since then *Monostroma* has been shown to have a heteromorphic life history, alternating with a "zygocyst" stage as does *Ulothrix* (Tatwaki, 1972). Also, some ulvaceous algae pass through a filamentous stage during their developmental, e.g., *Ulva, Enteromorpha, Percursaria, Capsosiphon* and *Ulvaria* (Bliding, 1968). Further evidence against the separation of the Ulvales from the Ulotrichales was provided by Singh (1945, 1947) when he found that *Fritschiella* and *Draparnaldiopsis* had isomorphic life histories. These and other branched filamentous green algae are either included in the Ulotrichales (Setchell and Gardner, 1920b; Scagel, 1966; Abbott and Hollenberg, 1976) or placed in a separate order, the Chaetophorales (Fritsch, 1935; Kylin, 1949; Round, 1963, 1971; Bold and Wynne, 1978). Fritsch (1935, 1944) and Papenfuss (1960) concluded that there was little justification for separating the Ulvales from the Ulotrichales. They have been followed by some authors (Chapman, 1964; Scagel, 1966; Abbott and Hollenberg, 1976), whereas others have retained the order Ulvales (Doty, 1947; Kylin, 1949; Smith, 1944; Bliding, 1968; Gayral, 1971; Vinogradova, 1974; Bold and Wynne, 1978).

Kornmann (1965) considered life histories to be of primary importance
and placed the heteromorphic species of Monostroma in the Ulotrichales, at the same time maintaining the Ulvales for isomorphic ulvaceous algae. This treatment was followed by Round (1971). Later Kornmann (1973) elevated the Monostromataceae to order level, Monostromatales, and placed it in the new class Codiolophyceae along with the Ulotrichales, Codiolales and Acrosiphonales. These groups, though diverse in morphology and development of the macrophytic gametophyte, all had a unicellular "Codiolum" sporophyte. Previous to this, the ulvaceous algae had always been placed in the Chlorophyceae.

Recently considerable attention has been given to cell structure and in particular the mitotic and cytokinetic apparatus of green algal cells (Pickett-Heaps and Marchant, 1972; Stewart, Mattox and Floyd, 1973; Pickett-Heaps, 1975; Stewart and Mattox, 1975a, 1975b; Mattox and Stewart, 1977). Stewart and Mattox (1975a) suggested that most of the classical classifications of the green algae were superficial and that a natural system must incorporate data on mitosis, cytokinesis, the ultrastructure of reproductive cells and biochemical characteristics. According to the work of Stewart and Mattox (1975b, 1978) the Ulvaceae (Ulva, Enteromorpha, Percursaria, Pseudendoclonium and Trichosarcina) are distinctly different from ulotrichalean algae and possibly represent a phylogenetic line separate from the Chlorophyceae. They have proposed that the ulvaceous algae be placed in a new class, the Ulvaphyceae. However, they have not studied any of the members of the Monostromataceae, and the position of the heteromorphic ulvaceous algae remains unclear in their scheme. Comparative ultrastructure studies of these algae will hopefully help clarify the relationship of the Monostromataceae to the Ulvaceae.

C. NORTHEAST PACIFIC SPECIES OF ULVA

Prior to the 20th century phycologists assigned northeast Pacific spe-
specimens of *Ulva* to already established Atlantic species. Harvey (1858) listed in his Nereis Boreali-Americana two species from the west coast: *U. fasciata* Delile and *U. latissima* Linnaeus. From Harvey's description of *U. fasciata* as undulate and irregularly toothed, it seems certain that the specimens he examined were *U. taeniata* (Setchell) Setchell et Gardner. *Ulva latissima* was used as a catch-all species for thalli of various shapes. In 1862 Harvey added two more species, *U. rigida* C. Agardh and *U. linza* Linnaeus, from herbarium specimens collected by Dr. D. Lyall on Vancouver Island and neighboring areas. Anderson (1891) recorded from California *U. fasciata*, *U. lactuca*, *U. latissima* and several species presently placed in Enteromorpha.

The Phycotech Boreali-Americana, issued and distributed by Collins, Holden and Setchell (1895-1919), included specimens of *U. lactuca* var. *latissima* and var. *rigida* as well as several new taxa from the west coast. *Ulva californica* Wille (1899) was described from minute, cuneate thalli collected at Pacific Beach, California. Setchell described four forms of *U. fasciata*: f. *expansa* (1905), f. *lobata* (1901), f. *taeniata* (1901) and f. *caespitosa* (1901) (Collins et al., 1895-1919). Collins (1903) included all of these taxa in his paper on the Ulvaceae of North America.

Setchell and Gardner are responsible for the concepts of most of the species presently recognized for the northeast Pacific. In 1903 Setchell and Gardner reported only one species with two varieties (*U. lactuca* var. *latissima* and var. *rigida*). They summarized their conclusions at that time (1903, p. 210): "A very considerable study of the species of *Ulva* along the entire western coast of North America indicates that, while there may be many forms, there is probably only one species and very few varieties. The habit, size, color and even the character of cell depends so much on the age and the environment of the specimen, that it is possible to trace a series
from the quiet water inside a point of land to the exposed localities outside of it which may include all the forms and intermediate conditions between the most distinct species as yet proposed under the genus."

However, after further study Setchell and Gardner (1920a, 1920b) concluded that a number of species could be distinguished, and they listed thirteen for the northeast Pacific of which four were new, three were new combinations and one had not been reported from this area (Table 3). Their work remains the last extensive study of *Ulva* on this coast, and subsequently phycologists have retained the same species with a few minor changes. *Ulva vexata* Setchell et Gardner was transferred first to *Enteromorpha* (Doty, 1947), and later to *Blidingia* as a variety of *B. mimina* (Norris, 1971). *Ulva linza* has been placed in *Enteromorpha* by most authors. Scagel (1966) suggested that *U. latissima* be reduced to a synonym of *U. lactuca* based on Papenfuss' report (1960) that the type of *U. latissima* was actually a *Laminaria*.

In 1968 Chihara described *U. scagelii* primarily on germination and developmental patterns. Hollenberg (1971) elevated Howe's *U. fasciata f. costata* Howe (1914) to species level, *U. costata* (Howe) Hollenberg, and reported it from southern California.

Other authors that have discussed the species of *Ulva* in the northeast Pacific are Smith (1944), Doty (1947), Scagel (1966), Norris (1970) and Abbott and Hollenberg (1976).

D. EVALUATION OF TAXONOMIC CRITERIA

The criteria used in the past to separate species of *Ulva* in the northeast Pacific (Setchell and Gardner, 1920b; Smith, 1944; Doty, 1947; Scagel, 1966; Abbott and Hollenberg, 1976) are outlined in Figure 1. The emphasis was placed on thallus size, shape, thickness, and cell height to width ratio in
Table 3. Species of *Ulva* reported for the northeast Pacific.

<table>
<thead>
<tr>
<th>Pacific Coast of North America</th>
<th>British Columbia</th>
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<tr>
<td><em>U. angusta</em> Setchell et Gardner&lt;sup&gt;1,2&lt;/sup&gt;</td>
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<td><em>U. californica</em> Wille&lt;sup&gt;1,2,3&lt;/sup&gt;</td>
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<td><em>U. costata</em> (Howe) Hollenberg&lt;sup&gt;2,4&lt;/sup&gt;</td>
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<td><em>U. dactylifera</em> Setchell et Gardner&lt;sup&gt;1,2&lt;/sup&gt;</td>
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<td><em>U. expansa</em> (Setchell) Setchell et Gardner&lt;sup&gt;1,2,3,5&lt;/sup&gt;</td>
<td><em>U. expansa</em>&lt;sup&gt;5,6,7&lt;/sup&gt;</td>
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<td><em>U. fenestrata</em> Postels et Ruprecht&lt;sup&gt;1,3,5&lt;/sup&gt;</td>
<td><em>U. fenestrata</em>&lt;sup&gt;1,5,6&lt;/sup&gt;</td>
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<td><em>U. lactuca</em> Linnaeus&lt;sup&gt;1,2,5&lt;/sup&gt;</td>
<td><em>U. lactuca</em>&lt;sup&gt;1,2,5&lt;/sup&gt;</td>
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<td><em>U. lobata</em> (Kützing) Setchell et Gardner&lt;sup&gt;1,2,3,6&lt;/sup&gt;</td>
<td><em>U. lobata</em>&lt;sup&gt;6,8,9&lt;/sup&gt;</td>
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<td><em>U. rigida</em> C. Agardh&lt;sup&gt;1,2,5&lt;/sup&gt;</td>
<td><em>U. rigida</em>&lt;sup&gt;1,2,5&lt;/sup&gt;</td>
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<td><em>U. scagelii</em> Chihara&lt;sup&gt;6,10&lt;/sup&gt;</td>
<td><em>U. scagelii</em>&lt;sup&gt;6,10&lt;/sup&gt;</td>
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<td><em>U. stenophylla</em> Setchell et Gardner&lt;sup&gt;1,2,3,8&lt;/sup&gt;</td>
<td><em>U. stenophylla</em>&lt;sup&gt;8&lt;/sup&gt;</td>
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<tr>
<td><em>U. taeniata</em> (Setchell) Setchell et Gardner&lt;sup&gt;1,2,3,7,9&lt;/sup&gt;</td>
<td><em>U. taeniata</em>&lt;sup&gt;7,9&lt;/sup&gt;</td>
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<sup>1</sup> Setchell & Gardner (1920b)
<sup>2</sup> Abbott & Hollenberg (1976)
<sup>3</sup> Doty (1947)
<sup>4</sup> Hollenberg (1971)
<sup>5</sup> Scagel (1966)
<sup>6</sup> Scagel (1973)
<sup>7</sup> Norris & Abbott (1972)
<sup>8</sup> Lee (1965)
<sup>9</sup> Widdowson (1965)
<sup>10</sup> Chihara (1968)
Figure 1. Criteria used to separate the 12 species of Ulva previously reported for the northeast Pacific. Cell H/W ratio refers to cell height to width ratio in transverse section. In thin specimens H/W ratios approach 1. In thick specimens H/W ratios > 1.5. During normal development ("Ulva lactuca-type") reproductive cells germinate directly and the upright germling begins to develop before the basal system. During abnormal development ("Ulva scaglioni-type") reproductive cells germinate by means of a germination tube and an extensive basal system develops before initiation of the upright germling (Chihara, 1968).
transverse section. Much of the original work on *Ulva* was based on herbarium specimens (Wille, 1899; Setchell and Gardner in Smith, 1947, p. 81; Hollenberg, 1971), and in a few instances species were apparently described from single collections (*U. californica* in Wille, 1899; *U. angusta* in Setchell and Gardner, 1920b). Because of this, little was known about intraspecific variation due to age, environmental conditions and genetic plasticity. Setchell and Gardner (1920b) and Scagel (1966) recognized the need for culture studies to determine the validity of morphological and anatomical criteria used to separate these species. The recent tendency is to use morphological and anatomical criteria along with studies of morphogenesis and interspecific hybridization potential to separate species (van den Hoek, 1964; Bliding, 1968; Kapraun, 1970; Rhyne, 1973). The validity of the various taxonomic criteria is discussed below:

1. **Thallus Morphology**

Considerable morphological variation has long been recognized for species of *Ulva* (Setchell and Gardner, 1903; van den Hoek, 1964; Chapman, 1964; Bliding, 1968; Kapraun, 1970; Steffensen, 1976a) and other ulvaceous algae (Klugh, 1922; Bliding, 1938; Arasaki and Shihira, 1959; Burrows, 1959). The parenchymatous, distromatic blade of *Ulva* offers few characteristics that can be used to separate species. Growth of the blade is by diffuse cell divisions, and the resulting shape is affected by numerous factors such as age, reproductive state, wave exposure, tidal factors, temperature, salinity, light and biological factors such as grazing. Steffensen (1976a) demonstrated that a single species from a New Zealand estuary could at various stages of growth fit the diagnoses for five different species. Morphology varied with age of the thallus, time of year, salinity and whether the thallus was attached or free-floating. Titlyanov et al. (1975) recorded
significant differences in the size of thalli of *U. fenestrata* Postels et Ruprecht from habitats of different wave exposure and at different times of the year. The largest thalli occurred in shallow, protected areas in winter and spring. *Ulva* species growing in the upper intertidal have been observed to be small and stunted (Lawson, 1956).

Photosynthesis and growth are affected by exposure to air (Johnson et al., 1974), eutrophication (Waite and Mitchell, 1972; Steffensen, 1976b), and changes in temperature and salinity (Ogata and Matsui, 1965; Kjeldsen and Phinney, 1972; Yokohama, 1972; Zavodnik, 1975; Steffensen, 1976a). These factors affect the size and probably the morphology of thalli. Numerous culture studies have been made of *Ulva* and other ulvaceous algae. In some studies cultured plants retained the morphological characteristics of the species (Foyn, 1955; Yoshida, 1965; Chihara, 1968, 1969). In other studies the morphology depended on the culture conditions (Provasoli, 1958, 1961; Kapraun, 1970, Rhyne, 1973; Bonneau, 1977). Foyn (1960, 1961) obtained morphological variants in culture caused by genetic mutations.

The preceding studies suggest that morphology must be used with caution and preferably with other characteristics. However, in areas where there are few species, morphology can occasionally be used effectively. Kapraun (1970) plotted thallus length against width for *U. fasciata* and *U. lactuca* from Port Aransas, Texas. For these two species there was little overlap. In the northeast Pacific the large number of species reported and their similarities in morphology make this type of analysis difficult. Some species have distinctive taxonomic characteristics such as perforations (*U. fenestrata*) and dentation (*U. rigida, U. taeniata*), but even these vary with environmental factors. According to Vinogradova (1974) the perforations in *U. fenestrata* were caused by molluscs such as *Littorina*. In "*U. lactuca" from New Zealand microscopic teeth were common in small attached plants but
absent in expanded plants (Steffensen, 1976a). Also, in Enteromorpha the tendency to branch is influenced by culture conditions (Burrows, 1959; Kapraun, 1970). A similar tendency might be expected for dentations, which are essentially short lateral branches of determinate growth.

2. **Thallus Thickness and Shape, Dimensions of Cells and Pyrenoid number**

The lack of good gross morphological characteristics led to the use of blade thickness; size, shape and arrangement of cells; and the number of pyrenoids in each cell for characterizing species (Bliding, 1968). However, as discussed by van den Hoek (1964) and Kapraun (1970), these characteristics often show considerable variation and overlap for different species. Steffensen (1976a) noted that changes in cellular morphology were associated with changes in thallus morphology for a given species. In *U. fenestrata* from the northwest Pacific, cells in surface view were either rounded or angular and varied significantly in dimensions for different localities and times of the year (Vinogradova, 1974). Cell dimensions in *U. fenestrata* were apparently also influenced by temperature as the dimensions increased from north to south, and during the summer months when water temperatures were up to 15°C warmer than during the winter months. Vinogradova also noted a decrease in thickness with an increase of wave exposure. Titlyanov et al., (1975) did not find a significant change in cell dimensions in *U. fenestrata* from localities of different wave exposures, and cell dimensions in surface view increased during the winter and early spring rather than in the summer. They suggested that low temperatures retarded division of cells and stimulated growth in dimensions as is reported in phytoplankton (Jorgensen, 1968).

The number of pyrenoids per cell has been used as a taxonomic criterion
(Bliding, 1968; Chihara, 1968, 1969). This criterion can be useful for species with one pyrenoid per cell, but for species with more than one, the pyrenoid number may vary considerably (van den Hoek, 1964). Pyrenoid numbers have in the past caused some confusion when errors were made in reporting numbers from herbarium material (Smith, 1947).

3. Reproductive Details and Interspecific Hybridization Potential

Bliding (1963), van den Hoek (1964) and Kapraun (1970) reported that reproductive details and the results of hybridization experiments were of great value for separating species. Most species have a life history consisting of an alternation of isomorphic sporophytic and gametophytic phases (Foyn, 1929, 1934, 1958, 1959; Bliding, 1968). The sporophyte typically produces quadriflagellated zoospores, and the heterothallic gametophytes produce biflagellated gametes. In a few species only one type of swarmer has been observed (Dangeard, 1957; Bliding, 1968), suggesting the loss of one of the two phases. Dimensions of swarmers (Chihara, 1969) and whether gametes are isogamous or anisogamous have also been used as taxonomic criteria. Smith (1947) studied the reproduction of five species from California and found that only one, *U. taeniata*, had isogamous gametes. All of the species in Europe for which sexual reproduction has been reported have anisogamous gametes (Bliding, 1968) except for isolated populations (Meowus, 1938; Foyn, 1955).

The results of hybridization experiments have proven useful for separating species. Foyn (1955), Bliding (1963, 1968) and Kapraun (1970) suggested the presence of interspecific fertility barriers. In their studies fusion occurred between gametes of different species, but the mating reaction was weak, and germlings never developed beyond a few cells. However, Dangeard (1963) successfully crossed isolates which he identified as *U. lactuca* and *U. rigida*. Ardre (1967) described a species of *Ulva* in which cells of one
layer resembled those of *U. lactuca* and cells of the other layer resembled those of *U. rigida*. She suggested the dimorphism was caused by a hybridization or "pseudo-hybridization" between *U. lactuca* and *U. rigida* resulting in a hybrid with genetically different layers. A similar dimorphism has also been observed in *U. conglobata* f. *densa* in Japan (Okamura, 1918). There is also the possibility of intraspecific fertility barriers. Such barriers have been demonstrated for other green algae (van den Hoek, 1964).

4. **Germination and Developmental Patterns**

Germination and early developmental patterns are often different for different species. In some instances these differences have been used as the basis for describing new species (Cauro, 1958; Chihara, 1968). Germination is direct in most species, but in a few a germination tube develops prior to cell division as described for *U. linearis* (Cauro, 1958), *U. scagelii* and *U. arasakii* (Chihara, 1968, 1969). After germination the germling differentiates into an upright filament and a basal disk. In most species the upright filament develops prior to the basal disk, but in *U. gayralii*, *U. linearis* (Cauro, 1958) and *U. scagelii* (Chihara, 1968) the basal system develops first. However, the relationship between the two may be influenced by culture conditions (Cauro, 1958; Baudrimont, 1961). The upright filament undergoes longitudinal divisions\(^1\) at right angles to the surface to form a tubular, monostromatic germling (Løvlie, 1964). Eventually the tube collapses producing a flattened distromatic blade (see Fig. 50c). Different species can be differentiated by the length of the filament when the first longitudinal division occurs, the persistence of the apical cell, and the morphology of the juvenile blade (Föyn, 1955; Bliding, 1968). Recent studies have shown that

\(^1\)Longitudinal divisions refers to the direction of cleavage during cytokinesis.
germling morphology may vary greatly in culture, particularly when grown axenically (Provasoli, 1958; Bonneau, 1977).

In the northeast Pacific only four species have been studied in culture: *U. lobata* (Strand et al., 1966), *U. fenestrata* and *U. scagelii* (Chihara, 1968), and *U. taeniata* (Provasoli, 1961).
III. MORPHOLOGICAL AND ANATOMICAL VARIATION

A. METHODS

1. Collections and Herbarium Studies

To determine the distribution and geographic variation of *Ulva* spp., general collections were made along the Pacific coast from northern British Columbia to southern California (Fig. 2). In addition to these collections large numbers of herbarium specimens, including many of the type specimens, from the northeast Pacific (defined for this study as the coast from the Aleutian Islands, Alaska, to the southern tip of Baja California, Mexico) and other areas were borrowed and studied (Table 4). These herbarium specimens provided valuable information regarding geographic and seasonal variation as well as being helpful in interpreting species descriptions and published distributions. Diagnostic characteristics such as size, shape, blade thickness, cell dimensions, pyrenoid number and the presence or absence and length of teeth were compared for specimens from different geographic localities. For microscopic observation of herbarium specimens, small pieces of blade were allowed to soak in seawater for 5 to 15 minutes. Thickness and cell dimensions were measured with an ocular micrometer at 1000x power.

Specimens resulting from personal collections were placed in the University of British Columbia Phycological Herbarium (UBC).

In addition to the geographic collections, seasonal collections were made over several years in Barkley Sound on the west coast of Vancouver Island, B.C. (Fig. 3). This large sound offers a wide variety of marine habitats as well as research facilities at the Bamfield Marine Station (Western Canadian Universities Marine Biological Station). Of the 12 species of *Ulva* in the northeast Pacific, 6 have been reported from Barkley Sound (Scagel, 1973). During the first year of the study different morphological types...
Table 4. Herbaria from which specimens were borrowed and studied.¹

<table>
<thead>
<tr>
<th>Code</th>
<th>Herbarium Name and Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHFH</td>
<td>Allan Hancock Foundation, University of Southern California, Los Angeles</td>
</tr>
<tr>
<td>AKU</td>
<td>Auckland University (New Zealand)</td>
</tr>
<tr>
<td>CANTY</td>
<td>Canterbury Museum, Christchurch (New Zealand)</td>
</tr>
<tr>
<td>DS</td>
<td>Dudley Herbarium (in UC)</td>
</tr>
<tr>
<td>GJH</td>
<td>George J. Hollenberg (now in US)</td>
</tr>
<tr>
<td>GMS</td>
<td>Gilbert Morgan Smith Herbarium (Hopkins Marine Station of Stanford University)</td>
</tr>
<tr>
<td>L</td>
<td>Rijksherbarium, Leiden University</td>
</tr>
<tr>
<td>LD</td>
<td>Institute of Systematic Botany, Lund</td>
</tr>
<tr>
<td>LE</td>
<td>Komarov Botanical Institute, Leningrad</td>
</tr>
<tr>
<td>MLML</td>
<td>Moss Landing Marine Laboratory of the California State Universities</td>
</tr>
<tr>
<td>M</td>
<td>Missouri Botanical Garden (specimens in UC)</td>
</tr>
<tr>
<td>NY</td>
<td>New York Botanical Garden</td>
</tr>
<tr>
<td>OSU</td>
<td>Oregon State University, Corvallis</td>
</tr>
<tr>
<td>PBA</td>
<td>Phycotheca Boreali-americana (in AHFH, UBC, UC, US; Collins et al., 1895-1919)</td>
</tr>
<tr>
<td>RS</td>
<td>Private Herbarium of Robert Setzer</td>
</tr>
<tr>
<td>UBC</td>
<td>University of British Columbia, Vancouver</td>
</tr>
<tr>
<td>UC</td>
<td>University of California at Berkeley</td>
</tr>
<tr>
<td>US</td>
<td>United States National Herbarium, Smithsonian Institute, Washington, D.C.</td>
</tr>
<tr>
<td>UW</td>
<td>University of Washington, Seattle</td>
</tr>
<tr>
<td>VJC</td>
<td>Private Herbarium of V. J. Chapman</td>
</tr>
</tbody>
</table>

¹Throughout this thesis numbers starting with (U) indicate personal collections from a given population on a given day.
Figure 2. Map of study area in the northeast Pacific. Open circles indicate locations of intertidal transects. Dots indicate collection sites.
Figure 3. Map of study area in Barkley Sound, Vancouver Island. Arrows indicate locations of intertidal transects. • = hydrographic stations. ■ = Bamfield Marine Station.
were collected from a variety of habitats and compared. During this initial period, several trends in seasonality and morphological variation were noted. Further studies were conducted to confirm these trends and isolate the causal factors.

2. Intertidal Transects

Four different transects perpendicular to the shoreline were established to determine the morphological and anatomical variation of *Ulva fenestrata* with vertical position and exposure to wave action. Three sites were chosen in Barkley Sound on the basis of accessibility by boat, exposure to wave action and abundance of *U. fenestrata* (Fig. 3,4; Table 5). A fourth transect was located at Brockton Point in Stanley Park, Vancouver. Permanent base points were placed by drilling holes with a gas-powered impact drill and sinking ½" starbolts. The vertical positions of the base points relative to the lowest low water level (chart datum) were determined by comparing the water level at each transect with that at the tide gauge in front of the Bamfield Marine Station by means of shortwave radios. The vertical positions of two base points (Kirby Point, Brockton Point) were determined from predicted water levels (Canadian Hydrographic Service, 1974). Meter marks along the transect lines were surveyed to the nearest tenth of an inch (2.54 mm) relative to the base points.

Specimens were collected from ¼ m² quadrats every meter (every 5 meters for Brockton Point) along the transect lines. The center of the top edge of the quadrat was placed on the meter marks. In the lab the length and width of the blades were measured. In most instances disks were cut from the center, and in larger thalli from the margins, and preserved in 5% Formalin to be sectioned later. Thallus thickness, cell dimensions and pyrenoid numbers were determined under 1000x power.
<table>
<thead>
<tr>
<th>Location</th>
<th>Species Collected</th>
<th>Date</th>
<th>Slope</th>
<th>Substrate</th>
<th>Exposure to Wave Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brockton Point, Burrard Inlet, B.C. 49°18'N, 123°07'W</td>
<td>U. fenestrata, U. scagelii</td>
<td>25-VII-76, 24-XI-76</td>
<td>5°, 11°</td>
<td>boulders, shell, sand, mud, bedrock, boulders, shell, sand, mud</td>
<td>protected, protected</td>
</tr>
<tr>
<td>Grappler Inlet, Barkley Sound, B.C. 48°49.92'N, 125°06.94'W</td>
<td>U. fenestrata</td>
<td>22-VII-75, 2-IX-75, 17-IV-75</td>
<td>11°, 26°</td>
<td>bedrock, shell, sand, mud</td>
<td>protected, semiprotected</td>
</tr>
<tr>
<td>Scott's Cove, S.W. of Aguilar Point, Barkley Sound, B.C. 48°50.07'N, 125°08.7'W</td>
<td>U. fenestrata</td>
<td>21-VII-75, 2-XII-75</td>
<td>26°</td>
<td>bedrock</td>
<td>semiprotected</td>
</tr>
<tr>
<td>North side of Kirby Point, Barkley Sound, B.C. 48°50.99'N, 125°11.97'W</td>
<td>U. fenestrata</td>
<td>11-VII-75, 2-XII-75, 16-I-76, 16-IV-76</td>
<td>24°</td>
<td>bedrock</td>
<td>semiexposed</td>
</tr>
<tr>
<td>Brady's Beach, Barkley Sound, B.C. 48°49.74'N, 125°09'W</td>
<td>U. taeniata</td>
<td>16-IX-74, 31-XI-74, 23-II-75, 11-V-76, 13-V-76, 16-VI-76, 27-VII-76</td>
<td>2°</td>
<td>sand beach, scattered boulders</td>
<td>semiexposed</td>
</tr>
</tbody>
</table>
To measure the yearly accumulation and loss of sand around a bed of *Ulva taeniata* on Brady's Beach, Barkley Sound, horizontal and vertical transects were surveyed periodically over a two year period relative to a permanent base point (Fig. 3, 4d; Table 5). The vertical ranges of *U. taeniata* and other dominant algae were noted, and collections of *U. taeniata* were made every 5 meters along a 30-meter vertical transect. As with *U. fenestrata* these specimens were measured and sectioned.

3. **Hydrographic Data**

Water temperature and water samples were taken from the surface and a depth of 3 meters during the daytime low and high tides every week or two weeks at two stations for a period of a year. The stations were located at the mouth of Bamfield Inlet and toward the head of Grappler Inlet (Fig. 3). The salinity of the water samples was measured with either a conductivity meter or a refractometer. The purpose of these stations was to determine if differences in salinity and temperature could account for some of the differences in morphology and thickness between plants in Grappler Inlet and plants from other areas.
B. HYDROGRAPHY OF STUDY AREA

During the summer months surface water temperatures and salinities along the west coast of North America are influenced by the south flowing California Current and upwelling. The California Current carries cold subarctic water from the Aleutian Current to as far south as 23° N where it converges with the Equatorial Current (Sverdrup et al., 1942). As they flow south the surface waters gradually increase in temperature. However, in the spring and early summer upwelling is a common phenomenon along the coast of California and in areas of Baja California, Mexico, resulting in relatively cold coastal water. This summer upwelling may be due in part to the north-west winds prevalent in the early summer or due to entrainment of water by the California Current (Emery, 1960). At Point Conception, California, the California Current encounters a northward flowing water mass and turns away from the coast to flow southwest (Emery, 1960). This results in an abrupt change of summer surface temperatures that is reflected by a change in the marine flora in southern California (Abbott and Hollenberg, 1976). In the fall and winter upwelling diminishes and a countercurrent, the Davidson Current, carries southern waters along the coast as far north as 48° N (Sverdrup et al., 1942).

These two currents and upwelling provide the coast north of Point Conception with relatively cold surface temperatures. The mean surface temperatures from the Aleutian Islands to Point Conception range from 2° to 11.5° C in February and 9.5° to 15° C in August (U.S. Dept. of Commerce, 1956). South of Point Conception the surface temperatures range from 10° C in January to 25.5° C in August with means of ca. 13.5° and 19.5° C (U.S. Dept. of Commerce, 1956). However, in Baja California pockets of cold upwelled water provide surface temperatures comparable to temperatures north of Point Conception (McEwen, 1916). The flora of these areas of upwelling
include species more typical of northern waters (Dawson, 1946a, 1950, 1951).

In the Strait of Georgia and in many of the inlets along the mainland coast of British Columbia, salinities and to a smaller degree temperatures are influenced by freshwater runoff with salinities varying from zero to that of open ocean waters (Pickard, 1961). Salinities vary seasonally with the lowest salinities occurring in the winter during peak coastal precipitation and in the summer following snowmelt (Tully and Dodimead, 1957). In the central part of the Strait of Georgia the discharge of the Fraser River has a major influence on surface salinities. At the mouth of Burrard Inlet (Vancouver) the surface salinities vary from 10% to 26% (Tully and Dodimead, 1957). Surface water temperatures in the Strait of Georgia near the mouth of the Fraser River range from 5°C to 16°C (Waldichuk, 1957).

Along the west coast of Vancouver Island river runoff also has a significant influence on the surface salinities of some inlets (Pickard, 1963). However, the salinities in these inlets are generally greater than that in the mainland inlets due to the relatively small river runoff on Vancouver Island.

1. Salinity and Temperature Measurements in Barkley Sound

Figure 5 shows the seasonal variation in salinities and temperatures from the two stations monitored in Barkley Sound. Salinities fluctuated dramatically, particularly at the surface between the months of September through April. In Grappler Inlet salinities at the surface dropped on several occasions to less than 5%. However, these dramatic drops always followed heavy rainfalls. At a depth of 3 meters salinities were less affected by rainfall and were similar for both stations. These data show that Grappler Inlet is not normally brackish except at the surface following heavy rainfalls. Water temperatures varied seasonally with a maximum temperature around 17°C in summer and minimum temperature around 7°C in winter and early spring.
Figure 5. Salinity (a,b) and temperature (c,d) at the surface and a depth of 3 meters at two stations in Barkley Sound between May, 1975, and May, 1976. a,c. In front of the Bamfield Marine Station. b,d. Grappler Inlet. Dots and open circles represent the averages between readings taken during the daytime high tides and low tides on a given day at the surface (dot) and at a depth of 3 meters (open circles).
C. RESULTS

Maximum, minimum and mean values of thallus thickness, cell dimensions and pyrenoid number for specimens of Ulva and Chloropelta caespitosa from the northeast Pacific are given in Table 6. Although U. expansa, U. lobata and U. rigida are reported in the literature (Table 3) for British Columbia, these species could not be distinguished from the different morphological types of U. fenestrata. The herbarium specimens of U. expansa and U. lobata from California also resembled U. fenestrata, but were kept separate for comparative reasons. Herbarium specimens from the northeast Pacific identified as U. lactuca were closer to other Pacific species of Ulva than to the European concept of this species (Bliding, 1968). In almost all instances these specimens were grouped and studied with other species.

The study of herbarium specimens and field collections revealed a large degree of morphological and anatomical variation for distromatic ulvaceous algae in the northeast Pacific. A few species, such as U. stenophylla, U. taeniata and Chloropelta caespitosa, were morphologically distinct, though in some instances they showed some variation with environmental factors. Other species showed similarities to each other and could not be easily distinguished. Throughout this thesis species that appear to be related will be discussed together.

1. Ulva californica, Ulva scagelii, Ulva angusta

Specimens fitting the description of Ulva californica were collected at several localities in southern California. These plants formed dense tufted mats on top of rocks in the mid to upper intertidal zones. Individual plants were small, less than 2 cm tall, and cuneate, but were often attached together by a common base giving a characteristic tufted appearance (Fig. 6). Ulva scagelii in British Columbia was also found primarily in the mid to upper
Table 6. Blade thickness, cell dimensions in transverse section and the number of pyrenoids per cell in herbarium specimens of *Ulva* and *Chloropelta* (thickness and cell dimensions in μm). Means are not given for fewer than 10 measurements.

<table>
<thead>
<tr>
<th>Species</th>
<th>CENTER OF BLADE</th>
<th>MARGIN OF BLADE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Thickness range</td>
<td>Cell Height range</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>U. angusta</em>¹</td>
<td>39-51</td>
<td>13-19</td>
</tr>
<tr>
<td><em>U. californica</em> (California)</td>
<td>25-70 42</td>
<td>10-22</td>
</tr>
<tr>
<td><em>U. scagelii</em> (British Columbia)</td>
<td>27-63 42</td>
<td>7-23</td>
</tr>
<tr>
<td><em>U. fenestrata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brockton Pt.</td>
<td>30-81</td>
<td>46</td>
</tr>
<tr>
<td>Grappler Inlet</td>
<td>29-90</td>
<td>48</td>
</tr>
<tr>
<td>Bamfield Inlet</td>
<td>36-100</td>
<td>70</td>
</tr>
<tr>
<td>Scott's Cove</td>
<td>31-87</td>
<td>55</td>
</tr>
<tr>
<td>Kirby Pt.</td>
<td>34-100</td>
<td>59</td>
</tr>
<tr>
<td><em>U. expansa</em> (California)</td>
<td>46-105 71</td>
<td>16-41</td>
</tr>
<tr>
<td><em>U. lobata</em> (California)</td>
<td>51-106 77</td>
<td>23-53</td>
</tr>
<tr>
<td><em>U. rigida</em>²</td>
<td>48-105</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹ Includes a single specimen from the San Francisco- Oakland area.
² Includes 2 specimens from Long Beach.
³ Includes one specimen from a NY specimen.
<table>
<thead>
<tr>
<th></th>
<th>CENTER OF BLADE</th>
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<th>MARGIN OF BLADE</th>
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<tr>
<td></td>
<td>Thickness range</td>
<td>Cell Height range</td>
<td>Cell Width range</td>
<td>Thickness range</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><strong>U. conglobata</strong></td>
<td>53-97</td>
<td>15-40</td>
<td>5-22</td>
<td>40-64</td>
</tr>
<tr>
<td><strong>U. stenophylla</strong></td>
<td>38-136</td>
<td>67</td>
<td>26</td>
<td>28-47</td>
</tr>
<tr>
<td>(180)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>U. taeniata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>British Columbia</td>
<td>40-90</td>
<td>57</td>
<td>14-35</td>
<td>34-52</td>
</tr>
<tr>
<td>Oregon and Calif. north of Pt. Conception</td>
<td>37-116</td>
<td>76</td>
<td>15-38</td>
<td>33-64</td>
</tr>
<tr>
<td>South of Pt. Conception</td>
<td>41-214</td>
<td>122</td>
<td>13-78</td>
<td>39-78</td>
</tr>
<tr>
<td><strong>U. fasciata</strong></td>
<td>82-100</td>
<td>37-43</td>
<td>10-15</td>
<td>85-88</td>
</tr>
<tr>
<td>Chloropelta caespitosa</td>
<td>23-60</td>
<td>6-17</td>
<td>6-25</td>
<td>17-35</td>
</tr>
</tbody>
</table>

1. Type material.
2. Dentate specimens.
3. Many of these specimens had eroded margins.
Figure 6. Herbarium specimens of Ulva californica and specimens morphologically intermediate between U. californica and U. scagelii
a. From Botany Beach, Port Renfrew, Vancouver IsT., B.C. (U308; 11-VII-76). b. From San Gregorio Beach, Calif. (U266.5; 31-XII-75). c. From Point Joe, Calif. (U303; 11-VII-76).
d. From Malibu, Calif. (AHFH 63053; 17-XI-56). E. From Point Mugu, Calif. (AHFH 66940; 26-X-57). f. From La Jolla, Calif. (NY; Lectotype of U. californica; no date of coll.).
a-c,e. Scale bar = 50 mm. d,f. Scale bar = 5 mm.
intertidal zones, often forming mats with up to 100% cover. However, individual plants were solitary rather than tufted, cuneate to narrowly oblanceolate and up to 20 cm or more in length (Fig. 7). Transitional specimens were encountered on the west of Vancouver Island (Fig. 6a) and in central and southern California (Fig. 6b-e). These transitional specimens could not be identified with certainty with one or the other species.

Thallus thickness and cell dimensions were similar for both species (Table 6) and could not be used to separate morphologically transitional forms. In both species the cells in transverse section were isodiametric to slightly taller than wide in both the center and margins of the blade (Fig. 8f-h). In many specimens the blade tapered to a short stipe-like base that was elliptical in transverse section due to the presence of rhizoidal protuberances between the cell layers. In other specimens rhizoidal cells originated at the base of the flattened blade (Fig. 8b,e). In surface view the cells of both species were 4-6 sided, rectangular, angular or with rounded corners (Fig. 8a,c). The cells often formed short longitudinal rows. Most cells had 1 pyrenoid per cell, though 2 pyrenoids were observed in some cells of several specimens.

No specimens were encountered while collecting or in herbaria that could with confidence be identified as *U. angusta* Setchell et Gardner, other than the type material. Most herbarium specimens labeled as such were found on examination to be *U. taeniata* (e.g. AHFH69365, US39015) or *U. stenophylla* (CMS8018). The type specimens are narrowly oblanceolate with ruffled margins (Fig. 9) and are similar in thickness, cell dimensions and pyrenoid number to specimens of *U. californica* and *U. scagelii* (Table 6; Fig. 8d,i).

Figure 10 shows the relationships between blade length and width, and blade length and geographic distribution for all three species.
Figure 3. Surface and sectional micrographs of *Ulva californica* from southern California, *U. scagelii* from British Columbia and *U. angusta* (Isotype material).  a. Surface view of *U. californica*.  b,c. Base and central surface view of *U. scagelii*.  d. Central surface view of *U. angusta*.  e,g. Transverse sections through the basal rhizoidal region and above the rhizoidal region in *U. californica*.  g,h. Central and margin transverse sections of *U. scagelii*.  i. Marginal transverse section of *U. angusta*.  a. Scale bar = 50 μm.  f. Scale bar = 100 μm.  b,e,g-i. Same scale bar as (a).  P = pyrenoid.  R = rhizoidal region.
Figure 9. a,b. Isotype material of *Ulva angusta*. a. US 57109
b. AHFH 60478. c. Specimen of *U. californica* (U266.5) grown in culture.
Figure 10. a. Relationship between blade length (cm) and blade width (cm) in herbarium specimens of *Ulva californica*, *U. scagelii* and *U. angusta*. b. Relationship between blade length (cm) and latitude in herbarium specimens of *U. californica* and *U. scagelii*. Each dot or circle represents measurements from a single specimen. Open circles indicate type material. *Uc* = *U. californica*. *Us* = *U. scagelii*. *Ua* = *U. angusta*. 
2. *Ulva fenestrata*, *Ulva expansa*, *Ulva lobata*

Numerous specimens from Alaska to southern California were encountered that were orbicular, lobed or expanded. These specimens varied considerably in morphology, blade thickness, cell dimensions and pyrenoid number, and formed a continuum that could not be clearly broken down into species (Figs. 12-14). Herbarium specimens from California had generally been identified as *U. expansa*, *U. lobata*, *U. lactuca* and *U. rigida*. In Oregon, Washington, British Columbia and Alaska most of these had been identified as *U. fenestrata*, *U. lactuca* and *U. rigida*. As shown in Figure 1 these species were separated by thickness, blade morphology and the presence or absence of perforations. Figure 11 shows the type specimens of some of these species. Initial field collections indicated that the variation of these specimens reflected environmental differences. Large expanded plants, that reached lengths of up to 1.5 meters, were encountered primarily in relatively protected shallow bays and inlets. Thick, lobed plants usually occurred in the mid to lower intertidal zones in areas of moderate wave exposure (Fig. 12c,d). In these same areas plants in the upper intertidal zone were orbicular and relatively thin. Along open coast beaches thalli in the mid to upper intertidal zones were small, thick and densely tufted (Fig. 12b). Many plants were observed to have numerous perforations, a feature considered diagnostic for *U. fenestrata* (Fig. 13). Perforations were more common in specimens in the northern part of the study area; however, many specimens from California were also perforate. These perforations appeared to be cause by grazing or abrasion in most instances. Specimens that were attached to floats or *Nereocystis* stipes always lacked perforations (Fig. 12a).

To determine if environmental factors related to vertical position and wave exposure could be responsible for part of the observed variation, several transects were established in Barkley Sound and one at Brockton Point.
Figure 11. Type material of lobed and expanded species of Ulva. a. U. fenestrata (Holotype; LE; photograph in UBC). b. U. fasciata f. expansa (Holotype; UC 98481). c. U. fasciata f. lobata (Holotype; UC 98491). d. Phycosiris Lobata Lectotype; L4114-3; Specimen illustrated by Kützing (1857)).
Figure 12. Lobed and expanded specimens of Ulva from the northeast Pacific. a. Specimen attached to a Nereocystis stipe, Barkley Sound, Vancouver Isl. (UBC 58337 (U283); 13-V-76). b. High intertidal specimen from an exposed beach, Moss Landing, California (U194; 27-IV-76). c,d. Low intertidal specimens. c. Aguilar Point, Barkley S., Vancouver Isl. (UBC 58101 (U60); 27-VI-73). d. Scott's Cove, Barkley S., Vancouver Isl. (UBC 58338 (U138b); 15-IX-74). a,c,d. Scale bar = 100 mm. b. Scale bar = 50 mm.
Figure 14. Surface and sectional micrographs of Ulva fenestrata and related species from the northeast Pacific. a-c. Surface views of the central area of the thalli. d. Marginal surface view. e. Surface view of "U. conglobata." f-h. Central transverse sections of herbarium specimens identified as U. fenestrata (f) U. expansa (g) and U. lobata (h). i. Transverse section near margin in U. fenestrata. j, k. Central and marginal transverse sections of "U. conglobata." a. Scale bar = 50 μm. b-k. Same scale as (a).
in Burrard Inlet. Table 5 gives the sampling dates, slope, substrate and exposure of each transect. Initially it was hoped that seasonal data could be collected from the transects, but the patchy distribution and general sparseness of *Ulva* in the winter months made it impossible to collect quantitative data year round.

Although a large amount of variation was encountered in each quadrat along the transects, there was in most instances a significant increase in size (Table 7; Fig. 15) and thickness (Table 8; Fig. 16) of thalli the lower the quadrats were located in the intertidal zone. Comparisons of the three Barkley Sound transects showed that the upper limit of *Ulva* was depressed in sites less exposed to wave action, and that the thickness of thalli decreased at a given vertical level in the less exposed sites (Table 8; Fig. 16). Figure 17a shows these three transects graphed against percent time exposed to air calculated from the tide level predictions for Bamfield Inlet for the 4 week period prior to sampling along the transects.

A change of shape and in some instances coloration was also observed along the transects. In those exposed to surf or swells (Kirby Point, Scott's Cove) thalli in the mid to upper intertidal zones tended to be small, and orbicular or ovate, often with ruffled margins (Fig. 18a). Thalli in the mid to lower intertidal zones became increasingly more lobed and expanded (Fig. 18b–d). Lobes appeared to result from uneven growth along the margins, often initiated by tears in the blade. In some instances slits in the middle of a blade resulted in a lobe overlapping the blade. In the two sheltered transects (Crappler Narrows, Brockton Point) thalli in the upper intertidal zone were often pale in coloration, soft in texture, tattered and heavily epiphytized. Plants toward the lower end of the transects were increasingly darker green, firmer, less epiphytized and more lobed in appearance. No correlation could be made between perforations and vertical position or wave
Table 7. Comparison of thallus length (cm) in transect samples showing
the number of measurements (n), the means (x), standard deviations (SD), and the value of "student t." Significant (t) values
indicate that the null hypothesis ($x_1 = x_2$) is false. The vertical
position of the samples in meters above chart datum is also
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Table 8. Comparison of thallus thickness (µm) in transect samples showing the number of measurements (n), the means (x), standard deviations (SD), and the value of "student t." Significant (t) values indicate that the null hypothesis (x₁ = x₂) is false. The vertical position of the samples in meters above chart datum is also given (H). Upper most sample = (U); lower most sample = (L)

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(U) 3.23
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(U) 3.23
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Figure 15. Relationships of blade length (cm; dots) and blade width (cm; open circles) with vertical position (m) above chart datum in Ulva fenestrata along three intertidal transects in Barkley Sound (a-c) and one in Burrard Inlet (d). a. Kirby Point; 11-VII-75, 16-IV-76. b. Scott's Cove; 21-VII-75. c. Grappler Inlet; 22-VII-75. d. Brockton Point; 5-V-77. Each dot or circle represents the mean of 4-82 measurements of specimens collected in \( \frac{1}{4} \) m\(^2\) quadrats. Refer to Table 7.
Figure 16. Relationship between blade thickness (µm) and vertical position (m) above chart datum in Ulva fenestrata along three intertidal transects in Barkley Sound (a-c) and one in Burrard Inlet (d). a. Kirby Point; 11-VII-75, 16-IV-76. b. Scott's Cove; 21-VII-75. c. Grappler Inlet; 22-VII-75. d. Brockton Point; 5-V-77. Each dot represents the mean of 4-45 measurements of specimens collected in \( \frac{1}{2} \) m² quadrats. Horizontal bars represent standard deviations of the means. Refer to Table 8.
Figure 17.  

a. Relationship between blade thickness (μm) of *Ulva fenestrata* along three intertidal transects perpendicular to the shoreline and time exposed to air calculated from the predicted tide level (Canadian Hydrographic Service, 1974). Kirby Point, 11-VII-75; Scott's Cove, 21-VII-75; Grappler Inlet, 22-VII-75.

b. Percentage of specimens of *U. fenestrata* with one pyrenoid per cell and percentage with 2-4 pyrenoids per cell at different vertical positions above chart datum along an intertidal transect (Kirby Point; 11-VII-75). Refer to Table 8.
Figure 18. Changes in morphology of Ulva fenestrata along a vertical transect (Kirby Point). a. 1.7 meters above chart datum. b. 1.2 m. c. 0.75 m. d. 0.3 m.
action.

Changes in thickness were reflected by changes of cell height in sectional view; however, other cell dimensions showed no observable relationships to vertical position or wave exposure. The pyrenoid number tended to increase slightly with a decrease of vertical position in the intertidal zone (Fig. 17b).

3. *Ulva rigida*

Specimens from southern California and Baja California were encountered that fit the description of *U. rigida* sensu Bliding (1968). These plants formed tufts or turfs in the mid to upper intertidal zones, sometimes mixed with *Chloropelta* or occasionally *Ulva californica*. However, thallus shape, size, thickness, cell dimensions and marginal microscopic dentation made these specimens easy to separate from *Chloropelta* and *U. californica* (Table 6; Fig. 19). Specimens of *U. rigida* from southern California were usually irregularly lobed and up to several cm tall (Fig. 19a). North of Point Conception only one broadly lobed specimen was observed that had dentation along the margins (Fig. 19d). Several collections were made in northern California, Oregon and British Columbia of nondentate densely tufted thalli growing in exposed locations in the upper intertidal zone (Fig. 12b). These plants fit the description of *U. conglobata* form *densa* Kjellman which Yendo (1916) and Setchell and Gardner (1920b, p. 270) considered to be a form of *U. rigida*. Specimens of *U. rigida* from southern California and *U. conglobata* from north of Point Conception both occasionally showed a difference in cell height in the two cell layers when collected from the upper intertidal zone in exposed areas (Fig. 14j). However, this differentiation of cell layer was also found in specimens more typical of *U. fenestrata*.
Figure 19. Morphology and anatomy of *Ulva rigida* from the northeast Pacific. a. Herbarium specimens from Pacific Beach, Calif. (U293; 26-V-76). b-d. Central (b) and marginal surface views. e,f. Central transverse sections. g,h. Marginal transverse sections. a. Scale bar = 50 mm. b. Scale bar = 50 µm. e-h. Same scale as (b). c. Scale bar = 50 µm. d. Same scale as (c).
4. **Ulva stenophylla**

*Ulva stenophylla* was found to be one of the most distinctive species of *Ulva* in the northeast Pacific. Specimens were relatively uncommon and were found from Barkley Sound, B.C., to Santa Barbara, California. Thalli were simple or occasionally lobed, linear, lanceolate, narrowly elliptical or rarely oblanceolate (Fig. 20). Young thalli were planular throughout but later usually developed ruffled margins, leaving a planular central axis 0.5 to 3.5 cm wide, as well as becoming spirally twisted. The blade tapered abruptly to a short flattened cuneate base, occasionally with a short cylindrical stipe in young plants. Thalli reached lengths of nearly two meters and were usually 2 to 26 times longer than wide (Fig. 22a).

As can be seen from Table 6 and Figure 21f-1 the central axis of most specimens was relatively thick compared to the margin. In the thicker specimens cells of the central axis were characteristically bullet-shaped, tapering toward the blade surface (Fig. 21f). In surface view cells along the central axis were rectangular to polygonal, or occasionally hemispherical with rounded corners, and in no observable order (Fig. 21b,d). Cells along the margins and in the central area of young thalli were rectangular or polygonal, often in curved rows (Fig. 21c). Although Setchell and Gardner (1920a) reported that *U. stenophylla* lacked pyrenoids, specimens examined usually had 2-3 or more pyrenoids in each cell. Examination of the type specimen (UC 98512) revealed the presence of pyrenoids (Fig. 21d).

In Barkley Sound *U. stenophylla* formed pure populations or was mixed with *Enteromorpha linza*, *U. fenestrata* or *U. taeniata*. In the winter and early spring only young plants were found attached to the stipes of *Nereocystis luetkeana*. In the spring and summer *U. stenophylla* colonized the mid intertidal to subtidal zones in moderately exposed (Brady's Beach) and protected areas (Grappler Inlet). In the late fall this species was generally
Figure 20. Herbarium specimens of *Ulva stenophylla*. a. Epiphytic on *Nereocystis*, Scott's Cove, Barkley S., Vancouver Isl. (U324; 3-IV-77). b. From Cable Beach, Barkley S. (U132; 13-IX-74). From Bolinas, Calif. (UC 393944; V-03). d. From Monterey, Calif. (Isotype; UC 98511; 10-VI-01). a-d. Scale bar = 100 mm.
Figure 21. Surface and sectional micrographs of Ulva stenophylla. a-c. Surface views of the base (a), central axis (b) and margin (c). d. Surface view of the Holotype. Note the presence of pyrenoids (P). e-i. Transverse sections through the base (e), central axis (f,g) and margin (h,i). a. Scale bar = 50 μm. b-i. Same scale as (a).
Figure 22. a. Relationship between blade length (cm) and blade width (cm) in Ulva stenophylla from Barkley Sound. b. Relationship between blade length (cm) and time of year in herbarium specimens of U. stenophylla from Barkley Sound. Each dot or circle represents measurements of a single specimen. Open circles indicate type material from Monterey, Calif. (UC).
absent from Barkley Sound during the period of the study (Fig. 22b). Like
*U. fenestrata* the length and thickness of the thalli tended to increase with
a decrease in vertical position; however, the patchy distribution of *U.
stenophylla* made it difficult to determine the degree of variation along a
transect. No variation could be correlated with geographic distribution.

5. **Ulva taeniata, Ulva costata, Ulva dactylifera, Ulva fasciata**

*Ulva taeniata, U. costata* and *U. dactylifera* were found to be similar
in morphology and anatomy. Thalli of all three were linear to lanceolate,
simple, lobed or branched from the base into several narrow lacinae (Fig. 23,
29). The blades were almost always spirally twisted and often had thickened
planar midribs or costae and thin ruffled margins. As can be seen in
Figure 30a for specimens of *U. taeniata* from Barkley Sound, specimens reached
lengths of over 1.5 meters with length to width ratios of 2:1 to over 80:1.
These morphologically and anatomically similar species were separated in the
literature primarily by the presence of marginal teeth in *U. taeniata* (Set-
chell and Gardner, 1920b; Smith, 1944) and the presence of distinct "costae"
taeniata* was usually reported to be distributed from southern British Colum-
bia to just south of Point Conception (Abbott and Hollenberg, 1976). South
of Point Conception *U. taeniata* was generally reported to be replaced by the
nondentate species, *U. costata* and *U. dactylifera*. However, herbarium stud-
ies of all three species revealed dentation in most specimens with a decrease
in the size of dentation south of Point Conception (Fig. 26a). The decrease
in the length of teeth appeared to be related to an increase of surface water
temperatures (Fig. 26a,c). North of Point Conception teeth ranged from about
50 μm to over 1.5 mm. In southern California between Point Conception and
the Mexican border, the teeth were much reduced or absent. Blade thickness
Figure 23. Herbarium specimens of Ulva taeniata (a–c) and U. fasciata (d) from California. a. From Monterey (Isotype; US 57112; 11-VI-01). b. From Loon Point, Santa Barbara Co. (AHFH 67481; 19-XII-57). Note pale and dark costae. c. Arroyo Sequit (AHFH 62940; 18-X-56). Note pale costae. d. Ulva fasciata from San Diego Bay (RS; 4-V-74). a,b,d. Scale bar = 100 mm. c. Scale bar = 50 mm.
Figure 24. Surface and sectional micrographs of *Ulva taeniata* and related species. 

**a.** Surface view of a dark costa. **b.** Surface view of a pale costa. **c,d.** Marginal surface views. **e.** Central transverse section. **f,d.** Transverse sections through lacinae showing the transition from the thickened midrib or costa to the thin margin. Note rhizoids between the cell layers in (f). **h.** Marginal transverse section showing a tooth. **i.** Microscopic dentation in the Holotype of *U. dactylifera* (UC 205622). **a.** Scale bar = 50 μm. **b-c,e,h.** Same scale as (a) **d.** Scale bar = 50 μm. **f.** Scale bar = 100 μm. **g.** Same scale as (f). **i.** Same scale as (d). **P** = pyrenoid. **R** = rhizoidal layer.
Figure 25. Morphology and anatomy of the type material of *Ulva fasciata* f. *costata*. a,b. Lectotype (NY). c. Surface view of *Lacinae* showing costae. d. Transverse section of transition area between costa and margin. e–g. Surface views of the costa (e), margin (f) and transitional area (g). c. Scale bar = 10 mm. d,e,g. Scale bar = 50 μm. f. Same scale as (e).
of these species also varied with geographic distribution and appeared to be related to water temperature (Fig. 26b,d). The thickest specimens occurred in southern California and areas of Baja California that lacked upwelling. Cell width did not vary appreciably with geographic distribution.

Many specimens, particularly those from southern California, had thick central costae that differed in color from the margin. In some the costae were paler than the margin; in others they were darker (Fig. 23a-c). In plants with pale costae the central cells contained large vacuoles (Fig. 24b). The pale coloration was due to the larger size of the cells and the greater distance between cells in the costae relative to the margin (Fig. 24g). In most plants with dark costae the central cells were packed with starch granules (Fig. 24a). In other plants a distinct dark costa was caused by a layer of rhizoids between the cell layers that in some instances extended to the tip of the lacinae (Fig. 24f). The type specimens of *U. fasciata* f. *costata* Howe (1914) from Peru had pale costae caused primarily by a change in the dimensions of the cells (Fig. 25). These specimens also had a dark band along the margin caused by a shift in position of the chloroplast. Specimens from California previously identified as *U. costata* had costae that were darker than the margins (see Hollenberg, 1971, Fig. 1). Many specimens of *U. taeniata* and *U. dactylifera* from California and Baja California had either pale or dark costae to varying degrees. This included an isotype of *U. taeniata* (US 57112; Fig. 23a) that had a pale costa. No correlation between morphology and the type of costae could be made.

Two specimens from southern California (P.B.A. 221b at UBC; unnumbered specimen in the Setzer Herbarium, Fig. 23d) were encountered that were closer to *U. fasciata* Delile than the three species discussed above. Both specimens were branched from the base into narrow planular lacinae that were approximately the same thickness along the margins as they were in the
Figure 26.  

a. Relationship between length (0.1 mm units) of marginal teeth and latitude in herbarium specimens of Ulva taeniata.  
b. Relationship between blade thickness (µm) and latitude in herbarium specimens of U. taeniata. a,b. Each circle represents the measurement of one specimen.  
c,d. Maximum (dots; average for August) and minimum (open circles; average for January) yearly surface water temperatures along the west coast of North America (McEwen, 1916; U.S. Dept. of Commerce, 1956).
Figure 27. Photographs of Brady's Beach transect in the late summer (a; 15-IX-74) and in the winter (b; 22-II-75).
Figure 28.  a. Seasonal variation in the height (m) of Brady's Beach relative to chart datum caused by the movement of sand. Each point represents the average of six measurements along a 30 m transect.
b. Relationship between blade length (cm) in *Ulva taeniata* and vertical position (m) above chart datum along a transect perpendicular to the waterline (Brady's Beach; 16-VI-76). Refer to Table 7.
Figure 29. Winter (a,b) and summer (c,d) specimens of *Ulva taeniata* from Barkley Sound. a-c. From Brady’s Beach. a. U153; 22-II-75. b. U268; 15-II-76. c. U124; 1-IX-74. d. From Second Beach (UBC 57975 (U246); 10-VII-75). a,b. Scale bar = 50 mm. c,d. Scale bar = 100 mm.
Figure 30. a. Relationship between blade length (cm) and blade width (cm) in herbarium specimens of *Ulva taeniata* from the northeast Pacific. b. Relationship between blade length (cm) and time of year in *U. taeniata* from Barkley Sound. Each point represents the measurement of a single specimen.
Seasonal studies were made of *U. taeniata* in Barkley Sound. This relatively uncommon species was generally found attached to boulders or bedrock partially buried in sand along exposed and semi-exposed beaches. In areas *U. taeniata* formed dense beds mixed with *Gracilaria verrucosa* during the spring, summer and fall. However, in late fall and winter these beds appeared to completely disappear, not to reappear again until spring (Fig. 27). Surveyed transect lines demonstrated that over 30 cm of sand was deposited on Brady's Beach during fall and winter of 1974-5 covering rocks to which an extensive bed of *U. taeniata* was attached (Fig. 28a). In the late fall it was not uncommon to find thalli buried with as much as 15 to 30 cm of sand with just their tips protruding. However, in January and February even these plants disappeared. On February 23, 1975 several boulders were dug out of the sand, but no indications of attached thalli or holdfasts could be found. A search of the neighboring rocky headland revealed a much reduced form of *U. taeniata*. These thalli, though mature as indicated by their fertility, were only 3 to 5 cm long and irregularly lobed (Fig. 29a,b) but were easy to recognize by their distinct dentation. In spring as the sand receded, swarmers from these winter plants were probably responsible for recolonizing newly exposed rock surfaces.

As can be seen in Figure 30b the length of *U. taeniata* thalli from Barkley Sound increased over the summer reaching a peak in early fall. Length also increased significantly with a decrease in vertical position in the intertidal zone along Brady's Beach (Table 7; Fig. 28b).

6. *Chloropelta caespitosa*

*Chloropelta caespitosa* was first encountered while collecting *U. californica* and *U. rigida* in southern California. This diminutive alga was
distromatic and closely resembled *Ulva* morphologically and anatomically (Table 6; Fig. 31). However, its peltate blade and distinctly different ontogeny (Section IVB-2) set this alga apart from *Ulva* and other ulvaceous algae.

*Chloropelta caespitosa* grew in the upper intertidal region of exposed beaches attached to bedrock, boulders, cement blocks and kelp stipes (Fig. 31a,b). On sandy beaches the plants formed low densely tufted mats on emergent rocks; on rock benches plants attained a larger size and were loosely tufted. *Chloropelta caespitosa* often grew mixed with *U. californica* and *U. rigida*, but it was usually easily distinguished by its peltate blade (Fig. 31d-f). Large specimens that had blades split to the base were more difficult to separate from species of *Ulva* but could be identified by the circular rhizoidal zone at the center of the blade and the lack of marginal dentation (Fig. 31f,g). Also the rhizoidal cells in the blade appeared more loosely organized in *Chloropelta* (Fig. 31i).

In addition to the collections made in southern California, specimens of *C. caespitosa* were found in collections of E. Yale Dawson deposited in the Allan Hancock Foundation Herbarium (AHFH) at the University of Southern California (Section VIC-8). These specimens, previously identified as *U. californica* by Dawson, were from southern California, between Los Angeles and San Diego.
Figure 31. Habit, morphology and anatomy of field specimens of *Chloropelta caespitosa*.  

a. Type locality (Point Fermin, San Pedro, Calif.).  
b. Habit of plants from type locality (scale bar = 50 mm).  
c-g. Herbarium specimens.  
c. Type material (U286; 26-V-76; scale bar = 2.5 mm).  
d. From La Jolla Cove, Calif. (U292; 27-V-76; scale bar = 1 mm).  
e-g. From Laguna Beach, Calif.  
e. AHFH 64566; 14-1-57; Scale bar = 1 mm).  
f,g. UBC 57968, 57967; 26-V-76; Scale bar = 10 mm.  
h.i. Surface views of the center of the blade (h) and near the base (i).  
j,k. Central and marginal transverse sections.  
h-k. Scale bar = 50 μm.
D. DISCUSSION

As discussed in Section IIIB the ulvaceous algae are known to vary considerably in their morphological and anatomical characteristics (Setchell and Gardner, 1903; Klugh, 1922; Bliding, 1938; Arasaki and Chihara, 1959; van den Hoek, 1964; Chapman, 1964; Bliding, 1968; Kapraun, 1970; Steffensen, 1976a). This is also true for species of *Ulva* from the northeast Pacific (Table 6), though some of the variation can be related to environmental factors and is predictable. Variation with various environmental factors and the use of morphological and anatomical characteristics as taxonomic criteria are discussed below.

1. **Geographic Variation in Morphology and Anatomy**

Morphological and anatomical changes with geographic location were particularly apparent in *U. taeniata*. The length of marginal teeth decreased and blade thickness increased the further south plants were collected. Water temperature appears to be a primary factor influencing these changes as other hydrographic factors are relatively constant, and the area of greatest temperature change (Point Conception; see Section IIIB) coincides with the largest shift in tooth length and thickness (Fig. 26). A similar change in tooth length for other species of *Ulva* has not been reported by other authors. Rhyne (personal communication) grew isolates of *U. rigida* from the northwest Atlantic on a temperature gradient table, but did not observe any change with temperature. A change of blade thickness with temperature has been reported for other species of *Ulva*. Titlyanov, et al., (1975) suggested that a seasonal change in blade thickness of *U. fenestrata* from three localities in the Sea of Japan was related to seasonal changes in water temperature. In their studies blade thickness increased with a decrease of temperature. They suggested that this was caused by the retardation of cell
division and increase in cell elongation at cold temperatures. Data presented in Figure 26b for U. taeniata and general observations of U. fenestrata and U. stenophylla suggest an opposite trend in the northeast Pacific. Specimens of U. fenestrata from Alaska and northern British Columbia tended to be thinner than specimens from Oregon and California (data not presented). However, these observations were made primarily of herbarium specimens that lacked complete collection data. As indicated by Table 8 and Figure 17a, thickness in U. fenestrata varies with intertidal position and wave exposure. Vinogradova (1974) reported that cell dimensions in surface view for specimens of U. fenestrata from the northwest Pacific increased from north to south and during the summer months. However, she did not mention whether this change was accompanied with a change in thickness. In U. taeniata the increase of thickness with an increase in temperature is accompanied with an increase of cell height in transverse section but not in cell width (Table 6).

Water temperature may also be responsible for the morphological differences between U. californica and U. scagelii. These species are similar in cell dimensions, pyrenoid number, thallus shape and habitat. The primary difference is the blade length and the habit of the thallus. The gradual decrease in blade length and the increase of tufted thalli the further south they are collected may be due to the increase in water temperature or, because both species grow in the upper intertidal zone, may be related in part to an increase in air temperature. The tufted habit of specimens from southern California allows the thalli to retain large quantities of water while exposed to the air. Hence, the tufted habit may reduce the rate of dehydration of the thallus while exposed to air. Other upper intertidal ulvaceous algae from southern California (U. rigida, Chloropelta caespitosa) also show a tufted habit.
2. **Wave Exposure and Intertidal Position**

All species studied in the field showed some variation with intertidal position and wave exposure. Species of *Ulva* from Barkley Sound reached a maximum size when subtidal or attached to floating objects and decreased in size and often in thickness with an increase in vertical position in the intertidal zone. This was particularly true for *U. fenestrata*. The decrease in length and thickness may be related to a reduced photosynthetic capacity when exposed to air as is reported for *U. expansa* (Johnson et al., 1974) and *U. pertusa* (Ogata and Matsui, 1965). Another possible hypothesis is that the plants in the upper intertidal zone are more frequently shocked into becoming fertile by exposure to air. In *U. fenestrata* all but the rhizoidal cells are capable of becoming fertile. After release of swarmers the fertile margin erodes away leaving a much smaller blade that continues to grow. This would result in smaller, thinner blades in the upper intertidal zone. Though the release of swarmers in *Ulva* is cyclic and often occurs during periods of spring tides (Smith, 1947), the formation and release of reproductive cells have been shown in some species to be independent of desiccation (Smith, 1947; Chihara, 1969). Also in some areas the formation and release of swarmers occurs during neap tides (Sawada, 1972; Sawada and Watanabe, 1974; Okuda, 1975). In Barkley Sound plants in the intertidal zone, subtidal zone and high intertidal tide pools all release swarmers at the same time during the month, so that it is apparent that some factor other than desiccation initiates reproductive cell formation.

If desiccation is a major factor affecting growth rate, then wave exposure, air temperature, tidal amplitude and tidal periodicity should influence the morphology and perhaps the thickness of thalli growing at a given level in the intertidal zone. In Barkley Sound plants collected at a specific level in the intertidal zone increased in thickness with an increase of wave
exposure (Fig. 16). This difference was less pronounced in the lower intertidal and subtidal zones (Fig. 17a). Vinogradova (1974) reported a decrease of blade thickness for *U. fenestrata* from areas of increasing wave exposure; however, she did not mention whether the plants were all collected at the same vertical position or not. Desiccation may determine the upper limit of *Ulva*, though other factors such as competition and grazing may also be important (Chapman, 1973). Townsend and Lawson (1972) showed that with a tide simulating apparatus the percent time exposed to air, influenced by the frequency of immersion and the salinity of the water, determined the upper limits of *Enteromorpha*. In subtropical and tropical areas wave action and desiccation appear to be important in establishing algal zones and upper limits (Lawson, 1957). *May et al.* (1970) found that removal of herbivores from a vertical transect in New South Wales increased the density of *Ulva* but not the vertical limits, suggesting physical limitations on its distribution.

Thalli also changed in shape and appearance with vertical position. This was particularly true in protected coves and inlets. Plants growing in the upper intertidal zone in Grappler Inlet were often heavily epiphytized, irregular in shape, bullate and pale in coloration. Continuously submerged, attached plants were lobed, grass green in color and healthy in appearance. Unattached plants grew into extensive expanded blades up to a meter or more across. Similar variation was observed by Steffensen (1976a) for a single species in an estuary in New Zealand. However, in Grappler Inlet this variation was unrelated to differences in salinity (Fig. 5a,b).

3. **Seasonal Variation**

In British Columbia most species showed a maximum abundance during the spring and summer. This was particularly true for *U. stenophylla* and *U. taeniata* which all but disappeared in the late fall. Thallus dimensions also
varied seasonally. Specimens of *U. stenophylla* reached a maximum length in later summer and early fall (Fig. 22b), whereas specimens of *U. taeniata* reached a maximum length during June through August (Figs. 29b, 30b). Winter forms in both of these species were considerably smaller than summer forms and in the instance of *U. taeniata* lacked distinct linear lacinae. Similar trends were not as easy to observe in *U. fenestrata* due to the considerable variation in specimens from different vertical positions, and seasonal patchiness along the transects in Barkley Sound. In the winter specimens along the transects were sparse and smaller than summer specimens. Titlyanov, et al., (1974) also observed a reduction in the size of specimens during the winter months in the northwest Pacific. In a similar expanded species in New Zealand Steffensen (1976a) observed rapid growth of specimens in spring and early summer (October through December). In the late summer thalli fragmented and broke away from the substrate.

4. **Morphological and Anatomical Characteristics as Taxonomic Criteria**

In the northeast Pacific some species can be identified with some confidence on morphological and anatomical characteristics. These specimens are more or less linear and vary in a predictable fashion. North of Point Conception *U. taeniata* can be separated from other linear species by the presence of marginal teeth. *Ulva stenophylla* can be confused with *U. scagelii*, particularly when immature. However, these two species differ in pyrenoid number and thallus shape. Blades of *U. stenophylla* are almost always lanceolate, tapering towards the apex. The larger specimens of *U. scagelii* are oblanceolate, tapering towards the base.

Kapraun (1970) graphically separated two species of *Ulva* using the relationship between length and width. However, because of the large number of species in the northeast Pacific and the variation encountered in some species
this method cannot be used. Taxonomic characteristics of the expanded species of *Ulva* from the northeast Pacific vary significantly according to their habitat, location in the intertidal or subtidal zones, wave exposure and time of year. At a given site specimens can fit the species descriptions of *U. expansa*, *U. fenestrata*, *U. lactuca*, *U. lobata* and *U. conglobata*. Special characteristics such as teeth in *U. rigida* appear to be valid taxonomic criteria whereas others such as perforations in *U. fenestrata* are not (Vinogradova, 1974).

All of the species from the northeast Pacific vary greatly in cell dimensions and blade thickness (Table 6). These characteristics should not be used alone for identifying species. Pyrenoid number is relatively consistent for *U. californica* and *U. scagelii*. However, other species with several pyrenoids in each cell show much variation from cell to cell and plant to plant. In *U. fenestrata* pyrenoid number changed with a change in intertidal position (Fig. 17b).

To summarize, morphological characteristics can be used to identify the less variable species such as *U. californica* (*U. scagelii*), *U. stenophylla*, *U. taeniata* and *Chloropelta caespitosa*. Expanded species, except for *U. rigida*, cannot be separated on morphology. Anatomical characteristics are extremely variable and must be used with caution.
IV. GROWTH, DEVELOPMENT AND LIFE HISTORIES

A. CULTURE METHODS

1. Media and Apparatus

Several different culture media were tried including an artificial seawater mix (Utility Seven-seas Marine Mix, Utility Chemical Company, 145 Pell St., Paterson, New Jersey), an Erdschreiber seawater enrichment medium (Fjeld, 1970), Suto's enrichment medium (Chihara, 1968) and a modified Provasoli's seawater enrichment medium (Provasoli, 1958). The best growth occurred in a modification of the last medium (Table 9) and was used for all reported studies. In all culture experiments seawater was taken from the Bamfield Marine Station seawater system. This water is pumped from the Bamfield Inlet at a depth of approximately 25 meters below the surface and has a salinity of 30-33%. Seawater was either filter-sterilized using 0.45 μm membrane filters or steamed for 1 hour and then filtered. In some instances germanium dioxide was added to the culture medium with a final concentration of 0.5 mg/l to control diatom contamination (Lewin, 1966). Although cultures were kept unialgal, no attempt was made to make them axenic. Different salinity media were made by diluting steam and filter-sterilized seawater with glass distilled water and then adding the stock enrichment solution. For salinities above 32%, seawater was boiled to concentrate the salts, filtered and then diluted with distilled water to the appropriate salinities.

For most of the studies four large walk-in environment chambers set at 7°, 10°, 15°, and 20° were used. For short term experiments a front opening Percival (Percival Manufacturing Corp., Box 249, Boone, Iowa, U.S.A.) or less dependable Psycrotherm incubators (New Brunswick Scientific Co., New Brunswick, N.J., U.S.A.) were used. All three types of chambers were illuminated with Sylvania F48T12 cool white 40 W fluorescent tubes. To produce
Table 9. Seawater enrichment culture medium.

<table>
<thead>
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<th>Solution A</th>
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<tr>
<td>NaNO₃</td>
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<table>
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<th>Solution B</th>
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<tr>
<td>thiamine</td>
<td>50.0</td>
</tr>
<tr>
<td>biotin</td>
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<table>
<thead>
<tr>
<th>Solution C</th>
<th>g/1000 ml</th>
</tr>
</thead>
<tbody>
<tr>
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<td>1.0</td>
</tr>
<tr>
<td>FeCl₃.6H₂O</td>
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</tr>
<tr>
<td>MnCl₂.4H₂O</td>
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</tr>
<tr>
<td>ZnSO₄.7H₂O</td>
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</tr>
<tr>
<td>CoSO₄.7H₂O</td>
<td>0.0048</td>
</tr>
<tr>
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</tr>
</tbody>
</table>


Culture Medium: 20 ml of stock solution to 1 liter of sterilized seawater.
a temperature gradient an aluminium gradient table modified from the design used by Edwards and van Baalen (1970) was constructed (Fig. 32a). One end of the plate was cooled by placing the entire apparatus in the 7°C chamber and pumping cold water from a 20 gallon holding tank through a copper pipe soldered to the bottom side at one end of the plate. The other end was heated with a 10", 60 watt strip heater controlled by a rheostat. For most experiments the gradient table was placed on top of a shaker table to reduce temperature stratification in the medium.

For the culture of large thalli a seawater flow table was constructed (Fig. 32b). Thalli were tied to a tilted plexiglass table with monofilament fishing line. Seawater from a holding tank flowed by gravity onto the table through pores in a plastic pipe at the top end of the table. The table was always used in conjunction with the open seawater system at the Bamfield Marine Station, though it could easily be modified to be used with a closed system. Clogging of the pores by diatoms was prevented by placing a few crystals of GeO₂ in the header tank.

2. Establishment and Examination of Cultures

Thalli collected in the field were wrapped in damp paper towels and placed in plastic bags or polypropylene jars in a refrigerator or cooler (2-10°C). Thalli stored in this manner remained viable for up to a week or more and usually released swarmers within 1 hour to 5 days after placing them in fresh seawater, and exposing them to light.

Many attempts were made at controlling the time of release of swarmers of both field-collected and cultured plants. Desiccation, aeration, fragmentation, antibiotic solutions, vitamin solutions (Thaidens and Zeuthens, 1967), fresh enrichment medium and changes of temperature, photoperiod and light intensity were all used in attempts to "shock" the thalli into pro-
Figure 32.  a. Temperature gradient table.  C = copper cooling pipe; H = 60 watt strip heater; R = rheostat; F = fuse.  
b. Flow table for culturing large specimens.  
T = holding tank; P = plastic pipe.
ducing reproductive cells. The most dependable method was similar to that used by Nordby and Hoxmark (1972) and involved a change of medium, temperature, photoperiod and illumination. Small thalli or pieces of thalli grown in culture at 7°, 10°, or 15° C or field material stored in dishpans at 10° C under a photoperiod of 12:12 LD and an illumination of 550-3250 lux were rinsed and placed in fresh medium in a "sporulating chamber" set at 18° C with a 17:7 LD photoperiod and an illumination of 4000 to 6500 lux. Most thalli released within 3 to 5 days at the start of the light period. Thalli that prematurely developed gametangia were kept from releasing gametes for 1 to 2 days by placing them in the dark at 7° C. Transfer of these thalli into the light and fresh culture medium brought about spontaneous release. Using this method the release of gametes from several different plants could be synchronized.

To establish uniform cultures several drops of swarmers, concentrated by their phototactic response to laterally oriented light, were placed in a 250 ml beaker stirred by an electromagnetic stirrer. One or 2 ml allotments were transferred into 50 ml petri dishes, and the swarmers were allowed to settle on coverslips in a dark box. After 24 hours the coverslips were rinsed and placed in fresh petri dishes and medium. To observe sexual fusion gametes from different plants were placed in a drop of seawater on a microscope slide oriented laterally to a high intensity light. Gametes are positively phototactic and collect on the side toward the light, whereas quadriflagellated zygotes are negatively phototactic and collect on the side away from the light. If the slide is mounted on a compound microscope gametes and zygotes can be easily observed and picked up with a micropipette. Cultures from zygotes were established either in this manner or by using a mating apparatus similar to that of Nordby (1976).

For development and life history studies germlings were grown in petri
dishes until they were 1-2 mm high and then transferred to 250 ml jars. Culture medium was renewed every 1 to 2 weeks for actively growing cultures and every month for cultures in storage at low temperatures and low light intensities. To determine optimal culture conditions and possible effects of physical parameters on development and morphology, isolates were grown under a variety of culture conditions. Most species were grown at three different temperatures (7°, 10°, 15° C), four different salinities, 5, 15, 25, 35%) or seven different salinities (5, 10, 15, 20, 25, 30, 35%), and three different illuminations (ca. 550, 1600 and 3250 lx) under a 12:12 LD photoperiod. In addition several species were grown on the temperature gradient table under seven or eight different temperatures (i.e. 9°, 11°, 12°, 14°, 16°, 18°, 20°, ± 1° C). Culture conditions (temperature and salinity) were chosen to reflect the range of conditions found in the field (see Section IIB).

Cultures were examined weekly and the germlings photographed and/or measured using an ocular micrometer and a 50x water immersible objective lens or by temporarily mounting the coverslips on sterile slides. In instances where the number of cultures in an experiment made it impossible to examine them all in one day, coverslips were mounted in 30% clear corn syrup dissolved in 5% Formalin. Such preparations, if checked occasionally to prevent the formation of air bubbles or if sealed around the outer edge, are good for several months when unstained and much longer when stained. In one experiment 1 cm disks were cut from thalli collected in the field, weighed and placed in agitated jars under different temperatures and salinities. Rate of growth was measured by changes in diameter, and wet and dry weights of the disks. Unfortunately the disks tended to become fertile and degenerate. In all other studies the rate of growth of germlings was determined by cell number or change in germling length.
Throughout this section isolates are identified by collection numbers beginning with the letter (U). Collection numbers represent one or more specimens collected at the same time from a given population (Tables 11-14).

B. LIFE HISTORIES, REPRODUCTIVE DETAILS AND DEVELOPMENTAL PATTERNS

1. Ulva

All species of Ulva from the northeast Pacific studied in culture demonstrated life histories typical of the genus (Föyn, 1929; Bliding, 1968). For each species three types of morphologically similar thalli were encountered. One type of thallus produced pear-shaped quadriflagellated zoospores that on release were usually positively phototactic but within a short period of time became negatively phototactic. However, in one instance quadriflagellated swarmers remained positively phototactic (U. scagellii, no. U315). Zoospores generally settled shortly after coming in contact with a solid substrate, dropping or absorbing their flagella and rounding up. The other two types of thalli produced biflagellated swarmers that could act either as gametes or spores when compatible gametes of the opposite mating strain were not present. Gametes of opposite mating strains were anisogamous except in U. taeniata where they were isogamous, and were produced by different thalli (unisexual). The female gametes were larger both in length and width, and darker in color than the male gametes. Both types of gametes were positively phototactic and remained motile in the absence of a compatible mating strain for several hours or longer if placed in the dark. Compatible gametes of opposite mating strains formed clumps of a few to 100 or more when mixed together. Fusion was lateral and the resulting quadriflagellated zygotes became negatively phototactic, quickly dropping or absorbing their flagella and rounding up after coming in contact with a solid substrate.

In culture zoospores always germinated into gametophytes capable of
producing female or male gametes. Zygotes germinated into sporophytes. Gametes that germinated parthenogenetically usually produced gametophytes of the same mating strain; however, female and male gametes occasionally produced thalli that released quadriflagellated zoospores.

Occasionally thalli released swimmers in the laboratory that had 6, 8, 10 or more flagella. These swimmers were generally irregular in shape, had more than one eyespot and were considered to be prematurely released swimmers that had not completely separated from one another (Fig. 36f).

Release of zoospores and gametes was preceded by a change in color of the fertile areas of the thalli. In sporophytes and female gametophytes the fertile areas were a dark olive green. In male gametophytes of most species the fertile area was a pale yellowish or brownish green. In Ulva taeniata the color of fertile areas in both mating strains was the same. In all species swimmers escaped from sporangia and gametangia through papillae in the outer wall with a circular or elliptical pore at the apex.

Morphogenesis in Ulva from the northeast Pacific followed a complex series of events that could be divided into four stages: 1) germination of reproductive cells; 2) differentiation into an upright filament and a prostrate basal system; 3) development of the upright system into a monostromatic tubular germling; 4) collapse of the tubular germling to form a distromatic blade. The general patterns of development observed are discussed below.

Under the microscope flagellated reproductive cells went through rapid spinning movements, always in a counter-clockwise direction, before attaching. Settled zoospores, zygotes and parthenogenetic gametes quickly rounded up, dropped or absorbed their flagella, and secreted a cell wall. Eyespots remained visible for a short period after settling. In most species of Ulva settled reproductive cells germinated directly by dividing into two similar
Figure 33. Different early developmental patterns in Ulva. a. Germination by a germination tube and development of the basal system prior to the upright system (i.e. *U. californica*, *U. scagelii*). b. Germination by a germination tube and development of the upright system prior to the basal system (i.e. *U. californica*, *U. scagelii*). c. Direct germination and development of the upright system prior to the basal system (i.e. *U. fenestrata*, *U. stenophylla*, *U. taeniata*). g = germination tube; p = pyrenoid.
cells, a basal initial and an upright initial (Fig. 33c). When a lateral light source was used the first division was perpendicular to the direction of the light with the basal initial away from it. In *U. californica* and *U. scagelii* reproductive cells either germinated directly or germinated indirectly by means of a germination tube (Fig. 33, 34). In the latter type of germination the protoplast migrated to the distal end of a long thin-walled protuberance. The formation of a transverse wall cut off the distal end of the tube with the protoplast from the empty spore or zygote wall and proximal tube. This secondary cell then divided as before into an upright initial and one or more basal initials, usually with the basal initials distal to the germination tube (Fig. 33a). The empty spore or zygote wall and proximal tube eventually disintegrated over a period of about a week.

The upright initials generally divided before the basal initials in a transverse plane, initiating the development of uniseriate filaments attached by single basal initials. The basal initials either remained short and round, or elongated into primary rhizoidal cells before dividing. Longitudinal and transverse divisions of the basal initials and resulting progeny cells followed by cell elongation eventually gave rise to multicellular rhizoidal attachment disks. Under some culture conditions the basal initials of *U. californica* and *U. scagelii* developed into extensive prostrate disks before the initiation of upright filaments (Fig. 33a).

The upright uniseriate filaments continued to grow by transverse divisions until lengths were reached that were specific to each species but influenced by culture conditions. At this point longitudinal divisions occurred perpendicular to the surface of each filament to produce multiseriate germlings, though in some species a single apical cell was retained until later on in the development. Further longitudinal divisions always at right

1In this thesis a perpendicular, longitudinal or transverse division refers to the orientation of the new cell wall.
angles to the surface resulted in rod-shaped or lanceolate germlings. In transverse section cells were arranged in a ring around a central lumen filled with an amorphous matrix (Fig. 50c). As the diameter of the ring of cells increased the matrix separated except at the base to produce monostromatic saccate germlings (Fig. 50c). In the lower part of the germling the cells produced rhizoidal extensions from their inner walls that grew downward and became part of the basal attaching disk.

When the upright germlings reached lengths of a few mm to a cm or more, the lumens of the hollow upright portions collapsed with the monostromatic cell layers fusing with one another to form distromatic blades (Fig. 50c). Further growth of the blade resulted from cell divisions perpendicular to the blade surface (Fig. 50a). In the species examined divisions in a plane parallel to the surface of the blade only occurred during the formation of marginal teeth (Fig. 50b). Cells in one cell layer never divided parallel to the surface to add cells to the other layer. Under some culture conditions the collapse of the hollow germlings was incomplete or absent resulting in hollow Enteromorpha-like plants.

Reproductive and developmental details for species studied in culture are presented below and in Table 10.

a. Ulva californica, Ulva scagelii

Isolates from British Columbia, Washington and California of these two species and intermediate forms released quadriflagellated zoospores and bi-flagellated gametes (Table 11; Fig. 34a–c). Zoospores developed into uni-sexual gametophytes that eventually released gametes. Female and male gametes were both capable of germinating parthenogenetically into either the same gametophyte strain from which the gametes were released or into sporophytes. Zygotes developed into mature thalli in culture, but the release of swarmers
Table 10. Reproductive and developmental details observed in isolates of Ulva and Chloropelta caespitosa.

<table>
<thead>
<tr>
<th></th>
<th>U. californica¹</th>
<th>U. fenestrata</th>
<th>U. stenophylla</th>
<th>U. taeniata</th>
<th>Chloropelta caespitosa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spore dimensions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>length/width (μm)</td>
<td>8-12.5/</td>
<td>7-15/</td>
<td>11-15/</td>
<td>8-12/</td>
<td>7-12 long</td>
</tr>
<tr>
<td>spores/sporangium</td>
<td>4-8</td>
<td>8-16</td>
<td>8</td>
<td>4-8</td>
<td>8-16</td>
</tr>
<tr>
<td>gametes/gametangium</td>
<td>≥16</td>
<td>≥16</td>
<td>8-32</td>
<td>8-16</td>
<td>?</td>
</tr>
<tr>
<td>gamete dimensions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>length/width (μm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀gametes</td>
<td>5-8/</td>
<td>6-10/</td>
<td>9.5-12</td>
<td>3.5-11/</td>
<td>?</td>
</tr>
<tr>
<td>♂gametes</td>
<td>3-4.5</td>
<td>3-5</td>
<td>9.5-12 long</td>
<td></td>
<td></td>
</tr>
<tr>
<td>germination tube</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>no. of cells in filament when first longitudinal division</td>
<td>9-16</td>
<td>3-8(11)</td>
<td>10-30</td>
<td>7-15</td>
<td>5-25</td>
</tr>
<tr>
<td>length of germling when apical cell is lost (mm)</td>
<td>0.5-1.0</td>
<td>0.1-1.5</td>
<td>5-20</td>
<td>1.0-10</td>
<td></td>
</tr>
<tr>
<td>other characteristics</td>
<td>conspicuous</td>
<td>marginal</td>
<td>see</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>basal develop.</td>
<td>dentation</td>
<td>Section IVB-2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹This includes isolates from both B.C. and California
²Isogamous gametes
from these was not observed.

In these two species all but the cells near the base were capable of releasing reproductive cells. Each sporangium released 4-8 zoospores, 8-12.5 μm long and 4-6.5 μm wide (Fig. 34a,b). Each gametangium held 16 or more gametes. The gametes were distinctly anisogamous with the female gametes 5-8 μm long and 3-4.5 μm wide and the male gametes 4-7 μm long and 2-3.5 μm wide (Fig. 34c). Reproductive cells from thalli collected from British Columbia were indistinguishable from those collected in southern California.

Zoospores and zygotes usually germinated a few hours after settling by means of a germination tube (Fig. 34d,c). Gametes were much slower to germinate, often taking several days. Parthenogenetic germination of gametes was usually direct, without a germination tube.

Early development in these two species varied with the different culture conditions used (see Section IVC-1a). In culture at relatively high temperatures an extensive prostrate basal system developed before the upright filament (Fig. 42). In this type of development the secondary cell at the distal end of the germination tube divided into a proximal upright initial and a distal basal initial or initials (Fig. 33). By a series of mostly transverse divisions and the formation of lateral rhizoidal branches that were often later cut off by cell divisions, the basal initials developed into a filamentous prostrate system (Fig. 34f,h). Eventually the upright initial divided to initiate the formation of the upright system. At lower temperatures the initiation of the upright system preceded the development of a basal system that was much less extensive (Fig. 42).

In these species the upright uniseriate filament was formed by diffuse transverse divisions as was indicated by the presence of the germination tube at varying positions along the filament (Fig. 34i). The first longitudinal
Table 11. Isolates of *Ulva californica* and *Ulva scagelii* studied in culture.

<table>
<thead>
<tr>
<th>Coll. No.</th>
<th>Collection Location</th>
<th>Date</th>
<th>Phase of Field Material</th>
<th>Cultures Started From</th>
</tr>
</thead>
<tbody>
<tr>
<td>U315</td>
<td>Brockton Point, Vancouver, British Columbia</td>
<td>24-XI-76</td>
<td>S, G</td>
<td>φ, φ, σ</td>
</tr>
<tr>
<td>U334</td>
<td>&quot;</td>
<td>3-VI-77</td>
<td>Gφ</td>
<td>σ</td>
</tr>
<tr>
<td>U335.5</td>
<td>&quot;</td>
<td>1-VII-77</td>
<td>S, Gφ</td>
<td>φ, φ</td>
</tr>
<tr>
<td>U326</td>
<td>Kitsilano Beach, Vancouver, British Columbia</td>
<td>23-IV-77</td>
<td>Gφ, Gσ</td>
<td>φ, σ, φ</td>
</tr>
<tr>
<td>U301</td>
<td>Departure Bay, Nanaimo, British Columbia</td>
<td>17-VI-76</td>
<td>S</td>
<td>φ</td>
</tr>
<tr>
<td>U308</td>
<td>Botany Beach, Port Renfrew, British Columbia</td>
<td>11-VII-76</td>
<td>S, G</td>
<td>φ, φ, σ, φ</td>
</tr>
<tr>
<td>134</td>
<td>Cattle Point, San Juan Island, Washington</td>
<td>19-X-72</td>
<td>S. G.</td>
<td>φ</td>
</tr>
<tr>
<td>U336</td>
<td>West side of Whidbey Island, Washington</td>
<td>23-VII-77</td>
<td>S. G.</td>
<td>φ, σ</td>
</tr>
<tr>
<td>U266.5</td>
<td>San Gregorio Beach, California</td>
<td>31-XII-75</td>
<td>S. G.</td>
<td>φ, σ, φ</td>
</tr>
<tr>
<td>U303</td>
<td>Point Joe, California</td>
<td>11-VII-76</td>
<td>S, G</td>
<td>φ, φ, σ, φ</td>
</tr>
<tr>
<td>U290</td>
<td>Wood's Cove, Laguna Beach, California</td>
<td>26-V-76</td>
<td>S. G.</td>
<td>φ, φ</td>
</tr>
<tr>
<td>U292</td>
<td>La Jolla Cove, La Jolla, California</td>
<td>27-V-76</td>
<td>?</td>
<td>?</td>
</tr>
</tbody>
</table>

S = sporophyte phase; G = gametophyte phase; φ = zoospore; φ = female gamete; σ = male gamete; φ = zygote.
Figure 34. Reproduction and development of *Ulva californica* and *U. scagelii*.  

a. Transverse section through marginal sporangia (scale bar = 10 μm). Note escape papillae.  
b. Zoospores.  
c. Fusing anisogametes.  
b. Scale bar = 10 μm.  
e. Same scale as (b).  
d, e. Formation of germination tubes (isolates from B.C.; scale bar = 10 μm).  
f. Development of basal system (U315).  
g. Development of the upright system prior to the basal system at 70°C (isolate from California (U266.5)).  
h. Development of the basal system at 10°C (U266.5).  
i−k. Development of the upright germling.  
m. Incomplete fusion of the two cell layers.  
f−i. Scale bar = 20 μm.  
j. Same scale as (i).  
k−m. Scale bar = 50 μm.
division usually occurred toward the base of the filament when it was 9-16 or more cells long (Fig. 34j) and quickly spread along the filament. A single apical cell was retained until the germlings reached a length of between 0.5 and 1.0 mm. The germlings quickly passed through the multiseriate stage to form flattened strap-like blades (Fig. 34k) that were distromatic in transverse section (Fig. 34m). In culture the germlings grew into long, spirally-twisted, linear blades up to 15 cm long and only a few mm wide (Fig. 9c). Blades often proliferated from the cells of the basal system, particularly under relatively high temperatures (Fig. 44).

b. *Ulva fasciata*

During this study no living specimens of *Ulva fasciata* were encountered in the northeast Pacific. However, in order to compare the development of this species to other linear species from the northeast Pacific (*U. stenophylla*, *U. taeniata*) specimens from Waimea Beach, Hawaii (21°38.8'N, 159°04.1'W), collected by Dr. P. A. Lebednik, were studied in culture.

Specimens from Hawaii released biflagellated swarvers from cells along the margins of the narrow lacinae. The swarvers were positively phototactic and ranged from 6-9 μm long and 3-4 μm wide. Though several plants released swarvers, no differences in size could be discerned between the swarvers from different plants and no sexual fusion occurred.

In addition to biflagellated gametes some plants demonstrated an unusual form of reproduction and a vegetative stage unlike the foliose thallus typical of *Ulva*. In these plants marginal cells rounded up and were released by erosion of the margin. Each released cell was surrounded by a thick layer of wall matrix material (Fig. 35a). By divisions within the matrix a free floating globose stage with a monostromatic cell layer surrounding a central lumen formed (Fig. 35b-f). These were irregular in shape, though often
Figure 35. Reproduction and development of *Ulva fasciata* from Hawaii. 
g. Release of biflagellated swarmers from globose stage. h,i. Development of normal thalli from biflagellated swarmers. 
a. Scale bar = 50 μm. b-d. Same scale as (a). e,g,h. Scale bar = 100 μm. f,i. Scale bar = 1 mm.
angular with sharply pointed corners. Over a period of about a month the globose stage grew to a size of a few mm, and then all of the cells formed gametangia (Fig. 35g). Gametes were released that were similar in appearance and size to those released by the foliose stage. These gametes developed into biflagellated swimmers, germinated directly and followed the "Ulva lactuca-type" pattern of development (Chihara, 1968) in which the upright filament developed before the basal system (Fig. 33c). Later development was typical for the genus. Cultured blades were similar in morphology to the thalli collected in nature and reached lengths of several cm (Fig. 35h,i). Germlings did not develop marginal dentation in culture.

c. Ulva fenestrata

Isolates tentatively identified as U. fenestrata from British Columbia, Washington and California released quadriflagellated zoospores and anisogamous biflagellated gametes (Table 12). In culture zoospores, zygotes, female gametes and male gametes germinated and grew into foliose blades similar to specimens collected in the field (Fig. 36,37). However, these blades always lacked perforations. In only a few instances were thalli grown in cultures observed to release swimmers. One plant (U264), grown from a gamete, released both quadriflagellated and biflagellated swimmers.

Swimmers were usually produced along the margins of the thalli, though at times all but the basal rhizoidal cells formed sporangia or gametangia. Each sporangium released 8-16 zoospores that were 7-15 μm long and 4-7 μm wide (Fig. 36d). Each gametangium held 16 or more gametes. Female gametes were 6-10 μm long and 3-5 μm wide; male gametes were 4-7 μm long and 2-4 μm wide (Fig. 36e).

Zoospores and zygotes settled shortly after inoculation into culture dishes, but motile gametes were occasionally observed 2-3 days later. Upon
Table 12. Isolates of *Ulva fenestrata* and related forms studied in culture.

<table>
<thead>
<tr>
<th>Coll. No.</th>
<th>Collection Location</th>
<th>Date</th>
<th>Cultures Started From</th>
</tr>
</thead>
<tbody>
<tr>
<td>U139B</td>
<td>Brockton Point, Vancouver, B.C.</td>
<td>3-XI-74</td>
<td></td>
</tr>
<tr>
<td>U140B</td>
<td>&quot;</td>
<td>3-XI-74</td>
<td></td>
</tr>
<tr>
<td>U316</td>
<td>&quot;</td>
<td>24-XI-76</td>
<td></td>
</tr>
<tr>
<td>U83</td>
<td>Ross Islets, Barkley Sound, B.C.</td>
<td>1-VIII-73</td>
<td></td>
</tr>
<tr>
<td>U141</td>
<td>S.E. side of Diani I., Barkley Sound, B.C.</td>
<td>14-XI-74</td>
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</tr>
<tr>
<td>U142</td>
<td>&quot;</td>
<td>14-XI-74</td>
<td></td>
</tr>
<tr>
<td>U168</td>
<td>Grappler Inlet, Barkley Sound, B.C.</td>
<td>29-III-75</td>
<td></td>
</tr>
<tr>
<td>U266</td>
<td>&quot;</td>
<td>2-XII-75</td>
<td></td>
</tr>
<tr>
<td>U64</td>
<td>Bamfield Inlet, Barkley Sound, B.C.</td>
<td>29-VI-73</td>
<td></td>
</tr>
<tr>
<td>U79</td>
<td>&quot;</td>
<td>28-VII-73</td>
<td></td>
</tr>
<tr>
<td>U82</td>
<td>&quot;</td>
<td>1-VIII-73</td>
<td></td>
</tr>
<tr>
<td>U86</td>
<td>&quot;</td>
<td>16-VIII-73</td>
<td></td>
</tr>
<tr>
<td>U147</td>
<td>&quot;</td>
<td>26-I-75</td>
<td>α, β, γ(γ' with U146)</td>
</tr>
<tr>
<td>U149</td>
<td>&quot;</td>
<td>26-I-75</td>
<td>α, β, γ'</td>
</tr>
<tr>
<td>U239</td>
<td>&quot;</td>
<td>26-VI-75</td>
<td></td>
</tr>
<tr>
<td>U267</td>
<td>&quot;</td>
<td>15-II-76</td>
<td></td>
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<tr>
<td>U19</td>
<td>Aguilar Point, Barkley Sound, B.C.</td>
<td>25-V-75</td>
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<td>U60</td>
<td>&quot;</td>
<td>27-VI-73</td>
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<td>U63</td>
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<td>29-VI-73</td>
<td></td>
</tr>
<tr>
<td>U146</td>
<td>S. end of Scott's Cove, Barkley Sound, B.C.</td>
<td>25-I-75</td>
<td>α (α' with U147)</td>
</tr>
<tr>
<td>U169</td>
<td>&quot;</td>
<td>28-III-75</td>
<td>α (α' with U165)</td>
</tr>
<tr>
<td>U85</td>
<td>Brady's Beach, Barkley Sound, B.C.</td>
<td>10-VIII-73</td>
<td></td>
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<tr>
<td>U165</td>
<td>&quot;</td>
<td>28-III-75</td>
<td>γ, β, α (β with U169 &amp; U171)</td>
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</tbody>
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Table 12. Continued

<table>
<thead>
<tr>
<th>Coll. No.</th>
<th>Collection Location</th>
<th>Date</th>
<th>Cultures Started From</th>
</tr>
</thead>
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<tr>
<td>U323</td>
<td>Cable Beach, Barkley Sound, B.C.</td>
<td>2-IV-77</td>
<td>♂, ♀, ♂, ♀</td>
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<tr>
<td>U171</td>
<td>Sooke Harbor, S. end of Vancouver I., B.C.</td>
<td>21-III-75</td>
<td>♂, ♀, ♂, ♀ (♀ with U165 &amp; U169)</td>
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<tr>
<td>U337</td>
<td>N. side of Smith I., W. side of Whidbey I., Washington</td>
<td>23-VII-77</td>
<td>♂, ♀, ♂, ♀</td>
</tr>
<tr>
<td>U194</td>
<td>Moss Landing, Calif.</td>
<td>27-IV-76</td>
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<td>U264</td>
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<td>7-XI-75</td>
<td>♀, ♂</td>
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<td>Pescadero Point, Carmel, California</td>
<td>12-VII-76</td>
<td>♀</td>
</tr>
<tr>
<td>U307</td>
<td>Mission Point, Carmel, California</td>
<td>13-VII-76</td>
<td>♀, ♀</td>
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</table>

♀ = zoospore; ♂ = gamete; ♀ = female gamete; ♂ = male gamete; ♀ = zygote.
Figure 36. Reproduction and development of *Ulva fenestrata* and related species. a,b. Surface and sectional views of sporangia (scale bar = 10 μm). c. Transverse section through marginal gametangia (scale bar = 20 μm). d. Zoospores. e. Fusing anisogametes. d. Scale bar = 5 μm. e. Same scale as (d). f. Incompletely separated gametes (scale bar = 10 μm). Note escape pores. g-r. Development of upright germling. g-m, p-r. Isolates from B.C. n,o. Isolates from California. g,j,k. Scale bar = 10 μm. h,i. Same scale as (g). l-o. Scale bar = 20 μm. p,q. Scale bar = 50 μm. r. Scale bar = 500 μm.
Figure 37. Culture of Ulva fenestrata. a,b. Transverse sections through a hollow germling (a) and a distromatic germling (scale bar = 50 μm). c-f. Field collected plants (c, U316; e, U139) and resulting progeny grown in culture (d,f). Note lack of perforations in cultured thalli. c. Scale bar = 100 mm. e-f. Scale bar = 50 mm.
settling swarmers rounded up and secreted a cell wall. Settled zoospores and zygotes were noticeably smaller than gametes. Zoospores and zygotes usually took 3–7 days to germinate, whereas parthenogenetic gametes usually took 7–14 days. During germination sporelings either divided directly into an upright initial and a basal initial or produced prior to division a short rhizoidal protuberance directed away from the source of light (Fig. 36g–i). The upright initial usually divided first to form an upright uniseriate filament (Fig. 36j), though in several germlings the basal initial divided longitudinally to form a basal pad of two cells previous to divisions in the upright system. The first longitudinal divisions in the upright filaments occurred towards the base when the filaments reached lengths of 3–8 (11) cells. Single apical cells disappeared at lengths of 100 μm to 1.5 mm, and the multiseriate germlings quickly became cylindrical with rounded apices (Fig. 36q).

During the development of the upright systems into uniseriate and pluri-seriate filaments, the basal initials usually divided a few times longitudinally to form small disks of 4 or more rounded cells (Fig. 26a). Further divisions and formation of short rhizoidal protuberances produced attachment disks much smaller than that of *U. californica* (Fig. 36p).

Collapse of the cylindrical germlings and adhesion of the cell layers produced short strap-like blades. By further growth of the blades, germlings developed into curved spatulate or ovate thalli (Fig. 36r, 37f). A few thalli grown in culture formed tufts similar in morphology to *U. conglobata* (Fig. 37d). No discernable differences were observed between isolates from different areas. Figure 37 shows fertile field-collected plants and their cultured progeny.
d. **Ulva stenophylla**

Isolates of *U. stenophylla* from British Columbia released quadriflagellated zoospores and anisogamous gametes (Table 13). In culture zoospores, zygotes and female gametes grew into long linear blades up to 22 cm or more in length that closely resembled thalli collected in the field. No attempts were made at growing male gametes in culture. Plants grown in culture could not be induced to release swarmers.

Swarmers were produced in cells along the margins of mature thalli. Each sporangium usually held 8 zoospores that were 11-15 μm long and 4-7 μm wide (Fig. 38a). The number of gametes in each gametangium varied from 8-32. Female gametes were 9.5-12 μm long and male gametes 5-7 μm long (Fig. 38b,c).

Zoospores and zygotes germinated between 2 and 5 days after settling, whereas female gametes were slightly slower to germinate, taking 5 or more days. Cell division was preceded by the development of a rhizoidal protuberance on one side of the sporeling. When clumped zoospores were grown under overhead lights, the rhizoidal protuberances were oriented toward the center of the clump. By a series of transverse divisions the sporelings developed into uniseriate filaments (Fig. 38f-h). The basal initials divided longitudinally to produce several rounded attaching cells after the upright filaments reached lengths of 6-40 or more cells (Fig. 38h). Later these cells produced rhizoidal protuberances, but rhizoidal attaching disks never became as extensive as in *U. californica*.

The first longitudinal divisions in the upright filaments occurred at the center or toward the base when the filaments reached lengths of 10-30 cells, though usually around 20 (Fig. 38i). The longitudinal divisions resulted in long, narrow, cylindrical germlings tapering to single apical cells (Fig. 38l). That these apical cells were important in controlling longitudinal growth was indicated by the tendency of some germlings to fork subdichot-
Table 13. Isolates of *Ulva* stenophylla studied in culture

<table>
<thead>
<tr>
<th>Coll. No.</th>
<th>Collection Location</th>
<th>Date</th>
<th>Cultures Started From</th>
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<td>U224</td>
<td>Grappler Inlet, Barkley Sound, B.C.</td>
<td>9-VI-75</td>
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</tr>
<tr>
<td>U318</td>
<td>Bamfield Inlet, Barkley Sound, B.C.</td>
<td>22-I-77</td>
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<td>U52</td>
<td>Scott’s Bay, Barkley Sound, B.C.</td>
<td>19-VI-73</td>
<td>♀</td>
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<td>U57</td>
<td>&quot;</td>
<td>27-VI-73</td>
<td>♀, ♂</td>
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<tr>
<td>U58</td>
<td>&quot;</td>
<td>27-VI-73</td>
<td>♀</td>
</tr>
<tr>
<td>U59</td>
<td>&quot;</td>
<td>27-VI-73</td>
<td>♀</td>
</tr>
<tr>
<td>U62</td>
<td>&quot;</td>
<td>28-VI-73</td>
<td>♀</td>
</tr>
<tr>
<td>U226</td>
<td>&quot;</td>
<td>9-VI-75</td>
<td>♀</td>
</tr>
<tr>
<td>U310</td>
<td>Brady's Beach, Barkley Sound, B.C.</td>
<td>27-VII-76</td>
<td>♀</td>
</tr>
<tr>
<td>U230</td>
<td>Cable Beach, Barkley Sound, B.C.</td>
<td>10-VI-75</td>
<td>?</td>
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</tbody>
</table>

♀ = zoospore; ♂ = gamete; ♀ = female gamete; ♀♀ = zygote
Figure 38. Reproduction and development of Ulva stenophylla. a. Sporangia. b. Gametangia. c. Fusing anisogametes. d. Incompletely separated gametes. e-λ. Development of the upright germling. k. Abnormal forked germling. m,n. Transverse sections through a hollow (m) and a partially distromatic (n) germling. a-c. Scale bar = 10 µm. d. Same scale as (c). e,f. Scale bar = 10 µm. g. Scale bar = 10 µm. h,i. Same scale as (g). j,n. Scale bar = 50 µm. k,λ. Scale bar = 200 µm. m. Scale bar = 50 µm.
omously at the tip (Fig. 38k). Single apical cells were retained until the germlings had reached lengths of 5 mm to 2 cm.

In culture germlings remained hollow until they were a few mm to a few cm in length. In many the collapse of the cylinder was incomplete resulting in blades with hollow areas (Fig. 38n). When grown on the flow table (Fig. 32b), thalli grew quickly to lengths of more than 20 cm. Plants grown in jars usually degenerated after reaching lengths of 1-5 cm. The basal cells of these thalli often produced new upright filaments.

e. *Ulva taeniata*

Isolates of *Ulva taeniata* from British Columbia released quadriflagellated zoospores and isogamous gametes from different thalli (Table 14). Under some culture conditions, zygotes and gametes grew into linear, dentate thalli that closely resembled plants collected in the field. Thalli (U126) grown from gametes produced gametes.

Swarmers were produced in cells along the margins and at the tips of mature thalli. Each sporangium held 4-8 zoospores that were 8-12 µm long and 4-7 µm wide (Fig. 39a,b). Each gametangium held 8-16 gametes (Fig. 39d). Gametes varied greatly in size, and, though fusing pairs were often of different dimensions, gametes from different thalli could not be distinguished (Fig. 39c). Gametes varied from 3.5-11 µm in length and from 2-6.5 µm in width.

Zoospores and zygotes germinated a few days after settling, whereas gametes germinated 4 or more days after settling. Rhizoidal protuberances developed on the side of the sporelings distal to the light source. Several transverse divisions produced upright filaments attached by single rhizoidal basal cells (Fig. 39f,g). The basal system developed further when the filaments were 100 µm or longer by the production of secondary rhizoids from cells...
Table 14. Isolate of *Ulva taeniata* studied in culture

<table>
<thead>
<tr>
<th>Coll. No.</th>
<th>Collection Location</th>
<th>Date</th>
<th>Cultures Started From</th>
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<tr>
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<td>Brady's Beach, Barkley Sound, B.C.</td>
<td>22-II-75</td>
<td>?</td>
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<tr>
<td>U229</td>
<td></td>
<td>10-VI-75</td>
<td>🍃</td>
</tr>
<tr>
<td>U280</td>
<td></td>
<td>13-V-76</td>
<td>🍃, 🍃</td>
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<td>U309</td>
<td></td>
<td>27-VII-76</td>
<td>🍃</td>
</tr>
<tr>
<td>U317</td>
<td></td>
<td>22-I-77</td>
<td>🍃, 🍃</td>
</tr>
<tr>
<td>U321</td>
<td></td>
<td>2-IV-77</td>
<td>🍃, 🍃</td>
</tr>
<tr>
<td>U126</td>
<td>Cable Beach, Barkley Sound, B.C.</td>
<td>13-IX-74</td>
<td>🍃, 🍃, 🍃</td>
</tr>
</tbody>
</table>

.isDefined = zoospore; 🍃 = gamete; 🍃 = zygote from isogamous gametes.
Figure 39. Reproduction and development of Ulva taeniata. 

- b. Marginal sporangia (scale bar = 25 μm).
- c. Fusing isogametes.
- d. Marginal gametangia. a,d. Scale bar = 5 μm.
- e. Clumping of gametes from compatible mating strains (scale bar = 100 μm).
- f-m. Development of upright germling. f. Scale bar = 100 μm. g. Scale bar = 10 μm. h. Same scale as (g).
- i,j. Scale bar = 50 mm.
- k. Germling grown in 10% culture medium. k,l. Scale bar = 100 μm. m. Scale bar = 200 μm.
- n,o. Transverse sections through a hollow germling (n, scale bar = 25 μm) and a distromatic germling (o, scale bar = 50 μm).
in the lower part of the upright filaments.

The first longitudinal divisions occurred in the lower half when the filaments reached lengths of 7-15 cells (Fig. 39h,i). Continued longitudinal divisions produced cylindrical germlings tapering to single apical cells as in _U. stenophylla_ (Fig. 39j,l). The cylindrical germlings collapsed and developed into distromatic blades when 1-2 mm in length. The blades were attached by colorless unbranched rhizoidal cells, occasionally interrupted by series of small rectangular cells, resembling cells of the blade. At this stage under some culture conditions (see Section IVC-ld) scattered cells along the margin divided parallel to the surface to initiate the development of marginal teeth (Fig. 39m). Most teeth were determinate reaching a maximum size of a few mm. Other teeth showed indeterminate growth, developing into lobes or lacinae. Single apical cells were retained until the germlings reached lengths of 2 mm to over a cm. Marginal teeth and branches retained single apical cells up to lengths of a few mm. Thalli grown in jars reached lengths up to 28 cm.

2. _Chloropelta caespitosa_

Isolates of _Chloropelta caespitosa_, collected at Point Fermin, California, on May 26, 1976 and August 24, 1977, were cultured through several generations. Each generation was similar in development and morphology to the previous one. However, due to difficulties in controlling the time of release of swarmers in _Chloropelta_, all of the reproductive details were not clarified. Mostly quadriflagellated swarmers were observed, though on two occasions, once from field-collected plants and once from plants grown in culture, biflagellated swarmers were observed, but it was not possible to determine whether these came from different plants from those releasing quadriflagellated swarmers. Sexual fusion between biflagellated or quadriflagellated swarmers was not observed.
Figure 40. Reproduction and development in Chloropelta caespitosa. a. Escape pores for zoospores. b. Sporangia. c. Quadriflagellated zoospores. b. Scale bar = 10 μm. a,c. Same scale as (b). d. Clumps of settled zoospores (scale bar = 100 μm). e,f. Initial development of filamentous germling. e. Scale bar = 20 μm. f. Same scale as (e). g-k. Development of upright multiseriate germling. g-i,k. Scale bar = 50 μm. j. Germling grown at 35 %. Same scale as (i). l,m. Monostromatic saccate germlings (scale bar = 250 μm). n. Proliferation of germlings from basal rhizoids (scale bar = 100 μm). o. Dendroid basal system (scale bar = 100 μm). p. Germling grown at 5 % (scale bar = 25 μm). q. Distromatic saccate germling. r. Degeneration of cells at the apex. s. Germling releasing zoospores from apex (scale bar = 250 μm). t,u. Campanulate germlings. q,r,t. Scale bar = 1 mm. u. Scale bar = 2 mm.
Figure 41. Development of *Chloropelta caespitosa*. a–c. Transverse sections through multiseriate (a) and monostromatic hollow (b, c) germlings (scale bar = 5 μm). d. Transverse section through transition zone showing monostromatic and distromatic areas (scale bar = 100 μm). e. Transverse section through distromatic germling (scale bar = 100 μm). f, g. Transverse section through rhizoidal base (scale bar = 5 μm). j–m. Longitudinal sections. j. Distromatic saccate germling with a monostromatic apex (scale bar = 250 μm). Arrow indicates transition area. n, o. Outer and inner surfaces of campanulate germling. n. Scale bar = 10 μm. h, i, k–m, o. Same scale as (n).
Zoospores were pear-shaped, 7-12 \( \mu m \) long, with four flagella inserted at the narrow end (Fig. 40c). Each zoospore contained a single cup-shaped chloroplast with an orange eyespot. Eight to sixteen zoospores were produced in each sporangium along the margins of mature thalli and at the apex of saccate germlings in culture (Fig. 40b,s). Zoospores escaped from the sporangia through papillae with circular or elliptical pores at the apex from 5-9 \( \mu m \) in diameter (Fig. 40a). Zoospores were at first positively phototactic but quickly became negatively phototactic and tended to settle in clumps of a few to many cells (Fig. 40d).

Settled spores germinated directly without the formation of germination tubes into a basal attaching cell and an apical cell. Transverse divisions of the apical cell and resulting daughter cells gave rise to an upright uniseriate filament that reached lengths of 5-25 cells before the first longitudinal division occurred (Fig. 40a-h). Elongation of the basal cell formed at first a primary rhizoidal cell. Later divisions of this cell and resulting daughter cells, followed by cell elongation, gave rise to a loosely organized rhizoidal attaching system. Longitudinal divisions of the cells in the upright filament perpendicular to the surface produced a rod-shaped multiseriate germling (Fig. 40i-l,50d). In transverse section the cells of the multiseriate filament were arranged in a ring, the lumen of which was at first filled with an amorphous matrix (Fig. 41a,b). As the diameter of the ring of cells increased the matrix separated in the upper two thirds or more of the germling to produce a monostromatic saccate germling (Figs. 40m,41c). In the lower part the cells produced rhizoidal extensions from their inner walls that grew downward and became part of the attaching system (Fig. 41f,g). In some cultures the attaching system consisted of prostrate multiseriate filaments. These filaments were strand-like and branched in a dendroid fashion (Fig. 40o). The cells of narrow branches were elongate, but the cells
in the thicker strands lacked rhizoidal protuberances and resembled the cells of the upright system. New germlings often proliferated from these basal filaments producing clumps of germlings.

When the germlings were one to a few mm tall, each cell of the monostromatic cell layer divided once longitudinally in a plane parallel to the surface of the germling to form a distromatic cell layer around the enclosed lumen (Fig. 41d,e,i,j,k,l,m). The first of these divisions occurred above the solid rhizoidal base and proceeded toward the apex. In some germlings the apical end remained monostromatic, but degeneration of the apex resulted in a completely distromatic germling (Fig. 41r).

The distromatic saccate germlings eventually ruptured at the apex by one of two methods. In the first the cells of the monostromatic or distromatic apex degenerated and caused the apex to rip open (Fig. 40r). In the second method cells in an irregular disk at the apex developed into sporangia (Fig. 40s). A clear degenerative area developed between the fertile disk and surrounding vegetative cells and eventually, after release of the swarmers, caused the fertile disk to fall out of the germling. The opening was at first tattered and irregular, but continued growth of the distromatic blade resulted in a campanulate thallus 5-15 mm tall (Fig. 40t,u). At this stage all divisions in the blade were perpendicular to the surface so that each of the two layers of cells was independent of the other, and a distinct line of demarcation developed between cell wall material of each layer (Fig. 41i). Further growth led to a flattened orbicular or oblong blade up to a few centimeters in diameter attached in the center by a cone-shaped rhizoidal base.
C. RESPONSES TO VARIATION IN TEMPERATURE AND SALINITY

To study the effects of temperature and salinity on development and morphology, isolates of Ulva and Chloropelta were grown under a variety of culture conditions. These culture conditions are listed on Table 15. Results of the studies are given below.

1. Ulva californica, Ulva scagelii

Isolates from British Columbia (U315, U335.5, U301, U308) and southern California (U290) responded in a similar fashion to different salinities and temperatures, though some variation was observed between isolates. Only slight changes in germling morphology occurred between 10% and 35%. At 5% germlings were irregular in morphology and slow in growth. The prostrate basal system increased slightly in diameter with an increase of salinity along with the proportion of cells in the upright system producing rhizoidal protuberances. Little difference was observed in growth rate between 10% and 35% (Fig. 46a).

Ulva californica and U. scagelii demonstrated a marked amount of variation in development when grown at different temperatures. When grown at 10° or less the upright filament developed before the basal system (Fig. 42). The extent of development of the basal system increased rapidly with an increase of temperature (Figs. 42-45). Figure 45 shows that the increase in the basal system was not due simply to an increase in the growth rate. Maximum growth of the upright system occurred at 15° C in cultures of U335.5 and at 15° and 17° in U290 (Figs. 44,45). The degree of proliferation of new blades from the basal system also increased at higher temperatures (Figs. 43,44).
Table 15. Conditions under which isolates of Ulva and Chloropelta caespitosa were cultured to study the effects of temperature and salinity on development and morphology.

<table>
<thead>
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<th>Salinities (S %)</th>
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<td>U290</td>
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<td>U. fenestrata</td>
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<th>Salinities (S %)</th>
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<td>¥</td>
<td>10°, 15°</td>
<td>5, 10, 15, 20, 25, 30, 35</td>
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</tbody>
</table>

¹¥ = zoospores; ¥ = gametes; ¥ = female gametes; ¥ = zygotes.

²This includes isolates from British Columbia identified as U. scagelii (U301, U308, U315, U335.5) and isolates from California more typical of U. californica (U290).
Figure 42. Development of Ulva scagelii (U335.5) at different temperatures over a 3 week period after inoculation. At low temperatures (9.5°, 11° C) development of the upright filament preceded development of the basal system. At higher temperatures (13°, 15°, 17°, 19° C) basal development preceded initiation of upright filament.

One Week: 9.5°, scale bar = 50 μm; 11°-19° scale bar (11°) = 50 μm.
Two Weeks: 9.5°, scale bar = 50 μm; 11-13°, scale bar (11°) = 50 μm; 15-19°, scale bar = 100 μm.
Three Weeks: 9.5°, scale bar = 50 μm; 11°, scale bar = 100 μm; 13-19°, scale bar (13°) = 200 μm.
Figure 43. Morphology of 4-week-old germlings of *Ulva scagelii* (U335.5) grown at different temperatures. Note increasing size of basal disc with an increase of temperature.
Figure 44. Morphology of 8 week-old germlings of *Ulva californica* (U290) grown at different temperatures. Note the proliferation of new germlings from the base at higher temperatures. Part of the rhizoidal basal discs were lost when the germlings were removed from coverslips and mounted for examination.
Figure 45.  

a. Growth in diameter of basal discs of *Ulva scagelii* (U335.5) at different temperatures.  
b. Growth in length of blades of *U. scagelii* (U335.5) at different temperatures.  
Each point represents the average of 10-20 measurements.
2. *Ulva fenestrata*

Germlings grown at low salinities (5, 10%) tended to be either irregular in shape or relatively short and wide. Otherwise, *U. fenestrata* showed very little variation in morphology when grown at different salinities and temperatures. However, the rate of growth was affected by both of these factors. The fastest growth occurred between 20% and 30% (Fig. 46b) and at 16° and 18° C.

3. *Ulva stenophylla*

Development of germlings was normal between 15% and 35%. At 5%, few spores germinated and those that did grew into irregular clumps of cells. At 10%, germlings were often forked and had irregular outlines. The maximum rate of growth occurred at 25% and 30% (Fig. 47).

After a week of growth at different temperatures, normal development occurred between 10° and 16° with a maximum rate at 12° and 14° C. At 7° C most of the germlings were forked. Between 18° and 22° C the germlings were irregular and unhealthy in appearance.

4. *Ulva taeniata*

Development and morphology in *U. taeniata* were affected by both salinity and temperature in culture. All of the germlings died at 5%, and only a few survived at 10%. Maximum growth in length occurred at 25% (Fig. 46c, d). Determinate teeth developed on 3-week-old plants grown at 20%, 25% and 30% with a maximum development at 25%. At 10% and 15% teeth were few and indeterminate, developing into forks or branches. No teeth were observed in 3-week-old plants grown at 35%. The length and density of basal rhizoids increased with an increase of salinity.

At different temperatures maximum growth occurred between 14° and 18° C.
Figure 46. Growth of Ulva in culture at different salinities at 10° C.
a. U. scagellii (301; 1 week-old germlings).  b. U. fenestrata (U267); 1 week-old germlings).  c,d. U. taeniata (U280).
c. Two week-old germlings.  d. Three week-old germlings.
a–c. Relative growth was measured by the number of cells in the upright filament.  d. Relative growth was measured by germling length. Each point represents the mean of 22–83 measurements. Vertical bars represent the standard deviation of the means.
Figure 47. Growth of *Ulva stenophylla* (U310) at different salinities at 10° C (a,b; 2 and 3 weeks) and 15° C (c,d; 2 and 3 weeks). Relative growth was determined by germling length. Each point represents the mean of 21-40 measurements. Vertical bars represent the standard deviation of the mean.
Figure 48. Morphology of 7 week-old germlings of *Ulva taeniata* (U321) grown at different temperatures. Note the marginal dentation of germlings grown at low temperatures (9°, 11°, 12°, 14° C).
At 22° C and above all of the germlings died. The number and length of teeth and branches increased with a decrease of temperature (Fig. 48). Above 16° C germlings lacked teeth and branches. At 16° C germlings had short round teeth and no branches. Below this germlings became progressively more dentate and branched (Fig. 48).

5. *Chloropelta caespitosa*

Germlings grown in salinities of 15% or less became irregularly globose and produced less developed rhizoidal systems than at higher salinities (Fig. 40). None of these germlings developed beyond the monostromatic saccate stage. Germlings grown in salinities of 20% or greater all went through the developmental pattern described for *Chloropelta*. In cultures grown in salinities greater than 20%, rhizoidal cells extended further up the upright germling than in lower salinities (Fig. 40i,j).

D. HYBRIDIZATION EXPERIMENTS

Strict intersterility barriers between species of *Ulva* have been demonstrated by Föyn (1955), Bliding (1968) and Kapraun (1970). In their studies gametes of different species fused but the zygotes failed to develop more than a few cells. According to Bliding (1963, 1968) delayed fusion or lack of viable zygotes from fusion can be used to delimit species. During the study of northeast Pacific species of *Ulva*, hybridization experiments were used to confirm conclusions from field and culture studies. Figure 49 gives the results from crossing intraspecific and interspecific gametes.

1. *Ulva californica, Ulva scagelii*

Gametes from thalli collected in British Columbia and morphologically similar to type specimens of *U. scagelii* (U315; see Table 11) fused immediate-
ly after mixing with gametes from thalli collected in California (U303) and morphologically similar to type specimens of *U. californica* (Fig. 6c). This cross resulted in germlings similar to ones grown from zoospores. Isolates from California (U266.5, U303) also fused with an isolate from the west coast of Vancouver Island (U308; Fig. 6a) resulting in viable zygotes.

2. *Ulva fenestrata*

Thalli from different localities in British Columbia identified with *U. fenestrata* successfully crossed and produced viable zygotes (Fig. 49; Table 12). In some instances these thalli differed morphologically. For example small lobed plants (U167) crossed with large, orbicular, perforate plants (U169, U171). Gametes of a tufted high intertidal plant from California (U307) resembling *U. conglobata* did not clump or fuse with gametes of *U. fenestrata* from British Columbia (U323).

3. *Ulva fenestrata* with *Ulva californica* and *Ulva scagellii*

Gametes did not clump or fuse in attempted crosses of *U. fenestrata* (U316, U323, U335, U337) with *U. californica* and *U. scagellii* (U266.5, U303, U308, U315, U334, U336). The attempted cross between 'U. conglobata' (U307) from California and *U. californica* was also unsuccessful.

4. *Ulva lactuca*

Living specimens of *U. lactuca* from Helgoland (U333) were obtained from Dr. J. W. Markham. Thalli were induced to release female and male gametes, and attempts were made to cross these with gametes of *U. californica* (U303) and *U. fenestrata* (U335). Gametes from U333 and U303 did not clump or fuse. Gametes from U333 and U335 did not clump but a few laterally fused gametes were observed several minutes after the gametes were mixed together.
Figure 49. Results of crossing experiments. A plus (+) indicates a positive clumping and fusing response. A minus (−) indicates no mating response. U ca = U. californica. U sc = U. scagelii. U fen = U. fenestrata. U c = U. conglobata. U l = U. lactuca (from Helgoland). U st = U. stenophylla. U t = U. taeniata. U ca and U sc are distinguished on the basis of geographic location. Isolates of U ca are from California. Isolates of U sc are from British Columbia. Gametes of U t are isogamous and, therefore, cannot be separated into male and female strains.
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The delay in fusion and small number of fused gametes observed were interpreted as a negative mating response (see Bliding, 1963).

E. DISCUSSION

1. Life Histories and Reproductive Details

Life histories in *Ulva* from the northeast Pacific all follow the same pattern and cannot be used to separate species. The only deviation observed in culture was in *U. fasciata* from Hawaii in which cells (aplanospores) from the margin of blades developed into minute but multicellular, floating globose thalli. Growth in this stage was determinate and cells eventually released normal-appearing biflagellated swarmers. Föyn (1934) observed a similar stage in a culture of *U. lactuca*. However, in his study the globose stage developed from germlings that broke away from the substrate, and eventually released abnormal swarmers. Bonneau (1978) observed the formation of polymorphic globose thalli from isolated cells in degenerate germlings of *U. lactuca*. These occasionally produced swarmers that developed into normal germlings. The ability of the globose thalli of *U. fasciata* to float with water currents and produce swarmers suggests that they would be advantageous for the dispersal of the species. To my knowledge similar stages have not been observed in the field, possibly because of their diminutive size and floating habit. Unfortunately, *U. fasciata* from the northeast Pacific (west coast of North America) has not been studied in culture, and it is not known whether specimens from this area exhibit reproduction and development similar to specimens from Hawaii or other areas. Specimens from Morocco (Cauro, 1958) and the Gulf of Mexico (Kapraun, 1970) showed an alternation of unisexual gametophytes with sporophytes as is typical for the genus. These isolates were also anisogamous, a characteristic that can be used to separate *U. fasciata* from these areas from the morphologically similar *U. taeniata*. It
will be of interest to compare these two species in culture if living specimens of *U. fasciata* can be found in the northeast Pacific.

The complete life history of *Chloropelta caespitosa* has not been observed, though the presence of both quadriflagellated and biflagellated swarmers, the absence of a cyst-like stage and evidence for thalli with two different ploidy levels (see Section V) suggest an alternation of isomorphic sporophyte and gametophyte generations similar to that of *Ulva*.

The type and size of reproductive cells have been suggested as possible taxonomic criteria for separating ulvaceous species (van den Hoek, 1964; Bliding, 1964; Kapraun, 1970). In the northeast Pacific only one species differs in the type of reproductive cells. *Ulva taeniata* has isogametes, whereas all other species have anisogametes. The dimensions of swarmers could not be used to separate species as these varied considerably (Table 10), even from individual thalli.

2. Developmental Patterns

a. *Ulva*

Development and morphogenesis in *Ulva* has been studied in detail (Yamada and Saito, 1938; Cauro, 1958; Föyn, 1959; Baudrimont, 1961; Løvlie, 1964; Yoshida, 1965; Bliding, 1968; Løvlie, 1968; Chihara, 1968, 1969; Kapraun, 1970; Rhyne, 1973; Bryhni, 1974). Though germings show considerable variation when grown in axenic culture (Provasoli, 1958, 1961; Kapraun, 1970; Bonneau, 1977), isolates grown in unialgal nonaxenic culture often produce thalli similar to specimens collected in the field (Bliding, 1968; Chihara, 1968, 1969; Kapraun, 1970). In several instances development has proven valuable in describing or separating species (Cauro, 1958; Bliding, 1968; Chihara, 1968, 1969).

In the northeast Pacific developmental patterns were useful for sepa-
rating species and for understanding how environmental factors such as temperature and salinity modify morphology. Differences between species were observed in germination of reproductive cells, development of the basal attaching system, and development of the upright germling. In the latter length of uniseriate filaments when the first longitudinal divisions occurred and the persistence of apical cells were important (Table 10). *Ulva stenosphylla* and *U. taeniata* can be separated from other species on the above criteria. Specimens tentatively assigned to *U. californica* and *U. scagelii* respectively from California and British Columbia demonstrated similar developmental patterns. Chihara (1968) designated the germination pattern of *U. scagelii* as the "*Ulva-scagelii-type" to differentiate it from "*Ulva-lactuca-type" germination found in most species. Orbicular, lobed and expanded specimens, identified as *U. fenestrata*, *U. expansa* and *U. lobata*, also showed similar developmental patterns to each other. Development in this group resembled that reported for *U. conglobata* (Yamada and Saito, 1938). This lends support to Vinogradova's (1974) placement of *U. pertusa* as a synonym of *U. fenestrata* and Hommersand's (1972) suggestion that *U. conglobata* might be a small form of *U. pertusa*.

In some species temperature modified developmental patterns and morphology of the resulting thalli. In *U. californica* and *U. scagelii* the diameter of the basal disk increased with an increase of temperature. Associated with this was an increasing proliferation of blades from the basal disk. The modification of development of these species can be related to the tufted appearance of *U. californica* in southern California and the solitary habit of *U. scagelii* in British Columbia. Dentation in *U. taeniata* was also modified by temperature in culture. The number and length of teeth decreased with an increase of temperature. This relates well to the reduction in the length of teeth of plants in the field the further south that they were collected (see
Section IIID-1). Normally blades develop by diffuse divisions perpendicular to the blade surface (Bryhni, 1974). Teeth, on the other hand, are initiated by divisions parallel to the margin surface which is equivalent to the blade surface (Fig. 50a,b). Bryhni (1974) suggested that the orientation of cellulose fibrils in the cell wall may be important in determining the orientation of division planes. If this is true then temperature might be expected to affect wall deposition around cells along the blade margin.

Culture studies indicate that **U. stenophylla** grows normally in a relatively narrow range of temperatures (10-16° C). This corresponds well with herbarium and field studies. Though it has been collected as far south as Santa Barbara, **U. stenophylla** is rare south of Monterey. Its northern limit is Vancouver Island. The mean coastal surface temperatures in this area (Vancouver I. to Monterey) range from 9°-14.5° C (Naval Oceanographic Office, 1969). In Barkley Sound rapid growth occurred in this species when water temperatures were between 9° and 16° C (Figs. 5c,d,22b). When temperatures were below 8° C plants were scarce and small. Unlike **U. stenophylla**, **U. fenestrata** showed a wide tolerance to temperatures in culture. Though growth rate was influenced by culture temperature, germling morphology was not.

Culture studies suggest that the distribution of **U. fenestrata** along the west coast of North America is not limited by temperature. Biebl (1972) has shown that **U. pertusa** is tolerant of extremely high and low water temperatures.

Species of **Ulva** also differed in their tolerance to different salinities in culture. **Ulva stenophylla** and **U. taeniata** had narrow tolerances, whereas **U. californica** and **U. fenestrata** had wide salinity tolerances. Again these differences reflect the distribution of the species in the field. **Ulva taeniata** and **U. stenophylla** are restricted to the open coast or bays with high salinities. **U. californica** (**U. scagelii**) and **U. fenestrata** have been collected both on the open coast and in brackish inlets along the British
Columbia coast. Kjeldsen and Phinney (1973) reported that *U. taeniata* grew at the mouth of Yaquina Bay, Oregon, and that *U. lobata*, *U. rigida*, *U. fenestrata* and *U. expansa* occurred increasingly further back in the estuary. I suspect that the last four species represent morphological variations of a single species. Kapraun (1970) reported a gradation of morphological forms of *Enteromorpha* depending on salinity. Druehl (1967) suggested that in estuaries salinity and temperature stratifications affected the upper limits of *Ulva* and other algae. Although the studies in this thesis indicate that some species are more tolerant than others, caution must be used in applying salinity tolerances in culture to field plants. Ogata and Matsui (1965) found that tolerance differed when different culture media were used, and Zavodnik (1975) reported that tolerances differed when spring water was used instead of distilled water to dilute sea water.

b. Chloropelta

Although the initial stages of development in *Chloropelta* resemble that of *Ulva* and other members of the "natural family", Ulvaceae (Bliding, 1968), the formation of the distromatic blade by divisions parallel to the blade surface is a clear departure from these genera or other ulvaceous algae.

When the uniseriate filaments of the Ulvaceae and *Chloropelta* reach specific lengths influenced by environmental factors, longitudinal divisions perpendicular to the surface of the germling at first produce multiseriate germlings. This is followed by the formation of monostromatic cylindrical germlings. Most other members of the Ulvales sensu Bliding (1963, 1968), with the exception of *Percursaria* (Kornmann, 1956) and a few species of *Monostroma* (Kornmann and Sahling, 1962; Tatewaki, 1972), also pass through a hollow stage. However, in most members of the Monostromataceae the hollow stage develops from horizontal divisions in the center of the prostrate disk
Figure 50. a,b. Planes of division along nondentate (a) and dentate (b) margins in transverse section. Divisions are normally perpendicular to the surface except during the formation of teeth.

c. Developmental patterns in various genera belonging to the Ulvaceae. Transverse sections starting with a uniseriate filament.

d. Development of *Chloropelta* in longitudinal section.
followed by an upheaval of the upper monostromatic layer of cells. In *Monostroma undulatum* Wittrock a uniseriate filament develops directly into a monostromatic blade without passing through a hollow stage (Kornmann and Sahling, 1962).

It is at the hollow stage that *Chloropelta* departs from the type of development characteristic of the Ulvaceae. Contrary to what is stated in several books on the algae and lower plants (Fritsch, 1935; Scagel et al., 1965; Morris, 1967; Chapman and Chapman, 1973; Bold and Wynne, 1978; Trainor, 1978) divisions never occur in a plane parallel to the surface of the germling in the Ulvaceae to produce a distromatic blade. Instead the distromatic blade of *Ulva* forms by the collapse of the hollow germling and the adhesion of the cell layers (Løvlie; 1964; Fig. 50c). The two layers, however, remain independent. In *Chloropelta* the distromatic blade forms by a single division of each cell in a plane parallel to the surface of the blade (Fig. 50c,d). Subsequent development in *Chloropelta* closely resembles that of *Monostroma fuscum* (Dube, 1967).

3. Hybridization Experiments

Results of hybridization experiments were consistent with studies from other areas (Bliding, 1968; Kapraun, 1970) and helped to test observations made during field and culture studies. Isolates typical of *U. scagelii* from British Columbia and isolates typical of *U. californica* from California crossed and produced viable zygotes. Likewise, lobed and expanded specimens of *U. fenestrata* crossed and produced viable zygotes. These crosses provide supportive evidence for the placement of *U. scagelii* as a synonym of *U. californica* and *U. fasciata f. lobata* as a synonym of *U. fenestrata* (see Section VIA). Attempted crosses between species that are morphologically and developmentally distinct failed, indicating the presence of interspecific sterility barriers.
V. CYTOLOGICAL STUDIES

Several cytological studies have been reported on for species of *Ulva* and other ulvaceous algae, yielding haploid numbers that varied from 8 to 13 (Table 16). These earlier studies were concerned primarily with confirming the alternation of a diploid sporophyte with a haploid gametophyte and did not attempt to assess the potential of using chromosome numbers for delimiting species. Few species of *Ulva* were studied, and the resulting counts were often conflicting (Table 16).

During this study chromosome counts were made for five species of *Ulva* from the northeast Pacific and for *Chloropelta caespitosa* to determine if chromosome numbers could be used to delimit species.

A. METHODS

For chromosome counts thalli were fixed in either 3:1 ethanol: acetic acid or in Buffaloe's fixative (Buffaloe, 1958) and stained with either aceto-carmine (Godward, 1966) or aceto-iron-haematoxylin-chloral hydrate (Wittmann, 1965). The best combination was Buffaloe's fixative with haematoxylin stain. Buffaloe's fixative tended to stain the chloroplast, decreasing the overall contrast, but the fixed material was not as brittle as it was in ethanol: acetic acid and demonstrated superior staining qualities.

Mostly gametophytes grown in culture from zoospores and parthenogenetic gametes, or gametophytes collected from the field undergoing gametogenesis were used for this study as the primary purpose was to determine haploid numbers. Thalli were fixed in the field and in culture over 24 hour periods to determine when cells were most actively dividing. As reported by several other investigators (Ramanathan, 1939; Yabu and Tokida, 1960; Linskens and Vennegoor, 1967; Kapraun, 1970; Løvlie and Braten, 1970; Sarma and Chaudbury, 1975) the maximum number of vegetative divisions occurred during the dark
Table 16. Chromosome numbers in the Ulvaceae.

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period. Thereafter, germlings were grown under a long day photoperiod in which the dark period ran from 12:00 noon to 7:00 pm. Germlings were fixed at \(\frac{1}{2}\) hour intervals between 12:00 noon and 4:00 pm.

B. RESULTS

Mitotic events in species of *Ulva* and *Chloropelta* from the northeast Pacific generally agreed with reports by researchers for other ulvaceous algae. Vegetative cells were usually uninucleate, though some, but by no means all, rhizoidal cells were multinucleate. In two isolates of *U. fenestrata* started from parthenogenetic gametes, large round multinucleate cells about 25 \(\mu\)m in diameter were scattered among uninucleate cells in the blade of germlings (Fig. 51f). In these isolates and others started from gametes, haploid and diploid sets of chromosomes were observed in different cells in the same germlings. Other cells in the same germlings were observed to contain two sets of chromosomes undergoing division, each with its own spindle apparatus (Fig. 51e). These were either in the same stage of mitosis or in different stages.

Mitotic divisions were generally observed a half hour to four hours after the end of the light period. Nuclear membranes persisted throughout mitosis. Nucleoli disappeared during gametogenesis but persisted through early prophase during vegetative mitosis.

The diminutive size of the chromosomes (0.5-2 \(\mu\)m) and the persistent nucleolus and nuclear membrane made counting chromosomes difficult. For each species the number of chromosomes observed varied, even in different cells from the same plant. However, in all species studied the chromosome numbers were in the same range. Counts of haploid chromosomes ranged from 5 to 11 for *U. californica*, *U. fenestrata*, *U. rigida*, *U. stenophylla*, *U. taeniata* and *Chloropelta caespitosa* (Fig. 51). In most cells of these species 8 or 9
Figure 51. Chromosome studies of Ulva and Chloropelta. a,b. Haploid sets of chromosomes in Ulva califonia. c,d. Haploid sets of chromosomes in U. fenestrata. e,f. A dikaryotic cell (e, in metaphase) and a multinucleate cell (f, in prophase) in parthenogenetic germings of U. fenestrata. g,h. Haploid set (g) and diploid set (h) of chromosomes in U. stenophylla. i,j. Haploid sets of chromosomes in U. taeniata. k,l. Haploid set (k) and diploid set (l, some chromosomes out of focus) in Chloropelta caespitosa. a. Scale bar = 10 µm. b–l. Same scale as (a). P = persistent nucleolus.
chromosomes were observed. Germlings of *U. fenestrata*, *U. stenophylla* and *C. caespitosa* started from parthenogenetic gametes gave haploid counts of 5 to 9 chromosomes and diploid counts of 12 to 18 chromosomes.

C. DISCUSSION

Mitotic events and chromosome numbers in species of *Ulva* from the northeast Pacific were similar to those observed for other ulvaceous algae (Table 16). However, the difficulty in counting chromosomes and the similarities in chromosome number made chromosome studies an unlikely method for delimiting species.

Of interest is the variable nuclear state observed in parthenogenetic germlings. Parthenogenetic gametes either develop into gametophytes of the same mating strain, diploid sporophytes, haploid sporophytes or thalli that are both haploid and diploid and can produce both zoospores and gametes (Föyn, 1958, 1959; Hoxmark and Nordby, 1974; Hoxmark, 1975; Løvlie and Bryhni, 1978). Gametes of plus or + mating strains are more likely to produce diploid sporophytes than minus or − mating strains (Hoxmark and Nordby, 1974). Föyn (1962) also observed the formation of diploid sporophytes from diploid gametes. The presence of parthenogenetic germlings with ln, 2n and n+n cells in species from the northeast Pacific suggest that the doubling of the chromosome number is progressive and does not occur in the first or second nuclear divisions of the settled gamete. This is supported by Föyn's (1958) and Hoxmark's (1975) observations of parthenogenetic plants with both haploid and diploid cells. Doubling of the chromosome number, referred to as "diploidization" by Hoxmark and Nordby (1974), may occur through karyogamy following nuclear division without cytokinesis. If inhibition of cytokinesis continued, then multinucleate cells such as were observed in parthenogenetic germlings of *U. fenestrata* would form. Factors responsible for initiating
and controlling "diploidization" are not clear (Hoxmark and Nordby, 1974).
VI. GENERAL DISCUSSION

A. SPECIES AFFINITIES

The distromatic ulvaceous species from the northeast Pacific can be divided into four groups based on similarities in habitat, morphology, anatomy and development.

1. *Ulva californica*, *Ulva scagelii*, *Ulva angusta*

The species in this group grow in the upper intertidal zone, are cuneate to narrowly oblanceolate, are relatively thin and generally have one pyrenoid in the single chloroplast of each cell. The two species that have been cultured, *U. californica* and *U. scagelii*, also show similar germination and developmental patterns. The primary differences between the three species are size and shape of the blade. The results presented in this thesis indicate that these differences are related to differences in environmental conditions.

Specimens of *U. californica* from southern California form densely tufted turfs in the upper intertidal zone. Specimens of *U. californica* from northern California and *U. scagelii* from Washington and British Columbia form mats in the upper intertidal zone, but the thalli are decumbent and solitary. In culture both species produce extensive basal disks that proliferate new upright blades to form tufts at temperatures above $15^\circ$ C. Below $15^\circ$ C basal disks are less extensive and the blades tend to be solitary. The changes in development at different temperatures relate well to changes in morphology and temperature in the northeast Pacific. Along the Pacific coast of North America the most abrupt change in surface water temperatures occurs at Point Conception, California. North of Point Conception surface temperatures along the open coast rarely exceed $15^\circ$ C, whereas surface temperatures south of Point Conception are usually above $15^\circ$ C (U.S. Dept. of Commerce, 1956). It
is south of Point Conception that *U. californica* usually forms densely tufted turfs. The differences in morphology and habit appear to reflect the adaptation of thalli to different climatic conditions. As pointed out by Abbott and Hollenberg (1976, p. 6) for red algae, intertidal seaweeds in southern California are predominately short, densely branched and often in turfs. North of Point Conception large foliose forms are more common. The turfs are able to hold water among the branched or tufted thalli and are probably less susceptible to drying out or burning-off during summer low tides. These factors are less important north of Point Conception because of the cooler summer temperatures and coastal fogs. The extensive basal disks of thalli grown at relatively high temperatures may also show adaptation to the climatic conditions in southern California. In culture cells of the disk often produce new upright thalli, particularly at relatively high temperatures. As has been suggested for a similar turf species of *Ulva* from Morocco (Cauro, 1958), the basal disks are probably perennial and resistant to desiccation, providing a means of vegetative propagation following summer burn-offs.

In culture both *U. californica* and *U. scagelii* grow into long strap-like thalli that reach lengths up to 15 cm. Again, climatic conditions probably account for the decrease in blade length with a decrease in latitude (Fig. 10b). Another factor that possibly affects size and morphology is wave exposure. Specimens of *U. scagelii* from protected shores in the Strait of Georgia and Burrard Inlet reach lengths of 15 cm or more. Specimens from exposed beaches on the west coast of Vancouver Island and from northern California are almost all under 3 cm.

As discussed above, the morphological differences between *U. californica* and *U. scagelii* can be related to environmental differences. Because these species also show similar developmental patterns and are capable of hybridizing, it is proposed here that *U. scagelii* is a synonym of the
older species, *U. californica*.

It is also suggested here that *U. angusta* is a synonym of *U. californica*. Most of the specimens identified as *U. angusta* in various herbaria (AHFH, GMS, UC, US) were found to be either *U. stenophylla*, *U. taeniata* or species of *Enteromorpha*. Doty (1947) examined one of the isotypes of *U. angusta* and stated that the margins were sometimes hollow. He transferred this species to *Enteromorpha*. However, I examined holotype and isotype material and found them to belong in *Ulva*. Occasionally the cell layers separated at the margins after rehydration, but this also occurred in other species more typical of *Ulva*. The type specimens of *U. angusta* show similarities to *U. californica* and, as noted by Chihara (1968), to *U. scagelii* in their thickness, cell dimensions and pyrenoid number. Furthermore, they are almost identical morphologically to specimens of *U. californica* grown in culture. Setchell and Gardner (1920b) gave the type habitat of *U. angusta* as shallow pools in the upper intertidal zone. Continued submergence of these plants could explain why these specimens developed into long oblanceolate blades.

Plants similar to *U. californica* in habit, structure and development have been reported from other areas of the world. Dangeard (1958b) tentatively assigned a diminutive tufted alga from near Dakar, Senegal, to *U. californica*. Chapman (1956) suggested that *U. parva* Chapman from New Zealand was closely related to *U. californica*, differing primarily in thickness. Dangeard (1958a) and Chihara (1968) noted similarities between *U. linearis* Dangeard from Rabat, Morocco, and *U. californica* (*U. scagelii* in Chihara, 1968). Cauro (1958) described developmental patterns for *U. linearis* and *U. gayralii* Cauro that were similar to that of *U. californica*. Germination in these two species was usually direct, though germination by means of a germination tube did occasionally occur in *U. linearis*. Cauro suggested that the germination tubes only formed under unfavorable culture conditions (Chihara,
1968). However, Cauro reported that the cultures for both species were started from biflagellated swarmers. As reported in Section IVB-la, parthenogenetic gametes from *U. californica* rarely formed germination tubes. The same may apply to both *U. linearis* and *U. gayralii*.

2. *Ulva stenophylla*, *Ulva taeniata*, *Ulva costata*, *Ulva dactylifera*, *Ulva fasciata*

These species show similarities in habit, morphology, anatomy and development. All are usually found on exposed beaches in the lower intertidal and subtidal zones, though they are sometimes found in the upper intertidal zone or in protected waters with high salinities. The thalli are composed of simple or branched lacinae. With the exception of some specimens of *U. fasciata*, the lacinae have a thickened central midrib or costa and relatively thin margins and apex. Vegetative cells contain a single chloroplast, each with 2, 3 or more pyrenoids. *Ulva stenophylla*, *U. taeniata* and *U. fasciata* (from Hawaii) germinate directly, and in the first two species from the northeast Pacific single apical cells are retained until the germlings are 2 mm to a few cm in length.

The morphology and anatomy of these species appear well adapted to survival on surf-swept beaches. Linear lacinae present little resistance to moving water and shifting sand. The thickened central axis adds strength to the lacina, allowing it in the instance of *U. stenophylla* to reach lengths of nearly 2 meters. Occasionally, the midrib of these species is reinforced by the growth of rhizoidal protuberances from the axial cells between the cell layers. The morphological adaptability of these species is probably best exemplified by *U. taeniata*. This species is generally restricted to exposed sandy beaches. The long lacinae remain intact even when buried with up to

\[1\] The presence of a rhizoidal layer throughout the length of the lacinae of some specimens supports Papenfuss' (1960) conclusion that the taxon described as *Letterstedtia* belongs with *Ulva*. 
10 cm or more of sand.

The similarities in structure and habit indicate that these species are closely related. Three of the species, *U. taeniata*, *U. costata* and *U. dactylifera*, represent morphological variants of the same species.

a. *Ulva stenophylla*

Its linear form, ruffled margins, planar longitudinal axis and lack of dentation are enough to make *U. stenophylla* one of the easier species of *Ulva* to identify on this coast. Some specimens closely resemble *U. taeniata*, but examination of the base for dentation is usually sufficient to separate the two. Unfortunately, an inaccurate species description and an atypical holotype has caused considerable confusion regarding the identity of this species. Setchell and Gardner (1920a) described *U. stenophylla* as lacking pyrenoids. However, subsequent examinations of the type (Chihara, 1969; personal observations, Fig. 21d) and other specimens (Smith, 1947) have revealed the presence of pyrenoids. Smith (1947) suggested that Setchell and Gardner overlooked pyrenoids because their description was based entirely on herbarium specimens. The holotype of *U. stenophylla* (UC 98512) is a broadly lanceolate specimen similar to specimens found in quiet waters in Barkley Sound. The isotype (UC 98511; Fig. 20d) and other specimens collected by Gardner (UC 98477, 393944) are more typical of the species. The confusion over the identity of this species led Smith (1944) and Abbott and Hollenberg (1976) to consider this species rare, "known only from the type specimens" (Smith, 1944). However, their illustrations and descriptions of *U. angusta* as well as specimens in the GMS Herbarium labelled as *U. angusta* represent *U. stenophylla*. Doty (1947) interpreted *U. stenophylla* as a broadly lanceolate or elliptical species with margins about the same thickness as the center. A specimen (UC 307228) from Chetco Cove, Oregon, identified by Doty as
U. stenophylla, is actually a specimen of U. fenestrata.

A species that bears a strong resemblance to U. stenophylla is U. arasakii Chihara (1969) from Japan. Chihara compared the two but concluded that they differed primarily because U. arasaki had 1-4 pyrenoids in the chloroplast of each cell whereas, according to his examination of the type, U. stenophylla had only 1 pyrenoid. However, my studies of the type specimens and numerous other herbarium and living specimens show that U. stenophylla usually has 2-3 pyrenoids in the chloroplast of each cell and less commonly 1 or 4 pyrenoids. Chihara also noted that according to dimensions given by Smith (1947) gametes of U. stenophylla were smaller than gametes of U. arasaki. My measurements of gametes for Ulva species are consistently larger than Smith's, and for U. stenophylla are closer to the dimensions given by Chihara for U. arasaki. The primary difference between these two species is the type of germination. Ulva stenophylla germinates directly, whereas U. arasaki germinates by means of a germination tube. Subsequent development in the two species is very similar. The affinities of these two species need to be studied further through culture and hybridization experiments. Unfortunately, during the course of my research, live specimens of U. arasaki could not be obtained.

Two species from New Zealand also bear strong similarities to U. stenophylla. Several specimens including the types of these two species, U. geminoidea v. crispa (Chapman, 1956) and U. phyllosa (Chapman) Papenfuss (1960), were examined. Chapman (1952) based his genus Lobata on U. phyllosa as "L. phyllosa". He justified the separation by claiming that reproductive bodies were produced in the cells along the central axis. Papenfuss (1960) noted that Chapman's drawings of reproductive bodies resembled storage granules in rhizoidal cells, and placed Lobata with Ulva. I found that the holotype of Lobata phyllosa, which is the type species
of the genus, possessed reproductive structures along the margins typical of the genus Ulva. Reproductive bodies in the central cells were not observed.

At present information is lacking about the life histories and development of U. geminoidea v. crispa and U. phyllosa.

b. Ulva taeniata

*Ulva taeniata* collected north of Point Conception is easy to recognize because of its linear spirally-twisted form and dentate margins. Some specimens develop planular midribs and ruffled margins similar to *U. stenophylla*, but close examination of the base and margins are usually sufficient to separate them. South of Point Conception the specimens are usually smaller and either lack or have reduced dentation. In the past, most of these specimens were placed in *U. angusta* or *U. dactylifera*. Careful observation with a dissecting microscope or compound microscope usually reveals microscopic dentation along the margins. It is important to distinguish between teeth formed by divisions of marginal cells and teeth caused by erosion of the margins.

Doty (1947) stated that dentation was visible in a photograph of the type of *U. dactylifera* (Setchell and Gardner, 1920a, Plate 26, Fig. 1). Although the type does have microscopic teeth (up to 70 μm long), the macroscopic "teeth" visible in the photograph were caused by erosion.

Setchell and Gardner (1920a) separated *U. dactylifera* from *U. taeniata* for the following reasons: 1) the absence of dentation; 2) an expanded basal portion with lacinae growing out from the margin; 3) a thicker midrib along the lacinae; 4) cell dimensions in the midrib. Examination of the type and isotypes has revealed the presence of microscopic dentation similar to the dentation in morphologically more typical specimens of *U. taeniata* at a similar latitude. Herbarium studies indicate that the thicker midrib and different cell dimensions in transverse section are related to an increase of tem-
perature south of Point Conception. The majority of specimens, including the isotypes of *U. dactylifera*, from southern California and Baja California lack the expanded base displayed by the type of *U. dactylifera*. This morphology appears to be atypical and is not a sufficient reason for separating *U. dactylifera* from *U. taeniata*.

Howe (1914) described specimens from Peru as *U. fasciata f. costata* based on the presence of pale thickened midribs or costae along the central axes of lacinae. He noted that when costae were less distinct, "the resemblance of the plants to the California *U. fasciata f. taeniata* Setchell, as exhibited in Phycotheca Boreali-Americana 862, is marked, though they are less dentate-marginated than that." Hollenberg (1971), after examination of a few costate specimens from southern California, designated this form as a species. However, the plants he examined had costae that were darker than the surrounding tissue (Hollenberg, 1971, Fig. 1). In the AHF Herbarium there are a number of specimens from southern California and Baja California with either pale costae, dark costae or both to various degrees. Most of these plants have microscopic or macroscopic dentation and in no other way differ from other plants identifiable as *U. taeniata*. The costae in these specimens are caused either by the accumulation of starch or the lack of starch and the development of large vacuoles in the enlarged cells of the midrib. These conditions appear to reflect the physiological state of the cells. For example in cultures of *Ulva* where conditions inhibit rapid growth, cells accumulate large quantities of starch. Further support for identifying *U. costata* with *U. taeniata* comes from the presence of pale costae in an isotype of the latter (US 57112; Fig. 23a). However, of the specimens of *U. costata* examined from Southern America (Peru, Chile) only the type material and a few specimens from Peru can be identified with *U. taeniata*. Other specimens more closely fit *U. fasciata* Delile or *U. nematoidea* Bory.
(see Levring, 1941).

Chapman (1956) reported specimens of *U. taeniata* from New Zealand. Several specimens were examined from New Zealand during my study, and, although teeth were less distinct in these specimens, they were found to agree closely with *U. taeniata* from California. The type specimen of *U. brevistipita* Chapman (1956; CANTY, Laing H. 5421) was also examined and found to agree closely with *U. taeniata*. Chapman's description of this species contains several inaccuracies. He described this species as being 60 μm thick, with a cell length to width ratio in transverse section of 1.25. He also reported that *U. brevistipita* had "scarcely thickened" walls and adhered well to paper. Examination of the type specimen revealed a lanceolate blade that had microscopic teeth, was 75 μm thick in the center and had a cell length to width ratio of 1.3 to 2.5. Also, the cell walls in this specimen were extremely thickened and the blade did not adhere to the herbarium paper.

c. *Ulva fasciata*

*Ulva fasciata* and *U. taeniata* show marked similarities, particularly in southern California where both species occur. *Ulva fasciata* is a warm water species occurring in tropical and subtropical waters around the world. *U. taeniata* is primarily a cold water species, but can grow at temperatures as high as 20° C. *Ulva taeniata* is characterized by dentate margins, but Delile (1813) also described *U. fasciata* as "briefly dentate". Though the teeth of *U. fasciata*, when present, are never as large or numerous as the teeth of *U. taeniata* growing north of Point Conception, in southern California this characteristic cannot be used to separate the two species.

Howe (1914) noted that Montagne found in his studies of *U. fasciata* from Algeria that the margins of the lacinae were thickened. In *U. taeniata* the margins are always much thinner than the central axis. The two specimens
of *U. fasciata* examined from southern California have thickened margins that differ only slightly from the central axis. However, specimens from Cuba (AHFH 58331) and Hawaii (UBC 58036) were found to have margins about half the thickness of the central axis. Setchell and Gardner (1920a) separated *U. taeniata* from *U. fasciata* because the former was usually crisply ruffled or spirally twisted, whereas *U. fasciata* from other areas was almost always planular.

My observations of the two species suggest that *U. fasciata* can be separated from *U. taeniata* by its planular lacinae with margins about the same thickness as the central axis. *U. fasciata* also tends to be highly branched from the base into long linear lacinae of similar lengths. With few exceptions, *U. taeniata* tends to be sparsely and irregularly branched.

3. *Ulva fenestrata*, *Ulva expansa*, *Ulva lobata*, *Ulva rigida*, *Ulva conglobata*

These species are orbicular, ovate, irregularly lobed or expanded. They vary greatly in their cell dimensions and usually have 1, 2, 3 or more pyrenoids in the single chloroplast of each cell.

a. *Ulva fenestrata*

Setchell and Gardner (1920a, 1920b) noted similarities between *U. fenestrata*, *U. expansa* and *U. lobata*. They separated *U. lobata* from *U. expansa* because of its smaller size, its thicker blade and because it was less ruffled. Both species were distinguished from *U. fenestrata* because they lacked regular perforations. Vinogradova (1974) stated that perforations in *U. fenestrata* from the northwest Pacific were caused by grazing molluscs such as *Littorina* and were not a valid taxonomic characteristic. Her observations are supported by my own and by the lack of perforations in
cultured plants and plants growing epiphytically on *Nereocystis* pneumatocysts or stipes. The separation of *U. lobata* from *U. expansa* or *U. fenestrata* on the basis of size, thickness or presence of lobes no longer appears valid because of the large amount of variation noted for plants grown under different environmental conditions. I have not observed any specimens of *U. expansa* or *U. lobata* from the northeast Pacific that did not fit into the morphological and anatomical range of *U. fenestrata*.

It is difficult to determine the distribution of *U. fenestrata*. In most coastal areas there are species that closely resemble *U. fenestrata*. Chapman (1956) reported *U. lobata* from New Zealand, and Saifallah and Nizamuddin (1977) reported *U. fenestrata* from Pakistan. The type locality of *U. lobata* is reported to be Chile (Setchell and Gardner, 1920a); however, the specimen illustrated by Kützing (1849) as *Phycoseris lobata* (L 4114-3; Fig. 11d) has written on it: "C.B. Spei". According to a personal communication from Dr. G. M. Lokhorst to Dr. R. F. Scagel, this means: "Cape the Good Hope, South Africa". Obviously, extensive culture and hybridization studies are required to determine the relationships of expanded thalli from various geographic localities.

b. *Ulva rigida*

*Ulva rigida* is a ubiquitous species found primarily in tropical and subtropical waters. Although the concept of *U. rigida* has varied greatly, it is now considered by most phycologists to be characterized by lobed or expanded blades with dentate margins (Bliding, 1968). In the northeast Pacific this name has been used for thick, ovate or deeply divided plants, ranging in distribution from Alaska to Mexico (Setchell and Gardner, 1920b; Smith, 1944; Scagel, 1966; Abbott and Hollenberg, 1976). In not one of these floras have teeth been listed as a species characteristic,
though Abbott and Hollenberg illustrated a dentate specimen (1976, Fig. 41). Yendo (1916) noted that "the plant which passes as *U. lactuca* var. *rigida* among American botanists appears to me certainly different from *U. rigida* Ag." Although this appears true for most specimens identified with this species, dentate specimens from southern California closely resemble *U. rigida* from other areas and most certainly belong with this species.

c. *Ulva conglobata*

*Ulva conglobata* was described by Kjellman (1897) for a tufted plant growing in the upper intertidal zone in Japan (see Okamura, 1918). Yendo (1916) considered this species to be a synonym of *U. rigida*. He noted that *U. fasciata* f. *caespitosa* Setchell from California closely resembled *U. conglobata* f. *densa* Kjellman and suggested that this taxon should also be combined with *U. rigida*. Setchell and Gardner (1920b) also noted the similarities between *U. fasciata* f. *caespitosa* and *U. conglobata*; however, they referred these species to *U. lactuca*.

Specimens of *U. conglobata* from the northeast Pacific show similarities to both *U. fenestrata* and *U. rigida*. They differ from the latter by the lack of marginal dentation. Unlike *U. taeniata*, the teeth in *U. rigida* do not appear to be influenced by temperature (Rhyne, personal communication), at least for specimens from the northwest Atlantic. *U. conglobata* could possibly be a high intertidal form of *U. fenestrata*. This is supported by the occasional formation of tufted plants similar to *U. conglobata* in culture from isolates of *U. fenestrata*. However, as noted in Section IVD-2 gametes of *U. conglobata* failed to mate with gametes of *U. fenestrata*. The results from this experiment were inconclusive but suggest that *U. conglobata* may be genetically distinct from *U. fenestrata*. 
4. Chloropelta caespitosa

Chloropelta caespitosa superficially resembles tufted species of Ulva from southern California such as U. californica and U. rigida. However, C. caespitosa differs from species of Ulva in its peltate blade and distinctly different development. From the discussion in Section IVE-2 it is clear that although Chloropelta is a different taxon from Ulva, it has close affinities with members of the Ulvaceae. At present, development, life histories and the method of release of swarmers are the primary criteria for separating families within the Ulvales (Bliding, 1968; Gayral, 1971; Tatweaki, 1972; Vinogradova, 1974). By these criteria Chloropelta is closest to the Ulvaceae. The strong similarities in development between Chloropelta and Ulvaria (Dube, 1967) suggest to me that Chloropelta may have evolved from an Ulvaria-like ancestor. Ulvaria is restricted to cold water regions, whereas Chloropelta has only been found in warm-temperate waters. The ability of cells to divide longitudinally to form a distromatic blade may have developed in response to climatic pressures. The distromatic campanulate blade and tufted habit of Chloropelta no doubt increases its resistance to desiccation as has been suggested for U. californica in Section IVA-1. It is unlikely that a monostromatic ulvaceous alga such as Ulvaria could survive in the upper intertidal zone of subtropical or tropical regions.
B. KEY TO THE DISTROMATIC ULVACEOUS ALGAE FROM THE NORTHEAST PACIFIC

Species of *Ulva* and *Chloropelta* are morphologically plastic and often overlap in taxonomic characteristics. When collecting *Ulva* or *Chloropelta* several mature specimens from each population should be collected, and environmental factors such as water temperature, salinity, exposure to surf and tidal position should be noted. Identifications using the following key should be confirmed by comparing specimens to species descriptions and figures. For studies requiring positive identifications isolates should be cultured and their developmental patterns checked against those described for the different species (Section IV).

1. Thallus either a distromatic vesicle a few mm in diameter or a peltate, distromatic blade, occasionally torn to the base .................................

.................................................. *Chloropelta caespitosa*

1. Thallus a distromatic blade with a basal holdfast, though often with new blades proliferating from the base ................................. 2

2. Thallus cuneate, oblanceolate, linear or lanceolate; ± branched...3

2. Thallus orbicular, ovate, irregularly lobed or expanded ............6

3. Thallus spirally twisted, often branched and marginally dentate, in water of temperatures above 18° C the teeth microscopic or occasionally absent ................................. *Ulva taeniata*

3. Thallus generally not spirally twisted, though often with densely ruffled margins; marginal dentation absent ................................. 4

4. Thallus with several long, linear lacinae originating from near the base; planular throughout; south of Point Conception, California ..

.................................................. *Ulva fasciata*

4. Thallus usually not branched at base, though occasionally with a single fork; planular or with ruffled margins ..................... 5
5. Thallus cuneate to oblanceolate, always expanding in width towards the apex; planular or slightly ruffled; mature thallus less than 1 cm to 25 cm long; chloroplasts usually with one pyrenoid. ... *Ulva californica*

5. Thallus linear to lancolate, almost always tapering at the apex; often with a thickened planular midrib and densely ruffled margins; mature thallus 20 to 180 cm long; chloroplasts usually with 2–3 pyrenoids ... ........................................... *Ulva stenophylla*

6. Thallus with microscopic marginal dentation; often lobed and densely tufted; growing in the mid to upper intertidal zone. ... *Ulva rigida*¹

6. Thallus without marginal dentation; orbicular, ovate, irregularly lobed or expanded, often with numerous perforations ...................

......................................................... *Ulva fenestrata*¹

¹Also see discussion of *Ulva conglobata* Kjellman in Section VIA-3c.
ULVALES\textsuperscript{1} Blackman and Tansely (1902)

This order classically includes biseriate or parenchymatous thalli one to two cells thick attached by rhizoids or a basal disk. Cells of the thallus are primarily uninucleate with single parietal chloroplasts usually containing one or more pyrenoids. Sexual reproduction is by biflagellated isogamous or anisogamous gametes, and asexual reproduction is usually by quadriflagellated or occasionally biflagellated zoospores. Germination of the reproductive cells is either direct or by germination tubes. Life histories can be isomorphic or heteromorphomorphic, and developmental patterns are variable.

ULVACEAE Lamouroux orth. mut. Dumortier (1822)

This family includes biseriate and parenchymatous thalli one to two cells thick. Life histories consist of an alternation of isomorphic unisexual gametophyte and sporophyte stages, though one or the other stage is occasionally lost. Reproductive swarmers are released from sporangia and gametangia through circular or elliptical pores. Reproductive cells germinate directly or by means of a germination tube into an upright uniseriate filament and a prostrate ± rhizoidal attaching system. Through longitudinal divisions at right angles to the surface the germling develops into a biseriate (e.g. Percursaria) or a multiseriate filament. In most genera continued longitudinal divisions lead to a tubular saccate germling one cell thick. The monostromatic tubular germling either remains saccate (e.g. Blidingia, Enteromorpha), tears open to form a flattened monostromatic blade (e.g. Ulvaria) or

\textsuperscript{1}Recent, but as yet incomplete work, suggests that this order should be modified to include filamentous and parenchymatous algae that divide vegetatively by means of a precocious furrow and differ from other green algae in the structure of the reproductive cells (Stewart and Mattox, 1975a, 1978).
collapses to form a distromatic blade (e.g. Ulva). In Chloropelta cells of the monostromatic tubular germling undergo a single longitudinal division in a plane parallel to the surface to produce a distromatic tubular germling that eventually tears to become a peltate blade.

**ULVA Linnaeus (1753)**

The thallus is a flattened, foliose, distromatic blade that is usually attached at the base by rhizoidal cells. Vegetative cells are uninucleate, though rhizoidal cells are occasionally multinucleate, and have single parietal chloroplasts with one or more pyrenoids. Sporangia and gametangia form either throughout the blade or are restricted to the margin. Zoospores, zygotes and parthenogenetic gametes germinate directly or by a germination tube and develop into a monostromatic tubular germling. Collapse of the tubular germling produces a flattened distromatic blade. The cell layers remain separated by a mucilaginous matrix, and the blade expands by diffuse transverse divisions within each cell layer.

**TYPE LOCALITY:** On rocks near high water mark, Pacific Beach, south of La Jolla, California.

**TYPE MATERIAL:** Lectotype: NY; no date of collection. Isotypes: distributed as P.B.-A. no. 611.

**REFERENCES:**

- Wille, in Collins, Holden and Setchell, 1899, Fasc. 13, no. 611.
- Collins, 1903, p. 9.
- Setchell and Gardner, 1920b, p. 264.
- Dawson, 1945, p. 23.
- Doty, 1947, p. 11, Plate 2, Figs. 6-10.
- Dangeard, 1958a, p. 166-167.
- Dawson, 1959a, p. 186-188, 190.
- Dawson, 1960, p. 31.
- Sparling, 1971, p. 236.
- Abbott and Hollenberg, 1976, p. 78, 80, Fig. 35.

**SYNONYM:**

*Ulva scagelii* Chihara, 1968.

**TYPE LOCALITY:** Kitsilano Beach, Vancouver, British Columbia.

**TYPE MATERIAL:** Holotype: TNS-AL 10011, collected June 29, 1968. Isotypes: UBC 34568, 34569, 34570; UC M110589.

**REFERENCES:**

- Chihara, 1968, p. 87-102, Figs. 3-8.
PROBABLE SYNONYMS:

Ulva angusta Setchell et Gardner, 1920a.

TYPE LOCALITY: Published as Moss Beach, San Mateo Co., California, but the holotype is labeled as being from Sausalito, Marin Co. The isotype labels agree with the published locality.


REFERENCES:

Setchell and Gardner, 1920a, p. 283, Plate 27, Plate 31, Fig. 1.
Setchell and Gardner, 1920b, p. 264-5, Plate 22, Plate 26, Fig. 1.

Ulva linearis Dangeard, 1957.

TYPE LOCALITY: Rabat, Morocco.

REFERENCES:

Dangeard, 1958a, p. 28-31, Figs. 9-10.
Gayral, 1960, p. 85-95, Plate 1, Plate 3, Figs. a,b.

DISTRIBUTION:

N.E. Pacific: Alaska Peninsula to Isla Magdalena, Baja California.
N.E. Atlantic: Morocco?

REPRESENTATIVE SPECIMENS:

ALASKA:
Khantaak Isl., 8-VI-60, UBC 9231, 9232.

BRITISH COLUMBIA:
Brockton Point, Vancouver (49°18'N, 123°07'W), 16-V-76, UBC 58356 (U285);
Ferguson Point, Vancouver (approx. 49°18'N, 123°13'W), 24-VII-68,
UBC 34826; English Bay, Vancouver (49°17'N, 123°14'W), 8-VII-76, UBC 58076 (U302); Kitsilano Beach, Vancouver (48°17'N, 123°23'W), 29-VI-68, UBC 34568, 34569, 34570; Departure Bay, Vancouver Isl. (49°10'N, 123°55'W), 17-VI-76, UBC 58077 (U301); Sidney Harbor, Vancouver Isl. (approx. 48°39'N, 123°55'W), 8-X-76, UBC 58359; Botany Beach, Port Renfrew, Vancouver Isl. (approx. 48°33'N, 124°28'W), 10-VII-76, UBC 58346 (U308); Victoria Breakwater, Vancouver Isl. (approx. 48°25'N, 123°21'W), 23-V-63, UBC 18430, 18431.

WASHINGTON:

CALIFORNIA:
S. of San Gregorio Beach (approx. 37°20'N, 122°28'W), 31-XII-75, UBC 58347 (U266.5); Point Joe, Pacific Grove (approx. 36°37'N, 121°54'W), 25-VII-76, UBC 58349, 58350 (U303); Montana de Oro State Beach, San Luis Obispo Co. (approx. 35°15'N, 120°51'W), II-74, Setzer 8080 (AHFH); Montecito (approx. 34°25'N, 119°34'W), 5-II-59, AHFH 70000; West Malibu (approx. 34°03'N, 118°57'W), 17-XI-56, AHFH 63053; Point Mugu (34°06'N, 114°07.5W), 26-X-57, AHFH 66940; Pitas Point (34°17.2'N, 119°23.2'W), ?, AHFH 67867; Sunset Blvd., Los Angeles (approx. 34°01'N, 118°29'W), 14-II-58, AHFH 67911, 15-XI-56, AHFH 63176; Wood's Cove, Laguna Beach (33°32'N, 117°46'W), 26-V-76, UBC 58075 (U290); N. of Scripts Pier, La Jolla (approx. 32°51'N, 117°16'W), 27-V-76, UBC 58344 (U295); Pacific Beach, La Jolla (approx. 32°50'N, 117°17'W), ?, NY (Lectotype), P.B.-A. 611 (isotypes), UC 77858.
2. *Ulva conglobata* Kjellman, 1897.

**TYPE LOCALITY:** Yokohama, Goto and Amaska, Japan.

**TYPE MATERIAL:** The type material could not be located.

**REFERENCES:**

Kjellman, 1897, p. 11-14, Plate 2, Figs. 1-11, Plate 3, Figs. 15-18.


Okamura, 1921, p. 58-9, Plate 165, Figs. 1-10.

Fujiyama, 1950, p. 222-3.


**SYNONYMS:**

*Ulva fasciata* f. *caespitosa* Setchell\(^1\)

**TYPE LOCALITY:** "Forming a close covering on sandy rocks, midway of the littoral zone," Pacific Grove, California.

**TYPE MATERIAL:** P.B. - A. no. 809, collected May, 1900.

**REFERENCES:**

Setchell, in Collins, Holden and Setchell, 1901, Fasc. 17, no. 809.

Setchell and Gardner, 1920b, p. 270.

**DISTRIBUTION:**

N.E. Pacific: Vancouver Island, B.C. to Monterey, California?

N.W. Pacific: Japan

**REPRESENTATIVE SPECIMENS:**

**BRITISH COLUMBIA:**

Flores Isl., Clayoquot Sound, Vancouver Isl. (49°26.65'N, 126°14.0'W), 13-V-75, UBC 58186 (U201); S.E. side of Diana Isl., Barkley S.

\(^1\)This name lacks a published diagnosis and is therefore invalid.
Vancouver Isl. 48°50.1'N, 125°10.1'W), 17-VI-75, UBC 58190 (U234).

OREGON:
Yaquina Head (44°41'N, 124°05'W), 22-IX-75, UBC 58195 (U260); S. of Newport (approx. 44°39'N, 124°02'W) 22-IX-75, UBC 58187 (U258).

CALIFORNIA:
Moss Beach (approx. 37°35'N, 122°30'W), 28-IV-75, UBC 58188, 58189 (U194); Point Joe, Pacific Grove (approx. 36°37'N, 121°54'W), 5-VII-28, AHFH 78344; Pacific Grove (approx. 36°37'N, 121°54'W), V-1900, GMS 8044, P.B.A. 809 (UBC).
3. **Ulva fasciata** Delile, 1813.

**TYPE LOCALITY:** Port of Alexandria, Egypt.

**TYPE MATERIAL:** Could not be located.

**REFERENCES:**

Delile, 1813, p. 297, Plate 58, Fig. 5.

Chapman, 1956, p. 396.

Dangeard, 1958a, p. 23-28, Figs. 5-7.

Gayral, 1958, p. 150-1, Plate 4.


Krishnamurthy and Joshi, 1969, p. 126, Figs. 3,9,15.


Saifullah and Nizamuddin, 1977, p. 522, Plate 1c, Fig. 6.

**DISTRIBUTION**

World-wide in tropical waters.

N.E. Pacific: only two herbarium specimens from southern California were observed (P.B.-A. No. 221b at UBC, unnumbered specimen in the Setzer Herbarium).
4. **Ulva fenestrata** Postels et Ruprecht, 1840.

**TYPE LOCALITY:** Port St. Petri and Pauli, Kamtschatka.

**TYPE MATERIAL:** Holotype: LE; UBC 57002 (photograph and small pieces of the type); no date of collection. Isotype: LD 14419.

**REFERENCES:**
- Postels and Ruprecht, 1840, p. 21, Plate 37.
- Nagai, 1940, p. 8-9.
- Doty, 1947, p. 9-10, Plate 2, Fig. 3.
- Scagel, 1957, p. 43.
- Scagel, 1966, p. 59, Plate 29, Figs. C-E.
- Chihara, 1968, p. 87-102, Figs. 1,2 and 8.
- McRoy et al., 1971, p. 7.
- Vinogradova, 1974, p. 70-4, Plate 19, Figs. 1-6, Plate 10, Figs. 1-9.

**SYNONYMS:**

*Ulva expansa* (Setchell) Setchell et Gardner, 1920a.

**TYPE LOCALITY:** "Floating in great abundance and apparently attached to sandy rocks, Monterey", California.

**TYPE MATERIAL:** Lectotype: UC 98481; collected June 4, 1901 Isotype:
REFERENCES:


Collins, 1909, p. 216 (as *U. fasciata* f. expansa).


Setchell and Gardner, 1920b, p. 268.


Smith, 1944, p. 46.

Dawson, 1945, p. 23.

Dawson, 1946b, p. 170.


Doty, 1947, p. 10.


Scagel, 1966, p. 58-9, Plate 29, Figs. A,B.


Abbott and Hollenberg, 1976, p. 80-3, Fig. 38.


*Ulva fasciata* f. *lobata* Setchell, 1901.

TYPE LOCALITY: On rocks in the lower intertidal zone, Pebble Beach, Carmel Bay, California.


REFERENCES:

Setchell, in Collins, Holden and Setchell, 1901, Fasc. 18, no. 863.

Collins, 1903, p. 10.

Collins, 1909, p. 216.
Setchell and Gardner, 1920a, p. 284 (this and the following references as *Ulva lobata* (Kützing) Setchell et. Gardner).


Smith, 1944, p. 46-7, Plate 4, Figs. 4-5.

Dawson, 1945, p. 23.

Taylor, 1945, p. 43.

Dawson, 1946b, p. 170.

Doty, 1947, p. 10.


Chapman, 1956, p. 394-5.

Dawson, 1957, p. 4.

Dawson, 1959a, p. 186, 188.


Norris, 1970, p. 50, Plate 19C.

Abbott and Hollenberg, 1976, p. 85, 87, Fig. 40.


*Ulva pertusa* Kjellman, 1897.

**TYPE LOCALITY:** Hakodate, Yenoshima and Yokahama, Japan.

**TYPE MATERIAL:** could not be located.

**REFERENCES:**

Kjellman, 1897, p. 4, Plate 1, Figs. 1-5, Plate 3, Figs. 1-8.

Okamura, 1921, p. 79-81, Plate 169, Fig. 8, Plate 170, Figs. 1-14.

Yamada and Saito, 1938, p. 36-40.

Nagai, 1940, p. 8.

Segawa, 1959, p. 3, Plate 2, Fig. 8.

Vinogradova, 1974, p. 70.
DISTRIBUTION

N.E. Pacific: Alaska to southern California.

N.W. Pacific: Kamchatka to Taiwan(?)

REPRESENTATIVE SPECIMENS:

ALASKA:

Shapard Point, Orca Bay, Prince William Sound (approx. 60°30'N, 145°40'W), 31-V-65, M 155339; Sitka (approx. 57°3'N, 135°18'W), 19-VII-17, UC 205680.

BRITISH COLUMBIA:

Hope Island (approx. 50°58'N, 127°55'W), 15-IV-75, UBC 58227 (U181); Squire Point, Call Inlet (50°35'N, 126°09'W), 17-IV-75, UBC 55226 (U183); Isi. S.E. of Grassy Isl., at mouth of Kyuquot S., Vancouver Isl. (49°55.4'N, 127°15.0'W), 14-V-75, UBC 58212 (U205); Flores Isl., Clayoquot S., Vancouver Isl. (49°26.6'N, 126°14.0'W), 13-V-75, UBC 58216 (U200); Brockton Point, Vancouver (49°18'N, 123°07'W), 3-XI-74, UBC 58332 (U140); Belle Chain Islets, Strait of Georgia (49°08.4'N, 123°40.24'W), 29-X-73, UBC 58201 (U105); S.E. of Diana Isl., Barkley S., Vancouver Isl. (48°50.1'N, 125°10.1'W), 15-II-76, UBC 58113 (U267); S.E. of Aguilar Point, Barkley S., Vancouver Isl. (48°50.4'N, 125°10.9'W), 27-VI-73, UBC 58101 (U60); Scott's Cove, Barkley S., Vancouver Isl. (48°50.1'N, 125°08.72'W), 15-IX-74, UBC 58338 (U136); Sooke Harbor, Vancouver Isl. (48°21.6'N, 123°42.5'W), 31-III-71, UBC 58107, 58108.

WASHINGTON:

Utsalady, Camano Isl. (approx. 48°10'N, 122°31'W), VII-08, UC 132729;

1In addition to those listed, there are numerous specimens from Alaska and B.C. in the UBC herbarium.
Steam Boat Isl., Thurston Co., 9-VII-67, UW 244339; Lincoln Park, Seattle (approx. 47°30'N, 122°22'W), 14-VIII-55; Willapa Harbor (approx. 47°00'N, 124°00'W), ?, UW 249554

OREGON:
Yaquina Bay (approx. 44°39'N, 124°02'W), 9-IX-65, OSU 21; Chetco Cove, Brookings (approx. 42°04'N, 124°16'W), 5-VII-44, DS 307228.

CALIFORNIA:
Sausalito, San Francisco Bay (approx. 37°51'N, 122°29'W), V-20, UW 137763; Elkhorn Slough, Moss Landing (approx. 36°48'N, 121°47'W), 3-X-69, GMS 10858; Monterey Harbor (approx. 36°48'N, 122°01'W), 16-VII-42, GMS 8028; Pebble Beach, Carmel (approx. 36°33'N, 121°55.9' W), 23-V-71, GMS 11655, 7-XI-75, UBC 58229 (U264); Dana Point Harbor (approx. 33°24'N, 117°40'W), 26-V-76, UBC 58230.
5. *Ulva rigida* C. Agardh, 1822.

**TYPE LOCALITY:** Cadiz, southern Spain (see Papenfuss, 1960, p. 305).

**TYPE MATERIAL:** Lectotype: at Lund (LD).

**REFERENCES:**

Agardh, C., 1822, p. 410-11.
Setchell and Gardner, 1920b, p. 269-70.
Dangeard, 1958a, p. 22-3.
Gayral, 1958, p. 148, Plate 3.
Dangeard, 1959, p. 141-5, Figs. 10-11.
Papenfuss, 1960, p. 305, Fig. 4, Plate 1, Fig. 11.
Bliding, 1968.
Krishnamurthy and Joshi, 1969, p. 124, Fig. 1,7,13.
Vinogradova, 1974, p. 69-70, Plate 18, Figs. 1-8.
Abbott and Hollenberg, 1976, p. 87, Fig. 41.
Saifullah and Nizamuddin, 1977, p. 224, Plate 2c, Fig. 15.

**DISTRIBUTION:**

World-wide.
N.E. Pacific: Southern California and Mexico.

**REPRESENTATIVE SPECIMENS:**

**CALIFORNIA:**
Lechuza Point, 12-XI-58, AHFH 69124; Lunada Bay, 30-XI-57, AHFH 65905;
Catalina Isl. (approx. 33°32'N, 118°29'W), 23-23-III-48, AHFH 26608;
5-IV-70, DS 12209; La Jolla Cove, La Jolla (approx. 32°51'N, 117°16'W),
26-V-76, UBC 58184,58185 (U291); Bird Rock, Pacific Beach (approx.
32°50'N, 117°17'W), 26-V-76, UBC 58183 (U294).

BAJA CALIFORNIA:


**TYPE LOCALITY:** Floating, Monterey, California.

**TYPE SPECIMENS:** Holotype: UC 98512; collected June 10, 1901. Iso-
type: UC 98511.

**REFERENCES:**

Setchell and Gardner, 1920a, p. 282, Plate 26, Fig. 2, Plate 29.
Setchell and Gardner, 1920b, p. 271, Plate 21, Fig. 2, Plate 24.
Smith, 1944, p. 45, 47, Plate 4, Fig. 1-3 (as *Ulva angusta*).
Smith, 1955, p. 62, Fig. 24.
Papenfuss, 1960, p. 308.
Abbott and Hollenberg, 1976, p. 87, Fig. 42, p. 78, Fig. 34 (as *U.
angusta*).

**PROBABLE SYNONYMS:**


**TYPE LOCALITY:** Tauranga Bay, New Zealand.

**TYPE SPECIMEN:** Holotype: CANTY 38129; collected Nov. 7, 1942.

**REFERENCES:**

Chapman, 1952, p. 49, Fig. 3 (as *Lobata phyllosa*).
Chapman, 1956, p. 398, Fig. 41 (as *L. phyllosa*).
Papenfuss, 1960, p. 312.

*Ulva arasakii* Chihara, 1969.
TYPE LOCALITY: Inuwaka, Choshi, Chiba-ken, Japan.

TYPE MATERIAL: Holotype: TNS; collected May 1, 1965.

REFERENCES:


DISTRIBUTION:

N.E. Pacific: Vancouver Island, British Columbia to Santa Barbara, California.

N.W. Pacific: Choshi Peninsula, Japan (as U. arasakii)?

S.W. Pacific: New Zealand (as U. phyllosa)?

REPRESENTATIVE SPECIMENS:

BRITISH COLUMBIA:

E. side of Diana Isi., Barkley S., Vancouver Isi. (48°51'N, 125°11'W), 17-I-76, UBC 58032, 16-IV-76, UBC 58033 (U276); S.E. of Diana Isi., Barkley S., Vancouver Isi. (48°50.1'N, 125°101'W), 13-IX-74, UBC 58080 (U133), 13-V-76, UBC 58034 (U284); Scott's Cave, Barkley S., Vancouver Isi. (48°50.1'N, 125°08.72'W), 17-IX-73, UBC 58069, 18-VIV-74, UBC 58082 (U121), 3-IV-77, UBC 58041, 58042 (U324); Grappler Inlet, Bamfield, Vancouver Isi. (48°49.94'N, 125°06.94'W), 16-VI-75, UBC 58048, 22-VII-75, UBC 58027, 58028, 58029; Brady's Beach, Bamfield, Vancouver Isi. (48°49.74'N, 125°09'W), 24-VI-75, UBC 58086 (U238), 13-V-76, UBC 58022 (U282); Second Beach, Bamfield, Vancouver Isi. (48°48.85'N, 125°09.7'W), 10-VII-75, UBC 58021 (U247); Whiffen Spit, Vancouver Isi. (approx. 48°21'N, 123°43'W), 14-VII-73, UBC 55731, 55732.

CALIFORNIA:

Buhue Point, Humboldt Bay (approx. 40°48'N, 124°25'W), 29-VII-72, UBC 47117, 47118; Bolinas, (approx. 38°54'N, 122°42'W), ?-V-03,
UC 393944; Durbury Reef (approx. 38°54'N, 122°42'W), 29-V-03, UC 98477; Monterey (approx. 36°48'N, 122°01'W), 10-VI-01, UC 98511 (Isotype); Coal Oil Point, Santa Barbara Co. (approx. 34°26'N, 119°43'W), 6-VII-70, AHFH 76120; Santa Barbara (approx. 34°26'N, 114°43'W), 26-XII-32, AHFH 78392.

NEW ZEALAND:
Steuart Isl. (approx. 46°50'S, 168°36'E), 6-V-45, Auckland 0100S (Lobata phyllosa); Tauranga Bay, Westport, West Coast of South Island (approx. 43°15'S, 167°00'E), 7-X-42, CHR 38129 (holotype of Lobata phyllosa).

**TYPE LOCALITY:** "On sandy rocks, in small tideways, lower littoral and upper sublittoral zones, Monterey, California."

**TYPE SPECIMENS:** Holotype: UC 98493; collected June 11, 1901. Iso-types: US 57112; P.B.A. no. 862.

**REFERENCES:**

- Harvey, 1858, p. 58-9 (as *U. fasciata*, in part).
- Harvey, 1862, p. 161 (as *U. fasciata*).
- Anderson, 1891, p. 218 (as *U. fasciata*).
- Setchell, in Collins, Holden and Setchell, 1901, Fasc. 18 no. 862 (as *U. fasciata f. taeniata*).
- Collins, 1903, p. 10 (as *U. fasciata f. taeniata*).
- Collins, 1909, p. 216 (as *U. fasciata f. taeniata*).
- Setchell and Gardner, 1920b, p. 273, Plate 23.
- Sanborn and Doty, 1944, p. 12,20,24.
- Smith, 1944, p. 48, Plate 3, Figs. 1-3.
- Dawson, 1946a, p. 59-64.
- Dawson, 1946b, p. 170.
- Doty, 1947, p. 8-9, Plate 2, Figs. 11-12, Plate 4, Figs. 3-4.
- Smith, 1947, p. 8-9, Figs. 26-7.
- Chapman, 1956, p. 387, Fig. 31I.
- Dawson, 1959a, p. 186.
- Papenfuss, 1960, p. 308, Plate 5, Fig. 19.
SYNONYM:

**Ulva dactylifera** Setchell et Gardner, 1920a.

**Type Locality:** San Pedro.

**Type Specimens:** Holotype: UC 205622; collected Sept., 1908. Isotypes: UC 40287, AHFH 58852, 60403, US 57107, UW 64239.

**References:**

Setchell and Gardner, 1920a, p. 285-6, Plate 26, Fig. 1.
Setchell and Gardner, 1920b, p. 272-3, Plate 21, Fig. 1.
?Dawson, 1944, p. 201.
Dawson, 1945, p. 23.
Dawson, 1945b, p. 170.
?Chapman, 1956, p. 395, Fig. 39I.
?Dawson, 1959b, p. 6,11.
Papenfuss, 1960, p. 308.
Abbott and Hollenberg, 1976, p. 80, Fig. 37.

**Probable Synonym:**

**Ulva brevistipita** Chapman, 1956.

**Type Locality:** Midlittoral pool, Titahi Bay, New Zealand.

**Type Specimens:** Holotype: CANTY (Laing H. 4321); no collection date.
REFERENCES:

Chapman, 1956, p. 387, Fig. 30d.


TYPE LOCALITY: Surf-washed rocks, Chincha Islands, Peru.

TYPE SPECIMENS: Lectotype: NY (Coker no. 193); collected June 18, 1907. Syntypes: NY, UC 197872.

REFERENCES:

Howe, 1914, p. 20-2, Plate 1, Plate 2, Fig. 10-23 (as U. fasciata f. costata Howe).

Taylor, 1947, p. 60 (as U. fasciata f. costata).

Dawson, Acleto and Foldvik, 1964, p. 8-9, Plate 3 (as U. fasciata f. costata).

Hollenberg, 1971, p. 283, Fig. 1.

Abbott and Hollenberg, 1976, p. 80, Fig. 36.

DISTRIBUTION:

N.E. Pacific: Vancouver Island, British Columbia to southern Baja California, Mexico.

S.E. Pacific: Peru (as U. fasciata f. costata)?

S.W. Pacific: New Zealand.

REPRESENTATIVE SPECIMENS:

BRITISH COLUMBIA:

Port Harvey, E. Crancroft Island (50°33.5'N, 126°16.0'W), 11-IX-70, UBC 48805; Middle Point, Duncan Bay, Vancouver Isl. (50°05.3'N, 125°18.2'W), 10-IX-70, UBC 48803; Isl. S.E. of Grassy Isl., Kyuquot S., Vancouver Isl. (49°55.4'N, 127°15.0'W), 14-V-75, UBC 56998; Miracle Beach, Vancouver Isl. (49°51'N, 125°05'W), 16-IX-59, UBC
11445; E. side of Diana Isl., Barkley S. (48°50.03'N, 125°11.11W), 25-VII-75, UBC 58007 (U253); Brady's Beach, Barkley S., Vancouver Isl. (48°49.74'N, 125°09.9'W), 13-X-73, UBC 56999, 15-XI-74 57969 (U143a); Cable Beach, Barkley Sound (48°49.46'N, 125°09.4'W), 15-II-76, UBC 57976 (U268); Second Beach, Bamfield, Barkley S. (48°48.85'N, 125°09.7W), 10-VII-75, UBC 57975 (U246).

OREGON:
North Jetty, Yaquina Bay (approx. 44°39'N, 124°002'W), 6-I-66, OSU 25; Seal Rocks (44°29.5'N, 124°06.3'W), 10-VI-66, UBC 24958; Cape Perpetua (approx. 44°17'N, 124°07'W), 10-VI-68, OSU 1422; Fossil Point, Coos Bay (approx. 43°21'N, 124°21'W), 8-II-68, HP 2429.

CALIFORNIA:
Dillons Beach, Tomales Bay (approx. 38°14'N, 122°55'W), XI-15, UC 205625; Duxbury Reef, Bolinas (38°54'N, 122°42'W), IV-1896, UC 98494; Pescadero (37°15'N, 122°25'W), 7-XI-1891, DS 304423; Santa Cruz (36°58'N, 122°01'W), no date, US 54924; North Jetty, Moss Landing (approx. 36°48'N, 121°47'W), 14-VI-72, MLML 1104; Monterey (approx. 36°48'N, 122°01'W), 11-VI-01, UC 98493; Carmel Beach (approx 36°33'N, 121°55.9'W), 22-VII-39, GMS 7754; E. side of Loon Point, Santa Barbara Co. (approx. 34°25'N, 119°34'W), 19-XII-57, AHFH 67481; Carpinteria (34°23.5'N, 119°31.5'W), 26-IX-57; Ventura (34°16.7'N, 119°17'W), 28-VI-57, AHFH 66014; W. Malibu (approx. 34°03'N, 118°57'W), IX-08, UC 305622; S. of Point Fermin, San Pedro (33°42.35'N, 118°17.10'W), 24-VIII-77, UBC 58040, (U339); San Nicolas Isl. (33°15'N, 119°30'W), 13-III-32, UC 633413; La Jolla (approx. 32°51'N, 117°10'W), 1-VI-46, US 38995; Coronado (approx. 32°42'N, 117°12'W), VIII-03, US 34586.

BAJA CALIFORNIA:
Punta Descanso (approx. 32°16'N), 30-XI-63, AHFH 78432, 8-IV-45, UC
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694036; Bahia de Todos Santos, Ensenada (approx. 31°48'N, 116°42'W), 29-X-51, US 41727, VII-24, UC 395360; Rio San Telmo Reef (approx. 30°57'N, 116°15'W), 12-III-45, UC 693937; near Punta Maria (28°55'N, 114°32'W), 14-IV-46, US 39015; Isla Cedros (approx. 28°12'N, 115°15'W), 19-IV-51, UC 940035; Bahia Tortuga (approx. 27°39'N, 114°51'W), 26-VII-57; Punta Abreojos (approx. 26°42'N, 113°30'W), 30-IV-50, AHFH 54523; San Roque (approx. 25°36'N, 100°09'W), VII-1899, UC 98506.

PERU:
Playas de Barranco, 18-IX-48, M 61522; Pucusans, 9-IV-63, AHFH 75447; Chincha Islands (approx. 11.27'S, 79.05'W), 18-VI-07, NY (Coker no. 193), UC 197872.

NEW ZEALAND:
Eastbourne, Port Nicholoson (approx. 41°17'S, 174°54'E), 17-VIII-58, UW 244317; Lyall Bay (approx. 41°19'S, 174°48'E), 06-V-?, VJC 1137; The Bluff, Ninety Mile Beach (approx. 34°41'S, 172°55'E), 16-I-41, AKU 010002; Titahi Bay (approx. 41°06'S, 174°50'E), no date, CANTY (Laing H. 4321); St. Clair, 13-I-33, CANTY (Laing Herb. 4322).
8. **Chloropelta caespitosa** gen. et sp. nov. ined.

**TYPE LOCALITY:** Forming densely tufted mats on boulders, cement blocks and kelp stipes in the upper intertidal zone, Point Fermin, San Pedro.

**TYPE MATERIAL:** Holotype: UBC 57963; collected May 26, 1976. Iso-
types: UBC 57965, 1101.

**DISTRIBUTION**

N.E. Pacific: Los Angeles to Pacific Beach, California.

**REPRESENTATIVE SPECIMENS:**

Sunset Blvd., Los Angeles (34°02.2'N, 118°34.45'W), 15-XI-56, AHFH 63176; Point Fermin, San Pedro (33°42.35'N, 118°17.10'W), 26-V-76; UBC 57963, 57965, 1108¹ (U286), 24-VIII-77, UBC 57964 (U338); Laguna Beach (33°32'N, 117°46'W), 26-V-76, UBC 57967, 57968 (U290); Bird Rock, La Jolla (32°48.9'N, 117°16.4'W), 25-II-57, AHFH 64802; Tourmaline Surfer Park, Pacific Beach (32°48.1'N, 117°15.6'W), 27-V-76, UBC 57966.

**Chloropelta**

Thallus at maturity a membranous peltate distromatic blade attached by a central rhizoidal disk; quadriflagellated and biflagellated reproductive swarmers produced in cells along the blade margins; reproductive cells germinate into uniseriate filaments that later develop into multiseriate germlings by repeated longitudinal divisions perpendicular to the surface of the filament; separation of the cells along the longitudinal axis lead to the development of a clavate monostromatic saccate germling; a division of each cell of the monostromatic cell layer in a plane parallel to the germling surface produces a distromatic saccate germling; degeneration of the apical end produces ¹preserved in 70% alcohol.
at first a campanulate thallus; continued growth of the thallus results in a flattened peltate blade.

**Chloropelta caespitosa**

Thalli orbicular or ovate, peltate or split to the base; planar or ruffled along the margins; forming dense tufts or tufted turfs; plants from a few mm to 60 mm or more in diameter; cells in surface view angular, irregular, randomly arranged, between 4 and 29 μm across; rhizoidal cells near attachment disk loosely arranged; blade from 17 μm thick at the margins to 95 μm or more near the base, mostly around 30-35 μm thick; cells in sectional view nearly isodiametric, usually wider than tall near the margin and taller than wide near the center; 1-2 or rarely 3 pyrenoids in the single parietal chloroplast of each cell; grass green in color.
VII. SUMMARY

Results of studies on the taxonomy and morphological variation of distromatic ulvaceous algae from the northeast Pacific are summarized below:

1. Six species of Ulva (U. californica, U. fasciata, U. fenestrata, U. rigida, U. stenophylla, U. taeniata) are recognized for the northeast Pacific using morphological, developmental and anatomical criteria. One of these species, U. fasciata, was not previously recognized for this area. The validity of a seventh species, U. conglobata, remains unclear. Six of the previously recognized taxa (U. angusta, U. costata, U. dactylifera, U. expansa, U. fasciata f. lobata, U. scagelii) are reduced to synonyms of other species, and another species, U. lactuca, is thought not to occur on this coast.

2. Some morphological and anatomical characteristics previously used to separate species were found to vary with environmental factors.

   a. Development and morphology in Ulva californica varied with temperature. This has resulted in the previous placement of northern specimens into U. scagelii (Chihara, 1968).

   b. In U. taeniata the number and length of teeth decrease and the blade thickness increases with an increase of water temperature. Non-dentate specimens south of Point Conception were previously identified as U. angusta, U. costata or U. dactylifera. In Barkley Sound U. taeniata showed considerable seasonal variation in size and morphology.

   c. Size, shape and thickness of thalli in U. fenestrata varied with vertical position, wave exposure and time of year. The range in morphology and anatomy of this species included the criteria pre-
viously used to delimit *U. expansa* and *U. lobata*.

3. An unusual form of reproduction was observed for *Ulva fasciata* from Hawaii similar to that reported for *U. lactuca* by Bonneau (1978). Aplanospores developed into a floating multicellular stage that eventually released biflagellated swarmers. The globose stage, if produced in nature, would greatly increase the species' potential for dispersal.

4. A new genus and species of distromatic ulvaceous algae were described from the northeast Pacific. *Chloropelta caespitosa*, when mature, closely resembles *Ulva*. However, the developmental pattern is distinctly different and places this alga closer to *Ulvaria*. 


Bryhni, E. 1974. Genetic control of morphogenesis in the multicellular


Kützing, F. T. 1849. Species algarum... vi+922 PP. Leipzig.


Survey of macrophyte resources of the coastal waters of Alaska. Institute of Marine Science, University of Alaska, Fairbanks, IMS R71-6, 40 pp.


Postels, A. & F. Ruprecht. 1840. Illustrationes algarum in itinere circa orbem... St. Petersburg. iv+22 pp., 40 pls.


