NOAA Technical Memorandum OMPA-4

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Completion Report Submitted to
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by

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Bellingham, Washington

## DISCLAIMER

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ABSTRACT

A literature search on growth rates of benthic algae and invertebrates in Puget Sound showed relatively little is known about growth and productivity. Field studies were initiated to examine growth in populations of intertidal and subtidal *Laminaria saccharina* and subtidal *Nereocystis luetkeana* from Shannon Point, Puget Sound. Based on the movement of holes punched 10 cm from the stipe, maximum growth rates of *L. saccharina* were observed during May and June (approximately 100 g wet wt. biomass per day). Evidence indicated growth also occurred beyond 10 cm from the stipe and that values must be considered conservative.

Stipes of *N. luetkeana* started growth late in April. Stipe growth was most rapid in May and June (8-9 cm per day), and decreased through to September. Biomass production in August and September was approximately 250 g wet weight per day.

# 1. INTRODUCTION

From 1972 to 1979 several extensive studies on the structure of intertidal and shallow subtidal benthic communities of the Puget Sound region have been made (Battelle Northwest, 1974, DOE 1978, MESA 1978). These studies have been primarily motivated by the potential of oil spills, and have emphasized species occurrences, numbers of individuals and biomass. In order to evaluate the sensitivity of these benthic communities to serious environmental disruption, such as an oil spill, their functional characteristics also need to be described. One of the most important functional characteristics of these communities is the flow of energy (productivity) through trophic levels. Growth and growth rates are important components of the analysis of productivity.

To evaluate the knowledge on growth and growth rates of benthic communities in Puget Sound a literature search of growth in algae, marine plants, and invertebrates was conducted. As well, field studies on growth in *Laminaria* and *Nereocystis* were initiated. As is evident in the results, the literature search showed relatively little is known of growth and productivity of either benthic algae or invertebrates. In many cases only estimates of longevity of animal species was available. In only a few cases were annual productivity rates determined.

Two important and convenient algae species in the benthic communities of Puget Sound are *Nereocystis luetkeana* and *Laminaria saccharina*. *N. luetkeana* is convenient because, since it is an annual, estimate of annual productivity can be made by determining maximum standing crop. *Nereocystis* has been conservatively estimated (Rigg, 1915) to have a maximum standing crop in Puget Sound of 390,000 tons (this area included U.S. waters of the Strait of Juan de Fuca and San Juan Islands).

In this study stipe elongation of *N. luetkeana* was followed at a site in Puget Sound (Shannon Point) from May to September 1978 and February to May 1979. Blade elongation was followed for a short period in August and September 1978.

*Laminaria* is a convenient genus to evaluate growth rate because the meristematic area between stipe and frond is responsible for the majority of growth (Parke, 1948). Parke showed the greatest rate of growth in *L. saccharina* was in the proximal 25 cm of the frond. Mann (1973) followed growth in a closely related species (*L. longicruris*) by following the migration of holes punched just distally (10 cm) of the meristematic tissue.

In this study growth of *L. saccharina* was followed in an intertidal and subtidal area of Puget Sound from May 1978 to June 1979.

## 2. METHODS

### 2.1 Literature Search

A number of literature sources were examined, including: Beak, 1975 - Oil Pollution and the Significant Biological Resources of Puget Sound; Collias and Andreeva, 1977 - Puget Sound Marine Environment, An Annotated Bibliography; The Oceanographic Institute, 1975-78 - Compendium of Current Environmental Studies in Puget Sound and Northwest Estuarine Waters; DOE, 1977 - Washington Coastal Areas of Major Biological Significance.

As well, a computer search for data on growth rates of invertebrates and algae in Puget Sound was made from the following sources: NTIS, Biological Abstracts, Oceanic Abstracts, Sci-Search, and Aquatic Science and Fisheries Abstracts.

Finally, individuals in academic institutions and state agencies were contacted for growth data.

### 2.2 Field Studies

#### 2.2.1 Study Area and Tagging

The study area was just easterly of Shannon Point (Fig. 1). Algae in two areas were examined: A group of intertidal *L. saccharina*; and a group of *L. saccharina* located at approximately 3-5 m depth below mean low water.

Algae were tagged with numbered plastic tags obtained from Hewitt Plastic Co. Tags were initially attached to the algae by stainless steel wire. However, with time, the wire tended to abrade the tissue of the plant. In an attempt to increase tag visibility and to keep the tag from the holdfast area, tags were attached to styrofoam balls (10-15 cm diameter). However, the effect of the current on the balls resulted in unacceptable abrasion to algae tissue. Finally plastic clips were used to attach tags to the algae. No damage was noted using this method.

#### 2.2.2 Laminaria Growth Studies

The method used to estimate growth rates was that described in Mann (1972). Holes were punched just distally of the meristematic region (10 cm) and the rate of migration was determined by periodic observation.

*Intertidal L. saccharina*. In May 1978, 30 algae were tagged, holes (approximately 5 mm diameter) were punched 10 cm from the stipe, and blade width at 10 cm recorded. Algae were checked every two weeks. Distance of the hole migration, and width at 10 cm were noted. New holes were punched as necessary. This experiment was terminated on July 5, 1979, because the *L. saccharina* were dead or badly damaged because of excessive exposure due to daytime low tides. At each observation period, when tagged algae could not be located, new plants were tagged to keep sample size at 10 or more algae.

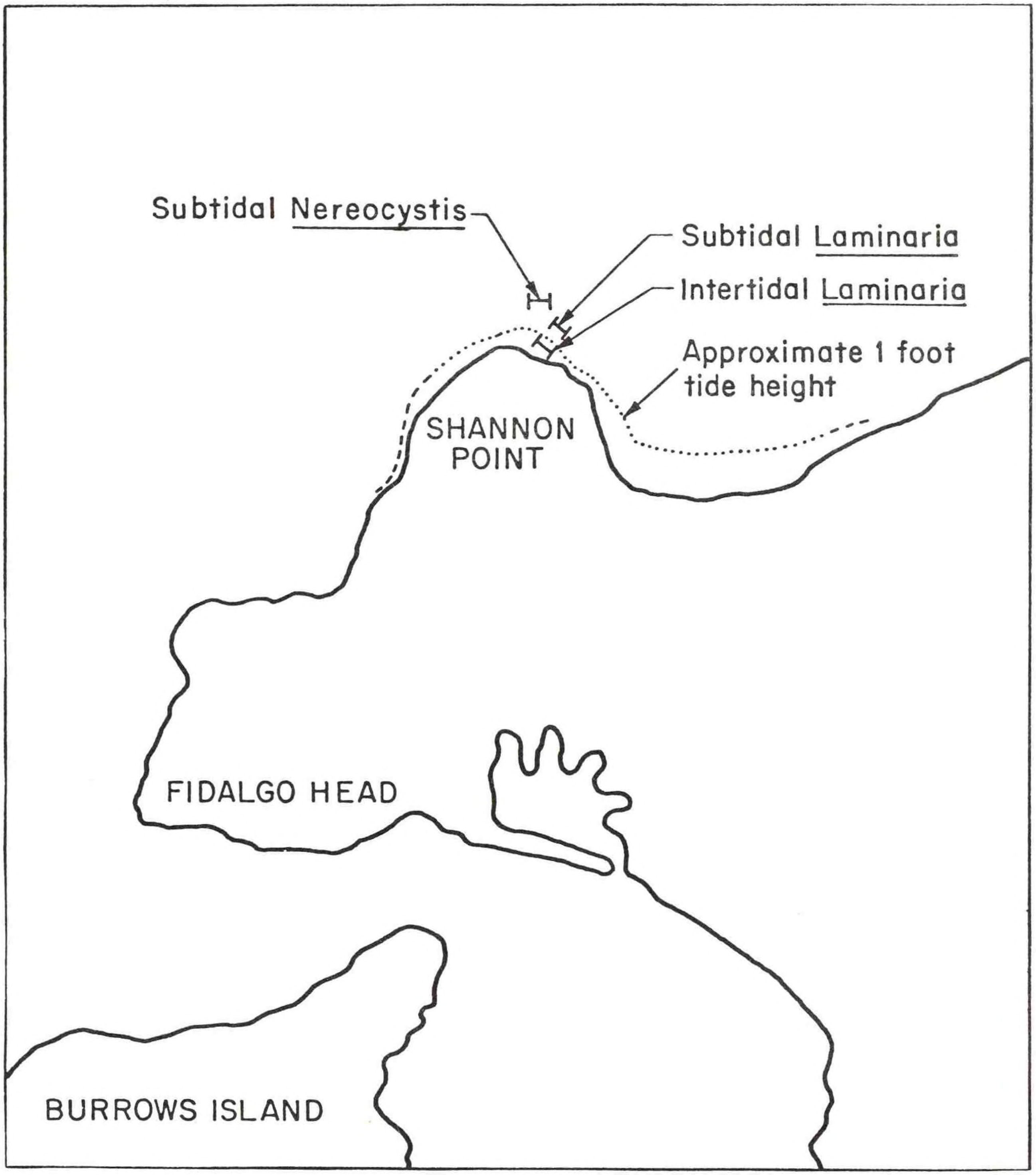


Figure 1. Location of Nereocystis and Laminaria sample sites.

Subtidal L. saccharina. In June 1968, a 50 m transect line was located at the 3 to 5 m depth (below 0.0 tide). Approximately 50 algae adjacent to the line were tagged. At each observation period, the migration of the hole and blade width at 10 cm from the stipe were taken. New holes were punched as necessary. At some observation times (November 1978 to April 1979) blade length was also recorded. The experiment was terminated June 1979.

### 2.2.3 Calculations

Wet Weight Correlations. In April 1978, 29 *L. saccharina* of all size classes were collected and the length, width at 10 cm, and wet weight recorded. In May 1979 the procedure was repeated with 30 *L. saccharina*. Various correlations of measurements to wet weight were made (Table 1). Linear regression between wet weight and each of length, width at 10 cm, and area ($cm^2$) gave acceptable correlation, but the intercept was unacceptable. However, a power curve ($y = ax^b$) where y was wet weight and x was length gave an acceptable correlation and an intercept near zero (Table 1).

Estimation of Biomass. The best correlation between wet weight and size was the power curve relationship between wet weight and length (Table 2). To estimate biomass accumulation for those observation periods in which algae lengths were available, the increase in length (by hole migration) was added to the initial length to calculate the final length. This method avoids the problem of erosion of the ends of the frond lowering biomass values.

### 2.2.4 Nereocystis Growth Studies

In June 1979 a 50 m transect line was located at 5 m depth (Fig. 1). Approximately 40 algae were tagged (see tagging). Stipe length was measured every two weeks until September 1978.

In August 1978, 14 *N. luetkeana* were tagged at the surface from a boat, and a hole (approximately 5 mm diameter) was punched at 10 cm from the bulb. Hole migration was followed until September 8, 1978. After this time recurring storms removed many *N. luetkeana* from the study site, making consecutive observations impossible. Further tagging was not attempted because of lack of algae.

Correlations of size measurements with wet weight of the total algae were conducted in May 1978 (25 algae) and August 1978 (22 algae). Stipe length, mean frond length, and wet weight were recorded. Linear regressions of mean length, and total length vs. wet weight gave unacceptable correlation coefficients (Table 2). The power curve ($y = ax^b$) was fitted to mean blade length vs. wet weight. A correlation coefficient of 0.97 with intercept of 0.03 was obtained.

Table 1. Regression of size measurements on wet weights for *Laminaria saccharina*. Twenty-nine algae were collected April 1978; 30 algae were collected in March 1979. The power curve ($y = ax^b$) was fitted on the length vs. wet weight of both groups of algae combined.

| | | | |
|---|---|---|---|
| I. April 1978 (n = 29) | | | |
| width (10 cm) vs. wet wt: | weight = | -4.1 + 4.6 width, | $r^2 = 0.79$ |
| length vs. wet wt: | weight = | -237.5 + 4.8 width, | $r^2 = 0.78$ |
| area vs. wet wt: | weight = | -46.8 + 0.16 area, | $r^2 = 0.87$ |
| II. March 1969 (n = 30) | | | |
| width (10 cm) vs. wet wt: | weight = | -139.2 + 18.4 width, | $r^2 = 0.69$ |
| length vs. wet wt: | weight = | -54.2 + 2.4 length, | $r^2 = 0.79$ |
| area vs. wet wt: | weight = | -63.9 + 0.2 area, | $r^2 = 0.90$ |
| III. Power Curve (n = 59) | | | |
| length vs. wet wt: | weight = | 0.03 length (1.86), | $r^2 = 0.90$ |

Table 2. Regression of size measurements on wet weight for *Nereocystis luetkeana*. Twenty-five algae were collected in May 1978 and 22 in August 1978. Both groups were combined.

I. Linear Regressions

Total blade length vs. wet weight:

Weight = -10.9 + 0.33 total length, $r^2 = 0.90$

Mean blade length vs. wet weight:

Weight = -1,342.4 + 19.1 length, $r^2 = 0.90$

II. Power Curve

Mean blade length vs. weight:

Weight = 0.02 length (2.1), $r^2 = 0.97$

## 3. RESULTS

### 3.1 Literature Review

#### 3.1.1 Brown Algae

a. Laminaria. Growth data for Laminaria are treated in the discussion section of this report (4.2).

b. Nereocystis. Growth of the sporophyte of this annual algae begins in early spring. Stipe growth is rapid with the following rate reported for N. luetkeana in Puget Sound: Frye (1906) - 10 inches per day; Hartge (1928) - 1 inch per day; Sheldon (1915) - 1 inch per day; and Scagel (1947) - 6 cm per day. For the California coast, Nicholson (1970) reported a rate of up to 6 cm per day for immature algae.

Once the stipe reaches the surface, its growth slows or ceases altogether (Nicholson, 1970). Hurd (1916) reported that the elongation of the stipe was more rapid for N. luetkeana in deeper water than those in shallower water.

Light has been found to be the most important factor in sporophyte growth (Vadas, 1972) although temperature also showed an effect. For algae from 0-20 m below low tide, growth was greatest at 15°C for the first three weeks of sporophyte development. After 6.5 weeks sporophyte growth was maximum at 10°C.

Field measurements of growth of fronds of N. luetkeana has been reported by Fallis (1915). Growth was maximum in the proximal two inches of the frond from the stipe. Fallis reported frond growth of 1.5 to 2 inches per day during the summer.

Since Nereocystis is an annual, estimates of annual production can be made by determining maximum standing crop. Rigg (1915) estimated that in late summer Puget Sound, the San Juan Archipelago, the Strait of Juan de Fuca and that part of the Strait of Georgia in U.S. waters had a maximum standing crop of 390,000 tons. Rigg cautioned that in his view the estimate was conservative.

More recent data on standing crop of N. luetkeana are available from the coast of British Columbia. Coon and Field (1976) report part of the results of an inventory program for British Columbia coastal waters. Data are area specific. As an example, densities of 3.1 kg/m$^2$ biomass density were given for kelp beds in Nootka Sound.

#### 3.1.2 Red Algae

a. Gigartina. Chan (1972) reported that the growth of Gigartina exasperata in San Francisco began in spring and that at 15°C three months were required to produce upright blades from carpospores. For G. papillata, Chan (1972) reported that growth also began in spring months.

For G. stellata from New Hampshire, Burns and Mathieson (1972) reported growth to begin in the period of February to May, with maximum biomass produced in August and September. Most rapid growth occurred with increasing summer temperatures. No data are reported for Puget Sound.

b. Iridaea. Fralick (1971) found the optimal growing season of Iridaea cordata in the Puget Sound region to be from March to September with a peak in August. Optimal growth occurred at a depth of -3 m below MLLW. In tank culture at 14-15°C, 40 kg of wet weight, I. cordata were produced in a 140 day period (Waalund, 1974).

In a study in Strait of Georgia waters, Austin et al. (1973) found a biomass of 170,000 kg along a 30 mile stretch of beach on the eastern shore of Vancouver Island (Kye Bay).

The standing crop of I. cordata in the Puget Sound region is not adequate to support a commercial harvest and culture procedures have been developed by the Washington State Department of Natural Resources (Mumford, 1977, 1978). Using these culture procedures, Mumford (1978) reports annual standing crop yields of between 1435 and 4920 g dry matter/$m^2$.

### 3.1.3 Angiosperms

a. Zostera. Zostera marina is estimated to cover about 9% of the bottom of Puget Sound or some $4.5 \times 10^8$ $m^2$ (Phillips, 1974). Phillips also found that seeds germinated in June while new turions and leaves started growth in February. Annual production was estimated by doubling the maximum standing crop (found from June to September). Phillips (1974) calculated that eelgrass beds fixed 1.5 g carbon/$m^2$/growing season day (15 hrs.) resulting in an annual production of 187-1078 g/$m^2$. Phillips also estimated that the annual production of Z. marina was $4.8 \times 10^5$ metric tons for all of the Puget Sound region.

### 3.1.4 Invertebrates

a. Polychaetes

1. NEREIS. Moore et al. (1974) reported for N. vexillosa from the North Pacific, a life span of four years with sexual maturity reached during the third year.

2. PECTINARIA. This genus is most commonly found in Puget Sound at depths greater than 100 m (Nichols, 1975). Nichols described a mean life span of six years. Nichols also reported an annual production of 1.4 to 1.8 g/c/$m^2$ for Pectinaria. Growth rates at various stations differed.

b. Bivalves

1. CRASSOSTREA. Chew (1961) found that growth in Crassostrea gigas slowed or stopped below 10°C. Growth began when water temperature reached 12°C. Growth was maximum in periods of highest temperature.

2. CLINOCARDIUM. C. nuttali has a life span of 5 to 7 years (Houghton, 1973; Qualye and Bourne, 1972).

3. MACOMA. Juvenile M. nasuta held 30 days under laboratory conditions

showed 24.1 mm increase in shell length (Hylleberg and Gallucci, 1975). Under field conditions, Gallucci and Hylleberg (1976) found greater growth of M. nasuta in "closed" areas compared to "open" areas of Garrison Bay, San Juan Island. "Open" areas were characterized by coarse sediment while "closed" areas were fine silt and clay. Average changes in shell length at the two sites over a 40 day period were:

| | Small size | Medium size | Large size |
|---|---|---|---|
| "closed" area | 4.1 cm | 0.4 cm | 0.15 cm |
| "open" area | 2.7 cm | 0.7 cm | 0.60 cm |

4. MYA. Houghton (1973) reported a life span of 8-9 years for M. arenaria while Moore et al. (1974) reported a life span of 7 years. Swan (1952) found that the M. arenaria grew 1.5 times faster in sand than in a mud/gravel/shell mixture. Animals from the sand had shells that were lighter in weight than those from a mud/gravel/shell mixture.

5. MYTILUS. Houghton (1973) reported a life span for M. edulis of 8 years. Moore et al. (1974) reported a life span of 4 years. For M. californianus Dayton (1970) found that mussels exposed to wave agitation grew faster than those in quiet waters.

6. PANOPE. P. generosa (the geoduck) is long lived with a life span in excess of 10 years, with males spawning after three, and females after four years (Anderson, 1971). Growth is relatively rapid for the first few years with clams adding approximately 30 mm shell length per year (Goodwin, 1973).

Anderson (1971) reported that clams at the end of their first year averaged 10 g, at their third year 300 g, and at the end of ten years, 1.6 kg. These data are similar to those of Goodwin (1973) who found it took 8 years for the first 10 cm of shell length (450 g weight) and by 10 years clams weighed around 900 g. Goodwin also noted that once 10 cm size was reached growth ceased or was very much reduced.

7. PROTOTHACA. Qualye and Bourne (1972) reported the life span of P. staminea as 10 years. Houghton (1973) reported 12 years. In an examination of growth of P. staminea at Kiket Island, Houghton (1973) found that there was increased growth at lower tide levels and that the growth rate was lower on the south side of the island than on the north. On the south side there was a standing crop of around 20 g/0.25 $m^2$ with an annual productivity of 4.3 g/0.25 $m^2$/yr. On the north side there was a standing crop of around 250 g/0.25 $m^2$ and an annual productivity of 45.6 g/0.25 $m^2$/yr. Values varied according to tide height.

8. SAXIDOMUS. Houghton (1973) reported a life span for S. giganteus of 13 years with reproductive maturity at 3-5 years. An annual productivity of 29 g/$m^2$/yr. was found for areas with a standing crop of 270 g/$m^2$.

9. TRESUS. T. capex has a life span in excess of 15 years (Bourne and Smith, 1971). The authors also reported the size (shell length) of these clams for various ages: 1 year, 28 mm; 3 yrs., 70 mm; 5 yrs., 100 mm (175 g), 7 yrs., 116 mm; 9 yrs., 125 mm; 11 yrs., 130 mm (420 g); 13 yrs., 143 mm; 15 yrs., 150 mm. Sexual maturity was reported to occur at 3 years of age.

10. VENERUPIS. The introduced V. japonica was reported by Houghton (1973) to have a generally higher rate of growth than the native P. staminea when the two species were found together (Houghton, 1973). Nosho and Chew (1971) reported the following growth data (shell length) for V. japonica: 1 yr., 24 mm; 2 yrs., 36 mm; 3 yrs., 40 mm; and 4 yrs., 44 mm. The authors also reported that most of the growth occurred in the summer and early fall.

c. Gastropods

1. HALIOTIS. The abalone H. kamtschatkana grows slowly. Mollet (1978) reported a minimum of four years to reach a shell length of 10 cm. Qualye (1971) gave shell length data for H. kamtschatkana from 1 to 10 years: 1 yr., 2.0 cm; 2 yrs., 3.5 cm; 3 yrs., 6.0 cm; 4 yrs., 6.8 cm; 5 yrs., 8.2 cm; 6 yrs., 9.0 cm; 7 yrs., 9.8 cm; 8 yrs., 10.5 cm; 9 yrs., 11.0 cm; 10 yrs., 11.5 cm. The first spawning was reported to occur in the third year.

d. Cephalopods

1. LOLIGO. Trumble (1973) reported a life span of 3 years for squid from the Northeastern Pacific Ocean.

e. Crustaceans

1. CANCER. The Dungeness crab C. magister, has a maximum age of 10 years with a probable life span of 8 years (MacKay, 1942). MacKay also noted that sexual maturity is reached by the female in the fourth year, although Prentice (1971) reported that females matured in the second year. The relationship between carapace width and age (MacKay, 1942) is given in Fig. 2.

Butler (1961) for C. magister from British Columbia gave the following age versus carapace width data for males: 1 yr., 24 to 31 mm; 2 yrs., 97 to 119 mm; 3 yrs., 147 mm; 4 yrs., 176 mm; 5 yrs., 207 mm. Growth in females for the first two years was similar to that of males. After two years, however, growth was slower.

Mayer (1973) found that the growth rate for C. magister around Kiket Island and Similik Bay was less than described for C. magister off the west coast of Washington State.

2. ORCHESTIA. Moore et al. (1974) reported a life span of less than one year for O. traskiana from the North Pacific.

3. PANDALUS. Dahlstrom (1970) gave a life span of 2-4 years for P. jordani. Butler (1970) gave a life span of 4 years for P. platyceros. For P. hypsinotus Butler (1964) reported that shrimp at 1.5 years were 124 mm in length and 10.2 gm. At 3 years length was 130 mm and weight 12.7 gm.

f. Echinoderms

1. DENDRASTER. Birkland and Chia (1971) reported 9 years as the maximum age of the sand dollar, D. exertricus. Growth was steady until the fifth year (8-9 cm test length). After the fifth year growth was much reduced. The authors reported a substrate effect on growth. At Alki beach (Seattle) growth

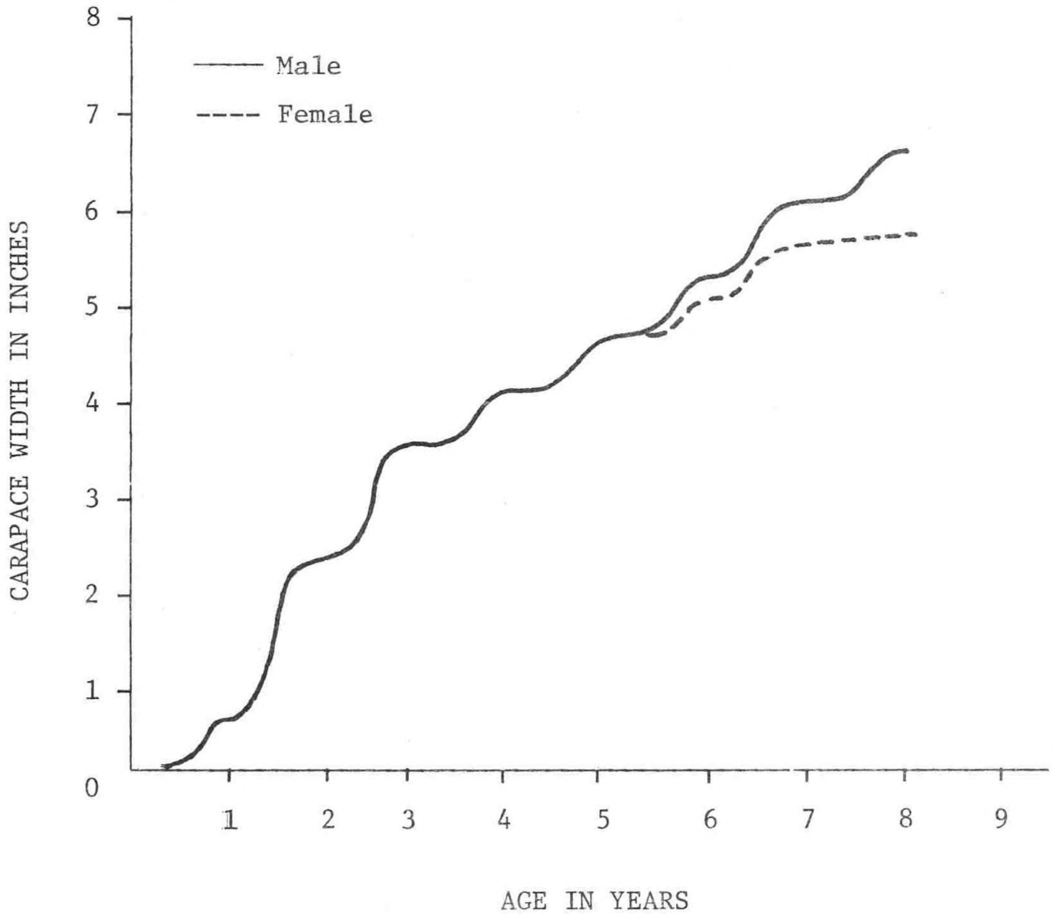


Figure 2. Carapace width (inches) and age of the Dungeness crab Cancer magister. (MacKay, 1942)

in those areas that were sandy was more rapid in young and slower in adults than in those areas that had sand between cobbles and clay 2-10 cm below the surface.

2. MEDIASTER. Birkland et al. (1971) reported four years to sexual maturity for the sea star, *M. aegualis*. In field conditions a growth of 2 mm per month was noted from November to January while 0.5 mm growth per month was noted from September to March. Under laboratory conditions growth of 0.3 to 0.4 mm per month was noted. For adult *M. aegualis* (12-14 cm size) growth under field conditions was found to be 0.7 to 1.1 mm per month.

3. STRONGYLOCENTROTUS. Moore et al. (1974) reported a life span of 4 years for the urchin *S. drobachiensis*.

g. Brachiopods

1. TERREBRATALIA. Paine (1969) reported a maximum age of 9-10 years for the lampshell *T. transversa*. Animals of 5 years of age averaged 43 mm in width.

## 3.2 Field Studies of Laminaria and Nereocystis

### 3.2.1 Intertidal Laminaria saccarina; Frond Elongation

Data on length of migration of punched holes and frond width at 10 cm are given in Table 3. A graph of the mean daily hole migration is shown in Fig. 3. There was little change in the first two weeks of June with mean hole migration of around 1.2 cm per day. In the latter two weeks the daily hole migration dropped markedly to around 0.5 cm per day. After the end of June no algae were available to continue the experiment. It is tempting to attribute this decrease in daily hole migration to the "summer burn off" that reduces intertidal algae during summer months. However, Fig. 3 shows that subtidal algae also showed a sharp decrease in daily distance of hole migration during this time.

### 3.2.2 Subtidal Laminaria saccharina; Frond Elongation

Data on migration of punched holes and width at 10 cm for subtidal *L. saccharina* are given in Table 4. The mean daily hole migration is shown in Fig. 3. A distinct seasonal pattern of hole migration is evident. Migration of around 1 cm per day was noted at the beginning of July. Daily elongation steadily decreased through to October to a low of less than 0.05 cm per day. Low values were observed until early January when daily elongation started to increase. Maximum daily elongation was noted in March with values of around 2.5 cm per day elongation.

### 3.2.3 Calculation of Increase in Area for L. saccharina

Conservative estimates of daily increase in area for intertidal and subtidal *L. saccharina* are given in Tables 3 and 4 and Fig. 4. Data are similar to those in Fig. 3, that is for subtidal *L. saccharina* the daily increase in area decreases from June through December. Starting in January there is a rapid rise in the daily increase in areas that peak in May. Standard deviations (Fig. 4) show that these seasonal changes are significant ($p = 0.05$).

Table 3. Summary of data for intertidal <u>L. saccharina</u>. Data for individual algae are given in Appendix 1. Area was calculated by using elongation and width at a point 10 cm from the stipe. S is the standard deviation.

| | May 25-June 7 | June 7-June 21 | June 21-July 5 |
|---|---|---|---|
| n | 12 | 13 | 6 |
| mean width | 15.2 | 15.4 | 16.5 |
| mean hole migration | 15.4 | 17.0 | 7.7 |
| mean area | 224.8 | 256.5 | 199.3 |
| no. of days | 13 | 14 | 14 |
| mean elongation/day (cm) | 1.2 | 1.2 | 0.6 |
| S | 0.7 | 0.7 | 0.4 |
| mean area/day ($cm^2$) | 17.4 | 18.6 | 14.2 |
| S | 9.5 | 9.0 | 5.8 |

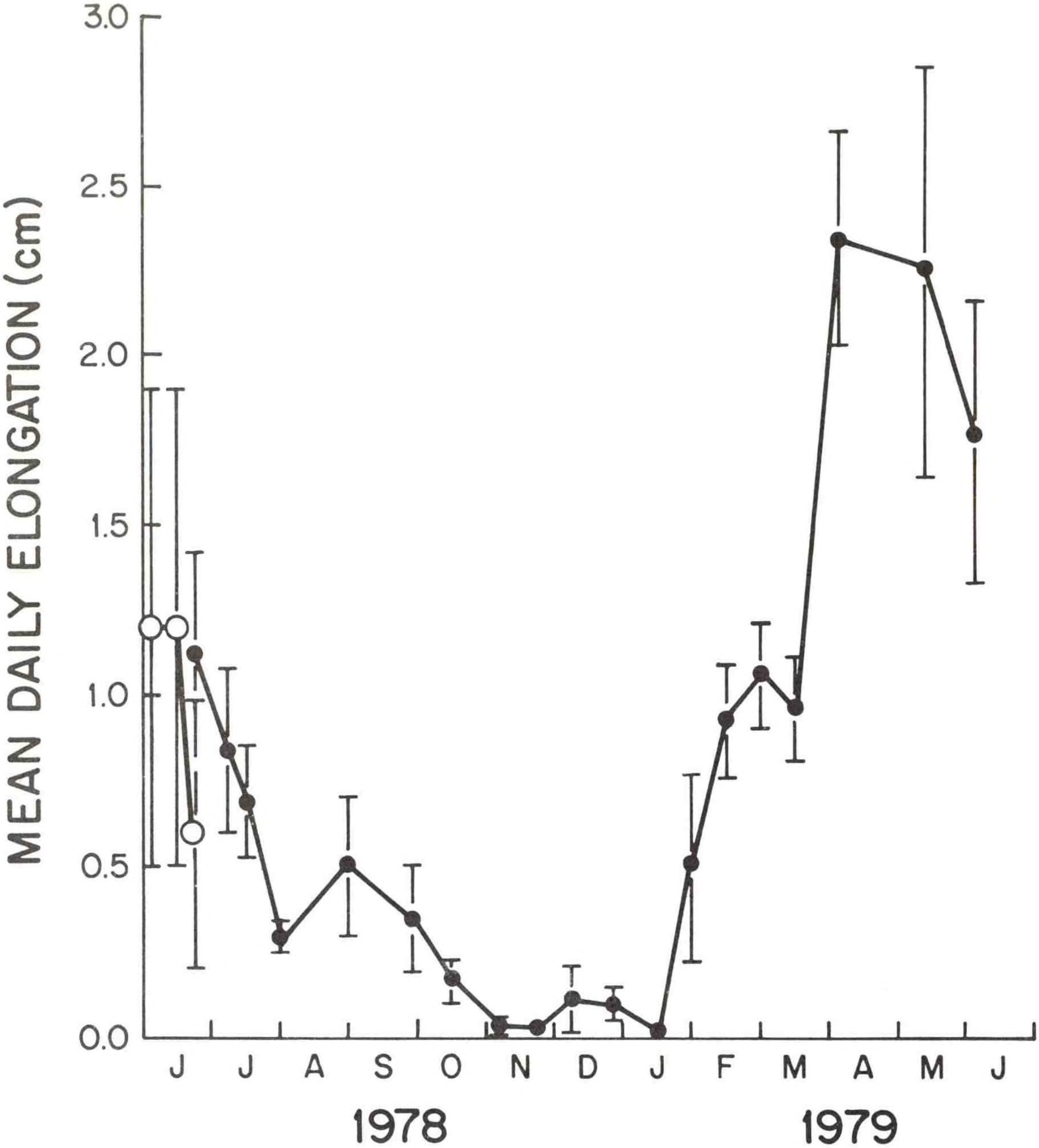


Figure 3. Mean daily hole migration of intertidal and subtidal Laminaria saccharina. Open circles are intertidal L. saccharina. Closed circles are subtidal L. saccharina.

Table 4. Summary of data for subtidal *L. saccharina*. Data for individual algae are given in Appendix 2. Area was calculated by using elongation and width at a point 10 cm from stipe.

| | June 16–June 28 | June 28–July 7 | July 7–July 19 | July 19–Aug. 16 | Aug.30–Sept.20 | Sept.20–Oct. 6 | Oct.6–Oct.27 | Oct.27–Nov.14 | Nov.14–Dec. 1 | Dec. 1–Dec. 15 |
|---|---|---|---|---|---|---|---|---|---|---|
| n | 22 | 10 | 30 | 31 | 19 | 18 | 19 | 24 | 19 | 15 |
| mean width | 22.8 | 26.0 | 21.0 | 21.6 | 17.0 | 16.4 | 14.9 | 16.3 | 15.0 | 14.9 |
| mean elongation | 13.4 | 7.6 | 13.0 | 7.9 | 10.6 | 5.2 | 3.5 | 0.5 | 0.53 | 1.6 |
| mean area | 294 | 185 | 162 | 181 | 163 | 69 | 49 | 6.2 | 5.4 | 17.6 |
| # of days | 12 | 9 | 12 | 28 | 21 | 16 | 21 | 18 | 17 | 14 |
| elongation/day | 1.12 | 0.84 | 0.68 | 0.29 | 0.51 | 0.35 | 0.17 | 0.03 | 0.04 | 0.12 |
| std. deviation | 0.62 | 0.43 | 0.35 | 0.14 | 0.38 | 0.30 | 0.13 | 0.06 | 0.06 | 0.20 |
| area/day | 24.5 | 20.5 | 13.5 | 6.4 | 5.9 | 4.8 | 2.6 | 0.4 | 0.4 | 1.5 |
| std. deviation | 15.8 | 9.3 | 7.2 | 3.7 | 4.0 | 3.7 | 1.8 | 0.8 | 0.6 | 1.7 |

| | Dec.15–Jan.6 | Jan.6–Jan.25 | Jan.25–Feb. 8 | Feb. 8–Feb.24 | Feb.24–Mar. 8 | Mar. 8–Mar.26 | Mar.26–April 7 | Apr.7–May 20 | May 20–June 7 |
|---|---|---|---|---|---|---|---|---|---|
| n | 11 | 7 | 17 | 17 | 17 | 20 | 20 | 16 | 15 |
| mean width | - | 11.6 | 12.1 | 13.4 | 14.6 | 20.1 | 18.4 | 22.7 | 20.7 |
| mean elongation | 2.2 | 0.43 | 7.2 | 14.9 | 12.8 | 17.5 | 28.0 | 96.0 | 31.9 |
| mean area | - | 4.43 | 88.5 | 206.5 | 194.9 | 345.9 | 510.5 | 2,098.6 | 670.9 |
| # of days | 22 | 19 | 14 | 16 | 12 | 18 | 12 | 43 | 18 |
| elongation/day | 0.10 | 0.02 | 0.51 | 0.93 | 1.06 | 0.97 | 2.33 | 2.25 | 1.77 |
| std. deviation | 0.09 | 0.03 | 0.27 | 0.28 | 0.30 | 0.32 | 0.62 | 1.20 | 0.44 |
| area/day | - | 0.2 | 6.3 | 12.9 | 16.2 | 19.2 | 42.5 | 48.8 | 37.3 |
| std. deviation | - | 0.3 | 3.8 | 5.8 | 6.7 | 6.7 | 15.8 | 24.5 | 12.7 |

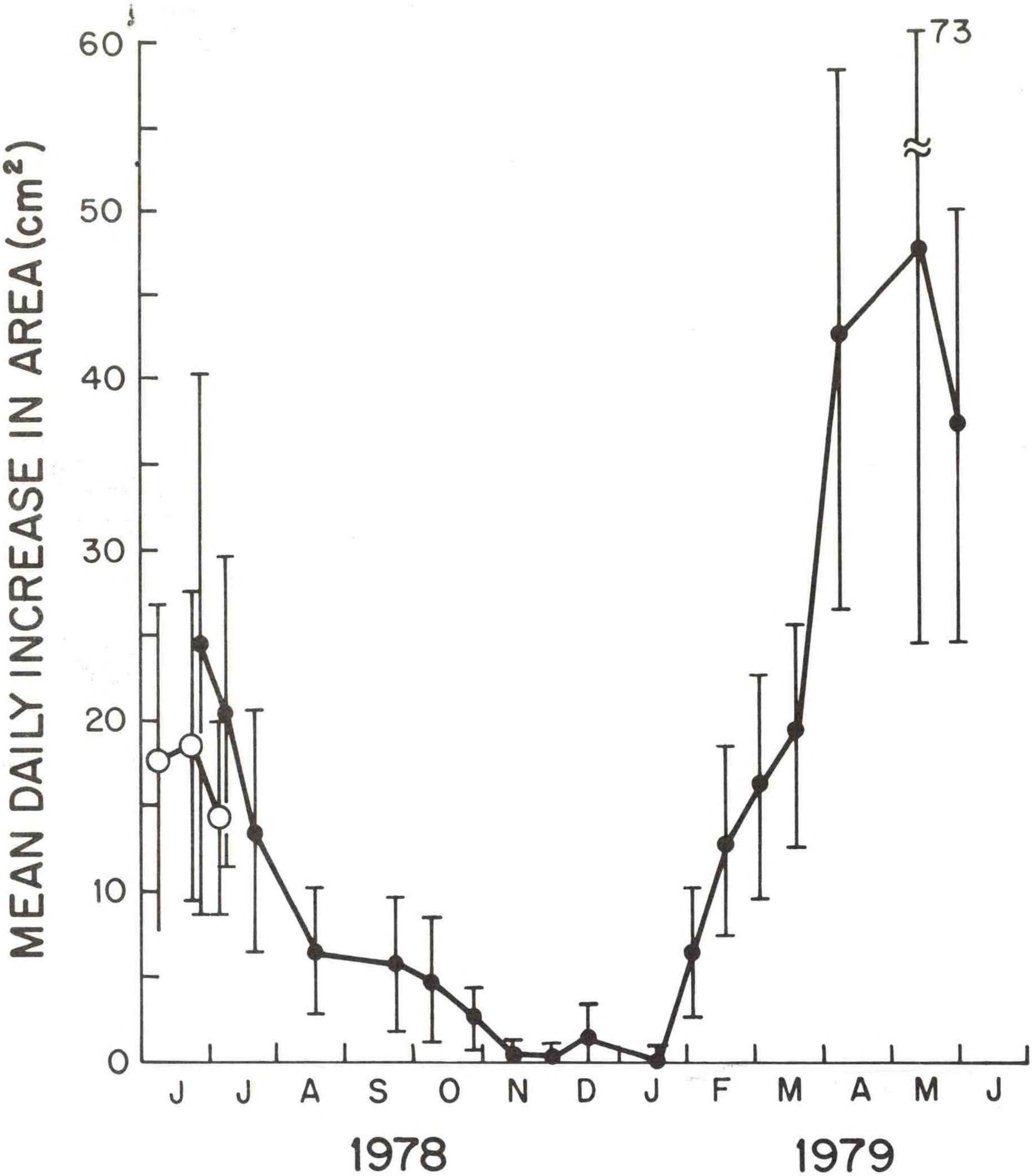


Figure 4. Mean daily increase in area of intertidal and subtidal <u>Laminaria saccharina</u>.

With appropriate data on wet weight it would be possible to estimate daily increases in biomass from area data. Linear regression curves of frond area to wet weight gave reasonable correlation coefficients (Table 1). However the Y intercept values indicated that for small values of area (as would be used to estimate growth) erroneous estimates of algae biomass might be made. If data were available on wet weight of the first 10-30 cm of fronds of *L. saccharina* the biomass could be calculated using these data.

### 3.2.4 Calculation of Increase in Biomass for L. saccharina

Length of *L. saccharina* were taken on algae during this period of December 1978 to June 1979 (Table 5). For this period daily increases in biomass were estimated using the regression of wet weight to the power curve of length (see methods). The results are shown in Fig. 5. The values of daily increase in grams of wet weight followed closely the curves of both increase in area (Fig. 4) and hole elongation (Fig. 3). One difference in the curves was that in the first period of the study (June 1979) both elongation and area showed a decrease from previous values, whereas biomass was greater.

### 3.2.5 Nereocystis luetkeana

a. Stipe Elongation. The first phase in the analysis of growth of *Nereocystis luetkeana* was to follow elongation of the stipe (Table 6). Figure 6 shows the mean stipe length from June 5 to September 8, 1978. During this time stipe length increased from around 250 cm to 600 cm. Data for algae from the spring of 1979 are also shown in Fig. 6. In May 1979 stipe length was around 75 cm, rapidly increasing to around 175 cm by May 17. Observation of the site during the period of February to April 1979 showed no sporophyte growth until the end of April.

Although mean stipe length continued to increase through to September 1978 (Fig. 6) the rate of increase slowed during this period. Fig. 7 shows the mean daily stipe increase through the study period. Values ranged from a high of between 7 and 9 cm per day in May and June to approximately 2 cm per day elongation in August and September.

b. Blade Elongation. Starting August 9, elongation of blades was followed by observing hole migration. Values were estimated for August 24 and September 8 (Table 7). Storms and resulting loss of algae after this time prohibited further measurement of elongation. Table 8 gives the data on blade elongation in *N. luetkeana*.

Table 5. Summary of length data for *L. saccharina*. Biomass was estimated using the power curve, wt = 0.32 length (1.86). Data for individual algae are given in Appendix 3. Biomass is in grams of wet weight.

| Date | Biomass | Number of days | Daily biomass |
|---|---|---|---|
| December 1 | 17 | 14 | 1.2 |
| December 15 | 57 | 22 | 2.6 |
| January 6 | 0 | 19 | 0 |
| January 25 | 155 | 14 | 11.1 |
| February 24 | 331 | 12 | 27.6 |
| March 8 | 449 | 18 | 28.0 |
| March 26 | 915 | 12 | 76.2 |
| April 7 | 3,880 | 43 | 90.2 |
| May 20 | 1,920 | 18 | 106.7 |

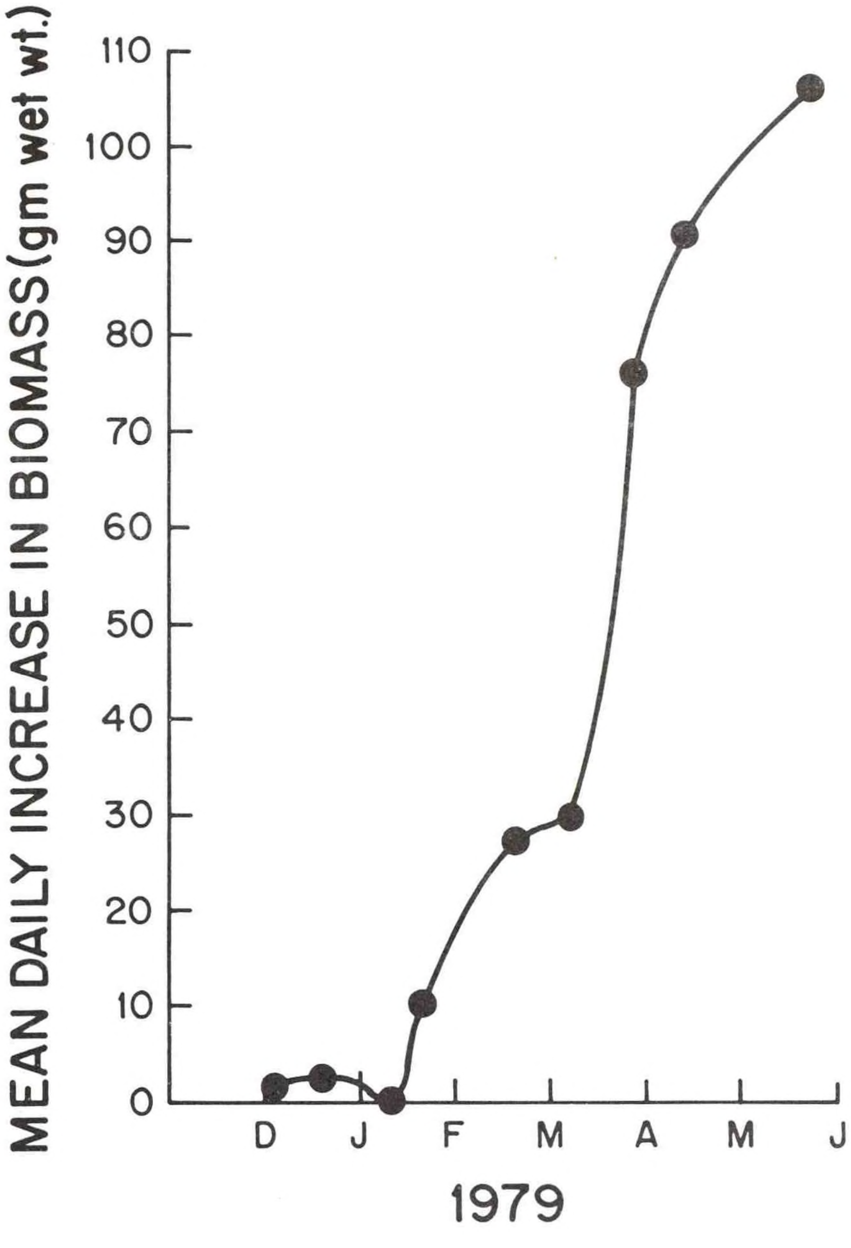


Figure 5. Daily increase in biomass of Laminaria saccharina.

Table 6. Summary of stipe growth in Nereocystis luetkeana. Data for each algae are given in Appendix 4.

| Date | n | mean increase (cm) | number of days | mean daily stipe increase (cm) | standard deviation |
|---|---|---|---|---|---|
| June 5 - June 13 | 8 | 68.5 | 8 | 8.6 | 2.5 |
| June 13- July 11 | 34 | 172.6 | 28 | 6.1 | 2.6 |
| July 11- July 28 | 29 | 37.3 | 17 | 2.2 | 2.2 |
| July 28- September 8 | 8 | 94.6 | 42 | 2.3 | 1.2 |
| May 3- May 17 | 9 | 96.4 | 14 | 6.9 | 2.1 |

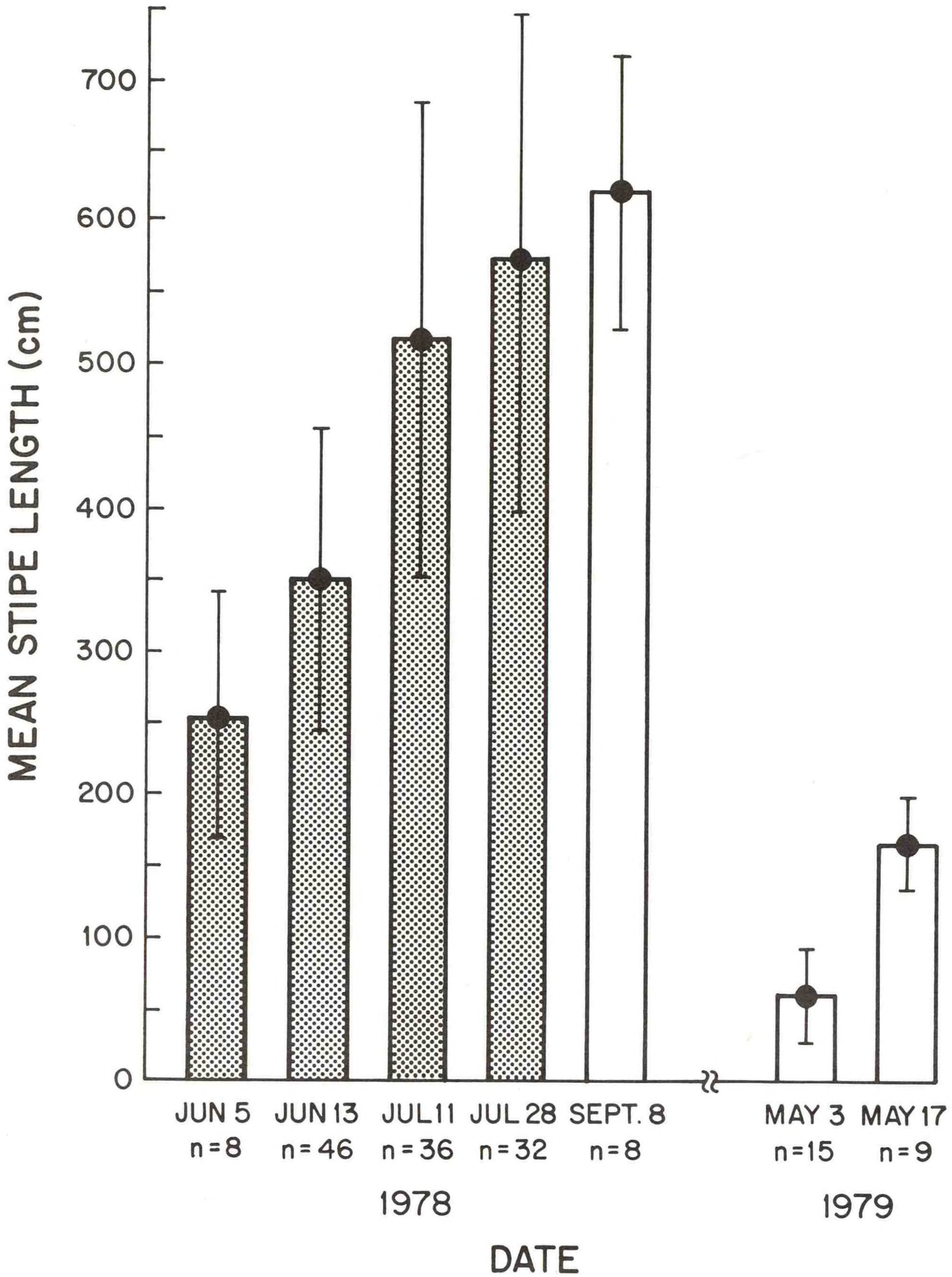


Figure 6. Mean stipe length of Nereocystis luetkeana.

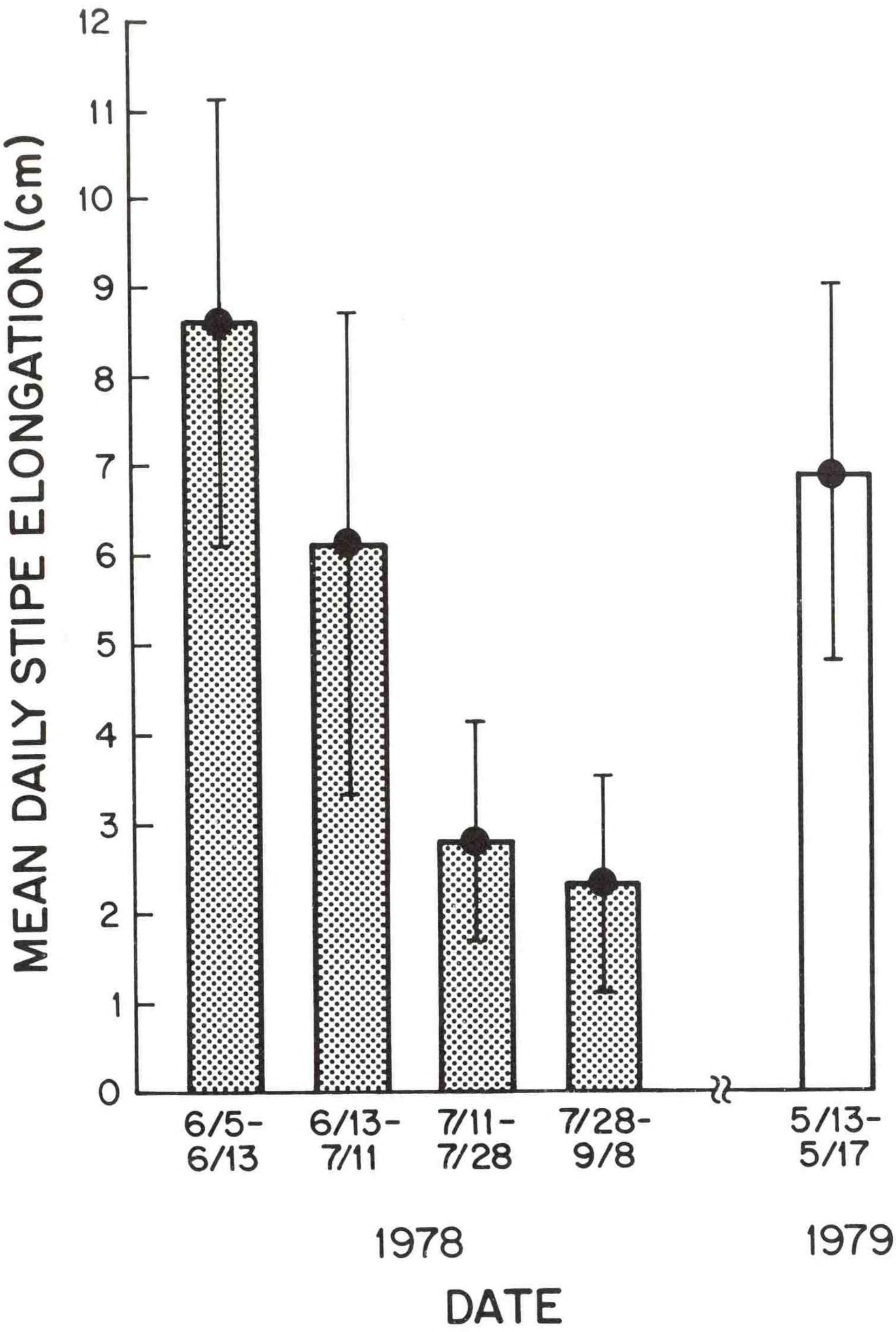


Figure 7. Daily stipe elongation of Nereocystis luetkeana.

Table 7. Summary of blade growth data for Nereocystis luetkeana. Data for individual algae are given in Appendix 5. Mean growth is elongation of blades. Biomass is grams of wet wt. tissue as estimated by a power curve (see Methods).

| | mean growth | biomass | daily biomass |
|---|---|---|---|
| August 9-24 | 276.1 | 4,041 | 269.1 |
| August 24-September 8 | 33.1 | 3,842 | 255.2 |

Table 8. Comparison of mean width of *L. saccharina* from July 7, 1978 and August 16, 1978 at 10 and 20 cm from stipe.

| | |
|---|---|
| July 7 n = 9 | |
| mean width at 10 cm | 25.3 cm |
| mean width at 20 cm | 30.2 cm |
| t = -1.89 | N.S. |
| July 19 n = 49 | |
| mean width at 10 cm | 21.4 cm |
| mean width at 20 cm | 27.6 cm |
| t = 5.09 | SIG |
| August 16 n = 36 | |
| mean width at 10 cm | 22.8 cm |
| mean width at 20 cm | 27.8 cm |
| t = 2.82 | SIG |

## 4. DISCUSSION

### 4.1 Evaluation of the Technique

One basic assumption in this study was that the growth of L. saccharina occurred in the first 10 cm of the frond from the stipe. This assumption was based on the work of Parke (1948), Mann (1972, 1973), and others (see Kain, 1976). Parke showed that the greatest growth of L. saccharina occurred in the first 25 cm of the frond. Mann (1972) found that the majority of growth of L. longicuris occurred in the first 10 cm of the frond and he punched holes at that location to follow rates of hole migration. L. longicuris is very similar to L. saccharina. Mann (1972) reported that juveniles of the two species could not be distinguished.

Based on these data, holes were punched at the 10 cm mark for this study. Two kinds of data collected during this study indicate that the assumption that all growth occurs in the first 10 cm is incorrect. First, for three time periods during the study (Table 8), frond width at 10 and 20 cm from the stipe was noted. At two of the three times the mean width at 20 cm was significantly greater ($p = 0.05$) than at 10 cm. That is, there was a significant increase in blade width that must have occurred as a result of growth beyond the 10 cm mark. Secondly, for observation periods from December 15 to June 7, both blade width and total blade length were recorded (Table 5, Appendix 3). These data show that at least some algae, during the time period of December 4 to June 1, had an increase in total length that was greater than the distance of movement of the punched hole. These data indicate the growth in L. saccharina occurs beyond 10 cm from the stipe.

There is another factor to consider in evaluating these growth data for L. saccharina. Algae release dissolved organic matter during photosynthesis. Sieburth and Jensen (1969) and Khailov and Burlakova (1969) showed that 30-40% of the gross primary productivity of algae in the coastal zone is in the form of dissolved organic matter.

Data on growth of L. saccharina reported in this study must be viewed as conservative estimates of total productivity because they do not consider growth beyond 10 cm, nor the extent of the production of dissolved organic material during photosynthesis.

### 4.2 Growth in Laminaria saccharina

Given these restraints, the growth rate of L. saccharina showed the species has a distinct growth period with times of virtually no growth (November - January) and that growth is maximum in May and June when individual L. saccharina had a growth of over 100 g of wet weight per day.

Comparison of these values to those of the literature is difficult because most studies give results in productivity per area. For example, Mann (1972) gave a rate of production for L. longicuris of 4.8 g $C/m^2$/day. Other values reported in the literature include: the turtle grass (Thalassia) 5.8 g $C/m^2$/day (Quasim and Bhattatliri, 1971); Cystoseira, 10.5 g $C/m^2$/day (Johnston, 1969);

west coast intertidal seaweeds, 20 g C/m$^2$/day (Kanwischer, 1966); Macrocystis, 1.5-2.5 g C/m$^2$/day (Clendenning, 1960); L. hyper borea, 3.4 g C/m$^2$/day (Bellamy et al., 1968); and Zostera marina, 1.59 g dry weight/m$^2$/day (Phillips, 1974). It is likely that the data reported here would yield similar values.

### 4.3 Other Puget Sound Laminaria Growth Data

Thom et al. (1977) gave values for rate of migration of holes punched 10 cm from the stipe in intertidal L. saccharina at West Point and Lincoln Park, Seattle. For the period of May 26 to June 10 Thom reported daily mean hole migration of 1.3 and 1.8 cm. For intertidal L. saccharina from Shannon Point during this time period mean daily hole migration fell from 1.2 cm per day to 0.6 cm per day. These values were very similar to those calculated in this study; 1.2, 1.2 and 0.6 cm per day (Table 3).

### 4.4 Nereocystis Stipe Elongation

Data from this study showed that the stipe of Nereocystis luetkeana grew most rapidly in spring (8-9 cm per day) and the rate decreased through the summer (approximately 2 cm per day). Thom et al. (1977) showed that the maximum growth of N. luetkeana from Lincoln Park, Seattle, was in May and June (4.2 cm per day) but that maximum stipe elongation at West Point, Seattle, was in June to August (2.8 cm per day). In general, Thom's values are lower. As well, one of Thom's sites was located adjacent to a sewage outfall (West Beach). The marked seasonal difference in growth of N. luetkeana stipes observed in this study was not apparent in Thom's report.

ACKNOWLEDGMENTS

Acknowledgment is due to those people involved with the often difficult task of collecting data by use of SCUBA--Gary Smith, Ken Dunton, David Gillingham, Rick Yackley and Jim Dougherty. As well, the staff of the Sundquist Marine Laboratory in Anacortes provided boats and support for diving. Finally, Alice Benedict directed laboratory analysis of samples and assisted in summaries of data.

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Appendix 1. Tag number, width at 10 cm, hole elongation (cm), and area (elongation x width at 10 cm) for intertidal *L. saccharina*.

| May 25-June 7 | | | | June 7-June 21 | | | | June 21-July 5 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm elongation | Area | Tag No. | Width 10 cm | cm elongation | Area | Tag No. | Width 10 cm | cm elongation | Area |
| 3 | 7 | 12 | 84 | 3 | 7 | 6 | 42 | 9 | 13 | 15 | 195 |
| 4 | 19 | 14 | 266 | 4 | 20 | 13 | 260 | 11 | 14 | 6 | 84 |
| 6 | 15 | 18 | 270 | 6 | 17 | 16 | 272 | 13 | 14 | 2 | 182 |
| 8 | 8 | 10 | 80 | 8 | 11 | 13 | 143 | 18 | 16 | 2 | 288 |
| 11 | 13 | 31 | 403 | 9 | 13 | 35 | 455 | 20 | 27 | 11 | 297 |
| 12 | 13 | 27 | 351 | 12 | 10 | 34 | 340 | 27 | 15 | 10 | 150 |
| 13 | 19 | 14 | 266 | 13 | 22 | 14 | 308 | | | | |
| 14 | 14 | 28 | 392 | 14 | 17 | 21 | 357 | | | | |
| 16 | 25 | 6 | 150 | 15 | 15 | 23 | 345 | | | | |
| 17 | 15 | 6 | 90 | 16 | 15 | 6 | 90 | | | | |
| 20 | 21 | 13 | 273 | 18 | 15 | 14 | 210 | | | | |
| 23 | 14 | 6 | 84 | 20 | 24 | 17 | 408 | | | | |
| | | | | 27 | 15 | 10 | 150 | | | | |

Appendix 2. Tag number, width at 10 cm (W10), hole elongation in cm and area (elongation x width at 10 cm) for subtidal L. saccharina.

| June 16-28 (12d) | | | | June 28-July 7 (9d) | | | | July 7-19 (12d) | | | | July 19-Aug. 16 (28d) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| 1 | 22 | 15 | 330 | 1 | 32 | 9 | 288 | 4 | 20 | 14 | 280 | 11 | 23 | 9 | 207 |
| 2 | 30 | 10 | 300 | 4 | 17 | 9 | 153 | 7 | 31 | 1 | 31 | 23 | 29 | 5 | 145 |
| 3 | 16 | 20 | 320 | 7 | 28 | 3 | 84 | 24 | 20 | 10 | 200 | 79 | 33 | 7 | 231 |
| 4 | 19 | 10 | 190 | 10 | 27 | 9 | 243 | 32 | 30 | 4 | 120 | 44 | 29 | 7 | 203 |
| 15 | 24 | 12 | 288 | 21 | 29 | 5 | 145 | 36 | 26 | 10 | 260 | 50 | 23 | 12 | 276 |
| 17 | 24 | 15 | 360 | 24 | 19 | 10 | 190 | 44 | 32 | 4 | 128 | 52 | 18 | 5 | 90 |
| 19 | 13 | 17 | 221 | 32 | 32 | 3 | 96 | 50 | 19 | 11 | 209 | 54 | 21 | 4 | 84 |
| 21 | 28 | 37 | 1,036 | 36 | 23 | 14 | 322 | 52 | 17 | 9 | 153 | 55 | 18 | 2 | 36 |
| 24 | 17 | 14 | 238 | 44 | 32 | 3 | 96 | 53 | 12 | 14 | 168 | 56 | 12 | 7 | 84 |
| 25 | 35 | 4 | 140 | 47 | 21 | 11 | 231 | 54 | 20 | 7 | 140 | 57 | 28 | 12 | 336 |
| 27 | 18 | 20 | 360 | | | | | 55 | 20 | 3 | 60 | 58 | 20 | 10 | 200 |
| 28 | 23 | 12 | 276 | | | | | 56 | 12 | 9 | 108 | 60 | 39 | 10 | 390 |
| 31 | 17 | 18 | 306 | | | | | 57 | 27 | 13 | 351 | 61 | 15 | 15 | 225 |
| 32 | 32 | 6 | 192 | | | | | 58 | 22 | 6 | 132 | 62 | 26 | 6 | 156 |
| 33 | 30 | 3 | 90 | | | | | 59 | 14 | 11 | 154 | 65 | 21 | 10 | 210 |
| 36 | 23 | 20 | 460 | | | | | 60 | 24 | 14 | 336 | 66 | 26 | 8 | 208 |
| 37 | 22 | 11 | 242 | | | | | 61 | 15 | 15 | 225 | 68 | 24 | 8 | 192 |
| 43 | 18 | 15 | 270 | | | | | 62 | 25 | 6 | 150 | 70 | 17 | 2 | 34 |
| 44 | 27 | 8 | 216 | | | | | 63 | 25 | 10 | 250 | 71 | 15 | 3 | 45 |

continued

Appendix 2--continued

| June 16-28 (12d) | | | | June 28-July 7 (9d) | | | | July 7-19 (12d) | | | | July 19-Aug. 16 (28d) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| 45 | 25 | 15 | 375 | | | | | 64 | 16 | 11 | 176 | 73 | 12 | 5 | 60 |
| 46 | 21 | 8 | 168 | | | | | 65 | 21• | 10 | 210 | 75 | 31 | 9 | 279 |
| 48 | 18 | 5 | 90 | | | | | 66 | 23 | 9 | 207 | 76 | 22 | 10 | 220 |
| | | | | | | | | 67 | 19 | 11 | 209 | 77 | 15 | 9 | 135 |
| | | | | | | | | 68 | 23 | 7 | 161 | 78 | 18 | 5 | 90 |
| | | | | | | | | 69 | 18 | 11 | 198 | 80 | 29 | 12 | 348 |
| | | | | | | | | 70 | 17 | 3 | 51 | 81 | 13 | 16 | 208 |
| | | | | | | | | 71 | 18 | 4 | 72 | 83 | 14 | 11 | 154 |
| | | | | | | | | 72 | 30 | 0 | 0 | 84 | 24 | 16 | 384 |
| | | | | | | | | 73 | 12 | 4 | 48 | 85 | 20 | 10 | 200 |
| | | | | | | | | 74 | 23 | 3 | 69 | 86 | 18 | 10 | 180 |
| | | | | | | | | | | | | 31 | 18 | 0 | 0 |

continued

Appendix 2--continued

| Aug. 30-Sept. 20 | | | | Sept. 20-Oct. 6 | | | | Oct. 6-Oct. 27 | | | | Oct. 27-Nov. 14 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| 55 | 17 | 1 | 17 | 51 | 23 | 4 | 92 | 51 | 21 | 4 | 84 | 51 | 21 | 1 | 21 |
| 60 | 20 | 10 | 200 | 63 | 27 | 0 | 0 | 54 | 21 | 1 | 21 | 54 | 21 | 0 | 0 |
| 63 | 27 | 5 | 135 | 150 | 15 | 0 | 0 | 150 | 15 | 0 | 0 | 127 | 12 | 0 | 0 |
| 75 | 30 | 11 | 330 | 151 | 11 | 11 | 121 | 151 | 10 | 7 | 70 | 128 | 12 | 1.5 | 18 |
| 76 | 20 | 3 | 60 | 152 | 14 | 11 | 154 | 152 | 13 | 5 | 65 | 129 | 11 | 0 | 0 |
| 150 | 15 | 5 | 75 | 153 | 13 | 10 | 130 | 153 | 13 | 4 | 52 | 130 | 11 | 1 | 11 |
| 151 | 11 | 20 | 220 | 154 | 12 | 11 | 132 | 154 | 11 | 8 | 88 | 131 | 10 | 1 | 10 |
| 152 | 14 | 26 | 364 | 156 | 14 | 3 | 42 | 156 | 13 | 2 | 26 | 132 | 21 | 0 | 0 |
| 153 | 14 | 23 | 322 | 157 | 20 | 2 | 40 | 157 | 22 | 2 | 44 | 133 | 39 | 0 | 0 |
| 154 | 11 | 16 | 176 | 159 | 14 | 8 | 112 | 158 | 14 | 10 | 140 | 134 | 21 | 0 | 0 |
| 156 | 14 | 7 | 98 | 160 | 13 | 6 | 78 | 159 | 12 | 2 | 24 | 135 | 24 | 0 | 0 |
| 157 | 20 | 2 | 40 | 161 | 16 | 7 | 112 | 160 | 12 | 1 | 12 | 136 | 22 | 0 | 0 |
| 159 | 14 | 21 | 294 | 162 | 13 | 15 | 195 | 161 | 14 | 5 | 70 | 150 | 16 | 0 | 0 |
| 160 | 13 | 15 | 195 | 163 | 15 | 3 | 45 | 162 | 13 | 4 | 52 | 151 | 10 | 1 | 10 |
| 161 | 17 | 16 | 272 | 164 | 25 | 1 | 25 | 163 | 14 | 3 | 42 | 152 | 13 | 0 | 0 |
| 162 | 13 | 9 | 117 | 166 | 19 | 1 | 19 | 165 | 12 | 5 | 60 | 153 | 13 | 0 | 0 |
| 163 | 16 | 8 | 128 | 168 | 19 | 1 | 19 | 166 | 18 | 1 | 18 | 154 | 11 | 2 | 22 |
| 166 | 19 | 0 | 0 | | | | | 167 | 17 | 4 | 68 | 156 | 13 | 0 | 0 |
| 168 | 19 | 5 | 95 | | | | | 175 | 19 | 0 | 0 | 158 | 12 | 5 | 60 |

continued

Appendix 2--continued

| Aug. 30-Sept. 20 | | | | Sept. 20-Oct. 6 | | | | Oct. 6-Oct. 27 | | | | Oct. 27-Nov. 14 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| | | | | | | | | | | | | 161 | 15 | 0 | 0 |
| | | | | | | | | | | | | 162 | 13 | 0 | 0 |
| | | | | | | | | | | | | 163 | 15 | 0 | 0 |
| | | | | | | | | | | | | 166 | 18 | 0 | 0 |
| | | | | | | | | | | | | 168 | 19 | 0 | 0 |
| | | | | | | | | | | | | 50 | 21 | 1 | 21 |

continued

Appendix 2--continued

| Nov. 14-Dec. 1 | | | | Dec. 1-Dec. 15 | | | | Dec. 15-Jan. 6 | | | | Jan. 6-Jan. 25 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| 51 | 22 | 0 | 0 | 54 | 21 | 1 | 21 | 127 | | 2 | | 127 | 9 | 0 | 0 |
| 54 | 20 | 0 | 0 | 127 | 12 | 1.0 | 12 | 128 | | 0 | | 129 | 9 | 0 | 0 |
| 127 | 12 | 0 | 0 | 128 | 12 | 2 | 24 | 129 | | 0 | | 130 | 8 | 1 | 8 |
| 128 | 12.2 | 0 | 0 | 129 | 10 | 0 | 0 | 130 | | 5 | | 131 | 7 | 0 | 0 |
| 129 | 10.5 | 0 | 0 | 130 | 11 | 1 | 11 | 131 | | 4 | | 135 | 25 | 0 | 0 |
| 130 | 10.8 | 3 | 32 | 131 | 9.0 | 12 | 108 | 132 | | 1 | | 161 | 14 | 1 | 14 |
| 131 | 9 | 3 | 27 | 132 | 23 | 1 | 23 | 135 | | 0 | | 163 | 9 | 1 | 9 |
| 132 | 22 | 0 | 0 | 134 | 21 | 0 | 0 | 158 | | 6 | | | | | |
| 133 | 20 | 0 | 0 | 135 | 26 | 0 | 0 | 161 | | 2 | | | | | |
| 134 | 26 | 0 | 0 | 151 | 10 | 1 | 10 | 163 | | 1 | | | | | |
| 151 | 10 | 2 | 20 | 152 | 13 | 2 | 26 | 166 | | 3 | | | | | |
| 152 | 13 | 1 | 13 | 153 | 13 | 1 | 13 | | | | | | | | |
| 153 | 13 | 1 | 13 | 157 | 13 | 2 | 26 | | | | | | | | |
| 154 | 10 | 2 | 20 | 162 | 13 | 2.0 | 26 | | | | | | | | |
| 156 | 15 | 0 | 0 | 166 | 18.0 | 1 | 18 | | | | | | | | |
| 158 | 13 | 0 | 0 | 163 | 15 | 1 | 15 | | | | | | | | |
| 162 | 13 | 0 | 0 | 156 | 14 | 2 | 28 | | | | | | | | |
| 165 | 14 | 0 | 0 | | | | | | | | | | | | |
| 166 | 19 | 0 | 0 | | | | | | | | | | | | |

continued

Appendix 2--continued

| Jan. 25-Feb. 3 | | | | Feb. 8-Feb. 24 | | | | Feb. 24-Mar. 8 | | | | Mar. 8-Mar. 26 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| 54 | 16 | 0 | 0 | 127 | 14 | 10 | 140 | 127 | 18 | 21 | 378 | 127 | 19 | 16 | 304 |
| 127 | 9 | 1 | 9 | 129 | 9 | 10 | 90 | 129 | 12 | 7 | 84 | 129 | 17 | 14 | 238 |
| 129 | 9 | 2 | 18 | 130 | 13 | 16 | 208 | 130 | 13 | 7 | 91 | 130 | 19 | 36 | 684 |
| 130 | 11 | 9 | 99 | 131 | 9 | 14 | 126 | 131 | 14 | 14 | 196 | 131 | 19 | 20 | 380 |
| 131 | 9 | 7 | 63 | 137 | 14 | 18 | 252 | 134 | 20 | 11 | 220 | 134 | 25 | 14 | 350 |
| 137 | 14 | 13 | 182 | 138 | 16 | 18 | 288 | 137 | 15 | 15 | 225 | 135 | 23 | 12 | 276 |
| 138 | 14 | 10 | 140 | 139 | 16 | 14 | 224 | 138 | 17 | 13 | 221 | 136 | 19 | 17 | 323 |
| 139 | 11 | 10 | 110 | 140 | 12 | 13 | 156 | 139 | 17 | 13 | 221 | 137 | 21 | 20 | 420 |
| 140 | 8 | 6 | 48 | 141 | 14 | 14 | 196 | 140 | 12 | 13 | 221 | 138 | 23 | 14 | 322 |
| 142 | 14 | 8 | 112 | 142 | 13 | 21 | 273 | 141 | 12 | 10 | 120 | 140 | 28 | 14 | 392 |
| 143 | 12 | 9 | 108 | 143 | 14 | 16 | 224 | 142 | 12 | 10 | 120 | 141 | 17 | 12 | 204 |
| 144 | 12 | 11 | 132 | 145 | 9 | 8 | 72 | 143 | 13 | 11 | 143 | 143 | 13 | 17 | 221 |
| 147 | 13 | 10 | 130 | 147 | 16 | 20 | 320 | 147 | 19 | 18 | 342 | 154 | 20 | 19 | 380 |
| 148 | 14 | 10 | 140 | 148 | 17 | 14 | 238 | 148 | 16 | 15 | 240 | 161 | 17 | 16 | 272 |
| 161 | 14 | 8 | 112 | 149 | 11 | 11 | 121 | 149 | 12 | 10 | 120 | 178 | 27 | 13 | 351 |
| 163 | 14 | 3 | 42 | 154 | 14 | 11 | 154 | 154 | 15 | 13 | 195 | 182 | 17 | 13 | 221 |
| 166 | 12 | 5 | 60 | 161 | 17 | 26 | 442 | 161 | 11 | 16 | 176 | 184 | 12 | 16 | 192 |
| | | | | | | | | | | | | 185 | 19 | 26 | 494 |
| | | | | | | | | | | | | 186 | 16 | 24 | 384 |
| | | | | | | | | | | | | 187 | 30 | 17 | 510 |

continued

Appendix 2--continued

| Mar. 26-April 7 | | | | April 7-May 20 | | | | May 20-June 7 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area | Tag No. | Width 10 cm | cm growth | Area |
| 127 | 16 | 25 | 400 | 127 | 20 | 53 | 1,060 | 127 | 18 | 27 | 486 |
| 129 | 18 | 19 | 342 | 129 | 24 | 62 | 1,488 | 129 | 19 | 28 | 532 |
| 131 | 13 | 34 | 442 | 131 | 20 | 124 | 2,480 | 131 | 20 | 32 | 640 |
| 134 | 23 | 30 | 690 | 137 | 25 | 109 | 2,725 | 140 | 22 | 33 | 726 |
| 135 | 27 | 15 | 405 | 139 | 30 | 64 | 1,920 | 141 | 21 | 23 | 483 |
| 137 | 15 | 35 | 525 | 140 | 22 | 194 | 4,268 | 142 | 19 | 32 | 608 |
| 138 | 21 | 37 | 777 | 141 | 17 | 40 | 680 | 147 | 18 | 20 | 360 |
| 139 | 19 | 30 | 570 | 142 | 21 | 39 | 819 | 154 | 16 | 26 | 416 |
| 140 | 16 | 37 | 592 | 143 | 21 | 24 | 504 | 175 | 22 | 33 | 726 |
| 141 | 14 | 27 | 378 | 145 | 18 | 135 | 2,430 | 176 | 24 | 26 | 624 |
| 143 | 14 | 33 | 462 | 154 | 20 | 123 | 2,460 | 178 | 23 | 34 | 782 |
| 154 | 21 | 31 | 651 | 175 | 14 | 151 | 2,114 | 180 | 22 | 47 | 1,034 |
| 161 | 16 | 23 | 368 | 176 | 26 | 131 | 3,406 | 182 | 25 | 48 | 1,200 |
| 162 | 16 | 16 | 256 | 178 | 39 | 38 | 1,482 | 185 | 22 | 39 | 858 |
| 178 | 25 | 21 | 525 | 180 | 20 | 161 | 3,220 | 196 | 19 | 31 | 589 |
| 182 | 9 | 21 | 189 | 182 | 26 | 97 | 2,522 | | | | |
| 184 | 22 | 20 | 440 | | | | | | | | |
| 185 | 18 | 32 | 576 | | | | | | | | |
| 186 | 17 | 35 | 595 | | | | | | | | |
| 187 | 27 | 38 | 1,026 | | | | | | | | |

Appendix 3. Tag number and total frond length for subtidal *L. saccharina*.

| Dec. 1 | | Dec. 15 | | Jan. 6 | | Jan. 25 | |
|---|---|---|---|---|---|---|---|
| Tag No. | Length | Tag No. | Length | Tag No. | Length | Tag No. | Length |
| 51 | 234 | 54 | 89 | 51 | 211 | 54 | 70 |
| 54 | 76 | 127 | 50 | 127 | 49 | 127 | 49 |
| 127 | 63 | 123 | 79 | 128 | 27 | 129 | 24 |
| 128 | 82 | 129 | 81 | 129 | 80 | 130 | 63 |
| 129 | 88 | 130 | 85 | 130 | 84 | 131 | 40 |
| 130 | 84 | 131 | 71 | 131 | 65 | 134 | 113 |
| 131 | 71 | 132 | 129 | 132 | 120 | 135 | 115 |
| 132 | 130 | 134 | 112 | 135 | 114 | 137 | 58 |
| 134 | 113 | 135 | 110 | 158 | 115 | 138 | 58 |
| 135 | 121 | 151 | 54 | 161 | 177 | 139 | 48 |
| 136 | 190 | 152 | 82 | 163 | 59 | 140 | 21 |
| 151 | 57 | 153 | 88 | 166 | 105 | 141 | 47 |
| 152 | 110 | 156 | 95 | | | 142 | 101 |
| 153 | 96 | 158 | 115 | | | 143 | 79 |
| 154 | 51 | 161 | 185 | | | 144 | 44 |
| 156 | 110 | 102 | 47 | | | 145 | 11 |
| 158 | 120 | 163 | 60 | | | 146 | 10 |
| 162 | 50 | 166 | 101 | | | 147 | 70 |
| 165 | 85 | 16 | 33 | | | 148 | 61 |
| 166 | 80 | | | | | 161 | 68 |
| | | | | | | 163 | 35 |
| | | | | | | 165 | 87 |
| | | | | | | 127 | 2 |

continued

Appendix 3--continued

| Feb. 24 | | Mar. 8 | | Mar. 26 | |
|---|---|---|---|---|---|
| Tag No. | Length | Tag No. | Length | Tag No. | Length |
| 54 | 14 | 127 | 70 | 127 | 59 |
| 127 | 62 | 129 | 51 | 129 | 56 |
| 129 | 46 | 130 | 109 | 130 | 194 |
| 130 | 87 | 131 | 78 | 131 | 146 |
| 131 | 62 | 134 | 132 | 134 | 85 |
| 137 | 83 | 137 | 102 | 135 | 60 |
| 138 | 87 | 138 | 108 | 137 | 170 |
| 139 | 73 | 139 | 87 | 138 | 62 |
| 140 | 37 | 140 | 51 | 139 | 148 |
| 141 | 225 | 141 | 154 | 140 | 106 |
| 142 | 61 | 142 | 72 | 141 | 161 |
| 143 | 105 | 143 | 123 | 143 | 212 |
| 145 | 23 | 147 | 113 | 154 | 111 |
| 147 | 91 | 148 | 107 | 161 | 101 |
| 148 | 90 | 149 | 41 | 162 | 52 |
| 149 | 31 | 154 | 48 | 175 | 68 |
| 154 | 37 | 161 | 97 | 176 | 99 |
| 161 | 133 | 178 | 118 | 178 | 129 |
| | | 182 | 36 | 182 | 53 |
| | | 184 | 19 | 184 | 40 |
| | | 185 | 42 | 185 | 103 |
| | | 186 | 45 | 186 | 116 |
| | | 187 | 78 | 187 | 89 |
| | | | | 189 | 55 |

continued

Appendix 3--continued

| Apr. 7 | | May 20 | | June 7 | |
|---|---|---|---|---|---|
| Tag No. | Length | Tag No. | Length | Tag No. | Length |
| 127 | 94 | 127 | 143 | 127 | 148 |
| 129 | 63 | 129 | 125 | 129 | 122 |
| 131 | 120 | 130 | 295 | 131 | 200 |
| 132 | 142 | 131 | 244 | 140 | 264 |
| 134 | 130 | 137 | 254 | 141 | 192 |
| 135 | 49 | 139 | 187 | 142 | 130 |
| 137 | 146 | 140 | 258 | 147 | 227 |
| 138 | 159 | 141 | 196 | 154 | 235 |
| 139 | 123 | 142 | 141 | 175 | 223 |
| 140 | 64 | 143 | 199 | 176 | 232 |
| 141 | 156 | 145 | 198 | 178 | 171 |
| 142 | 102 | 147 | 232 | 180 | 153 |
| 143 | 174 | 154 | 203 | 182 | 218 |
| 145 | 63 | 175 | 192 | 185 | 176 |
| 154 | 80 | 176 | 216 | 196 | 141 |
| 161 | 62 | 178 | 158 | 28 | 32 |
| 162 | 38 | 180 | 138 | | |
| 166 | 95 | 182 | 191 | | |
| 175 | 42 | 185 | 170 | | |
| 176 | 84 | 196 | 92 | | |
| 178 | 120 | 197 | 183 | | |
| 182 | 29 | | | | |
| 184 | 33 | | | | |
| 185 | 73 | | | | |
| 186 | 84 | | | | |
| 187 | 117 | | | | |
| 189 | 32 | | | | |
| 190 | 31 | | | | |

Appendix 4. Tab number and stipe elongation (cm) for <u>Nereocystis</u> <u>luetkeana</u>

| June 5-June 13 | | June 13-July 11 | | July 11-July 28 | | July 28-Sept. 8 | | May 3-May 17 | |
|---|---|---|---|---|---|---|---|---|---|
| 303 | 70 | 300 | 152 | 302 | 87 | 303 | 96 | 198 | 91 |
| 305 | 31 | 302 | 174 | 303 | 79 | 305 | 59 | | |
| 311 | 53 | 303 | 179 | 304 | 88 | 311 | 43 | | |
| 312 | 88 | 304 | 301 | 305 | 50 | 337 | 162 | | |
| 315 | 85 | 305 | 105 | 306 | 31 | 339 | 180 | | |
| 319 | 69 | 307 | 148 | 307 | 40 | 353 | 51 | | |
| 322 | 88 | 308 | 169 | 308 | 56 | 357 | 90 | | |
| 339 | 63 | 310 | 121 | 310 | 37 | 358 | 76 | | |
| | | 311 | 210 | 311 | 49 | | | | |
| | | 313 | 105 | 313 | 59 | | | | |
| | | 314 | 119 | 314 | 37 | | | | |
| | | 315 | 266 | 216 | 72 | | | | |
| | | 316 | 316 | 321 | 14 | | | | |
| | | 313 | 257 | 324 | 26 | | | | |
| | | 319 | 143 | 325 | 23 | | | | |
| | | 321 | 64 | 328 | 69 | | | | |
| | | 322 | 189 | 329 | 3 | | | | |
| | | 323 | 19 | 335 | 49 | | | | |
| | | 324 | 323 | 337 | 77 | | | | |
| | | | | 340 | 50 | | | | |
| | | | | 342 | 34 | | | | |
| | | 323 | 116 | 347 | 69 | | | | |
| | | 328 | 125 | 348 | 26 | | | | |
| | | 329 | 240 | 350 | 40 | | | | |
| | | 335 | 205 | 351 | 33 | | | | |
| | | 336 | 191 | 353 | 56 | | | | |
| | | 337 | 152 | 355 | 55 | | | | |
| | | 339 | 177 | 357 | 45 | | | | |
| | | 340 | 154 | 358 | 35 | | | | |
| | | 347 | 183 | | | | | | |
| | | 350 | 171 | | | | | | |
| | | 351 | 103 | | | | | | |
| | | 353 | 176 | | | | | | |
| | | 355 | 158 | | | | | | |
| | | 357 | 106 | | | | | | |
| | | 358 | 251 | | | | | | |

Appendix 5. Tag number, total length of fronds (cm), total hole migration (cm) for *Nereocystis luetkeana*.

| Aug. 8-24 | | | Aug. 24-Sept. 8 | | |
|---|---|---|---|---|---|
| Tag No. | Total length | Total elongation | Tag No. | Total length | Total elongation |
| 361 | 1,420 | 235 | 361 | 1,131 | 43 |
| 362 | 11,523 | 428 | 362 | 7,989 | 19 |
| 364 | 6,009 | 219 | 366 | 3,112 | 19 |
| 365 | 3,530 | 151 | 367 | 2,849 | 81 |
| 366 | 2,013 | 336 | 369 | 5,986 | 4 |
| 367 | 3,882 | 326 | 370 | 5,458 | 20 |
| 368 | 5,464 | 121 | 372 | 921 | 29 |
| 369 | 5,522 | 263 | 374 | 3,294 | 50 |
| 370 | 6,445 | 261 | | | |
| 371 | 14,265 | 421 | | | |