Age of drifting *Macrocystis pyrifera* (L.) C. Agardh rafts in the Southern California Bight

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Abstract

*Macrocystis pyrifera* plants that detach from the substratum float to the surface and, if they do not become entangled or washed immediately to the shore, may drift at the surface for an unknown period of time. These rafts provide habitat for a variety of coastal and pelagic fauna. The distances dispersed and the period available for species to utilize these habitats, however, depend on the longevity of the raft and methods for determining the age of rafts are unknown. A method to age drifting *M. pyrifera* rafts based on a change in length of blades (BL) following detachment is validated here. This technique determines the period of time since detachment and not the actual age of the plant. In general, average BL decreases from initial attached values of 50–60 to about 0 cm, when rafts sink. The rate of aging, or deterioration of BL, is related to water temperature, and sets the period a raft stays afloat. Maximal estimates of ages of rafts were between 63 and 109 days, depending on the exact method used. Their lifetime will limit the distances dispersed by kelp rafts in Southern California, and this methodology will be useful for determining the temporal patterns of abundance of fauna associated with rafts. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Faunal dispersal; *Macrocystis* rafts; Rafting

1. Introduction

Forests of giant kelp, *Macrocystis pyrifera*, are common along the west coast of North America and in temperate waters throughout the world (Dayton, 1985; Foster and Schiel, 1985). This brown alga attaches to rocky substrates with a root-like holdfast. Stipes or fronds intertwine to form a column until they reach the surface and spread out in a
floating canopy. Mature undamaged plants have extensive surface canopies, with up to 50% of the biomass within one meter of the surface (North, 1994). Kelp plants may become detached from the substrate by urchin grazing or storms (Dayton et al., 1992; Tegner et al., 1995). Detachment does not mean death for these plants, which may (i) become entangled in the kelp forest, (ii) drift free of the forest and then wash up on the beach, or (iii) drift for a period of time before sinking at sea or returning to the coast. Drifting rafts continue to function physiologically for some time following detachment (Hobday, 1998). The period that rafts stay afloat is unknown and is reported here for the first time. Determining the floating period of drifting kelp will allow estimation of distances traveled and interpretation of dispersal patterns and the changes in associated fauna.

Floating in kelps is enhanced by gas-filled pneumatocysts (Lobban and Harrison, 1994). Another rafting alga, Sargassum, also maintains its buoyancy by gas-filled vesicles and can probably remain afloat indefinitely unless killed by cold temperatures or submerged by wave action or excessive epibiont growth (Dooley, 1972). Older M. pyrifera pneumatocysts accumulate interior water, which may reduce buoyancy (Cribb, 1954). Sinking, ultimately due to reduced buoyancy, may be caused by physiological changes in the plant tissues that lead to deterioration of the plant or by the weight of encrusting epibionts. Edgar (1987) suggested that kelp rafts sink when nitrate levels become too low, and that low nitrate waters may restrict the dispersal of kelp rafts. Attached kelp absorbs nutrients from the passing flow of water and if this water is low in nitrogen, the plant may show signs of deterioration (North, 1994). M. pyrifera can use internal nitrogen reserves to maintain growth for up to 2 weeks (Gerard, 1982, 1984), however, the storage capacity of M. pyrifera (a laminarian kelp) is low compared to fucale kelps (Gerard, 1982). Drifting kelp is also likely to suffer from nitrogen depletion, due to reduced flow over its fronds, and will deteriorate over time. Drift algae that sinks provides significant organic inputs to the sea floor (Schoener and Rowe, 1970; Smith, 1983, and references within), especially below areas where oceanic or topographic features lead to surface aggregation (Kingsford, 1995). Kelp and other macrophyte detritus are especially important in the nearshore canyon regions of California where productivity of benthic assemblages is significantly enhanced by such inputs (Vetter, 1994, 1995; Harrold et al., 1998).

M. pyrifera plants that detach from the substrate retain some associated fauna, and the floating period of rafts influences the distances that fauna can be dispersed (Helmuth et al., 1994; Hobday, 2000a). While a detached M. pyrifera plant persisted for 18 months in a kelp forest (Dayton et al., 1984), the lifetime of kelp rafts that separate from kelp forests is unknown (Helmuth et al., 1994). Yaninek (1980) found that pneumatocysts lost their buoyancy after only 7 days, but stipes are buoyant and float even when the pneumatocysts have been compromised (Hobday, personal observation). Harrold and Lisin (1989) estimated floating time to be on the order of 7–9 days; however, most of their radio-tracked rafts washed ashore after this period. Researchers have misused these estimates to suggest floating periods of the same order of magnitude (Kingsford, 1995; Shaffer et al., 1995). Detached holdfasts tethered at the surface begin to disintegrate after between 3 months (Vasquez, 1993) and 6 months (Edgar, 1987). Kelp rafts are likely to float for similar time periods (Helmuth et al., 1994).
Previous efforts to age attached brown algae have focused on holdfast size (Graham et al., 1997), and stipe ring counts (Hymanson et al., 1990), with accuracy of around 1 year. Such measures are not suitable for aging drifting rafts over the expected time scales. Success in describing the variation in kelp morphology with biometric relations has been reported (Jackson et al., 1985), and some similar measures of blade properties were explored in this study. Helmuth et al. (1994) also attempted to describe raft age via blade length, with similar rationale to that presented here.

If a common baseline value for some property exists for all attached M. pyrifera plants, and if this property changes with time following detachment, drifting kelp rafts can be aged by measurement of this property and its rate of change from initial values. Ideally, an aging proxy should have, in addition to being time and cost effective, the following properties:

1. a baseline value for all attached plants corresponding to detachment age zero;
2. a monotonic change, either increasing or decreasing, in the property, allowing resolution over the full range of time, from detachment to sinking;
3. final values that are always measurable.

Nine potential raft aging proxies were identified in four categories, (i) biological (maximum faunal size, faunal abundance, epibiont cover), (ii) morphological (blade length, blade weight, tissue density), (iii) physiological (pigment content of blades, nitrogen content of blades), and (iv) physical (raft distance from the source). Of these aging proxies only blade length met all the criteria (Hobday, 1998), and is the only method used to age drifting kelp rafts presented in this paper.

2. Methods

2.1. Baseline sampling of attached plants

To age drifting rafts the baseline values of blade length (BL) when the kelp plant detaches must be known and consistent over the geographic range considered. Attached plants were surveyed monthly at the La Jolla and Pt Loma kelp forests, and opportunistically at southern California island kelp forests, between January 1995 and December 1997.

New blades are added at the elongating apical tip of a stipe on attached plants. After some time the stipe ceases growth, and a terminal blade is formed (Cribb, 1954; North, 1961). Blades below the tip grow to their maximum length. Preliminary attached plant sampling of BL showed that the maximum BL occurs and asymptotes about 2 m below the tip of a stipe (Fig. 1). Blades above this are still elongating (region 1), those in region 2 have ceased growth and are not senescing (or growth equals senescence) which gives a stable length on attached plants. Blades in region 3 are senescing on attached plants (Fig. 1). Thus, any reduction in BL in region 2 on drifting rafts can be attributed to senescence.

Baseline sampling for initial BL was carried out in region 2 of attached stipes with
Fig. 1. Blade length on an attached *Macrocystis pyrifera* stipe. Blade length increases with distance below the growth tip (region 1), is constant approximately 200 cm from the tip (region 2), then declines at about 400 cm from the tip (region 3). The solid black bar identifies the region of the stipe where 20 blades were measured to determine stipe BL.

growth tips at the surface (Fig. 1). Twenty consecutive blades on three to five stipes per attached plant were measured, beginning two meters from the terminal end of the stipe. At La Jolla, a single site was monitored, while at Pt Loma a site on the outer edge of the forest and a site in the middle were monitored so any differences in BL between the exterior and the interior of the forest could be evaluated. At the smaller island forests, plants were selected randomly. For each attached survey, three to six plants were sampled per site. Blades damaged by handling were not measured. The average stipe BLs were calculated and averaged to give overall plant BL (±S.E.). One-way ANOVA were used to test for differences over time at each location (Pt Loma, La Jolla, and all islands). A two-way ANOVA was used to compare differences between sites and over time for the months in which BL was measured at all three sites. A one-way ANOVA was used to test for seasonal differences in attached BL. A high-order polynomial was fitted to the BL data for all sampled months to provide an empirical description of the data and allow estimation of initial BL for any date in the sampling period. Regression analysis was used to examine the relationship between the Scripps pier average monthly sea surface temperature and BL.

2.2. Final sampling of drifting rafts

Drifting rafts were collected with a large net and deposited in a large bin for faunal removal (Hobday, 1998). Stipes with growth tips were carefully removed and up to 20 consecutive blades per stipe measured, beginning a distance 2 m from the tip. Up to 10 stipes were measured for each raft and averaged to provide a final BL (±S.E.). Blades
that were broken in collection could be identified and were not measured. Stipes that had more than five broken blades were not measured.

2.3. Rate of change in BL

The rate of change in BL from detachment to sinking must be evaluated in order to age rafts. Ideally a plant would be detached, followed and regularly sampled. However, because the floating time is on the order of months and the potential range is hundreds of kilometers (Helmuth et al., 1994; Hobday, 2000a), following a floating plant is impractical. One solution is to detach plants and tether them such that they can be located and sampled regularly.

Eleven experiments to determine the change in blade length over time were performed between July 1995 and December 1997. In each experiment between three and five attached plants with 10–20 stipes growing at a depth of 16–20 m in the La Jolla kelp forest were used. Plants of this size typically weigh 50–100 kg and form rafts 2–3 m in diameter, which is the median size of drifting rafts observed and collected in the Southern California Bight (Hobday, 2000a).

SCUBA divers removed each M. pyrifera plant from the substrate below the holdfast, and brought the plant to the surface. When all plants for an experiment were at the surface, they were gently loaded into a boat and quickly transported to a site 1 km distant, over a sand plain between the Scripps pier and the La Jolla kelp forest. Plants were returned to the water, where they floated at the surface. Three to five stipes were tagged with flagging tape at a point 2 m from the growth tip and labeled with the date of the measurements. As in the baseline sampling, 20 blades were measured on each of these stipes, beginning at this point. Each kelp plant was then gently bundled to mimic natural rafts and tied to surface floats, which were in turn attached to weights on the bottom at a depth of 15 m.

At approximately weekly intervals thereafter, the rafts were unbundled, up to five stipes with growth tips identified, and 20 blades measured beginning at a distance 2 m from the growth tip. A limited number of stipes with growth tips occur on each plant, and this necessitated some repeated measuring of stipes. Any growth of the stipe, however, meant that the same 20 blades would not be measured in subsequent weeks. On each sampling date an attempt was made to measure some new stipes, as well as ones measured previously. The number of times, and the date last measured was noted for each stipe, and it was tagged at a point 2 m from the growth tip. The distance between the tags from two sampling periods represented the stipe growth in the elapsed period. After measurements each raft was rebundled and tied to the float. The 20 blades were averaged to provide a stipe average, and the stipe averages provided an average raft BL for each date. The effect of repeated handling and measurement, as well as the growth rate for stipes, was obtained with this protocol. If handling alone led to a decrease in BL, then the average stipe BL for stipes that had been previously handled should be less than that for unmeasured stipes. Thus, the stipe BL anomalies (from the raft average for each measurement day) should not be less than zero for handled stipes or greater than zero for ‘virgin’ stipes. Rafts were sampled weekly until they sank, or broke free during storms.
The aging rate for each experiment was obtained from the slope of a linear regression on all the raft BL values for that experiment. The average sea surface temperature during an experiment was obtained from the Scripps pier time series.

2.4. Age determination

Because the rate of BL change was linear in all experiments (see Section 3.3), the age of natural rafts can be calculated as

\[ A = \frac{I - F}{R} \]  

where \( A \) is estimated raft age, \( I \) is the initial attached BL value, \( F \) is the final BL value as measured on the particular drifting raft, and \( R \) is the rate of BL change.

Raft age was estimated using two variations for determining the initial BL values. In method 1, the initial BL was found using the attached survey data. In method 2, the initial BL was assumed to be equal to the maximum BL found for any raft collected during a sampling cruise. This second method would allow estimates of raft age to be made in regions where no estimates of initial BL exist.

The average water temperature for the previous 50 days from the SCRIPPS pier, which is highly correlated with SST throughout the Southern California Bight (J. McGowan, pers. commun.) was used to select the appropriate aging rate. The initial BL, final BL, and aging rate, were then used to make an estimate of the age of the raft.

Because the initial and final BL and aging rate are measured with uncertainty, the uncertainty associated with the age estimate is calculated by combining the sums and quotients rules for the propagation of uncertainties (Taylor, 1982) to produce the following expression

\[ \delta A = |A| \sqrt{\left( \frac{\sqrt{(\delta I)^2 + (\delta F)^2}}{(I - F)} \right)^2 + \left( \frac{\delta R}{R} \right)^2} \]  

where \( \delta I \), \( \delta F \) and \( \delta R \) are the uncertainty in initial BL, final BL, and aging rate, respectively, and \( \delta A \) is the uncertainty in the estimated age, \( A \).

The magnitude of \( \delta R \) changed with the magnitude of the aging rate (see Section 3), and so a regression relationship was used to select the appropriate value for use in the uncertainty estimation.

The average maximum raft age estimated from the data collected in the 3 years of sampling was calculated for each season. Seasons were divided into fall (months September–November), winter (December–February), spring (March–May), and summer (June–August). The average sea surface temperature at the Scripps pier was used to generate a seasonal aging rate, \( \delta R \) was selected according to the aging rate (see Section 3). Average initial BL for the appropriate months were averaged to give a seasonal initial BL. Final BL was assumed to be zero and to be measured without uncertainty.
Average maximum age for each season was calculated using Eq. (1) and the seasonal variables.

### 2.5. Elasticity of age estimates

Improvements in the uncertainty of the age estimate were explored with elasticity analysis. Elasticity ($E$), represents the proportional change in one variable ($\delta A$) for a proportional change in another ($\delta V$), while all other variables are held constant. Initial BL was set at 65 cm for all simulations. Final BL was set at the average for all collected rafts, 42.25 cm, as well as at 52.25 and 32.25 cm. The aging rate was set at the minimum found in this study, $0.64 \text{ cm day}^{-1}$, and also at 1.00 and $0.30 \text{ cm day}^{-1}$. The uncertainty estimated for each variable ($\delta I$, $\delta F$ and $\delta R$) was changed by $\pm 25$ and $\pm 50\%$ for all the above parameter combinations. The elasticity for each of the combinations was calculated as

$$E = \left( \frac{\Delta \delta A - \delta A}{\delta A} \right) \frac{\delta V}{\left( \Delta \delta V - \delta V \right)}$$

where $\delta A$ is calculated as in Eq. (2), $\delta V$ is the uncertainty in initial and final BL and aging rate, and $\Delta \delta A$ and $\Delta \delta V$ are the $\pm 25$ or $\pm 50\%$ changes in $\delta A$ and $\delta V$, respectively.

### 3. Results

#### 3.1. Initial BL measurements

A 34-month survey of attached *M. pyrifera* BL was completed between March 1995 and December 1997. Each of the islands in the Southern California Bight, including the four northern (channel) islands, was surveyed at least once in this period. At the Pt Loma kelp forest there was a significant difference in BL over time and by site (exterior and interior forest sites, mean $53.66 \pm 5.38$ and $50.90 \pm 5.79$ cm, respectively) (Table 1). The significant interaction term (Time×Site) indicates that the differences were not consistent through time.

Plants from these two Pt Loma sites were combined to give average BL for Pt Loma each month. Because of the infrequent sampling, the islands were examined as a single

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>3647.418</td>
<td>28</td>
<td>130.265</td>
<td>3.344</td>
<td>0.001</td>
</tr>
<tr>
<td>Site</td>
<td>424.095</td>
<td>1</td>
<td>424.095</td>
<td>10.885</td>
<td>0.001</td>
</tr>
<tr>
<td>Time×Site</td>
<td>2452.271</td>
<td>28</td>
<td>87.581</td>
<td>2.248</td>
<td>0.001</td>
</tr>
<tr>
<td>Error</td>
<td>5727.099</td>
<td>147</td>
<td>38.960</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
‘location’. All three locations, Pt Loma (ANOVA \( F_{30.189} = 2.703, P < 0.001 \)), La Jolla (ANOVA \( F_{31.123} = 4.462, P < 0.001 \)), and the islands (ANOVA \( F_{6.52} = 2.755, P < 0.02 \)), showed a significant difference in BL over time. BL was also compared for just the 6 months where data was taken at all three locations (Table 2). Site and Time are marginally non-significant. In addition, the non-significant interaction term indicates that the relationship between time and site was consistent.

The individual plant BL values for all sites and all months were thus pooled (\( n = 434 \) plants) and the data fitted with a 10th-order polynomial for empirical description of the temporal variation. This provided a better empirical fit than any other function. Using 1 January 1995 as the first day of the study, an estimate of initial BL for any day can be found using this relationship (Fig. 2). The average monthly standard error for attached BL surveys was \( \pm 2.38 \) cm, and this number was used in the determination of the uncertainty in the age estimates. If the change in BL over time is ignored, then the S.E. of all attached plants was \( \pm 5.67 \) cm.

There was a significant difference between the four seasons in initial BL (ANOVA \( F_{3.29} = 8.127, P < 0.001 \)). There was a significant difference between seasons for the 36 months of surface temperature data (ANOVA, \( F_{3.32} = 23.73, P < 0.001 \)); however, average monthly sea surface temperature was not related to initial BL (Regression \( F_{1.31} = 1.502, P = 0.23 \)).

### 3.2. Final BL measurements

Fifty rafts were collected in five cruises (two summer, three winter) in the Southern California Bight between 1995 and 1997 and between 5 and 75 km from the nearest land (island or mainland) (see Hobday, 1998). All rafts collected had between one and 10 stipes with terminal ends; 20 blades were measured on each. Final BL ranged between 77.21 and 2.33 cm, and averaged \( 42.25 \pm 12 \) cm. The S.E. in final BL for each raft was used to calculate the uncertainty in raft age.

### 3.3. Aging rate experiments

The 11 BL aging rate experiments, using a total of 41 plants, ran for up to 63 days before the tethered rafts broke apart. All experiments showed a significant decrease in average BL with increasing time since detachment (\( P < 0.009 \) for all cases). Age

<table>
<thead>
<tr>
<th>Table 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Results of two-way ANOVA on attached plant BL at three locations for the months when all sites were sampled*</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Site</td>
</tr>
<tr>
<td>Time</td>
</tr>
<tr>
<td>Site×Time</td>
</tr>
<tr>
<td>Error</td>
</tr>
</tbody>
</table>

*Site is a fixed factor in the two-way ANOVA, and the F-ratio is obtained by dividing the Site MS by the interaction MS. For time, the F-ratio is obtained in the usual fashion (Time MS/Error MS).
accounted for a large amount of the variation in BL for all experiments (average $R^2 = 0.76$; range, 0.50–0.88) (Table 3). Aging rate was calculated from the slope of the regression line fit to all plants in an experiment, and ranged between 0.43 and 2.09 cm day$^{-1}$ (Table 3). The average aging rate was $0.94 \pm 0.48$ cm day$^{-1}$. Aging rate was temperature dependent (Fig. 3). At temperatures greater than 20°C, the rate increased sharply, and was calculated as $R = 0.1527T^2 - 6.0924T + 61.38$ ($R^2 = 0.98$), while below 20°C the rate did not change with temperature, and was estimated at 0.64 cm day$^{-1}$. The error associated with the aging rates (calculated from the fit of the regression line) increased with magnitude of aging rate, and so an error rate ($\delta R$) appropriate to the rate magnitude ($R$) was calculated for use in the final age estimate from a line describing the relationship ($\delta R = 0.1838R - 0.0032$, $R^2 = 0.83$). The aging rate was not dependent on the initial BL values for the experiment (regression, $F_{1,9} = 0.192$, $P = 0.67$).

Growth of stipes on the tethered rafts continued for some time following detachment. Maximum growth occurred in the week following detachment (0–12 cm day$^{-1}$), then declined sharply. By 40 days, average stipe growth on each detached plant was less than 1 cm day$^{-1}$. Above 20°C, growth was lower, and ceased more quickly than when water temperatures were less than 20°C.

There was no effect of handling detected in the experiments. Blades on stipes that had been measured and handled either once ($n = 143$), twice ($n = 63$), or more than twice
Table 3
Summary of all experiments for determining the aging rate (R) of rafts

<table>
<thead>
<tr>
<th>Expt.</th>
<th>Rafts</th>
<th>Start date</th>
<th>Time (days)</th>
<th>I (cm)</th>
<th>Temp. (°C)</th>
<th>R (cm day⁻¹)</th>
<th>S.E.</th>
<th>n</th>
<th>P &lt;</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3</td>
<td>7/25/95</td>
<td>42</td>
<td>55.77</td>
<td>20.67</td>
<td>0.66</td>
<td>0.10</td>
<td>19</td>
<td>0.0001</td>
<td>0.73</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>1/11/96</td>
<td>38</td>
<td>52.47</td>
<td>14.92</td>
<td>0.43</td>
<td>0.10</td>
<td>7</td>
<td>0.0087</td>
<td>0.78</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>9/27/96</td>
<td>35</td>
<td>55.79</td>
<td>18.15</td>
<td>0.65</td>
<td>0.12</td>
<td>9</td>
<td>0.0009</td>
<td>0.81</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>11/11/96</td>
<td>28</td>
<td>56.27</td>
<td>16.02</td>
<td>1.04</td>
<td>0.27</td>
<td>17</td>
<td>0.0015</td>
<td>0.50</td>
</tr>
<tr>
<td>5</td>
<td>4</td>
<td>4/17/97</td>
<td>63</td>
<td>56.68</td>
<td>20.31</td>
<td>0.64</td>
<td>0.09</td>
<td>11</td>
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<td>0.85</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>5/28/97</td>
<td>28</td>
<td>49.43</td>
<td>21.28</td>
<td>0.90</td>
<td>0.15</td>
<td>12</td>
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<td>0.79</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>7/2/97</td>
<td>36</td>
<td>47.71</td>
<td>21.43</td>
<td>1.01</td>
<td>0.18</td>
<td>16</td>
<td>0.0001</td>
<td>0.69</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>7/30/97</td>
<td>37</td>
<td>55.91</td>
<td>21.81</td>
<td>1.00</td>
<td>0.14</td>
<td>9</td>
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<tr>
<td>9</td>
<td>3</td>
<td>8/29/97</td>
<td>21</td>
<td>57.04</td>
<td>23.07</td>
<td>2.09</td>
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<tr>
<td>10</td>
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<td>9/24/97</td>
<td>15</td>
<td>51.55</td>
<td>22.14</td>
<td>1.42</td>
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<td>9</td>
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<tr>
<td>11</td>
<td>4</td>
<td>10/22/97</td>
<td>63</td>
<td>52.11</td>
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<td>26</td>
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<td>0.73</td>
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<tr>
<td>Ave.</td>
<td></td>
<td></td>
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<td>36.9</td>
<td>53.7</td>
<td>19.87</td>
<td>0.94</td>
<td>13</td>
<td>0.17</td>
<td>0.76</td>
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<tr>
<td>S.E.</td>
<td></td>
<td></td>
<td></td>
<td>15.1</td>
<td>3.21</td>
<td>2.61</td>
<td>0.48</td>
<td></td>
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</tbody>
</table>

*The number of rafts in the experiment is given in column 2, the time that the experiment ran is in the fourth column. The average initial BL (I) for the rafts, the average temperature during the experiment, estimated aging rate (R) from the regression, standard error of this estimated slope (S.E.), and the number of points in the regression (n) (i.e., one point for each raft each week) are provided. The associated P values for the hypothesis that the slope is not different from zero, and the R² for each experiment are also given. P values have been rounded to four decimal places, in many cases they were even smaller.

Fig. 3. *Macrocystis pyrifera* raft aging rate experiments and temperature. The aging rate is constant for temperatures below 20°C ($R = 0.64 \text{ cm day}^{-1}$), and increases sharply above this threshold ($R = 0.1527T^2 - 6.0924T + 61.38$, $R^2 = 0.98$).
(n = 24) during an experiment were not found to be shorter than those that had not been previously measured (n = 111) (regression $F_{1,339} = 0.499$, $P = 0.480$).

3.4. Age determination

The average age of rafts using initial BL derived from the attached plant survey (method 1) was 16 ± 21 days (range, −35 to 72 days, ±7–69). Using the maximum BL for any raft collected on the same cruise as initial BL (method 2) the average age was 38 ± 22 days (range, 0–99 days, ±11–69 days) (Fig. 4). The estimated average maximum floating period for rafts in summer, fall, winter and spring was 76.1 ± 14.5, 84.6 ± 16.1, 74.7 ± 14.3, and 88.6 ± 16.9 days, respectively.

3.5. Elasticity and improvements in age estimation

The elasticity analysis showed that the most improvement in the uncertainty of the age estimates would come from improvements in the uncertainty of final BL measurements (Fig. 5). Improving the uncertainty in the initial BL and aging rate estimates would lead to only minor improvements (see Hobday, 1998).

![Fig. 4. Estimated age of all *Macrocystis pyrifera* rafts collected in this study using method 1 (squares) and method 2 (circles) (see Section 3). Rafts 1–6 were collected before the aging methodology was developed and are not included. Bars are ±1 S.E.](image-url)
Fig. 5. Elasticity of *Macrocystis pyrifera* raft age estimates. Improvement in age uncertainty is shown for a range of percentage changes in the uncertainty of initial BL (I), final BL (F) and aging rate (R).

4. Discussion

4.1. Initial BL

A predictable initial BL value, necessary for aging *M. pyrifera* rafts, was found in one region of the stipe on attached plants (Fig. 1), however, there were differences in attached BL over time at each location. As a result, describing the initial BL cycle with a high-order polynomial allowed a better estimate of the initial BL value than just using an average initial BL value for the whole time period. Differences between locations in the Southern California Bight were close to significant (Table 2), thus, combining the BL for all sites prior to describing the time variation increases the uncertainty associated with the initial BL estimate. However, the elasticity analysis showed that reducing the uncertainty in the initial measurements would not markedly improve the uncertainty in
the age estimate (Fig. 5). The islands had a slightly higher average initial BL than the mainland sites, thus pooling all these plants will lead to a slight underestimation of the age of island-origin rafts, and overestimation of mainland-origin raft age. However, without better information on the raft origin, this bias cannot be corrected.

Although there were seasonal differences in initial BL, there was no consistent monthly initial BL cycle, nor any relationship between BL and water temperature detected in the three years of this study. North (1971) also failed to detect any seasonal morphological differences in *M. pyrifera*. Thus, a complicated function was selected to empirically describe the initial BL cycle, rather than trying to use a more simple predictive function (Fig. 2). For the purpose of this study, the goal was simply to describe the initial BL pattern, rather than explain it.

The initial BL found in this study was similar to that described in other regions of the range of *M. pyrifera*. In Tasmania an attached BL of 60 cm was typical (Cribb, 1954). He found that maximum BL was reached and growth stopped about 100 cm from the tip, and described attrition of blades with increasing distance down the stipe (as described in Fig. 1). Brown et al. (1997) found that there was no increase in BL on any mature blades (region 2) in New Zealand attached plants. They estimated erosion (deterioration) rates on mature attached blades to be matched by slight increases in length. Jackson et al. (1985) described similar blade elongation and deterioration patterns on attached stipes at La Jolla.

The reduction of flow within a kelp forest (Jackson and Winant, 1983) may lead to more shading of the understory and hence reduce growth rates and affect the blade lengths of plants in the inner portion of a forest. If these inner plants detach, they may produce ‘older’ rafts than plants detaching from the outer edge of a forest. In this study there was a significant difference of about 2 cm in average initial BL between plants found at the center and outer edge of the Pt Loma kelp forest (Table 1). However, detached plants at the center of a forest are more likely be tangled (P. Dayton, pers. commun.) and form fewer free floating rafts, which may reduce this potential aging bias. Pt Loma is the widest kelp forest in California: intra-forest differences are expected to be less or non-existent in smaller forests. Pooling the BL values for the inner and outer regions of the Pt Loma kelp forest only slightly increased the uncertainty of the initial BL estimate at that site.

4.2. Final BL

All rafts collected had stipes on which region 2 (Fig. 1) could be identified and blades measured. Rafts with an average BL $<2$ cm were never observed, which is consistent with the assumption that rafts sink when BL approaches 0 cm. The BL proxy fulfilled the criteria that the aging property has measurable values at all times.

While most rafts collected in this study had one holdfast, indicating formation from single plants (Hobday, 1998), rafts may also be composed of two or more plants (Helmuth et al., 1994). If a raft was formed from multiple plants that detached at the same time, then the aging method will still be valid. If the collected raft is an aggregation of two rafts that collided at sea and are of different ages, then the BL age estimate will approximate the average age of the two rafts. The raft fauna may have
mixed, and hence also be an averaged fauna. The uncertainty associated with the final BL measurements will be high, in turn increasing the uncertainty in the age estimate. Helmuth et al. (1994) reported that rafts collected further from the tip of South America also had more eroded blades, supporting the findings in this study.

Sunken _M. pyrifera_ stipes with BL>0 have been observed in submarine canyons and other nearshore habitats (Hobday, pers. obs.; C. Smith, E. Vetter, pers. commun.). ZoBell (1971) found that beached kelp sank when returned to the ocean; these fragments may represent previously beached material. If true, then the coast is an absorbing boundary for drifting rafts (Hobday, 2000a).

### 4.3. Aging rate determination

Experiments using tethered rafts showed that the aging rate was linear, and temperature dependent, with a change in the relationship at about 20°C (Table 3). Unfortunately, rafts were lost from all experiments before they were observed to sink. When average raft BL approached 10–15 cm, the stipes were also weak, and the rafts broke apart under the action of waves against the tethers. Thus, there is an assumption that the decline in BL below these BL values would continue to be linear.

Several biases may arise from tethering rafts. Since these kelp rafts will be anchored relative to water, their floating period may be extended as new water (and nutrients) move by, rather than the drifting raft moving in the same patch of water. If local nitrogen depletion in the patch is a major factor in raft deterioration the aging rate of tethered rafts will underestimate the natural rate. Because the experimental rafts are tethered close to the coast they may experience cloudier conditions, possibly extending the life of the kelp raft by reducing damage caused by sunlight (e.g., Jokiel, 1980). If, however, mechanical abrasion is more important, then the estimates of aging rate may be too high, as tethered rafts are fixed with regard to wave motion. The aging rates are likely to be raft size specific. The effect of increased raft size on aging rate is unknown, but greater differences in the stipe BL on larger rafts and hence greater uncertainty in rate measurements are likely.

Experimental rafts only had about 10 stipes with growth tips, and five stipe measurements were attempted each week for up to 7 weeks, and because each plant was measured many times, statistical independence was violated. This problem seems unavoidable at the scale of this experiment. The most rigorous experimental protocol would have required detaching and anchoring at least 40 plants per experiment, then measuring a new raft every week which would have required detachment and relocation of over 400 plants for this study.

Stipes on attached plants continue to grow as new blades are added. This growth also continued for a period of time when plants were detached. Typical growth rafts on detached plants in this study initially ranged between 0 and 16 cm day$^{-1}$ (averaged 4–6 cm day$^{-1}$ for a temperature range of 15–24°C) and declined with floating period. Maximum growth rates of 46 cm day$^{-1}$ were recorded by Gerard (1982) in Monterey (water temp 9–16°C), but average values were 10 cm day$^{-1}$. In Tasmania stipe growth was typically 3.4 cm day$^{-1}$ (Cribb, 1954), while in New Zealand attached plants have stipe elongation rates of between 1.2 and 2.0 cm day$^{-1}$ (Brown et al., 1997).
Zimmerman and Robertson (1985) measured elongation rates during periods of nutrient stress and found them to be lower than in normal nutrient conditions (3.0 vs. 11.0 cm day$^{-1}$). This stress mimics the change in conditions accompanying detachment and drifting. The observed decrease in stipe growth rate with increasing detachment time suggests that plant stress is higher, perhaps through nutrient depletion, or self shading. Whatever the cause, drifting M. pyrifera rafts are slowly dying.

4.4. Age estimates

A simple model based on a linear aging rate was used for age estimation. The maximum BL found for a raft collected on a cruise was often higher than the initial BL predicted from the empirical BL relationship (method 1). The initial BL value was an average for the month, and so some attached plants or rafts with higher and lower initial BL are expected. This is one problem with comparing individual final BL estimates with population level estimates for initial BL. Experiments showed that BL always declined with time following detachment, so those rafts must come from kelp plants with higher initial BL. Negative ages have little meaning: to correct this the estimated ages from method 1 can be bounded at zero, or the initial BL values can be changed. If the maximum BL found for a drifting raft on a cruise is used as the initial BL (method 2), then all rafts collected in that period have ages equal to or greater than zero. Raft ages estimated by method 2 were typically older than estimated by method 1; however, the relative ranking of raft ages did not change markedly (Hobday, 1998).

Maximum average raft floating period was estimated at between 74 and 88 days depending on the season. The uncertainty associated with seasonal estimates of maximum floating period ($\pm 14$ days), was lower than that found for collected rafts ($\pm 23$ days). This is because final BL (zero) was assumed to be measured without uncertainty, and the elasticity analysis showed this uncertainty contributed most to the uncertainty in the age estimate. There was very little difference between maximum ages because the temperature-dependent aging rate did not change for three of the seasons. The absolute maximum age for a raft in Southern California using initial BL = 70 cm, final BL = 0 cm, aging rate = 0.64 cm day$^{-1}$ (maximum or minimum values found in this study), is 109 days which is close to the maximum estimate found in this study and similar to disintegration times for tethered holdfasts (Edgar, 1987; Vasquez, 1993). Detachment and release of plants with satellite tags, such that they could be followed and measured at known times would allow true validation of this method. Ideally, with unlimited budget and ship time, free rafts could be followed for months, and sampled at weekly intervals.

To make similar estimates of raft age in the future, a researcher need only make a short time series of attached BL values in the region of study prior to collecting rafts to allow prediction of initial BL. Three to 6 months of pre-collection monitoring will cover the range of possible drift ages for all seasons. If the rafts are to be collected in southern California, no new aging rate experiments are necessary; however, in other regions where temperature and nutrient relationships may differ, some additional experiments are recommended. Final measurements of BL should be taken from region 2 of as many stipes per raft as is possible to reduce the uncertainty of the age estimate.
4.5. Elasticity analysis

Reduction in the uncertainty of the age estimate would be achieved with a decrease in the variability of the final raft BL measurements (Fig. 5). However, most of the available stipes were measured on collected rafts, and so the measured uncertainty is close to the true variability of final BL. An increase in the number of replicates in each aging experiment will reduce the variability of the aging rate estimates; however, little improvement to the variability in the age estimate would result. Similarly, decreasing the uncertainty in the estimate of initial BL would not improve the uncertainty in the age estimate (Hobday, 1998).

4.6. Conclusion

Natural rafts were estimated to float for a maximum of between 65 and 109 days depending on the aging method used. This study is the first attempt to age natural drifting algal rafts, and the resolution is greater than ever achieved with brown algae (Hymanson et al., 1990). The floating time of drifting M. pyrifera rafts will influence the possible dispersal distances and the distances that fauna may be transported (Helmut et al., 1994; Hobday, 2000a). Previous studies of the fauna of detached algae have just compared attached and drifting material, ignoring the temporal patterns (Kingsford and Choat, 1985; Bushing, 1994; Ingolfsson, 1995, but see Helmuth et al., 1994). Distance offshore and density of particular species has been used a proxy for algal raft age (Helmut et al., 1994; Ingolfsson, 1995), but does not allow the same rigor in estimation as with the methods developed in this study. The methods for aging the drifting kelp rafts developed in this study will allow the patterns of faunal abundance on natural rafts to be related to the time the raft has been drifting (Hobday, 2000b).

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