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# Prediction of the distribution of settled *Sargassum* propagules*

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**Abstract**: This paper investigated the way to predict the distribution of *Sargassum* propagules settled on the sea bottom using diffusion parameters obtained by current measurements. Solving a vertical transport equation, I estimated the vertical flux of propagules at the sea bottom and assumed that the lateral distribution of drifting propagules is expressed by the Gaussian distribution. Combining the vertical flux of propagules and horizontal diffusion, I proposed a model that predicts the distribution of *Sargassum* propagules settled on the sea bottom.

In order to obtain the diffusion parameters of this model, I made current measurements around *Sargassum* forests in Gokasho Bay, Mie Prefecture, Japan. Using these parameters, I predicted the distribution of settled propagules released instantaneously from the center of a *Sargassum* forest. I compared the predicted distribution with the field data obtained by using artificial substrata. The distribution predicted by the model using these diffusion parameters agreed well with the actually measured distribution of propagules of *S. horneri* around an offshore forest.

## 1. Introduction

One of the most precarious stage in the life of any benthic organisms is their dissemination phase. For most seaweeds, microscopic propagules with little or no powers of locomotion represent the most important, often the only dispersal mechanism. However, this aspect of algal ecology has been relatively little studied. This paper proposes a method for predicting the distribution of settled propagules of *Sargassum* by using diffusion parameters obtained from current measurements and compares the predicted distribution with the measured distribution of *S. horneri*.

## 2. Release, settlement and adhesion of propagules of *S. horneri*

*S. horneri*, a brown seaweed which is popular in central Japan, become fertile in April and May. Eggs are found on the surface of the receptacles, and after few days propagules are released from the surface of the receptacles before development of rhizoids, and sink with their base up. After propagules touch on substratum, the tenacity of adhesion increases with the length of the period for which the propagules have been in residence on the substratum (OKUDA, 1984). After two days the percentage of the propagules of *S. horneri* surviving exposure to a water flow of 90cm/s exceeds ninety percent (IHKURA, personal communication), and they are hardly dislodged from the substratum under ordinary wave conditions in *Sargassum* forests.

## 3. The model

The purpose of the model is to predict

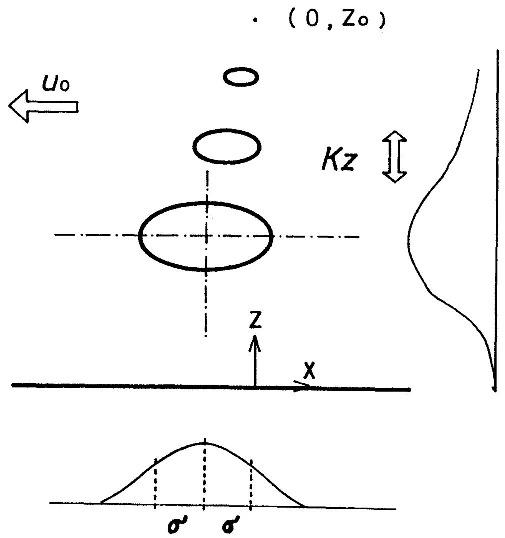


Fig.1. Schematic processes through which propagules released from a single point sink and diffuse in turbulent water.

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the distribution of settled propagules using the diffusion parameters obtained by current measurements. I intend the model to be simple, but capable of realistically predicting the distribution of settled propagules.

I deal with a two-dimensional diffusion problem. Consider the situation shown in Fig. 1. A propagule is shed at a moment ($t=0$) from a single point set at some distance from the sea bottom ($x=0$, $z=z_0$). For simp licity, I deal with vertical and lateral diffusion independently each other.

(1) *Vertical diffusion*

If $p_z(z, t)$ describes the probability that a propagule is at point $z$ at time $t$, then the equation describing the dynamics of the probability is given by

$$\frac{\partial p_z}{\partial t} + w\frac{\partial p_z}{\partial z} = K_z\frac{\partial^2 p_z}{\partial z^2}, \quad \cdots\cdots\cdots\cdots(1)$$

where $w$ is the sinking velocity of the propagule and is assumed to be a negative constant, $K_z$ is the vertical eddy diffusivity and is assumed to be constant. This equation can be solved if initial and boundary conditions are provided. First, I assume that the initial condition is $p_z(0, z) = \delta(0, z_0)$. The second assumption is that the propagule adheres when it contacts the sea bottom, $p_z=0$ at $z=0$, and the water depth is sufficiently deep to neglect surface effects. Solving Eq. (1), which applies the initial and boundary conditions, we see that

$$p_z = \frac{1}{2(\pi K_z t)^{1/2}}\left[\exp\left\{-\frac{(z-z_0)^2}{4K_z t}\right\} - \exp\left\{-\frac{(z+z_0)^2}{4K_z t}\right\}\right]\cdot \exp\left\{\frac{w(z-z_0)}{2K_z} - \frac{w^2 t}{4K_z}\right\}. \quad \cdots\cdots\cdots\cdots\cdots\cdots(2)$$

Calculating the flux at the sea bottom, we see that

$$f_z(t) = \left[wp_z + K_z\frac{\partial p_z}{\partial z}\right]_{z=0}$$

$$= \frac{1}{2(\pi K_z t)^{1/2}}\frac{z_0}{t}\cdot exp\left\{-\frac{(z_0+wt)^2}{4K_z t}\right\}. \cdots\cdots(3)$$

This $f_z(t)$ is the probability that the propagule released from $z=z_0$ at $t=0$ contacts the sea bottom at a time $t$, and is shown in Fig. 2 for values of $K_z$. The release height ($z_0$=5m) and sinking velocity ($w$=−5mm/s) are typical values for *S. horneri*.

From this figure, we can see that for the

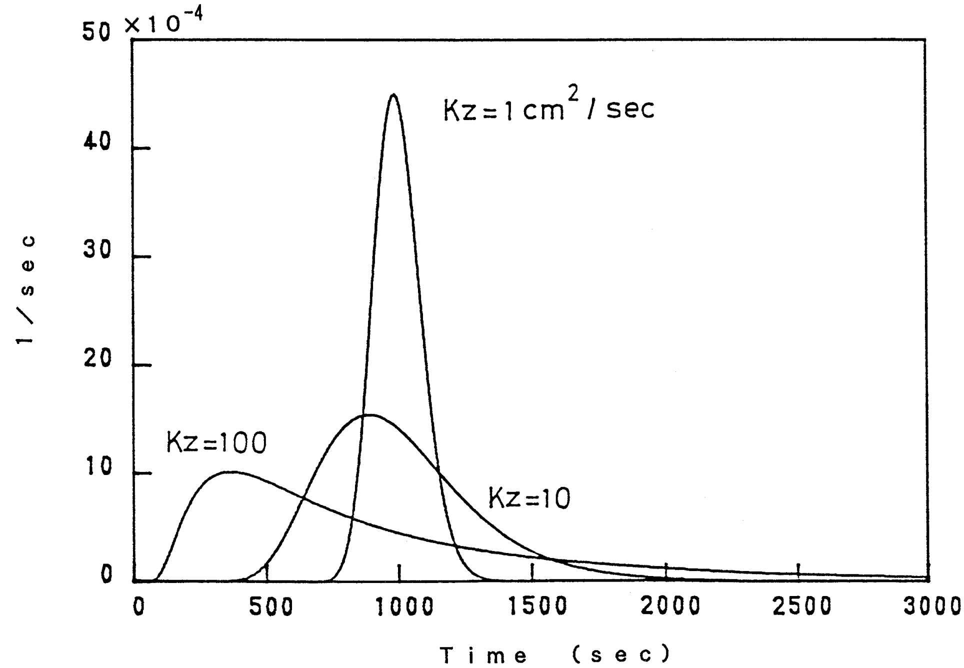


Fig. 2. Vertical flux of *Sargassum* propagules at the sea bottom estimated by Eq. (3) for $z_0$=500 cm and three values of $K_z$ .

increasing vertical eddy diffusivity most propagules settle more rapidly because of diffusive transport, while some propagules stay longer in the water column.

(2) *Lateral diffusion*

Lateral diffusion is variable due to inherent properties of fields of flow. I assumed that lateral distribution of the propagule is given by

$$p_x(x,t)=\frac{1}{(2\pi)^{1/2}\sigma}\exp\left\{-\frac{(x-u_0t)^2}{2\sigma^2}\right\},\cdots(4)$$

where $p_x(x,t)$ is the probability that the propagule is at point $x$ at time $t$, $u_0$ is a uniform flow, and $\sigma^2$ is the variance about the center of the distribution. The relationship between $\sigma^2$ and $t$ is determined from field observations.

(3) *Distribution of settled propagule*

The probability that the propagule released from a point $x=0$, $z=z_0$ settles finally at a distance $x$ is then given by

$$P(x)=\int_0^\infty f_z(t)\cdot p_x(x,t)dt.\cdots\cdots\cdots\cdots\cdots\cdots(5)$$

If we know the values of vertical diffusivity $K_z$ and can express the horizontal variance $\sigma^2$ as a function of time after release, we can predict the distribution of *Sargassum* propagules settled on the sea bottom by using Eqs. (3), (4) and (5). When the source of propagules is not a single point and the release of propagules is continuous, we can predict the distribution of the settled propagules by integrating Eq. (5) for space and time.

## 4. Estimation of the diffusion parameters

Diffusion in the ocean has been studied by using dye or drifters. This is essentially a Lagrangian approach which provides data related to diffusion processes. However, Lagrangian type field experiments are difficult to carry out for a long period of time around *Sargassum* forests. Hence I adopted the moored current meters, and estimated the diffusion parameters under the assumption that Eulerian process is approximately similar to Lagrangian one.

(1) *Distribution of Sargassum forests*

Field observations were carried out in Gokasho Bay, central Japan (Fig. 3). Figure 4 shows the study site. From April to May

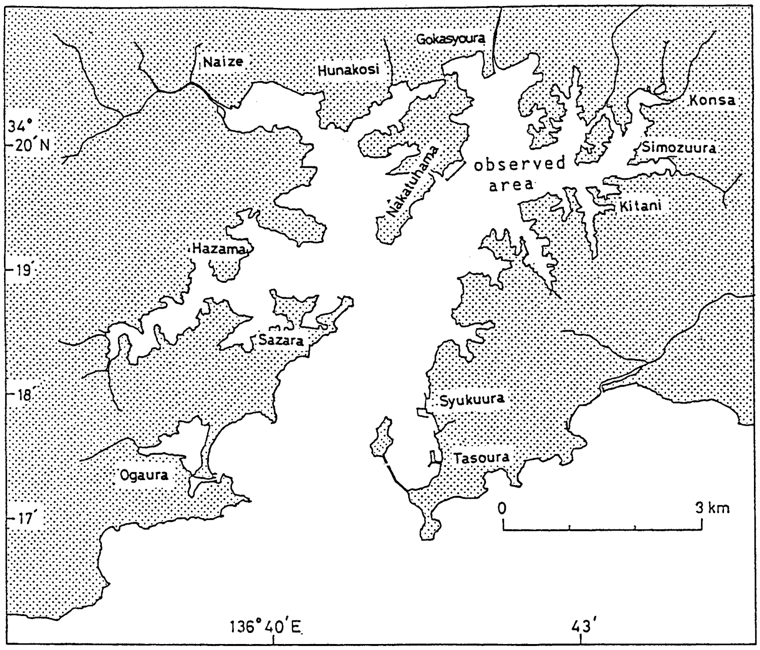


Fig. 3. Map of Gokasho Bay, Mie Prefecture, Japan.

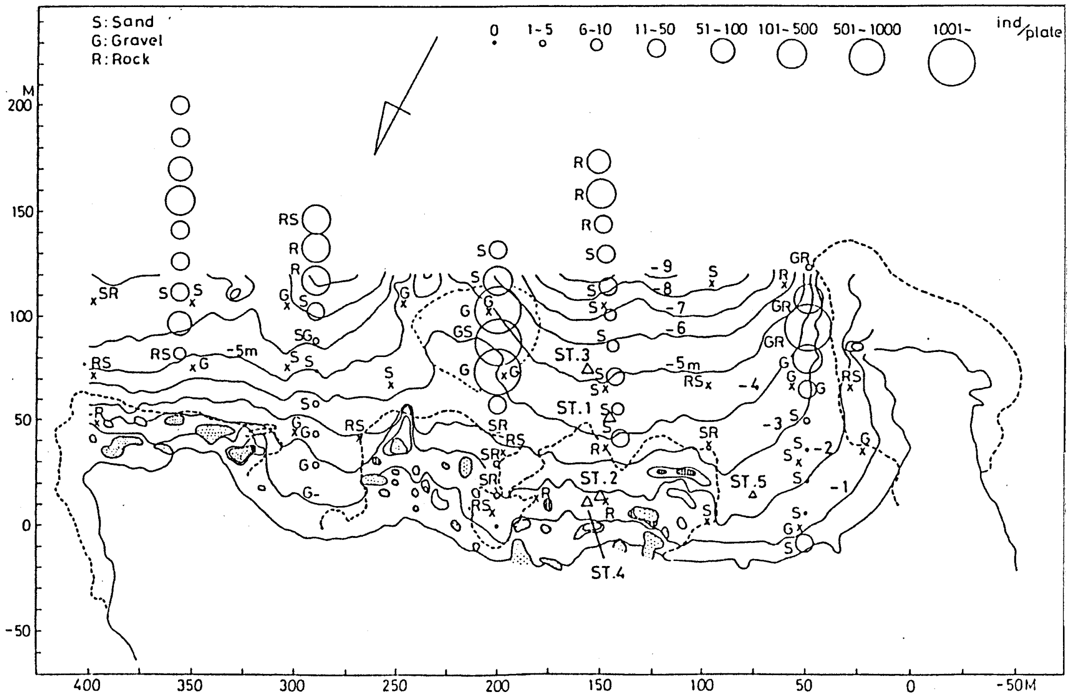


Fig. 4. Study site and numbers of *Sargassum* propagules per plate settled on artificial substrata put out on 9–18 April and sampled on 8–14 May 1985. Broken lines indicate rock or gravel regions determined by aerial photographs. Crosses are stations where bottom substrata were observed. Triangles are stations where water movement were measured.

*Sargassum* forests mainly composed by *S. horneri* and *S. piluliferum* grow luxuriantly in rock or gravel regions indicated by broken line in the figure. The density of *Sargassum* forests is about 4 kg wet weight per square meter (TODA *et al*., 1989).

(2) *Vertical diffusivity*

Locations of current measurement sites are shown in Fig. 4. Table 1 lists the bottom depth at the measurement sites, the height at which current meters were fixed and sampling time-intervals. I measured vertical velocity in a *Sargassum* forest (Run 1-1) and offshore (Run 1-2) of it. Waves were visually estimated to have a period of about 6 second, and the power spectra of vertical velocity showed strong peaks of frequency 0.17/s.

Values of vertical diffusivity are obtained by

$$K_z = < w'^2 > T_* \qquad \cdots\cdots\cdots\cdots(6)$$

and

$$T_* = \int_0^\infty r_w(\tau)\,d\tau\ , \qquad \cdots\cdots\cdots\cdots(7)$$

where $< w'^2 >$ is the mean squares of vertical component of the turbulent velocity obtained by subtracting the running mean from the measured data for 6.6 sec to cut off the effect of wave orbital velocity, and $r_w(\tau)$ is the auto-correlation function. The vertical distribution of $K_z$ is shown in Fig. 5. The mean of $K_z$ was 2.4 cm$^2$/s at offshore of the *Sargassum* forest and was 1.3 cm$^2$/s in it.

(3) *Lateral variance as a function of time after release*

I analyzed north component of lateral velocity which was dominant in the study site (Run 2,3; Table 1,2). The lateral displ acement of propagules $Y(t)$ is calculated by integrating the measured velocity under the assumption that Eulerian process is similar to Lagrangian one, namely

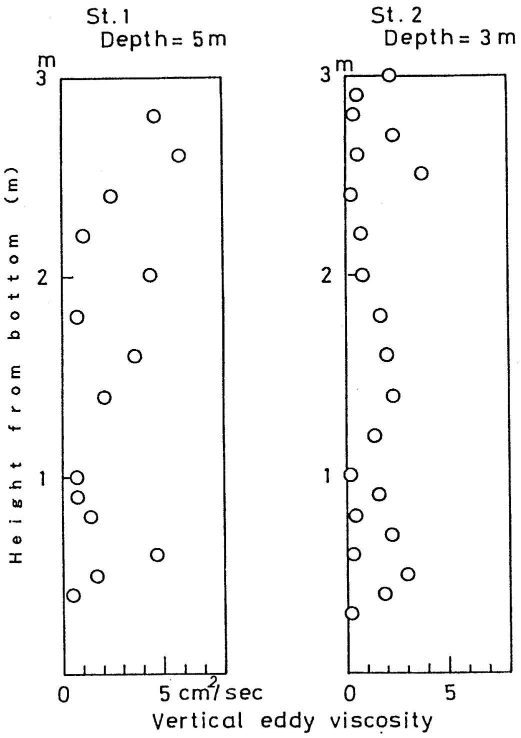


Fig. 5. Profiles of vertical eddy viscosity at St. 1 on 30 April (Run 1-1) and at St. 2 on 2 May (Run 1-2) 1985.

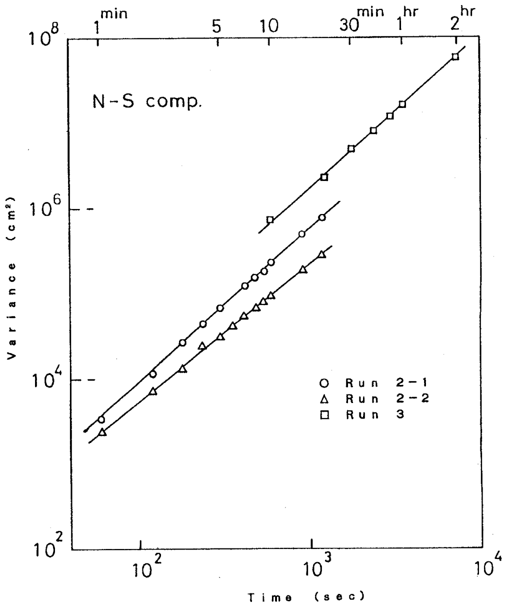


Fig. 6. Regressions of variance ($\sigma^2$) of lateral displacement of *Sargassum* propagules vs. time (open circles: Run 2-1, open squares: Run 2-2, open triangles: Run 3).

Table 1. List of current measurements around *Sargassum* forests. Location of the study site is shown in Fig. 4.

| Run | St. | Bottom depth (m) | Sensor height (m) | Sampling interval | Length of one record and duration of measurement |
|---|---|---|---|---|---|
| Run 1-1 | St. 1 | 5.0 | 0.4-2.8 | 0.317 sec | 3 min 1985 4/30 13:00-15:00 |
| Run 1-2 | St. 2 | 3.0 | 0.3-3.0 | 0.317 sec | 3 min 1985 5/ 2 12:30-16:00 |
| Run 2-1 | St. 3 | 6.2 | 2 | 1 min | 1 day 1987 3/ 9 11:00- |
| Run 2-2 | St. 3 | 6.2 | 2 | 10 min | 19 day 1987 4/14 0:00- |
| Run 3 | St. 4 | 2.5 | 1 | 5 sec | 1 day 1986 4/23 10:00- |

Table 2. Statistics for current measurements.

| | Run 2-1 | | Run 2-2 | | Run 3 | |
|---|---|---|---|---|---|---|
| | E-comp. | N-comp. | E-comp. | N-comp. | E-comp. | N-comp. |
| Mean (cm/s) | 0.13 | 0.68 | 0.37 | 0.30 | 0.42 | -0.35 |
| S.d. (cm/s) | 0.80 | 1.00 | 1.39 | 1.67 | 0.56 | 0.83 |
| Max. (cm/s) | 3.30 | 5.60 | 12.70 | 8.90 | 2.75 | 3.04 |
| Min. (cm/s) | -2.60 | -3.30 | -6.20 | -11.80 | -2.46 | -4.83 |
| $a$ | 1.54 | 2.56 | 15.37 | 6.45 | 1.09 | 3.42 |
| $m$ | 1.78 | 1.78 | 1.66 | 1.80 | 1.72 | 1.60 |

$$Y(t)=\int_0^t udt, \qquad \cdots\cdots\cdots\cdots\cdots(8)$$

Figure 6 shows the variance ($\sigma^2$) of $Y(t)$ plotted against time $t$. The regression line fitted to the bilogarithmic plot corresponds to $\sigma^2(t)$ proportional $t^m$.

$$\sigma^2=at^m \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots(9)$$

Values of the indices $a$ and $m$ are shown in Table 2.

The rate of relative lateral diffusion may be represented by a coefficient of eddy diffusion $K_x$ defined by

$$K_x=\frac{1}{2}\frac{d\sigma^2}{dt}\ . \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots(10)$$

From Eq. (9), $K_x$ is then given by

$$K_x=\frac{1}{2}mat^{m-1}=c\sigma^r\ , \qquad \cdots\cdots\cdots\cdots\cdots\cdots\cdots(11)$$

where $r=2(m-1)/m$ and $c$ is a constant. Equation (11) represents the dependence of $K_x$ on scale (BOWDEN, 1974). Theoretical treatment of diffusion shows the case $m=1$ is Fickian diffusion with $K_x$ constant while $m=2$ implies that $K_x$ increases linearly with $t$ or $\sigma$, corresponding to a constant diffusion velocity. The case $m=3$ corresponds to $K_x$ being proportional to 4/3, which is considered with inertial subrange conditions for locally isotropic turbulence, if $\sigma$ is identified with the scale of the process.

Values of the index $m$ lay between 1.6 and 1.8, that is a little smaller than 2. Anyway, we can estimate the variance of lateral diffusion by Eq. (9) and Table 2.

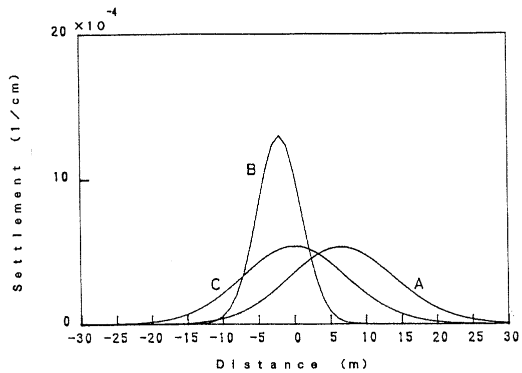


Fig. 7. Distribution of *Sargassum* propagules (1/cm) estimated to settle to the sea bottom by Eq. (5).
A: $z_0=500$ cm, $K_z=2.4$ cm$^2$/s, $u_0=0.68$ cm/s, $\sigma^2=2.56\ t^{1.78}$.
B: $z_0=300$ cm, $K_z=1.3$ cm$^2$/s, $u_0=-0.35$ cm/s, $\sigma^2=3.42\ t^{1.6}$.
C: $z_0=500$ cm, $K_z=0$ cm$^2$/s, $u_0=0$ cm/s, $\sigma^2=2.56\ t^{1.78}$.

(4) *Prediction of the distribution of settled propagules*

Combining the vertical flux and horizontal diffusion, I calculated the probability distribution of settled propagules by Eq. (3), (4) and (5) using the diffusion parameters obtained by current measurements (Fig. 7). The distribution curve A is calculated by using the vertical eddy diffusivity obtained by Run 1-1 and the relationship between $\sigma^2$ and $t$ obtained by Run 2-1 at offshore stations (St. 1 and St. 3) of the *Sargassum* forest. The curve B indicates that at St. 2 (Run 1-2) and St. 4 (Run 3) in the *Sargassum* forest. The curve C is calculated under similar conditions with A except uniform flow ($u_0$) and vertical diffusivity are neglected. The curves A and C are seen to be similar in shape, showing that the effect of sinking velocity of propagule ($w$) exceeds the one by vertical diffusion in this case.

## 5. Distribution of settled *Sargassum* propagules

I investigated the distribution of settled *Sargassum* propagules by using artificial substrata (vinyl chloride plate 10 cm ×5 cm, Fig. 8). Artificial substrata were put out on 9-18 April and sampled on 8-14 May 1985 in study site (Fig. 4). The majority of measured propagules was *S. horneri* and the number of propagules settled on the artificial substrata

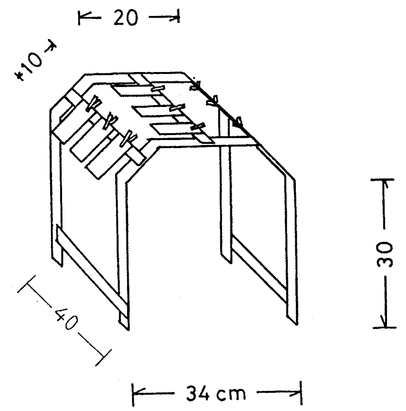


Fig. 8. Artificial substrata (vinyl chloride plate, 10 cm×5 cm) attached to a stainless grid.

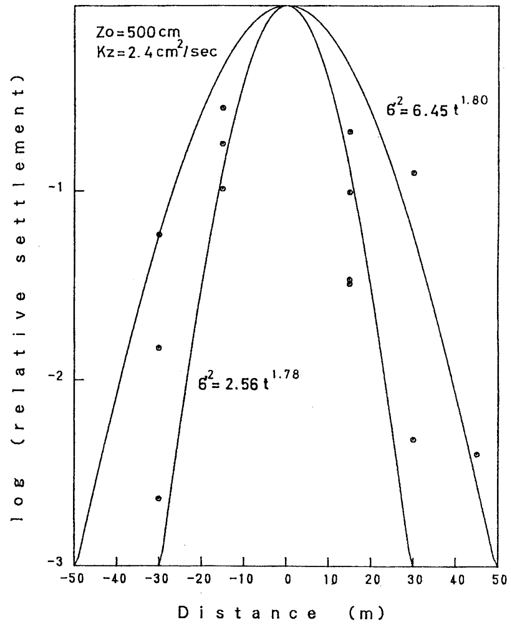


Fig. 9. Comparison of numbers of *Sargassum* propagules estimated to settle to the sea bottom with observed one (open circles). Solid lines show estimated distribution of propagules by Eq. (5).
A: $z_0=500$ cm, $K_z=2.4$ cm²/s, $u_0=0.68$ cm/s, $\sigma^2=2.56\ t^{1.78}$.
B: $z_0=500$ cm, $K_z=2.4$ cm²/s, $u_0=0.30$ cm/s, $\sigma^2=6.45\ t^{1.8}$.

ranged from 0 to 2197 individuals/50 cm². Numbers of propagule settled on the artificial substrata in a near-shore region were low, while numbers were high around an offshore *Sargassum* forest. These results indicate that wave motion effected the settlement of propagules on the artificial substrata in the following manners (TODA *et al.*, 1989). In a near-shore *Sargassum* forest where wave ray concentrates, the propagules that fell onto the substrata were carried out by wave motion. In a near-shore small bay where wave ray disperses and the sea bottom is muddy, settlement of silt on the substrata inhibited the settlement of propagules. On the other hand, in a offshore region where wave motion has little effect on the settlement of propagules, distribution of propagules reflected the dispersion from offshore mother plants.

I compared the actually measured distribution of propagules of *S. horneri* in a offshore region with the predicted distribution, under an assumption that the propagules are released from the single point set at a distance of 5 m from the sea bottom in the center of the offshore *Sargassum* forest. In Fig. 9, solid curves represent the estimated distribution of propagules using the power law obtained from two observations in a offshore region of *Sargassum* forests, while open circles show the relative number of propagules normalized by the maximum number of propagules in the center of the *Sargassum* forest. The predicted distribution agreed well with the distribution of relative number of propagules of *S. horneri* obtained from the field experiment in the offshore region.

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# ホンダウラ類幼胚の着底数密度分布の予測

杜　多　　哲

藻場中心の一定の高さから$\delta$関数的に放出された幼胚が、中心から一定の位置の海底に着底する確率密度分布を予測する手法を提案した。鉛直方向には拡散係数を定数として扱い、幼胚の沈降と拡散を考慮した輸送方程式を解いて、海底面での幼胚フラックスを幼胚放出後の時間の関数として求めた。水平方向への拡散による幼胚の水平分布は正規分布で近似できると考え、その広がりを表す統計的分散は幼胚放出後の時間の関数として観測結果から求めることとした。海底面でのフラックスと水平方向の拡散を組み合わせることによって、幼胚の着底確率密度分布を求める方法を示した。

このモデルの中の拡散パラメーターを求めるために、三重県五ヶ所湾のガラモ場周辺で流れの測定を行い、鉛直拡散係数および水平方向の広がりを表す統計的分散と時間の関係を求めた。これらの拡散パラメーターを用いて藻場の中心から$\delta$関数的に放出された幼胚の着底数密度分布を予測した。また人工的な付着基盤を多数海底に設置することにより、アカモク幼胚の着生数の分布を求めた。波の影響の少ない沖側の藻場周辺では、予測した分布と測定した分布はよく一致しこの手法の有用性が示された。