Journal of the Oceanographical Society of Japan
Vol. 42, pp. 22 to 29, 1986

Introduction of Accumulation-Dispersal Coefficient of Marine Organisms*

Hideo Kawai†

Abstract: Avoiding the subject for fish accumulation, the traditional view in fish population dynamics has ascribed immigration and emigration of fish to dispersal of fish. The main purpose of this paper is to find a quantity that represents the time rate of accumulation-dispersal of marine organisms, and also has some relation to the horizontal convergence of current velocity of the surrounding water. For this, the accumulation-dispersal coefficient is introduced not in the form of diffusion, but in the same form as the convergence. Since the accumulation-dispersal of organisms is a factor that changes its distribution density, all factors causing the change are first classified to locate the position occupied by the accumulation-dispersal. Each factor corresponds to each coefficient appearing in a linearized equation describing the rate of change in the density, averaged over a region or a group. The immigration-emigration coefficient is divided into three coefficients of passage, accumulation-dispersal and diffusion velocity. For the organisms ranging in a nearly horizontal layer, the accumulation-dispersal coefficient is shown to equal the area-averaged horizontal convergence of organismal velocity relative to land, which is the sum of the area-averaged horizontal convergences of swimming velocity relative to water and of current velocity. However, the area-averaged convergence of current velocity associated with the accumulation-dispersal coefficient for a region is shown to be somewhat different from the usual one.

1. Introduction

The majority of the accumulation-dispersal phenomena of marine organisms may disappear if they are simply averaged over a broad area and a long period; yet the phenomena are important for modes of organisms' life and fisheries, irrelevant of the spatiotemporal scale involved. For instance, while a contagious distribution of some phytoplankton induces a success in the initial feeding and subsequent survival of larvae, this may not necessarily be so for a homogeneous distribution of the same population (Lasker, 1975). When a fish stock is distributed homogeneously, it may be unavailable for a fishery due to excessive expenditures required for fishing operations, but when the same stock is distributed contagiously, it may become available. The accumulation-dispersal rate of fish is further related to the duration of fishing grounds, necessary for a fishery forecasting.

As will be shown in Sec. 2, the accumulation-dispersal coefficient over a region is included in the immigration-emigration coefficient, I, for that region. Related to I, various studies have been undertaken in fish population dynamics (Kawai, 1986a). According to the traditional view, not only emigration but also immigration has been regarded as dependent on the intrinsic rate of dispersal of fish (Beverton and Holt, 1957; Beverton and Gulland, 1958; Tanaka, 1960, 1985). They stated that the emigrating rate in a region is proportional to the density of that region, while the immigrating one is not. On the other hand, there has been another viewpoint that immigration as well as emigration can be described by using I. From the latter viewpoint this paper does not regard I as that related to diffusion but does it as a genuine one. According to Kawai (1986a), $|I|$ for various fish stocks is inversely proportional to sampling time-intervals, and dominates over other coefficients at short time-intervals.

The main purpose of this study was to find a quantity, which represents the rate of accumulation-dispersal of organisms, and which further has some relation to the horizontal convergence

* Received 15 April 1985; in revised form 10 September 1985; accepted 5 November 1985.
† Department of Fisheries, Kyoto University, Kyoto 606, Japan.

of current velocity of the surrounding water. In this paper, therefore, the accumulation-dispersal coefficient is introduced not in the form of diffusion but in the same form as the convergence. Although this is reasonable, the distribution and movement of organisms should be regarded as continuous for a mathematical expression. This idea has been published for the physical oceanography of particles (Kawai, 1976). Since such accumulation-dispersal of marine organisms is a factor that alters the distribution density, a classification of all factors causing the change is first made. This is related to the linearization of the equation describing the rate of change in the distribution density, averaged over a region or a group.

As mentioned above, the local accumulation of fish stocks is a weak subject for the traditional fish population dynamics. In dealing with the spatial variability of distribution density, general population dynamics also remains in the frame of some aggregation indexes in a static approach, such as Morisita's (1959) "index of dispersion," *Iδ*, and Lloyd's (1967) "index of patchiness," or it may emphasize diffusions even in a dynamic approach (Okubo, 1980). Introducing the accumulation-dispersal coefficient, a fundamental idea in this paper may find a clue for developing new population dynamics. At present, available data for analysis, based on the idea advanced in this paper, are few, but it may stimulate a development of instruments to measure not only the distribution density of fish but also its horizontal flux.

2. Classification of factors changing the distribution density

Stavn (1971) classified organismal distribution patterns to determine the major causes of patterns in nature. His classification was a modification of Hutchinson's (1953), which was composed of vectorial, coactive, reproductive, social and stochastic patterns. Haury *et al.* (1978), on the basis of Hutchinson's classification, assumed the stochastic elements to be contained in each of the other major mechanisms. In this paper, a new classification of factors that change the distribution densities averaged over a region and a group is systematically made (Fig. 1). Kawai (1981, 1982) tried to classify factors accumulating marine organisms, but the trial was based on such a group as a school, an elementary population, a race or a patch. It was also restricted to factors that increased the density, and some of the terms used were not appropriate. The analysis based on a group or a population sounds conceptionally logical, and looks convenient to the traditional population dynamics.

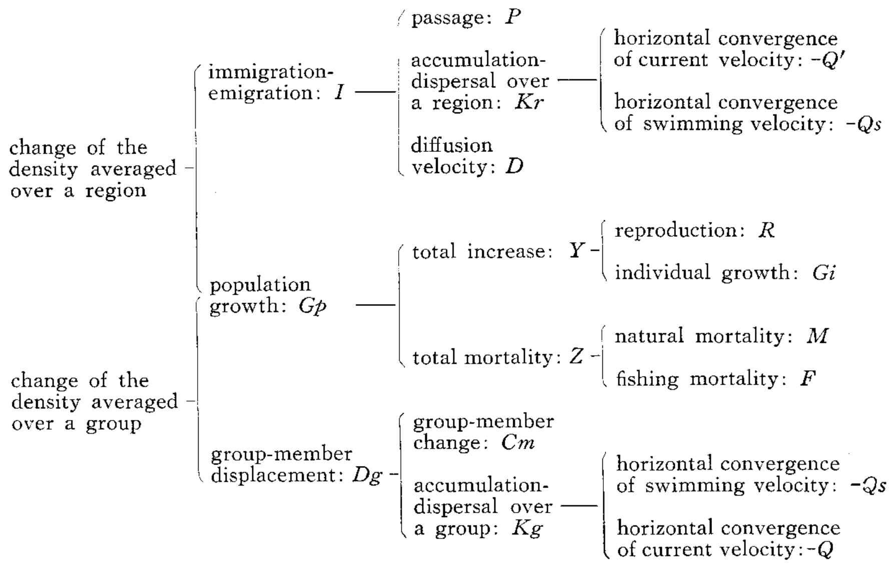

Fig. 1. Classification of factors affecting the distribution density, averaged over a region or a group, along with corresponding symbols of the coefficients appearing in the equations that describe the rate of change in the density.

However, difficulties are encountered with such problems as the identification of group members in the case of mergence, split and dissipation of the group. In addition, from a commercial standpoint, an analysis based on a region is indispensable to coastal fisheries (Ogawa, 1980) as well as international ones.

2.1. Factors changing the density averaged over a region

The top and middle of Fig. 1 shows the classification of factors affecting the density averaged over a region, along with corresponding symbols of the coefficients in Eqs. (4), (9) and (2), which describe the rate of density change (Sec. 3.1). The change is divided into two entirely different factors: immigration-emigration and population growth. The former is subdivided into three factors: passage, accumulation-dispersal over a region and diffusion velocity. Figure 2 represents a one-dimensional schema of the first two of the three factors in a special case where the density does not vanish at every point along the sections. Even if the organismal velocity relative to the land is constant, a difference in density between the two sections causes a difference in flux between immigration and emigration. This is a contribution of the passage to immigration-emigration. On the other hand, even if the density is constant, a difference in the velocity causes a flux difference. This is a contribution of the accumulation-dispersal over a region to immigration-emigration. Diffusion velocity is a contribution other than passage and accumulation-dispersal over a region to immigration-emigration.

2.2. Factors changing the density averaged over a group

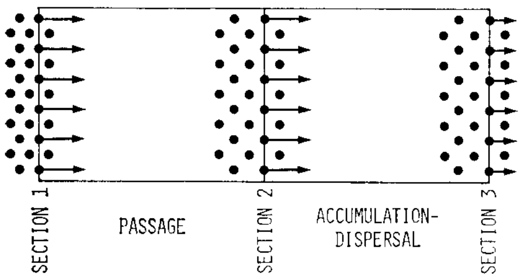

Fig. 2. One-dimensional schema of passage and accumulation-dispersal, two factors changing the distribution density averaged over a region. There is no difference in the organismal velocity between sections 1 and 2, and no difference in the density between sections 2 and 3.

The middle and bottom of Fig. 1 indicates the classification of factors that change the density averaged over a group, along with the corresponding symbols of the coefficients in Eqs. (18) and (19) that describe the rate of change in the density (Sec. 3.3). The change is divided into two entirely different factors: group-member displacement and population growth. The former is further subdivided into two: group-member change and accumulation-dispersal over a group, which is in reality a group-area change. As mentioned above, it is not possible to give analyses of such a disunited group as merges, splits or dissipates. Figure 3 represents a schema of the two factors. Even if the area occupied by a group is constant, the entrance of non-grouped individuals and exit of grouped ones causes a group-member change and consequently a group-member displacement. On the other hand, even if the members do not change, an area change causes an accumulation-dispersal and consequently a group-member displacement.

2.3. Population growth

The population growth shown in the middle of Fig. 1 participates in a change of the distribution density averaged over a region or a group. In human ecology, it includes not only birth and death, but also a social increase as immigration subtracted by emigration. In general ecology, however, it does not include immigration and emigration (Fig. 1). Corresponding to the traditional equation for a changing fish stock, the population growth in Fig. 1 is defined as the total increase subtracted by the total mortality. The total increase is the sum of reproduction and individual growth, but mostly the former is for single-celled organisms and the latter for the multicellular organisms. The total mortality is the sum of natural and fishing mortalities.

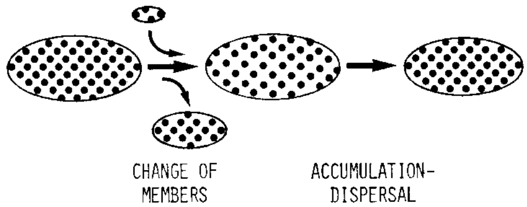

Fig. 3. A schema of the change of members and accumulation-dispersal, two factors that affect distribution density averaged over a group. The time sequence runs from left to right.

The above classification is applicable not only to fishery organisms, but also to such nonfishery ones as red-tide organisms when omitting the factor of fishing mortality. The factor of "recruitment" used in fish population dynamics is here included in immigration-emigration or group-member change.

2.4. Horizontal convergence

As the density treated in this paper is an average over a specific horizontal area, the rate of accumulation-dispersal over a region or a group is equivalent to the horizontal convergence of organismal velocity, when the organisms range in a nearly horizontal layer (Sec. 4).

3. Equation for the rate of change in distribution density

3.1. Coefficients in a region-averaged equation

The equation of the rate of change in distribution density of a population at a point in a two-dimensional sea is given by

$$\partial n/\partial t = -\boldsymbol{\nabla}\cdot(n\boldsymbol{V}) + Gp\, n \qquad (1)$$

and

$$Gp = Y - Z,\ Y = R + Gi,\ Z = M + F, \qquad (2)$$

where t is time; $\boldsymbol{\nabla}$ denotes the differential vector operator in the horizontal plane; n is the density, which equals a moving average of (the total biomass of the population in a water column under an element of the sea-surface / the area of the element); and $\boldsymbol{V}$ the horizontal velocity vector of organisms relative to land, which equals the moving average of (the horizontal momentum vector / the total biomass) for the population. The area of the element is assumed to be sufficiently small compared to that of the region to be considered below. The population growth coefficient, Gp, is defined by Eq. (2), where Y is the total increase coefficient, Z total mortality coefficient, R reproduction coefficient mostly for single-celled organisms, Gi individual growth coefficient mostly for multicellular organisms, M natural mortality coefficient, and F fishing mortality coefficient (Sec. 2.3).

Taking an average of Eq. (1) over a sea-surface region bounded by a closed curve c, and defining immigration-emigration coefficient I by

$$I = -\overline{\boldsymbol{\nabla}\cdot(n\boldsymbol{V})}/\bar{n}, \qquad (3)$$

we can write

$$\mathrm{d}\bar{n}/\mathrm{d}t = (I + Gp)\bar{n}, \qquad (4)$$

where the overbar denotes an area-average over the region. Here, positive and negative values of I correspond to immigration and emigration, respectively. When $n=0$, I disappears, because $\boldsymbol{V}=0$ in Eq. (3). By applying Green's theorem in the plane to Eq. (3), we find

$$I = -\int_c n\boldsymbol{V}\cdot\mathrm{d}\boldsymbol{B}/\bar{n}A, \qquad (5)$$

where A is an area of the region, $\mathrm{d}\boldsymbol{B} = \boldsymbol{b}\,\mathrm{d}c$, and $\boldsymbol{b}$ is the exterior unit normal to the curve c. When a portion of c coincides with coastlines and fronts acting as barriers for organisms, we can write Eq. (5) as

$$I = -\int_{c'} n\boldsymbol{V}\cdot\mathrm{d}\boldsymbol{B}/\bar{n}A, \qquad (5')$$

where $c' = c - c''$, and c'' is the sum of the integration paths that coincide with the coastlines and fronts, because $\boldsymbol{V}\cdot\mathrm{d}\boldsymbol{B}$ vanishes along c''.

Denoting a deviation from the average over the region by a prime, we have

$$n = \bar{n} + n' \text{ and } \boldsymbol{V} = \overline{\boldsymbol{V}} + \boldsymbol{V}'. \qquad (6)$$

Substitution of Eq. (6) into Eq. (5′) yields

$$I = -\overline{\boldsymbol{V}}\cdot\int_{c'} n'\mathrm{d}\boldsymbol{B}/\bar{n}A - \int_{c'} \boldsymbol{V}\cdot\mathrm{d}\boldsymbol{B}/A - \int_{c'} n'\boldsymbol{V}'\cdot\mathrm{d}\boldsymbol{B}/\bar{n}A. \qquad (7)$$

Defining passage coefficient, P, accumulation-dispersal coefficient for a region, Kr, and diffusion velocity coefficient, D, by

$$P = -\overline{\boldsymbol{V}}\cdot\int_{c'} n'\mathrm{d}\boldsymbol{B}/\bar{n}A, \qquad (8.1)$$

$$Kr = -\int_{c'} \boldsymbol{V}\cdot\mathrm{d}\boldsymbol{B}/A = -\overline{\boldsymbol{\nabla}\cdot\boldsymbol{V}}, \qquad (8.2)$$

$$D = -\int_{c'} n'\boldsymbol{V}'\cdot\mathrm{d}\boldsymbol{B}/\bar{n}A, \qquad (8.3)$$

respectively, we can write Eq. (7) to be

$$I = P + Kr + D. \qquad (9)$$

The derivation of the right side of Eq. (8.2) is based on the principle that either of c or c' can be taken as an integral path in this case. When $n=0$, each of P, Kr and D disappears, because $\boldsymbol{V}=0$ in Eq. (8).

3.2. Three coefficients for regions of special shape

For a region bounded by arbitrarily shaped coastlines and m straight sections (Fig. 4), the three coefficients can be defined. Denoting the exterior normal to the ith section ($i=1, 2, \dots, m$), whose length is B_i, by $\boldsymbol{B}_i$, and an average over the ith section by $[\ ]_i$, we can transform Eq. (8) into

$$P=-\overline{\boldsymbol{V}}\cdot\sum_{i=1}^{m}[n']_i\boldsymbol{B}_i/\bar{n}A\,,$$
$$Kr=-\sum_{i=1}^{m}[\boldsymbol{V}]_i\cdot\boldsymbol{B}_i/A\,, \qquad (10)$$
$$D=-\sum_{i=1}^{m}[n'\boldsymbol{V}']_i\cdot\boldsymbol{B}_i/\bar{n}A\,.$$

For a rectangular coastal or frontal region (Fig. 5a), Eq. (10) is transformed into

$$P=([n']_1-[n']_2)\bar{u}/\bar{n}C-[n']_3\bar{v}/\bar{n}B\,,$$
$$Kr=([u]_1-[u]_2)/C-[v]_3/B\,, \qquad (11)$$
$$D=([n'u']_1-[n'u']_2)/\bar{n}C-[n'v']_3/\bar{n}B\,,$$

where $\bar{u}$ and $\bar{v}$ are x (positive rightward) and y (positive offshore) components of $\overline{\boldsymbol{V}}$, respectively. Since density and velocity variations normal to the coastline or to the front are much greater than those parallel, for aggregated organisms along the coastline or the front we can write

$$(P+D)/Kr\sim([n']_3\bar{v}+[n'v']_3)/\bar{n}[v]_3$$
$$=[n'v]_3/\bar{n}[v]_3<1\,. \qquad (12)$$

For a rectangular strait region of width B bounded by coastlines of length C (Fig. 5b), the second term on the right side of each of Eq. (11) disappears.

For a bay with a narrow connection to the open sea (Fig. 5c), Eq. (10) is transformed into

$$P=[n']_1\bar{u}B/\bar{n}A\,,$$
$$Kr=[u]_1B/A\,, \qquad (13)$$
$$D=[n'u']_1B/\bar{n}A\,,$$

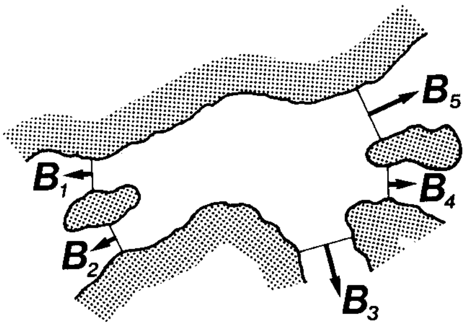

Fig. 4. A region bounded by arbitrarily shaped coastlines and 5 straight sections. $\boldsymbol{B}_i$ ($i=1, 2, \dots, 5$) is the exterior normal to the ith section, whose length is B_i.

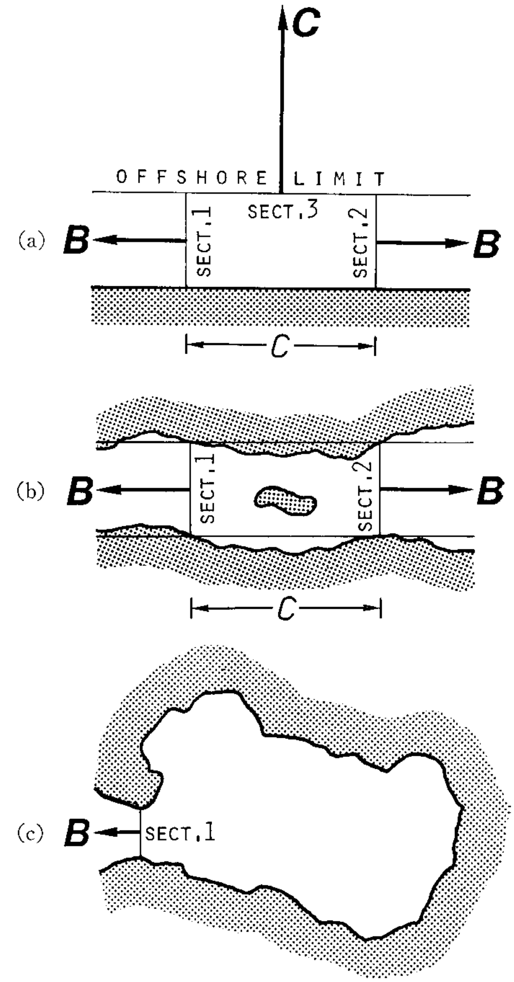

Fig. 5. Regions of special shape over which Eqs. (11) and (13) are derived. $\boldsymbol{B}$ and $\boldsymbol{C}$ are the same as $\boldsymbol{B}_i$ in Fig. 4. (a), a coastal or frontal region; (b), a strait region; (c), a bay with a narrow connection to the open sea.

where B is the width of a section across the bay mouth. For the organisms that have entered the bay, we have

$$(P+D)/Kr=[n'u]_1/\bar{n}[u]_1<1\,. \quad (14)$$

3.3. Coefficients in a group-averaged equation

The distribution density averaged over a group is given by

$$\bar{n}=N/Ag\,, \quad (15)$$

where the overbar denotes an average over the group, N is the total biomass of the group, and Ag an area occupied by the group. Tracking the moving group, the substantial differentiation of the natural logarithm of Eq. (15) with respect to time yields

$$(\mathrm{D}\bar{n}/\mathrm{D}t)/\bar{n}=(\mathrm{d}N/\mathrm{d}t)/N-(\mathrm{d}Ag/\mathrm{d}t)/Ag. \quad (16)$$

Defining group-member displacement coefficient Dg by

$$Dg=(\mathrm{D}\bar{n}/\mathrm{D}t)/\bar{n}-Gp\,, \quad (17)$$

from Eq. (16) we can write

$$Dg=Cm+Kg\,, \quad (18)$$

where the group-member change coefficient Cm and the accumulation-dispersal coefficient for a group Kg are defined by

$$Cm=(\mathrm{d}N/\mathrm{d}t)/N-Gp$$

and

$$Kg=-(\mathrm{d}Ag/\mathrm{d}t)/Ag\,, \quad (19)$$

respectively (Fig. 1). The coefficient Kg equals the time rate of fractional decrease of Ag.

4. Relation to the horizontal convergence of the current

We first consider the accumulation-dispersal of organisms ranging in a nearly horizontal layer along the sea-surface, a flat thermocline, a level bottom or flat optimum-isotherms. By denoting the swimming velocity of organisms relative to the surrounding water as $\boldsymbol{V}_s$, and the current velocity of the water relative to the land as $\boldsymbol{V}_c$, we can write the organismal velocity relative to the land as

$$\boldsymbol{V}=\boldsymbol{V}_s+\boldsymbol{V}_c \quad (20)$$

for the point where organisms exist, and from Eq. (8.2) we have

$$Kr=-\overline{\boldsymbol{\nabla}\cdot(\boldsymbol{V}_s+\boldsymbol{V}_c)}=-\int_c(\boldsymbol{V}_s+\boldsymbol{V}_c)\cdot\mathrm{d}\boldsymbol{B}/A\,. \quad (21)$$

However, if a closed curve c bounding a region contains some part where no organisms exist, we should calculate the line integral of Eq. (21) omitting that part, since it is necessary to regard $\boldsymbol{V}_c$ for the part of c as disappearing from $\boldsymbol{V}=\boldsymbol{V}_s=0$ in Eq. (20). The $\overline{\boldsymbol{\nabla}\cdot\boldsymbol{V}_c}$ calculated in such a manner is different from the usual definition of an area-averaged horizontal divergence of current velocity Q, and can be distinguished by attaching a prime, such that

$$Kr=-(Q_s+Q')\,, \quad (22)$$

where $Q_s=\overline{\boldsymbol{\nabla}\cdot\boldsymbol{V}_s}$, and $Q'=\overline{\boldsymbol{\nabla}\cdot\boldsymbol{V}_c}$.

For organisms distributed much heterogeneously in the vertical direction over a thick layer, Q' should be further modified according to the heterogeneity.

The group-member change coefficient Cm in Eq. (18) is not related to the horizontal convergence of current velocity, because the entrance of nongrouped individuals and exit of grouped ones is due mainly to biotic factors. Thus, having excluded Cm from Kg by definition (Sec. 3.3), we write

$$Kg=-\overline{\boldsymbol{\nabla}\cdot(\boldsymbol{V}-\bar{\boldsymbol{V}})}=-\overline{\boldsymbol{\nabla}\cdot(\boldsymbol{V}_s+\boldsymbol{V}_c-\bar{\boldsymbol{V}})}\,,$$

where $\bar{\boldsymbol{V}}$, an average of $\boldsymbol{V}$ over the group, is the translational velocity of the group. Since $\boldsymbol{\nabla}\cdot\bar{\boldsymbol{V}}=0$, it becomes

$$Kg=-\overline{\boldsymbol{\nabla}\cdot(\boldsymbol{V}_s+\boldsymbol{V}_c)}=-(Q_s+Q) \quad (23)$$

in the same form as Eqs. (21) and (22). In this case, however, Q is used instead of Q', because the organisms exist everywhere close to the boundary of the group.

Although Q or Q' seems to bring a passive accumulation-dispersal for organisms, somewhat active behaviors of organisms may participate, as it is effective only when the organisms range in such a nearly horizontal layer as mentioned at the beginning of this Section. Thus, we cannot regard the function of Q or Q' as completely passive for organisms. On the other hand, Q_s seems to bring a comparatively active accumulation-dispersal for organisms. It results from the biotic coaction or the structure of an abiotic environment, and the latter has a rather passive aspect. In short, terms of "active" and "passive" are of relative sense, and various factors are combined to work in such accumulation-dispersal.

As shown by Eqs. (22) and (23), both Kr and Kg are only the area-averaged horizontal convergence of organismal velocity. A simpler term "accumulation-dispersal coefficient" as denoted by K is sometimes used for Kr and/or Kg. By using the results of this paper, the scale dependent nature of K is discussed by Kawai (1986b).

Acknowledgement

I wish to thank Dr. Y. Ogawa for making valuable comments on the first draft of this manuscript.

References

Beverton, R.J.H. and J.A. Gulland (1958): Mortality estimation in partially fished stocks. Spec. Pub. Inter. Comm. Northwest Atlantic Fish., **1**, 51-66.

Beverton, R.J.H. and S.J. Holt (1957): On the Dynamics of Exploited Fish Populations. Her Majesty's Stationery Office, London, 533 pp.

Haury, L.R., J.A. McGowan and P.H. Wiebe (1978): Patterns and processes in the time-space scales of plankton distributions. p. 277-327. *In*: Spatial Pattern of Plankton Communities, ed. by J.H. Steele, Plenum Press, New York and London.

Hutchinson, G.E. (1953): The concept of pattern in ecology. Proc. Acad. Natur. Sci., Phila., **105**, 1-12.

Kawai, H. (1976): Convergence, divergence and the physical oceanography of particles. p. 103-155. *In*: Physical Oceanography II, ed. by T. Teramoto, Tokyo Univ. Press (in Japanese).

Kawai, H. (1981): Factors for the accumulation of marine organisms and the accumulation velocity responsible for fisheries productivity. Bull. Japan. Soc. Fish. Oceanogr., **39**, 75-82 (in Japanese).

Kawai, H. (1982): Scale dependence of the displacement accumulativity of red-tide organisms and the measurement-time intervals desirable for different scales. p. 187-195. *In*: Fundamental Studies on the Effects of Marine Environment on the Outbreaks of Red Tides (1980-1981), Report of Environmental Science, B148-R14-8, supported by the Ministry of Education, Science and Culture, Japan (in Japanese).

Kawai, H. (1986a): Dominancy of the immigration-emigration coefficient over other coefficients on a short time-scale. Bull. Japan. Soc. Sci. Fish., **52**.

Kawai, H. (1986b): Scale dependence of accumulation-dispersal coefficient of marine organisms. J. Oceanogr. Soc. Japan, **42**, 30-38.

Lasker, R. (1975): Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., **73**, 453-462.

Lloyd, M. (1967): Mean crowding. J. Anim. Ecol., **36**, 1-30.

Morisita, M. (1959): Measuring the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu U. Series E. (Biology) **2**, 215-235.

Ogawa, Y. (1980): Fishery fluctuations in relation to hydrography of coastal waters. Bull. Coast. Oceanogr., **17**, 131-144 (in Japanese).

Okubo, A. (1980): Diffusion and Ecological Problems: Mathematical Models. Biomathematics, **10**, Springer-Verlag, 254 pp.

Stavn, R.H. (1971): The horizontal-vertical distribution hypothesis: Langmuir circulations and *Daphnia* distributions. Limnol. Oceanogr., **16**, 453-466.

Tanaka, S. (1960): Studies on the dynamics and the management of fish populations. Bull. Tokai Reg. Fish. Res. Lab., **28**, 1-200 (in Japanese).

Tanaka, S. (1985): Elements of Fish Population Dynamics. Koseisha Koseikaku, 381 pp. (in Japanese).

海洋生物の集散係数の導入

川　合　英　夫*

要旨: 水産資源力学では魚類集積の問題をぬきにして，魚類の移出入は魚類の分散によるという見方が伝統的であった．本報の主目的は，海洋生物の集散速度を表すとともに，周囲水流速の水平収束と関係する量を見出すことにある．このため拡散の形としてではなく，水平収束と同じ形で集散係数を導入する．生物の集散は分布密度を変える一要因であるから，密度変化を起こす全要因の分類を最初に行い，集散が占める位置関係を明らかにする．各要因は，海域内や群内で平均した分布密度の変化速度を記述する線型方程式に現れる各係数に対応している．移出入係数は，通過・集散・拡散速度の3係数に分解される．ほとんど水平な層内に分布している生物にとって集散係数は，生物対地移動速度の水平収束の面積平均，つまり対水遊泳速度と流速の各々の水平収束の面積平均の和に等しいが，海域集散係数に係わる流速収束の面積平均は，通常のものとはやや異なることを示す．

* 京都大学農学部水産学教室
〒606 京都市左京区北白川追分町