

## Generating Complex Klinokinetic Movements of 2-D Migration Circuits Using Chaotic Model of Fish Behavior

Yong-Hae Kim

*Institute of Marine Industry, College of Marine Science, Gyeongsang National University,  
Tong-Young, Kyeognam 650-160, Korea*

The complex 2-dimensional movements of fish during an annual migration circuit were generated and simulated by a chaotic model of fish movement, which was expanded from a small-scale movement model. Fish migration was modeled as a neural network including stimuli, central decision-making, and output responses as variables. The input stimuli included physical stimuli (temperature, salinity, turbidity, flow), biotic factors (prey, predators, life cycle) and landmarks or navigational aids (sun, moon, weather), values of which were all normalized as ratios. By varying the amplitude and period coefficients of the klinokinesis index using chaotic equations, model results (i.e., spatial orientation patterns of migration through time) were represented as fish feeding, spawning, overwintering, and sheltering. Simulations using this model generated 2-dimensional annual movements of sea bream migration in the southern and western seas of the Korean Peninsula. This model of object-oriented and large-scale fish migration produced complicated and sensitive migratory movements by varying both the klinokinesis coefficients (e.g., the amplitude and period of the physiological month) and the angular variables within chaotic equations.

Key words: Klinokinesis, Migration model, Complex movements

### Introduction

Fish migration data are often collected using labor-intensive tagging techniques, including a recent method of applying transmitting tags that track individual fish (Sibert and Nielsen, 2001). These techniques have been used to determine the primary routes and timings of the migrations of many fish species, and individual tracking data may elucidate how fish decide upon these particular routes and timings. Previous fish-tracking studies have indicated that routes can differ in both scale and time for even a single species (McKeown, 1984; Itoh et al., 2003; McFarlane and King, 2003; Palsson and Thorsteinsson, 2003; Gutenkunst et al., 2007). Such variation in fish migratory patterns may result from complex environmental factors, complex behavior (Menczer and Belew, 1996), or individual differences or preferences that can shift during the life cycle (Lucas and Baras, 2001; Metcalfe et al., 2002).

Fish migration can be viewed as an evolved systematic displacement in underwater space that is

limited to a specific geographical circuit and linked to a regular seasonal or annual cycle. If underwater environmental changes are periodic, repeated migrations reinforce the responses to relevant stimuli and promote the emergence of predictable behavior, because fish orient almost immediately and relocate to an area with more favorable conditions (Lucas and Baras, 2001). In addition, memory and navigation (Giske et al., 1998) may enable fish to minimize the energetic costs of swimming and migration by instilling a bias in movement toward a particular geographical goal (Dodson, 1988).

Fish migration can be affected by internal and external factors, such as abiotic/physical (e.g., water temperature, salinity, dissolved oxygen, tidal or current stream, underwater light etc.) and biotic (e.g., prey and predators, feeding, spawning, sensitivity of the sensory organs) conditions (McKeown, 1984; Smith, 1984; Freon and Misund, 1999). Several models of fish migration have been used to predict primarily large-scale movements in response to different stimuli in the open sea. For example, the "comfort theory" is a principal equations model

\*Corresponding author: yonghae@gnu.ac.kr

demonstrating fish movement in response to environmental factors (Balchen, 1979). The migration of salmon in the open sea was simulated based on temperature, current velocity, turbidity, food, depth, etc. (Quinn, 1991). In addition, a computer simulation model of the movement of demersal fish (Arnold and Holford, 1995) was developed using tidal stream vectors, and Niwa (1998) modeled the migration dynamics of fish schools in heterothermal environments.

Other approaches to simulating large-scale movements include artificial neural networks in tuna (Dagorn et al., 1997; 2002), individual-based migration models (Hubbard et al., 2004), and advection-diffusion models (Magnusson et al., 2005). However, these models do not account for interactions between abiotic and biotic limiting factors. Small-scale coastal movements of sea bream and flounder (Takaba and Morioka, 1999; Kim and Ahn, 2002) were modeled by adapting a fish movement model (Kim, 2003) based on a three-step neural network allowing internal and external factors to be processed by chaotic decision-making that was incorporated as irregular and chaotic variation in moving speed and direction through time. This sea bream-flounder model reproduced fish movement patterns similar to those recorded in the field for a 5-km radius during one day. However, a more realistic model is required to account for spatial variation through time in movement associated with fish migration that occur in specific under-water environments.

A model was constructed to generate complex fish movements, building from a small-scale movement model (Kim, 2003). First in a 2-dimensional plane using a klinokinesis index in an object-oriented migration circuit and then it is extended to an entire large-scale annual migration. This large-scale migration model controlled and generated a wide range of variation in movements through time using klinokinesis coefficients (e.g., the amplitude and period of the physiological month) as well as angular and swimming speed variables within chaotic behavior equations.

## Materials and Methods

### Model foundation

A fish migration model was reconstructed and expanded from a small-scale chaotic fish-movement model Kim (2003) to generate complex movements of annual fish migration in a 2-dimensional under-water plane. The primary neural networks in this fish migration model involved three steps: input stimuli,

central decision-making, and response output (i.e., object-oriented movements for annual migration. The important components of these input variables are listed in Table 1 (modified from Lucas and Baras, 2001 and Kim, 2003).

The input stimuli (S) included aquatic physical and biotic factors, celestial and weather conditions, the physiological state of migrating fish and the imprinting memory of fish for migration (McKeown, 1984; Smith, 1984). The central decision-making process was generated using Lorenz chaos equations (Lorenz, 1979) by the aperiodic rotation of the psycho-hydraulic wheel activated by the stimuli parameters (Lorenz, 1981). The output response were controlled as three chaotic variables (movement components) that were categorized as specific migration patterns, including comfort or sheltering patterns, navigational and orientation tactics, swimming and biotic energy and memory and learning for complex annual migrations (Lucas and Baras, 2001; Metcalfe et al., 2002).

### Input stimuli

The input variables of stimuli processing for the complex fish migration model included abiotic and biotic factors, celestial and weather conditions, fish physiological state and imprinting memory etc (specific variables are listed in Table 1).

The specific aquatic physical factors were the temperature effect ( $E_T$ ) the salinity effect ( $E_S$ ) and the effect of flow velocity ( $E_V$ ). The primary biotic factors such as detection ratio ( $P_C$ ) by contrast of prey and the detection angle ratio ( $P_A$ ) of prey were the same as those used in the previous model (Kim, 2003). Additional variables, such as physiological state in the life cycle, celestial and weather conditions, object orientation and navigation by memory and learning were modified or added as novel factors, as described below.

### Biotic factors

The effect of prey density ( $E_P$ ) (Freon and Misund, 1999; Dagorn et al., 2002) was modified from Kim (2003) to an exponential form as the ratio of present prey density  $P_S$  to maximum prey density ( $P_M$ ) of zooplankton:

$$E_P = \exp(-P_S/P_M) \quad (0 \leq E_P \leq 1) \quad (1)$$

### Physiological state in the life cycle

Annual fish migration can be affected by the physiological state during the annual cycle or migration pattern (McKeown, 1984; Smith, 1984). Physiological factors ( $E_M$ ) is modified from Kim (2003) were

Table 1. The main and sub-elements of the three-step fish migration model

Step	Symbols	Elements
Stimuli input	S <sub>1</sub>	Aquatic physical factors: Water temperature, Salinity and dissolved oxygen, Tidal stream vector, Ground and geography
	S <sub>2</sub>	Biotic factors: Plankton, Prey or predator
	S <sub>3</sub>	Celestial and weather: Sun, moon, weather, season
	S <sub>4</sub>	Physiological state in life cycle
	S <sub>5</sub>	Object orientation and navigation
Decision-making	k, m	Normalized parameter from intensity of stimuli
	U	Output signal representing vertical moving speed
	V	Output signal representing horizontal moving speed
	W	Output signal representing horizontal direction
Out put response	R <sub>1</sub>	Migration pattern: Feeding, spawning, wintering
	R <sub>2</sub>	Comfort or sheltering pattern
	R <sub>3</sub>	Navigation and orientation pattern
	R <sub>4</sub>	Swimming pattern and biotic energy
	R <sub>5</sub>	Memory and learning by time, geography etc

calculated as follows:

$$E_M = (I_A + I_S + I_W) + \sin(M + N_R) \quad (0 \leq E_M \leq 1) \quad (2)$$

where  $N_R$ , indexes  $I_A$ ,  $I_S$  and  $I_W$  range from 0 to 1 and represent indices of the spawning season, sheltering habitat, and the over-wintering season respectively. The annual cycle is represented as a sine function with month ( $M$ ) and a random ratio ( $N_R$ ; ranges from 0 to 1). Higher values of a specific physiological factor ( $E_M$ ) indicate that fish could be more active until finding an optimum place.

#### Celestial and weather conditions

Fish can orient to move in a desired direction by the bearing and period of the sun, moon, underwater landmarks or current (McKeown, 1984). The detection of bearing or season can be estimated by underwater light polarity, light levels and duration of daylight when underwater (Shibert and Nielsen, 2001). Underwater light could be blocked by a cloudy and turbidity due to particles in the water. The masking effect of light ( $E_W$ ) by weather and water quality modelled using the cloud ratio ( $C_R$ ) and the vertical light attenuation coefficient  $c$  (Kim and Wardle, 1998) and the slope ( $\psi$ ):

$$E_W = \psi / (c + 0.5C_R) \quad (0 \leq E_W \leq 1) \quad (3)$$

$E_W$  ranges between 0 completely unable to determine time or bearing by sun or moon and 1 completely to determine.

#### Object orientation factors

To migrate via homing (e.g., salmon) or closed circuit (e.g., most pelagic fish) migration, fish could swim to specific objective locations at certain time

using landmarks, odours, or navigational aids (McKeown, 1984; Smith, 1984, Lucas and Baras, 2001; Metcalfe et al., 2002). Therefore, fish were assumed to recognize both direction and time, thus spend certain pre-set periods of time in feeding, spawning, or over-wintering by detecting environmental changes, etc. The sustained moving speed ( $V_M$ ) as swimming ability is estimated as the distance to the goal position by the arrival time. The effect of object orientation ( $E_O$ ) as a stimulus for migration, whether residency or travel (Itoh et al., 2003) can be re-presented as the ratio of temporal moving speed ( $V_T$ ) to ideal sustained speed ( $V_M$ ) to preset goal positions:

$$E_O = |V_M - V_T| / V_M \quad (0 \leq E_O \leq 1) \quad (4)$$

#### Central decision-making

The central decision-making process in biological behavior model can be formulated using Lorenz chaos equations by aperiodic rotation of the psychohydraulic wheel (Lorenz, 1979) which is activated by the stimuli parameters. The parameters  $k$  and  $m$  are generated to rotate the hydraulic wheel in chaotic behavior equations (Kim, 2003) as follows;

$$\begin{aligned} dU/dt &= k(W-U) \\ dW/dt &= mU - UV - W \\ dV/dt &= UW - V \end{aligned} \quad (5)$$

The output response by variables  $U(t)$ ,  $V(t)$  and  $W(t)$  are chaotic values of movement components that can be categorized as specific migration patterns, including comfort or sheltering patterns, navigational and orientation tactics, swimming and biotic energy and memory and learning for annual complex

migrations.

Parameters  $k$  and  $m$  are expressed as  $k_0$ ,  $k_1$ ,  $m_0$  and  $m_1$  within the cosine function (Kim and Stringer, 1992; Kim, 2003) using the above limited ranges of  $k$  and  $m$ :

$$\begin{aligned} k &= (1 + 5 k_0) \cos\{(2 + 6 k_1)t\} \\ m &= (5 + 15 m_0) \cos\{(5 + 6 k_1 + 7 m_1)t\} \end{aligned} \quad (6)$$

where  $k_0$ ,  $k_1$ ,  $m_0$  and  $m_1$  are modified as a hyperbolic tangent function from Kim (2003). These four parameters range between 0 and 1, and higher values indicate higher variation in the three variables in Eq(6). The first parameter ( $k_0$ ) is defined as a hyperbolic tangent function by biotic factors such as detection ratio ( $P_C$ ) by contrast of prey, detection angle ratio ( $P_A$ ) of prey (Kim, 2003), the effect of prey density ( $E_P$ ) in eq(1):

$$k_0 = \tanh(P_A + P_C + E_P) \quad (7)$$

The second parameter  $k_1$  is represented by physiological state and migration patterns  $E_M$  from eq(2) as follows:

$$k_1 = \tanh(E_M) \quad (8)$$

The third parameter  $m_0$  is affected by aquatic physical factors such as the temperature effect ( $E_T$ ), the salinity effect ( $E_S$ ) and the effect of flow velocity ( $E_V$ ) (Kim, 2003) as follows:

$$m_0 = \tanh(E_T + E_S + E_V) \quad (9)$$

The fourth parameter ( $m_1$ ) is represented by  $E_M$  from eq(2),  $E_W$  from eq(3) and  $E_O$  from eq(4) and as follows:

$$m_1 = \tanh(E_M + E_W + E_O) \quad (10)$$

### Response output

The primary output factors of the complex migration model are represented by five dominant patterns of movement (Table 1). These patterns correspond to specific destinations in space and time: as location and time such as migration patterns ( $R_1$ ) feeding, spawning, wintering; patterns for seeking favourable environment or sheltering habitat ( $R_2$ ), capabilities for navigation or orientation ( $R_3$ ), swimming patterns and biotic energy ( $R_4$ ) and object orientation using imprinted memory ( $R_5$ ).

### Migration patterns

Fish migration patterns are dominant by the need

to move between geographical zones and satisfy the seasonal requirements of the annual life cycle (McKeown, 1984; Freon and Misund, 1999; Huse et al., 2002; Metcalfe et al., 2002). The three main zones are those for feeding, spawning and over-wintering, each of which serves as an objective habitat within the migratory pattern. For long periods during each annual cycle, fish at an initial location have an objective to reach a particular landmark with bearing deviation depending on the season. The three objective directions are those toward a feeding habitat ( $A_F$ ), toward a spawning area ( $A_R$ ), and a habitat for over-wintering ( $A_W$ ). In addition, there is an end limit ( $A_L$ ) as upper and lower values. The temporal direction with respect to the timing of fish migration ( $A_T$ ) incorporates the klinokinesis coefficients such as the angular amplitude ( $\phi$ ) and period ( $\lambda$ ) with month ( $M$ ):

$$A_T = \angle(A_F + A_R + A_W \pm A_L) + \phi \sin(\lambda M) \quad (11)$$

Fish swimming speed to one destination among the several objectives in the memory can be represented as ideal sustained speed ( $V_D$ ) and speed deviation ( $V_E$ ).

### Comfort or sheltering patterns

Fish at an initial location in time have an objective direction ( $A_D$ ) away from hazardous environments toward sheltered or more comfortable destinations (Balchen, 1979). The temporal deviation of swimming speed ( $V_1$  from  $V_M$ ) and the deviation of the directional range ( $A_1$ ) can be represented with temperature effect ( $E_T$ ) and salinity effect ( $E_S$ ) from Kim (2003) as follows:

$$\begin{aligned} A_1 &= \pi \pm A_D \\ V_1 &= E_T E_S V_M \end{aligned} \quad (12)$$

### Navigation and orientation patterns

Although fish can orient or navigate using natural landmarks, light from the sun or moon, or geographic magnetic fields (McKeown, 1984; Quinn, 1991; Lucas and Baras, 2001; Metcalfe et al., 2002), the detection of light or magnetic fields could be limited by the sensitivity of the relevant sense organs as well as the environmental or weather conditions. The navigational ability of fish can be affected by the masking effects of light, landmarks, or bearing detection. The masking effect underwater can be derived from the cloud ratio ( $C_R$ ), the vertical attenuation coefficient  $c$  and the relative sensitivity ( $B_S$ ) of fish for bearing of celestial objects or landmarks. Therefore, the deviation of the temporal direction of fish migration ( $A_2$ ) can be estimated by

the light masking index ( $\psi$ ) from eq (2) and speed ( $V_2$ ):

$$\begin{aligned} A_2 &= \psi c C_R / B_S \\ V_2 &= V_M / (C_R + 3c) \end{aligned} \quad (13)$$

where  $B_S$  ranges from 0 to 1.

### Swimming patterns and biotic energy

The horizontal heading movement of fish ( $A_H$ ) is represented as a vector between temporal heading ( $A_T$ ) and current direction ( $A_C$ ). Thus, the horizontal movement velocity of fish ( $V_T$ ;  $\text{ms}^{-1}$ ) can be predicted from permanent current velocity ( $V_C$ ;  $\text{ms}^{-1}$ ) and direction ( $A_W$ ) as follows:

$$V_T = V_C \cos(A_T + A_C) \quad (14)$$

As a result, the directional deviation ( $A_E$ ) can be selected as a maximum value among  $A_1$ ,  $A_2$ ,  $A_3$  and the speed deviation ( $V_E$ ) can be selected as a maximum value among  $V_1$ ,  $V_2$ , and  $V_3$ . In addition, the instantaneous direction ( $A_H$ ) and moving speed ( $V_F$ ) of fish are calculated from the output signal  $W(t)$  and  $V(t)$  as the derivative of eq (5):

$$\begin{aligned} A_H &= \angle \{A_T + A_C + A_E W(t)\} \\ V_F &= V_T + V_D + V_E V(t) \end{aligned} \quad (15)$$

### Simulation method

The block diagram for this migration model was modified from Lucas and Baras (2001), and Kim (2003) as shown in Fig. 1. The model was programmed in FORTRAN 90 on a workstation (Alpha CPU 866 MHz). Sea bream [*Chrysophrys major* (Temminck et Schlegel), total length 60 cm, 7 years old] a demersal self-sea fish (Metcalfé et al., 2002), were used to test the developed model of fish migration. The results were compared with examples of recorded sea bream migrations (NFRDI, 1998).

Underwater abiotic factors such as temperature, salinity, tide, current and zooplankton given in Table 2 were collected at 1° intervals for latitudes from 30° to 40°N and for longitudes from 120° to 135°E around the Korean peninsula (NFRDI, 2001a; HO, 1982). Transparency measurements for the vertical attenuation coefficient were obtained by NFRDI (2001b). Cloud data were obtained from monthly meteorological reports. Therefore data for specific location and times were interpolated between the nearest observation points and times. Underwater light, current, tidal stream data and remaining factors were derived using the methods of Kim (2003).

Simulations were conducted for westward and

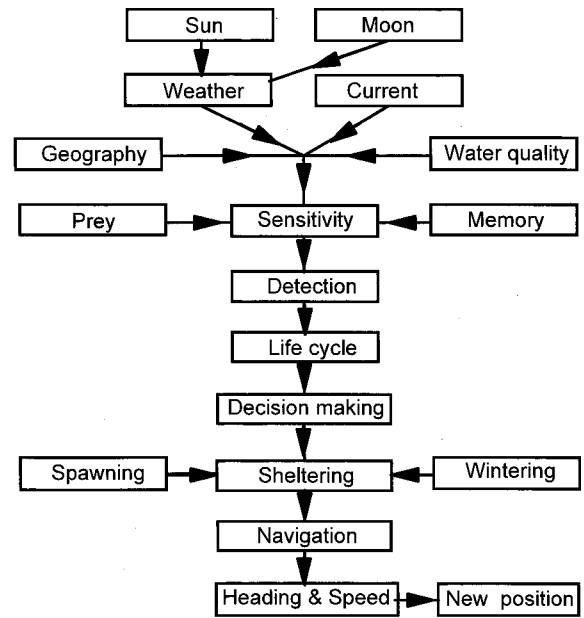


Fig. 1. The block diagram for the developed fish migration model using the chaos theory and neural networks modified from Kim (2003).

southwards migrating groups of sea bream (NFRDI, 1998) for 1 year using time steps of 0.1 days (2.4 h) or 0.01 days (0.24 h). Fish were assigned positions and period of time to reach over-wintering (from 1 January until the end of February) and spawning (1 June until the end of July), and relevant environmental factors are listed in Table 2. The random ratio in eq(2) was set as  $N_R=0.86$ , and the relative bearing sensitivity in eq(13) was set as  $B_S=0.71$ . The light masking index in eq(3) was set as  $\psi=0.1$  for  $0 \leq E_W \leq 1$  and the range of heading movements in eq(11) was limited to  $A_L=\pm 30^\circ$  for directional changes in seasonal migration patterns. The klinokinesis angular amplitude ( $\phi$ ) in eq(11) was varied from  $15^\circ$  to  $75^\circ$  in increments of  $15^\circ$  and the klinokinesis period coefficients ( $\lambda$ ) was varied from 0 to 9 in increments of 1.

### Results

The migration circuits as the horizontal tracks of two groups of sea bream one migrating westwards and the other southwards in the Korean sea were redrawn as given in Fig. 2 from NFRDI (1998). The simulated tracks from this model with the monthly klinokinesis period coefficient in eq(10) i.e.  $\lambda=0$  to 9 with a constant amplitude  $\phi=60^\circ$  were represented for both the southward in Fig. 3(A) and westward in Fig. 3(B). When the monthly period coefficient was set to  $\lambda=0$  (i.e., migration to the desired goal occurred without meandering), movements were

Table 2. Constants and parameters used in the migration model for sea bream

Parameter or constant (unit)	Description (equation)	Value
$T_L$ (°C)	Initial lowest temperature	12
$T_M$ (°C)	Upper limit temperature	20
$M_L$	Month when $T_L$	1 (Jan)
$M_M$	Month when $T_M$	8 (Aug)
$P_M$ (mg m <sup>-3</sup> )	Density of zooplankton (1)	500
$N_R$	Random ratio (2)	0.86
$\psi$	Light masking index (3)	0.1
$\phi$ (°)	Klinokinesis angular amplitude (11)	15-75
$\lambda$	Klinokinesis coefficients (11)	0-9
$A_L$ (deg)	Range of heading (11)	30
$B_S$	Relative bearing sensitivity (13)	0.71

Table 3. The deviation of the simulated tracks from a given fixed location shown in top figure in Fig. 3 with given Julian days in relation to monthly klinokinesis period  $\lambda$  in equation (11) when constant amplitude  $\phi=60^\circ$  for sea bream

Stock	Julian day	Give location (deg)		Deviation of position (km)									
		Long.	Lat.	$\lambda=0$	1	2	3	4	5	6	7	8	9
Southward	170.0	128.4	34.7	58.2	59.6	62.4	67.4	50.1	27.8	44.0	29.8	29.6	31.2
	300.0	128.7	34.4	5.0	5.6	7.0	15.2	10.8	3.8	15.6	12.5	4.9	4.6
	365.0	127.0	33.0	1.1	3.1	16.5	6.5	12.7	10.3	9.0	6.0	7.2	2.4
Westward	60.0	125.6	33.6	26.7	27.8	25.7	27.8	23.8	25.7	22.7	25.1	16.5	24.5
	123.0	125.2	36.5	8.9	10.6	9.1	14.6	7.9	12.7	9.5	7.5	11.3	16.8
	160.0	123.1	37.8	2.2	1.5	10.2	1.5	10.2	9.2	1.6	2.2	1.1	1.6
	250.0	123.8	36.3	11.7	11.1	18.9	11.7	17.6	18.2	12.6	22.9	13.6	11.0
	310.0	125.0	33.3	6.3	15.7	7.0	5.7	17.0	5.0	14.4	6.5	1.1	3.1
	365.0	125.9	32.5	0.0	1.1	2.4	6.7	6.5	13.4	3.1	1.1	3.1	1.1
Mean				13.3	15.1	17.7	17.5	17.4	14.0	14.7	12.6	9.8	10.7
S.D.				18.7	18.7	18.2	20.2	13.4	8.4	12.7	10.6	9.2	11.1

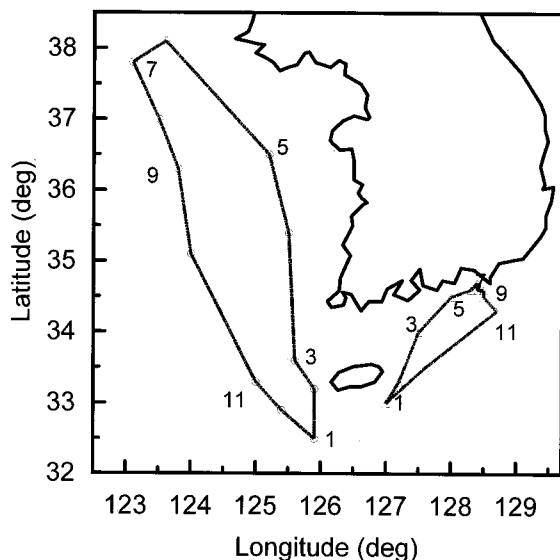


Fig. 2. The typical migration tracks of two groups of sea bream in the Korean sea (redrawn from NFRDI, 1998). The left-hand tracks of sea bream are called the westward group and the right-hand tracks are the southward group. Numbers near the tracks represent the month.

straight and similar to the monthly mean tracks derived from recorded migrations given in Fig. 2 (NFRDI, 1998). However when the monthly klinokinesis period coefficient  $\lambda > 0$ , movement tracks show more complex curves in accordance with increasing the coefficient  $\lambda$  and were similar to the field observations of the sea bream movements of approximately 1 day (Takaba and Morioka, 1999; Kim and Ahn, 2002).

Deviations in position between the simulated locations and the given fixed location of sea bream on particular Julian days are represented in Table 3 in relation to the coefficient  $\lambda$ . The deviations of movements of the southward group in June (Julian day 170) ranges from 28 to 67 km were larger than those of the westward groups. The deviations of the latter group were generally  $< 28$  km, because the westward migrating fish took longer than 170 days to reach the given migration goal. There was no linear relationship between the coefficients and the deviation of the tracks. The deviation at  $\lambda=8$  was significantly different ( $p < 0.05$ ) from deviations at  $\lambda=2-6$ , and the deviation at  $\lambda=9$  was significantly different

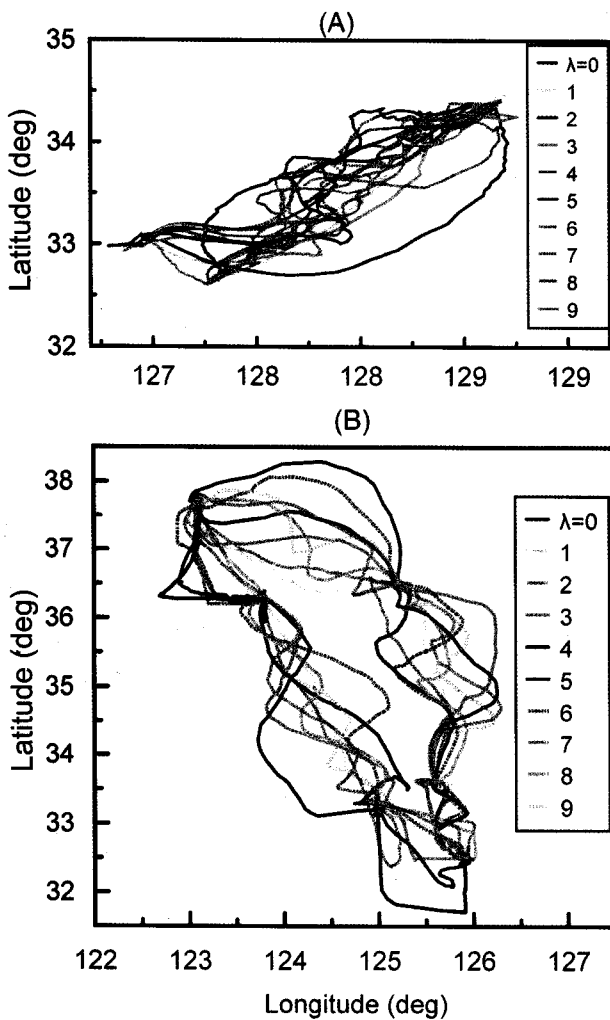


Fig. 3. The daily tracks of sea bream for a year as output from the chaotic migration model illustrating the effect of changing the monthly klinokinesis period coefficient  $\lambda$  in eq(11) varied from 0 to 9 when constant  $\phi=60^\circ$  for southwards (A) and westward (B) migration circuits.

from deviations at  $\lambda=2-4$ . All other comparison were not significantly different. These results indicate that this model produced more chaotic movements of the migration circuit presumably more realistic patterns of fish movements.

When the values of the monthly klinokinesis amplitude angle varied from  $\phi=15$  to  $75^\circ$  in eq(11) at a constant period  $\lambda=9$ , daily movements of westward migration circuits were shown in Fig. 4. As the monthly klinokinesis amplitude angle  $\phi$  or period  $\lambda$  increased, the movements became more complicated and meandering tracks.

The daily movements of sea bream over a period of 1 year using the angular variable  $W(t)$  within time function when  $\phi=60^\circ$  and  $\lambda=9$  are represented in Fig.

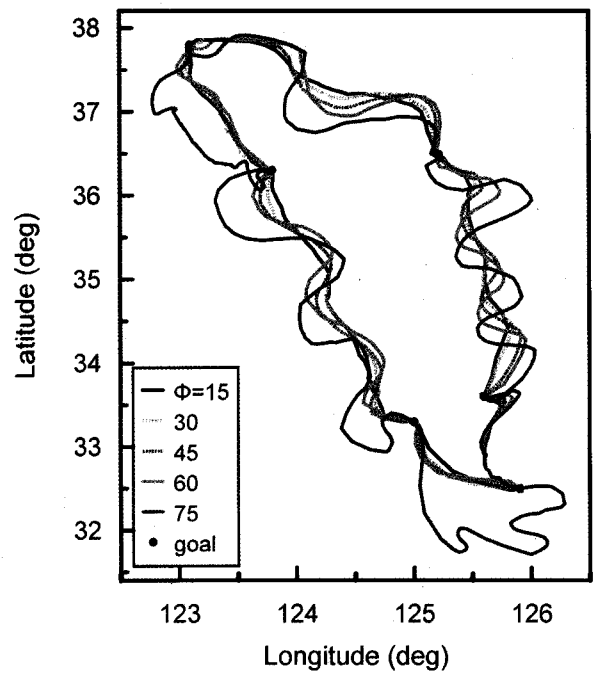


Fig. 4. The daily tracks of sea bream for a year as output from the chaotic migration model illustrating the effect of changing the monthly klinokinesis amplitude coefficient  $\phi=15-75^\circ$  when constant  $\lambda=9$  for westward migration circuits (The filled circles are given goal positions in Table 3).

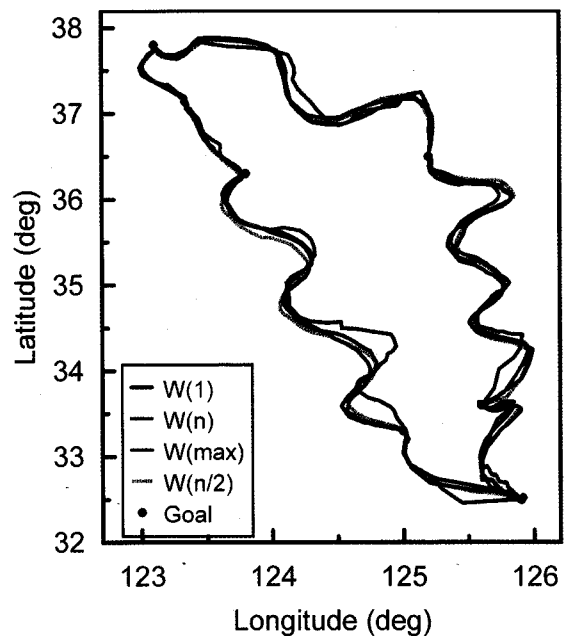


Fig. 5. The daily tracks of sea bream for a year as output from the chaotic migration model illustrating the effect by selecting the angular variable  $W(n)$  with time function  $dt$  when  $\phi=60^\circ$  and  $\lambda=9$  for westward migration circuits (The filled circles are given goal positions in Table 3).

5. The angular variable  $W(t)$  was represented as first value of  $W(1)$  from  $n$  values of  $W(t)$  by time steps  $n$ , as random values of  $W(n)$ , and as the maximum value  $W(\max)$  among  $W(n)$  for the westward migration circuits. Different values of  $W(t)$  changed irregularly and controlled the meandering of the migratory movements under the same conditions of the fish and the underwater environments.

The daily mean migration speed of the sea bream by this model as an example when the monthly klinokinesis coefficient  $\lambda=5$ ,  $\phi=60^\circ$  with time step 0.1 days was represented in Fig. 6(A) and when the time steps 0.01day for Julian days 160-163 in Fig. 6(B). The daily mean speeds over a period of 1 year using various values of the monthly klinokinesis coefficient  $\lambda$  were very low ranging between 0.051 and 0.076  $\text{ms}^{-1}$  for the westward and 0.027 to 0.032  $\text{ms}^{-1}$  for the southward migrating fish. The daily mean migration speed of sea bream during over-wintering (January and March) or during spawning (June and July) was slower than during the feeding period. The variation of daily heading movements as directional bearing as an example when the monthly directional coefficient  $\lambda=5$  in Fig. 3(A) in southward migrating

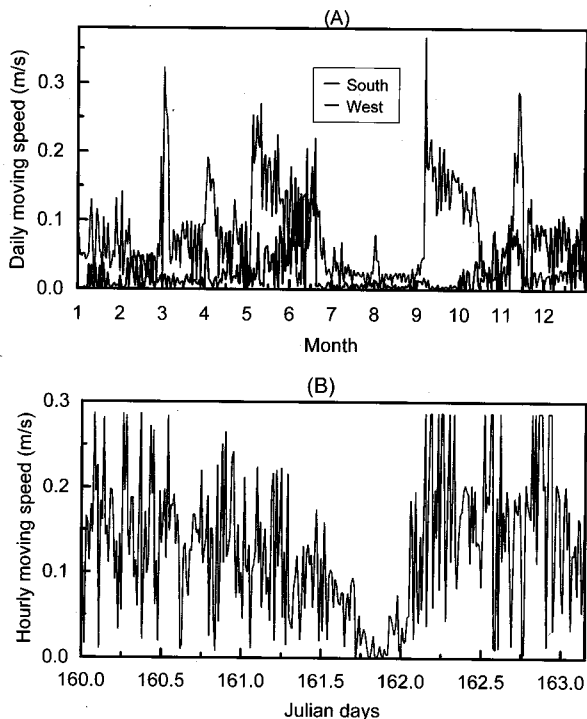


Fig. 6. Examples of the variation of daily mean migration speed in the southward sea bream from the simulation results when the klinokinesis coefficient  $\phi=60^\circ$  and  $\lambda=5$  for a year when time step 0.1day (A) and their parts of the variations of hourly migration speed when time step 0.01day (B).

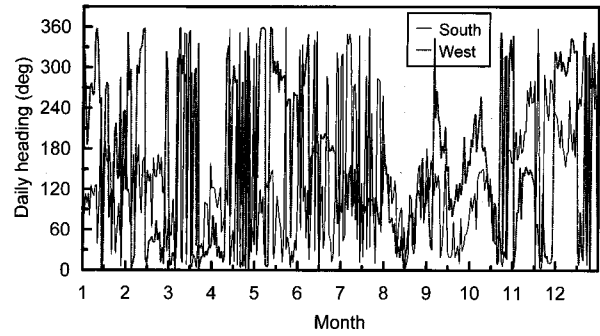


Fig. 7. Examples of daily variations of mean migration heading for the sea bream as southward and westward from the simulation results when the klinokinesis coefficient  $\phi=60^\circ$  and  $\lambda=5$  for a year.

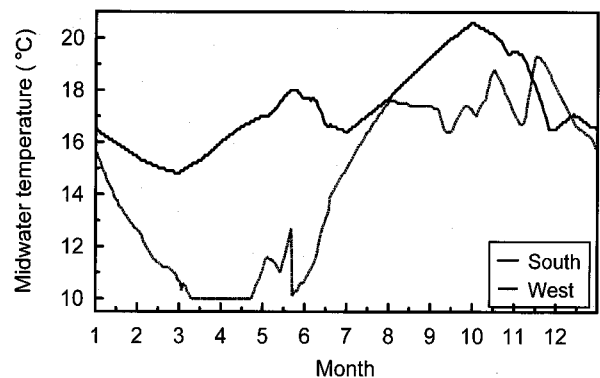


Fig. 8. Examples of daily variations of the sea temperature at depth 50 m along with the path of sea bream from the simulation results when the klinokinesis coefficient  $\phi=60^\circ$  and  $\lambda=5$  for a year.

fish is represented in Fig. 7.

The estimated water temperature, at the depth 50 m, along the simulated path of the daily locations of the example sea bream in Fig. 6(A) are shown in Fig. 8. The water temperatures at 50 m depth along with the location in southward migrating ranged between 15°C and 21°C in contrast to a wider range between 10°C and 21°C in westward migrating because of a cold water mass in the spring in the western sea of Korea.

## Discussion

The sea bream movements indicated that fish were located near the initial over-wintering habitat during January and February and close to the spawning habitat during June and July. This pattern occurred regardless of the values of the monthly klinokinesis angular amplitude or period coefficients or the chaotic angular variable  $W(t)$  likely due to preset positions of goals, with day as an object orientation.



In terms of small-scale movements, the change-able curves of the simulated movements appear similar to the observed small-scale movements of sea bream (Kim and Ahn, 2002), although such detailed observations of real fish were conducted for only 1 day during the pre-spawning season. More complicated locations of migratory movements can be observed using more precise positioning methods (Sibert and Nielsen, 2001), and the smaller time steps. This simulation could produce more variable locations of fish migration. These variable deviations could be modeled as complex characteristics of the simulated path generated from a fish migration model using chaos and neural networks.

The daily migration speeds of sea bream in this simulation were slower than the mean migration speeds observed over a period of 6 min in a small-scale coastal study as  $0.36 \pm 0.24 \text{ ms}^{-1}$  (Kim and Ahn, 2002), probably due to the differences in the mean sampling time. Due to the potential for generating variable speeds and paths, the model reported here can be tested by changing the appropriate constants and variables. Previous studies have documented diverse routes and timings of the migratory patterns and speeds of blue fin tuna (Brill et al., 2002; Davies and Stanley, 2002; Itoh et al., 2003) and big eye tuna (Schaefer and Fuller, 2002).

The variation in the estimated water temperature near the sea bottom (depth of approximately 50 m) from a previous study along the westward path of sea bream in spring and summer (Ho, 1982) was lower than variation along the path of southward migrating fish. These results can be attributed to the fact that the bottom of the Western Sea retained a cold water mass during spring and summer, whereas the South Sea was warmed by the Kuroshio current. However, variation of water temperature in relation to the path of sea bream should be monitored using direct -tag observations and considered as a diverting path in this model.

When flowing northward and eastward during the spring and summer, these currents may provide a distinct advantage to migrating fish, whereas the southward- and westward-migrating fish returning to the over-wintering habitat in autumn may encounter difficulties in swimming against these currents. However, these contrasting effects of current flow should be examined further in sea bream, because these demersal fish can swim near the bottom where current velocity is much slower than in waters at intermediate depths.

The migration model presented here includes object-oriented (Downing and Reed, 1996) and multi-

stimulus, multi-response concept (Johansson et al., 2001) using chaos equations and the neural network system over long periods of time. Future studies should focus on detailed precise data of underwater environments as well as movements in the field for longer periods of time for incorporation with remote sensing data (Dagorn, 1997) and stock dispersion or assessment data (Freon and Misund, 1999).

This fish migration model applied chaos theory and neural networks with kinokinesis movements to generate a variety of fish movement tracks that exhibited variation in both direction and speed. The model assumed that fish harbor both navigational and intrinsic memory for migratory goals in the given particular sea conditions. However, more experiments are necessary to compare field observations and model simulations to better understand the relationship between stimuli and the migratory behavior of marine fish. Future modeling efforts should incorporate the effects of environmental changes, the presence or absence of fish memory, differences in individual schools, and 3-dimensional movement patterns to produce a more real model.

### Acknowledgments

I would like to thank Mr. Bee-Ryong Lee, Jong-Hyuk Lim, and Byeong-In Song for help with data processing and Dr. C. S. Wardle for useful comments and English corrections. In addition, I am also grateful to the two anonymous reviewers for their helpful comments.

### References

- Arnold, G.P. and B.H. Holford. 1995. A computer simulation model for predicting rates and scales of movement of demersal fish on the European continental shelf. *ICES J. Mar. Sci.*, 52, 981-990.
- Balchen, J.G. 1979. Modelling, prediction and control of fish behaviour. In: *Control and Dynamic System*. Leondes, C.T. ed. Academic Press. London. 99-146.
- Brill, R., M. Lutcavage, G. Metzger, P. Bushnell, M. Arendt, J. Lucy, C. Watson and D. Foley. 2002. Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry. *Fish. Bull.*, 100, 155-167.
- Dagorn, L., M. Petit and J.M. Stretta. 1997. Simulation of large-scale tropical tuna movements in relation with daily remote sensing data: The artificial life approach. *Biosystems*, 44, 167-180.
- Dagorn, L., F. Menczer, P. Bach and R.J. Olson. 2002. Co-evolution of movement behaviours by tropical pelagic

- predatory fishes in response to prey environment: A simulation model. *Ecol. Model.*, 134, 325-341.
- Davies, T.L.O. and C.A. Stanley. 2002. Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian bight observed with ultrasonic telemetry. *Fish. Bull.*, 100, 448-465.
- Dodson, J.J. 1988. The nature and role of learning in the orientation and migratory behavior of fishes. *Environ. Biol. Fish.*, 23, 161-182.
- Downing, K. and M. Reed. 1996. Object-oriented migration modeling for biological impact assessment. *Ecol. Model.*, 93, 203-219.
- Freon, P. and O.A. Misund. 1999. Dynamics of Pelagic Fish Distribution and Behaviour. Effects on Fisheries and Stock Assessment. Fishing News Books. London, 21-55.
- Giske, J., G. Huse and Ø. Fiksen. 1998. Modelling spatial dynamics of fish. *Rev. Fish Biol. & Fish.*, 8, 57-91.
- Gutenkunst, R., N. Newlands, M. Lutcavage and L. Edelstein-Keshet. 2007. Inferring resource distribution from Atlantic bluefin tuna movements: An analysis based on net displacement and length of track. *J. Theo. Biol.* 245, 243-257.
- HO (Hydrographic Office of Korea). 1982. Marine Environmental Atlas of Korean Waters. Yoohanjengpan. Seoul, 1-21.
- Hubbard, S., P. Babak, S.T. Sigurdsson and K.G. Magnusson. 2004. A model of the formation of fish schools and migrations of fish. *Ecol. Model.*, 174, 359-374.
- Huse, G., S. Railsback and A. Ferno. 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *J. Fish. Biol.* 60, 571-582.
- Itoh, T., S. Tsuji and A. Nitta. 2003. Migration patterns of young Pacific bluefin tuna (*Thunnus orientalis*) determined with archival tags. *Fish. Bull.*, 101, 514-534.
- Johansson, R., M. Magnusson, P.A. Fransson and M. Karlberg. 2001. Multi-stimulus multi-response posturography. *Math. Biosci.*, 174, 41-59.
- Kim, J.H. and J. Stringer. 1992. *Applied Chaos*. John Wiley & Sons. New York, 1-546.
- Kim, Y.H. 2003. Numerical modelling of chaotic behavior for small-scale movements of demersal fishes in coastal water. *Fish. Sci.*, 69, 535-546.
- Kim, Y.H. and J.Y. Ahn. 2002. Analysis on chaotic behaviour of movements of sea bream and halibut in open Sea. *Fish. Sci.*, 68(suppl. 2), 1797-1800.
- Kim, Y.H. and C.S. Wardle. 1998. Modelling the visual stimulus of towed fishing gear. *Fish. Res.*, 34, 165-177.
- Lorenz, E.N. 1979. On the prevalence of a periodicity in simple systems. In: *Global Analysis. Lecture Notes in Mathematics*, no. 755. Dold, A. and B. Eckmann, eds. Springer-Verlag, Berlin, 53-75.
- Lorenz, K.Z. 1981. *The Foundations of Ethology*. Springer-Verlag, Berlin, 176-188.
- Lucas, M.C. and E. Baras. 2001. *Migration of Freshwater Fishes*. Blackwell Science, London, 1-136.
- Magnusson, K.G., S.T. Sigurdsson and E.H. Dereksdottir. 2005. A simulation model for capelin migrations in the North Atlantic. *Nonlinear Analysis: Real World Appl.*, 6, 747-771.
- McFarlane, G.A. and J.R. King. 2003. Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean. *Fish. Bull.*, 101, 358-367.
- McKeown, B.A. 1984. *Fish Migration*. Croom-Helm, Beaverton, USA, 1-224.
- Menczer, F. and P.K. Belew. 1996. From complex environments to complex behaviors. *Adapt. Behavior*, 4, 317-363.
- Metcalfe, J., G. Arnolds and R. McDowall. 2002. *Migration*. In: *Handbook of Fish Biology and Fisheries*. Hart, P.J.B. and J.D. Reynolds. eds, Blackwell Publishing, Oxford, UK, 175-199.
- NFRDI (National Fisheries Research and Development Institute, Republic of Korea). 1998. *Ecology and Fishing Ground of Main Fishes in Korean Waters*. Yemoonsa, Busan, 219-225.
- NFRDI (National Fisheries Research and Development Institute, Republic of Korea). 2001a. *Oceanographic Information of the Korean Waters in 2001*. Yemoonsa, Busan, 1-215.
- NFRDI (National Fisheries Research and Development Institute, Republic of Korea). 2001b. *Technique for quantifying abundance of primary organism around the Korean waters using ocean color satellite*. Report of Ministry of Maritime and Fisheries, 35-88.
- Niwa, H.S. 1998. Migration dynamics of fish schools in heterothermal environments. *J. Theo. Biol.*, 193, 215-231.
- Palsson, O.K. and V. Thorsteinsson. 2003. Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus mohua*): evidence from storage tag data. *Can. J. Fish. Aqua. Sci.*, 60, 1409-1423.
- Quinn, T.P. 1991. Models of Pacific salmon orientation and navigation on the open ocean. *J. Theo. Biol.*, 150, 539-545.
- Schaefer, K.M. and D.W. Fuller. 2002. Movements, behavior, and habitat selection of bigeye tuna (*Thunnos obesus*) in the eastern equatorial Pacific as ascertained through archival tags. *Fish. Bull.*, 100, 765-788.
- Shibert, J.R. and J.L. Nielsen. 2001. *Electronic Tagging and Tracking in Marine Fisheries*. Kluwer Academic

Publishers. Dordrecht, Netherland, 1-468.  
Smith, R.J.F. 1984. The Control of Fish Migration.  
Springer-Verlag, Berlin, 1-240.  
Takaba, M. and T. Morioka. 1999. Relationship between  
movements of tagged red sea bream 0 year-old group

and drift-cards in the Seto Inland Sea of Japan.  
Nippon Suisan Gakkaishi, 65, 200-208.

(Received September 2006, Accepted September 2007)