

Schooling and migration of large pelagic fishes relative to environmental cues

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ABSTRACT

A kinesis model driven by high-resolution sea surface temperature maps is used to simulate Atlantic bluefin tuna movements in the Gulf of Maine during summer months. Simulations showed that individuals concentrated in areas of thermal preference. Results are compared to empirical distribution maps of bluefin tuna schools determined from aerial overflights of the stock during the same time periods. Simulations and empirical observations showed similar bluefin tuna distributions along fronts, although interannual variations in temperature ranges occupied suggest that additional foraging factors are involved. Performance of the model is further tested by simulating the relatively large-scale annual north–south migrations of bluefin tuna that followed a preferred thermal regime. Despite the model's relatively simple structure, results suggest that kinesis is an effective mechanism for describing movements of large pelagic fish in the expansive ocean environment.

Key words: Atlantic bluefin tuna, kinesis, migration, spatial model

INTRODUCTION

Population migration was described by Dingle (1996) following Kennedy (1961, 1985) as a persistent directed movement of animals under their own power from one 'habitat' to another. Nakamura (1969) described two types of migratory movement for tunas:

one he considered passive, that is, movement within a habitat in response to local abiotic or biotic conditions; and the other, active or directed movements of fish between habitats following an ontogenetic change in biological requirements. The latter migration behaviour is often motivated by the needs of feeding and reproduction. Such migratory movement has been described for many tunas including Pacific skipjack *Katsuwonus pelamis* (Gauldie and Sharp, 1996), albacore *Thunnus alalunga* (Otsu and Uchida, 1962; Laurs and Lynn, 1977; Kimura *et al.*, 1997), southern bluefin tuna *Thunnus maccoyi* (Murphy and Majkowski, 1981) and Atlantic bluefin tuna *Thunnus thynnus* (Mather, 1980; Suzuki, 1991).

Atlantic bluefin tuna are currently managed as two discrete populations (East and West Atlantic) with limited mixing (Clay, 1991). Classic hypotheses on tuna ecology state that West Atlantic bluefin tuna undertake substantial annual migrations in the Atlantic Ocean, similar to those observed for many avian populations (see Alerstam, 1990 for a review of avian migration). For mature bluefin, low-latitude habitat is believed to correspond to warm-water breeding sites in the Gulf of Mexico and the Straits of Florida (Rivas, 1954; Mather *et al.*, 1995), while the northern extent ranges into the rich forage grounds found in cold mid- to high-latitude waters extending from Cape Hatteras to Newfoundland (Hamre, 1958; Rivas, 1978; Mather *et al.*, 1995). The extent of the migration varies with age. Age-0 bluefin are presumably spawned in the Gulf of Mexico in the spring and passively dispersed northward by the Gulf Stream. Active migratory behaviour is thought to commence at an age of 14 days, with fish less than 0.5 m moving out of temperate coastal waters and into warmer tropical waters of the Sargasso Sea (Rivas, 1978). In general, it takes about 6–8 years for fish to become giants (i.e. reaching lengths >2.5 m), when they routinely move into waters in the Gulf of Maine and the Gulf of St Lawrence (Hamre, 1958; Hurley and Iles, 1980; Mather *et al.*, 1995). It should be noted that recent data from archival and 'pop up' tagging suggest that alternative migration patterns or spawning grounds may exist for West Atlantic bluefin tuna (Lutcavage *et al.*, 1999).

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Spatial distributions of bluefin tunas in North Atlantic waters can change significantly over relatively short time scales (Lutcavage *et al.*, 1997). Though the timing of their annual appearance in the Gulf of Maine is somewhat predictable, spatial distributions of fish aggregations within that area do not necessarily show consistent patterns. Concentrations of fish are assumed to change position in response to a suite of local abiotic and biotic conditions. School positions of large pelagic fishes are often associated with sharp contrasts in sea surface temperature gradients associated with oceanic fronts (Olson and Podesta, 1987; Olson *et al.*, 1994). This behavioural pattern is fairly common among large pelagics such as swordfish *Xiphias gladius* (Podesta *et al.*, 1993), bluefin tuna (Roffer, 1987) and albacore (Lauris and Lynn, 1977; Kimura *et al.*, 1997). Strong temperature preferences have been shown for many marine and freshwater fishes (Bull, 1936; Magnuson *et al.*, 1979), including yellowfin tuna (Brill *et al.*, 1999). However, evidence is lacking for bluefin tuna, possibly owing to their endothermic capabilities (Carey and Teal, 1966; Carey *et al.*, 1971) and the difficulties of handling them in a controlled setting. Bluefin tuna are one of few endothermic fish capable of maintaining internal body temperatures ranging from 24°C to 35°C while inhabiting waters ranging from 6°C to 30°C (Carey and Lawson, 1973; Sharp, 1978; Cort and Liorzou, 1991). Their ability to exploit food resources well below the thermocline on coastal banks further indicates that temperature may not be a limiting factor in determining their vertical or horizontal oceanic distributions (Brill *et al.*, 1999). While some tunas such as albacore are known to concentrate along large oceanic temperature features (Lauris and Lynn, 1977; Kimura *et al.*, 1997), it may be that giant bluefin tuna in northern Atlantic waters are actually responding to prey distributions that are themselves determined by primary and secondary production concentrated along thermal fronts. In such cases, thermal features of the sea surface can be used as proxy indicators of the spatial distribution of prey abundance which subsequently affects tuna distribution.

In this paper, a simple kinesis model responding to spatial 'habitat' data is developed to investigate the possible mechanisms behind the migratory behaviours observed for bluefin tuna in the western North Atlantic. Migration from the Gulf of Mexico to the North Atlantic is modelled as kinesis (i.e. reaction to ambient conditions) by the fish relative to the space-time development of the physical temperature cue involved that results in modification of their swimming behaviour. The model is used to analyse two

kinds of behaviour: (1) large-scale annual migrations from tropical to boreal waters; and (2) the nature of local use of physical features in their Gulf of Maine foraging grounds for prediction of the space-time behaviour of the bluefin tuna stock.

METHODS

Movement model structure

Principles of klinokinesis can be employed to simulate 'behavioural thermoregulation' following Neill (1979). Kinesis is a nondirectional, behavioural response to external stimuli driven by inherent awareness of preferred conditions. Animals change their speed (orthokinesis), turning frequency, or average angle of turns (klinokinesis) depending on the intensity of stimulus in their spatial surroundings (Fraenkel and Gunn, 1940; Schöne, 1984). Harden Jones (1968) described this behaviour as one mechanism for movement in the absence of local landmarks for orientation. To use this technique for simulating the large-scale seasonal migration patterns of bluefin tuna, it was desirable to code the behaviour mathematically as opposed to the conditional statements used by Neill (1979) to determine the probability of turning. Mathematical coding increases model processing speed and allows the model to be run quickly on a high-speed digital computer.

The kinesis model was developed by modifying the 'time of flight' model for particle motion in a turbulent flow field (Dutkiewicz *et al.*, 1993). Table 1 explains the notation of the model. If an individual's movement at any given time t is defined by velocity V , then the probability of turning can inversely be described as the probability of maintaining the exact same value of V in the following timestep. To simulate turning, the dimensional components of V (i.e. $\Delta X/\Delta t$, $\Delta Y/\Delta t$ in two-dimensional Cartesian grid space) can individually be altered by some random magnitude. Therefore, the velocity of a fish in time, $V(t)$, can be modelled considering two components: the velocity from the previous timestep $V(t-1)$ (due to inertia or directional persistence), and some random velocity, ε . If the timestep length is short enough, a large, bilaterally symmetrical animal will tend to continue in generally the same direction as in the previous timestep (Okubo, 1980). In that case, the contribution of $V(t-1)$ to $V(t)$ would be much greater than that of the random component, ε . On longer time scales, or as the movement of the fish becomes less directed, $V(t)$ would be dominated by the random component and maintain little or none of the previous velocity.

To simulate this behaviour, the location of each fish at time t is defined by its position in Cartesian coordinates (x, y) . The fish's velocities $\Delta X/\Delta t$ and $\Delta Y/\Delta t$ are denoted as U and W , respectively. The inertial and random components of each dimensional velocity can then be manipulated to control changes in the movement of the fish at each time-step. The normally distributed random component ϵ is a real number whose mean absolute value is defined as:

$$|\epsilon| = \sqrt{(\Phi^2/2)} \quad (1)$$

where Φ is the maximum sustained swimming velocity, and ϵ has equal probability of being either positive or negative. Equation 1 reduces Φ to its average dimensional (x, y) components by Pythagorean Theorem. Velocity at time t can be described as:

$$V(t) = f(V_{t-1}) + g(\epsilon) \quad (2)$$

with either $U(t)$ or $W(t)$ substituted for $V(t)$. The functions $f(V_{t-1})$ and $g(\epsilon)$ define the relative contributions of each x or y component given the difference between immediate and optimal ambient temperature values (T and T_0 , respectively). These functions are both described by Gaussian distributions:

$$f(V_{t-1}) = V_{t-1} \times H_1 \left[e^{(-0.5)[(T-T_0)/\sigma]^2} \right] \quad (3)$$

$$g(\epsilon) = \epsilon \times \left[1 - \left(H_2 e^{(-0.5)[(T-T_0)/\sigma]^2} \right) \right] \quad (4)$$

where σ is a variance parameter which controls the width of the Gaussian distribution, H_1 and H_2 control height, and the 'peaks' of the distributions are centred where $T - T_0 = 0$ (i.e. where ambient temperature is equal to preferred temperature). Values of H_1 and H_2 are restricted to the range 0–1.0. If the model is parametrized such that $H_1 < H_2$, a negative orthokinetic response can be simulated, in which individuals reduce their speed as they encounter preferable conditions (Okubo, 1980).

Using these equations, the maximum contribution of the velocity $V(t-1)$ at any timestep t is equal to $H_1 \times V(t-1)$, which only occurs when $T = T_0$. Likewise, the random component would only contribute $(1 - H_2) \times \epsilon$ under those conditions. At the opposite extreme, if ambient temperature is well above or below the preferred temperature, the resulting velocity comes from the tails of the distributions: the previous velocity contributes nothing, and the new

velocity is entirely random [$0.0 \times V(t-1) + 1.0 \times \epsilon$]. In keeping with the assumption of kinesis, the response only depends upon local temperature, as there is no taxis ability to discern gradients. In the resulting behaviour, as a fish moves from areas of poor temperature to those more preferable, it will retain more of its previous velocity in the subsequent time-step: i.e. it will tend to continue in generally the same direction. As it moves into areas of less favourable conditions, the movement becomes more random. It is suggested that this lowest approximation to the fish's behaviour still allows effective migration over a wide range of spatial scales.

Design of model simulations

To test the model's performance and examine the potential mechanisms influencing spatio-temporal distributions of Atlantic bluefin tuna, three different types of simulations were run using the algorithm described above. The first was a simple test of the model behaviour in a single dimension. The model was run in a Cartesian plane, using position along the X -axis as the stimulus that influenced movement. By setting a target of $X = 0$ (unit = km), the kinesis behaviour influences fish to aggregate about the origin on the X -axis. Maximum sustainable swimming speed was set to 10 km h^{-1} for all model runs, which represents the search velocity for individuals outside their comfort range. This value is well within reported sustained swimming speeds for bluefin tuna (Wardle *et al.*, 1989; Lutcavage *et al.*, 1997). Model runs were initialized by uniformly distributing fish on the interval $(-50, 50)$ along the X -axis. Each fish was assigned a random velocity applied for the initial timestep. Models were then run following 1000 individuals for periods ranging from 30 to 625 days, sufficient time for the system to attain equilibrium. Model sensitivity was examined using various combinations of parameter values. The effectiveness of the model at inducing aggregations about the target area was determined by examining the structure of fish distributions at the conclusion of runs. For simulations in a Cartesian plane, this is represented as histograms of fish density along axes.

The second series of simulations considered long-distance migrations following a seasonally propagating temperature gradient. In the case of bluefin tuna, this model simulation mimics the hypothesized annual migration from south to north and back, starting from the Gulf of Mexico. Assuming that such a migration could be driven by affinity for a specific surface water temperature, the simulated location of optimal temperature along the abscissa changed, reflecting the seasonal north–south propagation of a preferred ther-

Table 1. Parameters of the Atlantic bluefin tuna spatial movements model.

Symbol	Description	Value	Units	Reference
V_t	Total velocity of an individual at time t	$f(T, T_0, V_{t-1}, \varepsilon)$	km h ⁻¹	
V_{t-1}	Total velocity of an individual at time $t-1$	Variable	km h ⁻¹	
ε	Random variate providing stochastic component of velocity	$ \varepsilon \cap N(\mu, \zeta)$	km h ⁻¹	
μ	Mean of $ \varepsilon $	$\mu = \sqrt{(\Phi^2/2)}$	km h ⁻¹	
ζ	Variance of $ \varepsilon $	4.5	km h ⁻¹	
U	Individual velocity in X-plane	$f(T, T_0, U_{t-1}, \varepsilon)$	km h ⁻¹	
W	Individual velocity in Y-plane	$f(T, T_0, W_{t-1}, \varepsilon)$	km h ⁻¹	
Φ	Maximum sustained swimming velocity	10	km h ⁻¹	Wardle <i>et al.</i> (1989) Lutcavage <i>et al.</i> (1997)
H_1	Height of Gaussian curve in $f(V_{t-1})$	0.75	Dimensionless	
H_2	Height of Gaussian curve in $g(\varepsilon)$	0.9	Dimensionless	
σ	Width of Gaussian curves	Variable by simulation	Dimensionless	
$T(x, y, t)$	Ambient temperature during timestep	Spatially variable	°C	AVHRR SST data
T_0	Target or optimal temperature	18	°C	Lutcavage <i>et al.</i> (1997)
δ	Timestep length	0.25	h	

mal regime along the eastern coast of North America. On the two-dimensional Cartesian grid, optimal temperature T_0 was initialized at the origin (0,0). While the preferred position along the abscissa was always located at $X = 0$, the target temperature moved up and down the ordinate on the interval $0 \leq Y \leq 1000$ km according to a sinusoidal function of time with a period of one year. This creates an overall shift of preferred conditions from the origin northward 1000 km and then back to the origin over the course of one year, roughly characterizing the annual movement of bluefin tunas in the north-western Atlantic and the thermal changes observed along the boundary of the West Atlantic. A modified version of this model was created in which the sinusoidal function was coupled to a stochastic delay in the propagation of the thermal regime. In model runs, the temperature profile remained static for a random number of days (5–15 days on average) then abruptly shifted to its updated position. This provided a possibly more realistic spatio-temporal transition of the thermal regime. In simulations, movements of 500 fish were modelled over a two-year period with parameter values $\sigma = 3.0$ and timestep $\delta = 0.25$ h. The model was allowed to run for a year to initialize from an initial distribution at the origin (0,0). Model domain along the ordinate was bounded on the interval $-500 \leq Y \leq 1500$. Positions of fish over the course of the second and third years were tracked to determine densities relative to the target positions.

The third set of model runs was constructed to simulate movements of 500 bluefin in the Gulf of

Maine [Cape Cod, MA north to Bar Harbor, ME (71.0°W to 66.5°W, 40.75°N to 45.25°N); see Fig. 3] using sea surface temperature (SST) as the stimulus for movement. SSTs from satellite data were used to map temperature distributions in the area at 0.009° latitude/longitude resolution (≈ 1 km). The SST maps employed were constructed from advanced very high resolution radiometer (AVHRR) data collected during the period August to October 1994, provided by the Rosenstiel School of Marine and Atmospheric Science remote sensing facility. Specifics of the AVHRR observation methodology were described by Schwalb (1978). In simulations, T_0 was set at 18°C, which reflects mean observed surface temperature of school locations during August and September 1994 and 1995 aerial survey data (Lutcavage *et al.*, 1997). This was chosen as our preferred stimulus level not only because it concurs with temperature data for these tuna; also, it is linked to the edge of Gulf Stream waters because of the large mass of subtropical mode water at 18°C to its south (Iselin, 1936; Warren, 1972; Worthington, 1976). Aerial surveys show a marked association of bluefin tuna concentrations with thermal front zones along the edge of the warm Gulf Stream water (Fig. 5) (Lutcavage *et al.*, 1997). Fish movements were simulated for up to four weeks under these conditions, allowing fish to disperse preferentially throughout the model domain. Combinations of σ and δ values were employed for purposes of sensitivity analysis. Final positions of fish in model runs were visualized using IDL software (Interactive Data Language, Research Systems, Boulder, CO), and were

compared with positions of schools determined from aerial survey data. Aerial survey methodologies were described in Lutcavage and Newlands (1999).

RESULTS

Model results from single dimension runs are shown in Fig. 1. Using a timestep of $\delta = 0.25$ h, the model produced excellent aggregations over the specified range of σ -values (Fig. 1a,e,i). The spread of individuals around the target value ($X = 0$) was proportional to the value of σ ; fish density appears to ‘flatten out’ at a distance 3σ from the target position, so that sharper aggregations were associated with the smaller sigma values, such as $\sigma = 10$. As timestep increased, the

effectiveness of the kinesis behaviour was reduced. Numbers of fish around the target decreased over all values of σ as the timestep increased. Using a timestep of 5.0 h, no significant aggregations were observed for any sigma value (Fig. 1d,h,l).

The two-dimensional annual migration model on a Cartesian surface produced similar results as above for static conditions on the X-axis. However, sinusoidal variation in the target position on the Y-axis from 0.0 to 1000.0 km and back produced an overall movement of highest fish densities between migration extrema over a period of one year. The results of this run are presented as histograms of densities along the Y-axis every 3 months for a one-year period (Fig. 2). Densities on the X-axis are excluded to avoid redundancy

Figure 1. (a–l) Results of one-dimensional analytical model runs with taxis to $X = 0$ parametrized to $\delta = 0.25, 0.50, 1.0$ and 5.0 h (rows), and $\sigma = 10, 30,$ and 50 (columns).

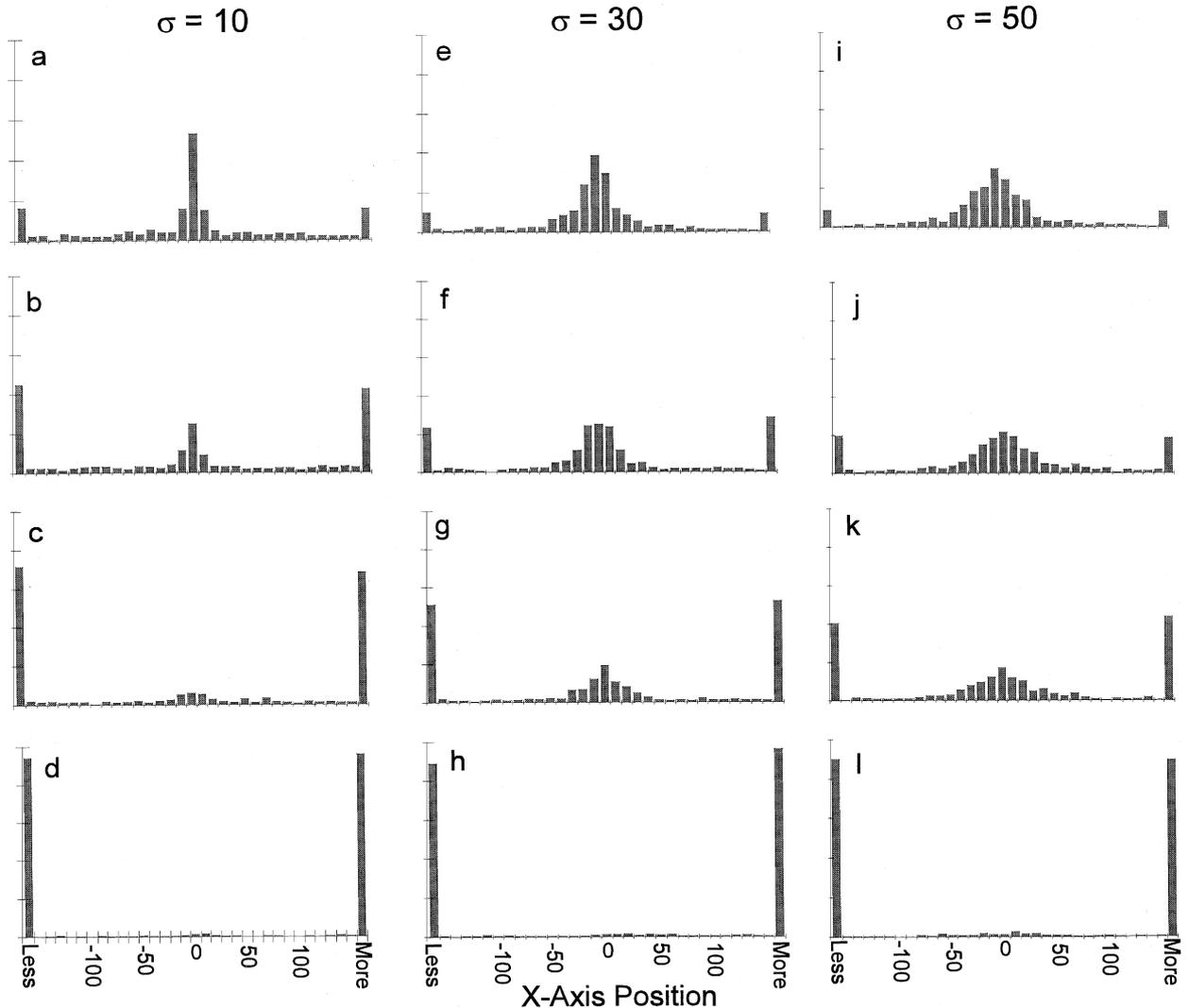
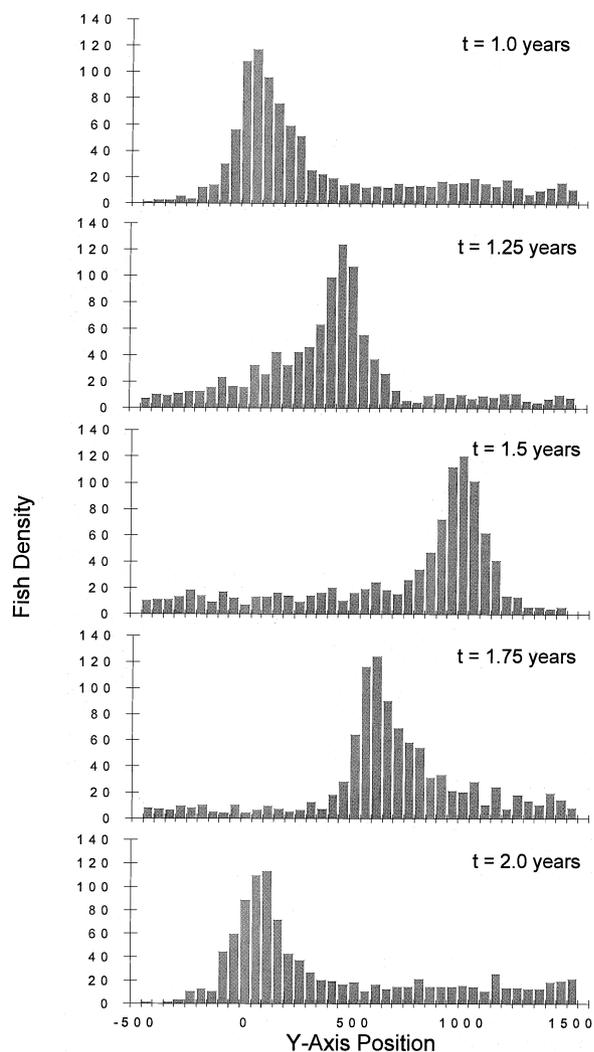


Figure 2. Result of two-dimensional analytical model run with migration along Y-axis. Position along Y-axis over period of 1 year is noted as distance (km) from origin.



with the previous example. Stochastic delays in thermal target propagation produced the same general result, although on average the number of fish lagging behind the general migration increased.

Simulations of bluefin tuna movement in the Gulf of Maine produced spatial distributions similar to those observed in aerial survey data. Individual fish positions at the start and end of runs are denoted on colour-coded maps of sea surface temperature, and the corresponding water temperatures occupied by fish at these times are shown as histograms (Fig. 3). The temperatures occupied by fish at the start of model runs generally ranged from 9°C to 24°C, with many fish evenly distributed between 13°C and 18°C. However, histograms of surface temperatures occupied

by fish at the end of model runs indicate highest concentrations of fish in surface waters of 18°C. The spread of thermal distributions of fish about this target temperature generally reflect the value of σ used for each run. Correlations between fish density and surface temperature from model runs showed temperature distributions comparable to those obtained from aerial survey data over annual observation periods (Fig. 4). Model results using this target temperature also showed marked aggregations along the edges of sharp thermal fronts (Fig. 3).

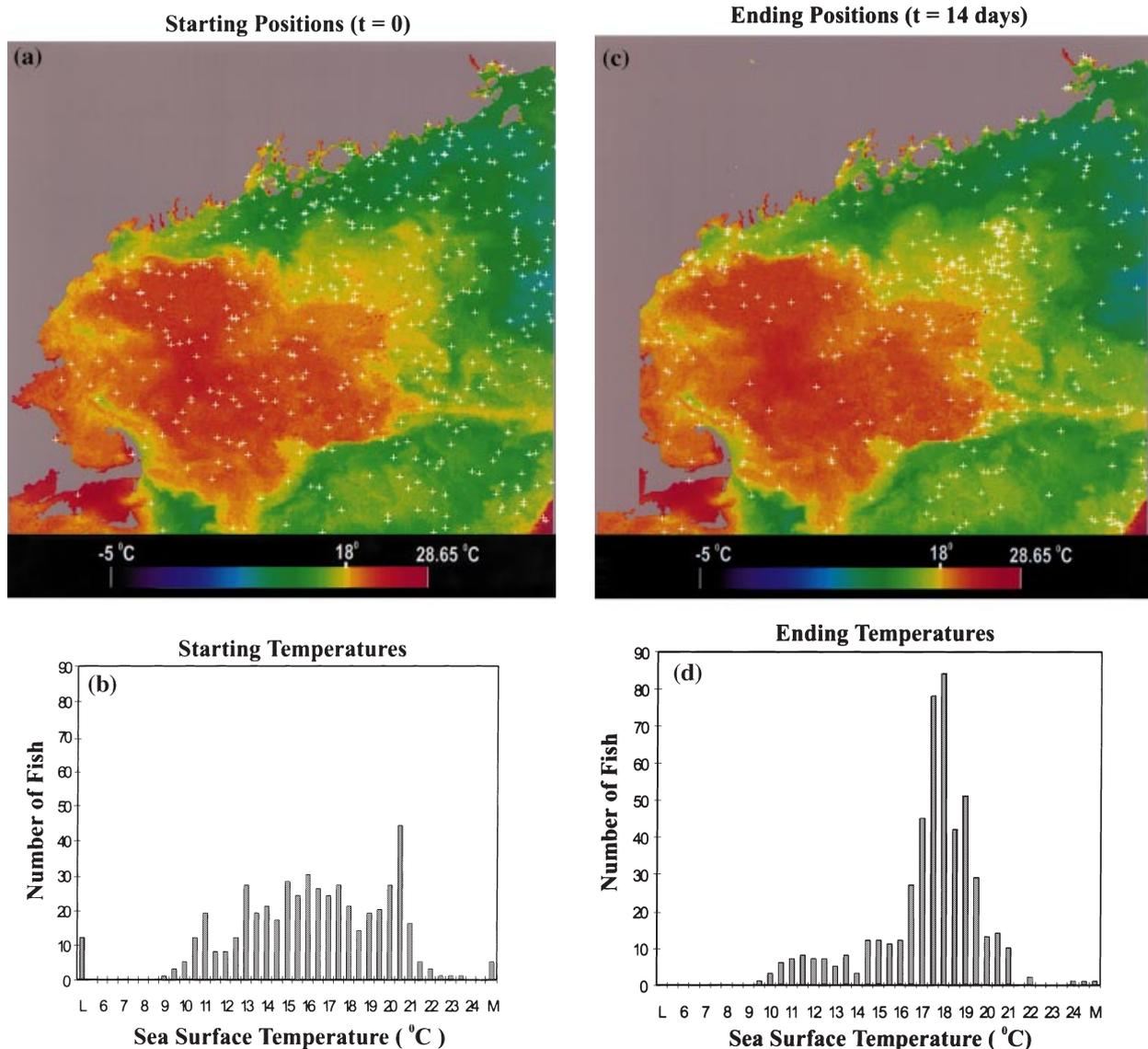
DISCUSSION

Some important aspects of large pelagic fish movement and migratory behaviours were illuminated by our simple model application. The advantages of the kinesis approach lie in its behavioural simplicity, yet results suggest that this approach can be used to reproduce a variety of complex movement patterns. While simulations in the Gulf of Maine provide a realistic format for evaluating model performance relative to field observations, the Cartesian model runs provide a simple format for examining model behaviour and sensitivity analysis.

The influence of the parameters σ and δ on the effectiveness of the kinesis behaviour is apparent from the distributions presented in Fig. 1. These parameters represent the sensitivity of the kinesis behaviour and the temporal resolution, respectively. Values of σ employed characterize the resulting concentration of fish around the target stimuli. Parametrization of σ is contingent upon the range of stimulus values in the data (e.g. surface temperature range). Timestep length likewise influenced model behaviour, and its parametrization depends upon data resolution and computational limitations.

By allowing the random component to contribute to velocity when individual fish were within the target area (although this contribution is minimal), a 'milling' behaviour was simulated when fish are within their target area. As the movement of the fish slows owing to the orthokinetic response, there is still the possibility of a stochastic influence which could propel the fish outside the target range of stimulus. Therefore, densities are balanced by the tendency to aggregate by kinesis vs the dispersive effect of random 'diffusion'. In the field, small numbers of fish are often observed in less probable areas for unknown reasons. Similarly, in these model results, the highest density of fish occurred in the area of optimal stimulus, with decreasing densities moving toward areas of less favourable stimulus. This condition was dynamic, with fish moving in and

Figure 3. Results of Gulf of Maine model runs illustrated as spatial position plots over sea surface temperature maps (3a,c), as well as histograms of sea surface temperatures occupied by individuals at start and end of run (3b,d). Starting positions were random (3a), and the ambient temperatures of all individuals are illustrated by the histogram in 3b. Model was run for 14 days with the parameter values $T_0 = 180$, $\sigma = 2$, $\delta = 15$ min and $N = 500$. Final positions are indicated in 3c. Sea surface temperature is colour-coded for the range -5°C (default masking value for land) to 28.65°C . Colour representation of 18°C surface water is denoted on colour scale. Panel 3(d) illustrates the ambient temperatures of final positions for all individuals.

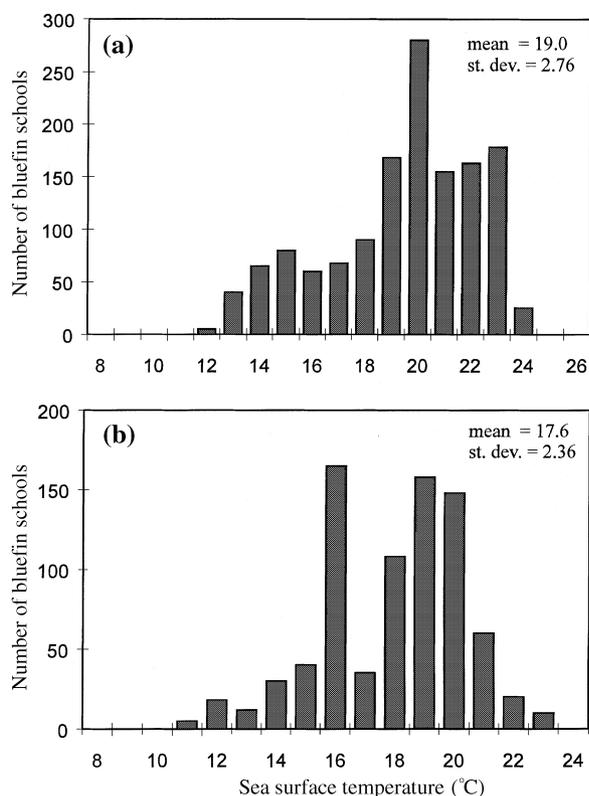


out of the target area owing to the aforementioned milling behaviour.

The results of the second series of simulations suggest that the kinesis model can produce aggregations in general agreement with observations for target areas under dynamic spatial conditions. While the spatial irregularities of thermal gradients in the coastal Atlantic are not ideally represented by the one-dimensional temperature forcing function, the kinesis

model can be employed to imitate fish migrating in response to a moving thermal target. Model results were most accurate when maximum swimming speed (Φ) was increased to 15 km h^{-1} . Because fish within target areas reduce their speed through an orthokinetic response, the average effective velocities over the course of model runs were well below this value. The histograms in Fig. 2 indicate that a number of individual fish do not keep up with the movement of the

Figure 4. Histograms of sea surface temperatures (°C) occupied by tuna schools in the Gulf of Maine as determined by aerial survey and daily SST data for the years 1994 (a) and 1995 (b). Note differing scales.

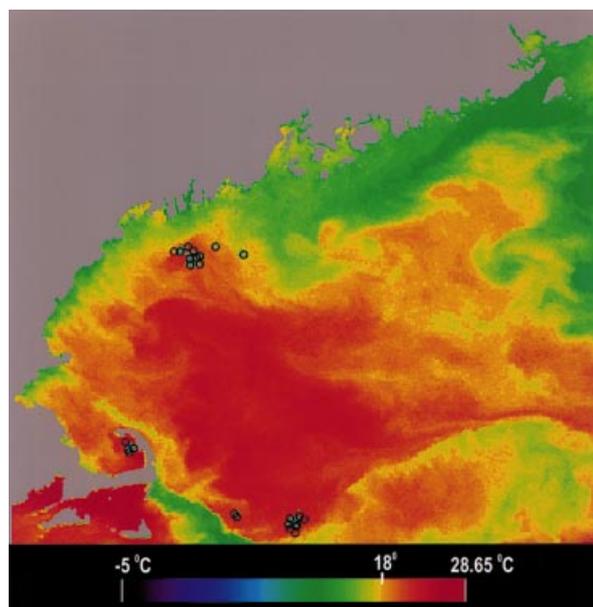


target Y-value (temperature cue). In this case, once the target Y-value has moved far away from an individual fish, its chances of finding the target again are decreased. When the target value moves back towards these lost fish, they are close enough to pick up the kinetic response which moves them into the target area. The highest densities of fish occurred at the target Y-value, but there were significant numbers of 'lost' fish throughout the target's range (0–1000 km). The number of fish outside the target temperature increased in the stochastic delay model, indicating that rapid movements of the preferred thermal regime may have reduced the effectiveness of the kinesis model. These results seem to be realistic, as the appearance of smaller numbers of fish either preceding or lagging behind the general migratory group has often been observed in anecdotal reports by fishermen. Back-calculated spawn dates of bluefin tuna larvae collected in the Gulf of Mexico have also indicated that some late adult spawning may occur well after the general northward migration has begun (Mather *et al.*, 1995). Our model results may accurately describe the

behaviour of fish that have lost the proper environmental cues necessary for directed migration. It has also been suggested that many tunas may employ magneto-sensory abilities in directing long-range migrations (Wiltchko and Wiltchko, 1995). If this behaviour was modelled as a seasonal directional bias in conjunction with the kinesis behaviour, the number of fish lagging behind the main migratory group would certainly diminish.

Our model produced reasonable spatial distributions of bluefin tuna when compared to the Gulf of Maine sea surface temperature maps. Figure 3(c) shows colour-coded surface temperature and positions of individual fish following a four-week simulation. The spatial aggregation of fish along SST frontal systems is very similar to what has been observed from aerial surveys (Fig. 5). Most fish are within $\pm 1^\circ\text{C}$ of the target temperature value of 18°C , as seen in Fig. 3(d). This temperature–density correlation is typical of results from the Gulf of Maine model; the greatest numbers of individuals are in 18°C surface temperature waters, and the spread of individuals about that target temperature reflects the value of σ used in the run. When compared to temperature distributions of schools in the Gulf of Maine as

Figure 5. Positions of tuna schools in the Gulf of Maine on 16 August 1994, plotted over sea surface temperature map from Reynolds data. Sea surface temperature is colour-coded for the range -5°C (default masking value for land) to 28.65°C . Colour representation of 18°C surface water is denoted on colour scale.



determined by aerial survey and daily SST data, the histograms show similarity in their general shapes. Though peaks appear out of phase, they are both characterized by highest concentrations between 18°C and 20°C, with a gradual decrease in numbers at progressively lower temperatures and a sharp drop in numbers as temperature increases. This reflects both the limitations of available surface water temperatures and the behaviour of the fish as they centre their activities on the location of thermal fronts. However, spotter plane data from the month of October in the Gulf of Maine indicate that largest surface assemblages may occur at 15°C surface temperature (Lutcavage *et al.*, 1997), which may suggest that preferred thermal ranges change seasonally.

Sensitivity analysis demonstrated that the model performs best when short timesteps (<1 h) are employed. This is also reasonable with respect to the cognitive time scales that influence fish movement behaviour. This temporal resolution can be a disadvantage when using this model to simulate fish distributions over extended periods of time (e.g. multigenerational population models). The increase in computing time required may make this model unfeasible for use, depending on available computing resources. The need for short timesteps arises from the fact that stimulus levels are only considered at the starting and ending points of an individual's movement during a timestep. If timesteps are long (1 h or greater), a fast-swimming fish such as a tuna could easily move over 10 km in a single timestep. It is then possible for fish completely to overshoot a preferred temperature, and the model is based on stimulus levels only at starting and ending points. In reality, the fish would be sensing changes in stimulus over the entire course of its movement, and would respond when it encountered a preferable area during its travel. Therefore, at longer timestep values this model behaviour becomes very unrealistic.

Because of the availability of remotely sensed SST data and temperature's hypothesized importance in influencing spatial distributions of tunas and other pelagic fish, this model uses sea surface temperature as the sole stimulus influencing spatial distributions, but other characteristics could easily be substituted or integrated using this basic kinesis model. As an example, if more than one stimulus were included in the model, the kinesis behaviour could be based upon some optimal combination of the available stimuli, including spatial and physiological variables. Weighting factors could be employed to create hierarchical responses to different stimuli. Because temperature fronts are employed in the Gulf of

Maine model as proxy indicators of prey aggregations, better knowledge of prey species behaviour with respect to thermal features might considerably enhance the performance of this model. Any model of individual movement can be strengthened by better knowledge of species behaviour, and emerging data from hydroacoustic tracking and 'pop up' satellite tags can yield significant data on fine- and larger-scale spatial distributions.

Bertignac *et al.* (1998) employed an advection-diffusion model to describe skipjack tuna distribution in the Pacific. A 'habitat index' incorporating forage prey distribution and sea surface temperature influenced the advective term of movement. Their model results were generally in good agreement with data. However, it tended to produce 'over-concentrations' of fish in areas of favourable habitat that were isolated within a poor surrounding environment. Using this movement behaviour, fish would not move away from favourable areas if it required crossing an expanse of less favourable habitat, remaining 'trapped' in such isolated areas. As the authors stated, this condition arose because advection is 'created by the habitat gradient.' The sharp gradient surrounding such areas prevents fish from venturing further to sample nearby waters. This type of bias would likely be reduced using a kinesis model, because it does not explicitly respond to gradients of stimulus. While the kinesis behaviour caused fish to aggregate in favourable areas, the influence of the stochastic component kept fish moving throughout the environment, allowing fish to sample their habitat more completely while still producing aggregations in preferred areas.

Bluefin tuna display complex, dynamic schooling behaviours in the Gulf of Maine (Partridge *et al.*, 1983; Lutcavage *et al.*, 1997). Though these schooling behaviours were excluded from this study, it would be possible to simulate such interactions within the same model context. The model could be identically run assuming that individual units are separate schools of fish, with size and structure varying according to defined probability functions. Final positions of schools at various points in the run could then be examined using cluster analysis techniques, and probability of schools combining or splitting could be applied based on proximity to one another. There also may be methods of incorporating such social interactions on a hierarchical basis in spatial models using kinesis principles. These possibilities are left to future exploration. The model may be better suited to fish species that form loose aggregations, rather than those that maintain highly structured schools. Inshore species such as the common snook (*Centropomus undecimalis*)

or spotted seatrout (*Cynoscion nebulosus*) exhibit congregation behaviour during spawning periods, certain life stages, or in areas of high productivity. However, they do not display the persistent, structured school behaviour characterized by species like tunas. These inshore species may be better subjects for a spatial model employing this kinesis behaviour. Spatial domains for modelling inshore species would naturally be smaller than those of wide-ranging pelagic species, which would facilitate high-resolution characterization of environmental stimuli. The heterogeneity of the inshore environment would lend itself well to this kinesis model.

The general agreement of simulations of kinesis behaviour with observed bluefin tuna spatial distributions presents an effective alternative to the use of taxis behaviour in fish movement models. The fundamental assumption of taxis behaviour is that individuals can sense directionality of stimulus gradients, either over the length of their body or within a defined search area, and thus can direct their motion towards preferred environmental conditions. Considering the relatively large spatial scales of ocean temperatures over 70% of the globe, it is probably unrealistic to assume that bluefin tuna could distinguish large-scale thermal gradients (e.g. >10 km) over the length of their bodies (Olson and Podesta, 1987). It likewise appears unrealistic to assume that these fish could reconstruct gradient directionality over large spatial and temporal scales from cognitive ability (i.e. memory of past events). Therefore, modelling movement as a kinesis behaviour is appropriate in that it assumes the simplest powers of sensory perception and cognitive ability on the part of the fish. The model assumes only that fish have a sense of their ambient conditions as well as 'inherent knowledge' of preferred ambient states, and can adjust their behaviour and spatial position accordingly.

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