

A dynamic optimisation model for the behaviour of tunas at ocean fronts

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ABSTRACT

We present a model that simulates the foraging behaviour of tunas in the vicinity of ocean fronts. Stochastic dynamic programming is used to determine optimal habitat choice and swimming speed in relation to environmental variables (water temperature and clarity) and prey characteristics (abundance and energy density). By incorporating submodels for obligate physiological processes (gastric evacuation, standard and active metabolic costs) and sensory systems (visual feeding efficiency), we have integrated into a single fitness-based model many of the factors that might explain the aggregation of tunas at ocean fronts. The modelling technique describes fitness landscapes for all combinations of states, and makes explicit, testable predictions about time- and state-dependent behaviour. Enhanced levels of searching activity when hungry and towards the end of the day are an important feature of the optimal behaviour predicted. We consider the model to be particularly representative of the behaviour of the warm-water tunas or *Neothunnus* (e.g. skipjack, *Katsuwonus pelamis*, and yellowfin, *Thunnus albacares*) and for surface-dwelling temperate tunas (e.g. young albacore, *Thunnus alalunga*), which are often observed to aggregate near fronts. For the bluefin group (i.e. older albacore; northern and southern bluefin, *Thunnus thynnus* and *Thunnus maccoyii*), for which extended

vertical migrations are a significant and as yet unexplained component of behaviour, the model is able to reproduce observed behaviour by adopting the lower optimal temperature and standard metabolic rate of albacore. The model cannot explain why physiological differences exist between and within the different tuna species, but it does show how differences in susceptibility to thermal stress will permit different behaviour.

Key words: behaviour, fronts, physiology, stochastic dynamic programming, tunas

INTRODUCTION

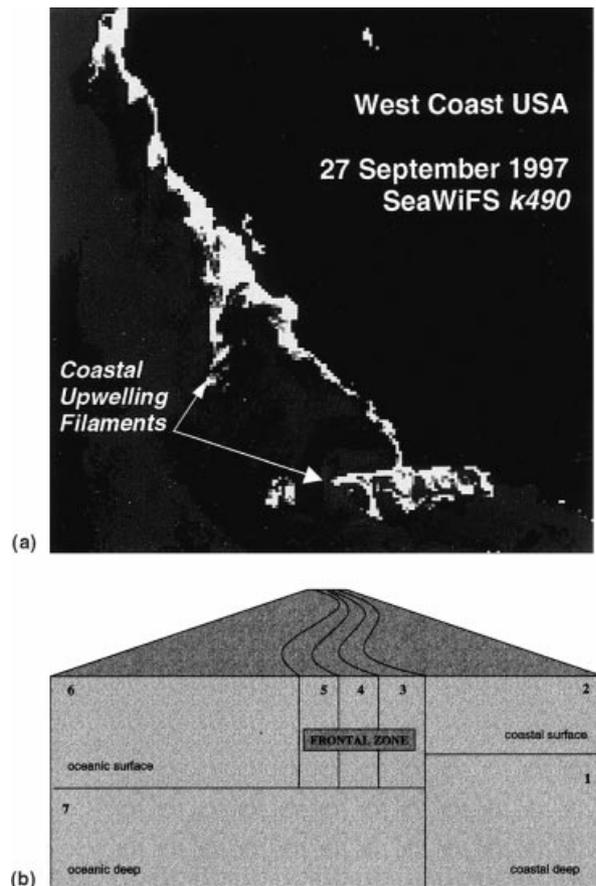
Ocean fronts are broadly understood to mark the boundary between two different water types (Fig. 1a) and are therefore usually manifested as a region of strong horizontal gradients in temperature, salinity, and chlorophyll, and concentration of zooplankton and micronekton. Blackburn (1965) noted that fronts are very important in the ecology of tunas and other macronekton, but that the reasons for this were rather poorly understood. Even now, there are no data sets that allow a definitive assessment of trophic interactions at fronts, particularly with regard to the behaviour of tunas (Olson *et al.*, 1994). Whilst it is generally accepted that tunas aggregate at fronts, presumably to feed (Laurs *et al.*, 1984; Fielder and Bernard, 1987), field observations do not always show that tunas and their prey are more abundant in or at fronts than in adjacent waters (Sund *et al.*, 1981; Power and May, 1991). Nonetheless, the observation that tunas are often associated with fronts, known in Japan as Kitahara's Law, is often used in present-day operational forecasting to direct fishing effort for tunas (Yamanaka *et al.*, 1988; Santos and Fiúza, 1992). Reasons offered as to why such association occurs include the following (Laurs *et al.*, 1984): confinement to a physiologically optimum temperature range (Thompson, 1917; Sund *et al.*, 1981), use of frontal gradients for thermoregulation (Neill, 1976), limitation of visual hunting efficiency owing to water clarity (Murphy, 1959; Magnuson, 1963), and the availability of appropriate food (Pinkas *et al.*, 1971). The relative importance of these factors has not been

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Figure 1. (a) Diffuse attenuation coefficient (k_{490}) derived from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). Turbid waters (white) are seen near the coast, being the result of wind-driven upwelling of cold, nutrient-rich waters and subsequent increase in phytoplankton density. Albacore aggregate and feed near these filaments (Laurs *et al.*, 1984; Fielder and Bernard, 1987). Pixel size is 4 km; image histogram has been stretched to discriminate water masses. (b) Schematic representation of habitat choice for tunas in the vicinity of a coastal upwelling front. Some realistic values for food abundance and quality and physical properties (turbidity, temperature) of the different habitats are suggested in Table 1.



investigated theoretically, experimentally or by field observation.

This model was developed as a tool that might help to guide and interpret future observations. We investigate tuna behaviour in the context of optimal foraging theory, where the individual is seeking to maximize energy return from foraging activity in a heterogeneous environment (Emlen, 1966; MacArthur and Pianka, 1966; Stephens and Krebs, 1986; Schoener, 1987). The objective of the exercise was to develop a model system for a generic tuna that would

predict optimal foraging behaviour in relation to the biophysical environment. Environmental cues and functional responses are linked, and obligate physiological processes are represented at an appropriate level of detail. Through this work, we wished to suggest a methodology for integrating tuna physiological and behavioural ecology within a quantitative framework, with a sound theoretical basis, and ultimately a predictive capability. We also asked two essential questions of the model.

- 1 Is the observed aggregation of tunas at ocean fronts predicted by any single property or combination of properties of the fish themselves or of their environment?
- 2 Are the observed inter- and intraspecific variations in behaviour also predictable?

By investigating these questions we hoped to provide explanations for tuna behaviour, placing observations in a theoretical context and identifying requirements for further observational and experimental study.

THE MODEL

Environment

The ocean environment is represented in two-dimensional space and time, with two vertical layers and two surface water masses with a frontal zone between them (Fig. 1b). The fish may therefore inhabit any one of seven possible habitats at any given time. As the time step used in the model is one hour, we allow the fish to move between all possible habitats without constraint. The properties of these habitats (Table 1) are used as inputs to the model. Temperature relates to the rate of various physiological processes, which are described in more detail below. Prey abundance and water clarity affect the rate of food encounter, whilst prey quality in terms of caloric (energy) density affects the rate of energy return. The energy density of northern anchovy, *Engraulis mordax*, a favourite prey of albacore foraging at the coastal upwelling fronts off California (Fielder and Bernard, 1987) is $\approx 7 \text{ kJ g}^{-1}$ (Boggs, 1991). Here we vary prey quality by decreasing energy density from this level. Tunas are predominantly visual predators, feeding opportunistically and unselectively on micronekton, including epipelagic fish, molluscs and crustaceans, and the larvae of these groups (Blackburn, 1968). For reasons largely concerning the difficulty of sampling micronekton (i.e. small, fast-swimming fish), direct assessment of tuna forage has not yet been possible (Roger, 1994). We estimated prey abundance as

Table 1. Some realistic values for habitat properties at the frontal zone: estimated values for food quantity (Prey) and quality (PED), turbidity (k) and temperature (T) are used. For different simulations these quantities were varied.

Patch	k (m ⁻¹)	T (°C)	Prey (shoals m ⁻³)	PED (kJ g ⁻¹)
1	–	–	–	–
2	0.04	18.00	0.40E-07	6
3	0.0325	19.00	0.20E-07	5.5
4	0.025	20.00	0.10E-08	5.5
5	0.0175	21.00	0	–
6	0.01	22.00	0	–
7	–	–	–	–

follows: taking prey concentration as $\approx 1\text{--}10\text{ g m}^{-2}$ (as used by Dagorn *et al.*, 1995) over a 100 m surface layer gives prey density of $1 \times 10^{-5}\text{--}10^{-4}\text{ kg m}^{-3}$. The feeding model described below simplifies prey encounter such that if a shoal of forage fish is encountered, up to 1 kg of food is consumed. Assuming a shoal of forage fish to have an average mass of 1000 kg, we obtain prey densities of $1 \times 10^{-8}\text{--}10^{-7}$ shoals m⁻³, which is the range of abundance used in this model. In clear water with realistic swimming speeds this gives an encounter rate and frequency of feeding of 1–2 meals day⁻¹.

Prey encounter

The probability p of finding food during any time step is deduced from the encounter rate, E , between the cruising tuna and its prey:

$$p = 1 - \exp(-E.t), \quad (1)$$

for:

$$E = 0.5(\pi.r^2.v.N) \quad (2)$$

The concentration of prey N is input to the model and reactive distance r is calculated below. Cruising velocity v is allowed to range from 1 to 10 body lengths s⁻¹ and is optimized in the fitness criterion. For visual predators such as tuna, the reactive distance is equivalent to the visual range of the fish. A mechanistic model for aquatic visual feeding has been derived (Aksnes and Giske, 1993; Aksnes and Utne, 1997), which includes much detail on the properties of the predator's eye, the optical properties of the water and prey characteristics. These are largely undetermined for tunas and their prey, so we have collected the parameters into a single constant c_1 and let visual range vary in relation to water clarity (diffuse

attenuation coefficient k at 490 nm), surface solar irradiance S and depth z :

$$r^2 \approx c_1.S.e^{-k.z}. \quad (3)$$

For the surface habitats we integrate r over the mixed layer depth h and for the deeper habitats we calculate r at depth h :

$$\int_0^h r^2 \approx c_1 \cdot S \int_0^h e^{-k.z} dz \quad (4)$$

$$r^2 \approx -c_1.S.(e^{-k.h} - 1)/k \quad (5)$$

We use diffuse attenuation coefficient at 490 nm, the peak wavelength for the spectral sensitivity of the yellowfin tuna eye (Kawamura *et al.*, 1981). This is also directly measurable with the satellite-borne Sea-viewing Wide Field-of-view Sensor (SeaWiFS).

Physiology

Owing to significant gaps in the literature, we have had to derive a generic or artificial tuna (ARTU), characteristics of which are given alongside those of 'real' tuna in Table 2. Bio-energetic equations, considering standard and active metabolic energy costs, and the role of food quality, quantity and availability, represent the physiology of the individual animal and are the state-space of the model. Temperature has a direct effect on standard metabolic rate (Brill, 1987) but also limits time spent in colder waters by its effect on heart rate (Brill, 1994b; Brill, 1997; Brill *et al.*, 1999). We account for the effect of cardiac stress by using an additional state variable.

State variable X (stomach fullness)

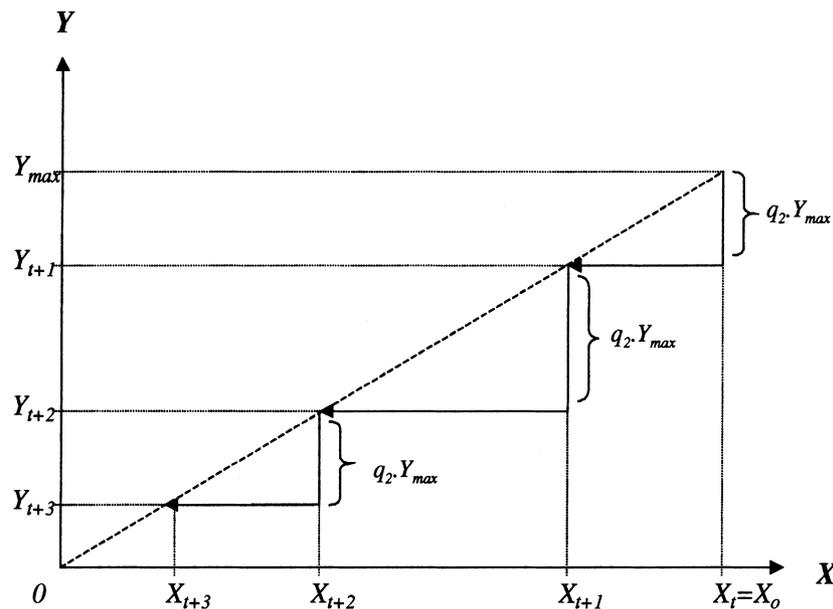
Experimental work has shown that when food is available, tuna will feed until satiated in less than an hour (Olson and Boggs, 1986). The model therefore allows the stomach to be refilled to capacity at each prey (shoal) encounter. Tunas have exceptionally high digestion rates, which is advantageous for species that must be able to exploit a food patch whenever one is found (Magnuson, 1969; Brill, 1987, 1996). Rapid energy absorption may occur for low-energy prey items (Olson and Boggs, 1986) and in warmer waters where metabolic rate – and therefore absorption efficiency – is higher (Jobling, 1994). In this model, rather than fixing a linear or logarithmic rate of gastric evacuation, we let it be determined by the rate of energy absorption from the stomach (Fig. 2). Energy absorption and gastric evacuation rates at

Table 2. Characteristics of our artificial tuna (ARTU) compared with published data^a. Omissions occur where no published information is available. ARTU is derived to have characteristics similar to those measured for skipjack and yellowfin.

Property	ARTU	Skipjack	Yellowfin	Albacore	Bigeye	S. bluefin
Maximum length (cm) ^b	100	110	280	130	250	225
Maximum weight (kg) ^b	20	35	200	45	210	200
Stomach capacity/body mass (%)	5	–	5.46–5.97 ^c	–	–	–
Somatic energy density (kJ g ⁻¹)						
Maximum	6	6.2 ^d	6.0 ^d	–	–	–
Minimum	3	3.1 ^d	3.7 ^d	–	–	–
Swimming speed (body lengths s ⁻¹)						
Maximum	10	14.4 ^e	10 ^e	–	–	–
Minimum	1	1.5 ^f	1.3 ^f	–	1.1 ^f	–
Preferred (optimal) temperatures (°C)	20–30	17 (20–29) 30 ^g	18 (24–30) 31 ^g	11 (16–19) 25 ^g	11 (23–28) 28 ^g	10 (13–15) 28 ^g
Standard metabolic rate (SMR) for 20 kg fish (kJ h ⁻¹)	22	30 ^h	22 ^h	15 ⁱ	–	–
Lethal limits of temperature: time (h) @temperature (°C)	5, 15	5, 15 ^j	–	–	–	–
Q ₁₀ for temperature effect on SMR (–)	2	2.2 ^h	2.2 ^h	–	–	–
Visual range (m)	1–30	–	–	–	–	–

^aSources: ^bCollette and Nauen (1983); ^cOlson and Boggs (1986); ^dBoggs and Kitchell (1991); ^eYeun (1966); ^fMagnuson (1973); ^gFreon and Misund (1999); ^hBrill (1987); ⁱBrill, unpublished, in: Graham and Laurs (1982); ^jDizon *et al.* (1977), Barkley *et al.* (1978).

Figure 2. Energy absorption from the stomach and gastric evacuation. Starting with a full stomach (X_0) with maximum stomach energy (Y_{max}), a proportion ($q_2 \cdot Y_{max}$) is absorbed during the first time step. An amount of stomach contents is then evacuated, such that the energy density of the stomach contents (Y/X) is unchanged. The amount of energy absorbed in each time step varies because the absorption coefficient (q_2) depends on metabolic rate. This doubles two hours after feeding and then decreases to the pre-feeding rate.

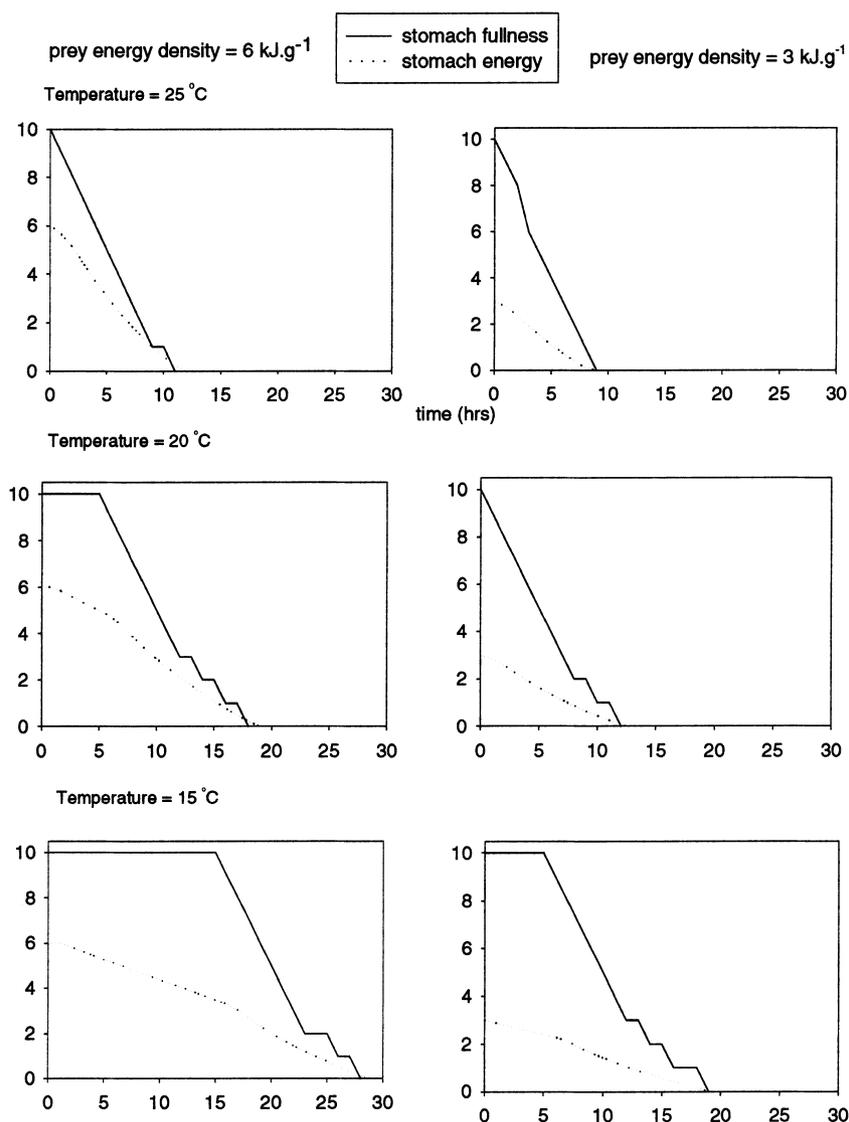


different temperatures and prey densities are shown in Fig. 3. The stomach is capable of absorbing a fixed amount of energy in each time step. Poor-quality food is evacuated more quickly than is high-quality food. While the slopes for gastric evacuation are the same, the time taken to empty the stomach is less for lower-energy food. What this implies is that energy absorption in the stomach is a continuous process but gastric evacuation is not – some variation in the energy density of the stomach contents occurs during digestion, but this slight accumulation of waste precedes a pulse of evacuation.

State variable Y (stomach energy)

The energy in the stomach is determined by the relative amounts of the possible prey types and their respective energy densities. The amount of energy absorbed from the stomach contents in each time step is determined by the absorption coefficient, q_2 , which varies with metabolic rate as described below. Previous work (Kitchell *et al.*, 1978) found that absorption efficiency, in terms of energy absorbed from energy ingested, was 90% for a diet of fish and 80% for a diet of invertebrates. Here we assume 100% absorption, an approximation that allows us to use the amount of

Figure 3. Rates of energy absorption and gastric evacuation for different prey qualities at different temperatures. Note the rapid evacuation of stomach contents when prey quality is poor and the slower absorption and evacuation rates at lower temperatures. Energy absorption is a continuous process; gastric evacuation is pulsed.



energy absorbed per time step to determine the rate of gastric evacuation as described above and in Fig. 2.

State variable Z (body energy)

Total body energy is the product of body mass and somatic energy density, and it represents the accumulation of energy reserves as fat, as energy stored in muscle, and as sugar. Body energy is increased by absorption from stomach contents and is decreased by standard and active metabolic energy costs. The total energy cost in a time step (α) is the sum of energy cost due to standard metabolic rate (E_M), the energetic cost of converting food (specific dynamic action, SDA) and the energetic cost of locomotion (E_L):

$$\alpha = E_M + SDA + E_L. \tag{6}$$

Standard metabolic rate, E_M , falls with decreasing temperature, with a $Q_{10} \approx 2$ (Brill, 1987). Specific dynamic action is a function of stomach fullness, X . Jobling (1994) described the effects of feeding on the metabolic rate of fish and noted a sharp increase shortly after ingestion of a meal, peaking at ≈ 2 times the pre-feeding rate within a few hours. Over the first two hours following ingestion we let SDA increase from zero (i.e. no food is being converted) to a value equivalent to the standard metabolic rate; total metabolic energy costs therefore double and then decrease to the pre-feeding level over the time that it takes for the stomach to empty.

The energy cost through locomotion E_L is a function of body length, swimming speed cubed and drag (Sharp and Francis, 1976, after Streeter, 1962):

$$E_L = 2.59 \times 10^{-5} \cdot L^2 \cdot v^3 \cdot C_d \text{ (mg O}_2 \text{ h}^{-1}\text{)}. \tag{7}$$

The drag coefficient, C_d , is also a function of body length and velocity (Gerritsen, 1984, after Webb, 1975) and can be approximated as:

$$C_d = 0.55 L^{-1/2} v^{-1/2}. \tag{8}$$

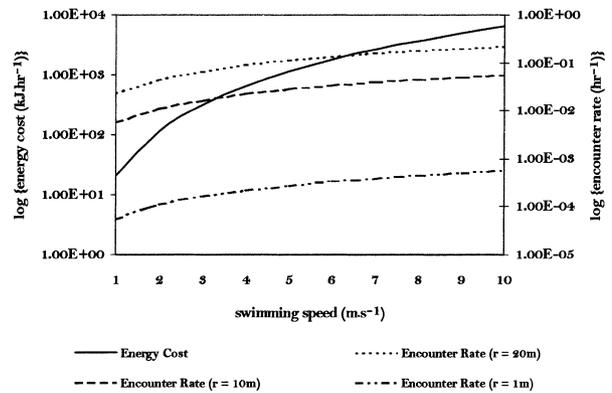
For our generic tuna, with length 100 cm, this then gives:

$$E_L = 0.2002 v^{2.5} \text{ (J h}^{-1}\text{) for } v \text{ in cm s}^{-1} \tag{9}$$

(NB : 1 joule = 14.054 mg O₂).

We can compare the energy cost of foraging with the encounter rate for various velocities (Fig. 4). This illustrates the trade-offs that operate, as encounter rate

Figure 4. The trade-off between energy cost and encounter rate for various swimming speeds. Swimming speed is included in the optimization criterion and is not usually predicted to be above 4 m s⁻¹.



is a linear function of v (eqn 2) and energy cost varies with $v^{2.5}$ (eqn 9). We have included swimming speed in the optimization criterion, allowing the trade-offs to operate and using any increase in v from the minimum as an indication of active foraging behaviour.

State variable Q (thermal stress)

Captive skipjack could not survive more than a few hours in waters only 5°C outside the optimal temperature range, i.e. 15°C and 35°C (Dizon *et al.*, 1977; Barkley *et al.*, 1978). Death under thermal stress is most likely caused by falling heart rate and cardiac output, rather than by effects on muscle temperature and efficiency and energy losses (Brill *et al.*, 1998). We have therefore treated the subject separately from the other bioenergetic state variables. The state variable Q is increased with time spent in waters outside the preferred temperature range, and decreased when the fish returns to warmer waters. The rates of increase (Table 3) are set such that Q reaches the lethal maximum in the time given by the experiments referred to above (Dizon *et al.*, 1977; Barkley *et al.*, 1978). The rates of increase and recovery may be non-linear and variable. The ability of bigeye tunas to tolerate colder waters for longer periods than other tropical tunas has been attributed to rapid increase in blood temperature when in warmer waters (Holland *et al.*, 1992; Dewar *et al.*, 1994) but also to the unique properties of bigeye blood itself (Brill, 1997). We therefore adopted a recovery rate for Q that is a factor of 10 greater than the rate of increase (Table 3). We also included a direct effect of Q on overall fitness (see below).

Table 3. Increment/decrement of state variable Q by coefficient q_3 (see eqn 15): q_3 is the increase of Q that results after one time step (i.e. one hour) in this habitat. When $Q = 5$ the fish is dead. The rate of change of Q (i.e. $dQ/dt = q_3$) is such that the fish dies after 5 h in water 5°C colder than the minimum value of the preferred temperature range. Two scenarios for increase and recovery are used. In Scenario 1, increase and recovery rates are linear and identical. In Scenario 2, increase is slow and recovery is rapid. Time periods permitted in colder waters based on these rates are given.

Water temperature (°C)	Hourly increment/decrement of thermal stress, Q (i.e. q_3)	Time until death (h)
15	1	5
16	0.64	8
17	0.36	14
18	0.16	31
19	0.04	125
20	0	—
21	-2	—
22	-4	—
23	-5	—
24	-5	—
25	-5	—

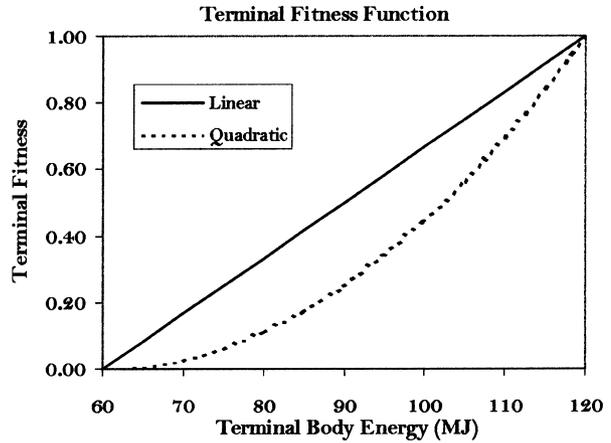
Evaluation of fitness

The technique used for the study is *stochastic dynamic programming* (SDP). The outputs of an SDP model are the state- and time-dependent choices that maximize some measure of fitness, and the technique is particularly appropriate to behavioural studies incorporating different components of fitness (McFarland, 1977; Mangel and Clark, 1988; Krebs and Davies, 1991; Giske et al., 1998). The fitness criterion used here is not a true measure of Darwinian fitness, but is a proxy for the general health of the fish, and therefore its reproductive ability. We do not consider issues of allocation of energy to somatic and gonadal growth, which would need to be incorporated into a model of tuna life history, but assume that at low levels of total body energy, growth, reproduction and migration are limited. We therefore define the ‘terminal fitness function’ (Mangel and Clark, 1988) such that fitness F is scaled according to the level of somatic energy density above a critical level:

$$F(x, y, z, Q, H, H) = \begin{cases} \left(\frac{z - z_{crit}}{z_{max} - z_{crit}}\right)^\zeta & \text{if } z > z_{crit} \\ 0 & \text{if } z \leq z_{crit} \end{cases} \quad (10)$$

where x, y, z and Q are the state variables described above, H is the time horizon and z_{max} and z_{crit} are

Figure 5. Terminal Fitness Function (linear and quadratic). By changing the shape of the function, higher body energy is required to obtain high fitness values; this increases the motivation for active foraging.



the maximum and minimum (critical) levels of somatic energy density. We can vary the shape of the Terminal Fitness Function by raising it to various powers ζ to maximize the motivation for foraging (eqn 10; Fig. 5).

By backward iteration from terminal fitness, we then obtain fitness values for all combinations of state, habitat i , and swimming speed s over time t using the ‘dynamic programming equation’ (Mangel and Clark, 1988):

$$F(x, y, z, Q, t, H) = \begin{cases} \max_i (1 - p_2) \left[p_1 F(x', y', z', Q', t + 1, H) + (1 - p_1) F(x'', y'', z'', Q'', t + 1, H) \right] & \text{for } z > z_{crit} \\ 0 & \text{for } z \leq z_{crit} \end{cases} \quad (11)$$

where p_1 is the probability of finding food, and the dynamics of the state variables are:

If food is encountered (with probability p_1):

$$x' = X_0 \quad (12a)$$

i.e. stomach is filled,

$$y' = y - q_2 \cdot y_{max} + (X_0 - X) \cdot \rho E \quad (12b)$$

i.e. energy is absorbed from the stomach and new energy is ingested.

If food is not encountered (with probability $1 - p_1$):

$$y'' = y - q_2 \cdot y_{max} \quad (13a)$$

$$x'' = y'' \cdot x \cdot y^{-1} \tag{13b}$$

i.e. energy is absorbed from the stomach and the new stomach energy, y'' determines the new stomach fullness (see Fig. 2), as waste (i.e. mass with negligible energy) is evacuated.

For all cases:

$$z' = z'' = z + q_2 \cdot y_{\max} - \alpha \tag{14}$$

i.e. body energy increases by absorption from the stomach, minus total energy costs,

$$Q' = Q'' = Q + q_3 \tag{15}$$

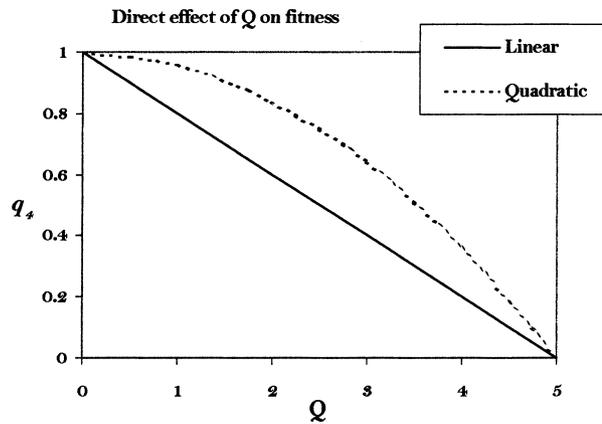
i.e. thermal stress changes depending on ambient temperature (Table 3) The level of thermal stress may then have a direct effect on fitness through the coefficient q_4 (Fig. 6):

$$q_4 = (Q_{\max} - Q)/Q_{\max} \tag{16a}$$

$$q_4 = 1 - (Q/Q_{\max})^2 \tag{16b}$$

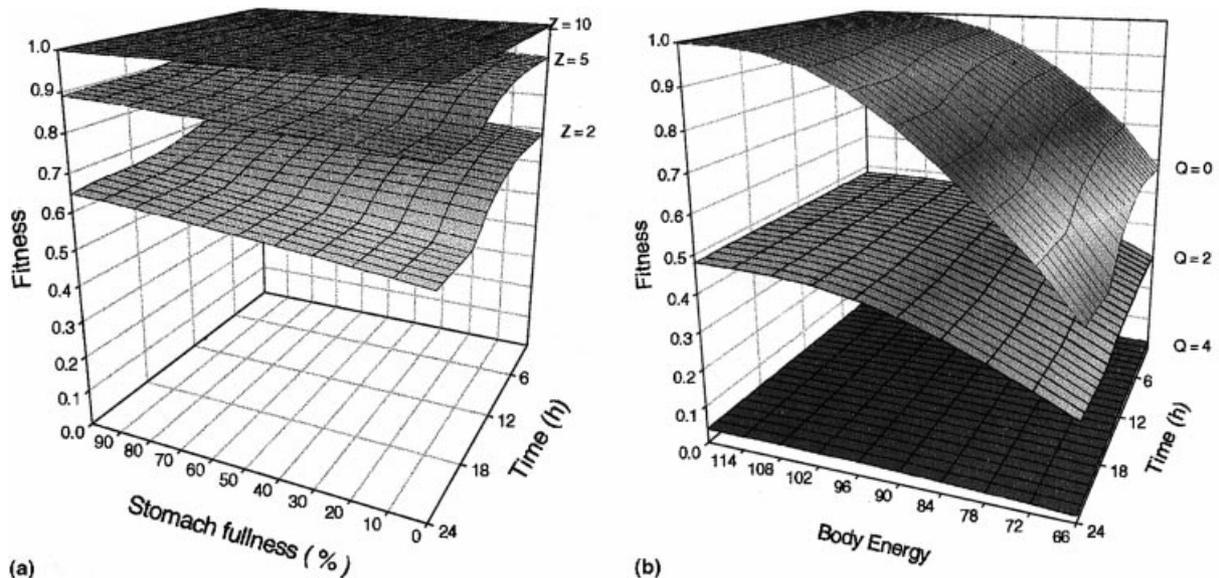
Once the fitness values for all possible solutions are calculated, the optimal solutions (i.e. optimal habitat

Figure 6. The direct effect of thermal stress Q (linear and quadratic) through the coefficient q_4 . This makes the effect of thermal stress immediate and non-linear.



and swimming speed for any combination of states and time) are saved. An individual-based model (IBM) can then run forward in time, simulating foraging with stochastic prey encounter; the state dynamics and behaviour may be recorded. Some results for fitness landscapes, optimal behaviour and foraging simulations are presented below.

Figure 7. Fitness landscapes representing the fitness values of combinations of the four state variables over time. (a) Fitness for different values of stomach fullness X over time, at different levels of body energy Z ; thermal stress Q is set to zero. Although there is a small diurnal effect, fitness values are fairly constant with stomach fullness, but are significantly affected by the level of body energy. (b) Fitness for different values of body energy Z over time, at different levels of thermal stress Q ; stomach fullness is 50%. At any time t there is significant variation in fitness as body energy is varied; as thermal stress increases, all fitness values are much reduced.



RESULTS

Foraging at fronts

Fitness landscapes

These represent the fitness values for combinations of the four state variables over time, and are illustrated in Fig. 7. Figure 7(a) shows fitness for different values of stomach fullness X over time, at different levels of body energy Z . Fitness decreases slightly with stomach fullness and there is a small diurnal effect, such that fitness is lower for an unfilled stomach towards the end of the day than it is for the same level of stomach fullness at the start of the day. These fitness landscapes are significantly affected by the level of body energy. In Fig. 7(a), if body energy is high, it matters little whether or not the stomach is full. As body energy decreases, variations in stomach fullness become more important determinants of fitness. Figure 7(b) shows fitness for different values of body energy Z over time, at different levels of thermal stress Q . At any time t , there is significant variation in fitness as body energy is varied, and as thermal stress increases, all fitness values are reduced.

Foraging simulations

For conditions where only single properties varied between habitats, we have simply described the results. For scenarios where all properties vary between habitats (Table 1), we have included plots of optimal habitat and swimming speed and of foraging simulations. Swimming speed greater than the minimum value indicates active foraging.

Effect of temperature variations

If food quality and quantity do not vary between habitats, but temperature varies from 25°C offshore to 15°C inshore, the optimal habitat to inhabit is the one where temperature is just above the threshold for the accumulation of thermal stress. Here, metabolic energy costs are lowest and no thermal stress is incurred.

Role of food quantity and quality

If there is food in only one habitat and all other conditions are equal, then it is optimal to be in that habitat. If there is equal abundance in all habitats but food quality varies, then the optimal habitat is the one with the most energetic food. If there is an unequal distribution of food and quality also varies, then the best place to be is an intermediate habitat, which has good-quality food and higher-than-average abundance.

Effect of visual range and light

Swimming speed is generally faster during the day, when light intensity – and therefore visual range – is

high. If food has not been encountered as daylight is fading, swimming speed may increase for a few hours before falling again, a prediction that follows from the fitness landscapes described above. At night, when visual range is near zero, swimming speed usually dropped to the minimum value. Diffuse attenuation coefficient k , being in the exponent of the visual feeding model, was a major determinant of foraging behaviour.

Foraging simulations for a quasi-realistic scenario

We ran simulations for the environmental properties listed in Table 1 with three different representations of the effect of thermal stress (eqn 16a,b). In the first case (Fig. 8), Q was treated as the other state variables in the dynamic programming equation (eqn 11), i.e. there was no direct effect on fitness ($q_4 = 1$).

Figure 8. Foraging simulation with no direct effect of thermal stress (i.e. $q_4 = 1$). Horizontal axes, time of day. The top graph shows the bioenergetic state dynamics, the next two graphs show optimal habitat and swimming speed, respectively, and the bottom graph shows thermal stress Q . Habitat characteristics vary across the front (Table 1). The fish is predicted to inhabit the cooler, food-rich waters of Habitat 2 most of the time, increasing its swimming speed to forage actively during daylight hours. Because there is no direct effect of Q , the fish can stay in Habitat 2 even under high stress levels.

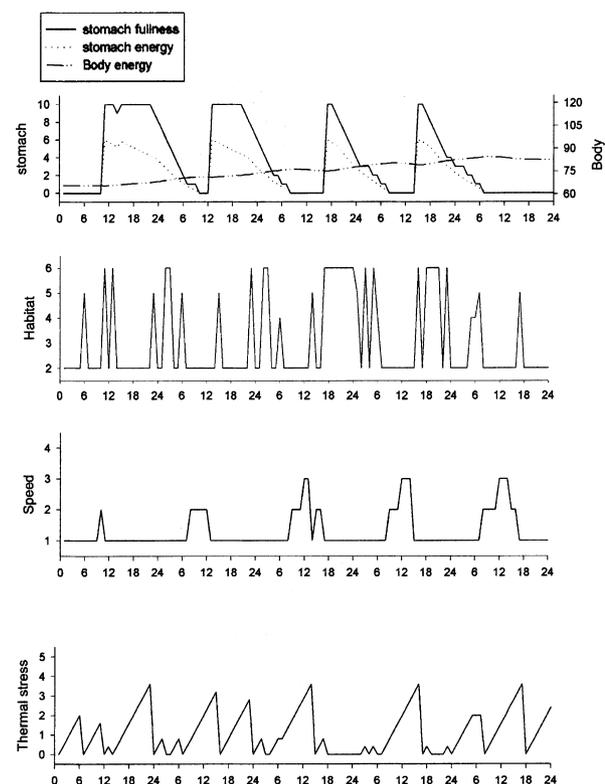
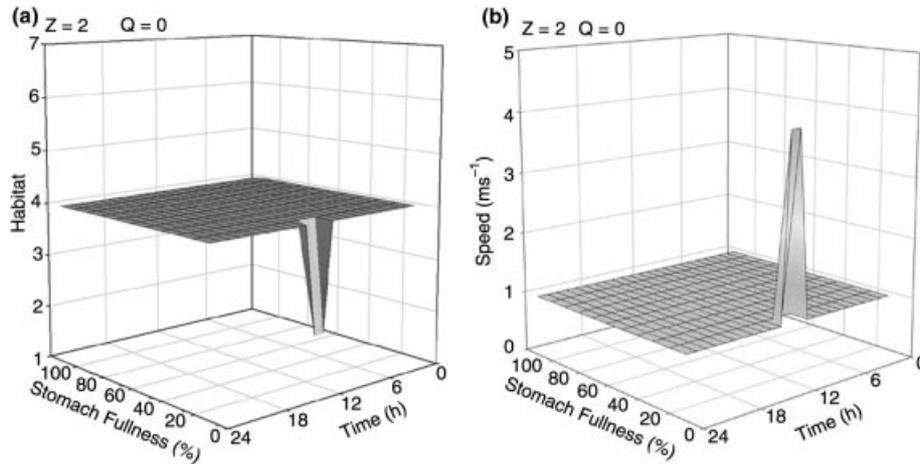


Figure 9. (a) Optimal habitat and (b) swimming speed for various times and hunger states (stomach fullness); body energy is low (72 MJ) and thermal stress is zero.



Active foraging occurred only during daylight hours, but the fish stayed in colder waters for the majority of the time, only occasionally returning to warmer waters to reduce Q . We did not consider this original formulation to represent the physiological mechanisms well, and the behaviour that resulted did not seem realistic. We therefore incorporated a direct, linear effect of Q on fitness through eqn 16a, representing the immediate effect of temperature change on heart rate (Brill, 1994b, 1997; Brill *et al.*, 1999). This resulted in much more conservative behaviour (Fig. 9a,b; Fig. 10). The optimal solutions (Fig. 9a,b) show that tuna should only forage actively in coastal waters if the stomach is empty and during the middle 4 h of the day (10:00–14:00); the rest of the time they should stay in warmer offshore waters, swimming at their minimum speed. Foraging is still a diurnal activity, peaking around midday, but time spent in colder waters is extremely limited (1–2 h). Again, this behaviour did not seem very realistic.

We then varied the shape of the function determining the direct effect of Q on fitness, implementing eqn 16b rather than eqn 16a (Fig. 6). The time permitted in colder waters is prolonged (Fig. 11a,b; Fig. 12) and behaviour is then not so conservative. Active foraging occurs from 07:00 to 17:00 when the stomach is less than 70% full; if stomach fullness is below 20% between 09:00 and 15:00, the fish should also move to the coastal waters (Fig. 11a,b). At night, active foraging does not occur; the warmest offshore waters (Habitat 6) are occupied if there is food ($\geq 20\%$) in the stomach; otherwise the fish should stay in Habitat 4. Within the constraints of the model environment, we are satisfied that this best

represents the motivation, physiological imperatives and behavioural options for tunas foraging at fronts, and that the resulting behaviour is as realistic as it can be.

Figure 10. Foraging simulation for the direct linear effect of Q on fitness. Horizontal axes, time of day. Time spent in colder water is extremely limited (1–2 h).

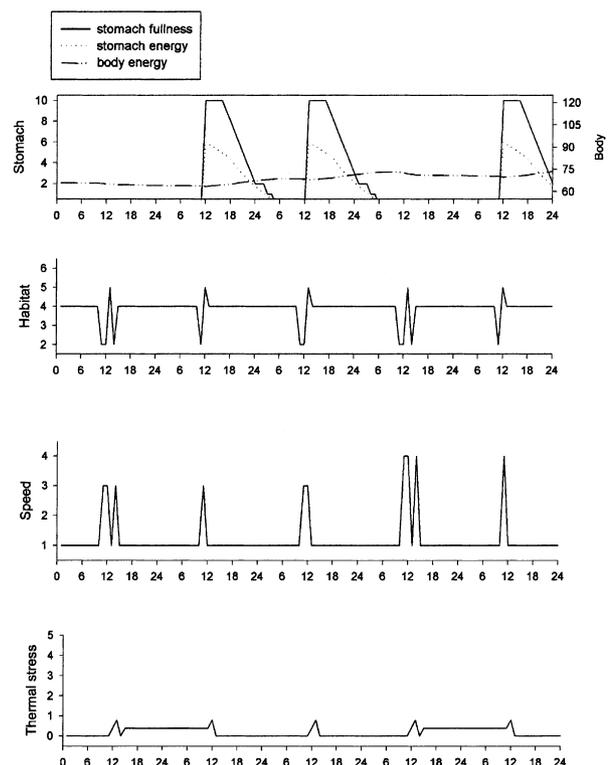
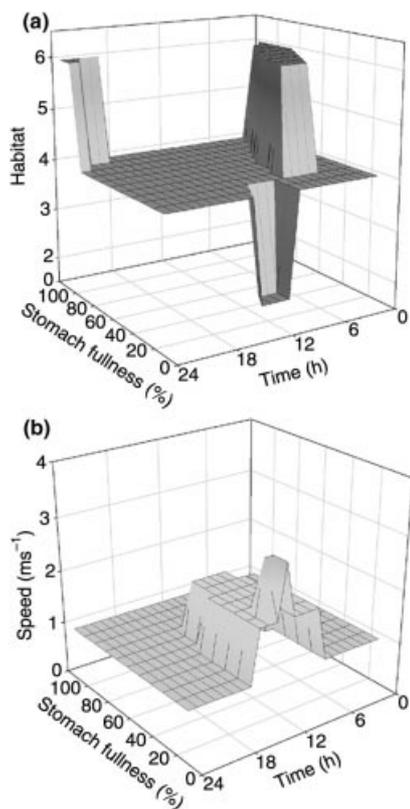


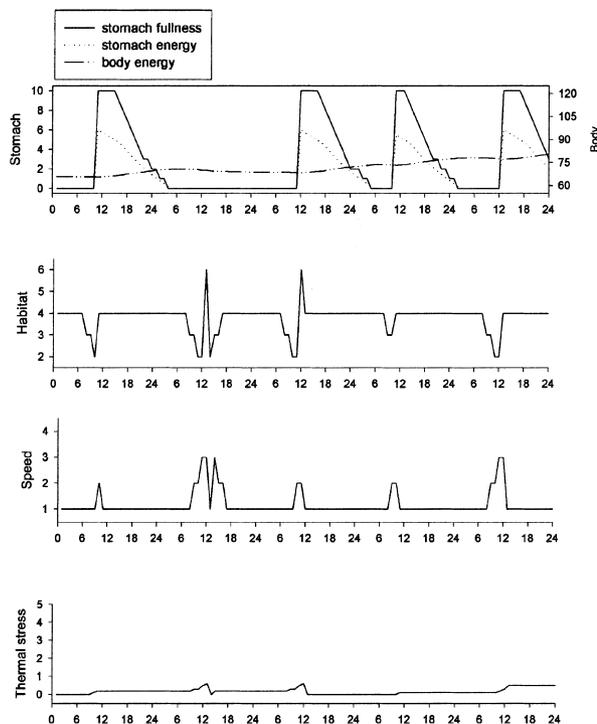
Figure 11. (a) Optimal habitat and (b) swimming speed for varying time and hunger state (stomach fullness); body energy is low (72 MJ) and thermal stress is zero. The implementation of a direct quadratic effect of Q on fitness leads to less conservative behaviour, with active foraging predicted from 07:00 to 17:00 if stomach fullness is less than 70%. At most other times the fish should stay in Habitat 4, unless it still has food in its stomach prior to dawn. Then it should seek warmer waters, where digestion is more efficient and it may absorb stomach energy more quickly, before foraging again.



Vertical movements

We then ran some simulations to examine vertical movements. For these, food was only available in the deeper, cold habitats. By varying the optimal temperature and metabolic rate for ARTU, we were able to provoke different behaviour patterns analogous to the differences between the behaviours of tropical and temperate tunas. We implemented the same representation of thermal stress that we used above, i.e. thermal stress was incurred slowly and had a direct effect on fitness, and recovery rate in warmer waters was rapid. The behaviour that results is analogous to that of tropical tunas, with most time spent in the surface waters and occasional excursions into deeper,

Figure 12. Foraging simulation for the direct quadratic effect of Q on fitness. Horizontal axes, time of day. Time spent in colder water is less limited (1–6 h). This behaviour is more realistic.



colder waters (Fig. 13). In the second case, we used metabolic rate and optimal temperature for albacore (Table 2). ARTU then spent most time in deep waters, with occasional vertical excursions to surface waters (Fig. 14).

DISCUSSION

This model integrates environment, physiology and behaviour within a single, quantitative framework, thus providing a theoretically sound perspective from which to make and interpret observations. We were able to make realistic simulations of observed behaviour by having a slow increment and fast decrement of thermal stress, representing the well-documented thermal inertia of tunas (Neill *et al.*, 1976; Holland *et al.*, 1992), and by including the effect of thermal stress directly on fitness. In reference to the questions we asked at the start of the exercise, we can say that the observed aggregation of tunas at ocean fronts is not predicted by temperature alone, and when turbidity is high on the cold side of the front it is not profitable to be in those waters unless they are higher in food abundance or quality than are the warmer waters. By

Figure 13. Foraging simulation for vertical movements. Horizontal axes, time of day. Only the open ocean habitats are available. Food is only available in deeper waters, where the temperature is 8°C less than at the surface. With metabolic rate and optimal temperature similar to skipjack and yellowfin, ARTU spends most of the time in the surface waters, with short excursions to deeper water to forage.

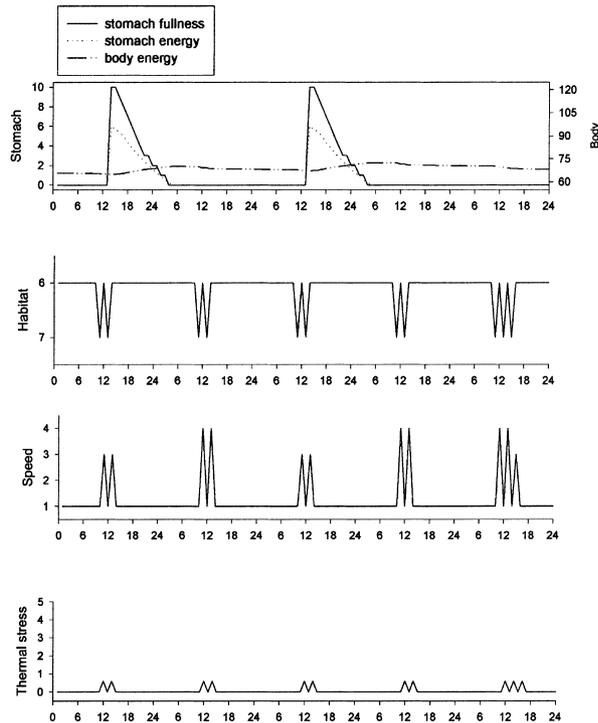
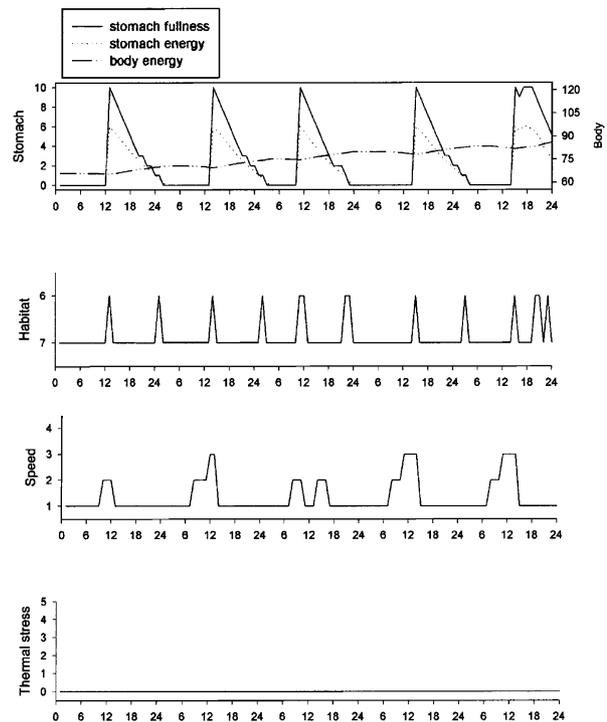


Figure 14. Foraging simulation for vertical movements. Horizontal axes, time of day. Only the open ocean habitats are available. Food is only available in deeper waters, where the temperature is 8°C less than at the surface. With metabolic rate and optimal temperature similar to albacore, ARTU spends most of the time in the deeper waters, with short excursions to shallow water to obtain a 'gulp of heat' (Brill, 1994a).



varying optimal temperatures and the representation of thermal stress in the determination of fitness, we generated differences in behaviour that are akin to the observed differences between surface-dwelling tropical tunas such as skipjack and yellowfin and deeper foragers such as bigeye and bluefin.

An inherent property of dynamic optimization models is that at each stage, the individual has perfect knowledge of the fitness values of its present and future states and the consequences of alternative behaviours. Learning and physiological cues would explain knowledge of the past and present, and olfactory sense could explain knowledge of future prey concentrations, through medium- to long-range detection of prey prior to visual encounter (Atema, 1980; Atema *et al.*, 1980). The encounter rate between predator and prey is then determined by the visual feeding model (Aksnes and Giske, 1993; Aksnes and Utne, 1997). This is yet to be fully parametrized for tunas. It would be necessary to measure the visual capacity and sensitivity threshold of

tuna eyes, as well as to characterize the inherent and apparent contrasts of their prey.

The model also predicts state-dependent behaviours that have not yet been investigated in the field or laboratory. Simultaneous measurements of both state and environmental variables (stomach contents, heart rate, temperature, light) as well as the behaviours predicted (location, swimming speed, swimming mode) would provide a more detailed picture of the behavioural ecology of tunas than now exists. Some work has been done in this area (Holland *et al.*, 1992; Brill *et al.*, 1999) but in no study have all relevant variables been measured simultaneously. By contrast, for Weddell seals (*Leptonychotes weddelli*), heart rate, body temperature, depth and swimming velocity have been measured during free-diving, while a peristaltic pump withdrew blood samples and injected radio-labelled metabolites (Guppy *et al.*, 1986; Hill, 1986). Although more difficult for fish than mammals, such work could be repeated for tunas with measurements

logged and transmitted by acoustic or satellite telemetry (e.g. Lutcavage *et al.*, 1999).

Better information on the interplay of vital rates would justify more detailed modelling efforts. A smaller time step than that used (1 h) would allow burst and cruise swimming to be more clearly resolved, and additional habitats would add spatial resolution. Food types and concentrations will vary over time and water mass structure is dynamic. There will be a time and energy cost associated with moving between discrete habitats, which would depend on the scale of the oceanic front. Instant escape to a favourable habitat may not be possible, and this will limit foraging range. The conservative nature of the behaviour predicted here may therefore be an artefact of the model environment. We have simulated behaviour from individual motivation to optimize energy balance in the presence of various factors that must be traded off against each other. In life-history models, spatial population dynamics derive from evolutionary motivation through the use of a truly Darwinian fitness measure (Fiksen *et al.*, 1995; Huse and Giske, 1998). Further work, considering populations of individuals over large space and time scales, should seek to connect the biophysical dynamics of the oceanic environment with fish behaviour motivated by evolutionary as well as physiological imperatives.

CONCLUSIONS

We have applied an established paradigm in behavioural ecology, with an associated computational method, and brought together competing hypotheses into a single model to improve our understanding of why tunas and other fish may aggregate at fronts. This work has been anticipated in the literature for some time (Hunter *et al.* 1986; p. 30) but has not previously been realised. We have predicted time- and state-dependent optimal foraging behaviour (i.e. slow swimming in warm, clear waters when not foraging, and foraging excursions into colder waters when hungry) that is broadly consistent with observation (Block *et al.*, 1997) and other modelling work (Dagorn *et al.*, 1995). Sharp and Francis (1976) commented that "The utility of simulation studies lies in the process of linking together observations, using generalised principles where possible, to generate testable hypotheses which ultimately lead to resolution of cause and effect relationships." We have suggested a modelling framework which, if developed further and properly parametrized, would allow testable hypotheses to be made and cause-and-effect relationships to be

clearly resolved; we have also identified areas of research into tuna vision and physiology that will facilitate progress in tuna behavioural ecology and we have suggested investigations to test theoretical predictions for free-living animals.

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