Co-evolution of movement behaviours by tropical pelagic predatory fishes in response to prey environment: a simulation model

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Abstract

Predatory fishes, such as tunas, billfishes, and sharks, coexist in pelagic regions of the tropical oceans. In situ experiments have revealed horizontal and vertical movement patterns for different pelagic species, but the influence of the biotic environment on movement behaviour has not been studied. In this paper, we propose a simple model in which the movement behaviour of these fishes is driven entirely by the biotic environment, without implementing physiological constraints. We explore this concept via computer simulations based on the Latent Energy Environments model [Menczer, F., Belew, R.K., 1996a. From complex environments to complex behaviors. Adapt. Behav. 4(3/4), 317–63]. In our model, multiple behaviours for artificial fishes evolve in a three-dimensional environment where spatial and temporal distributions of prey are patterned after hydroacoustic data taken during ultrasonic telemetry experiments on tunas in the open ocean in French Polynesia. Interactions among individuals are modeled through their shared prey resources. Movement patterns of the adapted individuals are analyzed to: (i) compare artificial individuals with real fishes (three species of tuna, three species of billfishes, and one species of shark) observed by ultrasonic telemetry; and (ii) examine how the artificial fishes exploit their environment. Most of the individuals evolved vertical patterns virtually identical to those exhibited by fishes in the wild. The agreement between our simple model and the ethological data validates the use of computational models for studies of the characteristics of multiple species inhabiting a common ecosystem. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pelagic oceanic environment; Multi-species behaviour; Tropical predator fish; Neural networks; Evolutionary algorithms; Artificial life

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1. Introduction

Large predatory fishes, such as tunas, billfishes, and sharks, dwell in the open sea, and their habits are a challenge to observe. Because of their eco-

nomic importance, there is a great body of knowledge about them from fishery activities. However, before the development of ultrasonic telemetry techniques, little was known of their fine-scale movements. By attaching sonic transmitters to the animals and listening to the echoes produced by these devices, it became possible to describe the vertical and horizontal movement patterns of these fishes in their natural habitats (see Yuen, 1970 for one of the first experiments). In most cases, these studies showed diverse movement patterns for different species (Carey and Olson, 1982; Carey and Robison, 1981; Cayré and Chabanne, 1986; Carey, 1990; Carey and Scharold, 1990; Holland et al., 1990a,b; Cayré, 1991; Brill et al., 1993; Block et al., 1997; Bach et al., 1998; Josse et al., 1998; Brill et al., 1999; Dagorn et al., 2000). The next challenge is to understand why these species evolved such different movement behaviours.

There are large temperature differences between the warm upper layers of the ocean and the cold deep waters. By moving a few hundred meters vertically, an animal may encounter a greater temperature change than it experiences seasonally or while moving thousands of miles horizontally (Carey, 1992). Most fish species are stenotherms, but large fishes like billfishes are able to partially control their body temperatures because thermal diffusion through a large mass is a slow process, and convective heat transfer is reduced in parts of the body by a modified circulatory system (Stevens and Neill, 1978). Moreover, tunas and lamnid sharks are able to maintain their body temperatures warmer than the ambient water temperature by means of countercurrent heat exchangers in the circulatory system between the gills and muscle tissues. The vertical movements of some oceanic fishes, observed by ultrasonic telemetry, have been interpreted in relation to the vertical structure of the abiotic environment, mainly water temperature and dissolved oxygen concentration (Holland et al., 1990a, 1992; Cayré and Marsac, 1993; Block et al., 1997; Brill et al., 1999).

Tunas, billfishes, and sharks require large amounts of energy (Olson and Boggs, 1986; Boggs and Kitchell, 1991; Brill, 1996; Cortés, 1997), and

they must be efficient predators to survive. Prey distribution may, therefore, have an important influence on the movement patterns of these species. Due to the difficulties in observing these predators and their prey in their habitat, little effort has been devoted until recently to study the role of the biotic environment in explaining their movements. During the ECOTAP[1] program in French Polynesia, experiments were developed to collect simultaneously ultrasonic telemetry data for yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tunas and acoustic data on their prey (Josse et al., 1998; Dagorn et al., 2000). These data show that the three-dimensional distribution of the prey can account for an important part of the small-scale movement patterns of the tunas, but more studies are clearly needed.

Tunas, billfishes, and sharks have evolved different strategies to exploit the same environment. Are different movement behaviours the result of different physiological mechanisms in these animals, or is it possible to explain the movement patterns by the dynamics of the prey, without considering their physiological limits? Menczer and Belew (1994), Sims (1994), Terzopoulos et al. (1994) have addressed the evolution of morphology in artificial life organisms. Menczer and Belew (1996a) showed theoretically that both abiotic and biotic environmental structure can play a key role in shaping the evolution of behaviours. In this study, we explore the structure of the prey environment in shaping the evolution of behaviour patterns, without considering physiology. Such studies can help us understand the role of the biotic environment in behavioural adaptations and how multiple behaviours can emerge in a common ecosystem.

The purpose of this study is to develop a computational model of the movements observed in multiple predator species sharing the pelagic oceanic environment. Our approach is to abstract

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[1] ECOTAP (studies of tuna behaviour using acoustic and fishing experiments) is a joint program between EVAAM (now Service des Ressources Marines, SRM), Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) and Institut de Recherches pour le Développement en Coopération (IRD).

away from the physiological details of the different species and focus on an individual based model with minimal assumptions about prey distribution and dynamics. The objective is to simulate a co-evolutionary process and analyze the different behaviours emerging in a realistic prey environment. We assess the predictive power of the model in accounting for the heterogeneous set of behaviours displayed by several tropical predatory fishes. We are not interested in modelling a specific behaviour, but rather in studying the range of behaviours that can result from co-adaptation in a shared biotic environment with given characteristics. Such a model can be applied to different environments where the same species occur (e.g. the eastern Pacific Ocean), which would be impossible if it were encumbered with area-specific details.

In Section 2, we outline the three components of the model: the shared prey environment, the artificial fishes, and the evolutionary algorithm used to adapt their behaviours. In Section 3, the behaviours that evolved from the model are compared against our knowledge of actual species from ultrasonic telemetry experiments. We also analyze the emergent patterns in relation to the artificial environment, and consider the sensitivity of our model with respect to its assumptions. In Section 4, we discuss our main findings, and Section 5 concludes with a look at future work.

2. Model

We employ an agent-based model to simulate the evolutionary process of a population of fish situated in a dynamic environment, and analyze the diverse set of adaptive behaviours that are generated by the model.

Our model is based on the latent energy environments (LEE) framework (Menczer and Belew, 1996a,b). The agents share a three-dimensional biotic environment, gathering resources to survive. The resources are replenished independently of the behaviours of the agents, determining the carrying capacity of the artificial ocean. Selection for survival is based on a localized and endogenous form of density-dependent fitness, because

competition is limited to the spatially-distributed resources. Individuals with behaviours that allow them to make good use of the resources, survive and reproduce. Individuals that exploit independent resources do not interact.

Artificial life models based on individuals (Judson, 1994), such as LEE, are appropriate to test hypotheses like the one suggested in this paper because they allow modelers to easily generate heterogeneous populations and to explore the relationships between co-evolving species and environmental resources. For example Echo, a computational framework that shares many features with LEE, was used by Hraber and Milne (1997) to study how environmental and biotic factors regulate species abundance and the composition of ecological communities. The absence of centralized control and global selection in LEE allows for many efficient behaviours to coexist, without the bias of an optimization process that would push toward a single solution. This approach is similar to the 'animats' model of Krebs and Bossel (1997), while it differs from models such as dynamic programming, where the objective is to find optimal solutions (e.g. Baker, 1996).

Other modeling efforts have focused on the responses of population and community structure and behaviour governed by species interactions and prey environments (Dodds and Henebry, 1995; Matsumoto and Seno, 1995; Kawata, 1997; Spencer, 1997). Because our objective is to generate behaviours based on assumptions about the biotic environment, as opposed to testing different models of animal decisions, the proposed approach also differs from ecological models in which the rules governing the behaviour of individuals are pre-programmed (e.g. Downing and Reed, 1996; Letcher and Rice, 1997; Beecham and Farnsworth, 1998; Lorek and Sonnenschein, 1998; Ziv, 1998). We follow the suggestion of Beecham and Farnsworth (1998), that individual-based models that refer to pre-programmed rules should be extended to use evolutionary methods, where each individual would evolve an individual-specific algorithm, in order to gain insight into the evolutionary origins of alternative behaviours.

2.1. Biotic environment

To model the biotic environment, we use general knowledge about the prey fauna of the open ocean in French Polynesia and specific acoustic observations made in French Polynesia during the ECOTAP program. These data have not yet been fully analyzed. In the absence of precise details on prey characteristics, we model only two types of prey. Type 1 prey are low in energy, typical of those inhabiting the deep scattering layer (DSL), and composed mainly of crustaceans, small fishes, and jellies. It is well-known that, during the nighttime, the organisms of the DSL ascend to the surface layer (Longhurst, 1976). At sunrise, the community descends to deep waters, where it spends the daytime. The DSL structure might be characterized as very large and dispersed patches. Prey of type 2 are more energetic and are found in smaller, denser patches composed mostly of small pelagic fishes and squids. They do not migrate as deep as type 1 prey; they usually live in an intermediate layer during the day, and also occupy surface waters at night.

The vertical distributions of the two types of prey during day and night are used to define the vertical environment of the model. The artificial ocean of our predatory fishes is modeled vertically by three depth layers: a surface layer, an intermediate layer, and a deep layer, corresponding to the waters occupied by the two types of prey at night and day. In French Polynesia, for example, the lower boundaries of these layers are found at approximately 150, 350 and 500 meters (the latter

depth is the vertical limit of the acoustic observations in the ECOTAP program). Horizontally, each of these layers is modeled by a grid of 400 by 400 cells, representing an area of 40 by 40 n.mi. (~ 75 by 75 km), and opposite sides are joined to avoid edge effects and to form a torus.

A schematic representation of the biotic environment assumed for this model is presented in Fig. 1. This is admittedly a very simplified model of a prey community. For example, it disregards the amount of time that it takes for different prey taxa to move between depth layers. More importantly, it assumes that no prey are present in the surface layer during the daytime, although it is known that predatory fishes feed in the surface layer of the ocean, especially in areas where the surface layer is thin. However, during 2000 h of acoustic surveys between 0 and 500 m in the exclusive economic zone (EEZ) of French Polynesia, we did not find abundant prey in the surface layer during the daytime. Therefore, our simplified model is generally consistent with those field observations.

The energy density of type-2 prey is set at five times that of type-1 prey in our simulations. We set the number of prey to 150 items within a circle of 8 n.mi. (~ 15 km) radius for patches of type-1 prey and 50 items within a circle of 1 n.mi. (~ 2 km) radius for patches of type-2 prey. One prey item in our model does not represent one prey item in the wild, but rather a combination of several prey items. A more realistic representation of the numbers of real prey (which is not known) would have forced the model to consider millions of prey items. To simplify the computation of prey items in our model, we used the concept of 'super-individuals' proposed by Scheffer et al. (1995). The prey population is then represented by a smaller number of units. The super-individuals are classes of individuals for which parameters are identical in the model (e.g. same energy content). Because we do not know the exact spatial dimensions of these patches in the ocean, the radii and spatial distributions of the patches are somewhat arbitrary, but consistent with our observations in French Polynesia.

Following the LEE approach, we adopt a constant prey replenishment rate: four patches of
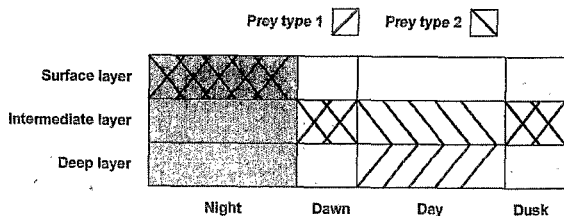
Fig. 1. Model of the vertical dynamics of the biotic pelagic environment. All the prey (types 1 and 2) are in the surface layer during nighttime and in the intermediate layer during dawn and dusk. At daytime, prey of type 1 are in the deep layer while prey of type 2 are in the intermediate layer. Prey types are described in the text.
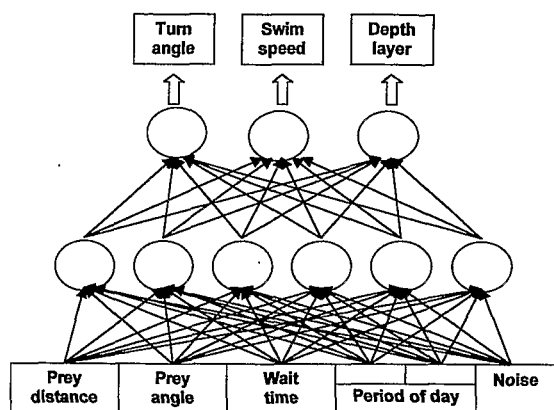
Fig. 2. Architecture of the neural networks used to model fish behaviours.

type-1 and two patches of type-2 prey regularly appear at random positions every half day. This replenishment rate is independent of prey consumption. As in actual environments, competition occurs only among individuals who share prey resources. Other features that discriminate between prey types, such as size, palatability, and ease of capture (i.e. swim speed), are either neglected in the model or accounted for indirectly through the energy content.

One time step is defined as 15 min. Therefore, the duration of the 11-h day and night periods is 44 time steps each, while the 1-h dawn and dusk periods correspond to four steps each (Fig. 1). A 24-h cycle is represented by 96 time steps. Each type of prey has a vertical distribution pattern that depends on the period of the day (day, night, dawn, and dusk), as observed in the wild (Fig. 1). We simplify the computation of the model by ignoring horizontal movements of prey, which is reasonable when comparing the relative sizes (100:1) and relative mobility of pelagic predators and prey.

2.2. Fish behaviour

The behaviour of the artificial predatory fishes that we consider in this model is three-dimensional movement. Movements by an organism causes its view of the surrounding habitat and its spatial relationships with respect to the habitat to

change. In our experiment, we represent the mapping from sensory states to motor actions using the well-known computational model of feed-forward neural networks (Rumelhart and McClelland, 1986). Generally speaking, these networks are collections of simple units connected by weighted links, which can compute arbitrary nonlinear functions. The organization of the individual networks used to model each artificial oceanic predator is described in Fig. 2.

The artificial neural network is comprised of two layers of units and connections. The behaviour of an artificial fish is characterized by the weights of the connections. In our case, each connection weight is represented by a floating-point number. Because feed-forward networks have no recursive connections, the behaviours of the simulated fishes are strictly reactive. Although interactions between different forms of learning and evolution have been explored in the artificial life community, and even in the LEE framework (Menczer and Belew, 1994; Cecconi et al., 1996), our present model neglects any effect of individual learning for the sake of simplicity; we first want to focus our attention on the behaviours that can emerge by way of evolution.

The neural network inputs represent internal and external information provided by five sensors (Fig. 2). The presence of a prey item can be detected when (i) the prey item and the fish are located in the same depth layer, and (ii) the prey item is within a circle of a specified radius around the predator. The distance at which a tuna or billfish responds to a prey, by odor or vision, is not known. Studies on Atlantic cod (*Gadus morhua*) have shown that fish positioned as far as 700 m upstream of fishing gear can sense baited hooks (Bjordal and Løkkeborg, 1996). Although baited hooks are not the same as free-swimming prey, and Atlantic cods are not the same as tropical tunas or billfishes, we adopt this order of magnitude and set the detection distance to five cells (~ 900 m).

The 'prey–distance' sensor indicates the Euclidean distance between the predator and the closest prey item, and has continuous values between 0 and 1. The value is 1 for distances greater than the detection distance. The 'prey–angle' sen-

sor indicates the angle between the direction the predator is facing and that of the closest prey item. It also has continuous values between 0 and 1, corresponding to the range $[-\pi, +\pi]$ (the discontinuity occurs behind the predator). If no prey item is detected, the value is random. The 'wait-time' sensor counts the number of time steps (up to 20, or 5 h) since the last prey item was eaten. The actual value is normalized to the interval [0, 1].

The two 'period-of-day' sensors have boolean values that are combined to indicate the period of the 24-h cycle, night, dawn, day, or dusk. Day and night are not necessarily synonymous with light and dark in aquatic environments, as light depends on depth, brightness at the surface, turbidity, and other factors. (Helfman, 1993). Therefore, our time sensors could be viewed as sensory perceptions combining information about light intensity, depth, and internal-clock mechanisms.

Finally, because real sensory systems are noisy, we include a random noise source as an additional input. By omitting sensors that provide information such as prey size or speed, we make the simplifying assumption that predators do not select for specific prey in the model. All predators exploit the same prey fauna. Considering that

```
initialize fish population
repeat until behaviour distribution is stable {
    for each alive fish i {
        sense world
        propagate network activations
        perform action a
        energy(i) += benefits(a) - costs(a)
        if (energy(i) > THETA) {
            i' := mutate(clone(i))
            energy(i) /= 2;
            energy(i') := energy(i)
        }
        elsif (energy(i) < 0) {
            kill(i)
        }
        update prey resources
    }
    replenish prey resources
```

Fig. 3. Pseudo-code of the LEE evolutionary algorithm at the basis of the proposed model. Note that energy is always conserved; it enters the system through the replenishment of prey resources and leaves the system in the form of work costs for performed actions. Also note that the reproduction constant, THETA, is independent of population size. Therefore the size of the population quickly converges to the carrying capacity of the environment, determined by the prey replenishment rate.

tunas and other pelagic fishes are widely believed to be opportunistic predators (Alverson, 1963; Roger, 1994), this seems a reasonable assumption.

The network has one hidden layer with six units and an output layer of three units. The first output unit produces a change in direction of the horizontal movement relative to the current heading. The second output unit indicates the swimming speed, between 2 and 10 cells per time step, or between 0.4 and 2.2 m/s, consistent with ranges of swimming speeds measured during field observations (Olson and Boggs, 1986; Brill et al., 1993). The third output unit determines the depth layer where the fishes swims: surface, intermediate, or deep. The fact that the network outputs of all artificial fishes correspond to identical ranges in movement behaviours, mirrors our simplifying assumption of identical physiological abilities across the modeled population of predators.

2.3. Evolution

As stated above, our use of the LEE model is justified, in part, by our goal to study the evolution of a heterogeneous range of behaviours, rather than the convergence to a single optimal behaviour. While the latter would be appropriate in a single-species model, we want to account for the realistic situation whereby several species of predators co-evolve different behaviours while sharing a common habitat. LEE models allow co-adaptation by an evolutionary algorithm based on an endogenous fitness measure (Menczer and Belew, 1996a,b). The model does not select directly on the behaviour evolved by a predator, but on its resulting efficiency (net energy intake rate) in the shared environment. To illustrate these aspects of our model, our LEE evolutionary algorithm is outlined in Fig. 3. The evolved set of behaviours resulting from this co-adaptive process represents the model's prediction of movement behaviours, which we compare with real data.

We now illustrate, in further detail, the evolutionary algorithm of Fig. 3. To begin a simulation, we created 200 fishes, each with different random weights uniformly distributed between -0.5 and $+0.5$. All fishes are initialized with 2000 units of energy. The internal energy state of

Table 1
Categories used to characterize vertical movement patterns

Category	Vertical pattern
A	More than 90% of the time in the surface layer
B	More than 90% of the time in the intermediate layer
C	More than 90% of the time in the deep layer
D	Movements between the deep and intermediate layers
E	Movements between the surface and intermediate layers
F	Movements between all three layers
G	Movements between the surface and deep layers

a fish can vary between 0 and 4000 units. The fishes gain energy when they eat a prey item: 30 units for type 1 prey, and 150 units for type 2 prey. The fishes lose 1 unit of energy per cell moved; i.e. the energy cost of swimming is proportional to the distance.

When a fish depletes its energy stores, it is eliminated from the population. When a fish's internal energy reaches 4000 units, it reproduces one offspring asexually. The parent divides its energy with its progeny; i.e. each offspring starts with 2000 units of energy. At birth, offspring and parent are located at the same location. The evolution of behaviours depends only on random mutations because there is no sexual recombination or cross-over. The offspring inherits its parent's weights. Then, $\sim 2\%$ of the weights are randomly selected and mutated by adding random noise drawn from a uniform distribution between -1 and $+1$. All weights are bounded to the interval $[-5, +5]$.

3. Results

Ten runs of 150 000 time steps each resulted in a total of 2489 artificial fishes. Each individual was analyzed to characterize its vertical and horizontal movements. Next, we report on the movements exhibited during nighttime and daytime to classify general movement patterns and to compare them to behaviours of real predatory fishes in the wild. Then, we evaluate the evolved artificial individuals in relation to the way they exploit their environment. Finally, we analyze the sensitivity of the results.

3.1. Artificial versus natural movement patterns

To analyze movement behaviours, we fed the sensors of the evolved individuals with a randomly generated input sequence. The sequence corresponds to a succession of 30 model night periods and 30 model day periods (2640 steps), and it models a situation in which individuals do not detect prey and have not eaten for a long period of time (i.e. the 'prey-distance' and 'wait-time' sensors are set to 1). Then, we analyzed their searching behaviours while the fishes looked for prey.

3.1.1. Vertical movements

Our objective was to classify the vertical behaviours emergent from the ten runs into groups which exhibited similar vertical patterns during the various periods of the day. Each individual was classified according to its swimming depth, i.e. by its output when submitted to the pre-determined inputs outlined above. Seven categories of vertical behaviours were considered, each category corresponding to the ocean layers where the fishes swam most of the time (Table 1). Layers in which a fish spent less than 10% of the time were disregarded. The 10% threshold is arbitrary, but helpful in visually classifying real species. We considered different criteria (thresholds between 0 and 10%), and the classification was effectively the same. Each individual was classified by one letter corresponding to a vertical pattern category for the daytime and another letter for the nighttime. We first focus on nighttime and daytime patterns.

For each run, we computed the frequencies of the 49 possible combinations (7×7 categories) of vertical patterns during nighttime and daytime. Because there was large variability across runs (cf. Section 3.3), we ranked the behaviours by frequency of occurrence in each run, and used the median of the rank distributions to classify the results of the ten runs (Table 2). Only 19 of the 49

classes of possible patterns were represented in the ten final artificial populations. The five most frequent classes are highlighted in Table 2, and the typical vertical movements in these five classes are shown in Fig. 4. All five top classes include the A pattern during the nighttime, which corresponds to movements within the surface layer. The five possible vertical patterns during the daytime, combined with the surface nighttime pattern, correspond to the most frequent classes. The emergence of behaviours D and E (alternative movements between different layers) is interesting because it suggests a precise adjustment of the weights of a neural network, and is discussed further in Section 4.

We compared the behaviours that evolved in these simulations with ultrasonic telemetry data on movements of real fishes from experiments conducted in French Polynesia or Hawaii. These experiments provide us with accurate depth data. In cases where ultrasonic telemetry data from the tropical Pacific Ocean were not available, we used data from other areas. We considered seven dif-

Table 2
Vertical movement behaviours of the artificial individuals during nighttime and daytime, respectively, ranked by frequency across ten simulations[a]

Class	Rank distribution median
AB	2
AA	2.5
AE	2.5
AD	3.25
AC	6
ED	7
EB	7.25
CC	9.5
EC	13
AF	18
BB	27.75
EA	28.75
EE	28.75
BC	29.5
BD	29.5
EF	29.5
BE	30
DC	30
FF	30

[a] The five most frequent classes are bold.

Table 3
Classification of seven oceanic predator species according to their vertical movement patterns during the daytime and nighttime, respectively[a]

Species	Class	Reference
Skipjack tuna	AA	French Polynesia, Pacific Ocean (Cayf and Chabanne, 1986)
Yellowfin tuna	AE	French Polynesia, Pacific Ocean (Bach et al., 1998) Hawaii, Pacific Ocean (Holland et al., 1990a) Eastern Pacific Ocean (Carey and Olson, 1982)
Bigeye tuna	AC	French Polynesia, Pacific Ocean (Dagorn et al., 2000) Hawaii, Pacific Ocean (Holland et al., 1990a)
Swordfish	AC	Off Cape Hatteras, Atlantic Ocean (Carey and Robison, 1981)
Striped marlin	AA	Hawaii, Pacific Ocean (Brill et al., 1993)
Pacific blue marlin	AA	Hawaii, Pacific Ocean (Holland et al., 1990b)
Blue shark	AD	Between George's Bank and Cape Hattera, Atlantic Ocean (Carey and Scharold, 1990)

[a] Behaviour categories are as defined in Table 1. The classification criteria are the same used for the artificial fishes (cf. Table 2), and are based on data from the references shown.

ferent species known to be predators in this environment. They include three tuna species: skipjack (*Katsuwonus pelamis*), yellowfin (*T. albacares*) and bigeye tunas (*T. obesus*); three billfish species: swordfish (*Xiphias gladius*), striped marlin (*Tetrapturus audax*) and pacific blue marlin (*Makaira nigricans*); and one shark species, blue shark (*Prionace glauca*).

It is difficult to generalize a regular vertical pattern for individuals of any particular species because individual behaviour is not rigid, but rather composed of adaptive actions. Nevertheless, we used published data to classify the vertical patterns of the above species according to the criteria used for our artificial fishes (Table 3). The behaviours that emerged in our simulations are consistent with the behaviours exhibited in nature; the seven species considered were categorized in the top five classes of the artificial population.

Depth

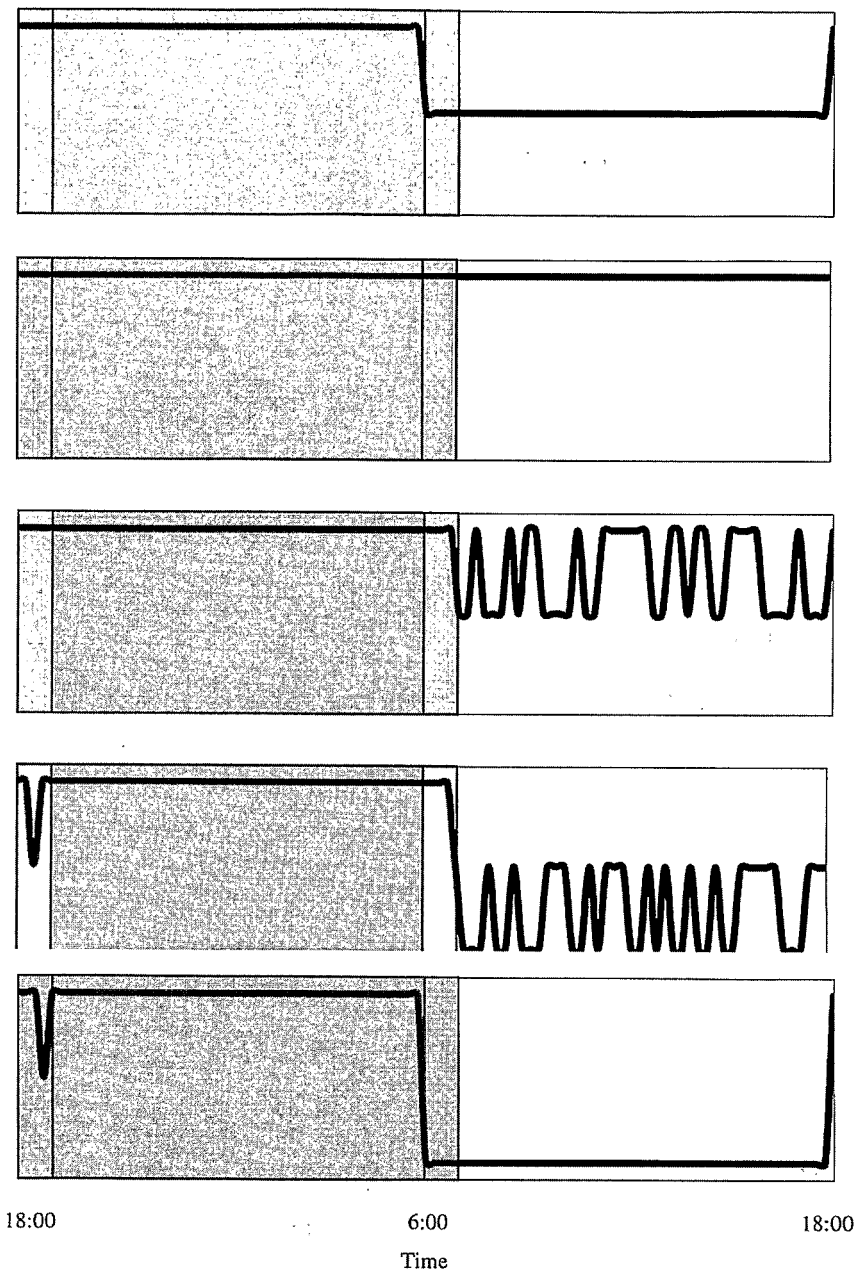18:00   6:00   18:00

Time

Fig. 4. Typical vertical movements of artificial individuals in the five most represented classes (from top to bottom: AB, AA, AE, AD and AC). The horizontal axis corresponds to time (the 24-h period, from 18:00 to 18:00 h), with the four periods of the day marked by the background levels of gray. The vertical axis corresponds to the depth layer.

The only behaviour predicted by our model but not observed in the real fishes by ultrasonic telemetry is AB. However, longline catch data suggest that albacore tuna utilize the AB pattern (see Section 4).

3.1.2. Horizontal movements

To perform quantitative analysis of horizontal movement patterns, we measured two statistics for each individual and for each 11-h period (day or night):

- path length *L*, the linear distance covered along the horizontal trajectory (proportional to the average swimming speed);
- diffusion distance *D*, the Euclidean distance between the two extreme points of the horizontal trajectory.

The distributions of these measures, obtained by combining all 2489 individuals from the final populations of the ten runs, are shown Fig. 5. The respective distributions of daytime and nighttime individual path lengths have the same mode (88 cells), which corresponds to an average swimming speed of two cells per time step (the lowest swimming speed in our simulations). Nevertheless, nocturnal movements were usually more extensive than diurnal ones. During the daytime, individuals did not cover long distances (maximum value of *L* is 180 cells) and 76% of the individuals had a path length *L* of 88 cells. During the nighttime, this path length value (88 cells) is only observed in 15% of the individuals and *L* values range up to 320 cells.

From this data we conclude that the model selected for animals with low horizontal speeds. Several tracking studies found that, in general, fishes do not adopt high speeds for their movements (Carey and Robison, 1981; Carey and Olson, 1982; Cayré and Chabanne, 1986; Carey, 1990; Carey and Scharold, 1990; Holland et al., 1990a,b, 1992; Cayré, 1991; Brill et al., 1993, 1999; Block et al., 1997; Bach et al., 1998; Josse et al., 1998; Dagorn et al., 2000). Although it is known that fishes can move rapidly when attacking prey or avoiding danger (Walters and Fierstine, 1964), there is probably little routine use for high speeds, as suggested by Carey (1992). This suggests that the convergence toward low speed is consistent with reality.

The diffusion distance *D* was longer during the nighttime than during the daytime (Fig. 5). During the daytime, 75% of the individuals have a diffusion distance less than or equal to 10 cells. During the nighttime, however, 80% of the individuals have a diffusion distance greater than 10 cells. This suggests high sinuosity and exploitative behaviours (Benhamou, 1992) during the daytime, as opposed to more extended, exploratory behaviours during the nighttime.

No conclusive data about the horizontal movement patterns of actual oceanic predatory species are yet available to assess the validity of the predictions of diffusion distance. While some sonic tagging experiments with yellowfin and bigeye tunas in Hawaii (Holland et al., 1990a) and with yellowfin tuna in the Indian Ocean (Cayré, 1991) seem consistent with our model, these data are for coastal areas. A few tracking experiments with large bigeye tuna in the open ocean (Dagorn et al., 2000) suggest the need for further experiments on predators in the open ocean.

3.2. Analysis of evolved strategies

To examine the vertical behaviours exhibited by the artificial individuals during a complete 24-h cycle, we consider the depth of predators during night, day, dawn, and dusk. Individuals were subjected to an input sequence representing 30 24-h cycles. We used the codes in Table 1 for the vertical patterns during all four periods. For the analysis, one individual is characterized by four letters, one for each period of the day in the above order. The classification of the final populations in the ten runs includes 70 out of 2401 possible classes. These are ranked by frequency of occurrence, and the median of the rank distributions for the ten runs is shown in Table 4 for the top ten classes.

The most frequently observed 24-h movement class is AAAA, which corresponds to individuals swimming in the surface layer most of the time. The artificial fishes exhibiting this behaviour forage efficiently only during the night period, because in our artificial ocean no prey are present in the surface layer during the day, dawn, or dusk. We conclude that, while this strategy is the sim-
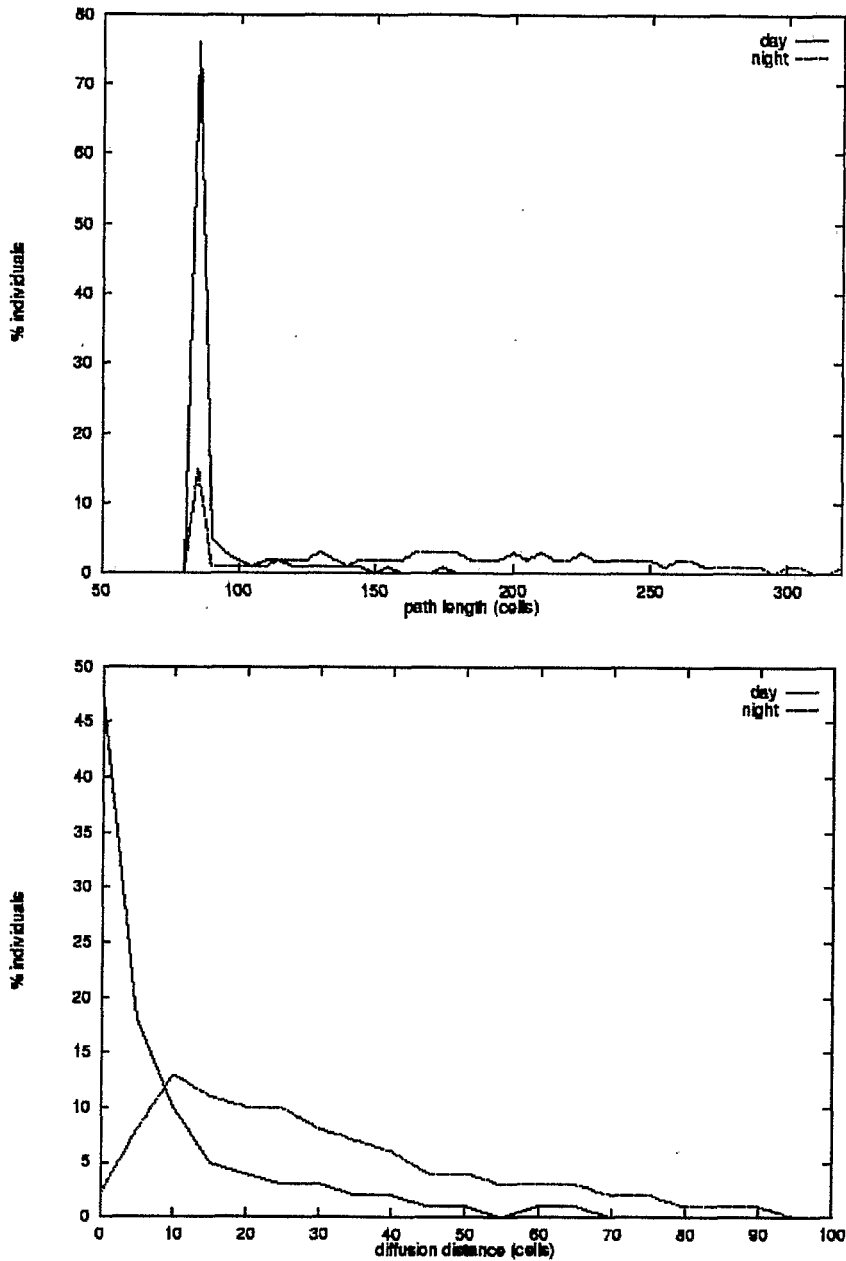
Fig. 5. Distributions of path length *L* (top) and diffusion distance *D* (bottom), characterizing the population's horizontal movements.

plest possible with respect to vertical movements, it provides individuals with sufficient energy for survival from prey caught during the nighttime alone. This exclusively nocturnal activity pattern

might correspond to primitive predator species (Helfman, 1993).

The top eight classes include the A pattern at night, indicating that the fishes are active during

the nighttime. All patterns except AAAA indicate that the predators forage during the daytime as well. Such diurnal foraging capabilities correspond to more advanced species (Helfman, 1993).

The dawn and dusk patterns are the same for each of the top ten classes, reflecting the same environmental conditions in spite of different inputs from the time-of-day sensors. Six of the top ten patterns indicate that the fishes are active during the twilight periods as well as during night and day. Helfman (1993) points out that such activity patterns represent opportunistic behaviours, which characterize many fishes, particularly predatory ones. Our model agrees with Helfman's conclusion that the activity patterns of fishes in the wild may be strongly determined by the activity patterns of their prey.

Table 4
Classified vertical movement behaviours of the artificial individuals during the four periods of the day (night–day–dawn–dusk), ranked by frequency across ten simulations[a]

Class	Rank distribution median
AAAA	1.5
ABAA	3
AEAA	4
ABEE	5.75
AEEE	6.25
ADBB	8.25
ADEE	8.75
ABBB	11
EBBB	12.5
CCCC	20.75

[a] Only the ten most frequent classes are shown. The median of the frequency rank distribution drops below 610 from the 11th class.

Table 5
Values of the prey distribution parameters held constant during the original simulations, as well as the four sensitivity analysis runs

Prey type	N_{patches}	E_{tot}
1	8/day	36 000/day
2	4/day	30 000/day

3.3. Sensitivity analysis

Using an individual based model, such as LEE, to represent a population of artificial individuals and their environment entails a number of assumptions. The purpose of some of the assumptions is to keep the model simple, while others are required by several aspects of the model. Therefore, it is critical to determine how sensitive the model predictions are to the assumptions.

Ideally, one would repeat the simulations several times while varying each parameter by some amount, and assess the variability of the results with respect to the assumption denoted by that parameter. Because such a full-scale sensitivity analysis is computationally prohibitive[2], we decided to focus our analysis in a couple of ways. First, we looked at the population dynamics from the original runs to determine the number of time steps necessary for the population size to stabilize around the carrying capacity of the environment. We concluded that after 10 000 time steps the fluctuations in population size were essentially reduced to noise. Second, we focused on the two critical parameters whose initial values were assigned with less confidence than the others in the original runs: (i) the relative amounts of energy in the two prey types, and (ii) the detection distance. In the original simulations, the ratio of energy between the two types of prey was $E_2/E_1 = 5$. The formula that correlates the energy of an item of a given prey type with the total replenishment energy per unit time, the number of patches, and the number of prey items per patch of the same prey type is given by:

$$N_{\text{prey/patch}}^{X} = \frac{E_{\text{tot}}^{X}}{E_X N_{\text{patches}}^{X}}$$

where $X \in \{1, 2\}$ is the prey type. The number of patches (N_{patches}) and total energy (E_{tot}) were fixed at their original values (Table 5). Thus, we used the energy values of the prey (E_X) as independent variables, which determined the ratio, and derived the numbers of prey items per patch ($N_{\text{prey/patch}}$) as dependent variables. We ran four additional simu-

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[2] A single 150 000-step run of our C++ simulation code required ~40 CPU h on a 400 MHz P2 Linux workstation.
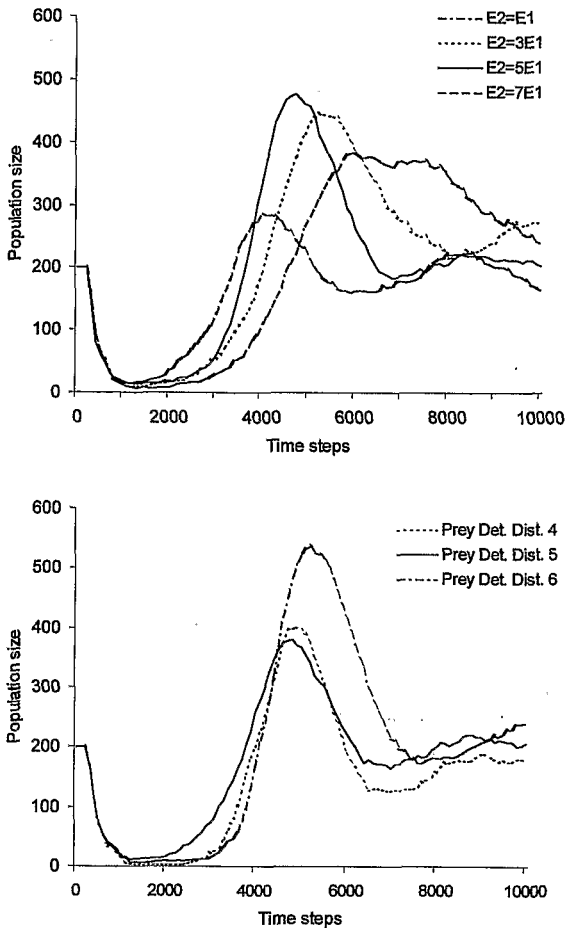
Fig. 6. Size of the artificial population in the four sensitivity-analysis runs for various ratios of energy between the two prey types (upper graph), and the three sensitivity-analysis runs for various detection distances of prey (lower graph).

lations with energy ratios $E_2/E_1 \in \{1, 3, 5, 7\}$. In the original runs, the prey detection distance was 5 cells, i.e. 900 m. We also ran three additional simulations with prey detection distance at 4, 5 and 6 cells, i.e. 720, 900 and 1080 m. All the seven sensitivity runs were stopped after 10 000 steps (see Fig. 6).

An important observation from our simulations is that few of the individuals in a starting population happen to be initialized with a random behaviour that is efficient enough to allow them to survive (Fig. 6). All the individuals at the end of a run are descendants of these few ancestors, an

effect that we call 'ancestor bottleneck.' Consequently, genetic drift causes a large variability in the behaviours evolved by the populations across different runs (Menczer and Belew, 1994). This is why we focused on rank when analyzing vertical movement behaviours (cf. Section 3.1.1). For the same reason, we used the Spearman correlation coefficient, R_s, to see whether the results of the four additional runs were consistent with those of the ten original runs. The rank correlation was calculated between (i) the vertical movement behaviours emerged at the end of the seven sensitivity runs (percentages), and (ii) the medians of rank distributions across the original ten runs. Table 6 shows that all rank correlation values are highly significant. Therefore, our model is not sensitive to variations in the energy ratio of the prey types nor to the distance at which a fish responds to a prey item.

4. Discussion

Most large oceanic predators live in all of the oceans, in different oceanographic conditions. Usually, habitats of these species are defined in relation to the physical and chemical structure of the ocean, rarely as a function of the biotic environment (see Longhurst, 1998 for large-scale oceanic provinces defined from hydrology and phytoplankton distribution). Acoustic data have

Table 6
Spearman rank correlation coefficients, R_s, between the rank of the median of the ranks of the behaviour frequencies in the original ten runs, and the rank of the behaviour frequencies in each of the seven sensitivity analysis runs[a]

Run	R_s	Probability
$E_2 = E_1$	0.67	>0.9999
$E_2 = 3E_1$	0.55	0.9999
$E_2 = 5E_1$	0.69	>0.9999
$E_2 = 7E_1$	0.78	>0.9999
Prey detection distance = 4 cells	0.64	>0.9999
Prey detection distance = 5 cells	0.52	0.9998
Prey detection distance = 6 cells	0.49	0.9997

[a] The control runs with $E_2 = 5E_1$ and prey detection distance = 5 cells have identical conditions to the ten original runs (except for the seed of the random number generator).

traditionally been used for stock assessment or direct observations of animal behaviour, but have largely been ignored in ecological modelling (Brandt and Mason, 1994). The biotic environment of the present model was inspired by the results of acoustic experiments conducted in French Polynesia under the ECOTAP program, which was designed specifically to study the ecology and behaviour of tropical tunas. The aim of the present study was not to represent exclusively the ocean in French Polynesia, but to draw from real observations a realistic model of the environment in which different pelagic predatory fishes live. The various tropical oceanic zones have different abiotic factors, such as temperature and dissolved oxygen, which influence the depths reached by different types of prey. Our model can be applied to different biotic environments that have similar prey macro-structure even if the micro-scale details (e.g. the depths of the layers) vary between environments. This explains our preference for general terms ('surface', 'intermediate', and 'deep') to model the depth layers rather than specific values in meters.

We used tracking results for only few individuals per species to define one pattern per species, but these data clearly indicate the existence of behavioural variability across individuals of the same species, as well as within a single individual depending upon the variability of the environment. We focus our discussion only on the interspecific variability observed in the wild, but our modelling approach also provides a means to study intra-specific and intra-individual variability.

Physiology is generally considered the key determinant of the vertical movement patterns of fishes. For example, skipjack and yellowfin tunas occupy shallower depths than bigeye tuna during the daytime (Cayré and Chabanne, 1986; Holland et al., 1990a; Cayré, 1991; Dagorn et al., 2000). Bigeye tuna have the ability to physiologically and behaviourally thermoregulate (Holland et al., 1992), allowing them to expand their niche into deep, cold water below the thermocline (Dagorn et al., 2000). During the daytime, bigeye tuna make frequent, regular upward excursions to warm up, as indicated by the ultrasonic telemetry

experiments of Holland et al. (1992). Because of different physiological capabilities, different species are not able to exploit the same vertical habitats.

The modelling work presented here, on the other hand, indicates that predator adaptations to prey dynamics can also lead to the same vertical movement dynamics, without any physiological constraints. Our simulations suggest that diverse behaviours can emerge due to adaptation to the prey environment alone. All the artificial fishes had the opportunity to develop movements in deep and cold waters (the intermediate and deep layers). The structure and the dynamics of the biotic environment alone were responsible for the simultaneous differentiation of several strategies for survival in the artificial ocean. The model suggests the possibility that behaviours evolved first, creating progressive selective pressure for changes in physiological capabilities, or, at least, that behaviours and physiology might have co-evolved simultaneously.

The absence of tracking data corresponding to the most frequently observed vertical behaviour pattern predicted by our model may seem discouraging. However, there is evidence that the albacore tuna (*T. alalunga*) fits this category. Albacore is the most abundant tuna species in French Polynesia. However, no published tracking data for this species in a tropical area yet exist. Therefore, we examined experimental longline fishing data, with quasi-uniform vertical distribution of hooks, to assess the vertical movement behaviour of albacore tuna. Based on this data, albacore tuna in tropical waters utilize mostly the intermediate layer during the daytime, i.e. the AB pattern (Fig. 7). Thus, all five behaviours most frequently predicted by our model are found in nature.

Behaviours D and E (rapid changes between depth layers) deserve special attention. The emergence of these behaviours requires a very precise adjustment of the synaptic weights, which suggests that these behaviours are especially adaptive to the structure of the environment. The ability to make rapid, frequent changes in depth is a special adaptation in some pelagic fishes. Special sonic-tracking experiments were developed to study why these animals exhibit these striking vertical move-
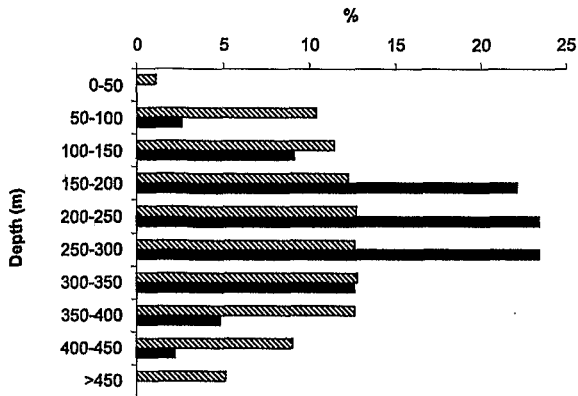
Fig. 7. Depth distribution of albacore tuna catches (black bars) and fishing effort (shaded bars) based on 53 daytime fishing experiments (281 individuals captured). The experiments used an instrumented longline, with a total of 27 750 hooks set between 9 and 14° south in the French Polynesian EEZ.

ments. Thermoregulation was demonstrated for bigeye tuna, for example (Holland et al., 1992). Carey and Scharold (1990) proposed that sharks moved vertically to search for food using olfaction. A combination of factors may be involved in explaining frequent, rapid vertical movements, and these factors may differ from species to species. Our model indicates that this particular vertical behaviour could have evolved to efficiently exploit the biotic environment.

5. Conclusions

We presented a minimal computational model to explore the hypothesis that the biotic environment may have played a major role in the evolution of movement behaviours of tropical oceanic predatory fishes. The model illustrated that realistic vertical movement patterns can evolve based on simple, yet robust assumptions about prey distributions. The success of this approach confirms the promise of individual-based artificial life models for this kind of study (Judson, 1994), and particularly the use of approaches like LEE to study co-evolution of animals living in a same environment (Menczer and Belew, 1996b).

A second objective of this work was to determine whether the biotic environment could induce the emergence of several co-adapted behaviours. Our results suggest that the variety of behaviours exhibited by individuals or species corresponds to different solutions for exploiting the same environment. While it remains important to study the physiological limits of predatory species, our modelling suggests the need for more research to characterize the biotic environment of tropical oceanic fishes and its relationship with behaviour.

This minimal model lends itself to numerous refinements and extensions. Incorporating additional data about the French Polynesia EEZ would benefit the model. For example, data on the depth distributions of additional predatory species is becoming available from fishing experiments. Predator diet data will also be available soon from stomach content analyses. The model of the prey environment could be made more precise using information on horizontal and vertical prey distributions and dynamics, which is currently being analyzed from underwater acoustics surveys combined with trawl sampling. This kind of data will allow a more accurate, continuous three-dimensional model of the environment, and consequently a more refined model of fish movement behaviour.

Another direction for future work is to apply this modelling approach to different environments. This would not be possible if the model was specific to a particular area. Our assumptions about the biotic environment could easily be adjusted to reflect conditions more realistic in other areas. For example, in this paper we assumed that no prey are found in the surface layer during the daytime while the opposite is true in the eastern Pacific Ocean. Yellowfin tuna feed on epipelagic prey throughout the daylight hours in the eastern Pacific (Olson and Boggs, 1986). By simulating biotic environments corresponding to alternative areas and comparing the emergent behaviours with the known movement patterns of actual fishes in those areas, we can test the generalization power of the model.

Finally, the model could be extended to include factors such as predator size, prey selection, and physiological constraints corresponding to differ-

ent individuals and species. We chose to disregard predator size and prey selection in our model as a simplifying assumption, albeit somewhat unrealistic. One way to address these problems would be to include some adaptive physiological capabilities into the genotypic model, and study the relationship between the evolutions of behaviour and physiology in heterogeneous populations. This modelling approach might also be appropriate to tease apart the variability observed in diet data for different predatory species and different individuals of the same species in different environments. In this sense, our approach would be a precursor for models that assume given trophic relationships to study ecosystem dynamics (Pauly et al., 1998).

Acknowledgements

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