

The migration game in habitat network: the case of tuna

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Abstract Long-distance migration is a widespread process evolved independently in several animal groups in terrestrial and marine ecosystems. Many factors contribute to the migration process and of primary importance are intra-specific competition and seasonality in the resource distribution. Adaptive migration in direction of increasing fitness should lead to the ideal free distribution (IFD) which is the evolutionary stable strategy of the habitat selection game. We introduce a migration game which focuses on migrating dynamics leading to the IFD for age-structured populations and in time varying habitats, where dispersal is costly. The model predicts migration dynamics between these habitats and the corresponding population distribution. When applied to Atlantic bluefin tunas, it predicts their

migration routes and their seasonal distribution. The largest biomass is located in the spawning areas which have also the largest diversity in the age-structure. Distant feeding areas are occupied on a seasonal base and often by larger individuals, in agreement with empirical observations. Moreover, we show that only a selected number of migratory routes emerge as those effectively used by tunas.

Keywords Structured population · Ideal free distribution · Game theory · Habitat selection · Bluefin tuna

Introduction

Many populations of animals and plants exhibit characteristic distributional patterns that are related to the ability of the organisms to move and explore their environment. Temporal environmental fluctuations result in changes in population distributions (Morris 2011). Moreover, competition is among the major driving forces shaping animal distributions. Passive dispersal from more populated to less populated habitats reduces intra- and inter-specific competition thus promoting species coexistence and diversity (MacArthur and Levins 1964; Rosenzweig 1981). Dispersal also often involves active habitat selection, which is a widespread phenomenon in nature and has been described in many animal populations such as birds (Svårdson 1949), terrestrial mammals (Wecker 1963; Morris 1987b, 1996), and fish (Milinski 1979; Berec et al. 2006).

Fitness-based arguments are commonly used to describe the process of habitat choice (e.g., MacArthur and Levins 1964; Morris 1989; Křivan et al. 2008). When moving between different habitats, organisms should prefer those sites that provide them with the highest payoff, i.e., where their fitness is maximized (Rosenzweig 1981).

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Nevertheless, both individual fitness and habitat selection typically depend on interactions among individuals, which usually have the form of a density-dependent relation linking habitat quality and species distribution (Rosenzweig and Abramsky 1985).

Under negative density dependence (described by logistic growth), if dispersal is cost free and individuals are omniscient and free to settle at any habitat, the evolutionarily stable strategy corresponds to the ideal free distribution (IFD) (Fretwell and Lucas 1969; Křivan et al. 2008; Morris 2011). At the IFD, payoffs in all occupied habitats are the same and larger or equal than those in the unoccupied habitats. Thus, no individual can improve its fitness by choosing a different habitat.

Although the IFD is a strong theoretical tool to analyze animals' spatial distributions, over the past decades, attempts to validate it led to equivocal results (Matsumura et al. 2010). For example, several studies reported “under-matching” when animals underuse better habitats and overuse poorer habitats (for a review see Kennedy and Gray 1993). These discrepancies between the IFD and observed distributions are attributed to, e.g., the cost of moving (Morris 1987a; Åström 1994), imperfect information (Matsumura et al. 2010), or stochastic fluctuations in environmental conditions (Schreiber 2012). An important aspect that is usually neglected in theoretical studies of habitat selection and migration (but see, e.g., Sutherland and Parker 1985; Hugie and Grand 1998; Grand and Dill 1999; Tregenza and Thompson 1998) is the variability among individuals. In particular, factors related to age or energetic state can contribute to individuals' perception of the environment and affect the ability to migrate between habitats. Moreover, the current location of an individual can also affect the habitat selection process. Indeed, while the IFD assumes freely moving individuals between habitats, habitat-connectivity can often be constrained by specific geographical (e.g., topography) or temporal (e.g., seasonal) patterns, which can then limit the ability to migrate towards better habitats. A network of habitats is often a more realistic and general description of habitat connectivity for migratory species (Taylor and Norris 2010; Betini et al. 2015).

For example, migratory species such as the Atlantic bluefin tuna (BFT) have widely separated feeding and spawning areas that are distributed over a large latitudinal gradient. Those habitats are typically exposed to changes in seasonality and habitat productivity that can affect habitat payoffs and dispersal dynamics. The species appears to have evolved a migration strategy that alternates rapid movement between neighboring regions with periods of continuous feeding in those areas before a new migration occurs (Block et al. 2001, 2005; Wilson et al. 2005). Thus, the dispersal dynamic between distant habitats appears as a multiple step

process by which tunas explore several habitats rather than a single direct movement toward higher payoff areas.

In this manuscript we present a game theoretical approach, called the “migration game,” to model migration dynamics of an age-structured population on a network of interconnecting habitats that undergo seasonal variation. In addition, we assume a travel cost that is age specific. Then, we apply this concept to BFT to predict their seasonal distribution and their migration routes across the Atlantic.

Theoretical framework

The migration game

We consider an unstructured migratory species in an heterogeneous environment consisting of a network with n habitats.

Distributional processes are assumed to be discrete in time, and the time step is scaled so that it equals 1. In each habitat, i , and at each time step, the population abundance, p_i , changes due to migration dynamics:

$$p_i(t+1) = p_i(t) + \sum_{j=1}^n p_j(t)x_{ji}(t) - \sum_{j=1}^n p_i(t)x_{ij}(t) \quad (1)$$

where $x_{ij}(t)$ ($x_{ij}(t) \geq 0$, $\sum_{j=1}^n x_{ij}(t) = 1$ for every $i = 1, \dots, n$) is the per capita migration rate from habitat i to habitat j within the unit time interval. Thus, total population abundance $P = \sum_i^n p_i(t)$ stays constant. We note that if two sites i and j in the network are not linked, we set $x_{ij} = x_{ji} = 0$.

To define migration rates, we assume that each habitat is characterized by a negative density-dependent payoff, u_i . If there is a direct link between habitats i and j in the network, then for individuals migrating from i to j , we define a reward function:

$$\Phi_{ij}(p_i, p_j) = u_j(p_j) - c_{ij} - u_i(p_i) \quad (2)$$

where $c_{ij} \geq 0$ is the migration cost. This cost includes the energy needed to migrate between habitats i and j as well as the energy required for habitat selection and decision making processes (Bonte et al. 2012).

We consider directed (non-random) movements on the network and we assume that along migration routes the reward must be positive, i.e., an individual currently in habitat i will move to habitat j only when the reward of doing so is positive. Hence at each time step, t , dispersal rates x_{ij} must result in a population distribution that satisfies:

$$\Phi_{ij}(p_i, p_j) \geq 0. \quad (3)$$

In the model, motility is restricted by the topology of the network and we assume that in a single time unit individuals can migrate to neighboring habitats only (i.e.,

habitats directly connected to the current animal habitat). We observe that the rewards (Φ_{ij} , Eq. 2) are frequency dependent. Indeed, individual strategies, x_{ij} , influence population distribution (p_i , Eq. 1), which in turn influences the rewards.

We define a non cooperative migration game, in which individuals (players) are characterized by their current habitat i , and strategies of a player in i are given by probabilities x_{ij} , ($j = 1, \dots, n$) with which the individual moves to one of the neighboring habitats. The reward of player i is defined as $\sum_j x_{ij} \Phi_{ij}$ where the sum is restricted to those habitats that are directly connected to habitat i . Solutions are migration rates x_{ij}^* that are the Nash equilibria (NE) of the migration game.

The equilibrium strategy is such that any unilateral change in the strategy of any individual would result in a lower reward for the player who changes its strategy. This implies that for any two habitats j and j' such that $x_{ij}^* > 0$ and $x_{ij'}^* > 0$, the rewards must be the same and maximal (i.e., $\Phi_{ij}^* = \Phi_{ij'}^* \geq \Phi_{ik}^*$ for any connected habitat k such that $x_{ik} = 0$). A general method to calculate the migration rates uses linear complementarity problem (LCP; Mullen 2013; Facchinei and Pang 2003).

Migration rates x_{ij}^* are then used in the model (Eq. 1) to define population dynamics on the network.

Distributional equilibrium in a cost-free migration game

We start with the assumption that migration is cost free, i.e., $c_{ij} = 0$ in Eq. (2). Then the reward function is similar to those used in habitat selection games (e.g., Hugie and Dill 1994; Křivan et al. 2008) and the solution of the migration game converges to the IFD (Pan and Nagurney 1994; Cressman and Křivan 2006). However, because dispersing animals are constrained in their movements by existing links in the habitat network, depending on the topology of the network, it can take several steps to reach the global IFD. Indeed at each time step, individuals can move only to habitats that are directly connected to their current habitat. Thus,

at each time step, individuals reach a local IFD in the sense that directly linked habitats have the same payoffs as we do not consider the cost of dispersal. As time increases, the IFD becomes more global, that is, payoffs in additional habitats get equalized.

To illustrate the relation between migration equilibrium and distributional equilibrium, we consider a simple case of three habitats denoted as A, B, C , and two different network topologies: (a) a fully connected network (Fig. 1a); (b) a network where habitat B is disconnected from C (Fig. 1b). Each habitat is characterized by a negatively density-dependent payoff

$$u_i = 1 - \frac{p_i}{K_i} \tag{4}$$

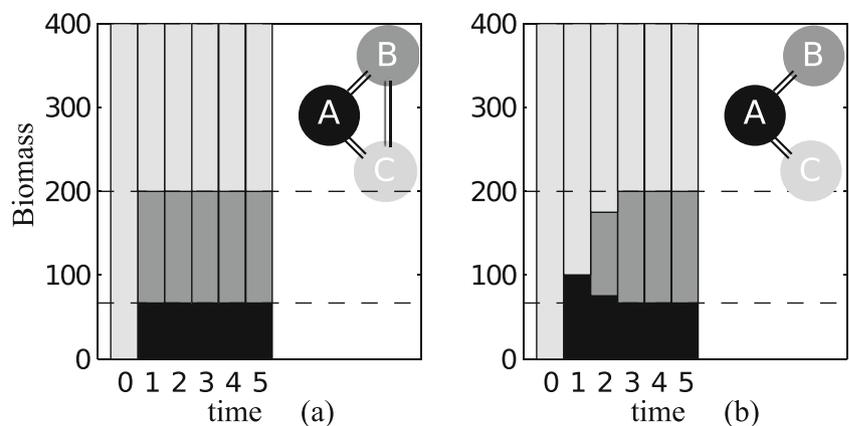
where K_i is the habitat carrying capacity and p_i is the number of individuals in habitat $i = A, B, C$. We assume that initially all individuals, P , occupy habitat C only, i.e., $p_C = P, p_A = p_B = 0$.

When the network is fully connected, our model converges to the IFD in a single time step (Fig. 1a). Since individuals are free to move in all the habitats in the network, the strategies resulting from the migration game are those needed to balance the reward function in Eq. (2) for all the three habitats.

When the network is not fully connected, three time steps are needed to reach the global IFD (Fig. 1b).

In the first time step, only movements between C and A are possible on the network because we assume that individuals can move only between neighboring habitats in a single time step. Thus, individuals from habitat C can move in habitat A only, and they do it so that the payoffs in both habitats are the same ($u_C = u_A$). This defines the migration rates x_{CA} as those that balance rewards ($\Phi_{CA} = \Phi_{AC}$), i.e., a local IFD conditions is reached between the two habitats. In the second time step, individuals that are now in habitat A have the possibility to migrate into B since $\Phi_{AB} > 0$. Moreover, because of this emigration from habitat A , habitat A payoff will increase compared to habitat C

Fig. 1 Convergence of population distribution to the IFD in three habitats A (black), B (dark grey), and C (light grey). Panel **a** assumes fully connected network while panel **b** assumes a partially connected network. Dashed lines show the IFD. Parameters: $K_A = 100, K_B = 200, K_C = 300$, and total population $P = 400$



causing migration from habitat *C* to *A*. For example, after the migration, the payoff in habitat *A* can be written as

$$u_A = 1 - (p_A + x_{CA} - x_{AB})/K_A \tag{5}$$

with similar expressions for the payoff in habitats *B* and *C*. In this second time step, all individuals that were initially in habitat *A* move to habitat *B*, but this is not enough to equilibrate payoffs in these two habitats. Thus, after time step 2, payoffs in habitats *C* and *A* are the same and smaller than is the payoff in habitat *B*. Only in the third time step, payoffs in all habitats are equalized and the global IFD is reached (Fig. 1b).

This example documents that when dispersal is local at each time step, several steps are needed to reach the global IFD. In fact, this is because the number of emigrants cannot be larger than the number of inhabitants.

The effects of costs on the IFD

When travel costs are zero and habitat payoffs are negative density-dependent, there is a single IFD (Křivan et al. 2008). However, if migration costs are positive, there may be infinitely many possible IFDs. Indeed, let us consider an environment consisting of two habitats (*i* = 1, 2), and let the habitat payoffs be described by Eq. 4.

The reward of an individual currently in habitat 1 to migrate to habitat 2 is

$$\Phi_{12}(p_1, p_2) = u_2(p_2) - u_1(p_1) - c_{12}$$

and, similarly, the reward of an individual currently in habitat 2 to migrate to habitat 1 is

$$\Phi_{21}(p_1, p_2) = u_1(p_1) - u_2(p_2) - c_{21},$$

Under the IFD, there is no incentive for individuals to move and none of these two rewards can be positive. In particular, when travel costs are neglected, a single IFD

exists at which $\Phi_{12}(p_1, p_2) = \Phi_{21}(p_1, p_2) = 0$ (Fig. 2a). When travel costs are positive (Fig. 2b), there is a region of possible distributions under which the reward in neither habitats is positive. Thus, all these distributions correspond to IFDs.

The LCP method that we use to calculate numerically the NE of the migration game selects a single IFD from the set of possible IFDs. The selected point is on the boundary of the set of all IFDs, i.e., in the above example it is one of the two boundary points.

Coupling migration and demographic processes

So far we have considered migration dynamics only. Now, we combine migration with population demography. This means that we do not assume anymore that the overall population abundance is fixed. We consider an age structured population with *S* age classes. We assume that in each time step the population first undergoes migration and after that it undergoes demographic changes. This can be represented as $P_i(t) \rightarrow P'_i(t) \rightarrow P_i(t + 1)$, where $P_i(t) = (p_{i,1}(t), \dots, p_{i,S}(t))$ is the vector describing age structure of the population in habitat *i* at the beginning of a time step, $P'_i(t) = (p'_{i,1}(t), \dots, p'_{i,S}(t))$ is the population distribution, once individuals have redistributed themselves according to the migration equilibrium, and $P_i(t + 1) = (p_{i,1}(t + 1), \dots, p_{i,S}(t + 1))$ is the new population distribution after the demographic processes (birth, death, and growth). To represent these processes, in each habitat, we use a Leslie matrix, i.e., $P_i(t + 1) = L_i P'_i(t)$ where:

$$L_i = \begin{pmatrix} q_{i,1} & r_{i,2} & r_{i,3} & \dots & r_{i,S-2} & r_{i,S-1} & r_{i,S} \\ g_{i,1} & q_{i,2} & 0 & \dots & 0 & 0 & 0 \\ 0 & g_{i,2} & q_{i,3} & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & g_{i,S-2} & q_{i,S-1} & 0 \\ 0 & 0 & 0 & \dots & 0 & g_{i,S-1} & q_{i,S} \end{pmatrix} \tag{6}$$

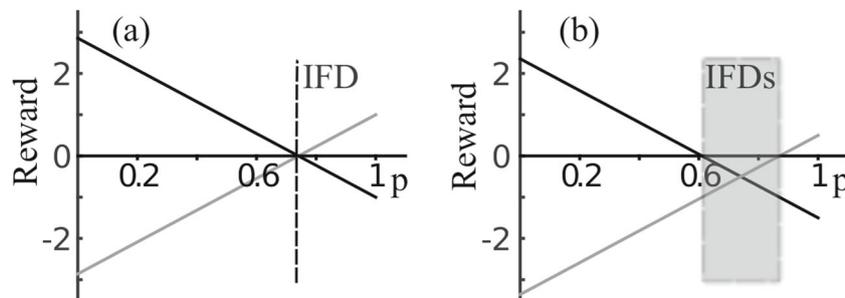


Fig. 2 Reward functions (Φ_{ij}) without (panel a) and with (panel b) migration costs. The plots show rewards of migration for individuals in habitat 1 (black) and in habitat 2 (grey) as the proportion *p* of individuals in habitat 1. For values of *p* such that the black (grey) line

is above the x-axis, individuals of population 1 (2) have incentive to migrate. In panel (a), migration costs are zero and a single equilibrium distribution $p = 0.74$ exists. In panel (b), migration costs are positive and there is a set of equilibrium distributions

The probability that a fish in age class $a - 1$ at time t will grow into class a at time $t + 1$ in habitat i is $g_{i,a}$. Similarly, $q_{i,a}$ is the probability that a fish will continue to stay in the same class, while $r_{i,a}$ is the average number of newborns (belonging to the class $a = 1$) produced by individuals at ages $a > 1$ in habitat i .

Case study

The ecology of Atlantic bluefin tuna

The Atlantic bluefin tuna (*Thunnus thynnus*) has evolved a migratory behavior in which spawning and feeding sites are separated by large distances, typically spanning 100s to 1000s of kilometers and several degrees of latitude (Mather et al. 1995; Cury et al. 1998). Spawning sites are located in temperate-tropical waters (i.e., Mediterranean Sea, Gulf of Mexico), but feeding sites used by the largest and oldest individuals are located in northern temperate-boreal waters (Mather et al. 1995). During the narrow reproductive period, individuals often display fast trans-Atlantic migrations to reach the Mediterranean spawning ground (Block et al. 2005; Fromentin 2009). The seasonal south-north migratory behavior exhibited by bluefin tuna has likely evolved

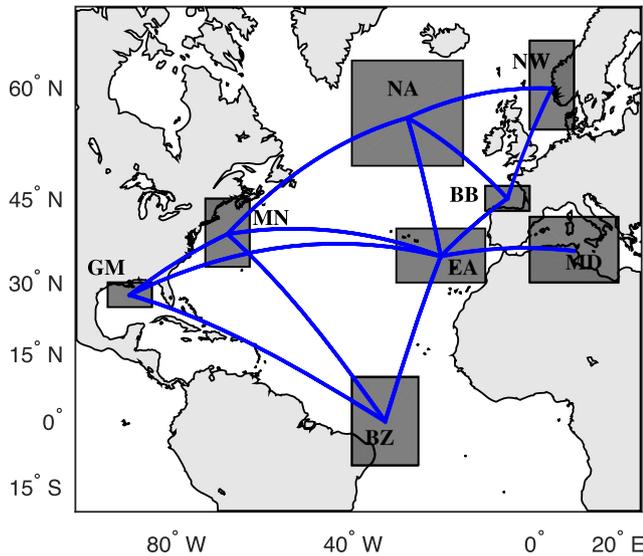


Fig. 3 Network for the bluefin tuna migration game. We consider eight habitats: GM Gulf of Mexico, BZ Brazil, MN Maine, NA North Atlantic, NW Norway, BB Bay of Biscay, EA Eastern Atlantic, and MD Mediterranean. Habitats are defined within a certain spatial range (grey areas) for which we calculate the average biological productivity that is assumed to be proportional to the habitat’s carrying capacity. Links between habitats show the potential migration routes assumed in the present study

Table 1 Biological characteristics of age classes

Age class a	Weight w (kg)	Fertility r^a (month ⁻¹)	Growth g (month ⁻¹)	Survival q (month ⁻¹)
Young	1	0	0.02	0.9
Juvenile	30	0.125 s	0.02	0.9
Adult	100	0.25 s	0.02	0.9
Mature	200	0.5 s	0.02	0.9
Old	500	s	0.02	0.9

to allow individuals to benefit from large biomasses of prey species in these regions (Cury et al. 1998).

Model implementation

We implement the theoretical framework described above, to illustrate the spatial dynamics of the Atlantic bluefin tuna. The time step for the dynamic system is set equal to one month, and the simulations are extended up to 20 years. We chose a network of $n = 8$ habitats (Fig. 3): Gulf of Mexico (GM), Brazil (BZ), Maine (MN), North Atlantic (NA), Norway (NW), Bay of Biscay (BB), eastern Atlantic (EA), and Mediterranean (MD). The links between habitats are selected based on historical migration routes of bluefin tuna and defined to represent feasible distances that individuals can cover in 1 month. Moreover, the migratory population is structured in five age classes: young of the year, juvenile, adult, mature, and old. We denote by w_a the mean weight of tuna at age class a (Table 1).

Habitat payoffs for an individual of class a in habitat $i \in \{GM, BZ, MN, NA, NW, BB, EA, MD\}$ at month t are density dependent:

$$u_i = 1 - \frac{\sum_a w_a p_{i,a}}{K_i} \tag{7}$$

Here, $p_{i,a}$ is the population of age a living in habitat i , K_i is the time varying carrying capacity of habitat i described as $K_i(t) = K_i(1 + \theta_i \cos(\pi + t\pi/6))$, where $\theta_i \leq 1$ is a seasonality parameter specific for each habitat (Table 2). The seasonality parameter is calibrated using mean values (2003–2011) of the seasonal biological productivity (Westberry et al. 2008) averaged over the area covered by the habitat (Fig. 3). Larger coefficients reflect larger seasonal fluctuations typically at higher latitudes.

The costs for exploring adjacent habitats, c_{ij} in Eq. 2, are difficult to set. This is because the term includes several processes such as traveling between habitats, comparison of habitat qualities, and decision-making process to select one specific habitat (Bonte et al. 2012). Tuna are efficient swimmers (Dewar and Graham 1994) and can travel thousands

Table 2 Characteristics of habitats

Habitat <i>i</i>	Mean carrying capacity K_i	Seasonal effect θ_i
Gulf of Mexico (GM)	130,000	0.2
Brazil (BZ)	20,000	0.1
Maine (MN)	60,000	0.5
North Atlantic (NA)	60,000	0.9
Norway (NW)	40,000	0.8
Bay of Biscay (BB)	100,000	0.6
Eastern Atlantic (EA)	50,000	0.3
Mediterranean (MD)	200,000	0.2

of kilometers within a few days (Block et al. 2001). Hence, the cost of traveling and exploring different habitats is not negligible but probably low and most likely depends on the distance between habitats. Indeed, we assume here that the cost for habitat identification and selection is a function of the distance between habitats and we approximate it as:

$$c_{ij,a} = \mu \frac{d_{ij}}{w_a^{0.06}} \tag{8}$$

where d_{ij} is the distance in kilometers between habitat i and j , while w_a is the age-specific average weight that is proportional to the individual swimming speed. We consider migrations performed at an optimal velocity and it can be shown (Appendix) that for tunas the optimal swimming speed scales as $w_a^{0.06}$ (Ware 1978). We set the range of $\mu = 5 - 150$ to analyze the migration game under different habitat selection costs, and we test the sensitivity of our results to this parameter.

The demographic rates in the Leslie matrix (survival q_a , fertility r_a , growth g_a ; Eq. 6) are given in Table 1. Fertility coefficients, r_a , are non zero only in the spawning areas: Gulf of Mexico (GM) and Mediterranean (MD). In our definition of the Leslie matrix (Eq. 6), we assume that older individuals have higher fertility proportional to some spawning intensity s (i.e., fecundity). In the model, we test how the results are affected by different values of s (Appendix).

Results

Tuna migrations in a stable environment

We first run the model using only the demographic processes, without migration or environmental variability, and set the total bluefin tuna biomass ($M = 330$ kton). The

simulation converges toward a stable age distribution in the spawning areas (Gulf of Mexico and Mediterranean) and zero biomass otherwise. This is the initial condition used in all the subsequent simulations.

From this initial distribution, we simulate the migration game in the case of a stable environment with no seasonality (K_i constant, Table 2). We assume no demographic changes in the tuna population structure (i.e., the Leslie matrix is the identity matrix) but consider different costs in the habitat selection process. Under such assumptions, the migration

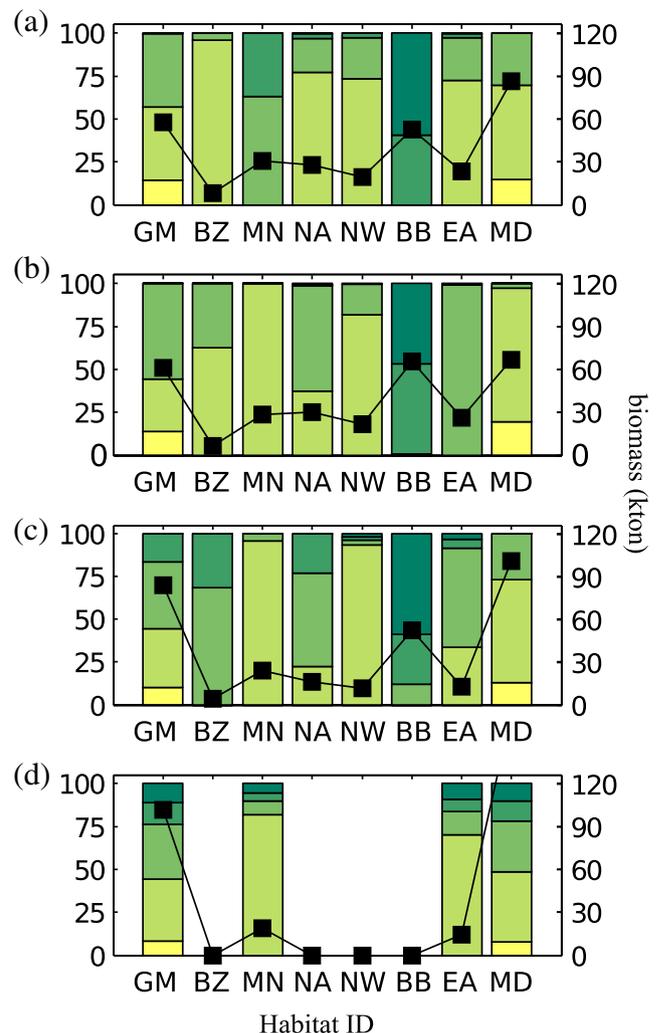


Fig. 4 Distribution of total biomass ($M = 330$ kton, lines) and age structure (bars) in the bluefin tuna population across habitats, as predicted from the migration game equilibrium when no demography or seasonal changes are considered. Panel **a** assumes very low ($\mu = 20$) habitat selection costs, **b** low ($\mu = 50$) cost, **c** medium cost ($\mu = 100$), and **d** high cost ($\mu = 150$). Different colors (yellow to dark green) denote the five different age classes (Young, to Old). In panel (d), the biomass for the Mediterranean habitat is larger than the scale and equal to $M_{MD} = 172$ kton

game on the network converges toward a stable IFD (shown as the solid line in Fig. 4).

At very low costs ($\mu = 20$), most of the biomass is aggregated in the spawning areas ($M_{GM} = 61$ kton and $M_{MD} = 89$ kton) and in the Bay of Biscay ($M_{BB} = 47$ kton) while the sum of all the other habitats accounts for $\approx 35\%$ of the total biomass (Fig. 4a). In this case, the largest tuna are on both sides of the Atlantic and mainly in habitats MN and BB with Mediterranean (MD) and Gulf of Mexico (GM) showing the most structured population distribution. The youngest class (light yellow color) is present only in the spawning areas and does not migrate to other habitats.

Increasing the habitat selection costs ($\mu = 50$, Fig. 4b) has no major effects on the biomass distribution. The distributions of age classes are also similar to the previous case with relative changes only in habitats EA and MN. With a further increase of the cost ($\mu = 100$, Fig. 4c), the

population tends to accumulate in the spawning areas while the most distant habitats tend to become unoccupied. At very high cost ($\mu = 150$, Fig. 4d), only few habitats are significantly populated and the majority of tuna biomass is in the spawning area ($M_{GM} = 102$ kton, $M_{MD} = 172$ kton).

Migration game in a seasonal environment

We simulate the habitat selection process under changing carrying capacity (K_i) and accounting for tuna population demography (L , Eq. 6, and Table 1).

Seasonal fluctuations in the tuna biomass are evident in all habitats with the spawning habitats having the lowest relative biomass variation (Fig. 5). The habitat in Norway (Fig. 5e) and Brazil (Fig. 5b) are occupied by the larger/older classes, but have the lowest of the biomasses. The age-structure in each habitat changes less than the variability in total biomass, but throughout the season significant changes in the age-structure can occur in the eastern Atlantic and Maine (Fig. 5c, g). Interestingly, the peaks in biomass in the spawning areas are in April–May while in the feeding areas they are in July–August as it is commonly reported (Table 3).

The intensity of migration on the habitat network depends on the cost of the habitat selection process and the spawning intensity of the species (Fig. 6). When costs are low and spawning intensity high (Fig. 6a) the population distributes in all available habitats and all migratory routes are used with the exception of the transatlantic route MN–EA. The age-structure is different in each area and highly diversified in the spawning area and in the central Atlantic. When the spawning intensity (s) is reduced (Fig. 6b), the total global biomass also decreases and some of the routes are used less frequently. In particular, the connections between Brazil and the western Atlantic are much weaker but the transatlantic connections (GM–EA and MN–EA) have higher migration flows. This is mainly driven by very low biomass in Brazil habitat (Fig. 6b). At higher habitat selection costs (Fig. 6c, d), the direct transatlantic routes connecting habitats GM and MN to EA break down and, in general, migration rates decrease. Moreover, only larger individuals appear to exploit the farthest habitats BZ and NW. Further cost increase (Fig. 6e, f) further diminishes migration with majority of individuals staying in the spawning habitats. Distant habitats such as Brazil and Norway have a very low biomass or are completely unoccupied.

In the case of high cost and low spawning intensity, the migration strategy is only selected by larger individuals while the majority of the population will not distribute outside the spawning grounds. Most of these patterns are confirmed also when a more extensive sensitivity analyses is performed (Appendix).

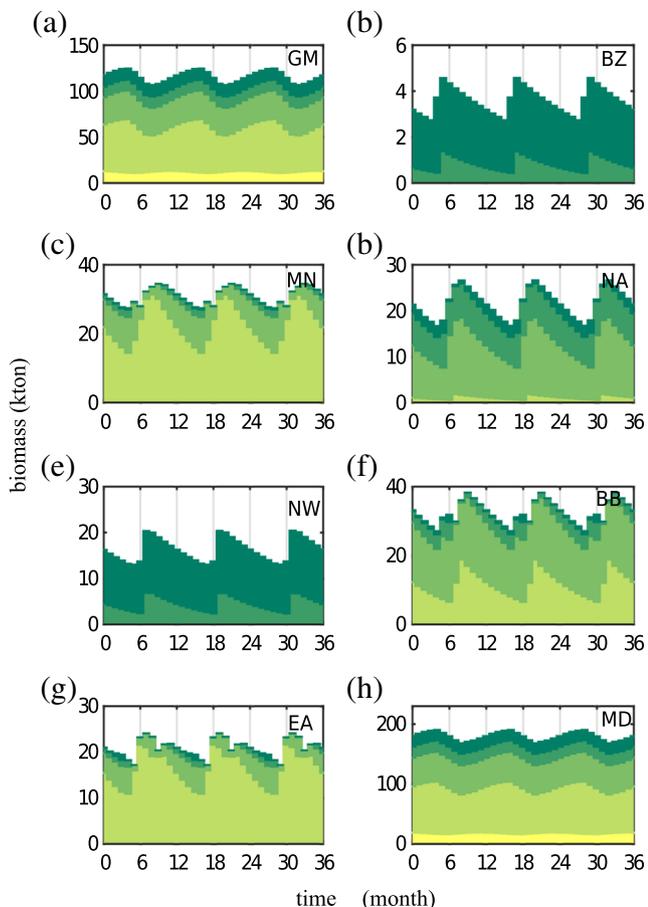


Fig. 5 Time series of the biomass per age in the eight habitats: **a** Gulf of Mexico, **b** Brazil, **c** Maine, **d** North Atlantic, **e** Norway, **f** Bay of Biscay, **g** Eastern Atlantic, and **h** Mediterranean, calculated with $\mu = 100$ and $s = 30$. Different colors (yellow to dark green) for the five different age classes (Young to Old)

Table 3 Seasonal migration phenology of bluefin tuna in the north Atlantic Ocean

Years	Region	Timing of presence in northern feeding areas	References	Notes
1999–2004	West Atlantic; Bay of Biscay	July–September	(Block et al. 2005)	Data storage tags (DSTs)
1981–2005	Bay of Biscay	Day 180–230 (approx.)	(Dufour et al. 2010)	Timing of immigration to region based on commercial CPUE data
2005–2009	NWAtlantic (Maryland to Cape Cod)	Summer months	(Galuardi and Lutcavage 2012)	DSTs applied to juveniles
1950s–1970s	Norwegian Sea	July–September	(Aloncle et al. 1972; Mather et al. 1995)	Based on commercial catch data.
2012	East Greenland (Denmark Strait)	August–September	(MacKenzie et al. 2014)	Based on bycatch in commercial mackerel fisheries
1996–2003	Contl. shelfbreak south of Iceland	August–October (few in November)	(Olafsdottir and Ingimundardottir 2003)	Based on commercial CPUE data
1923–1931	Dogger Bank, North Sea	Day 190–290 (approx.)	(Murray 1932; MacKenzie and Myers 2007)	Based on at sea observations of schools; similar patterns seen from 1912–1922.
1950s–1970s	North Sea	July–September	(Tiews 1978)	Based on commercial fisheries
	Southern Gulf of St. Lawrence, Canada	August–October	(Vanderlaan et al. 2014)	Based on commercial CPUE data
1996–2006	Whole west Atlantic from G. Mexico–Newfoundland,	Seasonal during year	(Walli et al. 2009)	DSTs

Discussions

Migration modeling

In this article, we introduce a game-theoretical approach to model habitat selection in migratory populations in environments consisting of a network of habitats. The model describes population-migration dynamics in age-structured populations and in temporally varying environments. The model is parametrized and applied to study the seasonal migration of the Atlantic bluefin tuna.

The results show how changes in the resource level, population demography, and cost of migration can alter population distribution across large distances. We further show that only some subset of the available links on the network are effectively selected as migratory pathways while many other routes are not utilized. This allows us to identify emerging fish migration routes and to compare these predictions with observed migration behavior.

The ability of the model to capture some of the features of tunas migration suggests that this widespread phenomenon might often emerge as a migration game that explicitly accounts for active habitat selection.

A fundamental assumption in the model is that migration is described as a sequential process by which, at each time step, individuals increase their fitness. This is because in the migration game, each individual in a given habitat can—in a single time step—move only to the neighboring habitats, i.e., those that are locally connected to the one where the individual is currently located. The migration occurs when there is an advantage to move, i.e., when the reward function is positive. Since this function is negatively density-dependent, its value is affected by the strategies of other individuals in the populations and it is also affected by the cost of assessing and commuting between different habitats. At each time step, individuals tend to reach a local IFD by trying to equalize the local reward functions. In some cases, this equilibrium cannot be reached in a single time

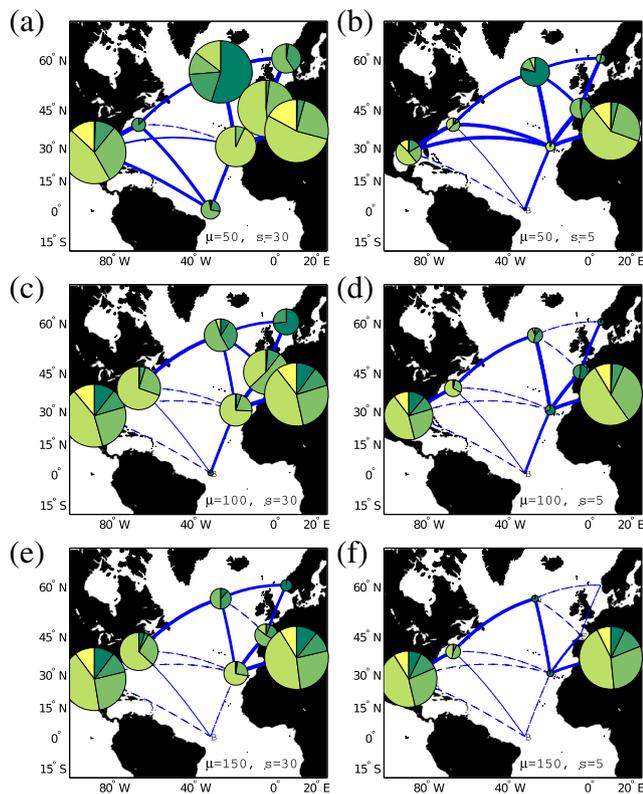


Fig. 6 Map of the network structure at different spawning intensity (s) and habitat selection cost μ . Simulations are run for 10 years under seasonal effects and the distribution in December is shown. Habitats are illustrated with *circles* proportional to the total tuna biomass and color representing different age classes (between *yellow* and *dark green* from Young to Old age, respectively). *Lines* connecting the habitats show integral biomass flux during the entire simulation and are thicker for larger fluxes, while *dashed lines* are used when no flow is predicted along the path. **a** $\mu = 50$ and $s = 30$ and a total global biomass $M = 496$ kton, **b** $\mu = 50$ and $s = 5$ and $M = 128$ kton, **c** $\mu = 100$ and $s = 30$ and $M = 424$ kton, **d** $\mu = 100$ and $s = 5$ and $M = 166$ kton, **e** $\mu = 150$ and $s = 30$ and $M = 374$ kton, **f** $\mu = 150$ and $s = 5$ and $M = 174$ kton

step, because there are not enough individuals living in a given habitat that can migrate towards connected habitats with a higher payoffs.

It is relevant to note that the IFD is the ESS of the habitat selection game (Křivan et al. 2008). However, the IFD describes the spatial population distribution without details about the migration process leading to such distribution. Several mechanisms that can lead to IFD have been described in Cressman and Křivan (2006). In the present study, we illustrate another possible mechanism assuming that individuals are myopic and the dynamics are discrete over time and constrained within a network of habitat. Depending on the local constraints and the set of individual strategies, individuals might or might not migrate and reach a local IFD in each time step of our model. This game on network is then called the migration game.

The assumption of describing habitat connectivity by discrete network structure is a generalization of migration models assuming movements between all pairs of habitats (a fully connected graph). The network approach easily captures the existence of geographical, bioenergetic, or life history constrains, which often break potential migration routes (Henningsson and Alerstam 2005; Alerstam et al. 2003; Alerstam 2001). The model is also flexible enough to allow the effects of ocean currents, temperature variability, or other environmental changes to be represented using different costs on each link. Indeed, the cost of migration between two habitats can affect the reward function and then can modify the migration equilibrium on the network; a mechanism which is in agreement with the hypotheses that changes in migration routes can be driven by climate change (Walther et al. 2002; Rijnsdorp et al. 2009; Doney et al. 2012).

Equalization of the local reward functions is consistent with the ideal free distribution theory (Fretwell and Lucas 1969). We show that at each time step, individuals in the population distribute according to a local IFD among connected habitats and, in case of stable environment with no demographic effects, the local equilibrium converges, in several steps, toward a global IFD on the network (Pan and Nagurney 1994; Cressman and Křivan 2006). The migration dynamic we use in the model describes when and how individuals update their strategies over time. This is known as revision protocol in game theory (Sandholm 2010) and is based on two assumptions: myopia and inertia. Myopia means that individuals assess their strategy based on local information on costs and payoff opportunities only. Inertia postulates that individuals do not update their strategy continuously but instead re-evaluate their decision sporadically, mainly because very often the environment in which they live provides a multiplicity of concerns to be solved rather than a single-minded focus on one strategy (Sandholm 2010). We think that the discrete form of time and space in our model describes naturally myopic and inertial processes which are likely to occur in fish populations. Moreover, compared to a continuous model, the discrete representation of the space with the network of habitats appears to be more consistent with the idea of migration corridors, habitat hot spots, and migration stopovers which are typically found in many species (Rose 1993; Hunter et al. 2003). However, it is worth noting that, in some species, behaviors such as migration and dispersal can be genetically predetermined and act independently from local environmental conditions (Dingle and Drake 2007; Dingle 2014). These “innate evolutionary responses” (Howard 1960) might be the main drivers for long distance migrations and overcome the competition response assumed in our study. Identifying the balance between the role of innate, social, and learning behaviors in natural migratory species is a challenging task

which could be a key area for future empirical study (e.g., Scott et al. 2014).

Environmental and demographic effects

Seasonality in the resource distribution and competition for resources are both important mechanisms for the selection on migration traits. Indeed, in weak seasonal environments, residency is the behavioral strategy that is selected (Shaw and Couzin 2013). Our results support those findings and show that in case of a stable environment, the distribution of the populations between heterogeneous habitat converges to the IFD. At the IFD, there is no net dispersal between habitats unless demographic effects are present. Indeed, changes in population structure can elicit changes in the reward functions that result in migration. The coupling between demographic and environmental effects are critical for the results. Generally, if dispersal dynamics are much faster than are changes in habitat payoffs, the global IFD at the current environmental conditions is likely to be reached. When migration and environmental variability operate on similar or slower time scales, the animal spatial distribution may never reach the IFD at the current environmental state. For this to happen, additional assumptions on dispersal are needed to hold (Mobæk et al. 2009; McLoughlin et al. 2010). In our model, we assume that the population can reach a local IFD condition, which translates into assuming a fast behavioral response to explore neighbor habitats. The time step used to integrate the discrete model sets the time scales for behavioral response and environmental variability. An alternative approach would be to describe demographic and environmental dynamics as continuous processes both affecting the migratory behavior with feedback on the population dynamics. In such cases, however, we would have a revision protocol lacking the inertia of the decision process which we think is common in most natural populations and could be verified experimentally by, for example, examining existing data on tagged fish.

The presented model does not explicitly account for the feedbacks between migration dynamics and fecundity of the individuals. Indeed, in habitats with higher payoff, one could expect individuals to grow faster than those in lower payoff habitat. Whereas we assume fixed demography that does not depend on habitat occupancy. A more general model would require accounting for the lifetime integral fitness of the migrating individuals and would also make use of inclusive fitness (Hamilton 1964) when migration spans several generations, e.g., monarch butterfly (Chapman et al. 2015). In the simple case here, fitness is modeled as a reward function proportional to carrying capacity while only the individuals present in the spawning habitats have positive fecundity values in the Leslie matrix. A finer spatial habitat subdivision and an improved description of the

fitness measure might still be able to capture some of these complications described above, when the assumption of time scale separation between demography and behavior holds.

Relevance to the ecology of the Atlantic bluefin tuna

As we have seen before, Atlantic bluefin tunas have a wide distribution in the Atlantic Ocean from tropical to sub-polar areas. Migration has likely evolved to allow migrants to benefit from the seasonal highly productive environment at higher latitude while reproducing in different regions. Being excellent swimmers, bluefin tuna can potentially be present in all parts of the Atlantic. Nonetheless, evidence suggests that the species distributes within several hotspot areas, where tunas are present all year round, while their abundance outside those areas is minimal. Moreover, the same individual can visit these hotspots several times during the feeding period before going back to spawning areas for reproduction. Those patterns in distribution and migration behavior are in part captured by the habitat network approach used in our model, with a series of hotspot areas connected by a range of migratory pathways. Moreover, the model appears to describe reasonably well the peaks in distribution in the different areas. For example, in the spawning areas, the maximum abundance is achieved mainly at the beginning of summer and precedes the peaks in abundances in the feeding areas. Habitats such as Norway or Brazil are visited only by the larger individuals (200–500 kg) and are very sensitive to changes in fishing pressure or cost of migrations (Fromentin 2009; Safina and Klinger 2008).

Thus, our modeling approach allows to represent, in a quite realistic way, spatial population dynamics of the Atlantic bluefin tuna including the disappearance of some feeding habitats and changes in migration routes.

The modeled estimate of the timing of appearance at summer feeding areas is similar to the tuna migration phenology observed in nature (Table 3). In addition, the size composition of the modeled populations arriving in several of these areas compares favorably with the size composition of bluefin tuna observed and/or caught in such regions.

For example, modeled size distributions for Brazil and Norway are centered at large (≈ 200 cm) sizes. Catch data from these areas (Mather et al. 1995) show that most bluefin captured in fisheries in these areas were generally >150–200 cm, thus similar to model predictions.

Our modeling approach is potentially a useful framework for investigating how exploitation and environmental variability including climate change could affect the large-scale migratory behavior and spatial distribution of bluefin tuna. For example, environmentally driven changes in regional productivity and environmental carrying capacity would affect habitat suitability, migration costs (e.g., due to

temperature changes), and migratory rewards. These changes can lead to reduced use of some habitats and stronger preferences for other habitats, thereby potentially influencing fishery opportunities and costs for different nations. Such changes may already be underway because migration phenology for the Bay of Biscay is linked to large-scale climate conditions (e.g., the North Atlantic Oscillation, NAO) that affect sea temperatures (Dufour et al. 2010) and bluefin tuna have recently been observed in east Greenland where they have not previously been observed (MacKenzie et al. 2014). Moreover, our modeling framework, if coupled to integrated oceanographic biogeochemical models (Dragon et al. 2015), can also potentially derive new insights on the relative roles of oceanographic variability and exploitation leading to past major changes in bluefin tuna distributions and fisheries such as those off Brazil, Norwegian-North Sea, and south of Iceland.

Recent advances in group behavior and information sharing and transfer between individuals of the same group also show how habitat choice can be influenced by the knowledge content or migratory experience of the individuals, and how group behavior (e.g., migration to particular habitats) can be driven by a subset of informed individuals (De Luca et al. 2014). A future challenge for migratory behaviour modeling is therefore to develop ways to integrate individual-level and group dynamics in migration game modeling frameworks such as that developed here. Given that bluefin tuna is such a highly migratory species, and migrates across ocean zoning boundaries of several jurisdictions, and also across stock management boundaries, migration models that quantify rates and timing of exchanges among areas could potentially have practical application in fishery management and conservation. The migratory behavior of this species is complex. Our modeling approach, although moderately complex, is based on some simplified considerations of population dynamics, regionally dependent ecosystem carrying capacities and bioenergetics of energy intake and utilization, and is a step towards process-oriented migration and distribution models. Further advances in process knowledge and implementation are needed, and if implemented, could support management and conservation decision-making for this species.

Although our model has been configured primarily to represent the large-scale movement dynamics and spatial distribution of bluefin tuna, the migration game, as defined here, can be potentially applied to a wide range of highly migratory species, including other fish species, marine mammals, and reptiles (e.g., turtles). The persistent migratory cycle of the Pacific white sharks (*Carcharodon carcharias*) among a network of coastal hotspots and the open Pacific (Jorgensen et al. 2009) suggests that the seasonal movements of the species might be the result of individual optimization dynamics. The migration game could also be

used to disentangle the relation between migration routes and wintering strategies in Arctic shorebirds that routinely perform long distance (>10,000 km) migrations between the Arctic regions and southern warmer habitats (Henningsson and Alerstam 2005). Although migratory routes in marine turtles appear to have been shaped by passive dispersion during the hatchling phase (Hays et al. 2010), the effects of changing conditions in ocean currents (Hays et al. 2014) and food availability (Hawkes et al. 2009) could be investigated using a theoretical framework similar to what we describe here. Likewise, migrations of seals, whales, and other marine apex predators (Block et al. 2011) might be possibly described by similar migratory dynamics.

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Appendix: Model calibration for Atlantic bluefin tuna

Migration costs

The time needed to migrate between two habitats regulates the cost of migration in fish population since the energy consumed will be higher the longer is the migration time. The

Table 4 Scaling of physiological rates with size and parameter values for tuna from (1) (Overholtz 2006), (2) (Ware 1978), (3) (Dewar and Graham 1994), and (4) (Block and Stevens 2001)

Parameter	Symbol	Value	Ref.
Max. Energy intake	$I(w)$	cw^ϕ	–
Standard metabolic rate	$M(w)$	$\alpha_1 w^\gamma$	–
Swimming power	$P(w)$	$\alpha_0 w^\eta U^\beta$	–
Constant for energy intake	c	$1 \cdot 10^{-2}$	[1]
Exponent for energy intake	ϕ	0.8	[1]
Constant for power cost	α_0	$1.8 \cdot 10^{-8}$	[2]
Exponent for power cost	η	0.47	[2]
Exponent for power cost	β	$1.4 < \beta < 2.8$ ($\beta = 2$)	[3]
Constant for metabolic cost	α_1	$3.76 \cdot 10^{-4}$	[4]
Exponent for metabolic cost	γ	0.6	[4]

power rate consumed while swimming at an optimal speed (P) is:

$$P = \alpha_0 w^\eta U^\beta \tag{9}$$

where w is the mass of the fish, while the estimates for allometric constants α_0 and η assume fish swimming in a turbulent regime (i.e., high Reynolds number) (Ware 1978, Table 4).

We can assume that during migration fish swim at the optimal speed (U^*) at which the total energy expenditure per unit distance is minimized. Using an allometric function for the metabolic costs $M = \alpha_1 w^\gamma$, a general form of U^* can be derived by an optimisation procedure relating the swimming cost to the total cost of moving (metabolic cost plus power output):

$$U^* = \left[\frac{-\alpha_1 w^\gamma}{\alpha_0 w^\eta (1 - \beta)} \right]^{\frac{1}{\beta}} \tag{10}$$

where α_1 and γ are allometric constants for fish metabolism (Table 4). This results in an allometric scaling for the optimal swimming speed as:

$$U^* \approx w^{\frac{\gamma-\eta}{\beta}} \tag{11}$$

In tuna, the exponent β has been found to range between $1.4 < \beta < 2.8$ (Dewar and Graham 1994) and we assume $\beta = 2.1$, which provides swimming speeds in the range reported for several tuna species (1.2 – 2.4 body length per second) (Block and Stevens 2001). Thus we obtain a scaling $U^* \approx w^{0.06}$.

Demography

Uncertainties exist on the definition of demographic parameters for the bluefin tuna population (Simon et al. 2012). In our model, the young-of-the-year stage (0–1 years) excludes the egg phase and does not have reproductive potential while at juvenile stage (1–5 years), a small fraction is mature

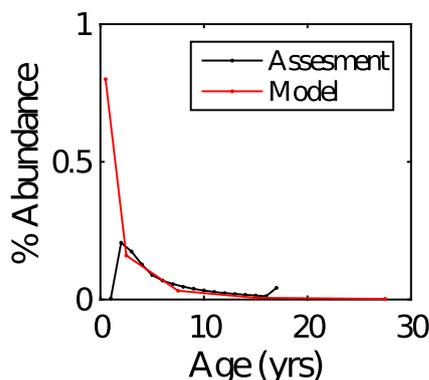


Fig. 7 Age structure data from the ICCAT assessment group (black) on bluefin tuna and from the model using the Leslie matrix estimates (red)

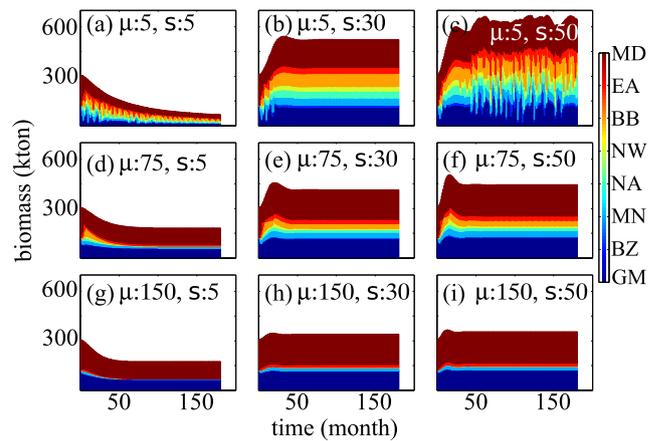


Fig. 8 Sensitivity of the population structure and total biomass in different habitats under different spawning intensity s and habitat selection cost μ in aseasonal environments

for reproduction. The reproductive maturity increases up to 50 % at the adult stage (5–10 years) while mature (10–20) and old (20–35) stages are fully reproductive but the latter has a lower survival rate. Those rates are consistent with observed maturity at age data for western and eastern Atlantic bluefin tuna (SCRS 2012) and are used to define the values of r_k . Moreover, the value survival (q) and growth (g) values used in the Leslie matrix are consistent with reported values for the yearly mortality rates (SCRS 2012) and provide a realistic bluefin tuna age-structure (Fig. 7) with a maximum population growth rate (0.15) that is in the range of previous estimates (Simon et al. 2012). Finally, we constrain the global bluefin tuna population using a given total carrying capacity K_T and assume a density dependent function on the spawning factor s .

Extended sensitivity analyses

At low spawning intensity and high migration costs (Fig. 8g), only the spawning areas are occupied. Decreasing habitat selection costs allows tuna to migrate in adjacent feeding areas (G and C) but reduce the total biomass and increase fluctuations in the migration behaviour (Fig. 8a, d). On the other hand, at high spawning and low migration costs (Fig. 8a, b), the biomass reaches the total carrying capacity over few months, and all habitats are occupied although at different levels of biomass.

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