Overview, Design Concepts and Details for:
An Individual-Based Model of Basking Sharks in Ireland

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1. Purpose and Patterns

This research will develop the first individual-based model (IBM) of basking sharks (*Cetorhinus maximus*). Basking sharks are currently endangered worldwide, and in 2022 Ireland, a hotspot of basking shark activity, protected basking sharks under the Wildlife Act of 1976. The country is now looking to expand their MPA network and develop stronger marine conservation efforts.

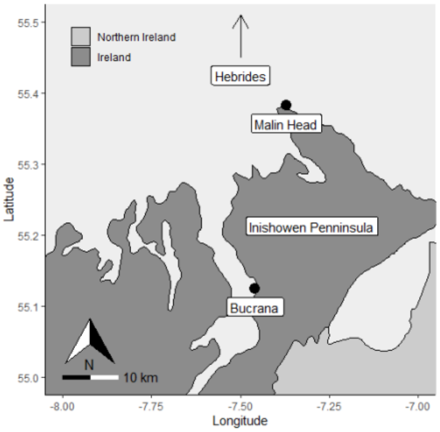

Figure 1: Map of the modeled area. Map created by Alexis Garretson at Tufts University.

Basking Sharks gather in aggregations, ranging from a small (2+) to a large number (100+) of individuals. They do so unpredictably (i.e. in one location, at the same time of year, on any given year, there can be a single shark, five sharks, or 100 sharks). When in groups, sharks are known to interact (echelon swimming, parallel swimming, nose to tail swimming), indicating that aggregations may be intentional and serve a social or even reproductive function. This model seeks to understand the environmental and/or social drivers of this shoaling behavior.

The coast of the Inishowen Peninsula (Figure 1), located in Country Donegal, Ireland, and part of the Malin-Hebrides shelf, will be used as a localized case study for this research, as basking sharks visit this area most years and are known to aggregate there. This IBM will be used to assess whether this aggregating behavior is solely based on food availability, a social function, or both.

By understanding environmental and social drivers of these aggregations, we can understand their conservation importance. This may inform geographic or temporal protective measures (i.e. ideal areas for MPAs, seasonal boat speed limits) by identifying times of year or environmental conditions when aggregations are most likely.

Purpose

This model seeks to reproduce basking shark aggregation behavior in the Inishowen Peninsula and to test what environmental and/or behavioral drivers lead to basking shark aggregations.

It is important to understand why sharks come to an area, especially in large aggregations which can increase the risk of human-wildlife conflicts, such as ship strikes or harassment (Speedie, Johnson, and Witt 2009). It is also documented that zooplankton, the main food source for basking sharks, are gradually shifting North due to climate change (Cotton et al. 2005), potentially altering the preyscape for sharks. Therefore, policymakers may need to shift the conservation strategies in response to changes in environmental conditions. If these aggregations are prey-driven, this could mean that the aggregations themselves could shift (geographically and/or temporally) in future decades. If they serve a reproductive purpose, protecting areas where these during peak aggregation times could potentially increase reproductive success. If these aggregations are a combination of social or prey-driven, then climate change could create a future timing mismatch between food availability and reproductive needs.

To understand the drivers of aggregations, the model reproduces a 10,545 km^2 area around the Inishowen Peninsula of Ireland (Figure 1), divided into 1 km x 1 km patches of only the top 10 meters of the water column. The model contains a maximum of 200 sharks (sharks migrate in/out of the model so the number at any time is variable between 0-200 sharks).

Research Questions

1. What environmental factors lead to basking shark aggregations*?
2. What social conditions lead to basking shark aggregations?

*An aggregation is defined as two or more sharks. Singular sharks are also separately documented.

Patterns

Shark Aggregations

Research and sightings data has shown that sharks return to the same area on a semi-regular basis and exhibit site fidelity (Berrow and Heardman 1994; Crowe et al. 2018; Doherty 2017; Skomal et al. 2009). Generally, basking sharks are sighted in Ireland between April and October (though some outliers exist). Individuals have been documented returning to a site after 1+ years and sharks have also been verified to travel across the Malin-Hebrides shelf, between Inishowen and Hebrides Scotland (Johnston et al. 2019; Sims and Reid 2002). Shark aggregations are unpredictable, though well documented (Sims et al. 2022). According to sightings data collated by the Irish Basking Shark Group (IBSG) and Irish Whale and Dolphin Group (IWDG), groups of 4-60 individuals have been sighted around the Inishowen Peninsula, while aggregations of up to 150 have been sighted in other areas of Ireland. Sea surface temperature (SST) and Zooplankton have both been correlated with basking shark abundance, but not consistently. Research indicates that SST is better for understanding large scale movements and trends, while zooplankton are better for small scale trends (Braun, Skomal, and Thorrold 2018; Miller et al. 2015; Sims et al. 2000; Sims and Quayle 1998).

While publicly reported sightings have limitations, the IBSG/IWDG sightings data set is the widest and longest running data set available on basking shark movements in Ireland.

Zooplankton Patchiness

Zooplankton exhibit localized patchiness, which has been documented to impact basking shark movements and behavior, as basking sharks are more likely to be found in areas with higher *Calanus* species (Sims and Merrett 1997). Zooplankton in the North Atlantic exhibit a boom and bust cycle (Bonnet et al. 2005; Conover 1988; Häfker et al. 2018).

The majority of zooplankton research uses biomass and looks at large scale populations. There is no real-world long-term study on localized, zooplankton patchiness/distribution in the north Atlantic. Therefore, this model will reproduce localized patchiness by randomly distributing different amounts of zooplankton throughout the model area, based on the percentage of patches that will have zooplankton (set by the user) and the estimated average amount of zooplankton for that day. Daily average zooplankton is based on data supplied by the Continuous Plankton Recorder (CPR).

2. Entities, State Variables, and Scales

Entities

Spatial Units

Model area represents 56n, 55n, & -8w, -6.5w, an area of 10,545 km^2, with patches of 1 km x 1km x 10 m(depth). This area was chosen as it is largely understudied compared to basing sharks research in the south. The Hebrides, directly across from the Inishowen Peninsula, have recently been declared an MPA, due in large part because basking sharks exhibit aggregation behavior there. Therefore, this area is in key need of more conservation-focused research. As this is the first model of its kind, only a small area was selected.

The Inishowen Peninsula was chosen as it's a known tourist attraction, as well as a local hiking spot, and has been highlighted in international media as a hotspot for basking sharks. There is also a large fishing community in the area. Long-term local partnerships between the IBSG (formeraly the Inishowen Basking Shark Study Group) and community leaders and organizations have ensured a high rate of reports in the area.

1 km x 1 km patches were selected to keep patch sizes small, but manageable, and to account for shark movements within 24 hours. The 10m depth was chosen as that's the maximum depth of the Continuous Plankton Recorder, and the sightings reports are of surfacing sharks.

- State variables
    - The amount of zooplankton per patch
    - Land/water

Agents

Individual basking sharks are the agents. Each shark represents a single shark.

- State variables:
    - Hidden/not hidden (represents migration into/out of the model area)
    - Number of days without eating
    - Number of days spent outside the model area

Time

Each time step in the model is 24-hours. Aggregations can last up several hours, or even days, and sharks can come/leave (Sims et al. 2022). The research question is not interested in duration of the aggregation, nor in the length of time individual sharks spend in the aggregation. Instead, it is simply interested in whether or not an aggregation occurred on a single day and the size of the aggregation.

The model depicts April 1 through October 31, from 1982 to 2018. This is because the majority of sightings reports in the IBSG/IWDG data set corresponds to this time. While some basking sharks may remain in Ireland during the winter, the ones that do likely to remain well below 10m depth (Doherty 2017), and therefore are unlikely to be accounted for in publicly reported sightings. The model ends on October 26, 2018, because that was the last October sampling day for CPR in 2018.

- State variables:
    - Month
    - Day
    - Year

Zooplankton

Data from the Continuous Plankton Recorder (CPR) for 50-60 N and ~ 3-12W was used. This data is slightly lager than the model area but was included in order to maximize the amount of input data that could be used. The CPR data included species, date, time, and abundance. *Calanus finmarchicus* and *Calanus helgolandicus* were totaled together (labeled "Cal" in the model). *Pseudo Calanus* and *Centropages typicus* were totaled together (labeled "Otherzp" in the model). Daily abundance was combined for these two groups of species. The input data of zooplankton differentiates *Calanus* copepods from other species of zooplankton, as basking sharks are documented to prefer *Calanus* copepods, but are also documented to each other larger zooplankton species (Sims 2008).

The daily abundance of zooplankton was multiplied by 50, per CPR methods (Richardson et al. 2006) with true zeros recognized. However, due to a lack of data points for many days required in the model, a linear interpolation was performed, to estimate zooplankton amounts between CPR sampling dates.

State Variables

Zooplankton

The percentage of patches which contain zooplankton (*Calanus* species, and the other species) is set by the user. Every time the model updates (every 24 hours), the abundance of zooplankton is taken from a csv file containing the CPR data that has been linear interpolated. The abundance is divided by 3 (CPR samples 3m^3 of water per sample), then divide by the percentage of patches that should have zooplankton (set by the user). The results of this equation are then distributed throughout the model by multiplying that previous result by the standard deviation, so the patches have a range of zooplankton values. Zooplankton are counted in individuals (population size) not biomass.

Two zooplankton variables are set by the user (Table 2):

1. Cal_%: The percentage of patches that contain *Calanus finmarchicus* and *Calanus helgolandicus*
    a. Slider variable
2. Otherzp_%: The percentage of patches that contain *Pseudo Calanus* and *Centropages typicus*
    a. Slider variable

Sharks

Shark behavior is determined by the submodel (Table 1 and Figure 2).

Sharks are either hidden or not hidden. Hidden indicates that they have left the model area, and do not execute any behavior functions.

Sharks maintain a list of previous patches with high zooplankton (this is utilized in submodel Food and submodel Food/Social).

Multiple shark variables are set by the user (Table 2). These include:

1. Sense-distance: how far a shark can “see”.
    a. Sense-distance is doubled when sharks are sensing other sharks.
    b. Slider variable
2. Swim-speed: how far sharks swim in a 24 hour period.
    a. The speed is set to (swim-speed + 1) when sharks are not eating.
    b. Slider variable
3. Thresohold_zp: The amount of zooplankton required to make a patch worth visiting and is used to determine if a shark should leave a patch.
    a. Sharks assess if the amount of zooplankton in a patch meets the threshold level of zooplankton *when divided by the total amount of sharks in the patch*.
        i. Sharks will not move to or remain in a patch if the amount of zooplankton cannot support all the sharks in the patch
    b. A rough estimate of individual zooplankton weight was used to calculate the threshold population size (CPR data counts individuals, not weight).
        i. It is estimated that basking sharks can eat ~3,000 grams zooplankton / 24 hours.
        ii. A rough estimate converts 3,000 grams of zooplankton to approximately 1.5E+11 individual copepods.
4. No_eat_min: the number of days it takes for a shark to not eat (be in a patch below threshold_zp) before they leave.
    a. Slider variable
    b. This does not account for number of sharks in a patch.

    c. This number resets once a shark visits a patch that contains zooplankton above the threshold_zp level.
5. Return-season: The number of days it takes a shark to return after leaving for the season.
    a. Leaving determined by no_eat_min
    b. Slider variable
6. Friend_min: The number of sharks required to attract a shark to an area.
    a. Slider variable

Ideal Range of Variables:

Still to be determined. Preliminary sensitivity testing indicates that the following variables produce the most realistic model outputs. See Table 3 for the ideal settings as determined by preliminary testing.

3. Process overview and scheduling

1. At each time step, the model imports the zooplankton data and date (month, year, day).

2. If it is the start of the season (April 1), sharks are assigned a random number of days (between 0 and 60) to wait before entering the model (‘migrate”). When they first enter the model, they are distributed in the north, east, and west edges of the model, to mimic “swimming” into the area.

3. Zooplankton data from the CSV file is distributed throughout the percentage of patches set by the user.

4. Sharks assess whether they need to leave where they currently reside (Figure 2). They will only do so if the total amount of zooplankton in their 1 km x 1 km patch cannot support the number of sharks in the same patch (calculated by dividing total zooplankton by (number of sharks * threshold_zp)).

    a. If sharks do not need to move, they remain put.

5. If they need to move, sharks will select patches in their sense-distance to move to. Their choice of patch is determined by each submodel (Table 1 and Figure 2).
    a. In the Food submodel, sharks will select a new patch to move to that contains zooplankton (both cal and otherzp) that exceeds the threshold_zp level. If such a patch cannot be identify, the shark will choose the closest match from its memory of high zooplankton patches.
    b. In the Social submodel, sharks will select a new patch to move to that contains a number of sharks that exceeds the friend_min level.
    c. In the submodel Food/Social, sharks will first select a patch that contains zooplankton that exceeds that amount set by threshold_zp. If it cannot find such a patch, it will look for a patch that contains more sharks than the friend_min level. If a shark cannot, it will then select a high zooplankton patch from memory.
    d. If sharks can’t find any patches that fulfill the requirements to move to a patch (set by submodels), they will select a random patch in their sense-distance to move to.

6. For all movements, sharks assess whether or not land is an obstacle, and will keep searching for a patch until they find one they can reach without crossing land (see: *method of avoiding land*).

7. After moving, sharks then determined if they are in a patch with enough food or not (track-no-eat). If they are in a patch without sufficient food, they count +1 for days they have not eaten.
    a. If they are in a patch with food, they reset the no-eat count to 0.

8. If a shark has not eaten for the minimum number of days (set by the user), it leaves the model (sets itself to hidden). Sharks count each day that they are hidden. Sharks will migrate back into the model area after a period of time set by the user (return-season). They will enter the model from north, east, west, the location is randomly chosen.

9. The sharks assess whether the patch they are in contains zooplankton above the (threshold_zp multiplied by three). If it does, the patch is added to the list of of high zooplankton patches.

10. The model tracks if any sharks have crossed over land (for visual debugging).

11. The model samples 10 random patches for zooplankton (this is averaged).

12. Total number of sharks and number of single sharks is recorded.

13. Any aggregations of sharks are recorded. Aggregation size, latitude and longitude, and the zooplankton amount of each patch with an aggregation is recorded.

14. 10 random patches are sampled for sharks and recorded if and how many sharks are in the patch. Latitude and longitude, and the zooplankton amount of each area is also recorded.

15. If the patch they are currently in contains sufficient zooplankton, sharks record the location of the patch.

16. If the year is 2018 and the date is October 26, the model stops. Three sample files are exported.

Method of Avoiding Land

(1) Sharks select patches that meets their submodel requirements (Table 1 and Figure 2)
(2) Sharks sort the list of qualifying patches by descending amount of patch_cal, number of sharks, or memory of a patch with high zooplankton (determined by submodel).
(3) Sharks then select the first patch on the list.
    (a) Sharks Assess if there is any land between them and the target patch.
    (b) If there is land between shark and patch, sharks select next patch on the list.

    (c) Sharks repeat this process until there is no land between them and a target patch.

(4) If there is no land between sharks and the target patch, sharks determine if the target patch is more or less than the number of patches equivalent to the [swim_speed] away.

(5) If the patch is more than number of patches equivalent to the [swim_speed] away, sharks move towards it; if less than that, move directly onto the patch

(6) If there are no patches that meet the requirements set by the submodel, or if there are no patches that can be reached without land, the sharks move at random

    (a) Random-move follows the same list/avoid land method, but only selects random patches of water and does not sort based on any criteria.

4. Design Concepts

Basic Principles

Classical mathematical models and ecosystem modeling (e.g. EcoPath with Ecoism) do not generally allow for adaptive behavior or environmental stochasticity (Christensen and Walters 2004; Coll et al. 2015; Natugonza et al. 2020). Therefore, some researchers have argued that individual-based models (IBMs) are better suited to highly mobile marine species (Codling 2008). IBMs can allow for more complex intra- and inter-specific relations, as well as environmental stochasticity.

Basking sharks have not been extensively modeled. In one example, though, Ensemble Ecological Niche Modeling (EEM) has been applied to basking sharks (Doherty 2017). While the model was effective at predicting the suitability of foraging locations, this didn’t always correspond with shark sightings or with tagged data. Doherty noted that tagged basking sharks displayed a “dispersive nature” (pg. 126) and did not appear to make consistent, group migrations, especially with regard to areas where sharks winter and are assumed to be largely solitary (Sims 2008). Doherty suggested that the model be refined to include a “exploration-refinement” hypothesis (2017). Exploration-refinement is a framework to understand the behavior of long-lived migratory species (Guilford et al. 2011), especially those that mature late in life, assuming younger individuals will feel less impulse to return to breeding sites (Fayet 2020). It is assumed that these individuals explore different migratory routes before settling on a preferred one. Such a framework would require individualized agents and environmental stochasticity to accurately reflect basking shark behavior. While Doherty (2017) suggests the use of it, no mechanism for the inclusion of this hypothesis is suggested. Individual-based models (IBMs) are a potential method of testing this.

Emergence

- Aggregations (number, size, location)

Adaptation

- Avoiding obstacles (land)
  - Choosing a new patch to move to if land is in the way
- Selecting patches within a defined area that meets specific criteria
  - Criteria defined by submodel
  - Defined area = sense-distance radius
- Keeping a list of patches that had a high amount of zooplankton
- Leaving if they haven't eaten enough

Objectives

- Size and frequency of aggregations
  - This is driven by sharks seeking food or other sharks

Learning

- Memory, but only in Food and Food/Social
  - Otherwise, they're responding to environmental cues
- Number of days they haven't eaten
  - Migrate out when that minimum has been set and migrate back in when needed

Prediction

- Model does not currently predict anything

    - Implies correlation between zooplankton and aggregation size/frequency that can potentially be predictive

Sensing

- “Sense” distance
    - Likely using smell to find zooplankton but smell in water is highly dependent on a variety of factors (Sims 2008; Sims et al. 2022). This can include the source of the smell, currents, and density of particles in the water. This is why it is a slider variable.
- Memory retention
    - List of patches that 3x the amount of zooplankton compared to the threshold_zp set by the user
- Swim Speed:
    - Based on swim speeds from Sims 2000 who calculated the swimming speed of both feeding and non-feeding basking sharks to be an average of $0.85ms^{-1}$ and $1.08ms^{-1}$ respectively, it is estimated that a feeding shark can travel 73 km in one day. The model assumes that the distance traveled is *not* a straight line. Research from Sims and Quayle 1998 found that sharks traveled 1-2 km per hour, which would be 24-48 km/h. (Skomal et al. 2009) tracked sharks for (avg) 203 days, with an average straight line distance of 1904 km = 9.3 km/day. This is why swim speed is a silder variable.

Interaction

- Mediated interaction between sharks
    - In the Social submodel, the number of sharks in a patch determines which patch a shark will move to (more sharks increases likelihood a shark will choose that patch)

Stochasticity

- The percentage of patches that have zooplankton (set by the user)
- Fine scale location of zooplankton
    - Patches are randomly chosen to have zooplankton each day

    - The amount of zooplankton is randomly assigned, based on the CPR average and the standard deviation of the CPR data.

Collectives

- Shark aggregations [emergent property]
    - Sharks may select patches that have aggregations of sharks already in the Social and Food/Social submodels

Observation

- Hiker list (Psuedo Sighting Reports)
    - Every day, 10 patches are randomly selected and sampled. The number of sharks in each sampled patch is recorded. This is to mimic reports from boaters and hikers. Data is only recorded if sharks were seen. Date and zooplankton amounts are recorded.
    - Sampled daily.
- Shark list (Total Aggregations)
    - Any time that a shark shares a patch with another shark, the model records the number of sharks in that patch along with the zooplankton amount, lat/long and date.
    - The number of patches with single sharks are recorded separately.
    - Sampled daily.
- Zp sample (Psuedo CPR Sampling)
    - The average of ten patches are sampled and the average Cal and Otherzp are calculated.
    - Sampled daily.

5. Initialization

Set-up loads the General Bathymetric Chart of the Oceans (GEBCO) map, which includes depth. It opens up the CPR data and begins pulling from the respective day. It also loads up the latitude and logitude only at setup. *Set-up* starts all three observational lists, which are updated each time step. It sets up 200 sharks to migrate in.

Go sets the sharks migrating in. Sharks randomly migrate from east, west, and north in the model. The sharks do not migrate in at once but migrate in at a randomly determined rate. This process is repeated every April (the start of the model season).

On *Go* the sharks are randomly distributed on the west east and north sides of the model. This is to mimic migration from the south and from Hebrides, Scotland. The model sets the date zooplankton are loaded as environmental variables in each patch.

Initialization is the same for every submodel.

GEBCO:
- Contains depth data
- Upload once at start

Lat/lon
- Manually calculated in excel
- Upload once at start

6. Input Data

Zooplankton
- Daily CPR average
- Updates every day
- Chosen for species specific abundance (not biomass)
- Long-term study sample
- In individual zooplankton (abundance)

GEBCO map
- Uploaded once.

User settings:

See Table 2.

7. Submodels

The model consists of five submodels, including a Random control. The difference between each submodel is the behavior and decision making of the sharks within the model. All zooplankton and patch characteristics remain consistent in each submodel. All non-random submodels operate the same, with the exception of how sharks choose a new patch to move to. In the random submodel, sharks do not decide to leave a patch based on food availability, but instead move at every time step.

Food Submodel

In the Food submodel the sharks only seek areas that contain zooplankton that exceed the threshold zooplankton (Threshold_zp, set by the user).

In the food submodel, sharks retain a list of high zooplankton patches. If they cannot find a patch with sufficient zooplankton, they will select the closest patch from their memory list. They choose the patch with the least distance. If this patch faces land, they choose the patch with the second least distance, etc. If no patch can be found, the shark swims at random.

Social Submodel

In the Social Model (submodel Social), sharks are still urged to move from a patch if there is not sufficient zooplankton. However, they only select a patch based on the number of sharks in the patch (this must be greater than or equal to the friend_min set by the user). It is assumed that sharks can "sense" other sharks from a further distance than zooplankton, due to the significantly larger size of basking sharks and because of the sharks' slime coat (Lieber et al. 2020), which likely contains sensory information. It is also hypothesized that sharks may be attracted to aggregations via pheromones from other sharks (Sims et al. 2022). Therefore, when seeking other sharks, the sense-distance is set to double. Sharks sort potential patches by number of sharks (highest first) and assess if land is an obstacle. If it is, they choose the second highest number of sharks, etc. If no patch can be found, the shark swims at random.

Food/social Submodel

The Food/social Model (submodel Food/Social) is a combination of the Food Model (submodel Food) and the Social Model.

In this submodel, sharks first search for a patch with zooplankton. They sort patches by the highest amount of *Calanus* (“cal” in the model). If they cannot find one that contains zooplankton above the threshold zooplankton level set by the user, they then search for a patch with other sharks that meet the friend_min (the assumption being either that other sharks indicate food, or perhaps that they desire to mate). They sort those patches by amount of sharks. If the sharks cannot find a patch with a sufficient amount of other sharks (in sense-distance x 2), they then search for a patch from memory. If no patch can be found, the shark swims at random.

Random Submodel

Sharks select a random patch to move to. They will assess if land is an obstacle and re-select patches until it is not. Shark will still complete migration in and out of the model area, based on food availability and the time set in no-eat-min and leave-season.

8. Tables & Figures:

Submodel	Seek Zooplankton	Seek Other Sharks
Random	No	No
Food	Yes	No
Social	No	Yes
Food/social	Yes	Yes

Table 1: Key differences between submodels.

Parameter	Explanation	Setting
threshold_zp	Minimum amount of zooplankton (cal and other_zp combined) required for a shark to feed for ~15 hours	0-1000000000000
No_eat_min	Number of days a shark must encounter a patch that is less than the threshold_zp before leaving the model	0-100
sense-distance	How "far" a shark can see (in km)	0-100
Swim-Speed	The distance a shark can swim (in km)	0-100
return-season	How many days it will take a shark to return after they have left in response to reaching the no_eat_min	0-100
Cal_%	Percentage of patches with Calanus copepods	0-100
other_zp_%	Percentage of patches with other large zooplankton	0-100
friend_min	Number of other sharks a patch must have to attract a shark (only used in the "Social" version)	0-100

Table 2: User input into model

Cal	Otherzp	Threshold ZP	Sense Distance	Swim Speed	Friend Min	No Eat	Return
10	10	1.00E+11	20	9	5	14	20

Table 3: Ideal settings, determined by preliminary testing.

Shark Decision Pathway

If total zooplankton in patch is less than the threshold_zp when divided by the number of sharks in the patch	If Yes	→	Food	→	Seek patch with zooplakton above the threshold	→	If no patches with zooplankton > threshold_zp, Seek patch from memory of high ZP patches, choose closest patch	→	if no patches in memory, Random Swim		
	If Yes	→	Social	→	Seek patches with other sharks >= friend_min	→	If no patches with sharks >= friend_min, random swim	→	Random Swim		
	If Yes	→	Food/Social	→	Seek patch with zooplakton above the threshold	→	If no patches with zooplankton > threshold_zp, Seek patches with other sharks >= friend_min	→	If no patches with friend >= friend_min, Select high zooplankton patch from memory	→	If no patches with high zooplankton patch in memory, random swim
	If No	→	All model Versions	→	Stay put						

Figure 2: Shark Decision Pathway under different submodels. Note that if a patch that meets the condition is identified, under all versions, sharks make the following action: If within swimming distance, move to it, if out of swimming distance, swim towards it. Random is not included in this table as sharks make no decision under the random version.

9. References

Berrow, Simon, and Clare Heardman. 1994. "The Basking Shark *Cetorhinus Maximus* (Gunnerus) in Irish Waters: Patterns of Distribution and Abundance." *Biology and Environment: Proceedings of the Royal Irish Academy* 94B:101–7.

Bonnet, Delphine, Anthony Richardson, Roger Harris, Andrew Hirst, Gregory Beaugrand, Martin Edwards, Sara Ceballos, Rabea Diekman, Angel López-Urrutia, Luis Valdes, François Carlotti, Juan Carlos Molinero, Horst Weikert, Wulf Greve, Davor Lucic, Aitor Albaina, Nejib Daly Yahia, Serena Fonda Umani, Ana Miranda, Antonina dos Santos, Kathryn Cook, Susan Robinson, and Marie Luz Fernandez de Puelles. 2005. "An Overview of <i>Calanus Helgolandicus<i> Ecology in European Waters." *Progress in Oceanography* 65(1):1–53. doi: 10.1016/j.pocean.2005.02.002.

Braun, Camrin D., Gregory B. Skomal, and Simon R. Thorrold. 2018. "Integrating Archival Tag Data and a High-Resolution Oceanographic Model to Estimate Basking Shark (Cetorhinus Maximus) Movements in the Western Atlantic." *Frontiers in Marine Science* 5. doi: 10.3389/fmars.2018.00025.

Christensen, Villy, and Carl J. Walters. 2004. "Ecopath with Ecosim: Methods, Capabilities and Limitations." *Ecological Modelling* 172(2):109–39. doi: 10.1016/j.ecolmodel.2003.09.003.

Codling, Edward A. 2008. "Individual-Based Movement Behaviour in a Simple Marine Reserve-Fishery System: Why Predictive Models Should Be Handled with Care." *Hydrobiologia* 606(1):55–61. doi: http://dx.doi.org.mutex.gmu.edu/10.1007/s10750-008-9345-9.

Coll, M., E. Akoglu, F. Arreguín-sánchez, E. A. Fulton, D. Gascuel, J. J. Heymans, S. Libralato, S. Mackinson, I. Palomera, C. Piroddi, L. J. Shannon, J. Steenbeek, S. Villasante, and V. Christensen. 2015. "Modelling Dynamic Ecosystems: Venturing beyond Boundaries with the Ecopath Approach." *Reviews in Fish Biology and Fisheries* 25(2):413–24. doi: http://dx.doi.org.mutex.gmu.edu/10.1007/s11160-015-9386-x.

Conover, R. J. 1988. "Comparative Life Histories in the Genera Calanus and Neocalanus in High Latitudes of the Northern Hemisphere." *Hydrobiologia* 167(1):127–42. doi: 10.1007/BF00026299.

Cotton, Peter, D. W. Sims, Sam Fanshawe, and Mark Chadwick. 2005. "The Effects of Climate Variability on Zooplankton and Basking Shark (*Cetorhinus Maximus*) Relative Abundance off Southwest Britain." *Fisheries Oceanography* 14(2):151–55. doi: https://doi.org/10.1111/j.1365-2419.2005.00331.x.

Crowe, L. M., O. O'Brien, T. H. Curtis, S. M. Leiter, R. D. Kenney, P. Duley, and S. D. Kraus. 2018. "Characterization of Large Basking Shark Cetorhinus Maximus Aggregations in the

Western North Atlantic Ocean." *Journal of Fish Biology* 92(5):1371–84. doi: https://doi.org/10.1111/jfb.13592.

Doherty, P. D. 2017. "Basking Shark Movement Ecology in the North-East Atlantic." ProQuest Dissertations Publishing.

Fayet, Annette L. 2020. "Exploration and Refinement of Migratory Routes in Long-Lived Birds." *Journal of Animal Ecology* 89(1):16–19. doi: https://doi.org/10.1111/1365-2656.13162.

Guilford, Tim, Robin Freeman, Dave Boyle, Ben Dean, Holly Kirk, Richard Phillips, and Chris Perrins. 2011. "A Dispersive Migration in the Atlantic Puffin and Its Implications for Migratory Navigation." *PLOS ONE* 6(7):e21336. doi: 10.1371/journal.pone.0021336.

Häfker, N. Sören, M. Teschke, K. S. Last, D. W. Pond, L. Hüppe, and B. Meyer. 2018. "*Calanus Finmarchicus* Seasonal Cycle and Diapause in Relation to Gene Expression, Physiology, and Endogenous Clocks." *Limnology and Oceanography* 63(6):2815–38. doi: 10.1002/lno.11011.

Johnston, Emmett M., Paul A. Mayo, Paul J. Mensink, Eric Savetsky, and Jonathan D. R. Houghton. 2019. "Serendipitous Re-Sighting of a Basking Shark *Cetorhinus Maximus* Reveals Inter-Annual Connectivity between American and European Coastal Hotspots." *Journal of Fish Biology* 95(6):1530–34. doi: 10.1111/jfb.14163.

Lieber, Lilian, Graham Hall, Jackie Hall, Simon Berrow, Emmett Johnston, Chrysoula Gubili, Jane Sarginson, Malcolm Francis, Clinton Duffy, Sabine P. Wintner, Philip D. Doherty, Brendan J. Godley, Lucy A. Hawkes, Matthew J. Witt, Suzanne M. Henderson, Eleonora de Sabata, Mahmood S. Shivji, Deborah A. Dawson, David W. Sims, Catherine S. Jones, and Leslie R. Noble. 2020. "Spatio-Temporal Genetic Tagging of a Cosmopolitan Planktivorous Shark Provides Insight to Gene Flow, Temporal Variation and Site-Specific Re-Encounters." *Scientific Reports* 10(1):1661. doi: 10.1038/s41598-020-58086-4.

Miller, P. I., K. L. Scales, S. N. Ingram, E. J. Southall, and D. W. Sims. 2015. "Basking Sharks and Oceanographic Fronts: Quantifying Associations in the North-east Atlantic." *Functional Ecology* 29(8):1099–1109. doi: 10.1111/1365-2435.12423.

Natugonza, Vianny, Cameron Ainsworth, Erla Sturludóttir, Laban Musinguzi, Richard Ogutu-Ohwayo, Tumi Tomasson, Chrisphine Nyamweya, and Gunnar Stefansson. 2020. "Ecosystem Modelling of Data-Limited Fisheries: How Reliable Are Ecopath with Ecosim Models without Historical Time Series Fitting?" *Journal of Great Lakes Research* 46(2):414–28. doi: 10.1016/j.jglr.2020.01.001.

Richardson, A. J., A. W. Walne, A. W. G. John, T. D. Jonas, J. A. Lindley, D. W. Sims, D. Stevens, and M. Witt. 2006. "Using Continuous Plankton Recorder Data." *Progress in Oceanography* 68(1):27–74. doi: 10.1016/j.pocean.2005.09.011.

Sims, D. W. 2000. "Filter-Feeding and Cruising Swimming Speeds of Basking Sharks Compared with Optimal Models: They Filter-Feed Slower than Predicted for Their Size." *Journal of*

Experimental Marine Biology and Ecology 249(1):65–76. doi: 10.1016/S0022-0981(00)00183-0.

Sims, D. W. 2008. “Chapter 3 Sieving a Living.” Pp. 171–220 in *Advances in Marine Biology*. Vol. 54. Elsevier.

Sims, D. W., and D. A. Merrett. 1997. “Determination of Zooplankton Characteristics in the Presence of Surface Feeding Basking Sharks *Cetorhinus Maximus*.” *Marine Ecology Progress Series* 158:297–302.

Sims, D. W., and Victoria A. Quayle. 1998. “Selective Foraging Behaviour of Basking Sharks on Zooplankton in a Small-Scale Front.” *Nature* 393(6684):460–64. doi: 10.1038/30959.

Sims, D. W., and Philip C. Reid. 2002. “Congruent Trends in Long-Term Zooplankton Decline in the North-East Atlantic and Basking Shark (*Cetorhinus Maximus*) Fishery Catches off West Ireland.” *Fisheries Oceanography* 11(1):59–63. doi: 10.1046/j.1365-2419.2002.00189.x.

Sims, D. W., E. J. Southall, V. A. Quayle, and A. M. Fox. 2000. “Annual Social Behaviour of Basking Sharks Associated with Coastal Front Areas.” *Proceedings of the Royal Society B: Biological Sciences* 267(1455):1897–1904. doi: 10.1098/rspb.2000.1227.

Sims, David W., Simon D. Berrow, Ken M. O’Sullivan, Nicholas J. Pfeiffer, Richard Collins, Kev L. Smith, Brianna M. Pfeiffer, Paul Connery, Shane Wasik, Lois Flounders, Nuno Queiroz, Nicolas E. Humphries, Freya C. Womersley, and Emily J. Southall. 2022. “Circles in the Sea: Annual Courtship ‘Torus’ Behaviour of Basking Sharks Cetorhinus Maximus Identified in the Eastern North Atlantic Ocean.” *Journal of Fish Biology* 1–22. doi: 10.1111/jfb.15187.

Skomal, Gregory, Stephen Zeeman, John Chisholm, Erin Summers, Harvey Walsh, Kelton McMahon, and Simon Thorrold. 2009. “Transequatorial Migrations by Basking Sharks in the Western Atlantic Ocean.” *Current Biology* 19(12):1019–22. doi: 10.1016/j.cub.2009.04.019.

Speedie, C. D., L. A. Johnson, and M. J. Witt. 2009. Basking Shark Hotspots on the West Coast of Scotland: Key Sites, Threats and Implications for Conservation of the Species. Commissioned Report No.339.