Thesis

Why Fish form Shoals (and schools):

Detection Avoidance $P_R = P_O - (x't'C_R)$

Allen Philips

Abstract

California Sealions hunting Pacific Herring in Little Manzanita Bay, Bainbridge Island, Washington. 3/17/2024 photo by Author

Fish have been observed to form shoals (swimming together), and schools (compact swimming together with coordinated motion) throughout recorded history. Predation is an acknowledged driving force for fish shoaling and schooling. What is open to investigation is the 'how' and 'why' this should be so.

This paper identifies and describes a new mechanism: **Detection Avoidance.**

Detection Avoidance is a subset of predation abatement.

Detection Avoidance function within both temporal and spatial domains.

This paper discussion of **Detection Avoidance** significant differences:

- Demonstrates aggregating behavior is effective pre-predatorial contact.
- Demonstrates aggregating behavior is effective against predation without an associated escape behavior.
- Formally links spatial aggregations with temporal aggregations.
- Provides a general mathematical form that models real world observations.

This paper's description of Detection Avoidance:

Utilizing the Fourier relationships between Time Frequency Data and Spatial Frequency Data, this paper develops the mathematical general form:

- Provides multivariant computer models (available to the readership):
    - predicting the effectiveness of Detection Avoidance within the real world.
    - show equivalency (and the mapping and overlaying) of Time Frequency Data and Spatial Frequency Data
- Presents multiple graphic examples:
    - The equivalency between time-frequency and spatial frequency.
    - The author's background in acoustics created the initial false understanding that frequency has an inherent component of time itself. <u>It does not</u>. This misunderstanding caused a delay in development. A number of talks to educated audiences has shown that this concept requires multiple attempts to adequately overcome the mental entanglement that occurs when describing the concept: 'frequency over time'.
- Provides video evidence of Detection Avoidance process within fish school events.

The author states:

IF the readership can appreciate the lifecycle of the American cicada and recognize that its ability to hide for long periods of time is a significant contribution to the cicada's ability to avoid predation (temporal separation),

THEN, this paper, using mathematical models and real-world examples, will show that a shoal or school of fish hiding in an opaque ocean is the equivalent of a cicada brood hiding (temporal separation) and that the spatial separation is a significant contribution to the school's ability to avoid predation.

Primary Conclusion: This paper identifies a significant heretofore undescribed mechanism that drives this evolutionary forcing function: **Detection Avoidance.**

Furthermore: This paper develops the mathematical model that concisely describes this function:

$$P_R = P_O - (x't'C_R)$$

Detection Avoidance is defined as: reduction of predation by reducing the availability of attacks on bait fish by: 'prey group hiding', either in time, or in space. i.e. Individual fish in shoals and schools cannot be eaten if they are not in the same location as the predators.

Secondary Conclusion: Detection Avoidance is significantly different from previous explanations in that it does not depend on whether the aggregation is in the school or shoal form, nor does it depend on fish behavior during or after predatorial attacks. It functions before predators find the shoal or school. It is not a subset of Attack Abatement as defined by Jussi Lehtonen & Kim Jaatinen.

Introduction

Detection Avoidance:

Statement: This research indicates fish form shoals to reduce predation by minimizing their footprint to a negligible amount within the spatial domain and thereby 'avoiding detection' by the predator population. This is significantly different from other descriptions. The evasive behavior by a fish school is a different process.

Definitions:

- **Shoaling** is observed to be a large aggregation of individuals of the same species swimming calmly together with enough spacing to allow foraging, breeding, and perhaps other social activities. Although large by human standards, the shoal becomes insignificant and invisible to predators on an oceanic scale.
- **Schooling** is when fish contract the **shoal** group size significantly into smaller size, a **school,** (often when encountering predation) and beginning to swim energetically in coordinated motion in random swirls and eddies making their positions difficult to predict.

Detection Avoidance is accomplished by small forage fish (anchovy of the family *Engraulidae,* etc) by coalescing their distributed population into aggregates of small spatial footprints ($<10^3$-10^5 square meters) within a large ocean ($>10^{12}$ square meters) and utilizing the opacity of the sea (spatial separation).

Detection Avoidance is not calculated to be just a function of the "school" but primarily that of the "shoal". The ocean is so large that the difference of the grouping footprint, before contact, between the larger shoal and smaller school is small.

This survival technique is accomplished by 'hiding' (from basic non-directed predatorial random-path search techniques) in the smallest functional region of a large opaque space.

This model can be mathematically represented by $\mathbf{P_R = P_O - (x't'C_R)}$, where $\mathbf{P_O}$ is the original population, $\mathbf{P_R}$ is the population remaining after predation, $\mathbf{C_R}$ is the consumption rate (normalized), and **x'** and **t'** is the magnitude of exposure (in units of time and space).

Articulated in a straight forward way: The survival of individual forage fish is improved when they form groups that **'hide significantly beyond detection range'** within the incredibly large spatial plane that is the ocean. The group, whether school or shoal, is attempting to **never have contact** with predators. This conclusion provides an alternative explanation to earlier assumptions that the school itself is the primary protection against predation.

In conjunction, if predators are detected, prey behavior collapses the shoal into the significantly smaller spatial footprint of a randomly fast moving 'school'. This increases the odds to reestablish prey-predator separation and disappear again into the murky depths.

As delineated in many other studies, the high concentration of prey can also overwhelm the predator population (satiation/dilution) when contact does occur.

Discussion - Significance

Significance of Detection Avoidance:

Detection Avoidance is the ability for animal aggregations to avoid the same location as predators, thereby reducing the availability of attacks on the group.

For fish, this is accomplished by reducing their spatial footprint within a large ocean. It occurs whether in foraging shoals or when formed up into coordinated motion schools. I.E. The **Detection Avoidance Model** shows shoaling by itself can reduce predation.

Thus is a significant statement: Fish shoals, not just schools, avoid predation by achieving separation from unsophisticated predators by reducing their spatial footprint to perhaps $1:10^3$ to $1:10^6$ of the search area, substantially reducing their risk of detection.

This model can be mathematically represented by $\mathbf{P_R = P_O - (x't'C_R)}$, a new formula.

What does previous research suggest?

A review of Research Gate identified a cogent model[1] developed by Travis and Palmer which demonstrated increasing difficulty of prey detection over large spatial domains if partial predation causes the prey to coalesce into smaller and smaller regions.

Additionally, below is a representative summary[2,3] by Lehtonen, Jaatinen, Ioannou and others, of the other predominant hypotheses for the predatorial forcing influences that drive fish schooling behavior. None mention the utility of the shoal as predation avoidance, all hypotheses assume prey behavior during predation.

- Selfish Gene:
  - Individuals within school fight for safest location within school using other individuals as sacrifice.
- Group Awareness:
  - Multiple aware individuals within the school improves predator detection.
  - Initiates early group escape behavior when in proximity to predators/detection.
- Predator Confusion:
  - Improved survival by making it harder for predator success on individual within a school versus against the solitary individual.
- Saturation/Dilution:
  - Schools are larger than can be consumed by predators. Reduces average attack rate on individuals within the group. Improves average group individual's

survival from predation over that of solitary fish.

Discussion - Differences

The **key differences** between the Travis/Palmer[1] model and the **Detection Avoidance Model** are:

The **Detection Avoidance Model** identifies the equivalency between spatial and temporal domains of animal aggregates.

The **Detection Avoidance Model** articulates that spatial hiding occurs before prey detection.

The **Detection Avoidance Model** articulates that spatial hiding does not require prey behavior modification after detection such as coalescing into schools.

None of the hypothesis stated before propose a mechanism that is in effect prior to contact between predators and prey. **Detection Avoidance** is unique.

What is **Detection Avoidance** exactly? Is it truly an evolutionary forcing function?

During research it turned out that by formulating and comparing the concept of spatial-frequency and temporal-frequency domains made manipulating the concepts and mathematics much easier, allowing a better intuitive understanding. What this meant was, the author searched for analogs that would shed illumination on the functionality of spatial hiding. It was determined that some behaviors that occurred over time could be compared to behaviors that occur across a space.

Applying the concept of **'Detection Avoidance'** to termites is illustrative. Termites and Cicadas reduce predation for the vast majority of their life cycle by hiding successfully from predators over long stretches of time and limiting their exposure.

AN EXAMPLE: Within the Puget Sound Native Tree Conservancy, the author's study area, termites, **hiding all year** is a dominant survival strategy. Yet, since they eventually deplete their food supply, they must move on. Flying in late fall for a short period each year

ASSUME: a **temporal frequency process** (contacts between predator and prey across time) within a space-time domain of a twenty acre wood, over a year's period, and predators using random walk searches, uniformly distributed. From this given condition it will be demonstrated **by mathematical model** that termites are successful because on many calendar days they are simply not available to predators because they are hiding away behind their wood barriers. The **'frequency'** of detections between termites and predators is small over the **temporal** (time) domain, even though when detection does occur, it occurs across the large spatial axis.

CONCLUSION: Termites use **Detection Avoidance** behavior to prevent predation by not being available the vast majority of days, allowing the population to increase, and adopting saturation protection when contact does occur.

Discussion - Mapping

Mapping termite behavior over the behavior of fish is also illuminating.

ASSUME: a **spatial frequency process** (contacts between predator and prey across space) within a space-time domain of an ocean of twenty square miles, over a year's period, and predators using random walk searches, uniformly distributed. From this given condition it will be demonstrated by **mathematical model** that fish schools are successful because over the many square miles of ocean they are simply not available to predators because they are hiding behind the opacity of a very large opaque ocean. The **'frequency'** of detections between fish and the predators is small over the **spatial (**space) domain, even though when detection does occur, it occurs across the temporal axis (i.e. there may be small amount of contact between predator and prey over most of the days-time).

CONCLUSION: Fish shoals use **Detection Avoidance** behavior to prevent predation by not being available the vast majority of space, allowing the population to increase, and adopting saturation protection when contact does occur.

The **temporal behavior** of termites restricts predator-prey interactions over a year's time even though when they do occur, they can occur over the full space domain, is the equivalent to the **spatial behavior** of fish restricting predator-prey interactions over the full spatial domain even though when they do occur, they could occur any time during the year.

Both processes are **Detection Avoidance.**

These previous examples assist the audience in understanding the equivalency between 'hiding behind a wood wall', and hiding behind an opaque curtain. It is easy to conceptualize the effectiveness of a wood wall for protection, less intuitive: the protection from an opaque curtain of a large ocean.

In the appendices, the Fourier Transforms, Gaussian Analysis, Graphic Models and programs will also demonstrate the equivalencies.

$$P_R = P_O - (x' t' C_R)$$

Population **R**emaining = **O**riginal **P**opulation – (**x'** region of predation x **t'** time of exposure x **C**onsumption **R**ate)

It is not clear initially, however, which evolutionary force drives schooling activities more: detection avoidance or coordinated escape behavior (group shielding). Most observation shows both. Which came first, 'the chicken or the egg'?

Model Example: Imagine a fish species that school, but when attacked, just huddle together unresponsive to attack (unsophisticated). In such a scenario, the common argument that schooling confuses predators would not apply, yet detection avoidance and predator dilution would still be valid. . The author does not have a clean example of living fish species that school, but do not practice coordinated escape behavior. However, a possible example is the Goliath Grouper *Epinephelus itajara,* in part of its life cycle (example 2).

Discussion - Examples

Living Example (1): Cicadas

Fortunately, there is an insect analog that might. The periodic cicadas, Magicicada ssp[4], common in Eastern United States, has improved escape detection by significantly reducing the frequency in time that they are eligible to predatorial attacks. Most observers note that the temporal frequency of emergence is the predominate survival strategy. The author has observed that it is relatively easy to hand catch these cicadas compared to attempting to hand catch *Schistocerca americana*, the American grasshopper, an insect of similar size. There are so many cicadas in an emerging 'brood' that predation is overwhelmed. So much so, that the cicadas show diminished escape reflex compared to grasshoppers. After emerging, they can said to be huddling, without escaping.

The Fourier equivalence of the temporally hiding cicadas with diminished escape behavior would be a spatially hiding fish species, that when found, has little or no escape behavior.

The existence of a living species with substantial **Detection Avoidance** behavior but with very little escape behavior implies to the author, that amongst bait fish that school, Detection Avoidance is at least as much of a fundamental evolutionary forcing function as is group shielding and escape behavior.

Living Example (2): Goliath Groupers

Returning to the 'chicken or the egg' question. Are eggs the way chickens create more chickens? Or are chickens the way eggs make more eggs? This is a valid issue. The Atlantic Goliath Grouper[5], *Epinephelus itajara,* are individually dispersed sparsely over large regions, yet they coalesce into a very small location to spawn. Their eggs, an essential element of the species survival, have little or no escape behavior, yet by combining both spatial and temporal **Detection Avoidance** as survival techniques in this phase of their life-cycle, they demonstrate a world-wide successful environmental strategy. **Even without having 'schooling defense mechanisms'**, the grouper, then, is a species that 'aggregate' and enough juveniles successfully avoid the egg 'predators' of the reef using Detection Avoidance..

Therefore, citing these two examples of hiding, followed by dilution/satiation when discovered, but without group shielding behavior, implies **Detection Avoidance** is of a magnitude as significant as any other proposed evolutionary forcing function and since it applies to shoaling as well as schooling, may have to be included in future evolutionary models of animal aggregations.

Conclusions: **Detection Avoidance**

Pelagic foraging fish species display grouping in shoals and schools that is representative of many other animal aggregations such as herds of migrating mammals and flocks of birds.[12]

An accurate understanding of the forcing functions that drive animal aggregations is essential to the understanding of the evolutionary mechanisms that mold animal behavior.

Observations show fish that aggregate into groups with a small common footprint (shoals) demonstrate greater reproductive success than individual fish that are evenly distributed across the spatial domain (ocean).

This paper identifies and describes a significant process driving the formation of fish shoaling and schooling: **Detection Avoidance.**

Detection Avoidance is a mechanism that fish use to avoid predation by utilizing the enormous scale and opacity of the ocean to create effective separation between predator and prey sufficient enough to enhance overall fitness and reproductive success of the average fish within the school.

Fish achieve this effect by forming shoals allowing foraging while still reducing their presence in the murk. The formation of schooling occurs after predators have been encountered and evasion techniques further reduce the scale of the prey footprint.

Conclusions: Detection Avoidance (spatial and temporal) is a newly described evolutionary mechanism for fish (and possibly other animal aggregations).

- A significant reason why fish form shoals and schools is to reduce predation by **Detection Avoidance** through **spatial separation** (hiding in space) by coalescing into a small footprint within the opaque ocean.
- This behavior is the mathematical equivalent of cicadas reducing predation by **Detection Avoidance** through **temporal separation** (hiding in time) and emerging only once every few years.
- This behavior is even evolutionary advantageous **while in shoals,** without having to form schools, and without having to perform escape behavior when detected.
- A **general mathematical form** has been found that models both the temporal and spatial domains of the Detection Avoidance mechanism: $P_R = P_O - (x' * t' * C_R)$ see appendices for derivation

Population **R**emaining = **O**riginal **P**opulation – (**x'** region of predation x **t'** time of exposure x **C**onsumption **R**ate)

If valid, the results are a significant contribution to the modeling of animal aggregations as well as to the understanding of animal behavior and the function of evolutionary forcing .

Author

Allen Philips has a unique educational path

- Fisherman. sailor, explorer of the worlds' oceans, 1980 to now
- Steward and Conservator of Dolphin Place, a PNW Nature Conservancy, since 1973
- Master's Degree, Oceanography, University of Washington, 1990
    - Sub-contractor, J.K. Parish, Coordinated Fish Motion Studies, University of Washington. 2004
    - Sub-contractor, J.K. Parish, Marine Biology Laboratories, University of Washington, 2010
    - Natural Philosopher, 1980-date

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I wish to thank my community and family in supporting my efforts to caretake this small plot of wildness, allowing fifty years of observations of this evolving habitat.

I wish to thank Dr's Coachman and Andersen promoting my acceptance into the University of Washington's Oceanography graduate program.

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I also wish to thank Dr's J. M. J. Travis and S. C. F. Palmer for their illuminating 2005 paper
Spatial processes can determine the relationship between prey encounter rate and prey density
Biology Letters (2005)

'Look deep into Nature and then you will Understand everything better'[13]

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Model Methods

Math Models

Fourier Series and Transforms

Gaussian and Normal Distributions

Normalized Cross-Dimensional Solution

Graphic Model

Venn Diagram Intersections

Interactive Computer Model

MODEL Variable Definitions

C_R	Prey consumption rate per Predator	$P_O(x,t)_i$	Initial prey population as distributed across **(z)**
$C_R(z)$	Prey consumption rate per Predator per **z**	**PPI**	Predator-Prey Interactions
D	Domain magnitude = **n** * **m**	P_R	Final prey population
F(x)	Spatial Frequency Function: also F(x,t), t nonvarying	**R**	ratio unit space/domain = **z/D**
G(t)	Temporal Frequency Function: G(x,t), x nonvarying	**S**	Predators (sharks, etc)
GPM	Group Protective Measures	$S_D(z)$	Predator density per **(z)**
m	magnitude of space domain	S_O	Predator initial population
n	magnitude of time domain	**T, t**	time, the time axis of units (t)
P	Prey	**t'**	time of prey exposure
P_C	Prey consumed	**T**(g)	temporal unit, a specific grid location in **T** domain
$P_C(t)$	Prey consumed on a date	T_E	time of emergence
P_D	Prey density	**X, x**	space , the spatial axis of units (x)
$P_D(x')$	Space of prey exposure	**X**(g)	spatial unit, a specific grid location in **X** domain
$P_D(z)_i$	Initial prey population per **z** (unit space*time)	**x'**	Location of prey exposure
$P_D(z)$	Prey density per **z**	**Z, z**	unit space * time
$P_E(x,t)$	Prey emergence on a date at a location	**Z**(g)	a specific grid location in the space-time domain
PF	Prey Footprint **= (n' * m')**	**Z**(i)	**z** at initial time
P_O	Initial prey population		

Model Development

Background

Examining the natural world and assessing the relationships of what we observe is critical to the understanding of causes and consequences of the events of our world.

For five decades the author has resided at the Puget Sound Nature Conservatory and Observatory located within the Little Manzanita Bay estuary, Bainbridge Island, Washington, USA, (www.DolphinPlaceOpen.Space).

Over the years at this site, the author has observed salmon runs (*Oncorhynchus kisutch)*, eulachon smelt spawning aggregations (*Thaleichthys pacificus*), termite swarms (*Zootermopsis augusticollis),* and fall orb web spiders (*Araneus diadematus*).

During this time the author postulated there may be similar root causations for the aggregations of fish spawning and termite nuptial flights.

This study indicated that termites overwhelm the predatorial population during their swarms (predator satiation effect). They also show that, by hiding in wood, termites simply are not available (Detection Avoidance) during most of the year for predators to consume. Initial conclusions indicated termite survival significantly depends on both **Detection Avoidance** and **Satiation Effect.**

At the outset, it was not obvious that schooling fish, like termites, are successfully avoiding detection. However, having spent considerable time underwater, the author is aware of the substantial opacity of the ocean, especially considering the scale of the predatorial detection distances verses the scale of the environment (often exceeding 1:10,000 or greater). Perhaps fish schools create spatial separation. As such, it is possible that similar predatorial pressures might create the behaviors the author observed in schooling fish and swarming termites.

Development of Math Models

Mapping mathematical models over real world observations helps in our understanding. Beginning fifteen years ago, the author began the effort to articulate the problem of fish aggregations and to develop the math and models to assist describing these processes. Evolutionary processes and forcing functions are multi-dimensional, multi-variable systems of substantial complexity. Sorting out the significant attributes from the fine detail and noise is difficult. The author spent considerable time investigating functionalities that were not intuitively obvious.

A quick review of the processes of various mathematical frequency analysis

Fourier Series and Transforms

Both the local eulachon (type of smelt, a small forage fish) schools, and the termite swarms, exist in an environment that repeats on hourly and daily cycles (day, dusk, night, dawn), moon cycles (phase, illumination), and yearly cycles (four seasons, etc). These frequencies, such as spawning at twilight on the first full moon in fall, can also be co-associated.

As an undergrad the author participated in the creation of Fourier Transform software for the University of Washington's survey ship RV Thomas G Thompson; in the 1990s he was a sonar officer in the Navy working with the development of acoustic imaging of the ocean; and in the early 2000's was a minor participant in the University of Washington's Coordinated Fish Motion Studies for the Applied Physics Laboratory.

His experience in developing software and signal analysis initially suggested Fourier Series and Transforms could be promising tools in the investigation of why fish school. Fourier Transforms allows analysis of frequencies within a data set, and Fast Fourier Transforms allows an approximate calculation of what would otherwise be an infinite series with some uncertainty.

By using Fourier Transforms, it was hoped that the frequencies of these events could be extracted and rigorously compared mathematically to demonstrate an exact equivalency.

Where

$$Be^{i(2\pi ft+\theta)} = Acos(2\pi ft + \theta) + iAsin(2\pi ft + \theta)$$

f = frequency
T = time
Θ = phase shift
A = magnitude in a rectangular coordinate domain
B = magnitude in a polar coordinate domain

However, after much research, it was determined, these mathematics could not be directly applied to the separate behaviors of the local fish and insects because Fourier Analysis requires the manipulations to be different facets of the same set of events.

Nevertheless, it was shown that an equivalency could be made between the processes forcing the frequency of predatorial events in a spatial domain of the smelt and the processes forcing the frequency of predatorial events of the termites in a temporal domain.

Gaussian Functions

A gaussian function is a mathematical model that describes the distribution of events that often are observed in nature, where the number of occurrences rise to a maximum, then fall off somewhat symmetrically. This mathematical model's scale can be adjusted in height and width to conform to the data to determine if the model actually describes the real world with some accuracy. Since both fish schools and termite population increase from zero to a maximum and then taper off, describing these events using a gaussian model is appropriate.

t = **Time** of events
a = **Amplitude** of events
***F*(t)** = **Function of Time:** Mathematical model describing the shape and relationships between the data, typically a magnitude for every value on the time axis
μ = **Mean:** the position of the middle point of the data, the highpoint of the model
σ = **Standard Deviation**: Mathematically describes the region that contains 68% of the events. Also can be understood as the majority of the data surrounding the center ot the events
σ^2 = **Variance:** the extent the date spreads away from the center
μ ± 2σ = The area described by these values contains 95% of population

$$F(t) = \frac{a}{[\sigma\sqrt{2\pi}]} * e^{\frac{-1}{2}(\frac{(t-\mu)^2}{\sigma^2})}$$

Note: When time (t) is at the center of our data (t = μ), ***F***(t) = $\frac{a}{[\sigma\sqrt{2\pi}]}$

The first math model selected will be a gaussian function, capable of reasonable assessment across domains.

And finally, since the Fourier transform of a Gaussian function is another Gaussian function, it should be easier to analyze.

Why Fish School (and form shoals)

Model Hypothesis (Gaussian):

Assuming a model where there are:

- three domains, of time and space and frequency
- a gaussian function G of time and frequency for termites
- a gaussian function F of space and frequency for fish
- F and G both have domains that share the frequency of events
- and parameters that can be normalized,

This means that

IF

termite behavior can be described as a gaussian function, and

fish behavior can be described as a gaussian function, and

their domains contain common fields of space, time and frequency, and

the models can be mapped and correlated,

THEN an equivalency can be inferred.

Termites population described by gaussian function $\mathcal{G}$(t)

Assuming termite swarms have a density on a given day (frequency per unit time), spread evenly across space, and that frequency builds up from a very low number, increasing while approaching the day of maximum and then tapering off. This real world step-wise function of the population can be modeled by in a normal distribution as one moves away from the center.

$$g(\mathbf{t}) = \frac{\mathbf{a}}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\frac{(\mathbf{t}-\mu)^2}{\sigma^2}\right)$$

σ = standard deviation; $\boldsymbol{\sigma^2}$ = variance
μ = mean
μ ± 2σ = 95% of population
t = Julian calendar date
a = amplitude

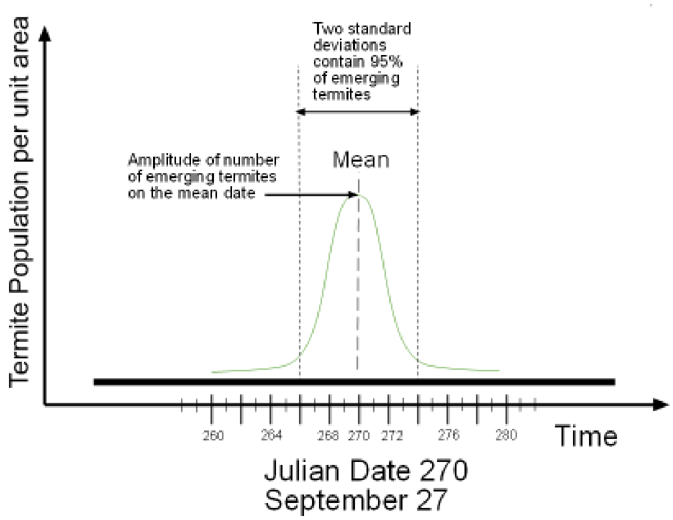
A hypothetical set of values: select 9 square meters of the **Dolphin Place Forest;** select the day of maximum termite emergence (μ) to be "t = 270 = September 27th"; a standard deviation (σ) of two days; then two standard deviations (2σ) is 4 and therefore a window 8 days wide will contain 95% of all emerging termites; and the amplitude of emerging termites is a number "a" that will be normalized with fish later

a = amplitude = 120
t = Julian calendar date
μ = mean = day 270 of 365 days

σ = standard deviation = 2 days
2σ = 4 days (Sep 23 - Sep 30 contain 95% of population)
$\boldsymbol{\sigma^2}$ = variance = 4 days

$$G(270) = \frac{120}{2\sqrt{2\pi}}\, e^{-\frac{(t-270)^2}{2(2)^2}} \sim 24 \text{ day 270}$$

Example:



Population Frequency vs Time

Termite predation described by gaussian function G(t)

The model can be modified by incorporating a function for predation. A simplified predator model can be added to interact with the termites:

Assuming:

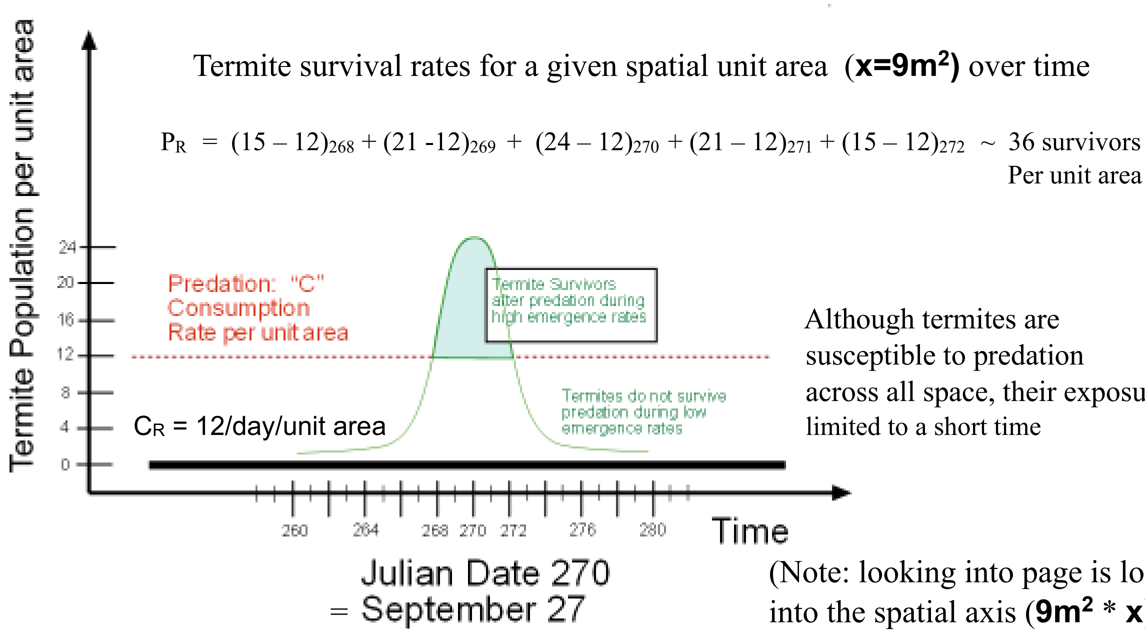
- Predator population remains constant over time
- Predator population evenly distributed over space
- Predator consumption rate is a constant

This model can be shown to be valid even if termites flights and predators are shown to be randomly distributed over time.

The predators will eat all termites when termite population is less than predator consumption rate (**C_R**). In a given space and time, all termites above the consumption rate survive.

Below is a hypothetical depiction of the emergence of termites within a unit space ($9m^2$) over time, as well as the predatorial consumption within the same time/space. **t'** = number of days

The total termite population (**P_R**) that remains at the end of the year is equal to the survival of termites per unit area times the total area. In this example, **C_R** = 12 termites/day/unit area



Although termites are susceptible to predation across all space, their exposure is limited to a short time

(Note: looking into page is looking into the spatial axis (**$9m^2$ * x**)

Note: This diagram is a single temporal slice through the entire termite emergence across the whole spatial plane within the forest. Termites will encounter some predation in each spatial unit Total termite survival = unit survival x number of spatial units.

Fish population described by gaussian function f(t)

Assuming fish shoals have a density of a given area (frequency per unit area), spread evenly across time, and that frequency builds up from a very low number, increasing while approaching the unit space of maximum density and then tapering off. This real world step-wise function of the population can be modeled by in a normal distribution as one moves away from the center. We can also map the previous termite model onto the fish model (note: to ease the mapping of the models, the x-y coordinates are normalized to one length value, '**x**'):

$$\mathcal{F}(\mathbf{x}) = \frac{\mathbf{a}}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\frac{(\mathbf{x}-\mu)^2}{\sigma^2}\right)$$

σ = standard deviation
σ² = variance; **μ ± 2σ** = 95% of group
μ = mean
x = spatial location
a = amplitude

A hypothetical set of values: above the **Hakurei Seamount** 140°49'E**,** one minute (') of longitude is a little less than a kilometer, a possible size for a forage fish shoal; the location of maximum fish density (μ), "x =49'; a standard deviation (σ) of 1 minute; then two standard deviations (2σ) is 2 minutes and therefore a space 4 minutes (3.5 km) square will contain 95% of all fish of the shoal; and the amplitude of fish is a number "a" that will be the magnitude of millions of fish

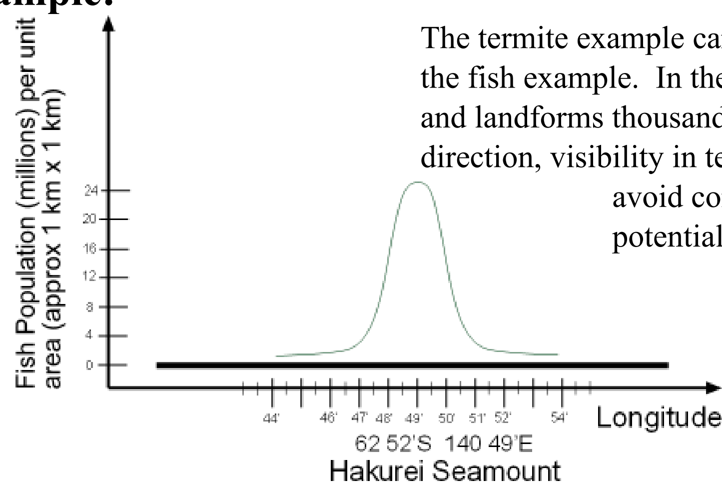
a = amplitude = 120 (million)
x = spatial location
μ = mean = 140°49'E,

σ = standard deviation = 1° of latitude ~ 1 nautical mile
2σ = 2 minutes of latitude (contains 95% of population)
σ² = variance ~ 1 nautical mile

$$F(49') = \frac{120}{2\sqrt{2\pi}}\, e^{-\frac{(x-49)^2}{2(1)^2}} \sim 24 \text{ million}$$ long 62 52'S lat 140 49'E

Example:

The termite example can be mapped directly over the fish example. In the southern ocean, with distances and landforms thousands of kilometers away in each direction, visibility in tens of meters, the fish shoal will avoid contact with the vast majority of potential predators.



Population Frequency In Spatial Domain

Fish predation described by gaussian function F(t)

The model can be modified by incorporating a function for predation. A simplified predator model can be added to interact with the shoal of fish:

Assuming:

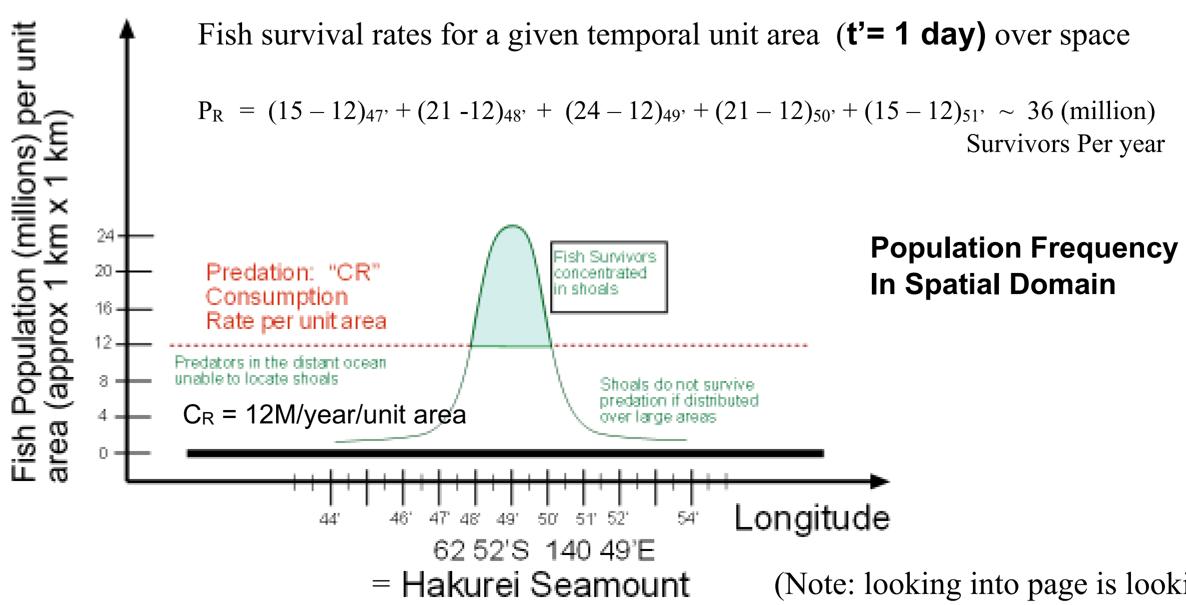
- Predator population remains constant over time
- Predator population evenly distributed over space
- Predator consumption rate is a constant
- Normalize the spatial dimension x/y just to a single variable of magnitude x

This model can be shown to be valid even if fish shoals and predators are shown to be randomly distributed over space.

The predators will eat all the fish when the fish population is less than predator consumption rate (**C_R**). All fish in a given space and time above the consumption will survive.

Below is a hypothetical depiction of a shoal of fish within a unit space over time, as well as the predatorial consumption within the same time/space. **x'** = space fish exposed; **x-x' = region** fish are not exposed.

The total fish population (**P_R**) that remains at the end of the year is equal to the survival of fish per unit area times the time the unit area is exposed. In this example, **C_R** = 12 million/year/unit area



(Note: looking into page is looking into the temporal axis (**one day * t)**)

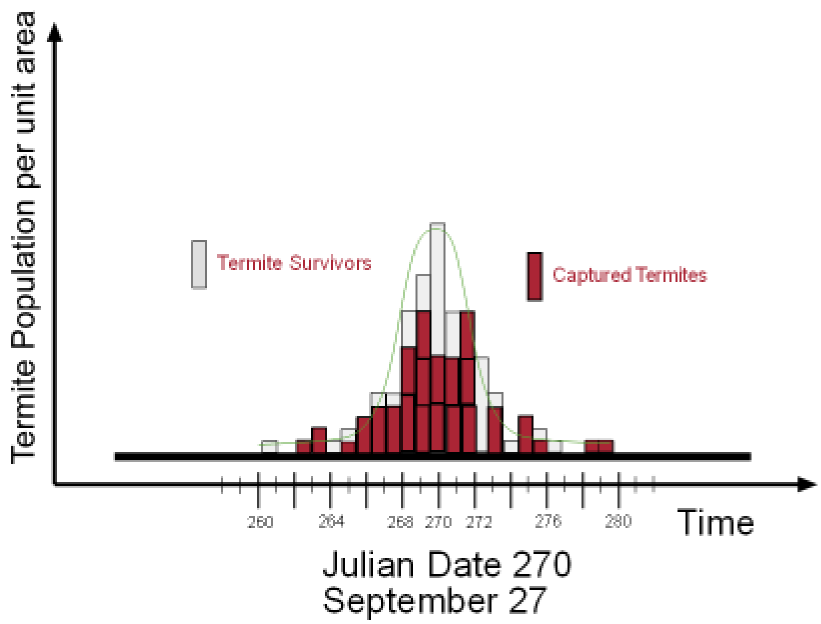
Normalized Cross-Dimensional Solution

Hypothetical Stepwise function

Real world fish and termites come in discrete packages, and collecting real world data would entail summations instead of integration.

At the Dolphin Place Open Space a five year real data set for termites is in progress. Observation are being made within a three meter by three meter section of the wet forest in the fall of each year (SEP-OCT) from 15 minutes prior to sunset to 15 minutes after sunset, counting observed termites and observed captures by spiders. Data has not be formally analyzed.

Below is a hypothetical chart of what the termite data may look like:



$$PR = Po - Pc = \sum_{t=1}^{365}[EDt] - \sum_{t=1}^{365}[Ct] = \sum_{t=1}^{365}[EDt - Ct]$$

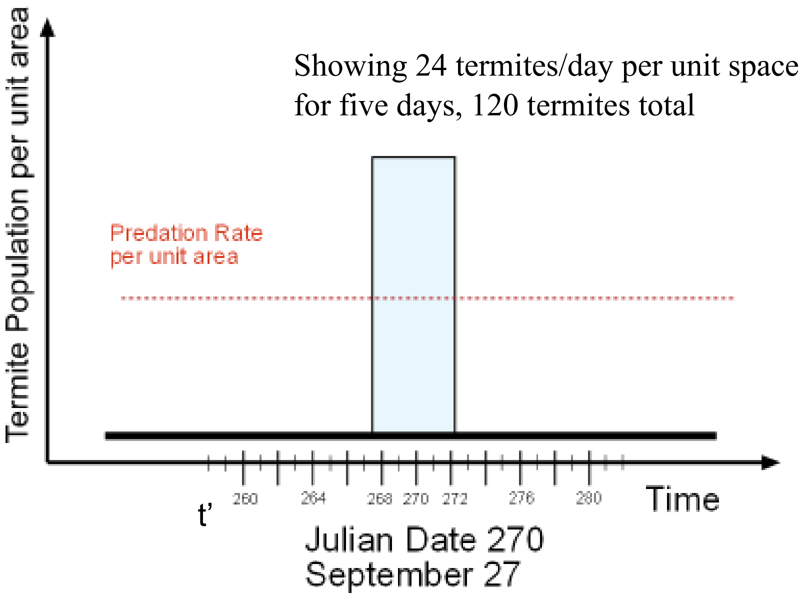
Where:

PR = Population Termites Remaining **Po** = Original Termite Population

Pc = Total Termites Consumed **P**E(x,t) = Prey Emerging on a date

Pc(t) = Number of Termites Consumed on a date

Hypothetical Termite Stepwise Function Model



Time vs Population Frequency

The occurrence of termite flights has been observed at the Dolphin Place Forest for decades. These events occur only a short period of time in the late fall, otherwise the termites evade predation by hiding within the wood of injured or decaying trees. Although the termite availability is limited over time, their emergence is spread across the full landscape of the forest.

This behavior can be modeled by a simplified step function of predator/prey interactions.

IF a summary of the observations can be made with the following assumptions:

Assuming:

- The example for termites can be simplified
- The example is a stepwise function, allowing binary analysis
- A space*time domain (**D**)
- A time axis of units (**t**)
- A space axis of units (**x**)
- A unit space*time (**z**)
- Prey population is distributed across space domain (**x**)
- Initial Prey population per unit space (**$P_{D(x)i}$**) is a constant
- **$P_{D(z)i}$ =** initial prey population per unit space time
- Predator population **S_D**(z) remains constant over space*time **(x * t)**
- Predator population evenly distributed over space*time **(x * t);** one predator per unit space*time (**S_D**(z))
-
- A function **G (x,t),** within Domain **D**, that describes the occurrence, of termites within each unit space*time, (**z**), (**G** = frequency),
-
- Predator and Prey interactions can be calculated in each unit time/unit space (**x', t'**) and thereafter extended across the whole time/space domain
- If Prey exist in an unit space*time (**z**), then Predator consumption rate **C_R,** is a constant within (**z**), not to exceed **P_D(z)**, otherwise, **C_R = 0** (units: prey/z)
- Prey population exposure is a constant value on days (**t'**), zero otherwise

Stepwise function example for termites (Detection Avoidance)

IF values for the example:

- **Po** is the initial population (for the purposes of this example, = **12,000** Total
- **PR** is the remaining population,
- **x** is the space domain where the termites are exposed, **x = 100 m**^{2}
- The spatial unit in this example **x**$_s$ **= 1 m**^{2}
- The time domain (**t**) = 365 days
- **P**$_D$(x)i **= 120** (initial population per unit space)
- **P**$_E$(x,t) **= 24 (**emergence over 5 days, 24 per day)
- **T**$_E$ **(**time of first emergence) **= 268**
- **t'** is the number of days exposed to predation, **t' = 5,**
-
- G(t) = **frequency function of temporal distribution** $G(t) = \begin{cases} 1: & t = 268\text{-}272 \\ 0: & \text{if not} \end{cases}$
-
- **C**$_R$ is the consumption rate per unit space per unit time, **C**$_R$ **=10**
- **C**$_R$ will be normalized and defined at the maximum number of prey all predators can consume in a unit space*time **(z)**
- **P**$_C$ is the population of termites consumed

THEN:

The population of termites remaining **P**$_R$ can be calculated by determining the original population **Po** and subtracting the number of termites consumed by predation **C**$_R$.

$$P_R = P_O - P_C$$

Survivors = Initial Population – area of predation * time of predation * consumption rate

$$P_R = P_O - (x * t' * C_R)$$

$$PR = Po - Pc = \left(\sum_{x=1}^{100} Po(x)\, i\right) - \left\{\left(\sum_{x=1}^{100} x\right) * \left|\sum_{t=1}^{365} G(t)\right| * CR\right\}$$

$$P_R = (100\ m^2 * 120\ prey/m^2) - \{100\ m^2 * [5\ days * 10\ prey/(m^2 * day)]\}$$

$$P_R = 12{,}000 - 5{,}000 = 7{,}000 \text{ termites}$$

Stepwise function for fish (Detection Avoidance) (mapping termite model):

IF values for the example:

- **Po** is the initial population (for the purposes of this example, = **12M** Total)
- P_R is the remaining population,
- **x** is the space domain where the fish are exposed, **x = 100 km**^{2}
- The spatial unit in this example x_s **= 1 km**^{2}**,** the time unit t_s is one day
- The time domain (**t**) = 365 days
-
- P_D **(x)i** = Initial prey population in each unit space $P_D(x)i = \begin{cases} 2.4M: x = 68\text{-}72 \\ 0: \text{ if not} \end{cases}$
-
- **F(x) = frequency function of spatial distribution:** $F(X) = \begin{cases} 1: x = 68\text{-}72 \\ 0: \text{ if not} \end{cases}$
-
- **x'**= area where fish school is exposed to predation **= 5 km**^{2}
- X_E **(**location (grid number of fish school) **= 68** (arbitrary grid number for this example)
- **t** is the number of days exposed to predation, **= 365**
- C_R is the consumption rate per unit space per unit time, assume a school of 250 tuna, each capable of consuming 20 bait/day, C_R **= 5,000 per km**^{2} **per day**
- P_C is the population of fish consumed

THEN:

The population of fish remaining P_R can be calculated by determining the original population **Po** and subtracting the number of termites consumed by predation C_R .

$$P_R = P_O - P_C$$

Survivors = Initial Population – area of predation * time of predation * consumption rate

$$P_R = P_O - (x' * t * C_R)$$

$$PR = Po - Pc = \left(\sum_{x=1}^{100} Po(x)\, i \right) - \left\{ \left(\sum_{x=1}^{100} F(x) \right) * \left[\sum_{t=1}^{365} t \right] * CR \right\}$$

$$P_R = [(2.4 \text{ fish}*10^6/\text{km}^2 \ ) * 5 \text{ km}^2] \ - \ 5 \text{ km}^2 * [365 \text{ days} * (5 * 10^3) \text{ fish}/ (\text{day} * \text{km}^2)]$$

$$P_R = 12 * 10^6 - (5 * 365 * [5 * 10^3]) = 2.875 * 10^6 \text{ fish}$$

Summary of spatial and temporal stepwise models

The investigator will note that the termite and the fish models re similar and have common terms.

$$P_R = P_O - P_C$$

The general solution has a broader application than just for the unit space*time. Both the frequency-time function G(t) and the frequency-space function F(x) can operate in the same space*time Domain **D**.

$$P_R = P_o - (F(x) * G(t) * C_R)$$

Since $F(X) = \begin{cases} 1: x = 68\text{-}72 \\ 0: \text{if not} \end{cases}$ is stepwise 1 for all x' and zero for all else, **F(x)** can be replaced by x'

And since $G(t) = \begin{cases} 1: t = 268\text{-}272 \\ 0: \text{if not} \end{cases}$ is stepwise 1 for all t' and zero for all else, **G(t)** can be replaced by t'

$$P_R = P_o - (x' * t' * C_R)$$

Detection Avoidance

General Form

Conclusion: 'Simplicity is the Ultimate Sophistication'[13]

This general stepwise solution for **Detection Avoidance** is applicable when animal aggregates are isolated from predation by either time, or space, or both.

It indicates that evolutionary forcing functions select for animal aggregations by reducing the capture of individuals by random search predation.

Detection Avoidance is believed to be at least as much of a fundamental evolutionary forcing function as is group shielding and escape behavior.

NOTE: This solution for survivors does not depend upon the size of the domain **D.** P_R and P_O are independent of the size of the environment or the length of time within the environment. P_R is wholly dependent on the area of contact and the length of time of contact.

Graphic Model :

This paper includes the initial description of the **Detection Avoidance** developed a decade ago.

A very simple graphic model was described to explore the attributes of predatorial avoidance by animal aggregations. Two domains were selected: spatial frequency vs time, and temporal frequency vs time. Because the concepts of temporal and spatial frequency isn't intuitive, the graphic model was selected to improve understanding by providing a visual representation of the processes.

A visual display of population densities over time was determined best, allowing side-by-side comparisons by normalizing the time-axis of the temporal-frequency model with the spatial-frequency model.

Their graphical equivalency has a mathematical basis using Fourier transforms.

The termite temporal-frequency-time model has a greater correlation to the experience of most investigators and is displayed first. Then, a model demonstrating fish shoaling over a normalized spatial-frequency-time domain is displayed. Finally the two models are step-wise compared.

The deep woods setting in the Pacific Northwest are exposed annually to termite nuptial flights. In the fall, they flitter almost at random in the forest. However, termites are not available to predation by arachnids except certain times a year. Local observations indicated that the frequency of capture of the insects by spiders was more dependent on the time of year than the location within the forest.

To create a time-space-frequency domain that could be mapped to the real world, a rectangular column, with time the vertical axis, and the base and cross section as the spatial plane, was created. The population frequencies would be plotted on this domain.

A time axis displaying one year is appropriate, since that was the observational period for watching termites, 365 days.

To visualize the results of the model, a normalized (made equivalent numerically) 2-dimensional area with similar units, a square of 19 x 19 acres, which resulted in 361 square acres for the space (a little less than a square mile) was selected.

To ease the visualization of this model, the time and scales were then rounded up by about 12% to 400 units on the temporal axis, and 400 units (20 x 20) on the spatial plane, resulting in numbers most people can manipulate in their head.

Finally, the model was reduced to a minimalistic sample while maintaining relationships, a 4x4 square spatial dimension, and a 16-day temporal dimension. The results of this small model can be rescaled without distortion to reflect the behaviors by termites within a 361 acre wood over a year's time.

Set minimum behavior rules

- Initially, prey and predator are constrained to initial assigned spaces
- prey and predators are distributed evenly about the spatial domain
- predators can consume up to 10 prey per day that are in their box
- more prey (an arbitrary number: one prey for each unit space-time was chosen) than predators (one per unit area).

An analysis on the reduced model was conducted, then expanded the analysis to the large models.

Terms:

- Spatial Frequency – how often an event occurs across a landscape
- Temporal Frequency – how often an event occurs over time

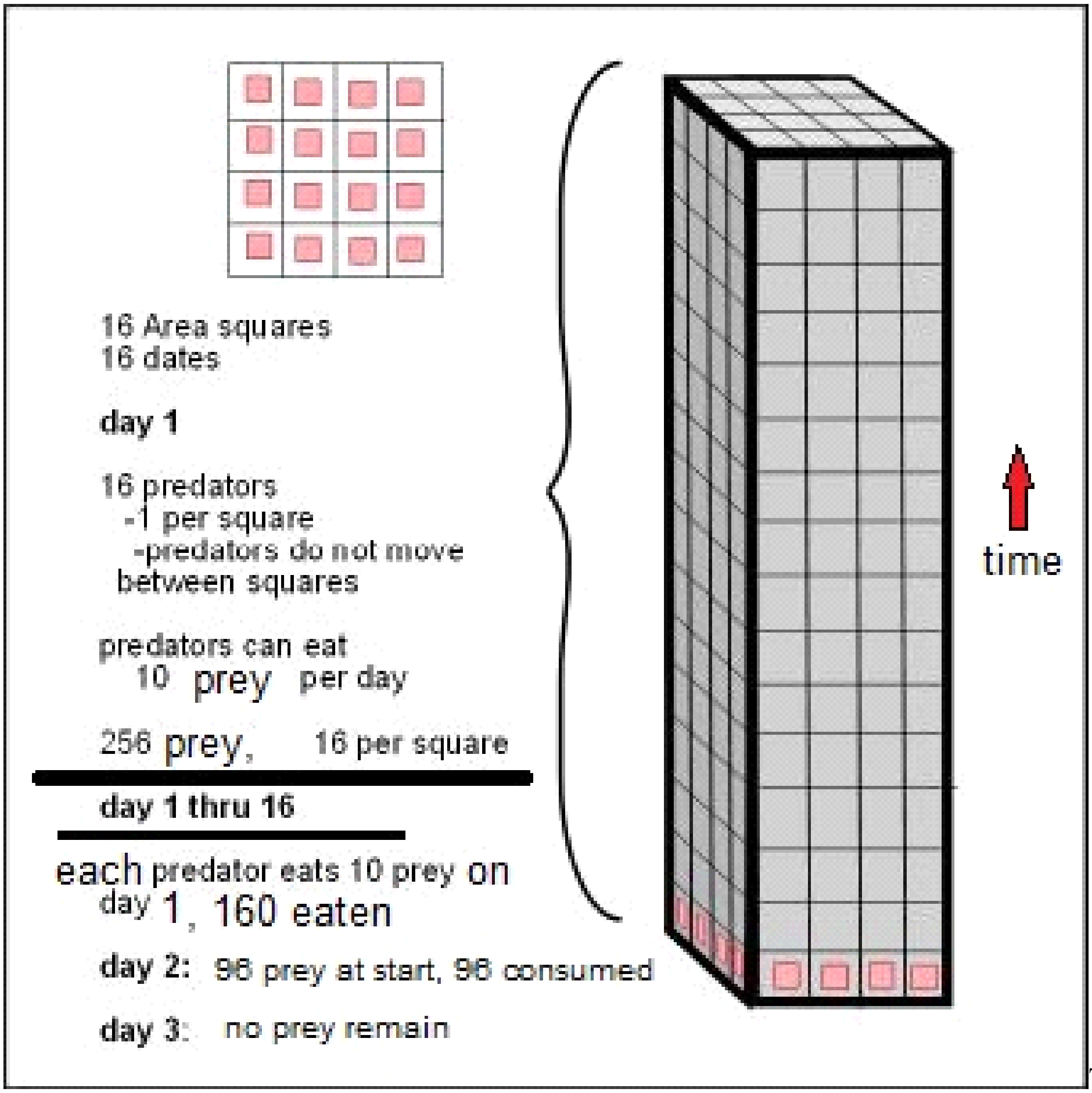
Prey and predators are initially placed at random at time=1 within the domain. Over sufficiently long time, the random walks of prey and predators can be modeled by an even placement and the randomness has no influence for the purposes of this model and can be ignored

Figure 1: Graphic analysis of (x,y,t) = (4,4,16) model of arbitrary prey and predators demonstrating extinction of prey population with initial random distributions of both prey and predators

Figure 2: Graphic analysis of (x,y,t) = (4,4,16) model of termite prey and arachnid predators. The frequency distribution of the termites over the spatial domain equals the full scale = x*y = 16. The frequency distribution of the termites over the temporal domain equals just one period (such as two weeks in the fall). This demonstrates the survival of the prey population with full interactions with predators over the spatial plane but a restricted frequency over the temporal axis. **Termites survive by using 'temporal hiding' and overwhelming predation when contact occurs.**

Figure 3: Graphic analysis of (x,y,t) = (4,4,16) model of anchovy prey and shark predators. The frequency distribution of the anchovies over the spatial domain is just one spatial unit. The frequency distribution of the anchovies over the temporal domain equals the full time scale. (such as one acre out of 361). This demonstrates the survival of the prey population with full interactions with predators over the time axis but a restricted frequency over the spatial plane. **Anchovies survive by using 'spatial hiding' and overwhelming predation when contact occurs.**

Graphic Results



The initial run of the model was a 4x4 square spatial dimension, and a 16-day temporal dimension. The metrics were that predators and prey were evenly distributed spatial on day one.

Figure 1

Day one: 16 predators, one per square, 256 prey, 16 per square

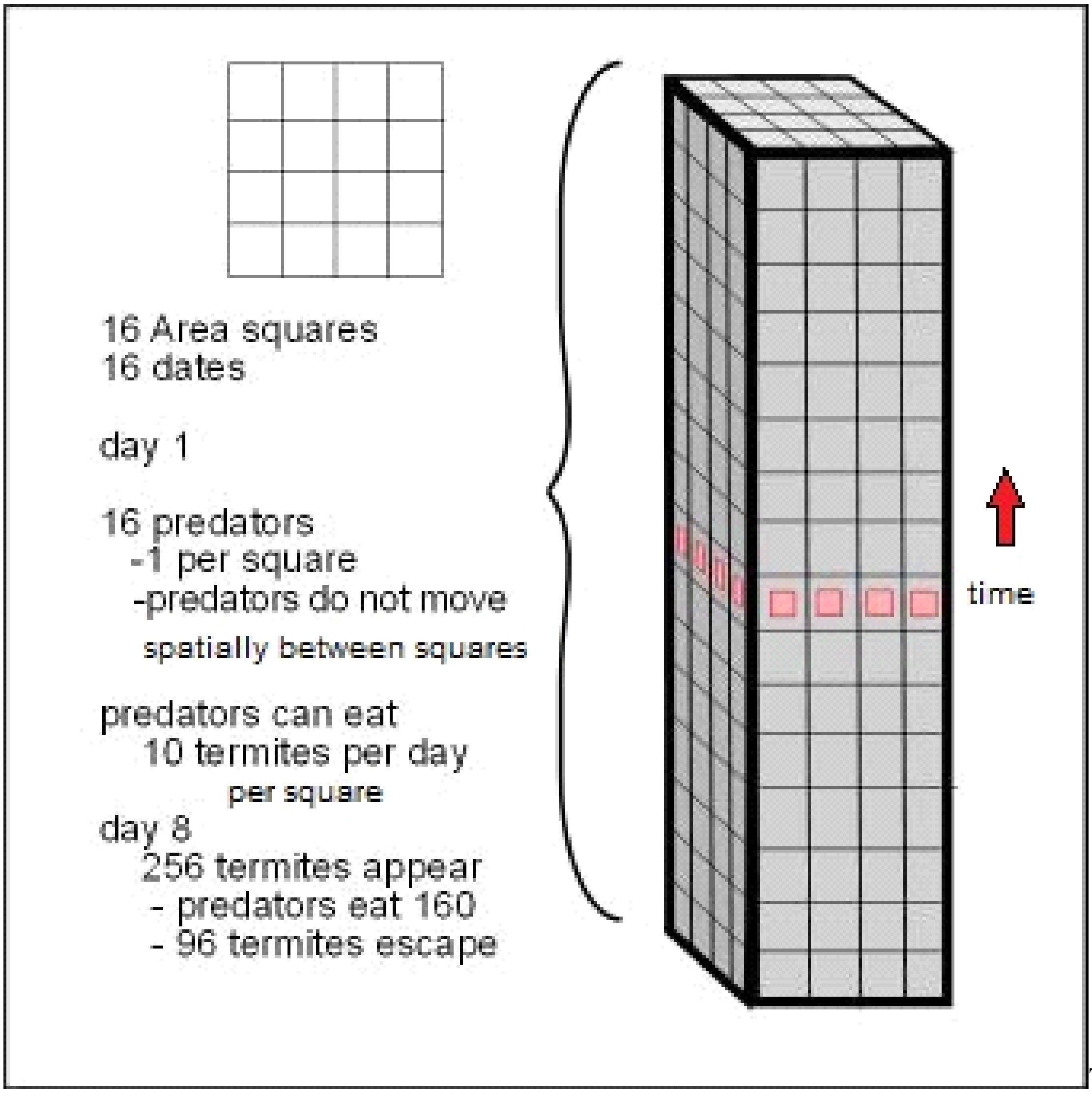
Day two: 16 predators, one per square, 96 prey, 6 per square

Day three: 16 predators, one per square, 0 prey, no survivors …..

Day sixteen: 16 predators, one per square, 0 prey, no survivors

Conclusion: In this model, the prey do not survive, without temporal or spatial separation from the predators

Note: Throughout this simple model, the dynamics of prey and predator boom and bust population fluctuations were not attempted to be shown because, although they may impact absolute numbers, they do not affect relationships or ratios.



The **temporal-frequency** run of the model was a 4x4 square spatial dimension, and a 16-day temporal dimension. The metrics were that termites only appear on one date.

Figure 2

Day one: 16 predators, 256 termites in hiding, 16 per square

Day seven: 16 predators, 256 termites in hiding, 16 per square

Day eight: 16 predators, 256 termites show up, all across the landscape, 16 per square

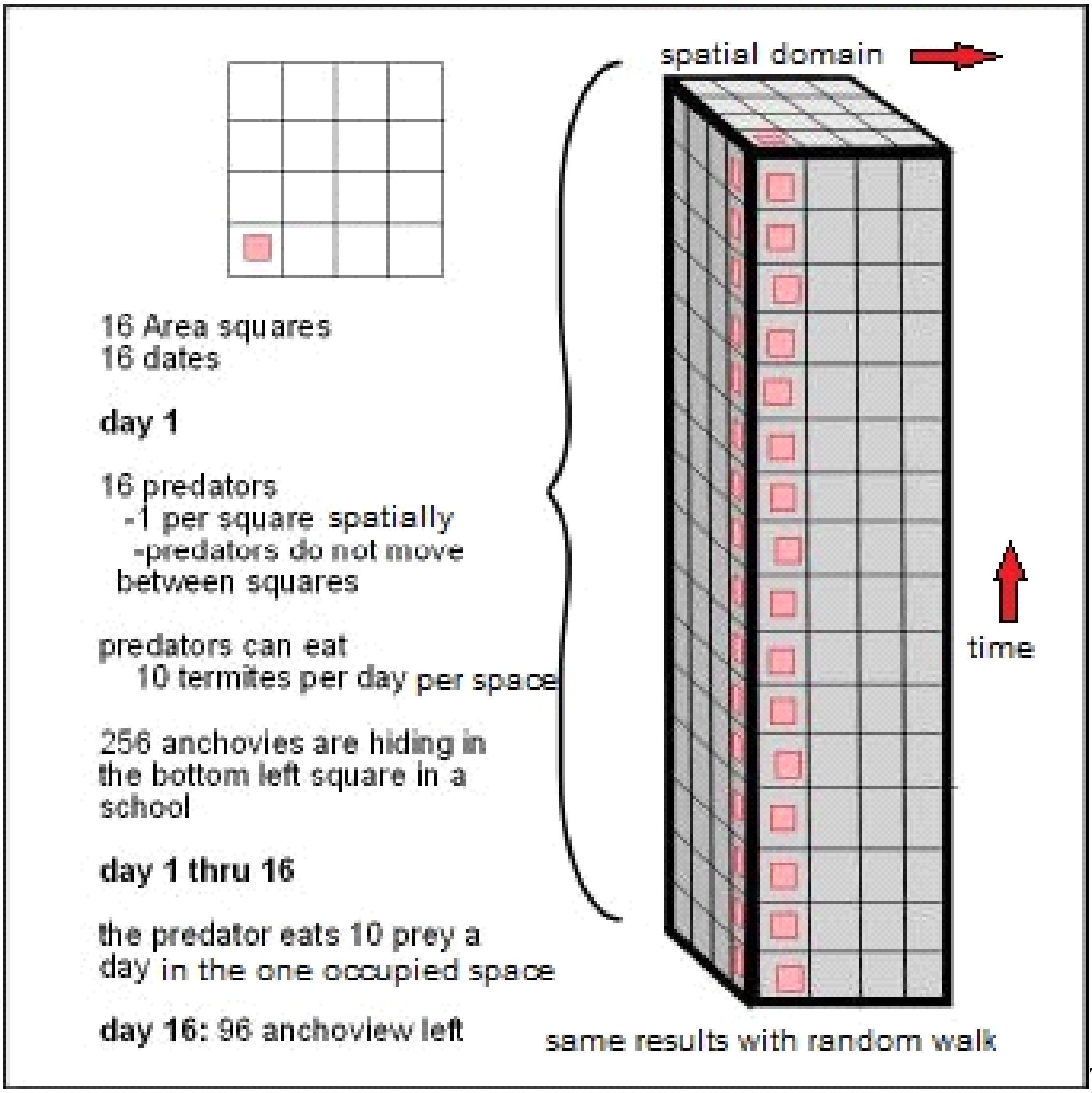
Each predator eats 10 termites, 160 termites eaten

Day nine: 16 predators, 96 termites in hiding, 6 per square

Day sixteen: 16 predators, 96 termites in hiding, 6 per square

Conclusion: This demonstrates the survival of the prey population with full interactions with predators over the spatial plane but a restricted frequency over the temporal axis. **Termites survive by using 'temporal hiding' and overwhelming predation when contact occurs.**

This model is easy to understand and is 'intuitive'.



The **spatial frequency** run of the model was a 4x4 square spatial dimension, and a 16-day temporal dimension. The metrics for sardines were that they only appear in one square.

Figure 3

Day one:	16 predators, 256 anchovies in hiding, 256 on one square
	One predator eats 10 anchovies, 246 remaining
Day two:	16 predators, 246 anchovies in hiding, 246 on one square
	One predator eats 10 anchovies, 236 remaining
Day eight:	16 predators, 186 anchovies in hiding, 186 on one square
	One predator eats 10 anchovies, 176 remaining
Day nine:	16 predators, 176 anchovies in hiding, 176 on one square
	One predator eats 10 anchovies, 166 remaining
Day sixteen:	16 predators, 106 anchovies in hiding, 106 on one square
	One predator eats 10 anchovies, 96 remaining

Conclusion: This demonstrates the survival of the prey population with full interactions with predators over the time axis but a restricted frequency over the spatial plane. **Anchovies survive by using 'spatial hiding' and overwhelming predation when contact occurs.**

Discussion

Comparing models: if we enlarge the boundaries of the simple model to match that of the year-long design, our numbers are increased (based on one prey per box), to 400 predators and 160,000 prey, but the ratios stay the same.

One can easily describe the predominate termite behavior as 'hiding' for most of the time, then hiding from, or overwhelming, the predator population during the infrequent interactions.

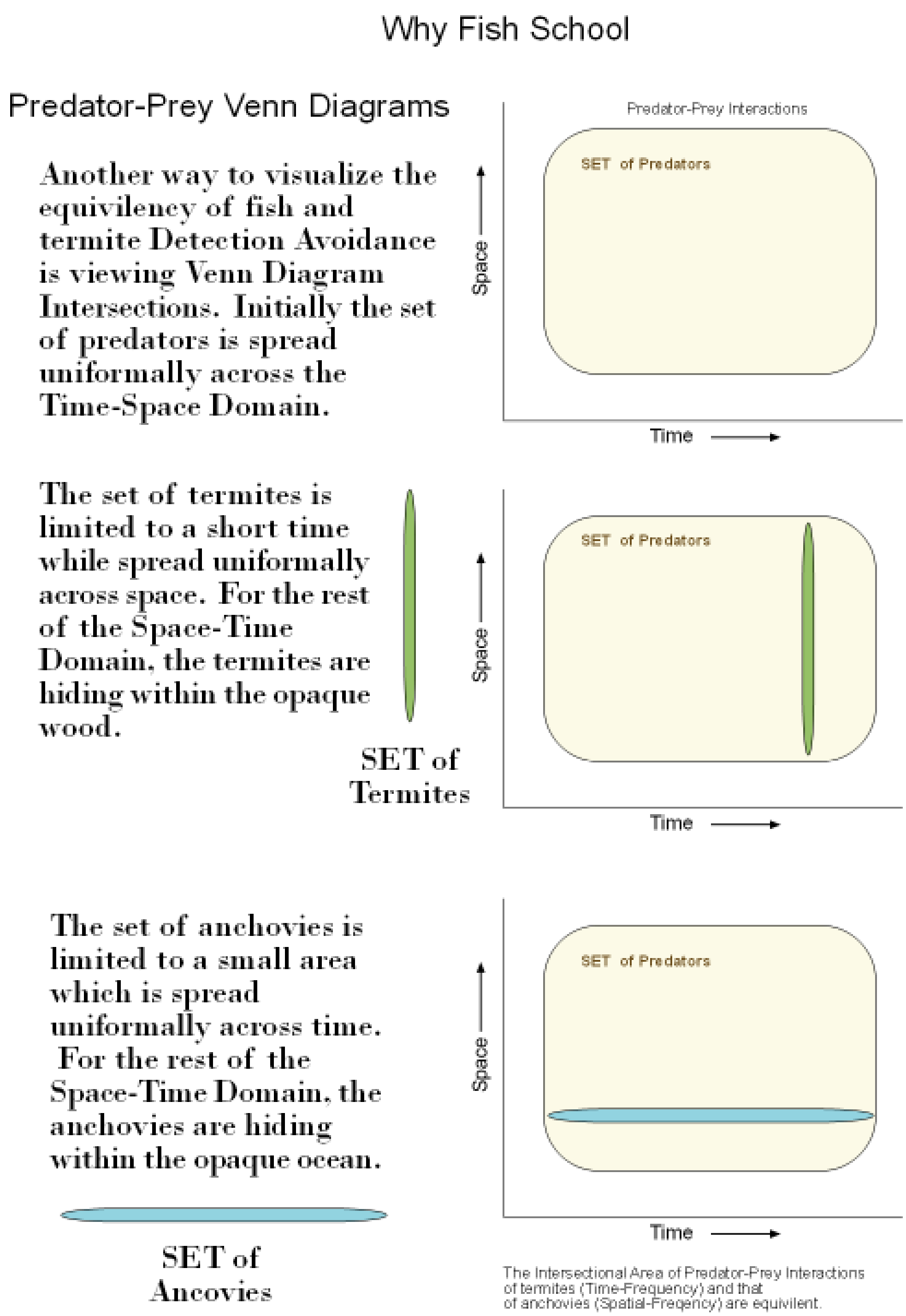
Note: Using the same parameters between temporal termites and spatial anchovies results in the same numbers of survivors.

The interactions within Earth's Biome evidently contribute to the evolutionary forces that drive the grouping of prey, whether in a spatial-frequency domain or temporal-frequency domain.

We conclude there is a Fourier equivalency between the temporal frequency of the nuptial emergence of termites, and the spatial frequency of fish shoals.

It is not clear initially, however, which evolutionary force drives schooling activities more: detection avoidance or coordinated escape behavior (group shielding). All schooling shows both. Which came first, 'the chicken or the egg'?

‘The Noblest of Pleasures is the Joy of Understanding’[13]



ONLINE INTERACTIVE COMPUTER MODELS

These computer models and interactive programs are available online for use or downloading.

The program is MS Excel

This software was chosen because of its worldwide availability and ease of use.

Investigators will be able to enter population, predator consumption rates, time of exposure, location exposure values, and then see immediately the impacts on population over time.

The cells in pink allow user input of data, the cells in grey with orange text are the resulting population changes due to predation.

NOTE: Contrasting Detection Avoidance with other fish school mechanism proposals:

A paper, ***Safety in numbers: the dilution effect and other drivers of group life in the face of danger***[16] ***,*** by Jussi Lehtonen & Kim Jaatinen, has been one of the best source of information and summaries[16] of causes of fish aggregation.

Below, Table 1 is extracted from their paper

Note: none of the processes are the equivalent of group detection avoidance , i.e. "hiding in space".

Detection Avoidance is distinctly different than the behaviors summarized by Jussi Lehtonen & Kim Jaatinen in their 2016 paper in Springer. It is effective while in shoal activity

Table 1 Summary table of processes yielding safety in numbers

	Rationale	Effect on individual	Effect on group
Dilution effect/attack abatement	Stay in larger groups to 'dilute' predation pressure among individuals in the group	Increases fitness relative to a solitary individual	Group average fitness can increase if initially below optimum size or decrease if already at or above optimum. Does not imply fitness differences within the group
Satiation effect	Congregate in groups (in space and/or time) that are larger than the maximum predator intake, leading to dilution	Increases fitness relative to solitary individual, or those in groups smaller than the maximum predator intake	Increases average survival in group relative to groups smaller than the maximum predator intake
Selfish herding	Moving to a safer position relative to other group members and predator	Increases fitness of focal individual moving to a safer position	Creates mortality differences within the group. Can potentially increase group average survival
Confusion effect	Large numbers of moving prey can hamper predator target selection and accuracy.	Increases individual fitness	Decreases predator attack success, thereby generally increasing group average survival. Can create mortality differences within the group
Group vigilance/alarm calls	Many individuals are more efficient at detecting predators.	An individual giving an active warning signal may increase its own risk, but benefit by being warned by other group members[a].	Can evolve via kin selection, increasing survival of a group of relatives. Can also create within-group differences in survival when collective detection is not perfect

The author of this paper finds it easier to compare and contrast the impact/ mechanism effect on a population in the time domain (termites/cicadas), then reflect what that means in the spatial domain (fish). The impact of predatorial pressure on termites/cicadas in a restricted time is similar to those pressures on fish in restricted space.

	Termites/Cicadas	Fish
Group vigilance:	No observed behavior	Yes
Confusion effect:	No observed behavior	Escape into opaque sea
Selfish herding:	Termites Yes, Each one independent during the short time exposed (Cicadas do not display significant escape behavior, no)	Game theory suggests that schooling breaks over generational time frames
Saturation effect:	Yes	Yes
Dilution effect:	Yes	Yes

Discussion - Examples - Mutualism

Living Example (3): Mutualism: Fish, an unusually Intelligent Mammal, and Dinosaurs.

Below is an example to what lengths living creatures will cooperate to be successful against the **Detection Avoidance** strategy.

Boney fish, *Osteichtyes,* separated from the ancestors of terrestrial vertebrates over 400 million years ago, while the ancestors of dinosaurs and mammals split apart over 300 million years ago. My mind races to consider the forcing functions of cooperation that selected these seemingly separate species into not only into a beneficial mutual relationship, but one that relies on the astounding level of cooperation and sophistication of hunting packs.

Why do dolphins, tuna, and seabirds work together to find fish schools[6]? As noted in this thesis, fish form shoals and schools to evade predation by disappearing in the enormously large and opaque ocean (hiding). Tuna (highly mobile, extremely fast, apex predators) cannot find them efficiently. Seabirds (dinosaurs) with the ability to fly quickly far and wide, can find the shoals easier, but, cannot maximize the opportunity because the schools disappear deeper into the ocean when attacked.

Dolphins (highly intelligent) jumping out of the water can see the birds from miles away and journey to them, accompanied by the tuna. As a team (cooperation), the three species improve their foraging success rates: the birds act as scouts, the dolphins a messengers, and the tuna form a 'basement' under the fish school to contain the prey at the surface so all three can feed.

Predatorial cooperation by species separated by 400 million years to counter the prey's cooperative schooling behavior. In both cases, the average fitness within the groups are improved over that of solo individual.

Sidebar: The success of the large fish aggregations within shoals and schools may have assisted in the evolution of tuna swimming in packs. The size of fish schools are basically immune to individual predators during a single event, benefiting from the saturation/dilution process. In addition, the individual predator being fully satiated, would not suffer losses from additional cooperating predators, and would benefit from expanded search abilities.

The packs of tuna would scour the oceans of individual fish while searching for the shoals, creating feedback time and time again against the gene pool of bait fish whose genetic directives would allow them to strike out on their own, eliminating successful reproduction of those selfish genes of individual fish trying to abandon the school. Offence vs defense on evolutionary scales.