Living in Fear: An Individual-based model of a killer whale-dusky dolphin behavioral game

Mridula Srinivasan

Office of Science and Technology

Protected Species Science

NOAA Fisheries




Roadmap

- Background
- Research Objectives
- Model Description
- Model Evaluation
- Model Simulation
- Results
- Summary and Conclusions

Scared Prey- Fierce Predators

- Predators don't have to consume prey to have an effect on prey lifestyle decisions (Sih 1987, Lima and Dill 1990, Brown et al. 1999)
  - i.e. physiology, **behavior**, morphology, life history

- Can be more consequential than lethal predation (Preisser et al. 2005, Luttbeg & Kerby 2005, Creel and Christianson 2008) affecting population dynamics and demographics, and ecological communities

Trophic Cascades (Paine 1980)

- Examples

Wolf-moose-balsam fir (Post et al.1999)

- Killer whales- sea otter- urchins – kelp (Estes and Palmisano, 1974)
- Tiger sharks –dolphins-dugongs- sea grass (Dill et al. 2003)
- Bass-minnows-zooplankton-phytoplankton (Carpenter et al.1987)

Predation Risk Effects

- Habitat shift (Heithaus and Dill 2002)
- Prey and Predator dispersal (Sih et al. 2007)
- Foraging behavior (Brown and Kotler, 2004)

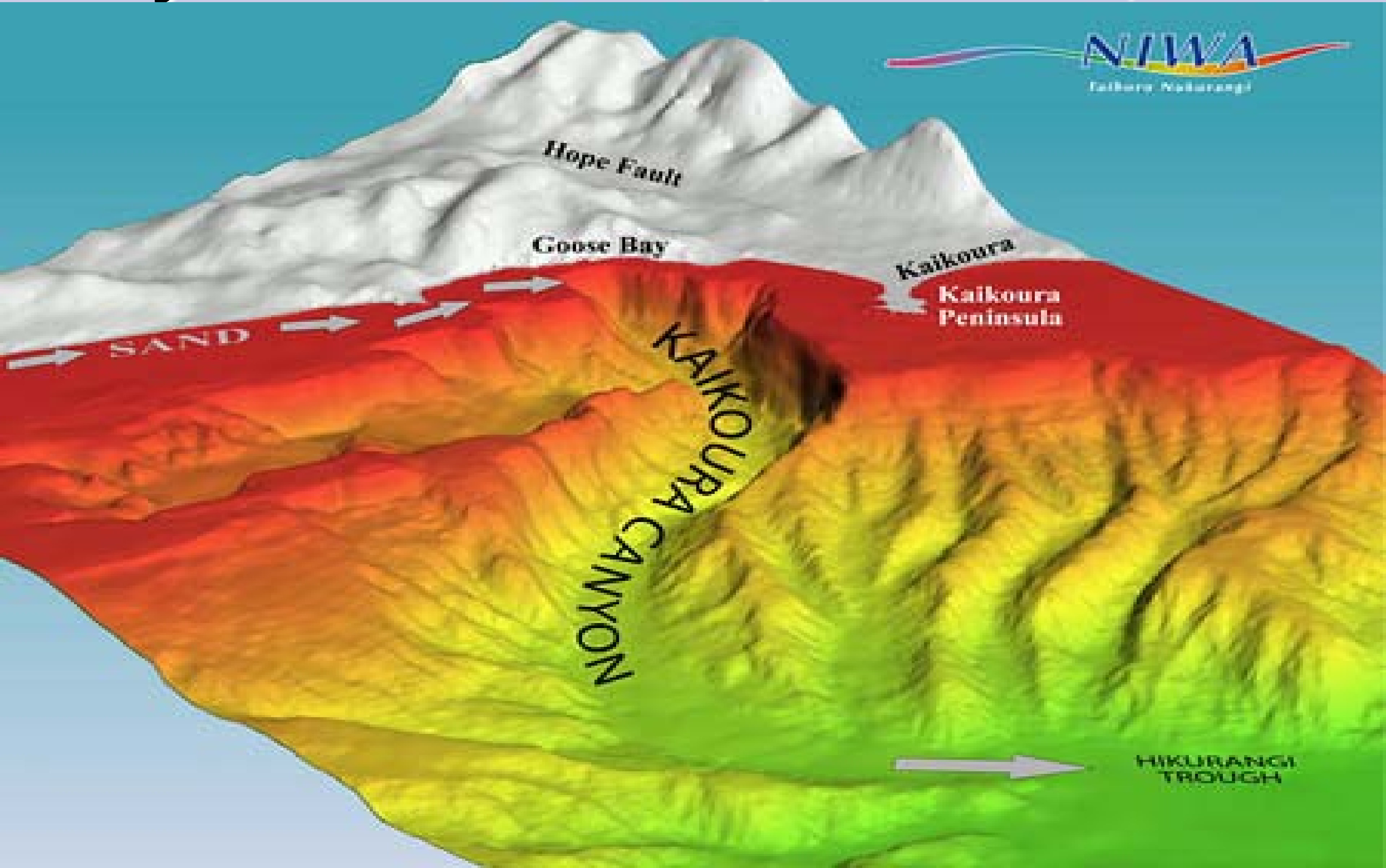
Predation Risk affecting the species rather than cascade or ecological effects (Creel and Christianson 2008)

- Stress e.g. snow shoe hare-lynx (Boonstra et al. 1998)
- Reproductive physiology in elk (Creel et al. 2007)

Terminology

- Non-consumptive effects (NCE)
- Risk effects
- Fear effects
- Indirect predation risk effects
- Non-lethal effects
- Sub-lethal effects

System of Interest, Kaikoura,NZ



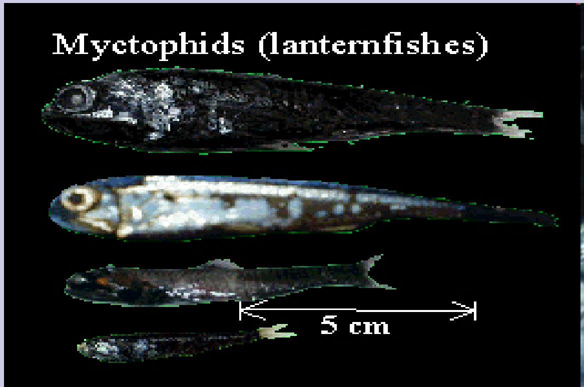
Ecological Players

Prey - Dusky dolphin (*Lagenorhynchus obscurus*)

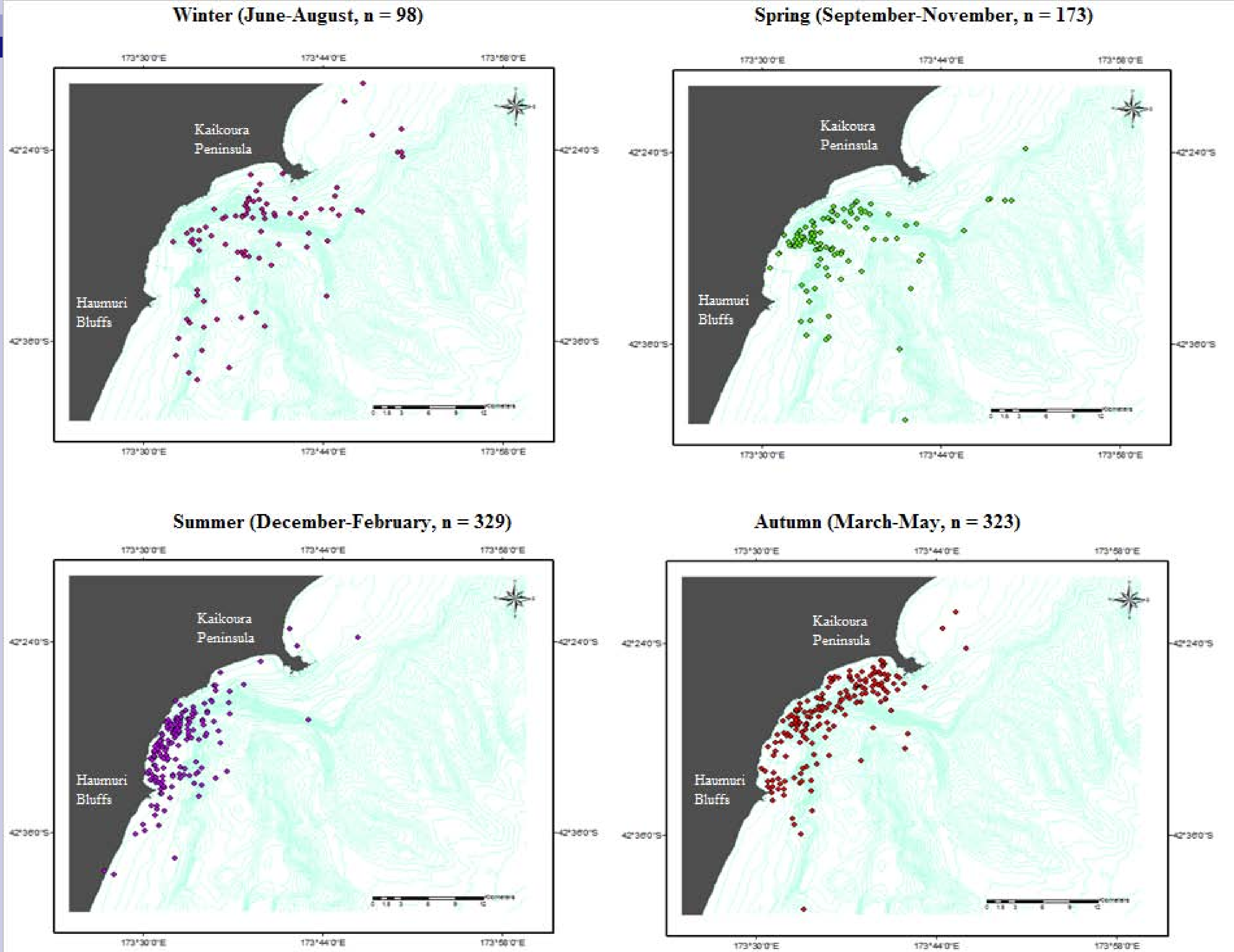
Predator- Killer whale (*Orcinus orca*)

Deep Scattering Layer (DSL)

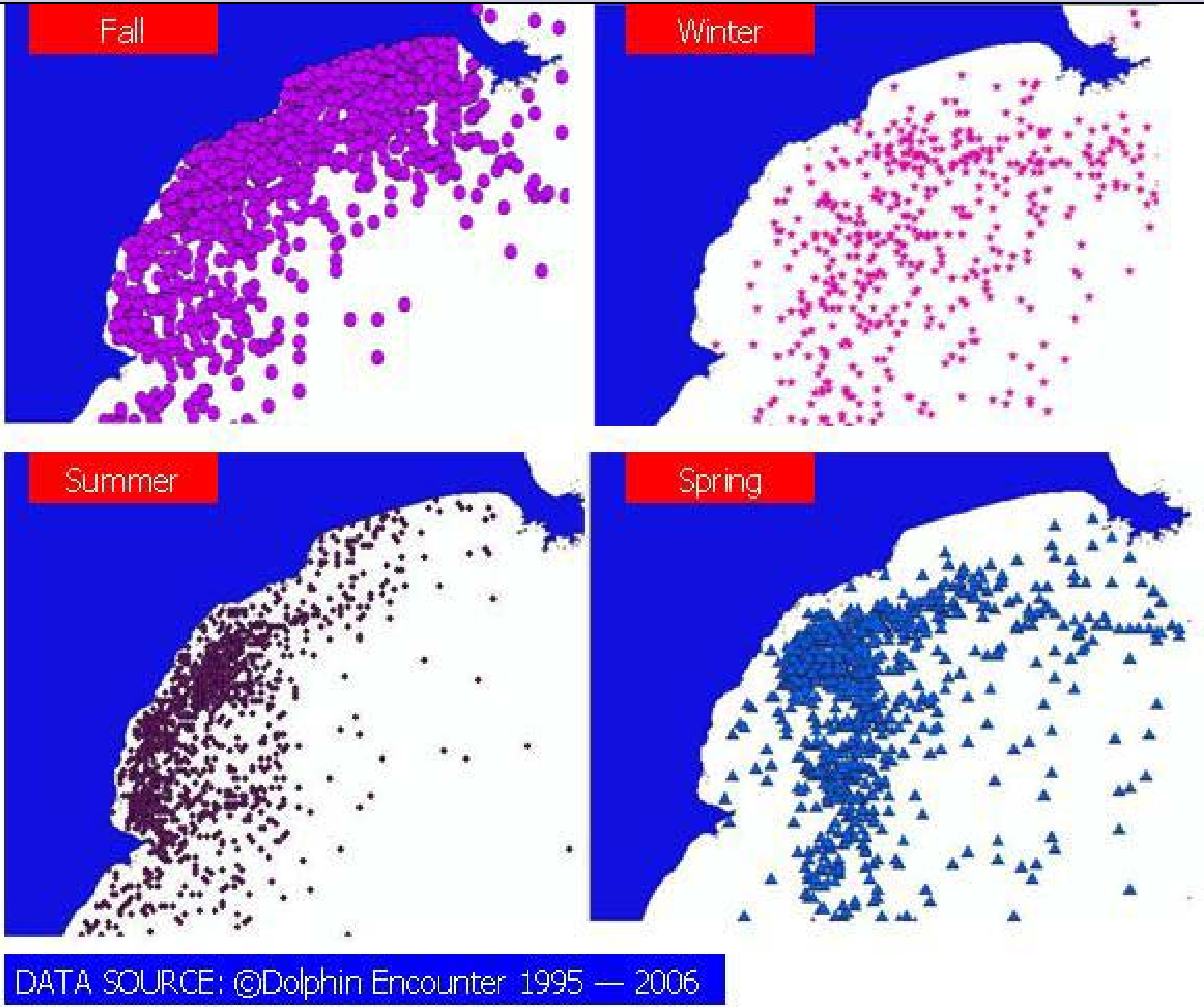
Benoit-Bird©



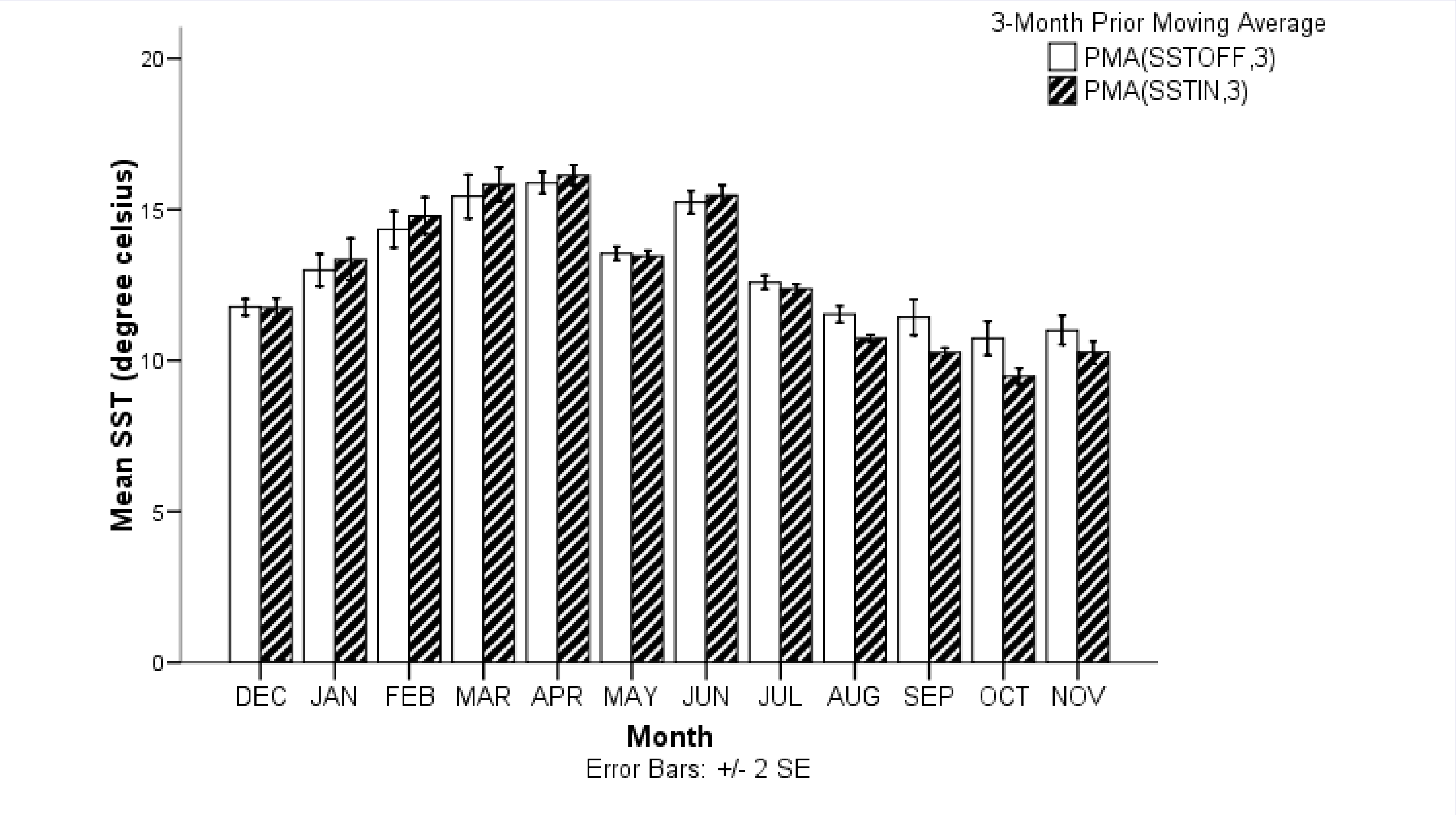
Benoit-Bird©



From Markowitz (2004) [Data period: 1995-2003]

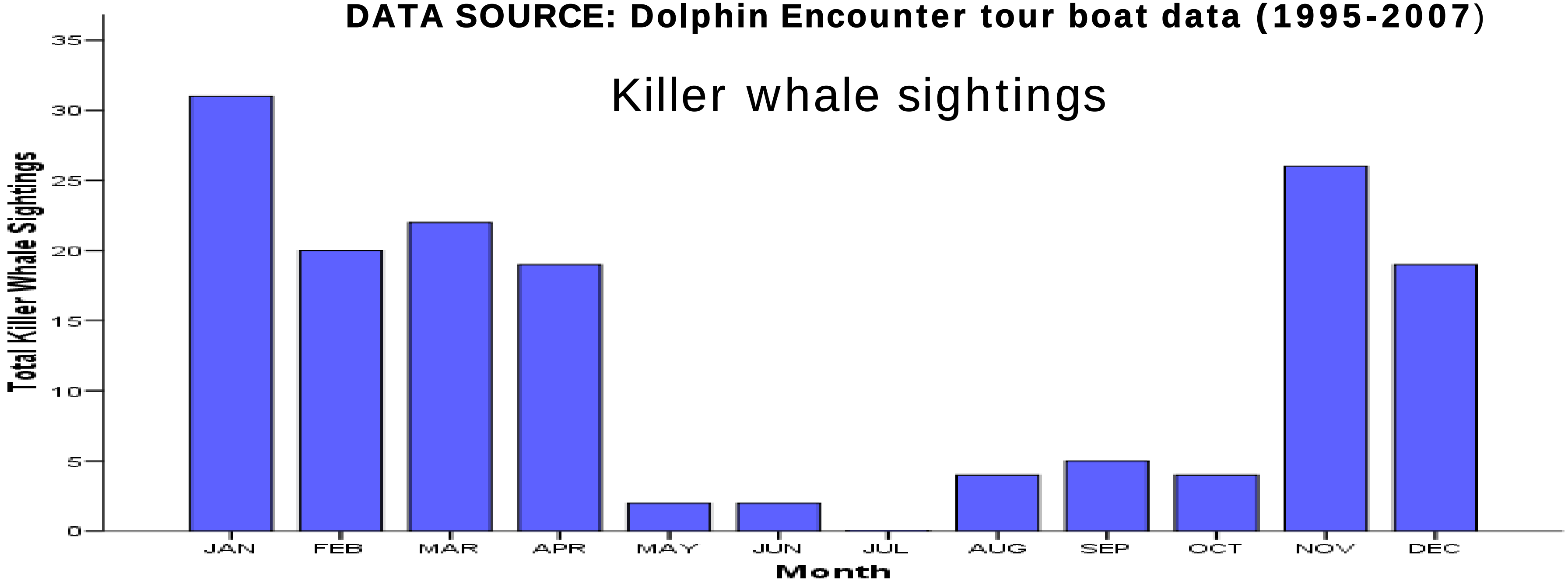

Fall
Winter
Summer
Spring
DATA SOURCE: ©Dolphin Encounter 1995 — 2006

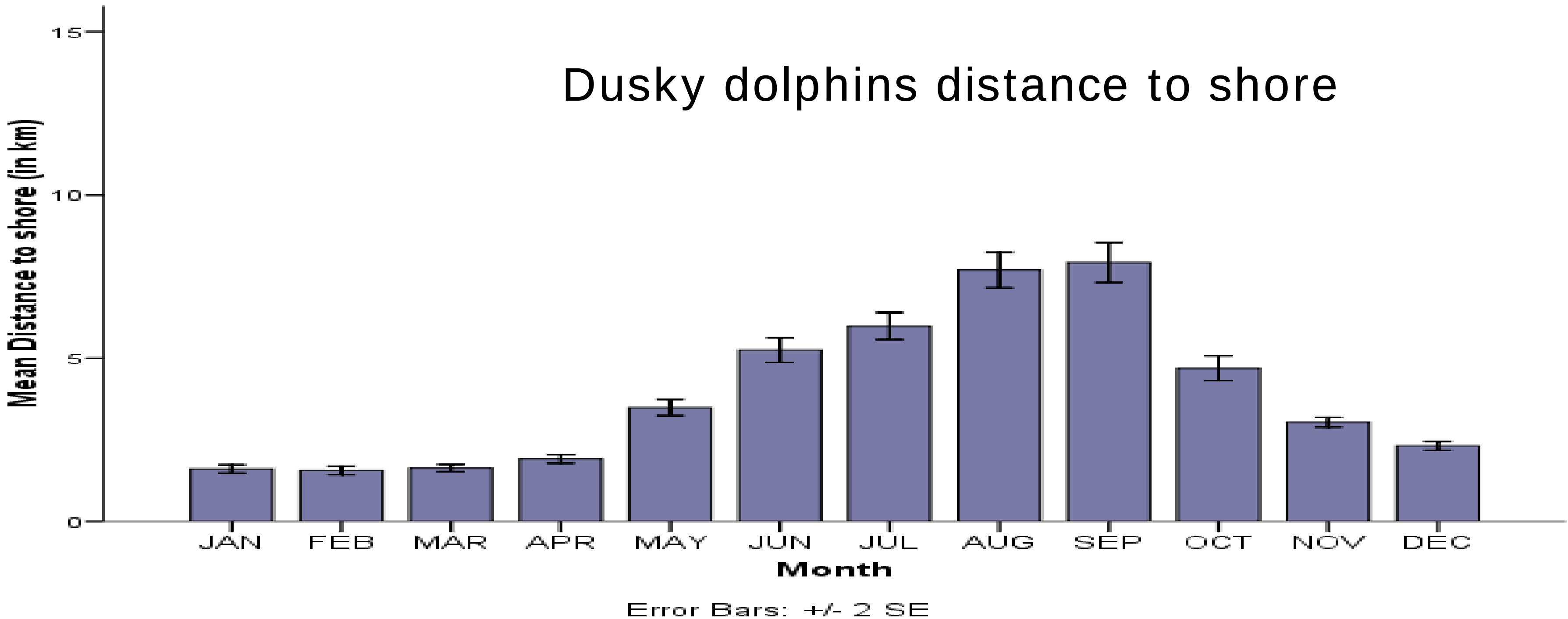
Sea Surface Temperature (SST) Trends



5-year SST data (2003-2007)

DATA SOURCE: Dolphin Encounter tour boat data (1995-2007)

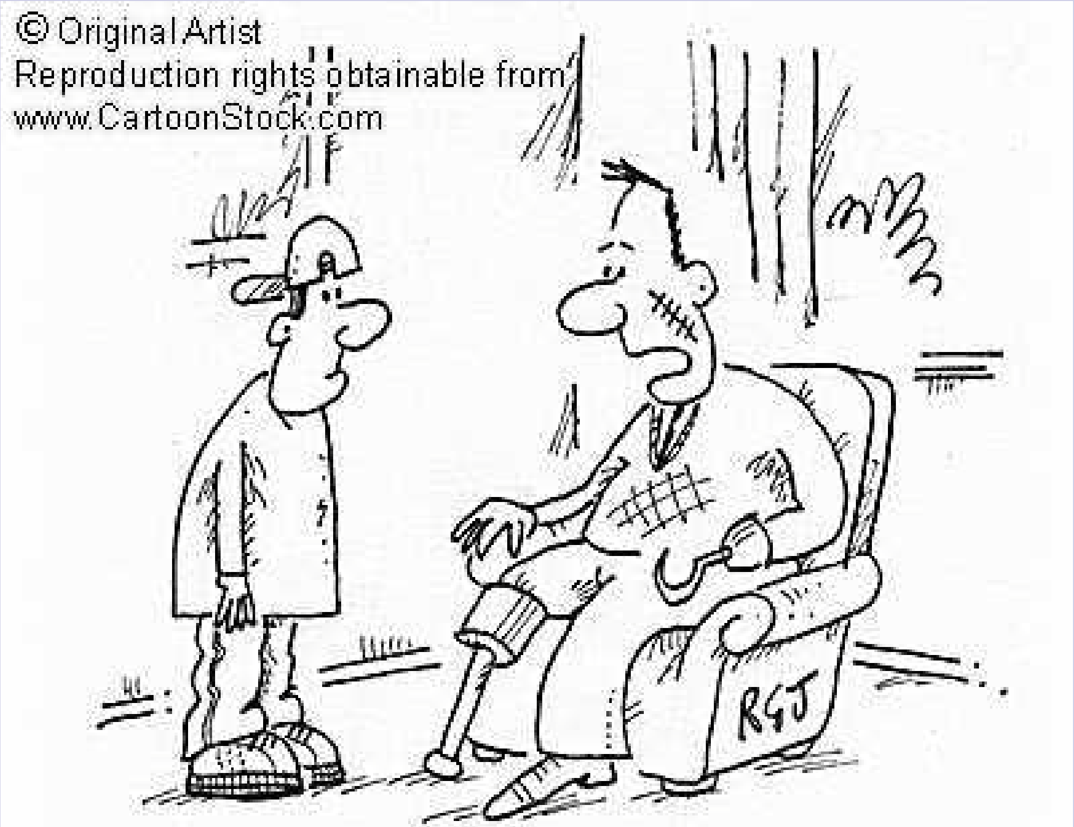




Research Objectives

- Develop a spatially explicit, individual-based model (IBM) simulating a dusky dolphin avoiding killer whales in a heterogeneous marine habitat near Kaikoura, New Zealand based on our current level of understanding of the system.
- Use the model to compare evolutionary costs vs. benefits focusing principally on **foraging time** and **number of killer whale encounters** for dusky dolphins adopting short and long-term anti-predator behaviors.

What does ‘fear’ mean to you?



"Son, when I was your age my dad told me to see the world, to swim with the dolphins and the sharks, and now I'm telling you...just stick to the dolphins."

Fear-driven behavior

Costs

- Commute time and distance
- Spend more fuel – energy

Benefits

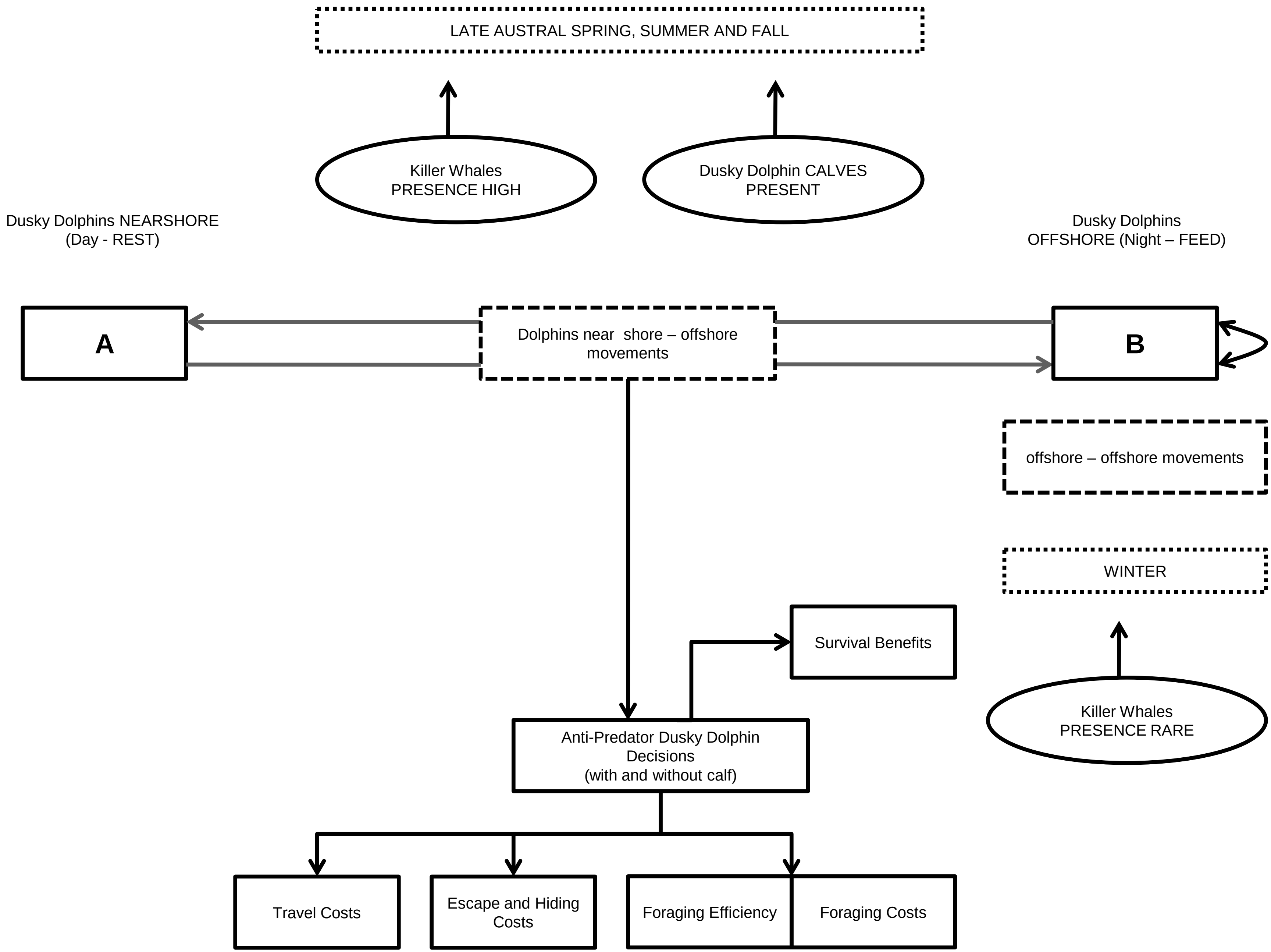
- Staying safe-peace of mind

Why it matters?

- Focus has been on lethal predation
- Quantifying anti-predator decisions as costs vs. benefits
- Making predator-prey behavior consequential – a behaviorally responsive interaction
- Ecologically relevant
- Foster better management practices

Measuring fear effects

- Develop and evaluate an IBM capturing the dynamic behavioral interaction between a clever prey avoiding a clever predator.
- Examine evolutionary costs *vs.* benefits in terms of foraging time and number of encounters with killer whales.


LATE AUSTRAL SPRING, SUMMER AND FALL
Killer Whales PRESENCE HIGH
Dusky Dolphin CALVES PRESENT
Dusky Dolphins NEARSHORE (Day - REST)
Dusky Dolphins OFFSHORE (Night – FEED)
A
Dolphins near shore – offshore movements
B
offshore – offshore movements
WINTER
Killer Whales PRESENCE RARE
Survival Benefits
Anti-Predator Dusky Dolphin Decisions (with and without calf)
Travel Costs
Escape and Hiding Costs
Foraging Efficiency
Foraging Costs

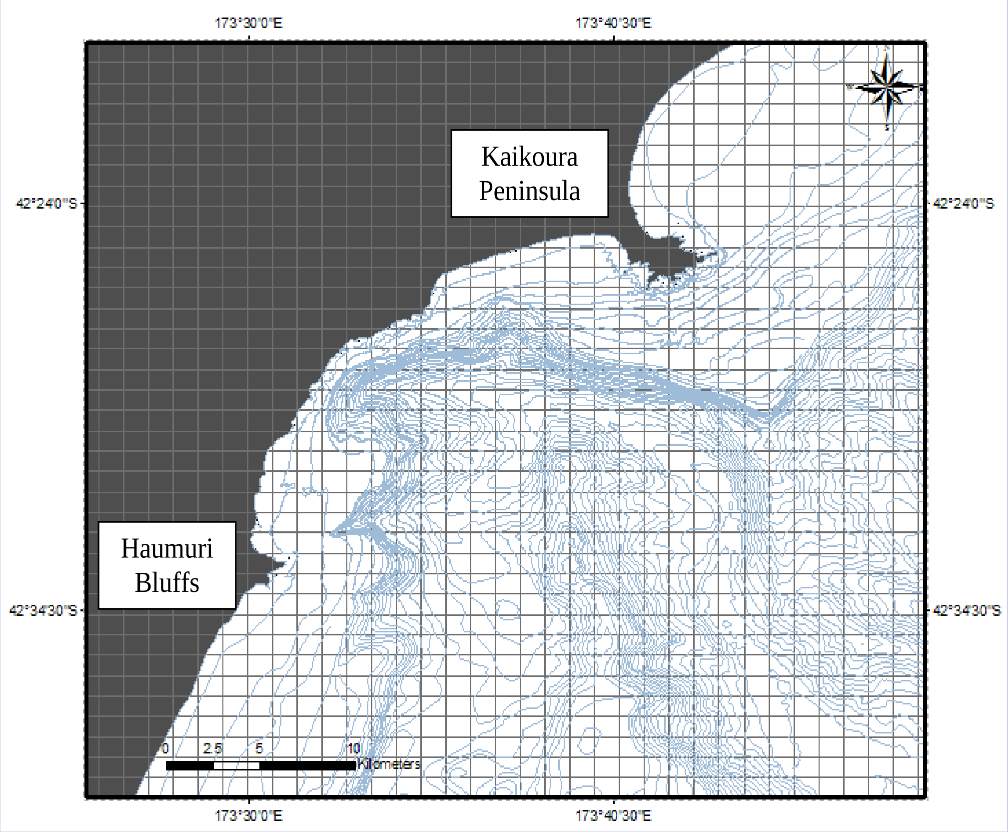
Individual-based model (IBM)

- Basis: Individual properties is representative of the population

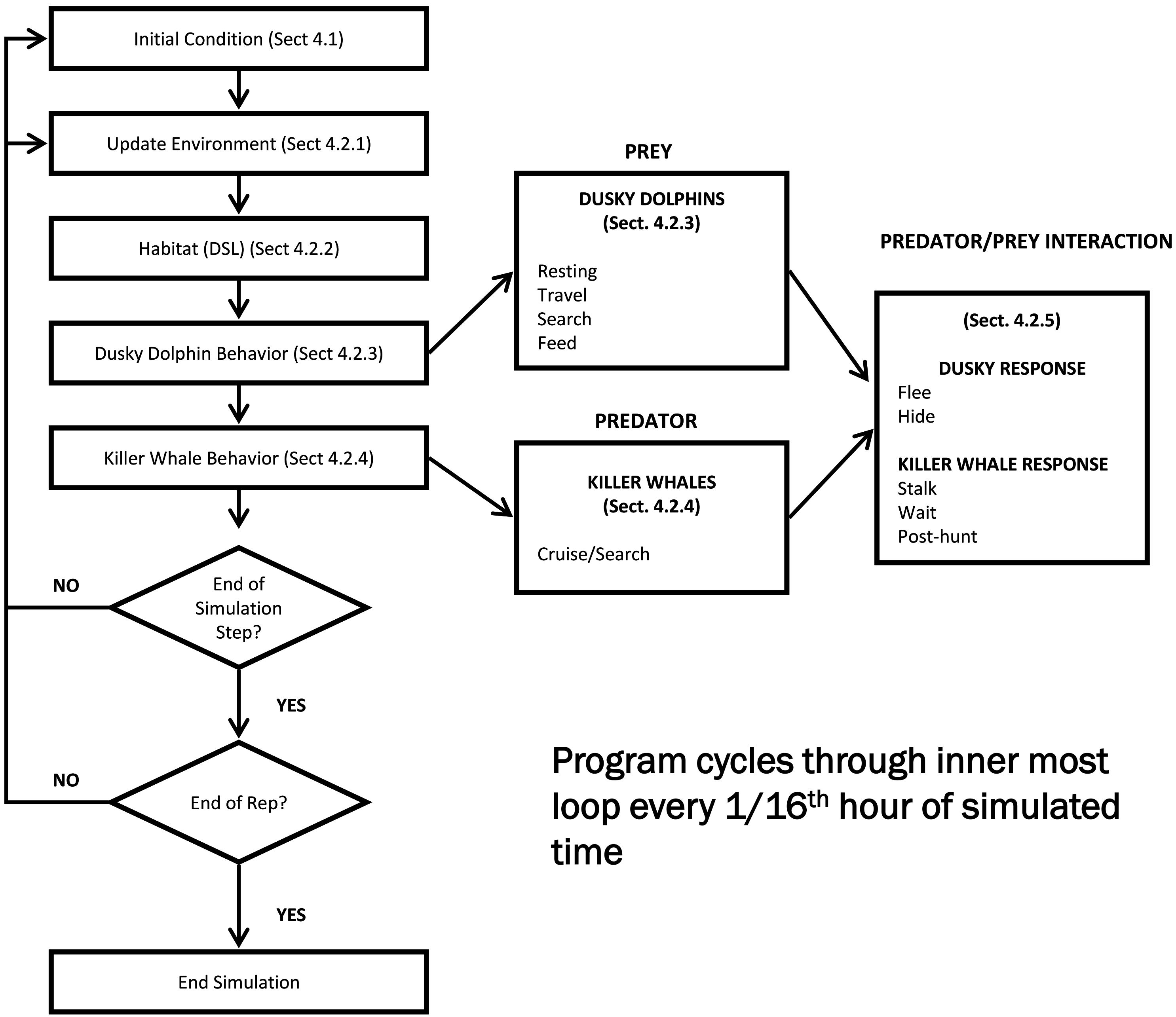
  (IBM, Adams and DeAngelis 1987)
- Programmed in VB.net (Microsoft®, 2003)
- Geo-referenced, grid-based, stochastic model

Model Features

- 3 classes
  - Dusky dolphin
  - Killer Whale
  - Habitat (food)
- Habitat: 1468 instances 1 km x 1 km cells, depth defined by bathymetric contour lines



Model Process



Program cycles through inner most loop every 1/16th hour of simulated time

Class Attributes	Values
(b) Dolphin class	
Location	X-Y coordinates
Behavioral state	Resting, Traveling, Foraging, Fleeing, or Hiding
Distance to detect killer whales (km)	5 (1, 5, 7, 10)
Hiding time (hr)[a]	1 (0.25, 0.5, 1, 3, 5, 7, 9)
Resting velocity (km hr^{-1})[a, b]	4
Foraging velocity (km hr^{-1})	5
Traveling velocity (km hr^{-1})[b]	8
Fleeing velocity (km hr^{-1})[b,]	18
(c) Killer Whale class	
Location	X-Y coordinates
Behavioral state	Cruising, Stalking, Waiting, or Post-hunting
Distance to detect dolphins (km)	5
Reentry Interval (days)[d, e]	3
Post-hunt time (hr)	1
Waiting time (hr)	1
Average Cruising velocity (km hr^{-1})[f,g]	8
Average Stalking velocity (km hr^{-1})[f-h]	16
(a) Habitat class	
Spatial location	X-Y coordinates
Depth	m
DSL	Yes or No[*]
(d) Aggregated variables	
Total Distance	km
Distance Traveling	km
Distance Resting	km
Distance Foraging	km
Distance Fleeing	km
Time Resting	Proportion
Time Traveling	Proportion
Time Hiding	Proportion
Time Fleeing	Proportion
Time Foraging	Proportion
Total Killer Whale Days in System	Number
Predator-prey Encounters	Number

[a] Ciprano (1992); 1 to 4 hr

Time Hiding	Proportion
Time Fleeing	Proportion
Time Foraging	Proportion
Total Killer Whale Days in System	Number
Predator-prey Encounters	Number

[a] Ciprano (1992); 1 to 4 hr

[b] Markowitz (2004); between 16 and 22 km hr^{-1}

[c] Dahood et al. (2008)

[d] Srinivasan and Markowitz (2009)

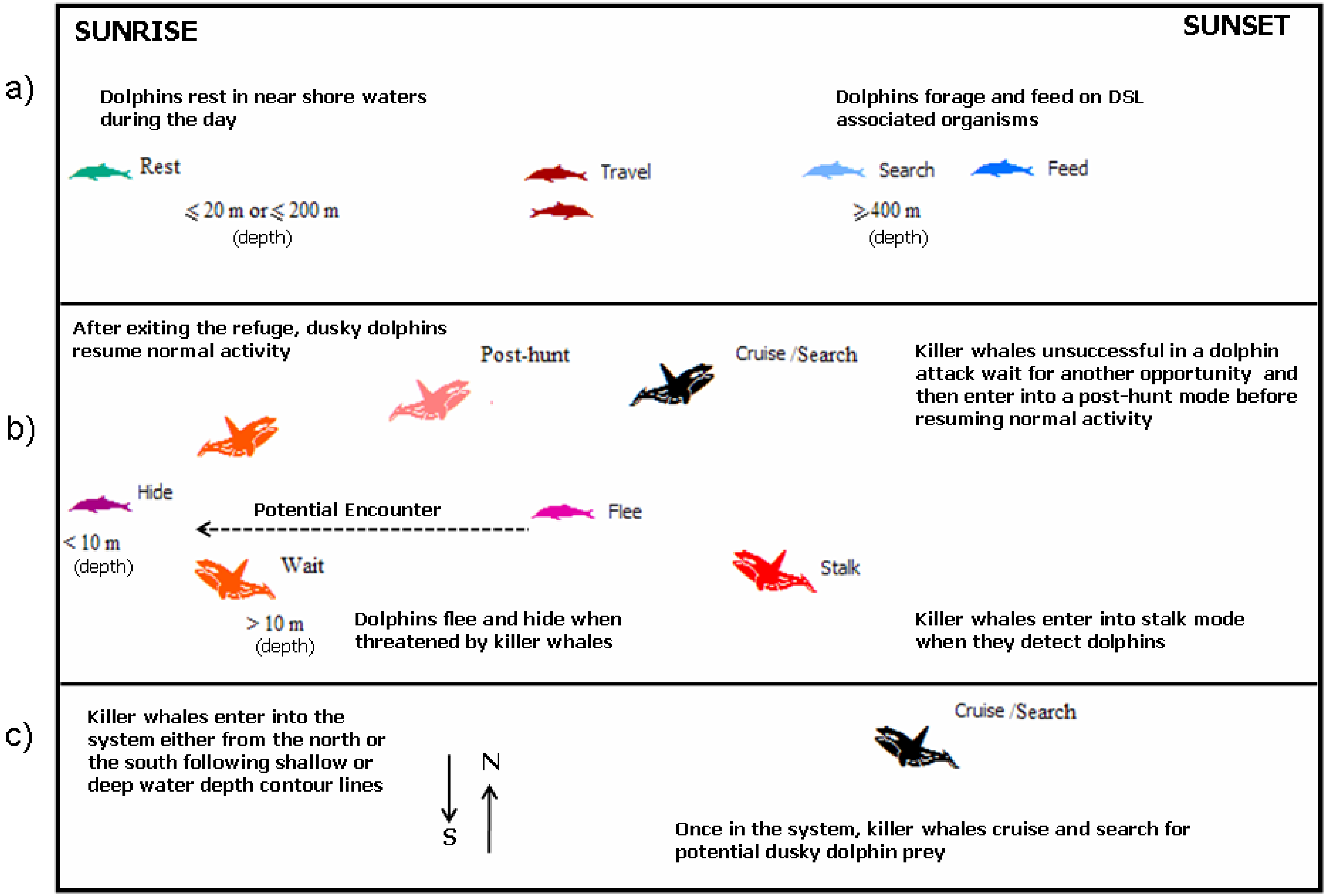
[e] Dolphin Encounter tour boat data (1995 - 2007)

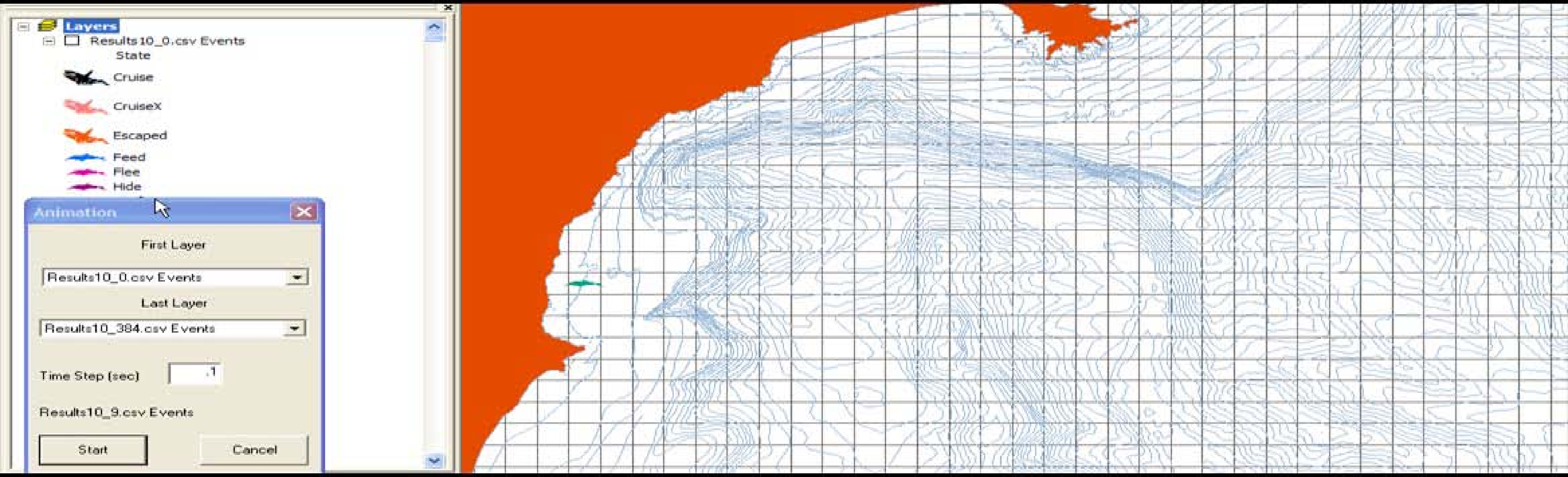
[f] Williams (2002); 12.6 (cruising) – 43 (sprinting speed) km hr^{1}

[g] Ford et al. (2005); 15 to 30 km hr^{1} (Stalking/chasing velocity)

[h] Ford and Reeves (2008); >15 to 20 km hr^{1} (Stalking/Chasing Velocity)

*stochastic variable

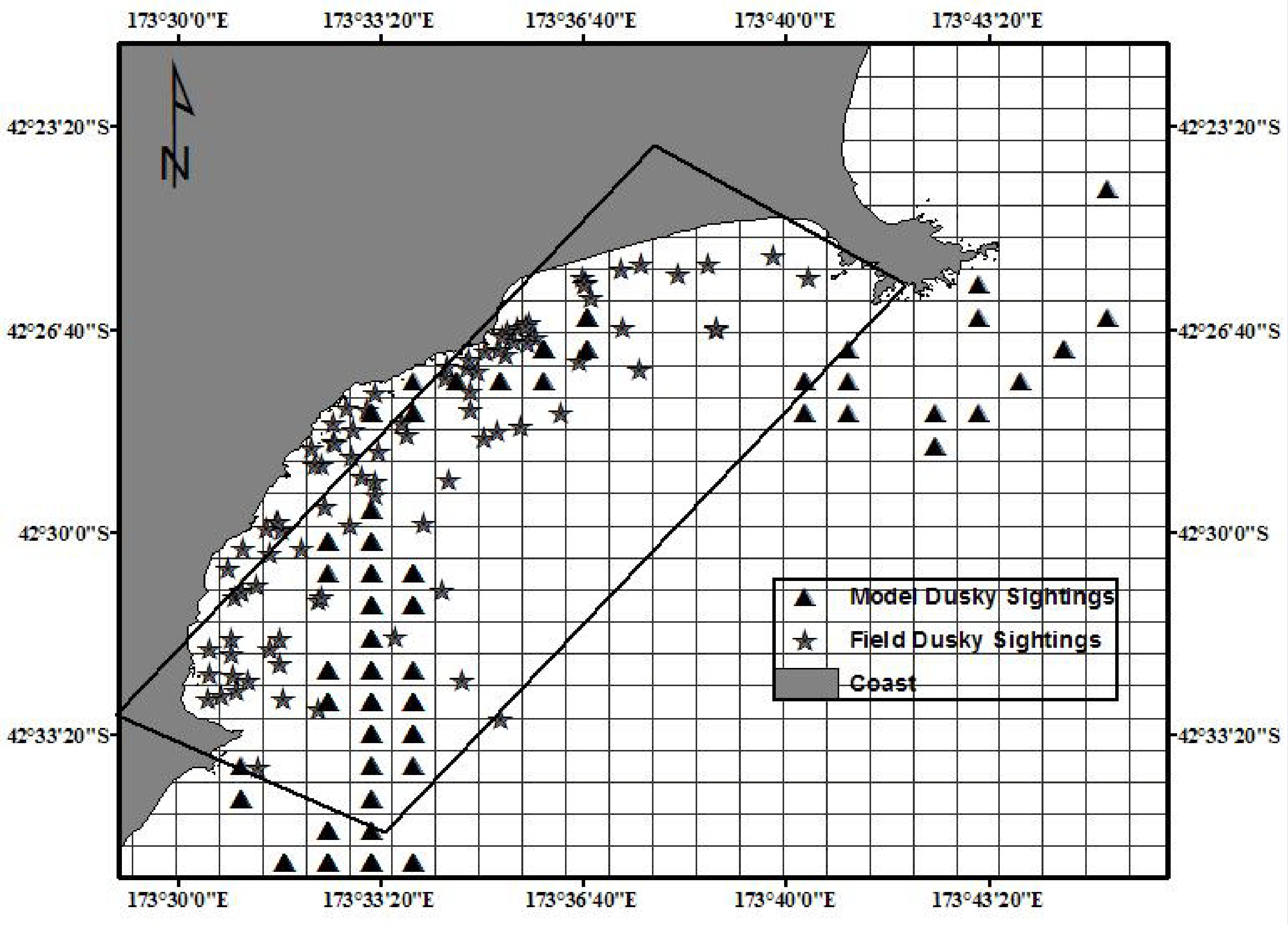

SUNRISE
SUNSET
a)
Dolphins rest in near shore waters during the day
Dolphins forage and feed on DSL associated organisms
Rest
Travel
Search
Feed
≲ 20 m or ≲ 200 m
(depth)
≳400 m
(depth)
b)
After exiting the refuge, dusky dolphins resume normal activity
Post-hunt
Cruise /Search
Killer whales unsuccessful in a dolphin attack wait for another opportunity and then enter into a post-hunt mode before resuming normal activity
Hide
Potential Encounter
Flee
< 10 m
(depth)
Wait
Stalk
> 10 m
(depth)
Dolphins flee and hide when threatened by killer whales
Killer whales enter into stalk mode when they detect dolphins
c)
Killer whales enter into the system either from the north or the south following shallow or deep water depth contour lines
N
S
Cruise /Search
Once in the system, killer whales cruise and search for potential dusky dolphin prey


Layers
Results10_0.csv Events
State
Cruise
CruiseX
Escaped
Feed
Flee
Hide
Animation
First Layer
Results10_0.csv Events
Last Layer
Results10_384.csv Events
Time Step (sec)
.1
Results10_9.csv Events
Start
Cancel

video

Model Evaluation

- Turing Test (Turing 1950)
- Model verification
- Sensitivity Analyses



Mantel test (Mantel, 1967) (426 x 426 distance matrix, km^2) spatial patterns of dolphins show an 88% spatial correlation (Observed Z = 1793.60, t = 28.96113, α = 0.01 $p < 0.0001$).

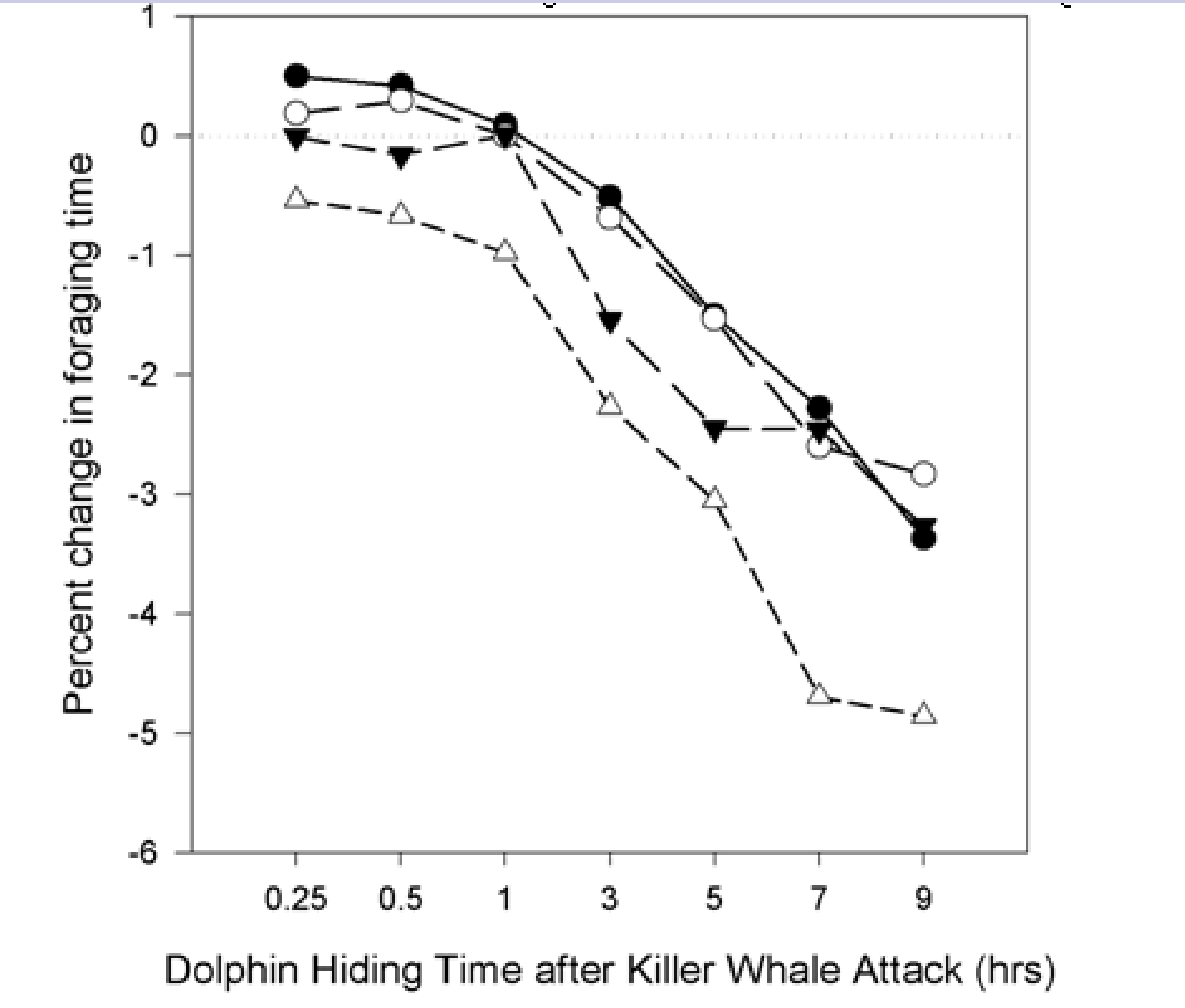
Sensitivity analyses

- Ran 28 sets of 20 Monte Carlo simulations using different combinations of values of:

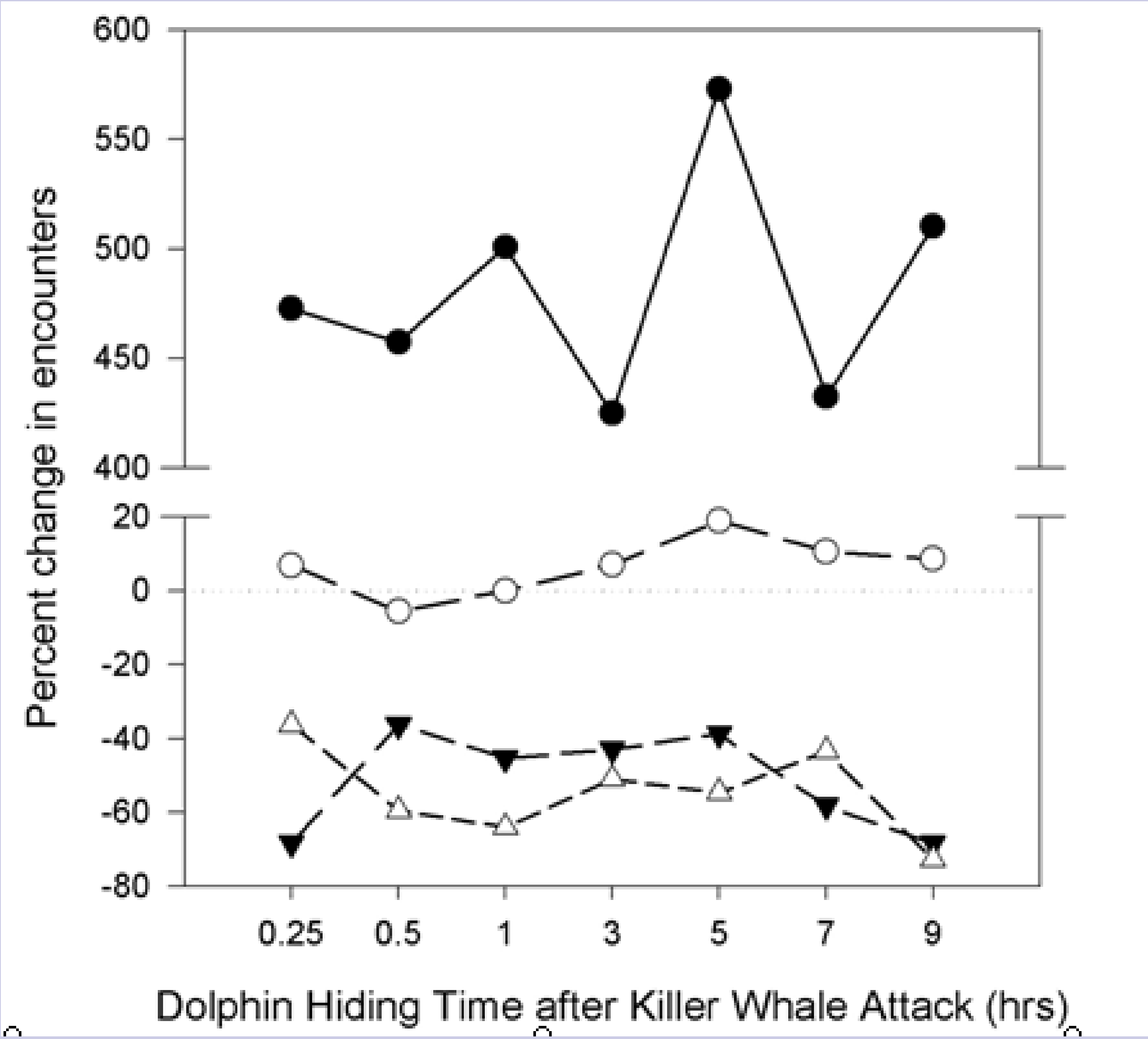
(1) distance at which duskies detect killer whales,

(2) hiding time of duskies post killer whale encounter (4 detection distances x 7 hiding times)

(3) monitored the effect on dusky dolphin activity budgets: foraging time and the number of killer whale encounters



Detection distances of 1, 5, 7 and 10 km are represented by solid circles, open circles, closed triangles and open triangles. Values represent percent change from baseline (zero) value.



Detection distances of 1, 5, 7 and 10 km are represented by solid circles, open circles, closed triangles and open triangles. Values represent percent change from baseline (zero) value.

Model Experimental Design

Scenario	Movement behavior	Killer whales	Detection Distance (km)	Hiding Time(hrs)
Reference 1	No	No	N/A	N/A
Reference 2	Yes	No	N/A	N/A
Reference 3	No	Yes*	N/A	N/A
Max. detection/Min. hiding	Yes	Yes*	10	0.25
Min. detection/Max. hiding	Yes	Yes*	1	9
Fear impulse strategy	Yes	Yes*	1	0.25
Fear driven strategy	Yes	Yes*	10	9
Baseline strategy	Yes	Yes*	5	1

*For each scenario, we simulated 6 different killer whale presence times: appearing 1, 2, 4 times per day and every 3, 5, or 10 days

Pre and Post encounter strategies

- *“Fear-driven”* - long hiding time and large detection distances
- *“Fear-impulse”* - short hiding time and short detection distances
- *“Fear-driven”* - long detection distance and short hiding time
- *“Fear-impulse”* - long hiding time and short detection distances
- “Baseline scenario” - best hypothesis for current strategy exhibited by dusky dolphins

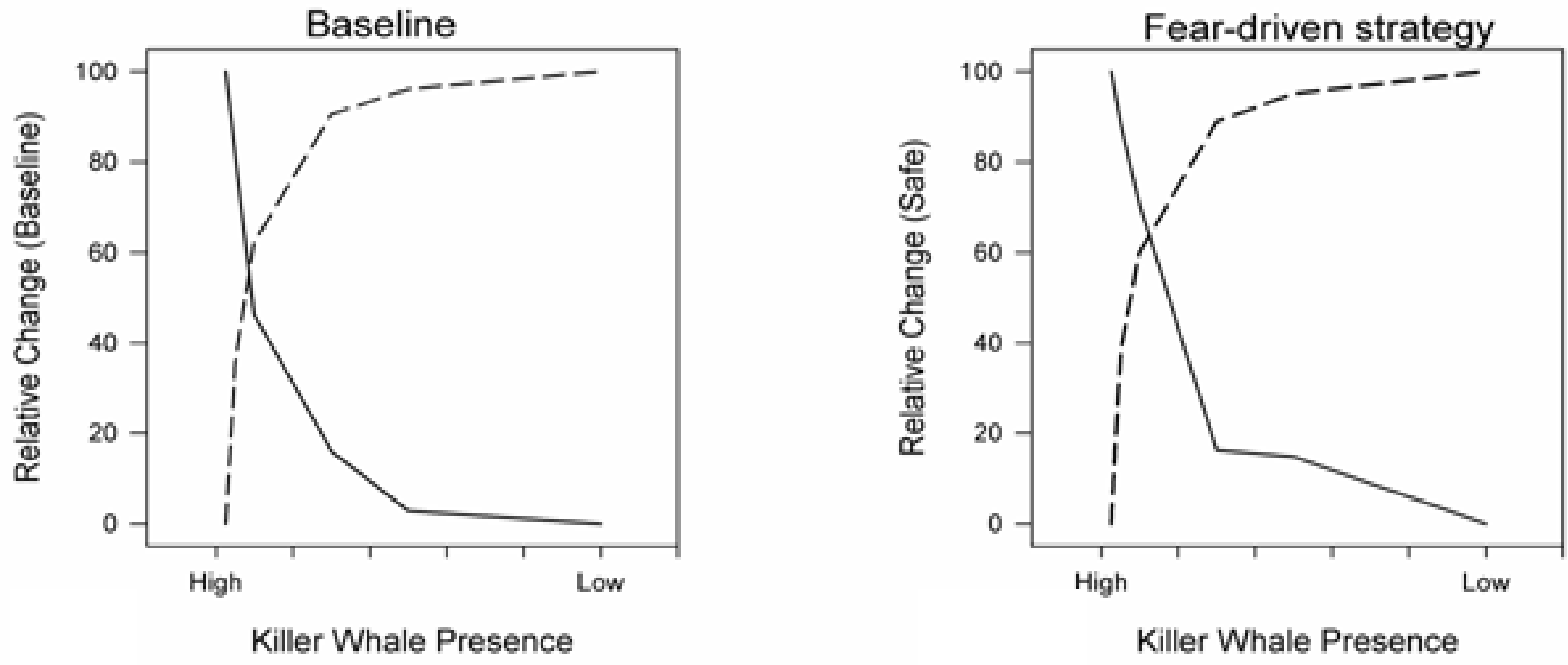
Model simulation summary

- 8 scenarios (3 reference and 5 strategies)
- 20, one-year, Monte Carlo (replicate stochastic) simulations for a total of 160 simulations
- Each simulation began 1 hr before sunset on 1 November and ran over a 210-day period (through the end of May).
- We recorded mean foraging time and mean number of killer whale encounters for each set of simulations to assess evolutionary costs vs. benefits.

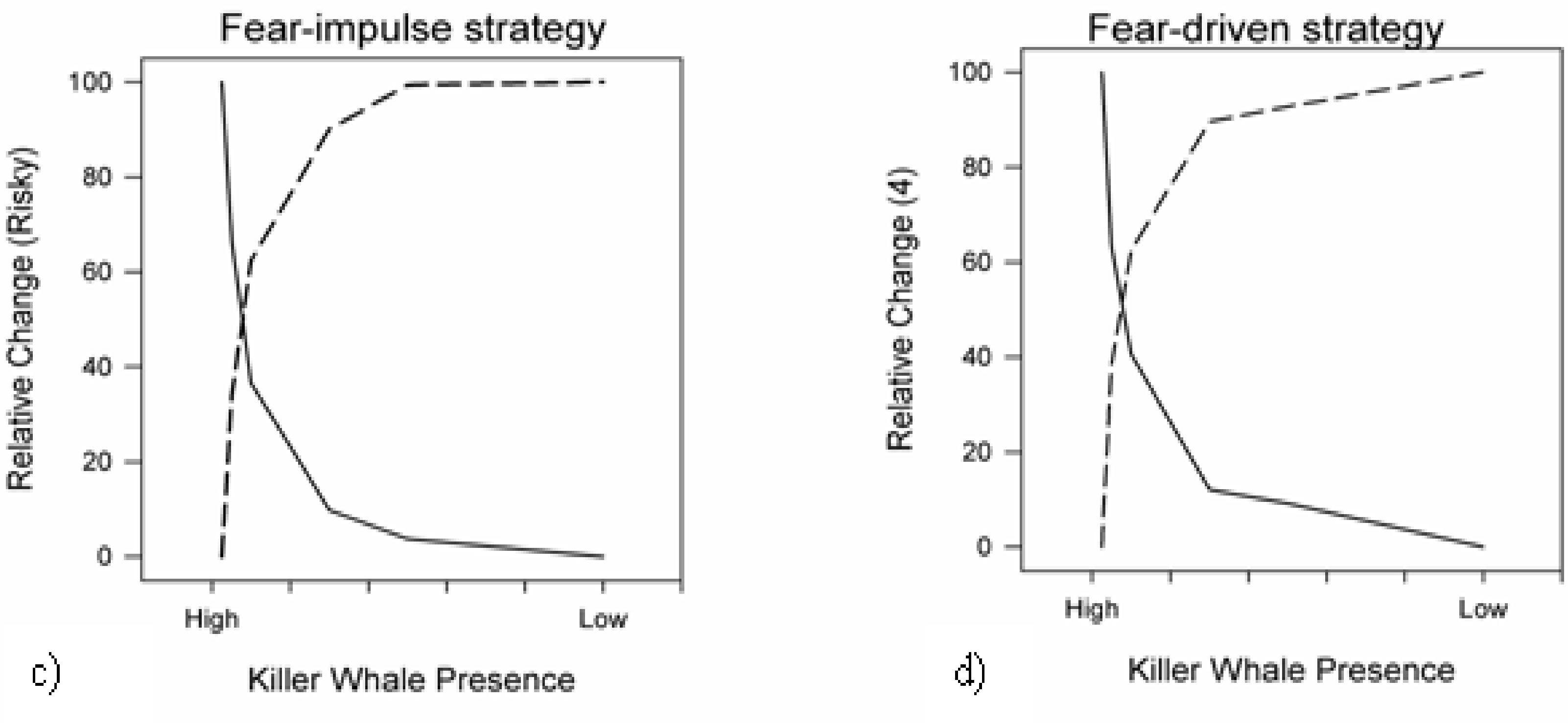
General Results

- Simulation results indicated that relative changes in dolphin behavior were similar across all five strategies
- Mean foraging time decreased as killer whale presence increased

Relative change of time spent foraging (dashed line) and encounter rate (solid line) for each strategy

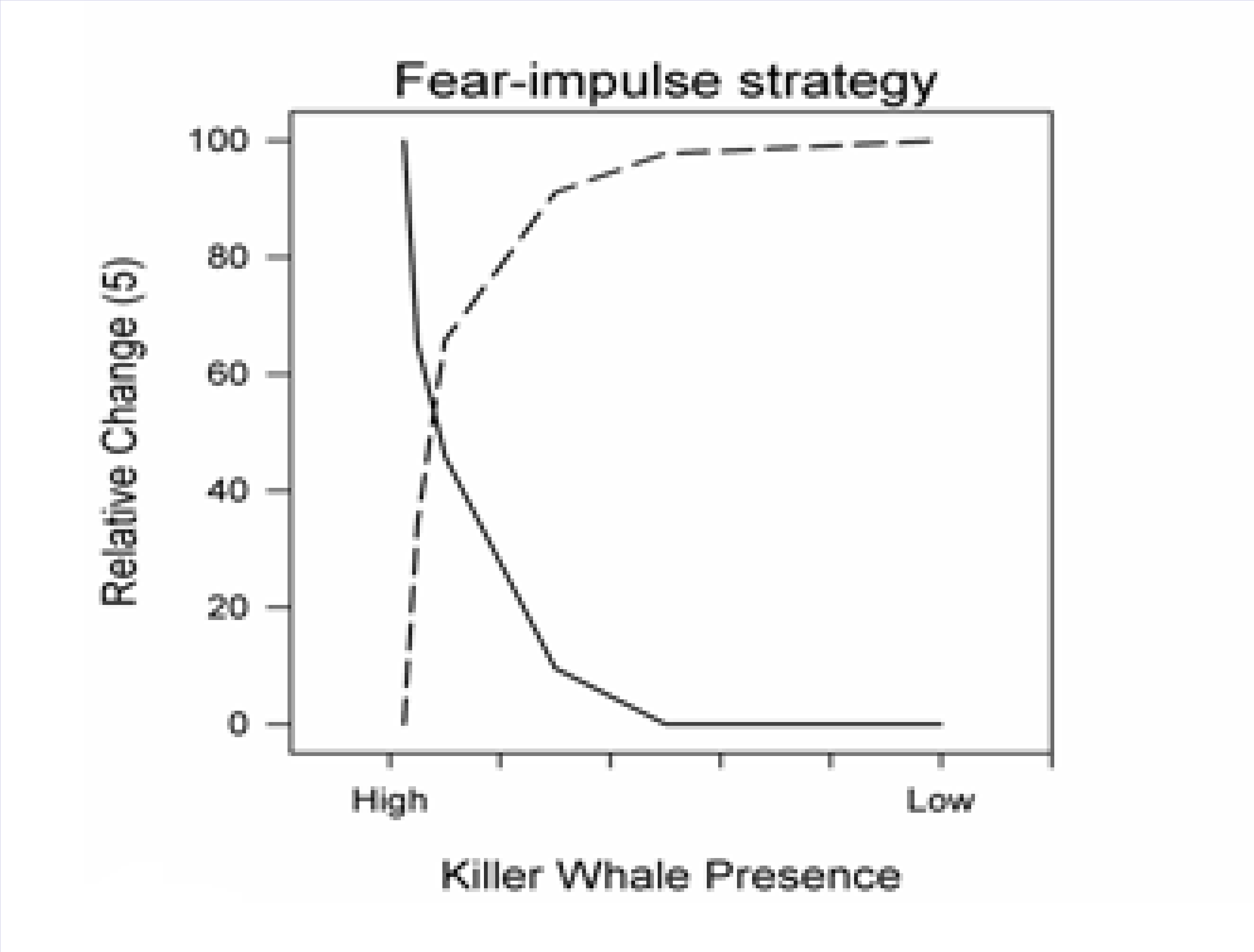


Long Hiding Time/Long Detection Distance



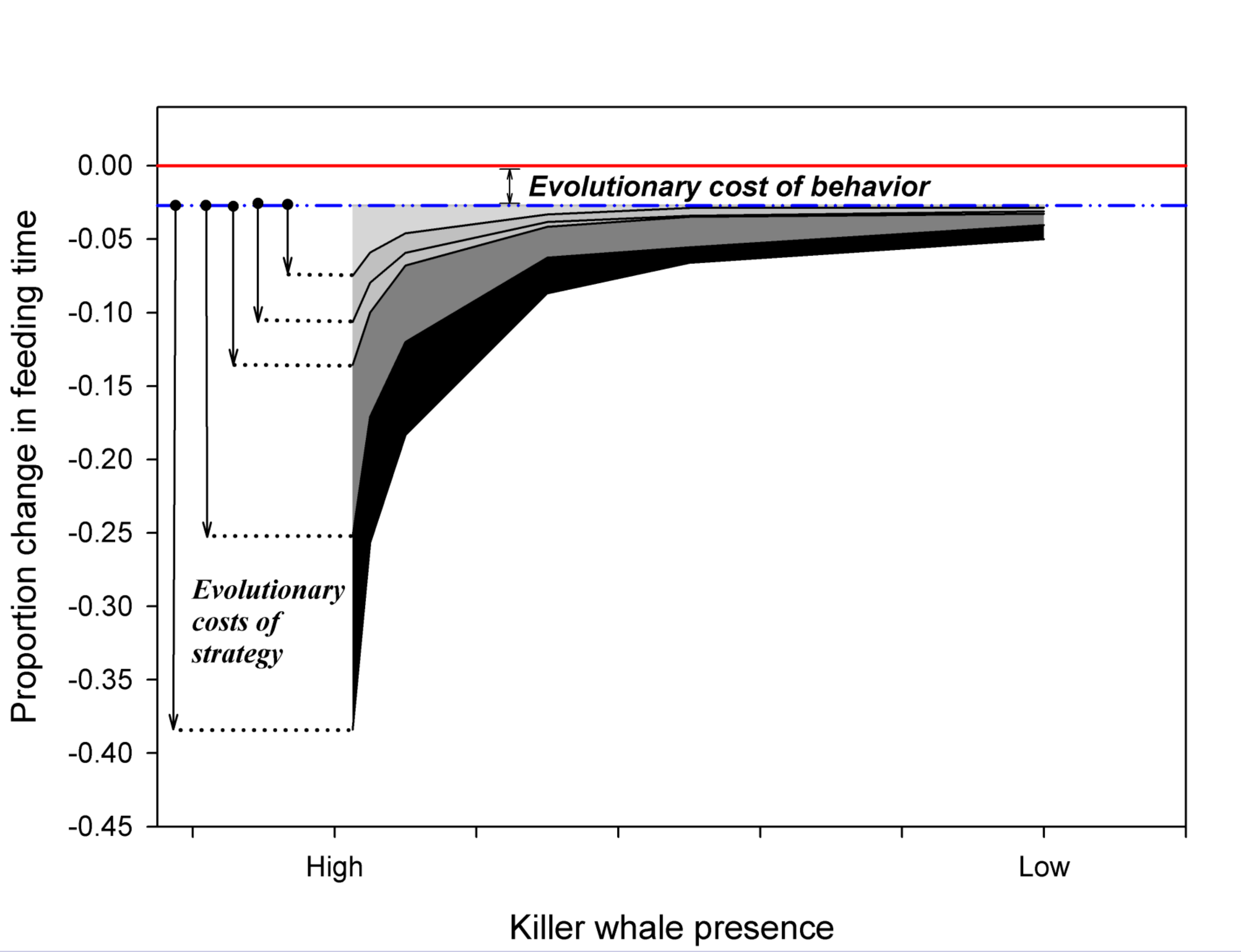
Short Hiding and Detection Distance

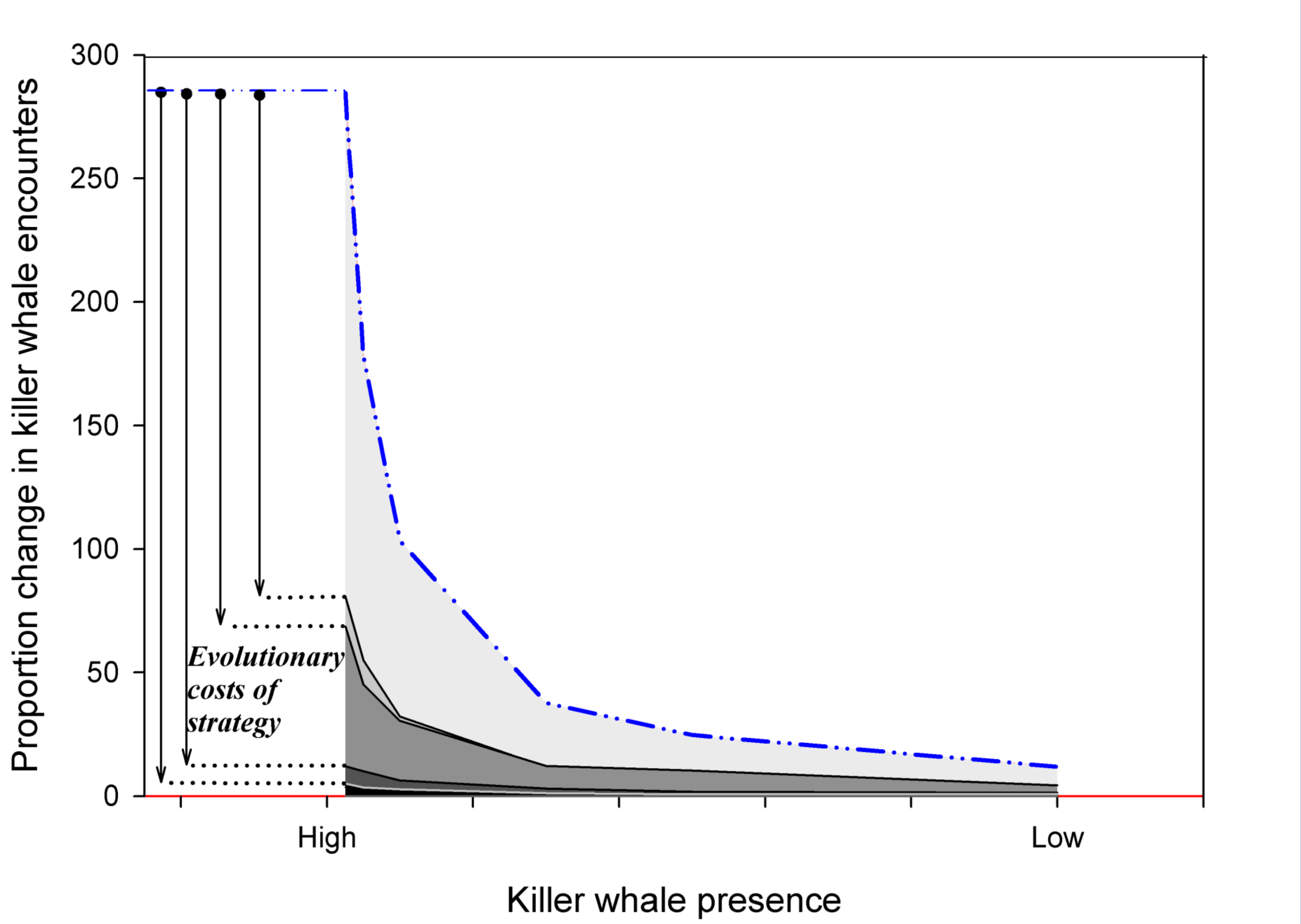
Short Hiding Time/Long Detection Distance



Short Detection Distance/Long Hiding Time

Evolutionary costs vs. benefits





Proportion change in killer whale encounters
300
250
200
150
100
50
0
Evolutionary costs of strategy
High
Low
Killer whale presence

Evolutionary Costs vs. Benefits

- Dusky dolphins incur a 2.7% loss in feeding time by evolving the anti-predator behavior of moving to and from the feeding grounds
- "*Fear-driven*" strategies resulting in the highest decrease in mean foraging time, and the "*fear-impulse*" the least
- At the highest level of killer whale presence, the "*fear-driven*" strategies resulted in 38% and 25% decreases in foraging time and the "*fear-impulse*" strategies resulted in 7.5% and 14% decreases
- The "*fear-driven*" strategies had approximately a 98% reduction in killer whale encounters regardless of the level of killer whale presence

Discussion

- Baseline model hypotheses approximates *fear-driven* - reduced encounters and *fear-impulse* limited decrease in foraging time

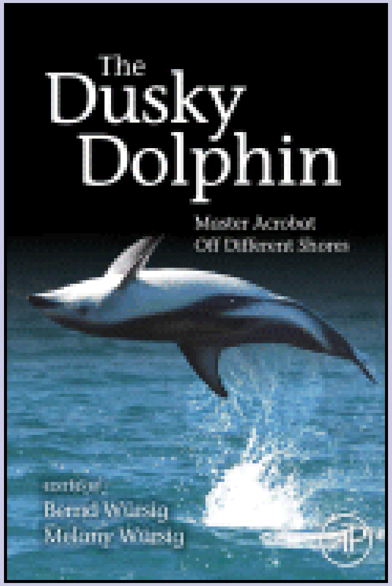
Model Benefits

- Applicable to other species of interest
- Test theoretical concepts
- Stress on predator-prey behavior
- Visualization of interaction
- Applies to both direct and indirect predation risk effects
- Capability to incorporate more specificity and explore new questions

Research & Management Issues

- Dusky dolphins are an IUCN *data deficient* species (36% of marine mammal sp. are threatened, 38 % data deficient, Schipper et al. 2008).
- Habitat alterations and bad management practices can adversely affect stable habitat choices & behavior that contribute to dolphin survival.

- *Srinivasan, M. W.E. Grant, T. Swannack, and J. Rajan. Behavioral games between a clever prey avoiding a clever predator: An individual based model of dusky dolphins and killer whales. Ecological Modelling (in press).*



Srinivasan and Markowitz. 2009. Predator threats and dusky dolphin survival strategies. In: Dusky Dolphin: Master Acrobats off Different Shores. Elsevier, Academic Press.

Acknowledgments

Dr. Bernd Würsig, Dr. Bill Grant, Dr. Jane Packard, and Dr. Ben Wu

Dr. Todd Swannack and Jolly Rajan

Funding: Earthwatch Institute, SWSS, USDA, NSF, Mooney Foundation, WB Davis and International Scholarship, and other TAMU College Station and Galveston Research and Travel Grants, and the Würsigs

Earthwatch volunteers and assistants, especially Jennifer Bennett

Adrian Dahood, Sierra Deutsch, Heidi Pearson, Robin Vaughn, Dave Lundquist, and other lab mates

Dennis Buurman, **Victor and Colette Foster**, Dr. Tim Markowitz, Clinton Duffy, NIWA, Dr. Michael Uddstrom, Dr. Rochelle Constantine, Dr. Ingrid Visser, *Dolphin Encounter* crew and staff

WFSC and TAMUG Staff, specially **Shirley Konecny** and **Stacie Arms**

thank you ....