VIGILANCE LEVELS & HEALTH IN HAWAIIAN SPINNER DOLPHINS

By

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Abstract

Over the past several decades, Hawaiian spinner dolphins have become a species of interest for both scientists and tourists alike. Spinner dolphins can be found resting in the bays of coastal Hawaii almost daily, and their habits have been noted by the burgeoning ecotourism industry and increased human presence. While no in depth studies have been performed on the dolphin populations, these increased interactions have researchers concerned about the vulnerability of the dolphin population.

Dukas & Clark (1995) hypothesize that a key unexplored factor in animal health is vigilance level, or the ability of the animal to process complex patterns such as foraging or detecting predators based on the amount of rest they are able to obtain. As the lifestyle of spinner dolphins puts them at extreme risk for lowered vigilance levels, the equations put forward in the article were used to create a bio-energetics model that would illustrate its potential effects on their ability to capture prey and evade predators.

While short-term vigilance loss does not appear to be significantly damaging to the dolphin's ability to feed and protect itself, a long-term loss may greatly affect a spinner dolphin's overall health. These findings indicate that the current human presence in the bays during the spinner dolphins' resting hours has the potential to detrimentally affect their health and consequently their population numbers and should serve as a starting point for further vigilance based research.

Introduction

Spinner dolphins have been studied for over forty years, but still much about their biology is unknown. The federal government provides for their wellbeing under the Marine Mammal Protection Act (1972) but no state laws or programs provide the same legal coverage. In the bays near Kona, Hawaii, the presence of spinner dolphins is an everyday occurrence. In addition to the pods of dolphins, hundreds of people, both tourists and locals, swimming and boating also fill the bays each day (Timmel et al. 2008). The increasing presence of humans in bays is causing more frequent interactions between the humans and the dolphins, but the effects of these interactions are still largely unknown. The western side of Hawaii's big island is one of the most notable places where human interaction with spinner dolphins occurs daily (Delfour 2007).

To better understand the unique nature of the spinner dolphin and their susceptibility to human activities, their daily habits should also be addressed. Spinner dolphins are small cetaceans easily identified by a three tone-grey pattern and get their common name from the axial spins and leaps they perform during social encounters ("Spinner Dolphin" 2011). They are unique in that unlike most other cetaceans they forage at night in the open ocean feeding on mesopelagic fish, shrimp, and squid (Benoit-Bird & Au 2009) and spend the day resting and socializing in bays (Norris & Dohl 1980). Prey of the spinner dolphin live at about 400 to 700m beneath the surface of the water during the day but because spinners are thought to only be able to dive to depths of 400m maximum they must wait until nightfall, when the mesopelagic layer rises to depths easily reached by the dolphins for about 11 hours per day (Benoit-Bird 2003). The leading hypothesis for resting in the bays is that by resting in the bays during the day, the predation risk is much lower than in the open ocean because of the enclosed area as well as the increased ability to see the shadow of a predator on the sandy bottom (Heenehan 2010). Just as with people, resting allows the dolphins to recover from their daily, or nightly efforts. The dolphins rest with uni-hemispheric sleep meaning only one half of the brain is shut down at a time while the other enables the animal to perform functions necessary for survival (Cirelli & Tononi 2008). The ability to sleep with only one half of their brain at a time allows the dolphins to continue swimming and return to the surface to breathe while also watching for predators so the other half of their can brain rest (Cirelli & Tononi 2008). Currently, their behavior is to come into these bays to rest where they will be less likely to be attacked by predators and can sleep with less interruption. However, with the growing presence of humans, this behavior is being disrupted as they wake up due to the unexpected commotion.

Most studies focus on the western side of the big island of Hawaii. The four bays that are currently being studied in depth are Keauhako, Kealeakekua, Honaunau, and Makako bays. Each of these bays historically have had frequent spinner dolphin presence during the day and so have become favored to study spinner dolphin and human interactions (Norris et al. 1994). These bays are characterized by shallow water, sandy bottoms, are protected from wind and strong ocean currents, and are all less than 1.5km across. By having this set of characteristics, the bays are ideal locations for spinner dolphin resting areas (Norris et al.1994).

Additionally, Kona bays are also home to an isolated sub-stock of spinner dolphins. According to the National Marine Fisheries Service (NMFS) , the entire chain of Hawaiian islands is host to a single stock of spinner dolphins, but recent data indicates that six individual stocks are most likely present along the islands (Andrews et al., 2010). The MMPA definition of a stock is "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature," and Andrews et al. found that little genetic mixing of individuals in between the sub-stocks occurs. Consequently, should one of the individual populations around Hawaii become unsustainably small, it is unlikely like that the dolphin stocks elsewhere in Hawaii would be able to bolster the dwindling population through emigration to the smaller stock. Additionally, spinner dolphins have been observed to have "long-term site fidelity," meaning that even if conditions of the bays deteriorate to the point where the dolphins are detrimentally affected, the animals will not seek better resting bays which could exacerbate the issue of isolated stocks (Marten & Psarakos 1999). By not moving to more restful, less human-influenced areas the dolphins not only will be continuing their exposure to poor conditions but will also eliminate the possibility of mixing with a healthier population.

With the increased interactions between humans and dolphins comes increased concern for the dolphins' wellbeing and whether people's activities such as kayaking or scuba have an effect on their behavior and consequently their health. The human presence in the bays is unlike to abate anytime in the foreseeable future as millions of dollars a year are brought into Hawaii from tourists who wish to be able to see and or swim with the spinner dolphins

No official population estimate is available for the Hawaiian spinner dolphin (Department of Commerce 2011). However, a recent study puts the best available population estimate for the big island between 600 and 700 dolphins in the area (Hill et al. to be published). The estimate is concerning when compared to the initial abundance estimate done by Norris of 1000 to 2000 dolphins about thirty years ago (Norris et al. 1994). The decrease, however, cannot be attributed to any specific factor for several reasons. Little is known on trends of the dolphin population changing over time due to a lack of consistent research and difficulty finding conclusive correlating factors.

For many people, swimming with the dolphins has now become viewed as a right, whether it is because they are on their dream vacation or they've done it all their lives. Some feel a spiritual need to swim with the dolphins while others view them as aliens from another world. Boating tours that advertise swimming with dolphins began in Hawaii around 1991 and have now become a major portion of the tourism industry. Ecotourism as a whole has been increasing annually at a rate of about 10% (Delfour, 2007). Whatever the reason, each day dolphins and humans share these bays and with increasing frequency will interact with each other.This includes tourism in Hawaii, much of which occurs on the water and highlights all varieties of marine mammals including pilot whales, beaked whales, and spinner dolphins. Fabienne Delfour conducted a study in which the effects of kayaking, boating and swimming in the bays on spinner dolphin behavior (2007). The study found that as the number of human activities in the bay increased, the number of times a change in dolphin swimming direction occurred following an encounter with humans (Delfour 2007). Other studies have found alterations in animal distribution (Lammers 2004), speed (Ribeiro et al. 2005), swimming patterns (Acevedo 1991), and behavior at the surface (Hastie et al. 2006). Additionally, Samuels et al (2000) reported that the number of dolphins returning to the bays with highest human presence decreased over time, indicating poor conditions for dolphin resting. Human activity is clearly affecting the behavior of the dolphins, but the extent to which this may affect their health is still unknown.

In many cases, laws on conservation or environmental issues have both federal and state counterparts. However, with marine mammals this is not the case. On the state level, Hawaii has laws forbidding interaction with animals within sanctuaries, but as none of the bays are protected the state does not have any enforcement power. Of the four bays studied off of the Big Island of Hawaii, at least one is considered a Marine Life Conservation District by the state of Hawaii, but their laws make no mention of dolphins within the bay, they only apply to non-marine mammal species. In 2006, the state of Hawaii was authorized to assist in the enforcement of dolphin protection but so far this has been mostly limited to spreading the awareness of MMPA guidelines ("Department of Land and Natural Resources" 2006).

The only legislation that currently applies to spinner dolphins is the Marine Mammal Protection Act (MMPA). This is because the MMPA prohibits the creation of any state policies dealing with the management of marine mammals, and so Hawaii cannot create their own regulations to deal with any potential issues arising from human interactions with the dolphins. The enforcement of dolphins under the MMPA falls to NMFS Protected Resources, and then is divided up into six regions, with the Pacific Island Regional Office (PIRO) dealing with the Hawaiian Spinner dolphins. Under Title I, which addresses the conservation and protection of marine mammals, the MMPA makes it illegal to harass or attempt to harass marine mammals. This includes the altering of their behaviors, which may occur in these bays when people are come into close contact with the dolphins (MMPA 1994). As the rates of human activities in the Hawaiian bays are increasing, NMFS is receiving higher number of complaints that the swimmers and boaters are harassing the dolphins (Timmel et al. 2008). While the 1994 amendments to the MMPA essentially makes swimming with dolphins illegal under Level B harassment, or "having the potential to disturb a marine mammal stock in the wild by causing a disruption of behavioral patterns" (MMPA 1994), lack of conclusive findings on the part of researchers as well as the difficulty of proving such occurrences in court have kept the regulation difficult to enforce. Many of the studies performed in the Hawaiian bays are therefore attempting to prove this portion of the MMPA is being violated in order to prove a cause for stricter policy or more enforcement in these bays.

Another one of the goals of the Marine Mammal Protection Act is to maintain the stocks of marine mammals above the optimum sustainable population (MMPA 1994). "Optimum sustainable population" is the number of animals that will result in the maximum productivity of the population keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element. Spinner dolphins are currently considered as "depleted" by NMFS, which means that the species have fallen below their optimal sustainable level ("Spinner Dolphin" 2011). This degradation of their status prompted NMFS PIRO to look for ways to mitigate human interactions with the dolphins on a regular basis.

Lack of enforcement in the bays as well as the difficulty of proving whether an interaction has altered the behavior of the dolphins prompted NMFS to publish voluntary Spinner dolphin viewing guidelines. These guidelines, which are no more than the normal suggested behavior when encountering any marine mammal, are distributed to tour operators as part of an outreach program to increase awareness of the MMPA and the possible effects of human interactions in an attempt to deter human pursuit of dolphins without new regulations. The guidelines instruct boats to stay over 50 meters away from the dolphins at all times, to limit observation time to half an hour, and to make sure the dolphins are not encircled or trapped between boats or the shore at any time ("Spinner Dolphin" 2011). Additionally, outreach programs to tourists exploring the areas alert them to the nocturnal nature of the spinner dolphins as well as the requirements of the MMPA. In the summer of 2011, NOAA began implementation of the Dolphin SMART program in Hawaii, where tourists are able to find a list of dolphin tour operators who have agreed to abide by the NOAA dolphin viewing guidelines ("Swimming with Spinner Dolphins," 2011).

In 2006, NMFS issued a notice of intent to create new policies to deal with human interactions with the spinner dolphins in these bays (Department of Commerce, 2006). In early 2011, NMFS announced their plan of closing Kealakekua, Honaunau, Makako and Kauhako bays during the morning hours when spinner dolphins have most frequently been observed to be resting (Johnston, 2011). These four bays have been studied intensively for the past two years in order to collect data for analysis on the behavior of dolphins in the presence of humans. After the closure the study will continue in an attempt to determine whether the absence of human activity brings about any change in behavioral patterns. Already backlash has been seen against this new policy, and not without warrant. A 2009 report by the International Fund for Animal Welfare estimates the annual revenue for tourist related boating activities in Hawaii is over $40 million. An order to shut down four of the major tourist bays on the big island during prime business hours could cause millions of dollars in losses for the tour operators frequenting those areas ("Whale Watching" 2009). While protecting marine mammals is a priority for NMFS, the alienation of a large revenue stream in Hawaii may not be the best long term plan if protection of spinner dolphin habitat is to coexist with the tour boat industry. This is especially contentious as NMFS is often unable to prove the MMPA has been violated.

One concept which has not been explored in depth as a way to measure spinner dolphin health and could greatly aid in the discussion of potential ramifications of human activities is the effect the amount of sleep, or lack thereof, has on the spinner dolphin. In Dukas & Clark's 1995 article *Sustained vigilance and animal performance*, they discuss the concept that a lack of rest leads to the inability of the central nervous system to "sustain a high quality of information processing for an extended period of time." A 2008 study concluded that dolphins subject to sleep deprivation were more likely to have slower response times to stimuli, indicating that a continuous interruption of sleep patterns could potentially increase the mortality risk of spinner dolphins due to inability to successfully forage or predation (Cirelli & Tononi 2008). However, the severity or proportional response to lack of sleep has not yet been measured. Dukas & Clark created a model which measures the vigilance, in this instance defined as a "state of behavioral alertness to predators…a general condition of enhanced ability to process information" and a series of equations which correlate measures of health such as ability to forage for food, mortality risk, and net energy gain. Using a technique such as modeling would allow for the study of possible effects of human presence in the bays without interfering by becoming a presence themselves. From these equations, a model was created specifically targeted towards the spinner dolphin in an attempt to assess the relationship between rest, vigilance level, and health.

Materials and Methods

In order to display spinner dolphin behavioral data within a modeling framework, the environmental modeling program STELLA was used. Equations created by Dukas and Clark (1995) were employed with some slight modifications due to the need to take into account characteristics specific to the spinner dolphins in addition to the feasibility of creating a working model from equations that have previously only been applied theoretically. Because the equations in the paper are designed for animals in general, when creating a Stella model values such as metabolic cost of living and prey density while foraging have to be altered in order to tailor the model to spinner dolphins. Values for these parameters were taken from multiple papers discussing the foraging, socializing, and sleeping habits of the dolphins (e.g. references and see below).

The Basic Model

The first simulation run from the model demonstrated an ideal situation in which the vigilance of a dolphin begins at the maximum vigilance level before foraging and ends at maximum vigilance level after a resting bout (see Table 1).

Table 1. Symbols and values used in the initial model

Symbol	Description	Value
t	Time	$0 \leq t \leq 24$
υ	Vigilance level	$0 \leq \upsilon \leq 100$
γ	Resting multiplier	
τ	Time delay between foraging and resting	8 hours
η	Time Delay multiplier	
α	Rate of vigilance decrement during foraging activity	.07/hr
β	Rate of vigilance recovery during rest	.19/hr
θ	Foraging multiplier	
λ	Number prey encountered per hour	215.7 animals
f	Long-term average rate of food intake	

$\overline{\mu}$	Predation risk	
μ	Chance of encountering a predator	
$\overline{\rho}$	Percent chance of encountering a predator while resting	0.002
ρ	Percent chance of encountering a predator in the open ocean	0.02
M	Overall mortality risk	
c	Metabolic cost per hour foraging	173.75 kcal/hr
E_{prey}	Calories of prey item	
E	Net rate of energy gain	
F	Total expected lifetime energy gain	
L	Length of prey	

The first step in demonstrating the variations in vigilance in spinner dolphins is determining the rate of change of vigilance over the course of their activities. Constant proportional rates of change are assumed in the equations by Dukas & Clark of:

$$\frac{d\upsilon}{dt} = \begin{cases} -\alpha\upsilon & \text{while foraging} \\ \beta(1-\upsilon) & \text{while resting} \end{cases}$$

Vigilance level in this model is demonstrated by ν, where $0 \leq \upsilon \geq 100$, with 0 representing the dolphin at a depleted vigilance level and 100 representing maximum vigilance (Dukas & Clark 1994). The model was run for a simulation period 24 hours with the starting point using a vigilance level of 100, assuming maximum vigilance after a period of rest as the dolphins switch to foraging behaviors. The value for rate of vigilance decrement, or α, is set at a proportion of vigilance of .07 per hour and β is set at a rate of 0.19 vigilance recovery per hour. While the values of α and β have not been recorded in any study, the assumption is made that the rate of recovery would be much higher than the rate of decrement in animals as a much larger proportion of time is spent awake than asleep. For simplicity purposes, vigilance level only increases during resting periods and only decreases during foraging bouts. Given that the dolphins forage for an approximately 11 hours each night while the mesopelagic layer is available to them (Benoit-Bird), it would mean that the dolphin's decrement time, for the purpose of this model, would be limited to those 11 hours. Additionally, Kenneth Norris observed resting spinner dolphins to remain in the bays for a minimum of 5 hours (1994). Therefore, the window of time in which vigilance recovery occurs is set to 5 hours per 24 hour cycle. To create the ideal simulation, any decrement that occurs during the foraging period would need to be fully recovered during the resting bout. Therefore, with an initial placeholder rate of decrement of .07 percentage of vigilance lost per hour over an 11 hour period, the rate of recovery would have to be .19 per hour in order to create the baseline. In addition to having bouts of foraging and resting, a time delay is also taken into account for the transitions between foraging and resting. As dolphins do not forage in the same location they rest, travel is taken into account as well as socialization time. For the purposes of this model, moving from the resting location to the foraging location or vice versa and any time spent socializing is categorized as a time delay in which the vigilance level neither diminishes nor increases. For this model, the time delay is set at 4 hours between each transition, totaling 8 hours per day. Consequently, the model would run with the foraging period for the first eleven hours, a four hour time delay for travel and socializing, a resting period for the next five hours and then switching from rest to foraging for 21:00-24:00hrs.

The equation used to model the vigilance dynamics over a 24 hour period is then

$$\upsilon = -\alpha\upsilon\theta + \gamma\beta\upsilon + \eta\upsilon$$

where

$$\theta = \begin{cases} 1 & t \leq 11 \\ 0 & t > 11 \end{cases}$$

$$\gamma = \begin{cases} 0 & t < 16, t > 20 \\ 1 & 16 \geq t \leq 20 \end{cases}$$

$$\eta = \begin{cases} 0 & t \leq 11,\ 16 \leq t \leq 20 \\ 1 & 11 > t < 16, t > 20 \end{cases}$$

Assuming the average rate of food intake during a foraging bout is proportional to the vigilance level at that time and that any prey encountered by the dolphin is caught and consumed

Average rate of food intake = $\lambda\upsilon$

we can then calculate the theoretical amount of food a dolphin would be able to consume during any given foraging period

$$f(\upsilon) = \sum_{0}^{24} \lambda\upsilon$$

According to Dukas & Clark (1995), increasing the amount of time spent foraging should increase the rate at which they are able to consume prey due to increased time to encounter food. Food intake is also used to estimate the overall health of the dolphin assuming that the amount of prey caught can indicate future success in terms of gaining size and thus becoming less at risk from predation as well as being an indicator of future reproductive health (Read 2011). Therefore, the higher the food intake over the dolphin's daily foraging period, the higher the assessment of the dolphin's health.

Mortality Risk and Metabolic Costs

Up until this point, predation and metabolic cost are not accounted for in the equations, but by utilizing another equation by Dukas & Clark (1995) predation risk, or the dolphin's susceptibility to a predation attempt can be calculated by

$$\bar{\mu} = \mu(1 - \upsilon)$$

This equation simply illustrates that as foraging time progresses and causes vigilance to decrease a dolphin's risk of predation will rise. Foraging time in this instance includes the activities of "both feeding and scanning the environment for predators" (Dukas & Clark, 1995). Without rest this activity reduces the capacity of the dolphin to both feed and look out for predators in the future. Assuming there are no other causes of mortality and at maximum vigilance the dolphin will be able to escape any predation attempts, Dukas and Clark translate this predation risk into an overall mortality risk (*M*) shown as an increasing function of foraging effort by

$$M(\upsilon) = \rho\theta\bar{\mu}(\upsilon) + \rho\tau\bar{\mu}(\upsilon) + \bar{\rho}\gamma\bar{\mu}(\upsilon)$$

A metabolic cost (c) is then taken into account. By including the metabolic cost into the equation, overall energy gain can be calculated and an estimated overall caloric intake can be produced, leading most likely to a more accurate prediction of future dolphin health (Dukas & Clark 1995). Net daily energy gain is modeled by the equation

$$E(\upsilon) = \lambda\theta\upsilon - c$$

The metabolic cost of living also varies between resting and foraging states. At all times, the dolphin is moving as well as performing involuntary bodily processes which require energy of maintenance. Because no studies have been published on the metabolic rates of spinner dolphins, the calculated values came from studies on bottlenose dolphins. Yazdi, et al (1999) discuss the various energy costs associated with baseline swimming as well as the cost of increased speeds and diving. For the simulation, the model is divided into two metabolic rates, the rates while foraging and the rates while not foraging (during the time delay and resting bouts). The resting metabolic rate of bottlenose dolphins was found to be an energy consumption rate of 2.15 W/kg (Yazdi et al., 1999). However, during periods of efficient swimming Yazdi et al. found the metabolic rate to be about 10% higher. Assuming that the dolphins are swimming efficiently for the periods while not foraging, the metabolic cost must factor in the cost of transport while the dolphins travel and rest (as they are still swimming during resting bouts). The metabolic cost of transport during these periods is then set to be at 1.16 $Jkg^{-1}m^{-1}$, which converts to 0.00027 $\frac{kcal}{kg * m}$ (Yazdi et al., 1999). If the average spinner dolphin weighs 65 kg and is swimming at the most efficient rate of 2.5 m/s (Yazdi et al. 1999), then the dolphin will be using 157.95 kilocalories per hour while travelling and resting. Williams et al. (1999) found that the metabolic rate of dolphins increases up to 20% from the resting metabolic rate during diving causing the metabolic cost of foraging to be set at 173.75 kilocalories per hour. Between these two metabolic rates, the average daily maintenance requirement for a spinner dolphin is about 61 kcal/kg.

Using the results of Benoit-Bird (2003) on prey caloric values and assuming a 61kcal/kg maintenance requirement, the daily energy needs are calculated to be about 3,965 kilocalories per day. The main prey items of spinner dolphins are known to be fish, shrimp and squid, with an average equation measuring the caloric content of the dolphin's diet being

$$E_{prey} = 388 \times L - 1{,}139$$

A majority of the prey found in spinner dolphins' stomachs were myctophid fish with an average length of 7.8cm (Benoit-Bird 2003) and so this was used as the length for the average prey item obtained. When plugged into the equation above, the caloric content of the average prey of a spinner dolphin is 1,975 calories or 1.975 kilocalories and so this value was used as the parameter for the calories of each food item eaten. Using the 11 hour period as the limit for how long the dolphin will have to obtain 3,965 kilocalories we can determine that in order for this energy requirement to be met, at least 2,007.59 prey items must be eaten every day. With the assumption stated for the average rate of food intake, the spinner dolphin will eat all prey it comes into contact with should it be at its highest vigilance level. As the vigilance level diminishes, the smaller percentage of prey the dolphin will be able to capture. Therefore, the number of prey encountered per hour used in earlier equations would need to be at least the minimum amount of food a dolphin needs per day. Using this data, the number of prey encountered per hour is set at 215.7 animals so that with its varying vigilance under ideal circumstances the dolphin can meet its minimum maintenance energy needs. As food availability is not a limiting factor for dolphin energy maintenance (Benoit-Bird 2003), this number would

actually be a low estimate of prey encounters. Additionally, spinner dolphins actively seek high aggregations of prey (Benoit-Bird & Au 2008) as well as cooperatively forage so their foraging areas would have higher chances of encountering prey than the open ocean or the mesopelagic layer as a whole.
By using a conservative estimate of how much a spinner dolphin would eat in a single foraging period and adding in the metabolic cost, we can then see whether the dolphin is able to fulfill its caloric needs over the course of the day and are able to have another criteria by which to measure spinner dolphin health.

Creating suboptimal conditions

The first simulation of the model was run under optimal conditions in which the dolphin was able to rest until its vigilance was fully restored in order to create baseline numbers for outputs such as food intake per foraging bout as well as net energy gain over the lifetime of the animal. Subsequent simulations when the dolphin is only able to obtain 80, 60, and 40 percent of the minimum amount of sleep observed by Norris (1994). These simulations will depict possible consequences of prevalent tourist disruption of dolphins resting in the bays.

While mimicking optimal conditions, the model is set up to restore vigilance to its original level at the end of each day which provides the dolphin with the optimal amount of vigilance to perform the next day's activities. While these conditions continue, the dolphin will be able to restore its vigilance indefinitely. Should suboptimal conditions occur, vigilance levels would then be altered within the model. Taking into account the possibility that long term effects of sleep deprivation may be different than short term, foraging ability as well as mortality risk may be more evident when looked at from a long term perspective and so the simulation will be extended from its original 24 hour period to a thirty day period in order to view potential long term effects.

Results

Optimal Scenario

Vigilance level in the optimal scenario is shown to begin at 100% with the dolphin being fully able to process its surroundings, decrease over the course of the foraging bout and not rise again until the dolphin is able to rest again in the bays with the vigilance level returning to maximum capacity at the end of the resting period (Figure 1).

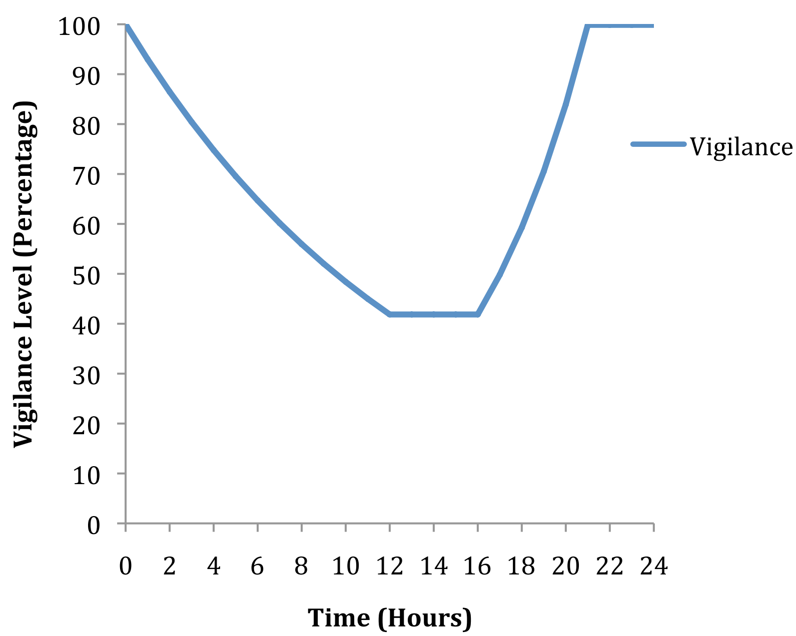

Figure 1. Vigilance dynamic over a 24 hour period

The vigilance dynamic was then used to model the rate of food intake a dolphin would be able to perform, as *f* is positively correlated with vigilance level. The rate of food consumption is highest at the beginning of the foraging bout and decreases as vigilance levels lower. After the foraging bout ends, the rate of food intake consequently drops to 0 for the rest of the day (Figure 2).

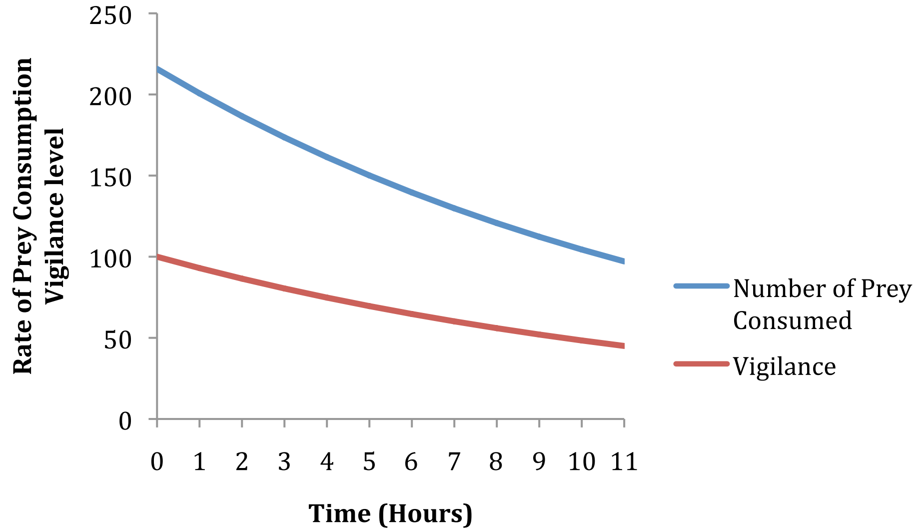

Figure 2. Rate of prey consumption per hour over a foraging bout compared with vigilance level

As can be seen in Table 2, the longer the foraging bout the more food the dolphin is able to obtain. However, the rate at which the dolphin is able to capture its prey decreases over time and it becomes a less efficient predator.

Table 2. Rate of prey intake and total prey intake during a foraging bout

Time (hours)	Prey Consumed per Hour	Total Prey Intake (number of animals)
0	215.76	215.76
1	200.66	431.52
2	186.61	632.17
3	173.55	818.78
4	161.40	992.33
5	150.10	1153.73
6	139.59	1303.83
7	129.82	1443.42
8	120.73	1573.24
9	112.28	1693.98
10	104.42	1806.26
11	97.11	1910.68
Final		**2007.80**

Mortality Risk and Net Energy Gain

Predation risk was found to be negatively correlated with vigilance levels and so as the foraging bout progressed, the dolphin's risk of predation rises as it is no longer be able to process its surroundings as thoroughly as it could at the beginning of the foraging bout. Additionally, as the dolphin rests and its vigilance would rise, the risk of predation lowers (Figure 3).

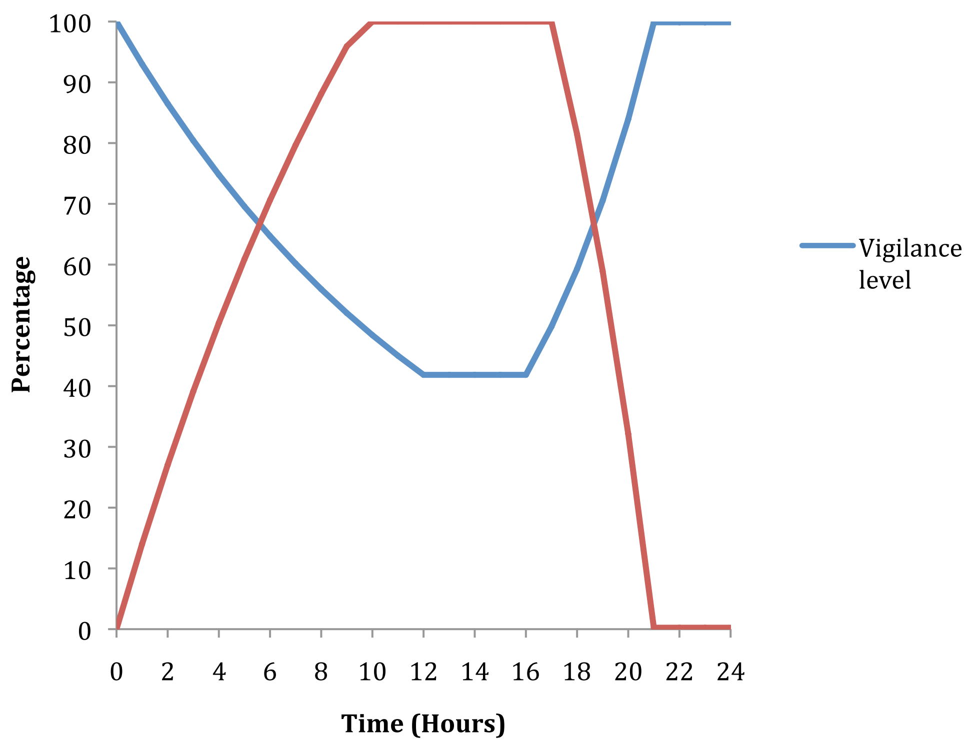

Figure 3. Predation risk and vigilance level over a 24-hour period where the predation risk represents the percent chance, should a predator attack that the dolphin fails to notice the predator.

Next analyzed was the overall mortality risk, which differs from the predation risk in that it takes into account the likelihood of the dolphin encountering a predator rather than just its risk of being predated should an interaction occur. From this equation it will be noticed that the mortality risk is on the rise while the dolphin forages and its vigilance level lowers. However, the mortality risk drops drastically when reaching the resting period because of the highly improbable presence of predators in the resting bays (Figure 4).

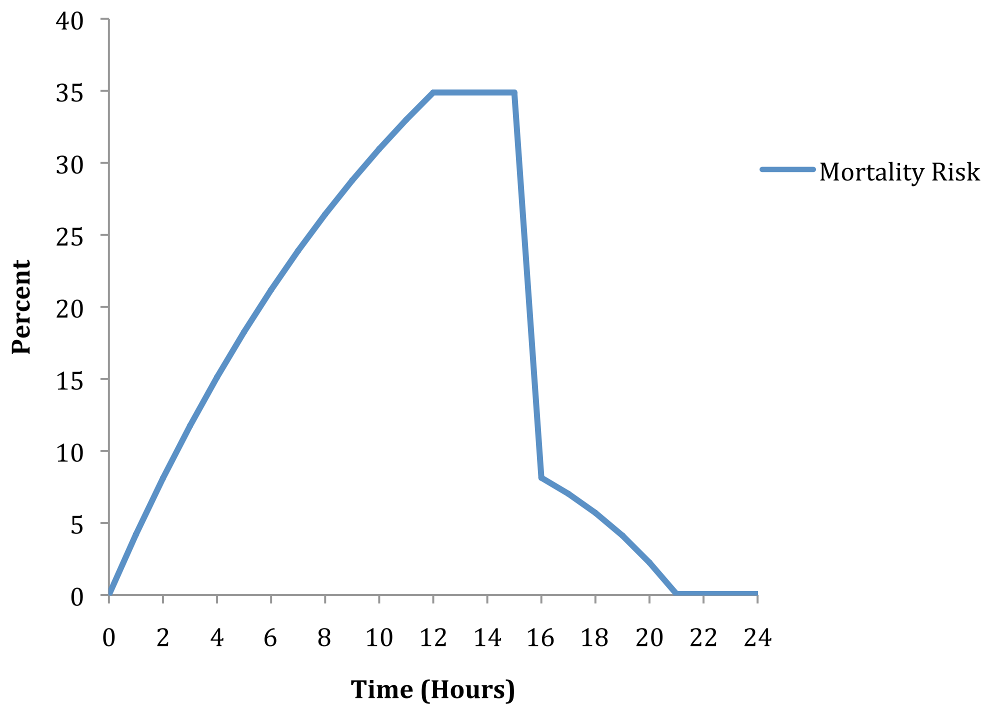

Figure 4. A dolphin's mortality risk due to predation over a 24-hour period

The final way spinner dolphin health was measured is through the animal's ability to obtain its minimum energy requirements in order to maintain its metabolic needs. The modeled equation demonstrates that the dolphin is able to capture enough food for itself over the foraging bout to provide itself with enough energy to perform daily functions. As the model is set to the dolphin eating only enough to maintain its energy needs, the overall energy gain is around 0 at the end of the day, just in time for the dolphin's next foraging bout to begin (Figure 5).

However, this is a conservative approach, as the animals would likely exceed their daily minimum requirements.

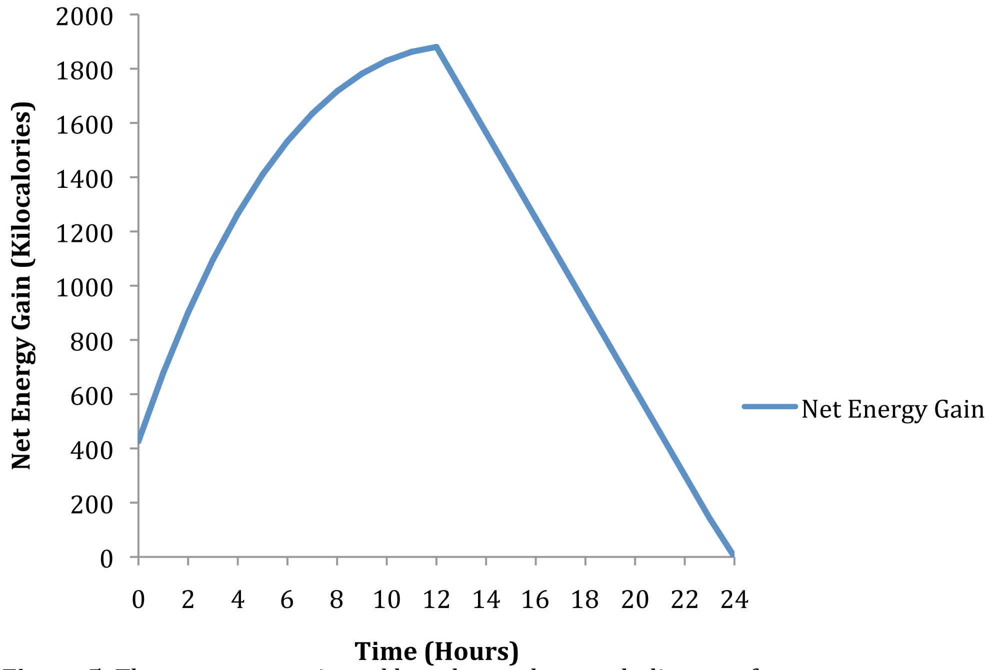

Figure 5. The net energy gain and loss due to the metabolic cost of a spinner dolphin

Using this optimal situation in which the dolphin is able not only to replenish its vigilance levels at the end of each day as well as capture enough prey to meet its metabolic needs now allows for a comparison to simulations in which the dolphin is not able to obtain as much rest as is needed.

Suboptimal Simulations

In order to study the potential effects of disrupted sleeping time simulations were then run at 80%, 60%, and 40% of the dolphin's original 5 hours of sleep. As shown in Figure 6, the shorter the resting period means the dolphins leave the bays earlier in the day and to a longer foraging bout. Less rest and more time searching for prey means the dolphin's vigilance is lower at the end of each foraging bout with less time to recover, and when the dolphin's next foraging bout begins its vigilance is not restored to its optimal level. The amount of rest lost is proportional to the amount of vigilance not restored at the end of each day (see Figure 6).

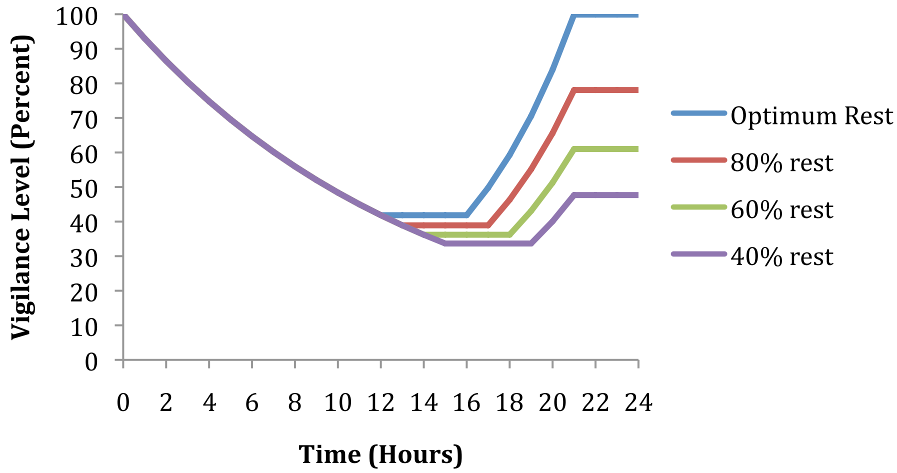

Figure 6. Comparative vigilance levels at varying lengths of rest

With lowered vigilance levels, the dolphin continues to capture food during its extra hours of foraging but at lower rates as time wears on (Table 3).

Table 3. Rate of prey intake and total prey intake during a foraging bout

Time (hours)	Prey Consumed per Hour	Total Prey Intake
0	215.76	215.76
1	200.66	431.52
2	186.61	632.17
3	173.55	818.78
4	161.40	992.33
5	150.10	1153.73
6	139.59	1303.83
7	129.82	1443.42
8	120.73	1573.24
9	112.28	1693.98
10	104.42	1806.26
11	97.11	1910.68
12	90.32	
13	83.99	
14	78.11	
Final (optimal)		**2007.80**
Final (80% rest)		**2098.11**

Final (60% rest)	**2182.11**
Final (40% rest)	**2260.22**

While in the short term, foraging for longer periods of time may be beneficial to the dolphin as increased caloric intake can be used as a measurement of overall fitness (Dukas & Clark 1994) but if the longer foraging bouts and shorter rest periods continue long term it may affect their health in different ways, a possibility that will be analyzed later in the paper.

Mortality Risk and Net Energy Gain

As vigilance levels fail to increase back to their maximum level at the end of a resting period, the amount of food gained is not the only aspect of the dolphin's day that is affected. Mortality risk, a function of vigilance level, also demonstrates markedly different results with less sleep than from that found in the optimal scenario. Figure 2, which shows the mortality risk of the dolphin falling back to zero at the end of the day, is compared with the differing mortality risks as a result of a loss of sleep time. Figure 7 illustrates the drastic difference on the level of mortality risk based on the lowered vigilance levels. Previously, even when the dolphins left the resting bays at hour 20 their risk of mortality due to increased chance of encountering a predator did not rise significantly because their vigilance level was so high it kept their predation risk extremely low. Due to a shorter resting period, the vigilance level is lowered and as a result their mortality risk jumps exponentially as they exit the bays causing what was previously almost nonexistent mortality risk to be as high as 31% (Figure 7).

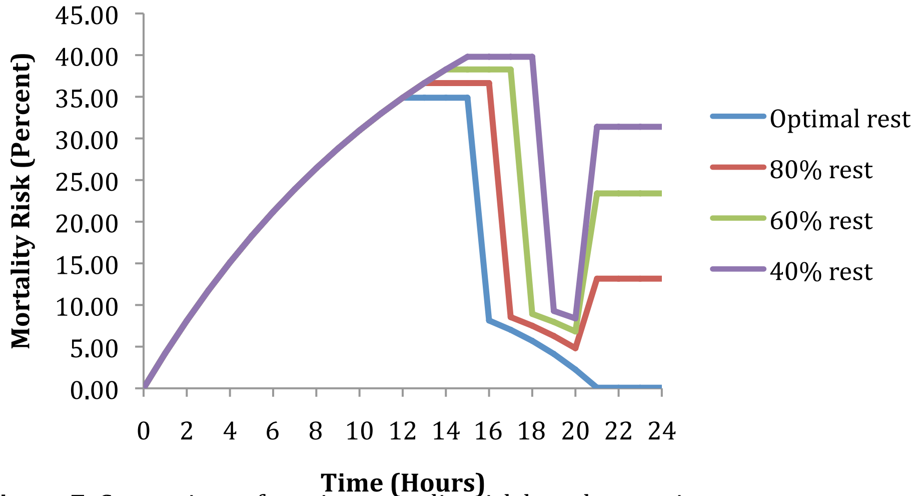

Figure 7. Comparison of varying mortality risk based on resting lengths

In terms of energy gain, while using it as a measure of the dolphin's overall health it would seem that in the short term longer foraging bouts and shorter resting periods would suit the dolphin's needs of growth and reproductive behaviors as it produces a greater net energy gain at the end of the day (see Figure 8) as the metabolic cost remains the same regardless of vigilance level.

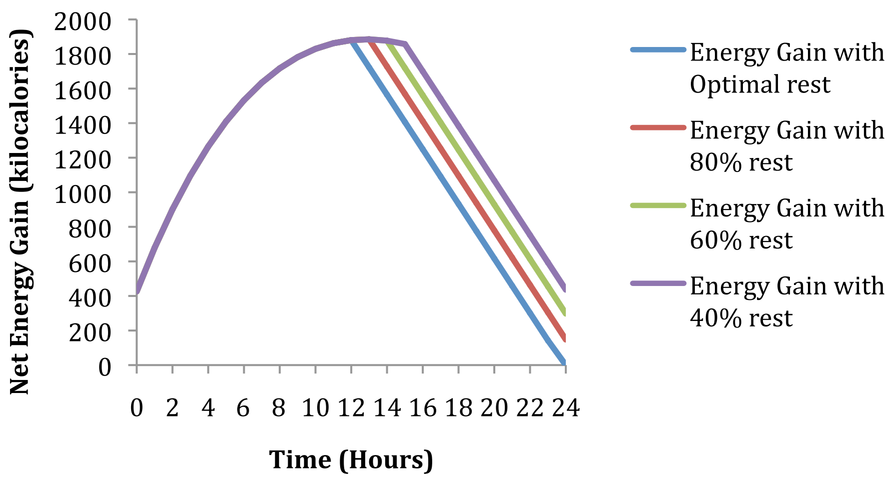

Figure 8. Comparison of net energy gain with varying resting lengths

However, while the net energy gain may be higher at the end of a single day the overall health of the dolphin may suffer even with regards to energy gain in the long term.

Extended Simulation

For the purposes of this model, an extended simulation of the data was run for 30 days with the dolphin being able to obtain 80% of its ideal resting period. When run for only one day, vigilance level was restored to 78% of its maximum level, enough for the dolphin to still maintain its energy needs as well as keep its mortality risks to a reasonable level. However, after being run for 30 days the dolphin's vigilance level ends at 0.74% of its maximum level and quite frequently hits zero during foraging bouts (see Figure 8). Vigilance levels dropping to zero does not mean death and in reality a spinner dolphin would most likely never reach a vigilance decrement that severe. The scale from zero to one hundred percent is merely an arbitrary scale used to demonstrate the decrement and recovery of vigilance rather than a precise measurement.

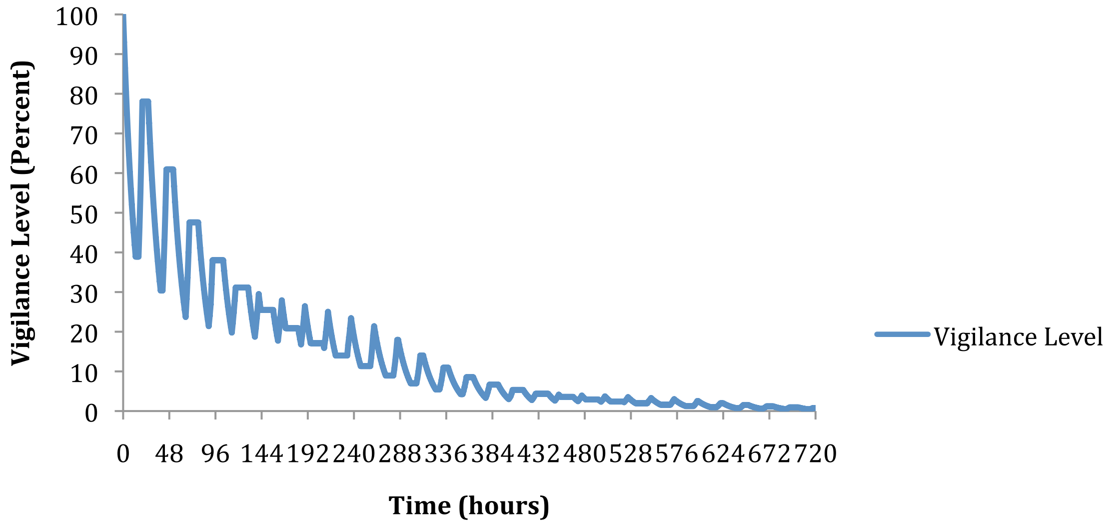

Figure 9. Simulation run for 30 days (or 720 hours) with the dolphin resting at 80% of its ideal length

The rate of food intake was also drastically affected over the long term. Previously, when run at the optimal resting time, the dolphin is able to catch 71.68 prey items per hour, but at the end of 30 days losing only 20% of its resting time the dolphin only catches an average of 15.79 prey items per hour due to the decreased rate at which it is able to catch prey because of lowered vigilance levels. In the latter half of the month the data often indicates the dolphin's ability to capture only one to two prey items per hour of foraging. On the thirtieth day of the simulation, the total prey intake is just under 19 prey items, a fraction of the 2008 prey items captured under the optimal scenario or even after a single day of 80% rest (See Table 4).

Table 4. Rate of prey intake and total prey intake during a foraging bout after 30 days at 80% optimal sleep

Time (hours)	Prey Consumed per Hour	Total Prey Intake
0	2.02	2.01
1	1.88	3.89
2	1.74	5.63
3	1.62	7.26

4	1.51	8.76
5	1.40	10.17
6	1.30	11.47
7	1.21	12.69
8	1.13	13.82
9	1.05	14.87
10	0.98	15.84
11	0.91	16.75
12	1.02	17.77
Final		**18.78**

Mortality Risk and Net Energy Gain

As shown the optimal scenario (Figure 4), the dolphin begins each day with its lowest mortality risk it will have for the next 24-hours until it is able to recover vigilance during the resting period. However, when sufficient rest is not possible the dolphin fails to regain maximum vigilance by the end of the day and consequently its mortality risk does not fall to its ideal levels around zero. Over time, the lowest level of mortality risk rises as the dolphin is not able to regain all of its lost vigilance and the amount unrecovered grows larger as the month wears on. Figure 10 shows this gradual increase in overall mortality risk over a 30 day period as the dolphin's vigilance levels continue to decrease.

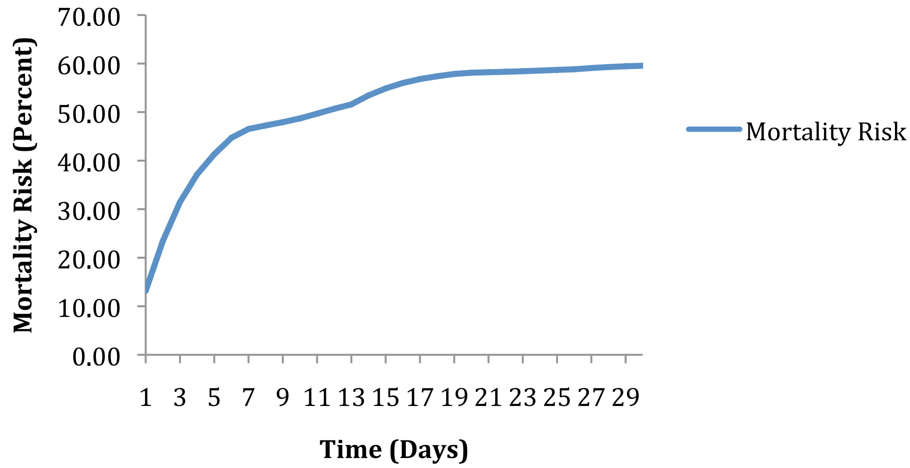

Figure 10. Mortality risk over a month period with 80% optimal sleeping time

In the short-term simulations, it would seem that the longer the foraging bout, the better off the dolphin is in terms of food capture and energy gained. However, if the behavior of longer foraging bouts is expanded to look at the dolphin's net energy gain over the period of a month the benefit quickly disappears and what in the short term was beneficial becomes detrimental to the dolphin's overall health (Figure 11).

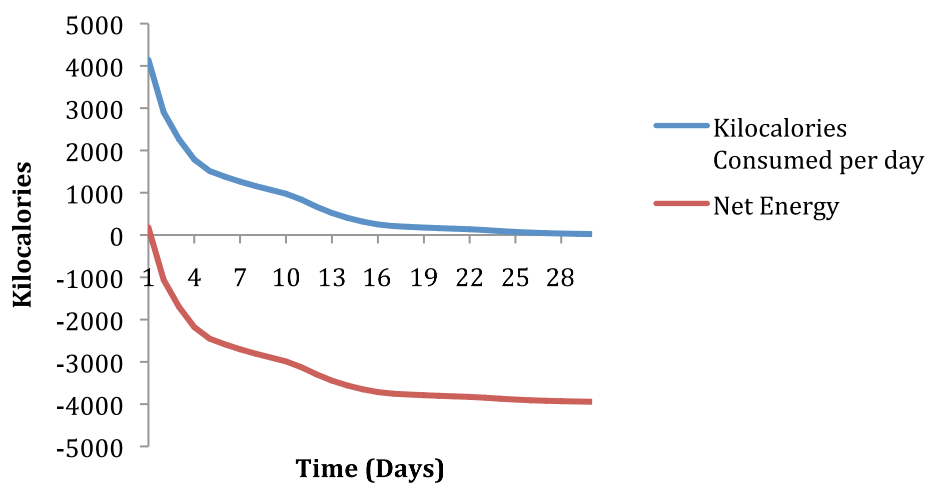

Figure 11. Total kilocalories consumed per day and net energy

Of course, the model does not take into account a multitude of factors including the knowledge spinner dolphins often participate in cooperative foraging (Benoit-Bird et al 2009) which would reduce the amount of effort expended per prey item captured. While this is an extreme projection and is highly unlikely to be accurate it shows a general trend that long term loss of sleep and consequently vigilance will severely affect the ability of the dolphin to provide food for itself.

Discussion

As dolphins perform various activities throughout the day, their decisions to participate in certain behaviors are due to a variety of factors. Some of the behavior may be attributed to food availability or energy conservation or even predation risk, but Dukas & Clark (1995) argue that vigilance decrement is another one of these important determining factors. Their equations simulate a scenario in which much of the life of a spinner dolphin is affected by vigilance levels. While certainly not the only determining factor, Dukas & Clark may have touched on an aspect of an animal's life that has not been explored and is possibly quite pertinent to the spinner dolphin controversies.

Vigilance may be defined concisely as "complex pattern recognition" (Dukas 2002), but the scope of its influence is clearly much greater than it initially may appear. From these simulations it would seem that the vigilance level of an animal affects more than just its awareness of its surroundings; it affects how the animal is able to care for and protect itself every day. The optimal scenario provides under some general assumptions the factors which are accepted to be affected by vigilance level and how they respond to its rise and fall. In the ideal scenario, the dolphin is able to regain all of the vigilance it has lost over the course of the foraging bout, keep mortality risk to a minimum and consume enough prey items to meet its metabolic needs.

As soon as the amount of rest is diminished, the dolphin's vigilance level fails to return to its maximum level at the end of its daily resting period. Initially, the consequence of failure to obtain 5 hours of rest does not seem of consequence, as even getting 40% of its optimum sleeping period the vigilance level only drops to around fifty percent. However, it is not the level of vigilance that indicates the dolphin's overall health but rather the other factors which are a function of the vigilance level that indicate the true effects of a lack of rest. The rate of prey capture is positively correlated with vigilance level (Figure 2) and so the longer the foraging bout the lower the vigilance level meaning the dolphin is slower to detect and capture prey. On the first day, the longer foraging bout with the shorter resting period is demonstrated to be beneficial for the dolphin in terms of energy gain. However, the mortality risk indicates that even with minimal loss of sleep, the dolphins are significantly more at risk to predation than with a full resting bout. As shown in Figure 7, with a full resting period of 5 hours, the vigilance level is restored to the point that even after the dolphin leaves the bays for the open ocean, where the chance of encountering a predator jumps exponentially, the mortality risk is still very close to zero. With less rest vigilance is not restored to 100% and consequently the predation risk remains higher so that the mortality risk after losing only 20% resting time leads to a jump in mortality risk just by leaving the resting bays (see Figure 7).

While the short-term scenarios provide insight into how sensitive the various factors are to the dynamics of vigilance levels, a long-term view demonstrates into the potential effects of human interruption of a dolphin's resting time. The thirty day simulation was run with the dolphin sleeping 4 hours per day in order to get a better idea of long term ramifications of sleep deprivation while using a low estimate of the amount of sleep lost. However, the results are still quite drastic. As can be seen in Figure 9, vigilance levels decrease over the thirty day period until maximum vigilance achieved at the end of a resting bout is only a quarter of a percent of the maximum potential. Additionally, the mortality risk grows as the month progresses the dolphin is unable to have enough resting time to recover its vigilance levels and is therefore less likely to be able to detect a predator in time to fend off the attack or escape as its response time will be slowed.

In the most extreme outcome of the extended simulation, the model predicts that a spinner dolphin having slept for four hours a day for 30 days in a row will only be able to capture approximately 19 prey items over a twelve hour foraging bout on account of diminished vigilance. While this is unrealistic to expect this in a real world scenario, the indication is clear that a long-term loss of sleep and consequently vigilance will severely affect the ability of the dolphin to provide food for itself. Additionally, Figure 11 shows the net gain of energy to fall below zero after only the second day of getting 80% of optimal resting time. Results such as this may indicate long term effects on the dolphin's health due to poor nutrition or reproductive health. Once net energy gained falls below zero, it indicates that the dolphin must utilize energy from its stores in its blubber in order to meet its metabolic needs. Dolphin blubber provides the animal with insulation and positive buoyancy (Struntz, et al 2004), important characteristics for a life lived under the water. If the dolphin is a juvenile, this would also diminish growth capacity as all energy would be used merely for maintenance purposes.

There are multiple weaknesses in this model and much room for improvement. Firstly, a minor problem in this model is its failure to address the vigilance decrement which surely occurs during the travel and socialization time which occurs between foraging and resting bouts. Additionally, at the current rate of vigilance decrement, even the slightest loss of sleep leads to huge jumps in the mortality risk of the dolphins as well as long term energy gain. The parameters may have to be changed to reflect the fact that the dolphins are not starving to death even though they appear to be getting less than 4 hours of sleep over a period longer than one month. However, failure to address this in the model does not negate the potential ramifications of lack of rest, as the general trends are still pertinent and valuable information to those studying the spinner dolphins. With less sleep will come less ability to detect prey and over the long term the dolphin's nutrition will suffer but perhaps not to the extent indicated by the model.

Furthermore, the net energy gain equations and parameters could be made more accurate. By only calculating the minimum amount of food captured and eaten in a single day by a spinner dolphin, the model is most likely too sensitive to a lowered vigilance level in that it almost immediately indicates that the dolphin will suffer from malnutrition from two bouts of poor sleep. However, this would introduce another problem in that instead of having a calculated number based on studies and estimates for maintenance needs of the spinner dolphin a more arbitrary number would have to take its place, making the model less based on facts and more based on assumptions of how much over its maintenance needs a dolphin may eat.

Of course, as with all models, these results must be taken as more of a guideline than fact that with vigilance decrement comes an exact proportional response in all other aspects of a dolphin's life. Even if the amount of vigilance lost leads to a decrease in foraging ability less severe than the data from the model indicates, the trend is clear: long term vigilance decrement, no matter the amount, can in fact cause a sizeable decrease in the ability to detect both prey and predators and lead to higher instances of mortality in the spinner dolphin. Vigilance level is not the only factor that affects dolphin health and mortality, but as one of many this model can provide an insight into the potential ramifications of near constant human presence in their resting bays. If other factors were taken into account, the results from a lack of sleep would not be as drastic. However, the models created give an idea of how vigilance may factor in and be a part of the dolphin's declining health in the wild.

This model could be taken even one step farther and perhaps attempt some sort of optimal foraging so that when the mortality risk becomes too high for the dolphin and it is not able to capture enough prey it would cease foraging and start another activity. By adding this to the model, perhaps it would create a more realistic scenario in which the dolphin would not forage until its vigilance level is so low that it would be almost impossible to recover to its maximum capacity.

Conclusion

Vigilance in this instance does not provide a solution to these issues nor an additional problem. It merely serves as another stepping stone to better understanding potential factors in the decrease in spinner dolphin health in these bays. Additionally, the drastic decrease in all of the spinner dolphin health measures (mortality risk, total prey capture, net energy gain) may provide additional leverage on the part of the federal government to illustrate that the constant human presence in the bays is in fact a violation of the MMPA. The data produced by the model supports the action on the part of the federal government to have partial closures in bays known to have resting spinner dolphins.

Additional research must be done in order to fully understand the biology and life history of the spinner dolphin not only to help make this model more accurate but also because without further knowledge it is possible that all actions to protect the dolphins could prove futile and subsequent regulation of the area would be premature. Greater controls, possibly through regulation and enforcement need to be enacted in the bays. Spinner dolphin health is declining and the numbers of people in the bays are increasing without adequate management of activities or thought to consequences of human presence. The number of complaints related to spinner dolphin harassment increases each year and yet enforcement has not reacted accordingly. For many tour operators a filed complaint simply leads to a slap on the wrist, and the business is too lucrative for such a small governmental response to cease their behavior. Vigilance modeling provides yet another insight into a complex problem with a growing need for a solution. Dolphin conservation is one of the unique environmental topics that in terms of the issue-attention cycle (Downs 1972), it is able to maintain long-term public enthusiasm. This status provides tremendous opportunity to prevent the gradual decline of a species into an endangerment of extinction and should not be wasted.

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