

**MODELING THE ENERGETICS
OF STELLER SEA LIONS (*Eumetopias jubatus*) ALONG THE OREGON COAST**

by

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RESEARCH REPORT

Submitted To

Marine Resource Management Program
College of Oceanic & Atmospheric Sciences
Oregon State University
Corvallis, Oregon 97331

2002

in partial fulfillment of
the requirements for the
degree of

Master of Science

Commencement June 2003

ABSTRACT

A dynamic bioenergetic model for Steller sea lions (*Eumetopias jubatus*) was built using the STELLA simulation modeling system. The model is intended as an aid for the exploration of ecological questions regarding growth and survival of immature Steller sea lions (ages 1-3) living along the Oregon coast under different nutritional scenarios. The ultimate goals were: 1) to identify features of the Oregon ecosystem that could contribute to the growth of the Steller sea lion population in contrast to the declining population in Alaska and 2) to provide a basis for examining the various hypotheses that have been put forward regarding the causes of the Steller sea lion decline in Alaska.

The dynamic energetic model was composed of coupled submodels, created or adapted from the literature, that describe the energetic inputs and outputs of the animal. It is a mechanistic model based on biological principles that attempts to describe the connections and feedbacks between the different components and the allocation of energy to them under suboptimal nutrition.

The model predicted that both changes in prey abundance and quality would have a more pronounced effect in one-year-old animals than in two- and three-year-old sea lions. A reduction in prey density could delay the attainment of sexual maturity, and this could have a significant negative effect on the population rate of increase. The seasonal migration of Pacific whiting was shown to be very important as a biomass influx into the system. In general, the model predictions were consistent with observations on the declining population of Steller sea lions in Alaska.

ACKNOWLEDGEMENTS

I would like to extend a special and warm thank to my supervisor, Dr. David B. Sampson. His scientific as well as human qualities made working with him in this project a real pleasure.

I would like to thank my graduate committee Dr. Charles B. Miller and Dr. Daniel Roby for their time and insightful comments on my report. Thanks to Dr. James W. Good and Laurie Jodice for their great job in making the Marine Resource Management such an outstanding program. My special thanks to Laurie Jodice for her help and guidance and for always being there for anything a MRM student could possibly need. Thanks also to Irma Delson for her warmth and support.

I would also like to thank Robin F. Brown, Susan D. Riemer and Brian E. Wright from the Oregon Department of Fisheries and Wildlife for their sharing of data with me. Special thanks to Brian for providing me with great pictures for my student presentations.

Financial support for this project was provided by the North Pacific Universities Marine Mammal Consortium. I would also like to thank Oregon State University for providing me with an Oregon Laurels Supplemental Graduate Scholarship during my first year at OSU.

Changing continents, a very special thanks to my parents and family for their love and support and for their unconditional belief in me. A very warm thank you to my friends Ana, Ines, Patricia, Leo & Baba, Marina & Rafa for showing me that friendship is a gift that stands over distance. It would have been so much harder to leave my country without knowing that, whenever I come back, we can still have some 'minis' at 'Los Moteros' and laugh about life as if it were yesterday. And thanks to my new friends here (yes, Armando, specially you) for making my stay so pleasant and for showing me that there is more in life than science.

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*Este trabajo está dedicado a mis padres,
a los que se lo debo todo.*

CHAPTER 1: GENERAL BACKGROUND

The Steller sea lion, *Eumetopias jubatus*, breeds from the Kuril Islands and Okhotsk sea through the Aleutian islands and Gulf of Alaska, and south to California (Loughlin *et al.* 1987). The breeding colonies of Steller sea lions on the Oregon coast have been increasing for the last decades at an average annual rate of 3.9% (Riemer *et al.* 2001). In contrast, the Alaskan population of Steller sea lions has decreased by over 70% between 1980 and 1992 (Loughlin *et al.* 1992, Trites and Larkin 1996). This dramatic decline led to the classification of the Steller sea lion as a threatened species under the U.S. Endanger Species Act in 1990. In 1997, it was reclassified as endangered in the western portion of its range because of a continuing decline and concern about the long-term viability of these populations, while the eastern portion remained as threatened as a possible reservoir for the conservation of the entire species.

The cause(s) of the decline remains uncertain (NMFS 1995). One of the leading hypotheses to explain the decline is the nutritional stress hypothesis (Alverson 1992, Merrick *et al.* 1997, Calkins *et al.* 1998). This hypothesis states that Steller sea lions could be suffering from nutritional stress due to reduced availability and or quality of prey. There are some pieces of evidence in support of this hypothesis, such as a reduced body size of females in the Gulf of Alaska during the 1980s compared to the 1970s (Calkins *et al.* 1998). There has been an apparent switch in the diet of Steller sea lions in the Gulf of Alaska from mostly small fatty schooling fishes (such as herring, sandlance, capelin and smelt) in the 1950s and 1960s to mostly gadid species (such as walleye pollock) in the 1980s and 1990s (Alverson 1992, Merrick *et al.* 1997). In addition, the sharpest decline in the Steller sea lion populations occurred in areas with the lowest diversity of diet (Merrick *et al.* 1997). However, evidence in support of the nutritional stress hypothesis has been inconclusive and sometimes contradictory. Studies on Steller sea lion's health have found no significant differences between adult females and pups in summer in the Gulf of Alaska (a declining population) versus southeastern Alaska (an increasing population) (Castellini 1993, Davis *et al.* 1996). When female attendance patterns were compared in an area of declining population versus an area of stable population, the perinatal period was longer and foraging trips were shorter in the area of

population decline, countering the predictions of the nutritional stress hypothesis (Milette 1999).

The Oregon coast offers an excellent framework for a comparison with Alaska. Many of the demersal and pelagic fish species that form the food base for Steller sea lions in Oregon are harvested by industrial scale fisheries, and several of these fish stocks have been declining (*e.g.*, coho salmon, lamprey and several species of rockfish). The diet diversity of Steller sea lions in Oregon is not high, at least during the summer months. They rely on a few prey items: Pacific whiting (*Merluccius productus*) and Pacific lamprey (*Lampetra tridentata*) alone can comprise on average 60% of the diet (Riemer and Brown 1997, this study in a latter section). Yet, the population of Steller sea lions in Oregon has been increasing over the last decades.

This study is aimed at identifying features of the Oregon coast that are important for the maintenance and health of the local population of Steller sea lions. This will provide a basis for examining the various hypotheses that have been put forward regarding the causes of the Steller sea lion decline in the Aleutian Islands. The approach is the building of a dynamic bioenergetic model using the STELLA simulation modeling system (High Performance Systems, <http://www.hps-inc.com>). The model is used to explore the implications of changes in prey abundance and or quality in the growth and survival of immature Steller sea lions (ages 1-3 years) living along the Oregon coast. The study focuses on immature female Steller sea lions for two reasons:

- 1) A reduction in the survival of immature animals has been suggested as a possible cause of the decline in conjunction with moderate reductions of female fertility (York 1994).

- 2) Once females reach sexual maturity and are impregnated, they incur the costs of pregnancy and lactation. The modeling of lactation under nutritional stress requires a resolution and understanding of Steller sea lion biology that is currently unavailable.

Females are chosen because of their greater contribution to the reproductive potential of the population. The Steller sea lion is a polygynous species (Loughlin *et al.* 1987) and one male can impregnate several females.

This study addresses some ecological questions: 1) the implications of changes in prey abundance and quality in the growth and survival of immature Steller sea lions;

2) the possible implication of a reduction of prey density in the attainment of sexual maturity and the consequences for the population and 3) the role of the seasonal migration of Pacific whiting (*Merluccius productus*) into Oregon waters for the stability of the population of Steller sea lions.

Secondarily, the model allows for exploring other questions such as the role of metabolic depression as an energetic strategy for minimizing weight loss under nutritional deficiencies, the role of compensatory growth in free ranging animals, and which foraging strategy (just enough foraging to satisfy energy needs versus forage to maximize energy intake) better resembles the observed Steller sea lion behavior.

In Chapter 2, I describe how the model was constructed and the basic underlying equations and biological principles. This chapter is divided in two main sections: 2.3 Outflows and 2.4 Inflows. The first describe the submodels used in the representation of the energetic costs for the animal. There are three main submodels: activity, thermoregulation and growth (positive and negative phases). Section 2.4 describes the foraging model chosen to represent how the animal acquires energy from its environment. In Chapter 3, I describe some simulation experiments and the results obtained. Detailed information about the justification of the approaches taken, the assumptions and parameters chosen, can be found in the Appendices.

CHAPTER 2: THE DYNAMIC BIOENERGETIC MODEL

2.1 Introduction

Essential to understanding how organisms interact with their environment and respond to perturbations is the study of internal allocation of energy under different scenarios. To facilitate such an understanding I constructed a bioenergetic model that is dynamic in many of its parameters.

Bioenergetic models divide the energy expenditures of the animal into different components. They usually distinguish two main components, production or storage and maintenance or respiration (Costa and Williams 1999, Lavigne *et al.* 1982). Storage includes somatic and reproductive growth, while respiration includes basal metabolism, the heat increment of feeding, thermoregulation and work and activity (Costa and Williams 1999).

Most bioenergetic models for marine mammals (*e.g.*, Ashwell-Erickson and Elsner 1981, Doidge and Croxall 1985, Lavigne *et al.* 1985, Olesiuk 1993, Winship *et al.* 2002) are applied to estimate food consumption of individuals or populations, as direct estimates are methodologically very difficult to obtain and studies on captive animals may not be very representative. These approaches, with varying degrees of complexity, are similar in their methodology. They involve a backward calculation of the energy ingested by the animal based on estimates of the energetic costs of the different physiological functions. The energy needed for each physiological function is estimated independently of the others, based usually on experimental (field or laboratory) observations. These models are static in the sense that the parameters used (either point values or intervals that accommodate uncertainty in the estimates) are fixed and independent of variations in the other parameters. There are no feedback loops among the variables or parameters and the energy flow is linear, from the observed outcomes to the inferred energy consumed.

A dynamic bioenergetic model takes that approach further and includes the links among the different energetic components and the shifts in the allocation of energy to them under environmental stress. This can provide an insight into the environmental window where an individual can survive and the consequences of nutritional stress for its

future performance. The set of individual responses to stress will influence the trajectory of the entire population, as animals of different developmental and reproductive status have different energetic needs and options, and also make a varying contribution to the population dynamics.

The development of a dynamic model is difficult because of the many gaps in the understanding of the biology of Steller sea lions (or similar marine mammals). Direct experimentation with an endangered species such as the Steller sea lion is problematic, and observations of free ranging animals are difficult and limited. Nevertheless, some basic biological principles can be inferred from studies of other animal groups, for which much more intensive research has been done. Specifically, the animal production literature has proven very useful for inferring those principles, and this shows great potential in adapting animal production models to understand the functioning of wild populations, which has not been fully explored before.

The model is mechanistic as it is mainly based on general biological principles rather than on empirical observations. The advantage of a mechanistic model over an empirical model is that they are more flexible, they can be applied over a wider range of conditions than are experimentally feasible (France *et al.* 1987).

However, even “borrowing” principles from other animal groups, some competing and mutually exclusive hypotheses could not be discerned due to the lack of evidence. Some other gaps had to be overcome by untested assumptions and deductions. Nevertheless, I consider that the advantages of building a dynamic model override the disadvantages. Wherever possible, I have identified weaknesses and highlighted assumptions, and I have built an open model that incorporates alternative hypotheses that cannot be judged among at present. There are some parts of the Steller sea lion's biology that are unknown. Nevertheless, many of them might be unimportant when understanding the animal as a whole and might have little influence on the population dynamics.

The many uncertainties in some of the parts of the model limit its applicability. It should be clear that the objective of the modeling exercise is increased understanding, rather than quantitatively accurate predictions. Even though the model may seem numerical in its outputs, it should be regarded as a qualitative model. While this model is

not suitable as a basis for setting management regulations, it can be useful for defining new lines of research.

Given the dramatic and continuous decline of the western stock of the Steller sea lion population, and the no less dramatic economic consequences of the management regulations in the area (*e.g.*, no fishing zones around most rookeries and haulouts and modified fishing seasons, NOAA 2002), it is important to identify gaps in the current knowledge and evaluate the most immediate needs for research.

2.2 Dynamic Modeling

A dynamic bioenergetic model is similar to a traditional static one in that it separates the energy requirements of the animal into different components. It is different in that it is not linear and unidirectional in its connections. That is, in static models the energy ingested, and therefore food ingested, is inferred from the energetic costs. A dynamic model is circular in the sense that it is not the description of one state, but the representation of a series of states where the output (ingested energy) becomes an input for the next time step. Intake is dependent upon physiological functions, and physiological functions are dependent upon intake. This circularity is broken when environmental conditions are considered as one of the inputs. These conceptual differences are represented in Figures 2.1 and 2.2.

There is no good starting point to describe a dynamic bioenergetic model. For simplicity, I will start with the outflows.

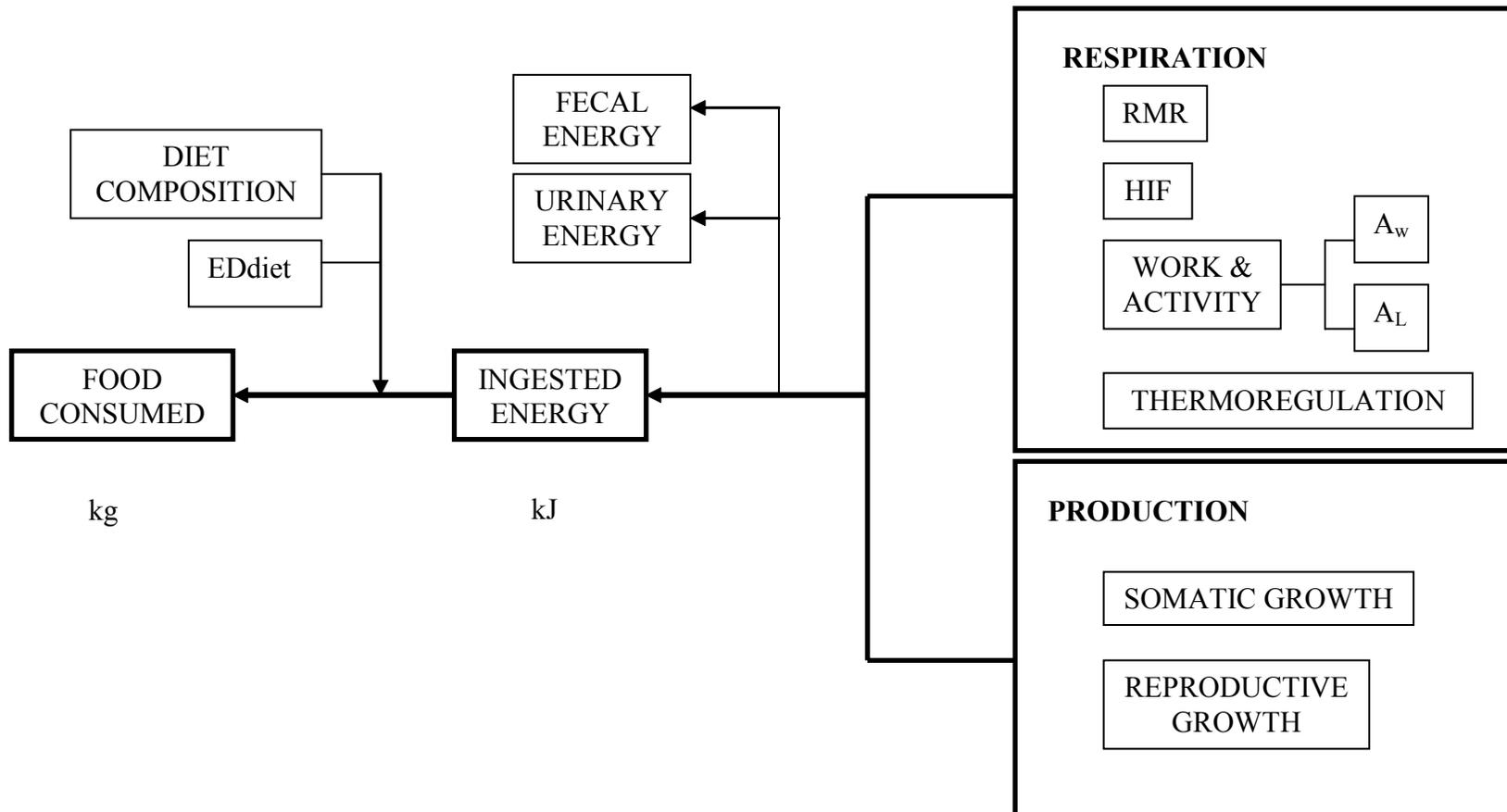


Figure 2.1: Traditional static bioenergetic model adapted from Costa and Williams (1999). The flow of energy is unidirectional, from the observed outputs (respiration and production) to the inferred inputs (ingested energy and food consumed). There are no connections among the animal physiological functions (RMR is resting metabolic rate, HIF is the heat increment of feeding, A_w is activity in water and A_L is activity on land and EDdiet is the energy density of the diet).

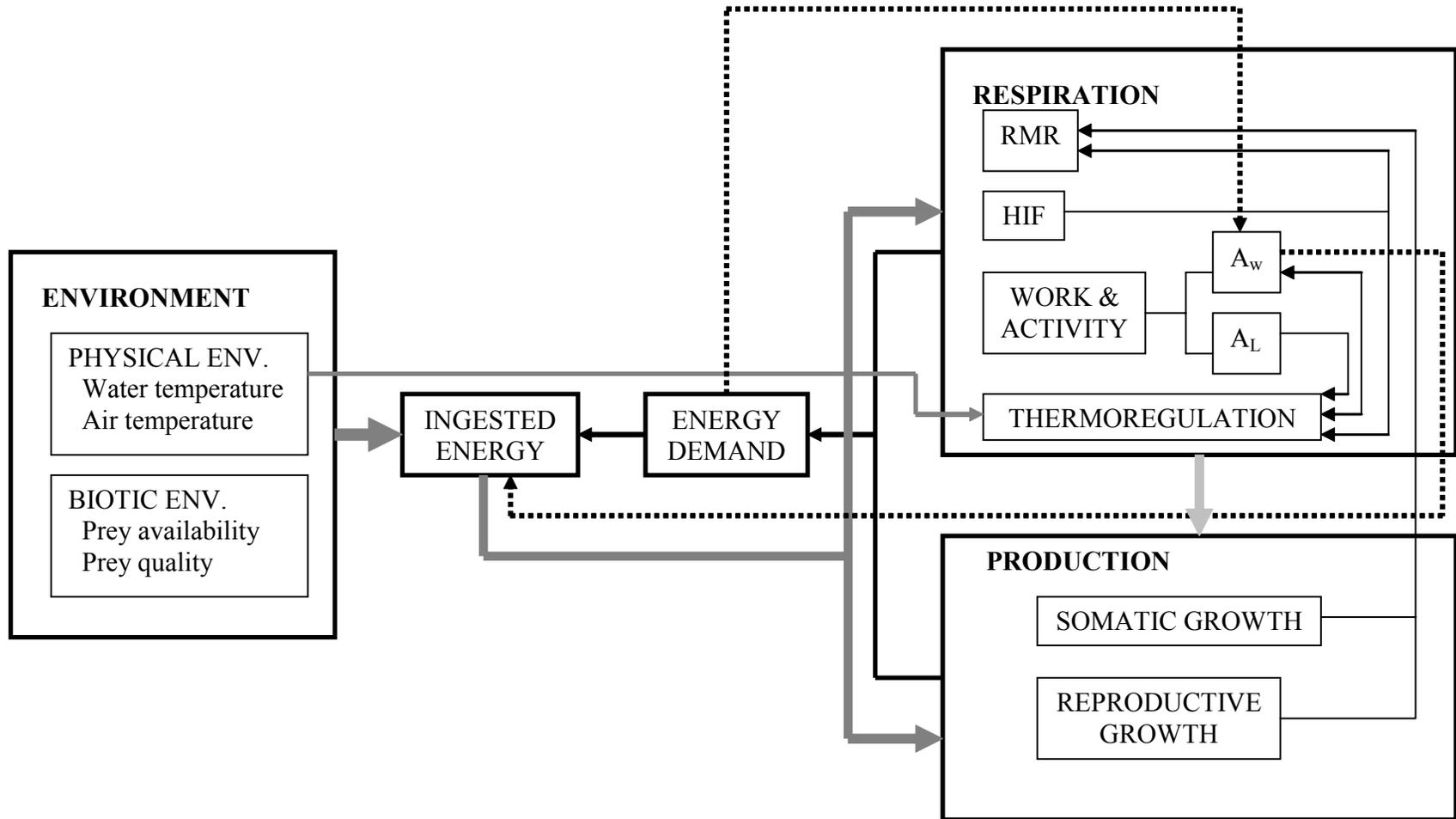


Figure 2.2: Dynamic bioenergetic model showing some of the feedback loops among its components. The animal's physiological functions are dependent upon ingested energy, and ingested energy is dependent itself on the sea lion physiological functions. The circularity is broken when environmental conditions are taken into account. The ingested energy then results from internal mechanism (energy demand) and external mechanisms (environmental conditions).

2.3 Energetic Outflows

To describe the energetic outflows of the animal, I will follow the scheme proposed in Costa and Williams (1999) in which energetic costs are separated into respiration (basal metabolism, heat increment of feeding, work and activity and thermoregulation) and storage (somatic and reproductive growth).

2.3.1 Energetic costs for respiration:

2.3.1.1 Basal metabolism:

Lavigne *et al.* (1986) have shown that under standard conditions, marine mammals have metabolic rates similar to those of other mammals and can be represented by Kleiber's (1975) "from mouse to elephant" equation. Therefore, I use Kleiber's equation to provide a baseline level for sea lion metabolic rates:

$$[2.1] \quad BM = 292.88 * (Bodywt^{0.75})$$

where BM is the basal metabolic rate (kJ/day) and *Bodywt* is body weight (kg).

This baseline level is modified by use of multipliers or additive terms depending on the departure from standard conditions:

- Immature growing animals have higher metabolic rates. To account for that the model uses a multiplier similar to the one in Winship *et al.* (2002), based on observations of growing Steller sea lions conducted at the Vancouver aquarium. One-year-old animals are assumed to have a resting metabolic rate double that predicted by Kleiber's equation, and the rate declines linearly to the standard rate when the animals are 8 years old.
- An activity multiplier and additive terms are introduced to account for the elevation in resting metabolic rate when the animal is not resting (Section 2.3.1.3)
- The cost of thermoregulation in water and air is calculated and added to the cost of activity to account for the increase in metabolic rate when the animal is outside its thermoneutral zone (Section 2.3.1.4).
- The higher metabolic rates derived from the absorptive state are assumed to be represented by the heat increment of feeding (Section 2.3.1.2).

The resultant metabolic rate is called the resting metabolic rate (RMR) as opposed to the active metabolic rate.

2.3.1.2 Heat Increment of Feeding (HIF):

Not all the energy ingested as food is available to an animal for growth and maintenance. Some energy is lost because of a rise in metabolism during the digestive process. This increase in metabolism is thought to result from both the mechanical and biochemical processes of digestion (Blaxter 1989).

Although the heat increment of feeding is not always a fixed proportion of gross energy intake (Beamish and Trippel 1990), and can vary for different meal sizes and for different food items (Rosen and Trites 1997, 1999, 2000a), there are not enough data to model how HIF would vary as a function of meal size and composition. In addition, the model does not have enough resolution to account for individual meals. Therefore, HIF is considered in the model to be a constant proportion of gross ingested energy (GIE).

I use the midpoint (0.125) of the interval given in Blaxter (1989) for monogastric animals (0.02 to 0.23) for the HIF for maintenance as a proportion of gross ingested energy. This value is the same as the midpoint of the interval used in Winship *et al.* (2002).

Growing animals may experience higher HIF as a consequence of inefficiencies in the synthesis of tissues. The HIF during periods of growth is incorporated indirectly in the model as the inefficiencies in the retention of protein and fat, discussed later in the section on somatic growth. The quantitative effect of activity upon the HIF is unknown and it is not incorporated in the model.

2.3.1.3 Work and Activity:

A Steller sea lion's activities are diverse and might include activities in water such as foraging, traveling between food patches, rafting or escape from predators, and activities on land such as sleeping, resting, playing, or breeding. For simplicity, activity costs are separated into activity cost on land and activity cost in water. On land, all activities are considered equivalent from an energetic point of view. In water, it is assumed that all activity is foraging. The proportions of time the animal devotes to land and water activities are calculated from its energetic needs and prey availability and quality, as explained in Section 2.4.

2.3.1.3.1 The cost of activity in water (A_w).

The model assumes that all activity in water is foraging, with the animal swimming at a sustained foraging speed while feeding on the prey encountered. To estimate the cost of locomotion, I use an integrated locomotion and thermoregulation model, as proposed in Hind and Gurney (1997). They calculated total metabolic rate when swimming (M) as:

$$[2.2] \quad M = M_B + M_T(V) + M_L(V)$$

where $M_T(V)$ is the metabolic cost of maintaining a constant body-core temperature and is a function of the swimming velocity. As the animal increases its swimming velocity, forced convection is greater and will dissipate heat faster. $M_L(V)$ is the metabolic cost of locomotion and is also a function of the swimming velocity. M_B is the cost of all other activities, which they called the basal metabolic rate. Because by definition the basal metabolic rate only applies to adult animals in the post-absorptive state, I use the resting metabolic rate (RMR) for M_B , which incorporates the multipliers according to the state of the animal as explained above. The calculation of $M_T(V)$ is explained in Section 2.3.1.4. The metabolic cost of locomotion $M_L(V)$ is estimated by hydrodynamic calculations as explained next.

In order to maintain a constant swimming speed, an animal must exert a propulsive force that exactly balances the drag force resulting from its movement. The magnitude of this drag force depends on the animal's size, its shape, the physical properties of the water and the swimming speed (Hind and Gurney 1997). The equation that determines the drag forces is (Hoerner 1958):

$$[2.3] \quad D = 1/2 * \rho * S * C_d * V^2$$

where ρ = density of the water at a given temperature.

S = animal's wetted surface area

C_D = drag coefficient

V = speed at which the animal is swimming.

From the drag force experienced by the swimming animal, the force exerted by the animal can be estimated because the thrust forces required for swimming at a constant velocity will equal the drag forces encountered by the animal (Feldkamp 1987). The

mean rate of energy expenditure in overcoming fluid resistance will be the product of body drag and average swimming velocity (Webb 1975, Yates 1983). The required power output P_o is then given by (Webb 1975, Yates 1983):

$$[2.4] \quad P_o = 1/2 * \rho * S * Cd * V^3$$

To relate the metabolic cost of the mechanical effort required to propel an animal at speed V , Hind and Gurney (1997) used the equation:

$$[2.5] \quad M_L = \lambda * \frac{\rho * S * Cd * V^3}{2 * \epsilon_A * \epsilon_p}$$

where λ = ratio of the drag of an active swimmer to that of a passive one moving at the same speed;

ϵ_A = aerobic efficiency, which is the efficiency with which chemical energy is transformed into muscular work;

ϵ_p = propeller efficiency, which is the efficiency with which muscular movements are translated into forward thrust.

The model uses the following parameter values (sources and a detailed discussion about these values are in Appendix 1): λ : 1; C_D : 0.0056; ϵ_p : 0.80 and ϵ_A : 0.15.

2.3.1.3.2 The cost of activity on land (A_L).

With the exception of the breeding season, sea lions on land are usually resting or sleeping. The metabolic cost of activities on land is therefore low. The model applies a multiplier to the resting metabolic rate, but this multiplier is set to 1 as animals on land are normally resting. I included the multiplier, though, to allow for the study of the implications of divergence from that value. The model does not account for sleep, which reduces the resting metabolic rate by about 10% (Mason and Benedict 1934, cited in Blaxter 1989).

In addition to resting metabolic rates, when the animal is on land, it can also face thermoregulatory needs. In general, these needs will be low or zero, as the animal's adaptations for thermoregulation in water tend to minimize heat losses in air as well. Only under extreme low temperatures or very strong wind will animals incur an extra

cost for temperature regulation on land. The energetic cost for thermoregulation is added to the metabolic costs of activity on land.

The total cost of activity (A) is given by:

$$[2.6] \quad A = A_W * P_f + A_L * (1 - P_f)$$

where A_W is the cost of activity in water, A_L the cost of activity on land and P_f the proportion of time in water.

2.3.1.4 Thermoregulation:

Marine mammals are homeotherms and maintain body temperatures within the typical mammalian range of 36° to 40°C (Costa and Williams 1999, Schmidt-Nielsen 1997). The aquatic environment represents an energetic challenge for homeotherms, as heat flow in water is much greater than in air. This heat loss is further increased by forced convection when the animal is swimming. Thermoregulation is, therefore, an essential trait in the life of marine mammals. A wide variety of adaptations has evolved to control heat loss to the environment (Irving 1969, Schmidt-Nielsen 1997). These adaptations are either morphological (a thick blubber layer, fur, heat exchangers at the base of the flippers) or behavioral (avoiding thermally stressful situations). However, it is sometimes not clear whether, in spite of those adaptations, they still need to increase their metabolic rates to maintain body temperature under certain circumstances.

Thermoregulation is often ignored in bioenergetic models for pinnipeds (Olesiuk 1993, Mohn and Bowen 1996, Stenson *et al.* 1997, Winship *et al.* 2002). Some models assume that animals in the wild are within their thermoneutral zones, between the lower critical T_{lc} and upper critical T_{uc} temperatures, where the animal does not need to expend additional energy to maintain body temperature. Other models assume that the cost of thermoregulation is imbedded in the costs of activity. However, the extent to which these assumptions are valid has not been considered.

Otariids are in general temperate pinnipeds (Costa and Williams 1999) with relatively thin blubber layers. Liao (1990, cited in Costa and Williams 1999) found that the T_{lc} for California sea lions in water was from 14.8°C to 16.4°C. This is above the average temperature experienced by Steller sea lions along the Oregon coast, and is certainly higher than the temperatures experienced by their counterparts in Alaska.

Juvenile Steller sea lions are about the same size of California sea lions, so it is possible that they incur thermoregulatory costs. A reduced condition (as indicated by blubber thickness) arising from nutritional deficiencies might affect the thermoregulatory capabilities of the animal and compromise its survival.

A comprehensive heat loss model for aquatic animals of different sizes and conditions, in different mediums and at different levels of activity, has been missing and is an essential part of a dynamic bioenergetic model. Such a model is derived from general equations of heat transfer.

It is assumed that heat is lost due to conduction, convection, and evaporation (only evaporation during respiration is considered). Heat losses by conduction and convection are calculated by assuming a cylindrical shape for the sea lion, where there is an inner core and an outer layer of blubber and fur. This approach is similar to that used in Lavigne *et al.* (1990), Ryg *et al.* (1988) and Watts *et al.* (1993). The model assumes that all heat is produced in the body core and that the insulating layer of blubber does not produce any heat. Heat is dissipated from the inner core by conduction that only takes place in a radial direction. In the skin of the animal, heat can be dissipated by free convection (when the animal is stationary in water or on land with no wind) or forced convection (when the animal is swimming or on land with wind).

The heat dissipation model is derived by coupling the general equations for heat transfer by conduction and convection. I use the following set of equations:

- The heat loss from the body core to the blubber-skin interface is modeled assuming a cylindrical shape and dissipation by conduction according to the equation (Kreith 1958):

$$[2.7] \quad H_1 = [k_1 * 2 * \pi * L * (T_{cb} - T_{bs})] / \ln(R_b / r_c)$$

where R_b is the radius of the sea lion

r_c is the inner core radius

T_{cb} is the temperature at the core-blubber interface.

T_{bs} is the temperature at the blubber-skin interface, which is not known.

k_1 is the thermal conductivity of the blubber.

- The heat loss by conduction from the blubber-skin interface to the surface of the skin can be calculated assuming a flat plate model (Kreith 1958) as the thickness of the skin is very thin and the difference in surface areas is minor. The factor f accounts for the surface of the foreflippers as explained in Appendix 1.

$$[2.8] \quad H_2 = f \cdot 2 \cdot \pi \cdot R_b \cdot L \cdot (k_2 / \Delta R_b) \cdot (T_{bs} - T_s)$$

where T_s is the skin temperature and is unknown, k_2 is the thermal conductivity of the fur and ΔR_b the thickness.

- The heat loss from the surface of the skin to the medium (water or air) can also be calculated as a flat plate model and depends on the kinetics of the animal. It is in generic form given by:

$$[2.9] \quad H_3 = f \cdot h_{conv} \cdot 2 \cdot \pi \cdot R_b \cdot L \cdot (T_s - T_a)$$

where T_a is the ambient temperature (water or air temperature) and h_{conv} is the convective heat transfer coefficient, which is different for water or air and for forced or free convection. For the animal to be in thermal equilibrium H_1 , H_2 and H_3 must equal. From the equality and solving for the unknowns (H , T_{cb} and T_s) the heat loss rate (H) can then be calculated as:

$$[2.10] \quad H = (T_{cb} - T_a) \cdot 2 \cdot \pi \cdot L \cdot [\ln(R_b / r_c) / k_1 + \Delta R_b / f \cdot k_2 \cdot R_b + 1 / f \cdot h_{conv} \cdot R_b]^{-1}$$

or its equivalent but simpler expression:

$$[2.11] \quad H = U \cdot S \cdot (T_{cb} - T_a)$$

where S is the corrected surface ($S = 2 \cdot \pi \cdot L \cdot R_b \cdot c$, where c is a surface correction factor explained in Appendix 1) and U is the overall heat transfer coefficient:

$$[2.12] \quad U = 1 / (R_b \cdot \ln(R_b / r_c) / k_1 + \Delta R_b / f \cdot k_2 + 1 / f \cdot h_{conv})$$

The calculation of h_{conv} for forced and free convection in water and air is explained in the Appendix 1.

The heat loss by evaporation through respiration is added to the estimated heat loss by conduction and convection. The model assumes that heat loss by evaporation through respiration accounts for 10% of the total heat loss (Folkow and Blix 1987) and that this source of heat loss is constant and does not vary with workload.

The heat budgets are calculated independently when the animal is in water and on land. For heat loss on land, an exposure ratio of 65% is assumed as in Luecke *et al.* (1975) for California sea lions at temperatures at or below 5°C.

The heat budgets are calculated as the difference between the heat gain rate and the heat loss rate (kJ/day). The heat gain rate is determined by all the sources of heat production. Those are, for water, the resting metabolic rate, the inefficiency of activity, the inefficiencies of growth and the heat increment of feeding; for land, the metabolic rate (which on land is simply the resting metabolic rate) and the inefficiencies of growth. It is also assumed that all feeding and, consequently, all heat increments of feeding, take place in water.

The inefficiency of activity while swimming represents the portion of work that is not translated into motion. That fraction is calculated as: $(1 - \epsilon_A) * M_L$ where M_L is given by Eq 2.5 and ϵ_A is the aerobic efficiency. This approach is similar to the one in Hind and Gurney (1997) and Luecke *et al.* (1975).

The inefficiencies of growth are calculated separately for fat and protein growth as:

$$\text{Pr_Growth} * (1 - k_p) \quad \text{for protein}$$

$$\text{Fat_Growth} * (1 - k_f) \quad \text{for fat}$$

where Pr_Growth and Fat_Growth is the energy allocated to protein and fat mass growth during that time step, and k_p and k_f are the efficiencies of protein and fat retention respectively.

If the heat budget is negative, there would be an additional energetic cost for thermoregulation equivalent to the amount of the deficit. This amount is added to the activity costs of the animal.

A detailed discussion about the parameters used can be found in the Appendix 1.

2.3.2 Energetic costs for production:

The energetic costs for production can be separated into somatic growth and reproductive growth. The model is only concerned with somatic growth.

This section refers to body growth from weaning (assumed to occur at one year of age) to adult size. I consider separately lean (protein and water) mass growth and fat mass growth. Those body components have different dynamics and functions.

Different growth paths are possible considering the present conditions of diet and the nutritional history of the animal. I distinguish between positive phases of growth, under both optimal and suboptimal nutritional conditions, and negative phases of growth. Optimal nutritional conditions mean that the energetic intake allows for the full development of the sea lion's growth potential.

2.3.2.1 Positive growth phase under optimal nutritional conditions:

Studies of farm animals have shown that there is a maximum capacity for protein growth. This maximum capacity cannot be exceeded even when food is not limiting and it is intrinsic to the species and sex (*e.g.*, Black 1988, Campbell *et al.* 1985a,b, Dunkin *et al.* 1986, Dunkin and Black 1987, Campbell and Taverner 1988, Black 2000, de Vries and Kanis 1992). The concept of a maximum protein deposition rate is applied in most animal production models (*e.g.*, Black *et al.* 1986, De Vries and Kanis 1992, Whittemore and Fawcett 1976, Whittemore 1983, Moughan and Smith 1984, Moughan *et al.* 1987).

Although no similar detailed studies exist for marine mammal growth, I assume that this is a general principle of mammalian growth. This idea is also consistent with intuition: a five-year-old child fed to excess of his needs won't reach adult body size at the age of six. He will probably become obese rather than taller.

The assumed maximum growth rates for protein are explained in Appendix 1 (under reference growth models).

With regard to the rate of fat deposition, more speculation is involved. Studies of farm animals do not show a concomitant intrinsic growth curve for fat or a physiological limit for fat tissue accretion. It is generally assumed that the total body mass of fat is a function of the energy surplus given to the animals (Kielanowski 1976, Whittemore 1998). This has to do with the major role of adipose tissue, the long-term storage of

energy (Leat and Cox 1980). Some portion of the adipose tissue serves as a reservoir to buffer temporary mismatches between energy intake and energy demand. Therefore, there is more flexibility in the rate at which fat is deposited, as well as in the optimum weight of body fat for a given developmental status.

Nonetheless, this flexibility has lower limits, as a certain minimum level of fat is necessary for the animal to function. Depending on what is necessary, what is desirable, and what is accessory, Whittemore (1998) differentiated total body lipid into three compartments: essential fat, a minimum preferred level of target fat and depot fat. Essential fat is the irreducible base level of fat necessary to normal metabolic function. The preferred level of target fat is the minimum level of fatness required to partition and prioritize available nutrients toward lean tissue growth and other functions such as pregnancy and lactation. At levels of fatness below the target, achieving target lipid levels will detract from the attainment of potential rates of protein retention, as the physiological priority would be for fat deposition. Depot fat is a means of either dealing with excess energy from an imbalanced diet or creating a store of energy in the body in preparation for some prospective food shortage (Whittemore 1998).

There are not enough data to address how the composition of body mass changes with age and sex for Steller sea lions. The data for different ages are cross-sectional, instead of longitudinal, and from different locations, which makes it difficult to infer how composition changes in the growing animal. A description of the available data is in Appendix 1. In addition, in Steller sea lions, as in other aquatic mammals, adipose tissue has a thermoregulatory function besides energy storage. Therefore, it is difficult to infer to what extent fat is used for storage of energy as in other mammals, or as a coat for thermoregulation.

Given the lack of more detailed data, the model makes certain assumptions. It is assumed that the physiological distinction among essential fat, minimum preferred level of target fat, and depot fat applies also to the growth of Steller sea lions, although the values might differ from those of other mammals. Assigning values to those fat levels is almost a guess. However, I considered it necessary to make those distinctions to evaluate possible strategies and different growth paths when nutrition is not optimal. Although the values assigned might not be accurate, the model can at least provide a qualitative insight

into the relative development and use of the different body components when diet is not optimal.

The model assumes the following values for the fat levels: essential fat is 5% of total body weight and the minimum preferred level of target fat is 15% of total body weight. For simplicity, these values are referred to in the model as the minimum level of fat and the target level of fat. They are allowed to vary according to thermoregulatory needs. Therefore, they depend on the size, season and level of activity of the animal.

The value of depot fat as a percentage of total body weight depends on the foraging strategy. One of the functions of depot fat is storage of energy in anticipation for some prospective food shortage (Whittemore 1998). This definition raises the question of what is a prospective food shortage. Certainly, the breeding season means a food shortage for the reproductive animal, as giving birth, breeding, and the first days of lactation occur on land and are incompatible with feeding. For Steller sea lions in Oregon, the winter migration from the region of Pacific hake (Stauffer 1985), one of the preferred Steller sea lion food items (Riemer and Brown 1997), might result in a food shortage that is also predictable on a regular yearly basis. El Niño years, which occur at a wider temporal frequency, might fall within the range of predictability for a Steller sea lion. How long a time span are Steller sea lions capable of anticipating? Most importantly, how much does a sea lion value the future compared with the present? How much is a Steller sea lion willing to risk today in exchange for a future increase in fitness?

Given the lack of answers to those questions, two extreme hypotheses, which underlie two alternative foraging strategies (Schoener 1971), are tested in the model: (1) Steller sea lions are "time minimizers", meaning their goal is to minimize the time spent obtaining a fixed energy requirement. This fixed energy requirement is the energy that satisfies maintenance, maximum protein growth accompanied by the target fat level and a certain amount of depot fat. Depot fat could be related to reproductive activities, but as the model is only concerned with immature animals, in this case depot fat is zero.

It is assumed that a fixed energy requirement will drive the "hunger" signal, and that this signal will determine the foraging effort. Once that energy requirement is met, the hunger signal is turned off and the animal stops eating. This approach implies that the

final weight of the animal is completely internally regulated, although environmentally modulated. Alternatively:

(2) Steller sea lions are "energy maximizers", meaning they feed so long as there is an energetic profit from their feeding activity. Excess energy is accumulated in the form of depot fat, and there is no limit for this accumulation. Sea lions stop feeding when the rise in costs offsets the rise in gains. This way, animals acquire as much energy as they can, when there is abundant food, to be fitter in anticipation of future shortages. The final weight of animals is, in this instance, environmentally determined, as the environment primarily determines what is profitable and what is not.

Most certainly, real Steller sea lions would show an intermediate behavior between these extremely "cautious" and extremely "greedy" strategies, which represent the opposite ends in a gradient of behaviors. Another variable, which has not been considered in the model, the perceived risk of predation, could modulate where in that gradient real animals would operate. The perceived risk of predation is different from the real risk of predation in that it is how the risk is perceived by the animal. However, predation risk and energy intake are expressed in different currencies that cannot be evaluated directly in the model.

2.3.2.2 Positive phase of growth under suboptimal nutritional conditions:

When the sea lion cannot get enough energy from its diet, it won't be able to grow at its maximum potential rate. Its recent nutritional past will condition its growth path under these circumstances. If the animal has depot fat, those fat deposits can be catabolized while protein growth proceeds at its maximum potential rate until the fat is catabolized to the target level. This behavior has been observed in some farm animals (Whittemore 1998, Trowbridge *et al.* 1918). When the fat content of the modeled sea lion is at the target fat level (the animal has no more depot fat) the resulting growth rate is that which incorporates the energy available for growth to both protein and fat tissue at a target Fat/Protein ratio. This target ratio is simply the one that allows for maintaining the target fat level. The resulting weight gain rate depends on how much energy is available for growth. The energy available for growth is the difference between metabolizable energy (proportion of ingested energy that is utilizable by the animal, explained in

Appendix 1) and maintenance costs. The reduction of growth relative to its potential is proportional to the reduction in energy intake.

Therefore, any positive increment of body mass will be such that it meets the target level of fat. The animal would grow slower in all its components while maintaining its “health”. This is, the animal would keep the preferred proportions rather than growing at the maximum potential for one component at the expense of the others. This idea is based on evidence in Whittemore (1998), Orden *et al.* (1999), Wallace (1948), Wilson (1952, 1954a,b), Elsey *et al.* (1964), Tulloh (1964), Allden (1968a,b), Ledger and Sayers (1977) and Drew and Reid (1975) from studies of different farm and laboratory animals.

2.3.2.3 Compensatory growth:

It has been noticed that some animals, when rehabilitated after periods of undernutrition, may show growth rates that exceed those of control animals that were continuously fed. This has been called compensatory or catch-up growth. Examples are numerous in the animal science literature (for a review see Allden 1970 and O’Donovan 1984). However, the evidence is often equivocal. Periods of undernutrition leading to growth arrest or to weight loss are sometimes considered equivalent and not clearly distinguished. Another source of confusion is that sometimes comparisons are done on animals of the same chronological age but different weights (Allden 1970). Generally, underfed animals are lighter and grow faster than controls of the same age. But they are in a steeper portion of their normal growth curve.

For animals in the wild, the situation is more complicated because food intake is in certain cases linked to a relatively costly foraging activity (either from an energetic or from a predation risk point of view). Would there be any advantage for compensatory growth?

In the model, both possibilities are included.

- Real compensatory growth occurs. When the animal is off its growth schedule because it has grown at a lower rate or has lost weight, it may accelerate its growth rate to keep pace with its chronological growth curve. In this view, the growth curve is determined by the chronological age of the animal.
- There is no real compensatory growth. Mature size can be reached, nevertheless, by lengthening the growing period (and there is evidence that this is possible, Allden 1970).

The growth curve of the animal is determined by its physiological age (as inferred by its length) instead of by its chronological age. The concept of physiological age is discussed in Section 2.3.2.6.

However, independently of the hypothesis chosen, when the animal is recovering from weight loss, the assumed maximum protein growth rates can be temporarily exceeded in the model.

2.3.2.4 Negative phase of growth:

During periods of insufficient nutrition for maintenance, body mass is catabolized to meet the energetic demands. Therefore, negative growth will occur. Negative growth is not the reverse of positive growth. An animal of a certain length will not shrink to a younger stage, but it will become thinner instead.

During phases of negative growth, the different body components will evolve separately, and their relative proportions will change depending on the intensity and duration of the energy restriction. The assumed catabolic process in the model follows the stages of starvation as described in Castellini and Rea (1992). However, phase I of starvation, when the hepatic glycogen reserves are utilized, is not considered. It is assumed that the animal will first catabolize non-essential fat, that is, the fat above the minimum level. This stage would be equivalent to phase II of starvation as described in Castellini and Rea (1992), characterized by increased oxidation of lipids and partial sparing of proteins. Once the animal is at the minimum level of fat, if the energetic deficiency persists, the animal will catabolize protein and fat simultaneously, maintaining fat at the minimum ratio (phase III). There is some evidence that several marine mammal species use core reserves (non-fat tissue) during periods of fasting and undernutrition (Markussen 1995, Whorty and Lavigne 1987). In any case, once the animal has catabolized all fat to the minimum ratio, its survival is seriously compromised independently of the proportions of fat and protein that it catabolizes. If it catabolizes fat, thermoregulatory cost will rise very rapidly. If it catabolizes protein, a considerable mass loss will occur as protein has less energetic density than fat. This will shorten its survival time. It is assumed that when 1/3 of the initial lean body mass has been catabolized, the modeled animal dies (Ruch and Patton 1973). Recovery from phase III starvation is long and difficult (Castellini and Rea 1992), and unlikely to happen in the wild. The model

treats protein and fat catabolism as occurring with an energetic efficiency of 100%, so that no energy is dissipated during the mobilization of body mass.

2.3.2.5 Metabolic depression:

It has been well documented that many starving animals show a reduction in the resting basal metabolic rate below normal levels (Keys *et al.* 1950, Grande *et al.* 1958, Gallivan and Best 1986, Markussen *et al.* 1992, Boily and Lavigne 1995, Montemurro and Stevenson 1960, Cahill 1978, Harlow 1981, cited in Rosen and Trites 1999). This reduction is higher than would be explained by the loss of body mass alone. Whether this metabolic depression is an adaptative strategy aimed at saving energy during periods of energy restriction, or the inevitable consequence of the loss of tissues with high metabolic rates (especially liver and guts), is not clear.

Studies of Steller sea lions and other pinnipeds do not offer much light on this question. Animals showed metabolic depression when on total fasting or reduced energy intake trials (Rosen and Trites 2000b, Rosen and Trites 1999, Markussen 1995) but not when the food was restricted to 10% of their *ad libitum* diet (Rosen and Trites 1998, Markussen 1995).

With the available evidence, it is difficult to discern if metabolic depression could happen in free ranging animals under nutritional stress. Øritsland and Markussen (1990) and Øritsland (1990) noted that metabolic depression is important in minimizing mass loss and lengthening the survival time during starvation. Therefore, the inclusion or exclusion of metabolic depression can have important consequences for the performance of the modeled animal. Given the lack of clear evidence, the model considers both options. The calculation of the magnitude of the metabolic depression is explained in Appendix 1.

2.3.2.6 Length and mass growth models:

The model follows both the evolution of growth in mass and growth in length. The classical mass-at-age and length-at-age models are not of much use to predict growth when the animal has experienced growth retardation or weight loss because of inadequate nutrition and it is, therefore, out of its chronological growth schedule. Another approach must be found to free the growth curves from their chronological schedules and link them

to nutrition. This is done in the model by means of an "hybrid" growth model employing two growth equations: one for length as a function of age and one for mass as a function of length. This approach works as follows:

If there is growth in protein mass, the length of the animal increases. It is assumed that this increase is allometric according to the theory of allometric growth proposed by Huxley (1932). This is because muscular, skeletal and other supporting structures will all have to grow accordingly for the animal to remain functional. The length of the animal will not increase more than what its skeletal body structures can support. The allometric relationship between mass and length is used in reference to protein rather than total body mass because total body mass is more variable due to the greater variability in the fat compartment. Seasonal fattening may happen without an accompanying increase in length.

Total body mass and protein mass gains are functions of the energetic transactions of the animal. There will be growth in mass if the animal has enough energy to do so, the resultant gain being a function of the energy available to growth as:

$$[2.13] \quad \Delta W_{dry} = \frac{Er}{pFat * EfatGr + pPr * EprGr}$$

where ΔW_{dry} is the dry mass gain (without water), Er is the remaining energy available for growth (metabolizable energy minus respiration), $EfatGr$ and $EprGr$ are the energy needed to build a kilogram of fat and protein tissue respectively and $pFat$ and pPr are the targeted proportions of protein and fat in the body respectively (these values are discussed in Appendix 1).

If protein mass growth has not been the maximum possible because of environmental constraints, length growth won't be maximal either. The extent to which length growth would diverge from the ideal depends on the allometric relationship with respect to protein mass. This relationship is as follows:

If total body mass as a function on length is:

$$[2.14] \quad W(L) = a \cdot L^b$$

then protein mass as a function of length is

$$[2.15] \quad Pr\ wt(L) = RefpPr \cdot a \cdot L^b$$

using a reference proportion of protein mass in the body ($RefpPr$) and assuming it remains constant from weaning to adulthood in the specified reference growth model (described in Appendix 1). This is certainly not true as body composition changes over time and by season, but there are no detailed data to describe the equation of protein mass growth as a function of time or length.

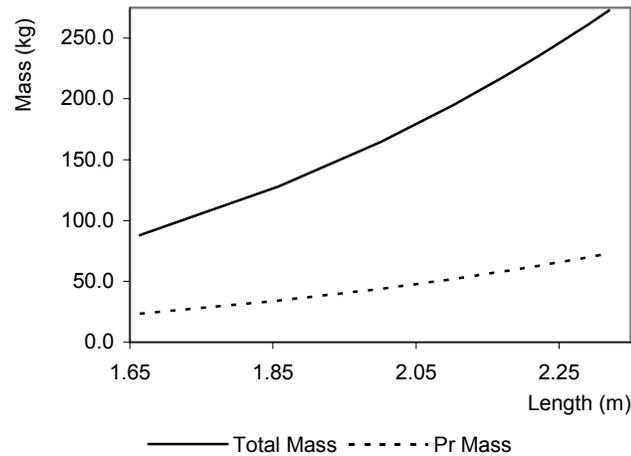


Figure 2.3: Allometric relationship between total body mass and protein body mass. Parameters a and b are taken from Winship *et al.* (2001) and the reference proportion of protein mass in the body from Davis *et al.* (1996).

By inverting eq. 2.15, length becomes a function of protein mass ($Pr\ wt$):

$$[2.16] \quad L(Pr\ wt) = \left(\frac{Pr\ wt}{Re\ fp\ Pr \cdot a} \right)^{\left(\frac{1}{b} \right)}$$

In the model, rather than using protein mass, the maximum protein mass (the maximum protein mass once attained) is used to avoid a shrinking in length when there is

protein mass loss. Maximum protein mass can only increase, it cannot decrease. When there is protein mass loss, maximum protein mass stays stationary.

Equation 2.15 then predicts how the length of the animal increases. The increment in length is a result of the increment in protein mass, which is itself a result of the energetic transactions of the animal as defined by eq. 2.13.

The model assumes that under ideal circumstances, the animal would have consumed enough energy to grow ideally. How does the animal know how much it has to eat to grow ideally during the next time step?

The length of the animal is used to calculate the desired increment in protein mass for the next time step based on:

$$\frac{d \text{Pr wt}}{dt} = \frac{d \text{Pr wt}}{dL} * \frac{dL}{dt} \quad \{\text{the chain rule}\}$$

$d \text{Pr wt} / dt$ is the assumed maximum potential daily rate (dt in the model is one day) of protein deposition for the sea lion as discussed in Section 2.3.2.1.

$d \text{Pr wt} / dL$ can be calculated from eq. 2.15 as:

$$[2.17] \quad d \text{Pr wt} / dL = b * \text{RefPr} * a * L^{(b-1)}$$

dL/dt is calculated from the reference growth model (Appendix 1), which is a Gompertz length at age model:

$$[2.18] \quad L(t) = A * \text{EXP}(-\text{EXP}(-k * (t - t_0)))$$

and,

$$[2.19] \quad dL/dt = A * \text{EXP}(-\text{EXP}((-k) * (t - t_0))) * ((k) * \text{EXP}((-k) * (t - t_0)))$$

From equations 2.17 and 2.19, $d \text{Pr wt} / dt$ can be calculated. Knowing $d \text{Pr wt} / dt$, the specified proportions of fat and protein and the cost of tissue accretion, the energy required to growth optimally in the next dt can be calculated.

In this manner, the temporal schedule for growth is determined in the model by the length of the animal. The length at age relationship is chosen to determine the future increments in length and mass rather than using a mass at age relationship because length is a better indicator of the developmental status of the animal. Mass (either as total body mass or protein mass) is very dependent on the energetic inputs and can increase or

decrease independently of the age of the animal. Growth in length can be retarded if nutrition has been inadequate, but length cannot decrease, and thus provides a better estimate of the animal's developmental status relative to its mature size. The length at age model is used to determine the desired increments and accompanying energy demand, while energetic intake ultimately determines the accomplished increments in both length and mass.

The variable t in eq. 2.19 is either the chronological age of the animal (if there is compensatory growth) or its physiological age (if there is no compensatory growth). The physiological age is derived from the length of the animal by inverting the length at age model (eq. 2.18) such that:

$$[2.20] \quad t(L) = ((\text{LOGN}(-\text{LOGN}(\text{Length}/A)))/(-k)) - (t_0))$$

What physiological age means is that, if an animal is the length of a six-year-old, it is considered six years old independently of the time it took to reach that length. Under optimal growth, the animal will advance one physiological day with every chronological day, but under suboptimal conditions, its growth would be slower. The idea of physiological age has been adopted in some animal production models (Loewer *et al.*, 1983, 1987) resulting in better predictions at extreme nutritional conditions.

A summary of this growth model can be found in Figure 2.4.

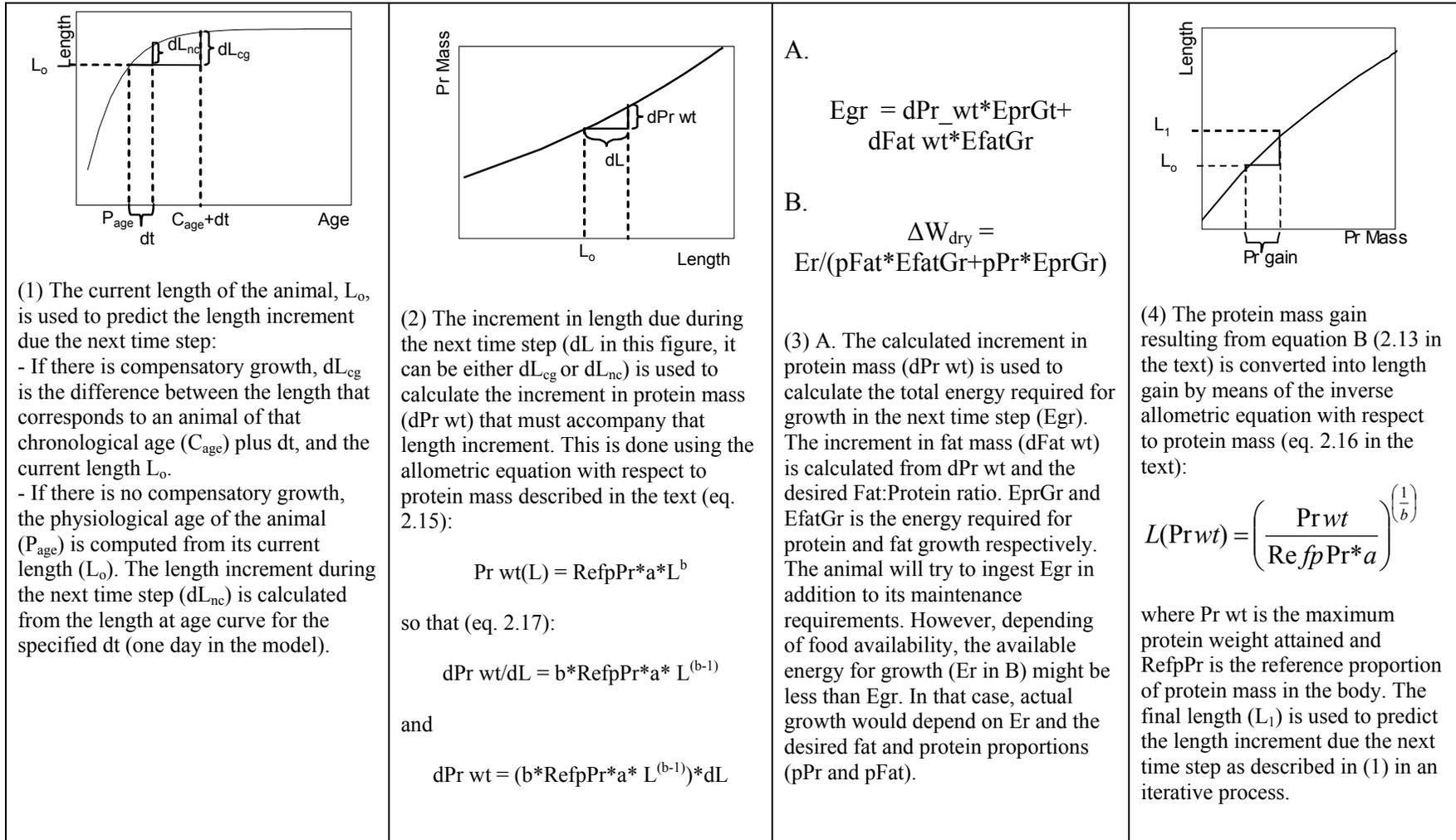


Figure 2.4: Summary of the combined growth model to predict increments in length and mass as a function of nutrition. The model incorporates the options of compensatory growth happening and not happening.

2.4 Energy Inflow

The previous section dealt with the approaches for modeling the sea lion's energetic outflows. This section deals with the approaches for modeling the simulated sea lion's response to match its energetic input to its outputs.

2.4.1 Ingested Energy:

Ingested energy is the energy acquired by the animal from its environment. This simple definition contains one of the fundamentals of the energy flow dynamics: energy flow depends on the animal as well as on its environment. How much it depends on the animal versus how much on the environment is a difficult question. Animals have evolved tightly coupled to their environment and their biological traits are strongly shaped by environmental characteristics. This makes it difficult to discern to what extent observed behaviors are internally or externally driven. Sometimes animals have internalized external signals and a particular behavior pattern persists even when the external forcing is removed. For example, the seasonal cycles in food intake shown in many captive animals that have a constant food supply provide evidence of internal regulation independent of ambient food availability (*e.g.*, Kastelein *et al.* 1990, 2000, Lager *et al.* 1994). Although this internal mechanism could have been shaped during the course of evolution in response to predictable external environmental variations, its persistence in the absence of external forcing shows that the animal has internalized the forcing. But many times it is not so evident whether environmental signals have been entirely internalized into the “genetic programs” of the animals, or if the animals still have some flexibility to adapt their behaviors to a varying environmental clue.

2.4.2 Dual regulation system:

In the model, this dependence of the energy flow on both the animal and the environment is represented by a dual regulation system. Ingested energy is determined by two functions, an energy demand function (internally determined) and a food intake function (externally determined). Evidence in support of internal regulatory systems comes from different fields, including ecology and physiology, and some of this evidence is discussed in Appendix 2.

Internal regulatory mechanisms set the upper limit of what an animal seeks to eat. But what they actually eat also will be determined by what is available to them. The evidence in support of an external or environmental regulation is obvious: if there is no food available, animals starve.

When animals face a reduced intake because of either decreased prey availability or quality, they adapt their foraging effort. The extent to which they can do so will be limited by two types of constraints:

- Limitation to foraging rate. This limitation can be external, when the prey availability is so low that the rate of energy intake cannot match the rate of energy use. Or it can be internal, when the animal can only process a certain amount of food that provides less energy than the animal needs.
- Restriction of the time available to foraging. Animals can increase the time they expend on feeding but there are certain limits. Although it is difficult to discern the limit, it is obvious that the time devoted to foraging cannot exceed 100% of the total activity budget.

The animal, as an energetic system, will seek an optimal rate that allows it to meet its energetic outflows. Accomplishing this optimal rate will be ultimately determined by environmental conditions (the amount, quality and accessibility of prey that is available to the animal).

The demand function describes the rate of energy intake that will allow the animal to meet its maintenance and production needs. The food intake function describes the amount of energy the animal can get depending on prey density and/or quality and level of effort. In other words, the demand function sets the targeted energy ingestion rate that the food intake function will try to meet by modifying foraging effort. The demand function is what the animal “wants” and the food intake function is what the animal gets.

2.4.3 The energy demand function:

There is no single equation that predicts an animal's energetic requirements through the year in a varying environment. For that reason, instead of using a simple equation, the energy demand function is the sum of all the energetic requirements:

- Energy requirements for maintenance: the animal will seek a feeding rate that allows it to meet its demand for metabolism, activity and thermoregulation.
- Energy requirements for growth: the model assumes that in growing animals, food intake under optimal conditions would be adjusted to sustain growth to a set rate. That is, the animal will adjust its energy intake to grow according to the growth equations discussed in Section 2.3.2.6. The animal will have a predetermined, targeted growth rate. This idea of a "genetic program for growth" (Weston and Poppi 1987) has been implicitly or explicitly assumed in many publications in animal science.
- Energy requirements for maintaining a set protein and fat body weight: the animal will eat as necessary to defend the body weight attained.

This representation of the energy demand allows for changes in any of the variables and it is recalculated after each time interval.

2.4.4 The food intake function:

This is the link between the animal and its environment, the link between the energetic needs of the individual and the prey available to it. Animals "think" in Joules, but they get Kilograms. The food intake function sets the conversion between these two currencies.

The model assumes that the relationship between the sea lion feeding rate and prey density follows a Type II functional response (Holling 1959, 1965), in which the feeding rate is dependent upon prey density at low prey densities, and approaches an asymptotic value with increasing prey density. This asymptotic value in the model is determined by the physical capacity of the animal to process food, that is, how many kilograms of fish can the sea lion process in a given time period.

The Type II functional response is considered to be representative of the invertebrate response, in contrast to the Type III functional response equation, which is

considered representative of a vertebrate response. Nevertheless, Abrams (1982), Sih (1984) and Dunbrack and Giguère (1987) among others showed that it is possible to get a Type III functional response if foraging effort varies adaptatively at high prey densities. In the model foraging effort is allowed to vary, therefore I assume that the Type II equation will generate a Type III response and is a correct representation of the feeding process even though that equation is usually associated with invertebrate predators.

The equation relating food intake and prey density should be regarded in a dynamic manner. The animal's daily energetic requirements are discrete points that vary through time as the animal grows or changes its activity budget in response to variations in prey density. Energetic requirements (kJ) are transformed into food requirements (kg) from the overall energetic density of the diet (eq. 3.1). The animal's food requirements (in kg) will vary depending on the composition of the diet, as sea lions would have to eat greater amounts of the prey items that have lower energetic content. The animal will modify its foraging effort to lower or raise the food intake curve until the curve fits its food requirements. It can do so until it hits a limit (such as the maximum amount of food it can process in a day or the maximum time it can be foraging) or until the increased cost of foraging offsets any increase in the energy gained. In that case, the animal would have a negative energy budget and if the situation persists, it could die. Therefore, the relationship between food intake and prey should be envisioned as a dynamic area that sets what is possible and what is not for a foraging animal rather than a curve.

The parameters I use for the feeding rate equation are derived from a general Type II functional response equation such as the one described in Valiela (1995):

$$[2.21] \quad I(a, P, b) = \frac{a * P}{1 + a * b * P}$$

where I = ingestion rate

P = prey density

a = encounter rate coefficient

b = “handling” time

The “handling” time in some models is defined as the time expended attacking, capturing and consuming a food item. In the model here the meaning is different and only

considers the time needed to process food items once ingested. This time constraint is called processing time instead of handling time (this parameter is discussed in Appendix 2).

The encounter rate coefficient (a in eq. 2.21) is a measure of the animal's contribution to a successful encounter. No matter how much prey is in the sea, the sea lion won't get any unless it exerts a certain amount of foraging effort. Foraging effort is measured in the model as the volume of water searched for food per unit of time. In the volume searched, only a fraction of the biomass of prey present is actually seen, captured successfully and ingested. Then:

$$[2.22] \quad a = Vol * ppi$$

where Vol is the volume searching rate (m^3/day) and ppi the probability of successful capture. The volume searched for food is simply a function of the time spent foraging and the foraging velocity and is given by

$$[2.23] \quad Vol = Pf * V$$

where Pf is the proportion of time in the water foraging and V is the foraging velocity. This assumes that for every meter that the animal advances in the forward direction, a volume equal to $1m^3$ is searched.

The resulting equation then is:

$$[2.24] \quad I = \frac{Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

The assumptions underlying this foraging model are outlined in Appendix 2.

A variation in one of the variables will lead to a readjustment in the values of the other variables if food intake is to remain constant. Conversely, if food intake is to increase, the values of the variables have to change. There is little the animal can do with respect to processing times and prey densities, so it will have to increase the encounter rate, either by spending more time foraging or by foraging more actively (by increasing its foraging speed). The relationship between ingestion rate, foraging speed and proportion of time foraging depends on the animal's foraging optimization criterion.

2.4.5 Optimization:

The virtual sea lion will adjust its foraging effort variables in a manner that meets the targeted ingestion rate (I_t) that would have satisfied its energetic needs for the previous day. The number I_t is accommodated into equation 2.24 such that:

$$I_t = \frac{Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

I_t is a discrete value known in advance from the energy demand function and the composition of the diet. There are two variables associated with foraging effort that can be modified to adjust the food intake to the targeted value. Those are the foraging time (Pf) and the foraging speed (V). There are infinite combinations of Pf and V yielding the same encounter rate (encounter rate being defined as: $ppi * Pf * V * P$), yet not all would have the same energetic implications. Increasing velocity will be accompanied by a rapid increase in activity cost, since those costs are related to velocity to the third power. The cost of foraging, on the other hand, is linearly related to the time spent foraging Pf . But an increase in the time foraging could be accompanied by an increased risk of predation.

The optimal combination of Pf and V depends, therefore, on the optimality criteria, which comes back to whether the animal conforms to the energy maximizer versus the time minimizer strategy. Energy maximizers would try to optimize the rate at which energy is acquired. Time minimizers would try to optimize survival by minimizing the time spent foraging (assuming that there is an increased risk of predation when in the water). The solutions could be significantly different.

In the model, time spent foraging and foraging speed are derived according to those optimization criteria in a dynamic fashion. The interaction between those parameters is not straightforward, as under certain circumstances they are inversely related (an increase in one would lead to a decrease in the other) and in others they are directly related. In general, there has been very little attention in the foraging literature about the interaction between those parameters. However, the interaction changes the shape of the optimization solution. To understand how this happens, it is convenient to consider first optimization solutions with respect to only one of the parameters (the other is assumed to be fixed).

2.4.5.1 Optimization with respect to time spent foraging (Pf) for a fixed foraging velocity (V).

The solution for the time minimizer is straightforward. It will feed the minimum amount of time necessary to fill a fixed energetic requirement. From eq. 2.24, everything is known but Pf (the calculation of ppi is explained in Chapter 3, in the section on tuning the model). From the energy demand function, the energy requirement is inferred. From the diet composition, that energy is translated into the targeted ingestion rate (I_t). It is only a matter of inverting the equation to solve for Pf so that:

$$[2.25] \quad Pf = \frac{I_t}{V * ppi * P * (1 - I_t * b)}$$

The solution for an energy maximizer is different in that the animal does not have a targeted ingestion rate (I_t), but it adjusts Pf depending on the energetic profitability of its foraging activity. This can be solved in terms of maximizing the energetic revenue. The animal will increase its proportion of time spent foraging until the point where a further increase in Pf will increase the costs over the gains. That point can be found by equating the derivative of the gain function with the derivative of the cost function and solving for Pf. The gain function with respect to Pf is again eq. 2.24, or in its energetic equivalent, it is:

$$[2.26] \quad G(Pf) = \frac{diet * Eff * Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

where *diet* is the overall energetic density of the mixed diet (kJ/kg) and *Eff* the efficiency of the digestive process (explained in Appendix 1). The cost function with respect to Pf is:

$$[2.27] \quad C(Pf) = A_w * Pf + A_L * (1 - Pf)$$

where A_w is the cost of activity in water and A_L the cost of activity on land (estimated as explained in Section 2.3.1.3).

Then

$$[2.28] \quad \frac{dG}{dPf} = \frac{diet * Eff * V * ppi * P}{(1 + b * Pf * V * ppi * P)^2}$$

and

$$[2.29] \quad \frac{dC}{dPf} = A_w - A_L$$

Equating those two expressions and solving the quadratic equation gives the optimal value of Pf for an energy maximizer.

2.4.5.1 Optimization with respect to foraging velocity (V) for a fixed proportion of time foraging (Pf).

Following the same reasoning, the velocity at which a time minimizer should swim for a fixed Pf is:

$$[2.30] \quad V = \frac{I_t}{Pf * ppi * P * (1 - I_t * b)}$$

The optimal velocity for an energy maximizer depends on its energetic gain and cost functions with respect to V. The gain function with respect to V is derived from eq. 2.24 as:

$$[2.31] \quad G(V) = \frac{diet * Eff * Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

and

$$[2.32] \quad \frac{dG}{dV} = \frac{diet * Eff * Pf * ppi * P}{(1 + b * Pf * V * ppi * P)^2}$$

The cost function with respect to V in this case is (derived from eqs. 2.2 and 2.5, for simplification thermoregulation costs are not included):

$$[2.33] \quad C(V) = \left(\frac{tr * (\lambda * \rho * S * Cd * V^3)}{2 * ea * ep} + RMR \right) * Pf$$

where tr is a transformation parameter (Appendix 1). Then:

$$[2.34] \quad \frac{dC}{dV} = \frac{3 * tr * (\lambda * \rho * S * Cd * V^2) * Pf}{2 * ea * ep}$$

Equating eq. 2.32 and eq. 2.34 and solving the quartic equation for V gives the optimal swimming velocity for an energy maximizer. Some interesting properties of these solutions and the interaction of Pf and V are outlined in Appendix 2.

Both optimal analytical solutions (for Pf and for V either for time minimizers or energy maximizers) are incorporated into the model. For the software to solve the equations, it is necessary to set starting values for Pf and V, so it can calculate in the next iteration the optimal V based on the given Pf and vice versa. Those new optimal calculated values of Pf and V are used as reference values to calculate new optimal Pf and V in a dynamic fashion and the process is repeated until values stabilize around a certain Pf and V (which doesn't necessarily mean that they are fixed, as they can change following a change in energy needs). The stable solution is quite independent of the starting values of Pf and V.

These solutions mean that the energy maximizer behavior is primarily externally determined. For the time minimizer, the linkage of the energetic needs of the animal and the foraging model is as follows: The energetic needs of the animal at time $t-1$ are used to calculate the energy demand at time t (there is always a time lag, the animal won't know the energy it has to acquire until it has expended it). This energy demand is converted into mass of food from the overall energetic density of the diet. This desired food intake is used as explained above to calculate the optimal Pf and V. Those values are inserted into eq. 2.24 and the real ingestion rate at time t is calculated. This ingestion rate is converted into gross energy intake from the overall energetic density of the diet. Under optimal circumstances, the desired and real ingestion rate would be equal. However, when a ceiling is found (if the estimated $Pf > Pf_{max}$ or $V > V_{Mmax}$, where Pf_{max} in the model is set to 0.9 and V_{Mmax} is equal to the V that elevates the metabolic rate 10 times RMR), the real ingestion rate would be less than the desired rate.

2.5 Summary

A dynamic bioenergetic model was built to explore the implications of changes in prey abundance and or quality in the growth and survival of immature Steller sea lions living along the Oregon coast. The model couples a physiological model describing the energetic outputs of the animal to a foraging model describing the foraging behavior of the animal aimed at meeting those energetic needs.

Within the physiological model, three main submodels were adapted. These are activity, thermoregulation and growth. The submodels are intended, rather than to make accurate quantitative predictions, to capture the connections among them. Therefore, they are mainly based on biological, thermodynamic and hydrodynamic principles rather than on empirical quantitative observations, and they include variables that are common to the other submodels. The activity model describes the cost of activity as a function of the animal's size, its activity budget and foraging speed. The thermoregulation model describes heat losses as a function of the animal's size and body composition, its activity budget and foraging speed. The growth model describes growth in length and in mass as a function of the nutrition of the animal rather than as a function of its age.

The coupling of the physiological to the foraging model allows the animal to adapt its behavior to meet its energetic needs depending on the current prey availability and quality. The variables that the animal can adapt are proportion of time foraging (P_f) and foraging speed (V). The model allows for the exploring of the set of possible responses to environmental perturbations while considering different behavioral strategies. This aids our understanding of the environmental window where sea lions can live and how it varies for sea lions of different sizes.

CHAPTER 3: SIMULATIONS

In this chapter, the model is used to assess questions of interest about the energetics of immature Steller sea lions along the Oregon coast. In order to do so, the environmental conditions of the Oregon coast were recreated, the model was tuned, and simulations were run under different experimental conditions directed to answer the specific questions.

3.1 Oregon conditions

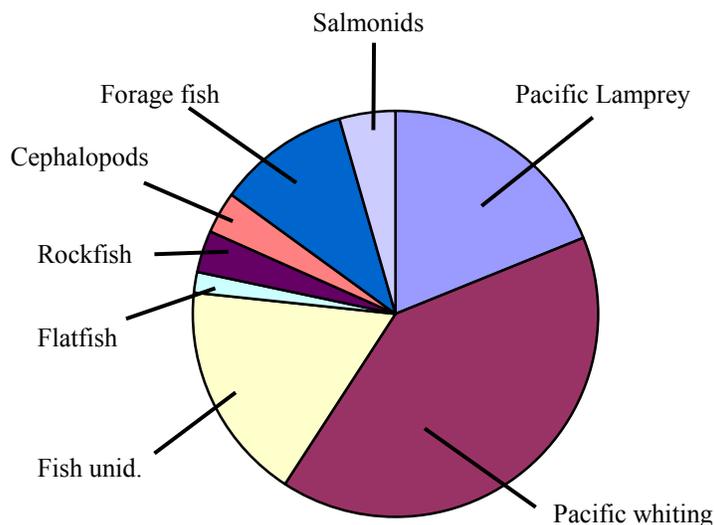
3.1.1 Physical environment.

The physical characteristics of interest in the model are the water and air temperatures. Oregon conditions were recreated by plotting the seasonal variation in seawater and air temperatures, corresponding to the average monthly values from the NODC Coastal Water temperature database for seawater temperatures and from the Western Regional Climate Center database for air temperatures at Port Orford. Port Orford was chosen as a representative point because of its close location to the main Steller sea lion rookeries in Oregon. The precision of the data was deemed acceptable for modeling purposes given all other uncertainties. The waters off the Oregon coast are dominated by an upwelling system, and water temperatures do not show a strong seasonal variation. There is also no pronounced temperature gradient with depth.

3.1.2 Trophic environment.

The trophic environment of concern for the model is related to the prey species eaten by Steller sea lions. The prey species composition in the diet of Steller sea lions was calculated by applying the split-sample frequency of occurrence analysis described in Olesiuk *et al.* (1990) to the detailed records of the scat data described in Riemer and Brown (1997). The split-sample frequency of occurrence method was chosen because it approximates better the importance of prey items to the diet than a simple frequency of occurrence analysis. The split-sample frequency of occurrence analysis considers not only the frequency of a prey type in the samples, but also if the prey type occurs by itself or with others.

The data used in the model were collected in June and July between 1986 and 1993 at Pyramid Rock, Rogue Reef, Oregon. The different prey species were separated into categories that were intended to resemble those in Winship *et al.* (2002) to allow for comparisons.



All scats were collected during summer months (June and July). Little is known about what Steller sea lions in Oregon eat during winter. But one thing is for certain, it is not Pacific whiting. Pacific whiting undergo an extensive seasonal migration offshore and to their spawning grounds off California during the winter (Bailey *et al.* 1982, Stauffer 1985).

The migration of Pacific whiting was recreated using a sine function such that their presence in the simulated system was 1 at the beginning of the sea lion year (starting 15th June), dropped to 0 at the middle and returned to 1 at the end.

The relative proportions of prey items in the diet and their energetic densities are used to calculate the overall energetic density of the diet using

$$[3.1] \quad ED_{diet} = \sum_{i=1}^8 prey_i * ED_{prey_i}$$

Energetic densities for the prey items are taken from Winship *et al.* (2002). The calculation of the relative proportions of the different prey items is explained next.

3.2 Tuning the model

The purpose of tuning is to recreate an initial framework that resembles the natural behavior of Steller sea lions. The tuning process is intended to overcome two of the most uncertain components in the model: how much fish is there and what is the probability of successful capture of prey (ppi)?

The first question could be approximated by estimations of fish abundance from stock assessment documents. However, not all the species eaten by Steller sea lions in Oregon are assessed on a regular basis, and many of them are not assessed at all. In the best case, stock assessment documents could provide estimates of total abundance. Nevertheless, total fish abundance is not a reflection of prey availability to the sea lion. Not all fish sizes are eaten by the sea lion (Fritz *et al.* 1995, Frost and Lowry 1986). Spatial (both in location and depth) and temporal changes in distribution can also affect the real availability of the fish to the sea lion.

An attempt to incorporate directly an estimation of the probability of successful capture is impossible. There is not enough current knowledge about the Steller sea lions' (or a similar species) foraging methods and abilities.

However, as far as the model is concerned, it is not in the absolute numbers of fish that is important, but rather the relationships between prey abundance and or quality and sea lion performance. For modeling purposes, it is irrelevant to know the real fish abundance or the real probability of successful capture. An approximation that resembles relatively closely the observed behaviors is adequate, from that perspective, to explore the implications of perturbations in resource prey. The variable used as a reference to tune the model was the proportion of time spent foraging (Pf). The time minimizer strategy was chosen because the energy maximizer could not respond appropriately to

seasonal variations in abundance. Instead, the model animal reduced its velocity and Pf was always the maximum possible value (this is discussed in Appendix 2).

The reference model framework starts with a fictitious area. The absolute abundance values of the different prey items are included in a manner such that their relative proportions are those in which they appear in the sea lion's diet. This is an artifact, because sea lions could have food preferences that do not mirror the relative abundances of the fish. But, for modeling purposes, the relative abundance of the prey items controls the proportions in the diet of the sea lion. The prey items absolute abundance values are referenced with respect to Pacific whiting. The absolute abundance of Pacific whiting is taken to be 1.7 million tons at the beginning of the sea lion year, based on the estimates for the most recent years assessed in Dorn *et al.* (1999). The absolute abundance values for the rest of the prey items are calculated relative to that value. From their absolute abundance values, their relative abundance values are calculated. When Pacific whiting is present, their relative abundance values are as shown in Figure 3.1. However, when whiting is absent, the relative abundance values change. The only item that changes its absolute abundance is Pacific whiting, the rest remain constant throughout the year.

To adjust the prey abundance to the observed Sea lion behavior, I ran a series of simulations in which I systematically changed the probability of successful capture (ppi) in order to get plausible proportions of time foraging (Pf). The model was tuned for one-year-old sea lions. The reference proportions of time foraging (midpoint 0.565, range:0.37 to 0.76) were based on behavioral studies conducted in Alaska of time budgets for immature Steller sea lions, cited in Winship *et al.* (2002). It is quite artificial to fit Alaskan time budgets to Oregon prey distributions and abundances. However, there are no detailed time budgets for Oregon as there are for Alaska. This 'hybrid' approach presents another problem: the migration of Pacific whiting introduces a variation in total prey biomass of almost 40% during a year. The model was tuned such that the proportions of time foraging during winter, when Pacific whiting is absent, resemble those observed in Alaska. The proportion of time foraging is then, highly dependent on season in the model. The initial conditions are described in Table 3.1.

Once the probability of successful capture (ppi) was set, it was considered fixed for the immature animals studied (1-3 years old). It is not clear if that probability should be the same for animals of different ages. Foraging is a process that involves learning, and older and more experienced animals could have a greater probability of capturing fishes. However, sea lions are intelligent animals and learn fast, especially when their lives depend on it. On the other hand, smaller animals could have a narrower range of possible prey when compared to bigger animals. Frost and Lowry (1986) noticed that sea lions less than 4 years old ate significantly smaller fish (22.4 cm) than did older animals (26.9 cm). But smaller animals can have more maneuverability and agility when chasing fishes. There are reasonable justifications for all the options: ppi as a decreasing or increasing function of age. However, for a maximum age difference of two years in the sea lions under study, the probability of successful capture could be expected to change little, if any. That probability could also be an inverse exponential function of prey abundance. In any case, in the model it is considered fixed.

Table 3.1: Initial conditions in the STELLA model for the simulations. These are the reference levels at which immature sea lions (ages 1-3) start all simulations.

Age 1	Length (m)	1.66
	Protein wt (kg)	25.44
	% Fat	15
Age 2	Length (m)	1.86
	Protein wt (kg)	35.01
	% Fat	15
Age 3	Length (m)	2.00
	Protein wt (kg)	43.33
	% Fat	15
All animals	ppi	0.00725
	Initial Prey density (kg/m ³)	0.049
	Lowest Prey den (kg/m ³)	0.029
	EDdiet range (kJ/kg)	5203-6012

3.3 The simulations

Once the model was tuned, I ran simulations to assess different ecological questions. Some questions of interest were:

- 1) How do declines in prey abundance affect immature female Steller sea lions (age 1-3 years) along the Oregon coast?
- 2) How important is the seasonal availability of whiting for the Oregon Steller sea lion population?
- 3) How do declines in prey abundance affect the attainment of sexual maturity?
- 4) How are the immature female sea lions (age 1-3 years) affected by changes in prey quality?

To assess these questions, I introduced perturbations into the model system and then studied the responses.

In all cases, the sea lion year was assumed to start on the 15th of June, as that is the mean Steller sea lion pupping date (Calkins *et al.* 1998, Pitcher and Calkins 1981). All simulations were run assuming the time minimizer strategy for the Steller sea lion behavior. The methods and results for each question are described next.

3.3.1 The effect of overall prey density reduction in immature Steller sea lions (age 1-3):

Methods:

The overall prey density was reduced from baseline levels systematically by 5% increments. The simulation was started for one-, two- and three-year-old sea lions and run for an entire year for the different levels of perturbation. At the beginning of the year the animal's length, weight and fat percentage were those of a healthy reference animal of that age (Table 3.1). The perturbation was held constant during the entire year. Four possible combinations relating to the hypothesis of compensatory growth and metabolic depression were tested for each age class and level of perturbation. Reductions in prey abundance were done sequentially, starting with the lowest reduction and increasing the magnitude of the perturbation until animals in one age class died under all scenarios. The effect of reduced prey density was measured in terms of normal growth, growth retardation (when the difference between chronological age and physiological age is greater than 5 days), weight loss and death (Table 3.2). The numbers in parentheses after

the "growth retardation" label indicate the number of physiological days lost as an indication of retardation (difference between chronological age and physiological age). The numbers in parentheses after the "death" label indicate the day when death occurred.

Results:

As expected, reductions in prey abundance have an effect on the performance (growth and survival) of the immature sea lions. However, the effect was different for different ages (Table 3.2). This age effect holds regardless of the hypothesis chosen (compensatory or no compensatory growth, metabolic depression or not). One-year-old sea lions are the most susceptible to reductions in abundance. In all scenarios, they are not able to survive reductions of 20% in prey abundance. Two- and three-year-olds are capable of surviving such reductions, with minor growth retardation for two-year-old sea lions and no effect for three-year-old animals. Animals of all age classes are capable of overcoming minor reductions of 5 and 10% in prey abundance by adjusting their foraging effort.

It is interesting to note the relative unimportance in the results of this particular simulation of the hypothesis chosen (compensatory or no compensatory growth, metabolic or no metabolic depression). Another interesting result is that severe growth retardation (that should be detectable in wild animals) is associated with considerable weight loss rather than with slow growth.

Table 3.2: Effect of different levels of reduction in the overall prey abundance in one-, two-, and three-year-old sea lions under different scenarios: with and without compensatory growth, and with and without metabolic depression (MD). The numbers in parentheses after the "growth retardation" label indicate the number of physiological days lost as an indication of retardation. The numbers in parentheses after the "death" label indicate the day when death occurred.

% Prey Abundance Reduction	Compensatory Growth		No Compensatory Growth	
	MD	No MD	MD	No MD
<u>One-year-old sea lions</u>				
5%	Normal growth	Normal growth	Normal growth	Normal growth
10%	Normal growth	Normal growth	Normal growth	Normal growth
15%	Normal growth	Normal growth	Growth retardation (19 days)	Growth retardation (19 days)
20%	Death (297)	Death (299)	Death (295)	Death (293)
<u>Two-year-old sea lions</u>				
5%	Normal growth	Normal growth	Normal growth	Normal growth
10%	Normal growth	Normal growth	Normal growth	Normal growth
15%	Normal growth	Normal growth	Normal growth	Normal growth
20%	Normal growth	Normal growth	Growth retardation (32 days)	Growth retardation (32 days)
25%	Death (273)	Death (271)	Death (271)	Death (271)
<u>Three-year-old sea lions</u>				
5%	Normal growth	Normal growth	Normal growth	Normal growth
10%	Normal growth	Normal growth	Normal growth	Normal growth
15%	Normal growth	Normal growth	Normal growth	Normal growth
20%	Normal growth	Normal growth	Normal growth	Normal growth
25%	Weight loss Growth retardation (214 days)	Weight loss Growth retardation (214 days)	Weight loss Growth retardation (213 days)	Weight loss Growth retardation (213 days)
30%	Death (231)	Death (230)	Death (231)	Death (230)

3.3.2 The importance of Pacific whiting:

Methods:

To assess the importance of the Pacific whiting, both as an influx of biomass and as the driver of seasonality in the system, a new set of similar experiments was done. This time the Pacific whiting absolute abundance was zero for the entire year. Again, simulations were run for every age class for a year. Only one scenario (the one with metabolic depression and no compensatory growth) was considered, as the previous results showed the unimportant effect of the hypothesis chosen. Starting animals were healthy at the beginning of the year as in Table 3.1. Perturbations were introduced as 5% reductions of overall prey density. Results were recorded as normal growth, growth retardation (and magnitude), weight loss and death (and day of death). The trials were compared to the previous ones in which there is no compensatory growth and there is metabolic depression.

Results:

The results from this set of trials are summarized in Tables 3.3 and 3.4. Table 3.3 is a summary of the experiments in 3.3.1 under similar circumstances (no compensatory growth and metabolic depression).

Table 3.3: Summary of the prey abundance results in experiment 3.3.1 assuming that there is no compensatory growth and there is metabolic depression.

Age Class	Prey abundance				
	95%	90%	85%	80%	75%
1 year old	Normal growth	Normal growth	Growth retardation (19 days)	Death (295)	Death (201)
2 years old	Normal growth	Normal growth	Normal growth	Growth retardation (32 days)	Death (271)
3 years old	Normal growth	Normal growth	Normal growth	Normal growth	Weight loss Growth retardation (213 days)

Table 3.4: Simulations of the effects of prey abundance reductions on Steller sea lions (ages 1-3 years) in the absence of Pacific whiting. It is assumed that there is no compensatory growth and there is metabolic depression.

Age Class	Prey abundance				
	95%	90%	85%	80%	75%
1 year old	Normal growth	Normal growth	Growth retardation (157 days)	Death (126)	Death (74)
2 years old	Normal growth	Normal growth	Normal growth	Growth retardation (223 days)	Death (114)
3 years old	Normal growth	Normal growth	Normal growth	Growth retardation (11 days)	Death (156)

The importance of Pacific whiting is reflected in Tables 3.3 and 3.4. In the absence of whiting (Table 3.4), animals of all ages die with a 25% reduction in the abundance of the other prey species. There are two ways to interpret that situation. It could be that sea lions die because there is no whiting. Whiting represents 40% of the biomass in the simulated system, and a further reduction of biomass could be excessive for sea lions. However, the model was tuned for the winter situation when whiting are absent. It seems more plausible that animals survived in the former experiments because of the seasonal return of the whiting.

Again, the age effects are patent. With or without whiting, one-year-old sea lions die with a 20% reduction of prey abundance, while other age classes can survive. Moderate reductions of 10% do not affect the survival or growth of any age animal.

The system in the absence of Pacific whiting is more unstable in the sense that high reductions in biomass have catastrophic consequences for the sea lions, with the animals dying in all three age classes.

3.3.3 Effect of declines in prey abundance on the attainment of sexual maturity.

Methods:

Laws (1956) noted that length at sexual maturity as a percentage of final size, was remarkably constant among female pinnipeds at 87%. That criterion was applied as the indicator of reaching sexual maturity. A healthy one-year-old sea lion (according to the reference Table 3.1) started the simulation under different levels of overall prey abundance relative to the baseline level. Perturbations in prey abundance were held constant in every simulation. As in the previous simulation, four scenarios (with and without metabolic depression, with and without compensatory growth) were considered. The presence and absence of Pacific whiting was also considered. Simulations were run until the animal reached sexual maturity and the day when that happened was recorded and transformed into the animal's age. If the animal died before reaching maturity, the day of death was recorded.

To explore the possible effects at the population level of delays in attaining sexual maturity, a population submodel was constructed using the STELLA simulation modeling system. Details about this submodel are given in Appendix 3. This model is the

representation in STELLA of the life tables derived for Steller sea lion in Winship *et al.* (2002), based on Trites and Larkin (1992) and York (1994). The finite rate of population increase obtained with those values was 1.0. The discrete maturity at age values given in Winship *et al.* (2002) were transformed into a continuous function with two parameters (age50 and β) and the model was retuned to produce a 0.0% increase in the population numbers. Once retuned, the age50 parameter was modified by adding 1, 2, 3 and 4 years (so that $\text{age50} = \text{initial age50} + \text{perturbation}$). An initial number of 100,000 males and 100,000 females both of age 1 was used. All simulations were run for a transition period long enough to allow for attaining a stable age structured population (40 years). Then the perturbations in the age50 parameter were introduced and the simulations were continued for another 40 years. The resulting rate of population change was recorded as the percentage change in the total number of animals.

Results:

The effects of the prey abundance reductions on the attainment of sexual maturity are shown in Tables 3.5 and 3.6:

Table 3.5: Age at which a one-year-old female Steller sea lion would achieve sexual maturity under different constant levels of reduction in prey abundance. Four possible scenarios were considered: with/without compensatory growth, and with/without metabolic depression (MD). The seasonal migration of Pacific whiting was maintained. The model considered a female to be mature when her length was $0.87 \cdot A$, where A is the parameter in the Gompertz length at age model for female Steller sea lions fitted in Winship *et al.* 2001).

Prey Abundance	Compensatory Growth		No Compensatory Growth	
	MD	No MD	MD	No MD
100%	9 th August (3 years)			
95%	10 th August (3 years)	10 th August (3 years)	9 th August (3 years)	9 th August (3 years)
90%	10 th August (3 years)			
85%	10 th August (3 years)	10 th August (3 years)	30 th August (3 years)	30 th August (3 years)
80%	Death (297)	Death (299)	Death (295)	Death (293)

Table 3.6: Similar experiments in the absence of Pacific whiting.

Prey Abundance	Compensatory Growth		No Compensatory Growth	
	MD	No MD	MD	No MD
100%	10 th August (3 years)	10 th August (3 years)	10 th August (3 years)	10 th August (3 years)
95%	10 th August (3 years)	10 th August (3 years)	10 th August (3 years)	10 th August (3 years)
90%	10 th August (3 years)	10 th August (3 years)	11 th August (3 years)	11 th August (3 years)
85%	16 th August (3 years)	16 th August (3 years)	11 th February (3 years)	11 th February (3 years)
80%	Death (126)	Death (124)	Death (126)	Death (126)

The results are quite interesting. The mating season in Oregon is over by the middle of July, at which time breeding males give up maintaining their territories and leave the rookery areas (Mate 1973). Under the best circumstances, females become sexually mature in the model on the 9th August, when there are no males available to mate with. This, of course, depends on the configuration of the model and the assumed growth models. If the model was stochastic instead of deterministic, some females might become sexually mature in time to be impregnated. A growth retardation like the one caused by a 15% reduction in prey abundance could cause a female to lose an entire year of reproductive potential. In animals with continuous mating year round, slight delays in maturation would not have much effect. However, in animals that mate just once a year, the effect could be greater.

In these simulations, the introduced perturbation was held constant. Mild perturbations did not delay growth considerably, while strong ones caused the death of the sea lion. In the real world, perturbations are irregular. It is probable that a seasonal perturbation accompanied by considerable weight loss would cause a longer delay in the attainment of sexual maturity.

The effect of a delay in sexual maturation at the population level has usually been ignored. Reductions in juvenile survival accompanied by slight decreases in female fertility have been posed as the most plausible causes for the decline at the demographic level in Alaskan populations of Steller sea lions (York 1994). However, the results of the population simulation in the study here show that the effect of delayed sexual maturation could be significant, as can be seen in Figure 3.2.

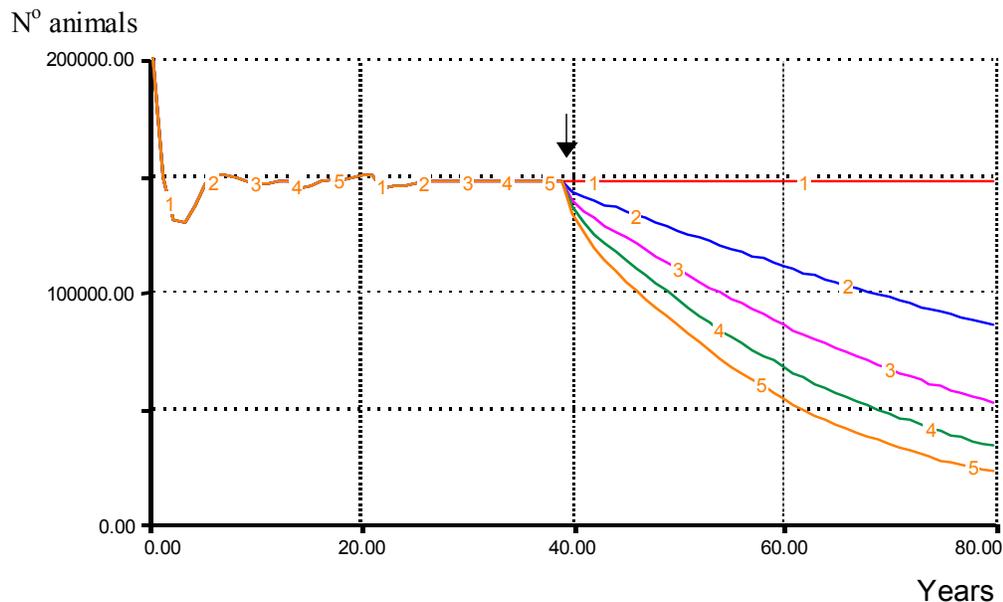


Figure 3.2: Comparison of trajectories of a simulated sea lion population given changes in the parameter for the age at 50% maturity (age50). Simulations were run for a sufficient period (40 years) to ensure that a stable age structured population was attained and then four different perturbations were introduced, indicated by the arrow. Curve 1 is a population with the baseline parameters (described in Appendix 3). In curve 2, the age at 50% maturity was delayed by 1 year; in curve 3 the delay was two years, and so on. The resulting rates of population increase were respectively 0.0%, -1.34%, -2.57%, -3.73% and -4.80%.

3.3.4 Effect of changes in prey quality.

Methods:

Not only prey availability (approximated in the model by prey abundance) but also prey quality can play a role in the feeding ecology of the Steller sea lion. To address the influence of prey quality, I ran a set of experiments in which I varied the energetic content of the sea lion prey. As in the other experiments, animals of different ages experienced the perturbation for a year. Only the scenario with no compensatory growth and metabolic depression was examined. Starting animals were healthy at the beginning of the year according to the reference Table 3.1. The overall energetic density of the sea lion diet (given by Eq.3.1) was reduced by increments of 5%. That was the only perturbation; the overall prey density was held at the baseline level. A second set of similar trials was conducted, this time varying only the energetic density of Pacific whiting to study the interaction of seasonality and reduction in prey quality. It was reduced by 25 and 50%. Results in all trials were recorded as normal growth, growth retardation (and magnitude), weight loss and death (and days to death).

Results:

The results were remarkable in that a reduction in prey quality had a considerable effect on young animals, even though the overall prey density was at the baseline levels. The age effect was very pronounced. With a minor reduction, the one-year-old sea lion died, whereas the same reduction was almost unnoticed by the two- and three-year-old sea lions. This effect can be seen in Figures 3.3, 3.4 and 3.5, and is quantified in Tables 3.7 and 3.8.

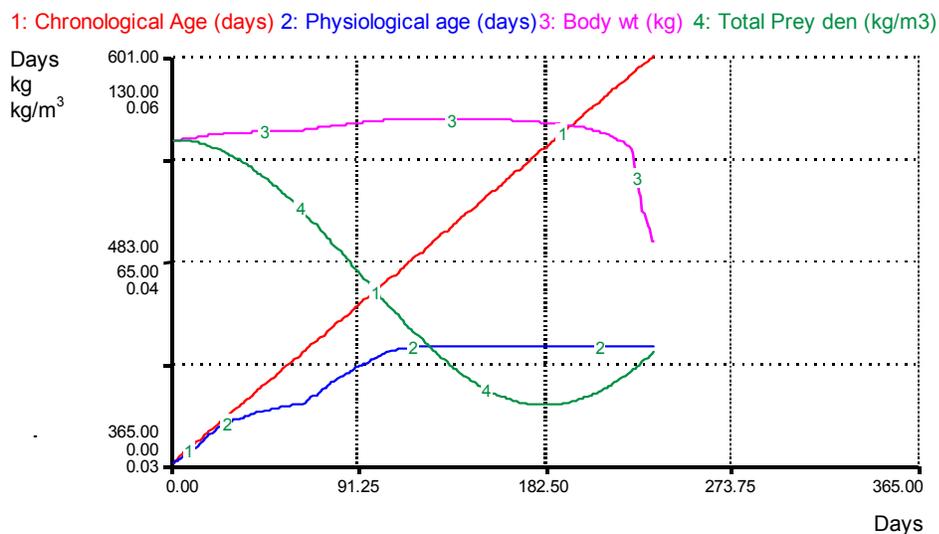


Figure 3.3: One-year-old sea lion facing a 10% reduction in overall prey quality. The comparison in the evolution of chronological age (line 1) and physiological age (line 2) indicates the effect of the perturbation on the developmental status of the animal. The simulation stops when the animal dies after considerable weight loss.

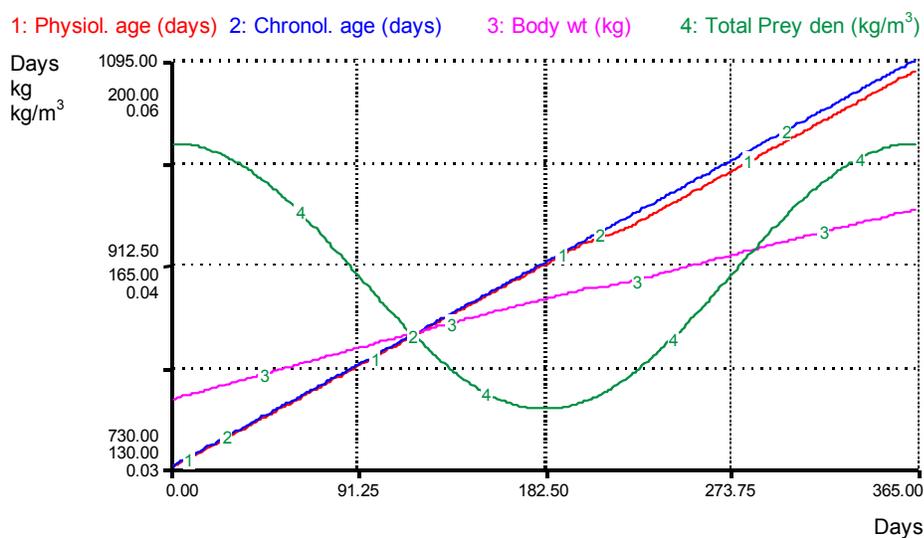


Figure 3.4: Two-year-old sea lion facing a 10% reduction in overall prey quality. A slight retardation of growth (as shown by the difference in chronological and physiological age) happens after the point of lowest prey density during winter. There is no weight loss.

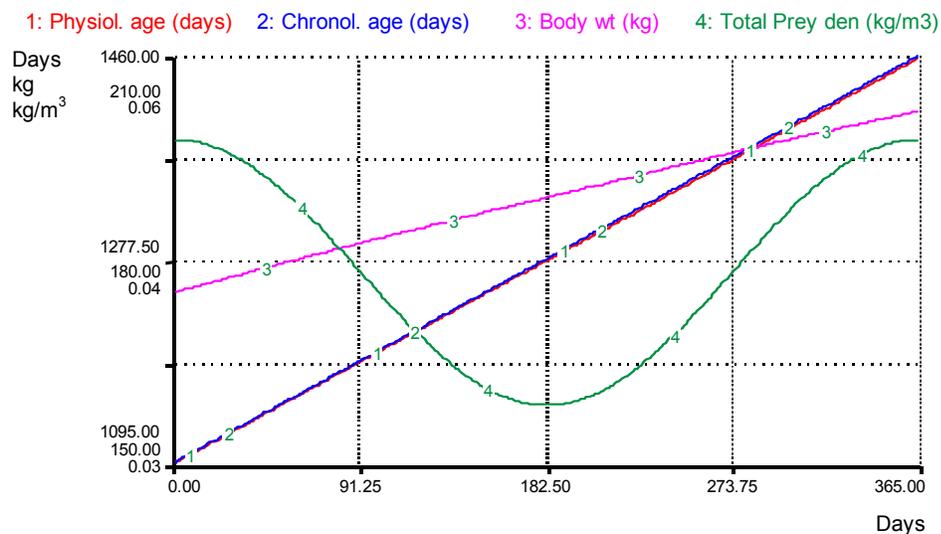


Figure 3.5: Three-year-old sea lion facing a 10% reduction in overall prey quality. The perturbation has no effect on growth of total body mass.

Table 3.7: Effect of reductions in the overall energetic density of the prey on immature female Steller sea lions (age 1-3).

Age Classes	Reduction in the overall energetic density of the diet		
	5%	10%	15%
1 year old	Normal Growth	Death (235)	Death (74)
2 year old	Normal Growth	Growth retardation (9 days)	Death (229)
3 year old	Normal Growth	Normal Growth	Death (327)

Table 3.8: Effect of reductions in the Pacific whiting energetic density on immature female Steller sea lions (age 1-3).

Age Classes	Reduction in Pacific whiting energetic density	
	25%	50%
1 year old	Normal Growth	Death (74)
2 year old	Normal Growth	Normal Growth
3 year old	Normal Growth	Normal Growth

3.4 Discussion

1) The effect of overall prey density reduction on immature Steller sea lions (age 1-3):

The age effect was evident in this set of trials: perturbations to prey density did not affect sea lions of different ages equally. This feature was also persistent among the other simulations. The model indicated the existence of a bottleneck in the survival of Steller sea lions, with the first year in the life of a sea lion being the most difficult. Of course, we do not need a model to believe this to be so. It is fairly intuitive. What is interesting is that perturbations that caused the one-year-old animals to struggle or die were relatively easily overcome by the older animals. Although the validity of these results depends crucially on the model assumptions, and a more thorough analysis should be conducted, this finding could lead to a reexamination of the symptoms expected in a nutritionally stressed population.

The nutritional stress hypothesis and its predictions are often mentioned without any quantitative specification to the magnitude of the perturbation that would cause a given symptom. There are many degrees in the range of possible perturbations that can cause nutritional stress to a population. Conversely, there should be a range of expected symptoms and effects associated with those different degrees. Predictions of the nutritional stress hypothesis usually refer to a moderate to high degree of stress. Those are generally based on analogies with short and intense episodes of nutritional shortages to pinniped populations, such as the ones caused by El Niño events (Trillmich and Ono 1991). However, the model in this study predicted that mild perturbations could show symptoms that are more difficult to notice, and still have a considerable effect on the population demography. York (1994) analyzed rates of decline and associated changes in the age structure of the Marmot Island population for 1975-1985 and showed that the simplest explanation for both phenomena was a 20% decline in the annual survival of juvenile females. If animals were nutritionally stressed to a point that could be easily measured in adults or nursing pups (dependent on their mothers), it is probable that there would be no Steller sea lions left alive now. The effect and symptoms of a mild but persistent shortcoming are not comparable to an intense but short perturbation. The model predicts that a mild nutritional perturbation could have a considerable effect on one-year-old animals, while having an almost unnoticeable effect on older sea lions.

It would be very interesting to expand the range of age classes considered. However, at this stage, the difficulties in modeling the energetics of lactation preclude such an analysis. Some of those difficulties deal with the variability in Steller sea lion postnatal growth rates and the variability in the lactation length. Studies of Steller sea lion pup growth (Higgins *et al.* 1988, Davis *et al.* 1996) are restricted to the very first weeks after birth (4 to 6) and yield variable growth rates. On the other hand, although female-offspring bonds appeared to last less than one year in most instances, some individuals suckle for up to two years (Gentry 1970, Sandegren 1970, Calkins and Pitcher 1982). It is possible that there is an inverse relationship between pup growth rates and lactation length, as has been reported for California sea lions (Francis and Heath 1991), Galapagos fur seals (Trillmich 1986) or Peruvian fur seals (Majluf 1987). Lee *et al.* (1991) found that the process of weaning was related to a critical or threshold body weight attained by off-spring among large bodied mammals, the anthropoid primates, ungulates and pinnipeds. It could be that if the process of weaning is not tied to an environmental cue (*e.g.*, an abrupt change in water temperature or the break of the ice shelf as for other pinnipeds), lactating Steller sea lion mothers will nurse their pups until the pups reach a threshold body size that facilitates their future survival. The length of the lactation period would then be determined by the mother's ability to provide energy to sustain her pup's growth.

If there are no predetermined pup growth rates or a fixed lactation length, the modeling of the lactating mother's foraging trip duration is extremely complicated. When does the lactating mother decide that she has eaten enough and has to return to land? Steller sea lions, as other otariids, forage while lactating (Costa and Williams 1999) and can leave their pups onshore for several days. Trip duration determines how much energy the mother can acquire to deliver to her pup, but also how often she can feed her pup. It is generally believed that the ability of the pup to survive is what determines the mother's foraging trip duration. However, if the mother spent too much time foraging at sea, her pup could lose too much weight and the extra gain obtained by the longer foraging trip would be offset by the cost of recovering weight by her pup. At the end, her pup would show slower net growth rates because continuous growth is not equivalent to a cycle of gains and losses due to the inefficiencies in the building of body mass. From an energetic

point of view, it is more efficient to deliver smaller amounts of energy at shorter intervals than larger amounts less frequently. However, as the pup grows and is more energetically demanding, the mother needs to undergo longer foraging trips to meet her own and her pup energetic requirements, so that foraging trip duration is not fixed during the lactation period.

A minimum foraging trip duration, dependent on prey availability, allows the mother to meet her own energetic requirements. This probably changes over the lactation season if there is local prey depletion. In addition, there is a maximum foraging trip duration determined by the ability of the pup to survive. The optimal foraging trip duration would fall somewhere in the middle (although it could be that the minimum trip duration that allows the mother to meet her requirements is longer than the maximum trip duration that allows the survival of the pup, in which case the pup would die). However, at this stage I could not find an adequate basis for determining the optimal foraging trip duration for a lactating mother. The modeling of this trip duration is crucial, as the growth rate and survival of the pup depend on it. And not only of the current pup, but also of future ones, because if the lactation has been extended for more than a year, that could interfere with the nursing of the new pup.

2) The importance of Pacific whiting:

The seasonal migration of Pacific whiting was shown to be very important in the model. The system was more stable with whiting than without whiting. The migration of Pacific whiting into Oregon waters during the spring is probably one of the most important features of the ecology in the area (Livingston and Bailey 1985). It is certainly important for Steller sea lions. Whiting start arriving off Oregon by the third week in April. Ermakov, cited in Stauffer (1985), reported that schools begin to move shoreward over the shelf to depths of 90 m or less in June. Few remain over the slope during July and early August. The peak of the pupping season in Oregon takes place during the first week in June (Mate 1973). That is a perfect timing. Lactating mothers would not have to make great efforts to find food to support nursing. There is another aspect of Pacific whiting that makes it an asset as a food item. They also undertake strong diurnal migrations, apparently in response to the vertical migrations of euphausiids. At sunset schools disperse and rise toward the surface, and at night they are scattered from near the

surface to 20 m depth (Stauffer 1985). At Oregon rookeries Steller sea lions are nocturnal foragers, leaving around sunset and returning in the morning (Mate 1973). In that sense, Pacific whiting is the sea lion's manna. It comes when it is most needed, and it is relatively easy to catch, as the sea lions don't need deep dives. This is consistent with its high incidence in the Steller sea lion's scats and was also indicated by the model results.

3) Effect of declines in prey abundance on the attainment of sexual maturity.

If reaching sexual maturity were linked to attaining a certain size, retardation in growth would be accompanied by a retardation of sexual maturation.

The criteria applied in the model for the attainment of sexual maturity (when the animal reaches 87% of the final length) was quite arbitrary. It was based on interspecific comparisons conducted by Laws (1956) in pinnipeds. The use of interspecific comparisons to predict intraspecific behavior, starting with the use of Kleiber's (1975) mouse-to-elephant equation to predict basal metabolism at an individual level, is a recurring temptation in the study of animal biology. However, when no other measurements exist for the species of interest, it can provide insights, although not accurate predictions, into the observed behavior. On the other hand, the model's use of such a criterion implies causality: reaching a given size induces sexual maturity. However, the causality could be in the opposite direction: the onset of sexual maturity could be what slows the growth rates. Therefore, the results from this experiment should be interpreted with caution.

The model predicted a slight retardation in the age of sexual maturity when prey density was substantially reduced. This retardation could be on the order of some days to several months. Although these particular simulations predicted only moderate delays in the attainment of sexual maturity, longer delays could be plausible with stronger seasonal perturbations. Lavigne *et al.* (1985) noted that the mean age of maturity of Northwest Atlantic harp seals has apparently declined from more than 6 years in the early 1950s to less than 4 years in the late 1970s. Calkins *et al.* (1998) reported a reduced body size of females in the Gulf of Alaska during the 1980s compared to the 1970s. If body size is related to sexual maturity, it is possible that females in Alaska could have suffered a delay in the attainment of sexual maturity.

The effect of a delay in sexual maturity was significant at a population level. This offers an alternative (or complementary) explanation to the population decline being caused by increased mortality. It is tempting to suggest that such an effect could have contributed to the decline of the Steller sea lion population in Alaska.

4) Effect of changes in prey quality.

The effect of a reduction in prey energetic density was remarkable. The prey abundance remained constant in the experiments and only the quality was reduced. Nevertheless, the effects on the sea lions were drastic, especially for the young ones. Age effects were again noticeable.

The effect of a reduction in prey quality is, of course, linked to the assumptions in the model. Probably the most important assumptions deal with the maximum food processing capacity for the sea lion. The value was chosen quite arbitrarily, although based on circumstantial evidence (outlined in Appendix 2). Sea lions have fast digestive passage rates (Helm 1984) that can contribute to rapid food processing. However, even though the assumed value could be incorrect, conceptually there must be a maximum processing capacity. A reduction in prey quality (maybe not of the same magnitude as in the simulations) will force the animal to increase its foraging effort if energy intake is to remain constant. An increase in foraging effort will raise the energetic demand, leading to a further increase in foraging effort. The animal could compensate for a reduction in prey quality, so long as it was under its maximum processing capacity (and under Pf_{max} and V_{Mmax}). But, depending on the magnitude of the reduction in prey quality and or interactions with reductions in prey abundance, the animal would eventually hit that limit. Once constrained by the food processing limit, there is nothing the animal can do to increase its energy intake further. Younger animals have higher mass specific energy requirements and are more susceptible to reach ceilings to their foraging effort.

Another interesting result of these trials is that the increase in foraging effort (as measured by the proportion of time foraging Pf) resulting from a reduction in prey abundance was higher than for a 'comparable' reduction in prey quality. For the simulated 3-year-old sea lion, a reduction in prey abundance of 20% from baseline levels was overcome by an increase in Pf and caused an insignificant growth retardation of 3 days. A reduction in the energetic prey density of 10% caused a similar insignificant delay of 2

days. However, the increase in the proportion of time foraging was less noticeable as can be seen in Figure 3.6.

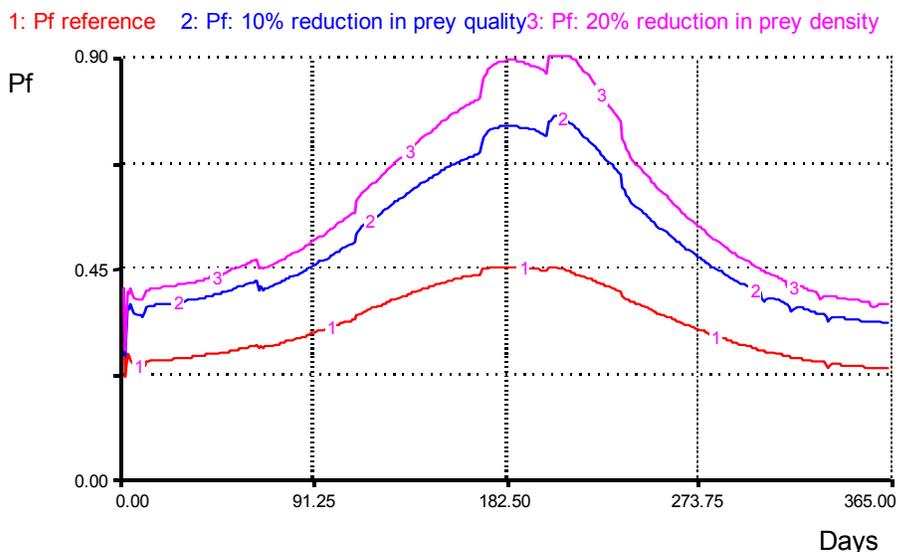


Figure 3.6: Proportion of time foraging (Pf) for a 3-year-old sea lion under different scenarios. Curve 1 represents the baseline conditions, where Pf increases in winter in response to the seasonal migration of Pacific whiting off Oregon. Curve 2 represents the foraging effort of the sea lion when facing a reduction of 10% in the overall prey quality. Curve 3 represents the foraging effort of the sea lion when facing a reduction of 20% in the overall prey density. Both perturbations had a similar insignificant effect on the growth performance of the sea lion.

It is interesting to note that, although it is difficult to compare perturbations in prey quality and prey abundance, a 10% reduction in prey quality versus a 20% reduction in prey abundance caused earlier death of the one-year-old sea lion (at day 235 versus day 297). Yet, the reduction in prey quality could be overcome more easily for the three-year-old sea lion.

This might mean that a reduction in prey quality, although it could have considerable effects on one-year-old sea lions, would be even harder to detect in older animals than a reduction in prey abundance. This reduces our capability to assess mild and chronic nutritional stress in wild animals caused by a reduction in prey quality. Even more, if there were strong seasonality as in the Oregon coast, the effects would be more difficult to assess depending on the season.

Interactions of prey quality with prey abundance are also possible. Low prey quality in addition to a decline in the abundance of the high-energy prey could be very detrimental for the youngest sea lions. Both effects seem to have happened in the Bering Sea ecosystem. The abundance of pollock, a fish with low caloric content, has increased with respect to historical levels, simultaneous with a reduction in the abundance of fatter fishes (Trites 1998, Alverson 1992). According to the model, a reduction in the energetic density of the prey alone could cause the death of one-year-old sea lions, while leaving the two- and three-year-old sea lions quite unaffected. The effect on lactating mothers could be also important, especially for the youngest ones.

5) General discussion and future directions.

The dynamic bioenergetic model developed in this study has proven very useful for examining ecological questions regarding the growth and performance of immature female Steller sea lions living along the Oregon coast. Such a model is the first integrated attempt to describe the energetics of free ranging Steller sea lions under varying scenarios. The simulations run in this report are only examples of some possible experiments. Nevertheless, there are ample other possibilities. This study shows the potential of using mechanistic models to improve our understanding of the energetic options of wild animals facing environmental perturbations.

One interesting result from the study here is that mutually exclusive hypotheses about certain unknown aspects of the biology of Steller sea lions yielded the same general results. This finding encourages the development of open theoretical models that incorporate different hypothesis. Even more, a model of this type allows one to explore circumstances that might not be experimentally feasible. This would be crucial in urgent cases such as the decline of the western stock of Steller sea lions, in which the fast rate of the population decline does not allow for waiting until all experimental results are provided to develop a complete model and explore its implications.

The model could aid in the interpretation of different nutritional stress symptoms. As was shown in the results, the age effect is very conspicuous. The youngest sea lions are the most susceptible to suffer nutritional stress while older animals could remain relatively unaffected. In the model, environmental perturbations were held constant for a year. However, in the natural world perturbations would vary in intensity and duration

through the years. This could create pulses in the increased mortality by age classes, with mild perturbations affecting only the youngest sea lions, while further perturbations would spread the effect to other age classes and could also delay the attainment of sexual maturity. This would certainly influence the trajectory of the population.

The model did not incorporate competition or predation effects, but certainly, an increase in the proportion of time foraging forced by environmental perturbations could be accompanied by an increased mortality by predation. McNamara and Houston (1987) found from a modeling exercise that incorporated predation that the number of animals dead from starvation might not provide a reliable indication of the importance of food. This, along with the findings of this study, suggests that it is necessary to reassess the expected symptoms of a nutritionally stressed population under different degrees of stress. That would be necessary for evaluating appropriate methods for the detection of nutritional stress in wild populations.

The model also shows the great potential of mechanistic models for unraveling the metabolic requirements of different behaviors. Field and laboratory metabolic measurements provide values that are a composite of different activities: thermoregulation, swimming, diving or resting at sea. A model like the one in this study provides insights into the relative contributions of the different activities and behaviors to the overall metabolic rate.

Certainly, such a model needs experimental validation of its individual submodels. There is much room for improvement as new findings are produced. Individual contributions could certainly enrich the model. The model structure is prone to the assimilation of alternative views or different resolutions, as well as expansion to other age classes and linkage to population dynamics.

An improved and validated model could be used to explore the implications of different management strategies regarding the fisheries that target the same prey species as the Steller sea lions. The metapopulation structure of the Steller sea lion population (Raum-Suryan *et al.* 2002) is prone to adaptative management strategies, given that the current regulations have had not an effect on the recovery of the population. In that case, it would be necessary to define a time frame for the detection of any improvement in the

situation and a scale of plausible and expected effects to evaluate the success of the different management measures.

3.5 Conclusions

A dynamic energetic model was developed to assess the effects of changes in prey availability and or quality on the performance (growth and survival) of immature Steller sea lions (ages 1-3) living along the Oregon coast. The goal was to identify possible traits of the Oregon ecosystem that allow for the growth of the population of Steller seal lions in spite of the decline in numerous of their prey species. This model could be used to evaluate possible causes of the decline of the western stock of Steller sea lions in Alaska.

A general trait of the simulations was that animals of different ages are affected very differently by environmental perturbations. The most extreme example was caused by changes in the quality of prey that could resulted in the death of the simulated one-year-old animals while having practically no effect on the older animals. The results have to be taken with great caution, as they depend on the validity of the underlying assumptions.

The seasonal influx of fish biomass to Oregon coastal waters, mediated by the migration of Pacific whiting, was a key factor in the performance of the model Steller sea lion. Increasing whiting abundance in the spring allows the animals to recover from weight loss caused by diminished prey densities and lower temperatures in winter. Probably the migrations of other prey items, such as lamprey, could also play an important role in the feeding ecology of the Steller sea lion in Oregon, as suggested by other authors (Roffe and Mate 1984).

The model suggests that moderate nutritional stress, caused by a reduction in either prey availability or prey quality, would not be expressed similarly in animals of different ages and sizes. The most affected animals would be the one-year-olds, and, depending on the magnitude and timing of the perturbation, animals could die relatively fast without showing prolonged signs of malnutrition. This, along with fat sparing and the retention of high levels of fat in the blubber for thermoregulation, would make it difficult to diagnose nutritional stress in the wild.

The results of the model suggest a mechanism linking the nutritional stress hypothesis with the demographic hypothesis as an explanation for the decline of the Steller sea lions in the western stock; at the same time the model might explain why some of the evidence has been so contradictory to date. In addition, nutritional deficiencies could retard growth, and consequently, the attainment of sexual maturity. The effect of this at the population level could be significant.

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APPENDIX 1

Activity in water

- Parameters:

The cost of locomotion was calculated according to eq. 2.5 as:

$$[2.5] \quad M_L = \lambda * \frac{\rho * S * C_d * V^3}{2 * \varepsilon_A * \varepsilon_p}$$

The definition of those parameters and the justification of the values chosen are explained below:

λ : is the ratio of the drag of an active swimmer to that of a passive one moving at the same speed. This is because C_D cannot be measured directly from swimming animals, but is calculated from experiments with towed or gliding animals. However, when the animal is actively swimming, total drag changes and this is accounted by λ . Williams and Kooyman (1985) found that alteration in the body configuration of swimming harbor seals (*Phoca vitulina*), as occurs during stroking movements, resulted in an increase in body drag. In their calculations, body drag during gliding phases could double during active swimming.

Sea lions and fur seals of the family Otariidae use their foreflippers for swimming (Robinson 1975). When the sea lion is actively stroking, total drag will be slightly greater than passive drag due to resistive forces acting on the foreflippers (Feldkamp 1987). However, since these forces arise only when the flippers are extended, they are likely to be small in comparison to total body drag (Webb 1975, Yates 1983). California sea lions do not stroke continuously but modulate swimming speed by gliding between flipper beats (Feldkamp 1985). Steller sea lions swim with an essentially rigid body and move only their foreflippers to generate lift and thrust (Stelle *et al.* 2000). Therefore, passive drag estimates should provide a reasonable estimate of the drag for rigid body-swimmers (Webb 1975, Blake 1983), such as actively swimming sea lions. I then assume a value of 1 for λ .

ρ is the density of the water (in kg/m^3) at a given temperature ($^{\circ}\text{C}$) and S is wetted surface area (m^2). The values chosen to represent those parameters are explained next under thermoregulation.

C_D : is the drag coefficient. It depends significantly on velocity if the boundary layer flow is laminar, but if it is turbulent, this dependence is much weaker (Hoerner 1958). Drag coefficients vary with Reynolds numbers, gradually decreasing with increasing Reynolds numbers, dropping dramatically in the transition region 5×10^5 - 5×10^6 , and then stabilizing in the region of turbulent flow (Blake 1983).

According to the experiments in Stelle *et al.* (2000), it is likely that at the mean swimming speed of Steller sea lions observed in captivity, the boundary layer is turbulent (Reynolds number 5.5×10^6).

The range of swimming velocities of Steller sea lions in the wild is not well documented. If velocities in the wild were lower than those reported in Stelle *et al.* (2000) and the flow were laminar, the drag coefficient C_D could be considerably higher. This would impose an energetic penalty for swimming at low velocities, as the overall cost of locomotion would be increased.

In any case, there are no data to quantify the effect of velocity on C_D , so there was no good alternative than to consider C_D constant and independent of velocity. This would certainly bias the estimation of velocity.

C_D is also a function of the object size and shape (Hind and Gurney 1997), so it will presumably be different for Steller sea lions of different ages. But again, there are not enough data to account for this variation, so the model assumes that C_D is shape independent.

The model takes C_D for all sea lions as the average value of 0.0056 at a mean Reynolds number of 5.5×10^6 in Stelle *et al.* (2000).

V is the speed at which the animal is swimming (m/s) and its calculation was explained in Section 2.4.5.

ϵ_p : is the propeller efficiency, which is the efficiency with which muscular movements are translated into forward thrust. Fish *et al.* (1988) calculated a propeller efficiency of 85% for ringed seals and thrust calculations for the swimming seals showed no

systematic variation of ϵ_P with velocity. But Feldkamp (1987) calculated the propeller efficiency for California sea lions and it rose with speed reaching a plateau of 80% at the highest velocities. This value is consistent with the approximate value of 80% for cetaceans and pinnipeds given in Fish (1994). The model takes a propeller efficiency of 80% and assumes it is independent of velocity.

ϵ_A : is the aerobic efficiency, which is the efficiency with which chemical energy is transformed into muscular work. Very few studies have attempted to estimate the aerobic efficiency and its relationship with workload. Feldkamp (1987) found for two California sea lions swimming in flume tanks that it rose with velocity reaching a maximum value of 15% and 12%. With so little information, any estimate is little more than a guess. The model uses for the aerobic efficiency coefficient a constant value of 0.15, independent of velocity.

The assumed independence of the parameters C_D , ϵ_P and ϵ_A from velocity will certainly bias the model's estimates of velocity, as the penalties for swimming at very low or very high velocities are lost.

This model formulation for the energetic cost of swimming has other weak points. Drag parameters have been obtained from captive animals. But the energetic cost of overcoming drag will vary with changing conditions for animals swimming in the wild (Stelle *et al.* 2000).

The resultant cost of locomotion (M_L) calculated with eq. 2.5 is given in watts. This cost is transformed to kJ/day (the energetic unit of the model) using a converter (**tr**).

Thermoregulation:

- Calculation of h_{conv} :

h_{conv} is the convective heat transfer coefficient. It is different for heat loss in air or in water and by forced or free convection. It is a function of a dimensionless number, the Nusselt number, the thermal conductivity of the medium (k_m) and the length of the animal (L) such that:

$$[A.1] \quad h_{\text{conv}} = \text{Nu} * k_m / L$$

and $\text{Nu} = f(\text{Re}, \text{Pr})$ for forced convection

$\text{Nu} = f(\text{Gr}, \text{Pr}) = f(\text{Ra}, \text{Pr})$ for free convection

where Re is the Reynolds number, Gr is the Grashof number, Pr the Prandlt number and Ra the Rayleigh number.

For forced convection (either on water or air), the calculation of the heat transfer coefficient ($h_{\text{conv forc w}}$ and $h_{\text{conv forc air}}$) is straightforward. It only depends on the velocity of the animal or of the wind (through the Reynolds number) and the characteristics of the medium (the Prandlt number), which are known in advance in the model. The Reynolds number can be easily calculated as:

$$[A.2] \quad \text{Re} = V * L / v$$

where V = swimming or wind velocity (m/s)

L = length of the animal (m)

v = kinematic viscosity of the medium (m²/s)

The Nusselt number, Nu, is equal to (Research Education Association 1987):

$$[A.3] \quad \text{Nu} = 0.0296 * (\text{Re}^{0.8}) * \text{Pr}^{(1/3)}$$

To calculate heat loss by free convection, the following set of equalities are taken from Chapman (1987):

$$[A.4] \quad h_{\text{conv free}} = \text{NuD} * k_m / D$$

$$[A.5] \quad \text{NuD} = (0.60 + 0.387 * (\text{RaD}^{(1/6)}) * ((1 + (0.559 / \text{Pr})^{(9/16)})^{(-8/27)}))^{(1/4)}$$

$$[A.6] \quad \text{RaD} = \text{GrD} * \text{Pr}$$

$$[A.7] \quad \text{GrD} = D^3 * g * \beta * (T_s - T_a) / v^2$$

where NuD = Nusselt number for the diameter

k_m = thermal conductivity of the medium (W/m°C)

D = diameter of the sea lion (m)

RaD = Rayleigh number of the diameter

Pr = Prandlt number

GrD = Grashof number of the diameter

β = medium coefficient of thermal expansion (K^{-1})

ν = kinematic viscosity of the medium (m^2/s)

T_s = temperature at the skin ($^{\circ}C$)

T_a = temperature at the medium ($^{\circ}C$)

Calculations become complicated by the fact that the heat transfer coefficient ($h_{conv\ free}$) is itself a function of the temperature difference between the skin and the medium ($T_s - T_a$). Therefore, $h_{conv\ free}$ cannot be calculated without knowing T_s . However, T_s is itself dependent on the heat loss, which depends on $h_{conv\ free}$. The system of equations does not have an analytical solution. Another approach must be used to find a numerical solution. This is done by means of an iterative process as described in Chapman (1987) such that a tentative value for T_s is used. Then, $h_{conv\ free}$ can be calculated and therefore the overall heat transfer coefficient (U). Heat loss (H) can then be calculated using eq. 2.11 as:

$$[2.11] \quad H = U * S * (T_{cb} - T_a)$$

where S is the corrected surface of the animal (explained below).

The tentative value for free convection in water is $T_w + 1^{\circ}C$, as under most circumstances the temperature of the skin approximately equals the water temperature (Hokkanen 1990), although that is not always the case (Boyd 2000). For free convection in air, a tentative value equal to the temperature of the core (T_{bc}) is used.

With the tentative value for T_s and the calculated free convection coefficient $h_{conv\ free}$, the heat dissipated at the skin by free convection (H_3) can be calculated as:

$$[2.9] \quad H_3 = f * h_{conv\ free} * 2 * \pi * R_b * L * (T_s - T_a)$$

or

$$[A.8] \quad H_3 = f * h_{conv\ free} * S * (T_s - T_a)$$

Equating eqs. 2.11 and A.8 gives:

$$[A.9] \quad f * h_{conv\ free} * (T_s - T_a) = U * (T_{cb} - T_a)$$

From that expression, T_s can be recalculated as:

$$[A.10] \quad T_s = (U*(T_{cb} - T_a) / (f*h_{conv\ free})) + T_a$$

With that new value for T_s , a new value of $h_{conv\ free}$ can be recalculated, and the calculations of U and H are repeated, getting new recalculations of T_s and $h_{conv\ free}$.

Preliminary simulations were run for different starting values of T_s in air and in water to ensure that the same final T_s was reached independently of the initial tentative value given. In all cases, after a few iterations (around five), T_s stabilized around the same final value independently of the tentative value used.

The heat losses calculated with those equations are given in watts. A converter to kJ/day is used (tr).

- Parameters:

The values of the parameters and the characteristics of the medium at a given temperature are tabulated from Radnjevic (1976) and Chapman (1987). They correspond to pure water at atmospheric pressure and dry air at atmospheric pressure for different temperatures. The parameters are the Prandlt number for air and water (**Pr_{air}**, **Pr_w**), the thermal conductivity of air and water (**k_w** and **k_{air}**), the kinematic viscosity of air and water (**v_w** and **v_{air}**) and the coefficient of thermal expansion for water (**β_w**). The coefficient of thermal expansion for air (**β_{air}**) is calculated by the ideal gas approximation as:

$$[A.11] \quad \beta_{air} = 1/T_f$$

where T_f is the ambient fluid temperature in K, calculated as $(T_s + T_a)/2$ as in Chapman (1987). The variations due to the salinity of the seawater and to the humidity of air are not considered.

The animal's shape is approximated to a cylinder for the heat loss calculations. **L** is the length of the animal. It is an output of the model, calculated as explained in Section 2.3.2.6. The diameter is calculated by geometry from the body composition of the animal and the densities of the different tissues. The core radius (**rc**) and the total radius (**Rb**) are:

$$[A.12] \quad rc = \sqrt{\text{Lean wt} / (DL * \pi * L)}$$

$$[A.13] \quad Rb = \sqrt{\text{Fat wt} / (DF * \pi * L) + rc^2}$$

where **Lean wt** is the mass of lean tissue, **Fat wt** is the blubber mass, which are outputs of the model. **DL** is the density of the lean tissue (1100 kg/m³ as in Keys and Brozek 1953) and **DF** is the density of blubber, 930 kg/m³ (Øristland *et al.* 1985), similar to the value for Steller sea lions in Olesiuk and Bigg (1987).

f is a factor introduced to account for the surface of the foreflippers. Foreflippers represent a considerable percentage of total body surface area as sea lions use them for swimming. In the model, it is assumed that foreflippers do not produce any heat, but contribute to dissipation of heat to the environment. The surface of the flippers is included in the calculations of heat flows H₂ and H₃ (eqs.2.8 and 2.9).

The multiplier *f* is assumed to be equal to 1.165, as 16.5% was the average percentage of the total wetted surface area accounted by the foreflippers as measured in six Steller sea lions in Stelle *et al.* (2000). This percentage is almost identical to the mean value of 16.2% for California sea lion foreflippers (Feldkamp 1987).

S is the surface of the animal. It is equal to 2* π *L*Rb*c where **c** is a surface area correction factor. This correction is needed because when the surface of the animal is estimated assuming a cylindrical shape, some error is introduced. To estimate that error, I calculated surface areas according to the cylindrical model and compared them to Stelle *et al.* (2000) measurements of surface area from six juvenile Steller sea lions. The multiplier **c** chosen to minimize the difference between the observed and predicted values was 1.21.

k₁ is the minimum effective conductivity of the blubber in W/m°C.

The thermal conductivity of live blubber can be modified according to the animal's needs by modifying the peripheral blood flow. As the model is intended to capture the cost of thermoregulation when the heat budget is negative, the conductivity of the blubber in this circumstance is assumed the minimum effective conductivity, or in other words, the minimum possible conductivity. It is assumed that, when an animal is at, or below its lower critical temperature, peripheral blood flow is reduced to a level where

the thermal conductivity of the blubber approaches the value determined in dead blubber. Studies by Kanwhisker and Sundnes (1965) and Kvasdheim *et al.* (1997) validate this assumption.

The conductivity of blubber varies between and within species, possibly as a function of the fat content of the blubber (Worthy and Edwards 1990). It also varies depending on the position in the body (Kvasdheim and Folkow 1997). I am not aware of measurements for Steller sea lions. The values found in the literature are mainly related to phocids. Ryg *et al.* (1988) found a thermal conductivity of $0.2 \text{ W/m}^{\circ}\text{C}$ for ringed seals (*Phoca hispida*). Scholander *et al.* (1950) and Worthy (1985) describe similar values of $0.185 \text{ W/m}^{\circ}\text{C}$ for harbor seals. Kvasdheim and Folkow (1997) recorded a value of 0.17 W/mK^1 for two harp seals and Kvasdheim *et al.* (1997) report a similar average value for two harp seals of 0.195 W/mK .

Sea lions are temperate water animals and generally have a thinner blubber layer than arctic phocids of similar size (Bryden and Molyneux 1978). Therefore, it may be expected that blubber conductivity would be at the lower end of that for seals, maybe lower. A value of $0.17 \text{ W/m}^{\circ}\text{C}$ for blubber conductivity in Steller sea lions was taken, although that value is quite arbitrary.

k_2 is the thermal conductivity of the fur. It is taken to be that of hair, $0.37 \text{ W/m}^{\circ}\text{C}$, used in Hind and Gurney (1997) from Lage and Bejan (1991).

ΔR is the hair mat depth (ΔR) and it is taken to be 1 mm as described for wetted hair in Luecke *et al.* (1975) for California sea lions. This is the same value taken in Hind and Gurney (1997).

T_w and T_a are the water and air temperatures and are inputs to the model depending on the time of the year (taken from the National Oceanographic Data Center coastal water temperature database for seawater, <http://www.nodc.noaa.gov/dsdt/cwtg/npac.html>; and from the Western Regional Climate Center database for air, <http://www.wrcc.dri.edu/htmlfiles/or/or.avg.html>; both at Port Orford).

T_{cb} is the core temperature. Small cetaceans and pinnipeds have low thermal inertia and are more likely to have a T_{cb} that approaches core temperature (Watts *et al.* 1993).

¹ The use of $^{\circ}\text{C}$ or K is equivalent when applied to temperature gradients, as $\text{K} = 273 + ^{\circ}\text{C}$.

Nevertheless, it can be a few degrees below the core temperature. In immersed harbor seals, this temperature appears to be a few degrees below that of the core at the lower critical temperature (Irving and Hart 1957, Hokkanen 1990, Worthy 1991, Kvadsheim *et al.* 1997). T_{cb} is set to 35°C as in Watts *et al.* (1993) for pinnipeds.

Steller sea lion body composition

The model considers protein and lipid mass separately. The water content is calculated from the protein mass assuming a constant ratio of 0.65:0.267 (water:protein mass) as in Davis *et al.* (1996). Water and protein constitute lean tissues. The ratio of lipid to protein or to lean mass is not fixed and it varies depending on the nutritional status of the animal. The model assumes certain levels of lipids in the body as distinguished in Whittemore (1998) and described in Section 2.3.2.1. The following initial values are used in the model:

- For essential fat, a value of 5% of total body weight is assumed as in Whittemore (1998). It is assumed that this value reflects the minimum needed for metabolic functioning, in common with other mammals. However, the minimum percentage varies in the model according to thermoregulatory needs. Losing too much fat when all food sources are in the water would be a pernicious strategy for a sea lion. Utilization of blubber beyond a minimum thickness would cause unacceptable heat loss (Øritsland *et al.* 1985, Ryg *et al.* 1988). The idea of a minimum fat insulation thickness has also been used in Øritsland and Markussen (1990). They note that animals might die with considerable fat deposits remaining in the body.
- The minimum preferred level of target fat is set to 15% of body mass.

Traditionally, Steller sea lions have been regarded as large pinnipeds with a relatively thin blubber layer (Pitcher *et al.* 2000). Steller sea lion body composition has been studied in different locations and for animals of different ages. Davis *et al.* (1996) found an average percentage of body lipids of 2.4 % of total body mass in pups (0-5 days of age) at locations in Alaska. In the same study, post parturient female total body lipid was on average 8.3% of total body mass. Total body lipid was measured with labeled water. Olesiuk and Bigg (1987) found that for a sample of male Steller sea lions taken in British Columbia an average blubber percentage of 5.9% (fall) and 16.4% (spring). Based

on that study, Pitcher *et al.* (2000) assumed a similar relationship between percentage of blubber and percentage of sculp and concluded that the average percentage of blubber in the Steller sea lions in their study was 10-14% of body mass. Winship *et al.* (2002), based on the mentioned studies, assumed an adult lipid proportion in the body of 0.07-0.14.

However, post parturient females and males in fall have fasted for a considerable amount of time and, in the case of the females, they are nursing an energetically demanding pup. The percentages of body fat reported in those studies might be closer to minimum percentages of fat in the body than to targeted ones. This idea is supported when one considers that for humans an "ideal" fat content in the body is in the region of 14-20% for males and 21-27% for females (Blaxter 1989). A human dies in near freezing water in a matter of minutes. Steller sea lions in Alaska certainly swim in near-freezing water for up to 76% of their time (Trites and Porter 2002). The values reported are also low for typical values for mammals in general. Pitts and Bullard (1968) in Blaxter (1989) derived a generic allometric equation of % fat as a function of body mass from analysis of the bodies of 49 species. The resultant generic equation was:

$$[A.14] \quad \% \text{fat in the body} = 6.01 * W^{0.2}$$

where W is body weight in kg. If that relationship is applied to the weight at age Gompertz model fitted in Winship *et al.* (2001), the predicted percentages of fat in the body would range from 14.7% to 18.5%. As previously shown, thermoregulation in the aquatic environment would impose a greater need for fat content in the Steller sea lion's body.

Most recent studies (Dunlap-Harding *et al.* 2001) found that Steller sea lions 14-15 months of age had average percentages of body fat of 17.1% (western, declining stock) and 19.0% (eastern stock). Those differences were not significant. The overall range of percentage body fat found was 4.3-33.7%, the lowest being the ones for 2-month old pups. In the experiment in Rea *et al.* (2001), prior to fasting trials, animals had a percent body fat from 11 to 28%, although these animals were captive.

It is difficult to infer which would be the minimum preferred level of target fat for a growing Steller sea lion. It is possibly dependent on season and size of the animal, as those variables would influence its thermoregulatory needs and needs for energy storage. A tentative value of 15% was chosen as a representative initial value for the minimum

preferred level of target fat. However, it is also allowed to vary according to thermoregulation needs in a similar fashion than the minimum level of fat. It then depends on the size, season and level of activity of the animal.

For simplicity, in the model essential fat is called minimum level of fat while the minimum preferred level of target fat is called simply the target level of fat.

Both levels vary from their initial values in a similar manner according to thermoregulatory needs, as explained in Section 2.3.2.1. They are increased when excessive heat is lost to the environment and decreased when the situation is the opposite. Excessive heat loss is considered when the heat dissipated to the environment exceeds the resting metabolic rate. In that case, the minimum and target levels of fat are increased by 0.001 units in every time step that this is happening. When the resting metabolic rate is greater than two times the heat dissipated to the environment, both levels are decreased by 0.002 units per time step. These limits and magnitudes of increase and decrease are arbitrary and were set in a manner that allowed for a reasonable behavior of the virtual sea lion.

The cost of tissue accretion

The available energy for growth is allocated according to the specified fat/protein ratio. The final increment in dry mass was given by eq. 2.13:

$$[2.13] \quad \Delta W_{dry} = \frac{Er}{pFat * EfatGr + pPr * EprGr}$$

Er is the remaining energy available for growth once maintenance needs have been satisfied. $EfatGr$ and $EprGr$ is the energy needed to build a kilogram of fat and protein tissue respectively. Those are different from the energetic densities of fat and protein in that there is some energy dissipation during the tissue building process. $EfatGr$ and $EprGr$ are then ED_{fat}/kf and ED_{pro}/kp , with ED_{fat} and ED_{pro} being the energetic content of the retained body lipid and body protein respectively, and kp and kf the efficiencies of protein and fat retention respectively. $pFat$ and pPr are the targeted proportions of protein and fat in the body, the ones that ensure that the target level of fat is met.

There are some minor discrepancies in the literature about the values of the energetic contents of the different tissues. I take the values in Blaxter (1989) as

representative. These are $ED_{\text{pro}} = 23600 \text{ kJ/kg}$ and $ED_{\text{fat}} = 39300 \text{ kJ/kg}$. This falls within the range determined experimentally by Olesiuk and Bigg (1987) in Steller sea lions ($9400\text{-}9450 \text{ Kcal/gr} = 39330\text{-}39539 \text{ kJ/kg}$) for fat.

The discrepancies about the deposition efficiencies are even greater. ARC (1981) establishes an efficiency of 0.74 for fat and 0.54 for protein deposition. Webster (1985) gives a value 0.75 for fat and 0.45 for protein. Blaxter (1989) noted that these efficiencies depend on the dietary source of energy and may be higher, around 0.78-0.90 for fat and 0.56 for protein. He believes that representative values would be 0.76 for fat and 0.56 for protein. Whittemore (1998) recommends a value of 0.44 for protein. However, he acknowledges that many nutritionists believe it is higher, up to 0.54 for young pigs, and to have values as low as 0.38 for heavier pigs of 100 kg or more. He uses an efficiency for fat retention of 0.75. Nevertheless, he notes that when lipid in the diet is high, efficiency may be as high as 0.90; deVries and Kanis (1992) took $k_p = 0.45$ and $k_f = 0.75$ based on Mougan and Smith 1984 and Metz *et al.* (1986).

What these discrepancies may be representing is that the values can vary depending on the energy source and on the developmental status of the animal, as suggested in Beamish and Trippel (1990). For a fixed diet, the efficiency could be higher for young animals because the proportion of protein in the gain is higher and aminoacids can be incorporated into new tissue without much cost. In older animals where growth is mostly fat, aminoacids have to be deaminated, which incurs higher energetic losses. While it is almost certain that these values are not fixed, there are not enough data to quantify how they vary depending on the energy source (fat or protein) or the fate (deposition or breakdown). I consider the deposition efficiencies to be fixed as 0.56 for protein and 0.76 for fat as in Blaxter (1989).

Then, a kilogram of protein will contain 23600 kJ, while it would cost 42143 kJ to build. Similarly, a kilogram of fat contains 39300 kJ, but it costs 51710 kJ. During weight loss, a kilogram of fat would provide 39300 kJ, but the rebuilding cost is 31.5% higher. This means that the penalties for losing weight are as high as those for exceeding credit on a credit card. Gaining and losing weight is not an energetically efficient strategy.

Reference growth models

The model follows both the evolution of total body mass as well as body length. The use of both measurements, weight and length, is essential for modeling the negative phases of growth. The animal can lose weight, but it cannot “shrink” in the sense that once it has reached a certain length, it maintains it.

The model uses a combined growth model employing two growth equations: one for length as a function of time and one for mass as a function of length (the use of these equations was described in Section 2.3.2.6).

The allometric equation is taken from Winship *et al.* (2001) but is used in reference to protein mass rather than total body mass:

$$[2.15] \quad \text{Pr wt}(L) = \text{RefpPr} * a * L^b$$

RefpPr is the reference proportion of protein in the body and is taken to be 0.267 from Davis *et al.* (1996). Parameters a and b are taken as those from the mass at length model for Steller sea lions fitted in Winship *et al.* (2001), $a=10^{1.34}$ and $b = 2.89$.

Length is used in the model to predict how much the animal “wants” to grow in the next time interval. I use the Gompertz model of length at age fitted in Winship *et al.* (2001) as a reference ‘genetic program for growth’:

$$[2.18] \quad L(t) = A * \text{EXP}(-\text{EXP}(-k * (t - t_0)))$$

Parameter’s values are $A = 2.32$, $k = 0.404$ and $t_0 = -1.726$.

Table A.1 : Reference length at age relationship. It is the Gompertz model fitted in Winship *et al.* (2001).

Age (years)	Female Length (m)	Age (years)	Female Length (m)
1	1.66	13	2.31
2	1.86	14	2.32
3	2.00	15	2.32
4	2.10	16	2.32
5	2.17	17	2.32
6	2.22	18	2.32
7	2.25	19	2.32
8	2.27	20	2.32
9	2.29	21	2.32
10	2.30	22	2.32
11	2.31	23	2.32
12	2.31	24	2.32

Female Length at age (Gompertz model)

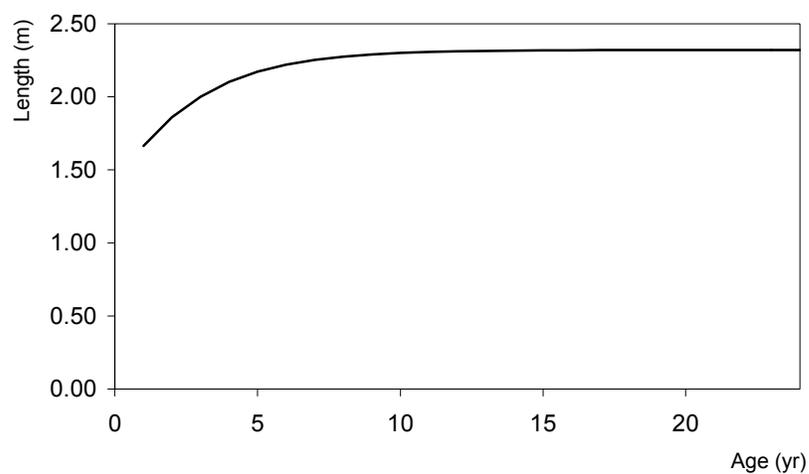


Figure A.1: Reference length at age model from the Gompertz model fitted in Winship *et al.* (2001).

The underlying assumptions are that the growth models derived in Winship *et al.* (2001) from animals in Alaska also apply to the eastern stock, including the animals in Oregon. It is also assumed that this model represents the ideal growth under no nutritional limitation, which is not the case as it is possible that the wild animals on which the model was based would have experienced food limitation during some stages of their lives.

Metabolic depression

The model considers the option that there is metabolic depression in the wild when animals are energetically restricted and weight loss occurs (it also considers the alternative option). Nevertheless, metabolic depression it is only considered to occur when there is lean body mass loss. There is evidence that the resting metabolic rate is related to body composition, and specifically to lean body mass (*e.g.*, Tess *et al.* 1984. Olthoff and Dickerson 1989).

The magnitude of the metabolic depression is related to lean body mass loss in a similar manner as in Øritsland (1990). He uses an empirical equation:

$$[A.15] \quad MBF = -0.33 + (1.33 W)/W_s$$

where MBF is the metabolic depression factor limited to [0.6,1], W = body weight (kg) and WS = standard or initial body weight (kg). In the Stella model this expression is modified in that the standard body weight is the maximum protein mass attained. Instead of considering total body mass, only protein mass is considered so that W is Pr wt.

Øritsland's (1990) equation has provided a reasonable fit to the values observed in Rosen and Trites (1998), although it underestimated the change in resting metabolic rate at high losses of body mass.

It is interesting to note that Markussen *et al.* (1992) found that starvation causes a depression in the basal metabolic rate in harbor seals that was still evident during activity. The model maintains metabolic depression also during periods of activity. The metabolic rate is assumed to return to its normal rate when the protein mass is regained.

Metabolizable Energy

Not all the energy contained in the food is available to the animal. Part of it is dissipated during digestion. Metabolizable Energy (ME) is the net energy remaining after fecal and urinary energy loss and represents the energy available for growth and supporting metabolic processes. Mathematically ME is described by: $ME = IE - FE - UE$ (Costa and Williams 1999), where IE is ingested energy and FE and UE the energy present in the feces and urine respectively.

Fecal digestive efficiency varies with prey type and composition. Rosen and Trites (2000a) found that for juvenile Steller sea lions fed on diverse items, fecal digestive efficiency ranged from 0.904-0.954. It varied with prey type, but differences among prey types were small. I took the midpoint of this range, 0.929. This is quite close to the value used in the Winship *et al.* (2002) bioenergetic model, based on various studies of captive pinnipeds (Keiver *et al.* 1984, Ronald *et al.* 1984, Fisher *et al.* 1992, Mårtensson *et al.* 1994, Lawson *et al.* 1997). They used a range of 0.90-0.96, with a midpoint of 0.93. For the urinary digestive efficiency, I used the midpoint of the range in Winship *et al.* (2002) (range 0.90-0.93, midpoint 0.915).

The resulting overall efficiency of gross energy utilization (the multiplication of both values) would be 0.85. This value would be equivalent to the midpoint of the overall range in Winship (2000), who uses a range of 0.81-0.89. It is also equivalent to the midpoint of the widest range I found in the literature for pinnipeds, that of Costa (1988) in Costa and Williams (1999) for California sea lions (84.95, range 78.3-91.6). It is also consistent with other studies reported in Costa and Williams (1999): Costa (1988) found that it was 88.2% for California sea lions fed on herring, 91.6% when fed on anchovy, 91.4% for mackerel and 78.3% for squid; Keiver *et al.* (1984) found it was 87.1% for harp seals fed on herring; Ronald *et al.* (1984) found a value of 82.7% for gray seals fed on herring; Parsons (1977) found it was 89.8% for ringed seals fed on herring and Ashwell-Erickson and Elsner (1981) found it was 80.3% for harbor and spotted seals fed on pollock or herring.

APPENDIX 2

Evidence in support of the dual regulation system

Animals of different ages and reproductive status have different energetic requirements. Many times they live in the same environment and yet they are able to extract differentially the precise amount of energy they need at the different stages of their lives. In general, mammals do not seem to extract energy at their maximum possible rates. The ability of many mammals to increase their food intake in certain situations (*e.g.*, during cold stress, lactation, poor feed quality) show that they could eat more, but they chose not to do so (for a critical review in this issue see Ketelaars and Tolkamp 1992). Animals must have regulatory mechanisms that allow them to adjust their feeding rates to their internal needs at different stages of their lives. Physiological studies locate these regulatory functions in the hypothalamus (Steffens and Strubbe 1987, Schmidt-Nielsen 1997, Nicolaidis 1987). Destruction of the ventromedial hypothalamic area (VMH) causes hyperphagia and obesity (Hetherington and Ranson 1940, Brobeck *et al.* 1943, cited in Steffens and Strubbe 1987), whereas the destruction of the lateral hypothalamic area (LHA) results in aphagia and decline of body size (Anand and Brobeck 1951, cited in Steffens and Strubbe 1987). These brain areas receive information from the alimentary tract and the circulation, and about the size of the reserves (Steffens and Strubbe 1987).

While the exact mechanisms and possible mediators are not clearly identified, all views coincide in that information about the energetic status of the animal along with stimuli produced in the digestive tract interplay to regulate feed intake and weight through the central nervous system. Physical satiation mediated by hormones produced in the digestive tract may play a role in the short-term response and promote a stop-feeding behavior; other sources of information about the energetic status of the animal may play a role in the long-term response and promote a resume-feeding behavior. As a result, in the long run, food intake and consequently body weight are regulated accurately. Most adult animals maintain their body weight within narrow limits even in variable environments.

In this respect, it is interesting to note that captive pinnipeds are often unable to maintain their body mass when switched to a lower energy diet, despite being fed *ad*

libitum (Mårtensson *et al.* 1994, Rosen and Trites 2000b). This could be due to the short duration of the experiments (only several weeks). Curll and Davison (1983) suggested that appreciable time might be required for herbivores to adapt behaviorally to a change in herbage biomass. It could also have happened because, even though they were fed *ad libitum*, the frequency of feeding was fixed. Physical satiation stimuli of the type discussed earlier could have acted in response to the amount eaten in one sitting, while stimuli from the energetic status of the animal would have acted in connection with the frequency of feeding, which was set for the animals in the experiment. Some other explanations are possible. Whittemore (1998) described that an excessive protein content in food (such as in pollock as in the Rosen and Trites 2000b experiment) leads to increased heat production from the deamination of aminoacids, which may depress food intake if heat dissipation becomes limiting and body temperature rises or if the product of deamination become marginally toxic.

Assumptions of the foraging model

The foraging model described in Section 2.4.4 assumes that for every meter that the animal advances in the forward direction, a box with a volume of 1 m^3 is searched. This is unrealistic as the volume in the corners in the box is probably not in the scope of the animal. The volume searched has probably a spheroid shape. Nonetheless, that simplification should not affect the final output, as the parameter *ppi* was estimated during the tuning of the model (in Section 3.2) and the reduction on the effective volume searched should be accounted for by a reduced value of the estimated *ppi*.

The foraging model is very simple and some of the other assumptions of this model are:

- Transit times from and to foraging grounds are considered negligible. Diving behavior is not accounted for either. Prey items are at a certain depth and descending and ascending could also be considered transit times, especially ascending. The need to surface to breath limits effective foraging times, which will be ultimately limited by the sea lion's aerobic capabilities. However, Steller sea lions in Oregon seem to be preferentially nocturnal feeders (Mate 1973). They might be taking advantage of the

nocturnal migrations of some fishes, such as Pacific whiting (Stauffer 1985), and they probably feed close to the surface rather than undertaking deep dives.

All speed is considered foraging speed. There are no transit speeds when the animal is moving from foraging grounds. All activity in the water is associated with feeding.

- Foraging speed is assumed constant. I did not consider instantaneous changes in speed, which are very likely to happen during the fish-chasing process, and or during ascent and descent. Burst-glide swimming versus constant swimming has been shown to reduce considerably the swimming cost in fish (Weihs 1974 cited in Ware 1978). Similarly, gliding while diving appears to be a general phenomenon in diving marine mammals that conserve energy and increase aerobic dive duration (Williams *et al.* 2000, Williams 2001). Other diving physiological strategies such as bradycardia are not taken into account either.

- It is assumed that the prey distribution is homogeneous in space. Prey density is used as an approximation to prey availability. This is quite simplistic. Many of the prey items found in the Steller sea lions' diet at the Oregon coast are schooling fishes (Riemer and Brown 1997). Once they find a school, sea lions may feed on it for a considerable amount of time. School density as opposed to fish density would be a better measurement to describe the foraging success of sea lions. This will have a considerable effect when fish density is at low levels, as a reduction in fish abundance may not be homogenous, but can concentrate the fish into a few relatively large isolated patches that are difficult for the sea lion to find.

On the other hand, all prey items are combined into a single index of prey density with the same associated probability of successful capture (ppi). In fact, that probability would depend on the prey item, as slow swimming animals would be easier to catch. Roffe and Mate (1984) noted that Steller sea lions at the Rogue river mouth could be following the slow moving lamprey in their seasonal migrations.

Certainly, Steller sea lions have food preferences and might follow their preferred food items (preferred because they are more abundant, easier to catch or more palatable). Only when their preferred food items are below a certain abundance threshold, would they shift to others.

- The probability of successful capture (ppi) is independent of prey density. It seems reasonable to assume that the probability of seeing, reacting and capturing a prey successfully would depend on prey density. The shape of that relationship would probably be dome-shaped, as at low or high prey densities, the probability would be lower. Or if, in connection with one of the former assumptions, reduced prey density concentrates the prey in isolated patches, ppi could be an inverse exponential function of prey density.

- All units in the proportion of time foraging (P_f) are considered equivalent from the energetic gain point of view. However, when the prey items undergo daily migrations (as Pacific whiting), this assumption is not valid.

The poverty of this foraging model reflects the current understanding about diving and foraging behavior for Steller sea lions in the wild. There are no detailed diving profiles as the ones for other species (*e.g.*, Gentry *et al.* 1986, Boyd 1996, Costa and Gales 2000), and there is not much known about their capture strategies and techniques. Nevertheless, the model is intended to accommodate the energetic trade-offs and options that exist for an animal when it has to increase its food intake. The qualitative relationship between the energetic cost and gains is hopefully intact despite those uncertainties.

Processing time

The rate at which food is ingested is described in the model by a Type II functional response, like the one described in Valiela (1995):

$$[2.21] \quad I(a, P, b) = \frac{a * P}{1 + a * b * P}$$

In this type of equation, parameter b is the handling time, traditionally defined as the time expended attacking, capturing and consuming a food item. It introduces a temporal limitation in the rate at which food can be ingested (the curve drawn by eq. 2.21 has an asymptote at $1/b$).

In the model here the meaning is different, as the time resolution is on the order of days and not minutes, which would be range of the expected time intervals needed by the sea lion to attack and eat a food item. In any case, there are no direct observations for free

ranging Steller sea lions of the time required to attack and capture fish. I assume that this time is negligible and I only consider the time needed to process food items once ingested. This time constraint is called processing time instead of handling time. This term is introduced to account for the upper limit in the food that can be ingested and processed during the one-day time step.

There is certainly a limit to the amount of food an animal can ingest daily, although monogastric animals are traditionally believed not to be physically constrained in their intake (Ketelaars and Tolkamp 1992). However, there is evidence that some monogastric animals may be physically limited in their intake, at least during some stages of their life. Black *et al.* (1986) reviewed for their pig production model previous experiments; they concluded that there is considerable support for the assumption that there is a maximum intake for pigs that is determined by the capacity of the digestive tract. Those studies showed a weight dependent capacity to increase intake when the digestible energy content of the diet was reduced for pigs of different sizes. Small pigs were unable to compensate for a decline in the energy concentration of the diet (and neither were juvenile Steller sea lions in Trites and Rosen 2000b experiment).

Kastelein *et al.* (1990) found that the maximum intake (the *ad libitum* intake after one day of fasting) for a 16-year-old male was approximately 26 kg/day, while for two 16-year-old females was around 15 kg/day, 11 kg/day for a 3-year-old female and 7 kg/day for a 2-year-old female. They did not weight the animals, but taking values of weight at age from the model fitted by Winship *et al.* (2001) it can be seen that while for small animals those values are 5.5, 7 and 5.7% of body weight, for the male it would be 3.8 %. Fiscus and Baines (1966) reported a 2-year-old male taken at sea with a stomach content of 9.4% of body weight. In the pollock feeding trial (Rosen and Trites 2000b), animals during the recovery periods (which can be approximated to maximum intake rates) ate 5.9 and 5.8% of their body mass a day. The maximum food intake per day of California sea lion reported by Kastelein *et al.* (2000), when expressed as a function of typical adult sizes (390 kg for males, 110 kg for females) gives values of approximately 9% for one male and 14.5% for one female. This value may seem a little bit high, but this female was a reproducing animal (and its real weight is unknown).

The maximum daily processing capacity should not be understood as the absolute maximum digestive capacity of the animal, but as the maximum voluntary daily food intake. It seems reasonable to assume that an animal, even though it might be in a negative energy budget, would not feed at a level that causes discomfort to it. As discussed before (in evidence of internal regulatory systems), physical stimuli released by the digestive tract when it is approaching fullness, act over the centers at the hypothalamus to inhibit the hunger sensation. Therefore, even though the animal might have not consumed enough kilojoules to support its activities, it may stop eating because of the physical sensation of fullness. The idea that animals feed at rates that maximize comfort rather than energy acquisition has been proposed for ruminants (Forbes 1995).

On the other hand, this maximum capacity is not only related to the volumetric capacity to ingest food. Pinnipeds have very fast digestive passage rates (Helm 1984) and the potential to eat great amounts of food. In general, Steller sea lions do not feed on a daily basis, so they must have a high volumetric capacity to consume food. However, there can be limitations in other parts of the digestive process, such as the intestine's capacity to absorb nutrients, the liver's capacity to process absorbed nutrients, the capacity to transport, use and store the processed nutrients and the kidneys' capacity to excrete the resulting wastes (Hammond and Diamond 1997).

There are not enough data to infer the shape of a function for the maximum daily processing capacity relative to body size or age. But it seems reasonable that this capacity will be size dependent. It is not clear if that relationship would be an allometric or isometric function of total body weight. Given the lack of data, I assume that the maximum food intake won't exceed 15% of body mass and that this is constant for animals of all ages. This value is practically a guess. For that reason, it is left open in the model to user modifications, as it can be influential.

In this sense, it is interesting to note that the estimated daily food requirements of pregnant females with pups of the youngest reproductive ages (4 and 5 years old) calculated in Winship *et al.* (2002) are above 15% of body mass. This may indicate that the youngest pregnant lactating females are working very close to or past their maximum capabilities and are at risk of having problems getting enough food. They might be very susceptible to losing their pup, having an abortion or both. Abortion has been suggested

to be associated with female condition during late pregnancy in Steller sea lions (Pitcher *et al.* 1998). Even though they are fertile, the youngest females could be energetically incapable of successfully rearing a pup when there are minor environmental perturbations. The effect of that at a population level might be similar to a delay of two to three years in the age of first reproduction. This effect could have significant consequences for the population as was seen in Section 3.3.3 in Chapter 3.

Processing time in the model is then the inverse of the maximum food intake capacity. It is the assumed minimum time required to process 1 kg food.

Interaction Pf-V

In Chapter 2 Section 2.4.5 the optimal proportion of time foraging (Pf) and foraging speed (V) were calculated according to different optimization criteria. It is interesting to have a look at how those optimal V and Pf are related. To understand the relationship, it is useful to represent the net gain curve as a function of Pf and V. The net gain function is the energetic gain minus all the energetic costs:

$$[A.16] \text{ Net E Gain} = \text{Ingested E} * \text{Efficiency} - (\text{E loss in water}) * \text{Pf} - \text{E loss on land} * (1 - \text{Pf}) - \text{E prod}$$

The net gain in energy is just the difference between the energy acquired and the energy expended. The energy acquired is that available to the animal after accounting for losses in the digestive process. This is what the multiplier *Efficiency* represents, the overall efficiency of the digestive process.

The energetic costs to the animal include: those in water times the proportion of time the animal is in water; those on land times the proportion of time the animal is on land; and the energetic costs of production (either in the form of somatic or reproductive growth, somatic growth in this case as only immature animals are considered). For simplicity, the cost of thermoregulation is not included in this equation.

Replacing the nominal concepts by their mathematical expressions, that equation is equivalent to:

[A.17]

$$NetGain = \frac{Pf * V * ppi * P * diet * Eff}{(1 + Pf * V * ppi * P * b)} - \left(\frac{tr * (\lambda * \rho_w * S * Cd * V^3)}{2 * \epsilon_A * \epsilon_P} + RMR \right) * Pf$$

$$- [LM * RMR * (1 - Pf)] - Eprod$$

where *NetGain* is expressed in kJ/day; *Pf* is the proportion of time foraging; *V* is the foraging velocity (m/d); *ppi* is the probability of successful capture; *P* is the overall prey density (kg/m³); *diet* is the energetic density of the mixed diet (kJ/kg); *Eff* is the digestive efficiency; *b* is the processing time (day/kg); *tr* is the converter of watts into kJ; λ is the ratio of the drag of an active to passive swimmer; ρ_w is the density of the water at a given temperature (kg/m³); *S* is the wetted surface area (m²); *C_D* is the drag coefficient; ϵ_A is the aerobic efficiency; ϵ_P is the propeller efficiency, *RMR* is the resting metabolic rate (kJ/day); *LM* the land multiplier of the resting metabolic rate and *Eprod* the total cost of production (kJ/day).

If this net gain function is plotted with respect to foraging velocity (for a fixed *Pf*), it shows a characteristic pattern (Fig. A.2). The height of the curve depends on the prey abundance (*P*). As velocity increases, the net gain increases to a maximum value and then starts to decline. Positive net gain means an extra energetic profit that can be stored in the form of depot fat. Negative net gain means that the animal is in a negative energy budget and it would need to metabolize body tissue to meet its energetic needs. Net gain equal to zero means that the animal is in energetic balance, it uses all the energy that is ingesting. There are then three important velocities, V_{min} , V_{opt} and V_{max} .

V_{min} is the minimum velocity that allows the animal to meet its energetic demands for a fixed proportion of time foraging (*Pf*). If the animal increases its velocity beyond V_{min} , it would make an extra energetic profit. This profit is maximized at V_{opt} . If the animal increases further its velocity, net gain starts to decline again till V_{max} , as the increment in the energetic cost of locomotion would offset any increase in ingested

energy. V_{\max} is the maximum velocity that allows the animal to get enough food to meet its energetic demands².

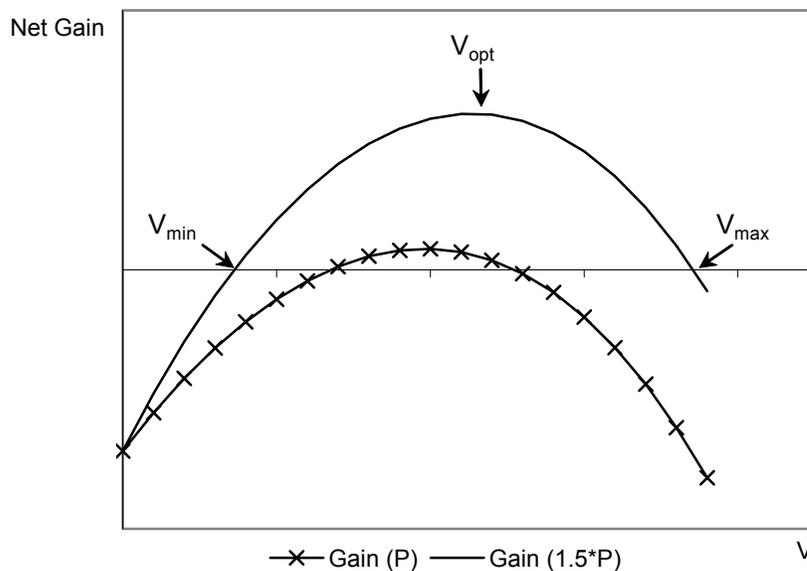


Figure A.2: Representation of the net energetic gain for a foraging sea lion as a function of foraging speed (V) at two levels of prey density.

If an animal is swimming at V_{\min} and increases its velocity to $V_{\min} + \delta$, it displaces itself along the net gain curve. It has two options. An energy maximizer would keep the extra profit in the form of fat. A time minimizer would prefer to make no extra profit and instead, go home earlier by reducing Pf and displacing the whole curve downwards. Then, it can still increase its velocity by another δ and consequently, reduce Pf more. It is possible to repeat the process until it gets to V_{opt} . At that point, a further increase of V will raise cost over benefits. To avoid being in a negative energy balance, it would have to increase Pf . To the left of V_{opt} , velocity and Pf are inversely related. To the right, they are directly related, and an increase in V has to be followed by a faster increase in Pf . Therefore, V_{opt} is also the velocity that minimizes Pf . When the optimal velocity for the time minimizer is calculated using eq. 2.30 or solving for V_{opt} in the net gain function,

² This V_{\max} is different from the metabolic maximum velocity, $V_{M\max}$ (in Section 2.4.5), which is the velocity that raises the metabolic rate to the maximum metabolic rate, assumed to be ten times the resting metabolic rate.

solutions are identical in most circumstances (at extremely low prey densities the solution of eq. 2.30 can result in a higher V than V_{opt} as it does not consider the increase in locomotion costs).

It is important to note that this V_{opt} is the optimal foraging speed and is dependent upon prey density. When other optimality criteria are applied, the solutions can be different. It is quite common to find allusions in the literature to optimal speeds, referring to optimal cruising speeds. Those are calculated as the speed that allows covering the maximum distance with the minimum energetic cost. There is no connection with energy intake, only costs are considered. Those speeds are independent of prey density and might be the ones used to travel from patch to patch. I did not consider those optimal speeds as in the model the animals are assumed to be continuously feeding. This coupled foraging-physiological model is not intended to predict sea lion swimming speeds, but to get an average estimation of the energetic cost of foraging and how that relates to energy intake.

Other possible optimality criteria would be the speed that minimizes heat loss. Heat dissipation in the water is a function of swimming velocity, and heat production is a function of velocity as well. There is an optimal speed, dependent on water temperature, at which the heat loss is minimized. I did not include thermoregulation considerations in the optimization solution.

For the energy maximizer the solution found by the optimization is peculiar. As the cost of activity increases to the third power with an increase in velocity but increases linearly with an increase in the proportion of time swimming, it is more profitable in energetic terms to increase P_f instead of V when prey abundance is reduced (also, the gain increases more slowly with an increment in V than in P_f). Even more, it is more profitable to reduce V in order to further increase P_f . The result is that, under most situations, the energy maximizer reduces its velocity so that it can feed at low energetic cost the maximum possible amount of time. Such a strategy is energetically very profitable (at least in the model) and the animal gains fat rapidly, which reduces further foraging costs (due to reduced thermoregulatory costs). This relationship between P_f and V can be seen in Figures A.3 and A.4, where net gain is higher for higher P_f and lower speeds.

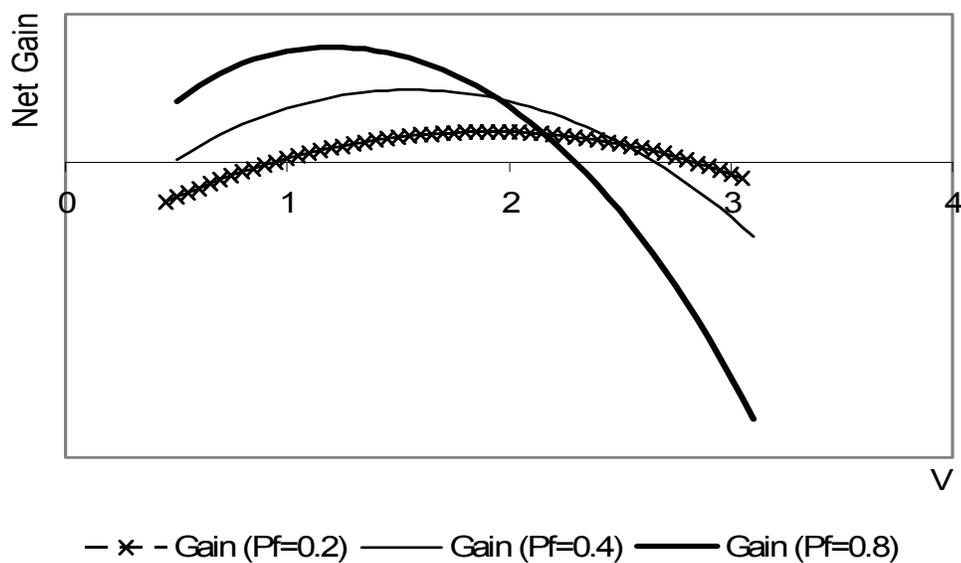


Figure A.3: Net energetic gain for a foraging sea lion as a function of foraging speed (V) at different proportions of time foraging (Pf).

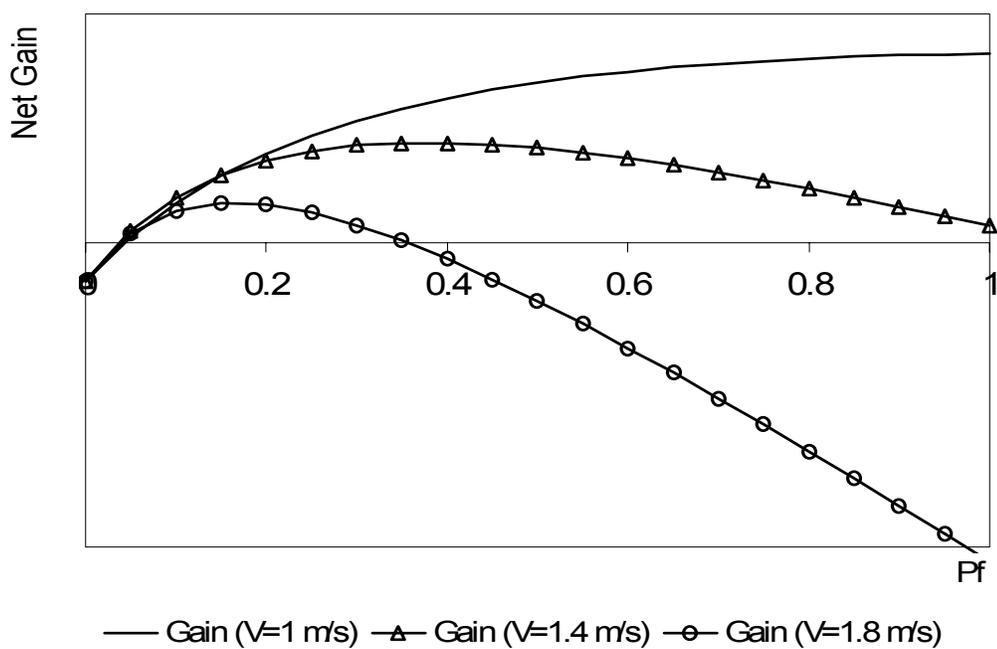


Figure A.4: Net gain for a foraging sea lion as a function of proportion of time foraging (Pf) at three different foraging speeds (V).

Time minimizer vs. Energy maximizer

One interesting feature of the model is an indication that Steller sea lions' behavior could be better approximated by a time-minimizing strategy, or equivalently, that their foraging behavior is driven by a hunger satiating behavior. When the virtual sea lion is allowed to behave as an energy maximizer, its immediate response is a drop in the foraging velocity and a rise in foraging time. Under most circumstances, the animal is swimming close to or at the minimum possible speed (set arbitrarily to 1m/s in the model) and the maximum possible proportion of time (set to 0.9 in the model). This behavior is maintained even with strong seasonal variations in prey density.

The 'velocity reduction and increasing time' foraging strategy is certainly energetically profitable. With the same basic parameters as the time minimizer, the energy maximizer could double its percentage of fat at the end of one year. After several years, the sea lion could get extraordinarily fat. This could be due, of course, to an inadequate tuning of the model parameters. It may also be that negative feedback loops were missed. For example, there would certainly be penalties for excessive fat, which are not considered in the model: increased buoyancy, overheating, and loss of maneuverability, to mention a few. The risk of predation is not considered either. Wild animals might be more cautious depending on the state of their reserves.

The problem with the optimization of Pf and V is that two different currencies are being optimized separately, which are time and extra energy gains. The solutions represent probably the extremes of a gradient between extremely cautious (time minimizers) and extremely greedy (energy maximizers) animals. If the perceived risk of predation could be quantified in energetic terms, it is probable that an intermediate solution be found.

APPENDIX 3

The STELLA population submodel

To assess the possible population effects of a delay in the age of attainment of sexual maturity, a population submodel was build using the STELLA simulation modeling system. This submodel has a stock variable for every age class. There are twenty-two age classes for females and fourteen for males. The inflows to each stock is the number of animals from the previous age class that survived according to the life tables in Winship *et al.* (2002) based on Trites and Larkin (1992) and York (1994) (Table A.2). The outflow from each stock is the number of animals that die and the number of animals that survives and become one year older. The time step is one year. The number of pups produced is the multiplication of the number of females of the different age classes alive at the beginning of the year times the proportion mature at age in the previous year. The summation of all those is multiplied by the assumed fertility of 0.63 (as in York 1994, based on Pitcher and Calkins 1982). Pups are assumed to be born in a ratio of 1:1 males to females. An initial number of 100,000 females and 100,000 males one-year-olds is given (the initial number of animals for other age classes was zero), and simulations are run for a transition period to ensure that a stable age structured population is attained before perturbations were introduced.

The discrete data for maturity at age given in Winship *et al.* (2002) were transformed into a continuous function with two parameters (age50 and β):

$$[A.18] \quad Mat(age) = \frac{1}{1 + \exp(-\beta * (age - age50))}$$

The values of age50 and β for which the finite rate of population increase was 1 were age50 = 2.786 and $\beta = 1.42$. Perturbations were introduced over that baseline level. The low value for age50 is somehow a mathematical artifact of the transformation of discrete values into a continuous function, as the earliest evidence of female sexual maturity has been recorded at 3 years of age (Pitcher and Calkins 1981). Equation A.18 predicts that at 2.8 years of age 50% of the females are mature. However, those values for

age50 and β produce a finite rate of population increase of 1, and the goal was to assess how this rate change as a function of changes in age50.

Age	Annual Survival		Proportion mature (female)
	Male	Female	
0	0.52	0.671	0
1	0.65	0.824	0
2	0.78	0.915	0
3	0.86	0.946	0.321
4	0.87	0.924	0.57
5	0.85	0.91	0.83
6	0.831	0.899	1
7	0.814	0.89	1
8	0.798	0.882	1
9	0.782	0.874	1
10	0.768	0.867	1
11	0.754	0.861	1
12	0.74	0.855	1
13	0.727	0.85	1
14	0	0.845	1
15		0.841	1
16		0.836	1
17		0.832	1
18		0.828	1
19		0.824	1
20		0.821	1
21		0.817	1
22		0	1

Table A.2: Median annual survival rates for male and female Steller sea lions and proportion mature at age as in Winship *et al.* (2002). This survival rates were used in the population submodel. The proportion mature at age was calculated using a continuous function (eq.A.18) such that produced a finite rate of population increase of 1 given those survival rates.

List of equations

$$[2.1] \quad BM = 292.88 * (Bodywt^{0.75})$$

$$[2.2] \quad M = M_B + M_T(V) + M_L(V)$$

$$[2.3] \quad D = 1/2 * \rho * S * Cd * V^2$$

$$[2.4] \quad P_o = 1/2 * \rho * S * Cd * V^3$$

$$[2.5] \quad M_L = \lambda * \frac{\rho * S * Cd * V^3}{2 * \epsilon_A * \epsilon_p}$$

$$[2.6] \quad A = A_w * Pf + A_L * (1 - Pf)$$

$$[2.7] \quad H_1 = [k_1 * 2 * \pi * L * (T_{cb} - T_{bs})] / \ln(Rb/rc)$$

$$[2.8] \quad H_2 = f * 2 * \pi * Rb * L * (k_2 / \Delta Rb) * (T_{bs} - T_s)$$

$$[2.9] \quad H_3 = f * h_{conv} * 2 * \pi * Rb * L * (T_s - T_a)$$

$$[2.10] \quad H = (T_{cb} - T_a) * 2 * \pi * L * [\ln(Rb/rc) / k_1 + \Delta R / f * k_2 * Rb + 1 / f * h_{conv} * Rb]^{-1}$$

$$[2.11] \quad H = U * S * (T_{cb} - T_a)$$

$$[2.12] \quad U = 1 / (Rb * \ln(Rb/rc) / k_1 + \Delta Rb / f * k_2 + 1 / f * h_{conv})$$

$$[2.13] \quad \Delta W_{dry} = \frac{Er}{pFat * EfatGr + pPr * EprGr}$$

$$[2.14] \quad W(L) = a * L^b$$

$$[2.15] \quad Pr wt(L) = RefpPr * a * L^b$$

$$[2.16] \quad L(Pr wt) = \left(\frac{Pr wt}{Re fp Pr * a} \right)^{\left(\frac{1}{b} \right)}$$

$$[2.17] \quad dPr wt/dL = b * RefpPr * a * L^{(b-1)}$$

$$[2.18] \quad L(t) = A * EXP(-EXP(-k * (t - t_o)))$$

$$[2.19] \quad dL/dt = A * EXP(-EXP((-k) * (t - t_o))) * ((k) * EXP((-k) * (t - t_o)))$$

$$[2.20] \quad t(L) = ((LOGN(-LOGN(Length/A)) / (-k)) - (t_o))$$

$$[2.21] \quad I(a, P, b) = \frac{a * P}{1 + a * b * P}$$

$$[2.22] \quad a = Vol * ppi$$

$$[2.23] \quad Vol = Pf * V$$

$$[2.24] \quad I = \frac{Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

$$[2.25] \quad Pf = \frac{I_t}{V * ppi * P * (1 - I_t * b)}$$

$$[2.26] \quad G(Pf) = \frac{diet * Eff * Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

$$[2.27] \quad C(Pf) = A_w * Pf + A_L * (1 - Pf)$$

$$[2.28] \quad \frac{dG}{dPf} = \frac{diet * Eff * V * ppi * P}{(1 + b * Pf * V * ppi * P)^2}$$

$$[2.29] \quad \frac{dC}{dPf} = A_w - A_L$$

$$[2.30] \quad V = \frac{I_t}{Pf * ppi * P * (1 - I_t * b)}$$

$$[2.31] \quad G(V) = \frac{diet * Eff * Pf * V * ppi * P}{1 + b * Pf * V * ppi * P}$$

$$[2.32] \quad \frac{dG}{dV} = \frac{diet * Eff * Pf * ppi * P}{(1 + b * Pf * V * ppi * P)^2}$$

$$[2.33] \quad C(V) = \left(\frac{tr * (\lambda * \rho * S * Cd * V^3)}{2 * ea * ep} + RMR \right) * Pf$$

$$[2.34] \quad \frac{dC}{dV} = \frac{3 * tr * (\lambda * \rho * S * Cd * V^2) * Pf}{2 * ea * ep}$$

$$[3.1] \quad ED_{diet} = \sum_{i=1}^8 prey_i * ED_{prey_i}$$

$$[A.1] \quad h_{\text{conv}} = \text{Nu } k_m / L$$

$$[A.2] \quad \text{Re} = V * L / \nu$$

$$[A.3] \quad \text{Nu} = 0.0296 * (\text{Re}^{0.8}) * \text{Pr}^{(1/3)}$$

$$[A.4] \quad h_{\text{conv free}} = \text{NuD} * k_m / D$$

$$[A.5] \quad \text{NuD} = (0.60 + 0.387 * (\text{RaD}^{(1/6)}) * ((1 + (0.559 / \text{Pr})^{(9/16)})^{(-8/27)}))^{(1/4)}$$

$$[A.6] \quad \text{RaD} = \text{GrD} * \text{Pr}$$

$$[A.7] \quad \text{GrD} = D^3 * g * \beta * (T_s - T_a) / \nu^2$$

$$[A.8] \quad H_3 = f * h_{\text{conv free}} * S * (T_s - T_a)$$

$$[A.9] \quad f * h_{\text{conv free}} * (T_s - T_a) = U * (T_{\text{cb}} - T_a)$$

$$[A.10] \quad T_s = (U * (T_{\text{cb}} - T_a) / (f * h_{\text{conv free}})) + T_a$$

$$[A.11] \quad \beta_{\text{air}} = 1 / T_f$$

$$[A.12] \quad rc = \sqrt{\text{Lean wt} / (DL * \pi * L)}$$

$$[A.13] \quad Rb = \sqrt{\text{Fat wt} / (DF * \pi * L) + rc^2}$$

$$[A.14] \quad \% \text{fat in the body} = 6.01 * W^{0.2}$$

$$[A.15] \quad \text{MBF} = -0.33 + (1.33 W) / W_s$$

$$[A.16] \quad \text{Net E Gain} = \text{Ingested E} * \text{Efficiency} - (\text{E loss in water}) * P_f - \text{E loss on land} * (1 - P_f) - \text{E prod}$$

$$[A.17]$$

$$\text{NetGain} = \frac{P_f * V * ppi * P * \text{diet} * \text{Eff}}{(1 + P_f * V * ppi * P * b)} - \left(\frac{tr * (\lambda * \rho_w * S * Cd * V^3)}{2 * \epsilon_A * \epsilon_P} + \text{RMR} \right) * P_f$$

$$- [LM * \text{RMR} * (1 - P_f)] - \text{Eprod}$$

$$[A.18] \quad \text{Mat}(\text{age}) = \frac{1}{1 + \exp(-\beta * (\text{age} - \text{age50}))}$$