

Steller sea lions *Eumetopias jubatus* and nutritional stress: evidence from captive studies

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ABSTRACT

1. Numbers of Steller sea lions *Eumetopias jubatus* in the North Pacific have declined. According to the nutritional stress hypothesis, this decline is due to reduced food availability. Data from studies conducted on pinnipeds in the laboratory are used here to test if the nutritional stress hypothesis can explain the decline of Steller sea lions.

2. Overall, there is strong evidence for biologically meaningful differences in the nutritional quality of major prey species. Steller sea lions can partly compensate for low-quality prey by increasing their food consumption.

3. There appear to be no detrimental effects of low-lipid prey on sea lion growth or body composition when sea lions can consume sufficient quantities of prey. However, the ability to increase consumption is physiologically limited, particularly in young animals. Overall, it is more difficult to maintain energy intake on a diet of low-quality prey than on a normal diet.

4. Under conditions of inadequate food intake (either due to decreased prey availability or quality, or increased energy requirements) the overall impacts of nutritional stress are complex, and are dependent upon season, prey quality, age and the duration and intensity of the nutritional stress event.

5. Studies on pinnipeds in the laboratory have been instrumental in identifying the conditions under which changes in sea lion prey can result in nutritional stress and the nature of the physiological impacts of nutritional stress events.

Keywords: conservation, diet, metabolism, nutrition, pinnipeds

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INTRODUCTION

The precipitous decline of Steller sea lions *Eumetopias jubatus* in the North Pacific has generated a tremendous scientific effort to understand the reasons for the population change, supported by an unprecedented level of funding for conservation-directed research (see Morell, 2008). The numerous individual hypotheses put forward to explain the decline are concerned with both proximate and ultimate factors that range in scale from ecosystem changes to individual sea lion physiology (Anonymous, 2008). To make things more complex, many of these hypotheses are inter-related (Guenette *et al.*, 2006; Atkinson, DeMaster & Calkins, 2008b).

One hypothesis that has received a great deal of attention has become known as the nutritional stress hypothesis. Calkins & Goodwin (1988) are generally credited with first providing evidence of nutritional concerns among wild Steller sea lions. They noted:

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Standard length, girth and weight for female sea lions taken in the Kodiak area were significantly smaller in the 1980s than in the 1970s. (. . .) Reduced body size indicates a reduced state of overall physical condition which, in turn, indicates a state of lowered nutritional plane.

They also noted a decrease in certain aspects of haematology (packed cell volume and haemoglobin, although this finding has been disputed by others), and a subsequent analysis showed that sea lions in the 1980s had less body fat and/or a different body shape as determined by body volume/weight relationships than those in the 1970s (Castellini & Calkins, 1993). The findings were summarized in the statement:

When viewed together, the changes in food habits, reduced body size, and poorer physical condition indicate a lowered nutritional plane. Most of the evidence we have found supports a theory that a reduction in carrying capacity for sea lions in the Gulf of Alaska has occurred. (Calkins & Goodwin, 1988).

In its simplest form, the nutritional stress hypothesis suggests that the decline in Steller sea lions is linked to inadequate nutrition induced by changes in the quality and/or quantity of available prey (Anonymous, 1993). It arises from limited observations on temporal (pre-decline and post-decline) changes in dominant prey items, differences in the diet of geographically separated declining and stable populations, statistical relationships between diet diversity and local population trends, cross-sectional changes in body condition and physiology, and differences in the chemical composition of prey species (Anonymous, 2008). It does not specify the cause of these ecosystem changes or differences (e.g. global warming, regime shifts or fisheries competition).

An impressive range of field studies have been carried out to investigate the validity of this hypothesis from various perspectives, including diet reconstruction, prey species composition analysis, and physiological and behavioural measurements of sea lions (Anonymous, 2003). These studies are invaluable as they provide direct evidence for interactions between individual sea lions and the natural environment. However, as with almost all field studies, experimental manipulations – and therefore conclusions regarding cause and effect – are somewhat limited in scope. In addition, nearly all field research has taken place after the population decline had started.

In other research, the nutritional stress hypothesis has been investigated by using captive pinnipeds. In most of this research, dietary manipulations of animals in the laboratory have been used to study the physiological consequences of such changes. These studies were not designed to test if nutritional stress is occurring, but to ascertain the effect of certain feeding conditions on individual sea lions. In other words, sea lions are physiologically challenged in ways that mimic different types of changes in food supplies (availability and/or quality) that might be occurring in the wild. The results of such studies can present evidence on whether certain environmental conditions may cause particular physiological difficulties for Steller sea lions in the wild, and provide tools and metrics for evaluating the health and nutritional status of animals in the field. They cannot, however, be used directly to determine if nutritional stress is occurring (or has occurred) among wild sea lions, except in their ability to provide data for the development and evaluation of tools and indices. They are restricted in their scope by a number of inherent factors, including the inability to include prey capture costs or animal preferences, limited sample sizes and age and sex classes, limited duration and the inability to evaluate the ultimate (reproductive and survival) consequences of the dietary manipulations.

The experimental designs employed in studies evaluating the nutritional stress hypothesis with captive pinnipeds are varied. Methods involve using different feeding regimes (both type and quantity of prey) for various durations, a range of age groups and even different focus

species. However, this variety in research design provides a wealth of information, although the task of interpreting the sum of these studies is a difficult one.

In the present paper I summarize the data from the majority of dietary studies conducted with pinnipeds in the laboratory that can be used to evaluate the validity of the nutritional stress hypothesis. I attempt to present impartially as much evidence as possible from the studies published to date, and to summarize the collective results into a coherent consensus.

WHAT IS THE NUTRITIONAL STRESS HYPOTHESIS?

A great deal of the debate regarding the validity of the nutritional stress hypothesis centres on the various interpretations of the purported mechanisms. Indeed, as with most scientific theories, the nutritional stress hypothesis has evolved in response to both empirical evidence and continued intellectual consideration. One could argue that there is no single nutritional stress hypothesis, but that a spectrum of potential types (and mechanisms) of nutritional stress have been proposed to be negatively affecting Steller sea lion populations, as well as populations of other species in the North Pacific experiencing population declines. The spectrum of possible interpretations of the nutritional stress hypothesis can be categorized into four distinct, testable variants.

Variant I – pollock equals death

In this extreme variant, the nutritional stress hypothesis is interpreted to mean that sea lions eating walleye pollock *Theragra chalcogramma* do not survive (or reproduce) because there is something inherently ‘wrong’ with pollock (and by extension with other key species such as Atka mackerel *Pleurogrammus monopterygius*). Some scientists have labelled this the junk food hypothesis, a term popularized in the public media and usually incorrectly attributed to Alverson (1992). Although Alverson never used the specific term (after much popular use it first appeared in the primary literature in Rosen & Trites, 2000b) or suggested such an extreme interpretation as ‘pollock equals death’, he was the first to highlight the potentially deleterious effect that a pollock-dominated diet might have on Steller sea lions (see Variant II). The logic behind the ‘pollock equals death’ variant is that either a diet of pollock cannot supply sufficient energy or nutrition to sea lions regardless of how much is available, or there is something in pollock that is inherently harmful to sea lions. As an extreme interpretation it is also the easiest to test: a direct relationship between the amount of pollock consumed and key life history parameters would provide evidence for this variant. Although most scientists may distance themselves from such an extreme interpretation, the justifications and conclusions of several studies come tenuously close to this line of reasoning.

Variant II – deleterious effects of low prey quality

The suggestion is that low quality prey items make it more difficult for individuals to survive and reproduce. The quality of the diet can be measured as energy density or as some other nutritional aspect (e.g. lipid content, amino acid composition), although discussions tend to be focussed on the former, given the prominent differences in energy density between key prey items (e.g. herring or salmon vs. pollock or Atka mackerel) (see ‘All fish are not equal’ below). For example, a diet of pollock, because of its low energy density, means animals must consume large numbers of fish to meet their energy demands. Therefore, eating pollock makes it more difficult to make a living, not because there is something ‘wrong’ with pollock, but because it is a suboptimal food source compared with other prey species. Hence, when supply is limited or energy demands are high, the life history characteristics (survival or reproduction) of a segment of the population will be altered.

The prevalence of low-quality prey in the diet might result in population declines through increases in individual sea lion food requirements, decreases in prey availability (including changes in capture costs or prey predictability), or shifts in the composition of prey types available to sea lions in the local ecosystem. Alverson (1992) suggested that:

There indeed may be a nutritional deficiency, but it is more likely associated with the decline in abundance or availability (or both) of fatty fish resources that have much higher caloric value and perhaps other nutritional attributes not available in pollock and other low-fat species (p. 254).

The difference between this interpretation and the ‘pollock equals death’ variant of the nutrition stress hypothesis is the concept that in the ‘deleterious effects of low prey quality’ variant, a low-quality diet simply makes it more difficult, but not impossible, for animals to fulfil their optimal nutritional needs. Hence, only those individuals with the most difficulty meeting those demands are significantly affected by it. These could be young animals, with higher relative energy and nutritional requirements and poor foraging skills, or lactating (and possibly simultaneously pregnant) females with high absolute energy requirements and restricted foraging opportunities due to pup maintenance. However, a low quality diet would not equally affect all segments of a population, or all members of a particular subset.

In early research, there was a tendency for scientists to focus on starvation as the ultimate manifestation of nutritional stress. However, poor nutrition and low energy intake can result in a host of physiological effects that can ultimately impact life history parameters (either immediately or in the future), such as adverse body composition changes, inappropriate energy budgets, lower growth rates, deferred reproduction and various physiological disorders (explored further in the section ‘Evaluating the nutritional stress hypothesis’). In addition, given the adaptability of mammals, nutritional stress may reveal itself as an alternative viable life history strategy (e.g. pupping in alternate years – see Speculation on ultimate causes) rather than as a complete failure to survive or reproduce.

Variant III – insufficient prey quantity

In this scenario, nutritional stress arises from a lack of adequate prey (regardless of quality) on a local geographical and temporal scale. This variant may also be associated with an inability to compensate for past suboptimal conditions when times are good. ‘Sufficient prey’ can be broadly defined as the amount required for sea lions to fulfil their optimal energetic and nutritional requirements, and the effects of insufficient prey can either be immediate or impact future life history events. Prey quality enters into the equation only in the sense that animals must consume more low-quality than high-quality prey to attain equal nutritional or energetic intake (the required biomass is inversely proportional to quality). Changes in prey availability may result from changes in overall prey density (lowered carrying capacity or localized depletion) or from changes in oceanographic distribution (distance from the shelf or depth) that makes it more costly for sea lions to capture fish (thus reducing the net energy gain per ingested unit of biomass).

Variant IV – interaction between prey quantity and quality

This paradigm suggests that consuming low-quality prey has additional inherent detrimental effects when energy is limiting. When sea lions are not able to ingest sufficient prey to meet their energy requirements, the chemical nature of certain prey items may induce additional physiological effects on sea lions beyond those attributable directly to energy deficits that impact survival and/or reproduction. The nature of the differences in chemical composition between prey species is not specified in this variant, but characteristics of interest include lipid

and protein contents. Energy density may be another important factor if differences in the relationship between biomass and energy intake affect hormonal and behavioural attributes (e.g. hunger and satiation signals).

The results from studies in which the diet of pinnipeds in the laboratory is manipulated can be used to test these variants of the nutritional stress hypothesis. More specifically, the results can be used to answer one or more of the following questions:

1. If food intake is sufficient to meet energetic and nutritional needs, can sea lions maintain mass and health on a low-lipid diet? (Variant I and partly Variant II).
2. Is it difficult to maintain energy intake on a low-lipid diet? (Variant II).
3. Do factors such as age and season affect how sea lion health and condition change in response to temporal changes in energy? (Variant III).
4. If energy is limited, does prey quality affect health and condition? (Variant IV).

ALL FISH ARE NOT EQUAL

The theory that Steller sea lion population declines may be related to diet originally arose from several pieces of evidence. Firstly, it has been shown that the summer dietary diversity of females is statistically correlated to the rate of localized population decline (Merrick, Chumbley & Byrd, 1997). Sea lions from stable or increasing populations have a diverse prey base (including many types of forage fish), whereas those from the areas of greatest decline have more uniform diets dominated by either walleye pollock or Atka mackerel. Complicating this observation is the fact that, given the nature of key prey species, there is also an inverse correlation between the average energy density of the diet and the rate of population change (Winship & Trites, 2003). Further evidence for the potential role of diet derives from the suggestion that the diet of sea lions in the (declining) Western population may, historically, have been more similar to the current diet of the healthy, increasing Eastern population (a diversity of fatty forage fish; Alverson, 1992; Trites, Calkins & Winship, 2007).

The link between diet and sea lion population dynamics also rests on the observation that different key prey items for Steller sea lions may contain vastly divergent nutritional content. This was first elucidated by Alverson (1992), whose writings appear, in many respects, surprisingly progressive more than a decade later:

... the food 'energy value (kcal/g)' of pollock, cod, and sole is very low in comparison to herring, capelin, and salmon. Pollock, along with cod and flounders, have on average a relatively low fat content. It seems likely that the fatty species provide significantly greater gross energy and other nutritional requirements per-unit-weight of prey consumed than the gadoids and flounders (Alverson, 1992 p. 250).

Alverson's argument was based upon exceedingly limited data that, among other things, highlighted the differences in lipid and protein content of herring (*Chupea pallasii*, 12.8% lipid and 16.4% protein) and pollock (1.0% lipid and 18.9% protein). He notes that 'It is also apparent from Stansby (1976) (Table 5) that the oil content of potential prey may vary by area, season, etc.'

Alverson summarized the nutritional stress hypothesis as follows:

... what species are most likely to provide the nutrition needed to support and maintain a healthy Steller sea lion population? In this respect, it may well be that small forage fishes that display classic schooling behavior are easier to capture and are nutritionally superior. Steller sea lions may have flourished during periods of higher abundance of small fatty fishes and became increasingly distressed as they turned to pollock and other whitefish as their major food sources (Alverson, 1992 p. 249).

This statement highlights the importance of two aspects of prey 'quality': actual chemical composition and the cost of capture. Following the growing interest in the nutritional stress hypothesis, a number of researchers examined the proximate composition and energy content of different key Steller sea lion prey species (see references reviewed in Winship & Trites, 2003; Logerwell & Schaufler, 2005). In their review, Winship & Trites (2003) re-iterated that the average energy density of herring (6.19 kJ/g wet weight) was greater than that of pollock (3.85 kJ/g), and reported an intermediate value (4.34 kJ/g) for a smaller sample of Atka mackerel. There was a natural range for these values (herring 3.4–11.7; pollock 2.7–5.9 kJ/g) that could partly be explained by age, gender, location and season (reproductive phases), but overall there was clearly a substantial difference in the proximate composition of these species. Fritz & Hinckley (2005) updated the Winship & Trites (2003) data set from subsequently published studies and concluded that the range of energy densities for these prey species was greater than reported by Winship & Trites (2003). Unfortunately, they (figure 8 in Fritz & Hinckley, 2005) do not provide mean values or variance, but only graphically illustrate a range of potential values. They argue that, since there is substantial potential overlap between energy densities, it is inappropriate to label certain species as high- or low-energy. This is partly true – for instance a large gravid pollock may have a similar lipid and energy content to a spent herring. However, as the database of prey species continues to expand, it is evident that prey energy densities vary with size, location and season (Logerwell & Schaufler, 2005), but that within a given time period pollock almost always has a lower average energy or lipid density than herring, whereas Atka mackerel has moderate energy density (Vollenweider, 2004). This is particularly true for the size of prey consumed by sea lions (Sinclair & Zeppelin, 2002; Zeppelin *et al.*, 2004).

An expanded database of the proximate composition of prey species would be useful, but could not directly define the nutritional value of these items to individual sea lions. Many elements contribute to complex nutritional profiles (vitamins, essential fatty acids, etc), few of which have been adequately studied in otariids. Studies of prey species' composition and the effects of different prey types on sea lions tend to concentrate on differences in energy, lipid and protein content. This is partly due to the obvious differences in composition, the relative ease of measurement and the clearer understanding of the potential physiological impacts of these attributes. Alverson (1992) recognized that predicting the effects of different prey species on sea lion physiology went far beyond knowledge of basic proximate composition of the fish:

Nutritional support and energy requirements for marine mammals are much more complicated issues than just availability of fats, proteins, and carbohydrates in prey species, but there seems to be little specific information that addresses this for Steller sea lions (p. 250).

The most basic attribute of prey is its gross energy content, which can be determined directly through bomb calorimetry or indirectly through extrapolation from proximate composition analysis. However, this value does not necessarily reflect the biologically useful energy. Net energy content is a more relevant measure, and differs from gross energy content by the energy lost through the various processes of digestion (Lavigne *et al.*, 1982). This includes faecal energy loss (FE, often calculated in its inverse form, digestive efficiency DE), urinary energy loss (UE, often used to calculate metabolizable energy) and the heat increment of feeding (HIF; Anonymous, 1981). Although net energy and gross energy content are related, one cannot be predicted from the other unless the various costs of digestion (FE, UE and HIF) are known (Blaxter, 1989).

A series of studies with captive animals was carried out to quantify the biological (bioenergetic) value of different types of fish to Steller sea lions. Although previous studies had

examined changes in digestive efficiency in various pinnipeds for a variety of prey items (summarized in table 3, Rosen & Trites, 2000a), Rosen & Trites (2000a) published the first measures of DE in an otariid. They measured DE in juvenile Steller sea lions variously fed diets of herring, pollock, squid *Loligo opalescens* and farmed pink salmon *Oncorhynchus gorbuscha*. There were significant differences in DE between prey species, such that DE appeared to increase with energy density of the prey item. This suggests that Steller sea lions digest prey of high energy density more efficiently than prey of low energy density. However, overall DE values were high for all prey species (species' averages from 90.4 to 95.4%). This is consistent with results from other pinnipeds (table 4 in Lavigne *et al.*, 1982; table 3 in Rosen & Trites, 2000a). Dry matter digestibility (also called apparent assimilation efficiency) has also been studied in otariids (Fadely, Worthy & Costa, 1990; Fadely, Zeligs & Costa, 1994). This is a measure of the efficiency of biomass digestibility, and is neither equivalent to digestive efficiency (Rosen & Trites, 2000a) nor as bioenergetically relevant.

As noted by Lawson, Miller & Noseworthy (1997), the high digestive efficiency of pinnipeds is surprising, given their rapid passage rates (Helm, 1984; Krockenberger & Bryden, 1994; Goodman-Lowe, Atkinson & Carpenter, 1997). Trumble, Barboza & Castellini (2003) hypothesized that, as food intake increased to compensate for lower energy density, increased protein and lipid loads would decrease digestion efficiency. In studies in which pollock, herring and mixed diets were fed to captive harbour seals *Phoca vitulina*, their hypothesis of a trade-off between intake and digestion was not supported for protein. However, lipid digestibility of herring declined from 90 to 50% when lipid intake exceeded 60 g kg^{-0.75}/day. A follow-up study reported that a mixed diet of herring and pollock – which had moderate protein and lipid levels – had the greatest overall digestibility (Trumble & Castellini, 2005).

Another source of energy loss during digestion is the heat increment of feeding (HIF). HIF is the increase in metabolism resulting from both the mechanical and biochemical processes of digestion (Harris, 1966). HIF is not a fixed amount, and is at least partly dictated by the size and composition of the meal. In general, the energetic cost of processing food is lowest for lipid (4–15%) and carbohydrate (4–30%), and highest for protein (30–70%; Blaxter, 1989), and has been shown to increase curvilinearly with total ingested energy (Blaxter & Boyne, 1978). Studies on Steller sea lions confirmed that HIF (as a proportion of gross energy intake) increased with decreasing prey quality. HIF for 4 kg meals of squid (19.4%, Rosen & Trites, 1999) was higher than for equal sized meals of pollock (15.7%, Rosen & Trites, 2000b), which was greater than for similar meals of herring (12.4%, Rosen & Trites, 1997). There was also a significant effect of meal size, whereby the HIF from 4 kg herring meals was greater than that from 2 kg herring meals (12.4% vs. 9.9%, Rosen & Trites, 1997). A similar effect of meal size was reported for northern elephant seals *Mirounga angustirostris* (Barbour, 1993). No other researchers have investigated HIF in otariids, but comparative data are available from other marine mammals (see table 3 in Rosen & Trites, 1997).

The cumulative effect of these differences in the efficiency of digestive processes can lead to substantially different estimates of prey requirements compared with values calculated on the basis of gross energy content. For example, Rosen & Trites (2000b) compared estimates of gross energy content differences in pollock and herring with estimates based on net energy. They combined experimentally derived estimates of digestive efficiency, HIF and urinary energy loss (5%, Ashwell-Erickson & Elsner, 1981). They calculated that Steller sea lions would have to consume approximately 56% more pollock than herring to maintain an equal net energy intake, compared with estimates of 46% based on gross energy content. The difference in estimates may be even more substantial, given that sea lions that attempt to maintain net energy intake by increasing the quantity of the lower energy density prey must

absorb the additional HIF cost associated with larger meal sizes (Blaxter & Boyne, 1978; Webster, 1981; Rosen & Trites, 1997). Similarly, Trumble *et al.* (2003) report that the daily energy intake of harbour seals eating pollock *ad libitum* was 22–26% higher than that of those eating herring, and that no differences in growth resulted.

INDIRECT EXPERIMENTS

As fisheries researchers were conducting more complete analyses of sea lion prey, several experiments were being carried out that could be used to evaluate if captive pinnipeds consuming low-quality prey had difficulty maintaining body mass and/or lipid stores. These studies were not originally designed to address this issue specifically, but the results can be used on a *post hoc* basis to provide important clues (pertinent details of each experiment are given in Table 1). For example, in a study quantifying assimilation efficiencies of different prey, Fadely *et al.* (1994) reported that two subadult or adult California sea lions *Zalophus californianus* alternately fed pollock or herring over short periods (3–11 days) maintained similar rates of mass change by eating more pollock than herring.

In contrast, Kirsch, Iverson & Bowen (2000) investigated the effects of a change from a high-fat herring diet to a low-fat pollock diet on the body composition and blubber fatty acid patterns of five juvenile harp seals *Phoca groenlandica*. Their study was predominantly designed to test the effects of prey lipid content on the turnover of the fatty acid signature in the blubber layer. They found that the young seals lost lipid stores when switched from the herring to the pollock diet, and were unable to maintain previous high growth rates on the pollock diet despite feeding *ad libitum*. Unfortunately, because food intake could not be individually tracked, it was not possible to ascertain if the failure to maintain growth was the result of a decrease in gross energy intake, an inability to process the pollock adequately or both.

In another study on phocid seals, five adult harbour seals (7–20 years) were placed on a 4-week high-lipid (15.1% wet weight) herring diet, followed by 4 weeks on a low-lipid (3.6% wet weight) diet (Stanberry, 2003). Significant differences in changes in body mass (+8.4% vs. –2.4%) were found between the high- and low-lipid diets; there were no differences in body composition index (percent lipid content), although the author did not test for changes in absolute lipid or protein mass. The changes in body mass were deduced to have partly resulted from an insufficient increase in gross energy intake despite an *ad libitum* feeding regimen. In contrast, in a longer study of the digestive efficiencies of harbour seals, animals sufficiently increased their food intake when consuming pollock to maintain similar energy intakes and body mass compared with when they were consuming herring with a greater lipid and energy density (body composition was not measured, Trumble *et al.*, 2003).

Rosen & Trites (2000b) reported on a study designed to test their previous work on digestive efficiency (Rosen & Trites, 2000a) and heat increment of feeding (Rosen & Trites, 1997), and the resulting relationship between gross energy and net energy intakes in Steller sea lions. Six juvenile Steller sea lions were switched from an *ad libitum* herring-dominated (or pure herring) diet to a pollock diet for 11–24 days, and then switched back to a pure herring diet for 14 days (each animal completed multiple trials, separated by extended rests). The assumption of the experiment was that the sea lions would self-regulate their food intake to compensate for any changes in prey quality and/or net energy density. Hence, the study was of limited duration, and did not measure certain physiological parameters such as changes in lipid mass or realignment of energy budget. The main result is that, although the sea lions increased their ingested food mass slightly when consuming pollock, this increase was not statistically significant nor was it physiologically sufficient to offset the lower energy density

Table 1. Details of *ad libitum* or maintenance level feeding experiments that can be used to evaluate the nutritional stress hypothesis. Specifics shown include the energy density of the high- and low-energy prey (kJ/g wet weight), the ratio between these values, the number of animals used and whether the animals adequately adjusted food intake between diets to maintain similar growth rates. In the study by Rosen & Trites (2005) the animals were on a fixed food intake whereby the amount of food offered assured isocaloric intake between prey groups

Species	Age	High energy	Low energy	Ratio	No. of animals	Trial length (days)	Adjustment	Source
California sea lion	Subadult, adult	6.00	4.40–4.80	1.30	2	3–11	Yes	Fadely <i>et al.</i> , 1994
Harp seal	1–3 years	7.8	4.97	1.57	5	30	No	Kirsch <i>et al.</i> , 2000
Steller sea lion	0.9–4.5 years	7.58–6.40	4.54–4.72	1.51	6	11–24	No	Rosen & Trites, 2000b
Harbour seal	7–20 years	8.82	5.47	1.61	5	28	No	Stanberry, 2003
Harbour seal	3–23 years	7.70	4.92	1.57	8	90	Yes	Trumble <i>et al.</i> , 2003
Steller sea lion	2.5–3.0 years	9.57	5.36–5.81	1.68	3	42	Yes	Rosen & Trites, 2005
Steller sea lion	6–9 years	5.76	4.65	1.23	3	120	Yes	Atkinson <i>et al.</i> , 2008a

of the pollock over the period of the study. As a result, the sea lions consuming pollock had significant losses in body mass compared with that during the control or recovery (herring) periods. However, it was unclear whether this was due to some innate physiological restriction (digestive capacity or inability to ascertain and respond to physiological changes), a by-product of the artificial environment (inadequate motivation to consume additional pollock) or the result of the limited duration of the diet regimes.

As previously noted, this group of studies were not specifically designed to test the potential physiological effects of diet quality, and so have inherent limitations in experimental design and data analysis. However, the results of these studies seem to indicate that pinnipeds cannot overcome differences in prey quality simply via increased digestive efficiency. In fact, animals appear to be less efficient at digesting low-quality prey (although high lipid intake may also cause inefficiencies; Trumble & Castellini, 2005) than at digesting higher-quality prey. The results of these studies also indicate that pinnipeds may not sufficiently alter food intake to overcome differences in prey quality. The *ad hoc* nature of these studies makes it difficult to evaluate whether the inconsistent results between studies were related to age, season, experimental design or animal handling. What was clearly required were controlled, laboratory experiments on sea lions, explicitly designed to evaluate these aspects of the nutritional stress hypothesis.

DIRECT EXPERIMENTAL EVIDENCE

Experiments that were specifically designed to evaluate the effect of different prey on sea lion physiology were formulated around two divergent approaches. In one set of studies, short-term switches took place between single prey item diets, fed on a controlled intake basis. In other studies, long-term, *ad libitum* intake of mixed-item diets was used. Each of these approaches has inherent strengths and weaknesses.

Ad libitum feeding purports to represent a more 'natural' situation where the animals are not restricted by 'prey availability', but intake levels can be affected by handler bias and individual animal food preferences. This approach also makes it difficult to separate the effects of energy intake and diet quality. Controlled feeding levels serve to separate out the effects of prey quality and intake levels, but place unnatural restrictions on the animals' ability to make dietary adjustments. Long-term, mixed-item diets aim to mimic parallel changes in prey availability in the environment, and can reveal subtle physiological changes that would develop over extended periods. Short-term, single prey item manipulations may be used to mimic the effects of short-term local changes in prey availability, and/or may magnify the potential effects of changes in diet composition to deal with low sample sizes. Both approaches have been used in laboratory studies of the effects of prey quality on sea lion physiology, and the combined results provide different – but not incompatible – perspectives.

Atkinson *et al.* (2008a) rotated three subadult or adult Steller sea lions between three mixed-item diets designed to mimic various diets described in the wild. Treatments were designed to reflect diets of wild Steller sea lions around Kodiak, Alaska, prior to and following the beginning of the documented decline in that area, and the diet of wild Steller sea lions in southeast Alaska where the population was increasing. The diets contained four to seven different prey species or groups, although the energy density of the diets only differed by a maximum of 23%. The sea lions were fed *ad libitum* (within training requirements) and maintained on a single diet for 4 months, and each animal experienced each diet during the three experimental 'seasons'. Atkinson *et al.* (2008a) reported that animals continued to grow on all three diets, and changes in body mass did not differ significantly between the three diet regimes or between seasons. This was largely achieved by the animals self-regulating their

food intake; gross energy intake was not significantly different between diets. Although food biomass intake was significantly different between diets, there was also a significant interaction between diet and season in both biomass and caloric intakes. Mean change in relative body condition (lipid mass as a proportion of total mass) was not significantly different among diets or seasons; however, the interactions between diet and season tended toward significance. The authors noted that the presence of a single large male greatly affected the results.

Rosen & Trites (2005) used controlled food-intake protocols in a series of experiments designed to determine if there was something inherently 'inadequate' in low-lipid prey, once differences in energy density were controlled. In one experiment three juvenile Steller sea lions were alternately switched between isocaloric diets of herring and pollock (the animals were on each diet for 42 days). In contrast to the Atkinson *et al.* (2008a) study, food intake for both diets was set at a constant, isocaloric level, estimated to be near the animals' maintenance energy levels. The researchers reported no significant effects of prey type on body mass, lipid mass or overall body composition. The lack of statistical effect of prey type occurred despite the fact that, while the animals gained the same amount of lean tissues on both 'maintenance' diets, they concurrently lost 3.6 kg of lipid reserves on pollock but only 0.9 kg of lipids on herring. The statistical results may partly be the result of small sample size, but they are also due to the tremendous effect of season on changes in body composition that occurred largely driven by the male sea lion who, as in the Atkinson *et al.* (2008a) study, had the greatest growth rate. This individual put on a tremendous amount of mass solely in the form of lean tissue in the spring while on the herring diet. In the summer, while consuming pollock, he continued to put on lean tissue at the expense of sacrificing lipid mass stores. This may have been an artefact of the fact that food intake was held constant across seasons, despite the fact that energy requirements were higher in the summer and the level of food available may not have met the sea lions' energy demands for somatic growth.

In another experiment detailed in Rosen & Trites (2005), the researchers wanted to determine if the lipid composition of pollock might differentially affect sea lion physiology, taking into account differences in lipid concentration (and energy density). They 'supplemented' pollock by inserting capsules of non-processed pollock oil, so that it attained approximately the same lipid content as herring. This design also served to control for the potential effects of fish mass intake, as the resulting prey items were now isocaloric. Seven female Steller sea lions were divided into two treatment groups, and fed either herring or 'fatty pollock' for 34 days.

Rosen & Trites (2005) reported that, as expected for isocaloric diets, there were no significant differences in changes in total body mass between trials when the sea lions consumed herring or fatty pollock. However, there were significant differences in changes in body composition during the trials. The sea lions lost 2.7 ± 0.9 kg lipids while consuming fatty pollock, but gained 5.2 ± 2.7 kg lipids while consuming herring. More surprisingly, the herring-fed sea lions gained body lipids at the expense of an equal amount of lean tissues, whereas lean tissue mass in the fatty pollock-fed group stayed constant. This translated into a decrease in relative body composition (ratio of lipid to total body mass, $-2.2 \pm 0.7\%$) on fatty pollock diets, and an increase on herring diets ($3.5 \pm 1.5\%$).

The different patterns of tissue growth and catabolism between the fatty pollock vs. herring study and the pure pollock vs. herring study may be due to the fact that the fatty pollock was artificially supplemented and may not have accurately mimicked natural high-lipid pollock. However, a comparison with other studies also strongly suggests that season played an important role in how animals reacted to different types of prey items. In retrospect, this may seem obvious. Pinnipeds, like many mammals, have highly seasonal life histories that require

seasonal changes in energy budgets and bioenergetic priorities. Allen (2009) synthesized the offset seasonal cycles in both body mass and food intake in captive Steller sea lions. Therefore, it is not surprising that their requirements and/or metabolic capacity for processing differing levels of lipids and proteins also vary seasonally. Although past studies either ignored the effects of season or were designed to mitigate potential effects, the combined effects of season and level of energy intake were specifically investigated in a series of subsequent studies (see further discussion).

Overall, neither Atkinson *et al.* (2008a) nor Rosen & Trites (2005) provided compelling proof of any inherent differences in maintaining body mass or lipid mass due to prey quality under conditions when sea lions could ingest sufficient food to meet their energy requirements. However, Rosen & Trites (2005) did suggest that prey quality might differentially affect physiology and health when energy intake was insufficient to cover 'optimal' energetic costs (because of either decreased intake or increased energy budget demands). This led to a series of experiments in which the potential for differential effects of prey composition on sea lion health under suboptimal bioenergetic conditions was specifically addressed.

THE COMPLICATION OF RESTRICTION

While much of the focus of early diet manipulations had been on pollock, Rosen & Trites (2005) also conducted a study of the effects of Atka mackerel on Steller sea lion health. Atka mackerel is a dominant prey among Steller sea lions in the western Aleutians, and has an average energy density and lipid content intermediate between those of herring and pollock (Logerwell & Schaufler, 2005). The aim was to investigate if there was an additive effect of prey quality on the physiological consequences of restricted energy intake. The Atka mackerel used had only 48% of the lipid content and 67% of the energy density of the herring. Four sea lions were switched from an *ad libitum* herring diet to isocaloric, restricted diets of either Atka mackerel or herring for 29 days (each sea lion completed trials with each prey type). The level of energy restriction was set so that the sea lions lost an average of 10.4% of their initial body mass. As predicted for isocaloric diets, there was no difference in body mass loss between trials when sea lions were consuming restricted levels of either Atka mackerel or herring. However, more of the total mass loss was derived from decreases in lipid stores when the animals were consuming Atka mackerel than when they were eating herring (63.6% vs. 40.3%). There also appeared to be a seasonal component overlying this trend, although the study was only conducted in autumn and winter.

In a subsequent study (Kumagai, Rosen & Trites, 2006) the combined effects of food composition and season were tested during short (9 days) periods of more intense food restriction in seven juvenile Steller sea lions. The sea lions were switched from an *ad libitum* herring diet to restricted, isocaloric diets of either pollock or herring. Each sea lion was given alternative restricted diets during four successive seasons. Given the same level of restricted energy intake, the rate of body mass loss was significantly higher during winter (1.6 kg/day) than during summer (1.2 kg/day). These differences were also mirrored by greater increases in cortisol levels (a stress hormone) after the winter restriction (Rosen & Kumagai, 2008). Diet did not affect the amount of mass lost (as predicted for isocaloric diets) but a significant season x diet interaction was a source of variation in mass loss. For most seasons, the majority of the body mass that was lost when eating pollock derived from decreases in lipid mass, whereas a greater proportion of the mass lost when eating herring derived from decreases in lean tissue. However, the pattern was reversed in the summer. Intensely restricted energy intake may be more detrimental to Steller sea lions in the winter months, and the type of prey consumed may have seasonal-specific effects on body composition.

CAPACITY FOR COMPENSATION AND RECOVERY

The potential effects of specific types of restricted food intake at certain times of the year have been investigated in several studies on sea lions in the laboratory. However, how applicable are such scenarios to wild sea lions? Specifically, might the failure of sea lions in captivity to increase food intake on different diets sufficiently to maintain body mass and condition be a by-product of their artificially predictable access to food? In theory, when faced with low-energy prey, sea lions in the wild should simply consume more food. This strategy should also apply when animals are faced with periodic disruptions in their food supply: they should simply consume more prey when food again becomes available, to make up for previous energy deficits, regardless of the quality of the prey itself.

However, animals are inherently limited in their ability to increase their food intake by a finite digestive capacity (Weiner, 1992). Rosen & Trites (2004) tested the ability of sea lions to alter their food intake in response to short-term changes in prey quality and availability. They found that sea lions quickly and accurately altered their food intake to maintain a constant average energy intake when either prey quality (herring vs. capelin) or availability (daily vs. alternating days) was altered. For example, when switched from herring to capelin, their food biomass intake increased 89%, which was almost exactly what was predicted by differences in energy content. However, it became apparent that the capacity of the young sea lions to increase their daily food intake was quickly reached at a level equal to ~15–20% of their own body mass. Remarkably, this amount of daily food intake is approximately equal to the estimated daily intake required by wild sea lions to fulfil their bioenergetic needs on known, lower-quality diets (Winship, Trites & Rosen, 2002). Therefore, it was quite feasible that young sea lions in the wild – with, compared with adults, their higher energetic demands and lower foraging capabilities – would have difficulty consuming and processing sufficient prey following a period of food restriction, when required food biomass would be even greater to overcome the previously induced energy deficit. This also highlights the importance of prey predictability in the natural environment (Malavear, 2002; Gende & Sigler, 2006): ‘missed’ feeding days necessitate increased food intake on subsequent days that may be beyond the animals’ physiological capacity.

Prey quality during the period of food restriction and the ability of the sea lions to recover from such a period was the subject of a subsequent study (Jeanniard du Dot, Rosen & Trites, 2008, 2009b; Jeanniard du Dot *et al.*, 2009a). Eight sea lions were first put on a 28-day restricted diet of either herring or pollock, and then monitored through a 28-day controlled recovery period during which they were given the same amount of herring they ate during an *ad libitum*, pre-restriction period. Seasonal changes in body composition, hormone levels and the responses of the animals’ energy budgets to the restriction and re-feeding were monitored four times per year. Overall, the sea lions seemed to make seasonally appropriate changes in their body composition and energy budgets (such as by increasing foraging activity during summer when fish are naturally abundant and by decreasing thermoregulation capacity in summer when waters are warmer) while consuming restricted levels of herring, but not while consuming pollock (Jeanniard du Dot *et al.*, 2008, 2009b). In addition, when given increased amounts of herring during the controlled re-feeding phase, the capacity of both groups to compensate for the previous mass loss was found to depend on season and was independent of previous diet (Jeanniard du Dot *et al.*, 2008). All of the sea lions increased their rates of mass gain and returned to their pre-experimental weight during winter, but not during summer. This suggests that, although food intake was sufficient to promote recovery in winter, some digestive or bioenergetic constraint precluded converting food into biomass in summer. Therefore, although animals may suffer greater mass loss in the winter than in the

summer under some conditions of nutritional stress (Kumagai *et al.*, 2006), some intrinsic energetic plasticity related to seasonal adaptation to the environment may render winter an easier period to recover from this type of nutritional stress.

EVALUATING THE NUTRITIONAL STRESS HYPOTHESIS

Question 1: If food intake is sufficient to meet energetic and nutritional needs, can sea lions maintain mass and health on a low-lipid diet?

YES. When the food intake of sea lions is controlled so that they are obtaining identical net energy through different quality prey items, there is no apparent effect on body mass or composition as long as energy intake is sufficient to meet their energy requirements (Rosen & Trites, 2005). The results of *ad libitum* feeding studies on captive pinnipeds indicate that they have the capability to alter food intake in response to changes in prey energy density. Several studies have demonstrated that pinnipeds can maintain body mass by increasing food mass intake to provide sufficient energy intake (Trumble *et al.*, 2003; Atkinson *et al.*, 2008a). However, this capacity to adjust food intake adequately has not been universal (Kirsch *et al.*, 2000; Rosen & Trites, 2000b; Stanberry, 2003). The reasons for these discrepancies between experimental results are unclear. However, they should not be simply dismissed as ‘dissimilarity between protocols’, but rather the results should be used as a comparative data set to further our understanding of the effects of prey quality. For example, the ability of animals to adjust food intake levels sufficiently might be related to the length of time that animals were given to adjust to different diets. Although there is a general trend for animals to adjust food intake adequately during studies with longer or less numerous diet switches (Table 1) other studies demonstrate an exceedingly rapid alteration in food intake (Rosen & Trites, 2004) and digestive efficiency (Trumble *et al.*, 2003) in response to changes in prey quality.

Other factors to consider include the age of the subjects and differences in energy density of the diets. However, both of these factors relate to the question of the difficulties in ingesting sufficient prey, and are addressed in the next section. On the whole, there appears to be no evidence that a low-quality diet differentially affects sea lion mass or body condition if food intake is increased to maintain energy intake. However, care should be taken in evaluating sea lion health solely on the basis of body mass or composition. There are studies that indicate a low-lipid diet in pinnipeds is associated with other disorders including anaemia (Thompson *et al.*, 1997) and vitamin deficiency (Mazzaro *et al.*, 2003).

It is also critical to understand that testing if sea lions can thrive on a pollock-dominated diet is not the same as testing if a pollock-dominated diet can cause problems. The extreme interpretation of the nutritional stress hypothesis – wherein eating pollock will, in itself, cause health problems – is clearly not supported by the available evidence. Yet, conditions that induce nutritional stress rarely affect all members of a population equally. Classically, such episodes are most likely to impact members of the population with the highest nutritional requirements and those least able to adapt to suboptimal conditions behaviourally and physiologically.

Question 2: Is it difficult to maintain energy intake on a low-lipid diet?

YES. The conclusion that low-quality prey does not adversely affect sea lion health if food intake is not limited (Question 1) is often misinterpreted to suggest that food quality is never a critical factor. In fact, other ecological and physiological factors may effectively limit food intake to the point at which it is not possible for sea lions to obtain and process sufficient prey. For example, increasing energy requirements, decreasing prey quality, and increased capture costs each result in increasing required ingested prey biomass. Yet the amount of prey

that an animal can capture and process over a set time period is limited by numerous factors, including prey patch dynamics, available foraging time and digestive capacity.

Captive studies have shed light on several of these parameters, including the fact that the biochemical differences between prey species are biologically relevant – and often magnified – for Steller sea lions. Numerous studies have demonstrated that pinnipeds cannot overcome differences in prey quality by increasing the efficiency of digestion. Rather, lower quality prey generally has a higher relative cost of digestion (via faecal energy loss and heat increment of feeding; Rosen & Trites, 1997, 1999, 2000a,b), although too much high-lipid prey may also decrease efficiency (Trumble *et al.*, 2003). Larger or more frequent meals may also lead to decreased digestive efficiencies (Barbour, 1993; Rosen & Trites, 1997; Trumble *et al.*, 2003). Although it is obviously not a concern in captive studies, the cost and efficiency of capture cannot be ignored as this affects both net energy gain and the potential limiting effect of foraging time.

Captive studies have also demonstrated the concept that food intake is physiologically limited. Sea lions show a remarkable capacity for quickly adjusting food intake to maintain energy intake levels when faced with changes in prey quality or feeding frequency (Rosen & Trites, 2004; Atkinson *et al.*, 2008a). However, this capacity is not infinite (Rosen & Trites, 2004) nor universal among studies. These results may reflect the fact that digestive capacity forms a real physiological limit to the amount of prey that can be consumed (Karasov & Diamond, 1988; Weiner, 1992; Hilton *et al.*, 1999; Rosen & Trites, 2004). As previously noted, the amount of food required (and hence the chance of approaching a physiological capacity) depends upon both energy requirements and prey quality. Therefore, situations in which energy or nutritional requirements are highest are most likely to lead to an inability to meet those requirements with low quality prey. The range of experimental protocols used in captive pinniped feeding studies can provide insight into some of these limitations.

For example, the differences in the experimental results might reflect the greater inherent difficulty for younger animals to increase sufficiently the amount of low quality prey ingested to maintain adequate levels of nutrition (Table 1; see modelled effects in Malavear, 2002). Since younger animals have higher relative energy demands without commensurate increases in digestive capacity (Kleiber, 1975; Calder, 1984; Schmidt-Nielsen, 1984) they are more likely than adults to become physically satiated before they reach their required level of food intake when consuming low energy prey. For example, the Steller sea lions in the study by Rosen & Trites (2000b; 0.9–4.5 years) were substantially younger than those studied by Atkinson *et al.* (2008a; 6–9 years). However, it should also be noted that in the studies by Stanberry (2003) and Trumble *et al.* (2003), many of the same harbour seals, comprising a wide range of ages, were used.

Energy demands – and therefore food biomass requirements – also change on a seasonal basis. It has been demonstrated in numerous studies that pinnipeds have seasonal food intake requirements (that may or may not match seasonal energy requirements; Rosen & Renouf, 1998; Allen, 2009). In most captive feeding studies, repeated measures are used to control for seasonal effects. However, in these same studies season \times diet interactions occur; diet quality seems to affect body composition differently during periods of high and low growth (particularly in large males). This may be a reflection of a nutritional inadequacy during periods of highest energy or nutritional demand.

Another noticeable variation between captive experiments is the net difference in energy content between the ‘high-quality’ and ‘low-quality’ treatments (Table 1). For example, in the Atkinson *et al.* (2008a) study, the sea lions would have to consume 23% more fish on the

lowest quality diet to achieve the same gross energy intake as on the highest quality diet. In contrast, other researchers (Kirsch *et al.*, 2000; Rosen & Trites, 2000b; Stanberry, 2003) used prey quality differences that required animals to consume 51–61% more fish while on the low-quality diet than on the high-quality diet (as did the study by Trumble *et al.*, 2003 where animals did adequately compensate). However, the relatively low difference in energy density of the diets used in the Atkinson *et al.* study was partly the result of a lower ‘high-quality’ diet rather than a higher ‘low-quality’ diet. Regardless, the difference in required fish biomass – and the interaction with energy requirements – probably affected the outcomes of the various captive feeding studies.

Question 3: Do factors such as age and season affect how sea lion health and condition change in response to temporal limitations in energy?

YES. There is no particular need for captive pinniped studies to tell us that nutritional stress adversely affects sea lion condition and health. Nutritional stress is, by definition:

... a situation in which an animal's nutrient demands exceed its nutrient ingestion, resulting in net catabolism in body tissues to the extent that one or more vital physiological functions are impaired. Any depletion of reserves short of this result does not reflect ‘stress’ (. . .), but merely the functioning of an animal within its limits of tolerance (King & Murphy, 1985).

By the laws of the conservation of matter, any change in energy intake necessitates physiological and behavioural adjustments to compensate for the deficit. There is a range of options that individuals can employ to minimize the effects of decreased energy intake. However, at some point, the responses to the energy deficit result in changes in reproductive and survival parameters, particularly if that restriction is unexpected or beyond the scope of normal experience. Studies on captive sea lions have been useful to define the range of physiological options utilized and to evaluate potential bioindicators of nutritional stress in captive sea lions’ wild counterparts.

Changes in body mass are an expected result of energy intake deficits. In fact, the hypodermal blubber layer of pinnipeds serves as a primary energy reserve, particularly for seasonally predictable periods of low food intake (e.g. during moulting or breeding periods). Just as the energy budgets of pinnipeds are seasonal, so are the responses of animals to experimental food restrictions. In addition, captive studies indicate that the seasonal response to nutritional stress depends also on the nature of the restriction. For example, in a pair of studies of seasonal differences in response to a similar total mass loss (~10% of initial body mass), the loss was induced by different intensities of food restriction. Although the rates of mass loss in captive Steller sea lions during moderate (28 days) restrictions did not differ by season (summer vs. winter, Jeanniard du Dot *et al.*, 2008), severe, short-term (9 days) shortages in winter seemed to induce the greatest rates of mass loss, accompanied by the greatest responses in stress hormones (Kumagai *et al.*, 2006; Rosen & Kumagai, 2008). Juvenile Steller sea lions fasted for 7–14 days had significantly greater rates of mass loss than subadults during the breeding season (Rea, Rosen & Trites, 2007), but there were no such age-related differences during the non-breeding season. Moreover, biochemical evidence suggests these lack of differences in mass loss during the non-breeding season were due to the ability of juvenile animals to start protein-sparing sooner (perhaps due to higher initial lipid mass) and maintain it for longer than the subadult sea lions (Rea *et al.*, 2009).

Although the patterns of mass loss during restriction may be important, the seasonal ability of individuals to recover from such episodes is also critical. Following food restrictions in the winter, Steller sea lions exhibit significant growth (compensatory growth) on what was previously ‘maintenance level’ food intake (Jeanniard du Dot *et al.*, 2008). However, in the

summer months, they appear less able to recover from similar episodes of food restriction without a large influx of food that may be required to 'kick-start' the physiological processes. Therefore, it is important to realize that the definition of a 'critical' period depends on whether one is more concerned with the period of restriction itself or with the ability of an animal to recover from that restriction.

The source of mass loss during periods of nutritional stress must also be considered. During both moderate and intense restrictions, sea lions tended to spare more lipids in the winter than in the summer (although this relationship was affected by the type of prey they were consuming – see the next section; Kumagai *et al.*, 2006; Jeanniard du Dot *et al.*, 2008). It is believed that lipid stores are primarily catabolized as an energy source by pinnipeds during nutritional stress, except for a small amount of protein required for gluconeogenesis (Castellini & Rea, 1992), due to the higher energy density of lipid and the structural importance of proteins. Although the relative energy densities of lipid and protein make the projected mass loss marginally less lopsided, this pattern seems to hold for phocid seals and fasting Steller sea lions (Rea *et al.*, 2007). The source of mass loss has noteworthy impacts on the physiological consequences of nutritional stress, since catabolism of each type of tissue has its own risks and consequences. Lipid reserves can only be depleted so far without impinging on thermoregulatory abilities, which can lead to an increasing spiral of escalating maintenance costs (Rosen, Winship & Hoopes, 2007). It should not be surprising then that sea lions conserved lipid stores more in the winter when the thermoregulatory consequences of depletion were more acute, than in the summer. Insufficient lipid reserves ultimately lead to catabolism of non-lipid sources, which provide less energy (and ultimately have a greater direct health effect), thereby requiring greater rates of mass loss. Rea *et al.* (2007) reported that 85% of the variation in rates of mass loss in fasting Steller sea lions could be explained by initial body lipid stores. Therefore, variation in body condition leading up to a nutritional stress event also plays a role in the subsequent effect of the episode, whether this variation is due to natural changes or previous environmental conditions.

For these reasons, body condition – lipid mass as a percentage of total body mass – has been used as an indicator of health and nutritional status in pinniped field studies. However, experimental food restrictions with Steller sea lions have shown that a significant proportion of the mass loss also derives from non-lipid sources, effectively blunting the extent of changes in body condition. For example, Rosen & Trites (2005) report that relative body condition in Steller sea lions decreased only 3.7% during periods of imposed nutritional stress, despite a 10.4% decrease in body mass (a smaller change in body composition than that due to natural seasonal variation). Similar changes in body condition are reported by Kumagai *et al.* (2006) and Jeanniard du Dot *et al.* (2008), with the additional complication of interactions with season and prey type (see the next section). Such responses impact scientists' ability to detect nutritional stress through measures of relative body composition.

Nutritional stress can also be detected through blood haematology and biochemistry. Rea, Rosen & Trites (2000) demonstrated that traditional markers [blood urea nitrogen (BUN), plasma ketone bodies, non-esterified fatty acids] can be used to evaluate the nutritional status of fasted animals. However, the complex reaction of specific bioindicators may be dependent upon species, season, age and the type of restriction, thereby limiting their effectiveness. For example, BUN levels are a product of both internal protein catabolism and food protein intake and are also affected by season and age (Jeanniard du Dot, 2007; Rosen & Kumagai, 2008; Rea *et al.*, 2009). An alternative approach is to develop multi-parameter indices that can be validated through data from captive pinnipeds subject to known nutritional stresses (e.g. Trumble *et al.*, 2006).

Question 4: If energy is limited, does prey quality affect health and condition?

YES. Nutritional stress results when an animal receives insufficient materials from its food supply. The most basic of these requirements is energy, and the potential of sea lions receiving inadequate energy from their prey has been a central focus of many scientific studies. As well as varying in energy, key prey species may differ in terms of a number of other parameters, including lipid, protein and essential fatty acid content. Previously described studies have demonstrated that sea lions appear to be able, under optimal conditions, to fulfil all of their nutritional requirements while consuming prey of different qualities. However, when prey intake is inadequate, the animals may suffer the consequences of specific unfulfilled energetic requirements in addition to the effects of decreased energy intake.

The most apparent differences in the proximate composition of key experimental prey items are lipid and protein content. Given the perceived importance of the sea lions' hypodermal blubber layer, most researchers have concentrated on the effects of decreased lipid intake, but other potential nutritional difficulties – such as increased or decreased protein intake – should not be discounted (Zhao, Castellini & Schell, 2006).

Studies that use controlled, restricted diet regimes allow the comparison of isocaloric diets to evaluate whether prey quality has additional impacts on sea lion health and condition beyond those imposed by restricted energy intake (e.g. Rosen & Trites, 2005; Kumagai *et al.*, 2006; Jeanniard du Dot, 2007). The cumulative results of these studies suggest that there is an additional effect of prey quality, but that the specific consequences vary by season and with the intensity of the restriction.

For example, during episodes of intense food restriction, sea lions fed pollock lost a greater portion of their mass from body fat than those fed herring within each season (Kumagai *et al.*, 2006). The only exception was the herring-fed group in summer that lost body mass exclusively from body fat. The catabolism of lipid stores in the herring-fed group was sufficient to permit critical lean tissue growth during periods of reduced energy intake. In contrast, during trials in which a more moderate, longer restriction was imposed, sea lions consuming restricted levels of herring lost more lipid mass than sea lions consuming pollock in both winter and summer (Jeanniard du Dot *et al.*, 2008). However, in a pattern similar to that from previous rapid restriction trials (Kumagai *et al.*, 2006), the high level of lipid catabolism in the summer herring-fed group was sufficient to permit critical lean tissue growth. In the winter, the sea lions consuming pollock lost almost all of their body mass from body protein.

Prey quality can have other bioenergetic consequences. As detailed earlier, Jeanniard du Dot *et al.* (2009b) found that sea lions consuming herring appeared to make seasonally appropriate adjustments to food restriction, whereas those consuming pollock appeared to make no such bioenergetic optimizations. Another factor that emerged from captive feeding studies is the physiological effects of the discord between energetic and physical satiation induced by prey with low energy densities. When faced with decreased food intake, free-ranging animals can either increase activity to increase foraging success (foraging response) or decrease metabolic expenditure, including by decreasing activity levels and metabolic depression (the controlled decrease in resting metabolic rate, the so-called fasting response; Guppy & Withers, 1999). This latter response serves to decrease the potential energy deficit by decreasing energy expenditure, thereby decreasing rates of mass loss (and postponing eventual death). Captive fasting Steller sea lions clearly demonstrated metabolic depression, with animals decreasing their resting metabolic rate by up to 30% (Rosen & Trites, 2002). However, the results from studies of animals on restricted diets are more complex. Sea lions consuming energetically insufficient, low-energy prey (pollock or squid) also demonstrated

significant metabolic depression (Rosen & Trites, 1999, 2000b). However, sea lions eating restricted levels of high-energy herring appeared to exhibit a foraging response, with increased activity levels and resting metabolic rates (Rosen & Trites, 2002).

As noted by Jeanniard du Dot *et al.* (2009b), the 'correct' response is probably dependent upon what is most appropriate for the seasonal conditions. In summer (when most of the studies were undertaken), a foraging response would be more beneficial, given the high prey availability in the wild. In winter, a fasting response would be more beneficial, as decreased prey availability and quality make increased foraging efforts less effective. Certainly this seasonal trend has been consistent across all captive sea lion studies in which restricted diets of herring have been used. However, in trials with low-energy density prey, there has been either a lack of seasonal response or a fasting response in summer months. The difference may be due to the fact that, when sea lions consume low levels of energy from prey such as squid and pollock, the ingested food biomass remains high. This may lead to conflicting signals, whereby animals feel physically satiated (e.g. due to stomach distension) but have not yet achieved energetic satiation (Rosen & Trites, 2002).

Hence, the overall result of feeding experiments on captive sea lions suggest that prey quality has additional physiological consequences during episodes of restricted energy intake. The differences in response are likely to be the result of differences in both the intake of key nutritional components and the ingested biomass. However, the exact nature of the physiological responses differs according to season and level of restriction.

SPECULATION ON ULTIMATE CAUSES

Experiments with captive pinnipeds are designed to investigate the link between different types of imposed nutritional scenarios on the physiology of individual animals. It is difficult to carry out studies on captive animals that can directly link nutritional profiles to changes in reproduction or survival, but it is appropriate to speculate on how episodes of nutritional stress may ultimately affect these key life history parameters. Some scientists have suggested that, although nutritional stress may have been a major factor causing the initial decline of Steller sea lions, it is not currently a factor in their continued decline or lack of recovery (see Anonymous, 2003). This hypothesis is based largely on two points.

1. Population models suggest that earlier declines were due to decreased juvenile survival (York, 1994), whereas current population trends appear to be driven by decreased reproductive rates (Holmes *et al.*, 2007).
2. There was a significant change in population trajectories, from an initial steep decline until ~1985, to a more gradual decline or stabilization after this point.

However, other scientists have argued that neither of these observations is inconsistent with long-term nutritional stress (Pitcher, Calkins & Pendleton, 1998; Holmes *et al.*, 2007). There is evidence of nutritional stress affecting reproducing females in the 1980s (during the period of initial decline) as well as in the 1990s (when the decline rate slowed), as evidenced by a chronic decline in reproductive rates over almost 30 years (Holmes *et al.*, 2007) that may be the cumulative result of the long-term nutritional stress. Alternatively, the apparent 'shift' in the main dynamics affecting population levels may have resulted from increases in juvenile survival due to decreased incidental (bycatch) and intentional (hunting, shooting) takes (Loughlin & York, 2000).

Although nutritional stress may have led to decreasing fecundity, it may have also played a role in effectively increasing juvenile survival. Historically, Steller sea lions weaned their pups at ~9–12 months in anticipation of an annual birth (Pitcher & Calkins, 1981). These newly weaned pups were relatively naïve foragers with poor diving capabilities (Richmond,

Burns & Rea, 2006). Therefore, if foraging opportunities were diminished – either due to decreased food availability or a requirement to catch more, low-quality prey – a certain additional portion of the population would not thrive. The mathematics of population dynamics requires only a relatively small additional portion of the juvenile population failing to survive to reproductive age to drive the observed population decline (York, 1994; Loughlin & York, 2000).

However, recent studies have suggested that some females in the population now do not produce a pup every year, and therefore continue to nurse their pup for extended periods (2 years and beyond; Trites *et al.*, 2006). This change in fecundity might result from mothers who, being unable to maintain body condition due to nutritional restrictions (due to decreased energy intake and/or increased lactational demands from young who need additional supplementation), are not giving birth every year, due to either spontaneous abortions or nutrition-related anoestrous. This would lead to the weaning of older, larger pups that are more experienced and physically capable of foraging (and therefore have a higher juvenile survival rate) and a concomitant decrease in natality rates.

CONCLUSION

The evidence from captive pinniped studies suggests that diet quality does not affect body mass and condition if intake is sufficient to meet energy demands. While sea lions possess the ability to alter food intake in response to prey quality and availability, sufficient intake may be limited by ecological factors (prey availability or distribution) and/or physiological factors (increased energy demands or digestive capacity). Under conditions of inadequate food intake, the overall impacts of nutritional restriction are dependent upon season, age and prey quality. Younger animals, with their increased energy requirements and more limited digestive capacities, are less able to increase food intake sufficiently when consuming low quality prey to obtain sufficient nutritional intake. Adults are less limited by digestive capacity, but their ability to make seasonally appropriate adjustments to their energy budget (which minimize the bioenergetic consequences of food restriction) is impeded when consuming low-quality prey. Additionally, it appears that, although severe food restriction in the winter may induce greater rates of mass loss and physiological stress than in the summer, sea lions have greater difficulty recovering from more moderate restrictions in the summer months. Although captive studies cannot be used to identify the source of nutritional stress, they have been instrumental in validating the potential physiological effects of specific ecological scenarios.

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