

Size Selectivity in Marine Mammal Diets as a Guide to Evolutionarily Enlightened Fisheries Management

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Abstract.—Commercial fisheries have a long history of nonsustainable harvests—not through deliberate mismanagement but through an inability to simultaneously account for the complexity of relevant factors, including the ecological and coevolutionary interactions within ecosystems. We argue that these factors (e.g., natural selection and coevolution) are among the structuring processes behind the patterns of predation exhibited by species such as marine mammals. As such, these patterns provide an indication of harvest practices that are sustainable in the long term—that is, normal for the systems and circumstances involved. Thus, patterns in selectivity exhibited by predators in their consumption of prey species meet the needs for evolutionarily enlightened guidance in management, long seen as missing in current practice. Our analysis of data characterizing the diets of 63 species of marine mammals indicates that the majority of prey consumed are 30 cm or less in length. This pattern is common to all marine mammal taxa and is apparently independent of the body size of predator species and largely independent of the body size range of prey species, many of which exceed 100 cm in maximum length. The size selectivity of commercial fisheries differs from that of marine mammals for all but the smallest prey species and is positively correlated with size. When possible, commercial fisheries tend to target individuals greater than 30 cm. The selective pressure this exerts on large-bodied prey species is abnormal in comparison with that of the natural predator–prey systems that have evolved to sustain consumption of individual prey items of 30 cm or less. To minimize the abnormal effects of selective pressure imposed by fishing, we argue that the targeted size composition of catches should be modified to more closely match the patterns exhibited by marine mammals as another example of the application of systemic management, a holistic alternative to conventional management.

An increasing number of studies suggests that in many cases, the commercial harvest of fish stocks is managed in a way that is not sustainable (Rosenberg 2003; U.S. Commission on Ocean Policy 2004; Worm et al. 2006; Jørgensen et al. 2007). Lack of sustainability prevails (Pauly et al. 2002), regardless of whether it is observed in significant reductions in stock biomass (Myers and Worm 2003); reductions in mean age or age at maturity (Jørgensen 1990); changes in mean and maximum size (Wysokinski 1984); or irreversible changes in the genetic makeup of the exploited stock (Law 2000; Olsen et al. 2004; Fenberg and Roy 2008; Hutchings and Fraser 2008). Such problems persist at the ecosystem and biosphere scales when observed in reduced consumer populations or, in the extreme, extinction. Common to these problems is the fact that commercial fisheries have a tendency to remove more biomass each year than is sustainable in

the long term (Fowler and Hobbs 2003; Fowler 2008). However, fishing intensity (e.g., the rate of removal of biomass or numbers, or the portion of standing stock or production harvested annually) is but one component of the nonsustainable harvest of fisheries resources. In this paper, we deal exclusively with size selectivity based on the argument that selective removals of any subset of a resource species are a problem if the selectivity is an outlier in comparison with the patterns of selectivity by other species. We emphasize that both total removals and size selectivity are management issues that must be considered simultaneously; addressing one in the absence of the other is unlikely to result in sustainability, particularly when one or both of these components is abnormal relative to the patterns of consumption by nonhuman predators (Fowler 2003).

The management of size selectivity may be seen as another example of systemic management (Fowler 2003; Hobbs and Fowler 2008). Such management is based on naturally occurring patterns that directly match the management questions being addressed. This match involves completely consonant guiding information wherein there is a one-to-one mapping between

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Received June 24, 2009; accepted December 17, 2009
Published online May 17, 2010

the question and the pattern, thus avoiding much of the subjectivity of conventional management (as discussed by Belgrano and Fowler 2008; Fowler and Hobbs 2009). As such, systemic management is an expansion of the concept of biomimicry (Benyus 1997) to the species level, wherein our species mimics the sustainability evident in others. In fisheries management, this results in recommendations for changing commercial harvest practices in such a way that long-term sustainability is a more likely outcome. Systemic management is pattern-based management in which examples of sustainable interactions between nonhuman animals and their ecosystems or the biosphere are used for guidance where humans interact with ecosystems or the biosphere in the same way. Thus, systemic management goes beyond popular adaptations of biomimicry that identify useful products and processes. In systemic management, information is provided regarding the quantity of the products that can be produced or harvested sustainably. In addition to knowing that it is important to consume resources with selectivity similar to that of other species, we also know that it is important to consume them at rates similar to the rates at which they are consumed by other species (Fowler 2008).

With specific reference to fisheries management, perhaps some of the more serious effects of commercial fishing involve genetic change caused by selective harvest practices that preferentially target individuals with a particular demographic characteristic (or other phenotype) while preferentially excluding others (Conover 2000; Law 2000; Conover and Munch 2002; Olsen et al. 2004; Kendall 2007; Fenberg and Roy 2008). Temporally selective harvests, for example, appear to have resulted in altered migratory schedules (Quinn et al. 2007). Likewise, recent research focuses on size selectivity and its effect on life history traits (e.g., Conover et al. 2005; Edeline et al. 2007; Fenberg and Roy 2008). Because genetic effects are related to selective mortality, various pleas for evolutionarily enlightened management have been made repeatedly (e.g., Hutchings 2000; Stokes and Law 2000; Thompson 2005; Conover 2007; Jørgensen et al. 2007; Swain et al. 2007). Selectivity in coevolutionary interactions is one of the processes that maintain ecosystem structure and function. Many patterns within ecosystems are interrelated (Cohen et al. 2003), and if the integrity of ecosystems is to be preserved, then the genetic effects of selective fishing must be included among the factors dealt with in management. Thus, one of the main challenges to management is to address both direct and indirect consequences of selectivity (Smith and Bernatchez 2008), either of which can lead to coevolutionary effects on ecosystems (Kuparinen

and Merilä 2007). Selectivity is not easily addressed in any specific management action, however, because the term can relate to a wide variety of attributes of a species (e.g., sex, age, size, location, growth patterns, and maturation rates). Whatever we do in research to supply management advice, it must involve a measurable (Fowler 2003) aspect of selectivity and it must be a component of fishing practices that can be managed (e.g., season, total catch, geographic region, and mesh size).

Here, we address the specific issue of size selectivity to exemplify one of the many facets of fisheries management that must be dealt with to provide quantitative guidance to managers. In most cases, commercial fishing as currently practiced in many of the world's oceans is not sustainable over the long term; total removals are typically set at highly abnormal rates (Fowler 2008), and fishery collapses are increasingly evident (e.g., Worm et al. 2006). In contrast, predator-prey relationships in marine ecosystems have evolved over thousands of generations and persist as links in coevolutionary webs (Thompson 2005) over evolutionary time scales. In addition to being products of their evolutionary and coevolutionary history, most or all of these ecosystems have experienced some level of anthropogenic perturbation. As such, these systems exhibit emergent properties that simultaneously account for the effects of a wide range of variables at various spatial and temporal scales (Belgrano and Fowler 2008). Importantly, in addition to reflecting sustainability in the face of anthropogenic effects, these systems reflect evolutionary and coevolutionary processes that are important to the consideration of all management questions. Such questions include, of course, those regarding sustainable selectivity itself and size selectivity in particular.

The management question we address in this paper is "What mean size of fish should be taken in commercial fisheries to achieve sustainability?" Although size selectivity is but one of many aspects of harvest practices, all of which must be considered simultaneously, it is a crucially important component in assessing our impact on individual resource species or ecosystems. Here, we identify patterns in size selectivity among other mammalian predator species as a means to provide evidence of what is normal and what works (sustainability) and, conversely, what is abnormal and does not work (nonsustainability). Variability in such pattern(s) as related to other predator species, life history strategies, trophic levels, and other ecological variables would provide more specific insight and would require additional research to elucidate.

Methods

We searched the literature published before 2004 for information regarding the size composition (here limited to length data) of fish, cephalopod, and crustacean prey species in the diets of marine mammals throughout the world. Some of the prey size data are based on measurements of whole prey items taken directly from the gastrointestinal tracts of the predator species (through forced and natural regurgitation or from recently deceased animals). However, in most cases prey size data are estimated using correlations (most of which were uncorrected for size reduction of hard parts through erosion) relating prey body size to the size of those tissue types that remain intact in the digestive systems of marine mammals (e.g., cephalopod beaks, fish otoliths, and bones; Fitch and Brownell 1968). This approach is known to have several inherent biases (reviewed by Etnier and Fowler 2005), such as systematic underrepresentation of small-bodied taxa and underestimation of the body size of large-bodied taxa because of erosion of characteristic skeletal elements (Bowen 2000; Tollit et al. 2004; Zeppelin et al. 2004). Nevertheless, the use of regression to derive body size from the size of measurable body parts is the standard approach in the literature and provides the basis for the overwhelming majority of the available data. Insofar as the data we obtained may be an imperfect representation of the patterns we are attempting to document, they are currently the best available data for this purpose; more importantly, they illustrate the kind of information needed to address the management question we have posed.

Prey size data were extracted directly from the text and tables of available publications when possible. When prey size data were presented only in graphical format (e.g., length-frequency distributions or box plots), the figures were digitally scanned and estimates of prey size were then determined with digitizing software (see Etnier and Fowler 2005).

The maximum size that different prey species were likely to attain was used to develop an index of the degree to which marine mammals are selective with respect to either the body size of the resource species or the size of individuals selected from the prey population. In most cases, maximum reported size was obtained from online searchable databases hosted by FishBase (Froese and Pauly 2003) and CephBase (Wood and Day 1998). In cases where the maximum reported size either was not listed in the databases or was smaller than the maximum reported size from food habits studies, the upper end of the size range reported in the food habits studies was used as a minimum estimate for the maximum attainable size.

In the interest of comparing size selectivity across prey species of differing size, the relationship between targeted prey size and maximum attainable size for each prey species was characterized using Holling's disk equation (Holling 1959), which is a curvilinear asymptotic relationship of the form:

$$y = \frac{ax}{1 + bx}, \quad (1)$$

where y = mean prey size and x = maximum reported prey size. The shape parameters a and b were estimated using nonlinear regression in the Statistical Package for the Social Sciences (Norusis 1998).

For any given prey species for which marine mammal food habits data were available, relevant commercial catch data were also obtained. This typically is possible only for commercially targeted species because size composition of nontarget species encountered as bycatch usually is not reported. Furthermore, data from commercial catches were chosen so as to be comparable both spatially and temporally with the food habits data. Because many of the world's fisheries actively attempt to minimize the degree of spatial overlap with marine mammals (Kaschner and Pauly 2004), comparable spatial data were often available only at a regional level (i.e., only as a portion of the full geographic ranges of harvested species).

Finally, we wanted to evaluate and compare the degree to which both marine mammals and commercial fisheries are selective in the size composition of the prey they consume or harvest in contrast to the size composition of prey available in their environment. To accomplish this, survey data were obtained, where possible, for prey species in our food habits database. As with the commercial data, survey data were required to be comparable both spatially and temporally with the food habits data.

Although prey size information was included in our data when available, statistical analyses were conducted only on size data derived from samples of 10 or more individuals of any given prey species. Sample means based on 10 or more prey items were then used to calculate the unweighted mean of means (i.e., all sample means were weighted equally regardless of the underlying sample size) for various subsets of prey taxa. Information on otolith or cephalopod beak size was used only if the appropriate regression equations were available to allow conversion to prey body size. Body size for cephalopods is listed as dorsal mantle length. Conventions on the measure of body size used for fish (e.g., total length, fork length, and standard length) tend to be species-specific. As a consequence, we did not consistently use one over the other, but we did use a consistent length convention within each fish

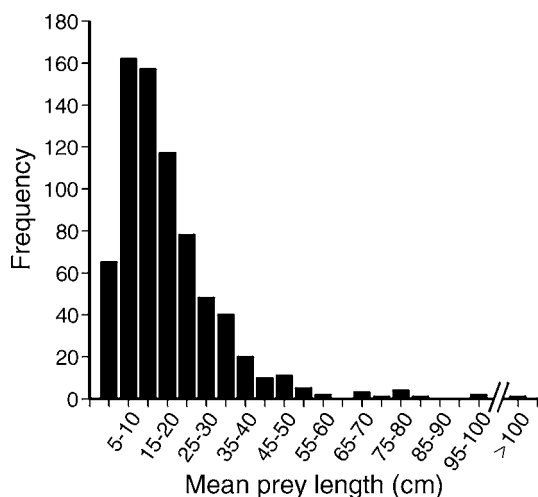


FIGURE 1.—Frequency distribution of the mean size of fish, cephalopod, and crustacean prey consumed by marine mammal predators ($N = 727$ cases) of varied sizes (small seals to sperm whales). See Methods for description of size measurements used within each prey taxon.

species. Body size for crustaceans is listed as total length for shrimp and krill, carapace width for crabs, and carapace length for lobsters. In this document, we use the terms “prey length,” “prey size” and “size” interchangeably, regardless of the taxonomic group.

Results

Size Composition of Marine Mammal Predation

Our search of materials published before 2004 yielded 1,166 records of prey size data distributed across 63 marine mammal species (Etnier and Fowler 2005). Data on targeted prey body size were obtained for 17 species of crustaceans representing 12 families, 140 base taxa (i.e., a mix of genus-level and species-level identifications) of cephalopods from 28 families, and 223 base taxa of fish representing 71 families (Table A.1 lists major prey species). The marine mammal predators included 13 species of otariid (eared) seals, 15 species of phocid (earless) seals, four

species of mysticete (baleen) whales, and 31 species of odontocete (toothed) whales (Table A.2 presents major predator species; see Etnier and Fowler 2005 for complete listing of prey and predator taxa). Of the 1,166 records of prey size, 727 consisted of mean prey size based on sample sizes of 10 or more. Comparable commercial fisheries data were available for 120 of the 727 cases, and comparable survey data were available for 152 of the 727 cases. There were 85 cases common to all three databases (marine mammal food habits, commercial catches, and surveys; Etnier and Fowler 2005).

The precision with which we were able to estimate prey size from published graphical representations was high. In cases where both graphical and textual representations of the data were available, mean prey size estimated from figures was within ± 0.5 cm of the stated mean in 85% of the cases (103 of 121) and was within ± 1.0 cm in 91% of the cases (110 of 121). Estimation errors of this magnitude are not expected to significantly bias our results.

When viewed in the aggregate, our results indicate that marine mammals tend to consume prey that are 30 cm or less in length. Although mean prey size ranges from 1.3 cm (Antarctic fur seal predation on the lanternfish *Gymnoscopelus piabilis*) to 115.9 cm (sperm whale predation on giant squid *Architeuthis dux*), the distribution has a strong positive skew and an overall unweighted mean of means equal to 17.63 cm (Figure 1). Indeed, 501 of 727 cases (69%) had a mean prey size of 20 cm or less, and 627 of 727 cases (86%) had a mean prey size of 30 cm or less.

Although the aggregate data may mask considerable taxonomic variability in mean consumed prey size, several lines of evidence suggest that this is not a significant bias in our study. With the exception of the relatively small mean size of crustaceans preyed upon by marine mammals (3.99 cm), mean prey size of the aggregate data (17.63 cm) is similar to the mean size of cephalopods (17.99 cm) and fish (18.34 cm) targeted by subsets of the major taxonomic groups of predators for which we have data (Table 1). Likewise, the

TABLE 1.—Mean size (cm; calculated as the unweighted mean of means for samples composed of 10 or more prey items) of different marine prey taxa consumed by mammalian predator taxa. Number of sample means is in parentheses. See Methods for size measurements used within each taxon.

Predator taxonomic group	Prey taxonomic group			
	Crustaceans	Cephalopods	Fish	Overall
Otariid seals	4.79 (15)	12.86 (39)	17.35 (183)	15.82 (237)
Phocid seals	3.23 (8)	15.77 (18)	20.11 (121)	18.66 (147)
Mysticete whales	3.75 (4)	—	14.5 (1)	5.9 (5)
Odontocete whales	1.45 (2)	19.09 (219)	18.08 (117)	18.64 (338)
Overall	3.99 (29)	17.99 (276)	18.34 (422)	17.63 (727)

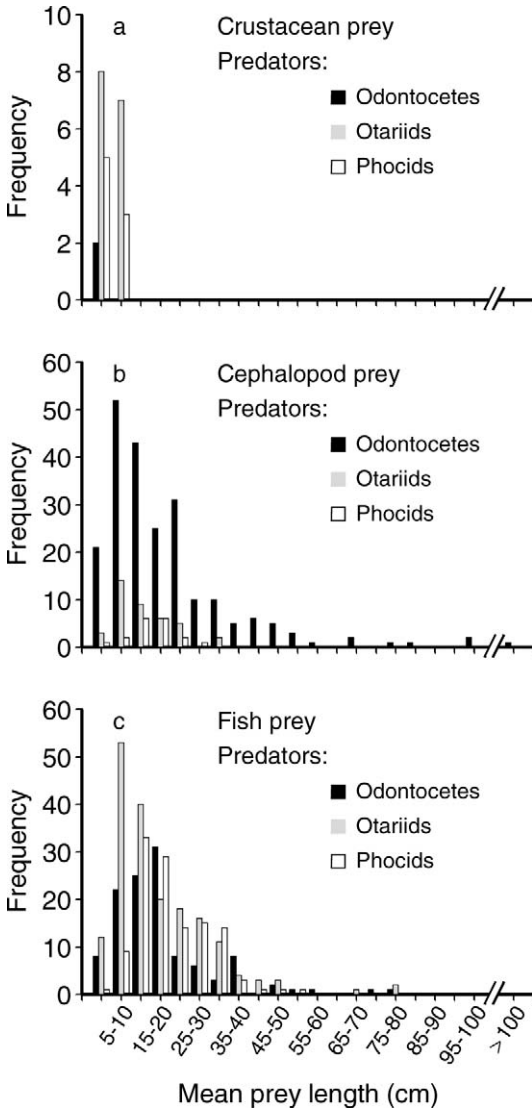


FIGURE 2.—Frequency distributions of the mean size of (a) crustacean prey, (b) cephalopod prey, and (c) fish prey consumed by three marine mammalian taxa (odontocete whales, otariid seals, and phocid seals; sample sizes are given in Table 1). See Methods for description of size measurements used within each prey taxon.

frequency distributions of mean prey size of cephalopods and fish targeted by marine mammals are similar to the aggregate frequency distribution of means (Figure 2). Species-specific frequency distributions of prey size means for different predators constitute smaller and smaller subsets of these data but generally repeat the overall pattern observed here (Etnier and Fowler 2005).

Generally, large-bodied prey items are ingested in small numbers relative to small-bodied prey items. Thus, our minimum sample size requirement could bias against large-bodied prey items. However, in cases where size could be determined for single prey items ($N = 254$ individual prey items), mean prey size was 30 cm or less for all major taxonomic groups of predators (Table 2) and was broadly similar to the unweighted mean of means based on the larger samples (Table 1). Thus, the preponderance of prey items averaging 30 cm or less is not a function of our arbitrary sample size requirement.

Furthermore, the preponderance of prey items averaging 30 cm or less appears to be independent of the prey species in marine mammal diets. That is, marine mammals are not targeting only small-bodied species (i.e., selecting species rather than individuals). Although the majority of prey species consumed by marine mammals reach a maximum length of less than 50 cm (Figure 3; Table 3), mean prey size increases only slightly with increasing maximum prey size. This is most clearly illustrated by predation of marine mammals on fish (Figure 3D–F), where mean prey size approaches an asymptote at around 40 cm despite the presence of prey species that can reach sizes well over 100 cm.

The food habits data also clearly show that marine mammals tend to consume prey items of 30 cm or less independent of the body size of the predator species. Our data show that the tendency to consume prey items of 30 cm or less holds for the largest of whales, the smallest of seals, and everything in between (see Etnier and Fowler 2005 for species-specific data).

Size Composition of Commercial Catch

We now address how this recurring pattern among marine mammals compares with the patterns exhibited by commercial fisheries. The potential for patterns in marine mammal predation to inform the management of commercial fisheries is quite high; of the 380 distinct prey taxa for which we have data, 218 of these (57%) are harvested commercially (Etnier and Fowler 2005).

The abundance and size composition of prey species vary spatially and temporally for all predatory species (Pauly 1985; Castonguay and Mercille 1988; Overholtz and Waring 1991; Livingston 1993; Reid et al. 1996). Thus, it is important for comparisons between fisheries and marine mammals to involve data from the same regions and seasons if possible. It is difficult to obtain commercial catch data that are comparable spatially and temporally with marine mammal prey size data because of the wide-ranging habits of most marine mammal species coupled with the often fragmentary record of dietary data. Only 17% of the cases (120 of

TABLE 2.—Mean size (cm) of individual prey items from marine taxa consumed by different mammalian predator taxa. Sample size (individuals) is in parentheses. There were no reported data for single prey items of the mysticete whales; no crustacean species were reported as single prey items. See Methods for size measurements used within each taxon.

Predator taxonomic group	Prey taxonomic group		
	Cephalopods	Fish	Overall
Otariid seals	11.80 (34)	17.50 (46)	15.08 (80)
Phocid seals	20.07 (16)	23.44 (31)	22.29 (47)
Odontocete whales	14.61 (82)	15.88 (33)	14.98 (115)
Overall	14.55 (132)	18.69 (110)	16.43 (254)

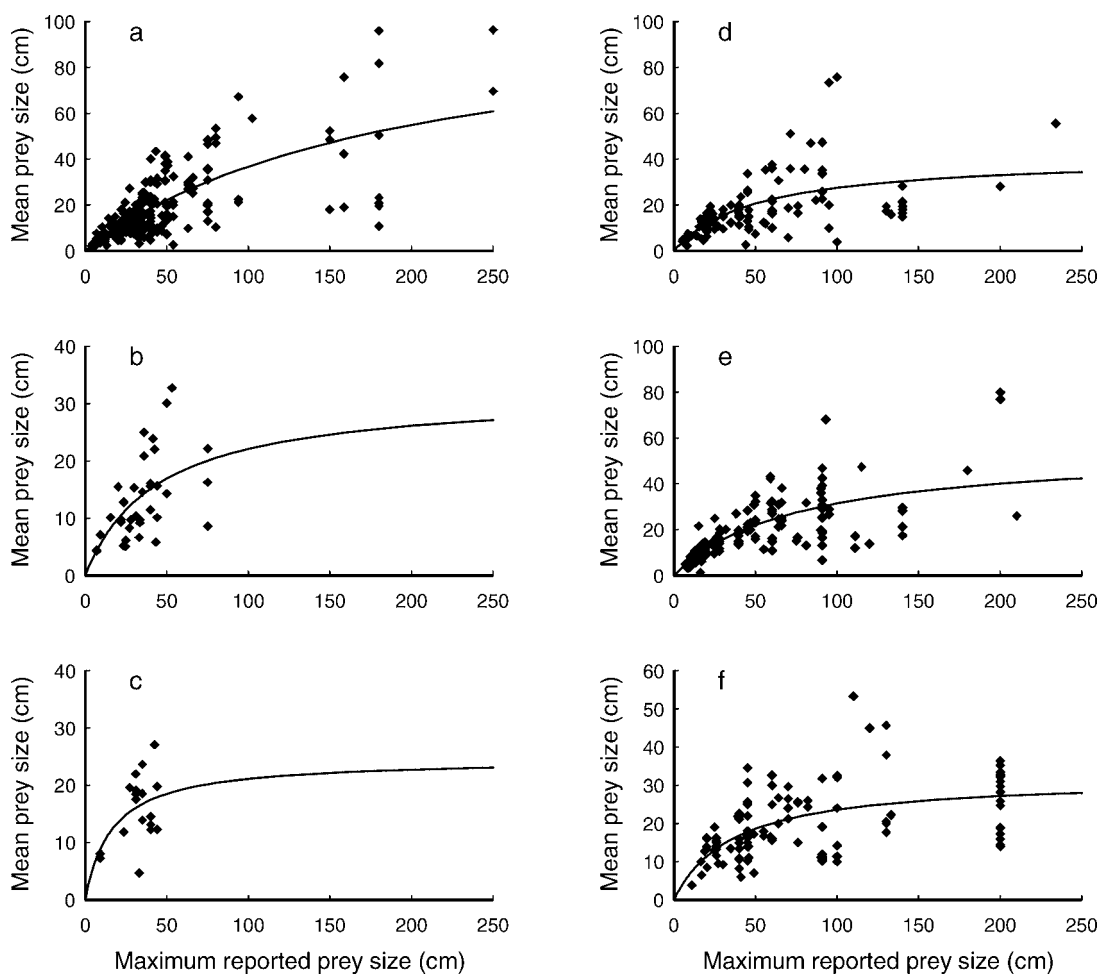


FIGURE 3.—Relation between maximum reported size and mean prey size of (a) cephalopods consumed by odontocete whales (outlier for a 600-cm giant squid removed), (b) cephalopods consumed by otariid seals, (c) cephalopods consumed by phocid seals, (d) fish consumed by odontocete whales, (e) fish consumed by otariid seals, and (f) fish consumed by phocid seals. Sample sizes and parameter estimates for Holling's disk equation describing the relations are listed in Table 3. Prey species are occasionally represented by multiple data points (e.g., Atlantic cod *Gadus morhua* and European ling *Molva molva* in panel f). See Methods for description of size measurements used within each prey taxon.

TABLE 3.—Sample sizes and parameter estimates for Holling’s disk equation (Holling 1959) describing the relationship between mean prey size and maximum reported prey size for different pairings of marine mammal predator groups and cephalopod or fish prey. Parameters *a* and *b* determine the shape of the asymptotic curve plotted in Figure 3.

Pairing	<i>N</i>	Parameter	Parameter estimate	Asymptotic SE	95% confidence limits	
					Lower	Upper
Odontocetes × cephalopods ^a	218	<i>a</i>	0.5575	0.0439	0.4711	0.6440
Odontocetes × cephalopods ^a	218	<i>b</i>	0.0052	0.0012	0.0028	0.0075
Otariids × cephalopods	38	<i>a</i>	0.7197	0.2466	0.2196	1.2198
Otariids × cephalopods	38	<i>b</i>	0.0225	0.0160	-0.0099	0.0550
Phocids × cephalopods	18	<i>a</i>	1.5031	1.1567	-0.9489	3.9552
Phocids × cephalopods	18	<i>b</i>	0.0612	0.0697	-0.0865	0.2088
Odontocetes × fish	114	<i>a</i>	0.8230	0.1676	0.4910	1.1549
Odontocetes × fish	114	<i>b</i>	0.0199	0.0069	0.0063	0.0336
Otariids × fish	181	<i>a</i>	0.7283	0.0766	0.5772	0.8795
Otariids × fish	181	<i>b</i>	0.0132	0.0027	0.0078	0.0186
Phocids × fish	120	<i>a</i>	0.8828	0.1520	0.5817	1.1838
Phocids × fish	120	<i>b</i>	0.0275	0.0067	0.0143	0.0406

^a A 600-cm outlier was removed from calculations.

727) involved commercial catch data that corresponded to marine mammal food habits data. Nevertheless, the available data show that in species-specific comparisons, the mean size of the commercial catch (28.45 cm, SE = 1.0556) is significantly larger than the mean size consumed by marine mammals (21.08 cm, SE = 1.3757), with an overall 7.37-cm difference in means (Figure 4; paired $t = -6.599$, $P < 0.001$). Furthermore, the magnitude of the difference between means (commercial mean minus food habits mean) shows a significant and positive correlation with maximum reported size of the target (prey) species ($P < 0.001$). That is, as the overall size of the target species

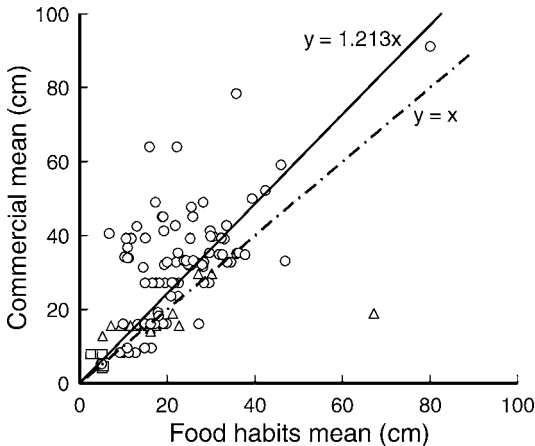


FIGURE 4.—Relationship between mean size of crustacean prey (squares; $N = 5$), cephalopod prey (triangles; $N = 17$), and fish prey (circles; $N = 95$) consumed by marine mammal predators versus the mean size of the same taxa in the commercial catch from the same region and time period. The dashed line ($y = x$) depicts a 1:1 relationship. See Methods for description of size measurements used within each prey taxon.

increases, the mean size of the commercial catch is increasingly divergent from and larger than the mean size consumed by marine mammals (Figure 5).

The relationship between (1) the difference in the mean size of harvested versus predator-consumed individuals and (2) the maximum reported size of the target species has important management implications. Although it has yet to be linked correlatively to sustainable total biomass removals (covered by Fowler and Hobbs 2003; Belgrano and Fowler 2008; Fowler 2008), this relationship suggests that, at least in terms of size composition of the commercial catch, little

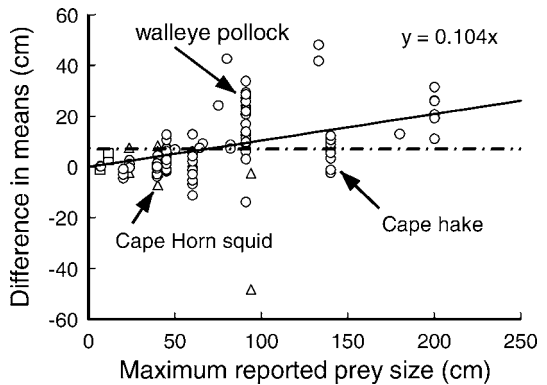


FIGURE 5.—Distribution of differences in mean size of prey taxa (size in the commercial catch minus size consumed by marine mammals) plotted as a function of maximum reported size for each prey taxon (squares: crustaceans, $N = 5$; triangles: cephalopods, $N = 17$; circles: fish, $N = 95$). The horizontal line indicates the mean difference in means (7.37 cm). Prey taxa with 10 or more entries (appearing as vertical clusters of points) include Cape Horn (chokka) squid, walleye pollock, and Cape hake. See Methods for description of size measurements used within each prey taxon.

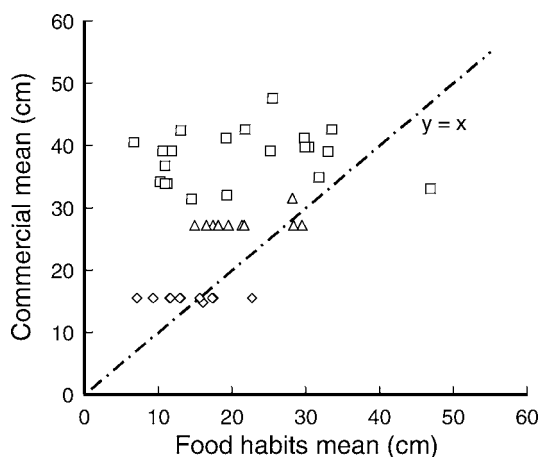


FIGURE 6.—Relationship between mean size of prey consumed by marine mammal predators and mean size of the same taxa in the commercial catch from the same region and time period: Cape Horn (chokka) squid (diamonds; $N = 11$), walleye pollock (squares; $N = 21$), and Cape hake (triangles; $N = 11$; all three species are represented by ≥ 10 data points in Figure 5). See Methods for description of size measurements used.

management action is needed to change size selectivity in commercial fisheries at the smaller end of the size spectrum. For example, mean size of Cape Horn (chokka) squid in the commercial fishery averages only 1.4 cm larger than the mean size consumed by marine mammals in 10 cases from the Benguela ecosystem (off the SW coast of Africa), with a nearly equal number of cases occurring above ($N = 6$) and below ($N = 5$) the 1:1 regression line (Figure 6; see Etnier and Fowler 2005 for a full list of predator species). However, for larger-bodied resource species, there is cause for concern because we see an increasing frequency of abnormal selectivity with increasing prey size. The increasing divergence in Figure 5 is shown more clearly in species-specific plots (Figure 6) for Cape hake (i.e., an aggregate of shallow-water Cape hake and deepwater Cape hake; mean difference of 6.1 cm, with 2 cases below and 9 cases above the regression line) and walleye pollock (mean difference of 17.1 cm, with 1 case below and 20 cases above the regression line).

Another way of examining the degree to which commercial fisheries diverge from marine mammals in mean prey size is to return to patterns represented by our use of Holling's disk equation (equation 1). In these patterns, Holling's disk equation characterizes the asymptotic increase in mean prey size as the maximum attainable size of those taxa increases (Figure 3; Table 3). Plots for commercial data (Figure 7) reinforce our findings: The mean size of fish taken commercially is

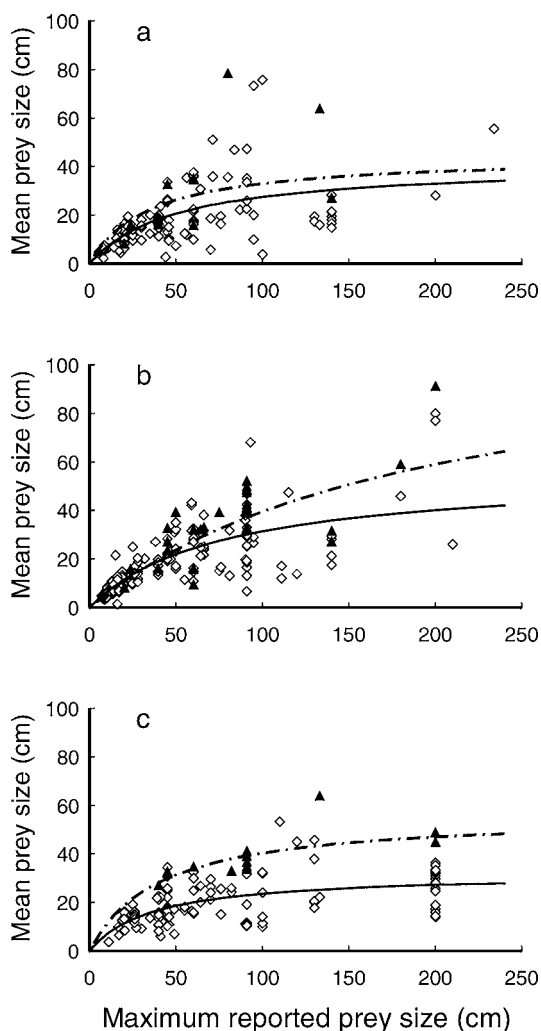


FIGURE 7.—Relationship between maximum reported size of fish prey taxa and the mean size consumed by (a) odontocete whales, (b) otariid seals, and (c) phocid seals (open diamonds, solid line) presented in comparison with the mean size in the commercial catch (solid triangles, dashed line). The curves describing the relationships are nonlinear regressions based on Holling's disk equation; see Table 4 for sample sizes and regression statistics. See Methods for description of size measurements used.

significantly larger than the mean size of fish consumed by marine mammal predators (Table 4), and the degree of difference increases with increasing maximum body size of the prey species.

Selectivity of Marine Mammals and Commercial Fisheries

Our analyses clearly show that commercial fisheries have a tendency to catch larger fish than are consumed

TABLE 4.—Statistical significance (two-sample *t*-test) of comparisons of Holling's disk equation (Holling 1959) parameter estimates for marine mammal food habits data versus commercial fishery data. Parameters *a* and *b* determine the shape of the asymptotic curve plotted in Figure 4. Although the estimates of *b* are not significantly different for the pairing of phocid seals and commercial catch, the overall curves are significantly different.

Pairing	<i>N</i>	Parameter	Parameter estimate	Asymptotic SE	<i>P</i>
Odontocetes × fish	114	<i>a</i>	0.8230	0.1676	<0.01
Commercial × fish × odontocetes	27	<i>a</i>	2.8511	2.7453	
Odontocetes × fish	114	<i>b</i>	0.0199	0.0069	<0.01
Commercial × fish × odontocetes	27	<i>b</i>	0.1121	0.1234	
Otariids × fish	181	<i>a</i>	0.7283	0.0766	<0.01
Commercial × fish × otariids	44	<i>a</i>	0.5983	0.1133	
Otariids × fish	181	<i>b</i>	0.0132	0.0027	<0.01
Commercial × fish × otariids	44	<i>b</i>	0.0051	0.0028	
Phocids × fish	120	<i>a</i>	0.8828	0.1520	<0.01
Commercial × fish × phocids	23	<i>a</i>	1.4189	0.2910	
Phocids × fish	120	<i>b</i>	0.0275	0.0067	0.07
Commercial × fish × phocids	23	<i>b</i>	0.0252	0.0072	

by marine mammals and thereby have selective effects on the prey species and coevolutionary impacts on the ecosystem that are unusual (abnormal) for these systems. This tendency is especially prevalent for large-bodied prey species. A possibility remains, however, that either marine mammals or commercial fisheries are not selectively targeting specific size-classes as much as they are sampling the prey available in the immediate vicinity where prey segregate according to size. Marine mammals are often described in the food habits literature as opportunistic foragers that simply consume prey in direct proportion to their encounter rates (Kajimura 1985; Addink and Smeenk 2001; Stockin and Burgess 2005). However, various studies (Croxall and Pilcher 1984; Sinclair et al. 1994, 2005; Reid et al. 1996; Sinclair and Zeppelin 2002) suggest that marine mammal foraging behavior reflects some level of decision making within the options available temporally and spatially. Commercial fisheries exhibit a wide range of size selectivity dictated by the location and time at which gear is set as well as the minimum mesh or hook size utilized. In view of such context-specific selectivity, we next examine the available survey data to evaluate the degree to which marine mammals and commercial fisheries exhibit size selectivity in any given situation.

Similar temporal and spatial coverages were crucial to our comparisons between the commercial and food habits data. Again, it is important that survey data have roughly the same temporal and spatial coverage represented by the foraging of the marine mammals in evaluating their selectivity. From our list of 727 entries of mean prey size, we were able to locate comparable survey data for 152 cases (see Etnier and Fowler 2005 for a full listing). Using the same metric as in Figure 5, we subtracted the mean size consumed by marine mammal predators from the mean size of the

same prey species found in appropriate surveys. Although the mean difference is 4.67 cm, the magnitude of the difference increases with maximum attainable body size of the prey species (Figure 8a). This suggests that not only are marine mammals consistently consuming prey that are 30 cm or less, as we have already shown (Figures 1, 2), but they are also systematically targeting these small-bodied prey even when larger individuals are available. This tendency involves selectivity both within and among prey species; as with other marine species (Link 2004), marine mammals are size selective in their feeding.

Commercial fisheries show a quite different tendency. In the 85 cases for which we had data from all three sources (food habits, commercial, and survey; see Etnier and Fowler 2005 for a full listing), the mean size of prey caught commercially is only slightly larger (0.43 cm) than that of prey captured in surveys. There is no relationship between the difference in means (i.e., mean size of prey taxa caught commercially versus that of prey taxa caught in surveys) and increasing maximum attainable body size of the prey species (Figure 8b).

The difference between marine mammals and commercial fisheries is emphasized in Figure 9, where the mean targeted size of prey or commercial catch is plotted against the survey mean size for the 85 cases in which data were available. The slope of the regression line describing the relationship between commercial mean size and survey mean size is statistically indistinguishable from 1.0 ($P < 0.001$), whereas the slope of the regression line describing the relationship between mean sizes in mammalian diets and in surveys is significantly lower than 1.0 ($P < 0.001$) and is significantly lower than the slope of the regression line for commercial mean size ($P < 0.001$).

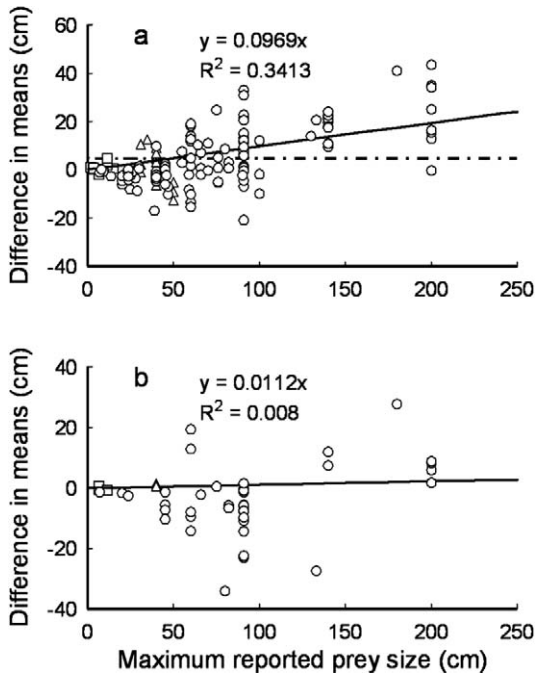


FIGURE 8.—Distribution of differences in mean size of prey taxa plotted as a function of maximum reported size for each prey taxon: (a) mean size in surveys minus mean size consumed by mammalian predators (squares: crustaceans, $N = 17$; triangles: cephalopods, $N = 18$; circles: fish, $N = 117$); and (b) mean size in surveys minus mean size harvested by the commercial fishery (crustaceans, $N = 5$; cephalopods, $N = 11$; fish, $N = 69$). The dashed horizontal line in panel a represents a mean difference of 4.67 cm; the mean difference of 0.43 cm in panel b is not represented. The regression line shown in panel b is not significantly different from $y = 0$. See Methods for description of size measurements used within each prey taxon.

Discussion

There are many reasons to think that the data we have presented are an imperfect representation of the ways in which marine mammals and commercial fisheries do or do not differ in their selective removal of individuals from the populations of prey (resource) species. For example, the marked similarity between the commercial and survey means is almost certainly an artifact of the similarity (often intentional) between the sampling gear used to generate the survey data and the gear used commercially. In similar fashion, the degree of size selectivity exhibited by marine mammals may be overstated by our data if survey sampling gear systematically underrepresents small-bodied individuals. Nevertheless, comparisons between the mean size of commercial catches and the mean size of prey consumed by marine mammals are unaffected by the

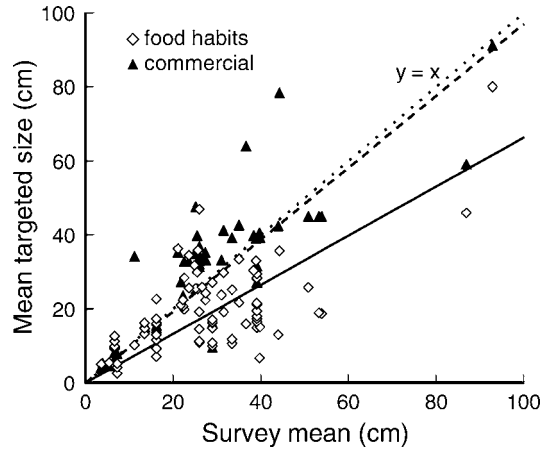


FIGURE 9.—Relationship between mean size of prey taxa (crustaceans, cephalopods, and fish) in surveys and the mean size targeted by marine mammals (i.e., represented in food habits data; open diamonds, solid line) or by the commercial fishery (i.e., catch data; black triangles, dashed line) for 85 cases. The dotted line ($y = x$) depicts a 1:1 relationship. See Methods for description of size measurements used within each prey taxon.

sampling of surveys designed to determine what is available.

Even so, it can be argued that food habits studies in general, and our subset of those studies in particular, suffer from too many inherent biases to provide a clear picture of the size composition of marine mammal dietary preferences (e.g., Dellinger and Trillmich 1988; Zeppelin et al. 2004; reviewed by Etnier and Fowler 2005). Future studies of larger-bodied species of marine mammals (e.g., male Steller sea lions *Eumetopias jubatus* and sperm whales) could reveal greater consumption of large-bodied prey than was evident in our data. Nevertheless, considering that existing data consistently show a dominance of prey items of 30 cm or less regardless of taxonomic group (including species with a wide range of body sizes), ocean basin, or period, it seems safe to conclude that there are real differences in size selectivity between commercial fishing and marine mammal diets, even if future refinement of sampling and analytical methods shows the differences to be larger or smaller than indicated here. In any case, our study emphasizes the need for careful attention to the methods involved in dietary studies; results are consonant with the management question regarding selectivity posed earlier and exemplify the best kind of scientific information to address such questions (Belgrano and Fowler 2008).

Because our study draws on data from a wide diversity of marine mammal and prey species and

because the pattern of targeting small-bodied prey is so pervasive, we argue that this emergent pattern is characteristically stable (i.e., characteristically emergent from the self-organizing nature of the complex biological systems in marine environments) and reflects the simultaneous influence of macroevolutionary, coevolutionary, and ecological factors—processes that are systemic in their combination. As such, this pattern of predation can be interpreted as indicative of (1) what is stable over evolutionary time scales and (2) what is sustainable under current circumstances. Unlike most conventional fisheries management programs, the emergent pattern of marine mammal size selectivity automatically incorporates and integrates the effects of a wide range of variables (climatological, oceanographic, etc.) acting at various spatial and temporal scales.

Based on this emergent pattern, our recommendation for restructuring fisheries management policies in an evolutionarily enlightened way is to regulate commercial selectivity such that the patterns in mean size of individual fish harvested are more closely aligned with those observed in marine mammal predation. Doing so would achieve one of the objectives of management: attaining health by avoiding the abnormal (i.e., systemic health as normalcy for other species, ecosystems, and our interactions with them; Fowler and Hobbs 2002; Fowler 2003). It would also avoid any correlated selective pressures intrinsic to random size selectivity (e.g., behaviors, growth, or distribution; see Conover and Munch 2002). Any abnormal ecosystem effects would also be avoided so that evolutionary and coevolutionary interactions would remain intact. As we have pointed out, this change requires little or no shift in size selectivity of smaller-bodied prey species. For larger-bodied species, however, the harvested proportion of large—and presumably older—sexually mature individuals needs to be reduced in favor of smaller, younger, and generally more abundant size-classes to achieve a downward shift in the mean size of harvested individual prey items.

The expanding literature on the effects of selectively harvesting large-bodied individuals has documented consequences of concern, often leading to the argument that large individuals should be protected more than they are in current management practice (e.g., Law 2007; Swain et al. 2007; Hutchings and Fraser 2008). Such work emphasizes the need for protection and supplies information about the cause-and-effect relationships between selectivity and its consequences. However, this work does not supply direct and specific or quantifiable management advice. Much of the contemporary thought about evolutionarily enlightened

management in fisheries is confined to the context of maximizing yields rather than sustainability (e.g., Conover and Munch 2002; Conover et al. 2005), thus perpetuating the problems of that approach and failing to provide operational standards. The advice we present here not only has a quantitative basis but also accounts for the full complexity of ecological and evolutionary consequences, including those not yet documented or understood (Belgrano and Fowler 2008). There is a firm scientific basis for reducing the harvest rates on large-bodied fish.

We are currently seeing a decline in the harvest of large-bodied fish in many of the world's fisheries, a phenomenon that has been termed "fishing down the food web" (Pauly et al. 1998), wherein harvests of taxa from lower trophic levels have increased dramatically. However, this has been the result of or a symptom of at least two factors, neither of which is derived from conscious action to achieve such results but both of which are amenable to management. The first factor is that fishing rates in general (i.e., portion of the stock harvested per year) are many times higher than the consumption rates of marine mammals (Fowler and Hobbs 2002; Fowler 2003, 2008). These high removal rates cause large-bodied, high-trophic-level fish stocks to dwindle (Myers et al. 1997; Myers and Worm 2003) and are typically not a conscious management decision aimed at reducing the abundance of large, reproductively mature individuals. The second factor is the selectivity we have documented in this paper. If both problems are dealt with simultaneously as part of a conscious management decision and if the harvest rates of large individuals are reduced (though not necessarily to zero: see Figures 1, 2), it is safe to predict that the disproportionately high fecundity of these individuals would make significant contributions to recruitment and that large-bodied individual fish would be part of their ecosystem in greater numbers than now observed. This would at least partly deal with situations wherein poor population recovery has followed the genetic influence of commercial fishing (Walsh et al. 2006). In such cases, our recommendations are as preventative and restorative as management measures can be, insofar as size selectivity is concerned (some changes caused by previous management are probably irreversible).

Following the traditional logic of conventional management, a number of arguments can be made in reaction to our conclusions. Two, both involving competition, are worthy of note. First, it can be argued that harvesting fish the same size as those found in the diets of marine mammals puts us into more (rather than less) direct competition with such species (e.g., Mecenero et al. 2007), many of which are already

declining. Second, it can be argued that we should actively reduce the populations of species with which we compete, thereby making a larger share of mutually consumed resources available to humans (as may be the position of whaling nations in the context of management by the International Whaling Commission; Gerber et al. 2009). Although there is simplistic logic behind such arguments, each can easily be judged to be problematic. Each alternative serves as an example of how we often judge one factor to be more important than another in the subjectivity of conventional management. If, on the basis of such an argument, managers were to avoid correcting the abnormal selectivity we have identified, it would involve the assumption that one particular form of competition is more important than, for instance, the genetic effects of selectivity. Such value-based decisions are often designed into current decision-making processes, even to the extreme of being required by law.

By contrast, in systemic management, rather than debate the relative merits of such issues, the issues are used as motivation to refine existing management questions or to ask new ones (Fowler and Hobbs 2009). Systemic management deals with “both-and” rather than “either-or” solutions to management questions; that is, systemic management deals with both competition (e.g., Fowler 2003) and size selectivity (the topic of this paper) rather than one or the other. After asking the pertinent questions, scientific data exemplified by the kind we have presented here can provide answers regarding selectivity, and different sets of data can serve to provide answers regarding the harvest rates involved in competition. In both cases, the answers involve an objectivity that avoids the above-mentioned judgments (Belgrano and Fowler 2008; Fowler and Hobbs 2009).

Concerns such as those raised above involve niche overlap and direct competition with other mammalian species. However, if we take fish differing in size from those taken by marine mammals, we are directly competing with other predator species and quite likely competing indirectly with marine mammals (e.g., through reductions in overall prey availability, fecundity, etc.). Avoiding competition entirely is unrealistic, and we are forced to ask management questions about the sustainability of harvests wherein we put ourselves in competition with other species. Nonhuman species compete with each other; it is part of what happens in ecological systems, and empirical information about consumption rates involving competition reveal sustainability (Fowler 2003). There may be niche separation based on the suite of species consumed, and related patterns can be used to allocate consump-

tion across alternative prey species available in an ecosystem (Fowler 1999). If there are patterns in the size range of prey taken by individual nonhuman predators, these would be used to confine the range of sizes taken in commercial harvests. To deal with complexity, we must treat both selectivity and competition—in all of the ways they can be measured—along with other factors. In all cases, we would strive to avoid the abnormal.

Another factor that weighs heavily in conventional management is the matter of economics. In the USA, federal law requires consideration of economic issues in setting environmental policy and in managing our use of resources. Our recommendations would produce extraordinary economic cost to the commercial fishing industry and, as such, will probably be rejected by many with no further consideration. It is worth pointing out, however, that similar approaches have been used successfully in U.S. sport fisheries since the 1970s (e.g., the use of “slot” limits; see Brousseau and Armstrong 1987) and in purse seine fisheries for Cape horse mackerel *Trachurus trachurus capensis* (Meceño et al. 2007). Use of economic considerations to override progress toward actual sustainability (both ecological and economic; Belgrano and Fowler 2008) serves as an excellent example of conventional management (see also Rosenberg 2003). In systemic management, sustainability is paramount to economics, and economic factors and their influence are accounted for a priori in the patterns used to make management decisions; as discussed earlier, empirical patterns reflect abnormal human influence. Abnormal human influence (including economic forces) and circumstances independent of human influence are reflected in the patterns we observe. Using these patterns to guide management is progress toward achieving the health of ecosystems, avoiding abnormality among other species, and finding success in dealing with matters of long-term concern (e.g., evolutionary and coevolutionary processes).

Thus, to correct past mistakes exemplified by considering economic factors to be of greater importance than sustainability, we recommend that the selectivity of human resource use be managed based on empirical patterns that reveal the selectivity at work in natural systems. Our paper has focused on size selectivity, and we recommend that commercial harvests of fish be changed on a target-species-specific basis to mimic the size selectivity found among nonhuman mammalian predators. Parallel applications will work for any form of selectivity, whether it is selectivity among alternative prey species, geographic locations, depth, or seasons. For instance, in harvesting fish, we need to regulate the ratio of females to males

in the catches, the ratio of one phenotype to another, and the ratio of reproductive to pre-reproductive age categories. To deal with the complexity of ecosystems, there is a long list of such factors. The evolutionary enlightenment deemed by so many experts to be a necessary addition to or modification of management is now a realistic and attainable option. It is part of systemic management to involve both ecological and evolutionary applications—not simply one or the other.

Acknowledgments

This study benefited greatly from numerous discussions with our colleagues at the Alaska Fisheries Science Center, Seattle, Washington, most notably Beth Sinclair, Pat Livingston, and William Walker. We thank Gary Duker, Jeff Hard, Neala Kendall, James Lee, Beth Sinclair, the editors, and two anonymous reviewers for providing very insightful comments on drafts of this paper. We recognize that some may find the ideas presented here disconcerting, which makes it all the more noteworthy that there have been those willing to discuss them in a scholarly, friendly manner. Such discussions lead to new and important management questions. For that, we are thankful.

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Appendix 1: Prey Size Data, Combined Across Marine Mammal Predator Taxa

TABLE A.1.—Summary of prey size data for marine prey species with 10 or more cases in the analysis, combined across mammalian predator species.

Prey species	Number of cases		Mean prey size (cm) ^c
	Total	In analysis ^b	
Crustaceans ^a	34	29	3.99
Euphausiidae			
Antarctic krill <i>Euphausia superba</i>	15	15	4.53
Cephalopods ^a	487	275	18.94
Loliginidae			
Market squid <i>Loligo opalescens</i>	15	10	11.58
Chokka squid <i>Loligo vulgaris reynaudii</i>	13	11	14.04
Bony and cartilaginous fishes ^a	645	421	18.46
Clupeidae			
Atlantic herring <i>Clupea harengus</i>	11	10	27.49
Pacific sardine <i>Sardinops sagax</i>	14	11	16.72
Myctophidae			
Lanternfish <i>Electrona antarctica</i>	13	12	7.83
Lanternfish <i>Electrona subaspera</i>	13	10	8.04
Nichols' lanternfish <i>Gymnoscopelus nicholsi</i>	15	15	12.06
Gadidae			
Atlantic cod <i>Gadus morhua</i>	24	19	26.15
Walleye pollock <i>Theragra chalcogramma</i>	36	26	24.10
Merlucciidae			
Shallow-water Cape hake <i>Merluccius capensis</i>	12 ^d	10 ^d	20.84 ^d
Deep-water Cape hake <i>M. paradoxus</i>			
Nototheniidae			
Antarctic silverfish <i>Pleuragramma antarcticum</i>	14	11	14.40
Overall total ^a	1,166	727	17.63

^a Summary results include all data presented in Etner and Fowler (2005).

^b Includes only those cases where mean prey size was based on a sample size of 10 or more.

^c Unweighted mean of means.

^d Shallow- and deep-water Cape hakes are combined as "Cape hake."

Appendix 2: Prey Size Data for Individual Species of Mammalian Predators

TABLE A.2.—Summary prey size data for marine mammal predator species with 10 or more cases in the analysis.

Predator species	Number of cases		Mean prey size (cm) ^c
	Total	In analysis ^b	
Otariid seals ^a	361	237	15.82
Antarctic fur seal <i>Arctocephalus gazella</i>	142	99	12.33
Australian fur seal <i>A. pusillus doriferus</i>	14	11	19.97
South African fur seal <i>A. pusillus pusillus</i>	72	49	17.98
Sub-Antarctic fur seal <i>A. tropicalis</i>	22	12	9.47
Northern fur seal <i>Callorhinus ursinus</i>	46	18	12.90
California sea lion <i>Zalophus californianus</i>	14	12	14.27
Phocid seals ^a	234	146	18.64
Grey seal <i>Halichoerus grypus</i>	78	52	24.64
Southern elephant seal <i>Mirovunga leonina</i>	33	12	14.72
Harp seal <i>Phoca groenlandica</i>	26	11	20.31
Harbor seal <i>Phoca vitulina</i>	36	33	15.45
Odontocete whales ^a	556	338	18.64
Baird's beaked whale <i>Berardius bairdii</i>	19	15	36.64
Long-finned pilot whale <i>Globicephala melas</i> (= <i>G. melaena</i>)	21	10	16.43
Risso's dolphin <i>Grampus griseus</i>	24	15	12.08
Southern bottlenosed whale <i>Hyperoodon planifrons</i>	71	44	25.04
Pygmy sperm whale <i>Kogia breviceps</i>	27	12	15.85
Harbor porpoise <i>Phocoena phocoena</i>	50	31	16.99
Dall's porpoise <i>Phocoenoides dalli</i>	43	37	12.88
Sperm whale <i>Physeter macrocephalus</i> (= <i>P. catadon</i>)	69	47	31.35
Tucuxi <i>Sotalia fluviatilis</i>	20	10	9.71
Pan-tropical spotted dolphin <i>Stenella attenuata</i> ^a	42	37	12.74
Overall ^a	1,166	727	17.63

^a Summary results include all data presented in Etnier and Fowler (2005).^b Includes only those cases where mean prey size was based on a sample size of 10 or more.^c Unweighted mean of means.