Ecosystem Impact of the Decline of Large Whales in the North Pacific

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Biodiversity loss can significantly alter ecosystem processes (Chapin et al. 2000), and ecological extinction can have similar effects (Jackson et al. 2001). For marine vertebrates, overharvesting is the main driver of ecological extinction, and the expansion of fishing fleets into the open ocean has precipitated rapid declines in pelagic apex predators such as whales (Baker and Clapham 2002), sharks (Baum et al. 2003), tuna, and billfishes (Cox et al. 2002; Christensen et al. 2003), leading to a trend in global fisheries toward exploitation of lower trophic levels (Pauly et al. 1998a). Globally, many fish stocks are overexploited (Steneck 1998), and the resulting ecological extinctions have been implicated in the collapse of numerous nearshore coastal ecosystems (Jackson et al. 2001). Nevertheless, although the declines of apex predators in pelagic ecosystems are well documented, the ecosystem impacts of such declines are unclear (Steneck 1998, Jackson et al. 2001).

The ecological role of large whales (baleen and sperm whales) in pelagic ecosystems and the consequences of the decline of their populations from whaling has been the focus of debate for pelagic ecologists, conservation biologists, fisheries managers, and the general public. The severe depletion of stocks of large whales is one of the best documented examples of the overexploitation of apex predators. In the North Pacific, at a minimum estimate, 62,858 whales, representing 1.8 million tons of whale biomass, were removed over a 150-year period (Springer et al. 2003). Although large whales are significant consumers of pelagic prey, such as schooling fish and euphausiids (krill), the trophic impacts of their removal is not clear (Trites et al. 1999). Indeed, it is possible that the biomass of prey consumed by large whales prior to exploitation exceeded that currently taken by commercial fisheries (Baker and Clapham 2002), but estimates of prey consumption by large whales before and after the period of intense human exploitation are lacking. Given the large biomass of pre-exploitation whale populations (see, e.g., Whitehead 1995; Roman and Palumbi 2003), their high mammalian metabolic rate, and their relatively high trophic position (Trites 2001), it is likely that the removal of large whales over a 150-year period by human harvest had cascading effects, leading to changes in energy flow and species composition at other trophic levels (Bowen 1997).

In Antarctica, Laws (1977, 1984, 1985) speculated that the removal of baleen whales increased krill availability to fur seals and penguins by as much as 150 million tons annually, and May et al. (1979) modeled how this could lead to significant increases in seal populations. Several studies have provided estimates of the prey requirements of current populations of cetaceans across multiple geographic areas using a variety of approaches (Sergeant 1969; Brodie 1975; Lockyer 1981; Lavigne et al. 1986; Innes et al. 1987; Vikingsson 1990; Armstrong and Siegfried 1991; Ichii and Kato 1991; Kawamura

1994; Vikingsson 1995; Sigurjónsson and Vikingsson 1997; Trites et al. 1997; Vikingsson 1997). However, with the exception of Laws' (1977) estimates for Antarctica and Trites et al.'s (1999) estimates for the Bering Sea, few studies have attempted to assess the impacts of commercial whaling on energy flow in pelagic ecosystems by comparing the percent of marine primary productivity consumed by whales before and after the period of intensive commercial whaling.

In the absence of empirical observations, one method to examine the trophic impact of consumers on ecosystems is to assess changes in the amount of net primary production required (PPR) to sustain them (Vitousek et al. 1986; Pauly and Christensen 1995; Kenney et al. 1997; Trites et al. 1997). Using this approach, Vitousek et al. (1986) estimated that humans consume 35%–40% of terrestrial primary production. In marine systems, Pauly and Christensen (1995) estimated that commercial fisheries required 8% of global aquatic primary production to sustain them, and Brooke (2004) estimated that seabirds consume 7% of global primary production. In this chapter we use a similar approach to assess the potential trophic impact of the historical removal of large whales from the North Pacific pelagic ecosystem.

Approach

An assessment of the impact of the removal of large whales on energy flow requires (1) estimates of prey biomass consumption rates for each whale species, (2) estimates of pre- and postexploitation whale populations, (3) estimates of the trophic level and trophic transfer efficiencies of individual whale species, and (4) estimates of the net primary production of the ecosystem.

Whale Prey Biomass Consumption

We used two approaches to estimate whale prey biomass consumption per individual whale of each large whale species: allometric estimates of whale metabolic rates and allometric estimates of whale ingestion rates. For the metabolic rate approach, we combined allometric estimates of resting/basal metabolic rates of whales with known diet, prey energy estimates, and assimilation efficiencies to calculate the mass of prey required daily by individuals of each large whale species. Three independent allometric metabolic rate models were used. The first model (Hemmingsen 1960) relied upon empirically derived measures of mammalian resting metabolic rates,

$$\text{Active Metabolic Rate (W)} = 12.3(\text{Body Mass (kg)})^{0.75}, \quad (16.1)$$

as did the second model (Kleiber 1961),

$$\text{Active Metabolic Rate (W)} = 9.84(\text{Body Mass (kg)})^{0.756}. \quad (16.2)$$

In both cases, we assumed that daily metabolic rates in free-living animals were 3 times resting/basal rates (Costa and Williams 1999). The third approach (Nagy et al. 1999) relied upon an allometric model of empirically measured field metabolic rates using doubly labeled water:

$$\text{Field Metabolic Rate (W)} = 8.88(\text{Body Mass (kg)})^{0.734}. \quad (16.3)$$

Prey energy required was converted to prey biomass required (PBR) using published data on diet composition (Pauly et al. 1998b), prey energy density (Clarke 1980; Boyd 2002), and consumer assimilation efficiency (84%; Lockyer 1981).

For the ingestion rate approach we used two allometric models of prey ingestion rates. The first model (Innes et al. 1987) was based upon empirically measured biomass ingestion rates in marine mammals:

$$\text{Prey Biomass Required (kg)} = 0.42(\text{Body Mass (kg)})^{0.67}. \quad (16.4)$$

The second model (Nagy 2001) was based upon empirically measured biomass ingestion rates in terrestrial and aquatic mammals using doubly labeled water:

$$\text{Prey Biomass Required (kg)} = 0.17(\text{Body Mass (kg)})^{0.773}. \quad (16.5)$$

An important caveat is that in all approaches, allometric estimates were calculated from extrapolations well beyond the range of empirically measured subjects.

Whale Population Estimates

We restricted our analysis to the North Pacific/Bering Sea region. Population numbers of this region prior to exploitation and at current levels were taken from published estimates (Table 16.1). Such estimates are difficult to derive, can be speculative, and can lead to inaccuracies in our estimates of trophic impact. Ranges of population estimates prior to exploitation are not published in the literature (only point estimates are available). Measures of dispersion of estimates of current populations in the study region have been published as confidence intervals, ranges, or standard deviations. To account for uncertainty in current population estimates, we estimated population prey consumption rates based on the high, low (i.e., dispersion) and published best estimates of the current population. Generally, dispersion measures varied by less than 25% of the best population estimate. For example, Perry et al. (1999) reviewed population estimates of large whales, and the largest maximum-minimum range difference in North Pacific large-whale populations they examined (fin whales) differed by only 22%. Differences of this magnitude have minimal impacts on biomass consumption estimates.

TABLE 16.1

Body Mass, Population Estimates, and Population Biomass of North Pacific Large Whales Used to Estimate Prey
Consumption Rates

	Blue	Fin	Sei	Bryde's	Humpback	Minke	N. Right	Gray	Sperm
Body mass (kg)[a]	69,235[b]	55,600[c]	16,811[d]	16,143[d]	30,400[c]	6,600[c]	23,400[c]	15,400[c]	18,500[c]
Population									
Current Low	2,475[e]	14,620[e]	7,260[e]	22,500[f]	6,000[e]	22,500[g]	404[e]	24,477[h]	75,648[i]
Current High	4,125	18,630	12,620	37,500	8,000	37,500	2,108	28,793	83,958
Current Best	3,300	16,625	9,110	30,000	7,000	30,000	1,256	26,635	79,803
Pre-exploitation	4,900	43,500	42,000	39,000	15,000	30,000	31,750	26,635	204,454
Reference	4	4	4	5	4	6	4	5	7
Biomass (metric tons)									
Current Best	228,476	924,350	153,157	484,290	212,800	198,000	29,390	410,179	1,476,356
Pre-exploitation	339,252	2,418,600	706,062	629,577	456,000	198,000	742,950	410,179	3,782,399

[a]Body masses are averages of male and female values.

[b]Lockyer (1976).

[c]Pfister and DeMaster, Chapter 10 of this volume.

[d]Trites and Pauly (1998).

[e]Population estimates from Perry et al. (1999).

[f]Because of complexities of population structure and reporting uncertainty (i.e., confusion between whale stocks and other species such as sei whales), it is difficult to estimate the Northern Pacific population of Bryde's whales confidently. We used pre- and postexploitation estimates of the western North Pacific from the International Whaling Commission and combined these with an estimate of postexploitation numbers for the entire eastern tropical Pacific provided by Wade and Gerrodete (Carretta et al. 2002). Thus, both our pre- and postexploitation estimates are likely overestimates for Bryde's whales.

[g]Population estimates from Ohsumi (1991).

[h]Population estimates from Carretta et al. (2002).

[i]Sperm whale population estimates are derived from areal extrapolations of estimates published by Whitehead (2002).

TABLE 16.2

Allometric Estimates of Daily Metabolic Rates of Large Whales of the North Pacific

	Estimated Daily Metabolic Rate (W)					
	Eq. (16.1), 3 × Basal	Eq. (16.2), 3 × Basal	Eq. (16.3), Average Daily	Mean	SD	CV
Blue	52,499	44,904	31,720	43,041	10,514	24.4%
Fin	44,536	38,043	27,003	36,527	8,864	24.3%
Sei	18,159	15,401	11,223	14,928	3,492	23.4%
Bryde's	17,615	14,936	10,894	14,482	3,384	23.4%
Humpback	28,318	24,102	17,337	23,252	5,540	23.8%
Minke	9,007	7,596	5,650	7,418	1,685	22.7%
Northern right	23,271	19,775	14,307	19,118	4,518	23.6%
Gray	17,004	14,413	10,524	13,980	3,262	23.3%
Sperm	19,511	16,557	12,040	16,036	3,763	23.5%

TABLE 16.3
Prey Biomass Requirements for North Pacific Large Whales Derived from Five Different Models

Whale	Prey Biomass Requirements (kg individual^{-1} day^{-1})							
	Eq. (16.1)	Eq. (16.2)	Eq. (16.3)	Eq. (16.4)	Eq. (16.5)	Mean	SD	CV
Blue	1607	1375	971	735	913	1120	359	0.32
Fin	1259	1076	763	635	771	901	258	0.29
Sei	513	435	317	285	306	371	99	0.27
Bryde's	417	354	258	277	296	320	65	0.20
Humpback	711	605	435	423	483	532	123	0.23
Minke	235	199	148	152	148	176	39	0.22
Northern right	712	605	438	355	395	501	152	0.30
Gray	521	441	322	268	286	368	109	0.30
Sperm	476	404	294	304	329	361	77	0.21

When only ranges were available, we used median values as the best estimate of the population.

Trophic Level and Trophic Transfer Efficiencies

To estimate the PPR to sustain pre- and postwhaling populations, we converted estimated prey biomass requirements of whales (PBR) to PPR using estimates of whale trophic levels and trophic transfer efficiencies. We estimated whale trophic levels by combining whale diet composition with prey trophic level estimates (Pauly et al. 1998b). Using these estimates, we converted prey biomass requirements of whales to PPR using whale trophic level (TL) and an estimate of trophic transfer efficiency published by Pauly and Christensen (1995):

$$PPR = (PBR/9) \times 10^{(TL-1)} \qquad (16.6)$$

Net Primary Production

Net primary production (NPP) for the North Pacific was estimated using the vertically generalized production model (VGPM) derived from global samples of ^{14}C measures of primary production (Behrenfeld and Falkowski 1997). The VGPM provides a method to estimate primary production using satellite-derived measures of chlorophyll concentration. We used estimates of chlorophyll concentration from SeaWiFS satellite images of the North Pacific/Bering Sea, averaged 1998–2001, to estimate annual net primary production using the VGPM.

Model Results

Large-whale populations in the North Pacific declined to 47% of pre-exploitation levels—from approximately 437,000 pre-exploitation to the current level of approximately 204,000 (Table 16.1). This resulted in a 58% decline in large-whale biomass from 9.7 million metric tons to 4.1 million metric tons.

Individual Whale Prey Biomass Consumption

Based upon estimates from allometric models of respiration rate, the metabolic rates of large whales range from 43 kW for blue whales to 7.4 kW for minke whales (Table 16.2). Using these values, we estimated the mean PBR to sustain individual whales ranged from 1,120 kg day^{-1} (blue whales) to 176 kg day^{-1} (minke whales) (Table 16.3).

Whale Population Prey Biomass Consumption

Combining individual whale prey biomass consumption values with population estimates, we calculated the average daily prey biomass required to sustain the North Pacific populations of large whales before and after their declines from exploitation (Table 16.4). These numbers have uncertainties related to extrapolations of allometric equations beyond empirical data and errors in published estimates of whale populations. Given these caveats, we estimated daily population prey biomass requirements ranged from 629 metric tons day^{-1} to sustain the current population of northern right whales to approximately 74,000 metric tons day^{-1} to sustain the pre-exploitation population of sperm whales. Because of the large pre-exploitation population size of sperm whales, this species has the highest gross prey biomass requirements of North Pacific large whales. We estimate that whaling reduced the total daily prey biomass consumption for all North Pacific large-whale populations by 57%: Pre-exploitation daily prey biomass consumption totaled some 185,000 metric tons day^{-1}, whereas postexploitation consumption totals some 80,000 metric tons day^{-1}.

Primary Production Required to Sustain Whale Populations

We estimated average daily net primary production for the North Pacific to be 2.54×10^{10} kg C day^{-1}. Published information on the diet of North Pacific whales (Table 16.5) was combined with published trophic levels for whale diet items: large zooplankton, 2.2; fish, 2.7, small squid, 3.2, large squid, 3.7,

TABLE 16.4
Estimated Daily Prey Biomass Requirements (thousands of metric tons day^{-1}) for North Pacific Large-Whale Populations

	Estimated Daily Prey Biomass Requirements (thousands of metric tons per day)											
	Respiration Models						Ingestion Models					
	Eq. (16.1)		Eq. (16.2)		Eq. (16.3)		Eq. (16.4)		Eq. (16.5)		Mean	
Whale	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation
Blue	5.3	7.9	4.5	6.7	3.2	4.8	2.4	3.6	3.0	4.5	3.7	5.5
Fin	20.9	54.8	17.9	46.8	12.7	33.2	10.5	27.6	12.8	33.5	15.0	39.2
Sei	4.7	21.6	4.0	18.3	2.9	13.3	2.6	12.0	2.8	12.8	3.4	15.6
Bryde's	12.5	16.3	10.6	13.8	7.7	10.1	8.3	10.8	8.9	11.6	9.6	12.5
Humpback	5.0	10.7	4.2	9.1	3.0	6.5	3.0	6.4	3.4	7.3	3.7	8.0
Minke	7.1	7.1	6.0	6.0	4.4	4.4	4.6	4.6	4.5	4.5	5.3	5.3
Northern right	0.9	22.6	0.8	19.2	0.6	13.9	0.4	11.3	0.5	12.5	0.6	15.9
Gray	13.9	13.9	11.8	11.8	8.6	8.6	7.2	7.2	7.6	7.6	9.8	9.8
Sperm	38.0	97.3	32.2	82.5	23.4	60.0	24.2	62.1	26.3	67.3	28.8	73.8
Total	108.2	252.0	91.9	214.2	66.6	154.8	63.2	145.4	69.7	161.6	79.9	185.6

TABLE 16.5
Trophic Position of Prey, Whale Diet, and Estimated Trophic Level of North Pacific Large Whales

Prey Species	Prey Trophic Position	Diet Composition (Proportion)[a]								
		Blue	Fin	Sei	Bryde's	Humpback	Minke	N. Right	Gray	Sperm
Large zooplankton	2.2	1	0.8	0.8	0.4	0.55	0.65	0	1	0
Fish	2.7	0	0.15	0.15	0.6	0.45	0.35	0	0	0.25
Small squid	3.2	0	0.05	0.05	0	0	0	0	0	0.1
Large squid	3.7	0	0	0	0	0	0	0	0	0.6
Small zooplankton	2.0	0	0	0	0	0	0	1	0	0.05
Trophic Level[b]		3.20	3.33	3.33	3.50	3.43	3.38	3.00	3.20	4.22

[a]Based on Pauly et al. (1998b).

[b]Based on weighted mean trophic position of diet items.

small zooplankton, 2.0 (Trites et al. 1999). This yielded estimates of the trophic position of North Pacific large whales (Table 16.5). We assumed a trophic transfer efficiency of 0.1 (Pauly and Christensen 1995) and used our estimates of trophic position and population prey biomass requirements to calculate biomass of PPR to sustain each whale species prior to and after exploitation (Table 16.6). For all large-whale populations in the North Pacific, we estimate that pre-exploitation populations required a total of 16 million metric tons of fixed carbon per day, whereas current populations require a total of 6.5 million metric tons of fixed carbon per day. Combining our estimates of primary production required to sustain large-whale populations with our estimate of average daily net primary production for the North Pacific, we estimated the percentage of average daily net primary production (NPP) required to sustain North Pacific large-whale populations at current numbers and at pre-exploitation numbers (Table 16.7). For all North Pacific whale populations, pre-exploitation populations required approximately 64.5% of NPP, whereas current populations require 26.3% of North Pacific NPP.

Discussion

Rapid Removal of Large Whales

Because of the large range, long-distance movement patterns, and logistical difficulties in conducting population surveys for large cetaceans, it is difficult to assess their current population numbers accurately (Clapham et al. 1999; Perry et al. 1999; Clapham et al. 2003). It is even more difficult to assess pre-exploitation population numbers accurately (Gerber et al. 2000). We used available estimates for current and postexploitation population numbers from the literature, which likely introduced error into our calculations. However, the magnitude of error introduced by

inaccuracies in population estimates is relatively small compared to the effect of whaling. Indeed, the range of estimated percent daily net primary production required (Table 16.7) varied by less than 2% using high, low, and best estimates of current population sizes from the literature. Regardless, there is a clear consensus that commercially exploited North Pacific whale populations experienced severe declines to a fraction of their original sizes during the past two centuries (Clapham et al. 1999). Thus, even substantial adjustments in pre-exploitation and current estimates of large-whale populations do not seriously affect conclusions drawn from the consumption estimates on which they are based.

Using best available population estimates, large-whale populations in the North Pacific were reduced by approximately 53% (from approximately 437,000 to 204,000 individuals) (Table 16.1). This reduction occurred in less than 150 years, with most of it taking place during approximately 100 years (from the mid-nineteenth to the mid-twentieth century; Clapham et al. 1999). Because larger species were preferentially harvested, total whale biomass in the North Pacific was reduced 58% from approximately 9.7 million metric tons to 4.1 million metric tons. A comparable decline took place in Antarctica, where commercial whaling was estimated to have removed 65% (Laws 1977) of whale stocks, reducing whale biomass by 85%.

Commercial whaling not only reduced the population and biomass of large whales in the North Pacific; it also changed the large-whale community composition. Pre-exploitation whale biomass of sperm whales represented 47% of total whale biomass, whereas sperm whales represent 39% of the present-day biomass in large whales. This may have important trophic implications, because the large-whale community has shifted from one dominated primarily by squid predators (sperm whales) to one dominated primarily by fish and zooplankton predators (rorquals). Sperm whales are almost a full trophic level above rorquals (Table 16.5) in marine food webs. Thus,

TABLE 16.6
Estimated Primary Production Required to Sustain Large-Whale Populations in the North Pacific

	Primary Production Required (thousands of metric tons per day)											
	Respiration Models						Ingestion Models					
	Eq. (16.1)		Eq. (16.2)		Eq. (16.3)		Eq. (16.4)		Eq. (16.5)		Mean	
Whale	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation	Current	Pre-exploitation
Blue	93	139	80	119	56	84	43	63	53	79	65	97
Fin	492	1286	420	1099	298	780	248	648	301	787	352	920
Sei	110	506	93	429	68	313	61	281	65	302	79	366
Bryde's	440	572	373	485	272	353	292	380	312	406	338	439
Humpback	147	315	125	268	90	193	88	188	100	214	110	236
Minke	186	186	157	157	117	117	120	120	117	117	140	140
Northern right	10	251	8	214	6	155	5	125	6	139	7	177
Gray	244	244	207	207	151	151	126	126	134	134	172	172
Sperm	6,921	17,732	5,873	15,047	4,271	10,943	4,416	11,314	4,790	12,272	5,254	13,462
Total	8,643	21,232	7,337	18,024	5,329	13,088	5,398	13,245	5,879	14,451	6,517	16,008

TABLE 16.7
Percentage of Average Daily Net Primary Production of the North Pacific Required to Sustain
North Pacific Large-Whale Populations

	Model Results						
	Respiration Models			Ingestion Models		*Summary*	
	Eq. (16.1)	Eq. (16.2)	Eq. (16.3)	Eq. (16.4)	Eq. (16.5)	Mean	SD
Mysticetes and Sperm Whales							
Current N. Pacific Low	32.1%	27.3%	19.8%	20.1%	21.9%	24.2%	5.3%
Current N. Pacific High	37.5%	31.9%	23.1%	23.4%	25.5%	28.3%	6.2%
Current N. Pacific Best	34.8%	29.6%	21.5%	21.7%	23.7%	26.3%	5.8%
Pre-exploitation N. Pacific	85.5%	72.6%	52.7%	53.4%	58.2%	64.5%	14.2%
Mysticetes Only							
Current N. Pacific Low	5.7%	4.8%	3.5%	3.2%	3.6%	4.2%	1.1%
Current N. Pacific High	8.2%	7.0%	5.0%	4.7%	5.2%	6.0%	1.5%
Current N. Pacific Best	6.9%	5.9%	4.3%	4.0%	4.4%	5.1%	1.3%
Pre-exploitation N. Pacific	14.1%	12.0%	8.6%	7.8%	8.8%	10.3%	2.7%
Rorquals Only							
Current N. Pacific Low	4.8%	4.0%	2.9%	2.7%	3.1%	3.5%	0.9%
Current N. Pacific High	7.1%	6.0%	4.3%	4.1%	4.6%	5.2%	1.3%
Current N. Pacific Best	5.9%	5.0%	3.6%	3.4%	3.8%	4.4%	1.1%
Pre-exploitation N. Pacific	12.1%	10.3%	7.4%	6.8%	7.7%	8.9%	2.3%

their removal may have had more profound implications on marine ecosystems than the removal of rorquals.

Whale Metabolic Rates and Prey Consumption Rates

Our calculations of prey and primary production requirements are influenced by population estimates, estimates of trophic positions, and assumptions regarding metabolic rates. Boyd (2002) points out that error in such estimates is both additive (e.g., metabolic rates, assimilation efficiency) and multiplicative (e.g., populations, time). We used 3 independent allometric models to estimate whale metabolic rates. All models provided similar estimates: Across all species, the coefficient of variation was consistently around 24% (Table 16.2). Based upon various methods, Lockyer (1981) estimated the basal metabolic rate for a 70,790 -kg blue whale at 12,269 to 24,539 W. Assuming an active metabolic rate of 3 times basal and using Lockyer's estimates yields a range of approximately 36.8 to 73.6 kW, within which our average estimate of 43.0 kW for a 69,200-kg blue whale falls. Lockyer also used a muscle equivalent method to estimate active metabolic rate. Her estimate of 232,778 W was considerably greater than our average estimate. However, it is unlikely that blue whales sustain an active metabolic rate 9.5 to 18 times basal. Our estimate for the daily metabolic rate

for minke whales (7.4 kW) lies within Markussen et al.'s (1992) estimates of the average daily energy requirements for minke whales of 9,214 W for females and 6,789 W for males.

Sigurjónsson and Vikingsson (1997) used two allometric methods to estimate the metabolic rates of blue, fin, sei, minke, humpback, and sperm whales. For each of these species, our estimates of metabolic rate were 3% (blue whale) to 52% (sperm whale) lower than their estimates of daily energy consumption made using two models. Costa and Williams (1999) concluded that the basal metabolic rate of marine mammals is actually 1.2 to 2 times Kleiber's (1961) allometric estimates. If that conclusion is true, then our estimates would be 20 to 100% lower than a calculation based upon Costa and Williams's values for marine mammal basal metabolic rates. Nonetheless, our values can be considered within the range of values estimated by most studies and tend to be somewhat conservative (i.e., lower).

Our estimates of individual consumption of prey biomass (Table 16.3) are also comparable to others'. Armstrong and Siegfried (1991) estimated Antarctic minke whale daily prey consumption using metabolic rate during the feeding season as 212 kg day^{-1} for males and 252 kg day^{-1} for females. These can be compared to our estimate of 176 kg day^{-1}. Markussen et al. (1992) estimated minke whale prey consumption at 204 kg day^{-1} for males and 277 kg day^{-1} in females. Vikingsson

(1997) estimated fin whale prey consumption from stomach volume and passage rates at 677–1,356 kg day^{-1}, comparable to our estimate of 901 kg day^{-1}.

Trophic Importance of Current Populations of Large Whales

We estimate that large whales in the North Pacific currently consume some 80,000 metric tons of prey per day (Table 16.4). Several studies have estimated the prey biomass requirements for individual species as well as communities of marine mammals for a variety of marine areas, and these provide useful comparisons for our estimates. Based on our estimates, large whales in the North Pacific currently consume approximately 19% of the 418,688 metric tons day[-1] Trites et al. (1997) estimated is consumed by marine mammals (including mysticetes, odontocetes, and pinnipeds) in the entire Pacific Ocean. Armstrong and Siegfried (1991) estimated the minke whale population prey biomass requirement in the Antarctic at 97,260 metric tons day[-1], whereas Markussen et al. (1992) estimated that northeast Atlantic minke whales consumed 14,667 metric tons day[-1].

The maximum biomass extracted by commercial fisheries in the North Pacific occurred in 1998 and averaged 75,468 metric tons of fish day[-1] (FAO 2002). This is comparable to our estimate of prey biomass consumed by current populations of large whales in the North Pacific. It has been argued that most commercial fisheries, including the North Pacific fishery, are overexploited (Pauly et al. 1998a, Steneck 1998). Because commercially targeted species are often top predators, their declines can have cascading trophic impacts (Dayton et al. 1998, Worm and Myers 2003). The mean trophic level of commercial fisheries in the North Pacific was estimated by Pauly et al. (1998b) to have declined from a maximum of 3.4 in the early 1970s to 3.2 by 1994. Combining trophic level values (Table 16.5) with prey biomass consumption estimates (Table 16.4); we estimate the weighted mean trophic level of North Pacific large whales to be 3.4. Thus, in terms of both prey biomass consumption and trophic level, it can be argued that current populations of large whales are of similar importance in the North Pacific marine ecosystems to commercial fisheries. The impact of pre-exploitation levels of great whales in this area would have been much greater.

Several studies have estimated the primary production required to sustain consumer populations in other regions: Kenney et al. (1997) estimated that cetaceans in some coastal regions of the northwestern Atlantic consume 11.7%–20.4% of net primary production, while Trites et al. (1997) estimated that marine mammals in the Pacific consume 12%–17% of net primary production. We estimate that current populations of large whales (smaller odontocetes and pinnipeds excluded) in the North Pacific consume approximately 26% of net primary production. This is considerably greater than the weighted mean primary production required to sustain world fisheries (8% of net primary production; Pauly and Christensen 1995). Thus, assuming that commercial fishing has important trophic impacts in marine ecosystems, current populations of large whales also appear to be important trophic interactors.

Community Implications of the Decline of Large Whales

Virtually every ecosystem is characterized by both bottom-up (resource limitation) and top-down (consumer control) interactions (Hunter and Price 1992). The bottom-up view holds that populations of organisms on each trophic level are resource limited by nutrients or food, while the top-down view focuses on predators' control of their prey leading to the situation where, at successive trophic levels, populations are alternately resource or predator limited (Fretwell 1977). Traditionally, oceanographers have characterized pelagic marine ecosystems as being bottom-up regulated (Verity and Smetacek 1996), whereas the top-down view has dominated our understanding of freshwater and coastal ecosystems (Paine 1966; Estes and Palmisano 1974; Carpenter et al. 1987; Power 1992). Indeed, evidence of trophic cascades in coastal ecosystems has been documented from the removal of large vertebrates such as cod (Worm and Myers 2003), predatory reef fish (Hughes 1994), and sea otters (Estes and Palmisano 1974).

A key element of most trophic cascades is the dependence upon strong interactions by particular species (Pace et al. 1998). Because of their large body size and relatively high metabolic rate, marine mammals have the potential to be strong trophic interactors (Bowen 1997). However, although strong predator-induced trophic cascades have long been recognized in pelagic lake systems (Carpenter and Kitchell 1993), evidence of trophic cascades resulting from predator removals in pelagic marine systems is rare (Micheli 1999a; Pace et al. 1999; Estes et al. 2001). Lack of evidence in pelagic systems may be a result of the logistical difficulty of documenting cascades in the open ocean (Estes et al. 2001), nonexistent baselines (Dayton et al. 1998; Jackson et al. 2001), weak coupling between phytoplankton and herbivores (Micheli 1999b), or more reticulate pelagic food webs with higher degrees of omnivory that dampen classic trophic cascades (McCann et al. 1998).

The removal of large whales from pelagic food webs had several nonexclusive possible outcomes: (1) replacement of the trophic role of large whales by other predators, (2) changes in carbon turnover rates as longer-lived cetaceans are replaced by smaller species with shorter life spans, and (3) the initiation of trophic cascades. Laws (1977) proposed that the removal of large whales from the Southern Ocean ecosystem resulted in increases in their prey and their replacement by other krill predators such as penguins, fur seals, and seals. Essington (Chapter 5 in this volume) used a food web model to show that large whales—primarily sperm whales—were replaced by large squid in the tropical North Pacific. Unfortunately, information on trends in abundance, diet, and trophic interactions of pelagic species is lacking for most systems (DeMaster et al. 2001). This lack, coupled with the problems of assessing change in pelagic ecosystems outlined above, makes an evaluation of

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the relative importance of trophic replacement and trophic cascades initiated by the removal of large whales problematic.

It is certain, however, that whaling severely reduced the prey requirements of large whales. We estimate that North Pacific large whales currently consume approximately 43% of what they consumed prior to whaling (80,000 metric tons per day of prey biomass compared to 186,000 metric tons per day at prewhaling numbers). Laws et al. (1977) estimated that large-whale populations in Antarctica consume 17% of the levels they consumed prior to whaling (30,300 metric tons per day compared to 178,000 metric tons per day prewhaling) and that this decline in krill consumption increased the availability of krill to other consumers in the relatively simple Antarctic ecosystem (see also Ballance et al., Chapter 17 in this volume).

Trites et al. (1999) developed a mass balance model to examine complex trophic interactions resulting from marine mammal declines in the Bering Sea. They estimated that the commercial harvest of large whales in the Bering Sea accounted for 43.4% of Bering Sea net primary production during the 1950s. This does not account for the amount required to sustain the entire population of large whales (that is, it does not include the portion not harvested). Thus, our estimate of 64.5% of primary production requirement for the entire large-whale population of the North Pacific prior to large-scale population declines appears relatively congruent with theirs. In spite of these high consumption rates, Trites et al. (1999) concluded that the overall impact of marine mammal declines had little effect on other species in the Bering Sea ecosystem. They concluded that the removal of large whales may have had a positive effect on pollock *(Theragra chalcogramma)* abundance by reducing competition for food, but this could not explain the dramatic increase in pollock that occurred between the 1950s and 1980s. Instead, they attributed large-scale changes observed in the Bering Sea ecosystem to shifts in primary production due to oceanographic regime shifts.

However, recent studies are providing growing evidence that top-down interactions do play an important role in pelagic marine food webs (Pace et al. 1999). For example, fisheries exploitation has been shown to result in significant changes in the plankton community structure in the North Sea (Reid et al. 2000); microzooplankton have been hypothesized to control plankton community structure in the Bering Sea (Olson and Strom 2002); the relative biomass of phytoplankton and zooplankton in the North Pacific has been attributed to top-down control by pink salmon (Shiomoto and Hashimoto 2000); the profound changes witnessed recently in the Black Sea have been attributed to a trophic cascade initiated by the severe depletion of pelagic predator stocks (Daskalov 2002); and experimental studies have demonstrated that the top-down effect of copepod predation and grazing can profoundly affect pelagic community structure and primary production (Stibor et al. 2004).

While the food web models of Trites et al. (1999) and Essington (Chapter 5 in this volume) predict trophic replace-ment rather than trophic cascades from the removal of large whales, one assumption of their models is that no radical changes in ecosystem organization occurs. Scheffer and van Nes (2004) proposed that dramatic state shifts in marine systems can result from diffuse interactions among many species and feedbacks between organisms and the abiotic environment—scenarios not captured in typical food web models. Thus, it is possible that large changes in food web structure initiated by whaling coupled with large-scale climate changes (e.g., regime shifts) could lead to dramatic state shifts in pelagic ecosystems, including trophic cascades. Scheffer and van Nes (2004) speculated that open ocean state shifts might not arise easily but would tend to be impressive in magnitude and scale when they did occur. Both our estimates and those of Trites et al. (1999) demonstrate that a significant shift in energy flow occurred as a result of whale harvest. Large whales were (and continue to be) important consumers of North Pacific prey biomass; the decline of their populations certainly altered energy flow and trophic interactions; and such perturbations, coupled with climatic changes, have the potential to alter pelagic food web structure dramatically.

Sperm Whale Demands on Marine Ecosystems

Sperm whales may be one of the most important predators in pelagic ecosystems. At pre-exploitation levels, we estimated that sperm whales accounted for 84.1% of the 64.5% of average daily North Pacific NPP consumed by large whales. At current population sizes, we estimate that sperm whales require 80.6% of the total 26.3% of average daily North Pacific NPP consumed by large whales (see Table 16.7). We estimate that whaling has reduced sperm whale consumption of average daily North Pacific NPP to 39% of pre-exploitation levels. The impact of sperm whale reduction may be more significant than that of reductions in other whale species because of sperm whales' large body size, large population size, high trophic level, and potentially important role in top-down control of cephalopods.

Based upon their diet and NPP requirements, sperm whales in the North Pacific are significant cephalopod predators. Cephalopods (1) are active, fast-moving predators; (2) feed on a wide range of prey including crustaceans, fish, and other cephalopods; (3) generally live only one year and die after a single spawning event; (4) have rapid growth rates and high metabolic rates; (5) undergo rapid ontogenetic shifts in prey species within a year; and (6) have been estimated to consume 2.09 to 4.03 Gt of prey each year globally (Rodhouse and Nigmatullin 1996). Rodhouse and Nigmatullin (1996) AUQ 3 argued that these traits indicate that predation by squid significantly affects pelagic ecosystem structure. For example, in the Gulf of California, Ehrhardt (1991) found that a strong migration of *Dosidicus gigas* led to high predation rates in the Gulf and a subsequent decline in sardine landings.

High rates of cephalopod predation by sperm whales, combined with the trophic importance of cephalopods in pelagic

ecosystems, could lead to cascading trophic impacts as squid are released from top-down predation by sperm whales through whaling. Essington (Chapter 5 in this volume) predicted that declines of sperm whales in the tropical and subtropical North Pacific would lead to dramatic increases in the abundance of large squid (as they replace the trophic role vacated by sperm whales). Even in the absence of trophic cascades, the replacement of extremely large, long-lived predators (sperm whales) by smaller, short-lived predators (large squid) should dramatically increase interannual variability in large-predator abundance and thus both the resistance and resiliency of the ecosystem to change. In the presence of a strong trophic cascade, the removal of sperm whales would have an even greater capacity to alter food web structure significantly. This may be particularly important for less productive open-ocean systems, where sperm whale abundance is relatively high.

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In summary, our estimates of NPP requirements demonstrate that large whales are important trophic interactors and that their declines from commercial harvest have significantly altered energy flow in marine food webs. However, a lack of historical data on pelagic ecosystems precludes assessing the relative importance of trophic replacement, trophic cascades, or other major ecosystem changes from this large alteration of energy flow. Nonetheless, there is recent support for the importance of top-down processes in pelagic ecosystems, and the high consumption rates of high-trophic-level species by large whales, particularly sperm whales, suggests that trophic cascades are possible. At the least, the reduction of large whales has probably led to increases in trophic competitors (Worm et al., Chapter 26 in this volume). Some of these competitors (e.g., squid) have short generation times and undergo dramatic interannual variability in abundance. Increased variability may alter the resilience and resistance of pelagic ecosystems to change and ultimately increase susceptibility to dramatic state changes.

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[AUQ1] (Discussion, Community implication of the decline of large whales, 2nd paragraph) Your Micheli 1999a and Micheli 1999b are the same reference. If you mean for one of them to be different, please change it. Otherwise, delete "a" here.

[AUQ2] (Discussion, Community implication of the decline of large whales, 2nd paragraph) Your Micheli 1999a and Micheli 1999b are the same reference. If you mean for one of them to be different, please change it. Otherwise, delete "b" here.

[AUQ3] (Discussion, Sperm whale demands on marine ecosystems, 2nd paragraph) Rodhouse and Nigmatullin (1996) correct? If not, please add Rodhouse 1996 to Lit Cited.

[AUQ4] (Discussion, Sperm whale demands on marine ecosystems, 3nd paragraph) Thus increase both the resistance and the resilience or *reduce* them?

[AUQ5] (Lit Cited, Laws 1984) Please supply page range.

[AUQ6] (Lit Cited, Micheli 1999a) See AUQ1.

[AUQ7] (Lit Cited, Micheli 1999b) See AUQ2.