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). Likewise, ecological extinction through over harvest, particularly of large vertebrates, has been implicated in the collapse of numerous nearshore coastal ecosystems (Jackson et al. 2001). 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 towards exploitation of lower trophic levels (Pauly et al. 1998a). While most fish stocks are overexploited (Steneck 1998), the ecosystem impacts of such declines are unclear (Steneck 1998, Jackson et al. 2001).

The ecological role of large whales in pelagic ecosystems and the consequences of the decline of their populations from whaling has been the focus of interest and debate for pelagic ecologists, conservation biologists, fisheries managers, and the general public. The severe depletion of virtually all global stocks of baleen whales is one of the best documented examples of the overexploitation of apex predators. A minimum estimate of 62,858 whales representing 1.8 million tons of whale biomass was removed from the northern North Pacific (Springer et al. 2003). The biomass of pelagic prey consumed by baleen whales prior to exploitation likely exceeded that currently taken by commercial fisheries (Baker and Clapham 2002). Although large whales are significant consumers of pelagic prey such as schooling fish and euphausiids, the trophic impacts of their removal is not clear (Trites et al. 1999). However, an abrupt change in whale populations due to harvest may have had cascading effects leading to changes in energy flow and species composition at other trophic levels (Bowen 1997).

Roman and Palumbi (2003) recently speculated that pre-whaling North Atlantic baleen whale populations may have been much larger than previous estimates - as much as 6 to 20 times greater than current numbers. Thus, whaling likely significantly reduced predation pressure on pelagic schooling prey resources and
thus altered pelagic ecosystems. 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 may have led 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, Sigurjonsson and Vikingsson 1997, Trites et al. 1997, Vikingsson 1997). However, with the exception of Laws’ (Laws 1977) estimates for Antarctica and Trites et al’s (Trites et al. 1999) estimates for the Bering Sea, few studies have attempted to assess the impacts of commercial whaling on pelagic ecosystems.

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 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 and Pauly and Christensen (1995) estimated that commercial fisheries required 8% of global aquatic primary production to sustain them. In this chapter we use a similar approach to assess the potential trophic impact of rapid removal of large whales from the North Pacific pelagic ecosystem.

**Approach**

An assessment of the primary production impact of the removal of large whales requires: 1) an estimate of the prey consumption rates of pre- and post-whaling whale populations, 2) estimates of the trophic level and trophic transfer efficiencies of the consumer, and 3) estimates of the net primary production of the ecosystem.
Whale Prey Biomass Consumption

We used two approaches to estimate whale prey biomass consumption of individual whales 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. Two of these (Hemmingsen 1960, Kleiber 1961) relied upon allometric models of empirically derived measures of mammalian resting metabolic rates. We assumed that daily metabolic rates in free-living animals were 3 times resting/basal rates (Costa and Williams 1999). The third (Nagy et al. 1999) relied upon an allometric model of empirically measured of field metabolic rates using doubly labeled water.

Hemmingsen (1960) Model

\[
\text{Active Metabolic Rate (W)} = 12.3 \left( \text{Body Mass (kg)} \right)^{0.75}
\]

Kleiber (1961) Model

\[
\text{Active Metabolic Rate (W)} = 9.84 \left( \text{Body Mass (kg)} \right)^{0.756}
\]

Nagy et al. (1999) Model

\[
\text{Field Metabolic Rate (W)} = 8.88 \left( \text{Body Mass (kg)} \right)^{0.734}
\]

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 based upon empirically measured biomass ingestion rates in marine mammals (Innes et al. 1987), or empirically measured biomass ingestion rates in mammals (all mammals) using doubly labeled water (Nagy 2001).
Innes (1987) Model
Prey Biomass Required (kg) = 0.42(Body Mass (kg))^{0.67}

Nagy (2001) Model
Prey Biomass Required (kg) = 0.17(Body Mass (kg))^{0.773}

It should be noted that in all approaches, allometric estimates were calculated from extrapolations well beyond the range of empirically measured subjects. Population numbers of N. Pacific large whales prior to exploitation and at current levels were taken from published estimates (Table 1).

Trophic Level and Trophic Transfer Efficiencies
To estimate the primary production required (PPR) to sustain pre- and post-whaling populations requires the conversion of 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 primary production required using whale trophic level (TL) and an estimate of trophic transfer efficiency published by Pauly and Christensen (1995):

\[ \text{PPR} = \left( \frac{\text{PBR}}{9} \right) \times 10^{(\text{TL} - 1)} \]

Net Primary Production
Net primary production 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 model provides a method to estimate primary production using satellite-derived measures of chlorophyll concentration, sea surface temperature, and irradiance. We used monthly estimates of chlorophyll concentration from SeaWiFS satellite images of the North Pacific averaged 1998-2000, global equal-angle best SST from the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder
project, and irradiance from the climatology of Bishop and Rossow (1991) to estimate annual net primary production using the VGPM model.

**Model Results**

Whale populations declined from 431,390 pre-exploitation to current levels of 133,689 (Table 1). Large whale biomass in the N. Pacific declined from 9.5 million metric tons to 2.9 million metric tons.

*Whale Prey Biomass Consumption*

Based upon estimates from allometric models of respiration rate, the metabolic rates of large whales ranged from 43,041 W for blue whales to 7,418 W for minke whales (Table 2). Using these values, we estimated the mean prey biomass required to sustain individual whales ranged from 1,120 kg day\(^{-1}\) (blue whales) to 176 kg day\(^{-1}\) (minke whales) (Table 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 N. Pacific populations of large whales prior-to and after their declines from exploitation (Table 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 25 metric tons day\(^{-1}\) to sustain the current population of N. Right Whales to 70,434 metric tons day\(^{-1}\) to sustain the pre-exploitation population of Sperm Whales. Due to the large pre-exploitation population size of sperm whales, this species has the highest gross prey biomass requirements of N. Pacific large whales. We estimate that whaling reduced the total daily prey biomass consumption for all N. Pacific large whale populations by 70%: pre-exploitation daily prey biomass consumption totaled 183,112 metric tons day\(^{-1}\), while post exploitation consumption totaled 55,155 metric tons day\(^{-1}\).
Primary Production Required to Sustain Whale Populations

Using daily prey biomass consumption values for each whale species, we estimated average daily net primary production for the N. Pacific. Diet of N. Pacific whales (Table 5) was based upon data published in Pauly et al. (1998b). We combined this information with published trophic levels for whale diet items: large zooplankton 2.2; fish 2.7, small squid 3.2, large squid 3.7, small zooplankton 2.0 (Trites et al. 1999). This yielded estimates of the trophic position of N. Pacific large whales (Table 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 primary production required to sustain each whale species prior to and after exploitation (Table 6). For all large whale populations in the N. Pacific, we estimate that pre-exploitation populations required a total of 15,405,419 metric tons fixed Carbon day\(^{-1}\) while current populations require a total of 2,232,524 metric tons fixed Carbon day\(^{-1}\).

Combining our estimates of primary production required to sustain large whale populations with our estimate of average daily net primary production for the N. Pacific, we estimated the percentage of average daily net primary production required to sustain N. Pacific large whale populations at current numbers and at pre-exploitation numbers (Table 7). For all N. Pacific whale populations, pre-exploitation populations required approximately 62\% while current populations require 9\% of N. Pacific net primary production.

Discussion

Rapid Removal of Large Whales

Due to their large range, long distance movement patterns, and logistical difficulties in conducting population surveys, it is difficult to accurately assess current population numbers of large cetaceans (Clapham et al. 1999, Perry et al. 1999, Clapham et al. 2003). It is even more difficult to accurately assess pre-exploitation population numbers (Gerber et al. 2000). We used available estimates for pre- and post-exploitation population numbers from the literature,
but recognize the error that these estimates introduce into our calculations. However, it is universally agreed that virtually all commercially exploited N. 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 upon which they are based.

Using these population estimates, large whale populations in the N. Pacific were reduced by approximately 69% (431,390 to 133,689 individuals) (Table 1). This reduction occurred in less than 150 years, with most of the reduction taking place during approximately 100 years (mid 19th to mid 20th century) (Clapham et al. 1999). Based on our population estimates, total whale biomass in the N. Pacific was reduced 70% from approximately 9.5 million metric tons to 2.9 million metric tons. The decline of large whales in the N. Pacific is comparable to that experienced 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 N. Pacific, it also changed the large whale community composition. Pre-exploitation whale biomass was dominated by sperm whales (38% of total), while post-exploitation biomass is dominated by fin whales (35% of total). This may have important trophic implications as the large whale community shifted from one dominated by teuthophagous predators (sperm whales) to piscivorous or zooplanktivorous predators (fin whales).

**Whale Metabolic Rates and Prey Consumption Rates**

Our calculations of prey and primary production requirements are strongly influenced by population estimates, trophic positions, and assumptions regarding metabolic rates. This introduces uncertainty due to inadequate empirical data (e.g. metabolic rates, population numbers) and natural variability. Boyd (2002)
points out that error is both additive (e.g. metabolic rates, assimilation efficiency) as well as 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 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 for Lockyer’s estimates (36,808 to 73,616 W), our average estimate of 43,041 W for a 69,235 kg blue whale falls within her estimate. 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 18 to 9.5 times Lockyer’s basal estimate. Our estimate for the daily metabolic rate for minke whales (7,418 W) 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.

Sigurjonsson 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. Overall, our values can be considered within the range of values estimated by most studies, and tend to be conservative (i.e. lower) estimates of large whale average daily metabolic rates.

Our estimates of individual consumption of prey biomass (Table 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 compared to ours 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$^{-1}$ compared to our estimate of 901 kg day$^{-1}$.

*Trophic Importance of Current Populations of Large Whales*

We estimate that large whales in the N. Pacific currently consume 55,155 metric tons day$^{-1}$ (Table 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 N. Pacific currently consume approximately 13% 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$^{-1}$ while Markussen et al. (1992) estimated that NE Atlantic Minke whales consumed 14,667 metric tons day$^{-1}$.

The maximum biomass extracted by commercial fisheries in the N. 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 N. Pacific. It has been argued that most commercial fisheries, including the N. Pacific, 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 N. Pacific was estimated by Pauly et al. (1998b) to have declined from a maximum of 3.4 in the early 1970’s to 3.2 by 1994. Combining trophic level values (Table 5) with prey biomass consumption estimates (Table 4); we estimate the weighted mean trophic level of N. Pacific large whales is 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 N. Pacific marine ecosystems to commercial fisheries.
One method to assess trophic importance is to assess the primary production required to sustain consumer populations. Marine mammals are important consumers of marine primary productivity: Kenney et al. (1997) estimated that cetaceans in some coastal regions of the NW 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 N. Pacific consume approximately 9% of net primary production. This is comparable to the weighted mean primary production (8% of net primary production) required to sustain world fisheries (Pauly and Christensen 1995). Thus, assuming that commercial fishing has important trophic impacts in marine ecosystems, current population numbers large whales also appear to be important trophic interactors.

_Trophic Impacts of Whaling_

In terms of prey biomass consumed, whaling severely reduced the trophic impact of large whales. We estimate that N. Pacific large whales currently consume approximately 30% of what they consumed prior to whaling (55,155 metric tons day^{-1} of prey biomass compared to 183,112 metric tons day^{-1} at pre-whaling 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 day^{-1} compared to 178,402 metric tons day^{-1} from current to pre-whaling). Changes at one trophic level can have cascading effects on others (Power et al. 1996). To the degree that large whales are important consumers of N. Pacific prey biomass, the decline of their populations may have significantly altered trophic interactions, and their trophic importance in N. Pacific food webs prior to whaling was almost certainly greater than that of current commercial fisheries.
Estimates of primary production requirements also provide insight into the possible impact of commercial whaling in the N. Pacific. We estimate that the primary production requirement of N. Pacific large whales declined from 62% of net primary production at pre-exploitation populations to 9%. Trites et al. (1999) estimated that the amount of primary production required to sustain the commercial harvest of large whales in the Bering Sea was 43.4% of net primary production during the 1950’s. This does not account for the amount required to sustain the entire population of large whales (i.e. it does not include the portion not harvested). Thus, our estimate of 62% of primary production requirement for the entire large whale population of the N. Pacific prior to large scale population declines appears reasonable. 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.

Sperm Whale Demands on Marine Ecosystems
Due to their large pre-exploitation population sizes and high trophic level, sperm whales are important components in terms of energy flow dynamics in the N. Pacific ecosystem. We estimate that sperm whales account for approximately 83% of the total 62% of net primary production required to sustain pre-exploitation large whale populations. While our model is sensitive to error in population estimates and trophic level, a 25% reduction in our assumed pre-exploitation population size or decline in trophic status 0.5 a trophic level would only result in a shift of sperm whale importance from 83% to approximately 60% of total net primary production required to sustain large whales.

Little is known about pelagic food webs and the role of squid in structuring trophic interactions. It is likely that squid are important predators in pelagic systems, and they also form a significant proportion of the diet of apex predators in open ocean ecosystems, including sperm whales. To the extent that predation by squid may have cascading impacts on the food webs of which they are a part, the rapid removal of sperm whales may have significantly altered pelagic ecosystems.
This may be particularly important for less productive open ocean systems where sperm whale abundance is relatively high.

**Community Implications of the Decline of Large Whales**

Virtually every ecosystem is characterized by consumer-prey interactions. While top-level predators are generally rare because of their high trophic status, they often act as keystones - strongly influencing ecosystem structure and function as their effects are magnified through the food web via trophic cascades (Strong 1992, Estes 1996, Power et al. 1996). Coastal trophic cascades have resulted 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). While trophic cascades in coastal ecosystems have shaped our understanding of the role of apex predators as keystone species, examples of similar effects in pelagic systems are rare (Estes et al. 2001).

Laws (Laws 1977) proposed that the decline of large whales from the Southern Ocean ecosystem resulted in increases in food availability and thus populations of penguins, fur seals, and seals. May et al. (May et al. 1979) developed a simple model to explain how trophic interactions may have shifted due to whale declines. Both of these approaches rely upon fairly simple food webs. Given a simple system, one would predict that the rapid removal of large whales would initiate trophic cascades.

A key element of most trophic cascades is the dependence upon strong interactions by particular species (Pace et al. 1998). Due to their large body size and relatively high mammalian metabolic rate, marine mammals have the potential to be strong trophic interactors (Bowen 1997). Strong predator-induced effects in plankton food webs have been long recognized in lake systems (Carpenter and Kitchell 1993), and it is not unreasonable to expect changes in pelagic ecosystem food web structure due to the removal of a taxonomic group.
that is a strong trophic interactor such as large whales. Thus, the rapid removal of large whales may have led to changes in pelagic ecosystems.

However, while the demise of large whales may have led to changes in the diet of their predators (Springer et al. 2003), there is no evidence that this also led to pelagic trophic cascades. Trites et al. (Trites et al. 1997) developed a mass-balance model to examine complex trophic interactions resulting from marine mammal declines in the Bering Sea. Their model demonstrated that most primary production flowed through large whale populations in the 1950’s, and that marine mammal declines may have had positive effects on some species (e.g. Pollock). However, they found that the overall impact of marine mammal declines had little effect on other species in the Bering Sea ecosystem, and could not explain major changes that occurred in the system between 1950 and 1980. Instead, they attributed changes in the Bering Sea ecosystem to shifts in primary production due to oceanographic regime shifts.

Trites et al.’s (Trites et al. 1997) model results appear to contrast with those of trophic interactions in coastal systems where substantial changes in species composition and trophic interactions have been attributed to changes in apex predator abundances. 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), or nonexistent baselines (Dayton et al. 1998, Jackson et al. 2001). However, it may also be that strong trophic cascades are less common in pelagic systems. Micheli (1999) found that coupling was weak between phytoplankton and herbivores and thus resource and consumer effects attenuate in marine pelagic food webs. McCann et al. (1998) proposed that non-linearity in more reticulate pelagic food webs due to omnivory and interference precludes classic trophic cascades. It is likely that bottom-up changes in primary production in the Bering Sea due to regime shift (Napp and Hunt 2001) occurred simultaneously with apex predator declines due to commercial harvest. This may confound predictions based solely upon top-down effects.
Information on diet, trophic interactions, and trends in abundance is lacking for most pelagic species, including large whales (DeMaster et al. 2001). This makes predictions about the impact of the removal of large whales on commercial fish stocks and the impact of commercial fisheries on large whale recovery problematic. While the removal of apex predators such as large whales may have increased the availability of krill to other consumers – including species of commercial importance – in the relatively simple Antarctic ecosystem, similar scenarios are not supported by models of the more complex Bering Sea ecosystem (Trites et al. 1999). Thus, the notion that the removal of large whales may have facilitated that expansion of some world fisheries (e.g. Bering Sea) cannot be supported. However, commercial exploitation of other apex predators has been shown to result in dramatic changes in trophic interactions and species abundances (Worm and Myers 2003). We cannot demonstrate that similar changes occurred in the N. Pacific due to the commercial exploitation of large whales. Regardless, our model demonstrates that, in the N. Pacific pelagic ecosystem, large whales are important trophic interactors, and commercial harvest of large whales significantly altered energy flow dynamics.
Literature Cited


Keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. Bioscience 46:609-620.


Table 1. Body mass of N. Pacific large whales. Body mass references: \(^1\)Lockyer (1976), \(^2\)Jones and DeMaster (this volume) \(^3\)Trites and Pauly (1998). Population references: \(^4\)Carretta et al. (2002), \(^5\)Ohsumi (1991), \(^6\)Jones and DeMaster (this volume). \(^7\)Due to complexities of population structure and reporting uncertainty (confusion between whale stocks and other species such as sei whales) it is difficult to confidently estimate the N. Pacific population of Bryde’s whales. We used pre and post exploitation estimates of the Western N. Pacific from the International Whaling Commission and combined these with an estimate of post exploitation numbers for the entire E. Tropical Pacific provided by Wade and Gerrodete (Carretta et al. 2002). Thus, both our pre- and post exploitation estimate are likely overestimates of the N. Pacific Bryde’s whale population.

<table>
<thead>
<tr>
<th>Body Mass (kg)</th>
<th>Blue</th>
<th>Fin</th>
<th>Sei</th>
<th>Bryde's</th>
<th>Humpback</th>
<th>Minke</th>
<th>N. Right</th>
<th>Gray</th>
<th>Sperm</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reference</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Population</td>
<td>4,900</td>
<td>43,500</td>
<td>42,000</td>
<td>39,000</td>
<td>15,000</td>
<td>32,000</td>
<td>31,750</td>
<td>28,240</td>
<td>195,000</td>
<td>431,390</td>
</tr>
<tr>
<td>Reference</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>7</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Biomass (metric tons)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-exploitation</td>
<td>339,252</td>
<td>2,418,600</td>
<td>706,062</td>
<td>629,577</td>
<td>456,000</td>
<td>211,200</td>
<td>742,950</td>
<td>434,896</td>
<td>3,607,500</td>
<td>9,546,037</td>
</tr>
<tr>
<td>Current</td>
<td>276,940</td>
<td>1,034,160</td>
<td>212,155</td>
<td>484,290</td>
<td>121,752</td>
<td>211,200</td>
<td>1,170</td>
<td>268,176</td>
<td>277,500</td>
<td>2,887,342</td>
</tr>
</tbody>
</table>

*Body mass is average of male and female body masses
Table 2. Allometric estimates of daily metabolic rates (W) of large whales of the N. Pacific based upon 3 times estimates of basal metabolic rate (Hemmingsen 1960, Kleiber 1961) or average daily metabolic rate (Nagy et al. 1999).

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Blue</td>
<td>52,499</td>
<td>44,904</td>
<td>31,720</td>
<td>43,041</td>
<td>10,514</td>
<td>24.4%</td>
</tr>
<tr>
<td>Fin</td>
<td>44,536</td>
<td>38,043</td>
<td>27,003</td>
<td>36,527</td>
<td>8,864</td>
<td>24.3%</td>
</tr>
<tr>
<td>Sei</td>
<td>18,159</td>
<td>15,401</td>
<td>11,223</td>
<td>14,928</td>
<td>3,492</td>
<td>23.4%</td>
</tr>
<tr>
<td>Bryde's</td>
<td>17,615</td>
<td>14,936</td>
<td>10,894</td>
<td>14,482</td>
<td>3,384</td>
<td>23.4%</td>
</tr>
<tr>
<td>Humpback</td>
<td>28,318</td>
<td>24,102</td>
<td>17,337</td>
<td>23,252</td>
<td>5,540</td>
<td>23.8%</td>
</tr>
<tr>
<td>Minke</td>
<td>9,007</td>
<td>7,596</td>
<td>5,650</td>
<td>7,418</td>
<td>1,685</td>
<td>22.7%</td>
</tr>
<tr>
<td>N. Right</td>
<td>23,271</td>
<td>19,775</td>
<td>14,307</td>
<td>19,118</td>
<td>4,518</td>
<td>23.6%</td>
</tr>
<tr>
<td>Gray</td>
<td>17,004</td>
<td>14,413</td>
<td>10,524</td>
<td>13,980</td>
<td>3,262</td>
<td>23.3%</td>
</tr>
<tr>
<td>Sperm</td>
<td>19,511</td>
<td>16,557</td>
<td>12,040</td>
<td>16,036</td>
<td>3,763</td>
<td>23.5%</td>
</tr>
</tbody>
</table>
Table 3. Prey biomass requirements (kg individual\(^{-1}\) day\(^{-1}\)) for N. Pacific large whales derived from 5 different models (see text for explanation of models).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue</td>
<td>1607</td>
<td>1375</td>
<td>971</td>
<td>735</td>
<td>913</td>
<td>1120</td>
<td>359</td>
<td>0.32</td>
</tr>
<tr>
<td>Fin</td>
<td>1259</td>
<td>1076</td>
<td>763</td>
<td>635</td>
<td>771</td>
<td>901</td>
<td>258</td>
<td>0.29</td>
</tr>
<tr>
<td>Sei</td>
<td>513</td>
<td>435</td>
<td>317</td>
<td>285</td>
<td>306</td>
<td>371</td>
<td>99</td>
<td>0.27</td>
</tr>
<tr>
<td>Bryde's</td>
<td>417</td>
<td>354</td>
<td>258</td>
<td>277</td>
<td>296</td>
<td>320</td>
<td>65</td>
<td>0.20</td>
</tr>
<tr>
<td>Humpback</td>
<td>711</td>
<td>605</td>
<td>435</td>
<td>423</td>
<td>483</td>
<td>532</td>
<td>123</td>
<td>0.23</td>
</tr>
<tr>
<td>Minke</td>
<td>235</td>
<td>199</td>
<td>148</td>
<td>152</td>
<td>148</td>
<td>176</td>
<td>39</td>
<td>0.22</td>
</tr>
<tr>
<td>N. Right</td>
<td>712</td>
<td>605</td>
<td>438</td>
<td>355</td>
<td>395</td>
<td>501</td>
<td>152</td>
<td>0.30</td>
</tr>
<tr>
<td>Gray</td>
<td>521</td>
<td>441</td>
<td>322</td>
<td>268</td>
<td>286</td>
<td>368</td>
<td>109</td>
<td>0.30</td>
</tr>
<tr>
<td>Sperm</td>
<td>476</td>
<td>404</td>
<td>294</td>
<td>304</td>
<td>329</td>
<td>361</td>
<td>77</td>
<td>0.21</td>
</tr>
</tbody>
</table>
Table 4. Estimated daily prey biomass requirements (metric tons day\(^{-1}\)) for N. Pacific large whale populations using 5 different prey requirement models (see text for explanation of models).

<table>
<thead>
<tr>
<th>Respiration Models</th>
<th>Ingestion Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemmingsen</td>
<td>Kleiber</td>
</tr>
<tr>
<td>Current</td>
<td>Pre-exploitation</td>
</tr>
<tr>
<td>Blue</td>
<td>6,428</td>
</tr>
<tr>
<td>Fin</td>
<td>23,420</td>
</tr>
<tr>
<td>Sei</td>
<td>6,479</td>
</tr>
<tr>
<td>Bryde's</td>
<td>12,513</td>
</tr>
<tr>
<td>Humpback</td>
<td>2,847</td>
</tr>
<tr>
<td>Minke</td>
<td>7,536</td>
</tr>
<tr>
<td>N. Right</td>
<td>36</td>
</tr>
<tr>
<td>Gray</td>
<td>9,064</td>
</tr>
<tr>
<td>Sperm</td>
<td>7,137</td>
</tr>
<tr>
<td>Total</td>
<td>75,460</td>
</tr>
</tbody>
</table>
Table 5. Diet and estimated trophic level of N. Pacific large whales. Diet composition based on Pauly et al. (1998b).

<table>
<thead>
<tr>
<th>Diet Composition</th>
<th>Blue</th>
<th>Fin</th>
<th>Sei</th>
<th>Bryde's</th>
<th>Humpback</th>
<th>Minke</th>
<th>Right</th>
<th>Gray</th>
<th>Sperm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large Zooplankton</td>
<td>1</td>
<td>0.8</td>
<td>0.8</td>
<td>0.4</td>
<td>0.55</td>
<td>0.65</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Fish</td>
<td>0</td>
<td>0.15</td>
<td>0.15</td>
<td>0.6</td>
<td>0.45</td>
<td>0.35</td>
<td>0</td>
<td>0</td>
<td>0.25</td>
</tr>
<tr>
<td>Small Squid</td>
<td>0</td>
<td>0.05</td>
<td>0.05</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Large Squid</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
</tr>
<tr>
<td>Small Zooplankton</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0.05</td>
</tr>
<tr>
<td>Trophic Level</td>
<td>3.20</td>
<td>3.33</td>
<td>3.33</td>
<td>3.50</td>
<td>3.43</td>
<td>3.38</td>
<td>3.00</td>
<td>3.20</td>
<td>4.22</td>
</tr>
</tbody>
</table>
Table 6. Estimated primary production required (metric tons day$^{-1}$) to sustain large whale populations in the N. Pacific.

<table>
<thead>
<tr>
<th></th>
<th>Respiration Models</th>
<th>Ingestion Models</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hemmingsen</td>
<td>Kleiber</td>
<td>Nagy et al.</td>
</tr>
<tr>
<td></td>
<td>Current</td>
<td>Current</td>
<td>Current</td>
</tr>
<tr>
<td>3Blue</td>
<td>113,204</td>
<td>138,675</td>
<td>96,826</td>
</tr>
<tr>
<td>Fin</td>
<td>549,988</td>
<td>1,286,263</td>
<td>469,801</td>
</tr>
<tr>
<td>Sei</td>
<td>152,156</td>
<td>506,383</td>
<td>129,042</td>
</tr>
<tr>
<td>3ryde's</td>
<td>439,660</td>
<td>571,558</td>
<td>372,782</td>
</tr>
<tr>
<td>3lumpback</td>
<td>84,156</td>
<td>315,189</td>
<td>71,626</td>
</tr>
<tr>
<td>N. Right</td>
<td>396</td>
<td>251,312</td>
<td>336</td>
</tr>
<tr>
<td>3ray</td>
<td>159,624</td>
<td>258,859</td>
<td>135,304</td>
</tr>
<tr>
<td>3perm</td>
<td>1,300,950</td>
<td>16,912,347</td>
<td>1,103,961</td>
</tr>
<tr>
<td>Total</td>
<td>2,998,683</td>
<td>20,439,136</td>
<td>2,547,126</td>
</tr>
</tbody>
</table>