Cetacean biomass, prey consumption, and primary production requirements in the California Current ecosystem

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ABSTRACT: To better understand the role played by cetaceans as top-level predators in the California Current ecosystem, we estimate the fraction of annual net primary production (NPP) required to support the prey consumed by cetaceans, using a simple trophic transfer model. The biomass of cetacean species in the California Current is calculated as the product of their mean summer and fall abundance during 1991 to 2005 and estimates of mean mass ind.$^{-1}$. Total prey consumption by cetaceans is estimated from a mass-specific consumption model. NPP is estimated from remote satellite measurements using the Behrenfeld-Falkowski vertically-generalized production model for each of 4 geographic regions. The total biomass of baleen whales exceeds the biomass of toothed whales by a factor of ~2.5; however, the estimated prey consumption by these taxa is nearly equal. Assuming 10% trophic transfer efficiency, cetaceans are estimated to require 32.2 g C m^{-2} yr^{-1} of primary production, or ~12% of the NPP in the study area, to sustain the prey that they directly consume. Because they feed at a lower trophic level, the primary production requirement (PPR) of baleen whales is ~13% of that of toothed whales, despite their 2.5-fold greater biomass. Uncertainty in trophic transfer efficiency results in the greatest uncertainty in estimating PPR for these upper trophic predators.

KEY WORDS: Cetaceans · Whales · Dolphins · Porpoises · California Current ecosystem · Biomass · Food web · Trophodynamics · Primary production · Trophic efficiency

INTRODUCTION

Estimates of animal abundance and biomass density are vital to understanding the trophodynamics of marine ecosystems (Ryther 1969, Steele 1973). Marine mammals play an important role as top predators within marine ecosystems (Bowen 1997) and have been included in a number of ecosystem models; however, their abundance is often based on 'order of magnitude' estimates (Trites et al. 1997) or are 'guess-estimated' (Neira & Arancibia 2004). More precise estimates of cetacean abundance are becoming available for many areas of the world's oceans as a result of an increase in line-transect survey effort (Wade & Gerrodette 1993, Kasamatsu & Joyce 1995, Forcada & Hammond 1998, Hammond et al. 2002, Mullin & Fulling 2004, Gerrodette & Forcada 2005). Most

recently, Barlow & Forney (2007) estimated the summer/fall abundance and density of most cetaceans in the California Current ecosystem based on 5 surveys conducted from 1991 to 2005, which now allows us to more precisely examine the trophic role of cetaceans in that ecosystem.

There have been several previous estimates of the consumption and primary production requirements (PPR) of cetaceans in a variety of ecosystems worldwide. Bax (1991) reviewed 6 previous studies and found that the fraction of fish consumed by marine mammals varied greatly from 0 to 30% of the total fish consumption in the study area (including human catches). Reilly et al. (2004) estimated that, at current reduced densities, baleen whales in the South Atlantic sector of the Southern Ocean consume 4 to 6% of the biomass of krill in that area. Kenney et al. (1997) esti-

mated that cetacean consumption was larger than human catches in the northeastern US continental shelf ecosystem and that their PPR was 11.7 to 20.4% of the total net primary production (NPP). Trites et al. (1997) estimated that the prey consumed by all marine mammals in the Pacific Ocean exceeded the catch in all fisheries by a factor of 3 and that the primary production required to support their prey is 15 to 22% of the total NPP. Morissette et al. (2006) estimated that marine mammals in the Gulf of St. Lawrence require 14.1% of NPP to support their prey. Croll et al. (2007) estimated that current populations of large whales (the Balaenopteridae plus sperm whales) in the North Pacific require 26% of the primary production and that pre-exploitation whales levels would have required 64% of the current primary production. In that study, 64 to 84% of the PPR of large whales was attributed to sperm whales. There have been no previous studies of the trophic needs of cetaceans that were specific to the California Current ecosystem.

Here we examine the trophodynamic role of cetaceans in the California Current ecosystem by estimating their prey consumption and the fraction of NPP required to support that prey. Because cetacean abundance estimates are not available for all species off the coasts of Canada or Mexico, we define our California Current study area to be from the US west coast to 555 km offshore (Fig. 1). We use recent estimates of cetacean abundance for 23 species (Table 1) to estimate cetacean biomass in the California Current using species-specific estimates of mass ind.$^{-1}$. The consumption of prey by cetaceans is estimated from their biomass using a prey consumption model. NPP in the California Current is estimated from remote satellite measurements using the Behrenfeld-Falkowski vertically-generalized production model (VGPM; Behrenfeld & Falkowski 1997). The PPR of cetaceans was estimated from their prey consumption using a simple trophic energy transfer model based on the trophic levels of their prey (Trites et al. 1997). We examine the uncertainty in our estimates by exploring a range of plausible values for cetacean abundance, cetacean consumption, and ecosystem trophic transfer efficiency.

MATERIALS AND METHODS

Cetacean abundance. Our study area included waters along the US west coast out to a distance of ~555 km. For most species, we used cetacean abundances in that area estimated from ship line-transect surveys from 1991 to 2005 (Barlow & Forney 2007). The abundance of harbor porpoise and the coastal stock of bottlenose dolphins could not be estimated from these
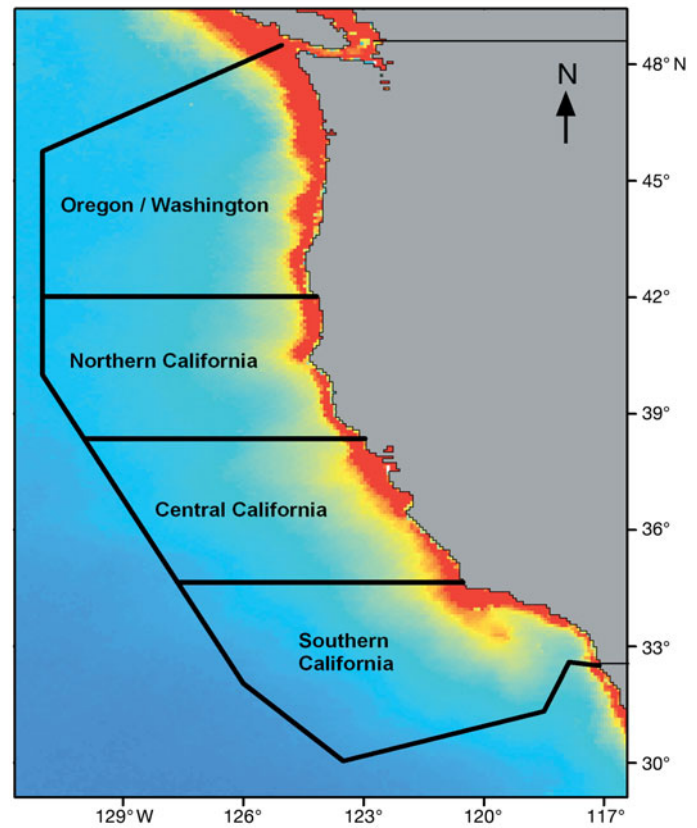

Fig. 1. Mean net primary production (NPP) from November 1996 to March 2006, estimated using the Behrenfeld-Falkowski vertically-generalized production model within the California Current study area boundaries (bold lines). Colors from blue to red indicate increasing levels of primary production. Regions are the same as the geographic strata used by Barlow & Forney (2007). Horizontal lines (across the land) indicate Canadian (top) and Mexican (bottom) borders

ship surveys because they occur too close to shore for safe navigation; their abundance was estimated from aerial surveys during the same time period (Carretta et al. 1998, Laake et al. 1998, Carretta & Forney 2004).

Biomass estimation. For most species, the mean species-specific body mass of individuals was estimated from measured values where available (Trites & Pauly 1998, their Table 2) or from a regression model of mean body mass as a function of maximum length (Trites & Pauly 1998, their Table 4). For fin and blue whales, measurements of mass are dominated by samples from Antarctic waters where these species are appreciably longer (mean length = 21.6 and 25.6 m, respectively) than in the California Current (mean length = 19.0 and 20.9 m, respectively) (Clapham et al. 1997, Gilpatrick & Perryman 2008). For these 2 species, we used the lengths of whales taken by whalers from the California Current populations (Clapham et al. 1997, Gilpatrick & Perryman 2008) and estimated the mass of each measured individual using Lockyer's weight/length rela-

Table 1. Families and common names of cetacean species in the present study. Odontocetes (toothed whales) include all species listed here except Balaenopteridae

Family	Species	Common name
Delphinidae	*Delphinus delphis*	Short-beaked common dolphin
	Delphinus capensis	Long-beaked common dolphin
	D. delphis or *D. capensis*	Unclassified common dolphin
	Stenella coeruleoalba	Striped dolphin
	Lagenorhynchus obliquidens	Pacific white-sided dolphin
	Lissodelphis borealis	Northern right whale dolphin
	Tursiops truncatus	Bottlenose dolphin (offshore)
	Tursiops truncatus	Bottlenose dolphin (coastal)
	Grampus griseus	Risso's dolphin
	Globicephala macrorhynchus	Short-finned pilot whale
	Orcinus orca	Killer whale
Phocoenidae	*Phocoenoides dalli*	Dall's porpoise
	Phocoena phocoena	Harbor porpoise
Ziphiidae	5 *Mesoplodon* spp.	*Mesoplodon* spp.
	Ziphius cavirostris	Cuvier's beaked whale
	Berardius bairdii	Baird's beaked whale
	Z. cavirostris or *Mesoplodon* spp.	Unidentified ziphiid whale
Physeteridae	*Kogia breviceps* or *K. sima*	*Kogia* spp.
	Physeter macrocephalus	Sperm whale
Balaenopteridae	*Balaenoptera acutorostrata*	Minke whale
	Balaenoptera edeni	Bryde's whale
	Balaenoptera borealis	Sei whale
	B. borealis or *B. edeni*	Sei/Bryde's whale
	Balaenoptera physalus	Fin whale
	Balaenoptera musculus	Blue whale
	Megaptera novaeangliae	Humpback whale

tionships for these species (Lockyer 1976, their Table 2). The resulting average masses (42.1 and 58.2 t, respectively, for fin and blue whales) were much lower than those given by Trites & Pauly (1998) (55.6 and 102.1 t, respectively, for fin and blue whales, with both sexes pooled). For most species, estimates of male and female body mass were averaged based on assumed parity in sex ratios, but for sperm whales, killer whales, and pilot whales, which exhibit extreme sexual dimorphism, masses were averaged assuming that females comprise 60% of their populations (as Trites et al. 1997 assumed for sexually dimorphic pinnipeds). Total population biomass was estimated as the product of this mean body mass and estimates of total abundance for each species.

Prey consumption by cetaceans. The food requirements of cetaceans has been reviewed recently by Reilly et al. (2004) and Leaper & Lavigne (2007). Many models have been proposed, and considerable uncertainty remains, especially for large baleen whales.

Typically, models either directly estimate the average daily ration (R in kg wet wt) or estimate food requirements indirectly from the average daily metabolic requirement (ADMR in kJ d^{-1}). ADMR is sometimes modeled as a function of basal metabolic rate (BMR in kJ d^{-1}). For a wide range of homeotherms, BMR is related to mass (M) according to the Kleiber (1975) function:

$$BMR = 293.1M^{0.75} \qquad (1)$$

and there is no compelling evidence that marine mammals do not follow this relationship (Leaper & Lavigne 2007). Lavigne (1996) proposed that, for marine mammals, ADMR (or, comparably, field metabolic rate [FMR] in kJ d^{-1}) might scale linearly with Kleiber's BMR:

$$ADMR = FMR = \beta(293.1M^{0.75}) \quad (2)$$

Several authors have estimated ADMR or FMR for cetaceans using Eq. (2) with $\beta = 2.5$ (Kenney et al. 1997, Hooker et al. 2002, Laidre et al. 2004) or $\beta = 3$ (Costa & Williams 1999, Croll et al. 2007). Leaper & Lavigne (2007) argue that ADMR and R should increase with mass no faster than BMR (i.e. to the power of 0.75) and likely at a slower rate because the costs of locomotion and thermal homeostasis decrease with mass. Based on allometric relationships, Boyd (2002) suggested a model for FMR based on mass to a lower power:

$$FMR = 2529^{0.524} \qquad (3)$$

R can be estimated from ADMR (or FMR) by converting energy needs to wet weight of food (typically 5450 kJ kg^{-1} for fish and squid and 3900 for crustaceans kJ kg^{-1}) and adjusting for assimilation efficiency (typically 80%) (Leaper & Lavigne 2007):

$$R = ADMR / \{0.8[3900Z + 5450(1 - Z)]\} \qquad (4)$$

where Z is the fraction of crustaceans in their diet.

Models for the direct estimation of R also take the same general form:

$$R = A M^B \qquad (5)$$

and versions of this model for marine mammals have been suggested by several authors: $A = 0.1$, $B = 0.8$ (Trites et al. 1997); $A = 0.42$, $B = 0.67$ (Innes et al. 1986); and $A = 1.66$, $B = 0.559$ (Reilly et al. 2004).

Eight models of prey consumption were compared (Fig. 2). Relative to the other models, the model from
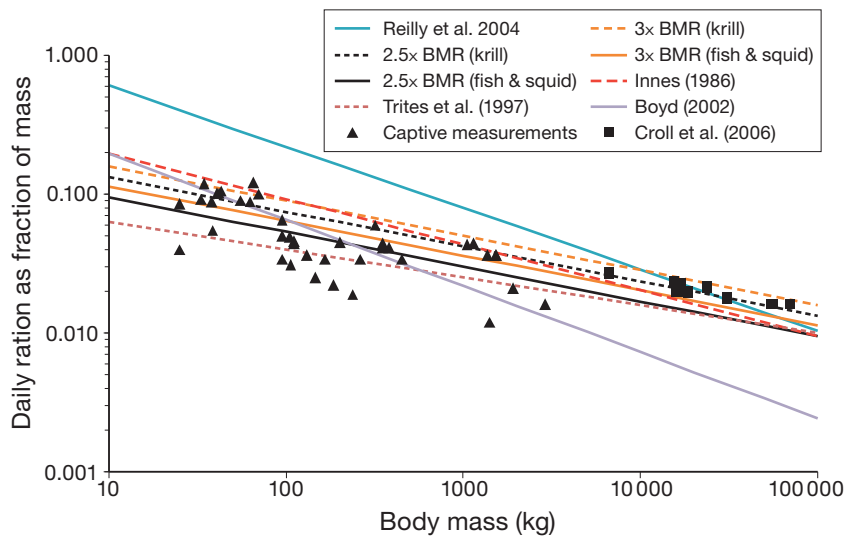
Fig. 2. Models of average daily ration required to meet the energetic require-
ments of wild cetaceans, expressed as a fraction of body mass. Models based on
metabolic rates (average daily metabolic requirement [ADMR] or field metabolic
rate [FMR]) are converted from energy needs (kJ d^{-1}) to daily ration (kg wet wt
d^{-1}) based on an assimilation efficiency of 80% and assumed prey energy densi-
ties of 5450 kJ kg^{-1} for fish and squid and 3900 kJ kg^{-1} for krill and other crusta-
ceans. The estimated daily rations averaged from 5 models used by Croll et al.
(2007) for 8 baleen whale species and sperm whales are also shown (■). The daily
rations measured for captive cetaceans (▲) are shown for comparison (Kastelein
et al. 1993, 1994, 1997, 1999, 2000a,b,c,d, 2002, 2003a,b)

10% trophic transfer efficiency for car-
bon between all trophic levels (Pauly
& Christensen 1995, Trites et al. 1997).
Cetacean prey were divided into 8 cat-
egories with different trophic levels.
The PPR$_i$ for each species, i, is given
by:

$$\mathrm{PPR}_i = Q_i \sum_{g=1}^{8} d_{i,g} c_g \left(\frac{1}{T_e} \right)^{(L_g - 1)} \qquad (6)$$

where Q_i is the total prey consumption
in kg wet weight, $d_{i,g}$ is the proportion
of prey category g in the diet of species
i, c_g is the proportion of carbon per wet
weight for prey category g, T_e is the tro-
phic transfer efficiency, and L_g is the
trophic level of the prey category. Our
Eq. (6) differs from that used by Trites
et al. (1997) (their Eq. 5) by explicitly
including a carbon:wet weight conver-
sion factor and trophic efficiency as
variables. We used the same prey cate-
gories and the corresponding values of
d and L given by Pauly et al. (1998). We
assumed that the carbon:wet weight
ratio is 1:9 for all prey species (Pauly &
Christensen 1995). The trophic level of
the cetacean species was computed as 1
plus a weighted average of the trophic levels of their
prey (Pauly et al. 1998). These values are generally in
good agreement with the estimated trophic level from
isotope studies (Pauly et al. 1998, Das et al. 2003).

Primary production in the California Current. For
each of 4 regions in the study area, a mean daily NPP
rate (mg C m^{-2} d^{-1}) was obtained for a 10 yr period (No-
vember 1996 to March 2006). NPP fields were derived
for each of 111 mo using the Behrenfeld-Falkowski
VGPM (Behrenfeld & Falkowski 1997), using surface
chlorophyll *a* (chl *a*, mg m^{-3}) from the Ocean Color and
Temperature Scanner (OCTS) and Sea-viewing Wide
Field-of-view Sensor (SeaWiFS), photosynthetically
active radiation (PAR, Einstein m^{-2} d^{-1}) from SeaWiFS,
and sea surface temperature (SST, °C) from the ad-
vanced very high resolution radiometer (AVHRR)
Pathfinder, moderate resolution imaging spectroradio-
meter (MODIS)-Terra and MODIS-Aqua (Kahru &
Mitchell 2002). Estimates have ~9 km spatial resolu-
tion. To avoid bias caused by seasonal changes in
cloud coverage, daily NPP values within each region
were averaged by calendar month and these monthly
values were averaged to give an annual estimate of
daily NPP. The mean annual NPP was estimated as
365× the mean daily value. The Windows Image Man-
ager (WIM) software program (www.wimsoft.com) was
used to calculate NPP, obtain the average NPP, create

Reilly et al. (2004) overestimated consumption by small
cetaceans and the model of Boyd (2002) underesti-
mated the consumption by large cetaceans. In general,
consumption models were consistent with or slightly
higher than measured consumption rates for small and
medium-sized cetaceans kept in captivity (Fig. 2). Cap-
tive cetaceans would be expected to have lower aver-
age consumption rates than wild animals because ac-
tivity levels are generally lower and they are often fed
fish with a very high energy content (such as herring,
with an energy density of 8880 kJ kg^{-1}) (Kastelein et al.
2000d). In the present study, we used the model given
by Eqs. (2) & (4) with β = 2.5 as our primary model, but
included this model with β = 3 and the Trites et al.
(1997) model (Eq. 5, *A* = 0.1, *B* = 0.8) as plausible
models in our sensitivity analysis.

The total annual prey consumption was estimated as
the product of the mean annual ration (365 × *R*) and the
estimated abundance of each species. For baleen
whales, which migrate outside of the study area, we
used Lockyer's (1981) estimate that 83% of the annual
intake occurs in the summer feeding areas (i.e. in the
California Current ecosystem).

Primary production requirement. The primary pro-
duction required to support the prey consumed by
cetaceans was estimated using a simple model of
energy transfer between trophic levels that assumes a

Table 2. Estimates of abundance (number of individuals, N), coefficient of variation for abundance (CV(N)), average individual mass (kg), and population biomass (t) for cetaceans within the California Current study area. Abundance estimates and CVs are from Barlow & Forney (2007) except for coastal bottlenose dolphin (Carretta et al. 1998) and harbor porpoise (Laake et al. 1998, Carretta & Forney 2004). The Families Delphinidae and Phocoenidae are collectively referred to as delphinoids

Species	N	CV(N)	Mass	Biomass
Short-beaked common dolphin	352 069	0.18	80	28 218
Long-beaked common dolphin	21 902	0.50	80	1755
Unclassified common dolphin	5629	0.64	80	451
Striped dolphin	18 976	0.28	116	2201
Pacific white-sided dolphin	23 817	0.36	78	1861
Northern right whale dolphin	11 097	0.26	62	682
Bottlenose dolphin (offshore)	2026	0.44	188	380
Bottlenose dolphin (coastal)	206	0.12	188	39
Risso's dolphin	11 910	0.24	224	2662
Short-finned pilot whale	350	0.48	608	213
Killer whale	810	0.27	2219	1798
Dall's porpoise	85 955	0.45	61	5269
Harbor porpoise	64 515	0.27	31	2003
Mesoplodon spp.	1177	0.40	449	529
Cuvier's beaked whale	4342	0.58	829	3597
Baird's beaked whale	1005	0.37	3137	3152
Kogia spp.	1237	0.45	177	219
Sperm whale	1934	0.31	16 834	32 558
Minke whale	823	0.56	6566	5404
Bryde's whale	7	1.01	16 143	109
Sei whale	98	0.57	16 811	1647
Sei/Bryde's whale	18	0.65	16 477	293
Fin whale	2099	0.18	42 150	88 473
Blue whale	1548	0.16	57 230	88 592
Humpback whale	942	0.26	30 408	28 644
Unidentified delphinoid	4968	0.36	79	394
Unidentified ziphiid whale	463	0.50	748	346
Unidentified small whale	528	0.50	1286	679
Unidentified roqual whale	270	0.20	44 096	11 906
Unidentified large whale	189	0.25	36 162	6835
Subtotal: Delphinoids	604 230	0.14		47 927
Subtotal: Ziphiidae	6987	0.37		7624
Subtotal: Physeteridae	3171	0.26		32 777
Subtotal: Balaenopteridae	5805	0.12		225 068
Total	620 910	0.14		320 910

alternative consumption models (the Trites et al. 1997 model and a model based on 3 times BMR) that encompass a plausible range of uncertainty. Finally, Pauly & Christensen (1995) reviewed previous estimates of trophic energy transfer efficiencies for aquatic ecosystems and found a wide range of estimated values between 2 and 24% and a mean of ~10%. To explore the sensitivity of our results to a plausible range of uncertainty, we added or subtracted 1 SD (5.8%) around a central value of 10% for a range of 4.2 to 15.8%. Less uncertainty exists in estimating the average mass of cetaceans than for the other parameters in our model, so we did not explore uncertainty in the length/mass relationships.

RESULTS

Cetacean biomass estimates

The total abundance of small cetaceans in the California Current (Table 2) was clearly dominated by 2 species, short-beaked common dolphins and Dall's porpoises, which together comprised ~72% of all delphinoids and 71% of all cetaceans. Baleen whales (Balaenopteridae) comprised only ~1% of the total estimate of cetaceans along the US west coast (Table 2). The picture was, however, reversed if biomass was considered (Table 2). Baleen whales comprised ~70% of the cetacean biomass and delphinoids comprised only 15%.

Prey consumption estimates

Estimated prey consumption was greatest for short-beaked common dolphins followed closely by blue and fin whales (Table 3). Collectively, of the 4 summary taxa, consumption was highest for Balaenopteridae, with delphinoids as a close second (Table 3). In general, the prey consumption by large whales was relatively less than might be expected because *R* was proportionately less for larger animals. The prey categories consumed by these cetaceans varied greatly among species (Table 4). Blue whales feed almost exclusively on euphausiids (Christensen et al. 1992,

masks corresponding to each region of our study area, and calculate NPP statistics for each region.

Sensitivity analysis. A number of uncertainties affected our estimates of the consumption and PPR of cetaceans. We explored the effect of these uncertainties by using a plausible range of inputs for 3 areas of uncertainty. Many of the abundance estimates had high coefficients of variation (Table 2), and we explored this uncertainty by using the upper and lower log-normal 68% CIs for the estimates of all species, simultaneously (roughly equivalent to ±1 SD). There are many models for estimating marine mammal consumption from their mass, but little consensus on which model is best. To examine sensitivity, we explored 2

Fiedler et al. 1998), fin and humpback whales feed on a mixture of euphausiids and small pelagic fish (Mitchell 1978, Christensen et al. 1992), beaked whales and sperm whale feed largely on epi- and mesopelagic squid species (Smith & Whitehead 2000), and delphinoids feed mostly on a mixture of epi- and mesopelagic fishes and squids (Fitch & Brownell 1968, dos Santos & Haimovici 2001). Large zooplankton (krill) was consumed at a rate 3 or more times greater than that of any of the other 7 prey categories (Table 5).

Table 3. Estimates of cetacean prey consumption within the California Current study area using 3 models. The 2 models based on scaled basal metabolic rate (BMR, Eq. 2) depend on the proportion of crustaceans in the diet (Eq. 4), and here we use the estimated proportion of large zooplankton (Trites et al. 1997) to estimate the proportion of crustaceans. Consumption estimates for Balaenopteridae assume that 83% of their diet is consumed in the California Current feeding area

Species	Proportion large zoo-plankton in diet	—— Annual consumption (t) ——		
		2.5× BMR	Trites et al. (1997)	3× BMR
Short-beaked common dolphin	0.00	578519	428591	694223
Long-beaked common dolphin	0.00	35989	26662	43187
Unclassified common dolphin	0.00	9250	6852	11099
Striped dolphin	0.00	41144	31050	49373
Pacific white-sided dolphin	0.00	38401	28413	46082
Northern right whale dolphin	0.00	14949	10929	17939
Bottlenose dolphin (offshore)	0.00	6297	4868	7557
Bottlenose dolphin (coastal)	0.00	640	495	768
Risso's dolphin	0.00	42231	32933	50677
Short-finned pilot whale	0.00	2629	2155	3155
Killer whale	0.00	16066	14052	19279
Dall's porpoise	0.00	115512	84437	138615
Harbor porpoise	0.00	52056	36779	62467
Mesoplodon spp.	0.00	7044	5688	8452
Cuvier's beaked whale	0.00	41131	34247	49357
Baird's beaked whale	0.00	25838	22994	31006
Kogia spp.	0.00	3682	2838	4418
Sperm whale	0.00	175334	169710	210401
Minke whale	0.65	45176	28224	44995
Bryde's whale	0.40	667	474	665
Sei whale	0.80	11489	7130	11443
Sei/Bryde's whale	0.80	2055	1274	2046
Fin whale	0.80	490329	318582	488367
Blue whale	1.00	491002	300083	489038
Humpback whale	0.55	157735	110106	157104
Unidentified delphinoid	0.00	8100	5998	9720
Unidentified ziphiid whale	0.00	4061	3364	4874
Unidentified small whale	0.00	6957	5921	8348
Unidentified roqual whale	0.80	65244	42487	64983
Unidentified large whale	0.80	39358	30574	47229
Subtotal: Delphinoids		961784	714216	1154141
Subtotal: Ziphiidae		78074	66293	93689
Subtotal: Physeteridae		179016	172548	214819
Subtotal: Balaenopteridae		1263696	808359	1258641
Total		2528885	1797910	2776868

Primary production leading to cetaceans

The mean values of annual NPP did not vary much among the 4 regions (Table 6). Values showed a strong offshore gradient in all regions, with higher net production closer to the coasts (Fig. 1). The overall mean value weighted by the size of each region was 266.8 g C m^{-2} yr^{-1}. Assuming a 10% trophic transfer efficiency, an NPP of ~32.2 g C m^{-2} yr^{-1} was needed to support the prey that were directly consumed by cetaceans in this study area (Table 5). This PPR represented ~12% of the total NPP. Of this PPR for cetaceans, ~60% was required for delphinoids and only 14% was required for Balaenopteridae, despite the greater biomass consumed by the latter.

Sensitivity analysis

In exploring plausible ranges of uncertainty in input values (Table 7), it was clear that uncertainty in estimates of trophic transfer efficiencies have the greatest effect on estimates of cetacean PPR. Values of PPR ranged from 4 to 99% of NPP as trophic efficiency varied from 15.8 to 4.2%, respectively. Uncertainties in estimates of cetacean abundances and consumption rates had roughly equivalent effects on uncertainty in cetacean PPR (Table 7). As abundance varied between its lower and upper 68% CI, cetacean PPR ranged between 10 and 15% of NPP. Two models were used to bracket the uncertainty in estimates of cetacean consumption rates (Table 7), and the range of cetacean PPR estimates varied between 9 and 14% of NPP for these 2 models.

DISCUSSION

Based on our estimates of cetacean biomass consumption and an assumed trophic efficiency of 10%, the PPR for cetaceans is on the order of 12% of the NPP in the California Current study area. This is less than most estimates from the studies cited in the 'Introduction'. The cetacean densities used in most of those previous studies were only rough estimates, and some of this difference can be attributed to the

Table 4. Annual consumption, prey proportions, effective trophic level, and annual primary production requirement (PPR) for each species of cetacean in the study area. Annual consumption values from Table 3 (wet weights for the entire study area) were converted to consumption of carbon biomass m^{-2}. Prey proportions for each of 8 prey categories (BI: benthic invertebrates, LZ: large zooplankton, SS: small squid, LS: large squid, SP: small pelagic fish, MP: mesopelagic fish, MF: miscellaneous fish, HV: higher vertebrates) are from Pauly et al. (1998). The effective trophic level is equal to 1 plus the average prey trophic level (Table 5) weighted by the prey proportions. Annual PPR is estimated from Eq. (6), assuming a trophic transfer efficiency of 10%

Species	Annual consumption (mg C m^{-2} yr^{-1})	BI	LZ	SS	LS	SP	MP	MF	HV	Trophic level	Annual PPR (g C m^{-2} yr^{-1})
Short-beaked common dolphin	56.42			0.15	0.15	0.10	0.40	0.20		4.2	11.69
Long-beaked common dolphin	3.51			0.15	0.15	0.10	0.40	0.20		4.2	0.73
Unclassified common dolphin	0.90			0.15	0.15	0.10	0.40	0.20		4.2	0.19
Striped dolphin	4.01	0.05		0.20	0.15	0.05	0.30	0.25		4.2	0.83
Pacific white-sided dolphin	3.74			0.30	0.05	0.30	0.20	0.15		4.1	0.56
Northern right whale dolphin	1.46			0.30	0.20		0.40	0.10		4.3	0.34
Bottlenose dolphin (offshore)	0.61			0.20	0.05	0.15		0.60		4.2	0.11
Bottlenose dolphin (coastal)	0.06			0.20	0.05	0.15		0.60		4.2	0.01
Risso's dolphin	4.12	0.05		0.50	0.35	0.05		0.05		4.3	1.10
Short-finned pilot whale	0.26			0.30	0.30	0.10	0.10	0.20		4.3	0.07
Killer whale	1.57			0.05	0.05	0.10		0.40	0.40	4.5	0.81
Dall's porpoise	11.26	0.05		0.30	0.10	0.20	0.20	0.15		4.1	1.92
Harbor porpoise	5.08	0.05		0.10	0.10	0.30		0.45		4.2	0.87
Mesoplodon spp.	0.69			0.20	0.30		0.30	0.20		4.4	0.19
Cuvier's beaked whale	4.01	0.10		0.30	0.30		0.15	0.15		4.3	1.02
Baird's beaked whale	2.52	0.10		0.30	0.25	0.10	0.10	0.15		4.2	0.57
Kogia spp.	0.36	0.05		0.35	0.40		0.10	0.10		4.4	0.11
Sperm whale	17.10	0.05		0.10	0.60	0.05	0.05	0.15		4.4	6.12
Minke whale	4.41		0.65			0.30		0.05		3.4	0.16
Bryde's whale	0.07		0.40			0.20	0.20	0.20		3.7	0.01
Sei whale	1.12		0.80	0.05		0.05	0.05	0.05		3.4	0.05
Sei/Bryde's whale	0.20		0.80	0.05		0.05	0.05	0.05		3.4	0.01
Fin whale	47.82		0.80	0.05		0.05	0.05	0.05		3.4	1.96
Blue whale	47.88		1.00							3.2	0.76
Humpback whale	15.38		0.55			0.15		0.30		3.6	1.17
Unidentified delphinoid	0.79			0.15	0.15	0.10	0.40	0.20		4.2	0.16
Unidentified ziphiid whale	0.40	0.10		0.30	0.30		0.15	0.15		4.3	0.10
Unidentified small whale	0.68	0.10		0.30	0.30		0.15	0.15		4.3	0.17
Unidentified roqual whale	6.36		0.80	0.05		0.05	0.05	0.05		3.4	0.26
Unidentified large whale	3.84		0.80	0.05		0.05	0.05	0.05		3.4	0.16
Subtotal: Delphinoids	93.8										19.4
Subtotal: Ziphiidae	7.6										1.9
Subtotal: Physeteridae	17.5										6.2
Subtotal: Balaenopteridae	123.2										4.4
Total	246.6										32.2

Table 5. Estimated annual prey consumption for 4 cetacean taxa stratified by prey categories (for abbreviations, see Table 4). Mean tropic levels for each prey category are from Pauly et al. (1998)

Taxon	Consumption by prey category (mg C m^{-2} yr^{-1})								Total
	BI	LZ	SS	LS	SP	MP	MF	HV	
Delphinoids	1.2	0.0	17.8	13.6	11.8	29.5	19.3	0.6	93.8
Ziphiidae	0.7	0.0	2.2	2.2	0.3	1.1	1.2	0.0	7.6
Physeteridae	0.9	0.0	1.8	10.4	0.9	0.9	2.6	0.0	17.5
Mysticetes	0.0	106.7	3.0	0.0	6.6	3.0	7.8	0.0	127.1
Total	2.9	106.7	25.1	26.4	19.5	34.6	31.0	0.6	246.6
Trophic level	2.2	2.2	3.2	3.7	2.7	3.2	3.3	4.0	

greater precision of estimates in the present study. This PPR of 12% is still a very significant fraction of primary production, especially considering that up to 50% of net production might not enter the cetacean food web except via indirect pathways of detritus and dissolved organic matter (Azam et al. 1983).

The absolute magnitude of annual prey consumption by cetaceans is also large, ~2 million metric tonnes. We avoid the usual comparison of this

Table 6. Mean annual net primary production (NPP) in each of 4 geographic regions. The total mean annual NPP is an average of the 4 regions (Fig. 1) weighted by their areas

Region	Area (km^2)	Mean annual NPP (g C m^{-2} yr^{-1})
Oregon/Washington	321 471	285.5
Northern California	257 368	257.4
Central California	241 420	292.5
Southern California	317 827	235.9
Total	1 138 086	266.8

quantity with the size of fisheries catches because the majority of this prey is krill and other species with no commercial harvest. It is, however, interesting to compare the cetacean PPR (~12%) with the primary production that is required to support the commercial fisheries catches. Pauly & Christensen (1995) estimated that worldwide fish catches and bycatch require ~8% of the global marine NPP but that the PPR for fisheries in upwelling and shelf ecosystems range from 25 to 35% of the NPP. For the northern California Current, Field et al. (2001) estimated the PPR for fisheries was ~20% in the 1960s. It appears, therefore, that the cetacean PPR is on the order of half of that required by commercial fisheries; when pinnipeds are added, it is likely that the total PPR for marine mammals will be of similar magnitude as that of fisheries.

The already large level of prey consumption by cetaceans is likely to increase. The abundance of delphinoids is likely reduced by fisheries bycatch which was high in the 1980s and early 1990s but has decreased recently (Julian & Beeson 1998, Carretta et al. 2005). Consumption by delphinoids should increase as they recover to previous levels. More significantly, large

whale populations were greatly depleted by commercial whaling, and populations are still growing (Calambokidis & Barlow 2004) to resume the role they once held in the California Current ecosystem. In just 7 years (1919 to 1926), 1871 humpbacks were removed by whalers working from shore stations in central California (Clapham et al. 1997), which is roughly twice the 1991 to 2005 abundance used here. Baleen whale biomass might double or quadruple before reaching pre-exploitation levels. Euphausiids are consumed in massive quantities by baleen whales, especially blue whales, which appear to be krill specialists (Christensen et al. 1992). Krill standing biomass (27 g wet wt m^{-2}) and production (216 g wet wt m^{-2} yr^{-1}) has been estimated for a northern, inshore portion of the California Current by mass balance using an Ecopath model (Field et al. 2006). Based on these values, the annual krill consumption by baleen whales (~0.1 g C m^{-2} yr^{-1}) would be <0.05% of the net krill production. However, this estimate was for highly productive inshore waters and would not be characteristic of our entire study area. In contrast, based on net tow data, Brinton (1976) estimated the density of *Euphausia pacifica* in the Southern California Bight to be only 0.01 to 1.0 g wet wt m^{-2}; given these estimates, krill consumption by baleen whales would be relatively much more important. More work is needed to directly estimate krill standing biomass and production in the entire California Current ecosystem.

Seasonality

Primary production is highly seasonal in the California Current study area, with highest rates of NPP in the spring and early summer. Here we have chosen to use an annual average of NPP rather than values for summer and fall seasons that correspond to the timing of the cetacean surveys. We did this because all cetaceans prey are 1 or more trophic level above phytoplankton and most feed on prey that are 6 mo to several years old. Although most baleen whales may not arrive in the area until early summer, they are certainly feeding on accumulated krill production that resulted from the spring phytoplankton bloom. Odontocetes are feeding on production that accumulated over much longer time periods. Because of the time lag between primary production and the subsequent consumption by cetaceans, an annual average of NPP is most appropriate.

Table 7. Estimates of the cetacean primary production requirement (PPR) given a variety of plausible inputs for cetacean abundance (lower and upper 68% CIs), the Trites et al. (1997) prey consumption model (Eq. 5 with $A = 0.1$, $B = 0.8$), the prey consumption model based on 3× the basal metabolic rate (BMR) (Eq. 2 with $\beta = 3$ and Eq. 4), and with trophic efficiencies of 4.2 and 15.8%. Percentages of the PPR are based on an estimated average net primary production (NPP) of 266.8 g C m^{-2} yr^{-1}. The base model uses the best estimates of cetacean abundance, a prey consumption rate based on 2.5× BMR, and a trophic efficiency of 10%

Model	Prey consumption by cetaceans (mg C m^{-2} yr^{-1})	PPR (g C m^{-2} yr^{-1})	PPR (% NPP)
Base model	246.6	32.2	12
Abundance = Lower 68% CI	153.4	25.0	10
Abundance = Upper 68% CI	387.1	40.2	15
Consumption model = Trites et al. (1997)	175.3	25.2	9
Consumption model = 3× BMR	270.8	37.7	14
Trophic efficiency = 4.2%	246.6	264.2	99
Trophic efficiency = 15.8%	246.6	11.1	4

Here we have assumed that the baleen whales that feed in the California Current consume 83% of their annual ration in that area. This assumption was based only on studies in the Antarctic (Lockyer 1981). Our abundance estimates are based on surveys in summer and fall when the majority of baleen whales are expected to be in their feeding areas. However, we know that blue whales migrate south and congregate in high-productivity areas in winter and spring and thus are likely to feed in those areas (Reilly & Thayer 1990). In contrast, humpback and minke whales migrate south in winter to very low-productivity areas, and are not likely to feed at all in those areas. Little is known about the migration patterns of fin whales that feed in the California Current, but a few fin, blue, and humpback whales are present off the shore of California in winter (Forney & Barlow 1998). Overall, a value of ~80% appears to be a reasonable estimate of a baleen whale's annual food consumption within the California Current, but the value of this parameter for individual species might range from 60 to 100%.

Less is known about the seasonal movement patterns of odontocetes. Most species are thought to be year-round residents, but their numbers may vary as some shift seasonally in distribution. In a comparison between summer and fall ship surveys and winter aerial surveys, Forney & Barlow (1998) found that common dolphins (both species pooled), Pacific white-sided dolphins, Risso's dolphins, and northern right whale dolphins were significantly more abundant in winter. Common and Risso's dolphins are a warm-temperate and tropical species whose distributions extend south and west of the cold California Current study area, so their higher abundance in winter is unexpected. However, these comparisons were based on a more narrow coastal study area in California, and, at least for common dolphins, the higher abundance in winter was probably caused by their movement towards the coast from within the California Current. Pacific white-sided dolphins and northern right whale dolphins are cold-temperate species whose distribution extends north and west of our California Current study area. Their increased numbers in winter may reflect their movement into the California Current. Our estimates of cetacean consumption and PPR in the California Current may be underestimates if abundances are generally higher in winter and spring.

Resolving uncertainties

By far the greatest uncertainty in evaluating the trophodynamic role of cetaceans lies in the trophic transfer efficiency of the trophic pathways leading to their prey. Ryther (1969) assumed trophic transfer efficiencies of 10% for marine oligotrophic areas and 20% for upwelling ecosystems. Pauly & Christensen (1995) estimated a mean trophic efficiency of 10.1% based on a review of models of aquatic ecosystems and showed that values as high as 20% were rare. The same study showed, however, that estimates of trophic efficiencies as high as 16% are common. The range of trophic efficiencies used in our sensitivity study (±1 SD from Pauly & Christensen's [1995] mean) is clearly within the range observed in aquatic ecosystems (Pauly & Christensen 1995), although it might be an extreme case if the trophic efficiencies of all trophic levels were a full SD away from the mean value. Using a trophic efficiency of 4.2% results in the conclusion that cetaceans require 99% of the NPP to support their prey base (Table 7), which is clearly untenable when considering the removals by other top-level predators (e.g. pinnipeds, seabirds, sharks and humans). Detailed knowledge of marine mammal abundance can therefore aid in ecosystem studies by limiting the range of feasible values for trophic efficiency. Nonetheless, there are no direct measures of trophic efficiency within the California Current, and obtaining such estimates should be a priority for improving trophic models of that system.

Uncertainty in estimating cetacean abundance (by using 68% CIs) resulted in PPR estimates from 10 to 15% of NPP. In this case, it would be statistically implausible for the abundance of all species to be simultaneously at their upper or lower CIs due to sampling variability. Such a situation could only occur if a substantial bias existed in the estimation procedures. The close agreement between estimates of blue and humpback whale abundance by independent methods (line-transect and mark-recapture, Calambokidis & Barlow 2004) suggests that such bias is unlikely.

Uncertainty in cetacean consumption rates (represented by a range in models) results in PPRs ranging from 9 to 14% of NPP. Directly measuring the consumption rates of large whales is extraordinarily difficult, and there are no immediate prospects of improving these estimates. However, cetacean PPR is dominated by consumption by small cetaceans. Food consumption and metabolic rates can be measured for captive dolphins and porpoises (Kastelein et al. 2002), and additional studies of this kind are likely to help refine estimates for wild cetaceans.

In the present study, we have assumed that all prey consumed within the bounds our study area was the net result of primary production within that area. In fact, no area of the open ocean is an entirely closed system. Advection of biomass in the California Current ecosystem is generally in a southward direction, with some production from the north flowing into our study area and some production from within that area flow-

ing out to the south. Measurement or models of current-driven biomass flux could also help refine our understanding of the trophodynamics of cetaceans as well as other components of the ecosystem.

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