

Trophic Levels of North Pacific Humpback Whales (*Megaptera novaeangliae*) Through Analysis of Stable Isotopes: Implications on Prey and Resource Quality

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Abstract

Trophic levels of 1,105 humpback whales from six geographically and isotopically distinct North Pacific feeding groups were calculated using $\delta^{15}\text{N}$ of humpback whales and regional primary consumers. The overall mean trophic level for North Pacific humpback whales was 3.6 ± 0.02 , indicating a diet of both fish and zooplankton, and, thus, supporting assumptions of humpback whales as generalist predators. The highest mean trophic level was calculated for the north Gulf of Alaska group (4.0 ± 0.03), while the lowest was found for the Russian and the western Aleutian Islands group (3.3 ± 0.08). Differences in mean trophic levels suggest that feeding groups differ in the proportion of fish and zooplankton in their diets.

Key Words: North Pacific, prey quality, stable isotopes, trophic level, humpback whales, *Megaptera novaeangliae*

Introduction

Most seasonal or long distance migrations occur in response to seasonal peaks in regional resource availability and, at least with respect to land mammals, are generally characterized by the availability of resources at both ends of the migration (Fryxell, 1995; Murray, 1995; Corkeron & Connor, 1999; Alerstam et al., 2003). Large baleen whales undergo seasonal migrations between high-latitude foraging grounds and low-latitude breeding grounds. In contrast to their land-based relatives, sources of nutrition are rarely available on the breeding grounds and, as a result, many baleen whale species undergo long periods of fasting (Corkeron & Connor, 1999). Migration is

an energetically expensive behavior, and energy demands likely increase further when coupled with fasting. Activities on the breeding grounds, such as breeding, gestation, and lactation, require an increase in energy demands above standard metabolic requirements (Read, 2001). The physical condition of migrant whales when they arrive on their respective breeding grounds is thus critical to survival and reproductive success. Poor body condition of migrants, including baleen whales, has been implicated in reduced reproductive success, changes in offspring sex ratios, delays in migratory timing, and lower annual survival rates (Perrins, 1970; Price et al., 1988; Wiley & Clapham, 1993; Moller, 1994; Stolt & Fransson, 1995; Lozano et al., 1996; Sandberg & Moore, 1996).

Stores of adipose tissue contribute the majority of energy in times of fasting. Migratory birds, for example, increase fat stores prior to migration by increasing food intake and by selecting diets based, in part, on nutrient content. Changes in the fatty acid composition of migratory bird depot fat is affected by diet composition and has direct consequences for the energetic cost of migration (Pierce & McWilliams, 2005). It follows that migratory whales should optimize intake of high-quality prey that will contribute most to their fat or blubber layer. For marine mammals, the blubber layer serves many functions, including defining hydrodynamic shape, providing buoyancy, insulating from cold water temperatures, and storing energy in the form of lipids (Worthy & Edwards, 1990; Koopman et al., 2002). As a result, prey choice for baleen whales on their feeding grounds can have significant impacts on future events, including migration, survival, and reproduction.

In the North Pacific, humpback whales (*Megaptera novaeangliae*) migrate from low-latitude breeding

grounds to geographically distinct feeding aggregations in higher latitudes. Segregation on the feeding grounds has been attributed to the cultural transmission of fidelity to a feeding ground as a result of a calf's early maternal experience (Martin et al., 1984; Baker et al., 1987; Clapham & Mayo, 1987). At low latitudes, humpback whales may lose one third to one half of their body mass (Dawbin, 1966; Lockyer, 1981; Baraff et al., 1991; Laerm et al., 1997). During this period of fasting, humpback whales rely almost exclusively on the blubber stores accumulated while foraging on the high-latitude feeding grounds (Lockyer, 1981).

Humpback whales are considered to be generalist in their prey selection and are known to feed on zooplankton (including euphausiids) and small schooling fish, such as Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*). Despite this apparently generalized diet, there are likely significant differences between the specific diets of feeding aggregations, with some groups targeting forage fish and others euphausiids. Previous analysis of humpback whales' stable isotope ratios identified six geographically distinct feeding grounds in the North Pacific (Witteveen et al., 2009b). These findings suggest that feeding grounds differ with respect to prey availability and/or the feeding groups differ in their feeding behavior or prey choice. Location of foraging will thus directly impact the variety and quality of prey available to humpback whales. The quality of prey and its ability to contribute to this energy reserve is therefore critical to the survival and reproductive success of humpback whales. As a result, clarifying the number and boundaries of feeding locations can have important implications in management and conservation efforts.

The analysis of stable carbon and nitrogen isotope ratios is an inexpensive and effective method for exploring trophic position, diet, and feeding origins of migratory animals (Hobson, 1999). Stable nitrogen isotope ratios become enriched by ~2 to 5‰ between trophic levels and can, therefore, predict relative trophic position (Minagawa & Wada, 1984; Fry, 1988; Hobson et al., 1993, 1994; Sydeman et al., 1997; Kurle & Worthy, 2002). In this study, we investigate the relative trophic levels of the North Pacific humpback whale feeding groups through comparison of stable nitrogen isotope ratios of their skin and the tissue of primary consumers of regional food webs. This study marks the first attempt to employ stable isotope analysis to infer how differences in regional diets and prey choice may influence aspects of the humpback whale life history.

Materials and Methods

Sample Collection, Preparation, and Stable Isotope Analysis

Humpback whale skin samples were collected for isotopic analysis as part of the Structure of Populations, Levels of Abundance, and Status of Humpback whales (SPLASH) project. The SPLASH sampling effort covered the known range of humpback whales in the North Pacific basin. On the feeding grounds, the SPLASH effort occurred between 17 May and 4 December 2004 and 22 April and 4 December 2005 (Calambokidis et al., 2008). Samples were collected using a hollow-tipped biopsy dart fired from either a crossbow or modified .22 rifle, and identification photographs of the tail flukes of sampled animals were collected whenever possible. In total, 5,604 samples were collected during SPLASH field efforts on the feeding grounds, of which 1,105 were used for stable isotope analysis (Calambokidis et al., 2008; Witteveen et al., 2009b).

Upon collection, samples were preserved by either freezing or storage in dimethyl sulfoxide (DMSO) or ethanol. Method of preservation has been shown to have no effect on stable isotope analysis when lipids are extracted (Hobson et al., 1997; Todd et al., 1997; Marcoux et al., 2007). All skin samples were oven dried and lipids extracted (Witteveen et al., 2009b). Samples were analyzed for stable carbon and nitrogen isotope ratios using a Finnigan MAT Delta Plus XL isotope ratio mass spectrometer (IRMS). Stable isotope ratios are reported as per mil (‰) using the standard delta (δ) notation according to $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, where X is ^{15}N or ^{13}C and R is the corresponding ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. Standard reference materials were carbon from Pee Dee Belemnite and atmospheric nitrogen gas. Replicate measurements of internal laboratory standards indicated a measurements error of ± 0.10 for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Feeding Groups and Migratory Connections

A previous analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ classified North Pacific humpback whales into six feeding groups (Witteveen et al., 2009b). These groups were defined as COW (California, Oregon, Washington, and southern British Columbia), NBC (northern British Columbia), SEAK (southeastern Alaska), NGOA (northern Gulf of Alaska), CENT (western Gulf of Alaska, eastern Aleutian Islands, and Bering Sea), and WEST (western Aleutian Islands and Russia) (Figure 1). Variables from these groups, including $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were used in classification tree analysis to assign breeding areas to feeding groups based on similarities in stable isotope ratios, describing migratory connections. Breeding areas were Asia (Philippines, Okinawa, and Ogasawara, Japan), the U.S. (Hawaiian Islands), Mexico (Revillagigedos

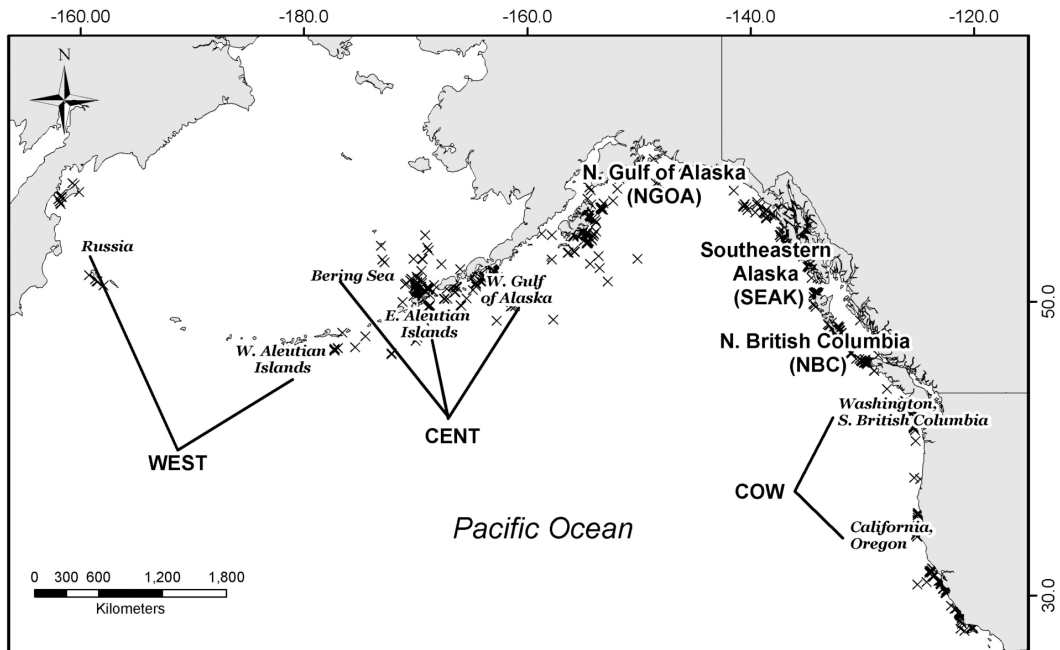


Figure 1. Map of the North Pacific showing ten regions of SPLASH sampling on feeding groups of humpback whales; also shown are the six feeding groups (in caps) defined previously in the text, with solid lines showing feeding region membership (Witteveen et al., 2009b).

Islands, Baja Peninsula, and Mainland), and Central America (Witteveen et al., 2009a).

Baseline $\delta^{15}\text{N}$ of Regional Food Webs

Comparisons of the $\delta^{15}\text{N}$ values of humpback whale skin cannot be made without knowledge of the $\delta^{15}\text{N}$ values at the base of food webs for each feeding group. Previous studies have used primary consumers, such as copepods (*Calanus* sp.) and filter-feeding bivalves, as good surrogates of food web bases (Kling et al., 1992; Cabana & Rasmussen, 1996; Post, 2002; Matthews & Mazumder, 2005; Andrews, 2010). In the present study, at least one primary consumer from the geographic region of each feeding group, except WEST, was used to set the baseline $\delta^{15}\text{N}$ level of regional food webs. If more than one primary consumer was available for the region, the mean value of all consumers was used for that region. With respect to WEST, the $\delta^{15}\text{N}$ value obtained for CENT was used in the absence of specific data for that region. Primary consumers used were copepods (Copepoda, *Neocalanus* spp., *Calanus* spp.), weathervane scallops (*Patinopecten caurinus*), mussels (*Mysticallus californiana*), and salps (Salpidae) (Table 1).

Trophic Ecology

The trophic levels of individual humpback whales were calculated using the following equation:

$$\text{Trophic Level} = 2 + (\delta^{15}\text{N}_{\text{specimen}} - \delta^{15}\text{N}_{\text{primary consumer}})/2.4$$

where 2 is the trophic position of the primary consumer and 2.4 is the average $\delta^{15}\text{N}$ enrichment per trophic level for marine mammals (Hobson et al., 1994; Post, 2002). Mean trophic-level values for each feeding group were calculated by averaging the trophic levels of individuals within feeding groups.

Statistical Analysis

Data were tested for normality and homogeneity of variance using Kolmogorov-Smirnov and Levene's test, respectively. One-way analyses of variance (ANOVA) were used to explore differences in trophic level between feeding groups. Homogeneous subsets were determined through Tukey's post-hoc tests following analysis. All statistics were conducted within *Predictive Analysis Software (PASW) 18.0* for Windows (IBM, SPSS, Inc., Somers, NY, USA) with a critical value of $\alpha = 0.05$ for all analyses (Moran, 2003). Values presented are mean \pm SE.

Results

The overall mean trophic level for North Pacific humpback whales was 3.6 ± 0.02 . Feeding groups' means ranged from a low of 3.3 ± 0.08 (WEST) to a high of 4.0 ± 0.03 (NGOA) (Figure 2). The lowest individual trophic level was 1.4 and was estimated

Table 1. Mean (\pm SE) stable nitrogen isotope ratios (‰) and sample sizes for humpback whales and primary consumers for each of the six distinct feeding groups of humpback whales in the North Pacific (Witteveen et al., 2009b); also shown are the trophic levels (TL) of humpback whales for each group.

Group	Humpback whales				1° consumers		
	<i>n</i>	$\delta^{15}\text{N}$	TL	<i>n</i>	$\delta^{15}\text{N}$	Species	Sources
WEST	81	12.3 \pm 0.19	3.3 \pm 0.08	--	9.1*	--	--
CENT	282	12.6 \pm 0.07	3.5 \pm 0.03	57	9.1 \pm 0.13	<i>Neocalanus</i> spp., <i>Calanus</i> spp., <i>Patinopecten caurinus</i>	Hirons, 2001; Andrews, 2010
NGOA	199	13.6 \pm 0.07	4.0 \pm 0.03	86	8.8 \pm 0.04	<i>Calanus</i> spp., <i>Patinopecten caurinus</i>	Hirons, 2001; Andrews, 2010
SEAK	227	12.7 \pm 0.06	3.4 \pm 0.03	10	9.3 \pm 0.10	<i>Patinopecten caurinus</i>	Andrews, 2010
NBC	135	13.0 \pm 0.08	3.5 \pm 0.03	42	9.4 \pm 0.09	<i>Mystilus californiana</i>	Markel, unpub. data
COW	181	14.7 \pm 0.07	3.9 \pm 0.03	15	10.2 \pm 0.69	Salpidae, Copepoda	Miller, 2006; CSCAPE 2006 project
Total	1,105	13.2 \pm 0.04	3.6 \pm 0.02	210			

*No data from primary consumers in the WEST feeding group were available. The value shown is from the CENT.

for an animal sampled in SEAK in 2004. The highest individual trophic level came from NGOA in 2004 and was estimated at 5.1. The mean values of $\delta^{15}\text{N}$ for primary consumers ranged from 8.8 in NGOA to 10.2 in COW, and $\delta^{15}\text{N}$ of humpback whale skin increased by an average of 3.9 ‰ over primary consumers (Table 1). This difference signified humpback whales were foraging approximately 1.6 trophic levels higher than primary consumers.

Trophic levels differed among feeding groups ($F_{5,1099} = 62.0$, $p < 0.001$). Post-hoc tests showed that mean trophic levels for NGOA and COW were significantly different than for all other groups. The trophic levels of the remaining four feeding groups did not differ significantly (Figure 2).

Discussion

Using stable isotopes to explore the trophic levels of humpback whales can lend insight into regional differences in prey availability or choice. A mean trophic level of 3.6 supports the assumption that on a basin-wide scale, North Pacific humpback whales are generalist predators and likely exploit both fish and zooplankton species. If the humpback whales sampled in this study were feeding primarily on zooplankton, it is likely that estimates of trophic level would be closer to those of cetacean species adhering to a more strict plankton diet such as the bowhead whale (TL = 2.8 to 3.0; Hoekstra et al., 2002). Trophic levels of strict ichthyophagous marine mammals tend to be higher such as those estimated for beluga whales (TL = 4.4 to 4.8; Lesage et al., 2001) and ringed seals (TL = 4.4 to 4.6; Hobson et al., 2002; Figure 2). Trophic levels estimated in this study further suggest that humpback whales are feeding

at levels similar to those of piscivorous pelagic fish: trophic levels between 3 and 4 and one to two trophic levels above zooplankton (Lesage et al., 2001; Das et al., 2003; Morissette et al., 2006).

Though COW exhibited the highest mean value of $\delta^{15}\text{N}$ (14.7), it had the second highest trophic level (3.9). The highest trophic level was seen in NGOA (4.0), where average $\delta^{15}\text{N}$ was 1.1 ‰ lower than COW. The discrepancy between $\delta^{15}\text{N}$ and trophic levels is due to the substantial difference in the $\delta^{15}\text{N}$ values of the primary consumers in each feeding region. While the stable nitrogen isotope ratios of primary consumers (trophic level = 2) were near 9.0 ‰ for most feeding groups, the COW value was 10.2 ‰ (Table 1 & Figure 3). It should be noted that the primary consumers used were not consistent between regions due to limited availability of samples or data. Thus, differences may have been the results of regional differences in $\delta^{15}\text{N}$ or due to differences in how primary consumers assimilate their food. Regardless, differences need to be estimated using the best means possible. Failing to account for differences at lower trophic levels and basing estimates of trophic level on $\delta^{15}\text{N}$ alone would result in the assumption that COW was feeding at a trophic level considerably higher than all other North Pacific feeding groups (Figure 3). Thus, it is very important to account for differences in the baselines of food webs before making trophic-level comparisons (Post, 2002).

Species of prey available to humpback whales can vary widely by season and location and, while considered generalists as a species, the trophic levels of feeding groups of humpback whales suggest significant regional differences in the types of prey being targeted. With a trophic level at or near

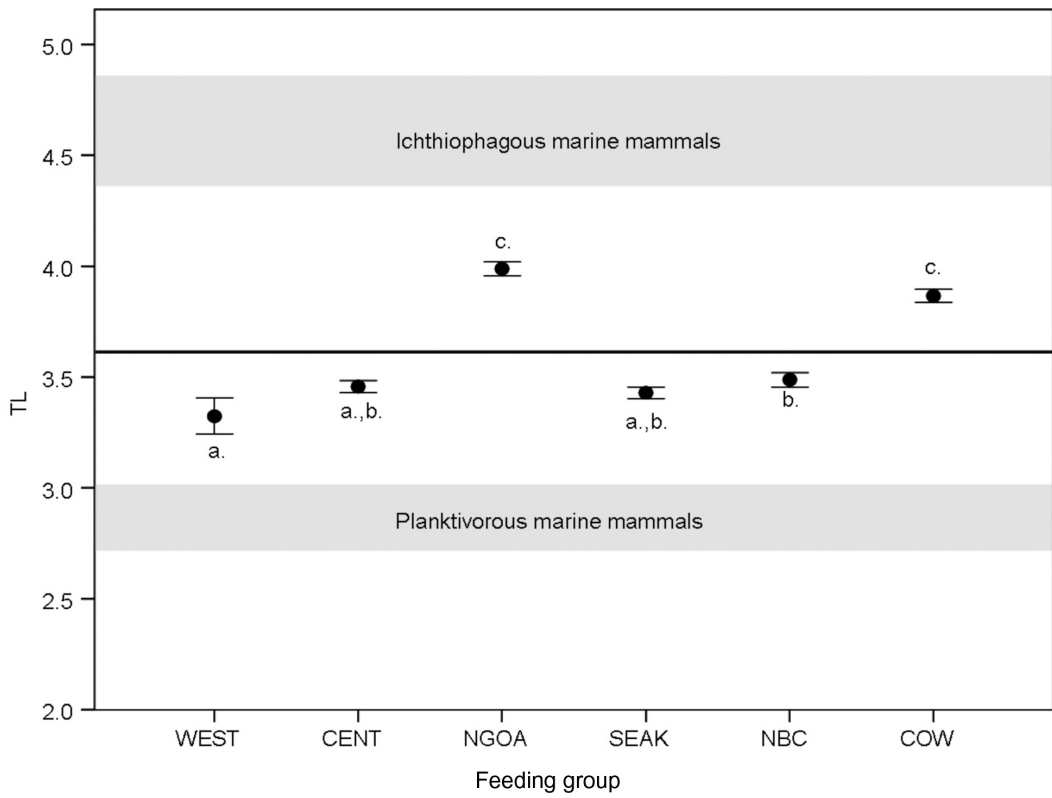


Figure 2. Mean (\pm SE) trophic level (TL) for each of the six feeding groups of North Pacific humpback whales; the solid black line represents the overall mean values for all groups. Shaded regions represent the range in trophic levels for strictly fish eating (4.4 to 4.8) and strictly plankton eating (2.8 to 3.0) marine mammals.

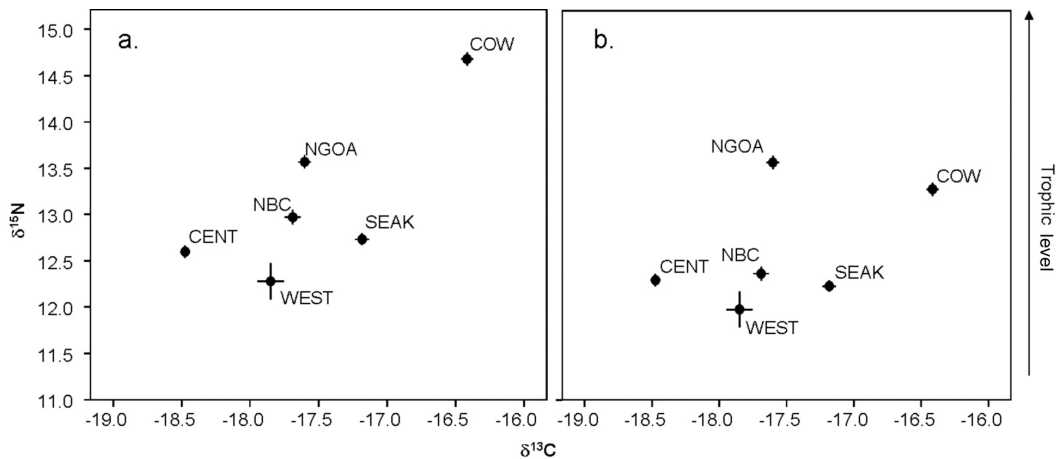


Figure 3. Mean values (\pm SE) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each feeding group (see Table 1; Figure 1) without (a) and with (b) adjustments to $\delta^{15}\text{N}$ based on primary consumers

4.0, it is likely that the diet of the NGOA and COW groups had a diet proportionally higher in fish species than zooplankton, while the remaining groups all had trophic levels closer to 3.5, indicating a more mixed diet of both fish and zooplankton. Field observations provide support for relative trophic-level differences. For example, humpback whales have been seen foraging extensively on euphausiid swarms in the eastern Aleutian Islands, an area included in the CENT feeding group with an estimated trophic level of 3.5 (C. Matkin, North Gulf Oceanic Society, pers. comm.). In contrast, the higher trophic level of COW is substantiated by recent observations of a switch from zooplankton (prior to 2004) to fish for animals feeding off California (J. Calambokidis, Cascadia Research, pers. comm.). Further, humpback whales foraging near Kodiak Island, Alaska, within the NGOA feeding group, have been shown to target aggregations of capelin (Witteveen et al., 2008).

Such variation in prey availability and use may significantly influence the life history parameters of feeding groups. Humpback whales depend on high-quality forage to sustain migratory and breeding behaviors through lengthy periods of fasting. Diets of poor quality or quantity may not contribute enough lipid to adipose tissue reserves, which are catabolized during migration and periods of limited nutrient intake (Lockyer, 1986; Bairlein, 1987; Izhaki & Safriel, 1989; Castellini & Rea, 1992; Parrish, 1997). Lipid content is the primary determinant of energy density, both of which can vary widely across taxa (Anthony et al., 2000). For example, the energy content of euphausiids is relatively low at 0.74 kJ/g (Davis et al., 1998) but can be greater than 5 kJ/g for some forage fish (Anthony et al., 2000). Assuming lipid content and energy density are surrogate measures of prey quality, it would follow that humpback whales in the COW or NGOA feeding groups may receive more benefits in the form of stored energy from their predation of fish or require smaller quantities of prey than groups foraging on euphausiids such as WEST or SEAK. However, other factors in addition to lipid content, such as energy required for capture and density of aggregations, are also likely to contribute to the overall quality of a prey source.

While the benefits of foraging are accrued on feeding grounds, they are realized on breeding grounds and, as such, the impact of foraging location on breeding animals must also be considered. Lockyer (2007) reviewed how food energy storage in the form of blubber can be vital to a number of functions, including insulation and reproductive efficiency, in both large migratory and small non-migratory cetaceans. Body condition was shown to be tightly linked to fertility in the closely related fin whales (Lockyer, 1986, 1987a, 1987b, 1990). Anthony et al. (2000) states that "by selecting for prey quality, in conjunction with maximizing

quantity, piscivorous predators can potentially increase their own fitness and the productivity of the population" (p. 67) if all prey resources require the same energy to capture. Thus, based on assumptions regarding energy density and prey quality, animals breeding in Central America and Mainland Mexico, which feed in COW (Rasmussen et al., 2007; Witteveen et al., 2009a), should benefit from higher trophic-level prey, perhaps in the form of increased survival or fecundity. Conversely, animals breeding in one of the western Pacific areas may not incur the same energetic benefits because stable isotope ratios indicated that their primary foraging locations were CENT and WEST where they were feeding on lower trophic-level prey (Witteveen et al., 2009a). While our results do not provide evidence of differences in prey quality, they do show differences in trophic level, which may be the first step in the process of determining how prey availability of choice may affect the life history parameters of humpback whales.

Sampling of humpback whales occurred across two feeding seasons and, thus, represent only a portion of any single whale's feeding history. This narrow sampling window may be limiting because, as stated previously, humpback whale prey can be highly variable both temporally and spatially, as well as in their energy content. The availability and abundance of prey within the boundaries of each feeding group likely dictates which prey humpback whales actually ingest. If certain prey types are predictably available, it is not unreasonable to believe that feeding groups of humpback whales could develop into regional prey specialists. Such specialties would easily become fixed since segregation of feeding groups has occurred as the result of a cultural transmission of migration routes from mother to calf (Aidley, 1981; Martin et al., 1984; Baker et al., 1987; Clapham & Mayo, 1987). Thus, predator selection of a prey resource with relatively low available energy may have significant long-term population effects resulting from reductions in body condition and reproductive success (Urton & Hobson, 2005; Inger et al., 2006).

There are limitations in this exploration of stable isotope ratios and trophic levels. Discussion of diet composition and trophic position depend on an accurate estimate of stable isotope enrichment of ^{15}N between humpback whales and their prey. Unfortunately, there are presently no published trophic enrichment factors for humpback whales. Other studies have used enrichment factors ranging between 2.4 to 3.8‰ (Hobson & Welch, 1992; Hoekstra et al., 2002; Born et al., 2003; Das et al., 2003). We used the lowest value of 2.4‰ because it has been applied to previous studies of marine mammals, including cetaceans (Hobson et al., 1996; Das et al., 2003). Choosing a higher trophic

enrichment factor would decrease our estimates of trophic level, changing our assumption of a fish-based diet for COW and NGOA to a mixed diet and from a mixed diet to a zooplankton-dominated diet for the remaining feeding groups. However, despite these changes, the relative differences and conclusions about differences in prey types between feeding groups would remain the same.

Calculations of trophic level also depend highly on the turnover rate of assimilated tissues if diets are not constant throughout the feeding season. The turnover rates of tissues are proportional to their metabolism, with active tissues (i.e., skin or muscle) showing faster turnover than inert tissues (i.e., baleen or bone) (Tieszen et al., 1983; Schell et al., 1989a, 1989b; Hobson & Clark, 1992; MacAvoy et al., 2006; Podlesak & McWilliams, 2006). Though never empirically tested, the skin of rorqual whales likely exhibits high metabolic rates, and a turnover rate of 7 to 14 d for humpback whale skin has been suggested (Todd, 1997). Thus, estimates here may reflect the trophic level of only the past 2 wks to 1 mo of foraging.

Information is needed to elucidate how prey use may be influencing life history factors such as reproductive success. First, more specific diet composition for each feeding group needs to be described. With the recent advancements in stable isotope mixing equations, feeding group diets could be modeled if a variety of prey resources from each region were available for analysis (Phillips & Gregg, 2001, 2003; Newsome et al., 2004; Phillips et al., 2005). Dietary mixing models in this manner would allow for more specific diet comparisons to be made, rather than comparing generalized fish vs zooplankton diets. If data on life history parameters, including, but not limited to, calf and adult survival, fecundity, and body condition, were available, correlations between these parameters and dietary differences could be explored. With the growing number of long-term datasets for regional humpback whale populations and the recent efforts of SPLASH, some parameters may be obtainable.

Analysis of stable carbon and nitrogen isotope ratios has shown that there may be significant differences in the prey being utilized between feeding groups of humpback whales in the North Pacific. These results highlight the need for additional research focused on diet composition within each feeding group as previous studies have shown that diet composition can have significant impacts on fitness.

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