



The morphology of euphausiid mandibles used to assess selective predation by blue whales in the southern sector of the California Current System

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ABSTRACT

We describe the mandibular morphology of the eight most abundant euphausiid species in the California Current and report regression relationships between mandible size and body total length. We applied these species-specific characters to the mandibles recovered from fecal samples of 18 blue whales (*Balaenoptera musculus* (Linnaeus, 1758)) collected between 1998 to 2015 off Southern California to test for selective feeding on the euphausiid assemblage. The diets of blue whales were consistently and overwhelmingly dominated by the large neritic euphausiid *Thysanoessa spinifera* Holmes, 1900, even when other species were present or dominant in closely collected net samples. More than 99% of the ingested euphausiids were longer than 10 mm, indicating that blue whales in this region are highly selective by prey species and size class, and dependent upon aggregations of juveniles or adults of a limited number of coastally associated euphausiid species.

Key Words: Euphausiacea, fecal-sample analysis, krill, prey selection

INTRODUCTION

Blue whales, *Balaenoptera musculus* (Linnaeus, 1758), are the largest animals on earth but possibly have one of the most restricted diets, preying almost entirely on euphausiids (Nemoto, 1970; Kawamura, 1980; Schoenherr, 1991; Croll *et al.*, 2005), although occasionally additional prey have been reported (Del Ángel Rodríguez, 1997; Jiménez Pinedo, 2010). Like other rorquals, blue whales lunge feed, collecting planktonic organisms from volumes of engulfed water during discrete feeding events (Kawamura, 1980; Goldbogen *et al.*, 2012). Lunge feeding occurs at the water surface and at depth, and the average blue whale dive depth off the California coast is 190 m (Goldbogen *et al.*, 2012). Northeast Pacific blue whales migrate annually between Baja California and an area west of the Costa Rica Dome in winter to as far north as Washington state during summer, likely tracking their prey (Bailey *et al.*, 2009). Blue whales commonly occur between June and October in the southern sector of the California Current System (Bissell 2013), when they are thought to feed actively (Bailey *et al.*, 2009). Of the thirty-nine euphausiid species present in this region (Brinton *et al.*, 2000), eight dominate the potential prey field for blue whales: *Euphausia eximia* Hansen, 1911, *E. gibboidea* Ortmann, 1893, *E. pacifica* Hansen, 1911, *E. recurva* Hansen, 1905, *Nematocarcinus difficilis* Hansen, 1911, *Thysanoessa gregaria* (G. Sars, 1883), *Nyctiphanes simplex* Hansen, 1911, and *T. spinifera* Holmes, 1900.

The euphausiid *Thysanoessa spinifera* is over-represented in whale fecal material in comparison with net samples from the water column near where the whales were feeding in Monterey Bay and the Channel Islands, California (Fiedler *et al.*, 1998; Croll *et al.*, 2005). The more abundant euphausiid *Euphausia pacifica* was consumed at both locations, but in significantly lower proportions than the present in the water column. The mean size of both euphausiid species was larger in the whale diet than in the water column in Monterey Bay (Croll *et al.*, 2005). Blue whales nevertheless occur well beyond the geographic ranges of *Thysanoessa spinifera* and *Euphausia pacifica* and are known to consume other euphausiids in other locations. Blue whales feed on *Euphausia superba* Dana, 1850 and *E. crystallorophias* (Kawamura, 1980) in the Southern Ocean, both of which aggregate near the surface under pack ice (O'Brien, 1987). Blue whales have also been observed feeding on surface aggregations of *Nyctiphanes simplex* in the Gulf of California, Mexico (Gendron, 1992) and *N. simplex* mandibles have been documented in blue whale feces there (Del Ángel Rodríguez, 1997; Jiménez Pinedo, 2010). Surface swarms may provide accessible aggregations of mature adults (Smith & Adams, 1988); however, euphausiid aggregation density is a more important factor in determining the energetic benefit of a particular lunge than the depth of the aggregation (Goldbogen *et al.*, 2011). A deeper, but denser aggregation of euphausiids would provide the whale with

more net energy gain, despite the added cost of swimming deeper compared to a shallow but sparse aggregation.

Analysis of fecal samples is a non-invasive method of assessing the diet of baleen whales. Whale fecal plumes contain unassimilated prey remains, including the siliceous mandibles of euphausiids (Kieckhefer, 1992; Del Ángel Rodríguez, 1997; Croll *et al.*, 2005; Jiménez Pinedo, 2010). While previous researchers have investigated the feeding specificity of whales through analysis of mandibles in fecal material (Kieckhefer, 1992; Del Ángel Rodríguez, 1997; Fiedler *et al.*, 1998; Croll *et al.*, 2005; Jiménez Pinedo, 2010), there are no published descriptions of mandibular morphology for most of the euphausiid species we describe here, limiting the range of identifiable prey species. We for the first time describe mandible morphologies for all eight numerically dominant species of euphausiids in the California Current System. We developed isometric scaling relationships that relate mandible size to body total length of the euphausiids, and use these species-specific descriptions and scaling relationships to test the hypothesis that blue whales feed selectively on the available euphausiid prey assemblage in the southern sector of the California Current System from San Diego to Cordell Bank, California (Fig. 1).

MATERIALS AND METHODS

Dissection and identification of mandibles

We completed mandible dissections with the use of a Nikon SMZ 1500 stereomicroscope (Nikon, Tokyo, Japan). Total length from the tip of the rostrum to the end of the telson (Boden *et al.*, 1955; Brinton, 1962; Brinton *et al.*, 2000) was measured for each adult euphausiid before mandibles were dissected. Each pair of mandibles was dissected and cleared of the labrum, mandibular palps, first and second maxillae, and associated musculature so that accurate measurements could be made. We measured total mandible length (TML), total incisor length (TIL), and total molar width (TMW; Fig. 2) so that the mandibular edge index (MEI) could be calculated (Nemoto, 1977). Once cleaned, each pair of mandibles was then placed in glycerin on a slide for measurements and assessment of morphological characteristics.

The adult size range of *Euphausia pacifica* coincides with the size range of the euphausiids blue whales have been shown to ingest (Croll *et al.*, 2005). Mandibles were initially dissected from intact

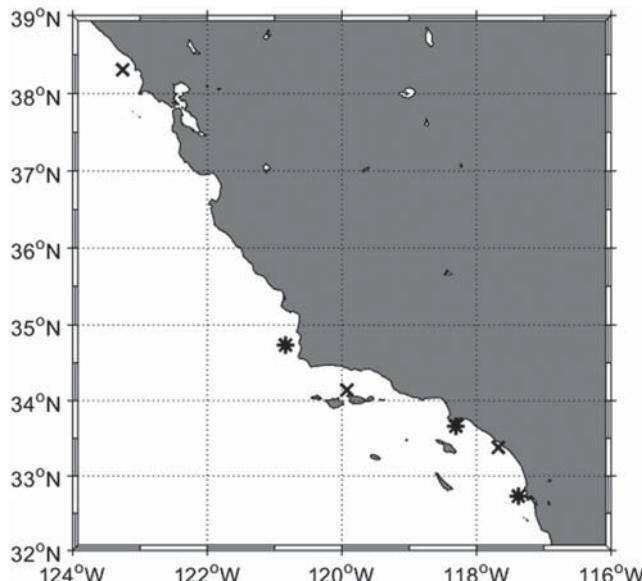


Figure 1. Locations of the collection of fecal samples from blue whales; x, only fecal samples, *, fecal samples and net samples.

E. pacifica males and females at each 11–22 mm increment across the size range of adults, to assess morphological changes through adult development. This analysis revealed a similar mandibular morphology across sexes and throughout the adult life history. We then chose specimens at the lower, middle, and high end of the adult size range of each of the eight species with both sexes represented equally.

Each species exhibited consistent morphology throughout their adult size range and between sexes, with only minor variations, making species identifications reliable. A median adult size individual was used for taxonomic descriptions, line drawings (Fig. 3), and digital images (Fig. 4). Mandible drawings were made with Adobe Illustrator CS6 from line drawings made from a camera lucida and a compound microscope at 10 \times magnification.

Mandible-to-body-length regressions

The relationship between mandible length and body total length for the eight dominant California Current System (CCS) species (Brinton & Townsend, 2003) was determined using linear regressions. Regressions with larger sample sizes were developed for *T. spinifera* and *E. pacifica*, which proved to be the dominant prey. A total of 300 *T. spinifera* individuals, from furcilia to adults, were dissected and the lengths of the right mandible and body (total length) were measured; 136 adult *E. pacifica* and 30 individuals of the remaining six species were similarly dissected and measured. Statistics were performed in SigmaPlot vers. 10.0 (Systat Software, San Jose, CA, USA). Model I regressions were calculated because of the high precision and accuracy of both x and y variables.

Collection and enumeration of fecal samples

The whale fecal material was obtained from three sources (Nickels, 2017; Fig. 1, Table S1). The Cascadia Research Collective gathers whale fecal samples during photo identification of cetaceans off California. Clumps of newly discharged, floating fecal material were skimmed off the water's surface using a dip net with approximately 63 μ m mesh and either frozen at 20° C or preserved in isopropyl alcohol. Samples were transferred into 1.8% formaldehyde buffered with sodium tetraborate for long-term fixation.

Fecal samples were also obtained in partnership with the Ocean Institute, Dana Point, California, during public whale watching cruises in 2013. The fecal material was collected with a 183 μ m mesh plankton filtering funnel attached to a boat hook and frozen at -20° C before transfer to buffered 1.8% formaldehyde at room temperature.

A third source took place on 31 July 2014 in association with a larger effort (SKrillEx I) at Nine Mile Bank, near San Diego, California. During the second year of that effort (SKrillEx II) in 2015, fecal samples were collected on a small boat mission and opportunistically during a small-boat visual survey using a 183 μ m plankton filtering funnel. Fecal material was immediately preserved in buffered 1.8% formaldehyde.

The date of collection and the species of whale whence the sample originated was documented in all fecal samples. The location where the sample was collected was also recorded, but some location information is missing from older records (Supplementary material Table S1).

Fecal material was sorted for euphausiid mandibles and other identifiable prey parts using a dissecting microscope with a calibrated ocular micrometer. To prevent double counting, only right mandibles were identified and measured. Aliquots were removed from well-mixed samples and all right mandibles were identified and measured. Sorting continued until at least 300 right mandibles were found or all of the right mandibles from the sample were identified. Mandibles that were too damaged for identification were not included. The length distribution of consumed euphausiids was reconstructed from right-mandible lengths based upon the species-specific linear regressions (see below).

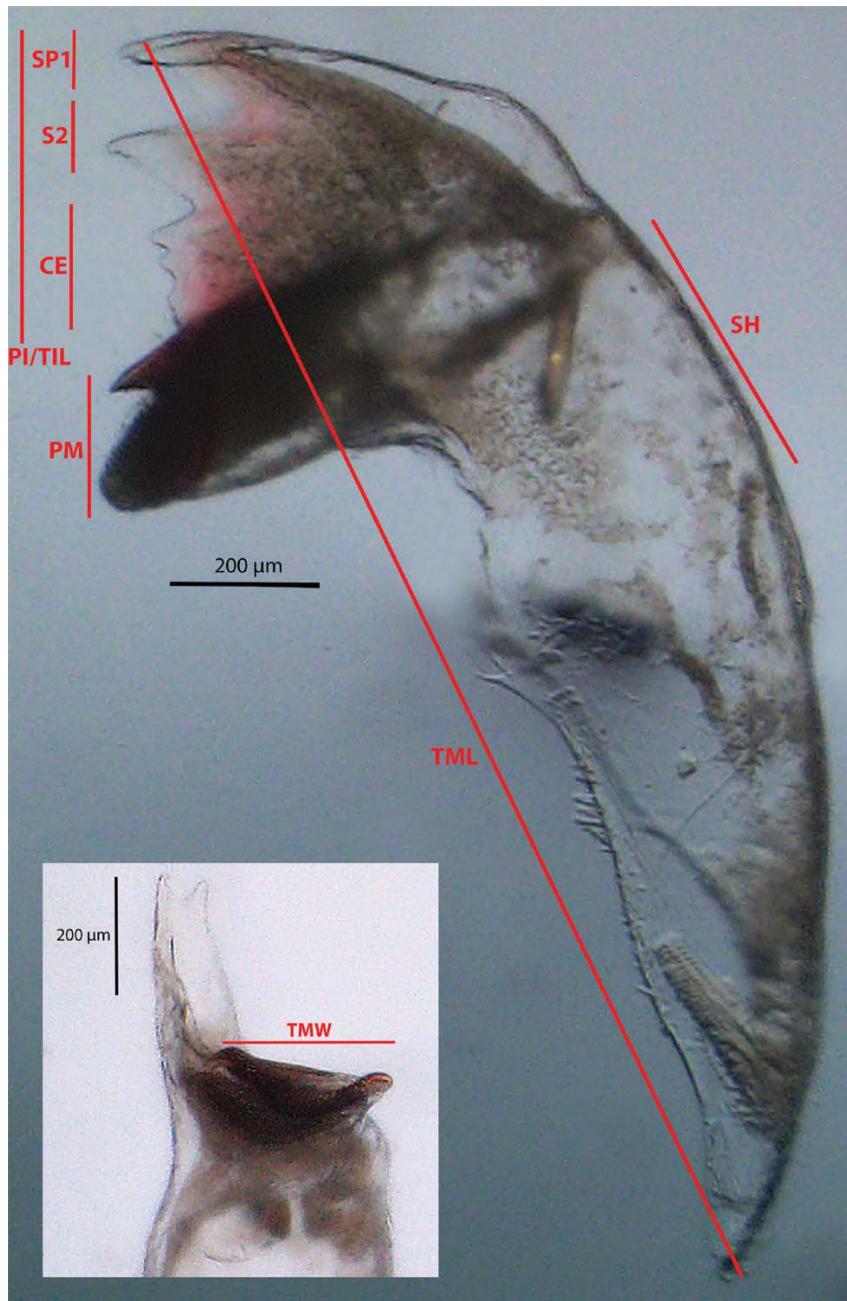


Figure 2. Digital images of euphausiid right mandible showing total mandible length (TML), total incisor length (TIL), and total molar width (TMW). Diagnostic characters include first pair of spines (spine pair one, SP1), spine two (S2), cutting edge (CE), pars incisiva (PI), pars molaris (PM), root shoulder (SH).

Description of mandibles

We chose the right mandible as our reference standard for taxonomic identifications, line drawings, descriptions, and digital images as in [Nemoto \(1977\)](#) and [Mauchline \(1989\)](#). The diagnostic characters described were the spacing of the first pair of spines (spine pair one, SP1), shape and length of the second spine (spine two, S2), the shape, angle, and length of the cutting edge (CE) proximal to the grinding region, the *pars molaris*, and the shoulder structure (SH) where the main cusp of the mandible connects to the root or posterior leading arced section of the mouthpart (Fig. 2).

Net-sample collection and enumeration of euphausiids

Net samples were also collected, whenever possible, to compare the size and species of euphausiids present where the whales were

feeding with those consumed by the whales, as inferred from fecal analysis. The Cascadia Research Collective sampled ambient euphausiids with a 333 μm mesh bongo net towed obliquely from ~300 m to the surface (21 September 2009; [Supplementary material Table S1](#)) or with a dip net (approximately 63 μm mesh) (15, 16, 26 August 2010; [Supplementary material Table S1](#)). These euphausiids were initially preserved in ethanol but then transferred to buffered 1.8% formaldehyde. Additional sampling as part of SKrillEx I and II ([Nickels, 2017](#); [Supplementary material Table S1](#)). Bongo-net transects with calibrated flowmeters were performed across a steep bathymetric feature thought to be a blue whale aggregation center. The 202 μm mesh bongo nets were lowered to 200 m or 10 m above the sea floor and towed obliquely as the ship moved at 0.5–1 m s⁻¹) to preserve a 45° degree wire angle. These samples were immediately preserved in buffered 1.8% formaldehyde.

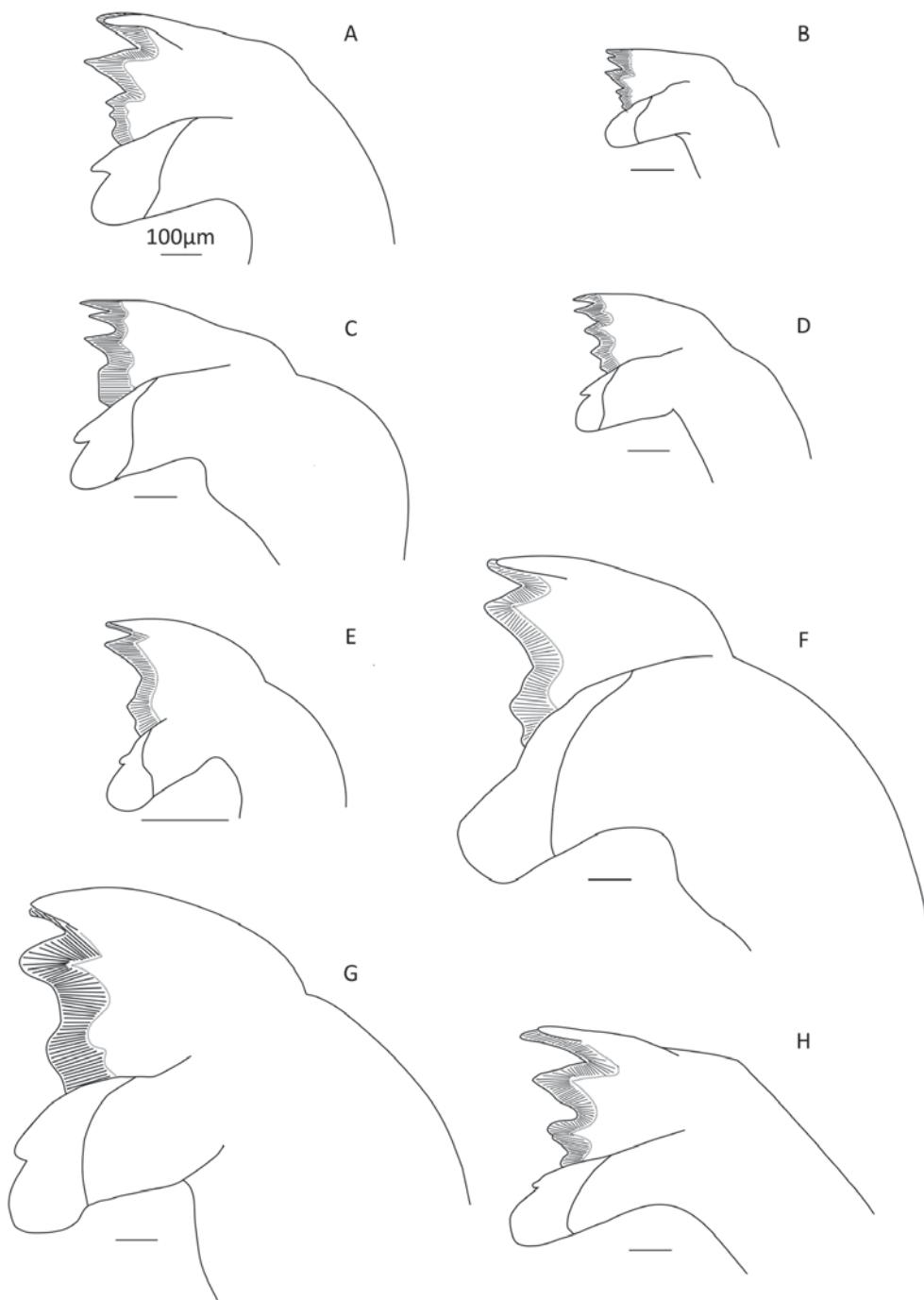


Figure 3. Right mandibles of *Thysanoessa spinifera* (A), *Thysanoessa gregaria* (B), *Euphausia pacifica* (C), *Nyctiphanes simplex* (D), *Euphausia recurva* (E), *Euphausia eximia*, *Euphausia gibboidea* (G), and *Nematocelis difficilis* (H). Scale bars = 100 μ m.

Net samples were enumerated under a dissecting microscope with a calibrated ocular micrometer. From each sample, either all euphausiids were identified to species and life history phase (furcula, juvenile, adult) or they were subsampled with a Folsom splitter so that approximately 200 individuals were identified. The identified euphausiids were measured for body total length (Boden *et al.*, 1955; Brinton, 1962; Brinton *et al.*, 2000).

For fecal samples paired with net samples from the same time period and region, we compared the size distribution of euphausiid prey consumed (reconstructed from fecal samples) with the size distribution of euphausiid prey available (determined by net samples) using a Kolmogorov-Smirnov test. The mean size distribution was used for comparison where multiple fecal or net samples were

collected from similar dates and locations. Ratio of species were compared between fecal and net samples with pairwise G-tests. Statistics were performed in R vers. 3.1.2 (R Core Team, 2014).

RESULTS

Mandible descriptions

All eight common species of euphausiid had distinctive mandibular morphology (Figs. 3, 4), making it possible to identify the species.

The cusp of the mandible is made up of a cutting region referred to as the *pars incisiva*, and the grinding region, the *pars*

molaris (Fig. 2). The cusp leads to a basis, which is connected to robust musculature. Within the *pars incisiva*, there are multiple spines and a cutting edge useful for taxonomic identifications.

The first spine pair (SP1) is the anteriomost process and is typically a combination of two either overlapping or slightly offset spines.

Each *pars incisiva* of the mandible was placed as flat as possible in the same orientation to the observation dish so that the presence or absence of overlapping SP1 could be assessed. This placement left the incisor region in the background and the molar region in the foreground. The *pars molaris* from whale fecal samples was often either filled with fecal material or somewhat filed down due to abrasion during digestion and gut passage, thus making the characteristics of the *pars molaris* generally unsuitable for rapid or precise taxonomic identifications. Although the *pars incisiva* possessed enough taxonomic information to serve as the main region for identification of mandibles from whale fecal samples, we also describe a unique character of the *pars molaris* for *E. gibboidea* and *N. difficilis*.

Thysanoessa spinifera: *Pars incisiva* spines of SP1 overlap. S2 large, acute, fully extending to and sometimes beyond terminal end of SP1. Deep acute groove between SP1, S2. CE three-acutely pointed process descending in height as it approaches margin of *pars molaris*. CE varies, in some cases possessing 1 or 2 processes, with longest reaching approximately half length of S2 (Figs. 3A, 4A).

T. gregaria: *Pars incisiva* spines of SP1 offset (primary difference between *T. gregaria* and *T. spinifera*), besides overall size of right mandible. S2 large, acute, fully extending to, sometimes beyond terminal end of SP1. CE three- acutely pointed process descending in height as it approaches margin of *pars molaris*. CE varies, in some cases possessing 1, 2 processes, with longest reaching approximately half length of S2 (Figs. 3B, 4B).

Euphausia pacifica: *Pars incisiva* with slightly offset SP1. Acute S2 located tightly to SP1, extending to just before or to terminal end of SP1 but not extending beyond it. CE typically diagnostic wide plateau or slightly corrugated ridge, sometimes lacking this character or possessing low-lying ridge with 2 small peaks as S2. Swollen shoulder (SH) present, forming convexity plus noticeable protrusion of chitinous material toward lateral margin. SH forms from anteriomost end of *pars incisiva* leading to posterior end of individual (specimen must be rotated to see this three-dimensional character). SH sets *E. pacifica* (Figs. 3C, 4C) apart from the similar mandible of *N. simplex* (Figs. 3D, 4D).

Nyctiphanes simplex: *Pars incisiva* spines of SP1 slightly offset. Very acutely pointed S2 does not fully extend to terminal end of SP1. CE series of 2 processes 2/3 length of S2. No SH protrusion present. Anterior edge of *pars incisiva* continuous, more gradual approach towards SH of the basis of mouthpart (Figs. 3D, 4D).

Euphausia recurva: *Pars incisiva* spines of SP1 fully overlap. Acute S2 located tightly to SP1, terminal end extending fully to, even slightly beyond SP1. Deep, wide trough between S2, CE. Obtuse process CE approximately 1/3 length of S2. Lateral approach from cusp to basis more gradual, rounded than *E. eximia*. (Figs. 3E, 4E).

Euphausia eximia: *Pars incisiva* spines of SP1 fully overlap. Acute S2 located tightly to SP1, terminal end extending fully to, even slightly beyond SP1. CE widely separated from S2, with and obtuse blunt curved process. Deep, wide trough between S2, CE. Obtuse process CE approximately 1/3 length of S2. Lateral approach from cusp to basis more angular than rounded (Figs. 3F, 4F).

Euphausia gibboidea: *Pars incisiva* spines of SP1 fully overlap. S2 located closely to SP1, terminal end forming less acute, more blunted end than other species of *Euphausia* of similar size and *T. spinifera* mandibles. CE forms single or double rounded process widely separated from S2. *Pars molaris* ornamented with highly serrated marginal edge (Figs. 3G, 4G).

Nematoscelis difficilis: *Pars incisiva* spines of SP1 overlap but length of dorsal spine does not extend fully out to ventral spine. Each spine of SP1 very elongated, acute. S2 acute, much wider than SP1, does not fully extend out to terminal end of SP1. CE is third large, acute process, not fully extending to terminal end of S2. Overall length, shape of main mandible cusp structure leading to SH1, root more elongated than other species described herein. SH1 forms sharp 160° angle. *Pars molaris* ornamented with highly serrated marginal edge (Figs. 3H, 4H).

Mandible to body length regressions

All eight species showed significant ($P < 0.01$), positive linear regressions between right mandible total length and body total length for the adult reference individuals (Fig. 5). The r^2 values were all above 0.85. The r^2 values of *T. spinifera*, *E. pacifica*, *E. eximia*, and *N. simplex* were above 0.90.

Species and size composition of ingested euphausiids

All fecal samples of blue whales were dominated by mandibles positively identified as those of *T. spinifera* (Fig. 6). Of the 18 fecal samples analyzed, 2/3 of them were composed of 100% *T. spinifera* prey. The remaining third contained between 1% and 19% *E. pacifica*. One 2015 sample from near San Diego contained two *N. difficilis* mandibles. One *N. simplex* mandible was found in the sample from an unknown location in 1998. These two samples

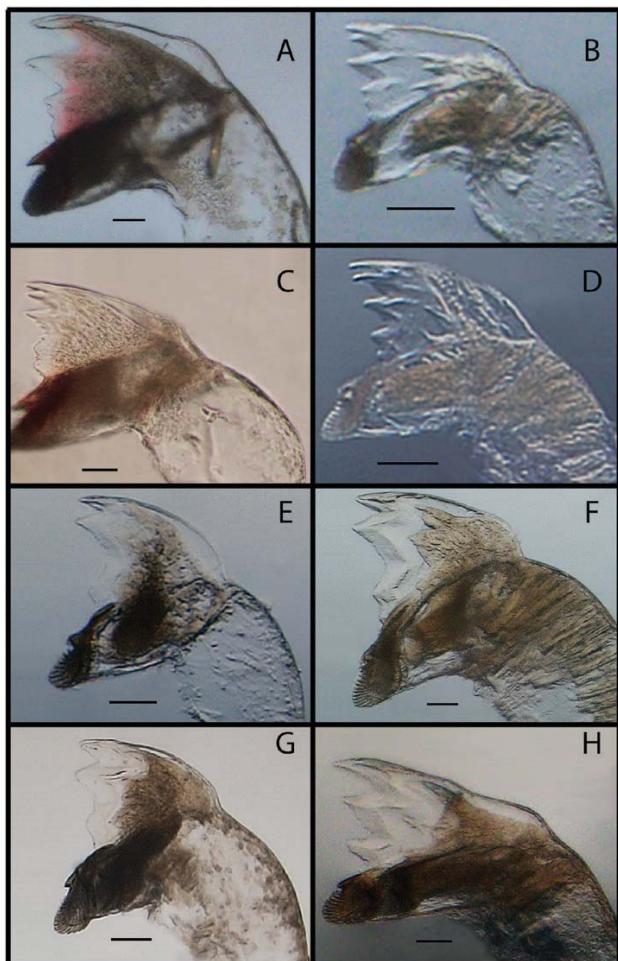


Figure 4. Digital images of right mandibles of *Thysanoessa spinifera* (A), *Thysanoessa gregaria* (B), *Euphausia pacifica* (C), *Nyctiphanes simplex* (D), *Euphausia recurva* (E), *Euphausia eximia*, *Euphausia gibboidea* (G), and *Nematoscelis difficilis* (H). Scale bars = 100 μ m.

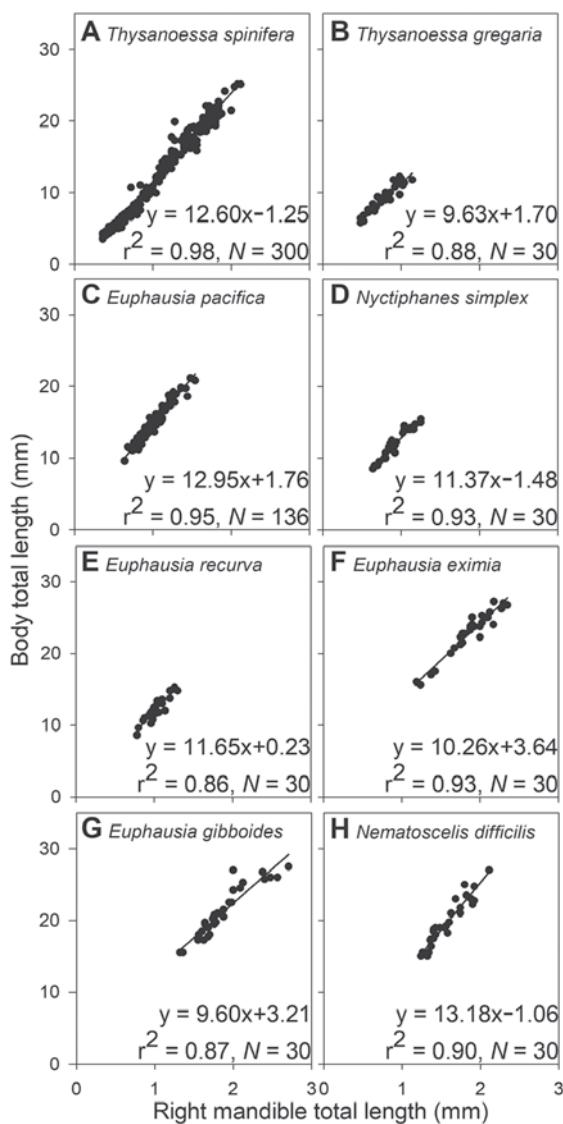


Figure 5. Relationship between body total length and total mandible length in *Thysanoessa spinifera* (A), *Thysanoessa gregaria* (B), *Euphausia pacifica* (C), *Nyctiphanes simplex* (D), *Euphausia curvata* (E), *Euphausia eximia*, *Euphausia gibboidea* (G), and *Nematocarcinus difficilis* (H). All regressions are significant ($P < 0.01$).

containing minor contributions from species other than *T. spinifera* also contained *E. pacifica*.

Some fecal samples also contained identifiable material other than euphausiid mandibles. The fecal sample from near Long Beach (14 September 2010) contained a single *N. difficilis* carapace. A colony of *Pyrosoma atlanticum* Péron, 1804 (Tunicata, Thaliacea) was found in a fecal sample from near Dana Point (18 July 2013). The 26 June 1999 had an antenna from the pelagic red crab, the squat lobster *Pleuroncodes planipes* Stimpson, 1860 (Anomura, Munididae). More substantial crustacean remains were found in the 23 June 2015 sample near San Diego, including *P. planipes* pereiopods and chelipeds as well as appendages of another unidentified decapod.

The reconstructed body lengths of ingested euphausiids (Fig. 7) ranged from 7.1 mm to 29.6 mm. The smallest and largest individuals belonged to *T. spinifera*, with a median of 17.46 mm. The modal size and size distributions of ingested euphausiids varied considerably by collection date (Fig. 7). Of all euphausiid sizes reconstructed from mandible measurements, less than 0.01% were smaller than 10 mm body length.

Comparison of prey digested to prey available

Whales did not ingest species not represented in dip net samples (August 2010; Fig. 8) when feeding on surface swarms composed of 100% *T. spinifera*. When bongo nets were used to sample prey at depth, the species composition of ingested euphausiids was less diverse than the available euphausiids. In all cases when other euphausiid species were also present, *T. spinifera* was over-represented in the diet compared to its availability in the water column ($P \leq 0.05$, pairwise G-test). *Euphausia pacifica* was the most abundant euphausiid in the water column in July 2014 and June 2015 but was highly under-represented in the blue whale diet on both occasions ($P < 0.001$, pairwise G-test).

There were often significant differences in size distributions between ingested euphausiids and euphausiids present in the water column (Fig. 9). Whales consumed significantly larger euphausiids than were available ($P < 0.05$, Kolmogorov-Smirnov (K-S) test, Fig. 9A, C, E) in all three comparisons between fecal samples and deeper bongo tows. Of the two instances when surface euphausiid aggregations were sampled by dip nets, there was no difference in size distributions in one case ($P > 0.05$, K-S test; Fig. 9D), and the other was the only instance where larger euphausiids were available than those ingested ($P < 0.05$, K-S test; Fig. 9B).

DISCUSSION

Our results agree with previous studies (Fiedler *et al.*, 1998; Croll *et al.*, 2005) indicating that blue whales appear to target large *T. spinifera* as prey in the southern and central sectors of the California Current System. *Thysanoessa spinifera* has been documented to form dense daytime surface aggregations (Brinton, 1981; Smith & Adams, 1988) and grow to a relatively large size in the southern CCS, which likely leads them to be high-value, low-cost prey for lunge feeding whales. Even when *E. pacifica* dominated deep net samples numerically, *T. spinifera* was over-represented in fecal material. The smallest previously reported prey size was estimated at y 10 mm (Croll *et al.*, 2005). We found several mandibles from euphausiids between 7 and 10 mm, but these accounted for less than 0.01% of the total euphausiid prey. Smaller sizes may be occasionally ingested but are relatively unimportant both numerically and energetically and are not targeted as prey by blue whales. Other than *T. spinifera* and *E. pacifica*, we occasionally identified mandibles of *N. simplex* (during an El Niño year) and *N. difficilis* in fecal material of blue whales, but these species are also minimal dietary components. The nearly monospecific diet of the blue whales in the region, despite the occurrence of other more abundant euphausiid species in the water column, suggests that euphausiids occur in monospecific aggregations at depth at finer scales than can be resolved by current net sampling techniques. Although Décima *et al.* (2010) detected only modest levels of patchiness in *T. spinifera*, that study was conducted on a much larger spatial scale than in our study.

Del Ángel Rodríguez (1997) and Jiménez Pinedo (2010) found blue whale diets to be composed primarily of *N. simplex* in the Gulf of California, Mexico, where *T. spinifera* is absent. *Thysanoessa simplex* must therefore form aggregations that are large or dense enough to make them exploitable and energetically valuable prey in the absence of *T. spinifera*, despite their smaller size. The documented occurrence of *N. simplex* mandibles from individuals less than 10 mm long indicates that these smaller euphausiids can be ingested and that their mandibles can survive digestion. We did not find smaller euphausiids, indicating that euphausiids may be self-segregating by size as well as species and the whales are able to take advantage of these aggregations of large adults.

Some non-euphausiid prey remains were found in the fecal samples. We interpret these as incidental ingestions rather than alternative targeted prey. Pyrosomes are passive drifters and would neither have been able to avoid engulfment by a whale nor

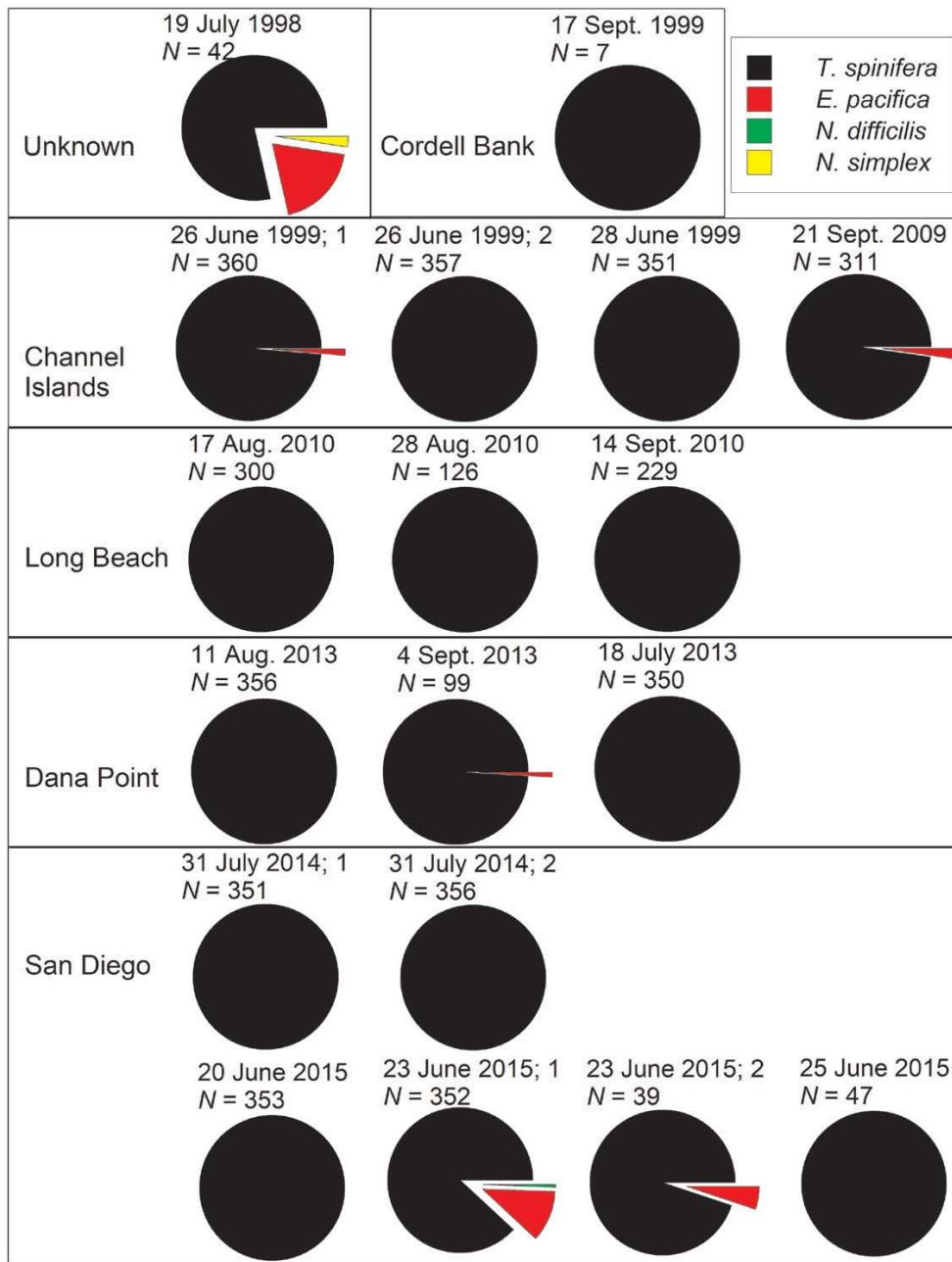


Figure 6. Percentage euphausiid species composition reconstructed from mandibles identified from fecal samples of the blue whale at different localities.

provided significant nutritional value. *Pleuroncodes planipes* occurs off Southern California in higher abundances during El Niños (Boyd, 1962; McClatchie *et al.*, 2016), and its presence in the area as evidenced by blue whale diet is therefore not surprising. This observation appears to be the first evidence of blue whales feeding on *P. planipes* to be confirmed by fecal contents. If *P. planipes* had been the target of whales, we would not have expected to see as many euphausiid mandibles, as these two taxa occupy different depths during the day, when whales feed (Nickels, 2017). We found no evidence of myctophid prey in contrast to the Gulf of California (Del Ángel Rodríguez, 1997; Jiménez Pinedo, 2010). While we did not attempt DNA analysis, the majority of unidentifiable material in the fecal samples was red pigmented and chitinous, suggesting that it was composed of euphausiids rather than fishes.

We chose to pair the samples that are closest in space and time when comparing the prey ingested by a whale to the available prey. These comparisons assume, however, that the aggregations of

euphausiids where a whale was feeding are a good representation of the prey field at the time the material in the feces was ingested. The gut passage time for blue whales has not been estimated, but the closest approximation is 18 h for their smaller relative, the fin whale, *Balaenoptera physalus* (Linnaeus, 1758) (Vikingsson, 1997). The larger blue whale is likely to have a longer digestive tract, and therefore may have a longer passage time, or the time may vary depending on the quantity and rate of prey engulfed. Gut passage times longer than 24–48 h or high variability in the composition of available euphausiids on a shorter timescale than gut passage would decrease the likelihood that the net samples represent the prey available when the whale was feeding.

We estimated the size distribution of available euphausiids from bongo tows, although there could be associated biases. Studies of the catch efficiency of euphausiids in the region by bongo nets in relation to other nets, the MOCNESS (Wiebe *et al.*, 1985) and Matsuda-Oozeki-Hu trawls (Oozeki *et al.* 2004) suggest that the

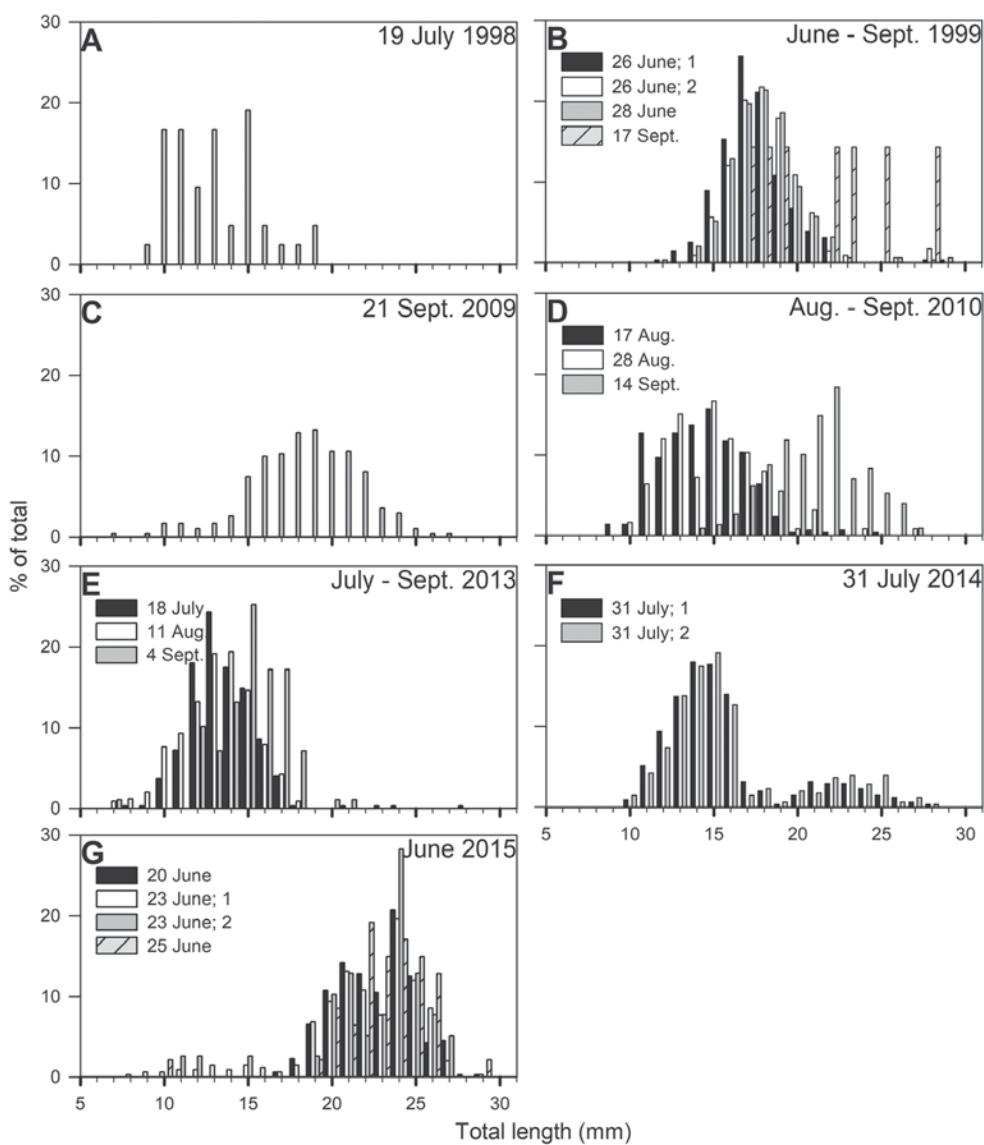


Figure 7. Reconstructed distributions of prey euphausiid body total length (mm) from mandible total lengths found in whale fecal samples.

size distributions of the smallest euphausiids is well represented by bongo tows (M. Ohman and A. Townsend, unpublished). Although the largest euphausiids may sometimes be under sampled by a bongo tow, these individuals consistently constitute a very small fraction of the euphausiid population. The total body length for adults of each species from this region was reported by Brinton *et al.* (2000) as *Thysanoessa spinifera* (15–26 mm), *T. gregaria* (7–12 mm), *Euphausia pacifica* (11–22 mm), *Nyctiphanes simplex* (7–17 mm), *E. recurva* (7–16 mm), *E. eximia* (15–30 mm), *E. gibboidea* (16–26 mm), and *Nematoscelis difficilis* (15–25 mm) (Brinton & Townsend, 2003). We encountered a small number of larger individuals.

Sizes were estimated by Croll *et al.* (2005) using linear regressions developed by Kieckhefer (1992) for *T. spinifera* and *E. pacifica*. Our slope is slightly steeper (12.6 compared to 11.3) and y-intercept slightly lower (~1.25 compared to 1.30) for *T. spinifera*. Our *T. spinifera* equation is the result of a larger body size range (3–25 mm versus 10–29 mm) and a larger number (300 versus 166). Both regressions for *E. pacifica* have the same slope (12.95), although we have a slightly smaller y-intercept (1.76 versus 2.84). The two *E. pacifica* regressions are the result of similar body size range coverage (9–21 mm versus 10–22 mm) and similar numbers

(136 versus 144). Del Ángel Rodríguez (1997) developed a regression equation for estimating the lengths of *N. simplex* from mandible lengths but used the body length measurement from the base of the eye to the base of the telson, thus our equations are not comparable.

We unambiguously identified the euphausiid species and closely estimated the sizes consumed by blue whales. In other regions or for euphausiid predators with more varied diets, complete absence of uncertainty may be more difficult. The *Euphausia* species 1a group defined by Brinton (1975), which includes *E. eximia*, *E. recurva*, and *E. mutica*, have very similar larval morphology (Brinton *et al.*, 2000), but in some cases not be identifiable (M.D. Knight, unpublished). The mandible morphology of the group is also similar. Definite identifications may be made for specimens where only one species is known to be present either from biogeography or concurrent net sampling, or where the range of mandible lengths does not overlap between species. The larger *E. eximia* are distinctive in relation to their total mandible length from non-overlapping adult sizes and the lateral approach from cusp to basis being more angular than rounded. Specimens without these additional characters may need to be pooled into a common *Euphausia* species 1a grouping.

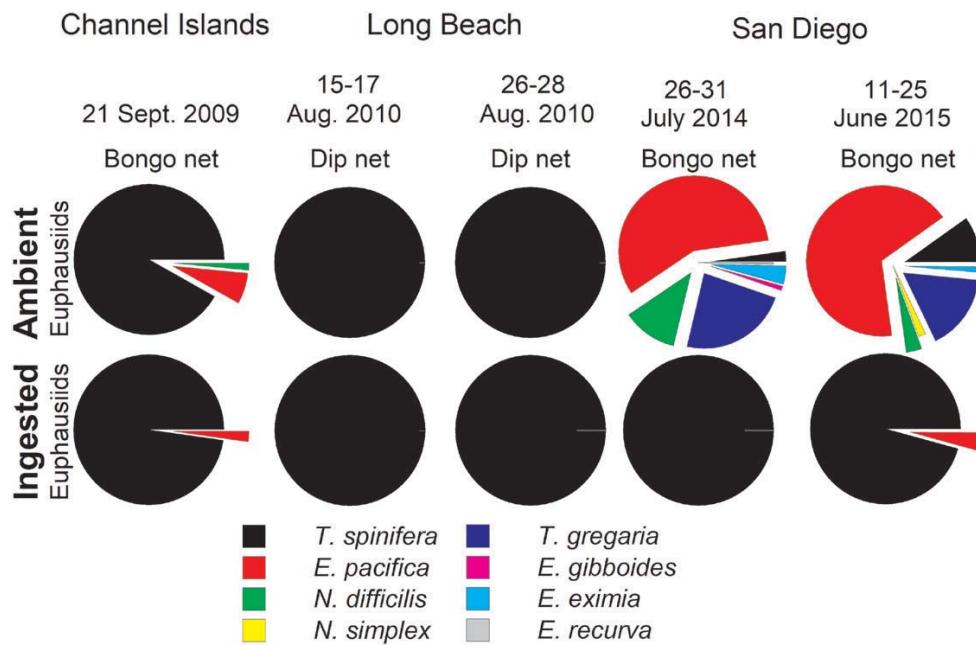


Figure 8. Euphausiid prey species compositions from mandibles in blue whale fecal samples compared to ambient available euphausiids collected by bongo nets or dip nets (August 2010 only) at different localities and dates.

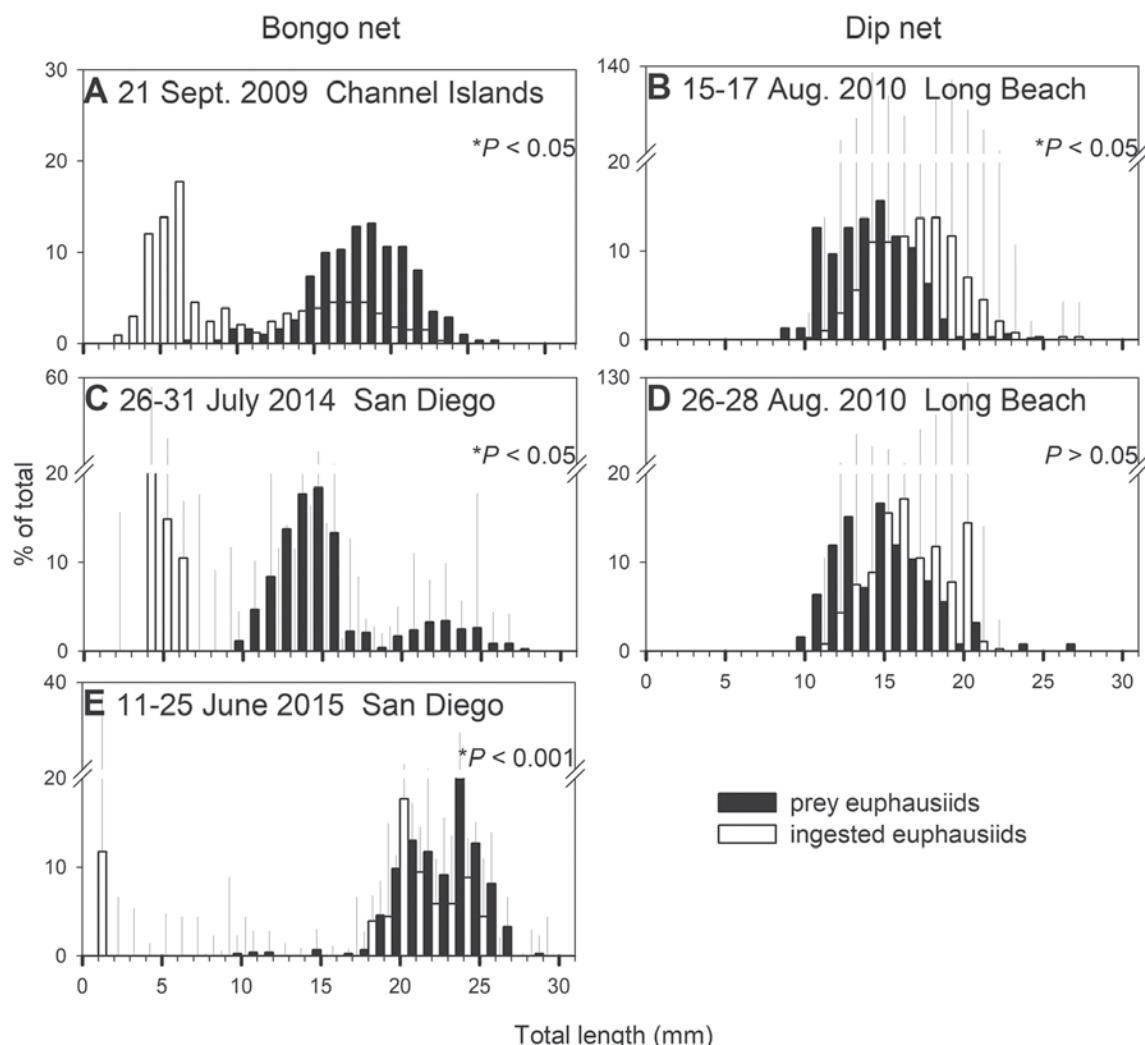


Figure 9. Comparison of reconstructed distributions of prey euphausiid body total length from mandibles found in blue whale fecal samples (solid bars) with ambient available euphausiids collected by bongo or dip nets (open bars);* statistically significant Kolmogorov-Smirnov test.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Table S1. Collection dates, approximate times, and locations for fecal samples used to assess ingestion of euphausiids by blue whales.

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REFERENCES

Bailey, H., Mate, B.R., Palacios, D.M., Irvine, L., Bograd, S.J. & Costa, D.P. 2009. Behavioural estimation of blue whale movements on the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research*, **10**: 93–106.

Bissell, M.W. 2013. *Using volunteered geographic information to model blue whale foraging habitat, Southern California Bight*. M.S. thesis, University of Southern California, Los Angeles, CA, USA.

Boden, B.P., Johnson, M.W. & Brinton, E. 1955. The Euphausiacea (Crustacea) of the North Pacific. *Bulletin of the Scripps Institution of Oceanography*, **6**: 287–400.

Boyd, C.M. 1962. *The biology of a marine decapod crustacean, Pleuroncodes planipes Stimpson*. PhD, University of California, San Diego, San Diego, CA, USA.

Brinton, E. 1962. The distribution of Pacific euphausiids. *Bulletin of the Scripps Institution of Oceanography*, **8**: 51–269.

Brinton, E. 1975. Euphausiids of southeast Asian waters. *Naga Report, Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand*, **4**: 1–287.

Brinton, E. 1981. Euphausiid distributions in the California Current during the warm winter-spring of 1977–78, in the context of a 1949–1966 time series. *California Cooperative Oceanic Fisheries Investigations Reports*, **22**: 135–154.

Brinton, E. & Townsend, A. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep-Sea Research II*, **50**: 2449–2472.

Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D. & Bridgeman, A.L. 2000. Euphausiids of the World Ocean. *World Biodiversity Database CD-ROM Series*. ETI, University of Amsterdam and UNESCO Publishing, Paris.

Croll, D., Marinovic, B., Benson, S., Chavez, F., Black, N., Ternullo, R. & Tershy, B. 2005. From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series*, **289**: 117–130.

Décima, M., Ohman, M.D. & De Robertis, A. 2010. Body size dependence of euphausiid spatial patchiness. *Limnology and Oceanography*, **55**: 777–788.

Dana, J.D. 1850. Synopsis generum crustaceorum ordinis "Schizopoda." *American Journal of Science and Arts*, ser. 2, **9**: 129–133.

Del Ángel Rodríguez, J.A. 1997. *Hábitos alimentarios y distribuciones espacio-temporal de los orcas comunes (Balaenoptera physalus) y azul (Balaenoptera musculus) en la Bahía de La Paz, BCS México*. M.S. thesis, Instituto Politécnico Nacional, Mexico City, Mexico.

Fiedler, P., Reilly, S., Hewitt, R., Demer, D., Philbrick, V., Smith, S., Armstrong, W., Croll, D., Tershy, B. & Mate, B. 1998. Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Research II*, **45**: 1781–1801.

Gendron, D. 1992. Population structure of daytime surface swarms of *Nyctiphanes simplex* (Crustacea: Euphausiacea) in the Gulf of California, Mexico. *Marine Ecology Progress Series*, **87**: 1–6.

Goldbogen, J., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N., Schorr, G. & Shadwick, R. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *Journal of Experimental Biology*, **214**: 131–146.

Goldbogen, J.A., Calambokidis, J., Croll, D.A., McKenna, M.F., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G., Shadwick, R.E. & Tershy, B.R. 2012. Scaling of lunge-feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Functional Ecology*, **26**: 216–226.

Hansen, H.J. 1905. Preliminary report on the Schizopoda. *Bulletin de l'Institut Océanographique de Monaco*, **30**: 1–32.

Hansen, H.J. 1911. The genera and species of the order Euphausiacea, with account of remarkable variation. *Bulletin de l'Institut Océanographique de Monaco*, **210**: 1–54.

Holmes, S.J. 1900. California stalk-eyed Crustacea. *Occasional Papers of the California Academy of Sciences*, **7**: 1–262.

Jiménez Pinedo, N.C. 2010. *Hábitos alimentarios y relación interespecífica entre la ballena azul (Balaenoptera musculus) y la ballena de aleta (B. physalus) en el suroeste del Golfo de California*. M.S. thesis, Instituto Politécnico Nacional, Mexico City, Mexico.

Kawamura, A. 1980. A review of food of balaenopterid whales. *Scientific Reports of the Whales Research Institute*, **32**: 155–197.

Kieckhefer, T.R. 1992. *Feeding ecology of humpback whales in continental shelf waters near Cordell Bank, California*. M.S. thesis, San Jose State University, San Jose, CA, USA.

Mauchline, J. 1989. Functional morphology and feeding of euphausiids. In: *Functional morphology of feeding and grooming in Crustacea* (B.E. Felgenhauer, L. Watling & A.B. Thistle, eds.), pp. 173–178. A.A. Balkema, Rotterdam, The Netherlands.

McClatchie, S., Goericke, R., Leising, A., Auth, T., Bjorkstedt, E., Robertson, R., Brodeur, R., Du, X., Daly, E., Morgan, C., Chavez, F., Deibach, A., Hildebrand, J., Field, J., Sakuma, K., Jacox, M., Kahrh, M., Kudela, R., Anderson, C., Lavanegos, B., Gomez-Valdes, J., Jimenez-Rosenberg, S., McCabe, R., Melin, S., Ohman, M., Sala, L., Peterson, B., Fisher, J., Schroeder, I., Bograd, S., Hazen, E., Schneider, S., Golightly, R., Suryan, R., Gladics, A., Loredo, S., Porquez, J., Thompson, A., Weber, E., Watson, W., Trainer, V., Warzybok, P., Bradley, R. & Jahncke, J. 2016. State of the California current 2015–16: comparisons with the 1997–98 El Niño. *California Cooperative Oceanic Fisheries Investigations Reports*, **57**: 5–61.

Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. In: *Marine food chains* (J.H. Steele, ed), pp. 241–252. University of California Press, Berkeley, CA, USA.

Nemoto, T. 1977. Food and feeding structures of the deep sea *Thysanopoda* euphausiids. In: *Ocean sound scattering prediction* (R. Andersen & B.J. Zahuranc, eds), pp. 457–480. Plenum Press, New York and London.

Nickels, C.F. 2017. *The co-location of blue whales and their euphausiid prey across multiple spatial scales*. Ph.D. thesis, University of California, San Diego, CA, USA.

O'Brien, D.P. 1987. Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic Spring of 1985. *Journal of Crustacean Biology*, **7**: 437–448.

Oozeki, Y., Hu, F.X., Kubota, H., Sugisaki, H. & Kimura, R. 2004. Newly designed quantitative frame trawl for sampling larval and juvenile pelagic fish. *Fisheries Science*, **70**: 223–232.

Ortmann, A.E. 1893. Decapoden und Schizopoden. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, **2**: 1–120.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna [<http://www.R-project.org/>].

Sars, G.O. 1883. Preliminary notices on the Schizopoda of H.M.S. "Challenger" Expedition. *Forhandlinger i Videnskabs-selskabet i Christiania*, **7**: 1–43.

Schoenher, J.R. 1991. Blue whales feeding on high concentrations of euphausiids around Monterey Submarine Canyon. *Canadian Journal of Zoology*, **69**: 583–594.

Smith, S.E. & Adams, P.B. 1988. Daytime surface swarms of *Thysanoessa spinifera* (Euphausiacea) in the Gulf of the Farallones, California. *Bulletin of Marine Science*, **42**: 76–84.

Stimpson, W. 1860. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. *Annals of the Lyceum of Natural History of New York*, **7**: 177–246, pls. 2, 5.

Vikingsson, G.A. 1997. Feeding of fin whales (*Balaenoptera physalus*) off Iceland – diurnal and seasonal variation and possible rates. *Journal of Northwest Atlantic Fisheries Science*, **22**: 77–89.

Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Barber, V., Cowles, T.J. & Fiedl, G.R. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and microneuston. *Marine Biology*, **87**: 313–323.