

DIET OF GRAY WHALES (*ESCHRICHTIUS ROBUSTUS*) IN CLAYOQUOT SOUND, BRITISH COLUMBIA, CANADA

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ABSTRACT

In Clayoquot Sound, British Columbia, gray whales (*Eschrichtius robustus*) forage for pelagic, hyperbenthic, and benthic invertebrates. Prey types were collected near feeding whales and at sites where no whales were observed to ascertain whales' diets and to describe prey populations and distributions. Characteristics of prey that are examined include species composition, density, biomass, and size. Whales foraged for mysids, *Holmesimysis sculpta* being the most abundant species collected. Whales foraged near concentrated patches of porcelain crab zoeal larvae, composed primarily of *Pachycheles rudis*, 21–294 times the average density and biomass normally collected. Amphipod biomass, composed primarily of *Ampelisca agassizi* and *A. careyi*, was 160 ± 150 g/m² where whales foraged. Larger amphipods, rather than higher density, resulted in higher amphipod biomass between years. Whales foraged where there was a high proportion (61%) of amphipods >6 mm in length. Whales initially foraged for amphipods along the 20-m depth contour line; amphipod biomass was best developed and least variable at depths between 16 and 20 m.

Key words: gray whale, *Eschrichtius robustus*, diet, porcelain crab larvae, mysids, amphipods, ghost shrimp, *Cryptomya*, Clayoquot Sound.

Every spring gray whales (*Eschrichtius robustus*) migrate along the west coast of North America from their calving/breeding grounds in the bays and lagoons of Southern California, Baja California, and the Gulf of California to their primary feeding grounds located in the Bering, Chukchi, Beaufort, and Eastern Siberian seas (Rice and Wolman 1971, Swartz 1986). However, not all gray whales reach the primary feeding grounds every summer. Small numbers of whales end their northward movements upon reaching the waters of Clayoquot

Sound, Vancouver Island, Canada (Duffus 1996, Darling *et al.* 1998). In this part of the tertiary feeding grounds, foraging is the dominant activity of whales. Gray whales are generalist foragers (Nerini 1984) and have been observed throughout the Sound feeding on planktonic porcelain crab larvae (Family Porcellanidae), hyperbenthic swarming mysid crustaceans (Family Mysidae), benthic amphipods (Family Ampeliscidae), and benthic ghost shrimp (*Callinassa californiensis*) (Duffus 1996, Darling *et al.* 1998).

Porcelain crabs are suspension-feeding anomurans (Knudsen 1964) found in a variety of habitats (Haig 1960). *Pachycheles* spp. generally live in burrows and rock crevices in the lower intertidal region, whereas *Petrolisthes* spp. live beneath loosely bedded rocks and rubble higher in the intertidal zone (Gonor and Gonor 1973). Porcelain crabs have extended planktonic larval development (Jensen 1991) which means that the larvae of these crabs pass through two zoeal stages and one megalopal stage. Gonor and Gonor (1973) provide a complete review of the life history of porcelain crabs.

Mysids are shrimp-like crustaceans often called "opossum shrimps" because females carry their young in a brood pouch under the thoracic region (Kozloff 1996). Mysids are hyperbenthic in nature; aggregations of these organisms form layers 1–10 cm (Guerrero 1989, Kim and Oliver 1989) to 1 m deep (Murison *et al.* 1984, Kim and Oliver 1989) over the sea floor. Mysids are usually present in lagoon eel grass (Murison *et al.* 1984) and kelp forests (Wellington and Anderson 1978, Murison *et al.* 1984, Guerrero 1989). This latter habitat preference explains the apparent association of gray whales and kelp (Murison *et al.* 1984).

Amphipods which belong to the gammaridean family Ampeliscidae construct and live in mucous tubes that penetrate several centimeters into the sandy bottom (Rice and Wolman 1971, Nerini 1984). Most of the prey utilized by gray whales in the Arctic are ampeliscid amphipods, which includes a number of circumboreal species that inhabit shallow coastal seas (Dickinson 1982, Coyle and Highsmith 1989). On the west coast of Vancouver Island, sandy-bottom bays provide habitat for amphipods analogous to the vast benthic habitats prevalent in the primary feeding grounds. In specific bays throughout central Clayoquot Sound, amphipods are located in the immediate subtidal region, from the surf zone to a depth of approximately 35 m.

Ghost shrimp (*Callinassa californiensis*) are burrowing crustaceans abundant in sandy muddy habitats of estuaries located along the west coast of North America (MacGinitie 1934). They inhabit the intertidal zone in burrows that they excavate; these burrows have at least two openings at the surface which provides for some circulation of sea water through the tunnels. Ghost shrimp obtain much of their food from detritus in the mud. When burrows are under water at high tide, shrimp fan water through their burrows by means of their abdominal appendages. When burrows are exposed at low tide, the organisms are believed to be relatively inactive. In association with *Callinassa* spp. is the small clam, *Cryptomya californica*, whose siphons open into shrimps' burrows instead of to the surface. These clams collect food from water currents created by ghost shrimp (Kozloff 1996).

In this paper we identify four prey habitats located in central Clayoquot Sound where gray whales have repeatedly foraged during the 1990s. Porcelain crab larvae, mysids, amphipods, ghost shrimp, and clams are abundant in these habitats. We quantified species composition, density, biomass, and size of these invertebrates near feeding whales, and also at sites where no whales were observed, to determine the diet of gray whales and to describe prey populations and distributions.

METHODS

We classified four gray whale prey habitats in central Clayoquot Sound based on observation from 1987 to the present. The study area is encompassed by Rafael Point, which is situated on Flores Island, and Grice Bay, which is situated 10 km east of Tofino (Fig. 1). Prey habitats are distinguishable according to distance from shore, type of substrate, and depth. Free-swimming porcelain crab larvae were collected >1 km from shore over boulder substrate around Rafael Point in water depths ranging between 10 and 30 m. Mysids were collected <1 km from shore near kelp beds and reefs on the south-southwest side of Flores Island in water 0–15 m deep. Amphipods were collected from the sandy substrate that covers about 10 km² of the bottom of Cow Bay in water 0–35 m deep. Ghost shrimp and clams were collected from littoral sand/mud flats in Grice Bay in water <3 m deep.

Prey-sampling coordinates were determined using the Canadian Hydrographic Service Field Sheet number 3603 (1996). Each prey habitat was divided by lines whose intersections created a minimum of 100 possible sampling coordinates. From these coordinates, six–eight sampling sites were randomly chosen before each sampling period. In the field a GPS was used to navigate the research vessel to each sampling site. Gray whales were not observed at the randomly selected sampling sites; prey estimates determined at these sites were assumed to reflect average prey productivity in each habitat. Where whales were observed foraging, we opportunistically collected samples near the animals to quantify patch characteristics of the various prey species. Feeding whales were defined as whales which remained within a restricted area of a particular habitat and exhibited constant directional changes in movement (Mallonée 1991).

We fixed all invertebrates in formaldehyde and stored them in 70% ethanol. Small individuals and species that were not known to be potential gray whale prey and contributed little to overall biomass were not identified and counted. Biomass was measured to 0.001 g as blotted wet weight. We used both parametric and non-parametric tests to analyze our data. Significantly skewed data sets (K-S Test, $\alpha = 0.05$) were analyzed with non-parametric statistical tests.

Porcelain Crab Larvae

Sampling sites were chosen from 146 possible sampling coordinates located within an area encompassing Rafael Point (from Siwash Point to an area lo-

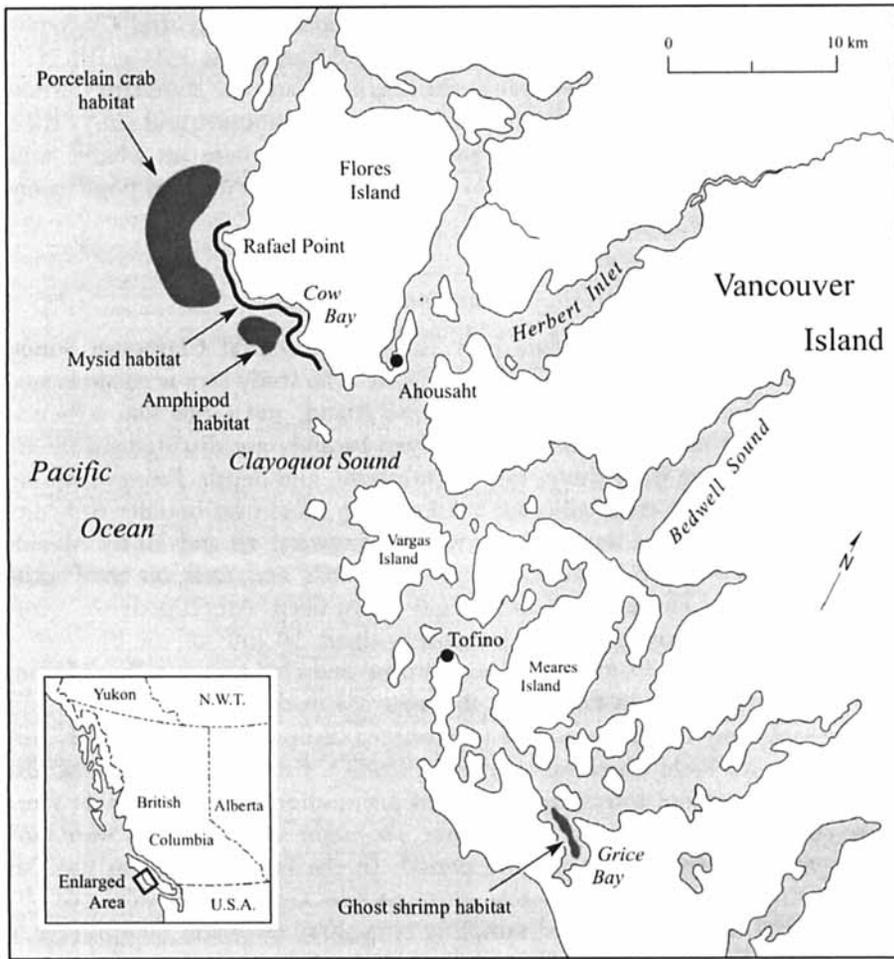


Figure 1. Gray whale prey habitats in central Clayoquot Sound, British Columbia.

cated north past Dagger Point, to the 30-m depth contour; Fig. 2). From these coordinates seven sampling sites were chosen randomly before each sampling period. One of the seven sampling locations was randomly selected to be the site for three replicate plankton tows.

In 1996 porcelain crab larvae were sampled on a semimonthly basis which resulted in five sampling periods between 4 July and 9 September (*i.e.*, seven sites were sampled every two weeks). In 1997 three sampling periods occurred between 3 July and 28 August (*i.e.*, seven sites were sampled every four weeks). Thirteen locations where gray whales foraged were sampled opportunistically; sampling for porcelain crab larvae occurred within 20 m of diving whales.

We collected plankton samples with a 2×20 -cm diameter bongo style plankton net, 80 cm long, with a 500- μ m mesh size. A mechanical flowmeter (General Oceanics model 2030R) determined the volume of water (m^3) to

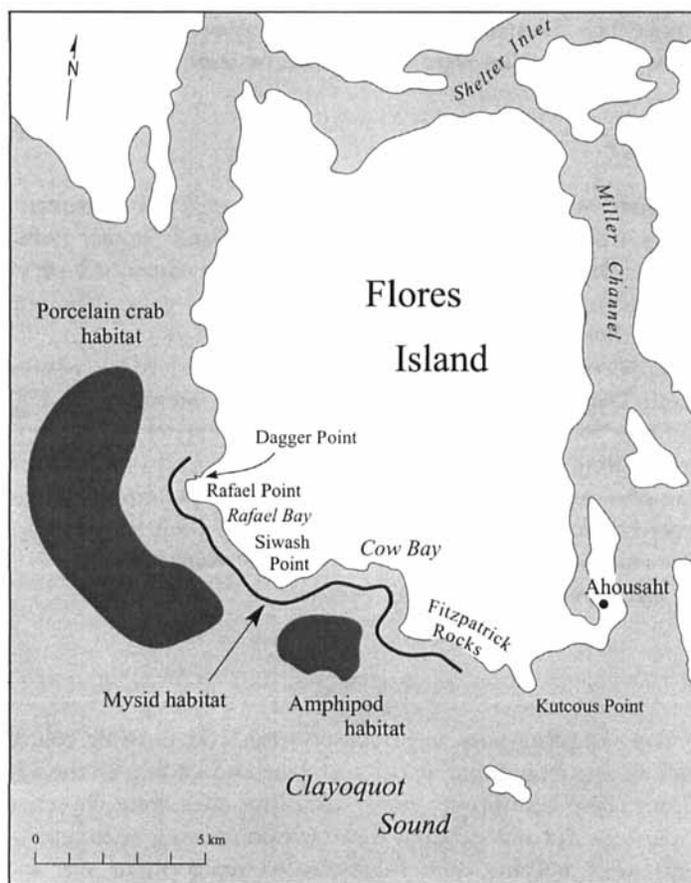


Figure 2. Gray whale prey habitats near Flores Island, Clayoquot Sound, British Columbia.

calculate standardized density and biomass estimates for the invertebrates. We collected porcelain crab larvae by towing the plankton net from the sea floor to the surface (maximum depth = 30 m) in oblique tows through the water column.

Large samples were subdivided using a Folsom plankton splitter. The zoea I, zoea II, and megalopal larval stages were separated and counted. In 1996 zoea II individuals were identified to genus using the method described by Gonor and Gonor (1973). This gave an overall indication of the relative abundance of *Pachycheles* spp. and *Petrolisthes* spp. In 1997 all porcelain crab larvae collected randomly, and subsamples of crab larvae collected near feeding whales, were identified to species using the different numbers of primary red chromatophores visible on freshly obtained specimens (Gonor and Gonor 1973). Subsamples for identification purposes were randomly selected from collections obtained near feeding whales (one subsample of approximately 100

larvae/sample). The biomass of porcelain crab larvae, other planktonic organisms, and the total biomass were determined for each sample.

Mysids

Mysid habitat near Flores Island was divided into five subareas: the Fitzpatrick Rocks, Cow Bay, Rafael Bay, Rafael Point, and Dagger Point (Fig. 2). Mysids were collected with the same plankton net described previously for sampling porcelain crab larvae. To collect mysids we towed the net horizontally along the bottom.

In 1996 opportunistic samples were collected near feeding whales between Cow Bay and Dagger Point from 30 June to 1 September. In 1997 opportunistic samples were collected between the Fitzpatrick Rocks and Dagger Point from 17 June to 1 September.

Large samples were subdivided using a Folsom plankton splitter. Mysids were separated from other planktonic material and their biomass determined. Mysids were counted, identified to species [using Kathman *et al.* (1986) as an authority], and gravid females were counted.

Amphipods

In Cow Bay sampling sites were chosen from 102 possible coordinates located within an area beginning at the surf zone and ending at the 35-m depth contour. From these coordinates seven sampling sites were chosen randomly. If a particular site did not produce a sample containing sediment (*i.e.*, rocky or too deep), then another randomly selected replacement site was chosen. Four replicates were obtained at one of the seven sites; the number of replicates was determined from Downing (1979).

In 1996 random sampling occurred once every two weeks between 29 June and 2 September (*i.e.*, five sampling periods during the field season). In 1997 sampling occurred approximately once every six weeks between 2 July and 2 September (*i.e.*, two sampling periods during the field season). Samples were collected opportunistically in 1997, between 2 July and 21 August, where gray whales were observed bottom-feeding in Cow Bay. Samples were either collected within 100 m of a feeding whale or not more than one day later at the location of a previously observed feeding whale.

Amphipods were collected with a 0.06-m² core sampler (WILDSCO Ogeechee Sand Pounder) lowered from the anchored research vessel. Sediment from each sample was rinsed through a 1-mm mesh screen to remove amphipods and other invertebrates. These organisms were preserved, counted, and the volume of sediment recorded. Amphipods were identified according to Dickinson (1982). They were categorized into one of two size classes: individuals 0–5.9 mm in length were designated “small” and individuals 6–11 mm in length were designated “large.” This classification originates with Rice and Wolman’s (1971) stomach content analysis where prey items measured >6

mm in length. Amphipods were weighed to determine the biomass per unit area.

Ghost Shrimp

In Grice Bay sampling sites were chosen from 177 possible coordinates. In 1996 eight sites were randomly chosen throughout the bay on 25 July (three days after the whales left the bay) and 3 September. Eight replicates were obtained at one of the sites; the number of replicates was determined from Downing (1979). We collected ghost shrimp with a section of PVC tubing 17 cm long and 10 cm in diameter. The tubing was pushed into the sediment and the core and sampler removed with a shovel. All samples were collected at low tide in water depths ranging from 0.5 to 1.5 m. Shrimp were measured from the tip of the telson to the eye. Ghost shrimp and clams were weighed to determine biomass per unit area.

RESULTS

Porcelain Crab Larvae

Larvae of *Pachycheles* spp. and, to a lesser extent, *Petrolisthes* spp. were important components of the plankton community around Rafael Point (Table 1). In 1996 there was a lower proportion of the smaller zoea I larval stage than the larger zoea II stage in plankton samples. The postlarva megalopal stage was sparse in all samples. There was no significant difference ($t = -0.21$, $df = 74$, $P = 0.84$) between the biomass of plankton (not including porcelain crab larvae) collected at sites where whales did and did not forage.

Plankton collected near gray whales consisted almost exclusively of porcelain crab larvae (95%–99%: Table 1). In 1997 the zoea I larval stage was more numerous than the zoea II stage at three of four sites near feeding whales. Whales were observed at the surface diving near patches of porcelain crab larvae which exhibited density and biomass estimates between 15 and 465 times the average values normally present in the water column. There was a moderate to strong positive correlation between the number of feeding gray whales observed and the biomass of porcelain crab larvae collected (Pearson's, $r = 0.68$, $n = 76$, $P < 0.001$).

Minimum threshold porcelain crab larvae density and biomass estimates were determined by observing gray whales' foraging behaviors at locations where plankton samples were obtained (Fig. 3). When gray whales were present, two distinct behaviors were observed. First, whales either traveled through the sampling area or foraged sporadically over large areas. Second, whales foraged in small areas for the entire observation period. There was also a range of densities where whales exhibited a mixture of these two behaviors. This region is bounded by biomass estimates of porcelain crab larvae ranging from 1.47 to 2.03 g/m³. These biomass estimates correspond to density estimates of crab larvae ranging from 1,295 to 1,528/m³. Gray whales were ob-

Table 1. Characteristics of porcelain crab larvae where gray whales did and did not forage. Mean \pm SD.

Characteristics of porcelain crab larvae	Feeding whales			No whales	
	1996 <i>n</i> = 17	1997 <i>n</i> = 8	1996 <i>n</i> = 84	1997 <i>n</i> = 48	
Percentage					
Crab larvae in the plankton	99	95	64		
<i>Pachycheles</i> spp.	95	90	86	87	
<i>Pachycheles rudis</i>		57		44	
<i>Pachycheles pubescens</i>		30		34	
<i>Petrolisthes</i> spp.	5	10	10	13	
Zoea I	27	63 and 19*	34	45	
Zoea II	70	37 and 81*	62	52	
Megalopae	0.1	0.1	0.4	3.6	
Density (/m ³)					
Mean	3,006 \pm 3,718	4,726 \pm 4,598	72 \pm 70	11 \pm 13	
Maximum	10,520	13,198	334	56	
Biomass (g/m ³)					
Mean	4.61 \pm 6.09	6.16 \pm 7.54	0.10 \pm 0.12	0.01 \pm 0.02	
Maximum	16.73	20.56	0.59	0.07	

* Determined from 3 dates (1, 13, and 18 August 1997). Data collected on 1 and 13 August were combined because zoea I stage was more abundant than zoea II stage. Data obtained from 18 August presented separately because there were fewer individuals in zoea I stage (19%) than zoea II stage (81%).

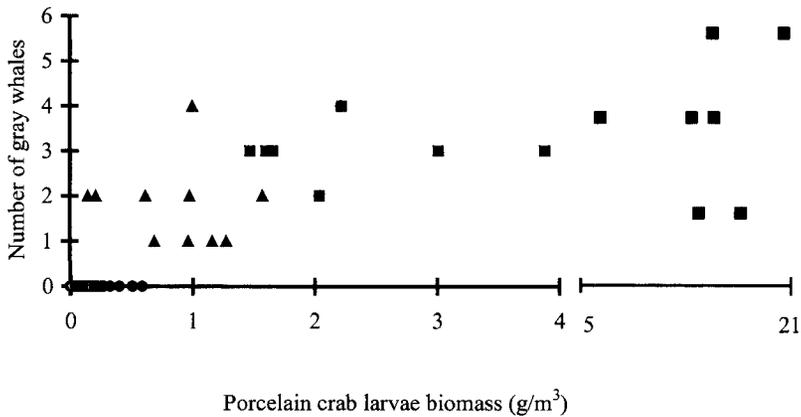


Table 2. Characteristics of mysids where gray whales foraged. Median [IQR^a].

Characteristics of mysids	Feeding whales	
	1996 <i>n</i> = 25	1997 <i>n</i> = 36
Percentage		
<i>Holmesimysis sculpta</i>	90–99	56–100
<i>Neomysis rayi</i>	0.8–1.2	0.2–1.5
<i>Acanthomysis columbiae</i>	4–10	1–100
<i>Disacanthomysis dybowskii</i>	1	14
<i>Columbiaemysis ignota</i>		1–86
<i>Exacanthomysis davisii</i>		0.1–0.8
Gravid individuals	0–42	0–49
Density (/m ³)		
Median	10 [53]	175 [746]
Maximum	326	2,249
Biomass (g/m ³)		
Median	0.32 [1.56]	1.43 [6.00]
Maximum	2.56	22.60

^a Inter-quartile range.

every sample obtained from the bay. Where whales foraged, 78% of the biomass consisted of amphipods and 22% consisted of polychaetes. Amphipods were collected in 100%, whereas worms were collected in 19%, of the samples. Amphipod density was similar where whales did and did not forage (Kruskal-Wallis test, $\chi^2 = 0.35$, $n = 63$, $df = 2$, $P = 0.84$). In 1997, where whales did and did not forage, amphipod populations were similar in every respect, except for biomass CV.

Amphipod populations were generally different in 1997 compared to 1996. Amphipod biomass was significantly higher in 1997 ($F = 10.52$, $df = 62$, $P < 0.001$), especially where whales foraged. Gray whales foraged where there was 160 ± 150 g/m² of benthic biomass. "Small" amphipods (0.1–5.9 mm in length) were significantly bigger (by 0.8 mm) in 1997 than in 1996 (Kruskal-Wallis test, $\chi^2 = 77.54$, $n = 1,569$, $df = 2$, $P < 0.001$). In contrast, "large" amphipods (6–11 mm) were significantly smaller (by 0.6 mm) in 1997 (Kruskal-Wallis test, $\chi^2 = 27.07$, $n = 524$, $df = 2$, $P < 0.001$). Where gray whales foraged, 61% of the amphipods were "large" individuals. In contrast, in 1996 there was a low proportion of "large" amphipods (6%) and a corresponding high proportion of "small" amphipods. In general, benthic biomass was least variable where gray whales foraged.

Amphipod biomass in Cow Bay was significantly greater at depths ranging between 16 and 20 m compared to depths ranging between 0 and 10 m ($F = 7.04$, $df = 85$, $P < 0.001$; Table 4). The water column depth where samples were initially obtained near feeding gray whales was 20 ± 1 m (mean \pm SD). Thus, gray whales initially foraged in areas of Cow Bay where amphipod communities were best developed.

Table 3. Characteristics of amphipods where gray whales did and did not forage. Mean \pm SD.

Characteristics of Amphipods	Feeding whales		No whales	
	1997 <i>n</i> = 21	1996 <i>n</i> = 47	1997 <i>n</i> = 19	1996 <i>n</i> = 87
Percentage benthic biomass	78	60		
Density (/m ²)				
Mean	11,054 \pm 4,151	16,121 \pm 20,187		10,332 \pm 6,704
Maximum	21,326	112,396		20,750
Biomass (g/m ²)				
Mean	113 \pm 28	48 \pm 54		97 \pm 80
Maximum	173	244		277
Coefficient of Variation	0.27	0.93		0.65
Mean length 0-5.9 mm	<i>n</i> = 157	<i>n</i> = 1257	<i>n</i> = 155	<i>n</i> = 155
	4.3 \pm 1.3	3.4 \pm 0.7	4.1 \pm 1.2	4.1 \pm 1.2
Mean length 6-11 mm	<i>n</i> = 246	<i>n</i> = 83	<i>n</i> = 207	<i>n</i> = 207
	7.1 \pm 1.0	7.9 \pm 1.2	7.5 \pm 1.2	7.5 \pm 1.2
Proportion (%) 0.1-5.9 mm	39	94	43	43
Proportion (%) 6-11 mm	61	6	57	57

Table 4. Comparisons between depth and amphipod biomass. Mean \pm SD, median [IQR^a].

Depth (m)	Biomass (g/m ²)	Coefficient of variation (CV)	<i>n</i>
0–10	2 \pm 3	1.42	5
11–15	35 [73]	1.22	13
16–20	98 \pm 49	0.51	57
21–25	57 \pm 47	0.82	11

^a Inter-quartile range.

Ghost Shrimp and Clams

In 1996 one gray whale foraged in Grice Bay for 47 d (from 5 June to 22 July). Benthic samples were collected on 25 July (three days after the whale departed from the bay) and on 3 September. Ghost shrimp (*Callinassa californiensis*) and clams (*Cryptomya californica*) contributed 98%–99% of the benthic biomass (Table 5). Ghost shrimp represented 15% and 25% of the biomass on 25 July and 3 September, respectively. Clams represented 84% and 73% of the benthic biomass on 25 July and 3 September. There was significantly less ghost shrimp than clam biomass (Mann-Whitney *U* test, $Z = -2.41$, $n = 32$, $P = 0.02$). No gravid ghost shrimp were collected on the two dates.

DISCUSSION

We found 13 species of invertebrates to be abundant near foraging gray whales. Darling *et al.* (1998) reported three other prey items to be abundant near feeding gray whales. These items include dungeness crab megalops (*Can-*

Table 5. Characteristics of ghost shrimp and *C. californica*. Mean \pm SD, median [IQR^a].

Prey characteristics	No whales	
	Ghost shrimp	<i>C. californica</i>
	<i>n</i> = 30	
Density (/m ²)		
Mean/median	634 \pm 523	1,082 [1,592]
Maximum	2,546	13,878
Biomass (g/m ²)		
Mean/median	64 \pm 45	178 [309]
Maximum	176	1,038
Length (mm)	<i>n</i> = 188	<i>n</i> = 431
Mean	13 \pm 9	8 \pm 4
Maximum	38	18

^a Inter-quartile range.

cer magister), swimming amphipods (*Atylus borealis*), and herring eggs/larvae (*Clupea harengus pallasi*). This raises the total to 16 recognized prey species of gray whales in the central region of Clayoquot Sound. However, this is probably not yet a complete list as anecdotal reports suggest other prey items are sought. For example, gray whales do lunge through schools of needlefish or sandlance, and other larval fish, but we cannot ascertain whether they seek the same prey as the fish, or seek the fish themselves.

Porcelain Crab Larvae

Planktonic crabs and their larvae are important prey for gray whales. In Baja California gray whales may forage on the planktonic red crab, *Pleuroncodes planipes* (Norris *et al.* 1983). Rice and Wolman (1971) reported that a northward migrating female gray whale killed in 1964 contained 20 liters of the zoea stage larvae of the crab *Pachycheles rudis* and a few brachyuran zoeae. In addition, these researchers reported that an immature female taken in 1968 had in its stomach about 50 liters of the zoea stage larvae of a pinnotherid crab and a few porcellanid zoeae.

Porcelain crab zoeae remain relatively close to shore compared to some brachyuran zoeae (Lough 1975, Jamieson and Phillips 1988), possibly due to their strong horizontal swimming ability (Gonor and Gonor 1973). Since gray whales primarily feed close to shore in relatively shallow water, dense patches of porcelain crab zoeae provide a source of food which is easily accessible to whales. In addition, both porcelain crab zoeal stages have long rostral and posterior spines as extensions of the carapace which are the primary defense structures of the crab larvae against planktivorous fish (Morgan 1989). These spines make the crab larvae large enough to be trapped and retained by gray whales' baleen plates.

Pachycheles pubescens Holmes, *Pachycheles rudis* Stimpson (Newcombe, cited in Haig 1960), *Petrolisthes cinctipes* Randall (Hart and Newcombe, cited in Haig 1960), and *Petrolisthes eriomerus* Stimpson (Hart 1940, cited in Haig 1960) are the only four species of porcelain crabs known to exist along the Pacific coast of North America north of California (Gonor and Gonor 1973). *P. rudis*, *P. cinctipes*, and *P. eriomerus* have been previously collected in Clayoquot Sound (Haig 1960, Jamieson and Phillips 1988). In this study the zoeal larval stages of both *Pachycheles* spp. and *Petrolisthes* spp. were consistent components of the plankton community near Rafael Point between June and September. Ninety–95% of the porcelain crab zoeae collected near feeding whales was *Pachycheles* spp., of which 57% was *P. rudis*. Although *Petrolisthes* spp. normally represented 5%–10% of the crab larvae collected in samples, *Petrolisthes* spp. larvae are still an important component of the planktonic prey base for gray whales at certain times of the year, particularly in August. For example, on 20 August 1996 near Dagger Point, 34%–60% of the crab larvae in the zoea II larval stage collected near feeding gray whales were *Petrolisthes* spp.

In 1996 there was a higher proportion of the larger zoea II stage collected in samples at seven of nine sites near feeding gray whales. This led us to

speculate that whales were targeting swarms of crab larvae that contained larger individuals. However, in 1997, the smaller zoea I stage was collected in greater numbers at three of four sites near feeding gray whales. Consequently, it is unclear whether gray whales target the larger zoea II stage, especially since collections made in 1996 at sites where no whales were observed also contained a high proportion of zoea II larvae. We suspect the proportion of the different zoeal stages collected in plankton samples was an artifact of the time during the season when sampling was conducted. However, since the postlarva megalopal stage was not abundant in any plankton tows, this stage of porcelain crab development is probably not an important source of food for gray whales.

Porcelain crab larvae were consistently present in the plankton community during summer months. We estimate there were 41–81 mt in 1996 and 4–10 mt in 1997 of porcelain crab larvae continually present near Rafael Point [based on 0.066–0.130 g/m³ (95 % CI; 1996) and 0.006–0.016 g/m³ (95 % CI; 1997) in an area 27 km² with an average depth of 23 m]. However, crab larvae biomass was generally diluted throughout a large area which made foraging for these invertebrates potentially energetically unprofitable for cetaceans. Gray whales foraged only at sites where porcelain crab larvae density and biomass were significantly higher than normally present in the water column. Whales foraged where 95%–99% of the planktonic biomass was comprised of porcelain crab larvae. The abundance of these invertebrates determined around feeding whales was 21–294 times the average abundance normally collected throughout the habitat.

At Rafael Point a submerged rocky ledge with shallow sites 2–6 m deep extends approximately 1.2 km offshore. Crab larvae may concentrate at the point because of the local topography. Wind-induced upwelling (Peterson and Miller 1977, Mackas *et al.* 1980) is dependent on local topography (Freeland and Denman 1982) and is known to enhance phytoplankton production and lead to energy transfer up the food chain (Durbin *et al.* 1995). Payne *et al.* (1986) determined that bottom topography influences the feeding behavior of humpback whales by concentrating prey. Other physical processes that may play an important role in concentrating crab larvae into swarms include mechanisms for nutrient enrichment of surface waters such as tidally induced mixing, internal waves (Haury *et al.* 1978), and tidal flow (Freeland and Denman 1982, Payne *et al.* 1986).

Mysids

Researchers, who have observed gray whales feeding on mysids, report similar depths (<5–10 m: Wellington and Anderson 1978, 4–10 m: Guerrero 1989, 8–16 m in 1996, and 3–20 m in 1997: this study) which suggests that mysids are found in shallow nearshore areas. Although *Holmesimysis sculpta* was the most numerous mysid species collected in Clayoquot Sound, *Neomysis rayi* was also collected, but in small numbers only. Yet *N. rayi* was collected from 71% of the mysid subareas and in 26% of all plankton samples. Guerrero

(1989) states that *N. rayi* is more active than *H. sculpta* and, therefore, will be more successful at avoiding a collection device. Consequently, although *H. sculpta* was more abundant in samples than the other five species of mysids, *H. sculpta* may not have been more abundant, only easier to catch. Swimming speeds of mysids range between 1 and 20 cm/sec (Mauchline 1980) which is slower than the mean speed the plankton net was pulled through the water during this study (24 cm/sec). Generally, however, when more plankton samples were collected from a particular area, a greater number of mysid species was also collected from that area. One reason may be mysid swarms are dominated by one or two species (Wellington and Anderson 1978, Murison *et al.* 1984).

Gravid female mysids are larger than other life stages and, according to Mauchline (1980), have a higher caloric value than males or other life stages. In 1996, on 19 August in Cow Bay, 42% was the maximum proportion of gravid individuals collected in one sample. The maximum proportion of gravid mysids collected in 1997 was 49%; this sample was obtained on 18 July at Rafael Point. On average during 1997, between 9% and 32% of the mysids collected from different regions in our study area were gravid. Mauchline (1980) suggests that the proportion of gravid mysids often varies seasonally in temperate regions; crustacean zooplankton growth and development rates depend strongly on water temperature.

We found gravid mysids to be more numerous as the summer progressed, yet there was no correlation between the number of gravid individuals collected and the number of feeding whales observed. It is still possible, however, that gray whales targeted larger gravid mysids rather than other individuals. Although the feeding morphology of baleen whales precludes prey selection at the level of individual prey items, prey selection may occur at the patch level (Dolphin 1988). Concentrated patches of gravid individuals may exist within mysid shoals; Guerrero (1989) reports that, although mysids often occur in large mixed-species shoals, within a shoal these organisms are usually segregated by species and size into smaller swarms. Plankton samples we collected support Guerrero's observations because many tows contained only similar-sized individuals. Gray whales may possess the ability to identify and target swarms within mysid shoals that contain high numbers of gravid females.

Population dynamics of mysids are not well known. In our study area mysids appeared to be more abundant in 1997 than in 1996. For example, *Exacanthomysis davisii* was observed in one of four samples collected from Cow Bay during 1997, but was not observed in any of the 19 samples collected from the same bay during 1996. Thus, *E. davisii* was probably more abundant in Cow Bay during 1997. Moreover, in 1997, *E. davisii* was collected in 42% of the samples obtained at the Fitzpatrick Rocks, which is an area that neighbors Cow Bay. In successive summers Guerrero (1989) noted that the occurrence of dense mysid swarms varied greatly in the Pachena Bay-Barkley Sound region.

Amphipods

Benthic biomass where gray whales foraged in Cow Bay was comprised predominantly of amphipods and, to a lesser extent, polychaetes. Garner (1993) reported that the most abundant benthic invertebrates in Cow Bay in 1992 were amphipods, clams, and polychaetes.

Similar to arctic communities of amphipods (Highsmith and Coyle 1991), biomass of amphipods in Clayoquot Sound may be related to individual size more so than population density. Amphipods in Cow Bay increased in biomass between the 1996 and 1997 field seasons, yet density remained similar. Therefore, the increase in amphipod biomass in 1997 was due to the presence of more "large" individuals. The numerous small individuals present in 1996 may have matured into larger individuals in 1997, suggesting that amphipods in Clayoquot Sound may have a two-year life-cycle, as indicated by Highsmith and Coyle (1991). Amphipod life histories are related to latitude (Morino 1978) because temperature plays an important role in determining adult size, brood size, and generations per year (Highsmith and Coyle 1991). Although amphipods in temperate latitudes should have annual life histories (Morino 1978, Highsmith and Coyle 1991), amphipods in cold temperate latitudes, such as those in Clayoquot Sound, should have a two-year life-cycle (Highsmith and Coyle 1991).

We found that amphipod biomass was higher in water depths ranging between 16 and 20 m than at other depths. In 1996 two extreme biomass estimates (244 and 178 g/m²) were obtained from depths of 20 and 17 m while, in 1997, the largest biomass estimate (277 g/m²) was obtained from a depth of 14 m. Benthic samples obtained near feeding gray whales were collected from a mean depth of 20 m. Thus, whales initially foraged in areas of Cow Bay which supported high benthic biomass. Duffus (1996) reported that the mean depths of feeding areas in Cow Bay in 1992 and 1993 were 15 and 22 m, respectively. Amphipod biomass was also less variable at depths ranging between 16 and 20 m. If homogenous amphipod communities exhibiting high biomass exist at particular depths, then gray whales should be expected to forage along these depth contours. This behavior was observed in this study, by Kvitek and Oliver (1986) at Long Beach, and by Guerrero (1989) in Ahous Bay. Since benthic biomass was significantly lower at depths between 0 and 10 m in Cow Bay, whales should not be expected to feed in these areas first. This expectation was confirmed by whale movement patterns we observed during 1996 and 1997. Duffus (1996) did not observe a shallow-to-deep water feeding pattern in Cow Bay in 1992 or 1993 as well.

In conclusion, we describe the diet of gray whales foraging in a small area of their tertiary feeding grounds located approximately midway along their coastal migration route. In central Clayoquot Sound, British Columbia, gray whales are not primarily benthic foragers, as they are described as being in their northern primary feeding grounds. Rather, gray whales are highly opportunistic foragers that utilize for food a variety of pelagic, hyperbenthic, and benthic prey types with different life histories. Species composition, density,

biomass, and size are characteristics of these invertebrate prey that influence the diet of foraging gray whales.

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