



Forage Plankton

(of the Kitimat Fjord System)

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Abstract

Because the scope of our study is focused on trophic interactions, we must first determine which zooplankton taxa are implicated in the foraging ecology of local whales, either directly or by degrees of trophic separation. The best starting point, therefore, is the known diets of locally sampled whales. We can then consider these preferences in light of current knowledge about zooplankton community composition in the region to make educated guesses about the prey preferences for whales within the Kitimat Fjord System.

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¹ **Bangarang Backgrounders** are imperfect but rigorous reviews – written in haste, not peer-reviewed – in an effort to organize and memorize the key information for every aspect of the project. They will be updated regularly as new learnin' is incorporated.

Introduction

In a study of foraging ecology (which is what the Bangarang Project hopefully will be), it is obviously important to know who is eating whom, but also to understand something about the natural history of the prey. The whales and seabirds of the Kitimat Fjord System are probably eating some mixture of fish and plankton. The “Forage Fish” Backgrounder dealt with the former and the present Backgrounder deals with the latter. Zooplankton are pivotal components of pelagic ecosystems, and their dynamics are governed by both “bottom-up” processes like oceanography and “top-down” processes like predation and competition. The “Plankton Processes” Backgrounder focused on the former and provides the oceanographic context for how fjord dynamics influences zooplankton population. It also outlines the overall zoogeography of the coast, reviewing north-south and inshore-offshore trends in community composition and life strategy. Furthermore, it discusses the anomalies in these patterns that accompany periodic climate oscillations.

Here I am interested in the nitty gritty of 1) whom specifically among the zooplankton the Bangarang whales are most likely targeting, and 2) how their natural history may guide trophic interactions. To these ends I first focus on published reports of whale diets from the region along with the known diets of any fish species that may also be targeted as prey in the Kitimat Fjord System. I then consider which zooplankton species are likely to be present in the Kitimat Fjord System based on published knowledge (no zooplankton studies have ever taken place here). Taken together, some educated guesses about the nature of trophic interactions in the study area should fall out.

The euphausiid images are from Baker et al. (1990).

Whale Diet

Because the scope of our study is focused on trophic interactions, we must first determine which zooplankton taxa are implicated in the foraging ecology of local whales, either directly or by degrees of trophic separation. The best starting point, therefore, is the known diets of locally sampled whales.

Fin Whales

The majority of North Pacific diet studies pertain to regions farther offshore or north of BC (Kawakami 1980, Kawamura 1980, 1982; Nemoto and Kasuya 1965, Pike 1950), but British Columbia’s historical whaling database reveals regional prey preferences (Nichol et al. 2002). Stomach data comes from studies between 1963 and 1967, when data collection was higher in quality and more consistent (Flinn et al. 2002). 578 of 650 killed fin whales were examined for stomach contents between 1963 and 1967 (Flinn et al. 2002). Non-empty FW stomachs contained mainly (sometimes exclusively) euphausiids in all five years (Flinn et al. 2002), but the proportion of diet components changed significantly between years. In 1964 and 65, higher percentages of copepods, fish, and cephalopods were found. The euphausiids preyed upon by fin whales included *Euphausia pacifica*, *Thysanoessa spinifera*, *T. longipes*, and *T. inermis*. Important calanoid species include (Neo)*Calanus cristatus*, *C. plumchrus*, *C. finmarchicus*, and *Metridia lucens* (Flinn et al. 2002).

Compared to fin whale stomach content data from other regions in the North Pacific, BC fin whales rely less on fish and more on zooplankton for their nutritional needs (Flinn et al. 2002). Fish in the diet of the whales killed off the BC coast were primarily found in stomachs of whales killed in the spring (Flinn et al. 2002). General North Pacific studies indicate that calanoid copepods are also primary prey (Kawamura 1980, 1982; Nemoto 1957, 1959; Nemoto and Kasuya 1965). Kawamura (1982) hypothesized that fin whales in the nearby Gulf of Alaska prey switch from euphausiids (abundant in late spring and early summer) to copepods (most abundant in

summer and fall). Other species known to be fin whale prey include the euphausiids *T. longipes* and *T. inermis* and the copepods *Calanus cristatus*, *C. plumchrus*, *C. finmarchicus*, and *Metridia lucens*.

Humpback Whales

Humpbacks in B.C. and Gulf of Alaska waters have been observed feeding upon sardine, herring, capelin, pollock, eulachon, Pacific mackerel (*Scomber japonicas*), and euphausiids (Nemoto 1959, Fisheries & Oceans Canada 2010). Stomach content records (summarized by Ford et al. 2009) were dominated by the euphausiids *E. pacifica* and *T. spinifera*. One stomach was found to contain a species of small squid (Ford et al. 2009). Pacific hake (*Merluccius productus*) is also dominantly abundant in coastal waters (Mackas et al. 1997) and may be preyed upon by humpbacks. Relative to the specialized diets of other rorquals, humpback whales forage opportunistically (Calkins 1986).

From previous experience in the study area, the author can attest that humpback whales are bubble-net feeding intensively on schooling fish – almost definitely herring -- in early and mid-summer. There is a marked change in their feeding behavior later in the summer (Keen et al., unpubl. data), suggesting that humpbacks switch to a krill-dominated diet in the late summer (Janie Wray, pers. comm.). It has been suggested elsewhere that humpbacks can prey switch between years (Krieger & Wing 1985).

Just north of the study area in Fredericka Sound, AK, the euphausiids *T. raschi* and *E. pacifica* constitute 50-80% of humpback diet (Dolphin 1987). *T. longipes* have also been found in stomachs in the Gulf of Alaska, sometimes hundreds of kilograms of the species (Tomilin 1957, in Russian; cited in Calkins 1986). Euphausiid patches consisting of high concentrations of *T. raschi* were more likely to be humpback prey than those patches with relatively less *T. raschi* (Dehault 1985). Dolphin (1988) wrote: “The primary prey species of the humpback whales in southeast Alaska have been identified as the euphausiid crustaceans *Thysanoessa raschi* (Dolphin 1987c; Wing and Krieger 1983), *Thysanoessa longipes* (Wing and Krieger 1983); Bryant et al 1981), *Thysanoessa spinifera* (Nemoto and Kasuya 1965; Bryant et al. 1981; Wing and Krieger 1983), *Euphausia pacifica* (Jurasz and Jurasz 1979; Bryant et al. 1981; Wing and Krieger 1983), and the fishes Pacific herring, *Clupea harengus* (Jurasz and Jurasz 1979; Wing and Krieger 1983), capelin, *Mallotus villosus* (Jurasz and Jurasz 1979; Wing and Krieger 1983), Pacific sand lance, *Ammodytes hexapterus*, and juvenile walleye pollock, *Theragra chalcogramma* (Dolphin 1988), based on stomach contents, analysis of fecal samples, and visual observation of feeding.”

Diets of Whale Prey

It takes a food web to attract large cetaceans to an area, and it would be impossible to design a sampling regime that adequately samples all of the zooplankton (or phytoplankton or fish, for that matter) tied up in that web. But it is nonetheless prudent to take the steps necessary to acknowledge what is being left out of the picture that we hope to paint with our data. Without such precautions, we cannot substantiate claims of which taxa are major “players”, and which it is acceptable not to monitor. In this vain, reviewing which zooplankton are consumed by the fish species of cetacean diets is the least I can do. It is also interesting that some of the fish targeted by whales are also competitors for zooplankton. Refer to the “Forage Fish” backgrounder for more about these species.

Herring

Adult pacific herring feed primarily on euphausiids (Tanasichuk 1998). Juvenile herring from Prince William Sound were found to prey upon Cirrepedia nauplii, fish eggs, small and large calanoids, euphausiids, and larvaceans (Foy & Norcross 1998). In BC, they are known to prey upon “planktonic crustaceans, copepods, euphausiids, amphipods, marine worms, and small fishes. Important forage species include *Calanus* and *Pseudocalanus copepods*, *Thysanoessa inermis* and *T. raschii* (euphausiids) and amphipods *Themisto spp.*” (Gjøsæter 1998).

Sardine

The most important prey items for the sardine (*Sardinops sagax*) in British Columbian waters are diatoms, euphausiids, euphausiid eggs, copepods, and oikopleurids (larvaceans; McFarlane et al. 2005). In one study from 1997 fieldwork, euphausiids were found in over 55% of sardine stomachs and contributed nearly 60% of the overall stomach contents volume (McFarlane et al. 2005).

Pacific Hake

Of all the abundant schooling fish in B.C. waters, hake may exert the greatest predation pressure on their krill prey, *Euphausia pacifica* and *Thysanoessa spinifera*, by sheer dint of their biomass (Mackas et al. 1997). Hake and euphausiids are known to co-occur in great aggregations in coastal B.C. throughout summer months.

Sand lance

Sand lances (reviewed thoroughly in Robards et al. 1999) are actively pelagic as they feed in the daytime, but they rest in the benthos at night. In the winter, a higher proportion of their diet tends to come from epibenthic prey (Rogers et al. 1979). During their vertical migration, they are preyed upon intensively.

Larval sand lance feed on phytoplankton, from diatoms to dinoflagellates (Trumble 1973). When longer than 10 cm, they feed upon the nauplii of copepods in the summer and euphausiids in the winter (Craig 1987). Adults feed predominantly on *Calanus* copepods, but also on a range of species, including chaetognaths, mysids, amphipods, and fish larvae (Field 1988, O'Connell and Fives 1995, Scott 1973). In the winter, more of their food comes from fellow epibenthic organisms (Rogers et al. 1979).

Expected Zooplankton

Mackas & Galbraith (2002) outlined zoogeographic classifications for BC plankton (for details, see the "Plankton Processes" Background). There are southern and boreal groups, and within each there is an onshore-offshore gradient of neritic (coastal or inland waters), shelf, and oceanic species. In each zoogeographic province the plankton assemblage exhibits convergent similarities in size, diet, life history, etc., that have arisen from co-existing in similar physiographic conditions throughout evolutionary time (see Mackas & Coyle 2005 too).

The zoogeography of the boreal shelf and neritic provinces are most relevant to the Kitimat Fjord System. Mackas and Galbraith define the area as the shelf from latitudes 42-60 degrees North. Many boreal shelf taxa have diel and/or ontogenetic migration strategies that aid retention and population maintenance in a strongly advective shelf environment (Mackas and Galbraith 2002). For the boreal neritic province, "taxa in this group normally complete their life cycle, and reach their maximum abundance, either within inner-coast estuaries and straits or along the innermost part of the outer-coast continental shelf" (Mackas and Galbraith 2002). Note, however, that during climatic anomalies southern species may occur in the adjacent shelf waters.

In both the above diet review and in the zooplankton literature for BC waters, two dominant groups stand out: copepods and euphausiids (Mackas & Tsuda 1999), and the euphausiids the most of the two. Copepods make up a large portion of the total biomass of the zooplankton community in all areas of the British Columbia coast, especially in spring and early summer (Mackas and Tsuda 1999), but they are less of a target for the whales of interest. Euphausiids also dominate the zooplankton community, though their abundance is more dependent on the season and local bathymetry (Mackas & Tsuda 1999), and they are targeted by whales (and fish and seabirds too).

Of course, groups other than these are present in the study area, occasionally in dominant numbers. Those most commonly mentioned in studies of predator diets and regional studies are amphipods, chaetognaths, and tunicates.

Hyperiid amphipods: Of the few regional studies that were found (Lorz & Pearcy 1975; Schulenberger 1978; Yamada et al. 2004), sampling protocols were similar to euphausiid studies (571u 1m diameter single-net; 333u 0.7 diameter BONGO; 333u .7 diameter, respectively). In the North Pacific gyre, hyperiid amphipods have been observed to remain primarily within the upper 100m (Schulenberger 1978). In the Oyashio region, 99% of the population was collected above 300m (Yamada et al. 2004).

Chaetognaths can also occur in abundance throughout the water column in the study area. They are important predators of larval fish and copepods, among other plankters, and in coastal BC they can be indicative of the excursion of the typically “offshore” assemblage into neritic habitats (see Mackas & Galbraith 2002). These predatory zooplankters are long (2-120mm, Bone et al. 2001) and slender. 333 micron-mesh nets seem adequate for quantitatively sampling all chaetognath life stages (Terazaki & Miller 1986; Johnson & Terazaki 2003). The chaetognaths expected on BC’s boreal shelf are *Sagitta elegans*, *Sagitta scrippsae* (Mackas et al. 2007), *Parasagitta elegans* and *P. euneritica* (Mackas and Coyle 2005). An oceanic chaetognath, *Eukrohnia hamate* also occurs in BC waters but is not expected in fjords (Mackas & Galbraith 2002).

Oikopleurid larvaceans have been observed in high densities at depth in British Columbia fjords (see Trevarrow et al. 2005). The author has seen salps, as well as ctenophores and cnidarians, in abundance at the surface near the mouths of inlets in the study area. Although these gelatinous plankters are not consumed by the target cetaceans of our study, they are a primary prey of herring. Furthermore, their presence suggests shifts in community dynamics, and could be suggestive of a shifting dominance in phytoplankton size class (Andersen 1998). However, because they break up in towed nets, gelatinous plankters are notoriously difficult to sample quantitatively using our approach. At the most, their presence can be noted and identification should be possible to the class-level.

Ctenophores (including the neritic *Pleurobrachia bachei*, Mackas and Galbraith 2002) and **cnidarians** are often dominant zooplankton predators on the continental shelf, especially in “green-water” conditions (Suchman and Brodeur 2003, Larssen 1987). Aurelia (probably *labiata*) is an abundant neritic scyphomedusa that is rare in the continental shelf and absent in Haida Eddies (Mackas & Galbraith 2002). The tunicates *Salpa fusiformis/aspera* and pteropod *Clio pyramidata* occur on the BC shelf (Mackas and Galbraith 2002). In Knight Inlet, pteropods, chaetognaths, ctenophores, and cnidarian are known to be present, and known to migrate diurnally from the surface through depths of 250m (Trevarrow et al. 2005).

Relevant Euphausiids

Euphausiids are pelagic shrimp-like eucarids that aggregate in high densities and provide the basis of many trophic webs. In BC waters, euphausiids “often account for 10-25% of net-caught zooplankton biomass and secondary production (e.g. Heath 1977; Harrison et al. 1983; Fulton and LeBrasseur 1984; Mackas 1992; Tanasichuk 1998a,b).”

Life History

The euphausiid reproductive cycle has a strong annual periodicity (Kathman et al. 1986). Mating typically occurs in spring, after which fertilized eggs are either broadcast or brooded depending on the species. There are four principle development stages before adulthood (Kathman et al. 1986): the nauplius, metanauplius (or pseudometanauplius), calyptosis, and the furcilia. On the BC coast, two peaks in larval abundance have been observed: May-June, at the onset of the upwelling season, and August-September, at its end (Mackas 1992).

Distribution

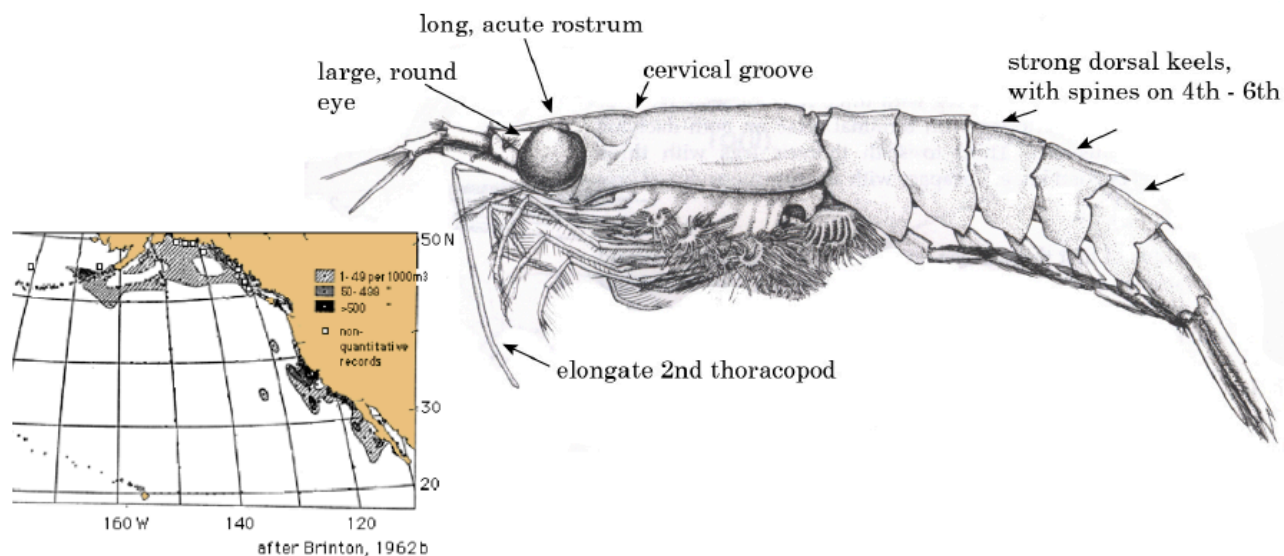
In BC coastal waters, euphausiid distribution does not seem limited by temperature or salinity, except in the very shallow surface layer at the heads of some inlets (Kathman et al. 1986). But species do have general salinity preferences and seem to aggregate accordingly. Differences between coastal regions in species composition are primarily tied to bathymetry both onshore and off (Mackas 1992, Mackas and Tsuda 1999). Simard & Mackas (1989), who mapped summer season euphausiid distributions using a high-frequency echo sounder, found that the highest concentrations of all taxa in the immediate vicinity of steep depth gradients such as the shelf break and along the margins of banks and submarine canyons. Depth patterns can also be a function of species-specific ontogeny: for example, later life history stages in *T. spinifera* in California may occur deeper in the water column, e.g. 150-200 m (Croll et al. 2005).

Expected Species

Twelve or more euphausiid species occur off the outer B.C. coast (Mackas 1992, Brinton et al. 2000), but the three dominant species there, from the Juan de Fuca area (Mackas 1992) to Prince William Sound (Coyle & Pincuk 2005), are *Euphausia pacifica*, *Thysanoessa spinifera*, and *T. inspinata* (Mackas 1992). All three species are epipelagic, endemic to the North Pacific, and vertical migrators (Bollens et al. 1992). For more information about the taxonomy, identification and distribution of northeast Pacific euphausiids, see their Backgrounder.

The regional literature and experts say that the two most abundant euphausiids in the Kitimat Fjord System are likely to be *T. spinifera* first, then *E. pacifica* (Galbraith, pers. comm.; Mackas 1992; Cooney 1986). Any other euphausiids in the area are likely to be a mix of *T. longipes* (Flinn et al. 2002, Galbraith, pers. comm.), *T. inermis* (Flinn et al. 2002, Cooney 1986, Galbraith, pers. comm.), and *T. raschi* (Dolphin et al. 1987, Cooney 1986, Galbraith, pers. comm.). *T. inspinata* may also be present (Mackas 1992) but is likely to be the most rare (Galbraith, pers. comm.). So there are a total of six species to watch out for.

Thysanoessa spinifera



Eggs are as small as 380 μ . Adults are as small as 18mm (Brinton et al. 2000). Adults are generally larger than adults of *E. pacifica*.

Thysanoessa spinifera (Holmes, 1900) is the only local species usually found in less than 100m of water, and it is the most common euphausiid on the BC shelf (Mackas & Anderson 1986). Its range is restricted to northeast Pacific coastal waters (Regan 1968). Broadly speaking, *T. spinifera* is considered an inner shelf and fjord

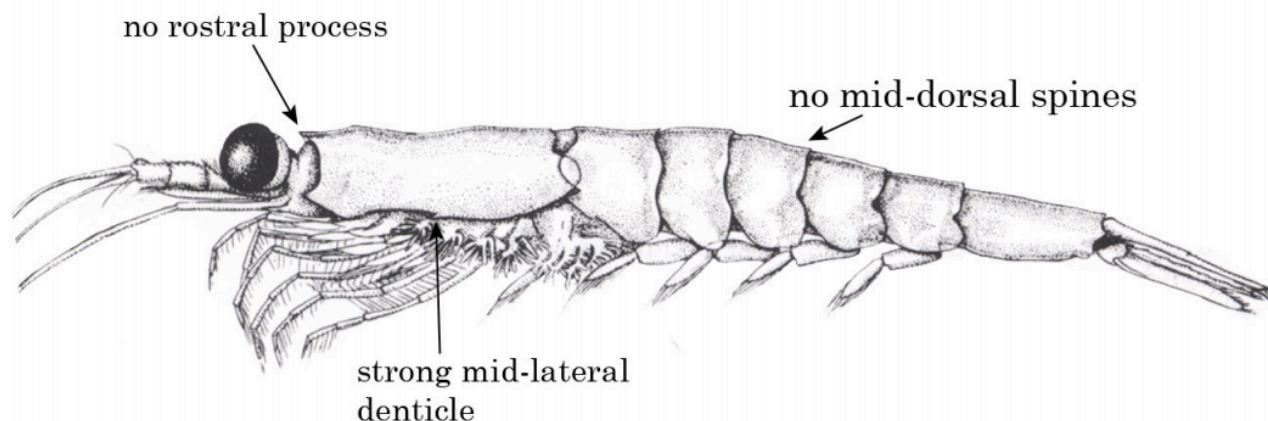
species, while *E. pacifica* is more abundant off the shelf; this is the case both in the Juan de Fuca area (Mackas & Galbraith 1992) and the Gulf of Alaska (Coyle et al. 2005).

In BC *T. spinifera* is common in fjords and inlets, in which it can occur in salinities between 14.3 and 27.3 o/oo (Regan 1968). *T. spinifera* in California may occur deeper in the water column, e.g. 150-200 m (Croll et al. 2005). In S. California, *T. spinifera* has a discrete spawning season that extends from May to July off California, also coincident with strongest upwelling (Brinton 1981).

Thysanoessa spinifera exhibit seasonal swarming behavior, possibly related to sexual development (Brinton, 1981; Smith and Adams 1988). From May to July during the peak of the upwelling season, fully mature adults form extensive inshore surface swarms (Smith and Adams 1988). These reproductive adults are thought to swarm, breed and then presumably die at the end of their three-year life cycle (Nemoto 1957).

Both *T. spinifera* and *T. inspinata* are dominant food items for baleen whales in the coastal waters of the eastern Aleutian Islands (Ponomareva 1963), for blue, fin, and humpback whales of the Gulf of Alaska (Mauchline & Fisher 1969), and for fish. It is thought that blue whales off the southern California coast take advantage of these swarming events to forage in shallow waters (Fiedler et al. 1998).

Euphausia pacifica



Egg capsules can be as small as 360 μ . Life stages become progressively large. The final furcicula stage (7) can be as small as 5.3 mm. Adults can be as small as 11 mm (Brinton et al. 2000).

Euphausia pacifica is common along the entire northeast Pacific coast, though it is more rare to absent in the Bering Sea and Aleutian Islands' waters. In BC coastal waters *E. pacifica* is almost always the dominant species and can occur in very large numbers (Regan 1968). This has been confirmed in the Strait of Georgia (Heath 1977), among other places.

E. pacifica is considered a primarily oceanic species, widely distributed throughout the N Pac, but also occurring in neritic waters (Regan 1968). In southern B.C., *E. pacifica* (and occasionally *T. inspinata*) were the dominant euphausiids at the deeper locations along and seaward of the shelf break and in the Juan de Fuca submarine canyon system (Mackas 1992). In the Gulf of Alaska, if *E. pacifica* does occur in Prince William Sound, it is thought to be related to deep-water renewal in the sound (Coyle & Pinchuk 2005).

However, there are confounding exceptions. In Observation Inlet, near the Alaskan border, *E. pacifica* were found in the upper reaches of the fjord, in the turbid waters near the river mouth (Mackas & Anderson 1986). These *E. pacifica* were larger than those in the outer areas of the inlet, suggesting better survival. It has been hypothesized that these tannin-rich waters provide a visual refuge from predation.

The species exhibits an annual or biannual life cycle (Brinton 1976, Heath 1977). Vertical behavior is known to differ substantially between ontogenetic stages (Bollens et al. 1992, see below). In Dabob Bay, WA (e.g., Bollens et al. 1992), a pulse of larvae is thought to occur in the spring, followed sequentially by pulses of juveniles and adults in late summer to early fall. All size classes aggregate at or near the surface at night, and juveniles and adults are thought to vertically migrate to 100-200m depths during the day. There is also thought to be an ontogenetic migration, with a trend towards deeper depths with larger body sizes.

Off of Oregon, *E. pacifica* larvae are most abundant between October and December, with no major concentrations during winter or spring (Smiles and Percy 1971). In S. California, *E. pacifica* has continuous recruitment year round with peaks associated with upwelling periods (Brinton 1976). Individuals live about 1 year, although in some areas a second, non-breeding year has been observed (Ponomareva 1963, Heath 1977). Larvae have also been found from May to September in the Strait of Georgia and Saanich Inlet by Heath (1977), which lends evidence to the hypothesis of a two-year life cycle.

“Like many other euphausiids species, adult and late juvenile stages of *E. pacifica* undergo a pronounced diel vertical migration, rising to the surface layer at night to feed, then descending at dawn to a dimly lit depth strata (between 80 and 150m in the Strait of Georgia) to avoid visual detection by predators during daylight hours (Mauchline 1980). Their horizontal spatial distribution is also extremely patchy, with a large fraction of the total population biomass aggregated in a small fraction of the habitat (Romaine et al. 2002). In coastal and continental margin regions, patch location and morphology are strongly affected by seabed topography and currents. But because of the strong diel vertical migration, these spatial aggregations form, dissipate, and reform on a daily basis (Romaine et al. 2002).”

In Southern California *E. pacifica* juveniles and adults occur from 150-400m during the day (Brinton 1967). Banner (1950) and Fulton & LeBrasseur (1985) found this species most common in the upper 300m during the spring in B.C. In Saanich Inlet, which has an anoxic bottom layer, *E. pacifica* remains at 100m during the day in concentrations up to 10,000 individuals per cubic meter (Mackie & Mills 1983). Another study found *E. pacifica* even shallower in Saanich Inlet daylight hours: 70-90m (Boden and Kampa 1965). In Knight Inlet, the scattering layer is at 60-90m depths, and is generally composed of larger crustacean zooplankton including euphausiids (primarily *Euphausia pacifica*), amphipods (both hyperiid and gammariid), copepods, and decapod shrimp (Mackie and Mills 1983, Trevorrow et al. 2005).

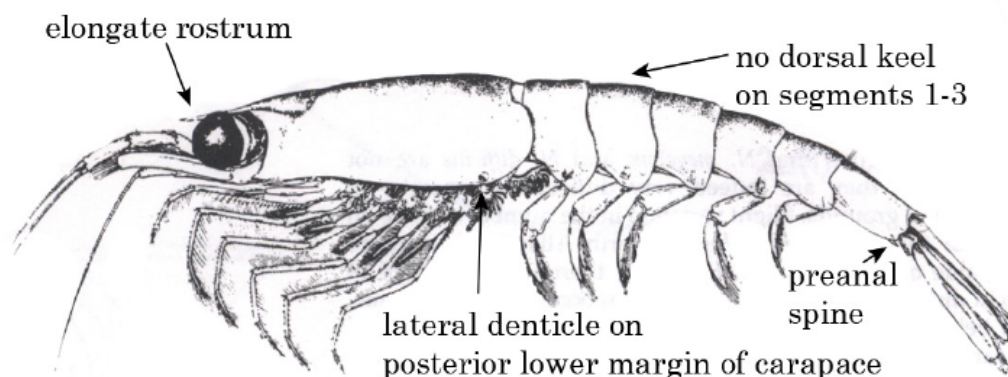
E. pacifica feeds mostly at night; it is a filter feeder that consumes detritus, algae, chaetognaths, echinoderms and crustaceans (Mauchline & Fisher 1969). It is an important prey species for blue, fin, humpback and right whales, as well as squids, decapods, and birds (Mauchline 1980, Vermeer 1981, Vermeer 1985, Vermeer et al. 1985).

Other *Thysanoessa* spp.

Thysanoessa is cosmopolitan in subtropical and subpolar waters, but generally does not occur within the tropics (Kathman et al. 1986). Relative to other abundant north Pacific euphausiid genera (Stylocheiron, Nematobrachion, and Euphausia), *Thysanoessa* is considered the most northerly, and dominates euphausiid assemblages in the mid- and high-latitudes (Boden 1950). All *Thysanoessa* species are epipelagic, found at depths ranging from 0 to 1000m (Kathman et al. 1986). This adaptive ability to span a considerable depth range may be reflected in the bilobate eye of the genus (Kathman et al. 1986).

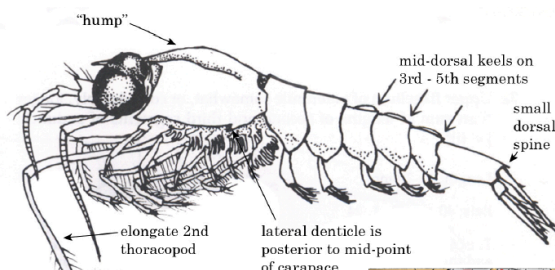
There are 10 species within the genus *Thysanoessa*, 6 of which occur in the North Pacific. Of this subset, 3 are endemic to the north Pacific (*T. inspinata*, *T. longipes*, and *T. spinifera*; Kathman et al. 1986).

Thysanoessa inermis (Kroyer, 1846)



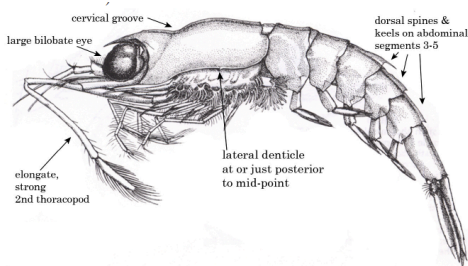
An epipelagic species. It has been reported from the North Atlantic, North Pacific, Arctic, Beaufort Sea, and the Svalbard Archipelago. In the Pacific this species occurs south of ~43 degrees N (Brinton 1962, Mauchline & Fisher 1969). Most occur between 140-280m during the day, and shallower at night, but have been found as deep as 400m. Their habitat is restricted to 32.1-33.4 o/oo salinity in the northern North Pacific (Fukuchi 1977). *T. inermis* is a predator; it feeds upon diatoms, dinoflagellates, tintinnids, radiolarians, medusa, chaetognaths, molluscs, echinoderms, and crustaceans, as well as detritus (Mauchline 1980, Mauchline & Fisher 1969). It is an important component of the diets of blue, fin, sei, and humpback whales, as well as seals, fish, and birds (Mauchline 1960, Mauchline & Fisher 1969). This species composed 90% of the diet for whales sampled in a study at the whaling station of Akutan, Alaska (Banner 1950).

Thysanoessa inspinata (Nemoto 1963)



Eggs and larvae of *T. inspinata* are undescribed. Adults are as small as 12mm (Brinton et al. 2000). An epipelagic species. This species is endemic to the North Pacific, occurring south of 50 degrees N in the Gulf of Alaska and occurring as far west as the Sea of Japan. North of Vancouver Island, this species' range gives way to the less abundant subarctic *Thysanoessa longipes* (Brinton et al. 2000). In the Queen Charlotte Islands region, it has been known to co-occur with *T. longipes* (Fulton & LeBrasseur 1984). It usually occurs in <300m of water. *T. inspinata* is a relatively important food item for blue, fin, sei, and humpback whales (Mauchline & Fisher 1969).

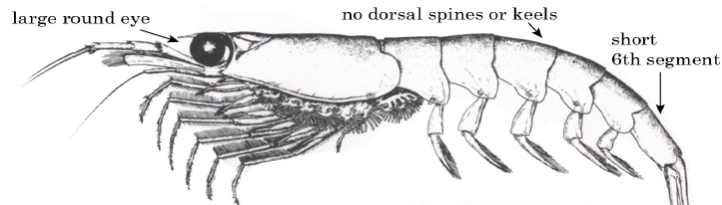
Thysanoessa longipes (Brandt, 1851)



An epipelagic species. *T. longipes* is endemic to the North Pacific, and has been recorded from California to Alaska as well as in the Sea of Japan, Okhotsk Sea and Bering Sea (Banner 1950, Fulton & LeBrasseur 1984). San Diego is the southernmost record (as of the 1950s) and the species seems to occur here only as an

occasional straggler (Boden 1950). Usually inhabits depths ranging from 0 to 500m, and salinities ranging from 32.6-34.1 o/oo in the northern N. Pacific (Fukuchi 1977). *T. longipes* is primarily an oceanic species, widely distributed throughout the North Pacific, but also occurring on occasion in neritic waters (Regan 1968). In coastal B.C. inlets, it has been found in salinities of 24.5-27.2 o/oo (Regan 1968). *T. longipes* consumes detritus, diatoms, dinoflagellates, tintinnids, chaetognaths, echinoderms, and crustaceans (Mauchline 1980). It is an important food item for birds (Vermeer 1981, Vermeer 1985, Vermeer et al. 1985) and blue, fin, sei, and humpback whales (Mauchline 1980, Mauchline & Fisher 1969).

***Thysanoessa raschii* (M. Sars, 1864)**



An epipelagic euphausiid. This species occurs in the North Atlantic, North Pacific, and Arctic, including Svalbard. It has been recorded at higher latitudes, off Oregon, British Columbia, and Alaska, as well as the Clyde Sea near Britain (Hardy 1956). It inhabits the continental shelf or the neritic shore waters in the Arctic regions (Nemoto 1966). It is a shallow epipelagic species, found from 0-200m. In the coastal inlets of B.C., it can be found in salinities of 25.7 – 26.8 o/oo (Regan 1968). *T. raschii* is filter-feeding omnivore, relying upon detritus, algae, diatoms, dinoflagellates, tintinnids, radiolarians, chaetognaths, and crustaceans.

Relevant Copepods

The most numerically dominant zooplankters of at least the southern fjords of BC are the copepods (Trevorrow et al. 2005). The same goes for the nearby Gulf of Alaska (Cooney 1986). There are 294 species of pelagic copepods in the northeast Pacific (Razouls et al. 2005-2014). Cooney (1986) lists 26 copepod species that are numerically dominant in the Gulf of Alaska.

Life History

Although local current-bathymetry interactions can aggregate copepods in much the same way they do euphausiids, on larger scales large-bodied copepods (e.g., *Neocalanus spp.*) occur in higher abundance farther offshore and farther north in deeper ocean regions (Flinn et al. 2002). The annual life history of BC copepods is more variable than that of its euphausiids, both across species and among populations of the same species. Copepod reproduction seems more closely tied to annual cycles in production, and there may even be a plastic response to blooms; in Dabob Bay, WA, for instance, copepod egg production is higher during blooms (Osgood & Frost 1994).

At the same study site, three predominant shelf copepods exhibit three markedly different ontogenetic cycles (Osgood and Frost 1994). *Calanus marshallae* emerges from diapause in mid-winter, produces one major generation in early spring that spawns very early and diapauses by late May. *C. pacificus* emerges from diapause in late winter and produces a new generation soon after *C. marshallae*. Two more generations occur in coincidence with late spring and autumn phytoplankton blooms, then C5 diapause occurs in late fall. *Metridia lucens*, a deeper-dwelling omnivore, does not undergo winter diapause. The fall and winter population was chiefly adult females at depth, but nauplii are present year-round and reproduction never seems to cease. Perhaps by remaining active at depth, this species was able to avoid offshore advection and could therefore

afford a more continuous turnover of generations. Elsewhere on the coast, however, the same species can have different ontogenetic cycles. While the life history *C. marshallae* of southern Dabob Bay closely resembles that of Indian Arm to the north (Woodhouse 1971), in Oregon upwelling regions this species goes through 3 generations within a year rather than 1 (Osgood & Frost 1994).

The vertical and horizontal occurrence of diapause stages are influenced by the species' C5 buoyancy, the seasonal timing of its diapause, and its vertical behavior during its active life stages. Both active and diapausing phases of many species, including *N. cristatus* and *E. bunggi*, tended to predominate in the pycnostad between the halocline and the thermocline (20-80m depth) (Coyle et al. 2005). Many of the dominant NE Pacific copepod species spend their early life stages almost entirely within the upper 50m (Mackas and Coyle 2005).

Metridia is a genus of large-bodied copepod, similar in size to *Calanus* and *Neocalanus*. *Metridia lucens* is a dominant copepod that may be present at any life stage during the summer. The species feeds upon fecal pellets, detritus and radiolarians, and is thought to be less associated with surface layers (Osgood & Frost 1994). Although it does vertically migrate (up to 150m, Mackas & Galbraith 2002), its mean depth is deeper and it does not linger in surface waters (Falkenhaus et al. 1997). This species is also thought to reproduce continuously, and has no overwintering diapause stage (Osgood & Frost 1994). In Dabob Bay, southern British Columbia, *Metridia lucens* does not appear to enter a diapause state (Osgood & Frost 1994). The fall and winter population was chiefly composed of adult females, which remained at depth and were reproductively immature. Nauplii were found on all sampling dates, meaning reproduction never ceased and *M. lucens* phenology is more continuous than in other major calanoids in the region (Osgood & Frost 1994).

Because copepod life stages vary in size, it is difficult to sample all stages in the water column, from egg to nauplius to copepodite, quantitatively. Late copepodites of calanoid copepods can be millimeters in length, but their eggs and nauplii are much smaller. Osgood & Frost (1994) observed that 216 μ nets missed calanoid nauplii in the North Pacific's subpolar gyre. To capture copepodites of *Calanus*, Harris et al. (2000) recommend a mesh size of no more than 124 μ . For copepodites of *Pseudocalanus*, a smaller genus that is also common to BC waters, they recommend 61 μ mesh. Some studies (e.g. Coyle & Pincuk 2005, Peterson 1979, Miller & Clemons 1988) deploy two nets of differing mesh size and diameter in order to capture all life stages present; but the primary objectives of these studies pertain to geographic, vertical, and seasonal patterns. Tsuda et al. (2001) used mesh sizes varying from 333 μ to 1mm, the largest found from our literature review in studies of *N. plumchrus* and *flemingeri*; while they could not quantify naupliar stages, they maintained that "all later copepodite stages were retained".

With the Bangarang Project's sampling set up, only the most relevant life stages of copepods – copepodites (specifically C4, 5, & 6) and, in some cases, the final naupliar stages, will be sampled. Fortunately, other studies suggest that the timing of the Bangarang project's sampling plan is ideal. By late May, when sampling would begin, only copepodites 4 and 5 of the dominant *Neocalanus plumchrus* are expected to be in the study area (Mackas et al. 2007). The biomass maximum for pre-dormant C5's of this species can be expected to occur somewhere between late April and late May (Mackas et al. 2007), meaning there may not much need to cater equipment design to earlier, smaller life stages.

Distribution

The larger subarctic oceanic species of the slope, usually endemic to subarctic gyres, can sometimes be transported onto the shelf by onshore flow patterns (Mackas and Galbraith 2002). These include: *Neocalanus plumchrus*, *N. cristatus*, *N. flemingeri*, and *Metridia pacifica*. These species are also listed as dominant in Mackas and Anderson (1986), along with some of the shelf species mentioned above.

The most common species in BC shelf and slope waters is *Neocalanus plumchrus* (Harrison et al. 1983). Because this species was split by Miller (1988) into two species, *N. plumchrus* and the slightly smaller *N. flemingeri*, studies previous to that must be read with a grain of salt. In addition to these, Mackas et al. (2007) also mention *Metridia lucens*, and *Calanus marshallae* as dominant in BC waters (Mackas et al. 2007). To the north, *Eucalanus bungii* is numerically dominant in the Gulf of Alaska (Cooney 1986). *Neocalanus* dominate

copepod biomass in the GOA shelf during spring, but largely disappear by early summer (Coyle and Pimncuk 2003, Mackas and Coyle 2005). Prosome lengths of *N. plumchrus* and *flemingeri* species' copepodites range from 650 μ (C1) to 4.9 mm (C5)(Tsuda et al. 1999). Miller et al.'s (1991) 20-year study in the Gulf of Alaska corroborates these data: mean prosome lengths for these species varied between 3.0 and 3.5mm for *N. flemingeri* adults, and 3.55 and 3.9mm for *N. plumchrus* C5s. Tsuda et al. (2001) reported prosome lengths for C5 *N. cristatus* between 6.39 and 7.58mm; for C6, between 5.6 and 6.1mm.

Expected Species

In the boreal shelf zoogeographic province, Mackas & Galbraith (2002) list the following species.

Acartia longiremis (noted as a neritic species; also in Mackas et al. 2007)

Pseudocalanus mimus (the most common species, also in Mackas et al. 2007)

Pseudocalanus moultoni (noted as a neritic species)

Calanus marshallae (also southern)

Paracalanus parvus, (noted as neritics; Mackas et al. 2007 classifies it as a southern species)

Mesocalanus tenuicornis (also southern)

These species, which are those most likely to be found in the Kitimat Fjord System, are generally small. Relatively little information on distribution and life history is available for most of these species.

Calanus marshallae: This copepod has multiple generations within a year, diel vertical migration patterns differ among males and females, and is thought to rely upon ontogenetic vertical migration to return to shelf habitat after being advected offshore (Peterson 1998). Studies of *C. marshallae* in the Oregon upwelling system spurred the hypothesis that the timing of ontogenetic vertical behavior employs the offshore-onshore advection cycle to maintain shelf populations (Peterson et al. 1979), and this was later proposed as the mechanism of spatial retention for some BC zooplankton species (Mackas 1992). Observations from several studies seemed to corroborate this (Woodhouse 1971, Osgood & Frost 1994, Coyle et al. 2005). Osgood & Frost (1994) states that 216 μ mesh cannot be quantitative for nauplii of *Calanus marshallae* and *pacificus*. Peterson's (1979) dissertation on *C. marshallae* relied on 120 μ and 240 μ mesh nets. Based on his data collection in the laboratory and in the field, he concluded that this species' first naupliar stage is ~220 μ . The third naupliar stage was the first to be longer than 333 μ . The first copepodite stage is ~1mm. C5 is 2.5mm, and C6 can be as little as 3.0mm.

Literature Cited

- Andersen, V. 1998. Salp and pyrosomid blooms and their importance in biogeochemical cycles, p. 125-137. In Q. Bone [ed.], *The biology of pelagic tunicates*. Oxford University Press, Oxford.
- Banner, A.H. 1950. The Mysidacea and Euphausiacea. Pages 447-448 in *Gulf of Mexico, its origin, waters, and marine life*. Fisheries Bulletin 89. Fish. Wildl. Serv., Washington.
- Boden, B. P. and Kampa, E. M. (1965) An aspect of euphausiid ecology revealed by echo-sounding in a fjord. *Crustaceana*, 9, 155–173
- Bollens, S.M., B.W. Frost, B.W., and T.S. Lin. 1992. Recruitment, growth, and diel vertical migration of *Euphausia pacifica* in a temperate fjord. *Marine Biology* 114: 219–228.
- Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California Current. *Limnology & Oceanography* 12:451-483.
- Brinton, E., 1976. Population biology of *Euphausia pacifica* o. southern California. *Fishery Bulletin*, U.S. 74, 733-762.
- 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., M.D. Ohman, A.W. Townsend, M.D. Knight, and A.L. Bridgeman. 2000. Euphausiids of the World Ocean. World Diversity Database CD-ROM Series. Windows Version 1.0. ETI Expert Center for Taxonomic Identification: Mauritskade, Netherlands.
- BRYANJ T. ,P ., NICHOLS, G ., and MILLERK., 1981. Krill availability and the distribution of humpback whales in southeast Alaska. *J. Mammal.* 62: 427 -430
- Calkins, D.G. 1986. Marine Mammals. In Hood, D.W., and S.T. Zimmerman, eds. 1986. *The Gulf of Alaska: physical environment and biological resources*. NOAA Alaska Office OCS Study MMS 86-0095.
- Croll et al. 2005. From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series* 289:117-130.
- Coyle, K.O., A.I. Pinchuk. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep-Sea Research II* 32:217-245.
- Coyle, K.O., and A.I. Pinchuk. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. *Fisheries Oceanography* 12, 327–338.
- Craig, P.C. 1987a. Forage fishes in the shallow waters of the north Aleutian shelf. In: *Forage fishes of the southeastern Bering Sea: Proceedings of a conference*; [dates of meeting unknown]; [location unknown]. OCS Study MMS 87-0017. [Place of publication unknown]: [publisher unknown]: 49-54.
- Dehalt, A., C. 1985. Zooplankton resources and humpback whale, *Megaptera novaeangliae*, foraging ecology in southeast Alaska. M.Sc. thesis, University of British Columbia, Vancouver.
- Dolphin, W.F. 1988. Foraging dive patterns of humpback whales, *Megaptera novaeangliae*, in southeast Alaska: a cost-benefit analysis. *Can. J. Zool.* 66: 2432-2441.
- Falkenhaus, T., K.S. Tande, T. Semenova. 1997. Diel, seasonal, and ontogenetic variations in the vertical distributions of four marine copepods. *Marine Ecology Progress Series* 149:105-119.
- Fiedler, P.C., S.B. Reilly, R.P. Hewitt, D. Demer, V.A. Philbrick, S. Smith, W. Armstrong, D.A. Croll, B.R. Tershy, B.R. Mate. 1998. Blue whale habitat and prey in the California Channel Islands. *Deep-Sea research II* 45:1781-1801.
- Field, L.J. 1988. Pacific sand lance, *Ammodytes hexapterus*, with notes on related *Ammodytes* species. In: Wilimovsky, N.J.; Incze, L.S.; Westrheim, S.J., eds. *Species synopses, life histories of selected fish and shellfish of the northeast Pacific and Bering Sea*. [Place of publication unknown]: [publisher unknown]: 15-33. Available from: Washington Sea Grant Program, 3716 Brooklyn Ave. NE, Seattle, WA 98105.
- Fisheries and Oceans Canada. 2010. Recovery Strategy for the North Pacific Humpback Whale (*Megaptera novaeangliae*) in Canada [DRAFT]. Species at Risk Act Recovery Strategy Series. Fisheries and Oceans Canada, Ottawa. x + 51 pp.
- Fleminger, A., and R.I. Clutter. 1965. Avoidance of towed nets by zooplankton. *Limnology & Oceanography* 10:96-104.
- Flinn, Rowenna, A.W. Trites, E.J. Gregr. 2002. Diets of fin, sei, and sperm whales in British Columbia: an analysis of commercial whaling records, 1963-1967. *Marine Mammal Science* 18(3):663-679.

- Ford, J.K.B., A.L. Rambeau, R.M. Abernethy, M.D. Boodaards, L.M. Nichol, and L.D. Spaven. 2009. An assessment of the potential for recovery of humpback whales off the Pacific Coast of Canada. Canadian Science Advisory Secretariat Research Document 2009/015.
- Foy, R.J., B.L. Norcross. 1998. Spatial and temporal differences in the diet of juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. In *Juvenile Herring Growth and Habitats: Exxon Valdez Oil Spill Restoration Project Annual Report*.
- Fulton, J., and R. LeBrasseur. 1984. Euphausiids of the continental shelf and slope of the Pacific coast of Canada. *La Mer* 22:268-276.
- Gjørseter, H. (1998) The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia* 83:453– 496.
- Harris, R.P., P.H. Wiebe, J. Lenz, H.R. Skjoldal, M. Huntley, eds. 2000. *ICES Zooplankton Methodology Manual*. Academic Press: London.
- Harrison, P., J. Fulton, F. Taylor, and T. Parsons. 1983. Review of the biological oceanography of the Strait of Georgia: Pelagic environment. *Canadian Journal of Fisheries and Aquatic Science* 40: 1064-1094.
- Heath, W.A. 1977. The ecology of harvesting of euphausiids in the Strait of Georgia. Ph.D. Thesis, University of British Columbia. 187 pp.
- Ianson, D, SE Allen, DL Mackas, MV Trevorrow, and MC Benfield. 2011. Response of *Euphausia pacifica* to small-scale shear in turbulent flow over a sill in a fjord. *Journal of Plankton Research* 33(11):1679-1695.
- Johnson, T.B. and M. Terazaki. 2003. Species composition and depth distribution of chaetognaths in a Kuroshio warm-core ring and Oyashio water. *Journal of Plankton Research* 25(10): 1279-1289.
- JURASZ, C., , and JURASZ, V., 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Sci. Rep. Whales Res. Inst. Tokyo*, 23: 91 – 101
- Kathman, R.D., W.C. Austin, J.C. Saltman, and J.D. Fulton. 1986. *Identification Manual to the Mysidacea and Euphausiacea of the Northeast Pacific*. Canadian Special Publication of Fisheries and Aquatic Sciences 93.
- Kawamura, A. 1980. A review of food of balaenopterid whales. *Scientific Report of the Whales Research Institute* 32:155-198.
- Kawamura, A. 1982. Food habits and prey distributions of three rorqual species in the North Pacific Ocean. *Scientific Report of the Whales Research Institute* 35:59-91.
- Keen, E.M. 2012. *Euphausiidae of the coastal northeast Pacific: A Field Guide*. Unpublished. SIO275 Taxon Project.
- Krieger, K.J., and B.L.Wing. 1985. Location and assessment of humpback whale forage in southeastern Alaska with sonar echo sounding. Unpublished report, Auke Bay Laboratory, NOAA. National Marine Fisheries Service, Auke Bay, AK. 66pp.
- Lorz, H.V., & W.G. Percy. 1975. Distribution of hyperiid amphipods off the Oregon coast. *J. Fisheries Research Board of Canada* 32: 1442-1447.
- Mackas, D.L. & E.P. Anderson. 1986. Small-scale zooplankton community variability in a northern British Columbian fjord system. *Estuarine, Coastal, and Shelf Science* 22:115-142.
- Mackas, D.L. and K.O. Coyle. 2005. Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography* 52(5-6): 707-725.
- Mackas, D.L., 1992. Seasonal cycle of zooplankton off southwestern British Columbia. *Canadian Journal of Fisheries and Aquatic Science* 49: 903–921.
- Mackas, D.L., and A. Tsuda. 1999. Mesozooplankton in the eastern and western subarctic Pacific: Community structure, seasonal life histories, and interannual variability. *Progress in Oceanography* 43:335-363.
- Mackas, D.L., R. Kieser, M. Saunders, D.R. Yelland, R.M. Brown, and D.F. Moore. 1997. Aggregation of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. *Can. J. Fish. Aquat. Sci.* 54: 2080–2096.
- Mackas, D.L., R.E. Thomson, and M. Galbraith. 2000. Changes in the zooplankton community of the British Columbia continental margin, 1985-1999, and their covariation with oceanographic conditions. *Canadian Journal of Fisheries Aquatic Sciences* 58:685-702.
- Mackas, D.L., S. Batten, M. Trudel. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the northeast Pacific. *Progress in Oceanography* 75: 223-252.
- Mackas, David L., & M.D. Galbraith. 2002. Zooplankton Distribution and Dynamics in a North Pacific Eddy of Coastal Origin: I. Transport and Loss of Continental Margin Species. *Journal of Oceanography* 58:725-738.

- Mackie, G.O. and C.E. Mills. 1983. Use of the Pices IV submersible for zooplankton studies in coastal waters of British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 40:763-776.
- Mauchline, J. 1980. The biology of mysids and euphausiids. *Advanced Marine Biology*. 18:1-681.
- Mauchline, J., and L.R. Fisher. 1969. The biology of Euphausiids. *Advanced Marine Biology* 7:1-454.
- McFarlane, G.A., MacDougall, L., Schweigert, J., Hrabok, C. 2005. Distribution and ecology of Pacific sardines (*Sardinops sagax*) off British Columbia, CA. *Cal-COFI Report*, Vol. 46.
- Miller, C.B., J. Fulton, B.W. Frost. 1991. Size variation of *Neocalanus plumchrus* and *Neocalanus flemingeri* in a 20-yr sample series from the Gulf of Alaska.
- Nemoto, T. 1957. Foods of baleen whales in the northern Pacific. *Scientific report of the Whales Research Institute* 12:33-89.
- Nemoto, T. 1959. Food of baleen whales with reference to whale movements. *Scientific Report of the Whales Research Institute* 14:149-290.
- Nemoto, T. 1966. *Thysanoessa* euphausiids, comparative morphology, allomorphy, and ecology. *Sci. Rep. Whales. Res. Inst. Tokyo*. 20:109-155.
- Nemoto, T. and T. Kasuya. 1965. Foods of baleen whales in the Gulf of Alaska of the North Pacific. *Scientific Report of the Whales Research Institute* 19:45-51.
- O'Connell, M.; Fives, J.M. 1995. The biology of the lesser sand-eel *Ammodytes tobianus* L. in the Galway Bay area. *Biology and Environment*. 95b(2): 87-98.
- Osgood, K.E., and B.W. Frost. 1994. Comparative life histories of three species of planktonic calanoid copepods in Dabob Bay, Washington. *Marine Biology* 118: 627-636.
- Peterson, W. 1998. Life cycle strategies of copepods in coastal upwelling zones. *Journal of Marine Systems* 15:313-326.
- Peterson, W.T. 1979. Life history and ecology of *Calanus marshallae* Forst in the Oregon Upwelling Zone. Dissertation at Oregon State University.
- Peterson, W.T., C.B. Miller, & A. Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep-Sea Research* 26: 467-494.
- Pike, G. 1950. Stomach contents of whales caught off the coast of British Columbia. *Fisheries Research Board Canadian Pacific Progress Report* 83:27-28
- Ponomareva, L.A. 1963. The euphausiids of the North Pacific, their distribution and ecology. *Dok. Akad. Nauk SSSR*:1-142. Transl. from Russian by Israel Programme for Science Translation, Jerusalem, 1966.
- Razouls C., de Bovée F., Kouwenberg J. et Desreumaux N., 2005-2014. - Diversity and Geographic Distribution of Marine Planktonic Copepods. Available at <http://copepodes.obs-banyuls.fr/en> [Accessed March 18, 2014]
- Regan, L. 1968. *Euphausia pacifica* and other euphausiids in the coastal waters of B.C.: relationships to temperature, salinity, and other properties in the field and laboratory. Ph.D. Thesis, University of British Columbia. 274 p.
- Rogers, D.E.; Rabin, D.J.; Rogers, B.J. [and others]. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island including ichthyoplankton, meroplankton (shellfish), zooplankton, and fish. [Seattle, WA]: University of Washington, Fisheries Research Institute, final report FRI-UW-7925: 291 p.
- Romaine, SJ, DL Mackas, and MC MacAulay. 2002. Comparison of euphausiids population size estimates obtained using replicated acoustic surveys of coastal inlets and block average vs. geostatistical spatial interpolation methods. *Fisheries Oceanography* 11:2, 102-115.
- Schulenberger, E. 1978. Vertical distributions, diurnal migrations, and sampling problems of hyperiid amphipods in the North Pacific central gyre. *Deep-Sea Research* 25: 605-623.
- Scott, J.S. 1973. Food and inferred feeding behavior of northern sand lance (*Ammodytes dubius*). *Journal of the Fisheries Research Board of Canada*. 30: 451-454.
- Simard, Y., and D.L. Mackas. 1989. Mesoscale aggregations of euphausiid sound scattering layers on the continental shelf of Vancouver Island. *Can.J. Fish. Aquat. Sci.* 46: 1238-1249.
- Smiles, M.G. Jr., and W.G. Pearcy. 1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. *U.S. Fisheries Bulletin* 69:79-86.
- Smith, S.E., and P.B. Adams. 1988. Daytime surface swarms of *Thysanoessa spinifera* (Euphausiacea) in the Gulf of the Farallones, California. *Bulletin of Marine Science* 42: 76-84.
- Tanasichuk, R. W. 1998. Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Marine Ecology Progress Series* 173: 181-195.

- Tanasichuk, R.W. (1998a) Interannual variations in the population biology and productivity of *Euphausia Pacifica* in Barkley Sound, Canada with special reference to the 1992 and 1993 warm ocean years. *Mar. Ecol. Prog. Ser.* 173: 163±180.
- Tanasichuk, R.W. (1998b) Interannual variations in the population biology and productivity of *Thysanoessa Spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Mar. Ecol. Prog. Ser.* 173: 181±195.
- Terazaki, M., C.B. Miller. 1986. Life history and vertical distribution of pelagic chaetognaths at Ocean Station P in the subarctic Pacific. *Deep-Sea Research* 33: 323-337.
- Tomilin, A.G. 1957. Kitoobraznye [Cetacea]. Vol. 9 of *Sveri SSSR I Prilezhaschchikh stran* [Mammals of the U.S.S.R. and Adjacent Countries]. Izedatel'stvo Akademi Nauk SSSR, Moscow. 756 pp. (Translated by Israel Program for Scientific Translations, 1967, 717 pp., NTIS No. TT 65-50086.)
- Trevorrow, Mark V., D.L. Mackas, M.C. Benfield. 2005. Comparison of multifrequency acoustic and in situ measurements of zooplankton abundances in Knight Inlet, British Columbia. *Journal of the Acoustical Society of America* 117 (6):3574-3588.
- Trumble, R.J. 1973. Distribution, relative abundance, and general biology of selected underutilized fishery resources of the eastern north Pacific Ocean. Seattle, WA: University of Washington. 178 p. M.S. thesis.
- Tsuda, A., H. Saito, H. Kasai. 1999. Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. *Marine Biology* 135: 533-544.
- Tsuda, A., H. Saito, H. Kasai. 2001. Geographical variation of body size of *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri* in the Subarctic Pacific and its marginal seas: implications for the origin of large form of *N. flemingeri* in the Oyashio area. *Progress in Oceanography* 57:341-352.
- Vermeer, K. 1981. The importance of plankton to Cassin's auklets during breeding. *Journal of Plankton Research* 3:315-329.
- Vermeer, K. 1985. The diet and food consumption of nestling Cassin's auklets during summer, and a comparison with other plankton-feeding alcids. *Murrelet* 65:65-77.
- Vermeer, K., J.D. Fulton, and S.G. Sealy. 1985. Differential use of zooplankton prey by ancient murrelets and Cassin's auklets in the Queen Charlotte Islands. *Journal of Plankton Research* 7:443-459.
- WINGB, . L., and KRIEGERK., J. 1983. Humpback whale prey studies in southeast Alaska, summer 1982. Northwest and Alaska Fisheries Center, Auke Bay Laboratory, NMFS, NOAA, Auke Bay, AK
- Woodhouse, C. D., Jr. (1971). A study of the ecological relationships and taxonomic status of two species of the genus *Calanus* (Crustacea: Copepoda). Ph. D. thesis. University of British Columbia, Vancouver.
- Yamada, Y., T. Ikeda, A. Tsuda. 2004. Comparative life history study on sympatric hyperiid amphipods (*Themisto pacifica* and *T. japonica*) in the Oyashio region western North Pacific. *Marine Biology* 145: 515-527.