Plankton Processes
(Zoogeography on the BC Coast)

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Abstract
The British Columbia zooplankton interact with their physical environment in remarkable ways. The same currents that provide plankters with phenomenal seasonal blooms in productivity are constantly threatening to whisk them away to foreign waters. To persist and thrive in BC’s rich waters, each zoogeographic group has evolved innovative life strategies that scientists are only beginning to understand. The result is a highly structured mosaic of boreal zooplankton communities that finds it hyperbole in the dynamic fjords of the BC coast. All this spatial and temporal variability attracts an ecosystem of predators, including the great whales.

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1 Bangarang Backgrounders are imperfect but rigorous reviews – written in haste, not peer-reviewed – in an effort to organize and memorize the key information for every aspect of the project.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.
Oceanographic Context

Marine biota are closely tied to their physical environment in innumerable ways, and their interaction is particularly strong in the plankton (Mann & Lazier 1996, Yamazaki et al. 2003). The oceanography of the BC coast has been covered in its own Backgrounder, but there are some features that are especially relevant to the geography and population dynamics of zooplankton. Mackas & Coyle (2005), the seminal review of zooplankton geography in BC waters, emphasizes the importance of the following:

1. Coastal upwelling/downwelling,
2. Estuarine circulation driven by freshwater runoff
3. Current interactions with submarine canyons
4. Filaments and meanders in boundary currents.
5. Mesoscale geostrophic eddies.

Latitudinal Differences

The importance of these processes changes by latitude. The BC coast is host to a transition zone between southern and northern oceanic and atmospheric systems whose positions relative to the coast oscillate seasonally and interannually. The result is distinct southern and northern communities.

Off southern BC and Washington state, coastal waters are dominated by wind-driven upwelling for a significant portion of the year (Benmank et al. 1981, Freeland 1983). Nutrients are pumped onshore and upwelled. The buoyancy-driven coastal current, the Vancouver Island Coastal Current (Thompson et al. 1989), exists but is not well established this far south, and waters are low temperature and highly saline (Mackas and Coyle 2005). Much of the deep alongshore flow on the BC coast comes from the California Undercurrent. In the winter, this current shallows and surface flows switch to poleward (Mackas and Galbraith 2002).

Off northern BC and Alaska, onshore downwelling winds prevail most of the year, establishing persistent shoreward and northwestward alongshore transport (Mackas and Coyle 2005). The Aleutian Low overhead brings inordinate precipitation year round, which drives the intense Alaskan Coastal Current (ACC; Weingartner et al. 2005, Mackas and Coyle 2005). In the Gulf of Alaska (GOA), the ACC broadens and occupies most of the continental shelf (Coyle & Pinchuk 2005). Summer upwelling on the northern GOA shelf is episodic and weak, if present at all (Royer 1998). Ekman transport still adds macro-nutrients to the coastal zone in the north via shoreward transport of nutrient-rich but low-iron water from High-Nutrient Low-Chlorophyll regions in the offshore gyre (Weingartner et al 2005, Whitney et al. 2005).

Meridional Differences

Nearshore shelf habitats differ markedly from those offshore in the deep ocean (reviewed thoroughly in Mackas & Coyle 2005). The nearshore environment is generally shallow (with the exception of deep sections of fjords), enabling strong physical and biological interactions with the benthos. Protected from oceanic winds, the mixed layer is usually shallow or absent but a freshwater lens can be found within the fjords. Strong alongshore currents are found, perturbed only by small-scale tidal and wind events and periods of intense freshwater discharge. Thanks to episodic upwelling, nearshore waters enjoy high primary productivity, with strong episodic blooms of large phytoplankton species (Mackas 1992).

Generally, offshore areas are comparatively very large, broad, homogenous and deep. The deep water column suits specialists of diel vertical migration (DVM), which drives considerable interaction between upper and bottom communities. Strong winds maintain a deep surface mixed layer atop a strong pycnocline. Currents are slow and circulate around geostrophic gyre features rather than run equatorward or poleward as those found on the coast. Relative to nearshore habitats, the seasonal signal is weaker offshore (Mackas 1992). Because offshore waters are often iron-limited and strongly stratified, productivity following the spring bloom is lackluster (Mackas and Coyle 2005). The early spring blooms locally deplete nutrients by March and April. Phytoplankton are dominated by small cells and blooms become less frequent. Periodic wind events temporarily degrade the pycnocline and allow nutrients to leak into the photic zone (Mackas and Coyle 2005). Productivity is less variable throughout the year but there is still a steady increases throughout the summer as episodic shoreward transport occurs (Mackas 1992). An annual productivity maximum occurs in September (Mackas 1992).
The Problem of Retention

The geography of zooplankton communities is governed as much by physical forcing as it is by day-to-day trophic interactions (competition and predation; Mackas et al. 2000). Zooplankton typically swim one to a few centimeters per second and lack the sensory capacity to detect the speed and direction of the large horizontal flows in which they live (Mackas and Coyle 2005). But for communities between the mainland and the continental margin, those flows can easily move zooplankton between starkly different environmental conditions within a single generation – or even a single life stage (Mackas and Coyle 2005). Seasonal alongshore currents can move surface zooplankters tens of kilometers to the north or south in a day and cross-shore currents, which are particularly important in neritic environments like fjords and straits, can do the same (Mackas and Coyle 2005). Seasonal seaward winds are often countered by shoreward forcing later in the year, but the duration and intensity of the opposing processes are almost never equivalent (Mackas and Coyle 2005). Other current features like mesoscale eddies add to the fray; eddies trap nearshore species within their warm core and sweep them offshore, entraining shelf and slope species as they go (Mackas and Galbraith 2002).

The problem of retention unites vertical and cross-shelf patterns and will inform all aspects of the biogeography of BC’s zooplankton. The persistence of geographically stable populations depends upon consistent exposure to the same variety of environmental conditions and consistent access to nutrients, prey, and conspecifics for reproduction. How then do planktonic species persist if currents are constantly challenging their spatial retention? Margin, shelf and neritic species must achieve retention and life-cycle closure over the time scale of a full generation (several weeks to a year). This problem is particularly acute for nearshore species who are most exposed to strong seasonal currents (Mackas 1992, Kline 1998). It is even worse for those established in BC’s fjords. For benthic meroplanktonic species whose larvae have only a few days to combat advection and settle within their historical range, the critical time window is very much shorter (Mackas and Coyle 2005).

Currents can be particularly challenging for those species who have specialized to proliferate in the surface Ekman layer or in upwelling zones, where surface currents are strongly seaward at certain latitudes (Mackas and Coyle 2005). Many zooplankton life cycle events occur in spring (probably to take advantage of the seasonal increase in food availability) at about the same time wind and current patterns are undergoing rapid seasonal transitions (Mackas and Coyle 2005). Because life cycles and depth distributions are seasonal, the retention problem could drive “large match-mismatch variations in distribution and survivorship of both zooplankton and their predators” (Mackas and Coyle 2005).

Observations

The problem was first posed by Hardy (1956) and is given an excellent review in Mackas and Coyle (2005). It has been explored in many papers in between, including Peterson et al. (1979), Mackas (1992) and Peterson (1998), among others.

The lack of retention has been observed or inferred in many studies, adding to the mystery of how it occurs nonetheless. As established above, southern BC waters experience large inputs of upwelled water (and nutrients) to the continental shelf in spring and summer (Mackas et al. 2000). Phytoplankton biomass is high, especially in mid- to late summer, and there is ample food to support the growth of herbivorous zooplankton (Mackas et al. 2000). However, instead of seeing a subsequent increase in zooplankton biomass throughout the summer, this upwelled water “washes out” neritic surface populations into oceanic waters throughout the course of the productive season, causing a coastal decline in grazer biomass (Mackas et al. 2000). Upwelled water, containing relatively little zooplankton, replaces this sea-borne water, and zooplankton biomass falls in May and June at rates comparable to the expected autumnal decline (Mackas 1992).

The advection of nearshore species into offshore waters effectively “dilutes” nearshore populations, a process that plays a critical role in coastal ecology, and is thought to govern coastal zooplankton abundances moreso than predation (Mackas et al. 2000). Both BC and the GOA experience summer-time declines in “shelf” species, though the mechanisms in each region differ. On the BC coast it is a result of upwelling, offshore advection, and
subsequent dilution (Mackas 1992). In the GOA, declines are probably due to the cross-shelf broadening and mixing of the alongshore Alaska Coastal Current combined with biological effects like predation and food limitation (Coyle et al. 2005).

As seaward advection causes nearshore populations to decline, their influence offshore is expected to increase. Mackas (1992) found that offshore zooplankton biomass increases rapidly from February through April due to local blooms, but then continues to increase slowly through August-September due to the import of “shelf” species. Offshore species are thus forced to compete with shelf species (Mackas et al. 2000). At any one time, the zooplankton in an area can be composed of residents and advected immigrants in proportions that vary seasonally (Mackas and Coyle 2005). This has been observed in Prince William Sound (Kline 1998).

In periods of downwelling (winter to the south and most of the year to the north), the converse occurs: offshore species are advected inshore. Each year the Alaskan continental margin receives a large advective input of large oceanic copepods in the spring (e.g., Neocalanus; Cooney 1986) that dissipates throughout the summer (Coyle and Pinchuk 2003).

**Solutions**

_Evolutionary adaptations reflect what has happened persistently and repeatedly in the past._

-Mackas and Coyle (2005)-

Because BC zooplankton are obviously persisting, we know that advection away from their preferred habitats is countered by some reverse process. On the BC coast, most established currents have associated countercurrents: the seaward flow of estuarine circulation has a deep shoreward flow; to the south, equatorward flows in the summer are paired with winter poleward flows. These countercurrents, particularly deep shoreward flows, surely are involved in reseeding and retaining zooplankton species in coastal habitats (a hypothesis developed by Peterson et al. 1979, Mackas 1992, and Peterson 1998). Mesoscale estuarine-type circulation therefore create an annual cycling of neritic and oceanic planktonic species, with poorly understood implications for seasonal succession and the adaptive life histories of resident species (Mackas et al. 2000, Mackas & Coyle 2005).

This hypothesis requires that affected species exhibit behaviors that are timed well enough with onshore-offshore flow regimes to survive throughout the cycle and achieve retention. Mackas and Coyle (2005) group these behaviors into two categories:

- Diel and ontogenetic vertical migrations that span shears of horizontal currents.
- Life cycle timing, seasonal dormancy and reproductive strategy.

To emphasize, this idea that vertical behavior and phenology serve to achieve retention hinges entirely upon exact timing, especially in dynamic environments like coastal BC (Mackas and Coyle 2005). Lu et al. (2003) observed that euphausiid larvae are transported shoreward before the spring transition and seaward after it. If eggs hatch at the wrong time, the effect could be disastrous for the population.

The potential of certain behaviors to achieve retention has been tested using computer modeling with encouraging results (Wroblewski 1982, Batchelder et al. 2002), and some isotope data also support the hypothesis (Kline 1998), but it has yet to be tested in the field.

**Vertical Behavior**

The vertical structure of seaward and landward currents in estuarine conditions makes it easy for zooplankton to swim vertically between very different transport regimes (Mackas and Coyle 2005). Most continental margin, shelf and neritic zooplankton exhibit vertical position behavior that could, in theory, enhance their probability of spatial retention and life-cycle closure (Mackas and Coyle 2005).

Avoidance of the surface layer where currents are strongest should reduce transport speed and favor local retention (Mackas and Coyle 2005). Diel vertical migrators, with mesopelagic depth preferences in the day,
would seem less vulnerable to being flushed from the sound by surface advection and storms (Coyle et al. 2005). If they do become advected, morning migration below the halocline will advect species back towards shore. In addition to shoreward bottom currents, internal wave trains at depth can aggregate, accelerate and transport zooplankton at depth (Pineda 1999, Shanks 1983).

Deep zooplankton scattering layers are commonly observed in BC fjords; many species composing this layer perform DVM into surface waters at night. The vertical behavior of a species varies with ontogenetic phase, local water properties, season, regional plasticity (e.g. for copepods, Falkenhaug et al. 1997; for euphausiids, Regan 1988). 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). Other species of pteropods, chaetognaths, ctenophores, and cnidarian are sometimes present, and known to migrate diurnally from the surface through depths of 250m (Trevorrow et al. 2005).

Because patterns in vertical migration are linked to feeding modes, we can infer that feeding modes also govern a species’ susceptibility to offshore advection. Herbivorous zooplankton are more dependent upon surface waters than omnivorous or detritivorous species. In Dabob Bay, herbivorous Calanus spp. migrated to the upper 50m at night, while the omnivorous Metridia lucens, which feeds upon fecal pellets, detritus and radiolarians, was less associated with seaward-flowing surface layers (Osgood & Frost 1994). While both species vertically migrate, the different depth ranges they inhabit may affect their cross-shelf distributions (Coyle et al. 2005).

Latitudinal gradients in day length can have important effects on migration/advection interaction. The timing of DVM is governed by day-length, which may serve to achieve retention over the course of a year. In the summer, when days are long, nights are short, and an upwelling regime is in place, zooplankton spend more time at depth in shoreward-flowing currents. In the winter, when days are short, nights are long, and downwelling is occurring, zooplankton spend more time in the surface waters that have switched to flowing shoreward flow (Mackas and Coyle 2005). In both scenarios, daily horizontal movements are “two steps shoreward, one step back.”

The annual cycle of Metridia pacifica is an example of this. During the longer nights of winter and early spring, M. pacifica probably spend more time in surface waters. While winter storms do mix waters across the shelf (Coyle et al. 2005), there is little risk of offshore advection in the absence of upwelling conditions. The cross-shelf mixing erases any significant cross-shelf differences in abundance. As day-length increases, M. pacifica are forced to spend a greater portion of their diurnal cycle in their deep daytime habitat. As winds relax and discharge increases in summer, the along-shelf transport weakens, resulting in a net onshore transport of sub-halocline water over the shelf (Weingartner et al. 2005). Metridia are probably transported onshore with bottom waters and aggregate on the inner shelf during spring and early summer (Coyle et al. 2005).

**Phenology**

Because the reproductive state of zooplankton life stages affects their vertical behavior, it follows that the timing of their ontogeny affects their spatial retention in neritic waters. It is thought that shelf species that have been advected offshore in a seasonal surface currents replenish their larval bank on the inner shelf by remaining in a landward bottom current at depth during a diapause stage (Peterson et al. 1998, Mackas & Coyle 2005). While summer surface currents are being pumped seaward, the water underneath is flowing back to shore and contains a mixture of overwintering zooplankton species (Coyle et al. 2005). This explains how many of the dominant northeast Pacific copepod species spend their early life stages almost entirely within the seaward surface currents in the upper 50m but are found again in nearshore waters year after year (Mackas and Coyle 2005).

During cross-shelf surveys in the Oregon coastal upwelling system, Peterson et al. (1979) found that stage 5 copepodids of C. marshallae were found offshore, while eggs and nauplii were found at the surface very nearshore. Drawing on work by Peterson & Miller (1976) to explain this strange phenomenon, they suggested that overwintering C5 copepodids returned to shelf habitat by remaining at depth and being advected in deep
shoreward flows. Wroblewski (1982) used computer models to test the viability of Peterson’s conclusion, with positive results.

The three most common subarctic copepod species (Neocalanus plumchrus, Neocalanus cristatus, Eucalanus bungii) share a common life history: several summer generations followed by prolonged and deep ontogenetic migration and autumn-winter dormancy (Mackas et al. 2000). At the onset of the upwelling season, surface-frequenting adult Neocalanus species in the Gulf of Alaska are among those advected out to sea. Then, between May and July the Neocalanus begin their ontogenetic migration out of the surface waters to enter their C5 diapause (Coyle et al. 2005). Diapausing animals on the shelf are thought to reside in the bottom layer below the halocline, which is moving shoreward (Coyle et al. 2005). They are therefore likely to concentrate in the submarine canyons that cross the shelf. Bottom water renewal in the coastal inlets would then reseed deep layers with overwintering Neocalanus C5s, adding to reproductive populations for the following cycle (Coyle et al. 2005). In Prince William Sound, overwintering copepods contain isotope tracers typical of offshore habitats (Kline 1998).

Returning to Metridia lucens a deeper-dwelling omnivore studied in Dabob Bay, WA: this species does not appear to enter a diapause state (Osgood & Frost 1994). The fall and winter population was chiefly adult females which mostly remained at depth and were reproductively immature. Nauplii were found on all sampling dates, meaning reproduction never ceased (Osgood & Frost 1994). By remaining at depth, this species was able to avoid offshore advection and could therefore afford a more continuous turnover of generations and a less rigidly scheduled ontogeny.
In contrast, euphausiids 1) do not have deep diapause stages in their life cycle, 2) their larvae are restricted to the upper 100m (Kathman et al. 1986), and 3) all life stages in general are more restricted to surface waters. They must therefore rely more on vertical migrations for retention. This may explain why BC euphausiids over the shelf appear more dominant in areas where offshore advection (and hence, upwelling) is minimal (Mackas et al. 2000).

Other phonological tactics may be invoked to achieve retention. Some species phase their primary reproductive activities before the strongest upwelling (Connolly et al 2001). In the California Current behavioral aggregation occurs at the upwelling front, which transgresses shoreward during episodes of weakened alongshore wind stress and returns advected species closer to land (Roughgarden et al. 1988).
Zoogeography

Spatial variability in zooplankton is small compared to its variability over the course of a year (Mackas & Anderson 1986), but geographic patterns are still stark.

Patterns

The interaction of latitudinal and meridional patterns creates four zoogeographic provinces in the northeast Pacific: boreal coastal, boreal offshore, southern coastal, and southern offshore (after Mackas and Galbraith 2002).

Latitudinal

General characteristics of the zooplankton community change with latitude, but not as markedly as the cross-shelf cline discussed below. Some taxa can be found in both the Gulf of Alaska and off the west coast of Vancouver Island (Coyle et al. 2005). That said, the differences can be stark in some areas: most California Current species are rare or totally absent from the Alaska Coastal Current in the Gulf of Alaska (Cooney 1986, Coyle and Pinchuk 2003). The southern zooplankton biota is characterized by copepods and chaetognaths typically endemic to the California Current. To the north is a subarctic species complex, characterized by alternating abundances of euphausiids and subarctic copepods (Mackas et al. 2000). Euphausiids are generally more abundant further north and inland along the BC coast (Mackas and Galbraith 1992, Flinn et al. 2002). This suggests that fin whales may prefer the higher-latitude coastal corridor as a feeding ground.

North-south patterns are influenced by seasonal alongshore currents. After months of strong winter polar transport in surface coastal waters, the southern zooplankton endemic to the California Current and more offshore waters are carried north and inland, with the ironic result that “warmer” species are found in the wintertime waters of Oregon, Washington and British Columbia (Mackas and Galbraith 2002). This is especially pronounced in “warm” species that dominate over the continental margin, where poleward transport is strongest (Mackas and Galbraith 2002).

Interannual and decadal climatic variations cause the boundary between north-south modes in meteorology, oceanography, and zooplankton to oscillate up and down the B.C. coast, with a transition zone roughly near Haida Gwaii and Hecate Strait (west of the Bangarang study area)(Crawford et al. 2007, Lucas et al. 2007). This planktonic transition zone probably corresponds to transitions in higher trophic levels. While most zooplankton studies have taken place in the Vancouver Island area and in the Gulf of Alaska, relatively few have been conducted in the expansive coastline in between, particularly within the transitional inlets.

Meridional

The cross-shelf distribution of species is influenced by their depth preferences, vertical migratory behavior, salinity-temperature preferences, water-mass distribution and movement (Coyle et al. 2005). Three cross-shelf regions can be considered: the inner shelf, outer shelf (which, in the Gulf of Alaska, is delineated by the western boundary of the ACC), and the continental margin (slope). Of these, the inner shelf has the lowest average biomass, the narrowest seasonal peak in productivity (May-June, coinciding with the timing of the upper layer temperature maximum), and the lowest winter levels (Mackas 1992). Biomass in the southern outer shelf region has been observed to be much greater than the inner shelf and slightly higher than the shelf break (Mackas 1992). Inner and outer shelf biomass peaks had the same timing (May-June), but the subsequent biomass decline was less dramatic to seaward, probably due to the stronger surface currents near-shore that advect herbivorous zooplankton out to sea even as dissolved nutrients and phytoplankton biomass increase (Mackas 1992).

In evolutionary response to near-shore oceanography and the imperative of retention, coastal zooplankton have shorter generations, are smaller, are less diverse, rely more on phytoplankton in their diets, have restricted vertical ranges and are have more facultative (flexible) ontogenetic timings. The stratified, less productive and deeper offshore waters support zooplankton with longer generations, deep and prolonged pre-adult ontogenetic
migrations, larger bodies, high diversity, more carnivory, and common and extensive vertical migrations (Mackas and Coyle 2005, McGowan & Walker 1985).

From Mackas and Coyle (2005):

<table>
<thead>
<tr>
<th>Environment</th>
<th>Nearshore-continental shelf</th>
<th>Offshore—deep ocean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life span/life history</td>
<td>1–4 generations year⁻¹</td>
<td>1–2 generations year⁻¹</td>
</tr>
<tr>
<td>Individual body size</td>
<td>Smaller than offshore, similar to further south</td>
<td>Large</td>
</tr>
<tr>
<td>Taxonomic richness</td>
<td>Slightly less diverse</td>
<td>Slightly more diverse</td>
</tr>
<tr>
<td>Feeding type</td>
<td>Omnivorous, but obtaining much of their ration from phytoplankton</td>
<td>Mix of omnivores and carnivores, with omnivores obtaining much of their ration from micro-zooplankton</td>
</tr>
<tr>
<td>Major predators</td>
<td>Cnidarians, ctenophores, chaetognaths, juvenile and adult epipelagic fishes</td>
<td>Chaetognaths, crustacean zooplankton, migratory micro-nektob</td>
</tr>
<tr>
<td>Vertical migration</td>
<td>Less consistent and narrower vertical range, may aid spatial retention</td>
<td>Very common, probably mostly for predator avoidance</td>
</tr>
<tr>
<td>Ontogenetic</td>
<td>Facultative, may aid spatial retention</td>
<td>Obligate and deep when present, aids seasonal survival</td>
</tr>
</tbody>
</table>

Table 2: Comparison of life history, morphological, and trophic characteristics of nearshore (continental shelf) vs. deep ocean copepods in the NE Pacific.

In the north, the mid-shelf boundary of the Alaska Coastal Current provides a strong meridional transition zone (Cooney 1986). Overall abundance tends to be greater within the productive Alaskan Coastal Current than in adjacent offshore waters (Nap et al 1996, Coyle and Pinchuk 2005). Inland of the mid-shelf break, in the ACC and the coastal fjords, a neritic community prevails (Pseudocalanus spp., Metridia pacifica, Calanus marshallae, etc.). Seaward of the ACC boundary, oceanic species dominate (e.g., Neocalanus cristatus, Eucalanus bungii). Between the two realms is a mid-shelf transition zone with a mixture of the two communities (Coyle et al. 2005). Because the ACC broadens over the shelf throughout the summer upwelling season, highest neritic abundances occur in the early upwelling season, and the ratio of oceanic to neritic species fluctuates with the breadth of the transition zone.

In both the north and south, the continental margin serves as a transition zone for nearshore-offshore communities, but the cline is complicated, nonmonotonic and often disrupted (Mackas and Coyle 2005). The community found at the margin includes mixtures of species endemic to both nearshore and open-ocean environs, and meroplanktonic larvae of shallow-water benthos and demersal fish are abundant in the spring and early summer (Mackas and Coyle 2005). On the shelf side of the margin zone, ctenophores and cnidarians are
often dominant zooplankton predators, especially in “green-water” conditions (Suchman and Brodeur 2003, Larssen 1987). Seaward of the continental shelf break, migratory micro-nekton and chaetognaths become more important.

At certain times of the year offshore species can cross the transition zone and invade shelf habitats. During spring, shelf biomass in the Gulf of Alaska is dominated by offshore species that are advected in during spring (Coyle and Pinchuk 2003, Incze et al 1996, Cooney 1986, 1988).

**Vertical**
The vertical distribution of water properties, especially salinity, temperature and dissolved oxygen, serve to structure the geography of nearshore zooplankton communities. In shelf waters, the thermocline and halocline are often decoupled. In summertime Gulf of Alaska, when solar radiation is more intensive, a shallow seasonal thermocline (20-30m) is in place, while the halocline occurs deeper (typically >60-90m). Several zooplankton species that can tolerate lower salinities, including *Neocalanus cristatus* and *E. bunggi*, occupy the space between these two clines (Coyle et al. 2005). Also, the depth and stratification of the pycnocline can define sinking rates and resting depths for overwintering species, whose diapause stage densities are thought to be species-specific (Davies et al. 2014). This likely has important implications for the attraction of these coastal habitats for migratory predators like whales.

**Anomalies**
The strongest anomalies in biomass and community composition occur on the seasonal scale. As may be expected, there is a winter minimum and spring-summer maximum of zooplankton biomass in BC waters (Mackas 1992, Thomas & Emery 1986). On the interannual scale, zooplankton anomalies have been correlated with changes in several physical environmental indices.

Decadal oscillations in oceanographic conditions along the northeast Pacific coast cause region-wide shifts in zooplankton communities. In a 15-year study of large interannual variations in species biomasses, Mackas et al. (2000) observed two dominant modes: the first, a southerly copepod and chaetognath fauna including several species normally endemic to the California Current, and the second consisting of boreal shelf species and inversely fluctuating abundances of euphausiids and subarctic copepods. During warming events, southern species are transported into BC waters via the shoaling, poleward California Undercurrent and become major components of zooplankton biomass (Mackas 1992).

Interannual variation is compounded by the periodic development of mesoscale, anti-cyclonic eddies in BC waters (Thomson 1984; Ikeda et al. 1984, Crawford 2002). These can persist for several years and occasionally mix neritic communities into blue waters offshore, adding ephemeral spatial heterogeneity in community structure (Mackas & Galbraith 2002, Coyle et al. 2005). A downside to pronounced vertical behavior is that eddies seem especially effective at entraining and retaining species that undergo DVM (Mackas and Galbraith 2002).

The generally dominant zooplankton taxa in the northeast Pacific fjordland are euphausiids (the generally offshore *Euphausia pacifica*, the coastal *Thysanoessa spinifera*, and the more southern *T. inspinata*) and copepods (e.g., *Neocalanus plumchrus, N. cristatus*, and *Metridia spp.; Mackas & Tsuda 1999*). In general, these two crustacean taxa have very different life histories and respond quite differently to the periodic forcing along temperate coasts, such that anomalies in their abundance tend to occur inverse to each other (Mackas et al. 2000). Onshore concentrations of euphausiids are known to occur adjacent to an offshore proliferation of copepods (Flinn et al. 2002). The southern dominance of copepods is often coupled with a northerly dominance of euphausiids (Mackas and Galbraith 1992). Strong upwelling seems to favor copepods while weak upwelling favors euphausiids (Mackas et al. 2000). This may seem surprising, considering that *E. pacifica* and *T. spinifera* both inhabit upwelling environments, and within these environments, their adult stages tend to aggregate where upwelling is strongest (Mackas et al. 1997). The relationship between ontogenetic timing and advection probably plays an important role in explaining these inversely related anomalies.
Fjord Factors

In physical, chemical, and biological respects, fjords are bizarre and dynamic environments. Their oceanography has been reviewed in a dedicated Backgrounder. Strong flows are pushed and pulled through confined channels compartmentalized by shallow sills. Substantial freshwater discharge lends unique structure to the water column. The deep variegation of fjordland coasts undoes the homogenizing forces of the shelf's open waters and preserves distinct communities of zooplankton in adjacent inlets (Mackas & Anderson 1986, Burrell 1986). Unfortunately, the zoogeography of plankton in fjords requires high-resolution sampling plans to study, and few such publications were found by this author.

Productivity Patterns

In fjords, copious terrigenous nutrients and extensive mixing (wind-, estuarine- (Mackas et al. 1980) and tide-driven) lead to exceptionally high average chlorophyll concentrations throughout the spring, summer, and early autumn both within fjords (Gilmartin et al. 1984) and on the adjacent inner shelf (Gilmartin et al. 1984, Mackas 1992). Primary production can vary in phase with the lunar cycle (Balch 1981), which is probably quite pronounced in temperate fjords where spring tidal currents can be rapid and can induce strong mixing over constrictions like sills.

In Indian Arm, a fjord in central BC, Gilmartin et al. (1984) found that over 90% of the primary production could be attributed to the nanoplanckton. Harmful algal blooms (HAB) are not uncommon and have recently been observed in the Kitimat Fjord System (this author; Chris Picard, pers. comm.).

Gilmartin et al. (1984) found that the primary factor in controlling primary production was the stability of the water column, which influences the mean light intensity and nutrient supply received by phytoplankters. Heavily silted systems such as glacial fjords are thought to have suppressed fall blooms (Burrell 1986).

In Indian Arm, Regan (1988) concluded that euphausiids species tolerated the seasonal variability of the fjord’s physical environment to varying degrees, and that these tolerances informed the vertical distribution and general abundance of each species. In Saanich Inlet, southern BC, photosynthetic rates begin increasing rapidly in late March, reach their peak in June and July, then fall precipitously from mid-August to mid-September (Hobson 1981). Euphausiid populations in fjords, such as E. pacifica in Dabob Bay, WA, produce a pulse of larvae immediately following the spring bloom (Bollens et al. 1992).

Along-Fjord Patterns

The spatial scale of community variability within fjords is finer than that found on the open shelf (Mackas & Anderson 1986). In Observation Inlet, northern BC, species distribution was consistently structured throughout the fjord (Mackas & Anderson 1986). Euphausiids (primarily *Euphausia pacifica*) were more abundant in the turbid upper reaches of the inlet’s arms, while large-bodied copepods, including *Neocalanus plumchrus*, dominated samples in the seaward portions of the inlet. Also, the euphausiids (and other taxa, including amphipods, chaetognaths, pteropods, and migratory copepods) in the upper inlet were larger, suggesting better survival.

Aggregative Forces

The distribution of biomass within fjords is highly clumped. The intense tidal forcing over the bathymetry of coastal inlets is thought to aggregate zooplankton at the boundaries of water masses, isotherms and bathymetric features (Davies et al. 2014) including fjord sills (Cummins 2003, Ianson et al. 2011). Aggregations of euphausiids along steep bathymetric slopes form and disperse daily (Simard et al 1986, Mackas et al 1997,
Simard and Lavoie 1999). In Knight Inlet, central BC, daytime layers of euphausiids and amphipods have been observed near 70-90m depths, concentrated in the frontal mixing zone at the inlet’s sill (Trevorrow et al. 2005, Ianson et al. 2011). Filter-feeders like mysticetes may be taking advantage of these tidal aggregations to forage more efficiently.

Zooplankton do not always aggregate solely based on food supply; some studies have found their distribution more tightly associated with bathymetry (which may be a proximate variable for some other environmental feature) than primary productivity (Macks et al. 1980). Frontal zones, often centered around the sill at the fjord’s mouth, are characterized by high primary productivity (Steele 1978) but the geography of zooplankton within fjords is often offset from such features (Parsons et al. 1983). In Saanich Inlet, southern BC, the abundance and heterotrophic activity of both euphausiids and large-bodied copepods were found to be higher within more stable waters deeper inside the inlet, away from the phytoplankton maximum found at the sill’s frontal zone (Mackas et al. 1980, Parsons et al. 1970, Parsons et al. 1983). The fact that zooplankton have been found aggregated away from local productivity maxima suggests that forces other than hunger are at work. Perhaps euphausiids and other taxa prefer upper arms of inlets because the turbid water, still with tannins in suspension from the river runoff, provides some refuge from salmonid smelt and other predators (Mackas & Anderson 1986, Healy 1980).

The presence of turbulence may also influence aggregation (Mackas et al 1993, Franks 2001, Tsurumi et al 2005). The relationship of plankton to turbulence is uncertain, and is probably species- and context-specific (Franks 2001). In small-scale turbulence, zooplankters like *Euphausia pacifica* (e.g. Patria and Wiese 2004) can sense and avoid velocity gradients in fluid motion caused by predators (Kiorboe et al. 1999), but in turbulent zones predator presence might be masked by ambient fluid motion. Turbulence theoretically increases encounter rates of predators and prey (Rothschild and Osborn 1998), which may encourage predators to seek out turbulent areas and prey to avoid them (Ianson et al. 2011). Plankters may also avoid turbulence because the velocity shear is uncomfortable and cause them to lose control over their motion (Yen et al 2008), thus impacting their ability to feed (Tsurumi et al 2005). Euphausiids in Knight Inlet were observed in a bottom boundary layer at the sill, below their normal depth preference, into which they must have actively swum (Ianson et al. 2011). This behavior may have served to aid retention near productive features and enhance aggregations in strong flows at sills and on shelves (Ianson et al. 2011).

**Bottom Waters**

Fjord sills are barriers to the exchange of nutrients, salinity and oxygen in the deep waters of fjords. Conversely, sills also contribute to the retention and concentration of river-borne nutrients within fjords, which is a primary cause of their remarkable productivity (Thomson 1981; read the Bangarang Backgrounder “Fjords!” for more.) Stagnant bottom water resides behind sills, largely isolated from the estuarine circulation, and develops unique water properties that serve to structure zooplankton populations within the fjord.

**Oxygen Minimum Layers**

Midwater hypoxic layers are common features in deep coastal inlets like fjords (Mackie & Mills 1983). Such Oxygen Minimum Layers (OMLs) provide vertical habitat structure that can govern community interactions (Hutchinson 1957, Childress and Seibel 1998, Fujiwara and Yamada 2002). Differences in species-specific oxygen tolerances (Keister et al. 2000; Taylor & Rand 2003, Bell & Eggleston 2005) may stratify zooplankton communities and separate predators from their prey in low-oxygen refuges (Horppila et al. 2000; Klumb et al. 2004; Bertrand et al. 2006). The presence of an OML has the potential to represent both an upper and lower barrier to diel migrations (Parker-Stetter & Horne 2008). For example, *Euphausia pacifica* has been found to aggregate during the day just above the oxycline in Saanich Inlet (Mackie & Mills 1983).

With metabolic demands as a constraint, OMLs are thought to serve as a seasonal vertical barrier moreso for fish populations than invertebrates (Parker-Stetter & Horne 2008). Nekton may alter their horizontal and/or vertical locations based on oxygen levels (Horppila et al. 2000; Keister et al. 2000) or modify their schooling/swimming behavior (Bertrand et al. 2006; Taylor et al. 2007).
Anoxic bottom waters are common in some fjordlands but are rare in British Columbia (Picard 1961, Thomson 1981). When these features do occur, however, they offer unique niches to residents of the entire water column. DeRobertis et al. (2001) studied bathypelagic amphipods in Saanich Inlet, one of the only BC fjords where the midwater hypoxic layer grades into an anoxic environment at the bottom. The gammarid amphipod *Orchomene obtusus* was found to exhibit a bimodal vertical distribution, with one peak in the midwater hypoxic zone (right above 130m), and a much larger peak (by an order of magnitude) within the anoxia of the seafloor. This peculiar distribution reveals a fascinating reverse vertical migration, in which *Orchomene* dives below the hypoxic zone and enters anoxic waters to feed; its body can withstand these anoxic conditions for about a day before it must return to hypoxic waters to relieve its oxygen debt. This small percentage of time spent at their hypoxic “surface” explains the smaller abundances in the hypoxic layer than at the bottom.

**Refugia**

Cold, deep waters in fjords provide suitable habitat for species that would otherwise require environs typical of higher latitudes. As one of many examples in the Gulf of Alaska, *Parathemisto libellula* is an Arctic amphipod but can occur in the northeast Pacific’s fjords, where deep temperatures are persistently <8 degrees C (Coyle et al. 2005). Such coldwater species probably arrive in fjord deep waters by the summertime transport of bottom waters onto the shelf and into inlets and sounds (Coyle et al. 2005).

Fjords also contain some of the deepest waters on the BC mainland's coast. The deep, dense bottom waters of fjords are an ideal overwintering habitat for diapausng species. In Knight Inlet, for example, a dense population of *Neocalanus plumchrus-flemingeri* copepodid 5’s occurs at depths of 500m in winter and early spring (Cooney et al. 2001). The use of fjords as deepwater refugia may assist in nearshore retention.

The great depth of fjords can be sufficient to accommodate oceanic species who perform obligate ontogenetic migrations. These larger species can establish year-round populations in the deepest inland channels and provide an important food source for coastal predators like juvenile salmon, herring (Mackas and Coyle 2005) and whales.
Literature Cited


Davies, KTA, CT Taggart, RK Smedbol. 2014. Water mass structure defines the diapausing copepod distribution in a right whale habitat on the Scotian Shelf. Marine Ecology Progress Series 497:69-85.


