Krill & Light

(Blind-side samplin' the squirrely buggers)

Eric Keen

Abstract

Adult euphausiids (krill) are probably the most important prey item for humpback and fin whales in the Kitimat Fjord System, but their avoidance makes them extremely difficult to sample thoroughly from small, low-cost platforms like the SV *Bangarang*. But they *must* have a weakness, and we *will* find it! This brief Backgrounder reviews the way avoidance works and why it is so bad for zooplankton studies, then evaluates the efficacy of two possible measures for mitigating avoidance: sampling at night, or sampling with lights. Both would come at considerable expense and risk for the Bangarang – but desperate tows call for desperate measures!

Contents

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[1] **Bangarang Backgrounders** are imperfect but rigorous reviews – written in haste, not peer-reviewed – in an effort to organize and memorize the key information for every aspect of the project.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

Avoidance

The situation

The catch of a zooplankton sampler is not necessarily representative of the water through which it is towed. A variety of processes contribute to the deviance of the sample from reality. Barkley (1972) outlined some of those processes in a basic equation:

Catch = (volume sampled) x (no. of organisms unit volume) x (probability of capture) -- (escapement)

Escapement is the loss of captured organisms through the mesh. The "probability of capture" term can be broken down further into a variety of factors (indeed, Barkley complicates this equation considerably in the details of his paper), but of them avoidance is by far the most influential (Wiebe et al. 1982). Net avoidance – zooplankton actively dodging the net -- is a serious concern in macrozooplankton studies.

Euphausiids, or krill, are excellent at avoiding predators including nets (Brinton 1962). Many species, including the common northeast Pacific species *Euphausia pacifica*, have large eyes that are extremely sensitive to light (Mauchline 1980). They use these eyes to detect the luminescing photophores that bespeckle their conspecifics (Warner et al. 1979) and to maintain a position in the water column within the same low level of light. To stay at a preferred isolume, krill undertake diel migrations on the order of 100m or more (Boden and Kampa 1965). Vision is also an obvious guard against approaching predators (Wiebe et al. 1982).

Krill are also quite sensitive to small-scale fluid motions (Patria and Wiese 2004), including small-scale shear (Kiorboe et al. 1999). This sensitivity serves both to maintain swarm cohesion and to remotely detect nearby predators (Ianson et al. 2011). Euphausiids are usually highly aggregated in the water, leading to patchy distributions on many scales. Such aggregations confer increased surveillance capacity and the ability to respond with advanced, concerted action (Manning 1979). Avoidance responses tend to be an effective defense at the level of both an individual and the swarm.

When krill detect a nearby predator, they exhibit various degrees of avoidance behavior (mysids do too; O'Brien and Ritz 1988). O'Brien (1987b) outlines three such levels of avoidance as observed in *E. superba* and other Antarctic species of krill. The primary and least desperate response (first described in Hamner 1984, then Hanamura et al. 1984) is avoidance, in which krill use their pleopods to swim away and avoid detection by a proximate predator that is not within striking range.

The secondary response (described by O'Brien 1987a) is a more concerted and coordinated escape effort, invoked when the disturbance becomes more intense and the predator comes within striking distance. There are three general forms of this response: flash expansion of a single school (in which the school condenses then suddenly expands using both pleopods and tail-flips; Pavlov 1969, O'Brien 1987a), the splitting of a larger school into smaller coordinated swarms (O'Brien 1987a), and a coordinated but short-lived tail-flip reaction in the region of the swarm closest to the disturbance (Ragulin 1969, Hanamura et al. 1984, O'Brien 1987a and b). The first two forms, flash expansion and swarm splitting, would disorient charging aggressors. They would also require predators like whales to filter a larger volume of water for the same intake of prey and thus degrade the suitability of a prey patch. To counter this, whales have developed a variety of herding behaviors (e.g., humpbacks encircling swarms with their blinding-white pectoral fins, as observed in the Bangarang study area).

The tertiary and most desperate response (first described by Hamner 1984, also observed in Kils 1979, Kils 1981 and Nicol and O'Dor 1984) is an individualized, repeated tail-flip scramble. This last resort can lead to the total disruption of a swarm within ten seconds (Hamner 1984, O'Brien and Ritz 1988).

In the literature

Holt and Tattersall (1905) were one of the first to propose that their low daytime capture rates were due to avoidance. MacKintosh (1934) described *Euphausia superba* leaping backward to avoid the approaching net. Together, Tattersall (1924), Hardy (1936), Moore (1950), Barham (1957), Marr (1962), Fleminger and Cutter (1965), McGowan and Fraundorf (1966), Wiebe and Holland (1968), Pavlov (1969), Wiebe (1971), Kils (1979), Wiebe et al. (1982), Everson (1983), Bityukov (1984), Witek et al. (1985), Everson and Bone (1986), Daly and Macaulay (1988), Mathew (1988), Hovekamp (1989), Daly (1990) and Shaw and Robinson (1998) represent only a fraction of published studies that have observed or inferred that euphausiids were actively avoiding their samplers. Moore (1950) estimated an avoidance factor of at least 10 by comparing catch data and in-situ visual estimates of bioluminescence. Brinton (1967) found associations between avoidance and vertical migratory behavior in euphausiids and incorporated avoidance tendencies into taxonomic/ecological guilds in the southern California Current. Sameoto (1980) was among the first to note that net catches were drastically low compared to biomass estimates derived from concurrent active acoustics. Cochrane et al. (1991) observed the same.

Context-dependence

The impact of net avoidance upon a sampler's performance depends upon many factors (Weibe et al. 1982). These are thought to include time of day (Fleminger and Clutter 1965); light regime of a latitude or season (Isaacs 1965, Hovekamp 1989); moonlight conditions (Shaw & Robinson 1998), tidal state (Shaw & Robinson 1998); size, shape, and color of the net (McGowan and Fraundorf 1966); speed of tow (Brinton 1967); species (Clutter and Anraku 1968); sex or developmental stage of the organisms; their physiological state (Laval 1974); sampling error (Watkins et al. 1985); and absolute density (Boyde et al. 1978). O'Brien (1987b) visualized the context-specificity of the euphausiid avoidance response with this flowchart:
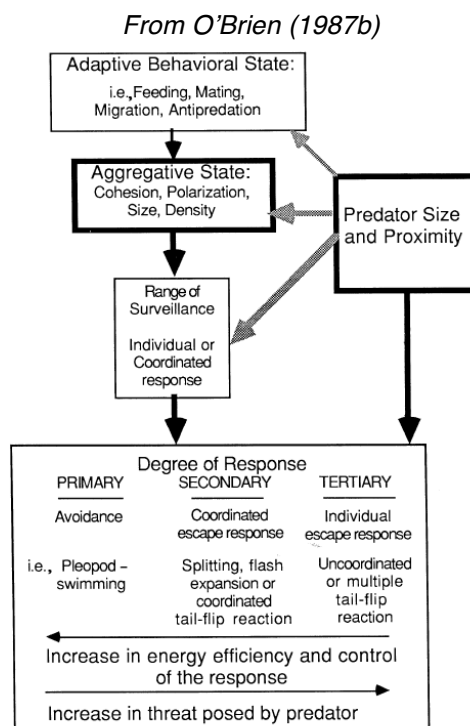
From O'Brien (1987b)

Fig. 2. Flow chart demonstrating the relationships between the major influences determining the degree of escape response in euphausiids. Stippled arrows = feedback path, thickness of arrow = relative importance (subjective).

Avoidance & Error

"The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate to any given problem, so that it catches the right organisms, and rejects others, with known efficiency."

- Barkley (1972)

Avoidance causes a sampler to be selective; it will only catch the species or the life stages that can't avoid it. All samplers are selective in some sense (mesh size guarantees that), but if the selectivity cannot be measured (which for avoidance is obviously difficult; how do you count how many things you aren't catching?), then a serious bias is introduced to results.

The context-dependence of avoidance behavior can be confounded with the natural patchiness of euphausiid aggregations. Patchiness of zooplankton may cause large differences between successive tows taken at a single station (Wiebe 1971, Wiebe et al. 1973, Wiebe et al. 1982, Watkins et al. 1985). This is not sampling error because it reflects the natural distribution of the target population (Wiebe 1982), but when populations are distributed according to life-stage and when avoidance capacity depends on the current behavior of a swarm, it is difficult if not impossible to disaggregate the effects of patchiness from the varying effects of avoidance (Wiebe 1971, Wiebe and Holland 1968).

Active acoustic methods for biomass assessments have suggested that nets grossly under-sample euphausiid stocks (Sameoto 1980, Sameoto 1983, Daly & Macaulay 1988). Daly & Macaulay (1988) found that their plummet net catches were 1/20th of acoustic biomass estimates. However, neither method is perfect; downward-looking acoustics cannot detect zooplankton activity near the surface or concentrations that are below a certain threshold concentration (e.g., 0.2g per cubic meter; Daly and Macaulay 1988). Nets are avoided and therefore selective, and relatively few data are collected for inordinate effort – however, they can sample near the surface and detect very low concentrations, as well as provide life history and size-class information in some cases (Daly and Macaulay 1988). Hovekamp (1989) wrote: "*Comparison with acoustic data (Daly and Macaulay 1988) suggests that even the most careful net sampling seriously underestimates euphausiid abundance. Acoustic techniques appear to be very applicable to euphausiid distribution and abundance study (Macaulay 1977). But the necessity of ground-truthing acoustic data still leaves a need for accurate net sampling.*" It thus behooves researchers to sample using both methods.

Avoidance makes the sampling with single-net systems practically useless in quantifying euphausiid biomass or size distributions in any way that reflects reality (Wiebe et al. 1982). However, diversity surveys and descriptive (relative) patterns in densities and size distributions can be inferred from simple samplers that are not 100% avoided by target organisms.

Mitigation

There are two usual strategies to reduce net avoidance: increase net speed or increase net size (Wiebe et al. 1982). The strategy of increasing tow speed is useful only up to a point; any speeds above 3 knots will risk damage to the specimens, unwieldy wire angles and wire lengths (especially for deep tows), and the increased likelihood of escapement (specimens being forced through and out of the net's mesh)(Wiebe et al. 1982).

Increasing net size can be problematic too. As with high tow speeds, larger nets can be cumbersome for smaller research platforms. Barkley's (1972) avoidance theory indicates that the potential advantage of greater mouth area in a larger net is effectively cancelled by individuals reacting to the approach of the net at a greater distance (Wiebe et al. 1982). That said, size has been found to be influential. Jerde (1967) compared catch rates between a 2.3m^2 micronekton net and 1m^2 macrozooplankton sampler and concluded that adult euphausiids were avoiding his 1m^2 net. However, no difference in the number of species sampled was found between the two net sizes (although the large mesh size of the micronekton net did allow some escapement, which may have reduced the apparent diversity of its catch).

McGowan & Fraundorf (1966) focused on the efficacy of different net sizes in sampling for diversity and abundance, and the susceptibility of various designs to biases introduced by species patchiness and their ability to avoid. Mouth diameters in their study ranged from .2m to 1.4m. Their sampling design held other variables constant, including mesh size (550 micron), tow speed (3.4 km/hr, 1.85 knots, 0.9 m/s) and volume sampled, in order observe the sole effect of mouth diameter on net efficacy and disaggregate biases due to the patchiness of plankton aggregations from those due to active avoidance. The size of the sampling device did in fact have an effect on estimates of zooplankton diversity. With regards to diversity sampling, the nets performed in the following ranked order: 1.4 > 1.0 = 0.4 = 0.8 > 0.6 > 0.2 m. In terms of abundance estimates, the nets yielded biomass estimates that increased with their diameter: 1.4 > 1.0 > 0.8 > 0.6 > 0.4 > 0.2 m. Both patterns could be explained by the fact that the largest macrozooplankton species (which are the best avoiders), are better caught in the largest nets and therefore contribute substantially more biomass to those tows.

Avoidance effects may also be mitigated during analysis; because euphausiid capture efficiency is believed to differ between day and night samples due to visual net avoidance (see next section), some studies (e.g. Mackas et al. 2000) apply a correction factor to euphausiid results.

Two field methods for minimizing avoidance deserve special attention: sampling at night and adding lights to the net. The next sections weigh these options.

Day vs. Night

Many oceanographers have investigated the effect of time of day on rates of zooplankton avoidance. Their results have varied but they fall neatly within a few broad categories.

Published Studies

Catch rates much better at night (esp. for larger krill)
Shaw & Robinson (1998) compared copepod and euphausiid abundance estimates from night and day tows with an oblique BONGO net. At each station, bongo tows were conducted every 2 hours over a 24 hour period in 1994 and 1995. They found that euphausiids were caught much better at night. The maximum night to day (N:D) catch ratios were 10.6 for *Euphausia pacifica* (though they varied by an order of magnitude) and 4.9 for *Thysanoessa spinifera*. They also found that the larger animals have higher catches at night. With the copepods, the majority of calanoid genera had near-equal N:D ratios. Some of the large female copepods (e.g. *Metridia pacifica* or *Eucalanus bungii*) had N:D ratios of 2 to 8, but some smaller calanoid species had higher day catches than night catches. In their conclusion, Shaw & Robinson (1998) recommend "that coastal studies using bongo nets to discretely sample copepods or euphausiids should include a 24 h component in the sampling program to quantify difference between night and day abundance estimates."

Wiebe et al. (1982) compared night and day catch rates of the euphausiid *Nematoscelis megalops* by towing a MOCNESS alternating its configuration between a small ($1m^2$) net and a micronekton ($10m^2$) net. Night catches exceeded day catches, especially with the small net. Wiebe et al. (1982) interpreted this result as greater avoidance during the day.

No day-night difference
Sameoto et al. (1987) compared euphausiid catch rates between day and night tows in the eastern tropical Pacific. Their day tows out-performed their night tows, yielding higher biomass and total numbers of krill. This suggests that avoidance was either non-existent or constant between day and night. It should be noted that rarer species were only caught at night. It should also be acknowledged that a BIONESS sampler (composed of 10 $1m^2$ nets) was used at a speed of 3 knots. With a sampler that size, it is not surprising that avoidance was negligible.

Daly and Macaulay (1988) reported no significant difference between night and day plummet catches of *E. superba*.

Daly (1990) sampled for euphausiids in the Antarctic marginal ice zone both day and night and did not report any catch differences.

Seasonal change in daytime catch performance
Hovekamp (1989) quantitatively assessed the avoidance of euphausiids in various contexts by conducting both up-hauled and down-hauled vertical tows day and night in a deep-water bay of Puget Sound. The predominant euphausiid in his study area was *E. pacifica*, but *Thysanoessa longipes* and *Tessarabrachion oculatus* were also present. Nets were fished as near to noon and midnight as the ship schedule would allow. Hovekamp found that differences between day and night catches varied by season. In the summer, day catches actually performed better: "Daylight increases the catch on the summer cruises almost three-fold. On October 1 daylight makes little difference. Darkness increases average mean catch by factors of three [for down-haul casts] and 12 [for up-haul casts] in late October and February" (Hovekamp 1989). When night catches did out-perform day catches, Hovekamp concluded that avoidance was occurring and that it varied as a function of animal size. He also found that time of day influenced the efficacy of towing methods; down-fishing plummet nets always out-performed up-hauled vertical tows, but even more so at night.

Avoidance varies greatly by life stage

To compare avoidance behavior across euphausiid life stages, Mathew (1988) performed repeated vertical tows from 5m above the seafloor to the surface both day and night. Since the entire water column was sampled, the effect of vertical migration could not be a reason for catch differences (though he did not consider that vertical position may influence the behavioral state and/or alertness of the animals). Mathew found that larvae catches did not differ between day and night tows. Adult (and to a lesser extent, juvenile) catches were much higher in night than in day (2x to 63x difference, depending on species).

Brinton (1967) concluded that in the case of California Current euphausiids, furcilia larvae are less active, more nearly limited to surface layers, and well-sampled both day and night; adults, on the other hand, are avoided more in the day.

Other Taxa
Fleminger and Clutter (1965) experimentally observed the effect of time, day and sampler size on avoidance by copepods and mysids. They found that smaller samplers were more avoided but that avoidance rates were species-specific. Copepods showed no relative avoidance in light. Mysids were up to 8.8x better caught in dark than in light.

Conclusions

Though there are exceptions, the general pattern is that euphausiids are more easily sampled at night, especially the larger ones. The reason for this remains unclear. The most obvious possibility, that it is darker at night and therefore easier to catch krill off-guard, is probably not it. Euphausiids adhere to an isolume and schedule their vertical migrations accordingly, so the light conditions in which they reside should not change between day and night (Westin and Aneer 1987). The ability to detect an oncoming net may be hampered by darkness (Everson and Bone 1986), but bioluminescence on and near a net can render it at least as visible in the dark as in the light (Hovekamnp 1989). Data from Wiebe et al. (1982), when plugged into Barkley's (1972) catch model, suggest that significant avoidance is also happening at night in the absence of sunlight. Wiebe et al. (1982) conclude that the euphausiid *Nematoscelis megalops* detects nets visually, seeing a shadow in daylight and bioluminescence at night. Hovekamp (1989) agreed that euphausiids (in his case, *E. pacifica*) are visually detecting nets and avoiding them accordingly, and that there is no reason to think that visual detection rates differ substantially between day and night.

If the ability to detect a net does not change between day and night, catch differences between day and night must be results of patterns in distribution and behavior (Westin and Aneer 1987). It is possible that more euphausiids are caught at night simply because more have migrated into the sampled depths, though Mathew's (1988) study, in which he samples the entire water column from surface to seafloor and still finds day-night catch differences, suggests otherwise. All things considered, diel change in behavioral state is the most probable culprit. During the day, krill are found at depth in dense aggregations and they are not feeding; they are probably much more alert, preoccupied with becoming prey, and able to detect predators (or nets) from greater distances thanks to the greater surveillance capacity and transitive fluid motions of a swarm. At night euphausiids migrate to the surface and feed intensively, at which time their neighbors become competitors and they disperse in search of forage. They are therefore preoccupied and without the advantages of a swarm. This alone may explain the differences between night and day catches.

Regardless of the reason, night sampling usually yields more success. It should be remembered, however, that euphausiid abundances are substantially underestimated by net sampling, regardless of time of day (Wiebe et al. 1982).

Net-mounted Lights

"It is known from recent evidence (Warner et al. 1979) that decapod crustacea…are easily 'blinded' by even moderate amounts of light. This suggests the possibility of equipping the mouth of a net with a "blinding" light system to be used to periodically illuminate a region ahead of the net with enough light to temporarily blind individuals in the net. With the light out, individuals so affected by the light pulse would be unable to see and, therefore, to respond to the much lower light generated by zooplankton being captured by the net.

We postulate that individuals outside the zone of temporary blindness may respond by electing a startle response, but, because the volume illuminated would be so large, their movement would be random with respect to the volume to filtered by the net. Clearly, considerably more research is required before this strategy could be considered feasible."

- Wiebe et al. (1982)

Published Studies

Do mounted lights increase krill catch rates in net tows? Several but not many studies have investigated this for euphausiids, mysids, decapods and mesopelagic fishes. Their results have varied.

No effect
Clark & Pascoe (1985) used a 70W continuous light (a Viking Sealight diver's light) on a midwater trawl down to 800m; while fish were caught with more success when the light was on, euphausiid and mysid catch rates were not different at all, and decapod catch rates significantly *decreased*. Mesopelagic fish catch has been significantly increased using continuous lights elsewhere (Swinney et al. 1986), but in other studies light had no effect was seen in midwater (800m) mysid and decapod catch rates (Hargreaves & Herring 1992).

Dramatic increase in catch
Sameoto et al. (1993) found that a continuous light (125W, 30 degree beam) atop their BIONESS significantly increased their catch of *Meganyctiphanes norvegica* by 10-20 times. A video camera mounted on the frame revealed that avoidance reactions were greatly reduced with the light on. The light increased capture rates in both day and night sampling, but the light was less effective in nighttime tows. They concluded that "the use of artificial lights markedly reduces net avoidance by euphausiids."

Wiebe et al. (2004) used a high-powered strobe light (150W/s, model 1500SXD, Photosea Systems, flash duration ca. 10–20 μs, 4 second intervals, 30 degree beam) on a MOCNESS frame, which was towed through acoustically detected krill patches between 50 and 90m depth in the Southern Ocean. A flashing light was chosen to minimize the effect of attracting organisms to the net, although no studies have reported attraction of euphausiids to moving light. ROV studies have shown that euphausiids only begin moving toward a stationary light 1 minute or more after the light is established (Sameoto et al. 1990). Wiebe et al. (2004) analyzed euphausiid capture rates for "big" (e.g. *E. superba*, >15mm) and for "small" (5-15mm) species (*E. superba, E. crystallorophias*, and *Thysanoessa macroura*). *E. superba* was caught 2x better with the strobe light on, but there was no difference at all in small euphausiid species. The size distribution within the large and small euphausiid categories did not change with the flashing light on or off.

Conclusions

To this author's knowledge, two studies have confirmed that lights increased euphausiid catch rates; one of these used a strobe light, the other a continuous light. The strobe-light study had increased capture rates only for larger (15mm+) euphausiids; in smaller euphausiids they found no difference. Other studies have found no effect, but no studies reported a negative effect. The effect of strobe vs continuous lighting has never been compared. Current evidence suggests that a continuous light is more effective at capturing small- to medium-sized euphausiids. Euphausiids are probably not attracted to a moving light, so Wiebe et al.'s (2004) purpose of using a strobe light probably does hold; one might also expect a flashing light to be more effective at stunning or confusing krill. All studies to date have used high-power lights (70-150 W), but they have all been conducted on multiple net systems. A smaller light may be suitable for a single net. If the logistical complications of adding a light to a signle-net system are overwhelming, it's not the end of the world; it might not have made a difference anyway.

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