Biological drivers of zooplankton patchiness

Carol L. Folt and Carolyn W. Burns

The plankton of oceans and lakes is distributed unevenly (“patches”), and the importance of spatial heterogeneity to plankton ecology and evolution is well recognized. Recent attention to processes driving zooplankton aggregation stems from the likelihood of patchiness on species interactions, the modelling of population dynamics and assessment of community function. Zooplankton were long considered passive members of patches that were the product of large-scale physical processes. The prevailing viewpoint has shifted to accepting that biological processes also contribute to zooplankton patchiness. The most recent studies even grapple with quantitative assessment of the relative contributions of biology and physics to patchiness and the extent to which biological processes counteract physical drivers. Why has scientific opinion changed?

First, physical processes are proving to be insufficient to explain many spatial patterns (Box 1). For example, recent work showed that large-scale horizontal (100 km) chlorophyll patchiness was better explained by correlation with primary production (a biological process) than with passive tracers (indicative of physical processes). In another instance, zooplankton community structure persisted during horizontal transport for three hours despite periods of turbulent mixing. Only 52% of the spatial variation in community structure was attributable to physical transport; the remaining variance was ascribed to behavioural processes (predation and food searching) capable of counteracting dissipative physical forces.

Second, advanced modelling studies are establishing the inadequacy of physical models to explain some patch dynamics. For example, Zhou et al. examined patch cohesion using data on krill (Euphausiacea) swarms (Box 2) and estimated that the biological component necessary to maintain a swarm was quite large relative to purely physical processes.

Third, novel studies of small-scale biological processes are altering our perception of the behavioural capacity and flexibility of zooplankton. There have also been breakthroughs in field monitoring of both large- and small-scale processes and spatial patterns (Table 1), which have improved our resolution of zooplankton patchiness and spatial dynamics under natural conditions.

What are zooplankton patches and swarms?

Patches, density gradients, aggregations, swarms and layers all refer to zooplankton distributions. Zooplankton are normally sparse in much of the water column, with a few high-density aggregations where abundance can reach levels 10^4 times the median (Fig. 1). Patches are loosely described as the regions of higher abundance, usually composed of several taxa and with 10^2–10^3 times as many phytoplankton as zooplankton.

Density (abundance and spacing between individuals), composition, dimension and persistence are used to characterize patches. The most recent work shows that spacing and composition can be driven by small-scale behavioural processes. The most recent studies even grapple with quantitative assessment of the relative contributions of biology and physics to patchiness and the extent to which biological processes counteract physical drivers. Why has scientific opinion changed?

Box 1. Why is scale important?

The spatial scale over which patchiness is measured defines the patterns and processes that can be observed. To appreciate the significance of biological drivers to zooplankton patchiness, we need an understanding of the way in which their influence on aggregation relative to physical drivers varies with spatial scale. For example, over large scales (10 m to 1 km), behavioural processes (e.g. migration) are believed to be more important than with passive tracers (indicative of physical processes). In another instance, zooplankton community structure persisted during horizontal transport for three hours despite periods of turbulent mixing. Only 52% of the spatial variation in community structure was attributable to physical transport; the remaining variance was ascribed to behavioural processes (predation and food searching) capable of counteracting dissipative physical forces.

Until recently, biological drivers of plankton aggregation were underappreciated, because most studies concentrated on physical processes. New technological advances, novel experiments and theory have shifted focus to the pivotal role of behaviour in plankton patch dynamics. Our review highlights four biological drivers of zooplankton spatial patchiness and brings together recent research on well studied marine and freshwater taxa, primarily copepods and cladocerans. Diverse and powerful behavioural responses by zooplankton to physical and chemical signals are shown to contribute to the formation and breakdown of zooplankton patches over several different spatial scales.

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Spatial structure or dynamics within zooplankton aggregations is not well documented, but patches within patches at scales from <0.5 m to ~10 m to 200 m have been measured.116 (Fig. 2a). Also, little is known about the dimensions or persistence of particular patches.22 Swarms are a special case and provide the most compelling evidence for biologically driven and maintained patchiness (Box 2). They are dense, discrete patches (five to 103 times denser than normal patches), often composed of a single species, sex or instar, where movement and orientation, but not necessarily spacing, are random.1,20 Copepods (e.g. Acartia tonsa) and cladocerans (e.g. Daphnia) only swarm occasionally, but some euphausiids (krill)3 and mysids are obligate swarmers.

What are the most important biological drivers of zooplankton patchiness?

Four mechanisms and their underlying behaviours (i.e. drivers) are consistently cited for their potential to cause zooplankton patchiness: diel vertical migration, predator avoidance, finding food and mating. There is now strong evidence that these drivers alone, or in combination, drive spatial heterogeneity in numerous situations.

Diel vertical migration

Common among all phyla of motile plankton, diel vertical migration (DVM) is the tendency for organisms to swim upwards and downwards at certain times during the 24-h day. As a result of DVM, organisms aggregate periodically and somewhat predictably at certain depths. In this sense, DVM is one of the most widespread and powerful biological causes of patchiness. Zooplankton usually aggregate near the surface by night and at greater depths by day, but patterns differ by taxa and stage. In marine systems especially, the surface by night and at greater depths by day, but patchiness: diel vertical migration, predator avoidance, finding food and mating. There is now strong evidence that these drivers alone, or in combination, drive spatial heterogeneity in numerous situations.

Much current research focuses on distinguishing the physical or biological signals (e.g. predator cues) that alter DVM behaviours (e.g. light responses) and DVM-driven patterns of distribution. For instance, migration amplitude and aggregation depth depend on optical properties of the water and, possibly in cladocerans, on changes in light intensity at dawn and dusk.20 However, the degree of migration can be modified by zooplankton behavioural responses to variations in predators, food, temperature, oxygen and their endogenous rhythms.22-23 Within-taxa differences in DVM appear likely. For example, cladoceran

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Table 1. Technological aids to studies of zooplankton patchiness

(Examples and references are representative only.)
DVM seems to depend on the presence of predator cues, although there are pronounced clonal differences in the extent to which Daphnia phototaxis varies in the presence of predators. A particularly active research area in freshwater systems is in the effect of chemicals from predators (kairomones) on DVM. Kairomones from fish or invertebrates induce vertical migration in many taxa, but not all species or genotypes respond similarly to these signals. Kairomones are far less well studied in marine systems, and the few studies that are available suggest that marine species might not migrate vertically in response to kairomones. If generally true, this raises the question as to why freshwater and marine taxa differ in such a striking way.

**Predator avoidance**

Predators can create patchiness in prey spatial distributions directly, by removing individuals. Indirectly, by eliciting avoidance or escape responses, predators can have even greater effects on zooplankton distributions. For example, Daphnia can aggregate in high food patches in aquaria. Novel research has also recently revealed that predator chemicals increase the tendency of some cladocerans to aggregate horizontally, although predator-induced aggregation might also require light for expression. For example, dense swarms (>4000 per litre) of the cladoceran, *Daphnia longispina*, form in the littoral zone during the day and dissipate at night. These swarms probably coalesce in response to chemicals released by predatory midge larvae (*Chaoborus flavicans*), because *Daphnia* aggregated in aquaria in the light when midge kairomones were present. *Daphnia* did not aggregate in response to kairomones in the dark, even though they are capable of moving horizontally to avoid them. Other cladocerans and some copepods are now also known to aggregate in the littoral zone of lakes by day and to dissipate by night. More work on horizontal aggregation in general and predator-induced horizontal aggregation in particular is warranted, especially with marine species.

The evolutionary explanation for zooplankton aggregation (including DVM) in response to predators is that individual predation risk is diluted at high density. Indirect support for predator avoidance being the ultimate driver of patchiness comes from studies demonstrating energetic and demographic costs of conspecific aggregation. Mutual interference (reduced feeding or reproduction at high conspecific density) might be common among crustacean zooplankton. If so, there is a distinct disadvantage to remaining in dense aggregations, especially if food becomes limited. Nevertheless, these species often aggregate, even in the presence of physical mechanisms to dissipate patchiness, and aggregation occurs independent of mating (juveniles and mixtures of species also aggregate) or of the risk of predator aggregation.

**Locating food patches**

Aggregating in regions of high food concentration is another potentially strong driver of zooplankton patchiness. However, no single pattern of dispersion of zooplankton relative to phytoplankton is routinely measured. Observations differ, partly because of differences in scale and design of sampling programmes. Mechanistic studies might be a more direct approach for examining the influence of food on zooplankton distribution. If food is patchy, then several processes could concentrate zooplankton in regions of high food density. First, physical mechanisms might aggregate zooplankton with algal prey, particularly if the organisms are similar in shape, buoyancy or locomotory ability, and when physical processes overwhelm zooplankton locomotion. Second, most zooplankton orient to food patches under some conditions. Aggregation might result when individuals use similar behaviours to locate, or remain in, food patches. Third, high food concentrations might support high growth, leading to high concentrations of consumers over time.

Copepods appear capable of a greater variety of physical and chemical responses for food location than cladocerans. At different food concentrations, copepods change swimming speeds, turning angles or hopping rates, interspersed bouts of jumping with periods of resting or sinking, and actively locate and remain with food patches over small scales. Copepods, and possibly cladocerans, respond to odour and use chemical exudates to locate food, but pertinent data for Cladocera are scarce.

Some cladocerans do adjust swimming speeds or trajectories at different food concentrations. For example, *Daphnia magna* aggregated in high food patches in aquaria
in the light because individuals reduced their swimming speed at high food concentrations. At low food concentrations, in the light, they swim faster and more horizontally, which also increased the probability of moving to a more favourable food patch. However, in the dark, *D. magna* did not aggregate in patches of high food concentration, raising the question as to why cladoceran aggregation might differ diurnally.

The underlying reasons for differences in day and night aggregation remain speculative. For instance, *Daphnia pulex* also aggregate at high food concentrations and disperse at low food concentrations in laboratory experiments. However, unlike the study with *D. magna*, aggregation in response to food (but not predators) also occurred in the dark. Possibly, both species can aggregate in the dark, but aggregation with food might be observed less commonly at night simply because daphnids swim more slowly in the dark and hence aggregations rarely result. Slower swimming by small cladocerans could also explain why it takes longer for small species to locate and aggregate in food patches.

It now appears that the behavioural responses of zooplankton to food are often moderated, or even eliminated, when predators are present. This might also lead to lack of correlation between spatial distributions of zooplankton and phytoplankton, because daphnids swim more slowly in the dark and hence aggregations rarely result. Slower swimming by small cladocerans could also explain why it takes longer for small species to locate and aggregate in food patches.

Finding mates

Mate seeking is another powerful incentive for aggregation, and swarming and mating are frequently linked. Zooplankton are often sparse in oceans and lakes, and encounters among receptive mates would be rare without aggregative mechanisms.

Advances in understanding the mating behaviours of crustacean zooplankton have arisen largely from studies employing advanced optical systems to study marine copepods (Table 1). For some zooplankton, mating frequency might depend entirely on chance encounters in patches generated by large-scale physical processes and migrations. Others, like many copepods, track mates over small distances by chemoreception, using water-borne pheromone trails, and by mechanoreception, following fluid disturbances produced by species-specific mating behaviours. For example, females of the calanoid copepod *Temora longicornis* respond to male chemical exudates by increasing the frequency of ‘hops’, which alerts males to their presence and increases their chance of encounter. A comparison of flow fields generated by females indicated that such hops created detectable signals in a volume...
Box 3. Future studies in zooplankton patchiness: contrasts, multiple scales and multiple drivers

New technologies, experiments, in situ measures, theory linking biophysical processes and optical techniques to examine individual behaviours have advanced our understanding of biological drivers of plankton patchiness. Several contrasting patterns have emerged that are likely to fuel continued research interest in this topic. Some possible questions include:

- **What are the links between small- and large-scale patchiness?**
  - Current understanding suggests that different behaviours drive patchiness at large versus small spatial scales. Understanding how individual biophysical responses interact with larger physical and migratory processes to drive zooplankton patchiness over all scales is a major goal. Determination of the consequences of spatial patchiness to ecosystem productivity and zooplankton diversity would be of considerable value.

- **How do turbulent motions affect aggregative and dispersive behaviours?**
  - Water movements have the potential to confound mechanore- and chemoperception. Contrasting individual and aggregative behaviours under calm versus turbulent conditions and across taxa will provide insight into the way physical and biological processes form and break down patches and drive aggregation.

- **What is the role of light to aggregative behaviours?**
  - Recent experimental studies contrasting behaviour in light versus dark conditions underscores the need to look at multiple drivers to understand patch dynamics. For example, the tendency to aggregate, the speed of aggregation and the density of individuals in patches tend to increase in the light. Several common patterns can be explained by taking a multiple process approach, and a hierarchy of biological drivers might emerge.

- **How do predators drive aggregation at small versus large scales?**
  - Exploration of the direct effects of predators on horizontal movements and aggregation has just begun. Contrasting responses to different predators (e.g. invertebrate versus vertebrate) across and within taxa and under different biophysical drivers might be explained by taking a multiple process approach, and a hierarchy of biological drivers might emerge.

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