Biological drivers
of zooplankton patchiness

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The plankton of oceans and lakes is distributed unevenly ('patchily'), and the importance of spatial heterogeneity to plankton ecology and evolution is well recognized. Recent attention to processes driving zooplankton aggregation stems from the likely influence 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[1]. 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[1,2] 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 aggregative processes)[5]. In another instance, zooplankton community structure persisted during horizontal transport for three hours despite periods of turbulent mixing[6]. Only 52% of the spatial variation in community structure was attributable to physical transport; the remaining

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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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.[2] 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[11–13] 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 10^3 times the median[21,22] (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[21].

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 (Fig. 2a). As patch density increases, the minimum nearest neighbour distance (MNND) decreases. Species-, sex- and stage-specific MNNDs are linked to taxa-specific fluid disturbance and perception[12,18,29]. However, observed spacing within patches usually exceeds MNND estimates (i.e. densities are lower than predicted). Recent work[29] on copepod reactive distances (Fig. 2b) helps resolve this paradox. Some male copepods sense females at distances well beyond their perceptive range by slowly tracking diffusing pheromone trails[29]. Thus, spacing in patches might relate more to reactive than to perceptive distances[29]. Reactive distances are also hypothesized to vary with the signal type (mate, competitor or predator), highlighting the way in which biological interactions may control patch composition and density. Small-scale turbulence can also affect signal persistence, which might further alter patch density under particular conditions.

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 requires 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 combine with physical processes (e.g. turbulence, currents and eddies) to create spatial heterogeneity[1]. Over smaller scales (1 mm to 10 m), individual behaviours (e.g. mating and predator avoidance) are judged to be crucial, and capable of overriding physical processes in some instances[2].

Linking aggregative processes and their influences across spatial scales is a pressing goal. Ecologists have begun to quantify the influence of behaviours that drive small-scale patchiness to aggregation at greater scales. For instance, point-source releases of dissolved organic matter associated with predation events and cell lysis (at scales <1 ml) might create tiny persistent (several hours) patches of high nutrient concentration that can be exploited by rapidly growing, mobile chemotactic bacteria[3]. Models suggest that this small-scale patchiness would significantly alter the effect of concentration-dependent rate processes (e.g. production, nutrient uptake and predation) at larger scales[4].

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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 10 m to 200 m have been measured[1,16] (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 10^3 times denser than normal patches), often composed of a single species, sex or instar, where movement and orientation, but not necessarily spacing, are random[18,28]. Copepods (e.g. *Acartia tonsa*[29]) and cladocerans (e.g. *Daphnia*) only swarm occasionally, but some euphausiids (krill[7]) 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, advective processes together with DVM control large-scale spatial and temporal dynamics of many species[17].

> **Box 2. Mysids (Mysidacea) and euphausiids (Euphausiacea): the classic swarmers**
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> Mysid (e.g. *Anisomysis* spp.) and euphausiid (krill) swarms form and are maintained in response to individual behaviours and social interactions (active aggregations); hydrological processes only create a background favourable to their formation. Obligate aggregations are caused solely by internal biological mechanisms, whereas those caused by both intrinsic (e.g. migration and dispersion) and extrinsic (e.g. internal waves) factors are facultative[7]. Swarm, school, shoal and cluster describe mysid aggregations, depending on spatial arrangement of individuals, their directional orientation and the extent of group movement. Recent studies of swarm morphology illustrate, or imply, the importance of individual behaviours to the formation and maintenance of mysid and euphausiid swarms.
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> **Mysidacea:** Aggregations can be composed of one dominant species comprising 50–100% of the individuals, and up to five 'guest' species[8]. Swarms differ in shape and mobility, being primarily either stationary or migratory. The degree of mobility changes seasonally and with sexual maturity. Most swarms include various developmental stages, but some swarms consist of a single stage. Swarm volume changes in response to biological drivers such as hunger and predation risk; changes are brought about by alterations in swimming speed and escape behaviours[9].
>
> **Euphausiacea:** Daytime densities of Antarctic krill (*Euphausia superba* Dana)[10] can reach 30 000 m^{-3}. Aggregations range from small, discrete swarms and schools to layers and superswarms that extend horizontally for several kilometres. These layers vary in size, sex, maturity and moult and feeding states, and comprise a series of krill swarms that have touched but not merged, so that the properties of the individual swarms are retained.

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[30]. However, the degree of migration can be modified by zooplankton behavioural responses to variations in predators, food, temperature, oxygen and their endogenous rhythms[31,32]. Within-taxa differences in DVM appear likely. For example, cladoceran

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Table 1. Technological aids to studies of zooplankton patchiness[a]

Technology	Knowledge gained	Refs
Spatial Information Preservation method (SIP): rapid freezing of water samples to preserve 3-D particle distribution	Spatial distributions and abundance of microorganisms (bacteria, flagellates and phytoplankton); nanoscale patchiness	4
Laser-illuminated, optically-synchronized, single 3-D video recording system and blue laser central positioning of zooplankton	3-D time series of copepod movements during mating	11
In situ video camera with opposing stroboscope produces dark-field images of plankton >0.3 mm that can be used down to 100 m depth	Distribution and abundance of plankton >0.3 mm; patchiness and aggregations; *in situ* view of pelagic environment experienced by zooplankton	13
Continuous, high-speed zooplankton sampler (U-Tow): collects discrete samples at a range of depths	Spatial distributions and abundance of species; size and composition of patches	14
Moored, Acoustic Doppler Current Profiler (ADCP)	Time-course of appearance and disappearance of dense aggregations of zooplankton at depth	15
Video Plankton Recorder (VPR): towed video microscopy	Sizes, composition of zooplankton patches in the sea such as taxa-specific copepod aggregations <20 cm	16
Large-volume, water-filled towers with control of amount and vertical position of temperature, light and food; video cameras used; for example, Plankton Towers (Ploen, Germany), Aquatron (Halifax, Canada)	Locomotion behaviours of zooplankton groups and individuals (vertical migration speeds, directions, turns, etc.); responses to physical and chemical gradients at natural scales	17
Laser-illuminated, electronically synchronized, dual CCD (charged-coupled device) camera, video recording system	Positions of individual copepods (nauplii, copepodites) in a swarm; nearest neighbour distances; speeds of swimming, sinking and jumping	18
2-D and 3-D filming combined with automatic frame-by-frame analysis: sufficient resolution to distinguish moving appendages and features for individual animal recognition	Swimming speeds, paths and turns of individuals; quantification of behavioural responses that alter encounter probability in response to chemical cues	19
Particle Image Velocimetry (PIV)	Hydrodynamic signals created by short-lived movements of individual zooplankton	20

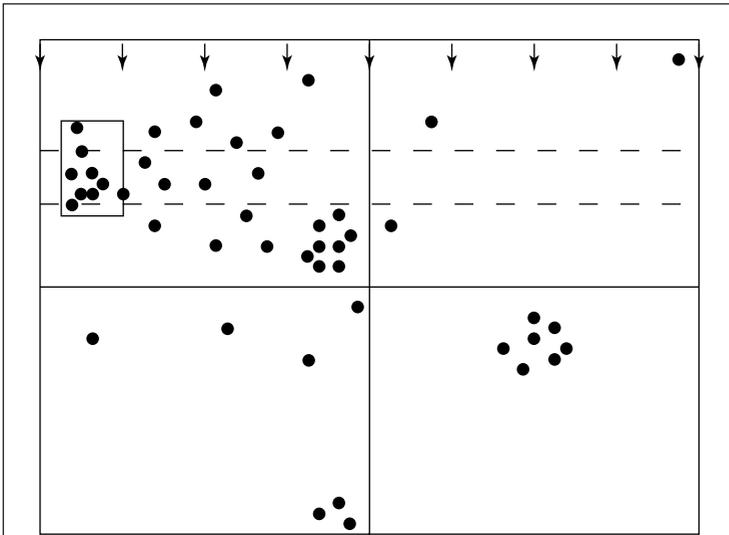[a]Examples and references are representative only.

Fig. 1. Diagram of a 'typical' zooplankton spatial distribution for species A (filled circles). Each of the four large boxes represents a plankton trap or tow sample. Densities of A in 75% of the sampled area are less than the average (12 per sample). Smaller-scale patches (indicated by the small box) would not be discerned from these four samples. Arrows depict the greater sampling resolution that is possible using new techniques; dashed lines represent a transect sampled acoustically. Although the persistence of most zooplankton patches is not well known, numerous studies show that this level of heterogeneity is common[1,21]. Individual membership in patches might change but overall spatial configuration is more stable. Precise estimates of patchiness depend on the scale and conditions under which they are measured (Box 1), and evidence suggests that patchiness is greater under calm conditions or when measured over larger spatial scales[1,21,22]. The merits of several statistical measures routinely used to characterize patchiness have been compared by Pinel-Alloul[1]. In this illustration, Lloyd's 'patchiness index'[1] is ~1.8, which means that individuals are aggregated and that they experience a density that is actually 1.8 times greater than the average.

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[33].

A particularly active research area in freshwater systems is the effect of chemicals from predators (kairomones) on DVM. Kairomones from fish or invertebrates induce vertical migration in many taxa[25,34], but not all species or genotypes respond similarly to these signals[32,33]. 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[35]. 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[21]. Indirectly, by eliciting avoidance or escape responses, predators can have even greater effects on zooplankton distributions (e.g. by triggering DVM, which, in turn, results in large-scale aggregative patterns). Predator avoidance also regulates movement at smaller scales (<10 mm) in ways that influence aggregation. Known responses include escape hops, increased swimming speeds and vertical movements or a halt to movement, each of which affects aggregation and spacing. However, new research has revealed taxa-specific responses to mechanical disturbances, such as those produced by predators. Species from more 'energetic, physical regimes' require larger mechanical stimuli to elicit an escape reaction, or respond only when closer together[12].

Novel research has also recently revealed that predator chemicals increase the tendency of some cladocerans to aggregate horizontally[36], 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[24]. *Daphnia* did not aggregate in response to kairomones in the dark, even though they are capable of moving horizontally to avoid them[24,37]. Other cladocerans and some copepods are now also known to aggregate in the littoral zone of lakes by day and to dissipate by night[23]. 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[38,39]. 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[21]) 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 spatial scale and design of sampling programmes[1]. 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[29]. First, physical mechanisms might aggregate zooplankton with algae passively, 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, intersperse bouts of jumping with periods of resting or sinking, and actively locate and remain with food patches over small scales[40]. Copepods, and possibly cladocerans, respond to odour and use chemical exudates to locate food[41,42]; however, pertinent data for Cladocera are scarce.

Some cladocerans do adjust swimming speeds[43,44] or trajectories[44,45] 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[44]. At low food concentrations, in the light, they swam 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*[37] also aggregate at high food concentrations and disperse at low food concentrations in laboratory experiments. However, unlike the study with *D. magna*[44], aggregation in response to food (but not predators) also occurred in the dark[37]. Possibly, both species can aggregate in the dark, but aggregation with food might be observed less commonly at night simply because daphniids 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[44].

It now appears that the behavioural responses of zooplankton to food are often moderated, or even eliminated, when predators are present[37]. This might also lead to lack of correlation between spatial distributions of zooplankton and phytoplankton in the presence of predators – a topic of current attention.

Finding mates

Mate seeking is another powerful incentive for aggregation, and swarming and mating are frequently linked[34]. Zooplankton are often sparse in oceans and lakes, and encounters among receptive mates would be rare without aggregative mechanisms[11].

Advances in understanding the mating behaviours of crustacean zooplankton have arisen largely from studies employing advanced optical systems[27] 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
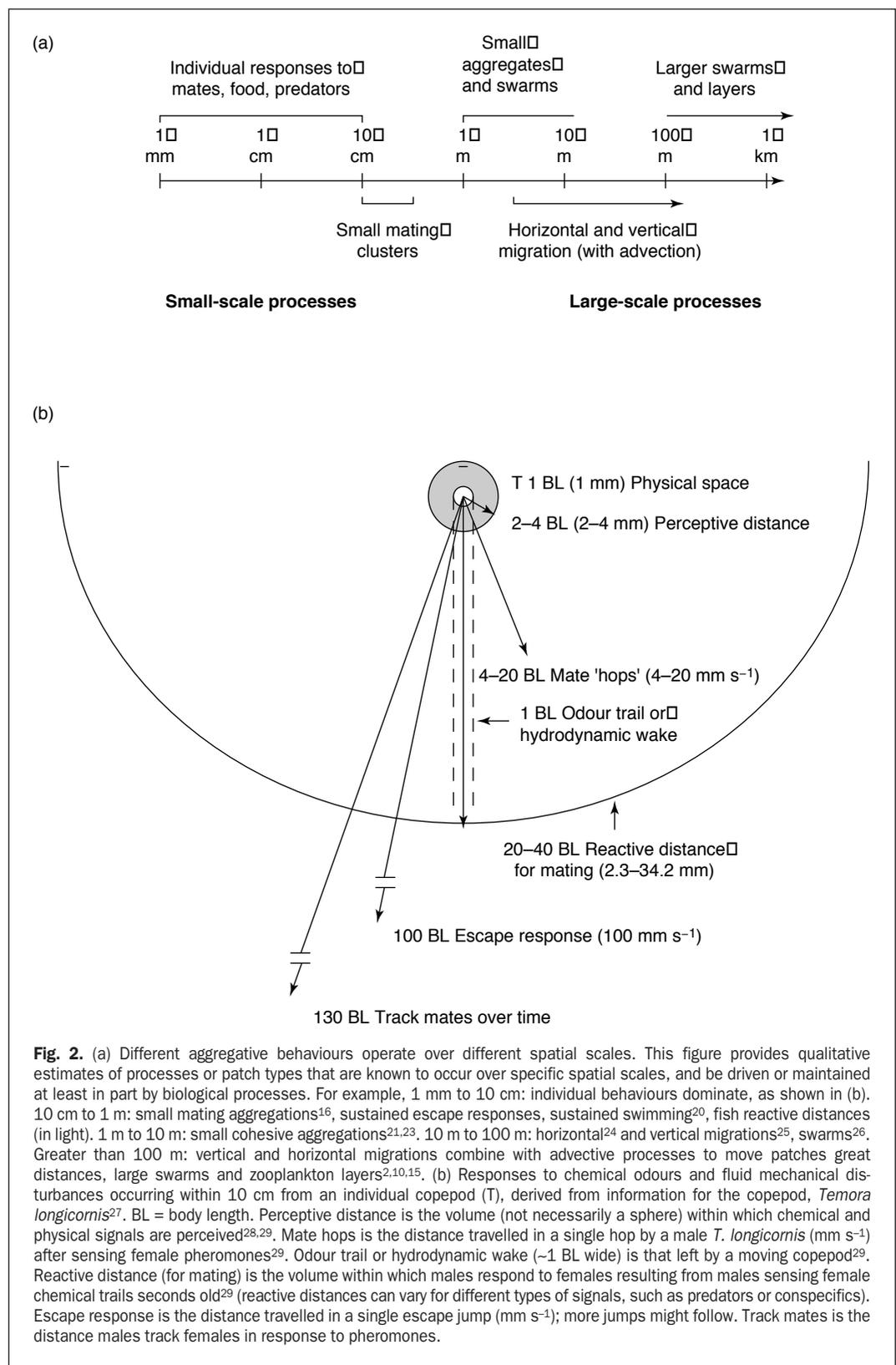
migrations. Others, like many copepods, track mates over small distances by chemoreception, using water-borne pheromone trails, and by mechanoreception, following fluid disturbances produced by species-specific mating behaviours. For example, females of the calanoid copepod *Temora longicornis* respond to male chemical exudates by increasing the frequency of 'hops', which alerts males to their presence and increases their chance of encounter[20]. A comparison of flow fields generated by females indicated that such hops created detectable signals in a volume

Fig. 2. (a) Different aggregative behaviours operate over different spatial scales. This figure provides qualitative estimates of processes or patch types that are known to occur over specific spatial scales, and be driven or maintained at least in part by biological processes. For example, 1 mm to 10 cm: individual behaviours dominate, as shown in (b). 10 cm to 1 m: small mating aggregations[16], sustained escape responses, sustained swimming[20], fish reactive distances (in light). 1 m to 10 m: small cohesive aggregations[21,23]. 10 m to 100 m: horizontal[24] and vertical migrations[25], swarms[26]. Greater than 100 m: vertical and horizontal migrations combine with advective processes to move patches great distances, large swarms and zooplankton layers[2,10,15]. (b) Responses to chemical odours and fluid mechanical disturbances occurring within 10 cm from an individual copepod (T), derived from information for the copepod, *Temora longicornis*[27]. BL = body length. Perceptive distance is the volume (not necessarily a sphere) within which chemical and physical signals are perceived[28,29]. Mate hops is the distance travelled in a single hop by a male *T. longicornis* (mm s^{-1}) after sensing female pheromones[29]. Odour trail or hydrodynamic wake (~1 BL wide) is that left by a moving copepod[29]. Reactive distance (for mating) is the volume within which males respond to females resulting from males sensing female chemical trails seconds old[29] (reactive distances can vary for different types of signals, such as predators or conspecifics). Escape response is the distance travelled in a single escape jump (mm s^{-1}); more jumps might follow. Track mates is the distance males track females in response to pheromones.

approximately 12 times greater than that of feeding signals. These energetically costly manoeuvres are displayed more often when a male chemical signal is perceived. Both the male chemical and the female hydrodynamic 'response' signals dissipate rapidly[29] (within seconds), reducing the likelihood that individuals will 'search' for mates when chance of encounter is low or that these mating behaviours will produce patches on a large scale. Nevertheless, recent work by Davis *et al.*[16] suggests that mate searching might enhance aggregation at small scales, because they observed small (<20 cm) monospecific clusters of copepods, probably associated with mating.

Unlike copepods, cladocerans have not been shown to use chemosensory behaviours to locate mates. However, males swim faster and orthogonally to females or employ area-restricted spiral swimming upon encountering other individuals, which maximizes encounter rate and increases aggregation[46]. In cladocerans, the production of males is associated with crowding. If mating takes place primarily in dense aggregations or monospecific swarms, the chance of failed mating attempts will be low[47]. This could be especially valuable for taxa that lack chemosensory or species-specific rheotactic mechanisms for discerning appropriate mates.

Biological and physical processes work in combination to drive patchiness

Studies of the effects of single processes on zooplankton patchiness have yielded insights, but new work considering drivers in combination is more rapidly advancing our understanding. For example, the effect of light on the formation and maintenance of patches now appears to be best understood in combination with information on tides, predators and endogenous rhythms:

• Scallop larvae migrate vertically and concentrate near the surface in response to both light and tidal cues[17]. By migrating vertically with both diel and tidal periods, the larvae aggregate where currents might transport them horizontally to appropriate settlement sites.
• Fish kairomones drive changes in spatial distribution and habitat use of zooplankton prey. Light might act with these cues to drive cladocerans to aggregate among macrophytes during the day (to avoid fish) and disperse into open water at night[23,24,48].
• Directed and undirected movements by a marine copepod drive it to form swarms in shafts of light among mangroves[26]. However, endogenous diurnal rhythms are also important, because it does not swarm at night, even with light shafts.

In a like manner, it is now appreciated that the effect of food abundance on zooplankton aggregation and dissipation can be modified by factors such as turbulence and predators:
• Small copepods in marine coastal waters aggregate in a food layer during calm conditions, but, when winds are strong, both copepods and algae are dispersed throughout the surface layer[13].
• Downward swimming by a clone of *Daphnia* in response to changing light intensity is enhanced by the presence of food, which counteracts hunger, and by fish kairomones without, surprisingly, any interactive effect of food and predators[30]. Similarly, in the absence of chemicals from a dipteran predator, a clone of *D. pulex* aggregates only under high food conditions. Predator kairomone stops the aggregation at high food concentrations, although animals swim horizontally away from predator scent[37]. The presence of a predator also reduces the amount of time the copepod, *Acartia tonsa*, remains in food patches in laboratory experiments[49]. Finally, the swimming behaviour of two *Chaoborus* species is better understood as the combined response to dual cues from prey and predator. When both cues are present, movement rates are intermediate – that is, slower than with food alone and greater than with either predator alone[50].

What lies ahead?

Ample evidence for the pervasiveness of small-scale behaviours as drivers of zooplankton aggregation now exists. These behaviours need to be recognized in experiments, analyses and predictive models of plankton patchiness (Box 3). A major challenge will be to incorporate the effects of multiple drivers, and the interactive effects of these drivers, on plankton patchiness.

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