Patchiness of the Plankton

Within the geographical boundaries inhabited by any species, the individuals of that species are not distributed uniformly or randomly, but are usually aggregated into discrete 'patches' of variable size. This patchiness is true of both phytoplankton and zooplankton, as well as of other types of marine and terrestrial species.

More frequently, patchiness can be defined only statistically: individuals are found more frequently together than one could predict from an expectation of randomness.

Problems of Patchiness:
- Difficulties in sampling, because plankton nets should be towed over long distances to collect sufficient material for analysis.
- Variation in abundance causes inaccuracies in numbering whole communities in a representative manner.

Spatial scale of Patchiness

Spatial distribution of patchiness that concentrate plankton vary from thousands of kilometres to very small-scale patches of 10 m or less, such scales ranging from oceanic gyres to Langmuir cells of circulation. Differences in scale are shown in Figure 1, which illustrates changes in numbers of zooplankton and phytoplankton on a scale of kilometers, and in Figure 2, which shows smaller-scale of patchiness of zooplankton on a scale of meters. These figures illustrate patchiness on a horizontal axis, but zooplankton also form discrete aggregates in the vertical dimension. Figure 3 shows the vertical distribution of copepods in the Bering Sea (northern extension of the Pacific ocean); note the vertical separation of the species within the epipelagic and mesopelagic zones, as well as the discrete depths inhabited by different life stages and by males and females.

Figure 1 Patchiness in phytoplankton (as indicated by chlorophyll a concentration) and in zooplankton, on a kilometer scale. Based on night-time data taken from 3 m depth in the northern North Sea, May, 1976.
Figure 2 Examples of small-scale (in metres) patchy distribution of zooplankton off the California coast, (a) A shelled pteropod, *Limacina*; (b) a chaetognath, *Sagitta*; (c) a copepod, *Corycaeus* and (d) euphausiid larvae.
Figure 3 Vertical zonation of the copepod community in the Bering Sea during summer. Samples were collected during daylight hours. ♀, females; ♂, males; CV, copepodite stage V.

The major causes of patchiness in plankton
Patchiness is created mainly by biological and physical processes. The following are the major causes of patchiness in the plankton:

1. Spatial changes in physical conditions, such as light, temperature, and salinity. Patchiness in phytoplankton distribution is related to physical processes that control nutrient availability and thus phytoplankton production. Zooplankton patchiness may be correlated with phytoplankton concentrations, or it may be caused by other factors.

2. Water turbulence and current transport
- Various types of turbulent and mixing can result in aggregation or dispersion of planktonic populations. Some types of mixing (upwelling) result in elevated surface nutrient concentrations, high primary production, and increased numbers of zooplankton (Fig. 4); other forms of mixing (downwelling) have the opposite effect on production and aggregation of organisms.
• **Langmuir circulation**

This pattern of circulation is set up when wind blows steadily across the surface of relatively calm seas. As a result, vortices of several meters in diameter start to revolve around horizontal axes and lead to both upwelling and downwelling of water (**Figure 5**). The phenomenon of Langmuir circulation is often visibly apparent as a series of parallel foam lines extending for great distances. Figure 5 shows Langmuir vortices and plankton distributions. Neutrally buoyant particles are randomly distributed, but downward swimming organisms are aggregated in high velocity upwellings (A); particles that tend to float are aggregated in downwellings (B); particles that tend to sink are aggregated in upwellings (C); upward swimming organisms are aggregated in low-velocity downwellings (D); and horizontally swimming organisms are aggregated where there is less relative current velocity than within the vortices (E).
Patchiness due to Langmuir circulation will persist only as long as wind velocity and direction remain constant; and wave action may cause constantly changing patterns of aggregation and dispersal in near-surface plankton.

- **Vortices formed downstream** of a current moving past an island.
- **Vortices** formed as a tidal current moves through a narrow pass, such as the mouth of an estuary.

In all these cases, plankton would be entrained in these currents and eddies.

- **Wind-generated turbulence and water currents**

A concentrated patch of phytoplankton must inevitably diffuse outward because of the transfer of wind and current energy that moves a phytoplankton cell away from a specific point. Dye that is placed in even relatively quiet water will gradually disperse in all directions (Figure 6.a). If the dye is placed in a current, the dispersion of dye will be mainly in the direction of the current (Figure 6.b).

However, a phytoplankton population is obviously not a jar of dye; phytoplankton reproduce, often with a few generations per day. As the rate of water dispersal decreases, and the rate of phytoplankton reproduction increases, there is an increased likelihood of appearance of a concentrated patch of phytoplankton. Thus, the introduction of a rapidly growing phytoplankton population into a sluggish body of water is the probable condition necessary for a rapid growth of phytoplankton, called a bloom.

Fig. 6  The spread of a concentrated patch of dye, when added to the water: size and shape of patch are shown at the start and at several subsequent times. (a) Case of no current and random turbulence; dye is diffusing equally in all directions. (b) In a unidirectional current, shape of dye patches becomes larger and elongated in the direction of the current.
3. Grazing in some areas and reduced grazing in others (Exclusion theory)
Exclusion theory of Bainbridge (1953): High food concentration attracts zooplankton that will diminish food concentration inside the patch; outside the zooplankton patch, phytoplankton can grow faster than zooplankton to form a new patch of food; eventually zoo-plankton will move to new food patch, etc (Fig. to right).

4. Localized reproduction
Reproduction may also play a role in causing patchy distribution in some species. Aggregations of zooplankton formed for purposes of breeding will cause a small-scale heterogeneous distribution, although the mechanisms in which the members of the swarm unite are not understood. Also, all the progeny hatching from one swarm, or even from one egg mass, tend to remain together for some period of time before they become dispersed.

5. Feeding and schooling behavior
When feeding, the Antarctic krill Euphausia superba forms swarms in which the individuals are closely packed but move independently of each other. At other times, the euphausiids are organized in schools, in which the individuals are uniformly oriented and swim together at a uniform speed.
The formation of schools is thought to offer some defense against certain predators but, on the other hand, some predators may force schooling in order to concentrate their prey. For example, some temperate-water species of euphausiids may be driven into tight schools by sharks, or by whales which produce a 'net' of bubbles to encircle and concentrate their prey. In general, extremely high concentrations of predators (e.g. swarms of medusae or ctenophores, or fish schools) will quickly cause local decreases in the numbers of their prey and thus create a patchy distribution of the prey.

6. Swimming behavior
In the zooplankton, swimming behavior and other forms of adjustments of water depth are the major causes of patchiness. Because of regular daily migrations (to be discussed in the following section), many zooplankton groups are aggregated as they move up and down.
Persistence (time scale) of patches
The length of time a particular patch of plankton may persist varies from thousands of days to momentary periods according to the cause of the distribution. Very large patches of zooplankton, such as those caught in rings spun off from the Gulf Stream, may persist for months or even years. Mating aggregations of macrozooplankton (e.g. euphausiids) may persist for only a few days, but the planktonic offspring that hatch from spawning aggregations may remain together for many days or months. Patchiness due to Langmuir circulation will persist only as long as wind velocity and direction remain constant; and wave action may cause constantly changing patterns of aggregation and dispersal in near-surface plankton. Table 1 summarizes some of the physical and biological processes that cause the patchy distribution of planktonic organisms.

Table 1 Approximate spatial and temporal scales of some important processes that cause patchy distribution of zooplankton.

<table>
<thead>
<tr>
<th>Spatial length scale (km)</th>
<th>Physical processes</th>
<th>Biological processes</th>
<th>Persistence time scale (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1000+</td>
<td>Gyres (e.g. Sargasso Sea); continental upwelling (e.g. Peru Current); water mass boundaries (e.g. Antarctic Convergence)</td>
<td>Regional ecosystems defined by the water mass</td>
<td>1000+</td>
</tr>
<tr>
<td>100</td>
<td>Warm and cold core rings; tidal fronts; seasonal coastal upwelling</td>
<td>Seasonal growth (e.g. spring blooms); differential growth between phyto- and zooplankton</td>
<td>100</td>
</tr>
<tr>
<td>10</td>
<td>Turbulence (e.g. estuarine mixing; island wake effects)</td>
<td>Lunar cycles (e.g. fish spawning)</td>
<td>10</td>
</tr>
<tr>
<td>1</td>
<td>Tidal mixing</td>
<td>Reproductive cycles</td>
<td>1</td>
</tr>
<tr>
<td>0.1</td>
<td>Wind-induced vertical mixing</td>
<td>Grazing/predation</td>
<td>0.1</td>
</tr>
<tr>
<td>0.01</td>
<td>Langmuir circulation; wave action</td>
<td>Diel events (e.g. vertical migration)</td>
<td>0.01</td>
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<td></td>
<td></td>
<td>Physiological adaptation (e.g. buoyancy; light adaptation)</td>
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<td></td>
<td></td>
<td>Behavioural adaptation (feeding swarms)</td>
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