

Chapter 10

COPEPOD BEHAVIOR: OCEANOGRAPHIC CUES, DISTRIBUTIONS AND TROPHIC INTERACTIONS

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ABSTRACT

In order to fully understand the role copepods play in marine ecosystems, we delve into the sensory world of copepods, and build on this foundation to show how copepods utilize their environment to bridge the gap between dispersed prey and fast-moving predators. We begin by describing in detail the copepod's environment and the cues that we know are employed based on available literature. We then explore the implications of these behaviors on copepod distributions, trophic interactions, and overall marine ecosystem production. As we learn more about copepod sensory capabilities, it is becoming clearer, that copepods provide a critical link between physical and behavioral determination of organism distributions in the ocean. This link has profound effects on higher trophic level production and top-down *versus* bottom-up control in marine ecosystems.

INTRODUCTION

Copepods have evolved behavioral responses to their environment over millions of years that can have profound effects on their distributions, trophic interactions, and ultimately marine fishery production [1,2]. This is largely because copepods play a unique role in many marine food webs due to their position as secondary consumers [3,4], where they provide a critical intermediary link between photosynthesis (primary production) and higher trophic levels. Copepods are also prey for a wide variety of tertiary consumers such as predatory

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zooplankton, larval and adult fishes, and filter-feeding marine mammals [5-8]. Consequently, copepod behavior can have dramatic direct and indirect consequences through marine ecosystems. For this reason, there has been intense effort by oceanographers to understand the dynamics of copepod behavior relative to their environment for many decades.

Early work on copepod behavior focused on explaining the role of strong diel vertical migration (DVM) patterns that many species exhibit [9-12]. Researchers explained this behavior as the interplay between feeding and predation where copepods would ascend from depth to the surface at night to feed and back down at dawn to avoid visual predators, all cued predominantly by light intensity. The motivation behind this behavior, predator avoidance, was a catalyst to the next few decades of research on copepod behavior [4,13,14].

As experiments and observations became more sophisticated, it appeared that copepods utilize the full suite of environmental stimuli available to them, and that while predation may be the evolutionary driving force for individual behavior, it may not be, as recent studies suggest, the most important factor in driving population structure and trophic dynamics [1,8,15]. Responses to cues such as light, fluid density (changes in temperature or salinity), gradients in velocity, turbulence, chemicals from prey, and prey presence in combination with ocean circulation patterns across a range of scales can lead to aggregation in patches defined by vertical or horizontal orientations [7,16-18]. Direct responses to mating cues and predator disturbances can lead to changes in population distributions as a function of depth [5,19-21]. In many cases, we are just beginning to understand how copepod behavior can influence the productivity of both lower and higher trophic levels, the organization of food webs, and pelagic ecosystem functioning [1,8,22,23].

Our understanding of copepod behavior has grown dramatically over the past few decades through critical collaborations between copepod ecologists, oceanographers, and fluid dynamists and through application of new technology to observation, experimentation, and analysis [24-26] and through the aid of increasingly sophisticated individual-based models [22,23,27]. From the fluid physics standpoint, we now understand how turbulence can affect both copepod feeding and predation rates [28-30], how fluid velocity gradients can elicit escape responses from predators [31,32], and how copepods utilize the properties of flow to develop feeding currents and minimize energetic expenditure [33]. Application of three-dimensional imaging systems and fractal analysis of trajectories has provided new insights into subtle responses of copepods to environmental cues, and how these responses persist through time [25,34]. These advances have led to a variety of new questions about how the marine environment functions. How do copepods translate environmental cues to particular behaviors? How do these responses directly affect distributions of copepods, their predators, and their prey? How do these changes affect production of higher trophic levels and the maintenance of biodiversity? Increasingly sophisticated computer models of pelagic ecosystems [27,35] are beginning to address these questions and new technologies for imaging copepod behavior [36-38] will enable oceanographers to test hypotheses developed by these models in the near future.

In this chapter, we review the basic cues that an individual copepod is exposed to from changes in light intensity and duration to ephemeral disturbances due to predator movements. For each cue, we begin with the basic physics behind the cue generation and propagation through the environment and reception by an individual copepod. We then discuss observed behavioral responses to the cue, and the potential implications for ecological function. Once we have reviewed the state-of-knowledge of copepod sensory and behavioral ecology, we

delve into the how these behaviors affect distributions and predator-prey interactions. We then discuss, based on available literature, the cascading effects of physics, behavior, and consequent distributions on trophic cascades and ecosystem functioning. Finally, we discuss the current state-of-the-field and future directions for understanding the role copepods play in the marine environment. Our intention is to give the reader a bottom-up view of the ocean in order to catalyze interest and research in pelagic ecosystem functioning as it relates to copepods and their behaviors especially in the light of new studies that suggest a much different role of copepods in marine systems that is not driven by predation response behaviors, but more closely tied to the spatial structure of prey in the ocean [1,2,8].

OCEANOGRAPHIC CUES AND BEHAVIORAL RESPONSES

In the ocean, an individual copepod is exposed to a myriad of environmental, chemical, and biological cues, which it must receive and respond to in order to survive. Copepods have a number of sensory capabilities that facilitate behavioral responses to cues and structure in the ocean. These include sensitivity to light, temperature, salinity, fluid density, velocity gradients, and chemicals. This section will review our knowledge of copepod behavioral response to each of these cues in order to set the stage for the subsequent discussion of organism distributions and interactions.

Before discussing particular cues, it is important to discuss the scales over which a copepod interacts with its environment. A single individual copepod can typically swim at $ca. 5 \text{ mm s}^{-1}$ allowing it to cover at most $ca. 400 \text{ m}$ in a day. The relative scales of horizontal (km s^{-1}) and vertical (m s^{-1}) gradients and flows in the ocean therefore largely constrain copepod behavior to sensing vertical structure and moving vertically. However, this is not always the case especially in the vicinity of fluid density fronts (common in estuaries, river plumes, and in upwelling regimes) where horizontal gradients can be of the same magnitude as vertical gradients. For now, we consider predominantly vertical structure in the ocean, with the caveat that there are potential situations where copepods may be able to directly respond and interact along horizontal gradients [39].

Environmental Cues: Light

Light in the ocean plays important roles in both primary and secondary production. In this section, we briefly cover the role that light plays in copepod behavior in order to describe the 'world through a copepod's eyespot'. The treatment here is not meant to be exhaustive, but simply to familiarize and remind the reader that light plays a unique role in copepod behavior that can have large effects on their sensory response, distributions, and productivity. Copepods use light in many ways because it can affect prey distributions, predation risk, and habitat quality [40-42]. Light as a cue in the ocean is an omnipresent factor that provides copepods with a mechanism to locate prey and avoid predators. By using light cues, copepods can deal with the wide range of light attenuation in different water masses easily and utilize light to accomplish many basic life processes.

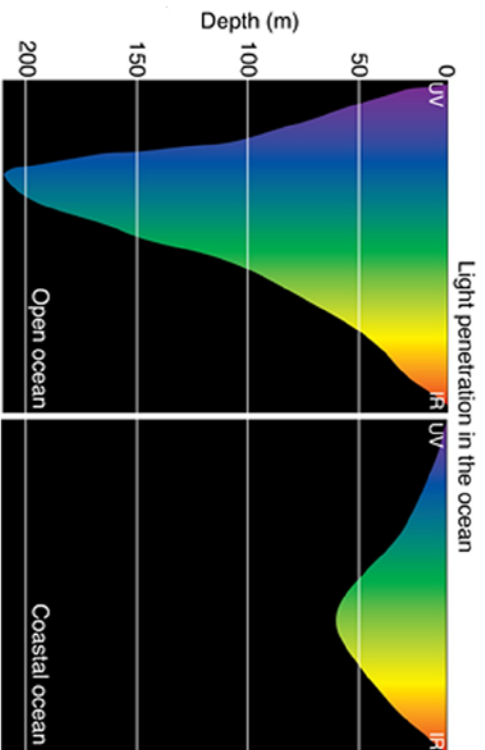


Figure 1. Light attenuation in the ocean. Attenuation is much higher in coastal waters due to increased turbidity associated with runoff, increased primary productivity, and increased sediments. Copepods are most sensitive to blue-green light that can penetrate much deeper into the ocean.

Light is absorbed rapidly over depth in the ocean (Figure 1). Consequently, light provides an ideal cue for sensing susceptibility to visual predators with gradients that scale reasonably well to copepod behavior and swimming capabilities. However, other factors such as turbidity and colored dissolved organic matter (CDOM) can have dramatic effects on the attenuation of light in the ocean. Regardless of the particular decay constant (dependent on water clarity and content), copepods can utilize light gradients to maintain position within the water column relative to predator visual acuity, and they may use different aspects of the light distribution to cue particular behaviors as will be discussed below.

Copepods are generally sensitive to light and numerous copepod species, such as *Acartia tonsa*, demonstrate a broad range of sensitivity and are positively phototactic [43]. Copepods sense light through a single eyespot located centrally on the main body or head of the animal. The eyespot senses light intensity generally in the range of visual light (400–700 nm), and can provide weak infrared and UV sensitivity depending on species [4]. Light intensity can be used in a variety of behaviors and can also mediate responses to other environmental cues [42]. Perhaps the most fundamental use of light by copepods is in either changes in photoperiod inducing dormancy [44] or in the use of light intensity to initiate DVM and depth maintenance [9,12].

Light is generally considered the primary proximate cue controlling DVM [41,45]. Lampert [46] observed that DVM is intrinsically linked to light-dependent mortality in surface waters, and typically occurs only in the presence of such predation pressure. Further, DVM is a flexible behavior that allows for balancing various constraints including effectiveness of protection, energy input, and other environmental variables [47]. Four major hypotheses have been suggested to explain DVM. First, the preferendum or isolume hypothesis corresponds to zooplankton following a preferred light level during migration.

Buskey et al. [48], for example, observed copepod behavior consistent with this hypothesis. Second, the absolute intensity threshold hypothesis suggests that DVM is at least partly controlled by an absolute threshold. *Calanopia americana* is an example of a copepod that follows behavior consistent with this hypothesis [49,50]. Third, the rate of change hypothesis suggests that the relative rate and direction of light intensity change from ambient level mediates DVM. This behavior has been observed in *A. tonsa* [51] among other species [41]. Fourth, the transparency-regulator hypothesis emphasizes the role of water transparency in regulating structural drivers and dynamic drivers [52]. Williamson et al. [52] argue that this hypothesis allows for more accurate explanation of the broad range of observed DVM behaviors.

Species that undergo DVM are most sensitive to wavelengths (blue/green) that are prevalent at sunset when migration often occurs [53]. While light is the primary proximate cue, exposure to predators can additionally influence migrations by affecting the magnitude of movement and inducing migrations in previously non-migrating species. For many species, the behavioral response is commonly activated from chemical or (possibly) mechanical cues from fish predators [41]. Recent studies have also found that some copepods are more sensitive to predator flow disturbances when exposed to higher illumination, which suggests that copepods are sensitive to their visual susceptibility to predation [42]. In this study, the copepod, *Calanus finmarchicus*, tunes its response to predator-like flow disturbances based on the ambient light intensity, which illustrates individual copepods awareness of their particular environment.

Many species of copepods are known to modulate their depth based on the phase of the moon, again a response to ambient light levels that appears related to predator avoidance. Avoidance behavior (vigorous downward swimming) to ultraviolet light has also been observed in some species likely to avoid ultraviolet radiation damage [54]. Responses to light have also been shown to induce swarming behavior in many estuarine and coastal species of copepods [55]. Swarming in response to light has been proposed as a mechanism for mating aggregation [20]. In the light shafts of mangroves, Buskey [56] observed intense swarms of the copepod, *Dicathona oculata*, and illustrated increased mating success within the swarms. However, whether swarming behavior is a true response to environmental changes or an artifact associated with intense light beams is still unclear [45].

Finally, a potential example of the use of light affecting horizontal distributions is the increased abundance of estuarine copepods, such as *Eurytemora affinis*, within the estuarine turbidity maxima (ETM) region [40,57,58]. Although ETMs are also often regions of other convergent oceanographic processes, they can be sensed using light by copepods. In shallow estuaries, light can penetrate the entire water column with minimal attenuation. However, changes in turbidity often occur at scales (10's m) similar to that of vertical structure in the open ocean. However, whether copepods actively employ light as a cue to maintain position within these regions as a mechanism for reducing predation risk is still an open question.

Environmental Cues: Temperature, Salinity, and Fluid Density

Gradients in temperature, salinity, and fluid density in many ways form the most consistent environmental cues available to copepods in the ocean. In the ocean, temperature and salinity follow distinct profiles that lead to the development of gradients in fluid density

called 'frons' in the horizontal, and 'clines' in the vertical [2]. Regions of strong vertical gradients or clines are common throughout the ocean, are often associated with subsurface chlorophyll maxima, and occur at scales (m's) that can be exploited by individual copepods [59,60]. Due to the strong associations between temperature, salinity and prey resources, it is expected that copepods employ these cues in foraging behavior. However, recent studies have suggested that this is not necessarily the case, at least for several common coastal species [15,60,61].

The presence of a salinity gradient has long been recognized as affecting copepod swimming behavior with the organism consistently reeling from the salinity gradient layer [62]. The most important factor in creating patchiness of copepods in this context is modified swimming behavior [63]. Harder [64] observed species-dependent distributions in the presence of a fluid density gradient and documented minimum threshold levels for several species to accumulate at salinity gradient layers. Most copepods tended to accumulate near the fluid density gradient layer. Interestingly, *Temora longicornis* showed no accumulation at salinity gradient layers in the absence of a coincident fluid density gradient. *T. longicornis* did, however, show aggregation at a fluid density gradient layer in absence of a coincident salinity gradient. Thus, fluid density appears to be the most important property controlling behavior that leads to aggregation, at least for this species. Lougee et al. [65] observed similar influence of haloclines on copepod distributions and argued that in estuaries, salinity and fluid density gradients are generally coincident. In that scenario, the results of the proximate cue being salinity or fluid density would ultimately be the same. Many estuarine copepods are suspected of using fluid density cues, often in the form of salinity, to maintain position within the estuary that can trigger tidally-driven vertical migration [66-68]. These responses enable copepods to undergo small-scale (2-6 m) vertical movements triggered by changes in salinity. Migrations at these scales enable the copepods to maintain position within the ETM [57,69].

There is also similar, but not as exhaustive, evidence that copepod swimming behavior is influenced by temperature, however the response may be linked to changes in water viscosity associated with temperature changes. *T. longicornis*, for instance, demonstrates higher swimming speed, fewer break periods, and more frequent jumps for higher fluid temperature [70]. Temperature can also directly affect metabolic rates and lead to dormancy [44]. Changes in temperature have also been shown to affect responses of estuarine copepods to salinity [71].

Regarding the mechanism of aggregating, Woodson et al. [60] observed that individual copepods rarely cross a fluid density gradient layer, when strength is at supra-threshold levels, and rather swim along a layer boundary or turn around. They reported behavior threshold levels for *A. tonsa* and *T. longicornis* crossing the fluid density gradient layer. The behavior around salinity gradient and fluid density gradient layers is also species-dependent. Woodson et al. [15] observed that *E. affinis* behaved differently than the other copepod species tested. *E. affinis* often crossed the fluid density gradient layer, changed swimming patterns, and increase residence time in the layer region. For this species, Seuront [68] observed increased complexity of swimming path with increasing salinity and concluded that *E. affinis* employs salinity gradients as a proximate cue to maintain position near regions of high productivity in estuaries. The state of the adult may also be a factor for the behavioral response. Michalec et al. [69] found an optimal salinity range for swimming activity in the copepod *Pseudodiaptomus amandaelet*, which differed for ovigerous females compared to other females and males.

$$\text{Simple Shear Flow} = \text{Rotation} + \text{Deformation}$$

$$u_1 = a x_2$$

$$(u_1)_{rot} = \frac{a}{2} x_2$$

$$(u_2)_{rot} = -\frac{a}{2} x_1$$

$$(u_1)_{def} = \frac{a}{2} x_2$$

$$(u_2)_{def} = \frac{a}{2} x_1$$

Figure 2. Shearing motion will rotate and stretch any straight material line as demonstrated by this example illustration. The decomposition of this simple example can be generalized to three-dimensions via Eqn. (1).

The ecological result of aggregations around steep salinity gradient or fluid density gradient layers may vary as well. For instance, Hetch [72] observed salmon louse copepod aggregations at steep salinity gradients and suggested that the aggregations may increase the frequency of host/parasite encounters. The response for this copepodid seems to be influenced by both the absolute salinity and the change in salinity with depth. In another example, Boedansky and Bollens [73] suggested that it may be advantageous for copepods to respond to physical cues rather than searching for ephemeral food patches. The observations of Woodson et al. [15] support this suggestion, at least for *E. affinis*, for whom the fluid density gradient layer appears to act as the initiation of a cue hierarchy in the search for food and high resource patches.

Environmental Cues: Fluid Motion

In any flow field there are multiple fluid mechanical cues that a copepod could sense, namely fluid acceleration, vorticity, and deformation rate. A general three-dimensional velocity gradient, can be decomposed into its irrotational and rotational components defined by the deformation rate (or strain rate) tensor, e_{ij} , and the rotation tensor, r_{ij} as (Figure 2):

$$\frac{\partial u_i}{\partial x_j} = e_{ij} + \frac{1}{2} r_{ij} \quad (1)$$

where u_i is the velocity vector and the indices i and j indicate the three coordinate directions [74].

The deformation rate tensor can be thought of as the relative velocity gradient due to pure deformation and can itself be decomposed into the linear deformation rate (diagonal terms) and the shear deformation rate (off-diagonal terms):

$$e_{ij} = \begin{vmatrix} \frac{\partial u_i}{\partial x_i} & \frac{1}{2} \left(\frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i} \right) & \frac{1}{2} \left(\frac{\partial u_i}{\partial x_k} + \frac{\partial u_k}{\partial x_i} \right) \\ \frac{1}{2} \left(\frac{\partial u_j}{\partial x_i} + \frac{\partial u_i}{\partial x_j} \right) & \frac{\partial u_j}{\partial x_j} & \frac{1}{2} \left(\frac{\partial u_j}{\partial x_k} + \frac{\partial u_k}{\partial x_j} \right) \\ \frac{1}{2} \left(\frac{\partial u_k}{\partial x_i} + \frac{\partial u_i}{\partial x_k} \right) & \frac{1}{2} \left(\frac{\partial u_k}{\partial x_j} + \frac{\partial u_j}{\partial x_k} \right) & \frac{\partial u_k}{\partial x_k} \end{vmatrix} \quad (2)$$

The rotation tensor can be thought of as the relative velocity gradient due to fluid rotation:

$$r_{ij} = \frac{\partial u_i}{\partial x_j} - \frac{\partial u_j}{\partial x_i} = -\epsilon_{ijk} \omega_k \quad (3)$$

hence,

$$r_{ij} = \begin{vmatrix} 0 & -\left(\frac{\partial u_k}{\partial x_i} - \frac{\partial u_i}{\partial x_k} \right) & \left(\frac{\partial u_k}{\partial x_j} - \frac{\partial u_j}{\partial x_k} \right) \\ \left(\frac{\partial u_k}{\partial x_i} - \frac{\partial u_i}{\partial x_k} \right) & 0 & -\left(\frac{\partial u_k}{\partial x_j} - \frac{\partial u_j}{\partial x_k} \right) \\ -\left(\frac{\partial u_k}{\partial x_i} - \frac{\partial u_i}{\partial x_k} \right) & \left(\frac{\partial u_k}{\partial x_j} - \frac{\partial u_j}{\partial x_k} \right) & 0 \end{vmatrix} \quad (4)$$

and

$$r_{ij} = \begin{vmatrix} 0 & -\omega_3 & \omega_2 \\ \omega_3 & 0 & -\omega_1 \\ -\omega_2 & \omega_1 & 0 \end{vmatrix} \quad (5)$$

where ω_i is the vorticity vector and ϵ_{ijk} is the alternating tensor. For the example shear flow shown in Figure 2 (i.e., $u_i = ax_j$), the deformation rate and rotation tensors are, respectively, given by

$$e_{ij} = \begin{vmatrix} 0 & \frac{1}{2}a & 0 \\ \frac{1}{2}a & 0 & 0 \\ 0 & 0 & 0 \end{vmatrix} \quad (6)$$

and

$$r_{ij} = \begin{vmatrix} 0 & a & 0 \\ -a & 0 & 0 \\ 0 & 0 & 0 \end{vmatrix} \quad (7)$$

These results, and Figure 2, demonstrate that there is simple shear deformation aligned at 45° relative to the x_1 and x_2 axes and rotation aligned with the x_3 axis only.

Thus, any three-dimensional velocity field can be thought of as the superposition of rotational and deformational flow components, and the ability of a copepod to sense the magnitude and orientation of the flow disturbance allows it to distinguish, for instance, the suction force from a predator [75] versus the fluid mechanical signature of a phytoplankton cell entrained in its own feeding current [76]. Some authors suggest that copepod size has evolved to utilize specific flow characteristics [77], and many copepods have developed adaptive behaviors to remove signal noise from their immediate surroundings [77,78].

Copepods sense fluid motion using setae (bristle- or hair-like structures) that are mechanically sensitive along the first antenna. Deflection of the setae triggers neural signals (i.e., spikes) that possess amplitudes and sensitivity that suggest the capability for very rapid responses such as prey capture and escapes from predators [79,80]. Copepod setae are sensitive to fluid velocities as small as $20 \mu\text{m s}^{-1}$ and demonstrate response to stimuli in the range of 40 to 1000 Hz [81]. Copepod setae possess a wide range of lengths. Shorter setae are sensitive to rapid fluid motion, whereas long setae function as low velocity sensors [82]. The morphology (i.e., setal shapes, orientations, and degree of ornamentation) is spectacularly diverse among copepods, which indicates a vast range of mechanosensory capability [83,84]. This suggests that copepod setal morphology may be tuned to specific functionality. For instance, predatory copepods should have numerous short setae, with fewer long setae, in order to effectively detect the flow disturbance of rapidly moving prey [83].

A majority of studies of hydromechanical cues have focused on predator-prey detection interactions [13,85]. In fact, Kiorboe [1] mentions mechanoreception of predators and of prey as key factors in the success of copepods. Kiorboe and Visser [14] argue that predator perception of prey depends on the absolute magnitude of the velocity disturbance created by moving prey, whereas prey perception of predators is a function of the spatial gradients of velocity and the sensor span; see also [86]. In the prey-perception-of-predators scenario, the signal strength is proportional to the spatial gradient of velocity as well as the size of the prey (i.e., the spatial span of the sensors). Although it should be noted that observations of *A. tonsa* do not fully support the hypothesis that threshold for behavioral response solely depends on the velocity difference (i.e., the product of velocity gradient and sensor span; [87]).

Table 1. Thresholds for escape responses to fluid motion in several copepod species

Species	Fluid Stimulus	Threshold Deformation Rate (s ⁻¹)	Reference
<i>Acartia hudsonica</i>	Siphon	2.2	[90]
<i>Acartia hudsonica</i>	Oscillating bar	1.7	[204]
<i>Acartia hudsonica</i> , nauplii	Siphon	0.80	[85]
<i>Acartia tonsa</i>	Siphon	0.38	[19]
<i>Acartia tonsa</i>	Siphon	1.19-2.49	[87]
<i>Acartia tonsa</i> , nauplii	Siphon	0.38	[19]
<i>Calanus finmarchicus</i>	Rotating Cylinder	0.40	[205]
<i>Calanus helgolandicus</i> , nauplii	Siphon	0.52-3.24	[206]
<i>Centropages hamatus</i>	Siphon	1.2	[90]
<i>Centropages homatus</i>	Oscillating bar	1.4	[90]
<i>Centropages typicus</i> , nauplii	Siphon	2.60-2.79	[206]
<i>Euchaeta rimana</i>	Siphon	2.24	[19]
<i>Euchaeta rimana</i>	Pipette jet	3.3	[32]
<i>Eurytemora affinis</i>	Pipette jet	1.9	[13]
<i>Eurytemora affinis</i> , nauplii	Siphon	1.88-2.65	[206]
<i>Fluteerhina acediffrons</i> , nauplii	Siphon	1.92-4.25	[206]
<i>Labidocera madureae</i>	Siphon	6.3	[19]
<i>Orthona</i> spp.	Siphon	3.8	[19]
<i>Paracalanus parvus</i>	Siphon	6.2	[204]
<i>Pleuromamma xiphias</i>	Siphon	4.6	[19]
<i>Temora longicornis</i>	Pipette jet	6.5	[13]
<i>Temora longicornis</i>	Siphon	2.7	[90]
<i>Temora longicornis</i>	Oscillating bar	> 15	[90]
<i>Temora longicornis</i> , copepodid	Siphon	0.73-0.81	[31]
<i>Temora longicornis</i> , nauplii	Siphon	2.78-3.96	[31]
<i>Temora turbinata</i>	Siphon	3.9	[204]
<i>Tortanus discadatus</i>	Siphon	0.3	[90]
<i>Tortanus discadatus</i>	Oscillating bar	1.2	[90]

The most significant flow disturbance is quantified by the deformation rate (Eq. 2; [14,19]). Copepods appear to be capable of perceiving acceleration, but do not behaviorally respond to acceleration [87]. Similarly, the presence of fluid vorticity (Eqs. 3-5) did not elicit escape response [87]. The behavioral response does not depend on pure linear deformation rate versus pure shear deformation rate, but rather is mediated by the magnitude of the deformation rate. Numerous studies have used siphons [88], moving spheres [89], and other flow disturbance generators [87,90] to document threshold levels of deformation rate to evoke an escape response (Table 1). There is substantial variability among the reported threshold values. Much of the variability may be due to sensory differences (and setal morphology differences) among species, although there may also be an influence of measurement approach among various researchers. The escape response of *A. tonsa* also depends on the relative location of the flow disturbance, which indicates a directional bias and creates effective 'blind spots' of weaker perceptible ability [91]. The greatest susceptibility for *A. tonsa* is when attacked from the side. Thus, documenting a threshold deformation rate for

escape response requires flow measurements in a plane relevant to the copepod's orientation. In addition, the threshold deformation rate to elicit escape response appears to be mediated by ambient illumination level with a lower threshold in lighted conditions compared to dark conditions [42].

Known sensitivity of copepod setae appear to be consistent with the ability for remote detection of inert particles by feeding-current-generating and cruising copepods [86], although sensing of prey is strongly biased toward larger prey particles [14]. Consistent with the morphological diversity mentioned above, the combination of numerous mechanosensors facilitates the ability to spatially locate the flow disturbance of moving prey [92]. *Orthona plumifera*, for instance, show an ability to accurately project the prey's instantaneous location and velocity prior to attack with adaptable attack behavior based on the perceived signal patterns [93]. Sensing of prey within the capture region is facilitated by mechanoreceptive setae on the basal sector of the first antenna, whereas setae on the mid and distal regions are utilized to orient to prey located outside the capture region [84]. Detection of prey depends on the relative spatial location of the prey and the prey's motility [94]. Motile prey are detected in front of the copepod, whereas non-motile prey are detected ventrally or lateral-ventrally to the copepod.

Mechanoreception in copepods is important in contexts beyond predator-prey interactions as well. For instance, Jiang and Osborn [95] discuss the hydrodynamic signal between copepods of similar size. The signals in that case may not be symmetric with one copepod sensing another who is unaware of the first. Consistent with this scenario, Baggefin and Kjørboe [96] observed that *A. tonsa* use hydrodynamic signals to locate mates. Males and females appear unaware of the presence of a potential mate until one individual creates a flow disturbance by hopping. Copepods are capable of distinguishing the source of a hydrodynamic disturbance (prey, predator, mate, etc.) based on the information contained in the signal [76]. This suggests that different types of behavioral responses to different types and magnitudes of various hydrodynamic signals are likely. In another context example, Woodson et al. [61] observed copepods orienting to thin layers of velocity gradients with increased swimming speed and turning frequency that result in increased local residence time near the thin layer structure. The threshold deformation rate in this case was substantially smaller (roughly one to two orders of magnitude smaller) than the threshold to evoke an escape response. Woodson et al. [60] hypothesized that the response to the velocity gradient layer indicated the initiation of a cue hierarchy in the search for resource rich zones. Finally, sensing of turbulent fluid motion has been hypothesized to induce copepod behavioral responses such as sinking or swimming into less turbulent regions [97-99]. While the relevant mechanosensory signal in fluctuating turbulent velocity fields has been speculated [100,101], direct measurements have not yet been performed. Further, turbulent flow conditions may significantly affect the availability and reliability of hydrodynamic signals from predators, prey, and conspecifics.

Environmental Cues: Chemical and Biological

Chemosensing and chemical signals play important roles in copepod ecology. Chemical cues in the marine environment typically consist of highly soluble (molecular diffusivity $\sim 10^5$ cm² s⁻¹) compounds including amino acids, proteinaceous compounds, nucleic-acid

related compounds, glycerolipids, and pheromones [102-105]. The means of release and the hydrodynamically-regulated advection and diffusion of a chemical signal determine the amount and specificity of chemical information conveyed [104,106]. The focus of this section is on biophysical coupling concerning the release of chemical cues, subsequent hydrodynamic advection and diffusion, and finally cue perception and implications for behavioral responses.

The two most important parameters that define the appropriate regimes of fluid flow and chemical transport in an aquatic environment are the Reynolds number Re

$$Re = \frac{\rho UL}{\mu} = \frac{UL}{\nu} \quad (8)$$

and the Péclet number Pe

$$Pe = \frac{UL}{\Gamma} \quad (9)$$

where U is the characteristic velocity, L is the characteristic length scale, ρ is fluid density, μ is dynamic viscosity, ν is kinematic viscosity, and Γ is molecular diffusivity of the chemical. Re represents the ratio of inertial to viscous forces acting in a flow, and Pe describes the ratio of advective to diffusive effects acting on a passive scalar, such as chemical concentration, in a flow field.

Low and intermediate values of Re indicate laminar flow (i.e., less than the order of 100) with very low values (i.e., less than 1) indicating viscosity-dominated flow. Larger values of Re indicated turbulent flow in which random velocity fluctuations lead to enhanced chemical transport. Similarly, low values of Pe indicate a regime dominated by diffusive transport, whereas larger values of Pe indicate an advection-dominated regime. Thus, these parameters form the basis for a quantitative understanding of the relevant transport processes as well as the chemical concentration cue likely to be experienced by receivers [106].

The spread of chemicals emitted into a stagnant fluid environment is governed by Fickian diffusion in which chemical flux \vec{q} is proportional to the concentration gradient as:

$$\vec{q} = -\Gamma \nabla c \quad (10)$$

where c is chemical concentration, and the diffusion transport equation is given as:

$$\frac{\partial c}{\partial t} = \Gamma \nabla^2 c \quad (11)$$

Time scales of molecular diffusion are extremely long and gradients of chemical solute develop slowly. At low Re , the addition of flow advection is included in the chemical flux:

$$\vec{q} = \vec{u}c - \Gamma \nabla c \quad (12)$$

where \vec{u} is the velocity vector, and transport is described by the advection-diffusion equation:

$$\frac{\partial c}{\partial t} + \vec{u} \cdot \nabla c = \Gamma \nabla^2 c \quad (13)$$

Finally, chemical flux in high Re turbulent flows is additionally influenced by random velocity fluctuations. The turbulent time-averaged flux of a chemical solute, \vec{q} , is given as:

$$\vec{q} = \vec{u}c - \Gamma \nabla c + \vec{u}'c' \quad (14)$$

where the overbar notation indicates time-averaged and the prime notation indicates fluctuation away from the time-averaged value. Equation (11) reveals the additional turbulent flux term corresponding to the covariance of the velocity and concentration fluctuations. The time-averaged concentration field is now governed by the Reynolds-averaged advection-diffusion equation as:

$$\frac{\partial \bar{c}}{\partial t} + \vec{u} \cdot \nabla \bar{c} = \Gamma \nabla^2 \bar{c} - \nabla \cdot (\overline{u'c'}) \quad (15)$$

In many cases, the covariance term is replaced by a 'turbulent diffusivity' term that models the effect of turbulence as a diffusive process.

Copepods demonstrate sensory capability to detect dissolved chemicals and use the cues to respond to food, mates, and other items [107]. Food particle detection *via* chemosensation can be more efficient than hydrodynamic detection [108]. Copepod cruising strategy is more effective for smaller particles and chemical plume sensing is more effective for larger particles, although this conclusion is highly sensitive to the assumed detection threshold levels [108]. *T. longicornis*, for instance, can trail follow sinking marine snow particles from a distance of greater than 25 particle radii *via* chemosensation [109]. Copepod distributions are also influenced by chemical interactions with phytoplankton food particles [110]. When near to patches of food particles, *A. tonsa* demonstrated the ability to detect the patch edge and to maintain position precisely enough to take advantage of food presence [111]. In this context, Woodson et al. [60] reported threshold concentrations of chemical exudates of phytoplankton for *A. tonsa* and *T. longicornis* to initiate excited area-restricted search behavior (i.e., increased swimming speed and turning frequency). Similar behavior is observed in several other species as well [15].

Numerous studies have demonstrated mate detection *via* chemosensation, and the impressive mate locating ability may help explain copepod success in the ocean [112]. Males have the ability to chemically distinguish virgin females compared with mated females [113]. Copepods also appear to be unique in their ability to track chemical information in a three-dimensional space to locate a mate. In the trail following scenario, the female leaves a trail of pheromone that the male randomly intersects. Once the male intersects the trail, he accurately follows it and even corrects for heading in the wrong direction [104]. By leaving a pheromone trail, the female increases the probability of encounter with a mate by up to 100 times [114]. Male *T. longicornis* locate females by following chemical trails for up to 10 seconds and track over distances exceeding 13 cm or 130 body lengths [115,116]. *Centropages typicus* demonstrate similar behavior and track trails up to 31 seconds old and 17 cm long [96]. The freshwater species *Hesperodiptomus shoshone* demonstrate shorter (3.8 cm maximum) and

brifter (2.4 s maximum) tracks, which suggests either weaker chemical sensitivity or less persistence of the chemical cue [117]. Alternate to the trail following scenario, female *Pseudocalanus elongatus* create a nearly spherical cloud of pheromone with heterogeneous chemical distribution around their hovering position [118]. A male swims in the cloud surrounding the female with intermittent physical contact with the female. In another alternate behavior, female *Oithona davisae* distributes pheromone in a trail intermittently due to their hop-sink swimming behavior [119]. Males use local search strategies to bridge the gap between neighboring patches of pheromone.

Copepods also demonstrate chemosensory ability beyond sensing food or mates. For instance, female *T. longicornis* show a chemosensory response to dimethyl sulfide (DMS) suggesting that plumes of this gas may provide information about the nearby presence of algae food particles [120]. In another example, *T. longicornis* and *E. affinis* sense water-soluble diesel oil and avoid the contaminated region [121]. Further, chemosensation may be used in combination with other sensory modes including flow sensing [84]. The response to combined cues in this case is species dependent.

Environmental Cues: Multiple Stimuli and Interactions

The way in which behavioral responses change when multiple cues are combined leads to the idea of a cue hierarchy and provides a basic tool for quantifying the ecological implications of individual behavior. A central theme in sensory ecology is the idea of a cue hierarchy in triggering changes in behavior [122]. A cue hierarchy explains the relative importance of various types of sensory cues in triggering behavioral responses in relation to one another. For example, the presence of chemical cues induces *T. longicornis* to strengthen or cancel responses to velocity gradient cues, whereas combined chemical and velocity gradient cues evoke the same response in *A. tonsa* as the isolated cues [60]. The velocity gradient acts as an initial cue to restrict search area in a foraging copepod, and chemical cues then allow the copepod to refine the search area for a resource patch with greater effectiveness [60]. Finally, mechanical contact with individual prey cells initiates feeding behaviors [60]. Each cue allows an individual copepod to systematically and effectively search their local environment for prey or resources. Similarly, as mentioned above for predator-prey interactions, light can modulate the hydromechanical threshold for escape response among copepods [42].

BEHAVIOR AND DISTRIBUTIONS

In this section, we focus on how individual copepod behaviors when viewed collectively affect their distributions over the depth of the water column. As discussed previously, due to the disparity in vertical (meters) and horizontal (kilometers) scales in the ocean, most copepods interact with their surroundings in the vertical direction where scales are better matched to the foraging and swimming capabilities of an individual (e.g., ca. 5 mm s⁻¹, covering 10³ of m in a few hours). Two recent articles review the effects of behavior on zooplankton distributions and the implications on higher trophic levels [2,22].

Foraging and feeding behavior are driven by both mechano- and chemoreception in an effort to locate resource patches. Field studies by Mullin and Brooks [123] found that the copepod *Calanus pacificus* would not be able to survive in the water column except at a preferential depth with concentrated food resources. Similarly, Dero [124] found that a dominant copepod species was food limited at most depths and that minimum concentrations necessary for survival (200 mg cm⁻³ chl-*a*) were only found in one narrow depth range between 20 and 30 m. Furthermore, *in situ* evidence for microscale patchiness [17,125,126] shows that limited food resources inhibit copepod growth and thus copepods must be able to actively locate and exploit isolated resource patches in order to survive. Indeed, the idea of area-restricted search behavior [15,60,127] in individuals through altered swimming speed and increased turn frequency can often produce population scale aggregations. Many species of copepods including *Pseudocalanus minutus* [128], *T. longicornis* and *P. elongatus* [129], and *A. tonsa* [111], are observed to decrease swimming speed (or hop frequency) when encountering food patches. Leising et al. [130] also note predation risks for a foraging copepod exploiting different portions of the water column, and modeling studies by Leising and Franks [127,131] examined the effect of food concentrations and patchiness on copepod swimming behavior and found behavior consistent with area-restricted foraging.

Individual Behavior and Depth Distributions

Individual copepod behaviors, such as predator avoidance, foraging, and mating, have been shown to have dramatic effects on the distribution of copepods in relation to oceanographic properties. Some clear examples of this are in estuaries as described previously in the section on responses to salinity, and in the ‘thin layers’ literature; see e.g., [132-134]. Thin layers are a common feature of the ocean and represent fine-scale (m’s) distributions of both phytoplankton and zooplankton (Figure 3). These layers are often associated with similar scale gradients in temperature, salinity, fluid density, velocity, and turbulence. Copepods, through their behavioral adaptations, appear to be cued into the formation and maintenance of these high resource patches [61,135,136]. Simple individual-based models that simulate behaviors observed in the laboratory over longer time scales have further illustrated that these patches can lead to large-scale distribution patterns in copepods [15,131].

Habitat partitioning is thought to be a critical component in the ability of the pelagic environment to maintain observed levels of biodiversity especially in the plankton. Differences in DVM along with behavioral responses to fluid mechanical, chemical, and phototactic cues can have significant trophic consequences. Many calanoid copepods, like many other zooplankters, are diel vertical migrators, i.e., they exhibit large changes in depth on a diel cycle driven by phototactic cues [137]. When vertical migratory behavior is superimposed on the physical structure of the water column and coupled with individual behavioral responses to patchy cues, population-scale, high-population-density aggregations can result [18]. Experiments on a variety of zooplankton showed that almost every species tested aggregated at salinity and/or temperature interfaces (i.e., the pycnocline; [94]). Fieldwork also showed multiple species of copepods aggregating in the layer just above the permanent halocline [97]. Interestingly, depth distribution was species-segregated. Bollens et al. [138] tested the effects of a variety of mechanical, chemical, and visual cues in producing

patchy aggregations of the copepod *A. hudsonica*. Genin et al. [37] acoustically tracked over 375,000 zooplankters over a coral reef in the Red Sea and observed active swimming against vertical flows resulting in depth maintenance on a population scale could lead to dense aggregations. Finally, Pierson et al. [139] documented that copepods make periodic forays into deeper waters throughout the night, suggesting a higher frequency component to classical conceptualization of DVM.

Foraging behaviors in response to interacting cues in the form of a cue hierarchy can also lead to dense aggregations of copepods in vertical layers based on laboratory experiments and numerical modeling [15,127]. Acoustic data suggest these aggregations can form during a combination of DVM and foraging behavior for organisms in the copepod size classes (Figure 4; [18]). But to date, direct observation of copepod foraging behavior over time scales that could lead to dense aggregations of copepods have not been made.

Direct responses to predators can also affect the distribution of copepods. Bollens and Frost [5] documented the initiation of DVM in response to predators. In fact, recent evidence suggests that some copepod species make repeated migrations between the surface and depth in order to minimize predation risk and maximize feeding opportunity [139]. Whether these migrations are cued by local changes in light intensity or are intrinsic to copepod behavior after food saturation is an on-going question for biological oceanographers that would benefit greatly from advanced *in situ* imaging systems [36,38,126,140].

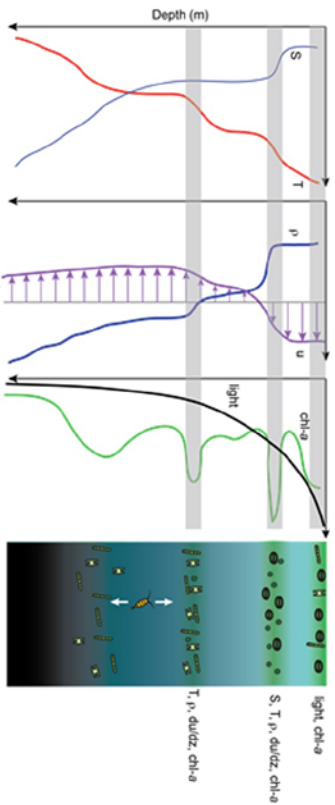


Figure 3. Gradients in the ocean at scales relevant for copepod behavior: Salinity (S), temperature (T), fluid density (ρ), velocity gradients (du/dz), Chlorophyll a ($chl-a$), and light all contribute to the copepod sensory environment, but not all will be associated with preferred prey items.

It is expected that convergent swimming behavior likely plays the largest role in the depth maintenance and distributions of copepods. Whether individual depth preferences develop into large-scale aggregations at the population level is often determined by an interaction between physics and biology [22]. Several mechanisms have been proposed for the development of patches of phytoplankton (e.g., gyro-lactic trapping, shearing, *in situ* growth, buoyancy, convergent behavior). However, at the scale of copepods, swimming speeds are greater than vertical velocities for most of the ocean [2]. Fine-scale cues associated with the formation of phytoplankton patches can differ depending on the mechanism causing the patchiness. Therefore, it is expected that some patches may lead to copepod aggregations,

while others may not. For example, *in situ* growth of phytoplankton can create a patch in the absence of a fluid density gradient or velocity gradient. Copepods therefore may not be able to sense the patch until much later when phytoplankton achieve sufficient density to elicit a chemical response.

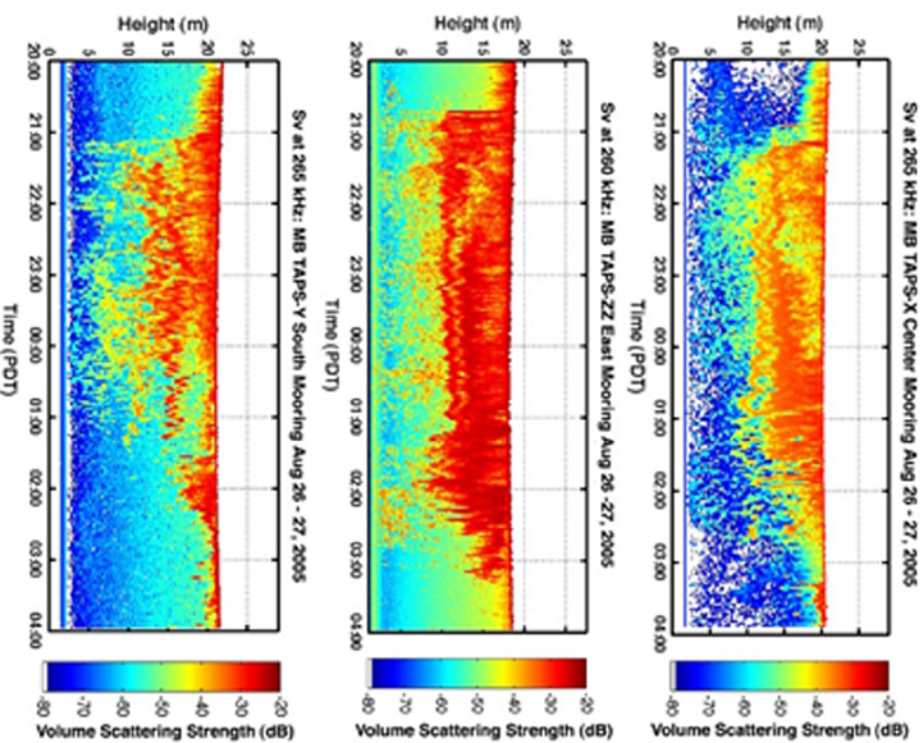


Figure 4. Three volume scattering strength records are displayed, centered on midnight on 26-27 August 2005. These patterns illustrate the similarities and differences in acoustic scattering at three sites in Monterey Bay showing aggregation in layers at night (adapted from [18]).

Aggregations: Physical and Behavioral Drivers

Aggregative behavior in zooplankton is often credited either to physical processes or to behavior [141]. Physical processes such as internal waves, currents, stratification, and turbulence, may affect aggregations, but only at relatively large spatial and temporal scales. However, behavioral interactions that promote aggregations and swarming act at small scales that may not be observed by typical oceanographic or biogeography studies. Behavioral responses that lead to aggregations are attributed to either social interactions, or individual responses to environmental cues [142,143]. These types of behavior differ in that the former is a response to signals/cues that are the product of animals at certain population density; whereas the latter is the result of attraction to a surroundings cue [141,144]. Copepods may exhibit social behavior during mating, but responses to environmental cues, such as fluid mechanical, chemical, and phototactic cues, appear to be the primary driving forces behind copepod swarms [144,145]. Copepod interaction with environmental conditions is directly affected by their ability to perceive and respond to fluid mechanical and chemical information in their surroundings [143,146]. The interaction of these processes at relevant scales affects observed community structure and, therefore, is an important aspect of plankton ecology [1,15,145].

Phytoplankton closely follow distributions of passive scalar quantities, whereas copepods show intense variability even at the smallest scales. On large scales, advective motions of currents can act to transport organisms into general areas [3]. On smaller scales, turbulent motions mix passive particles. Turbulent advection can explain plankton patchiness at large scales (order of kilometers), but variation at small scales is also present [147,148]. The patchiness, described at the inertial scales (scales of Coriolis parameter and Rossby radius) by Abraham [148], is the result of turbulent transport, or behavioral responses [97,149]. The strength of this process is often defined by the turbulence intensity or turbulent diffusivity. Surface winds play an important role in the variation of turbulence through the water column, with the highest turbulent intensity near the surface and lowest in the pycnocline [150]. Fluid density stratification acts to attenuate vertical velocity fluctuations, and thus may aid in creating vertical aggregations of passive particles, such as marine snow, and many phytoplankton species [133].

Fluid density and velocity gradients are more common and easily detectable cues for foraging at larger scales than chemical exudates or phytoplankton presence alone. The presence of fluid density and velocity gradients warrants brief searches for other information, thus focusing the search region, reducing energetic expenditure, and improving individual fitness [15,59,151,152]. Physical gradients are more common than chemical exudate patches, and therefore meet the criteria for detectability at larger scales. Additionally, momentum diffuses faster than scalar quantities (exudates, phytoplankton cells), thus velocity gradients often surround chemical exudate or food patches [59]. Gallagher et al. [152] proposed that aggregations at these layers are a result of copepods using this information to narrow search regions. In contrast, waterborne chemical exudates provide more reliable, but possibly less available cues that also induce swarming and area-restricted search behavior [107,110]. Finally, contact cues (mechanical or chemical) with individual prey cells are likely to provide the most reliable, close-range cues that initiate feeding response [111]. This detectability-reliability issue has been thoroughly addressed for specialist insects in terrestrial systems, and

suggests that foraging individuals employ a host of cues to improve search success and foraging efficiency [122].

TROPHIC INTERACTIONS AND PRODUCTION

If the ocean were well mixed, copepods would be solely dependent on their sensory capabilities and sensory space, which extends at most a few millimeters from the organism itself. In this case, an individual copepod would need to locate prey items (typically single phytoplankton cells) that would be located several meters apart with no other information to locate them. This situation would be equivalent to human beings being required to locate food that is similar in size to a cookie, and each cookie is located several kilometers apart with no information on where the next cookie might be if one is found. In such a situation, copepods would be largely extinct or rare. As it stands, copepods are the most abundant multi-celled organism on earth, largely due to the unique structure of the marine environment that is driven by flow physics and accentuated by biological processes [2].

Convergence and Aggregation

The importance of physical drivers in developing such structure to the marine environment is clearly portrayed in an example illustrated by McManus and Woodson [2] using an allegorical comparison between the scales described above through which copepods and humans interact with their world. The ocean is structured across multiple scales ranging from basin scale circulation to mesoscale eddies and filaments to fronts and clines to fine-scale distributions of phytoplankton [153,154]. These patterns are the result of flow, fluid dynamic instabilities, and stabilizing processes associated with fluid density discontinuities that are primary subjects of the field of physical oceanography. Here, we want to illustrate that the ocean is not well-mixed and is quite structured even at scales relevant to copepod foraging, and it is this structure that determines the production of copepods in the marine environment and how copepods fill a critical gap between primary and tertiary consumers.

Some of the clearest examples of the role copepods play in marine food webs comes from examining thin layers and fronts (e.g., [6,8,16,140]). The term '*thin layer*' in the context of biological and physical oceanography is more or less synonymous with biophysical coupling and has come to be defined as spatially coherent plankton patches (marine snow, bacteria, phytoplankton, zooplankton, ichthyoplankton; [59,155]) in which biomass can be several orders of magnitude greater than the water column immediately above or below the layer (Figure 5). Thin layers range in thickness from a few centimeters to a few meters vertically, span up to square kilometers horizontally, and can persist for days [132,156]. They are a widespread phenomenon occurring in virtually all marine environments where conditions are favorable including fjords, river mouths, continental shelves, and shelf basins [157]. Copepods are known to aggregate in or near thin phytoplankton layers, and aggregation can occur rapidly within a few hours [18,132]. In these regions of vertical aggregations of biological species, the population densities can be enormous (up to several thousand per m³; [158]). The extremely dense aggregation of biomass in thin layers has profound implications

on the health and vitality of marine ecosystems, specifically through its linkage of fine scale (< 1 m) individual behavioral processes and submesoscale (tens to hundreds of meters) processes that underlay the spatiotemporal distribution of marine fishery productivity [8].

As McManus & Woodson [2] point out, fronts are surface outcroppings of vertical fluid density gradients and consequently have similar characteristics to thin layers. Fronts are regions of horizontal gradients in oceanographic properties that have long been known as biological hotspots in the ocean [7,151,159]. Flows in fronts are often convergent with a frontal jet developing along one side of the front [3]. In these regions, phytoplankton are often aggregated and found in densities that can support large populations of copepods similar to those reported for thin layers [160-162].

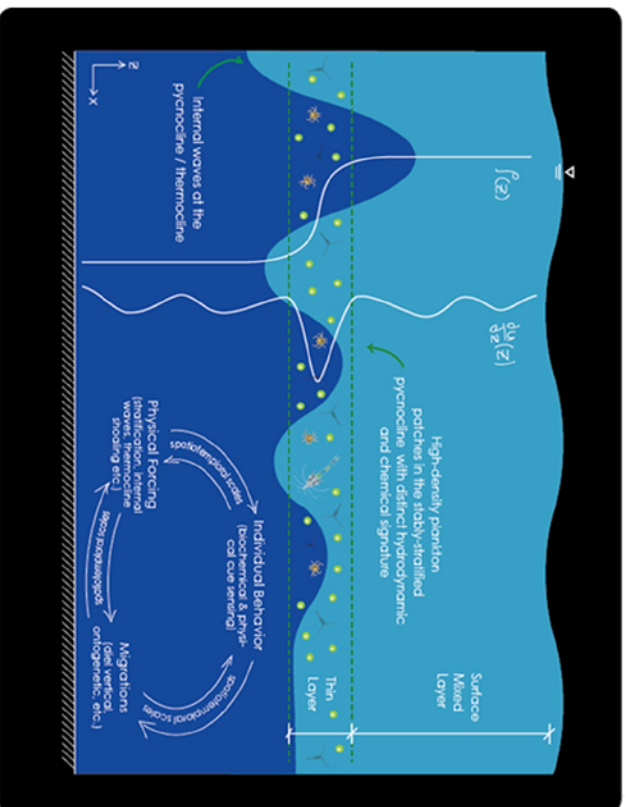


Figure 5. Thin layers are an example of biochemical-physical coupling in high-density plankton patches.

Foraging and Predation in a Turbulent Environment

Turbulence has a multi-faceted effect on copepod feeding and aggregation. At low levels, turbulence can act to increase prey encounter and ingestion rates for copepods simply by increasing the movement of prey items through the sensory sphere of the copepod [29,147,163,164]. However, at higher levels, turbulence can disrupt feeding by increasing handling rates. The bell-shaped response of feeding by small plankters such as

larval fish and copepods to turbulence during feeding also has implications for foraging and aggregation in regions of strong oceanographic gradients such as fronts and clines (Figures 3 and 5; [28]).

In the view of predator-prey interactions for copepods, turbulence acts roughly as a Brownian motion process by which particles are moved around at random and the degree to which this movement occurs is determined by the intensity level of turbulence, often reported as a dissipation rate [165]. At low levels, turbulence has no effect on feeding and ingestion rates among copepods. As turbulence increases due to changes in the flow environment, the contact rate of copepods with prey increases dramatically resulting in a concomitant increase in feeding and ingestion rates. However, as turbulence levels continue to increase, copepods themselves begin to be swept around, handling time for individual prey items increases, and consequently, feeding and ingestion rates begin to decline [28]. The bell-shaped nature of the effects of turbulence on feeding in copepods suggest an optimal feeding window that likely varies by species and may act as a modulator of species coexistence due to spatial variation in turbulence levels.

Moderate levels of turbulence enhance feeding rates for both filter feeding and direct prey capture copepods with stronger effects on the latter [33,166]. In fact, some species of copepods are known to switch dominant feeding mode based on intensity level of turbulence in the environment and can consequently affect the seasonal succession of phytoplankton communities [23,35,167]. This complex interaction between copepod behavior and turbulence provides yet another mechanism for maintaining diversity among copepod species.

Thin layers and fronts are often regions of increased turbulence within the range of enhanced copepod feeding (dissipation rates around $10^{-7} \text{ cm}^2 \text{ s}^{-3}$) as opposed to wind-affected surface layers where dissipation rates can be detrimental to copepod feeding. Interestingly, in most coastal regions, winds are often minimal overnight when copepods ascend to the surface to feed. The hypothesis that copepods may be cued into diurnal variation in turbulence levels as a cue for reverse (nocturnal) DVM in copepods has not been extensively explored. Near fronts and clines, turbulence is also often elevated due to the shearing of the flow, but is quickly dissipated due to the stratification present [168]. This situation may provide not only an optimal environment for phytoplankton growth since nutrients are mixed, but also optimal conditions for copepod feeding where turbulence levels are typically maintained at intermediary levels [28].

For copepods, the effects of turbulence play a similar role for predators (e.g., [28]). Larval fish ingestion rates also increase with increasing turbulence up until a certain point and then decline [30]. However, the optimal levels of turbulence differ for varying size classes of larval fish. In addition, copepod thresholds for escape are species-specific (Table 1), thus suggesting differential susceptibility to predators based on turbulence levels. Similarly, different predator species are likely to deal with turbulence in varying capacities. For example, a small larval fish would be strongly affected by turbulence, while an anchovy might only be moderately affected, and a filter-feeding whale would not be affected at all. Thus, the spatiotemporal dynamics of turbulence in the environment also will regulate predation pressure. The role of turbulence in structuring pelagic communities is still a critical gap in our knowledge, and an active area of ongoing research.

Predation Pressure

It has long been assumed that predation pressure is extremely high and that predation therefore controls copepod population dynamics because of the extreme behaviors exhibited by many species of copepods associated with predator avoidance such as DVM and escape response. However, aggregations of copepods can lead to intense predation pressure as tertiary consumers are able to more readily exploit them similar to the case for copepod grazing on phytoplankton aggregations. In spite of this predation pressure, copepods continue to aggregate at fronts and clines, and thrive [1]. This suggests that, much like for phytoplankton, predation pressure does not play a major role in the population dynamics of copepods.

Individual fitness, however, is important from an evolutionary standpoint thus assuring that predation pressure is a dominant force in determining copepod behaviors at evolutionary time scales. Overall, the increased predation pressure of the population is outweighed by the increased production due to aggregating in or near regions of high phytoplankton densities. Consequently, copepod behaviors associated with predator avoidance may actually be detrimental to the success of the population as a whole where feeding alone could lead to intense secondary production and consequently fueling higher trophic level production. Regardless, copepod behaviors associated with predator avoidance have received considerable attention in the scientific literature due to the prevalence and easily observed effects of avoidance [19,31,169].

The apparent minimal effect of consumers on copepods at the population level mimics the effects of copepods on their prey where copepod predation can cause changes in the structure of the phytoplankton community, although it rarely severely impacts the overall population dynamics or abundance [29,167]. This suggests that in the ocean, very few systems are fully resource limited, and that the structure of the ocean (organizing the available resources into finite, dense patches) is the primary driver of productivity, at least for secondary consumers such as copepods [1,150,163]. It appears that predation has more effect on the population structure and not persistence or population density in plankton communities largely due to the immense productivity in the ocean.

Higher Trophic Level Production

Recently, studies are pointing towards the importance of prey size structure and distributions, and not prey abundance, as the determining factors in higher trophic level foraging success [170]. Spatial aggregations act to increase prey-predator covariance, a critical parameter for transfer of energy through the food web. At small scales, phytoplankton patchiness is largely governed by flow physics, which can lead to spatial aggregations across multiple temporal and spatial scales. The formation and persistence of phytoplankton and microzooplankton patches is controlled by several parameters, namely dispersion, turbulence, shear, and buoyancy, as reviewed in Dunham & Stocker [22]. The size, population density, and longevity of prey patches then affects the ability of the next trophic level, copepods, to exploit the prey [2]. At the level of copepods, swimming and behavior are becoming more important in determining the spatiotemporal characteristics of aggregations. Beyond copepods, most organism aggregation is due to species-specific behaviors that involve

foraging, schooling, and mating. Putting all of this together, however, continues to be a difficult task for oceanographers.

Foraging success of copepods can have dramatic effects on phytoplankton community structure [29,167,171]. Changes in the size structure of the phytoplankton community can drive similar changes in the copepod community presenting an interesting feedback loop within the plankton alone where grazing by copepods on particular phytoplankton species changes the prey size structure and thus changes the dominant predator [23,27,35]. The pattern of this feedback loop presents interesting questions regarding the effects of copepods in multi-level, complex food webs found in natural environments and especially on top predator production.

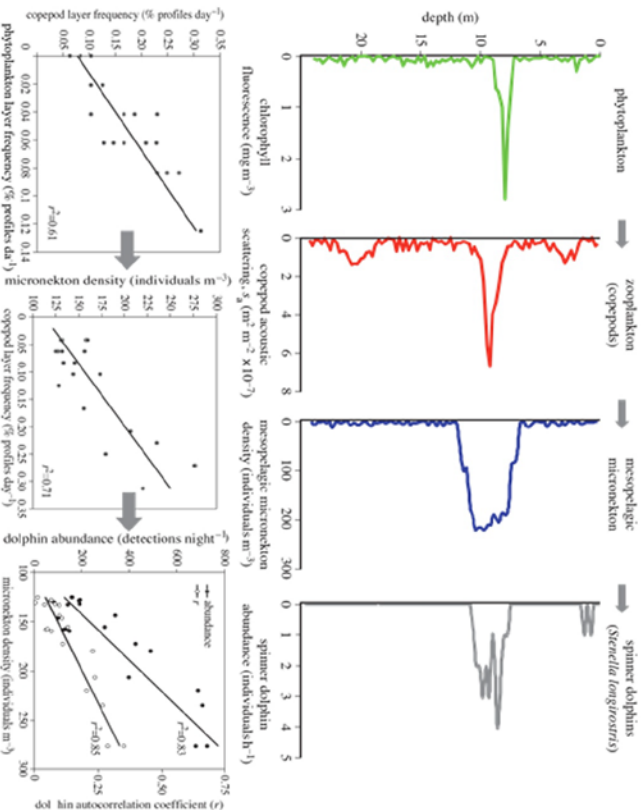


Figure 6. An example of covariation of predators and prey in Hawaii's nearshore pelagic ecosystem measured at 2300 on 4 May 2009 using instruments moored on the 25 m isobaths along with relationships between aggregation characteristics and predator-prey covariation. Adapted from [8].

Following the cookie allegory above, each trophic level requires a certain level of aggregation of its prey resource in order to survive in the ocean (Figure 6). As one moves up the trophic pyramid, the drivers of aggregation shift from physical to behavioral mechanisms [2]. Since copepods are uniquely positioned where their swimming capabilities are just beginning to match the scales of environmental cues in the ocean, they provide not only a critical link between phytoplankton and higher trophic levels, but they also provide the link between physical and biological drivers of production in marine food webs [1]. Regions that

have the physical and flow characteristics to promote intense aggregations of phytoplankton at scales that can be exploited by copepods are often regions that are also highly productive across higher trophic levels [7]. This effect has been observed for a wide range of taxa from predatory zooplankters to whales [8,16,172]. Recent observations of copepod-fish-dolphin interactions in the Hawaiian Islands suggest that spatial aggregations lead to strong bottom-up control of the pelagic community consistent with the idea that copepods play a key role in trophic dynamics of these systems [8].

A CASE STUDY: HARMFUL ALGAL BLOOMS, COPEPOD ECOLOGY, AND ECOLOGICAL IMPLICATIONS

A case study is presented of particular ecological and economic relevance: copepod ecology as it relates to harmful algal bloom (HAB) dynamics. HABs (also often called "red tides") are dense blooms of phytoplankton in fresh and marine waters commonly due to dinoflagellates and diatoms that contain toxic compounds. The frequency, intensity, and geographic distribution of HAB events worldwide have been increasing in the past two decades, with associated adverse effects on ecological, human, and economic health [173-176]. In their critical role as trophic mediators, copepods link primary producers and higher order trophic levels; thus they can significantly influence HAB dynamics and modulate large-scale ecological effects through their physiological and behavioral interactions with toxic blooms. Understanding the relevant, coupled biological, chemical, and physical processes at the correct spatiotemporal scales is critical for building accurate early detection and predictive management tools (coupled biophysical Individual-Based Models, e.g., [177,178]).

Many chemical compounds (e.g., domoic acid, paralytic shellfish poison, dimethyl sulfide; see e.g., [179]) associated with HAB species are known to have deleterious effects on copepod fitness [180] not only because of toxicity-related responses but also from typically low nutritional values. Among studies of copepod grazers fed harmful algae, decreased grazing and fecundity are the most common results, although the causes of decreased grazing (physiological incapacitation, behavioral avoidance or lack of stimulation) and/or decreased fecundity (toxic versus nutritional effect) vary among studies [181]. Prince et al. [182] looked at the effects of toxic *Karenia brevis* on fitness for the copepod *A. tonsa*, and found that on diets rich in *K. brevis*, copepods experienced decreased survivorship and decreased egg production per female, but the percentage of eggs that hatched was unaffected. Similarly, egg production rates of *A. tonsa* fed toxic *K. brevis* strains were similar to those of starved copepods, whereas those of copepods fed non-toxic strains along with beneficial *Rhodomonas salina* were significantly higher [183]. Jiang et al. [180] found an interesting physiological response with evolutionary implications in the copepod *A. tonsa* responding to the harmful dinoflagellate *Cochlodinium polykrikoides*: a rapid gain and loss of evolutionary toxin resistance as a population. After four generations of chronic exposure to toxic phytoplankton, copepods had evolved toxin resistances three times greater than pre-exposure generations; within two generations lacking exposure, all increased toxin resistance was lost. This suggests that copepods can rapidly adapt to dissolved toxic compounds and likely play a critical role in implementing some form of top-down grazer control on toxic phytoplankton blooms. These

findings also highlight how algal toxins may influence copepod feeding behavior and alter top-down control exerted by copepod grazers.

The idea of top-down grazer control (or the modification of it) is consistent across the currently available literature. Hong et al. [184] used digital holographic cinematography to compare feeding behavior of free-swimming copepods, *A. tonsa*, on nutritional prey (*Storsetula major*) to that occurring during exposure to toxic and non-toxic strains of *K. brevis* and *Karlodinium veneficum*. They found two different beating modes of the copepod's feeding appendages—a "sampling beating" of short durations and a longer duration "grazing beating" that generates feeding currents as well as a variety of behavioral regimes corresponding to the presence, absence, or combination of beneficial and harmful algal cells. This modification of top-down grazer control was also seen by Waggett et al. [183] whose data indicate that *K. brevis* influences copepod grazer populations via multiple synergistic mechanisms: (i) decreased ingestion rates, (ii) decreased egg production, and (iii) increased mortality of copepods through a combination of toxicity and nutritional inadequacy. In grazing and mortality experiments, Cohen et al. [185] found that *A. tonsa* exhibited minimal sublethal behavioral responses. However, there were significant effects on the swimming and photobehavior of *Temora turbinata* and *C. typicus* at the lowest sublethal concentrations tested (10^5 *K. brevis* cells l^{-1}), suggesting very low behavioral response thresholds. Their data suggest that sublethal effects of *K. brevis* and its brevetoxins on copepod behavior occur on a species-specific basis. Similarly, Schultz & Kjørboe [186] found that *A. tonsa* was capable of incredibly selective feeding behaviors by remotely identifying and rejecting toxic cells based on associated hydrodynamic or chemical signatures. In contrast, Leandro et al. [187] found that a lack of remote prey selection lead to the copepod *C. finmarchicus* becoming a preferential trophic vector for toxin accumulation, likely due to a lack of ability to remotely characterize toxic cells. Species-specific selective feeding behavior (or lack thereof) through active, remote prey selection can enhance or dampen bloom growth dynamics thus modulating ecological impacts on other trophic levels [186,188].

During toxic bloom conditions, anti-grazing deterrents act to lower predation rates by copepod grazers and sustain the bloom [189-192]. Teegarden et al. [193] showed that even though sloppy copepod grazing was effective at dispersing toxins to low concentration levels by aiding environmental advection and turbulent diffusion, toxins were still seen to bioaccumulate in copepods, acting as a preferential toxin accumulation vector. Extrapolating to higher trophic levels, Gammon et al. [194] examined the effect of HABs on nearshore fish communities through reduced fish abundance and health as well as changes in community structure. The effects are likely due to neurotoxic influences that cause zooplankton to act erratically, and thus become more conspicuous prey items and preferential vectors for trophic transfer of dissolved toxic compounds. These factors, on a species-specific basis, can act in concert to produce preferential vectors by which toxins accumulate at higher trophic levels.

Changes in copepod feeding and swimming behavior caused by toxic compounds can significantly influence predator, prey, and mate encounter rates by altering the fractality ("diffuseness" or "volume-fillingness", e.g., [195]) of a copepod's trajectory. Erratic, hydrodynamically conspicuous, diffuse swimming behavior (i.e., paths with high fractal dimensions) and inconspicuous, ballistic, steady swimming behavior (i.e., low path fractal dimensions) each have their ecological place for copepods; however, too much of one or the other can have deleterious effects on copepod life success (e.g., by decreasing mate or prey encounters or increasing conspicuity to predators). Changes in individual copepod behaviors

are quickly extrapolated to population scale phenomena with important implications for HAB dynamics (intensity/toxicity, duration, trophic transfers, etc.) and overall ecological effects.

Finally, HABs are intricately linked to fronts and clines and thus to copepod ecology; often dissolved toxic compounds should be considered as another biochemical factor in the numerous and biogeochemical dynamics of fronts [196,197] and clines [198-201]. There are numerous biological (phyto-, zoo-, and ichthyoplankton species, algal growth dynamics, zooplankton grazing), chemical (toxic compound, toxicity levels), and physical (hydrography, advection, turbulent and molecular diffusion) factors coupled over wide spatiotemporal scales that affect HAB dynamics and determine overall ecological impacts. These factors interact in a complicated manner, but it is clear that ecological effects and trophic implications are highly species-specific and dependent on toxicity level, mode of action (pathway of toxicity), morphology, and monospecificity of a particular toxic algal species and its associated toxic compounds. In addition, species-specific copepod physiological and behavioral responses (e.g., fitness, foraging, grazing, sampling, mating) as well as local physics (turbulence, stratification, surface waves, internal waves, tides, etc.) play significant roles influencing the duration, density, toxicity, and overall ecological impacts of a particular HAB event.

CONCLUSION

As the largest collective of multicellular organisms on earth and direct consumers of primary producers, copepods are an integral component of the marine ecosystem and are a critical aspect of the spatiotemporal distribution of productivity in the world's oceans. The extent that gradients in oceanographic properties affect populations and communities is still not fully understood, but recent findings suggest that from the perspective of a copepod, the ocean is a structured and patterned habitat at scales much smaller than historically accepted [59,151,202].

Future Directions

The influence of individual behavior on pattern in pelagic habitats warrants further investigation at the fine-to-intermediate scales (mm to m). Emphasis on better resolution in field measurements combined with continued laboratory investigations is imperative to developing our understanding of copepod behavior and ecology at appropriate scales. A continued drive toward understanding and answering some of these large-scale issues will benefit from collaborations between field studies and experimental investigations where specific aspects can be accurately isolated and controlled. As we become more aware of the importance of fine-scale structure in the ocean, it is necessary to begin to test the impact of these features on larger scale ecological processes. This oceanographic structure leads to distinct behavioral responses by copepods that can have immense effects on aggregations and large-scale distributions. Such aggregations provide a critical link to higher trophic level production and interactions.

Copepod behavior remains an important topic in oceanographic research due to its importance in determining predator-prey interactions at the base of an immensely productive

food web that is the primary source of sustenance for a large portion of the world's human population. Recent evidence suggesting that the immense role of structure and pattern in the marine environment (as a driver of production that determines trophic pathways) critically hinges on the ability of copepods to find and locate prey. We have identified through this chapter four areas that are important to furthering our understanding of the direct and indirect effects of copepod behavior on pelagic ecosystem dynamics. First, developing an understanding of how copepods may employ horizontal gradients in turbidity (light intensity) for position maintenance in regions where horizontal gradients are of appropriate scale (estuaries, coastal ocean fronts). Second, elucidation of the proximate cues for DVM as it relates to fine-scale foraging behavior. Third, the role of turbulence in structuring pelagic communities. Finally, the natural variability of predator-prey covariance affects the role of copepods in complex food webs. Many of these issues will require novel combinations of modeling and *in situ* observations. New emergent models of phytoplankton communities provide an important step in this direction [27,35,203]. Expanding these models to higher trophic level interactions should provide unique insights into zooplankton community dynamics. Although direct observation of copepod behavior in the field is still a difficult problem, some recent advances in imaging systems provide a ray of hope for this issue (Figure 7; [36,38,126]) that should allow testing and parameterization of large-scale ecosystem models in the near future.

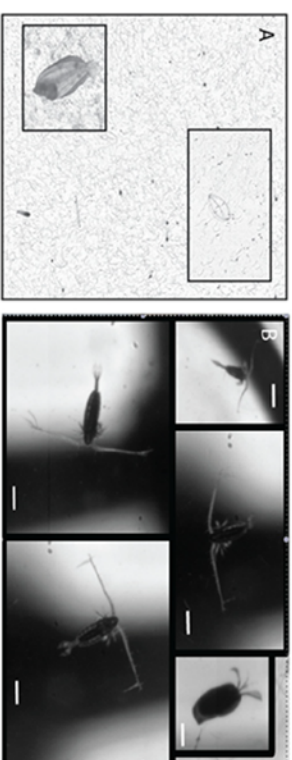


Figure 7. Images from (A) ISHS (In Situ Ichthyoplankton Imaging System; courtesy of R.K. Cowen and A.T. Greer; RSMAS), and (B) ZOOPlankton Sonar; courtesy of J. Jaffe and C. Brisenio-Scripts), new technologies that are allowing quantitative estimation of predator-prey dynamics in copepod ecology. Scales in (B) correspond to 1 mm.

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