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# Community Trait Distribution Across Environmental Gradients

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## ABSTRACT

Variability in community composition is often attributed to underlying differences in physical environments. However, predator–prey interactions can play an equally important role in structuring communities. Although environmental differences select for different species assemblages, less is known about their impacts on trait compositions. We develop a trait-based analysis of plankton communities of the southern California Current System across multiple trophic levels, from bacteria to mesozooplankton, and over a gradient of environmental conditions, from the oligotrophic open ocean to coastal upwelling. Across a factor of four differences in total community biomass, we

observe similarities in the size structure along the environmental gradient, with the most pronounced departures from proportional variations in the biomasses found in the largest protists (> 40 µm). Differences in the trait distributions emerge within a small range of size groups: greater biomass contribution of larger autotrophs (> 10 µm) is observed only for the upwelling region.

**Key words:** Activity traits; California current; community structure; feeding mode; multi-trophic interactions; plankton; resource acquisition; size distribution; upwelling.

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Data collected as a part of the California Current Ecosystem LTER programme can be found at <https://oceaninformatics.ucsd.edu/datazoo/catalogs/ccelter/datasets>.

**Author Contributions** KMK, KHA and AWV developed the concept of the trait-based analysis presented in the study. KMK conducted the analysis and prepared the first draft of the manuscript. KHA, AWV and MDO provided the supervision and guidance during the study progression. MDO contributed the mesozooplankton data and assistance with characterizations of zooplankton traits and ocean hydrography. MRL contributed pico-, nano- and microplankton data and guidance with characterizations of resource acquisition traits. All authors provided critical feedback and substantially contributed to manuscript revisions.

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## MANUSCRIPTS HIGHLIGHTS

- Multi-trophic analysis of plankton interactions using taxa-transcending activity traits.
- Striking similarities in trait distributions across a pronounced contrasts in biomass.
- Nutrient availability drives biomass, while grazer control stabilizes trait distribution.

## INTRODUCTION

The trait-based approach is gaining traction among terrestrial and marine ecologists (McGill and others 2006). Its central concept that ecological interactions are governed by the traits and trade-offs of individuals, rather than their taxonomic affiliations, creates a theoretical framework that can

predict the mechanisms structuring an ecosystem assemblage (Tilman 1990). This approach has been useful in a wide range of research topics, from modelling functional groups (Follows and Dutkiewicz 2011) to organizing empirical observations of communities (Westoby and Wright 2006; Gravel and others 2016).

Much of the potential of the trait-based approach lies in its ability to establish a mechanistic link between the trade-offs faced by individuals and the emergence of community structure and function (Tilman 1990). The challenge of developing a trait-based description of a community is in the inspired selection of a few traits that are most important for the individuals' success. For example, vegetation types can be described by leaf mass per area, stem-specific density, maximum size and seed mass (Westoby and Wright 2006), which have been used to explain environmentally driven contrasts in the dominant vegetation type (van Bodegom and others 2014), or in competition-based models (Falster and others 2017). In marine environments, an emerging understanding of the fundamental traits centres around cell and body size (Sheldon and others 1972; Andersen and others 2016), trophic strategy (Chakraborty and others 2017) and feeding behaviour (Kjørboe 2011). The classification using the above-mentioned traits for marine communities focuses on the importance of predator-prey interactions, in contrast to the competition-focused traits used to characterize terrestrial vegetation. However, in contrast to the trait-based description of vascular land plants, a trait-based classification has so far been implemented to a limited subset of taxonomic groups, often within the same or adjacent trophic levels (Barton and others 2013; Brun and others 2016; Kenitz and others 2017). A trait-based approach that utilizes taxa-transcending traits that could be used to characterize a wide range of sizes and trophic levels has not yet been applied to describe marine ecosystems.

Cell size is associated with the trophic strategies of marine protists, which together with turbulence and nutrient concentration are key determinants of the composition of protist communities (Margalef 1978; Irigoien and others 2004). In nutrient-limited regions, such as subtropical ocean gyres, smaller cells outcompete larger cells in diffusive uptake of nutrients. To compensate, larger cells often adopt mixotrophic resource acquisition strategy to meet their nutrient requirements (Hartmann and others 2012; Chakraborty and others 2017). In contrast, under turbulent and nutrient-rich conditions characteristic of subpolar

gyres and upwelling regions, larger autotrophic cells gain an advantage as nutrient uptake becomes less restrictive and larger size provides a temporary refuge from size-selective predation (Kjørboe 1993).

Predator-prey interactions exert equally important impacts in shaping communities as size-based competition (Verity and Smetacek 1996; Armstrong 1999). Larger organisms tend to eat smaller ones, and this size-dependent predation determines the size structure of communities and the biomass distributions among adjacent trophic levels (Sheldon and others 1972; Andersen and Beyer 2006). In addition to body size, interactions across trophic levels are strongly coupled to the feeding strategy expressed by predators. An active search for food increases an organism's encounter rate with prey, but invariably also exposes it to a greater risk of predation, while a passive feeding strategy is associated with lower predation risk, but also lower food encounter (Gerritsen and Strickler 1977; Kjørboe 2011). Passive feeding modes include 'sit-and-wait' hunting strategies that rely on motile prey to come within a predator's sensory reach. Active feeders cruise through the water or generate feeding currents to predominantly capture non-motile prey (Kjørboe 2011). Therefore, the activity traits—active or passive feeding strategy and motile or non-motile behaviour—in conjunction with size-based prey preferences, determine predator-prey interactions.

Here, we develop a trait-based description of planktonic communities spanning multiple trophic levels in terms of three key functional traits: organism size, trophic strategy (phototrophic, mixotrophic or heterotrophic) and activity (see Box 1). Size is considered the master trait, and we analyse the distributions of biomass, trophic strategy and activity according to size. Together, these three traits strongly influence an organism's ability to take up resources, its exposure to predators and encounters with prey. In other words, trade-offs are linked through trophic interactions, and the dominant trait combination (size, trophic strategy and activity level) depends not only on the physical drivers, but also on the distributions of the key traits in neighbouring trophic levels. We expect that these fundamental trophic arrangements are expressed as distinct patterns in trait distributions across gradients in physical environments.

We utilize observational data from the California Current System (CCS), spanning multiple trophic levels, from bacteria to large mesozooplankton (Figure 1). The CCS is a region characterized by steep environmental gradients that provide an ideal

**Box 1.** Classification of Activity Traits Across Taxa

Differences in the morphological complexities of organisms lead to a great diversity of feeding behaviours that organisms adopt to capture food across multiple trophic levels. Feeding modes can be categorized as ‘active’ and ‘passive’. For example, active feeders move through the water or generate some form of feeding current in pursuit of their prey, whereas organisms that rely on motile prey to enter their detection and capture volumes are considered passive. Clearance rate increases for more active strategists due to relatively higher encounter rates with their prey. However, organisms that exhibit higher activity while searching for food are more exposed to their predators, which introduces an important trade-off between feeding efficiency and predation risk (Kjørboe 2011). Therefore, the selection of suitable strategy is important in determining feeding success as well as predation risk for an individual organism, and shapes interactions across multiple trophic levels.

Below are some examples of multi-trophic classification of active and passive feeding behaviours within the marine food web:

*Passive feeders*

One category of passive feeding strategists is composed of prokaryotes and protists that take up organic or inorganic nutrients by diffusion across the cell membrane. This includes heterotrophic bacteria that take up dissolved organic compounds and autotrophic cyanobacteria (*Synechococcus* and *Prochlorococcus* (Figure 1A) spp.) and eukaryotic producers (such as diatoms; Figure 1B) that take up inorganic nutrients and synthesize organic compounds. Autotrophic protists often do not possess the ability and structures that would allow them to propel themselves, and are therefore considered non-motile. Some marine bacteria exhibit motile behaviour, with the occasional relatively high-speed bursts that allow them to keep up with the nutrient-rich patches (Mitchell and others 1995). Still, bacterial motility acts to enhance the diffusive nutrient uptake, and therefore bacteria are considered passive here.

For multicellular organisms, passive feeding behaviours include ‘sit-and-wait’ strategies. For example, pteropods (Figure 1C) secrete a sheet-like mucous web on which they collect sinking particulate material or trap motile prey (Gilmer and Harbison 1986). Similarly, copepods that collect sinking particulate matter, such as marine snow, so-called flux feeders, are considered passive strategists (Kjørboe 2011).

Passive feeders also include organisms that exhibit ambush-feeding behaviours, such as cyclopoid copepods (Figure 1D; for example, *Oithona* spp.) and chaetognaths (Figure 1E) that remain relatively motionless and wait for motile prey to come within their sensory fields (Kjørboe 2011). Although these two examples of ambush feeders exhibit carnivory, they differ significantly in trophic level: cyclopoid copepods feed mostly on microzooplankton, though supplement their diet with diatoms (Castellani and others 2005); chaetognath diets consist mainly of small copepods (Tönnesson and Tiselius 2005).

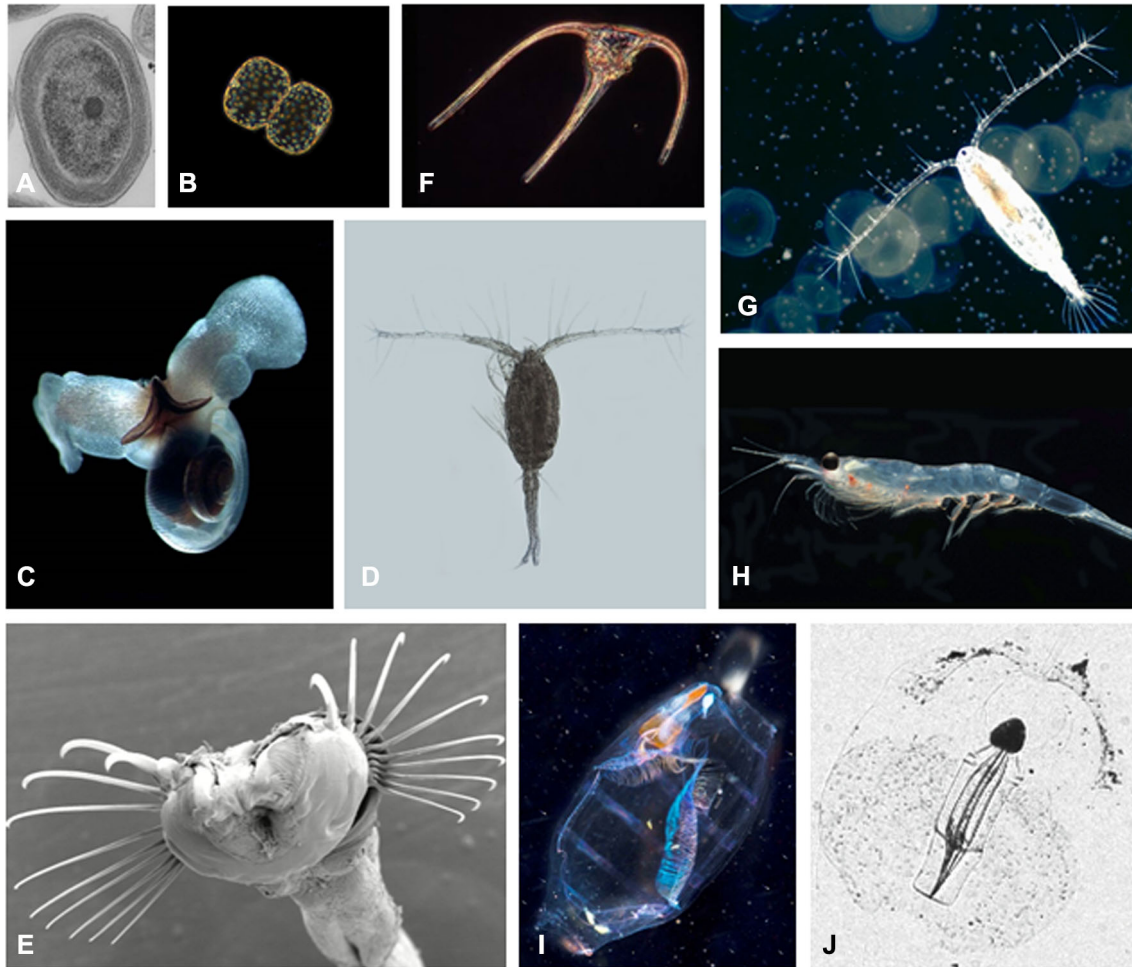
*Active feeders*

Among protists, active strategists include mixotrophic and heterotrophic cells such as flagellates (Figure 1F) or ciliates that use their flagella or cilia to generate propulsion or feeding currents to acquire food particles (Fenchel 1980; Boenigk and Arndt 2000). Active protists are the most important grazers of bacteria (Gonzalez and others 1990) and phytoplankton and exhibit predatory hunting behaviours as well (Pfister and Arndt 1998).

Among mesozooplankton, active feeders include calanoid copepods (Figure 1G) and krill (Figure 1H) that use appendages to generate feeding currents or to search actively for prey. Additionally, pelagic tunicates draw and expel water through their transparent, barrel-shaped housing using muscle contractions (for example, salps and doliolids; Figure 1I) or tail undulations (for example, appendicularia; Figure 1J), and filter food particles onto fine mucus webs (MacGinitie 1939).

testing ground for investigating the impacts of environmental variability on ecosystem structure (Rykaczewski and Checkley 2008; Checkley and Barth 2009; Taylor and Landry 2018). The contrasting physical environments of the CCS have been previously linked to distinct shifts in phytoplankton community structure (Mullin 1998; Taylor and others 2015; Taylor and Landry 2018), biomass of macrozooplankton taxonomic groups (Colebrook 1977) and community size spectra (Rykaczewski and Checkley 2008) across sampling transects from coastal upwelling to the open ocean.

With the large environmental gradient in the CCS, we expect that our trait-based analysis will reflect the major environmental contrasts in the oceans between oligotrophic and eutrophic regions. We would expect that nutrient-driven contrasts in the protist community structure cascade further up the food web and evoke alternating expression of activity traits across trophic levels (Kenitz and others 2017). However, across the contrasts in the physical environment, we discovered a somewhat conserved trait distribution of body size, trophic strategies and activity traits. We show how classic descriptions of the differences between oligotrophic



**Figure 1.** A variety of marine organisms, from bacteria to mesozooplankton: **A** *Prochlorococcus marinus* MED4, courtesy of Luke Thompson (MIT) and Nicki Watson (Whitehead Institute for Biomedical Research), copyright Chisholm Lab, MIT; **B** *Coscinodiscus* sp., image courtesy Jaffe Lab for Underwater Imaging, SIO; **C** *Limacina helicina*, courtesy of R.R. Hopcroft, UAF; **D** *Oithona similis*, courtesy of M.D. Ohman, SIO; **E** *Sagitta* sp., courtesy of S. Haddock, MBARI; **F** *Ceratium* sp., courtesy of Jaffe Lab, SIO; **G** *Acartia tonsa*, courtesy of T. Kiørboe, DTU Aqua; **H** *Euphausia pacifica*, courtesy of M.D. Ohman, SIO; **I** Doliolid, courtesy of M. Stukel, Florida State University; **J** Appendicularian, courtesy of M.D. Ohman, SIO.

and eutrophic oceanographic regions can be understood as deviations from this conserved structure.

## MATERIALS AND METHODS

To investigate the effects of the environment in shaping plankton community composition, we categorize the sampled communities based on their physical environmental properties. Further, each community is composed of several taxonomic groups, which we categorized according to their resource acquisition or feeding strategies. We then tested for systematic variability in feeding and activity trait distributions within size classes and ecosystem types as an indicator of shifting arrangements in trophic interactions.

## Sampling Area and Station Classification

The sampling area is located in the southern section of the CCS, where the southward-flowing California Current separates the inner region of coastal upwelling from the nutrient-limited open ocean. Physical and biological measurements are collected four times per year by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and California Current Ecosystem LTER (CCE-LTER) programmes from 66 stations. Of these, detailed analyses are conducted along two cross-shore transects: beginning at the upwelling centre off Point Conception (line 80) and originating in the coastal waters of the Southern California Bight (line 90) (Figure 2).

The highly dynamic hydrography of the CCS leads to strong temporal variability in environmental properties at each station, preventing classification of stations into constant hydrographic regimes based only on geographical location. Classification of stations was therefore done using the physical water properties at each station and each sampling event. Physical measurements are available from March 1990 to January 2011.

We used the random forest classifier to allocate stations into three categories: upwelling, core California Current and oceanic. Each category was distinguished based on temperature, salinity and oxygen measurements taken every 25 m from 50 to 200 m depth (Lynn and Simpson 1987). Inorganic nutrients were not included as classification parameters due to their direct effects on phytoplankton community structure. Trial inclusion of nutrients in the criteria for classification showed little effect on the station allocation. Upwelling waters are characterized by high salinity, low temperatures and low dissolved oxygen concentration. Waters transported by California Current are somewhat fresher and highly oxygenated. Oceanic waters are warmer, and the vertical temperature profiles of the oceanic stations reveal more pronounced thermal stratification (Figure 3; Supplementary Material S1). The training data for the random forest classifier were obtained by manual classification of the physical properties for stations most likely located within the defined hydro-

graphical features. Selected profiles at station 55 (line 80) provided the training data for the upwelling category, station 80 (line 80) for the California Current, and station 120 (line 90) for oceanic waters. The complete list of the training data is provided in Supplementary Material S2.

Selection of the hydrographic categories was conducted by excluding the sampling events located in the mixing regions between hydrographic features. At each sampling event, the station was assigned to a particular category based on probability. The exclusion of the mixing regions was implemented by considering only the sampling events where the water characteristics were classified with a probability of at least 0.7. This approach aimed to eliminate transient regions that could diminish emergent contrasts in the plankton community assemblages.

## Plankton Data

The plankton community data analysed by the CCE-LTER programme span multiple trophic levels from photosynthetic picoplankton to carnivorous mesozooplankton. Detailed information related to the collection and analysis methods is outlined in the CalCOFI and CCE-LTER Methods Manuals (<http://cce.lternet.edu/data/methods-manual>). For pico-, nano- and microplankton, we use the samples collected from November 2004 to December 2010, and for mesozooplankton, from November 2005 to January 2011.

Available picoplankton data include biomass estimates for heterotrophic bacteria and photosynthetic *Prochlorococcus* and *Synechococcus* spp. Picoplankton are sampled at multiple depths; however, only samples collected within the upper euphotic zone, with the depth range matching nano- and microplankton samples, are considered here. The cells are enumerated using an Altra flow cytometer. Abundance estimates are converted to carbon biomass using the literature-based carbon contents per cell for each taxon (Garrison and others 2000; more details in the CalCOFI Methods Manual).

Nano- and microplankton are routinely sampled at three depths, down to the deep chlorophyll maximum. Here, we consider only samples collected within the upper euphotic zone, which are the two shallowest samples. The abundance and biomass measurements are obtained using high-throughput digital epifluorescence microscopy (Taylor and others 2015). The community is divided into eight distinct taxonomic groups (Table 1), with heterotrophs distinguished by the

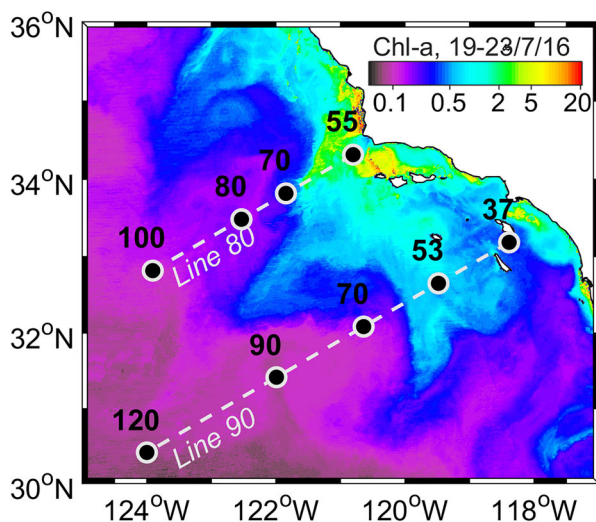
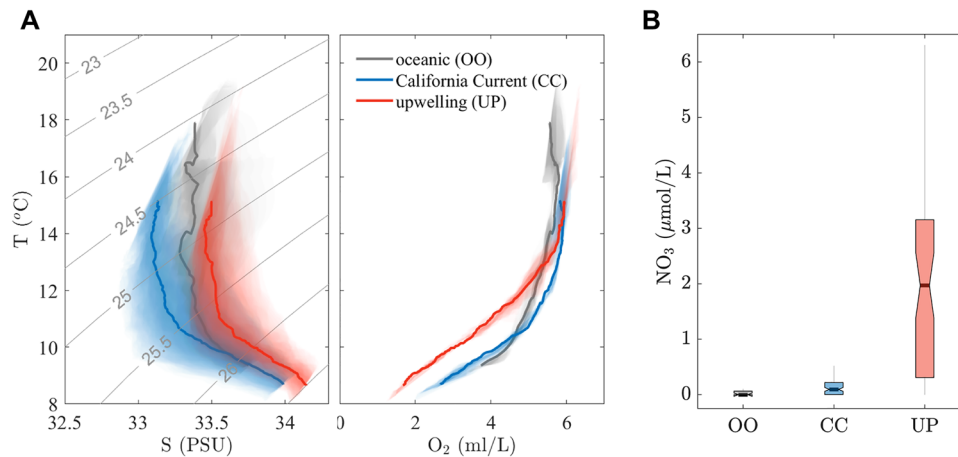


Figure 2. Location of the sampling stations along lines 80 and 90 in the California Current Ecosystem LTER region, superimposed on a satellite image of Chl-*a* ( $\text{mg m}^{-3}$ ). The image is a composite of NASA Level-2 datasets from MODISA, MODIST and VIIRS for 19–23 July 2016. Data courtesy of M. Kahru, SIO.



**Figure 3.** Physical properties of the three station groupings classified by the random forest algorithm: upwelling, California Current and oceanic water masses. Panel **A** highlights mean differences in temperature–salinity (T–S; *left*) and temperature–oxygen diagrams (T–O<sub>2</sub>; *right*) for the study period of November 2004 to January 2011. Coloured shaded areas are 95% confidence intervals. Panel **B** contrasts differences in nutrient (NO<sub>3</sub>) concentrations averaged over the upper euphotic zone (depth range corresponding to the sampling depth of protists). Seasonal contrasts in the physical properties of each region are provided in Supplementary Material S1.

absence of chlorophyll. Nano- and microplankton biomass estimates were obtained for five size classes based on the measured cell lengths: less than 5, 5–10, 10–20, 20–40 and greater than 40 μm. Size classification was based on measurements of the longest axis of individual cells, and therefore the organization of cells into chains is not accounted for. Additionally, one important limitation of the sampling procedures was the suboptimal preservation of ciliates, which led to an underestimation of their biomass.

Mesozooplankton samples were taken with a PRPOOS (Planktonic Rate Processes in Oligotrophic Ocean Systems) 0.5-m-diameter net with 202-μm mesh, hauled vertically from 210 m to the surface. Formalin-preserved mesozooplankton samples were classified into the taxonomic groups, listed in Table 1, using a ZooScan digital imaging system (Gorsky and others 2010) followed by 100% manual validation. The mesozooplankton community was grouped into three size classes: less than 1.5, 1.5–5 and greater than 5 mm based on feret diameter (FD; the longest dimension of an imaged object). Feret diameter is linearly related to body length (Gorsky and others 2010). Additionally, twenty logarithmically spaced size groups from 0.4 to 5 mm FD were extracted for the investigation of the size distributions of copepods only. C biomass was obtained from taxon-specific length-C relations in Lavaniegos and Ohman (2007).

The biomass (*B*) estimates for all plankton size classes were corrected for the widths of the size bins to assure uniform, logarithmically spaced size bins. For picoplankton, the limits include cells from 0.2 to 2 μm. For nano- and microplankton, we assume the cell size ranges from 2 to 80 μm. For mesozooplankton, the smallest organisms detected by ZooScan are 0.4 mm in feret diameter.

## Classification of Trophic Strategy Traits

In addition to body (cell) size, we focus on trophic strategy traits that are realized differently across trophic levels. For unicellular organisms, we consider resource acquisition strategy and motility. For more complex organisms, we characterize feeding mode. We characterize different trait groups in terms of their relative activity level. Whether the behaviour is considered passive or active depends on the relative magnitudes of hydromechanical disturbance generated by feeding activities. Plankton taxa are grouped according to their resource acquisition or feeding traits as listed in Table 1.

## Statistical Analysis

### *Tukey's HSD Test*

Tukey's honest significant difference (HSD) test was conducted to identify any significant contrasts in the trait compositions of sampled plankton community between the considered regional categories. The test was applied to each trait group within each plankton size class. The significance of

**Table 1.** Classification of Activity Traits for Plankton Taxonomic Groups

Trait classification	Taxonomic group
Picoplankton	
Passive	
Non-motile heterotrophs	Heterotrophic bacteria
Non-motile autotrophs	<i>Synechococcus</i> spp., <i>Prochlorococcus</i> spp.
Nano- and microplankton	
Active	
Motile heterotrophs	Dinoflagellates, flagellates, ciliates
Motile mixotrophs	Dinoflagellates, flagellates, cryptophytes, prymnesiophytes
Passive	
Non-motile autotrophs	Diatoms
Mesozooplankton	
Active	
Other	Cnidaria + ctenophores, ostracods, polychaetes
Cruise/feeding-current feeders	Euphausiids, calanoid copepods
Filter feeders	Doliolids + salps, appendicularians
Passive	
Mucous-web feeders	Pteropods
Marine snow/flux feeders	Harpacticoid and poecilostomatoid copepods
Ambush feeders	Oithonid copepods, chaetognaths

the observed contrasts is presented in Supplementary Material S4.

## RESULTS

### Plankton Biomass Distribution

The highly productive upwelling zone of the study region sustains roughly fourfold higher mean biomass than the oceanic provinces and over twice the biomass of the California Current waters (Figure 4A). Because biomass is compressed within shallow euphotic zones of the upwelling area, the actual peak concentrations of food resources available to consumers are even further elevated relative to the sparse and deeper euphotic zones of the oceanic and California Current areas. Despite this, the size distributions of biomass are similar across the sites and resemble a Sheldon spectrum, where the integrated biomasses within logarithmically spaced size bins approximately weakly decline with size (Sheldon and others 1972). There are, however, notable deviations for the picoplankton and the largest protists ( $> 40 \mu\text{m}$ ), particularly for the upwelling region. Picoplankton are relatively less abundant in the upwelling region than in the oceanic and California Current regions. In contrast, large protists ( $> 40 \mu\text{m}$ ) have biomass levels similar to those of smaller protists in the upwelling region, but are virtually absent in the oceanic regions.

### Spatial Contrasts in Plankton Community Trait Compositions

The overall distributions of the activity traits share a lot of similarities among regions, both in terms of the ratios of passive/active organisms (Figure 4B) and the full trait distributions of feeding modes (Figure 4C; see Supplementary Material S4). The main difference is a shift from small towards large autotrophs in the upwelling region. As with the size distributions, the most notable difference is confined to the largest protists ( $> 40 \mu\text{m}$ ), though statistically significant differences are seen for all groups of protists larger than  $10 \mu\text{m}$ .

Passive cells (non-motile autotrophs) in the size range  $10\text{--}40 \mu\text{m}$  are significantly more dominant in the upwelling area than in the California Current ( $p < 0.001$ ; see Supplementary Material S4) and oceanic ( $p < 0.01$ ) waters. This difference corresponds to an increasing dominance of autotrophs relative to heterotrophs and is mainly due to the occurrence of large diatoms in the upwelling area. For the largest size class of protists ( $> 40 \mu\text{m}$ ), community trait compositions exhibit strong seasonal variability, especially in the California Current and oceanic regions, with statistically significant differences for autotrophs and heterotrophs only for the California Current (see Figure S4 in the Supplementary Material). Aside from these differences, the trait distributions for the





protistan communities are similar between the California Current and oceanic regions.

Among mesozooplankton, passive feeding is somewhat more prevalent in oceanic waters for all considered size classes. Small and moderate size classes of flux feeders increase significantly ( $p < 0.001$ ) in the oceanic region, whereas the biomass contributions of small ambush feeders remain largely conserved across the environmental gradient. For the mid-size range (1500–5000  $\mu\text{m}$ ), we observe a slight increase in ambush feeders (mainly chaetognaths) from the upwelling to the California Current to the oceanic regions ( $p < 0.05$ ). Overall, for small and mid-sizes of mesozooplankton, upwelling and California Current regions show relatively similar community trait compositions, while oceanic waters exhibit statistically significant contrasts.

For the largest zooplankton size class, a statistically significant decline of passive feeders in upwelling waters emerges due to a decreasing proportion of ambush-feeding chaetognaths ( $p < 0.01$  when compared to California Current;  $p < 0.05$  when compared to the oceanic region). This is associated with an increased proportion of feeding-current/cruise feeders ( $p < 0.001$  when compared to California Current;  $p < 0.05$  when compared to oceanic waters). Oceanic and California Current communities show no significant differences in trait compositions of large mesozooplankton.

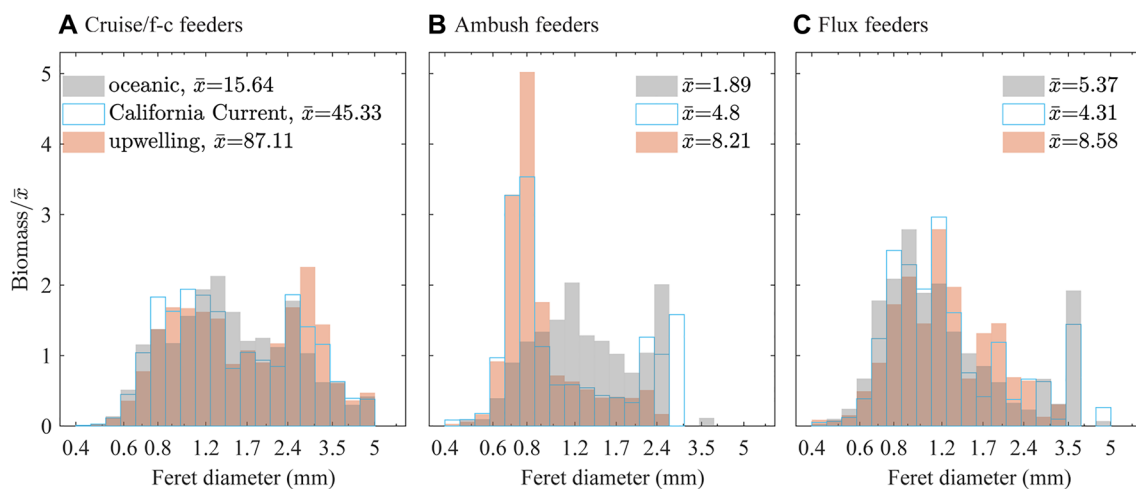
## Copepod Size Distributions

Copepods are the numerically dominant animals in most planktonic ecosystems, and their documented diverse feeding strategies provide an additional route by which we can evaluate potential environmental relationships in trait distributions.

Active copepods that generate feeding currents or exhibit cruise feeding (Figure 5A) are characterized by a bimodal size distribution, dominated by animals in the size ranges of 0.78–1.51 mm and 2.25–3.83 mm (FL). This distribution is a conserved feature across the range of environmental conditions in the CCS study region.

In contrast, significant differences are observed for the size distributions of ambush-feeding copepods (Figure 5B). For the oceanic assemblage, biomass is dominated by moderately sized individuals of 0.97–1.25 mm (FL). In the upwelling and California Current regions, the size structure shifts towards smaller individuals, 0.66–0.97 mm (FL). Additionally, the biomass contribution of larger animals, 2.07–3.02 mm (FL), increases in the California Current.

For flux-feeding copepods, size distributions show no pronounced spatial contrasts (Figure 5C). Across all three regions, the distributions are skewed towards smaller animals, with the flux-feeding community dominated by individuals of 0.75 to 1.25 mm (FL).



**Figure 5.** Size distributions of copepod taxa grouped according to their dominant feeding strategies for water masses classified as oceanic, California Current and upwelling: **A** cruise/feeding-current feeders (active), **B** ambush feeders (passive) and **C** marine snow/flux feeders (passive). For each region and feeding group, the biomass ( $\text{mg C m}^{-2}$ ) is normalized to the mean,  $\bar{x}$ .

## DISCUSSION

The three CCS regions in the present analysis differ on average by fourfold in total community biomass and sevenfold in biomass of primary producers at the food web base. Despite the contrasts in total community biomass and biomass distributions, the broad-scale trait compositions across all size groups of plankton show many similarities. There are no significant differences in the proportion of heterotrophs to autotrophs within the bacterial communities across the environmental gradient, as has been observed for picoplankton communities along the environmental gradient of the Atlantic Meridional Transect (Zubkov and others 2000). Similarly, the composition of the smaller-than-10- $\mu\text{m}$  nanoplankton varies little. The differences in total biomass among regions result from differences in nutrient levels, with the coastal upwelling region characterized by the order of magnitude higher nutrient concentrations than the oceanic region. This agrees with the theoretical prediction of a direct relation between productivity and the overall magnitude of the biomass size distribution (Andersen and Beyer 2006).

Environmental conditions are well known to shape community structure in pelagic marine ecosystems (Margalef 1978; Irigoien and others 2004). High-nutrient conditions lead to a dominance of larger autotrophic plankton, typically diatoms, either as single cells or chain colonies, whose morphologies allow for more efficient nutrient uptake in the turbulent regions of coastal upwelling (Margalef 1978; Pahlow and others 1997). On the other extreme, low-nutrient regions are dominated by very small cells, the superior competitors for nutrients (Raven 1986; San Martin and others 2006). The present results generally conform to these expectations, but only in a limited size range, by showing strong departures from proportional variations in the biomasses, particularly for the larger greater-than-40- $\mu\text{m}$  protists (Figure 4A). It should be noted, though, that the range of environmental conditions in the CCS region does not include extreme oligotrophic regions. Had the analysis included regions even further offshore, the contrast in the two larger groups of protists, and possibly also the smallest size group, might be larger. Although the trait-size-based analysis confirms previous findings of environmental shaping of community structure, it shows that these differences are only present in a relative narrow size range, and the dominant picture is that the overall size-trait distribution is mainly conserved across the environmental gradient.

Despite differences in total community biomass, one shared characteristic of the activity distributions among regions is the alternation of passive and active strategies in adjacent size classes, with the differences diminishing towards larger size categories. Thus, largely inactive bacteria (picoplankton) are fed upon by largely motile nano-heterotrophs and mixotrophs (< 10–20  $\mu\text{m}$  protists), and mostly passive microplankton are fed upon by more active small- and mid-sized zooplankton, and they by more passive larger zooplankton (Figure 4B, C). The trend for a greater proportion of passive large protists in the greater-than-20 and 40  $\mu\text{m}$  sizes in upwelling waters is also reflected in an elevated proportion of active smaller-than-1500 and 5000  $\mu\text{m}$  zooplankton consumers compared to oceanic waters.

The conservation of the proportion of mixotrophic cells across all size classes is at odds with mixotrophy being a superior trophic strategy in highly oligotrophic waters (Ward and others 2011; Chakraborty and others 2017). However, our analysis only reflects the potential biomass of mixotrophic cells and not the degree to which they express the extremes of mixotrophic behaviours under different environmental conditions. That is, depending on resource availability and a mixotroph's relative investment in autotrophy or phagotrophy, metabolism can be purely autotrophic or purely heterotrophic. We therefore cannot exclude the possibility that there is a difference in the actual proportion of protistan phagotrophy that occurs among the regions. Thus, although there are some differences in the trait distributions among the oceanographic regions, the similarities across sizes or regions are more apparent than deviations from the overall trait pattern.

Conservation of trait distributions in the CCS could be partially a consequence of lateral mixing among regions. The CCS is indeed characterized by large spatial and temporal variability due to the intermittent nature of upwelling events and the meandering of the California Current (Checkley and Barth 2009). We have accounted for this variability in part by associating stations with particular hydrodynamic features, rather than a particular geographic location. Nonetheless, coastal jets, filaments and mesoscale eddies in the CCE region (Peláez and McGowan 1986) are additional mechanisms with the potential for rapidly transporting water from productive coastal upwelling cells 100 s of kilometres offshore. Although the week-to-month timescales of zonal advection from these mechanisms substantially exceed the average generation times of protists, allowing the structure

and composition of these assemblages to adapt to changing conditions during advective transport offshore, the same cannot be said for the longer-lived zooplankton. This could explain why the larger protists in Figure 4A show biomass distributions that reflect the expected differences between productive coastal and oceanic habitats, while the zooplankton have similar trait and biomass distributions that vary mainly in magnitude across all regions.

The zooplankton communities are dominated by active feeders, mainly calanoid copepods. Apart from high clearance rates, there are other behavioural traits that benefit the active-feeding community and allow them to overcome the effects of offshore transport. These include diel vertical migration and diapause. Vertical migration by active feeders is an important defence mechanism against predators (Zaret and Suffern 1976; Ohman 1990) and can potentially allow migrating copepods to be transported back towards the productive, coastal upwelling zones (Batchelder and others 2002). Additionally, poleward transport of the diapausing late copepodite stages in the coastally entrained California Undercurrent has been identified as an important mechanism maintaining healthy populations of large calanoid copepods in the CCS (Johnson and Checkley 2004), which would further contribute to driving the observed bimodal biomass size distribution of active feeders.

The proportion of passively feeding groups within each zooplankton size class remains relatively invariant across the environmental provinces, with the only significant differences confined to flux-feeding copepods in the small to mid-size categories. For the two largest size classes, there is only a marginal decline in the proportion of ambush feeders, composed mainly of carnivorous chaetognaths, in the upwelling region, possibly a result of competition with more effective visual predators that are highly abundant in this region (Checkley and Barth 2009).

Increase in the flux-feeding population is recorded only in the oceanic waters and remains steady in the core California Current and upwelling waters, despite the environmental differences between the two regions. Higher abundance of flux-feeding copepods in oceanic regions could be due to lower turbulence, which facilitates easier detection of sinking material. In contrast, ambush-feeding copepods that dominate the ambush-feeding community in the corresponding size category maintain constant biomass contribution along the environmental gradient despite the predictions that their clearance rates are enhanced under moderately

turbulent conditions (Saiz and Kiørboe 1995; Kenitz and others 2017). This benefit, however, can be offset by increased predation mortality due to (i) enhanced feeding activity in the euphotic zone in the more turbulent and prey-rich upwelling areas (van Someren Gréve and others 2017) and (ii) the lack of migratory behaviour serving as a predation refuge (Ohman and Romagnan 2016). Higher predation on ambush-feeding copepods likely explains the shifts in population size distributions towards smaller individuals in the upwelling regions. This shift is only observed for the ambush-feeding copepods and therefore suggests that zonal advection does not act as a mechanism that selectively removes larger individuals (Peterson 1998).

The degree of effort expended by organisms to acquire resources (that is, feeding strategy quantified here in terms of activity) is a taxa-transcending trait that can be used to characterize a wide range of organisms. Feeding strategy is a trait with a clear mechanistic trade-off in that it affects not only feeding rates, but also predation risk, and therefore it has been a focal point of the multi-trophic analysis presented here. The lack of pronounced differences in the feeding traits (activity) distribution for mesozooplankton may indicate that, alongside feeding strategy, activity may strongly influence other aspects of an individual's life time fitness. Finding a mate, for instance, is strongly influenced by swimming activity, a trait that can be unequally distributed between the sexes (Kiørboe 2008). Thus, characterizing mesozooplankton communities by traits related to migratory behaviour, dormancy, or reproduction strategy may reveal some underlying separation of the assemblages along environmental gradients.

The relatively conserved size–trait structure of the California Current System raises the question as to what mechanisms stabilize the trait distributions. In terrestrial environments, resource competition shapes the distribution of distinctly different plant biomes and contrasts in inhabiting fauna are far more pronounced than observed here. Although bottom-up control of community structure is dominant in vegetated habitats, the composition of marine communities is strongly controlled by predator–prey interactions (Verity and Smetacek 1996). Despite higher plant biomass on land, aquatic herbivores consume a significantly larger proportion of primary production, with three times greater rates of herbivory reported for marine ecosystems (Cyr and Pace 1993; Polis 1999), and predation rates on herbivores expected to be higher in aquatic ecosystems than on land (Cyr and Pace

1993). Faster generation times and higher mass-specific consumption rates for aquatic organisms drive stronger regulatory control from consumers (Polis 1999; Shurin and others 2006). This strong regulation by predators could act to equilibrate biomass distributions between environment regimes. Without such regulation, we would expect that the strong differences in nutrient availability would drive even larger differences between the regimes. We therefore conjecture that it is the strong coupling of trophic interactions within marine food webs that balances the bottom-up effects of environmental variability on a regional scale by providing stronger predatory control and stability, especially for the lower trophic levels.

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