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Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean

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Functional trait diversity relates variation in the structure of biological communities to function and ecosystem processes. Zooplankton occupy a central position in marine food webs, modulating energy availability to higher trophic levels, while themselves affected by environmental variation. The use of traits with functional diversity potentially enables a more mechanistic understanding of variation and regulation of zooplankton communities than is possible with taxonomic diversity alone. Traits for 42 zooplankton species from the northeast subarctic Pacific were assembled from the literature and applied to a 16-year time series from the oceanographic Line P. We assembled traits on body size, ontogeny, habitat and feeding behaviours. Six major functional groupings were identified via a trait-based cluster dendrogram. Several functional diversity indices were also calculated, and compared with analogous taxonomic diversity indices. Analogue diversity indices were significantly correlated. Both types of diversity indices revealed some year-specific "anomalies" which were associated with broad-scale oceanographic and climatic regime shifts. We propose that the functional diversity approach may represent an additional ecological tool with which we can gain further understanding of zooplankton function and trophic linkages in a changing ocean, in part because functional traits are often based on easily measured morphological characters.

INTRODUCTION

Biodiversity studies have often relied on the number of species present within a given ecosystem, and to a lesser extent also on the number of individuals within each species, to assess wider community and ecosystem effects (Gaston, 2000; Hamilton, 2005). The majority of studies have focused on common taxonomic indices such as richness, evenness, and those indices that incorporate both aspects such as the Shannon and Simpson indices (Shannon, 1948, Simpson, 1949; Hill, 1973). Taxonomic diversity has been used to estimate biodiversity (alpha, beta and gamma; Whittaker, 1972) and changes over different spatial and temporal scales in relation to environmental or anthropogenic factors (e.g. Zhuravlev and Naimark, 2005; Blarquez *et al.*, 2014). This is a well-established approach, but it ultimately provides little information on how changes in biodiversity affect community composition and potentially ecosystem function. While taxonomic diversity indices have been recognized as a key element in the general understanding of global biodiversity patterns, the identity of the species present, as well as their biological and ecological roles might even be of greater importance in ecosystem studies and processes (Walker, 1992; McGill *et al.*, 2006).

Over the past decade, there has been a growing interest and recognition of the importance of the specific ecological roles of the species present in ecosystems to address questions of the relations between biodiversity and ecosystem functioning (Barton *et al.*, 2013; Litchman *et al.*, 2013; Stuart-Smith *et al.*, 2013). Functional diversity can relate biodiversity and ecosystem function as it characterizes the diversity of species traits (rather than species identity) (Diaz and Cabido, 2001), where traits are phenotypic characteristics that describe or relate to how organisms function (Petchey and Gaston, 2006). Functional diversity is a tool that can be used to explain variation in the structure and function of communities and relate these to ecosystem structure and processes in freshwater zooplankton (Barnett *et al.*, 2007; Vogt *et al.*, 2013). Perhaps one of the greatest advantages of functional diversity over traditional taxonomic diversity indices is that it allows for a more ecological/ecosystem-based point of view rather than a species one.

A functional approach allows us to move beyond a reliance on taxonomic identity and includes various indices that can be calculated using a range of qualitative, semi-quantitative and/or quantitative traits (Villéger *et al.*, 2008; Laliberté and Legendre, 2010). The approach is more forgiving to coarser taxonomic analysis because many functional traits are often shared by closely related species, and some can be measured or inferred from gross morphology, such as has been done for phytoplankton

(Kruk *et al.*, 2010). Functional diversity metrics include indices such as functional richness (*FRic*), functional divergence (*FDiv*), functional evenness (*FEve*) (Villéger *et al.*, 2008), Rao's quadratic entropy (Rao, 1982) and more recently, functional dispersion (*FDis*) (Laliberté and Legendre, 2010). Furthermore, community-level weighted means (CWM) of trait values can easily represent the dominant functional composition of communities (Ricotta, 2005; Cavender-Bares *et al.*, 2009). *FDis* and *RaoQ* are similar indices, both estimating the spread of species in trait space, weighted by their relative abundances (Laliberté and Legendre, 2010). *FRic* is an indicator of how much of potential niche space is occupied by the species present in a given community, providing information that can be related to productivity and environmental variability (Mason *et al.*, 2005; Schleuter *et al.*, 2010). *FEve* measures the distribution of mean species traits within the occupied trait space, where a high value indicates a regular distribution and a low value may be interpreted as an over-representation by certain traits (Mason *et al.*, 2005; Schleuter *et al.*, 2010). Traditional indices such as species richness *(S)* and species evenness *(J')* are the taxonomic analogues of their functional indices counterparts. *S* corresponds to the number of species while *J'* describes how evenly are biomass or abundances distributed across species (Smith and Wilson, 1996). *FDis* measures two parameters; the variance of functional traits and species' position in the cluster of trait space (Mason *et al.*, 2005). The Shannon diversity index (*H'*) is the taxonomic analogue of *FDis* and is commonly used to jointly characterize the number and evenness of species in a community, having a larger value when many species persist with similar abundances (or biomass) (Shannon, 1948).

Functional diversity has been used to characterize communities more mechanistically, and also often to relate community structure to ecosystem function, in a wide range of ecological studies. Studies have covered a wide variety of taxa and habitats including: plants and grasslands (Singh *et al.*, 2008; Biswas and Mallik, 2010; Pakeman, 2011; Jastrzębska *et al.*, 2012; Roscher *et al.*, 2013; Bhaskar *et al.*, 2014; Schittko *et al.*, 2014), fish (Stuart-Smith *et al.*, 2013; Hitt and Chambers, 2014; Wiedmann *et al.*, 2014), soil communities (Concostrina *et al.*, 2014; Li *et al.*, 2014), oceanic islands (Whittaker *et al.*, 2014), benthic invertebrates (Paganelli *et al.*, 2012), phytoplankton (Longhi and Beisner, 2010; Palffy *et al.*, 2013), to name only a few from a large list of recent studies. In terms of zooplankton functional diversity studies, most have been done on freshwater zooplankton (e.g. Barnett *et al.*, 2007, 2013; Barnett and Beisner, 2007; Vogt *et al.*, 2013). For marine zooplankton however, there has been little work to date incorporating a quantitative functional diversity approach to communities. To our

knowledge, there has been no quantitative comparison of functional trait diversity indices, nor of community types. Given the key role that marine zooplankton play as the major link between primary producers and fish, seabirds and marine mammals in marine ecosystems, it is important to evaluate new tools with which to further our understanding of the structure and function of zooplankton communities and the forces that influence these.

In this study, we first assembled a large new matrix of functional traits for marine zooplankton. We then used these traits to quantify zooplankton functional diversity in the long-term Line P data series from the northeast subarctic Pacific Ocean across sites and through time. The goal was to compare variation of traditional taxonomic diversity indices to variation of functional diversity indices. The Line P historical time series represents an ideal opportunity to assess the sensitivity of the diversity calculations, since long-term responses (16 years) of zooplankton biomass to major oceanographic and climatic events variation are well studied and understood.

METHOD

Zooplankton sampling and sites

Our analysis is based on a time series (1997–2012) of zooplankton abundance data sampled at locations along the Line P transect (Fig. 1) at seven stations (P02 ($n = 26$), P04 ($n = 51$), P08 ($n = 38$), P12 ($n = 46$), P16 ($n = 36$), P20 ($n = 42$) and P26 ($n = 51$)). Line P encompasses a series of oceanographic stations that start near the mouth of the Juan de Fuca Strait (P02) and extend off the shelf into the Gulf of Alaska ending at Station P (P26) in

the northeast subarctic Pacific. Zooplankton sampling along Line P has been previously described in detail by Mackas (Mackas, 1992) and Mackas and Galbraith (Mackas and Galbraith, 2002). Briefly, however, stations were sampled three times per year, typically in the spring (May/June), summer (July/August/September) and winter (February/March). Zooplankton samples were collected with vertical hauls of 0.6- or 0.42-m mouth-diameter bongo nets, fitted with 0.23-mm black mesh and a TSK flowmeter. For our purposes, we only considered vertical net hauls ≤250 m to the surface to ensure that the same depths were sampled across all sites. For shallow stations of the inner portion of the line, this meant that the entire water column was sampled, while for deeper stations off the shelf break (>1000 m depth) the sampled community is assumed to include surface dwelling and high-amplitude migrators (Mackas et al., 2007). The Line P transect is characterized by oceanic and boreal subarctic conditions. Water properties and seasonal zooplankton distribution and community composition have been studied and are known to differ along the transect: the outer Line P (Sites P16, P20 and P26) is an iron-limited high nitrogen−low chlorophyll (HNLC) environment, while the inner sites (P02, P04, P08 and P12) have depleted nitrogen during summer (Whitney et al., 1998; Mackas and Galbraith, 2002).

Functional traits

This study includes 42 species which were most representative of the zooplankton communities of the NE subarctic Pacific (Mackas and Coyle, 2005; Mackas et al.,
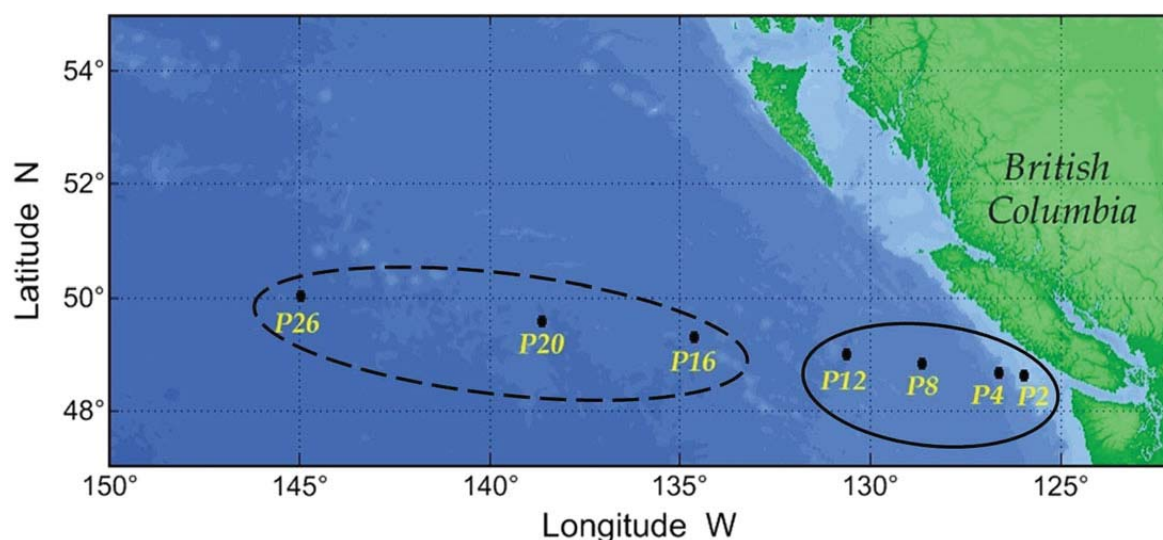

Fig. 1. Map of the study area (Line P) in the subarctic northeast Pacific Ocean. The non-dashed circle represents inner Line P stations (P2, P4, P8 and P12) and the dashed circle represents outer Line P stations (P16, P20 and P26) (Map, courtesy of Marie Robert, Fisheries and Oceans, Canada).

2007). The selection of these species was largely intended to reflect the main crustacean zooplankton community of the Gulf of Alaska and the subarctic northeast Pacific Ocean, as well as some northern California Current indicator species (See Mackas et al., 2001, 2004, 2007). Some non-crustacean groups common to the time series (e.g. *Limacina helicina*) were also included in our analyses. However, our treatment of non-crustacean groups is limited relative to that of crustaceans; thus, some traits and interrelationships with the zooplankton community will be under-represented. With this set of species, we carried out an extensive literature review for marine zooplankton functional traits in the northern subarctic Pacific Ocean (see Supplementary data, Table 1 for references to the trait matrix). In addition to these species representing most of the biomass, these are also the species for which we were able to find trait information. The seven functional traits for which we found information for all 42 species were: (i) average adult female body length (mm); (ii) feeding type (active ambush feeding, passive ambush feeding, current feeding, cruise feeding; as defined by Kiørboe, 2011); (iii) trophic group (herbivore, carnivore, omnivore, detritivore, herbivore−omnivore, omnivore−carnivore, detritivore−carnivore); (iv) reproduction mode (broadcast spawner, egg-brooding sac (copepod) and egg-brooding (non-copepod)); (v) vertical distribution preference [epipelagic (0−200 m), epimesopelagic (0−1000 m), mesopelagic (200−1000 m) and mesobathypelagic (200−4000 m); (vi) diel vertical migration (DVM) behaviour (Yes, No) and (vii) habitat type (nearshore, shelf, shelf break, offshore, inlet, oceanic, cosmopolitan]. These traits were selected because they are known to be functionally important, describing the life history and ecology of the species, and because they are expected to remain more or less constant through time and space. Note however, that the tendency to display DVM in any given context is thought to be driven mainly by conditions of light, food and predation (Lampert, 1989; Hays, 2003). Thus, this particular trait cannot be considered fixed but rather plastic and there is evidence that species can adjust their DVM behaviour according to other factors such as temperature (Cooke et al., 2008), oxygen levels (oxycline) (Keister and Tuttle, 2013), UV radiation (Willamson et al., 2011) and avoidance of toxic algae (Fernando, 1994). Our initial analyses including this trait yielded rather confusing results, and we therefore chose not to include DVM in further functional diversity analyses, given the plasticity of this trait among and within species.

Data analysis

We calculated three functional diversity indices: *FRic* (Villéger et al., 2008); *FEve* (Villéger et al., 2008) and *FDis* (Laliberté and Legendre, 2010). We also calculated the CWM of average female body-length, the only quantitative trait (Lavorel et al., 2008). Three analogous taxonomic diversity indices were also calculated: Shannon diversity index (H'), species evenness (J') and species richness (S). Functional and taxonomic diversity indices were calculated using the packages *FD* and *Vegan* (Laliberté and Shipley, 2011; Oksanen et al., 2013) within the R statistical framework (R Development Core Team, 2014). A species-by-traits matrix was calculated using the PCoA axes of a Gower (Gower, 1971) dissimilarity matrix (Villéger et al., 2008) since we considered both qualitative and quantitative traits. Major functional groupings of species were identified with a cluster dendrogram calculated using average linkage clustering of species based on the dissimilarity matrix. The number of functional groups was determined by using the Calinski−Harabasz criterion (Calinski and Harabasz, 1974) to select the optimal number of groups. The relationships between functional diversity indices and their corresponding taxonomic diversity indices as well as their non-corresponding taxonomic diversity indices were investigated using Pearson's correlation coefficients for the time series along the inner and outer sections of Line P. The strength of the relationships between the various indices is expressed by the correlation coefficient values and the associated P-values ($P < 0.05$). We calculated annual "anomalies" in each diversity index as the size of the annual residual value relative to the long-term temporal trend in each of the inner and outer portions of Line P. Finally, a Kruskal−Wallis test was used to assess the effect of year on CWM of average female body length within the inner and the outer portions of Line P.

RESULTS

Cluster dendrogram

We were able to assign six categorical and one continuous quantitative functional traits to the 42 most representative zooplankton species for our study region (Table I). The Calinski−Harabasz criterion identified six distinct functional groups from the cluster dendrogram constructed on the basis of functional trait dissimilarity (Fig. 2). Group 1 was composed of large-bodied carnivorous species (*Paraeuchaeta elongata*, *Themisto pacifica*, *Dimophyes arctica*, *Aglantha digitale*, *Eukronia hamata* and *Parasagitta elegans*). Group 2 consisted of only two species of the same genus, *Gaetanus simplex* and *G. tenuispinus*, both of which are mesopelagic broadcast spawning, omnivore−carnivore copepods. Group 3 was formed of four detritivore species (*Scaphocalanus* spp., *Scolecithricella minor*, *Conchoecia* sp. and *Disconchoecia elegans*). Group 4 was composed of small ambush feeding copepod species (*Acartia* spp.,

Table I: Functional traits of the 42 dominant zooplankton species from the subarctic Northeast Pacific Ocean community

Order/taxon	Length (mm)	Feeding type	Trophic group	Reproduction mode	Vertical distribution	DVM	Habitat
Copepod							
Acartia tonsa	1.03[8]	Active ambush feeding[29]	Herbivore – Omnivore[5]	Broadcast spawning[5,53]	Epipelagic[5]	Yes[57]	Nearshore[5]
Acartia longiremis	1.07[8,11]	Active ambush feeding[5]	Herbivore – Omnivore[5]	Broadcast spawning[5,53]	Epipelagic[5]	Yes[57]	Nearshore/shelf[5,48]
Aetidus divergens	1.8[2]	Active ambush feeding[40]	Omnivore[4,6]	Broadcast spawning[4,6]	Epimesopelagic[4,6]	Yes[57]	Shelf[5]
Aetideus pacificus	2.5[2,11]	Active ambush feeding[40]	Omnivore[4,6]	Broadcast spawning[4,6]	Epimesopelagic[4,6]	Yes[57]	Shelf[5]
Calanus marshallae	3.70[8,11]	Current feeding[40]	Herbivore – Omnivore[12]	Broadcast spawning[12]	Epipelagic[12]	Yes[58]	Shelf[42]
Calanus pacificus	3.00[8,11]	Current feeding[40]	Herbivore – Omnivore[12,13]	Broadcast spawning[12]	Epipelagic[12]	Yes	Inlet/offshore*
Centropages abdominalis	1.78[8,11]	Active ambush feeding[15]	Omnivore[15]	Broadcast spawning[15]	Epipelagic[15]	Yes[58]	Nearshore/shelf[15]
Calocalanus spp.	1.04[11]	Current feeding[50]	Herbivore – Omnivore[50]	Broadcast spawning[50]	Epipelagic[46,50]	Yes[57]	Shelf/shelf break[47]
Clausocalanus spp.	1.15[11]	Cruise feeding[62,64]	Herbivore – Omnivore[50]	Broadcast spawning[50]	Epipelagic[49,50]	Yes[55]	Shelf/shelf break[47,49]
Ctenocalanus vanus	1.20[11]	Current feeding[50]	Herbivore[50]	Egg-brooding sac[52,54]	Epipelagic[49,50]	No	Cosmopolitan[50]
Eucalanus bungii	7.03[8,11]	Current feeding[39]	Herbivore – Omnivore[5]	Broadcast spawning[5]	Epipelagic[5,28]	No[55]	Shelf break/offshore[5]
Eucalanus californicus	6.45[8,11]	Current feeding[20]	Herbivore – Omnivore[20]	Broadcast spawning[5]	Epipelagic[5]	No[55]	Shelf break/offshore[5]
Gaetanus simplex	3.3[1,8]	Current/ambush feeding[1,40]	Omnivore – Carnivore[1,5]	Broadcast spawning[1]	Mesopelagic[1,28]	Yes[59]	Shelf break/offshore[5]
Gaetanus tenuispinus	3.7[1,8]	Current/ambush feeding[1,40]	Omnivore – Carnivore[1,5]	Broadcast spawning[1,66]	Mesopelagic[1,66]	Yes[59]	Shelf break/offshore[5]
Mesocalanus tenuicornis	2.1[50]	Current/ambush feeding[50]	Omnivore[50]	Broadcast spawning[50]	Epipelagic[49,50]	Yes[55]	Shelf/shelf break[47,49,50]
Metridia pacifica	2.89[8,11]	Cruise feeding[39]	Omnivore[5]	Broadcast spawning[5]	Epipelagic[5,28]	Yes[55]	Inlets/offshore[5]
Microcalanus pusillus	0.80[8,11]	Current feeding[43]	Omnivore[1,43]	Broadcast spawning[1,43]	Epimesopelagic[1,43]	Yes	Inlets/offshore[1,43]
Microcalanus pygmaeus	0.86[8,11]	Current feeding[43]	Omnivore[1,43]	Broadcast spawning[1,43]	Epipelagic[1,43]	Yes	Inlets/offshore[5]
Neocalanus cristatus	9.23[8,11]	Current feeding[17]	Omnivore[12]	Broadcast spawning[32]	Epipelagic[12,28]	No[56]	Shelf break/offshore[5]
Neocalanus flemingeri	5.25[8,11]	Current feeding[25]	Omnivore[12]	Broadcast spawning[32]	Epipelagic[12,28]	No[56]	Shelf break/offshore[5]
Neocalanus plumchrus	4.98[8,11]	Current feeding[16]	Omnivore[12]	Broadcast spawning[32]	Epipelagic[12,28]	No[56]	Shelf break/offshore/inlets[5]
Oithona similis	0.94[8,11]	Active ambush feeding[14,29]	Herbivore – Omnivore[26]	Egg-brooding sac[26]	Epipelagic	Yes[55]	Nearshore/shelf[48]
Paracalanus spp.	1.0[11]	Current feeding[50]	Herbivore[50]	Broadcast spawning[50]	Epipelagic[49,50]	No[57]	Nearshore/shelf/shelf break[4]
Pareuchaeta elongata	6.85[8,11]	Active ambush feeding[61]	Carnivore[27,61]	Egg-brooding sac[8,54]	Mesobathypelagic[27,28]	Yes	Shelf[28]
Pseudocalanus mimus	1.52[8,11]	Current feeding[40]	Herbivore[5]	Egg-brooding sac[5,53]	Epimesopelagic[5]	Yes[55]	Nearshore/shelf[5,48]
Pseudocalanus minutus	1.46[8,11]	Current feeding[25]	Herbivore[5]	Egg-brooding sac[5,53]	Epimesopelagic[5]	Yes	Offshore/inlets[5]
Pseudocalanus moultoni	1.52[8,11]	Current feeding[40]	Herbivore[5]	Egg-brooding sac[5,53]	Epipelagic[5]	Yes	Nearshore[5]
Pseudocalanus newmani	1.24[8,11]	Current feeding[40]	Herbivore[5]	Egg-brooding sac[5,53]	Epipelagic[5]	Yes[62]	Nearshore/shelf[5]
Scaphocalanus brevicornis	2.28[8,11]	Current feeding[40]	Detritivore – Omnivore[45]	Broadcast spawning[1]	Mesobathypelagic[1,5]	No	Shelf/offshore[1,5]
Scaphocalanus magnus	4.61[8,11]	Current feeding[40]	Detritivore – Omnivore[1,45]	Broadcast spawning[1,66]	Mesobathypelagic[1,5]	No	Offshore/cosmopolitan[1,5]
Scolecithricella minor	1.4[1]	Current feeding[43,51]	Detritivore – Omnivore[43,51]	Broadcast spawning[1]	Epimesopelagic[1]	Yes[55]	Offshore/cosmopolitan[43,51]
Non-copepod							
Amphipod							
Themisto pacifica	6.5[1]	Active ambush feeding[37]	Carnivore[31,37]	Egg brooding[1,67]	Epipelagic[31]	Yes[55]	Cosmopolitan[33]
Chaetognath							
Eukrohnia hamata	22.5[22]	Active ambush feeding[21]	Carnivore[21]	Egg brooding[19]	Epimesopelagic[19]	Yes	Shelf break/offshore/inlets[19]
Parasagitta elegans	26.5[22]	Active ambush feeding[14]	Carnivore[22]	Broadcast spawning[1,68]	Epimesopelagic[22]	Yes	Nearshore/cosmopolitan[1]
Euphausiid							
Euphausia pacifica	20.5[30,34]	Current feeding[3]	Omnivore[3]	Broadcast spawning[35]	Epipelagic[3]	Yes[55]	Shelf/shelf break[3]
Thysanoessa inspinata	17.0[36]	Current feeding[41]	Herbivore[3]	Broadcast spawning[35]	Epipelagic[3,33]	Yes[55]	Offshore/shelf break[30,33]
Thysanoessa spinifera	21.0[1,38]	Current feeding[41]	Omnivore[3]	Broadcast spawning[35]	Epipelagic[3,33]	Yes[55]	Nearshore/shelf[30,33]
Pteropod							
Limacina helicina	5.0[63]	Passive ambush feeding[19]	Omnivore[24]	Broadcast spawning[24]	Epipelagic[19]	Yes[55]	Cosmopolitan[63]
Ostracod							
Conchoecia sp.	2.1[2]	Current feeding[1,65]	Detritivore[1,65]	Broadcast spawning[1]	Epimesopelagic[1]	Yes[61]	Shelf break/oceanic[1]
Discoconchoecia elegans	1.92[19]	Current feeding[19]	Detritivore[19]	Broadcast spawning[19]	Epimesopelagic[19]	Yes[55]	Shelf break/offshore/inlets[19]
Hydrozoa							
Aglantha digitale	11.0[9,10]	Active ambush feeding[9]	Carnivore[9,10]	Broadcast spawning[9]	Epimesopelagic[9]	Yes[55]	Cosmopolitan[9]
Dimophyes arctica	10[1,2]	Passive ambush feeding[2]	Carnivore[2]	Broadcast spawning[2]	Epimesopelagic[2]	Yes[55]	Inlet/offshore[2]

Length represents the average body length of adult females. References are indicated in superscript numbers and are found in Supplementary data.
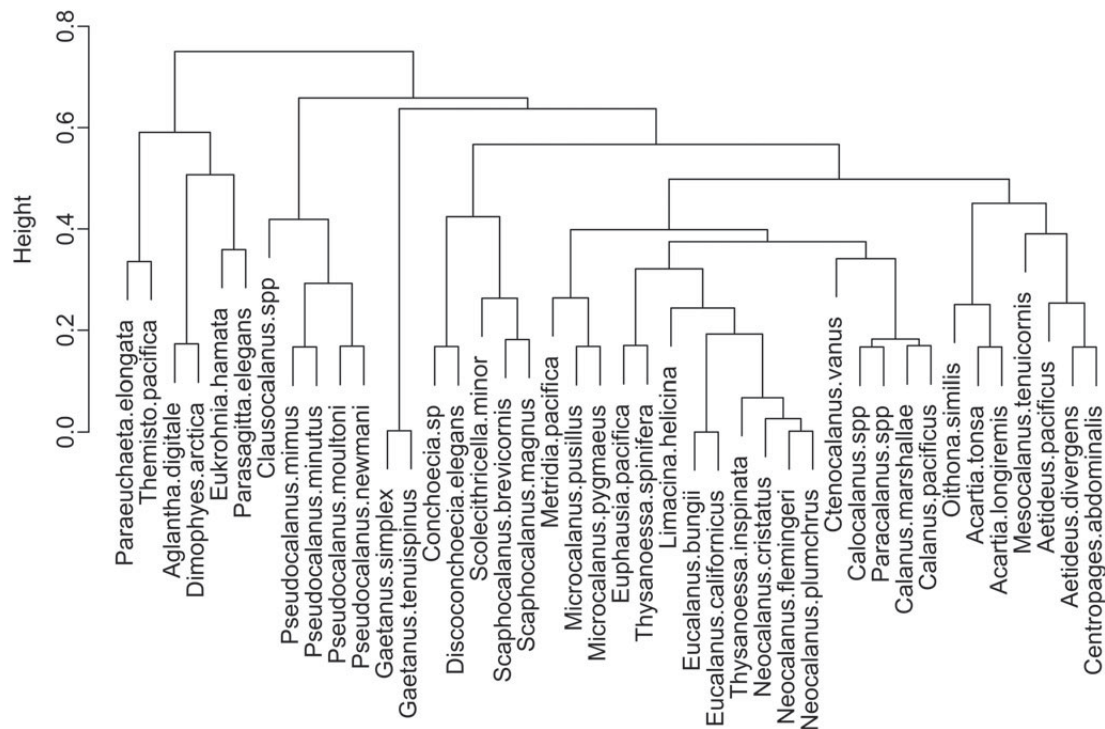
Fig. 2. Cluster dendrogram based on functional traits using average linkage clustering of 42 zooplankton species based on the Gower's distance matrix calculated on their functional traits (Table 1).

Aetidus spp., *Oithona similis*, *Centropages abdominalis* and *Mesocalanus tenuicornis*). Group 5 was the largest and included three sub-groups: small inlets/offshore copepod species (*Metridia pacifica* and *Microcalanus* spp.) formed Group 5a, a group (Group 5b) composed of three large-bodied herbivore−omnivore current feeding euphausiid species (*E. pacifica*, *T. spinifera*, *T. inspinata*), the pteropod *L. helicina*, and the large epipelagic omnivorous copepods: (*Neocalanus* spp. and *Eucalanus* spp.) and Group 5c included five epipelagic herbivorous copepod calanoid species (*Ctenocalanus vanus*, *Paracalanus* spp., *Calocalanus* spp., *C. pacificus* and *C. marshallae*). Finally, Group 6 consisted of small egg-brooding epipelagic species (*Pseudocalanus* spp., and *Clausocalanus* spp.).

Correlation between functional diversity and taxonomic diversity indices

Functional diversity indices calculated on the six traits (i.e. not including the DVM trait) correlated well with their corresponding taxonomic diversity indices (Fig. 3a−c). There was a significant positive correlation between *FDis* and the Shannon index (H') for both the inner (r 0.775, $P < 0.001$) and the outer portions of Line P ($r = 0.707$, $P < 0.001$). There was also a significant positive correlation between *FRic*

and taxonomic richness (S') within the inner ($r = 0.725$, $P < 0.001$) and the outer portion of Line P ($r = 0.615$, $P < 0.001$). There was a weak but significant correlation between *FEve* and community evenness (J') within the inner portion of Line P ($r = 0.243$, $P < 0.01$) and the outer portion of Line P ($r = 0.247$, $P < 0.001$).

Correlations between functional diversity indices and their non-corresponding taxonomic diversity indices were also found (Tables II and III). *FDis* and species richness (S') were positively correlated within the inner section of Line P ($r = 0.204$, $P < 0.05$), but not within the outer section ($r = 0.165$, $P = 0.064$). *FDis* and evenness (J') were strongly correlated in both sections of Line P (inner: $r = 0.798$, $P < 0.0001$ and outer: $r = 0.723$, $P < 0.0001$) (Tables II and III). *FEve* and species richness (S') and *FEve* and Shannon Index (H') were positively correlated in the inner Line P ($r = 0.206$, $P < 0.01$ and $r = 0.277$, $P < 0.001$). *FRic* and Shannon Index (H') were correlated in both parts of Line P ($r = 0.360$, $P < 0.0001$ and $r = 0.369$, $P < 0.0001$) (Table II). There was also a weak but significant correlation between *FRic* and species evenness (J') in the outer portion of Line P ($r = 0.227$, $P < 0.01$) (Table III).
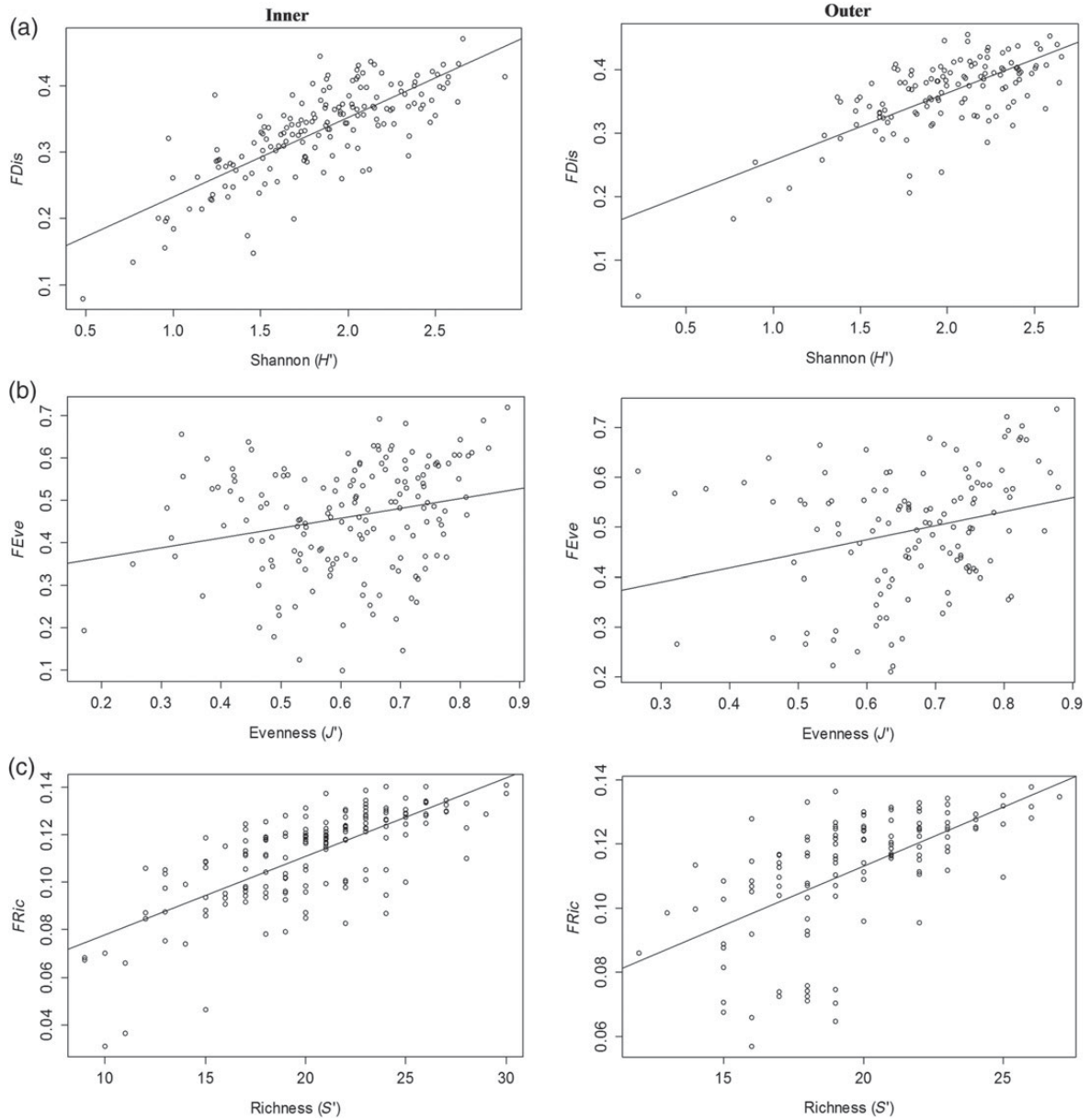
Fig. 3. Correlation between (**a**) functional dispersion (*FDis*) and Shannon's diversity index; (**b**) functional evenness (*FEve*) and species evenness and (**c**) functional richness (*FRic*) and species richness within the inner and the outer portion of Line P.

Table II: Pearson coefficients for correlations between all taxonomic and functional diversity indices within the inner section of Line P

Variables	FEve	FDis	Richness (S')	Shannon (H')	Evenness (J')
FRic	0.06	0.173[*]	0.725[***]	0.360[***]	0.142
FEve	–	0.194[*]	0.206[**]	0.277[***]	0.243[**]
FDis	–	–	0.204[**]	0.775[***]	0.798[***]
Richness (S')	–	–	–	0.453[***]	0.144
Shannon (H')	–	–	–	–	0.962[***]

* = P < 0.05; ** = P < 0.01; *** = P < 0.001.

Table III: Pearson coefficients for correlations between all taxonomic and functional diversity indices within the outer section of Line P

Variables	FEve	FDis	Richness (S')	Shannon (H')	Evenness (J')
FRic	−0.067	0.243[**]	0.615[***]	0.369[***]	0.227[**]
FEve	–	−0.038	−0.112	0.188[*]	0.247[**]
FDis	–	–	0.165	0.707[***]	0.723[***]
Richness (S')	–	–	–	0.419[***]	0.162
Shannon (H')	–	–	–	–	0.962[***]

* = P < 0.05; ** = P < 0.01; *** = P < 0.001.

More generally, when both inner and outer stations were considered together, taxonomic diversity indices and functional diversity indices were significantly correlated (Table II) with two exceptions: *FEve* with *FRic* and *FEve* with *S* (Table IV).

Inter-annual variation in taxonomic and functional diversity indices

Generally, the annual patterns of "anomalies" were similar for functional and taxonomic diversity indices (Figs 4 and 5). Within the inner section, negative anomalies were noted for all taxonomic and functional indices in 1997, with the exception of *FDis*. Negative anomalies persisted in 1998 for *FEve* and *FRic*. All indices exhibited

Table IV: Pearson coefficients for correlations between all taxonomic and functional diversity indices across the entire time and spatial series of Line P

Variables	FEve	FDis	Richness (S')	Shannon (H')	Evenness (J')
FRic	0.006	0.197***	0.716***	0.379***	0.175***
FEve	–	0.153*	0.081	0.234***	0.262***
FDis	–	–	0.176***	0.757***	0.777***
Richness (S')	–	–	–	0.420***	0.158*
Shannon (H')	–	–	–	–	0.960***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

positive anomalies in 2003, with the exception of *FEve* which had no anomaly on that year. Negative anomalies were observed in 2004−2006 in *FDis* and *H'* as well as in *FEve* and *J'* and negative anomalies were also noted in 2005−2006 in *FRic* and *S'*. Positive anomalies were observed in 2007, followed by negative anomalies in subsequent years in *FDis* and *FRic*. In the outer portion of Line P, negative anomalies were noted for all taxonomic and functional indices in 1997, with the exception of *FEve*. Positive anomalies were observed in 1998−2001 and 2004−2005 for *FDis* and *H'* followed by negative anomalies in 2006. Both *FRic* and *S'* exhibited positive anomalies in 2004−2007. *FDis* and *H'* as well as *J'* and *FRic* had positive anomalies in 2011−2012, while *FEve* and *S'* had negative anomalies. The similar temporal patterns for both *FDis* and *H'* anomalies were reflected in significant positive correlations between these two indices for both the inner ($r = 0.53$, $P < 0.05$) and outer portions ($r = 0.68$, $P < 0.01$) Line P (Tables V and VI). Similarly, *FRic* and *S'* anomalies, were positively correlated ($r = 0.50$, $P < 0.05$) for the inner but not for the outer stations (Table VI).

We also examined the annual variation in CWM values for female body length. There was a significant effect of year on CWM of female body length within the outer portion of Line P (KW chi-squared = 31.06, df = 15, P-value = 0.0086). Time (year) was not significant in the inner portion of Line P (KW chi-squared = 14.57 df = 15, P-value = 0.482) (Fig. 6).
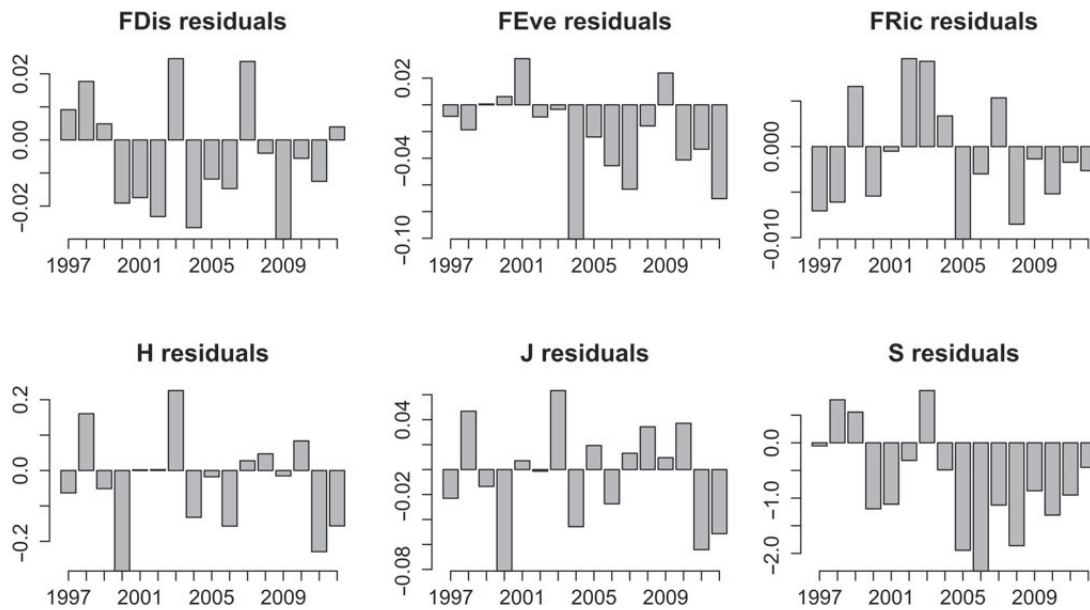

Fig. 4. Annual anomalies in taxonomic diversity and functional diversity indices within the inner portion of Line P.
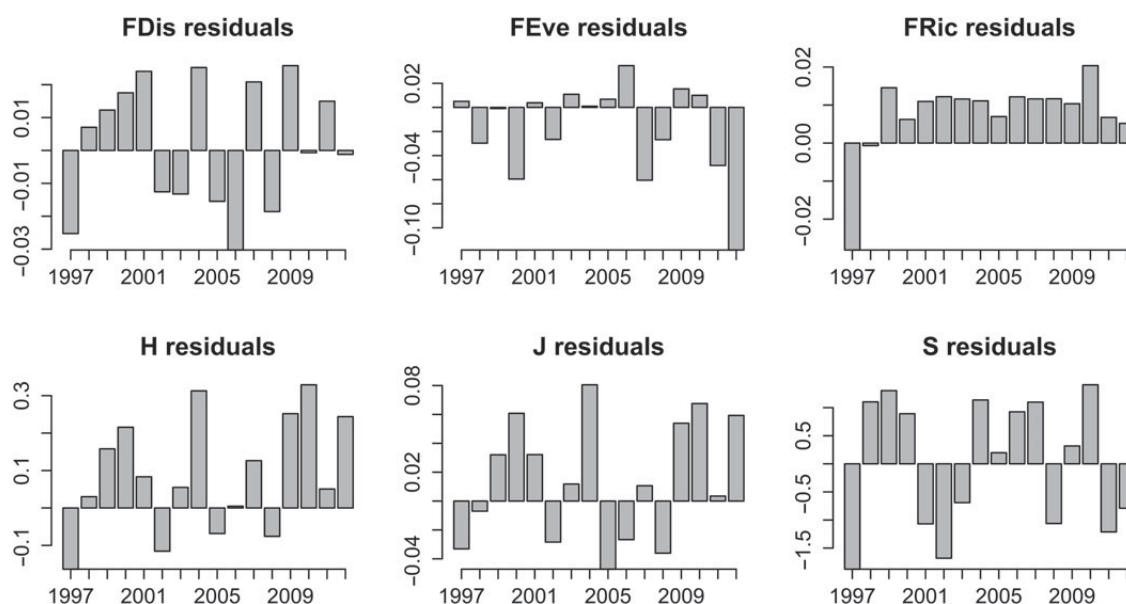
Fig. 5. Annual anomalies in taxonomic diversity and functional diversity indices within the outer portion of Line P.

Table V: Pearson coefficients for correlations between temporal residuals for all taxonomic and functional diversity indices the inner section of Line P

Variables	FEve	FDis	Richness (S')	Shannon (H')	Evenness (J')
FRic	−0.04	0.13	0.50[*]	0.20	0.07
FEve	–	−0.11	0.14	0.22	0.25
FDis	–	–	0.50[*]	0.53[*]	0.45
Richness (S')	–	–	–	0.40	0.20
Shannon (H')	–	–	–	–	0.97[***]

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Table VI: Pearson coefficients for correlations between temporal residuals for all taxonomic and functional diversity indices within the outer section of Line P

Variables	FEve	FDis	Richness (S')	Shannon (H')	Evenness (J')
FRic	0.07	0.29	0.44	0.49	0.35
FEve	–	−0.24	0.15	−0.17	−0.20
FDis	–	–	0.36	0.68[**]	0.71[**]
Richness (S')	–	–	–	0.62[**]	0.44
Shannon (H')	–	–	–	–	0.96[***]

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

DISCUSSION

In this study we took advantage of a long and well-studied zooplankton time series (Line P) to compare traditional taxonomic and functional diversity indices in a marine context for the first time, and to gain some insight into the relative sensitivity of each approach to environmental forcing as identified by earlier biomass-anomaly studies. Functional diversity can be viewed as a potential intermediate between taxonomic-based diversity estimates and *in situ* (direct) functional measurements such as secondary production and ingestion rates. The direct approach is preferable since it can ostensibly capture the true functional response of a community; however this approach is difficult and time-consuming and cannot be applied retrospectively. As a result, there are no long-term time series of

community-level functional rate measurements for marine zooplankton. A significant advantage of the functional trait approach is that functional diversity calculations can be applied retrospectively to existing time series of taxonomic identification and abundance. Our primary objective was to assess the potential of functional trait diversity as a new tool in our effort to understand community structure in a way that points to ecosystem processes and function.

Functional group of species

Six functional groups of species were identified on the basis of the functional trait database we present using: female body size; reproduction mode; feeding mode; trophic group; and distribution (vertical and habitat). A functional group of species can be defined as a group
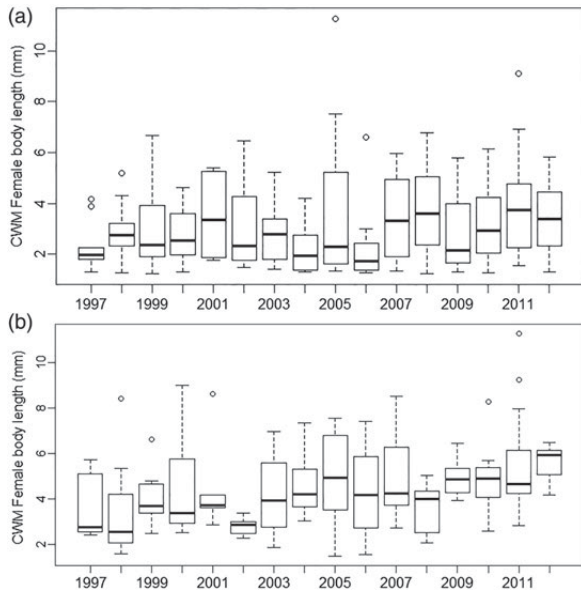
Fig. 6. Annual variation in community weighted means (CWM) of female body length within (**a**) inner Line P and (**b**) outer Line P. Each black line, white box and whiskers outside the box represent the mean, the standard deviation and the standard error, respectively. White dots represent outliers.

of species with similar traits that are likely to share similar roles in ecosystem processes (Gitay and Noble, 1997). The functional groups identified in this study can be related to processes with some ecological significance for ecosystem functioning.

One main functional group (Group 1) was composed of predatory species characterized by large-body size and a primarily ambush tactic feeding behaviour. Group members, the copepod *P. elongata*, the amphipod *T. pacifica*, the hydromedusae *A. digitale*, the siphonophore *D. arctica* and the two chaetognath species *E. hamata* and *P. elegans*, have an epimesopelagic distribution and can be found in various habitat types. These species are known to prey on smaller species such as copepodite stages of *Calanus* spp., *Pseudocalanus* spp. and *Acartia* spp. This functional group of predatory species can also feed on fish larvae and compete with juvenile and fish larvae for food (Bailey and Houde, 1989).

Group 2 consisted of two mesopelagic broadcast spawner omnivore–carnivore copepods, *Gaetanus simplex* and *G. tenuispinus*. Although these two species tend to be cosmopolitan in their distribution, they are more commonly found on the shelf break and offshore within the subarctic Pacific region. These copepods prey on copepod nauplii and rely to some extent on detritus. Group 3 was composed of broadcast spawning detritivores and are likely to have significant ecosystem function effects by contributing to recycling of organic matter by

feeding on copepod carcasses and other sources of food (Yamaguchi *et al.*, 2002). This group was composed of the copepods *S. brevicornis*, *S. magnus* and *S. minor*, and two ostracods *Conchoecia* sp. and *D. elegans*. Group 2 and 3 can contribute to the recycling of organic matter and, together with Group 1, exert a control on the mesozooplankton population (Auel, 1999). We found a group (4) of species composed of small ambush feeding copepods including *Acartia* spp. (*A. hudsonica*, *A. longiremis*), *Aetidus* spp. (*A. pacificus*, *A. divergens*), *Oithona similis*, *Centropages abdominalis* and *Mesocalanus tenuicornis*. These species are largely found nearshore and on the shelf. *M. tenuicornis* is a southern copepod with a usual distribution along the California coast, while *Acartia* spp., *Aetidus* spp. and *C. abdominalis* are common boreal shelf species (Mackas *et al.*, 2004). Despite their omnivorous character, phytoplankton still dominates their diet, and these copepods are in turn preyed upon by large carnivorous zooplankton and epipelagic fishes (Mackas and Coyle, 2005).

One group (5a) was formed by medium and small inlets/offshore copepod species including *Metridia pacifica* and *Microcalanus* spp. (*M. pusillus*, *M. pygmaeus*). These omnivorous species have an epipelagic distribution and are important food item for fish larvae. Hillgruber *et al.* (Hillgruber *et al.*, 1995) found that walleye Pollock larvae were feeding exclusively on copepod nauplii, with an emphasis on *M. pacifica* and *Microcalanus* spp. Also linked primarily to habitat was the functional group (5b) composed primarily of large subarctic oceanic copepods. This group consisted of euphausiid species (*E. pacifica*, *T. spinifera*, *T. inspinata*), the pteropod *L. helicina* and large epipelagic omnivore copepod species: *Neocalanus* spp. and *Eucalanus* spp. These copepod species dominate the offshore biomass of Line P in May–June while euphausiid maximum biomass is usually observed in early fall, after the summer feeding season (Mackas *et al.*, 2004). These species are key food items for higher trophic level species including pelagic fishes, seabirds and marine mammals such as humpback whales (Jahncke *et al.*, 2005). The group (5c) was formed of five predominantly herbivorous, broadcast spawning, epipelagic calanoid copepod species, including three small body size warm-water species (~1 mm); *Ctenocalanus vanus*, *Paracalanus* spp. and *Calocalanus* spp. that can be transported into Line P region by poleward transport along the continental slope (Mackas and Coyle, 2005) and two larger boreal species (~3 mm+); *C. pacificus* and *C. marshallae*. This group is formed of species mainly found near the shelf and the shelf break area.

In nearshore and shelf habitats, the most important contributors to secondary production by the zooplankton community is composed of the functional group (6) made up of small herbivorous copepods (*Pseudocalanus* spp.)

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along with another egg-brooding species *Clausocalanus* spp. *Pseudocalanus* spp. are ecologically significant as they are among the most numerically abundant taxa and among the top secondary producers (Napp *et al.*, 2005). The description of the functional groups identified in our study highlights species linkages in terms of their ecological function, including role in the various food webs of the northeast subarctic Pacific. By applying the functional groups identified here to other data from the same region, a functional trait approach could thus be used to understand or predict potential shifts in function and trophic linkages in a changing ocean, complementing more traditional approaches based on species assemblages (e.g. Dower and Mackas, 1996; Tommasi *et al.*, 2013) with mechanistic information.

Correlations between taxonomic and functional diversity indices

We used our trait database subsequently to compare variation of traditional taxonomic diversity indices and functional diversity indices by applying it to historical zooplankton community data from Line P, a long-term time-series. The general patterns of correlations between taxonomic and functional diversity indices revealed in the present study were generally as expected given the analogous way in which diversity is captured by each set of indices. The relatively strong and positive relationships between Shannon diversity and *FDis* indicates that within our marine zooplankton community a high species diversity value also reflect in a greater variety of traits. As the value of *FDis* increased, the species assemblage of functional traits can become overdispersed due to the larger number of functional traits represented (Wiedmann *et al.*, 2014). With respect to community evenness, *FEve* and $\mathcal{J}'$ were the least correlated of all analogous diversity index pairs. However, our results highlighted that they do vary positively in the Line P time-series. For community richness, *S* and *FRic* were well correlated indicating that a larger number of species tend to fill a greater volume of trait space in Line P (Villéger *et al.*, 2008). The Shannon diversity index (H′) relies on both relative species abundance and species richness in its calculation. While FDis also depends on relative species abundance but not on species richness. Thus, there should be some expectation that FDis will vary with H′, however, this correspondence need not be as strong as the correlations we measured, since there are no *a priori* reasons for expecting increased representation of functional traits when simply adding species to a community or increasing evenness. Note too that we also found a significant positive correlation between FDis and species richness (for the inner stations) indicating that variation in taxonomic diversity (its most

basic measure) is also reflected in variation in function. This result is similar to the correlations between RaoQ and species richness presented by Stuart-Smith et al. (Stuart-Smith *et al.*, 2013) for fish assemblages.

Our diversity index analyses results are similar to those observed in other studies from other ecosystems. Heino (Heino, 2008) found a strong correlation between *S* and *FRic* in littoral macro-invertebrate communities as did Ding *et al.* (Ding *et al.*, 2013) for bird communities. Mayfield *et al.* (Mayfield *et al.*, 2010) suggested that *S* and *FRic* are fundamentally linked based on the selection effect, where a large species pool size increases the likelihood of capturing the range of functional trait values in that pool of species. However, it has also been argued that other parameters, such as abiotic factors, may play a role in the relationships between *FRic* and *S*, as well as between other taxonomic and functional diversity indices. In fact, different functional traits can reflect individual responses to different environmental gradients with minimal change in richness, making *FRic* or other functional diversity indices better at capturing variation in ecosystem function (Cadotte *et al.*, 2011).

Time series anomalies

The Line P transect can be divided into two different sections on the basis of oceanographic and bathymetric properties; the outer Line P characterised by oceanic conditions and an iron-limited HNLC (high nitrate – low chlorophyll) environment, and the inner stations of Line P, which cover shelf waters with boreal subarctic conditions characterised by depleted nitrogen during the summer (Whitney *et al.*, 1998; Mackas and Galbraith, 2002). Several studies have examined variation in zooplankton distribution and community composition along Line P and have linked the observed differences primarily to inter-annual environmental variation, especially El Niño and La Niña events. In this current study, we examined functional and taxonomic diversity anomalies from 1997 to 2012. This 16 year time period covered several well documented extreme events including the very strong 1997−1998 El Niño event (peak occurred between December 1997 and October 1998), a strong La Niña event in 1999, a warm period between 2003−2005 (PDO positive), where 2005 was characterized as one of the warmest years on record, another La Niña event in 2007 followed by colder conditions in 2008, where 2008 was one of the coldest years over the past 50 years (Batten *et al.*, 2010). These oceanographic and atmospheric events have had a measureable influence of the species composition and spatial distribution of zooplankton communities (Mackas *et al.*, 2007; Batten *et al.*, 2010). In our analyses, negative anomalies were observed for most

taxonomic and functional diversity indices in 1997 and for some in 1998 within both sections of Line P. Negative anomalies were also observed during the warm phase of 2004−2005 within the inner portion of Line P. Our results demonstrate that during the first phase of the 1997−1998 El Niño event, there were fewer species (low S), variable in abundance (low H' and J'), with an unfilled niche space (low FRic). There was also a lower spread of species in trait space (low *FDis* indicates under-dispersion) within the outer section of Line P. It has been suggested that under-dispersion tends to occur in conditions of "environmental adversity" for instance, anomalies of abiotic factors (Weiher and Keddy, 1995) such as sea-surface temperature (SST) or under generally oligotrophic conditions (Vogt *et al.*, 2013). Our results corroborate analyses by Mackas and Galbraith (Mackas and Galbraith, 2002), which identified a reduction in zooplankton species as well as a shift in species assemblages towards warmer-water taxa. During warmer time periods such as 1997−1998 and 2003−2005, anomalously high abundances of warmer water species are found along Line P, while the abundance of boreal/northern species have negative biomass anomalies (Mackas and Galbraith, 2002).

The use of CWMs of average female body length suggest that useful information can be gained in terms of community function when traits are applied to a time series. Recent studies have demonstrated the value of CWM of trait values, for instance in linking amphibian responses to changes in plant litter communities (Cohen *et al.*, 2014). CWM is obtained by taking the mean trait value of a given species, weighted by its relative abundance within the community and summed across all species (Garnier *et al.*, 2014). Body length can be considered as a key structuring trait in zooplankton influencing, predator−prey relationship, energy content as well as metabolic rates such as growth and fecundity (Barnett *et al.*, 2007; Barton *et al.*, 2013). Here, we observed a significant increase in the overall community size in terms of adult females over time within the outer portion of Line P, towards a mean value of 6 mm in 2012. This may indicate a greater contribution in recent years of large oceanic copepod species such as *Eucalanus* spp. and *Neocalanus* spp. (Group 5b), which are known to be abundant in this region. Irvine and Crawford (Irvine and Crawford, 2013) similarly observed that large mesozooplankton species were more abundant in 2012 including the large copepods *Neocalanus* spp., euphausiids and hyperiid amphipods but using a purely taxonomic approach. This trend could be related to changes in oceanographic patterns such as the recent cooling within the outer section of Line P. The vast majority of SST daily values were below average in 2011 and 2012 (Irvine and

Crawford, 2012, 2013). Chiba *et al.* (Chiba *et al.*, 2015) have also recently found that larger copepod species dominated in the NE Pacific when SST was colder between 2007 and 2011. We want to emphasize that future studies should incorporate functional diversity in tandem with the more traditional species composition approach to develop a better understanding of species assemblages, community-level variations and the aggregate differences these can bring to the community (e.g. a quantifiable change in mean community body size).

Our study serves to illustrate the applicability of functional trait ecology in zooplankton studies. However, the assignment of traits can be problematic, since some traits vary ontogenetically (e.g. across nauplii, copepodite and adult stages), with gender, with season (e.g. winter omnivores, summer herbivore) and/or with region. A good example for the NE subarctic Pacific is the biomass-dominant copepod *Neocalanus* spp. In the Strait of Georgia, *Neocalanus* is defined as an herbivore (El-Sabaawi *et al.*, 2009), whereas the results of shipboard incubations classify the same species as detritivores in the outermost stations of Line P (Dagg, 1993; Homma and Yamaguchi, 2010). Following an iron enrichment experiment close to station P26 (Ocean station P) in 2002 (SERIES; Boyd *et al.*, 2004), a large diatom bloom developed and gut pigment analyses demonstrated that large copepods such as *Neocalanus* spp. switched from a detritivorous feeding habit to herbivory (Tsuda *et al.*, 2006). This is a prime example of environmental conditions shaping the behaviour and function of zooplankton species (e.g. Beaugrand *et al.*, 2002). Trait plasticity can therefore complicate the definitive assignment of a functional trait and indices that permit such variation (as well as central tendency values) to be accounted for are required (e.g. Albert *et al.*, 2011; Siefert *et al.*, 2014). We recommend caution while recognizing that ultimately, species/trait combinations may differ depending on the location and the objective of the study. Ideally, direct functional measurements such as ingestion rate and production rate measurements represent the best approach; however, these measurements are logistically difficult to apply at large spatial and temporal scales. Moreover, long-term time series of these types of measurements for zooplankton communities do not exist and there is thus still value in the approach we have adopted in this current study given the large number of long-term datasets of taxonomic information on species abundance. Thus, functional traits and diversity indices represent a potential alternative approach to direct measurement of function, by taking advantage of existing information on species abundances and compiling relevant functional traits available in the literature.

Using a well-studied time series allowed us to highlight the existence of temporal anomalies in functional and

taxonomic diversity indices that can be related to oceano-graphic and climatic events or shifts. Future studies are needed in order to understand the degree to which environmental conditions may shape the functional diversity within the zooplankton community and influence ecosystem processes and functioning at other time scales. Our results suggest that taxonomic and functional diversity indices represent complementary approaches where functional diversity indices may be useful in certain cases to capture more subtle changes in community structure and function. The description of the functional groups identified in our study highlights species linkages in terms of their ecological function rather than the most commonly described water-mass-based approach of species assemblages. The functional diversity approach may serve as a useful means to understand or predict potential shifts in function and trophic linkages in a changing ocean.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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