Unimodal relationship between biomass and species richness of deep-sea nematodes: implications for the link between productivity and diversity

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ABSTRACT: Describing large-scale patterns of biological diversity is a first step towards understanding the mechanisms that generate and maintain diversity. The highly diverse deep-sea floor is the largest ecosystem on Earth, but the productivity–diversity relationship in this biome is not well characterized. We investigated this relationship by using biomass of nematodes as a proxy for productivity (particulate organic carbon flux to the seabed). We used sample data collected from the New Zealand and Antarctic regions and combined these with published data from around the globe for broader analyses. There was a significant unimodal relationship between nematode biomass and diversity, i.e. expected number of species, ES(51) both within the New Zealand region and across ocean basins. This relationship remained significant after accounting for the effects of both water depth and nematode abundance. These findings support earlier suggestions of a unimodal productivity–diversity relationship in the deep sea that were based on other proxies (e.g. water depth, modelled particulate organic carbon flux). We argue that the 'productivity context' is of primary importance when determining the strength and nature of the relationship between other environmental factors and diversity. Studies that include either or both extremes of the productivity scale are likely to find that productivity is the main factor limiting deep-sea diversity, whereas those focusing on the intermediate productivity range are more likely to find that other factors (e.g. disturbance, habitat heterogeneity) play a role.

KEY WORDS: Southwest Pacific · Kaikoura Canyon · Ross Sea · Southern Ocean · Nematodes · Macroecology · Biomass

INTRODUCTION

Two major goals of ecology are to describe and explain patterns of species diversity (Lawton 1996). Species–energy theories, which have drawn considerable attention from ecologists seeking to explain large-scale diversity patterns, posit that species diversity (i.e. richness) is a function of one or multiple forms of energy variable(s) (e.g. temperature, evapo-transpiration, productivity; e.g. Currie 1991). The relationship between productivity and species diversity, in particular, has been the topic of numerous investigations in both terrestrial and aquatic ecosystems (Huston 1994, Rosenzweig 1995, Tittensor et al. 2011). Most such studies describe a unimodal relationship between productivity and local diversity (Waide et al. 1999, Dodson et al. 2000, Chase & Leibold 2002), but positive and negative linear relation-

ships are also common (Mittelbach et al. 2001, Witman et al. 2008). A number of underlying mechanisms have been proposed to explain productivity–diversity relationships, although there is much debate about their relative contributions (Rosenzweig 1992, Waide et al. 1999, Gross & Cardinale 2007). As the number of individuals increases with productivity, diversity may increase through higher proportions of rare (Preston 1962) and specialist species (Evans et al. 2006), lowered extinction rates and/or higher speciation rates (Rex 1973, Wright 1983). Negative productivity–diversity relationships may result from increased rates of competitive exclusion (Grime 1973, Rosenzweig & Abramsky 1993), temporal variability in productivity (Chown & Gaston 1999) or environmental stress (e.g. hypoxia, Levin & Gage 1998). A combination of these mechanisms, operating to increase and decrease diversity, might be responsible for the unimodal productivity–diversity relationship often observed.

Most of our knowledge of productivity–diversity relationships has been gained from terrestrial and shallow aquatic habitats (e.g. Mittelbach et al. 2001). Such relationships, however, have not been well characterized in the deep sea (>200 m water depth) owing to the challenges of conducting research in this environment and despite this ecosystem being the largest in areal extent on Earth. With the exception of chemosynthetic habitats, productivity in the deep sea is defined as particulate organic carbon (POC) flux from the euphotic zone. However, direct measurements of POC flux are rare. Consequently, investigations of productivity–diversity relationships in the deep sea are almost always conducted using productivity proxies. A decade ago, Levin et al. (2001, p. 60) noted that 'a unimodal relationship between diversity and productivity at large scales in the deep sea is plausible, but is not well substantiated'. This view remains essentially unchanged (Rex & Etter 2010), although some support was provided in a recent study by Tittensor et al. (2011), which showed a unimodal relationship between modelled POC flux and the diversity of deep-sea protobranch bivalves and gastropods.

One of the main problems with investigating productivity–diversity relationships in the deep sea is the difficulty of placing available studies on a continuous productivity gradient (Levin et al. 2001, Rex & Etter 2010). Most deep-sea studies are restricted to a single region, which limits the range of productivities sampled. The shape of the productivity–diversity relationship, however, may depend on the range of productivities considered (Huston 1999), which could

explain inconsistencies between studies (Rex & Etter 2010). Comparisons between investigations are also hampered by the wide range of productivity proxies used, such as water depth (e.g. Stuart & Rex 2009), latitude (e.g. Lambshead et al. 2002), modelled surface water productivity (e.g. Corliss et al. 2009), modelled POC flux (e.g. O'Hara & Tittensor 2010) or the organic matter/pigment content of the sediment itself (e.g. Berkenbusch et al. 2011, Leduc et al. 2012). Water depth is by far the most commonly used proxy for productivity because it is easy to determine, but depth is correlated with a number of other variables which can influence diversity patterns (e.g. temperature) and is not necessarily correlated directly with productivity at the seabed, particularly when compared across ocean basins (Rex & Etter 2010). Remotely sensed and modelled data have also become increasingly popular, despite limitations associated with spatial/temporal resolution and model validation (Balch et al. 1992, Banse & Postel 2003). POC flux to the seafloor depends on a variety of factors not included in these models, such as bottom micro- (Snelgrove et al. 1994) and macro-topography (e.g. canyons; De Leo et al. 2010), POC input from advective currents (Nodder et al. 2007) and the efficiency with which organic matter is remineralized and consumed in the water column (Buesseler et al. 2007).

Determining the relationship between productivity and local diversity at large spatial scales requires a proxy that can be meaningfully compared between ocean basins. Deep-sea standing stocks (i.e. biomass, abundance) of macrofauna (DeMaster et al. 1994, Cosson et al. 1997, Smith et al. 1997, Johnson et al. 2007) and meiofauna (Tietjen 1989, Danovaro et al. 1999) are strongly correlated with POC flux and could provide such a proxy (Rosenzweig 1995, Rex et al. 2005). Nematode biomass, in particular, is positively correlated with POC flux both within (Smith et al. 2008) and across ocean basins (Soetaert & Heip 1995). Thus, whilst biomass is most commonly used as a measure of secondary productivity, there is evidence to suggest that it is also a good proxy for POC flux. As Rex & Etter (2010, p. 25) noted, '[benthic] standing stock is the culmination of pelagic-benthic coupling, (…) and is the most directly relevant measure of ecological and evolutionary opportunity in the deep sea'. Few investigations, however, have been conducted on the relationship between standing stock and diversity (Haedrich et al. 1980, Boucher & Lambshead 1995).

Nematodes are by far the most abundant component of deep-sea faunal communities (Giere 2009)

and are arguably the most diverse (Lambshead & Boucher 2003). However, our knowledge of nematode diversity trends in the deep sea remains sketchy relative to the larger macro- and megafauna. The majority of studies have reported a positive relationship between productivity and deep-sea nematode diversity (Lambshead et al. 2002, Lampadariou & Tselepides 2006, Fonseca & Soltwedel 2007, 2009, Danovaro et al. 2008a), although the opposite trend has also been reported (Gambi et al. 2003), and several studies found no depth-related diversity gradients (Dinet & Vivier 1979, Jensen 1988, Lambshead et al. 2000). Whether these inconsistencies reflect the influence of other factors that have not been accounted for, or represent different portions of a larger unimodal curve, remains unclear. Nematodes are well suited for the study of diversity–productivity relationships in the deep sea because their standing stock is more closely linked to organic matter input than macrofauna and appears to be less affected by factors such as low oxygen conditions (Cook et al. 2000). Large-scale studies in the North Atlantic and the central Pacific have also led to the suggestion that, unlike larger organisms, nematode diversity in the deep sea is mostly unaffected by historical factors (e.g. glaciation events), which may otherwise confound analyses (Lambshead et al. 2000, 2002). Moreover, nematode biomass is typically estimated using the volumetric method (Giere 2009). This approach allows estimates of biomass and diversity to be derived from the same samples, thereby minimising any influence of small-scale variation in productivity.

The objective of the present study was to investigate the link between productivity and diversity in the deep sea by characterizing the relationship between nematode biomass and species richness. We used sample data collected from the New Zealand and Antarctic regions, and combined these with published data from the Mediterranean (Danovaro et al. 2008a, Pusceddu et al. 2009), Venezuela Basin (Tietjen 1984, 1989), Southeast Pacific (Danovaro et al. 2002, Gambi et al. 2003) and Southwest and central equatorial Pacific (Brown et al. 2001, Lambshead et al. 2002) for broader analyses.

MATERIALS AND METHODS

Sampling and laboratory methods

In total, 41 sites were sampled in the present study (Table 1, Fig. 1). New Zealand study sites (36 in total) were located on the Chatham Rise, Challenger Plateau and Kaikoura Canyon. The Chatham Rise is a broad submarine ridge extending eastwards from the South Island of New Zealand at water depths of ~350 to 3000 m. The highly productive Subtropical Front (STF) appears to be bathymetrically locked onto the southern flank of the rise near 44° S (Murphy et al. 2001, Sutton 2001). Meio- and macrofaunal biomass peaks on the southern flank of the rise near the STF and declines rapidly below 1200 m depth, particularly on the northern flank of the rise (Probert & McKnight 1993, Nodder et al. 2003, Grove et al. 2006, Berkenbusch et al. 2011). Nine sites on the Chatham Rise were sampled in September to October 2001 along a transect at 178° 30′ E (350 to 3100 m water depth; Table 1) during National Institute of Water and Atmospheric Research (NIWA) cruise TAN0116 (Nodder et al. 2007). Sixteen sites (422 to 1238 m water depth) were sampled on the Chatham Rise in March to April 2007 during NIWA cruise TAN0705. One additional site (990 m water depth) was sampled in February 2009 during NIWA cruise TAN0902. This site is located in a large, near-circular depression ('pockmark', ~10 km diameter, 80–100 m deep; Davy et al. 2010) on the southern flank of the rise and is characterized by episodic accumulations of fresh phytodetritus (S. Nodder unpubl. Ocean Survey 2020 data). The Challenger Plateau encompasses water depths ~400 to 3000 m in an area of generally low biological productivity to the northwest of the South Island, New Zealand (Murphy et al. 2001). Six sites (237 to 1213 m water depth) were sampled on the Challenger Plateau in May to June 2007 during NIWA cruise TAN0707. Five sites (405 to 1420 m water depth) were sampled along the Kaikoura Canyon axis in May 2010 during NIWA cruise TAN1006. The Kaikoura Canyon lies to the east of the South Island (~42° S), and has been described as one of the most productive deep-sea benthic habitats known (De Leo et al. 2010). Antarctic study sites included 2 sites on the Ross Sea continental shelf and slope (849 and 1604 m water depth, respectively), and 3 sites on the abyssal plain adjacent to Scott and Admiralty seamounts farther to the north (3245 to 3543 m water depth). These sites were sampled in February to March 2008 during NIWA cruise TAN0802. The abyssal site near Admiralty seamount is in an area of relatively lower surface productivity than the other Antarctic sites (Bowden et al. 2011).

Samples were taken using an Ocean Instruments MC-800A multicorer (MUC; core internal diameter = 9.52 cm). For faunal analyses, 1 to 2 replicates (i.e. samples from different MUC deployments) per site were obtained. Each faunal sample consisted of a

Table 1. Details of study sites, with mean nematode abundance, biomass and diversity data (n = 1–5 replicate samples). DW: dry weight; ES(51): expected number of species for a sample of 51 ind. Asterisks (*) are diversity data from Leduc et al. (2012)

Region Voyage	Habitat	Water depth (m)	Latitude (S)	Longitude (E or W)	Abundance (ind. per 10 cm^{-2})	Biomass (µg DW per 10 cm^{-2})	Diversity (ES(51))
New Zealand							
TAN0116	Chatham Rise	350	43°43.33′	178°50.00′ E	1355	168.5	36.7*
		450	42°96.81′	178°50.00′ E	795	47.9	41.5*
		450	43°81.81′	178°50.00′ E	972	99.5	35.7*
		750	44°00.00′	178°50.00′ E	1314	70.7	38.3*
		1000	42°81.67′	178°50.00′ E	476	31.9	40.7*
		1200	44°33.33′	178°50.00′ E	1521	53.8	39.6*
		2300	42°30.00′	178°30.00′ E	391	31.2	37.6
		2800	46°40.00′	178°30.00′ E	239	13.2	34.7
		3100	41°00.00′	178°30.00′ E	165	17.9	38.6
TAN0705	Chatham Rise	530	43°97.92′	179°63.33′ E	1711	129.2	32.8*
		644	43°29.30′	175°54.53′ W	549	19.9	37.4*
		1016	42°78.60′	176°7149′ W	560	39.2	37.6*
		1210	42°62.16′	175°92.62′ E	1324	222.5	35.8*
		532	42°99.03′	178°98.64′ E	2487	229.1	38.4*
		515	44°13.01′	174°84.55′ E	2828	322.8	35.0*
		1238	44°48.64′	177°14.07′ E	1698	216.0	33.1*
		478	43°82.66′	176°70.43′ E	989	317.9	30.2*
		422	43°51.62′	178°61.67′ W	1109	149.0	37.2*
		770	44°01.68′	178°51.93′ E	1837	177.3	37.2*
		1200	42°61.16′	178°33.93′ W	889	39.8	40.0*
		792	42°76.15′	178°34.86′ W	598	23.4	37.9*
		980	42°78.18′	177°21.03′ W	222	7.7	36.7*
		896	42°80.80′	177°22.82′ W	226	10.9	37.9*
		799	42°84.68′	177°22.47′ W	376	15.6	33.8*
TAN0707	Challenger Plateau	480	38°61.82′	168°94.31′ E	669	37.2	40.3*
		1213	36°92.14′	167°52.56′ E	641	36.8	33.4*
		264	39°64.63′	172°15.30′ E	893	63.6	31.2*
		532	40°88.14′	170°86.03′ E	737	33.9	34.7*
		804	40°12.64′	170°22.17′ E	575	87.5	32.1*
		237	39°64.09′	172°37.15′ E	669	40.3	32.4*
TAN0902	Chatham Rise 'pockmark'	990	44°06.60′	178°35.62′ E	3269	719.5	26.4
TAN1006	Kaikoura Canyon	404	42°29.38′	173°33.06′ E	3315	304.7	12.2
		706	42°28.86′	173°33.49′ E	2801	161.7	11.5
		1017	42°29.03′	173°36.88′ E	3226	1326.5	16.6
		1061	42°30.49′	173°37.95′ E	1661	1352.9	21.5
		1320	42°31.42′	173°43.68′ E	2011	849.9	18.6
Antarctic							
TAN0802	Ross Sea continental shelf	849	74°43.92′	167°06.17′ E	7023	116.9	21.5
	Ross Sea continental slope	1604	72°05.30′	175°33.51′ E	777	23.2	29.8
	Abyssal plain, near Admiralty seamount	3403	66°43.43′	171°11.18′ E	338	13.3	34.1
	Abyssal plain, near Scott seamount	3245	67°37.18′	178°12.12′ W	236	22.2	31.4
	Abyssal plain, near Scott seamount	3543	68°31.12′	178°48.70′ W	450	11.6	19.8

subcore (2.6 cm internal diameter) taken to a sediment depth of 5 cm. All samples were preserved in 10% formalin and stained with Rose Bengal. Samples were rinsed through a 1 mm mesh to remove macrofauna and through a 45 µm mesh to retain nematodes. Nematodes were extracted from the remaining sediment by Ludox flotation, transferred to pure glycerol and mounted on slides (Somerfield & Warwick 1996).

All nematodes present in each sample were counted under a compound microscope at 100× magnification. Nematode body volumes were estimated from
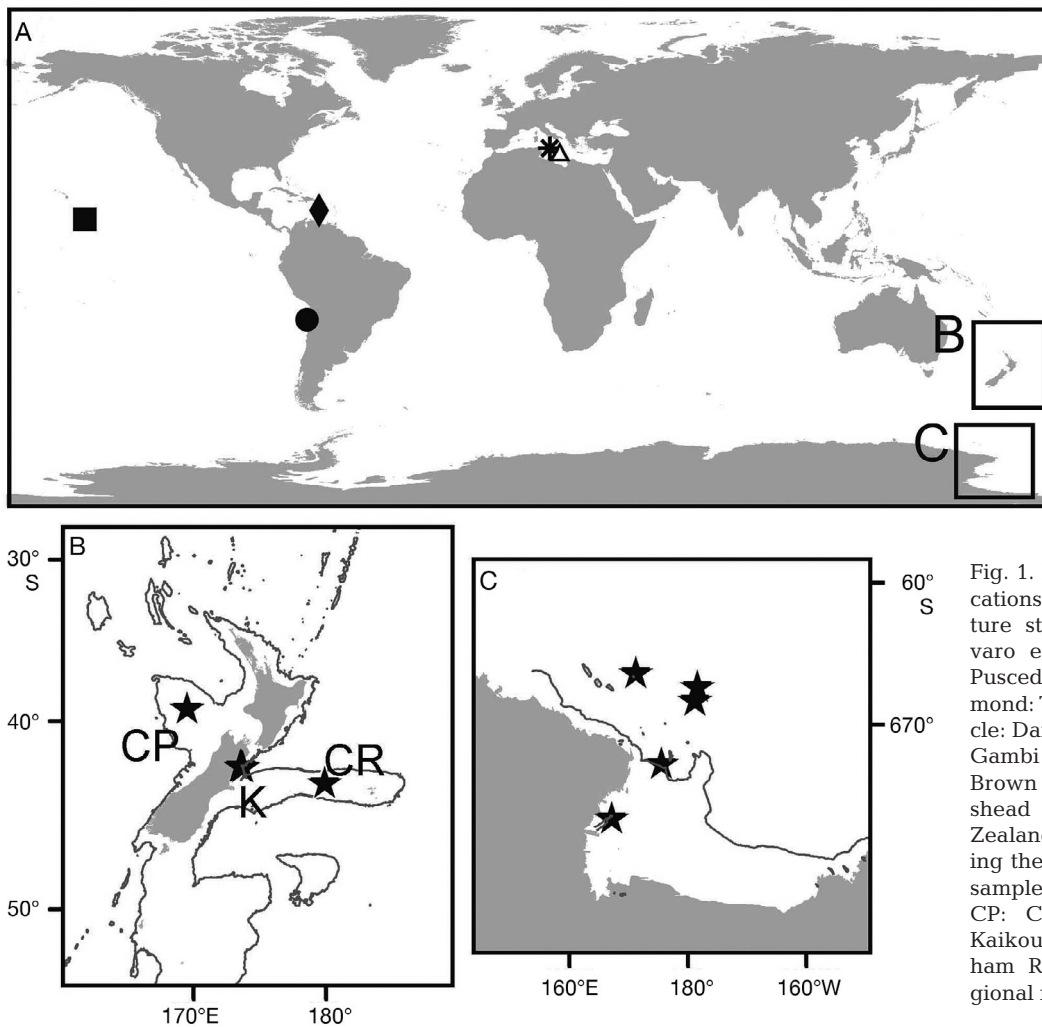
Fig. 1. Nematode sampling locations. (A) Locations of literature studies. Asterisk: Danovaro et al. (2008a), triangle: Pusceddu et al. (2009); diamond: Tietjen (1984, 1989); circle: Danovaro et al. (2002) and Gambi et al. (2003); square: Brown et al. (2001) and Lambshead et al. (2002). (B) New Zealand regional map, showing the 3 bathymetric features sampled for this study (stars; CP: Challenger Plateau, K: Kaikoura Canyon, CR: Chatham Rise). (C) Ross Sea regional map, showing sampling sites (stars)

length and maximum body width measurements obtained by video image analysis (Nodder et al. 2003, Grove et al. 2006). Body volumes were converted to dry weight (DW) based on a relative density of 1.13, and a dry:wet weight ratio of 0.25 (Feller & Warwick 1988). Estimates of mean body weight were based on a minimum of 100 individuals, or all individuals if fewer were present. Nematode diversity was estimated based on the identification of 120 to 150 randomly selected individuals (or all individuals if fewer were present) per sample and quantified using Hurlbert's (1971) rarefaction method for estimating the expected number of species for a sample of 51 individuals, ES(51). This measure is among the most commonly used diversity indices in deep-sea nematode investigations (e.g. Danovaro et al. 2008b) and allows comparison of samples with different abundances. Nematodes were identified to genus and putative species using descriptions of Warwick et al. (1998), as well as the primary literature.

Literature data

We collated data from all deep-sea studies for which nematode diversity expressed as ES(51) could be found and which also provided biomass and abundance data (Table 2). Data were obtained from the Mediterranean (12 sites; Danovaro et al. 2008a, Pusceddu et al. 2009), Venezuela Basin (8 sites; Tietjen 1984, 1989), central equatorial Pacific (5 sites; Brown et al. 2001, Lambshead et al. 2002) and southeast Pacific (4 sites; Danovaro et al. 2002, Gambi et al. 2003). Samples in these studies were obtained using either a multicorer or box corer (see Table 2 for details), which may yield different abundance estimates (Bett et al. 1994). Some studies, however, have reported no difference between the 2 sampling methods (Brown et al. 2001, Mokievskii et al. 2007). All of these studies sampled with a core ≤10 cm in diameter and determined biomass using the volumetric method (Giere 2009). All studies used a mesh

Table 2. Details of literature data sources included in the study showing mean nematode abundance, biomass and diversity. DW: dry weight; ES(51): expected number of species for a sample of 51 ind. *: from top 1 cm of sediments; **: estimated from graph; ***: from Danovaro et al. (2008b)

Region Source	Water depth (m)	Abundance (ind. per 10 cm^{-2})	Biomass (µg DW 10 cm^{-2})	Diversity (ES(51))
Mediterranean				
Danovaro et al. (2008a)[a]	3870	45	3.6	16.9*
	3055	38	0.8	16.2*
	2950	74	3.0	19.8*
	3200	109	6.6	21.0*
	4000	33	2.0	22.0*
	1290	326	65.1	26.8*
	2850	161	12.9	23.0*
	2755	92	11.0	23.9*
Pusceddu et al. (2009)[a]	3581	32**	0.6**	15.0
	3430	25**	0.6**	12.0
	3550	55**	7.0**	20.3
	3550	56**	2.0**	22.0
Venezuela Basin				
Tietjen (1984)[b]	3858	65**	32.0**	27.4***
	5054	38**	30.0**	32.1***
	3517	90**	88.0**	31.8***
Tietjen (1989)[b]	5401	137**	15.5**	30.0***
	2217	92**	5.2**	26.8***
	7460	76*	8.0**	25.4***
	8189	69**	19.9**	22.4***
	8380	78**	16.8**	21.6***
Central equatorial Pacific				
Lambshead et al. (2002)[c]	4320	60*	3.1*	33.9
Brown et al. (2001)[c]	4400	96*	8.2*	32.4
	4390	64*	8.7*	32.4
	4990	45*	1.9*	31.3
	4880	40*	1.9*	28.2
SE Pacific				
Danovaro et al. (2002)[d]	1050	492	232	25.0
Gambi et al. (2003)[d]	1140	550	248	26.7
	1355	525	282	26.0
	7800	5072	810	18.4

[a]Multicore, 20 µm mesh; [b]box core, 44 µm mesh; [c]multicore and box core, 45 µm mesh; [d]box core, 20 µm mesh

size of 45 µm or less, which ensured minimal variation in biomass estimates since nematodes retained on a 45 µm mesh comprise >90% of total biomass in deep-sea samples (Leduc et al. 2010a,b). One study (Danovaro et al. 2008a) provided nematode diversity data only from the 0–1 cm sediment depth layer, while nematode abundance and biomass data were obtained from the 0–15 cm depth layer. Diversity estimates from Danovaro et al. (2008a) were adjusted assuming that diversity estimates based on the top 1 cm of sediments underestimate ES(51) values by 15% relative to whole cores (Leduc et al. 2010b). Another study (Lambshead et al. 2002) provided nematode diversity data based on whole cores (sediment depth not specified) but estimated biomass based on the 0–1 cm fraction only. In this case, we

assumed that biomass estimates were 33% of the total depth-integrated values (D. Leduc unpubl. data). All other diversity and biomass data were based on cores ≥5 cm deep.

Statistical analyses

Statistical analyses were conducted on the mean nematode biomass and diversity of each site. Analyses were conducted on all data combined (n = 70 samples) and on Chatham Rise sites only (n = 25), in order to compare the biomass–diversity relationship at different spatial scales (i.e. across and within regions). The Chatham Rise sites were chosen for separate analysis because they span a wide range of productivities within a single seabed feature.

Analyses were conducted using distance-based linear models (DistLMs) in PERMANOVA+ (Anderson et al. 2008). The DistLM routine is a semi-parametric, permutation-based method that does not rely on the assumption of normally distributed data (Anderson et al. 2008). Examination of predictor variables (i.e. water depth, nematode abundance and biomass) prior to analyses showed that they were not strongly correlated ($R^2 < 0.41$). Because water depth is the most commonly used productivity proxy in deep-sea studies (Rex & Etter 2010), we began by investigating the relationship between water depth and nematode diversity. Nematode abundance was also included in the analyses to examine its relationship with diversity and to take into account its potential influence on the biomass–diversity relationship. Both linear and quadratic relationships were modelled in DistLM (the latter by performing regressions on first- and second-order terms in sets, Anderson et al. 2008). The best-fitting relationship was chosen for the final regression models by comparing adjusted R^2 values (Quinn & Keough 2009). Relationships between water depth, nematode abundance, nematode biomass and diversity were initially examined by analysing each predictor separately (marginal tests). Partial regressions were used to better characterize the relationships

and to account for the effect of the other 2 variables. Similarity matrices used in DistLM analyses were built using Euclidean distance of untransformed diversity data (Anderson et al. 2008). The p-values for individual predictor variables were obtained using 9999 permutations. Water depth and nematode abundance/biomass data were $\log_{10}$-transformed to reduce skewness.

RESULTS

Nematode abundance and biomass at the New Zealand and Antarctic sites spanned about 1 and 3 orders of magnitude, respectively (Table 1). Nematode abundance was lowest at the deepest Chatham Rise site (3100 m water depth; 165 ind. 10 cm^{-2}) and highest at the Kaikoura Canyon sites (1661–3315 ind. 10 cm^{-2}). Biomass was lowest at sites on the northeastern Chatham Rise (7.7–15.6 µg DW 10 cm^{-2}) and at the Southern Ocean abyssal sites (11.6–22.2 µg DW 10 cm^{-2}). Nematode biomass was highest at the 3 deepest Kaikoura Canyon sites (850–1353 µg DW 10 cm^{-2}). ES(51) was lowest at the 2 shallowest Kaikoura Canyon sites (11.5–12.2) and highest at 2 sites on the northern flank of the Chatham Rise (40.7–41.5).

The range of nematode abundance and biomass for New Zealand, Antarctic and literature data combined spanned 2 and 4 orders of magnitude, respectively (32–7023 ind. 10 cm^{-2}, 0.6–1353 µg DW per 10 cm^{-2}, Tables 1 & 2). There was a weak but statistically significant negative relationship between water

depth and nematode diversity for all data combined (p = 0.002, R^2 = 0.14; Table 3) but not for the Chatham Rise sites alone (p > 0.05). Similarly, there was a significant quadratic relationship between nematode abundance and diversity for all data combined (p = 0.001, R^2 = 0.42) but not for the Chatham Rise sites alone (p > 0.05). There was a strong significant quadratic relationship between nematode biomass and diversity for all data combined and for Chatham Rise sites only (R^2 = 0.46 and 0.63, respectively, p = 0.001; Fig. 2). These relationships remained significant after controlling for water depth and abundance (Table 3).

DISCUSSION

Describing large-scale diversity patterns is a first step towards understanding the mechanisms that generate and maintain diversity. Many deep-sea studies span a comparatively limited productivity range (i.e. ≤1 order of magnitude; see Table 2). Combining data from oligotrophic (e.g. the Mediterranean) to highly eutrophic deep-sea habitats (e.g. Kaikoura Canyon) across a wide range of water depths (237–8380 m) and regions enabled us to characterize the relationship between nematode biomass and local diversity across the broadest possible spectrum.

Using biomass as a proxy of productivity (i.e. POC flux) has several advantages. Biomass, for example, provides a way to scale studies on a continuous productivity gradient and, for nematodes at least, provides a measure of productivity at a directly relevant

Table 3. Results of distance-based linear model (DistLM) analyses between water depth, nematode abundance, nematode biomass and nematode diversity (expected number of species for a sample of 51 ind., ES(51), for all data combined, and for Chatham Rise sites only. Marginal tests examine a single predictor separately, while partial tests take into account the effect of the other 2 predictors. Correlations are for linear (water depth) and quadratic (nematode abundance and biomass) relationships. Variables that are significantly correlated with nematode diversity are shown in **bold**. Prop.: proportion of the total variation in diversity, ES(51); res.: residual; regr.: regression

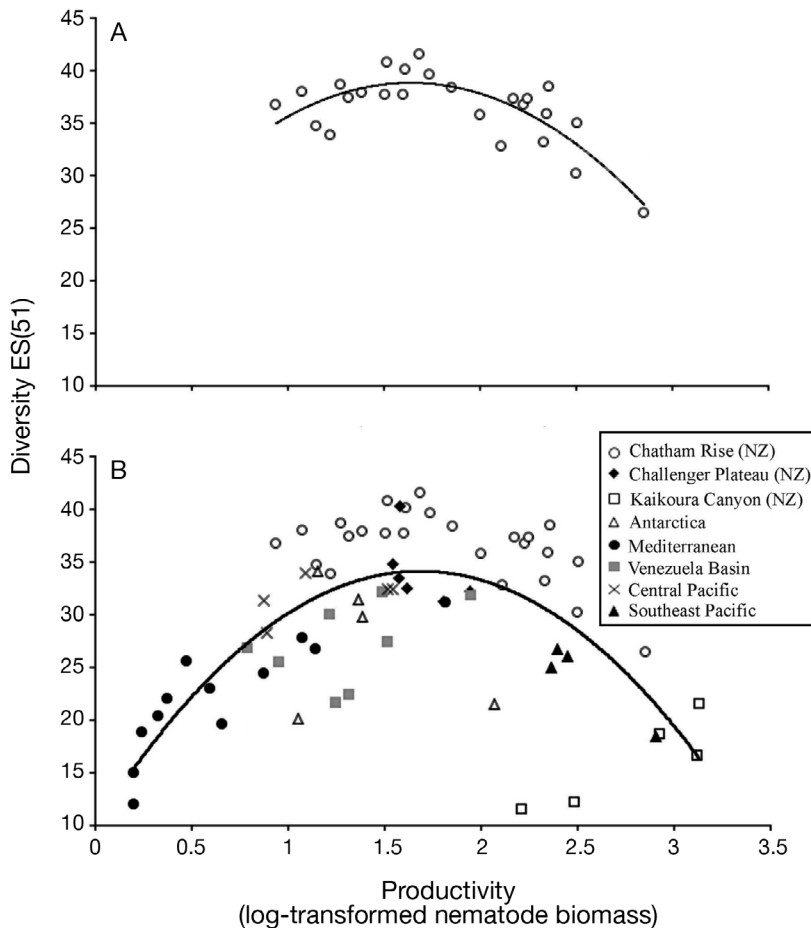|	Variable	SS (trace)	Pseudo-*F*	p	Prop.	Res. df	Regr. df
All data (marginal)	**Depth**	569.7	10.887	0.002	0.14	68	2
	Abundance	1719.9	23.928	0.001	0.42	67	3
	Biomass	1987.5	31.108	0.001	0.46	67	3
All data (partial)	Depth	56.6	2.027	0.152	0.01	64	6
	Abundance	140.8	2.521	0.109	0.03	64	6
	Biomass	551.1	9.870	0.001	0.13	64	6
Chatham only (marginal)	Depth	1.3	0.112	0.752	<0.01	23	2
	Abundance	59.7	3.195	0.071	0.23	22	3
	Biomass	167.5	18.818	0.001	0.63	22	3
Chatham only (partial)	Depth	3.7	0.867	0.351	0.001	19	6
	Abundance	16.137	1.894	0.171	0.06	19	6
	Biomass	124.6	14.682	0.001	0.47	19	6

Fig. 2. Relationship between productivity, $\log_{10}(1+$ nematode biomass), and nematode diversity, ES(51), on (A) the Chatham Rise and (B) across regions. Curved line in (B) shows the fit for all data points. See Table 3 for results of regressions analyses

less, biomass may be affected by factors other than productivity. Physical disturbance and predation, for example, could reduce biomass by removing individuals from the population. Quantifying the influence of these factors is difficult, but we might expect some habitats such as canyons to be subject to more intense disturbance regimes than open slope habitats (De Stigter et al. 2007, Garcia et al. 2007). Nematode biomass from the Kaikoura Canyon samples may, therefore, have been underestimated, although greater biomass values for this location would strengthen, rather than weaken, the unimodal relationship we observed (see Fig. 2).

Ideally, deep-sea productivity would be quantified using direct measurements of POC flux at a scale relevant to the system under study. Measuring POC flux in the deep sea, however, is labour-intensive, and site-specific data are generally scarce (e.g. Jahnke 1996, Lutz et al. 2007). Estimates of POC fluxes in the deep ocean from modelled (e.g. Usbeck et al. 2003) and satellite data (e.g. Lutz et al. 2007) are easier to obtain, but current methods do not take into account the potential decoupling between POC flux at the seabed and surface productivity (Buesseler et al. 2007), the influence of down-slope transport (Hecker 1990), lateral advection (Nodder et al. 2007), riverine input (Hansell et al. 2004) or bottom topography (e.g. canyons, Wei et al. 2010). It has also been argued that it is the quality rather than the quantity of the organic flux reaching the benthos that is critical in determining benthic secondary productivity (e.g. Nodder et al. 2003). Furthermore, parameters such as POC flux or sediment organic matter/pigment content do not take into account the partitioning of food resources between different components of the benthos. The relative contribution of smaller organisms to benthic secondary production, for example, increases substantially with depth (Rowe et al. 2008), implying that they incorporate varying proportions of available food resources.

The present study supports earlier suggestions of a unimodal productivity–diversity relationship in the

spatial scale because the same sample is used for both biomass and diversity estimates. The latter is particularly important for small animals with limited mobility, such as nematodes, because their distribution is likely driven by local (<10 cm) environmental conditions (Gallucci et al. 2009). As stated earlier, the strong link between measured POC flux and deep-sea benthic biomass is well established (e.g. Smith et al. 2008). In addition, nematode biomass on the Chatham Rise and Challenger Plateau is significantly correlated with other proxies of productivity, such as surface chlorophyll *a* concentrations ($R^2 = 0.54$, p < 0.01) and chloroplastic pigment concentrations in the sediments ($R^2 = 0.67$, p < 0.01; D. Leduc unpubl. data). Positive relationships between sediment pigment concentrations and nematode biomass have been described in other regions (e.g. Brown et al. 2001), providing further support for the use of nematode biomass as a proxy for productivity. Neverthe-

deep sea that were based on water depth (Levin et al. 2001, Rex et al. 2005, Rex & Etter 2010). The depth-based evidence for a unimodal productivity–diversity relationship in the deep sea showed a peak in diversity at intermediate depths (2000– 3000 m; Rex 1973, 1981, Etter & Grassle 1992, Boucher & Lambshead 1995, Rex et al. 2005), although positive and negative linear patterns have also been reported (see review by Stuart & Rex 2009). Besides productivity, several other factors that can vary with depth, such as sediment particle size diversity (Etter & Grassle 1992), macrohabitat heterogeneity (McClain & Barry 2010), oxygen concentrations (Levin et al. 2001), predation (Rex 1976) and speciation rates (Zardus et al. 2006), could explain these depth-related patterns. In the present study, diversity was either not correlated (Chatham Rise) or only weakly correlated (all data) with water depth. This finding adds to previous concerns that depth is not a particularly useful proxy for productivity. More work is required to test the generality of the unimodal productivity–diversity relationship in the deep sea using other productivity proxies.

Our results, based on biomass, suggest that the unimodal relationship between productivity (POC flux) and local diversity holds both within and across regions. Deep-sea regional diversity can influence local diversity (e.g. Stuart & Rex 1994) and may, therefore, have contributed to the pattern we observed across regions. However, because the relationship holds true when tested at the scale of the Chatham Rise sites, ecological factors acting at smaller spatial scales are more likely to be the main drivers. For instance, diversity at the least productive sites is likely to be limited by generally low population densities with consequently higher probability of local extinction (e.g. Rosenzweig 1995, Rex et al. 2005). This is unlikely to be the only factor involved, however, since the unimodal relationship between biomass and diversity remained significant after accounting for nematode abundance. A variety of factors could be invoked to explain the low diversity at the most productive sites. Increased rates of competitive exclusion may be responsible (Rex 1983), but this possibility has not yet been tested in the deep sea. Highly productive benthic habitats are usually characterized by low oxygen concentrations and high sulphide levels, conditions which are often associated with low infaunal diversity (Bagarinao 1992, Levin 2003). Hydrothermal vents and seeps, probably the most extreme examples of such habitats in the deep sea, are usually characterized by low-diversity nematode assemblages, and are sometimes dominated by species of the family Monhysteridae and of the genus *Sabatieria*, respectively (Vanreusel et al. 2010). These taxa were also dominant at our most productive deep-sea sites: the Atacama Trench (Gambi et al. 2003), Kaikoura Canyon, Chatham Rise pockmark and the deepest site on the Ross Sea continental shelf (D. Leduc unpubl. data). Physical disturbance may also help explain the low diversity observed at some of the most productive sites (Widdicombe & Austen 2001). Canyon communities, for example, are often subject to repeated disturbance following sediment resuspension and deposition events along the canyon axis (e.g. De Stigter et al. 2007). Chronic disturbance could help explain the particularly low diversity observed at the shallower (400–700 m water depth) Kaikoura Canyon sites nearest the active head of the canyon (see Table 1). Variability in food availability may also depress diversity at high-productivity sites. High-productivity sites usually experience greater temporal variability in organic matter input, which may favour species able to quickly exploit pulses of phytodetritus and thus lead to lower diversity through competitive exclusion (Chown & Gaston 1999). Considerable temporal variability in current flows on the Chatham Rise, for example, may lead to highly episodic phytodetritus deposition events (Nodder et al. 2007), a process which may be accentuated by local seabed topography (S. Nodder unpubl.).

It has been suggested that the shape of the unimodal productivity–diversity relationship may be better conceived as an upper boundary rather than a line of fitted average values (Schmid 2002; see also Fig. 2). Gray (2002) also suggested that the role of productivity may lie primarily in setting the upper limit of species diversity, with other factors influencing the realised diversity at a given location. Habitat heterogeneity, for example, is thought to facilitate species coexistence and increase diversity (e.g. Rosenzweig 1995, Henry & Roberts 2007). The positive influence of habitat heterogeneity on diversity may, however, be limited in highly productive environments characterized by toxic sediment conditions (e.g. high sulphide and low oxygen levels) because only a limited number of species will be adapted to such conditions. Similarly, Huston's (1994) dynamic equilibrium model predicts that the effect of disturbance on diversity will be most limited at either productivity extremes. In a practical sense, the range of productivities included in a study may influence our ability to detect a relationship between diversity and other environmental factors. For example, a study of diversity that includes low and/or high productivity extremes but does not account for this situation in

analyses may be less likely to detect relationships between, say, habitat heterogeneity and diversity or disturbance and diversity than a study limited to the middle range of productivities, because of the over-riding effect of productivity extremes on absolute levels of diversity. The 'productivity context' is, therefore, of primary importance when determining (or comparing) the strength and nature of the rela-tionship between diversity and other environmental factors. Thus, such studies should include measures of productivity as a matter of course, or be designed to sample within a limited productivity range.

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