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Trophic status and condition of *Hyalinoecia longibranchiata* from two regions of contrasting oceanic productivity

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ABSTRACT: The Chatham Rise and Challenger Plateau are 2 regions of New Zealand's Exclusive Economic Zone with very different levels of productivity. The Chatham Rise is a physically dynamic region that sustains one of New Zealand's largest mid-deep water fisheries, whilst the Challenger Plateau is a region of low hydrodynamic activity and productivity. These contrasting regions of pelagic productivity are likely to influence the trophic status of their benthic communities, where downward coupling of pelagic resources to the benthos occurs. Populations of the benthic quill worm *Hyalinoecia longibranchiata* (Onuphidae) were sampled at a range of depths on the Chatham Rise and the Challenger Plateau. Stable isotope signatures, $\delta^{13}C$ and $\delta^{15}N$, and nutritional condition indices (DNA:dry weight, protein:DNA, RNA:DNA and C:N) of the quill worms were measured to: (1) determine whether regional-scale differences in surface productivity are reflected in the trophic status and condition of the quill worms; and (2) ascertain the extent to which other factors (e.g. depth, distance from the mainland) may affect this. Analysis revealed that *H. longibranchiata* collected on the Chatham Rise were more enriched in $\delta^{13}C$ and in better condition than those collected on the Challenger Plateau. The isotopic enrichment observed at the Chatham Rise is likely to arise from differences in the quality and quantity of the organic inputs to the benthos. Overall, regional productivity had a much greater influence on the trophic status and condition, reflective of the degree of pelagic–benthic coupling, rather than any depth or spatial considerations.

KEY WORDS: Bentho-pelagic coupling · Chatham Rise · Quill worms · Benthic nutrition · Challenger Plateau · Condition

INTRODUCTION

The downward transport of particulate organic matter (POM), originating from the euphotic zone, is an important source of organic matter to the deep sea (Billett et al. 1983, Gage & Tyler 1991), which can shape the structure and functioning of benthic communities (Gooday 2002). For example, growth and reproduction in the deep-sea echinoid *Echinus affinis* in the Atlantic Ocean is determined by the seasonal deposition of phytodetritus (Camposcreasey et al. 1994), whilst variability of fluxes in POM influence

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the fatty acid composition of deep-sea holothurians (Hudson et al. 2004, see also Lutze & Coulbourn 1984, Fontanier et al. 2002, Buesseler et al. 2008). Connections between ecological processes that occur in the pelagic ecosystem and the seafloor may be referred to as 'pelagic–benthic coupling' (Graf 1992, Smith et al. 2006) and in the present study we use this term to describe the relationship between primary productivity (via POM flux) and the trophic status and nutritional condition of benthic megafauna.

The amount and quality of organic resources produced in an oceanic region will be determined, in part, by oceanographic processes and their associated physical features. For example, seamounts or oceanic rises can facilitate upwelling, which will bring fresh nutrients to the surface and influence the amount of vertical and horizontal mixing (Genin 2004), thereby increasing pelagic productivity (McGowan & Hayward 1978). Correspondingly, the transport of water masses, by currents, to regions with different physico-chemical properties (e.g. salinity, temperature), biological compositions (Eckert & Stewart 2001) and/or terrestrial inputs (Darnaude et al. 2004) may all serve to release nutrients into the photic zone (Tait 1968). Increases in surface productivity, in turn, may be reflected in an increase in the amount of POM transported downwards to the benthos (e.g. Graf 1992).

Stable isotopes have been employed to investigate nutrient and energy flows in marine ecosystems (Post 2002) and to document trophic interactions in deep-sea communities (Fisher et al. 1994, Iken et al. 2001, Levesque et al. 2006, Limén et al. 2008, Stowasser et al. 2009). Hobson et al. (1995) have shown, using stable isotopes, that the benthic invertebrate communities of northeastern Greenland (~300 m) are supported by pelagic productivity. Similarly, in the Gulf of Mexico (212 to 3527 m deep), Morse & Beazley (2008) found that the organic content of sediments, even in the deep sea (>1000 m), is influenced by surface productivity. The stable isotopes $\delta^{13}C$ and $\delta^{15}N$ will generally show a stepwise enrichment for each trophic level (~1‰ and 3–4‰, respectively; De Niro & Epstein 1978, Fry & Sherr 1984, Minagawa & Wada 1984). Hence these values can be used to identify the resources consumed by and the trophic position of an organism. Any interpretation needs to be made with care, as variations in enrichment may be both species- and tissue-specific (Vanderklift & Ponsard 2003), while the efficiency of assimilation and fractionation of the isotopes within the tissues can also be variable (Gannes et al. 1997). Furthermore, animals that undergo food deprivation may become enriched in $\delta^{15}N$, making trophic differences difficult to distinguish from fasting and/or starvation events (Webb et al. 1998, Cherel et al. 2005, Williams et al. 2007), and it is possible that this will be an issue in a food-limited environment, such as the deep sea (Tyler 2003).

In light of such caveats, condition indices can aid the interpretation of stable isotope data, as they will reflect the nutritional state and composition of an organism, allowing trophic interactions to be more accurately linked to nutritional ecology. Traditionally the ratio of the carbon content of an organism to its nitrogen content (C:N) has been used as an indicator of nutritional 'condition' (Okumura et al. 2002), where low ratios reflect improved nutritional status (Schmidt et al. 1999). Further indices frequently used in marine ecology (Chícharo & Chícharo 2008) include those derived from nucleic acids, protein and dry mass ratios. Cell growth is determined by protein biosynthesis, which is controlled by RNA, and hence protein and RNA concentrations will vary with an organism's rate of growth and/or nutritional status (Bergeron 1997). The concentration of DNA within a cell is assumed to remain fairly constant (Chícharo & Chícharo 2008), such that ratios of RNA:DNA and protein:DNA reflect rates of protein synthesis. The ratio of DNA:dry weight (DW) is indicative of the relationship between cell size (growth/starvation/ontogenetic change) and DNA concentration (Bergeron 1997), where high ratios are indicative of poor condition and/or starvation and low ratios indicate good condition and/or growth (Chícharo & Chícharo 2008).

Oceanic fronts are narrow bands of strong physical gradients where pelagic productivity is generally high (Longhurst 1998). In New Zealand, the Subtropical Front (STF) separates warm, highly saline, macronutrient-poor subtropical surface water masses, derived from the Tasman and Coral Seas, from cooler, less saline, macronutrient-rich subantarctic water masses (Heath 1985, Boyd et al. 1999). The nominal position of the front is at 44° S (Uddstrom & Oien 1999), although it is perhaps best regarded as a frontal zone (Sutton 2001). To the east of New Zealand, the STF is constrained bathymetrically by the elevated Chatham Rise, where the shallow bathymetry on the top of the rise generates a dynamic mixing regime that results in persistently high levels of productivity (Murphy et al. 2001). This is reflected in an increased flux of POM to the benthos (McClatchie et al. 1997, Nodder & Northcote 2001), with a subsequent impact on benthic communities (Probert & McKnight 1993, Nodder et al. 2003). In contrast, the Challenger Plateau that lies to the

west of New Zealand and to the north of the STF is less productive than the Chatham Rise and reflective of less dynamic, oligotrophic oceanic conditions (Murphy et al. 2001). In contrast to the considerable research on the Chatham Rise (see Carney 2005 for details), little work has been carried out on the Challenger Plateau and consequently the ecology of its pelagic and benthic communities is poorly studied (Longhurst 1998).

In terms of productivity, the mean annual sea surface chlorophyll *a* (chl *a*) concentrations on the Chatham Rise (0.6–0.7 mg chl *a* m^{-3}) are 3 times greater than those on the Challenger Plateau (0.2–0.3 mg chl *a* m^{-3}) (Murphy et al. 2001, Tilburg et al. 2002). Productivity on the Chatham Rise is spatially and temporally variable with a pronounced seasonality (Murphy et al. 2001). Primary production typically peaks during spring (0.8 mg chl *a* m^{-3}) due to the release of nutrients following deep autumn/winter mixing, remaining low throughout the rest of the year (0.1 mg chl *a* m^{-3}) (Murphy et al. 2001). Primary production tends to be higher on the southern flank compared with the northern flank, with peaks occurring during spring and autumn (1.2 mg chl *a* m^{-3}), with an elevated minimum for the rest of the year of 0.2 mg chl *a* m^{-3} (Murphy et al. 2001). For the Challenger Plateau (extended region of the Tasman Sea), Murphy et al. (2001) reported a production peak during spring (0.5 mg chl *a* m^{-3}), with little biomass accumulation occurring throughout the rest of the year (0.1 mg chl *a* m^{-3}).

With regard to particle flux or the downward transport of POM, Nodder & Gall (1998) found that phytopigments (predominantly chl *a*) contributed to the flux measured at 220 m water depth on the Chatham Rise. Fluxes ranged from 17 µg m^{-2} chl *a* d^{-1} during spring to 11 µg m^{-2} chl *a* d^{-1} during winter. Nodder & Northcote (2001) also recorded episodic particulate fluxes on the Chatham Rise at 300 and 1000 m depths, with an estimated particle sinking rate of 100 m d^{-1}. Fluxes were generally lower on the southern flank and were postulated to be richer in protein (reflected in overall higher molar N:P ratios), with a higher proportion of organic carbon sinking out of the surface ocean than that on the northern flank (e.g. organic carbon comprised 17% of the total annual mass flux at 300 m on the southern flank, compared with 14% on the northern flank) (Nodder & Northcote 2001).

Accordingly, these patterns in production and downward flux are also reflected in infaunal benthic biomass (Probert & McKnight 1993, Nodder et al. 2003, 2007), sediment bacterial production and community oxygen consumption (Nodder et al. 2003). However, for the Challenger Plateau and many other regions in New Zealand's deep sea, there are no comparable studies of particle flux. Notwithstanding, considering the lower productivity of the surface waters, it is likely that over annual time scales downward fluxes on the Challenger Plateau will be less than that occurring on the Chatham Rise.

Sarda et al. (2009) has postulated that the flux of organic matter to the benthos is a significant food resource for deep-water polychaetes (Cosson-Sarradin et al. 1998, Glover et al. 2001, Glover et al. 2002). On the Chatham Rise, polychaetes are a conspicuous and ecologically important component of the infaunal benthic community (Probert et al. 1996, Glasby & Alvarez 1999, Probert et al. 2009). The quill worm *Hyalinoecia longibranchiata* is a common megafaunal benthic polychaete found ubiquitously on New Zealand's continental slope (Read & Clark 1999). Members of the *Hyalinoecia* genus have been poorly studied, but they are considered to be motile epibenthic scavengers, predated upon by other deep-sea benthic fauna such as asteroids (Read & Clark 1999). During 2 research voyages in 2007 a high number of individuals were observed and collected from a wide range of sites on both the Chatham Rise (16.34 ± 6.73 ind. 1500 m^{-2}, mean ± SE) and the Challenger Plateau (7.13 ± 3.98 ind. 1500 m^{-2}) (Bowden 2011). The aims of the present study were: (1) to determine whether regional-scale differences in surface productivity are reflected in the trophic status and condition of a deep-sea benthic organism, the quill worm *H. longibranchiata*, thereby providing evidence of pelagic– benthic coupling; and (2) to ascertain the extent to which other factors (e.g. depth, distance from the mainland) may influence this.

MATERIALS AND METHODS

Specimens of *Hyalinoecia longibranchiata* were collected from 14 sites from depths of 451 to 853 m on the Chatham Rise and the Challenger Plateau (Fig. 1) using a beam trawl and epibenthic sled as a part of the New Zealand Government-funded 'Oceans Survey 20/20 Chatham-Challenger Hydrographic, Biodiversity and Seabed Habitat project' conducted between April and June (austral late autumn/early winter) 2007 over 2 voyages. The first was to the Chatham Rise (NIWA voyage TAN 0705) and the second was to the Challenger Plateau (TAN 0707) (Table 1). Once retrieved, *H. longibranchiata*

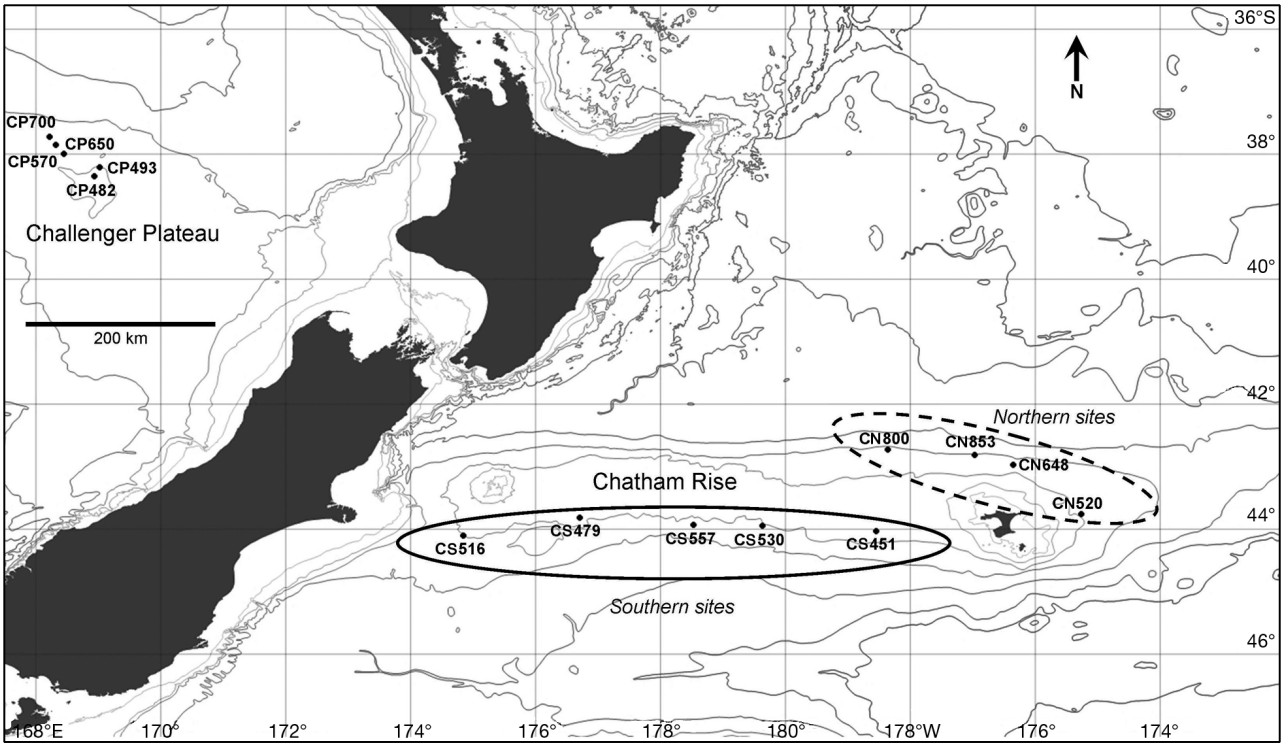

Fig. 1. Locations of the sample sites on the Challenger Plateau and Chatham Rise

Table 1. Location and depth of the sample sites. Sample sizes (n) are given for both the nucleic acid derived condition indices (CI; DNA:DM, protein:DNA, RNA:DNA ratios) and isotope analysis (SI; $\delta^{13}C$, $\delta^{15}N$, C:N ratio)

Site code	Location	CI	SI	Depth (m)	Latitude	Longitude
CP482	Challenger Plateau	8	8	482	38°22′58″S	168°56′14″E
CP493	Challenger Plateau	12	10	493	38°13′59″S	169° 1′24″E
CP570	Challenger Plateau	22	10	570	38° 1′25″S	168°26′49″E
CP650	Challenger Plateau	26	10	650	37°52′37″S	168°18′51″E
CP700	Challenger Plateau	28	10	700	37°45′22″S	168°12′53″E
CN520	Chatham Rise north	6	6	520	43°47′44″S	175°15′7″W
CN648	Chatham Rise north	25	10	648	42°59′55″S	176°20′53″W
CN800	Chatham Rise north	19	10	800	42°45′44″S	178°33′37″W
CN853	Chatham Rise north	11	10	853	42°50′34″S	176° 3′39″W
CS451	Chatham Rise south	12	10	451	44° 3′51″S	178°33′0″W
CS479	Chatham Rise south	30	10	479	43°50′24″S	176°42′25″E
CS516	Chatham Rise south	30	10	516	44° 7′52″S	174°50′40″E
CS530	Chatham Rise south	3	3	530	43°58′39″S	179°38′4″E
CS657	Chatham Rise south	3	3	657	43°57′46″S	178°32′5″E

specimens were frozen at –20°C. In the laboratory, specimen length was measured and body tissue was taken by removing the polychaete body from its quill and dissecting a 2 cm segment from below the head. This tissue was then weighed to 0.01 mg wet mass and subsequently freeze-dried. Once dry, samples were re-weighed and homogenised.

For the majority of sites, surface sediment was collected using either an Ocean Instruments MC-800 deep-sea multi-corer or a pipe dredge attached to the outside of the epibenthic sled or beam trawl. Determination of total organic matter (TOM) was made by weight loss-on-ignition, $CaCO_3$ content using vacuum-gasometry and phytopigment concentrations

(phaeopigments, chl *a*) by standard spectrophotometric methods (see methods in Nodder et al. 2003).

To elucidate differences in the major macronutrient composition of *Hyalinoecia longibranchiata* (proteins and lipids only), lipid content was determined from ~5 mg of dried whole tissue with samples extracted 3 times in 1 ml of chloroform. The remaining tissue was re-dried and assumed to represent the lipid-free fraction. Determination of the protein content was made using a modified procedure based on the methodology of Clissold et al. (2006) by extracting protein from 5 mg of dried ground sample in 500 µl of 1 M NaOH, followed by sonication and heating at 90°C. The supernatant was than diluted prior to determining the amount of protein using the Bradford assay (Bradford 1976).

For isotopic analysis ($\delta^{13}C$ and $\delta^{15}N$) and to determine C:N ratios (mg C:mg N), up to 10 individuals were randomly selected from each site. Lipids were not extracted from *Hyalinoecia longibranchiata* tissue, as preliminary work determined that lipid content was less than 5% (Post et al. 2007). When available, sedimentary organic material from each site was dried, homogenised and washed in 2 M phosphoric acid to remove carbonates prior to analysis (Yokoyama et al. 2005, Post et al. 2007). Isotopic analysis of $\delta^{13}C$ and $\delta^{15}N$ was undertaken by analysing the resulting N_2 and CO_2 gases with an Isoprime isotope ratio mass spectrometer to determine isotope values (see Yohannes et al. 2008). Delta values were expressed relative to Pee Dee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. Egg albumin of a known isotopic composition was used as a standard that was run for every 11 unknowns in sequence. Replicate assays of internal laboratory standards (albumin) gave a measurement precision (SD) of ±0.2‰ and ±0.5‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

The extraction and quantification of DNA and RNA for nucleic acid-derived indices was performed using a modified procedure based on the Schmidt-Thannhauser method of Dagg & Littlepage (1972) as follows: samples were first washed in 1.4 ml of ice-cold 0.2 M perchloric acid ($HClO_4$; PA) followed by vortexing and incubating on ice for 15 min, before being centrifuged at 6000 × *g* for 10 min at 4°C. The resultant supernatant was discarded and the entire step was repeated. The remaining pellet was resuspended in 1.12 ml of 0.3 M potassium hydroxide, vortexed and then incubated at 37°C for 1 h. RNA was extracted by adding 280 µl of ice-cold 2.0 M PA to the sample before vortexing, incubating on ice for 30 min and centrifuging at 6000 × *g* for 10 min at 4°C. The supernatant containing the RNA was measured for its absorbance at 260 nm using a NanoDrop full spectrum spectrometer (Thermo Scientific NanoDrop 2000c). The remaining pellet was then washed twice, by adding 1.4 ml of 0.2 M PA, followed by vortexing and centrifuging at 6000 × *g* for 10 min at 4°C. DNA was extracted by adding 600 µl of ice-cold 0.6 M PA, followed by vortexing and incubating at 70°C for 30 min. Once cooled to room temperature, samples were centrifuged at 6000 × *g* for 10 min prior to the removal of the supernatant, which contained the DNA fraction. The concentration of DNA was measured as for the RNA, at an absorbance of 260 nm.

Data analysis

An initial visualisation of the data was made using a principal coordinates analysis (PCO) in PRIMER v.6.4., and the significance of any differences between the 3 regions evaluated using PERMANOVA in PRIMER v.6.4 (Anderson, 2001), followed by post hoc pair-wise comparisons. Because ontogenetic changes in size have been found to influence isotopic signatures in a number of species (Kolasinski et al. 2009, Cummings et al. 2010, Ruiz-Cooley et al. 2010), including polychaetes (Hentschel 1998), the size (length) of specimens between regions (Chatham Rise and Challenger Plateau) for each suite of measurements (e.g. $\delta^{13}C$, protein:DNA, RNA:DNA) where appropriate, were compared using *t*-tests. If a significant difference in size was encountered, linear regression was applied to determine whether the variable of interest was linearly correlated with size.

To determine if differences in the isotopic signatures and condition indices existed between the 2 regions (Chatham Rise and Challenger Plateau), region-specific data were compared using a *t*-test for each variable of interest. In order to elucidate if there was any relationship between depth and isotopic signature ($\delta^{13}C$ and $\delta^{15}N$), linear regression was applied to the depth and isotope data for each region. Comparison between the slopes of the derived (valid) regressions was made using the method of Zar (1984). Analysis of the correlation between isotopic signatures, water depth and the distance from the mainland (geographic position), controlling for one of the 3 factors, was made using partial Mantel tests (Mantel & Valand 1970). Between-flank comparisons on the Chatham Rise (north and south, Fig. 1) were made in a similar fashion as for the between-region comparison.

RESULTS

Sediment organic matter isotopic signatures, TOM and phytopigment concentrations

TOM and phytopigment concentrations were both higher on the Chatham Rise than on the Challenger Plateau (Table 2). Comparison of the values suggests that sites on the northern flank of the Chatham Rise were more similar to the Challenger Plateau (both relatively lower) than they were to those on the southern flank of the Chatham Rise (Table 2). Sediments from the Challenger Plateau, together with some from the northern flanks of the Chatham Rise, were high in $CaCO_3$ (Table 2), and as a consequence, despite repeated phosphoric acid treatments, reliable $\delta^{13}C$ values were only obtained for 2 sites. On the Challenger Plateau, the mean sediment organic matter (SOM) isotopic signatures were −19.7‰ (n = 2) for $\delta^{13}C$ and 5.2‰ (±0.3, n = 13) for $\delta^{15}N$. On the Chatham Rise, the mean SOM isotopic signatures were −19.7‰ for $\delta^{13}C$ (±0.5, n = 13) and 4.5‰ (±0.3, n = 15) for $\delta^{15}N$.

Protein and lipid composition of the quill worms

Examination of the tissue macronutrient content of *Hyalinoecia longibranchiata* between the 2 regions, based on pooled regional data using a *t*-test, determined that there was no difference in their relative protein concentrations (t = 1.269, p = 0.897, n = 208), with 65.3% DW (±1.5) recorded for quill worms on the Challenger Plateau and 65.6% DW (±1.3) for those on the Chatham Rise. Analysis of the lipid concentrations from both regions, in the same manner, showed no difference (t = 0.421, p = 0.663, n = 113), with values of 4.0% DW (±0.7) and 4.8% DW (±1.1) recorded for the Challenger Plateau and Chatham Rise, respectively.

Table 2. Sediment analyses for the study sites on the Challenger Plateau and Chatham Rise (see Fig. 1). Data include total organic matter (TOM), calcium carbonate ($CaCO_3$), chl *a* and phaeopigment (μg g^{-1} DW sediment)

Site code	TOM (%)	$CaCO_3$ (%)	Chl *a* (μg g^{-1} DW)	Phaeopigment (μg g^{-1} DW)
CP482	2.479	90.400	0.000	0.608
CP493	1.869	93.400	0.003	0.495
CP650	1.709	87.000	0.010	0.871
CP700	1.215	86.700	0.008	0.366
Overall mean	1.818	89.375	0.005	0.585
SE	0.226	1.370	0.002	0.093
CN520	1.754	85.500	0.137	0.796
CN648	2.147	75.800	0.016	2.348
CN800	1.961	52.000	0.003	0.199
CS479	4.032	14.700	0.054	7.128
CS516	2.622	10.200	0.069	6.952
CS530	2.521	19.500	0.063	5.170
CS657	2.374	19.500	0.041	2.307
Overall mean	2.487	39.600	0.055	3.557
SE	0.282	11.815	0.016	1.078

Isotopic signatures and condition of the quill worms

Analysis of the isotopic and condition index data using PCO, revealed that the first 3 axes accounted for 73% of the variance before subsequent axes began to asymptote. Examination of the loadings for each axis (see Fig. 2) revealed that the first axis was defined by the positive relationship of the 2 isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) and inverse to the condition indices, i.e. as the condition of *Hyalinoecia longibranchiata* increased so did the enrichment of its isotopic signature. The second axis was defined by the positive correlation of the majority of the other variables with each other, but inversely against the index of DNA:DW, i.e. as the ratio of DNA:DW decreased (indicating better condition), all other variables increased. The third axis was defined by the positive relationship of protein:DNA and DNA:DW against each other, but inversely to C:N, i.e. increasing protein:DNA, DNA:DW and decreasing C:N all indicate improved nutritional condition.

A plot of the first 2 axes revealed that the data fell into 3 broadly discernable clusters: Challenger Plateau, Chatham Rise north and Chatham Rise south (Fig. 2). Examination of extent to which these clusters (regions) were differentiated from each other using PERMANOVA determined that there were differences between the regions (pseudo-F = 7.27, p ≤ 0.0001, unique no. of permutations = 9932, n = 98) and that all regions were different from each other (from the pair-wise comparisons, p ≤ 0.0039, unique no. of permutations ≥ 9933).

For specimens where isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) and C:N were measured, no significant differences, based on the pooled data for each region, were detected for the quill worm body lengths between regions (Challenger Plateau and Chatham Rise) (t = −0.374, p = 0.709, n = 142). Analysis of the body size of quill worms, pooled for each region and used to calculate the nucleic acid-derived condition indices (DNA:DW, protein: DNA, RNA:DNA), indi-

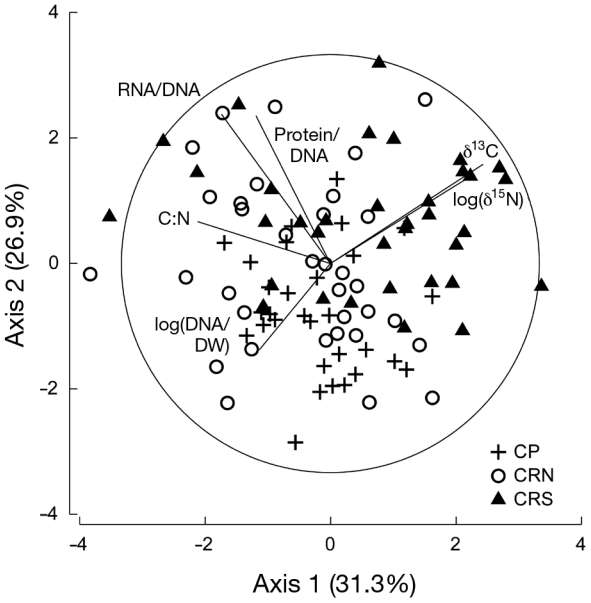

Fig. 2. Biplot of the first 2 axes showing the loadings derived from the principal coordinates analysis. Crosses denote samples from the Challenger Plateau (CP), open circles denote samples from the northern flank of the Chatham Rise (CRN) and solid triangles samples from the southern flank of the Chatham Rise (CRS)

cated a statistically significant difference (t = −2.978, p ≤ 0.01, n = 234) between regions, with quill worms from Chatham Rise (115 ± 2 mm) being larger than those from the Challenger Plateau (105 ± 3 mm). Linear regression analysis carried out for all samples, to determine whether there was a relationship between worm length and each of the nucleic acid-derived condition indices, revealed no linear trends for DNA:DW (r^2 = 0.004, F = 0.963, p = 0.328), protein:DNA (r^2 = 0.012, F = 2.404, p = 0.123) or RNA:DNA (r^2 = 0.039, F = 8.269, p ≤ 0.01); i.e. although differences in size exist, these are not thought to confound the actual variables.

Analysis of the $\delta^{13}C$ signatures, based on the pooled data for each region, showed that the Chatham Rise specimens (−18.4 ± 0.1‰) were more enriched than the Challenger Plateau specimens (−19.2 ± 0.1‰; t = −6.262, p ≤ 0.001, n = 134; Table 3). Linear regression of depth against the mean $\delta^{13}C$ signature recorded at each site for each region revealed decreasing enrichment of $\delta^{13}C$ with increasing depth for both the Challenger Plateau (r^2 = 0.866, F = 14.618, p ≤ 0.05) and the Chatham Rise (r^2 = 0.329, F = 6.164, p ≤ 0.05; Fig. 3). Comparison between the slopes found no difference in the effect of depth between regions, i.e. the slopes were equal. Partial correlations between depth and the mean $\delta^{13}C$ signature for each site, controlling for the distance from the mainland using a partial Mantel test, found depth to have a significant effect on $\delta^{13}C$ signatures on the Challenger Plateau (r = 0.836, p ≤ 0.05), but not on the Chatham Rise (r = 0.080, p = 0.384). Examination of the partial correlation between the distance from the mainland and the mean $\delta^{13}C$ signature recorded for each site, whilst controlling for depth, found no significant relationship for either the Chatham Rise (r = 0.003, p = 0.589) or the Challenger Plateau (r = −0.525, p = 0.100), i.e. the effect of depth on $\delta^{13}C$ signatures on the Challenger Plateau is independent of site location relative to the mainland.

Differences between the $\delta^{15}N$ signatures on the Chatham Rise (11.4 ± 0.1‰) and the Challenger Plateau (11.0 ± 0.1‰) were statistically different (t = −2.738, p ≤ 0.01, n = 139), but the <0.5‰ measurement precision for $\delta^{15}N$ measurements means that it cannot be concluded that these estimates are different (Table 3). Linear regression of the $\delta^{15}N$ signatures with depth for each site produced no significant relationship on the Chatham Rise (r^2 = 0.375, F = 3.819, p = 0.092) or the Challenger Plateau (r^2 = 0.010, F = 0.022, p = 8.920) (Fig. 3). A partial Mantel test of the mean $\delta^{15}N$ signature for each site and depth, whilst controlling for the distance from the mainland, failed to discern any underlying relationship for the Chatham Rise (r = 0.230, p = 0.121) or the Challenger Plateau (r = −0.018, p = 0.458). However, examination of the correlation of the mean $\delta^{15}N$ signature for each site with the distance from the mainland, whilst controlling for depth, revealed that there was a significant effect on $\delta^{15}N$ enrichment as distance from the mainland increased on the Chatham Rise (r = 0.525, p ≤ 0.001), but not on the Challenger Plateau (r = 0.082, p = 0.483). That is, on the Chatham Rise, $\delta^{15}N$

Table 3. Mean (±SE) values recorded for the stable isotope signatures and condition indices

Location	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N	DNA:DW	Protein:DNA	RNA:DNA
Challenger Plateau	−19.2 (0.1)	11.0 (0.1)	4.3 (0.1)	2.30 (0.08)	14.31 (0.54)	0.81 (0.03)
Chatham Rise	−18.4 (0.1)	11.4 (0.1)	4.6 (0.1)	1.96 (0.06)	16.50 (0.53)	0.95 (0.03)
Chatham Rise north	−18.9 (0.1)	11.1 (0.1)	4.7 (0.1)	1.78 (0.08)	17.61 (0.83)	0.93 (0.06)
Chatham Rise south	−17.9 (0.1)	11.7 (0.1)	4.5 (0.1)	2.10 (0.08)	15.56 (0.67)	0.97 (0.04)

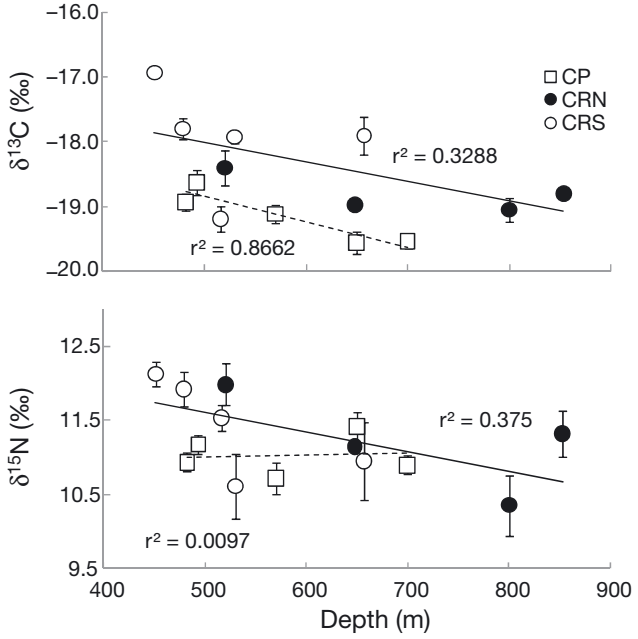

Fig. 3. Mean (±SE) $\delta^{13}C$ and $\delta^{15}N$ values of *Hyalinoecia longibranchiata* for each site. CP: Challenger Plateau, dashed line denotes regression line; CR: Chatham Rise sites, solid line denotes regression; N: north; S: south

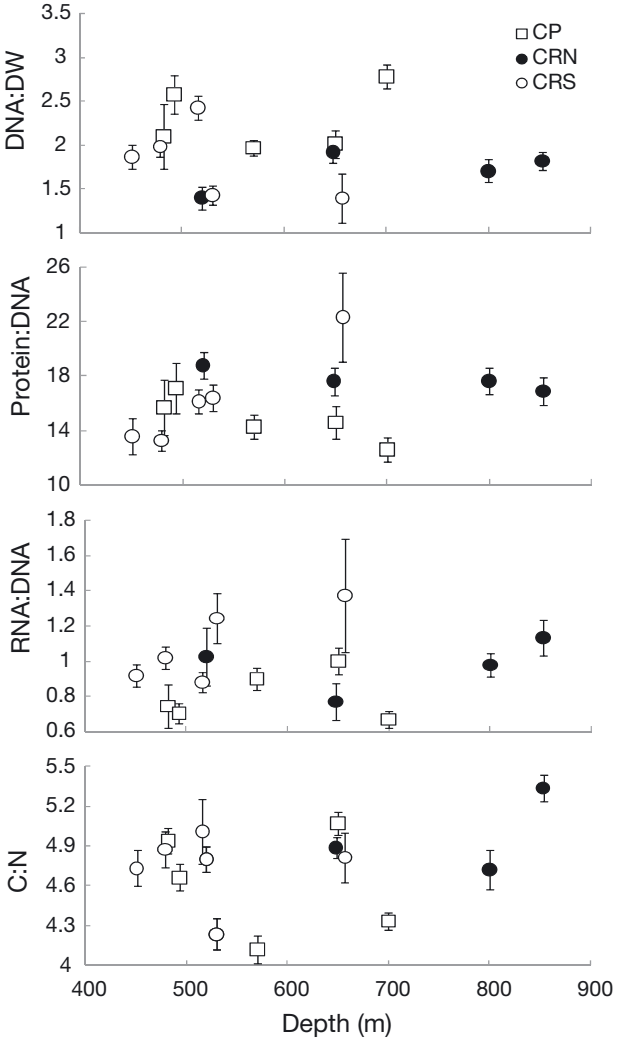

Fig. 4. Mean (±SE) DNA:DW, protein:DNA, RNA:DNA and C:N ratios of *Hyalinoecia longibranchiata* for each site. See Fig. 3 for symbol details

enrichment in quill worms is correlated with distance from the mainland.

Examination of the nucleic acid-derived ratios, based on the pooled data for each region, revealed that *Hyalinoecia longibranchiata* had better nutritional 'condition' on the Chatham Rise than on the Challenger Plateau. For Chatham Rise, the DNA:DW ratio was lower ($t = 3.613$, $p \leq 0.001$, $n = 227$) than that observed on the Challenger Plateau, whilst higher ratios of protein:DNA ($t = -2.764$, $p \leq 0.01$, $n = 208$), RNA:DNA ($t = -3.171$, $p \leq 0.01$, $n = 210$) and C:N ($t = -2.809$, $p \leq 0.01$, $n = 141$) were all recorded on the rise (Table 3, Fig. 4).

Examination of the pooled $\delta^{13}C$ signatures from opposing flanks on the Chatham Rise revealed that quill worms from the southern flank were more enriched (−17.9 ± 0.1‰) than those on the northern flank (−18.9 ± 0.1‰; $t = -6.317$, $p \leq 0.001$, $n = 86$; Table 3). Likewise, comparison of the pooled $\delta^{15}N$ signatures between both flanks of the Chatham Rise revealed that the southern flank (11.7 ± 0.1‰) was slightly more enriched than the northern flank (11.1 ± 0.1‰; $t = -3.109$, $p \leq 0.01$, $n = 91$). To determine whether the differences in isotopic enrichment reflect the nutritional condition of *Hyalinoecia longibranchiata*, condition indices (pooled data) from opposing flanks on the northern and southern sides of the rise were also compared. The ratio of DNA:DW was found to be lower on the northern flank ($t = -2.803$, $p \leq 0.01$, $n = 135$), suggesting that *H. longibranchiata* were in better condition on that flank compared to the south. However, no differences were recorded for the protein:DNA ratio ($t = 1.930$, $p = 0.056$, $n = 126$), the RNA:DNA ratio ($t = -7.240$, $p = 0.470$, $n = 127$) or C:N ratios ($t = 1.559$, $p = 0.123$, $n = 86$; Table 3, Fig. 4).

DISCUSSION

Examination of the sediments from the Chatham Rise revealed that they were more enriched in organic matter, with 2.5 ± 0.3% TOM, and contained 5 to 10 times more photosynthetic pigments than those from the Challenger Plateau (Table 2). The

ratio of chl *a* to phaeopigments can be used to assess the lability of POM, where higher values indicate a better quality of POM (Nodder et al. 2007), i.e. a more labile organic fraction. A straightforward comparison between the mean phytopigment ratios calculated for the Chatham Rise (0.02) and that for the Challenger Plateau (0.09) indicates that POM on the Chatham Rise was of a higher quality (Table 2). Accordingly, the $\delta^{13}C$ signature of *Hyalinoecia longibranchiata* was different between regions, with isotopic enrichment on the Chatham Rise compared with on the Challenger Plateau. The enriched $\delta^{13}C$ values of the Chatham Rise are likely to indicate differences in the primary carbon source (i.e. differences in composition of the primary phytoplankton communities). Differences in $\delta^{15}N$ values of *H. longibranchiata* between the 2 regions could not be interpreted further as they were less than the expected isotope measurement precision (0.5‰).

Typically the $\delta^{13}C$ signature for phytoplankton ranges from −24 to −18‰ (Fry & Sherr 1984). Data collected from the Chatham Rise have indicated phytoplankton signatures that range from −24 to −22‰ for $\delta^{13}C$ and 2.5 to 5‰ for $\delta^{15}N$ (S. D. Nodder unpubl. data, Fig. 5). Phytoplankton are the primary source of POM and SOM on the Chatham Rise, with episodic phytodetritus deposition observed on the seafloor following spring blooms in the vicinity of the STF (e.g. Nodder et al. 2007). The trophic position of *Hyalinoecia longibranchiata* was estimated by examining their isotopic signatures relative to SOM. On both the Chatham Rise and the Challenger Plateau,

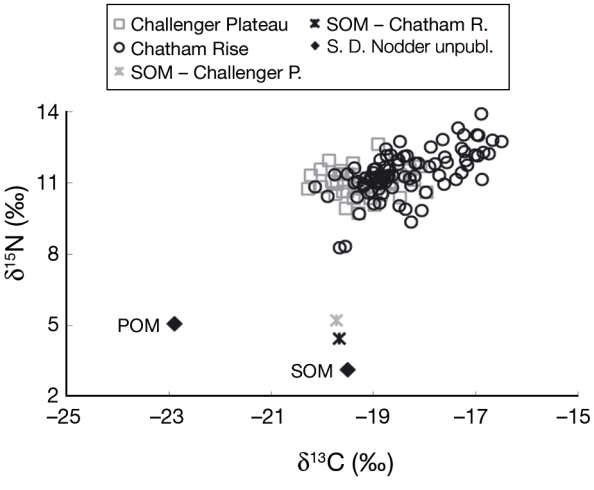

Fig. 5. $\delta^{13}C$ vs. $\delta^{15}N$ signatures of *Hyalinoecia longibranchiata* and sediment organic matter (SOM) from the Challenger Plateau and Chatham Rise. Also shown are isotope values of SOM and particulate organic matter (POM) from the Chatham Rise collected by S. D. Nodder (unpubl. data)

SOM $\delta^{13}C$ was similar to *H. longibranchiata* $\delta^{13}C$, with a mean value of −19.7‰ for both regions. Stable isotopes from SOM collected in the present study conform with other SOM data collected from the Chatham Rise, with values of approximately −21 to −18‰ for $\delta^{13}C$ and 2 to 4‰ for $\delta^{15}N$ (S. D. Nodder unpubl. data, Fig. 5). Further comparisons of SOM values are not possible because very few samples collected from the Challenger Plateau were able to be analysed; however, the values that were obtained do provide an indication as to the trophic position of *H. longibranchiata*. These values suggest that SOM is important as a basal source of energy to the benthic food web in both regions. For $\delta^{15}N$, the quill worms were more enriched than SOM by between 1 and 2 trophic levels (~4.4 to 5.2‰), indicating that they are secondary consumers (Fig. 5), and are most likely scavenging carnivores (e.g. Read & Clark 1999). These data indicate that *H. longibranchiata* from New Zealand's continental slope appear to be ecologically similar to other members of the *Hyalinoecia* genus, such as the carnivorous *H. artifex* from the Atlantic, which feeds on small fauna such as amphipods (Gaston 1987), and *Hyalinoecia* sp. from the Arabian Sea, which were 1 to 2 trophic levels above POM and SOM based on $\delta^{15}N$ values (Jeffreys et al. 2009).

Condition indices can be used to examine the effect of different trophic resources on consumers, which in turn may reflect pelagic productivity and downward POM flux. The higher ratios of protein:DNA, RNA:DNA and C:N, and lower ratios of DNA:DW, indicate that *Hyalinoecia longibranchiata* on the Chatham Rise were in better nutritional condition than those from the Challenger Plateau. As RNA is likely to be degraded from the storage of specimens at −20°C, data from the RNA measurements should be interpreted with care; however, in this study the rate of degradation is likely to be consistent for all specimens. Furthermore, a range of other condition indices were used, and were found to be consistent with the results from RNA:DNA ratios, reflecting the smaller cell size and poorer condition where ratios are higher (Chícharo & Chícharo 2008). The differences in these condition indices coincided with differences in $\delta^{13}C$ signatures of *H. longibranchiata* between the Chatham Rise and the Challenger Plateau. These observations suggest that the poor nutritional state of *H. longibranchiata* from the Challenger Plateau is likely to reflect differences in protein turnover rates (lower) and hence in their $\delta^{15}N$ signatures, although no difference within the resolution of the methodology applied was determined

here. These data indicate that differences in pelagic productivity will have implications for both the isotopic signature and nutritional condition of benthic communities.

Pelagic productivity and fluxes on the Chatham Rise have been extensively investigated (McClatchie et al. 1997, Chang & Gall 1998, Boyd et al. 1999, Bradford-Grieve et al. 1999, Murphy et al. 2001, Nodder & Northcote 2001, Nodder et al. 2003, 2007). Remote sensing in particular has indicated that phytoplankton biomass, as inferred from chl *a* concentrations on the Chatham Rise, can display high temporal and spatial variability (Murphy et al. 2001). Data collected for the present study may reflect this spatial variability, with $\delta^{13}C$ from *Hyalinoecia longibranchiata* being more enriched on the southern flank compared to the northern flank, and with specimens from this northern flank being more similar to specimens collected from the Challenger Plateau. More localised differences are likely to reflect the location of the southern boundary of the STF on the southern flank of the Chatham Rise (Uddstrom & Oien 1999, Sutton 2001), which typically has higher benthic biomass (Probert & McKnight 1993, Nodder et al. 2003, 2007). On the Chatham Rise, differences in biomass are attributed to nutritional quality of POM rather than its quantity (Nodder et al. 2003) because over annual time scales organic carbon fluxes are lower on the southern flank compared to the northern flank of the rise (Nodder & Northcote 2001). In addition, the analysis of the data indicates that the distance offshore may influence $\delta^{15}N$ enrichment of *H. longibranchiata* on the Chatham Rise. This may reflect spatial variability in productivity on the Chatham Rise rather than point sources and/or may reflect region-specific upwelling (Montoya et al. 2002).

Decreasing enrichment of $\delta^{13}C$ with increasing water depth was found for *Hyalinoecia longibranchiata* from both the Challenger Plateau and the Chatham Rise. For the Challenger Plateau, this effect was independent of any regional terrestrial inputs, i.e. the distance of the sites from the mainland. These differences are reflective of the changing composition of POM as a result of fractionation that may occur as the organic material sinks to the sea floor. The $\delta^{13}C$ values of POM is heavily dependent on the size, growth rate and CO_2 availability and assimilation of phytoplankton, which are established during photosynthesis, but are affected by other processes, such as remineralisation, with increasing water depth (Keller & Morel 1999, Trull et al. 2008). For $\delta^{15}N$, no significant relationships were found with depth on either the Chatham Rise or the Challenger Plateau. Previous studies have shown that differences in microbial degradation will cause increasing $\delta^{15}N$ values with depth (Voß et al. 1997, Mintenbeck et al. 2007). Large particles may avoid $\delta^{15}N$ enrichment with depth as they sink more rapidly, avoiding bacterial degradation, and hence are likely to become more rapidly deposited on the seafloor and integrated within the SOM. However, smaller particles will sink slowly with a greater residence time, allowing preferential consumption by microbial bacteria and a resulting enrichment of POM $\delta^{15}N$ (Mintenbeck et al. 2007). Consequently, filter feeders, which ingest fine particles, have been found to be more heavily influenced by enrichment of POM $\delta^{15}N$ with depth than deposit feeders (Mintenbeck et al. 2007).

Pelagic–benthic coupling can be a significant process for deep-water communities (Graf 1992), and the flux of POM to the seafloor can act as an important energy source to benthic communities in the deep sea (Gage 2003). The present study has compared 2 regions of contrasting productivity: the Chatham Rise, with high productivity, and the Challenger Plateau, with low productivity. Seafloor sediments indicate that the POM flux to the seafloor is of higher quality on the Chatham Rise compared with that on the Challenger Plateau. The stable isotope signatures and condition indices of *Hyalinoecia longibranchiata* appear to reflect these observations as well. This provides strong evidence that downward pelagic–benthic coupling is an important process in determining the trophic status and condition among deep-sea megafauna. This is one of 4 recent studies (see Leduc et al. 2010, Lörz 2011, Knox et al. 2012) that has linked the ecology or trophic status and/or condition of benthic megafauna to pelagic productivity in these areas. These findings demonstrate the importance of connectivity between pelagic resources and the seafloor through the flux of POM, allowing links between pelagic productivity and the trophic status and condition of benthic megafauna to be established.

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