Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa

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Biological traits analysis (BTA) is considered to be a powerful technique for describing the ecological functioning of marine benthic assemblages. This study is the first to apply BTA to assess differences in the traits of benthic faunal assemblages between areas exposed to heavy and light trawling in a major upwelling ecosystem along the west coast of southern Africa. The data were collected from two sampling locations in Namibia and six sampling locations in South Africa. The intensity of trawling varied from area to area. Significant differences in biological traits (BT) were detected between heavily and lightly trawled areas. Weighted infaunal traits showed significant differences between heavily and lightly trawled areas for 17% of the traits investigated, while 24% of epifaunal traits investigated were significantly different between areas of different trawling intensities. This suggests that the measured BTs of the epifauna might be more sensitive to trawling disturbances than BTs of the infauna. The infaunal traits differed significantly between areas with larger or smaller proportions of sand and mud. Nevertheless, more of the significant differences in infaunal BTs were related to variations in trawling intensity than to variations in sediment composition. Significant modifications of BTs are likely to lead to modified functioning of the community and provide more general potential indicators for management than those based on species. The study confirms the need for more basic biological and life history data on macro-benthic invertebrates but nevertheless shows that BTA detected specific features that correlate with trawling intensity and that these features may be important for epifaunal assemblage functioning.

INTRODUCTION

An ecosystem approach to fisheries management requires not only evaluation of fish stocks but also assessment of the state of ecosystems in order to monitor the integrity of the marine habitats influenced by fishing operations (FAO, 2003). Thus, practical methods are needed to evaluate and monitor the overall health of the ecosystem (FAO, 2003; Garcia *et al.*, 2003). Benthic invertebrates are considered to be suitable organisms for assessing ecosystem quality and environmental changes (Gray & Mirza, 1979; Gray *et al.*, 1990, 1992; Rosenberg & Resh, 1993) because they occur in a wide variety of forms and habitats and are known to respond to many types of environmental pressures, e.g. pollution, habitat degradation and disturbance (Pearson & Rosenberg, 1978; Mirza & Gray, 1981; Warwick *et al.*, 1987; Gray *et al.*, 1992, 2006). Benthic invertebrates tend to be confined to relatively small areas due to their limited mobility and

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effectively integrate historical environmental conditions (Warwick, 1993; Salas *et al.*, 2006). For example, certain species can suffer from the effects of predators or competitors or their own inability to tolerate the prevailing physical conditions. Only species having traits optimized for the altered environment will survive (Townsend & Hildrew, 1994). Certain combinations of general biological traits and life history strategies are favoured, depending on the environmental characteristics of the habitats in question (Southwood, 1977). Understanding the link between species traits and environmental variability will help to predict community responses (Bremner *et al.*, 2006a, b; Bremner, 2008).

Demersal trawl fishing activities are considered to be one of the greatest sources of anthropogenic disturbance to marine benthic communities (Watling & Norse, 1998; Kaiser *et al.*, 2000; Thrush & Dayton, 2002; Gray *et al.*, 2006). A number of studies have investigated the impact of trawling on various components of marine ecosystems (e.g. Hansson *et al.*, 2000; Drabsch *et al.*, 2001; Jennings *et al.*, 2001; Sparks-McConkey & Watling, 2001; Thrush & Dayton, 2002; Nilsson & Rosenberg, 2003; Rosenberg *et al.*, 2003; Tillin *et al.*, 2006). In general, these studies have concluded that large-scale trawling leads to less biomass and poorer

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diversity of benthic organisms, resulting in reduced productivity. Repeated habitat disturbance, e.g. large-scale demersal trawl fishing, has been shown to lead to an abundance of small-bodied, opportunistic, short-lived (r-selected) species with a concomitant loss of larger-bodied, longer lived, slower growing (K-selected) species (Jennings *et al.*, 1999, 2001; Ball *et al.*, 2000; Sparks-McConkey & Watling, 2001). Changes in the composition of benthic assemblages may result in changes in the ecological functioning of the system. Apart from conserving general biodiversity, functional diversity and redundancy should also be considered in management of the integrity of a biological community (Bellwood *et al.*, 2003; FAO, 2003). Indeed, the range and contribution of the functional traits of species in a community will determine its ecosystem functional diversity (Tillin *et al.*, 2006). Maintaining an ecosystem's functional diversity can provide a buffer against large environmental shifts caused by either natural effects or anthropogenic factors (Folke *et al.*, 2004; Bremner, 2008). Although less is known about functional redundancy, it too is likely to be linked with diversity and to be an important factor in functional performance following environmental disturbances.

The roles performed by benthic species are important in regulating ecosystem processes and can be portrayed by the biological traits they exhibit (Snelgrove, 1998). Biological traits analysis (BTA) uses a series of life history, morphological and behavioural characteristics of the species present in assemblages to indicate aspects of their ecological functioning (Chevenet *et al.*, 1994; Doledec *et al.*, 1999; Charvet *et al.*, 2000; Bremner *et al.*, 2006b). No single parameter can provide a complete measure of ecosystem functioning as a whole; simultaneously considering multiple variables is considered to be more effective (Bremner, 2008). The BTA incorporates information both on the relative biomass of species and on a wide variety of biological characteristics (trait information). Changes in the biomass (or abundance) of taxa resulting in changes in the patterns of trait expression within assemblages, may be indicative of the effects of human impacts on ecological functioning (Bremner *et al.*, 2006a) and are often reflected by an increase in those species able to withstand the impacts. Hence, BTA is a useful tool to study the effects of anthropogenic impacts (e.g. fishing) on benthic assemblage functioning, and can also be used to monitor changes in ecosystem functioning (Bremner *et al.*, 2003; Bremner, 2008).

Tyler *et al.* (2012) have assessed the availability of biological trait data for the well-documented demersal marine fauna of the British Isles. Based on data of 973 species from 15 phyla and 40 classes from extensive surveys around the UK, they quantified the availability of data on eight basic biological traits for each species from online databases. They found full biological data for only 9% of species (mostly fish) and 20% of species lacked any trait data. This indicates the need for basic biological data on marine species in order to properly understand their roles in marine communities and ecosystems. The need for basic trait data is even more acute in the less-known waters of southern Africa.

In order to understand the long-term impacts of fishing, studies at the scale of the fishery are required (Berkes *et al.*, 2001). However, only a few BTA studies of faunal functional traits in relation to ecological functioning and the effects of fishing have been conducted, and these have only been conducted in European or Canadian waters: temporal changes in benthos of the North Sea (Bremner *et al.*, 2005); epifaunal changes in demersal trawl grounds of the North Sea (Tillin *et al.*, 2006); infaunal and epifaunal changes in fished areas of the Mediterranean Sea (de Juan *et al.*, 2007); long-term changes in epifauna in the Bay of Fundy, Canada (Kenchington *et al.*, 2007); and dredging recovery of macrofauna in the English Channel (Cooper *et al.*, 2008).

This study is the first application of BTA to examine impacts of demersal trawling on marine benthic assemblages in deep-water fishing grounds (348–436 m) in a major upwelling ecosystem along the west coast of southern Africa.

Atkinson *et al.* (2011) analysed benthic species biomass and abundance data to assess the effects of different levels of trawling on assemblage composition, compared benthic assemblage spatial differences (over a north–south area in excess of 800 km) and the effects of sediment type. The analyses were complicated by pseudo-replication difficulties, which are addressed by Atkinson *et al.* (2011). This study re-analyses some of the same data but at the level of biological traits to address the following questions:

1. Do biological traits of infauna and epifauna respond to trawling effects in the same way?
2. What traits are characteristic of heavily and lightly trawled areas?
3. Do more intensely fished areas result in fewer K-selected species and/or more r-selected species?
4. Can BTA serve as a useful indicator for monitoring changes in fished communities?

MATERIALS AND METHODS

Sampling design

A detailed description of the sampling design and procedure is described in Atkinson *et al.* (2011). In summary, benthic macrofauna were collected from aboard the RV 'Dr Fridtjof Nansen' in April 2007 and FRS 'Ellen Kuzwayo' in February 2008 (Figure 1). The dates of sampling were fortuitous, depending upon ship availability. Four sites were sampled for infauna: Namibia (Nam); Childs Bank (Child); Cape Columbine (Col); and Cape Point (Point). Two sites were sampled for epifauna (Nam and Child) with areas of heavy trawling (HT) and light trawling (LT) being sampled at each site. Atkinson *et al.* (2011) defined heavily trawled sites to be those trawled between 1.5 to 2.7 times per year, while lightly fished sites were trawled between 0.1 to 1.1 times per year. Atkinson *et al.* (2011) provides further detail on the distinction between HT and LT areas in terms of trawl tracks, hours fished and proportion of swept area at each site sampled in this study.

A 0.2 m² van Veen grab was used to collect five quantitative replicate macro-benthic infaunal samples at each of the HT and LT area sites with all infauna retained after sieving with a 1 mm mesh sieve. Macro-benthic epifauna were sampled with three semi-quantitative replicate trawls with a 1 cm mesh net liner in HT and LT areas at the Namibian and Childs Bank sites. Sediment samples collected by grab at each area were analysed for particle grain size and total organic carbon (TOC) content. Details of field sampling and laboratory processing are reported in Atkinson *et al.* (2011). In brief, the sediments at both HT and LT areas at Namibia, Childs Bank and Cape Point sites were classified as 'sand' or
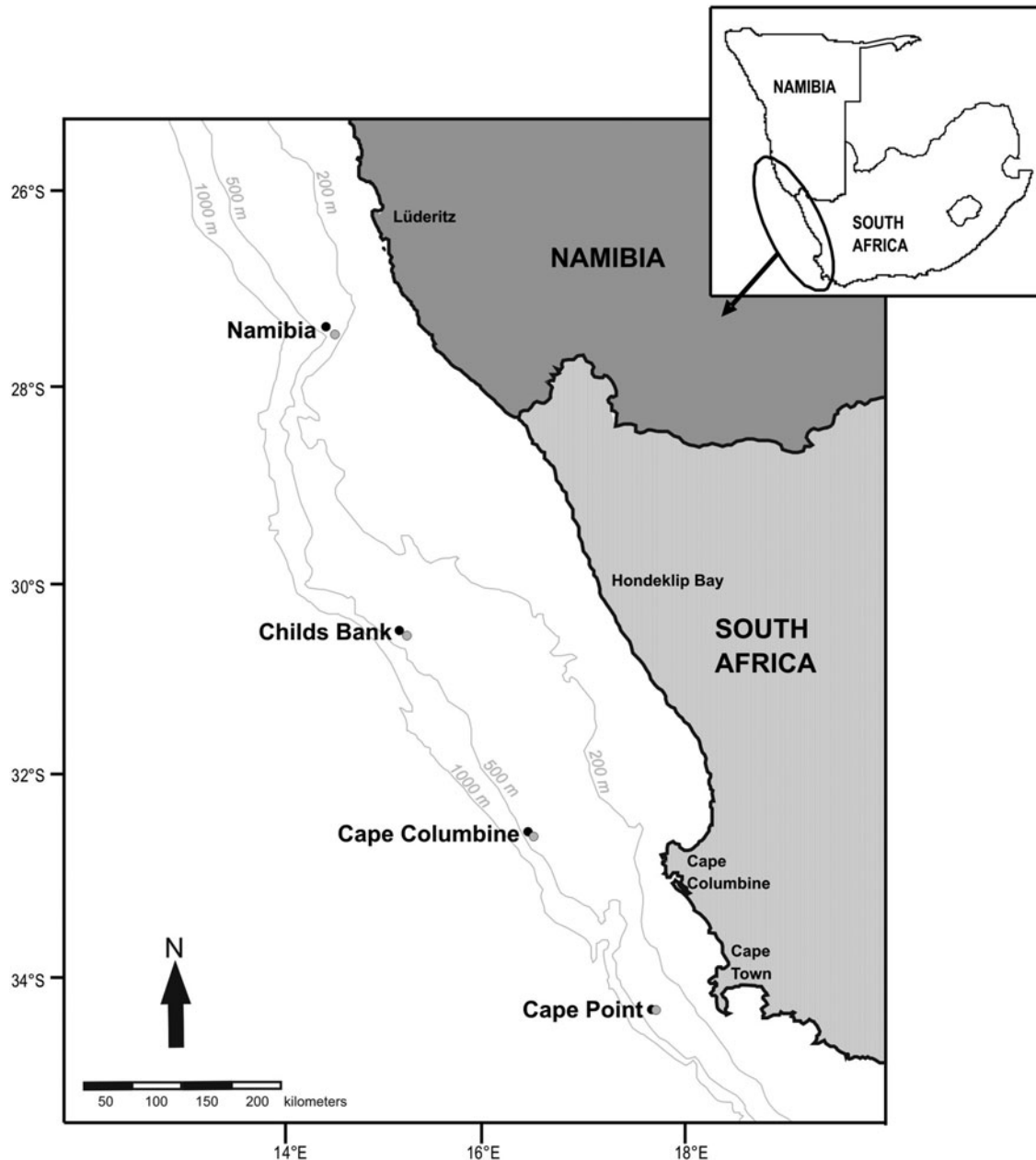
Fig. 1. Location of four selected sample sites. Black circles represent heavily trawled areas and grey circles represent lightly trawled areas (Atkinson *et al.*, 2011).

'muddy sand', comprising 72–89% sand, whereas at Cape Columbine, both HT and LT areas were more silty, with 52% and 21% sand, respectively. The level of TOC content varied between 0.64% and 5.55% for HT and LT areas at Namibia, Cape Columbine and Cape Point sites. However, higher TOC content was noted for HT (14.23%) and LT (11.37%) areas at Childs Bank.

Biological traits analysis (BTA)

The analysis of results generally followed the method reported in Bremner *et al.* (2006a) and Tillin *et al.* (2006). A biological trait database of all species sampled in this study was developed by compiling information from a range of literature sources, e.g. scientific publications, theses, web databases, general field books, technical papers and expert knowledge. Most of the trait information came from the species level since many traits were recorded through observations and measurements, e.g. size, body form, etc. However, the feeding types were categorized by genus or family level from published literature, mostly from the northern hemisphere. In this study, eight biological traits with a total of 42 categories were identified for the infaunal species analysis (Table 1) while nine biological traits with 41 categories were selected for the epifaunal analysis (Table 2). These basic traits are very similar to those analysed by Tyler *et al.* (2012), although we were unable to find enough data on fecundity and lifespan to include these traits. Each category was scored according to the affinity of each taxon for each trait category, ranging from 0–3, where 0 = no affinity and 3 = complete affinity. A taxon could be allocated several scores for the same trait, referred to as 'fuzzy coding' (Chevenet *et al.*, 1994), e.g. one species with two types of

Table 1. Infauna: biological traits and categories used in the analysis. Each category is allocated affinities ranging from 0–3 where 0 = no affinity and 3 = complete affinity. Size was analysed for both measured size at capture (NSA) and normal adult size (NSB) obtained from literature.

Trait	Code	Classification
Size (NSA & NSB)	NS_1	<5 mm
	NS_2	5 mm–1 cm
	NS_3	1–3 cm
	NS_4	3–6 cm
	NS_5	6–10 cm
	NS_6	>10 cm
Larval type	LT_1	Planktotroph
	LT_2	Lecithotroph
	LT_3	Direct development
Mobility	AM_1	None
	AM_2	Low
	AM_3	Medium
	AM_4	High
Body form	BF_1	Short/cylindrical
	BF_2	Dorsally flat
	BF_3	Laterally flat
	BF_4	Ball shape
	BF_5	Long thin
	BF_6	Irregular
Attachment	DA_1	None
	DA_2	Temporary
	DA_3	Permanent
Life habitat	AH_1	Sessile
	AH_2	Tube permanent
	AH_3	Tube semi-permanent
	AH_4	Burrower
	AH_5	Surface crawler
Feeding	FH_1	Suspension/filter
	FH_2	Scraper/grazer
	FH_3	Surface deposit feeder
	FH_4	Subsurface deposit feeder
	FH_5	Symbiont/deposit
	FH_6	Detritus/sandlicker
	FH_7	Carnivore/detrivore
	FH_8	Scavenger
	FH_9	Parasite/commensal

Table 2. Epifauna: biological traits and categories used in the analysis. Each category is allocated affinities ranging from 0–3 where 0 = no affinity and 3 = complete affinity. Maximum adult size (MS) was obtained from literature.

Trait	Code	Classification
Sampled size	SS_1	1–10 g
	SS_2	11–100 g
	SS_3	101–1000 g
	SS_4	1001–10,000 g
	SS_5	>10,000 g
Maximum adult size	MS_1	1–3 cm
	MS_2	>3–6 cm
	MS_3	>6–10 cm
	MS_4	>10 cm
Adult longevity	AL_1	<2 years
	AL_2	2–5 years
	AL_3	>5 years
Larval type	LT_1	Planktotroph
	LT_2	Lecithotroph
	LT_3	Direct development
Mobility	AM_1	None
	AM_2	Low
	AM_3	Medium
	AM_4	High
Body form	BF_1	Cylindrical
	BF_2	Dorsally flattened
	BF_3	Laterally flattened
	BF_4	Spherical
	BF_5	Long thin
	BF_6	Irregular
Attachment	DA_1	None
	DA_2	Temporary
	DA_3	Permanent
Adult habitat	AH_1	Sessile
	AH_2	Burrower
	AH_3	Surface crawler
	AH_4	Swimmer
Feeding	FH_1	Suspension/filter
	FH_2	Scraper/grazer
	FH_3	Surface deposit feeder
	FH_4	Subsurface deposit feeder
	FH_5	Dissolved matter
	FH_6	Large detritus
	FH_7	Scavenger
	FH_8	Carnivore/omnivore
	FH_9	Parasite/commensal

feeding strategies was given the affinity 2 in both feeding categories. In the event that no information was available for a trait at the species level, a search was conducted at the genus level, and if still no information was found, then at the family level. To investigate any differences in body size between heavily and lightly trawled sites, the average length of each infaunal taxon was measured and scored as affinities. As an indication of the body size of epifaunal species, the average biomass of taxa occurring was categorized on a log-based scale, because the trawl samples were not fully quantitative (see Atkinson *et al.*, 2011) and scored as affinities.

The 'fuzzy coded' species by traits matrices were weighted by their biomass at each site through matrix multiplication. The biomass-weighted trait category scores were summed over all taxa present at the area, providing a measure of frequency of occurrence of trait categories over the whole assemblage (Charvet *et al.*, 2000; Bremner *et al.*, 2006a). The traits weighted by biomass matrices were analysed independently for infaunal and epifaunal assemblages.

The non-parametric Mann–Whitney *U*-test, which ranks data on an ordinal scale and makes a comparison between two allocated groups, was used to test for significant

differences in infaunal and epifaunal biological traits weighted by biomass for each trawling treatment (HT and LT). The same test was then used to detect significant differences in biological traits of infauna between low (≤72%) and high (>72%) proportions of sand and low (<20%) and high (≥20%) proportions of mud using STATISTICA v.8 software. The classification of sediment (i.e. low or high percentage sand or mud) was identical at paired HT and LT areas except at Cape Columbine where the sand content was classified as high in HT areas and low in LT areas (Atkinson *et al.*, 2011).

Bubble plots, scaled to represent the biomass of infaunal species exhibiting significant traits at each site, were overlaid on principal coordinate analysis (PCO) plots of 4th root transformed infaunal biomass. The conservative 4th root transformation was adopted in this study to down-weight the excessive contributions of abundant species to the similarities calculated between species (Field *et al.* 1982; Clark & Gorley,

2006). Similarly, epifaunal species with significant traits were represented by vectors overlaid on a PCO plot of log-scale categorized biomass at each area. The PCO routine ordinates the data onto Euclidean axes by minimizing residual variation in the dissimilarities of the Bray–Curtis measure (Clarke & Warwick, 2001; Clarke & Gorley, 2006). The PCO was performed using PRIMER v.6 and its add-on package PERMANOVA+ (Clarke & Warwick, 2001; Clarke & Gorley, 2006; Anderson et al., 2008).

RESULTS

Infaunal BTA

A total of 248 infaunal species was identified and assigned traits scores. Seventeen per cent of infaunal biological traits tested were significantly different at the 5% level between areas of heavily and lightly trawled intensities (Table 3). Comparing the summed rank values for each significantly different infaunal trait between heavily and lightly trawled areas (calculated with the Mann–Whitney U test), it is evident that smaller (<5 mm) suspension and surface deposit feeders had a higher biomass at heavily trawled areas (Table 3). More surface crawlers with a long thin body form and high mobility occurred at lightly trawled areas. Ten and seven per cent of infaunal biological traits were significantly different at the 5% level in areas with low or high sand or mud compositions, respectively (Tables 4 and 5). Species between 5 mm and 1 cm in size, sessile, having lecithotrophic larval phases and a detritus/sandlicking feeding strategy had greater biomass in areas with more than 72% sand composition (Table 4). Surface crawlers and species having no larval life phases (direct development) had significantly greater biomass in areas with more than 20% mud composition. Sessile species had significantly less biomass in areas with high proportions of mud (Table 5). The first two axes of the infaunal biomass PCO account for only 33.6% of the total variation, suggesting a poor reflection of the structures occurring in the multivariate space in two-dimensions (Figure 2A). Nonetheless, HT and LT areas separate out at three of the four sites. An overlay of circles, scaled to represent the biomass of species with specific traits, was used to investigate the relationship of significant traits to trawling intensity. Species having small body size (<5 mm measured and 1–3 mm from literature) had greater biomass at the HT areas off Namibia and Cape Columbine (Figure 2B, C).

Table 3. Infauna: heavily vs lightly trawled areas. Significantly different biological traits (17% of traits tested) tested by non-parametric Mann–Whitney U between heavily and lightly trawled areas for biological traits weighted by infaunal biomass. LT, lightly trawled; HT, heavily trawled. Higher rank indicates larger biomass.

Trait	Classification	Code	Significant value	Rank LT/HT
Size (A)	<5 mm	NS1A	$P = 0.037$, $U = 123$	333/487
Size (B)	1–3 cm	NS3B	$P = 0.010$, $U = 105$	315/505
Mobility	High	AM4	$P = 0.003$, $U = 91$	519/301
Body form	Long thin	BF5	$P = 0.037$, $U = 123$	487/333
Habitat	Surface crawler	AH5	$P = 0.023$, $U = 116$	494/326
Feeding	Suspension	FH1	$P = 0.006$, $U = 99$	309/511
Feeding	Surface DF	FH3	$P = 0.015$, $U = 110$	320/500

Table 4. Sand content: significantly different infaunal biological traits (10% of traits tested) tested by non-parametric Mann–Whitney U between low and high sand content groups for biological traits weighted by infaunal biomass. Sand content was classified as high if $>72\%$ and low if $\leq72\%$. Higher rank indicates larger biomass.

Trait	Classification	Code	Significant value	Rank high/low
Size (A)	5 mm–1 cm	NS2A	$P = 0.030$, $U = 111$	573/247
Larval type	Lecithotroph	LT2	$P = 0.040$, $U = 118$	566/254
Mobility	None	AM1	$P = 0.028$, $U = 112$	571/248
Feeding	Detritus sandlicker	FH6	$P = 0.030$, $U = 114$	414/406

Table 5. Mud content: significantly different infaunal biological traits (7% of traits tested) tested by Mann–Whitney U between low and high mud content groups for biological traits weighted by infaunal biomass. Mud content was classified as high if $\geq20\%$ and low if $\leq20\%$. Higher rank indicates larger biomass.

Trait	Classification	Code	Significant value	Rank high/low
Larval type	Direct development	LT3	$P = 0.034$, $U = 122$	488/332
Mobility	None	AM1	$P = 0.040$, $U = 133$	343/476
Habitat	Surface crawler	AH5	$P = 0.020$, $U = 111$	499/321

Similarly, species that suspension-feed or deposit-feed near the sediment surface also had higher biomass at HT areas (Figure 2G, H). Species of high mobility (AM4), long thin body form (BF5) and surface crawlers (AH5) had larger biomass at the LT areas of Namibia and Childs Bank (Figure 2D–F).

Epifaunal BTA

A total of 60 epifaunal species was identified to genus or species level and assigned traits scores. Twenty-four per cent of traits tested were significantly different at the 5% level between HT and LT areas (Table 6). Most (80%) of the significant traits had greater biomass in the LT areas with only traits of temporary attachment and cylindrical body form having higher biomass in the HT areas (Table 6). Species weighing less than 10 g in the samples, but able to reach a body size of 6–10 cm had greater biomass at LT areas. Similarly, a species having either medium mobility, dorsally flattened, laterally flattened or spherical body form or having feeding strategies of scraper/grazer and sub-surface deposit feeder had significantly greater biomasses at LT areas in comparison to paired HT areas (Table 6).

The first two axes of the PCO plot account for 74% of the total variation indicating a good portrayal of the epifaunal biomass multivariate analysis in two dimensions (Figure 3). By superimposing a vector overlay (Pearson correlation) of significant traits onto the PCO plot, it is evident that the traits temporary attachment (DA2) and cylindrical body form (BF1) feature in species with greater biomasses at the Namibian HT area (Figure 3). The length and direction of each vector indicate the strength and sign of the relationship between that trait and the PCO axes. All other significant traits (SS1, MS3, AM3, BF2, BF3, BF4, FH2 and FH4) are as
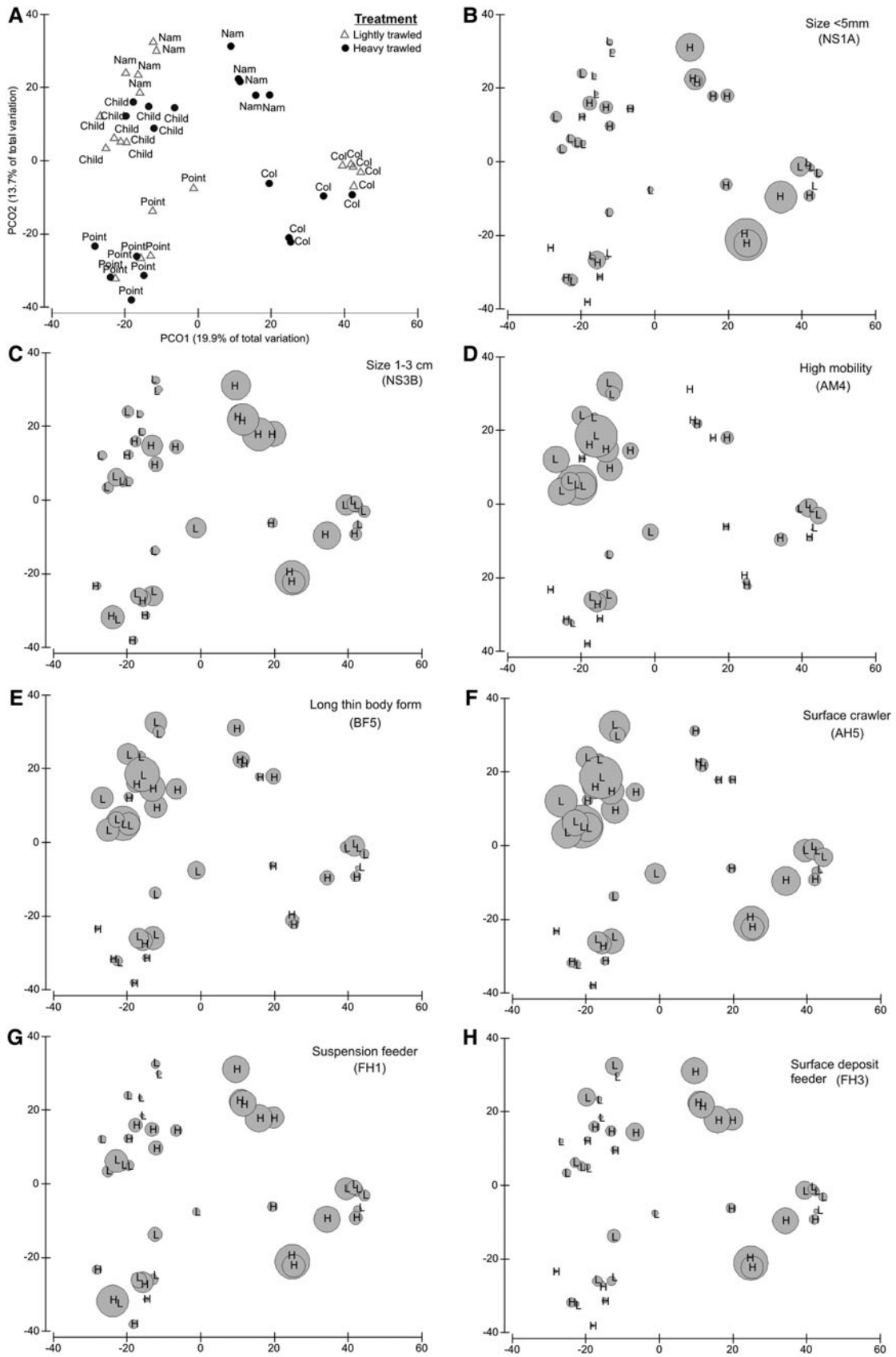
Fig. 2. Infauna: principal coordinate ordination graphs reflecting 4th root transformed infaunal biomass weighted by significant biological traits from Table 1. Panel 1A shows the PCO of 40 site and area replicates using Euclidean distance on the biomass-weighted biological traits matrix. Panels 1B–11B–G show bubble plots superimposed on 1A and scaled to represent biomass distribution of each trait of each replicate sample at each site and area. PCO1, PCO2, 1st and 2nd principal coordinates; H, heavily trawled; L, lightly trawled.

Table 6. Epifauna: significantly different biological traits (24% of traits tested) tested by non-parametric Mann–Whitney U between heavily and lightly trawled areas for biological traits weighted by epifaunal biomass. Higher rank indicates larger biomass.

Trait	Classification	Code	Significant value	Rank LT/HT
Size (sampled)	1–10 g	SS1	$P = 0.013$, $U = 2$	55/23
Size (maximum)	6–10 cm	MS3	$P = 0.013$, $U = 2$	55/23
Mobility	Medium	AM3	$P = 0.005$, $U = 0$	57/21
Attachment	Temporary	DA2	$P = 0.005$, $U = 0$	21/57
Body form	Cylindrical	BF1	$P = 0.005$, $U = 0$	21/57
Body form	Dorsally flat	BF2	$P = 0.008$, $U = 1$	56/22
Body form	Laterally flat	BF3	$P = 0.005$, $U = 0$	57/21
Body form	Spherical	BF4	$P = 0.005$, $U = 0$	57/21
Feeding	Scraper/grazer	FH2	$P = 0.005$, $U = 0$	57/21
Feeding	Subsurface deposit feeder	FH4	$P = 0.005$, $U = 0$	57/21

a result of species with these traits having greater biomass at either Childs Bank or Namibian LT areas.

Links between benthic communities and demersal fish

The diets of the 32 most commonly trawled demersal fish species occurring in the region (from Atkinson *et al.*, 2011, 2012) were assessed from available literature (MacPherson *et al.*, 1983; Russell *et al.*, 1983; Meyer & Smale, 1991; Punt *et al.*, 1992; Punt & Leslie, 1995; Pillar & Barange, 1997; Bianchi *et al.*, 1999) and from information provided through *FishBase* (Table 7). The majority of the trawled fish community feeds mainly on pelagic species occurring in the water column (44%), 37% feed mainly on benthic species, while 19% feed on both pelagic and benthic species. Thus, although the demersal trawled fish community is associated with the benthic community, much of this association occurs indirectly through small fish species and planktonic invertebrates that occur just above the seabed or in the water column. It is probable that the trawled fish community has a stronger association with the seabed habitat than as a dominant source of prey.

DISCUSSION

To increase our understanding of the effects trawling may have in changing ecosystem functioning, it is essential to recognize the relationship between the biological functions of species and their vulnerability to trawl disturbance (Tillin *et al.*, 2006). The BTA is considered to be a powerful technique to evaluate aspects of the ecological functioning of benthic assemblages (Bremner *et al.*, 2006a) and was chosen in this study to compare significant biological traits in HT and LT environments. Other studies have reported on changes in some of the same traits as those investigated in this study. For example, species with smaller body sizes appear to occur more in impacted areas (Kaiser *et al.*, 2000), a result similar to this study (Tables 3 and 4). Feeding type is another trait that differs between heavily and lightly trawled areas (Tables 3 and 4) and appears to significantly reflect the adaptation
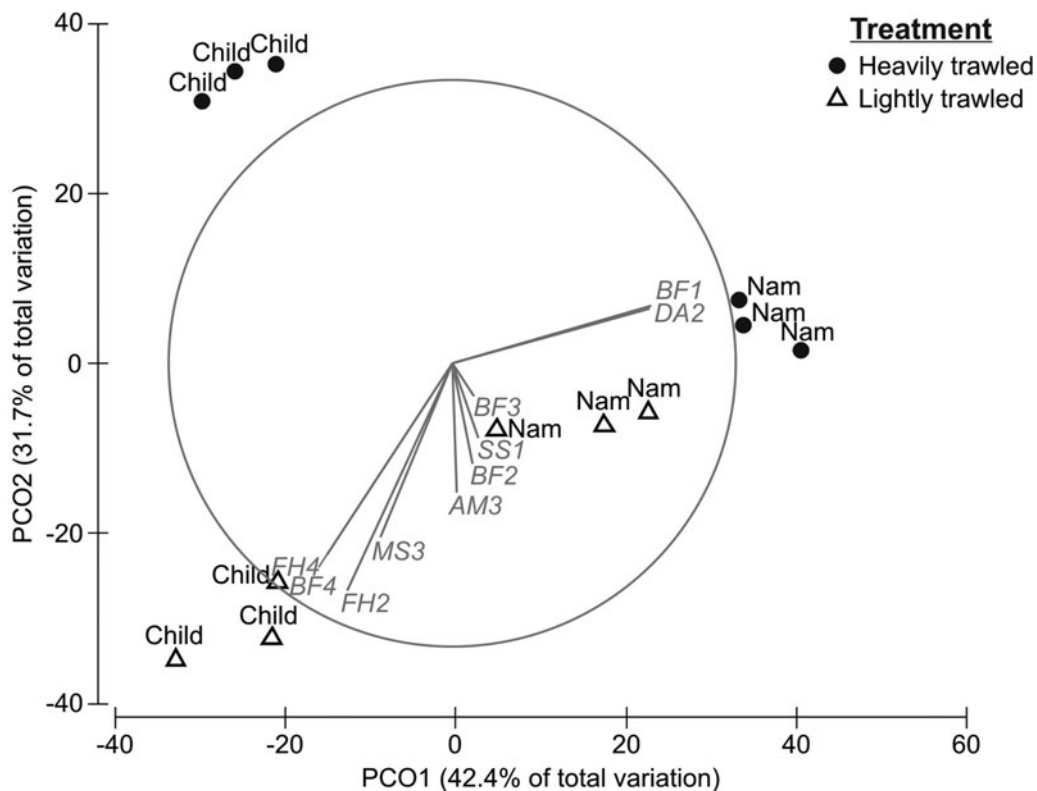

Fig. 3. Epifauna: principal coordinate ordination plot with vector overlays scaled to represent epifaunal biomass of each significant trait distribution (see Table 2) between heavily and lightly trawled areas after log-scale categorization, based on Bray–Curtis resemblance measure. PCO1, PCO2, 1st and 2nd principal coordinates; Nam, Namibia; Child, Childs Bank.

Table 7. Southern Benguela demersal trawl fish diets: most abundant trawl fish species in southern Benguela fish communities taken from Atkinson *et al.* (2011, 2012) with diets from literature and *FishBase* as indicated in table. Last column indicates classification of fish into those feeding on benthic species (fish and invertebrates occurring in, on or near the seabed) (37%), pelagic species (fish and invertebrates occurring in the water column) (44%) or both (19%).

Species	Diet	Reference	Feeding classification
Bassanago albescens	Brachyuran crabs (*Chaceon* sp.), pennatulacids (seapens), brittle stars, small crustaceans	Meyer & Smale, 1991	Benthic species
Brama brama	Opportunistic feeder on small fish, cephalopods amphipods, and euphausiids	*FishBase*	Pelagic species
Coelorinchus sp.	Variety of benthic organisms, such as polychaetes, brittle stars, gastropods, cephalopods and fish	Meyer & Smale, 1991, *FishBase*	Benthic species
Callorhinchus capensis	Feeds on small fish and a wide variety of invertebrates	Bianchi *et al.*, 1999, *FishBase*	Benthic species
Chelidonichthys capensis	Fish (mostly dragonet *Paracallionymus costatus*) and mantis shrimp	Meyer & Smale, 1991	Benthic species
Chelidonichthys queketti	Mysids, crustaceans (including macrurans), cephalopods and fish	Meyer & Smale, 1991	Benthic species
Conger wilsoni	Fish, crabs, other crustacea and cephalopods	Russell, 1983	Both
Emmelichthys nitidus	Feeds mainly on larger zooplankton	*FishBase*	Pelagic species
Epigonus sp.	Carnivorous, feed on small fish and planktonic invertebrates	*FishBase*	Pelagic species
Etmopterus sp.	Mid-water bony fish, also squid, octopus, shrimp and brittle stars	*FishBase*	Both
Galeorhinus galeus	Feeds mainly on fish (demersal as well as pelagic species) also crustaceans, cephalopods, worms and echinoderms	*FishBase*	Both
Genypterus capensis	Feed on dragonets, mantis shrimps, crabs, cephalopods and various fish including *M. capensis*	MacPherson, 1983, *FishBase*	Both
Helicolenus dactylopterus	Mysids, euphasids, small crustceans, pennatulicids, polychaetes, small fish including lantern fish	Meyer & Smale, 1991	Both
Holohalaelurus regani	Feeds mainly on pelagic bony fish, also fish offal, hagfish eggs, crustaceans, and cephalopods	*FishBase*	Pelagic species
Lepidion capensis	Mainly feeds on benthic org.ansisms—crustaceans (shrimp) and polychaetes	EOL page	Benthic species
Lepidopus caudatus	Feed on crustaceans, small squid and fish	*FishBase*	Pelagic species
Lophius vomerinus	Feeds mainly on bottom-living fish often on sardine, round herring and horse mackerel	Bianchi *et al.*, 1999, *FishBase*	Benthic species
Lucigadus ori	Likely small crustaceans, cephalopods, small fish	*FishBase*	Benthic species
Malacocephalus laevis	Ostracods, small crustaceans, mantis shrimps, small fish, cephalopods and occasionally deep-water hake	Meyer & Smale, 1991	Both
Merluccius capensis	Anchovy and pelagic crustaceans in small fish; hake, redeye and horse mackerel in larger fish	Punt *et al.*, 1992, Punt & Leslie, 1995, Pillar & Barange, 1997	Pelagic species
Merluccius paradoxus	Anchovy, horse mackerel and pelagic crustaceans in small fish; hake, horse mackerel, redeye and cephalopods in larger fish	Punt *et al.,* 1992, Punt & Leslie, 1995, Pillar & Barange, 1997	Pelagic species
Mustelus mustelus	Feeds mainly on crustaceans, but also cephalopods and bony fish	*FishBase*	Benthic species
Mustelus palumbes	Feeds on crustaceans, cephalopods, bony fish, and fish offal	*FishBase*	Benthic species
Notacanthus sexspinis	Feeds on benthic copepods and polychaetes	*FishBase*	Benthic species
Rajiidae	Small crustaceans, mysids, crabs, polychaetes, cephalopods and small bony fish	Bianchi *et al.*, 1999, *FishBase*	Benthic species
Ruvettus pretiosus	Feeds on fish, crustaceans and squid	*FishBase*	Pelagic species
Schedophilus sp.	Jellyfish, amphipods, krill and small fish	IUCN *Red List*	Pelagic species
Scomber japonicus	Feed on copepods and other crustaceans, fish and squid	*FishBase*	Pelagic species
Squalus acanthias	Mostly bony fish and some crustaceans	*FishBase*	Pelagic species
Squalus megalops	Feeds on bony fish, shrimps and other crustaceans, cephalopods and other elasmobranchs	*FishBase*	Pelagic species
Squalus mitsukurii	Feeds on bony fish including hake, snoek, conger eels and lantern fish, cephalopods and crustaceans	*FishBase*	Pelagic species
Zeus capensis	Feeds on a variety of fish, cephalopods and crustaceans	*FishBase*	Pelagic species

of the organisms to the habitat (de Juan *et al.,* 2007). As in this study, others have also found significant increases of motile scavengers (Kaiser & Spencer, 1994; Collie *et al.*, 1997; Ramsay *et al.*, 1998; Demestre *et al.*, 2000) and deposit feeders (Frid *et al.*, 2000) in trawled areas. The movements and the organisms' positions in the sediments were also considered important with regard to nutrient flux (Widdicombe *et al.*, 2004; Olsgard *et al.*, 2008). Body form was found to

differ between HT and LT areas for infauna (Table 3) and this trait may be useful to detect resilience to higher levels of trawling disturbance. No records were found in the literature of the significance of larval type affected by trawling but variations in latitude have been shown to influence this trait for several planktonic larvae of benthic invertebrates (Thorson, 1936; Schluter, 1998).

Infaunal versus epifaunal responses to trawling

Atkinson *et al.* (2011) showed that epifaunal assemblages respond more significantly to the impacts of heavy trawling than infaunal assemblages. This result appears to manifest in particular in deeper water trawling (>200 m), since studies in shallower waters have found the opposite response (Collie *et al.*, 2000; Jennings *et al.*, 2001; Hinz *et al.*, 2009). The results from the present biological traits analysis support the findings of Atkinson *et al.* (2011) with significant differences detected in a greater number of epifaunal traits (24% of traits measured) than infaunal traits (17% of traits measured) in HT and LT areas of the southern Benguela region. This indicates that an assessment of benthic assemblage biological traits is sufficiently sensitive to detect changes in benthic community function resulting from a trawling disturbance. The current study reports on the analysis of four sites for infauna and two sites for epifauna. In spite of the small sample size, the response of the biological traits suggests a likely effect on benthic community functioning, manifesting to a greater extent in epifaunal species. Significant differences in infaunal biological traits also occurred with differences in the proportions of sand (12% of biological traits) and mud (7% of biological traits). This suggests that infaunal community functioning is also influenced by the sediment properties. Schratzberger *et al.* (2007) used trait composition in meiofauna to investigate which environmental variables influenced the communities. In their study, biological traits were also found to be significantly correlated to proportions of sand and mud.

Epifaunal species having biological traits of temporary attachment and cylindrical body form occur in greater biomass in areas of more intense trawling. In this study, the burrowing anemone, *Actinauge granulata*, is largely responsible for these traits and indeed appears to prevail in areas subjected to heavy trawling (see Atkinson *et al.*, 2011). All other significant biological traits analysed were represented by a greater biomass occurring in LT areas. In this study, most of the species with a dorsally flattened body form were represented by starfish and crabs, while laterally flattened body forms were represented by three prawn species known to feed on or near the seabed. Various sponge species were categorized as having a spherical body form and occurred in greater biomass in LT areas. Similarly, three urchin species (*Echinus gilchristi*, *Brissopsis lyrifera capensis* and *Spatangus capensis*) with feeding strategies of either scraper or subsurface deposit feeder occurred in greater biomass in the LT areas. These widely diverse species (starfish, crabs, benthic prawns, sponges and urchins) appear to be sensitive to intense levels of trawling.

Traits related to LT areas

The long, thin body form of species like polychaetes, predicted to proliferate in areas of disturbance where larger macrofauna are removed (Bergman & van Santbrink, 2000; Kaiser *et al.*, 2000), were more abundant in the LT areas in this study (Table 3). Similarly, other studies (Jennings *et al.*, 2001; Hinz *et al.*, 2009) did not show consistent increases in small polychaete species in response to trawl disturbance. Jennings *et al.* (2001) reported that at moderate levels of disturbance there was some evidence for proliferation of small polychaetes, but at higher levels of disturbance, their biomass was reduced. Hinz *et al.* (2009) reported that overall small polychaetes did not respond positively to increasing trawl disturbance. *Nephtys* spp. and *Chloeia inermis* accounted for the high polychaete biomass in the LT areas in this study. Such species may be vulnerable to physical damage due to intense trawling levels whilst being able to withstand lighter levels of disturbance, as proposed by Jennings *et al.* (2001). This may similarly explain the greater prevalence of surface crawlers and highly mobile species in the LT areas in this study. These traits are also largely represented by *Nephtys* spp. and *Chloeia inermis*.

Habitat modification and changes in the proportions of mud and sand are reported to occur when the seabed is frequently trawled (Steele *et al.*, 2002), which, in turn, can change the suitability of habitats for the organisms. Significant differences in biological traits between high and low proportions of mud detected in this study suggest that surface crawlers and species having direct larval development are more prevalent in LT, muddier environments. Such environments would be expected to be more stable due to reduced physical disturbance, thus retaining finer sediment particles (Steele *et al.*, 2002). When trawling disturbs the sediment, fine mud particles are most likely to be transported away in suspension by currents near the seabed, leaving coarser particles to settle out near the trawled areas. Surface crawlers (infauna) generally occurred in greater biomass in the LT areas of this study (Table 3), indicating their vulnerability to heavier trawl activities through exposure to the passing gear on the surface of the sediment. Species with direct larval development are also likely to be vulnerable to higher levels of disturbance as the emerging juveniles, usually small in size, are more prone to local extinctions due to failure of new recruitment.

Traits related to HT areas

Several biological traits show a positive response to higher levels of trawling disturbance. Infaunal surface deposit feeders, suspension feeders and species having a small body size (<5 mm and maximum adult size of 1–3 cm) were significantly more abundant in HT areas (Table 3), possibly attracted by the increased disturbance levels leading to increased suspended food supply (Dayton *et al.*, 1995; Steele *et al.*, 2002) or able to readily escape the impact of the fishing gear due to their small body size. Epifaunal species with cylindrical body form and temporary attachment (i.e. the burrowing anemone *Actinauge granulata*) had a significantly greater biomass in heavily trawled areas (Table 4). Tillin *et al.* (2006) reported significantly more burrowers and scavengers in areas of high fishing impact and more filter feeders and attached fauna in less disturbed areas. de Juan *et al.* (2007) found greater abundance of mobile burrowing traits in the trawled area, while the untrawled area had more surface crawlers, highly mobile (similar to results of this study) and filter-feeding and deposit feeding organisms. Kenchington *et al.* (2007) observed increases in mobile species, burrowers and scavengers with a decrease in sessile,

filter feeders and species having permanent tubes (e.g. fan worms) with the onset of low intensity trawl fishing in the Bay of Fundy, Canada. Species with biological traits of mobility, burrowing life habit and scavenging feeding mode appear to respond similarly to fishing disturbance by increasing in biomass (Bremner *et al.*, 2005; Tillin *et al.*, 2006; de Juan *et al.*, 2007; Kenchington *et al.*, 2007). As discussed above, this study has some similar findings to other studies conducted in fished environments (e.g. burrowing life habit) whilst an increase in scavengers in heavily fished areas was not detected in the present work.

Trawling effects on K- and r-selected traits

In this study and as predicted, infauna with smaller body size (<5 mm), an r-selected trait, occur in significantly greater biomass in the HT areas. Other studies on benthic trawling impacts have also observed a shift from large, slow growing fauna to smaller and faster growing animals with varying levels of trawl disturbance (e.g. Kaiser *et al.*, 2000; Rumohr & Kujawski, 2000; Jennings *et al.*, 2001; Hinz *et al.*, 2009). Sessile species, filter feeders and those with larger body sizes (K-selected traits) appear to be more negatively impacted by fishing disturbance. The results of this study are similar to previous studies with respect to some of the traits measured (e.g. body size and mobility), but not with respect to others for which we have little or no data (e.g. feeding strategies and life habits). Some species with K-selected traits (e.g. high mobility, surface crawler) reflect high vulnerability to the impacts of trawling, whilst others (e.g. permanent attachment, large size) do not. This suggests that a simple r–K selected classification will not necessarily provide an appropriate indication of the species' vulnerability to trawling. The variability in results obtained from BTA further illustrates the uncertainty of true quantification of the effects of fishing with respect to functional diversity, as suggested by Bremner (2008). Additionally, different studies have different baseline environmental conditions against which change is measured, necessitating site-specific studies in fished habitats with appropriate comparisons to similar unfished habitats.

Application of BTA in an approach to fisheries management

Protection of habitats and their ecological functioning is fundamental to ensuring ecological sustainability and thus a key element in applying the ecosystem approach to fisheries management (Shannon *et al.*, 2006; Frid *et al.*, 2006, 2008). The use of BTA to describe and quantify ecological functioning is growing in popularity. However, Bremner (2008) cautions that such analytical methods should not be viewed as a panacea to define ecological functioning. Whole ecosystem functioning should contain elements of physical, chemical and biological components and should include all organism groups, i.e. micro-, meio-, macro- and mega-organisms, their interactions and energy flows. As an example of interactions, the diet assessment of demersal trawl fish shows only some level of interaction with benthic invertebrates and a greater reliance on small, benthic dwelling fish for food. Changes in benthic invertebrate species as a result of trawling are unlikely to greatly affect demersal trawl fish communities in terms of prey availability. However, the interaction between demersal trawl fish and benthic habitat structure and features is likely to be stronger (Auster *et al.*, 1997; Steele *et al.*, 2002). Such interactions should be considered when taking whole ecosystem functioning into account. The BTA only addresses a small component of whole ecosystem functioning and its limitations are acknowledged. In particular, this study underlines the lack of information on basic biological traits and life history studies of macro-benthic invertebrates in southern African waters and worldwide (Tyler *et al.*, 2012). Nevertheless, BTA is considered to be a useful tool to distil important benthic faunal information for further development into indicators of community functioning in fished marine systems and therefore is pertinent for implementation of fisheries management based on an ecosystem approach.

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