

RESEARCH ARTICLE

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A new comparative study of zooplankton from oceanic, shelf and harbour waters, south-east coast, Jamaica

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Abstract

Background: Zooplankton samples were collected fortnightly from four locations representing oceanic, shelf and harbour waters off Kingston, Jamaica in 2004, approximately 40 years after a similar study was concluded in 1964. The present sampling was conducted using vertical hauls with plankton nets of three different mesh sizes: 64, 200 and 600 μm between April and November 2004.

Results: Mean zooplankton abundances across the stations ranged from a maximum (5,858.5 individuals m^{-3}) at Harbour Shoal Beacon, mouth of Kingston Harbour, to a minimum (2,124.2 individuals m^{-3}) at California Bank, an offshore bank. One hundred forty-seven different taxa of zooplankton were identified during this study. Eighty-one taxa were identified from Harbour Shoal Beacon (HSB), 106 from South-East Cay (SEC), 114 from the shelf-edge station, called Windward Edge (WE), and 94 from California Bank (CB). The pattern obtained from the clustering of stations using percent similarity coefficient (PSC) and Jaccard community coefficient (JCC) showed the presence of two distinct groups of stations: one with HSB and the other containing all other stations. The abundance of individual species was also examined for their potential to characterize the different water masses. As found 40 years ago, *Lucifer faxoni* and *Penilia avirostris* were indicators of eutrophic Kingston Harbour waters, while *Microsetella norvegica* and *Farranula carinata* were identified as indicators of offshore waters. Zooplankton parameters across the area clearly distinguished the eutrophic Kingston Harbour waters from the shelf and offshore sites but could not differentiate between the mesotrophic shelf and the offshore bank. Larval forms were numerically dominant across all stations with copepod nauplii, fish eggs and echinoderm larvae being major constituents.

Conclusions: The zooplankton communities in the harbour, shelf and offshore areas of Jamaica's south-east coast still show significant spatial differences; however, the zooplankton community at the offshore bank was more similar to the shelf than was expected. Such banks although located offshore, receive enrichment due to associated circulation patterns. Therefore, they should not be considered oligotrophic and based on the zooplankton community distribution would be more accurately classified as mesotrophic.

Keywords: Zooplankton; Kingston Harbour; Shelf; Offshore bank

Background

There have been several zooplankton studies conducted off the south coast of Jamaica; however, these have focused on Kingston Harbour, the Port Royal Cays area and the nearby Hellshire Coast. The studies have involved numerous stations located within and in close proximity to Kingston Harbour (Lindo 1991; Webber et al. 1996; Dunbar and Webber 2003; Persad et al. 2003;

Francis et al. 2013). Through these studies, Kingston Harbour has been characterized as eutrophic and as a source of enrichment for other areas of the south coast shelf. On the basis of prevailing winds and surface circulation patterns (Webber et al. 2003; Narinesingh 2007), outflow from the Harbour, mainly affects the Hellshire coastline with the Port Royal Cays area being affected only in extreme rainfall events (Webber et al. 1996). The south-east coast shelf of Jamaica and the Port Royal Cays area have therefore been classified as mesotrophic,

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receiving enrichment limited in duration and extent (Webber et al. 1996).

Studies comparing oceanic zooplankton with those of eutrophic and mesotrophic coastal areas of Jamaica are rare. In this area of the south-east coast, only one such study has been previously conducted (Moore and Sander 1979). They sampled the zooplankton and physicochemical parameters between 1962 and 1964 at four stations located in Kingston Harbour as well as in offshore, oceanic waters. Moore and Sander (1979) found an increase in the number of zooplankton species from the harbour stations (66) towards the oceanic site (87). They also observed an increase in total zooplankton abundances from offshore areas towards Kingston Harbour and attributed this to an 'island mass' effect. The island mass effect, as noted by various authors, is recognized as a general increase in biological parameters (e.g. zooplankton biomass/abundances) in the vicinity of an island, bank or land mass (Sander and Steven 1973; Sander 1981; Hernández-León 1988, 1991; Hernandez-Leon et al. 2001). This increase in the biological parameters in the vicinity of islands was found to be due to various factors such as upwelling, land run-off of nutrient-rich waters and local current dynamics which had the effect of increasing the overall productivity of waters associated with the island.

The objectives of the present study were therefore to re-examine the spatial variation in zooplankton communities across an expected eutrophication gradient, comparing the water quality of the eutrophic Kingston Harbour with mesotrophic shelf and oligotrophic oceanic waters, as was previously done 40 years ago by Moore and Sander (1979). In this study, we aim to identify zooplankton indicators for the different water masses found throughout the area (Hsieh et al. 2004) and to indicate whether there is still a gradual change in progressing from Kingston Harbour to offshore areas as is expected of the island mass effect.

Methods

Field sampling

Four stations were selected off the south-east coast of Jamaica representing areas expected to have a range of water qualities. These were therefore cited at the mouth of the eutrophic Kingston Harbour (Harbour Shoal Beacon (HSB)), the southern-most of the Port Royal Cays (South-East Cay (SEC)), near the edge of the south-east coast shelf (Windward Edge (WE)) and California Bank (CB), an offshore bank located 20 km away from the mouth of Kingston Harbour and surrounded by deep waters (Figure 1). Sampling was conducted at each of the four stations at approximately 2-week intervals over a 6-month period, which began in April 2004 and ended in October 2004. All stations were visited between 0830 and 1300 hours on the same day. Stations were located in areas of approximately 30 m depth, except for HSB where the station was 7 m deep.

Physicochemical variables were recorded using a Hydro-lab multi-parameter probe (Loveland, CO, USA) at 5-m intervals throughout the water column for the upper 20 m. However, due to depth at HSB, readings were taken at 1-m intervals through the water column for 5 m. The parameters sampled were temperature, light extinction, salinity, dissolved oxygen, oxidation reduction potential (ORP) and pH. These were collected contemporaneously with the zooplankton samples at all stations and on all occasions.

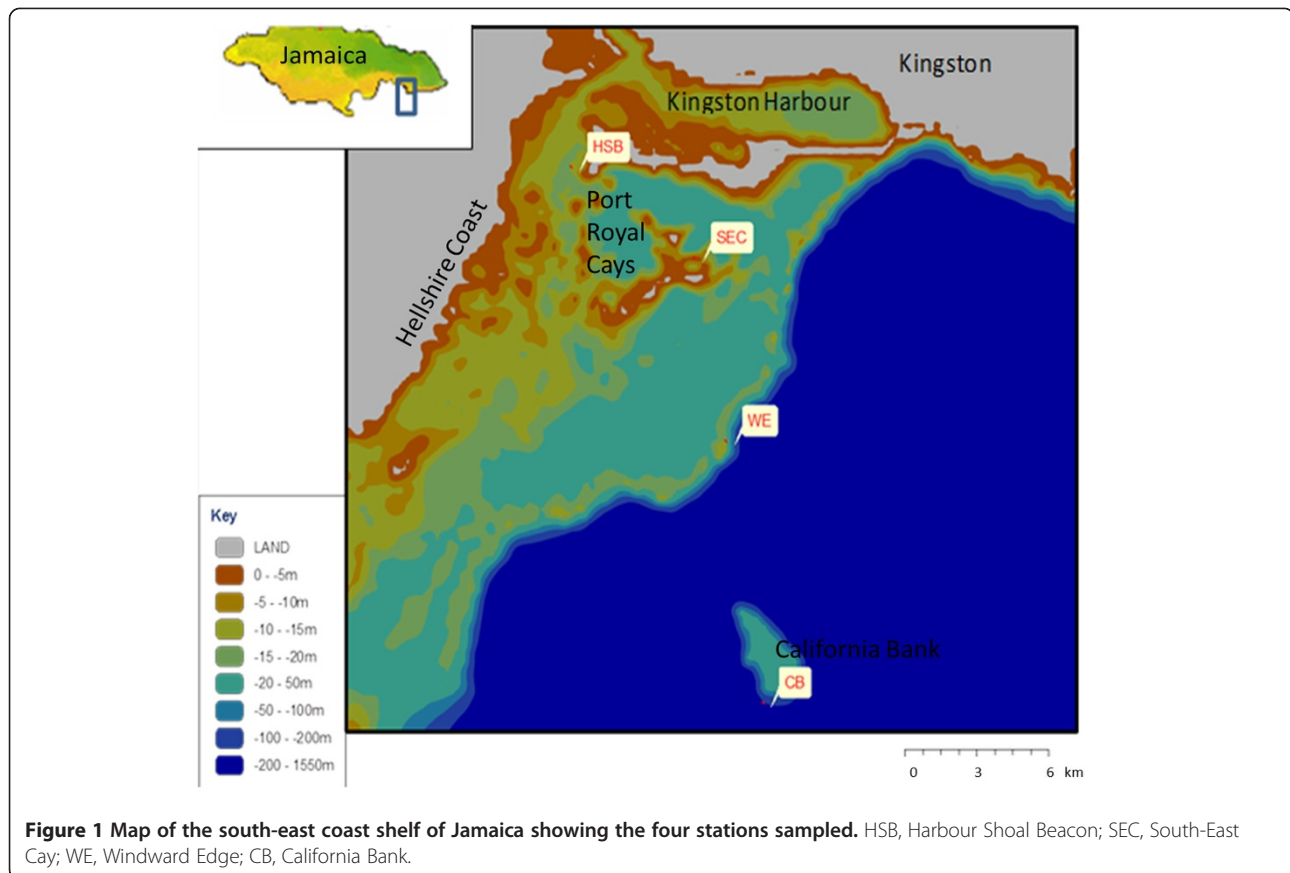
Zooplankton sampling was conducted as replicate hauls from 20-m depths at all stations except HSB where hauls were taken from 5 m, using plankton nets of three different mesh sizes: 64, 200 and 600 μm . The 600- μm net had a hoop diameter of 1.0 m, while the 200- and 64- μm nets both had hoop diameters of 0.5 m (UNESCO 1968). Sampling always commenced at what was believed to be the most oligotrophic site, CB, to minimize the effects of clogging of the nets. Nets were rinsed between sites to reduce carry-over of organisms. Samples were fixed in the field with 10% formalin. The volume of water filtered by the net was calculated using the formula: Volume of water filtered = $\Pi r^2 h$, where h is the depth of the water column filtered and r is the hoop radius of the plankton net.

The entire zooplankton sample was processed with taxa being identified to species (where possible), enumerated and their sample numbers converted to numbers m^{-3} . Where necessary, sub-samples were processed, these being obtained from the parent sample using the beaker-split method (Van Guelphen et al. 1982). The sample or subsample was poured into a Bogorov tray and taxa identified to species, where possible, with the aid of a Wild M7 binocular microscope (Heerbrugg, Switzerland).

Nitrate and phosphate levels present were determined from whole water samples which were processed according to the methods outlined in Parsons et al. (1984). Illumination readings were taken with a LI-COR light meter (Fondriest Environmental, Inc., Fairborn, OH, USA) and were used to calculate extinction coefficient (EC) values for the four stations using the following equation: $EC = 2.3 \times (\text{Log}_{10}L_1 - \text{Log}_{10}L_2) / D_2 - D_1$, where L_1 = light reading at the surface (depth 1), L_2 = light reading at depth (depth 2), D_1 = depth 1 and D_2 = depth 2.

Community analysis

Two community analysis tests, Jaccard community coefficient (Clifford and Stephenson 1975) and percent similarity coefficient (Kwiatkowski and Roff 1976), were applied to the zooplankton community to indicate the degree of similarity between stations. The JCC is given by the equation: $JCC = [c / (a + b - c)] \times 100$, where a is the number of all species occurring at one station, b is the number of



all species occurring at the other station being compared and c is the number of species common to both stations. JCC is based on the presence or absence of a species, not the number of times present or the quantity, as such single rare occurrences will carry the same weight as regular and numerically dominant species. The percent similarity coefficient (PSC) was applied using the following equation: $PSC = 100 - [0.5 \times \sum |a - b|]$, where a and b are the percentage of each species at each pair of stations.

When similarity is high, the PSC value approaches 100%. PSC is biased toward the more abundant species, neglecting single rare occurrences and thus may compensate for the weakness of the Jaccard community coefficient. The results of the community coefficients were displayed as a dendrogram with stations clustered in relation to both JCC and PSC values. Finally, Shannon-Wiener index of diversity (H) was determined for the zooplankton community at each station (e.g. Hsieh et al. 2004) using the following equation: $H = -\sum [(p_i) \times \ln(p_i)]$, where p_i = proportion of total sample represented by species i . The range for the index is normally 0 to 5.

Statistical analyses

Multifactor analysis of variance tests (MANOVA) were applied to normally distributed or $\log_{(x+1)}$ transformed

data using STATISTICA (Statsoft Inc., 1998). This test analysed the effect of one independent variable (station) on the dependent variables (physical and biological parameters) and tested whether there were significant differences between parameters at each station. The 95% confidence interval was used and therefore differences were considered significant if the p value was greater than 0.05 ($p > 0.05$). Pearson's product moment correlation matrix was used to show the relationship between physicochemical variables and the zooplankton community (Hwang et al. 2010).

Results

Physicochemical parameters

The physicochemical data for each station represented the mean of values taken through the water column as this was the path through which the zooplankton net was hauled. There was no significant temporal variation or evidence of seasonality in these parameters and so the means of fortnightly collections are presented for each station. Eleven physicochemical parameters were investigated, of which nine showed significant variation between stations (Table 1).

The physicochemical parameters that varied significantly between stations did not all show the expected

Table 1 All physicochemical and biological variables examined during the study

Variable	ANOVA significance value (95%)	Number	Means at each station with standard error			
			HSB	SEC	WE	CB
Physicochemical variables (water quality)						
Temperature (°C)	<0.001	108	29.63 ± 0.29	29.01 ± 0.29	27.82 ± 0.32	28.79 ± 0.35
Salinity (‰)	<0.001	108	36.10 ± 0.08	36.18 ± 0.05	36.21 ± 0.03	36.20 ± 0.04
DO (mg l ⁻¹)	<0.001	108	4.55 ± 0.04	4.44 ± 0.09	5.14 ± 0.14	5.14 ± 0.09
pH (pH units)	<0.001	107	8.27 ± 0.01	8.24 ± 0.01	8.24 ± 0.01	8.17 ± 0.01
Specific conductivity (mS cm ⁻¹)	<0.001	108	53.94 ± 0.11	54.51 ± 0.08	54.14 ± 0.04	54.51 ± 0.07
TDS (ppm)	<0.001	108	34.54 ± 0.07	34.89 ± 0.05	34.89 ± 0.04	34.92 ± 0.04
Log _(x + 1) extinction coefficient	0.031	41	0.53 ± 0.16	0.07 ± 0.01	0.05 ± 0.01	0.04 ± 0.01
Log _(x + 1) turbidity (NTU/mg l ⁻¹)	0.164	108	0.87 ± 0.11	0.64 ± 0.12	0.80 ± 0.21	0.14 ± 0.02
Log _(x + 1) ORP (mV)	0.011	108	518 ± 4.91	532 ± 8.80	552 ± 7.39	605 ± 10.43
Nitrates (µg at l ⁻¹)	0.079	108	0.34 ± 0.11	0.31 ± 0.10	0.22 ± 0.06	0.32 ± 0.09
Phosphates (µg at l ⁻¹)	0.027	108	0.09 ± 0.02	0.08 ± 0.01	0.05 ± 0.01	0.07 ± 0.01
Total chlorophyll a (µg l ⁻¹)	<0.001	108	1.001 ± 0.15	0.262 ± 0.02	0.127 ± 0.01	0.081 ± 0.01
Biological variables (zooplankton)						
Mean number of species	<0.001	41	53 ± 1.5	70 ± 1.9	71 ± 1.6	68 ± 1.7
Total abundance (numbers m ⁻³)	<0.001	41	5,963 ± 398	2,251 ± 193	2,491 ± 240	2,150 ± 122
Calanoida (numbers m ⁻³)	<0.001	41	1,497 ± 299	587 ± 80	568 ± 104	338 ± 22
Cyclopoid (numbers m ⁻³)	<0.001	41	375 ± 61	303 ± 30	349 ± 80	275 ± 24
Harpacticoid (numbers m ⁻³)	<0.001	41	33 ± 11	19 ± 9	50 ± 11	44 ± 7
Larvae (numbers m ⁻³)	<0.001	41	2,428 ± 411	930 ± 136	1,058 ± 218	1,480 ± 115
Decapod (numbers m ⁻³)	<0.001	41	102 ± 21	13 ± 1	2 ± 4	8 ± 2
Log _(x + 1) Cladocera (numbers m ⁻³)	<0.001	41	289 ± 81	5 ± 2	13 ± 7	5 ± 1
Log _(x + 1) Cnidaria (numbers m ⁻³)	<0.001	41	117 ± 31	30 ± 11	17 ± 3	32 ± 5
Log _(x + 1) Larvacea (numbers m ⁻³)	0.418	41	566 ± 220	607 ± 143	436 ± 226	225 ± 33
Log _(x + 1) Mollusc (numbers m ⁻³)	0.095	41	177 ± 30	140 ± 24	120 ± 16	57 ± 13
Chaetognath (numbers m ⁻³)	0.389	41	56 ± 12	47 ± 6	41 ± 7	33 ± 8

Means with standard error values are also given for each station. HSB, Harbour shoal beacon; SEC, South-East cay; WE, Windward edge; CB, California bank.

trend of gradual change with distance from the HSB to CB. Only ORP (Figure 2) showed gradual change with increasing distance offshore. Extinction coefficient and total chlorophyll *a* (Small et al. 2013) had a similar pattern with the highest mean values at HSB, but this was followed by a sharp decline at SEC and the stations further offshore. For most other physicochemical parameters, there was no clear pattern, and in some cases (e.g. phosphates, Figure 3), CB, located furthest offshore, often had mean values that were higher than WE or SEC, located on the shelf.

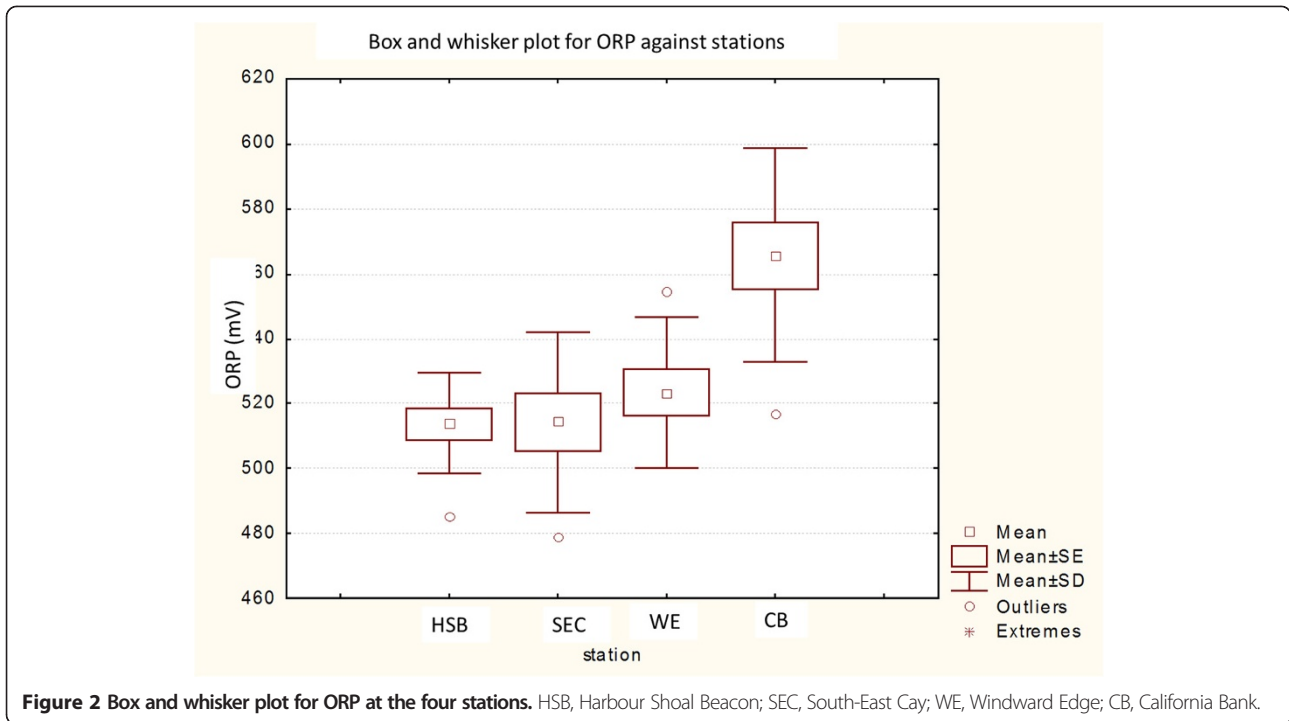
Zooplankton parameters

Several numeric indices were used to describe the variability in the zooplankton across stations, which include the following: number of species/taxa, mean total abundance and mean abundance of major groups and individual species. Ten zooplankton parameters were tested

for significant spatial variability, and seven were found to vary significantly between stations (Table 1).

Taxonomic richness and diversity

One hundred forty-seven different taxa of zooplankton were identified during the study (Table 2), which is 22% more than the 114 taxa found by Moore and Sander (1979). As expected, the Copepoda was the most diverse group (76 species) of which the order Calanoida (37 species) was the most dominant. The rare order Monstriloida was represented by one species. The group comprising larval stages was also very diverse with representatives from most taxonomic groups, including copepods. Although zooplankton organisms were identified to the species where possible (*cf.* 'Methods' section), the members of the group 'larvae', which were not easily identified to species, were represented as orders.



When stations were compared, HSB had the lowest total number of species (taxonomic richness) with 81. SEC with 106 different taxa and WE with 114 had the greatest total taxonomic richness. The furthest station from the island shelf, CB, had 94 different taxa (Table 3). The mean values

for the number of species or taxa for the sampling period varied significantly (MANOVA, $p < 0.001$) between stations (Figure 4). Shannon-Weiner diversity index values (Table 2) followed a somewhat similar trend to richness, but with CB having the lowest diversity (2.61) which was

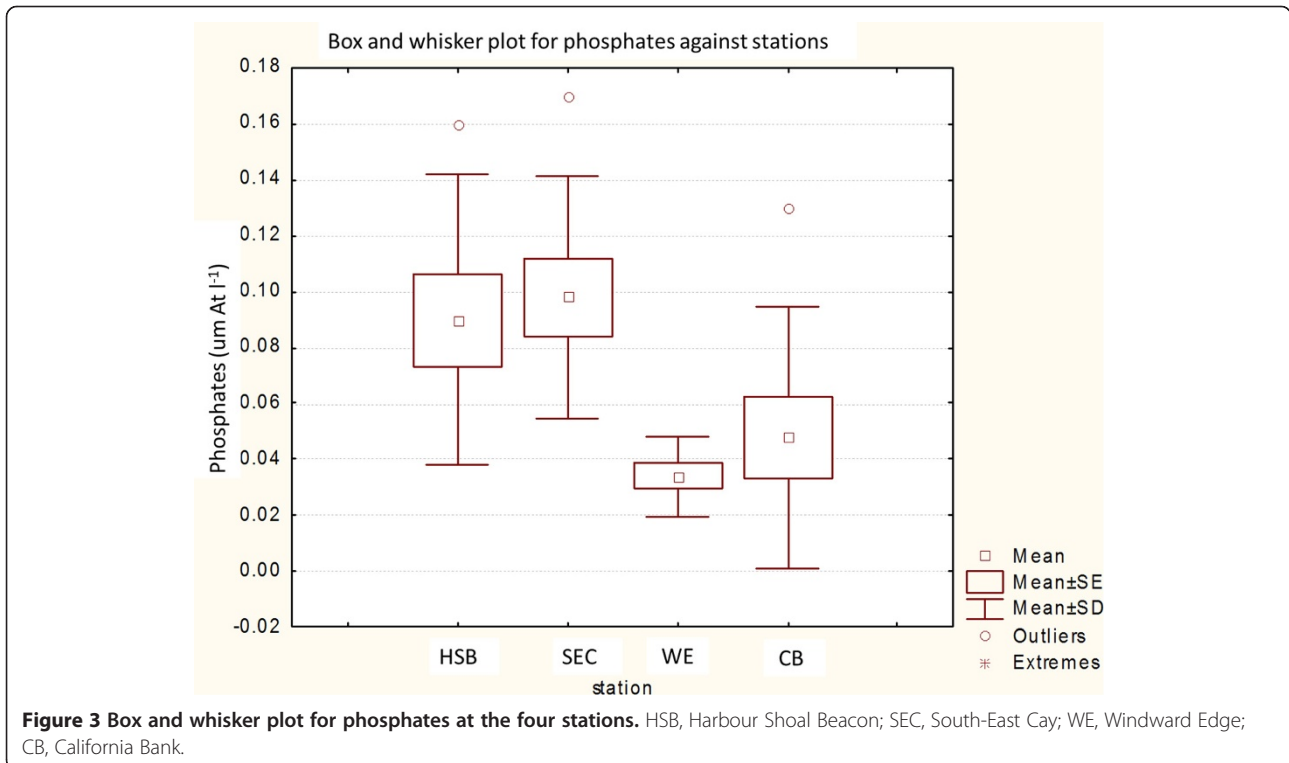


Table 2 Zooplankton species list, percentage occurrence of each species and Simpson's diversity index for each station

Taxa	HSB	SEC	WE	CB
Cnidaria				
<i>Abylopsis</i> spp.		30	50	60
<i>Aglama</i> sp.	20	40	80	60
<i>Aglaura</i> spp.	10	40	90	90
<i>Clytia</i> sp.	20			
<i>Cordagalma</i> sp.			20	10
<i>Ephysa aurata</i>				10
<i>Eudoxid</i> sp.		80	80	100
<i>Euphysora gracilis</i>			10	10
<i>Eutima</i> sp.	10		10	
<i>Liriope tetraphylla</i>	100	40		
<i>Loadicea pulchra</i>	70		20	
<i>Muggiea</i> sp.		50	70	80
<i>Obelia</i> sp.	60	30	30	10
<i>Phialopsis diegensis</i>			10	10
<i>Phialucium</i> sp.	10			
<i>Solamaris</i> sp.	90			
<i>Solmunella</i> sp.	10	10		
<i>Steenstrupia</i> sp.	10	40	30	
Ctenophora				
<i>Beroe</i> sp.			10	40
Cladocera				
<i>Penilia avirostris</i>	100	40	30	20
<i>Evadne tergestina</i>	40	30	70	70
Chaetognatha				
<i>Eukhronia proboscidea</i>		10		
<i>Eukhronia bathypelagica</i>		10		
<i>Khronitta subtilis</i>	30	20		
<i>Sagitta bipunctata</i>		10		
<i>Sagitta decipens</i>		20	10	
<i>Sagitta enflata</i>	100	100	100	100
<i>Sagitta hispida</i>	80	70	70	70
<i>Sagitta megalophthalma</i>		70	10	10
<i>Sagitta serratodentata</i>		10	10	
<i>Sagitta tenuis</i>			20	10
<i>Pterosagitta draco</i>	10		20	30
Amphipoda				
Amphipod		30	20	20
<i>Hyperia</i> sp.		40		10
Calanoida				
<i>Acartia lilljeborji</i>	10			
<i>Acartia spinata</i>	50	50	60	30

Table 2 Zooplankton species list, percentage occurrence of each species and Simpson's diversity index for each station (Continued)

Taxa	HSB	SEC	WE	CB
<i>Acartia tonsa</i>	80	50		10
<i>Acrocalanus</i> sp.	10	70	70	90
<i>Aetideus</i> sp.		10		
<i>Calocalanus</i> spp.		10	60	90
<i>Calocalanus pavo</i>	30	80	100	70
<i>Calocalanus pavoninus</i>		40	60	40
<i>Calanopia americana</i>	10	30	10	10
<i>Candacia bipinnata</i>	10		20	
<i>Candacia bispinosa</i>			10	
<i>Candacia curta</i>		20	10	
<i>Candacia longimana</i>		20		
<i>Candacia pachydactyla</i>	10	20	50	60
<i>Candacia paenelongimana</i>	10			
<i>Candacia varicans</i>		10	10	
<i>Centropages bradyi</i>				10
<i>Centropages velificatus</i>	100	100	40	20
<i>Centropages violaceus</i>	10	20		40
<i>Clausocalanus</i> sp.		90	80	10
<i>Euaugaptilus nodifrons</i>			10	
<i>Eucalanus</i> sp.		10	10	20
<i>Eucalanus micronatus</i>				60
<i>Eucalanus subtenuis</i>				10
<i>Euclata marina</i>		60	40	100
<i>Eutima</i> sp.	10		10	
<i>Labidocera aestiva</i>		10		
<i>Labidocera nerri</i>		10	10	
<i>Mecynocera</i> sp.			10	50
<i>Neocalanus robustior</i>				20
<i>Paracandacia bispinosa</i>			10	
<i>Paracalanus</i> sp.	80	100	90	70
<i>Paracalanus aculeatus</i>	20		20	30
<i>Paracalanus parvus</i>	100	50	30	60
<i>Paraeucalanus</i> sp.			20	
<i>Pontella mimocerami</i>		10	10	
<i>Pontellina</i> sp.		10	30	
<i>Rhincalanus cornutus</i>			10	
<i>Scolecithrix</i> sp.	10	20	60	70
<i>Subeucalanus mucronatus</i>		10	30	
<i>Subeucalanus pileatus</i>	30			
<i>Subeucalanus subcrassus</i>	30	30	10	10
<i>Temora longicornis</i>	70		20	
<i>Temora stylifera</i>	20	60	50	20
<i>Temora turbinata</i>	10	50	10	

Table 2 Zooplankton species list, percentage occurrence of each species and Simpson's diversity index for each station (Continued)

<i>Undinula vulgaris</i>	80	90	100	100
Cyclopoida				
<i>Copilia</i> sp.		40	50	60
<i>Corycaeus carinata</i>			10	10
<i>Corycaeus catus</i>	40	40	50	40
<i>Corycaeus clause</i>			40	30
<i>Corycaeus latus</i>		10	10	20
<i>Corycaeus lautus</i>		30	60	70
<i>Corycaeus limbatus</i>			20	10
<i>Corycaeus speciosus</i>	100	90	100	90
<i>Corycaeus typicus</i>			10	
<i>Dioithona oculata</i>	30	10		20
<i>Farranula carinata</i>		50	100	100
<i>Farranula gracilis</i>	70	70	70	60
<i>Farranula rostrata</i>	40	100	100	50
<i>Lubbockia</i> sp.	10	10	20	10
<i>Oithona hebes</i>			80	
<i>Oithona nana</i>	90	100	70	40
<i>Oithona similis</i>		10	10	
<i>Oithona plumifera</i>	60	90	60	50
<i>Oncea mediterranea</i>	10	10	50	30
<i>Oncea media</i>		10	10	
<i>Sagitella</i> sp.		10		
<i>Saphirella tropica</i>	10	50	10	
<i>Sapphirina</i> spp.	10	10	10	50
Harpacticoida				
<i>Clytemnestra</i> sp.	10	10	30	20
<i>Euterpina acutifrons</i>	80	50	40	30
<i>Macrosetella gracilis</i>		20	40	60
<i>Microsetella norvegica</i>	30	70	90	100
<i>Miracia efferata</i>	40	20	20	30
<i>Oculosetella</i> sp.		20		
Monstrilloida				
<i>Monstrilla</i> sp.	10	20		
Decapoda				
Decapod (unidentified)	60	80	40	20
<i>Lucifer faxoni</i>	100	60	30	20
Larvacea				
<i>Oikopleura dioica</i>	100	100	100	100
<i>Fritillaria</i> sp.	40	100	80	90
Pteropoda				
<i>Creseis acicula</i>	70	100	80	30
<i>Diacria</i> sp.		10		20

Table 2 Zooplankton species list, percentage occurrence of each species and Simpson's diversity index for each station (Continued)

Thaliacea				
<i>Doliolum</i> sp.	10	20	20	30
<i>Thalia</i> sp.	20	20	60	70
Larvae				
Actinula		20	10	
Auricularia	20	80	60	70
Bipinnaria larva of starfish	10	60	70	90
Copepodites	90	100	100	100
Copepod nauplii	100	100	90	100
Cirripede	10	10	30	
Euphausiid	10	20	60	90
<i>Echinocardium cordatum</i>			10	20
Echinopluteus larvae	60	60	80	60
Fish eggs	20	70	90	100
Fish larvae	20	70	60	50
Gastropod larva	70	100	100	100
Heteropod larvae	50	10	40	
Lanice larvae		40		20
Ophiopluteus larvae	10	60	80	70
Pontellid nauplius		30	60	10
Phylossoma larvae	10	30	10	
Polychaete spp.	50	90	90	80
Porcellanid larvae	60	40	10	40
<i>Sagitta</i> juvenile	10		40	30
Sergestid			10	
Spionid larvae		90	40	30
Stomatopod larvae	20	10	10	
<i>Tomopteris</i> sp.	10	10	20	20
Zoea	50	80	90	90
Number of species (richness)	81	106	114	94
Shannon-Weiner index	2.63	2.68	3.66	2.61

HSB, Harbour shoal beacon; SEC, South-East cay; WE, Windward edge; CB, California bank.

similar to HSB (2.63). WE therefore had the highest diversity value (3.66) as well as the highest taxonomic richness.

The percentage occurrence determined for each taxon at each station (Table 2) facilitated the identification of potential indicators. Only two species (*Sagitta enflata* and *Oikopleura dioica*) showed 100% occurrence at all four stations, while most other taxa, if found at all four stations, showed varying percentage occurrence. The Cnidaria and Ctenophora tended to have greatest occurrence at offshore areas, except for *Liriope tetraphylla* which was found at HSB on all sampling occasions. Organisms and groups which displayed dominance in both

Table 3 Zooplankton taxa with potential for use as indicators of water masses

Taxa	Mean numbers m ⁻³ with standard error			
	HSB	SEC	WE	CB
<i>Evadne tergestina</i>	10.3 ± 5.6	0.5 ± 0.4	2.9 ± 1.9	4.4 ± 1.9
<i>Penilia avirostris</i>	278.4 ± 77.1	3.9 ± 2.2	10.3 ± 8.1	0.3 ± 0.2
<i>Sagitta enflata</i>	45.6 ± 10.1	36.7 ± 5.3	34.2 ± 5.2	29.0 ± 7.6
<i>Clausocalanus</i> sp.	0	45.3 ± 18.3	154.1 ± 42.4	9.9 ± 9.9
<i>Paracalanus parvus</i>	734.6 ± 222.4	88.9 ± 18.1	48.9 ± 32.4	73.8 ± 21.4
<i>Undinula vulgaris</i>	19.1 ± 8.1	87.1 ± 26.5	40.6 ± 7.3	85.2 ± 23.4
<i>Farranula carinata</i>	0	4.8 ± 2.0	34.1 ± 9.7	40.4 ± 12.1
<i>Oithona nana</i>	192.5 ± 42.9	119.7 ± 15.4	6.3 ± 1.7	5.9 ± 2.7
<i>Microsetella norvegica</i>	4.3 ± 2.7	9.4 ± 2.7	30.7 ± 6.1	37.2 ± 5.6
<i>Lucifer faxoni</i>	23.9 ± 7.4	0.6 ± 0.2	0.4 ± 0.2	2.8 ± 2.1

HSB, Harbour shoal beacon; SEC, South-East cay; WE, Windward edge; CB, California bank.

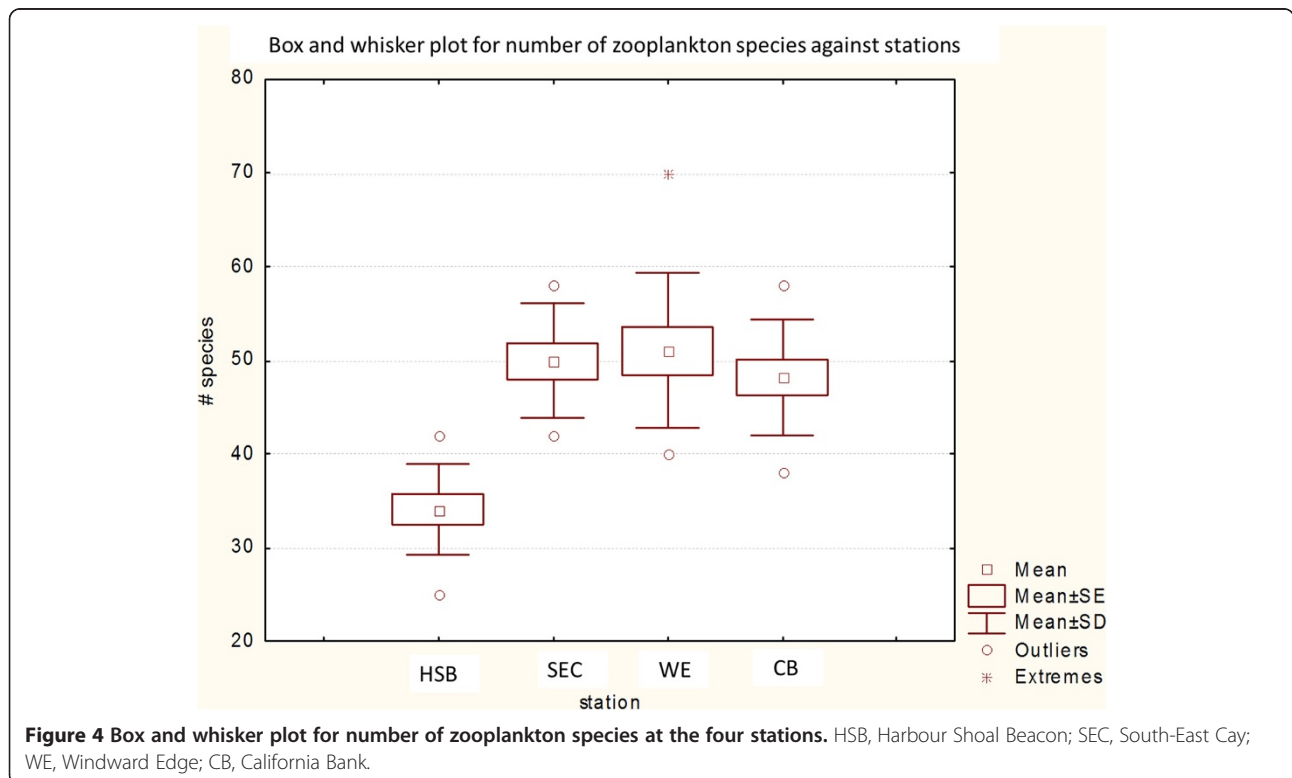
abundance and percentage occurrence at particular stations and which showed significant spatial variation (MANOVA, $p \leq 0.001$) were identified as potential indicators. These taxa were as follows: *Penilia avirostris*, *Clausocalanus* sp., *Paracalanus parvus*, *Undinula vulgaris*, *Farranula carinata*, *Oithona nana*, *Microsetella norvegica* and *Lucifer faxoni*.

Penilia avirostris, which was a previously described Kingston Harbour indicator (Grahame 1976), was always

found at HSB and showed decreasing percentage occurrence and abundance with distance from the Harbour; however, there was no pattern of gradual decline. *L. faxoni*, also previously identified as a Kingston Harbour indicator (Lindo 1991), showed the greatest percentage occurrence and abundance near the Harbour but again lacked the pattern of decline with increasing distance offshore. *M. norvegica* showed the opposite pattern with the lowest percentage occurrence and abundance at HSB, highest at CB and gradual increase with increasing distance offshore (Figure 5). *F. carinata* was similar to *M. norvegica* (Figure 6) and showed a gradual increase from zero at HSB to the highest mean abundances at station CB.

Total zooplankton abundances

Overall greatest total abundances (numbers m⁻³) were obtained at station HSB which had a mean value of 5,963 individuals m⁻³, while stations SEC, WE and CB had similar mean values of just over 2,000 individuals m⁻³ (Figure 7). Larvae were the most abundant fraction at three of the four stations and accounted for more than half of the total zooplankton abundance at California Bank. The group ‘larvae’ was dominated by copepod nauplii, fish eggs and echinoderm larval stages. Copepods made the second largest contribution to the overall abundances but exceeded the larvae only at WE.



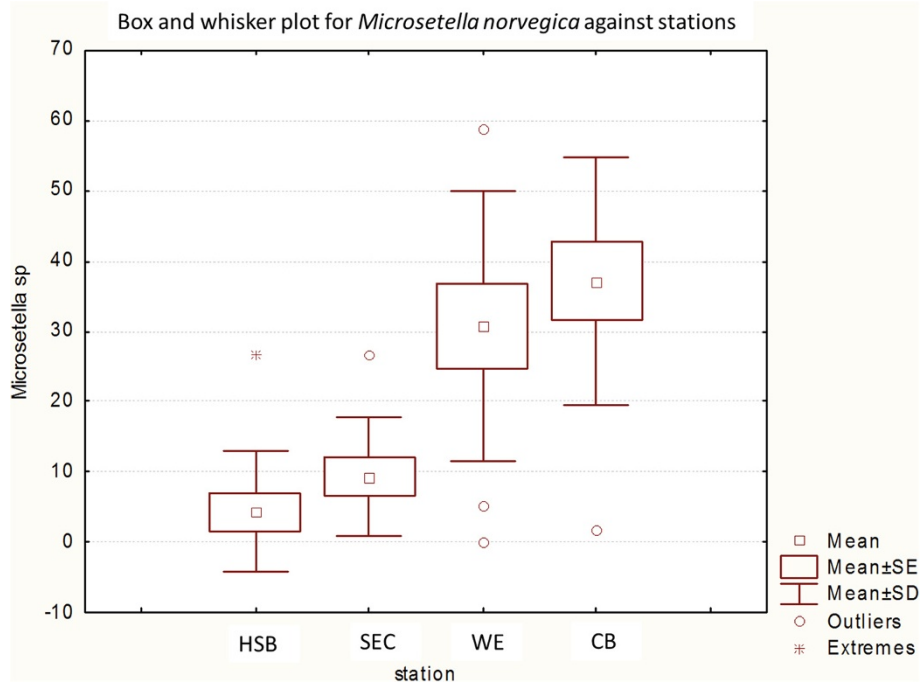


Figure 5 Box and whisker plot for *Microsetella norvegica* at the four stations. HSB, Harbour Shoal Beacon; SEC, South-East Cay; WE, Windward Edge; CB, California Bank.

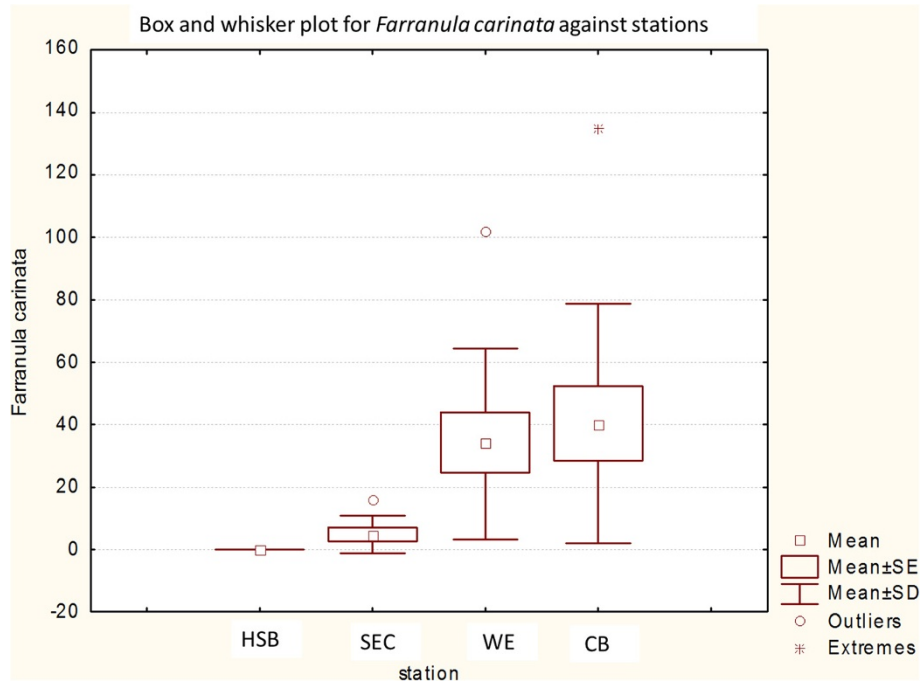


Figure 6 Box and whisker plot for *Farranula carinata* at the four stations. HSB, Harbour Shoal Beacon; SEC, South-East Cay; WE, Windward Edge; CB, California Bank.

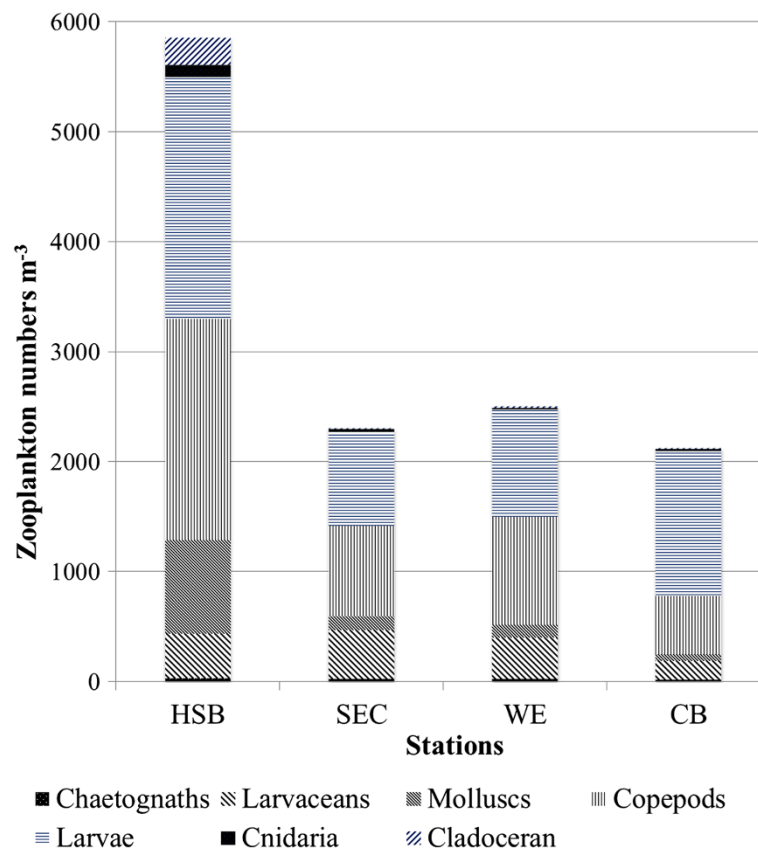


Figure 7 Mean abundances of the major zooplankton taxonomic groups found at each station. HSB, Harbour Shoal Beacon; SEC, South-East Cay; WE; Windward Edge; CB, California Bank.

Correlation analysis

Physicochemical parameters were correlated with the biological and size-fractionated phytoplankton biomass from a concurrent study (Small et al. 2013). The resultant correlation matrix (Table 4) indicated that specific conductivity and total dissolved solids showed a strong correlation with the biological variables. The phytoplankton size classes also correlated strongly with the number of species and total abundance of zooplankton.

Community coefficients

The cluster analysis dendrograms generated using the community coefficients JCC and PSC both showed two general groups of stations based on the zooplankton community, one with station HSB as the sole member and the other with the remaining three stations (Figure 8A,B). JCC, however, showed this trend of general increase in community similarity from stations HSB to CB, and station HSB had the least similar communities compared to the other stations with values all less than 38% (JCC < 0.38). The highest similarity (66%) was seen between stations CB and WE with a JCC value of 0.66. Stations SEC and WE were also found to be quite similar with an index of 0.63. PSC values were all higher (>53%),

but HSB still had overall lowest similarity compared to other stations (Table 5) with only SEC being 60% similar.

Discussion

The zooplankton communities of Jamaica's bays and harbors have been studied extensively for use in water quality monitoring as well as to indicate the influence of different water masses (Grahame 1976; Lindo 1991; Dunbar and Webber 2003; Webber et al. 2005; Campbell et al. 2008). However, only Moore and Sander (1979) previously made direct comparison between inshore stations and those beyond the coastal shelf. Webber and Roff (1995) conducted an intensive study of plankton and water quality offshore Discovery Bay, north coast of Jamaica, but this was facilitated by the coastal shelf of Jamaica's north coast being narrow (maximum of 1.6 km wide) compared to the south coast where the shelf has a maximum width of 24 km (Aiken and Kong 2000).

With the relatively large distances between the stations of this study and their linear arrangement, the expectation was that significant spatial differences would be obtained for all parameters and that values would gradually increase or decrease with increasing distance

Table 4 Correlation matrix relating physicochemical and biological parameters found to be significantly different across stations

Variable	Station	Distance	Temperature	Salinity	DO	pH	Specific conductivity	TDS	ORP	Phosphorus	Number of species	Abundance	Calanoida	Cladocera	Larvae	Cnidaria	Decapoda	Net	Nano	Pico	
Station	1																				
Distance	0.99	1																			
Temperature	-0.35	-0.35	1																		
Salinity	0.62	0.57	-0.05	1																	
DO	0.37	0.37	-0.49	0.21	1																
pH	-0.5	-0.55	0.53	-0.3	-0.44	1															
Specific conductivity	0.56	0.51	-0.12	0.95	0.35	-0.37	1														
TDS	0.62	0.59	-0.08	0.95	0.33	-0.3	0.92	1													
ORP	0.57	0.6	-0.74	0.11	0.46	-0.84	0.18	0.11	1												
Phosphorus	-0.44	-0.42	0.68	-0.29	-0.51	0.2	-0.36	-0.33	-0.38	1											
Number of species	0.53	0.46	-0.33	0.6	0.14	-0.27	0.61	0.57	0.28	-0.21	1										
Total abundance	-0.6	-0.53	0.16	-0.62	-0.15	0.22	-0.61	-0.57	-0.19	0.16	-0.65	1									
Calanoida	-0.59	-0.56	0.22	-0.68	-0.24	0.39	-0.69	-0.68	-0.37	0.25	-0.54	0.68	1								
Cladocera	-0.55	-0.5	0.09	-0.38	-0.05	0.15	-0.34	-0.32	-0.17	0.13	-0.42	0.73	0.55	1							
Larvae	-0.32	-0.26	0.07	-0.32	-0.04	0.01	-0.3	-0.25	0.02	0.03	-0.47	0.82	0.16	0.48	1						
Cnidaria	-0.46	-0.41	-0.01	-0.56	-0.08	0.1	-0.57	-0.51	-0.14	0.08	-0.41	0.45	0.71	0.54	0	1					
Decapoda	-0.56	-0.51	0.05	-0.51	-0.11	0.08	-0.48	-0.48	-0.17	0.01	-0.56	0.6	0.33	0.2	0.56	0.31	1				
Net	-0.69	-0.66	0.66	-0.57	-0.5	0.49	-0.62	-0.6	-0.6	0.54	-0.67	0.57	0.45	0.22	0.45	0.22	0.69	1			
Nano	-0.76	-0.73	0.48	-0.51	-0.33	0.55	-0.48	-0.4	-0.62	0.43	-0.5	0.56	0.58	0.59	0.29	0.46	0.27	0.52	1		
Pico	-0.54	-0.52	0.73	-0.44	-0.45	0.66	-0.47	-0.35	-0.7	0.5	-0.58	0.48	0.44	0.28	0.33	0.18	0.3	0.71	0.69	1	

All marked station correlations are significant at $p < 0.05000$, $N = 40$ (casewise deletion of missing data). Significant correlations indicated by coefficient of determination values ≥ 0.50 .

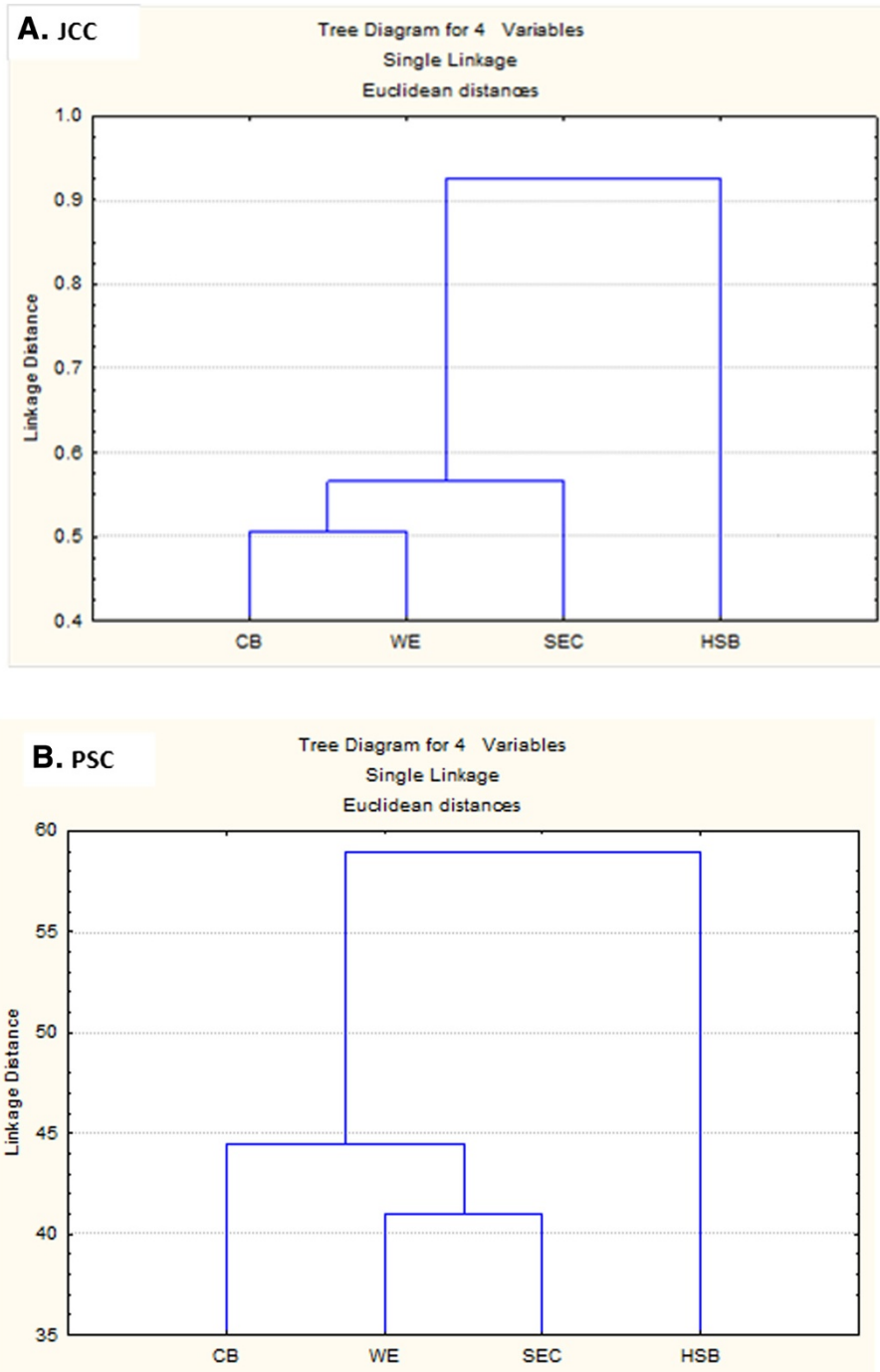


Figure 8 Dendrogram showing the mean station association using (A) JCC and (B) PSC. HSB, Harbour Shoal Beacon; SEC, South-East Cay; WE, Windward Edge; CB, California Bank.

offshore. The study was also intended to use the zooplankton as indicators of different water masses with differing trophic conditions. Previous studies have used the physicochemical parameters and chlorophyll *a* (Vollenweider et al. 1998; Fehling et al. 2012) or the zooplankton (e.g. Hwang and Heath 1997; Lougheed and

Chow-Fraser 2001; Hwang et al. 2006, 2010) to characterize the trophic status and water quality of marine areas. However, in this study, the physicochemical parameters were found to be unreliable with key parameters either not showing significant spatial differences (e.g. nitrates, turbidity) or not having the expected trend of decreasing/

Table 5 Jaccard community coefficient (JCC) and percentage community coefficient (PSC) values for the four stations

	Station	HSB	SEC	WE	CB
JCC	HSB	1			
	SEC	0.378	1		
	WE	0.360	0.626	1	
	CB	0.348	0.463	0.661	1
PSC	HSB	100			
	SEC	60.19	100		
	WE	55.52	72.14	100	
	CB	53.70	59.44	69.89	100

HSB, Harbour shoal beacon; SEC, South-East cay; WE, Windward edge; CB, California bank.

increasing with distance offshore (e.g. temperature/salinity, phosphates, specific conductance). The zooplankton were therefore expected to be useful indicators of the different water masses along the Harbour, shelf and offshore gradient by showing lower taxonomic richness/diversity coupled with higher abundances at the eutrophic Harbour station, progressing to higher richness/diversity with lower abundance at the shelf and offshore areas (Zhang et al. 2009). Individual zooplankton taxa by the variation in their abundance and percentage occurrence were also expected to indicate the different water masses.

Taxonomic richness and diversity

The number of species (taxonomic richness) and diversity were expected to show significant variation between stations, with the highest values at stations furthest offshore (WE and CB) and lowest at the mouth of Kingston Harbour (HSB), and SEC being an intermediary along the eutrophication gradient (Zervoudaki et al. 2009; Zhang et al. 2009). However, while SEC and WE were similar in terms of richness and diversity values, HSB and CB were also similar. Due to the distances involved, it is unlikely that taxonomic similarities between these stations were indicative of a common water mass. SEC and WE are likely to be enriched by waters of the south coast shelf as well as upwelled nutrients as both are associated with the edge of the south-east coast shelf, beyond which depths immediately fall from 44 to 347 m, or the edge of the Port Royal Cays area, beyond which depths fall from 5.8 to 31 m (Admiralty Chart number 456, 1992). California Bank, while not associated with the island shelf, would also come under the influence of enrichment from upwelled waters as it rises to 30 m from the ocean floor depths of 245 m. The increase in nitrates and phosphates confirm nutrient enrichment which would influence taxonomic richness and diversity. The effect of these upwelled waters at the offshore bank with the associated increase in zooplankton parameters

and decrease in diversity, would lead to the bank being classified as mesotrophic rather than oligotrophic.

The community indices, Jaccard community coefficient and percentage similarity coefficient, in conjunction with the cluster analyses also showed a general similarity between stations SEC, WE and CB and a high dissimilarity of that group with station HSB. Webber et al. (1996) identified the Harbour mouth as a discrete region with different characteristics from other areas on the Jamaican south coast shelf which included the South-East Cay. The harbour mouth region comes under the direct influence of waters originating from the Kingston Harbour, which has for a long time been considered a source of eutrophic waters (Moore and Sander 1979; Webber et al. 1996; Dunbar and Webber 2003; Webber and Wilson-Kelly 2003). In the present study, the community composition clearly separated the Harbour mouth station from the shelf and offshore areas.

Zooplankton abundance

The highest mean zooplankton abundances would be expected from station HSB at the Harbour mouth with lower abundances at the stations outside of the influence of the harbour. Moore and Sander (1979) observed this trend, with numbers at their harbour mouth station (3 J) being the highest overall, with the lowest numbers being recorded off the shelf (station 1 J). Hopcroft and Roff (2003) reported that the availability of nutrients plays an important role in varying phytoplankton populations and inherently zooplankton numbers. The high availability of nutrients due to the proximity to sources of nutrient input (Webber and Wilson-Kelly 2003) would lead to a highly productive phytoplankton community able to support a large zooplankton community at HSB. The outer stations would be considered nutrient deficient as sources of input are minimal and nutrient concentrations typically low (Moore and Sander 1979; Hopcroft and Roff 2003). At these stations, local processes and the upwelling of nutrients would be the main factors controlling the numbers of zooplankton.

Moore and Sander (1979) had reported 450.5 individuals m^{-3} for their offshore site (1 J), which was approximately one fifth of what was reported during this study at CB (2,125 m^{-3}). While 40 years separate the two studies, we believe such a large increase in abundances is more likely due to differences in sampling methods rather than solely to increased enrichment and productivity at the offshore stations. Higher numbers in the present study could be because station CB was located above an underwater bank, which could disrupt the current flow and cause vertical mixing and introduction of nutrients into the surface waters. Carleton et al. (2001) also found that interference of water currents by banks affected zooplankton communities, whereby higher numbers were found but with similar

richness when compared to offshore sites not associated with banks.

It was expected that copepods would be numerically dominant, as has been reported by numerous authors (Moore and Sander 1979; Youngbluth 1980; Chisholm and Roff 1990; Webber et al. 1996; Dunbar and Webber 2003; Hsieh et al. 2004; Lan et al. 2004; Hwang et al. 2006). However, larvae were numerically dominant at three of the four stations, with numbers being higher than all other taxa combined at CB. The copepods were the second most dominant taxon at all stations except WE, where their numbers exceeded the larvae. This dominance of copepods and larvae was also reported by Hwang et al. (2010) from the Danshuei Ecosystem of northern Taiwan, an area with riverine, estuarine and marine conditions. The dominance of larval forms at the offshore bank (station CB) further supports the area as having high biological productivity (Heywood et al. 1990; Hernández-León 1991). Furthermore, the high numbers of passive zooplankton, mainly fish eggs, echinoderms and mollusc larvae, would suggest reduced flushing at these sites. A few authors have noted that circulation patterns near submerged structures, such as banks, could lead to retention and increased numbers of especially larval forms with limited means of movement (Cowen and Castro 1994; Carleton et al. 2001).

Indicator species

Within each taxonomic group, a few species displayed significant variation in abundance and percentage occurrence across stations. These species were identified as indicators of different water masses. *P. avirostris* and *L. faxoni* have previously been identified as indicators of Kingston Harbour waters in previous studies, and these species have been again shown to characterize the waters at the harbour mouth. In addition, *M. norvegica* and *F. carinata* are now being identified as indicators of offshore waters, using percentage occurrence and abundance.

The cladoceran *P. avirostris* has been previously reported in high numbers in Kingston Harbour (Moore and Sander 1979; Dunbar and Webber 2003). The distribution of the species appears to be affected by salinity and food availability. Moraitou-Apostolopoulou and Kiortsis (1973) found that salinity and water depth had an effect on the distribution of *P. avirostris*, thereby limiting its presence to shallow areas with low-salinity waters, like Kingston Harbour. The Harbour is influenced by freshwater and high nutrient input from various sources (Webber et al. 2003; Webber and Wilson-Kelly 2003). *P. avirostris* generally feeds on particles <15 µm (Lipej et al. 1997), and within the Harbour, the most suitable size phytoplankton (nano-plankton 2 to 20 µm) would be readily available (Ranston et al. 2003).

The distribution of *L. faxoni* also appears to be affected by salinity levels, and therefore, *L. faxoni* has been found to be abundant near areas with freshwater inputs (Webber et al. 2005). Moore and Sander (1979) did not report the species at their offshore stations, but it was reported at their harbour stations with similar mean abundance values to the present study. Lindo (1991) and Webber et al. (1996) reported this species as being numerically dominant with maximum numbers at the mouth of the Harbour. Rakesh et al. (2006) noted that salinity was important in affecting zooplankton assemblage, and the enrichment of coastal waters by fluvial inputs led to changes in the phytoplankton which in turn affected the zooplankton. In this study, phytoplankton size classes correlated with the number of species and total abundance of zooplankton.

The copepod *M. norvegica* which is now being proposed as an indicator of the offshore stations was previously reported by Moore and Sander (1979) as occurring only at stations outside of the Harbour, while Chisholm and Roff (1990) did not record *M. norvegica* in their study of the cays area near Kingston Harbour. Webber and Roff (1995) reported *M. norvegica* as accounting for 2% of the total copepod abundance at their offshore station in Discovery Bay, Jamaica. Another proposed offshore indicator, the copepod *F. carinata*, was also found to be important in oceanic waters off the north coast at Discovery Bay, Jamaica by Webber and Roff (1995).

The indices used (species composition, community similarity indices, species density, total zooplankton abundance and individual indicator species) gave clear indication of the variation in distribution of the zooplankton communities in inshore, shelf and oceanic waters. In general, there was an increase in the species richness with a concomitant decrease in the abundance towards the open sea. The trend observed was similar to that caused by the island mass effect, and based on these indices, the identification of different areas with different levels of eutrophication was possible. It indicated that station HSB is the most eutrophic site, but there was no consistent pattern of increasing oligotrophic conditions with increasing distance from Kingston Harbour.

When all the indices were considered, the most pristine station was WE followed by SEC, both located on the south-east coast shelf. Although furthest offshore, CB showed signs of enrichment and therefore could not be considered as oligotrophic. While the current study therefore showed that there were significant differences between oceanic, shelf and Harbour waters off Jamaica's south-east coast, the inclusion of an offshore bank indicated that offshore areas with features such as banks support zooplankton communities that may be similar to the shelf area. Thus, these banks would be more accurately characterized as mesotrophic.

Conclusions

While the expectation of the study was to separate the water masses into oceanic, shelf and Harbour waters, along a eutrophication gradient, most indices identified only two contrasting water masses (eutrophic Kingston Harbour and mesotrophic shelf/offshore bank). The water masses were best separated using taxonomic richness, total zooplankton abundance and community similarity. Four species were also identified as good indicators of the water masses of the area. These were *L. faxoni* and *P. avirostris*, indicators of eutrophic Kingston Harbour waters, and *M. norvegica* and *F. carinata*, indicators of mesotrophic shelf and offshore waters.

Abbreviations

SCOR: Scientific Committee on Oceanic Research; UNESCO: United Nations Educational, Scientific and Cultural Organization.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MKW designed the investigation, while sampling and analysis was conducted by KAL. Both authors conducted the data analysis and prepared the figures and manuscript, but MKW finalized and submitted the latter. Both authors read and approved the final manuscript.

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