Abstract

Unique applications of plankton ecology and productivity in Jamaican waters are presented. While traditional indices were inadequate descriptors of mangrove lagoon water quality, planktonic indices (total Chlorophyll $a$, zooplankton groups and species) were more reliable. Phytoplankton biomass was used to indicate a longitudinal gradient along the Hellshire Coastline, identifying non-point sources of enrichment, and movement of water masses in the absence of expensive Eulerian current meters. Along that same coast, mean primary production, determined by $^{14}$C techniques, confirmed a gradient from the eutrophic Kingston Harbour (21.1 g C m$^{-2}$ year$^{-1}$) to the oligotrophic control site (0.52 g C m$^{-2}$ year$^{-1}$). Maximum inshore station values (36.75–18.39 g C m$^{-2}$ year$^{-1}$) were more than 20 times greater than offshore and exceeded Harbour values, confirming non-point sources and localized mechanisms as important inshore sources of eutrophication. The novel use of Ecopath with Ecosim (EwE) software to model trophic flows within planktonic communities was done in two bays. For Discovery Bay, on Jamaica’s north coast, the model indicated a developing ecosystem with open mineral cycles and poor nutrient conservation while in Foul and Folly Bays on the southeastern coast the model indicated greater resilience and ability to recover from perturbations. These applications have facilitated informed management decisions for sustainable use in Jamaican coastal ecosystems.

Keywords: Jamaica, mangrove lagoons, plankton, production, Ecopath, non-point sources, Kingston Harbour

1. Introduction

Jamaica is an archipelagic state with territorial waters approximately 24 times its land mass. Consequently, the range of water masses and associated water qualities include eutrophic...
bays and harbours, mangrove lagoons, pristine and mesotrophic bays as well as oligotrophic offshore waters. These have provided a vast and varied expanse for plankton ecology research. Plankton research in Jamaican waters has traditionally used species composition and abundances to characterize the different water masses, indicate eutrophication levels and distribution as well as to indicate the trophic status of areas and their ability to support fisheries.

Kingston Harbour, the seventh deepest natural Harbour in the world, borders Jamaica’s capital city, Kingston and is distinctive for the inflow of 21 identifiable gullies and streams [1] that carry storm water, partially treated sewage, agriculture run off and now large quantities of solid waste. Kingston Harbour is the most extensively studied bay in Jamaica and consequently the plankton have been used to characterize the Harbour as eutrophic [2–6] as well as indicate the influence of these waters on the south coast shelf [4, 7]. Kingston Harbour waters have been tracked using planktonic indices as leaving the Harbour and flowing south west towards the Hellshire coastline. Relative abundance of *Lucifer faxoni* and *Penilia avirostris* [4] have been used as indicators of Kingston Harbour waters in areas of the south-east shelf of Jamaica.

Early research [8] sought to indicate distinct assemblages of zooplankton that characterize offshore (oceanic), shelf and Kingston Harbour waters along with associated “indicator species”. More recent studies have also compared oceanic, shelf and Kingston Harbour waters using zooplankton abundances as well as community composition [9]. However, novel uses of zooplankton to indicate water quality have involved exploring the use of these indices in mangrove lagoons threatened by anthropogenic stress.

The new and unique uses of plankton as indicators around Jamaica involve their use in characterizing the eutrophication status of mangrove lagoons, their use to assess coastal dynamics and water movement as well as the use of plankton productivity in the characterization and understanding of ecological functions and trophodynamic flows in different water masses.

### 2. Plankton as indicators in mangrove lagoons

Mangroves are a diverse species of tropical woody trees found primarily in Tropical and Sub-tropical intertidal (wetland) environments. They are estimated to cover a global area of between 137,760 and 152,000 km² [10]. Mangroves provide a suite of regulating, supporting and provisioning ecosystem services [10] including shoreline protection, carbon sequestration and storage, water quality enhancement and promoting high biodiversity by providing food and shelter for fish, marine invertebrates, and birds. Mangrove forests are threatened globally by deforestation due to coastal development, mariculture (primarily shrimp farming), timber harvest, water diversion and over-exploitation. Jamaica’s wetland area has been estimated at ~17,700 ha with 9731 ha being mangrove dominated forests [11]. Mangroves are reported to be found along 290 km or 29% of Jamaica’s coastline and covering approximately 97 km² [12]. Unfortunately, many areas of Jamaica’s mangroves are threatened by eutrophication which if left undetected and unchecked, also leads to reduction and loss of this vital ecosystem and the services it provides.
Water quality monitoring of mangrove waters is particularly problematic because natural conditions in mangrove lagoons often yield unexpected or confounding values for indices commonly used in coastal water quality monitoring. Traditional coastal water quality indices used extensively in Jamaica’s coastal waters include: nutrients, water clarity (light penetration), biochemical oxygen demand (BOD), bacterial content as well as the planktonic communities, especially the phytoplankton [13]. Mangrove lagoons have natural low light conditions, high turbidity, high detritus, and often low salinity associated with land runoff. The existing indices would therefore identify all mangrove lagoons as polluted, relative to the non-mangrove areas of the bay [14]. Also, there is the danger of not indicating eutrophic conditions in mangroves because they are “masked” or modified by the natural physiographic conditions. For example, while high phytoplankton biomass is a reliable index of eutrophication, mangals may have low phytoplankton biomass because of the inhibitory effects of the phenolic materials (tannins) in the water [15]. Several studies have attempted to identify appropriate water quality indicators for use in Jamaica’s mangrove lagoons [14, 16–18]. These have explored using planktonic communities instead of traditional water quality indices, or mangrove root communities as water quality indices for mangrove lagoons.

2.1. The methods used

The methods used to investigate planktonic communities as effective water quality indices in mangrove lagoons required sites with mangroves experiencing different levels of nutrients and in relatively close proximity. Sampling was done at six contrasting mangrove areas in the south-east coastal areas of Jamaica which ranged from eutrophic, disturbed lagoons in Kingston Harbour and Hunts Bay to pristine mangrove areas in Wreck Bay (Figure 1). All the lagoons, however, share the characteristics of low light penetration because of tannin coloured waters, fluctuating salinities, high turbidity, and high detritus with associated microbial activity. Sampling was usually conducted for 1 year or to represent the wet and dry seasons and parameters included physicochemical: depth (±0.08 m), temperature (±0.10°C), dissolved oxygen (DO) (±0.2 mg l⁻¹), Salinity (±0.2‰), pH (±0.2 units) and Reduction/Oxidation potential- REDOX (±20 mV), phytoplankton biomass (Chlorophyll a), zooplankton abundance and species composition as well as species composition and abundance of mangrove foot fouling communities. The suite of physicochemical variables was read in situ using Hydrolab® or YSI® Mulit-parameter data loggers. For phytoplankton biomass water samples were collected in replicate at all stations using a horizontal Niskin sampler (3.5 l). Samples were filtered through a fractionating tower of nitex screening 20 μm, Whatman GFD glass fibre filters 2.7 μm and Whatman GFF glass fibre filters 0.7 μm at approximately 15 mmHg pressure [19]. Chlorophyll a extraction was conducted at room temperature in the dark for 24 h using 6 ml of 90% acetone [20] and was read using a Turner Designs TD700 Version 1.8 laboratory fluorometer.

Zooplankton samples were collected using a range of standard plankton nets including 64, 100, 135 or 200 μm. Replicate (n = 2) oblique or vertical hauls (depending on station depth) were done at each station as close to the mangrove roots as was possible. Animals were always
preserved immediately in the field after collection using 10% formalin. Samples were enumerated and identified for all taxa present using binocular microscopes (mag. ×10–×40) and with the aid of zooplankton guides [21–26]. In most studies, in addition to species lists, community analysis tests were employed which used species composition to investigate station affinities and identify possible associations. These included Jaccard Community Coefficient (JCC), Percentage Similarity Coefficient (PSC), and Principal Components Analysis (PCA). Cluster analysis diagrams/dendrograms were used [18] for to display station linkages using the PSC and JCC values. Mangrove root fouling communities were examined in the range of lagoons using both natural and artificial substrates (settlement panels) placed in the same area as the mangrove roots. Species composition and biomass of these root fouling communities were analysed contemporaneously with other parameters.

2.2. Findings and significance

2.2.1. Physicochemical parameters

Plankton is sensitive to many environmental influences such as salinity, temperature, dissolved oxygen levels, turbidity, and other factors [2, 13, 15, 27]. It was expected that these
influences would be significantly different between mangrove lagoons due different levels of anthropogenic stress in each area. Hunts Bay (in Kingston Harbour) is a known eutrophic site while Wreck Bay is pristine [28, 29]. Consequently, the ideal water quality indices were expected to indicate a range of conditions (with Wreck Bay mangal as the pristine extreme and Hunts Bay mangal as the eutrophic extreme).

Most physicochemical parameters used in these mangrove water quality studies showed significant differences between stations, with the exception of particulate organic matter (POM). However, the distribution of these parameters between lagoons did not show the expected pattern. Furthermore, the lack of significant difference in POM values between stations was not expected since this parameter is often an important indicator in water quality analyses [30, 31]. POM is usually suspended matter of organic and inorganic origins. Usually the mixing of fresh water with sea water involves a marked change in pH and increases the level of dissolved salts, which promote the coagulation of fine particulate matter [30]. With the diverse sources and the shallow nature of mangrove lagoons, high POM may be a constant feature; irrespective of the eutrophication levels being experienced in the lagoons. Thus, POM may not be an adequate descriptor of the eutrophic status in mangrove lagoons.

When examining the physicochemical variables used across studies, depth at the station should be considered because of the influence of this variable on mixing and therefore on several physicochemical parameters (e.g. dissolved oxygen (DO), temperature, salinity). The studies showed that shallow and more exposed stations (e.g. Hunts Bay – HB) would consistently have extreme and episodic values for variables like temperature and salinity [18]. While other mangrove areas like the Great Salt Pond (GSP) which was also shallow did not have high temperatures because of the constant shading provided by mangrove trees. Temperature, therefore, is not an adequate descriptor of eutrophication status.

Dissolved oxygen (DO) behaved in a similar manner to temperature and was thus equally unreliable with only the high variability in DO values about the mean (episodic variability) at polluted stations being a consistent indicator. The eutrophic Hunts Bay (HB) had a high oxygen concentration (averaging >7 mg l\(^{-1}\)) but also with the greatest fluctuation about the mean. Poor water quality was expected at this station [13, 32, 33]; with constant blooms of sometimes toxic phytoplankton species. Ranston and Webber [32] further reported a rapid decline in DO from super-saturation at the surface to almost anoxic conditions at depth. Dissolved oxygen in natural waters varies with temperature, salinity, turbulence, the photosynthetic activity of algae and plants, and atmospheric pressure. The solubility of oxygen decreases as temperature and salinity increase. Significant variations in DO can occur over 24-h periods, in response to variation in temperature and biological activity (i.e. photosynthesis and respiration). Biological respiration, including that related to decomposition, reduces DO concentrations [34]. Increases in DO relate to phytoplankton concentrations as algal blooms in eutrophic waters can cause DO concentrations to raise dramatically. According to Gordina et al. [35], oxygen super-saturation is indicative of a degree of eutrophication and Borsuk et al. [36] suggested that oxygen depletion in estuarine bottom waters resulted from chemical and biological oxygen consumption associated with the decomposition of organic matter in the sediments and water column. This makes dissolved oxygen (DO) values in coastal systems
difficult to explain as both extremes in DO (very high or very low values) may be indicative of deteriorating water quality. Hence, the diurnal fluctuation in this parameter has been suggested to be a better index than the absolute value.

Reduction/Oxidation Potential (REDOX) characterizes the oxidation state of natural waters. Oxygen, iron, and sulphur, as well as some organic processes can affect REDOX. Anaerobic respiration and the resultant increase in hydrogen sulphide are usually associated with a sharp decrease in REDOX and is evidence of reducing conditions [34]. REDOX values ranged between 250 and 300 mV for the mangrove stations sampled across the studies and while the variation between stations was statistically significant the overall similarity of the relatively low REDOX values [18] suggested that high reducing conditions are a constant feature of all these mangrove lagoons. More pristine bays like Discovery Bay on Jamaica’s north coast have been reported to have REDOX values in excess of 500 mV [37]. Not all studies analysed nutrients across stations, however, where sampled Nitrates and Phosphates varied significantly between stations, however, where sampled Nitrates and Phosphates varied significantly between stations but with no consistent spatial pattern [14].

2.2.2. Biological variables

The biological variables that have been used to assess mangrove water quality in Jamaica include zooplankton species composition, frequency of occurrence, zooplankton community coefficients, total abundances and totals of numerically important sub-groups (e.g. Calanoids, harpactocoids, larvae), Chlorophyll $a$ (phytoplankton biomass) and number of zooplankton “indicator species” m$^{-3}$. In some studies sessile root fouling organisms (epibiota) were analysed for their value in indicating ecosystem health, however, these were deemed unreliable for water quality. According to Hoilett and Webber [14] epibiota on the roots of the red mangrove which hang into the lagoon or are found on artificial substrates show interesting trends but the natural physiographic conditions (substrate type, degree of exposure, presence of rivers etc.) associated with each lagoon must be taken into consideration before conclusions can be made relating eutrophication to epibiota distribution. They indicated, however, that there is some value in the use of sessile fauna of individual taxonomic groups and Todd and Webber [16] also found Phallusia nigra (a solitary black ascidian) to be a useful indicator of varying eutrophication in the Kingston Harbour mangroves being found in high concentrations at the more disturbed sites like Buccaneer Swamp. However, the absence of $P. \text{nigra}$ is not in itself an indicator of pristine conditions as the species does not occur in the eutrophic Hunts Bay.

Total phytoplankton biomass most consistently showed the expected eutrophication gradient [14, 18] across mangrove lagoons. According to Campbell et al. [18] Chlorophyll $a$ was the most reliable planktonic index distinguishing stations as oligotrophic (0.21–0.55 mg m$^{-3}$) mesotrophic (0.57–2.55 mg m$^{-3}$) eutrophic (3.00–6.55 mg m$^{-3}$) and extremely eutrophic (>31.17 mg m$^{-3}$). However phytoplankton size fractions (which are extensively used in coastal water qualities) may be unreliable as the effect of low light negates the effect of high nutrients that would make the larger fractions, ≥ 20 μ in diameter, dominate. Hence, eutrophic mangrove lagoons have been shown to have greater proportions of the picoplankton fraction (0.2–2 μ diameter) than expected [14, 18].
Principal Components Analysis (PCA) used by Campbell et al. [18] showed harpacticoids and the animal *Dioithona oculata* (a cyclopoid) were major components for all stations as well as the larval plankton. *Acartia tonsa* (a calanoid) was identified by Hoilett and Webber [14] as consistently occurring across mangrove areas and varying along an eutrophication gradient. Mean total numbers of zooplankton varied significantly between stations. Campbell et al. [18], for example, showed total values ranging between 789 animals m$^{-3}$ at pristine Wreck Bay (WB) to 114,970 animals m$^{-3}$ at eutrophic Hunts Bay (HB). HB also had maximum fluctuations about the mean. The group Larvae followed a similar pattern of distribution to the total numbers.

The zooplankton in mangrove lagoons has been consistently found to be dominated by copepods and larvae [14, 18]. However, harpacticoid copepods and individual species like *A. tonsa* and *D. oculata* show greatest potential as indicators of eutrophication in mangrove lagoons.

Taxonomic richness (number of species) varied significantly across mangrove areas for most studies but did not seem to follow the expected eutrophication trend. For example, Fort Rocky lagoon (FRL) in the Port Royal mangroves which would be considered mesotrophic, had highest taxonomic richness [14, 18]; while Wreck Bay, a pristine mangrove area had consistently low richness. High diversity or high richness in zooplankton communities is usually a reliable index of pristine conditions [37]. However, the similarities in taxonomic composition between studies and across different lagoons, seem to suggest that mangrove lagoons have a ‘basal group’ of commonly occurring zooplankton species, where individual species or sub-groups (like larvae and harpacticoids) may only be used as indicators if they vary in relative abundance according to the levels of eutrophication of each lagoon. The entire group Harpacticoida, though sometimes small in total numbers, occurred with great frequency throughout the sampling period at all mangrove lagoons.

Some zooplankton species may also be useful as indicators of the influence of mangrove waters on other systems. For example, *D. oculata* is known to form swarms in water <30 cm deep among the prop roots of red mangroves (*Rhizophora mangle*) [38] and these swarms persist and remain with the mangrove water [39]. Another important species in this regard could be *A. tonsa* which was reported by Dunbar and Webber [5] to be one of the ‘hardier’ euryhaline species which dominated the eutrophic Hunts Bay and so has the potential to be indicative of the eutrophic conditions associated with the mangrove lagoons. However, *A. tonsa* may be indicative of eutrophic bays in general and not necessarily eutrophic mangrove areas [40, 41].

Total zooplankton abundances in mangrove lagoons can be extremely high reaching $10^5$ individuals m$^{-3}$ [42]. This was comparable to values found in some mangrove lagoons in Jamaica. However the values did not follow the eutrophication gradient. Total abundance of zooplankton in the eutrophic Hunts Bay was found to be as high as 563,339 animals m$^{-3}$ [18]. However, Francis et al. [33] found values of 16,499 animals m$^{-3}$ in Hunts Bay and Hoilett and Webber [14] reported means in excess of 1,000,000 animals m$^{-3}$ found in the immediate area of the *R. mangle* roots at Wreck Bay. The latter being the most pristine mangrove site examined during the study. Hunts Bay receives nutrient rich water as well as high levels of pollution from several gullies [32] and areas of the mangroves have also been disturbed by “dredge and fill” activities occurring in the Bay. This disturbance of the sediments will also lead to
significant enrichment of the water column. The pristine mangrove areas of Wreck Bay (WB) by contrast have no consistent enrichment sources and the sediments are made of coarse calcareous material. Total zooplankton abundances therefore were not shown to be reliable as indicators of eutrophication in mangrove lagoons.

Mangroves are tightly bound to the coastal environments in which they occur [43, 44]. They are influenced by physical and chemical conditions and can, also help to create them. As a result, changes to the system can have cascading long-term effects. Monitoring of these changes must be efficiently and accurately done and elements of the phytoplankton and zooplankton communities are here shown to be reliable indices for such monitoring exercises. The use of planktonic indices (e.g. Chlorophyll a, zooplankton groups like harpacticoids and larvae as well as individual species) have here been shown to be more reliable indicators of mangrove lagoon water quality than many physicochemical variables and the sessile root community. Furthermore, species like *D. oculata* and *A. tonsa* can be used to indicators of penetration of mangrove waters to other parts of the coast.

### 3. Phytoplankton and coastal dynamics

#### 3.1. Phytoplankton biomass along the Hellshire coast

Coastal circulation, in tropical waters, has been attributed to astronomical tides, river discharge and meteorological forces of which wind is most important [45]. The strength and significance of each are dependent on a wide range of topographic, hydraulic and meteorological controls [46]. Gravitational circulation can also be a major contribution to the dynamics of an estuary at sub-tidal scales; however this is not usually evident in small, shallow, well mixed bays with weak freshwater inflows. This study seeks to use the phytoplankton biomass and distribution as a descriptor in the coastal dynamics of the Hellshire Coastline. The distribution and influence of Eutrophic Kingston Harbour waters has been of interest in Jamaica as the Hellshire Coastline has tremendous potential for tourism development. Understanding the sources of water to this area is critical to managing the resource.

The Hellshire coastline (Figure 2) is located to the southwest of Kingston Jamaica and covers approximately 27 km, of which the eastern portion (15 km). It has six major bays each with white sand beaches and coral reefs associated with the seaward edge of the bay [4]. To the north-east of the Hellshire coast is the Kingston Harbour which is highly eutrophic and believed to be a potential source of degradation to the Hellshire area.

Sherwin and Deeming [47] reported that flow from Kingston Harbour is initially to the south and then west towards the Hellshire coastline. Water is advected through this area along a path of least resistance and should experience oceanic dilution with increasing distance from the harbour. This knowledge, along with the observation of deterioration of coral reef and seagrass bed communities along the Hellshire Coastline, led to postulating that the influence
of eutrophication from the Kingston Harbour was the source of high nutrient waters which flowed along the Hellshire coastline.

The bays investigated along Hellshire were Half Moon Bay (HMB), Two Sister’s Bay (TS), Sandhills Bay (SH), Engine Head Bay (EH) and Wreck Bay (WB), which are in order of increasing distance from the Kingston Harbour as illustrated in Figure 3. The overall purpose is to
indicate whether the bays are primarily influenced by the Eutrophic Kingston Harbour via or indicate whether there are other sources and conditions that influence in the phytoplankton distribution and hence water quality along the coastline.

3.1.1. The methods used

Thirteen stations were investigated over the study period November 1999 to January 2001. Station positions were selected based on the location of the shoreline irregularities in order to investigate the longshore current and so trace water masses throughout the area. Six stations were located outside of the reef system, approximately 2 km from the shoreline (within the continental shelf), which were termed ‘nearshore stations’. A second set of seven stations were located within the embayments, between the shoreline and the reef system, which were termed ‘inshore stations’ (Figure 3). Nutrient loads exiting the Kingston Harbour are restricted to the upper 7 m of the water column [4, 7, 48–50] hence samples were collected in surface layers only. These stations were included to allow for a more accurate assessment of the phytoplankton biomass distribution between bays and the potential retention time of each bay.

Sampling occasions were selected based on the tidal phase, i.e. rising tide and falling tide. This was thought to represent extremes of circulation within the region as high tide would account for a fast turn over time or retention time and low tide accounting for longer retention time. Tidal cycle data were obtained from the Port Royal Tide Gauge and the Port Royal Jamaica Tide Charts.

At each station, surface water samples were collected within the first meter of the water column for all inshore and nearshore stations and the phytoplankton biomass determined as Chlorophyll a using fluorometry, as previously described in this chapter.

3.1.2. Findings and significance

It was expected that with improved water quality or increased distance from the eutrophic influence of the Kingston Harbour, phytoplankton total biomass would gradually decrease [42]. It was also expected that with increased distance from the Kingston Harbour, a decrease in netplankton biomass and an associated increase in picoplankton would also be observed. This would be a result of netplankton being able to proliferate in nutrient rich area, whereas picoplankton would dominate in nutrient poor area due to their surface area to body ratio. It was also expected that total biomass should decline with distance from nutrient source. This trend would also be expected as stations change from inshore/bay towards the nearshore and offshore areas.

Analysis of 112 whole water samples revealed that, as expected, mean phytoplankton biomass showed a gradual decrease with increased distance from the eutrophic source (Kingston Harbour) and at nearshore stations (Figure 4). This supports the theory of dilution of Harbour waters by oceanic with increased distance from the harbour. The biomass at inshore stations, however, fluctuated with distance from Kingston Harbour, with a few stations found further along the coastline having a higher biomass than stations found closer to the harbour (Figure 5). This suggests that stations such as Engine Head Bay and Wreck Bay are atypical of expected trends even when weak trends exist.
To properly analyse the variations in phytoplankton biomass collections had to be separated based on tidal cycle as it was found that the phytoplankton biomass during a rising tide varied significantly from those collected during a falling tide (ANOVA $p < 0.001$; Figure 3. Hellshire Coast showing nearshore (2 km from shore) and inshore (within the bay) phytoplankton sampling stations.

Figure 3. Hellshire Coast showing nearshore (2 km from shore) and inshore (within the bay) phytoplankton sampling stations.
Average total biomass for nearshore surface stations collected during a rising tide showed the expected decrease along the coastline with increased distance from the Harbour (Figure 6).

In the case of the inshore stations the three stations closer to the Harbour showed a general decrease in biomass from the Great Salt Pond station to the Two Sister’s Bay station followed by an increase from the Sandhills Bay to Wreck Bay stations (Figure 7). When nearshore stations were compared to the inshore stations it was found that moving from the Kingston Harbour towards Sandhills Bay the nearshore stations were generally higher than that of the

Figure 4. Mean total phytoplankton biomass (μg l⁻¹) for all samples for nearshore surface stations along the Hellshire Coastline, St. Catherine.

Figure 5. Mean total phytoplankton biomass (μg l⁻¹) for all samples for inshore stations along the Hellshire Coastline, St. Catherine.
A gradual decrease in total biomass with increased distance from the Kingston Harbour was observed, although this pattern was not consistent. In some instances it was found that stations further away from the harbour on occasion had a higher biomass than that of the stations found closer to the harbour. Data indicate that the Two Sister’s nearshore station with the exception of Engine Head Bay and Wreck Bay where the biomass were slightly higher in the inshore areas. This pattern was even more evident when sampling occasions were analysed independent of each other. The variation in phytoplankton total biomass was found to be significantly different between inshore and nearshore stations by way of ANOVA (p < 0.001; df = 74).

Figure 6. Total phytoplankton biomass (µg l⁻¹) for nearshore surface stations during rising tide events along the Hellshire Coastline, St. Catherine.

Figure 7. Total phytoplankton biomass (µg l⁻¹) for inshore station during rising tide events along the Hellshire Coastline, St. Catherine.
station had a higher biomass than that of the Half Moon Bay Station which is closer to the Kingston Harbour, followed by the Wreck Bay, which is located the furthest away from the harbour.

Further Analysis of variance tests showed the falling tide event to be significantly different from the data collected during the rising tide events. The general pattern in phytoplankton distribution was completely different from that of trends observed on the rising tide occasions. The nearshore stations showed no significant difference between the total biomass of the surface stations (Figure 8). Total biomass for these stations seemed to be constant in moving from Half Moon Bay to Sandhills with a reduction in biomass found at the Engine Bay Station, followed by an increase at Wreck Bay which was greater than Half Moon Bay, Two Sisters Bay and Sandhills but less than Hellshire Bay.

At the inshore stations (Figure 9), values demonstrated an initially decrease in total biomass moving southwest along the coastline towards Sandhills followed by an exponential increase for the rest of the coastline. Wreck Bay had the highest biomass of all the stations. Statistically, inshore stations were significantly different from the nearshore stations (p < 0.001).

Interestingly Figures 6–9 illustrated that during both rising tide and falling tide occasions, the biomass observed at Wreck Bay was not the lowest along the Hellshire Coastline as would be expected. In fact, during the falling tide event the biomass at Wreck Bay was the highest biomass collected on that occasion.

When percentage biomass was plotted for each station based on biomass it was seen that this trend was observed at some stations but not all. During the rising tide events it was seen that in some instances netplankton biomass decreased for some locations when inshore biomass were compared with nearshore biomass (Figures 6 and 7). This was evident for the stations associated with Two Sisters Bay, Sandhills Bay, Engine Head Bay and Wreck Bay when

![Figure 8](Image). Total biomass (μg l⁻¹) for nearshore surface station during falling tide events along the Hellshire Coastline, St. Catherine.
inshore stations were compared with nearshore stations, with a corresponding increase in picoplankton. Similar trend was observed for the percentage of netplankton during a falling tide where increases were observed when inshore stations were compared with nearshore. However, this was not observed for the picoplankton size class and there was no consistent pattern as percentage composition fluctuated along the coastline.

Phytoplankton distribution fluctuates along the Hellshire coastline with bay stations differing significantly from nearshore stations. In some instances it has been seen that regardless of tidal regime phytoplankton biomass at some down-coast stations was greater than up-coast (close to Kingston Harbour) stations with variables being observed especially at Wreck Bay, which is the furthest bay from the Kingston Harbour. This observed variability may be accounted for based on localized activity and retention due to circulation patterns in the inshore waters of some bays, especially Wreck Bay. Phytoplankton biomass was therefore successfully used to identify the existence of non-point sources of enrichment along Hellshire and proved to be a useful tool in coastal assessment that could inform management practices in an area. Therefore, in the absence of difficult to track Lagrangian devices or expensive Eulerian current meters, the phytoplankton have been used to indicate the influence of eutrophic waters on down-current well mixed bays on the south coast of Jamaica.

4. Primary productivity

4.1. Phytoplankton production along the Hellshire Coast South-east Jamaica

There has been a paucity of plankton productivity studies in Jamaican waters for both phytoplankton and zooplankton and direct production assessment of phytoplankton have only been conducted along the Hellshire area, south coast of Jamaica.
Phytoplankton are important components of any marine ecosystem as they are responsible for significant portions of the primary production in that environment. Three principal properties; species composition, biomass and production, have been commonly used in the assessment of the phytoplankton community [51]. Tropical oceanic waters are typically high diversity, low biomass and low production environments while Caribbean coastal and inshore waters are characterized by lower diversity (few species dominating and proliferating) resulting in relatively higher biomass and productivity values [52]. This high biomass and production in nearshore waters is often induced by sudden enrichment from land run off from point and non-point sources [53]. These considerations are important in understanding the ecosystem whether this understanding is needed for water quality analysis, conservation, development, ecosystem energetics or fisheries management. The Hellshire coast of the southeastern Jamaica (Figure 2) with a eutrophic Kingston Harbour to the north [13] and an oligotrophic Caribbean Sea to the south provided an ideal setting to evaluate the expected gradient of impact from a point source of land based run off on the primary production of a multiple use coastal area.

4.1.1. The methods used

Six litre samples of water were taken from a standard depth equivalent to 20–40% of surface illumination at three inshore stations (Hellshire Bay, Half Moon Bay, and Wreck Bay) three offshore stations equidistant from the Kingston Harbour and a control far removed from both Harbour and Hellshire influences [50]. These stations were selected on the basis of their estimated productivity since they all enjoy no light limitation. The samples were kept in a cool dark place while being transported to the laboratory where 250 mL portions from each of the seven stations were preserved for identification and enumeration, one litre replicates were filtered for chlorophyll a biomass determination and triplicate 300 ml portions were placed into BOD bottles. Four milliliter aliquots were removed from each filled BOD bottle to allow for the addition of the radioactive material. One milliliter of Sodium Bicarbonate solution containing 20 micro curies of radioactive carbon \(^{14}\)C was added to each BOD bottle using a 5 ml hypodermic syringe [54]. One milliliter of 3(3,4-dichlorophenyl1)-1,1-dimethylurea (DCMU), a photosynthesis inhibitor was added to one of each triplicate [19, 55]. The sealed bottles were incubated for 4 h in the sea at various depths which simulated 20–40% of surface illumination at their original stations [56]. This was done to ensure that the algal cells remained at light intensities similar to their natural habitat.

Determination of Primary production by \(^{14}\)C technique was carried out as described by Steemann Nielsen [57], modified for scintillation counting by Wolfe and Schelske [58], and as reported by Parsons et al. [54]. The scintillation count was carried out on a Beckman liquid scintillation system counter (model no LS 100). Size fractionating was conducted by filtering 250 mL of the incubated sample through nucleoprep filters of three pore sizes (20, 2 and 0.2 μm). Components less than 0.2 μm in size were treated by the acid bubbling method before the addition of the scintillation fluid [59, 60].
4.1.2. Findings and significance

The mean primary production for the sampling period was greatest at the Kingston Harbour (21.1 g C m\(^{-2}\) year\(^{-1}\)) and lowest at the oligotrophic control site (0.52 g C m\(^{-2}\) year\(^{-1}\)) confirming the expected difference eutrophic and oligotrophic primary production. Although these values are not high when compared globally [61] the comparisons between the values recorded at different areas of the Hellshire coast are important.

Primary production values and size distribution at offshore stations (2.63–0.88 g C m\(^{-2}\) year\(^{-1}\)) were lower with increasing distance from the Harbour and indicated an exponential decline in production with distance from the Harbour point source. This is expected based on the volume, consistency and significance of the point source as reported in similar studies [61]. Values at inshore stations (36.75–18.39 g C m\(^{-2}\) year\(^{-1}\)) were more than 10 times greater than offshore stations at the same distance from the Harbour, with primary production values at one station (Hellshire Bay) exceeding that at the eutrophic Kingston Harbour and other turbid and enriched estuaries [62, 63]. Inshore waters are therefore much more productive than offshore waters and on occasion demonstrated higher productivity than eutrophic waters without significant point source inputs.

At all seven stations the nanoplankton fraction (2–20 μ diameter cells) dominated production, especially at the Harbour and inshore stations. Production in the picoplankton (0.2–2 μ diameter cells) and netplankton fractions (greater than 20 μ diameter cells) together contributed 40–50% of the primary production indicating some, but not great diversity in the composition responsible for the primary production throughout the area.

Mean assimilation numbers, which are an indication of the efficiency of the biomass in primary production, were found to be similar at the offshore stations and the control station (17–19 g C g Chl\(^{-1}\) h\(^{-1}\)). At all offshore stations picoplankton and nanoplankton assimilation were marginally higher than netplankton assimilation which indicates a homogenous system with no differential efficiency with marginal dominance in efficiency by the nanoplankton at the control station. Assimilation numbers at the inshore stations (45–70 g C g Chl\(^{-1}\) h\(^{-1}\)) were significantly greater (2–3 times greater) than those recorded at offshore stations and surprisingly even higher than the Harbour and three time greater than assimilation values reported by Glover in cultures in 1980. Phytoplankton at inshore stations influenced by non-point sources of enrichment are therefore significantly more efficient at primary production than the phytoplankton influenced by the enrichment from the known point source at the Harbour.

Within the inshore stations the picoplankton fraction (0.2–2.0 μm diameters cells) dominated the assimilation with highest values, not at stations close to the Harbour. This size fraction dominates where nutrient enrichment is low but consistent either from the non-point sources or by retention and regeneration mechanisms to facilitate proliferation [64, 65]. These results indicate that the non-point sources and the mechanisms operating at the inshore stations bays are significant sources of primary production to the Hellshire coast, a feature which is not uncommon where ground water percolates into the coastal waters [66].
4.1.3. An extreme rainfall event

Primary production values associated with the extreme rainfall event were variable at the offshore stations but only significantly higher at the offshore station furthest from the Harbour. Production at the Harbour declined from 21.1 to 8.76 g C m\(^{-2}\) year\(^{-1}\) while values increased dramatically, ten times higher than values over the normal period, to 11.39 g C m\(^{-2}\) year\(^{-1}\) at the station furthest from the Harbour. The reduced primary production at the Harbour even in the presence of increased point source enrichment may be the result of reduced light climate and reduced salinity [67] as silt laden fresh waters engulfed the entire coast. The increased production at great distance from the point source demonstrates the influence of the point source in flushing and providing significant enrichment but with reduced siltation to an offshore body of water resulting in algal proliferation. The occurrence of the extreme rainfall event resulted in marked changes in the size fractionated primary production pattern at offshore stations. The nanoplankton fraction which normally represented 50–60% of the production year round was as high as 90% after the rainfall event. The effect of this event on the phytoplankton production along the Hellshire coast was the result of exploitation of the changed condition by one genus Protoperidinium sp. which dominated the samples observed confirming the work of Zeeman [68], Webber et al. [49] and Adolf et al. [69].

The point source of the Kingston Harbour is an important contributor to the primary production of the Hellshire coast and under extreme rainfall events becomes the overwhelming feature determining the quantity, efficiency and location of primary production. The non-point sources along the Hellshire coast are also important but become significant localized impacts limited to inshore waters with significance determined by persistence of non-point release and nearshore mechanisms which facilitate retention and regeneration of especially picoplankton cells.

5. Modelling trophic flows through the plankton using Ecopath

While several studies have been done on these individual ecosystems, few, if any, have attempted to link or compare the areas, in terms of energy flow (as is possible using Ecopath). Ecopath was first developed to estimate the standing stock and production budget of a coral reef ecosystem in the Hawaiian Islands [70, 71]. It was further modified for use in any kind of aquatic ecosystem [72] and requires the input of at least four basic parameters as well as the diet composition for each consumer group. These parameters included: biomass; production/biomass ratio; consumption/biomass ratio and ecotrophic efficiency. Once these inputs of the basic parameters and diet compositions are completed, a mass-balanced trophic model of the ecosystem was produced by balancing the model, that is, modifying the entries until input = output for each consumer group.

One of the most important applications of this software is its ability to apply a selection of Odum’s twenty four attributes of ecosystem maturity [73] to the mass-balanced model [72, 74] in order to facilitate a description of the stage of an ecosystem’s stage of development. This
can be a very important tool to be used for effective management of the fisheries in these areas. The economies of a large number of countries are dependent on, or partially dependent on, the fisheries of these countries. If any attempts are to be made to effectively manage these fisheries, the systems which support these fisheries must be understood.

5.1. The methods used

A fairly novel use was made of the software when Ecopath 5.1 and Ecopath with Ecosim (EwE) were used to model the trophic flows within the plankton communities in Discovery Bay, on Jamaica’s north coast [75] and Foul and Folly Bays located in the Morant Wetlands on the extreme eastern end of the island [76], respectively. Ecopath with Ecosim is usually used to model trophic flows through fish and other macrofauna, with the plankton being used as an input or source of food.

Discovery Bay was considered to be a fairly pristine bay, with mean zooplankton abundances between $1077 \pm 91$ and $3794 \pm 87$ animals m$^{-3}$ and phytoplankton biomass between 0.4 and 0.8 mg m$^{-3}$. Foul and Folly Bays were found to be even more pristine with mean total zooplankton abundances ranging from $282 \pm 56$ to $3459 \pm 752$ animals m$^{-3}$ and phytoplankton biomass between $0.14 \pm 0.04$ and $0.34 \pm 0.2$ mg m$^{-3}$ [76].

5.2. Findings and significance

The Ecopath model for Discovery Bay indicated that “it was clear that this was still a developing ecosystem with open mineral cycles and poor nutrient conservation” [75]. Furthermore, the bay “would not be particularly resistant to perturbations. It would therefore be unable to easily recover from significant stresses (eutrophication; increased fishing efforts etc.) imposed on the ecosystem” [75]. This was thought to be indicative of the need for management strategies to control the use of the bay.

On the other hand, the Ecopath model of Foul and Folly Bays (Morant wetlands) indicated greater resilience in these bays than in Discovery Bay. They would therefore be better able to recover from stresses such as eutrophication [76]. The assessment of the plankton further identified the presence of high abundance of larvae, which when coupled with fast flowing currents through the bays, provides evidence that this area could be an “important source of larvae to other areas of Jamaica’s south coast” [76]. Therefore, a strong recommendation for the area’s protection could be made.

6. Overall conclusion

The new and unique uses of plankton ecology and productivity around Jamaica has been wide and varied with some interesting examples are demonstrated in this chapter. The specialized zooplankton communities which allow water quality characterization in mangrove lagoons, the description of coastal dynamics and the identification of point and non-point
sources which result in spatial variation in primary production and the modelling of coastal trophodynamic flows to influence conservation and fisheries management are all unique and important. Through plankton ecology and production Jamaica’s coastal ecosystem has benefited significantly from the improved understanding, meticulous monitoring, enhanced descriptions and innovative applications. This has facilitated informed management decisions for the sustained use of coastal ecosystems around Jamaica which can be extrapolated to other small islands and archipelagic states.

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References

[1] Webber DF, Wilson-Kelly P. Characterization of sources of organic pollution to Kingston Harbour, the extent of their influence and some rehabilitation recommendations. Bulletin of Marine Science. 2003;73:257-271

[2] Grahame J. Zooplankton of a tropical harbour: The numbers, composition, and response to physical factors of zooplankton in Kingston Harbour, Jamaica. Journal of Experimental Marine Biology and Ecology. 1976;25:219-237

[3] Moore E, Sander F. Nutrient-phytoplankton-zooplankton relationships at a highly eutrophic tropical station. Caribbean Journal of Science. 1982;18:95-102

[4] Lindo MK. The effect of Kingston Harbour outflow on the zooplankton populations of Hellshire, South-East Coast, Jamaica. Estuarine, Coastal and Shelf Science. 1991;32:597-608

[5] Dunbar FN, Webber MK. Zooplankton distribution in a tropical embayment, Kingston Harbour, Jamaica. Bulletin of Marine Sciences. 2003;73:343-360

[6] Webber MK, Ranston ER, Webber DF, Dunbar FN, Simmonds RA. Changes in water quality and plankton in Kingston Harbour after 20 years of continued eutrophication. Bulletin of Marine Sciences. 2003;73:361-378

[7] Webber MK, Roff JC, Chisholm LA, Clarke C. Zooplankton distribution and community structure on the southern shelf of Jamaica. Bulletin of Marine Science. 1996;59:259-270

[8] Moore E, Sander F. A comparative study of zooplankton from oceanic, shelf and harbor waters of Jamaica. Biotropica. 1979;11:196-206
[9] Lue K, Webber MK. A new comparative study of zooplankton from oceanic, shelf and harbour waters, South East-Coast, Jamaica. Zoological Studies. 2014;53:18. DOI: 10.1186/s40555-014-0018-2

[10] Webber MK, Calumpong H, Ferreira B, Granek E, Green S, Ruwa R, Soares M. Mangroves. Chapter 48. In: World Ocean Assessment – I. United Nation Publication – Cambridge University Press; 2016. 18 pp. Available form: http://www.un.org/depts/los/global_reporting/WOA_RPROC/Chapter_48.pdf

[11] FAO. The World’s Mangroves 1980-2005. FAO Forestry Paper No. 153. Rome: Forest Resources Division, FAO; 2007. p. 77

[12] NRCA. Development Trends in Jamaica’s Coastal Areas and the Implications for Climate Change. 1987. Available from: http://www.pioj.gov.jm/Portals/0/Sustainable_Development/Climate%20Change%20and%20Jamaica.pdf

[13] Webber DF, Webber MK. The water quality of Kingston Harbour: Evaluating the use of the planktonic community and traditional water quality indices. Chemistry and Ecology. 1998;14:357-374

[14] Hoilett K, Webber MK. Can mangrove root communities indicate variations in water quality? Jamaica Journal of Scientists and Technologists. 2001/2002;12/13:16-34

[15] Herrera-Silvera JA, Ramirez-Ramirez J. Effects of natural phenolic material (tannins) on phytoplankton growth. Limnology and Oceanography. 1996;41:1018-1023

[16] Todd S, Webber MK. The spatial distribution of Phallusia nigra, Savigny, 1816 (Tunicata: Asciidiacea) in the Port Royal and Buccaneer Swamp Mangroves, Kingston Harbour, Jamaica. Jamaica Journal of Science and Technology. 2007;18:2-18

[17] Elliott T, Persad G, Webber MK. Variation in the colonization of artificial substrates by mangrove root fouling species of the Port Royal mangrove lagoons in the eutrophic Kingston Harbour, Jamaica. Journal of Water Resource and Protection. 2012;4:377-387. DOI: 10.4236/jwarp.2012.46043. Published Online June 2012. Available form: http://www.SciRP.org/journal/jwarp

[18] Campbell P, Manning J, Webber MK, Webber DF. Planktonic communities as indicators of water quality in Jamaican mangrove lagoons: A case study. Transitional Waters Bulletin. 2008;3:39-63

[19] Li W, Dickie K. Growth of bacteria in sea water filtered through 0.2 μm Nucleopore membranes: Implications for dilution experiments. Marine Ecology Progress Series. 1985;26:245-252

[20] Lorenzen CJ, Jeffery SW. Determination of chlorophyll in seawater. Report of inter-calibration tests, sponsored by SCOR and carried out in Sep–Oct 1978. UNESCO Technical Papers in Marine Science. 1978;35:86

[21] Todd CD, Laverack MS, Boxshall GA. Coastal Marine Zooplankton. A Practical Manual for Students. Cambridge University Press; 1996. 106 pp
[22] Gonzales JG, Bowman TE. Planktonic copepods from Bahia Fosforescente, Puerto Rico, and adjacent waters. In: Proceedings of U.S. National Museum. Vol. 17. Smithsonian Institution; 1965. pp. 241-304

[23] Yeatman HC. Marine littoral copepods from Jamaica. Crustaceana. 1996;30:201-219

[24] Newell GE, Newell RC. Marine Plankton: A Practical Guide. Huthinson and Co Ltd; 1969; 244 p

[25] Owre HB, Foyo M. (1967) Copepods of the Florida current. Fauna Caribaea No. 1. Crustacea, Part 1: Copepoda. Institute of Marine Science, University of Miami. 1967; 137 pp

[26] Gerber RP. An Identification Manual to the Coastal and Estuarine Zooplankton of the Gulf of Maine Region from Passamaquoddy Bay to Long Island Sound. Freeport Village Press; 2000; part 1, 80 p; and part 2, 98 p

[27] Satsmadjis J. Comparison of indicators of pollution in the Mediterranean. Marine Pollution Bulletin. 1985;16:395-400

[28] McDonald-Senior KO. Differences in the Structure of Jamaican Mangrove Forests. [MPhil thesis] University of the West Indies. 2000. 256 p

[29] McDonald K, Webber DF, Webber MK. Mangrove forest structure under varying environmental conditions. Bulletin of Marine Sciences. 2003;73:491-506

[30] Phillips J. Chemical processes in estuaries. In: Barnes RSK, Green J, editors. The Estuarine Environment. London: Applied Science Publishers; 1972. pp. 33-50

[31] Thomas R, Mevbeck M. The use of particulate material. In: Chapman D, editor. Water Quality Assessments: A Guide to the Use of Biota, Sediments and Water in Environmental Monitoring, 2nd ed. 1996. pp. 127-129

[32] Ranston ER, Webber DF. Phytoplankton distribution in a highly eutrophic estuarine bay, Hunts Bay, Kingston Harbour, Jamaica. Bulletin of Marine Science. 2003;73:307-324

[33] Francis P, Webber M, Maxam S. Rapid reassessment of zooplankton communities for the resource management of Kingston Harbour, Jamaica. Revista de Biologia Tropical. 2014;62:231-239

[34] Chapman D, Kimstach V. Selection of water quality variables. In: Chapman D, editor. Water Quality Assessments: A Guide to the Use of Biota, Sediments and Water in Environmental Monitoring. 2nd ed. 1996. pp. 59-126

[35] Gordina AD, Pavlova EV, Ovsyany EI, Wilson JG, Kemp RB, Romanov AS. Long-term changes in Sevastopol bay (the Black sea) with particular reference to the ichthyoplankton and zooplankton. Estuarine, Coastal and Shelf Science. 2001;52:1-13

[36] Borsuk ME, Stow CA, Lueltich Jr RA, Paerl HW, Pinckney JL. Modelling oxygen dynamics in an intermittently stratified estuary: Estimation of process rates using field data. Estuarine, Coastal and Shelf Science. 2001;52:33-49
Webber MK, Edwards-Myers E, Campbell C, Webber DF. Phytoplankton and zooplankton as indicators of water quality in Discovery Bay, Jamaica. Hydrobiologia. 2005;545:177-193

Ambler JW, Ferrari FD, Fornshell JA. Population structure and swarm formation of the cyclopoid copepod *Dioithona oculata* near mangrove cays. Journal of Plankton Research. 1991;13:1257-1272

Ambler JW. Zooplankton swarms: Characteristics, proximal cues and proposed advantages. Hydrobiologia. 2002;480:155-164

Bianchi F, Acri F, Aubry FB, Berton A, Boldrin A, Camatti E, Cassin D, Comaschi A. Can plankton communities be considered as bio-indicators of water quality in the Lagoon of Venice? Marine Pollution Bulletin. 2003;46:964-971

Tester PA, Turner JT. Why is *Acartia tonsa* restricted to estuarine habitats? In: Proceedings of the 4th International Conference on Copepod. Bulletin of Planktonic Society of Japan. (Spec. Vol.). 1991. pp. 603-611

Small H, Lue K, Webber DF, Webber MK. The planktonic communities of the Jamaican South-East Coast: A comparison of harbor, shelf and oceanic areas. Revista Biologica Tropical. 2014;62(Suppl. 3):259-272

Kathiresan K, Bingham B. Biology of mangroves and mangrove ecosystems. Advances in marine biology. 2001;40:81-251

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. The value of estuarine and coastal ecosystem services. Ecological Monographs. 2011;81:169-193

Kitheka JU. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. Estuarine, Coastal and Shelf Science. 1997;45:177-187

Gaard E, Hansen B, Heinesen SP. Phytoplankton variability on the Faroe Shelf. ICES Journal of Marine Science. 1998;55:688-696

Sherwin J, Deeming KR. Water Circulation and its Relation to Pollution in Kingston Harbour, Jamaica. Project Report U 80-1. Menai Bridge, Angsley: UCES Marine Sciences Laboratories; 1980. 97 p

Morrison B, Greenaway AM. Nutrient dynamics. In: Goodbody I, editor. Caribbean Coastal Management Study: The Hellshire Coast, St. Catherine, Jamaica. Mona: University of the West Indies; 1989. pp. 19-31

Webber DF, Webber MK, Roff JC. The effects of flood waters on the planktonic community of the Hellshire coast, Southeast Jamaica. Biotropica. 1992;24:362-374

Webber DF, Roff JC. The influence of Kingston Harbor on the Phytoplankton community of the Hellshire coast, Southeast Jamaica. Bulletin of Marine Science. 1996;59:245-258
[51] Mukai T, Takimoto K. Effects of environmental gradients concerning water qualities on the structure of the phytoplankton community in the coastal sea. Estuarine, Coastal and Shelf Science. 1985;20:169-181

[52] Sander F, Steven DM. Organic productivity of inshore and offshore waters of Barbados: A study of the island mass effect. Bulletin of Marine Sciences. 1973;23:771-792

[53] Azevedo I, Duarte P, Bordalo A. Pelagic metabolism of the Douro estuary (Portugal) – Factors controlling primary production. Estuarine Coastal and Shelf Science. 2006;69:133, 2006-146. DOI: 10.1016/j.ecss.2006.04.002

[54] Parsons TR, Maita T, Lalli CM. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press; 1984. p. 173

[55] Legendre LS, Demers CM, Yentsch CM. The $^{14}$C method: Patterns of dark CO$_2$ fixation and DCMU correction to replace the dark bottle. Limnology and Oceanography. 1983;28:996-1003

[56] Harrison WG, Platt T, Lewis MR. The utility of light saturation models for estimating marine primary productivity in the field – A comparsion with conventional simulated in-situ methods. Canadian Journal of Fisheries and Aquatic Sciences. 1985;42:864-872. DOI: 10.1139/f85-110

[57] Steemann Nielsen E. The use of radioactive carbon (C$^{14}$) for measuring organic production in the sea. Journal du Conseil – Conseil International pour l’Exploration de la Mer. 1952;18:117-140

[58] Wolfe DA, Schelske CL. Liquid scintillation and Geiger counting efficiencies for carbon $^{14}$C incorporated marine phytoplankton in productivity measurements. Journal du Conseil/Conseil Permanent International pour l’Exploration de la Mer. 1967;31:31-37

[59] Schindler DM, Scgmit RV, Reid RA. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the $^{14}$C method. Fisheries Research Board Canada. 1972;29:1627-1631

[60] Sondergaard M. On the radiocarbon method: Filtration or the acidification and bubbling method? Journal of Plankton Research. 1985;7:391-397

[61] Cloern JE, Foster SQ, Kleckner AE. Phytoplankton primary production in the world’s estuarine – Coastal ecosystems. Biogeosciences. 2014;11:2477, 2501

[62] Kocum EG, Underwood J, Nedwell DB. Simultaneous measurement of phytoplanktonic primary production, nutrient and light availability along a turbid, eutrophic UK east coast estuary (the Colne Estuary). Marine Ecology Progress Series. 2002;231:1-12

[63] Ara K, Yamaki K, Wada K, Fukuyama S, Okutsu T, Nagasaka S, Shiomoto A, Hiromi J. Temporal variability in physicochemical properties, phytoplankton standing crop and primary production for 7 years (2002-2008) in the neritic area of Sagami Bay, Japan. Journal of Oceanography. 2011;67:87-111. DOI: 10.1007/s10872-011-0010-y
[64] Glover HE, Smith AE, Shapiro L. Diurnal variations in photosynthetic ratios: Comparison of ultraphytoplankton with a larger phytoplankton size fraction. Journal of Plankton Research. 1985;7:519-535

[65] Moran S, Silke J, Salas R, Chamberlain T, Lyons J, Shannon S. Review of Phytoplankton Monitoring. Marine Institute; 2006

[66] Álvarez-Góngora C, Herrera-Silveira JA. Variations of phytoplankton community structure related to water quality trends in a tropical Karstic coastal zone. Marine Pollution Bulletin. 2006;52:48-60

[67] Burford M, Webster A, Revill IT, Kenyon AT, Whittle RA, Curwen G. Controls on phytoplankton productivity in a wet-dry tropical estuary. Estuarine, Coastal and Shelf Science. 2012;113:141-151. DOI: 10.1016/j.ecss.2012.07.017

[68] Zeeman SI. The effects of tropical storm Dennis on coastal phytoplankton. Estuarine, Coastal and Shelf Science. 1985;20:403-418

[69] Adolf JE, Yeager CL, Miller WD, Mallonee ME, Harding LW Jr. Environmental forcing of phytoplankton floral composition, biomass, and primary productivity in Chesapeake Bay, USA. Estuarine Coastal and Shelf Science. 2005;67:108-122. DOI: 10.1016/j.ecss.2005.11.030, 2006

[70] Polovina JJ. An overview of the ECOPATH model. Fishbyte. 1984;2:5-7

[71] Polovina JJ, Ow MD. ECOPATH: A user’s manual and program listings. Southwest Fisheries Center Administrative Report. 1983;H82-23:46

[72] Christensen V, Pauly D. ECOPATH II – A software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modeling. 1992;61:169-185

[73] Odum EP. The strategy of ecosystem development. Science. 1969;164:262-270

[74] Christensen V, Pauly D. Changes in models of aquatic ecosystems approaching carrying capacity. Ecological Applications. 1998;8:S104-S109

[75] Persad G, Webber MK. The use of Ecopath software to model trophic interactions within the zooplankton community of Discovery Bay, Jamaica. The Open Marine Biology Journal. 2009;3:95-104

[76] Webber MK, Persad G, Harris N, Wilmot I, Webber DF. An ecological assessment of Foul and Folly Bays, Morant wetlands area, Jamaica, using Ecopath with Ecosim. Ocean and Coastal Management. 2015;105:127-137
