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Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Structure and nutrient transfer in a tropical pelagic upwelling food web: From isoscapes to the whole ecosystem

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ABSTRACT

Little is known about ecosystem structure and nutrient flux in the pelagic zone of seasonal upwelling systems in the tropics, despite their global importance to marine production. The Tropical Eastern Pacific (TEP) is responsible for around 10% of global ocean productivity, largely due to wind-driven seasonal upwelling areas between Mexico and Panama. The Gulf of Panama has a detectable outflow for hundreds of kilometres into the Pacific Ocean and the upwelling system there is an important productivity source in the TEP. In this study, we aim to determine the spatio-temporal patterns in variability of carbon and nitrogen stable isotope composition throughout the pelagic ecosystem of the Bay of Panama in upwelling and non-upwelling conditions, and how these patterns are recorded throughout the ecosystem from primary producers to apex predators. We characterise the stable isotope composition of basal production in the ecosystem to quantify spatial variability during the non-upwelling season. We use the $\delta^{15}\text{N}$ composition outside of upwelling season as an ecosystem baseline and quantify the overall $\delta^{15}\text{N}$ separation between all trophic levels (TL) from primary producers to apex predators (e.g. yellowfin tuna and mahi mahi) within the pelagic ecosystem ($2.9 \pm 0.1\%$ per TL). The ecosystem has a relatively simple, linear structure with size-based TL increase. We calculate the predator-prey mass ratio of this ecosystem (c. 113:1 for fishes, 376:1 for the whole ecosystem, uncertainty range: 77:1–1272:1). These values are low for existing estimates in other marine ecosystems, although within the expected range for animals of the mass sampled. The calculated predator-prey mass ratios and maximum TL indicate that this pelagic ecosystem may have a relatively long trophic chain, with inefficient nutrient transfer from low to high TLs.

Using a monthly time series of stable isotope values of resident, planktivorous fishes and co-occurring sea surface temperature measurements, we determine nutrient transfer time between primary production and TL3 fish. We calculate a rapid nutrient turnover time within this ecosystem as 0.5–1 month per TL. The incorporation of upwelled nutrients, which are enriched in the ^{13}C , leads to higher consumer $\delta^{13}\text{C}$ values. Carbon isotopes can therefore be used to track timing, duration, and use of upwelling zones. Our findings give novel, empirical insights into the functional ecology of the pelagic ecosystem in the Gulf of Panama, and provide a baseline for comparison and quantification of ecosystem structure and dynamics in the tropics, and in other pelagic upwelling systems.

1. Introduction

The Tropical Eastern Pacific Ocean (TEP) is a highly productive marine environment, responsible for around 10% of global marine productivity (Pennington et al., 2006). This region and adjacent areas contain some of the world's largest fisheries, such as the Peruvian anchoveta fishery (Chavez et al., 2003; Chavez and Messié, 2009). Much of this productivity is driven by seasonal upwelling events that draw nutrient-rich, cooler water to the photic zone (Pennington et al., 2006). Many species of commercially and ecologically important animals rely on the high productivity of these upwelling-influenced areas, including tunas, dolphinfishes, marlins, turtles, marine mammals, and migratory elasmobranchs (Block et al., 2011; Dewar et al., 2011; Martin et al., 2016; Moteki et al., 2001), although the relative reliance of this high productivity on upwelling periods remains largely unquantified. These organisms in turn have significant conservation, economic, and

nutritional value to human populations, including sport and food fisheries, fishmeal, and fish oil production. For example, fishery and aquaculture production in Central America alone generate an average of around 400k tonnes per year, with a mean annual value over 2 billion US dollars (Lauri et al., 2014), accounting for almost 3% of the economy for this entire region. These values include only small contributions from the Caribbean Sea (e.g. < 1% of vessels in Panama (Lauri et al., 2014)), and the great majority of production occurs in Pacific waters.

Despite the importance of upwelling pelagic ecosystems documented in temperate regions, such systems remain poorly understood in the tropics. In the North Pacific Ocean, apex predator movements have been found to intercept upwelling areas (Block et al., 2011). Of the few studies that have been conducted on upwelling systems, most investigate either the whole ecosystem within one time period (e.g. Bode et al., 2003; Coelho-Souza et al., 2012), or temporal dynamics of one or

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<https://doi.org/10.1016/j.pocean.2019.102145>

Received 1 February 2019; Received in revised form 21 June 2019; Accepted 7 August 2019

Available online 22 August 2019

0079-6611/ © 2019 Published by Elsevier Ltd.

two ecosystem components (e.g. Bode et al., 1996; Ekau et al., 2018; Madigan et al., 2012), often using one or two sampling points in multiple years rather than repeated sampling throughout a year. Often such studies are also reliant on modelled rather than empirical data to characterise trophic ecology (e.g. Cury et al., 2000; Duarte and García, 2004), and measure population dynamics rather than direct trophic and nutrient flows (e.g. Santos et al., 2007). Few studies have empirically measured and described whole ecosystem nutrient dynamics and the timing of nutrient transfer throughout the year in tropical pelagic ecosystems. Increasing the knowledge in these areas will allow more accurate tracking of behavioural, e.g. migration and feeding, and nutrient ecology throughout ecosystems.

Coastal upwelling systems in the TEP are responses to a combination of a deep pool of water with high nutrient concentrations in that region (<https://www.nodc.noaa.gov/OC5/woa18/>) and a regionally shallow thermocline, ~30–50 m deep (Fiedler and Talley, 2006), which facilitates rapid movements of nutrient-rich deeper waters to surface areas. There are three major seasonal upwellings in the TEP, all of them active during the northern hemisphere winter when tradewinds blow across low areas of the central American isthmus and move surface waters offshore: the Gulf of Tehuantepec off southern Mexico, the Gulf of Papagayo off northern Costa Rica and the Gulf of Panama (Fig. 1). The Panama upwelling system is the only one that includes a broad area of continental shelf on its inshore side, represented by the shallow (~50 m deep) Bay of Panama, in which our study was based. The Gulf of Panama is an important area of upwelling in the TEP. This ecosystem is highly productive, in large part due to large nutrient input from wind-driven seasonal upwelling (D’Croz and O’Dea, 2007; D’Croz and Robertson, 1997; McCreary et al., 1989; Pennington et al., 2006), and is an important nutrient source within the TEP. There is strong seasonality in this system between the cooler, wet months of the non-upwelling season between May and December with light and variable winds, and the hot, dry months between January and April with strong offshore trade winds, resulting in marked contrasts in temperature and nutrient availability in the pelagic zone. In the non-upwelling season, the relatively still oceanic conditions allow the local surface waters to absorb solar radiation, which increases temperatures, while the strong offshore trade winds of the dry season push the surface waters out to sea, drawing cooler waters up from the deep ocean (D’Croz and O’Dea, 2007; D’Croz and Robertson, 1997; and see McCreary et al., 1989 for the Tehuantepec and Papagayo systems). This upwelling stimulates productivity within the Bay and out into the open Pacific Ocean, carried on the Panama Current (Legeckis, 1988; Samuelsen and O’Brien, 2008; Stuhldreier et al., 2015). Primary productivity, measured as chlorophyll- α (mass of photosynthetic pigment, Chl- α), increases up to fivefold in upwelling season compared to the non-upwelling season (D’Croz and O’Dea, 2009, 2007; D’Croz and Robertson, 1997), when the

thermocline shoals almost to the surface. This increase in primary production is likely due to a release from the nitrate-limitation during the non-upwelling season, with an order of magnitude increase in dissolved nitrate in surface waters during upwelling season. Outside of the upwelling season, warm, low salinity surface waters originating from high rainfall along the Pacific coast of eastern Panama and, especially, Colombia, can be detected as far as 95° W, and cool waters from the upwelling detected in a south-westward direction for over 1500 km, as far as the Galapagos Islands (Alory et al., 2012; Legeckis, 1988), meaning that production in the waters of the Panama Bay has wide-ranging influence in the TEP.

The Bay of Panama upwelling system attracts a megafauna that is amongst the most diverse in the Tropical Eastern Pacific area (Lezama-Ochoa et al., 2017), and features a rich variety of fish species (Robertson and Allen, 2015). The increase in primary productivity due to upwelled nutrients concurrently drives high production in resident forage fishes such as the industrially fished Pacific anchoveta, *Cetengraulis mysticetus*, and Pacific thread herring, *Opisthonema* spp.. These small fishes show the greatest size-based aggregations for spawning in this area during upwelling season, with more diffuse distribution offshore and in deeper waters out of upwelling times, possibly making them less accessible to predators (Bayliff, 1963; Saetersdal et al., 1999). Around 80 thousand tonnes of these fishes are taken annually, which are important to both the economy of Panama and to the pelagic food web (CeDePesca, 2015; Csirke and Tandstad, 2005; Cury et al., 2000). These smaller fish support commercially important, migratory, upper trophic level predators such as yellowfin tuna, *Thunnus albacares*, and mahi mahi, *Coryphaena hippurus* (Block et al., 2011; Lasso et al., 1999; Thompson et al., 2012). Yellowfin tuna are known to spawn offshore in the Panama bight in the non-upwelling season (Wexler et al., 2007), possibly after having built up nutrient reserves from the increased abundance of forage fishes during upwelling. Larval tuna are also thought to be reliant on upwelled production around the TEP and show reduced survival in El Niño years when upwelling is suppressed, although the species shows increased spawning stock recruitment following El Niño events (Lehodey et al., 2006; Pedraza and Díaz Ochoa, 2006).

The stable isotope composition of primary production integrated by successive consumers during upwelling differs from that derived directly from atmospheric sources, and therefore provides a natural marker for upwelling-derived nutrients throughout the trophic web (Argüelles et al., 2012; Minami and Ogi, 1997). Upwelled waters carry higher levels of nutrients than non-upwelled waters, and these nutrients generally have higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values due to a combination of different environmental conditions during fixation by phytoplankton and isotopic alteration associated with remineralisation of sinking and settling particulate organic matter at depth. The C and N stable isotopic

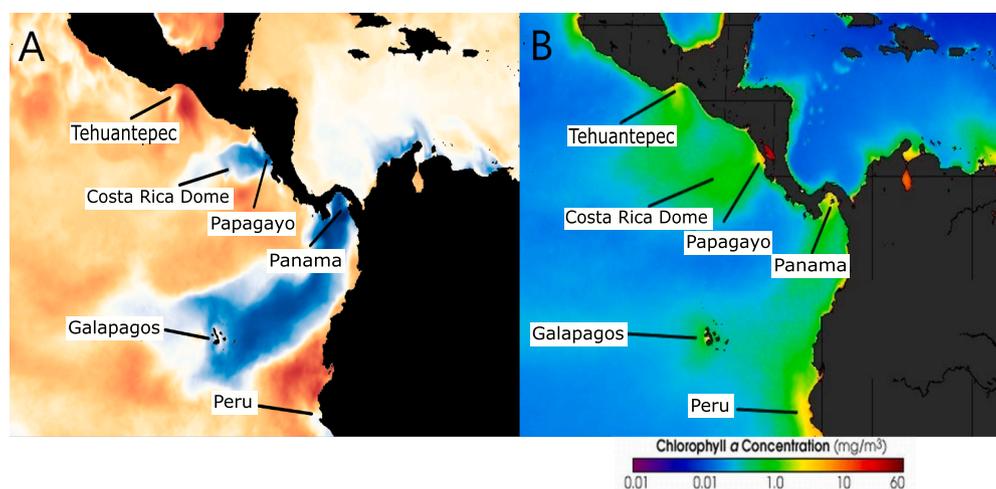


Fig. 1. Examples of (A) weekly sea surface temperature anomaly (11–17.03.2019, blue: colder and orange: warmer than the historical average for 1985–2012; image credit: NOAA) and (B) chlorophyll- α concentration (01.01.2004; image credit: SeaWiFS Project) during upwelling, showing major upwelling areas in the Eastern Pacific.

composition of primary production in upwelling regions is therefore significantly different to that of non-upwelling regions (Altabet et al., 1999; Graham et al., 2010; Libes and Deuser, 1988; Wu et al., 1999). These isotopic differences in dissolved nutrient source are transferred to organic compounds fixed during primary production in surface waters (Goericke and Fry, 1994; Lara et al., 2010) and subsequently transferred up the food web to higher trophic level consumers. Takai et al. (2000) and Argüelles et al. (2012) found that squid captured close to eastern Pacific upwelling systems were, for example, up to 6‰ higher in $\delta^{15}\text{N}$ and up to 3‰ higher in $\delta^{13}\text{C}$ values than those sampled from non-upwelling regions. The seasonality of the pelagic ecosystem in the Bay of Panama, with its strong contrasts between a cooler, nutrient-rich upwelling period and warmer, nutrient-poor conditions during non-upwelling (rainy) periods is likely to be expressed in the stable isotope composition of animals feeding in the area.

The carbon isotope composition of pelagic bulk primary production is strongly related to the isotope composition of the basal carbon source, such as upwelled dissolved inorganic carbon, and to the temperature of the seawater in which it grows (Magozzi et al., 2017; Tagliabue and Bopp, 2008). The relationship between carbon isotope composition and temperature is due to factors such as growth rate, cell geometry, and amount of available dissolved inorganic carbon (Lara et al., 2010; Tagliabue and Bopp, 2008). Upwelled waters are cooler, with more dissolved inorganic carbon due to respiration, which often originates from sources that have been remineralised by the actions of bacteria at depth (Cavan et al., 2017). The predictable relationship between temperature and carbon isotope composition of basal production means that changes in sea surface temperature due to upwelling should alter the isotopic composition of primary production, and subsequently of animals feeding within the ecosystem reliant on this primary production. In this way, upwelling-derived nutrient use can be detected within higher trophic levels of the pelagic ecosystem (Lopez-Lopez et al., 2017; Thompson et al., 2012). To detect upwelling signals, however, it is first important to have information on the baseline, without the influence of upwelling.

Our understanding of tropical inshore upwelling ecosystems, such as that typified by the Bay of Panama, is hindered by a lack of quantitative ecological measurements on nutrient sources, nutrient transfer between trophic levels, and measurements of trophic level spacing, particularly in the pelagic zone. Pelagic animals, however, are the customary targets of both commercial and recreational fisheries. For example, the most abundant and exploited fish in the world, the Peruvian anchoveta, is a pelagic consumer reliant on upwelled nutrients in the temperate eastern Pacific off Peru (Cury et al., 2000; Cushing, 1971). To understand the ecology of an ecosystem, it is necessary to understand the flow of nutrients through the trophic positions of the food web. Stable isotope analysis is a relatively recently developed tool that has become useful for determining ecosystem-level patterns in size-based structure and movement of energy between trophic levels (Blanchard et al., 2017; Reum et al., 2019).

In this study, we aim to determine the spatio-temporal patterns in variability of carbon and nitrogen stable isotope composition throughout the pelagic ecosystem of the Bay of Panama in upwelling and non-upwelling conditions, and how these patterns are recorded in organisms throughout the ecosystem from primary producers to apex predators. We present the baseline stable isotope variability in a tropical pelagic ecosystem in a time of relatively stable environmental conditions, outside of the influence of upwelling. We subsequently determine the relative enrichment of stable isotopes from this baseline between each trophic step and give a clear picture of the pelagic ecosystem structure, including measures of predator-prey mass ratio. We use a monthly time series of the stable isotope composition of resident fish species in conjunction with environmental data to analyse the timing and duration of nutrient transfer and integration from the baseline into the consumers within this ecosystem. The information we present here can be used to determine trophic behaviour and movement

patterns in animals using this area, and to assess ecosystem-scale response times to the influences of climate change, alterations in fishing pressures, and El Niño events.

2. Materials & methods

2.1. Sample collection

Samples were collected throughout the pelagic ecosystem of the Bay of Panama, out to a distance of ~120 km from the Panama Canal (see Table 1).

Pelagic particulate organic matter (POM) samples were taken on a relatively regularly-spaced grid across the Gulf of Panama to ~120 km from the Smithsonian Tropical Research Institute's marine station at Isla Naos, between September and early December 2014, to determine variability in the isotopic baseline of carbon and nitrogen stable isotope compositions outside of the wind-driven upwelling season (Bode et al., 2003; O'Reilly et al., 2002; Vokshoori et al., 2014). The isotopic composition of plankton during this period should be representative of the prevailing environmental and taxonomic conditions in the Gulf in non-upwelling season. These samples were taken by horizontal tow at ~10 m below the surface for 10 min using a straight conical SEA GEAR plankton net with 125 μm mesh, towed behind a motorised boat at ~9 km h^{-1} . The samples were rinsed from the cod-end into a labelled plastic container and immediately fixed with ethanol. In the laboratory, samples were subsequently filtered through a 200 μm sieve to divide the sample into larger plankton > 200 μm , for ease of reference subsequently denoted zooplankton (ZP), from which visible detritus (e.g. plastics, plant matter) and macroplankton (medusas, siphonophores and salps) were removed, and smaller plankton < 200 μm , subsequently denoted phytoplankton (PP) (Moloney and Field, 1991), from which visible zooplankton and detritus were removed. POM samples were taken throughout the Bay of Panama (Fig. 2) from September to December 2014.

All non-POM sampling was opportunistic. Bulk gelatinous zooplankton (scyphomedusae and salpidae) were sampled between the surface and c. 10 m using a 3 mm mesh landing net. Benthic predatory reef fishes Pacific graysby *Cephalopholis panamensis*, starry grouper *Epinephelus labriformis*, and pelagic planktivorous fish rainbow chub *Kyphosus ocyurus* were taken by spearfishing. The benthic reef fishes were collected opportunistically and included within these analyses to determine the connectivity of reef systems to pelagic production in the Bay. Benthopelagic planktivorous fish Pacific anchoveta *Cetengraulis mysticetus* and benthic predatory fish tallfin croaker *Micropogonias altipinnis* were subsampled from a commercial seine catch taken by ProMarina S.A. for fish meal and oil. Finally, pelagic predatory fishes mahi mahi *Coryphaena hippurus*, sierra mackerel *Scomberomorus sierra*, and yellowfin tuna *Thunnus albacares* were sampled from the Mercado de Mariscos (Seafood Market) in Panama City for the reliability of obtaining samples from these pelagic species; these predatory species were not always available, or very few animals were for sale during market sampling, resulting in low sample sizes. Rainbow chub *Kyphosus ocyurus* is a resident, zooplanktivorous pelagic fish (Knudsen and Clements, 2013) that was sampled for carbon and nitrogen stable isotope composition at least once per month from April 2014 to January 2015, inclusive, from locations near Islas Saboga and Pachequilla, within 4 km of one another in Las Perlas archipelago. This period incorporated both upwelling and non-upwelling months. All samples were immediately stored chilled in an insulated box with freezer packs for transport, then frozen at $-20\text{ }^{\circ}\text{C}$ within one to three hours of collection. Fish total length, jellyfish diameter, salp length (cm), and location of capture were recorded at point of collection, along with depth; whole wet mass of gelatinous plankton and fishes (g) were measured and recorded before laboratory dissection.

Gelatinous plankton (jellyfish and salp) were dissected to remove all organs, leaving only the bell of the jellyfish and the tunic of the salp,

Table 1

Details of all collected samples. Categories are defined as follows: Primary production (PP) is the bulk plankton size fraction < 200 µm, treated as pelagic phytoplankton; zooplankton (ZP) is the bulk plankton size fraction > 200 µm, treated as pelagic zooplankton; benthopelagic planktivores are fishes feeding on plankton from both benthic and pelagic sources; pelagic planktivores are fishes feeding on pelagic plankton; benthic predators are demersal fishes taking prey items from benthic habitats; and pelagic predators are pelagic fishes whose prey is other pelagic fishes.

Sample/species name	Date(s) of sampling	Season	N	Size	Category	Resident/migrant					
Phytoplankton (n = 36)	24.09.2014	Non-upwelling	4	< 200 µm	Primary production (PP)	Resident					
	10.10.2014		4								
	14.10.2014		1								
	16.10.2014		1								
	30.10.2014		5								
	31.10.2014		8								
	27.11.2014		1								
	04.12.2014		1								
	10.12.2014		11								
	Zooplankton (n = 75)		24.09.2014				Non-upwelling	10	≥ 200 µm	Zooplankton (ZP)	Resident
			10.10.2014					7			
14.10.2014		9									
16.10.2014		8									
30.10.2014		8									
31.10.2014		10									
27.11.2014		11									
04.12.2014		1									
10.12.2014		11									
Salp (n = 1)		13.03.2014	Upwelling	1	NA	ZP (Salp)		Resident			
Scyphozoa (<i>Aurelia</i> sp., <i>Chrysaora fuscescens</i> , unid. Scyphozoan) (n = 3)		03.03.2014	Upwelling	1	NA	ZP / planktivore (Jelly)		Resident			
	09.06.2014	Non-upwelling	1	116.5 g							
Pacific anchoveta <i>Cetengraulis mysticetus</i> (n = 72)	02.10.2014	Non-upwelling	1	NA	Benthopelagic planktivore	Resident					
	03.04.2014	Upwelling	52	37.1 g (mean) ± 17.7 (sd)							
Rainbow chub <i>Kyphosus ocyurus</i> (n = 37)	23.05.2014	Non-upwelling	20	422.5 g (mean) ± 181.5 (sd)	Pelagic planktivore	Resident					
	09.04.2014	Upwelling	5								
	06.05.2014	Non-upwelling	5								
	09.06.2014	Non-upwelling	3								
	03.07.2014	Non-upwelling	3								
	04.08.2014	Non-upwelling	3								
	02.09.2014	Non-upwelling	3								
	02.10.2014	Non-upwelling	3								
	30.10.2014	Non-upwelling	3								
	28.11.2014	Non-upwelling	3								
	29.12.2014	Upwelling	3								
	27.01.2014	Upwelling	3								
	Pacific graysby <i>Cephalopholis panamensis</i>	11.03.2014	Upwelling				3	258.3 g (mean) ± 45.4 (sd)	Benthic predator	Resident	
Starry grouper <i>Epinephelus labriformis</i>	11.03.2014	Upwelling	4	287.5 g (mean) ± 85.4 (sd)	Benthic predator	Resident					
Tallfin croaker <i>Micropogonias altipinnis</i>	03.04.2014	Upwelling	1	875 g	Benthic predator						
Mahi mahi <i>Coryphaena hippurus</i> (n = 6)	21.03.2014	NA – open Pacific Ocean	1	2448.6 g (mean) ± 315.5 (sd)	Pelagic predator	Migrant					
	06.06.2014	Non-upwelling	3								
Sierra mackerel <i>Scomberomorus sierra</i> (n = 14)	22.10.2014	Non-upwelling	2	1461.0 g (mean) ± 1045.4 (sd)	Pelagic predator	Resident					
	23.03.2014	Upwelling	5								
	06.06.2014	Non-upwelling	4								
	22.10.2014	Non-upwelling	3								
Yellowfin tuna <i>Thunnus albacares</i> (n = 4)	26.02.2014	Upwelling	2	5067.6 g (mean) ± 2828.4 (sd)	Pelagic predator	Migrant					
	21.03.2014	NA – Chiriquí	1								
	06.06.2014	Non-upwelling	2								
	22.10.2014	Non-upwelling	1								
	26.02.2015	Upwelling + Chiriquí	2								

which were thoroughly and repeatedly washed in Millipore water prior to dissection for isotope analysis (MacKenzie et al., 2017).

Bulk phytoplankton and zooplankton samples were rinsed using Millipore water through a vacuum pump onto pre-combusted Whatman glass fibre filters. These plankton samples were acidified by fuming with 1 M HCl for 24 h in a glass desiccation chamber to remove inorganic carbonates. Samples of dorsal white muscle were dissected from the fishes and cleaned repeatedly and thoroughly in Millipore water. Filters, fish muscle, invertebrate, and plankton samples were dried to a constant mass for 24–48 h in a 60 °C oven. All samples were then ground to fine, homogenous powder with a pestle and mortar or automated ball mill for stable isotope analysis.

2.2. Organism ecology

Phytoplankton are subject to seasonal blooms due to increased nutrient availability from thermocline shoaling almost to surface waters during the upwelling season, when a fivefold increase in Chl- α has been observed within the Bay of Panama (D'Croz and O'Dea, 2007). The isotopic compositions of these baseline organisms reflect a combination of taxonomy, the environmental conditions in which they grow, e.g. temperature, and the isotopic composition of the nitrogen and carbon nutrient sources that they integrate (Lara et al., 2010; Montoya, 2008; Tagliabue and Bopp, 2008)

Zooplankton respond to the increased grazing availability of phytoplankton with a concurrent seasonal bloom pattern. This category of animals is considered largely herbivorous within this ecosystem (Marra et al., 1987)

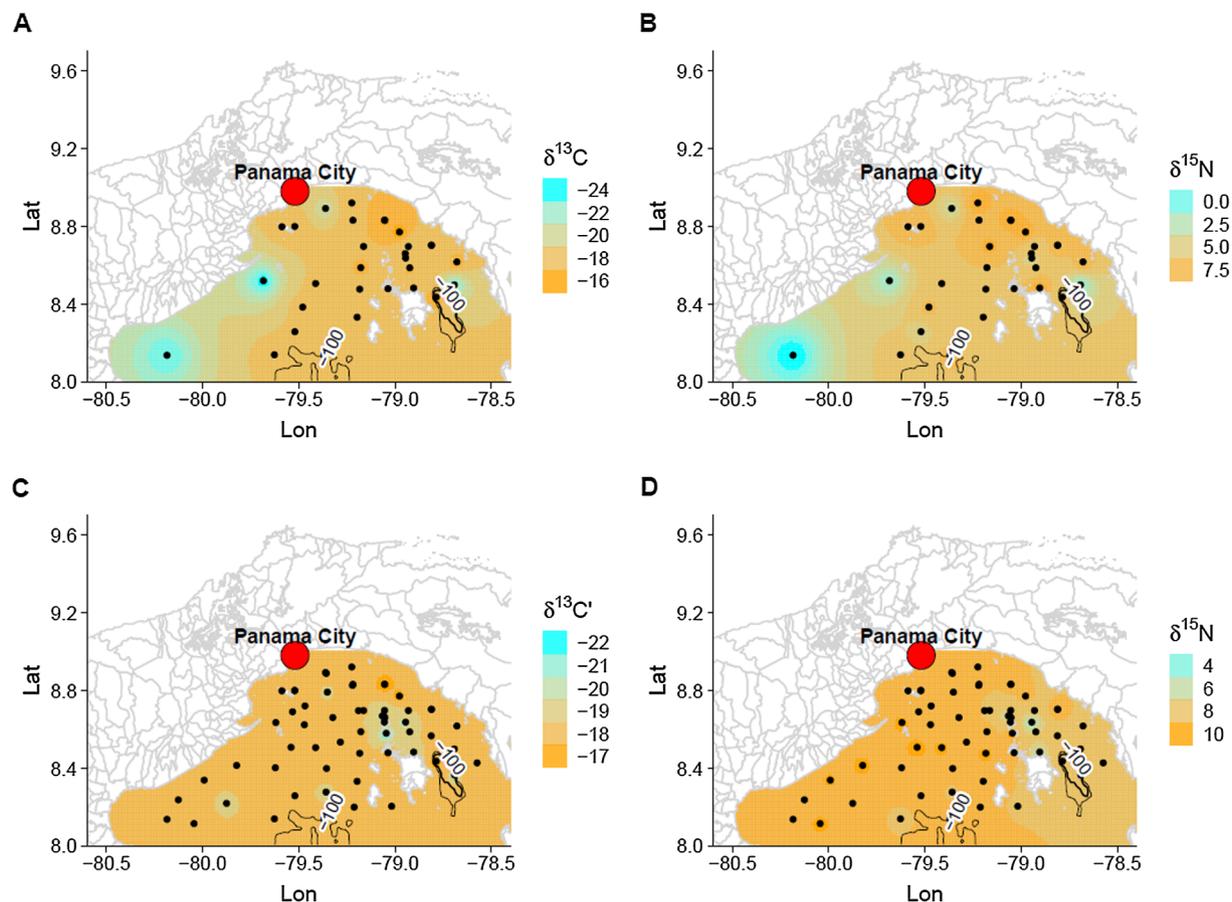


Fig. 2. Bay of Panama isoscape maps of inverse-distance weighted interpolated values of bulk (A) phytoplankton (< 200 μm) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$, and (C) zooplankton (> 200 μm) $\delta^{13}\text{C}$ and (D) $\delta^{15}\text{N}$ ‰. Black circles denote sampling locations, black lines indicate bathymetry.

Gelatinous zooplankton, here salps and jellyfishes (medusae) are pelagic macrozooplankton, that feed by filtering small planktonic organisms from the water (salps and jellyfish), and by capturing small pelagic animals in their tentacles. Due to this generalist feeding mode, potentially spanning multiple trophic positions, trophic level assignment is not given for these organisms, although salps are largely herbivorous and medusae are largely carnivorous (Kruse et al., 2015; Molina-Ramírez et al., 2015). These animals are, similar to smaller plankton, known to produce blooms during upwelling season (Miglietta et al., 2008).

2.2.1. Planktivores

The Pacific anchoveta *Cetengraulis mysticetus* is a benthopelagic fish that feeds on plankton by filtering water through its gill rakers. Unusually for anchovy-type filter feeders, *C. mysticetus* actively consumes both pelagic and benthic plankton, particularly benthic diatoms in adult fish. This species has a specialised muscular gizzard-like stomach for crushing hard-shelled diatoms to render the contents accessible, and appears to feed more benthically with increasing age/size (Bayliff, 1963). It might be speculated that the large schools aggregating in shallow waters could stir up the benthic surface layer, allowing access to filter benthic diatoms using their gill rakers, but further investigation would be necessary to determine whether this is the case. This fish appears to be largely phytoplanktivorous, based on Bayliff's (1963) stomach contents analyses.

Rainbow chub *Kyphosus ocyurus* is another tropical planktivore, although this species is largely zooplanktivorous and epipelagic-feeding (Dominici-Arosemena and Wolff, 2006; Robertson and Allen, 2015). This species is often associated with rocky shores and offshore reefs,

and a widespread resident in the study area throughout the year.

2.2.2. Benthic predators

The Pacific graysby *Cephalopholis panamensis* and starry grouper *Epinephelus labriformis* are reef-associated benthic-feeding carnivorous fishes, with a diet comprising small fishes and invertebrates (Craig et al., 1999; Dominici-Arosemena and Wolff, 2006). These fishes are considered resident throughout the year within the study area. Tallfin croaker *Micropogonias altipinnis* is another benthic fish, although with a broader habitat range covering sandy, muddy, and estuarine areas. These fish are carnivorous, with prey including fishes and benthic invertebrates (Fischer et al., 1995), and considered resident within the study area.

2.2.3. Pelagic predators

Mahi mahi *Coryphaena hippurus* is an epipelagic, circumtropical and sub-tropical predator, consuming fishes, squid, and crustacea (Tripp-Valdez et al., 2010; Varela et al., 2017). These fishes are highly itinerant, and found mainly in the study area during December to April (Lasso et al., 1999), coinciding with upwelling season. Sierra mackerel *Scomberomorus sierra* is another epipelagic, predatory fish, preying largely on smaller fishes such as anchovies (Collette and Nauen, 1983). This species is believed to have strong population structure, with localised genotypes linked to spawning area proximity (Domínguez López et al., 2010), thus is considered resident in the study area. Yellowfin tuna *Thunnus albacares* is, like mahi mahi, a migratory circumtropical and sub-tropical predator, also feeding on fishes, crustacea and squid (Olson and Boggs, 1986). These fish are considered migrants to the study area.

2.3. Seasonality and environmental data

Mean monthly SST values were calculated from sea surface temperature measurements at STRI's Isla Pacheca monitoring station (lat. 8.662, lon. -79.054, https://biogeodb.stri.si.edu/physical_monitoring/research/sst). Data here have been recorded at 30-min intervals continuously since 1995 using Onset Hobo temperature loggers, at a depth of 6 m below the surface. This station in Las Perlas is within 3 km of the capture locations for the time series of *K. ocyurus* samples. Monthly data were calculated as means of all recorded SST data within each month from November 2013 to February 2015. From these Isla Pacheca data, the SST values from May – December within each year were between 27.8 and 28.8 °C, while values from January – April 2014 and January – February 2015 were lower, between 22.4 and 26.3 °C. As upwelled waters are cooler than surface waters (Lehodey, 2001) and SST better reflects the conditions directly experienced within the marine ecosystem than measures of wind stress, SST values were used to temporally define upwelling and non-upwelling seasons. The months of January to April are therefore considered to be the upwelling period.

To test for spatially resolved anthropogenic and open oceanic contributions to the stable isotope composition of plankton in the Bay of Panama, shortest linear distances were measured to the nearest 100 m using Google Maps tools (©2018 Google Imagery, TerraMetrics) between plankton sample locations and:

- the closest shore,
- the closest settlement,
- the closest area of mainland Panama,
- Panama Canal (taken as a point in the centre of the Canal, next to the Bridge of the Americas, and used as a proxy for distance from the influence of Panama City),
- the open Pacific Ocean (taken as a point in the centre of the entrance to the Bay of Panama, on the continental shelf at approximately 10 km from the continental slope),

Bathymetry data were obtained from the ETOPO1 dataset (Amante and Eakins, 2009) hosted on the NOAA server, using the 'marmap' package in R (Pante and Simon-Bouhet, 2013).

High resolution chlorophyll- α concentration data at the surface of the ocean (0 m altitude) were obtained from MODIS/Aqua dataset (http://coastwatch.pfeg.noaa.gov/erddap/tabledap/erdMBchla8day_LonPM180.html) on a 0.025 degree latitude-longitude resolution; full acknowledgements to the NOAA CoastWatch Program and NASA's Goddard Space Flight Center, and OceanColor Web (Fu et al., 1998; Gordon and Wang, 1994; O'Reilly et al., 2000; Shettle and Fenn, 1979).

2.4. Stable isotope analysis

Samples were analysed for carbon and nitrogen stable isotope composition using a Flash-HT elemental analyser coupled to a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer (EA-IRMS) in the Smithsonian Tropical Research Institute Stable Isotope Laboratory. Samples were run concurrently with the following in-house standards of known isotope composition: ammonium sulfate, NIST peach leaves, aspartic acid, STRI-sugar B, STRI-C3, and, sucrose; and with international standards IAEA-N1 and IAEA-N2, IAEA-polyethylene with precision of 0.4 and 0.1‰ (\pm SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

2.5. Data analysis

All statistical analyses were run using R software version 3.4.3 (R Development Core Team, 2011).

2.5.1. Lipid correction

For animals (excluding salps which have a carbohydrate tunic), $\delta^{13}\text{C}$ values were arithmetically corrected for lipid content to allow

comparability with other values if atomic C:N ratio was ≥ 4.0 , otherwise measured values were used. Lipid correction was carried out according to the final revised equation from Kiljunen et al. (2006). Lipid-corrected $\delta^{13}\text{C}$ values are denoted $\delta^{13}\text{C}'$ hereafter. Phytoplankton $\delta^{13}\text{C}$ values were not corrected as it is not possible to separate cellulose from lipid content through atomic C:N ratios. Excluding phytoplankton samples, 46% of the samples required lipid correction. Post-correction, there was no significant relationship between $\delta^{13}\text{C}'$ values and C:N ratios.

2.5.2. Mass correction

To remove the effect of mass on $\delta^{15}\text{N}$ values and make the animals directly comparable, $\delta^{15}\text{N}$ values were corrected to a standard mean mass for pelagic predators according to Eq. (2):

$$\delta^{15}\text{N}' = \left(\frac{\delta^{15}\text{N}}{\delta^{15}\text{N}_{\text{calc}}} \right) \delta^{15}\text{N}_{\text{mean}} \quad (2)$$

where $\delta^{15}\text{N}'$ is the mass-corrected isotope value, $\delta^{15}\text{N}$ is the original measured value, $\delta^{15}\text{N}_{\text{calc}}$ denotes the expected isotope value for the body mass of that fish given the regression coefficient of the relationship between mass and $\delta^{15}\text{N}$ values for the pelagic predator fishes, and $\delta^{15}\text{N}_{\text{mean}}$ denotes the calculated isotope value for the mean body mass of the pelagic predator fishes.

2.5.3. Mapping

Phytoplankton and zooplankton stable isotope values were mapped using inverse distance weighted interpolation in the R gstat package (Gräler et al., 2016; Pebesma, 2004), where closer values are given higher weighing in interpolation than values measured further away, i.e. a greater likelihood of similarity, as is expected from spatial patterns in stable isotope composition (e.g. Bowen, 2010), see Fig. 2. Maps were created in the R ggplot2 package (Wickham, 2016).

Predator-prey mass ratio (PPMR) calculation

$$\text{Community PPMR} = \log \text{base}^{\frac{\Delta^{15}\text{N}}{\text{slope}}} \quad (1)$$

(Jennings et al., 2002), \pm SD between differences in trophic levels or tissue-diet fractionation (TDF) and around the slope of the $\delta^{15}\text{N}$ -log₂ mass relationships.

2.5.4. Nutrient transfer time

To determine the lag time between SST-controlled $\delta^{13}\text{C}$ values in primary production and the integration of that signal, via zooplankton consumption and integration of the primary production, and subsequent consumption and integration of the zooplankton by *K. ocyurus*, mean $\delta^{13}\text{C}$ values measured in *K. ocyurus* dorsal muscle for every month from April 2014 to January 2015 inclusive were cross-correlated with mean monthly sea surface temperature records from January 2014 to February 2015, calculated from measurements taken at the Isla Pacheca monitoring station, within 3 km of the *K. ocyurus* sampling sites.

All data are available from the online PANGAEA repository (MacKenzie et al., 2019).

3. Results

All data are available in Appendix A.

3.1. Plankton baseline stable isotope composition

Stable isotope values for separated bulk plankton size fractions, denoted phytoplankton (< 200 μm) and zooplankton (> 200 μm), show the baseline spatial isotopic variability outside of upwelling influence. The range in $\delta^{13}\text{C}$ ($\delta^{13}\text{C}'$) and $\delta^{15}\text{N}$ values is very high for both phytoplankton and zooplankton, although higher in $\delta^{15}\text{N}$ (Table 2). For comparison, the zooplankton isoscapes of Graham et al. (2010) show a total $\delta^{15}\text{N}$ range of 10‰ for the entire Atlantic Ocean. The overall

Table 2Summary statistics of stable isotope values for plankton size fractions; arithmetic lipid correction was applied to the $\delta^{13}\text{C}$ values of the zooplankton fraction.

	n	$\delta^{13}\text{C}$ (PP) or $\delta^{13}\text{C}'$ (ZP) ‰					$\delta^{15}\text{N}$				
		min	max	mean	range	SD	min	max	mean	range	SD
Phytoplankton (< 200 μm)	36	-27.4	-19.5	-21.2	7.9	1.4	-1.5	11.4	6.2	12.9	2.9
Zooplankton (> 200 μm)	75	-22.1	-16.4	-18.4	5.6	1.1	-3.1	10.5	8.3	13.6	1.6

geographic pattern is, however, relatively stable in isotopic composition of both C and N, as detailed below, with a small number of extreme values driving the large range (Table 2, Fig. 2).

Total variability in non-upwelling months
Isoscapes

3.1.1. Phytoplankton (< 200 μm)

The spatial patterns in phytoplankton carbon (Fig. 2A) and nitrogen (Fig. 2B) stable isotope compositions are similar, with some depletion in both isotopes measured in the westernmost parts of the Bay of Panama, particularly around Isla Taboguilla (lat. 8.801, lon. -79.521; -27.4‰ $\delta^{13}\text{C}$, -1.2‰ $\delta^{15}\text{N}$), near Punta Chame (lat. 8.522, lon. -79.684; -22.2‰ $\delta^{13}\text{C}$, 1.3‰ $\delta^{15}\text{N}$), and offshore from Parita Bay (lat. 8.138, lon. -80.185; -23.5‰ $\delta^{13}\text{C}$, -1.5‰ $\delta^{15}\text{N}$). More enriched values were measured towards the north and west, particularly offshore from Rio Chepo (lat. 8.773, lon. -78.977; -19.5‰ $\delta^{13}\text{C}$, 8.9‰ $\delta^{15}\text{N}$). For $\delta^{15}\text{N}$ only, the highest values are around Punta Chame (lat. 8.637, lon. -79.620; 11.4‰ $\delta^{15}\text{N}$, -22.6‰ $\delta^{13}\text{C}$) and c. 20 km offshore from Panama City (lat. 8.889, lon. -79.357; 9.9‰ $\delta^{15}\text{N}$, -21.1‰ $\delta^{13}\text{C}$), $\delta^{13}\text{C}$ values at these points are around the mean. The spatial compositions were overall relatively homogenous, with 66% of the phytoplankton $\delta^{13}\text{C}$ values between -22 and -20‰, and 56% of the $\delta^{15}\text{N}$ values between 4.5 and 7.5‰.

No significant relationships were found by linear regression between the composition of either carbon or nitrogen phytoplankton isotopes and depth or surface Chl- α concentration, or direct linear distance (km) from: the closest shore, the closest settlement, the mainland, the freshwater-fed Panama Canal, or the open Pacific Ocean.

3.1.2. Zooplankton (> 200 μm)

The geographic patterns of zooplankton lipid-corrected carbon (Fig. 2C) and nitrogen (Fig. 2D) stable isotope compositions are similar to one another. Unlike in phytoplankton, however, the lowest values of $\delta^{13}\text{C}'$ (-22.1, -22.0) co-occur, however, with the highest values of $\delta^{15}\text{N}$ (10.5, 10.4) close to Islas Chapera (lat. 8.581, lon. -79.045) and Pacheca (lat. 8.662, lon. -79.053) in Las Perlas. Highest values of $\delta^{13}\text{C}'$ were found between Las Perlas and Rio Chepo (lat. 8.773 to 8.834, lon. -79.054 to -78.977; -16.4 to -16.8‰ $\delta^{13}\text{C}'$, 8.8 to 9.4‰ $\delta^{15}\text{N}$). The lowest $\delta^{15}\text{N}$ values were found next to Isla Pacheca (lat. 8.6623, lon. -79.0535; -20.4‰ $\delta^{13}\text{C}'$, -3.1‰ $\delta^{15}\text{N}$), and between Isla Taboga and mainland Panama (lat. 8.842, lon. -79.565; -21.6‰ $\delta^{13}\text{C}'$, 2.1‰ $\delta^{15}\text{N}$) where the $\delta^{13}\text{C}'$ value was also low. The zooplankton spatial compositions were more homogenous than in the phytoplankton with 75% of the $\delta^{13}\text{C}$ values between -19.3 and -17.3‰, and 68% of the $\delta^{15}\text{N}$ values between 7.5 and 9.5‰.

There was a detectable positive relationship between zooplankton $\delta^{15}\text{N}$ values and shortest linear distance from the nearest shore ($F = 4.921$, $R^2 = 0.05$, $p = 0.03$), and the nearest settlement ($F = 6.855$, $R^2 = 0.07$, $p = 0.01$), although this relationship is driven almost entirely by six depleted measurements between 0 and 10 km from the shore around the northern islands of Las Perlas Archipelago, and between Isla Taboguilla and mainland Panama. There were no significant relationships between $\delta^{15}\text{N}$ values and depth, or shortest linear distance to the mainland, Panama Canal/City, or the open Pacific Ocean, nor with surface Chl- α concentration. There were no statistically significant relationships found between zooplankton $\delta^{13}\text{C}'$ and depth,

or direct linear distance (km) from: the closest shore, the mainland, Panama Canal, or the open Pacific Ocean. There is a marginally significant, positive relationship between $\delta^{13}\text{C}'$ and shortest linear distance to the closest settlement ($F = 3.086$, $R^2 = 0.03$, $p = 0.08$), which, in combination with the positive relationship between settlement proximity and $\delta^{15}\text{N}$ values, is suggestive of anthropogenic depletion of C and N isotope values in zooplankton.

3.2. Ecosystem structure: Trophic spacing

We collected stable isotope values across four trophic levels (TL) in a tropical pelagic ecosystem. Based on broad diet category, trophic levels are assigned as follows: phytoplankton (primary producers) are at TL1, zooplankton (primary consumers) at TL2, planktivorous fishes (zooplanktivores) at TL3 (Bayliff, 1963; Dominici-Arosemena and Wolff, 2005; Robertson and Allen, 2015), and predators (piscivores) at TL4 (Collette and Nauen, 1983; Craig et al., 1999; Dominici-Arosemena and Wolff, 2006; Fischer et al., 1995; Olson and Boggs, 1986; Tripp-Valdez et al., 2010; Varela et al., 2017). Statistical comparison of the mean stable isotope values for each trophic level in this data set gives the tissue-diet spacing between each TL, and for the whole ecosystem, with differences tested using Wilcoxon rank sum tests. Separation in stable isotope values for each TL are reported in Table 3 and shown in Fig. 3.

All fishes that could be categorised as potentially feeding on prey that included or was comprised entirely of benthic nutrient sources (*Cetengraulis mysticetus*, *Cephalopholis panamensis*, *Epinephelus labriiformis*, and *Micropogonias altipinnis*) had relatively elevated $\delta^{13}\text{C}'$ values compared with other fishes of similar trophic level with strictly pelagic diets, with the exception of one *C. panamensis*, which was similar in both $\delta^{13}\text{C}'$ and $\delta^{15}\text{N}$ values to pelagic predators, and therefore may have a diet of anomalously pelagic nutrient sources.

3.2.1. Tissue-diet fractionation

The isotopic spacing, or putative tissue-diet fractionation (TDF, Δ) between phytoplankton and zooplankton is 2.1 in $\Delta^{15}\text{N}$ and 2.9 in $\Delta^{13}\text{C}'$ (zooplankton fraction subject to lipid-correction, see Tables 2 and 3).

K. ocyurus mean $\delta^{13}\text{C}'$ value in October 2014 to January 2015 was -17.6‰, while the zooplankton mean value in September to December was -18.4‰, giving an average tissue-diet spacing of 0.8‰ between rainbow chub and zooplankton. For $\delta^{15}\text{N}$ values, the *K. ocyurus* mean was 13‰, while the zooplankton mean was 8.3‰, giving a

Table 3

Mean differences \pm SD, and p-values (Wilcoxon rank sum test) for $\delta^{15}\text{N}$ and lipid-corrected $\delta^{13}\text{C}'$ between trophic levels in the Bay of Panama pelagic ecosystem (note: benthic predators and gelatinous zooplankton were excluded from this analysis due to unclear assignment of trophic position, as were fishes with a reported capture location elsewhere than the Gulf of Panama).

	$\Delta^{15}\text{N}$			$\Delta^{13}\text{C}'$		
	mean	\pm SD	p	mean	\pm SD	p
TL1 - TL2	2.1	0.12	< 0.001	2.9	0.03	< 0.001
TL2 - TL3	4.3	0.01	< 0.001	2.2	0.02	< 0.001
TL3 - TL4	2.3	0.01	< 0.001	0.1	0.01	0.9
All	2.9	0.09	< 0.001	1.7	0.08	< 0.001

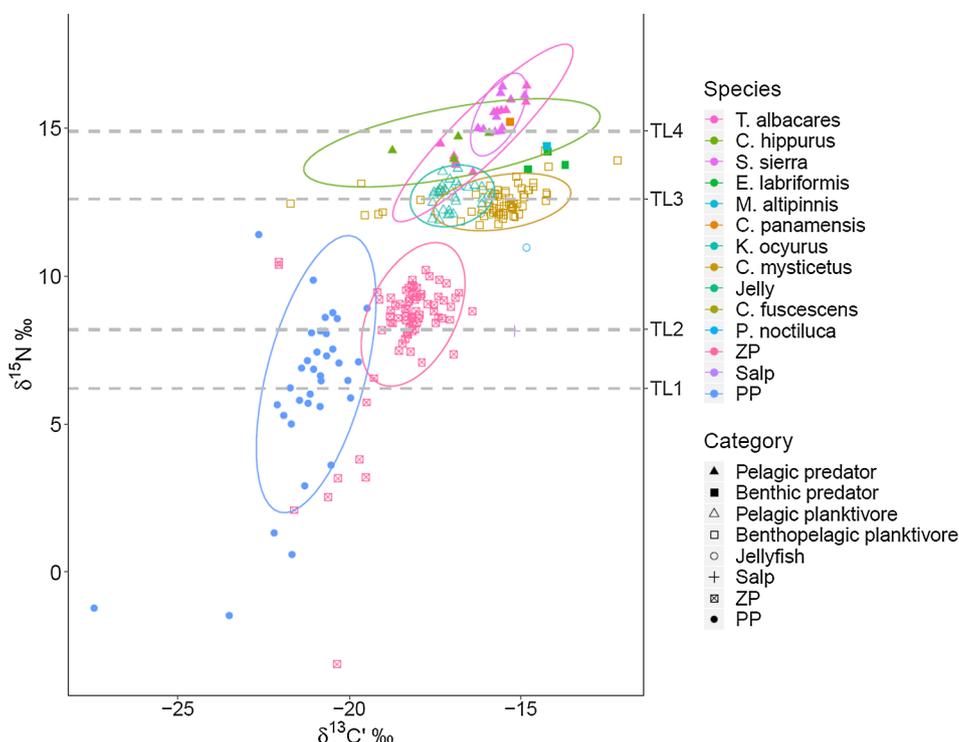


Fig. 3. Carbon (lipid-corrected for C:N elemental ratio $\geq 3.9\text{‰}$ for all organisms except phytoplankton and salps) and nitrogen stable isotope data of Bay of Panama organisms; colour denotes species, with ellipses showing 95% confidence interval values for each species with sufficient data points, and point shape denotes organism category (see also Table 1); dashed lines show mean $\delta^{15}\text{N}$ values for each approximate trophic level (TL) 1–4 from low to high on the y-axis.

contemporaneous tissue-diet fractionation of 4.7‰ from pelagic planktivorous fish to zooplankton. *C. mysticetus* had slightly enriched $\delta^{13}\text{C}$ values relative to *K. ocyurus* sampled during the same time period (April–May 2014), with respective means of -16.4 and -16.8‰ . Values of $\delta^{15}\text{N}$ were, however, very similar at 12.5‰ for *C. mysticetus* and 12.7‰ for *K. ocyurus*. Combined *K. ocyurus* and *C. mysticetus* give tissue-diet fractionation values of 1.8 to 4.6‰ in $\delta^{13}\text{C}$, and 4.3 to 6.4 ‰ in $\delta^{15}\text{N}$ from all planktivorous fish to zooplankton and phytoplankton (see Table 2 for mean values).

The TDF between planktivorous and pelagic predatory fishes is 2.3‰ $\Delta^{15}\text{N}$ and 0.1‰ $\Delta^{13}\text{C}$ (see Table 4). For only non-migratory pelagic fishes within the Bay of Panama, these differences are 2.7‰ $\Delta^{15}\text{N}$ and 0.5‰ $\Delta^{13}\text{C}$.

Overall, the mean TDF for this ecosystem is 2.9‰ $\Delta^{15}\text{N}$ and 1.7‰ $\Delta^{13}\text{C}$. Using this value of 2.9‰ to calculate trophic level based on the total range in $\delta^{15}\text{N}$ values, starting with the lowest phytoplankton $\delta^{15}\text{N}$ value of -1.5‰ at TL1, the maximum calculated trophic level in this ecosystem is 6.2, based on the maximum $\delta^{15}\text{N}$ value measured from an animal (*S. sierra*) within the Gulf of Panama (see Appendix for full data).

These data provide values for isotopic offsets that may be used to determine the baseline values and trophic behaviour within this food web throughout the year.

3.3. Predator-prey mass ratio (PPMR) and ecosystem structure

The predator-prey mass ratio (PPMR) for all animals with recorded

Table 4
Summary statistics of stable isotope values for fishes by broad functional group.

	n	$\delta^{13}\text{C}$ ‰		$\delta^{15}\text{N}$ ‰	
		mean	SD	mean	SD
Pelagic planktivores	37	-17.5	0.54	12.7	0.42
Benthopelagic planktivores	72	-15.8	1.42	12.5	0.50
Pelagic predators	31	-16.0	0.90	14.9	0.92
Benthic predators	8	-14.6	0.65	14.3	0.64

mass sampled in the Bay of Panama ecosystem was 375:1, based on measured $\delta^{15}\text{N}$ values against \log_2 mass and calculated using Eq. (1), using the mean value of $\Delta^{15}\text{N}$ between trophic levels for the whole ecosystem (Fig. 4a). By excluding non-fishes from the analysis and thereby changing the value of $\Delta^{15}\text{N}$, this value drops to 113:1. Excluding migratory fishes (mahi mahi, $n = 3$, and yellowfin tuna, $n = 4$), possibly importing $\delta^{15}\text{N}$ values from areas outside of the Bay of Panama, however, changes both the $\Delta^{15}\text{N}$ and the slope of the relationship between $\delta^{15}\text{N}$ and mass, thereby increasing the PPMR to 376:1 (Fig. 4b), an almost identical value to that calculated for the whole ecosystem.

$$\text{PPMR}_{\text{all}} = \frac{2.9 \pm 0.01}{20.34 \pm 0.03} = 375:1 \text{ (range: 233 – 657)}$$

$$\text{PPMR}_{\text{allfishes}} = \frac{2.3 \pm 0.01}{20.34 \pm 0.03} = 113:1 \text{ (range: 77 – 178)}$$

$$\text{PPMR}_{\text{residentfishes}} = \frac{2.7 \pm 0.18}{20.32 \pm 0.04} = 376:1 \text{ (range: 253 – 1272)}$$

3.4. Pelagic planktivore carbon isotope composition driven by SST

3.4.1. Fishes

Temporal trends and mean values of *K. ocyurus*.

Rainbow chub average $\delta^{13}\text{C}$ values were highest in April and May 2014 (April: $-16.9\text{‰} \pm 0.38$ sd, $n = 4$; May: $-16.6\text{‰} \pm 0.14$ sd, $n = 5$), and lowest in June 2014 ($-18.1\text{‰} \pm 0.18$ sd, $n = 3$), although the total range was 2.1‰, (Figs. 3 and 5). Average values of $\delta^{13}\text{C}$ showed cyclicity (Fig. 5b), with highest values in April to May 2014, immediately after the December to April upwelling season, lowest values in June 2014, and steady increase from the low in June towards higher upwelling season values (Table 2 and Fig. 5). There was noticeable variation in the composition of both isotopes throughout the 11-month period, however there was no significant correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Overall, the C and N isotope values of rainbow chub appear to be higher during and after the upwelling season and lower through the dry season.

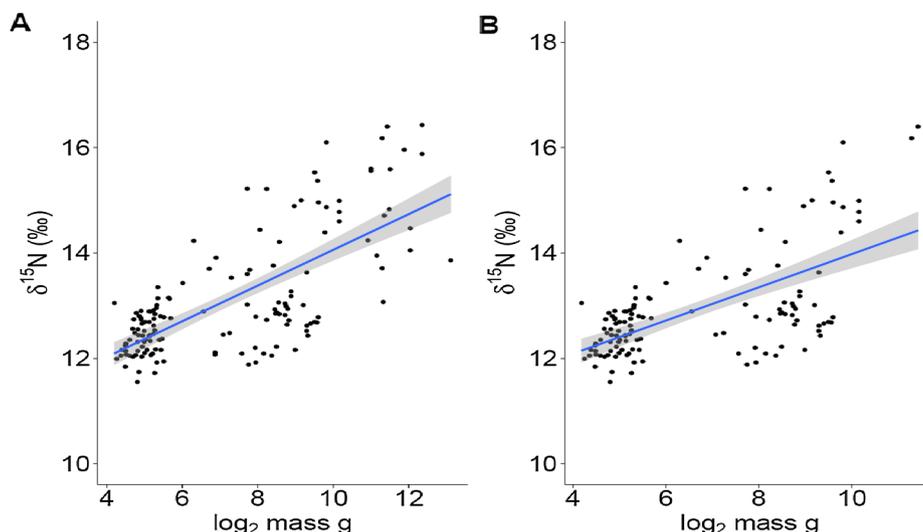


Fig. 4. Organism $\delta^{15}\text{N}$ values (‰) over \log_2 mass (g) for (A) all Bay of Panama animals, and (B) only fishes considered resident in the Bay of Panama (excluding non-fishes, *C. hippurus*, and *T. albacares*). The relationship between all fishes $\delta^{15}\text{N}$ and mass is not shown as it is almost identical to (A).

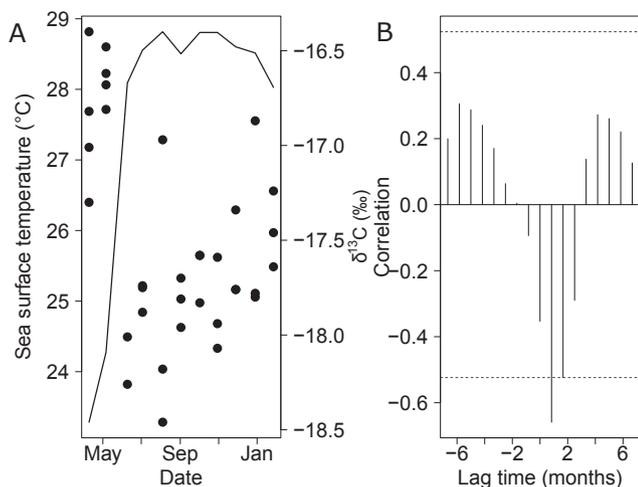


Fig. 5. (A) Rainbow chub $\delta^{13}\text{C}$ values (black filled circles) and Isla Pacheca mean monthly sea surface temperature values (black line); and (B) cross-correlation at different lag times between rainbow chub $\delta^{13}\text{C}$ values and mean monthly SST at Isla Pacheca, within 3 km of where the chub were sampled (lat. 8.662, lon. -79.054), each vertical line is one month of lag time from SST to mean $\delta^{13}\text{C}$ value, dashed line indicates significance threshold ($p = 0.05$).

3.5. Nutrient transfer time from SST to rainbow chub

A significant negative correlation was found between monthly rainbow chub $\delta^{13}\text{C}$ values and mean monthly sea surface temperature within 3 km of capture location, with a lag time of one to two months (one month: $F = 43.04$, $R^2 = 0.56$, $p < 0.001$; two months: $F = 19.58$, $R^2 = 0.36$, $p < 0.001$) (Fig. 5b). As rainbow chub are largely zooplanktivores, feeding around trophic level (TL) 3, this suggests a trophic transfer time for carbon of 0.5 to 1.0 month per TL in this pelagic ecosystem.

There was no significant correlation between rainbow chub $\delta^{15}\text{N}$ values and SST, neither before nor after correction of the isotope values to *K. ocyurus* mean mass to remove the relationship between size and ^{15}N composition. A longer time series would be needed to robustly test whether there is a temporal pattern in $\delta^{15}\text{N}$ values related to upwelling.

3.6. Isotope patterns in predatory fishes

Of the three species of pelagic predatory fishes, *C. hippurus* and *T.*

albacares did not differ from one another in lipid-corrected $\delta^{13}\text{C}$ values across all sampled areas (Bay of Panama, Gulf of Chiriquí, and open Pacific Ocean), nor did *S. sierra* *T. albacares*. We did find that *C. hippurus* values were significantly different from those of *S. sierra* (Wilcoxon sum rank test: $W = 2$, $p < 0.005$); however caution is advised on this result as only $n = 4$ *C. hippurus* were sampled.

Similar patterns were found in mass-corrected $\delta^{15}\text{N}$ values to those found in $\delta^{13}\text{C}$ values: significant differences were only found between *C. hippurus* and *S. sierra* (Wilcoxon sum rank test: $W = 0$, $p < 0.001$), although there is some suggestion of a difference between *S. sierra* and *T. albacares* at 90% significance ($W = 72$, $p = 0.09$). The values were separated at each contemporaneous sampling point except February 2015, when they converged at a value of around 15‰ (Fig. 6). More samples, could further resolve this potential difference. All pelagic predatory fishes showed minimal temporal differences in carbon isotope composition, although the values measured in October were overall slightly lower, largely driven by one *C. hippurus*. *S. sierra* show no obvious change in isotope composition through time, having similar within-month composition regardless of sample location. *C. hippurus* and *T. albacares* are relatively depleted in both isotopes compared to *S. sierra*, with the exception of *T. albacares* samples in February 2015, which are isotopically indistinguishable from *S. sierra*. There are too few months of sampling, however, to draw either statistically robust conclusions, or inferences on lag time between these predators and smaller fish that constitute their potential prey. Interestingly, both carbon and nitrogen isotope composition in all pelagic predators sampled (*C. hippurus*, *S. sierra*, and *T. albacares*) appear largely unrelated to their reported location of capture (Fig. 6).

4. Discussion

Ecosystem structure and nutrient flows can be measured and estimated by coupling stable isotope analyses to biological and environmental data. We describe the trophic structure and temporal nutrient transfer of a pelagic ecosystem subject to seasonal upwelling in the Tropical Eastern Pacific, covering size classes over three orders of magnitude. Here, we found low estimates of tissue-diet fractionation and of predator-prey mass ratio, which suggest high trophic transfer efficiency and rapid trophic assimilation of nutrients within this ecosystem (Barnes et al., 2010; Jennings et al., 2002). We see very rapid nutrient movements of between 0.5 and 1.0 month on average per trophic level. While there are many estimates of production and biomass residence rate per unit of time (e.g. Gascuel et al., 2008; Maureaud

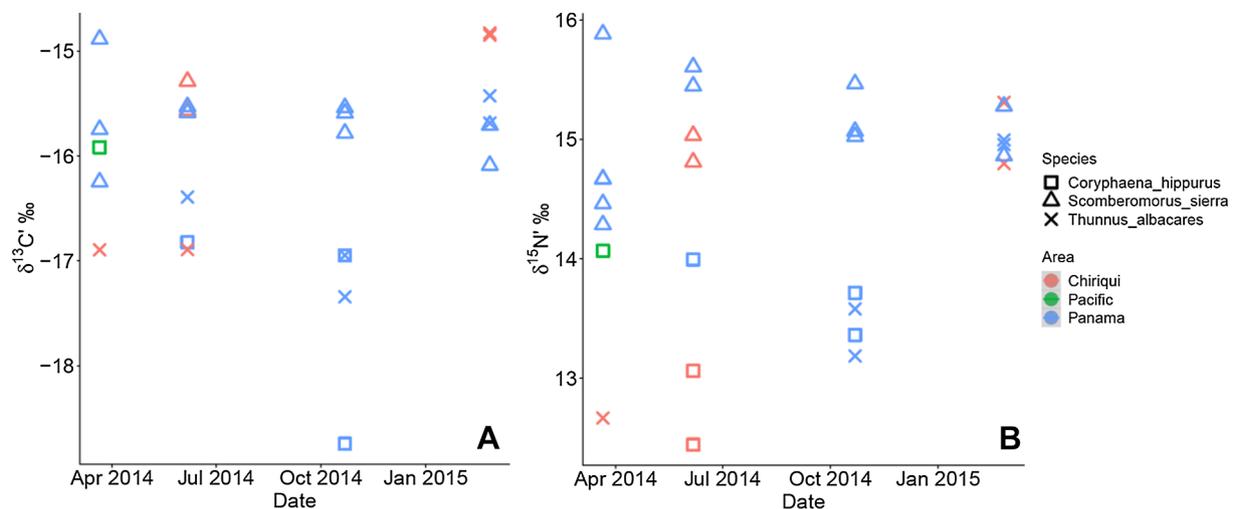


Fig. 6. Time series of (A) lipid-corrected carbon isotope values, and (B) mass-corrected nitrogen isotope values in piscivorous fishes; squares are mahi mahi, triangles are sierra mackerel, and crosses are yellowfin tuna; red is the Gulf of Chiriquí, green is the open Pacific Ocean, and blue is the Bay of Panama.

et al., 2017; Quillfeldt et al., 2015), particularly for individual species, there are few direct measurements of the duration of nutrient movement between trophic levels within marine ecosystems.

4.1. Baseline plankton

We found no strong drivers that spatially covary with the stable isotope composition of plankton across the Bay of Panama during the non-upwelling season. The overall isoscapes of the Bay of Panama were relatively spatially homogenous in both phyto- and zooplankton samples, although they showed localised depletions in $\delta^{13}\text{C}$ and, most strongly, $\delta^{15}\text{N}$ values. The depletions were generally quite close to shore, and likely caused by blooms of nitrogen-fixing cyanobacteria (Capone et al., 2005; Takai et al., 2000). This finding has implications for isoscapes based on POM and plankton measurements, as the localised variability can be high. If possible, time-series replicates should be taken to gauge the persistence of extreme isotopic values before inferences can be made on the influence of these values throughout the ecosystem.

Zooplankton showed relatively similar spatial variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to phytoplankton, although the greater spatial homogeneity in zooplankton values may reflect longer-term integration of isotopic composition than phytoplankton, and integration of a range of taxa and compositions in the primary producers (Smyntek et al., 2007). Isotopic fractionation between primary producers and herbivores is expected to be lower than the commonly used ecosystem averages of c. 3.4‰ in ^{15}N and c. 1‰ in ^{13}C (Sweeting et al., 2007; Vander Zanden and Rasmussen, 1999). This minimal spacing may be caused by a number of factors, such as low prey nitrogen content (Gaye-Siessegger et al., 2003), high nutrient availability (particularly in nutrient-rich, e.g. upwelled, waters), or abundance of large or colonial herbivores such as salps (Adams and Sterner, 2000; Henschke et al., 2015). Similar carbon and nitrogen isotope separations to those measured in this study ($\delta^{13}\text{C}$: 2.9 ± 0.03 , $\delta^{15}\text{N}$: 2.1 ± 0.12) have been recorded between phyto- and zooplankton fractions that were split by size at or below 200 μm , with minimally enriched isotope ratio values in the larger size classes (Fry and Quinones, 1994; Goering et al., 1990; Sholto-Douglas et al., 1991). The Δ values from this study suggest the $\delta^{15}\text{N}$ fractionation between primary producers and primary consumers is towards the low end of ecosystem estimates, in accord with that observed between primary producers and herbivores elsewhere, but relatively high $\delta^{13}\text{C}$ fractionation. While the zooplankton fraction was corrected for lipid content, the complex carbohydrates in the phytoplankton mean that arithmetic lipid correction is not possible; we suggest that the

carbohydrate and lipid content of the phytoplankton is the cause of this relatively high $\Delta^{13}\text{C}$ value between phyto- and zooplankton. The extreme depleted values we record are similarly low for both size fractions of plankton (Table 2, Figs. 2 and 3). These low values may be caused by localised nitrogen-fixation by cyanobacteria, such as *Trichodesmium* (Capone et al., 2005; Montoya, 2008), although it is possible that they are linked to anthropogenic nitrogen inputs as these can also have values close to 0‰ $\delta^{15}\text{N}$ (Morin et al., 2009). The small, significant relationship between $\delta^{15}\text{N}$ and marginally significant relationship between $\delta^{13}\text{C}$ values in zooplankton and proximity to settlements (driven by values in northern Las Perlas Archipelago) suggests that there may be some very localised effect of anthropogenic nutrients, possibly over short timespans as it is not apparent in the phytoplankton component, indicating that the zooplankton isotopic depletion may be due to nutrients from one to two months earlier. Interestingly, we do not find any isotopic effect of proximity to Panama City, indicating that nutrients from the City and the Canal may sediment rapidly out of pelagic circulation, may be mixed by the strong tidal currents, or may be swept rapidly out from the Bay for deposition elsewhere (Thompson, 2007). The Bay of Panama is subject to strong tidal flushing due to the large, regular, semidiurnal tides (Kirkpatrick, 1931), which may be the reason that no isotopic trace of the City is observed here. Alternatively, as suggested in the upwelling system off Morocco (Waser et al., 2000), low $\delta^{15}\text{N}$ values may be due to primary producers using more ammonium than nitrate for growth, where ammonium may originate from upwelled waters, or from bacterial action in waters with low oxygen content (McMahon et al., 2013). The lack of relationship between distances to anthropogenic nutrient sources and stable isotope compositions in phytoplankton is indicative that diazotrophs or ammonium uptake may be more likely explanations for the very depleted values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

4.2. Ecosystem structure

Simplification of complex and difficult to describe food web interactions into nutrient fluxes through trophic levels of an ecosystem enables understanding of the ecological processes structuring that ecosystem; stable isotope data provide information on such nutrient fluxes with relatively simple sampling requirements. Both for management of marine resources and for behavioural and dietary ecology, it is important to know the connectivity of an ecosystem and its inhabitants to different nutrient sources, for example pelagic versus benthic production (France, 1995; France and Peters, 1997; Trueman et al., 2014). Based on the stable isotope compositions of carbon and nitrogen, the

Bay of Panama pelagic ecosystem shows relatively linear, positive relationships with size and trophic level, suggesting a size-structured ecosystem. The patterns of nutrient transfer imply a single isotopic nutrient source with minimal evidence of modularity or separate food chains between open pelagic, reef-dwelling, or benthopelagic organisms. Enrichment along the $\delta^{15}\text{N}$ axis is related to trophic level (Fig. 3), with planktivores feeding above plankton, and predators feeding above planktivores. Enrichment in $\delta^{13}\text{C}$ also has a trophic component, but the most enriched consumers tend to be those using a combination of benthic and pelagic resources, *C. mysticetus*, *C. panamensis*, *E. labriiformis*, and *M. altipinnis* (Bayliff, 1963; Craig et al., 1999). Exclusively pelagic-feeding fishes had lower $\delta^{13}\text{C}$ values than those fishes whose diet may also contain some benthic prey items. Due to bacterial remineralisation, benthic ecosystem components are often enriched in the heavy isotopes of carbon (and sometimes nitrogen) relative to fresh, pelagic production (Cavan et al., 2017; France, 1995). Pacific anchoveta foraging on benthic diatoms in shallow waters, for which they have specialised gill rakers (Bayliff, 1963), and starry grouper, Pacific graysby, and tallfin croaker feeding on benthic fishes and invertebrates might be expected to show higher carbon isotope values than the measured pelagic fishes, as we observed in this study. These fishes were all, however, sampled towards the end of, or immediately following, upwelling season, which resulted in higher $\delta^{13}\text{C}$ values in rainbow chub; the enrichment seen in benthopelagic-feeding fishes could therefore be due to benthic nutrient input, upwelled nutrient enrichment, or a combination of both although the results should be treated with caution because of the low number and irregular temporal sampling. The $\delta^{13}\text{C}$ values of *C. mysticetus* were, however, higher than those of contemporaneous *K. ocyurus*, which suggests a component of benthic feeding in the isotopic composition of the anchoveta. We therefore suggest that relatively elevated values of $\delta^{13}\text{C}$ are likely to be a good indicator of benthic nutrient use in this system, with relatively lower values indicative of a more pelagic feeding strategy. This enrichment in ^{13}C composition from pelagic- to benthic-feeding organisms is a commonly observed trait in marine systems (Duffill Telsnig et al., 2018; e.g. France, 1995; Trueman et al., 2014). The lack of difference between *K. ocyurus* and *C. mysticetus* $\delta^{15}\text{N}$ values also suggests that these fishes feed at a very similar trophic position in the ecosystem, which implies greater algal use by rainbow chub or greater zooplankton consumption by Pacific anchoveta than recorded by previous studies (Bayliff, 1963; Dominici-Arosemena and Wolff, 2006). Greater zooplanktivory in *C. mysticetus* might also explain the large TDF (4.3‰) in $\Delta^{15}\text{N}$ between TL2-3.

4.3. Predatory fish ecology

Temporal similarity in the stable isotope composition of piscivorous fishes, particularly between sierra mackerel individuals, despite putative spatial segregation could indicate one of four issues:

- (a) misreporting of capture location,
- (b) fishes captured in the Gulf of Chiriquí or the open Pacific Ocean were very recent migrants from the Bay of Panama,
- (c) the Bay of Panama is the primary driver of pelagic environmental conditions (Alory et al., 2012; Legeckis, 1988; McCreary et al., 1989) and therefore nutrient source for this part of the TEP, influencing the stable isotope composition of the open Pacific Ocean and into the Gulf of Chiriquí, or
- (d) seasonal thermocline shoaling in the south-eastern part of the Gulf of Chiriquí, while weaker than the upwelling in the Gulf of Panama (Tao et al., 2013), may result in similarity in carbon and nitrogen stable isotope composition between animals feeding in each Gulf.

Migratory *C. hippurus* and *T. albacares* had a range of $\delta^{15}\text{N}$ values that were not correlated with their size, and so more likely related to their area of feeding. The piscivorous fishes, *C. hippurus*, *S. sierra*, and *T.*

albacares, had temporally similar $\delta^{13}\text{C}$ values from March 2014 to February 2015. Following correction to a mean mass for all piscivores, both *C. hippurus* and *T. albacares* were, however, depleted in ^{15}N relative to *S. sierra* when considering the entire time series. *T. albacares* that were sampled during February 2015, however, in the upwelling season, overlapped entirely in their nitrogen isotope composition with that of *S. sierra*. The similarity between these two species, with the *S. sierra* all resident in the Bay of Panama at this time, might suggest that the capture location of the tuna was misreported (e.g. erroneously reported as either Bay of Panama or Gulf of Chiriquí, see appendix), and that these predatory fishes had converged on the productive upwelling zone at this time, integrating upwelled nutrients from their prey. Capture locations were assigned to a broad oceanographic area (Bay of Panama, Gulf of Chiriquí, open Pacific Ocean) based on reported capture location by the fish market stall holder, therefore analyses based on these locations may not be as robust as analysis of time, which was firmly established. Alternatively, given the extension of upwelled waters westward to 95° W, and over 1500 km from the Gulf of Panama during this season (Alory et al., 2012; Legeckis, 1988), the *T. albacares* may have been caught in Chiriquí after integrating upwelled nutrients that originated in the Bay of Panama then flowed rapidly through this area of the TEP. The relative depletion of *T. albacares* and *C. hippurus* in ^{15}N suggests that $\delta^{15}\text{N}$ values are a better measure than $\delta^{13}\text{C}$ values of local versus open ocean production source in migratory fishes around the Panama area. Both explanations suggest the Bay of Panama is a productivity hotspot within the TEP during upwelling season. *T. albacares* appear to be sufficiently reliant upon upwelling and integrate local $\delta^{15}\text{N}$ values from upwelling-sourced nutrients sufficiently rapidly to be isotopically indistinguishable from local piscivorous fishes within 1.5–3 months of upwelling onset based on our calculated nutrient transfer times between trophic levels within this ecosystem.

We find it less likely that the seasonal shallowing of the Gulf of Chiriquí thermocline would cause similarity in carbon and nitrogen isotope compositions between animals caught here and in the Gulf of Panama, as previous research on oxygen isotope composition in bivalves between these areas did not observe similarity (Tao et al., 2013). It is, however, possible that organic isotope measurements in more rapidly grown tissues may find the smaller influence of temperature and nutrient chemistry than that observed in slower growing, inorganic bivalve minerals with somewhat more dampened signals of environmental variation. For future work on the reliance of migratory pelagic fishes on upwelled nutrients, more samples taken from fishes at known locations and over longer, more frequently sampled time scales within the Bay of Panama, the Gulf of Chiriquí, and in the open Pacific Ocean would be necessary to quantify the magnitude and timing of changes in isotopic composition of migratory predators that are due to feeding on upwelling-sourced nutrients. Fin clips, scales, or muscle biopsies would be useful means of gaining samples from catch-and-release sport-fished species such as *T. albacares* and *C. hippurus* (Williams et al., 2015).

4.4. Time series data and predator–prey mass ratios (PPMR)

Empirical measurements of the timing of nutrient transfer are lacking above the single species level, outside of experimental systems, and are largely absent for marine ecosystems. We found that the isotopic composition of rainbow chub measured monthly throughout the year in Las Perlas Archipelago is correlated with mean monthly sea surface temperature records with a lag of one to two months. Marine baseline carbon isotope values on a broad geographic scale are strongly linked to sea surface temperature (Lara et al., 2010; Magozzi et al., 2017; Tagliabue and Bopp, 2008), which are subsequently integrated through the trophic web. The isotopic composition of higher trophic level consumers is therefore linked to the location and environmental conditions of the ecosystem in which the consumers' tissues were grown (Bowen, 2010; Hobson, 1999; West et al., 2006). The significant negative correlation between *K. ocyurus* $\delta^{13}\text{C}$ values and SST, with a one-

to two-month lag, indicates a nutrient transfer time of one to two months from primary producers (TL1) to planktivorous (TL3) fishes, thus a mean transition time of 1 TL per 0.5 – 1 month in this tropical pelagic ecosystem. Similarly rapid integration of upwelled nutrients has also been measured in other warm water systems, including Lake Tanganyika and the South China Sea (Jiang and Wang, 2018; O'Reilly et al., 2002). This short period of time indicates a rapid transition of nutrients through the Bay of Panama Ecosystem, but it would be useful to collect a longer time series to enable tests of inter-seasonal variability in nutrient incorporation times.

The relatively low predator–prey mass ratio (PPMR) calculated for resident fishes of 376:1, may be indicative of inefficient, although rapid, transition of nutrients through the ecosystem (Barnes et al., 2010; Trebilco et al., 2013). The maximum trophic level of 6.2 indicates that this ecosystem supports a relatively inefficient, long trophic chain within this ecosystem with multiple discrete trophic levels. To confirm and clarify the full temporal extent of the cycles, however, it would be useful to obtain a longer time series. Knowledge of temporal dynamics in nutrient source and integration time are essential for the assessment of source contributions to the ecosystem and its components, determination of temporal stability in nutrient transfer, and for prediction of responses to change (Jennings et al., 2008; O'Reilly et al., 2002; Woodland et al., 2012).

The calculated PPMR of 113:1 for all fishes is relatively low for marine ecosystem PPMR measurements globally (Barnes et al., 2010), which, in combination with the low tissue-diet fractionation (TDF) in $\delta^{15}\text{N}$, suggests that the fish component of the pelagic system within the Bay of Panama is potentially inefficient in trophic transfer, likely with multiple trophic levels, and implies high species richness between predators and prey (Barnes et al., 2010; Jennings et al., 2002; Trebilco et al., 2013). Additionally, given that the PPMR value is lower when migrant fishes are included, this implies that the migratory predators may be consuming larger, more predatory species that are relatively similar in size to their predators. Reducing the $\Delta^{15}\text{N}$ (TDF) between trophic levels, or reduction of the slope of the relationship between $\delta^{15}\text{N}$ and \log_2 mass have similar effects, both increasing the efficiency of nutrient transfer by effectively shortening the food chain length, meaning that, for a given change in mass, there will be a smaller change in trophic level, implying a less efficient use of the prey resource (Barnes et al., 2010). Measurements of $\delta^{15}\text{N}$ - \log_2 mass within the entire ecosystem, and between known resident fishes in the Bay of Panama both increase the TDF relative to that of the entire fish community, thereby increasing the PPMR to 375:1 for the whole ecosystem, or 376:1 for resident fishes. For the resident fishes, the slope is slightly reduced relative to that of the whole ecosystem and to the entire fish community, also indicating greater nutrient transfer efficiency. The measured slopes are similar to those of North Sea fishes (slope = 0.335, (Jennings et al., 2001)), suggesting similar size structuring between the two ecosystems, but much higher than the slope of 0.263 measured in the tropical upwelling system in the Western Arabian Sea (Al-Habsi et al., 2008). The PPMR values (all fish = 113:1, resident fish = 376:1, whole ecosystem = 375:1) in the Bay of Panama are, however, orders of magnitude lower than the majority of literature studies. Reported values include the North Sea fish community (PPMR = 1136:1), which is a productive and highly seasonal temperate system, the southwest subtropical Pacific near New Caledonia (PPMR = 148,000:1) (Hunt et al., 2015), and in the seasonal upwelling systems of the Western Arabian Sea (PPMR = 7792:1), along the Atlantic margin of the Iberian Peninsula (PPMR = c. 200,000:1), and, more specifically, the Galician upwelling system (PPMR = 4500:1) (Bode et al., 2007, 2003), although the latter two studies included a much broader range of organism sizes. The Bay of Panama results are quite low in a global context (Al-Habsi et al., 2008; Barnes et al., 2010), and indicative of rapid, although somewhat inefficient nutrient transfer from low to high trophic levels within this ecosystem. Compared to other pelagic systems, these low values suggest a relatively mid-length and bottom-heavy pyramid or

column-shaped ecosystem, indicative of nutrient export at low trophic levels, and import at higher trophic levels (Trebilco et al., 2013). This result supports the relationship between sea surface temperature and $\delta^{13}\text{C}$ values in resident pelagic planktivores which suggest a mean nutrient transfer time of 1 TL per 0.5 – 1 month within this ecosystem.

5. Conclusions

Spatial phyto- and zooplankton carbon and nitrogen isotope compositions are relatively homogenous in non-upwelling season, but with localised point depletion, likely due to blooms of nitrifying primary producers or to localised uptake of ammonium rather than nitrate as a growth medium. As this study cannot provide information on the temporal stability at the base of the ecosystem, isoscapes should also be measured during upwelling to determine the extent of isotopic change due to changes in the environmental conditions, nutrient availability, and different isotopic composition of upwelled nutrients. This information would provide a more holistic view of the spatio-temporal influence of upwelling on ecosystem structure and nutrient transfer, and on the degree of integrated stable isotope signal dampening from primary production to higher trophic levels.

Upwelling-driven temperature changes and nutrients are recorded in the $\delta^{13}\text{C}$ values of resident fishes and integrated rapidly into the tissues of migrant consumers. The nutrient transfer time of carbon sources is c. 0.5 to 1 month per trophic level for this tropical pelagic ecosystem. Accounting for such lags in temporal dynamics of nutrient transfer and stable isotope composition can dramatically improve estimates of nutrient sources and timing of production at different levels of an ecosystem.

Together, isoscapes and *K. ocyurus* stable isotope compositions set a geographic, non-upwelling baseline and a temporal proxy baseline for the characterization and comparison of resident versus migrant organisms, pelagic versus benthic feeding, and upwelled versus non-upwelled nutrient use. The isotopic compositions, tissue-diet fractionation factors, and duration of nutrient transfer are essential but difficult to obtain information for comparative studies of pelagic, tropical, and upwelling-influenced marine ecosystems.

This ecosystem has a linear trophic structure, recorded in its $\delta^{15}\text{N}$ values, with both benthic and upwelling enrichment in $\delta^{13}\text{C}$ values. Carbon stable isotope composition is therefore useful to track pelagic versus benthic nutrient sources, and particularly to track upwelled nutrient use through time. Nitrogen stable isotope composition of migratory fishes, however, may be a better indicator of recent local versus imported nutrient use, i.e. whether the fish has fed within this ecosystem in recent months, or whether it is newly arrived.

The predator-prey mass ratios calculated in the system, in combination with the estimated maximum trophic level of 6.2, suggest that the Bay of Panama pelagic ecosystem has a relatively long trophic chain, with inefficient nutrient transfer between trophic levels. This result should be considered in the context of ecosystem management, particularly for fisheries, during less productive conditions such as years when El Niño events prevent upwelling in the area.

Given the taxonomically independent relationship between body size and trophic level, as measured in $\delta^{15}\text{N}$ values within organisms resident in this pelagic ecosystem, we suggest that size is a driving factor in determining behavioural and trophic ecology in pelagic animals within this area, and that size-based models and trophic ecology should be key in ecosystem models and impact assessments.

Acknowledgements

KMM was funded through a Smithsonian Stable Isotope Postdoctoral Fellowship. JNA was funded through the Smithsonian Tropical Research Institute Short-Term Fellowship Program. Thanks to the staff of the STRI Stable Isotope Laboratory, particularly Dayana Agudo, to Anthony Coates at STRI for fieldwork funding, to Jean

Philippe Belanger for assistance with sample preparation, and to ProMarina S.A. for access to samples. We would also like to thank the two anonymous reviewers whose comments and suggestions have greatly improved this manuscript. Samples were collected in the Bay of Panama under an ARAP permit.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2019.102145>.

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