

Effects of hydrological forcing on the structure of a tropical estuarine food web

Trisha B. Atwood, Tracy N. Wiegner and Richard A. MacKenzie

T. B. Atwood (trishaa@interchange.ubc.ca), Tropical Conservation Biology and Environmental Sciences Graduate Program, Univ. of Hawaii at Hilo, 200 W. Kawili St., Hilo, HI 96720, USA. Present address: Dept of Forest Sciences, Univ. of British Columbia, 3041 - 2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada. – T. N. Wiegner, Marine Science Dept, Univ. of Hawaii at Hilo, 200 W. Kawili St., Hilo, HI 96720, USA. – R. A. MacKenzie, USDA Forest Service, Inst. of Pacific Islands Forestry, 60 Nowelo St., Hilo, HI 96720, USA.

River flow can impact which sources of particulate organic matter (POM) fuel estuarine food webs. Here, we used stable carbon (C) and nitrogen (N) isotope analyses to compare how contributions of different POM sources (terrestrial, estuarine, and marine) to the diets of zooplankton and juvenile fishes differed between low and high river flow conditions, as well as spatially across a tropical estuary, Hilo Bay, Hawaii, USA. Diets of zooplankton and juvenile fishes were affected by river flow conditions, but the magnitude and the change in the basal resources depended on the location of the station in the estuary relative to the ocean and the river mouths. Consumers from the station most isolated from the ocean and with groundwater and overland flow inputs, utilized a combination of estuarine and terrestrial POM during both low and high river flow conditions and exhibited less variability in their basal resources than stations with direct ocean exchange. Consumers from stations in the Bay most affected by ocean exchange and river inputs utilized a combination of estuarine, terrestrial, and marine POM during low flow conditions, but shifted to marine and terrestrial POM during high river flow conditions. This shift to using terrestrial POM during high river flow conditions was substantial and up to 40% higher than values measured in other estuaries. Factors suspected to be affecting which POM source(s) consumers use in Hilo Bay are gross primary production, biological availability of exported terrestrial OM, and estuarine bacteria biomass, all of which are affected by river flow. Overall, our results suggest that Hilo Bay's food web and possibly those from other tropical estuaries are vulnerable to changes in hydrology, which may be further enhanced by global climate change.

Estuaries are dynamic ecosystems whose physical, chemical, and biological characteristics are greatly influenced by freshwater runoff from land and water exchange with the ocean (Day et al. 1989). As a result of their dynamic nature, estuaries support high levels of biological diversity, with multiple interconnected trophic links that result in complex food webs (Day et al. 1989, Cohen 1994). However, the spatial, temporal, and regional mechanisms governing the structures of these complex food webs remain unclear. One aspect under investigation is the importance of different organic matter (OM) sources to the base of estuarine food webs (Deegan and Garritt 1997, Mulkins et al. 2001, Pagano et al. 2006), and how the relative importance of these OM sources changes with natural and anthropogenic perturbations (Chanton and Lewis 2002, Hoffman et al. 2008, Schlacher et al. 2009).

Organic matter within estuaries is comprised of both autochthonous OM (i.e. in situ phytoplankton, marsh vegetation, benthic macroalgae), as well as allochthonous OM of terrestrial origin, which is transported into the estuary via rivers. It has been well documented in streams, rivers, and lakes that allochthonous OM subsidies increase secondary production (Wallace et al. 1997, Pace et al. 2007). However, several studies suggest that terrestrial OM is only a minor contributor to the diets of estuarine organisms, especially those feeding in

the water column (Deegan and Garritt 1997, Sobczak et al. 2002, Van den Meersche et al. 2009). The current consensus that pelagic estuarine food webs are endogenously fueled suggests that these communities may be less affected by the availability of allochthonous OM sources across spatial, temporal, and regional scales. In addition, studies have suggested that primary and secondary consumers are adaptive foragers that select high quality, low quantity autochthonous OM over more abundant, but lower quality terrestrial OM (Martineau et al. 2004, Delong and Thorp 2006). However, broad generalizations about estuarine food webs may limit our understanding of persistence and stability of estuarine ecosystems in the face of perturbation, especially global climate change.

Traditionally, estuarine food web studies focused on characterizing the trophic structure of a system at a single point in time. More recent studies have examined how temporal variation in hydrologic variables (i.e. river discharge) define and restructure food webs (Hoover et al. 2006, Hoffman et al. 2008, Schlacher et al. 2009). Fluctuations in river discharge affect the quantity and quality of terrestrial OM exported to estuaries (Wiegner et al. 2009), as well as estuarine phytoplankton growth, which may trigger responses in estuarine food webs (Hoover et al. 2006). River discharge and distance from

river mouths are also thought to influence the spatial scale of estuarine food web structure by governing across-ecosystem subsidies to estuarine consumers (Chanton and Lewis 2002, Hoffman et al. 2008, Schlacher et al. 2009, Tallis 2009). To date, the majority of these studies have mainly focused on temperate and subtropical estuaries, leaving tropical estuaries largely uncharacterized.

The dynamics among trophic levels in tropical estuaries are generally thought to be more tightly coupled than temperate systems due to their nearly continuous high temperatures and abundant light availability year round (Roman et al. 2002, Hoover et al. 2006). As a result of this tight coupling, secondary production within tropical estuaries responds quickly (e.g. days or weeks) to changes in phytoplankton communities caused by hydrological perturbations (Hoover et al. 2006). However, increases in river discharge caused by storm runoff can create two opposing changes to estuarine food web structure. If storm runoff contains high concentrations of dissolved nutrients that otherwise limit primary production and light availability is not significantly reduced by suspended solid inputs, then estuarine primary production may be stimulated and may fuel secondary production (Mallin et al. 1993, Hoover et al. 2006). In contrast, if storm runoff has high concentrations of suspended solids and water residence time in the estuary is long, then light limitation may reduce estuarine primary production (May et al. 2003, de Swart et al. 2007, Mead and Wiegner 2010). In order for secondary production to be sustained in the face of reduced primary production under high river flow conditions, organisms must receive terrestrial or marine OM subsidies. However, more regional data sets are needed to determine the extent to which river discharge structures estuarine food webs by altering contributions of autochthonous and allochthonous OM sources to consumers and how the importance of these sources is affected by changes in hydrology.

The present study used Hilo Bay, Hawaii, USA, to determine the impact of river flow on the structure of a tropical, estuarine, pelagic food web. Being a tropical system, Hilo Bay has abundant light and warm temperatures throughout the year, allowing for favorable phytoplankton growing conditions. Additionally, the Hilo Bay watershed has one of the highest annual rainfall rates in the USA and is the largest watershed in the state of Hawaii (Juvik and Juvik 1998). As a result, food web responses to increased river flow may be rapid and on the order of days (Mead and Wiegner 2010). The main objective of this study was to characterize the contributions of terrestrial, estuarine, and marine OM to secondary production of mesozooplankton in Hilo Bay under low and high river flow conditions. We specifically focused on particulate organic matter (POM) because it is directly consumed by mesozooplankton and based our design on previous estuarine food web studies (Deegan and Garritt 1997, Hoover et al. 2006, Schlacher et al. 2009). However, we recognize that dissolved organic matter (DOM) may indirectly fuel estuarine consumers through the microbial loop. Our hypothesis for this study was that terrestrial POM subsidies to consumers' carbon (C) and nitrogen (N) demands would increase with increasing river flow, as a result of reduced estuarine and marine POM availability, and increased terrestrial POM availability. This study also characterized the contributions of POM sources to dominant pelagic juvenile fishes of

economical, recreational, and cultural importance during low flow conditions. To accomplish these objectives, we measured stable C and N isotopes from POM sources, zooplankton, and fishes to identify which POM source(s) were the major contributors to primary and secondary consumers' diets.

Material and methods

Site description

Hilo Bay is a salt-wedge estuary located on the eastern side of Hawaii Island (Fig. 1). The surface area of the Bay is ~6.4 km² and ranges in depth from 0–15 m. Hilo Bay is semi-enclosed by a three-km long breakwall that affects water circulation and increases residence time of sediments and POM (Dudley and Hallacher 1991, USACOE 2009). Major surface freshwater inputs to the Bay are from the Wailoa and Wailuku Rivers. The Wailoa River is an perennial river with continuous groundwater inputs nears its mouth and its watershed drains 481 km², which is predominantly forest, but also contains a significant percentage of developed and cultivated land (Table 1). The Wailuku River is a perennial river and its watershed drains 574 km², which is predominantly forest (Table 1). The Hilo Bay area receives almost equal amounts of daylight between summer and winter months, with only a two hour difference between seasons, and has an average temperature of 23.3°C, with only a 3° change seasonally (Juvik and Juvik 1998). Additionally, Hilo Bay and its watershed have one of the highest precipitation rates within the USA, receiving on average 330 cm of rain nearshore and 508 cm of rain upslope annually (Juvik and Juvik 1998).

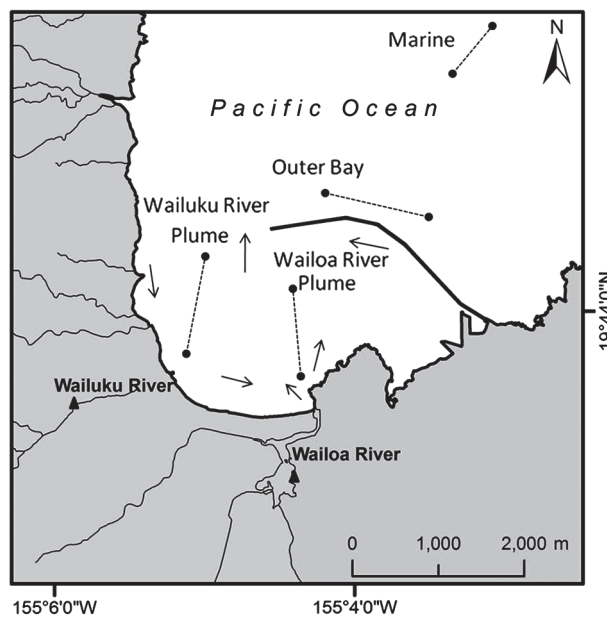


Figure 1. Map of stations and transects sampled from Jan 2007–Feb 2008 within Hilo Bay, Hawaii, USA, the Wailoa and Wailuku Rivers, and adjacent marine environment. Triangles represent single point sampling, while dotted lines represent transects. Arrows represent the general direction of currents in Hilo Bay and were obtained from Dudley and Hallacher 1991.

Table 1. Characteristics of the Wailuku and Wailoa Rivers' watersheds, Hawaii, USA. Land cover data were obtained from < www.csc.noaa.gov/crs/lca/hawaii.html > and are from 2001. To our knowledge, there were no significant changes to land cover from 2001 to 2008. N/A = not available.

Parameter	Wailoa River	Wailuku River
Watershed area (km ²)	481	576
Headwater elevation (m)	762	3500
Riparian land cover (% of each river)		
high-intensity developed	3.3	0.1
low-intensity developed	7.7	0.2
cultivated land	3.9	0.8
grassland	27.3	26.0
evergreen forest	40.7	59.0
scrub/shrub	14.6	10.7
bare land	0.3	2.9
emergent wetland	N/A	0.3
water	2.3	N/A

Samples of POM sources and consumers were collected from 2007–2008 from two riverine stations (Wailoa and Wailuku Rivers), three estuarine stations (Wailoa River plume, Wailuku River plume, and Outer Bay), and one off-shore marine station (Fig. 1). Multiple stations within the Bay were chosen to spatially characterize food web variability. The Wailoa River plume station, located in the southeastern portion of the Bay, was the inner most station in Hilo Bay and is isolated from direct surface water exchange with the ocean (Fig. 1). The Wailuku River plume station was located in the southwestern portion of the Bay, with a 1.5 km opening connecting it to the Pacific Ocean (Fig. 1). The Outer Bay station was located on the outside of the breakwall, outside the harbor, and had direct surface water exchange with the Pacific Ocean (Fig. 1). Riverine and estuarine samples were collected under eight low ($< 8.0 \text{ m}^3 \text{ s}^{-1}$) and four high ($> 10.0 \text{ m}^3 \text{ s}^{-1}$) river flow conditions, as measured at the Wailuku River gage (USGS Station no. 16704000) at Piipihonua (Table 2). Due to high surf advisories, the Outer Bay station was not accessible during two of the high river flow events. The marine station was located two km outside the Bay and was sampled on two low flow and one high flow events (Fig. 1).

Sample collection

Terrestrial, estuarine and marine POM were collected using a 20- μm mesh plankton net. Particulate organic matter samples were later size fractionated into a 20–50 μm size group. Here, terrestrial POM was a mixture of both riverine and land-derived POM. Terrestrial POM from the Wailoa and Wailuku Rivers were collected one day prior to collection of estuarine consumers during low river flow conditions and two days prior during high river flow conditions. A two day gap should have allowed for terrestrial POM to be incorporated into Hilo Bay's estuarine food web, as a previous study in Kaneohe Bay on Oahu Island, Hawaii, found that the food web responded to increased river flow on the order of days (Hoover et al. 2006). Nets were placed in a flowing portion of the river for ten minutes or until a minimum of five mg dry mass of sample was collected. Estuarine POM was collected along three transects at each estuarine station during

Table 2. Daily discharge from the Wailuku River, Hilo, Hawaii, USA, on low and high river flow sampling days during this study. Wailuku River data were obtained from USGS gage no. 16704000 < <http://hi.water.usgs.gov/data/adrweb/2005/sw/portal/16704000.html> >.

River flow condition	Date	Wailuku River discharge ($\text{m}^3 \text{ s}^{-1}$)
Low	03/14/2007	1.13
	05/03/2007	1.50
	06/18/2007	0.85
	07/08/2007	7.65
	07/30/2007	1.36
	09/05/2007	1.84
	10/10/2007	1.93
	11/07/2007	1.53
High	01/10/2007	10.56
	03/01/2007	45.59
	12/12/2007	22.23
	01/29/2008	26.73

low and high river flow conditions (Fig. 1). Plankton nets (20- μm mesh) were towed approximately one meter below the surface at two knots for ten minutes along each transect. Extensive picking and filtering was used to remove terrestrial material from estuarine POM samples. However, despite our best attempts to remove terrestrial material, fine particles may have remained in the estuarine sample. Thus, in this study, estuarine POM was a mixture of riverine, estuarine and marine POM. Marine POM was collected from eleven overlapping transects using methods described above for estuarine POM. All samples were immediately placed on ice and stored frozen until further analyses.

Zooplankton and larval fishes were collected simultaneously with the estuarine POM samples using 150- μm and 500- μm mesh plankton nets towed approximately one meter below the surface at two knots for three consecutive ten minute intervals along designated transects (Fig. 1). Samples were immediately placed on ice. Plankton were later size fractionated into 150–500 μm and $\geq 500 \mu\text{m}$ bulk samples, and a sub-sample of each size group was stored frozen until analysis. Dominant secondary consumers (i.e. calanoid copepods, crab megalops, *Sagitta* sp. (chaetognaths), and larval fishes) were removed from the remaining bulk sample for individual analysis. Dominant zooplankton groups were determined from visual surveys and M and E Pacific's report on Hilo Bay (1980).

Pelagic juvenile fishes of economical, recreational, and cultural importance (i.e. *Herklotsichthys quadrimaculatus* blue stripe herring, *Encrasicholina purpurea* nehu, *Kuhlia sandvicensis* Hawaiian flagtail, and *Scomberoides lysan* leatherback) were also collected from multiple stations within the Wailoa and Wailuku Rivers' plumes by throwing a 0.60-cm mesh cast net from shore, a method used by Hawaii's Dept of Aquatic Resources. Fish species of interest were not found at the Wailuku River station. Isotopic turnover of fish tissue is relatively slow compared to larval fish and zooplankton, and estimates of isotopic turnover are unknown for these species. Therefore, dietary analyses of juvenile fishes were done for low flow days only. Fish were only collected on days that had > 30 consecutive days of low river flow ($< 8.0 \text{ m}^3 \text{ s}^{-1}$). All samples were stored frozen until analyzed for stable C and N isotopes.

Table 3. Average (SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of particulate organic matter (POM) sources within Hilo Bay, Hawaii, USA, during low and high river flow conditions. Wailoa and Wailuku River samples are comprised of terrestrial POM, river plumes and outer Bay samples consist of estuarine POM, and marine samples consists of marine POM.

POM sources	n	Low flow		n	High flow	
		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Wailoa River	8	−28.590 (0.249)	3.689 (0.155)	4	−28.132 (0.251)	3.277 (0.099)
Wailuku River	8	−19.995 (0.313)	0.870 (0.073)	4	−25.554 (0.102)	0.827 (0.071)
Wailoa River plume	8	−22.277 (0.492)	3.560 (0.148)	4	−23.966 (0.238)	3.343 (0.523)
Wailuku River plume	8	−20.952 (0.408)	3.405 (0.312)	4	−24.880 (0.689)	3.387 (0.181)
Outer Bay	8	−20.983 (0.629)	3.699 (0.120)	3	−23.461 (0.399)	3.509 (0.422)
Marine	2	−20.641 (0.129)	3.643 (0.328)	1	−20.821	3.497

Stable isotope analyses

Particulate organic matter, zooplankton, larval fishes, and muscle tissue from juvenile fishes were analyzed for stable C and N isotopes. Samples that were collected multiple times on a single day were pooled and the average C and N isotopic signatures were used in analyses. Samples with insufficient biomass were pooled across transects when possible. Prior to stable isotope analysis, samples analyzed for C were acid digested with 10% HCl to remove calcium carbonate (Jacob et al. 2005). Pooled POM samples were filtered onto pre-combusted (500°C, 6 h) Whatman GF/F filters, dried at 70°C to a constant mass, and packaged in 9 × 10 mm tin capsules. Zooplankton and fishes samples were dried following the above procedures and then homogenized using a mortar and pestle, weighed, and packed into 5 × 9 mm tin capsules. All samples were analyzed for stable C and N isotopic composition using an elemental analyzer coupled to a isotope ratio mass spectrometer. Stable isotope results are presented as deviations from a standard (VPDB for C and atmospheric N_2 for N). Reproducibility at natural abundance levels were $\pm 0.04\text{‰}$ and $\pm 0.07\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Food web analyses

We examined differences in the POM base of food webs between low and high river flow conditions and among estuarine stations by estimating the percent contribution of different POM sources (terrestrial, estuarine and marine) to consumers' diets within Hilo Bay. Percent contributions of different POM sources to consumers' organic C and N demands were calculated using the SIAR ver. 4.0 mixing model (stable isotope analysis in R) (Parnell et al. 2010). Percent contributions are reported as the 50% Bayesian credibility interval. Due to the position of the breakwall and currents within Hilo Bay (Dudley and Hallacher 1991, USACOE 2009), marine POM was excluded as a possible POM source for consumers within the Wailoa River plume (Fig. 1). Station-specific (Wailoa River plume, Wailuku River plume and Outer Bay) stable isotopic values of estuarine POM were averaged within river flow conditions and used in dietary analysis of consumers collected from that location. Consumers' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were also averaged within river flow conditions. Because the aim of this study was to determine which POM source was fueling the base of the food web, POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were corrected for isotopic trophic shifts using Eq. 1:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}_{\text{adj}} = \delta^{13}\text{C}_i \text{ or } \delta^{15}\text{N}_i - (\alpha \times \text{TL} - 1) \quad (1)$$

where $\delta^{13}\text{C}_i$ or $\delta^{15}\text{N}_i$ is the corrected POM value, $\delta^{13}\text{C}_i$ or $\delta^{15}\text{N}_i$ is the initial stable C or N isotopic signature of the POM source, α is the mean discrimination factor (DF) ($-0.2 \pm 0.21\text{‰}$ for C and $2.2 \pm 0.30\text{‰}$ for invertebrate consumers, and $1.3 \pm 0.30\text{‰}$ for C and $3.3 \pm 0.26\text{‰}$ for N for fishes (McCutchan et al. 2003)), and TL is the trophic level of the consumer being analyzed, which was determined using gut content and dietary analysis from the literature (Table 4). The 150–500- μm bulk plankton, $\geq 500\text{-}\mu\text{m}$ bulk plankton, and larval fishes were not identified to species, and therefore, TL could not be estimated using literature. The TLs of these consumers were estimated by plotting C and N isotopic signatures on an x–y scatterplot. This analysis showed that 150–500- μm bulk plankton and one group of larval fishes grouped closely with calanoid copepods and $\geq 500\text{-}\mu\text{m}$ bulk plankton and the remaining larval fishes grouped closely with *Sagitta* sp. As a result, these consumers were given the same TL as copepods and *Sagitta*, respectively.

Statistical analyses

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of POM sources were compared between river flow conditions (low vs high) and among stations (Wailoa River, Wailuku River, Wailoa River plume, Wailuku River plume, Outer Bay, Marine) using a two-way analysis of variance (ANOVA). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumers (i.e. 150–500- and $\geq 500\text{-}\mu\text{m}$ bulk plankton, copepods, crab megalops, *Sagitta* sp. (chaetognaths), larval fishes) were also compared between river flow conditions and among stations using a two-way ANOVA. Fixed effects for both analyses included river flow condition and station, along with the two-way interaction term. Post hoc analyses were conducted using the Tukey HSD multiple comparisons test and all statistical analyses were performed in Statistica ver. 9.0 (StatSoft, Tulsa, OK) at an α level of 0.05.

Results

Stable isotope characterization

POM sources

The stable C and N isotopic composition of POM sources to Hilo Bay exhibited significant hydrological and spatial differences (Table 3, Fig. 2). In general, $\delta^{13}\text{C}$ signatures of POM sources were significantly more depleted in ^{13}C during

Table 4. Average (SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, number of samples (n), trophic level (TL), and literature source for TL of consumers collected from three stations (Wailoa River plume, Wailuku River plume, and Outer Bay) within Hilo Bay, Hawaii, USA, during low and high river flow conditions. (-) indicates where no samples were taken.

Consumers	Wailoa River plume				Wailuku River plume				Outer Bay				TL	TL source
	n	Low flow	n	High flow	n	Low flow	n	High flow	n	Low flow	n	High flow		
150–500- μm bulk plankton	8		4		8		4		8		4		2	
$\delta^{13}\text{C}$		-21.224 (0.233)		-22.740 (0.515)		-21.392 (0.400)		-22.190 (0.340)		-19.470 (0.076)		-20.560 (0.099)		
$\delta^{15}\text{N}$		5.173 (0.225)		4.061 (0.497)		5.092 (0.190)		3.860 (0.415)		4.527 (0.296)		3.583 (0.120)		
Calanoid copepods	8		4		8		4		8		4		2	Flemming 1939, Anraku and Omori 1963, Roman 1977, Downs and Lorenzen 1985, Turner 1986, Kleppel 1993, Cornils et al. 2007
$\delta^{13}\text{C}$		-21.704 (0.102)		-22.294 (0.404)		-21.992 (0.270)		-22.082 (0.499)		-21.482 (0.036)		-22.213 (0.050)		
$\delta^{15}\text{N}$		5.168 (0.334)		5.403 (0.161)		4.813 (0.231)		4.682 (0.123)		5.245 (0.347)		5.469 (0.068)		
Crab megalops	8		4		8		4		8		0		2	Harms et al. 1994, Perez and Sulkin 2005, Schwaborn et al. 2006, Burnett and Sulkin 2007, Coelho et al. 2009
$\delta^{13}\text{C}$		-20.176 (0.319)		-20.330 (0.308)		-20.146 (0.254)		-20.465 (0.311)		-20.460 (0.190)		-		
$\delta^{15}\text{N}$		4.791 (0.719)		4.413 (0.316)		4.170 (0.401)		3.548 (0.563)		4.513 (0.491)		-		
T2 larval fishes	4		4		4		4		4		0		2	
$\delta^{13}\text{C}$		-20.561 (0.377)		-22.343 (0.810)		-20.546 (0.471)		-19.640		-20.772 (0.456)		-		
$\delta^{15}\text{N}$		5.605 (0.295)		4.732 (0.235)		5.247 (0.200)		6.297		5.608 (0.827)		-		
$\geq 500\text{-}\mu\text{m}$ bulk plankton	8		4		8		4		8		4		3	
$\delta^{13}\text{C}$		-20.088 (0.210)		-22.182 (0.357)		-19.344 (0.097)		-20.594 (0.291)		-19.111 (0.343)		-20.256 (0.278)		
$\delta^{15}\text{N}$		7.129 (0.176)		6.723 (0.582)		7.255 (0.201)		6.313 (0.104)		6.495 (0.235)		5.614 (0.507)		
<i>Sagitta</i> sp	8		4		8		4		8		4		3	Pearre 1973, Canino and Grant 1984, Geisecke and González 2004
$\delta^{13}\text{C}$		-19.712 (0.119)		-21.233 (0.518)		-19.771 (0.139)		-19.835 (0.049)		-20.139 (0.455)		-19.718 (0.533)		
$\delta^{15}\text{N}$		8.002 (0.167)		6.880 (0.323)		7.885 (0.097)		6.881 (0.248)		7.776 (0.150)		6.331 (0.087)		
T3 larval fishes	3		3		1		4		0		0		3	
$\delta^{13}\text{C}$		-19.582 (0.304)		-22.330 (1.201)		-19.645		-19.109 (0.505)		-		-		
$\delta^{15}\text{N}$		8.759 (0.542)		8.225 (0.889)		7.68		8.578 (0.068)		-		-		
<i>Herklotsichthys quadrimaculatus</i>	8												3	Williams and Clarke 1983, Milton et al. 1994
$\delta^{13}\text{C}$		-18.469 (0.318)		-		-		-		-		-		
$\delta^{15}\text{N}$		9.319 (0.077)		-		-		-		-		-		
<i>Encrasicholina purpurea</i>	9												3	Clarke 1989, James and Findlay 1989, Bacha and Amara 2009, Islam and Tanaka 2009
$\delta^{13}\text{C}$		-18.402 (0.284)		-		-		-		-		-		
$\delta^{15}\text{N}$		9.130 (0.230)		-		-		-		-		-		
<i>Kuhlia sandvicensis</i>	8												3	Tester and Trefz 1954
$\delta^{13}\text{C}$		-18.295 (0.463)		-		-		-		-		-		
$\delta^{15}\text{N}$		8.955 (0.328)		-		-		-		-		-		
<i>Scomberoides lysan</i>	6												4	Major 1973, Blaber and Cyrus 1983, Lucas and Benkert 1983
$\delta^{13}\text{C}$		-16.296 (0.175)		-		-		-		-		-		
$\delta^{15}\text{N}$		10.723 (0.383)		-		-		-		-		-		

high river flow conditions than during low river flow conditions ($F_{1,50} = 42.23$, $p < 0.001$; Table 3, Fig. 2). Carbon isotopic signatures of POM sources were significantly different among stations ($F_{5,50} = 47.06$, $p < 0.001$). Additionally, there was a significant interaction between station and river flow condition ($F_{5,50} = 9.51$, $p < 0.001$), which showed that a station's $\delta^{13}\text{C}$ POM signature was affected by river flow conditions. During low river flow conditions, the Wailoa River's POM was significantly more depleted in ^{13}C (down to 8.60‰) compared to POM from the Wailuku River, estuarine (Wailoa River plume, Wailuku River plume and Outer Bay), and marine stations. The Wailuku River's POM was enriched in ^{13}C compared to other POM sources, but was only significantly different than POM from the Wailoa River and the Wailoa River plume during low river flow conditions. Despite the depletion of ^{13}C in all POM sources during high river flow conditions, the Wailoa River's POM was still significantly more depleted in ^{13}C relative to POM from the Wailuku River, estuarine and marine stations. With the exception of Wailoa River's POM, the Wailuku River's POM was more depleted in ^{13}C up to ~5‰ relative to other POM sources, and was significantly different than the Wailoa River and marine POM sources during high river flow conditions.

Stable isotopic N signatures of POM sources were not significantly different between low and high river flow events ($F_{1,50} = 1.227$, $p = 0.273$) and there was no interaction between station and river flow condition ($F_{5,50} = 0.227$, $p = 0.949$). POM from high river flow events was depleted in ^{15}N compared to POM from low river flow events; however, this difference was not significant. The $\delta^{15}\text{N}$ signatures of POM sources varied significantly among stations ($F_{5,50} = 42.358$, $p < 0.001$), which was due to Wailuku River's POM being significantly more depleted in ^{15}N during low (up to 2.83‰) and high river flow conditions (up to 2.68‰) conditions compared to all other stations (Table 3, Fig. 2).

Consumers

Similar to POM sources, $\delta^{13}\text{C}$ signatures of consumers from estuarine stations exhibited significant hydrological and spatial differences and there was a significant interaction between station and river flow condition ($F_{2,168} = 4.16$, $p = 0.017$), which again suggests that consumers' $\delta^{13}\text{C}$ signatures at a given station were affected by river flow. Pooled consumers' $\delta^{13}\text{C}$ signatures were significantly more enriched in ^{13}C during low river flow conditions than high ones ($F_{1,168} = 6.18$, $p = 0.014$; Table 4, Fig. 2). Consumers' $\delta^{13}\text{C}$ signatures were similar among all three estuarine stations during low river flow conditions, but Wailoa River Plume's consumers were significantly different than Wailuku River Plume's consumers during high river flow conditions. ($F_{2,168} = 4.44$, $p = 0.013$). The $\delta^{13}\text{C}$ values of consumers from the Wailoa River plume were depleted by as much as 2.8‰ compared to consumers from the Wailuku River plume during high river flow conditions.

Stable isotopic N signatures of consumers were not significantly different between river flow conditions ($F_{1,168} = 0.578$, $p = 0.448$) or among stations ($F_{2,168} = 1.689$, $p = 0.188$; Table 4, Fig. 2), and there was no significant interaction between station and river flow condition ($F_{2,168} = 0.625$, $p = 0.537$). Although not significantly different, $\delta^{15}\text{N}$ signatures of consumers were more depleted in ^{15}N during high river flow conditions compared to low flow ones.

Food web analysis

The SIAR mixing model indicated that POM source utilization by consumers varied spatially and with hydrological conditions within Hilo Bay (Table 5, Fig. 3). Because of the significant interaction between river flow condition and station for POM and consumers' $\delta^{13}\text{C}$ signatures, food web analysis results are presented by station below. Estuarine POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures from all stations within the Bay were pooled as there were no significant differences among them.

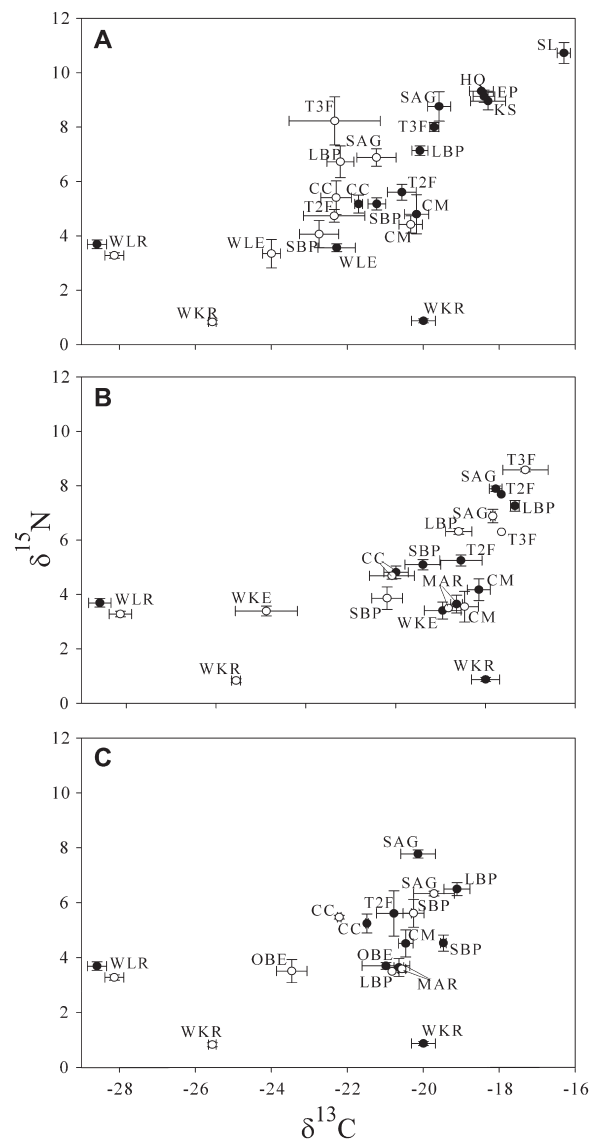


Figure 2. Mean ($\pm$ SE) stable carbon (C) and nitrogen (N) isotopic signatures of particulate organic matter sources (POM) and consumers from the Wailoa River plume (A), Wailuku River plume (B), and Outer Bay (C) stations during low (filled circles) and high (open circles) river flow conditions. Codes are as follows: WLR = Wailoa River POM, WKR = Wailuku River POM, WLE = Wailoa River plume estuarine POM, WKE = Wailuku River plume estuarine POM, OBE = Outer Bay estuarine POM, MAR = marine POM, SBP = 150–500- μm bulk plankton, CC = calanoid copepods, CM = crab megapods, T2F = trophic level two larval fishes, LBP = $\geq 500\text{-}\mu\text{m}$ bulk plankton, SAG = *Sagitta* sp. T3F = trophic level three larval fishes, HQ = *Herklotischthys quadrimaculatus*, EP = *Encrasicholina purpurea*, KS = *Kuhlia sandvicensis*, SL = *Scomberoides lysan*.

Table 5. Range of percent dietary contributions of particulate organic matter (POM) sources (WL = Wailoa River POM, WK = Wailuku River POM, E = estuarine POM, and M = marine POM) to consumers collected from three stations (Wailoa and Wailuku River plumes and Outer Bay) within Hilo Bay, Hawaii, USA, during low and high river flow conditions. Percent contributions were determined using SIAR ver. 4.0. (–) indicates where no samples were taken. Values are reported as the 50% credibility interval.

Condition	Consumer	Wailoa River plume			Wailuku River plume				Outer Bay			
		WL	WK	E	WL	WK	E	M	WL	WK	E	M
Low flow	150–500- μ m bulk plankton	0–1	35–40	59–64	6–9	23–26	29–38	30–38	0–1	45–49	4–19	30–40
	calanoid copepods	5–8	40–48	43–52	15–17	32–36	26–34	22–30	9–10	15–21	2–6	62–70
	crab megalops	1–3	44–57	33–45	0–1	52–62	2–10	12–22	0–1	44–51	3–10	32–41
	T2 larval fishes	1–36	20–26	38–50	1–4	23–29	28–36	29–37	1–3	12–20	31–39	33–42
	$\geq$ 500- μ m bulk plankton	0–1	95–97	1–3	0–1	0–1	1–8	87–94	0–1	1–4	9–22	70–84
	<i>Sagitta</i> sp.	0–1	91–97	2–7	0–1	1–5	26–39	41–54	0–2	1–6	33–44	35–45
	T3 larval fishes	1–6	36–55	35–46	23–33	24–33	24–33	24–33	–	–	–	–
	<i>Herklotsichthys quadrimaculatus</i>	1–2	34–38	60–64	–	–	–	–	–	–	–	–
	<i>Encrasicholina purpurea</i>	0–2	44–49	47–53	–	–	–	–	–	–	–	–
	<i>Kuhlia sandvicensis</i>	1–3	46–52	41–49	–	–	–	–	–	–	–	–
	<i>Scomberoides lysan</i>	0–3	85–94	1–9	–	–	–	–	–	–	–	–
High flow	150–500- μ m bulk plankton	0–1	47–52	47–51	0–1	40–46	0–1	49–54	0–2	74–78	1–3	14–19
	calanoid copepods	34–47	7–12	41–52	1–4	33–36	1–7	34–51	1–3	5–10	16–25	65–71
	crab megalops	2–12	33–43	35–46	1–6	28–38	1–9	27–38	–	–	–	–
	T2 larval fishes	25–35	31–37	36–44	23–32	22–32	24–33	23–32	–	–	–	–
	$\geq$ 500- μ m bulk plankton	2–8	86–92	1–2	0–1	0–2	0–2	89–92	0–1	1–3	0–2	90–93
	<i>Sagitta</i> sp.	3–12	36–47	36–45	1–6	0–3	1–31	33–47	1–5	2–10	25–36	33–46
	T3 larval fishes	31–41	32–43	28–39	1–9	1–7	24–33	29–39	–	–	–	–

Wailoa River plume

Estuarine and terrestrial POM were both large contributors of organic C and N to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of primary consumers within the Wailoa River plume during both low and high river flow conditions (Table 5, Fig. 3A–B). Overall, the Wailuku River was the major source of terrestrial POM to consumers' signatures during both low and high river flow conditions (Table 5). However, the contribution of terrestrial POM from the Wailoa River increased during high river flow up to $6\times$ for all consumers within the Wailoa River plume, except 150–500- μ m bulk plankton which had no detectable change in contribution (Table 5).

Similar to primary consumers, estuarine and terrestrial POM were also important sources of POM to secondary consumers in the Wailoa River plume, regardless of river flow condition (Table 5, Fig. 3A–B). Additionally, the Wailuku River was also the largest contributor of terrestrial POM to secondary consumers for both flow conditions (Table 5). Estuarine POM made a substantial contribution to the organic C demands of T3 larval fishes during low river flow conditions, and *Sagitta* sp. and T3 larval fishes during high river flow conditions (Table 5). An increase in the contribution of terrestrial POM in the Wailoa River's secondary consumers' signatures were also observed during high river flow conditions (Table 5). The three secondary consumer juvenile fish species (*H. quadrimaculatus*, *E. purpurea* and *K. sandvicensis*) from the Wailoa River plume all had similar POM source contributions to their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, with both estuarine and terrestrial contributing substantially to their organic C and N demands (Table 5). *Scomberoides lysan* differed from the other juvenile fish species in that Wailuku River POM was the only major contributor to their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (Table 5).

Wailuku River plume

In general, most primary consumers from the Wailuku River plume utilized a combination of terrestrial, estuarine, and

marine POM almost equally during low river flow conditions, and terrestrial and marine POM during high river flow conditions (Table 5, Fig. 3C–D). The Wailuku River was the largest contributor of terrestrial POM to consumers' C and N demands for both low and high river flow conditions (Table 5). Both 150–500- μ m bulk plankton and calanoid copepods had similar contributions of terrestrial, estuarine, and marine POM during low flow conditions. However, during high river flow conditions, the contribution of organic C and N to these consumers from estuarine POM decreased $\sim 40\times$, while marine POM contributions increased up to $2\times$ (Table 5). Crab megalops primarily utilized terrestrial POM during low flow conditions, but had similar contributions from terrestrial and marine POM during high river flow conditions (Table 5). T2 larval fishes had similar contributions of terrestrial, estuarine, and marine POM to their organic C and N demands during both low and high river flow conditions (Table 5).

Secondary consumers from the Wailuku River plume utilized estuarine and marine POM during both low and high river flow conditions (Table 5, Fig. 3C–D). $>500\text{-}\mu\text{m}$ bulk plankton obtained their organic C and N from marine POM during both low and high flow conditions (Table 5). *Sagitta* sp. had similar contributions from both estuarine and marine POM during both river flow conditions. T3 larval fishes had similar contributions from terrestrial, estuarine, and marine POM during low flow conditions, but their terrestrial POM contribution was substantially reduced during high river flow conditions (Table 5).

Outer Bay

Primary consumers from the Outer Bay station utilized a combination of terrestrial and marine POM during low river flow conditions; however, there was no consistent pattern with regards to POM source utilization during high river flow conditions (Table 5, Fig. 3E–F). Terrestrial and marine

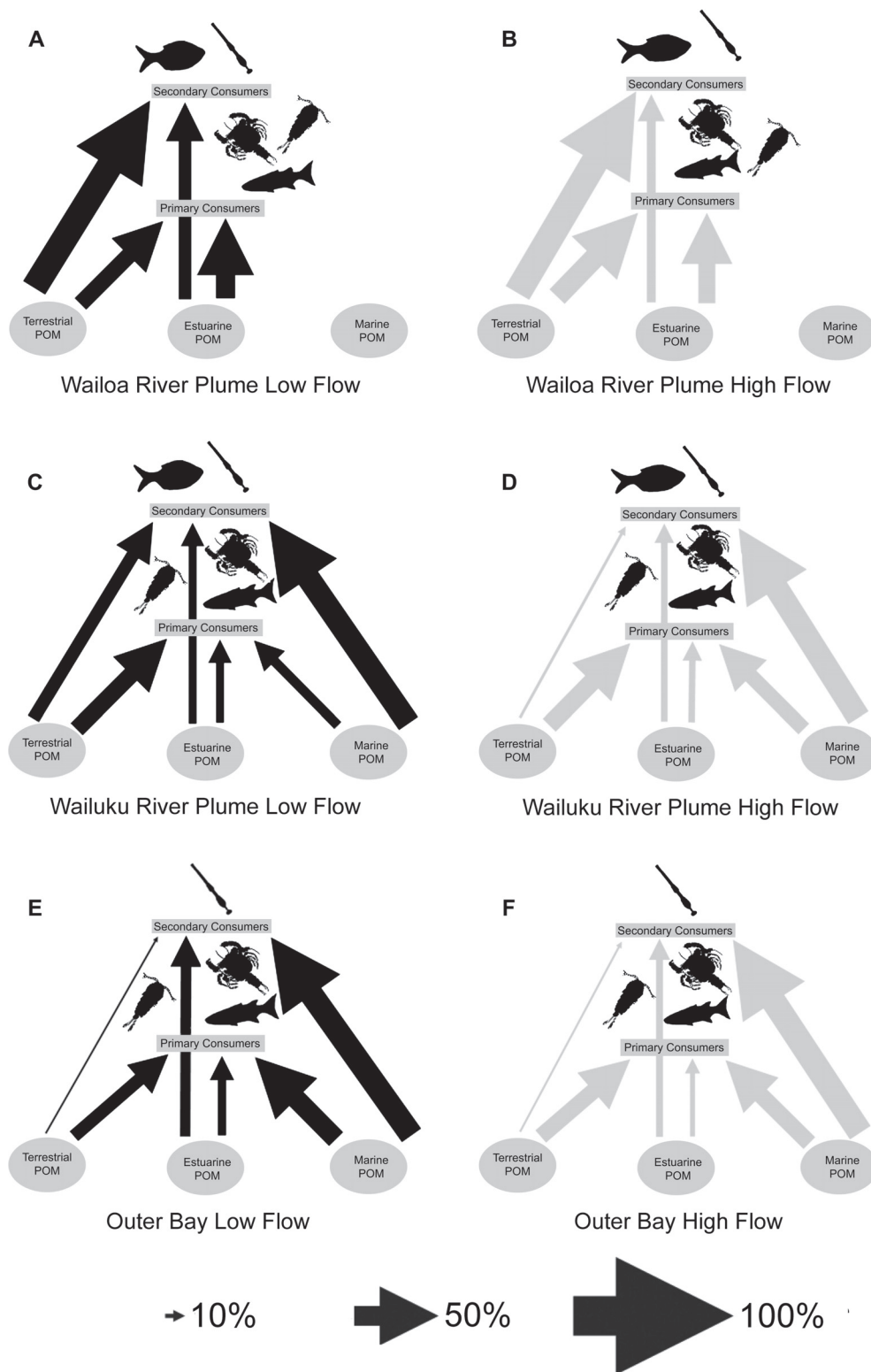


Figure 3. Dominant patterns in flux of particulate organic matter (POM) sources (terrestrial, estuarine, and marine) to Wailoa River plume [low flow (A) and high flow (B)], Wailuku River plume [low flow (C) and high flow (D)], and Outer Bay [low flow (E) and high flow (F)] to primary and secondary consumers. Black arrows represent low river flow conditions and grey arrows represent high river flow conditions. Thicknesses of arrows are proportional to the median percent contribution of the POM source to a consumer group and the relative thickness scale is shown at the bottom of the figure. Groupings of primary and secondary consumers were determined using trophic levels from Table 4. Median percent contributions were determined from the minimum and maximum contributions reported in Table 5. Percent contributions of terrestrial POM sources were determined by summing values from the Wailoa and Wailuku Rivers. Due to current direction and position of the breakwall (Fig. 1) contributions of marine POM were not estimated for consumers in the Wailoa River plume.

POM contributed a similar proportion to the organic C and N demands of the 150–500- μm bulk plankton during low river flow conditions, while terrestrial POM was primarily used during high flow conditions (Table 5). Calanoid copepods primarily utilized marine POM during both low and high river flow conditions (Table 5). Crab megalops and T2 larval fishes were not found at this station during high river flow conditions, and therefore, no comparisons could be made for these consumers between river flow conditions.

Secondary consumers from the Outer Bay station consisted of only >500- μm bulk plankton and *Sagitta* sp.; T3 larval fishes were not found at this station. While >500- μm bulk plankton and *Sagitta* sp. used different proportions of POM sources, marine POM was generally the greatest contributor during both river flow conditions (Table 5, Fig. 3E–F). For >500- μm bulk plankton during low river flow conditions, marine POM contributed 88% to their organic C and N demands, while estuarine POM contributed the remaining 22%. During high river flow conditions, estuarine POM contributions dropped to 0–2%, while marine POM contributions stayed high for the >500- μm bulk plankton. Estuarine and marine POM contributed the most and a similar percentage to *Sagitta* sp.'s organic C and N demands during both low and high river flow conditions (Table 5).

Discussion

While the effect of riverine discharge on estuarine food web structure has been documented in temperate and subtropical regions (Chanton and Lewis 2002, Hoffman et al. 2008, Schlacher et al. 2009), its role in tropical estuarine food webs, which are thought to be tightly coupled, is largely unknown. In Hilo Bay, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of POM and consumers revealed a spatially and temporally dynamic food web largely influenced by hydrology. While our hypothesis that contributions of terrestrial POM to consumers' diets would increase during high river flow conditions was generally true, this increase was not reflective of the eleven-fold increase in terrestrial POM previously documented in Hilo Bay during high river flow conditions (Wiegner et al. 2009). Additionally, there were also several consumers who exhibited a large decrease or had little change in the contribution of terrestrial POM to their organic C and N demands during high river flow conditions. Shifts from estuarine and terrestrially-derived POM to marine-derived POM during high river flow conditions occurred in portions of the Bay with a direct connection to the ocean and river input (Wailuku River plume and Outer Bay); more isolated areas of the Bay (Wailoa River plume) exhibited a more static food web that was dependent upon both estuarine and terrestrial POM regardless of hydrological regime. Shifts in organic C and N sources between low and high river flow conditions were less pronounced in secondary consumers compared to primary ones, and in many cases, a shift was not observed. This may have been due to secondary consumers being more mobile and expressing higher levels of selective feeding (Alvarez-Cadena 1993, Saito and Kiorboe 2001, Tønneson and Tiselius 2005), or because isotopic tissue turnover times of secondary consumers may have exceeded the two day sampling regime. Tissue turnover times for this study were

estimated using Hoover et al. (2006), which showed up to a six-fold increase in zooplankton biomass just one day following a high flow event. However, the zooplankton community measured in Hoover et al. (2006) primarily consisted of primary consumers, with the exception of a single species of Chaetognaths, whose biomass increased between 2–4 days depending on the life stage. Because we do not have a good understanding of isotopic tissue turnover in secondary consumers in Hawaii, it is hard to determine whether they have lower temporal variability in their diet than primary consumers, or whether dietary shifts were not reflected in their tissues because they had not come into isotopic equilibrium with the new POM source(s). Below, we present possible mechanisms for the observed patterns largely seen in primary consumers' diets within Hilo Bay with regards to contributions from estuarine, terrestrial, and marine POM.

Estuarine POM contributions

Increases in freshwater discharge to estuaries can restructure food webs in part by regulating estuarine phytoplankton growth (Mortazavi et al. 2000). The importance of estuarine POM in Hilo Bay's pelagic food web under high river flow conditions differed greatly among stations. Stations in the Bay most affected by ocean exchange and river inputs (Wailuku River Plume and Outer Bay) generally relied less on estuarine POM than the more isolated Wailoa River plume station during low flow conditions, but also had substantial reductions in the utilization of estuarine POM during high flow conditions. High river flow conditions within Hilo Bay decreased gross primary production (GPP) by a factor of four (Mead and Wiegner 2010), which likely resulted in the reduction in the percent contribution of estuarine POM to consumers' organic C and N demands from the Wailuku River plume and Outer Bay stations. The reduction in the use of estuarine POM by consumers in the Wailuku River plume and Outer Bay stations is further supported by greater heterotrophic surface water metabolism, indicative of allochthonous organic matter utilization, at these stations compared to the Wailoa River plume (Mead and Wiegner 2010). Decreased GPP was attributed to increased turbidity and decreased salinity, water temperatures, and nutrient concentrations from the Wailuku River (Wiegner and Mead 2009, Mead and Wiegner 2010). Direct surface water exchange with the Pacific Ocean could have also decreased retention time of dissolved nutrients for phytoplankton growth within the Wailuku River plume and Outer Bay stations (Dudley and Hallacher 1991, USACOE 2009). The combination of high turbidity coupled with low retention time of nutrients may make the Wailuku River plume and Outer Bay stations unfavorable for substantial phytoplankton growth during high river flow conditions, reducing the availability of estuarine POM to consumers at these stations (Snow et al. 2000, Warrick et al. 2005, Mead and Wiegner 2010).

In contrast to the Wailuku River plume and Outer Bay stations, the Wailoa River plume had a more static food web that was fueled by both estuarine and terrestrial POM. Percent contribution of estuarine POM to consumers' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in the Wailoa River plume did not change or slightly increased during high river flow conditions, suggesting that enough estuarine POM was produced at this station

to maintain a similar food web structure as during low river flow conditions. This was likely the result of higher nitrate concentrations from developed and cultivated land within the Wailoa River watershed (Fig. 1), coupled with longer retention times of nutrient-rich waters within this station compared with the Wailuku River plume and Outer Bay stations, and greater water clarity compared to the Wailuku River plume (Dudley and Hallacher 1991, USACOE 2009, Wiegner and Mead 2009).

Terrestrial POM contributions

In addition to regulating phytoplankton growth, increases in freshwater discharge to estuaries can increase the transport of terrestrial POM to these systems (Chanton and Lewis 2002, Wiegner et al. 2009). In Hilo Bay, high river discharge conditions deliver >90% of the organic C and N annual yields from the Wailuku River to Hilo Bay and POM concentrations can increase by a factor of eleven compared to low flow conditions (Wiegner et al. 2009). However, high river flow conditions had a minimal influence on the contribution of terrestrial POM to Hilo Bay's consumers' diets, as its contribution to their diets remained consistent regardless of station location or river flow condition. While the contribution of terrestrial POM to consumers' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures generally increased during high river flow conditions and were up to 40% higher than values measured in other estuaries (Deegan and Garritt 1997, Chanton and Lewis 2002, Schlacher et al. 2009), this increase was not proportional to the increased availability of terrestrial POM as a food source, nor did it compensate for the decrease in contributions of estuarine POM to consumer isotopic signatures. Additionally, some consumers expressed a decrease in contribution of terrestrial POM by as much as 50% (Fig. 3). The observed pattern in Hilo Bay contrasts with findings from temperate and subtropical studies, where the relative importance of terrestrial POM to food webs substantially increased with increasing river flow (Chanton and Lewis 2002, Hoffman et al. 2008, Schlacher 2008). One reason for this could be that we underestimated the total contribution of terrestrial POM to consumers, as estuarine POM is a mixture of terrestrial, estuarine, and marine POM. However, we do not believe that this was the case, as contributions of estuarine POM to many consumers at the Wailuku River plume and Outer Bay stations during high river flow conditions were minimal, and even if 90% of the estuarine POM signature was terrestrial, this would still not explain why terrestrial POM's contribution to Hilo Bay's food web did not substantially increase with increasing river flow. Thus, a more likely explanation as to why terrestrial POM's contributions to consumers' diets did not substantially increase during high river flow is that more refractory OM was discharged by the Wailuku (Wiegner et al. 2009) and Wailoa Rivers during high river flow conditions compared with low river flow conditions. Additionally, there was a 47% reduction in bacteria biomass in the water column of Hilo Bay during high river flow conditions (Wiegner et al. unpubl.). Bacteria are pivotal organisms in the link between the microbial loop and classical food webs (Pomeroy 1974, Paves and Gonzalez 2008) and a substantial reduction in their biomass could reduce the amount of organic C and N from terrestrial OM that can be transferred to higher trophic levels via the

microbial loop (Pomeroy 1974). However, for this to occur in Hilo Bay, the question arises as to whether or not terrestrial OM is primarily entering its pelagic food web indirectly via the consumption of bacteria who consume DOM, as opposed to direct consumption of terrestrial POM by zooplankton.

The emerging pattern from past studies is one emphasizing coupling of the microbial loop and classical food webs and deemphasizing direct consumption of terrestrial POM by pelagic zooplankton (Pace and Glasse 1984, Azam et al. 1994, Sherr and Sherr 1994). In order to determine whether a 47% reduction in bacteria biomass could inhibit contributions of terrestrial OM despite their increased availability to Hilo Bay consumers, a modified model from Deegan and Garritt (1997) was used to estimate the likelihood of bacteria as an indirect pathway for the transfer of terrestrial DOM from the microbial loop to the classical grazing food web of Hilo Bay. While the $\delta^{15}\text{N}$ of terrestrial DOM was not measured in this study, Coffin et al. (1989) and McClelland and Montoya (2002) showed that the discrimination factor from plant leaves (POM) $\rightarrow$ leachate (DOM) $\rightarrow$ bacteria was 0–2‰. Next, assuming a discrimination factor of ~2‰ per trophic level (McCutchan et al. 2003), the difference between the $\delta^{15}\text{N}$ signatures of mesozooplankton (~3.5–6.0‰) and Wailuku River's POM (~0.8‰), the largest terrestrial POM contributor to Hilo Bay during high river flow conditions, was approximately three to four trophic levels. Using the intermediate value of 1‰ for the bacterial fractionation of organic N, the predicted $\delta^{15}\text{N}$ isotopic values are as follows: terrestrial POM (~0.8‰) $\rightarrow$ terrestrial DOM, 'leachate,' + bacteria (~1.8‰) $\rightarrow$ microzooplankton (~3.8‰) $\rightarrow$ mesozooplankton (~5.8‰). The predicted $\delta^{15}\text{N}$ isotopic values fall within the measured isotopic values for these consumers in Hilo Bay (Table 4), suggesting that this could be a likely pathway for terrestrial OM into the system, and that a decrease in contributions of terrestrial OM used by consumers in Hilo Bay could be explained by the significant reduction in bacterial biomass during high river flow conditions.

Marine POM contributions

High river flow conditions are often associated with high surf brought on by storm systems (Sanderson 1993). The influence of high river flow conditions on marine POM's contributions to Hilo Bay consumers differed between stations, where marine contributions greatly increased in the Wailuku River plume station during high river flow and remained fairly constant between flows in the Outer Bay station. Hydrological forcing from increased wave action and mixing between estuarine, marine, and riverine waters in the Wailuku River plume during high river flow conditions was likely responsible for the increase (up to 40%) in marine POM subsidies to consumers at this stations. Studies have shown that marine phytoplankton in nearshore coastal waters can be stimulated by fluvial nutrient exports during high river flow conditions, and can support up to 90% of the organic C and N demands of zooplankton (Schlacher et al. 2009). Wiegner and Mead (2009) found that the Outer Bay and Wailuku River plume stations had similar increases in nitrate concentrations during storms, but the Wailuku River plume had nearly five times greater turbidity than the Outer Bay station. This suggests

that unlike the estuarine stations in Hilo Bay where primary production was likely inhibited by turbidity during storms, marine primary production could have been stimulated by river-born nutrients without being light-limited. Additionally, nutrients (e.g. N and iron) in rainwater have also been shown to stimulate primary production in offshore waters (Paerl et al. 1999). The use of marine POM over the abundant, lower quality, terrestrial POM suggests some level of selective feeding by Hilo Bay consumers. Selective feeding during high river flow conditions would be advantageous to ensure the highest level of energy transfer efficiency (Paves and Gonz  lez 2008) and even reproductive success in some consumers (Burdloff et al. 2002).

Conclusions

Many studies have emphasized the importance of estuarine and marine POM sources to estuarine consumers, modeling estuaries as a classical food web, where C flux primarily occurs from phytoplankton to zooplankton to fishes and offers a short and energy efficient pathway (Chanton and Lewis 2002, Sobczak et al. 2002, Van den Meersche et al. 2009). While consumers from Hilo Bay utilized a combination of estuarine, terrestrial, and marine POM, the increase of terrestrial POM contributions to consumers' diets were substantial and significant during high river flow conditions, and were up to 40% higher than values measured in other estuaries (Deegan and Garritt 1997, Chanton and Lewis 2002, Schlacher 2008). This suggests that terrestrial POM subsidies could be more important in tropical estuaries compared to temperate and subtropical ones. Although food webs emphasizing the transfer of C by way of phytoplankton to fishes are thought of as having high trophic transfer efficiency (Pomeroy 1974, Paves and Gonzalez 2008), studies have found that a mix of direct consumption of detritus and bacteria can yield high trophic transfers as well (Carman and Thistle 1985, Danovaro and Fabiano 1997), which would allow tropical estuaries to maintain a relatively high level of secondary and tertiary production.

The structure of food webs can fundamentally influence community dynamics and stability, and are greatly affected by natural and anthropogenic perturbations (Belgrano et al. 2005). However, the current paradigm on the POM base of estuarine pelagic food webs in response to hydrological forcing is that they are relatively static and remain largely endogenously fueled (Chanton and Lewis 2002, Hoffman et al. 2008, Schlacher 2008). Hilo Bay represents a dynamic and spatially complex food web, for which its topology largely arises from location specific mechanisms related to hydrological and biological interactions. Our study found that the POM base of the estuarine mesozooplankton food web in Hilo Bay was not static; it varied temporally and spatially with river flow conditions. Our results showed that subsidies to consumers' organic C and N demands from terrestrial and marine POM were significant at the stations with a direct connection to the ocean and affected by river inputs. In addition, strong temporal variability was evident in several consumers from stations influenced directly by river flow and ocean exchange, who shifted from primarily utilizing terrestrial or estuarine POM during low river flow conditions to marine POM during high river flow. These marked shifts in POM

source utilization support the idea that estuarine consumers are to some degree selective feeders that optimize energy transfer efficiency by selecting for quality over quantity (Martineau et al. 2004, Delong and Thorp 2006). Results from this study in conjunction with Mead and Wiegner (2010) suggest that variability in GPP, biological availability of terrestrial OM, as well as estuarine bacterial biomass associated with changes in river hydrology were the main factors driving POM source utilization by consumers in Hilo Bay, and that stations located in more isolated areas of the Bay appeared to have a more stable OM base in their food web regardless of river flow condition. If Hilo Bay is representative of tropical estuaries, our results suggest that food web structure within these systems may be vulnerable to changes in hydrological conditions, physical structure of the estuary, and watershed land-use.

Acknowledgements – We thank E. Hammil, C. Phillis, L. Shizuma, C. Kelley, K. Seiber, L. Mead, E. Hart, M. Netze, S. Molloy, R. Schneider, R. Tubal, C. Settlemier, T. Bambico, J. Coney, T. Soares, D. Roberts and A. Dunn. We would also like to thank J. Adolf, B. Nishimoto and J. Turner whom provided guidance in the final design of the project. J. Richardson and J. Moore provided comments on earlier drafts of this manuscript. This material is based upon work supported in part by Hawaii County and the National Science Foundation (NSF) under grants no. EPS0554657, DBI0453630, HRD02-23040 and DEB0453630. Additional support came from the Univ. of Hawai'i Sea Grant College Program under grant no. NA050AR4171048 from National Oceanic and Atmospheric Administration (NOAA) Office of Sea Grant, Dept of Commerce.

References

- Alvarez-Cadena, J. N. 1993. Feeding of the chaetognath *Sagitta elegans* Verrill. – *Estuar. Coast. Sci.* 36: 195–206.
- Anraku, M. and Omori, M. 1963. Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods. – *Limnol. Oceanogr.* 8: 116–126.
- Azam, F. et al. 1994. Bacteria-organic matter coupling and its significance for oceanic carbon cycling. – *Microb. Ecol.* 28: 167–179.
- Bacha, M. and Amara, R. 2009. Spatial, temporal, and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). – *Estuar. Coast. Shelf Sci.* 85: 257–264.
- Belgrano, A. et al. 2005. Aquatic food webs: an ecosystem approach. – Oxford Univ. Press.
- Blaber, S. J. M. and Cyrus, D. P. 1983. The biology of Carangidae (Teleostei) in Natal estuaries. – *J. Fish Biol.* 22: 173–188.
- Burnett, N. and Sulkin, S. 2007. Characteristics of feeding on dinoflagellates by newly hatch larval crabs. – *Mar. Biol.* 151: 851–861.
- Burdloff, D. et al. 2000. Particulate food value and its biological implication in estuarine ecosystems: effects on *Eurytemora affinis* copepod. – *Oceanografia* 3: 203–215.
- Canino, M. F. and Grant, G. C. The feeding and diet of *Sagitta tenuis* (Chaetognatha) in the lower Chesapeake Bay. – *J. Plankton Res.* 7: 175–188.
- Carman, K. R. and Thistle, D. 1985. Microbial food partitioning by three species of benthic copepods. – *Mar. Biol.* 88: 143–148.

- Chanton, J. P. and Lewis, F. G. 1999. Plankton and dissolved inorganic carbon isotopic composition in a river-dominated estuary: Apalachicola Bay, Florida. – *Estuaries* 22: 575–583.
- Chanton, J. and Lewis, F. G. 2002. Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, USA. – *Limnol. Oceanogr.* 47: 683–697.
- Clarke, T. A. 1989. Species profiles: Life histories and environmental requirements of coastal vertebrates and invertebrates, Pacific Ocean region. Report 4. The Hawaiian anchovy or nehu, *Engrasicholina purpurea* (Engraulidae). – Hawaii Inst. Mar. Biol. Kaneohe, Tech. Rep.
- Coelho, H. et al. 2009. Nondestructive quantification of phytoplankton gut content of brachyuran crab megalopae using in vivo chlorophyll a fluorescence. – *J. Plankton Res.* 31: 577–581.
- Coffin, R. B. et al. 1989. Carbon isotopic composition of estuarine bacteria. – *Limnol. Oceanogr.* 34: 1305–1310.
- Cohen, J. E. 1994. Marine and continental food webs: three paradoxes? – *Phil. Trans. R. Soc. B.* 343: 57–69.
- Cornils, A. et al. 2007. Feeding of Clausocalanids (Calanoida, Copepoda) on naturally occurring particles in the northern Gulf of Aquaba (Red Sea). – *Mar. Biol.* 151: 1261–1274.
- Danovaro, R. and Fabiano, M. 1997. Seasonal changes in quality and quantity of food available for benthic suspension-feeders in the Gulf of Marconi (northwestern Mediterranean). – *Estuar. Coast Shelf Sci.* 44: 723–736.
- Day, J. W. et al. 1989. Estuarine ecology. – Wiley.
- de Swart, H. E. et al. 2007. Initial growth of phytoplankton in turbid estuaries: a simple model. – *Cont. Shelf Res.* 29: 136–147.
- Deegan, L. A. and Garritt, R. H. 1997. Evidence for spatial variability in estuarine food webs. – *Mar. Ecol. Prog. Ser.* 147: 31–47.
- Delong, M. D. and Thorp, J. H. 2006. Significance of instream autotrophs in trophic dynamics of the upper Mississippi River. – *Oecologia* 147: 76–85.
- Downs, J. N. and Lorenzen, C. J. 1985. Carbon: pheopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. – *Limnol. Oceanogr.* 30: 1024–1036.
- Dudley, W. C. and Hallacher, L. E. 1991. Distribution and dispersion of sewage pollution in Hilo Bay and contiguous waters. – County of Hawaii Public Works.
- Fleming, R. H. 1939. The control of diatom populations by grazing. – *J. Conserv. Int. Explor. Mer.* 2: 210–227.
- Giesecke, R. and González, H. E. 2008. Reproduction and feeding of *Sagitta enflata* in the Humboldt Current system off Chile. – *ICES J. Mar. Sci.* 65: 361–370.
- Harms, J. et al. 1994. Growth and physiology of *Carcinus maenas* (Decapoda, Portunidae) larvae in the field and laboratory experiments. – *Mar. Ecol. Prog. Ser.* 108: 107–118.
- Hoffman, J. C. et al. 2008. Organic matter sources supporting lower food web production in the tidal freshwater portion of the York River Estuary, Virginia. – *Estuar. Coast Shelf Sci.* 31: 898–911.
- Hoover, R. S. et al. 2006. Zooplankton response to storm runoff in a tropical estuary: bottom-up and top-down controls. – *Mar. Ecol. Prog. Ser.* 318: 187–201.
- Islam, M. S. and Tanaka, M. 2008. Diet and prey selection in larval and juvenile Japanese anchovy *Engraulis japonicus* in Ariake Bay, Japan. – *Aquat. Ecol.* 43: 549–558.
- Jacob, U. et al. 2005. Stable isotope food web studies: a case for standardized sample treatment. – *Mar. Ecol. Prog. Ser.* 287: 251–253.
- James, A. G. and Findlay, K. P. 1989. Effect of particle size and concentration on feeding behavior, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. – *Mar. Ecol. Prog. Ser.* 50: 275–294.
- Juvik, S. P. and Juvik, J. O. 1998. Atlas of Hawaii, 3rd ed. – Univ. of Hawaii Press.
- Kleppel, G. S. 1993. On diets of calanoid copepods. – *Mar. Ecol. Prog. Ser.* 99: 183–195.
- Lucas, J. R. and Benkert, K. A. 1983. Variable foraging and cleaning behavior by juvenile leatherjackets, *Oligoplites saurus* (Carangidae). – *Copeia* 1: 151–154.
- M and E Pacific 1980. Geological, biological and water quality investigations of Hilo Bay. Final project report submitted to Hawaii County.
- Major, P. F. 1973. Scale feeding behavior of the leatherjackets, *Scorpaenoides lysan* and two species of genus *Oligoplites* (Pisces: Carangidae). – *Copeia* 1: 151–154.
- Mallin, M. A. et al. 1993. Regulation of estuarine primary production by watershed rainfall and river flow. – *Mar. Ecol. Prog. Ser.* 93: 199–203.
- Martineau, C. et al. 2004. Primary consumers and particulate organic matter: isotopic evidence of strong selectivity in estuarine transition zone. – *Limnol. Oceanogr.* 49: 1679–1686.
- May, C. L. et al. 2003. Effects of spatial and temporal variability of turbidity on phytoplankton blooms. – *Mar. Ecol. Prog. Ser.* 254: 111–128.
- McClelland, J. W. and Montoya, J. P. 2002. Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. – *Ecology* 83: 2173–2180.
- McCutchan, J. H. et al. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. – *Oikos* 102: 378–390.
- Mead, L. H. and Wiegner, T. N. 2010. Surface water metabolism in a tropical estuary, Hilo Bay, Hawaii, USA, during storm and non-storm conditions. – *Estuar. Coasts* 33: 1099–1112.
- Milton, D. A. et al. 1994. Diet prey selection and their energetic relationship to reproduction in the tropical herring *Herklot-sichthys quadrimaculatus* in Kiribati, central Pacific. – *Mar. Ecol. Prog. Ser.* 103: 239–250.
- Mortazavi, B. et al. 2000. Control of phytoplankton production and biomass in a river-dominated estuary: Apalachicola Bay, Florida, USA. – *Mar. Ecol. Prog. Ser.* 198: 19–31.
- Mulkins, L. M. et al. 2002. Carbon isotope composition of mysids at a terrestrial marine ecotone, Clayoquot Sound, British Columbia, Canada. – *Estuar. Coast Shelf Sci.* 54: 669–675.
- Pace, M. L. and Glasser, J. E. 1984. A simulation analysis of continental shelf food webs. – *Mar. Biol.* 82: 47–63.
- Pace, M. L. et al. 2007. Does terrestrial organic carbon subsidize the planktonic food web in a clear-water lake. – *Limnol. Oceanogr.* 52: 2177–2189.
- Paerl, H. W. et al. 1999. Rainfall stimulation of primary production in western Atlantic Ocean waters: roles of different nitrogen sources and co-limiting nutrients. – *Mar. Ecol. Prog. Ser.* 176: 205–214.
- Pagano, M. et al. 2006. Herbivorous and microbial grazing pathways of metazooplankton in the Senegal River Estuary (West Africa). – *Estuar. Coast Shelf Sci.* 67: 369–381.
- Parnell, A. C. et al. 2010. Source partitioning using stable isotopes: coping with too much variation. – *PLoS One* 5: e9672.
- Paves, H. J. and González, H. E. 2008. Carbon fluxes within the pelagic food web in the coastal area off Antofagasta (23°S), Chile: the significance of the microbial versus classical food webs. – *Ecol. Model.* 212: 218–232.
- Pearre S. Jr. 1973. Vertical migration and feeding in *Sagitta elegans* Verrill. – *Ecology* 54: 300–314.
- Perez, M. F. and Sulkin, S. D. 2005. Palatability of autotrophic dinoflagellates to newly hatched larval crabs. – *Mar. Biol.* 146: 771–780.
- Pomeroy, L. R. 1974. The ocean's food web, a changing paradigm. – *BioScience* 24: 499–504.
- Roman, M. R. 1977. Feeding of the copepod *Acartia tonsa* on the diatom *Nitzschia closterium* and brown algae (*Fucus vesiculosus*) detritus. – *Mar. Biol.* 42: 149–155.
- Roman, M. R. et al. 2002. Latitudinal comparisons of equatorial Pacific zooplankton. – *Deep-Sea Res. II* 49: 2695–2711.

- Saito, H. and Kiørboe, T. 2001. Feeding rates in the chaetognath *Sagitta elegans*: effects of prey size, prey swimming behavior and small-scale turbulence. – J. Plankton Res. 23: 1385–1398.
- Sanderson, M. 1993. Prevailing trade winds: Climate in Hawaii. – Univ. of Hawaii Press.
- Schlacher, T. A. et al. 2009. Can export of organic matter from estuaries support zooplankton in nearshore, marine plumes? – Aquat. Ecol. 43: 383–393.
- Schwamborn, R. et al. 2006. Ingestion of large centric diatoms, mangrove detritus, and zooplankton by zoeae of *Aratus pisonii* (Crustacea: Brachyura: Grapsidae). – Hydrobiologia 560: 1–13.
- Sherr, E. B. and Sherr, B. F. 1994. Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. – Microb. Ecol. 28: 223–235.
- Snow, G. C. et al. 2000. Effect of river flow on estuarine microalgal biomass and distribution. – Estuar. Coast Shelf Sci. 51: 255–266.
- Sobczak, W. B. et al. 2002. Bioavailability of organic matter in a highly disturbed estuary: the role of detrital and algal resources. – Proc. Natl Acad. Sci. USA 99: 8101–8105.
- Tallis, H. 2009. Kelp and rivers subsidize rocky intertidal communities in the Pacific northwest (USA). – Mar. Ecol. Prog. Ser. 389: 85–96.
- Tester, A. L. and Trefz, S. M. 1954. The food of the Aholehole, *Kuhlia sandvicensis* (Stendachner), in Hawaiian waters. – Pac. Sci. 8: 173–188.
- Tönnesson, K. and Tiselius, P. 2005. Diet of chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. – Mar. Ecol. Prog. Ser. 289: 81–95.
- Turner, J. T. 1986. Zooplankton feeding ecology: contents of fecal pellets of the Cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the northern Gulf of Mexico. – Mar. Ecol. 7: 289–302.
- USACOE 2009. Hilo Bay water circulation and water quality study. – County of Hawaii Public Works.
- Van den Meersche, K. et al. 2009. Autochthonous and allochthonous contributions to mesozooplankton diet in a tidal river and estuary: integrating carbon isotope and fatty acid constraints. – Limnol. Oceanogr. 54: 62–74.
- Wallace, J. B. et al. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. – Science 277: 102–104.
- Warrick, J. A. et al. 2005. Nutrient contributions to the Santa Barbara Channel. – Estuar. Coast Shelf Sci. 62: 559–574.
- Wiegner, T. N. and Mead, L. 2009. Water quality in Hilo Bay, Hawaii, USA, under baseflow and storm conditions. – Final project report submitted to Hawaii County.
- Wiegner, T. N. et al. 2009. Bioavailability and export of dissolved organic matter from a tropical river during base- and storm flow. – Limnol. Oceanogr. 54: 1233–1242.
- Williams, V. R. and Clarke, T. A. 1983. Reproduction, growth and other aspects of the biology of the gold spot herring, *Herklotsichthys quadrimaculatus* (Clupeidae), a recent introduction to Hawaii. – Fish. Bull. 81: 587–597.