

The distribution of estuarine and oceanic water masses on the southern shore of O'ahu, Hawai'i: Ecological and coastal management implications, and novel methodology

P. Ed Parnell¹

University of Hawaii, Department of Oceanography, 1000 Pope Road, Honolulu, Hawaii 96822

Abstract

The distribution of estuarine and oceanic water masses along the shelf of Mamala Bay, O'ahu, Hawaii, were determined by use of larval supply and recruitment patterns of benthic invertebrate species, stable C and N isotopic compositions of the suspension-feeding bivalve, *Spondylus tenebrosus*, turbidity, drifter, and CTD data. The recruitment of different species among estuaries was used to associate larval species with particular estuarine waters. Recruitment patterns of these species along the shelf were then used to infer water-mass distributions along the shelf. The spatial recruitment pattern of an oceanic lepadomorph barnacle, *Conchoderma virgatum*, was useful to infer shelf areas exposed to oceanic waters. Water-mass distributions inferred from the recruitment distribution of these species concurred with spatial patterns of turbidity and stable C and N isotopic compositions of *S. tenebrosus*, as well as drifter observations. Water-mass distributions observed in this study also concurred with biological distributional patterns observed in other studies, such as distributions of phytoplankton and zooplankton and the distribution of coral bio-erosion in the Bay. The ecological implications of this work include further evidence of the physical control of recruitment and biological pattern and the possible control of patch dynamics on the scale of kilometers due to significant recruitment variability at this scale. The prevailing distribution of water masses determined in this study also has important implications for the management of watersheds associated with Mamala Bay.

Coastal zones receive waters whose sources include groundwater seepage, terrestrial runoff, and oceanic water. The distribution of waters from these various sources can profoundly impact the distribution of benthic (McLusky et al. 1993; Moreira et al. 1993; Albani et al. 1998) and pelagic (LeFevre 1986; Van Der Spoel 1994) organisms and are therefore of interest to ecologists. Water-mass distributions along coastlines are also of interest to coastal engineers and managers so that the deleterious effects of pollutants can be effectively managed (Colwell et al. 1996).

The discrimination of water masses is typically accomplished by use of source-characteristic signatures of dissolved, particulate, or sedimented tracers and/or hydrographic surveys (Broecker and Peng 1982). The utility of various tracers is variable among locations and applications and therefore must be chosen carefully. The most important criterion for choosing an appropriate tracer is that it has characteristic and distinguishable values among water masses. In some cases, it is necessary to use more than one tracer be-

cause no single tracer has distinguishable values among the water masses of interest. In this case, the use of additional tracers enables the discrimination of water masses by plotting tracer values in multi-dimensional space (Wada et al. 1987). Another important consideration when choosing tracers is that tracers should enable the determination of water-mass distribution over the timescales of interest. For example, if disturbance due to storm runoff is of interest, then instantaneous distributions of salinity and temperature after a rainstorm are likely useful. However, if prevailing (c.f., chronic) processes are of interest, then instantaneous values of salinity and temperature may not be useful because of temporal variability. Here, long-term averages are appropriate, which would require repetitive sampling. One way to minimize repeated sampling is to choose tracers whose values are indicative of signal-integration over time, such as sedimented tracers (Andrews et al. 1998) or tracers incorporated into the tissues of organisms (Spies et al. 1989; Canuel et al. 1995; O'Connor and Beliaeff 1995).

The distribution of larval supply and recruitment may be another useful time-integrative tracer in many coastal areas. The use of larvae as tracers has been previously discussed (Roman and Boicourt 1999; Smith et al. 1999), and, in some cases, larval associations with estuarine plumes have been established (Kingsford and Suthers 1994). The benefits of using larval supply and recruitment patterns as indicators of coastal water mass distributions include (1) the time-integrative nature of collecting recruits on recruitment substrates for periods that are relevant to the timescales of interest, (2) no expensive field or laboratory equipment is needed, and (3) several species may be available for discrimination of water masses—each species may be considered a separate tracer.

The work presented in this paper began as an effort to use the distribution of benthic invertebrate larval supply and re-

¹ Corresponding author (edparnell@ucsd.edu). Present address: Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0227.

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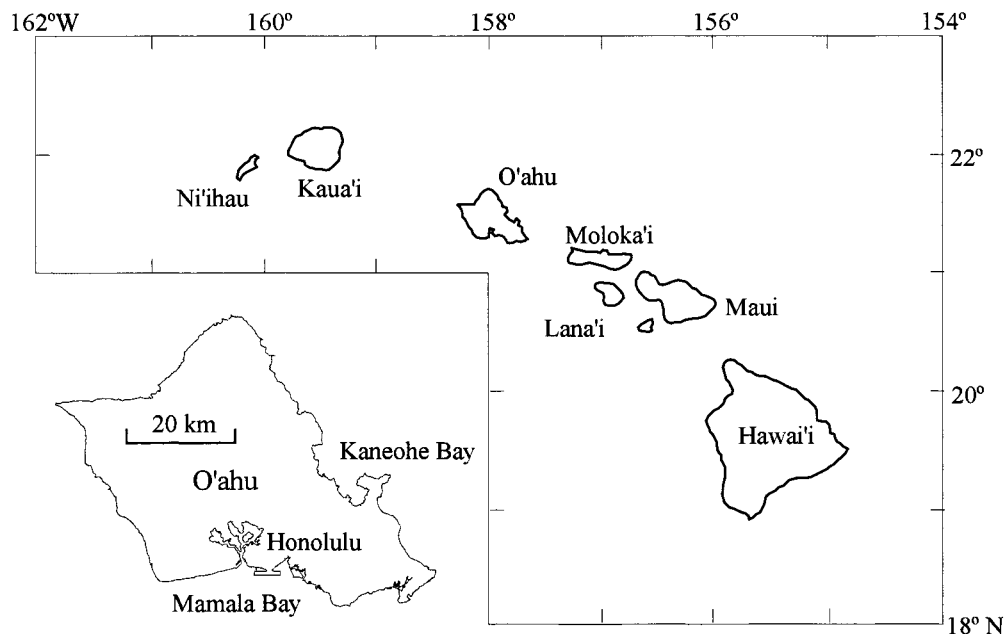


Fig. 1. Map of the Main Hawai'ian Islands with O'ahu enlarged. The locations of Mamala Bay and Kane'oh'e Bay are shown.

cruitment as an indicator of exposure to pollution in the bay that borders the most heavily industrialized and urbanized watershed in Hawaii—Mamala Bay, located on the southern shore of O'ahu (Fig. 1). In the process, it was discovered that the distribution of the supply and recruitment of larval benthic invertebrates can be an effective tracer of coastal water masses and their sources. The distribution of water masses along the Mamala Bay shelf was also examined by use of traditional tracers such as temperature, salinity, and turbidity, as well as the use of stable C and N isotopic ratios of a suspension-feeding bivalve. The combination of larval supply and recruitment patterns, the distribution of traditional tracers, and drifter data enabled the determination of prevailing water-mass distributions in Mamala Bay. The resultant distribution of water masses concurred with biological patterns that were observed in other studies of Mamala Bay, such as the bio-erosion of corals (Grigg 1995), phytoplankton distributions (Laws et al. 1999), and the distribution of coastal and oceanic appendicularians (Scheinberg pers. comm.).

Methods

Setting—Mamala Bay is an open-ocean embayment. Estuarine harbors located along the Bay include Pearl Harbor, Ke'ehi Lagoon, Honolulu Harbor, Kewalo Basin, and the Ala Wai Canal (Fig. 2); all are located along <15 km of coastline and receive runoff from urban, industrial, and/or agricultural zones. The Mamala Bay shelf gradually deepens offshore from fringing reefs to a depth of 30–50 m (2–4 km offshore), where the bottom slope becomes steeper. The water column over the shelf is typically well mixed, except during summer, when a seasonal thermocline is present at depths ranging from 5–10 m (pers. obs.). Primary currents in Ma-

mala Bay are tidally driven (ranging in magnitude from ~10 to 44 cm s⁻¹), oriented along shore, and reverse with the semidiurnal M2 tide. The maximal tidal range for the Bay is ~1 m. The M2 tidal wave approaches Oahu from the northeast and diverges near Kane'oh'e Bay (Larsen 1977). The wave then wraps around O'ahu and converges in western Mamala Bay (Hamilton et al. 1995). Tidal flows in western Mamala Bay are complex because of a tidal wave convergence/divergence, topography, and outflows from Honolulu Harbor, Ke'ehi Lagoon, and Pearl Harbor (Hamilton et al. 1995). Mean circulation over the shelf west of the Ala Wai Canal is westward (3–5 cm s⁻¹) and is eastward east of the Ala Wai (Hamilton et al. 1995). The prevailing wind patterns are the northeastern trade winds that predominate throughout the year, and episodic reversals of the trade winds, termed southwestern "Kona" winds, which are associated with the passage of cold fronts during late fall and winter. Mean circulation patterns over the shelf appear to be unrelated to prevailing wind patterns (Hamilton et al. 1995).

Study sites—Larval supply and recruitment were quantified at a depth of ~5 m on permanent subsurface moorings at several locations within the Bay and in estuaries bordering the Bay (Fig. 2). The permanent subsurface moorings (buoy depth ~4 m) were placed in three areas: (1) along the 16-m contour (shelf sites) at distances of 3–4 km, (2) in the Pearl Harbor channel, and (3) in Ke'ehi Lagoon (see Fig. 2). The shelf sites were located along suspected gradients of exposure to different estuarine plumes, which were considered sources of non-point-source pollution. The moorings were taut-line moorings consisting of 800-kg concrete aggregate anchors and ~1-m diameter steel buoys. Moorings were equipped with aluminum frames (larval frames; depth ~4–5 m) that housed ceramic tiles for collecting recruits and

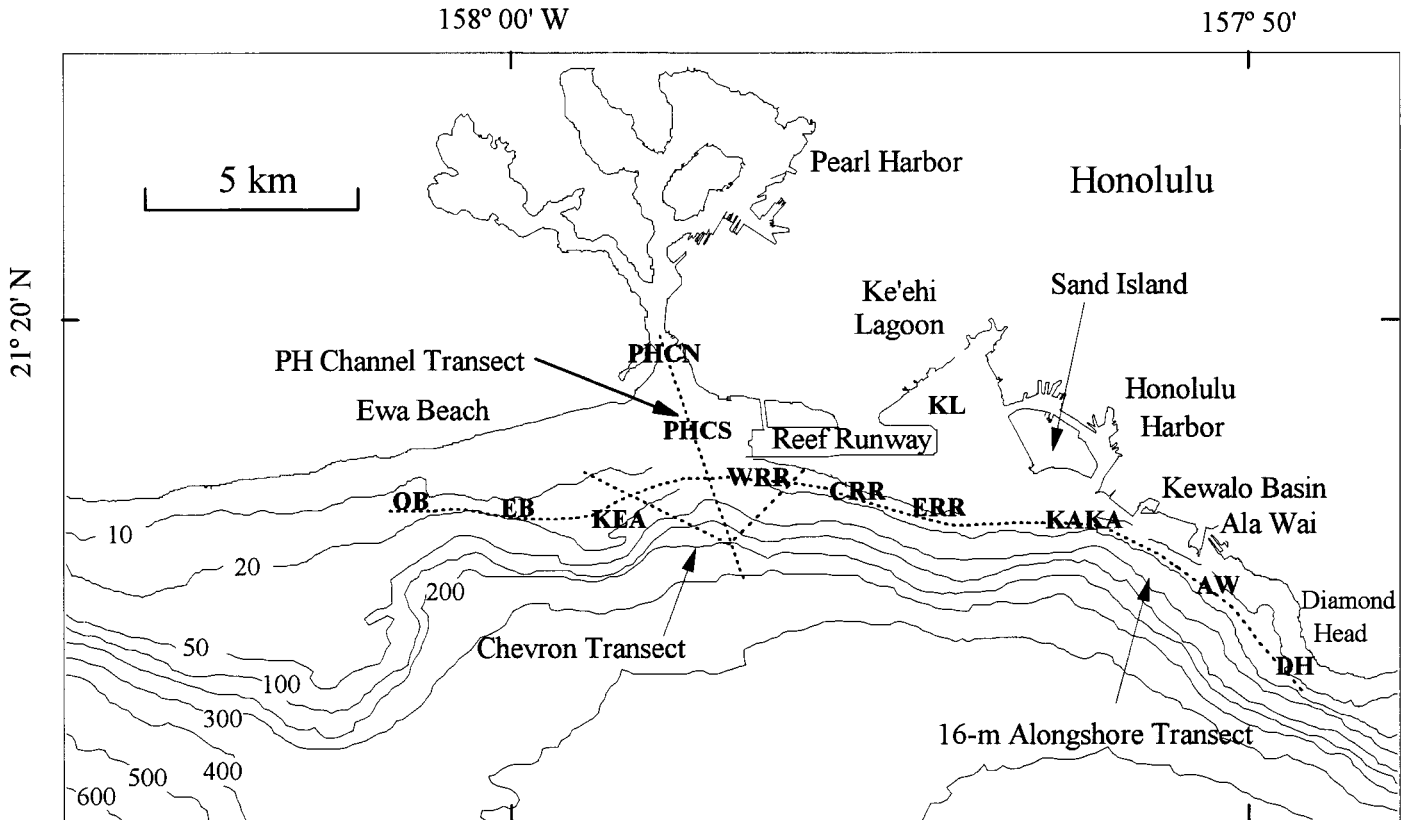


Fig. 2. Map of Mamala Bay showing the location of recruitment study sites (OB = Oneula Beach, EB = Ewa Beach, KEA = Ke'ahi Pt., PHCN = Pearl Harbor Channel North, PHCS = Pearl Harbor Channel South, WRR = West Reef Runway, CRR = Central Reef Runway, ERR = East Reef Runway, KL = Ke'ehi Lagoon, KAKA = Kaka'ako, DH = Diamond Head) and CTD transects (dotted lines and curves). Depth contour units are meters.

plastic map tubes for trapping larvae as a measure of larval supply (Yund et al. 1991). Ryan Tempmor thermographs were also housed on the larval frames so that temperature could be used as a tracer. Aluminum frames were swiveled and were equipped with vanes so that recruitment tiles were always oriented into the current.

Recruitment and larval supply—The recruitment and supply of larval benthic invertebrates at a site can be highly variable over many timescales (Jones and Epifanio 1995; Eggleston et al. 1998; Jenkins et al. 2000). Larval traps and settlement substrates conceivably integrate instantaneous values of larval supply and recruitment over some timescales at a particular site. Larval supply as quantified by use of sediment traps (e.g., Yund et al. 1991) conceivably integrates the arrival of larvae at a site (relative to other sites) over the period of trap deployment—i.e., larvae remain in the traps once they are trapped. On the other hand, the integration of instantaneous larval recruitment rates onto artificial substrates is not as straightforward. There are many possible sources of bias when this method is used. Two of these sources include larval settlement behavior and juvenile mortality. Larval settlement behaviors can be complex and are under the control of several possible mechanisms (Pechenik 1990). However, for the purposes of this study, one could argue that bias due to larval settlement behavior can be min-

imized by choosing species that readily recruit onto artificial substrates (i.e., fouling species). The second possible source of bias in estimates of recruitment rates, juvenile mortality, can lead to underestimates of recruitment. However, this bias may be minimized by decreasing the period of substrate deployment, thereby minimizing density-dependent sources of mortality. Predation, another source of juvenile mortality, may be minimized by decreasing the exposure of juveniles to benthic and water-column predators.

Recruitment was quantified by use of ceramic tiles (recruitment plates; dimensions, $20 \times 9.5 \times 1$ cm) that were soaked in filtered ($202 \mu\text{m}$ mesh) running seawater at the Kewalo Marine Laboratory for several weeks prior to deployment, to allow the development of a settlement-inducing biofilm. Seawater was continuously pumped from coastal waters near Kewalo Basin and was filtered to remove larvae, which could otherwise have settled on the tiles prior to their deployment. Recruitment tiles were deployed on moorings by SCUBA divers. Attempts were made to deploy tiles at 14-d intervals. However, because of logistical constraints and weather conditions, tile deployment periods ranged from 7 to 21 d (mean $\cong 13.8$, $s \cong 3.65$, median = 14). A deployment period of 14 d was targeted for comparisons with an earlier study of invertebrate recruitment on the southern shore of O'ahu (Bailey-Brock 1989) and to minimize recruit mortality and interactions. The number of recruits was di-

vided by deployment period (days) for statistical comparisons of recruitment rates among sites. Two to four replicate tiles were deployed at each site. Upon retrieval, tiles were placed in individual hard plastic containers and immediately sealed underwater. Upon return to the lab, tiles were inspected for recruits by use of a dissecting microscope, and the water remaining in the plastic containers was sieved ($1\ \mu\text{m}$ mesh) for juveniles. Juveniles on the tiles and those filtered by use of the sieve were identified to the lowest possible taxonomic level.

Larval supply was determined by use of larval traps that were deployed and recovered at the same time as recruitment tiles. Two replicate upward-facing plastic tubes (diameter = 5 cm, length = 60 cm) were fastened onto mooring frames and then injected with ~ 250 ml of a hypersaline (~ 100 ppt) 37% formalin solution underwater. The formalin solution was dyed with Rhodamine to verify sample integrity. Trap samples that did not have an intact layer of Rhodamine were not analyzed. Tubes were capped upon retrieval before they were removed from the moorings. At the lab, the formalin solution was sieved by use of a $101\text{-}\mu\text{m}$ mesh sieve. Larvae that were captured by the sieve were then counted and identified to the lowest taxonomic level possible. The number of larvae in the traps were divided by the deployment period for statistical comparisons of larval trapping rates among sites. Larval trapping rates were considered an index of larval supply (see Yund et al. 1991). As such, the relative magnitudes of larval trapping rates among sites were of interest. Larval trapping and recruitment work was conducted over a 31-month period (with brief interruptions) from February 1994 to September 1996.

Recruitment data for all taxa pooled and individual tracer species were statistically analyzed for seasonal and spatial differences. Nonparametric methods were used to analyze seasonal and spatial recruitment rates, because the variances of raw and transformed data grouped by season and site were not homogeneous (Levene's test, $P < 0.001$). Seasonal and spatial statistical tests were performed by use of Minitab. Seasonal effects on recruitment rates were tested by use of Mood's median test. Residuals from these tests were then used to test for significant spatial differences in recruitment by use of Kruskal-Wallis tests. Seasonal and spatial comparisons that were significant ($P < 0.05$) were then further tested by use of multiple pairwise unplanned comparison tests (Conover 1980) to determine which sites were significantly different from one another.

Stable isotopic ratios of a suspension-feeding bivalve—Early in the study, it became evident that circulation patterns near Ke'ehi Lagoon and Pearl Harbor were complex, and sharp gradients in recruitment and larval trapping rates were observed for several taxa, which indicates complex hydrographic conditions in this area. To aid the discrimination of complex water-mass distributions in this area, additional temporary moorings, equipped only with recruitment plates, were deployed in Ke'ehi Lagoon, the Pearl Harbor Channel, and along a transect from Ke'ehi Lagoon to Ewa Beach. Recruitment plates were left out for 3 months so that a common suspension-feeding oyster, *Spondylus tenebrosus*, could recruit onto the plates and grow while feeding on suspended

particulate algae. After 3 months, the plates were retrieved, and oyster tissues were analyzed for their stable carbon and nitrogen isotopic ratios. The rationale for this work was twofold. First, it is well established that dietary stable isotopic ratios primarily determine organismal ratios (DeNiro and Epstein 1978, 1981). This phenomenon has proved quite useful in determining food web structure (reviewed in Michener and Schell 1994) and in the identification of nutrient sources associated with coastal and offshore water masses (e.g., Sammarco et al. 1999). Second, earlier work by Laws and Ziemann (1996) showed that the $\delta^{15}\text{N}$ of POM in Pearl Harbor was distinct from Ke'ehi Lagoon (mean $\delta^{15}\text{N}$ values for Ke'ehi Lagoon and Pearl Harbor were $\sim 5\text{‰}$ and 6‰ , respectively). It was hoped that the tissues of *S. tenebrosus* would record the stable carbon and nitrogen isotopic ratios of particulate algae associated with these estuarine water masses and thereby help determine the offshore distributions of plumes emanating from Ke'ehi Lagoon and Pearl Harbor.

There are two main advantages of using stable isotopic ratios of suspension feeders as tracers of water mass. First, the fieldwork required is minimal compared with other tracer methodologies. All sites must be visited only twice—once to deploy the recruitment plates and once to retrieve them. This enables a greater number of sites to be studied, effectively increasing the possible spatial resolution. Second, the isotopic compositions of suspension feeders may provide a time-integrative indicator of the spatial distribution of suspended organic matter and therefore naturally filter high frequency variability, which is of little interest for studies of water-mass distribution over seasonal or longer timescales.

The method of signal integration in the stable isotopic ratios of suspension feeders is clearly different from that of larval supply and recruitment. The time-integrative signal of larval supply and recruitment is due to the continuous accumulation of larvae in traps and recruits on tiles and is therefore a sum of possibly highly variable instantaneous values over time. The processes contributing to the stable isotopic composition of an organism are much more complex, and the response-time of signal integration can vary even among tissues within the same organism (Tieszen and Boutton 1983). In this sense, the stable isotopic compositions of suspension feeders are due to the complex convolution of metabolic processes and the instantaneous isotopic compositions of particulate organic matter (POM) upon which these oysters feed.

The stable isotopic work was conducted over a 3-month period during the fall, because the spatial distribution of water masses during dry periods (the prevalent conditions on the southern shore of O'ahu) were of interest for this integrative technique. The distribution of water masses in Mamala Bay during rainfall events are ephemeral and are easily observed from distributions of salinity determined from CTD transects. Therefore, the stable isotopic technique is not necessary to discriminate offshore distributions of estuarine water masses during and immediately after rainfall events. The period of least annual rainfall on O'ahu includes summer and fall (Price 1983). Fall was chosen because the greatest rates of recruitment for many species occurred during fall (see Results), thereby maximally facilitating spatial com-

parisons of recruitment patterns with stable isotopic values of suspension feeders.

Temporary moorings were deployed on 27 September 1995 and situated along shore from Ewa Beach to Ke'ehi Lagoon (~500 m apart), in the mouth of Pearl Harbor and in Ke'ehi Lagoon. The moorings consisted of a scrap-iron weight for an anchor, polypropylene line, and a surface float. Recruitment tiles (four replicates) were placed on each mooring at a depth of ~4–5 m. The spatial resolution of the along shore moorings was two to three times greater than that of the along shore permanent moorings where larval supply and recruitment were measured. The moorings in Pearl Harbor and Ke'ehi Lagoon were intended as end-member sites. Larval *S. tenebrosus* recruited onto the tiles and were allowed to grow for three months until recruitment plates were retrieved on 17 December 1995. Upon retrieval, individual animals were picked off the tiles by use of a putty knife and were subsequently dissected so that their adductor muscles could be removed and dried for isotopic analysis. Muscles from several animals were pooled together (because of their small size) and ground into a fine powder by use of an acid-rinsed mortar and pestle. The resultant powder was divided into two to four replicate samples (dependent on the amount of powdered tissue). Sample preparation and analysis is described in Altabet (1988, 1990). Isotopic analysis was performed by use of a Finnigan Mat 252 mass spectrometer.

Turbidity—Two water samples were collected directly above the permanent moorings for turbidity analysis by use of 125-ml Nalgene bottles placed just below the surface. Turbidity sampling was typically conducted whenever the study sites were visited for the deployment and retrieval of larval samples. The water samples were placed in a cooler until they were analyzed the same day by use of a Laboratory Turbidimeter Model No. 2100A upon return to the lab. Statistical testing of turbidity differences among shelf sites was tested by use of the Kruskal-Wallis test. Sites that were significantly different from others were identified by use of multiple pairwise unplanned comparison tests (Conover 1980).

CTD transects—CTD transects were conducted to determine the instantaneous trajectories of plumes in the vicinity of the recruitment sites. Transects were conducted during both rainstorm and nonrainstorm (“dry”) periods, to determine the temporal variability of plume distribution. Three transects were repetitively sampled on different days (see Fig. 2), (1) along the 16-m contour from Ewa Beach to Diamond Head; stations were located ~500 m apart, (2) along the Pearl Harbor channel, and (3) a chevron transect near the mouth of Pearl Harbor. CTD transects were conducted from a small boat using a Seabird SBE-19 CTD. Along shore and Pearl Harbor Channel transects were conducted within 48 h of rainstorms (storm totals > 5 cm) on 14 February 1995 and 5 March and 6 November 1996 and during dry periods on 11 and 18 July 1995 and 10 August 1996. Chevron rainstorm transects were conducted on 5 March and 6 November 1996, and dry chevron transects were conducted on 11 and 18 July 1995.

Drifters—Surface drifters, similar to CODE (Coastal Dynamics Experiment) drifters (Davis 1985), were used to aid the resolution of complex tidal flows between Ke'ehi Lagoon and Ewa Beach. In an earlier study by Hamilton et al. (1995), it was suggested that the position of the M2 tidal divergence/convergence was located between Ewa Beach and Sand Island. Drifters were deployed from a small boat during both flood and ebb tides at several locations along the 16-m contour and followed for 10–15-min periods. Release and retrieval positions were fixed by use of DGPS (Differential Global Positioning System) from which current vectors were calculated. Drifters were deployed during both dry and postrainstorm periods because tidal current patterns during both conditions were of interest. Drifter studies were conducted during dry periods on 1 and 5 August and 18 November 1995 and 9 May and 22 September 1996 and during wet periods on 8 February 1995 and 6 April 1996.

Results

Recruitment and larval supply—A total of 372,837 larvae were captured in the traps and identified to 14 taxa, 7 of which were species. There were 93,184 recruits identified to 29 taxa (15 species). Recruits on tiles were more useful as tracers than trapped larvae because more species of recruits were identifiable than larvae. The larvae of only two tracer species were identifiable, *Finella pupoides* (gastropod) and *Balanus amphitrite* (barnacle). Recruitment rates were significantly correlated ($P < 0.05$) with larval trapping rates for both these species (*F. pupoides*, $r \cong 0.915$; *B. amphitrite*, $r \cong 0.889$). Bivalves and gastropods accounted for ~90% of larvae and recruits. Polychaetes and barnacles each accounted for ~3.5%; echinoderms, brachyurans, nonbarnacle arthropods, bryozoans, and tunicates made up the remaining ~3%.

Recruitment rates of all taxa pooled were significantly different among seasons ($P < 0.001$, Fig. 3). Mean recruitment rates were significantly the greatest during fall ($P < 0.005$) and significantly the lowest during winter ($P < 0.01$). Mean recruitment rates during spring and summer were approximately equal and were intermediate to winter and fall. Spatially, recruitment rates of all taxa pooled were significantly different among sites ($P < 0.001$). In fact, recruitment rates varied among sites by up to one order of magnitude (Fig. 3). Highest recruitment rates were observed in Ke'ehi Lagoon (KL), and lowest rates were observed just west of Pearl Harbor at Ke'ahi Point (KEA). Recruitment rates at KEA were significantly less than all other shelf sites ($P < 0.001$) and were significantly the greatest at East Reef Runway (ERR; $P < 0.005$), where mean recruitment rates were greater than KEA by a factor of ~4.2. Recruitment rates at KL were significantly greater than both Pearl Harbor Channel sites ($P < 0.001$).

The spatial pattern of larval recruitment for three species of benthic invertebrates included KL and sites just to the west and offshore of KL. These species were *Armandia intermedia* (polychaete), *F. pupoides*, and *B. amphitrite*, all estuarine and/or coastal species, whose recruitment rates were significantly the greatest at KL ($P < 0.01$; Fig. 4, Table

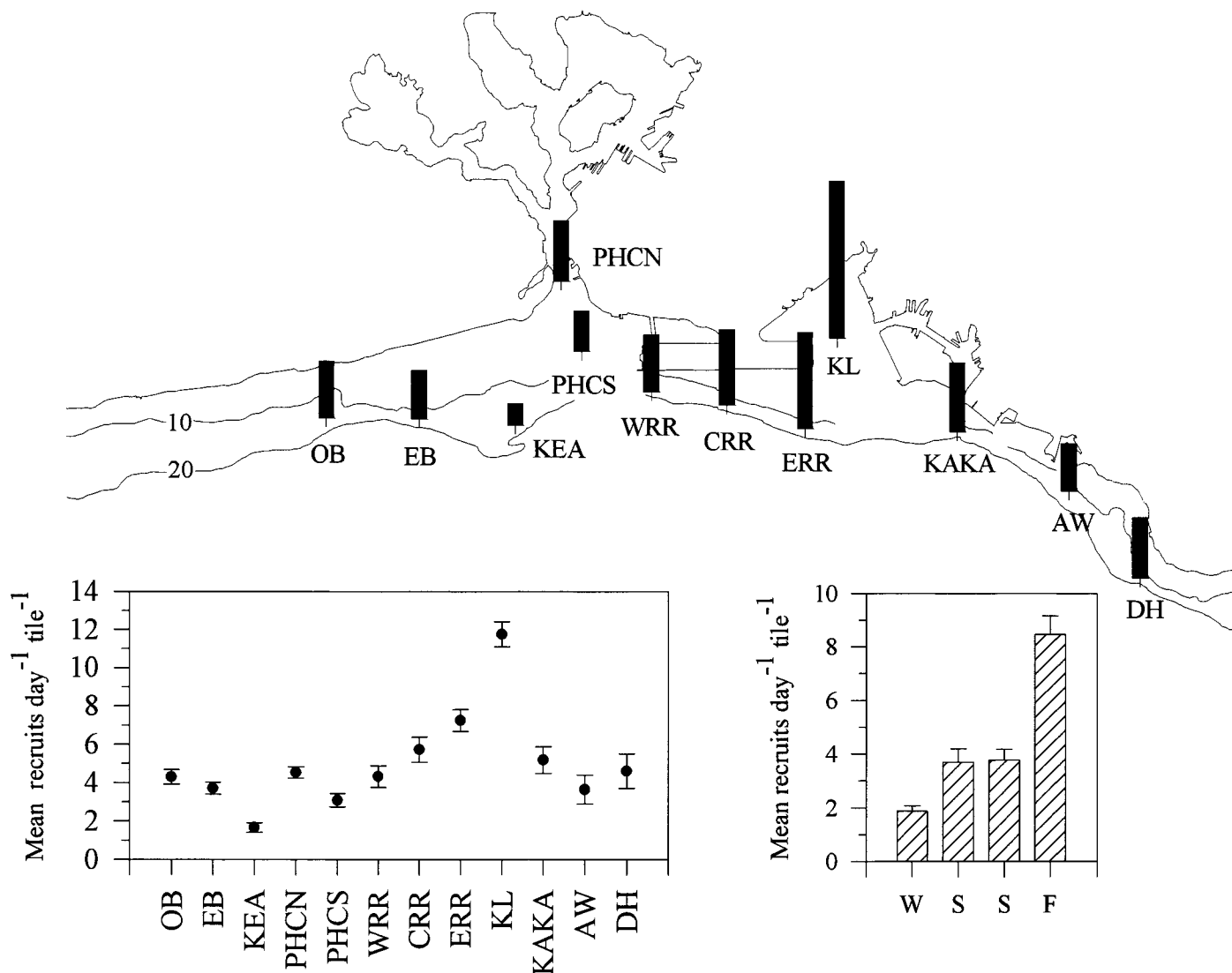


Fig. 3. Mean recruitment rates of all taxa pooled (number tile⁻¹ d⁻¹) by site and season. Site means are plotted as bars in map (lengths of bars indicate relative recruitment rates among sites) and are plotted as circles in line graph (bottom left). Seasonal mean recruitment rates at all sites are illustrated in the histogram (bottom left). Error bars are standard errors.

1). Recruitment of these species was also common at ERR, Central Reef Runway (CRR), and West Reef Runway (WRR). The same spatial pattern was observed for larval supply rates of *B. amphitrite* and *F. pupoides*. Larval *A. intermedia* were either not caught in the traps or are not readily distinguishable from other polychaete larvae. Therefore, the pattern of larval supply is not known for this species. Larval recruitment of *F. pupoides* was also observed at Diamond Head (DH). Recruitment of all three species was rare or nonexistent at all remaining sites, as were the larval supply of *B. amphitrite* and *F. pupoides*. A survey of adult *B. amphitrite* along the coastline of Mamala Bay from DH to Ewa Beach (EB) revealed a large population in KL (10%–50% cover), with much smaller populations near the mouth of Pearl Harbor (<5% cover), and in Kewalo Basin and the Ala Wai Marina (each <1%–5% cover).

Recruitment rates for all three species were seasonally variable, but recruitment was observed during all seasons.

Recruitment rates for all three species were significantly different among seasons ($P < 0.005$; Fig. 4). Recruitment rates of *A. intermedia*, *F. pupoides*, and *B. amphitrite* were significantly the greatest during winter ($P < 0.005$), fall ($P < 0.001$), and summer ($P < 0.001$), respectively. Recruitment rates of *F. pupoides* and *B. amphitrite* were significantly the lowest during winter ($P < 0.005$) and spring ($P < 0.001$), respectively. The seasonal patterns of larval supply for *F. pupoides* and *B. amphitrite* were the same as their respective seasonal recruitment patterns.

The spatial distribution of larval recruitment for two species of benthos included the Pearl Harbor Channel, and sites EB and Oneula Beach (OB), located west of Pearl Harbor (Fig. 5, Table 1). Recruitment rates of *Salmacina dysteri* (estuarine polychaete) and *Pinctada radiata* (oyster) were significantly the greatest at Pearl Harbor Channel north (PHCN) and Pearl Harbor Channel south (PHCS; $P < 0.001$). Recruitment of both species was also observed at EB

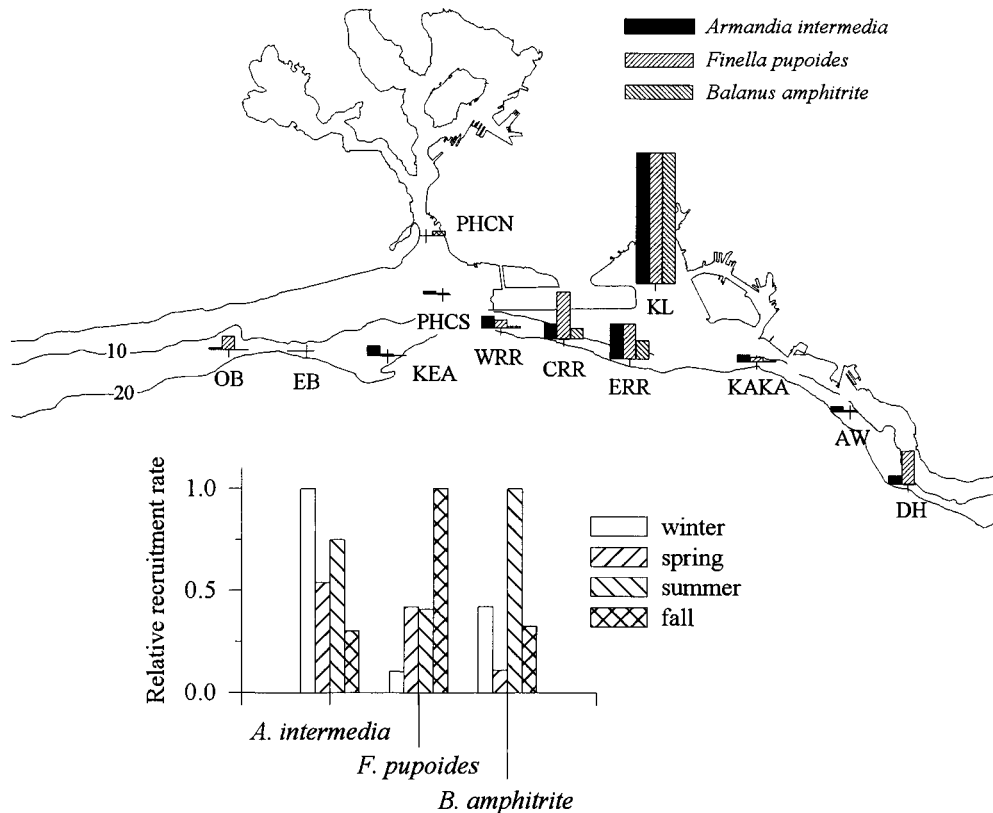


Fig. 4. Relative mean recruitment rates of *A. intermedia*, *F. pupoides*, and *B. amphitrite* by site (top) and season (bottom). Bar lengths in map indicate mean recruitment rates at each site relative to recruitment for each species at KL where recruitment rates for all three species were greatest (mean recruitment rates for each species at each site/mean recruitment rates for that species at KL). Seasonal relative mean recruitment rates are relative to seasonal mean maximum for each species. Relative recruitment rates are presented rather than actual means to reduce the number of graphs necessary. See Table 1 for values.

and OB, and nowhere else including site KEA, whose meridian is between Pearl Harbor and sites EB and OB. Unfortunately, the larvae of these two species were either not caught in the traps, or are not distinguishable from related species.

The recruitment rates of *S. dysteri* and *P. radiata* were seasonally variable. Recruitment rates of *S. dysteri* were significantly the greatest during spring ($P < 0.001$) and lowest

during fall. Recruitment rates of *P. radiata* were greatest during summer and significantly the lowest during fall ($P < 0.005$).

The lepadomorph barnacle, *Conchoderma virgatum*, a fouling and ectoparasitic open-ocean barnacle found in temperate and tropical zones (Newman 1980), recruited most heavily at EB, KEA, and Ala Wai Canal (AW; Fig. 6). Recruitment rates of *C. virgatum* were significantly greater at

Table 1. Summary statistics of recruitment rates for tracer species. Means and SD were calculated as the weighted means and SD of average recruitment rates for each species by site. Weighted values were calculated because tiles were occasionally lost or damaged, and it was not always possible to visit all sites on all sampling days because of weather conditions or logistical considerations. Maximal and minimal site means are also given for each species, as is the site where mean recruitment rates were maximal for each species.

Species	Weight mean (recruits day ⁻¹ tile ⁻¹)	Weighted SD	Maximum site mean	Minimum site mean	Maximum site
<i>Armandia intermedia</i>	0.12	0.228	0.76	0.01	KL
<i>Finella pupoides</i>	0.09	0.130	0.49	0	KL
<i>Balanus amphitrite</i>	0.52	0.246	4.77	0	KL
<i>Salmacina dysteri</i>	0.02	0.006	0.14	0	PHCN
<i>Pinctada radiata</i>	0.09	0.021	0.70	0	PHCN
<i>Conchoderma virgatum</i>	0.02	0.051	0.11	0	EB

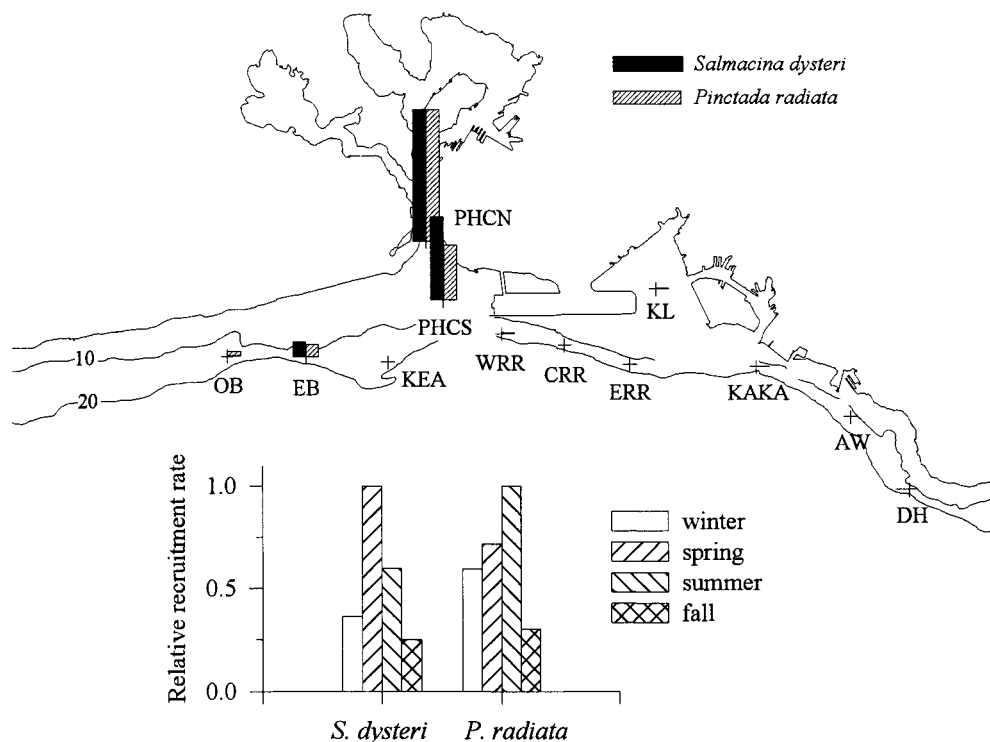


Fig. 5. Relative mean recruitment rates of *Salmacina dysteri* and *Pinctada radiata* by site and season. The plots are similar to Fig. 4 except that relative mean recruitment rates were calculated by use of the mean recruitment rates for each species at PHCN where mean recruitment rates of these species were maximal. See Table 1 for values.

these sites ($P < 0.001$) than all remaining sites. Recruitment of *C. virgatum* was rarely observed at OB and WRR and never observed at PHCN, PHCS, ERR, CRR or KL. Recruitment of *C. virgatum* was observed year round but was significantly the greatest during fall ($P < 0.05$). The larvae of *C. virgatum* were either not caught in the larval traps or were not distinguishable from other barnacle larvae.

Stable isotopes of *Spondylus tenebrosus*—Mean stable C and N isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) are plotted against each other for each site in Fig. 7. Unfortunately, the samples from KL had too much carbon and nitrogen, and, because the analysis is destructive, were irretrievably lost. The Pearl Harbor (PH) samples had too much nitrogen, but $\delta^{13}\text{C}$ values averaged -20.59 ($s \cong 0.254$). The values plotted for sites A and H are for single samples because analysis of the replicates failed. Only one replicate analysis for $\delta^{15}\text{N}$ was successful at site I. Despite the analytical problems, three groupings of sites are apparent: (1) A and B, (2) C–G, and (3) H and I. Multivariate cluster analysis of site means for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Euclidean single-distance analysis conducted with use of Matlab, Fig. 8) confirm these groupings. The first node distinguishes sites H and I from the others, and the second node distinguishes sites A and B from the remaining sites (C–G). A general MANOVA test was performed on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in Minitab by use of site as the model factor. The MANOVA test was significant ($P = 0.011$).

Turbidity—Turbidity was highly variable in space (see Fig. 9) and time. Turbidity was typically the greatest in KL (range 0.6–2.1 NTU). Mean turbidity was next greatest at the PH Channel sites (range 0.4–1.3 NTU). Greatest turbidities were observed after rainstorms at all sites. Increased turbidity was also observed at all shelf sites during and immediately after large swell events. The southern shore of O'ahu is subject to swell events during summer that are generated by storm systems off New Zealand. Increased turbidity during swell events is due to the resuspension of sediment and microalgae. Among the shelf sites, turbidity was consistently the lowest at KEA and AW ($P < 0.05$), significantly the greatest at ERR and CRR ($P < 0.05$), and most variable at EB. There were sharp turbidity gradients between WRR and CRR and between AW and DH.

CTD transects—The spatial distribution of salinity was a useful indicator of estuarine plumes along the Mamala Bay shelf shortly after rainstorms. For example, the distribution of salinity along the 16-m contour on 5 March 1996 (~36 h after a ~5 cm rainstorm; Fig. 10) clearly shows the positions of the PH, KL, and Honolulu Harbor plumes. However, the spatial distribution of these plumes was not evident during dry periods from either salinity or temperature plots. Salinity distributions along the chevron transect during ebb tides after rainstorms clearly indicated the plume moving offshore and slightly eastward from the mouth of PH (Fig. 11). The trajectory of the PH plume was not obvious during

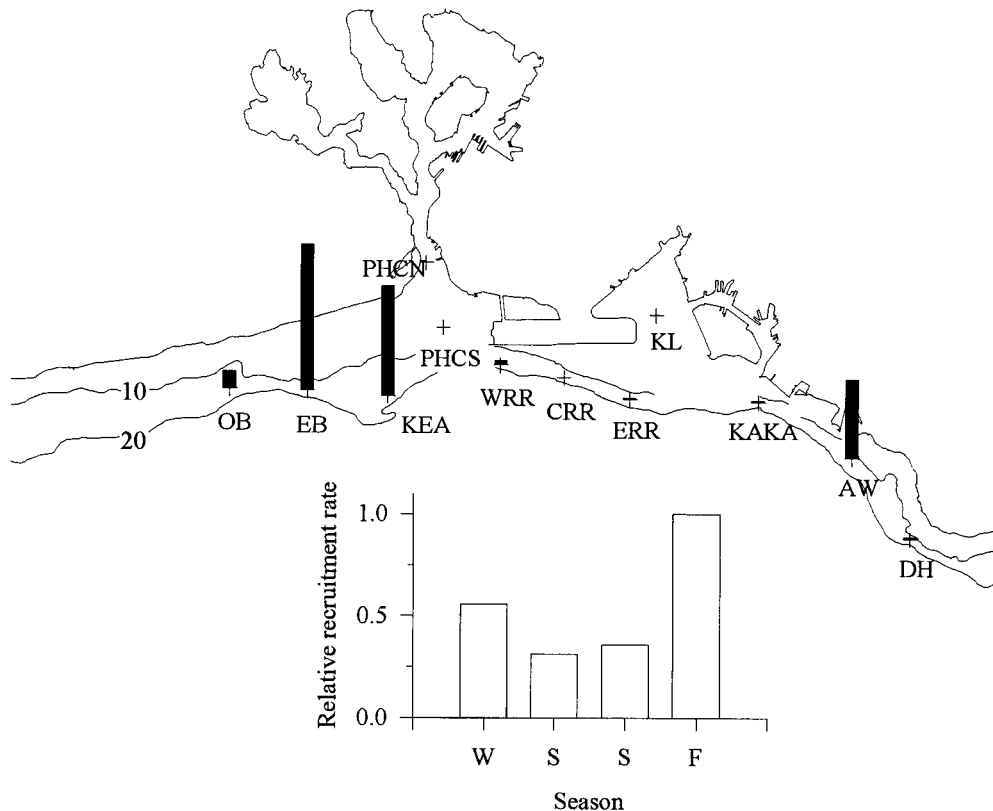


Fig. 6. Mean recruitment rates of the oceanic lepadomorph barnacle, *C. virgatum* by site and season. Site means are plotted as bars in map (lengths of bars indicate relative recruitment rates among sites). Seasonal relative mean recruitment rates are relative to the season having the highest recruitment rate (fall). See Table 1 for values.

dry periods (Fig. 11). However, slightly depressed salinities at the western end of the transect indicate that the plume may typically move west and inshore of the 16-m contour during dry periods.

Temperature differences between clearly distinct water masses, indicated by sharp color fronts, were typically $<0.1^{\circ}\text{C}$ (pers. obs.). Temperature and salinity were not useful tracers of water masses in Mamala Bay during dry periods because of this and because of the high temporal and spatial variability in salinity and temperature.

Drifters—Drifter trajectories were similar among days within ebb and flood tides. An example of current patterns observed on 1 August 1995 is provided in Fig. 12. Ebb currents consistently diverged or were complex near EB. Ebb currents were typically eastward, east of EB, and westward, west of EB. Flood currents were primarily westward throughout the drifter study area, which indicates that the M2 convergence is located further west. In general, the largest cross-shore current components were observed near EB. These general patterns were observed during dry and post-rainstorm periods. No sampling was possible during storms or the first 24 h after storms because of strong winds.

Discussion

The multiple types of data that were collected in this study provide information that is useful for determining both the

spatial and temporal distributions of water masses in Mamala Bay. This temporal and spatial view of water masses within the Bay is not possible when individual tracers or methodologies are used. The reason, each tracer is indicative of a particular water mass or type of water mass (e.g., turbid coastal water vs. clear offshore water), over a particular timescale and therefore provides only a portion of the view in space and time. The combination of tracers and methodologies yield a more complete view. The timescales of the methodologies presented here range from hours (the period of CTD and turbidity data collection within a day) to semi-monthly (larval recruitment and supply sampling frequency) to 3 months (deployment period of stable isotopic moorings). The repeated collection of these data over a multiyear period provides information on the spatial distribution of water masses within the Bay over longer than annual timescales. The following discussion addresses each type of data in order of timescale, progressing from the shortest timescales to the longest. As each methodology is included for interpretation, the spatial and temporal distributions of water masses along the shelf of Mamala Bay become more apparent.

CTD and turbidity—The distributions of temperature and salinity from the CTD transects were useful for determining the spatial distribution of estuarine plumes immediately after large rainfall events. However, this methodology was not useful for dry periods, because patterns of temperature and

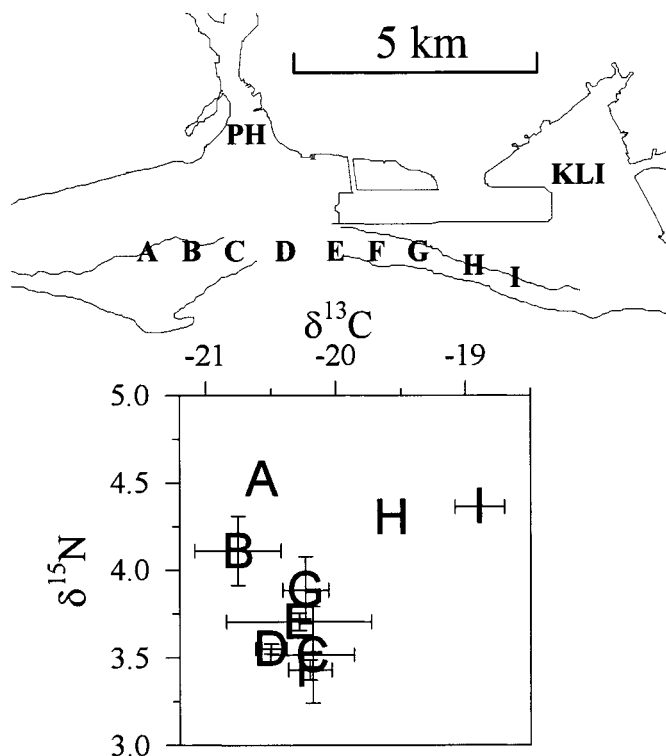


Fig. 7. Map of stable isotope study sites (top) with graph of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (units ‰) plotted against each other by site. Mean values are plotted with study site identifiers, and error bars are SDs. A and H are single samples, and the $\delta^{13}\text{C}$ of I is from one sample only because of analytical problems (see text). Three groups are apparent: group 1 (A and B), group 2 (C–G), and group 3 (H and I).

salinity were not obviously attributable to estuarine outflow during dry periods. Dry conditions predominate on the leeward sides of the Hawai'ian Islands (Mamala Bay is located on the leeward side of O'ahu), where significant rainfall mainly occurs during episodic winter storms (Price 1983). Rainfall onto the leeward sides of the Hawai'ian Islands during episodic storms can be quite heavy, sometimes accounting for up to half of the average annual rainfall in an hour or day (Price 1983). Because dry conditions prevail on the leeward side of O'ahu, CTD data do not provide information on the distribution of estuarine water masses for most of the year. This is also true for temperature records from thermographs deployed on the permanent moorings, because temperature differences along the 16-m contour were negligible. In fact, temperature differences between clearly distinct water masses, indicated by sharp color fronts, were typically $<0.1^\circ\text{C}$ (pers. obs).

Plumes emanating from Honolulu Harbor, KL, and PH after major rainstorms were always evident from the spatial distribution of salinity along the 16-m contour (Fig. 10). The plumes advected offshore from their sources into coastal waters, where oscillating along-shore tidal currents spread them along the shore. The movement of the PH plume after rainstorms is clearly visible from the chevron transects. The plume typically moved eastward and was clearly distinguishable up to 4 km from shore (Fig. 11). The trajectory of the PH plume was not as obvious during dry periods (Fig. 11). However, slightly depressed salinities at the western end of the chevron transect were occasionally observed, which suggests that the centerline of the plume occupies the area west and inshore of the 16-m contour during dry periods.

Temporal and spatial patterns of turbidity were apparent from the repetitive sampling program that was conducted at

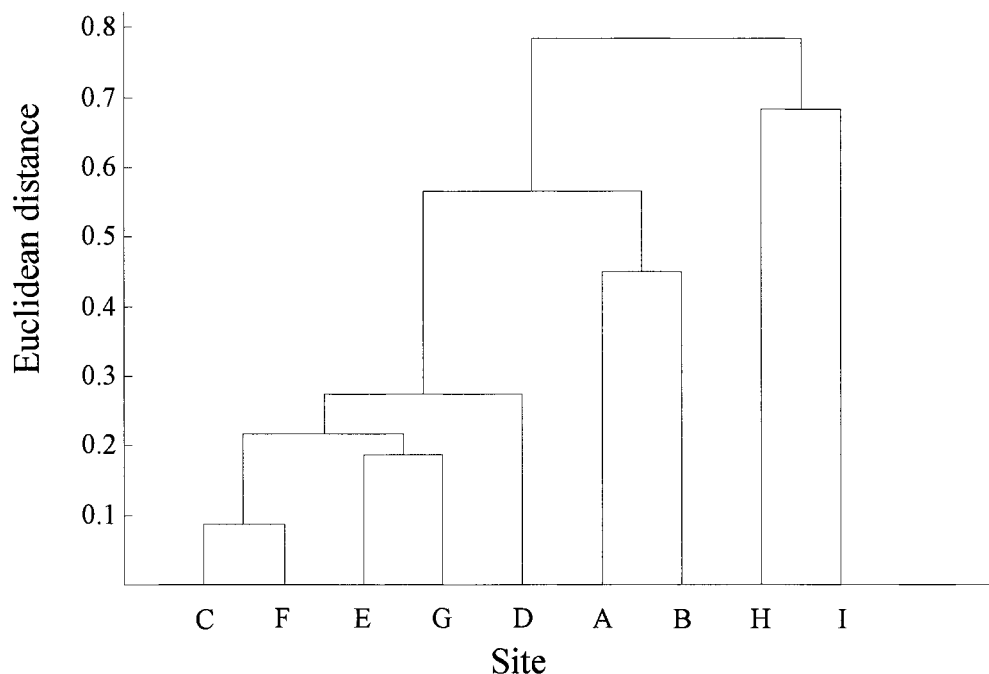


Fig. 8. Results of multivariate cluster analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among sites. The metric used for the analysis was Euclidean distance among site means for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

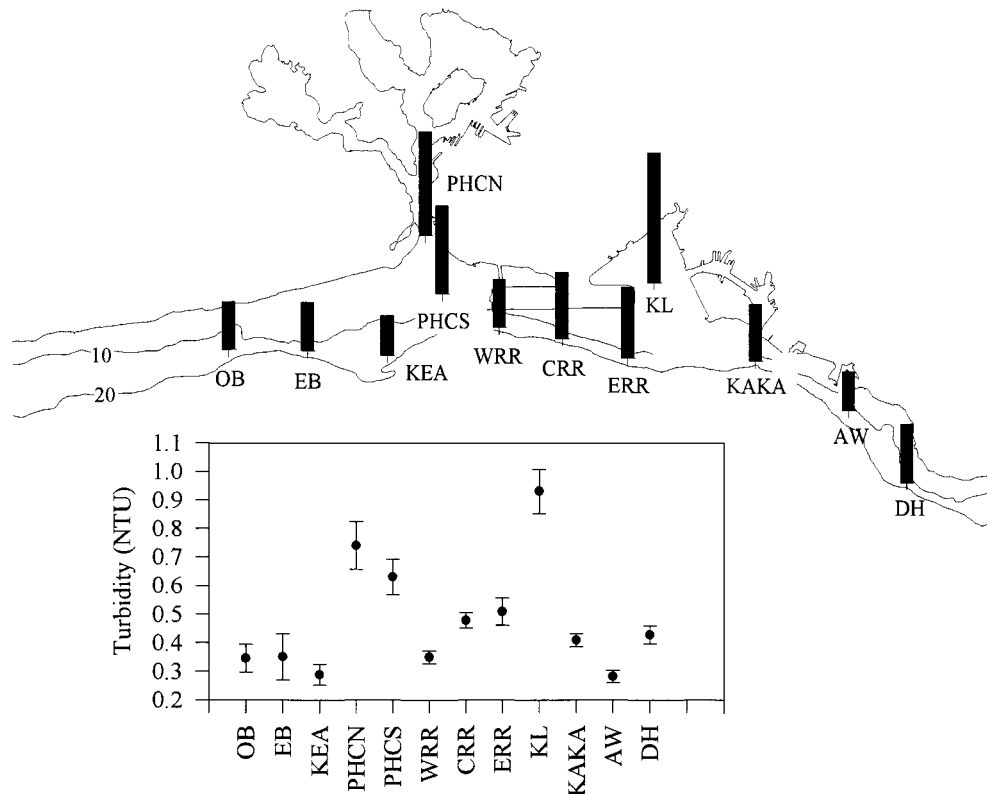


Fig. 9. Mean turbidity (NTU) values at study sites. Bar lengths indicate relative mean turbidity values among sites. Actual means are plotted in line graph at bottom with standard error bars for each site.

the permanent moorings. High turbidity events were observed after rainstorms and during swell events. Seasonally, these events occur during winter and summer for rainstorms and swell, respectively. Turbidity increased at all shelf sites after rainstorm events, and the greatest values during these periods were observed in the central portion of the Bay between PH and Honolulu Harbor. The same pattern was observed by Grigg (1995). Spatially, prevailing (nonwave and nonstorm periods) turbidity patterns are best illustrated by mean turbidity values among the sites (Fig. 7). Highest turbidities were observed along the PH Channel and in KL, as one would expect. Among the shelf sites, turbidity was consistently the lowest at KEA and AW, where turbidity was significantly different from the remaining shelf sites ($P < 0.05$). The low turbidity values observed at AW and KEA indicate that these sites are bathed by clearer water masses than all other shelf sites and that the source of this water mass may be offshore. The highest turbidities were observed at CRR and ERR, where turbidity values were significantly different from the rest of the shelf sites ($P < 0.05$), which indicates that these sites are typically bathed by an estuarine plume or a high-turbidity general coastal water mass. The sharp turbidity gradients observed between WRR and CRR and between AW and DH suggest that water-mass discontinuities are typically located between these pairs of sites.

Thus far, the integration of observed patterns of salinity and turbidity reveal short-term estuarine plume distributions after rainfall events and the persistence of high and low tur-

bidity water-masses among the shelf sites. Paradoxically, the site that is the closest down stream site from Pearl Harbor (recall westward mean drift within this portion of the Bay), KEA, is typically bathed by low-turbidity water. The interpretation of these patterns improves with the inclusion of integrative tracers.

Recruitment and larval supply—The spatial variability of total recruitment rates, as well as patterns of larval supply and recruitment of individual species, strongly suggests that different water masses typically bathe different areas of Māhala Bay. Recruitment rates of all taxa pooled exhibited significant seasonal and spatial variability (Fig. 3). Of greatest interest is the observation that the sites with the lowest mean turbidity values, sites KEA and AW, also had the lowest mean rates of recruitment and larval supply, whereas the shelf sites with the highest mean recruitment rates, ERR and CRR, also had the highest mean turbidity. Furthermore, the sharp turbidity gradient observed between KEA and CRR was also observed for recruitment rates. Similar persistent spatial patterns of turbidity and recruitment strengthen the hypothesis that different water masses typically bathe different areas of the shelf.

Larval supply and recruitment patterns of individual species appear to identify the spatial distribution of some water masses bathing the shelf. The highest mean recruitment rates of *A. intermedia* and *F. pupoides* were observed in KL. The highest mean rates of larval supply and recruitment for *B.*

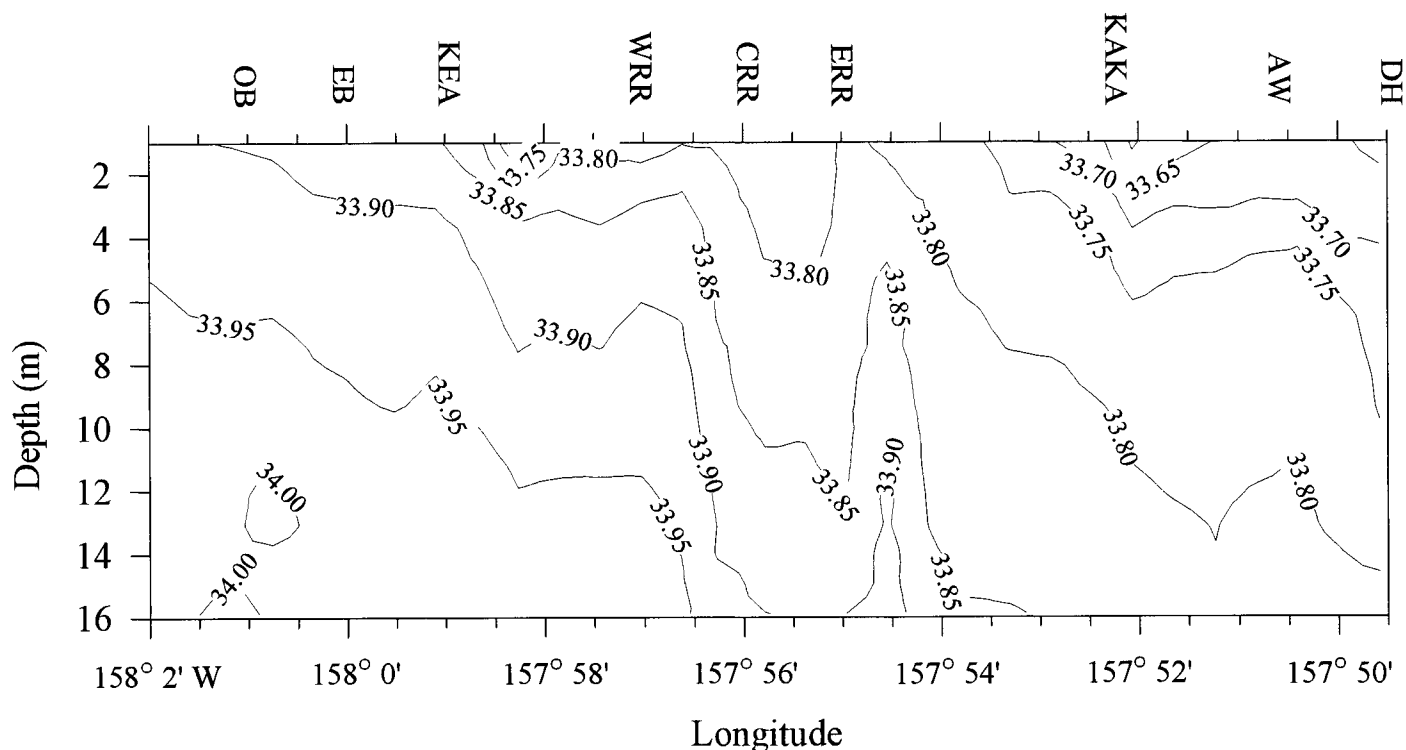


Fig. 10. Distribution of salinity along the 16-m contour on 5 March 1996 during ebb tide and ~36 h after a rainstorm (~7.5 cm of rain). Transect track is shown in Fig. 2. Casts were conducted ~500 m apart. The positions of shelf sites are indicated at the top. The PH plume is located between KEA and WRR, the KL plume extends deeper into the water column and is located between ERR and CRR, and the Honolulu Harbor plume is evident near KAKA.

amphitrite were also observed in KL. Furthermore, the largest adult populations of *B. amphitrite* on the southern shore of O'ahu were observed in KL (adult populations of *A. intermedia* and *F. pupoides* were not surveyed; adult populations of *B. amphitrite* were surveyed as part of another study). Together, these observations indicate that larval *A. intermedia*, *F. pupoides*, and *B. amphitrite* are present in KL waters. This was true throughout the year, because these species were observed to recruit most heavily in KL year round. The affinity of larval *A. intermedia*, *F. pupoides*, and *B. amphitrite* with KL waters enables their use as tracers of the KL water mass. Recruitment patterns of these species over the shelf indicate that the KL plume moves westward after it exits the mouth of the lagoon and bathes ERR and CRR. This is consistent with turbidity patterns observed at these sites and with westward mean flows over the shelf westward of AW (Hamilton et al. 1995). Some recruitment of *F. pupoides* was observed at DH, but this was believed to be from larvae moving westward from Moana'lua Bay (the bay east of DH). A plume of turbid water moving westward from Moana'lua Bay was frequently observed near DH.

Similar arguments hold for *Salmacina dysteri* and *P. radiata* as tracers of the PH plume. Recruitment rates for these species were consistently the greatest in the PH Channel, which indicates affinities with PH waters. The recruitment patterns of these two species over the shelf indicate that the PH plume typically moves westward from the mouth of PH toward EB and OB but does not bathe KEA, given that little or no recruitment of these species was observed at KEA.

Again, westward movement of the PH plume is consistent with observed westward mean flows, west of AW.

Recruitment patterns of *C. virgatum* appear useful as tracers of oceanic water masses. The distribution of larval *C. virgatum* is likely oceanic, because flotsam and megafauna in open ocean waters are habitats for adults of this opportunistic species (Newman 1980). Recruitment patterns of *C. virgatum* indicate that EB, KEA, and AW are typically bathed by offshore water throughout the year. Recruitment of *C. virgatum* at KEA and AW are consistent with low mean turbidities and recruitment rates of all taxa pooled. Taken together, these observations strongly indicate that KEA and AW are sites where offshore waters impinge on the shelf. Recruitment of *C. virgatum* was also observed at EB, where mean recruitment rates were the highest for this species. This result conflicts with the observation that species from PH also recruited at this site. The only possible explanation for this paradox is that EB is exposed to both offshore waters and PH plume waters. Furthermore, because recruits of both *C. virgatum* and the PH species were observed on the same tiles, the periodicity of this exposure was less than the tile deployment period (14 d). Examination of recruitment data for *C. virgatum* reveals that the high mean at EB is heavily influenced by a single pulse of settlement at this site. If this event is removed from the mean, then mean recruitment rates are greatest at KEA. Recall that mean turbidity values of EB were intermediate to KEA and the PH Channel sites and that turbidity was most variable at site EB, compared with all other shelf sites. These observations

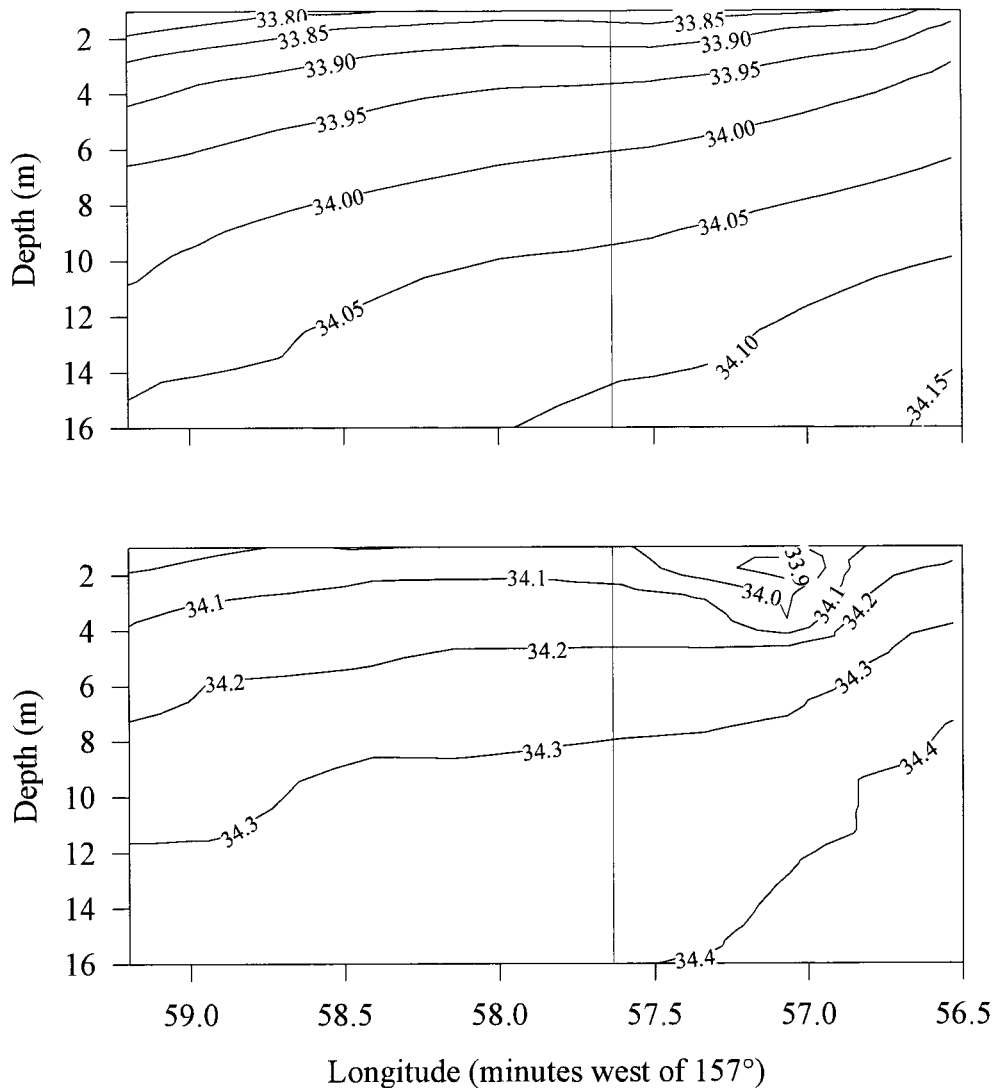


Fig. 11. Distribution of salinity during ebb tide along the chevron transect on: (1) 11 July 1996 during a nonrainstorm period (top), and (2) 5 March 1996 after an ~ 7.5 cm rainstorm (bottom). The track of the chevron transect is shown in Fig. 2. The vertex of the chevron is indicated here with a vertical line.

support the argument that EB is exposed to both PH and offshore waters.

Although recruitment of the tracer species discussed above were significantly different among seasons, recruitment of all these species was observed throughout the year. This means that the spatial distributions of offshore, PH, and KL waters persist year round, with little variation at periodicities greater than the recruitment-sampling interval (14 d).

One final point is warranted in the discussion of larval data. The relative difficulty of larval identification compared with recruit identification means that the recruitment method is more useful for water-mass discrimination than larval trapping. This is exemplified by the data presented here. Larval *F. pupoides* and *B. amphitrite* were the only larval species

that were available as larval tracers, whereas six species of recruits were available.

Stable isotopes—The stable isotopic data contribute additional information about the spatial distributions of water masses located between EB and KL. However, caution must be exercised in the interpretation of these data because of the analytical problems with end-member samples. These problems complicate the interpretation of the stable isotopic data because the patterns of stable isotopic ratios of *Spondylus tenebrosus* that were observed along the isotopic mooring transect cannot be directly attributed to exposure to waters from KL and PH. Instead, exposures must be inferred from patterns observed in the other types of data that have been presented thus far. The fact that spatial patterns ob-

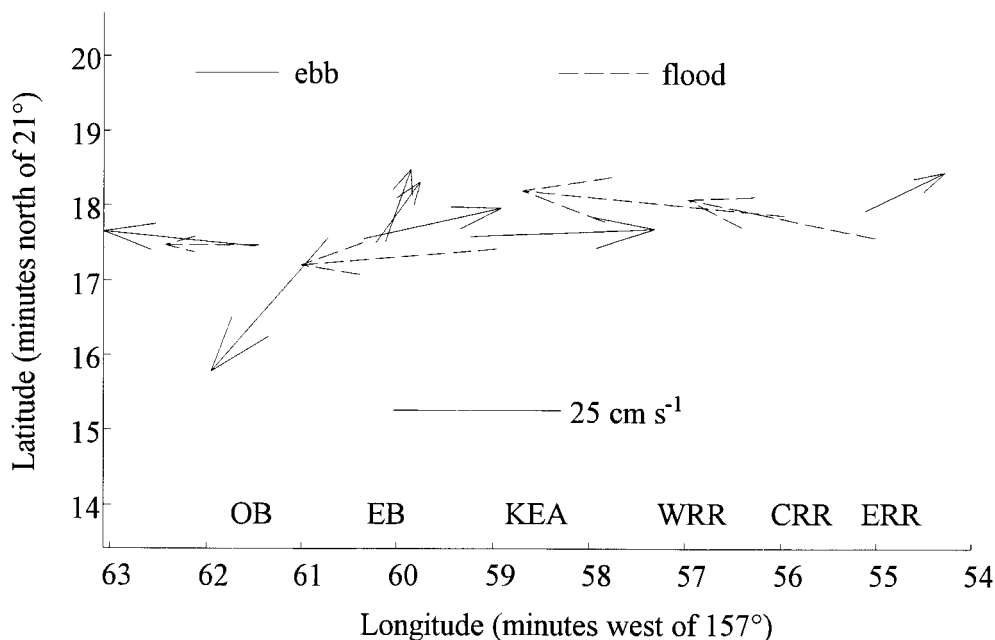


Fig. 12. Current vectors calculated from drifter trajectories during ebb tide (solid line) and flood tide (dashed line) on 1 August 1995. Shelf site locations are indicated just above the abscissa. Current divergences were typically observed near site EB during ebb tide. Scale bar indicates a current magnitude of 25 cm s^{-1} .

served in the stable isotopic data were similar to the spatial patterns observed for the other types of data supports such an interpretation.

Three groups of spatially coherent sites are evident from the plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figs. 7 and 8): group 1 (sites A and B), group 2 (sites C–G), and group 3 (sites H and I). These groupings suggest that the mooring transect is typically bathed by different water masses that have distinct stable isotopic compositions of POM. The spatial boundaries of these groups coincide with patterns of recruitment and turbidity that were observed during the both the entire study and during the period that isotopic moorings were deployed (Fig. 13). Sites A and B, located inshore of KEA, are likely bathed by the plume emanating from PH. Mean $\delta^{13}\text{C}$ values from PH were -20.59 , which is similar to the values observed at sites A and B. However, this value is also similar to mean $\delta^{13}\text{C}$ values for sites C–G. The $\delta^{15}\text{N}$ values of samples from PH are needed to discriminate PH waters from group 1 and 2 sites. Nonetheless, the discontinuity of stable isotopic values between sites B and C suggests that a water-mass boundary is typically located between these sites and that this boundary is likely the eastern boundary of the PH plume. Low turbidity, high recruitment rates of *C. virgatum*, low recruitment rates of all taxa pooled, as well as no recruitment of PH species at KEA indicate that the PH plume typically moves westward before it gets as far offshore as KEA.

The discontinuity of stable isotopic values between sites G and H indicates that the western boundary of the plume emanating from KL is typically located between these sites. However, the recruitment of KL species at sites as far west as WRR (Fig. 13) indicates that the KL plume occasionally

encroaches further west than site G. The method of signal integration in the recruitment and stable isotopic methodologies likely accounts for these observed differences. The recruitment method, which integrates instantaneous values of larval recruitment over the period of settlement-plate deployment (14 d), is more likely to record short-period variation in water-mass distributions than the stable isotopic method, because the turnover times of stable isotopic tissue compositions of *S. tenebrosus* are likely longer than the tile deployment period. (Laboratory feeding studies of stable isotopic turnover times for *S. tenebrosus* would strengthen this discussion.) Therefore, the patterns of recruitment and stable isotopes offshore from the Reef Runway indicates that the KL plume typically bathes sites CRR, ERR, H, and I and infrequently bathes WRR, E, F, and G. The differences between the recruitment and stable isotopic methodologies in this area exemplify the inherently lowpass-filtered nature of the stable isotopic method and points to the usefulness of this application where longer-term signals are of greater interest than shorter-term signals.

The interpretation of stable isotopic data would have been strengthened if an oceanic end member were available to interpret the stable isotopic compositions of group 2 sites. This would have required a mooring over deep water in areas subject to heavy ship traffic. The resources to deploy such a large and expensive mooring with the requisite navigational aids were not available. Another problem with the stable isotope data is that they do not conform to the dogma that the $\delta^{15}\text{N}$ of oceanic POM is enriched relative to terrestrial POM (Thornton and McManus 1994). Groups 1 and 3, which, it has been argued here, are exposed to PH and KL waters, respectively, are enriched in $\delta^{15}\text{N}$ relative to group 2

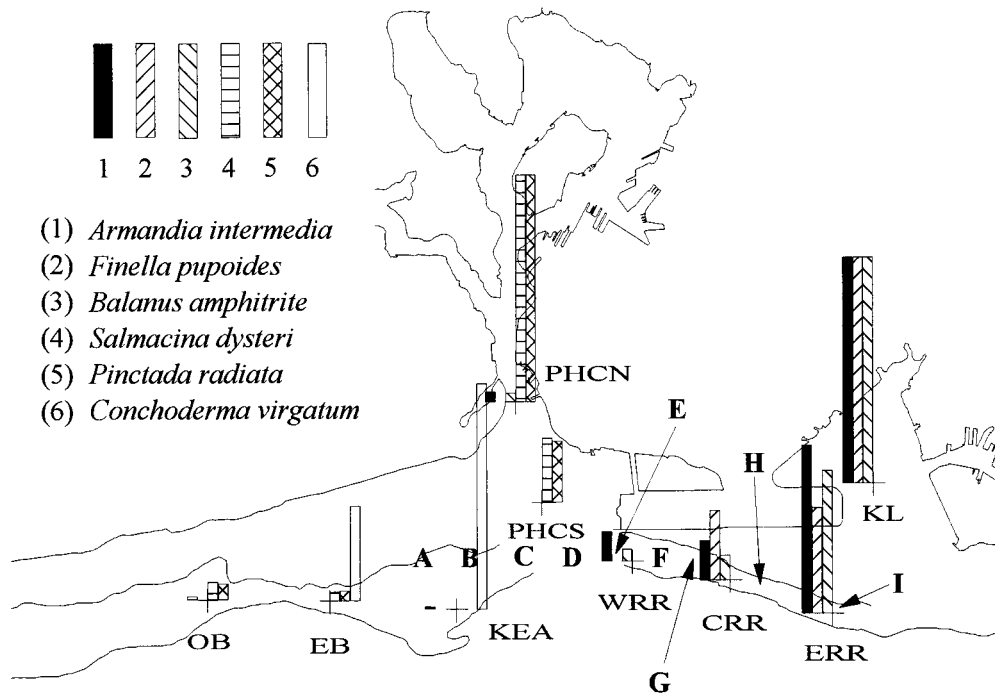


Fig. 13. Relative mean recruitment rates for all tracer species during the deployment period of stable isotopic moorings. Bar lengths indicate mean recruitment rates for each species relative to the site where mean recruitment rates for each species were maximal. Maximal mean recruitment rates for *A. intermedia*, *F. pupoides*, and *B. amphitrite* were observed at KL, maximal mean recruitment rates for *S. dysteri* and *P. radiata* were maximal at PHCN, and recruitment rates for *C. virgatum* were maximal at KEA. The locations of the stable isotopic moorings are also indicated.

sites, which appear to be bathed by more oceanic waters, judging by recruitment and turbidity data. Despite these problems, the spatial correspondence of recruitment and turbidity data with the stable isotopic data is intriguing and suggests that the stable isotopic patterns that were observed are likely attributable to water-mass effects. The results of this study indicate that the use of stable isotopic compositions of suspension feeders warrants further investigation. The use of stable nitrogen isotopic compositions of bivalves has already been used to determine sources of organic matter along estuarine gradients (Riera 1998) and particulate food sources within an estuary (Yelenik et al. 1996).

Drifters—The recruitment of *C. virgatum* and the PH species, *Salmacina dysteri* and *P. radiata*, at EB appear paradoxical until drifter data are considered. The major patterns observed from the drifter releases were that cross-shore circulation was typically the greatest near EB and that ebb currents frequently diverged near EB, with ebb currents going eastward east of EB and westward west of EB (Fig. 12). These patterns were similar among days and among dry and post-rainstorm periods. These observations are consistent with the argument that EB is exposed to offshore and PH waters. The periodicity of exposure to these waters is certainly less than the tile-deployment period of 14 d, as evidenced by the recruitment of species associated with both water masses on the same tiles, and may sometimes be as short as tidal periodicities. The observation that turbidity

was most variable at EB is also consistent with the argument that EB is exposed to both offshore and PH waters. The along shore border between offshore and PH waters apparently migrates in a cross-shore manner near EB, resulting in the alternate exposure of EB to these different water masses.

Conclusions—The value of using integrative tracers of water mass distribution, such as larval recruitment patterns and the stable isotopic values of suspension feeders, is that high frequency variability is naturally removed. This enables the determination of prevailing patterns or conditions, which are typically of interest when explaining the distribution of plants and animals or managing coastal ecosystems. The use of nonintegrative tracers as indicators of prevailing conditions would require either moorings, equipped with tracer sensors and data loggers, deployed with adequate spatial resolution, or frequent water sampling trips. Both alternatives are typically not practical.

The difference between prevailing and rainstorm-induced water mass distributions in Mamala Bay is illustrated by comparison of water-mass distributions inferred from larval recruitment patterns with patterns inferred from CTD data. First, it should be noted that CTD data were not useful to determine water-mass distributions during dry (prevailing) conditions because salinity and temperature differences among water masses were too small and variable to be useful. The distribution of the PH plume after rainstorms appeared to be quite different from its distribution during dry

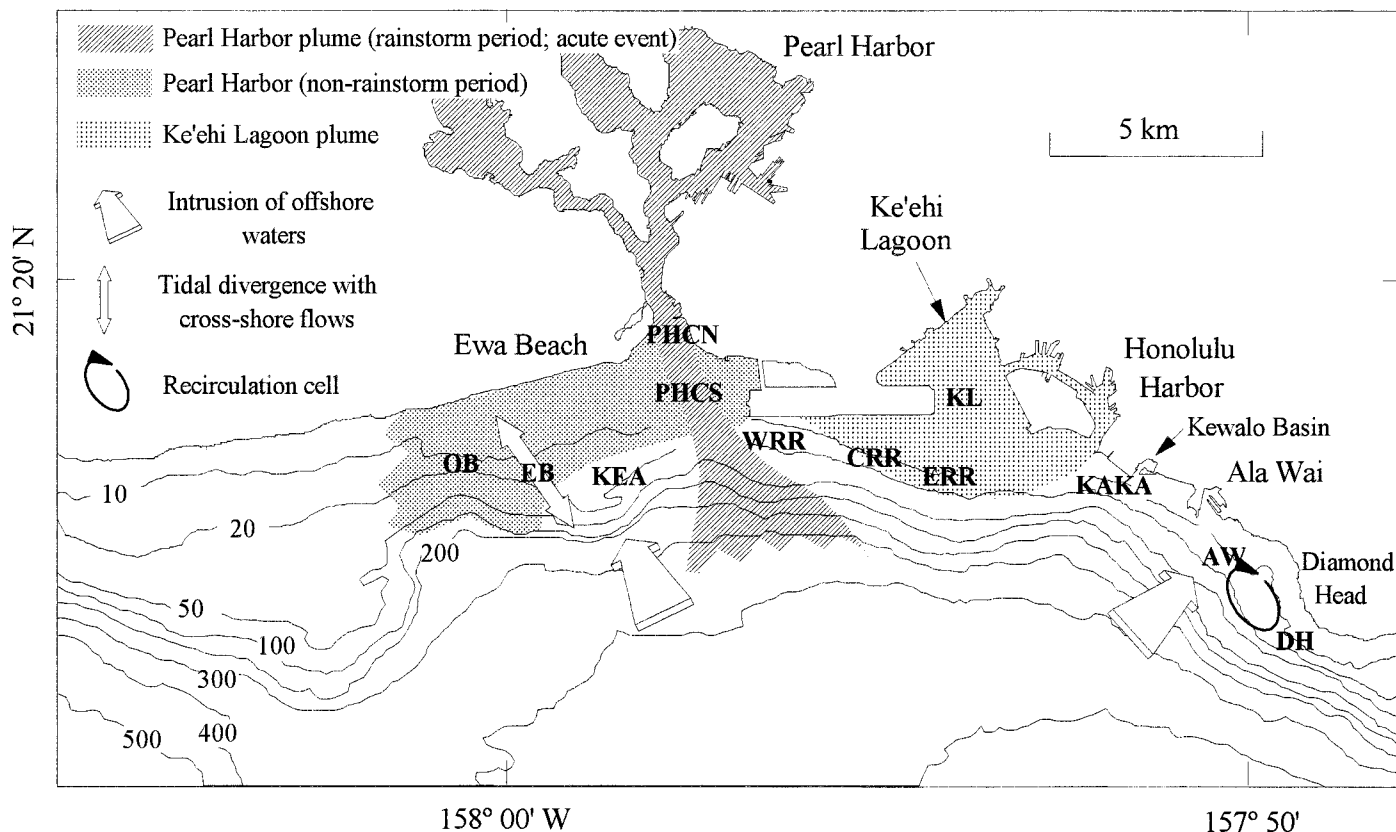


Fig. 14. Conceptual model of water-mass distribution and circulation features inferred from recruitment patterns of benthic invertebrates, CTD transect data, stable isotopic compositions of the suspension-feeding bivalve, *Spondylus tenebrosus*, turbidity, and drifter data.

conditions. The PH plume did not extend offshore to the 16-m contour until it advected far to the west near EB. On the contrary, the plume moved directly offshore and sometimes slightly to the east during and immediately after rainstorms. In contrast to the PH plume, the distribution of the KL plume did not appear to differ between rainstorm and dry conditions. These patterns are illustrated in Fig. 14, in which the spatial distributions of the PH and KL plumes are shown, as well as some circulation features that were evident from turbidity, CTD, recruitment, and drifter data.

The illustration in Fig. 14 is presented as a conceptual model of water-mass distributions and circulation features within Mamala Bay. As such, it is of use to ecologists interested in the distribution of animals and plants and to coastal managers who wish to remediate the effects of source-specific pollutants on particular ecosystems within the Bay. The prevailing distribution of the PH plume closely parallels the distribution of coral bio-erosion observed by Grigg (1995). Coral bio-erosion is primarily caused by suspension feeding animals. Rates of bio-erosion typically increase with increasing food supply. PH is likely the source of such particulate food. The prevailing distributions of oceanic waters and the plumes emanating from PH and KL coincides with the distribution of phytoplankton observed by Laws et al. (1999). Phytoplankton assemblages are chlorophyte dominated in eastern Mamala Bay, where an oceanic water mass appears to bathe the shelf (inferred from turbidity

data, the reduced recruitment rates of coastal species and the recruitment of *C. virgatum* at AW). Whereas phytoplankton assemblages are dominated by diatoms in waters west of Sand Island, where eutrophic estuarine waters are located. The distribution of coastal and oceanic appendicularian species also coincide with the patterns of water-mass distribution presented in Fig. 14 (Scheinberg pers. comm.). The coincidence of biological distributional patterns observed in these studies with water-mass distributions in the present study suggests physical control of Mamala Bay ecosystems by runoff-induced plumes and gross circulation features within the Bay. The distribution of water masses in Mamala Bay inferred from this study may also be of use to coastal managers, who, at present, are considering reclassifying areas of western Mamala Bay as "wet" (Laws pers. comm.), effectively lowering the standards for acceptable water quality. This would alter present water quality management strategy for Mamala Bay and its watersheds.

The physical control of recruitment pattern is evident from the distributions of water masses and recruitment patterns that were observed in this study. The physical control of recruitment has been demonstrated in the past (e.g., Farrell et al. 1991; Pineda 1991; Gaines and Bertness 1992). The degree of spatial variability in recruitment and larval supply pattern over scales of ~2–3 km that was observed in this study is striking and may have important implications for

adult patch dynamics at similar or smaller spatial scales, especially when recruitment processes are limiting.

References

- ALBANI A. D., V. M. FAVERO, AND R. S. BARBERO. 1998. Distribution of sediment and benthic foraminifera in the Gulf of Venice, Italy. *Estuar. Coast. Shelf Sci.* **46**: 251–265.
- ALTABET, M. 1988. Variations in nitrogen isotopic composition between sinking and suspended particles: Implications for nitrogen cycling and particle transformation in the open ocean. *Deep-Sea Res. I* **35**: 535–554.
- . 1990. Organic C, N, and stable isotopic compositions of particulate matter collected on glass-fiber and aluminum oxide filters. *Limnol. Oceanogr.* **35**: 902–909.
- ANDREWS, J. E., A. M. GREENAWAY, AND P. F. DENNIS. 1998. Combined carbon isotope and C/N ratios as indicators of source and fate of organic matter in a poorly flushed, tropical estuary: Hunts Bay, Kingston Harbour, Jamaica. *Estuar. Coast. Shelf Sci.* **46**: 745–756.
- BAILEY-BROCK, J. H. 1989. Fouling community development on an artificial reef in Hawaiian waters. *Bull. Mar. Sci.* **44**: 580–591.
- BROECKER, W. S., AND T. H. PENG. 1982. Tracers in the sea. Lamont-Doherty Geological Observatory.
- CANUEL, E. A., J. E. CLOERN, D. B. RINGELBERG, J. B. GUCKERT, AND G. H. RAU. 1995. Molecular and isotopic tracers used to examine sources of organic matter and its incorporation into the food webs of San Francisco Bay. *Limnol. Oceanogr.* **40**: 67–81.
- COLWELL, R. R., G. T. ORLOB, AND J. R. SCHUBEL. 1996. Mamala Bay Study management. In R. R. Colwell, G. T. Orlob, and J. R. Schubel [eds.], Mamala Bay Study final report, V. 1. Mamala Bay Study Commission.
- CONOVER, W. J. 1980. Practical nonparametric statistics, 2nd ed. John Wiley and Sons.
- DAVIS, R. 1985. Drifter observations of coastal surface currents during CODE: The method and descriptive view. *J. Geophys. Res.* **90**: 4741–4755.
- DENIRO, M. J., AND S. EPSTEIN. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* **42**: 495–506.
- . 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* **45**: 495–506.
- EGGLESTON, D. B., R. N. LIPCIUS, L. S. MARSHALL, AND S. G. RATCHFORD. 1998. Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: Lunar and seasonal periodicity, spatial coherence, and wind forcing. *Mar. Ecol. Prog. Ser.* **174**: 33–49.
- FARRELL, T. M., D. B. BRACHER, AND J. ROUGHGARDEN. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol. Oceanogr.* **36**: 279–288.
- GAINES, S. D., AND M. D. BERTNESS. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**: 579–580.
- GRIGG, R. W. 1995. Coral reefs in an urban embayment in Hawaii—a complex case history controlled by natural and anthropogenic stresses. *Coral Reefs* **14**: 253–266.
- HAMILTON, P., J. SINGER, AND E. WADDELL. 1995. Ocean current measurements. In R. Colwell, G. Orlob, and J. Schubel [eds.], Mamala Bay Study. Mamala Bay Study Commission.
- JENKINS, S. R., AND OTHERS. 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (Crustacea: Cirripedia) over a European scale. *J. Exp. Mar. Biol. Ecol.* **243**: 209–225.
- JONES, M. B., AND C. E. EPIFANIO. 1995. Settlement of brachyuran megalopae in Delaware Bay: An analysis of time series data. *Mar. Ecol. Prog. Ser.* **125**: 67–76.
- KINGSFORD, M. J., AND I. M. SUTHERS. 1994. Dynamic estuarine plumes and fronts: Importance to small fish and plankton in coastal waters of NSW, Australia. *Cont. Shelf Res.* **14**: 655–672.
- LARSEN, J. C. 1977. Cotidal charts for the Pacific Ocean near Hawaii using f-plane solutions. *J. Phys. Oceanogr.* **7**: 100–109.
- LAWS, E. A., AND D. ZIEMANN. 1996. Effects of sewage discharges and stream runoff on phytoplankton communities and water quality in Mamala Bay. In R. R. Colwell, G. T. Orlob, and J. R. Schubel [eds.], Mamala Bay Study final report, V. 3. Mamala Bay Study Commission.
- , ———, AND D. SCHULMAN. 1999. Coastal water quality in Hawaii: The importance of buffer zones and dilution. *Mar. Env. Res.* **48**: 1–21.
- LEFEVRE, J. 1986. Aspects of the biology of frontal systems. *Adv. Mar. Biol.* **23**: 164–281.
- MCLUSKY, D. S., S. C. HULL, AND M. ELLIOTT. 1993. Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper Forth Estuary. *Neth. J. Aquat. Ecol.* **27**: 101–109.
- MICHENER, R. H., D. M. SCHELL. 1994. Stable isotope ratios as tracers in marine aquatic food webs. In K. Lajtha and R. H. Michener [eds.], Stable isotopes in ecology and environmental science. Blackwell Scientific Publications.
- MOREIRA, M. H., H. QUEIROGA, M. M. MACHADO, AND M. R. CUNHA. 1993. Environmental gradients in a southern Europe estuarine system: Ria De Aveiro, Portugal, implications for soft bottom macrofauna colonization. *Neth. J. Aquat. Ecol.* **27**: 465–482.
- NEWMAN, W. A. 1980. Cirripedia: The barnacles. In R. H. Morris, D. P. Abbott, and E. C. Haderlie [eds.], Intertidal invertebrates of California. Stanford Univ. Press.
- O'CONNOR, T. P., AND B. BELIAEFF. 1995. Recent trends in coastal environmental quality: Results from the Mussel Watch Project. US Dept. of Commerce, NOAA.
- PECHENIK, J. A. 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: Does it occur, is there a price to pay? *Ophelia* **32**: 63–94.
- PINEDA, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* **253**: 548–551.
- PRICE, S. 1983. The natural environment: Climate. In R. W. Warwick [ed.], Atlas of Hawaii. Univ. of Hawaii Press.
- RIERA, P. 1998. Del 15-N of organic matter sources and benthic invertebrates along an estuarine gradient Marennes-Oleron Bay (France): Implications for the study of trophic structure. *Mar. Ecol. Prog. Ser.* **166**: 143–150.
- ROMAN, M. R., AND W. C. BOICOURT. 1999. Dispersion and recruitment of crab larvae in the Chesapeake Bay Plume: Physical and biological controls. *Estuaries* **22**: 563–574.
- SAMMARCO, P. W., M. J. RISK, H. P. SCHWARCZ, AND J. M. HEIKOOP. 1999. Cross-continental shelf trends in coral $\delta^{15}\text{N}$ on the Great Barrier Reef: Further consideration of the reef nutrient paradox. *Mar. Ecol. Prog. Ser.* **180**: 131–138.
- SMITH, K. A., M. T. GIBBS, J. H. MIDDLETON, AND I. M. SUTHER. 1999. Short term variability in larval fish assemblages of the Sydney shelf: Tracers of hydrographic variability. *Mar. Ecol. Prog. Ser.* **178**: 1–15.
- SPIES, R. B., H. KRUGER, R. IRELAND, AND D. W. RICE. 1989. Stable isotope ratios and contaminant concentrations in a sewage-distorted food web. *Mar. Ecol. Prog. Ser.* **54**: 157–170.
- THORNTON, S. F., AND J. MCMANUS. 1994. Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter provenance in estuarine systems:

- Evidence from the Tay Estuary, Scotland. *Estuar. Coast. Shelf Sci.* **38**: 219–233.
- TIESZEN, L. L., AND T. W. BOUTTON. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}\text{C}$ analysis of diet. *Oecol.* **57**: 32–37.
- VAN DER SPOEL S. 1994. The basis for boundaries in pelagic biogeography. *Prog. Oceanog.* **34**: 121–133.
- WADA E., M. MINAGAWA, H. MIZATANI, T. TSUJI, R. IMAIZUMI, AND K. KARASAWA. 1987. Biogeochemical studies on the transport of organic matter along the Otsuchi River Watershed, Japan. *Estuar. Coast. Shelf Sci.* **25**: 321–336.
- YELENIK S., J. MCCLELLAND, N. FEINSTEIN, AND I. VALIELA. 1996. Changes in N and C stable isotope signatures of particulate organic matter and Ribbed Mussels in estuaries subject to different nutrient loading. *Biol. Bull.* **191**: 329–330.
- YUND P. O., S. D. GAINES, AND M. BERTNESS. 1991. Cylindrical tube traps for larval sampling. *Limnol. Oceanogr.* **36**: 1167–1177.

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