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Contribution to the Themed Section: '*Mesopelagic resources—potential and risk*' Original Article

Vertical distribution and active carbon transport by pelagic decapods in the North Pacific Subtropical Gyre

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Pelagic decapods were sampled during August 2011 in the central North Pacific Subtropical Gyre (NPSG). Depth-stratified samples using a MOCNESS-10 (10 m^2 Multiple Opening/Closing Net and Environmental Sensing System) were collected at two stations to the west and north of the Hawaiian island of Oahu: Station Kahe: $21^{\circ}20.6'N$ – $158^{\circ}16.4'W$ and Station ALOHA: $22^{\circ}45'N$ – $158^{\circ}00'W$. Total decapod abundance and biomass were 4.3 ind. m^{-2} and 0.71 gDW m^{-2} . While 40 decapod taxa were identified, only 22 species were sampled sufficiently to study quantitatively their vertical migrations. All species were classified into three migration groups: full migrators (6 species); partial migrators (13 species); and non-migrators (3 species). Using measured local temperature profiles along with decapod densities and published models of respiration, excretion and mortality as well as gut fullness data, the individual and total active downward carbon flux was calculated. Active carbon flux of migrating decapods ranged from 383 to $625\text{ }\mu\text{gC m}^{-2}\text{ day}^{-1}$. This active flux was equal to 4.8–7.8% of passive flux at the mean nighttime residence depth of $\sim 711\text{ m}$, 2.1–3.4% of passive flux at the mean daytime residence depth ($\sim 262\text{ m}$), and 1.5–2.4% of passive flux at the base of the euphotic zone ($\sim 173\text{ m}$). Mortality flux accounted for $\sim 70\%$ of total active flux, followed by gut flux— $\sim 18\%$.

Keywords: active carbon flux, pelagic decapods, tropical Pacific, vertical distribution

Introduction

The oceans are estimated to have absorbed approximately half of total anthropogenic CO_2 emissions since the beginning of the industrial revolution (Sabine *et al.*, 2004; Le Quéré *et al.*, 2018). The physical and biological processes that mediate the transfer of carbon from the surface of the ocean to the ocean's interior are a key component of the global carbon cycle and the biological pump is one of the most important pathways for carbon transported vertically in the ocean and buried in the sediments. The biological pump includes the passive sinking of particulate organic matter (POM), diffusion and advection of dissolved organic matter (DOM), and active transport by the vertical migration of animals (Hidaka *et al.*, 2001). In the past, passive POM sinking, also known as “gravitational flux” or “passive flux”, and diffusion and advection of DOM were considered the most important processes mediating vertical transport (Longhurst, 1991).

However, since the 1990s the importance of active transport of carbon by vertical migrators has been increasingly recognized (Dam *et al.*, 1995; Hansen and Visser, 2016). This mechanism involves the transfer of organic matter consumed by zooplankton and nekton at the surface to their daytime residence depths through a combination of respiration, excretion, defecation, and mortality (Lampert, 1989; Longhurst, 1991). To date however, the majority of empirical studies assessing active carbon transport concentrated on the mesozooplankton and estimated flux out of the upper mixing layer only (Supplementary Table S1).

Microneuston are actively swimming marine organisms, generally larger than drifting mesozooplankton ($< 2\text{ cm}$), but smaller than larger nekton ($> 10\text{ cm}$) (Brodeur *et al.*, 2005). While they can be defined precisely based on Reynolds numbers, operationally microneuston include taxa too small to be caught by most large meshed pelagic trawls, but too mobile to be caught

efficiently by conventional plankton gears (Brodeur *et al.*, 2005). Their patchy distribution and high mobility makes them very difficult to sample without bias (Pakhomov and Yamamura, 2010). For these reasons, micronekton tend to be poorly sampled and understood (Brodeur and Yamamura, 2005). Micronekton nevertheless are the most conspicuous members of the mesopelagic community (Brodeur *et al.*, 2005), and significant nighttime residents of the epipelagic (Brodeur and Yamamura, 2005; Pakhomov and Yamamura, 2010). Functionally, micronekton are a primary food source for a wide variety of nektonic species, including commercially harvested species, and their active vertical migrators link smaller zooplankton with both large epipelagic (such as tuna, swordfish, and sharks) and meso/bathypelagic predators (Brodeur *et al.*, 2005; Brodeur and Yamamura, 2005).

Pelagic decapods are an abundant and important component of the micronekton community throughout many regions of the world's oceans (Maynard *et al.*, 1975; Hopkins *et al.*, 1989; Flock and Hopkins, 1992; Hopkins and Sutton, 1998). In the central North Pacific Subtropical Gyre (NPSG), previous studies have shown penaeid and caridean shrimps to be the second and fifth most abundant micronekton groups in deep (0–1200 m) net tows, and the first and fifth most abundant micronekton groups in shallow (0–400 m) nighttime tows (Maynard *et al.*, 1975; Hopkins *et al.*, 1994). Despite the high local abundance and functional importance of micronekton, very little is known about the diets or trophic role of pelagic decapods in the central NPSG. Active carbon flux attributed to migrant zooplankton in various areas of the world's oceans has been comparable to local gravitational fluxes (Longhurst *et al.*, 1990; Longhurst and Williams, 1992; Dam *et al.*, 1995; Le Borgne and Rodier, 1997; Zhang and Dam, 1997; Steinberg *et al.*, 2000, 2002; Al-Mutairi and Landry, 2001) suggesting a potentially important role for abundant pelagic decapods.

Longhurst *et al.* (1990) were among first to quantify the active flux attributed to migratory zooplankton. Using data from tropical and subtropical stations in the northwestern Atlantic and eastern Pacific, they showed that respiratory carbon flux due to zooplankton migrations across the pycnocline was equal to 13–58% of gravitational flux. A significant component of downward carbon flux had thus been completely missed in previous carbon models (Longhurst *et al.*, 1990). That study also indicated that active flux was highly variable between locations, and depended strongly upon the zooplankton community composition (Longhurst *et al.*, 1990, see also Supplementary Table S1). Most previous estimates of active flux were made using sampling gears well suited to sample mesozooplankton. Only a handful studies have attempted to assess the contribution of micronekton, or its main taxonomic groups, to vertical carbon flux pointing that pelagic decapods and myctophids may support significant active carbon transport to depths exceeding 300 m (Hidaka *et al.*, 2001; Davison *et al.*, 2013; Schukat *et al.*, 2013).

Previous studies of micronekton active carbon flux have been conducted in ecosystems where decapods contributed modestly to total micronekton density. During summer 2004, micronekton communities were sampled off the west coast of Oahu Island and both pelagic decapod diversity and contribution to the micronektonic community were found to be comparable to euphausiids, myctophids, and other fish (Kwong *et al.*, 2018). Stations ALOHA and Kahe have been regularly sampled since October 1988, under the auspices of the Hawaii Ocean Time-series (HOT) program (Karl and Lukas, 1996). These stations were chosen as

sites representative of the NPSG, which is the earth's largest contiguous biome (Karl, 1999; Karl and Lukas, 1996), but until now, the carbon flux through micronekton vertical migrations has not been adequately measured. The aims of this study were twofold: (a) to describe the composition, vertical distribution, and diel vertical migrations of pelagic decapods in the central NPSG, and (b) assess decapod contribution to local vertical carbon flux.

Material and methods

Samples were collected between August 19 and 25 of 2011 aboard the *R/V Kilo Moana* at two stations near the Hawaiian Island of Oahu, Station Kahe and Station ALOHA (Figure 1).

Station Kahe was located ~10 km from land (at 21°20.6'N 158°16.4'W), with a bottom depth of ~1500 m, while Station ALOHA is considered an open ocean station and located ~100 km from land (at 22°45'N 158°00'W) with a bottom depth of approximately 4800 m (Karl and Lukas, 1996).

Micronekton were collected using a MOCNESS-10 gear (Multiple Opening/Closing Net and Environmental Sensing System): a frame trawl with a 10 m² mouth opening and 6 mm mesh that was towed at a speed of 2 kts, and equipped with a SeaBird CTD to measure the physical properties of the water column. The MOCNESS-10 was outfitted with six nets: five of these nets were used to sample five discrete depth intervals, while the sixth net performed an oblique tow on the way down over the entire depth range. In this article, all decapods from the nets sampling discrete depths were identified to the lowest taxonomic level possible, counted and their carapace lengths measured. Carapace length was measured from the posterior middorsal margin to the posterior edge of the orbit using digital calipers with a resolution of 0.1 mm. Six depth-stratified tows were conducted, four at Station ALOHA and two at Station Kahe. Tows were made to depths of up to 1500 m during the day and up to 2500 m at night (Figure 2a). Due to limited sampling effort, data from Kahe and ALOHA stations were pooled. This was justified because the physical setting as well as decapod species composition

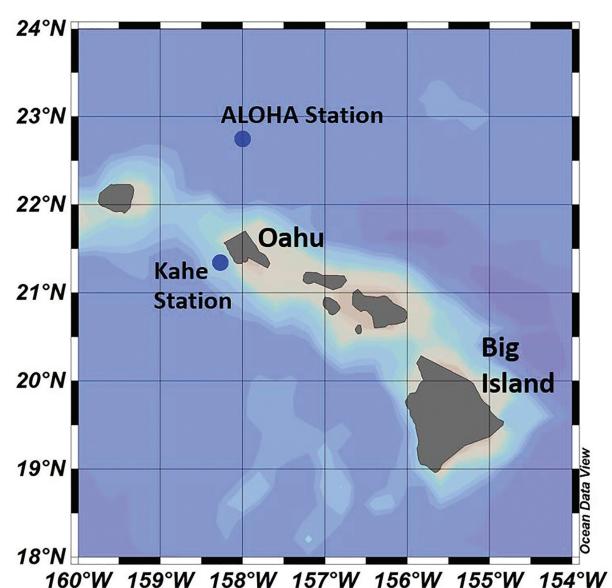


Figure 1. Sampling positions during August 2011 *R/V Kilo Moana* voyage in the NPSG off Hawaii.

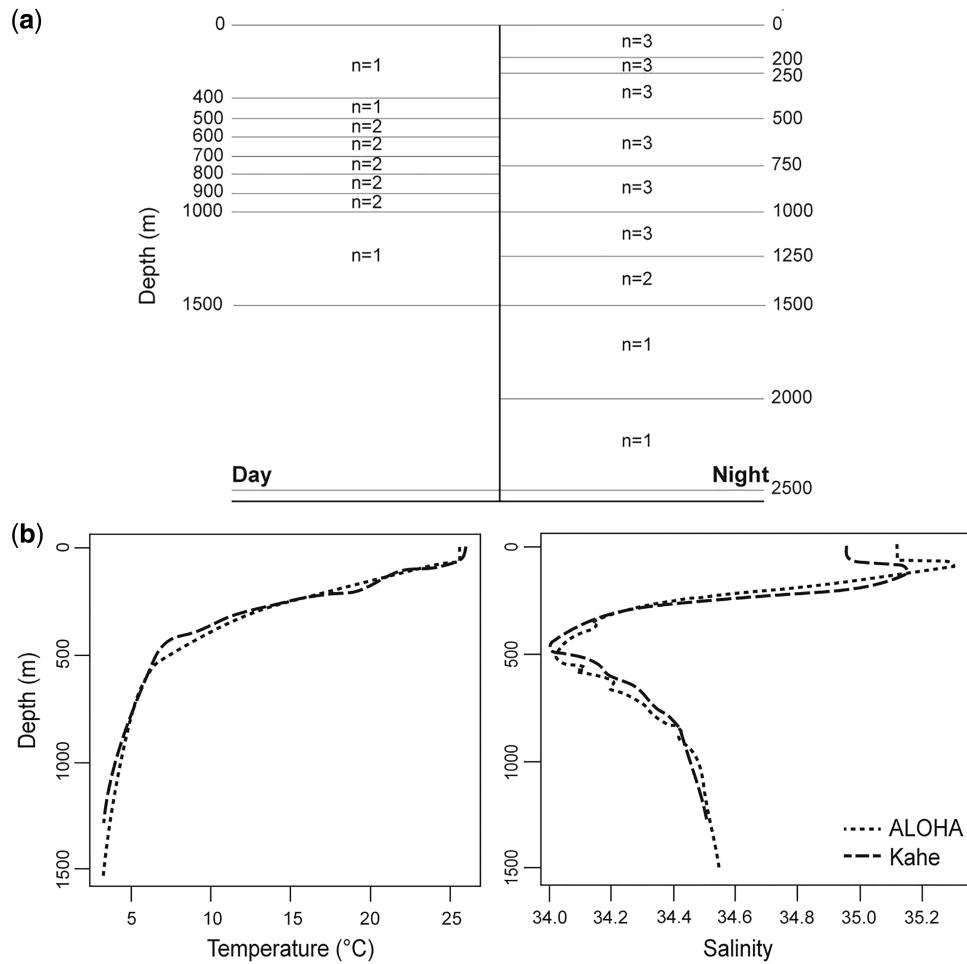


Figure 2. Stations Kahe and ALOHA combined sample size at each depth interval (a) and typical temperature and salinity profiles (b) during the 2011 R/V *Kilo Moana* voyage.

at both stations were highly similar (Figure 2b). Nevertheless, daytime sampling in the top 500 m only yielded one sample (Figure 2a). While it may be considered a low effort, recent study showed that daytime micronekton decapod density in the upper 500 m layer is insignificant (Kwong *et al.*, 2018).

Additional samples used to calculate length-weight relationships and carbon weight to dry weight ratios were collected at the Kahe Station during the 2004 *Oscar Elton Sette* cruise (Podeswa and Pakhomov, 2015). From the samples preserved in 6% buffered formalin roughly 75 individuals per species were used to determine species-specific carapace length to dry weight relationships. Individuals were rinsed thoroughly, carapace lengths were measured as described above, and wet weights were measured to 0.1 mg after blotting each individual with KimWipes to remove excess water. The decapods were then dried in an oven at 50°C for 24–72 h (24 h for small individuals, 48 h for moderate-sized individuals, 72 h for large individuals), then reweighed on the same balance to determine their dry weights. It was necessary to determine wet to dry weight ratios for decapods for two reasons. First, for species used for gut content analysis the dry weight of stomach content and the decapod was directly available. However, for species where no gut content analysis was performed, carapace lengths and wet weights were measured. In

such situations, dry weights were not directly measured to avoid unnecessary destruction of specimens. Instead, wet weights were converted to dry weights mathematically using predetermined wet to dry weight ratios. Second, the wet to dry weight ratios are affected by dry weight loss during formalin preservation, which has been well documented for zooplankton and micronekton in the literature (Pakhomov, 2003). Dry weight loss could be estimated based on body water content through a parabolic equation (Pakhomov, 2003):

$$\text{Dryweightloss} = 0.045 * (\text{body water content})^2 - 6.898 \\ * (\text{body water content}) + 289.4 \quad (1)$$

Dry weight loss is taken as a percentage of the mass of the unpreserved individual, while body water content is equal to the percentage of mass lost when an individual is dried completely in an oven. Relationships between carapace length and corrected dry weight were then derived for each species (Table 1). “Corrected dry weights” refer to both (a) dry weights that have been corrected for dry mass loss and (b) to wet weights that first have been converted to dry weights, and then corrected for dry weight loss.

To estimate the abundance of each decapod species at depth intervals, the catch was divided by the volume of water filtered.

Table 1. Relationship between carapace length (CL, mm) and corrected dry weights (DW, mg) for all pelagic decapod species found to perform diel vertical migrations.

Species	Mass units	a	B	p-value	R ²
<i>Acanthephyra smithi</i> *	DW	0.2862	2.7956	<0.0001	0.968
<i>Allosergestes pectinatus</i>	WW	0.1415	2.7634	<0.0001	0.849
<i>Allosergestes sargassi</i>	WW	0.4947	2.0937	<0.0001	0.950
<i>Deosergestes erectus</i>	WW	0.0575	2.8279	<0.0001	0.997
<i>Gennadas</i> spp.**	DW	0.7724	2.2225	<0.0001	0.949
<i>Janicella spinicauda</i>	DW	0.3375	2.6935	<0.0001	0.708
<i>Neosergestes consobrinus</i>	WW	0.0450	3.2939	<0.0001	0.955
<i>Neosergestes orientalis</i>	DW	0.2956	2.3369	<0.0001	0.792
<i>Notostomus elegans</i> ***	DW	0.0121	3.4175	<0.0001	0.987
<i>Parasergestes armatus</i>	DW	0.0743	2.8101	<0.0001	0.893
<i>Sergestes atlanticus</i>	WW	0.0421	3.2794	<0.0001	0.993
<i>Sergia bigemmeus</i>	WW	0.1345	2.8011	<0.0001	0.993
<i>Sergia gardineri</i>	DW	0.6103	2.1930	<0.0001	0.820
<i>Sergia scintillans</i>	DW	0.2389	2.5427	<0.0001	0.778
<i>Stylopandalus richardi</i>	DW	0.1108	3.1685	<0.0001	0.907
<i>Systellaspis debilis</i>	WW	0.0985	3.1415	<0.0001	0.990

"a" and "b" are constants derived by regression analysis for the equation DW = a * CL^b.

*Also used for *Acanthephyra curtirostris*;

**used for all *Gennadas* species (*bouvieri*, *clavicarpus*, *capensis*, *incertus*, and *tingarei*);

***also used for *Notostomus gibbosus*.

Due to the logistical challenge of accommodating various research group's needs, somewhat different depth intervals were sampled during different tows (Figure 2a). For example, in different series either 600–700 m or 700–800 m or 600–800 m depth intervals were sampled. It was thus necessary to either interpolate or extrapolate when estimating abundance for each depth interval and interpolation was deemed more appropriate. For example, data from the 600–700 m, 700–800 m, and 600–800 m depth intervals were analysed using the following equations:

$$\begin{aligned} \text{Estimated } 600 - 700 \text{ m abund.} &= 2/3 * (600 - 700 \text{ m abund.}) \\ &\quad + 1/3 * (600 - 800 \text{ m abund.}) \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Estimated } 700 - 800 \text{ m abund.} &= 2/3 * (700 - 800 \text{ m abund.}) \\ &\quad + 1/3 * (600 - 800 \text{ m abund.}) \end{aligned} \quad (3)$$

It has been well established that nets underestimate the densities of zooplankton, micronekton, and nekton. The catch efficiency of a net should therefore be taken into account when deriving abundance from net data (Aron and Collard, 1969; Misund *et al.*, 1999; Itaya *et al.*, 2001, 2007; Wiebe *et al.*, 2004). The catch efficiency of the MOCNESS 10 was conservatively assumed 33.3% due to the following considerations. First, Itaya *et al.* (2007) tested the effect of towing speed on catch per unit effort (CPUE) for a variety of frame trawls. They found that a frame trawl with a 4 m² mouth opening had a CPUE for two myctophid species (*Benthosema suborbitale* and *Diogenichthys atlanticus*) 2.8–3.4 fold higher at a towing speed of 3–4 kts versus 2 kts (Itaya *et al.*, 2007). Since it is unlikely that a 4 m² frame

trawl towed even at 4 kts has a 100% catch efficiency, the assumed catch efficiency of 33.3% was likely an overestimate. Second, the CUPE of 4 and 12.3 m² frame trawls towed at 4 kts was similar for *D. atlanticus*, while for *B. suborbitale* it was approximately double in the latter trawl compared with the 4 m² trawl (Itaya *et al.*, 2007). While this would suggest that, for certain species, the 10 m² net used in this study may somewhat offset the net avoidance incurred by the lower tow speed, the assumed 33.3% efficiency is still on the conservative side. Third, the 33.3% sampling efficiency could be arrived at based on studies that used a strobe light attached to the front of a MOCNESS net to "stun" euphausiids increasing catch by up to three times (Sameoto *et al.*, 1993; Wiebe *et al.*, 2004). Finally, direct MOHT and MOCNESS 10 inter-comparison in the northwestern Pacific showed that the latter net sampled only ~10% and ~20% of myctophids and euphausiids, respectively (Pakhomov and Yamamura, 2010, Table 3.2). Based on the available evidence, applying a catch efficiency of 33.3% for micronektonic decapods sampled with a 10 m² MOCNESS towed at 2 kts seemed conservative and acceptable.

Finally, it was necessary to account for reduced catches during the day. Due to increased visibility of the net during the day, avoidance is expected to be greater. It has been suggested that nighttime estimated abundances often exceed daytime densities due to visual net avoidance, and thus daytime abundances should be assumed equal to nighttime abundances. During our study, large day/night difference in density was only observed for 1 out of 19 migratory decapod species (e.g. *Sergia bigemmeus*), so overall this was a minor adjustment.

To determine whether a population is performing diel vertical migrations, the weighted mean depth (WMD) of each species must be calculated during both the day and the night as follows:

$$\text{WMD} = \sum (n_i * z_i * d_i) / \sum (n_i * z_i), \quad (4)$$

where, d_i is the depth of a sample i (the depth at the centre of the depth interval, in m), z_i the thickness of the interval (in m), and n_i is the abundance of individuals at that depth (ind. 1000 m⁻³) (Andersen *et al.*, 2001).

Welch's two-sample *t*-test was performed to determine statistically significant differences between day and night WMDs of individual species (Sawiowsky, 2002). In general, *t*-tests are highly robust in terms of both Type I and II errors to departures from the assumption of normality. Therefore, non-normal distributions for some species should not have been a significant issue (Sawiowsky, 2002). Species with significantly different day and night WMDs were classified as vertical migrators. Some species did not show significant migration toward the surface at night, while others performed partial migration. Partially migrating species were identified based on a bimodal distribution at night, with one peak at the daytime depth (non-migrating portion of population) and another peak (migrating portion) closer to the surface. For such species, the upward migrating portion was expressed as the percentage of the total nighttime population and its WMD calculated. Estimates of active flux (see below) were calculated based only upon the migratory portion of the population.

Active flux of carbon by migrating micronekton is composed of four major components: respiratory (RC), excretory (EC), mortality (M_{flux}), and gut (G_{flux}) flux. Each of these fluxes was calculated using individual rate processes that were scaled

up to the migrating densities, accounting for the amount of time migrating decapods resided in the mesopelagic depths (see below).

- (1) Respiratory flux was calculated using an empirical allometric relationship derived by [Ikeda \(1985\)](#), which predicts the respiration rate of a zooplankton/micronekton based on ambient temperature and the organism's biomass.

$$\ln RO = -0.2512 + 0.7886 * \ln DW_{mg} + 0.0490 * T, \quad (5)$$

where RO is the respiratory oxygen uptake ($\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$), DW_{mg} is the dry weight of the organism (mg), and T is the environmental temperature ($^{\circ}\text{C}$). This hourly respiration rate was then converted to a daily respiration rate by the number of hours of daylight, which at Station ALOHA over the study period was 12.6 h. Once rates of oxygen uptake were determined, it was necessary to convert these rates into respiratory equivalents following [Al-Mutairi and Landry \(2001\)](#) and scale up to total decapod density:

$$RC = RO * RQ * 12/22.4 * TD * N, \quad (6)$$

where RC is the respiratory carbon flux ($\mu\text{g C m}^{-2} \text{ day}^{-1}$), RQ is the respiratory quotient (assumed 0.97 after [Gnaiger, 1983](#)), which is the molar ratio of carbon produced to oxygen utilized, 12 is the molecular weight of carbon, and 22.4 is the molar volume of an ideal gas at standard pressure and temperature, TD is the number of hours per day the organism spends at depth (12.6 h) and N is the decapod migrating density (ind. m^{-2}).

- (2) Active excretory flux was calculated based on the findings of [Steinberg et al. \(2000\)](#). The authors measured CO₂ respiration and DOC excretion of a wide variety of diel migratory crustacean species at the US JGOFS Bermuda Atlantic Time-series Study. Respiration and excretion rates were found to vary similarly, with both rates depending on environmental temperature and the dry weight of the organism ([Steinberg et al., 2000](#)). In the case of diel migratory decapods, DOC excretion averaged 32% of CO₂ respiration in terms of $\mu\text{g C}$ respired or excreted per mg dry weight ([Steinberg et al., 2000](#)). Thus, for this study, excretory DOC (excretory flux, EC) was assumed equal to 32% of respiratory CO₂.
- (3) Decapod mortality was calculated by estimating the hourly weight-specific mortality rate using the organism's dry weight, based on the model of [Peterson and Wroblewski \(1984\)](#).

$$HM = 2.196 * 10^{-4} * DW_g^{-0.25}, \quad (7)$$

where HM is the hourly weight-specific mortality rate (h^{-1}), and DW_g is the dry weight of the animal (g). This was converted into a mortality flux using the following equation from [Zhang and Dam \(1997\)](#):

$$M_{\text{flux}} = HM * DW_{\mu\text{g}} * CR * TD, \quad (8)$$

where, M_{flux} is the daily mortality flux, DW_{μg} is the dry weight of the animal (μg), CR is the carbon weight to dry weight ratio, and TD is the number of hours (12.6 h) per day the organism spends at depth. Carbon to dry weight ratio for

pelagic decapods captured at Kahe Station was measured to be 0.42 (CR) during the 2004 *Oscar Elton Sette* cruise ([Podeswa and Pakhomov, 2015](#)).

- (4) Gut flux (G_{flux}) was estimated primarily using Equation (9), empirically derived using decapods captured during the 2004 *Oscar Elton Sette* cruise, predicting stomach content dry weight based on organism dry weight and stomach fullness ([Podeswa and Pakhomov, 2015](#)).

$$FB_{DW} = 0.020 * Org_{DW} * Fullness, \quad (9)$$

where FB_{DW} is the food ball dry weight (mg), Org_{DW} is the organism's dry weight (mg), and Fullness is the visually estimated stomach fullness. The food ball dry weight for all migratory individuals (G_{flux}) was determined using Equation (9) and species-specific values for peak nighttime stomach fullness. For a few species where no stomach content data was obtained, the mean peak nighttime stomach fullness of 0.52 averaged across all species was used. To convert food ball dry weights to food ball carbon, a mean ratio of 0.46 (obtained for fish, squid, euphausiids and copepods) was employed ([Podeswa and Pakhomov, 2015](#)). It was assumed that the highest nighttime stomach content of a migrant shrimp was carried from the euphotic to the mesopelagic zone, digested and remains egested at depth ([Clarke, 1980](#)). An assimilation efficiency of 88% was adopted and thus max average food ball weight (in mg C) was multiplied by 0.12 to estimate the carbon weight of the egested material ([Hopkins and Baird, 1977](#)).

Once active fluxes of all species were summed, a weighted average taken to determine the mean depth of carbon transport. Weighting was based on the size of the active flux. For example, if "Species A" migrated to a daytime WMD of 800 m, with a total active flux of 90 $\mu\text{gC m}^{-2} \text{ day}^{-1}$, while "Species B" migrated to a daytime WMD of 700 m, with a total active flux of 10 $\mu\text{gC m}^{-2} \text{ day}^{-1}$, there would be a total of 100 $\mu\text{gC m}^{-2} \text{ day}^{-1}$ transported to a WMD of 790 m. Once active flux was determined, it was related to the previously estimated passive flux at the same depth. A 5-year time-series study performed at Station ALOHA found that, below the base of the euphotic zone, long-term passive carbon flux could be accurately modelled based on depth using the following equation ([Karl et al., 1996](#)):

$$PC - FLUX(Z) = 28.7 * (Z/150)^{-0.818}, \quad (10)$$

where PC-FLUX(Z) is the particulate carbon flux to a depth of Z meters, in $\text{mgC m}^{-2} \text{ day}^{-1}$. The same study also found the base of the euphotic zone to be located at 173 ± 7 m.

Results

Temperature and salinity

Temperatures at Station ALOHA remained steady at $\sim 25.5^{\circ}\text{C}$ in the mixed layer (~ 0 –60 m), before rapidly declining in the thermocline to $\sim 6.3^{\circ}\text{C}$ at the base of the thermocline (~ 530 m) ([Figure 2b](#)). Temperatures continued to decline below the thermocline reaching $\sim 2.9^{\circ}\text{C}$ at 1500 m ([Figure 2b](#)). Salinity remained constant at ~ 35.1 in the mixed layer, rising to ~ 35.3 at

~100 m, before falling rapidly to ~34.0 at the base of the halocline (~500 m) (Figure 2b).

Temperature and salinity profiles at Station Kahe were very similar to those found at Station ALOHA. The main differences were lower salinity in the mixed layer at Station Kahe (34.5 at Kahe vs. 35.1 at ALOHA), and a shallower base of the thermocline (490 m at Kahe vs. 530 m at ALOHA) (Figure 2b).

Pelagic decapod diversity

The diversity of pelagic decapods was high at both sites with 40 taxonomic groups identified to species or genus level (Table 2). In total, 21 genera and 5 families were represented: Oplophoridae, Pasiphaeidae, Penaeidae, Sergestidae, and Sicyoniidae. All species ≥ 20 mm for which fewer than 10 individuals were caught were excluded from the analysis of fluxes. In total, 22 species/groups were included in the analysis.

Abundance, biomass, and diel vertical migrations

A highly significant linear relationship between dry weight (DW) and wet weight (WW) using all migrating decapod species collected at Kahe Station was observed ($DW = 0.179 * WW; p < 0.0001 [t = 140.9, df = 479], R^2 = 0.976$). Equation (1) implied a dry mass loss of 26.4% when water content is 82.1%. Thus before preservation in formalin, the decapods would have had a dry weight 35.9% higher than measured after preservation, as $1/(1 - 0.264) = 1.359$. After all dry weights were corrected for dry mass loss, length weight relationships for 22 pelagic decapod species were calculated (Table 1).

Total decapod abundance and biomass were 4.3 ind. m^{-2} and 0.71 gDW m^{-2} and rare species in total accounted for ~5% of both abundance and biomass (Table 2). Using Welch's two-sample *t*-test, it was determined that there was no evidence of significant diel vertical migrations for three of the species, indicated that they resided in mesopelagic zone through the day (Table 3). For six species the entire population migrated upwards at night, and the remaining 13 species migrated partially with 50–92% of the population migrating upwards during the nighttime (Table 3). Among the 22 species that were included in the analysis, migrating biomass (migrators as well as the portion of partial migrators) was 0.24 gDW m^{-2} , accounting for ~37% of their total biomass (Table 2).

Acanthephyra curtirostris, *Notostomus gibbosus*, and *Systellaspis debilis* belonged to the non-migratory group (Figure 3). All non-migratory species were relatively large (*A. curtirostris* being the smallest with an average mass of $220.4 \text{ mgDW ind.}^{-1}$), and all belonged to the family Oplophoridae (Table 2). *A. curtirostris* and *N. gibbosus* resided at similar depths, with WMDs ranging from 904 to 974 m during both the day and nighttime, while *S. debilis* resided at shallower depths, with daytime and nighttime WMD being 685 m and 681 m, respectively (Figure 3, Table 3). Of the non-migratory decapods, *A. curtirostris* was the most abundant with a mean abundance of $0.256 \text{ ind. m}^{-2}$ throughout the water column, while *N. gibbosus* made up the most biomass, mean biomass of $275.9 \text{ mgDW m}^{-2}$ (Table 2).

Acanthephyra smithi, *Allosergestes sargassi*, *Gennadas bouvieri*, *Gennadas incertus*, *Neosergestes orientalis*, and *Parasergestes armatus* belonged to fully migratory decapod group (Table 3). For all six species, the entire population migrated toward the surface at night. Unlike the non-migratory species, which all belonged to

Table 2. Pelagic decapod species composition and density during the 2011 R/V Kilo Moana voyage.

Species	No	Mean DW mg ind. $^{-1}$	Abundance ind. m $^{-2}$	Biomass mgDW m $^{-2}$
<i>Acanthephyra curtirostris</i>	41	209.16	0.256	56.438
<i>Acanthephyra smithi</i>	17	626.34	0.0934	59.287
<i>Allosergestes pectinatus</i>	38	12.10	0.152	1.771
<i>Allosergestes sargassi</i>	10	31.32	0.049	1.571
<i>Deosergestes erectus</i>	26	154.26	0.146	25.253
<i>Gennadas bouvieri</i>	95	84.96	0.481	41.773
<i>Gennadas capensis</i>	48	94.27	0.331	35.780
<i>Gennadas clavigarpus</i>	33	67.76	0.121	8.265
<i>Gennadas incertus</i>	13	50.70	0.071	3.694
<i>Gennadas spp.</i>	80	58.98	0.372	22.496
<i>Gennadas tinayrei</i>	10	51.45	0.048	2.753
<i>Janicella spinicauda</i>	18	40.15	0.105	4.378
<i>Neosergestes consobrinus</i>	26	10.56	0.132	1.426
<i>Neosergestes orientalis</i>	29	29.76	0.146	4.202
<i>Notostomus gibbosus</i>	23	1746.01	0.166	275.861
<i>Parasergestes armatus</i>	44	67.76	0.278	19.117
<i>Sergestes atlanticus</i>	19	25.55	0.073	1.719
<i>Sergia bigemmeus</i>	17	77.72	0.118	10.544
<i>Sergia gardineri</i>	117	35.62	0.560	20.376
<i>Sergia scintillans</i>	24	45.60	0.092	4.120
<i>Stylopandalus richardi</i>	28	65.76	0.167	12.171
<i>Systellaspis debilis</i>	28	362.29	0.151	54.920
Total			4.108	667.915
Total non-migrating biomass				423.421
Total migrating biomass				244.494
<i>Acanthephyra prionota</i>	4	212.83	0.012	2.553
<i>Acanthephyra sp.</i>	7	53.22	0.015	0.798
<i>Bentheogenenema sp.</i>	4	164.97	0.012	1.979
<i>Funchalia taanangi</i>	3	401.31	0.010	4.013
<i>Glypus sp.</i>	2	35.35	0.005	0.176
<i>Heterocarpus ensifer parvispina</i>	1	113.15	0.004	0.452
<i>Meningodora marptocheles</i>	1	283.94	0.004	1.135
<i>Oplophoridae sp. larvae</i>	3	15.48	0.010	0.154
<i>Oplophorus gracilirostris</i>	4	824.93	0.012	9.899
<i>Parapasiphae sulcatifrons</i>	1	476.44	0.004	1.905
<i>Parasergestes vigilax</i>	4	16.40	0.012	0.196
<i>Penaeidae sp.</i>	7	40.22	0.015	0.603
<i>Petalidium sp.</i>	3	31.08	0.010	0.311
<i>Sergia bisulcatus</i>	3	534.03	0.010	5.340
<i>Sergia inequalis</i>	4	272.13	0.012	3.265
<i>Sergia spp. (<20 mm)</i>	12	56.50	0.050	2.825
<i>Sergia tenuiremis</i>	4	475.53	0.012	5.706
<i>Sicyonia sp.</i>	1	148.50	0.004	0.594
Total (excluded)			0.213	41.911

Abundance and biomass values listed for each species are the mean of daytime and nighttime estimates. Species in bold accounted for < 6% of total abundance and biomass and were not included in the active carbon transport calculations.

Table 3. Summary of diel migratory data for all pelagic decapod species in this study.

Species	DWMD (m)	NWMD (m)	t	df	p	M (%)	NWMDm (m)
Species for which tde entire population migrates							
<i>Acanthephyra smithi</i>	678	370	3.53	15.45	0.003	100	n/a
<i>Allosergestes sargassi</i>	475	235	5.02	7.89	0.001	100	n/a
<i>Gennadas bouvieri</i>	803	459	11.00	81.33	<0.001	100	n/a
<i>Gennadas incertus</i>	898	248	12.61	8.55	<0.001	100	n/a
<i>Neosergestes orientalis</i>	508	113	18.26	7.89	<0.001	100	n/a
<i>Parasergestes armatus</i>	562	281	3.86	17.31	0.001	100	n/a
Species for which part of the population migrates							
<i>Allosergestes pectinatus</i>	543	314	3.17	15.23	0.006	69.4	110
<i>Deosergestes erectus</i>	671	255	4.86	14.57	<0.001	92.2	167
<i>Gennadas capensis</i>	1103	541	6.69	39.68	<0.001	71.0	324
<i>Gennadas clavicarpus</i>	700	234	9.18	27.7	<0.001	78.7	114
<i>Gennadas</i> spp.	726	420	5.73	50.82	<0.001	49.6	107
<i>Gennadas tinayrei</i>	759	249	13.92	6.88	<0.001	80.4	121
<i>Janicella spinicauda</i>	483	186	24.88	9.00	<0.001	87.8	104
<i>Neosergestes consobrinus</i>	564	394	2.18	23.71	0.040	55.4	108
<i>Sergestes atlanticus</i>	592	194	3.95	3.99	0.017	88.2	116
<i>Sergia bigemmeus</i>	900	224	7.90	6.22	<0.001	89.7	149
<i>Sergia gardineri</i>	748	275	10.19	100.74	<0.001	76.4	113
<i>Sergia scintillans</i>	660	261	6.55	19.00	<0.001	76.7	105
<i>Stylopandalus richardi</i>	572	195	5.84	14.96	<0.001	88.1	116
Non-migratory species							
<i>Acanthephyra curtirostris</i>	974	923	0.50	13.13	0.627	0	n/a
<i>Notostomus gibbosus</i>	904	955	0.52	18.61	0.606	0	n/a
<i>Systellaspis debilis</i>	685	681	0.06	6.25	0.953	0	n/a

DWMD and NWMD: daytime and nighttime weighted mean depth for the entire population; M (%): proportion of the population migrating. For the partially migratory species, the nighttime WMD for only the portion that migrates is also provided (NWMDm). Results of Welch's two-sample t-tests are provided for each species (t, df, p), with the test comparing daytime WMDs to night time WMDs for the whole populations.

the family Ophophoridae, the fully migratory species were taxonomically diverse, with one species from the family Ophophoridae (*A. smithi*), two species from the family Benthesicymidae (*G. bouvieri* and *G. incertus*), and three species from the family Sergestidae (*A. sargassi*, *N. orientalis*, and *P. armatus*). Other than *A. smithi*, all were of a small to moderate size, ranging from 29 mgDW ind⁻¹ for *N. orientalis*, to 87 mgDW ind⁻¹ for *G. bouvieri* (Table 2).

Among this group, *G. bouvieri* and *G. incertus* resided at the deepest depths during the day, at 803 m and 898 m WMD, respectively (Figure 4, Supplementary Figure S2). *A. smithi* resided at a shallower daytime depth of 678 m (Supplementary Figure S2), while *A. sargassi*, *N. orientalis*, and *P. armatus* resided at the shallowest daytime depths, at 475 m, 508 m and 562 m, respectively (Figure 4, Supplementary Figure S2). Of all six fully migratory species, only *N. orientalis* migrated into the euphotic zone (shallower than 173 m) during the night, with a nighttime WMD of ~113 m (Figure 4). *G. incertus*, *A. sargassi*, and *P. armatus* migrated to just below the base of the euphotic zone, with daytime WMDs of 235 m, 248 m, and 281 m, respectively (Figure 4, Supplementary Figure S2). Of the fully migratory species, *G. bouvieri* was the most abundant (0.481 ind. m⁻²), while *A. smithi* had the highest biomass, 59.3 µgDW m⁻², as well as the highest biomass per individual, 634.5 µgDW ind⁻¹ (Table 2).

Allosergestes pectinatus, *Deosergestes erectus*, *Gennadas capensis*, *Gennadas clavicarpus*, *Gennadas* spp., *Gennadas tinayrei*, *Janicella spinicauda*, *Neosergestes consobrinus*, *Sergestes atlanticus*, *Sergia bigemmeus*, *Sergia gardineri*, *Sergia scintillans*, and *Stylopandalus richardi* were all found to be migratory species (Table 3). All were partial migrants showing bimodal nighttime distributions

(Figure 5, Supplementary Figures S3–S5). Of these, only *G. capensis* migrated to a nighttime depth below the base of the euphotic zone (WMD 324 m) (Figure 5). The remaining 12 species migrated to a WMD within the epipelagic (<173 m) zone (Figure 5, Supplementary Figures S3–S5).

The other three members of the genus *Gennadas*, *G. clavicarpus*, *G. tinayrei*, and *Gennadas* spp. (damaged individuals) showed similar migratory patterns, migrating from daytime depths of 700–759 m to nighttime depths of 107–121 (Supplementary Figure S3). Decapods of the now defunct genus *Sergestes* displayed similar migratory distributions. The genus *Sergestes* has been recently re-classified into six separate but closely linked genera: *Allosergestes*, *Deosergestes*, *Eusergestes*, *Neosergestes*, and *Parasergestes* (Juddins and Kensley, 2008), which appears to be reflected in their migratory distributions. *A. pectinatus*, *N. consobrinus*, and *S. atlanticus* were particularly similar in their vertical distributions: all migrated to 108–116 m WMD during the night and to depths of 543–592 m WMD during the day (Figure 5, Supplementary Figure S4). In contrast, *D. erectus* was found at deeper depths during both the day and night (671 m and 167 m, respectively) (Figure 5). It should be noted that *D. erectus* is a relatively large species (Table 2). Three members of the genus *Sergia* displayed differing migratory distributions. While all three were partial migrants, ascending to similar depths within the euphotic zone at night, *S. bigemmeus* resided at 900 m during the day, while *S. gardineri* and *S. scintillans* resided at 748 m and 660 m WMD, respectively (Supplementary Figure S5). *J. spinicauda*, of the family Ophophoridae, and *S. richardi*, of the family Pandalidae, also displayed similar migratory distributions with daytime and nighttime WMDs of 483–572 m and 104–

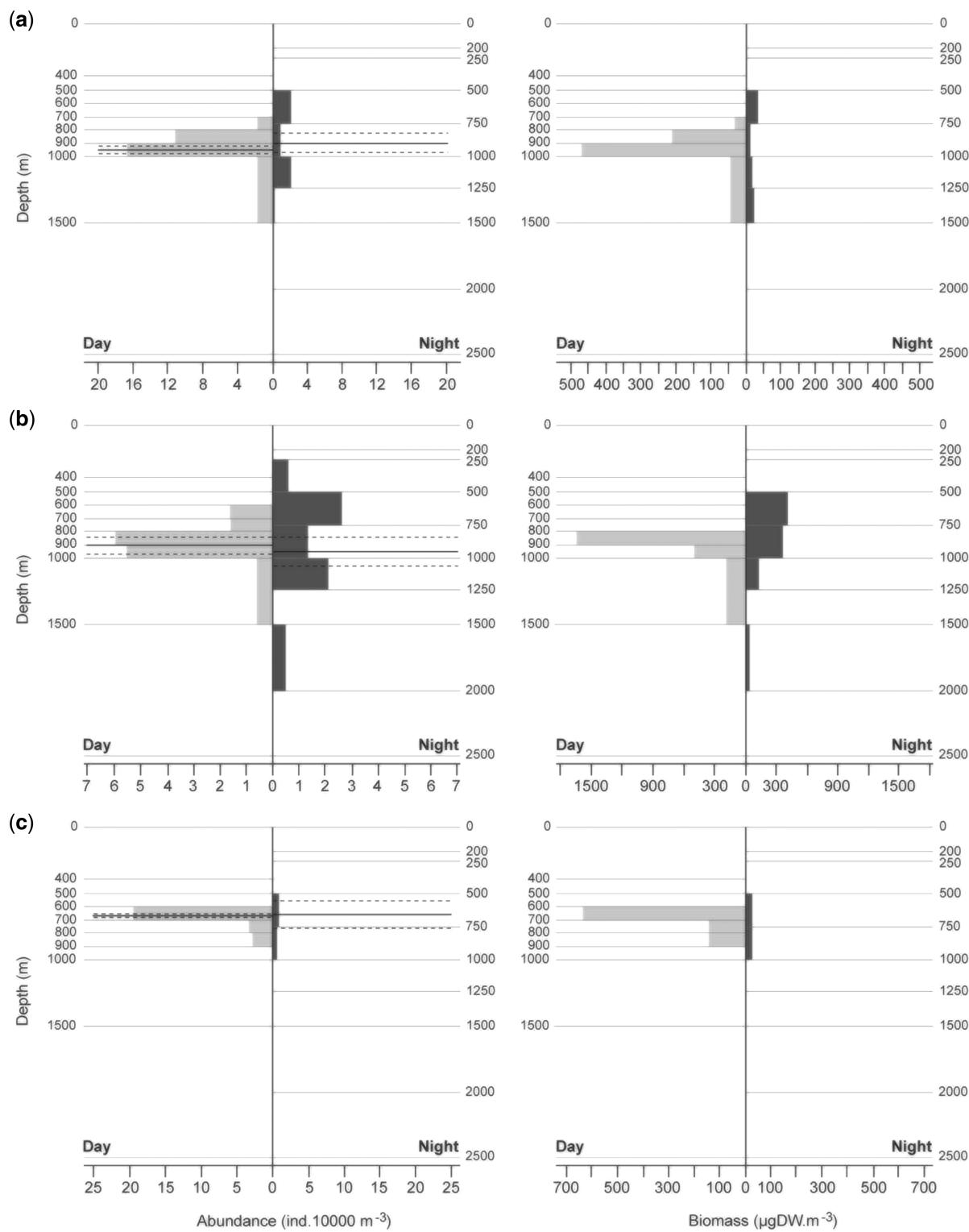


Figure 3. Abundance and biomass depth profiles of non-migrating decapods *Acanthephyra curtirostris* (a), *Notostomus gibbosus* (b), and *Systellaspis debilis* (c). For the abundance profile, daytime and nighttime WMDs are shown as solid lines, with dotted lines indicating standard errors.

116 m, respectively (Supplementary Figures S4 and S5). Both species were of similar size (Table 2). *S. gardineri* was the most abundant in this group but *A. pectinatus* made up highest biomass (Table 2).

There was a positive significant ($R^2 = 0.473$, $p = 0.00228$, $F = 13.46$, $df = 1$ and 15) correlation between decapod mean dry weight and the WMD to which they migrate to during the daytime, for < 100 mg individuals. However, when species with a

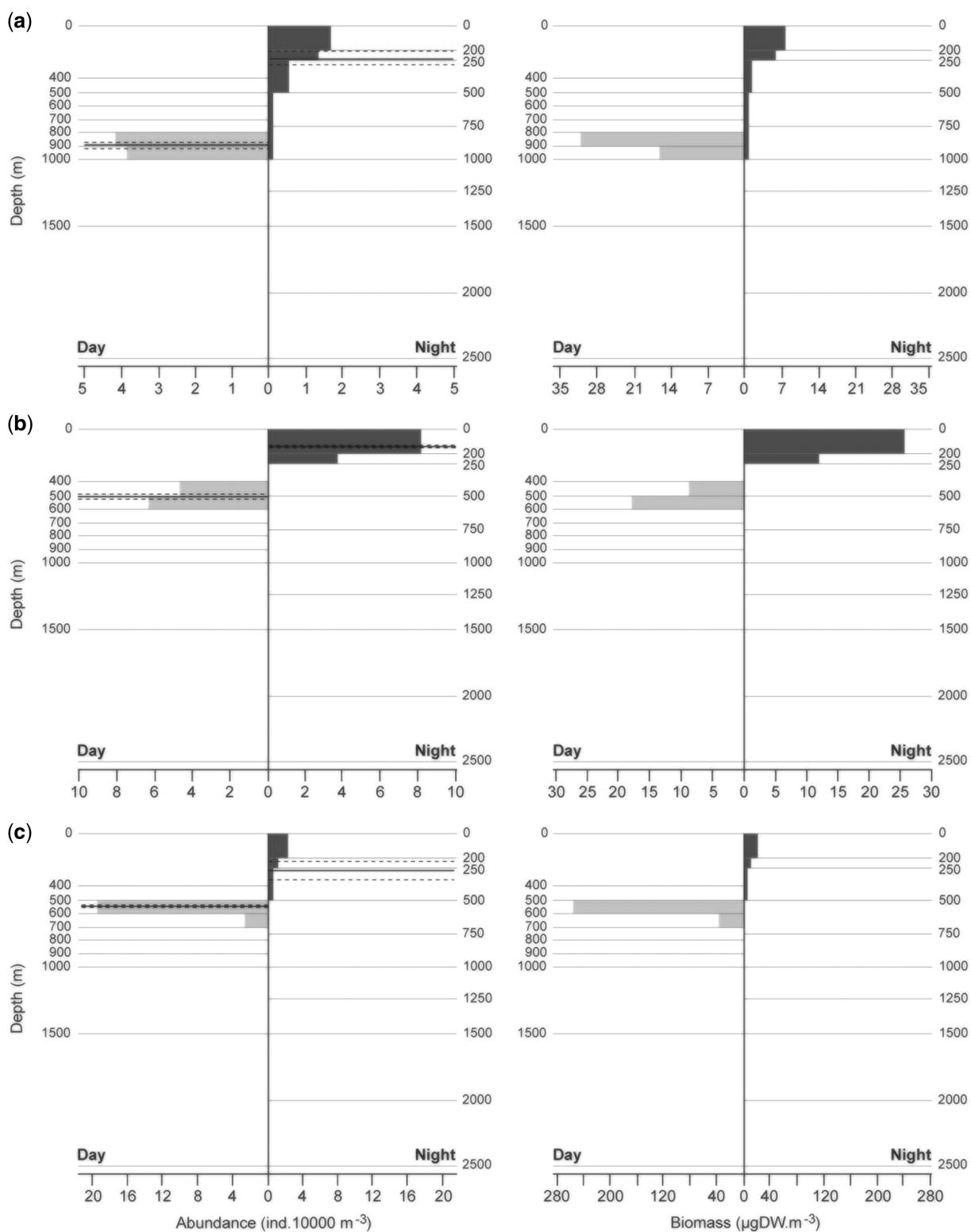


Figure 4. Abundance and biomass depth profiles of fully migrating decapods *Gennadas incertus* (a), *Neosergestes orientalis* (b), and *Parasergestes armatus* (c). For the abundance profile, daytime and nighttime WMDs are shown as solid lines, with dotted lines indicating standard errors.

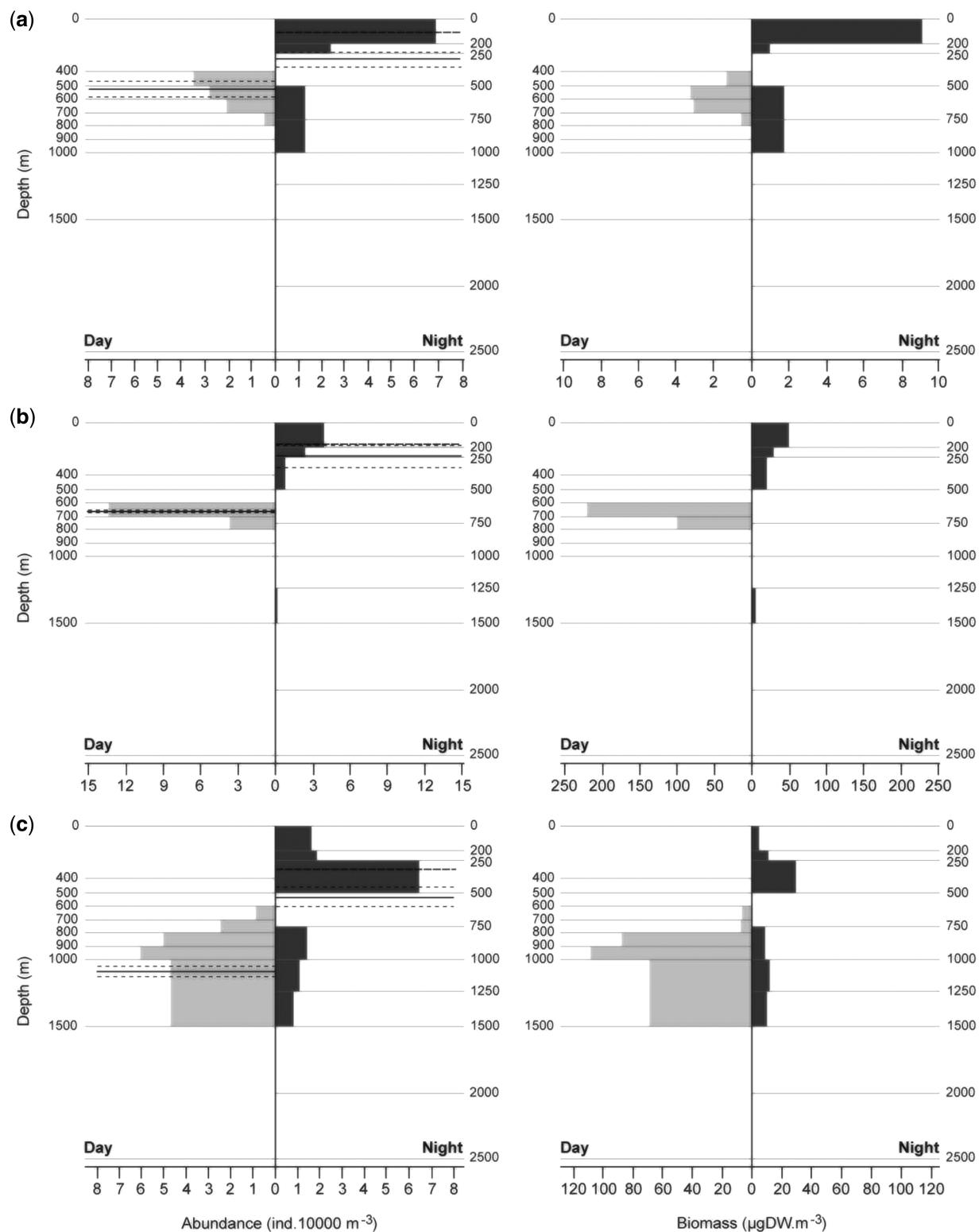


Figure 5. Abundance and biomass depth profiles of partially migrating decapods *Allosergestes pectinatus* (a), *Deosergestes erectus* (b), and *Gennadas capensis* (c). For the abundance profile, daytime, and nighttime WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the nighttime WMD for only the portion of the population that migrates to the surface.

Table 4. Active downward carbon flux components for all diel migratory decapod species, from a mean nighttime depth of 262 m to a mean daytime depth of 711 m.

Species	Respiratory flux ($\mu\text{gC.m}^{-2}.\text{day}^{-1}$)	Excretory flux ($\mu\text{gC.m}^{-2}.\text{d}^{-1}$)	Mortality flux ($\mu\text{gC.m}^{-2}.\text{d}^{-1}$)	Gut flux ($\mu\text{gC.m}^{-2}.\text{d}^{-1}$)
<i>Acanthephyra smithi</i>	3.11	1.01	76.44	30.91
<i>Allosergestes pectinatus</i>	1.38	0.45	4.30	0.64
<i>Allosergestes sargassi</i>	0.92	0.30	4.28	0.82
<i>Deosergestes erectus</i>	3.58	1.16	41.55	12.14
<i>Gennadas bouvieri</i>	11.0	3.57	88.57	21.78
<i>Gennadas capensis</i>	5.57	1.81	51.01	13.25
<i>Gennadas clavicularis</i>	2.08	0.67	14.65	3.39
<i>Gennadas incertus</i>	1.42	0.46	8.80	1.93
<i>Gennadas spp.</i>	3.90	1.27	25.92	5.83
<i>Gennadas tinayrei</i>	0.80	0.26	5.21	1.15
<i>Janicella spinicauda</i>	1.84	0.60	9.80	1.53
<i>Neosergestes consobrinus</i>	0.92	0.30	2.82	0.41
<i>Neosergestes orientalis</i>	2.61	0.85	11.75	1.89
<i>Parasergestes armatus</i>	6.13	1.99	42.93	9.97
<i>Sergestes atlanticus</i>	1.06	0.34	4.45	0.79
<i>Sergia bigemmeus</i>	2.43	0.79	19.92	4.93
<i>Sergia gardineri</i>	7.89	2.6	41.03	5.84
<i>Sergia scintillans</i>	1.38	0.45	7.90	1.97
<i>Stylopandalus richardi</i>	3.30	1.07	23.75	6.40
Total flux for all species	61.31	19.90	485.16	125.56

Total active carbon flux was $0.692 \text{ mgC m}^{-2} \text{ day}^{-1}$.

mean dry weight $> 100 \text{ mg ind.}^{-1}$ were included (*D. erectus* and *A. smithi*), the correlation was no longer significant ($R^2 = 0.0121$, $p = 0.654$, $F = 0.209$, $\text{df} = 1$ and 17).

Active carbon flux

In total, decapods transported $0.692 \text{ mgC m}^{-2} \text{ day}^{-1}$ through active carbon flux, from a mean depth of 262 m at night to a mean depth of 711 m during the day (Table 4). Mortality flux accounted on average for $\sim 70\%$ of total active flux. This was followed by the gut flux ($\sim 18\%$) and respiration flux ($\sim 9\%$) (Table 4). The excretion flux did not exceed 3% of total active flux. *G. bouvieri* and *A. smithi* were the greatest contributors to all four classes of active flux, followed by *D. erectus*, *G. capensis*, *Gennadas spp.*, *P. armatus*, *S. gardineri*, and *S. richardi* (Table 4).

Using Equation (10), the passive particulate carbon flux at the mean daytime depth (711 m), mean nighttime depth (262 m), and at the base of the euphotic zone (173 m, Karl and Lukas, 1996), was calculated to be 8.05 , 18.2 , and $25.54 \text{ mgC m}^{-2} \text{ day}^{-1}$, respectively. Therefore, total decapod-mediated active carbon flux were equal to 8.6% of the passive flux to the mean daytime depth (711 m), 3.8% of the passive flux to the mean nighttime depth (262 m), and 2.7% of passive flux at the base of the euphotic zone.

Discussion

Density and vertical migrations

Decapod community density estimated by this study (4.3 ind. m^{-2} in the upper 1000 m) in the NPSG near Hawaii was close to the middle range of similar estimates 0.9 – 10 ind. m^{-2} in various parts of the world ocean (see below). It was 2–4-fold higher than previous estimates (0.1 – 1.8 ind. m^{-2}) near Hawaii and in the Gulf of Mexico (Maynard et al., 1975; Walters, 1976; Flock and Hopkins, 1992), comparable to abundances (3.3 – 3.9 ind. m^{-2}) recorded for the Arabian Sea and near Azores (Domanski, 1986; Mincks et al., 2000; Ariza et al., 2015), and about twofold lower

than densities ($\sim 10 \text{ ind. m}^{-2}$) found in the Benguela upwelling system (Schukat et al., 2013). As in previous studies, the majority of decapod species undertook extensive vertical migrations and generally showed very similar migration patterns to those reported near Hawaii and elsewhere. An exception was *Systellaspis debilis*, which was classified as a non-migrating species in our study but a strong vertical migrator in other studies (e.g. Maynard et al., 1975; Hopkins et al., 1989, 1994; Schukat et al., 2013). This suggests that, possibly due to low sampling effort, we may have underestimated the migrating portion of the decapod community. Nevertheless, the proportion of migrating biomass based on individual species (50–92% of the total population in partially migrating species) compared reasonably well with overall micronekton migrating biomass (range 20–90% of total) estimated using acoustics in major basins of the world ocean (Klevjer et al., 2016).

Comparison to previous active flux estimates

It is difficult to reconcile decapod active flux with published values that are generally estimates for total zooplankton. Three available respiratory flux assessments for this group were 2 to >40 -fold higher, e.g. ~ 0.1 (this study) vs. <0.5 – $4.4 \text{ mgC m}^{-2} \text{ day}^{-1}$ (Hidaka et al., 2001; Schukat et al., 2013; Ariza et al., 2015), than estimates in our study. These discrepancies are much higher than differences in the decapod total density in various parts of the world ocean (see above) and can only be explained by the inconsistencies in the respiratory flux estimates adopted in different studies. The study that attempted measuring excretion, mortality, and gut flux yielded active carbon transport of 1 – $6 \text{ mgC m}^{-2} \text{ day}^{-1}$ (Angel and Pugh, 2000), which was 1.5–9.5-fold higher than our estimate and that could be explained by the differences in the decapod standing stock in the regions investigated. Our decapod respiratory flux estimates [$0.06 \text{ mgC m}^{-2} \text{ day}^{-1}$ or 0.2 , 0.3 , and 0.7% of total passive flux at 173, 262, and 700 m depths, respectively (Supplementary Table S1)] are on the low

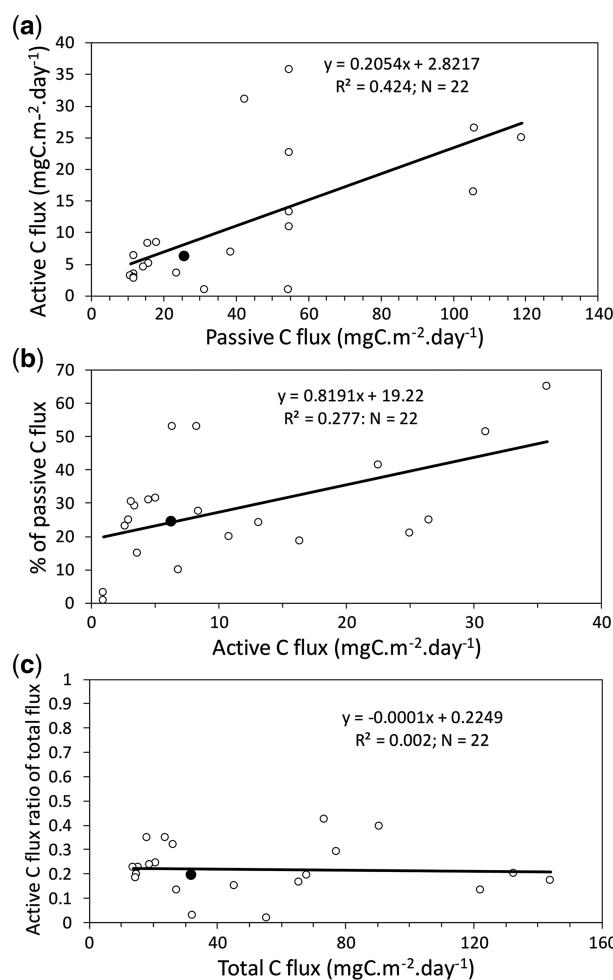


Figure 6. Importance of active carbon flux by zooplankton and micronekton at the base of mixed layer from published sources: (a) active vs. passive carbon flux; (b) active carbon flux vs. percentage active flux of passive flux; and (c) active carbon flux contribution to total flux (combined passive and active flux). Data are combined from Table 3 in Ariza *et al.* (2015) and Supplementary Table S1 (this study). Solid circle belongs to the mean estimate obtained in this study.

end of similar assessments in the North Pacific and near the Azores (0.5–1.2%, Hidaka *et al.*, 2001; Ariza *et al.*, 2015). However, they are significantly lower than similar estimates (26–36%) in the Benguela upwelling system (Schukat *et al.*, 2013).

Previous studies reported that decapod biomass makes up 3.2–32.1% of the total migratory biomass (corrected for a sampling efficiency of 14%; Hidaka *et al.*, 2001; Pakhomov and Yamamura, 2010; Ariza *et al.*, 2015). Within our study region, Pakhomov and Yamamura (2010) collected micronekton using three different sampling gears with variable mouth and mesh sizes as part of the Micronekton Intercalibration Experiment (MIE-1). On average, they found that decapod biomass made up $\sim 12 \pm 9\%$ of the total migratory biomass. The Isaacs-Kidd Midwater Trawl (IKMT) used in MIE-1 had the same mesh size as the MOCNESS-10 used in this study. IKMT migratory biomass during MIE-1 was dominated by cephalopods (32%), myctophids (14%), euphausiids (10%), stomatopods (9%), and decapods (8%) (Kwong *et al.*, 2018). Based on the above values, during our study we estimated

total active carbon flux to ~ 700 m mediated by micronekton to be within $5.1\text{--}7.4 \text{ mgC m}^{-2} \text{ day}^{-1}$. This would be comparable to 20–29%, 28–41%, and 63–92% of passive flux at 173, 262, and 711 m, respectively. While it is a coarse estimate (simple scaling-up from the decapod contribution to biomass assuming that other groups migrate/behave similarly), it provides a starting point for comparison with other assessments published in the literature (Supplementary Table S1).

Published active and passive carbon flux estimates at the base of the euphotic zone, plotted ignoring the enormous diversity of assessment methods, geographical and taxonomic variability, show that there is a general positive linear relationship between both flux types, and between active transport and its proportion of passive transport (Figure 6a and b). Steinberg and Landry (2017) found a similar pattern (likely compiling data from similar sources) but also showed that active carbon transport is positively related to migratory biomass. Finally, within the literature the active flux proportion of total carbon flux (active and passive) appeared to be stable, averaging $\sim 22\%$, with most estimates falling in the range of 15–40% (Figure 6c). It is notable that the total active flux estimated in this study fell close to the average literature values (Supplementary Table S1, Ariza *et al.*, 2015) as well as to modelling approximations of respiratory fluxes assessed by Bianchi *et al.* (2013a). Nevertheless, it should be acknowledged that most active flux measurements were based on respiratory and excretion fluxes alone, and very few accounted for mortality or gut flux (Supplementary Table S1). Assuming a dominant contribution of both mortality and gut flux, our estimates would have fallen into the lower end (likely $< 10\%$) of other estimates (Figure 6c).

In the past, there have been large (orders of magnitude) discrepancies in studies reconciling carbon demands of the mesopelagic fauna and its availability via passive carbon flux pointing to high uncertainty in both estimates (e.g. Boyd *et al.*, 1999; Steinberg *et al.*, 2008; Burd *et al.*, 2010). These could be improved by removing from the mesopelagic fauna active vertical migrants (Giering *et al.*, 2014). Currently, it is believed that besides passive carbon flux, mesopelagic plankton demands could be met through suspended (0.7–52 μm) particles and active vertical carbon flux (e.g. Hannides *et al.*, 2009, 2013, 2015; Steinberg *et al.*, 2000, 2002; Choy *et al.*, 2015; Gloeckler *et al.*, 2018). Despite high uncertainty, active flux mediated by zooplankton is an important contributor to the total carbon flux (Steinberg and Landry, 2017). Yet, most estimates were made using migrating tropical and temperate mesozooplankton and generally assessed active transport out of the upper mixed (<200 m) layer of water (Supplementary Table S1, Steinberg and Landry, 2017). However, (a) mesozooplankton generally do not migrate below 300 m, (b) they have short gut passage time, and (c) their mortality was not taken into account. Because in the majority of tropical regions production and consumption cycles are tightly aligned, the contribution of mesozooplankton active transport to total flux is substantial (Valencia *et al.*, 2018). Studies estimating similar contribution of large zooplankton and micronekton migrating below 300–500 m are rare and highly uncertain (Hidaka *et al.*, 2001; Davison *et al.*, 2013; Schukat *et al.*, 2013).

Micronekton indeed migrate much deeper than mesozooplankton, where passive flux is insignificant (Karl *et al.*, 1996). The importance of active transport is therefore expected to be greater at mesopelagic depths (400–800 m) across most of the world ocean (Bianchi *et al.*, 2013b). Few previous studies that

attempted to assess active carbon flux to mesopelagic layers (*Supplementary Table S1*) have shown that it can account for >70% of passive flux in the deeper part of the low mesopelagic zone (Steinberg *et al.*, 2000; Davison *et al.*, 2013; Schukat *et al.*, 2013; Hudson *et al.*, 2014). Those estimates are in line with modelling assessments made by Bianchi *et al.* (2013a, b), which only assessed respiratory active flux. The results of our study show that active carbon transport is not only important for nutrient regeneration and oxygen consumption in the mesopelagic zone but also provides critical food supply (reflected in high mortality contribution to total active flux) to the resident mesopelagic community. Decapods are an important part of active carbon transport, as they appear to migrate deeper than the majority of other macroplankton and micronekton (e.g. myctophids) (Davison *et al.*, 2013; Bianchi *et al.*, 2013a). Hence, when calculating active flux to mesopelagic layer it is critical to sample throughout the depth range of the organisms' migrations, to calculate the depth to which carbon is transported.

It is worth noting that this study provides quantitative evidence for the Vinogradov's ladder of vertical migrations (Vinogradov, 1962). This theory proposed that vertical migrations could be an important source of energy and materials to the mesopelagic, bathypelagic, and abyssopelagic zone residents (Allison *et al.*, 1996). While migrations from the bathypelagic to the surface are very rare, some deep living organisms perform upward migrations to mesopelagic depths (Vinogradov, 1962). The quantification of fluxes due to this vertical transfer ladder has proven difficult due to challenging bathypelagic and abyssopelagic sampling, and low fauna abundance (Haedrich and Henderson, 1974; Yamamura *et al.*, 1993; Allison *et al.*, 1996). It appears however, that active carbon flux may be at least as important in the mesopelagic realm as sinking phytoplankton and other detritus originating from the upper water column (Allison *et al.*, 1996).

Samples for this study were collected in the central NPSG, mostly at station ALOHA and secondly at station Kahe, two oceanographic locations that have been regularly monitored by the Hawaii Ocean Time-Series (HOT) program since October 1988 (Karl and Lukas, 1996). One of the central goals of the HOT program is to understand local biological processes and particulate matter fluxes (Karl and Lukas, 1996). However, up until now the contribution of diel migratory micronekton flux to the total downward carbon flux in the area has not been assessed. The central NPSG is a study site with very low passive gravitational flux typical of the oligotrophic oceanic realm and indicative of a weak traditional biological pump (Francois *et al.*, 2002). It is thus not surprising that active flux in this region is particularly significant contributor to the overall local downward carbon flux. An interesting finding of this study points to a lower than expected variability of active flux proportion of total (active and passive) flux at the base of the euphotic zone over a wide range of plankton communities globally (Figure 6c). Such measurements should however be more methodologically consistent and extended to temperate as well as Polar Regions of the world ocean.

Potential sources of error

A wide variety of models and assumptions were used in this study, which could lead to potential sources of error and uncertainty. The largest potential uncertainty likely relates to the net catch efficiency. It is generally recognized that acoustic biomass

estimates may exceed net estimates by an order of magnitude and only fast towing large nets could provide biomass values a few folds lower than acoustics (Pakhomov and Yamamura, 2010). Catch efficiency assumptions thus remain a significant source of uncertainty in this and other studies.

While net catch efficiency represents a potentially significant source of error, the uncertainty due to the models used to estimate respiratory flux, excretory flux, mortality flux, and gut flux should also be discussed. Respiratory and excretion rates were estimated as a function of body mass and temperature, based on data from a wide variety of zooplankton and micronekton, and could explain >90% of their variation (Ikeda, 1985; Steinberg *et al.*, 2000). In the gut flux estimates, the main source of error would relate to the locally obtained relationship that predicted food ball dry weight from dry weight of the organism and stomach fullness. However, while highly variable, ~82% of the variance in the data was explained by the model. On the one hand, the gut flux estimate could be an underestimate, because only prey mass in the stomach was taken into account, ignoring material in the intestines. On the other hand, it could be an overestimate if deep water feeding occurred (Podeswa and Pakhomov, 2015). Lastly, mortality flux estimates were based on a size-dependent mortality rate model developed for particles in the size range of fish eggs (~0.1 mg DW) to adult fish (~1000 g DW) (Peterson and Wroblewski, 1984). There is a considerable error associated with predictions made by this model for the smallest and largest organisms. However, for the mass range of the individuals in this study (roughly 0.01–0.6 gDW ind.⁻¹) the model predictions tend to be closest to empirical values. Furthermore, sensitivity analysis conducted by Zhang and Dam (1997) showed that mortality flux is highly sensitive to the residence time of migrants below of the euphotic zone and may vary by a factor of two.

Lastly, low number of samples ($N=1$) in the top 500 m during daytime should also be considered as a shortcoming of the current study. However, general micronekton absence in the upper layers during daytime is well documented (e.g. Kwong *et al.*, 2018).

Concluding remarks

The estimated active flux due to the diel vertical migrations of decapods was low compared with most previous estimates for zooplankton and micronekton communities as a whole, but comparable to previous estimates of decapod specific active flux. The relatively high abundance of migratory decapods, combined with the low passive flux in the central NPSG, suggests that this estimate for active flux due to migrant decapods may be more important relative to local passive flux in this region than in other areas of the world's oceans. Despite differences in community structure between the study area and other locations, this study emphasizes the importance of local micronekton migrations to vertical carbon flux on a global scale. The deep daytime migrations as well as the relatively high prevalence of species that did not migrate all the way up to the euphotic zone, highlights the importance of sampling of the entire water column, not just migrations into and out of the euphotic zone, as has been the case in many previous studies. Overall, the active flux estimates produced by this study show that total micronekton, including migrant decapods, are a sizable contributor to downward carbon flux in the open ocean. Currently, active flux is still poorly

defined and requires new and standardized approaches (e.g. biomass spectra combined with acoustics and/or modelling; [Kwong and Pakhomov, 2017](#)) to narrow down uncertainties in empirical estimates and reliably quantify regional and global micronekton-mediated carbon contributions to the mesopelagic realm.

Supplementary data

[Supplementary material](#) is available at the ICESJMS online version of the manuscript.

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