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Vertical distribution and migration of euphausiid species in the Red Sea

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We addressed how the extreme environmental conditions of the Red Sea impact or alter patterns of vertical distribution and vertical migration of five euphausiid species that are known from other oceans. *Euphausia diomedeae* was abundant and performed diel vertical migration (DVM) from >200 m in daytime to <100 m at night, similar to its pattern in other ocean regions. *Euphausia sibogae* and *Euphausia sanzoi* also showed consistent patterns of DVM across their ranges in the Red Sea and elsewhere. Two species, *Stylocheiron affine* and *Stylocheiron abbreviatum*, did not exhibit DVM. DNA barcode sequences for mitochondrial cytochrome oxidase I (COI) were used to confirm species identifications for four species (no previous barcode data exist for *E. sanzoi*). COI sequence differences averaged 2.8% (SD 3.1%) within species and 16.6% (SD 0.7%) between species, similar to previous studies of euphausiids. Red Sea specimens of *S. affine* matched morphological descriptions of a western equatorial form and differed 14% from Atlantic and Pacific specimens, suggesting possible cryptic species-level variation within this taxon. Widely distributed species of zooplankton may exhibit broad tolerance ranges for key environmental variables, and have considerable potential to adapt to variable and changing conditions across their geographic range.

KEYWORDS: extreme environment; euphausiids; diel vertical migration; intraspecific variation; DNA barcodes

INTRODUCTION

The Red Sea represents an end point of environmental conditions in the world oceans, with high surface temperature and salinities most of the year, high water temperatures (~21.5°C) in mesopelagic and bathypelagic depths, very high salinities [>40 practical salinity unit (PSU)] in most parts of the water column, and hypoxic conditions in mid-depths (Sofianos and Johns, 2007). Thus, the Red Sea is a region with exceptional conditions that enables the study of the environmental controls on the distribution and abundance of both widely distributed zooplankton species and those endemic to the Red Sea.

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Some zooplankton species found in the Red Sea are known to occur in other regions of the world's oceans. The broad distributions of some Red Sea zooplankton are surprising in light of the exceptional environmental conditions and barriers to dispersal, including a sill depth of ~137 m in the Bab-el-Mandeb strait (Werner and Lange, 1975; Smeed, 2004; Lambeck *et al.*, 2011) that appears to limit exchange of mesopelagic and deeper living species between the Red Sea and the Indian Ocean (van Couwelaar, 1998).

Euphausiids (krill) are an abundant and ecologically important component of pelagic ecosystems. Interest here is in two genera, *Euphausia* and *Stylocheiron*. Species of the genus *Euphausia* exhibit diel vertical migration (DVM) and generally live at depths of 500–200 m during daytime and in the upper 100 m at night (Brinton, 1962; Mauchline and Fisher, 1969). In contrast, a number of the species of the genus *Stylocheiron* do not perform DVM, but instead have specific depth ranges in which they reside both day and night (Brinton, 1962). In the North Atlantic, *Stylocheiron carinatum* and *Stylocheiron suhmii* live in the upper 100 m, *Stylocheiron affine* has a center of distribution between 200 and 300 m, and *Stylocheiron elongatum* and *Stylocheiron maximum* are generally found below 300 m (Mauchline and Fisher, 1969; Wiebe and Flierl, 1983; Endo and Wiebe, 2007). Likely because the Red Sea represents an end point in the spectrum of environmental conditions that tropical/subtropical euphausiids experience and because of its isolation from the Indian Ocean, only a few euphausiid species (~10) have been reported here (Weigmann, 1984; Casanova, 1990; van Couwelaar, 1998; Mathew *et al.*, 2003). In many tropical/subtropical ocean regions, including the Indian Ocean, between 20 and 30 euphausiid species occur in the water column (Reid *et al.*, 1978; Brinton *et al.*, 2000; Sutton and Beckley, 2015). Species listed as frequently caught include *S. affine*, *Stylocheiron abbreviatum*, *Stylocheiron armatum* (*S. carinatum* sibling species) and *S. suhmii*. Several species of *Euphausia* are also known to occur in the Red Sea (*Euphausia sanzoi*, *Euphausia sibogae*, *Euphausia diomedeae*) and one species of *Pseudeuphausia*, *P. latifrons*. The extent to which the patterns of vertical distribution and migratory behavior of these species observed in most oceans differ in the Red Sea in response to the extreme hydrographic conditions can provide valuable insights into the impacts of climate change that may be expected throughout the world's oceans, as well as in the Red Sea, in the coming decades.

The primary objectives of this study were (i) to determine the vertical distribution and migration behavior of euphausiids in relation to hydrographic structure and environmental conditions of the Red Sea and (ii) to use DNA barcodes to confirm species identification and compare with conspecific populations in other ocean regions (Pacific, Atlantic and Arabian Sea). In addition, the vertical distribution, abundance, and environmental conditions of the two Red Sea *Stylocheiron* species were compared to the same species in the Northwest Atlantic Ocean where comparable information was available. We addressed the hypotheses that (i) the extreme environment of the Red Sea mesopelagic zone, with high temperatures and low oxygen concentration, will restrict the vertical daytime distribution of *Euphausia* species to shallower depths than in other ocean regions; (ii) species of *Stylocheiron*, which are known to reside in the mesopelagic zone both day and night would take up nocturnal upward migrations in the Red Sea or would occur at shallower depths than in other ocean regions where they occur. We furthermore hypothesized that (iii) species of Red Sea euphausiids have identical cytochrome oxidase subunit I (COI) barcode sequences to individuals of the same species in other geographic regions; i.e. there is no taxonomically significant genetic differentiation of Red Sea euphausiid populations. This study is specifically designed to yield insights into the effects of climate change on marine zooplankton, based on the unique opportunity provided by the exceptional environmental conditions of the Red Sea.

METHOD

In January 2014, sampling for zooplankton was conducted near the King Abdullah University of Science and Technology (KAUST) campus (Thuwal, Saudi Arabia). Three 1-day trips were made aboard the R/V *Thuwal* to a location referred to as the Economic City Deep (ECDEEP), which is a ~700-m-deep basin located in north of KAUST at 22.5°N, 39.03°E (Fig. 1).

Field sampling

A 1/4-m MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System; Wiebe *et al.*, 1985) with 200 μm mesh nets was used to sample the zooplankton. The MOCNESS was obliquely towed four times from the stern A-frame using 11.43 mm conducting cable to 600 m depth with a ship speed nominally of 2 kt (62 m min^{-1}; Table I). Two MOCNESS tows were taken during daytime, one each on 7 and 8 January 2014 and two night tows were taken on 12 January 2014. The first day tow (M-25-001) was equipped with five nets that sampled 0–600, 600–400, 400–200, 200–100 and 100–0 m. The second-day tow (M-25-002) and the two night tows (M-25-003, M-25-004) each had six nets that sampled 0–600, 600–400, 400–200, 200–100, 100–50 and 50–0 m. GPS positions were logged, except

for the first tow when positions from the bridge were obtained for the tow start and end and at each opening of a net. The MOCNESS system was equipped with the standard SeaBird temperature and conductivity probes. Volume of water filtered by each net was determined based on the net frame angle and flowmeter counts using equation 10 b in Wiebe *et al.* (1985).

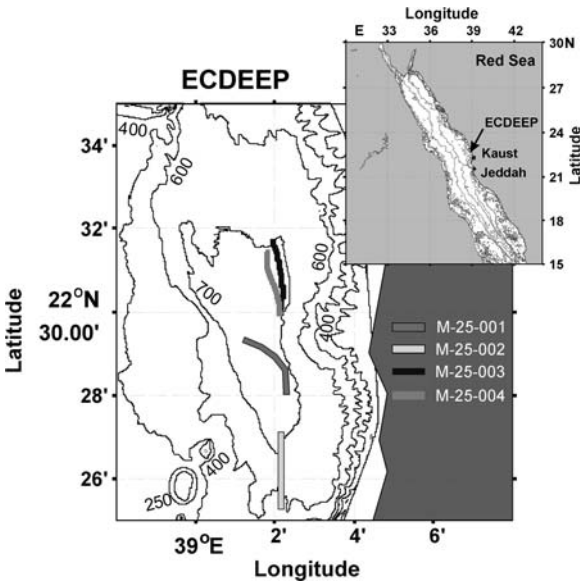

Fig. 1. Sampling locations of MOCNESS tows using to collect samples for this study. Positions shown are of the up-trace of the MOCNESS tows taken in the ECDEEP, Saudi Arabia in January 2014. KAUST is 85 km north of Jeddah.

In addition to the temperature and salinity data collected during MOCNESS tows, an Idronuat Ocean Seven 316Plus CTD was used to measure temperature, salinity, chlorophyll *a*, and dissolved oxygen from the surface to near the bottom (700 m) of the ECDEEP (Fig. 2).

The samples from the first tow were all preserved in 95% alcohol suitable for genetic analysis (Bucklin, 2000). Those from the other three tows were first split in a Folsom splitter (McEwen *et al.*, 1954); one-half was preserved in alcohol and one-half preserved in buffered 10% formalin. In the KAUST Red Sea Center laboratory, the adult and juvenile euphausiids in the alcohol fraction of each of the stratified oblique samples were removed, identified, and counted using a dissecting stereomicroscope and the (Baker *et al.*, 1990) guide. The counts of each euphausiid species for each net were standardized to the number of individuals/1000 m^3 for each depth stratum using the volume filtered by each net. The cumulative percent abundance (Baker, 1970; Pennak, 1943) was calculated for each tow using the bottom of the first depth stratum where a species occurred as 0% and the top of the final depth stratum

Table I: R/V Thuwal *cruise summary of MOCNESS towing statistics. Times (given as year-day and time in fractions of a day) are GMT (Local + 3 h). Tows 1 and 2 were taken during the day and tows 3 and 4 were taken at night*

Tow	Month local	Day local	Time start end (year-day·time)	Lat. (N) start end	Long. (E) start end	Net: depth_open-depth_closed	Volume filtered (m^3)
M-25-001	1	7	7.455590	22.4453	39.0403	Net 0: 0–600	606
			7.520718	22.4890	39.0203	Net 1: 600–400	391
						Net 2: 400–200	251
						Net 3: 200–100	256
						Net 4: 100–0	260
M-25-002	1	8	8.372106	22.4669	39.0339	Net 0: 0–600	2012
			8.492824	22.4209	39.0363	Net 1: 600–400	337
						Net 2: 400–200	352
						Net 3: 200–100	193
						Net 4: 100–50	119
						Net 5: 50–0	112
M-25-003	1	12	12.64576	22.4811	39.0331	Net 0: 0–600	307
			12.70711	22.5293	39.0327	Net 1: 600–400	288
						Net 2: 400–200	323
						Net 3: 200–100	202
						Net 4: 100–50	98
						Net 5: 50–0	133
M-25-004	1	12	12.74358	22.4785	39.0322	Net 0: 0–600	378
			12.80034	22.5236	39.0298	Net 1: 600–400	257
						Net 2: 400–200	297
						Net 3: 200–100	151
						Net 4: 100–50	115
						Net 5: 50–0	112

Times (given as year–day and time in fractions of a day) are GMT (Local + 3 h). Tows 1 and 2 were taken during the day and tows 3 and 4 were taken at night.

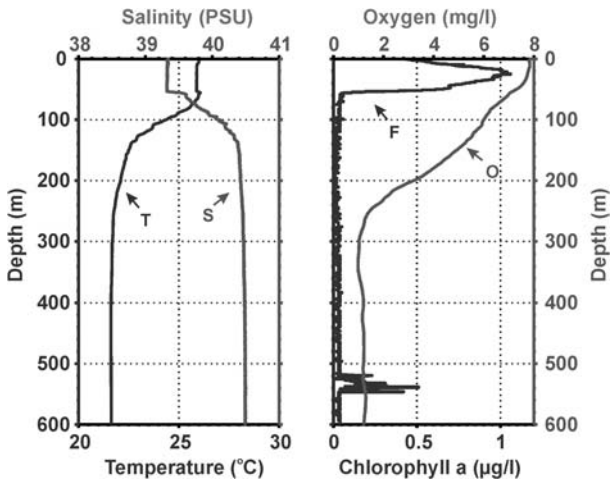

Fig. 2. Vertical distribution of temperature (°C), salinity (PSU), chlorophyll *a* (mg/L) and oxygen (mg/L) based on the CTD up-trace conducted on 13 January 2014.

of occurrence as 100%. Depth (m) values at 25%, 50% and 75% occurrence were interpolated based on the cumulative curve for each species and tow.

Brinton (1962, 1975) recognized five forms of *S. affine* distributed in the Pacific Ocean. He termed these ecophenotypes because of the existence of morphological intermediates in the geographic regions occupied by each form (Brinton, 1975). The forms were distinguished by the ratio of the widths of the lower part versus the upper part, size of the eye and ratio of the length to depth of the sixth abdominal segment. Corresponding morphological measurements were made of *S. affine* to determine which of the five morphological forms as defined by Brinton (1962) were present in the Red Sea. Photographic images of six individuals (three from M-25003, Net 3; three from M-25004, Net 3) were made using a Wild M5A stereomicroscope equipped with a Cannon Rebel EOS T2i camera. The measurements were made on the images in CorelDraw X6 scaled using a stage micrometer image taken at the same magnification as the specimens.

Genetic analysis

Selected specimens of each of the five euphausiid species identified from the alcohol-preserved samples were prepared for genetic analysis, including DNA extraction, PCR amplification and DNA sequencing. DNA sequences for the COI barcode region were determined for *E. diomedeae* (four individuals), *E. sanzoi* (six), *E. sibogae* (four), *S. abbreviatum* (three) and *S. affine* (six). The sequences were submitted to the NCBI GenBank database. GenBank Accession Numbers can be used to access sequence data and collection metadata for all specimens (Table II). Additional specimens of each species (except *E. sanzoi*) were identified from archived samples collected during cruises in the NE Pacific; NW, NE and SE Atlantic; and Arabian Sea (Fig. 3), and analyzed using the same methods.

DNA was purified from individual euphausiids using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA) using standard protocols, except that elution volumes were reduced usually to 100–200 µL. A ~708 base-pair region of the mitochondrial COI gene was amplified using consensus primers (Folmer *et al.*, 1994) and published PCR amplification protocols (Bucklin *et al.*, 2010). The PCR products were run on 2% agarose gels and purified using the QIAquick Gel Extraction Kit (Qiagen) following the manufacturer's instructions, with an elution volume of 35 µL. DNA sequencing was done using a commercial service (Eurofins MWG Operon, Louisville, KY, USA) following all manufacturer's instructions and protocols provided.

DNA sequences were manually checked for accurate machine reading using the Molecular Evolutionary Genetics Analysis (MEGA, Ver. 6) software package (Tamura *et al.*, 2013). DNA sequences to be analyzed were aligned and forward and reverse reads were reconciled using CLUSTAL-W, as implemented in MEGA (Thompson *et al.*, 1997). MegaBLAST searches were conducted in GenBank to confirm the accuracy and validity of the sequences. DNA sequences that could not be verified and validated, including aberrant or highly divergent sequences, were omitted from the data set. Published DNA sequences for the COI barcode region were obtained from GenBank (Bucklin *et al.*, 2007) and included in the sequence alignment for comparative analysis. Both the original alignment and an alignment trimmed to a 500 bp region in common among all sequences were used. In the latter case, any sequence shorter than the target 500 bp region was removed from further analysis, with the exception of several shorter sequences for Red Sea specimens.

Proportional sequence differences (p-distances), with means and standard deviations, within and between species were calculated. Pairwise p-distances were visually displayed as a pairwise distance matrix and as heat maps. A Neighbor Joining tree analysis was carried out in MEGA Ver.6 (Tamura *et al.*, 2013) with Kimura-2-Parameter distances (α = 0.5). Node support was obtained after 1000 bootstraps.

Comparison of samples from Red Sea and North Atlantic

Stylocheiron species collected in the Red Sea also occur in other oceans including the North Atlantic (Mauchline

Table II: Collection information for euphausiid DNA barcodes analyzed in this study

Species name	Voucher number	GenBank AC#	Region	Date	Latitude	Longitude	Depth (m)
S. affine	Eu51.12.4	KT864843	NE Pacific	13 September 2012	34.526 N	135.073 W	101–400
S. affine	Eu51.12.3	KT864844	NE Pacific	13 September 2012	34.526 N	135.073 W	101–400
S. affine	Eu51.12.2	KT864845	NE Pacific	13 September 2012	34.526 N	135.073 W	101–400
S. affine	Eu51.12.1	KT864846	NE Pacific	13 September 2012	34.526 N	135.073 W	101–400
S. affine	Eu51.12.5	KT864847	NE Pacific	13 September 2012	34.526 N	135.073 W	101–400
S. affine	Eu51.1.1	AF371984	Gulf Stream	22 April 1993	39.692 N	54.000 W	0–200
S. affine	Eu51.8.1	KT864848	Sargasso Sea	11 August 2011	34.996 N	52.027 W	150–367
S. affine	Eu51.8.2	KT864849	Sargasso Sea	11 August 2011	34.996 N	52.027 W	150–367
S. affine	Eu51.5.3	KT864850	Red Sea	7 January 2014	22.445 N	39.040 E	0–100
S. affine	Eu51.5.1	KT864851	Red Sea	7 January 2014	22.445 N	39.040 E	0–100
S. affine	Eu51.5.2	KT864852	Red Sea	7 January 2014	22.445 N	39.040 E	0–100
S. affine	Eu51.5.4	KT864853	Red Sea	7 January 2014	22.445 N	39.040 E	0–100
S. affine	Eu51.14.1	KU752550	Red Sea	12 January 2014	22.481 N	39.033 E	200–400
S. affine	Eu51.14.2	KU752551	Red Sea	12 January 2014	22.481 N	39.033 E	200–400
S. abbreviatum	Eu11.10.6	KT864854	NE Pacific	11 September 2012	35.552 N	135.009 W	0–150
S.abbreviatum	Eu11.10.2	KT864855	NE Pacific	11 September 2012	35.552 N	135.009 W	0–150
S. abbreviatum	Eu11.10.1	KT864856	NE Pacific	11 September 2012	35.552 N	135.009 W	0–150
S. abbreviatum	Eu11.9.4	KT864857	S Atlantic	20 March 2008	37.540 S	09.200 E	0–750
S. abbreviatum	Eu11.5.1	KT864858	N Atlantic	11 November 2007	03.213 N	14.602 W	49–100
S. abbreviatum	Eu11.4.1	GU183775.1	Sargasso Sea	21 April 2006	25.056 N	60.626 W	0–5000
S. abbreviatum	Eu11.1.1	EF467301	Sargasso Sea	21 April 2006	25.056 N	60.626 W	0–5000
S. abbreviatum	Eu11.13.2	KT864859	Red Sea	12 January 2014	22.481 N	39.033 E	200–400
S. abbreviatum	Eu11.11.2	KT864860	Red Sea	12 January 2014	22.479 N	39.032 E	100–200
S. abbreviatum	Eu11.12.2	KT864861	Red Sea	12 January 2014	22.479 N	39.032 E	50–100
E. sibogae	Eu18.1.1	EF467305	Arabian Sea	26 March 1995	14.450 N	65.000 E	50
E. sibogae	Eu18.3.1	KT864862	Red Sea	7 January 2014	22.445 N	39.040 E	200–400
E. sibogae	Eu18.5.1	KT864863	Red Sea	12 January 2014	22.481 N	39.033 E	50–100
E. sibogae	Eu18.7.1	KT864864	Red Sea	12 January 2014	22.481 N	39.033 E	0–50
E. sibogae	Eu18.6.1	KT864865	Red Sea	8 January 2014	22.467 N	39.034 E	200–400
E. diomedeae	Eu40.5.1	AY601077.1	SE Pacific	14 November 2000	16.941S	102.617 W	3600
E. diomedeae	Eu40.4.1	KT864866	Arabian Sea	26 March 1995	14.450 N	65.000 E	0–50
E. diomedeae	Eu40.4.2	KT864867	Arabian Sea	26 March 1995	14.450 N	65.000 E	0–50
E. diomedeae	Eu40.2.2	KT864868	Red Sea	7 January 2014	22.445 N	39.040 E	200–400
E. diomedeae	Eu40.2.3	KT864869	Red Sea	7 January 2014	22.445 N	39.040 E	200–400
E. diomedeae	Eu40.3.1	KT864870	Red Sea	8 January 2014	22.467 N	39.034 E	200–400
E. diomedeae	Eu40.2.1	KT864871	Red Sea	7 January 2014	22.445 N	39.040 E	200–400
E. sanzoi	Eu73.2.1	KT864872	Red Sea	7 January 2014	22.445 N	39.040 E	200–400
E. sanzoi	Eu73.1.5	KU752552	Red Sea	7 January 2014	22.445 N	39.040 E	100–200
E. sanzoi	Eu73.4.1	KU752553	Red Sea	8 January 2014	22.467 N	39.034 E	200–400
E. sanzoi	Eu73.4.3	KU752554	Red Sea	8 January 2014	22.467 N	39.034 E	200–400
E. sanzoi	Eu73.5.1	KU752555	Red Sea	12 January 2014	22.479 N	39.032 E	50–100
E. sanzoi	Eu73.7.2	KU752556	Red Sea	12 January 2014	22.481 N	39.033 E	50–100

DNA sequence data were obtained from specimens in new collections from the Red Sea, archived collections from other ocean regions, and published barcodes accessed from the NCBI GenBank database. Mitochondrial COI sequences and collection metadata can be accessed using the GenBank Accession Numbers (AC#) or by going to http://www.bco-dmo.org/project/620092.

and Fisher, 1969). Data from samples collected in the Northern Sargasso Sea (Wiebe and Flierl, 1983) and in a Gulf Stream Warm-Core ring (Wiebe *et al.*, 1992) were used to compare the day/night vertical distributions of the two Red Sea species. The Northern Sargasso Sea was sampled with a nine-net 1-m^2 MOCNESS with 335 μm mesh (Wiebe *et al.*, 1985). The data are from two day/night pairs of tows taken in the summer of 1997 on R/V Endeavor 11 and in the fall of 1977 on R/V Knorr 71 [see Table 1 in Wiebe and Flierl (1983) for details]. Oblique tows were made to 1000 m with the Net 0 open during the downhaul from the surface to the maximum depth of tow, and the Nets 1–8 opened and closed sequentially so as to sample 150-m intervals from 1000 to 400 m and 100-m intervals from 400 m to the surface. A modified Neil Brown CTD system (Wiebe *et al.*, 1976) was used to acquire conductivity, temperature and depth data during each tow.

The Gulf Stream Warm-Core Ring with a core of Sargasso Sea water was sampled during Fall 1982, with day- and night-time tows of a double 1-m^2 MOCNESS carrying 20 nets with 335 μm mesh and equipped with SEABIRD temperature and salinity sensors (Wiebe *et al.*, 1992). Oblique tow sampling was at 100-m intervals from 1000 to 200 m and at 25-m intervals from 200 m to the surface.

All of the Red Sea data sets used in this article are online and accessible from the Biological and Chemical

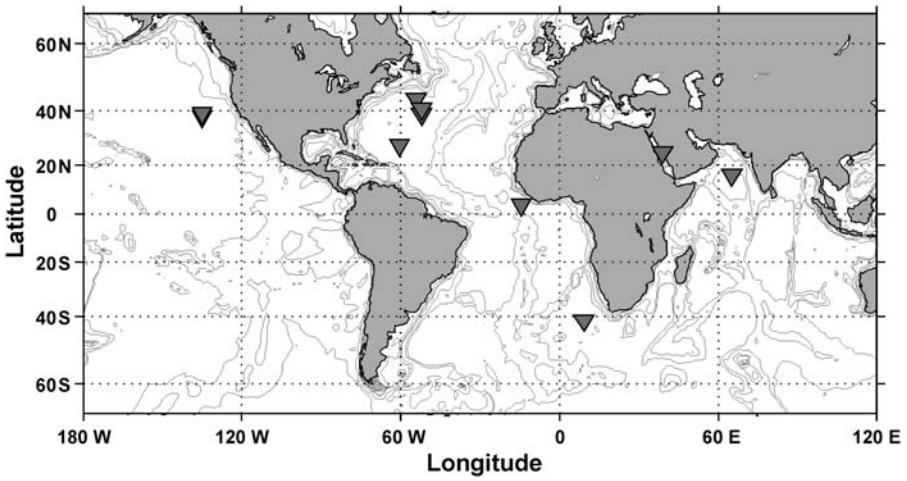

Fig. 3. Locations of analyzed archived samples from cruises in the NE Pacific; NW, NE and SE Atlantic; and Arabian Sea from which specimens of the five euphausiid species were identified and barcoded for comparison with DNA barcode data from the Red Sea specimens. See Table II for details.

Oceanography Data Management Office (BCO-DMO) under the project name "Red Sea Krill" (http://www.bco-dmo.org/project/620092.).

RESULTS

Hydrography

At the ECDEEP sampling site, surface temperatures (0–50 m) were high (~26°C) and decreased rapidly from 50 to 200 m (Fig. 2). Below 200 m, temperature decreased slowly until reaching the near-isothermal conditions (~21.5°C) that extended to the bottom (~700 m). Salinity was ~39.4 PSU from the surface to 50 m; increased rapidly to over 40 PSU at 150 m; and became nearly isohaline below 200 m. Oxygen as measured by the CTD was above 7.5 mg/L at the surface down to 50 m, and rapidly declined from 50 to 220 m from 7.3 to 2.3 mg/L. Below 220 m, low oxygen values averaged ~1.21 mg/L (range: 0.98–2.3) to the bottom of the cast. Chlorophyll *a* increased from the surface to a peak at about 35 m, and decreased rapidly to almost zero below 50 m (Fig. 2).

Euphausiid vertical distributions

Adult specimens of five euphausiid species were identified in the samples: *E. diomedeae*, *E. sanzoi*, *E. sibogae*, *S. affine*, and *S. abbreviatum*. *Euphausia diomedeae* and *S. affine* were the most abundant species (Fig. 4; Table III). The other species occurred in much lower abundances (Table III). The abundances of most species did not differ significantly between day and night. Only *S. affine* had night-time abundances that were significantly ($P < 0.05$) higher than the day values, while *S. abbreviatum* (Fig. 4) was caught only in the two night-time tows.

The vertical distributions of the *Euphausia* species generally ranged from below 200 m to 400 or 600 m during the daytime and above 200 m at night (Fig. 5). The central 50% of the population (i.e. between the 25th and 75th percentiles) occurred in a narrower depth zone, generally ~100 m during the day and ~50 m at night (Table IV). *Euphausia diomedeae* exhibited DVM from below 200 m in the daytime to the upper 100 m at night, with highest abundance in the upper 50 m. There were many *Euphausia* (probably *E. diomedeae*) larvae (furcilia) and juveniles in the upper 50 m at night that are not reflected in the counts presented in Fig. 4 and Table III. These were not as apparent in the samples taken in the daytime. The other *Euphausia* species appeared to migrate, but neither *E. sanzoi* nor *E. sibogae* were caught in the upper 50 m (Figs 4 and 5). The relatively low abundance of these two species contributes to this uncertainty. The entire population of *S. affine* had a broad depth range and was most abundant between 100 and 400 m both day and night, with no evidence of DVM. The central 50% depth range was narrower and ranged from 100 to 250 m. *Stylocheiron abbreviatum* (Fig. 5) was only caught in the two night-time tows in depths between 50 and 400 m.

The temperature and salinity data recorded during the R/V *Thuwal* MOCNESS tows matched the CTD data, so the CTD data (including oxygen concentrations) were used to characterize the pelagic environment of the sampled domain (Table IV). During the day, all

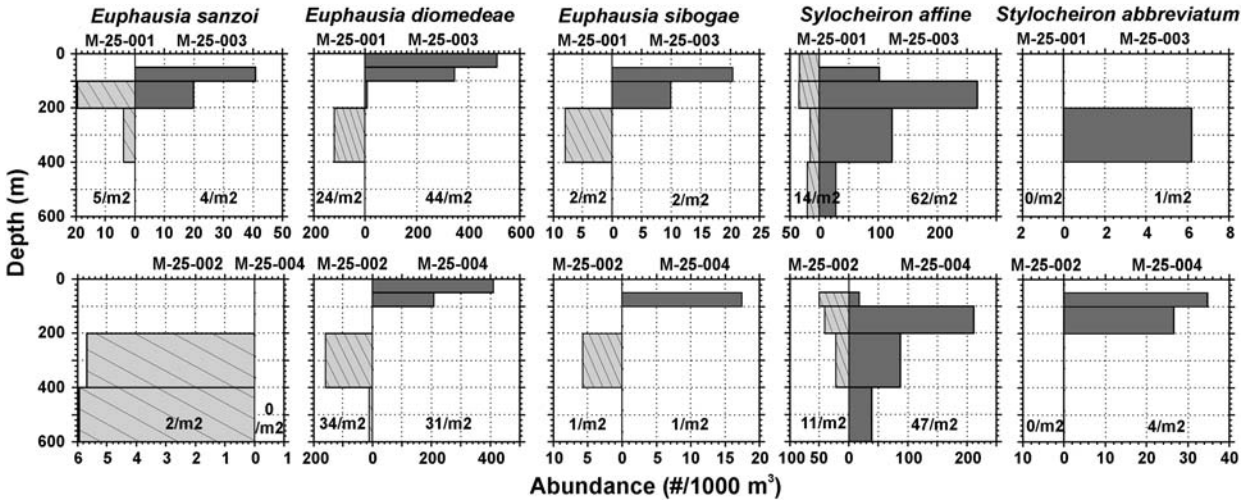

Fig. 4. Vertical distributions and abundances (individuals per 1000 m^3) of the five euphausiid species identified in the MOCNESS samples from the Red Sea ECDEEP. The cross-hatched profile bars are for day tows; the solid profile bars are for night tows. For each tow, the total number of individuals per m^2 is given at the bottom of the plot.

Table III: Abundance of euphausiids collected in the ECDEEP basin of the Red Sea northwest of KAUST, Saudi Arabia in January 2014

	Daytime abundance # (m^2)		Night-time abundance # (m^2)	
Species	m-25-001	m-25-002	m-25-003	m-25-004
E. diomedeae	24	34	44	31
E. sanzoi	5	2	4	0
E. sibogae	2	1	2	1
S. affine	14	11	62	47
S. abbreviatum	0	0	1	4

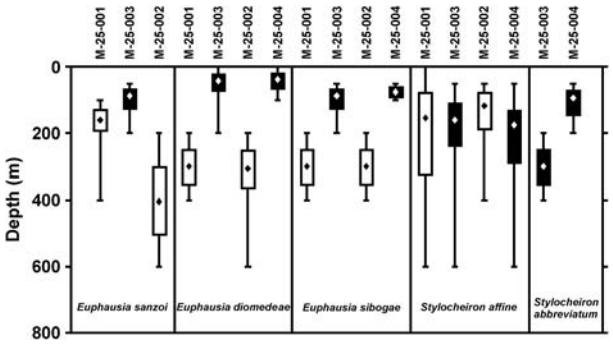

Fig. 5. Comparison of the cumulative percentages of euphausiids from the day and night MOCNESS tows taken in the ECDEEP region of the Red Sea. Cumulative abundances were calculated from bottom to surface, vertical lines represent depths of first occurrence; the bottom and top lines of the box represent the 25th and 75th percentiles of the population, respectively; the diamond marks the 50th percentile; the top of the vertical line represents the shallowest occurrence. The night samples are shown by black boxes; day samples are shown by white boxes. Tow numbers are given above each box plot.

species were caught below 50 m, in temperatures ranging from ~21.5 to 26°C. Salinity ranged from 39.3 to 40.5 PSU. The ranges of temperature and salinity for the night-time vertical distributions were similar for all species, including *E. diomedeae*, of which some individuals occurred in the upper 50 m (Fig. 5). Three quarters of the *E. diomedeae* and *E. sibogae* populations (0–75%) were caught in water with oxygen concentrations of 1.2–1.45 mg/L at their daytime depths, while *E. sanzoi*, which occurred on average closer to the surface, was found in somewhat higher oxygen concentrations (1.21–3.5 mg/L; Table IV). In contrast, the central 50% of the *S. affine* daytime population (25–75%) was found at shallower depths than *Euphausia* species and occurred in more moderate oxygen concentrations of 2.40–6.45 mg/L (Table IV). At night, most of the *Euphausia* species were found in well-oxygenated waters above 100 m, while the central 50% of *S. affine* and *S. abbreviatum* remained at depths with more moderate concentrations (1.52–5.62 and 3.08–4.03 mg/L, respectively; Fig. 5; Table IV).

Morphological form of *S. affine*

The morphometric measurements made on *S. affine* provided evidence that the Red Sea individuals have characteristics that place them in the "Western Equatorial Form" *sensu* Brinton (1962) (Fig. 6 and Table V). In addition, the number of crystalline cones in a transverse row in the upper eye is five, which also is a character of this form (Table V).

Table IV: Temperature, salinity and oxygen values for the cumulative percent depths of occurrence of the five euphausiid species collected in the ECDEEP basin

		Day				Night			
Species	Cumulative (%)	Depth (m)	Temperature (°C)	Salinity (PSU)	Oxygen (mg/L)	Depth (m)	Temperature (°C)	Salinity (PSU)	Oxygen (mg/L)
E. sanzoi	0	500	21.6	40.49	1.21	200	22.1	40.42	3.21
	25	346	21.9	40.46	2.42	123	23.2	40.30	5.57
	50	282	22.0	40.45	2.92	87	25.1	39.91	6.22
	75	216	22.3	40.40	3.25	69	25.8	39.67	6.72
	100	150	23.2	40.26	4.59	50	25.9	39.32	7.30
E. diomediae	0	500	21.6	40.49	1.21	150	23.2	40.26	4.61
	25	356	21.7	40.47	1.03	67	25.9	39.65	6.78
	50	304	21.7	40.47	1.03	40	25.9	39.32	7.58
	75	252	21.8	40.46	1.42	20	25.9	39.33	7.78
	100	200	22.1	40.42	3.20	0	26.0	39.33	7.89
E. sibogae	0	400	21.6	40.49	1.20	150	23.2	40.26	4.61
	25	350	21.7	40.47	1.00	106	24.1	40.11	5.90
	50	300	21.7	40.47	1.03	81	25.4	39.83	6.38
	75	250	21.8	40.46	1.45	66	25.9	39.64	6.82
	100	200	22.1	40.42	3.20	50	25.9	39.32	7.31
S. affine	0	500	21.6	40.49	1.21	600	21.6	21.64	1.22
	25	255	21.9	40.45	2.40	260	21.8	21.78	1.52
	50	135	23.0	40.32	5.29	168	22.3	22.32	4.39
	75	78	25.6	39.77	6.45	122	23.3	23.29	5.62
	100	26	26.0	39.33	7.55	50	25.9	25.89	7.29
S. abbreviatum	0	0	ND	ND	ND	300	21.9	40.45	2.21
	25	25	ND	ND	ND	246	22.1	40.43	3.08
	50	50	ND	ND	ND	197	23.2	40.23	3.56
	75	75	ND	ND	ND	162	23.8	40.08	4.03
	100	100	ND	ND	ND	125	24.0	39.87	5.25

Day and night values averaged when pairs of day or night values were available.

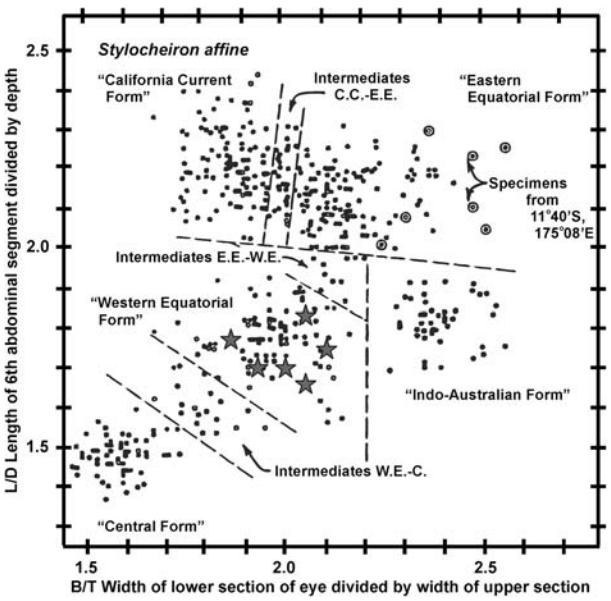

Fig. 6. Morphometric measurements of Red Sea *S. affine* plotted on a redrawn figure of the same measurements made by Brinton (1962, Fig. 93b) to distinguish five ecophenotypic forms in the Pacific Ocean. The stars mark the measurements made on six Red Sea individuals (see Table V for an expanded set of measurements).

Red Sea Euphausiid genetics

With the exception of *E. sanzoi*, for which no other DNA sequences were available, the COI barcode sequences for the Red Sea euphausiids confirmed species identifications based on comparisons with published and unpublished data. Pairwise DNA sequence differences (percent nucleotides) between individuals of the same species were typical of other euphausiid species similarly analyzed (Bucklin *et al.*, 2007) for *S. abbreviatum* (average = 3.76%, SD = 2.28%); sampling was not sufficient to allow accurate evaluation of intraspecific variation for *E. sibogae* (average = 1.0%, SD = 0.42%); *E. diomedeae* (average = 0.80%, SD = 0.50%), or *E. sanzoi* (average = 0.75%, SD = 1.1%). *Stylocheiron affine* showed larger intraspecific differences (average = 7.91%, SD = 6.58%), especially between the Red Sea specimens and those of other ocean regions (mean = 14.08%; SD = 0.39%; Table VI). Pairwise interspecific differences between the five species were typical of other crustacean zooplankton sampled over similar geographic domains: *S. abbreviatum* (average = 16.68%, SD = 1.54%), *S. affine* (average = 17.53%, SD = 1.48%), *E. sibogae* (average = 16.71%, SD = 1.41%), *E. diomedeae* (average = 15.61%, SD = 1.71%), and *E. sanzoi*

Table V: Morphometric measurements of S. affine *from the Red Sea MOCNESS samples*

Individual	No. of cones in upper eye	Total length of adult (mm)	Eye length (mm)	Eye length/total body length	Width lower part eye/ width upper part lobe	Length 6th abd. seg/ depth 6th abd. seg.	Length 6th abd. seg./ length of 5th abd.
M-25-003_1	5	6.80	0.80	0.12	2.05	1.83	1.50
M-25-003_2	5	6.30	0.82	0.13	1.87	1.78	1.60
M-25-003_3	5	7.00	0.78	0.11	2.10	1.75	1.40
M-25-004_1	5	6.50	0.83	0.13	2.05	1.67	1.40
M-25-004_2	5	6.35	0.88	0.14	2.00	1.70	1.60
M-25-004_3	5	6.30	0.89	0.14	1.92	1.70	1.37
Average	5	6.54	0.83	0.13	2.00	1.74	1.48

Three individuals are from M-25003 and three are from M-25-004. Total individual length measured from the tip of rostrum to the tip of the telson (Brinton, 1975, p. 216).

Table VI: Pairwise DNA sequence differences (percent nucleotides) within and between the five species of euphausiids identified from the Red Sea samples for a 500 base-pair section of the COI barcode region

	Mean	SD	Min	Max
Within species				
S. affine	7.91	6.58	0.00	14.82
S. abbreviatum	3.76	2.28	0.00	6.58
E. sibogae	1.00	0.42	0.40	1.60
E diomedeae	0.80	0.50	0.00	1.40
E. sanzoi	0.75	1.10	0.00	2.26
Between species				
S. affine	17.53	1.48	13.45	20.20
S. abbreviatum	16.68	1.54	13.82	19.40
E. sibogae	16.71	1.41	13.82	20.20
E diomedeae	15.61	1.71	11.90	19.40
E. sanzoi	16.28	1.82	11.60	19.20
Red Sea vs others				
Red Sea *S. affine* vs other *S. affine*	14.08	0.39	13.24	14.82
Red Sea *S. abbreviatum* vs other *S. abbreviatum*	4.47	1.67	1.09	6.58
Red Sea *E. sibogae* vs other *E. sibogae*	0.75	0.44	0.40	1.40
Red Sea *E. diomedeae* vs other *E. diomedeae*	0.94	0.36	0.40	1.40

Analysis includes new sequences for specimens from several ocean regions, as well as published sequences for the same species (see Table II and Figs 7 and 8). "Other" refers to individuals of the same species collected other oceans.

(average = 16.28%, SD = 1.82%). Patterns of within and between species differences are displayed as a heat map, with color-coded ranges (Fig. 7).

The Neighbor Joining tree showed clustering of barcodes for each species, including collections from the Red Sea and elsewhere, with 100% bootstrap support for each species, with the exception of the node between the two clades of *S. affine* (80%) (Fig. 8). There was evidence of clustering of individuals by ocean region for *S. abbreviatum* and especially for *S. affine*, which showed two distinct clusters of barcodes reflecting the Atlantic/Pacific versus Red Sea collections.

DISCUSSION

We have shown that the extreme environmental conditions of the Red Sea did not substantially effect or alter patterns of vertical distribution and vertical migration of five euphausiid species that are known from other oceans. These results have reconfirmed observations made by van Couwelaar (1998) and Casanova (1990) of the vertical distributions of the euphausiid species occurring in the Red Sea. The five species collected in the ECDEEP tows were also noted by these authors as the primary species in their Red Sea collections. Casanova (1990) also listed the neritic *P. latifrons* as indigenous in the Red Sea, but it was neither caught by van Couwelaar (1998), nor present in the ECDEEP samples. Both authors noted the presence of DVM for *Euphausia* species and the lack thereof for *Stylocheiron*, similar to our observations.

Pelagic environment of the Red Sea compared with other oceans

One of the most saline water masses in the world's oceans is found in the Red Sea, produced by very high evaporation rates of ~2 m/y, with very little freshwater run-off (Sofianos and Johns, 2002, 2007). Winter cooling and overturning circulation in the northern Red Sea give rise to the Red Sea Deep Waters (RSDW) below the Bab-el-Mandeb Strait sill (depth: ~137 m) which separates the Red Sea from the Gulf of Aden. The temperature of the RSDW varies only slightly around 21.5°C, with salinities above 40.4 PSU (Cember, 1988; Yao et al., 2014). Oxygen concentrations distinguish different types of RSDW: waters from 100 to 300 m have decreasing oxygen concentrations reaching a low that continues to the bottom (Fig. 2). In deeper waters further offshore, oxygen again increases below 1000 m (Yao *et al.*, 2014). The five euphausiid species likely experience very similar ranges of temperature and salinity during day and night in the ECDEEP. However, at ECDEEP the *Euphausia* species as a group are distributed deeper in

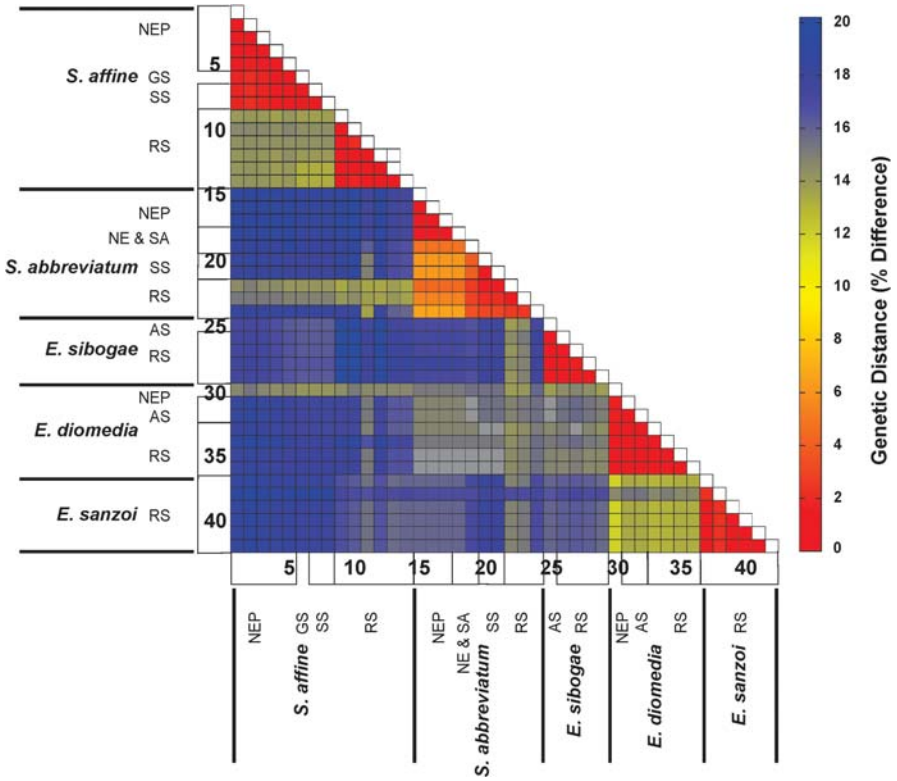

Fig. 7. Pairwise DNA sequence differences, represented as a heat map, within and between the five species of euphausiids collected in the Red Sea. Numbers/colors are percentages of nucleotides (p-distances) calculated for a 500 base-pair section of the COI barcode region. Intraspecific differences were typical of other crustacean zooplankton species analyzed, with the exception of *S. affine* (~14% difference between specimens from the Red Sea versus Atlantic/Pacific).

the water column during the day than most *Stylocheiron species* (Fig. 5 and Table IV), likely to avoid daytime predators. As a result, they experience lower oxygen concentrations during the day than do the *Stylocheiron*. This situation is reversed at night, with the upward migration of the *Euphausia* to the upper 100 m. The fact that the central portion of the *Stylocheiron* species distributions is mostly between 100 and 300 m, in moderately low oxygen concentrations, may reflect their avoidance of the lower oxygen concentrations at deeper depths, which they may be unable to tolerate for extended periods in the warm Red Sea waters (Fig. 5 and Table IV).

The environmental conditions of the Red Sea are substantially different from those of other subtropical/tropical ocean regimes. For example, in the central Arabian Sea, temperatures in the upper 100 m are similar to those in the Red Sea, varying between 24.9 and 28.5°C, although salinities are substantially lower (range: 34.5–36.6 PSU, Morrison, 1995, 1996a, 1996b, 2002). At depths below 100 m, temperatures decrease rapidly to ~11°C at 600 m and salinities range between 35.4 and 36.4 PSU. Oxygen values are high in the surface waters, but drop to much lower values below 100 m than observed in the ECDEEP. Discussing Indian Ocean euphausiid distributions, van Couwelaar (1998) said, "The present study fails to confirm the oxygen minimum as a barrier for downward migration. Epipelagic migrators during the day, and mesopelagic species, either migrating or not, stay under low oxygen concentrations at greater depths." In particular, he found *E. diomedeae* and *E. sibogae* to vertically migrate with weighted mean depths during the day of 200–400 m in the Gulf of Aden; he found similar patterns in the Banda Sea (van Couwelaar, 1994). *Euphausia sanzoi* showed less clear patterns, although the species was found at mesopelagic depths during the day and shallower at night. Casanova (1990) found all three *Euphausia* species dielly migrating.

Migrating euphausiids in the Eastern Tropical Pacific Ocean are also able to tolerate low oxygen conditions during the day (Brinton, 1979; Sameoto *et al.*, 1987; Gonzalez and Quiñones, 2002; Escribano *et al.*, 2009; Maas *et al.*, 2014). *Euphausia diomedeae* in this region has evolved to tolerate low oxygen water at daytime depths from 230 to 400 m and migrate at night into the upper

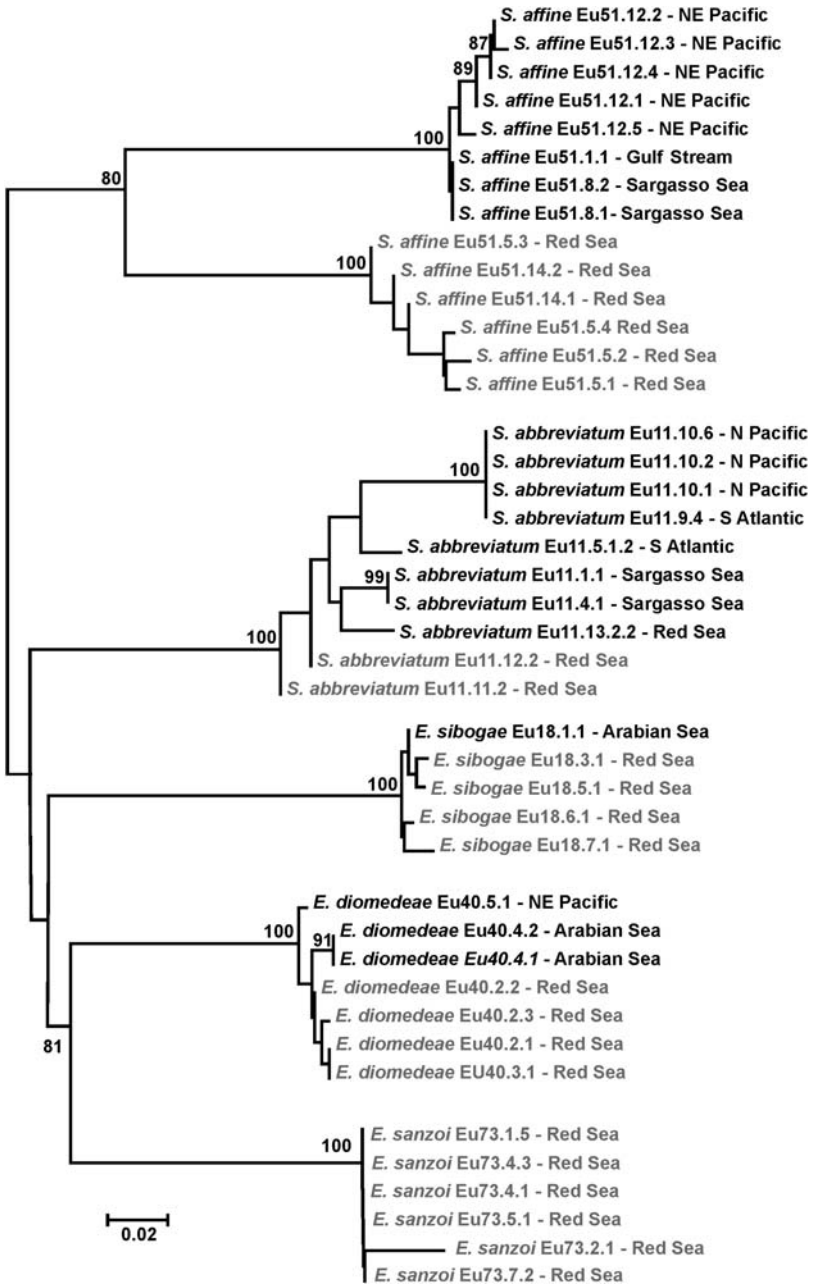

Fig. 8. Neighbor Joining tree with Kimura-2-Parameter genetic distances, with bootstrap values shown for nodes supported by >80% bootstrap values. With the exception of *S. affine*, species are resolved with 100% bootstrap support. Some regional differentiation of populations is shown for *S. abbreviatum*; the Red Sea population of *S. affine* shows 14% difference from conspecific populations in other ocean regions.

70 m (Brinton, 1962, 1975, 1979), while *E. mucronata* can tolerate low oxygen for extended periods of time in the OMZ in the Peru Current and carry out anoxic respiration to survive in the low oxygen conditions (Gonzalez and Quiñones, 2002). *Megancytiphanes norvegica* is able to survive in low oxygen conditions in fjords during the day, but mortality was up to 100% if kept at depth overnight (Spicer *et al.*, 1999). Migration to surface oxygenated waters is essential to dispose of the end-products of anaerobic metabolism.

The vertical distributions of *S. affine* and *S. abbreviatum* from the Northwest Atlantic, as reassessed in samples from the Sargasso Sea and a Warm-Core Ring with Sargasso Sea water at its core, provide another comparison with those in the Red Sea (Fig. 9). Similar to the Red Sea, the two species sampled in day and night show

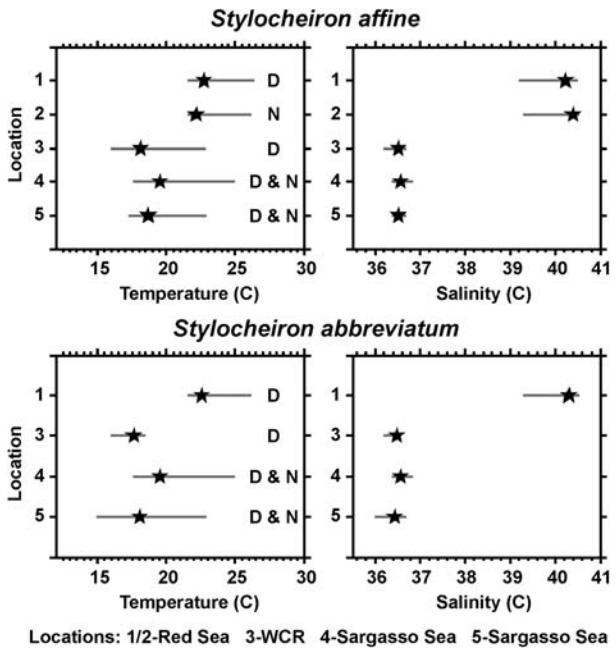

Fig. 9. *Stylocheiron affine* and *S. abbreviatum* temperature and salinity ranges. Maximum, minimum and average temperature and salinity values (marked by stars) based on the vertical distribution of the species in the Red Sea, in a Warm-Core Ring in 1982, and in the Northern Sargasso Sea in August and October 1977. The "D", "N" and "D & N" indicate data from day tows, night tows, or both day and night tows averaged together. The species in the Red Sea experienced significantly higher mean temperatures and salinities.

no evidence of vertical migration (Fig. 10), although the vertical distribution of *S. affine* in the Sargasso Sea is somewhat deeper than observed in the Red Sea. The low oxygen concentrations of the Red Sea combined with the high temperatures and high salinities at depth may have interactive effects (i.e. higher oxygen demand) that have negative consequences (Hofmann and Todgham, 2010). Despite this, both species had similar abundances in terms of numbers/m^2 in the North Atlantic and Red Sea (Figs 4 and 10).

Morphological forms of *S. affine*

Brinton (1962) recognized five geographical ecophenotypical forms of *S. affine* living in the Pacific Ocean. He determined that *S. affine* in the Arabian Sea and Bay of Bengal was similar to the Indo-Australian form, and showed the "Western Equatorial Form" in the more southern portion of the Indian Ocean (Brinton, 1975; Brinton *et al.*, 2000). The morphological characteristics of *S. affine*, collected in the Red Sea ECDEEP, however, are consistent with the Western Equatorial Form (Fig. 6). Casanova (1990) also noted that the Red Sea and Gulf of Aden forms had morphological characters consistent with the Western Equatorial Form. In addition, she noted that in contrast to the smaller gills of a form found in West equatorial regions off the coast of Somalia, the form of *S. affine* occurring in the Red Sea and Gulf of Aden had exceptional development of the gills, which she suggested was an adaptation to the low oxygen environment. Other Red Sea euphausiid species studied by Casanova (1990), including *S. abbreviatum*, *E. diomedeae* and *E. sibogae*, also had enhanced development of the gills, which she suggested may reflect incipient speciation driven by the distinct and extreme environmental conditions of northern regions of the Indian Ocean and Red Sea. Expanded gill surface area was observed by Antezana (2002) in *Euphausia mucronata*, which lives during the day in the Humboldt Current oxygen minimum zone. Natural selection adaptions to low O_2 may include high gill surface areas (Seibel, 2011).

Genetics

DNA barcodes have been widely used to identify species of metazoans, delimit species boundaries, reveal cryptic species, and discover new species among marine metazoans (Bucklin *et al.*, 2011). The mitochondrial COI gene is the most frequently used sequence for DNA barcoding of animals (Hebert *et al.*, 2003). Patterns and levels of COI barcode variation within and between species vary widely across the Crustacea: Hebert *et al.* (2003) reported an average difference of 15.4% (SD = 6.6%) based on 1781 pairwise comparisons between congeneric species. For euphausiids in particular, Bucklin *et al.* (2007) reported on COI barcode sequence variation for 40 species of five genera: pairwise percent differences within species averaged 1.7% (SD = 2.0%), although it should be noted that this value is highly dependent on geographic distribution of sampling and sample sizes (Bergsten *et al.*, 2012). COI differences between euphausiid species averaged 14.9% (SD = 4.0%), with average differences between 10 species of *Euphausia* of 16.2% (SD = 3.5%) and between seven species of *Stylocheiron* of 15.2% (SD = 2.3%) (Bucklin *et al.*, 2007).

Comparisons with available DNA sequences for the COI barcode region (Figs 3, 7 and 8; Table II, VI) clearly support the identifications of four of the five euphausiid species collected from the Red Sea. No barcode sequences are available for comparison for the fifth species, *E. sanzoi*. One species, *E. sibogae*, has only one barcode sequence available for comparison.

Stylocheiron abbreviation shows typical levels of intraspecific variation (~4%), although the COI gene tree (Fig. 8) shows some evidence of genetic differentiation of geographic populations and our analysis is hampered by

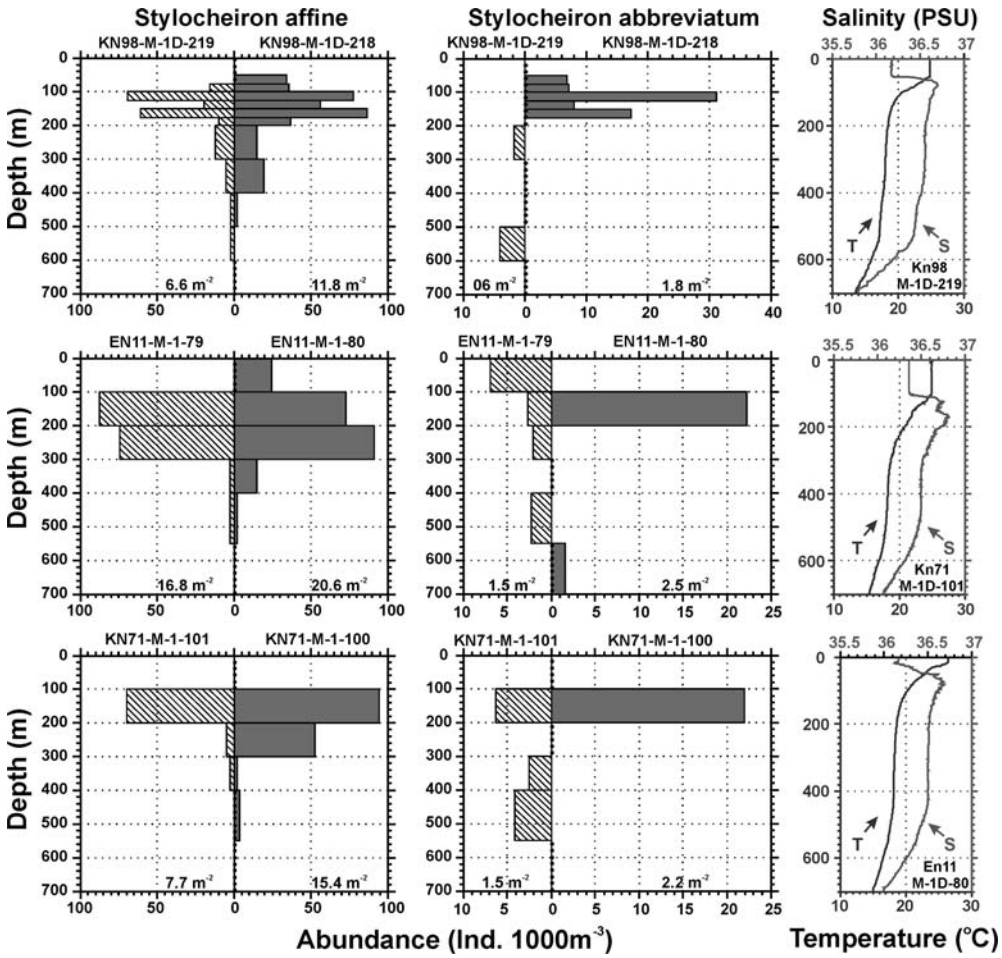

Fig. 10. *Stylocheiron affine* and *S. abbreviatum* North Atlantic vertical distributions. These two species are non-migrators in the North Atlantic and have centers of distribution below the mixed layer and seasonal thermocline. On KN98, the tows were taken in a Warm-core ring. On EN11 and KN71, the tows were taken in the Sargasso Sea. Day profiles (left) are cross-hatched and night profiles (right) are solid. Also plotted are the temperature and salinity data collected at the tow locations. These data were used in computing T and S data used in Fig. 8.

shorter barcode sequences for two individuals. In contrast, COI sequences for the Red Sea specimens of *S. affine* differed by about 14% from conspecific individuals from Atlantic and Pacific Ocean regions. This level of sequence divergence is consistent with species-level differences among euphausiids (Bucklin *et al.*, 2007). The observed levels of COI sequence variation between *S. affine* of the Red Sea and other ocean regions, including the NE Pacific and NW Atlantic (Gulf Stream and Sargasso Sea), with clustering of *S. affine* barcodes by ocean region, suggests that cryptic, species-level variation may be found within the global ocean populations of this taxon. Given the DNA sequence divergence of the Red Sea population observed in this study and the morphological differences described by Casanova (1990), *S. affine* warrants a world-wide integrated molecular and morphological taxonomic and phylogeographic analysis.

Implications for understanding and predicting zooplankton responses to climate change

The mesopelagic zone of the Red Sea represents an extreme environment with high temperatures, low food concentrations and hypoxic conditions with associated low pH. This environment provides an excellent extreme environment to study how zooplankton, especially those species that are also found in other ocean regions with less extreme conditions, respond to these conditions. High mesopelagic temperatures (~22°C) cause high metabolic demands, making the low food supplies and oxygen concentrations stressful. A mismatch between the demand for oxygen and the capacity of oxygen supply to tissues appears to be the first mechanism to restrict whole-animal tolerance to thermal extremes (Pörtner and Knust, 2007; Hofmann and Todgham, 2010; Somero, 2011). Recent studies in the

Red Sea have indicated that >95% of the mesopelagic fish perform vertical migrations to the upper ~200 m at night (Klevjer *et al.*, 2012; Dypvik and Kaartvedt, 2013). Klevjer *et al.* (2012) suggested that food limitation due to very low zooplankton concentrations (Weikert 1982; Halim 1984; Böttger-Schnack, 1990; Böttger-Schnack *et al.*, 2008) and rapid digestion in the very warm waters require the entire population of mesopelagic fish to migrate to upper layers each night to feed. Although similar effects might be expected for macrozooplankton, causing species not known to vertically migrate in other ocean regions to carry out DVM in the Red Sea, this was not the case for the two species of *Stylocheiron* examined in this study, one of which (*S. affine*) maintained the same depth ranges day and night and were similar to the species in other ocean regions. *Stylocheiron abbreviatum* was found at night in depths typical for the species in other oceans. Furthermore, the fact that the Red Sea *Euphausia* species exhibit DVM patterns similar to the species populations in other ocean regions suggests their physiological flexibility to tolerate much more extreme environments than they usually experience. The physiological and biochemical mechanisms by which widely distributed euphausiid species respond to the Red Sea environment are known in general (Seibel, 2011), but need to be studied in more detail to understand and predict these species responses to climate change.

CONCLUSIONS

Five euphausiid species previously reported from the Red Sea were collected with vertically-stratified sampling during January 2014. Three species of *Euphausia* (*E. diomedeae*, *E. sanzoi*, and *E. sibogae*) exhibited clear patterns of DVM, while two species of *Stylocheiron* (*S. abbreviatum* and *S. affine*) did not. The *Stylocheiron* species were found at depth ranges similar to those they occupy in other oceans (North Atlantic, Indian Ocean), albeit under very different environmental conditions (much higher temperature and salinity; lower oxygen concentration).

DNA sequences for the mitochondrial COI barcode regions supported the species identification of four of the five species, based on comparison with available barcode data (no comparative barcode data are available for *E. sanzoi*). Levels of intraspecific variation were typical of crustacean zooplankton analyzed previously, with the exception of *S. affine*, for which Red Sea specimens differed by 14% from those collected in the Atlantic and Pacific Oceans, suggesting the presence of cryptic, species-level variation within the taxon.

These results demonstrate exceptionally broad tolerance ranges of widely distributed euphausiid species for key parameters (temperature, salinity, and dissolved oxygen) in the pelagic environment. Whether these patterns reflect physiological plasticity or genetically mediated adaptation of populations and species remains unclear. The distinct and extreme conditions of the Red Sea offer a unique opportunity to examine these questions, and to gain new insights into how zooplankton populations and species may be able to tolerate, acclimate, and/or adapt to changing conditions in other ocean regions.

DATA ARCHIVING

All of the Red Sea data sets used in this article are online and accessible from the Biological and Chemical Oceanography Data Management Office (BCO-DMO) under the project name "Red Sea Krill" (http://www.bco-dmo.org/project/620092.).

GenBank Accession Numbers can be used to access sequence data and collection metadata for all specimens (Table II).

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