

## Living in suboxia: Ecology of an Arabian Sea oxygen minimum zone copepod

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### Abstract

Oxygen minimum zones (OMZs) are permanent suboxic features of the oceanic water column that strongly influence zooplankton distributions and biogeochemical cycles. The lower interface of prominent OMZs is characterized by a subsurface zooplankton biomass peak and high biological activity. The calanoid copepod *Lucicutia grandis* is an indicator species for this habitat. Its ecology in the Arabian Sea was studied during the U.S. Joint Global Ocean Flux Study (JGOFS) program to understand planktonic distributional and developmental adaptations to oxygen gradients in suboxic environments and the role of the OMZ zooplankton in food webs, vertical flux processes, and carbon cycles. Zooplankton samples were obtained in vertically stratified multiple opening-closing net and environmental sensing system (MOCNESS) tows to 1,000 m during four seasonal cruises. The vertical distribution of *L. grandis* was associated with the steep oxygen gradient from 0.07 to 0.15 ml L<sup>-1</sup> at the base of the OMZ about 600–1,000 m. There was a clear progression with age of the depths and oxygen levels inhabited by different developmental stages within this zone, a phenomenon attributed to both physiological constraints and ecological interactions. The seasonal and spatial pattern of reproduction and development was keyed in part to the seasonal monsoon cycle, with final maturation of young stages into reproducing adults probably triggered by the direct and indirect effects of the seasonal or episodic input to depth of sinking particles. Gut contents included surface flux material, deep-sea detrital material, zooplankton remains, and deep-sea aggregate material, indicating that *L. grandis* occupies at least four different trophic levels. This was an active, not a diapausing, population, since both adults and immature stages fed and reproduced during all seasons. In contrast to the pelagic fauna that are severely impacted by coastal episodic hypoxia, the animals of the oceanic OMZ are uniquely adapted to the very low oxygen and strong spatial and temporal patterns of this widespread suboxic environment.

Interest in the zooplankton ecology of suboxic or hypoxic (low oxygen) marine environments has been sparked by recent episodic hypoxic events in coastal waters such as Chesapeake Bay and the U.S. Gulf Coast. Episodic hypoxia in these locations frequently results in deleterious effects on zooplankton or exclusion of the normal fauna from the hypoxic zone (reviewed in Marcus in press). In contrast, oceanic oxygen minimum zones (OMZs), which are ubiquitous features of the midwater ocean, have a pelagic fauna that is adapted to permanent suboxic waters. These adaptations include morphological or physiological features facilitating

oxygen absorption (Childress and Seibel 1998), distributions related to specific oxyclines (Longhurst 1967; Brinton 1979; Wishner et al. 1998), and behavior, such as vertical migration or diapause, by which some animals move in and out of the most suboxic water on a regular basis (e.g., Judkins 1980; Saltzman and Wishner 1997b; Herring et al. 1998; Smith et al. 1998b; Morrison et al. 1999).

The terms “hypoxic,” “suboxic,” and “micro-oxic” refer to water with lower than normal oxygen concentrations. Hypoxic is used commonly for coastal events, suboxic is the preference of chemists dealing with OMZs (Morrison et al. 1999), and micro-oxic often relates to the process of measuring low oxygen. The oxygen values defining these waters in different studies are variable (reviews by Diaz and Rosenberg 1995; Marcus in press). We chose the definition of Morrison et al. (1999) of suboxic as <4.5 μM (about 0.1 ml L<sup>-1</sup>) oxygen, which defined the boundary of the core of the Arabian Sea OMZ.

The Arabian Sea is one of several world regions with an extensive and pronounced OMZ, where oxygen values below 0.1 ml L<sup>-1</sup> extend for hundreds of m vertically and thousands of km horizontally (Wyrski 1973; Morrison et al. 1999). This clearly affects the vertical distribution of total zooplankton biomass (Vinogradov and Voronina 1961; Böttger-Schnack 1996; Wishner et al. 1998). Zooplankton biomass is substantially reduced in the part of the water column

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### Acknowledgements

We thank the many people who helped at sea and in the lab during the JGOFS program (Wishner et al. 1998; Gowing and Wishner 1998). Specific assistance with the *Lucicutia* project was given by D. Outram, M. Rapien, J. Saltzman, and D. Schreiber in Rhode Island and by Laurie C. Van De Werfhorst, Paula Sicurello, Reena Zalpuri, Steve D'Angelo, Doug Davis, Sally Ann Rodriguez, Lani Watson, and Alaina Kipps in California. F. Ferrari provided taxonomic advice on *Lucicutia*, and P. W. Johnson and P. Hargraves provided taxonomic advice on the picoautotrophs. This work was funded by National Science Foundation grants OCE-9310591 to K.W. and OCE-9310590 to M.G. This is JGOFS contribution number 551.

Table 1. Cruise and season dates, station locations, and tow numbers. All tows were taken at night, unless indicated by (D) for day tows. Tows marked (S) have special sampling depths described in the text. (G) marks tows used only for gut content analyses. ND = no data (tows were not successful to depth). Season dates are from Weller et al. (1998).

	Cruise			
	TN043	TN045	TN050	TN054
Season	Late NE monsoon	Spring intermonsoon	Late SW monsoon	Early NE monsoon
Abbreviation	late NEM	SIM	late SWM	early NEM
Cruise dates (1995)	8 Jan–4 Feb	14 Mar–10 Apr	17 Aug–15 Sep	29 Nov–27 Dec
Season dates	1 Nov 94–15 Feb 95	16 Feb–31 May	1 June–15 Sep	16 Oct 95–15 Feb 96
Tows (by cruise)				
Sta. N7	19°12'N 67°10'E	ND	302 (D,G)	403
Sta. S15	10°00'N 64°54'E	106	305	406
Sta. S11	14°27'N 65°00'E	107	306(D)	408
Sta. S7	16°02'N 62°00'E	109, 111(S)	309	409, 410(D)
Sta. S4	17°12'N 59°46'E	113	311	411
Sta. S2	18°05'N 58°00'E	116	313	414

where oxygen values are lowest, but there is a subsurface peak in zooplankton biomass at the base of the OMZ (usually around 600–800 m depth) coincident with the increasing oxygen gradient from 0.05 to 0.1 ml L<sup>-1</sup> (Wishner et al. 1998). A similar vertical biomass distribution occurs in the OMZ of the Eastern Tropical Pacific (Wishner et al. 1995; Saltzman and Wishner 1997a).

The specific oxyclines coincident with the limits of the fine-scale distributions of different organisms remain poorly known. Oxygen gradients between suboxic and more oxygenated water can be sharp and spiky (only centimeters thick in some shallow water basins) (Donaghay et al. 1992), and micro-oxic concentrations are difficult to determine accurately in association with organism distributions. An oxygen level of about 0.1 ml L<sup>-1</sup> is usually considered the boundary for oceanic OMZ effects (Longhurst 1967; Childress 1975; Judkins 1980; Wishner et al. 1995, 1998). In this paper, we document a life history distributional strategy, strongly attuned to the oxygen gradient from 0.07 to 0.15 ml L<sup>-1</sup>, of a common OMZ copepod living at 600–1,000 m depth in the Arabian Sea.

The major seasonal signal in the Arabian Sea is the wind-driven monsoon cycle, with the northeast monsoon (NEM) occurring from December to January and the southwest monsoon (SWM) (with the strongest sustained winds of the year) occurring from July to September (Weller et al. 1998) (Table 1). High primary productivity occurs year round, peaking somewhat during the SWM and with seasonal and geographic changes in the phytoplankton composition and size (Campbell et al. 1998; Garrison et al. 1998, 2000). A major peak in export flux of organic material to depth occurs during and just after the SWM, with a smaller peak after the NEM and occasional intermonsoonal flux events (Lee et al. 1998; Honjo et al. 1999).

The lower interface of strong OMZs appears to be a location of high rates, as well as high abundances. We previously hypothesized that the zooplankton biomass peak at the base of the OMZ was a localized zone within the deep sea of enhanced processing of the sinking particulate material because zooplankton feeding rates measured in situ in this zone in the Eastern Tropical Pacific were high (Wishner et

al. 1995). In the Arabian Sea, we hypothesized that deep-sea zooplankton population dynamics might be linked to the seasonal monsoon cycle of vertical flux.

The copepod *Lucicutia grandis* (Giesbrecht 1895), the subject of this paper, is a common inhabitant of the subsurface biomass peak in both the Arabian Sea and Eastern Tropical Pacific and is being studied intensively as a deep-sea indicator species of oceanic OMZs. It lives mainly at depth from about 600–1,000 m near the lower interface of the OMZ, where it actively feeds and reproduces (Wishner et al. 1995; Saltzman and Wishner 1997b). It is a generalized omnivore that eats a variety of zooplankton and particulate material, both surface-derived items and particles produced in situ (Gowing and Wishner 1992, 1998). We expected that it would show strong relationships to the oxygen gradients of the OMZ and illustrate seasonal linkages between the pelagic deep-sea fauna and the vertical fluxes associated with the Arabian Sea monsoon cycle.

Biological, physical, and biogeochemical processes and the distributions of organisms, particles, carbon, nutrients, and hydrographic parameters in the Arabian Sea were intensively studied during the 1995 U.S. Joint Global Ocean Flux Study (JGOFS) (Smith et al. 1998a). This large multidisciplinary project, whose goals are quantifying carbon cycling and fluxes in the world's oceans, included over a year of research cruises in the northern Arabian Sea. The zooplankton studies reported here are a part of the U.S. JGOFS Arabian Sea project.

## Materials and methods

*Sampling*—Zooplankton were collected with a double 1 m<sup>2</sup> MOCNESS (two 1 m<sup>2</sup> MOCNESS systems side by side), a multiple opening-closing net system with environmental sensors and control of the nets from shipboard (Wiebe et al. 1976). The nets were 153- $\mu$ m mesh. Although cod ends with 333- $\mu$ m mesh drainage holes were inadvertently used on the first two cruises, the copepods in this study were all larger than this. Electronic data from the MOCNESS included time, volume filtered, depth, temperature (Sea-Bird SBE 3), salin-

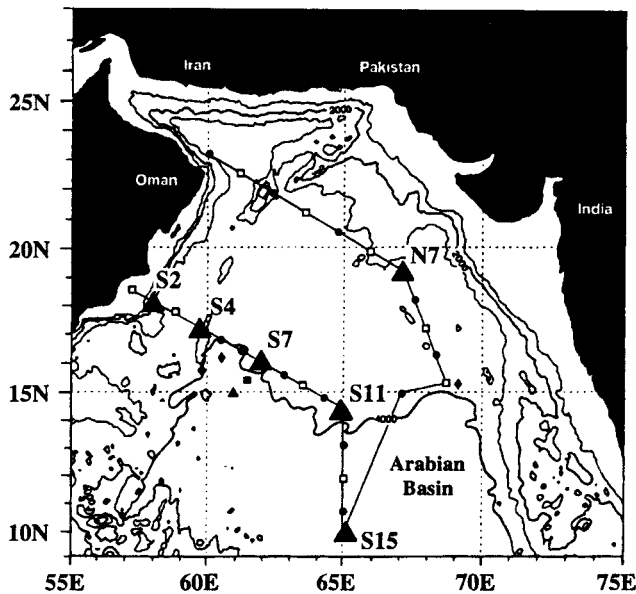


Fig. 1. Map of the northern Arabian Sea showing the JGOFS transect. Zooplankton samples came from stations marked with triangles.

ity (Sea-Bird SBE 4), light transmission (SeaTech 25-cm beam transmissometer), and oxygen (Sea-Bird SBE 13). Typically, about 500–800 m<sup>3</sup> were filtered for the samples discussed here.

Usually 16 discrete samples were collected in an oblique haul from 1,000 m to the surface, with 100-m intervals at depth and 50- or 25-m intervals in the upper 400 m. Depth intervals considered in this paper were 1,000–900, 900–800, 800–700, 700–600, 600–500, 500–400, 400–350, and 350–300 m. Another lab is processing the upper water column samples. Typically, a day and a night tow were taken at each of the six intensively studied stations (N7, S15, S11, S7, S4, S2) along the JGOFS track line spanning the Arabian Sea (Fig. 1). Samples were obtained clockwise along the track during four seasonal cruises in 1995: the late northeast monsoon (late NEM) in January (TN043), the spring intermonsoon (SIM) in March (TN045), the late southwest monsoon (late SWM) in August–September (TN050), and the early northeast monsoon (early NEM) in December (TN054) (Table 1). Occasional additional tows at these and other stations, samples down to 1,700-m depth, and special tows with narrowly spaced depth intervals near the base of the OMZ were also taken. Tow times, geographic locations, the depth range and volume filtered for each net, and zooplankton biomass are in the cruise event log and Wishner/Gowing files in the JGOFS database on the World Wide Web (<http://usjgofs.whoi.edu>). Further details on the zooplankton sampling and processing are in Wishner et al. (1998) and Gowing and Wishner (1998).

Cod ends were placed on ice immediately after retrieval. Nets were hosed down with filtered (nominally 2  $\mu$ m) seawater. For most day tows, the entire sample was preserved in 4% borate-buffered formaldehyde. For most night tows, the samples were split in an NMFS-style (flat-bottomed) plankton splitter. Half the sample was preserved as above

for displacement volumes, wet weights, and distributions. One quarter (or the entire remaining half for surface or very small samples) was refrigerated for dry weight and CHN subsampling, and one quarter (when available) was preserved in cacodylate-buffered 2% paraformaldehyde for electron microscopy of zooplankton gut contents.

For this study, usually one tow from each station for each season for the depth range 300 m and deeper was analyzed (eight samples counted per tow) (Table 1). Usually, the nighttime tow from each station was used; a day tow was used in one instance (S11 in August) when the night tow was unsuccessful to depth. Sta. S7 was emphasized for some additional studies because it was near the Findlater wind jet of the SWM, had a strong well-developed OMZ, had high abundances of the target species, and was a location of JGOFS sediment traps measuring particle fluxes. Two day tows were analyzed from S7 for day–night comparisons (March and December). One special tow with narrower depth intervals in the OMZ was also analyzed from S7 to look at small-scale distributions; this tow (111) had 20-m depth intervals from 600 to 700 m. For Sta. N7 on the northern transect, only a single night tow (December) was analyzed for distributions because most other tows there did not reach the full depth range. Since the thickest layer of the most suboxic water occurred at this station (<0.05 ml L<sup>-1</sup> to over 1,000 m), this tow provided an interesting endpoint for the studies of distributions relative to oxygen gradients. Data from Sta. N7 and Tow 111 at Sta. S7 were not included in statistical tests.

In the lab, the preserved fraction was split further for distributional studies. Usually from 1/8 to the entire sample was counted for *Lucicutia* abundance. Animals were sorted to life stage (copepodite 1 and older). A target of 100 individuals per sample was used (for depths where the species was present), but often many more were counted in the split. Over 24,000 individuals of *Lucicutia grandis* were counted and staged. F. Ferrari (U.S. National Museum) provided taxonomic assistance. Body length of representatives of each lifestage was measured with an ocular micrometer. Further analyses dealt only with copepodite 2 (C2) and older lifestages because C1s were sparse.

Oxygen data from the MOCNESS sensor were calibrated separately for each cruise and station for the 150–1,050-m depth range to obtain a continuous profile of oxygen in the deeper water column. (The net frame and sensors were deployed below 1,000 m to set up the tow; plankton collection usually began at 1,000 m on the way up.) The upcast oxygen profile, obtained simultaneously with the plankton collection, was used in most cases. Electronic oxygen sensors, although showing excellent repeatability in the pattern of fine-scale details, are sensitive to drift and pressure effects. Thus it was necessary to calibrate the electronic curves with the Winkler values from the JGOFS CTD casts to directly compare sensor oxygen values between tows taken days apart and over a wide depth and geographic range. The calibration procedure, described in Wishner et al. (1998), resulted in oxygen profiles that broadly followed the Winkler values while preserving the small-scale features of the original data (Fig. 2). The use of a continuous oxygen sensor on the MOCNESS along with the excellent calibrations provided

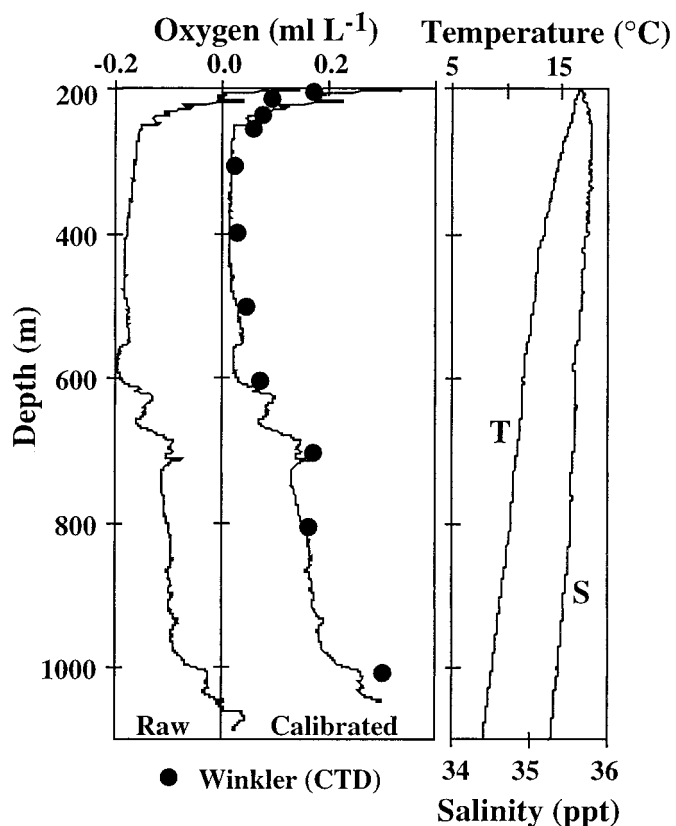


Fig. 2. Example of an original (raw) and calibrated MOCNESS oxygen profile from the upcast of Tow 109 along with Winkler values of oxygen from CTD casts taken during the same cruise at this station. Profiles of temperature and salinity from the same MOCNESS tow are also shown.

by the extensive JGOFS CTD data set (Morrison et al. 1998, 1999) proved essential for the fine-scale analyses in this paper.

**Data analysis**—Mean weighted depths (MWD), a measure of the center of a population's vertical distribution, were calculated for each lifestage from each tow using the equation of Perry et al. (1993):  $MWD = \frac{\sum (x_i \times z_i)}{\sum x_i}$  where  $x_i$  = abundance (no.  $1,000\text{ m}^{-3}$ ) and  $z_i$  = middepth of the net. The depth range used was 300–1,000 m or 300–1,100 m when noted, a depth range encompassing the abundance peak and oxygen gradients of the lower OMZ. For Tow 313 (late SWM Sta. S2), the depth range was 400–1,000 m because there were no data from 300 to 400 m. For each MWD, the associated oxygen value at that depth was determined from the calibrated continuous oxygen profile from the MOCNESS sensor for that tow.

Variables used to examine seasonal (between cruise) patterns included abundances and proportions of each lifestage, rates of abundance change of each stage between cruises, and abundance ratios of successive lifestages at each station. Abundance change between cruises was calculated for each lifestage from each station as the difference in its abundance between successive cruises divided by the number of days between the sampling at that station. Differences in these

variables among cruises or stations were analyzed with Kruskal-Wallis tests. Data from Sta. N7 were not included in these tests because only one tow was available. Sta. S15 data were included in tests of differences among stations but not in tests of differences among cruises, which focused on the region of high *Lucicutia* abundance. As documented below, S15 was a very different habitat from the rest of the stations, and *Lucicutia* abundances were very low there. Mann-Whitney *U* tests were used to examine the significance of differences between S15 and the other stations and between onshore (S2, S4) and offshore (S7, S11, S15) stations. The onshore-offshore comparison was significant in previous studies of overall zooplankton biomass (Wishner et al. 1998). A significance level of 0.05 was used in statistical tests.

**Carbon budget**—A carbon budget was developed to quantify the potential energetic impact of the *Lucicutia* population on midwater carbon fluxes. Four possible estimates of *Lucicutia* activity were used: respiration rates of two other deep-sea *Lucicutia* species from the California Current OMZ (Thueson et al. 1998: mean of  $1.252\ \mu\text{mol O}_2\ \text{g wet weight}^{-1}\ \text{h}^{-1}$  at  $5^\circ\text{C}$ ), the in situ feeding rate of *L. grandis* from about 800 m in the Eastern Tropical Pacific OMZ (Wishner et al. 1995: mean of  $0.0482\ \mu\text{gC copepod}^{-1}\ \text{d}^{-1}$ ), in situ oxygen consumption rates of mixed zooplankton from the somewhat suboxic Santa Catalina Basin at 1,300 m (K. Smith 1982:  $0.324\ \mu\text{l O}_2\ \text{mg wet weight}^{-1}\ \text{d}^{-1}$ ), and bulk zooplankton respiration rates based on the electron transfer system (ETS) method from 1,050 m in the Arabian Sea (Koppelman et al. 2000: 445 [October] and 106 [April]  $\mu\text{gC g wet weight}^{-1}\ \text{d}^{-1}$ ). These activity rates were converted to an individual carbon use rate ( $\text{mgC copepod}^{-1}\ \text{d}^{-1}$ ) using a respiratory quotient of 0.85 (Wishner 1980) and a copepod wet weight of 0.00754 g. This weight was 2/3 of the midweight of *Lucicutia bicornuta*, a similar but slightly larger species weighed by Thueson et al. (1998). Total *L. grandis* activity, calculated separately for each rate, was the product of its abundance (number  $\text{m}^{-2}$  for the appropriate depth range) and the individual carbon use rate.

Seasonal values at each station of primary production, organic carbon export at 100 m (thorium method), and sediment trap flux were obtained from Lee et al. (1998) and Honjo et al. (1999) and applied to the appropriate cruises (no values for S11 or N7). The sediment trap flux comparisons used to calculate the total midwater use of sinking organic carbon were the differences between the seasonally averaged organic carbon fluxes from the shallowest to the next deeper sediment trap at each station. Midwater traps in the JGOFS program were deployed at about 700–800 m and 900–2,300 m for the MK-7G trap series and at about 500 m and 900–1,500 m for the IRSC trap series. Only trap pairs showing a decrease in flux with depth were used. Flux differences for each pair were linearly interpolated to 1,000 m. The organic carbon flux decrease from the shallowest trap to 1,000 m was compared with the *Lucicutia* activity rates for the same approximate depth range (500–1,000 m or 700–1,000 m). Primary production and carbon export were compared to *Lucicutia* activity from 300 to 1,000 m.

Table 2. Numbers and stages of animals analyzed for gut contents. F = female, M = male, I = immature, not staged. Target depths are given for tow intervals except where the beginning or end depth differed by more than 10 m from the target depths.

Station	Season	Depth (m)	Animals
N7	Late NEM	1,000–1,100	3M
	Late SWM	800–900	3I
		1,000–1,100	1M
S15	Late SWM	700–800	2I (probably C5)
		800–900	2M, 4F
		900–1,000	1M
S11	Late SWM	500–600	4I (1C4, C4+C5)
		600–700	1I (C4 or C5)
		700–800	1F
S7	Late NEM	600–700	4F, 5M, 6C5, 3C4
	Spring IM	800–940	7F, 4M, 8C5
	Late SWM	400–500	3C3, 1 probable C3
		800–900	4F, 4M, 5C5
	Early NEM	700–800	4F, 4I (C3+C4)
S4	Late SWM	650–800	1F, 2M, 3I
S2	Late SWM	700–800	3F, 1M, 6I (C3, C4, and C5)

*Gut contents*—Animals with gut contents visible with a dissecting microscope were sexed and sorted at sea when possible. Stations, depths of collection, and numbers of animals analyzed are shown in Table 2; animals from the depth of maximum abundance (Table 3) were used when available.

Some of the immatures were not staged at the time they were processed for microscopy. In some cases where sizes had been recorded or a tow contained only one stage or predominantly one stage, it was possible to assign a stage or possible stages to the animals as noted in Table 2. Some animals were embedded at sea in LR Gold resin (Ted Pella); others were embedded in Spurr's resin (Spurr 1969) after the cruises. Details of the embedding procedures, sectioning for transmission electron microscopy (TEM) and rationale for using TEM are given in Gowing and Wishner (1998).

Analysis of gut contents was semiquantitative. A photomontage of an oblique or cross section of the midgut or hindgut was taken at 1,700–2,000 times magnification, and negatives were enlarged 1.6 times when printed. The gut area was also visually scanned at 17,000 times magnification to look for bacteria, virus-like particles, and small eukaryotic cells. Gut contents were classified into four categories, based on the probable origin of the food. Surface flux included uniform intact or pulverized diatom frustules, picoautotrophs uniformly dispersed throughout a matrix, and clusters of picoautotrophs sometimes in association with bacteria, all assumed to have sunk from surface waters. Deep-sea detritus was degraded material that was probably suspended at depth. This included "olive green material," a mixture of pulverized diatom frustules mixed in with amorphous material, sometimes with scattered gram-negative bacteria and metal-precipitating bacteria, "olive green bodies" (compact, non-cellular spheres [Fournier 1970; Silver and Alldredge 1981]), and heterogeneous amorphous, unidentifiable material. Deep-sea zooplankton included remains of metazoans such as crustacean cuticle, cnidarian nematocysts, uniform amor-

Table 3. Water column abundances from 300–1,000 m, maximum abundances, and the depth interval of the maximum abundance for each station and cruise. The depths (m) of the 0.07 and 0.1 ml L<sup>-1</sup> oxyclines for each tow are also shown. The asterisked abundance is from 400–1,000 m.

	Station	Abundance (m <sup>-2</sup> )	Max abundance (1,000 m <sup>-3</sup> )	Depth of max abundance	Depth of 0.07 ml L <sup>-1</sup>	Depth of 0.1 ml L <sup>-1</sup>
Late NEM	S15	114	548	500–600	none	none
	S11	318	653	400–500	510	590
	S7	238	849	600–700	621	674
	S4	223	461	400–500	208	392
	S2	265	1,108	900–1,000	938	1,006
SIM	S11	298	1,264	500–600	597	668
	S7	615	1,776	800–940	847	900
	S4	557	1,904	700–800	452	580
	S2	377	1,519	600–700	none	none
Late SWM	S15	90	200	500–600	349	357
	S11	516	3,019	600–700	697	732
	S7	121	568	800–900	753	831
	S4	300	731	650–800	546	728
	S2	*470	1,419	700–800	392	924
Early NEM	N7	445	2,211	800–1,000	1,033	1,076
	S15	91	407	400–500	none	none
	S11	558	3,374	500–600	653	720
	S7	394	2,255	700–800	773	803
	S4	360	1,206	800–900	617	773
	S2	289	1,087	700–800	none	826

phous material, often with nematocyst cell walls, that was probably tissue, and radiolarian silica with or without minipellets (Gowing and Silver 1985). Deep-sea aggregates included clusters of gram-negative bacteria and aggregates of bacteria-like bodies, or BLBs (Gowing and Wishner 1992), that were not present in combination with algal cells and thus appeared to have been produced at depth.

For each animal, the micrographs were taped together and the percentage of the area of the gut section occupied by various food categories was visually estimated. The presence of rare food items, such as microheterotrophs and virus-like particles, was recorded. The seemingly ideal but labor-intensive method of digitizing contents had been performed previously on 77 animals from the SIM and SWM from Sta. S7; gut contents of these animals were diverse, and few significant differences in types of food occurred (Gowing and Wishner 1998). Therefore, we felt that visual estimation would be adequate for detection of any large differences in food types and enable assessment of the whole section from each animal.

A total of 1,460 micrographs from 100 animals were analyzed. Gut contents of 37 animals from the SIM and late SWM from the depths of maximum abundance at Sta. S7 that had been previously analyzed quantitatively (Gowing and Wishner 1998) were reanalyzed as described here. Average percentages of food categories were compared for cruises, stations, and lifestages using Mann-Whitney *U* tests for comparison of two samples and Kruskal-Wallis tests for comparison of more than two samples. A Bonferroni adjustment was used to compensate for multiple testing (Miller 1981); a significance level of 0.01 was used.

## Results

*Overview of the oxygen environment*—The overall hydrography and oxygen distributions of the region are well described (Morrison et al. 1998, 1999). Stations S4, S7, and S11 were located near the southern edge of the highly suboxic ( $<0.1 \text{ ml L}^{-1}$ ) geographic area north of  $14^\circ\text{N}$  and east of  $59^\circ\text{E}$ , with 25–81% of the deeper water column (200–1,000 m) having oxygen levels below  $0.1 \text{ ml L}^{-1}$  during these tows (Wishner et al. 1998). Sta. N7 farther north was in the core of the most suboxic region, with 100% of the deeper water column less than  $0.1 \text{ ml L}^{-1}$ . The oligotrophic Sta. S15 was south of the suboxic region, and 0–3% of its deep water column was below  $0.1 \text{ ml L}^{-1}$ . The coastal Sta. S2 was usually west of the suboxic zone (only 3–7% suboxic water), except in January when suboxic water encompassed 94% of its deeper water column. Vertical profiles at the lower OMZ interface showed a gradual increase in oxygen with depth as well as much small-scale variability (Fig. 2). The temperature and salinity profiles showed only gradual trends at the lower OMZ interface, and there was no evidence of a density discontinuity. This contrasts with the sharper narrower gradients at the upper OMZ interface (the thermocline) and elsewhere at oxic-anoxic interfaces associated with sills or basins (Donaghay et al. 1992).

The temporal variability of oxygen values at any single depth and station in the Arabian Sea was large. For example,

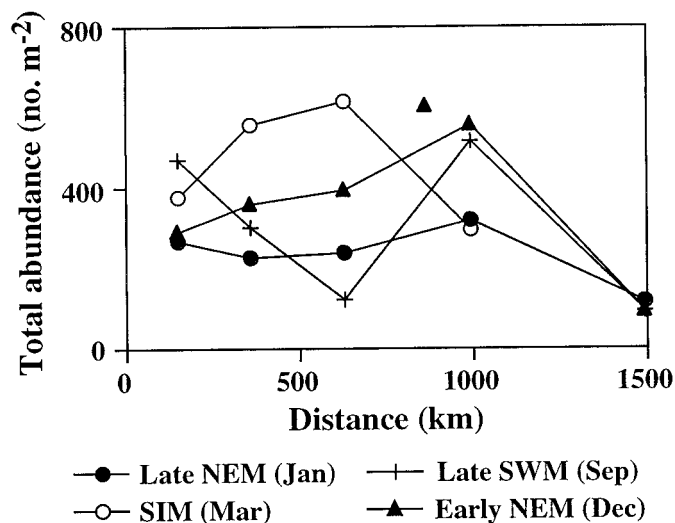


Fig. 3. The total abundance of *Lucicutia grandis* for the depth interval from 300 to 1,000 m. Each cruise is plotted separately (different symbols), and the values are positioned at the offshore distance of the station. Sta. S2 is on the left and Sta. S15 is on the right. Values are from night tows on the southern transect, except for a day tow at Sta. S11 during the SWM. The isolated triangle is from Sta. N7 on the northern transect.

the depths of the  $0.07$  and  $0.1 \text{ ml L}^{-1}$  oxyclines varied by several hundred m at the same station over time (Table 3). At a single depth, such as 700 m at S7, oxygen varied from  $0.04$  to  $0.14 \text{ ml L}^{-1}$  over time; similar variability occurred at the other OMZ stations. As described below, these oxygen values are within the range having strong biological significance to the animals living at the lower OMZ interface. Sta. S15 had consistently higher oxygen levels:  $0.37$ – $0.47 \text{ ml L}^{-1}$  at 700 m.

*Overall abundance and distribution*—In the Arabian Sea, *Lucicutia grandis* was a common member of the midwater copepod fauna, especially at stations within the center of the well-developed OMZ region (Fig. 3). The peak of its distribution geographically along the JGOFS southern transect was usually at the central Stations S4, S7, and S11, except during the SWM when S2 and S11 were peaks. N7 on the northern transect also was a location of high abundance. These stations generally corresponded to locations that had the strongest midwater oxygen gradients and the lowest midwater oxygen values ( $<0.05 \text{ ml L}^{-1}$ ) of the transect. Abundances at S15, overall and for each lifestage, were significantly lower than at other stations. S15 was the most oligotrophic station and farthest offshore, and oxygen remained relatively high in midwater compared to the other stations. *Lucicutia* abundance did not show a significant onshore (Stations S2, S4) versus offshore (other stations) difference, in contrast to total zooplankton biomass, which was significantly higher at the two onshore stations (Wishner et al. 1998). Thus, this copepod species appeared to be most strongly associated with the region of the strongest OMZ, rather than with the more eutrophic coastal upwelling zone or most oligotrophic offshore environment.

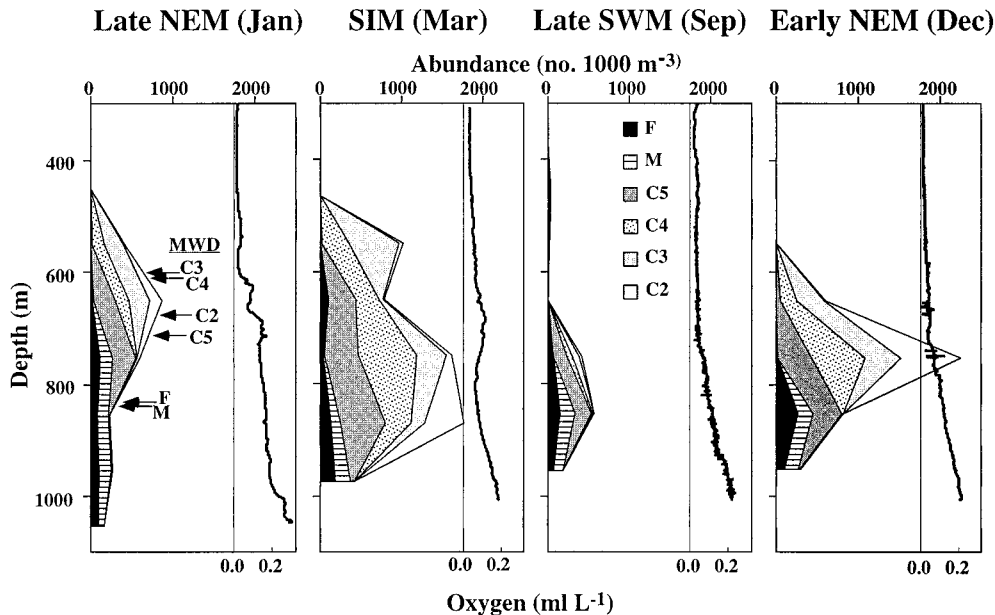


Fig. 4. Vertical distribution of *Lucicutia grandis* lifestages at Sta. S7 during the four seasons (night tows). The calibrated oxygen profiles from the same tows are also shown. The mean weighted depth (MWD) of each lifestage in that tow is indicated on the left graph as an example.

The vertical distribution of *L. grandis* was centered near the base of the OMZ where oxygen values started to increase with depth (Fig. 4). This species was a component of the subsurface zooplankton biomass peak, a characteristic feature of the Arabian Sea OMZ (Wishner et al. 1998). The depth of this feature and the peak abundance of *L. grandis* was generally between 600 and 1,000 m. However, the specific depth interval encompassing the peak abundance varied among tows, locations, and cruises, along with the depth range of the oxygen gradient (Table 3). In most tows, *L. grandis* abundance was sharply reduced (often no specimens) above 400 m, although rare individuals of various lifestages sometimes occurred in some shallower samples up to the surface. (Our lab analyzed only the samples from 300 m and deeper, but we were able to spot check a few shallow samples.) *L. grandis* specimens, primarily adult males and females, were also present in low abundance at the deepest depths (1,500–1,700 m) that were sampled only once or twice during the program.

Two tows highlighted additional distributional complexity. At Sta. N7 (Tow 403), where extreme suboxic water occurred to over 1,000 m, distributions were skewed deeper than elsewhere, and the subsurface biomass (and *L. grandis*) peaks probably extended below the 1,100 m tow depth (Fig. 5A) (Wishner et al. 1998). Tow 111 at Sta. S7 indicated that the *Lucicutia* abundance peak at depth was much narrower in vertical extent than was apparent in standard tows. This tow sampled 20-m thick layers from 600 to 700 m, compared to standard 100-m thick sampling strata. Abundance peaks of some lifestages were strongly associated with particular 20-m depth intervals (Fig. 5B).

Fresh samples from the subsurface zooplankton biomass peak were strikingly colored bright red (shrimp, copepods) and black (midwater fish), in contrast to the sparse pale de-

tritral mid-OMZ samples just above in the water column. In fresh samples, *L. grandis* was a large (4.6–4.8 mm adult length) bright reddish-orange copepod, easily visible, common, and indicative of this feature. At its depth of peak abundance in each tow (within the depth range 300–1,000 m), it represented a median of 12.8% (range 1.2–45.7%) of all calanoid copepods; its highest percentage in any sample was 89%. Over 93 other calanoid copepod species, some very rare, also occurred in the Arabian Sea subsurface biomass peak.

There was no evidence of diel vertical migration of *L. grandis* within the deeper water column (below 300 m), in contrast to the strong diel vertical migration observed in overall zooplankton and fish biomass in the upper 300 m of the water column (*see discussion*). *L. grandis* was abundant both day and night in the subsurface biomass peak near 600–1,000 m in the two day–night pairs examined (Fig. 6). Total water column abundances (300–1,000 m) were very similar day and night at this station when looked at in a regional context, although slightly higher in absolute numbers during the night than the day for each pair. The depth distribution of the different stages was slightly deeper during the night in one pair and during the day in the other pair. This depth variation was most probably related to the temporal variation in oxygen distributions described earlier rather than to any diel migration behavior of the plankton.

*Interactions with oxygen gradients*—Differences between tows and lifestages in the vertical distribution of *L. grandis* and interactions with the oxygen gradients were investigated using the mean weighted depth (MWD) of each lifestage from each tow (300–1,000 m) and its associated oxygen value. Figure 4 shows an example of the MWDs calculated for one of the tows. Adult males and females lived deepest,

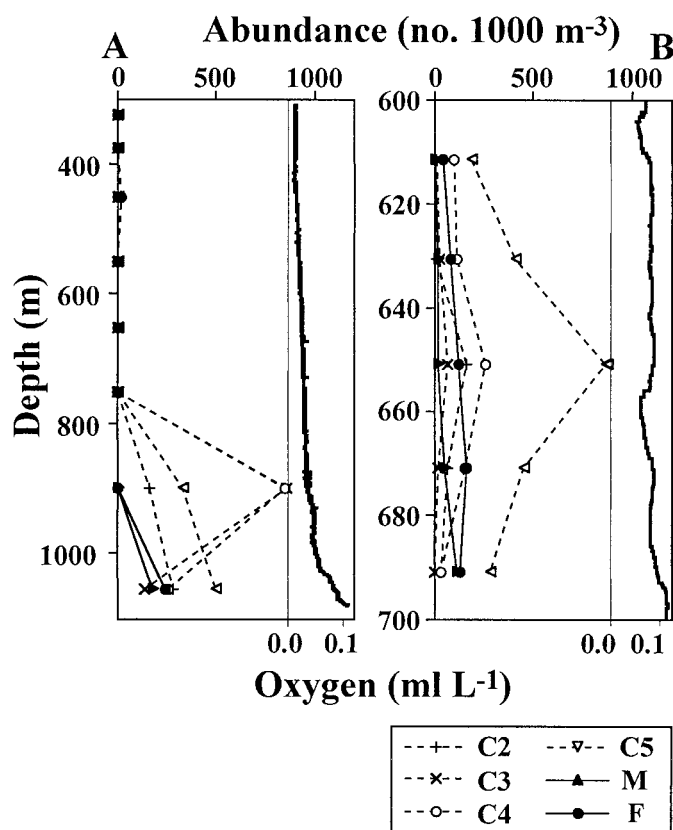


Fig. 5. Vertical distributions of *Lucicutia grandis* and the associated oxygen profiles in two special tows. Depth and abundance axes vary. (A) Distribution of the lifestages of *Lucicutia grandis* at Sta. N7 on the northern transect (Tow 403). This station was located in the region of the most vertically extensive suboxic OMZ. (B) Fine-scale distributions of each lifestage in the 600–700-m depth interval from Tow 111, which had sampling strata of 20 m within this interval.

whereas younger developmental stages occurred several 100 m shallower. Although the ordering of stages with depth was relatively consistent among tows, the specific MWDs for each lifestage varied over space and time. The vertical range in MWDs for all tows was almost 300 m for some lifestages.

The unique life history strategy of *L. grandis* relative to the oxygen gradients of the OMZ became apparent only when both the MWDs and associated oxygen concentrations were considered together (Fig. 7, Table 4). There was a clear progression with age of the depths and oxygen levels inhabited by the different developmental stages. Adult males and females lived and reproduced deepest where the oxygen was highest. They had mean MWDs of 863 and 825 m, respectively, with mean oxygen values at these depths of 0.149 and 0.133 ml L<sup>-1</sup> respectively. C2s (the youngest stage caught in abundance in the MOCNESS) rose up through the midwater column. C3s occurred shallowest (620 m) and at lowest oxygen concentrations (0.069 ml L<sup>-1</sup>). C4s and C5s sank back down to depth. The differences between lifestages in MWDs and oxygen concentrations were statistically significant.

Two outlying stations, S15 and N7, provided some inter-

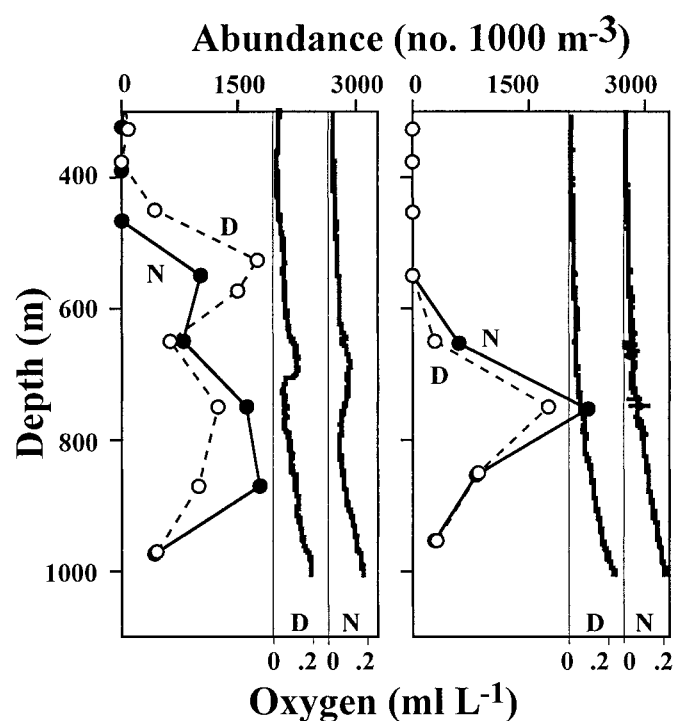


Fig. 6. Comparison between day (open circles) and night (closed circles) *Lucicutia grandis* vertical distributions and oxygen profiles. The left graph is from the SIM (March) and the right graph is from the early NEM (December) at Sta. S7.

esting contrasts, and tows from these stations were not included in the previous calculations for the following reasons. At Sta. S15, the midwater oxygen concentration was higher throughout the water column than at the other stations (Fig. 8). Mean oxygen concentrations at the MWDs for the three S15 tows for all stages were 0.412–0.480 ml L<sup>-1</sup>, significantly higher (by about 0.3–0.4 ml L<sup>-1</sup>) than at the other stations. However, the same relative depth distribution was maintained for the different stages, with the adults deepest and the C3s shallowest, although MWDs for the younger lifestages (C2–C4) were significantly shallower (by over 100 m) than at other stations. Despite the higher and less variable oxygen, S15 was apparently a less optimal habitat than elsewhere, because abundances of *L. grandis* were significantly lower here, as previously described.

At N7 most of the older individuals occurred in the deepest net (1,000–1,100 m) (Fig. 5A). When MWDs were calculated to 1,100 m, females at N7 were centered at 1,038 m with oxygen of 0.074 ml L<sup>-1</sup> and males at 1,050 m with oxygen of 0.081 ml L<sup>-1</sup>, but it is likely that most of their population was actually deeper and at higher oxygen levels. Younger lifestages at N7 were centered from 919 to 992 m (C3s and C4s shallowest) and at oxygen concentrations of 0.040–0.050 ml L<sup>-1</sup>.

*Seasonal and spatial development patterns*—*L. grandis* had a seasonal and spatial pattern of reproduction and development that was keyed to the monsoon cycle, especially in its central OMZ habitat. C2s, the youngest stage consistently seen and thus considered an indicator of recent repro-

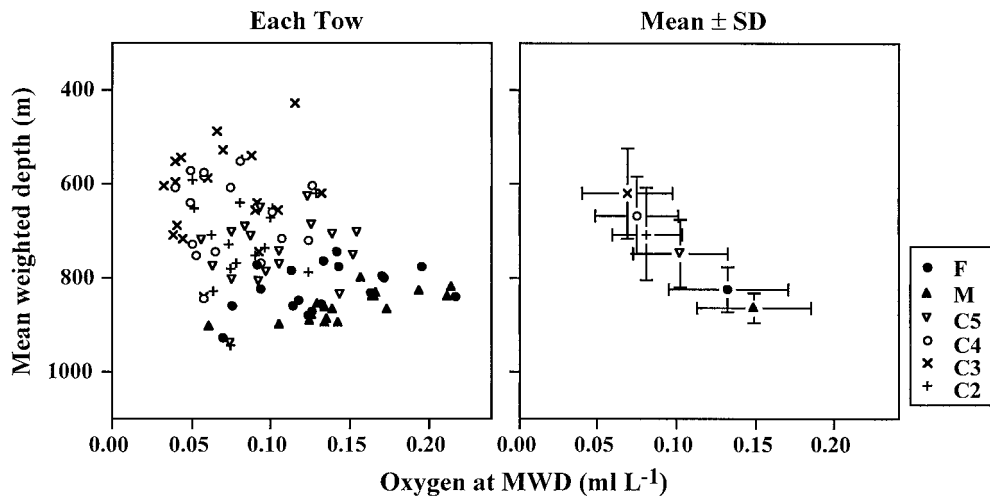


Fig. 7. The mean weighted depths (MWD) of each lifestage (different symbols) versus the oxygen value at that MWD. The left graph shows values for each lifestage and oxygen profile from each tow analyzed for abundance. The right graph shows the means of the depths and oxygen values ( $\pm$  standard deviations) for each lifestage. Values from Stations S15 and N7 are not included for reasons described in the text.

ductive activity, were highest in abundance and proportion (of total *L. grandis* individuals) at Stations S7 and S11, especially in March and December (Fig. 9). C2s increased from the late NEM (January) to the SIM (March), decreased from March to the late SWM (August), then increased again to the early NEM (December). Thus, January and August (the monsoon periods) were times of relatively low C2 abundance, whereas March and December (several months post-monsoon) were times of relatively high C2 abundance at most stations (Fig. 9). Differences in abundances and proportions among stations but not cruises were significant for C2s. However, there was a significant difference among cruises in the rate of change of C2 abundance with time, calculated for each station based on the actual sequential sampling dates at that station.

The C4 and C5 lifestages appeared to be “holding” stages, with final development through these stages to adults probably related to food availability. The abundance and proportion of C5s were significantly higher at the eutrophic

onshore stations (S2, S4) versus offshore (Fig. 9), suggesting that development past the C4 stage was facilitated by the higher food levels onshore. This was the only lifestage showing this significant spatial gradient. The C4/C5 ratio was lowest at S4, a eutrophic station, and highest at S15, the most oligotrophic station. The C5/F ratio was lowest at S15 and highest at the onshore stations. These patterns corresponded to the C5 abundance trends. Differences among stations were significant for these ratios. C5 and female abundances and rates of change at each station were significantly different among cruises, with March the time of peak abundance. At S15, abundances of all lifestages were significantly less than elsewhere (Fig. 9), but lifestage proportions were similar. Thus, although S15 appeared to be a less favorable habitat for *L. grandis* based on abundances, reproduction and development did occur there.

Significant differences among lifestage ratios (Table 4) suggested that developmental rates and residence times varied among successive stages such that some accumulated in

Table 4. Size, mean weighted depth (MWD), and oxygen concentration at the MWD for the different lifestages of *Lucicutia grandis*. Lifestage ratios are also listed. Values in parentheses are standard deviations and counts. All counts not shown are 18. Size measurements of C1s were provided by F. Ferrari.

	Lifestage						
	C1	C2	C3	C4	C5	F	M
Size (mm)	1.21	1.93	2.4	3.1	3.86	4.81	4.57
(SD, n)	(0.07, 7)	(0.12, 26)	(0.13, 36)	(0.16, 47)	(0.20, 51)	(0.34, 45)	(0.20, 41)
MWD (m)	ND	702	620	666	747	825	863
(SD)	ND	(100)	(100)	(82)	(74)	(49)	(32)
Ox at MWD (ml L <sup>-1</sup> )	ND	0.081	0.069	0.075	0.103	0.133	0.149
(SD, n)	ND	(0.023, 17)	(0.030)	(0.027, 17)	(0.031)	(0.04)	(0.037)
Lifestage ratio		C2/C3	C3/C4	C4/C5	C5/F	C5/M	F/M
Ratio value		0.4	0.94	1.08	2.49	3.11	1.13
(SD)		(0.28)	(0.41)	(0.66)	(0.91)	(3.15)	(0.61)

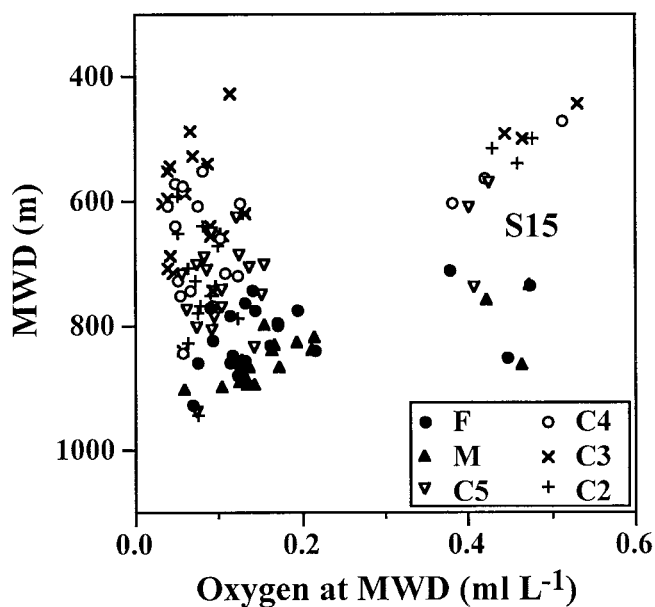


Fig. 8. Mean weighted depths (MWD) and associated oxygen values for each life stage for tows from Sta. S15 (right cluster of points) compared to the other stations (left cluster). N7 is not included.

the plankton more than others. Mean values ranged from 0.4 for C2/C3, about 1 for C3/C4 and C4/C5, and up to 2.5 for C5/female (Fig. 10). This is further evidence suggesting that C2s were relatively more ephemeral, and C4s and C5s more persistent, than other immature stages.

Both adult sexes were present and active year round. The female:male ratio was about 1 (range 0.6–3.4) (Table 4) and did not vary significantly among stations or cruises. It is likely, however, that much of the adult population was living

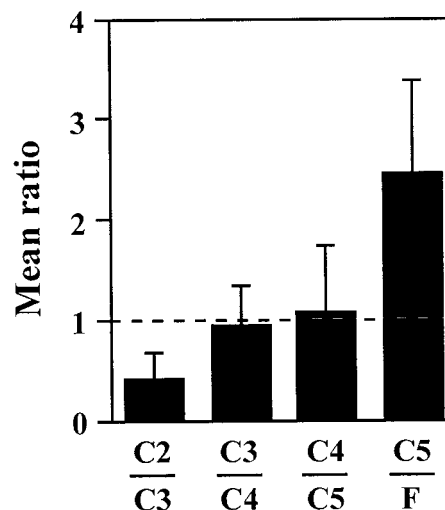


Fig. 10. Ratios between different successive life stages. Values are means (+ standard deviations) ( $n = 18$ ) and do not include data from Stations S15 or N7.

deeper than our standard sampling regime to 1,000 m, because adults were sometimes abundant in the few deeper samples taken. This was particularly obvious at N7 (Fig. 5A).

The timing of development and reproduction relative to the monsoon cycle is illustrated in Fig. 11, which shows the proportions of each life stage during each cruise at a station (S7) near the center of the species' distribution. During the late SWM in September, older stages were dominant. A major reproductive event occurred during or shortly after the SWM, resulting in the appearance of younger stages (C2s) a few months later (December). These stages grew and developed into older stages during the NEM in January. Re-

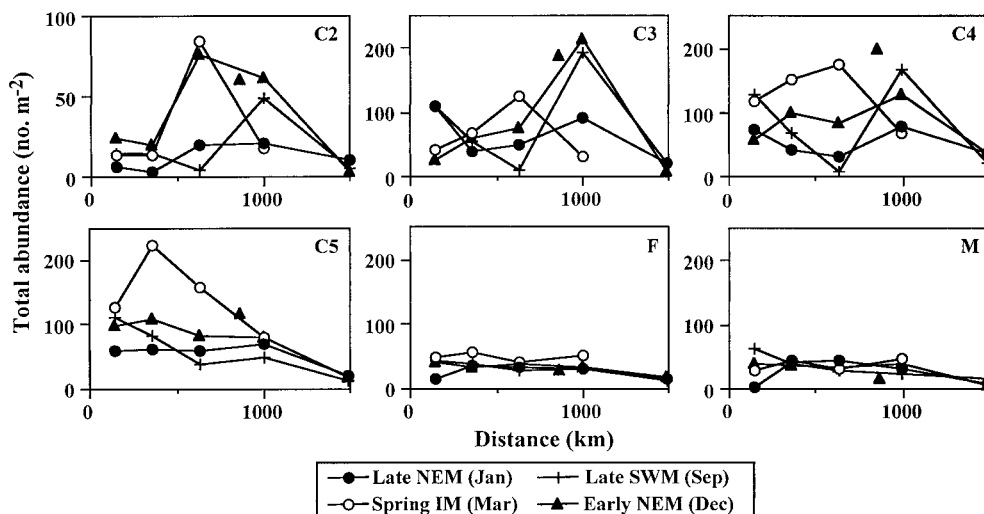


Fig. 9. Total abundance of the different life stages of *Lucicutia grandis* (300–1,000 m). Each cruise is plotted separately (different symbols), and the values are positioned at the offshore distance of the station (Table 1). Station S2 is on the left and Sta. S15 is on the right. Values are from night tows on the southern transect, except for a day tow at Sta. S11 during the SWM. The isolated triangle is from Sta. N7 on the northern transect. Abundance axes differ.

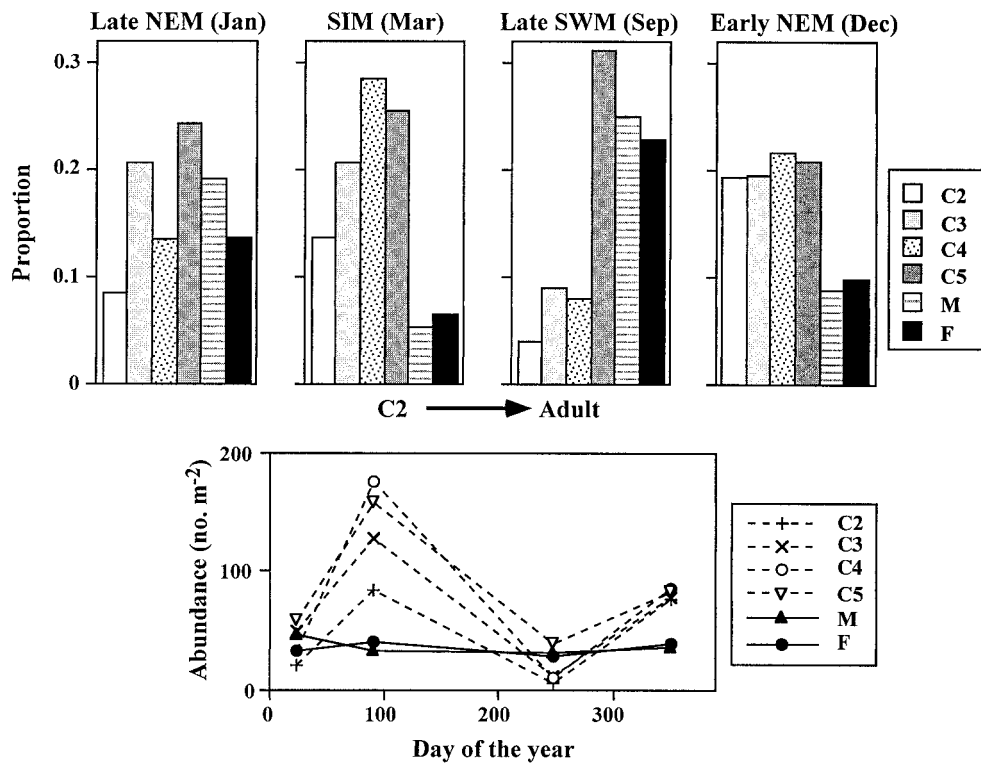


Fig. 11. Top: Proportion of the different lifestages from C2 to adult males and females (different patterns for each stage) at Sta. S7 during each of the four cruises. Bottom: Abundance (300–1,000 m) of each lifestage with time at Sta. S7.

production also occurred during or just after the NEM, resulting in the appearance of younger stages (C2s) a few months later in March. During the SIM (March), the immature stages developed and accumulated as C4s and C5s (Figs. 9, 11). A background level of continuous reproduction occurred all year, evidenced by the presence of C2s, females with spermatophores, and adults of both sexes during all cruises.

*Gut contents overview*—Surface flux, deep-sea detrital material, and zooplankton remains dominated gut contents of most animals of all lifestages from most stations examined, indicating that adults, C5, C4, and C3 stages are omnivorous generalists that do not diapause. The amount of deep-sea aggregate material was generally less than that of the other categories. Amounts of the different food categories were highly variable among individual animals within samples. There were few significant differences among food types within seasons and at stations and no significant differences in food categories among lifestages for any sample. Microheterotrophic cells and virus-like particles were observed sporadically and always in low abundance and will not be considered further.

*Station N7*—At N7 gut contents of the three adults from the late NEM contained mean percentages of 70, 18, 12, and 0 of surface material, deep-sea detritus, zooplankton remains, and deep-sea aggregates, respectively. The surface material was pulverized diatom frustules. The zooplankton

remains were predominantly cnidarian tissue. During the late SWM mean percentages of gut contents of the four animals were 3% surface material, 90% deep-sea detrital material, 6% zooplankton remains, and 1% deep-sea aggregates. Zooplankton material was predominantly cuticle. Differences among food types were not significant either time. Seasonal differences were not significant for any food type.

*Southern transect during the late SWM*—No significant differences in food types occurred between adults and immatures at any station along the southern transect during the late SWM (Fig. 12A). Adults and immatures were combined at each station for comparisons of amounts of food types. At S15 mean percentages of surface flux, deep-sea detritus, and zooplankton were similar in animals from 700 to 1,000 m. Although deep-sea aggregate material was less abundant than the other food categories, the differences among food categories were not significant. Surface flux was diatom silica. Zooplankton remains were predominantly cuticle and tissue-like material. Percentages of the different food categories did not differ significantly between S15 vs. all the other southern transect stations combined.

At S11 surface flux was predominantly diatom silica; one animal contained coccoliths, and a few animals contained a few picoautotrophs. Zooplankton remains were primarily cuticle. Deep-sea aggregate material occurred in two animals. One contained numerous BLBs, and one contained a large area of gram-negative bacteria in an amorphous matrix. Per-

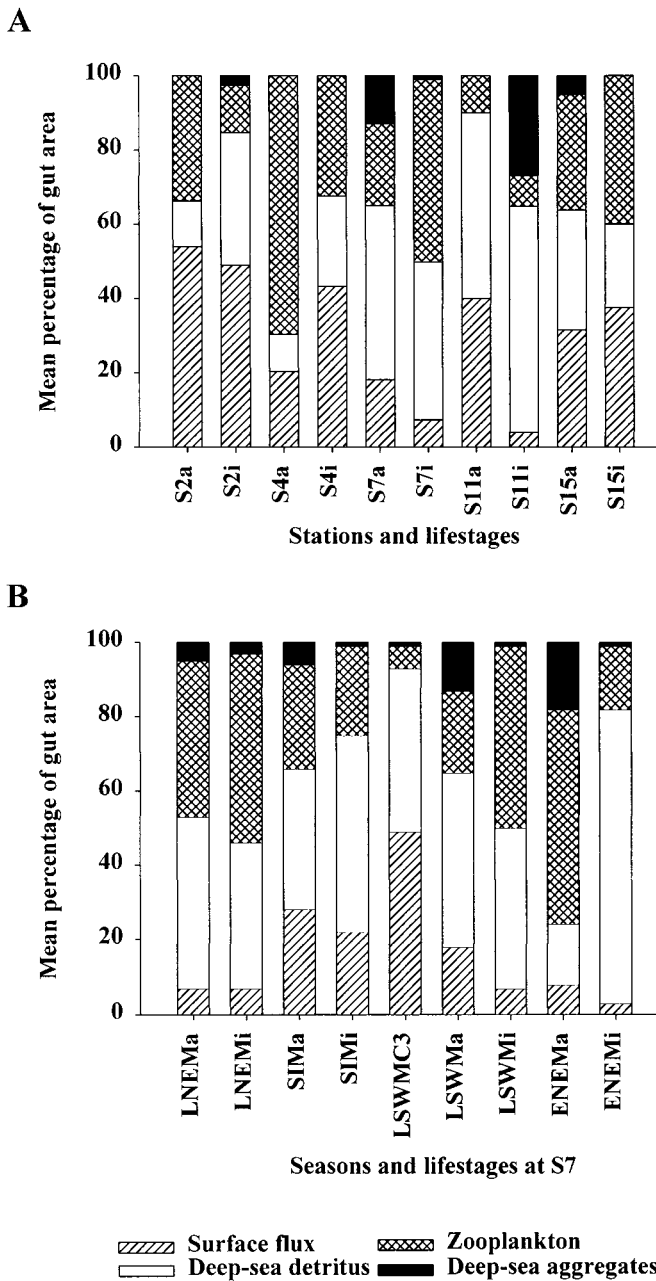


Fig. 12. Mean percentages of the various food types in gut sections from adults (a) and immatures (i). The number of animals is listed in Table 2. (A) Stations along the southern transect from on-shore to offshore. (B) Seasons at Sta. S7. C3 = lifestage C3.

centages of the different food types did not differ significantly.

At S7 surface flux material was generally siliceous, but four animals contained up to 14 picoautotrophs. Zooplankton remains were predominantly cuticle. Deep-sea aggregate material was BLBs. Detrital material and zooplankton remains in guts were significantly more abundant than aggregate material.

At S4 surface flux was predominantly picoautotrophs in a matrix in 2 animals and siliceous material in one animal.

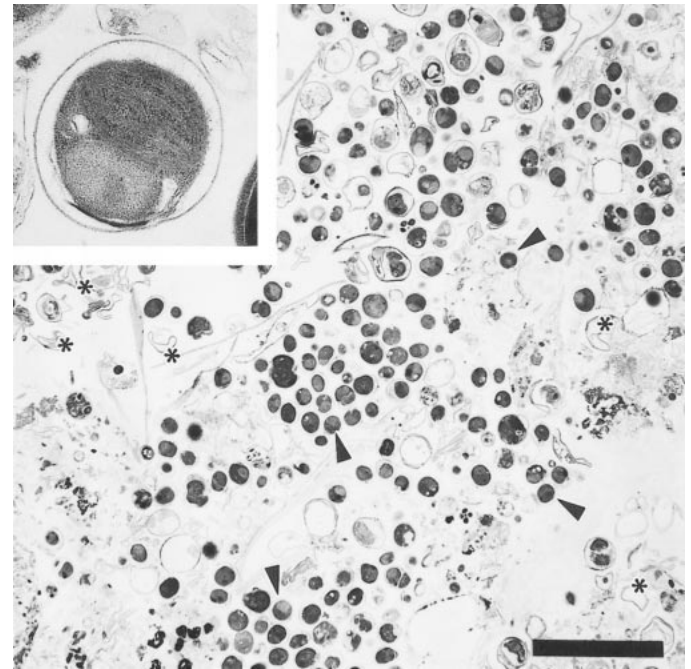


Fig. 13. Transmission electron micrograph of gut contents of a female from Sta. S2 during the late SWM showing numerous picoautotrophs (arrows) and a few remnants of cell walls (asterisks). Scale bar = 10  $\mu$ m. Inset: higher magnification of one of the *Nannochloropsis*-like picoautotrophs. Cell diameter inside cell wall = 1.2  $\mu$ m.

From 0 to 52 picoautotrophs were observed per gut section. Zooplankton remains were predominantly cuticle and tissue-like material. Deep-sea detrital material and zooplankton remains were significantly more abundant than aggregate material in guts.

At S2, in contrast to all the other samples examined, large numbers of intact and cell walls of digested picoeukaryotic cells occurred in gut contents of the 10 animals (Fig. 13). Sections generally contained over 50 cells and remnants; one animal contained over 800 cells in the section. Eight of the animals appeared to have consumed this material as surface flux. The picoeukaryotes in the other two animals occurred in minipellets, indicating that a phaeodarian radiolarian or its phaeodium had been consumed. Zooplankton remains were cuticle and radiolarian minipellets. Deep-sea aggregate material as BLBs occurred in one animal. Surface material, deep-sea detritus, and zooplankton remains were all significantly more abundant than deep-sea aggregate material.

Deep-sea aggregate material was significantly more abundant in guts from offshore stations (S15, S11, and S7) combined than in guts from onshore stations (S2 and S4) combined. Abundance of surface flux material, deep-sea detrital material, and zooplankton remains did not differ significantly between onshore and offshore stations.

*Seasonality at S7*—A summary of the mean percentages of the food categories for animals collected during different seasons is shown in Fig. 12B. Surface flux was predominantly diatom silica except for a few animals during the late NEM and four animals during the late SWM that also con-

tained clusters of picoautotrophs. Zooplankton remains were predominantly crustacean cuticle in all seasons. Deep-sea aggregate material was usually BLBs. During the late NEM detrital and zooplankton remains were significantly more abundant than surface flux and deep-sea aggregate material. During the SIM surface flux, deep-sea detrital material and zooplankton remains were all significantly more abundant than deep-sea aggregate material. During the late SWM, as noted above, deep-sea detrital material and zooplankton remains were more abundant than deep-sea aggregate material. During the early NEM no significant differences in abundance of food types occurred. Overall, there were no seasonal differences in food types for adults or for immatures.

## Discussion

The copepod *Lucicutia grandis* proved to be a good indicator species for the lower OMZ interface, and its ecology supported the hypothesis of high biological activity at this boundary. Its geographic distribution within the Arabian Sea was centered in the region of the strongest OMZ (Morrison et al. 1999), rather than the more eutrophic coastal upwelling zone or oligotrophic offshore environment. Its vertical distribution was most strongly associated with the steep oxygen gradient from about 0.07 to 0.15 ml L<sup>-1</sup> at the base of the OMZ, rather than with a particular depth. It was a component of the zooplankton biomass peak at the base of the OMZ (Wishner et al. 1998). Furthermore, the *L. grandis* population was an active, rather than a diapausing or resting, assemblage. Lifestages from C1 to adult males and females were present in the samples, and reproductive activity was evident from the occurrence of spermatophores during all seasons and seasonal peaks of abundance of younger lifestages. All lifestages examined for gut content analysis (C3 to adult males and females) had fed on a variety of food sources, further indicating an active population.

In the Eastern Tropical Pacific, *L. grandis* showed a similar distribution pattern and ecology, being most abundant from 700 to 1,000 m at the lower OMZ interface (Saltzman and Wishner 1997b) and feeding actively (Gowing and Wishner 1992; Wishner et al. 1995). Although the Eastern Tropical Pacific variant shows some morphological differences compared to the Arabian Sea form (Ferrari, pers. comm.), this species (or species group) seems to have a worldwide association with the steep oxygen gradients at the lower interface of oceanic OMZs. Its distribution may not be limited to this habitat, however, because it has been reported elsewhere (Hülsemann 1966). Taxonomic studies are needed to differentiate morphotypes and refine their precise distributional patterns and environmental associations.

In the Arabian Sea at Sta. S7, the annual cycle of lifestage abundance and proportion suggested that monsoon events triggered the final maturation of C4s and C5s to adults, their subsequent mating, and the development of the eggs and nauplii to young copepodites. The completion of these developmental processes apparently required about 1–3 months. The accumulation of C4s and C5s in March prior to the SWM (June–September) suggested that these stages were long lived and that maturation was delayed until suf-

ficient extra energy was available at these depths to support reproduction.

The required energetic input was probably the high vertical flux of sedimenting material associated with the monsoons. The flux measured in the JGOFS sediment trap at 821 m at S7 was especially high toward the end of the SWM (18–27 August) (Honjo et al. 1999). This trap subsequently clogged, but high fluxes continued to be recorded in deeper traps through mid-September. Smaller flux peaks in the 821-m trap occurred 15–23 December 1994, 1–10 March 1995, and 7–15 July 1995. Peak C2 abundances in the net tows occurred from 26 to 117 d after the midpoint of these flux events. Although the zooplankton sampling frequency was too coarse to resolve a tighter connection, the occurrence of peak C2 abundances from one to several months after each of the monsoon seasons (and other flux events) suggested that many individuals in the copepod population could amass sufficient energetic resources in a short period of time to continue their development and reproduce. Flux events between monsoon seasons, as well as the low level of continuous flux, could contribute the energy necessary for the year-round reproduction observed.

The episodic pattern of reproduction was not as obvious at other stations, where more continuous reproduction and development occurred. Perhaps the exact timing of the sampling at each station on each cruise relative to the flux and reproductive events at that location missed some of the peaks of the short-duration younger stages. At the oligotrophic station, weaker physical forcing would have provided less of a seasonal trigger.

An increase in feeding on surface flux material at the critical times was not apparent, however, because of the complex feeding ecology of *Lucicutia*. At S7, no seasonal differences in food types occurred for either adults or immatures, and surface flux material was more abundant in gut contents only in the SIM samples. Along the southern transect during the late SWM, S2 was the only station where surface flux material was more abundant than another food type (deep-sea aggregates).

There are three possible reasons for the lack of a distinct seasonal increase in surface flux material in guts. The first reason is related to sampling. Compared to the time scales of development of *Lucicutia* (months) and of sediment trap collection of sinking material (weeks), gut contents are a snapshot of gut passage of food (tens of minutes). Furthermore, our gut content analysis would not detect differences in nutritional quality of the different types of food. It is likely that “fresh” surface flux material would be more nutritious than deep-sea detrital material and would also require less energy to capture than zooplankton prey.

The second reason is related to *Lucicutia*'s feeding strategy. Gut contents were highly variable among and within individuals. In previous detailed analyses of late SWM and SIM animals, two areas of one individual's gut could be as different as guts from two individuals from the same sample (Gowing and Wishner 1998). This variability is probably not a result of long gut passage time because in situ feeding experiments on *L. grandis* in the Pacific suggested short gut passage times (Wishner et al. 1995; Gowing and Wishner 1998). *Lucicutia* populations are trophically versatile, oc-

cupying at least four trophic levels (herbivore, first and/or second level consumer [carnivore], detritivore, and microbivore on bacterial aggregates). They thus cannot be viewed as a simple "flux feeder" (sensu Jackson 1993); modeling (Burd and Jackson 1999) their feeding impact would be complicated. They feed on all the major particulate food sources available in their habitat and appear to be generalists even as immatures. No differences in food types occurred between immatures and adults for stages C3 and older in any of the samples. This generalism makes sense for feeding in the food-limited deep sea, but means that detection of subtle relative differences in food types requires a larger sample size.

The third reason is that an increase in surface flux material would probably also increase the other food types available to *Lucicutia*, making it difficult to detect a significant seasonal shift in food types. In addition to being available for direct consumption by *Lucicutia*, the surface flux material can be transformed into smaller sized suspended detrital material at depth during in situ zooplankton feeding and as a result of bacterial remineralization and abiotic dissolution and fragmentation. Rates of these processes are not known for the deep Arabian Sea, but could be higher during times of increased particle flux. Bacterial productivity in the upper 200 m showed a small increase during the SWM (Ducklow et al. in press.) Zooplankton consumed by *Lucicutia* included crustaceans and cnidarians. Biomass of total zooplankton in the 200–1,000- $\mu\text{m}$  size class (likely prey size) at the depth of maximum *Lucicutia* abundance was highest in the late NEM and lowest in the SIM at S7 (Wishner/Gowing files, JGOFS data base), suggesting the possibility of a relationship with surface flux. Abundance of deep-sea aggregate material could also be related to surface flux material. We believe that these aggregates originate within the OMZ or at one of its interfaces (see Gowing and Wishner [1998] for a detailed discussion of the aggregates). Their production could be fueled by components of the particulate flux. Although most of the siliceous material and bulk matter comprising the flux peaks sank rapidly to the deepest traps near the sea floor (Honjo et al. 1999), some of the labile components showed variability in midwater traps, suggesting possible use and processing by midwater organisms (Wakeham and Lee pers. comm.). Similar high microbiological activity and alteration of labile flux components occurred at the oxic–anoxic interface in the Black Sea (Karl and Knauer 1991; Wakeham and Beier 1991).

*L. grandis* was responsible for a small but measurable portion of the organic carbon use with depth. The carbon budget suggested that the activity of the *L. grandis* population alone consumed about  $0.05 \pm 0.03\%$  ( $n = 45$ , median = 0.05) of the primary production and  $1.4 \pm 1.9\%$  ( $n = 33$ , median = 0.7) of the organic carbon exported below 100 m. From 0.01 to 0.2% of the surface organic carbon production reached the sea floor (1,435–4,426 m) at these stations (Lee et al. 1998). Therefore, the *L. grandis* use alone was equivalent to the organic carbon input available to fuel the entire deep-sea benthic community. These means and medians exclude values calculated with the feeding rates of Wishner et al. (1995), which were 1–2 orders of magnitude less. Those feeding studies, using algal particles as detrital mimics

and tracers, probably measured only a component of the total range of feeding possibilities for these animals.

The apparent use by *L. grandis* of midwater sinking material as measured by the trap fluxes was much more variable. A median of 31% (mean  $54 \pm 60\%$ , range 4–239%,  $n = 27$ ) of the sinking organic carbon flux decrease in the midwater depths inhabited by *Lucicutia* could be accounted for by its estimated rate of carbon use. This high variability was due primarily to the variability in the flux measurements at midwater depths. Some midwater trap series, for example, did not record the expected decrease in flux with depth and even showed flux increases with depth (these pairs were not used in our calculation). This was attributed to particulate input via lateral advection in midwater or differential trapping efficiency related to currents at different depths (Lee et al. 1998). Alternatively, the biological activities of the midwater zooplankton, such as the ingestion and repackaging of detritus, prey, or in situ bacterial producers, could affect the types of sinking particles and provide an in situ source for new particles caught in deeper sediment traps (Karl and Knauer 1984; Wakeham et al. 1984). Regardless of the mechanism involved, the injection of new material in midwater would decrease the apparent loss in carbon with depth recorded in sediment traps and increase the apparent carbon use by the zooplankton. This could account for the surprisingly high and variable rates of midwater flux use by this species. This budget exercise highlighted the need for more research on midwater plankton–particle dynamics.

*Lucicutia's* gut contents can be used to detect and infer export of aggregates from surface waters. Surface assemblages of phytoplankton and microzooplankton varied seasonally and geographically, suggesting that the epipelagic microbial food web structure and its effect on carbon flux also varied (Garrison et al. 2000). As a generalist omnivore, *Lucicutia's* gut contents should monitor sinking surface material. Features relevant to the flux potential of SWM phytoplankton assemblages along the southern transect included (a) high abundances of the picoeukaryote *Prochlorococcus* at S15, (b) *Phaeocystis* colonies and mucus sheets from disrupted colonies, pennate diatom aggregates, and senescent diatoms at S11, (c) picoautotrophs and some diatoms, pennate aggregates and *Phaeocystis* colonies at S7, (d) diatoms and low *Phaeocystis* colonial biomass at S4, and (e) the highest diatom and picoeukaryote biomass along the transect at S2 (Campbell et al. 1998; Garrison et al. 1998, 2000). Diatoms, *Phaeocystis* colonies and mucus sheets, and diatom aggregates are large and dense enough to sink individually, whereas the picoautotrophs require an aggregating mechanism for export. Aggregating mechanisms include attachment of cells to flocs or extracellular sticky material produced by phytoplankton and concentration on zooplankton expendable feeding structures and into fecal pellets (reviewed by Alldredge and Silver 1988; see Kaltenböck and Herndl 1992; Pfannkuche and Lochte 1993; Lampitt et al. 1993; Alldredge and Jackson 1995; Wassmann 1998).

At S15, the lack of *Prochlorococcus* and scarcity of other picoeukaryotes in *Lucicutia* guts, despite their presence in surface waters, suggested the lack of an aggregation mechanism at this oligotrophic station. Epipelagic zooplankton abundances were lowest at S15 (Smith et al. 1998b; Wishner

et al. 1998), implying a limited influence of zooplankton feeding on particle export here. At S11, *Phaeocystis* colony mucus sheets could have provided a matrix for sinking aggregates that might scavenge picoplankton. However, only a few algal-bacterial clusters were observed in guts, indicating that aggregates were not commonly ingested. At S7, although diatom biomass was less than at S11 (Garrison et al. 1998), high silica fluxes in the trap at 821 m (Honjo et al. 1999) indicated that siliceous particulate material transited the zone of maximum *Lucicutia* abundance, and diatom silica occurred in *Lucicutia* guts. The presence of picoplankton in guts indicated that aggregation mechanisms probably associated with zooplankton feeding were also present here.

At S2, the most coastal and eutrophic station, the abundant picoeukaryotes and relatively low amount of silica in *Lucicutia* gut contents sharply contrasted with the other stations. The high abundance and diversity of both phytoplankton and zooplankton assemblages at this station would provide a variety of mechanisms for aggregate formation and subsequent delivery of the picoeukaryotes to depth. Massive sinking of picoplankton in aggregates of unknown origin was recently reported from 120 to 550 m in the Subtropical Front off New Zealand (Waite et al. 2000). In contrast to the Arabian Sea, picoprokaryotes, rather than picoeukaryotes, dominated the aggregates of the Pacific Ocean. Waite et al. (2000) also documented picoplankton within flagellate grazers in the aggregates and hypothesized that the reduction in picoplankton numbers with depth was due to heterotrophy within the aggregates. Our methods cannot distinguish ingestion of digested cell walls from digestion of cells by the copepods. The ultrastructural deterioration of the cells in guts is consistent with digestion by flagellates and copepods and also with deterioration of surface algae as they sink. The high numbers of picoeukaryotes in the hindgut of *Lucicutia* suggested that some of the cells would still have cytoplasm after incorporation into fecal pellets. *Lucicutia* populations thus repackage a portion of the organic carbon in aggregates into compact, probably faster sinking, fecal pellets at this station. This contrasts with fecal pellets produced from feeding on diatoms; diatom frustules and pieces in *Lucicutia* guts were always devoid of cytoplasm and thus repackaging would not affect carbon flux. Finally, the finding of abundant picoeukaryotes in *Lucicutia* guts at a station with the highest epipelagic diatom abundance and a high midwater silica flux raises the question of whether *Lucicutia* was feeding preferentially on aggregates containing picoplankton. Knowledge of the composition and abundance of aggregates present in *Lucicutia*'s habitat would be necessary to answer this question.

The environmental oxygen levels where this copepod (and the zooplankton community of the subsurface biomass peak) dwells ( $0.07\text{--}0.15\text{ ml L}^{-1}$ ) are among the lowest reported for active metazoans permanently living in suboxic waters. However, diapausing (inactive) stages of copepods or temporary residents such as vertical migrators are common in OMZs. For example, daily migrators from the upper water column of the Arabian Sea, averaging 10–19% of the total 0–1,000-m biomass in the same tows discussed in this paper (Wishner et al. 1998) and including mesopelagic fish and zooplankton, temporarily moved into the upper OMZ during

the day (200–400 m) (also see Herring et al. 1998; Smith et al. 1998b; Morrison et al. 1999; Luo et al. 2000). However, net tows that caught more animals at depth during the day than at the surface during the night suggested that these vertical migrators were relatively inactive while in the OMZ (Wishner et al. 1998). Diel vertical migration of some species into suboxic water also occurs in the Eastern Tropical Pacific, but the migration of other species is inhibited, and they remain confined to surface waters (Brinton 1979; Judkins 1980; Sameoto 1986; Saltzman and Wishner 1997b). Ontogenetic migrators, such as the copepod *Calanoides carinatus* in the Arabian Sea, diapause within and below the OMZ but feed, grow, and reproduce in well-oxygenated surface waters (S. Smith 1982; Smith et al. 1998b; Wishner unpubl. data).

In stable suboxic conditions, whether shallow or deep, some organisms appear able to live at much lower oxygen levels than species subject to episodic hypoxic events. Examples of layers at oxic–anoxic interfaces include diapausing *Calanus pacificus* in the Santa Barbara Basin (Alldredge et al. 1984,  $0.2\text{ ml L}^{-1}$  oxygen), high zooplankton metabolic activity in British Columbian fjords (Devol 1981,  $0.11\text{ ml L}^{-1}$ ), and zooplankton in the Black Sea (Vinogradov et al. 1986,  $0.5\text{--}1\text{ ml L}^{-1}$ ). Protozoan and microbial layers at oxic–anoxic boundaries in deep and shallow, pelagic and benthic, marine and freshwater environments are also well known (Vinogradov et al. 1986; Fenchel et al. 1990; Donaghay et al. 1992; Fenchel and Finlay 1995 and references therein). In the benthos within oceanic OMZs, large populations of nematodes, polychaetes, and occasional other taxa occur at oxygen levels of  $0.1\text{ ml L}^{-1}$  or less (Levin et al. 1991, 2000). In contrast, during shallow water coastal hypoxic events, the oxygen levels deleterious to copepods are often much higher, around  $1\text{--}2\text{ ml L}^{-1}$  (Roman et al. 1993; Stalder and Marcus 1997; Marcus in press). Coastal species may die at oxygen concentrations well within the survivability of OMZ copepods. In Chesapeake Bay,  $0.28\text{ ml L}^{-1}$  was considered anoxic and  $2.8\text{--}0.28\text{ ml L}^{-1}$  hypoxic for demersal fauna (Pihl et al. 1991). Community effects of episodic hypoxia in coastal ecosystems involve complex predator–prey interactions, as well as species-specific physiology (Breitburg et al. 1999).

In the ocean, most crustaceans adapted to life in OMZs apparently live aerobically and depend on specialized physiological and morphological adaptations to increase their effectiveness at removing oxygen from water (Childress and Seibel 1998). These adaptations include enhanced ventilatory capability, large gill surfaces, short diffusion distances, and respiratory proteins with very high oxygen affinity. Some vertical migrators, however, including some fish and the copepod *Gaussia princeps*, may use anaerobic metabolic pathways while temporarily in the OMZ and aerobic metabolism when in more oxygenated water (Childress 1977). In contrast, coastal crustaceans or demersal fish exposed to episodic hypoxic situations tend to avoid this water behaviorally by swimming away or reducing vertical excursions (Pihl et al. 1991; review by Marcus in press). When exposure is unavoidable, fecundity may be reduced and egg development times lengthened (Uye and Fleminger 1976; Lutz et al. 1994; Marcus and Lutz 1994). Some daphniids in lakes in-

crease their hemoglobin concentrations (Weider and Lampert 1985).

It is not obvious which of these mechanisms is employed by *Lucicutia grandis*. Two other OMZ *Lucicutia* species from the California Current were grouped as "thin-muscled floaters" on the basis of the relative activities of their lactate dehydrogenase (indicative of glycolytic or burst swimming potential) and citrate synthase (indicative of aerobic metabolic potential) (Thuesen et al. 1998). "Thin-muscled floaters" were considered sit-and-wait feeders, which is consistent with the diverse gut contents of *L. grandis*. Their relatively high lactate dehydrogenase activity may enhance the ability to live at low oxygen (Thuesen et al. 1998). After accounting for temperature effects, deep-sea copepods (and other nonvisual foragers) do not generally show decreased metabolic rates compared to shallow-living species, even within the OMZ (Childress 1995; Thuesen et al. 1998).

The sequence of environments inhabited by the different developmental stages of *L. grandis* is probably related to both physiological and ecological constraints, with a different balance at each stage. Adults may require higher oxygen levels especially for mating and egg and sperm production. In shallow water copepods, the mating process involves high speed bursts of activity (Yen et al. 1998). The development of spawned eggs may also require higher oxygen as described above. The occurrence of the C3s at the lowest oxygen levels is probably a predator-avoidance strategy. The C3s are large enough to provide a tasty morsel for the shrimp, fish, and other predators abundant at the lower OMZ interface, but probably small enough to have difficulty escaping an attacker. Since they may also be dependent on the timing of episodic flux events to provide sufficient food resources for continued development, they need a safe place to hide while waiting. Alldredge et al. (1984) in the Santa Barbara Basin and Vinogradov et al. (1986) in the Black Sea documented layers of copepods (some of them clearly diapausing stages) in oxic-anoxic boundaries with layers of gelatinous predators just above them, presumably at higher oxygen levels and sometimes with copepods in their guts. The diel vertical migration of nekton and zooplankton from the epipelagic zone into the OMZ is also a likely predator-avoidance strategy (from visually foraging epipelagic fish or squid). Diel migration of *Daphnia* into the suboxic hypolimnion, presumably to escape fish that cannot tolerate low oxygen, is a well-documented phenomenon in stratified lakes and ponds (Hanazato et al. 1989).

## Conclusions

The ecology of the copepod *Lucicutia grandis* is fine tuned to the small but stable oxygen gradients of the lower OMZ interface. Its abundance peaks in this zone despite the suboxic conditions. The unique features of *Lucicutia* life-stage distributions are that young stages migrate up in the water column to find a low oxygen refuge, and the timing of their vertical movement appears to be purely developmentally based, not diel or seasonal. *Lucicutia* occupies at least four trophic levels, and all stages studied actively feed even in low oxygen water. They respond to climatic cycles

and epipelagic events with their versatile trophic ecology and through reproduction. In contrast to the zooplankton negatively affected by coastal episodic hypoxia, *L. grandis*, and presumably the other species of the lower OMZ interface, have clearly adapted over evolutionary time to this widespread suboxic habitat.

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Received: 30 May 2000

Accepted: 13 July 2000

Amended: 15 August 2000