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FEATURE ARTICLE

Vertical distribution and diurnal migration of atlantid heteropods

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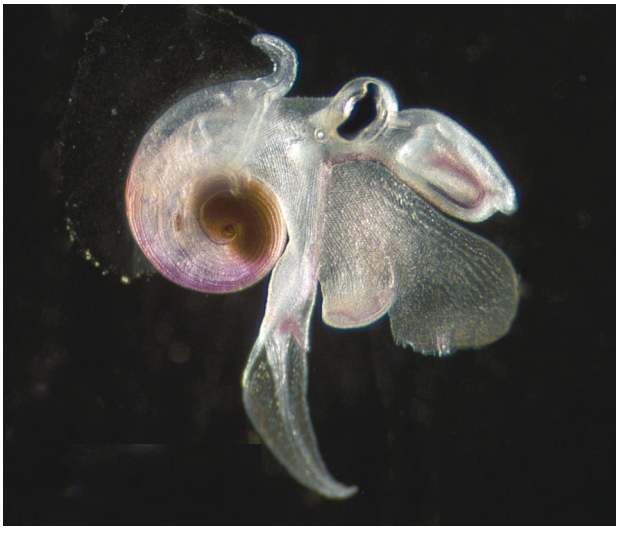
ABSTRACT: Understanding the vertical distribution and migratory behaviour of shelled holoplanktonic gastropods is essential in determining the environmental conditions to which they are exposed. This is increasingly important in understanding the effects of ocean acidification and climate change. Here we investigated the vertical distribution of atlantid heteropods by collating data from publications and collections and using the oxygen isotope ($\delta^{18}O$) composition of single aragonitic shells. Data from publications and collections show 2 patterns of migration behaviour: small species that reside in shallow water at all times, and larger species that make diurnal migrations from the surface at night to deep waters during the daytime. The $\delta^{18}O$ data show that all species analysed (n = 16) calcify their shells close to the deep chlorophyll maximum. This was within the upper 110 m of the ocean for 15 species, and down to 146 m for a single species. These findings confirm that many atlantid species are exposed to large environmental variations over a diurnal cycle and may already be well adapted to face ocean changes. However, all species analysed rely on aragonite supersaturated waters in the upper <150 m of the ocean to produce their shells, a region that is projected to undergo the earliest and greatest changes in response to increased anthropogenic CO_2.

KEY WORDS: Atlantidae · Gastropod · Vertical distribution · Diurnal migration · Oxygen isotopes · Calcification · Ocean acidification



Young adult atlantid heteropod *Oxygyrus inflatus* collected in the Atlantic Ocean during cruise AMT27. Maximum shell diameter (excluding keel) 1.6 mm.

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INTRODUCTION

Holoplanktonic gastropods spend their entire lives as drifting plankton, unable to swim against currents, but capable of adjusting their vertical position in the water column (Lalli & Gilmer 1989). This allows them to sink to depths, rise back to the surface or remain at a preferential depth. However, it is still unclear to what

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degree holoplanktonic gastropods take advantage of this vertical freedom, for example, to avoid predation, to reduce competition on finite food resources or to seek preferential environmental conditions.

Two groups of holoplanktonic gastropods are recognized: the pteropods (Thecosomata and Gymnosomata) and the heteropods (Pterotracheoidea). Both groups contain shelled, partially shelled and shell-less species, although even shell-less species have a shell in the larval stage, which is subsequently discarded (Lalli & Gilmer 1989). Holoplanktonic gastropod shells are composed of aragonite, a form of calcium carbonate that is susceptible to dissolution in waters undersaturated with respect to aragonite (Mucci 1983). These sensitive shells have highlighted the euthecosome (fully shelled) pteropods as being amongst the most vulnerable organisms to ocean acidification, with effects already being detected in field populations (Bednaršek & Ohman 2015). Ocean acidification research has not yet included the heteropods, which also rely on aragonite shells and inhabit the upper ocean, a realm of highly variable environmental parameters. This region will be greatly affected by ocean acidification and climate change, so it is beneficial to understand the vertical distribution of holoplanktonic gastropods. This will help scientists to determine the environmental conditions to which they are frequently exposed and may demonstrate, for example, that holoplanktonic gastropods are already exposed on a daily basis to undersaturated waters, with respect to aragonite, or to temperatures more variable than those predicted to affect oceans over the next 100 yr. Ultimately, holoplanktonic gastropods may already have mechanisms for dealing with a changing ocean (e.g. Maas et al. 2012). Conversely, ocean changes may present even more severe vertical environmental gradients than predicted, which holoplanktonic gastropods may be unable to adapt to, potentially forcing them to modify and constrain their vertical movements.

This study focusses on the shelled heteropods, or atlantids (family Atlantidae), which rely on a shell throughout their life. Atlantids are small (<14 mm) predatory holoplanktonic gastropods that feed on other metazooplankton, including euthecosome pteropods (Lalli & Gilmer 1989). Atlantids are able to fully retract into their thin-walled (1.5–8 µm, D. Wall-Palmer pers. obs.) aragonite shells, which are generally a broad, flat disk shape that is necessary for efficient swimming. The vertical distribution of atlantids has been speculated upon by many working in the field. It is generally accepted that atlantids live within the upper 250 m of the water column and often at much shallower depths (Lalli & Gilmer 1989, Seapy 1990, Michel & Michel 1991, Paulinose et al. 1992, Jivaluk 1998, Ossenbrügger 2010, Lemus-Santana et al. 2014, Wall-Palmer et al. 2016c). However, many atlantids are thought not to be static in their vertical position in the water column, but to undergo some degree of daily vertical migration. Studies based on sampling with plankton nets at different depths suggest that the depth and timing of this vertical migration are not only species specific, but also are specific to the ontogenetic stage and are probably influenced by seasonal changes (Wall-Palmer et al. 2016c and references therein). To date, the most extensive and thorough study of atlantid vertical distributions and migratory behaviour was conducted by Seapy (1990) offshore of Hawaii (USA). Seapy (1990) demonstrated 2 patterns of distribution: (1) small species that remained in shallow water of <140 m depth at all times, being active in the daytime and generally inactive at night, and (2) larger species that are inactive at depth during the daytime, but migrate to the surface at night to feed.

The shell geochemistry of some holoplanktonic gastropods has been used successfully to identify the depth at which shells are grown (e.g. Grossman et al. 1986, Juranek et al. 2003, Keul et al. 2017). The ratio of the oxygen isotopes ^{18}O and ^{16}O ($\delta^{18}O$) incorporated into an aragonite shell is a function of the $\delta^{18}O$ of the water in which a specimen lives ($\delta^{18}O_w$) and temperature (Grossman & Ku 1986). The $\delta^{18}O_w$ is a conservative water mass tracer related to input (e.g. precipitation and meltwater) and output (e.g. evaporation, sea-ice and brine formation), and therefore is directly relatable to seawater salinity (LeGrande & Schmidt 2006). Temperature plays a dominant role in the fractionation between ^{18}O and ^{16}O during the formation of aragonite. Therefore, the $\delta^{18}O$ equilibrium ($\delta^{18}O_{eq}$) at which aragonite is precipitated in seawater can be calculated from salinity and temperature. Euthecosome pteropods and atlantid heteropods calcify at or close to the aragonite–water isotopic equilibrium; therefore, the $\delta^{18}O$ of their shells directly records the $\delta^{18}O_{eq}$ of the water in which they live (Grossman et al. 1986, Juranek et al. 2003, Keul et al. 2017). Depth of calcification can be inferred by comparing the $\delta^{18}O$ of the specimen to a $\delta^{18}O_{eq}$ depth profile of the ambient water in which the specimen lived (calculated using temperature and salinity, LeGrande & Schmidt 2006). This technique has been used in a single study on atlantids (Grossman et al. 1986). Grossman et al. (1986) analysed 3 species of atlantid, *Atlanta inclinata, A. gaudichaudi* and an unidentified species. The isotopic compositions of the 3 species were comparable (apart from a single specimen) and indicated calcification in

the upper 75 m of the ocean. The geochemical methods of Grossman et al. (1986) have never been repeated or developed upon to include further atlantid species. Here we investigated the depth distribution of atlantid heteropods using 2 approaches. Firstly, sampling depth and time information gathered from publications and from collections was used to infer the likely depth distribution of each species and patterns of diurnal migration. Secondly, by building on the findings of Grossman et al. (1986), $\delta^{18}O$ values of single shells were used to determine the depth of calcification for 16 atlantid species at different life stages.

MATERIALS AND METHODS

Vertical distributions from published data and collections

Depth and (local) time data were gathered for 4086 specimens identified to species level in collections held at Plymouth Marine Laboratory (Plymouth, UK), Naturalis Biodiversity Center (Leiden, Netherlands), the Natural History Museum (London), the Natural History Museum of Denmark (Copenhagen) and material collected during the SN105 cruise of the OVR 'Sagar Nidhi' and the SO255 cruise of the RV 'Sonne'. Published depth and time data for 718 atlantid specimens were also used (Tesch 1910, Tokioka 1955, Furnestin 1961, Taki & Okutani 1962, McGowan & Fraundorf 1966, Van der Spoel & Troost 1972, Michel & Michel 1991, Hernández et al. 1993, Seapy & Richter 1993, Quesquén Liza 2005, De Vera et al. 2006, De Vera & Seapy 2006, Ayón et al. 2008, Ossenbrügger 2010, Howard et al. 2011, Wall-Palmer et al. 2016a,b, Burridge et al. 2017). The gathered data were from locations worldwide and from all seasons (Fig. 1). Only specimens that were collected live (using plankton nets) were included, and a maximum sampling depth of 600 m was applied due to poor temporal sample coverage below this depth. Samples collected over a long period of time (over 2 h) were also removed from the dataset. Depth measurements represent the maximum depth of each particular

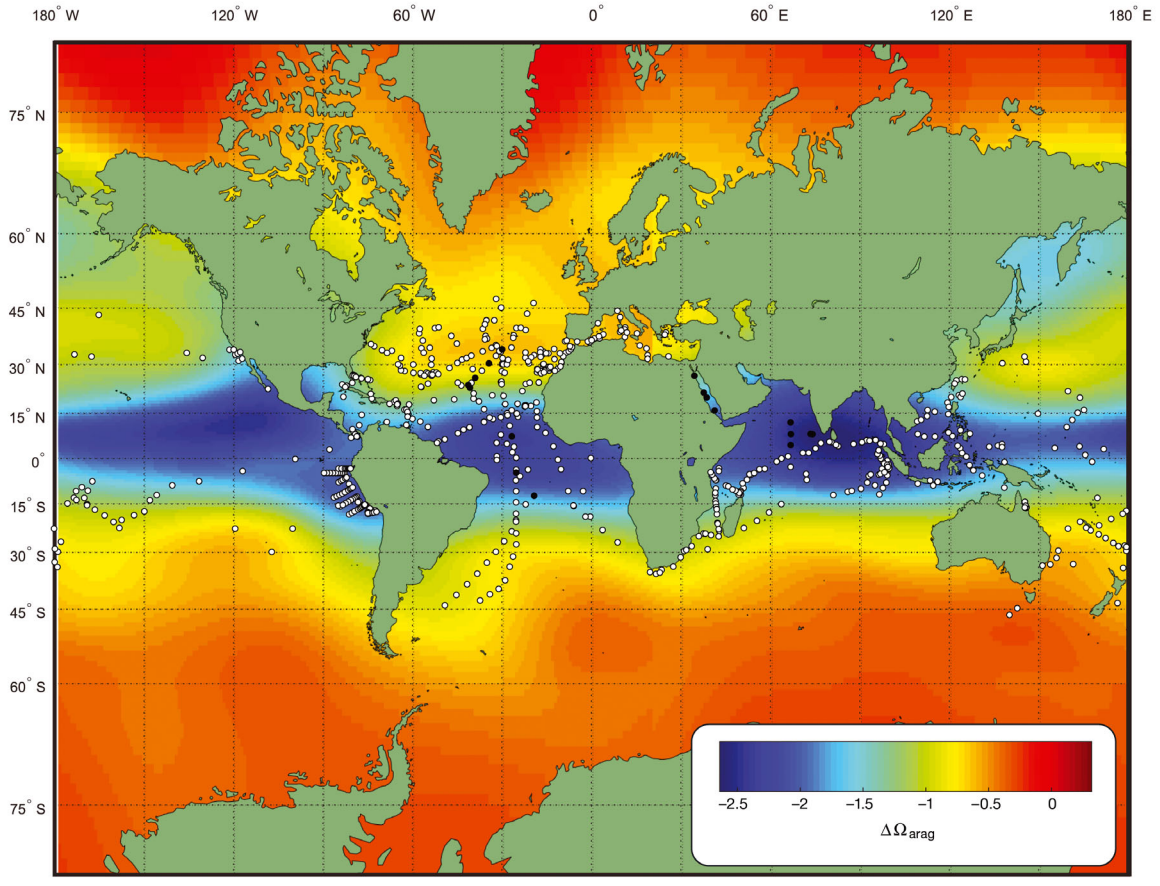


Fig. 1. Collection locations for atlantid specimens used in this study. White dots: specimens examined in collections and data gathered from publications. Black dots: specimens analysed for stable oxygen isotopes to determine the depth of calcification. Base map shows the difference in aragonite saturation state between the surface and 200 m created using data from Jiang & Feely (2015)

sampling. For example, a net may have been towed from 300 m to the surface, and therefore, specimens may have been caught at any depth between 0 and 300 m. For this reason, the shallowest record for each hourly interval was also determined (Table 1). This indicates the minimum depth at which each species has been found during each time interval.

Depth of calcification stable isotope analysis

For $\delta^{18}O$ analysis, a total of 63 specimens from 16 atlantid species were collected using a variety of methods during 4 cruises (Fig. 1): the Atlantic Meridional Transect in 2010 (AMT20) and 2014 (AMT24), the outbound Dutch-Indonesian 'Snellius II' G0 cruise (PG0) and the first cruise of IIOE-2 (SN105). All specimens were fixed and stored in ethanol prior to analysis. Ethanol has been found not to affect either $\delta^{18}O$ or the carbon isotope composition ($\delta^{13}C$) (Serrano et al. 2008). Specimens were prepared for analysis by rinsing thoroughly in MilliQ water, drying in an oven at 40°C and leaving in a desiccator for 24 h. Soft tissues were removed by placing specimens in an Emitech K1050X plasma asher in glass vials for 2.5 h. Plasma ashing does not affect the $\delta^{18}O$ and $\delta^{13}C$ of calcium carbonate (Serrano et al. 2008); however, the internal laboratory standard, Keyworth Carrera Marble (KCM), was also plasma ashed to check for any artefacts introduced using this method. The results of plasma ashed and non-plasma ashed KCM were within instrument error. A paired *t*-test found that $\delta^{18}O$ and $\delta^{13}C$ values were not significantly different between plasma ashed (pa) and non-plasma-ashed (n-pa) values for KCM ($\delta^{18}O$: pa M (mean) = −1.72, var = 0.01; n-pa M = −1.73, var = 0.01; $t = -0.33$, p = 0.75; $\delta^{13}C$: pa M = 2.01, var = 0.00; n-pa M = 2.00, var = 0.00; $t = -0.34$, p = 0.74), confirming no effect on the isotopic composition from this preparatory technique.

The stable isotope analysis was carried out at the Stable Isotope Facility (part of the NERC Isotope Geoscience Laboratory) at the British Geological Survey. Specimens ranging in weight between 13 and 200 µg were analysed individually, although the small size of

Table 1. Maximum depth (m) of shallowest plankton tows collected per hour for each species. Grey shading highlights general periods of darkness. Cells with '– ' denote time periods with no depth data. *A.* = *Atlanta*; *O.* = *Oxygyrus*; *P.* = *Protatlanta*

Time of day (h)	*A. ariejansseni*	*A. brunnea*	*A. californiensis*	*A. echinogyra*	*A. fragilis*	*A. frontieri*	*A. gaudichaudi*	*A. gibbosa*	*A. helicinoidea*	*A. inclinata*	*A. inflata*	*A. lesueurii*	*A. meteori*	*A. oligogyra*	*A. peronii*	*A. plana*	*A. rosea*	*A. selvagensis*	*A. tokiokai*	*A. turriculata*	*O. inflatus*	*P. sculpta*	*P. souleyeti*
00:00–00:59	–	50	15	300	50	100	50	50	50	50	50	50	–	300	25	–	–	200	300	50	10	100	–
01:00–01:59	70	50	–	50	400	50	35	50	300	50	–	35	600	50	25	50	400	–	50	50	0	–	50
02:00–02:59	–	50	–	50	50	50	50	50	50	50	50	25	200	50	0	–	50	100	50	50	0	50	50
03:00–03:59	216	50	–	50	50	50	50	50	50	50	50	0	50	50	25	50	0	100	50	50	50	0	50
04:00–04:59	200	50	210	50	50	50	50	50	50	50	55	50	50	0	50	50	0	200	50	50	50	50	100
05:00–05:59	–	100	–	55	100	55	50	55	55	18	55	18	–	55	25	55	–	300	18	55	25	–	100
06:00–06:59	–	–	–	100	100	50	10	–	–	100	10	50	–	100	10	50	100	100	100	10	100	–	100
07:00–07:59	–	400	–	–	–	–	50	10	10	10	400	10	–	–	10	–	–	–	600	–	100	–	400
08:00–08:59	–	–	–	–	–	–	50	–	–	100	–	50	–	–	32	–	–	–	–	–	100	–	100
09:00–09:59	–	–	–	396	396	–	50	459	396	–	–	10	–	459	32	–	396	–	396	10	25	–	459
10:00–10:59	–	100	–	100	200	100	50	–	100	150	100	50	–	100	32	100	100	100	100	100	50	–	100
11:00–11:59	–	–	–	376	376	–	50	–	–	–	–	50	–	–	32	–	376	200	376	376	105	–	376
12:00–12:59	–	–	–	–	–	–	50	–	–	150	140	50	–	–	31	–	–	200	–	–	140	–	–
13:00–13:59	–	200	–	–	–	–	50	–	–	300	–	50	–	–	32	–	100	200	–	–	110	–	–
14:00–14:59	–	400	150	–	–	–	50	411	411	366	411	50	–	–	32	411	–	–	411	411	2	–	200
15:00–15:59	–	140	–	–	–	–	140	–	–	400	140	140	–	566	32	566	–	100	–	140	140	–	–
16:00–16:59	–	140	–	–	200	370	50	400	200	600	140	50	–	370	140	–	370	200	–	140	100	–	100
17:00–17:59	–	140	–	–	–	–	50	–	–	310	140	10	–	–	140	–	–	–	–	–	140	–	–
18:00–18:59	–	100	10	100	50	50	10	50	50	10	10	10	50	50	10	100	50	11	50	0	0	50	10
19:00–19:59	20	50	–	50	23	50	0	50	50	50	50	23	100	50	23	50	50	80	0	0	10	50	50
20:00–20:59	–	10	–	50	15	50	50	50	50	0	10	50	60	0	0	50	50	100	25	50	0	50	10
21:00–21:59	–	50	–	50	50	50	50	40	50	19	50	0	50	50	0	50	19	200	50	50	0	19	50
22:00–22:59	–	50	50	50	50	50	50	50	50	50	140	25	50	50	25	100	50	–	100	50	50	–	50
23:00–23:59	–	50	210	0	100	50	50	50	50	50	0	0	50	50	0	50	50	–	100	0	50	–	100

some juvenile specimens meant that up to 3 specimens of a single species were analysed together (Table 2). Analysis was carried out using an IsoPrime dual inlet mass spectrometer with a Multiprep device. Specimens were loaded into glass vials and sealed with septa. The automated system first evacuated the ambient air within the vials and subsequently delivered anhydrous phosphoric acid to the carbonate at 90°C.

Table 2. Stable oxygen isotope analysis of atlantid specimens and the depth of calcification determined by comparison of specimen values to the aragonite equilibrium of the water column. Cells with '– ' denote stations with only a single specimen where mean and SD are not applicable. For a single specimen, the calculated depth of calcification was above sea level and therefore 'not possible'

Specimen code (Species_Cruise_ Station_Specimen)	Species	Specimens (n)	Description of specimens	Latitude	Longitude	Specimen $\delta^{18}O$ (‰) Calculated as aragonite	Mean station^{-1}	SD	Depth of calcification (m)
Abru_AMT20_07_01	*Atlanta brunnea*	1	Adult	34.23°N	29.73°W	−0.96	−0.84	0.17	46.92
Abru_AMT20_07_02		1	Adult			−0.72			61.91
Afro_SN105_01_01	*A. frontieri*	1	Adult	11.89°N	66.97°E	−1.85	−1.84	0.07	96.57
Afro_SN105_01_02		1	Adult			−1.91			91.94
Afro_SN105_01_03		1	Adult			−1.77			99.31
Agib_SN105_04_01A	*A. gibbosa*	0.5	Juvenile	8.02°N	67.08°E	−1.73	−1.69	0.06	88.40
Agib_SN105_04_01B		0.5	Adult whorl only			−1.71			88.91
Agib_SN105_04_02		1	Adult			−1.72			88.66
Agib_SN105_04_03		1	Adult			−1.60			93.93
Ahel_PG0_78_01	*A. helicinoidea*	1	Adult	26.62°N	34.72°E	−0.91	–	–	38.95
Ahel_PG0_86_01		1	Adult	21.45°N	37.87°E	−0.94	–	–	63.11
Ahel_PG0_88_01		1	Adult	19.93°N	38.87°E	−1.10	–	–	78.89
Ainc_AMT20_05/11_01	*A. inclinata*	1	Juvenile	4.89°S	25.03°W	−1.47	−1.44	0.30	101.24
Ainc_AMT20_05/11_02		1	Juvenile			−1.64			97.13
Ainc_AMT20_05/11_03		1	Juvenile			−1.65			96.69
Ainc_AMT20_05/11_04		1	Juvenile			−1.01			109.59
Ainf_PG0_141_01	*A. inflata*	1	Adult	8.00°N	74.34°E	−2.14	−2.34	0.28	66.23
Ainf_PG0_141_02		1	Adult			−2.54			58.45
Ainf_PG0_140_01		1	Adult	8.09°N	73.69°E	−2.12	–	–	66.54
Ales_PG0_94_01	*A. lesueurii*	1	Adult	15.78°N	41.51°E	−1.84	−1.79	0.29	78.16
Ales_PG0_94_02		1	Adult			−2.06			66.30
Ales_PG0_94_03		1	Adult			−1.48			106.68
Aoli_SN105_08_01	*A. oligogyra*	1	Adult	4.38°N	67.00°E	−2.30	−2.41	0.10	59.84
Aoli_SN105_08_02		1	Adult			−2.49			57.70
Aoli_SN105_08_03		1	Adult			−2.44			58.15
Apla_PG0_94_01	*A. plana*	1	Adult	15.78°N	41.51°E	−1.79	−1.81	0.02	82.54
Apla_PG0_94_02		1	Adult			−1.83			78.93
Aros_AMT20_23/10_01	*A. rosea*	1	Adult	30.29°N	34.17°W	−0.42	−0.49	0.10	95.50
Aros_AMT20_23/10_02		1	Adult			−0.46			92.77
Aros_AMT20_23/10_03		1	Adult			−0.60			80.93
Asel_AMT20_11_01	*A. selvagensis*	1	Adult	25.99°N	38.79°W	−0.94	–	–	74.35
Asel_AMT20_26/10_01		1	Adult	22.96°N	40.53°W	−1.28	–	–	Not possible
Asel_AMT20_23/10_01		1	Adult	30.29°N	34.17°W	−0.99	–	–	58.55
Atok_AMT20_09_01	*A. tokiokai*	1	Adult	30.29°N	34.19°W	−0.58	–	–	82.51
Atok_AMT20_26/10_01		1	Juvenile	22.96°N	40.53°W	−1.09	−1.16	0.06	81.30
Atok_AMT20_26/10_02		1	Juvenile			−1.22			72.73
Atok_AMT20_26/10_03		1	Juvenile			−1.17			77.12
Atur_SN105_01_01	*A. turriculata*	1	Adult	11.89°N	66.97°E	−1.69	−1.72	0.08	100.30
Atur_SN105_01_02		1	Adult			−1.74			99.69
Atur_SN105_01_03		1	Adult			−1.63			100.99
Atur_SN105_01_04		3	Juvenile			−1.83			97.46
Oinf_SN105_08_01	*Oxygyrus inflatus*	2	Juvenile	4.38°N	67.00°E	−1.90	−1.83	0.07	68.05
Oinf_SN105_08_02		1	Juvenile			−1.91			67.86
Oinf_SN105_08_03		2	Juvenile			−1.77			72.73
Oinf_SN105_08_04		2	Juvenile			−1.83			69.58
Oinf_SN105_08_05		2	Juvenile			−1.77			72.73
Pscu_AMT24_13_01	*Protatlanta sculpta*	4	Juvenile	7.29°N	26.49°W	−0.32	−0.38	0.08	100.56
Pscu_AMT24_13_02		5	Juvenile			−0.44			93.23
Psou_AMT20_23_01	*P. souleyeti*	1	Adult	12.54°S	19.03°W	−0.48	–	–	145.56
Psou_AMT20_11_01		1	Adult	25.99°N	38.79°W	−0.72	–	–	89.83
Psou_AMT20_12_01		1	Adult	23.77°N	41.11°W	−0.51	–	–	133.06

The evolved CO_2 was collected for 15 min, cryogenically trapped, cleaned of impurities and water vapour and passed to the mass spectrometer. Isotope values ($\delta^{13}C$ [not discussed herein], $\delta^{18}O$) are reported in per mille (‰) deviations of the isotopic ratios ($R = {}^{18}O/{}^{16}O$) against a standard gas calculated to the Vienna PeeDee Belemnite (V-PDB) scale using a within-run in-house laboratory standard calibrated against the National Bureau of Standards No. 19 (NBS-19). The aragonite-acid fractionation factor (1000 ln $\alpha_{CO2(ACID)\text{-}Aragonite}$) applied to the liberated gas values is 1.00855. Due to the long run time of 21 h, a drift correction was applied across the run, calculated using the KCM standards that bracket the samples. The correction of Craig (1957) was applied to account for ^{17}O. The average analytical reproducibility of the standard calcite (KCM) within run was <0.1‰ for $\delta^{18}O$.

Conversion of water column profiles into $\delta^{18}O_{eq}$

Calcification depth was determined by comparing the measured isotope values to a likely equilibrium oxygen isotope value ($\delta^{18}O_{eq}$) calculated using salinity and temperature (Grossman et al. 1986, Juranek et al. 2003). $\delta^{18}O_w$ was determined using salinity and temperature data collected with depth for each site (research cruises AMT20, AMT24, SN105). However, for PG0 sites, these data were not available. Therefore, seawater temperature and salinity profiles for these regions collected at a comparable time of year to the specimens analysed were extracted from the World Ocean Database (Boyer et al. 2013). For example, specimens were collected at station PG0-78 (26.62° N, 34.72° E) on 7 October 1988, and temperature and salinity data were collected in the same region (26.60° N, 34.98° E) on 26 September 1975. The regional $\delta^{18}O$-salinity relationships of LeGrande & Schmidt (2006) were applied (for example, Eq. 1). $\delta^{18}O_w$ was then converted from Vienna Standard Mean Ocean Water (V-SMOW) to V-PDB by subtracting 0.27‰ (Hut 1987). The method of Grossman et al. (1986), which uses the equation of O'Neil et al. (1969) with a correction factor of 0.6‰ for aragonite–calcite fractionation, was applied to calculate the aragonite equilibrium ($\delta^{18}O_{eq}$) with depth for each station (Eq. 2). Because atlantids produce aragonite in equilibrium with the seawater, the $\delta^{18}O$ of the specimen was directly compared to the $\delta^{18}O_{eq}$ depth profiles to determine the depth of calcification.

$$\delta^{18}O_w = (0.55 \times S) - 18.98 \text{ (for North Atlantic stations)} - 0.27 \quad (1)$$

$$\delta^{18}O_{eq} = [(-4.38 - \sqrt{\Delta}) / (2 \times 0.1)] + \delta^{18}O_w - 0.6‰ \text{ when: } \Delta = 4.38^2 - [(4 \times 0.1) \times (16.9 - T)] \quad (2)$$

In these equations, S is salinity and T is temperature.

These calculations do not take into account that the specimens may have formed their shells throughout different seasons of the year. The $\delta^{18}O_w$ is a function of salinity and therefore can vary seasonally, particularly in regions of high river runoff. However, in the open ocean where atlantids live, and away from polar regions that are greatly influenced by ice formation and melting, salinity does not show considerable seasonal or annual variation (Zweng et al. 2013). Therefore, we assumed here that there have been negligible seasonal and/or inter-annual variations in the $\delta^{18}O_w$ at each station.

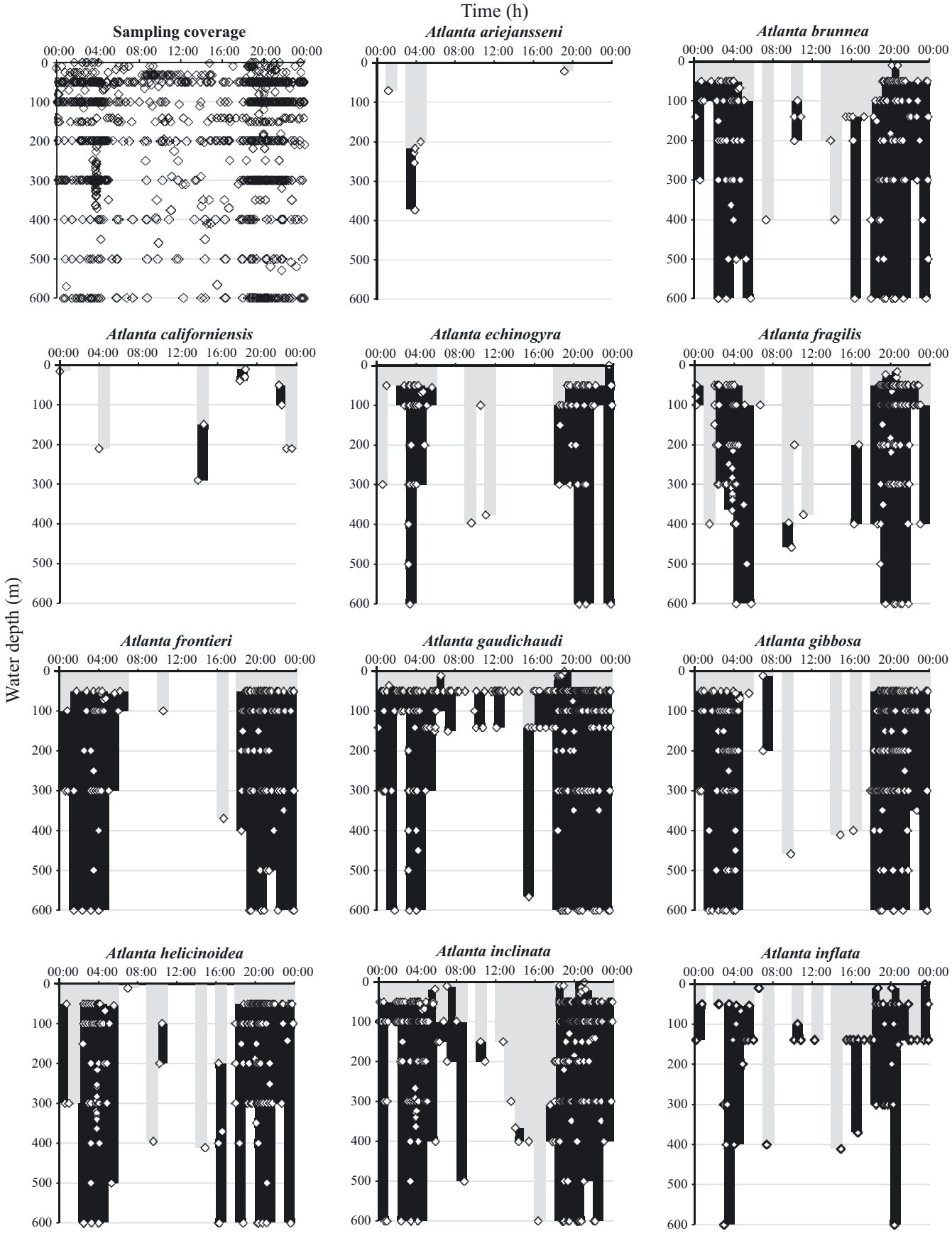
RESULTS AND DISCUSSION

Depth distributions and vertical migrations

Temporal and spatial sampling coverage of collection data was well spread, with 289 different time–depth points during the day (07:00–18:59 h) and 1092 different time–depth points during the night (19:00–06:59 h, Fig. 2). Spatial sampling included 409 time–depth points for the upper 99 m, and 341, 154, 258, 49, 170 and 120 time–depth points for depths of 100–199, 200–299, 300–399, 400–499 and 500–600 m, respectively (Fig. 2).

Most species have a good temporal coverage of sampling, with records available for the majority of hourly intervals. Only 4 species (*Atlanta ariejansseni*, *A. californiensis*, *A. meteori* and *Protatlanta sculpta*) have considerable gaps in sampling time, with <50% coverage for the hourly intervals (Fig. 2). The lack of sampling for 3 of these species (*A. ariejansseni, A. californiensis, P. sculpta*) can be explained because they occupy small regions relative to other atlantid species and have only been recently described (or reinstated). It is uncertain why there is a lack of sampling records of *A. meteori* during hours of daylight. For the remaining species, 2 main patterns of depth distribution

Fig. 2. Collated depth and time data from publications and collections. White diamonds: the maximum collection depth of all plankton net samples for each species. Black shaded areas: the maximum depth at which specimens were caught. Grey shaded areas: shallowest depth (sometimes the only depth) at which specimens were caught for each hourly interval. Original data are presented in Table S1 in the Supplement at www.int-res.com/articles/suppl/m587p001_supp.xlsx



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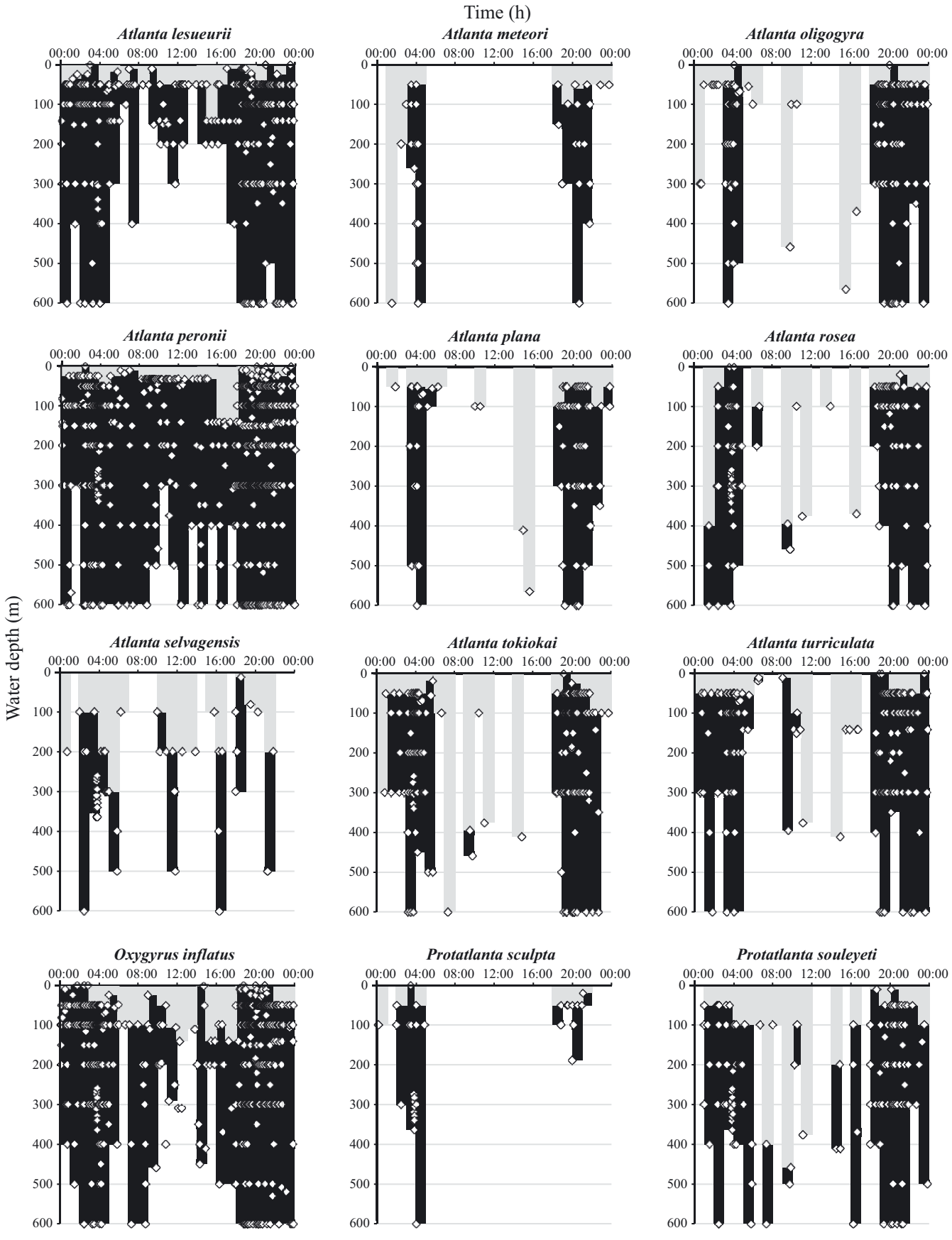

Fig. 2 (continued)

with time were found. These are generally in agreement with the patterns of depth distribution found by Seapy (1990) offshore of Hawaii, i.e. species that remain in shallow waters at all times, and species that migrate to deeper waters during the daytime.

Constant shallow water distribution

Three species (*A. peronii, A. gaudichaudi* and *A. lesueurii*) did not undergo any diurnal migration, being present in shallow waters of <50 m at most times (Fig. 2). The only deviation from this depth was between 15:00 and 18:00 h for all 3 species, when the maximum depth was <140 m. Although slightly deeper, *A. selvagensis* also showed a constant depth distribution, being present at <200 m during the day and at night. Seapy (1990) and Lalli & Gilmer (1989) also found that several smaller atlantid species were confined to shallow waters at all times. This supports the distributions of *A. gaudichaudi*, *A. lesueurii* and *A. selvagensis*. However, *A. peronii,* being one of the largest atlantid species, is generally considered to inhabit deeper waters (>200 m) and to be a diurnal migrator (Seapy 1990). Data presented here show that specimens were found in shallow water at all times (Fig. 2). Wall-Palmer et al. (in press) have shown that *A. peronii* is genetically diverse and may represent a collection of sub-species (or even species), each with a particular geographical distribution, and potentially each having a different depth distribution. Therefore, data presented here are probably a collation of all of these genetically different groups.

Two further species, *A. inflata* and *Oxygyrus inflatus*, were restricted to shallow water at all times, but also underwent a short-distance diurnal migration (Fig. 2). *A. inflata* showed a migration from <50 m at night to <140 m during the daytime; however, 2 periods of potentially deeper distribution occurred at 07:00–08:00 h and 14:00–15:00 h when the shallowest records were <400 m. *O. inflatus* varied in depth from <50 m during the night to <140 m during the day. Richter (1982) and Ossenbrügger (2010) also found *O. inflatus* to be restricted to the upper 100 m, and most abundant in the upper 50 m, and Seapy (1990) found *O. inflatus* to be restricted to the upper 90 m offshore of Oahu, Hawaii.

Deep water diurnal migration

Thirteen species displayed a consistent diurnal migration pattern (Fig. 2). These species had a shallow distribution, generally in the upper 50 m, between ~19:00 and 07:00 h, and a deeper distribution, in at least the upper 100 m, between 07:00 and 19:00 h. During parts of the daytime, each of these species was collected at depths of between 300 and 600 m but not in shallower water, despite the good temporal coverage of sampling at shallower depths. This suggests a diurnal migration that agrees with that proposed by several authors (Oberwimmer 1898, Seapy 1990, Michel & Michel 1991, Seapy & Richter 1993). However, a number of these species, including *A. brunnea*, *A. helicinoidea* and *A. oligogyra* were reported to be shallow non-migrators by Seapy (1990). None of the deep water migrating atlantid species exhibit the exact same migration path over time, reinforcing the view that migratory behaviour is species specific in atlantids (Richter 1973, Seapy 1990).

Despite the overall good spatial coverage of sampling points during the daytime, particularly in the upper 300 m, many of the migrating species were only caught in very deep net samples during the daytime, well below the 250–300 m assumed maximum depth. For example, *A. tokiokai* and *A. inclinata,* 2 species with very similar shell morphology, were only caught in net samples of >400 m during some time intervals during the daytime (Fig. 2). Some species were only caught at even greater depth, up to 1000 m. Michel & Michel (1991) also caught *A. inclinata* in opening-closing nets at a depth of 400–650 m during the daytime. These species are commonly caught in plankton samples (403 records presented here) and have a global distribution (Wall-Palmer et al. in press); therefore, if they were present in shallower waters during daylight hours, they would have likely been caught there. While it is improbable that atlantids descend into the aphotic zone (below 1000 m), because their complex eyes determine that they rely on light, it is possible that they do migrate well below the euphotic zone (200 m) into the deeper waters of the dysphotic zone (200–1000 m). Previous studies have noted that larger atlantid species, some with larger eyes that may be adaptations to low light levels (e.g. *A. fragilis*, *A. gibbosa*), are often caught in deeper waters than smaller species. Seapy (1990) found that larger species offshore of Oahu migrated to deeper waters during the daytime. Similar trends of larger taxa with depth have been found in other mesopelagic zooplankton (Dai et al. 2017), and larger eyes relative to body size are thought to increase photon capture (and hence detection of predators and prey) in deeper dwelling mesopelagic fishes (de Busserolles et al. 2013).

Deep water migrations over 300 m suggest that some atlantids are exposed to large environmental

gradients on a daily basis. The temperature difference from the ocean surface to 400 m is in the order of 5–20°C (from CTD data used in this study), far greater than the predicted anthropogenic change in ocean temperature. Even within the upper 200 m, and particularly in the tropical regions, atlantids are experiencing variation in the aragonite saturation state of up to 2.5 units during diurnal migrations (Fig. 1). This means that deep migrating species may already be adapted to cope with large environmental changes. However, deep water migrating species may also be affected by the shallowing of the aragonite lysocline, which is predicted to be within a few hundred metres of the ocean surface globally by the year 2300 (Caldeira & Wickett 2005, Orr et al. 2005, Raven et al. 2005). This will potentially alter atlantid migratory behaviour by reducing the depth to which they travel, and will undoubtedly have consequences for food availability, competition and predator interactions.

Nine of the deep water migrating species (*A. echinogyra, A. frontieri, A. rosea, A. fragilis, A. helicinoidea, A. oligogyra, A. selvagensis, A. tokiokai* and *P. souleyeti*), also display a brief deepening of their distribution at around midnight (Fig. 2). This phenomenon, described by Richter (1973) as the 'midnight sinking', has been observed by several authors (Oberwimmer 1898, Richter 1973, Seapy & Richter 1993) and is thought to be caused by a lack of illumination which causes disorientation (Russell 1927). However, Richter (1973) found that the timing of this brief movement to deeper waters was species specific in atlantid larvae, being approximately 2 h after a species appeared in surface waters and not correlating with light conditions. This behaviour may therefore be more of a resting period during feeding, rather than a general disorientation caused by low light levels. Six species (*A. brunnea, A. echinogyra, A. oligogyra*, *A. rosea, A. tokiokai* and *P. souleyeti*) displayed a shallowing in their distribution at around 10:00–11:00 h, which has not been observed in previous studies. This could potentially be a period of swimming in between resting to avoid sinking into much deeper waters where environmental conditions (e.g. temperature, pH) are more hostile.

Depth of calcification

$\delta^{18}O$ of atlantid heteropods yielded values between −0.32 and −2.54‰ (Table 2, Fig. 3). In agreement with the findings of Grossman et al. (1986), the $\delta^{18}O$ of specimens is comparable to the $\delta^{18}O_{eq}$ for each station. The calculated depth of calcification is remarkably consistent between species and between sta-

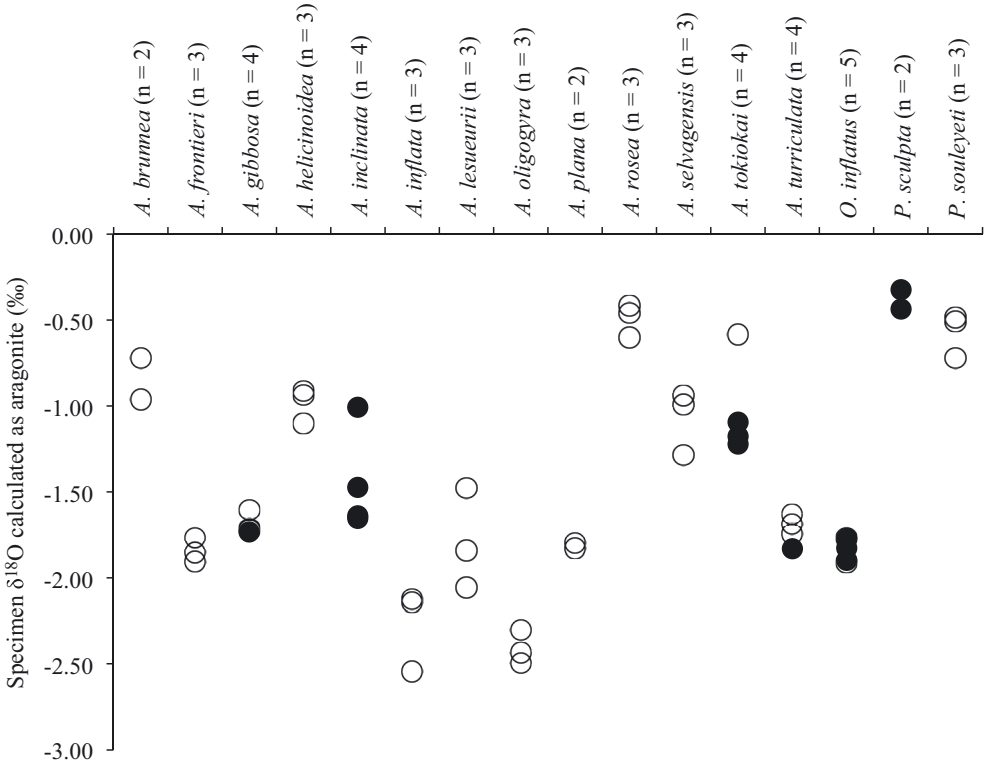

Fig. 3. Results of oxygen isotope analysis calculated as aragonite for all specimens. See Table 2 for values. These data include juvenile shells (filled circles) and adult shells (open circles). *A.* = *Atlanta*; *O.* = *Oxygyrus*; *P.* = *Protatlanta*

tions (Fig. 4). All species, with the exception of *P. souleyeti*, were found to calcify in the upper 38–110 m. These depths are comparable to the analysis of Grossman et al. (1986), who found calcification depths of 75 m for *A. inclinata* and *A. gaudichaudi. P. souleyeti* produced a range of depths of 89.83–145.56 m.

The smaller species of *Atlanta* (adult shell 1.5–3 mm), including *A. brunnea*, *A. helicinoidea*, *A. inflata*, *A. oligogyra* and *A. selvagensis*, consistently calcify in shallower water (38–79 m) relative to larger species (adult shell 5–10 mm) such as *A. frontieri*, *A. gibbosa*, *A. inclinata* and *A. rosea* (81–110 m). A significant correlation was found between the average calcification depth and maximum adult shell size for species of the genus *Atlanta* (Fig. 5a, r = 0.66, p = 0.015, n = 13). Calcification for all specimens, across all species and locations, was found to take place within the thermohalocline. For stations with chlo-

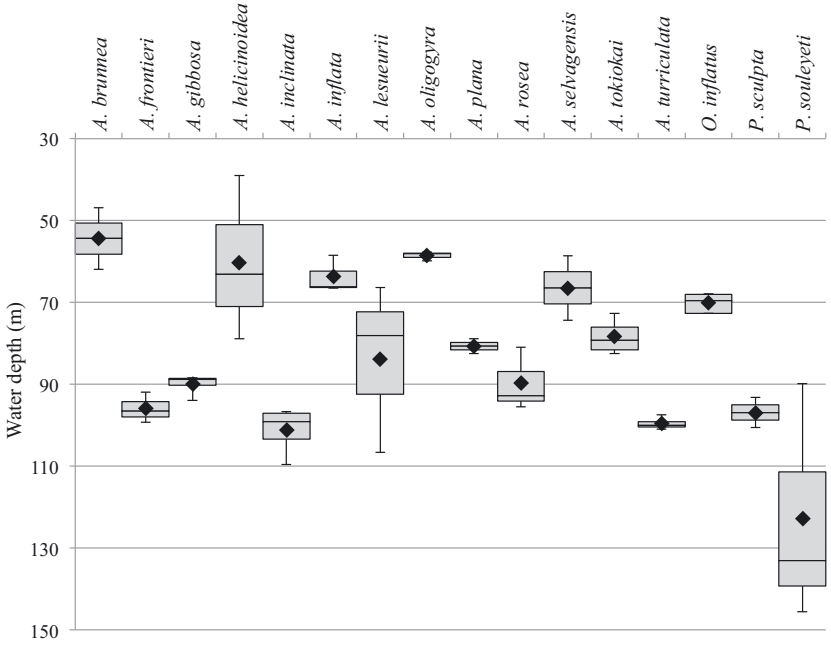

Fig. 4. Depth of calcification calculated using stable oxygen isotope analysis of atlantid shells, compared to the aragonite–seawater equilibrium (determined using seawater temperature and salinity). Original data are presented in Table 2. Black horizontal lines inside each box are the median depth, box limits are the first and third quartile, whiskers are the minimum and maximum depth, and black diamonds are the mean depth for each species. *A.* = *Atlanta*; *O.* = *Oxagyrus*; *P.* = *Protatlanta*

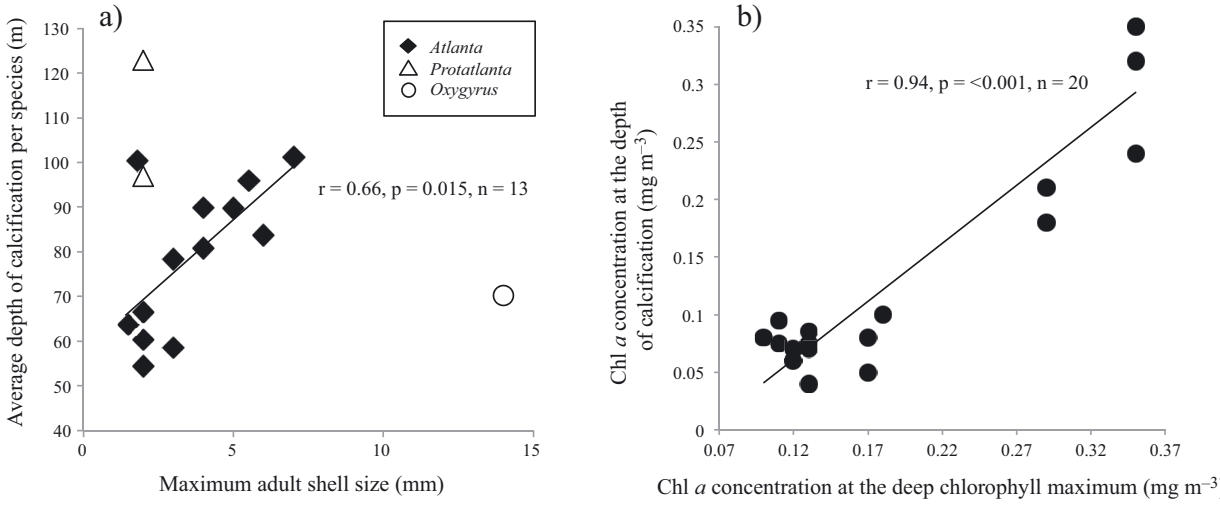

Fig. 5. (a) Average depth of calcification calculated for each species plotted against the maximum adult shell size for each species (Seapy 2011). Data for the genus *Atlanta* show a significant relationship. (b) Chlorophyll *a* concentration at the depth of calcification shows a significant relationship to the chlorophyll *a* concentration at the deep chlorophyll maximum (DCM) for specimens analysed from AMT20 and AMT24 stations

rophyll–depth data (stations from research cruises AMT20 and AMT24), the concentration of chlorophyll *a* at the depth of calcification was significantly correlated to the concentration of chlorophyll *a* at the deep chlorophyll maximum (DCM, Figs. 5b & 6). This could explain the deep calcification depth of *P. souleyeti* at stations AMT20-12 and AMT20-23 (133.06 and 145.56 m, respectively), where the thermohalo-

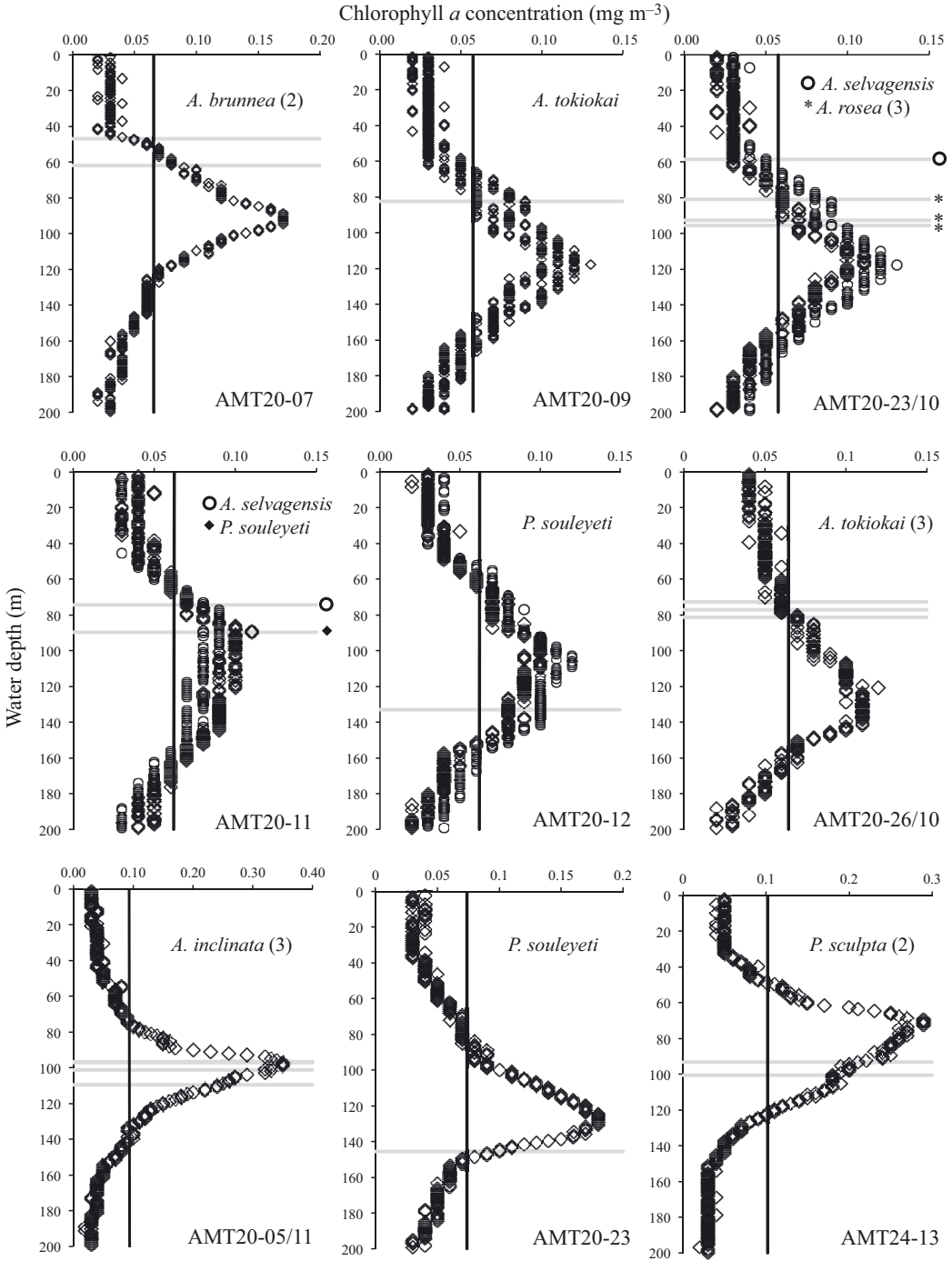

Fig. 6. Chlorophyll *a* concentrations over a water depth of 200 m for stations of Atlantic cruises AMT20 and AMT24 (data extracted from the British Oceanographic Data Centre). Black vertical lines: mean chlorophyll *a* concentration (over upper 200 m). Horizontal grey lines: depth of calcification of atlantids calculated from the $\delta^{18}O$ of shells, seawater temperature and salinity data. Where 2 species were collected from 1 station, the grey lines are labelled with symbols. Calcification takes place in regions with above mean chlorophyll *a* concentration, close to the deep chlorophyll maximum for most of the specimens analysed

cline and DCM are deep relative to other stations. Preference to calcify within this nutrient-rich layer is likely linked to food availability. This is consistent with the findings of Keul et al. (2017), who demonstrated that the pteropod *Heliconoides inflatus*, a potential prey species for atlantids, calcifies at a depth of ~75 m in the Atlantic Ocean.

Several of these data are based on whole adult shells; therefore, the calcifying depth is averaged over the entire life of the atlantid and may represent an average of deeper and shallower depths, as well as an average of different seasons and geographical areas. Particularly in adult specimens, shells may have been produced long before they were collected (e.g. in a different season when waters were warmer). The life cycle of atlantids is not well understood and the typical life span of an adult atlantid is unknown. The size and complexity of the velum in juvenile atlantids is characteristic of long-lived veligers (Thiriot-Quiévreux 1973, Lalli & Gilmer 1989) and may give an indication that their overall life span is long relative to other zooplankton groups. As a comparison, euthecosome pteropods are thought to have a life cycle of around 1.5–2 yr (Lalli & Gilmer 1989). In this study, juvenile specimens were used for 30% of the $\delta^{18}O$ analyses. In general, the depth of calcification in the juvenile stage (67.86 to 109.59 m) was comparable to the depth of calcification for the adult shells (38.95 to 106.68 m, excluding *P. souleyeti*) across different species and different geographical regions. For *A. turriculata* and *A. gibbosa*, both juvenile and adult shells were analysed for the same station. The $\delta^{18}O$ (and depth of calcification) for both life stages was comparable (Table 2, Fig. 3). Grossman et al. (1986) also found no difference in the $\delta^{18}O$ composition between 3 sections representing different life stages of a single *Atlanta* specimen. Therefore, although based here on a limited number of specimens, our results suggest that atlantids may calcify at the same depth throughout their lives (and stay within a small geographical region). This similarity between the $\delta^{18}O$ of juvenile and adult shells could also have been produced if atlantids do not calcify at or close to the aragonite–water isotopic equilibrium throughout their lives, having varying metabolic effects on the isotopic composition throughout ontogeny—for example, if atlantids preferentially incorporate a higher proportion of O^{16} that originates from their own respired CO_2 during shell growth. This has been found for some foraminiferan species (Pearson 2012). However, Grossman et al. (1986) found that the depths at which specimens were captured in sediment traps were in agreement with the depths at which the $\delta^{18}O$ values of specimens were recorded, suggesting that there are very few or no metabolic effects upon specimen uptake of $\delta^{18}O$.

CONCLUSIONS

This study combines collated collection data with stable oxygen isotope analysis of *in situ* collected material. Depth distribution data reveal 2 clear patterns of vertical distribution. The first pattern is of small atlantid species that reside in the upper 140 m of the ocean at all times and generally do not migrate. The second broad pattern of atlantid distribution, which the majority of species exhibit, is of larger species that carry out long diurnal migrations. During the night, these atlantids inhabit shallow waters, whereas during the daytime, they move to deeper waters. Some species may also move to very deep waters of over 300 m, and several migrating species exhibit a 'midnight sinking' and/or a 'midday shallowing'.

The $\delta^{18}O$ of the aragonite shells provides a first approximation to the depth of calcification, which appears to consistently represent a depth close to the DCM and within the upper 150 m, for juvenile and adult specimens. This region is projected to undergo the earliest and greatest change in pH in response to increased anthropogenic CO_2 and strongly indicates that atlantid heteropods will be adversely affected by ocean acidification of surface waters in the near future.

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