

## REVIEW ARTICLE

### A review of the ecology, palaeontology and distribution of atlantid heteropods (Caenogastropoda: Pterotracheoidea: Atlantidae)

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## ABSTRACT

Fewer than 1% of marine gastropod species live a holoplanktic life. Of these, the shelled heteropods of the family Atlantidae are among the most poorly understood. The atlantids potentially make up an important part of the ocean zooplankton, composing up to 69% of shelled holoplanktic gastropods in the Late Pleistocene to Recent fossil record. They are also likely to be at high risk from current and future global changes, including anthropogenic ocean acidification. However, due to their small size (<12 mm), difficulty of sampling and complicated morphology, we still lack key information about atlantid taxonomy and ecology. This makes it difficult to understand how important they are in the ocean foodweb and how they will be affected by environmental change. Although many studies have been carried out on the atlantids, these have generally been broad and unconnected. Here, we draw together this previous research, summarizing what is currently known about atlantid taxonomy, palaeontology, ecology and biogeography, and aiming to provide a foundation for future research on this group. The data indicate complex behaviours involving seasonal and vertical migration, and demonstrate extended geographical ranges, with implications for understanding the role of atlantids in the ocean foodweb and their sensitivity to environmental changes. This review highlights the urgent need for further taxonomic research on the atlantids, including molecular analysis, and for improved sampling techniques.

## INTRODUCTION

Heteropods have been studied for over 200 years, since the description of *Pterotrachea* by Forskål (in Niebuhr, 1775). The early oceanographic expeditions generated much interest in heteropods and entire chapters of cruise reports were often dedicated to their description (Smith, 1888; Tesch, 1910, 1949; Schiemenz, 1911; Tokioka, 1955a, b). However, in recent years, heteropods have often been overlooked in plankton studies, which is most likely a result of their small size and complicated taxonomy, combined with inadequate sampling techniques. The fragile shells of heteropods are easily broken during collection, resulting in incomplete descriptions and uncertain identifications. The ability of heteropods to evade capture by standard plankton nets, particularly those of small aperture, has also led to an underestimation of their abundance and diversity (McGowan & Fraundorf, 1966; Seapy, 1990a, b). Recent research on the fossil record of heteropods suggests that they can be quite abundant relative to other holoplanktic gastropods and more tolerant of temperate and cold waters than

previously thought (Wall-Palmer *et al.*, 2014). Recent plankton sampling during the 2014 Atlantic Meridional Transect in the Atlantic Ocean found that atlantid heteropods made up an average of 16% (up to 44% of individuals per sample) of calcareous holoplanktic gastropods at each station (A.K. Burridge, personal communication, 2015). This indicates that heteropods may be a more important component of the ocean foodweb than previously thought. Atlantids are also likely to be prone to the effects of current and future ocean acidification because they live in the most vulnerable habitat, the surface ocean and produce an aragonite shell, which is particularly susceptible to dissolution. However, no studies into the effects of ocean acidification have been carried out on atlantids. Research on a similar, but unrelated group of holoplanktic gastropods, the thecosome (shelled) pteropods, suggests that ocean acidification negatively affects shell growth and survival of aragonitic-shelled holoplanktic gastropods (Comeau, Alliouane & Gattuso, 2012; Wall-Palmer *et al.*, 2013; Bednaršek *et al.*, 2014).

This review collates information from published research on the taxonomy, palaeontology, ecology and biogeography of

the Atlantidae, extending and updating previous reviews by Thiriot-Quiévreux (1973), van der Spoel (1976), Lalli & Gilmer (1989) and Richter & Seapy (1999). Our aim is to provide a foundation on which future research on this group of potentially important and threatened holoplanktic gastropods can be developed. The collated data have been used to generate a series of biogeographical species maps and information on the complicated vertical and seasonal migrations of the atlantids. An overview of atlantid palaeontology is also presented, with the first stratigraphic chart for this group. We have not attempted to review the general biology, anatomy and larval development of atlantids, as this has been done by Thiriot-Quiévreux (1973), Martoja & Thiriot-Quiévreux (1975), Lalli & Gilmer (1989) and Jamieson & Newman (1989).

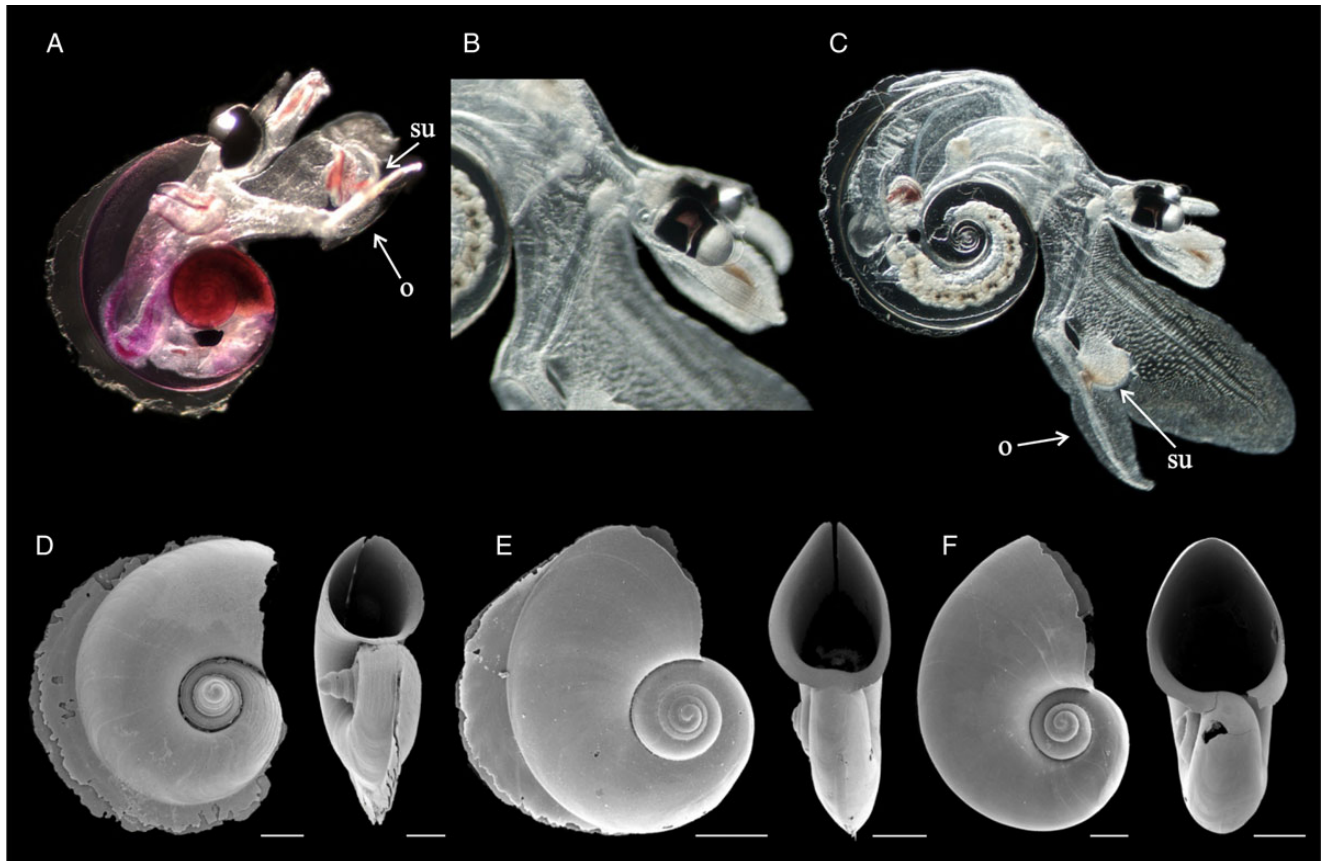
## TAXONOMY

The vernacular name ‘hétéropodes’ (meaning different foot) was created by Lamarck (1812), although Children (1824) formally introduced the order Heteropoda, placing it within the Mollusca next to ‘Gasteropoda’. The heteropods were identified as gastropods by Cuvier (1836), having previously been suggested as a link between cephalopods and fish (Lamarck, 1812). The subsequent taxonomic history of the group has been reviewed by Thiriot-Quiévreux (1973). Today, the order Heteropoda is invalid and has been reorganized as the superfamily Pterotracheoidea within the caenogastropod order Littorinimorpha (Gofas, 2015a). However, the term ‘heteropods’ is still widely used as an informal name for the group. The extant Pterotracheoidea are classified in eight genera in three families (Carinariidae, Pterotracheidae

and Atlantidae) (Seapy, 2011). An additional family, the Coelodiscidae, is known exclusively from the fossil record.

Of the three extant families of heteropods, the shell-bearing Atlantidae is considered to be the least specialized for a holoplanktic existence when compared with the other heteropod families, which have either reduced shells (Carinariidae) or lack shells in the adult stage (Pterotracheidae) and have a correspondingly larger body size (Thiriot-Quiévreux & Seapy, 1997). However, the Atlantidae are the most species-rich family, containing over 60% of all heteropod species (Seapy, 2011). Atlantids are also consistently found to be the most abundant heteropods in plankton samples (Richter, 1968; Seapy, Lalli & Wells, 2003; Ohman, Lavanigos & Townsend, 2009; Ossenbrügger, 2010). The family contains three genera (*Atlanta*, *Protatlanta* and *Oxygyrus*) and is characterized by dextrally-coiled, aragonitic shells into which the soft body can fully retract, sealed by a chitinous operculum that is attached to the foot (Fig. 1A, C). Apparent adaptations of the atlantids for a holoplanktic life include reduction in shell-wall thickness (3–40 µm) or (in the genera *Protatlanta* and *Oxygyrus*) a partially uncalcified (conchiolin) shell, a peripheral shell keel, a tendency for the body and shell to be transparent, well-developed eyes and the modification of the foot into a swimming fin (Lalli & Gilmer, 1989) (Fig. 1).

The genus *Atlanta*, including two species, was introduced by Lesueur (1817). Subsequently, many species, collected during the expedition of *La Bonite*, were beautifully illustrated by Eydoux & Souleyet (1841), but only indicated with vernacular names. However, before Souleyet (1852) was able fully to describe and name these species (13 of which were new), they were formally named by Gray (1850) from a collection of figures produced by M.E. Gray for the use of students. Tesch (1949) clarified the



**Figure 1.** Living heteropods (photographs taken by K.T.C.A. Peijnenburg and E. Goetze during the Atlantic Meridional Transect cruise, AMT22). **A.** *Atlanta helicinoidea* with eye type c (Seapy & Richter, 1993). **B, C.** *A. peronii* with eye type b. **D–F.** Scanning electron microscopy images. **D.** *A. turriculata*. **E.** *A. selvagensis*. **F.** *Protatlanta souleyeti*. Scale bars = 200 µm. Abbreviations: o, operculum; su, sucker used in predation.

systematics of the family, revising the number of species to 10, using specimens collected during the Dana Expeditions. Since then, a number of species have been reinstated or newly described, the latest being *A. selvagensis* de Vera & Seapy, 2006. There are currently 21 extant species (Seapy, 2011; Gofas, 2015b) and 9 extinct species of Atlantidae (Table 1). Extant species of *Atlanta* are organized into seven 'species groups' based on morphological features of the shell, eyes, operculum and radula (Seapy, 2011; Fig. 2). Species descriptions and keys have been published by Seapy (1990a, 2011) and Seapy *et al.* (2003).

The taxonomy of the Atlantidae largely relies on shell morphology, in particular protoconch shape (number of whorls) and ornamentation. However, shell morphology is often not sufficient to identify closely related species reliably, so that the eyes (Fig. 1A–C), radula and operculum are necessary for identification (Seapy & Richter, 1993). For example, in the Pacific Ocean the shells of *A. inflata* and *A. helicinoidea* are similar and eye type has to be used to differentiate the two species (Seapy, 2011). Three eye and three opercular types were originally described by Richter (1961) and these have been summarized for each species, together with radula type, by Seapy (2011).

So far there has been only a single molecular study including atlantids. Jennings *et al.* (2010) analysed four atlantid species, *A. gaudichaudi*, *A. inclinata*, *A. peronii* and *Oxygyrus inflatus*, from various locations in the Atlantic Ocean. They found molecular differences between two forms of *A. inclinata*, one with a golden shell keel sampled in the northwestern Atlantic Ocean and one with a colourless keel sampled in the northeastern and southeastern Atlantic Ocean, suggesting that these were distinct species. This indicates that identification based on traditionally used morphological features may not always be reliable.

Many areas of the world ocean have not been thoroughly sampled for atlantids (Richter & Seapy, 1999). The four most recently-described species, *A. fragilis*, *A. frontieri*, *A. californiensis* and *A. selvagensis*, all appear to have restricted distributions (de Vera & Seapy, 2006), so it is likely that there are additional atlantids still to be discovered. Improvements in sampling techniques and the application of combined morphological and molecular analyses are all necessary to improve understanding of atlantid taxonomy, evolution and biogeography.

## PALAEONTOLOGY

Although atlantid shells are frequently preserved in marine sediments, the age and origin of this group is uncertain. The oldest taxon (Fig. 3) considered to belong to the Atlantidae is *Bellerophina minuta* (Sowerby, 1814), described from the Cretaceous (Albian, Gault Clay Formation) of Britain (for illustration see Tracey, 2010: pl. 24, figs 16, 17; Janssen & Peijnenburg, 2014: fig. 19.6). This species is 75 myr older than any other known atlantid, but resembles the extant *Oxygyrus inflatus* so strongly that Forbes (1844) erroneously considered the two species to be synonymous. However, the fossil record of *O. inflatus* is not known to extend beyond the Pliocene (Janssen, 1998, 2007, 2012b). Therefore, if *B. minuta* is an atlantid, there is a large gap in the fossil record of atlantids for which we have no data, with the next oldest potential species appearing in the Oligocene.

Cossmann (1889) added the new extinct genus *Eoatlanta* to the Atlantidae, with the species *E. spiruloides* from the Eocene (Lutetian) of the Paris Basin. However, Lozouet (2012) and Schnetler (2013) have recently demonstrated the nonplanktic nature of this species and transferred it to the benthic Vanikoroidea. *Atlanta arenularia* Gougerot & Brailion, 1965, previously thought to be the oldest species in the genus *Atlanta*, is also found in the Eocene (Bartonian) of the Paris Basin. However, the shell morphology of this species suggests that it actually belongs within the Carinariidae.

The first certain representatives of the genus *Atlanta* (two unidentified species) were recorded from the Late Oligocene (Chattian)

and Miocene (Burdigalian–Serravallian) rocks of Malta (Janssen, 2012a). A slightly younger fossil genus, *Mioatlanta*, with one species, *M. soluta*, was described from the Miocene (Langhian) of Vetto d'Enza, northern Italy (Di Geronimo, 1974). However, additional material from the type locality demonstrates the close relationship between *Mioatlanta* and *Atlanta*, thus we are inclined to consider the two as synonymous. A further late Miocene species, known from only a few specimens, *A. cordiformis*, was found in the Dominican Republic (Janssen, 1999) and several unidentified *Atlanta* specimens (juveniles) have also been recorded from the late Miocene (Tortonian) of northern Italy (Janssen, 1995).

A number of *Atlanta* species have been recorded from Pliocene rocks worldwide. Woodring (1928) described two species, *A. diamasa* and *A. (Atlantidea) lissa*. However, the latter species, from the Bowden Beds of Jamaica, has now been interpreted as a synonym of *Protatlanta rotundata* by Janssen (2012a). These deposits were previously considered to be of Miocene age, but a much younger, Early Pliocene (Piacenzian) age has now been demonstrated using calcareous nannoplankton (Aubry, 1993), planktic foraminifera (Berggren, 1993) and holoplanktic Mollusca (Janssen, 1998). The species *A. plana*, until recently known exclusively from the extant Indo-Pacific fauna, has been recorded from Pliocene rocks in southern France and Estepona, southern Spain (Janssen, 2004, 2012b). A somewhat older occurrence (late Miocene–early Pliocene) of the same species is known from the Fiji Islands (Janssen & Grebneff, 2012). Pliocene (Piacenzian) rocks from Pangasinan (Philippines) contain a remarkable assemblage including 13 atlantid and 3 carinariid species (Janssen, 2007), among which 3 of the atlantids species were newly described (*A. lingayanensis*, *A. richteri* and *A. seapyi*). These are also the most recent atlantid species known to have become extinct. All other atlantid species found from the Pliocene of Pangasinan are extant, as are all atlantids identified from Pleistocene sediments in various localities (Fig. 3).

The genus *Protatlanta* has a single extant member, *P. souleyeti*, which is known from the Pliocene to the Recent. The oldest species, *P. rotundata* (synonyms *A. lissa* and *P. kakekawaensis*) is known from the middle to late Miocene (Mediterranean and Caribbean) and Pliocene (Mediterranean, Caribbean and Japan) (Woodring, 1928; Gabb, 1873; Shibata, 1984, 2008; Zorn, 1997; Janssen, 2004, 2007, 2012a; Janssen & Little, 2010). A second Miocene species, *P. kbiraensis* (Janssen, 2012a), is known only from Malta. However, extinct species of *Protatlanta* differ substantially from the extant type species and are likely, eventually, to be separated at genus level.

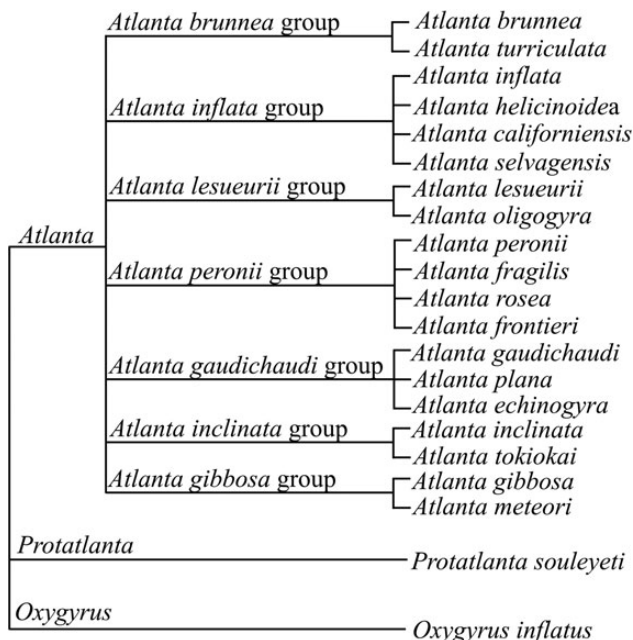
Although we do not know of any global atlantid species extinctions since the Pliocene, the distributions of extant species have changed during the Late Pleistocene. Data for *A. oligogyra*, *A. turriculata*, *A. echinogyra* and *A. plana* suggest that their current distribution is restricted to the Indo-Pacific. However, Wall-Palmer, Smart & Hart (2015) found all four species in Late Pleistocene sediments collected off Montserrat in the Caribbean Sea. These species seem to have ceased living in the Caribbean Sea during the period of climatic warming that followed the Last Glacial Maximum (LGM), potentially suggesting a localized atlantid extinction event. *Atlanta plana* was also present in the Mediterranean during the Pliocene (Janssen, 2012c), but is currently thought to be absent from the entire Atlantic Ocean.

These data emphasize the need for future research on atlantid palaeontology, in particular to investigate the large time gap during the Palaeogene. At present, atlantids are not used in palaeoceanography or as stratigraphic markers. However, our knowledge of the atlantid fossil record, though limited, has already added new insight into their abundance and temperature tolerance (Wall-Palmer *et al.*, 2014), as well as ecological relationships, such as preferred prey (Wall-Palmer *et al.*, 2015). Improving our knowledge of the atlantid fossil record is likely to prove useful in understanding the phylogenetic history of atlantids, as well as understanding how they have reacted to past environmental changes.



**Table 1.** List of all extant and extinct species of Atlantidae Rang, 1829.

<i>Atlanta brunnea</i> Gray, 1850
<i>Atlanta californiensis</i> Seapy & Richter, 1993
<i>Atlanta cordiformis</i> Gabb, 1873 <sup>a</sup>
<i>Atlanta diamesa</i> Woodring, 1828 <sup>a</sup>
<i>Atlanta echinogyra</i> Richter, 1972
<i>Atlanta fragilis</i> Richter, 1993
<i>Atlanta frontieri</i> Richter, 1993
<i>Atlanta gaudichaudi</i> Gray, 1850
<i>Atlanta gibbosa</i> Souleyet, 1852
<i>Atlanta helicinoidea</i> Gray, 1850
<i>Atlanta inclinata</i> Gray, 1850
<i>Atlanta inflata</i> Gray, 1850
<i>Atlanta lesueurii</i> Gray, 1850
<i>Atlanta lingayanensis</i> Janssen, 2007 <sup>a</sup>
<i>Atlanta meteori</i> Richter, 1972
<i>Atlanta oligogyra</i> Tesch, 1906
<i>Atlanta peronii</i> Lesueur, 1817
<i>Atlanta plana</i> Richter, 1972
<i>Atlanta richteri</i> Janssen, 2007 <sup>a</sup>
<i>Atlanta rosea</i> Gray, 1850
<i>Atlanta seapyi</i> Janssen, 2007 <sup>a</sup>
<i>Atlanta selvagensis</i> de Vera & Seapy, 2006
<i>Atlanta soluta</i> (Di Geronimo, 1974) <sup>a</sup>
<i>Atlanta tokiokai</i> Van der Spoel & Troost, 1972
<i>Atlanta turriculata</i> d'Orbigny, 1836
<i>Bellerophina minuta</i> (Sowerby, 1814) <sup>a</sup>
<i>Oxygyrus inflatus</i> Benson, 1835
<i>Protatlanta kbiraensis</i> Janssen, 2012a
<i>Protatlanta rotundata</i> (Gabb, 1873) <sup>a</sup>
<i>Protatlanta souleyeti</i> (Smith, 1888)

<sup>a</sup>Extinct taxa.**Figure 2.** Hypothesized organization of the extant species of the family Atlantidae, based on shell morphology (after Seapy, 2011).

## ECOLOGY

The importance of atlantids in the ocean foodweb is currently unknown. Atlantids are a family of specialized, mobile carnivores with large eyes that suggest selective predation (Lalli & Gilmer, 1989). Atlantids are also abundant relative to other shelled holoplanktic gastropods, making up an average of 16% (up to 44%) of shelled holoplanktic gastropods collected at each station during AMT24 (A.K. Burridge, personal communication, 2015) and up to 28% in net hauls collected off of Baja California (McGowan & Fraundorf, 1966). Atlantids are also consistently found to be the most abundant heteropods (Richter, 1968; Seapy *et al.*, 2003; Ohman *et al.*, 2009; Ossenbrügger, 2010), occurring at densities of up to 17 individuals of a single species (*Atlanta gaudichaudi*) per m<sup>3</sup> of water (Newman, 1990a). In plankton-net hauls, larval and juvenile atlantids are generally more abundant than adults (Thiriou-Quévieux, 1973; Newman, 1990a). This may, however, be an artefact of net avoidance, a phenomenon demonstrated by McGowan & Fraundorf (1966), who found that estimates of atlantid abundance and diversity were reduced when using nets with smaller apertures. They caught 37–350% more atlantid specimens per 1,000 m<sup>3</sup> of water with a 140-cm diameter ring net compared with a 20-cm diameter ring net. Seapy (1990b) found that specimens captured using a larger 4-m<sup>2</sup> aperture ring net were on average 50% larger in size than specimens caught using a 0.7-m<sup>2</sup> aperture bongo net (although the volume of water filtered was not comparable). Thus, it is likely that adult atlantids, and atlantids in general, are more abundant in our oceans than plankton hauls suggest.

The Late Pleistocene fossil record of holoplanktic gastropods reveals that atlantids are often abundant in sediments, relative to other shelled holoplanktic gastropods. This is particularly true during warm periods, when atlantids have been found to compose up to 69, 27 and 33% of holoplanktic gastropod shells in Mediterranean Sea, Caribbean Sea and Indian Ocean (Maldives) sediments, respectively (Wall-Palmer *et al.*, 2014). Numerically, atlantids can be as frequent as 3,333, 2,160 and 2,588 specimens per gram of sediment in the 150–500 µm fraction in material from these three areas, respectively (data extracted from Wall-Palmer *et al.*, 2014).

### Seasonal abundances

Limited published data suggest that atlantids can tolerate a range (c. 30–35 PSU) of salinities (Xu & Li, 2005; Xu, 2007; Cruz, 2012). However, they are sensitive to other environmental factors (Cruz, 1996, 1998) and exhibit distinct seasonal changes in abundance (Table 2) under the influence of water temperature and currents (Vane & Colebrook, 1962; Richter 1968; Thiriou-Quévieux, 1968; Cummings & Seapy, 2003; Xu & Li, 2005; Xu, 2007; Seapy, 2008; Angulo-Campillo *et al.*, 2011), monsoonal changes (Mathew *et al.*, 1990) and wet and dry seasons (Frontier, 1973a, b). Reproductive seasons do not appear to be strongly linked to seasonal abundances, because larval stages are often found throughout the year (Richter, 1968).

The effects of seasonal currents, both vertical and horizontal, upon atlantid abundances have been identified in several regions. In the Gulf of Naples, all heteropod species show the same seasonal changes in abundance, with a small, not always distinctive maximum in early spring, followed by a minimum in summer and a very distinct maximum in autumn (Richter, 1968). This pattern was inferred to be most likely influenced by hydrographic factors, in particular seasonal vertical convection. Cummings & Seapy (2003) also found a strong link between seasonal currents and the abundance of *A. californiensis* in the San Pedro Basin, CA. Highest abundances occurred during the summer, coinciding with the strongest seasonal flow of the California Current and Southern California Eddy. During the winter,

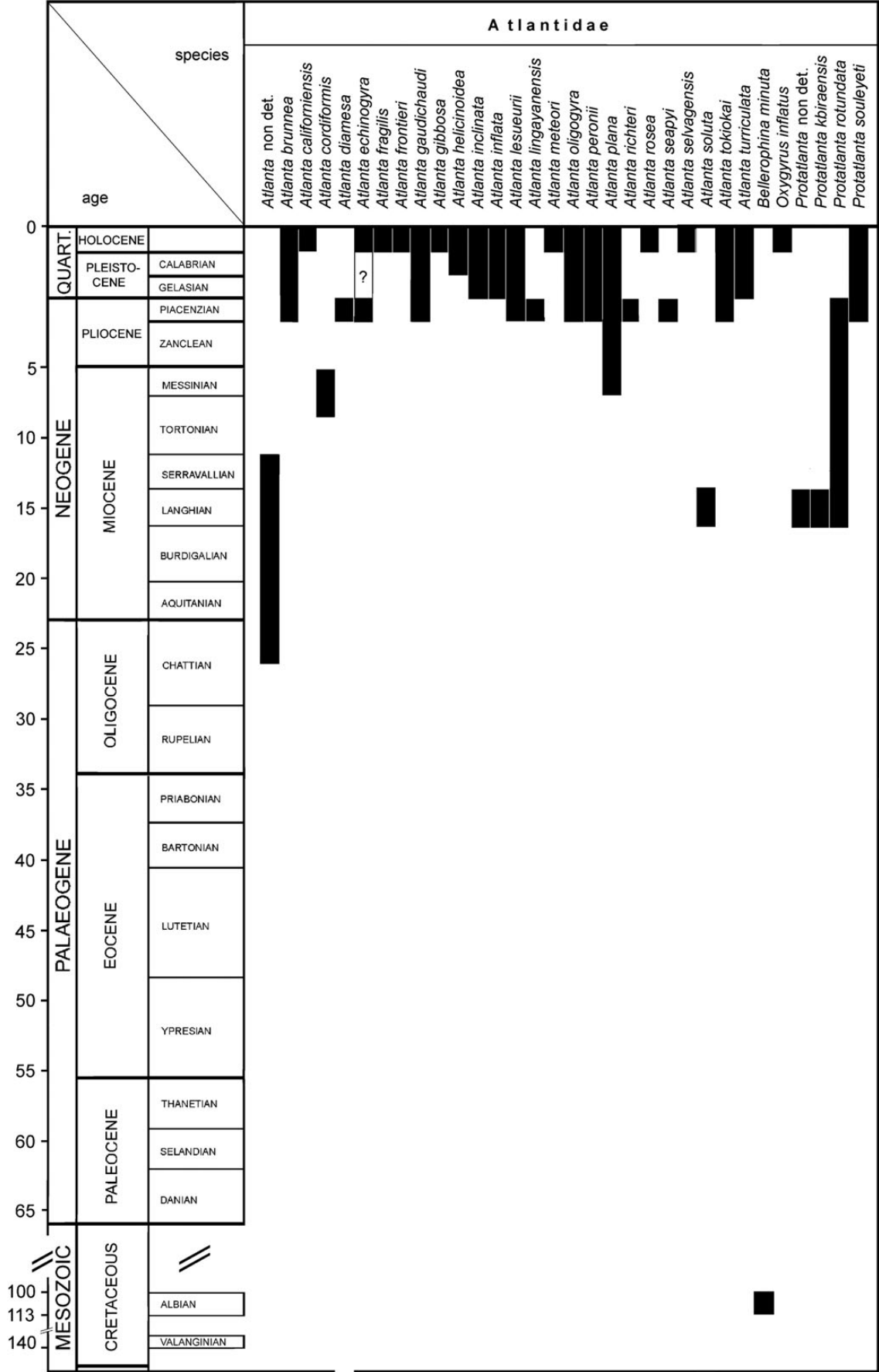


Figure 3. The known biostratigraphy of all extinct and extant atlantid species, compiled from published literature.

**Table 2.** Factors affecting seasonal abundances, compiled from published literature.

Location	Seasons during which atlantids are most abundant	Attributed reason	References
Gulf of Naples, Italy	Early spring and autumn	Seasonal vertical convection	Richter (1968)
San Pedro Basin, California	Summer	California current and Southern California eddy	Cummings & Seapy (2003)
East China Sea	Summer and Autumn	Water temperature related to shifting Taiwan warm current	Xu & Li (2005), Xu (2007)
West of UK	August to October	Water currents	Vane & Colebrook (1962)
Bay of Bengal	November and December, premonsoonal	Monsoonal changes	Mathew <i>et al.</i> (1990)
Arabian Sea	November and December, postmonsoonal	Monsoonal changes	Mathew <i>et al.</i> (1990)
Nosy-Bé, Madagascar	December to May	Wet season	Frontier (1973a, b)
Great Barrier Reef, Australia	Summer months	None given	Newman (1990a)
Gulf of Mexico	<i>A. selvagensis</i> May <i>A. gaudichaudi</i> November	None given	Lemus-Santana <i>et al.</i> (2014)
Banyuls-sur-Mer, S France	March to December, but some species all year	None given	Thiriot-Quiévreux (1970)
Castellón, E Spain	June to August	None given	Vives (1966)
Oahu, Hawaii	April	None given	Seapy (2008)

when the flow of these currents is weakest, the lowest abundances of *A. californiensis* were recorded. In the East China Sea (Xu & Li, 2005; Xu, 2007), higher abundances of atlantids (*A. rosea*, *A. lesueurii* and *A. peronii*) during the summer and autumn were found to be closely related to changes in the water temperature which, in common with other areas, is also related to shifting currents (Taiwan Warm Current).

In the Indian Ocean, Mathew *et al.* (1990) showed that the monsoon influenced heteropod abundance, with greatest numbers generally collected during November and December. This is during the Indian Ocean winter monsoon, characterized by dry weather and gentle, steady winds. However, the influence of the monsoon appears to be variable geographically. In the eastern Arabian Sea, post-monsoon increases in abundance have been reported, whereas in the Bay of Bengal the increases in abundance occur before the monsoon (Mathew *et al.*, 1990). Consequently, it is likely to be a combination of temperature, shifting water currents and food availability that influences heteropod abundance in these regions, rather than the monsoon *per se*. Frontier (1973a, b) identified a link between changing abundances of *A. gaudichaudi* and wet and dry seasons around the coast of Nosy-Bé, Madagascar. Highest abundances on the shelf coincided with the wet season, with the highest numbers occurring between December and May. It is thought that this link is caused when unusually prolonged dry periods detrimentally affect the juvenile population of the species (Frontier, 1973a, b).

These studies suggest that the seasonal abundance of atlantid heteropods is complex and closely linked to changes in water currents and food availability, rather than water temperature alone. While this may be a consequence of their weak swimming ability, it is more likely to be driven by movements and availability of prey. Newman (1990a) found that atlantids can remain suspended and stationary while currents flow over them. Therefore, atlantids are able to control how far they travel in currents. A number of studies have found that seasonal variations in atlantid abundance are species specific, with a seasonal succession of species (Evans, 1968; Thiriot-Quiévreux, 1968). Lemus-Santana *et al.* (2014) suggest that this seasonal succession is an ecological strategy to avoid competition for prey. Newman (1990b) found that three species of atlantid (*A. gaudichaudi*, *A. lesueurii* and *A. helicinoidea*) showed an opposing pattern of seasonality in two areas of the Great Barrier Reef, Australia, that are 1,180 km apart. In the north, the three species were more abundant during the winter sampling, whereas in the south the three were more abundant during the summer sampling. A similar pattern was found off the coast of the British Isles, where higher abundances of atlantids appeared in the northwest later

than in the southwest. Vane & Colebrook (1962) attributed this later arrival to currents passing from south to north, suggesting that atlantids travel in species-specific groups. Thiriot-Quiévreux (1968) found that off southeastern France larval and adult stages show the same seasonality, supporting this type of horizontal migration.

#### Vertical distribution and migration

The vertical distribution of atlantids is not well understood. Atlantids have been found to live within the epipelagic zone, the upper 250 m of the water column (Jivaluk, 1998; Michel & Michel, 1991; Paulinose *et al.*, 1992; Ossenbrügger, 2010) and often only at much shallower depths (Lalli & Gilmer, 1989; Seapy, 1990b; Ossenbrügger, 2010). Lemus-Santana *et al.* (2014) have provided the only detailed species-specific depth ranges for atlantids, but only for the Gulf of Mexico.

In an attempt to identify at what depth shell calcification takes place, Grossman *et al.* (1986) carried out geochemical analysis of stable oxygen isotopes of both whole atlantid shells (*A. gaudichaudi* and *A. inclinata*) and of specific parts of the shells that represent ontogenetic stages. The study found that *A. gaudichaudi* and *A. inclinata* precipitate their shells in shallow water at depths of less than 75 m, while another *Atlanta* species (not identified to specific level) did so at 75–125 m. Different sections of the shell were found to have similar oxygen isotopic compositions, suggesting that these atlantids precipitate their shells at the same depth throughout their lives. However, according to Lalli & Gilmer (1989) atlantids add to their shell thickness throughout their lives, which may explain why there was no difference in isotopic composition between the stages. Further geochemical analysis of shells at different stages of development, using new laser ablation techniques for example, is needed and will help to identify the vertical ranges of atlantids.

Based on plankton sampling using nets at different depths, it is thought that many (and potentially all) atlantid species show some degree of daily vertical migration within the epipelagic zone. However, many studies have shown conflicting results, suggesting that migration behaviours are often stage- and species-specific, with some species exhibiting nocturnal migration towards the surface and others exhibiting no migration at all (Fig. 4).

Oberwimmer (1898) was the first to suggest that heteropods, like pteropods, lived at depth during daylight hours and migrated to the surface during darkness. Larval atlantids appear to show the most consistent nocturnal migration patterns (Richter, 1973; Seapy & Richter, 1993) and Richter (1973) suggested that the numbers of migrating larvae are likely to be much higher than

the numbers of migrating adults. Seapy & Richter (1993) found that larval atlantids migrate in large groups and cover large vertical distances of up to 300 m. Larval atlantids display particular patterns of migration (Fig. 4) with species-specific timing. Generally sunset is followed by high numbers in the surface waters for around 2 h, much lower numbers for a further 2 h, then an increase to a maximum and finally dropping before sunrise (Seapy & Richter, 1993). Oberwimmer (1898) also observed two periods of high abundance (18:45–20:45 and 03:45–05:30), separated by a period of low abundance. Seapy & Richter (1993) hypothesized that the feeding behaviour of larval atlantids causes them to migrate in a ‘saw-tooth’ path. Ciliary movements of the velum propel the larvae, thus they must feed as they swim upwards. The larvae alternately feed and rest, which translates to alternating periods of upward swimming and passive sinking.

Large-sized (shell 6–12 mm) species that reside at greater depths (200–250 m) have also been found to migrate towards the surface during the night (Fig. 3), including *A. peronii* (Seapy, 1990b; Michel & Michel, 1991), *Oxygyrus inflatus* (Ossenbrügger, 2010) and *A. meteori* (Seapy, 1990b). Lalli & Gilmer (1989) suggested that, similar to the larvae, adults move in a saw-tooth path, swimming upwards for a brief period and then sinking a few centimetres. It is only during the sinking period that the adult atlantids use their scanning eye movements, which detect objects (prey or predators) within the water. Seapy (1990b) and Lalli & Gilmer (1989) proposed that atlantids probably use their large, elaborate eyes to detect prey in low light conditions at night and may feed on bioluminescent prey. Richter (1974) found that species with larger eyes tend to dwell deeper than species with smaller eyes, probably connected with the reduction in light with depth.

In contrast, *in-situ* observations of *O. inflatus* found it to be inactive at night, hanging motionless from strands of mucus, probably produced by the foot (Lalli & Gilmer, 1989). Newman (1990a) also observed individuals of *A. gaudichaudi* suspended in the water by mucous threads attached to the aperture or the foot. This, however, may not be a sign of inactivity, but a technique for detecting prey, because this behaviour is well suited to predators that use downwelling sunlight to locate prey and then pursue it. Newman (1990a) observed in the laboratory that *A. gaudichaudi* often swam upwards, hitting the water surface with the proboscis and ‘attaching’ for a few minutes. The function of this behaviour is not known.

Environmental factors such as seasonality have also been found to affect vertical migration behaviour. Seapy (2008) found that a number of Hawaiian atlantids (including *Protatlanta souleyeti*, *A. turriculata*, *A. meteori*, *A. peronii* and *A. helicinoidea*) only showed nocturnal migration during part of the year. Similarly, Vives (1966) reported an increase in the vertical stratification of *A. helicinoidea* (but not *A. peronii*) during the summer months off north-western Spain. Lemus-Santana *et al.* (2014) found that *A. selvagensis* and *A. gaudichaudi* show increased nocturnal abundances in May and November, respectively.

Seapy (1990b) found no difference between the numbers of small (shell 1.5–4 mm) atlantid species captured during the day and at night, when using a large 4-m<sup>2</sup> tow net. From this, it was suggested that small species do not exhibit diel migration and that the apparent migrations of some others may be an artefact of daytime net avoidance (Fig. 4). Similarly, Ossenbrügger (2010) reported species of *Atlanta* to be equally abundant during day and night off the Cape Verde Islands. Seapy (1990b) observed that nonmigrating atlantids off Hawaii tended to be the smaller species that reside in shallower waters (<140 m), as supported by *in-situ* observations of shallow-water species (Lalli & Gilmer, 1989).

From this collated information, it is clear that the vertical migrations of atlantids are complex, being seasonal, specific to stage and species, and also influenced by sampling method. The difficulty in comparing published data is not surprising, taking

into account the challenges encountered in collecting representative samples, of observing specimens *in situ* and the unfeasibility of keeping and accurately observing specimens in the laboratory. It is likely that new methods of observing (e.g. *in-situ* ROV and scuba observations) and sampling are needed to understand this complicated behaviour fully.

### Trophic relationships

Atlantids are carnivores and are known to prey selectively upon pteropods, other heteropods and copepods (Richter, 1982; Newman, 1990a). This selective predation makes atlantids an important component of the ocean foodweb (Thiriot-Quiévreux, 1973). The long proboscis suggests that they are adapted to preying on shelled organisms and they have been observed using their proboscis to reach into elongate pteropod shells (Newman, 1990a). However, the Late Pleistocene to Recent fossil record from the Caribbean Sea suggests that pteropods are not the preferred prey of atlantids. Wall-Palmer *et al.* (2015) found significant negative correlations between the abundance of shelled pteropods and atlantids, suggesting that atlantids were successful at times when pteropods were not (and *vice versa*). This indicates that shelled pteropods are unlikely to be the preferred prey. Noncalcifying zooplankton (such as copepods), which did not leave a fossil record, may be a more likely favoured food source (Wall-Palmer *et al.*, 2015). Frontier (1973b) reported juveniles of *A. gaudichaudi* at their highest abundance when phytoplankton and phytophagous zooplankton were also at their greatest abundance, which suggests that juvenile atlantids depend upon such prey.

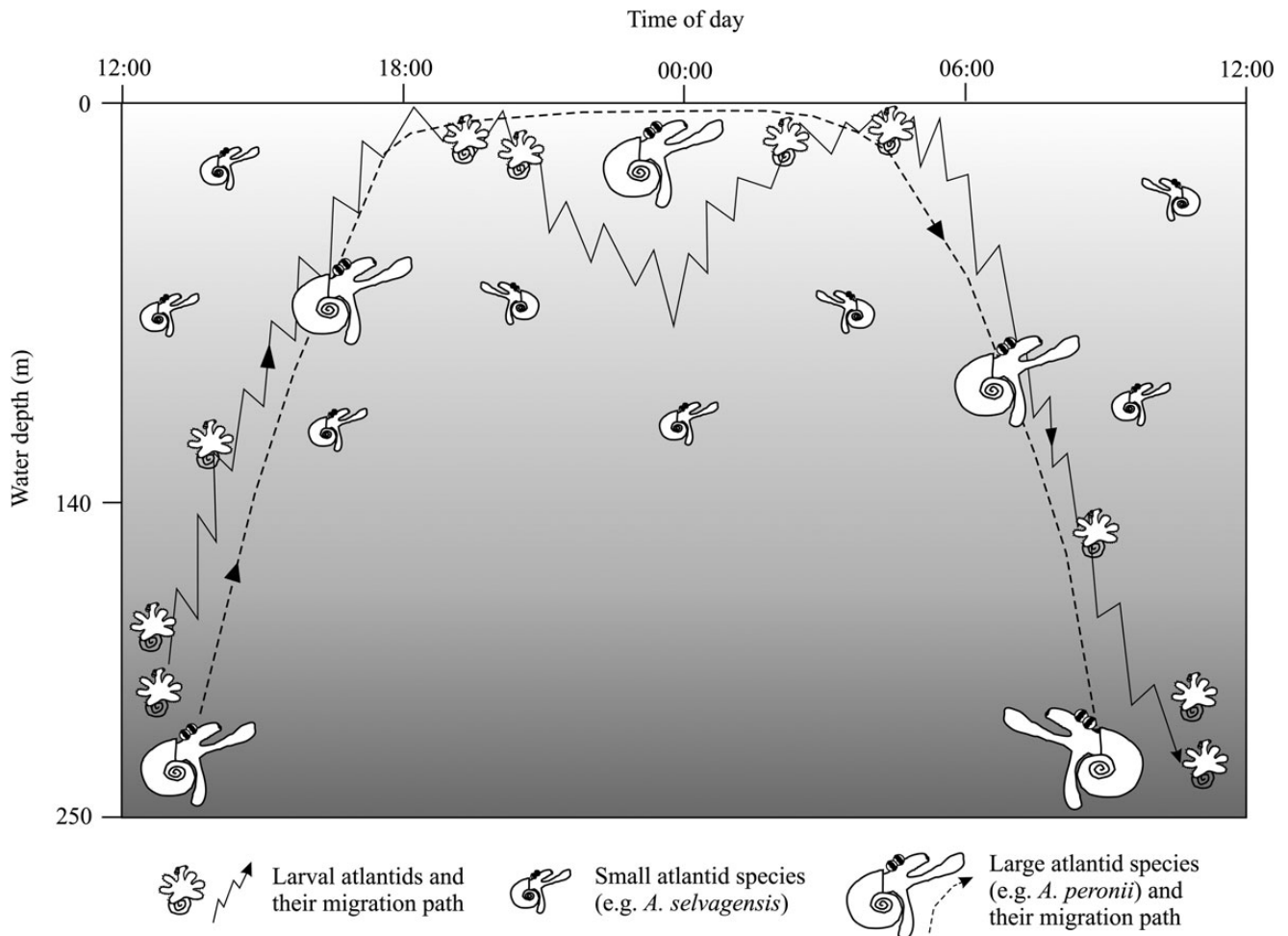
Atlantids use their specialized scanning eyes (Land, 1982) to detect prey and then snare it using both their sucker fin and hooked protrusible radula (Lalli & Gilmer, 1989; Newman, 1990a). They differ from the other heteropod families in their feeding behaviour, scraping and rasping their prey rather than swallowing it whole (Richter, 1968).

While currently there are not any studies quantifying the importance of atlantids in the ocean foodweb, they have been found in the stomach contents of commercially fished species, including dolphin-fish, for which *O. inflatus* is the favoured prey of immature adults (Richter, 1982), spiny lobsters (Wang, Mackenzie & Jeffs, 2014), bluefin tuna (Dragovich, 1970) and Pacific salmon (Nomura & Davis, 2005). In the East China Sea there is a link between high abundances of atlantids and the migration routes of mackerel, suggesting that atlantids are important to fisheries in the area (Xu & Li, 2005). In a study of the stomach contents of longnose lancetfish in the Central Pacific, Moteki, Fujita & Kohno (1993) reported heteropods (15.45% of prey individuals) to be the third most important prey after crustaceans and fish. Of these, the atlantids (*Atlanta* sp. and *O. inflatus*) made up 0.59% of the total prey individuals, which is comparable with the number of pteropods found (0.76%). While atlantids are known to be an important food source for planktivorous reef fish, they may also act as vectors of dinoflagellate toxins and as hosts of parasites detrimental to commercially important species of fish (Newman, 1990b).

### BIOGEOGRAPHY

With the caveats that there are still large areas of the oceans for which no data are available and that species identification can be subjective, available data (Fig. 5) largely support a warm-water distribution of atlantids as indicated by Thiriot-Quiévreux (1973), de Vera & Seapy (2006) and de Vera *et al.* (2006). No detailed biogeographical data were found for *Atlanta fragilis* (Richter, 1993; Seapy, 2011). Most species live mainly in the circumglobal warm-water region (Figs 5, 6), although around two-thirds show rare occurrences within transitional zones and cold-water regions.





**Figure 4.** Summary of atlantid migrations over 24-h cycle, compiled from published literature (Oberwimmer, 1898; Lalli & Gilmer, 1989; Seapy, 1990b; Michel & Michel, 1991; Seapy & Richter, 1993; Ossenbrügger, 2010). Larval atlantids exhibit a 'saw-tooth' nocturnal migration with two periods at the surface. Adults of large atlantid species also show a nocturnal migration from deeper waters to the surface. Adults of smaller atlantid species live in shallower waters and do not migrate.

Although there are few records of atlantids living in cold-water regions (Fig. 5), the Late Pleistocene fossil record demonstrates that they can be common in cold waters (Wall-Palmer *et al.*, 2014). During the LGM in the Mediterranean Sea, when sea surface temperatures were 7–10 °C (Sbaffi *et al.*, 2001; Hayes *et al.*, 2005), atlantids accounted for up to 17% of holoplanktic gastropod individuals (Wall-Palmer *et al.*, 2014). Howard *et al.* (2011) identified a small number (13 individuals at 2 stations) of *Atlanta gaudichaudi* (Fig. 5) from vertical net hauls south of Tasmania, just within the Subantarctic zone of the Southern Ocean (furthest south 44°53'S, 142°59'E). Atlantids have been found in this region during consecutive years (D. Roberts, personal communication, 2013), indicating that this is likely to be a long-term population. Pilkington (1970) also found heteropods, identified as *A. helicinoidea*, to be common and even abundant in plankton hauls off Taiaroa Head, New Zealand (45°46'12"S, 170°53'24"E). Vane (1961) and Vane & Colebrook (1962) discovered a number of atlantid species living off the west coast of the British Isles during the summer months, up to 57°N, but only identified *A. peronii* to species level.

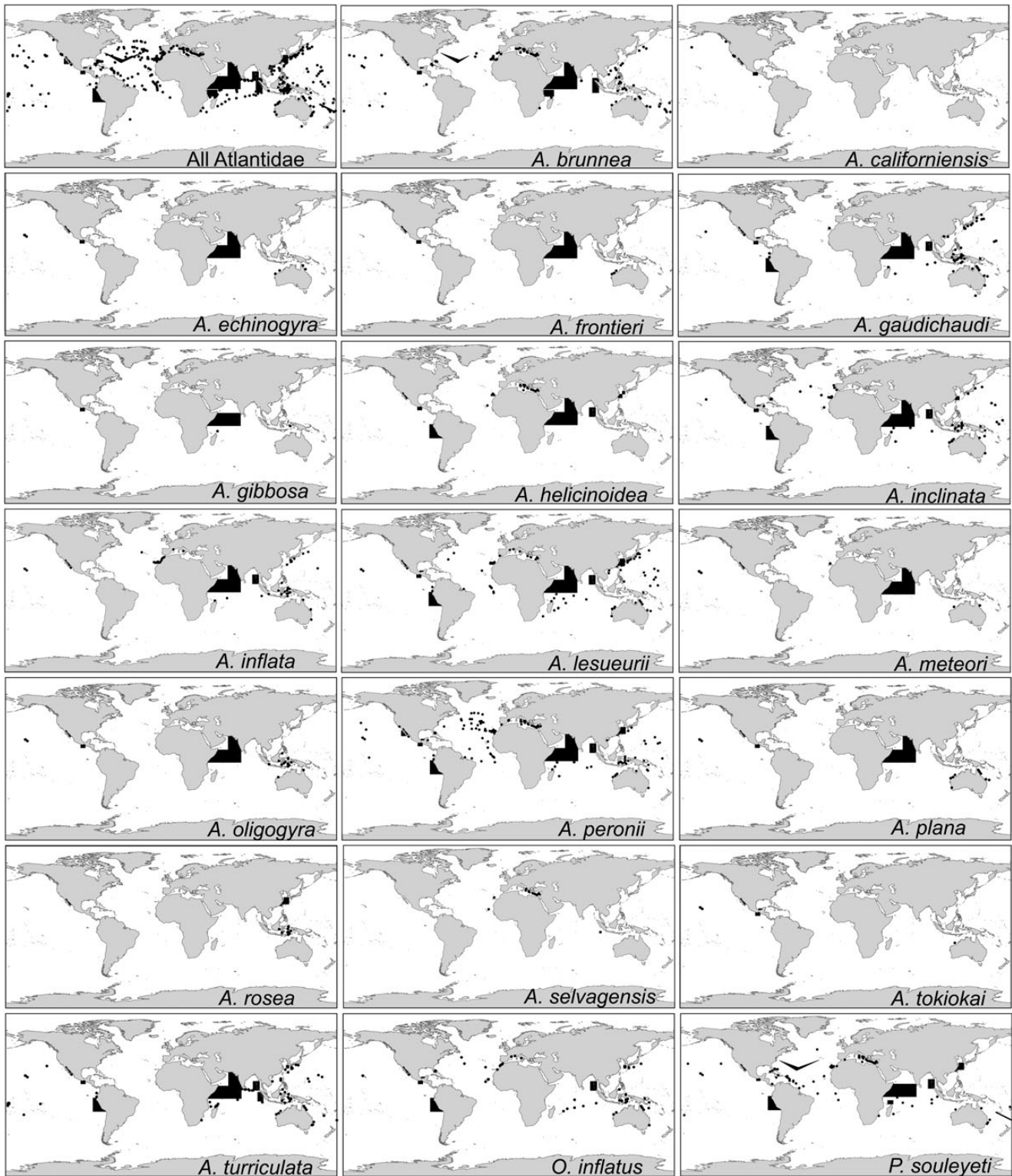
*Atlanta californiensis* is thought to prefer colder waters, being largely restricted to the cold California Current, from southern California to British Columbia (Seapy & Richter, 1993; Cummings & Seapy, 2003). However, Moreno-Alcántara *et al.* (2014) recently found that *A. californiensis* also lives in the warmer waters of the

Pacific Ocean off southern Mexico, suggesting a tolerance to a wide range of surface water conditions.

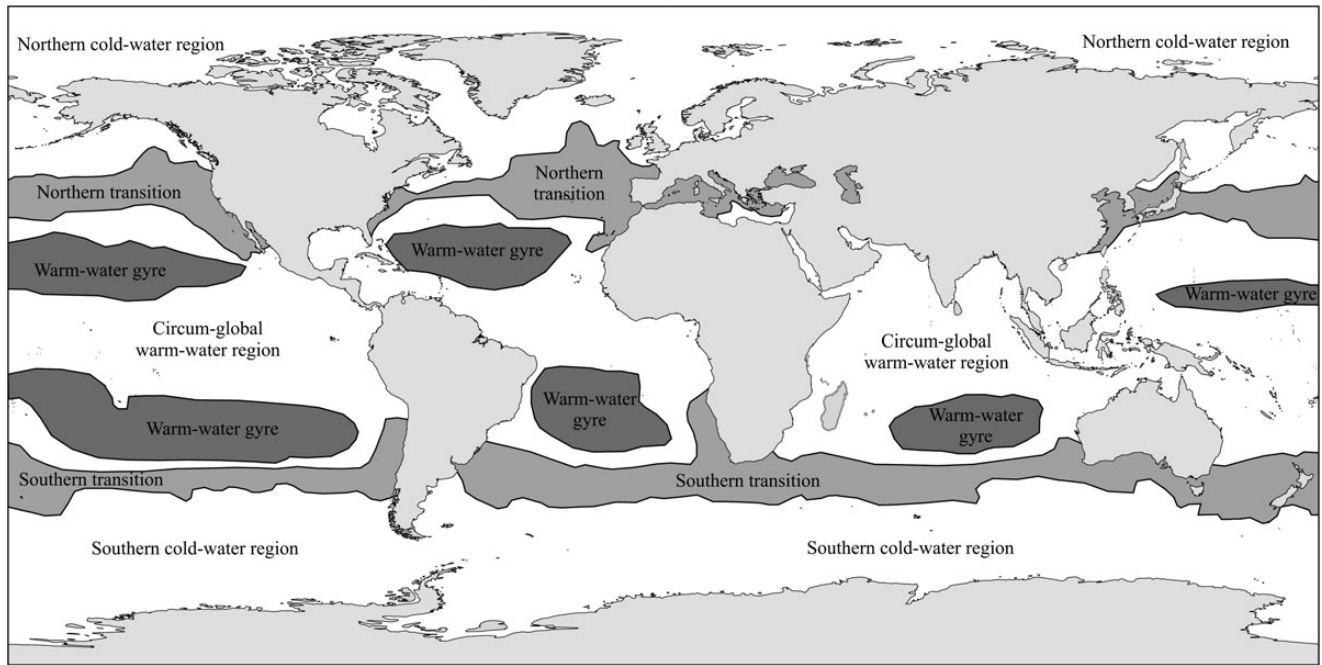
From the collated data (Fig. 5) it is not possible to determine temperature ranges for each species, but some geographical patterns can be seen. Nearly half of the species (*A. brunnea*, *A. gaudichaudi*, *A. helicinoidea*, *A. inclinata*, *A. lesueurii*, *A. meteori*, *A. peronii*, *Oxygyrus inflatus* and *Protatlanta souleyeti*) show a cosmopolitan, global distribution, occurring in the Atlantic, Indian and Pacific Oceans. The majority of the species (11 of 21) show a more restricted distribution and nine of these have not been recorded from the Atlantic Ocean, although some rare species, such as *A. rosea* and *A. tokiokai*, are likely to have a wider distribution than the data indicate.

The most restricted distribution is displayed by *A. californiensis*, which has only been reported along the west coast of North America, from Mexico to British Columbia (Fig. 5). However, this species has only recently been described and its occurrence may not have been identified in earlier studies (Seapy & Richter, 1993). A second species with a very restricted distribution, *A. fragilis*, has only been found in the tropical waters of the central Atlantic Ocean (Richter, 1993; Seapy, 2011). A species of thecosome pteropod, *Cuvierina cancapae*, is also known to be confined to the tropical Atlantic Ocean (BurrIDGE *et al.*, 2015), so *A. fragilis* may genuinely be confined to this small geographical area. However, *A. fragilis* has very similar morphological features to *A. peronii* and may have been misidentified elsewhere.





**Figure 5.** Distributions of 20 atlantid species compiled from published literature (Smith, 1888; Vayssi re, 1904; Tesch, 1906, 1910, 1949; Schiemenz, 1911; Bonnevie, 1920; Tokioka, 1955a, b; Ralph, 1957; Furnestin, 1961; Taki & Okutani, 1962; McGowan & Fraundorf, 1966; Evans, 1968; Richter, 1968, 1974; Pilkington, 1970; Thiriot-Qu ievreux, 1970; Frontier, 1973a, b; Grossman *et al.*, 1986; S nchez-Hidalgo y Anda, 1989; Newman, 1990a, b; Seapy, 1990a, b; Lozano Soldevilla & Hern ndez Hern ndez, 1991; Michel & Michel, 1991; Hern ndez *et al.*, 1993; Seapy & Richter, 1993; Aravindakshan & Stephen, 1996; Cruz, 1998; Gonz lez, 1998; Castellanos & Suarez-Morales, 2001; Cummings & Seapy, 2003; Seapy *et al.*, 2003;  evik *et al.*, 2006; de Vera, Seapy & Hern ndez, 2006; de Vera & Seapy, 2006; Xu, 2007; Ay n *et al.*, 2008; Seapy, 2008; Ossenbr gger, 2010; Angulo-Campillo *et al.*, 2011; Howard *et al.*, 2011; Lemus-Santana *et al.*, 2014; Moreno-Alc ntara *et al.*, 2014).



**Figure 6.** Zooplankton biogeographical provinces, modified from Oliver & Irwin (2008).

The occurrence of the most recently described species, *A. selvagensis*, was believed to be restricted to the eastern Atlantic Ocean. However, in a recent review of *A. inflata* and *A. selvagensis*, two species with similar shell morphology, Janssen & Seapy (2009) showed that *A. inflata* is restricted to the Pacific Ocean, while all specimens previously identified as *A. inflata* in the Atlantic and Indian Oceans are *A. selvagensis*, thus broadening the range of the latter. In addition to the tropical and subtropical distribution described by Seapy (2011) for these two species, they are also found within cooler transitional waters (Figs 5, 6).

The remaining species, *A. turriculata*, *A. frontieri*, *A. echinogyra*, *A. gibbosa* and *A. plana* have been reported only in the Indian and Pacific Oceans (Fig. 4). *Atlanta oligogyra* was previously thought to have a global distribution, but the data show that it is also restricted to Indo-Pacific waters.

#### Shelf vs open ocean

There are a number of conflicting findings on the preference of atlantids for onshore (neritic) and offshore (oceanic) waters. While some studies have found no preference (Frontier, 1973a, b; Mathew *et al.*, 1990), most have shown a difference between the abundances of atlantids in neritic and oceanic waters. Frontier (1966, 1973a, b) found that although adult *A. gaudichaudi* showed no preference of water depth, the more abundant juveniles preferred neritic waters and that, as a result, species richness and abundances generally decreased from the shelf to the open ocean. This trend was also reported by Van der Spoel (1996), who suggested that heteropods avoid the central areas of oceans. However, a number of studies have revealed the opposite trend, with increased abundance in oceanic waters. Seapy (2008) showed heteropods to be consistently more abundant at offshore stations (up to 15 nmi from the coast) than more coastal stations (less than 1 nmi) in southwest Oahu, Hawaii. Similarly, Ossenbrügger (2010) found heteropod abundances to be higher in the open ocean than on the flanks of a seamount in the Cape Verde Islands. Grice & Hart (1962) reported atlantids to be almost absent from coastal waters in the eastern Atlantic, with only a single species (*P. souleyeti*) in the neritic zone and 11

heteropod species in the oceanic Gulf Stream and Sargasso Sea. To the west of the British Isles *A. peronii* generally inhabits offshore waters over 180 m (Vane, 1961). These varying trends may be due to onshore and offshore currents, which strongly influence the position and abundance of atlantids. There could also be stage- and species-specific preferences for water depth. For instance, Newman (1990a) found veligers of *A. gaudichaudi* to be more abundant closer to the shore, whereas adults of the same species showed a preference for the deeper, open ocean.

In summary, the overall geographical area sampled for atlantids is still relatively small and much research is still required on atlantid biogeography. Data are currently not available for large areas of the southern Atlantic Ocean, southern Indian Ocean and much of the Pacific Ocean. There are also very few records for subpolar and polar waters (which may be because atlantids do not live in these areas). Most species have geographically restricted distributions, so it is important that all areas of the ocean are sampled. Improved sampling techniques and species identification will also reveal more accurate distributions.

#### NEXT STEPS

We suggest that the most pressing needs in atlantid research are in the basic, but fundamental areas of taxonomy, sampling techniques, vertical distributions and biogeography. Understanding these key areas will facilitate subsequent research on the response of atlantids to environmental changes, the importance of atlantids in the ocean foodweb and their significance to commercially fished species.

The improvement and updating of atlantid taxonomy is the most important priority. The development of combined molecular and morphological identification (e.g. Burridge *et al.*, 2015) will improve the quantity and quality of data on atlantids. In addition to the detailed scanning electron microscopy images of atlantids that are already available (e.g. Seapy, 2011; Janssen, 2012c), new methods should be considered, such as micro-CT imaging, which allows interactive examination of virtual specimens. Advances in DNA barcoding and application of molecular methods for identifying species boundaries are also extremely

important for improving atlantid taxonomy, to determine whether morphological variations indicate different species or variation within a species.

The second priority for future research is the improvement of sampling techniques. The use of larger-aperture nets reduces net-avoiding behaviour (McGowan & Fraundorf, 1966; Seapy, 1990a). Capture of atlantids will also be improved by adopting techniques used to catch small, fast-swimming fish (such as using slightly larger-mesh nets, up to 500 µm), sampling with horizontal net tows rather than vertical net hauls and by using faster towing speeds.

Determining the geographic ranges, depth distributions and migration behaviour of atlantids should also be considered as an important part of improving sampling techniques, so that nets can more accurately target the optimum depth and time of day. Discovering the vertical distribution of atlantids will involve a combination of stratified net collections, shell geochemistry and field observations. Knowledge of the biogeography, vertical distributions and migration behaviour of atlantids is also crucial to understanding their environmental requirements. This information will be fundamental to predicting how atlantids will be affected by global environmental changes. For example, it has been suggested that shelled pteropods that exhibit diel migration may be more resistant to the effects of ocean acidification (Maas, Wishner & Seibel, 2012) and this could also be true of atlantids. New information of ecology and biogeography will also improve our interpretation of the rich fossil record of atlantids, providing insights into their evolutionary history and past responses to global changes.

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