

A Historical Summary of the Distribution and Diet of Australian Sea Hares (Gastropoda: Heterobranchia: Aplysiidae)

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Matt J. Nimbs, Richard C. Willan, and Stephen D. A. Smith (2017) Recent studies have highlighted the great diversity of sea hares (Aplysiidae) in central New South Wales, but their distribution elsewhere in Australian waters has not previously been analysed. Despite the fact that they are often very abundant and occur in readily accessible coastal habitats, much of the published literature on Australian sea hares concentrates on their taxonomy. As a result, there is a paucity of information about their biology and ecology. This study, therefore, had the objective of compiling the available information on distribution and diet of aplysiids in continental Australia and its offshore island territories to identify important knowledge gaps and provide focus for future research efforts. Aplysiid diversity is highest in the subtropics on both sides of the Australian continent. Whilst animals in the genus *Aplysia* have the broadest diets, drawing from the three major algal groups, other aplysiids can be highly specialised, with a diet that is restricted to only one or a few species. Although the diets of some widespread, frequently-observed taxa have been investigated, those for lesser-known, endemic taxa remain unclear and require specific investigation.

Key words: *Aplysia*, *Dolabrifera*, *Dolabella*, Algae, Biogeography, Anaspidea, Herbivores.

BACKGROUND

The heterobranch family Aplysiidae Lamarck, 1809, encompassing the sea slugs collectively known as ‘sea hares’, currently comprises 64 species distributed among 11 genera (WoRMS 2017). All genera are found in Australian waters except for *Barnardaclesia* Eales & Engel, 1935 and *Paraplysia* Pilsbry, 1895. The Australian fauna is numerically uncertain, where, of the 25 species recorded, at least 12 are taxonomically insecure (Nimbs et al. 2017). For the Australian fauna, little is known of their specific diets, however, as with all sea hares, they are almost exclusively epifaunal herbivores (Thompson 1976: 102; Yonow 2008: 96; Gosliner et al. 2015: 100) consuming algae, angiosperms (seagrasses) and

filamentous cyanobacteria. As with other shallow-water herbivorous molluscs, polyphagy can occur with accidental ingestion of animal material during grazing (Camus et al. 2008).

Some species of sea hares can be highly selective and may specifically target non-plant foods (e.g. *Phyllaplysia taylori* Dall, 1900 is believed to consume diatoms (Beeman 1970)). Carefoot (1987) also noted that, when starved, captive animals of *Aplysia californica* J.G. Cooper, 1863 engaged in cannibalism and oophagy. Although the diets of some taxa have been well studied, most studies comprised feeding assays carried out in a laboratory as part of broader analyses of chemical ecology, physiology, or to explore the production of secondary metabolites (Carefoot 1970; Pennings and Paul 1992; Rogers

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et al. 2000; Ginsburg and Paul 2001; Capper et al. 2006). For those *in vitro* studies, the foods offered were based on observations of algae that were found to co-occur with the sea hare in its natural environment under the assumption that these were the most likely food sources.

Whilst aplysiids are predominantly creatures of the tropics and subtropics (Rudman and Willan 1998), their greatest diversity occurs where oceanographic and benthic conditions support suitable macroalgal habitats (Nimbs et al. 2017). Carefoot (1987) noted that the Australian region was the most biodiverse for animals in the genus *Aplysia* Linnaeus, 1767, and recent work indicates that this can be broadened to include the family Aplysiidae more generally, with the highest diversity occurring in the warm temperate waters of the central New South Wales (NSW) coast (Nimbs et al. 2017).

Documentation of Australian sea hare distribution at a regional scale has not previously been undertaken because of taxonomic uncertainties. Nevertheless, with tropical affinity (Rudman and Willan 1998), protracted larval duration (Kempf 1981), and high fecundity (Willan 1979; Wells and Bryce 2003), it is likely that settlement and metamorphosis may occur in novel temperate locations as oceanographic conditions (temperature, currents) change (Malcolm et al. 2011). Indeed, the compilation of a regionalised species inventory for the state of New South Wales by Nimbs and Smith (2017a) enabled the recognition of the southward range extension of the sea hare *Syphonota geographica* recorded for the first time south of Sydney, an observation that also represents the most southern global record (Nimbs and Smith 2017b).

Despite their high regional diversity, seasonal abundance, and occurrence in readily accessible habitats, much of the literature published on Australian sea hares concentrates on taxonomy. As a result, there is a paucity of information regarding their biology and ecology. Thus, in an effort to identify gaps in knowledge, a search of the literature on the distribution and diet of Australian Aplysiidae was undertaken. Notwithstanding the taxonomic insecurity of the Australian fauna, those species listed in Nimbs et al. (2017) were used as a foundation for this work.

The aims of this paper are twofold: (1) to explore the present Australian distribution of the Aplysiidae using historic and contemporary observation records and (2) to consolidate the information on diet by reviewing published literature

relevant to the Australian fauna and, where available, to supplement this with observations.

MATERIALS AND METHODS

Distribution of Aplysiidae in Australian waters

Australian distribution records were sourced from the literature, books, websites and personal records. The geographic extent includes the waters of continental Australia plus its oceanic islands and reefs (e.g. Lord Howe Island, Middleton and Elizabeth Reefs, Cartier and Ashmore Reefs) as well as external territories of Norfolk, Christmas and the Cocos (Keeling) islands.

Whilst many distribution records for the mainland can be pinpointed to individual locations, some give only broad regional descriptors. To accommodate this wide spatial range, presence/absence data for each taxon were consolidated into currently recognised marine bioregions - the IMCRA 4.0 shelf provinces (COA 2006) (Tables 1 and 2). A comparison of species richness among IMCRA provinces and between the east and west coasts, for the purposes of identifying latitudinal change, was facilitated by calculating the mid-point for each province as the summary independent variable.

Review of the diets of Australian Aplysiidae

The published literature was searched for information on the diets of the Australian aplysiid species. As some taxa exhibit ontogenic dietary plasticity (Carefoot 1987), the diets of veligers and juveniles were not considered.

RESULTS

Distribution of Aplysiidae in Australian waters

The western South Pacific Ocean has long been known to support the greatest diversity of aplysiids in the world (Eales 1960; Medina et al. 2004). In Australian waters there are the 25 described and undescribed species (23 listed in Nimbs et al. (2017)). Of these 25 taxa, 10 are in the genus *Aplysia* but, as these may include several synonymous taxa, the actual number is currently uncertain.

In a revision of the world species of *Aplysia*, Eales (1960: 380) listed 12 species from Australia

Table 1. List of the Australian IMCRA coastal shelf provinces (with the land based geographic limits of each geographic region), offshore islands and external territories (IMCRA Technical Group - Environment Australia for the Australian and New Zealand Environment and Conservation Council 1998)

IMCRA Province (IMCRA 4.0)	Extent (listed in IMCRA 3.3)
Northern Province	Cape Hotham, NT to Cape York, QLD
Northeast Transition	Cape York, QLD to Cooktown, QLD
Northeast Province	Cooktown, QLD to Port of Battle Creek, QLD
Central Eastern Transition	Port of Battle Creek, QLD to south of Coffs Harbour, NSW
Central Eastern Province	South of Coffs Harbour, NSW to south of Wollongong, NSW
Southeast Transition	South of Wollongong, NSW to Waratah Bay, Vic
Tasmanian Province	Cape Naturaliste, Tas to Cape Grim, Tas
Bass Strait Province	Cape Otway, Vic to Waratah Bay, Vic; Kangaroo Island, Tas to Little Musselroe Bay, Tas
Western Bass Strait Transition	Cape Otway, Vic to Cape Jervis, SA
Spencer Gulf Province	Cape Jervis, SA to Point Brown, SA
Great Australian Bight Transition	Point Brown, SA to Israelite Bay, WA
Southwest Province	Israelite Bay, WA to Perth, WA
Southwest Transition	Perth, WA to Geraldton, WA
Central Western Province	Gnaraloo, WA to North West Cape, WA
Central Western Transition	Geraldton, WA to Gnaraloo, WA
Northwest Province	North West Cape, WA to Cape Leveque, WA
Northwest Transition	Cape Leveque, WA to Cape Hotham, NT
Offshore Islands and territories	Extent
Lord Howe Island	Balls Pyramid, Lord Howe Island, Middleton and Elizabeth Reef, NSW (Tasman Sea)
Norfolk Island	Norfolk Island (Tasman Sea)
Cartier, Hibernia and Ashmore Reefs	Sahul Shelf, Timor Sea
Christmas Island	Christmas Island (Indian Ocean)
Cocos (Keeling) Island	Cocos (Keeling) Islands (Indian Ocean)

Table 2. List of data sources for distribution of Aplysiidae in Australian shelf waters

Published literature
Baker et al. (2015)
Benkendorff (2005)
Burn (2006; 2015)
Chalmer et al. (1976)
Cobb and Willan (2006)
Coleman (2008)
Eales (1960)
Gowlett-Holmes (2008)
Grove (2006)
Hedley (1916)
Nimbs and Smith (2017a b); Nimbs et al. (2017)
Shepherd and Thomas (1982); Shepherd (2013)
Wagele et al. (2006)
Wells and Bryce (1993)
Online databases
Atlas of Living Australia (ALA 2015)
Grove (2015)
OBIS (2016)
Rudman (2010)
Reports and personal communications
Baker et al. (2015)
Janine Baker, pers. comm. (SA)
Scoresby Shepherd, pers. comm. (SA)
Mark Scott, pers. comm. (Norfolk Island)

(*A. cronullae* Eales, 1960, *A. dactylomela* Rang, 1828 (syn. *A. argus* Rüppell & Leuckart, 1830), *A. denisoni* E. A. Smith, 1884, *A. extraordinaria* (Allan, 1932), *A. gigantea* G. B. Sowerby I, 1869, *A. juliana* Quoy & Gaimard, 1832, *A. nigra* d'Orbigny, 1837, *A. oculifera* A. Adams & Reeve, 1850, *A. parvula* Mörch, 1863, *A. reticulata* Eales, 1960, *A. sowerbyi* Pilsbry, 1895, *A. sydneyensis* G. B. Sowerby I, 1869). Later, Carefoot (1987: 170) listed 14 species, adding *A. keraudreni* Rang, 1828 on the east coast and *A. pulmonica* Gould, 1852 on the west. However, the latter was recently synonymised with *A. argus* (Alexander and Valdés 2013).

Eales (1960: 322) described a preserved individual of the east coast species *A. keraudreni* as “A small specimen, much contracted, but probably belonging to this species, [which] came from Sydney, Australia.” However, later in the work, as part of a global analysis of distribution (p. 380), it was omitted from a discussion of Australian animals and mentioned as occurring only in New Zealand. Furthermore, in a tabulated summary of species found in the South West Pacific (encompassing all Australian coastal waters), *A. oculifera* was omitted from the regional list (p. 381) despite being mentioned in the text (p. 380) as occurring in Western Australia (WA).

Whilst Carefoot (1987) and Eales (1960) both report *A. nigra* as an eastern Australian species, these records are most likely to be for *A. juliana*. Indeed, Eales discussed the numerous similarities between them. Later, Rudman also highlighted the probability that *A. nigra brunnea* Hutton, 1875 from NZ was most likely to be *A. juliana* (Rudman 2003a). Another *Aplysia*, *A. reticulata*, has not been mentioned in the literature or observed in Australian waters since Wells and Bryce (1993) recorded it and is also likely to be synonymous with another taxon.

In his treatise on the sea slugs from the Abrolhos Islands, WA, O'Donoghue (1924) described a new species, *Dolabrifera pelsaertensis*, using two specimens collected from Pelsaert Island. As “They do not appear to be referable to any described forms...” (1924: 535), he considered them to be a new taxon. Nevertheless, species of *Dolabrifera* can be highly variable in both colour and morphology (Rudman 2003b; pers. obs.), depending on diet and habitat. As with many of the Australian taxa described using preserved specimens, *D. pelsaertensis* is likely to be synonymous with another *Dolabrifera*. Few data are available regarding this species and a

thorough search of the literature failed to find any contemporary reference to, or observations of, *D. pelsaertensis*.

Aplysia argus and *A. parvula* are the most widespread aplysiids in Australian coastal waters, being found in 16 and 15 shelf bioregions respectively (Figs. 1A and 2A), and they are the only taxa recorded from the Great Australian Bight. *Dolabella auricularia* (Fig. 2G) and *Bursatella leachii* (Fig. 2E) also have wide distributions around much of Australia (Rudman 1998b) with both occurring in 12 bioregions. *Aplysia sowerbyi* (Fig. 2C), currently the only *Aplysia* recorded from the Northern Shelf Province, is probably circum-continental, however, some gaps remain, particularly in northern Western Australia. With just the single record, *Aplysia keraudreni* (Fig. 1G) has a highly restricted distribution and *A. cronullae* (Fig. 1B), *A. denisoni* (Fig. 1C) and *A. reticulata* (Fig. 2B), also found in only a few bioregions, are all likely to be synonymous with more widely observed species (Nimbs et al. 2017).

Petalifera petalifera (Fig. 3D), *Phyllaplysia* sp. (Fig. 3F) and the undescribed *Bursatella* sp. (Fig. 2F) from WA have comparatively short ranges, whereas *Dolabrifera brazieri* (Fig. 2H), *Petalifera ramosa* (Fig. 3E), *A. sydneyensis* (Fig. 2D), *A. juliana* (Fig. 1F) and *A. extraordinaria* (Fig. 1D) are more widespread, but restricted to the east coast. *Dolabrifera dolabrifera* (Fig. 3A), *A. oculifera* (Fig. 1H) and *Syphonota geographica* (Fig. 3I) are found on both the east and west coasts, but not in between, and *Notarchus indicus* (Fig. 3B) exhibits an apparently disjunct distribution: Central Eastern Province in NSW, Spencer Gulf Province in SA and three bioregions in WA.

Both *Stylocheilus striatus* (Fig. 3H) and *S. longicauda* (Fig. 3G) have been found in several bioregions; however, records are patchy and there are broad spatial gaps. Patchy distribution is also evident for the undescribed *Petalifera* sp. (Fig. 3C). The only *Aplysia* found exclusively on the west coast is *A. gigantea* (Fig. 1E), which occurs in both the Southwest Province and Southeast Transition bioregions.

All taxa mentioned above have been illustrated in Nimbs et al. (2017), except *Aplysia gigantea*, *Bursatella* sp. and *Phyllaplysia* sp. (presented here in Fig. 4). No images of *Aplysia cronullae*, *A. reticulata* or *A. keraudreni* were available.

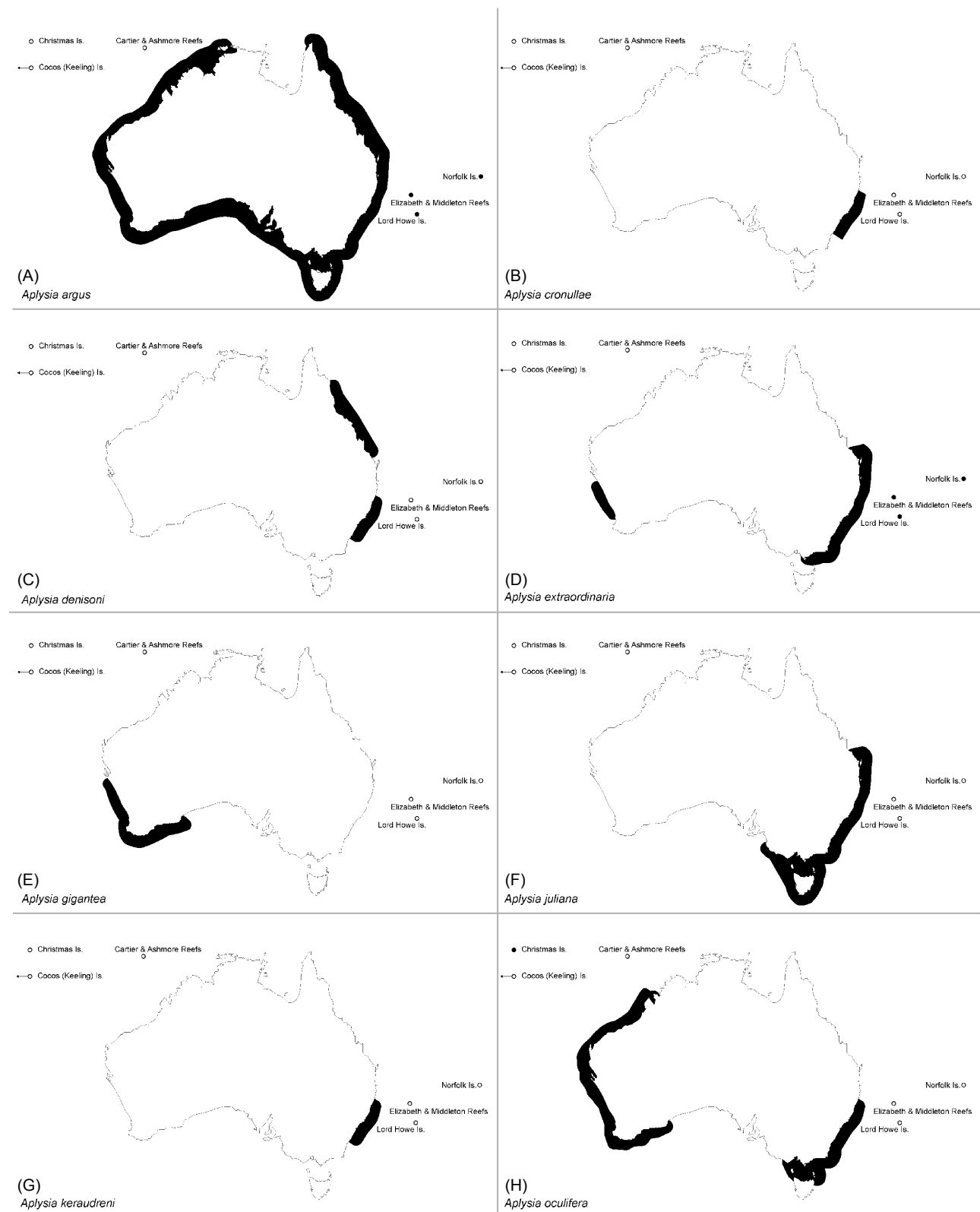


Fig. 1. Distribution of the Australian Aplysiidae. (A) *Aplysia argus*; (B) *Aplysia cronullae*; (C) *Aplysia denisoni*; (D) *Aplysia extraordinaria*; (E) *Aplysia gigantea*; (F) *Aplysia juliana*; (G) *Aplysia keraudreni*; and (H) *Aplysia oculifera*.

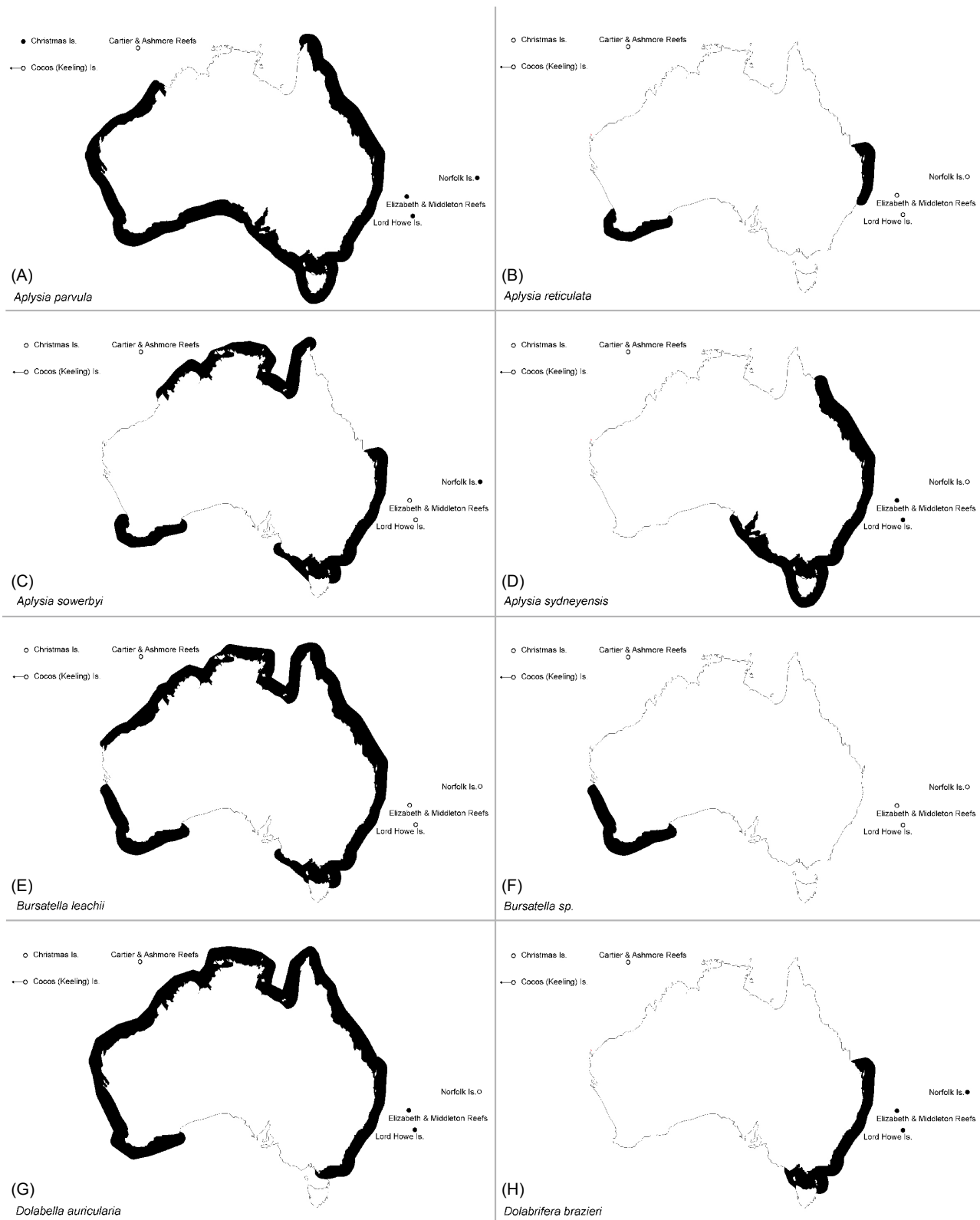


Fig. 2. Distribution of the Australian Aplysiidae. (A) *Aplysia parvula*; (B) *Aplysia reticulata*; (C) *Aplysia sowerbyi*; (D) *Aplysia sydneyensis*; (E) *Bursatella leachii*; (F) *Bursatella* sp.; (G) *Dolabella auricularia*; and (H) *Dolabrifer brazieri*.

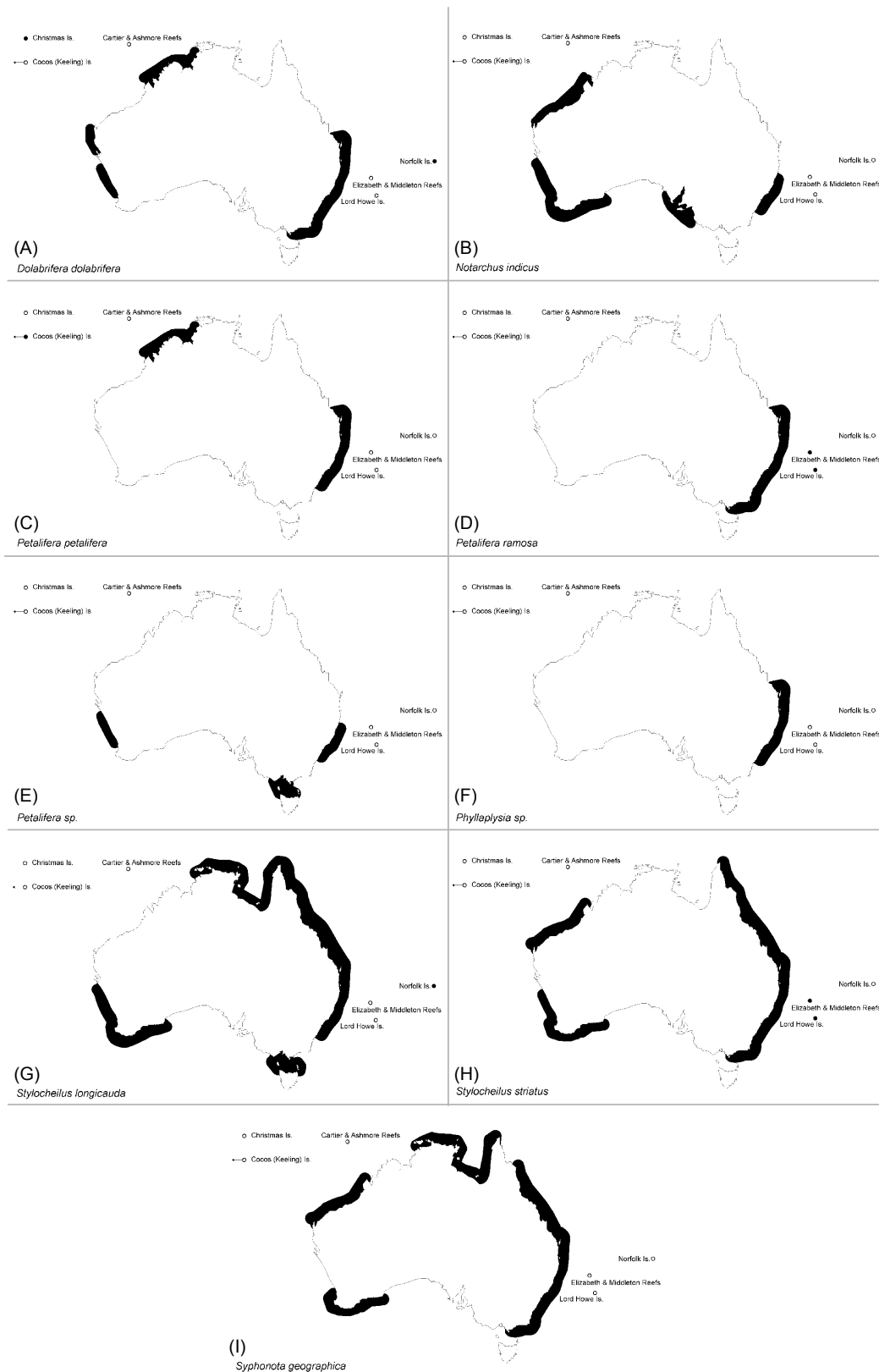


Fig. 3. Distribution of the Australian Aplysiidae. (A) *Dolabrifera dolabrifera*; (B) *Notarchus indicus*; (C) *Petalifera petalifera*; (D) *Petalifera ramosa*; (E) *Petalifera sp.*; (F) *Phyllaplysia sp.*; (G) *Stylocheilus longicauda*; (H) *Stylocheilus striatus*; and (I) *Syphonota geographica*.

Diet of Australian Aplysiidae

The diets of the Australian aplysiids are summarised in table 3.

DISCUSSION

Distribution of Aplysiidae in Australian waters

Aggregating data into IMCRA 4.0 shelf provinces revealed latitudinal patterns of distribution on both the east and west coasts that are consistent with those mentioned for NSW

alone (Nimbs et al. 2017), where aplysiid diversity increases with latitude, peaks in subtropical waters at 31–32°S and decreases in temperate waters. This pattern is stronger on the east coast (Fig. 5). Species of *Aplysia* are more diverse on the east coast, whilst other genera are more evenly distributed on both the east and west coasts.

In keeping with our hypothesis that the central NSW coast is possibly the most speciose region for aplysiids globally, Lord Howe Island and the nearby Middleton and Elizabeth Reefs, both with 8 recorded species, support the highest diversity among the offshore Australian islands and territories. This is followed by Norfolk Island,

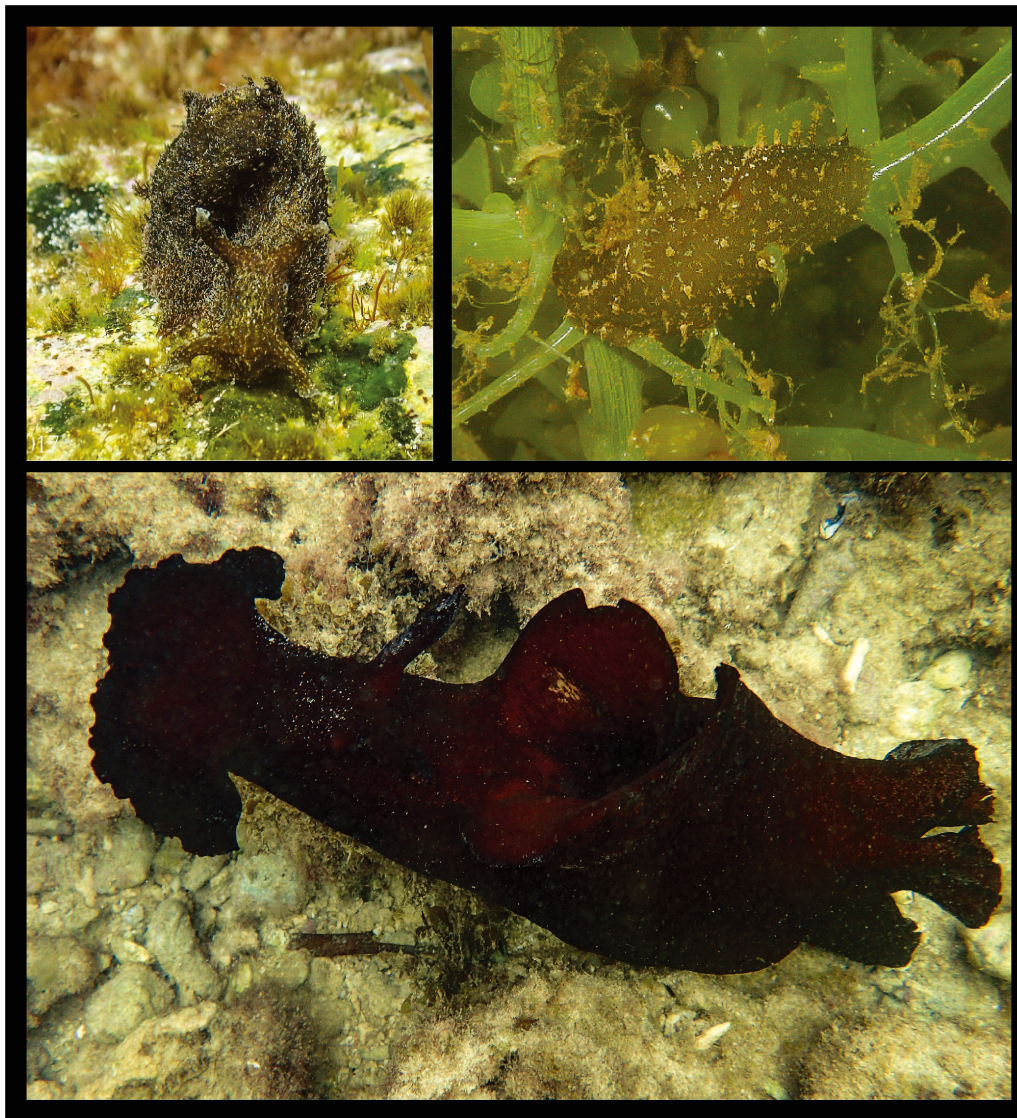


Fig. 4. Top left: *Bursatella* sp., Woodman Point, WA, 21 March 2017, photo: Matt Nimbs; top right: *Phyllaplysia* sp. Sydney Harbour, NSW, 4 February 2002, photo: Andrew Trevor-Jones (identified by W. B. Rudman (Rudman 2002), photo used with permission); bottom: *Aplysia gigantea*, Woodman Point, WA, 23 March 2017, photo: Matt Nimbs.

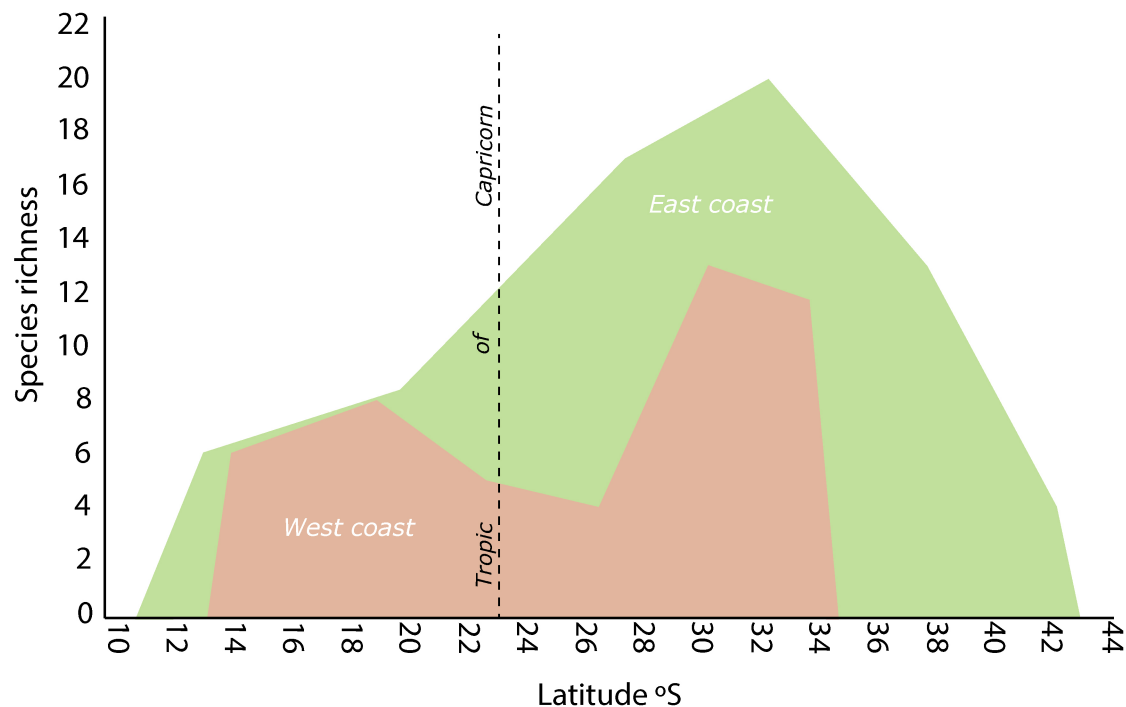


Fig. 5. Latitudinal diversity of the Aplysiidae on the eastern and western Australian coasts. Data represent aplysiid species richness for the middle latitude of each IMCRA 4.0 provincial shelf bioregion.

Table 3. Summary of dietary information for Australian Aplysiidae from field and laboratory observations (excluding larval stages). Algal species that were listed as 'host' were not necessarily deemed to be a food source

Aplysia

Aplysia argus Rüppell & Leuckart, 1830

Chlorophyta: *Cladophora* Kützinger, 1843; *Ulva* Linnaeus, 1753 [Morton and Miller 1973; Switzer-Dunlap and Hadfield 1979; Carefoot 1987].

Rhodophyta: *Corallina* Linnaeus, 1758; *Laurencia* J. V. Lamouroux, 1813; *Centroceras* Kützinger, 1842 '1841'; *Gracilaria* Grenville, 1830; *Acanthophora* J. V. Lamouroux, 1813; *Spyridia* Harvey, 1833 [Carefoot 1987, 1985, 1970; Morton and Miller 1973; Willan 1979; Switzer-Dunlap and Hadfield 1979; Rudman 1998a; Rogers et al. 2000]; red algae as adults [Switzer-Dunlap and Hadfield 1979; Carefoot 1987]; red and green turfing algae [Marshall and Willan 1999: 27].

Aplysia cronullae Eales, 1960

No data.

Aplysia denisoni E. A. Smith, 1884

No data.

Aplysia extraordinaria (Allan, 1932)

Chlorophyta: *Ulva* [personal observation, Sandy Beach, January 2017.]

Aplysia gigantea G. B. Sowerby I, 1869

No data.

Aplysia juliana Quoy & Gaimard, 1832

Ochrophyta: *Undaria* Suringar, 1873 [According to Saito and Nakamura (1961) in laboratory trials *A. juliana* preferred *Undaria pinnatifida* over green algae].

Chlorophyta: *Ulva* [Carefoot 1970; Usuki 1970; Sarver 1979; Rogers et al. 1995; pers obs. *Monostroma* [Usuki 1981].

Rhodophyta: Red algae [Willan 1979].

Aplysia oculifera A. Adams & Reeve, 1850

Chlorophyta: *Ulva* [Hurwitz and Susswein 1992; Yonow 2008: p. 97]; *Cladophora* [Plaut 1993].

Table 3. (continued)

<i>Aplysia parvula</i> Mörch, 1863
Chlorophyta: <i>Ulva</i> [Morton and Miller 1973; Shepherd and Thomas 1982; Marshall and Willan 1999].
Rhodophyta: <i>Delisea</i> J. V. Lamouroux, 1819 [Rogers et al. 1995; De Nys et al. 1996; Rogers et al. 2000]; <i>Laurencia</i> [Willan 1979; Shepherd and Thomas 1982; Marshall and Willan 1999; Rogers et al. 2003, 1995]; <i>Corallina</i> [Morton and Miller 1973]; <i>Plocamium</i> J. V. Lamouroux, 1813 [Willan 1979; Shepherd and Thomas 1982; Burn 1989]; <i>Solieria</i> J. Agardh, 1842 [Rogers et al. 2003; SDAS/MN pers. obs.]; <i>Portieria</i> Zanardini, 1851 [Ginsburg and Paul 2001].
<i>Aplysia reticulata</i> Eales, 1960
No data.
<i>Aplysia sydneyensis</i> G. B. Sowerby I, 1869
Rhodophyta: <i>Laurencia</i> [Rogers et al. 2003].
<i>Aplysia sowerbyi</i> Pilsbry, 1895
No data.
<i>Bursatella</i>
<i>Bursatella leachii</i> Blainville, 1817
Ochrophyta: <i>Vaucheria</i> A. P. de Candolle, 1801 [Paige 1988].
Chlorophyta: <i>Ulva</i> [Wu et al. 1980; only when starved according to Paige (1988)].
Cyanobacteria: <i>Lyngbya</i> C. Agardh ex Gomont, 1892 [Willan 1979; Switzer-Dunlap and Hadfield 1979; Paige 1988; Capper et al. 2006]; <i>Calothrix</i> [Clarke 2004, 2006].
<i>Dolabella</i>
<i>Dolabella auricularia</i> (Lightfoot, 1786)
Ochrophyta: <i>Dictyota</i> Dictyota J.V.Lamouroux, 1809 [Pennings and Paul 1992]; <i>Padina</i> Adanson, 1763 [Pennings and Paul 1992]; <i>Sargassum</i> (SDAS, pers. obs [video])
Chlorophyta: <i>Ulva</i> [Pennings and Paul 1992]; turfing green algae [Pennings et al. 1993; Marshall and Willan 1999: 28].
<i>Dolabrifera</i>
<i>Dolabrifera brazieri</i> G. B. Sowerby II, 1870
Chlorophyta: <i>Ulva</i> , turfing green algae. [MN pers. obs.].
<i>Dolabrifera dolabrifera</i> (Rang, 1828)
Chlorophyta: turfing green algae, [Marshall and Willan 1999: p. 29; Rudman 2010].
<i>Notarchus</i>
<i>Notarchus indicus</i> Schweigger, 1820
Chlorophyta: <i>Ulva</i> [Schuhmacher 1973].
<i>Petalifera</i>
<i>Petalifera</i> sp.
No data.
<i>Petalifera petalifera</i> (Rang, 1828)
Possibly consumes microalgal films growing on <i>Posidonia</i> or the macroalga itself [Martinez 1996; Clarke 2004].
<i>Petalifera ramosa</i> Baba, 1959
No data.
<i>Phyllaplysia</i>
<i>Phyllaplysia</i> sp.
No data.
<i>Stylocheilus</i>
<i>Stylocheilus longicauda</i> (Quoy & Gaimard, 1825)
Cyanobacteria: <i>Microcoleus</i> Desmazières ex Gomont, 1892 [Paul and Pennings 1991; Marshall and Willan 1999: 29]; <i>Lyngbya</i> [Nagle et al. 1998; Capper et al. 2006; Cruz-Rivera and Paul 2006].
<i>Stylocheilus striatus</i> (Quoy & Gaimard, 1832)
Cyanobacteria: <i>Lyngbya</i> [Paul and Pennings 1991; Nagle et al. 1998 from Clarke 2004].
<i>Syphonota</i>
<i>Syphonota geographica</i> (A. Adams & Reeve, 1850)
Angiospermae: <i>Halophila</i> Du Petit-Thouars, 1806 [Gavagnin et al. 2005].

Christmas Island and the Cocos (Keeling) Islands with 7, 3, and one species records respectively. *Aplysia argus*, *A. parvula* and *Petalifera* sp. have been recorded from Ashmore and Cartier Reefs, two of the emergent shoals in the northeastern Timor Sea (Willan 2005).

As with most other sea slugs, local distribution of sea hares is predominantly determined by the availability of their food (Edmunds 1977). However, with a tropical affinity (Rudman and Willan 1998), their broader geographic distribution is likely to be mediated by water temperature (Sunday et al. 2015). Whether on the east or west coast, conditions in the subtropics and warm-temperate regions appear optimal for the development and survival of sea hares, and this is reflected in their higher diversity. At these latitudes, warm water is supplied by southward-flowing boundary currents, the East Australian Current in the east and the Leeuwin Current in the west (Malcolm et al. 2011; Wernberg et al. 2013), which also carry a supply of larvae as potential recruits (Booth et al. 2007; Smith 2011). Further south, periods of coastal upwelling can provide nutrients (Gersbach et al. 1999; Roughan and Middleton 2002) and conditions conducive to the development and proliferation of algal food sources, whilst periodically adding considerable thermal stress to any tropical herbivores present (Pörtner 2010).

The vagaries of abiotic conditions can result in situations where, at any one time, a given sea hare species, potentially undetected for some time, can become the dominant heterobranch taxon in terms of abundance (pers. obs.). This phenomenon can result in community shifts in which one taxon becomes supplanted by another as populations wax and wane. Over longer temporal scales, these patterns can be visualised as a 'stochastic corkscrew' as described in Smith and Nimbs (2017).

Environmental conditions in large embayments are generally more conducive to settlement and development of sea hares - e.g. Port Stephens, NSW (Nimbs et al. 2017). In contrast to the large embayments on the coasts of southern QLD, NSW and south-western WA, aplysiid diversity in similar, calm-water habitats in Victoria, Tasmania and South Australia is comparatively low, despite high algal diversity and abundance. In fact, algal diversity in the Great Australian Bight and SA gulfs is amongst the highest in the world (Kerswell 2006) and yet, according to Shepherd and Thomas (1982), observations of aplysiids in South Australia are

very rare. Indeed: "Out of all the thousands of dives I have done in southern Australia... I have only seen sea hares once, although I have often dived in their habitat." (S. Shepherd pers. comm.). Low aplysiid diversity in these areas is unlikely to be driven by food availability but rather the effects of water temperatures which, particularly in winter, probably truncate or interrupt the aplysiid life-cycle.

Diet of Australian Aplysiidae

Aplysia species can be regarded as 'cutters of algae' (Purchon 1977), capable of masticating large pieces of food by the powerful gizzard, which renders the food into a state suited to cellular digestion. Thus, diet and consumption are not limited by the action of the radula. Feeding activity in the genus has been used as a neuronal model for systematic control of complex behaviour (Carefoot 1987) because it is easily observed and quantified (Hurwitz and Susswein 1992). As a result of numerous laboratory studies, the food of some taxa is very well known (though none of the taxa are from Australia), but due to the *in vitro* nature of these studies, these may not reflect natural diets.

Of all the aplysiids, species of *Aplysia* consume the broadest range of algae (Table 1) drawn from three phyla Chlorophyta (green algae), Rhodophyta (red algae), and Ochrophyta (brown algae). Most of the published literature relevant to the diet of Australian *Aplysia* is for the well-known, heavily investigated species with very extensive distributions (*A. argus*, *A. juliana* and *A. parvula*). Little information is available for endemic species, although *A. sydneyensis* was reported to consume the red algae *Laurencia obtusa* (Rogers et al. 2003). The diets of *A. cronullae*, *A. denisoni*, *A. extraordinaria*, *A. gigantea*, *A. sowerbyi* and *A. reticulata* remain unknown, but are likely to be similar to their sympatric congeners.

Often found in areas of low water movement or estuarine habitats, animals in the genera *Bursatella* and *Dolabella* have been observed to consume both ochrophyte and chlorophyte algae (Wu et al. 1980; Paige 1988; Clarke 2004, 2006) whilst the former also consumes cyanobacteria (blue-green algae) (Willan 1979; Switzer-Dunlap and Hadfield 1979; Paige 1988; Capper et al. 2006). In a study of *Bursatella leachii*, it was noted that this species *prefers* the cyanobacteria *Lyngbya majuscula* [= *Microcoleus lyngbyaceus*, *Schizothrix calcicola* and *Porphyrosiphon notarsii* (Paige 1988)]. These cyanobacteria

characteristically form mats on stable sediments and hard surfaces or occur as epiphytes on sea grasses. Found in similar habitats, the diet of the cosmopolitan *Stylocheilus striatus* has been found to be restricted solely to cyanobacteria (Paul and Pennings 1991; Nagle et al. 1998; Marshall and Willan 1999; Cruz-Rivera and Paul 2006; Capper et al. 2006).

The predominantly intertidal *Dolabrifera* species reportedly graze chlorophytes from among turfing algae (Marshall and Willan 1999; Rudman 2010). One author of the present paper (MN), observed and recorded *Dolabrifera brazieri* on a rocky reef in northern New South Wales, selectively consuming the chlorophyte *Ulva* whilst browsing amongst mixed turf algae. The diet of *Notarchus* is also, exclusively, species of *Ulva* (Schuhmacher 1973).

Species of the numerically small genus *Petalifera* are reported to graze films of epibiotic algal blooms growing on seagrass, although Hamatani (1962: 142) claimed that the Japanese *Petalifera punctulata* (Tapparone Canefri, 1874), may consume only the sap from *Zostera marina* and *Z. nana*. Some aplysiids, such as *Syphonota* and *Phyllaplysia* have been observed to consume sea grass leaves, the former *Halophila* sp. (Gavagnin et al 2005), and the latter, *Zostera* sp. Whilst *Aplysia* is the only genus found to consume Rhodophyta with regularity, there was one report of a *Phyllaplysia smaragda* K. B. Clark, 1977 from Florida, with pieces of the rhodophyte *Erythrocladida* in its caecum (Clark 1977).

Although the diet of the undescribed Australian *Phyllaplysia* sp. is unknown, observations of *Phyllaplysia taylori*, found in the north-eastern Pacific Ocean, indicate a diet dissimilar to all other aplysiids in that it is believed to comprise solely diatoms. Beeman (1970) carried out a comprehensive analysis of its diet and observed selective grazing of the epiphytic fauna on *Zostera*, noting a preponderance of sessile diatoms. A total of 14 diatom species were detected through examination of gut contents in specimens from several locations. Indeed, the digestive morphology of *P. taylori* is well suited to a diet constituting "...siliceous, abrasive material..." (Beeman 1970: 197).

CONCLUSIONS

Several important gaps remain in our knowledge regarding the distribution and diet of

the Australian aplysiids, and filling these is certainly hampered by the insecure taxonomic status of some species. Even well-known taxa such as *A. parvula* and *A. juliana*, with their purported circum-global distributions, have not been recorded from large sections of the Australian coastline. Thus, there is a clear need to develop basic species inventories, particularly for remote, sparsely populated areas. *Petalifera* and *Phyllaplysia* are the least known of the Australian fauna and, whilst their distribution is probably much more widespread than presently documented (Rudman 2002), there are very few records of the latter.

Even in areas adjacent to population centres, the diet of conspicuous species such as *Aplysia gigantea* and the wide-ranging *A. sowerbyi* remain unknown. Many of the Australian species have been observed to consume chlorophytes, particularly *Ulva* sp.; however, their diets are likely to be much broader and incorporate other foods in locations where, or at times when, *Ulva* is unavailable.

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