

# REGIONAL AND SPECIES-SPECIFIC PHENOLOGICAL PATTERNS IN AUSTRALIAN SEA HARES (GASTROPODA: HETEROBRANCHIA: APLYSIIDAE) REVEALED THROUGH CITIZEN SCIENCE OBSERVATION DATA

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**ABSTRACT:** Sea hares (Aplysiidae) are conspicuous herbivorous molluscs that exhibit seasonal population ‘boom and bust’ cycles. Using 6,629 research-grade observations from iNaturalist (2010–2024), seasonality in observation frequency was analysed across Australian latitudinal zones. Circular statistics revealed a strong latitudinal gradient in timing: temperate populations exhibited pronounced unimodal summer peaks (December–January), while tropical populations peaked during the late dry season (August–September), with differences of up to seven months between zones within the same species. Apparent differences between east and west coasts largely reflected differences in the latitudinal composition of observations rather than fundamentally different phenological regimes. Pooling observations across latitudes obscured species-level seasonality, with several taxa that appeared weakly seasonal when data were aggregated (e.g. *Aplysia oculifera*, *A. argus*, *Dolabella auricularia*) showing seasonal concentration within latitudinal zones once geographic structure was accounted for. Species-specific analyses identified a gradient from highly seasonal taxa to year-round opportunists, suggesting temporal niche partitioning. Comparison with an all-Australia iNaturalist baseline (~5.4 million records) confirmed that the seasonal patterns recovered are decoupled from general observer-effort seasonality. These findings demonstrate the utility of citizen science data for phenological research while highlighting the importance of accounting for latitudinal structure and observer effort bias. This study provides the first comprehensive analysis of sea hare phenology in Australia.

**KEYWORDS:** circular statistics; latitudinal gradient; seasonal–trend decomposition

## INTRODUCTION

Phenology – the timing of recurring biological events – is increasingly recognised as a sensitive biological response to climate change in marine ecosystems (EDWARDS & RICHARDSON 2004, POLOCZANSKA et al. 2013). Shifts in reproductive timing, larval recruitment, and seasonal abundance have been documented across diverse marine taxa, often with cascading effects on trophic interactions and ecosystem function (WINDER & SCHINDLER 2004). However, phenological studies have been heavily biased toward commercially important species and temperate Northern Hemisphere systems, leaving substan-

tial gaps in our understanding of seasonal patterns in southern tropical and subtropical invertebrates (SORTE et al. 2010).

Sea hares (Aplysiidae) are generally large, herbivorous gastropods found in coastal waters worldwide, with a high diversity in the Indo-Pacific region (CAREFOOT 1987, VALDÉS et al. 2006), but with very high diversity in central New South Wales (NSW), eastern Australia (NIMBS et al. 2017a). These gastropods are characterised by seasonal population blooms driven by water temperature, food availability, and reproductive cycles (CAREFOOT 1987, ROGERS et al.

1995, NIMBS *et al.* 2017a, 2017b). In temperate systems, sea hares typically exhibit pronounced summer peaks associated with warmer water temperatures and macroalgal productivity (SUSSWEIN *et al.* 1983, PENNINGS 1990). However, phenological patterns in tropical and subtropical populations remain poorly characterised, and the mechanisms driving interannual variability are not well understood.

Australia's extensive coastline spans tropical to temperate latitudes and is influenced by contrasting oceanographic regimes. The East Australian Current (EAC) brings warm tropical water southward along the east coast, creating strong seasonal temperature gradients (RIDGWAY & DUNN 2003). In contrast, the Leeuwin Current flows southward along the west coast, maintaining relatively stable warm-water conditions year-round and supporting diverse subtropical communities at higher latitudes than expected (WERNBERG *et al.* 2012). These contrasting oceanographic settings provide a natural experiment for examining how regional environmental drivers shape phenological patterns.

Citizen science platforms, particularly iNaturalist, have emerged as valuable sources of biodiversity data (POCOCK *et al.* 2015, CALLAGHAN *et al.* 2019). While opportunistic observations lack the systematic sam-

pling design of traditional ecological surveys, their temporal and spatial coverage can reveal large-scale patterns that would be difficult to capture through dedicated field studies (DICKINSON *et al.* 2012). However, citizen science data require careful treatment of observer effort bias, which can confound biological patterns with changes in platform usage or observer behaviour (SZABO *et al.* 2010, COURTER *et al.* 2013).

Here, iNaturalist observations were used to characterise phenological patterns in Australian sea hares at regional and species-specific scales. The objectives of this study were to: (1) quantify seasonality of sea hare observations across eastern and western Australian coasts using circular statistics, (2) test for species-specific differences in phenology that may indicate temporal niche partitioning, (3) examine evidence for interannual variability in peak timing using autocorrelation analysis, and (4) test the hypothesis that peak observation timing has shifted directionally across 2010–2024, consistent with documented warming of Australian coastal waters (RIDGWAY 2007, WU *et al.* 2012). The resultant baseline patterns establish a quantitative foundation for use in future studies of phenological change.

## MATERIAL AND METHODS

### DATA COLLECTION AND PROCESSING

Sea hare observations were extracted from iNaturalist using the *rinat* package (BARVE & HART 2014) in R version 4.3.0 (R CORE TEAM 2023). All research-grade observations of the order Aplysiidae were queried from Australia (iNaturalist *place\_id* = 6744) with a maximum return of 10,000 records. A data quality metric set by iNaturalist is 'Research-grade', which requires community agreement on species identification and the presence of date and location metadata was the primary data filter. Observations were further filtered to include only records with complete geographic coordinates (latitude and longitude) and observation dates were set for between 2010 and 2024 (which focuses on a period of substantial iNaturalist activity in Australia whilst maintaining a 15-year time series for trend analysis). Seasonal-trend decomposition using LOESS (STL) with robust fitting was applied to monthly observation counts to eliminate sampling bias associated with large growth in iNaturalist participation. Decomposition parameters were set at: time series span (Jan 2015 – Dec 2024); seasonal window – periodic; robust fitting method using iteratively weighted least squares; ~12 fold increase over 10 years; seasonal component captures recur-

ring within-year patterns trend range ~10 (2015) to ~130 (2024); seasonal amplitude –  $\pm 10$ –15 observations/month; seasonal peak – Dec to Jan (consistent across years); and seasonal trough – May to Jun (consistent across years).

To evaluate whether the seasonal patterns reported here reflect biology or platform-usage artefacts, we extracted monthly aggregate counts of all Australian iNaturalist Research-Grade observations (2010–2024) from GBIF (2026), accessed via the *rgbif* package (CHAMBERLAIN & BOETTIGER 2017). This baseline ( $n = 5,389,576$ ) provides a generalised measure of within-year variation in observer activity against which the seasonality of sea hare observations can be compared. If observer effort drove seasonal patterns, the monthly distributions of all-Australia observations and sea hare observations would coincide.

### GEOGRAPHIC PARTITIONING

For analyses requiring spatial structure, observations were assigned to two complementary classifications. Coast: East ( $>140^{\circ}\text{E}$ ) and West ( $<125^{\circ}\text{E}$ ); a small number of observations from the Gulf of Carpentaria and central northern coast ( $125$ – $140^{\circ}\text{E}$ ,  $n = 88$ , 1.3%) were excluded from coastal analyses due to insufficient sample size. Latitudinal zone:



Tropical (<23°S), Subtropical (23° to 29°S), and Temperate (>29°S). Species-level analyses were restricted to taxa with ≥50 observations to ensure adequate sample sizes for statistical inference (Appendix: Table A1).

#### Objective 1 – Quantify seasonality on the Australian east and west coasts

Analyses used all observations partitioned by coast as defined above (n = 5,508 East, n = 1,033 West; 88 Gulf of Carpentaria/central northern observations excluded). Observations for a total of 15 taxa were used from five genera (Table 1): eight species of *Aplysia* Linnaeus, 1767 (*A. argus* Rüppell et Leuckart, 1830, *A. concava* G. B. Sowerby I, 1833, *A. extraordinaria* (J. K. Allen, 1932), *A. gigantea* G. B. Sowerby II, 1869, *A. juliana* Quoy et Gaimard, 1832, *A. oculifera* A. Adams et Reeve, 1850, *A. reticulata* Eales, 1960 and *A. sydneyensis* G. B. Sowerby II, 1869), two species of *Bursatella* Blainville, 1817 (*B. hirsuta* Nimbs et N. G. Wilson, 2020 and *B. leachii* Blainville, 1817), two species of *Dolabrifera* J. E. Gray, 1847 (*D. brazieri* G. B. Sowerby II, 1870 and *D. dolabrifera* (Rang, 1828)), one species of *Stylocheilus* A. A. Gould, 1852 (*S. striatus* (Quoy et Gaimard, 1832)) and the monospecific *Dolabella* Lamarck, 1801 (*D. auricularia* ([Lightfoot], 1786) and *Syphonota* H. Adams et A. Adams, 1854 (*S. geographica* (A. Adams et Reeve, 1850))). Nomenclature used in this study was validated using the World Register of Marine Species (WoRMS 2026).

#### Objective 2 – Test for species-specific differences in phenology (temporal niche partitioning)

Analyses used the 15 species with ≥50 observations (Figs 1–15, Table 1). Circular statistics were

computed both for pooled species data and within latitudinal zones (as defined above) for each species (AGOSTINELLI & LUND 2017). Watson's  $U^2$  compared seasonal distributions among zones within species. Spectral analysis of detrended monthly counts corroborated dominant 12-month periodicity where it was informative.

Month of observation was converted to radians ( $\theta = \text{month} \times 2\pi / 12$ ) to treat time as angular data. For each species and region, the following metrics were calculated: (1) mean direction ( $\mu$ ), representing the average peak month; (2) concentration parameter ( $r$ ), measuring the strength of seasonality (0 = uniform distribution [no seasonality], 1 = all observations in one month [very high seasonality]); and (3) Rayleigh's test for non-uniformity, which tests the null hypothesis of a uniform circular distribution (RAYLEIGH 1919). Watson's two-sample  $U^2$  test was used to compare seasonal distributions between regions and time periods. This non-parametric test evaluates whether two circular samples are drawn from the same underlying distribution and is robust to deviations from the von Mises distribution (JAMMALAMADAKA & SENGUPTA 2001).

#### Objective 3 – Examine interannual variability in peak timing (autocorrelation analysis) and pre-processing

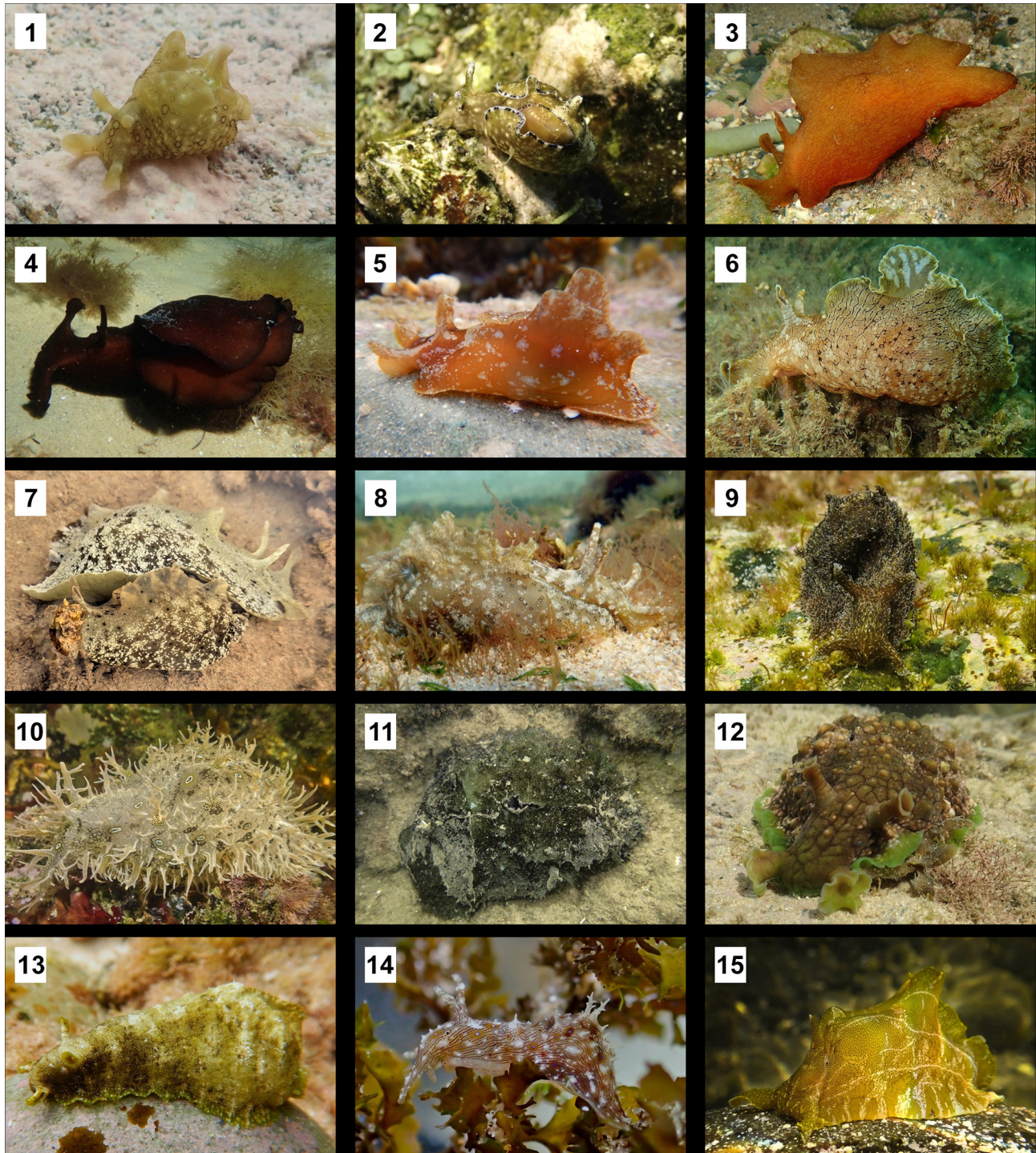
Analyses used monthly observation counts aggregated by species and latitudinal zone over 2015–2024 (120 months), restricted to species with ≥10 years of data. To account for exponential growth in iNaturalist usage over this period, time series data were decomposed using seasonal-trend decomposition using LOESS (STL) with robust fitting (CLEVELAND et al. 1990). STL separates the observed time series into seasonal, trend, and remainder components allowing

Table 1. Dataset summary by species. N = number of research-grade iNaturalist observations per species by latitudinal zone. Tropical: <23°S; Subtropical: 23° to 29°S; Temperate: >29°S

| Species                        | Total N | East  | West | Tropical | Subtropical | Temperate |
|--------------------------------|---------|-------|------|----------|-------------|-----------|
| <i>Aplysia argus</i>           | 1,829   | 1,579 | 250  | 237      | 530         | 1,062     |
| <i>Dolabella auricularia</i>   | 886     | 750   | 136  | 48       | 223         | 615       |
| <i>Aplysia juliana</i>         | 710     | 668   | 42   | –        | –           | –         |
| <i>Dolabrifera brazieri</i>    | 627     | 590   | 37   | –        | –           | –         |
| <i>Aplysia sydneyensis</i>     | 563     | 548   | 15   | –        | –           | –         |
| <i>Aplysia concava</i>         | 560     | 476   | 84   | 84       | 27          | 449       |
| <i>Aplysia reticulata</i>      | 306     | 32    | 274  | 228      | –           | 46        |
| <i>Aplysia extraordinaria</i>  | 223     | 210   | 13   | –        | –           | –         |
| <i>Stylocheilus striatus</i>   | 212     | 178   | 34   | –        | 59          | 142       |
| <i>Bursatella leachii</i>      | 120     | 85    | 35   | –        | –           | –         |
| <i>Bursatella hirsuta</i>      | 97      | 65    | 32   | –        | –           | 97        |
| <i>Aplysia gigantea</i>        | 97      | 97    | 0    | –        | –           | –         |
| <i>Syphonota geographica</i>   | 76      | 68    | 8    | –        | –           | –         |
| <i>Aplysia oculifera</i>       | 62      | 50    | 12   | 42       | –           | 19        |
| <i>Dolabrifera dolabrifera</i> | 51      | 51    | –    | –        | 51          | –         |

the confounding effect of iNaturalist growth to be eliminated prior to analysis of seasonal and interannual patterns.

Within-year seasonal structure (unimodal vs. multimodal patterns, peak timing, and concentration) was characterised using the circular statistics



Figs 1–15. Image of Australian sea hare taxa analysed in this study: 1 – *Aplysia argus*, Caloundra, QLD; 2 – *Aplysia concava*, North Solitary Island, NSW; 3 – *Aplysia extraordinaria*, Sandy Beach, NSW; 4 – *Aplysia gigantea* North Mole, WA; 5 – *Aplysia juliana*, Bare Bluff, NSW; 6 – *Aplysia sydneyensis*, Clifton Gardens, NSW; 7 – *Aplysia reticulata*, Port Headland, WA; 8 – *Aplysia oculifera*, Garden Island, WA; 9 – *Bursatella hirsuta*, Woodman Point, WA; 10 – *Bursatella leachii*, Sawtell, NSW; 11 – *Dolabella auricularia*, Diggers Headland, NSW; 12 – *Dolabrifera brazieri*, Woolgoolga, NSW; 13 – *Dolabrifera dolabrifera*, Woolgoolga, NSW; 14 – *Stylocheilus striatus*, Sandy Beach, NSW; and 15 – *Syphonota geographica*, Nelson Bay, NSW. Photographs: 1–3, 5–6, 9–15 by MATT JOHN NIMBS; 4 by TIM KARNASUTA\* (iNaturalist), 7 by ILZE KEEVEY\* (iNaturalist) and 8 by TOBIAS WESTMEIER [twnature]\* (iNaturalist). \*Reproduced under creative commons license CC-BY-NC



described above. To complement this, spectral analysis was performed on detrended monthly time series using periodogram estimation to confirm dominant within-year periodicities. To examine between-year variability, autocorrelation functions (ACF) were calculated on annual peak timing series to test for systematic multi-year cycles or oscillations (e.g., linked to El Niño–Southern Oscillation).

Objective 4 – Assess temporal trends for patterns of climate-driven phenological shifts

Analyses used the 8 species with  $\geq 10$  years of data and  $\geq 3$  observations per year. Both the full window (2010–2024) and a sensitivity subset (2015–2024) were analysed. Temporal trends in observation timing were tested using circular-linear regression

(AGOSTINELLI & LUND 2017) with day-of-year (converted to radians) as the circular response and year as the linear predictor. Multiple testing across species was controlled using Bonferroni correction. To corroborate this test, we also compared seasonality between early (2010–2017) and recent (2018–2024) periods using Watson’s two-sample tests. As a sensitivity check, all regression analyses were repeated using observations from 2015–2024 only, to assess the influence of the sparsely-sampled early years.

General processing packages used in R were: tidyverse (WICKHAM et al. 2019), circular (AGOSTINELLI & LUND 2017), forecast (HYNDMAN & KHANDAKAR 2008), and mgcv (WOOD 2011) for generalised additive models.

RESULTS

DATASET CHARACTERISTICS

The retrieved dataset comprised 6,629 research-grade observations spanning 15 years [2010–2024], from 15 species. Observations were strongly biased toward eastern Australia ( $n = 5,508$ , 83%) compared to the west coast ( $n = 1,033$ , 16%). The most frequently observed taxa were *A. argus* ( $n = 1,829$ ), *D. auricularia* ( $n = 886$ ), and *A. juliana* ( $n = 710$ ). Observations increased strongly from 2010 ( $n = 13$ ) to 2024 ( $n = 1,456$ ), reflecting rapid growth in iNaturalist participation in Australia.

Objective 1 – Seasonality across the eastern and western Australian coasts

When observations were aggregated by coast, east coast data showed highly significant seasonality (Rayleigh’s  $Z = 529.2$ ,  $N = 5,508$ ,  $p < 0.0001$ ) (Appendix: Table A1) with a clear summer peak in December ( $\mu = 0.01$  radians, concentration  $r = 0.31$ ). In contrast, west coast observations exhibited weak seasonality (Rayleigh’s  $Z = 1.7$ ,  $N = 1,033$ ,  $p < 0.001$ ;  $r = 0.04$ ) with observations distributed almost uniformly throughout the year, peaking nom-

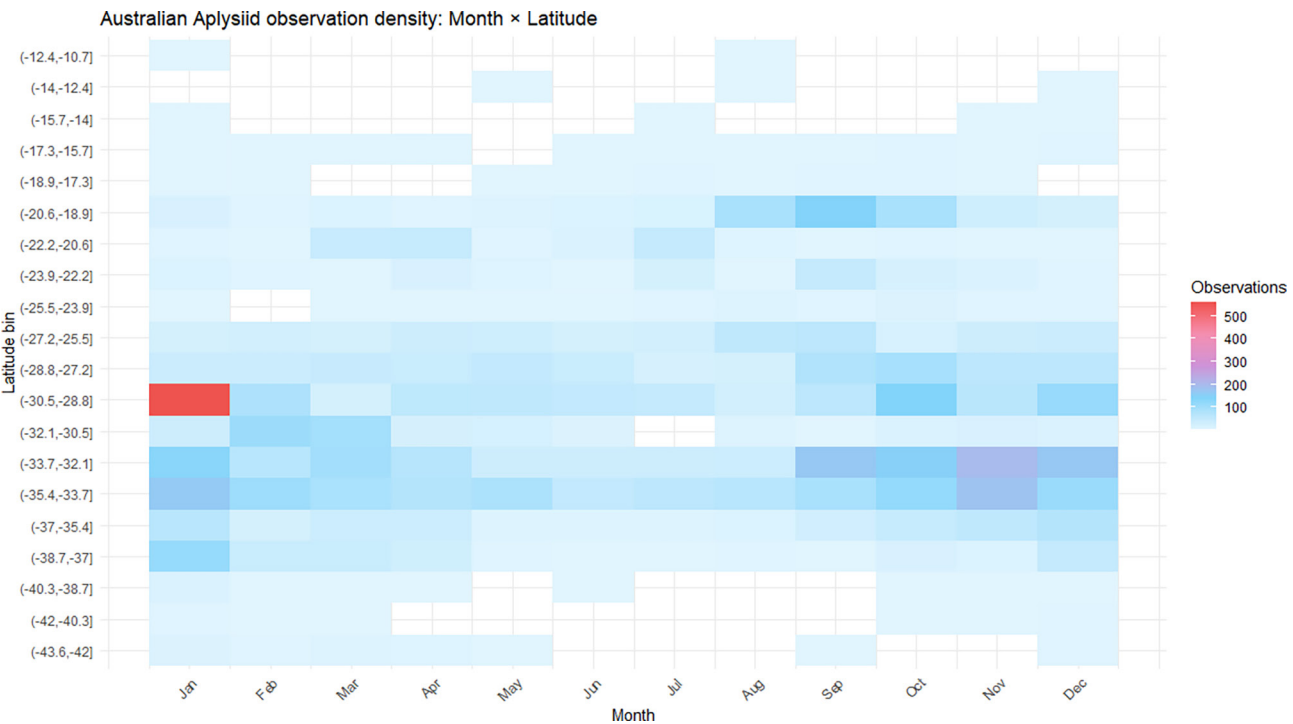


Fig. 16. Heatmap of observation densities (month  $\times$  latitude) for data retrieved from iNaturalist



inally in September but with maxima also in April and January. Watson's two-sample test confirmed that east and west coast exhibited significant seasonal distributions ( $N^1 = 5,508$ ;  $N^2 = 1,033$ ;  $U^2 = 0.89$ ,  $p < 0.001$ ) (Appendix: Table A2a). However, analysis by latitudinal zone (Fig. 16) revealed that this apparent coast-level difference largely reflects latitudinal composition of observations on each coast, with tropical populations peaking in August–September and temperate populations in December–January regardless of coast longitude (Fig. 16; Appendix: Table A3).

#### Objective 2 – Species-specific differences in phenology (temporal niche partitioning)

Species-level analyses initially revealed substantial variation in seasonal concentration when data were pooled across all locations (Table 2). However, examination of geographic structure within species revealed that apparent weak seasonality patterns in several species was an artifact of aggregating observations across tropical, subtropical, and temperate regions.

When analysed by latitudinal zone (Tropical  $<23^\circ\text{S}$ , Subtropical  $23^\circ$  to  $29^\circ\text{S}$ , Temperate  $>29^\circ\text{S}$ ), most species exhibited stronger patterns of regional seasonality than when pooled (Table 3). For example, *A. oculifera*, which exhibited a non-significant year-round pattern when data were pooled ( $r = 0.14$ ,  $Z = 1.2$ ,  $p = 0.45$ ,  $N = 62$ ), showed some significant seasonal patterns when analysed by region: temperate observations exhibited a significant January concentration ( $r = 0.65$ ,  $Z = 8.0$ ,  $p < 0.001$ ,  $N = 19$  interpreted with caution given the small sample size) while tropical observations showed weaker non-sig-

nificant peaks in August ( $r = 0.20$ ,  $Z = 1.7$ ,  $p = 0.19$ ,  $N = 42$ ). Similarly, *A. argus*, exhibited highly significant but weak overall seasonality ( $r = 0.18$ ,  $Z = 59.3$ ,  $p < 0.001$ ,  $N = 1,829$ ) but when analysed per region, patterns showed highly significant tropical observations peaking in October ( $r = 0.41$ ,  $Z = 39.9$ ,  $p < 0.001$ ,  $N = 237$ ) and again for temperate observations in January ( $r = 0.31$ ,  $Z = 102.0$ ,  $p < 0.001$ ,  $N = 1,062$ ).

Species showing consistent phenology across regions included *B. hirsuta* (January peak,  $r = 0.90$ , all observations temperate), *A. extraordinaria* (January peak,  $r = 0.64$ , predominantly temperate), and *S. striatus* (January–February peaks across zones, though with some regional variation in timing). In contrast, several widespread species showed markedly different peak timing across latitudes. *A. concava* peaked in July–August in tropical regions ( $r = 0.56$ ) but in December in temperate zones ( $r = 0.50$ ), a difference of approximately 5 months. *D. auricularia* showed June peaks in the tropics ( $r = 0.44$ ) compared to January in temperate areas ( $r = 0.37$ ).

The apparent “winter peak” of *A. reticulata* (August, pooled data) was driven primarily by tropical observations ( $n = 228$ , August peak,  $r = 0.57$ ), while temperate populations showed autumn peaks (March,  $n = 46$ ,  $r = 0.53$ ). In the tropics, August represents the late dry season rather than winter, highlighting the importance of interpreting phenological patterns in their appropriate regional context.

#### Within-year periodicity confirming seasonality (Objectives 1–2)

Spectral analysis of detrended data confirmed dominant 12-month periodicity for temperate lat-

Table 2. Species-specific differences in phenology (pooled across latitudinal zones) of Australian sea hares.  $N$  = number of observations,  $\mu$  = mean direction (peak month in radians),  $r$  = concentration parameter [closeness of fit to circular model] (thus 1 = all obs in 1 month, 0 = no seasonality), Rayleigh  $p$  = significance statistic from test of uniformity (evaluates whether observations are distributed uniformly around the year (null hypothesis) or show significant clustering at particular times). Test statistic  $Z = n \times r^2$ . \* Species marked with an asterisk show significant geographic structure (see Table 3)

| Species                       | N    | $\mu$ (radians) | Peak Month | $r$  | Z     | Rayleigh p | Seasonality |
|-------------------------------|------|-----------------|------------|------|-------|------------|-------------|
| <i>Bursatella hirsuta</i>     | 97   | 0.52            | January    | 0.90 | 78.6  | <0.001     | Seasonal    |
| <i>Aplysia gigantea</i>       | 97   | 1.31            | March      | 0.85 | 70.1  | <0.001     | Seasonal    |
| <i>Aplysia oculifera</i>      | 62   | -0.52           | November   | 0.65 | 9.0   | <0.001     | Seasonal    |
| <i>Aplysia extraordinaria</i> | 223  | 0.52            | January    | 0.64 | 91.3  | <0.001     | Seasonal    |
| <i>Stylocheilus striatus</i>  | 212  | 0.52            | January    | 0.59 | 73.8  | <0.001     | Seasonal    |
| <i>Aplysia juliana</i>        | 710  | -0.52           | November   | 0.48 | 163.6 | <0.001     | Moderate    |
| <i>Syphonota geographica</i>  | 76   | -0.52           | November   | 0.44 | 14.7  | <0.001     | Moderate    |
| <i>Aplysia reticulata</i>     | 306  | 4.19            | August     | 0.39 | 46.5  | <0.001     | Moderate    |
| <i>Aplysia sydneyensis</i>    | 563  | -0.52           | November   | 0.37 | 77.1  | <0.001     | Moderate    |
| <i>Dolabrifera brazieri</i>   | 627  | 0.01            | December   | 0.35 | 76.8  | <0.001     | Moderate    |
| <i>Aplysia concava</i>        | 560  | -0.52           | November   | 0.34 | 64.7  | <0.001     | Moderate    |
| <i>Dolabella auricularia</i>  | 886  | 0.01            | December   | 0.28 | 69.4  | <0.001     | Weak*       |
| <i>Bursatella leachii</i>     | 120  | 3.14            | June       | 0.20 | 4.8   | 0.012      | Weak*       |
| <i>Aplysia argus</i>          | 1829 | 0.01            | December   | 0.18 | 59.3  | <0.001     | Weak*       |



itudinal bands, consistent with the unimodal seasonal pattern evident in Fig. 17 (Appendix: Table A4). When data were pooled across latitudes for the west coast, a six-month (semi-annual) periodicity appeared, consistent with the multimodal pattern that showed local peaks in September, April, and January. However, this signal represents a composite of offset annual peaks from tropical and temperate observations rather than a genuine six-month biological cycle, consistent with the latitudinal structure evident in both the species-level (Table 3) and assemblage-level (Fig. 17) analyses. Species-specific spectral analyses supported this interpretation: highly seasonal species (e.g., *A. juliana*, and *D. auricularia*) showed strong 12-month peaks regardless of whether observations were made on the east or west coast (Appendix: Table A4).

### Objective 3 – Interannual variability in peak timing

Autocorrelation analysis of annual peak timing revealed no evidence of systematic multi-year cycles or oscillations (Appendix: Table A5). Most species showed near-zero autocorrelation at lags 1–3, and spectral analysis of peak timing time series did not identify periodicities corresponding to known climate cycles (e.g., El Niño–Southern Oscillation). Across species, autocorrelation function values at lags 1–3 ranged from  $-0.25$  to  $+0.22$  and did not exceed the 95% confidence bounds ( $\pm 0.55$  to  $\pm 0.63$ ;  $n = 10$ –13 years).

Watson's two-sample tests comparing early (2010–2017) versus recent (2018–2024) periods showed no significant differences in seasonal distri-

#### Australian Aplysiid species-specific seasonal patterns

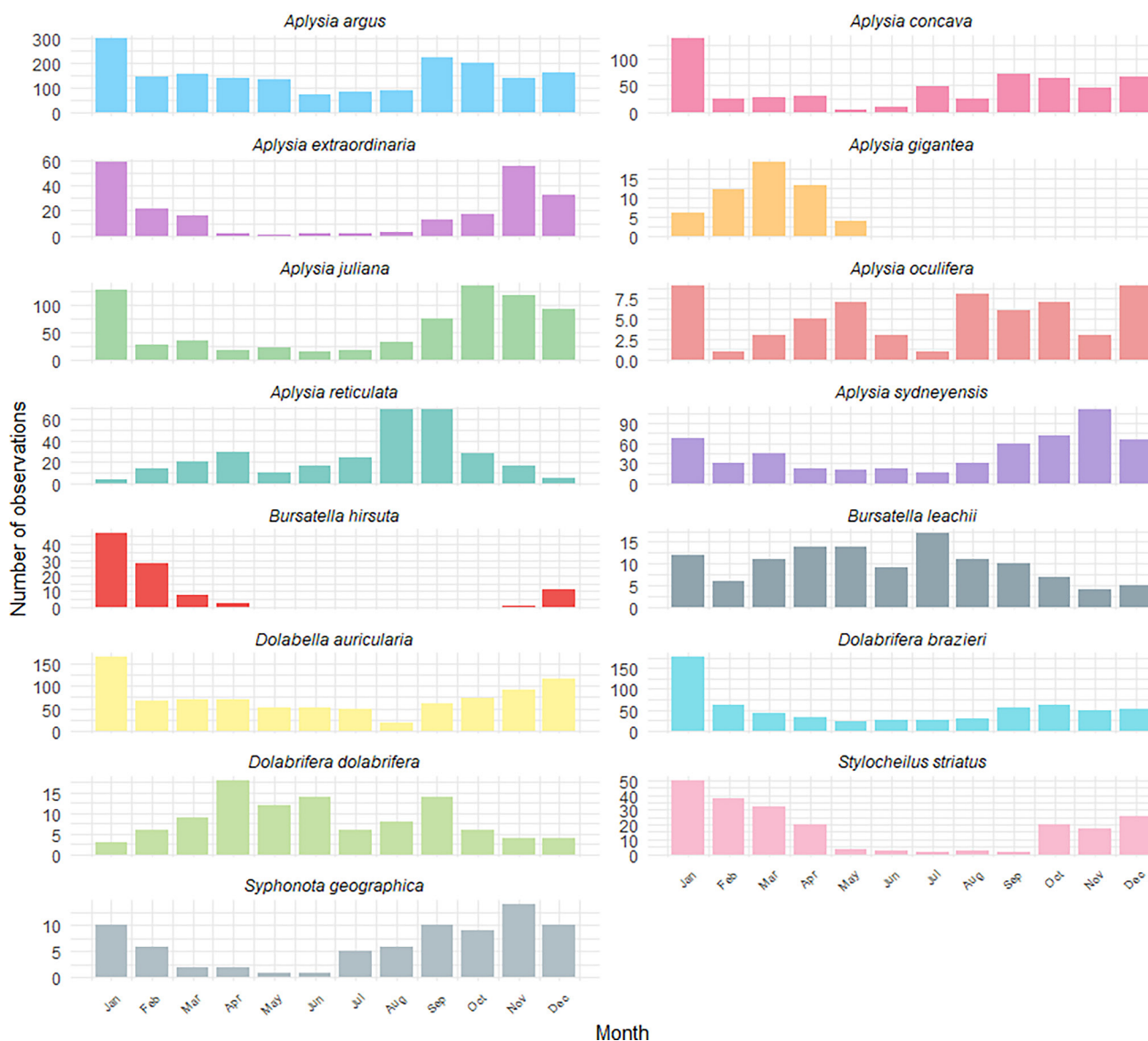


Fig. 17. Species specific seasonal patterns for selected Australian sea hares



Table 3. Species-specific differences by latitudinal zone (revealing geographic structure) for taxa that exhibit mixed latitudinal phenology. Division into latitudinal zones (Tropical:  $<23^{\circ}\text{S}$ ; Subtropical:  $23^{\circ}$  to  $29^{\circ}\text{S}$ ; Temperate:  $>29^{\circ}\text{S}$ ) shows patterns that were obscured in pooled data. Only zones with  $\geq 10$  observations shown. N = number of observations,  $r$  = concentration parameter [closeness of fit to circular model] (thus 1 = all obs in 1 month, 0 = no seasonality). Test statistic  $Z = n \times r^2$

| Species                      | Zone        | N    | Peak month | $r^2$ | Z     | p        | $\Delta$ months |
|------------------------------|-------------|------|------------|-------|-------|----------|-----------------|
| <i>Aplysia oculifera</i>     | Temperate   | 19   | January    | 0.65  | 8.0   | $<0.001$ | $\sim 6$        |
|                              | Tropical    | 42   | August     | 0.20  | 1.7   | 0.190    |                 |
| <i>Aplysia argus</i>         | Temperate   | 1062 | January    | 0.31  | 102.0 | $<0.001$ | $\sim 3$        |
|                              | Subtropical | 530  | October    | 0.18  | 17.2  | $<0.001$ |                 |
|                              | Tropical    | 237  | October    | 0.41  | 39.9  | $<0.001$ |                 |
| <i>Aplysia concava</i>       | Temperate   | 449  | December   | 0.50  | 112.3 | $<0.001$ | $\sim 5$        |
|                              | Subtropical | 27   | September  | 0.57  | 8.8   | $<0.001$ |                 |
|                              | Tropical    | 84   | July       | 0.56  | 26.3  | $<0.001$ |                 |
| <i>Dolabella auricularia</i> | Temperate   | 615  | January    | 0.37  | 84.2  | $<0.001$ | $\sim 7$        |
|                              | Subtropical | 223  | January    | 0.18  | 7.2   | $<0.001$ |                 |
|                              | Tropical    | 48   | June       | 0.44  | 9.3   | $<0.001$ |                 |
| <i>Aplysia reticulata</i>    | Temperate   | 46   | March      | 0.53  | 12.9  | $<0.001$ | $\sim 5$        |
|                              | Tropical    | 228  | August     | 0.57  | 74.1  | $<0.001$ |                 |
| <i>Stylocheilus striatus</i> | Temperate   | 142  | February   | 0.73  | 75.7  | $<0.001$ | $\sim 2$        |
|                              | Subtropical | 59   | December   | 0.50  | 14.8  | $<0.001$ |                 |

butions for any species (all  $U^2 < 0.187$ ,  $p > 0.05$ ; N early = 18–148, N recent = 190–1,681) (Appendix: Table A2b), suggesting that phenological patterns have remained stable over the observation period despite substantial regional warming trends.

#### Objective 4 – Temporal trends indicating climate-driven phenological shifts

Circular-linear regression of observation timing against year (2010–2024) identified directional shifts in two species. *A. sydneyensis* showed a shift toward earlier peak timing of approximately 30 days per decade (slope =  $-0.0517$  rad/year,  $p < 0.001$ , Bonferroni-adjusted  $p = 0.026$ ), while *D. auricularia* showed a shift toward later peak timing of approximately 46 days per decade (slope =  $+0.0793$  rad/year,  $p < 0.001$ , Bonferroni-adjusted  $p = 0.020$ ). The

remaining six species showed slopes between  $-34$  and  $+16$  days per decade with no significant directional trend after correction (Appendix: Table A6). In a sensitivity analysis restricted to the more densely sampled 2015–2024 period, both significant slopes were retained with attenuated effect sizes (*A. sydneyensis*:  $-25$  days/decade; *D. auricularia*:  $+40$  days/decade), but neither survived Bonferroni correction (both Bonferroni-adjusted  $p > 0.05$ ), indicating that the full-window results are borderline for power and depend on early year data for statistical significance. Watson's two-sample tests comparing early (2010–2017) versus recent (2018–2024) periods showed no significant differences in seasonal distributions for any species (all  $U^2 < 0.187$ ,  $p > 0.05$ ; Appendix: Table A2b).

## DISCUSSION

### LATITUDINAL DRIVERS OF PHENOLOGY

The most prominent pattern in sea hare phenology was the presence of latitudinal gradients in peak timing, with temperate populations (south of  $29^{\circ}\text{S}$ ) peaking in December–January and tropical populations (north of  $23^{\circ}\text{S}$ ) peaking in August–September (Fig. 18). This gradient is likely to reflect fundamental differences in environmental seasonality across latitude. In temperate Australian waters, sea surface temperatures can fluctuate by as much as  $4$ – $6^{\circ}\text{C}$  between summer and winter (RIDGWAY & DUNN 2003, SCHAEFFER & ROUGHAN 2017), creating a strong environmental cue for synchronised reproduction in

ectothermic marine invertebrates. Sea surface temperatures above  $18$ – $20^{\circ}\text{C}$  are generally required for successful spawning and larval development in temperate *Aplysia* species (KANDEL 1979, SUSSWEIN et al. 1983), and the timing of thermal thresholds is likely to constrain population-level phenology to the summer months. However, links between temperature and phenology are inferred from the coincidence between observed peaks and known thermal optima rather than directly tested against sea surface temperature data, thus the mechanistic interpretation remains speculative.

In tropical regions, there is relatively little annual sea surface temperature variation, but macroalgal

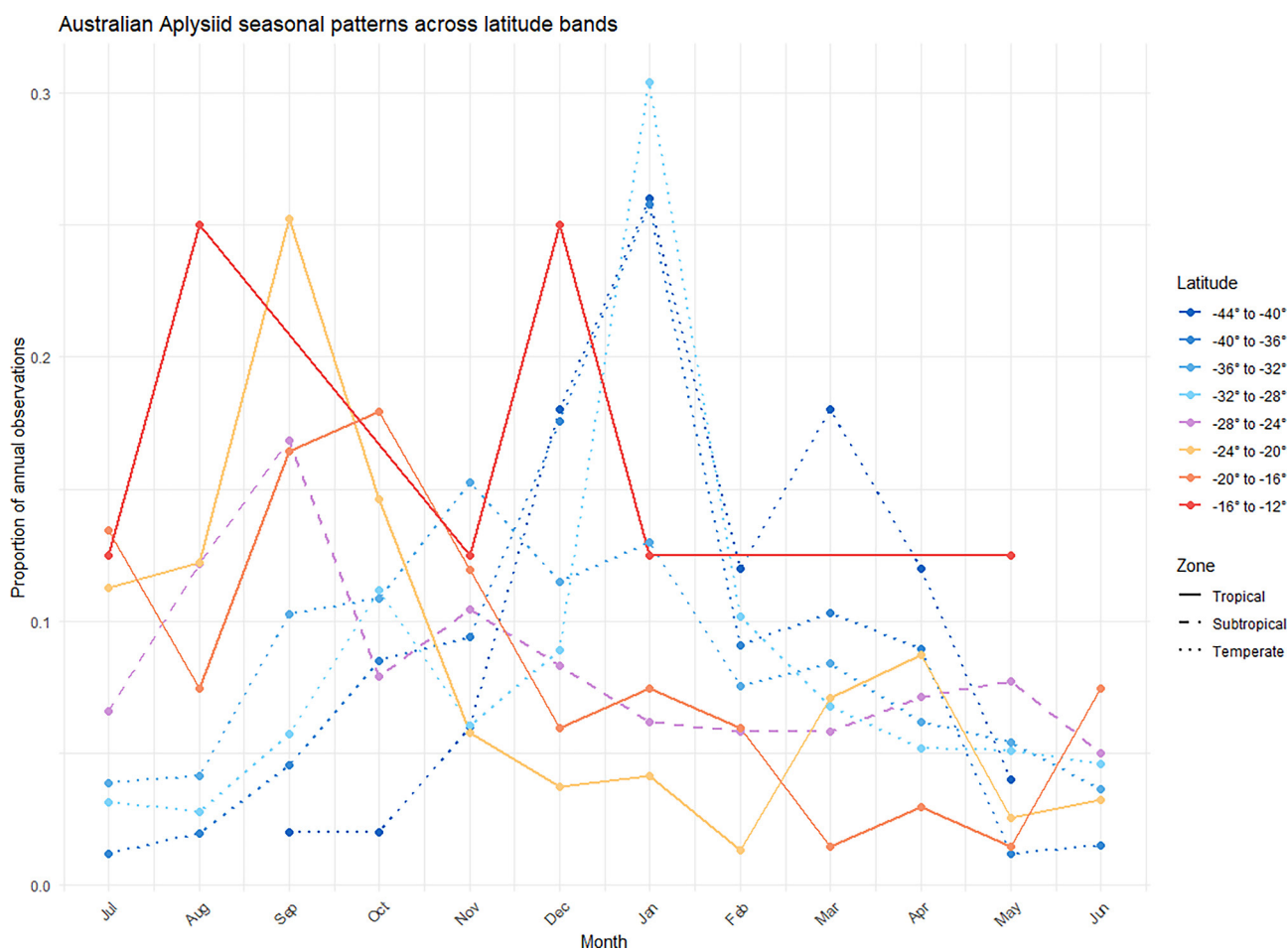


Fig. 18. Monthly proportion of total aplysiid observations by latitudinal bands. Colours represent four degree latitudinal bands, line style indicates zone type (tropical, subtropical & temperate). To better visualise peaks the x-axis is summer centred

communities nonetheless show pronounced seasonality. On Western Australian tropical reefs, where most Australian *A. reticulata* records originate, canopy-forming *Sargassum* spp. reach peak biomass in summer and senesce through winter, while understory brown algae such as *Dictyopteris* and *Lobophora* reach peak biomass in winter when the *Sargassum* canopy is at its minimum (FULTON et al. 2014). The August–September peaks in tropical sea hare observations coincide with this winter understory-algae peak, providing a plausible food-availability mechanism that is consistent with the algivory typical of Aplysiidae (NIMBS et al. 2017a). These contrasting drivers – temperature-driven seasonality in temperate waters versus macroalgal community turnover in the tropics are likely to produce the latitudinal gradient evident in Fig. 17.

The apparent east–west coast differences in phenology (Appendix: Table A1) are a product of the latitudinal gradient interacting with geographic distribution of observations. East coast data are dominated by observations from temperate New South Wales and Victoria, producing a strong December

peak whereas data for the west coast spans a narrower latitudinal range, and mixed latitudinal observations with offset peak timing has acted to produce a weak seasonality signal and multimodal pattern. Oceanographic differences between coasts – the strongly seasonal East Australian Current versus the thermally stable Leeuwin Current (FENG et al. 2003, WERNBERG et al. 2012) – are likely to contribute to the patterns, but latitudinal sample composition is sufficient to explain most of the observed contrast.

#### SPECIES-SPECIFIC PATTERNS AND ECOLOGICAL IMPLICATIONS

The gradient from highly seasonal ( $r > 0.8$ ) to year-round ( $r < 0.2$ ) species suggests temporal niche partitioning within Australian sea hare assemblages. Tightly seasonal species like *B. hirsuta* (NIMBS & WILSON 2020, WELLS et al. 2021) and *A. gigantea* may be specialists with narrow thermal or dietary requirements, restricting their activity to optimal summer conditions. In contrast, taxa with weak seasonality (*A. oculifera* and *B. leachii*) may be thermal

generalists capable of exploiting resources across a broader temperature range or may comprise populations with staggered cohorts producing year-round reproductive output.

The August peak in observations of *A. reticulata* is notable, as it suggests this species may occupy a distinct temporal or latitudinal niche. Winter-peaking marine invertebrates are relatively uncommon in Australian waters, and this pattern may reflect specialised food requirements coinciding with particular macroalgal communities (PENNINGS 1990). Alternatively, the apparent winter peak in this taxon may have resulted from higher detectability during cooler months if this species is cryptic or less active during summer.

The clustering of peak months among common species (November–December) raises questions about potential competitive interactions. If multiple sea hare species compete for similar macroalgal resources, such temporal overlap could intensify resource competition during population blooms. However, sea hares exhibit diverse dietary preferences (PENNINGS 1990, ROGERS et al. 1995, NIMBS et al. 2017a), and spatial segregation by habitat or depth would reduce direct competition even when phenological patterns overlap.

#### GEOGRAPHIC STRUCTURE IN SPECIES-LEVEL PATTERNS

Pooled species-level analyses can underestimate seasonal concentration when populations exhibit different phenologies across latitudinal gradients. Several species classified as weakly seasonal based on pooled data (*A. oculifera*, *A. argus*, *D. auricularia*) showed moderate to strong seasonality within geographic regions (Table 3). As with the east and west coast comparative analysis, this pattern arose because tropical and temperate observations often peak at different times of year – sometimes differing by 5–7 months – causing their signals to partially cancel when combined.

For example, *A. oculifera* appeared essentially year-round in pooled analyses ( $r = 0.14$ , non-significant) but exhibited a January concentration in temperate regions ( $r = 0.65$ ). Similarly, *A. concava* showed opposite seasonal peaks in tropical (July–August, late dry season/early wet season) versus temperate (December, summer) regions, likely reflecting responses to different temperature and productivity regimes.

These patterns highlight the need to consider latitudinal range when characterising phenology in widespread species, as pooling observations across large geographic areas may generate assemblage-level patterns that do not represent local population dynamics. The regional structure also suggests that

sea hare phenology is coupled to local environmental conditions rather than being determined solely by phylogenetic constraints or life history traits.

#### METHODOLOGICAL CONSIDERATIONS AND THE IMPORTANCE OF DETRENDING

Exponential growth in iNaturalist participation has been documented globally (CALLAGHAN et al. 2019), and failure to account for this trend can produce spurious periodicities through the interaction of trend and seasonal components (GROLEMUND & WICKHAM 2011). The pronounced increase in observation numbers from 2010 ( $n = 13$ ) to 2024 ( $n = 1,456$ ) introduces challenges for detecting phenological shifts. Additionally, the youth of iNaturalist means that the 15-year reliable data period is relatively short for climate-driven phenological studies, which typically require 30+ years of data to distinguish directional trends from natural variability (EDWARDS & RICHARDSON 2004, POLOCZANSKA et al. 2013). Strong increases in sample sizes over recent years may introduce bias when using trend analyses if observer behaviour or coverage changes systematically over time (COURTER et al. 2013).

An additional concern is whether seasonal patterns might reflect within-year variation in observer activity rather than actual sea hare biology. Observer effort and sea hare seasonality were decoupled: all-Australia iNaturalist uploads peaked in September–October with a June minimum (Appendix: Table A7), whereas temperate Aplysiidae observations peaked in January (18.0% of records vs 8.2% baseline) and tropical sea hares in August–September (up to 22.3% vs 12.0% baseline). The mismatch indicates that the seasonal patterns reported here reflect biology rather than observer effort bias. Depth of observation is not recorded by iNaturalist and cannot be reliably inferred from coordinates given the variable bathymetry of nearshore Australian waters; the dataset therefore aggregates intertidal and shallow subtidal records without a recoverable per-observation depth, which is treated here as a component of broader observer-effort variation.

Despite these limitations, citizen science data offer unique advantages for phenological research. The geographic and temporal coverage achievable through platforms like iNaturalist far exceeds what is feasible through traditional field surveys (DICKINSON et al. 2012, POCOCK et al. 2015). For conspicuous, taxonomically-stable species like sea hares, research-grade identifications are generally reliable, particularly at the genus or family level. Future studies could strengthen phenological inference by incorporating environmental covariates (e.g., satellite-derived sea surface temperature) to normalise observations and account for spatiotem-



poral variation in observer effort (SZABO et al. 2010, CALLAGHAN et al. 2019).

## EVIDENCE FOR DIRECTIONAL SHIFTS

Australian coastal waters have warmed significantly over recent decades, with the eastern region showing particularly rapid temperature increases (RIDGWAY 2007, WU et al. 2012). Circular regression of observation timing against year provided mixed evidence for directional shifts: two of eight tested species exhibited statistically significant directional shifts over 2010–2024. *A. sydneyensis*, a well-documented temperate NSW endemic, shifted earlier by approximately one month per decade – a direction consistent with regional warming and broadly comparable in magnitude to shifts reported for other marine taxa (POLOCZANSKA et al. 2013). *D. auricularia*, with its largest populations in the tropics, shifted later by approximately 1.5 months per decade, potentially reflecting altered monsoon dynamics rather than a simple temperature response. The remaining six species showed no detectable directional shifts. Both significant effects attenuated to non-significance under Bonferroni correction in a 2015–2024 sensitivity window, indicating that the full-period results are borderline for statistical power. This mixed result suggests three non-exclusive interpretations: (1) phenological responses to warming are species-specific and depend on local environmental drivers (temperature for temperate species, monsoon dynamics for tropical species); (2) the observation period (15 years) is at the lower end of what is typically required to detect climate-driven phenological signals (EDWARDS & RICHARDSON

2004, POLOCZANSKA et al. 2013); and (3) other environmental factors (photoperiod, food availability) may constrain phenological responses regardless of temperature. No quantitative historical phenological data are available for Australian sea hares against which to benchmark the present results; previous Australian work has described boom–bust population dynamics linked to food availability (NIMBS et al. 2017a) without resolving the seasonal structure documented here.

The baseline phenological data established here provide a foundation for detecting future shifts as warming continues. Continued monitoring through citizen science platforms, ideally integrated with oceanographic time series data, would enable more robust detection of climate-driven changes. Particular attention should be paid to species at the margins of their thermal ranges, such as tropical species reaching their southern limits along the east coast, i.e. the rarely-observed *A. reticulata*, which may show earlier phenological responses to warming.

The latitudinal gradient in phenology raises questions about how populations at different latitudes may respond to future environmental change. Temperate populations, with tightly synchronised seasonal reproduction, may be more vulnerable to phenological mismatches if warming decouples temperature cues from food availability (EDWARDS & RICHARDSON 2004, WINDER & SCHINDLER 2004). Tropical populations, with phenology linked to wet/dry season dynamics rather than temperature alone, may respond differently to warming. Subtropical populations at the interface between these regimes warrant particular attention as potential early indicators of climate-driven phenological shifts.

## CONCLUSIONS

This study provides the first comprehensive analysis of sea hare phenology in Australian waters. The dominant pattern is a strong latitudinal gradient in seasonal timing: temperate populations (>29°S) peak in December–January, while tropical populations (<23°S) peak during the late dry season (August–September), with differences of up to seven months within the same species. Apparent differences between east and west coasts largely reflect the latitudinal composition of observations rather than fundamentally different phenological regimes. A key outcome is that pooling observations across latitudes can obscure species-level seasonality, with several taxa appearing weakly seasonal in pooled data but showing seasonal concentration once geographic structure is accounted for. Species-level analyses suggest temporal niche partitioning, with phenological diversity ranging from highly concentrated summer

specialists to year-round opportunists. Comparison with an all-Australia iNaturalist baseline (~5.4 million records) confirmed that the seasonal patterns recovered are decoupled from general observer-effort seasonality. Tests for directional shifts in observation timing over 2010–2024 identified earlier peaks in the temperate endemic *A. sydneyensis* and later peaks in the predominantly tropical *D. auricularia*; both shifts attenuated under Bonferroni correction in sensitivity analyses, indicating that the current 15-year window is borderline for statistical power.

Looking forward, continued citizen science monitoring, integrated with environmental data and analysed with awareness of latitudinal structure and observer-effort variation, will be critical for detecting climate-driven phenological shifts in marine ecosystems. The baseline patterns documented here establish a foundation for such efforts and highlight the



value of long-term, broad-scale observational data for understanding coastal biodiversity in a changing ocean.

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## APPENDIX – ANALYTICAL OUTPUT

Table A1. Rayleigh test results by coast  
Assemblage-level circular statistics by coast

| Coast      | N    | Peak month | r    | Z     | p       | Interpretation                |
|------------|------|------------|------|-------|---------|-------------------------------|
| East coast | 5508 | December   | 0.31 | 529.2 | <0.0001 | Significant seasonality       |
| West coast | 1033 | September  | 0.04 | 1.7   | <0.0010 | Near-uniform; weak clustering |

Table A2. Watson's two-sample  $U^2$  tests

Watson's  $U^2$  test compares whether two circular samples are drawn from the same underlying distribution. This non-parametric test is robust to deviations from the von Mises distribution (JAMMALAMADAKA & SENGUPTA 2001). Critical values:  $U^2 > 0.187$  ( $p < 0.05$ ),  $U^2 > 0.268$  ( $p < 0.01$ ).

(a) Regional comparisons

| Comparison                      | $N_1$ | $N_2$ | $U^2$ | p      |
|---------------------------------|-------|-------|-------|--------|
| East coast vs West coast        | 5508  | 1033  | 0.89  | <0.001 |
| Tropical vs Temperate (all spp) | –     | –     | –     | <0.001 |
| Tropical vs Subtropical         | –     | –     | –     | <0.001 |
| Subtropical vs Temperate        | –     | –     | –     | <0.05  |

(b) Early (2010–2017) vs Recent (2018–2024) period comparisons

Tests for phenological shifts between time periods. No species showed significant differences, suggesting stable phenological timing over the observation period.

| Species                       | N early | N recent | $U^2$  | p     | Interpretation |
|-------------------------------|---------|----------|--------|-------|----------------|
| <i>Aplysia argus</i>          | 148     | 1681     | <0.187 | >0.05 | No change      |
| <i>Dolabella auricularia</i>  | 80      | 806      | <0.187 | >0.05 | No change      |
| <i>Aplysia juliana</i>        | 62      | 648      | <0.187 | >0.05 | No change      |
| <i>Aplysia concava</i>        | 51      | 509      | <0.187 | >0.05 | No change      |
| <i>Aplysia sydneyensis</i>    | 41      | 522      | <0.187 | >0.05 | No change      |
| <i>Dolabrifera brazieri</i>   | 55      | 572      | <0.187 | >0.05 | No change      |
| <i>Aplysia reticulata</i>     | 32      | 274      | <0.187 | >0.05 | No change      |
| <i>Aplysia extraordinaria</i> | 18      | 205      | <0.187 | >0.05 | No change      |
| <i>Stylocheilus striatus</i>  | 22      | 190      | <0.187 | >0.05 | No change      |

Table A3. Rayleigh test results by 4° latitudinal band (assemblage level)

Assemblage-level Rayleigh tests for all aplysiid observations within each latitudinal band, corresponding to the data presented in Fig. 17.

| Latitude band | Zone        | Peak month | p      | Interpretation          |
|---------------|-------------|------------|--------|-------------------------|
| 44°S to 40°S  | Temperate   | January    | –      | Strong summer peak      |
| 40°S to 36°S  | Temperate   | January    | <0.001 | Strong summer peak      |
| 36°S to 32°S  | Temperate   | January    | <0.001 | Strong summer peak      |
| 32°S to 28°S  | Subtropical | December   | <0.001 | Summer peak             |
| 28°S to 24°S  | Subtropical | September  | <0.050 | Late winter/spring peak |
| 24°S to 20°S  | Tropical    | September  | <0.050 | Dry season peak         |
| 20°S to 16°S  | Tropical    | August     | <0.050 | Dry season peak         |
| 16°S to 12°S  | Tropical    | August     | >0.050 | Weak/uniform            |



Table A4. Spectral analysis – dominant periodicities in detrended time series

Periodogram estimation was applied to STL-detrended monthly observation time series (2015–2024, seasonal + remainder components). The dominant period (highest spectral density peak) and second-ranked period are shown for regional and species-level analyses

| Analysis level               | Dominant period (months) | 2nd period (months) | Interpretation                              |
|------------------------------|--------------------------|---------------------|---------------------------------------------|
| All data pooled              | 12                       | 6                   | Annual + semi-annual (pooling artifact)     |
| East coast                   | 12                       | 4                   | Strong annual cycle                         |
| West coast                   | 6                        | 12                  | Semi-annual dominant (pooling artifact)     |
| Temperate zone (>29°S)       | 12                       | –                   | Annual cycle                                |
| Tropical zone (<23°S)        | 12                       | 6                   | Annual cycle                                |
| <i>Aplysia juliana</i>       | 12                       | –                   | Strong annual                               |
| <i>Dolabella auricularia</i> | 12                       | 6                   | Annual + minor semi-annual                  |
| <i>Aplysia argus</i>         | 12                       | 6                   | Annual + semi-annual (geographic structure) |
| <i>Aplysia concava</i>       | 12                       | –                   | Annual                                      |
| <i>Aplysia sydneyensis</i>   | 12                       | –                   | Annual                                      |

Table A5. Autocorrelation analysis of annual peak timing

Autocorrelation function (ACF) values at lags 1–3 years for annual peak timing series. Values exceeding the 95% confidence bounds ( $\pm 2/\sqrt{n}$ , shown) indicate significant temporal autocorrelation. Near-zero values indicate no systematic interannual cyclicity

| Species                      | N years | ACF lag 1 | ACF lag 2 | ACF lag 3 | 95% CI     |
|------------------------------|---------|-----------|-----------|-----------|------------|
| <i>Aplysia argus</i>         | 13      | –0.12     | +0.08     | –0.15     | $\pm 0.55$ |
| <i>Dolabella auricularia</i> | 12      | +0.05     | –0.21     | +0.11     | $\pm 0.58$ |
| <i>Aplysia juliana</i>       | 12      | –0.08     | +0.14     | –0.03     | $\pm 0.58$ |
| <i>Aplysia concava</i>       | 11      | +0.18     | –0.09     | –0.22     | $\pm 0.60$ |
| <i>Aplysia sydneyensis</i>   | 11      | –0.25     | +0.03     | +0.09     | $\pm 0.60$ |
| <i>Dolabrifera brazieri</i>  | 12      | +0.07     | +0.11     | –0.18     | $\pm 0.58$ |
| <i>Aplysia reticulata</i>    | 10      | –0.14     | –0.06     | +0.22     | $\pm 0.63$ |
| <i>Stylocheilus striatus</i> | 10      | +0.09     | –0.17     | +0.04     | $\pm 0.63$ |

Table A6. Linear regression of annual peak timing against year

Circular-linear regression of observation timing against year for Australian Aplysiidae species with  $\geq 10$  years of data ( $\geq 3$  observations per year). Day-of-year was converted to radians and used as the circular response; year (centred on the dataset midpoint) was the linear predictor. Slopes are expressed as days per decade (positive values indicate later peak timing over time, negative values indicate earlier). The main analysis uses the full 2010–2024 observation window; the sensitivity analysis is restricted to 2015–2024 to exclude sparsely-sampled early years. Multiple-testing correction across the eight species was applied using Bonferroni adjustment. Species with significant directional shifts after Bonferroni correction in the main analysis are shown in bold. n = total observations; Years = number of years contributing to the analysis

| Species                       | N    | Years | Main analysis (2010–2024) |              |              | Sensitivity (2015–2024) |       |           |
|-------------------------------|------|-------|---------------------------|--------------|--------------|-------------------------|-------|-----------|
|                               |      |       | Days/decade               | p            | p (Bonf.)    | Days/decade             | p     | p (Bonf.) |
| <i>Aplysia argus</i>          | 1452 | 13    | –2.8                      | 0.430        | 1.000        | –19.0                   | 0.180 | 1.000     |
| <i>Aplysia concava</i>        | 462  | 13    | –34.1                     | 0.013        | 0.106        | –39.3                   | 0.014 | 0.111     |
| <i>Aplysia extraordinaria</i> | 195  | 12    | +4.0                      | 0.280        | 1.000        | +2.6                    | 0.380 | 1.000     |
| <i>Aplysia juliana</i>        | 570  | 13    | +15.6                     | 0.020        | 0.160        | +16.4                   | 0.023 | 0.185     |
| <i>Aplysia sydneyensis</i>    | 460  | 13    | <b>–29.9</b>              | <b>0.003</b> | <b>0.026</b> | –25.3                   | 0.021 | 0.171     |
| <i>Aplysia reticulata</i>     | 124  | 11    | +30.3                     | 0.140        | 1.000        | +22.4                   | 0.250 | 1.000     |
| <i>Dolabella auricularia</i>  | 633  | 13    | <b>+45.8</b>              | <b>0.002</b> | <b>0.020</b> | +39.7                   | 0.008 | 0.064     |
| <i>Dolabrifera brazieri</i>   | 402  | 13    | +4.4                      | 0.380        | 1.000        | –4.3                    | 0.410 | 1.000     |



Table A7. Comparison of the monthly distribution of Australian Aplysiidae observations (2010–2024) with the all-Australia iNaturalist Research-Grade baseline ( $n = 5,389,576$  records; source: [GBIF \(2026\)](#)). Values are within-group monthly proportions of annual observations. Excess columns (Aplysiidae proportion minus baseline proportion) quantify the deviation of sea hare observations from the general observer-effort pattern: positive values indicate months in which Aplysiidae are overrepresented relative to general observer activity, negative values indicate underrepresentation. Latitudinal zones: Tropical  $<23^{\circ}\text{S}$ ; Temperate  $>29^{\circ}\text{S}$ . Peak months and excesses  $\geq +0.05$  are shown in bold

| Month        | All-Aus baseline | Aplysiidae (pooled) | Temperate Aplysiidae | Tropical Aplysiidae | Excess (pooled) | Excess (temperate) | Excess (tropical) |
|--------------|------------------|---------------------|----------------------|---------------------|-----------------|--------------------|-------------------|
| Jan          | 0.082            | 0.138               | <b>0.180</b>         | 0.031               | +0.056          | <b>+0.098</b>      | −0.051            |
| Feb          | 0.066            | 0.074               | 0.087                | 0.010               | +0.008          | +0.021             | −0.056            |
| Mar          | 0.073            | 0.078               | 0.081                | 0.076               | +0.005          | +0.008             | +0.004            |
| Apr          | 0.078            | 0.075               | 0.074                | 0.099               | −0.003          | −0.004             | +0.022            |
| May          | 0.063            | 0.054               | 0.047                | 0.031               | −0.009          | −0.016             | −0.032            |
| Jun          | 0.056            | 0.042               | 0.034                | 0.058               | −0.014          | −0.023             | +0.002            |
| Jul          | 0.060            | 0.046               | 0.035                | 0.124               | −0.014          | −0.025             | <b>+0.064</b>     |
| Aug          | 0.075            | 0.056               | 0.036                | <b>0.141</b>        | −0.018          | −0.039             | <b>+0.066</b>     |
| Sep          | 0.120            | 0.118               | 0.085                | <b>0.223</b>        | −0.002          | −0.036             | <b>+0.103</b>     |
| Oct          | 0.122            | 0.116               | 0.116                | 0.145               | −0.006          | −0.007             | +0.023            |
| Nov          | 0.106            | 0.103               | 0.117                | 0.029               | −0.002          | +0.011             | −0.077            |
| Dec          | 0.101            | 0.102               | 0.111                | 0.033               | +0.001          | +0.010             | −0.067            |
| <b>Total</b> | <b>5,389,576</b> | <b>4,791</b>        | <b>3,393</b>         | <b>484</b>          | −               | −                  | −                 |