ON THE ECOLOGY OF *CYSTOPHORA* SPP. FORESTS[1]

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Cystophora is the second largest genus of fucoids worldwide and, like many other forest-forming macroalgae, is increasingly threatened by a range of anthropogenic impacts including ocean warming. Yet, limited ecological information is available from the warm portion of their range (SW Western Australia), where severe range contractions are predicted to occur. Here, we provide the first insights on the abundance, diversity, productivity, and stand structure of *Cystophora* forests in this region. Forests were ubiquitous over more than 800 km of coastline and dominated sheltered and moderately-exposed reefs. Stand biomass and productivity were similar or greater than that of kelp forests in the temperate reef communities examined, suggesting that *Cystophora* spp. play a similarly important ecological role. The stand structure of *Cystophora* forests was, however, different than those of kelp forests, with most stands featuring an abundant bank of sub-canopy juveniles and only a few plants forming the canopy layer. Stand productivity followed an opposite seasonal pattern than that of kelps, with maximal growth in late autumn through early winter and net biomass loss in summer. Annually, stands contributed between 2.2 and 5.7 kg · m^{-2} (fresh biomass) to reef productivity depending on the dominant stand species. We propose that *Cystophora* forests play an important and unique role in supporting subtidal temperate diversity and productivity throughout temperate Australia, and urge a better understanding of their ecology and responses to anthropogenic threats.

Key index words: biogeography; biomass accumulation; canopy-forming macroalgae; *Ecklonia radiata*; Fucales; great southern reef; net primary production; photosynthesis; Sargassaceae; seaweed

Abbreviation: GSR, Great Southern Reef

Temperate Australia harbors a substantial fraction of the worlds underwater flora, comprising well over 1200 species of macroalgae with endemism levels >75% for some groups (Bolton 1994, Phillips 2001, Fragkopoulou et al. 2022). Macroalgae constitute the biological engine of the Great Southern Reef (GSR), an interconnected system of rocky reefs that extends across the lower third of the Australian continent (Bennett et al. 2016). In particular, large, canopy-forming brown algae form impressive underwater forests (sensu Wernberg and Filbee-Dexter 2019) that provide the foundation for habitat and underpin trophic food webs across the GSR (Shepherd and Edgar 2013). The underwater forests of this reef system are exceptional in their extreme diversity (e.g., >14 canopy-forming species in one forest; Collings 1996, Wernberg et al. 2003), and in that there can be no clear dominant species (Turner and Cheshire 2003)—as opposed to what is observed in many marine forests elsewhere (e.g., North America, Dayton et al. 1984; South Africa, Field et al. 1980; Europe, Smale and Moore 2017). Australian temperate forest-forming algae are, however, rapidly retreating polewards in response to ocean warming (Wernberg et al. 2011), with several species having lost substantial portions of their range in recent years (Smale and Wernberg 2013, Wernberg et al. 2016) or becoming functionally extinct (Pessarrodona 2022). Importantly, many more are predicted to undergo severe range contractions during this century (36–100% of range loss; Martínez et al. 2018), even under moderate warming scenarios. A sound understanding of the ecology and biology of the diverse Australian underwater forests is therefore critical to adequately predict and adapt to the challenges presented by climate change, as several areas along the GSR have been deemed global ocean warming hotspots (Hobday and Pecl 2014).

Large knowledge gaps remain, however, regarding the basic ecology and biology of many forest-forming species in the GSR (Coleman and Wernberg 2017). Research has traditionally focused on

laminarian kelps, particularly *Ecklonia radiata*, which tends to dominate the western and eastern coasts as well as exposed sites on the southern coast (Connell and Irving 2008, Bennett 2015, Wernberg et al. 2019). Yet, fucoids are often prevalent on sheltered and moderately exposed reefs, particularly along the longer (~6000 km) —more remote— south coast (Shepherd and Edgar 2013), exhibiting an exceptional richness (>60 species and 13 genera, many being monotypic or bitypic). Along this coastline, fucoid forests occur both as mono-specific or mixed assemblages with other fucoids or kelps across a wide range of wave exposure (Shepherd and Womersley 1981, Turner and Cheshire 2003, Goldberg and Kendrick 2004, Connell and Irving 2008). These fucoid forests constitute a prominent ecological element of the temperate subtidal unlike fucoids elsewhere, whose dominance is generally greatest in the intertidal habitats. Additionally, they play a unique ecological role compared to kelp forests, influencing understory environmental conditions and biota differently (Collings 1996, Irving and Connell 2006), and supporting distinct algal (Irving and Connell 2006), invertebrate (Taylor and Cole 1994, Fraser et al. 2020) and fish communities (McDermott and Shima 2006).

Cystophora is the second largest genus of fucoids globally (23 species, after *Sargassum*; Guiry and Guiry 2022) and is endemic to Australasia, where it is an ubiquitous constituent of its subtidal forests (Bennett 1921, Womersley 1947, 1949, Smith 1952). The majority of species occur in the warm- and cold-temperate regions of the Australian continent, while six species are found in New Zealand (Womersley 1987). *Cystophora* spp. are perennial plants occurring from the intertidal to around 30 m depth, with some species extending over extremely narrow biogeographical ranges (e.g., *Cystophora harveyi*, c.a. 350 km; Womersley 1987), while others occurring throughout temperate Australasia (e.g., *Cystophora monilifera*; Womersley 1987). *Cystophora* forests are typically composed of multiple species (Fig. 1a) and tend to dominate sheltered and moderately-exposed locations both in terms of percent cover and biomass (Shepherd and Womersley 1981, Collings and Cheshire 1998, Turner and Cheshire 2003, Goldberg and Kendrick 2004).

Despite their widespread distribution, little is known about the ecology and structure of *Cystophora* forests (Shepherd and Edgar 2013), particularly across the warm portion of their range (SW Western Australia) where *Cystophora* spp. remain severely understudied (Womersley 1964, 1987). Virtually all existing knowledge on their ecology and life history is derived from the South Australia coastline in the central (cooler) portion of their range (Shepherd and Womersley 1970, 1971, 1976, 1981, Cheshire et al. 1996, Collings and Cheshire 1998, Hotchkiss 1999). Worryingly, however, between 50 and 97% of the current distribution of *Cystophora* spp. (5000–9000 km of coastline) is projected to be lost under future climate change scenarios (Martínez et al. 2018), with rear (warm) edge populations having already become functionally extinct (Pessarrodona 2022).

Here, we provide the first account of the productivity and stand structure of *Cystophora* spp. forests across the warmer end of their distribution, together with fine-scale biogeographical notes on the distribution of different species. Our findings are placed in the context of the more intensively studied forest-forming macroalgae *Ecklonia radiata* (hereafter kelp), which typically dominates lower latitude reefs and more exposed locations (Goldberg and Kendrick 2004, Bennett 2015). This work contributes to understanding one of the most species-rich groups of forest-forming algae worldwide, and provides a basis for comparisons with other temperate algal assemblages. Additionally, our findings further our understanding of the forgotten forests of the Australian continent, providing a pivotal source of information to manage them in rapidly changing marine environment.

METHODS

Study area. The study area extended throughout the temperate coast of Western Australia. The west facing coastline of Western Australia features mostly limestone reefs of varied topographic complexity; the southwestern coast is characterized by both granite and limestone reefs, while the southern coast is mostly dominated by granite reefs. The temperate reefs of the region are exposed to large oceanic swells, with the southwestern corner experiencing the largest wave conditions (maximum significant wave heights of 11.5 m; Hemer 2006). Reefs are patchily interspersed with areas of sand and range in depth from the intertidal to >40 m.

The marine flora of the region is one of the richest in the world and features high levels of endemicity attributed to Australia's long isolation and the lack of mass extinction events (Phillips 2001, Fragkopoulou et al. 2022). The regional flora composition is markedly influenced by the Leeuwin Current, which seasonally flows southwards of the West-facing coastline bringing low-nutrient water and propagules from warmer areas to the temperate region (Kendrick et al. 2009). The marine forest canopies of the study area are dominated by kelp in the west coast, with *Cystophora* spp. and *Sargassum* spp. progressively becoming more abundant as one travels southeast (Goldberg and Kendrick 2004, Smale et al. 2010, Bennett 2015).

Forest distribution and abundance. To determine the current (2019–2021) extent of *Cystophora* forest stands across the western range edge of their distribution, we conducted a series of surveys across ca. 1600 km of coastline, from 27.5 to 35° S. Eighty-four survey locations were selected to cover the recorded historical distribution of *Cystophora* in Western Australia. Survey locations targeted shallow (i.e., 0–15 m depth), moderately-exposed and sheltered rocky reefs where *Cystophora* forests are known to dominate the seascape in other regions (Shepherd and Womersley 1970, 1981). Two types of surveys were conducted: (i) rapid underwater visual censuses (UVC) to determine the presence and composition of *Cystophora* stands (all sites), and (ii) seascape level surveys quantifying the abundance of *Cystophora* stands and other forest-forming algae (9 sites).
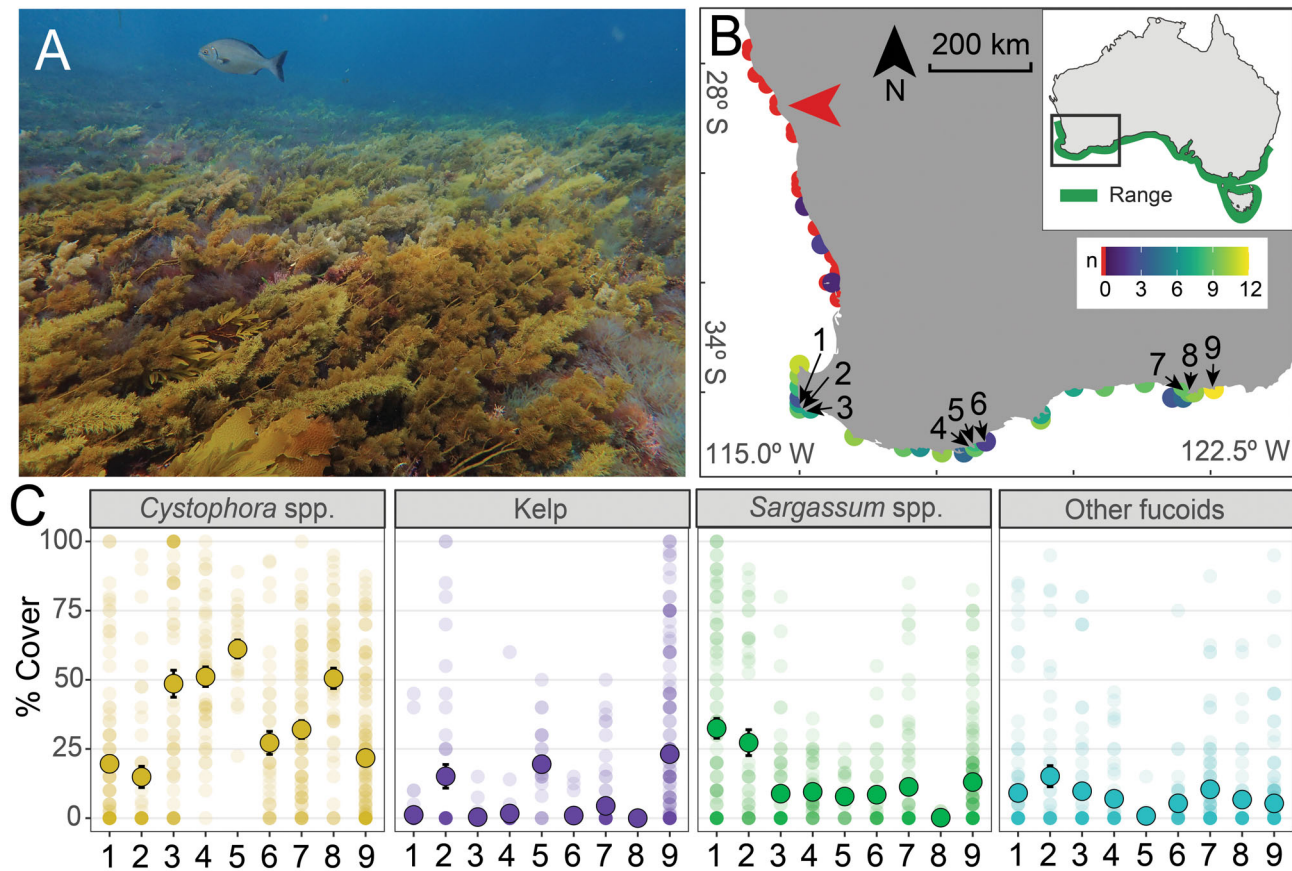
FIG. 1. (a) An underwater forest dominated by several species of *Cystophora* (Photograph: A. Pessarrodona). (b) *Cystophora* stand richness (*n* species) across all UVC survey locations in the western range edge of *Cystophora* distribution (line depicted in the insert). Letters denote locations of the abundance surveys, whilst the large arrow indicates the historical range edge. (c) Abundance (% cover) of different forest-forming groups across a subset of the studied sites within three regions (Cape Leeuwin, 1–3; Albany, 4–6; and Cape Le Grand, 7–9). Sites include Hamelin Bay (1), Cosy Corner (2), Augusta (3), Two People's Bay (4), Betty's Beach (5), Cheyenne Beach (6), Le Grand Beach (7), Black Island (8), and Wharton Beach (9). Large dots denote site-level means ± standard deviation, whilst smaller dots indicate quadrat-level values. Note the error bars of some sites are too small to be seen. [Color figure can be viewed at wileyonlinelibrary.com]

For the UVCs, the same observer (AP) swam along the shoreline or reef contour for approximately 30 min documenting the presence of as many species of *Cystophora* as possible. The majority (63%) of the UVC surveys included habitat reportedly occupied by *Cystophora* spp. in historical studies and herbaria specimens (i.e., intertidal-subtidal fringe down to 3 m depth; Smith 1952, PERTH5857759, AD-A51087, AD-A33330B, HO594202, note that early phycologists rarely accessed the subtidal). Additionally, a series of UVCs on SCUBA were conducted targeting a deeper (5–15 m) depth range. *Cystophora* spp. were found to be always present along the southern coastline (see Results section). For a subset of sites on that area (*n* = 9), the observer also surveyed their abundance (% cover). For these surveys, three to five transects were laid along the reef perpendicular to the shore, starting at the shallowest depth possible and extending until the rocky reef transitioned to sand or seagrass meadows (Connell and Irving 2008). Along each transect, a series of photographs of a 0.25 m² quadrat were taken at 2.5 m intervals (*n* = 22–55 photos per transect, varying depending on the reef total length and depth, capped at 15 m). Percent cover was measured in Adobe Photoshop CC (Adobe Systems Inc.) with the aid of a reticulum of 25 cells (5 × 5) superimposed over the photographed quadrats, where the cover within each cell in which a species appeared was recorded.

Forest structure and standing stock. To determine the stand structure, density and stock of *Cystophora* forests, we destructively sampled *Cystophora* stands dominated by eight different species (*C. brownii*; *C. harveyi*; *C. moniliformis*; *C. pectinata*; *C. racemosa*; *C. siliquosa*; *C. subfarcinata*; and a mixed stand of *C. expansa* and *C. monilifera*). Sampling targeted patches dominated (i.e., 90% cover) by each of the focal *Cystophora* species and was conducted across a range of sites (*n* = 7) and depths, depending on where the stands of each species were most abundant (Table S1 in the Supporting Information). In each stand type, six to sixteen 0.25 m² quadrats (Table S1) were randomly placed within the stand by a SCUBA diver and all nonencrusting algae inside the quadrat were collected inside a calico bag. Samples were at least 5 m apart and were processed within 6 h of collection. The maximum length (0.5 cm precision), weight (0.1 g precision), and species of each *Cystophora* individual was noted, while only the total weight of other species of algae was measured. This allowed us to quantify the mean *Cystophora* plant weight and length, density and size frequency, as well as assemblage total biomass.

Forest growth. To understand the contributions of *Cystophora* forests to the reef primary productivity, we measured plant growth and biomass accumulation in stands of four

abundant species (*C. racemosa*, *C. pectinata*, *C. moniliformis* and *C. brownii*) at sites near Albany (Betty's Beach, 34°56′08″ S 118°12′31″ E; and Two People's Bay, 34°58′16″ S 118°10′54″ E) from November 2020 to December 2021. Biomass accumulation constitutes a conservative measurement of true net primary productivity as it only quantifies the assimilated carbon destined to tissue growth (Krumhansl and Scheibling 2011, De Bettignies et al. 2013). Changes in plant biomass accumulation were estimated by tracking the thallus volume, as volume is better correlated to weight than plant length in fucoids (Åberg 1990). Measurements of randomly collected *Cystophora* plants from several species ($n = 28–219$ per species; Table 1) also confirmed a strong correlation between weight and volume (see Results section). According to Åberg (1990), an estimate of thallus volume can be obtained using the formula:

$$\text{Volume} = \text{maximum length} \times \text{circumference}^2$$

Maximum length (0.5 cm precision) was measured by running a measuring tape along the thallus from the top of the holdfast to the top of the largest frond. For the circumference (0.5 cm precision), all fronds of a given individual were laid parallel, a lasso was made with the measuring tape, and the circumference of the bundle of fronds measured by continuously moving the lasso along the length of the individual, noting the maximum value. The measuring tape was kept as tight as possible, and all measurements were performed by the same individual to minimize variation. For individuals smaller than 1.5 cm in circumference, the lasso was too small, and their circumference was set to 0.75 cm. Six to nine plants of each species were tagged and measured in situ periodically over a series of visits to the study sites (approximately every 2 months for 13 months).

In this way, the biomass accumulation rate of the tagged plants between two sampling visits was obtained by calculating the difference in weight (obtained by measuring the volume of tagged individuals in the field and the volume-weight relationships), divided by the number of days between visits. The tagged plants were located at depth where they were most abundant. *Cystophora racemosa*, *C. pectinata*, and *C. moniliformis* were sampled at Betty's Beach (5–6 m depth), and *C. brownii* was sampled at Two People's Bay (0.5–1.5 m depth). New plants were occasionally tagged to replace dead ones.

To compare *Cystophora* growth patterns with those of other forest-forming seaweeds, we also measured growth biomass accumulation in kelp. Growth was estimated at Betty's Beach following a modified methodology from Mann and Kirkman (1981), whereby individuals were hole-punched at 10 cm from the stipe-lamina transition zone. During each survey, 8 to 11 plants previously tagged and hole-punched were collected and new ones uniquely labeled and punched. The lamina elongation rate of each individual was determined by subtracting 10 cm to the final hole position, and dividing by the number of days between visits. To convert lamina elongation (cm) to biomass accumulation (g), we multiplied the average fresh biomass of three 5 cm length segments from the first 15 cm of each individual (g · cm^{-1}) by its elongation.

Finally, to determine biomass accumulation at the reef level, we multiplied the average annual growth of each species (i.e., positive growth) by their average density. Densities were estimated in July 2021 by haphazardly placing 0.25 m^2 quadrats in stands of different species (*Cystophora moniliformis*, $n = 10$; *C. racemosa* and *C. pectinata*, $n = 24$; *C. brownii*, $n = 15$; *Ecklonia radiata*, $n = 29$), and counting the number of adult (>30 cm thallus length) individuals within each quadrat.

RESULTS AND DISCUSSION

Distribution surveys. Overall, *Cystophora* stands were present across 43 of the 84 reefs sampled, extending from Cervantes (30° S, 115° E) through the southern coast of Western Australia (Fig. 1b, Fig. S1 in the Supporting Information). *Cystophora* spp. distribution was largely discontinuous along the (warm) range edge of its distribution (Perth Metropolitan Area to Geraldton; Smith 1952), with only a few isolated *Cystophora* plants found near Cervantes (30.5° S, 115° E), Seabird (31.5° S, 115° E), and Rottnest Island (32° S, 115° E). These findings align with surveys conducted between Jurien Bay and Lancelin (30–31° S 115° E), which also report a few scattered individuals (<2% cover) present only at 2 of the 42 sites surveyed (Edgar et al. 2009). In contrast, *Cystophora* spp. exhibited a continuous distribution along the southwestern and southern coast. The diversity of *Cystophora* stands on the range edge (up to 2 species per site, *C. brownii* and *C. monilifera*; Fig. 1b) was also lower compared to that of the southern coastline (up to 12 species per site; Fig. 1b). Overall, this suggests that, contemporarily, *Cystophora* play a minor ecological role across the range edge and are only ecologically relevant across the southwestern and southern coast.

At the subset of the sites examined within the south coast, *Cystophora* stands dominated the benthic cover at a majority (6 out of 9) of sites (Fig. 1c; 27–61% site cover). Across all these sites, kelps had cover below 25% and were never the dominant forest-forming group, while *Sargassum* spp., and other forest-forming fucoids typically had between 5–20% cover. Exceptions were two sites within the Cape Leeuwin region, whose forests were dominated by *Sargassum* (32% and 27% cover at Hamelin Bay and Cosy Corner, respectively; Fig. 1c). Our observations align with previous studies suggesting a transition from the kelp-dominated forests in the western coast to *Cystophora*- and fucoid-dominated forests in southern Australia (Collings and Cheshire 1998, Wernberg et al. 2003, Goldberg and Kendrick 2004, Bennett 2015), and reinforce the importance this genus plays in the subtidal ecology of the region. It is worth noting that, for logistical regions, most of the surveys conducted here targeted sheltered to moderately exposed sites, missing highly exposed sites where kelp forests may still be dominant (Goldberg and Kendrick 2004). Given that the same range of exposure was sampled across the entire coastline, however, our results suggests that *Cystophora* forests were at least dominant within areas of reduced wave exposure along the south coast.

In total, 13 *Cystophora* species were observed across all surveys (Fig. S1). Such rich diversity outnumbers that of other forest-forming groups such as kelps (1 species, *Ecklonia radiata*), *Sargassum* spp. (12 species), and other fucoids (7 species) occurring throughout the study region (Goldberg and

TABLE 1. Characteristics of *Cystophora* species encountered throughout the study region. Values indicate mean, while maximum values are indicated in parenthesis. FW = Fresh weight. DW = Dry weight.

| Species	Number of measured plants (n)	Length (cm)	Weight (g FW)	% DW (mean ± SD) [n]	Depth observed (m)	Distribution notes
C. brownii	207	16 (128)	54 (561)	22.4 ± 2.62 [23]	0–5	Widespread, abundant in the immediate sublittoral but rarely dominant. Moderate to rough wave action
C. expansa	161	22 (161)	60 (419)	NA	0–18	Locally abundant where it can sometimes dominate the shallow sublittoral. Moderate water movement
C. gracilis	54	11 (74)	15 (129)	NA	0–6	Abundant in the immediate sublittoral but rarely dominant, often mixed with other species.
C. grevillei	28	80 (154)	503 (1583)	16.19 ± 0.48 [4]	6–30	Rarely seen in the shallows, but common as drift. Possibly a deep water species
C. harveyi	128	48 (207)	143 (1295)	21.72 ± 2.65 [24]	0–5	Restricted to the SW corner, where it is one of the dominant species in the moderately exposed shallow sublittoral (0–5).
C. monilifera	111	20 (115)	65 (421)	17.61 ± 2.18 [15]	2–15	Widespread and abundant in some locations of moderate water movement
C. moniliformis	63	38 (326)	112 (475)	21.14 ± 4.03 [36]	2–15	Rarely dominant. Where abundant, it can form large patches near shallow areas of moderate wave action. Can withstand sand scour.
C. pectinata	144	19 (140)	136 (940)	15.36 ± 2.32 [15]	2–12	Locally abundant, where it can dominate shallow to deep sublittoral forests
C. racemosa	225	12 (150)	82 (735)	19.40 ± 2.98 [23]	2–14	Widespread and locally abundant in the shallow to deep sublittoral, although it rarely forms monospecific stands. Can occur along areas of rough wave action but at depth.
C. retorta	146	27 (233)	32 (521)	24.02 ± 3.28 [37]	2–15	Widespread but rarely abundant, often mixed with other species, where it co-occurs in the shallow to deep sublittoral.
C. siliquosa	191	32 (219)	61 (1469)	23.06 ± 3.20 [35]	1–8	Common in sheltered environments, often on rocks covered with sand.
C. subfarcinata	63	44 (167)	75 (480)	NA	0–3	Locally abundant, can dominate the assemblage in the immediate sublittoral in sheltered to moderately wave-exposed areas
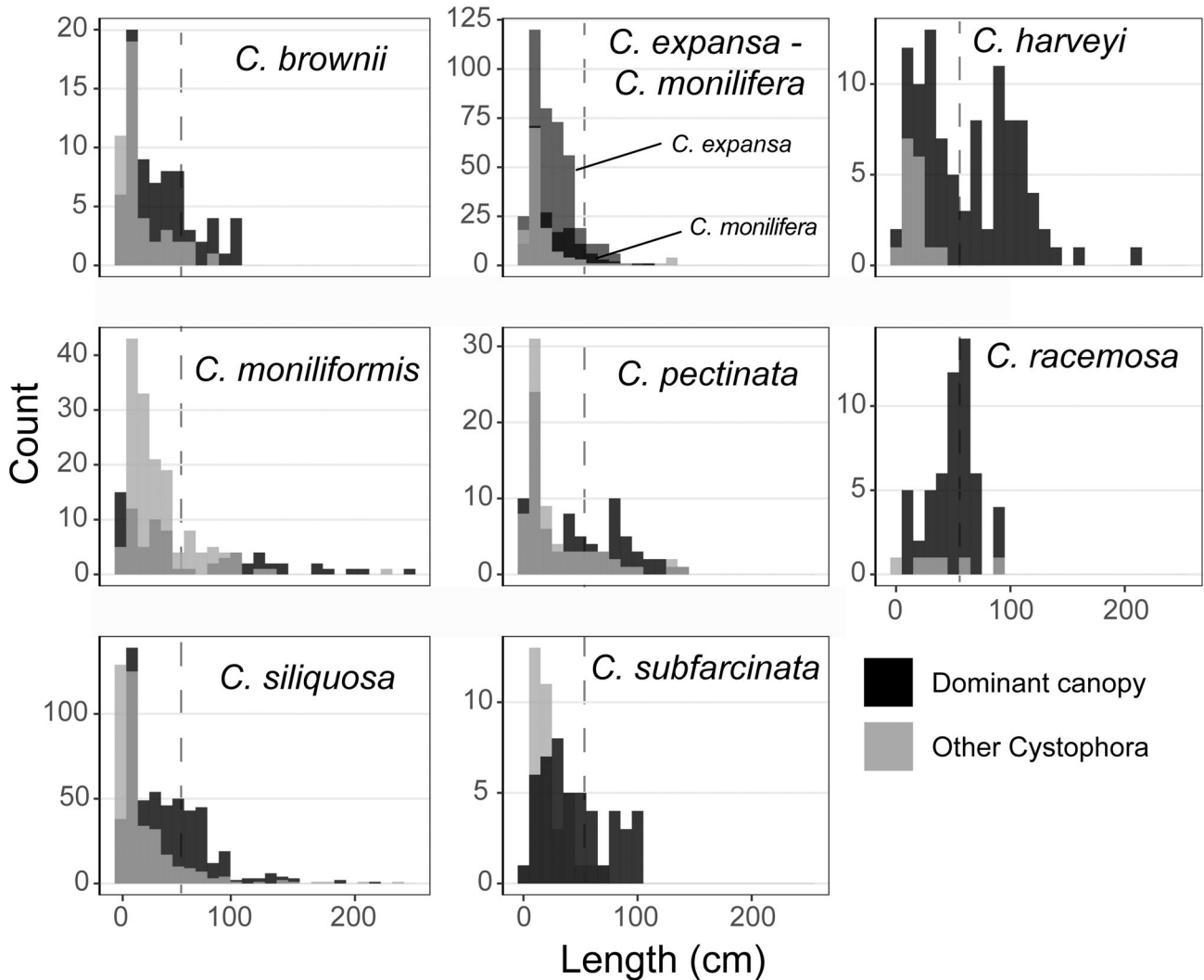
Fig. 2. Size frequency distribution of *Cystophora* stands dominated by different species across all the sites examined in Table S1. Bins are 10 cm. Dashed line indicates the lower limit of the canopy determined by the comprehensive studies of Hotchkiss (1999). Note that the scale of the y axis differs between panels.

Kendrick 2005). *Cystophora brownii*, *C. monilifera*, and *C. retorta* were the most widespread and commonly occurring species, present, respectively, at 28, 23, and 23 of the sites examined. The rarest species were *C. grevillei* and *C. retroflexa*, which are typically deeper water species (Womersley 1987; Table 1) and were found at 9 and 7 of the surveyed sites, respectively. Three additional *Cystophora* species have previously been reported in Western Australia (2 records for *C. tenuis* and 1 record for *C. polycystidea* and *C. botryocystis*; AVH 2021), but were not encountered during the study, making their presence in the study area dubious. Specimens of *Cystophora* intergrades were also found and require further investigation.

Forest structure and standing stock. Overall, 2806 *Cystophora* plants were measured and weighed. *Cystophora* spp. exhibited a wide range of lengths and

distinct morphological characteristics, ranging from 2 to 3 m tall canopies to smaller submeter bush-like canopies (Table 1). Plant length was a poor predictor of plant weight ($R^2 = 0.34$–0.83; Fig. S2 in the Supporting Information), while thallus volume exhibited strong relationships with weight ($R^2 = 0.84$–0.98; Fig. S3 in the Supporting Information) for all species. The use of thallus volume is, therefore, recommended in future nondestructive studies concerning demography, plant growth, or productivity.

The size structure of *Cystophora* stands was typically characterized by a few large plants constituting the bulk of the canopy (1–4 individuals · 0.25 m^{-2}), and numerous individuals from the dominant species, other *Cystophora* spp., and other fucoids (usually *Sargassum* spp.; A. Pessarrodona and C. Grimaldi, pers. obs.) forming a dense subcanopy
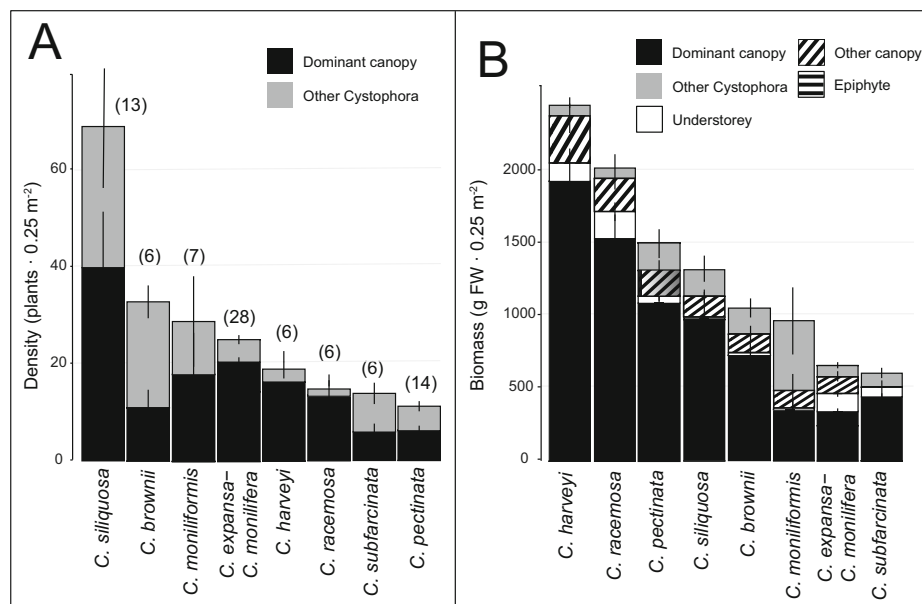
Fig. 3. (a) Density (plants · 0.25 m²) and (b) biomass (fresh weight or FW · 0.25 m²) of *Cystophora* stands dominated by different species across all the sites examined. The number of replicate quadrats examined within each stand are indicated in parenthesis.

and understory layer. These subcanopy juveniles constituted the majority of the total stand biomass, with large plants contributing only <25% of the total biomass in most stands (Fig. S4 in the Supporting Information). Recruits and juveniles from other *Cystophora* spp. were often as abundant as those of the dominant species, but rarely grew up to the canopy layer. Overall, most stands exhibited unimodal size distributions with peaks in the smallest size classes (0–20 cm length; Fig. 2), which suggests recruitment within the stand is continuous, and juveniles can readily maintain a closed canopy once adults die or are removed (Hotchkiss 1999). The only exceptions to the above pattern were *C. racemosa, C. harveyi, and C. racemosa* stands, whose

biomass was more evenly distributed within the stand and showed peaks at intermediate size classes (60–70 cm; Figs. 2 and S4). The stand structure of *Cystophora* forests contrasts with that of kelp forests in the study region, whose biomass and size structure is skewed toward a few larger plants (Kirkman 1981a, 1984, 1989), as few young recruits are able to establish themselves within dense canopies (Kirkman 1984, Irving and Connell 2006, Layton et al. 2019). Adult kelp plants strongly modify the environmental conditions beneath the canopy, with scouring and light reductions strongly limiting juvenile recruitment and growth (Layton et al. 2019, Tatsumi et al. 2021). In contrast, substrate abrasion is much lower within *Cystophora* and fucoid canopies,

TABLE 2. Comparisons of stand biomass (kg FW · 0.25 m⁻²) from a variety of kelp and fucoid forests in temperate Australia and the rest of the world.

| Forest dominant	Location	Stand biomass (kg FW · 0.25 m⁻²)	Reference
Subtidal			
Cystophora spp.	SW Australia	0.12–3.14	This study
Ecklonia radiata	SW Australia	0.4–2.2	Wernberg and Goldberg (2008)
Ecklonia radiata	SW Australia	1.5–4	Kirkman (1984)
Sargassum spp.	SW Australia	0.2–2.3	Hoang et al. (2016)
Scytothalia dorycarpa	S Australia	0.9–1.8	Goldberg and Kendrick (2004)
Phyllospora comosa	Tasmania	0.35–1.9	Sanderson (1990)
Mixed fucoid assemblages	S Australia	0.6–1.5[a]	Collings (1996)
Intertidal			
Durvillea potatorum	S Australia	1–27	Cheshire and Hallam (1988)
Ascophyllum nodosum, Fucus spp.	Nova Scotia	3.5	MacFarlane (1951)
Ascophyllum nodosum, Fucus spp.	Maine	2–7.8	Topinka et al. (1981)
Ascophyllum nodosum, Fucus spp.	Scotland	1.2–2.17	Walker (1947)

[a]Assuming a DW:FW ratio of 4.5 as per Table 1.
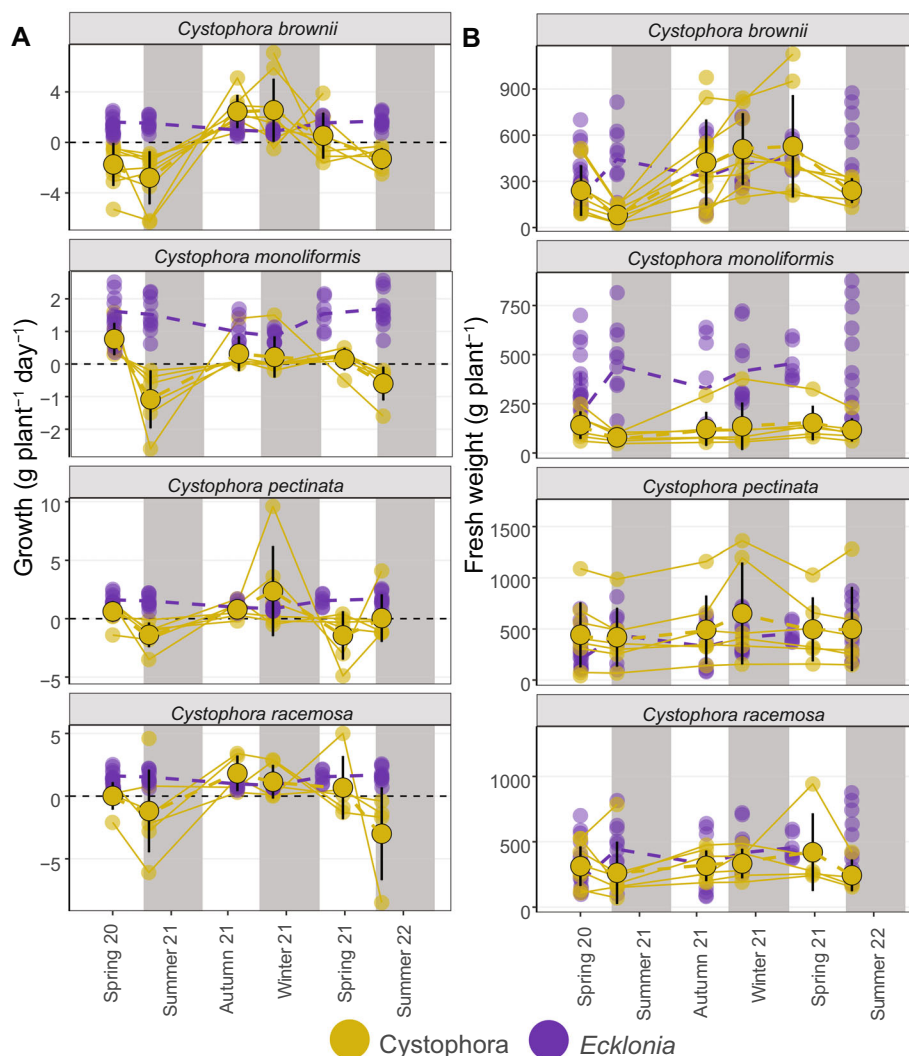
Fig. 4. Seasonal growth (g · plant^{-1} · d^{-1}; A) and plant biomass (B) of *Cystophora* spp. measured from November 2020 to February 2022 at Two People's Bay (C. *brownii*) and Betty's beach (rest of species), WA. Large dots indicate means ± standard deviation, while small dots indicate individual-level values, and lines follow individuals through time. The individual growth rates of the kelp *Ecklonia radiata* are also plotted in a darker shade, with the dotted line following the means. [Color figure can be viewed at wileyonlinelibrary.com]

which also allows more light to reach the seafloor (Irving and Connell 2006). *Cystophora* stands were also characterized by high stand densities compared to kelp forests, where densities >8 plants · 0.25 m^{-2} were very rare (Kirkman 1981a, 1984, 1989, Tatsumi et al. 2021). In contrast, the lowest plant density of all the stands examined in this study was that of *C. subfarcinata* (14.0 ± 8.44 plants · 0.25 m^{-2}), the highest being that of *C. siliquosa* assemblages (69.1 ± 58.5 plants · 0.25 m^{-2}; Fig. 3a).

The bulk of the standing stock was composed by the canopy and subcanopy individuals of the dominant *Cystophora* species (Fig. S3b), with understory algae comprising a relatively small proportion of the total biomass (3 ± 5%, range 0–25%). Such numbers are in line with other macroalgal studies in the area, where more than two thirds of the species

within an assemblage contribute minimally (e.g., < 5 g · 0.25 m^{-2}) to community biomass (Goldberg 2005, Westera et al. 2007). Exceptions were the *C. expansa–C. monilifera* stands, whose understory comprised 22 ± 19% of the total biomass. Standing stocks differed depending on the dominant species, with *C. harveyi* and *C. racemosa* stands having the highest biomass (2.31 ± 0.52 and 2.03 ± 0.16 kg FW · 0.25 m^{-2}), and *C. subfarcinata* and *C. expansa–C. monilifera* stands having the lowest (0.60 ± 0.33 and 0.67 ± 0.34 kg FW · 0.25 m^{-2}). Overall, forest standing stocks varied between 0.12 and 3.14 kg · 0.25 m^{-2} (Fig. 3b), which is well within the typical range of values reported for kelp or *Sargassum* spp. forests in the study area (Table 2). These values also fall within the range of other subtidal fucoid-dominated forests in South Australia, albeit

TABLE 3. Density, plant biomass accumulation (BA) and areal biomass production of different *Cystophora* species and the kelp *Ecklonia radiata* at the study sites. Densities were collected by randomly placing quadrats within each stand ($n = 24$, 24, 10, 29 and 15 respectively). Values indicate mean ± standard error, and are converted from fresh weight (FW) to dry weight (FW) using the values of Table 1. * Denotes a mixed stand (total density equals the sum).

Species	Density (ind. · m^{-2})	Average BA (g FW · plant^{-1} · y^{-1})	Average loss (g FW · plant^{-1} · y^{-1})	Areal BA (kg FW · m^{-2} · y^{-1})	Areal BA (kg DW · m^{-2} · y^{-1})
C. racemosa	9.3 ± 1.6*	333.7	380.9	3.1 ± 0.5	0.6 ± 0.1
C. pectinata	3.3 ± 1.0*	347.8	256.5	1.2 ± 0.3	0.2 ± 0.1
C. moniliformis	43.6 ± 14.9	132.0	153.2	5.7 ± 2.0	1.2 ± 0.4
C. brownii	4.3 ± 1.5	503.4	531.8	2.2 ± 0.7	0.5 ± 0.2
Ecklonia radiata	3.3 ± 1	717.5	NA	2.4 ± 0.7	0.3 ± 0.1

they appear to be somewhat lower than those of fucoid forests in the Northern Hemisphere, which are typically intertidal (Table 2). Our findings thus suggest that *Cystophora* forests play an ecological role akin to that of more well-studied groups in terms of habitat provision.

Forest growth. Biomass accumulation and net plant growth in the studied *Cystophora* stands exhibited a clear seasonal pattern, starting in early austral autumn to reach a maximum in austral winter ($2.5 ± 0.8$, $0.21 ± 0.3$, $2.4 ± 1.6$, $1.2 ± 0.6$ g · plant^{-1} · d^{-1} for *C. brownii*, *C. moniliformis*, *C. pectinata* and *C. racemosa*, respectively; Fig. 4a, Table S2 in the Supporting Information). Plants reached the highest biomass by late austral winter/early spring (Fig. 4b), then losing substantial amounts of biomass, having nil or negative net growth rates throughout austral spring until late summer ($-1.3 ± 0.3$, $-0.6 ± 0.2$, $0.0 ± 0.8$, $-3.0 ± 1.9$ g · plant^{-1} · d^{-1} for *C. brownii*, *C. moniliformis*, *C. pectinata* and *C. racemosa*, respectively; Fig. 4 a). This findings are largely consistent with observations from *Cystophora* forests in South Australia, which also reach their highest biomass in early austral spring (Hotchkiss 1999). Fucoids often allocate large proportions of their biomass to reproduction (Josselyn and Mathieson 1978, Mathieson and Guo 1992), and the growth patterns observed here are likely related to their reproductive cycle, which is also seasonal. Production of eggs and receptacles occurs during autumn and winter (Klemm 1988, Hotchkiss 1999; A. Pessarrodona and C. Grimaldi, pers. obs.), with plant biomass reaching maximum values in late austral winter when egg maturation and release occur (Smith 1952, Hotchkiss 1999). Plants then shed their spent reproductive tissue by summer (Womersley 1964, Klemm 1988, Hotchkiss 1999), which results in large pulses of detrital material (A. Pessarrodona and C. Grimaldi, pers. obs.). Over the annual cycle, *Cystophora* spp. plants lost between 74–144% of the accumulated biomass (Table 3), suggesting small allocation to perennial vegetative structures. Those observations agree with the findings of Hotchkiss (1999), who estimated that *Cystophora* spp. allocate up to 90% of their biomass to the production of eggs and receptacles.

Interestingly, *Cystophora* growth appears to show a negative relation to daily solar exposure and seawater temperature, being maximal during periods of low solar exposure (~2.5 kW · h^{-1} · m^{-2}) and cool (17–18°C) temperatures (Fig. 5). *Cystophora* growth allocation would, therefore, fall under the "season anticipator" strategy (sensu Kain 1989) whereby growth is slower than would be allowed by primary production in summer as excess fixed carbon is stored in reserve sugars to be used for rapid growth during periods of low irradiance. The fact that net primary production of *Cystophora* forests is maximal in austral summer (Cheshire et al. 1996), and mannitol levels increase in tissue during late austral summer and autumn (Hotchkiss 1999) offers support for this hypothesis. It must be noted, however, that Cheshire et al. (1996) quantified the production of the entire community (i.e., including understory algae and biota), so future studies should examine *Cystophora* photosynthesis in detail. This strategy contrasts with the patterns exhibited by other Australasian fucoids, where maximal growth occurs when light availability is greatest in summer (e.g., *Phyllospora comosa*, Sanderson 1990; *Sargassum lacerifolium*, Kirkman 1981b; *Sargassum* spp., Hoang et al. 2016). Similarly, kelps exhibit the largest growth rates in spring and early summer (Kirkman 1984, Wernberg and Goldberg 2008, Bearham et al. 2013), supporting observations made in the kelp-dominated patches in the study area (darker dots in Fig. 4). This finding is relevant because *Cystophora* spp. are complementing reef total productivity by accumulating and producing biomass at times when other forest-forming species are not.

We examined the contribution of *Cystophora* stands to reef biomass production by multiplying the average biomass accumulation rate of each plant during the positive growth season by their density (Table 3). A mixed stand of *C. racemosa* and *C. pectinata* produced $4.3 ± 0.34$ kg FW · m^{-2} · y^{-1}, while the stand dominated by *C. moniliformis*, despite having lower biomass accumulation rates per plant, produced $5.7 ± 2.0$ kg FW · m^{-2} · y^{-1} because of its very high plant density. These two values are substantially larger than the nearby kelp stands at Betty's Beach ($2.4 ± 0.7$ kg FW · m^{-2} · y^{-1}), suggesting that *Cystophora* stands are key contributors to reef primary productivity in the study area. *Cystophora* production is broadly comparable to that of other Australasian fucoids (e.g., 2.0–7.4 kg
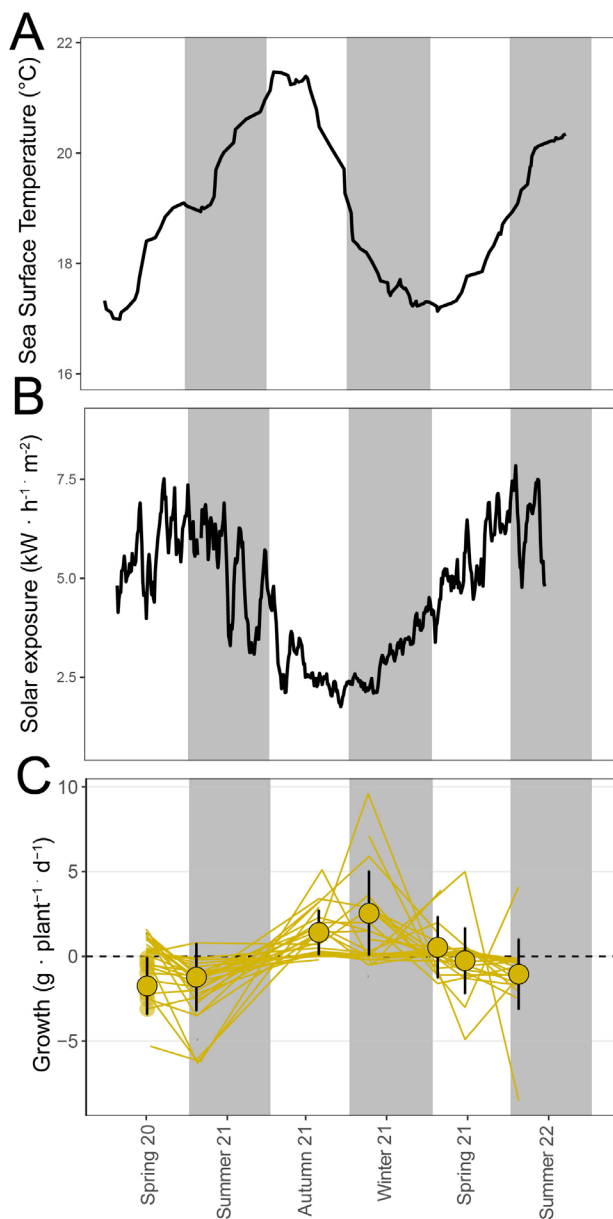
FIG. 5. Temporal variation in sea surface temperature (SST, a) and solar exposure (b), and *Cystophora* spp. growth (all species, c) near Betty's Beach over the duration of the study. Daily sea surface temperature (SST) data from November 2020 to March 2022 was extracted from the Integrated Marine Observing System (IMOS) multisensor SSTfnd L3S product at a $0.02 \times 0.02°$ resolution (IMOS 2022). Solar exposure was obtained from the weather station at Manypeaks, situated 11 km away from the study site (Australian Bureau of Meteorology). In panels a and b, black lines depict the 7 d running means. In panel c, large dots indicate mean ± SD, whilst lines follow individuals through time. [Color figure can be viewed at wileyonlinelibrary.com]

$FW \cdot m^{-2} \cdot y^{-1}$ for *Phyllospora comosa;* Sanderson 1990), and falls within the production range reported for *Ecklonia radiata* in other study areas (2–20 kg $FW \cdot m^{-2} \cdot y^{-1}$; Kirkman 1984, Novaczek 1984, Larkum 1986, Fairhead 2001, Bearham et al. 2013; Table 3). It is worth noting, however, that our

surveys were conducted in stands dominated by each of the examined species, and the overall contribution of *Cystophora* to reef productivity will ultimately depend on its density.

Overall, growth was not significantly different between *Cystophora* species (Table S2). This finding is in line with previous field observations from South Australia and Victoria, which also found large individual differences in plant growth and small variation between species (Klemm 1988, Hotchkiss 1999). These large variations could be due to the fact that individuals were randomly tagged from a range of sizes and positions in the forest canopy, resulting in larger canopy individuals suppressing the growth of smaller subcanopy plants (Kirkman 1981a, Layton et al. 2019, Tatsumi et al. 2021). Generally, larger individuals exhibited larger absolute growth rates, but there was no significant relationship between the biomass-specific growth rate and individual mass for most species (Fig. S5a in the Supporting Information), suggesting that smaller individuals can grow as fast as larger individuals. The same was true for biomass loss rates (Fig. S5b).

CONCLUSIONS

The importance of *Cystophora* forests in the subtidal ecology of the Australian continent has been equaled to that of *Eucalyptus* forests on land (Womersley 1949), which also exhibit an astounding diversity. Our understanding of the ecology of underwater forests in temperate Australia is, however, dominated by studies on kelps, with forests formed by fucoid seaweeds having received little attention. Here, we find that *Cystophora* stands are abundantly distributed in the southwestern and southern coasts of Western Australia, and can form forests similar to those of kelps. This suggests that they play a similarly important ecological role. Yet, their stand structure, biomass, and growth patterns differed in multiple ways, highlighting a unique and complementary contribution to habitat provision and reef productivity. Ongoing and predicted declines of these forests may thus represent an invaluable ecological loss for marine forest ecosystems worldwide, given that this exceptionally rich genus is found nowhere else.

AUTHOR CONTRIBUTIONS

A. Pessarrodona: Conceptualization (lead); data curation (lead); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (lead); project administration (lead); resources (lead); software (lead); validation (lead); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **C. Grimaldi:** Formal analysis (equal); funding acquisition (equal); investigation (equal); visualization (equal); writing – review and editing (supporting).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Distribution of different *Cystophora* spp. across the western range edge of their distribution.

Figure S2. Relationship between plant length and weight across multiple species of *Cystophora*.

Figure S3. Relationship between plant volume and weight across multiple species of *Cystophora*.

Figure S4. Cumulative frequency distribution of plant biomass in *Cystophora* stands dominated by different species across all the sites examined in Table S1.

Figure S5. Relationship between mass-standardized growth rate and plant biomass of *Cystophora* spp. (yellow) plants measured from November 2020 to February 2022 at Two People's Bay (C. *brownii*) and Betty's beach (rest of species).

Table S1. Details of the sampling sites and number of replicates for the forest structure and standing stock surveys.

Table S2. Results of the two-way ANOVA to test for differences in absolute growth rates between *Cystophora* seasons and sampling times. *P* values where $P < 0.05$ are indicated in bold.