

1 **Pteropods on the Edge: Cumulative Effects of Ocean Acidification, Warming, and**
2 **Deoxygenation**

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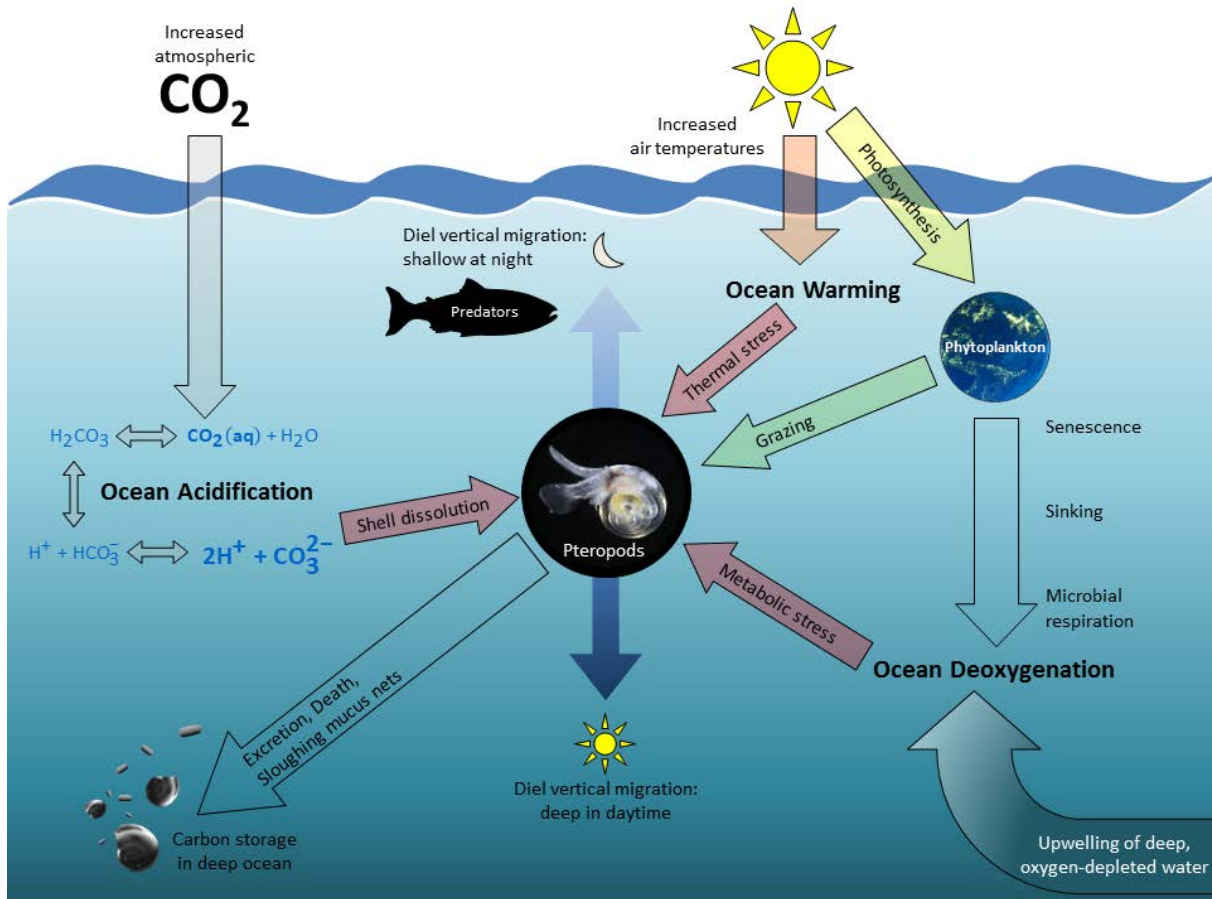
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25 Figure 1: Graphical abstract



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27 **Abstract**

28 We review the state of knowledge of the individual and community responses of euthecosome
29 (shelled) pteropods in the context of global environmental change. In particular, we focus on their
30 responses to ocean acidification (OA), in combination with ocean warming and ocean
31 deoxygenation, as inferred from a growing body of empirical literature, and their relatively nascent
32 place in ecosystem-scale models. Our objectives are: (1) to summarize the threats that these
33 stressors pose to pteropod populations; (2) to demonstrate that pteropods are strong candidate
34 indicators for cumulative effects of OA, warming, and deoxygenation in marine ecosystems; and
35 (3) to provide insight on incorporating pteropods into population and ecosystem models, which

36 will help inform ecosystem-based management of marine resources under future environmental
37 regimes.

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39 **1. Introduction**

40 Environmental change driven by rising anthropogenic CO₂ levels in Earth's atmosphere is
41 projected to have major effects on the world's marine ecosystems, at both global and local scales.
42 Abiotic changes may include, among others: temperature changes; alterations in circulation and
43 stratification; and changes in water chemistry, nutrient cycling, freshwater input, and water quality
44 (e.g., Harley et al., 2006; Sherman and McGovern, 2012). Changes to marine organisms may
45 include effects on physiology, growth, and respiration; changes in phenology of life history events
46 such as maturation and reproduction; shifts in abundance, depth, or latitudinal distribution; and
47 local extirpations if new conditions prove intolerable (Edwards and Richardson, 2004; Jackson,
48 2008; Pörtner and Farrell, 2008). Changes to individual species or populations likely will lead to
49 loss of biodiversity, community reorganization in many marine systems, and changes in
50 biogeochemical cycling and ecosystem services (Harley et al., 2006; Hoegh-Guldberg et al., 2007;
51 Bulling et al., 2010).

52 The myriad impacts of climate change on marine ecosystems will require effective
53 management responses, and those responses will draw heavily upon timely and rigorous scientific
54 research on key indicators and processes that are most affected by climate change (Schwing et al.,
55 2009). Three major marine stressors associated with climate change are ocean acidification (OA),
56 ocean warming, and ocean deoxygenation. These drivers are wide-ranging and often co-occur in
57 waters along continental margins (Feely et al., 2004, 2008; Fabry et al., 2008; Keeling et al., 2010;
58 Gruber, 2011; Seibel, 2011). Predicting and managing the effects of these stressors will require

59 considerable knowledge of the basic physiology, life history, ecology, and adaptability of marine
60 species, particularly of sentinel species that can indicate the onset of climate change effects in
61 marine ecosystems. Developing this knowledge will require coordinated laboratory studies, *in situ*
62 experiments and observations, large-scale/long-term monitoring, and integrative modeling (Le
63 Quéré et al., 2005, 2009; Fabry et al., 2008; Widdicombe and Spicer, 2008; Gruber, 2011; Seibel
64 et al., 2012).

65 Thecosome pteropods (Order Thecosomata), a group of marine, holoplanktonic, shell-
66 forming gastropods, are vulnerable to cumulative stressors like OA, especially in combination with
67 warming and deoxygenation (Figure 1). They exhibit a wide range of vertical and geographical
68 distributions, feeding habits, and metabolic rates (Byrne, 2011; Ikeda, 2014). They are considered
69 a key functional group to incorporate into marine biogeochemical models (Le Quéré et al., 2005,
70 2009; Hood et al., 2006; Gangstø et al., 2008), given their broad distribution and their role as
71 abundant planktonic consumers and calcifiers (Fabry, 1989; Lalli and Gilmer, 1989; Hood et al.,
72 2006; Doney et al., 2009; Bednaršek et al., 2012c). They also represent an important case study in
73 modeling of how different life history stages of pelagic organisms will be affected under global
74 ocean changes (Bednaršek et al., 2012a; Comeau et al., 2010b; Byrne, 2011; Lischka et al., 2011).

75 Here, we review empirical literature on the responses of shelled pteropod to global
76 environmental changes in the context of global environmental change, as cumulative stressors of
77 OA, ocean warming, and deoxygenation that are occurring simultaneously. We have collected
78 empirical data that are specifically required to incorporate pteropods into a stage-structured
79 population model, which will help inform ecosystem-based management of marine resources
80 under future environmental regimes. Finally, we demonstrate that pteropods are strong candidate
81 indicators for cumulative OA effects in marine ecosystems.

82 2. Overview of pteropod taxonomy, biology, ecology, and distribution

83 Pteropods are entirely pelagic gastropods comprising two orders—Thecosomata and
84 Gymnosomata—that differ in morphology, behavior, and trophic position (Lalli and Gilmer,
85 1989). Thecosomes include the suborders Euthecosomata and Pseudothechosomata. While most
86 thecosomes produce calcium carbonate (CaCO_3) shells, in some pseudothechosomes this feature is
87 replaced by a gelatinous internal pseudoconch, while the gymnosomes possess shells as veligers
88 but are unshelled following metamorphosis. While this review study focuses on euthecosomes, the
89 vital biological rates for both orders are presented in the Appendices (B1-B8). The life history of
90 pteropods varies greatly at different locations. Estimates of the life span of *Limacina helicina*, one
91 of the most studied species, range from 1 year (Van der Spoel, 1973; Wells, 1976; Fabry, 1989;
92 Gannefors et al., 2005; Hunt et al., 2008), to 1.2–1.5 years (Wang, 2014), to 1.5–2 years
93 (Kobayashi, 1974), to >3 years (Bednaršek et al., 2012a), depending on location. Most pteropod
94 are protandrous hermaphrodites, producing 1–2 pelagic egg masses per year. Veligers hatch within
95 2–6 days and begin feeding immediately (Lalli and Gilmer, 1989). Variation in environmental
96 conditions, such as temperature and food availability, likely leads to regional variability in traits
97 such as growth rate, maximum size, and maturation schedule and lifespan (e.g., Kobayashi, 1974;
98 Fabry, 1989; Lalli and Gilmer, 1989; Gannefors et al., 2005; Bednaršek et al., 2012a).

99 Pteropods are found throughout the world's oceans, with the greatest species diversity in
100 tropical and subtropical regions but the greatest abundance at high latitudes (Lalli and Gilmer,
101 1989; Fabry et al., 2008). They are predominantly epipelagic, occurring in the upper 200 m of the
102 water column (Stepien, 1980), though there are many mesopelagic species, and at least four
103 bathypelagic species are found exclusively below 1000 m (Van der Spoel, 1967; Wormuth, 1981).
104 Many species exhibit diel vertical migration (DVM), ascending (usually into the upper 100 m) to

105 feed at night and retreating to greater depths by day (Mackas and Galbraith, 2002; Hunt et al.,
106 2008; Flores et al., 2011). DVM patterns and ranges differ according to species (Wormuth, 1981;
107 Lalli and Gilmer, 1989), life-history stage and size (Mileikovsky, 1970; Bathmann et al., 1991),
108 season (Chen and Bé, 1964; Kobayashi, 1974; Lischka et al., 2011), wind and turbulence (Mackas
109 and Galbraith, 2002; Tsurumi et al., 2005), and availability of food (Kobayashi, 1974). Andersen
110 et al. (1997) observed mean DVM amplitude of *Clio pyramidata* to be greatest at oligotrophic sites
111 (475 m) and smallest at eutrophic sites (70 m). DVM is energetically costly, however, and is most
112 pronounced in the presence of significant predation pressure (Gliwicz, 1986; Ohman, 1990; Falk-
113 Petersen et al., 2008).

114 Pteropods are an important part of marine communities as consumers, prey, and
115 contributors to carbon cycling. They can reach densities of thousands of individuals per m³ across
116 numerous open ocean and shelf regions, including temperate regions (50–60 °S; 40–50 °N) and
117 tropical regions (0–10 °N; Bednaršek et al., 2012c), where they exceed global mean pteropod
118 biomass (Figure 2). Their contribution to total zooplankton biomass is significant, especially in
119 polar regions (Hopkins, 1987; Boysen-Ennen et al., 1991; Ward et al., 2003; Pakhomov and
120 Froneman, 2004; Pane et al., 2004; Bernard, 2006; Hunt et al., 2008). Estimates of global pteropod
121 biomass production range from 0.444 to 0.505 Pg C yr⁻¹ or 1.067 Pg CaCO₃ yr⁻¹ (Bednaršek et al.,
122 2012c), compared to the global observation-based CaCO₃ production range of 0.8–1.6 Pg CaCO₃
123 yr⁻¹ and model estimate of 0.87 Pg C yr⁻¹ (Gangstø et al., 2008). Furthermore, thecosomes
124 contribute greatly to regional carbon sequestration through high phytoplankton grazing (Hunt et
125 al., 2008; Bernard and Froneman, 2009) and large downward fluxes of fecal pellets (Manno et al.,
126 2010), mucus nets (Noji et al., 1997), and shells (Meinecke and Wefer, 1990; Tsurumi et al., 2005).
127 Thecosomes are the most important prey of gymnosomes (Conover and Lalli, 1972; Seibel and

128 Dierssen, 2003; Böer et al., 2005). Many other predators feed upon pteropods, including
129 carnivorous zooplankton (Lalli, 1970; Lalli and Gilmer, 1989; Pakhomov and Perissinotto, 1997;
130 Froneman and Pakhomov, 1998; Böer et al., 2005), amphipods (Pakhomov and Perissinotto, 1997;
131 Bernard, 2006), cephalopods (Hanlon and Messenger, 1998), fishes (Emmett et al., 1986; Lalli and
132 Gilmer, 1989; Armstrong et al., 2005; Aydin et al., 2005; Hunt et al., 2008; Doubleday and
133 Hopcroft, 2015), seabirds (Hunt et al., 2008), and marine mammals (Lalli and Gilmer, 1989).

134 **3. Relationships between pteropods and changing levels of CO₂**

135 The oceans have taken up approximately one third of all atmospheric CO₂ emitted by
136 human activities since the beginning of the Industrial Revolution (Sabine et al., 2004), significantly
137 altering seawater chemistry—a process termed ocean acidification. The elevated partial pressure
138 of CO₂ (*p*CO₂) is causing seawater pH and CaCO₃ saturation state to decrease (Feely et al., 2004;
139 Orr et al., 2005). By 2100, *p*CO₂ values are projected to reach between 420 and 940 μatm,
140 depending on the severity of the climate change scenario, with pH expected to decrease by 0.13 to
141 0.42 units (IPCC, 2013). Saturation horizons of CaCO₃ are expected to shoal, particularly at high
142 latitudes where buffering decreases as freshwater input from melting sea ice and greater
143 precipitation reduces total alkalinity (Feely et al., 2004, 2008; Orr et al., 2005; Steinacher et al.,
144 2009).

145 Changes in carbonate chemistry pose profound challenges to marine organisms that
146 produce calcareous shells, like pteropods. Pteropod shells are made of aragonite, a metastable form
147 of CaCO₃ that is ~50% more soluble in seawater than calcite (Mucci, 1983), and thus is more
148 sensitive to dissolution under acidified conditions (e.g., Orr et al., 2005; Bednaršek et al., 2012a,
149 2014b). Euthecosome shells are generally very thin, ranging from about a few μm in limaciniids
150 to ~100 μm thick in cavoliniids (Lalli and Gilmer, 1989). Shells are lightweight and transparent to

151 allow for pelagic lifestyle and camouflage, yet mechanically robust to endure a certain measure of
152 chemical and mechanical degradation (Sato-Okoshi et al., 2010; Li et al., 2015).

153 OA reduces the aragonite saturation state (Ω_{arag}) in seawater, thermodynamically favoring
154 dissolution over shell precipitation when Ω_{arag} falls below 1 (Appendix B8). This affects pteropods
155 through an increase in shell dissolution and a concurrent decline in calcification (Bednaršek et al.,
156 2014a). As dissolution exceeds calcification, pteropods may experience increases in shell
157 dissolution and reduction in shell growth; greater fragility, fragmentation, and porosity; and
158 mortality (Comeau et al., 2009, 2010a, 2012; Lischka et al., 2011; 2012; Bednaršek et al., 2012b;
159 Lischka and Riebesell, 2012; Manno et al., 2012; Busch et al., 2014). Partial shell dissolution has
160 been observed at $\Omega_{\text{arag}} \leq 1$ (Orr et al., 2005; Bednaršek et al. 2012b; Bednaršek and Ohman, 2015).
161 It is not clear if pteropods can sustain development, reproduction, and balance energy expenditure
162 at $\Omega_{\text{arag}} < 1$ given that they cannot achieve a positive balance between calcification and dissolution
163 in these conditions.

164 *In situ* studies suggest that OA is already affecting pteropods in some regions. Shell
165 dissolution in *Limacina helicina* has been observed along exposure gradients of $\Omega_{\text{arag}} \leq 1$ water in
166 the Southern Ocean (Bednaršek et al., 2012b) and along the North American West Coast
167 (Bednaršek et al., 2014b; Bednaršek and Ohman, 2015). In Australian waters, the tropical
168 euthecosomes *Creseis clava* (formerly *C. acicula*) and *Diacavolinia longirostris* experienced
169 degradation in shell thickness and integrity concurrent with long-term declines in Ω_{arag} , despite the
170 mean annual $\Omega_{\text{arag}} > 3.4$ (Roger et al., 2012). Fast shell dissolution occurs on the account of
171 extremely thin periostracum that allows dissolution to occur beneath it (Bednaršek et al., 2014a).

172 Responses to OA may be taxon-specific; shell thickness of *Limacina helicina antarctica*
173 in the Southern Ocean decreased while it increased in *Limacina retroversa australis* (Roberts et

174 al., 2014). Effects can also differ by life history stage. Greater vulnerability to elevated $p\text{CO}_2$ is
175 evident in the early life stages of many marine calcifiers (Byrne, 2011) with the shells of juvenile
176 *Limacina helicina ant.* dissolving more rapidly than adult shells at elevated $p\text{CO}_2$ (Bednaršek et
177 al., 2012a). Larvae of the Mediterranean pteropod *Cavolinia inflexa* reared at $\text{pH} = 7.82$ (857 ppm
178 $p\text{CO}_2$) experienced shell malformations but remained viable, while those reared at $\text{pH} = 7.51$ (1713
179 ppm $p\text{CO}_2$) lost their shells entirely, although they were otherwise viable (Comeau et al., 2010b).
180 Increased shell degradation and reduced shell size in juvenile Arctic *L. helicina* at elevated (up to
181 1150 ppm) $p\text{CO}_2$ was observed by Lischka et al. (2011). In addition to euthecosome, shelled
182 veliger of gymnosome and pseudothecosome could also be affected by OA with direct impacts on
183 shell growth and integrity (Fabry et al., 2008).

184 There is evidence that pteropods change depth distributions or DVM behavior in response
185 to OA. To minimize exposure to elevated $p\text{CO}_2$ and low Ω_{arag} , some pteropods may avoid layers
186 of $\Omega_{\text{arag}} \leq 1$ water, indicated by decreased abundances and species richness (Bednaršek and Ohman,
187 2015). On the other hand, calcification in the euthecosomes *Styliola subula* and *L. helicina* occurs
188 during the day when they are in deeper waters, particularly in the winter and spring. The adaptive
189 value of deep-water calcification is unknown, as the reduced Ω_{arag} and colder temperatures in
190 deeper waters lead to slowed metabolism and more energetically expensive shell formation. The
191 depth and timing of calcification most likely coincides with temperature optima and other factors
192 such as light intensity, food availability, and predator avoidance (Juraneck et al., 2003).

193 Increased $p\text{CO}_2$ levels in seawater will have other, less-visible effects on pteropods. At
194 elevated levels, dissolved CO_2 diffuses more readily across biological membranes and reacts with
195 intra- and extracellular fluids (Fabry et al., 2008; Maas et al., 2012a), creating internal acid-base
196 imbalances that can influence different physiological processes (Fabry et al., 2008; Widdicombe

197 and Spicer, 2008; Pörtner, 2008, 2010). Physiological responses to elevated $p\text{CO}_2$ vary widely
198 among studies. For example, oxygen consumption was suppressed by 20% in *Limacina helicina*
199 *ant.* at 1000 ppm $p\text{CO}_2$ and -1.8°C (Seibel et al., 2012). However, Comeau et al. (2010a) found no
200 effect of $p\text{CO}_2$ on respiration rates of Arctic *L. helicina* at 0°C , while Maas et al. (2012a) found
201 metabolic impacts of elevated $p\text{CO}_2$ in the non-migratory species *Diacria quadridentata* but no
202 impacts to species that underwent DVM (*Hyalocylis striata*, *Diacavolinia longirostris*, *Creseis*
203 *virgule*, and *Clio pyramidata*). Transcriptomic analyses indicated down-regulation of aerobic
204 metabolism and up-regulation of biomineralization during exposure to high $p\text{CO}_2$, which suggests
205 potential energy reallocation (Maas et al., 2015). Much more remains to be learned about the
206 physiological effects of acute and chronic exposure to OA stress.

207 At present, there are several published studies that document changes in pteropod
208 abundance trends, but few have conclusively linked population changes to OA impacts. *Limacina*
209 populations have declined in the North Pacific off Vancouver Island (Mackas and Galbraith, 2012),
210 and in the North Atlantic (Beaugrand et al., 2013). These declines occurred under cumulative
211 stressors of global climate changes, such as increased temperature concurrent with OA (Beaugrand
212 et al., 2013). In the North Sea, Beare et al. (2013) found that long-term declines in pteropods were
213 more strongly correlated to temperature, nutrients, and predators than to pH, although the authors
214 noted concerns about the pH data and the need for monitoring of carbonate chemistry. Importantly,
215 not all pteropod populations are declining; shelled pteropods near the Antarctic Peninsula were
216 highly variable but showed no long-term negative trends (Loeb and Santora, 2013), while pteropod
217 abundance increased in the northwestern Mediterranean Sea in $\Omega_{\text{arag}} > 1$ waters (Howes et al.,
218 2015). Continuing and expanding spatiotemporal monitoring of pteropod abundances and

219 indicators of OA and other environmental drivers is imperative for linking population responses
220 to global change drivers.

221 **4. The effects of ocean warming and deoxygenation**

222 The world's oceans are experiencing many other significant changes along with the
223 changes in carbonate chemistry. Due to uptake of surplus heat in recent decades, the temperature
224 in the surface layer has increased by $\sim 0.11^{\circ}\text{C}$ per decade, with the greatest warming in the 0–75 m
225 depth layer, resulting in strengthened density gradients and stratification in the upper ocean
226 (Gruber, 2011). CO_2 -induced warming is penetrating deeper in the North Atlantic than in the North
227 Pacific, Indian, and Southern oceans (Barnett et al., 2005; IPCC, 2007), with future warming
228 predicted to be strongest in the tropics and higher latitudes of the Northern Hemisphere (Gruber,
229 2011). Concurrently, deoxygenation of the ocean interior is occurring through mechanisms such
230 as reduced oxygen solubility in warmer waters, enhanced stratification of the upper ocean, and
231 increased biological oxygen demand (Keeling et al., 2010). According to model projections, the
232 global ocean oxygen concentration ($\sim 178 \mu\text{mol L}^{-1}$) could decline by 1–7% in the next 100 years
233 (Keeling et al., 2010). Oxygen minimum zones (OMZs), the relatively oxygen-depleted and poorly
234 ventilated portions of the water column generally found between 400 and 1200 m depths, are
235 already expanding and shoaling at lower latitudes (Stramma et al., 2008).

236 These large-scale patterns of warming and deoxygenation are already affecting
237 physiological processes and functions in marine ectotherms, including pteropods (Christou and
238 Moraitou-Apostolopoulou, 1995; Comeau et al., 2010a; Seibel, 2011; Maas et al., 2012b;
239 Appendices B1–B4). Individually, both temperature and oxygen are important drivers of pteropod
240 biology and ecology. Thermal tolerance and oxygen capacity are interconnected and are important
241 drivers of pteropod responses under global environmental changes. In addition, thermal and

242 oxygen gradients interact in the natural environment and affect pteropods in a physiologically
243 interactive manner, thus we consider the temperature and oxygen effects jointly. Like other
244 ectotherms, pteropod respiration rates are positively correlated with temperature (Smith and Teal,
245 1973; Seibel et al., 2007; Comeau et al., 2010a; Maas et al., 2012b; see also Appendices B1–B4).
246 Pteropods lower down their metabolic rates and energy requirements at cold temperatures, but the
247 extent of metabolic suppression is species-specific and likely dependent on physiological
248 adaptation or acclimatization to environmental conditions (Pörtner, 2008; Maas et al., 2012b). For
249 example, several tropical pteropod species (*Diacria quadridentata*, *Cavolinia inflexa*, *Creseis*
250 *virgula*, *Diacavolinia logirostris*, *Clio pyramidata*, and *Hyalocylis striata*) reduced their metabolic
251 rates by 60–75% when experimental temperatures decreased from 20°C to 11°C (Maas et al.,
252 2012b). In addition, species that undergo DVM generally experience greater temperature changes
253 than non-migrators (Wormuth, 1981; Seibel, 2011) and are thus expected to have broader thermal
254 niches (Seibel, 2011; Abele, 2012; Maas et al., 2012b). Thermal conditions also vary
255 geographically; pteropods at high latitudes naturally experience a narrow range of relatively low
256 temperatures (Pörtner, 2002; Seibel et al., 2007; Rosenthal et al., 2009) compared to those at
257 middle or low latitudes with broader temperature ranges. Increased metabolic rates of consumers
258 result in higher demand for food throughout the year (Christou and Moraitou-Apostolopoulou,
259 1995; Seibel et al., 2007; Comeau et al., 2010a; Maas et al., 2012b). Ocean warming during winter
260 may result in higher metabolic rates of overwintering pteropods (Smith and Teal, 1973; Seibel et
261 al., 2007; Comeau et al., 2010a; Maas et al., 2012b), consequently increasing energy demands at
262 times when food production is generally low. This is especially important in the case of high-
263 latitude species, where growth does not stop during the wintertime (Bednaršek et al., 2012a).

264 Similarly, oxygen requirements depend on particular physiological requirements of
265 different pteropod species and oxygen concentrations to which they are naturally adapted (Seibel,
266 2011; Maas et al., 2012b). Chronic exposure to high temperatures and oxygen constraints may
267 reduce somatic condition, activity, growth, and reproduction in pteropods (Pörtner, 2008, 2010;
268 Hofmann and Todgham, 2010; Abele, 2012; Maas et al., 2012b). Combined low temperature and
269 hypoxia consistent with the deep range of their DVMs slowed the metabolic rates of three species
270 of pteropods (*Hyalocylis striata*, *Diacavolinia longirostris*, and *Creseis virgula*) by ~80–90%
271 (Maas et al., 2012b). Suppressing metabolic rates prolongs survival during exposure to short-term
272 stressful conditions, such as hypoxic conditions at the deep range of their DVMs, hypercapnia,
273 food deprivation, or co-occurrence of these stressors (Guppy and Withers, 1999; Seibel et al.,
274 2012; Maas et al., 2012b). Depth may also be an important covariate; respiration rates of three
275 epipelagic species (*Diacria trispinosa*, *Cuvierina columnella*, and *Clio pyramidata*) responded
276 only to changes in temperature in normal pressure ranges, but pressures exceeding the greatest
277 depths of their DVMs caused a significant increase in respiration rates (Smith and Teal, 1973). In
278 the same study, the bathypelagic species *Thielea helicoides* was most sensitive to temperature at
279 shallow depths outside its normal range (Smith and Teal, 1973).

280 Given the important relationship of temperature and oxygen in ectotherm physiology, it is
281 likely that co-occurring warming and deoxygenation will have significant effects on species like
282 pteropods. Warmer waters may increase metabolic rates and oxygen requirements even as oxygen
283 concentrations are declining; alternatively, the metabolic suppression that some pteropods use to
284 conserve energy during times of hypoxia may be less effective in warmer waters, or infeasible in
285 cool waters that can only be found outside the pteropod's normal depth range. Reduced metabolism
286 can minimize or delay key behaviors and processes such as growth, development, locomotion, and

287 reproduction until environmental conditions are less stressful (Schalk, 1990; Guppy and Withers,
288 1999; Seibel et al., 2012; Maas et al., 2012b). Moreover, the effects of warming and deoxygenation
289 may be cumulative with those of altered carbonate chemistry. Chronic suppression of
290 reproduction, development and growth, coupled with shell dissolution, may induce severe impacts
291 on a population level (Guppy and Withers, 1999; Seibel et al., 2012; Byrne, 2011; Maas et al.,
292 2012a) unless pteropods are able to adapt by sustaining unchanged respiration rates. Experimental
293 studies on cumulative, interactive effects of these stressors have not yielded a clear consensus to
294 date. For example, neither Comeau et al. (2010a) nor Lischka et al. (2011) detected
295 $p\text{CO}_2$ /temperature interaction effects in their experiments; in contrast, Lischka and Riebesell
296 (2012) found that increasing temperature (from 2°C to 7°C) exacerbated the effect of their highest
297 $p\text{CO}_2$ treatment (880 μatm) on shell dissolution in overwintering Arctic *L. helicina*. While no such
298 interaction was found in the more eurythermal species *L. retroversa*, some evidence of increased
299 mortality in the warmest, highest $p\text{CO}_2$ treatment was reported (Lischka and Riebesell, 2012).

300 Importantly, the stressors of warming and deoxygenation, along with OA, will affect the
301 rest of the species with which pteropods interact. For example, these stressors will likely alter the
302 quality, quantity, and phenology of pteropod food (Appendix B7). Warming-induced increases in
303 ocean stratification (IPCC, 2007; Gruber, 2011) may reduce primary production in the tropics
304 (Martinez et al., 2009; Boyce et al., 2010) but not in the turbulent, nutrient-rich waters at higher
305 latitudes (Richardson and Schoeman, 2004). Phytoplankton community shifts from larger to
306 smaller cell sizes are anticipated in direct response to rising temperatures (Morán et al., 2010),
307 stratification-induced nutrient shortages, and temperature-mediated changes in grazing pressures
308 (Marañón et al., 2012; Chen et al., 2012). Euthecosomes may adapt readily to environmental shifts
309 that elicit variable food quality and abundance because they are opportunistic omnivores

310 (Wormuth, 1985; Perissinotto, 1992; Gilmer and Harbison, 1991; Gannefors et al., 2005).
311 Additionally, the gradual shift toward smaller phytoplankton may benefit species such as *Limacina*
312 spp. that preferentially graze on pico- and nanoplankton (Perissinotto, 1992; Bernard, 2006).
313 During productive seasons, the timing of phytoplankton blooms is crucial for stability of pteropod
314 populations (Seibel and Dierssen, 2003). However, if ocean warming alters phytoplankton bloom
315 phenology and results in temporal mismatches between phytoplankton availability and pteropod
316 abundance, the resulting food deprivation may suppress or delay vital biological processes as
317 reproduction, development, and spawning or affect local pteropod abundance (Seibel and
318 Dierssen, 2003; Bernard, 2006; Böer et al., 2006; Bernard and Froneman, 2009; Maas et al., 2011).
319 Moreover, changes in OA, temperature, and oxygen will affect consumption rates, spatiotemporal
320 distributions, and other ecological factors for pteropod competitors and predators (e.g., Seibel,
321 2011).

322 The gyres of the eastern tropical Pacific may present a natural laboratory in regard to the
323 combined effects of deoxygenation and concentrations of CO₂ on pteropod population that may
324 reach >1000 individuals per m³ (Maas et al., 2012a). Potentially hypoxic conditions (60 μmol O₂
325 L⁻¹) on average occur at < 200 m depths, occasionally as shallow as 50–100 m (Keeling et al.,
326 2010). Bednaršek et al. (2012c) found that the highest abundances and biomasses of pteropods
327 were at 50–500 m depths in the tropical Pacific; abundances were substantially lower at depths
328 shallower than 25 m and deeper than 500 m. Similarly, in the Indian Ocean, a high number of
329 pteropods were observed between 50 and 500 m depths (Bednaršek et al., 2012c), which overlaps
330 with low oxygen zones (60 μmol O₂ L⁻¹ at 100–600 m depths; Keeling et al., 2010). This could
331 indicate that certain tropical pteropod species are adapted to endure at least short-term exposure to
332 hypoxia and may be less vulnerable to the small changes in oxygen concentrations predicted for

333 tropical areas in the future (Keeling et al., 2010; Maas et al., 2012b). Conversely, future expansion
334 of deoxygenation and OA might affect pteropods differently in the North Pacific Ocean, where the
335 greatest pteropod biomass values were recorded between 50 and 200 m (Bednaršek et al., 2012c).
336 The hypoxic ($60 \mu\text{mol O}_2 \text{ L}^{-1}$) conditions occurred between 400 and 800 m (Keeling et al., 2010),
337 with undersaturated conditions below 200–1000 m (Feely et al., 2012; Jiang et al., 2015). These
338 differences could mean that high-latitude pteropod species avoid or do not undergo DVM through
339 OMZs or $\Omega_{\text{arag}} < 1$ waters due to lower tolerance to these conditions (Byrne, 2011; Seibel, 2011;
340 Maas et al., 2012b). Consequently, they may be vulnerable should deoxygenation and OA continue
341 to expand upward in the subarctic Pacific Ocean (IPCC, 2013). Any responses by these pteropods
342 to expanding hypoxia would also be influenced by the extent of surface ocean warming in the
343 North Pacific.

344 **5. Potential responses by pteropods to long-term changes in abiotic ocean conditions**

345 How pteropods respond to long-term ocean acidification, ocean warming, and deoxygenation
346 ultimately may define the outcome for their populations. Such responses may include:

347

348 ***5.1. Acclimatization and adaptation strategies***

349 Possible acclimatization and adaptations to OA include many mechanisms and strategies (Sunday
350 et al., 2014), such as changes in life cycle patterns, accelerated growth and maturation, increasing
351 the rate of shell formation, counteracting shell dissolution by increased calcification, or changing
352 the mineral polymorphism in the shell to more stable constituents (Bednaršek et al., 2012a; Lischka
353 et al., 2011). Under prolonged oxygen stress, pteropods will have to maintain aerobic metabolism
354 either by spending more time in waters with sufficient oxygen to pay off oxygen deficits, or by
355 changing their energy budgets, with associated changes in individual performance and species

356 ecology (Seibel, 2011; Maas et al. 2012b). A warming environment may cause a decrease in the
357 mean and maximum sizes of pteropods themselves, as an adaptation to the higher costs of thermal
358 stress mitigation (Daufresne et al., 2009; Abele, 2012). Such size decreases have been documented
359 in some pteropod species in regions with higher temperatures (Van der Spoel, 1970; Schalk, 1990;
360 Lebour, 1931, cited in Böer et al., 2005). Long-term increases in temperature may result either in
361 thermal acclimatization (a limited shift of optimal performance) or evolutionary adaptation (a shift
362 of the whole thermal niche) (Pörtner, 2008, 2010; Hofmann and Todgham, 2010). Evolutionary
363 adaptation might be facilitated by the patterns of intra- and inter-specific genetic variation
364 (Peijnenburg and Goetze, 2013), cryptic species (Jennings et al., 2010), and ecological
365 specialization. These parameters are considered to be major driving force for zooplankton
366 specialization, species adaptive capacity, and differential sensitivity to OA (Burrige et al., 2015).

367

368 ***5.2. Changes in distribution***

369 Pteropods may shift their distributions to regions with less stressful environmental conditions,
370 although it is difficult to anticipate what such shifts may look like, given the potential for
371 environmental stressors to interact. For example, some researchers hypothesize that pteropod
372 distributions in the Southern Ocean will shift northward to waters less affected by OA (Hunt et al.,
373 2008; McNeil and Matear, 2008; Comeau et al., 2012; Bednaršek et al., 2012b). However, high-
374 latitude pteropods migrating equatorward may be limited by their intolerance for warm
375 temperatures (Seibel et al., 2007; Fabry et al., 2008; Rosenthal et al., 2009; Byrne, 2011). Indeed,
376 many marine species, including at least 24 zooplankton species, have shown poleward
377 distributional shifts attributed to ocean warming (Parmesan and Yohe, 2003). Similar poleward
378 migrations might be expected from pteropods (e.g., Beaugrand et al., 2013), thus substantially

379 affecting their global distribution (Comeau et al., 2012). Shoaling of aragonite saturation horizons
380 and OMZs will affect vertical distributions of pteropods, particularly among polar species that are
381 restricted to aragonite-saturated waters (Orr et al., 2005; Seibel et al., 2007; Fabry et al., 2008;
382 McNeil and Matear, 2008) and species with low hypoxia tolerance (e.g., Maas et al., 2012b).
383 Pteropods are expected to change both their vertical and geographic distribution patterns to avoid
384 physiological stress in expanding OMZs (Seibel, 2011; Maas et al., 2012b) and aragonite-
385 undersaturated waters (Bednaršek and Ohman, 2015). Pteropods that are forced to change their
386 DVM habits due to shoaling of aragonite horizon and hypoxia may be unable to reach deep waters
387 during the day, which could expose them to greater predation rates (Seibel, 2011; Comeau et al.,
388 2012). Compounding this, warming may increase thermal stress and lower the supply of oxygen
389 in surface waters (Stramma et al., 2008; Gruber, 2011), further constraining vertical distributions.

390 ***5.3. Extirpation***

391 If shelled pteropods fail to adapt to changes in ocean conditions, or become less competitive under
392 local selective pressures following distributional shifts, they will most likely go locally extinct.
393 This is most likely in the polar oceans, where the entire water column could become undersaturated
394 in aragonite during this century (Orr et al., 2005; McNeil and Matear, 2008; Steinacher et al.,
395 2009), and in regions with extremely shallow aragonite saturation horizons, such as the North
396 Pacific Ocean, where periods of enhanced seasonal aragonite undersaturation associated with
397 upwelling have already been documented (Feely et al., 2008).

398 **6. Modeling pteropods in an ecosystem context**

399 Adapt, shift distribution, or disappear: how can we predict a pteropod species' response to
400 long-term OA, ocean warming, and deoxygenation? While empirical and experimental research

401 provides considerable insight, the expense, technical challenges, and slow rate of data acquisition
402 associated with such methods suggest that complementary modeling work is needed to address
403 this question. A variety of modeling approaches can offer insight into the future responses of
404 pteropods and related processes and species. As we have illustrated above and in the
405 supplementary appendices, there is an abundance of literature on many pteropod species, including
406 key parameters that lend themselves to several distinct types of models. Which model is chosen
407 depends on the intended application and the focal role of pteropods within that application. Below,
408 we consider two such roles, where pteropods are indicator species of ecosystem-scale perturbation
409 for OA, complemented by ocean warming or deoxygenation; and where pteropods are not just
410 indicators but also important food web components. Still other types of ecosystem models may
411 include pteropods, such as models of regional or global carbon cycling that might include
412 pteropods as a vector for storage of carbon in the deep ocean (Figure 1), but we do not consider
413 such models here.

414 ***6.1 Models of pteropods as indicator species***

415 Sensitivity to acidified conditions makes the euthecosome pteropods a suitable indicator
416 for OA. Because it does not occur in isolation from the other stressors, consideration of OA in
417 combination with warming or deoxygenation is warranted. Pteropods might serve as an early
418 warning signal for OA impacts on the ecological integrity of other groups that have similar biology
419 or ecology but lack the tell-tale signal of shell dissolution. Thus, from a modelling perspective, we
420 might consider how future projections of ocean conditions will impact pteropods, and how those
421 impacts might translate to co-occurring species like copepods, euphausiids, and other plankton that
422 typically form the energetic basis of marine ecosystems and fisheries. Such projections will inform

423 the design of monitoring programs that are put in place to detect the stressors, as well as
424 management actions to correct or mitigate the effects of those stressors.

425 One key to modelling pteropods as an indicator species is capturing spatial dynamics and
426 age structure. Explicit representation of age structure would allow prediction of how OA, warming,
427 and deoxygenation effect vital rates, such as survival and reproduction, and how these impact
428 overall population growth rate and demographics (Crouse et al., 1987; Caswell, 2001). Though
429 this approach has not typically been applied to plankton species, it is appealing in the case of
430 pteropods because acidification may have the strongest impacts on larval phases (Comeau et al.,
431 2010b), and therefore the value of larvae to overall demographics must be calculated.
432 Parameterizing such models for pteropods will require detailed estimates of survival and fecundity
433 rates for specific size or age classes, as illustrated below in our “straw man” model (Figure 3).
434 Representing spatial structure is important because, as outlined above, stressors have spatial
435 gradients or thresholds (e.g. Bednaršek et al., 2012b), and pteropod responses will differ along
436 those gradients and may involve movements to preferable conditions (Bednaršek and Ohman,
437 2015). Spatial structure may be best captured with individual-based models, which capture the
438 growth, consumption, and Lagrangian movements of individuals (or small groups of individuals)
439 across a model grid (DeAngelis and Mooij, 2005; Grimm et al., 2006). This spatial representation
440 is particularly attractive in the context of considering spatial monitoring schemes, though it has
441 most often been applied to fish and higher trophic levels rather than to plankton.

442 ***6.2 Models linking pteropods to higher trophic levels***

443 Pteropods may be important not just as indicators of environmental conditions, but also as
444 prey for species that are priorities for conservation or human harvest. This is most likely the case
445 in polar regions with high pteropod densities but also in the context of regional ecosystems (Figure

446 2). For instance, pteropods were seasonally important prey to pink salmon (*Oncorhynchus*
447 *gorbuscha*) and chum salmon (*O. keta*) in many studies in the North Pacific (Groot and Margolis,
448 1991). Food web models developed by Aydin et al. (2005, 2007) for several marine ecosystems
449 around Alaska estimated that salmon, sablefish (*Anoplopoma fimbria*), and rock sole (*Lepidopsetta*
450 *spp.*) all rely upon pteropods for substantial portions of their diets. Despite these case studies,
451 models of the plankton community often omit pteropods, or aggregate all zooplankton into a few
452 functional groups (Fennel, 1999; Chai et al., 2002; Le Quéré et al., 2005; Kishi et al., 2007). Due
453 in part to the movement toward ecosystem-based management of marine resources (McLeod and
454 Leslie, 2009) and to dramatic increases in computing capacity, there is a growing set of complex
455 “end-to-end” ecosystem models that link physics, plankton, fish, and fisheries, typically in a spatial
456 framework (Travers et al., 2007; Fulton, 2010). Such models often expand representation of
457 plankton groups to include pteropods, gelatinous zooplankton, and even mixotrophic groups such
458 as dinoflagellates (Aydin et al., 2007; Kaplan et al., 2012; Fulton et al., 2014).

459 End-to-end models are best viewed as coarse approximations of pteropod population
460 dynamics. These models can (1) link pteropods to their prey and predators; (2) allow three-
461 dimensional pteropod movement that captures potential horizontal and depth shifts in response to
462 altered temperature, oxygen, and Ω_{arag} ; and (3) represent some impacts of temperature and Ω_{arag}
463 on vital rates, such as survival and growth. Recent revisions to the Atlantis end-to-end model of
464 the California Current (Kaplan et al., 2012, 2013) suggest that deficiencies of these models to date
465 include the need for refined representation of vulnerable life stages, better diet information, and
466 incorporation of detailed observational literature related to physiological and feeding responses
467 (Appendices B1–B4, B6–B7). Simple demographic models of single pteropod species can be a
468 stepping stone toward these more complex models, either informing their parameterization or

469 being directly coupled to the end-to-end model.

470 **6.3 A “straw man” model of *Limacina helicina antarctica* demography**

471 To demonstrate the value of modelling pteropod responses to stressors, we created a “straw
472 man” stage-structured demographic model of *Limacina helicina antarctica*, one of the few species
473 for which survival and fecundity rates are relatively well-studied (Bednaršek et al., 2012a). (The
474 parameterization and data sources for this simple model are provided in Table 1.) Following the
475 methods of Caswell (2001) and Stubben and Milligan (2007), we divided the life cycle into seven
476 stages ranging from 30 to 335 d (Table 1), based on the stages described in Bednaršek et al.
477 (2012a). We divided age-1 (G1) individuals into four stages, to capture the hermaphroditic
478 transition from males to females, followed by a dormant winter period. We took daily survival of
479 the age-0 (G2) stage individuals from Bednaršek et al. (2012a), and assumed this survival rate also
480 pertained to all G1 individuals. Daily survival rates of eggs are unknown, but we estimated them
481 based on an assumption of stable population size ($\lambda=1$). Fecundity estimates provided by Lalli and
482 Wells (1978) ranged from 524 to 10,051 eggs per female over a 20 d period. We assumed that the
483 lower bound of this (26 eggs per female per d⁻¹) pertained to fully female G1 individuals with a
484 typical length of 2.74 mm and 0.62 mg dry weight. Length-weight relationships (Bednaršek et al.,
485 2012a) suggest the older G stage individuals at 10 mm length are a maximum of 4.33 mg dry
486 weight, 7 times the mass of G1 individuals, so we assume sevenfold higher daily fecundity rates
487 for the G stage. The final projection matrix that represents the demography of *Limacina helicina*
488 *ant.* on a daily timestep is presented in Figure 3A.

489 Results from the matrix model illustrate these main points. First, the daily survival rates of
490 0.99 leads to very low survival rates over an entire stage (1–7 months), and therefore, the stable
491 age structure of the population is expected to be numerically dominated by eggs and G2 (age-0)

492 individuals (Figure 3B). Thus, consideration of carbon flux or energy to predators should account
493 for this age structure, also taking into account the weight per individual or per egg.

494 Second, the elasticity matrix (Caswell, 2001; Stubben and Milligan, 2007) illustrates that
495 the largest effect on population growth rate will stem from proportional changes to survival rates
496 of G2 and the subsequent early stage of G1 (100% males; elasticity values of 0.274 and 0.284,
497 respectively). Demographics are less sensitive to proportional changes in other vital rates, such as
498 fecundities or the survival rates of older individuals and eggs (Figure 3C). For example, a
499 proportional reduction in survival rates of G2 individuals (e.g., under acidified conditions) will
500 have a stronger impact on the population than an equivalent proportional reduction in survival of
501 eggs to the G2 stage. This simple model also hints at the validity of our assumptions: the elasticity
502 analysis suggests that population growth is not sensitive (elasticity = 0.017) to egg survival, which
503 is fortunate since we estimated egg survival by assuming stable population size. On the other hand,
504 population growth rates—and the model output as a whole—are most sensitive to our assumption
505 that G2 survival rates could be applied to the first stage of G1 (“G1 early” stage, Table 1). Clearly,
506 additional empirical work is needed on this critical vital rate.

507 Similarly, summing the columns of the elasticity matrix yields the life stage weights, which
508 suggest that population dynamics are more strongly driven by the demographics of the youngest
509 individuals (G2 and the subsequent early stage of G1) than older individuals (Figure 3D). These
510 are the stages just prior to first reproduction. This is despite the high fecundity of the oldest
511 individuals, which is offset by additional months of mortality.

512 In summary, when combined in the model, the basic demographic data available (Table 1)
513 for *Limacina helicina ant.* illustrate that population dynamics are highly dependent on survival
514 and growth rates of the early stages. The empirical literature reviewed above suggests these are

515 the life stages most sensitive to acidification (Bednaršek et al., 2012a; Comeau et al., 2010b; Byrne,
516 2011; Lischka et al., 2011). Future work could incorporate ocean acidification effects directly into
517 the model. Other stressors such as increased temperature may decrease adult pteropod size (see
518 Schalk, 1990, reviewed above) and result in decreases in egg production that can also be tested in
519 the model. Another future step might be linking such models to maps of the overlap between spatial
520 distribution of each life stage and stressors, such as acidified water. This approach has been applied
521 to spatial risk assessments for other plankton species (Hodgson, 2014).

522 *6.4 Challenges and decisions for next steps in modeling pteropods*

523 Models that link OA, warming, and deoxygenation to pteropods and to higher trophic levels
524 via food web effects are necessary, but exhibit the general challenges of linking zooplankton to
525 vertebrate populations and ecosystem processes. Chief among these challenges is the lack of
526 targeted field and experimental work on many pteropod species—for instance, we found mortality
527 estimates for only a single pteropod species (Bednaršek et al., 2012a). In discussions of how to
528 link biogeochemically oriented zooplankton models to fisheries and end-to-end models, Carlotti
529 and Poggiale (2010) and Mitra et al. (2014) noted the disproportionately large number of studies
530 of copepod species, while other taxa such as pteropods are frequently omitted. For pteropods, there
531 have been few attempts at large-scale modeling, in particular because, until recently, there was a
532 real lack of information about their physiology, ecology, and distributions (Hood et al., 2006)—
533 all of which are required to move beyond simple “straw man” models such as the one here. One
534 of the major remaining challenges involves translating from short-term observations and
535 experiments, at the level of individual pteropods over days to weeks, into the population-level
536 understanding of the impacts of acidification, temperature, and oxygen.

537 Though it is clear that improved representation of pteropods and other zooplankton is a key
538 challenge to further development of ecological models (Rose et al., 2010), the level of detail
539 required to accomplish this is an open question. Mitra et al. (2014) identify a broad swathe of
540 physiological and ecological processes that they suggest must be studied empirically and brought
541 into plankton models; among these are variable assimilation efficiency, variable prey nutritional
542 quality, metabolic scaling of physiological rates, variable C:N:P ratios, and turbulence. However,
543 experience with ecosystem models suggests that additional complexity, particularly at the level of
544 physiological detail (Fulton et al., 2004), does not necessarily improve model performance or a
545 model's ability to capture key ecosystem features. In fact, in ecosystem models, there are well-
546 known trade-offs between model complexity and skill (Collie et al., 2014), particularly for
547 zooplankton (Carlotti and Poggiale, 2010; Rose et al., 2010).

548 **7. Conclusion and future needs**

549 The oceans continue to experience changes in physical and chemical conditions as a result
550 of multiple environmental drivers simultaneously at work, and teasing apart their relative impacts
551 will be challenging (Reum et al., 2015). How effectively we mitigate lost services or conserve
552 resources and processes will depend, in part, on our understanding of marine ecosystems and
553 stressors, and also on our ability to anticipate changes at appropriate time scales (e.g., Harley et
554 al., 2006). This understanding and predictive capacity will be built upon empirical, experimental,
555 and modelling sciences, working cohesively and across research disciplines. With better
556 understanding of the cumulative effect of global environmental stressors comes better prediction
557 of future pteropod responses on a global, regional, and local level. Maintaining pteropods in lab-
558 based experimental studies under multiple stressors for long periods of time is difficult, and multi-
559 factorial comparative studies are often challenging to interpret. *In situ* studies with co-occurring

560 multiple stressors, coupled with modeling, hold the promise to project these experimental studies
561 into ecosystem-scale dimensions that can be validated by monitoring programs. There are certain
562 gaps that near-future studies should address in regard to multiple stressors before pteropods
563 become critically affected. The short-list of gaps includes improved understanding of biomass
564 distribution, DVM patterns and trends, trophic interaction, carbonate fluxes, and long-term
565 population status and trends across spatial scales; biodiversity with related phylogenetics and
566 biogeography; life history rates for improved population and ecosystem models; acclimatization
567 and adaptation potential vs. vulnerability over short and long-term time scales related to particular
568 thresholds.

569 Addressing these gaps should be closely related to evaluating pteropods as indicators for
570 cumulative effects of OA and other stressors. Their role as an indicator has been recognized across
571 diverse ocean basins, including the Mediterranean Sea (Janssen and Peinjenburg, 2014), high-
572 latitudinal environments (Bednaršek et al., 2012b,c; Comeau et al., 2009, 2012; Lischka et al.,
573 2011) and upwelling systems (Bednaršek et al., 2014b). Our growing capacity to study *in situ*
574 pteropod responses (Bednaršek et al., 2012b, 2014b), coupled with the pteropod's ubiquitous
575 global distribution in the world's oceans, provides a basis for closing gaps, rigorous evaluation of
576 pteropods as indicators of ecosystem stress, and quantifying threshold values that can be used by
577 resource managers and regulators to inform environmental assessments and guide management
578 responses.

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582

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589

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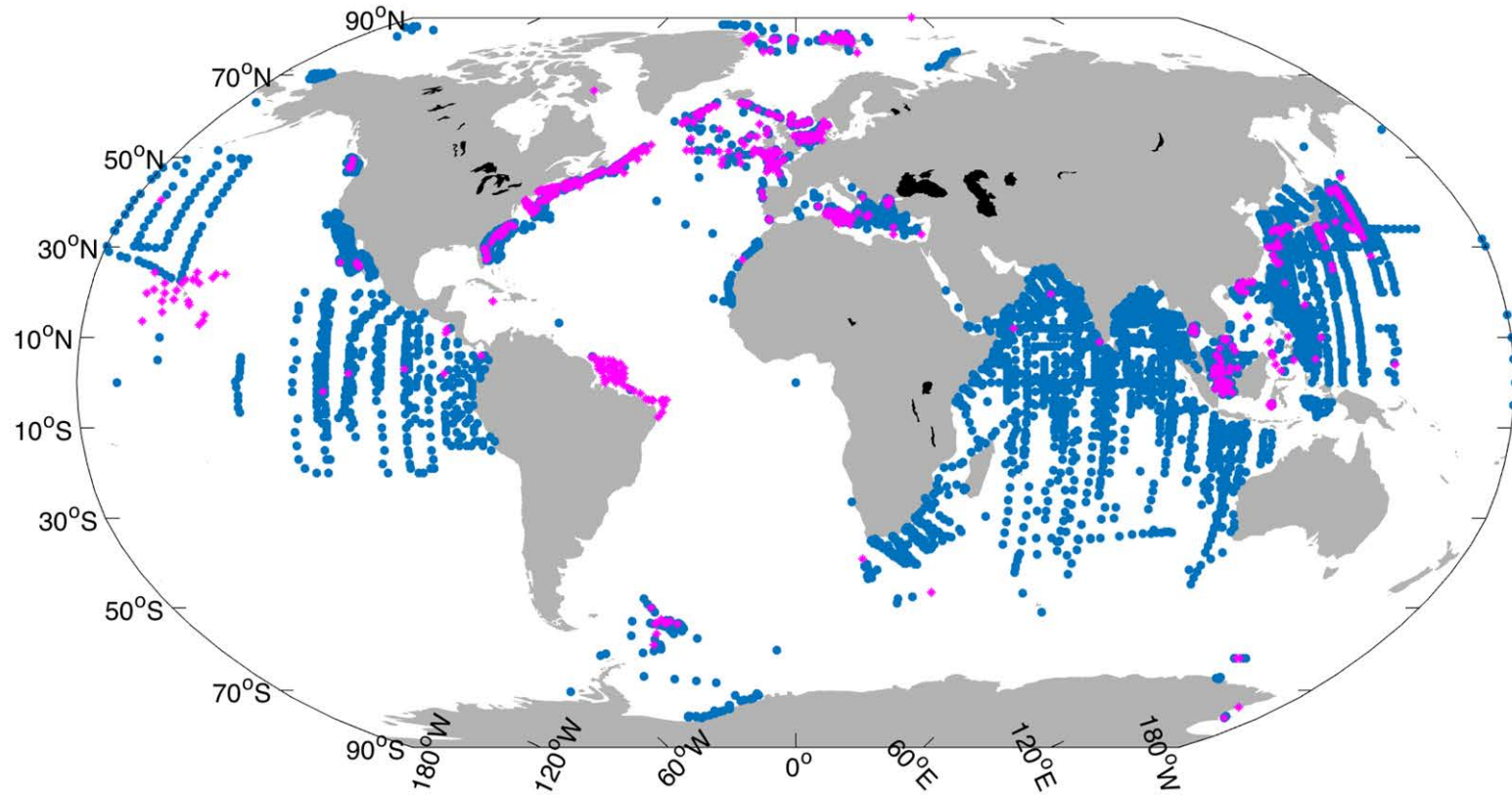
Table 1. Demographic rates for the stage-structured matrix model of *L. helicina ant*.
 The G1 stage (age-1 individuals) includes the transition from male to female for this protandrous hermaphroditic species.

Stage	% female†	Stage duration (d)†	Survival (d ⁻¹)†	Fecundity (eggs d ⁻¹)‡
Egg	0	30	0.858 (estimated)	0
G2	0	335	0.99	0
G1 early	0	51	0.99	0
G1 middle	50	51	0.99	13
G1 late	100	51	0.99	26
G1 (dormant)	100	212	0.99	0
G	100	120	0.99	182

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†Bednaršek et al., 2012a ; ‡Lalli and Wells, 1978.

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1122 Figure 2: Global pteropod distribution based on the pteropod dataset (blue dots of 15134 net-sampling stations; accessible in PANGAEA database

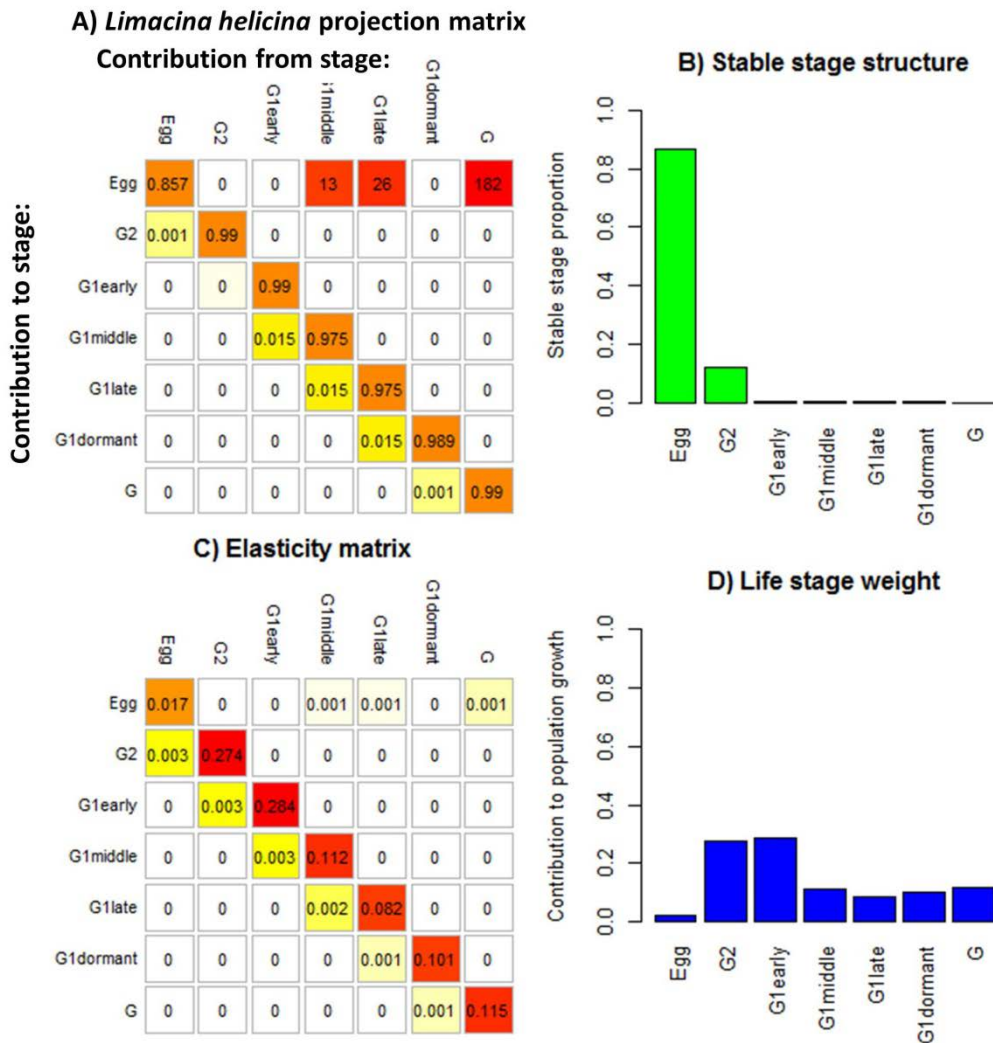
1123 doi.pangaea.de/10.1594/PANGAEA.777387). Pink dots indicate the location where pteropod biomass is higher than global mean pteropod

1124 biomass (modified from Bednaršek et al., 2012).

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Figure 3. Stage structured matrix model for *Limacina helicina antarctica*, on a daily time step. **a)** Projection matrix. First row is contribution to eggs (either fecundity, or probability of eggs remaining as eggs). Values on diagonal are survival probability, minus the probability of transitioning to next stage. Values directly below the diagonal represent probability of transitioning to the next stage. Daily transition probability for stage i calculated as $\frac{s_i^{d_i}}{\sum_{t=1}^{t=d} s_i^{t-1}}$, where s is daily survival, and d is duration of the stage in days. Note that in the third row, second column of the projection matrix, the actual value is 0.0003573. **b)** Stable age structure of the population. **c)** Elasticity matrix, representing the change in population growth rate stemming from proportional changes to the corresponding elements in the projection matrix. **d)** Life stage weight, the sum of columns of the elasticity matrix, representing the stage-specific contribution to population growth.

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Appendices:

Table B.1. Respiration rate as a function of temperature

Table B.1.1. Mass specific oxygen consumption rate ($\mu\text{mol O}_2 \text{ g wet mass}^{-1} \text{ h}^{-1}$)

Reference	Order	Taxa	Temperature [°C]	n (nb. of experiments/specimen)	Wet Mass [mg]*	MO ₂ [$\mu\text{mol O}_2 \text{ g wet mass}^{-1} \text{ h}^{-1}$]; mass specific oxygen consumption rate	SE (standard error)	Equation	Add. info	Temperature coefficients (Q ₁₀)	Notes
Seibel B.A. et al. (2007)	Thecosomata	<i>Limacina helicina</i>	-2	22	8.49	5.51	0.44				Oxygen consumption rates (MO ₂ . [$\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$]) decline with wet body mass (M, [g]) according to the power equation, $\text{MO}_2 = aMb$, where a is a normalization constant independent of mass and temperature, and b is a scaling coefficient that describes the slope of the relationship. Temperature coefficients [$Q_{10} = (a_1/a_2)(10/(T_2 - T_1))$] were determined from the normalization constants measured at different temperatures. Normalization constants for <i>C. antarctica</i> at 2°C and 28°C are higher than are those of <i>C. limacina</i> at 10°C and 58°C, respectively, suggesting that temperature compensation of some energetically expensive physiological process is reflected in whole-animal metabolic rates.
Seibel B.A. et al. (2007)	Thecosomata	<i>Limacina helicina</i>	-2	12	8.25	3.79	0.16		starved		
Seibel B.A. et al. (2007)	Thecosomata	<i>Limacina helicina</i>	5	10	3.2	6.37	0.868				
Seibel B.A. et al. (2007)	Thecosomata	<i>Cavolinia tridentata</i>	18	3	50.5	10.99	3.23				
Seibel B.A. et al. (2007)	Thecosomata	<i>Cavolinia tridentata</i>	24	2	6	17.25					
Seibel B.A. et al. (2007)	Thecosomata	<i>Cavolinia tridentata</i>	24	2	11	17.23					
Seibel B.A. et al. (2007)	Thecosomata	<i>Corolla spp.</i>	5	4	11305	0.226	0.11				
Seibel B.A. et al. (2007)	Thecosomata	<i>Corolla spp.</i>	18	1	0.327	0.582					
Seibel B.A. et al. (2007)	Gymnosomata	<i>Clione antarctica</i>	-2	31	140.4	2.04	0.116	$\text{MO}_2 = 0.84 M^{-0.29}$		3.6	
Seibel B.A. et al. (2007)	Gymnosomata	<i>Clione antarctica</i>	-2	30	70	0.99	0.05	$\text{MO}_2 = 0.84 M^{-0.29}$	starved	3.6	
Seibel B.A. et al. (2007)	Gymnosomata	<i>Clione antarctica</i>	2	20	123.8	2.83	0.177	$\text{MO}_2 = 1.50 M^{-0.23}$		3.6	

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Reference	Order	Taxa	Temperature [°C]	n	Wet Mass [mg]*	MO ₂ [μ mol O ₂ g wet mass ⁻¹ h ⁻¹];	SE	Equation	Add. info	Temperature coefficients (Q ₁₀)	Notes
Seibel B.A. et al. (2007)	Gymnosomata	<i>Clione limacina</i>	5	23	488.5	1.36	0.155	MO ₂ =0.58 M-0.43		4.26	*some of the wet mass values were calculated from the given range of measured wet mass values as mean wet mass values.
Seibel B.A. et al. (2007)	Gymnosomata	<i>Clione limacina</i>	5	9	217	1.01	0.09	MO ₂ =0.58 M-0.43	starved	4.26	
Seibel B.A. et al. (2007)	Gymnosomata	<i>Clione limacina</i>	10	20	343.5	1.95	0.149	MO ₂ =1.1 M-0.31		4.26	
Seibel B.A. et al. (2007)	Gymnosomata	<i>Pneumodermopsis spp.</i>	18	2	256	3.99					
Seibel B.A. et al. (2007)	Gymnosomata	<i>Pneumodermopsis spp.</i>	18	2	256	2.05					
Seibel B.A. et al. (2007)	Gymnosomata	<i>Pneumodermopsis spp.</i>	24	2	5	40.94					
Seibel B.A. et al. (2007)	Gymnosomata	<i>Cliopsis krohni</i>	5	3	789.5	0.06	0.02				
Seibel B.A. et al. (2007)	Gymnosomata	<i>Cliopsis krohni</i>	5	4	1775	0.055	0.014				
Seibel B.A. et al. (2007)	Gymnosomata	<i>Cliopsis krohni</i>	24	1	132	1.672					
Seibel B.A. et al. (2007)	Gymnosomata	<i>Thliptodon spp.</i>	5	1	740	0.067			deep		
Seibel B.A. et al. (2007)	Gymnosomata	<i>Thliptodon spp.</i>	20	1	56	0.693					
Seibel B.A. et al. (2007)	Gymnosomata	<i>Notobranchia grandis</i>	5	1	910	0.1			deep		

1149 Table B.1.2. Mass specific oxygen consumption rate ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$)

Reference	Order	Taxa	Temperature [°C]	n	Mean chl-a [mg m-3]	Oxygen consumption rate [$\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$]	SE	Equation	Add. info	Notes
Seibel B.A. and Dierssen H.M., (2003)	Thecosomata	<i>Limacina helicina</i>	-1.86	12	3.9 (and 1.5)**	5.51	0.4			**Chlorophyll measured twice (only relevant for <i>Limacina helicina</i> as a food source!); (Seibel B.A. and Dierssen H.M., 2003)
Seibel B.A. and Dierssen H.M., (2003)	Thecosomata	<i>Limacina helicina</i>	-1.86	22	1.0 (and 2.2)**	3.78	0.2			
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	<i>Clione antarctica</i>	-1.86	33		0.99	0.05	Oxygen consumption=0.4 (wet body mass)-0.28	food deprivation	
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	<i>Clione antarctica</i>	-1.86	31		2.04	0.12	Oxygen consumption=0.93 (wet body mass)-0.25		
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	<i>Clione antarctica</i>	-1.86	10		1.93	0.21			
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	<i>Clione antarctica</i>	-1.86	7		0.96	0.1		starved (lab experiment)	

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Table B.1.3. Mass specific oxygen consumption rate ($\text{mm}^3 \text{O}_2 \text{mg}^{-1} \text{hr}^{-1}$)

Reference	Order	Taxa	Temperature [°C]	n (nb. of experiments)	Ash-free dry weight [mg]	B	Seb (standard error of b)	a	Resp rate [$\text{mm}^3 \text{O}_2 \text{mg}^{-1} \text{hr}^{-1}$]	Equation and notes:	Notes
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	0	13	4.15	-0.3789	0.1915	1.6516	0.079165	Y=bX+a (y=respiration [$\text{mm}^3 \text{O}_2 \text{mg}^{-1} \text{hr}^{-1}$]; X=body weight [mg])	
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	5	8	4.15	-0.3936	0.2779	2.4904	0.85696		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	10	42	4.15	-0.4034	0.1163	3.0381	1.36399		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	15	14	4.15	-0.3838	0.2705	3.7014	2.10863		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	20	17	4.15	-0.3973	0.313	4.3798	2.731005		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	25	34	4.15	-0.3818	0.1013	4.7627	3.17823		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Diacria trispinosa</i>	30	8	4.15	-0.3834	0.2161	5.1301	3.53899		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Cuvierina columnella</i>	10	6	3.4	-0.3739	0.2154	1.5223	0.25104		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Cuvierina columnella</i>	15	35	3.4	-0.3895	0.1224	2.2877	0.9634		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Cuvierina columnella</i>	20	88	3.4	-0.3976	0.0562	2.8642	1.51236		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Cuvierina columnella</i>	25	54	3.4	-0.3816	0.0943	3.3264	2.02896		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Cuvierina columnella</i>	30	16	3.4	-0.3875	0.2258	3.8356	2.5181		Combined effects of pressure and temperature on respiration rate generally show increased respiration with increased pressure
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	0	17	5.05	-0.3332	0.1294	1.6971	0.01444		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	5	48	5.05	-0.3486	0.1008	2.3124	0.55197		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	10	28	5.05	-0.3405	0.1566	2.7271	1.007575		

Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	15	25	5.05	-0.3422	0.1304	3.4361	1.70799
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	20	30	5.05	-0.3332	0.1289	3.9971	2.31444
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	25	11	5.05	-0.3344	0.1475	4.4632	2.77448
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Clio pyramidata</i>	30	8	5.05	-0.3329	0.2116	4.9231	3.241955
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Thielea helicoides</i>	0	16	1.4	-0.4395	0.0983	2.1319	1.5166
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Thielea helicoides</i>	5	38	1.4	-0.4235	0.0621	2.3929	1.8
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Thielea helicoides</i>	10	23	1.4	-0.4326	0.0411	2.6516	2.04596
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	<i>Thielea helicoides</i>	15	4	1.4	-0.418	0.1456	3.8145	3.2293

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1170 **Table B.1.4. Respiration rates** ($\mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$) for Pseudothecosomata

Reference	Order	Taxa	Temperature [°C]	n	Respiration rate ($\mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$)	SD
Biggs D.C (1977)	Pseudothecosomata	<i>Corolla spectab</i>	26	5	0.91	3
Biggs D.C (1977)	Pseudothecosomata	<i>Corolla spectab</i>	26	8	0.82	3
Biggs D.C (1977)	Pseudothecosomata	<i>Corolla spectab</i>	26	3	0.55	3
Biggs D.C (1977)	Pseudothecosomata	<i>Gleba cordata</i>	26	1	0.83	3
Biggs D.C (1977)	Pseudothecosomata	<i>Gleba cordata</i>	26	1		0.44
Gilmer W.R. (1974)	Pseudothecosomata	<i>Gleba cordata</i>	26		5	0.5
Gilmer W.R. (1974)	Pseudothecosomata	<i>Gleba cordata</i>	20		3	0.5

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1183 **Table B.1.4. Respiration rates** ($\mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$) for Thecosomata and Gymnosomate

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Reference	Order	Species	Number of Experiments	Body weight (DM mg)	SD	Temp ($^{\circ}\text{C}$)	Respiration Rate ($\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}$)	SD
Maas AE et al. (2012)	Thecosomata	<i>Diacavolinia longirostris</i>	17	1.85	0.83	20	1.88	0.52
Maas AE et al. (2012)	Thecosomata	<i>Clio pyramidata</i>	23	2.05	1.1	20	2.03	0.53
Maas AE et al. (2012)	Thecosomata	<i>Creseis virgula</i>	18	1.53	0.86	20	1.18	0.35
Maas AE et al. (2012)	Thecosomata	<i>Diacria quadridentata</i>	23	2.18	0.74	20	2.31	0.42
Maas AE et al. (2012)	Thecosomata	<i>Hyalocylis striata</i>	36	2.36	0.95	20	1.72	0.34
Maas AE et al. (2012)	Thecosomata	<i>Cavolinia inflexa</i>	4	2.9	2.21	20	1.87	0.8
Maas AE et al. (2012)	Thecosomata	<i>Cavolinia uncinata</i>	6	10.2	6.8	20	4.07	2.89
Maas AE et al. (2012)	Gymnosorrata	<i>Clione limacina antarctica</i>	12	14.97	N/A	-1.8	5.93	0.41
Comeau S et al. (2012)	Thecosomata	<i>Creseis clava</i>	4	0.442	0	19	0.718	0.003

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B2) Growth rate as a function of temperature

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Table B.2.1. Growth rates (mm day⁻¹).

Reference	Taxa	Temp [°C]	Growth rate [mm day ⁻¹]	DW [mg]	g= exponential	Notes
Clarke C. and Roff J.C. (1990)	<i>Creseis virgula</i>		0.015	0.00025	0.015	Growth rates were not directly estimated but estimated from growth rate for pteropod <i>Creseis</i> (<i>C. virgula</i> from Wells, 1976), expressed as increase in shell length per day. Based on their length-weight relationship for <i>C. virgula</i> , they calculated g, but regarded it improbably low. (Clarke C. and Roff J.C., 1990).
Wells F.E. (1976)	<i>Creseis virgula conica</i>	27	0.01	0.00014	0.3	Collections twice monthly, from June 1971-May 1973 from 300 m to the surface (3 oblique tows). The size-frequency data was plotted on probability paper-the method utilizes fluctuations in the numbers of individuals in the various size classes to determine growth rates (over short period of time).
Wells F.E. (1976)	<i>Limacina bulmoides</i>	27	0.005	4.80E-05	0.15	
Wells F.E. (1976)	<i>Heliconoides inflatus</i>	27	0.004	3.43E-05	0.12	
Wells F.E. (1976)	<i>Limacina trochiformis</i>	27	0.0033	2.61E-05	0.1	
Bednaršek N. et al. (2012a)	<i>Limacina helicina antarctica</i>	4	0.009	0.00012		
Bednaršek N. et al. (2012a)	<i>Limacina helicina antarctica</i>	4	0.006	6.31E-05		interseasonal growth
Bednaršek N. et al. (2012a)	<i>Limacina helicina antarctica</i>	4	0.01	0.00014		
Bednaršek N. et al. (2012a)	<i>Limacina helicina antarctica</i>	4	0.009	0.00012		
Fabry V.J. (1989)	<i>Clio pyramidata</i>	10.7*	1.1			Notes: Equation: $Y=1.1 X$; $r^2=0.73$; $X=\text{time (h)}$, $Y=\mu\text{g Ca deposition/mg Ca shell}$ G measured in the ⁴⁵ Ca uptake experiment. G was calculated using data of Kobayashi (1974) on the mean shell diameter/month and the regression of the shell weight on shell diameter. (this estimate of growth rate is conservative - see pg.6); *Temperature was taken from the World Ocean Database as a mean annual surface temperature
Fabry V.J. (1989)	<i>Limacina helicina</i>	10.7*	0.7			

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B3.) Ingestion rate as a function of temperature (l, ng (pigm.) ind⁻¹ day⁻¹)

Reference	Taxa	Temp [°C]	Daily ingestion rate [ng pigm. ind ⁻¹ day ⁻¹]	k [h ⁻¹]	Notes
Pakhomov, E.A. and Perissinotto, R. (1997)	<i>Limacina</i> spp.	11.5	540.5	0.355	The actual temperature given in the article was 11-12 °C.
Pakhomov, E.A. and Perissinotto, R. (1997)	<i>Limacina</i> spp.	11.5	701.6	0.355	
Pakhomov, E.A. and Perissinotto, R. (1997)	<i>Limacina</i> spp.	11.5	170	0.355	
Hunt B.P.V. et al. (2008)	<i>Limacina</i> spp.	9.5	76.12	0.98	Original data from Perissinotto R. (1992)
Hunt B.P.V. et al. (2008)	<i>Limacina</i> spp.	9.5	301.87	0.98	
Hunt B.P.V. et al. (2008)	<i>Limacina</i> spp.	9.5	31.22	0.98	
Hunt B.P.V. et al. (2008)	<i>Limacina</i> spp.	9.5	134.01	0.98	
Pakhomov E.A. and Froneman P.W. (2004)	<i>Clio sulcata</i>	-0.901	27757	0.25	
Pakhomov E.A. and Froneman P.W. (2004)	<i>Limacina helicina</i>	-0.901	2103	0.25	
Pakhomov E.A. and Froneman P.W. (2004)	<i>Clio sulcata</i>	-0.544	16627	0.25	
Bernard K.S. and Froneman P.W. (2005)	<i>Limacina retroversa</i>	8.5		0.405	Where temperature is given as 8.5 it is actually given as >8.5 in the article. Where the temperature is given as 2.5 it is as <2. Temperature = subsurface (200 m).
Bernard K.S. (2006)	<i>Limacina retroversa</i>	4.94	4146.51	1.33	Daily ingestion rates were estimated using the following equation (Perissinotto 1992): $l = kG/(1-b1)$; l =ingestion rate, $b1$ = gut pigment destruction rate [ng (pigm) ind ⁻¹], k =gut evacuation rate [h ⁻¹]. The temperature was calculated as an average of sampling temperatures from each (one of the three) expeditions. Regression equations obtained from ingestion rates and integrated chl-a values measured during MOEVS II and IV expeditions were used to estimate ingestion rates of the copepods and pteropod for MOEVS V. ind. as weight in mg. $y = 4\ 231.9551 - 4.4327 * x$ ($p > 0.05$); y = individual daily ingestion rate, x = integrated chl-a concentration
Bernard K.S. (2006)	<i>Limacina retroversa</i>	5.79	4128.68	1.33	
Bernard K.S. (2006)	<i>Limacina retroversa</i>	4.28	4196.88	1.33	

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B4) Mortality rate as a function of temperature

Reference	Taxa	Temperature [°C]	Annual Beta Mortality rate [year ⁻¹]	Daily Beta mortality rate [day ⁻¹]
Bednaršek N. et al. (2012a)	<i>Limacina helicina ant.</i>	4	3.38	0.01

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B5) TIC/TOC ration

Reference	Taxa	Stage	Wet mass [mg ind. ⁻¹]	n	Mean Dry mass [mg ind. ⁻¹]	Mean Ash mass [mg ind. ⁻¹]	n	PIC/POC*	Notes
Gannefors C. et al. (2005)	<i>Limacina helicina</i>	juve	30.9	29	1.8	0.3	9	0.20	**Dry weight=all organics and inorganics; ash=inorganics, primarily CaCO ₃ (PIC - estimated from ash weight, assuming ash weight=CaCO ₃); Ash-free dry weight=all organics (Tsurumi M. et al., 2005) *PIC and POC were calculated** from the data in Gannefors C. et al. (2005).
Gannefors C. et al. (2005)	<i>Limacina helicina</i>	fem	259.5	60	28.2	10.2	20	0.57	
Gannefors C. et al. (2005)	<i>Limacina helicina</i>	fem	293.7	40	33	/	/	/	
Gannefors C. et al. (2005)	<i>Limacina helicina</i>	fem	332.5	71	33.9	14.9	29	0.78	
Gannefors C. et al. (2005)	<i>Limacina helicina</i>	fem	173.3	32	19.9	/	/	/	
Gannefors C. et al. (2005)	<i>Limacina helicina</i>	fem	202.6	52	19.3	7.9	18	0.69	
Bednaršek N. (2010)	<i>Limacina helicina antarctica</i>	juv	0.37					0.36	

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B6) Growth and Ingestion rate as a function of food concentration

Reference	Taxon	Temperature [°C]	Phytoplankton production [mg C m ⁻³ h ⁻¹]	Food concentration [surface level] [mg chl a m ⁻³]	Daily ingestion rate [µg pigm. m ⁻³ d ⁻¹]	Gut evacuation rate [k=h ⁻¹]	Equation	Ingestion equation	Notes
Perissinoto R. (1992)	<i>Limacina</i> sp.	9.5	1.2	2	23.6	0.98	Chl a ingestion = (ing. rate/food konc.)* 55 g Chl	I=KG/(1-b'); K=gut evacuation rate(day ⁻¹), G=pigment measurable in the gut; b'=non dimensional index for loss of pigment in digestion.	No measurements of K were carried out for year 1985 (first two I values) - cause of error. The community grazing impact for 1985 was then obtained by multiplying the gut pigment levels of C measured in 1989 by an average factor of 8.9 for the Natal Bank and 11.7 for the offshore samples. Temperature was taken from the experiments for obtaining K (=gut evacuation rate)
Perissinoto R. (1992)	<i>Limacina</i> sp.	9.5	0.7	1	32.3	0.98			
Perissinoto R. (1992)	<i>Limacina</i> sp.	9.5	<0.4	0.2	6.9	0.98			
Perissinoto R. (1992)	<i>Limacina</i> sp.	9.5	<0.4	0.3	18.5	0.98			
Pakhomov E.A. and Perissinotto R. (1997)	<i>Limacina</i> spp.	11.5	278.2	34.3	540.5	0.355			
Pakhomov E.A. and Perissinotto R. (1997)	<i>Limacina</i> spp.	11.5	261.4	45.9	701.6	0.355			
Pakhomov E.A. and Perissinotto R. (1997)	<i>Limacina</i> spp.	11.5	274.3	32.3	170	0.355	I=k G/(1-b'); G=integrated value (over 24h period) of gut pigment contents (ng (pigm) ind. ⁻¹), b'=nondiemsional index of the loss of pigment during digestion	Temperature was between 11-12	

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B7) Threshold food concentration and food preference

Reference	Order	Taxa	Food maintenance requirements [mg food ind ⁻¹ day ⁻¹]	Amount of food expressed as % of dry body weight per ind.	Notes
Gilmer,W.R. (1974)	Pseudothecosomata	<i>Gleba cordata</i>	0.6-1.5	0.7-1.8 %	In both cases, the lower value of food maintenance requirements given is that for a strictly fat diet and the higher value given is for pure carbohydrate uptake.
Gilmer,W.R. (1974)	Pseudothecosomata	<i>Gleba cordata</i>			
Gilmer,W.R. (1974)	Thecosomata	<i>Diacavolinia longirostris</i>	0.03-0.07	6.6-15.5 %	
Gilmer,W.R. (1974)	Thecosomata	<i>Diacavolinia longirostris</i>			
Reference	Order	Taxa	Food source	Additional info	
Gilmer R.W. and Harbison G.R. (1991)	Thecosomata	<i>Limacina helicina</i>	suspended material, motile prey (tintinnids, copepods, juvenile <i>Limacina helicina</i>)	It is possible the smaller specimen are herbivores and switch to omnivory at larger sizes. At large sizes <i>L. helicina</i> is opportunistic feeder. Crustacean prey might increase with the size of <i>L. helicina</i> .	
Gilmer R.W. and Harbison G.R. (1991)	Thecosomata	juvenile <i>Limacina helicina</i>	small suspended particles (phytoplankton and protozoans) and possibly also on suspended detritus.		
Gannefors C. et al. (2005)	Thecosomata	veliger <i>Limacina helicina</i>	particulate organic matter	POM is an important dietary component in this stage of life cycle.	
Flores H. et al. (2011)	Thecosomata	<i>Limacina helicina</i>		<i>Limacina helicina</i> mainly feed on phytoplankton in summer, but little is known how they survive the winter in Antarctic ice-covered waters (Lalli and Gilmer, 1989). In the Arctic, juvenile <i>L. helicina</i> have been reported to rely on particulate organic matter originating from the sea ice in winter (Gannefors et al., 2005; Kobayashi, 1974). If that is also the case in the Southern Ocean, <i>L. helicina</i> is likely to concentrate under ice in winter and prefer the phytoplankton-rich open waters in summer.	

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Reference	Order	Taxa	Food source	Additional info	Notes
Hunt B.P.V. et al. (2008)	Thecosomata	<i>Limacina retroversa</i>	Diatoms, Dinoflagellates, Coccolithophorid, Tintinnids	Dominance of diatoms, dinoflagellates and microzooplankton.	Hunt et al. (2008), Table 4. where the data source was Boas (1886. in Lalli and Gilmer, 1989)
Hunt B.P.V. et al. (2008)	Thecosomata	<i>Clio pyramidata f. sulcata</i>	Diatoms, Dinoflagellates, Tintinnids, Foraminiferans, Copepods, Polychaetes, Silicoflagellates	Diatoms important part of diet - predominantly herbivorous diet, but also larger motile organism contribute a substantial part of food - larger specimen of could have more omnivorous diet.	Hunt B.P.V. et al. (2008), Table 4
Hunt B.P.V. et al. (2008)	Gymnosomata	<i>Clione limacina antarctica</i>	Limacina helicina		Hunt B.P.V. et al. (2008), Table 4. where the data source was Hopkins (1987)
Hunt B.P.V. et al. (2008)	Thecosomata	<i>Limacina helicina antarctica</i>	Diatoms, Dinoflagellates	Diet phytoplankton dominated, but there is also some carnivory noted.	Hunt B.P.V. et al. (2008), Table 4. where the data source was Hopkins (1987))
Hunt B.P.V. et al. (2008)	Gymnosomata	<i>Clione limacina antarctica</i>	Limacina helicina antarctica	In the northern hemisphere <i>C. limacina</i> feeds on <i>L. helicina</i> in polar waters and <i>L. retroversa</i> in sub-polar/temperate waters (Lalli and Gilmer, 1989), and it is probable that <i>C. limacina antarctica</i> also feeds on <i>L. retroversa australis</i> in the SAZ and PFZ waters of the Southern Ocean.	Hunt et al. Article, Table 4. where the data source was Hopkins (1987)
Hunt B.P.V. et al. (2008)	Gymnosomata	<i>Clione limacina veligers</i>	phytoplankton	In the northern hemisphere, veliger stages of <i>C. limacina</i> were the only stage not feeding on <i>Limacina</i> . After metamorphosis from veliger to polytochous larvae (at 0.3 mm length), they begin feeding on <i>Limacina veliger</i> .	Data source Lalli and Gilmer, 1989.
Hunt B.P.V. et al. (2008)	Gymnosomata	<i>S. australis</i>	specialist predator on <i>C. pyramidata</i>	No gut content data available.	Data source Lalli and Gilmer, 1989.

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Reference	Order	Taxa	Food source	Additional info
Böer M. et al. (2005)	Gymnosomata	<i>Clione limacina</i>	<i>Limacina helicina</i> exclusively	Due to monophagy, <i>C. limacina</i> is exposed to long periods of food scarcity and consequently has to be adapted to starvation stress. Starvation experiments with <i>C. limacina</i> revealed that this species is able to survive in an aquarium for nearly a year without food. <i>C. limacina</i> has evolved various strategies as body shrinkage, utilization of body constituents not essential for survival, a very low metabolism and slow lipid consumption.
Marine species identification portal (http://species-identification.org)	Pseudothecosomata	<i>Corolla spectabilis</i>	A preference for particles > 10µm seems to occur.	
Marine species identification portal (http://species-identification.org)	Gymnosomata	<i>Pneumodermopsis</i> spp.	This carnivorous species of <i>Pneumodermopsis paucidens</i> p. feeds on <i>Limacina bulimoides</i> and especially <i>Creseis</i> spp.	<i>Pneumodermopsis</i> is a genus with fourteen species which are difficult to identify.
Marine species identification portal (http://species-identification.org)	Thecosomata	<i>Diacria trispinosa</i>	small plankton mainly phytoplankton in the epi- and mesopelagic zone	
Marine species identification portal (http://species-identification.org)	Thecosomata	<i>Cuvierina columnella atl.</i>	Copepod naupli, tintiniids, thecate dinoflagellates, <i>Globigerina</i> and centric diatoms were found in the gut.	
Marine species identification portal (http://species-identification.org)	Thecosomata	<i>Thielea helicoides</i>	The following organisms were found as food: <i>Fragilariopsis antarctica</i> , <i>Thalassiosira</i> , fragments of <i>Coscinodiscus</i> and <i>Chaetoceros</i> .	The recordings of food organisms indicate that planktonic organisms up to about 40 µm are caught as food, while other large organisms seem to be rejected as they were found in the surrounding plankton but not in the alimentary system i.e. larger specimens of <i>Chaetoceros</i> with bristles 1000µm long, and large dinoflagellates.
Marine species identification portal (http://species-identification.org)	Gymnosomata	<i>Thliptodon gegenbauri</i>	Carnivore	

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Reference	taxon	process	equation	notes
Bednarsek et al., 2014b	<i>L. helicina</i>	gross dissolution (% shell loss)	$65.76 * e^{-4.76 * \Omega_{\text{ar}}}$	
Comeau et al., 2009	<i>L. helicina</i>	gross calcification	$(0.57 \pm 0.4) * \ln(\Omega_{\text{ar}}) + 0.25 \pm 0.02$	% mg CaCO ₃ (g ww ⁻¹ day ⁻¹)
Bednarsek et al., in review	<i>L. helicina</i>	gross calcification	$\ln(\% \text{ glow} / (1 - \% \text{ glow})) = -4.34 + 5.07 * \Omega_{\text{ar}}$	
Bednarsek et al., 2014b	<i>L. helicina</i>	Weight-specific function for net calcification	$0.5705 + 0.5783 * (1 - e^{-4.1752 * \Omega_{\text{ar}}})$	
Bednarsek et al., 2014a	<i>L. helicina</i>	estimates of % ind affected by dissolution	$100 * (\exp(aa * \Omega_{\text{ar}} + bb)) / (1 + \exp(aa * \Omega_{\text{ar}} + bb))$	aa = -2.5779, bb=3.2105

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