Metabolic temperature compensation and coevolution of locomotory performance in pteropod molluscs

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Synopsis Gymnosomatous pteropods are highly specialized planktonic predators that feed exclusively on their thecosomatous relatives. Feeding behavior and the morphology of gymnosome feeding structures are diverse and have evolved in concert with the size, shape, and consistency of the thecosome shell. Here, we show that the metabolic capacity and locomotory behaviors of gymnosomes are similarly diverse and vary with those of their prey. Both gymnosomes and thecosomes range from gelatinous sit-and-wait forms to active predators with high-performance locomotory muscles. We find more than 10-fold variation in size-adjusted and temperature-adjusted metabolic rates within both the Gymnosomata and Thecosomata and a strong correlation between the metabolic rates of predators and of prey. Furthermore, these characteristics are strongly influenced by environmental parameters and predator and prey converge upon similar physiological capacities under similar selection. For example, compensation of locomotory capacity in cold waters leads to elevated metabolic rates in polar species. This highly coevolved system is discussed in terms of a predator–prey “arms race” and the impending loss of both predator and prey as elevated atmospheric carbon dioxide levels threaten to dissolve prey shells via oceanic acidification.

Introduction

The Pteropoda is a recently resurrected taxonomic designation meaning “wing-foot” (Massy 1920, 1932; Klussmann-Kolb and Dinapoli 2006). It includes pelagic snails of the closely related Gymnosomata and Thecosomata (Class Gastropoda: Mollusca). Both groups swim by flapping their parapodia (i.e., wings) to generate thrust, a behavior that has earned them the common name “sea angels.” The Thecosomata have shells that are calcified to varying extents and feed by extending a mucous web into the water column to trap food (Gilmer 1972; Gilmer and Harbison 1986). The Gymnosomata lack shells as adults and prey exclusively on thecosomes (Lalli 1970). In the most thoroughly studied example, Clione limacina feeds exclusively on Limacina helicina (Conover and Lalli 1972). The two species grow in concert throughout their life cycles, and sizes of predator and prey are correlated regionally (Lalli and Gilmer 1989). The coevolution of the gymnosome–thecosome clade has lead to the development of highly specialized mechanisms of prey-capture and predator-evasion in what appears to be a predator–prey arms race (a reciprocal relationship by virtue of its specificity) (Brodie and Brodie 1999). Predation involves tactile recognition of the prey species, its rapid capture using highly specialized buccal cones (equipped with cephalopod-like suckers in some cases), and complete extraction of the prey from its shell, using numerous hooks and a toothed radula. Highly efficient digestion and assimilation follow extraction (Conover and Lalli 1972, 1974; Lalli and Gilmer 1989).

Included among C. limacina’s impressive arsenal is a multi-geared swimming system that allows modulation between routine swimming at wing-beat frequencies of 1–2 Hz and higher speeds involved in predator–prey interactions (Satterlie and Spencer 1985). Locomotion is a quantifiable component of predator–prey interactions that has been described for several pteropod species (Morton 1954, 1958; Lalli and Gilmer 1989; Davenport and Bebbington 1990; Childress and Dudley 2004; Borrell et al. 2005). The underlying physiology, however, is well known only for C. limacina (Arshavsky et al. 1985a, 1985b; Satterlie
and Spencer 1985; Satterlie et al. 1985, 1990). During vertical ascent or station-holding, *C. limacina* swims continuously by sweeping its parapodia through an arc of approximately 180° (Borrell et al. 2005). During slow swimming, only small motoneurons that innervate slow-twitch ("red") muscle fibers in the parapodia are active (Satterlie et al. 1990). Two large motoneurons (general excitors) and fast-twitch ("white") muscle fibers are recruited into activity by serotonin during episodes of fast swimming (Arshavsky et al. 1985a, 1985b; Satterlie 1993). Ascent velocity is correlated with wing-beat frequency even over the small range of 1–2 Hz (Borrell et al. 2005).

A southern-ocean *Clione* species has been variously described as a variety, form or subspecies of the northern *C. limacina* (Massy 1920; van der Spoel 1976, 1999). Recently, Gilmer and Lalli (1990) supported the separation of these two as independent species based on subtle morphological differences. For convenience, we adopt this position and refer to the southern congener as *Clione antarctica*. Gilmer and Lalli (1990) noted that the behavior of *C. limacina* and *C. antarctica* is nearly identical, with similar routine wing-beat frequencies at their respective habitat temperatures, and both feed exclusively on regional forms of *Limacina helicina*. However, they noted the lack of a distinct escape swimming response in the southern species. Borrell et al. (2005) corroborated this important difference.

*Clione antarctica* in the Ross Sea, Antarctica, lives permanently at temperatures near −1.8°C, while the *C. limacina* populations we sampled routinely experience temperatures ranging from 5°C to 15.0°C. Low temperatures, such as those experienced by *C. antarctica*, typically depress production of mitochondrial ATP (Clarke 1980, 1983) and may influence output of muscle power as well (Rome 1984, 1990). In muscles doing repetitive work, the rate of ATP hydrolysis is directly proportional to frequency of contraction, all else being equal (Suarez 2003). Thus, in the absence of compensation, low temperature will limit the energy and power available for locomotion and the frequency of wing beating must decrease with a consequent reduction in swimming velocity.

The average consequences to fitness of failed foraging bouts that might result from such depression in temperature are probably much more severe for *Clione* spp. than for more generalist predators (Brodie and Brodie 1999). Thus, we expect strong selection for the maintenance of locomotory capacity in the face of thermal constraints on

the generation of ATP. Connover and Lalli (1972) found that the rates of capture of prey are temperature dependent and increase up to 17°C. In preliminary investigations, we found that feeding rates in the two congeners are similar at their respective habitat temperatures, but higher in *C. antarctica* than in *C. limacina* at similar temperatures (Seibel, unpublished data), supporting the idea that some compensation of ability to capture prey occurs at polar temperatures. Crockett and Sidell (1990) defined temperature compensation as the process permitting an organism living at low temperatures to attain greater active metabolic rates than an organism of similar ecotype from a warmer habitat acclimated to the same low temperature. The continuous locomotory activity in clionid pteropods is in stark contrast to the sedentary lifestyle of Antarctic nototheniid fishes that have been the basis for most metabolic studies of temperature compensation to date (see Clarke 1983; Eastman 1994 for reviews and Kawall et al. 2002 for a recent example). Active metabolism is not well constrained in pteropods, but is thought to be a substantial fraction of the total energy budget (Davenport and Trueman 1985). Thus, we expect temperature compensation of locomotion to be reflected in oxygen consumption by the whole animal, as well as at the neuromuscular and biochemical levels. Here, we take an integrative approach analyzing locomotory behavior and correlated metabolic expenditure in a new model system involving gymnosomes and their exclusive prey, the Thecosomata, each with divergent lifestyles and living in extremes of thermal environments.

**Materials and methods**

**Collection and maintenance of specimens**

Pteropods were collected in several locations and by many different methods. Specimens from Antarctica (*C. antarctica* and *Limacina helicina antarctica*) and from Newfoundland (*C. limacina* and *L. helicina*) were collected using a "jelly dipper" (small beaker attached to the end of a broom handle) at locations around Ross Island (Seibel and Dierssen 2003) and the Ocean Sciences Center in St Johns, respectively. A smaller number of specimens were collected using a plankton net towed through a hole drilled in the sea-ice near McMurdo Station, Antarctica. Specimens were transported to McMurdo Station and maintained at low densities in small plastic containers in filtered seawater in temperature-controlled environmental chambers until measurement (<48 h later). Other species were
collected by hand during blue-water SCUBA dives (Haddock and Heine 2005) near Mote Marine Laboratory (Florida), Monterey Canyon (California), or in the Gulf of California (Mexico). *Notobranchia grandis* and *Thliptodon* spp. were collected using detritus or suction samplers on the remotely operated vehicle (ROV) *Tiburon* from the Western Flyer, Monterey Bay Aquarium Research Institute (Robison 1993). Specimens were allowed at least 24 h to acclimate to the measured temperature (if different from the ambient temperature).

**Measurement of oxygen consumption rate**

During experiments, individuals were maintained in gas-tight glass syringes with volumes that were adjusted for animal mass (Thuesen and Childress 1994). Syringes were placed in temperature-controlled water baths set at the temperatures indicated in Table 1. Oxygen tension in the chambers was measured by injecting a water sample into a micro-respirometry chamber (75 µl sample volume) connected to a polarographic oxygen sensor maintained at the experimental temperature (Marsh and Manahan 1999). Individual duration of experiments varied from 6 to 24 h. Oxygen tension in the respirometry chambers never dropped below 50% air saturation. The critical oxygen partial pressure (the oxygen partial pressure above which the rate of oxygen consumption is independent of oxygen partial pressure) was determined for some species by continuously recording oxygen in a sealed chamber and was found to be <50% air saturation. No relationship was observed between either final oxygen tension or the duration of the experiment and oxygen consumption rate.

For comparison at common temperatures, rates were adjusted to 5°C assuming a temperature coefficient, $Q_{10} = (R_2/R_1)^{(10/(T_2-T_1)}$, of 2.5. This value is within the range typically occurring in the animals’ habitat. Significant differences between various species and temperatures were determined by analysis of covariance (ANCOVA, Statview inc.) performed on relationships between oxygen consumption rate and body mass. Significance is at the 95% confidence level.

### Table 1 Oxygen consumption rates (MO₂, µmol O₂ g wet mass⁻¹ h⁻¹) by pteropods

<table>
<thead>
<tr>
<th>Species</th>
<th>T°C</th>
<th>n</th>
<th>Wet Mass (mg)</th>
<th>MO₂ (± SE)</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Thecosomata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Limacina helicina</em></td>
<td>−2</td>
<td>22</td>
<td>2.4–14.9</td>
<td>5.51 (0.44)</td>
<td>Antarctica 1999</td>
</tr>
<tr>
<td><em>Limacina helicina</em></td>
<td>−2</td>
<td>12</td>
<td>1.5–15.0</td>
<td>3.79 (0.16)</td>
<td>Antarctica 2001 (starved)</td>
</tr>
<tr>
<td><em>Cavolinia tridentata</em></td>
<td>5</td>
<td>10</td>
<td>1.0–5.4</td>
<td>6.37 (0.868)</td>
<td>Monterey, CA</td>
</tr>
<tr>
<td><em>Corolla spp.</em></td>
<td>18</td>
<td>3</td>
<td>13–88</td>
<td>10.99 (3.23)</td>
<td>Gulf of California</td>
</tr>
<tr>
<td><em>Corolla spp.</em></td>
<td>24</td>
<td>2</td>
<td>6.11</td>
<td>17.25, 17.23</td>
<td>Atlantic Florida</td>
</tr>
<tr>
<td><em>Corolla spp.</em></td>
<td>5</td>
<td>4</td>
<td>1100–21510</td>
<td>0.226 (0.11)</td>
<td>Monterey, CA</td>
</tr>
<tr>
<td><em>Corolla spp.</em></td>
<td>18</td>
<td>1</td>
<td>0.327</td>
<td>0.582</td>
<td>Gulf of California</td>
</tr>
<tr>
<td><strong>Gymnosomata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Clione antarctica</em></td>
<td>−2</td>
<td>31</td>
<td>18.8–262</td>
<td>2.04 (0.116)</td>
<td>Antarctica 2001</td>
</tr>
<tr>
<td><em>Clione antarctica</em></td>
<td>−2</td>
<td>30</td>
<td>10.0–130</td>
<td>0.99 (0.050)</td>
<td>Antarctica 2002 (starved)</td>
</tr>
<tr>
<td><em>Clione antarctica</em></td>
<td>2</td>
<td>20</td>
<td>10.6–237</td>
<td>2.83 (0.177)</td>
<td>Antarctica 2001</td>
</tr>
<tr>
<td><em>Clione limacina</em></td>
<td>5</td>
<td>23</td>
<td>26.0–951</td>
<td>1.36 (0.155)</td>
<td>Newfoundland</td>
</tr>
<tr>
<td><em>Clione limacina</em></td>
<td>5</td>
<td>9</td>
<td>156–278</td>
<td>1.01 (0.090)</td>
<td>Newfoundland (starved)</td>
</tr>
<tr>
<td><em>Clione limacina</em></td>
<td>10</td>
<td>20</td>
<td>55.0–632</td>
<td>1.95 (0.149)</td>
<td>Newfoundland</td>
</tr>
<tr>
<td><em>Pneumodermopsis spp.</em></td>
<td>18</td>
<td>2</td>
<td>126–386</td>
<td>2.05, 3.99</td>
<td>Gulf of California</td>
</tr>
<tr>
<td><em>Pneumodermopsis spp.</em></td>
<td>24</td>
<td>2</td>
<td>5.18</td>
<td>40.94, 23.36</td>
<td>Atlantic Florida</td>
</tr>
<tr>
<td><em>Cloopsis krahnii</em></td>
<td>5</td>
<td>3</td>
<td>601–938</td>
<td>0.060 (0.020)</td>
<td>Pt. Conception, CA</td>
</tr>
<tr>
<td><em>Cloopsis krahnii</em></td>
<td>5</td>
<td>4</td>
<td>550–3000</td>
<td>0.055 (0.014)</td>
<td>Monterey, CA</td>
</tr>
<tr>
<td><em>Cloopsis krahnii</em></td>
<td>24</td>
<td>1</td>
<td>132</td>
<td>1.672</td>
<td>Gulf of California</td>
</tr>
<tr>
<td><em>Thliptodon spp.</em></td>
<td>5</td>
<td>1</td>
<td>740</td>
<td>0.067</td>
<td>Monterey, CA (deep)</td>
</tr>
<tr>
<td><em>Thliptodon spp.</em></td>
<td>20</td>
<td>1</td>
<td>56</td>
<td>0.693</td>
<td>Gulf of California</td>
</tr>
<tr>
<td><em>Notobranchia grandis</em></td>
<td>5</td>
<td>1</td>
<td>910</td>
<td>0.100</td>
<td>Monterey (deep)</td>
</tr>
</tbody>
</table>
Animal mass
Most animals were weighed on an analytical balance and frozen for further analysis. Those that were collected at sea were either frozen for subsequent determination of mass on land, or were weighed on a motion-compensated shipboard balance system (Childress and Mickel 1980). Respiration rates are reported in micromoles of O₂ consumed per gram wet weight per hour. Comparison with previous studies variously requires that respiration rates be expressed in terms of wet mass (WM), dry mass (DM), ash-free dry mass (AFDM), and/or protein content. Dry mass was determined for some species in the present analysis by drying specimens at 60°C until constant weight (48 h). For Limacina helicina antarctica, dried samples were then placed in a 500°C muffle furnace for 12 h and weighed on a precision analytical balance. The dry mass minus the ash weight equals the AFDW. Shells were included in all mass measurements. Wet mass was used as the primary measure of size because it is the parameter of physiological significance, i.e., it determines constraints on animal locomotion, behavior, and predator–prey interactions, among others. The use of other parameters as indicators of size can lead to misinterpretations of the biology of the whole animal. The relative values of different expressions of body size in this regard have been discussed fully by Childress (1977) and Childress and Somero (1979).

Results
Oxygen consumption rates
Mass-specific oxygen consumption rates (MO₂, μmol O₂ g⁻¹ h⁻¹) for 10 species of pteropods are presented in Table 1. A range of sizes sufficient to determine relationships between metabolism and body mass was available only for a few species (MO₂ = aMᵇ, where a is a normalization constant, M is wet body mass, and b is a scaling coefficient; see Figs. 1–3 for equations). Among gymnosomes, mean oxygen consumption rates ranged from 0.055 μmol O₂ g⁻¹ h⁻¹ in Cliopsis krohni at 5°C, to 40.94 μmol O₂ g⁻¹ h⁻¹ in Pneumodermopsis spp., at 24°C. Once corrected for temperature differences, assuming a Q₁₀ of 2.5 and estimating effects of body mass by comparing the normalization constants of scaling relationships, the highest rates were in C. antarctica (ANCOVA, P < 0.05), followed by C. limacina and Pneumodermopsis (Fig. 3A). Among thecosomes, rates were highest in tropical Cavolinia spp. measured at 18 or 24°C and lowest in the gelatinous pseudothecosome, Corolla spp. measured at 5°C (Fig. 3B). Rates were roughly equivalent between polar (5.51 ± 0.44 μmol O₂ g⁻¹ h⁻¹) and temperate specimens of L. helicina (6.36 ± 0.87 μmol O₂ g⁻¹ h⁻¹) measured at the
temperatures of their respective habitats (−2 and 5°C). Temperature coefficients (Q₁₀) were determined for *C. limacina* (Q₁₀ = 4.26, Fig. 1A) and *C. antarctica* (Q₁₀ = 3.6, Fig. 1B) by comparing normalization constants from scaling relationships.

**Feeding history**

Feeding history plays an important role in determining metabolic rates in pteropods. For thecosomes, feeding-related variation was not adequately controlled in the present analysis, so we cannot say with certainty whether compensation for low temperature took place and cannot make precise comparison with other studies. Because of their monophagous nature, feeding is much more easily controlled in gymnosophents and recent feeding history in field-caught specimens can be roughly discerned by the presence or absence of thecosomes at the time gymnosophents were collected (Seibel and Dierssen 2003). Food deprivation resulted in a 30 and 50% reduction in metabolic rate in *C. limacina* and *C. antarctica*, respectively (Fig. 2).

**Comparisons with published measurements**

The present results are within the range reported previously for species in each genus, despite very different techniques of collection and measurement. For example, respiration rates reported by Ikeda and Fay (1981) for limited numbers of *L. helicina* along the Antarctic Peninsula are similar to those we obtained, but not directly comparable due to large differences in body size of specimens in the two
Antarctic regions (Seibel, personal observation). *Limacina helicina* of comparable size, measured at similar temperatures, fall within the range of values we report here (Ikeda 1970, 1989). Smith and Teal (1973) measured metabolic rates in *L. helicoids* across a range of temperatures and hydrostatic pressures and found that, below 10°C, rates from this deep-living species are unaffected by either temperature or pressure. Those rates overlap with our values for *L. helicina*. As we report here, Biggs (1977) found that *Corolla* spp. has a much lower metabolic rate than do euthecosomes such as *Cavolinia* spp. Connover and Lalli (1974) presented extensive measurements for *C. limacina* at a range of temperatures that are consistent with our findings. We hesitate to draw conclusions about temperature compensation by comparing previously published data to our own, however, because subtle differences in body size, feeding history, and location of capture of the specimens measured, as well as differences in methods of collection and measurement, can greatly influence such conclusions.

**Swimming speed and behavior**

Mean wing-beat frequencies were similar in *C. limacina* (1.54 Hz, 10°C) and *C. antarctica* (1.36 Hz, 0°C) (Borrell et al. 2005) at their respective habitat temperatures. However, wing-beat frequency declined significantly with body length (Fig. 4A) and mean body length was greater in *C. limacina*. Thus, at a common body size, *C. limacina* swam nearly twice as fast at 10°C as did *C. antarctica* at 0°C. Furthermore, wing-beat frequencies were bimodal in *C. limacina* reflecting the multi-geared swimming system in this species. No evidence of different gears or gaits was observed in *C. antarctica*. When disturbed, *C. limacina* displays a burst escape response with wing-beat frequencies approaching 7 Hz (Satterlie and Spencer 1985), while *C. antarctic* exhibits a strong full-body withdrawal reflex instead (Borrell et al. 2005).

**Body mass**

Subsequently, we provide data on wet, dry, and ash-free dry mass as well as content of protein and lipid in select species so that others may make comparisons to previous studies. However, we refer only to wet mass normalized rates throughout the discussion because it is the parameter of physiological significance that determines constraints on such parameters as locomotion, behavior, and predator–prey interactions. For example, *Clione* and *Thliptodon* may have similar metabolic rates expressed as per-unit dry mass, but very different ones when expressed as per-unit wet mass because *Thliptodon* is much more gelatinous and, as a result, is a very sluggish swimmer.

For *C. antarctica*, dry weights were linearly related to wet weights (Dry weight = −0.17 + 0.13 Wet Mass; \( R = 0.99 \)). In *L. helicina*, dry mass (DM) was related to wet mass (M) as \( \ln(\text{DM}) = -1.26 + 0.87\ln(M) \), ash-free dry weight is equal to 0.38\ln(wet weight) + 0.16, and wet mass (M) is related to shell diameter (D) as \( M = -0.53 + 1.91\ln(D) \ (R^2 = 0.86) \). Mean protein content was 4.0% of wet weight for *L. helicina* but only 3% of wet weight for *C. antarctica*. When corrected for the contribution of shell to wet weight (ash, ~7%), the protein content is much higher for *L. helicina* than for *C. antarctica*. Using data on chemical composition, including lipid content (5.08 and 0.5% wet weight for *C. antarctica* and *L. helicina*, respectively (Phleger et al. 1997), the relative densities of each species were determined. *Limacina helicina* is negatively buoyant (1.18 g ml\(^{-1}\)), while *C. antarctica* was nearly neutral (1.04 g ml\(^{-1}\)) relative to sea water in McMurdo Sound (1.028 g ml\(^{-1}\)).

**Discussion**

**Metabolism**

The interspecific maintenance of physiological rates across temperature gradients, popularly known as “metabolic cold adaptation,” has a long and controversial history (e.g. Addo-Bediako et al. 2002). Whereas early studies may have over-estimated the degree of temperature compensation due to problems with experimental design (Scholander et al. 1953; Wohlshlag 1960, 1964; Holeton 1974; Steffensen 2002), more recent studies point out theoretical flaws in the concept of thermal compensation of whole-organism metabolism (Clarke 1998). Specifically, metabolic rates represent the sum of numerous energetic expenditures and arbitrarily elevating cost has no selective advantage (Clarke 1993). There is an advantage, however, in increasing metabolic capacity to a level consistent with required activity levels. Routine and basal rates typically mirror active or maximum sustainable rates (Reinhold 1999; Seibel and Drazen 2007). To the extent that locomotory costs are reflected in our routine measurements of whole-animal oxygen consumption, we expected to see elevated rates in actively swimming pteropods permanently adapted to cold temperatures.

In support of this hypothesis, *C. antarctica* measured at −2.0°C have metabolic rates similar to those of *C. limacina* measured at 5°C.
Similarly, *C. antarctica* measured at 2°C have rates equivalent to those of *C. limacina* measured at 10°C (Fig. 1A and B). However, an oxygen consumption rate measured at 30°C for a single unidentified tropical clionid pteropod (Ikeda 1970) and our own measurements of oxygen consumption by *Pneumodermopsis* spp. at 24°C suggest that compensation is, at best, only partial. Assuming a \( Q_{10} \) of 2.5, the normalization constant measured here for *C. antarctica* at −2°C (2.04) predicts a rate of 22.09 \( \mu \text{mol} \text{O}_2 \text{g}^{-1}\text{h}^{-1} \) at 24°C. This value is within the range of measurements on *Pneumodermopsis*, but considerably higher than the 12.8 \( \mu \text{mol} \text{O}_2 \text{g}^{-1}\text{h}^{-1} \) measured by Ikeda (1970). These results are consistent with those of Torres and Somero (1988) who demonstrated nearly complete compensation of metabolism in Antarctic fishes relative to Californian species, but only partial compensation relative to species from the warmer Gulf of Mexico. The actual temperature coefficients measured here were considerably higher than 2.5. For our data, this may indicate that the rates measured

Fig. 4 Wing-beat frequencies in polar and temperate clionids (A) as a function of body length (L, mm) in *Clione antarctica* [open circles; 1.4L^{−0.5}; 0 ± 2°C; Borrell et al. (2005)] and *Clione limacina* (closed circles; 2.4L^{−0.62}; 10 ± 2°C) during routine swimming (in the absence of obvious external stimuli). (B) Wing-beat frequencies in *C. limacina* at 10°C are bimodal with a peak representing slow swimming using slow-twitch muscle fibers, and a second peak at higher frequencies that recruit fast-twitch muscle fibers, thereby augmenting swimming power. (C) *Clione antarctica* at 0°C swims at routine slow speeds of approximately ~1 Hz, but lacks a fast swimming gear.
for *C. antarctica* at high temperatures, and for *C. limacina* at low temperatures, could have been elevated by the stress of being at temperatures outside those occurring in their normal habitat.

**Swimming speed**

Swimming speed, as indicated by wing-beat frequencies, does not appear to be fully temperature-compensated (Fig. 4). *Clione antarctica* at 0°C swims with wing-beat frequencies similar to that predicted for *C. limacina* by extrapolating to lower temperatures (Fig. 4C). A Q_{10} of only 1.7 could account for the difference in wing-beat frequency between the two species. This is a much smaller temperature effect than we observe for oxygen consumption intraspecifically, suggesting at least partial compensation in swimming speed. Nevertheless, wing-beat frequencies are lower in the polar species, compared to temperate species, at their respective habitat temperatures and body size. This observation is in apparent conflict with our hypothesized link between locomotory activity and elevated rates of oxygen consumption in *C. antarctica*. This discrepancy may be explained, however, by fundamental constraints associated with smaller size and low temperatures that require different mechanisms for producing thrust (Borrell et al. 2005). Furthermore, a multi-gear ed swimming system in *C. limacina* appears to be absent in *C. antarctica*. *Clione limacina* spontaneously switches between distinct fast gears and slow gears during routine swimming (Fig. 4B; Satterlie and Spencer 1985). Fast swimming is supported by additional recruitment of a fast-twitch, mitochondria-poor “white” muscle equivalent, while slow swimming relies principally on mitochondria-rich, slow-twitch red muscle equivalent. A third gait, a ballistic burst escape response, can be provoked by external stimulation of the tail. In *C. antarctica*, the fast and ballistic gaits appear to have been lost (Gilmer and Lalli 1990; Borrell et al. 2005; Fig. 4A). Thus, in our observations of “routine” swimming in *C. limacina*, we have inadvertently counted wing beats during both fast and slow swimming, the latter of which may be partially supported anaerobically and not entirely taken into account by measurements of oxygen consumption. *Clione antarctica* displayed only the slower speed, believed to be entirely supported by aerobic metabolism (Dymowska et al., manuscript in preparation). The apparent loss of the capacity for fast swimming is, we believe, due to physiological constraints within the neuromuscular system (Rosenthal et al., manuscript in preparation; Dymowska et al., manuscript in preparation) but may also result from kinematic constraints associated with viscosity at low temperatures (Borrell et al. 2005).

**Temperature compensation**

As discussed by Clarke (1998), energy production by mitochondria is generally constrained at low temperatures. Whereas significant rate-compensation characterizes some enzyme systems (Somero 1995), generation of mitochondrial ATP seems to be constrained at low temperatures, perhaps due to differing effects of temperature on processes relevant for ion transport in mitochondria (Guderley 1998; Johnston et al. 1998; Pörtner et al. 1998). In order to generate higher output of power by their muscles, cold-adapted organisms must compensate with more mitochondria, increased concentration of enzymes and/or greater surface area of the cristae (Peck 2002; Pörtner 2002). Compensation may also be achieved via recruitment of greater numbers of aerobic muscle fibers, as the power output and contraction rates of each muscle fiber are much reduced and animals may not achieve their potential performance at low temperatures (Bennett 1984; Rome et al. 1984; Rome 1990).

Mitochondrial proliferation has been demonstrated in a variety of Antarctic fishes (Johnston et al. 1998). In the sluggish Antarctic fish, *Pleuragramma antarcticum*, for example, mitochondria occupy 56.3% of the volume of red muscle fibers (Johnston et al. 1998) compared to a value of 32.4% for the red muscle fibers of skipjack tuna. Wing muscles from *C. antarctica* show a dramatic proliferation of mitochondria relative to *C. limacina* (Dymowska et al., manuscript in preparation). We believe, this is the primary cause of the elevated rates of oxygen consumption we see in the whole animal and is the basis for the observed loss of the escape response in *C. antarctica* via displacement of fast-twitch muscle fibers.

**Evolutionary “arms race”**

Evolutionary escalation of predator–prey interactions is often described anthropomorphically as “arms races.” For the interaction to endure, improved capabilities in one species demands compensatory improvements in the other (Brodie and Brodie 1999). However, coevolution requires that the interaction between predator and prey be reciprocal. This is rarely the case. The “life-dinner principle” suggests that predators may not respond evolutionarily to prey adaptations because selection...
in predator–prey interactions is typically asymmetrical (Brodie and Brodie 1999). If a predator fails to capture its prey, it loses that meal (i.e., dinner) but lives to hunt another day. Although the average consequence of losing a prey may be strong enough to drive an arms race, most predators can simply switch to a more available prey species and may experience higher fitness than if they had captured the original prey. If, on the other hand, the prey fails to escape, it loses its life and all future fitness. The consequences of these interactions are clearly more severe for prey. Exceptions to this rule may exist in cases where predation on other species is not possible.

Because gymnosomes are monophagous predators feeding exclusively on thecosomes, predator and prey interactions may more closely approximate a reciprocal relationship in pteropods. Thus, in gymnosomes the evolution of mechanisms of capturing prey may respond directly to changes in the strategy of avoiding predation on the part of their thecosomatous prey. Here, we have observed a close relationship between metabolic rates and locomotory capacity in pteropod predators and their prey. For example, *Clione* spp. and *Pneumodermpsis* spp. swim continuously and engage in tactile foraging for *Limacina* spp. and *Cavolinia* spp., respectively (Lalli and Gilmer 1989). Rates of encountering prey are presumably a direct function of swimming speed. Upon encountering prey, buccal cones are everted which strive to capture and manipulate the prey shell. If this initial attempt is unsuccessful, however, the thecosome prey evade predators via active swimming (Harbison and Gilmer 1992). Not surprisingly, these animals have relatively high locomotory capacity and metabolic rates relative to other gelatinous zooplankton (Seibel and Drazen 2007). In contrast, *Clioispis krohni* and *Thliptodon* spp. are among the slowest swimming gymnosomes (Lalli and Gilmer 1989). They are much more gelatinous and, at least in the case of *Clioispis*, forage by making direct contact with a prey species’ mucous feeding web, rather than by contacting the prey itself. *Clioispis* attaches to the feeding web and is slowly pulled toward its prey as the web is reabsorbed. They feed predominantly, if not exclusively, on *Corolla* spp. a slow-moving pseudothecosome. Both *Corolla* and *Clioispis* have metabolic rates at an order of magnitude lower than those of the more active pteropods described earlier (Fig. 3; Biggs 1977). This reduction in metabolic rate is clearly accomplished, in part, by elevated water content in these obviously gelatinous species. Gel plays an important role in buoyancy (Seibel et al. 2004), allows attainment of large size with little expense, and may play a role in the provision of oxygen in some species (Thuesen et al. 2005). However, reduced locomotory demand associated with their foraging strategy renders the accumulation of gel a cost-effective strategy (Seibel et al. 2004; Webber and O’Dor 2001).

**Conclusions**

The rates reported here for some species (e.g., *C. antarctica*) are higher than for many other gelatinous zooplankton of an equivalent size at similar temperature (Seibel and Drazen 2007). Just as visual predation in the pelagic realm drives selection for the highest metabolic rates among animals (Childress 1995; Seibel et al. 1997; Seibel 2007; Seibel and Drazen 2007), active predator–prey interactions among the nonvisual pteropods is a major factor in the evolution of their own high metabolic capacity. Furthermore, the present results reveal the power of this selection in overcoming hypothesized constraints associated with body size and temperature (Gillooly et al. 2001). Over the range of organisms studied to date, temperature and body size are relatively minor determinants of metabolic rate. The ecological roles played by organisms, and the associated energetic demands, drive selection for high metabolic capacity. Relaxation of this demand among sit-and-wait predators allows them to take advantage of opportunities to save energy.

Thescosomatous pteropods are of considerable ecological importance, reaching densities of thousands of individuals per cubic meter in some regions (Pane et al. 2004). They are important components of many ecosystems with a potential for influencing phytoplankton stocks (Hopkins 1987), carbon export (Noji et al. 1997), and dimethyl sulfide (DMS) levels (Levasseur et al. 1994) that, in turn, influence global climate through ocean-atmosphere feedback loops. They are prey to a variety of important predators besides gymnosomes, such as fishes, cephalopods, and mammals among others (Lalli and Gilmer 1989). As such, they are useful indicators of ecosystem health in some regions (Seibel and Dierssen 2003). Owing to rising atmospheric CO$_2$ concentrations and the acidification of ocean surface waters, the level of calcium carbonate (CaCO$_3$) in seawater is decreasing. Surface waters of some regions (e.g., the Southern Ocean) will become undersaturated within the next 50–100 years (Orr et al. 2005). Thescosome shells are made of aragonite, a type of CaCO$_3$ that is highly soluble, which suggests that these organisms may
be particularly sensitive to increasing CO₂ and reduced concentrations of carbonate ion. Thecosome pteropods are the main planktonic producers of aragonite in the world’s oceans. Within parts of their present-day geographic ranges, they will be the first major group of calcifying organisms to be adversely affected by undersaturation of CaCO₃ as a result of anthropogenic increases in CO₂ (Seibel and Fabry 2003; Drake et al. 2005; Orr et al. 2005). Because of the strict relationship between thecosomes and gymnosomes, the predator will also be susceptible. Despite this anthropogenic threat and the ecological importance of pteropods, our understanding of their life cycles, distributions, and general biology remains speculative (Kobayashi 1974; Gannefors et al. 2005). A major and immediate change in carbon dioxide emissions may be required to save the sea angels.

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