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Is post-feeding thermotaxis advantageous in elasmobranch fishes?

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The effects of post-feeding thermotaxis on ileum evacuation and absorption rates were examined in the laboratory using two elasmobranch species, the Atlantic stingray *Dasyatis sabina*, which inhabits thermally variable environments, and the whitespotted bamboo shark *Chiloscyllium plagiosum*, a stenothermic fish living on Indo-Pacific reefs. Experiments at temperatures similar to those experienced in nature revealed temperature change had no significant effect on *C. plagiosum* absorption or evacuation rates, suggesting stenothermic sharks cannot exploit temperature differences as a means to improve digestion efficiency. On the other hand, *D. sabina* showed significantly lower evacuation and absorption rates at lower temperatures. The relative decrease was greater for evacuation ($Q_{10} = 3.08$) than absorption rates ($Q_{10} = 2.20$), resulting in a significant increase in total absorption, suggesting *D. sabina* can benefit from using shuttling behaviour to exploit thermal variability in their environment to maximize energetic uptake.

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INTRODUCTION

Many elasmobranch species exhibit complex movement patterns over the course of their life history. The reasons for such behaviour probably vary among taxa and may be influenced by seasonal or diel fluctuations in environmental conditions and biotic resources (Nelson *et al.*, 1997; Sims *et al.*, 2001; Bonfil *et al.*, 2005; Rowat & Gore, 2007). Perhaps the most influential abiotic factor affecting elasmobranch movements is temperature (Matern *et al.*, 2000; Vaudo & Lowe, 2006; Wallman & Bennett, 2006). As ideal poikilotherms, most elasmobranchs lack the ability to maintain body temperature independent of ambient water. Considering most biological processes are temperature dependent (Magnuson *et al.*, 1979; Magnuson & Destasio, 1997), it is perhaps not surprising to find some elasmobranchs exploit habitat thermal variability to optimize physiological efficiency by shuttling between temperatures (Fry, 1947; Hight & Lowe, 2007), a process referred to as thermotaxis. Thermotactic behaviour has been clearly observed in several laboratory studies with

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elasmobranchs (Crawshaw & Hammel, 1973; Casterlin & Reynolds, 1979; Wallman & Bennett, 2006) and is strongly suspected in some free-ranging elasmobranch populations (Matern *et al.*, 2000; Sims *et al.*, 2006). These studies suggest that shuttling between temperatures can enhance feeding and digestion (Matern *et al.*, 2000; Sims *et al.*, 2005; Wallman & Bennett, 2006), reproduction (Harris, 1952; Economakis & Lobel, 1998; Wallman & Bennett, 2006; Hight & Lowe, 2007), swimming and muscle performance (Donley *et al.*, 2007), and nerve integration (Gordon, 2005). Although previous studies provide valuable insight into elasmobranch movement patterns, the conclusions that fishes benefit from the activity are based on evidence that is more correlative than direct.

Although many biological processes are probably influenced by thermal variability in the environment, it is the potential benefit of temperature change on feeding and digestion that has garnered the most attention. Laboratory studies with fishes clearly demonstrate changes in temperature have potential to alter nutrient diffusion and absorption rates (Ytrestøyl *et al.*, 2005) as well as evacuation rates (Wetherbee *et al.*, 1987). Several field studies and at least one laboratory study have investigated the possibility that elasmobranchs might exploit thermal heterogeneity in their environment to improve digestive efficiency. Field observations by Sims *et al.* (2006), for example, concluded that male lesser-spotted dogfish *Scyliorhinus canicula* (L.) adopt a 'hunt warm and rest cool' strategy by making diel vertical migrations in thermally stratified waters. Frequent vertical movements between cooler deep waters and warmer surface layers have also been observed in large pelagic fishes (Carey & Robinson, 1981; West & Stevens, 2001). Telemetry studies on bat ray *Myliobatis californica* Gill movement patterns (Matern *et al.*, 2000) and oxygen consumption measurements (Hopkins & Cech, 1994) suggest that these fish may experience digestive benefits by taking advantage of temperature gradients in Tomales Bay, California. In the only other batoid study, Wallman & Bennett (2006) were the first to empirically show that Atlantic stingray *Dasyatis sabina* (Lesueur) placed into a thermal gradient preferred warmer temperatures when fasted, but moved to cooler water once sated. Presumably feeding at relatively warm temperatures and resting in cool waters lower energy costs related to digestive processes and extend the time food is in contact with absorptive surfaces (Hopkins & Cech, 1994; Wallman & Bennett, 2006). In spite of the growing body of anecdotal evidence suggesting elasmobranchs may exploit temperature gradients to improve digestive efficiency, the mechanism and, therefore, possible benefits of post-feeding thermotaxis still remain open to question.

In poikilothermic animals, metabolic rates exhibit a stoichiometric relationship in which every 10° C increase in ambient temperature generally doubles the rate of biological functions (Cameron, 1989; Schmidt-Nielsen, 1997). This relationship is so consistent among poikilothermic organisms that it is referred to as van't Hoff's rule and can be mathematically expressed as the temperature quotient or Q_{10} . The temperature quotient is an index of temperature sensitivity for a given physiological rate. Unfortunately, in most field studies temperature cannot be controlled, leaving unanswered the question of how and to what degree thermal shuttling affects digestive rate processes. The thermotaxis hypothesis predicts for fishes to benefit from diel migrations they must first have access to thermal variability in their environment, and second, complementary digestive processes must differ in their response to changing temperature (Brett, 1971; Wallman & Bennett, 2006). For elasmobranchs that 'feed warm and rest cool' to recognize thermotaxic benefits, Q_{10} values must be

high for evacuation rates relative to absorption. Stated another way, as temperatures cool, evacuation rates must decrease faster (*i.e.* be more sensitive to temperature) than rates of absorption.

In the present study, the potential of thermotaxic behaviour to improve digestive efficiency was tested in two elasmobranch species found in dissimilar thermal environments, *D. sabina* and the whitespotted bamboo shark *Chiloscyllium plagiosum* [Anonymous (Bennett)], by quantifying Q_{10} values for ileum (spiral intestine) evacuation and absorption rates across a range of temperatures each experiences in its natural environment. *Dasyatis sabina* are ideal candidates for this study because they are found in thermally variable habitats, where water temperature may fluctuate from *c.* 3 to $>35^{\circ}$ C seasonally (Fangue & Bennett, 2003), and are known to exhibit feeding-related changes in temperature preference (Wallman & Bennett, 2006). In nature, these fish move freely over relatively long distances, where they experience rapid changes in depth and temperature (Teaf, 1980; Fangue & Bennett, 2003). On the other hand, *C. plagiosum* is a demersal stenothermic species inhabiting shallow coastal areas and coral reefs in the Indo-Pacific Ocean. Unlike *D. sabina*, *C. plagiosum* experience little seasonal or diel temperature fluctuation (Tullis & Ballie, 2005), with a minimum winter temperature of 18° C and a maximum summer temperature of 28° C (Chen *et al.*, 2008), and spend much of their time concealed in coral formations and crevasses from which they make relatively limited foraging excursions (Compagno, 2001). Testing species from dissimilar thermal habitats will provide a better understanding of the type and range of digestive adaptations seen in elasmobranchs. Data from this study are the first to quantify the effects of acute temperature change on evacuation and absorption rates in elasmobranchs, and thereby directly test the possible benefits of post-feeding thermotaxic behaviour in these species.

MATERIALS AND METHODS

CAPTURE AND HOLDING CONDITIONS OF EXPERIMENTAL ANIMALS

Dasyatis sabina ($n = 15$) were netted or trawled from shallow, near shore waters between Mobile County, Alabama ($30^{\circ} 41' N$; $88^{\circ} 2' W$) and Gulf County, Florida, in the north-west Gulf of Mexico ($29^{\circ} 48' N$; $85^{\circ} 20' W$). Fish were transported to the University of West Florida Marine Research Facility in a 950 l Rubbermaid (www.rubbermaid.com) polypropylene transport container filled with clean sea water treated with Amquel water conditioner (www.novalek.com) and continuously aerated by a Model 1200 Rule submersible pump (www.itflowcontrol.com/marine-and-rv/bilge). *Chiloscyllium plagiosum* ($n = 9$) were donated by SeaWorld, Orlando, Florida. Once at the Marine Research Facility, the fishes were transferred into separate biologically filtered 2000 l re-circulating tanks maintained at a salinity of 35 and a 12L:12D photoperiod. Fishes acclimated to a cyclic temperature prevented them from acclimating to a single temperature and they produce responses closer to those of seasonally acclimatized fish in nature (Hazel & Prosser, 1974; Carlson & Parsons, 1999; Neer *et al.*, 2006). The *D. sabina* holding tank was kept under a daily fluctuating temperature regime of 24 – 27° C simulating summer temperatures cycles common to bays in north-west Florida (Fangue & Bennett, 2003), whereas *C. plagiosum* were maintained at a 23 – 25° C daily cycle simulating temperature fluctuations in their natural habitat (Tullis & Peterson, 2000; Tullis & Baillie, 2005). Water temperatures in holding tanks were recorded at 30 min intervals *via* Onset StowAway XTI temperature loggers (www.onsetcomp.com) housed in waterproof cases. Water quality measurements including ammonia, pH, nitrite and nitrate levels were determined three times a week with 30% water changes made bimonthly or more

frequently if indicated by water quality measurements. During the acclimation period fishes were fed, every other day, a mixed diet of fresh-frozen shrimp (mainly *Litopenaeus setiferus*), fishes or squid until sated. All fishes were held for a minimum of 2 weeks before being used in experimental trials.

TEMPERATURE TREATMENTS

Prior to each trial, fishes were fasted for 96 h to ensure that the gut was clear (Wetherbee *et al.*, 1987). In all trials *D. sabina* and *C. plagiosum* were fed when temperatures in the holding tanks reached 26 and 24°C respectively, and immediately transferred to one of the three temperature treatments (21, 26 or 31°C for *D. sabina* and 20, 24 or 28°C for *C. plagiosum*). This protocol was used for all experimental trials. The acute change to high or low cycle temperatures was used to simulate temperature changes that fishes may experience by shuttling between different temperatures in nature (Carey & Robinson, 1981; Carey & Scharold, 1990). Each fish was exposed to a low, mid and high temperature for each digestive measurement, but was returned to holding conditions for a minimum of 10 days between trials.

ILEUM EVACUATION RATE DETERMINATIONS

Prior to the beginning of experimental trials, total ileum length (cm) was measured for each fish as the distance between the pyloric sphincter and the rectum using X-radiography. Total gut passage time as well as the time food was in contact with the ileum was estimated through sequential X-radiographs showing food position in the gut over time. At each experimental temperature, the ileum evacuation rate, as the distance travelled by the food across the ileum per hour (cm h^{-1}), was calculated to determine temperature quotient values.

Following the fasting period, fishes were offered de-shelled and de-veined *L. setiferus* containing a 0.5 mm diameter stainless steel ball. Meal size has been shown to affect digestion and evacuation rates (Fänge & Grove, 1979; Wetherbee & Gruber, 1990), but spurious errors are avoided by furnishing a quantity of food equivalent to 3% of fish body mass (Cortés & Gruber, 1992). Tongs were used to present the food so that fish would swallow the shrimp whole (Wetherbee *et al.*, 1987). Food intake was voluntary for all fishes in this study as force-feeding has been shown to influence evacuation rate and absorption efficiency (Wetherbee *et al.*, 1987). After being fed, each fish was placed in a Plexiglas X-ray chamber. To reduce handling stress, the fish remained in the chamber over the entire evacuation period. The X-ray chamber was housed in a model 43855A Hewlett-Packard Faxitron X-ray machine (www.hp.com). A dark cloth, across the front of the X-ray machine, reduced the potential disturbance to the fish. Water was continuously pumped between the X-ray tank and a 300 l biologically filtered reservoir to maintain good water quality and an EBO Jager 250-W submersible heater (www.eheim.com), placed in the reservoir, held water temperatures at the appropriate set point ($\pm 0.5^\circ\text{C}$). Each fish was then X-rayed a minimum of every 3 h (Wetherbee *et al.*, 1987) and more frequently as food entered the ileum. Dorsal images were made at 70 kV for 4 s on a Kodak Industrex MX125 Ready Pack II film (www.kodak.com).

ILEUM ABSORPTION TRIALS

Food absorption was determined by calculating the ratio of absorbed food to unabsorbable marker. Although a wide array of methods and markers have been used (Kotb & Luckey, 1972; Lied *et al.*, 1982; De Silva & Anderson, 1995), methods using chromic oxide (Cr_2O_3) have become the standard in digestion studies (NRC, 1993). The use of an inert marker is particularly important as it allows quantification of organic matter absorption with just a subsample of total faeces (Maynard & Loosli, 1969). Feeding regimens were similar to those of evacuation rate trials, but with the addition of chromic oxide (1% of total dry food mass; NRC, 1993) instead of the stainless steel ball. Fishes were then moved to individual 270 l faecal collection tanks and held at the appropriate constant temperature until evacuation was complete. Faeces were collected with a 1 mm mesh screen and analysed for unabsorbed food (dry mass) and chromic oxide. Collections were made at least every 2 h to minimize leaching

in the water (Sudaryono *et al.*, 1996; Weatherup & McCracken, 1998). Apparent digestibility coefficient (C_{AD}), digested to undigested matter ratio (Robbins, 1983), was estimated for each absorption trial using the equation suggested by Maynard & Loosli (1969): $C_{AD} = 100 [1 - (X_1 X_2^{-1})]$, where X_1 = per cent chromic oxide in the feed and X_2 = per cent chromic oxide in the faeces. C_{AD} represents the percentage of food absorbed by the fish.

Faecal samples were analysed for chromic oxide content using the technique described by Suzuki & Early (1991) and later modified by Lares (1999). Briefly, faeces were carefully washed with distilled water to eliminate salt and placed into a drying oven at 60° C for 72 h. Dried samples were then transferred to pre-weighed, borosilicate test tubes (16 mm × 100 mm) and weighed (mg). Test tubes and samples were heated for 5 h at 400° C in a muffle furnace (Lares, 1999). The difference between dry samples and ash masses was used to estimate the amount of organic matter (Suzuki & Early, 1991). Ashed samples were then prepared for spectrophotometric analysis (Sales & Britz, 2001; Laining *et al.*, 2003) by adding 2 ml of bleach (5.25% sodium hypochlorite) for each 10 mg of ash sample. Test tubes were maintained in an aluminium heating block at constant 110° C. After the bleach had evaporated, an additional 2 ml of bleach was added and allowed to evaporate (Lares, 1999). Samples were successively treated in the same way with hydrochloric acid to eliminate excessive hypochlorite. Once the samples were dry, 2 ml of distilled water was added and tubes centrifuged at 1250g for 10 min. Absorption readings from the solution were then compared with a potassium dichromate standard solution.

EVACUATION AND ABSORPTION Q_{10} DETERMINATIONS

Apparent digestibility coefficients and ileum evacuation rates at the three temperatures were used to quantify absorption rate as milligram food absorbed per hour. Temperature quotients were estimated for ileum evacuation and absorption rates to assess the effect of temperature on these physiological processes. In both species, Q_{10} values for each physiological process were estimated between high to mid, low to mid and low to high temperatures. Temperature quotients were calculated using mean rates from fishes in treatment groups. The population temperature quotient was determined using the following equation (Schmidt-Nielsen, 1997): $Q_{10} = (K_2 K_1^{-1})^{10(t_2-t_1)^{-1}}$, where K_1 is the mean rate at lower temperature, K_2 is the mean rate at higher temperature, t_1 is the lower temperature and t_2 is the higher temperature.

STATISTICAL ANALYSIS

All experimental values were reported as mean ± s.e. Data were tested for normality and non-normal data were rank transformed. The effect of temperature on C_{AD} , absorption and ileum evacuation rates was explored using repeated measures two-way ANOVA. Where appropriate, a Tukey–Kramer multiple comparison test was used to identify statistical differences in mean values between treatment groups. All statistical comparisons were based on $\alpha = 0.05$. All analyses were performed in SAS System, Version 9 (www.sas.com).

RESULTS

SIZE RELATIONSHIPS AND BEHAVIOUR OF FISHES IN DIGESTION TRIALS

Dasyatis sabina had a disk width of 24.4 ± 0.8 cm and a wet mass of 0.567 ± 0.060 kg. Pre-caudal lengths ranged from 17.5 to 31.6 cm (24.9 ± 0.8 cm). *Chilosyllium plagiosum* had pre-caudal length and wet mass values of 63.2 ± 0.5 cm and 0.586 ± 0.013 kg.

The fishes did not discriminate between untreated food and food treated with experimental markers (chromic oxide or a stainless steel ball) and promptly ingested

TABLE I. Thermal sensitivity (Q_{10}) for ileum evacuation and absorption rates calculated across three temperature ranges for *Dasyatis sabina* and *Chiloscyllium plagiosum*

| Temperature range ($^{\circ}$ C) | Ileum evacuation rate Q_{10} | Absorption rate Q_{10} |
|-----------------------------------|--------------------------------|--------------------------|
| | <i>D. sabina</i> $n = 15$ | |
| 31–21 | 3.08 | 2.20 |
| 31–26 | 3.07 | 2.33 |
| 26–21 | 3.09 | 2.07 |
| | <i>C. plagiosum</i> $n = 9$ | |
| 28–20 | 1.65 | 1.50 |
| 28–24 | 1.44 | 1.34 |
| 24–20 | 1.88 | 1.68 |

both when offered. Post-feeding, fishes remained in the experimental tank for between 1 and 4 days, depending on the temperature treatment. While in their respective experimental tanks, fishes showed no obvious signs of stress and were observed to remain quiescent on the tank bottom, with occasional movements to change position.

DIGESTION EXPERIMENTS

The effect of temperature on evacuation rate varied markedly between *D. sabina* and *C. plagiosum* (Table I). Rates of food movement through the gut were easily estimated for both species by observing the position of the stainless steel ball on sequential X-radiographs. The steel ball was egested with faecal matter at the end of each trial, signifying that the pellet passed through the gut at rates similar to that of food. Ileum evacuation rates in *D. sabina* decreased significantly with decreasing temperature (two-way ANOVA, $F_{2,28} = 31.48$, $P < 0.001$; Fig. 1). Mean evacuation rates at all three treatment temperatures were statistically distinct (Tukey–Kramer multiple comparison test, $\alpha = 0.05$). Conversely, evacuation rates in *C. plagiosum* showed no significant differences between temperature treatments (two-way ANOVA, $F_{2,16} = 0.96$, $P > 0.05$; Fig. 1).

Total evacuation times (h) also showed a different response to temperature in *D. sabina* and *C. plagiosum*. Total evacuation time in the former decreased from 77.0 ± 7.2 h at 21° C to 30.9 ± 4.3 h at 31° C. Total evacuation time in the latter, however, ranged from 85.8 ± 9.7 h at 20° C to 81.0 ± 16.7 h at 28° C.

The relationship between temperature and apparent digestibility and food absorption rate also differed between *D. sabina* and *C. plagiosum* (Table I). C_{AD} in *D. sabina* decreased from nearly 90% at 21° C to 60% for fish moved to 31° C (Fig. 2). The differences in coefficient means were significant (two-way ANOVA, $F_{2,28} = 15.03$, $P < 0.001$) and statistically distinct (Tukey–Kramer multiple comparison test, $\alpha = 0.05$) for each of the three temperatures tested. Absorption rates in *D. sabina* showed the opposite trend (Fig. 1), with absorption values increasing significantly as temperatures increased (two-way ANOVA, $F_{2,28} = 15.68$, $P < 0.001$). Mean values at each temperature treatment were also significantly different from one another (Tukey–Kramer multiple comparison test, $\alpha = 0.05$). *Chiloscyllium plagiosum*, on the other hand, showed no significant changes across temperature treatments

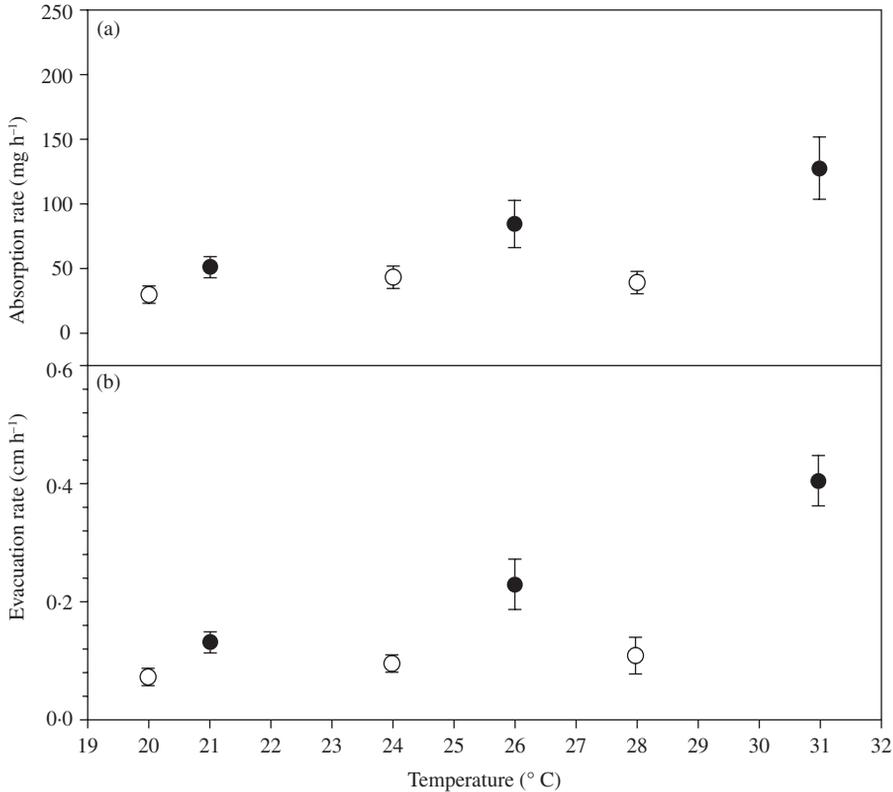


FIG. 1. Mean \pm S.E. (a) absorption rate and (b) evacuation rate for *Dasyatis sabina* (●) and *Chiloscylidium plagiosum* (○) at three temperature treatments. *Dasyatis sabina* absorption and evacuation rate values differed significantly at all three treatment temperatures, whereas values for *C. plagiosum* were statistically indistinguishable (two-way ANOVA followed by Tukey–Kramer multiple comparison test, $\alpha = 0.05$).

in either mean C_{AD} (two-way ANOVA, $F_{2,16} = 0.14$, $P > 0.05$; Fig. 2) or absorption rate (two-way ANOVA, $F_{2,16} = 1.05$, $P > 0.05$; Fig. 1).

Assessment of evacuation and absorption temperature quotients found that the digestive process in *D. sabina* showed varying degrees of thermal sensitivity, while the processes in *C. plagiosum* were largely unaffected by changing temperatures (Table I). *Dasyatis sabina* showed higher Q_{10} values for evacuation than absorption rates; however, Q_{10} values between temperature treatments remained relatively constant. *Chiloscylidium plagiosum* exhibited similar Q_{10} estimates for both evacuation and absorption rates, with minimal change between temperature treatments.

DISCUSSION

This represents, as far as is known, the first study to empirically demonstrate that post-feeding thermotaxis can improve digestive uptake in an elasmobranch. In fact, digestion efficiency studies on elasmobranchs are scarce and differ by methodology,

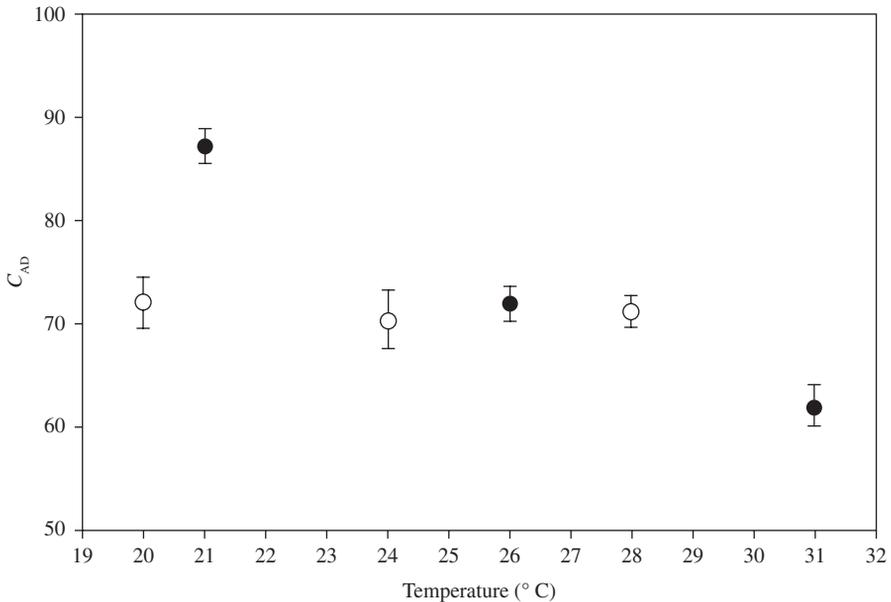


FIG. 2. Mean \pm s.e. apparent digestibility coefficient (C_{AD}) for *Dasyatis sabina* (●) and *Chiloscyllium plagiosum* (○) at three temperature treatments. *Dasyatis sabina* C_{AD} values were significantly different at all three treatment temperatures, whereas values for *C. plagiosum* were statistically indistinguishable (two-way ANOVA followed by Tukey–Kramer multiple comparison test, $\alpha = 0.05$).

experimental objectives and species tested, making it difficult to draw any meaningful conclusions on the effects of thermotaxis on physiological processes. Indeed, most studies assess gastric evacuation rates; however, gastric evacuation rates provide little insight into nutrient absorption and assimilation. To date, evacuation and absorption data are known only for the lemon shark *Negaprion brevirostris* (Poey). Wetherbee *et al.* (1987) and Wetherbee & Gruber (1990, 1993) estimated total evacuation times between 90.3 and 93.5 h and C_{AD} values between 68.9 and 73.2% in young *N. brevirostris* fed between 2.6 and 3.4% of their body mass at 25° C. *Dasyatis sabina* fed at 26° C and *C. plagiosum* fed at 24° C had C_{AD} values of *c.* 70%, very similar to the *N. brevirostris* values. Total evacuation times, however, were *c.* 20% shorter in *C. plagiosum* (74 h at 24° C) and nearly 40% lower in *D. sabina* (57.3 h at 26° C) than evacuation times estimated in *N. brevirostris*.

Wallman & Bennett (2006) suggested that, for thermotaxis to be useful, absorption rate Q_{10} values should be relatively higher than evacuation rate Q_{10} responses. In *D. sabina*, however, evacuation rate ($Q_{10} = 3.08$) was more sensitive to temperature than absorption rate ($Q_{10} = 2.20$). *Dasyatis sabina* moving from 31 to 21° C after feeding experienced an increase in overall food absorption of *c.* 30%. Although absorption per hour decreased with temperature, the much slower evacuation rate allowed the food to remain in contact with the ileum longer, resulting in an overall increase in absorption. *Chiloscyllium plagiosum* exhibited no significant improvement in digestion efficiency between temperatures, as absorption and evacuation rate showed similar changes in responses to decreasing temperature (evacuation rate: $Q_{10} = 1.65$; absorption rate: $Q_{10} = 1.50$). These results are not unusual

in fishes as several studies observed relatively insensitive absorption efficiencies over a wide range of temperatures (Windell *et al.*, 1978; Targett, 1979; Stevens & McLeese, 1984).

Generally, fishes are adapted to the thermal environment they experience, leading to specific ecological responses to temperature (Johnson & Kelsch, 1998). *Chiloscyllium plagiosum* may have never acquired the ability to exploit temperature gradients to improve digestive efficiency. These fish live in an environment lacking diel thermal fluctuations, always very close to the middle range of 24–26° C (Chen *et al.*, 2008). It is perhaps not surprising, therefore, that *C. plagiosum* do not exhibit thermotaxis or a significant digestive advantage when experimentally moved between temperatures after feeding. Many stenotherms maintain a metabolic set point over a defined range of temperatures, sometimes referred to as physiological plasticity (Hochachka & Somero, 2002). This strategy is thought to be most beneficial to strict stenothermic fishes, which secure optimal physiological efficiency at their preferred temperature, than to eurythermic fishes that forage in fluctuating thermal environment (Dent & Lutterschmidt, 2003).

Previous field studies have probably observed thermotaxis occurring in nature, but the effect of temperature could not be unequivocally separated from other environmental attributes such as prey availability or predator avoidance. *Myliobatis californica* (Matern *et al.*, 2000), *N. brevirostris* (DiGirolamo, 2008) and *S. canicula* (Sims *et al.*, 2006) are all believed to exploit temperature changes in their environment to improve digestive efficiency. The origin of this behaviour may very well be linked to, or at least influenced by, environmental factors other than temperature. In nature, when extreme differences in food availability exist, fishes may temporarily move into unfavourable thermal microhabitats in order to exploit productive feeding sites. In fact, it is not rare to observe fishes entering almost lethally warm temperatures to obtain food that was not abundant at their preferred temperature (Neill & Magnuson, 1974; Wildhaber & Crowder, 1990). Fishes may even gain some performance advantages by moving to these warmer waters. For example, field studies on *M. californica* and *S. canicula* (Matern *et al.*, 2000; Sims *et al.*, 2006) have suggested that elasmobranchs can increase metabolism and thereby maximize foraging efficiency by entering higher temperatures just prior to dusk when prey are most active. *Dasyatis sabina* may experience similar foraging benefits in metabolically expensive environments, but would ultimately lower metabolic rates by returning to cooler, preferred temperatures after feeding. In the face of these two competing selective pressures, it may be reasonable to suppose that fishes have modified both foraging and digestive physiology to optimize efficiency.

Interestingly, some bony fishes also exhibit a 'hunt warm–rest cool' strategy. Clark & Green (1990) observed juvenile cod *Gadus morhua* L. undertaking diel vertical migrations during summer when the thermocline allowed them to feed in warm shallow water and return to deeper cold water during non-feeding hours. When the thermocline disappeared, no vertical migrations were recorded, leaving the behavioural thermoregulation hypothesis a plausible explanation for shuttling behaviour. Not all bony fishes follow this same pattern. Wurtsbaugh & Neverman (1988) challenged the 'hunt warm–rest cool' hypothesis with their work on larval lake sculpins *Cottus extensus* Bailey & Bond in which they report that larval fish feed in cold lower strata and swim up in the warm water column to digest. Additional laboratory experiments indicate feeding in cold water could lower energetic

costs related to hunting and larval *C. extensus* that experience fluctuating temperature regimes grow at higher rates by feeding more frequently than larval fish kept in stable environments.

The respective strategies of 'hunt warm–rest cool' and 'hunt cool–rest warm' would give a metabolic advantage to fishes by either slowing down digestion and increasing overall absorption or by taking advantage of a faster evacuation time to forage more frequently. For elasmobranchs that are intermittent feeders (Wetherbee & Cortés, 2004), enhancing the efficiency of food uptake would be of greater benefit than foraging more frequently, especially if the cost of obtaining prey is high. It is possible, however, that elasmobranchs in need of feeding more frequently would benefit from a 'hunt cool–rest warm' strategy. Regardless of the reason, movements between temperatures could result in changes in physiological rate functions. Ironically, *D. sabina* may exploit thermotaxis to reduce their temperature dependence (Beitinger & Fitzpatrick, 1979) by reconciling effective feeding in metabolically demanding water temperatures with exceptional absorption efficiency at cooler temperatures as part of a successful foraging strategy. Overall, with respect to temperature, elasmobranchs seem to be more than just 'die Spielbälle der Umgebung' or the puppets of the environment (Krehl & Soetbeer, 1899), but rather manifest sophisticated behavioural and physiological adaptations to exploit specific thermal conditions.

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