The relationship between heat flow and vasculature in the dorsal fin of wild bottlenose dolphins *Tursiops truncatus*

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Summary

The dorsal fin of the bottlenose dolphin *Tursiops truncatus* contains blood vessels that function either to conserve or to dissipate body heat. Prior studies have demonstrated that heat flux, measured from a single position on the dorsal fin, decreases during body cooling and diving bradycardia and increases after exercise and at the termination of the dive response. While prior studies attributed changes in heat flux to changes in the pattern of blood flow, none directly investigated the influence of vascular structures on heat flux across the dorsal fin. In this study we examined whether heat flux is higher directly over a superficial vein, compared to a position away from a vein, and investigated the temporal relationship between heart rate, respiration and heat flux. Simultaneous records of heat flux and skin temperature at three positions on the dorsal fins of 19 wild bottlenose dolphins (with the fin in air and submerged) were collected, together with heart rate and respiration. When the fin was submerged, heat flux values were highest over superficial veins, usually at the distal tip, suggesting convective delivery of heat, *via* blood, to the skin's surface. Conversely, in air there was no relationship between heat flux and superficial vasculature. The mean difference in heat flux ($48\,\mathrm{W\,m^{-2}}$) measured between the three fin positions was often equal to or greater than the heat flux that had been recorded from a single position after exercising and diving in prior studies. Tachycardia at a respiratory event was not temporally related to an increase in heat flux across the dorsal fin. This study suggests that the dorsal fin is a spatially heterogeneous thermal surface and that patterns of heat flux are strongly influenced by underlying vasculature.

Key words: heat flux, vasculature, dorsal fin, bottlenose dolphin, *Tursiops truncatus,* thermoregulation, heart rate, respiration, temperature.

Introduction

Cetaceans, as aquatic endotherms, maintain a constant core temperature in an environment that conducts heat away from the body at a rate at least 25 times faster than air at the same temperature (Schmidt-Nielsen, 1997). Conductive heat loss, H', from a body to the ambient environment can be expressed as:

$$H' = A_{\mathrm{S}}C(T_{\mathrm{b}}-T_{\mathrm{a}}), \qquad (1)$$

where A_{S} is the surface area across which heat is lost to the environment, C is the body's thermal conductance, T_{b} is body temperature and T_{a} is the ambient temperature (for a review, see Pabst et al., 1999). Several adaptations enable cetaceans to minimize heat loss. In general, they have reduced surface area to volume ratios when compared to terrestrial mammals of similar size, and they maintain an insulating blubber layer that decreases their thermal conductance (Worthy and Edwards, 1990; Pabst et al., 1999). They also conserve heat using specialized vascular structures called countercurrent heat exchangers in their uninsulated appendages, the dorsal fin, pectoral flippers and flukes (Scholander and Schevill, 1955; Elsner et al., 1974). In each appendage, major arteries are located centrally within trabeculate, venous channels, called peri-arterial venous retia. Warm arterial blood flows past cooled venous blood returning from the periphery. The resulting temperature gradient between the two blood supplies allows the arterial blood to transfer its heat to the returning venous blood and, thus, conserves body heat (Fig. 1) (Scholander and Schevill, 1955).

To dissipate excess body heat, cetaceans bypass their thermal insulation and countercurrent heat exchangers. Under
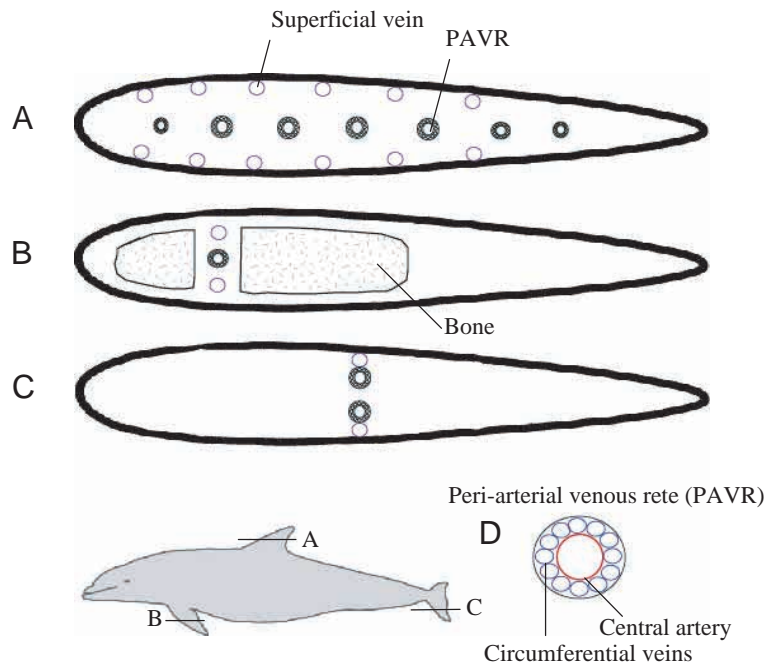
Fig. 1. Schematic representations of countercurrent heat exchangers in the appendages of a bottlenose dolphin. Cross-sections through (A) the dorsal fin, (B) the pectoral flipper and (C) the flukes. Inset below shows the positions of the cross-sections. Deep venous channels form peri-arterial venous retia (PAVR) surrounding central arteries (D). Superficial veins lie deep to the epidermis (thick black line) (modified from Pabst et al., 1999).

these circumstances, heat is transferred from the core by blood flow, through the blubber and to the skin's surface (Kvadsheim and Folkow, 1997). Cetaceans also bypass the venous return of the peri-arterial venous retia and return blood through superficial veins (Fig. 1) (Scholander and Schevill, 1955). In the dorsal fin and flukes, blood returning through the superficial veins functions to cool the reproductive tract (Rommel et al., 1994; Pabst et al., 1995). Thus, the blubber and the appendages function as dynamic thermal surfaces, allowing a cetacean either to conserve or to dissipate body heat, depending on its thermal requirements.

Several studies have examined the conditions under which cetaceans conserve or dissipate heat. These studies have reported heat losses as heat flux, a rate of energy transfer per unit area. McGinnis et al. (1972) found that a spinner dolphin (*Stenella longirostris hawaiiensis*) decreased heat flux across the dorsal fin as it was cooled in a water bath. Hampton et al. (1971) and Noren et al. (1999) found that bottlenose dolphins (*Tursiops truncatus*) more than doubled heat flux from their thermal windows (the pectoral flipper and dorsal fin) after exercise. A bottlenose dolphin, actively conserving body heat during cooling in a water bath, showed a decline in heat flow from the proximal to distal tip of each appendage, while a spinner dolphin actively dissipating body heat displayed heat flux values highest at the distal tip of the appendages (Hampton et al., 1971, 1976). These gradients in heat flow may be explained by the vascular anatomy of the appendage.

Scholander and Schevill (1955) suggest that the countercurrent heat exchange system would result in a steep proximal-to-distal temperature drop from the body into the appendage. Conversely, bypassing the countercurrent heat exchangers to dissipate excess body heat would result in the opposite temperature gradient as warm core blood reaches the distal periphery and is cooled as it returns along the surface of the appendage.

Noren et al. (1999) and Williams et al. (1999) have demonstrated that changes in respiration and heart rate also affect heat flow across the thermal windows. Marine mammals display sinus arrhythmia, a cycling of heart rate, which increases (tachycardia) during inspiration and decreases (bradycardia) during the interbreath interval (for a review, see Elsner, 1999). This sinus arrhythmia is most pronounced during diving (e.g. Elsner et al., 1966). Heat flux measurements across the dorsal fins of diving bottlenose dolphins were lower than values measured at the surface (Noren et al., 1999; Williams et al., 1999). The decrease in heat flux at depth was attributed to a suite of physiological responses that occur during diving, including bradycardia, decreased cardiac output and widespread peripheral vasoconstriction. In contrast, tachycardia experienced during ventilation events was associated with an increase in heat flux across the dorsal fin, suggesting an increase in blood flow resulting from peripheral vasodilation (Williams et al., 1999).

These studies have demonstrated that changes in heat flux across the thermal windows of dolphins are associated with changes in the pattern of blood flow. No study to date, however, has directly assessed the influence of the underlying vasculature on heat flux. Prior studies have measured heat flux at single, or in a few cases multiple, sites on the dorsal fin. None have noted underlying vascular structures in relation to their sites of measurement nor taken measurements at multiple sites simultaneously. Infrared thermal imaging suggests that the pattern of surface temperatures across the dorsal fin is influenced by the underlying vasculature (Fig. 2) (Pabst et al., 2002). Because blood flow is the force driving heat flux across the appendages, heat flux should vary across the fin depending upon the location from which it is measured, i.e. whether directly over or away from superficial veins.

Thus, the primary goal of this study was to investigate the role of vascular structures on heat flow by simultaneously and continuously measuring heat flux and skin temperature at three positions on the dorsal fins of bottlenose dolphins. These positions were chosen both to compare with prior studies and to assess the influence of underlying venous structures on heat flow across the height of the fin. Experiments were conducted in early summer in Sarasota Bay, FL, USA, a warm water environment; thus the predictions were that (1) heat flux would be higher when measured directly over a superficial vein and (2) heat flux would be highest at the distal tip of the fin. The second goal was to investigate the role of respiratory arrhythmia
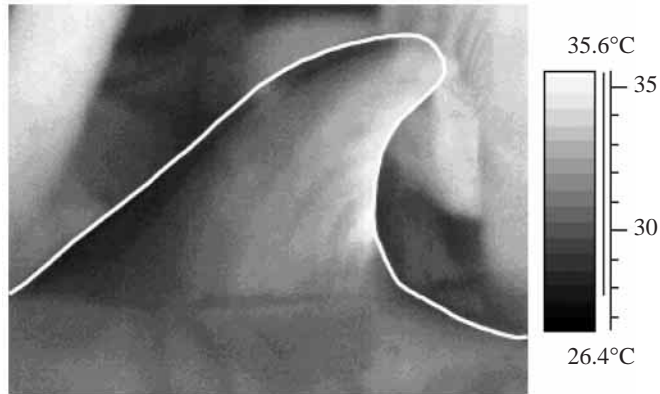
Fig. 2. Infrared thermal image of a bottlenose dolphin dorsal fin in Sarasota, FL, USA (FLIR systems AGEMA 570 IR Camera, Secaucus, NJ, USA). The white line has been added to outline the contour of the dorsal fin. Superficial veins are visible as the lighter (warmer) lines running from the distal tip and trailing edge of the fin to the base of the fin.

on the temporal pattern of heat flux across the dorsal fin in dolphins held stationary at the water's surface. Continuous, simultaneous measurements of heart rate and respiration were used to test whether heat flux across the dorsal fin increased during periods of tachycardia at inspiration and decreased during periods of bradycardia at interbreath intervals.

Materials and methods

Experiments were conducted in the shallow waters (approximately 1.5 m deep) of Sarasota Bay, Florida, USA on 19 wild bottlenose dolphins *Tursiops tursiops* Montagu 1821 that were briefly encircled, restrained and released as part of a health monitoring program conducted by the Chicago Zoological Society, under a National Marine Fisheries Service permit (Table 1). Animals used in this study were handled between 12–23 June, 2000. Water temperature during the period was 27.8–31.9°C and air temperature 30.2–32.2°C.

Experimental design

Heat flux and skin temperature were measured simultaneously and continuously at three positions on the dorsal fin of each dolphin: (1) the distal tip of the dorsal fin directly over a superficial vein, (2) the center of the fin directly over a superficial vein and (3) the center of the fin avoiding a superficial vein. All measurements were collected for periods of approximately 15 min under two experimental conditions: (1) the animal held stationary, with its dorsal fin above the surface of the water, for the first 7–8 min and (2) the animal held stationary with the head above water and the dorsal fin submerged just below the surface of the water for an additional 7–8 min.

To determine whether temporal changes in heat flux were associated with respiratory events and/or a change in heart rate, these measurements were collected simultaneously and continuously with heat flux and skin temperature.

Table 1. *Bottlenose dolphins used in this study*

Animal	Date of handling (June 2000)	Sex	Total length (cm)	Mass (kg)
FB101[A,W,V]	12	F	246	101
FB25[A,W,V]	13	F	270	206
FB178[V]	15	M	223	124
FB174[A,W,V]	15	M	254	230
FB58[A,W,V]	15	M	270	259
FB32[W,V]	16	M	253	198
FB11[W,V]	16	F	258	193
FB117[A]	16	F	239	156
FB109[A,W,V]	16	F	228	136
FB14[W,V]	19	M	267	227
FB15	20	F	N/E	N/E
FB155[W,V]	20	F	239	154
FB148	20	M	201	93
FB127[W,V]	22	F	234	N/E
FB13[A]	22	F	245	N/E
FB48[V]	23	M	252	196
FB33	23	F	252	195
FB26[A,V]	23	M	279	256
FB43	23	F	257	219

Lengths were straight-line measurements from tip of the rostrum to the fluke notch.

[V]Animals included in analyses relating to vasculature patterns.

[A]Animals included in heat flux *versus* respiration analyses for the dorsal fin in air.

[W]Animals included in heat flux *versus* respiration analyses for the dorsal fin submerged.

N/E, not measured.

Heat flux

Heat flow across the skin was measured with three square (2.54 cm length) heat flux transducers (B-episensor, Vatell Corporation, Christiansburg, VA, USA) waterproofed with a rubberized coating (Plastidip, PDI Inc., Circle Pines, MN, USA). Each heat flux disk had a unique calibration coefficient, supplied by the manufacturer, which was used to convert transducer output from mV to W m⁻². In addition, to ensure that the outputs of the three rubberized coated heat flux disks, as configured for the experiments, were consistent with each other, a series of calibration tests were run. The disks were immersed in a controlled water bath (RE-120 Lauda Ecoline, Brinkmann Instruments, Inc., Westbury, NY, USA) at six different water temperatures (20, 25, 30, 35, 40 and 45°C). The disks were allowed to stabilize at each water temperature, for approximately 45 s to 2 min. The output of each disk was then recorded at each of the six water temperatures to yield the disk's offset value (in W m⁻²). These offsets were averaged and used to make final calibration corrections in the data presented. To be conservative, heat flux measurements were considered different from each other if they differed by more than 10 W m⁻².

Heat flux measurements were collected from the left side of the dorsal fins. The positions of large-diameter, superficial

veins were determined by palpation and/or visual inspection of the fin. The heat flux transducers were then mounted in a plastic harness that held them on the dorsal fin in their correct position relative to the underlying vasculature (Fig. 3). The internal surface of the transducers pressed against the skin of the animal. To ensure that ambient air or water flowed freely on the external side of the transducers, they were mounted on thin springs, leaving a space of approximately 1 cm between skin and harness. The harness and heat flux disks added extra insulation to the dorsal fin, which introduced a negative bias in heat flux measurements (e.g. Kvadsheim and Folkow, 1997), but one that was expected to affect all measurements equivalently. Heat flux transducer outputs (in mV d.c.) were amplified (to V d.c.), downloaded to a Fluke Hydra data logger (Fluke Corporation, Everett, WA, USA) at 3 s intervals and logged onto a laptop computer.

Skin temperature

Skin surface temperature T_{skin} was determined using a copper-constantan (Type T) thermocouple implanted on the surface of each heat flux disk (Omega Engineering, Inc., Stamford, CT, USA). Thermocouples were connected to the Fluke Hydra data logger and outputs (in °C) were downloaded at 3 s intervals and logged onto a laptop computer. The thermocouples were calibrated in a water bath (RE-120 Lauda Ecoline) at the same six water temperatures
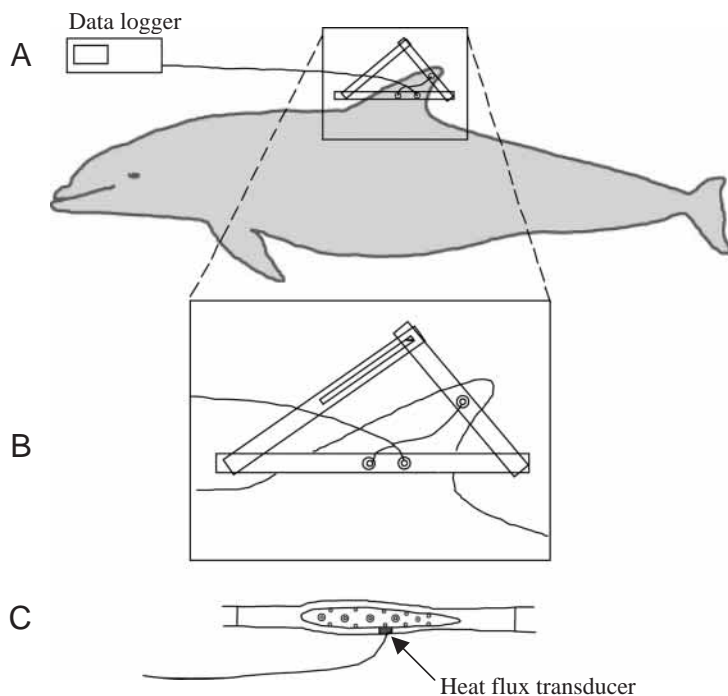

Fig. 3. Schematic representation of the heat flux harness placed on the dorsal fin of a bottlenose dolphin. (A) The harness, with a heat flux transducer attached to the Fluke Hydra data logger. (B) Locations of the heat flux transducers within the harness, which can change laterally and vertically. (C) The harness in a cross-sectional view. The heat flux transducer illustrated is placed directly over a superficial vein.

as the heat flux disks and found to be within 0.1°C of each other.

Heart rate and respiration

Heart rate was recorded during experimental sessions by a Polar Vantage NV heart rate monitor and standard watch receiver (Polar Electro, Inc., Woodbury, NY, USA). The monitor was fixed around the thoracic cavity of the dolphin by an elastic belt and transmitted information to the receiver attached directly to the belt. The Polar Vantage NV recorded R–R intervals (intervals between depolarization of the heart's ventricles), thus, effectively measuring each heart beat. After experimental sessions, heart rate data were downloaded from the receiver to a laptop computer for analysis *via* the Polar Vantage Interface system. Heart rate data were cleared from the receiver between each experimental session.

In the Polar Vantage Interface software, each R–R interval was converted to an instantaneous heart rate (beats min^{-1}). These data were then saved as text files and exported to spreadsheet software for analysis.

The time of each respiratory event, collected to the nearest second, was recorded on a datasheet by an observer. Each event was also recorded by another observer with an electrical trigger, connected to the data logger, which placed an event marker in the data file.

Analyses

Heat flux, skin temperature and heart rate data were examined using spreadsheet software (Excel, Microsoft Corporation, Redmond, WA, USA). To analyze the heat flux and skin temperature data from a full 15 min experiment, data for the fin in air and the fin submerged were separated. For each segment, a 2 min period was subsampled and analyzed, 2 min after recording for that segment began (Fig. 4). Because it took up to 2 min for the disks to stabilize during calibration experiments, this method of analysis allowed time for the transducers to equilibrate after the harness was put on the fin and after the fin was submerged. The data contained within each 2 min segment were averaged to yield a mean heat flux and skin temperature value at each of the three positions for each animal. These mean heat flux and skin temperature values could then be compared across different animals and between experimental conditions (fin in air or fin submerged).

Although a heat flux transducer could, with confidence, be placed directly over a superficial vein, it was more difficult to ensure that a transducer was definitely not over a vein, given the close spacing of large superficial veins on some fins (see Fig. 2). Thus, although experiments were conducted on 19 dolphins, in only 13 of these animals could the heat flux transducers be confidently placed away from a large, superficial vein in the center of the fin. For analyses relating to vascular structures in the dorsal fin only these 13 animals were examined (Table 1).
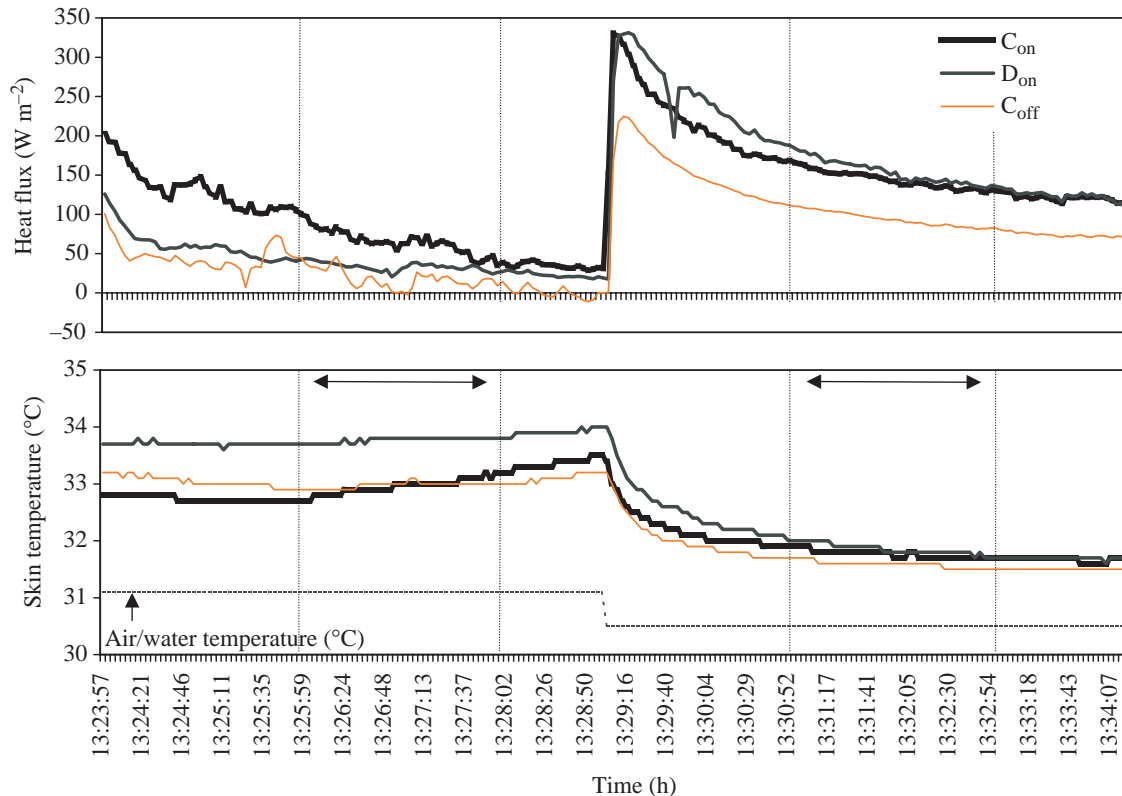
Fig. 4. Representative data record (for FB155). The three lines represent the different fin positions. C_{on}, a position at the center of the fin directly over a superficial vein; D_{on}, a position at the distal tip of the fin directly over a superficial vein; C_{off}, a position at the center of the fin away from superficial veins. The data streams begin recording with the dorsal fin in air. At fin submergence, all three heat flux values increase, while skin temperature values simultaneously drop. The two areas between the vertical dotted lines represent the 2 min segments of the record analyzed.

To analyze heart rate data, the instantaneous heart rates were first edited. Heart rate values below 20 beats min^{-1} and above 200 beats min^{-1} were deleted from the record, because these values appeared to be a result of the receiver missing heart beats or an inability of the receiver to record sudden increases. As heart rates were instantaneous values converted from R–R intervals, some seconds of real time contained multiple values of heart rate. In these cases, representing periods of tachycardia, peak heart rate values were selected. The heart rate data, after editing, had a value for each second of real time during the experiment and, thus, required alignment with the heat flux and skin temperature data, which were recorded at 3 s intervals. Heat flux and skin temperature values were averaged between 3 s intervals, yielding a value for each second of real time during the experiment.

Thus, eight simultaneous measurements (heart rate, respiration, heat flux and skin temperature at each of three positions) were recorded during each experimental session. As the Fluke Hydra data logger recorded heat flux and skin temperature every 3 s, this time interval was assumed to be the range of error in each synchronous time series.

The relationship between tachycardia and a respiratory event was determined by analyzing a time series of heart rate and respiration data. This examination revealed that the majority of tachycardic peaks occurred within 6 s before or after a respiratory event. Thus, the percentage of tachycardia events that fell within this time period was determined.

Investigating the relationship between tachycardia and increases in heat flux across the dorsal fin required additional data manipulation. Heat flux values tended to change throughout the length of the experiment, even after the 2 min stabilization period (see Fig. 4). Thus, overall increasing or decreasing trends in the heat flux time series were eliminated by fitting linear (for the dorsal fin in air) and quadratic models (for the dorsal fin submerged) to each heat flux record using statistical software (JMP IN, SAS Institute, Inc., Cary, NC, USA). Residuals were then calculated from these models. The residuals represented the changes in heat flux values that could potentially be temporally related to changes in heart rate. Because tachycardia was temporally related to respiratory events, respiration records were compared to those of heat flux to determine whether periods of tachycardia were related to increases in heat flux across the dorsal fin. The residuals were plotted with the respiration data in a time series to determine how often the highest heat flux residual value for the interbreath interval fell within 9 s, before or after, a respiratory event. The time window around each respiratory event was increased from 6 s to 9 s, in an attempt to account for delays that might exist between tachycardia and a change in peripheral vasodilation at the dorsal fin. The time window was limited to

9 s to prevent overlapping time periods between two separate respiratory events. Only changes in heat flux equal to or greater than $10\,\mathrm{W\,m^{-2}}$ were included in this analysis.

To determine whether mean heat flux and skin temperature differentials (temperature differential = $T_{\mathrm{skin}} - T_{\mathrm{amb}}$) varied by position and whether respiration rate differed when the fin was in air rather than submerged, the Shapiro–Wilk W-test was used to first test for normality. Once normal distributions were confirmed, one-way analyses of variance (ANOVAs) were performed to test for significant differences in these data sets. $P=0.05$ was used for all tests. All statistical tests were performed using JMP IN statistical software.

Results

Spatial variation in heat flux

Although the locations of superficial veins at the center of the fin could be confidently determined in only 13 out of 19 animals, all 19 animals were included in the following analysis to illustrate the overall variation in measured heat flux values across the dorsal fin. Thus, for this analysis, the two center positions do not necessarily relate to positions over or away from superficial veins. Within individuals, there was variation in heat flux between the three dorsal fin positions (Table 2).

Table 2. *Spatial differences in heat flux across the dorsal fin*

	Heat flux ($\mathrm{W\,m^{-2}}$)			
Animal	Center/Center in air	Center/Distal in air	Center/Center in water	Center/Distal in water
FB101	17.0	54.2	34.9	54.5
FB109	38.9	62.7	32.7	63.4
FB11	9.1	37.9	10.1	34.4
FB127	49.3	29.0	27.0	99.9
FB14	28.8	15.5	19.1	18.3
FB155	46.9	31.4	49.7	59.4
FB174	4.9	82.6	63.3	70.1
FB178	25.7	40.3	15.6	31.5
FB25	129.3	168.4	14.0	41.6
FB26	32.2	43.0	31.4	68.3
FB32	63.5	62.9	15.7	55.4
FB48	64.7	83.6	45.3	38.9
FB58	78.0	78.5	41.7	114.6
FB117	48.3	61.5	75.4	94.8
FB13	66.7	50.2	76.3	95.1
FB148	21.1	21.2	11.0	6.6
FB15	30.7	27.6	13.2	10.1
FB33	52.8	59.3	84.8	53.4
FB43	45.3	32.7	29.4	44.8
Mean ± S.D.	44.9±28.7	54.9±34.2	36.3±23.8	55.5±30.3

Shown are differences between the mean heat flux values measured at the two center fin positions (Center/Center) and the greatest differences between the mean values measured at the center of the fin and the distal tip (Center/Distal) for the dorsal fin in air and submerged.

The range of differences in the mean heat flux values measured between the two center fin positions was $4.9–129.3\,\mathrm{W\,m^{-2}}$ in air and $10.1–84.8\,\mathrm{W\,m^{-2}}$ when submerged. These positions were often separated on the fin by as little as 1 cm. Overall, for all dolphins pooled together ($N=19$), the mean differences in heat flux between the two positions at the center of the fin were $44.9±28.7\,\mathrm{W\,m^{-2}}$ in air and $36.3±23.8\,\mathrm{W\,m^{-2}}$ (means ± S.D.) when submerged. The greatest ranges of differences in mean heat flux values measured between the center of the fin and the distal tip were $15.5–168.4\,\mathrm{W\,m^{-2}}$ in air and $6.6–114.6\,\mathrm{W\,m^{-2}}$ submerged. For all dolphins pooled together, the mean values of the greatest difference between a center fin position and the distal tip were $54.9±34.2\,\mathrm{W\,m^{-2}}$ in air and $55.5±30.3\,\mathrm{W\,m^{-2}}$ (means ± S.D.) when submerged.

Heat flux over superficial veins

Although there was spatial variation in heat flux between the three dorsal fin positions within individuals, for all dolphins pooled together, the mean heat flux values measured at the three fin positions were not significantly different (d.f.=38, $F=1.69$, $P=0.20$) when the dorsal fin was submerged. The spatial pattern in heat flux within individuals was, however, related to patterns of superficial vasculature when the fin was submerged. Of the 13 dolphins where the placement of the heat flux transducers relative to superficial vessels had been confidently established, 12 (92%) showed heat flux values that

Table 3. *Mean heat flux values at the three positions for the dorsal fin in air and when submerged*

	Heat flux ($\mathrm{W\,m^{-2}}$)					
	Air			Water		
Animal	D_{on}	C_{on}	C_{off}	D_{on}	C_{on}	C_{off}
FB101	36.1	73.3	90.3	126.6	72.1	107.0
FB109	40.1	63.9	102.7	180.2	116.8	149.5
FB11	65.6	94.4	103.5	127.3	92.8	102.9
FB127	81.6	101.9	52.6	107.0	34.1	7.1
FB14	52.9	68.4	39.6	141.5	142.3	123.2
FB155	33.3	64.6	17.7	152.1	142.5	92.8
FB174	28.5	−49.1	−54.1	99.9	93.1	29.8
FB178	77.1	91.8	117.4	209.2	225.1	240.7
FB25	202.7	163.7	34.4	225.3	183.7	197.7
FB26	85.9	75.2	42.9	68.2	31.2	−0.2
FB32	43.2	42.6	106.1	169.5	114.1	129.9
FB48	−3.7	80.0	15.3	36.1	42.5	−2.7
FB58	50.3	49.7	−28.2	133.8	61.0	19.3

Positive values represent the condition of heat transfer from animal to ambient environment.

Negative values represent heat gain from the ambient environment.

D_{on}, measurements at the distal tip of the fin taken over superficial veins; C_{on}, measurements at the center of the fin taken over superficial veins; C_{off}, measurements at the center of the fin taken away from superficial veins.

Note that FB178 was the only animal that did not register heat flux values that were highest when measured over superficial veins under conditions of dorsal fin submerged.

were higher when measured over superficial veins (either distal or center) when the fin was submerged (Table 3). Eight of these 13 animals (62%) had the highest heat flux values at the distal tip of the fin. For the remaining four animals, measurements at the distal tip and the center of the fin over a superficial vein were within $10\,\mathrm{W\,m^{-2}}$ of each other.

For the dorsal fin in air, there were no significant differences in mean heat flux values measured between the three fin positions when all dolphins were pooled together (d.f.=38, F=0.60, P=0.55). There was also no predominant spatial pattern in heat flux values observed within individual dolphins. Three dolphins had heat flux values that were highest at the distal tip of the fin, four had heat flux values highest at the center of the fin when measured over a superficial vein and four had heat flux values highest at the center of the fin measured away from superficial veins (Table 3). The remaining two animals had highest heat flux values, within $10\,\mathrm{W\,m^{-2}}$ of each other, at two fin positions.

Skin temperature

For the dorsal fin submerged, the mean temperature differentials between the skin and the ambient environment did not vary between the three fin positions when all dolphins were pooled together (d.f.=35, F=0.23, P=0.79) (Table 4). There were, though, discernable patterns within individuals. For 11 out of 12 animals (92%) (no water temperature was determined for the 13th animal, FB101, thus only 12 were used for this

Table 4. *Temperature differentials between the skin and the ambient environment*

| | Temperature differential (°C) | | | | | |
| | Air | | | Water | | |
Animal	D_{on}	C_{on}	C_{off}	D_{on}	C_{on}	C_{off}
FB101	0.1	–1.7	–1.1			
FB109	1.8	–0.2	–0.3	–0.4	–0.7	–0.7
FB11	1.5	–0.2	–0.7	0.3	0.2	0.2
FB127	0.5	–0.7	–0.5	0.2	–0.3	–0.4
FB14	2.5	1.6	1.7	1.5	1.5	1.2
FB155	2.7	1.8	1.9	1.3	1.3	1.1
FB174	–0.4	–0.8	–2.1	0.2	0.1	–0.2
FB178	1.0	0.3	1.0	2.4	2.4	2.7
FB25	0.2	0.3	3.1	1.3	1.2	1.8
FB26	–0.2	–1.0	–0.9	1.1	0.9	0.7
FB32	2.6	0.9	–0.2	1.2	0.9	0.8
FB48	0.1	–0.4	–0.7	0.0	0.0	–0.3
FB58	–1.3	–2.9	–2.6	0.8	0.3	0.1
Mean ± S.D.	0.8±1.3	–0.2±1.3	–0.1±1.6	0.9±0.7	0.7±0.8	0.6±1.0

Positive values represent the condition of skin temperature greater than air or water temperature.

D_{on}, measurements at the distal tip of the fin taken over superficial veins; C_{on}, measurements at the center of the fin taken over superficial veins; C_{off}, measurements at the center of the fin taken away from superficial veins.

analysis), the highest temperature differentials corresponded to the highest heat flux values. A single animal, FB25, had the highest heat flux value at the distal tip of the fin, but the highest temperature differential at the center of the fin when measured away from a superficial vein. Of these 12 animals, 10 (83%) had both the highest temperature differential and highest heat flux values when measured over superficial veins in either the distal tip or the center of the fin. In addition, despite non-significant differences between the temperature differentials, heat flux at those three positions could vary greatly. Heat flux values measured directly over superficial veins could be $60\,\mathrm{W\,m^{-2}}$ higher than values measured away from superficial veins, with only a 0.2°C temperature difference between the three positions (see Fig. 4).

For the dorsal fin in air, the mean temperature differentials between the skin and the ambient environment also did not vary significantly across the fin when all dolphins were pooled together (d.f.=38, F=2.32, P=0.11) (Table 4). The highest temperature differentials, however, corresponded to the highest heat flux values in only one of 13 animals (8%) for the dorsal fin in air. Additionally, as the temperature differential between the skin and the ambient environment increased over time, heat flux across the surface of the dorsal fin decreased (see Fig. 4).

Heart rate and respiration

Heart rate data were successfully collected on six of the 19 dolphins. Mean heart rates were calculated from the longest periods of data for each animal. These periods were all longer than 4 min. Mean heart rates ranged from 72 to 101 beats $\mathrm{min^{-1}}$ (Table 5). Heart rates were arrhythmic, with periods of tachycardia associated with respiratory events and bradycardia during intervening interbreath intervals (Fig. 5). The highest heart rate value occurred within 6 s before or after a respiratory event, 89±7.5% (mean ± S.D.) of the time (range 75–97%).

Respiration rates were calculated under both experimental conditions (fin in air and fin submerged) for these six dolphins (Table 5), and there were no significant differences in the respiration rates under either condition (d.f.=11, F=3.04, P=0.11).

Table 5. *Mean heart rates and respiration rates*

| | Heart rate (beats $\mathrm{min^{-1}}$) | | Respiration rate (breaths $\mathrm{min^{-1}}$) | |
Animal	Mean ± s.d.	Range	Fin in air	Fin submerged
FB11	72±22	50–105	2.6	3.2
FB117	80±18	55–118	2.3	2.5
FB109	88±12	65–115	2.6	3.1
FB155	101±9	88–115	1.7	2.0
FB127	87±16	75–110	2.1	2.3
FB33	85±20	65–110	2.4	3.5

Mean heart rates were determined from the longest period of quality data (periods all >4 min in length).

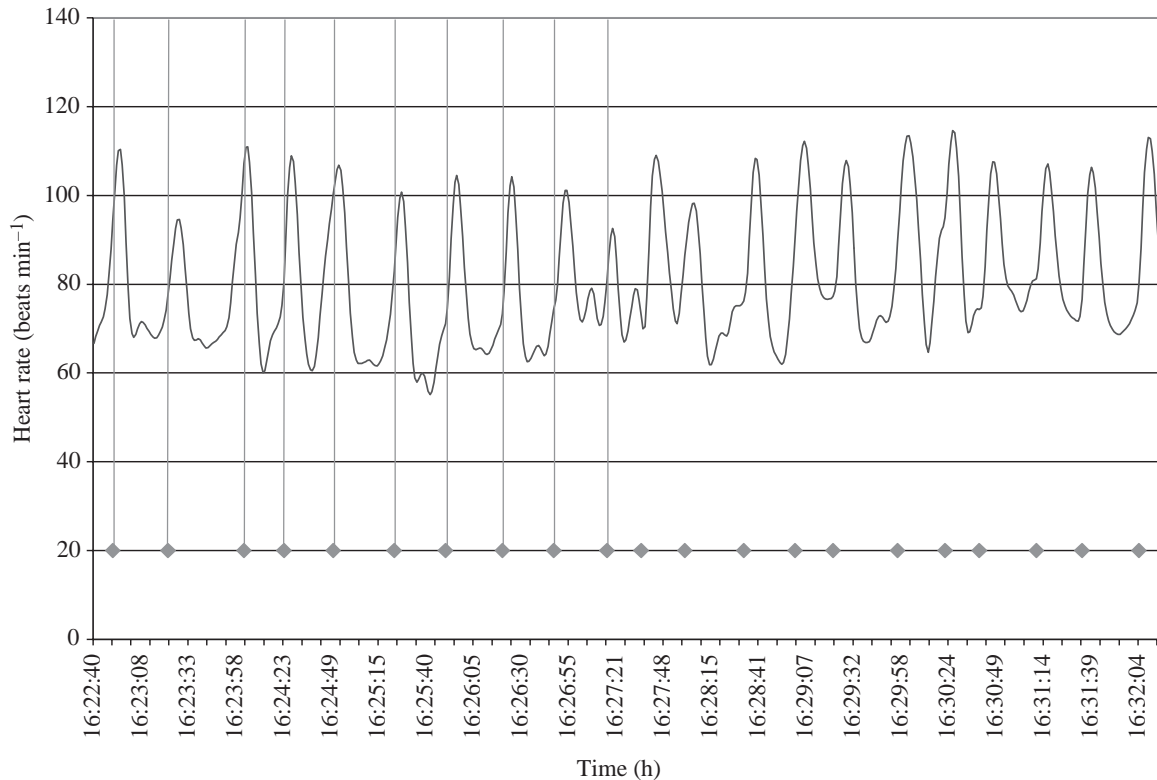Heart rate ranges do not include transient drops in heart rate.

Fig. 5. Representative record of heart rate and respiration (for FB117). The diamonds represent respiratory events. Vertical lines are added to the beginning of the data record to illustrate the temporal correlation between respiration and tachycardia. The heart rate data have been smoothed with a spline (λ=10, r^2=0.83) (JMP IN) to simplify visualization of the correlation. Smoothed data were not used for actual heart rate calculations (see Table 5).

Respiration and heat flux

Because tachycardia was temporally related to respiratory events, the respiration records were compared to those of heat flux to determine whether periods of tachycardia were related to increases in heat flux across the dorsal fin. No clear relationship between a respiratory event and an increase in heat flux across the dorsal fin, in either air or water, was observed (Fig. 6). A subsample of eight animals, representing a range of heat flux values, was selected for initial analyses of respiration and heat flux across the dorsal fin at the distal tip in air (Table 1). Heat flux data were first examined for the dorsal fin in air, as these records showed greater fluctuations than the submerged records. These fluctuations may have represented changes in heat flux across the surface of the fin or, alternatively, changes in the microenvironment surrounding the fin. The distal tip of the fin was selected for initial analyses, because it was expected that blood from the core would be delivered *via* the central arteries to this site first and, thus, any relationship between a respiratory event, tachycardia and a change in heat flux would be most obvious here. At the distal tip of the fin in air, the highest heat flux values were temporally related to a respiratory event only 37±21% (mean ± S.D.) of the time.

A sub-sample of ten animals, selected from those with the highest heat flux values, was examined to determine whether there was a relationship between respiratory events,

tachycardia and changes in heat flux across the dorsal fin when submerged (Table 1). At the distal tip of the fin measured over a superficial vein, 42±21% (mean ± S.D.) of the highest heat flux values were temporally related to a respiratory event. At the center of the fin measured over a superficial vein, this relationship reduced to 17±17% and at the center of the fin measured away from a superficial vein to 18±11%.

Discussion

Heat flux and superficial vasculature

The first objective of this study was to investigate the influence of vascular structures on heat flow across the dorsal fins of wild bottlenose dolphins. The results demonstrate that the dolphin dorsal fin is a spatially heterogeneous thermal surface. The mean differences in heat flux measured between the three positions on the dorsal fins of bottlenose dolphins in this study were often equal to or greater than the changes in heat flux recorded from a single position in dolphins before and after exercising and diving. For example, Noren et al. (1999) reported a mean increase in heat flux from the center of the dorsal fin of approximately 0–65 W m^{-2} following exercise, relative to resting values at the same water temperature. During dives there was a mean decrease in heat flux from the center of the dorsal fin of approximately 40–50 W m^{-2}, relative to values measured at the water's surface (Noren et al., 1999). In
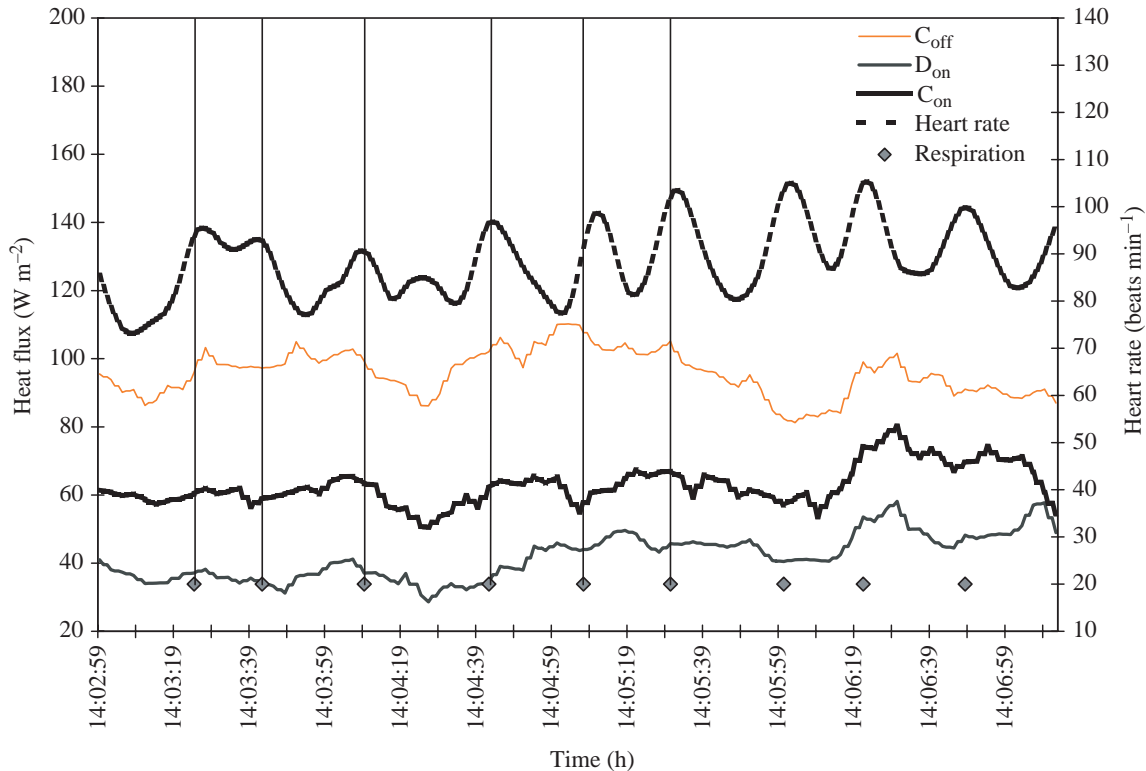
Fig. 6. Representative record of heat flux, heart rate and respiration for the dorsal fin in air (FB109). The diamonds represent respiratory events. Vertical lines are added to the beginning of the data record at each respiratory event to aid in the visual alignment of synchronous records. The heart rate data have been smoothed with a spline ($\lambda=100$, $r^2=0.49$) (JMP IN) to simplify visualization. C_{on}, a position at the center of the fin directly over a superficial vein; D_{on}, a position at the distal tip of the fin directly over a superficial vein; C_{off}, a position at the center of the fin away from superficial veins.

the current study, similar or greater differences in heat flux values were recorded between positions on the dorsal fin separated by as little as 1 cm (see Table 2).

When the fins were submerged, spatial differences in heat flux could be predicted based upon their position relative to underlying vascular structures – the highest heat flux values were recorded either at the distal tip of the fin directly over superficial veins or at the center of the fin over superficial veins. Thus, these results support the predictions that heat flux is higher over superficial veins and highest at the distal tip. The single individual (FB178) that had the highest heat flux at the center of the fin measured away from a superficial vein also had the highest combined total heat flux at all three positions (all >200 W m^{-2}) of any of the 13 animals, which suggest that this animal may have been using a greater proportion of the surface area of the fin to dissipate heat (see below).

Although the highest heat flux values during submergence were recorded over superficial veins at the distal tip of the fin, there was not as clear a pattern at the center of the fin. At the fin's center, heat flux measured over a superficial vein was not always higher than that measured away from a vein. This result may partially be explained by the vascular anatomy of the fin. Large superficial veins are the only ones that could have been assessed visually and/or by palpation during the experiments and, thus, avoided. Visual inspection of cross-sectioned dorsal

fins suggests that there are many smaller superficial veins at the dorsal fin's surface (Elsner et al., 1974; E. M. Meagher, personal observation). While the large veins could be avoided in the majority of the experiments (13 out of 19), these smaller superficial veins could not. Thus, the disks were most certainly measuring heat flux over small superficial veins at all three positions. Smaller vessels, particularly arterioles, capillaries and venules, act as ideal heat exchangers, while vessels of increasing diameter become less efficient at transferring heat to the surrounding tissue (Chato, 1980). Therefore, smaller vessels, including small superficial veins, could also have influenced the heat flux measurements.

The variables that affect conductive heat transfer are surface area, thermal conductivity and the temperature differential between the skin and the ambient environment (see Equation 1). Because a constant surface area was being assessed in these experiments, measured heat flux at the three dorsal fin positions was controlled by changes in skin temperature and/or changes in the conductivity of the skin. Although conductivity is a physical constant, and thus cannot be increased or decreased, convection, which is the movement of a fluid relative to an object, can substantially increase the rate of thermal diffusion (Kvadsheim and Folkow, 1997; Denny, 1993; Schmidt-Nielsen, 1997). For example, for the 13 animals investigated, 83% had the highest temperature

differentials and highest heat flux values measured at positions over superficial veins when the fin was submerged. This result suggests that increases in skin surface temperature and thus in heat flux, at these sites are due to the convective transfer of core heat *via* blood. In addition, when the complete heat flux and skin temperature records were examined for the dorsal fin submerged, it was apparent that as the temperature differential between skin and water decreased, heat flux also decreased (see Fig. 4). Small changes in the temperature differential between the dorsal fin and the ambient environment could also be associated with large differences in heat flux, further suggesting that when the fin was submerged there was active, convective delivery of heat to the surface of the skin.

The results for the dorsal fin in air were quite different. For example, there was no relationship between high heat flux values and high temperature differentials. Although the distal tip of the fin tended to have higher temperature differentials relative to the other two positions, only 8% of the dolphins had their highest heat flux values at this position. Additionally, as the temperature differentials across the dorsal fin increased over time, heat flux values decreased (see Fig. 4). The unexpected relationship between heat flux values and temperature differentials for the dorsal fin in air suggests that the conductivity of the ambient environment was affecting heat dissipation from the fin. The following equation reflects how the boundary layer, the layer of air or water with which the dolphin skin is in contact, affects heat dissipation:

$$H' = A_S(T_b - T_a) / [(L_1/C_1) + (L_2/C_2)], \qquad (2)$$

where L_1 and C_1 are the width and conductivity of the dolphin skin, respectively, and L_2 and C_2 are the width and conductivity of the boundary layer (Resnick and Halliday, 1966). Because the conductivity of water is approximately 25 times that of air, heat flux will be much greater in water when all other variables are held constant. In these experiments, when the fin was submerged, heat was dissipated to the conductive water medium as it was brought, *via* blood flow, to the skin's surface. Thus, heat flux values paralleled those of the temperature differential. Air, however, has relatively low conductivity. The results of this study suggest that in air, heat could not be dissipated from the fin as quickly as it was brought to the skin's surface. The high skin temperatures at the distal tip of the fin over superficial veins may have been caused by a build-up of heat, brought to the surface from the core *via* blood, that was not dissipated to the environment. The fin could also have experienced heat loading in air due to the effects of solar radiation, but this effect would not be expected to be site-specific, unlike the build-up of heat at the distal tip of the dorsal fin. The change in the conductivity of the ambient environment, from air to water, also accounts for the sudden increase in heat flux values at the moment of fin submergence. Although the temperature differentials between skin and ambient environment did not change greatly as the dorsal fin moved from air to water, heat flux values increased (sometimes by as much as sevenfold) as the fin moved into a more conductive water medium (see Fig. 4). Interestingly, this same pattern was observed in all animals, whether they were handled immediately after capture or after an extended period of being held calmly at the water's surface.

Heart rate, respiration and heat flux

The second objective of this study was to examine whether changes in heat flux across the dorsal fin were temporally related to periods of tachycardia and bradycardia. While respiring at the surface, some cetaceans, such as the harbor porpoise *Phocoena phocoena* (Reed et al., 2000) and bottlenose dolphin (Elsner et al., 1966; Kanwisher and Ridgway, 1983), display tachycardia at inspiration and bradycardia during interbreath intervals. The results from this study are similar, as 89% of respiratory events and the onset of tachycardia occurred within 6 s of each other.

Although the dolphins in the present study displayed respiratory arrhythmia, there was no relationship between respiration and increased heat flux across the dorsal fin, either when the fin was in air or when it was submerged. There are several potential reasons why this relationship was not observed. Williams et al. (1999) demonstrated that in a dolphin undergoing a dive response, bradycardia was associated with a decrease in heat flux across the dorsal fin. In those experiments, a bottlenose dolphin diving freely to 50 m showed a decline in mean heart rate from 102 beats min^{-1} to 37 beats min^{-1} (Williams et al., 1999). Upon surfacing and breathing, the dolphin displayed an increase in heart rate and heat flux. In the present study, the decline in heart rate measured during bradycardia at the surface was not as pronounced as that reported by Williams et al. (1999) during diving. The lowest heart rate value determined from the six dolphins in the present study was 50 beats min^{-1}; however, the mean heart rate during the interbreath interval for all six animals was 66 beats min^{-1} (Table 5). It appears that although the dolphins in these experiments were experiencing bradycardia during the interbreath interval, it was slight compared to that experienced during a dive response. Thus, the dorsal fin may not have experienced noticeably reduced blood flow during the interbreath intervals.

The dolphins in these experiments were also in a highly artificial behavioral setting. Stress, in any form, stimulates the sympathetic nervous system, leading to an increase in heart rate (Bullock, 1996). It is possible that the capture and restraint process inhibited bradycardia that would normally have been present during the interbreath interval. Respiration rates of captive, trained bottlenose dolphins are 2–3 breaths min^{-1}, and normal heart rates immediately after inspiration are 70–100 beats min^{-1} (Ridgway, 1972). According to Ridgway (1972), heart rate during the interbreath interval in bottlenose dolphins then falls to 30–40 beats min^{-1}, regardless of whether the animal is swimming or resting on a mat out of the water. While the average respiration rate of dolphins in the present study was within this range (see Table 5), heart rates during both tachycardia and bradycardia were higher than those reported by Ridgway (1972). Heart rates after inspiration in these experiments were 105–118 beats min^{-1}, while heart rates

during the interbreath interval were 50–88 beats min^{-1}. Thus, the relatively higher heart rates of the dolphins in these experiments may have affected the relationship between heart rate and patterns of heat flux across the dorsal fin.

In addition, these dolphins were in a warm environment and were actively dissipating body heat, as indicated by their heat flux values. Hampton et al. (1971) and Noren et al. (1999) recorded mean heat flux values of 27–70 W m^{-2} from the submerged dorsal fins of bottlenose dolphins at rest in water, with temperatures ranging from 26.5°C to 29.8°C, respectively. A heat flux value of 70 W m^{-2} was exceeded by at least two of the three dorsal fin positions, when the fin was submerged, in 15 out of the 19 dolphins in the present study. Noren et al. (1999) also measured mean heat flux values of 70–135 W m^{-2} from the submerged dorsal fins of bottlenose dolphins after surface swimming for 11–13 min at 4.3 m s^{-1}. A heat flux value of 135 W m^{-2} was exceeded by at least one of the three dorsal fin positions, when the fin was submerged, in 11 out of the 19 dolphins in the present study. Heat flow increases with increasing total skin blood flow through circulatory channels [e.g. venules, arterio–venous anastomoses (AVA), arterioles and capillary beds] and is highest when both capillary and AVA flows are at their highest levels (Grayson, 1990; Hales, 1985). While we did not directly measure blood flow through the dorsal fin, it is probable that these animals were maximizing the use of their circulatory channels to regulate their body temperature in the warm waters of Sarasota Bay. In this case, an increase in heat flux associated with tachycardia may not exist, or may be so small that the signal is lost in the background levels of overall high heat flow.

Although a relationship between an increase in heat flux and tachycardia has been demonstrated in diving dolphins (Williams et al., 1999), no study has attempted to detect the correlation in animals at rest on a breath-to-breath time scale. While the circulatory changes associated with diving result in pronounced vasoconstriction, it is possible that the modest changes in blood flow associated with non-diving respiratory arrhythmia may have no effect on heat flux across the dorsal fin. Understanding the large changes in heat flux that occur over time and between different behavioral states is important. Further research into the subtle changes in heat flux that occur within minutes could elucidate the dynamic control mechanisms that dolphins utilize to thermoregulate in their highly conductive marine environment.

The combined results of this study suggest that the dorsal fin of the bottlenose dolphin is a spatially heterogeneous thermal surface and that patterns of heat flux across the dorsal fin are strongly influenced by underlying vasculature, particularly at the distal tip of the fin. Heat flux across the dorsal fin can vary over small distances and care should be taken in future studies to record non-continuous measurements from a consistent location, particularly when comparing heat flux between different behavioral states. A single heat flux value recorded from the center of the dorsal fin may not provide an accurate representation of the amount of heat being dissipated by the animal. In addition, this study demonstrates that heat flux across the dorsal fin varies temporally in an animal under static conditions. Measuring heat flux and skin temperatures from dolphins under more natural conditions would provide further insights into the dynamic function of their thermal windows.

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