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UNIVERSITY OF CALIFORNIA, SAN DIEGO

The electrocardiogram and heart rate in three mid-sized whale species

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Natalie Bickett

Committee in charge:

Paul Ponganis, Chair
Gerald Kooyman
Martin Tresguerres

2017

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The Thesis of Natalie Bickett is approved and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2017

DEDICATION

This thesis is dedicated to the wonderful trainers, veterinarians, and staff at SeaWorld San Diego who share with the world so much love and joy. Thank you for all of the effort you put into promoting conservation and research to save these amazing animals.

I also dedicate this thesis to my parents who introduced me to the wonder of the ocean and inspired in me a passion for knowledge.

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Thank you to all who helped me collect and analyze data. Cassondra Williams, thank you for being so helpful and kind. You're always willing to share great advice when I need it. Joyce Smith, Kaila Pearson, and Laurel Kistler, thank you for helping me

sort through and make sense of the data we collected. You made this process much easier with your enthusiasm and dedication.

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ABSTRACT OF THE THESIS

The electrocardiogram and heart rate in three mid-sized whale species

by

Natalie Bickett

Master of Science in Marine Biology

University of California, San Diego, 2017

Paul Ponganis, Chair

Although there are many studies describing the behavior/ecology of whales, little is known of their physiology. Furthermore, the limited data available regarding cardiac function in whales have been collected under atypical conditions. To address this, we applied electrocardiogram (ECG) recorders with a suction cup attachment technique to a killer whale (*Orcinus orca*), pilot whale (*Globicephala macrorhynchus*), and beluga whale (*Delphinapterus leucas*) to investigate heart rate regulation. The PR and QRS

intervals of ECG signals were in the same range as previously published values in large mammals. Heart rates “at rest” in a pool were 83–140% of the allometrically predicted resting heart rates. Heart rates during swimming activities were higher than at rest in the killer whale and beluga whale, but lower in the pilot whale. Frequent fluctuations in apneic heart rate occurred during all activities, including rest and stationary submersions. We conclude that a) electrical impulse conduction in the hearts of whales does not scale allometrically as in small mammals, b) heart rates “at rest” can be elevated, probably secondary to non-fasting conditions, c) exercise does not always increase heart rate in whales, and d) beat-to-beat oscillations in apneic heart rate are common and can occur without exercise.

Introduction

The electrocardiogram (ECG) and heart rates of whales are relevant to our understanding of both cardiac function in large mammals and the diving ability of whales. Heart rate decreases with increasing body mass in mammals (Stahl 1967), and exceptionally rapid electrical impulses are postulated to account for shorter than predicted conduction times within the hearts of large mammals (Meijler & Janse 1988, Meijler *et al.* 1992a). Heart rate also plays a central role in the diving capacity and foraging ecology/behavior of whales and other marine mammals (Butler & Jones 1997, Kooyman & Ponganis 1998). The decline in heart rate (bradycardia) during dives decreases cardiac output and blood oxygen delivery to muscle and peripheral tissues, thus conserving blood oxygen stores and increasing the duration of aerobic metabolism in essential organs such as the brain and heart.

The degree of bradycardia during dives is variable and dependent upon interactions of the sympathetic and parasympathetic branches of the autonomic nervous system (Blix *et al.* 1983, Butler & Jones 1997, Ponganis 2015). Although there have been many studies of heart rate regulation and the cardiovascular dive response (bradycardia and peripheral vasoconstriction during breath-holds) in pinnipeds, there have been relatively few investigations in whales (Ponganis 2015). Most heart rate data for cetaceans have only been obtained from dolphins and porpoises (Williams *et al.* 1999, Teilmann *et al.* 2006, Noren *et al.* 2012, Williams *et al.* 2015, Elmegaard *et al.* 2016, Houser *et al*. 2010). The few available ECG recordings in larger cetaceans reveal that cardiac conduction intervals do not increase allometrically (in contrast to mammals less

than 1,000 kg in body mass) (Meijler & Janse 1988, Meijler *et al.* 1992a). These rare studies have been limited to whales in restricted or unusual situations, *e.g.*, harpooned (King *et al.* 1953), entangled in fishing nets (Meijler *et al.* 1992b), stranded on a beach (Senft & Kanwisher 1960), or during veterinary exams in shallow water (Ponganis & Kooyman 1999).

In this study, we sought to investigate heart rate regulation in three mid-sized odontocete species with suction cup attachment of an ECG bio-logger and ECG surface electrodes. Our goals were to characterize the ECG waveforms, to assess the allometric relationship of resting heart rates, and to determine the variability in heart rate profiles during several different spontaneous and trained activities. We hypothesized that 1) atrial and ventricular conduction times would not increase allometrically, as has been shown in similar studies with large mammals (Meijler & Janse 1988, Meijler *et al.* 1992a), 2) heart rate while resting in the pool would be greater than allometrically predicted resting heart rates (due to effects of recent feedings and activities) (Stahl 1967, Williams *et al.* 2017), 3) heart rates would vary in intensity during rest and exercise activities (Davis & Williams 2012, Noren *et al.* 2012), and 4) large beat-to-beat oscillations in heart rate, even during stationary breath-holds, would be common due to adjustments in parasympathetic tone in the presence of elevated sympathetic tone (Williams *et al.* 2015, Ponganis *et al.* 2017, Suzuki *et al.* 2017).

Methods

Animals

Data collection took place between 2015 and 2017 on a 3,807-kg, adult female killer whale (*Orcinus orca*), a 907-kg, adult female pilot whale (*Globicephala macrorhynchus*), and a 1,321-kg, adult male beluga whale (*Delphinapterus leucas*). All three animals were housed at the SeaWorld, San Diego marine facilities. Water temperature was maintained between 11–12° C for the killer whale, 14–18° C for the pilot whale, and 11–13° C for the beluga. No animals fasted for this study.

Equipment

We designed custom suction cup-ECG electrodes by mounting a silver-plated surface ECG electrode (E244 electrode, 1.2 cm-diameter, In Vivo Metric, Healdsburg, CA) in the base of a DTag suction cup (DTag3-V1.2-Cup-EPDM50 4.5 cm-diameter, silicone cup, Da/Pro Rubber, Inc., Tulsa, OK, USA). The electrodes were connected with a waterproof cable and connector (Teledyne - API, San Diego, CA) to an ECG bio-logger (UFI, Morro Bay, CA, USA; 209 g, 16 × 6 × 2.5 cm) with custom waterproof housing (Meer Instruments, Palomar Mountain, CA). The bio-logger was attached to a rigid, straight frame (26 x 3 x 0.1 cm) with plastic cable ties. The bio-logger frame was fixed to three of the DTag suction cups; the two outer cups were the custom suction cup-electrodes. The entire ECG-suction cup tag measured 26 cm in length with a mass of 320 g (Fig. 1A). The suction cup-electrodes were spaced 21.5 cm apart and placed ventrally

on the chest between the fore-flippers (Fig. 1B), near the estimated position of the heart (Piscitelli *et al.* 2010). Initially, the custom ECG electrode suction cups were not attached to the frame, and were extended as far apart as 3 m. However, signal quality and amplitude were unchanged with inter-electrode distances as short as 10.3 cm. We coated the electrodes with a thin layer of conductive electrode paste (Ten20 Conductive, Weaver and Co., Aurora, CO) prior to placement on the animal. The ECG sampling rate was 100 Hz.

Video and visual observations documented behaviors, breaths, and activity durations. An underwater Hero3 GoPro camera (GoPro, San Mateo, CA, USA) captured underwater behaviors, exhalations, and fluke-stroke actions during activities. The camera was either secured to the side of the pool for the beluga and pilot whales, or attached to the killer whale with a GoPro suction cup. Prior to the experiments, we synchronized the cameras and timepieces to the same computer clock used to deploy the bio-logger. The videos were used to count strokes and breaths to calculate stroke rates and respiratory rates.

Experimental design

The ECG was recorded during four activities: 1) resting, while the animal was inactive at the pool's surface, 2) submerged swimming, characterized by repeated spontaneous, shallow dives while the animal was freely swimming, 3) surface swimming, swimming while the animal's blowhole was above the surface, and 4) stationary

submersions, while the animal was stationed at an underwater viewing window (5 m) with a trainer on the other side of the glass to keep the animal stationary for certain durations. Activities 1–2 were spontaneous activities, and activities 3–4 were trained behaviors. ECGs were collected from the killer whale during activities 1–4 and from the pilot and beluga whales during activities 1–2.

Analysis

Data from the ECG bio-logger was downloaded to a PC via a UFI interface box (UFI, Morro Bay, CA, USA). We used the raw data to measure PR and QRS intervals (n = 20 consecutive beats per whale). R-waves were identified using a customized peak detection program (K. Ponganis; Origin 2017, OriginLab Co., Northampton, MA, USA) and represented individual heart beats. Each peak used in analyses was visually reviewed and verified. The instantaneous heart rate (f_H) in beats min^{-1} was then calculated (60/R-R interval), where the R-R interval (in seconds) was the time between two adjacent R waves. Instantaneous heart rate profiles were plotted with Origin software.

The heart rate during activities ≥ 1 min in duration were calculated as total beats/activity duration. These activity heart rates included heart rates during breath holds (apneas) and when the animals took a breath at the surface. Indistinct ECG signals and the associated time periods during an activity were excluded from calculations of the heart rate. Observational and video records were analyzed to calculate stroke rate (total

strokes/activity duration in minutes), and respiration rate (total breaths/activity duration in minutes).

The predicted resting heart rate was calculated with Stahl's allometric equation (Stahl 1967):

$$HR_{predicted} = 241 \times (Body\ mass_{\ (kg)})^{-0.25}$$

Values are reported as mean ± standard error of the mean (s.e.m.) unless otherwise stated.

Results

We obtained distinct ECG signals from each animal (Fig. 2). The amplitude of the ECG signal could vary dependent on either the emergence of an electrode above the water (Fig. 3) or body orientation underwater (Fig. 4 A, B). There were no obvious changes in signal amplitude during respirations.

In 20 heart beats of each animal, the mean PR intervals were 263 ± 6.0 ms (killer whale), 206 ± 5.6 ms (pilot whale), and 362 ± 6.9ms (beluga whale). QRS intervals were 263 ± 1.8 ms (killer whale), 233 ± 4.7 ms (pilot whale), and 204 ± 6.5 ms (beluga whale).

Heart rates and respiration rates of the three different animals during various activities are shown in Table 1. Heart rates at rest were 41.9 and 38.6% higher than the predicted resting heart rate of 31 and 44 beats min^{-1} for the killer whale and pilot whale, respectively (Stahl 1967). The beluga whale had a resting heart rate that was 17.5% lower than the predicted 40 beats min^{-1}. During swimming activities, heart rate was higher than measured resting values in the killer whale and beluga whale, but swimming heart rate was lower than heart rate at rest in the pilot whale (Table 1). The lowest heart rates seen in the killer whale (19 beats min^{-1}) occurred during trained stationary submersions. We also frequently observed large oscillations in apneic f_H during all activities, including rest (Figs. 5–7). The animals were in sinus rhythm during these oscillations in apneic heart rate (Figs. 5a, 6a, 7a). During respirations, the heart rate typically increased (Figs. 5–7). Video analysis allowed calculation of stroke rate during study periods in the killer whale (0.4 ± 0.07, n=7) and beluga whale (0.2 ± 0.03 Hz, n=3), and construction of simultaneous stroke rate and heart rate profiles in the killer whale (Fig. 8).

Discussion

ECG signal characterization

A) The ECG signal and PR and QRS intervals

A typical heartbeat begins with depolarization of the sinoatrial (SA) node, which is followed by spread of the depolarization through the atria (atrial contraction) to the atrioventricular (AV) node and then to the ventricles (ventricular contraction). The ECG signal of a heartbeat consists of a P wave (atrial depolarization), the QRS complex (ventricular depolarization) and the T wave (ventricular repolarization). The PR interval (time between the P and R waves) represents atrial conduction time while the QRS interval (time between the Q to S waves) is a measure of ventricular conduction time. Minor differences among studies may exist secondary to differences in the heart rate and difficulty in distinction of low amplitude P waves (Ponganis 2007). The PR and QRS intervals measured in this study were within the documented interval range for similarly sized mammals (camels, horses, elephants) and even larger whales (Noujaim *et al.* 2004) (King *et al.* 1953, Spencer *et al.* 1967, Meijler *et al.* 1992b, Ponganis & Kooyman 1999).

The results from this study are consistent with the observations of Meijler and co-workers that atrial and ventricular conduction times do not increase allometrically in mammals larger than 1,000 kg (Meijler & Janse 1988, Meijler *et al.* 1992a). Because heart size, and therefore the distance a cardiac impulse must travel, increases with body mass, it is notable that conduction intervals do not increase allometrically in mammals larger than 1,000 kg. However, the mechanisms that allow rapid depolarizations in such large hearts are unclear as anatomical and histological investigations show conduction

fibers in cetacean hearts are similar to conduction fibers of other mammals (James *et al.* 1995, Ono *et al.* 2009).

The size and shape of any given component of the ECG signal may also vary dependent on the ECG electrode locations, heart rate, and the origin of the depolarization (Detweiler 2010). Both PR and QRS intervals can also vary with heart rate (Detweiler 2010). The ECG signals from the three whales had the characteristic components of the mammalian ECG signal (Fig. 2). We suspect that the shapes (*i.e.*, biphasic) of the P waves and T waves are probably secondary to the electrode location relative to the heart.

B) ECG signal amplitude

The ECG records from captive animals, whose behavior could be closely monitored, have allowed several observations that are potentially useful for future interpretations of ECG signals from whales diving in the wild. Although it is known that saltwater short circuits and dampens the ECG signal (Kastelein & Meijler 1989, Ponganis 2007), it is notable that the amplitude of the ECG signal of the beluga whale can increase three-fold when even one ECG lead comes out of the water during spy-hopping activity (Fig. 3). The amplitude of the ECG signal can also change when a whale changes body orientation underwater, as indicated in Figs. 4A and 4B. While swimming underwater in a lateral position (45–90°), the ECG signal amplitude in the beluga whale decreased approximately three-fold (Fig. 4A). Signal amplitude in the killer whale decreased similarly when the whale was swimming upside-down underwater (Fig. 4B). Although it is unclear what factors caused these signal changes in ECG amplitude with body position, these unexpected findings may be useful in the analysis of ECG records from whales

diving in the wild. It is also possible that detection of such changes in ECG amplitude with body orientation may be dependent on the electrode location in this study. For this study, we placed the ECG-suction cup tag ventrally to optimize signal conduction.

Activity heart rate

Higher-than-predicted resting heart rates in the killer whale and pilot whale are not surprising because our data were not obtained during true resting conditions (*e.g.*, fasting). Although the animals were not active during recordings, the range of heart rates in the three whales at rest may be attributed to experimental conditions, such as interactions with trainers or other whales, non-fasting metabolic rate, and activity level. Indeed, reports of metabolic rates of killer whales at rest are 1.1 – 2.7x the predicted Kleiber basal metabolic rate (Williams *et al.* 2001, Worthy *et al.* 2014, Williams *et al.* 2017). Although we did not investigate the effect of vocalizations on heart rate in this study, it has been reported that there is a small metabolic cost associated with vocalizing in dolphins, which may therefore also contribute to higher than predicted resting heart rates (Noren *et al.* 2013).

The bradycardia associated with the onset of the apneic periods shown in the profiles is characteristic of the mammalian dive response (Figs. 5–7). Stationary, trained submersions in the killer whale resulted in a dive response with an apneic bradycardia (30 ± 0.5 beats min^{-1}) that approximated the allometrically predicted resting heart rate. Oscillations in instantaneous heart rate were common during these apneas (Fig. 5C).

The minimum heart rate of the killer whale in this study, 19 beats min^{-1}, was lower than previously documented heart rates of captive killer whales (30 beats min^{-1}), and the maximum heart rate in this study, 81 beats min^{-1}, was 35% higher than previously reported in the killer whale (Spencer *et al.* 1967). Minimum beluga whale heart rate values in this study (19 beats min^{-1}) were not as low as the 12 beats min^{-1} measured in a wild, harpooned beluga whale (King *et al.* 1953), but were consistent with reports of 20 beats min^{-1} in a captive beluga whale (Lyamin *et al.* 2016). Swimming elicited a slight increase in overall activity heart rates of the killer whale and beluga whale (Table 1).

These are the first reports of heart rate recordings of a pilot whale. Instantaneous heart rate in the pilot whale during rest was characterized by large and frequent oscillations during apnea (Fig. 6A). Unlike the killer whale and beluga whale, average heart rate during spontaneous, submerged swimming of the pilot whale was lower than that measured at rest, but it approximated the allometrically predicted heart rate. These lower values are probably secondary to a more intense dive response under these conditions in the pilot whale than in the killer whale and beluga whale (Fig. 6B).

The overall heart rates measured during these different activities of the three whale species either approximated or exceeded their allometrically predicted resting heart rates. For these short duration dives of up to four minutes in this study, it appears that heart rate is not reduced significantly below what would be considered a resting level. We expect that a more intense dive response and bradycardia would occur during prolonged dives to depth in the wild.

Instantaneous heart rate (f_H)

Frequent, often beat-to-beat, fluctuations in the apneic f_H profiles were apparent during all activities, including rest (Figs. 5–7). Similar fluctuations in heart rate between 30 and 60 beats min^{-1} had also been obtained previously from a captive killer whale during inactive, apneic periods (Spencer *et al.* 1967). As illustrated in the ECG rhythm strips in Figs. 5–7, these irregular heartbeats were of atrial origin (P waves present) in all three species from this study. Thus, the fluctuations in heart rate appeared secondary to changes in the rate of depolarization of the atrium that could result either in a slower heart beat (e.g., a longer heart beat interval or a pause) or a faster heart beat (e.g., a shorter heart beat interval). The faster heart beat after an abrupt short heart beat interval is termed a premature atrial contraction.

The rate of atrial depolarization is affected by the intrinsic rate of depolarization of the sinus node and the influence of the autonomic nervous system (Detweiler 2010). Parasympathetic stimulation slows heart rate while sympathetic stimulation accelerates heart rate. Premature atrial contractions are also often followed by a prolonged heart beat interval due to resetting of the sinus node (Catalano 2002). Although the sympathetic nervous system is activated during trained and spontaneous breath holds of short duration (Ponganis *et al.* 2008, Suzuki *et al.* 2017), we suspect that such abrupt changes in heart rate at low apneic heart rates are secondary to changes in parasympathetic stimulation of the heart for three reasons. First, the decrease in heart rate during a dive or breath-hold is secondary to parasympathetic stimulation (Butler & Jones 1997, Ponganis *et al.* 2017). Second, these fluctuations in heart rate were observed at rest and during leisurely underwater swimming with stroke-glide locomotory patterns and with stroke rates

predominantly less than 0.5 Hz (Fig. 8). The modulation of heart rate at such low exercise intensity is known to be primarily under parasympathetic control (Carter *et al.* 2003, Signore & Jones 1996, Ponganis *et al.* 2017). Third, despite activation of the sympathetic nervous system to constrict arteries and maintain blood pressure during dives (Scholander *et al.* 1942, Elsner *et al.* 1966), the parasympathetic system dominates over the sympathetic system in control of heart rate and produces a bradycardia (decrease in heart rate) during breath holds (Signore & Jones 1995, Signore & Jones 1996, Panneton 2013, Ponganis *et al.* 2017).

It has been proposed that effects of depth and exercise in marine mammals may result in autonomic conflict and cardiac arrhythmias, and that behavior modification during dives (*e.g.*, variable exercise intensity) can determine the risk of potential cardiac instability (Williams *et al.* 2015a, Williams *et al.* 2015b). The marked fluctuations in apneic heart rate observed in whales during rest, stationary submersions, and leisurely swims demonstrate that irregular heartbeats can routinely occur even without significant changes in depth and exercise intensity. Based on these findings, as well as the common occurrence of irregular heartbeats during deep dives of California sea lions (*Zalophus californianus*) and emperor penguins (*Aptenodytes forsteri*) (McDonald & Ponganis 2014, Wright *et al.* 2014), we suggest that benign fluctuations in heart rate are common in diving animals (Ponganis *et al.* 2017).

Conclusions

In this study, we found that the PR intervals and QRS intervals of these mid-sized whales did not increase allometrically, which supports previous studies that demonstrated the lack of such a relationship in mammals larger than 1000 kg (Meijler & Janse 1988, Meijler *et al.* 1992a). The adaptations responsible for rapid conductions times in larger mammalian hearts remain unknown. Heart rates of these whales at rest in the pool ranged from 17% less than (beluga whale) to 40% greater than (killer whale and pilot whale) allometrically predicted resting heart rates. We attributed this range of values to experimental conditions and often elevated metabolic rates previously measured in whales "at rest" in pools. Heart rates during swimming activities (which included apneas and respirations) were higher than those measured at rest in the killer whale and beluga whale, but less than that measured at rest in the pilot whale. Heart rates during spontaneous submerged swimming of the pilot whale and during trained, stationary breath holds of the killer whale approximated the allometrically predicted resting heart rate. Frequent fluctuations in heart rate occurred during all activities, even at rest and, in the killer whale, during stationary submersions. We attribute these fluctuations in heart rate to adjustments in parasympathetic tone.

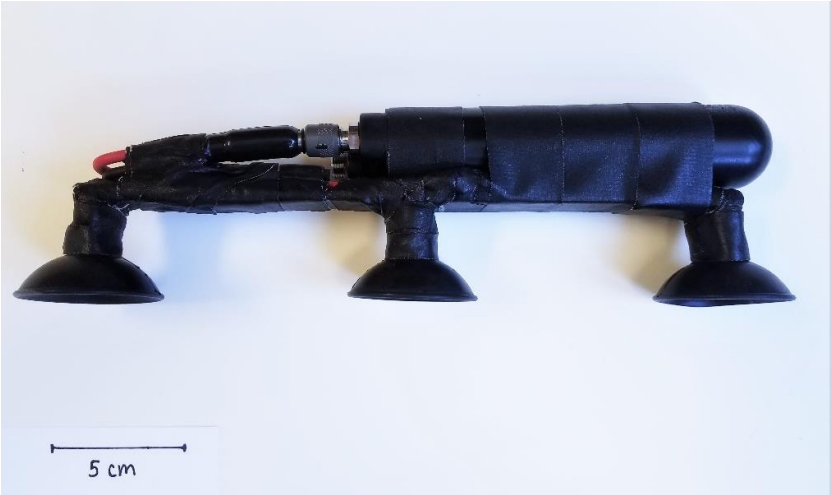
This thesis is being prepared for publication in 2017. Bickett, Natalie; Tift, Michael, St. Leger, Judy, Ponganis, Paul. (2017) The electrocardiogram and heart rate in three mid-sized whale species. The thesis author was the primary investigator and author of this paper.

Appendix

Table 1. Heart rate (beats min^{-1}) during different activities.
Except for the trained, stationary submersions of the killer whale, these heart rates include both apneic (breath-hold) and eupneic (breathing) heart rates. Heart rate was recorded during periods of rest, when the whale was motionless at the surface of the pool, and during submerged swims, when the whale was spontaneously swimming. Additional killer whale heart rate records were obtained during trained surface swims, when the whale's blowhole was at the pool's surface, and trained stationary submersions, when the whale was stationed motionless 5 m below the surface. During trained submersion of the killer whale, heart rate was analyzed from the time of submersion to the time of surfacing. Abbreviations: min – minimum; max – maximum.
*Stationary submersions were defined by an initial breath and a final breath.

Animal	Activity	Heart rate (beats min^{-1})	Min - max	Duration (min)	Respiration rate (breaths min^{-1})	N
Killer whale	Rest	44 ± 2.1	22-75	10.8 ± 1.43	1.3 ± 0.06	6
	Submerged swim	58 ± 1.2	23-81	19.1 ± 1.33	1.3 ± 0.06	3
	Surface swim	56 ± 3.1	30-73	2.7 ± 0.46	1.8 ± 0.30	7
	Stationary submersion	30 ± 0.5	19-70	2.3 ± 0.16	*	14
Pilot whale	Rest	61 ± 2.9	25-86	3.6 ± 0.43	1.5 ± 0.15	4
	Submerged swim	43 ± 2.1	20-77	3.7 ± 1.1	2.0 ± 0.17	5
Beluga whale	Rest	33 ± 2.0	19-74	4.5 ± 1.22	1.3 ± 0.03	2
	Submerged swim	46 ± 1.5	19-71	19.8 ± 4.0	2.3 ± 0.25	10

A



B



Figure 1. (A) ECG-suction cup tag. (B) Tag placement on a killer whale during data collection at SeaWorld, San Diego

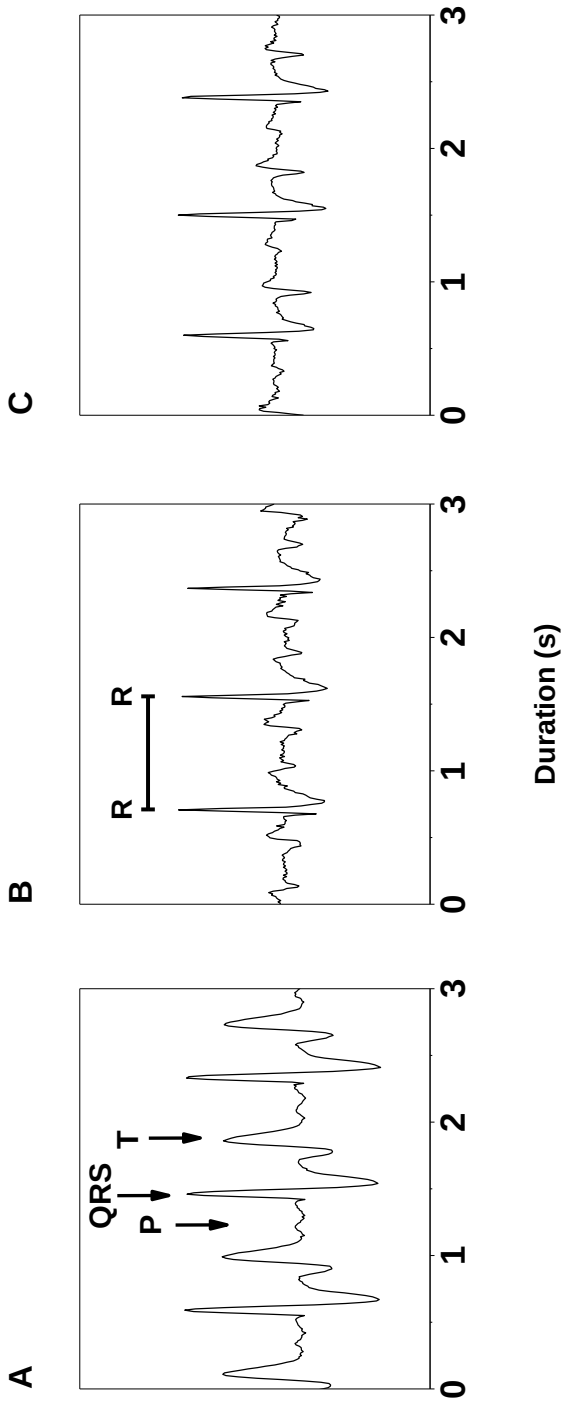


Figure 2. Examples of the ECG trace used to calculate PR intervals and QRS complex durations for a (A) killer whale, (B) pilot whale, and (C) beluga whale. The P wave (atrial depolarization), QRS complex (ventricular depolarization, and T wave (ventricular

repolarization) are indicated on the killer whale ECG trace (A). Instantaneous heart rate (f_H) was calculated using the time between two adjacent R waves (R-R interval) (B)

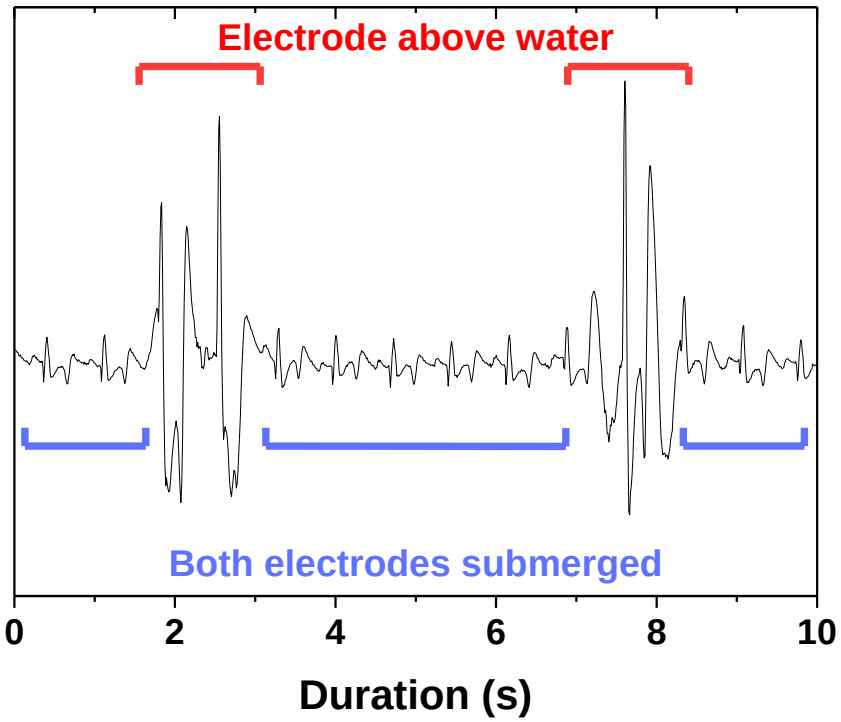


Figure 3. The effect of saltwater on the ECG signal: changes in signal amplitude associated with spy-hopping. The ECG signal increased almost 3-fold in amplitude when the cranial suction-cup electrode came out of the water during spy-hopping behavior in the beluga whale (no respirations).

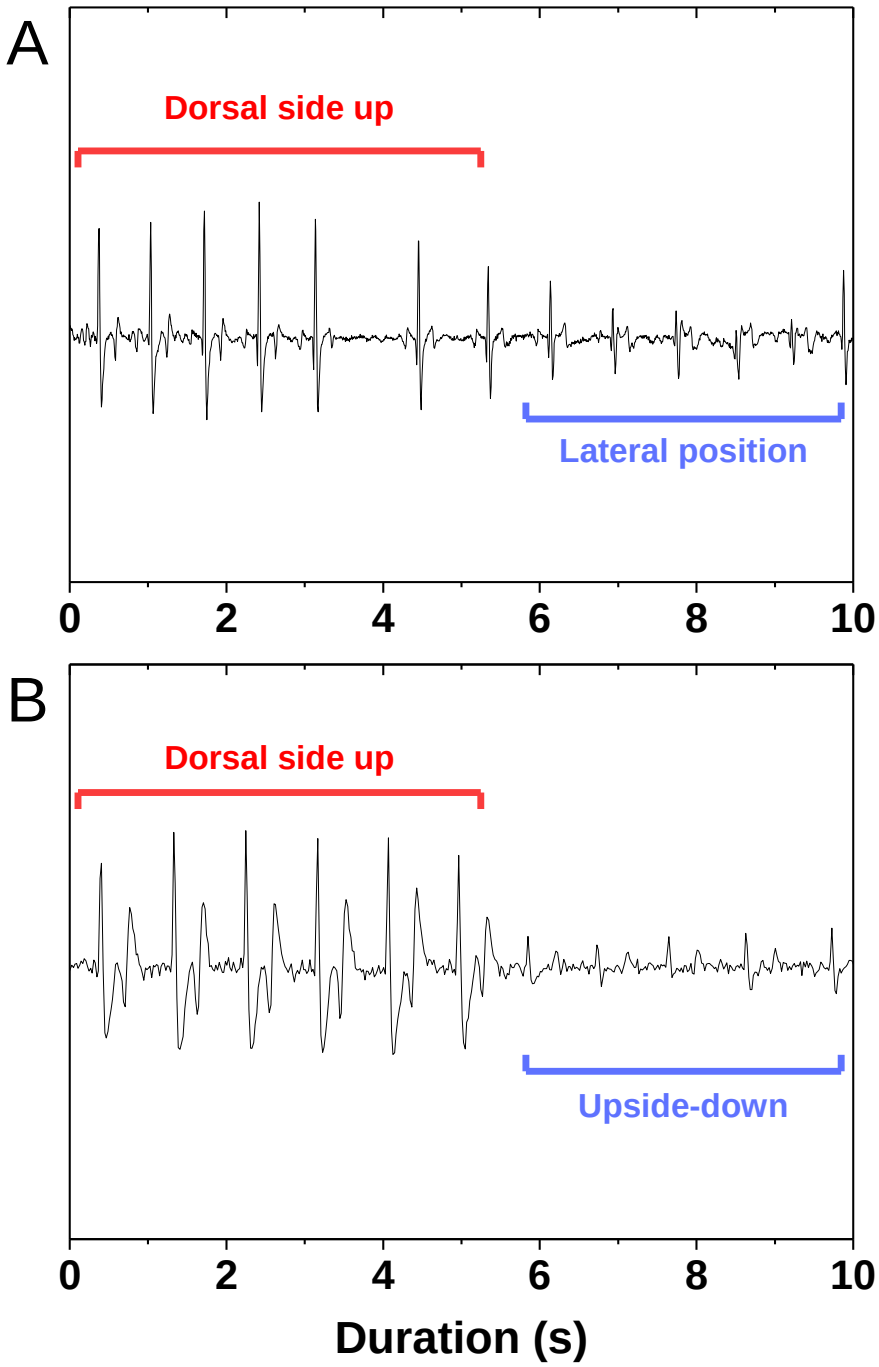


Figure 4. Changes in the ECG signal with body orientation. (A) The ECG of the beluga whale during submerged swims decreased in signal amplitude when the whale swam in a lateral position at an angle of 45° – 90°. (B) Amplitude of the ECG signal decreased when the killer whale turned upside-down while swimming underwater

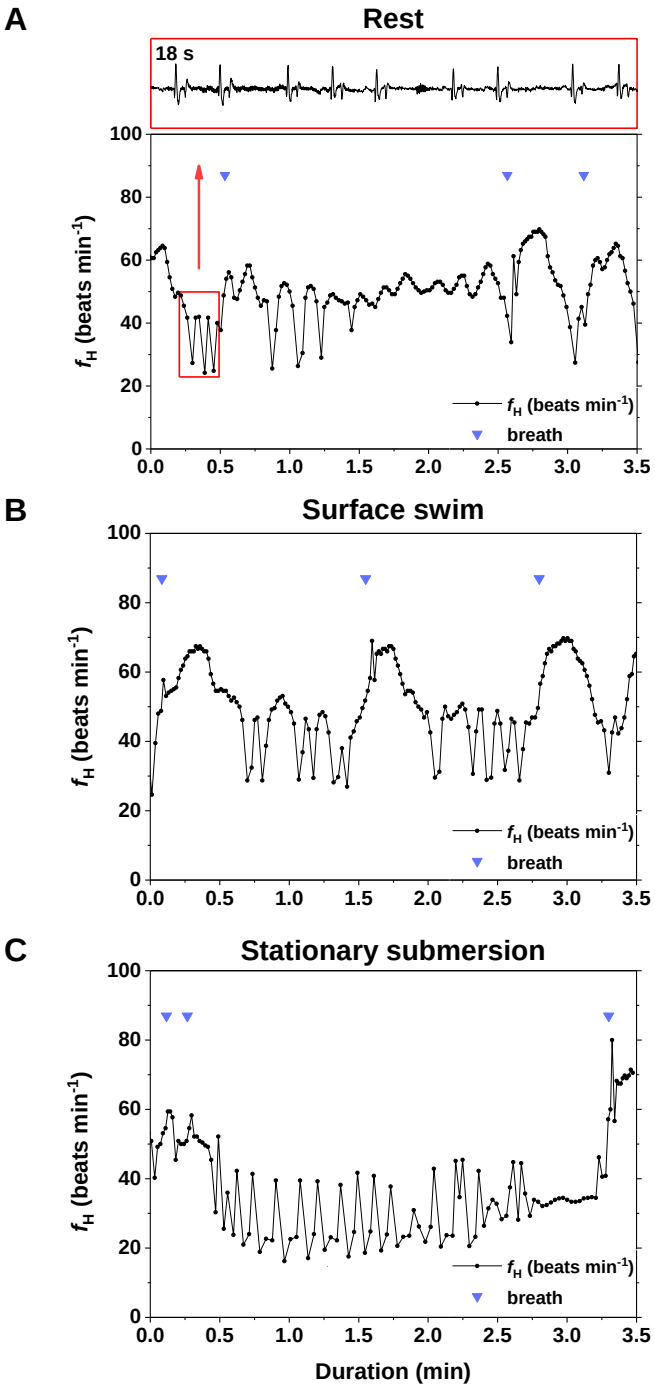


Figure 5. Instantaneous heart rate (f_H) profile per activity and samples of the corresponding ECG records of a killer whale during a spontaneous rest period (inactive, no stroking) (A), surface swimming (trained) (B), and trained, stationary submersion (C). Breaths are indicated by blue arrows. The 18-s ECG record directly above the rest f_H profile corresponds to the f_H outlined by the red box (A). Benign arrhythmias or fluctuations in heart rate occur during both stationary activities (A, C) and leisurely swimming (B). Stroke frequency was 0.5 ± 0.11 strokes s^{-1} (n = 4) during surface swims

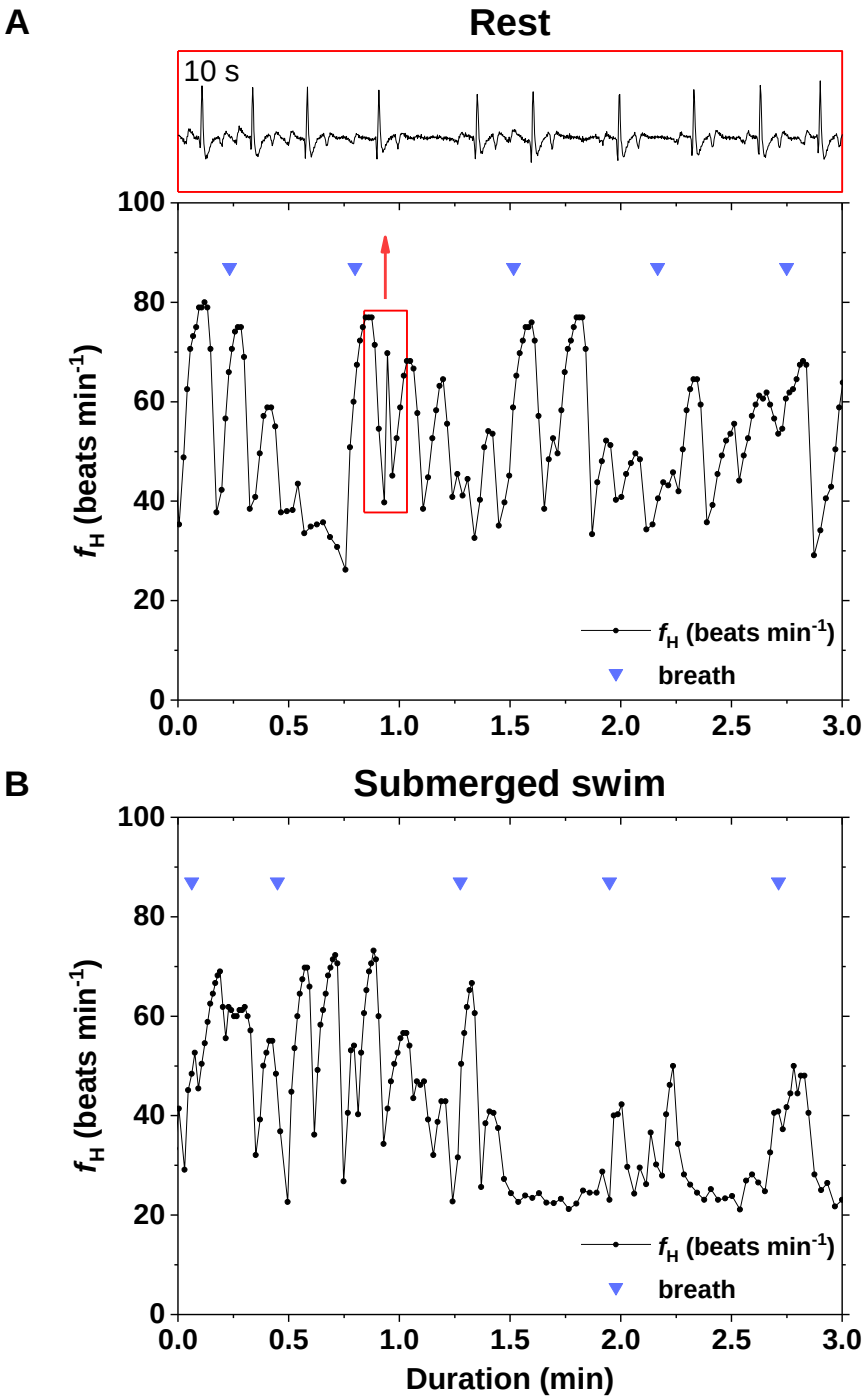


Figure 6. Instantaneous heart rate (f_H) profile per activity and samples of the corresponding ECG records of a pilot whale during two spontaneous activities: resting (A) and submerged swimming (B). Breaths are indicated by blue arrows. Benign arrhythmias (fluctuations in heart rate) occurred during both stationary (A) and leisurely swimming (B) activities.

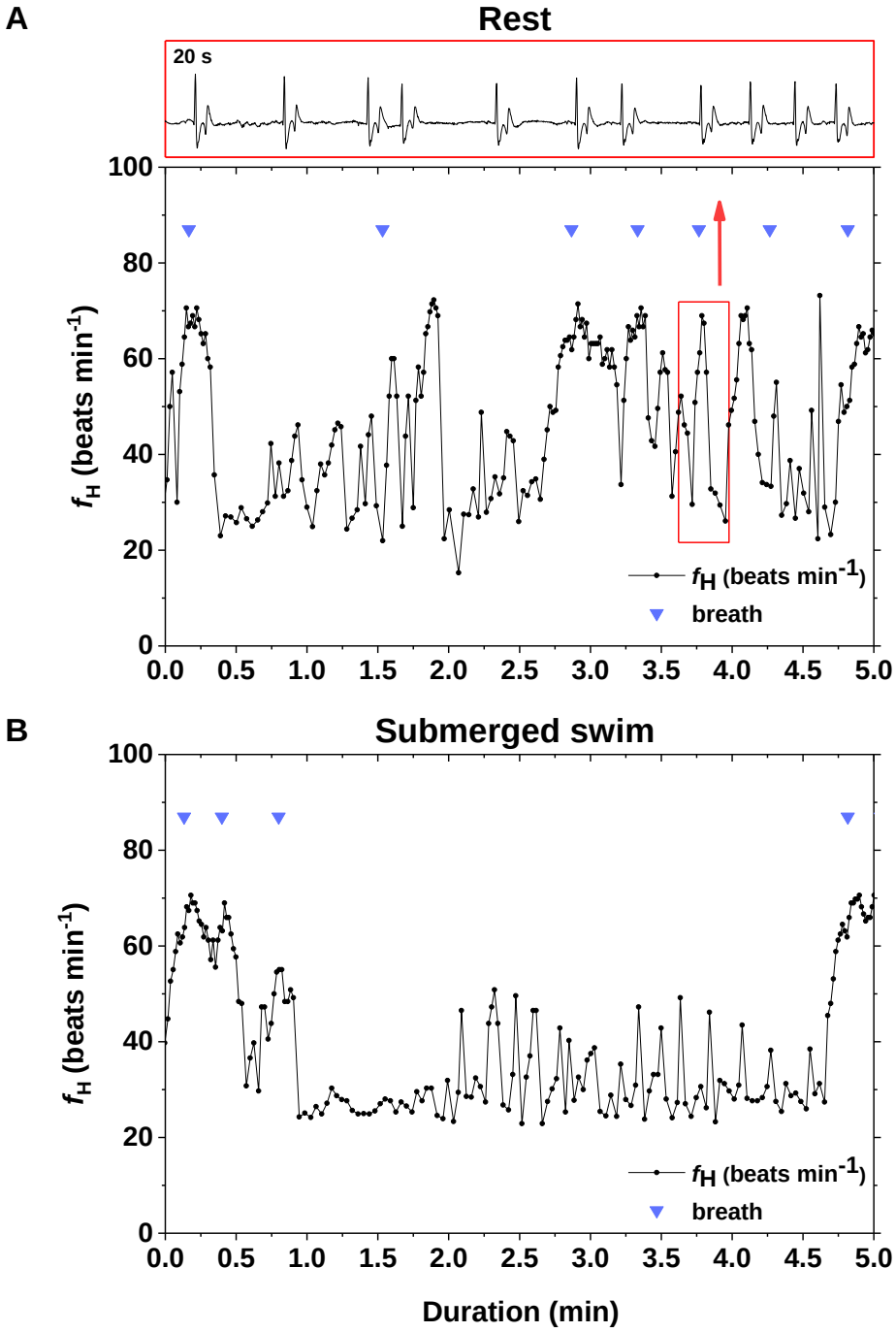


Figure 7. Instantaneous heart rate (f_H) profiles of a beluga whale during two spontaneous activities: rest (A) and submerged swimming, including a 4-min submerged swim (B). Breaths are indicated by blue arrows. The 20-s ECG record in A corresponds to the f_H profile in the red box. Benign arrhythmias (fluctuations in heart rate) occurred during both stationary (A) and leisurely swimming (B) activities. Stroke frequency was 0.18 ± .03 strokes s^{-1} during submerged swims

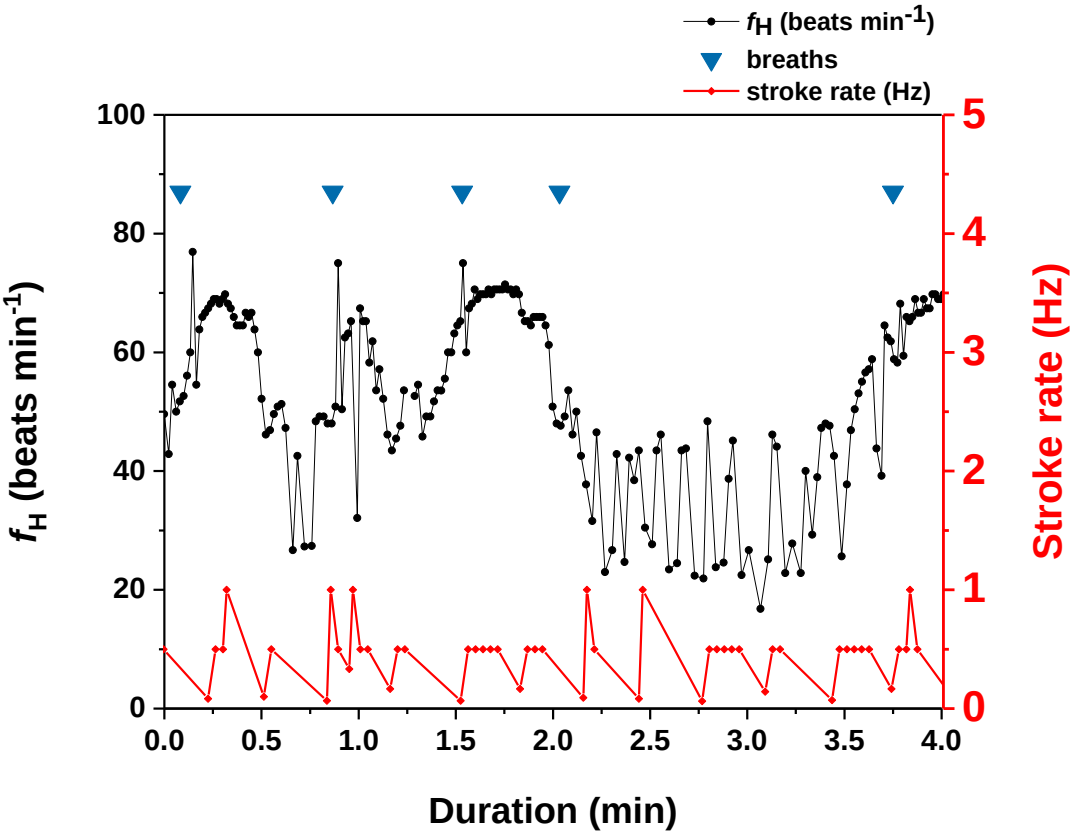


Figure 8. Instantaneous heart rate and stroke rate profiles during spontaneous submerged swimming of the killer whale, including an approximate 2-min submerged swim. Overall stroke rate for this submerged swim was 0.3 strokes s^{-1}

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