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The scaled sardine's unique metabolic phenotype and its implications for the susceptibility of small tropical pelagic fishes to climate change

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Small pelagic fishes (e.g., sardines, anchovies and their relatives) are preyed upon by large predatory fishes, birds and mammals, and thus, are key species in marine food webs and with respect to ecosystem health and productivity. However, we know little about their physiology, and such information will be critical to predicting how their populations may be impacted by human-induced rapid environmental change (HIREC) and in implementing effective conservation strategies. As a first step, we determined the maximum swimming speed, aerobic capacity [maximum metabolic rate (MMR) and aerobic scope (AS)] and cost of transport (COT; the energy required to swim a given distance) of scaled sardines (*Harengula jaguana*) collected in Eleuthera (The Bahamas). The scaled sardine's critical swimming speed (U_{crit}) was ~ 5–6 body length's per second, and this agrees with data collected on free-swimming schools of similar fishes in the wild. However, they had unexpectedly high values for MMR and AS (~ 25% and 70% greater than tuna, respectively), and for COT. These findings have important implications with regard to how these ecologically important fishes will potentially respond to HIREC-related challenges such as increased temperature and decreases in the biomass and size of plankton upon which they feed.

Keywords Metabolic capacity, Maximum metabolic rate, Aerobic scope, Cost of transport, Critical swimming speed, Tropical fish

Small plankton eating (i.e., planktotrophic) fishes such as anchovies, sardines, menhaden, pilchards, sprat and mullet play a crucial role in the trophic dynamics of marine ecosystems as they are an important food source for large predatory fishes [e.g., tuna (e.g., yellowfin, *Thunnus albacare*; skipjack, *Katsuwonus pelamis*), mahi mahi (*Coryphaea hippurus*), wahoo (*Acanthocybium solandri*) and greater amberjack (*Seriola dumerili*)], and marine mammals and birds[1–3]. There is some, but very limited, information on the bioenergetics and thermal physiology of these important fishes. For example, Faleiro et al.[4] examined how the survival, growth, metabolism and thermal tolerance of larval European sardine (*Sardina pilchardus*) were impacted by predicted future changes in average ocean temperature (i.e., + 2 °C). Van der Lingen[5] provides information on the effect of temperature (12–20 °C) and swimming speed in tanks on the metabolism of the pilchard (*Sardinops sagax*), and James and Probyn[6] detail the relationship between the latter parameter and metabolism of the anchovy (*Engraulis capensis*) at 16 °C. Thoral et al.[7] and Queiros et al.[8] described the metabolic consequences of temperature-dependent (10 vs. 20 °C) food deprivation, and feed size and temperature (16 and 21 °C), respectively, on the metabolism of *Sardina pilchardus*. Finally, Pribyl et al.[9] determined the upper thermal tolerance and optimal temperature of the Pacific sardine (*Sardinops sagax caeruleus*) when held at 15 vs. 17 °C.

However, additional information in this area is clearly needed given that small pelagic fish populations are known to respond rapidly to changes in ocean climate[10,11]. These species also live in tropical / subtropical regions where temperatures of > 25 °C are typical, and data suggests that tropical fish species may already be living close to their upper temperature limit[12,13]. Finally, a mechanistic understanding of biological / physiological processes, and how they respond to environmental challenges including human-induced rapid environmental

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change (HIREC), can inform management actions and ensure that they are effective with regard to conservation efforts[14,15].

In this study, we determined the swimming performance and metabolic capacity of small groups of scaled sardine (*Harengula jaguana*) in Eleuthera (The Bahamas) using a critical swimming speed (U_{crit}) test at 27 °C, after spending considerable effort in catching and holding these fish so that they were in good condition and suitable for performing such tests. This work reveals that the scaled sardine has the highest maximum metabolic rate (MMR) and aerobic scope (AS) recorded for any fish species (even when temperature and body mass are taken into account), but that their metabolic rate when swimming and cost of transport (COT, the energy required to swim a given distance) require considerable dietary caloric intake. In addition, it sets the stage for additional studies on this species' thermal tolerance (i.e., critical thermal maximum while swimming, CTS_{max}[16,17]) and on what cardiorespiratory and metabolic adaptations support this species' incredible metabolic capacity.

Results and discussion

Methodology considerations when working with these fish

One of the most relevant things we learned during this study was how difficult this species is to work with, and to use in metabolic and swimming performance studies. The scaled sardine becomes highly stressed very quickly as indicated by erratic behaviour, and loses large numbers of scales even when handled gently [as previously reported for the sprat (*Sprattus sprattus*)[18]. They do not recover well from even mild anaesthesia used for weighing and transfer into experimental chambers, and become highly agitated when alone or confined in small spaces. This knowledge, however, allowed us to make appropriate adjustments to how this species was caught from the wild, held in tanks and netted, and used in such experiments. First, we recommend using a seine net when catching the scaled sardine for scientific research as employing a monofilament cast net results in excessive scale loss and a large number of mortalities, and fish that are unable to perform well in such tests for prolonged periods post-capture (i.e., > 1–2 weeks). Second, sardines held in tanks require a moderate water flow/current, and covering the tanks with 'shade cloth' helps prevent stress associated with various husbandry and other activities. Lastly, the fish must be netted from the tanks carefully, as even lowering the water and limited chasing can result in mortalities in the population being held. To address this issue, we recently constructed a tank divider that can be inserted onto a tank's existing internal standpipe, and can be 'closed' so that the fish are confined in an ever smaller proportion of the tank. This allowed us to net fish even quicker without lowering the tank's water level and with little to no chasing, and thus, improve the welfare of fish being held / tested.

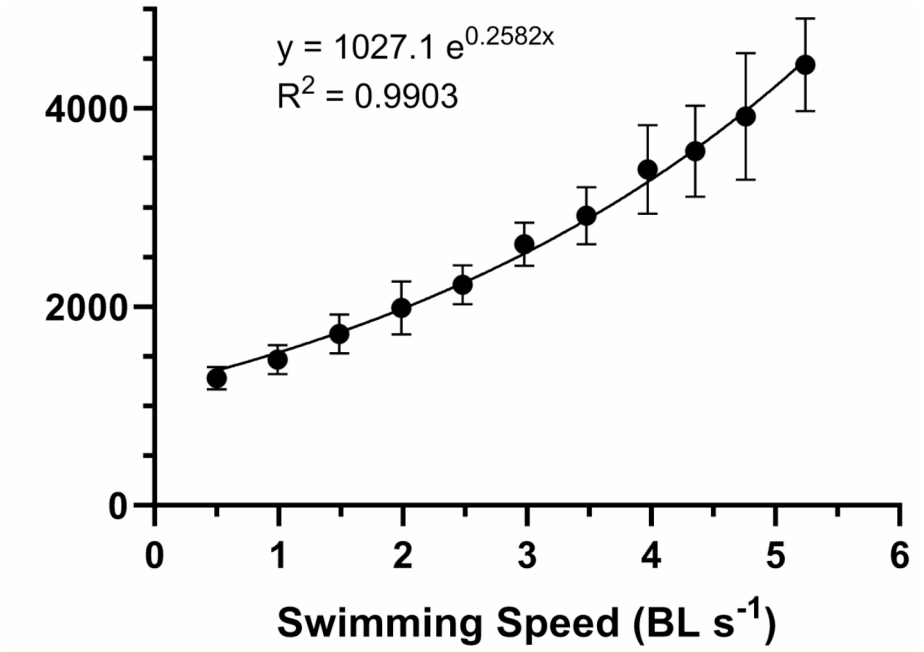
We also found that these fish do not 'rest' (i.e., they typically displayed foraging / searching behaviours) when put into a swim-tunnel when there is no, or a very slow, water current (e.g. < 2.0 body lengths per second; BL s^{-1}), regardless of the number of individuals in the tunnel. This makes it difficult to get relevant measurements of routine/resting metabolic rate (RMR), standard metabolic rate (SMR) by back-extrapolating to zero velocity, or metabolic rate at slow swimming velocities. Thus, measurements of SMR and RMR should probably be made in their holding tanks after a number of weeks post-capture as in Thoral et al.[7] and Queiros et al.[8]; although cylindrical respirometers (i.e. ~ 10 cm high x > 3 body lengths in diameter) may also work. Finally, when holding sardines for prolonged periods, we recommend that a supplementary diet of live organisms be offered given their high metabolic rates (see below). *Artemia*, calenoid copepods and diatoms have been provided in past studies[6,18–20], and enriched *Artemia* are extensively used in marine finfish aquaculture and may be a suitable nutritional source that can be easily cultured.

Standard and routine metabolic rates

The scaled sardine's SMR and oxygen consumption ($\dot{M}O_2$) at the slowest swimming speed (0.5 BL s^{-1}) were 1122 ± 133 and 1281 ± 155 mg O_2 kg^{-1} hr^{-1} at 27 °C, respectively (Fig. 1A). These values are approximately 2.5-fold higher than average values reported for sprat, northern anchovy (*Engraulis mordax*), pilchard (*Sardinops sagax*) and various species of sardine (average 420 mg O_2 kg^{-1} hr^{-1}; range 162–669 mg O_2 kg^{-1} h^{-1}) free-swimming in tanks at slow speeds (~ 0.3–0.9 BL s^{-1}) at 18-21 °C[5–7,18,20,21] when a temperature quotient (Q_{10}) value of 1.83 is used to temperature adjust the data[5,22]. This disparity is not due to poor condition[8] as the condition factor of the fish used in this study was 1.39 ± 0.03, but not surprising given their behavior at slow water velocities. The fish in this study were quite active and would often swim at an angle to the flow with their noses pressed against the wall of the swim tunnel (i.e., possibly looking for a way out; see Supplemental Fig. 1). However, this behaviour was reduced greatly, and then stopped, when swimming speed was increased (see video included in the Supplementary Material) and this resulted in an exponential swimming speed-oxygen consumption relationship (see Fig. 1A) typical of that seen in other fishes[23].

Swimming and metabolic capacity

The sardines in this study were swum in small groups at 27 °C, and the experiment stopped when the first or second fish became exhausted (see Methods section). While this likely resulted in an underestimation of their true U_{crit} and MMR, it is clear that this species has considerable swimming and metabolic capacities at this temperature. For example, the U_{crit} of the scaled sardine swum in groups was 5.01 ± 0.23 BL s^{-1} (range 4.48–5.80 BL s^{-1}) in this study, which falls between the values reported for smaller (~ 3.5 cm) tropical clupeiforms swum at 28–30°C (i.e., 7.54 BL s^{-1} for *Jenkinsia* spp. and 4.13 BL s^{-1} for *Spratelloides*;[24]), and for the maximum cruising speeds measured for sardines in the open ocean (3.8–5.9 BL s^{-1};[25–27]). Based on the above, we estimate that the true mean U_{crit} of sardines of this size likely approaches or exceeds 6.0 BL s^{-1}. This is considerably higher than that measured for wild chub mackerel (4.3 BL s^{-1}) of a similar size to the sardines tested in the present work[28], but lower than maximum voluntary swimming speeds (10.7 BL s^{-1}) reported for menhaden (*Brevoortia*



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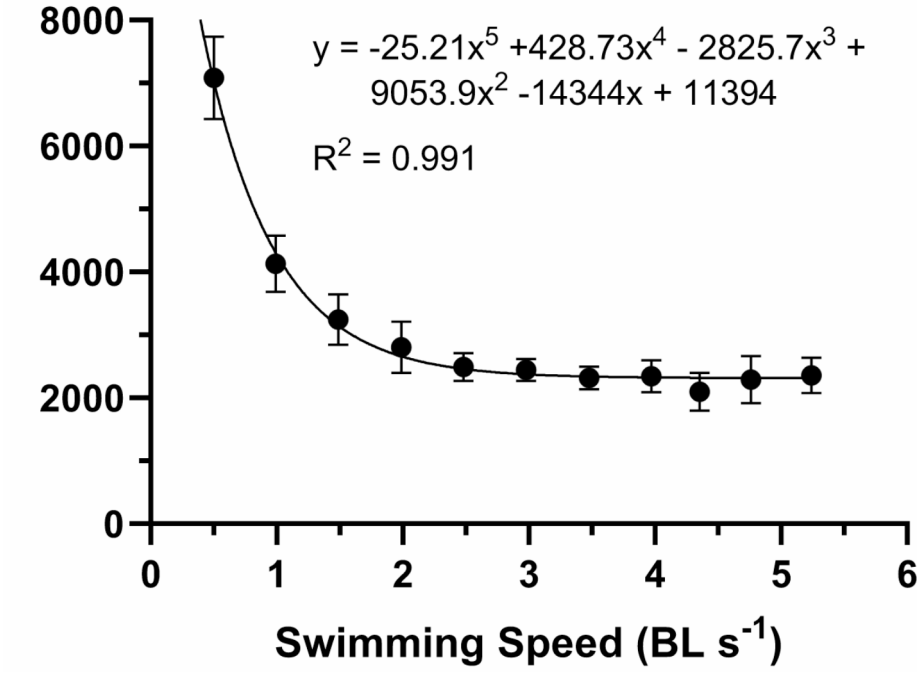

Fig. 1. Oxygen consumption and gross cost of transport for the scaled sardine during a critical swimming speed (U_{crit}) test at 27 °C. Values are means ± 1 standard error, $n = 6$ groups of fish.

tyrannus) during short-term (i.e., 2 min.) trials at 27 °C[29], and for sardines during avoidance/escape responses (i.e., 6.2[30] and 7.3 BL s^{-1}[16]).

With regard to the scaled sardine's active metabolic rate, MMR, AS and factorial aerobic scope (FAS; MMR/SMR), there are few data in the literature to which our values can be compared. However, there are metabolic data for a number of small planktotrophic fishes at various swimming speeds measured in tank respirometers. For example, van der Lingen[5] and Durbin et al.[20] measured the oxygen consumption of free-swimming sardines

(*S. sagax*) and menhaden, respectively, when actively feeding at speeds up to ~2.5 BL s^{-1}, and at this swimming speed they report $\dot{M}O_2$ values equivalent to 1750 and 1525 mg O_2 kg^{-1} hr^{-1} at 27 °C. These values are very similar to that reported for scaled sardines swimming at this speed in this study (1791 mg O_2 kg^{-1} hr^{-1}). However, the MMR, AS and FAS we measured were 4569 ± 350 mg O_2 kg^{-1} hr^{-1}, 3446 ± 290 mg O_2 kg^{-1} hr^{-1} and 4.2 ± 0.4, respectively. These MMR and FAS values are lower than those measured by James and Probyn[6] for spontaneously swimming Cape anchovies [(*Engraulis capensis*); 3000 mg O_2 kg^{-1} hr^{-1} (5831 mg O_2 kg^{-1} hr^{-1} at 27 °C) and ~10.7, respectively]. These differences may be simply explained by: (1) species and methodological differences; and/or (2) our value of MMR (range 3060 to 5392 mg O_2 kg^{-1} hr^{-1}) is likely an underestimation (see below). In addition, if we assume that our estimate of average SMR is ~2.5-fold higher than expected (as explained above), the adjusted FAS (i.e., 10.2) becomes very comparable to that reported by James and Probyn[6] for anchovies (i.e., 10.7). Collectively, these data show that small planktotrophic fish have an extremely high metabolic capacity. This is not surprising given their cruising speeds in the wild (1.2–5.9 BL s^{-1}), and that they are often doing so while filter feeding. When filter feeding, these fish have a large mouth gape and flared opercula, their body shape changes, and the resistance offered as the water passes through the gills makes constant swimming very energetically expensive[6,20].

However, one must compare their metabolic rate to a range of other fishes to truly appreciate this species' metabolic capacity. Thus, as part of this study, we searched the literature for data on other fishes that live in similar environments to the scaled sardine and/or are predators of these fish, and report the collected metabolic data after it was corrected for mass and temperature (to 25 °C) (see Table 1). Interestingly, the MMR values for these fishes appear to fall into 4 groups; small planktotrophic fishes (i.e., sardines and anchovies; > 3000 mg O_2 $Kg^{-0.937}$ hr^{-1}), tunas and other scombrids (~2300–2800 mg O_2 $Kg_{-}^{0.937}$ hr^{-1}), other pelagic predatory fishes (~1100–1300 mg O_2 $Kg^{-0.937}$ hr^{-1}) and other tropical fish species (400–600 mg O_2 $Kg^{-0.937}$ hr^{-1}). In fact, if the maximum value recorded for our scaled sardines and the data provided for Cape anchovy in van der Lingen et al.[5] are considered to be representative of the MMR values for these species (Table 1), our data suggest that the MMR of these fishes is at least 25% greater than that of tuna. In addition, these values are comparable to the highest reported MMR of which we are aware for any fish (i.e., 4450 mg O_2 $Kg^{-0.937}$ hr^{-1}; estimated for a single 40 kg sailfish during a pursuit dive when scaled to 25 °C)[31]. Collectively, these data suggest these small planktotrophic fish are amongst the ocean's 'elite athletes', and an exception to the dogma proposed by Killen et al.[32] that fish species from upper trophic levels have the highest maximum metabolic rates.

Although our finding that the scaled sardine's MMR is 25% higher than that for other tropical fish considered to be the 'top performers' is noteworthy, what is truly remarkable is the sardine's ability to increase their aerobic metabolism (i.e., both their AS and FAS). These values were 3730 mg O^2 $kg^{-0.937}$ hr^{-1} and 12.8, respectively, for the best performing group of sardines, and these values are ~70% and approach 2-fold greater, respectively, than those for tuna at the same temperature (Table 1). One could argue that this is partially due to the lack of good data for exercise-induced MMR values in tunas, and the possibility that the metabolic capacity of these species has been underestimated. However, it is likely that our estimates of AS and FAS are also low given that we swam the sardines in small groups, and stopped the experiments when weaker individuals reached their performance limits.

Common Name	Species	Mass (kg)	Study Temp. (°C)	MMR (mg O_2 $kg^{-0.937}$ h^{-1})	AS (mg O_2 $kg^{-0.937}$ h^{-1})	FAS	Reference
Scaled Sardine	*Harengula jaguana*	0.0145	27	3101*	3178ω	10.17ω	This study (mean data)
Scaled Sardine	*Harengula jaguana*	0.0104	27	3584*	3730ω	12.8 ω	This study (highest group value)
Cape Anchovy	*Engraulis capensis*	0.3	16	5168+	2533ω	10.7	James and Probyn[6]
Skipjack Tuna	*Katsuwanus pelamis*	1.7	25	2275+	1913	6.3	Dewar and Graham[46]
Skipjack Tuna	*Katsuwanus pelamis*	2	23.5	2859+	2246	7.14	Gooding et al.[47]
Yellowfin Tuna	*Thunnus albacares*	1.4	25	2758‡	2400	7.71	Bushnell and Brill[48]
Yellowtail Kingfish	*Seriola lalandi*	2.23	25	844*	633	4.0	Clark and Seymour[32]
Yellowtail Kingfish	*Seriola lalandi*	0.792	24	1260*	ND	ND	Palstra et al.[49]
California Yellowtail	*Seriola dorsalis*	0.0658	17.6	1022*	798	5.0	Wegner et al.[50]
Mahi Mahi	*Coryphaena hippurus*	0.04	28	1123*	984	3.71	Heuer et al.[51]
Bonefish	*Albula vulpes*	0.672	20.6	368*	150	2.23	Murchie et al.[52]
Schoolmaster Snapper	*Lutjanus apodus*	0.0345	26	582*	415	5.1	Nati et al.[17]
Green Jack	*Caranx caballus*	0.19	27	465*	399	3.6	Dickson et al.[53]

Table 1. Maximum metabolic rate (MMR), aerobic scope (AS) and factorial aerobic scope (FAS) for planktrotrophic fish species, their predators in tropical waters, and for other fishes in the Bahamas (at Cape Eleuthera). All data, but those for the mahi mahi and yellowtail kingfish, were collected on wild fish. The data were adjusted to a temperature of 25 °C using a Q_{10} of 1.83[5,22] and a mass scaling exponent of 0.937[31]. * Measured in a swim-tunnel respirometer; + maximum $\dot{M}O_2$ measured for fish in a tank; ‡ Estimated; ω Calculated using temperature adjusted routine metabolic rates reported for other sardine species (RMR estimated at 420 mg O_2 kg^{-1} hr^{-1}, see discussion); ND, not possible to determine based on the presented data.

Common Name	Species	Mass (kg)	Study Temp. (°C)	COT_{min} (mg O_2 $kg^{-0.54}$ h^{-1})	U_{opt} (BL s^{-1})	Reference
Scaled Sardine	*Harengula jaguana*	0.0145	27	283.89	3.24	This study
Chub Mackeral	Engraulis capensis	0.104	24	221.03	2.1–6.4	Guo et al.[28]
Green Jack	*Caranx caballus*	0.19	27	127.70	3.8	Dickson et al.[53]
California Yellowtail	*Seriola dorsalis*	0.069	24	260.35	3.65	Wegner et al.[50]
Mahi Mahi	*CoryPhaena hipparus*	0.04	28	321.48	4.05	Heuer et al.[51]
Yellowtail Kingfish	*Seriola lanalandi*	0.792	24	186.3	2.34	Palstra et al.[49]
Yellowtail Kingfish	*Seriola lanalandi*	2.35	25	159.35	1.7	Clark and Seymour[32]
Mackeral Tuna	*Euthynnus affinis*	0.122	24	409.22	5.0	Sepulveda and Dickson[54]
Bonito	Sarda chiliensis	1.19	18	333.04	1.4	Sepulveda et al.[55]
Yellowfin Tuna	*Thunnus albacares*	5.4	20	130.98	1.3–1.5	Blank al[56]
Pacific Bluefin Tuna	*Thunnus orientalis*	8.3	20	120.58	1.3–1.5	Blank al[56]

Table 2. Minimum cost of transport (COT_{min}) and optimum swimming speed (U_{opt}) data for the scaled sardine, and a number of tropical / subtropical pelagic fish species. All data but those for the Mahi mahi and Yellowtail kingfish were collected on wild fish. To allow comparison between the studies, the data were adjusted to a temperature of 25 °C using a Q_{10} of 1.83[5,22], and using a mass scaling exponent of 0.54[34].

Cost of transport

Another metabolic parameter that has considerable physiological and ecological implications is the cost of transport (COT), as it is an estimate of the fish's energetic demands when performing active behaviours (i.e., feeding, migrating etc.), and contributes greatly to the nutritional (energy) requirements of fishes. The relationship between COT and swimming speed is normally bell-shaped, with the greatest COT values at low and high speeds, and the lowest value (COT_{min}) occurring at the fish's optimum swimming speed (U_{opt}) somewhere in between. Indeed, this relationship has recently been shown for free-swimming sprat in a tank respirometer, with U_{opt} reported to be 0.4 BL s^{-1}[18]. However, this is not what we observed in this study for the scaled sardine. For this species, the gross cost of transport (COT_{gross}) was greatest at very low swimming speeds, decreased in an exponential fashion until approximately 3.0 BL s^{-1} and then remained relatively stable thereafter (Fig. 1B). Further, our estimate of U_{opt} was 3.24 ± 0.38 BL s^{-1}. That COT_{gross} was very high at slow swimming speeds and that our estimate of U_{opt} was much higher than in Meskendahl et al.[18] are not surprising. First, a lot of the activity of the scaled sardines at slow water velocities was not directly related to swimming against the current (as explained above). Second, voluntary swimming speed in a tank likely represents the minimum speed required to easily maintain hydrostatic equilibrium, not that when fish are trying to cover a required migratory distance at the most efficient cruising speed[20]. Third, our value for U_{opt} is in the range of other fishes, with the exception of some large tunas (Table 2). With regard to why we did not observe an increase in COT_{gross} as swimming speed increased above U_{opt} is not known. A similar swimming speed – COT relationship was reported for yellowtail kingfish (*Seriola lanalandi*) by Clark and Seymour[33], and they suggested that: specific aerobic processes (e.g., gut blood flow) are shut down at swimming speeds above U_{opt} to divert oxygen to the swimming muscles; and that energy saved from the progressive transition from opercular-buccal to ram ventilation may offset some of the costs associated with swimming at faster speeds. However, it is also likely that anaerobic metabolism was recruited to support swimming as current velocity increased, and that this limited increases in COT.

With respect to the COT_{min} of the scaled sardine, our value (2246.1 ± 106.1 mg O_2 kg^{-1} km^{-1} at 27 °C) is very similar to that reported for the sprat when their value recorded at 19 °C is adjusted to the same temperature (~ 2400 mg O_2 kg^{-1} km^{-1};[18]). However, this absolute value is 5 to 30-fold greater than the group of other fish species to which we have been comparing our metabolic data. This is largely due to the allometric scaling of COT with body mass. For example, if a mass scaling exponent of 0.54 for swimming animals is applied[34], and the data are adjusted to 25 °C, the resultant value for the scaled sardine (283.9 mg O_2 $kg^{-0.54}$ km^{-1}) is very comparable with most of the other species (~ range 220–410 mg O_2 $kg^{-0.54}$ km^{-1}) with the exception of the California yellowtail and larger tuna (~ 125 mg O_2 $kg^{-0.54}$ km^{-1}; see Table 2).

Nonetheless, the similar values when adjusted for the effect of body mass do not lessen the fact that swimming at these speeds is very expensive / energy demanding for this species. We estimate that if a scaled sardine swam at its U_{opt} for an entire day, they would require 221 cal g^{-1} day^{-1}, this value approximately 4.5 times that determined for the anchovy (*Engraulis encresicolus*) in tanks when adjusted to 27°C[35]. This finding has a number of implications. First, it is unlikely that the scaled sardine spends a large part of their day swimming at these velocities in the wild. This would be consistent with our observations on this species around Cape Eleuthera and data on other plankotrophic fish species. Relatively stationary schools / aggregations of the scaled sardine can be observed in small bays / inlets around the Island School at various times of the day. Further, Tudela and Palomera[35]) report that filter feeding primarily takes place during the day, and estimate that anchovies consume ~ 4% of their body mass per day. Based on the energy content of a sardine being 1560 cal g^{-1} (https://www.nutritionix.com/food/fresh-sardine), 4% of the daily energy intake of the scaled sardine is estimated to be ~ 62 cal g^{-1}. This energy intake would only support the scaled sardine swimming at U_{opt} for < one-fourth of the day. Second, they likely only engage in filter feeding when concentrations of phytoplankton and zooplankton are high as the energy content of plankton is approximately 4 cal g^{-1} dry weight[36].

Conclusions and perspectives

In this study, we have provided considerable insights into the swimming and metabolic capacity of the scaled sardine, a tropical/subtropical planktotrophic fish of great ecological importance in the Caribbean, Gulf of Mexico and on the northeast coast of South America. What is clear from our data is that this fish species (and probably other species of this ecotype), not tuna, should be considered the 'elite athletes' amongst fishes. This is due to their significant swimming capacity (U_{crit} likely up to or exceeding 6.0 BL s^{-1}), and the highest (by far) reported measures for MMR, AS and FAS. What morphological features and physiological mechanisms allow for this enhanced metabolic capacity, and determining this species' critical thermal tolerance while swimming (CTS_{max}), will be the focus of experiments and analyses soon to be conducted. Such studies will enable us to better understand the extent to which their physiology will amplify the consequences of HIREC on their biology and ecology versus make them climate resilient.

Based on recent research, it is clear that: ocean warming is leading to reduced phytoplankton biomass, zooplankton communities that increasingly favour gelatinous (i.e., less nutritious) species, and plankton populations that are composed of smaller-sized species and individuals[37–39]; and that these fundamental changes in plankton communities, concomitant with increased sea surface temperatures, will require planktotrophic fish species to spend more time filter feeding (e.g[40,41]). Thus, one might predict that fishes such as the scaled sardine will be hit particularly hard by HIREC, in part due to the large amount of energy they expend when swimming at velocities similar to those recorded in the wild (> 2000 mg O_2 kg^{-1} km^{-1}; Fig. 1). However, sardines also show positive acclimation responses [i.e., increased critical thermal maximum (CT_{Max}), and optimal temperatures (T_{opt}) based on stress-related biomarkers] to even brief periods of increasing temperatures[9]. They exhibit adaptive phenotypic plasticity (i.e., reduced energy expenditure) when long-term caloric restriction is imposed[41]. Further, even though it has been suggested that tropical fish species are more vulnerable to HIREC (increasing water temperatures) than temperate species[12,13]: such studies have not been conducted on species with such high metabolic capacity (i.e., AS and FAS); and we recently showed that while the tropical schoolmaster snapper (*Lutjanus apodus*) has a slightly (1.4 °C) lower CTS_{Max} compared to their CT_{Max} (i.e., measured at rest), swimming individuals achieved much higher values for MMR and AS when warmed[17]. Given the already high AS and FAS for the sardine, and this observation for the schoolmaster snapper, it is possible that the sardine's metabolic capacity might enable it to withstand further increases in ocean temperatures while still having enough metabolic currency to perform essential life functions (e.g., growth and reproduction) that determine population size and productivity.

Another important question to be addressed is what life history and evolutionary forces resulted in this exceptional aerobic capacity? This enhanced metabolic capacity does not appear to be related to the cost of digestion (specific dynamic action, SDA). The increase in post-feeding metabolic rate in fishes generally ranges from 2- to 3-fold[42], and Queiros et al.[8] report that this value is only 1.55-fold in *Sardina pilchardus* fed a meal of 1.8% body weight at 21 °C. However, these fishes live in an environment where temperatures reach or exceed 30°C, spend a substantial portion of the day swimming at considerable swimming speeds[35] (see above), and when filter feeding must overcome increased drag that undoubtedly requires additional aerobic capacity. Thus, is it likely that these factors, in addition to the metabolic demands involved in evading fast swimming pelagic predators, played a significant role in shaping their metabolic physiology.

Methods

Animals and preliminary experiments

This study was approved by the Animal Care Committee of Memorial University of Newfoundland and Labrador (protocol 22-01-KG) and by The Bahamas' Departments of Marine Resources and Environmental Protection and Planning (DEPP Research Permit BS-2023-100614). All procedures were performed in accordance with the Canadian Council on Animal Care's Guidelines on the 'Care and Use of Fish in Research, Teaching and Testing' (Canadian Council on Animal Care, 2005) and this study is reported in accordance with ARRIVE guidelines (https://arriveguidelines.org).

Wild scaled sardines (mean mass and fork length 14.53 ± 0.98 g and 9.95 ± 0.2 cm, respectively) were caught at < 1.5 m depth at the Island School (IS, Cape Eleuthera, The Bahamas) in May and October (2024) using a 30 m long beach seine with ¼ inch (~ 0.6 cm) mesh. This involved setting the net perpendicular to the beach, waiting for a small school of fish to position themselves between the end of the seine and the beach, manually bringing the end of the seine to the beach (trapping the fish), and then slowly and carefully hauling the seine to within a short distance of the shore / beach. At this point the seine was quickly lifted and the fish trapped in the seine were carefully put into a cooler filled with ambient seawater. The cooler was then transported a short distance to the Cape Eleuthera Institute (CEI) of the IS, where ~ 100 to 150 fish were put into a 1.3 m^3 cylindrical tank under natural photoperiod for 3–14 days prior to experimentation. This tank was supplied with 15 L min^{-1} of flow-through seawater (~33 ppt and > 95% air saturation) with temperatures averaging ~ 26.7 ± 0.9 °C (range 24.2–28.4; Supplementary Fig. 1). The fish were not fed during this period. However, the seawater was unfiltered and pumped into the facility from only approximately 100 m offshore (at a depth of ~ 2 m at high tide), and thus the sardines were able to feed upon the same zooplankton and other small organisms as where they were caught.

Prior to netting the fish for experiments, the water in the holding tank was lowered to a depth of approximately 20 cm, and two investigators with D-shaped nets quickly netted the fish and placed them into a swim-tunnel. We first tried swimming these fish individually in small Bläzka-type swim-tunnel respirometers (3.9 L, with a 6.8 cm internal diameter and 31.7 cm swimming section; Technical Services, Memorial University of Newfoundland and Labrador). However, this presented two issues. First, these tunnels had a maximum speed of ~ 6 BL s^{-1}, and it became apparent that some fish could outswim this current (at least for short durations). Second, and more importantly, the fish became agitated in the tunnel (likely due to confinement and isolation from the shoal[43])

and this resulted in mortalities. Thus, we decided to try and swim individual fish in a 108.9 L Bläzka-type swim tunnel (internal diameter 24 cm, working Sect. 100 cm; University of Waterloo, ON, Canada) where they had more room to swim. This approach was also unsuccessful, as their behaviour did not improve, we could not accurately (i.e., R^2 was < 0.8) record the oxygen consumption ($\dot{M}O_2$) of individual fish (i.e., due to their small size), and values recorded at the same swimming speed were highly variable. Thus, it was decided to swim the sardines in small groups.

U_{crit} experiments

After netting, small groups of sardines ($n = 3$–7) were transferred to the 108.9 L swim tunnel which had a plastic grid at the front to ensure uniform water flow in the swimming section, and was covered with black mesh to provide the fish with a dark refuge and to minimize stress from external stimuli. Current velocity was generated by an impeller (i.e., propeller), powered by a Leeson Washguard three-phase AC motor (model C182T17WK3D; Leeson Electric, Grafton, Wisconsin, USA) and controlled by a Leeson Speedmaster motor controller (model 174526, 0–120 Hz). Seawater was supplied to the swim tunnel from a temperature-controlled 208 L water reservoir at 10 L min^{-1} using a Little Giant® submersible pump (Model NK-1; Franklin Electric. Inc., Fort Wayne, IN, USA), and the O_2 content of the water was maintained at > 95% air saturation by bubbling the reservoir with air, or periodically with pure oxygen from a gas cylinder (i.e., at high swimming speeds). Temperature of the seawater in the reservoir was controlled by a 1800 W programmable immersion heater (Intelligent Heaters, Cumming, GA, USA) and a ½ HP Drop-In Chiller (Aqualogics Inc., Monroe, NC, USA).

Approximately 1 h after the fish were introduced into the swim-tunnel, water velocity was increased to 5 cm s^{-1} (approximately 0.5 BL s^{-1}), and the fish were left to recover overnight. The next morning (i.e., ~ 16 h post-transfer), a critical swim speed (U_{crit};[23]) test was used to measure resting/routine oxygen consumption (RMR), $\dot{M}O_2$ at increasing current velocities, and maximum $\dot{M}O_2$ (MMR). RMR of the sardines was initially measured at the baseline speed (~ 0.5 BL s^{-1}). Then, swimming velocity was increased by 0.5 BL s^{-1} (~ 5 cm s^{-1}) every 20 min until the first (or 2nd in the case of > 5 fish) fish reached exhaustion (i.e., the inability of the fish to move away from/off the back grid for more than 5 s). At this point, the current velocity was immediately reduced back to the baseline level, the fish were removed from the tunnel and euthanized [0.5 g L^{-1} tricaine methane sulphonate (TMS; Syndel Laboratories Ltd., Qualicum Beach, BC, Canada], and were measured for fork length and mass. The former measurement was used to adjust the U_{crit} of each fish. Prior to the test, it was assumed that each fish was 10 cm long (based on measurements made on fish in preliminary trials). These fish do not recover well from being anesthetized, and thus were not weighed before being put into the tunnel.

Measurements of $\dot{M}O_2$ and swimming capacity (U_{crit})

$\dot{M}O_2$ was measured at rest and at all swimming speeds by manually stopping the flow of water into the swim tunnel for a period of 30 (at 0.5 BL s^{-1}) or 12 min (at higher speeds)[44,45]. The partial pressure of oxygen (PO_2) in the swim tunnel was continuously measured using a fiber-optic sensor (dipping probe) connected to a PreSens O_2 meter (PreSens Precision Sensing GmBH, Resenberg, Germany) and a laptop computer running Fibox 3 LCD TRACE version 2.04 (PreSens). LoggerPro (Vernier® Science Education, Beaverton OR, USA) was then used to calculate the slope of the decrease in % saturation at each swimming speed after a 2-minute wait period. This slope typically had an R^2 value of > 95%, although there were a few values below this level at the slower swimming speeds. However, this was not unexpected given the limited mass of fish (40–80 g) compared to the volume of the swim tunnel.

The $\dot{M}O_2$ of a particular group of fish was calculated as:

$$\dot{M}O_2 = \frac{Slope \times 60\ \left(\min\ h^{-1}\right)\ \times\ water\ O_2\ content\ \left(mg\ O_2 L^{-1}\right)\ \times\ (V_c - V_f)}{Mass\ of\ the\ fish\ (kg)}$$

where $\dot{M}O_2$ was measured in mg O_2 kg^{-1} h^{-1}. Slope was measured in % air saturation per minute. V_c represents the volume of the chamber (measured in L), and V_f represents the volume of the fish (measured in L).

Note

(1) The oxygen content of 100% air saturated seawater of a salinity of 33 ppt and at a given temperature were calculated using LoligoSystem®'s on-line oxygen converter (https://loligosystems.com/resources/online-oxygen-converter/.
(2) We assumed that 1 g of fish = 1 mL of seawater.

The relationship between swimming speed and $\dot{M}O_2$ was first plotted for each group ($n = 6$), and the R^2 of the derived exponential equations were > 0.93. Standard metabolic rate (SMR) was then calculated by plotting the relationship between the log of $\dot{M}O_2$ and swim speed (BL s^{-1}) for each group, and extrapolating back to a swim speed of 0 BL s^{-1}. Absolute aerobic scope (AS) was calculated as the difference between the MMR of each group and SMR, while factorial aerobic scope (FAS) was calculated by dividing MMR by SMR. Measurements of background (microbial) $\dot{M}O_2$ were made several times after the U_{crit} tests were completed, and these comprised between 5 and 15% of sardine $\dot{M}O_2$ (assuming the tunnel held 50 g of fish). This value was subtracted from raw (absolute) values of $\dot{M}O_2$ recorded for the fish used in these experiments.

For each group of fish, the gross cost of transport (COT_{gross}, in mg O_2 km^{-1} kg^{-1}) was calculated by dividing their absolute $\dot{M}O_2$ at a given velocity by swimming speed. The optimal swimming speed (U_{opt}) was then calculated by fitting polynomial (4th to 6th power) equations to the COT_{gross} vs. swimming speed relationship for each group, and finding the swimming speed (using 0.01 BL s^{-1} bins) corresponding to the minimum COT_{gross} (i.e., the optimum swimming speed, U_{opt}).

A group's U_{crit} was calculated as in[23]:

$$U_{crit}\left(BL\ s^{-1}\right) = V + [(t_f \times V_i) / t_i]$$

where U_{crit} represents the speed at which the 1st (or 2nd) fish exhausted, and: V = highest velocity at which the fish swam the entire time increment; V_i = velocity increment (0.5 BL s^{-1}); t_f = time elapsed from the last change in current velocity to fatigue; and t_i = time increment (i.e., the time between increases in velocity; 20 min).

Data availability

The data that support the findings are housed at The Island School, but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. The data are, however, available from the corresponding author upon request and with permission of the Department of Environmental Planning and Protection of the Bahamas.

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Author contributions

AKG conceived the project, secured the funding and the required permits for this research, conducted the experiments, analyzed the data, prepared the figures and supplemental information, and wrote the first draft of the manuscript based on this research. ESP assisted with collecting the sardines and with experiments. ABB assisted in collecting the sardines, and with fish care and husbandry. All authors revised the manuscript and agree to its submission.

Declarations

Competing interest

The authors declare no competing interests.

Additional information

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