

A Comparison of Oxygen Consumption in Median-Paired fin swimming fish

A literary review on Total Cost of Transport and swimming gait transitioning in Labriform and Balistiform swimming fish.

Author: Manon den Haan

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Research Group: Faculty of Science and Engineering – Energy and Sustainability
Research Institute Groningen

Supervisor: Dr. K.N. Hoefnagel and Dr. E.J. Stamhuis



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Abstract

Underwater locomotion in fish can be divided into two categories: Body-caudal (BCF) and median-paired fin (MPF) locomotion. Within both the MPF and BCF functional groups there are different types of gaits and can be distinguished in two other groups: undulatory movements and oscillation. This literary review focuses on the oxygen consumption of median-paired fin swimming fish. Most species of fish that utilize MPF locomotion are species that live in or around complex structures, like (coral) reefs. Swimming plays a fundamental role in most ecological activities of a fish and spends a lot of energy in this. Therefore it is important to have a swimming gait that is energy efficient on a range of speeds. The aim of this study is to understand what the energetic cost of locomotion is over a range of velocities, and how do gait transitions affect these cost in fish species belonging to the MPF group. The hypothesis is that fish that change to a BCF swimming mode have a higher energetic cost than the fish would be swimming with a MPF mode at the same speed. This is done by comparing the oxygen consumption in the form of Total Cost of Transport (TCOT), Net Cost of Transport (NCOT) and the relative oxygen consumption of different fish species belonging to different habitats. The results show a lot of variety in both the TCOT, NCOT, relative oxygen consumption, and the swimming gait transition velocity. This can be explained by a number of factors, including the type of movement made by the pectoral fins, the form of the pectoral fins, the environment wherein the animals were housed and experimented on and experimental procedures of the individual studies.

Introduction

Since the 15th-century mankind was already using nature as inspiration for technical developments (Hwang et al. 2015). Leonardo da Vinci (1452-1519) used bird flight as a source for the design of a flying machine (Vincent et al. 2006). Since then technical advances only developed faster and further. An example of an application that was based on the aquatic environment are autonomous underwater vehicles (AUV's). These miniature submarines are used in a variety of applications, including for research purposes. The current underwater vehicles are propelled by screws, which have low performance in efficiency and maneuverability (Sfakiotakis et al. 1999; Sitorus et al. 2009). These propellers produce vortices and abrupt generation of thrust forces, this makes position control and motion difficult (Naomi Kato et al. 2002; Sitorus et al. 2009). In order to optimize the AUVs, it is desired that they are energetically efficient and highly maneuverable. Efficiency is important so that the submarine can stay underwater and perform its task for a longer period of time and maneuverable so it can make minute alterations without having to make a large detour.

Efficient swimming mechanisms of pelagic fish could be applied to propel forward for long distances. However is it insufficient to make slight local course alterations (Sfakiotakis et al. 1999). Currently, only a few studies have been done on motorized underwater vehicles with pectoral fin propulsion (Nbomi Kato and Furushima 1996; Sitorus et al. 2009; Zhou and Low 2012). These studies have primarily looked at the maneuverability and locomotion designs.

Underwater locomotion in fish can be divided into two categories: Body-Caudal and Median-Paired fin locomotion. The body-caudal fin (BCF) swimming gait is the most prevalent swimming style among fish and the ancestral state (Lauder 2000). It involves undulations of the body and the caudal fin to create thrust (Korsmeyer et al. 2002). Median-paired fin (MPF) swimming gait is evolutionary derived from the BCF swimming. While the fish hold their body rigid, one or more median or paired fish create thrust (Lauder 2000). The paired fins refer to the pectoral and pelvic fins, although the latter does not result in forward propulsion, but are more for stability and steering purposes. In general, there are three different specialized swimming functions: accelerating, cruising, and maneuvering (Webb 1984). These functions are closely related to the locomotion type used and since they are almost mutually exclusive, no single fish can have optimal performance in all three the functions (Sfakiotakis et al. 1999). MPF locomotion is primarily for maneuverability and stabilization and BCF is more for propulsion (Sfakiotakis et al. 1999).

Within both the MPF and BCF functional groups there are different types of gaits: undulatory movements and oscillation. Undulation is passing a wave along the propulsive structure. In oscillations, the propulsive structure swivels around its base without wave formations (Sfakiotakis et al. 1999). All the descriptions given next are based on the grouping of Breder's (Breder 1926). Oscillations can be in vertical, horizontal or an intermediate direction.

Labriform swimming is powered by oscillation of the pectoral fins, this type of locomotion is at relatively low speed (P. W. Webb 1973; Sfakiotakis et al.

1999; Korsmeyer et al. 2002), like in Parrotfish or Surf perches. In the tetraodontiform the anal and dorsal fin oscillate in a flapping motion as a unit to achieve propulsion (Sfakiotakis et al. 1999), for example in sunfish.

Balistiform swimming gait involves the undulations of anal and dorsal fins to generate thrust, this locomotion style is mainly seen in the family of the Triggerfish (Sfakiotakis et al. 1999). The rajiform gait is found in fish like rays and skates, it involves vertical undulations along the large and well developed pectoral fins to generate thrust. Diodontiform involves undulations down broad vertically placed pectoral fins. Fish that swim with the amiiform swimming mode usually have a long dorsal fin that undulates and in many cases, the body is held completely straight when swimming. Lastly the gymnotiform can be seen as the inverse of the amiiform, where propulsion is propagated by undulations of the anal fin.

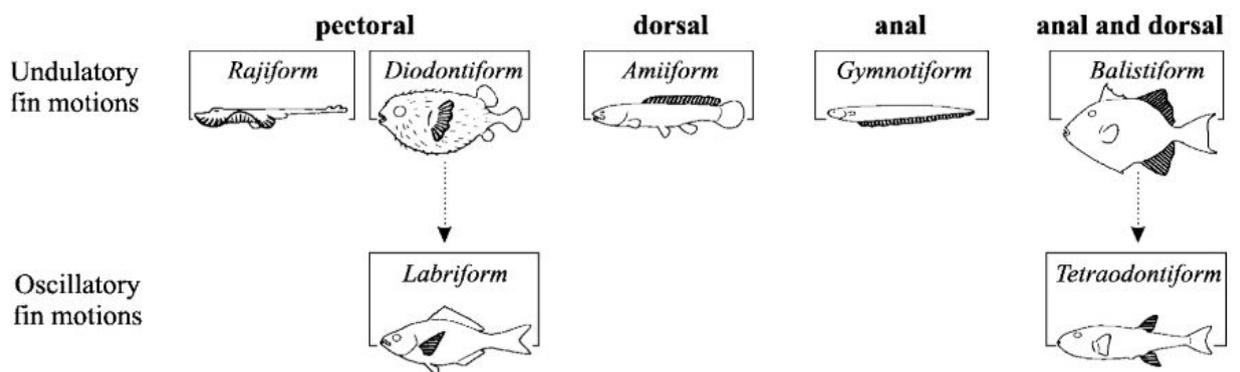


Figure 1. Different swimming gaits in median-paired fin propulsion. The darker shaded parts power propulsion, (adapted from Sfakiotakis et al. 1999, their fig. 5).

Most species of fish that utilize MPF locomotion are species that live in or around complex structures, like (coral) reefs. This type of habitat requires more in terms of mobility and maneuverability than speed and acceleration (Webb 1998). This study is on the MPF locomotion (Fig. 1). Because currently numerous research has been done on BCF swimming gait, and it is desired for the AUVs to have high maneuverability. MPF swimming is said to be energetically less efficient than BCF swimming for steady swimming at cruising speed (Korsmeyer et al. 2002). However, it has also been suggested that MPF swimming poses a lower energetic cost, because of a reduction in drag by keeping the body rigid while swimming (Webb 1975; Gordon et al. 1989). Even though some fish are specialized MPF swimmers, most species use a combination of BCF and MPF swimming gaits (Webb 1998; Korsmeyer et al. 2002; Tudorache et al. 2008; Svendsen et al. 2010). Two theories explain why gait transition occurs. One theory posits that, as the speed of locomotion increases, a gait transition occurs to minimize the energetic cost of transport and that the chosen gait minimizes the current energetic requirements and maximizes the endurance at the current speed (Alexander 1989; Webb 1998; Korsmeyer et al. 2002). This implies that MPF swimming gait is more beneficial at low speeds than BCF and BCF swimming becomes more efficient at high speeds (Blake 1980; Korsmeyer et al. 2002). The other theory posits that BCF swimming mode is only used for the recruitment of

additional muscles to reach higher swimming speeds and is less focused on energetic efficiency (Alexander 1989; Webb 1998; Kendall et al. 2007).

Swimming plays a fundamental role in most ecological activities of a fish, for example, foraging and reproducing (Blake 2004). Therefore it is imperative to have a swimming gait that is energy efficient on a range of speeds. The aim of this study is to understand what the energetic cost of locomotion is over a range of velocities, and how gait transitions affect these costs in fish species belonging to the MPF group. I expect that fish that change to a BCF swimming mode have a higher energetic cost for when the fish would be swimming with a MPF mode at the same speed. These results can then be projected on the AUVs and determine in which scenarios a certain swimming mode would be the most beneficial.

Material and Methods

A literary study is conducted to understand what the differences are in oxygen consumption and gait changes in different species belonging to the median-paired fin group. The search terms included "energetics", "median-paired fin" and "Labriform". Energy expenditure is calculated based on oxygen consumption rates (M_{O_2} ; mg O₂ kg⁻¹h⁻¹) of a solitary fish inside a flow respirometer. Swimming gait transitions are defined as the velocity at which the fish transitions from a Median-paired fin to an undulatory Body-caudal swimming gait (U_{p-c}) (Korsmeyer et al. 2002; Svendsen et al. 2010). For every species is this different and can have different underlying reasons. Ten different species were studied, of which 9 species had Labriform swimming gait and one had balistiform swimming gait, see table 1. In all studies, the fish were fasted before the experiments to guarantee that oxygen consumption is originated from standard metabolism and active swimming and not from digestion. The respiratory flow tanks wherein the fish were tested had a constant temperature, which ranged from 10 to 28°C depending on the species. Most of the studies give the length of the fish in body length (BL), which is the total body length of the fish from the tip of the nose to the end of the tail. Some studies (Table 1) give only the fork length (FL), which is the total length from the tip of the nose to the fork of the tail. In addition to that was the metabolic rate of the fish in the studies used not always in the same units. In order to compare species and studies, are all units converted to the same units mg O₂ kg⁻¹h⁻¹, see appendix 1 table 1A.

Standard metabolic rate (SMR) (mg O₂ kg⁻¹h⁻¹) was either calculated by letting the fish acclimate for a period or by extrapolating the SMR from the model. The acclimation inside the flow tank ranges between 6 and 24 hours. The acclimatization velocities inside the flow tanks were between the 0.3 and 1.2 body length per second (BL s⁻¹). After the fish is calmed down, the oxygen consumption inside the flume is measured as the standard metabolic rate. The second method of calculating the SMR is by taking the intercept of the oxygen consumption rates equation (Eq. 3) for when speed is zero (Parsons and Sylvester 1992). All studies have a slightly different way to calculate the rate of

oxygen consumption. It comes down to the equation below (Schurmann and Steffensen 1997; Korsmeyer et al. 2002; Roche et al. 2014).

$$MO_2 = sV_{resp}\alpha M^{-1} \quad \text{Eq.1}$$

Where s is the slope of the linear regression where oxygen saturation changes over time (Tudorache et al. 2008), V_{resp} is the volume of the respirometer corrected for the volume of the fish, α is the solubility of oxygen in seawater and M the mass of the fish.

Most of the studies have the relationship between oxygen consumption and the swimming speed U described based on either one of two models. The first model is a traditional exponential function (Brett 1964; Webb 1975; Beamish 1978; Korsmeyer et al. 2002).

$$MO_2 = a10^{bU} \quad \text{Eq.2}$$

$$\log(MO_2) = \log(a) + bU \quad \text{Eq.3}$$

Where a is SMR (at zero speed) and b the slope of the semi-logarithmic regression between the change in velocity and the oxygen consumption (Korsmeyer et al. 2002). The second model is based on a hydrodynamics-based power equation (Videler 1993; Korsmeyer et al. 2002; Svendsen et al. 2010)

$$MO_2 = a + bU^c \quad \text{Eq.4}$$

$$\log(MO_2 - a) = \log(b) + c \log(U) \quad \text{Eq.5}$$

Where a is SMR and c is the slope of the log-log regression (Eq.5). It contains information about the aerobic swimming efficiency (Wardle et al. 1996). ($MO_2 - a$) is the metabolic energy expenditure due to active swimming. The traditional exponential function (Eq. 2 and 3) is simpler than the power function (Eq. 4 and 5) because only two constants have to be derived. This makes it more reliable for making predictions based on measured values (Webb 1975; Korsmeyer et al. 2002). The advantage of the power function is that it takes into account difference in SMR between different species of fish. The power to which velocity is raised (c) can be used to compare the swimming cost between species (Korsmeyer et al. 2002). However, the SMR will be overestimated when the power function is fitted to the total MO_2 (Videler and Nolet 1990). Using the linear form (Eq. 5) will avoid the overestimation of lower values, but it requires an accurate SMR measurement (Korsmeyer et al. 2002).

However, it is not possible to compare species only based on the rate of oxygen consumption. In order to compare, oxygen consumption (metabolic rate) has to be transformed into Cost of Transport (COT) (Videler and Nolet 1990), because it is a dimensionless number. Where a large animal, like a whale, would cover 1 m within (a fraction of) one stride, a smaller animal, like a surfperch, would need 30 strides to cover that same distance. (Videler and Nolet 1990). The

metabolic cost of transport ($\text{mg O}_2 \text{ kg}^{-1}\text{km}^{-1}$) is the energy required to move one kg of animal over a certain distance in km (Alexander 2003).

$$\text{Net COT} = \frac{\text{Metabolic rate of moving an animal} - \text{SMR}}{\text{Mass} \cdot \text{Distance}} \quad \text{Eq.6}$$

$$\text{Gross COT} = \frac{\text{Metabolic rate of moving an animal}}{\text{Mass} \cdot \text{Distance}} \quad \text{Eq.7}$$

The Cost of Transport also reveals the most optimal speed for an animal to swim, at which velocity the energy expenditure is relatively at its lowest point. To make a link to the energy expenditure, the relative oxygen consumption is calculated by dividing the Net Cost of Transport by the SMR. It gives an indication of how much oxygen the fish needs to consume relative to the standard metabolic rate to swim at a certain velocity. Where the standard metabolic rate is the oxygen consumption primarily used for maintenance.

To calculate the rate of oxygen consumption and the COT, oxygen measurements are taken at multiple velocities. In order to compare studies and species, all the velocities are transformed from cm s^{-1} to BL s^{-1} (body lengths per second). In all studies, the fish were exposed to multiple velocities for a period of 5time so that the fish had time to stabilize its swimming gait. When an individual would fatigue the experiment must be terminated immediately. Fatigue is defined as when the fish could no longer maintain its position and drifted away to the back of the testing area (Korsmeyer et al. 2002). Table 1 gives an overview of the experimental procedure for every study.

The transitioning from a median-paired swimming gait to a body caudal swimming gait happens in fish species at a different velocity. The swimming gait changes are usually associated with mechanical and/or energetic factors (Kendall et al. 2007). The theory behind gait transitioning is to reduce energetic locomotion cost (Alexander 1989). If the switch of swimming gait is determined by mechanical factors such as additional muscle mass that is needed as the speed increases. If energy is the driving factor, BCF should be energetically more efficient than MPF (Kendall et al. 2007).

Table 1. Overview of the studies used for present research. Based on the material and methods and results of (Gordon et al. 1989; Parsons and Sylvester 1992; Gordon et al. 2000; Korsmeyer et al. 2002; Cannas et al. 2006; Kendall et al. 2007; Johansen et al. 2010; Svendsen et al. 2010; Fulton et al. 2013; Roche et al. 2014). FL= fork length. Cannas et al. 2006 and Johansen et al. 2010 did not provide total body length, instead only provided fork length.* Estimations of BL s-1 by transformation from cm s⁻¹. ** Sequence: 0.5, 0.8, 1.1, 1.4, 0.5, 1.9, 0.5, 2.3, 0.5 Lf/s. *** Note: Fish were allowed a 15 min rest between each bout

Author	Fish species	Fish details	Temperature seawater	Acclimation velocities	Standard metabolic rate (SMR) (mg O ₂ kg ⁻¹ h ⁻¹)	Measuring O ₂	S
Gordon et al. (1989)	Shiner Surfperch (<i>Cymatogaster aggregata</i>)	N=100; mass=10-30g; length=7-12 cm	10°C, 15°C, 20°C	0.75 BL s ⁻¹	102.7 106.7 171.6	-	O w sw sp
	Senorita wrasse (<i>Oxyjulis californica</i>)	N=40; mass=23-71g; length=13-17 cm	10°C, 15°C, 20°C	0.75 BL s ⁻¹	65.5 135.3 231.6	-	O w sw sp
Parsons and Sylvester (1992) ***	White crappie (<i>Pomoxis annularis</i>)	Mass=89-96 g mean=91g; length=16.5-17.5 cm	25°C	~ 0.3 BL s ⁻¹ (5 cm s ⁻¹)	121.5	-	2- te
Gordon et al. (2000)	Hawaiian spotted boxfish (<i>Ostracion meleagris</i>)	N=?; mass=25-60g; length= 10-16 cm	28°C	0.5 BL s ⁻¹	111.7	-	1- be te
Korsmeyer et al. (2002)	Parrotfish (<i>Scarus schegeli</i>)	N=7; mass=148-315 g; length=20.1-25.3 cm	26-27°C	~ 0.3-0.4 BL s ⁻¹ (7-10 cm s ⁻¹)	127.0	Every 10 min	O w sw sp

	Triggerfish (<i>Rhinecanthus aculeatus</i>)	N=5; mass=105-180 g; length=16.0-19.0 cm	26-27° C	~ 0.3-0. 4 BL s ⁻¹ (7-10 cm s ⁻¹)	74.7	Every 10 min	O w sv sp
Cannas et al. (2006)	Striped surfperch (<i>Embiotoca laterlais</i>)	N=6; mass= 480 ±90 g; length (fork)= 28.17 ± 2.04 cm	11°C	0.25 FL s ⁻¹	58.9	Every 10 min	O
Kendall et al. (2007)	Bluegill sunfish (<i>Lepomis macrochirus</i>)	N=9; mass=127.9 ±4.2g; length=19.3 ±0.4 cm	22°C		86.6	Every 15 s	O w sv sp
Johansen et al. (2010)	Striped surfperch (<i>Embiotoca laterlais</i>)	N=7; mass=169.2 ±24.5g; length (fork)= 19.2 ±0.9 cm	12°C (11.8-1 2.3°C)	0.5 FL s ⁻¹	90.8	Every 10 min	8 te
Svendsen et al. (2010)	Striped surfperch (<i>Embiotoca laterlais</i>)	N=11; length= 21.0 ±0.2 cm; mass= 296.0 ±8.7g	12.5°C (11.6-1 3.4°C)	0.5 FL s ⁻¹	109.4	Every 10 min	A ov
Fulton et al. (2013)	Bluelined wrasse (<i>Stethojulis bandanensis</i>)	N=7; mass=15.8 ± 1.1 g; length=10.1 ±0.2 cm	27-28° C In the tank 27 .7°C	0.5 BL s ⁻¹	231.2	-	O w sv sp
	Redbreasted wrasse (<i>Cheilinus fasciatus</i>)	N=7; mass=34.2 ± 7.7g; length=12 ±0.9 cm	27-28° C In the tank 27	0.5 BL s ⁻¹	179.5		O w sv sp

Roche et al. (2014)	Shiner Surfperch (<i>Cymatogaster aggreagata</i>)	N=20; mass=46.3 ±63g; length=14.84 ±0.49 cm	.7°C 12°C (11-13 °C)	0.5 BL s ⁻¹	129.9	Every 10 min	6 te
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Results

Oxygen consumption

After transforming every Total Cost of Transport to the same units of $\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$ it appears that every fish species, even under different circumstances, has the same shape of oxygen consumption (Fig. 2). The Bluelined wrasse (Fulton et al. 2013) has the highest energy expenditure and the Striped surfperch (Cannas et al. 2006) has the lowest oxygen consumption. In all species the oxygen consumption decreases with an increase in velocity, with a few exceptions i.e. in the Striped surfperch (Svendsen et al. 2010) or for when the fish transition in swimming gait from MPF to BCF; the Hawaiian spotted Boxfish (Gordon et al. 2000), the Parrotfish (Korsmeyer et al. 2002), the Triggerfish (Korsmeyer et al. 2002) and the Bluegill sunfish (Kendall et al. 2007). Besides the highest oxygen consumption, the Bluelined wrasse is also able to swim the highest relative velocities up to 12 BL s^{-1} (Appendix 2).

In the Net Cost of Transport (Fig. 3), the Bluegill sunfish with a BCF swimming gait has the highest NCOT when corrected for speed (Kendall et al. 2007). Both the Shiner surfperch (Roche et al., 2014) and the Striped surfperch (Johansen et al. 2010) have the lowest NCOT at lower velocities. The Bluegill sunfish with a MPF swimming gait (Kendall et al. 2007) and the shiner surfperch swimming in water with a temperature of 10°C (Gordon et al. 1989) appear to have no change in the net swimming cost with an increase in velocity. The oxygen consumption of the Redbreasted wrasse (Fulton et al. 2013) shows an optimum around a velocity of 1 BL s^{-1} , whereafter it slowly increases again, suggesting that the velocity of 1 BL s^{-1} is the optimum swimming speed.

Comparing the NCOT to the relative oxygen consumption gives similar images for most studies, there are small differences. For instance, the Striped surfperch (Cannas et al. 2006) has a lower NCOT than the Senorita wrasse (15 and 20°C) (Gordon et al. 1989). However, if compared to the relative oxygen consumption, the Senorita wrasse has a lower relative oxygen consumption than the Striped surfperch. The relative oxygen consumption (Fig. 4) shows again that the Bluegill sunfish with a BCF swimming gait has the relative highest oxygen consumption.

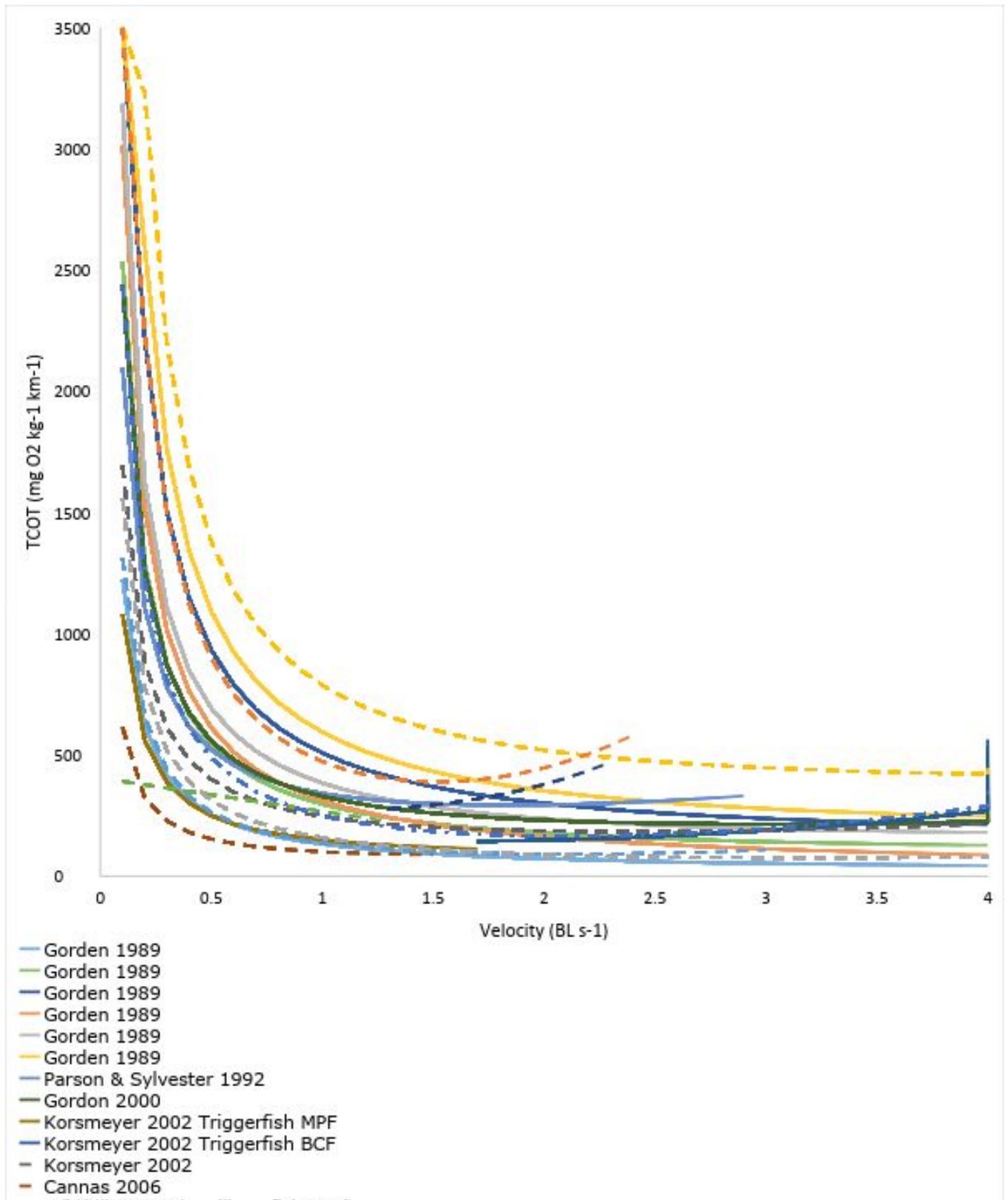


Figure 2. Total Cost of Transport (TCOT ($\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$)) against the relative velocity in (BL s^{-1}). Only speeds up to 4 BL s^{-1} and oxygen consumption till 3300 $\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$ are shown to give a better overview. The complete graph is shown appendix 2 figure 2A. Shiner surfperch (Gorden et al. 1989; Roche et al. 2014), Striped surfperch * (Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010), Redbreasted wrasse (Fulton et al. 2013), Bluelined wrasse (Fulton et al. 2013), Bluegill sunfish (Kendall et al. 2007), Parrotfish (Korsmeyer et al. 2002), Triggerfish

(Korsmeyer et al. 2002), *Boxfish* (Gordon et al. 2000), *Senorita Wrasse* (Gordon et al. 1989). * All values for velocity are in $FL s^{-1}$ instead of $BL s^{-1}$.

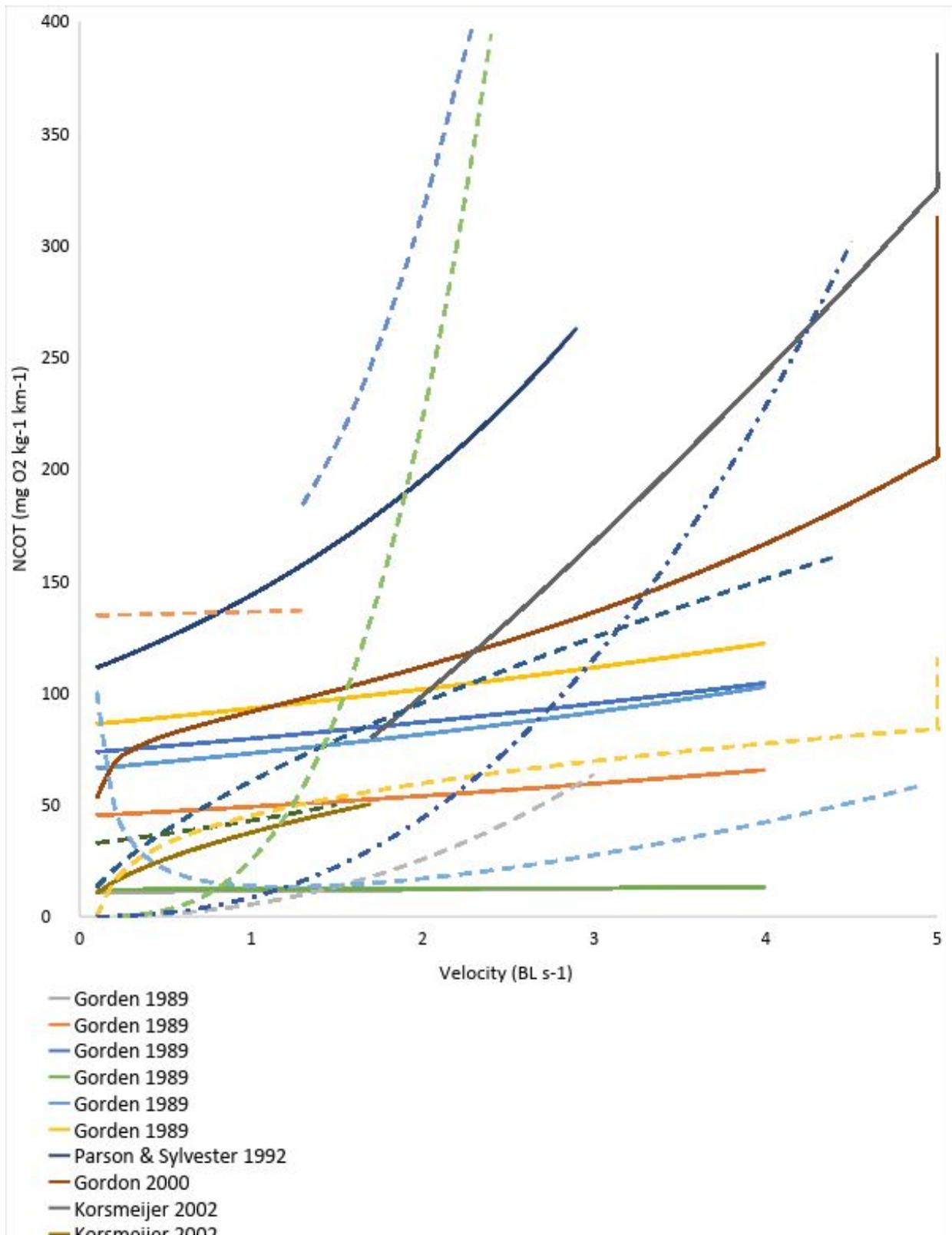


Figure 3. Net Cost of Transport ($NCOT (mg O_2 kg^{-1} km^{-1})$) against the relative velocity in ($BL s^{-1}$). Only speeds up to $5 BL s^{-1}$ and oxygen consumption to $400 mg O_2 kg^{-1} km^{-1}$ are shown to give a better overview. The complete graph is shown appendix 2 figure 2B. *Shiner surfperch* (Gordon et al. 1989; Roche et al. 2014), *Striped surfperch** (Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010), *Redbreasted wrasse* (Fulton et al. 2013), *Bluelined wrasse* (Fulton et al.

2013), *Bluegill sunfish* (Kendall et al. 2007), *Parrotfish* (Korsmeyer et al. 2002), *Triggerfish* (Korsmeyer et al. 2002), *Boxfish* (Gordon et al. 2000), *Senorita Wrasse* (Gordon et al. 1989). * All values for velocity are in $FL s^{-1}$ instead of $BL s^{-1}$.

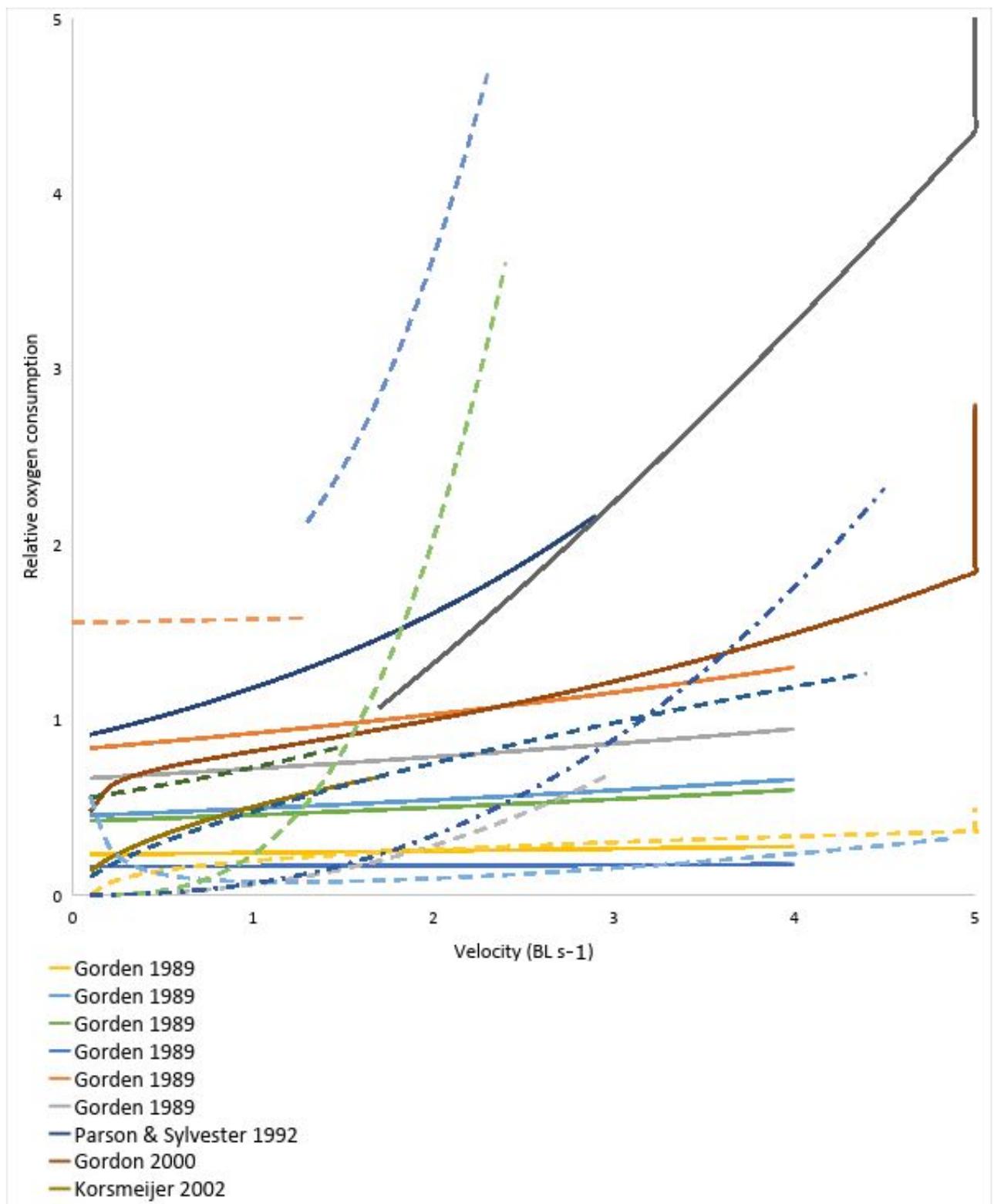


Figure 4. Relative oxygen consumption against the relative velocity in ($BL s^{-1}$). Only speeds up to 5 $BL s^{-1}$ and relative oxygen consumption to 5 are shown to give a better overview. The complete graph is shown appendix 2 figure 2C. *Shiner surfperch* (Gordon et al. 1989; Roche et al. 2014), *Striped surfperch** (Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010), *Redbreasted*

wrasse (Fulton et al. 2013), *Bluelined wrasse* (Fulton et al. 2013), *Bluegill sunfish* (Kendall et al. 2007), *Parrotfish* (Korsmeyer et al. 2002), *Triggerfish* (Korsmeyer et al. 2002), *Boxfish* (Gordon et al. 2000), *Senorita Wrasse* (Gordon et al. 1989). * All values for velocity are in FL s⁻¹ instead of BL s⁻¹.

Swimming gait transitioning

Even though the shape of Total Cost of Transport is very similar between the fish species, the velocity where the fish changes from a median-paired fin swimming gait to a body-caudal fin swimming gait is different (Table 2). Some fish species like the Bluelined wrasse, Redbreasted wrasse, and the Senorita wrasse appear to keep swimming even with high velocities with a MPF gait. The Shiner surfperch appears to have conflicting results, wherein Gordon et al. (1989) the swimming gait does not change but in Roche et al. (2014) it changes at a relative speed of around 3 BL s⁻¹. In three species there is a distinct transitioning from MPF to BCF with intermittent use of the caudal fin.

Table 2. Presenting the velocity where the fish species change in swimming gait from MPF to BCF and which type of pectoral fin movement.* Based on (Drucker and Jensen 1996). 1. (Jeirey A Walker and Westneat 2000), 2. (J. A. Walker and Westneat 2002), 3. (Lauder and Madden 2007), 4. Personal observations

Study	Fish species	Swim type	Velocity transitioning swimming gait (MPF
			□ BCF)
Gordon et al. (1989)	Shiner Surfperch (<i>Cymatogaster aggregata</i>)	Flapping ¹	Does not change
	Senorita wrasse (<i>Oxyjulis californica</i>)		Does not change
Roche et al. (2014)	Shiner Surfperch (<i>Cymatogaster aggregata</i>)	Flapping ¹	~ 3 BL s ⁻¹
Parsons and Sylvester (1992)	White crappie (<i>Pomoxis annularis</i>)		Transitioning at ~0.9 BL s ⁻¹ Completely > ~1.6 BL s ⁻¹
Gordon et al. (2000)	Hawaiian spotted boxfish (<i>Ostracion meleagris</i>)		Alternate > 5 BL s ⁻¹ > 6 BL s ⁻¹ caudal movement essential
Korsmeyer et al. (2002)	Parrotfish (<i>Scarus schegeli</i>)	Flapping ²	> 3.5 BL s ⁻¹
	Triggerfish (<i>Rhinecanthus aculeatus</i>)	Undulations of both the anal and dorsal fin	Intermittently 3.0-3.5 BL s ⁻¹ Continuously > 3.5 BL s ⁻¹
Cannas et al. (2006)	Striped surfperch (<i>Embiotoca laterlais</i>)	Flapping ⁴	≥ 1.75 FL s ⁻¹
Johansen et al. (2010)	Striped surfperch (<i>Embiotoca laterlais</i>)	Flapping ⁴	2.2 FL s ⁻¹ *
Svendsen et al. (2010)	Striped surfperch (<i>Embiotoca laterlais</i>)	Flapping ⁴	1.83 FL s ⁻¹ *

Kendall et al. (2007)	Bluegill sunfish (<i>Lepomis macrochirus</i>)	Complex movement ³	1.23 BL s ⁻¹
Fulton et al. (2013)	Bluelined wrasse (<i>Stethojulis bandanensis</i>)	Rowing ⁴	Does not change
	Redbreasted wrasse (<i>Cheilinus fasciatus</i>)	Rowing ⁴	Does not change

Discussion

Oxygen consumption

Even though the studied fish species live in different environments and have different swimming gaits, the Total Cost of Transport decreases with an increase in velocity in almost all studies. The Net Cost of Transport and the relative oxygen consumption portray a different picture. The values of the NCOT and the relative oxygen consumption of the fish increase with velocity. In all the used studies the oxygen consumption was significantly correlated with only velocity, with the exception of the Parrotfish in Korsmeyer et al. (2002). In this case, the Mass of the fish also significantly correlated with oxygen consumption. Nevertheless, those are that not the only factors that can cause a change in the oxygen consumption and thereby in the total cost of transport. The temperature of the water wherein the fish swims has an effect on the oxygen consumption of the fish as well (Gordon et al. 1989; Johansen and Jones 2011; Hein and Keirsted 2012).

These studies show that both the metabolic performance and swimming abilities decrease with an increase in ambient temperature. The metabolic performance, the total cost of transport (TCOT), increases consistently with temperature (Gordon et al. 1989; Ohlberger et al. 2007; Hein and Keirsted 2012). The standard metabolic rate also increases in warmer waters and so there is a significant interaction between water temperature and metabolism (Johansen and Jones 2011). The decline in swimming capabilities is evident from a declining critical swimming speed (U_{crit}). The critical swimming speed is a standard measurement to assess swimming capabilities of fish species (Plaut 2001). It is the velocity for which the fish does not fatigue. So the decline in swimming capabilities implies that temperature has an effect that the fish is fatigued earlier. The gait-transitioning velocity (U_{p-c}) is effected as well with an increase of water temperature, the U_{p-c} decreased with an increase in temperature (Johansen and Jones 2011) indicating that median-paired swimming fish go over to a BCF swimming mode earlier in warmer water temperature than in colder temperatures. These factors could suggest an explanation for the variety in the gross total cost of transport (Fig. 2). Even though a lot of studies are done with the same species, they were housed and experimented on in slightly different environments (Table 1).

Besides the fact that the animals were experimented on in different environments, the experimental procedures are different in all studies as well (Table 1). The largest difference between the studies is the step-wise increment in flow speed. The velocity increment ranges from 0.25 FL s⁻¹ to 1 BL s⁻¹. The time periods with which the increment is done ranges from 15 to 60 min, usually until the fish is fatigued. If an individual fish is swimming for a longer period of

time on a certain velocity, the individual would become fatigued earlier and have an increase in oxygen consumption (Cannon et al. 2011). This could be another explanation for the variety shown in the results between and within the species.

So it appears that there is no effect of ramping speed on the data of oxygen consumption. For future studies, the experimental procedure should be consistent to make a fair comparison between species. When the individual metabolic rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) is measured, this is only done at a few numbers of velocities. With these points, the exponential function (Eq. 3) and the power equation (Eq. 5) is fitted. So it is debatable whether these values are estimated with a high probability. Noticeable are the higher values of the NCOT at relatively low velocities, ranging to BL s^{-1} . These could be explained by the fact that some studies had the flow velocity of the flume to 0.5 BL s^{-1} , for when the standard metabolic rate is measured. At these velocities some species were already swimming (Gordon et al. 2000; Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010; Roche et al. 2014), while some the more coral reef species were resting at the bottom of the testing area (Korsmeyer et al. 2002; Kendall et al. 2007; Fulton et al. 2013).

Usually, only the aerobic metabolism is measured, but the anaerobic metabolism plays a major role in the total metabolic cost. Svendsen et al. (2010) have shown that measuring the excess post-exercise oxygen consumption (EPOC), around 25% of the total cost is made up of anaerobic metabolism. However, the EPOC only occurred at velocities higher than 1.9 FL s^{-1} , which was below the critical swimming speed for the Striped surfperch. It is assumed that the swimming gait transition velocity (U_{p-c}) is the point where the anaerobic power has a significant impact (Drucker and Jensen 1996) because additional muscle mass is required to propel forward. Even though the swimming gait transition velocity is similar to 1.9 FL s^{-1} , there is no evidence that the U_{p-c} was a threshold for anaerobic metabolism (Svendsen et al. 2010).

Whether the fish propels itself forward by using a flapping motion or a rowing motion has an influence on the oxygen consumptions (J. A. Walker and Westneat 2002). Research shows that in general rowing generates more thrust at low speeds than a flapping motion (Vogel 1996), resulting in the implication that rowing is mechanically more efficient. Contradicting is that simulations show that flapping has a higher mechanical efficiency than rowing at all speeds (Walker and Westneat 2002). At low swimming speeds ($<1 \text{ BL s}^{-1}$), the energetic efficiency of untwisted rowing and flapping are very close suggesting that rowing with an optimal fin shape could be more efficient than flapping with an optimal fin shape. This has been supported by the results of a physical model consisting of a stiff pectoral fin propelled by three motors (Kato and Liu 2003).

Swimming gait transitioning

The velocity for when the studied fish species transition from a Median-Paired fin swimming gait to a Body-Caudal ranges between 1.2 and 6 BL s^{-1} , or does not change at all and fish keep swimming at an MPF swimming gait even at high velocities (up to 12 BL s^{-1}). Even within the same species, the velocity at which the swimming gait changes is not really similar, **this could be explained by the differences in experimental procedures as mentioned above**. Generally, oxygen consumption increases when individuals transition from a MPF swimming gait to a BCF (Gordon et al. 2000; Korsmeyer et al. 2002; Kendall et al. 2007). Besides the fact that they swim at an increased velocity, predictions state that MPF will have a decreased oxygen consumption. However, Parson and Sylvester (1992)

show that when the White crappie switches from MPF to BCF the oxygen consumption decreases. But they can only maintain a MPF swimming gait up until 1 BL s^{-1} (Parsons and Sylvester 1992).

The variability in the swimming gait transitioning can be explained by the habitat of the studied fish. All fish species live in habitats that require movement. The Parrotfish, Triggerfish, Bluelined wrasse and Redbreasted wrasse live in coral reefs; the Shiner surfperch, Senorita wrasse and Striped surfperch live in kelp forest; and the White crappie and Bluegill sunfish live in freshwater where they take shelter in underwater structures like tree roots. They live at different water depths as well. Depending on the aspect-ratio of their pectoral fins they are predominately present at a certain depth in the water column (Gerstner 1999; Bellwood and Wainwright 2001; Korsmeyer et al. 2002). Fish with high aspect-ratio pectoral fins are more found above the reef and at higher positions in the water column, while species with a low aspect-ratio are found lower in the water column.

Kendall et al. (2007) suggest that the major underlying factor of swimming gait transitioning of the Bluegill sunfish is mechanically driven, so a need for additional muscle mass. Otherwise, the swimming power necessary to swim at high velocities cannot be met. Even though in terrestrial animals a gait switch is energetically efficient (Alexander 1989), Kendall et al. and the relative oxygen consumption in the present study show that the transition does not have an economic effect in the Bluegill sunfish (Kendall et al. 2007). The need for additional muscle mass can also be seen in other fish species, as they suggest in the Triggerfish (Korsmeyer et al. 2002). However, the White crappie shows that switching to BCF decreases the total cost of transport and thus suggesting that energetic factors play an important role in the gait transitioning of this species (Parsons and Sylvester 1992; Kendall et al. 2007).

Automated Underwater Vehicles

Translating a biological process to an underwater mechanical application faces some challenges. The main problem is the fundamental difference between a biological organism and a mechanical product. Biological organisms are in general soft, flexible and aquatic organisms are also wet. Biomimetic products are usually stiff and hard (Sitorus et al. 2009). Besides the morphological differences, biological processes are often very complex, and they can adapt effectively to their environment (Sitorus et al. 2009). Even though there is a gap between biological organisms and biomechanical products, organism can also be limited by some factors that biomechanics are not. As mentioned above, fish are affected by the temperature of the water. They have an increased oxygen consumption in warmer water (Gordon et al. 1989), on the contrary, biomechanical products probably do not have this proportionated increase in energy requirements in warmer waters (Davis et al. 2003). In addition, they don't have an increased energy expenditure with and a decrease in available energy. Further research is needed to make the gap between biological organisms/processes and biomechanical applications closer.

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Appendix 1

Table 1A. Conversion table used to convert all the units used in studies to mg O₂ kg⁻¹h⁻¹

Study	Units used	Conversion
(Gordon et al. 1989)	Metabolic rate is in ml O ₂ h ⁻¹ converting to mg O ₂ kg ⁻¹ h ⁻¹	P·V=n·R·T P= Pressure (atm) V= Volume (L) n= Moles of gas R= Gas constant (0.0821 L·amt mol ⁻¹ K ⁻¹) T= Temperature (K) Based on a combination of the Laws of Charles and Boyle and the Ideal Gas Law
		10°C T (K)= 283 K n= 1·0.001 L O ₂ / 0.0821·283 n= 4.3 ·10 ⁻⁵ mol O ₂ 4.3 ·10 ⁻⁵ * 32.00 1 ml O ₂ =1.38 mg O ₂
		15°C T (K)= 288 K n= 1·0.001 L O ₂ / 0.0821·288 n= 4.23 ·10 ⁻⁵ mol O ₂ 4.23 ·10 ⁻⁵ * 32.00 1 ml O ₂ =1.35 mg O ₂
		20°C T (K)= 293 K n= 1·0.001 L O ₂ / 0.0821·293 n= 4.16 ·10 ⁻⁵ mol O ₂ 4.16 ·10 ⁻⁵ * 32.00 1 ml O ₂ =1.33 mg O ₂
(Gordon et al. 2000)	Metabolic rate is in ml O ₂ h ⁻¹ converting to mg O ₂ kg ⁻¹ h ⁻¹	P·V=n·R·T P= Pressure (atm) V= Volume (L) n= Moles of gas R= Gas constant (0.0821 L·amt mol ⁻¹ K ⁻¹) T= Temperature (K)

		Based on a combination of the Laws of Charles and Boyle and the Ideal Gas Law
	28°C	$T (K) = 301 K$ $n = 1 \cdot 0.001 L O_2 / 0.0821 \cdot 301$ $n = 4.05 \cdot 10^{-5} mol O_2$ $4.05 \cdot 10^{-5} * 32.00$ $1 ml O_2 = 1.29 mg O_2$
(Korsmeyer et al. 2002)	Converting metabolic rate ($mg O_2 h^{-1}$) to ($mg O_2 kg^{-1}h^{-1}$)	By dividing the metabolic rate by the average body mass of the fish used in the study
(Kendall et al. 2007)	Converting metabolic rate in power ($W kg^{-1}$) to ($mg O_2 kg^{-1}h^{-1}$)	Based on (Elliott and Davison 1975) is in general $1 mg O_2 = 14.14 J$ (metabolic rate/14.14)*3600

Appendix 2

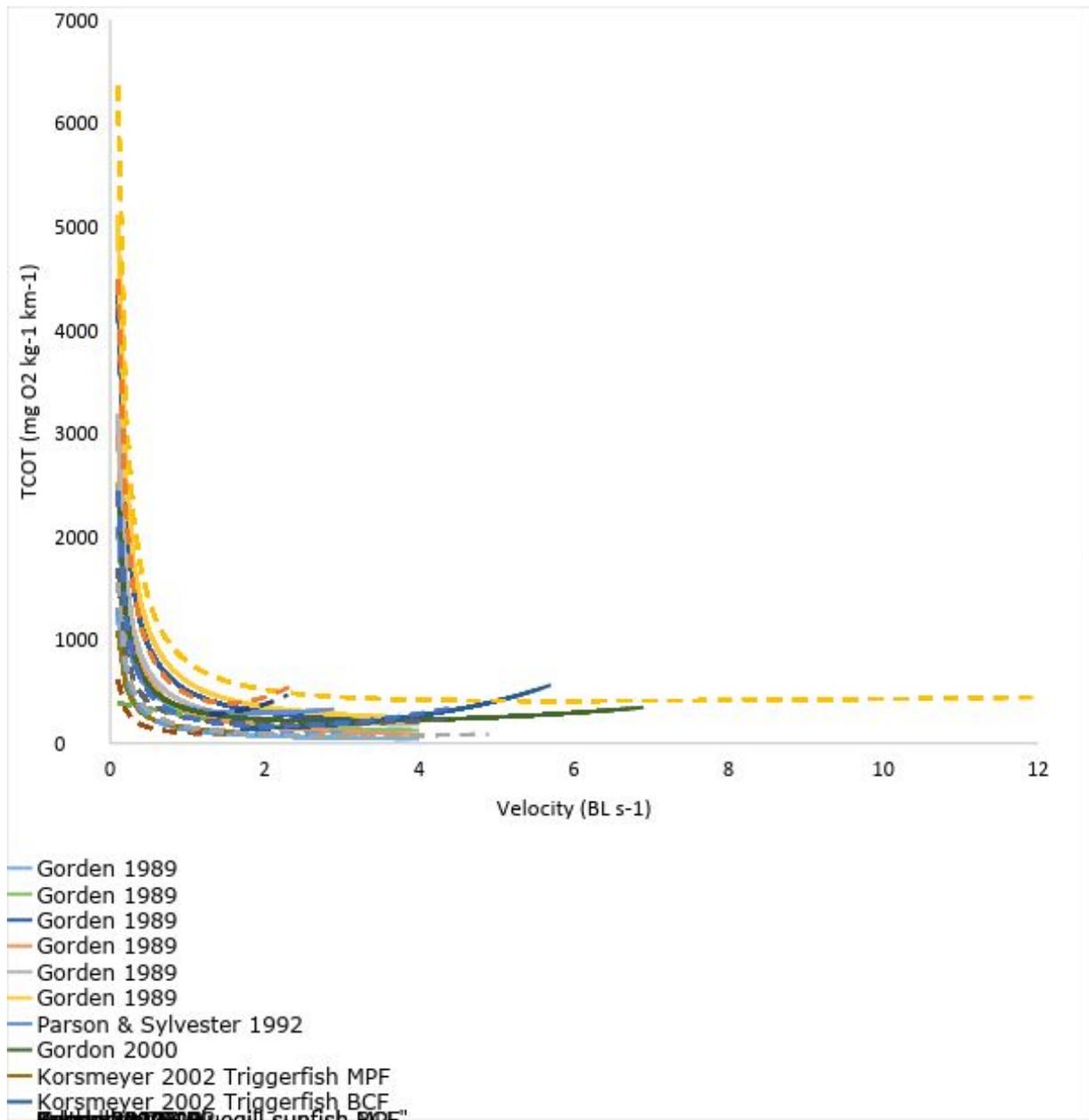


Figure 2A. A complete graph of the Total Cost of Transport (TCOT (mg O₂ kg⁻¹ km⁻¹)) against the relative velocity in (BL s⁻¹). Shiner surfperch (Gordon et al. 1989; Roche et al. 2014), Striped surfperch (Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010), Redbreasted wrasse (Fulton et al. 2013), Bluelined wrasse (Fulton et al. 2013), Bluegill sunfish (Kendall et al. 2007), Parrotfish (Korsmeyer et al. 2002), Triggerfish (Korsmeyer et al. 2002), Boxfish (Gordon et al. 2000), Senorita Wrasse (Gordon et al. 1989).

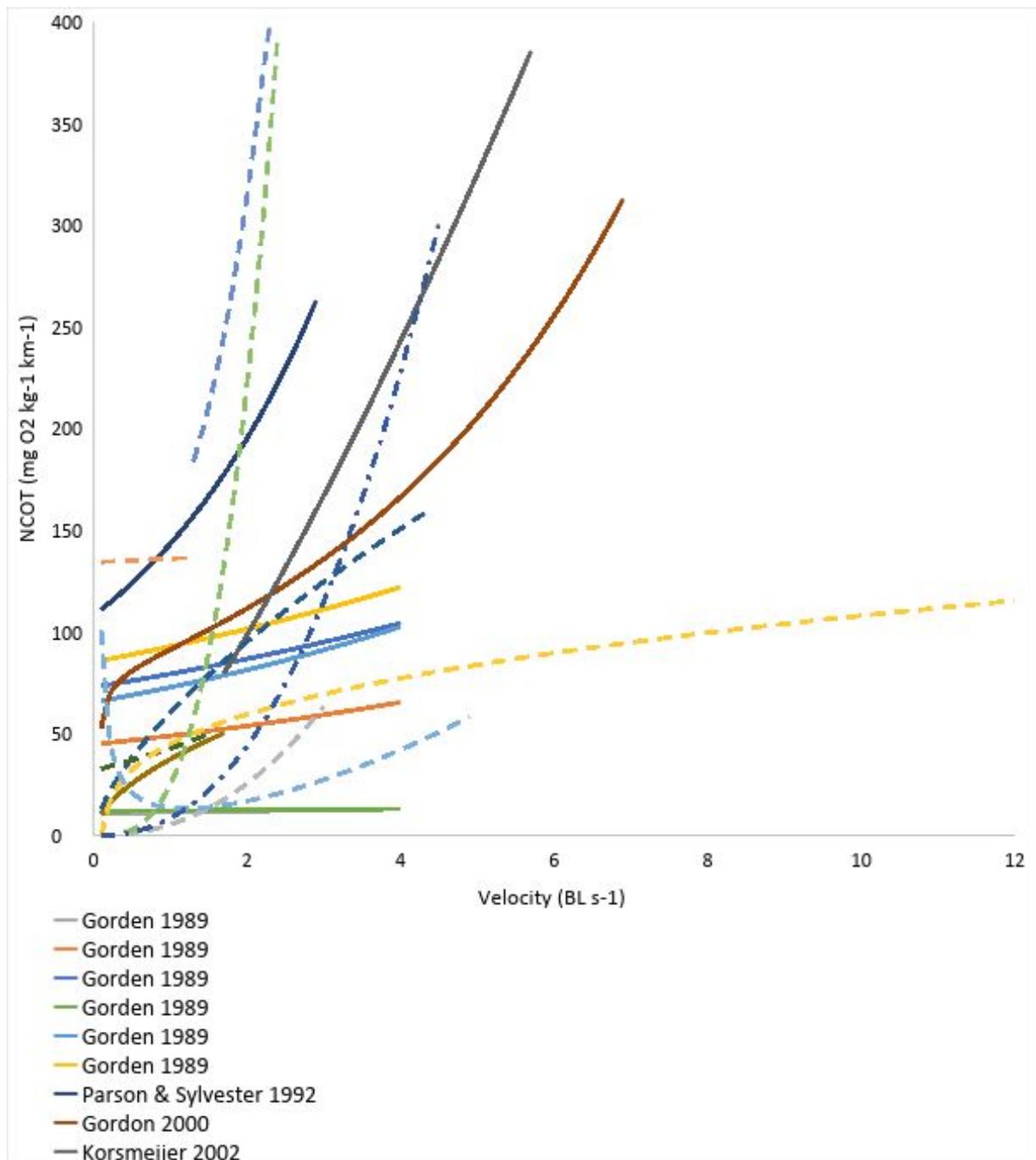


Figure 2B. A complete graph of the Net Cost of Transport (TCOT ($\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$)) against the relative velocity in (BL s^{-1}). Shiner surfperch (Gordon et al. 1989; Roche et al. 2014), Striped surfperch (Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010), Redbreasted wrasse (Fulton et al. 2013), Bluelined wrasse (Fulton et al. 2013), Bluegill sunfish (Kendall et al. 2007), Parrotfish (Korsmeijer et al. 2002), Triggerfish (Korsmeijer et al. 2002), Boxfish (Gordon et al. 2000), Senorita Wrasse (Gordon et al. 1989).

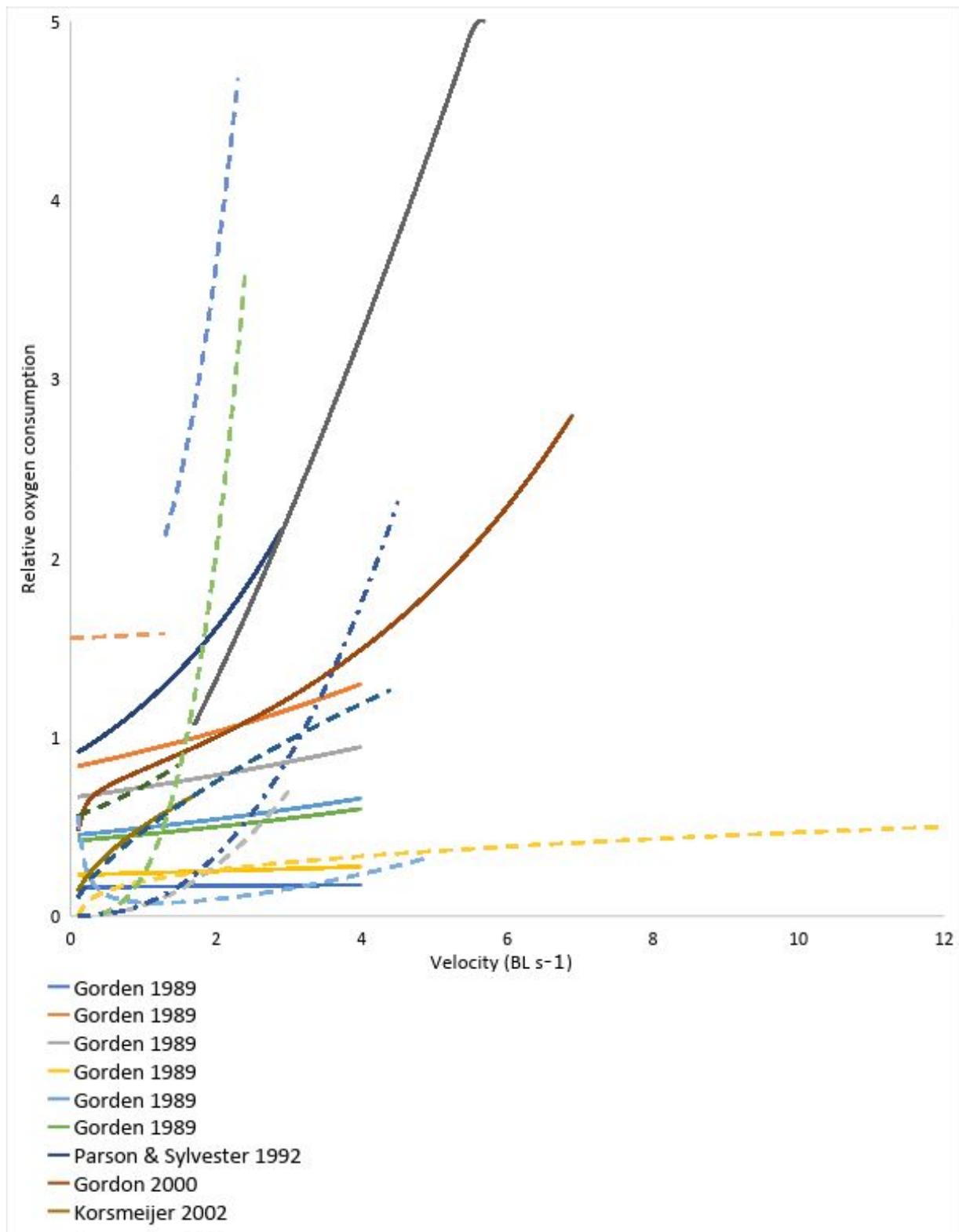


Figure 2C. A complete graph of the Net Cost of Transport (TCOT ($\text{mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$)) against the relative velocity in (BL s^{-1}). Shiner surfperch (Gordon et al. 1989; Roche et al. 2014), Striped surfperch (Cannas et al. 2006; Johansen et al. 2010; Svendsen et al. 2010), Redbreasted wrasse (Fulton et al. 2013), Bluelined wrasse (Fulton et al. 2013), Bluegill sunfish (Kendall et al. 2007), Parrotfish (Korsmeijer et al. 2002), Triggerfish (Korsmeijer et al. 2002), Boxfish (Gordon et al. 2000), Senorita Wrasse (Gordon et al. 1989).