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A Meta-Analytical Review of Muscle Glycogen Replenishment

Ian T. Macklin[1], Frank B. Wyatt[1], Malaeni Ramos[1], Grant Ralston[2]

[1]Department of Athletic Training and Exercise Physiology, Midwestern State University, Wichita Falls, US, [2]Institute for Clinical Exercise and Health Science, Applied Physiology Research Laboratory, School of Science and Sport, University of the West of Scotland, Hamilton, Lanarkshire, Scotland, UK

ABSTRACT

Macklin IT, Wyatt FB, Ramos M, **Ralston G**. A Meta-Analytic Review of Muscle Glycogen Replenishment. **JEPonline** 2019;22 (4):95-111. This study determined the mechanisms of muscle glycogen depletion and replenishment. A systematic literature review and meta-analysis research design was used. Inclusion and exclusion criteria consisted of the following: Glycogen depletion-replenishment studies; subjects in studies had no pathologies; human and animal studies were accepted; studies with diet manipulation were accepted; articles accepted for coding were peer reviewed, original publications. Coded studies were summarized and statistically analyzed. Coded variables were presented as means and standard deviations (±SD). Muscle glycogen depletion and replenishment were analyzed with Cohen's d effect size (ES). Fourteen studies were coded allowing for a total sample size of N=149. Subject demographics were: age, 29.0 ± 2.9 yrs; height, 180.4 ± 5) cm; and weight, 74.7 ± 3.6 kg. Pre-Post depletion rate ES was 10.29, which was considered huge. Post replenishment rate ES was 4.39, which was considered large. High intensity work led to the greatest depletion rates. High carbohydrates, with high kcal per meal showed the greatest replenishment rates.

Key Words: Depletion, Muscle biopsy, Performance, Recovery, Replenishment rates, Skeletal muscle glycogen

INTRODUCTION

During exercise performance, muscle glycogen is the dominant source for energy (12). The duration of exercise has been found to be closely related to the amount of glycogen stored in the muscle (41).

Depleted muscle glycogen levels during endurance events are associated with decreased performance and fatigue, even when other energy sources are available (26). During endurance exercise, skeletal muscles rely on localized storage of glycogen and whole-body glucose (34).

The formation of adenosine triphosphate (ATP) relies heavily on departmental muscle glycogen stores (36). Once a working muscle has depleted its stores of glycogen, glycogen must be replenished via the liver or through the consumption of food; a process which takes time (22,25,47). The purpose of this study was to determine via a meta-analysis the extent of muscle glycogen depletion through different modes of exercise, and what if any effect different diets have on the replenishment of depleted glycogen stores.

METHODS

Subjects

A total of fourteen (14) studies were used in the numerical coding of the meta-analysis. Seven were used to analyze glycogen depletion via an exercise protocol and 7 were used to analyze glycogen replenishment post-exercise protocol. Table 1 indicates the demographics of the subjects from the selected studies.

Table 1. Mean and Standard Deviation of the Demographics.

Age (yrs)	**Height** (cm)	**Weight** (kg)	**VO_2 max** ($mL \cdot kg^{-1} \cdot min^{-1}$)
29.0 ± 2.9	180.4 ± 5.0	74.7 ± 3.6	61.2 ± 4.0

Mean ± SD of the 14 studies used for numerical analysis (N=149)

Procedures

A systematic review of peer-reviewed articles was used to procure data for the subsequent meta-analysis. Initial searches focused primarily on muscle glycogen depletion via exercise and subsequent replenishment afterwards. SportDiscus, PubMed, and Google Scholar were search engines accessed during the discovery period with cross-referencing used for the additional peer-reviewed articles. Selected articles were then categorized, selecting those which focused primarily on muscle glycogen replenishment; inclusion and exclusion criteria were then applied to the articles. After the articles for coding were selected, they were qualitatively summarized and quantitatively coded for statistical analysis. Table 2 is a brief summary of the inclusion and exclusion criteria used for the current study.

Table 2. Inclusion and Exclusion Criteria for the Study.

Inclusion Criteria	Exclusion Criteria
• Original, peer reviewed articles • Articles focusing on muscle glycogen depletion or replenishment • Diet manipulation studies were accepted for coding • Human studies were accepted for coding • Review articles, while not used for coding, were accepted for citation purposes	• Articles not peer reviewed or published • Articles not measuring muscle glycogen • Dietary supplementation was not accepted for coding purposes • Non-human studies were omitted from coding • Pathologies were not accepted for coding purposes • Environmental factors

Statistical Analyses

All statistical analysis was performed using STATISTICA 7.0 (StatSoft Inc., Tulsa, OK) and shown as mean ± standard deviation. Pre- and post-measures used Cohen's Effect Size calculation (44).

$$d = \sqrt{\frac{[SD_2^2(n-1) + SD_1^2(n-1)]}{(n+n-2)}}$$

Equation 1. Effect size calculation, where SD is the standard deviation, d is the pooled effect size, and n=sample size. Effect size is a standardized value that determines the level of significance. Table 3 below depicts the significance of different values of d (6,43).

Table 3. Descriptors for Magnitude of d. (Statistical significance was set *a priori* at P≤0.05)

Effect Size	Very Small	Small	Medium	Large	Very Large	Huge
d	0.01	0.20	0.50	0.80	1.20	2.0

RESULTS

Pre to Post-Exercise and the Resulting Muscle Glycogen Depletion

The data from the 7 articles used for the pre- to post-muscle glycogen depletion was tabulated and graphed (Figure 1) to analyze differences found.

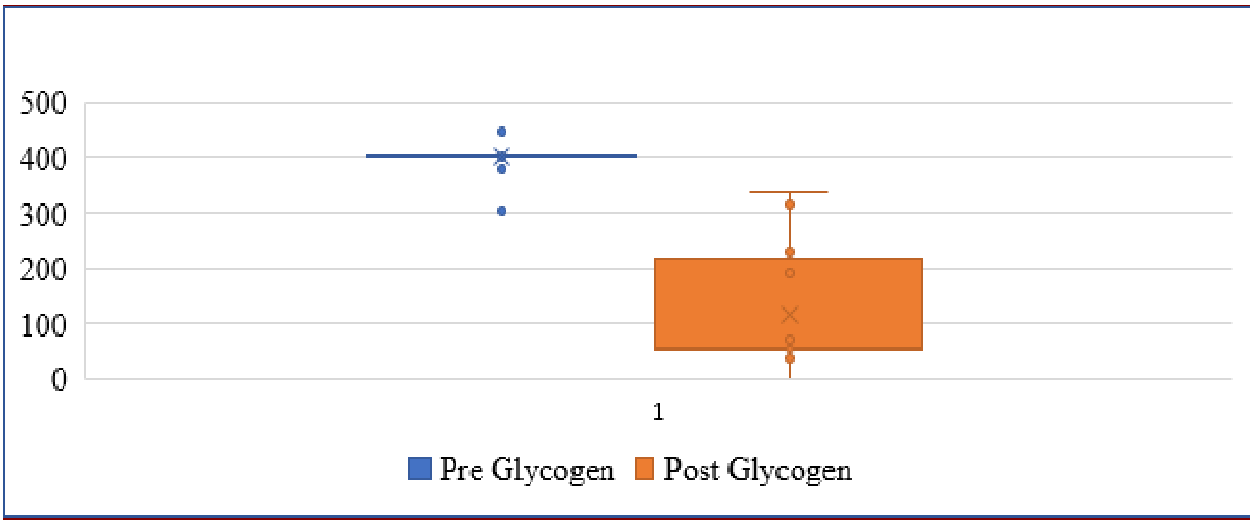

Figure 1. Pre vs. Post-Exercise Glycogen Levels.

The mean pre-exercise muscle glycogen for the studies analyzed was 402.3 ± 33.16 mmol·kg^{-1} wet weight. The mean post-exercise muscle glycogen was 124.2 ± 18.7 mmol·kg^{-1} wet weight.

By separating each study's pre- and post-exercise muscle glycogen levels the differences in training protocols can be discerned. The glycogen studies that looked at muscle glycogen levels pre- to post-exercise in rank order of percentage of muscle glycogen depleted are depicted in Figure 2.

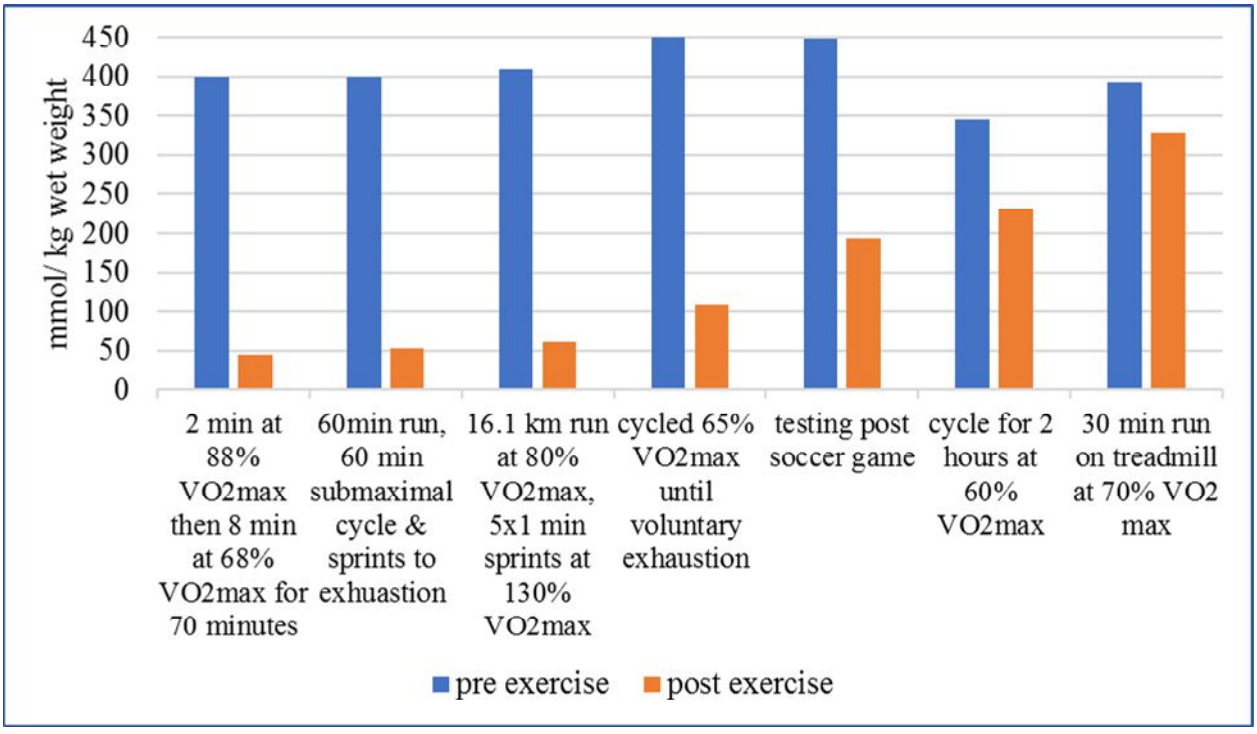

Figure 2. Muscle Glycogen Levels Pre- to Post-Exercise.

The general trends of the exercise protocols depicted in Figure 2 are the longer the duration and those that included both aerobic and anaerobic exercise resulted in greater glycogen depletion post-exercise. Descriptions of each exercise protocol from most to least depleted post-exercise are as follows. Ivy et al. (20) found that 70 min of interval training, cycling at 2 min at 88% VO_2 max followed by 8 min at 68% VO_2 max depleted cyclists muscle glycogen levels by 89%. Aulin et al. (2) found that 60 min of running followed by 60 min submaximal cycling with short sprints to exhaustion depleted muscle glycogen in well-trained athletes by 87%. Costill et al. (10) found that 16.1 km run at 80% VO_2 max followed by 5x1 min sprints at 130% VO_2 max depleted muscle glycogen in trained athletes by 85%. Gusba et al. (17) found that cycling at 65% VO_2 max until volitional exhaustion (118 min, ± 2.9) depleted muscle glycogen in physically active participants by 76%. Kustrup et al. (28) found that a division one European soccer match depleted highly trained athlete's glycogen levels by 57%. Williams et al. (47) found that 2 hrs cycling at 60% VO_2 max depleted trained cyclist muscle glycogen levels by 33%. Wee et al. (46) found that 30 min running on a treadmill at 70% VO_2 max depleted recreational runners muscle glycogen levels by 17%. The pooled effect size of pre to post-exercise for muscle glycogen depletion can be calculated from the data provided from each study. The resulting value of d was 10.29, which is considered huge.

Muscle Glycogen Replenishment Post-Exercise

The dietary intervention, timing of food intake, and length of time glycogen stores could replenish varied between studies. As noted in Figure 3, the utilization of various means of dietary manipulation affects glycogen replenishment 24 hrs post-exercise.

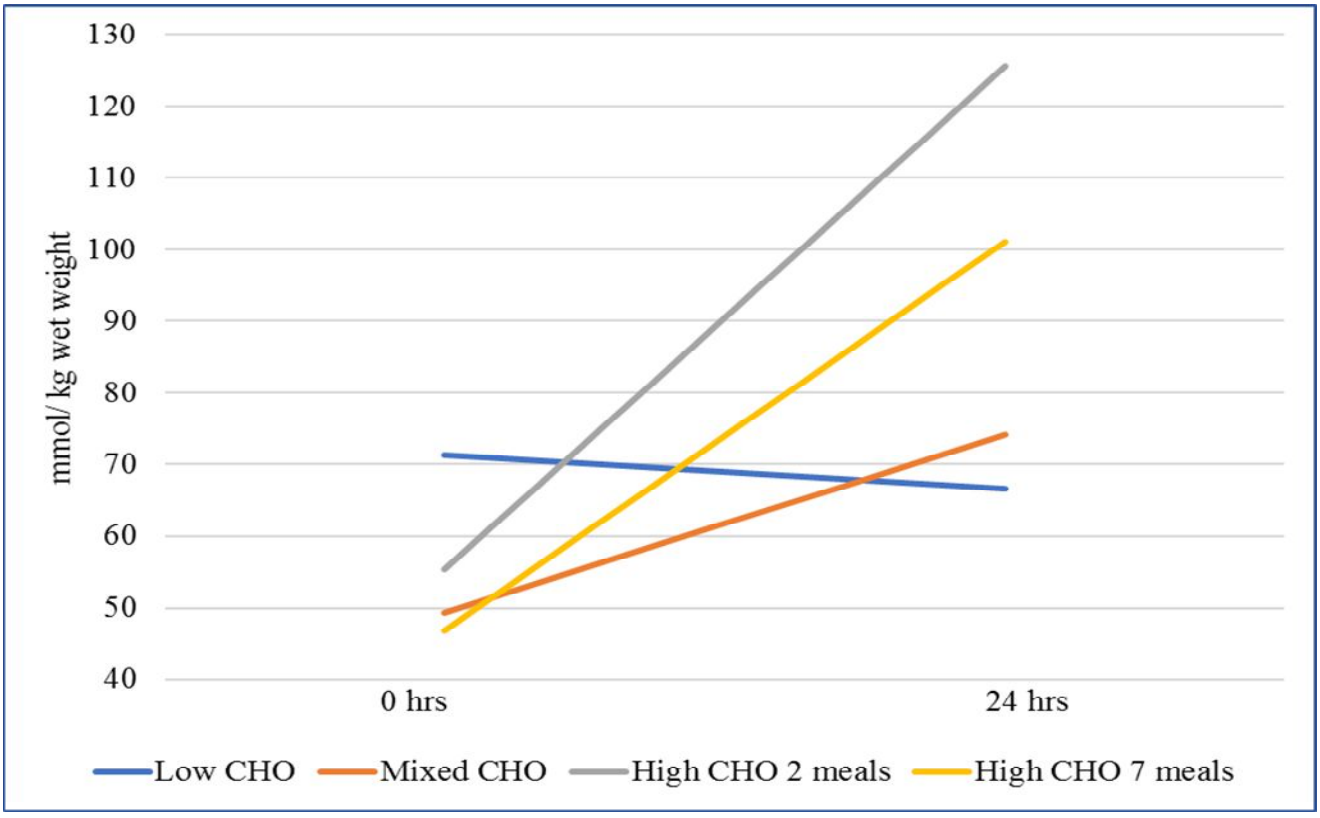

Figure 3. Glycogen Replenishment through Dietary Intervention (10).

Costill et al. (10) found that glycogen replenishment varied based on how much carbohydrates were consumed in post-exercise diet and the frequency of feeding. Each diet consisted of 3,000 kcals·d^{-1} with the total amount of carbohydrates being manipulated between groups. The low carbohydrate group contained 188 gm of carbohydrates over 2 meals, the mixed carbohydrate group contained 375 gm of carbohydrates over 2 meals, the high carbohydrate 2 meals contained 525 gm over 2 meals, and the high carbohydrate 7 meals contained 525 gm of carbohydrates over 7 meals.

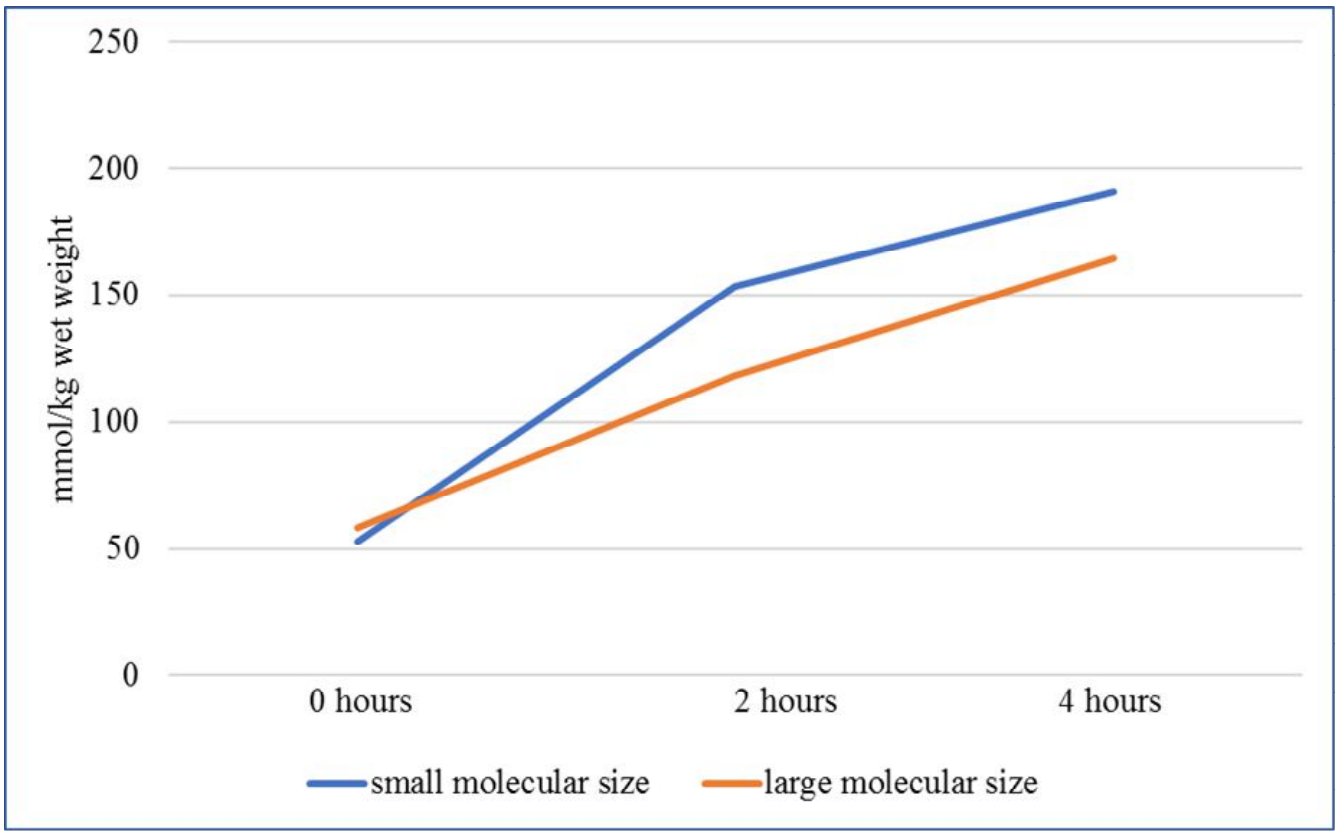

Figure 4. Isocaloric Drinks with Large vs. Small Molecular Size (2).

Aulin et al. (2) found that the consumption of carbohydrates of either small or large molecular mass following exercise resulted in different muscle glycogen replenishment rates. After a muscle glycogen depletion protocol either 300 gm of simple sugar or complex carbohydrates were consumed. Those that consumed simple sugars had significantly ($P<0.05$) greater muscle glycogen replenishment than those that had consumed complex carbohydrates. Studies looking at simple versus complex carbohydrates for longer periods of recovery found a different trend between the two groups. As noted in Figure 5 below are the skeletal muscle glycogen levels over 2 days as compared to simple versus complex carbohydrates.

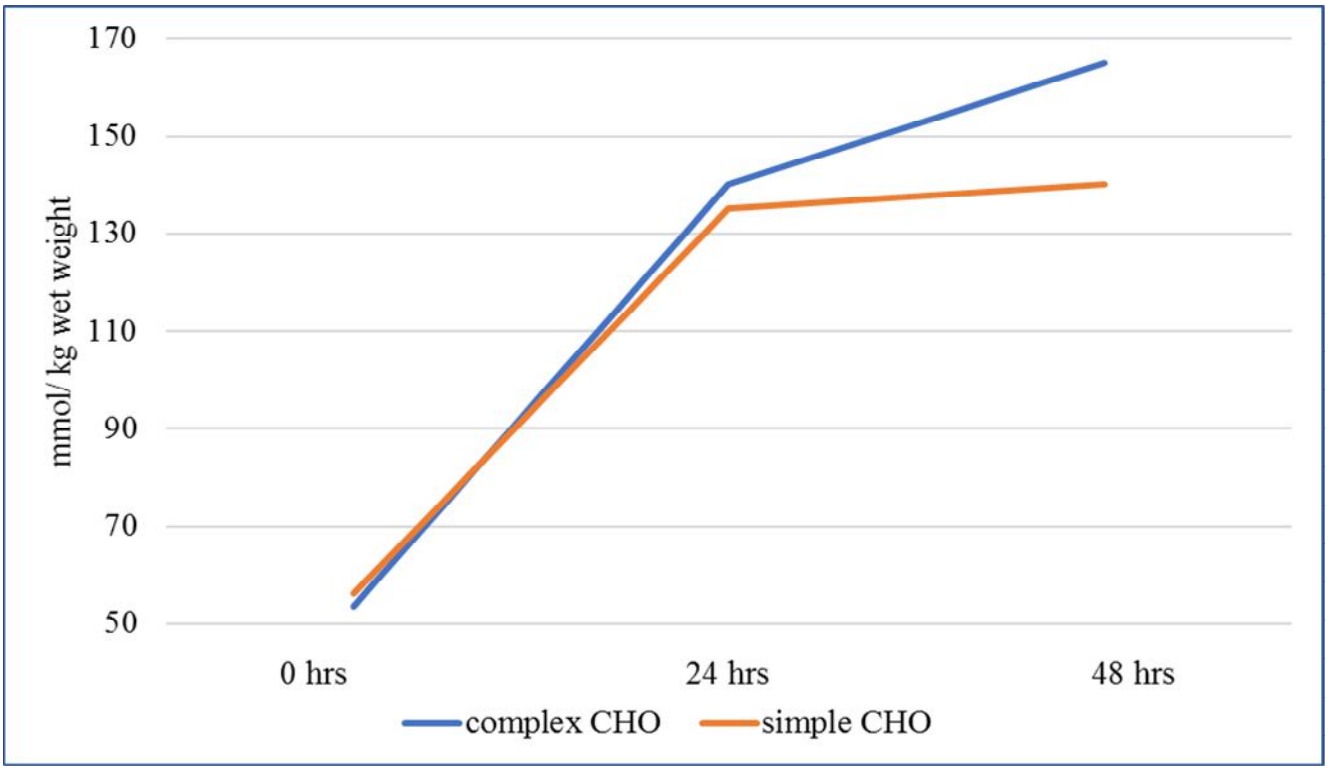

Figure 5. Simple vs. Complex Carbohydrate Consumption over 48 hrs (10).

Complex carbohydrates resulted in similar muscle glycogen replenishment up to 24 hrs post-exercise as compared to simple sugars but resulted in greater muscle glycogen replenishment in the 24 to 48 hrs post-exercise period. Costill et al. (10) fed participants a diet consisting of 70% carbohydrates, 20% fat, and 10% protein diet, with 3,700 kcals being administered in 2 meals in the first 24 hrs, and 2,400 kcals in 2 meals in the second 24 hrs. This equated to 648 and 415 gm of carbohydrates, respectively. The difference between the 2 groups was in the type of carbohydrates consumed, with the complex carbohydrate group consuming starches and the simple carbohydrate group consuming simple sugars. While glycogen levels began at relatively similar levels and were at the same relative level after 24 hrs, there was a significant ($P<0.05$) separation between the simple and the complex carbohydrate groups after 48 hrs. The effect size of muscle glycogen replenishment post-exercise was 4.39, which is considered huge.

Muscle Glycogen Resynthesis Rates

The rate at which muscle glycogen is replenished is affected by the amount of carbohydrates consumed, the complexity of the carbohydrates (simple or complex), and the timing of consumption post-exercise. Table 4 below is in ranked order of skeletal muscle glycogen resynthesis rate at 2 and 4 hrs post-exercise.

Table 4. Muscle Glycogen Resynthesis Rates in Order of Rate Found at the End of the Second Hour of Muscle Glycogen Replenishment Post-Exercise.

Authors	Total Amount of Carbohydrate (gm)	0-2 Hours ($mmol \cdot kg^{-1}$)	2-4 Hours ($mmol \cdot kg^{-1}$)
Aulin et al. (2)	300 split every 30 min	50.2	33
Blom et al. (4)	207 split 0-2 hrs	38.7	29
Ivy et al. (20)	140 split 0-2 hrs	33.1	25.6
Blom et al. (4)	103 split every 15 min	32.2	29
Maehlum et al. (30)	100 split every 15 min	30.5	
Reed et al. (39)	223 continuous infusion	30.1	24
Aulin et al. (2)	300 split every 30 min	29.9	26.6
Reed et al. (39)	223 split 0-2 hrs	27	23.6
Reed et al. (39)	223 split 0-2 hrs	26.2	21.9
Ivy et al. (20)	225 split 0-2 hrs	22.3	
Maehlum et al. (30)	Meal, after exercise		30.9

Aulin et al. (2) utilized 4.2 $gm \cdot kg^{-1}$ bodyweight glucose polymer and monomer, with the glucose polymer performing significantly better than the glucose monomer (50.2 vs. 29.9 $mmol \cdot kg^{-1} \cdot hr^{-1}$ at 2 hrs, 33.0 vs. 26.6 $mmol \cdot kg^{-1} \cdot hr^{-1}$ at 4 hrs post-exercise). Blom et al. (4) used 1.4 $gm \cdot kg^{-1}$ body weight and 0.7 $gm \cdot kg^{-1}$ body weight, with 1.4 $gm \cdot kg^{-1}$ body weight performing better at the 2-hr mark (38.7 vs. 32.2 $mmol \cdot kg^{-1} \cdot hr^{-1}$), with both providing a resynthesis rate of 29.0 $mmol \cdot kg^{-1} \cdot hr^{-1}$ at 4-hrs post-exercise. Ivy et al. (20) provided 1.5, 2.0, and 3.0 $gm \cdot kg^{-1}$ body weight of glucose polymer immediately post exercise with 22.3, 33.1, and 24.9 $mmol \cdot kg^{-1} \cdot hr^{-1}$, respectively. Maehlum et al. (30) provided solid food after exercise, producing a rate of resynthesis 4 hrs post-exercise of 30.9 $mmol \cdot kg^{-1} \cdot hr^{-1}$. Reed et al. (39) provided 0.8 $gm \cdot kg^{-1}$ body weight constant infusion for 4 hrs, 3.0 $gm \cdot kg^{-1}$ body weight solid food at 0 and 2 hrs post exercise, and 3.0 $gm \cdot kg^{-1}$ body weight glucose polymer at 0 and 2 hrs post exercise. Glycogen resynthesis rates were 30.1, 27.0, and 26.2 $mmol \cdot kg^{-1} \cdot hr^{-1}$ at 2 hrs, and 24.0, 23.6, and 21.9 $mmol \cdot kg^{-1} \cdot hr^{-1}$ at 4 hrs, respectively.

DISCUSSION

Pre to Post-Exercise and the Resulting Muscle Glycogen Depletion

Wasserman (45) found that on average skeletal muscles store 400 $mmol \cdot gm^{-1}$ wet weight of glycogen. The findings from this meta-analysis are consistent with Wasserman's (45) findings as the mean pre-exercise glycogen levels were 402.3 $mmol \cdot gm^{-1}$ wet weight. Pre-exercise skeletal muscle glycogen levels in the studies coded fell between 345 to 450 $mmol \cdot kg^{-1}$ wet weight, putting them within the 350 to 700 $mmol \cdot kg^{-1}$ wet weight range that Knuiman et al. (27) found. Figure 6 indicates various mechanisms used to deplete muscle glycogen levels. These mechanisms came from coded studies.

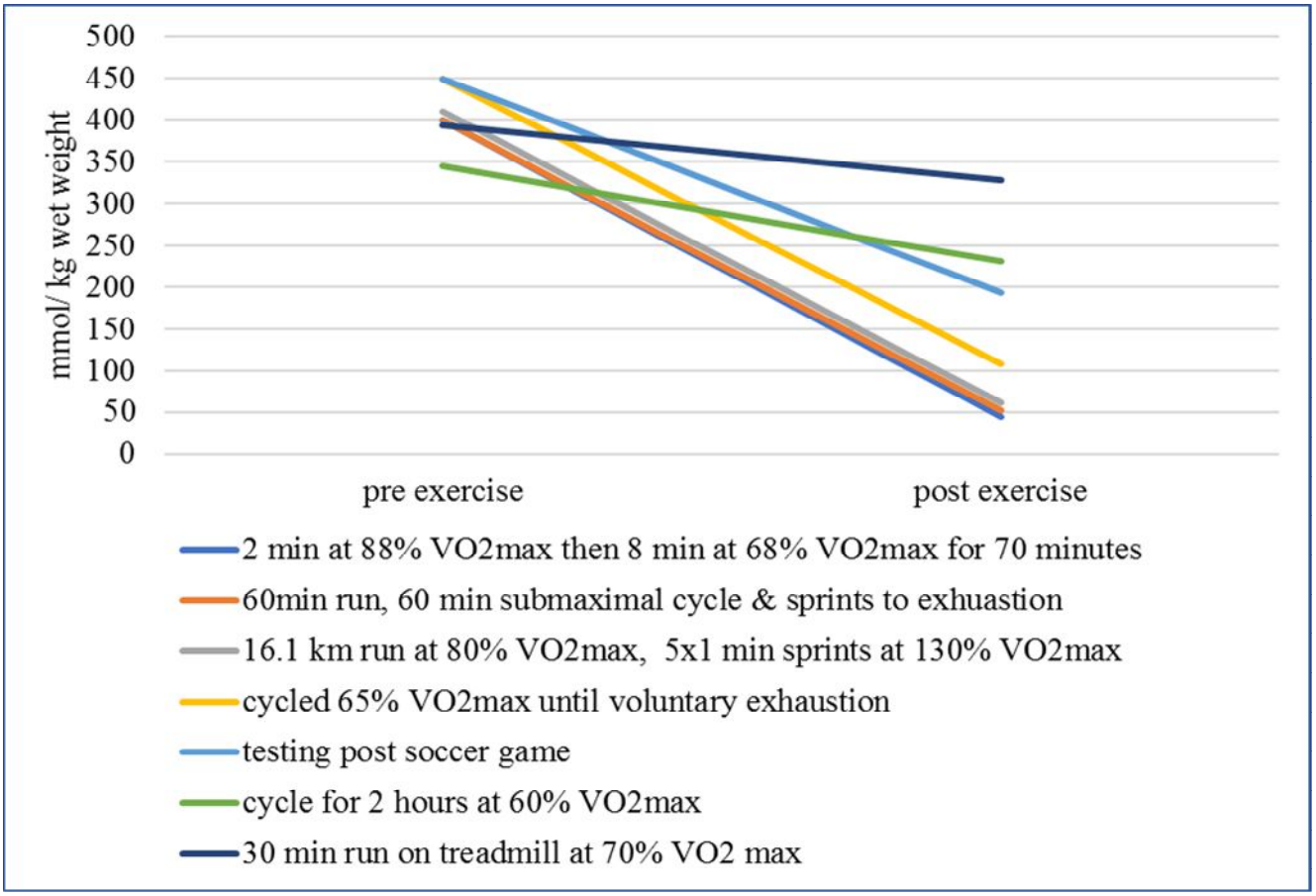

Figure 6. Muscle Glycogen Levels Pre to Post-Exercise.

Resting values are wide ranging and individualized based on training status, diet, muscle fiber type composition, specific muscles analyzed, sex, and body weight. The extent of muscle glycogen depletion via exercise depends on the mode, intensity, and duration. It has been established that the lactate threshold for exercise is approximately 70% VO_2 max (25). At this level of intensity, the energy substrate utilized is almost exclusively carbohydrates, thus the body is relying on blood glucose and glycogen stores rather than lipid stores (31). Muscle glycogen levels are stored in distinct sections of the muscle and within different fiber types (36). This has been termed compartmentalized as it relates specifically to muscle glycogen. Moreover, this means that to deplete muscle glycogen levels by performing endurance training at the lactate threshold followed by sprints allows both sites (i.e., specific muscle group, specific fiber type) of glycogen storage to be depleted.

The protocols that performed both aerobic and anaerobic exercise resulted in the lowest post-exercise glycogen levels as can be seen in Figure 6. Cycling has also been shown to facilitate greater glycogen depletion than running. Reasons for this include runners having to support their entire bodyweight while running, and eccentric loading during running that does not occur while cycling. With the breakdown of eccentric-concentric coupling as well as central fatigue, which occurs at a greater rate during running than in cycling, the mechanisms

for fatigue are different in the two movements. This explains the greater depletion of muscle glycogen in cyclists than in runners (33).

The lower intensity of the study by Williams et al. (47) can explain the higher post-exercise levels of glycogen (231.5 $mmol \cdot kg^{-1}$) as opposed to the regiments, which were of higher intensity (17) or those which included anaerobic intervals at the end of testing. The slope of each exercise intervention in Figure 6 illustrates the relationship between the intensity of exercise versus the amount of muscle glycogen depletion post-exercise.

During prolonged aerobic exercise the glucose uptake of exercising muscle fibers has shown to increase proportionally to the number of glycogen-depleted fibers. This results in a compensation for the reduced availability of muscle glycogen stores (16). This phenomenon occurs if there is in-exercise feeding to preserve glycogen stores or if the intensity is low enough to use free fatty acid and glucose oxidation as is the case of a 2-hr cycle at 60% VO_2 max (25). This increase in glucose uptake by the exercising muscles coincides with a decrease in glucose uptake in non-exercising muscles (13).

Coyle et al. (12) found that in-exercise feeding with carbohydrates allowed participants to oxidize carbohydrate sources at a high enough rate that they could spare muscle glycogen levels during the later stages of extended, strenuous aerobic exercise. This sparing of glycogen depletion allowed the postponement of fatigue, providing blood glucose levels could be maintained (5,49). In addition to in-exercise feeding, the timing of carbohydrate consumption plays a factor in the oxidation of carbohydrates during exercise. In the study by Costill et al. (10), it was found that while a high-carbohydrate diet facilitated muscle glycogen replenishment, only the cohort consuming 7 meals a day showed an increase of carbohydrate oxidation during exercise. The cohort consuming 2 meals a day with the same amount of carbohydrates per day did not show an elevation in carbohydrate oxidation.

It has also been found that lipid oxidation increases whenever glucose utilization is reduced, such as when longer duration but lower intensity exercise occurs (18,38,48). This is most common during lower intensity prolonged aerobic activities since the energy systems used for lipid oxidation are a more protracted process to produce the chemical form of energy utilized by the body, adenosine triphosphate, ATP (27).

Worthy of note in Figure 6 is the soccer game. After 90 min the players' muscle glycogen levels had fallen below the critical level (250-300 $mmol \cdot kg^{-1}$), thus impairing the function of the sarcoplasmic reticulum. This resulted in a 25% reduction in peak power post-game in the players tested (35). The sarcoplasmic reticulum impairment affected muscle glycogen replenishment, as after 24 hrs glycogen levels were at 75% of pre-game or 56% of their functional glycogen stores. At 24 hrs the maximal force production was at 90% of pre-game values. Of note is that functional glycogen is different than measured glycogen. Usable or functional glycogen is calculated by determining the difference between rested state glycogen and the glycogen remaining after fatigue (47). This is an important distinction, since once a participant has hit volitional fatigue there is still glycogen in the skeletal muscle, even if the person can no longer continue exercising. While glycogen is still present it is not used by the body to continue exercising.

Muscle Glycogen Replenishment Post-Exercise

The ability of the body to replenish glycogen stores post-exercise is predicated on several factors. These include but are not limited to the type of fuel, when it's consumed, how much is consumed, length of recovery period, hydration status of participant, plasma glucose and insulin levels, and level of glycogen depletion (11,13,15,23,20).

The findings by Costill et al. (10) are consistent with other research on the effects that diet and carbohydrate consumption have on glycogen replenishment (3,9,19,29). An ample amount of carbohydrates per body weight is necessary to facilitate the greatest replenishment of skeletal muscle glycogen stores. Studies have found that 1.2 to 1.5 gm carbohydrate per kg body weight per hour was adequate for glycogen replenishment provided an initial dose of 50 to 75 gm of carbohydrate is administered immediately post-exercise (14,21,24,40). If carbohydrate consumption concentrations are below optimal levels, a combination of carbohydrates and fat in a 2-2.9:1 ratio can be an acceptable replenishment source to aid in glycogen replenishment (21,22,50).

Costill et al. (10) found that a complex carbohydrate diet elicited greater muscle glycogen storage than simple sugars 24 hrs after exercise can be explained by the maintained elevation of serum insulin levels. Elevated insulin and blood glucose levels are not necessarily associated with the rate of glycogen replenishment, as blood measures factor in the demands for exercised and non-exercised muscles (8,13,23). Non-insulin-dependent muscle glucose transport increases via exercise, thus reducing over time post-exercise regardless of glycogen repletion levels (37). Even with elevated plasma glucose and insulin levels the rate of glycogen storage slows over time post-exercise, thus the administration of a carbohydrate supplement post-exercise is time sensitive (20).

While in-exercise feeding has not been shown to facilitate greater post-exercise synthesis rates of muscle glycogen, it has been shown to provide glycogen sparing during exercise (15). Glycogen sparing is a factor in post-exercise muscle glycogen levels and/or in the extension of time to exhaustion depending on the study. In-exercise feeding has been shown to allow muscle glycogen sparing by using either fat or blood glucose as the body's preferred fuel source for energy production (3). A combination of fat and carbohydrate has been shown to be optimal for both glycogen sparing and the rate of glycogen synthesis, especially in cases where the amount of ingested carbohydrate is less than current recommendations. The quantity of carbohydrates consumed post-exercise is an important factor in the replenishment of skeletal muscle glycogen stores. If the consumption of carbohydrates is restricted, muscle glycogen stores can take 8 to 10 days to return to normal (19).

Blood plasma volume has been found to be significant regarding muscle glycogen resynthesis, with lower levels of glycogen replenishment associated with dehydration (11). Furthermore, rather than water alone, the addition of electrolytes such as sodium, potassium, and chloride have been found to facilitate greater restoration of fluid retention (32). Hydration has been found to be of primary importance post-exercise, particularly if substantial water and electrolytes have been lost during exercise (47).

Muscle Glycogen Resynthesis Rates

The rate of glycogen replenishment rates has been shown to vary by study, diet intervention, time of feeding, and type of food provided. A selection of studies is displayed in Figure 7.

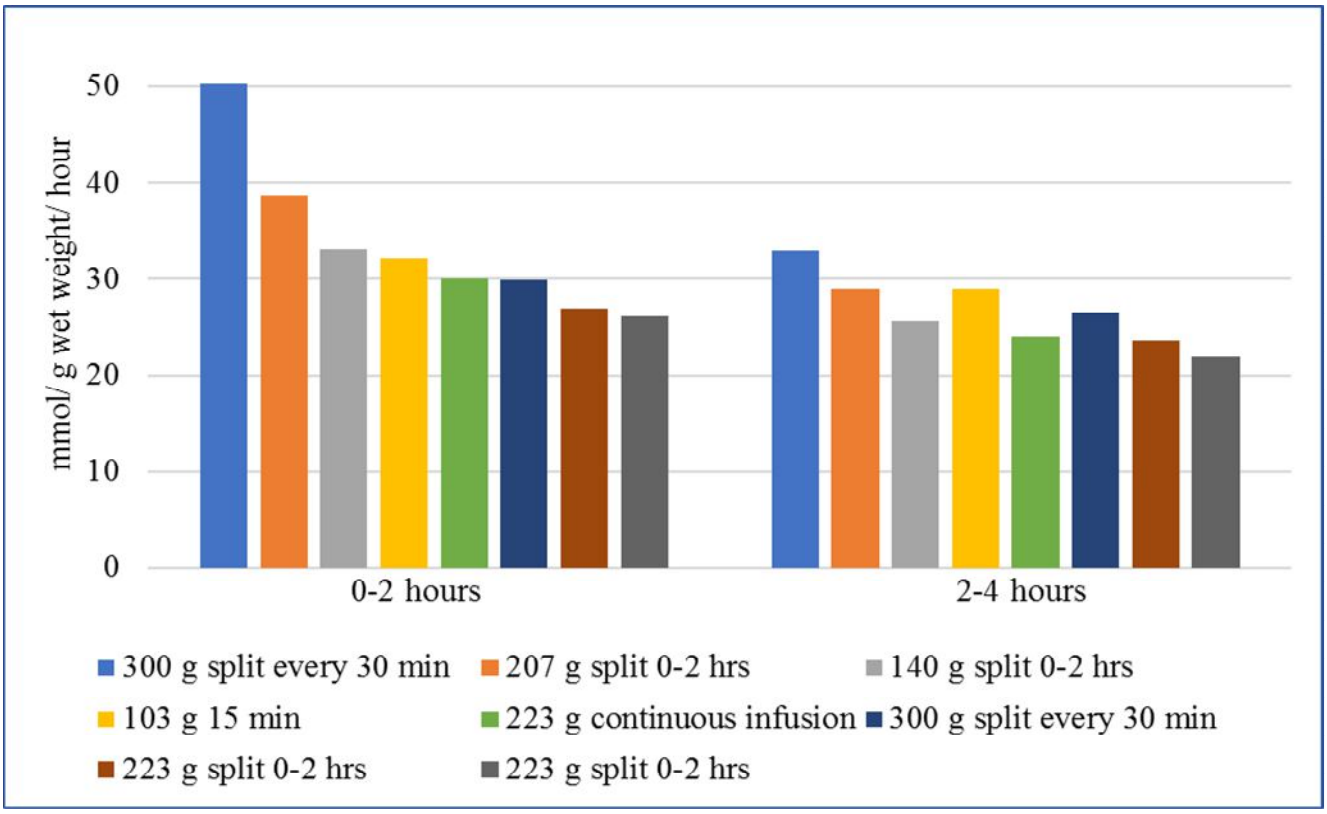

Figure 7. Glycogen Resynthesis Rates Post-Exercise.

As can been seen from Figure 7 and discussed in the results section there are several differences between studies which affected the glycogen resynthesis rates. There are some general trends across all studies coded, such as all synthesis rates declined from the 2-hr measurement to the 4-hr measurement. Also, the larger the amount of carbohydrate eaten soon after exercise cessation produced better glycogen synthesis rates than delayed consumption or smaller doses.

Ivy et al. (20) found that ingesting a 25% glucose polymer solution 2 hrs post-exercise reduced glycogen synthesis rates down to a third as compared to those that consumed the solution immediately post-exercise. As discussed early, blood flow, insulin, blood glucose levels, and the depleted muscles affinity for glucose uptake could have factored into this drastic reduction in glycogen synthesis rates in the group that delayed ingestion of glucose for 2 hrs. A factor which results from exercise is non-exercising muscles having significantly lower glucose uptake (arterial-venous glucose balance) as compared with their basal rate. This contrast with working muscles has been found to have an increase in their glucose uptake level (13). Blood flow to the lower extremity is quite low at rest but can increase by as much as a factor of 20 while exercising (1,42). Post-exercise blood flow rates decline rapidly to slightly above resting levels (1), followed by a slow reduction over the following hour (42).

Depleting muscle glycogen levels have been strongly associated with the development of fatigue during endurance training. The reduction in muscle glycogen availability is the main cause of perceived fatigue, as glycogen is essential for the resynthesis of ATP production during high-intensity endurance training. The length of time to exhaustion can be extended

via in-exercise feeding by sparing muscle glycogen through maintenance of the blood glucose levels.

While glycogen resynthesis rates do not increase post-exercise if in-exercise feeding takes place, muscle glycogen levels will be higher for any given duration due to the glycogen sparing effect of in-performance feeding while performing endurance training. The timing of post-exercise feeding is critical. With blood flow reducing rapidly after exercise, the muscles take in greater amounts of glucose to be converted into glycogen within the first hour and at a level much like pre-exercise levels after 2 hrs. If this 2-hr window is missed, the rate at which muscles resynthesize glycogen will be greatly reduced. Larger amounts of simple carbohydrates ingested during this 2-hr window will aid in the initial resynthesis. After 24 hrs, ingestion of complex carbohydrates seems to help keep insulin levels elevated for longer; aiding in the movement of blood glucose into the muscles for resynthesis of muscle glycogen. The consumption of protein with carbohydrates seems to help with muscle glycogen resynthesis due to the protein reducing the overall glycemic load of the food, steadying out the insulin spike which seems to be one of the mechanisms for long-term glycogen resynthesis after the initial 24 hrs. The role that blood glucose and insulin levels play in the resynthesis of muscle glycogen is complex. Blood glucose and insulin levels are consistent throughout the bloodstream even when working muscles are using both at a greatly increased rate while non-exercising muscle shut down their utilization of blood glucose during exercise.

Future Research

The study of blood glucose and insulin is a field of research that could be expounded upon, particularly in populations that have difficulty in regulating blood glucose and insulin. The fact that the demand for glucose increases or decreases depending on intensity and usage during exercise causes some obfuscation of results regarding exercising muscles specifically. Further research into how environmental factors affect glycogen utilization and replenishment is needed. With temperature and altitude affecting different populations and the body's acute and chronic adaptation to environmental stressors, knowing how glycogen storage and utilization is affected would help with training and recovery. Research into the elderly and frail populations is a direction that should be explored because there are very few articles that pertain to this population, and also since they have reduced muscle mass their ability to store glycogen may well be reduced.

Address for correspondence: Frank B. Wyatt, EdD, Department of Athletic Training and Exercise Physiology, Midwestern State University, Wichita Falls, TX 76308, frank.wyatt@msutexas.edu

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