Surf's up! The energetic costs of labriform swimming in unsteady flows

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ABSTRACT

Swimming represents the primary means through which fishes interact with their environment, and factors influencing swimming performance can profoundly affect their distribution and survivorship. Traditional measures of swimming performance are estimated under laboratory conditions using steady water flow. However, these experiments potentially underestimate the actual cost of swimming under unsteady water flows that characterize natural systems. Using a swimming respirometer and video recordings, we swam *Cymatogaster aggregata* using a standard U_{crit} swimming trial under one of three flow conditions with the same mean water velocity at each speed increment: steady flow (control), low amplitude water velocity fluctuations ($A=0.5BLs^{-1}$) and high amplitude water velocity fluctuations ($A=1BLs^{-1}$). We found that unsteady flows increase the metabolic cost of swimming, but only when high flows push a swimming fish beyond the threshold for exclusively aerobic metabolism (beyond U_{burst}). Furthermore, unsteady flows at the highest amplitude treatment decreased the maximum mean velocity (U_{crit}) and mean gait transition velocity (U_{pc}) achieved by individuals compared to the control and low amplitude unsteady flows. However, lower costs of swimming than predicted in low amplitude flows below U_{burst} suggest that fish are able to take advantage of the cyclical wave patterns and economize energy expenditure. Mean pectoral fin beat frequency did not differ significantly among treatments. This is the first study exploring the costs of swimming under unsteady flow in a marine labriform swimmer.

INTRODUCTION

The energetic costs of locomotion can form a large and variable component of the daily energy budgets of mobile organisms (Boisclair and Sirois, 1993). Environmental factors that influence locomotor performance can therefore have profound effects on individual fitness (Arnold, 1983; Irschick and Garland, 2001). In fishes, the energetic costs of swimming have traditionally been estimated by measuring oxygen consumption in steady-flow respirometers over a range of swimming speeds (e.g. Steffensen *et al.*, 1984). While steady-flow respirometry has provided invaluable insights into the swimming physiology of fishes, it may fall short of describing the true costs of swimming in nature, where water flows are often unsteady and can vary dramatically over short time-scales (Liao, 2007; Webb et al., 2010).

Water flow in the form of waves and currents is an important physical property of aquatic systems and has major effects on community structure and species distributions (Bellwood et al., 2002; Webb et al., 2010). Many fish species living in habitats routinely exposed to high intensity water motion have developed a range of morphological, physiological and behavioural adaptations to exploit these environments (e.g. Johansen et al., 2008; Langerhans, 2008). However, an increasing number of studies suggest that global changes in climate and water flow regimes are increasing both the frequency and intensity of climatic events such as storms, floods and wave surges (Bronstert, 2003; Harley et al., 2006; Seymour, 2011; Wang and Swail, 2001). The ability of fishes to adapt to changes in their hydrodynamic environment will therefore depend on whether and how increases in unsteady water flow affect the cost of locomotion. Recent work in freshwater systems has examined the performance and energetic costs of fish swimming in turbulent flows (Enders et al., 2003; Enders et al., 2005; Taguchi and Liao, 2011; Tritico and Cotel, 2010), yet similar studies in marine organisms are nonexistent. This oversight is surprising given the ubiquity and importance of unsteady, wave-driven water motion in coastal habitats around the globe (Fulton and Bellwood, 2005; Gourlay and Colleter, 2005).

Here, we examined whether the metabolic costs of fish swimming in unsteady water flow conditions is higher than (1) the costs of swimming in steady flows (standard U_{crit} trial) and (2) the costs of swimming predicted by theoretical models based on sinusoidal, wave-like flows with fixed amplitudes. We hypothesized that fish swimming in unsteady flows incur greater energetic costs than fish swimming in steady flows because the relationship between swimming speed (U) and oxygen consumption (MO^2) is non-linear (Brett, 1964). We also hypothesized that theoretical models based on the standard curve would underestimate the cost of locomotion in unsteady flows as fish may incur additional costs from maintaining their position and stability during changes in surrounding water velocity.

Study system

Members of the surfperch family (*Embiotocidae*) are near-shore swimmers with a wide distribution along the Pacific coast of North America, from Baja California to southern Alaska (Eschmeyer et al., 1983). Surfperches are labriform swimmers; they use their pectoral fins to generate thrust via positive and negative lift forces at each fin-beat cycle in a movement analogous to the wing-beat cycle of birds in flight (Webb, 1973; Webb, 1975). In labriform fishes, routine locomotion at low to intermediate speeds is powered by pectoral girdle muscles, which consist mostly of red-oxidative (aerobic) muscle fibres (Drucker and Jensen, 1996b; Westneat and Walker, 1997). At higher swimming speeds, these fishes exhibit a distinctive switch from pectoral only to caudle-assisted swimming, a gait transition known as $U_{p\text{-}c}$ (Cannas et al., 2006; Drucker and Jensen, 1996b). Recruitment of the caudle fin for fast steady swimming speeds appears to be achieved aerobically (Svendsen et al., 2010). However, unsteady fast swimming speeds (e.g., fast-starts, burst swimming) are powered by the segmented myotomal musculature along the body axis, consisting primarily of white-glycolytic (anaerobic) muscle fibres (Beamish, 1978; Kendall et al., 2007). This transition to anaerobic metabolic pathways at high swimming speeds can generate high mechanical power outputs, but comes with an elevated cost of transport and incurs an oxygen debt (Kendall et al., 2007; Svendsen et al., 2010). Consequently, these speeds can only be sustained for a short time and result in elevated rates of oxygen consumption post-exercise (excess post-exercise oxygen consumption; EPOC) in order to repay the oxygen debt (Beamish, 1978; Brett, 1964; Lee et al., 2003). Although beach surf zones are physically dynamic environments that routinely experience high amounts of wave exposure, previous studies on surfperches have only investigated the kinematics and physiology of swimming in steady state laminar flow conditions (Cannas et al., 2006; Drucker and Jensen, 1996a; Drucker and Jensen, 1996b; Mussi et al., 2002; Svendsen et al., 2010). Given this, we swam shiner surfperch (*Cymatogaster aggregata* Gibbons) in a flow-through respirometer at progressively higher speeds using traditional steady state flow and compared measures of oxygen consumption and swimming performance to those recorded in unsteady, undulating flow at set amplitudes. Our flow treatments mimicked a unilateral wave scenario (i.e., sinusoidal variations in water flow velocity in a single direction, around a constant mean velocity).

MATERIALS AND METHODS

We collected 20 adult *C. aggregata* (total length L_T= 14.84 ± 0.11cm; mass = 46.3 ± 1.4g; means ± s.e.) in August 2011 using a beach seine net at Fourth of July Beach and Jackson's Beach on San Juan Island, Washington, USA. Fish were immediately transported to the Friday Harbor Laboratories, University of Washington, and kept in flow-through tanks at an ambient light regime. Tanks were continuously supplied with filtered seawater (salinity 34 ppm) at a mean temperature of 12 °C (range 11 to 13 °C). Fish were acclimated for a minimum of 3 days and fasted for 24 h before experimental trials to ensure that satiation was standardized across individuals (Johansen et al., 2010; Niimi and Beamish, 1974).

Respirometry

We measured oxygen consumption (M_{O2}: mg $O_2 kg^{-1}h^{-1}$) for 20 solitary fish in a 8.31 l clear Plexiglas swimming respirometer with a working section of 9.0×26.0×10.0 cm (width × length × depth). Oxygen levels in the respirometer were recorded using a fiber optic oxygen meter (Presense Fibox 3) monitored with Oxyview v.5.31 (Presens). To reduce bacterial growth and respiration in the system, we rinsed the respirometer thoroughly in freshwater after every 6th trial. This procedure ensured that background respiration rates (measured at the beginning and end of each trial) remained below 20% of the oxygen consumption of fish.

We calibrated the flow in the working section of the respirometer from 0 to 80 ± 0.5 cm s^{-1} (mean ± SE) using a digital TAD W30 flow-meter (Höntzsch, Germany). Solid blocking effects of the fish in the working section were corrected by the respirometry software (AutoResp, Loligo Systems) following Bell & Terhune (1970). Fish were placed in the respirometer and left to acclimate for a minimum of six hours at a swimming speed of 0.5 body lengths per second (BLs^{-1}) until their oxygen consumption reached a steady state. We measured oxygen consumption at 0.5 BLs^{-1} by averaging the three MO^2 measurements immediately prior to the onset of the first trial (1 BLs^{-1}). These points fall within 10% of the average three lowest MO^2 measurements at 0.5 BLs^{-1} in over 50% of the fish tested.

We measured oxygen consumption as a function of swimming speed (U) following a standard critical swimming speed (U_{crit}) protocol for intermittent flow respirometry (Plaut, 2001; Steffensen, 1989; Steffensen et al., 1984). U_{crit} trials were initiated at 1.0 BLs^{-1} and swimming speed was increased by increments of 0.5 BLs^{-1} every 30 min. A swimming trial ended when the fish could no longer swim against the flow and was swept downstream onto a retaining grid for a minimum of 3s. We took three consecutive recordings of M_{O2} at every swimming speed; each determination consisted of a 225s flush, 75s wait and 300s measurement period, for a total of 10 minutes. We constructed a standard curve using six test subjects (treatment A=0; L_T= 14.92 ± 0.24cm; mass = 44.7 ± 2.2g), in which a constant velocity was maintained at each swimming speed increment (e.g. Johansen et al., 2010). We repeated the same step-wise procedure for the remaining 14 fish, but varied the swimming speed using low amplitude (A= 0.5BLs^{-1}) fluctuations (n=7, L_T= 14.89 ± 0.18cm; mass = 48.5 ± 3.46g) and high amplitude (A=1.0 BLs^{-1}) fluctuations (n=7, L_T= 14.64 ± 0.22cm; mass = 45.2 ± 1.2g) around the mean at each increment of 0.5 BLs^{-1} (e.g., 1.0 ± 0.5 BLs^{-1} and 1.0 ± 1.0 BLs^{-1}). These sinusoidal variations in water velocity were created by programming the propeller's rotational speed in the respirometer (TracerDAQ Pro^{TM} Software). Water velocities followed a sinusoidal function with a period of 5s, which is representative of moderate wave periods in the Puget Sound and San Juan Islands (Finlayson, 2006).

We measured EPOC after each U_{crit} trial by integrating the area under the curve of the relationship between MO^2 and time at U_{crit} until the time when the fish's oxygen consumption reached a steady state (Lee et al., 2003). Since most fish did not reach an oxygen consumption rate as low as that measured prior to the onset of the trial (see Svendsen et al., 2010), we determined the end of EPOC as the first 10 min time interval in which MO^2 increased by 5% after having stabilized. We added EPOC to each fish's MO^2 measurements proportionally to the count of burst swimming events at each distinct swimming speed during the U_{crit} trial. We attributed EPOC to burst swimming behaviours only, excluding pectoral and caudal fin swimming. In the confamilial, co-occurring striped surfperch *Embiotoca lateralis* Agassiz, Svendson et al. (2010) showed that the pectoral-caudal gait transition (U_{p-c}) is not a threshold for anaerobic swimming; instead burst activity is the single most important determinant of EPOC.

Video analysis: swimming performance and fin beats

We recorded the swimming behaviour of test subjects during each trial with a video camera (Canon Vixic HV30) positioned above the respirometer's working section. A mirror was placed at 45° adjacent to the working section in order to record the top and side view of the fish in a single frame. $U_{p\text{-}c}$ was determined when a fish changed from strictly pectoral to pectoral-and-caudal swimming for more than 5s (Johansen and Jones, 2011). For each speed increment of 0.5 BLs^{-1}, one observer (MT) examined the video footage using ODlog (Macropod Software) and recorded the frequency and amount of time each fish spent (1) swimming only with its pectoral fins (P), (2) swimming with a combination of its pectoral and caudal fins (P+C), or (3) bursting and coasting with caudle fin only (BC). One count was made for each pectoral fin beat (i.e. one full rotation of the pelvic fin) during both P and P+C swimming. One BC event was defined as a period of time that included caudal fin beats (typically 1, 2 or 3 beats) and the subsequent forward glide motion.

Statistical analysis

We calculated a fish's critical swimming speed (U_{crit}) and gait transition speed ($U_{p\text{-}c}$) following Brett (1964):

$$U_{crit} \text{ and } U_{p\text{-}c} = U + U_i \text{ x } (t/t_i) \tag{1}$$

where U is the penultimate swimming speed before the fish fatigued and stopped swimming (U_{crit}) or before the fish changed gait from P to P+C swimming ($U_{p\text{-}c}$); Ui is the swimming speed at which the fish was unable to continue swimming or changed swimming gait (i.e., swimming speed at increment i); t is the length of time the fish swam at the final swimming speed where fatigue or gait change occurred; ti is the amount of time fish were swam at each speed interval in the trial (30 min). We tested for differences in fish swimming performance ($U_{p\text{-}c}$, U_{burst}, U_{crit}) among treatments using one-way ANOVAs followed by a Tukey HSD post-hoc test.

The analysis of physiological response curves requires taking into account the temporal autocorrelation of data points (Peek et al., 2002). In our case, measurements of oxygen consumption for a given U_{crit} trial were not independent since we carried out repeated measurements on the same fish. Therefore, we used a linear mixed effect model to test for differences in the relationships between swimming speed (U) and oxygen consumption (MO^2) across flow treatments (Bolker et al., 2009; Peek et al., 2002). Relationships are based solely on the aerobic component of swimming trials (MO_2 measurements at speeds below U_{burst}). The data were log10 transformed to meet the assumptions of linearity, normality and homogeneity of variance. All analyses were conducted in R v2.11.1 (R Development Core Team, 2010).

RESULTS

Respirometry

Oxygen consumption rate (MO2) was best described as a power function for fish in all three flow treatments (Figure 1).

Treatment A=0 BLs^{-1} (steady flow treatment; standard curve):

$$MO_2 = 2.64 * Speed3.86 + 135.14 \tag{2}$$

Treatment A=0.5 BLs^{-1} (unsteady flow treatment with amplitude 0.5 BLs^{-1} around U_{mean}):

$$MO_2 = 3.66 * Speed^{3.45} + 127.52 \tag{3}$$

Treatment A=1.0 BLs^{-1} (unsteady flow treatment with amplitude 1.0 BLs^{-1} around U_{mean}):

$$MO_2 = 8.67 * Speed^{3.12} + 144.89 \tag{4}$$

The relationship between MO_2 and U_{mean} for the unsteady flow treatment (A=0.5 BLs^{-1}) was not significantly different from the standard curve steady flow (A=0) treatment ($t=-0.975$, $p>0.30$) as determined by the linear mixed effect model (Figure 2). In contrast, the relationship between MO_2 and U_{mean} for the 1.0 BLs^{-1} amplitude flow treatment significantly differed from the standard curve ($t=2.57$, $p=0.02$). The mean MO_2 differed significantly among treatment groups at swimming speeds of 2.5 BL/s ($F_{2,17}= 9.45$, $p<0.001$), 3.0 BL/s ($F_{2,17}= 9.66$, $p<0.001$) and 3.5 BL/s ($F_{2,16}= 5.92$, $p=0.012$). This was not the case at 4.0 BL/s ($F_{2,11}= 0.45$, $p=0.65$). Post-hoc tests revealed that fish in the high amplitude treatment consumed significantly more oxygen than fish in the control group at 2.5 BL/s and 3.0 BL/s (all ps<0.05), but not at 3.5 BL/s ($p=0.20$).

Swimming performance

Gait transition speed from P only to P+C propulsion (U_{p-c}) occurred at significantly different mean speeds among treatments (1-way ANOVA, $F_{2,17}=3.8158$, $p= 0.005$, Figure 3). Fish in large amplitude treatments (1BLs^{-1}) reached U_{p-c} at significantly lower mean speeds than fish in both low (A= 0.5BLs^{-1}) amplitude ($p=0.006$) and steady (A=0BLs^{-1}) flow ($p=0.027$) treatments. However, there was no difference in the mean gait transition speeds between fish in low amplitude and steady flow treatments ($p=0.847$). Transition speeds from pectoral-caudle swimming (P+C) to a burst and coast gait (U_{burst}) were not significantly different among treatments ($F_{2,17}=1.968$, $p= 0.17$). The mean maximum swimming speed (U_{crit}) reached by fish was significantly different among treatments ($F_{2,17}=3.871$, $p= 0.041$). Fish in the high amplitude treatment (A=1.0 BLs^{-1}) reached U_{crit} at significantly lower speeds than fish in the low amplitude treatment

($p=0.043$); fish in the steady flow treatment did not differ significantly in their maximum mean speed from either high ($p=0.129$) or low ($p=0.883$) amplitude treatments.

Fin beats

Pectoral fin beat frequency had a significant effect (LMM, $F = 489.100$, $P < 0.001$) and explained 60% of the variance in MO_2 when controlling for P+C and BC events (Figure 4, Table 1). P+C beat frequency was significant (LMM, $F = 112.887$, $P < 0.001$) and explained 26% of the variance in MO_2 when controlling for P and BC events. The frequency of burst and coast events was significant (LMM, $F = 13.752$, $P < 0.001$), but only explained 4% of model variance when controlling for all other predictors.

Mean pectoral fin beat frequency was greatest in the $A=1.0$ BLs^{-1} treatment, followed by the $A=0.5$ BLs^{-1} amplitude flow treatment and control treatment. However, the difference among flow treatments was not significant during pectoral only (LMM, $F = 2.272$, $P = .131$) and P+C fin swimming (LMM, $F = 2.393$, $P = 0.119$) even when controlling for swim speed (LMM, $F = .581$, $P = 0.560$).

DISCUSSION

We showed that *C. aggregata* incur greater energetic costs when swimming in high, unsteady wave-like flows ($A=1.0$ BLs^{-1}) than in steady flows with the same mean velocity ($A=0$ BLs^{-1}). However, our results suggest that C. *aggregata* are only affected by unsteady flows that vary in velocity beyond a certain threshold: fish swimming in unsteady flows with lower variations in velocity ($A=0.5$ BLs^{-1}) did not experience energetic costs superior to that of fish in steady flows ($A=0$ BLs^{-1}). Furthermore, swimming performance measures (U_{p-c}, U_{crit}) were lower for fish swimming at 1.0 BLs^{-1}

amplitude versus the control (U_{p-c}) and the 0.5 BLs^{-1} amplitude treatment. Considering that P+C and BC swimming are predictive of MO_2 consumption, fish swimming in high unsteady flows experience peak velocities that push them to recruit their caudal fin at lower mean velocities than in steady flows. We showed that some portion of the variance in aerobic oxygen consumption (26% and 4%) is likely caused by the recruitment of the caudal tail muscles. Therefore, we would expect that the increase in MO_2 consumption at a given speed of high amplitude water flow would be the result of a greater frequency of fin beats and/or a greater proportion of caudal fin beats. While P or P+C fin beats were highest in the 1.0 BL/s amplitude group, followed by the 0.5 BL/s amplitude and control group, the difference among treatments was not significant. A larger sample size may have been able to detect a significant change in fin beats among treatments.

Metabolic costs of swimming in unsteady flows

Traditionally, the field of fish swimming has described the kinematics, physiology, morphology and behaviour of fish movement. Increasingly, scientists have been able to apply this knowledge in practical ways such as developing more effective fishways for impounded rivers (e.g. Peake et al., 1997) and relating swimming performance measures to ecologically meaningful traits (Plaut, 2001). One limitation of this approach is that traditional performance measures taken under controlled laboratory conditions do not always accurately reflect the swimming abilities of fishes in natural conditions, where temperature and water flow velocity and turbulence are never constant. Freshwater researchers have attempted to replicate more natural conditions in swimming performance experiments, which may be more ecologically relevant and applicable to management objectives (Enders et al., 2003; Enders et al., 2005; Liao, 2007; Liao et al., 2003; Taguchi and Liao, 2011). However, similar experiments are lacking in marine systems. Studies of unsteady water flow on fishes have focused on body-caudle swimmers whereas the different swimming morphologies and kinematics of other locomotor modes may have a profound influence on the costs of unsteady swimming (Fulton, 2010; Webb and Cotel, 2010).

Of the few studies that have looked at the metabolic costs of fishes swimming in unsteady flows, the results are unclear. Enders et al. (2003) found a 1.3- to 1.6-fold increase in the metabolic cost of swimming in juvenile Atlantic salmon (*Salmo salar*) as turbulence increased. Under a more controlled type of turbulent condition (Von Karmen wake), Liao et al. (2003) demonstrated that rainbow trout (*Oncorhynchus mykiss*) are able to exploit the regular pattern of vortices and reduce the muscular activity needed to swim at a given speed. More recently, Taguchi and Liao (2011) suggest that turbulent flow can reduce the energetic costs of swimming in rainbow trout as long as certain energy-saving behaviours are employed. Our study represents the first attempt at measuring the metabolic costs of swimming in unsteady water flow for a marine, labriform fish. We found that unsteady flows increase the metabolic cost of swimming, but only at levels of flow that require burst swimming behaviour powered by the anaerobic body-caudal swimming muscles. In *C. aggregatea,* this change in energetic metabolic pathway was clearly visible in a change from P+C assisted population to BC propulsion powered solely by the caudle fin. However, all mean swimming speeds tested, low amplitude fluctuations (A=0.5 BLs^{-1}) did not increase the energy required to swim relative to steady flow. Rather, low amplitude fluctuations seem to require less energy for swimming at 3BLs^{-1} and 3.5BLs^{-1} than steady flow swimming or the predicted costs based on the sinusoidal function, although these trends were not significant. If water flow and wave patterns occur at regular intervals, it is possible that fish can anticipate the motion of the water and use the periods of low flow to economise energy and ride the wave. This behaviour may be similar to the energy-efficient wave and bow-riding behaviour observed in some cetaceans (Fish and Hui, 1991; Williams et al., 1992), and warrants further investigation.

Unsteady flows and swimming performance

Measures of swimming performance in the laboratory have been criticized by ecologists, who struggle to extrapolate the results of such tests to ecologically meaningful performance measures in natural systems (Peake, 2004; Plaut, 2001). However, as many fish species lack anti-predator defences other than effective escape and avoidance behaviours, swimming capability likely has a major impact on Darwinian fitness (Plaut, 2001). Although swimming capabilities measured under laboratory conditions may not accurately reflect an individuals' ability to outswim a predator or migrate upriver in the wild, these measures provide useful baselines that ecologists can then use to test against treatments that mimic more natural conditions. In our study, we used metabolic rates, swimming performance measures and fin beat frequencies in standard steady flow trials as a control for our two fluctuating speed treatments, which mimicked the unsteady water flow conditions a fish is likely to experience in rough or stormy weather days. The fact that only some of these performance measures differed among treatments provides interesting insights into the swimming behaviours of these fishes. For instance, the caudle fin was recruited earlier in the high amplitude treatment due to the destabilizing effect that maximum flows had on a fish swimming. However, once these fish were able to steady themselves with their caudle fins, they were able to continue swimming using aerobic energy pathways as long as the other two treatment groups, as indicated by the similar U_{burst} speeds in all treatments. The ability of labriform-swimming fishes to recruit their caudle fins for stability while still swimming aerobically with their pectoral fins may provide a substantial advantage over strictly body-caudle swimming fishes, which must use their caudle fins for thrust and stability during both aerobic and anaerobic swimming phases. Using a labriform swimmer in this study provided us with a unique means of partitioning aerobic from anaerobic energy metabolism given that pectoral fin beats correlate with oxygen consumption and gait transition speed (U_{burst}) can visually be used as an index of anaerobically-powered activity (Johansen et al., 2010; Svendsen et al., 2010; Tudorache et al., 2009). Interestingly, fish in the high amplitude group did not reach U_{crit} earlier than the control group, although they did fail at lower speeds than the low amplitude treatment fish. This discrepancy may be due to a lack of power to be able to detect significant differences among these treatment groups. However, a significant difference between high and low amplitude treatments suggests that fish do experience a higher cost of swimming when they are pushed beyond their aerobic capacities. Although these swimming performance measures do not represent all of the complexities and challenges of swimming in the wild, they can provide interesting insights into the effect of a single parameter that mimics natural conditions when compared with a highly controlled swimming trial that allows a fish to reach the theoretical maxima for a given measure.

Conclusion

Understanding the effects that waves and current have on the swimming capacity of fishes is important for both practical and theoretical reasons. Rivers are being increasingly degraded, and flow regimes altered as a result of numerous anthropogenic activities, compounded by climate change (Kingsford, 2011). Similarly, coastal marine systems are routinely exposed to intense bouts of water motion due to tidal action, wind-driven waves and weather patterns that are predicted to become more frequent and intense (Harley et al., 2006; Seymour, 2011). Whether or not fishes have the ability to adapt to these changes in their hydrodynamic environments depends on their swimming performance and physiology; traits which can be used to make predictions about the cost of locomotion in altered environments. Although controlled laboratory swimming trials under steady flow conditions have taught us much about the physical and physiological limits of swimming in fishes, this study provides an important advancement in our understanding of the costs of locomotion in unsteady flow conditions. Future studies should build on this research by exploring the influence of other important wave parameters such as periodicity on a variety of fishes with a range of swimming modes.

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REFERENCES

Arnold, S. J. (1983). Morphology, Performance and Fitness. *American Zoologist* **23**, 347-361.

Beamish, F. H. W. (1978). Swimming capacity. In *Fish physiology- locomotion*, eds. W. S. Hoar and J. R. Randall), pp. 101-187. New York: Academic Press.

Bell, W. H. and Terhune, L. D. B. (1970). Water tunnel design for fisheries research. *Fisheries Research Board of Canada* **195**, 1-69.

Bellwood, D. R., Wainwright, P. C., Fulton, C. J. and Hoey, A. (2002). Assembly rules and functional groups at global biogeographical scales. *Functional Ecology* **16**, 557-562.

Boisclair, D. and Sirois, P. (1993). Testing assumptions of fish bioenergetics models by direct estimation of growth, consumption, and activity rates. *Transactions of the American Fisheries Society* **122**, 784-796.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**, 127-135.

Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* **21**, 1183-1226.

Bronstert, A. (2003). Floods and climate change: Interactions and impacts. *Risk Analysis* **23**, 545-557.

Cannas, M., Schaefer, J., Domenici, P. and Steffensen, J. F. (2006). Gait transition and oxygen consumption in swimming striped surfperch *Embiotoca lateralis* Agassiz. *Journal of Fish Biology* **69**, 1612-1625.

Drucker, E. G. and Jensen, J. S. (1996a). Pectoral fin locomotion in the striped surfperch .1. Kinematic effects of swimming speed and body size. *Journal of Experimental Biology* **199**, 2235-2242.

Drucker, E. G. and Jensen, J. S. (1996b). Pectoral fin locomotion in the striped surfperch .2. Scaling swimming kinematics and performance at a gait transition. *Journal of Experimental Biology* **199**, 2243-2252.

Enders, E. C., Boisclair, D. and Roy, A. G. (2003). The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 1149-1160.

Enders, E. C., Boisclair, D. and Roy, A. G. (2005). A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1079-1089.

Finlayson, D. P. (2006). The Geomorphology of Puget Sound Beaches. In *School of Oceanography*, vol. PhD, pp. 216. Seattle: University of Washington.

Fish, F. E. and Hui, C. A. (1991). Dolphin swimming: a review. *Mammal Review* **21**, 181-195.

Fulton, C. J. (2010). The role of swimming in reef fish ecology. In *Fish Locomotion: An Eco-Ethological Perspective,* eds. P. Domenici and B. G. Kapoor), pp. 374- 406. Enfield: Science Publishers.

Fulton, C. J. and Bellwood, D. R. (2005). Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnology and Oceanography* **50**, 255-264.

Gourlay, M. R. and Colleter, G. (2005). Wave-generated flow on coral reefs - an analysis for two-dimensional horizontal reef-tops with steep faces. *Coastal Engineering* **52**, 353-387.

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L. and Williams, S. L. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters* **9**, 228-241.

Irschick, D. J. and Garland, T. (2001). Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system. *Annual Review of Ecology and Systematics* **32**, 367-+.

Johansen, J. L., Bellwood, D. R. and Fulton, C. J. (2008). Coral reef fishes exploit flow refuges in high-flow habitats. *Marine Ecology-Progress Series* **360**, 219-226.

Johansen, J. L. and Jones, G. P. (2011). Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology*, doi:10.1111/j/1365-2486.2011.02436.x.

Johansen, J. L., Vaknin, R., Steffensen, J. F. and Domenici, P. (2010). Kinematics and energetic benefits of schooling in the labriform fish, striped surfperch *Embiotoca lateralis*. *Marine Ecology-Progress Series* **420**, 221-229.

Kendall, J. L., Lucey, K. S., Jones, E. A., Wang, J. and Ellerby, D. J. (2007). Mechanical and energetic factors underlying gait transitions in bluegill sunfish (*Lepomis macrochirus*). *Journal of Experimental Biology* **210**, 4265-4271.

Kingsford, R. T. (2011). Conservation management of rivers and wetlands under climate change - a synthesis. *Marine and Freshwater Research* **62**, 217-222.

Langerhans, R. B. (2008). Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology* **48**, 750-768.

Lee, C. G., Farrell, A. P., Lotto, A., Hinch, S. G. and Healey, M. C. (2003). Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. *Journal of Experimental Biology* **206**, 3253-3260.

Liao, J. C. (2007). A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society B-Biological Sciences* **362**, 1973-1993.

Liao, J. C., Beal, D. N., Lauder, G. V. and Triantafyllou, M. S. (2003). Fish exploiting vortices decrease muscle activity. *Science* **302**, 1566-1569.

Mussi, M., Summers, A. P. and Domenici, P. (2002). Gait transition speed, pectoral fin-beat frequency and amplitude in *Cymatogaster aggregata*, *Embiotoca lateralis* and *Damalichthys vacca*. *Journal of Fish Biology* **61**, 1282-1293.

Niimi, A. J. and Beamish, F. H. W. (1974). Bioenergetics and growth of largemouth bass (Micropterus salmoides) in relation to body weight and temperature. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 447-456.

Peake, S. (2004). An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. *Transactions of the American Fisheries Society* **133**, 1472-1479.

Peake, S., Beamish, F. W. H., McKinley, R. S. and Katapodis, C. (1997). Relating swimming performance of lake sturgeon, *Acipenser fulvescens*, to fishway design. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1361-1366.

Peek, M. S., Russek-Cohen, E., Wait, D. A. and Forseth, I. N. (2002). Physiological response curve analysis using nonlinear mixed models. *Oecologia* **132**, 175-180.

Plaut, I. (2001). Critical swimming speed: its ecological relevance. *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* **131**, 41-50.

R Development Core Team. (2010). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, http://www.R-project.org.

Seymour, R. J. (2011). Evidence for changes to the northeast Pacific wave climate. *Journal of Coastal Research* **27**, 194-201.

Steffensen, J. F. (1989). Some errors in respirometry of aquatic breathers - how to avoid and correct for them. *Fish Physiology and Biochemistry* **6**, 49-59.

Steffensen, J. F., Johansen, K. and Bushnell, P. G. (1984). An automated swimming respirometer. *Comparative Biochemistry and Physiology a-Physiology* **79**, 437-440.

Svendsen, J. C., Tudorache, C., Jordan, A. D., Steffensen, J. F., Aarestrup, K. and Domenici, P. (2010). Partition of aerobic and anaerobic swimming costs related to gait transitions in a labriform swimmer. *Journal of Experimental Biology* **213**, 2177-2183.

Taguchi, M. and Liao, J. C. (2011). Rainbow trout consume less oxygen in turbulence: the energetics of swimming behaviors at different speeds. *Journal of Experimental Biology* **214**, 1428-1436.

Tritico, H. M. and Cotel, A. J. (2010). The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). *Journal of Experimental Biology* **213**, 2284-2293.

Tudorache, C., Jordan, A., Svendsen, J., Domenici, P., DeBoeck, G. and Steffensen, J. F. (2009). Pectoral fin beat frequency predicts oxygen consumption during spontaneous activity in a labriform swimming fish (*Embiotoca lateralis*). *Environmental Biology of Fishes* **84**, 121-127.

Wang, X. L. L. and Swail, V. R. (2001). Changes of extreme wave heights in Northern Hemisphere oceans and related atmospheric circulation regimes. *Journal of Climate* **14**, 2204-2221.

Webb, P. W. (1973). Kinematics of pectoral fin propulsion in *Cymatogaster aggregatta*. *Journal of Experimental Biology* **59**.

Webb, P. W. (1975). Efficiency of pectoral-fin propulsion in *Cymatogaster aggregata*. In *Proceedings of the symposium on swimming and flying in nature*, vol. 2 eds. T. Y. Wu C. J. Brokaw and C. Breenan), pp. 573-584. New York: Plenum.

Webb, P. W., Cotel, A. and Meadows, L. A. (2010). Waves and eddies: effects on fish behavior and habitat distribution. In *Fish Locomotion: An Eco-Ethological Perspective,* eds. P. Domenici and B. G. Kapoor), pp. 1-38. Enfield, NH: Science Publishers.

Webb, P. W. and Cotel, A. J. (2010). Turbulence: Does Vorticity Affect the Structure and Shape of Body and Fin Propulsors? *Integrative and Comparative Biology* **50**, 1155-1166.

Westneat, M. W. and Walker, J. A. (1997). Motor patterns of labriform locomotion: Kinematic and electromyographic analysis of pectoral fin swimming in the labrid fish *Gomphosus varius*. *Journal of Experimental Biology* **200**, 1881-1893.

Williams, T. M., Friedl, W. A., Fong, M. L., Yamada, R. M., Sedivy, P. and Huan, J. E. (1992). Travel at low energetic cost by swimming and wave riding bottlenose dolphins. *Nature* **355**, 821-823.

TABLES AND FIGURES

Table 1. Parameter estimates for Linear Mixed Model predicting Log(MO_2) based on pectoral only fin beat frequency, pectoral+caudal fin beat frequency and burst event frequency.

Parameter	Estimate (SE)	df	t	95% Confidence		Sig
				Lower	Upper	
Intercept	1.82520	111.565	68.004	1.77201	1.87838	0.00
Pectoral	0.00073	333.963	22.116	0.00066	0.00079	0.00
P+C	0.00138	339.468	10.625	0.01127	0.00164	0.00
Burst	0.00051	328.760	3.708	0.00024	0.00078	0.00

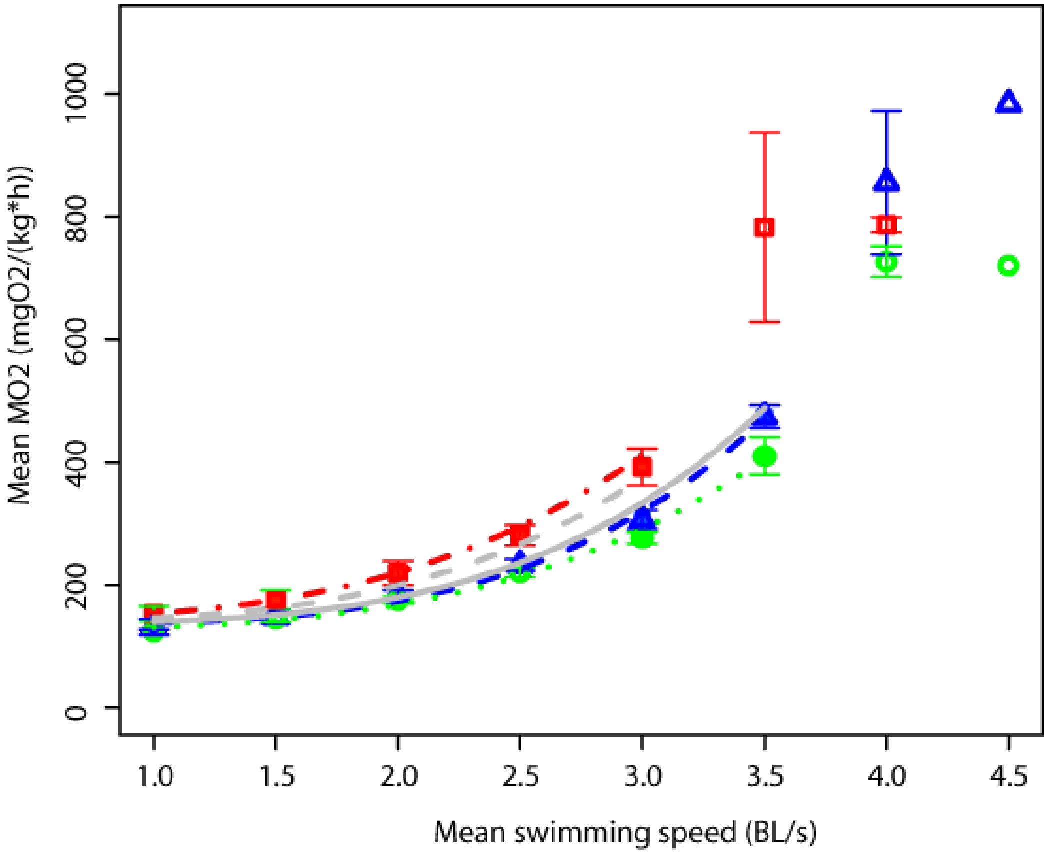

Figure 1. Mean oxygen consumption (MO_2 in mg O_2 $kg^{-1}h^{-1}$) as a function of mean swimming speed (U_{mean}) for *C. aggregata* in one of three treatments: constant flow velocity (standard curve) in red (n=6), unsteady flow with an amplitude of 0.5 BLs^{-1} around U_{mean} (n=7), and unsteady flow with an amplitude of 1.0 BLs^{-1} around U_{mean} (n=7). Relationships are based on the aerobic component of swimming trials and include MO_2 measurements at speeds below U_{burst} (filled symbols). Empty symbols are MO_2 measurements that include EPOC to provide the metabolic swimming cost that included both the aerobic and anaerobic swimming components. The three coloured lines are Eqn () (blue), Eqn () (green) and Eqn () (red), illustrating the relationship between exercise MO_2 and swimming speed. Error bars are standard errors. The grey lines are theoretical

predictions of MO_2 vs. speed based on the standard curve for the 0.5 BLs^{-1} amplitude treatment (solid) and the 1.0 BLs^{-1} amplitude treatment (dashed).

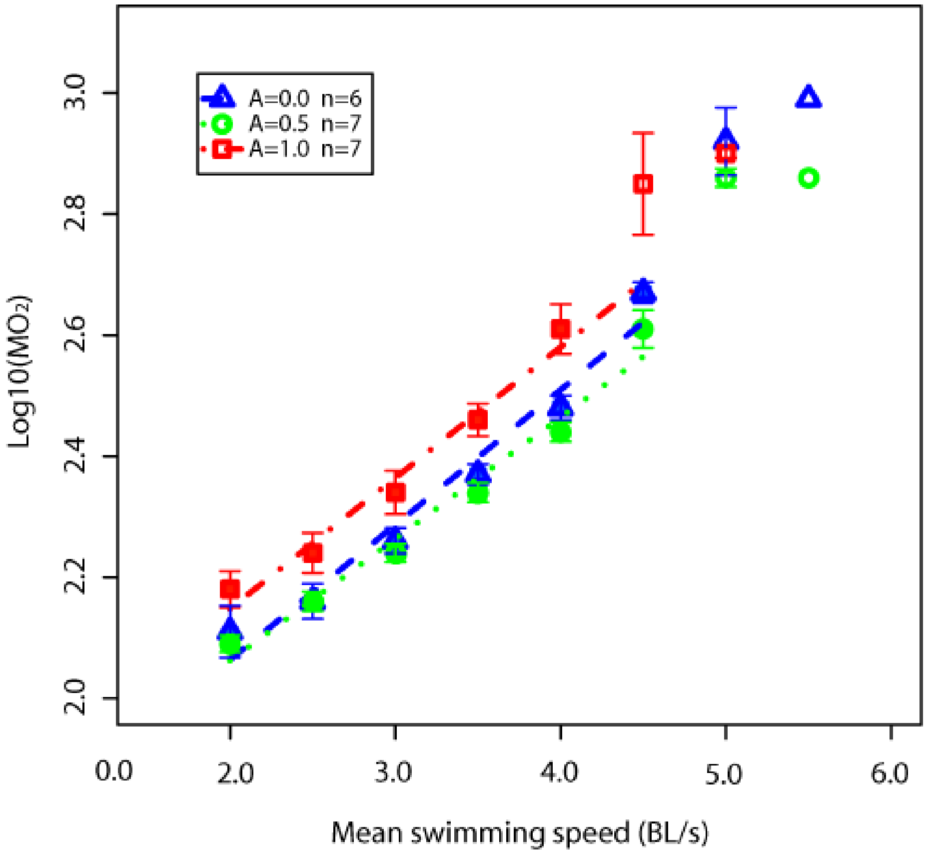

Figure 2. Same as Figure 1 – data was log10 transformed to meet the assumptions of the linear mixed effect model.

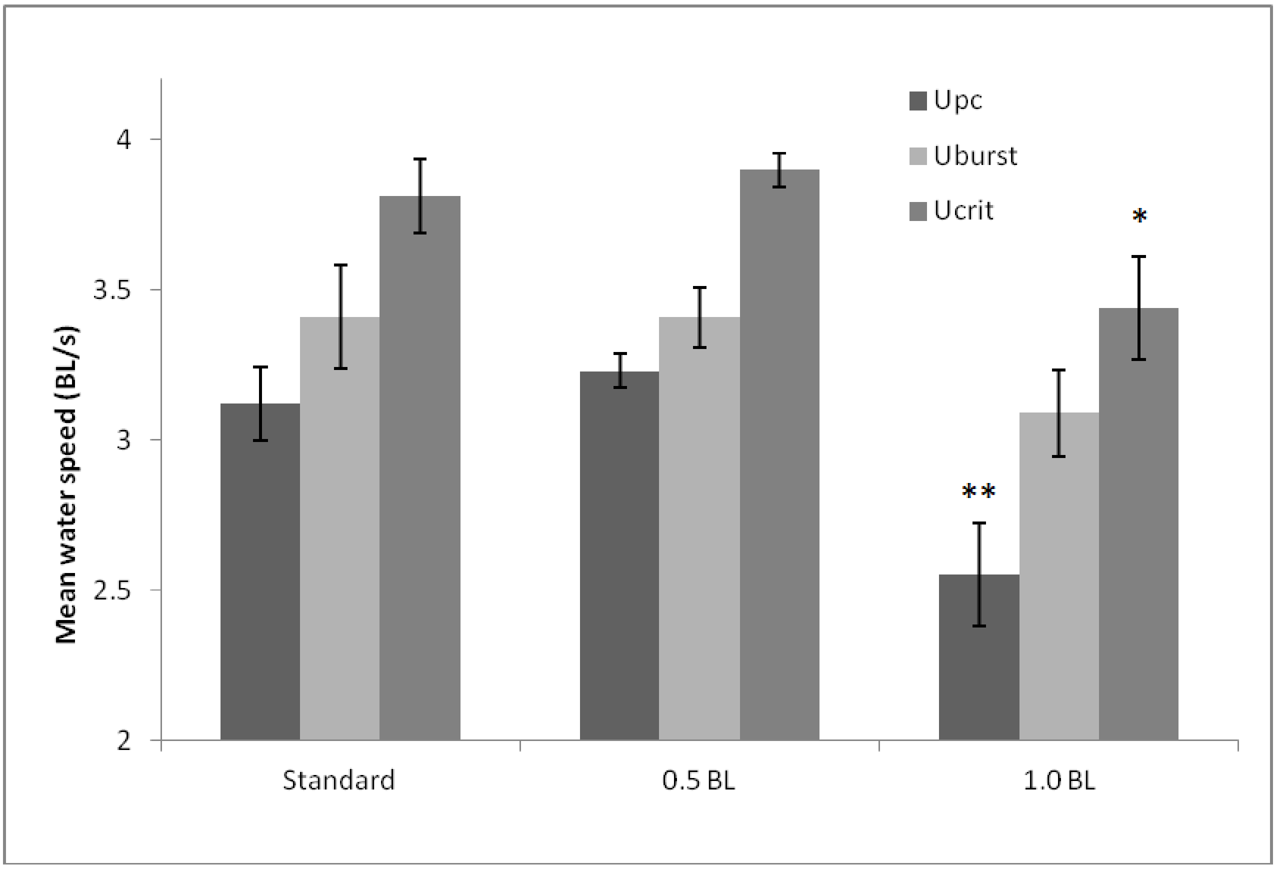

Figure 3: Mean water velocity achieved by fish for three different swimming performance measures (U_{pc}, U_{burst} and U_{crit}) in three different water flow treatments (control no fluctuation= standard, low amplitude fluctuation= 0.5BL, high amplitude fluctuation= 1.0BL). Asterisks indicate significant differences between the high fluctuation treatment and both low amplitude and control groups (**, p<0.01) and between high and low fluctuation treatments (*, P<0.05).

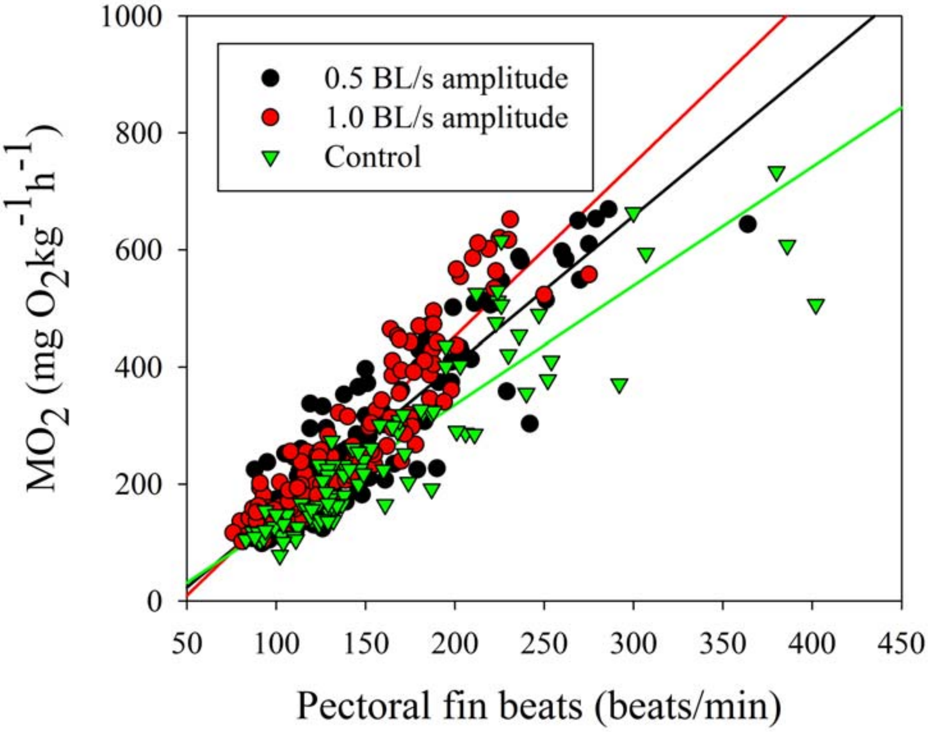

Figure 4: Scatterplot of the relationship between pectoral fin beat frequency and MO_2 grouped within three different flow treatments (control= $0BLs^{-1}$, low amplitude fluctuation= $0.5BLs^{-1}$, high amplitude fluctuation= $1.0BLs^{-1}$). MO_2 was log10 transformed for the model, but was back-transformed for this figure.