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RELATING CATCHABILITY OF FLATHEAD TO THEIR SEASONAL ACTIVITY AND MOVEMENT

K.M. Stehfest, J.M. Lyle, & J.M. Semmens
November 2014

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TRANSLATING**NATURE**INTO**KNOWLEDGE**

FINAL REPORT

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Executive summary

The sand flathead *Platycephalus bassensis* is one of the most important recreationally fished marine teleost species in Tasmania, comprising nearly two thirds of the total recreational finfish catch. The availability of the species to fishers has been reported to vary seasonally, yet, it is not known whether this seasonality is due to movement in and out of the species' summer spawning habitat in the shallow bays on the Tasmanian coast or seasonal changes in catchability.

Catchability is the likelihood of available fish to be captured by fishing gear, which can depend on the fishing gear used, fisher behaviour, management regulations or environmental variables. For rod and line gear, which is the predominant method of capture for the sand flathead, the catchability of the target species is highly dependent on the receptiveness to the bait and feeding motivation of the individual fish, both of which can vary with environmentally mediated changes in fish activity.

This study combines experimental catch data and telemetry data from Pittwater and Frederick Henry Bay (FHB) on the southeast coast of Tasmania as well as metabolic rate data collected in the laboratory to determine the nature and drivers of seasonal patterns in CPUE of the sand flathead:

- Firstly, we analysed CPUE data from two types of baited fishing gear (rod and line, longline) to determine area-specific, seasonal patterns in catch rates.
- Secondly, we collected and analysed data from both standard acoustic and accelerometer tags to establish seasonal movement patterns and measure activity and its relationship with environmental parameters.
- Thirdly, we measured resting and active metabolic rates of sand flathead at different temperatures in the laboratory to determine changes in metabolism and therefore feeding motivation with temperature.

The results showed significant seasonal variability in catches of the sand flathead which corresponded to seasonal patterns in both the horizontal movement and water temperature mediated changes in activity and metabolic rates. This suggests that for this species both movement and activity vary with season and environmental parameters, driving variability in catch rates.

Analysis of CPUE from both rod and line and longline data revealed that the seasonal variability in catches differed in magnitude by area, with a strong seasonal pattern in the shallow coastal estuary of Pittwater and a limited seasonal pattern in FHB, the deeper bay at the mouth of the estuary.

Low catch rates in Pittwater in winter were most likely caused by seasonal movement of flathead out of Pittwater into FHB at the start of winter, followed by a return to Pittwater at the start of the following spring. In FHB on the other hand, the fact that CPUE was slightly decreased in winter even though the movement data indicated this to be the species' winter habitat suggests that catches in this area are likely to be influenced by seasonal changes in the receptiveness of flathead to bait.

Activity data from acoustic telemetry and metabolic data collected in the laboratory show that both activity and metabolic rates increased significantly with temperature for the range of values encountered in this study with a 1 °C increase in temperature leading to a 14% increase in acceleration in the field and both resting and active metabolic rates increasing significantly with a temperature increase from 17 to 22 °C. This indicates that flathead have a higher probability of encountering a bait plume and locating and striking the bait at higher temperatures, which has previously been reported for other marine teleosts.

While it was not possible to fully tease apart the effects of horizontal movement and variations in activity on seasonal patterns in sand flathead catches, our findings make it clear that both are likely to be important factors which would need to be included in an accurate stock assessment for this important recreational fish species. To accomplish this, future studies with more continuous catch rate data as well as continuous activity data for fish tagged in FHB would allow the modelling of the relationship between activity and catch rates directly. Moreover, a laboratory study in which fish tagged with accelerometer tags are exposed to bait cues at different temperatures could allow us to calibrate an index of catchability based on temperature and activity which could be applied to data collected in the field.

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1. Introduction

Catch per unit effort (CPUE) is the most essential metric in fisheries science and assessment (Maunder et al. 2006), frequently used to address crucial management questions such as the health of fish stocks (Myers and Worm 2003), the historic trajectories of fisheries (Rosenberg et al. 2005) or the fishery effects of marine reserves (Kaunda-Arara and Rose 2004). Using CPUE data as an index of abundance requires the assumption that CPUE is directly proportional to fish abundance. However, this assumption is unlikely to hold for the majority of fisheries (Harley et al. 2001), as CPUE is highly dependent on both the availability and the catchability of the targeted fish species (Engås and Løkkeborg 1994), both of which can exhibit considerable variability in space and time (see Wilberg et al. (2009) for review). Availability describes local changes in fish abundance (Ricker 1975), primarily influenced by both vertical and horizontal movements of the target species and most stock assessment models of commercially exploited species include movement models to account for this (see Goethel et al. (2011) for review). Catchability on the other hand describes the likelihood of available fish to be captured by the gear, which can depend on the fishing gear used, fisher behaviour, management regulations or environmental variables (Wilberg et al. 2009). The inclusion of a catchability parameter is also a standard feature of nearly all stock assessment models (Arreguín-Sánchez 1996, Quinn and Deriso 1999) and much attention has been given to changes in catchability through the evolution of fishing technology and strategies (e.g. Sakagawa et al. (1987)), particularly in the analysis of historical catch data (e.g. Hampton et al. (2005)). Less common is the inclusion of environmentally driven variability in individual fish behaviour, which is a particularly important source of potential bias in the analysis of CPUE data from baited gear such as longlines, rod and line or baited traps (Stoner 2004).

For these types of fishing, the vulnerability of the target species to the gear is highly dependent on the release and transport rate of chemical cues from the bait as well as the receptiveness to the bait and feeding motivation of the individual fish (see Stoner (2004) for review). While the release and transport rate of chemical cues is mainly driven by abiotic variables, predominantly the current speed (Løkkeborg et al. 1995), receptiveness to bait and feeding motivation is highly dependent on the fishes' activity levels (Stoner et al. 2006). Activity can influence catchability in two ways: Firstly, fish have a greater probability of encountering a bait plume if they are more active; secondly, high activity will result in a higher metabolic debt and increase feeding motivation (Stoner 2004). Both, activity as measured by swimming speed and metabolic rate have been shown to be strongly influenced by environmental conditions, particularly temperature (Clarke and Johnston 1999, Gillooly et al. 2001), in a number of teleost fish species (e.g. sockeye salmon (Brett 1971), Atlantic cod (Castonguay and Cyr 1998)), generally increasing with temperature up to an optimum, followed by a rapid decline when thermal stress begins to set in (Brett 1971). Hence, individual behaviour mediated by ambient temperature is likely to have a significant effect on the relationship between fish abundance and CPUE (Stoner 2004).

Including information on fish activity and its relationship with environmental variables is therefore crucial for the accurate analysis of CPUE data from baited gear. However, even though some progress has been made in linking temperature and catchability of fish in the laboratory (Stoner and Sturm 2004, Stoner et al. 2006), few studies have addressed this relationship in the field due to the technological difficulties involved. Recent advances in biotelemetry techniques now allow researchers to monitor activity and by proxy metabolic rate of fish in the field over extended periods of time by implanting them with acoustic telemetry tags which contain tri-axial accelerometers. These tags measure acceleration in three axes, compute the root mean square of the three values as a proxy for activity, called the overall dynamic body acceleration (ODBA, (Gleiss et al. 2011)) and transmit the data to an acoustic receiver if the fish is within detection range. This technique has been used to determine activity patterns in the field for a number of different marine teleosts over the last few years (e.g. Pacific salmon (Wilson et al. 2013), barracuda (O'Toole et al. 2011), bonefish (Murchie et al. 2011)), can add considerable value to telemetry studies which are traditionally mainly focused on animal movement (Payne, Taylor et al. 2014) and has the potential to vastly improve our understanding of the relationship between environmental variables, activity and catchability.

Our study aims to use this technology in conjunction with results from metabolic experiments in the laboratory to determine whether seasonal patterns in CPUE of the sand flathead *Platycephalus bassensis* are driven by seasonal movements or environmentally mediated changes in activity. The sand flathead is one of the most important recreationally fished marine teleost species in Tasmania, comprising nearly two thirds of the total recreational finfish catch (1.07 million fish captured and killed and an additional 0.74 million captured and released in 2007/2008; (Lyle et al. 2009). The availability of the species to fishers has been reported to vary seasonally (Tracey et al. 2011). Yet, it is not known whether this seasonality is due to movement in and out of the species' summer spawning habitat in the shallow bays on the Tasmanian coast or seasonal changes in activity. Previous research in the laboratory showed that maximum swimming speed is positively correlated with ambient water temperature (Yanase et al. 2007) for this species and we aim to build on these findings and determine the causes of seasonal variability in CPUE through a three pronged approach:

> Firstly, we analysed CPUE data from two types of baited fishing gear (rod and line, longline) to determine area-specific, seasonal patterns in catch rates.
>
> Secondly, we collected and analysed data from both standard acoustic and accelerometer tags to establish seasonal movement patterns and measure activity and its relationship with environmental parameters.
>
> Thirdly, we measured resting and active metabolic rates of sand flathead at different temperatures in the laboratory to determine changes in metabolism and therefore feeding motivation with temperature.

2. Methods

2.1. Study site

All field data and fish for laboratory experiments were collected In Upper and Lower Pittwater (UPW & LPW) and Frederick Henry Bay on the southeast coast of Tasmania, Australia (Fig. 1). Pittwater (PW) is the shallow estuary (~4 m average depth) of the Coal River, comprised of mostly intertidal sand flats and river channels with a narrow entrance that connects to the deeper waters of FHB (~15 m average depth).

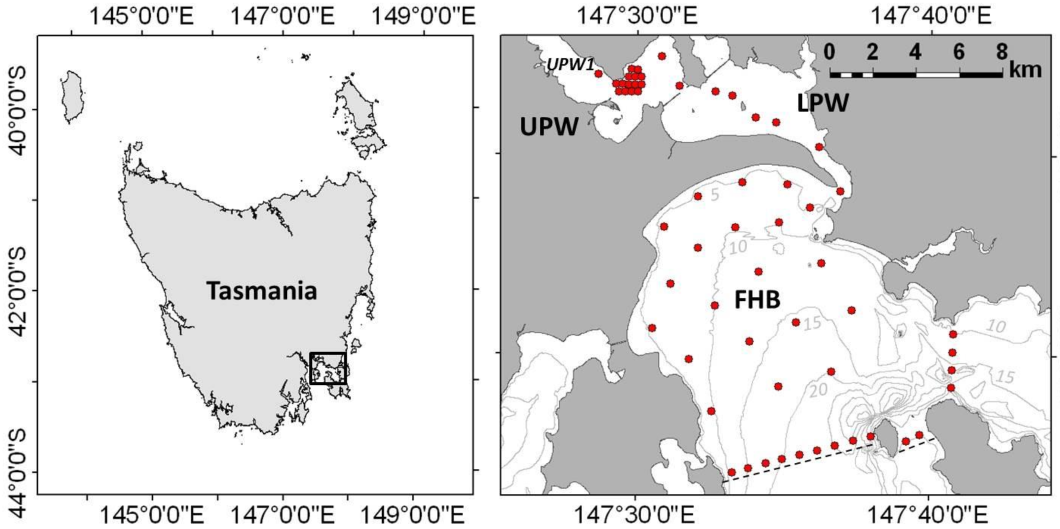

Figure 1. Acoustic receiver locations in the study area. Black rectangle in the map of Tasmania on the left indicates spatial extent of the high resolution map on the right. Red dots indicate locations of receivers. Receiver UPW1, used as a reference point for movement analyses is labelled.

2.2. Catch rate data collection and analysis

To determine seasonal variability in sand flathead catch rates, experimental rod and line fishing was carried out in UPW, LPW and FHB over several months in 2012/2013 as part of a linked Fishwise resource management grant (Project code 2011/124). Fishing was carried out at 7 sites in UPW, 5 sites in LPW and 15 sites in FHB and primarily occurred in February, May, September and December to coincide with periods when accelerometer were operational (refer below), with some additional fishing at select sites in March and June. Individual fishing events consisted of one to three researchers fishing continuously for flathead for 10 to 65 minutes. Catch counts were then averaged over all participating fishers and divided by fishing duration to compute standardized CPUE. To increase sample sizes, CPUE data was pooled for all sites within PW (UPW & LPW) and FHB and monthly variation in flathead catches for these two areas was examined.

To augment rod and line catch data, flathead catches from routine longline surveys of Chondrichthyan abundance in the shark refuge area which encompasses PW and FHB was also examined for seasonal variability. These data were collected by researchers at the Institute for Marine and Antarctic Studies, University of Tasmania in 2012/2013 using longlines with 18-50 baited hooks with soak-times of 55-240 minutes. Data was available for all months of the year except for June, August and September. Longline catch counts were standardized to CPUE rates by dividing the data by the number of hooks and the soak-time and then pooled for all deployments within PW and FHB.

To determine seasonal changes in catch rates, a generalized linear model (GLM) was fitted to each area in each dataset, resulting in a total of four models (2 datasets x 2 areas) with month of the year as the categorical predictor variable. Since the catch data presents a case of overdispersed count data, negative binomial models were used. All models were fitted using the glm.nb() function in the R package MASS (Venables and Ripley 2002). The month of February was used as the reference level to compare CPUE from the other months to, since this was the month with the highest CPUE in all cases apart from rod and line catches in FHB. Overall fit of the model was quantified by calculating the pseudo R^2 of the model as the percentage of the deviance explained by the model relative to the null model of no monthly variation (Dobson 2002). The significance of monthly changes in catch rates was determined by carrying out a likelihood ratio test between the monthly and the null model.

2.3. Acoustic telemetry data collection

To monitor the movement and activity patterns of sand flathead in the study area, an array of 58 acoustic receivers (VR2, VEMCO Ltd, Halifax, Canada) was continuously maintained from January 2012 to May 2013 in UPW, LPW and FHB. Acoustic receivers can detect uniquely coded VEMCO acoustic transmitters when within detection range of the receivers (approximately 400 to 500 m as determined through range testing, see Barnett et al. (2011) for details) and record timing of the tag's presence as well as any data collected and transmitted by the tag. Receivers were deployed either as a regular grid of receivers or as curtains with overlapping detection ranges so that animals could be detected moving across entrances and choke points of the coastal areas. At choke points where the distance between shorelines was less than the detection range diameter, a single receiver was placed halfway between the shorelines (Fig. 1). In each of the three areas, 1 receiver was fitted with an environmental data logger, collecting half-hourly temperature and salinity data near the seabed for the duration of the study.

A total of 30 sand flathead were tagged with acoustic tags, 20 with V9A-2L (9 x 46 mm; 6.3 g; power output = 145 dB; estimated tag life = 247-304 days) VEMCO accelerometer tags and the remaining ten with standard V9-2H VEMCO acoustic tags (9 x 29 mm; 4.7 g; power output = 151 dB; estimated tag life = 368 days). The VEMCO accelerometer tags deployed in this study measured acceleration in three axes with a sampling frequency of 5 Hz, removed static acceleration (i.e. acceleration due to variation in the tags orientation with respect to the earth's gravitational field) using a high pass filter, and amalgamated acceleration in the three axes into a single value by calculating the root mean square - the final measure of ODBA which is transmitted to the acoustic receiver. ODBA values were calculated and averaged for a sampling period of 80 seconds and transmitted every 190-290 seconds. To ensure the collection of acceleration data during all crucial stages of the flatheads' annual movement cycle despite the tags limited life, V9A tags were programmed to only collect data at the start (May-July) and end (August-October) of the austral winter and the spawning period in the summer (December-February). Outside of these periods, tags were switched off to conserve energy. Standard acoustic transmitters on the other hand, have a much longer battery life and the V9 tags were therefore transmitting continuously to provide an uninterrupted record of seasonal flathead movement in the study area.

Tagging was carried out in UPW and FHB over two years, between January and May 2012 and between December 2012 and April 2013. Animals were captured using bottom-set longlines, deployed for a maximum of 1 hour soak time to ensure that captured animals were in good condition for tagging. Upon capture, animals were hauled aboard the tagging vessel, hooks carefully removed from the animals' mouth and total length measured. Animals were then anaesthetised by placing them in a bath of Aqui-S (Aqui-S New Zealand Ltd) anaesthetic (0.03 ml per L of seawater) prior to surgery. To deploy the tag, a 1-2 cm incision was made in the abdominal wall and the tag inserted into the peritoneal cavity. For accelerometer tags, the tag was inserted with the acceleration sensor closest to the tail and the body of the tag aligned with the anterior-posterior axis of the animal. Consistent alignment of the tag with the animal's body is crucial to ensure measurements of acceleration are comparable across all tagged animals. To prevent the tag from shifting from its correct position, a suture thread was attached to the non-sensor end of the tag using epoxy resin. This tether was incorporated into the surgeons knot when the incision was closed with sutures. Aseptic techniques were used throughout the tagging procedure and the entire process lasted approximately 2-5 minutes. Running seawater was continuously pumped over the gills of the animals throughout tagging to facilitate breathing and a povidone-iodine antiseptic was applied to the wounds to aid healing. After tagging, animals were held in an aerated container of seawater until they had fully recovered from the anaesthetic and then returned to the water near the capture location in UPW. All methods used were approved by the University of Tasmania Animal Ethics Committee (Approval No A0011882).

2.4. Acoustic telemetry data processing and analysis

Prior to analyses, acceleration values from the first 24 hours after tagging were removed from the dataset to remove potentially abnormal behaviour associated with tagging-induced stress. To determine seasonal movement patterns in and out of PW, we calculated the shortest path distance through water from all receivers to receiver UPW1, the receiver furthest up the estuary in UPW (Fig. 1). This allowed us to assign estimated distance from the upper estuary to each flathead detection in the acoustic dataset. From this we calculated mean daily distance from UPW1 for all individuals tagged with standard acoustic tags and fitted a linear mixed effects model (LMM) to the data with distance from UPW1 as the dependent variable, month as the categorical fixed effect and individual fish ID as the random effect. January was chosen as the reference month to which all other months were compared as it had the shortest mean distance from UPW1. The analysis was only carried out for the standard acoustic tags, as the on/off cycle of the accelerometer tags would have resulted in considerable differences in sample sizes between certain months.

To determine the influence of seasonally changing environmental conditions on activity levels, we fitted an LMM to the accelerometer data with the logarithm of activity as the dependent variable, area-specific temperature and salinity as the fixed effects and individual fish ID as the random effect. We used the logarithm of acceleration as the dependent variable in our model since both normal Q-Q plot and Box-Cox transformation showed that the data approximately followed a log-normal distribution. Various versions of the LMM with different structures were computed in R using the package lme4 (Bates et al. 2014) and the best model selected using pairwise likelihood ratio tests. Significance of the fixed effects was determined using the Welch–Satterthwaite approximation of degrees of freedom as implemented in the lmerTest package (Kuznetsova et al. 2013) in R.

2.5. Metabolic data collection

To determine the effect of temperature on metabolic rates of sand flathead, we measured resting and post-exercise respiratory rates at three different temperatures in experimental tanks at IMAS Taroona. A total of 17 flathead (average total length (TL) = 314mm, SD = 27 mm, average wet weight = 193 g, SD = 54 g) were captured using gillnets, placed in tanks of seawater aboard the research vessel and transported to the laboratory. At the laboratory, fish were tagged with numbered external T-bar anchor tags (Hallprint, Hindmarsh Valley, SA, Australia) for easy identification of individuals and placed in large fibreglass holding tanks with a constant flow of filtered seawater. Fish were removed from the holding tanks and placed in acclimatisation tanks 48 hours prior to experimentation and were fasted to exclude digestive metabolic rates from the measurements. Acclimatisation tanks contained running seawater kept within 1°C of the temperature of the experimental treatment.

Metabolic rate measurements were carried out using an intermittent flow-through respirometer (see Fitzgibbon (2010) for details). This consisted of a 3.5 l cylindrical Perspex chamber in which oxygen levels were measured every 10 seconds by a dissolved oxygen probe. The respirometer chamber was submerged in a water tank with a continuous flow of seawater kept at a constant temperature. Water was continuously circulated between the chamber and the tank and the chamber was completely filled at all times. Every 4 minutes, water circulation through the chamber was shut off for 4 minutes and the reduction in dissolved oxygen in the chamber logged to determine respiratory rates. The interval length was chosen to avoid a drop in dissolved oxygen below 70 % saturation during the oxygen consumption measurement cycle.

Experimental animals were introduced into the chamber in the evening and measurements started the following morning to allow the fish to become accustomed to the chamber and recover from any handling stress. After 24 hours of respiratory rate measurements, fish were transferred to a circular open tank filled with seawater of the same temperature as the chamber and manually agitated to induce flight behaviour and cause burst swimming around the tank. Fish were agitated until exhaustion, as indicated by gasping and loss of balance was evident (Hyndman et al. 2003, Zeng et al. 2010) and then returned to the respirometer for a further 24 hours of measurements. Metabolic rates prior to agitation were defined as the resting metabolic rates and metabolic rates after agitation were defined as post-exercise metabolic rates. At the end of the experiment, fish were killed quickly by dissecting the brain with a sharp knife pushed through the top of the head and length and wet weight measured. Experiments were carried out at 12, 17 and 22 °C water temperature for 6, 6 and 5 fish respectively.

2.6. Metabolic rate data analysis

Oxygen consumption rates were determined for each replicate oxygen consumption cycle using linear regression. Any replicates where the fit of the linear model to drop in oxygen had R^2 values <0.96 were excluded from further analyses (Fitzgibbon 2010). From the slope of the linear regression, hourly drop in oxygen was computed and corrected for background respiration by subtracting the mean oxygen consumption from three empty chamber oxygen consumption cycles. Oxygen consumption rates were then corrected for fish size by dividing hourly drop in oxygen by the fish wet weight with a scaling factor of 0.79 (Clarke and Johnston 1999) resulting in the final respiratory rate value in mg/h/gWetWeight. From the large number of replicate cycles we calculated the standard metabolic rate (SMR) which is defined as the mean of the lowest 10% of pre-exercise oxygen consumption rate replicates, routine metabolic rate (RMR), which is the overall mean of all pre-exercise oxygen consumption rate replicates, the maximum metabolic rate (MMR), which is the mean of the highest 10 % of pre-exercise oxygen consumption rate replicates and active metabolic rate (AMR), which is the maximum post-exercise oxygen consumption rate.

Additionally, we computed excess post exercise oxygen consumption (EPOC), which is the total oxygen consumption in excess of the RMR during the recovery time. Recovery time was herby calculated as the time between the return to the chamber after agitation and the point where the post exercise metabolic rate was equal to the RMR +10 % (Zeng et al. 2010). EPOC was calculated by fitting a polynomial function to the change in post-exercise metabolic rates over time and calculating the area between the polynomial function and a linear function with slope = 0 and intercept = RMR, truncated to the left and right by the start and the end of the recovery period. In cases where recovery did not occur during the experiment, the end of the recovery period was estimated solving the polynomial for y = RMR +10% and using the resulting x value as the end of the recovery period in the subsequent EPOC calculation.

All calculations were carried out for individual fish and values within temperature treatments compared using one-way ANOVA followed by Tukey’s honest significant difference test. This was done after confirming approximate normality of the data through the visual inspection of Q-Q plots and equality of variances between temperature treatments through the Levene’s test (leveneTest() function in R package car; Fox and Weisberg (2011)).

3. Results

3.1. Seasonal catch rates

To determine seasonal patterns in catch rates, we analysed data from a total of 94 (48 in FHB, 46 in PW) rod and line and 160 (37 in FHB, 123 in PW) longline deployments. Data from neither gear type was continuous through the year and only 6 months of rod and line and 9 months of longline data were available for analysis (Fig.2). Area-specific differences in annual mean catch rates varied between the two gear types, with annual mean catch rate higher in FHB than in PW for the rod and line data, whereas the opposite was the case for the longline data (Fig.2).

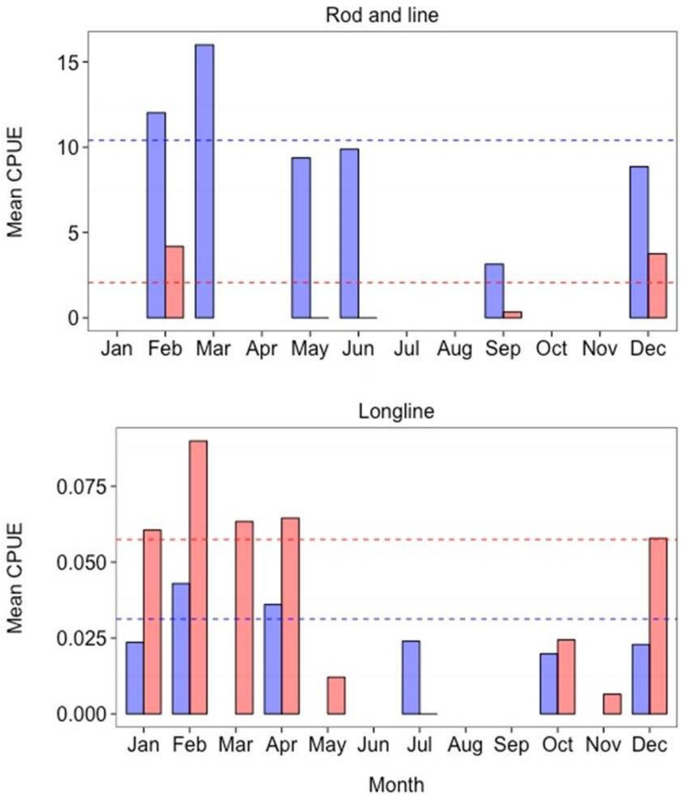

Figure 2. Monthly mean CPUE (vertical bars) and annual mean CPUE (dashed lines) in Pittwater (red) and Frederick Henry Bay (blue) for the datasets from the two gear types. Months with no bars indicate months without sampling, months with horizontal black lines indicate that sampling was carried out but no fish were caught.

The negative binomial GLM showed that month of the year was a significant predictor of CPUE ($p<0.05$) in all models bar one, the model for FHB from the longline data (Table 1). For both datasets, the seasonal signal was stronger in PW than in FHB, indicated by a larger pseudo R^2 (Table 1).

Table 1. Performance indicators of the four negative binomial generalized linear models fitted to the two CPUE datasets in the two different areas. The pseudo R^2 is an indicator of the proportion of deviance explained by the model, the likelihood ratio test statistic and associated p-value relates to the comparison of the model to the null model of no monthly differences in CPUE.

Dataset	**Area**	**Pseudo R^2**	**Likelihood ratio test statistic**	**p-value**
Rod and line	FHB	33%	22.68	<0.01
	PW	55%	30.67	<0.01
Longline	FHB	13%	6.11	0.3
	PW	32%	51.8	<0.01

February was the month with the highest CPUE in all cases apart from rod and line catches in FHB, which were highest in March (Fig.2). Rod and line CPUE in PW was similar in the two summer months (December & February), whereas in winter, catches were either 0 (May & June) or significantly lower than in February ($p<0.05$) as indicated by the GLM. Rod and line CPUE in FHB was significantly lower than the reference level in May, September and December, albeit only slightly so in May and December, whereas CPUE in March and June was not significantly different from CPUE in February. For the longline data, there was a clear seasonal separation between summer and winter CPUE in PW, with relatively uniform, high CPUE values in summer (December-April, $p>0.05$ for comparisons with the February reference level) and catches in winter either 0 (July) or significantly lower than the reference level (May, October & November). In FHB on the other hand, there was no seasonal pattern in longline CPUE, with no significant differences between any of the months and the reference level.

3.2. Seasonal movement

All 30 tagged flathead left PW during the course of the tags' battery life and moved into FHB, 16 of them returned to PW at a later date in the study. There was a clear seasonal pattern in departures from PW, with the monthly model performing significantly better than the null model (X^2= 523.9, p<0.05). Mean distances from the upper parts of PW (receiver UPW1) were significantly greater than the reference month during winter (May-August; Fig. 3), as animals departed PW sometime in May, were the furthest from UPW1 in July and returned to PW in September (Fig. 3).

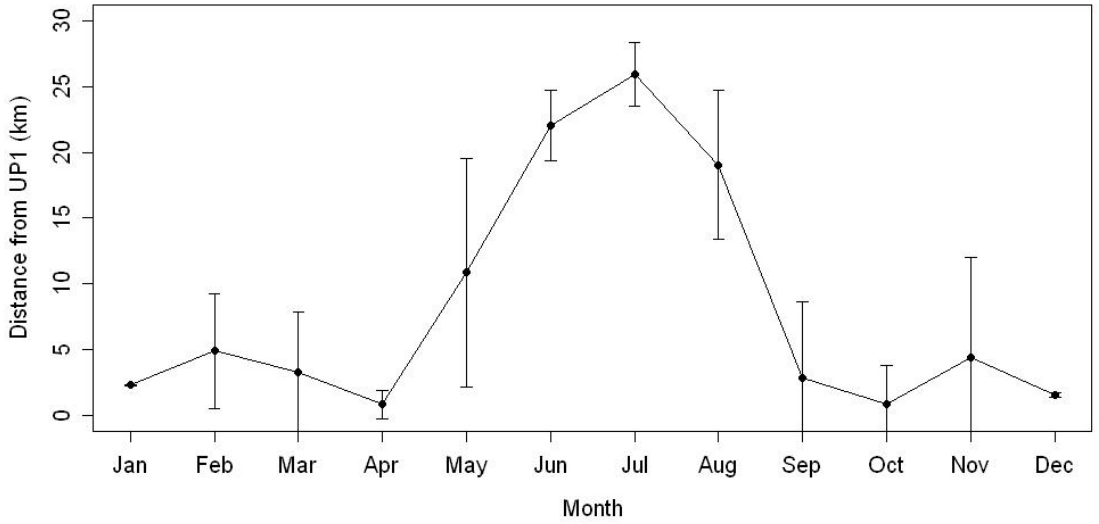

Figure 3. Mean monthly distance of flathead detections from the receiver furthest up the estuary in PW (UPW1). Vertical error bars indicate ± 1 standard deviation.

3.3. Influence of environmental parameters on activity patterns

During the study period, temperatures in the study area ranged from 8.2 to 22.0 °C (mean = 12.2 °C) and salinities ranged from 18.6 to 45.4 PSU (mean = 27.9 PSU). Both the upper and lower extremes of the temperature range were recorded in UPW, whereas minimum salinity was recorded in FHB and maximum salinity in UPW. Highest activity levels occurred at the highest temperatures (22 °C) and at the lower end of the salinity range (20-25 PSU), however, for most temperature and salinity values, variability in activity was considerable as indicated by large standard deviations for a large fraction of the temperature and salinity bins (Fig. 4).

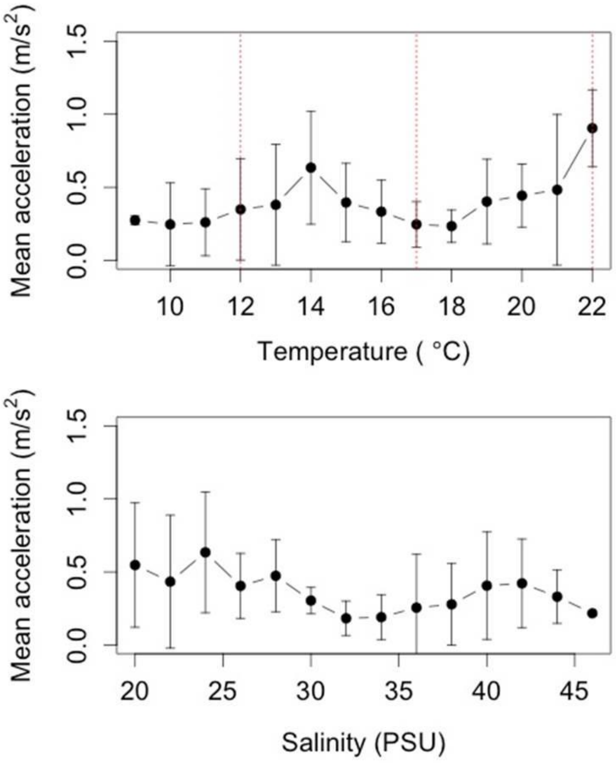

Figure 4. Mean acceleration by temperature (top panel) and salinity (bottom panel) bin. Temperature bin width is 1 °C, salinity bin width is 2 PSU. Vertical error bars indicate ±1 standard deviation. Vertical red lines in the top panel indicate temperature values used as treatments in the metabolic experiments.

The linear mixed model showed that both temperature and salinity had a significant impact on flathead acceleration (temperature: F = 75.47, $p<0.05$; salinity: F = 136.63, $p<0.05$) and the model including both parameters performed better than the null model or models containing only one of the parameters (table 2). However, there was no significant interaction between the two parameters and only the intercept varied between individuals, whereas the slope of the response curve was not significantly different between individuals (table 2).

Table 2. Performance indicators of different linear mixed models fitted to the relationship between acceleration and environmental parameters. Indicators relate to the comparison of each model to the model with the lowest Akaike information criterion (AIC), which included both salinity and temperature but no interaction between the terms (denoted by *) and a random intercept only. ΔAIC is the difference between the AIC of each model and the reference model. The top section shows more complex models than the reference model, the bottom section shows reduced models.

Model	**Likelihood ratio test statistic**	**p**	**ΔAIC**
Salinity + temperature (random intercept and slope)	1.96	0.86	8.1
Salinity + temperature + salinity*temperature	1.06	0.30	1
Salinity	4426.30	<0.05	4424.4
Temperature	121.87	<0.05	119.9
Null model	257.75	<0.05	253.8

The final model showed that temperature and salinity had opposite effects on acceleration and that the effect of temperature was stronger (Fig. 5). A 1 °C increase in temperature led to a 14% increase in acceleration whereas a 1 PSU increase in salinity led to a 6% decrease in acceleration for the temperature and salinity ranges encountered in this study.

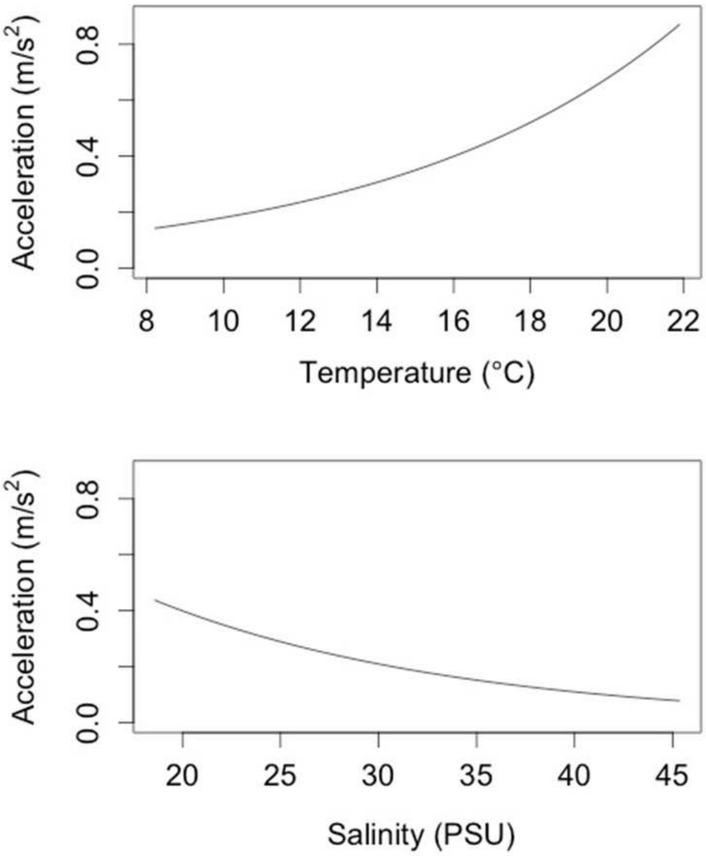

Figure 5. Effect of temperature and salinity on flathead acceleration from the linear mixed model fitted to the field data. Top panel shows effect of temperature on acceleration if salinity is held constant at the mean of all values encountered during the study (27.9 PSU). Bottom panel shows effect of salinity on acceleration if temperature is held constant at the mean of all values encountered during the study (12.2 °C).

3.4. Metabolic rates at different temperatures

The metabolic experiment showed that temperature had a significant impact on all four metabolic rate measures (SMR, RMR, MMR, AMR; table 3).

Table 3. Results of one-way ANOVA of metabolic parameters between temperature treatments

Variable	F-value	p-value
SMR	10.09	<0.05
RMR	9.579	<0.05
MMR	8.559	<0.05
AMR	15.49	<0.05
EPOC	0.342	0.57
Recovery time	11.74	<0.05

A rise in temperature caused a rise in both resting and active metabolic rates (Fig. 6), however, this was only significant for the 17 to 22 °C increase in temperature, not for the 12 to 17 °C increase (table 4).

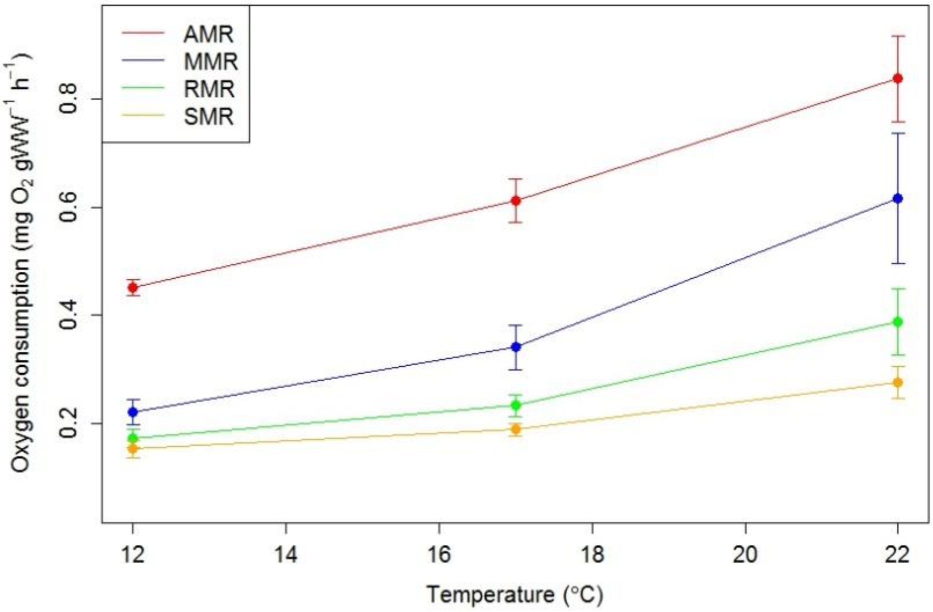

Figure 6. Differences in standard metabolic rate (SMR), routine metabolic rate (RMR), maximum metabolic rate (MMR) and active metabolic rate (AMR) between temperature treatments (see methods section for definition of metabolic rate parameters). Vertical error bars indicate ± 1 standard deviation.

Table 4. P-values for post-hoc Tukey's honest significant difference test of difference in metabolic parameters between pairs of temperature treatments. Test was not carried out for EPOC values since one-way ANOVA showed no significant difference between temperature treatments (see table 4). Grey shaded values indicate significant p-values ($p<0.05$).

Temperature	SMR	RMR	MMR	AMR	EPOC	Recovery time
12 – 17 °C	0.395	0.444	0.424	0.071	-	0.015
12 – 22 °C	0.002	0.002	0.003	0.000	-	0.008
17 – 22 °C	0.019	0.020	0.033	0.015	-	0.872

This is in agreement with the positive exponential relationship found in the field activity data, which also showed little difference in activity between the 12 and 17 °C bins and a marked increase from 17 to 22 °C (Fig. 6). In addition to metabolic rate means, the standard deviation also increased with increasing temperature (Fig. 6), indicating a greater degree of individual variation at higher temperatures. Despite significant differences in AMR, there was no significant difference in total EPOC between temperature treatments (table 3) due to high individual variation within treatments (Table 5). Recovery time on the other hand, decreased significantly with temperature (Table 4) and was more than twice as long at 12°C as at 17 and three times as long as at 22 °C (Table 5).

Table 5. Mean recovery time, defined as the time between exercise and return of the metabolic rate to within 10% of the RMR and mean excess post-exercise oxygen consumption (EPOC) for each temperature treatment. Standard deviation of the means is given in brackets.

Temperature treatment	Recovery time (hours)	EPOC (mg O_2 gWW^{-1})
12 °C	18.1 (7.9)	82.6 (37.7)
17 °C	7.6 (3.9)	72.6 (32.6)
22 °C	6.0 (3.2)	69.9 (36.8)

4. Discussion

The relationship between catch per unit effort from baited fishing gears and absolute fish abundance is strongly influenced by both the availability (i.e. vertical and horizontal distribution) and catchability (i.e. vulnerability of the fish to the gear) of the target species (Stoner 2004). Our study showed significant seasonal variability in catches of the sand flathead *Platycephalus bassensis* from two types of baited fishing gear as well as seasonal patterns in the horizontal movement and environmentally mediated changes in activity and metabolic rates. This suggests that for this species both availability and catchability vary with season and environmental parameters, which would have to be taken into consideration in any CPUE based stock assessment of this important recreational fish species.

Analysis of CPUE from both rod and line and longline data showed that the magnitude of the seasonal variability in catches that had previously been reported (Tracey et al. 2011) was highly area specific with a strong seasonal pattern in the shallow coastal estuary of Pittwater and limited to no seasonal pattern in Frederick Henry Bay, the deeper bay at the mouth of the estuary. This suggests that the two areas are affected differently by the factors driving changes in fish availability and catchability. Patterns in fish availability were strongly influenced by seasonal movement of flathead out of Pittwater and into Frederick Henry Bay at the start of the austral winter, followed by a return to Pittwater in spring. This seasonal departure from Pittwater is a pronounced characteristic of the predatory fish community in the estuary and a similar pattern has been observed for a number of other species, particularly elasmobranchs (Barnett and Semmens 2012). Seasonal changes in estuarine fish community structure is a common feature in temperate estuaries around Australia and worldwide (Claridge et al. 1986, Loneragan et al. 1989, Maes et al. 1998) and is generally attributed to seasonal changes in environmental parameters such as temperature, salinity or dissolved oxygen concentration (Thiel et al. 1995, Marshall and Elliott 1998).

The seasonal movement observed in this study indicates that the strong seasonal pattern in CPUE in Pittwater is predominantly driven by changes in fish availability, however, the fact that CPUE was still significantly lower in September and October, despite the fact that the majority of tagged fish had returned to within 10 km of the head of the estuary suggests that there are other factors at play. Moreover, there was also a seasonal pattern of lower CPUE in winter in the rod and line data from Frederick Henry Bay, albeit much less pronounced than in Pittwater. This is despite the fact that fish abundance would be expected to increase, as individuals that spent their summer in Pittwater are present in Frederick Henry Bay in winter.

Hence, it has to be assumed that changes in catchability also contribute to seasonal patterns in CPUE. Our activity data from acoustic telemetry and metabolic data collected in the laboratory show that both activity and metabolic rates increased significantly with temperature for the range of values encountered in this study. A previous study on *P bassensis* showed a significant increase in maximum swimming speed with temperature in the laboratory (Yanase et al. 2007) and an increase in activity with temperature has been shown for a number of other teleosts (Wardle 1980). If fish are less active in colder waters, they are less likely to encounter a bait plume and less likely to detect the bait after the chemical cue was received (Stoner et al. 2006). An increase in metabolic rate with temperature is also a common characteristic of many ectothermic fish species (Clarke and Johnston 1999) and it has been shown to increase feeding motivation (Stoner 2004) and rates (Russell et al. 1996, Buentello et al. 2000). Thus, temperature is likely to influence the probability of fish encountering a bait plume, detecting the bait and striking it. This was shown to be true in laboratory studies on Pacific halibut (Stoner et al. 2006) and sablefish (Stoner and Sturm 2004) where temperature had a larger effect on detecting a bait, the intensity of the search behaviour after detection and the likelihood to strike a bait than feeding history.

The seasonal movement and environmentally driven activity patterns described in this study are likely to have a significant impact on the availability and catchability of the target species which would need to be included in future stock assessment models. Availability is increasingly accounted for in fisheries management either by including large-scale movement models in stock assessment (Goethel et al. 2011) or by quantifying habitat preferences of the target species and including them in CPUE analyses, particularly for billfishes and tuna (Bigelow and Maunder 2007). For ectothermic fish species, some progress has also been made to account for temperature related patterns of availability in stock assessment models (e.g. yellowfin sole, (Stoner 2004)). However, few models exist that include environmentally mediated changes in catchability in the estimation of stock size from CPUE data, due to the difficulty of quantifying behavioural responses to environmental changes and their effect on catchability in the field. Yet, a number of laboratory studies have increased our knowledge of the response of fish to bait under varying conditions over the last ten years and the only recently developed acoustic accelerometer tags employed in this study are now allowing researchers to quantify the influence of environmental parameters on fish activity remotely in the field. This will hopefully allow the inclusion of an environmentally influenced catchability parameter in future stock assessment models, which is currently only done implicitly on a coarse temporal scale by accounting for changes in CPUE with season (e.g. Large (1992).

While in this study it was not possible to tease apart the effects of horizontal movement and variations in activity on the relationship between CPUE and fish abundance, our findings make it clear that both are likely to be important factors which would need to be included in an accurate stock assessment for the sand flathead. To accomplish this, future studies with more continuous catch rate data as well as continuous activity data for fish tagged in FHB in summer, which are likely to remain there year round would allow the modelling of the relationship between activity and catch rates directly. Moreover, a laboratory study in which fish tagged with accelerometer tags are exposed to bait cues at different temperatures could allow us to calibrate an index of catchability based on temperature and activity which could be applied to data collected in the field.

5. Acknowledgements

Funding assistance for this study was provided by the Fishwise Community Grant Fund administered by the Department of Primary Industries, Parks, Water and Environment.
The authors would like to thank Justin Bell, Keno Ferter, Edward Forbes and Graeme Ewing for their efforts during the collection of experimental catch data. Thanks are furthermore due to Adam Barnett, Amos Mapleston and Jaime McAllister for their assistance with the deployment of acoustic tags and maintenance of acoustic receivers.

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