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SURFING THE TIDE: HOMEWARD MIGRATION OF SEA TROUT (Salmo trutta) IN A PATAGONIAN RIVER.

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Corresponding Author:	Carolina Giese, Lic. Consejo Nacional de Investigaciones Cientificas y Tecnicas Puerto Madryn, Chubut ARGENTINA
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Consejo Nacional de Investigaciones Cientificas y Tecnicas
Corresponding Author's Secondary Institution:	
First Author:	Carolina Giese
First Author Secondary Information:	
Order of Authors:	Carolina Giese
	Martín Ignacio García-Asorey
	Miguel Ángel Casalinuovo
	María Marcela Amaya-Santi
	Brian Patrick Kennedy
	Miguel Alberto Pascual
Order of Authors Secondary Information:	
Abstract:	This study evaluates the influence of marine and freshwater conditions on the timing of river entry and upstream migration of sea trout (Salmo trutta) in the Grande River of Tierra del Fuego, Patagonia. We analysed the in-river catch-and-release records from a group of fishing lodges that dominate the Grande River fishery during January-April 2008 (n=5,029 fish) as a function of environmental variables: tidal amplitude, stage in the lunar cycle, river discharge, and river water temperature along the homeward migration season. We first discuss the value of the daily catch rate as an abundance index in the Grande river; then, we analyse the temporal structure of the tidal cycle in the Grande River estuary, a macro-tidal environment with a mean tidal amplitude of 5.7 m, and analyse the fit of a Generalized Additive Model to trout catches on a daily basis in four sections along the river to identify the environmental variables that may disproportionally affect trout abundance throughout the homeward migration. Fish catches in each section of the river were differentially affected by specific environmental variables: tidal amplitude had a positive and significant effect on catches in the three lower river sections, whereas water temperature and river discharge significantly affected catches in upper sections (positive effect of temperature; negative effect of discharge). Catches in the lower section clearly reflect the river entry stage of the homeward migration, with a bi-modal shape significantly correlated with the tidal cycle. The first peak was composed mainly of larger multi-sea-winter trout that move upstream, whereas the second one had a wider range of fish lengths, including a large proportion of small and maybe non-reproductive trout that overwinter in the lower river. Based on our results, we conclude that the large tides in the Grande River estuary strongly affect the river entry timing of sea trout. The underlying mechanisms of this effect may be a combination of increased odor recognition and increased tidal transport modulated by the seasonal tidal cycle, which operates on trout during coastal migration to produce the pulses observed in the Grande River sea trout run. In the middle and upper section of the river, where the tidal effect at river entry was

	dissipated as upstream migration progressed, trout catches increased with water temperature and decreased with river discharge, which may operate through their influence on in-river migration rate and abundance, but also through changes in catchability.

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Giese, Adriana Carolina. Giese, A. Carolina. 1
García-Asorey, Martín Ignacio. García-Asorey, Martín I. 2
Casalinuovo, Miguel Ángel. Casalinuovo, Miguel A. 3
Amaya-Santi, María Marcela. Amaya-Santi, M. Marcela. 4
Kennedy, Brian Patrick. Kennedy, Brian P. 5, 6
Pascual, Miguel Alberto. Pascual, Miguel A. 1, 7

1. Instituto Patagónico para el Estudio de los Ecosistemas Continentales. IPEEC-CONICET, Bvd. Brown 2915 (9120), Puerto Madryn, Argentina.
2. Grupo de Investigación y Desarrollo Tecnológico en Acuicultura y Pesca, Facultad Regional Chubut, Universidad Tecnológica Nacional, Av. del Trabajo 1536 (9120), Puerto Madryn, Argentina.
3. Dirección de Manejo de Recursos Ícticos Continentales, San Martín 1401 (9410), Ushuaia, Argentina.
4. Universidad Nacional de la Patagonia Austral, Unidad Académica Río Gallegos, Lisandro de la Torre 1070 (9400), Río Gallegos, Argentina.
5. Department of Fish and Wildlife Sciences, College of Natural Resources, University of Idaho, Moscow, ID 83844-1136, USA.
6. Departments of Biological Sciences and Geological Sciences, University of Idaho, Moscow, ID 83844-1136, USA.
7. Universidad Nacional de la Patagonia San Juan Bosco, Bvd. Brown 3051 (9120), Puerto Madryn, Argentina.

Corresponding author: Giese, A. Carolina. Bvd. Brown 2915 (U9120ACD), Puerto Madryn, Argentina. Email: giese@cenpat-conicet.gob.ar.

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ABSTRACT

This study evaluates the influence of marine and freshwater conditions on the timing of river entry and upstream migration of sea trout (*Salmo trutta*) in the Grande River of Tierra del Fuego, Patagonia. We analysed the in-river catch-and-release records from a group of fishing lodges that dominate the Grande River fishery during January-April 2008 (n=5,029 fish) as a function of environmental variables: tidal amplitude, stage in the lunar cycle, river discharge, and river water temperature along the homeward migration season. We first discuss the value of the daily catch rate as an abundance index in the Grande river; then, we analyse the temporal structure of the tidal cycle in the Grande River estuary, a macro-tidal environment with a mean tidal amplitude of 5.7 m, and analyse the fit of a Generalized Additive Model to trout catches on a daily basis in four sections along the river to identify the environmental variables that may disproportionally affect trout abundance throughout the homeward migration. Fish catches in each section of the river were differentially affected by specific environmental variables: tidal amplitude had a positive and significant effect on catches in the three lower river sections, whereas water temperature and river discharge significantly affected catches in upper sections (positive effect of temperature; negative effect of discharge). Catches in the lower section clearly reflect the river entry stage of the homeward migration, with a bi-modal shape significantly correlated with the tidal cycle. The first peak was composed mainly of larger multi-sea-winter trout that move upstream, whereas the second one had a wider range of fish lengths, including a large proportion of small and maybe non-reproductive trout that overwinter in the lower river. Based on our results, we conclude that the large tides in the Grande River estuary strongly affect the river entry timing of sea trout. The underlying mechanisms of this effect may be a combination of increased odor recognition and increased tidal transport modulated by the seasonal tidal cycle, which operates on trout during coastal migration to produce the pulses observed in the Grande River sea trout run. In the middle and upper section of the river, where the tidal effect at river entry was dissipated as upstream migration progressed, trout catches increased with water temperature and decreased with river discharge, which may operate through their influence on in-river migration rate and abundance, but also through changes in catchability.

KEY WORDS: *Salmo trutta*, anadromy, migration timing, spring-neap tidal cycle, GAM, Patagonia.

INTRODUCTION

Migration is a critically important behaviour within the life cycle of anadromous salmonids and has been a major theme in salmonid research for decades since the pioneering works of Hasler (1966) and Harden Jones (1968). Much has been learnt about the mechanisms guiding the migratory behaviour throughout different stages of the life cycle of salmonids, the environmental and genetic bases underlying the migratory behaviour, and how they give rise to population-specific migration patterns (Quinn, 2018). River entry is an essential phase in the life cycle of anadromous salmonids, during which fish are exposed to coastal, estuary and river conditions including pollution, fisheries, and various man-made obstructions. Understanding the seasonal timing in river entry and upstream migration and its dependence on environmental drivers can provide valuable information for space and time-specific fish conservation and management efforts, including fisheries regulations, restoration programs, dam operations, and effluent management. Disentangling the relative effect of marine and freshwater conditions during the ocean-river transition along the homeward migration, however, has proven to be a difficult challenge, mostly because of the multiple confounding factors operating at different domains and scales, and the complexities of interpreting responses from mixed-stock populations (Hays, 2013). The aim of this study is to analyse the effect of major marine and freshwater conditions during the homeward migration of a self-sustained population of sea trout *Salmo trutta* L. 1758 introduced in the Grande River in Tierra del Fuego, Patagonia, with a particular emphasis on the effect of the neap-spring tidal cycle.

The homeward migration in anadromous salmonids starts with the oceanic migration to coastal waters, continues along coastal waters to estuarine waters (Hansen *et al.*, 1993), followed by river entry and upstream migration (Quinn, 2018; Jonsson & Jonsson, 2011). The factors initiating the homeward migration from the high sea are not fully known (Sloman *et al.*, 2005; Jonsson & Jonsson, 2011); ocean conditions, sea-surface temperature (Hodgson *et al.*, 2006), and currents are known to have an influence, along with intrinsic factors such as sexual maturation or circannual rhythms, both synchronized to photoperiod (Bromage *et al.*, 1993; Ueda *et al.*, 2000). The timing of river entry has been associated with river discharge (Huntsman, 1948; Alabaster, 1970; Potter, 1988; Smith *et al.*, 1994; Jonsson & Jonsson, 2002), river water temperature (Jonsson & Jonsson, 2002), circadian rhythms and light intensity (Potter, 1988; Smith & Smith, 1997), winds (Hayes, 1953; Banks, 1969), daily tidal cycle (Hayes, 1953; Stasko, 1975; Potter, 1988; Smith & Smith, 1997; Erkinaro *et al.*, 1999; Karppinen *et al.*, 2004), and tidal currents (Potter, 1988; Bourque *et al.*, 1999). The upstream migration has been correlated with different environmental factors, the most important being river discharge (Huntsman, 1948; Hayes, 1953; Banks, 1969; Alabaster, 1970; Hodgson *et al.*, 2006; Jonsson *et al.*, 2018) and freshwater temperature (Trepanier *et al.*, 1996; Hodgson *et al.*, 2006). Other factors cited are circadian rhythms and light intensity (Banks, 1969).

The association between the spring-neap tidal cycle and spawning migration in anadromous salmonids is part of fishermen's lore, especially in places with large tidal amplitude such as Southern Patagonia, and it is anecdotally commented on by biologists around the world. However, such a relationship has seldom been demonstrated. Several studies have identified a relationship between river entry and the daily tidal cycle (Hayes, 1953; Stasko, 1975; Potter, 1988; Smith & Smith, 1997; Erkinaro *et al.*, 1999; Karppinen *et al.*, 2004), as well as the relationship of return timing and fish movement in estuarine waters with tidal currents (Potter, 1988; Bourque *et al.*, 1999). But only one work before ours analysed the influence of the spring-neap tidal cycle on salmonids migration; Hayes (1953) in a study conducted on *Salmo salar* in La Have River, Nova Scotia, found that peaks in the tidal cycles, representing daily increasing differences between high and low tides, seemed to be effective in concentrating Atlantic salmon in the estuary and initiating a run into the river. Spring-neap tidal cycle is particularly underestimated as an environmental influence on the spawning migration of anadromous fishes, perhaps because of the intricacies of disentangling the effects of tidal and lunar cycles (Jellyman & Lambert, 2003). The moon phase and the relative position of Sun-Earth-Moon are the driving factors of tidal forces on the earth's oceans, but tides respond locally in timing and range to the shape of the shoreline and the near-cost bathymetry (Knauss, 1978). Therefore, the potential of tides to operate as a significant driver of fish migrations varies greatly throughout the world, maybe playing an important role in some locations and not in others.

The aim of the present study was to evaluate the effect of marine and freshwater environmental factors on the timing of river entry and upstream migration of anadromous brown trout (*Salmo trutta*) in the Grande River of Tierra del Fuego. We use catch records from the local sport fisheries, collected throughout the migration season and along different river sections, from the estuary and upwards, as an abundance index to capture the relative effect of marine and freshwater variables over time and space. The characteristically wide tide amplitude of the Southern Atlantic Ocean, also highly variable along the spring-neap cycle, exposes the migrating fish to different tidal conditions, providing an excellent setting to evaluate the tidal influence.

MATERIALS AND METHODS

STUDY SYSTEM

The Río Grande is the largest river in Tierra del Fuego (53°47' S, 67°41' W), with a length of 180 km and an average annual discharge of 40 m3 s-1. It is a free-flowing stream that runs from the Andes range in Chile and across the steppe in Argentina to the Southern Atlantic Ocean. Its hydrography is dominated by snowmelt and rainfall, with important freshets in the spring and minimum flows in the summer. The estuary is 15 km long and shallow (Figure 1) with a strong tidal influence. The tides are semi-diurnal and present a neap-spring cycle with a two-week period, with an average amplitude of 5.6 m, a minimum amplitude of 1.9 m and a maximum of 8.6 m (SHN, 2011, for the period 2007-2011, Figure 2).

Brown trout is native to the Northeast Atlantic Ocean but has been widely introduced worldwide (MacCrimmon & Marshall, 1968). Brown trout populations have been established throughout Patagonia since 1909 (Pascual *et al.*, 2002). The southernmost populations, found in the Gallegos River, the Grande River, and other Atlantic rivers of Tierra del Fuego, have developed an anadromous cycle (called sea trout), with high marine growth and sustain important sport fisheries. The Grande River is the most important sea trout fishery in Argentina and it is usually considered by fishermen and international fishing magazines as the premier sea trout river in the world (Simpson, 2003; Purnell, 2016; Casalinuovo *et al.*, 2018), with an annual catch of well over 5,000 fish (O’Neal & Stanford, 2011). Within the Argentinean sector, catches take place mainly in six fishing lodges located along 70 km of the river that operate under a “catch and release” system.

FISH CAPTURE AND ENVIRONMENTAL DATA

The fish data used in this study correspond to records collected by trained fishing guides in the four most important lodges in the Grande River (María Behety, Toon Ken, Villa María and Kau Tapen, Figure 1) between January and mid-April 2008. The study area covered by the operation of these four lodges corresponds to the 52 km of the river where most of the fishing takes place, between river kilometres (RK) 25 and 77 from the ocean (Figure 1). Downstream from this area, there is a stretch with no fishing (the first 15 km) and a public fishing stretch (the next 10 km), here the river is strongly influenced by tides. Upstream from the study site, there is a 15 km river section up to the Chilean border with difficult access and light fishing. Fishing in Chile is much less significant than on the Argentinean side.

Trout were landed, measured (for fork length, girth anterior to the dorsal fin, and weight), and released back to the river by fishing guides from the four lodges that participated in the study, trained by biologists following a standard protocol (O’Neal & Stanford, 2011). The directions were to record every single fish caught so, besides the eventual missed individual, practically the whole catch in these four lodges was recorded. The daily catch rate (number of fish per day) in each section of the river was here used as an index of fish abundance throughout the season. The Grande River fishery is a highly-priced, fully booked fishery, where the number of rods allowed per lodge per day is regulated by provincial legislation (between four and nine). Lodges operate at total capacity throughout the season, and fishing takes place in two shifts (AM and PM) under all-weather conditions. Every lodge keeps a fishing log where catches are recorded daily, including information on the pools visited, trophy catches, type of flies and lines used, etc., at both daily shifts. The fishing logs in the lodges included in this study show no gaps in outings during the 2008 fishing season, so we are confident that fishing effort remained stationary throughout the season, not biasing catch rate as an index of fish abundance. Other factors potentially affecting catch rate or catchability besides abundance are accounted for during our analyses and interpretation of results. Catches registered in the public fishing stretch and in two other lodges in the river were purposely excluded from the analyses due to the lack of systematic and complete records. The area and lodges included in this study, on the other hand, produce most of the catches in the Grande River every year and throughout the season.

Angling has proved to be an adequate sampling method for monitoring several wild salmonid populations (Crozier & Kennedy, 2001; Thorley *et al.*, 2005). In particular, compared to other catch techniques (i.e. spinning and gillnet), fly-fishing is the least size-selective sampling method (Leclerc & Power, 1980; Hetrick & Bromaghin, 2006). In the Grande River, fly-fishing catches the full range of anadromous fish sizes with a slight bias towards larger size classes. The size-frequency of fly-fishing catches peaks at the 50-70 cm range compared to the size-frequency of migrating fish peaking at 40-60 cm as estimated by a Dual-frequency Identification Sonar scan (Niklitschek *et al.*, 2012).

The tidal height data were drawn from tidal charts of the Argentinean Navy Hydrography Service (SHN, 2011) for the Port of Río Grande (53°47’ S, 67°39’ W). The tidal amplitude was calculated on a daily basis throughout the upstream migration (December to April) as the difference between the maximum and the minimum tidal height registered on each day. Moon data, corresponding to the percentage of the moon illuminated each day at 8 pm, were provided by the Naval Observatory of Buenos Aires (Observatorio Naval de Buenos Aires). River discharge and freshwater temperature data come from a gauging station located at the river kilometre (RK) 130 (53º 53.5’ S, 68º

52.9’ W; Figure 1), managed by the Chilean National Water Administration (DGA, 2015), which was the unique station with hydrometric records for the Río Grande River in 2008. As tributaries within Argentina are relatively small and with the same general hydrologic regime as the main river, hydrological data at this station are expected to reflect conditions experienced by the fish within the study area. To consider the temporal delay between taking the measure (at RK 130) and its effect on catches (in RK 25-77), we applied a five-day moving average filter in our analyses (see below).

ANALYSES

In order to examine the effect of environmental factors on the timing of river entry and upstream migration, catch rates were considered in the context of potential explanatory variables. The length of the river where lodges operate and where catches were registered (river kilometres, RK, 25 to 77 from the sea) was divided into four sections of 13 kilometres long each, designated as A (closer to the sea) to D upstream (Table 1; Figure 1). Catches in the lower section are expected to represent river entry timing closely, while catches in the upper sections are expected to represent a combination of upstream migration with search and holding phase, as described in Finstad *et al.* (2005).

Tidal amplitude was first analysed to characterise the spring-neap tidal cycle in the study area; an auto-correlogram (Diggle, 1990) of tidal amplitude was used to summarise the general seasonal pattern. Then, the relationship between tidal amplitude and the percentage of moon illuminated was examined by linear and additive models in order to determine the degree of their association. Both analyses were conducted using data from 2007 to 2011. The lag of the effect of spring-neap tidal cycle on the abundance of *S. trutta* at different river sections from A to D was analysed by correlating daily catches in each section with daily tidal amplitude during the 2008 fishing season using cross-correlograms and varying time lags from 0 to 40 days. The lags producing the higher correlation were used to evaluate tidal amplitude in the model. River discharge and freshwater temperature data were included in the model with a five-day moving average filter to smooth local changes in the time series produced at RK 130; because they were expected to be irrelevant when affecting catches at RK 25-77, around five days later. The date of catch, as the day number within the year, was included in the model to account for the general pattern or run strength throughout the season.

The relationship of catch rate with water temperature, river discharge, tidal amplitude, percentage of the moon illuminated, and day number was evaluated separately for each river section using Generalized Additive Models (GAMs; Hastie & Tibshirani, 1990; Wood, 2006) as they are useful to model nonlinear relationships between fish species abundance and environmental variables (Wood, 2014; Alcaraz-Hernández *et al.*, 2016), and because an exploratory data analysis suggested a lack of linearity for some variables. Sea trout catch rates were described by a negative binomial distribution (Harris & Milner, 2007) to allow for overdispersion of the data. Multicollinearity of predictor variables was evaluated with Pearson correlation coefficients with a threshold of $|r| > 0.7$ among any pair of variables (Dormann *et al.*, 2013). In addition, the Variance Inflation Factor (VIF) was calculated and a cut-off value of VIF >5 (Zuur *et al.*, 2009) was used. The models were also tested for concurvity, a generalisation of collinearity that allows for nonlinear relationships among the set of predictor variables. GAMs were fitted using the penalized likelihood estimation method developed by Wood (2008) which has been proved highly robust to concurvity; therefore, values of estimate concurvity <0.6 were considered acceptable. When higher levels of concurvity were detected, one correlated variable was removed at a time, continuing with the reduced model having the lowest AIC and highest deviance explained. The GAMs were estimated using penalized cubic regression splines (Wood, 2014). Smoothing parameter estimation was achieved using restricted maximum likelihood (REML) following recommendations in Marra and Wood (2011). After fitting models, the shape of the relationship between each of the habitat parameters and daily catch was analysed. Variable selection was made by a backward stepwise elimination process based on Akaike's Information Criterion (AIC) as suggested in Zuur *et al*. (2009) applying parsimony and Delta-AIC <2 criterion. The percentage of deviance explained was used as a measure of model fit (Wood, 2006) and it was also considered in the model selection process.

Segregation in the migration timing by fish size was analysed within each river section through linear regressions (McCullagh & Nelder, 1989) between fish length or weight and day number. In addition, the distribution of fish length and weight by fortnight and by section throughout the season was inspected. All statistical analyses were carried out in R (version 3.3.0, 2016-05-03; R Core Team, 2016). GAMs were implemented using the gam function in the R package "mgcv" (Wood, 2006).

RESULTS

FISH CAPTURE AND ENVIRONMENTAL DATA

A total of 5,029 sea trout were caught between January 1 and April 13 during the 2008 fishing season, with a daily average of 49.3 ± 24.5 fish and a range of 1-122 fish day-1. The largest catches occurred in section A, decreasing towards the upstream sections (Figure 1, Table 1). Mean river discharge during the fishing season was 15.5 m^3 s^{-1} (range 11-28 m^3 s^{-1}), with a maximum during the first half of January, followed by a drop to level off at around 12 m^3 s^{-1} (Figure 3). Water temperature varied from 1.6 to

14.7º C with a mean of 9.3º C, a maximum around January 25 and then started to decrease (Figure 3).

The auto-correlogram of tidal amplitude (Figure 4, upper panel) shows a 15-day tidal cycle ($r = 0.008$, $p < 0.001$) and a more significant 29-day cycle ($r = 0.90$, $p < 0.001$). During the 2008 fishing season, at the mouth of the Grande River, tidal amplitude fluctuated from 2.5 to 8.0 m with a mean of 5.7 m. The 29-day tidal cycle is characterised by a low-neap, spring, high-neap, spring sequence (Figure 4, lower panel). There was not a strong linear relationship between tidal amplitude and percentage of moon illuminated at any lag (lag 0: $r = 0.0067$, $p = 0.117$; lag 15, stronger relationship found: $r = 0.012$, $p = 0.0432$), and the nonlinear relationship at a 12-day lag was the stronger one, with an explained deviance of 47.2% ($p < 0.001$).

DATA ANALYSES AND MODELS

Cross-correlograms between daily catches in different river sections and daily tidal amplitude during the 2008 fishing season show significant and positive correlations in the three lower river sections (Figure 5), with lags (in days) 7 in section A, 13 in section B, and 23 in section C. No significant correlation was found in section D. The general pattern is an increase in the time lag in the upriver direction with a decrease in the significance. Those lags were used in the inputs of GAM models to evaluate the effects on daily catches of tidal amplitude together with other variables.

Analysis of multicollinearity on predictive variables resulted in no critical problems of collinearity, and no variable surpassed the cut-off value of Variance Inflation Factor >5. The analysis of concurvity indicated that nonlinear relationships between predictive variables included in the best models appeared only in section D and related to “day number”, a variable that could be carrying the effect of river discharge and/or river temperature.

The fit of GAMs to daily catch rates with different explanatory variables indicates that fish catches in each section of the river are differentially affected by specific environmental variables (Figure 6 and Table 2). Day number had a significant effect on the daily catch in section A with two local maxima around day numbers 30 and 68, and a marginally significant effect in section D. Tidal amplitude had a positive and significant effect on catches in the three lower river sections (A, B and C). The percentage of moon illuminated was only marginally significant for section C. And, water temperature and river discharge significantly affect catches in upper sections (B, C and D), with a positive effect of temperature and a negative effect of discharge.

The mean length and weight of the trout caught decreased with time over the season in section A (linear regression; p-value <0.001). However, the proportion of variance explained by the models was low (length: $R^2 = 0.04$, weight: $R^2 = 0.012$). In section B, mean fish length also decreased over time (p-value = 0.02), but with an even higher unexplained variance ($R^2 = 0.005$), whereas mean fish weight did not change significantly over time (p-value = 0.59). In sections C and D, neither mean length nor mean weight changed over time (p-value >0.5). The length distribution registered in section A changed over time, from unimodal around 75 cm in January to bimodal around 40 and 75 cm in February and March. This shift in size frequency over time, from unimodal to bimodal, is preserved upstream, most clearly in section B and to some extent in upper sections (Figure 7). The weight frequency distribution shows a large increase in catches of smaller fish, below 2 kg, during the last fortnight of February and March, particularly in the lower section A. The pulse of small fish is also detected in section B during March, getting less important in the upper sections (Figure 8).

DISCUSSION

The strong relationship between fish catches and day number in the lower river section near the ocean, together with its characteristic two-peak pattern and the very low catches at the beginning and end of the season, suggests that the migratory *Salmo trutta* population in the Grande River is made up by an early and a late run. Although catchability is expected to change over the season responding to changes in fish physiology, behaviour and activity (Laughton, 1991; Young & Hayes, 2004), potentially affecting catch rate and therefore abundance estimation, we could not identify any driver that could have a two-peak effect on abundance. The catch rate pattern over the season is most likely reflecting actual changes of abundance due to pulses of fish entering the river from the estuary, with section A being a transition area to freshwater from the estuary. The less clear pattern in the next two upper sections or even increasing in the uppermost section supports the idea of these sections being holding areas or areas with more local migrations. Unlike other salmonids that migrate straight to the spawning grounds, it is common for sea trout to make a stepwise progression with erratic movements before establishing on spawning areas (Finstad *et al.*, 2005). As trout disperse along the river, the patterns at entry become weaker and unrecognised by the model. The increase in catches in the upper section with day number could be due to an accumulation of fish over time or could be an indirect effect of water temperature and/or river discharge that significantly affect catches in the three upper sections.

The change in size frequency making up the two peaks of the run indicates that different parts of the population are differentially involved in the two periods. The first peak is composed mainly of larger multi-sea-winter trout that progress upstream, whereas the second one is composed of a wider range of fish lengths, including a large proportion of small fish. The much lower representation of these small fish in upper sections used by mature fish suggests that they may be non-reproductive trout that overwinter in the lower river. This result is consistent with those of a radio-tracking study conducted in the Grande River where trout tagged later in the season were smaller and remained mostly in the lower reaches of the river (Casalinuovo, 2014). The negative relationship between the time of river entry and fish length or sea age has been reported before for *S. trutta* (Jonsson & Gravem, 1985) and *S. salar* (Jonsson *et al.*, 1990; Trepanier *et al.*, 1996; Jokikokko *et al.*, 2004; Quinn *et al.*, 2006; Borgstrøm *et al.*, 2010) elsewhere. Jonsson *et al.* (1990) found that one-sea-winter *S. salar* in the Imsa River returned later in the season than multi-sea-winter *S. salar*.

The abundance of trout in the lower section of the river was strongly dominated by the tidal cycle, an effect that, projected upstream, was detected in catches as far as 60 km upstream from the river mouth and 45 km above the limit of tidal energy penetration, with an expected increase in lag time. Since we controlled for the lunar cycle in the modelling exercise, which proved a non-significant effect on catches as observed in Kuparinen *et al.* (2009), we are very confident that the tidal effect is unrelated to changes in catchability but it is an actual effect on trout abundance. The association between migration timing and tides has received some attention in the past. Erkinaro *et al.* (1999) found that river entry of Atlantic salmon in the Tana River was more intense during high and ebbing tides. Smith and Smith (1997) found that river entry of Atlantic salmon in the Aberdeenshire Dee, Scotland, tended to occur during ebb tide. However, influences of tidal cycles on fish migration and movement were usually analysed either through the lunar cycle (Jellyman & Lambert, 2003) or considering only the diel cycle (Smith & Smith, 1997; Bourque *et al.*, 1999; Erkinaro *et al.*, 1999; Karppinen *et al.*, 2004) or the 15-day, spring-neap, cycle (Brenner & Krumme, 2007) without taking into account the full complexity of tidal cycles. In the Grande River, the auto-correlation of the 29-days cycle was found to be much stronger than the 15-days cycle (Figure 4, upper panel) due to the occurrence of high-neap and low-spring tides every other neap-spring cycle. River entry may be stimulated by extreme high spring tides and restricted by extreme low neap tides rather than by the regular spring and neap tides. To our knowledge, only one study in the literature had proposed that the seasonal tide cycle affects homeward migration in salmonids; Hayes (1953) observed that peaks in the tidal cycles representing increasing daily differences between high and low tides seemed to be effective in concentrating Atlantic salmon in the estuary and initiating a run into the LaHave River.

The specific mechanism by which increasing tidal amplitude may stimulate river entry in salmonids is unknown. The most straightforward conceivable mechanism would be tidal transport (Gibson, 2003) of fish concentrating in the estuary and coastal areas to upstream areas, producing pulses that mirror the strength of the tides. Stasko (1975) found that migrating Atlantic salmon in the Miramichi River estuary achieved overall upstream progress by drifting with flood tidal currents and by stemming the ebb currents. Bourque *et al*. (1999) using hydrodynamic and salmon migration models found that tidal currents directly affect return timing. But tides also affect the strength of the freshwater signal into the estuary and adjacent coastal areas. It is widely accepted that salmon and trout use their olfactory system to recognise their natal stream during the coastal phase of the spawning migration (Hasler, 1966; Døving *et al.*, 1985; Dittman & Quinn, 1996; Ueda *et al.*, 2007), and several studies have associated climatic, marine and fluvial conditions that increase the freshet (i.e., onshore winds, high tide, and increased flow) with an increase of salmonids concentration in river estuaries (Hayes, 1953; Banks, 1969; Smith & Smith, 1997; Erkinaro *et al.*, 1999). The large tidal amplitude characteristic of the Grande River estuary is likely to project a large tidal prism of freshwater into marine coastal areas, intercepting homeward migrating sea trout and acting as a gulping mechanism drawing them into the estuary. This increase in odor recognition combined with an increased tidal transport, both modulated by the seasonal tidal cycle, could produce the observed pulses in the Grande River sea trout run, where we found that tides are the dominant factor affecting trout abundance in the lowest section closest to the estuary.

Trout catches in the middle and upper section of the river, on the other hand, increase with water temperature and decrease with river discharge, which can operate through their influence on in-river migration rate and abundance (Trepanier *et al.*, 1996; Quinn *et al.*, 1997; Erkinaro *et al*., 1999; Forsythe *et al*., 2012; Jonsson *et al*., 2018), but also through changes in catchability (Clarke *et al.*, 1991; Aprahamian & Ball, 1995; L'Abée-Lund & Aspås, 1999). Low temperature is expected to lower metabolism, fish activity and, therefore, catchability (Jonsson & Jonsson, 2011), whereas high discharge in rivers typically affects the access of fishermen and their catching efficiency.

The Grande River sea trout fishery, with its detailed and spatially explicit catch record, simplified population and habitat structure, and strong tides, provides a unique setting for studying salmonid migration and fishery interactions at the ocean-freshwater interphase. We expect that the conceptual model of upstream migration of sea trout developed in this paper will provide valuable information to support fish conservation and management.

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CONTRIBUTIONS

Ideas: M.A.P. and M.M.A.S.

Data generation: A.C.G., M.A.C. and M.M.A.S.

Data analysis: A.C.G., M.I.G.A. and M.A.P.

Funding: M.A.P.

Manuscript preparation: A.C.G., M.I.G.A., M.A.C., B.P.K. and M.A.P.

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FIGURE CAPTIONS

Figure 1. Grande River in Tierra del Fuego in Southern Patagonia. The black lines delimit the sampling sections of sea trout catches, four river sections of 13 km long each: **Section A** from river kilometre (RK) 25 to 38; **section B**, from RK 38 to 51; **section C**, from RK 51 to 64 and; **section D**, from RK 64 to 77. The black point labelled as **HS** is the localisation of the hydrometric station at the RK 130. The white pentagons are the localisation of the four most important fishing lodges; María Behety (**MB1 and MB2**), Toon Ken (**TK**), Villa María (**VM**) and Kau Tapen (**KT**).

Figure 2. Neap-spring tidal cycle (solid line) at the mouth of the Grande River on the Atlantic Coast of Tierra del Fuego. Lunar cycle (dashed line) and lunar phases (white circle = full moon; black circle = new moon).

Figure 3. River discharge (dashed line) and freshwater temperature (solid line) at the Grande River during the 2008 fishing season; Jan 1-Apr 13.

Figure 4. Cyclicity of tidal amplitude at Grande River mouth. Upper panel: ACF, autocorrelation function, data from 2007 to 2011. Lower panel: Daily amplitude during 2008 and the 2008 fishing season (inside the rectangle).

Figure 5: Cross-correlograms between daily catches and daily tidal amplitude in each section of Grande River at lags from zero to 40 days, during the 2008 fishing season. a: section A, from river kilometre (RK) 25 to 38; b: section B, from RK 38 to 51; c: section C, from RK 51 to 64; and d: section D, from RK 64 to 77 from the river mouth in upstream wise (see Figure 1).

Figure 6: Generalized additive model output of environmental predictors showing their relationship with *Salmo trutta* daily catches during the 2008 fishing season in different

sections of the Grande River as depicted in Figure 1. Predictive variables are date (Day Number), tidal amplitude with 7 (section A), 13 (section B), 23 (section C) and 36 (section D) days lag (Tidal Amplitude), percentage of moon illuminated (Moon), freshwater temperature (Temperature), and river discharge (Discharge). Plots of significant variables correspond to best models (p-value<0.0001, ***; 0.001<p-value<0.01, **; 0.01<p-value<0.05,*) and plots of non-significant variables correspond to full models. Shaded areas are the 95% confidence limits. For more details see Table 2.

Figure 7: Length frequency in *Salmo trutta* catches by fortnight and river sections (as in Figure 1) in Grande River in 2008, from January 6 to April 12.

Figure 8: Weight frequency in *Salmo trutta* catches by fortnight and river sections (as in Figure 1) in Grande River in 2008, from January 6 to April 12.

Table 1. Total, daily average and daily range (minimum and maximum record for a single day) of sea trout (*Salmo trutta*) catches by section of Grande River. Kilometre of river (KR) is the beginning and the end of each river section from the estuary mouth upstream wise.

Section	KR	total catches	daily average	daily range
A	25 – 38	2,731	26.7	0 – 65
B	38 – 51	1,144	11.2	0 – 37
C	51 – 64	463	4.5	0 – 19
D	64 – 77	332	3.2	0 – 11
Total		5,029	49.3	1 – 122

Table 2: Summary of full and best Generalized Additive Models (GAMs) for *Salmo trutta* catches in each section of Grande River (section A, from river kilometre (RK) 25 to 38; section B, from RK 38 to 51; C: section C, from RK 51 to 64; and section D, from RK 64 to 77 from the river mouth in upstream wise, see Figure 1). Predictive variables are: date (Day Number), tidal amplitude with 7 (section A), 13 (section B), 23 (section C) and 36 (section D) days lag (amplitude_lag), percentage of moon illuminated (moon), freshwater temperature (temperature), and river discharge (discharge). Effective degrees of freedom (e.d.f.). Percentage of deviance explained (% dev.exp.). P-value significance: p-value<0.0001, ***; 0.001< p-value<0.01, **; 0.01<p-value<0.05, *.

River section	Predictive variable	Full model			Best model		
		% dev.exp.	e.d.f.	p-value	% dev.exp.	e.d.f.	p-value
Section A	Day Number	54.5	3.6	0.010*	52.4	5.5	<0.001***
	amplitude7lag		1	0.006**		1	0.005**
	Moon		1	0.072			
	temperature		1	0.347			
	discharge		2.6	0.152			
Section B	Day Number	28.4	2.1	0.745	27		
	amplitude13lag		1	0.027*		1	0.014*
	Moon		1	0.711			
	temperature		2.0	0.073		2.2	<0.001***
	discharge		3.3	0.046*		3.5	0.019*
Section C	Day Number	53.7	2.0	0.069	43.1		
	amplitude23lag		1	<0.001***		1	0.005**
	Moon		1	0.010**		1	0.033*
	temperature		1	0.007**		1	<0.001***
	discharge		4.1	<0.001***		4.2	<0.001***
Section D	Day Number	27.2	2.5	0.057	24.5	2.5	0.023*
	amplitude36lag		1.7	0.556			
	Moon		1	0.557			
	temperature		1.3	0.022*		1	0.003**
	discharge		1	0.020*		1	0.030*

Figure 1

Click here to access/download;Figure;Figure_1.png

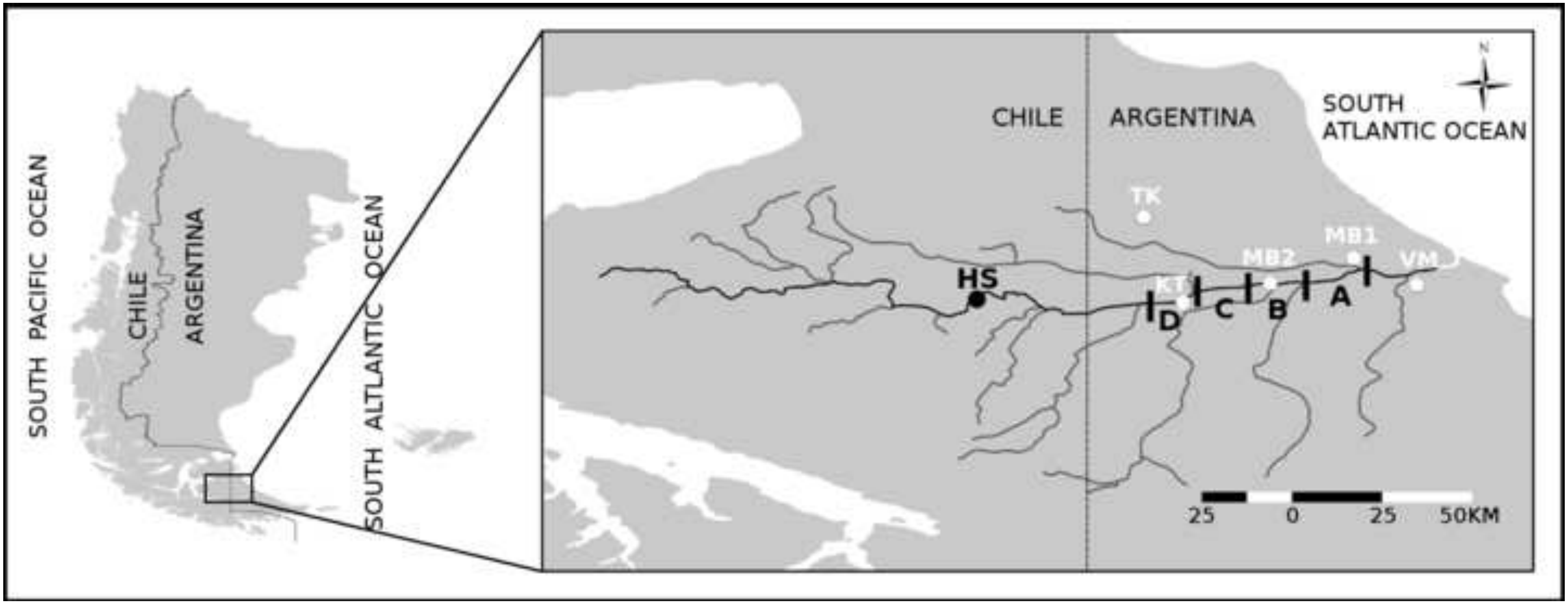
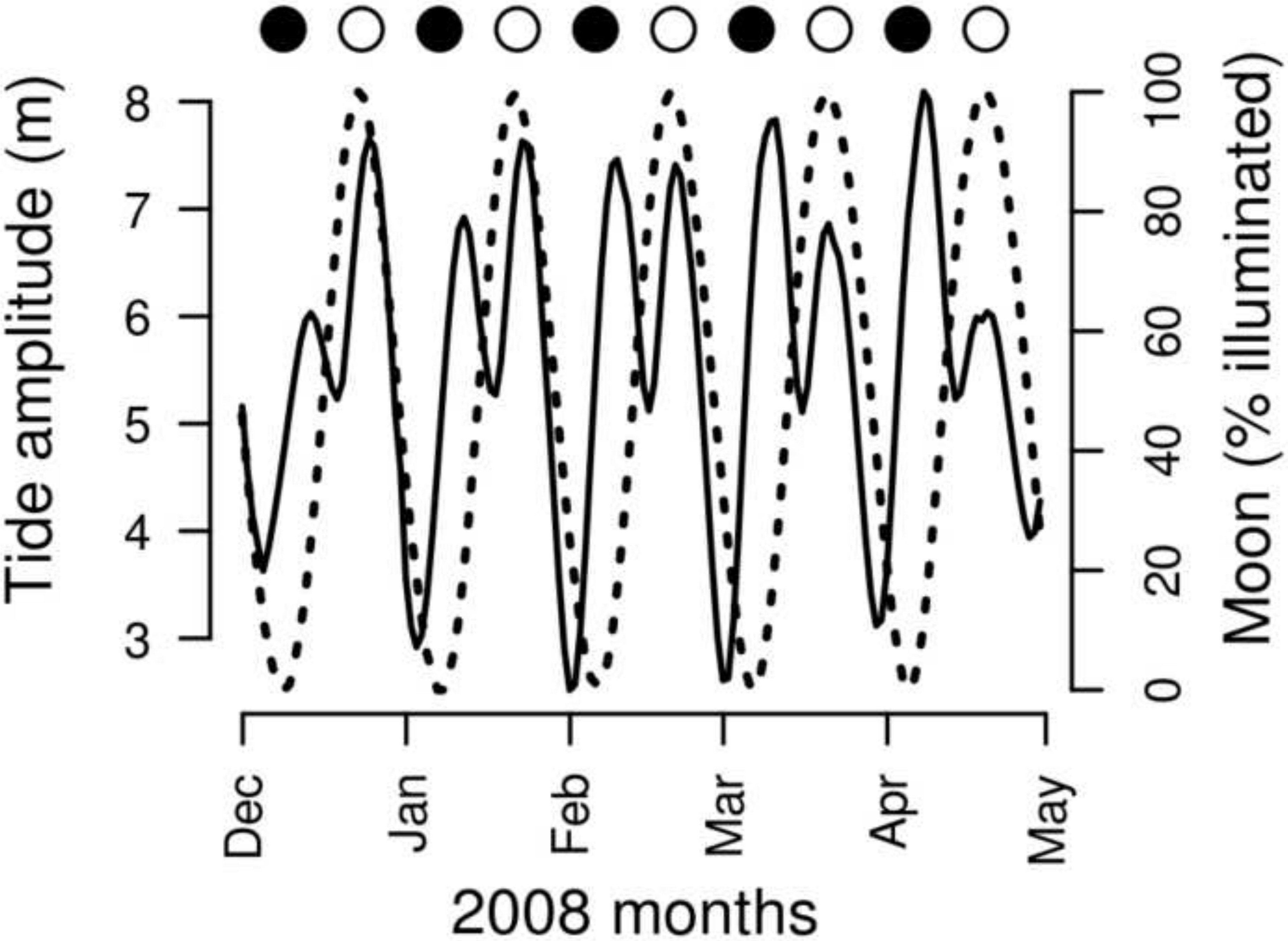


Figure 2

Click here to access/download;Figure;Figure_2.png



Click here to access/download;Figure;Figure_3.png

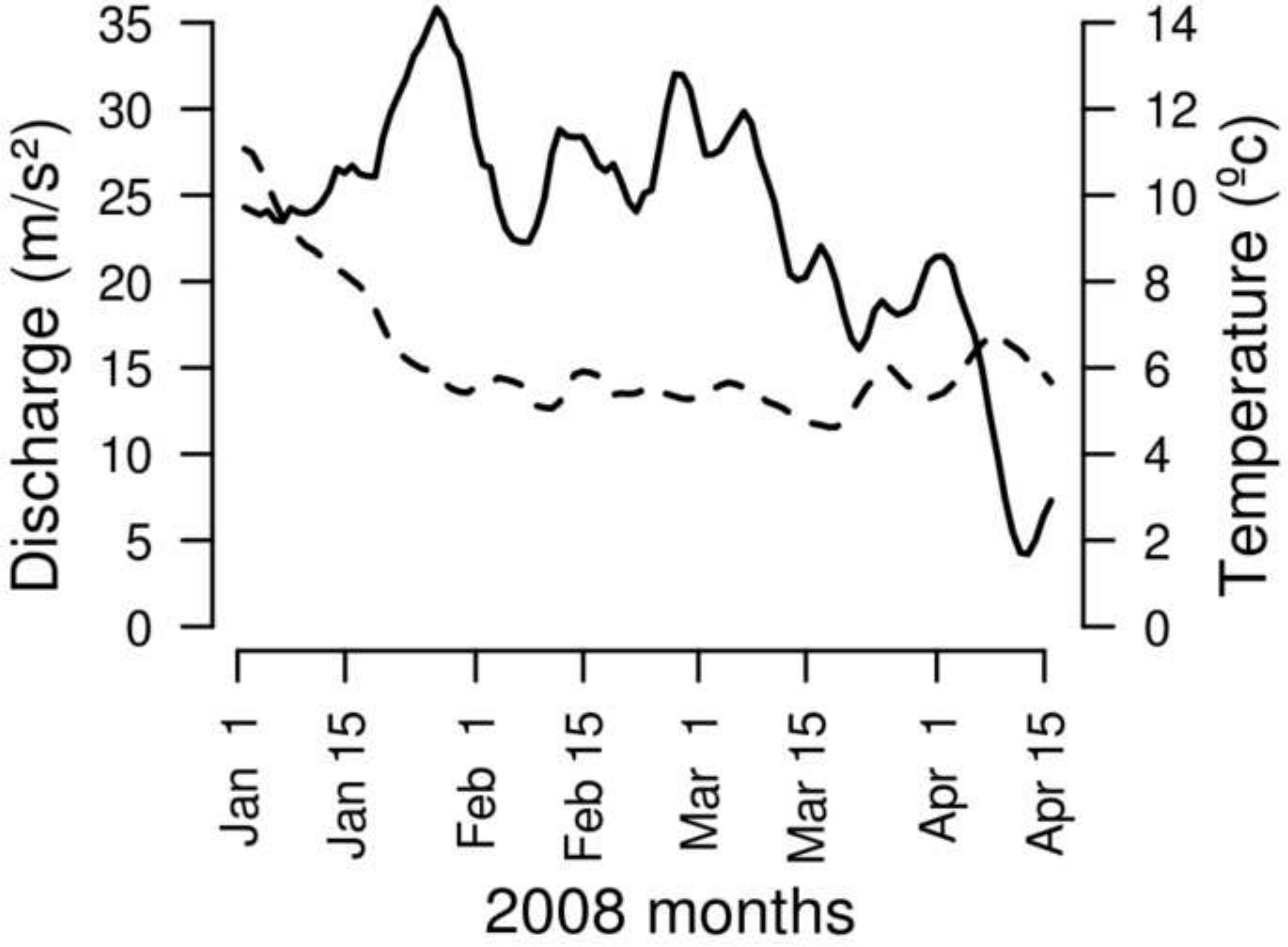


Figure 4

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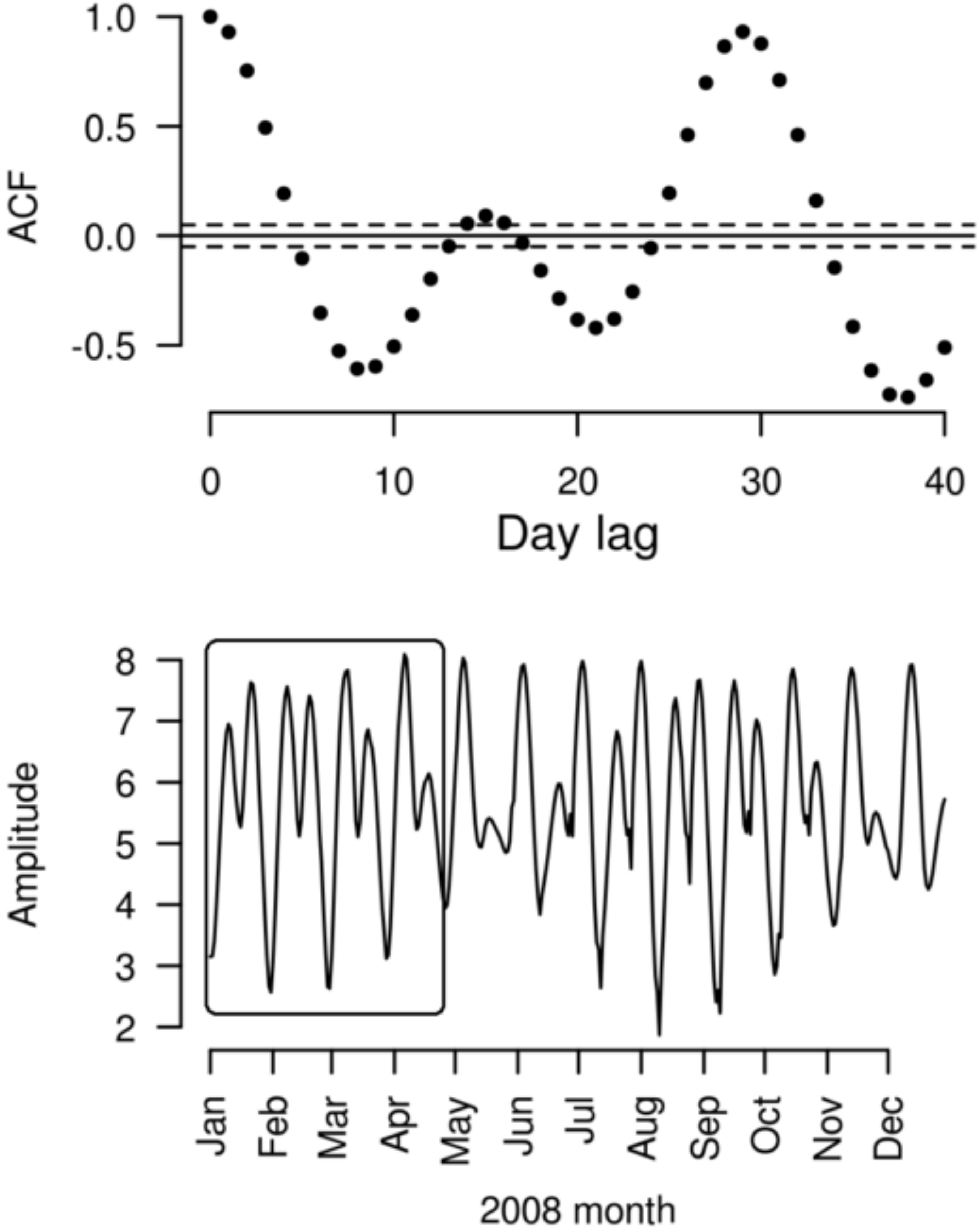
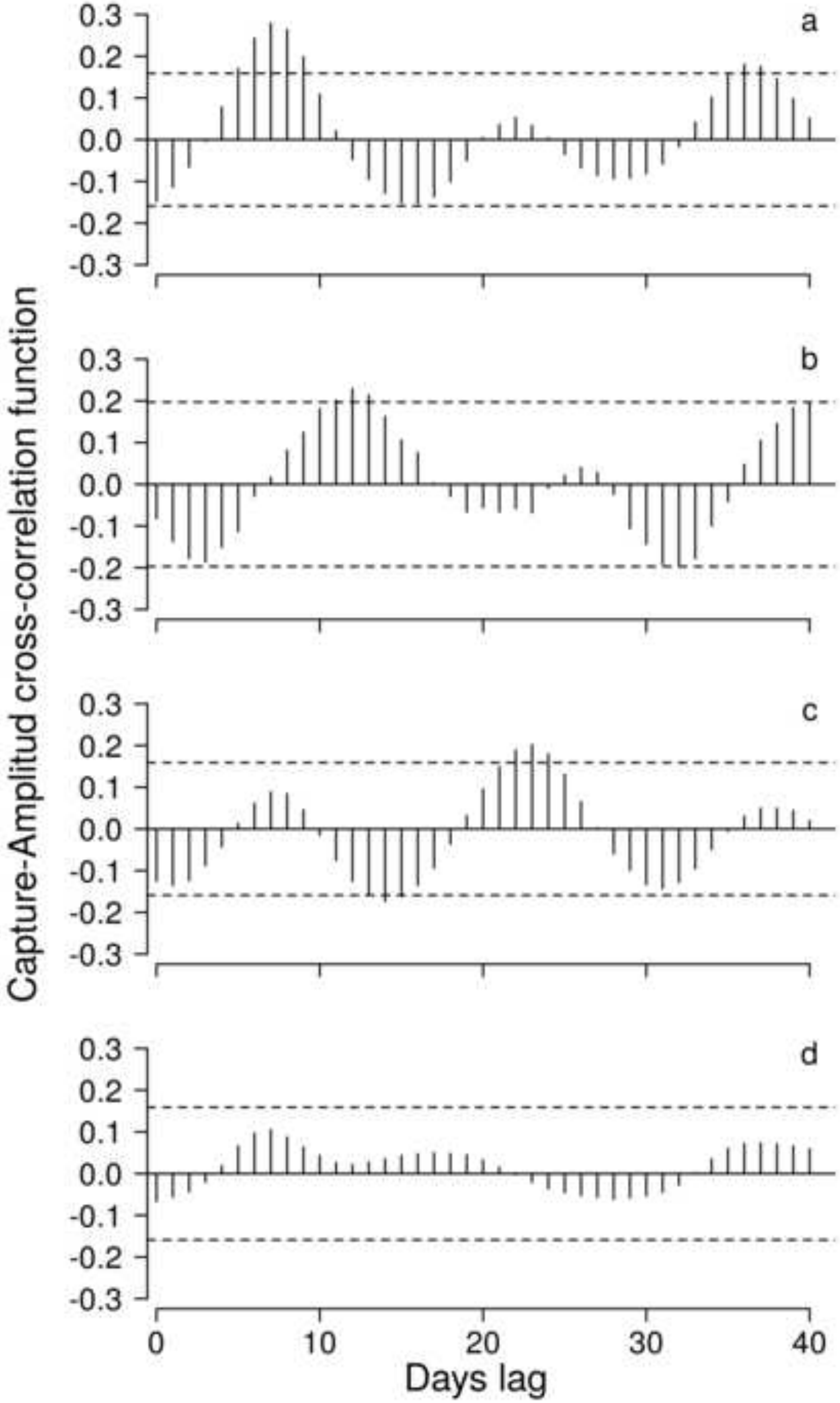



a
b
c
d
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0
10
20
30
40
Capture-Amplitud cross-correlation function
Days lag

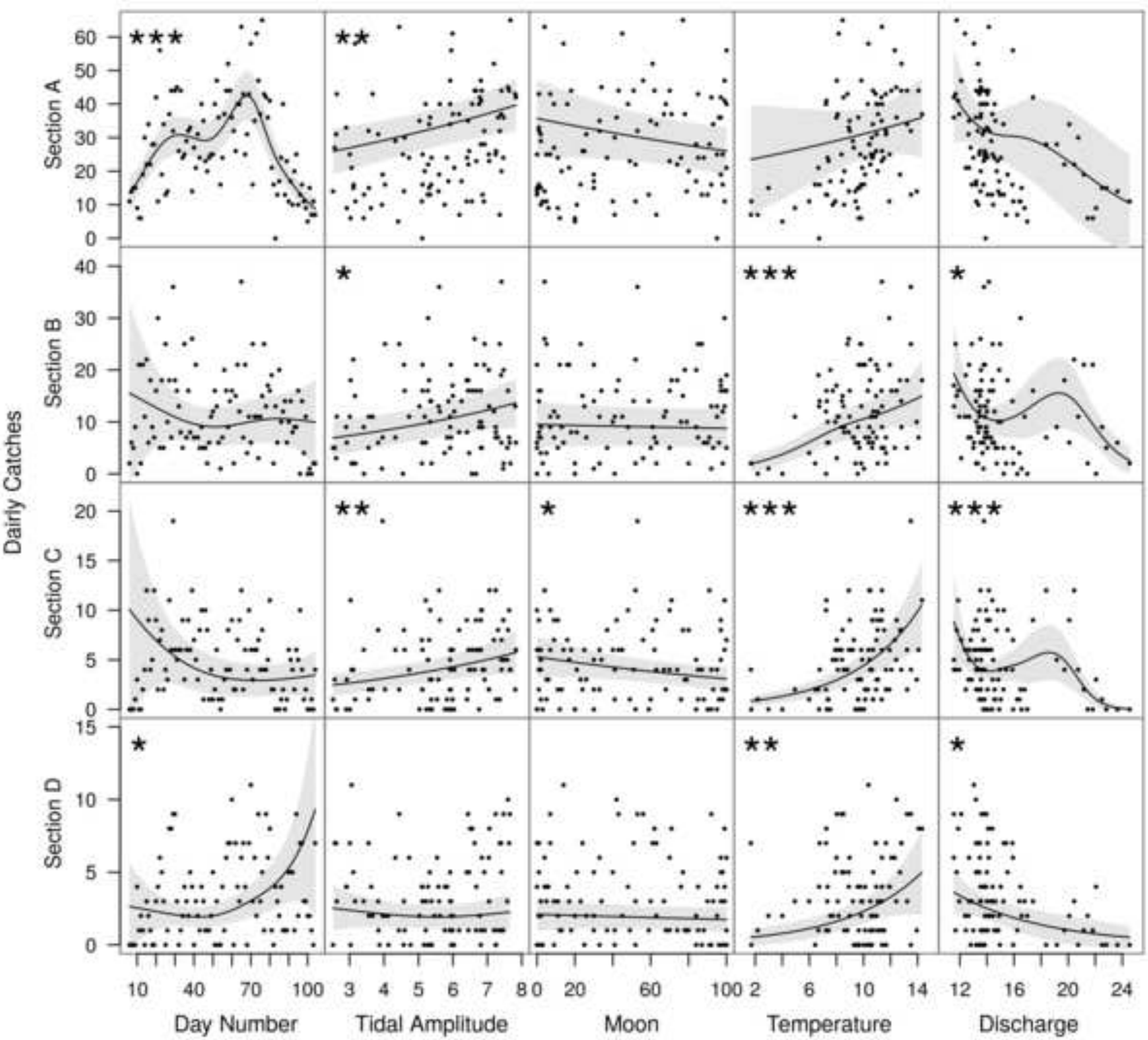
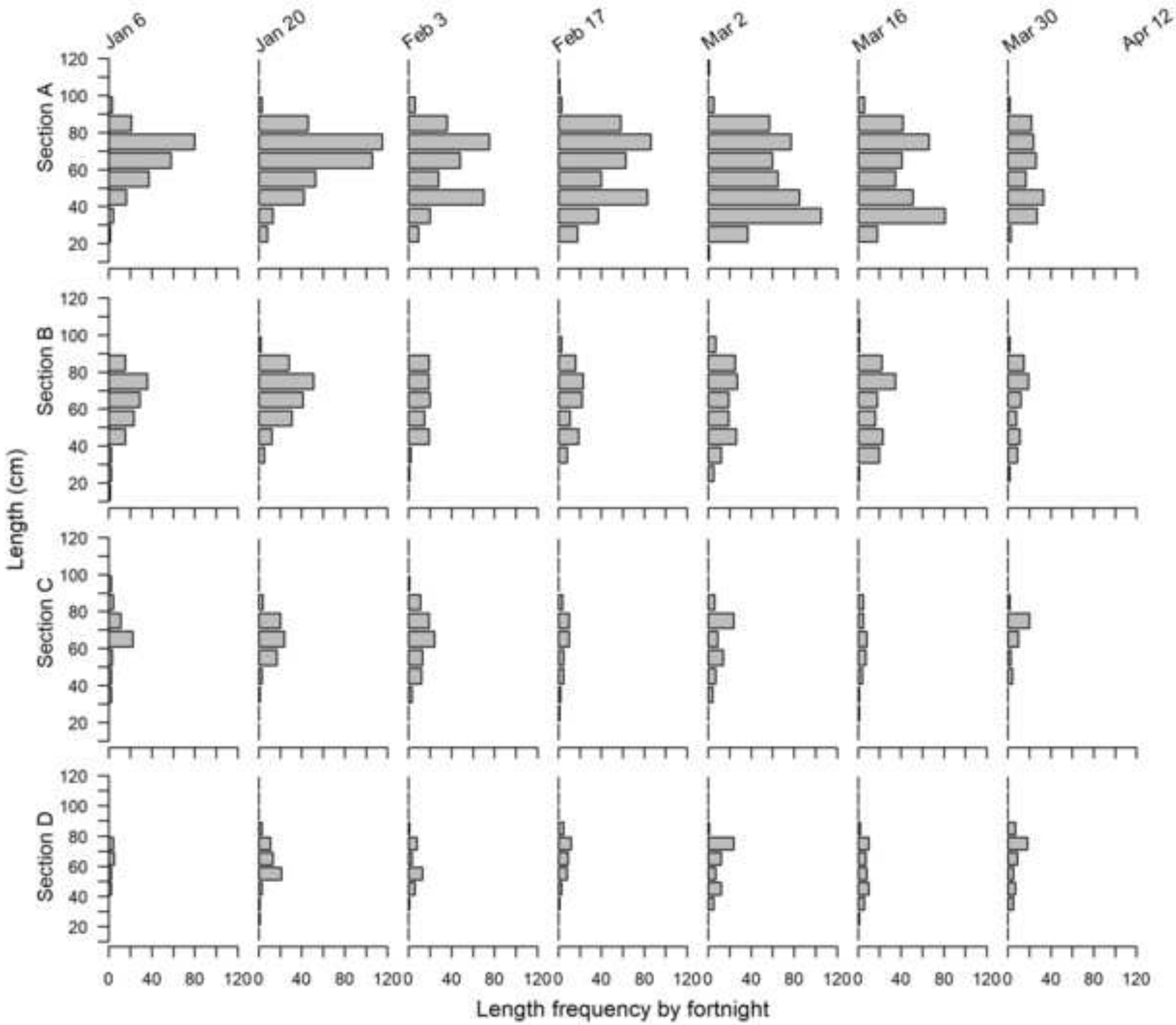

Dairly Catches
Section A
Section B
Section C
Section D
60
50
40
30
20
10
0
40
30
20
10
0
20
15
10
5
0
15
10
5
0
***
**
*
***
*
**
*
***
***
*
**
*
10
40
70
100
3
4
5
6
7
8
0
20
60
100
2
6
10
14
12
16
20
24
Day Number
Tidal Amplitude
Moon
Temperature
Discharge

Figure 7

Click here to access/download;Figure;Figure_7.png



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