

Rain-driven changes in fish dynamics: a switch from spatial to temporal segregation

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ABSTRACT: Niche segregation models underpin our understanding of speciation, population dynamics, and the evolution of foraging strategies. Many studies have evaluated changes in niche segregation dynamics over seasonal and decadal scales, but the influence of short-term stochastic processes like weather are poorly understood. This represents a problem for predicting ecosystem-level responses to the changes in weather patterns that are anticipated to occur over the coming decades. By simultaneously monitoring spatial and temporal segregation in a large estuarine piscivore and smaller benthic carnivore (mulloway *Argyrosomus japonicus* and sand whiting *Sillago ciliata*, respectively) before and after rainfall, we tested for disturbance-driven changes in species segregation. During non-rain conditions, both species were diurnally active but spatially segregated in the vertical plane (i.e. water depth). After rainfall, mulloway encroached on the whiting's vertical habitat and reversed their activity rhythm, while whiting did the opposite, strengthening their diel activity rhythm. Long-term fishery catch data were broadly consistent with this pattern, with rain-associated increases in mulloway catchability contrasting a decrease in catchability of whiting. Our example suggests short-term stochastic disturbances can drive drastic changes in fish dynamics, and highlights the significance of future changes to rainfall regimes in structuring ecosystem processes.

KEY WORDS: Accelerometer · Acoustic telemetry · Anti-predator behaviour · Biologging · Circadian rhythm · Context-dependent · CPUE · Interaction · Plasticity · Risk-allocation hypothesis

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INTRODUCTION

Central to identifying mechanisms that mediate predation pressure and facilitate coexistence among competitors, predators and prey are models of niche segregation, i.e. the differential selection of resources through space or time (Schoener 1974b, Lima & Bednekoff 1999, Kronfeld-Schor & Dayan 2003). Niche segregation dynamics that occur over seasons or years have received a great deal of attention in

ecology, but far less studied are the dynamics that occur over shorter temporal scales (i.e. hours or days), particularly with respect to stochastic disturbances such as weather (Lopez-Darias et al. 2012). A poor mechanistic understanding of animal responses to these disturbances hinders the prediction of ecosystem-level responses to the changes in weather that are expected in the coming decades (Allan & Soden 2008). Indeed, longer-term studies suggest that weather can induce major structural changes in

predator–prey dynamics, such as those between lizards and spiders (Spiller & Schoener 1995), predatory and non-predatory birds (Caldwell 1986, Sofaer et al. 2013), and carnivorous and grazing mammals (Owen-Smith et al. 2005, Letnic et al. 2009, Sinclair et al. 2013).

Resource partitioning through space is considered more common than that which occurs through time (at least with respect to competitors; Schoener 1974a, 1986, Kronfeld-Schor et al. 2001). This is intuitive for animals competing for similar resources because endogenous entrainment to environmental cues (i.e. circadian rhythms) allow organisms to exploit favorable conditions (Sharma 2003, Yerushalmi & Green 2009). If 2 animals are competing for the same resources, they should synchronize to the same fluctuations in exogenous factors (Schoener 1974a). Since endogenous circadian rhythms are thought to confer adaptive advantages (Sharma 2003, Woelfle et al. 2004, Yerushalmi & Green 2009), intraspecific reversals of activity (behavioural) rhythms should be relatively uncommon, and indicative of strong selective pressures. The few examples of such plasticity that do occur appear to be driven by a range of pressures, including changes in temperature or nutritional status in fish (Fraser et al. 1993, Metcalfe et al. 1998, Metcalfe & Steele 2001), social structure in insects (Bloch & Robinson 2001), and competitive interactions in mammals (Kronfeld-Schor et al. 2001). Rarely documented, however, are departures from regular activity rhythms that are driven by factors such as weather (but see Payne et al. 2013), even though these can cause dramatic changes to a range of biotic and abiotic ecosystem processes. If activity rhythms are indeed adaptive, their plasticity should confer significant advantages with respect to unpredictable exogenous fluctuations, but studies examining changes in niche dynamics in this context are scarce. This is not surprising, since identifying such changes requires the collection of high-resolution data in time and space simultaneously (because niche segregation occurs on both axes), which are difficult to collect for most free-ranging animals, particularly those in aquatic habitats (Barnett et al. 2010, Barnett & Semmens 2012).

In this study, we simultaneously compared the spatial and temporal segregation of 2 fish species before and after rainfall. A recent study documented consistent switches in activity rhythms of an estuarine fish after rain (Payne et al. 2013), so we examined segregation dynamics in an estuarine piscivore (mulloway *Argyrosomus japonicus*) and benthic carnivore (sand whiting *Sillago ciliata*). Specifically, we used accelerometer transmitters (Murchie et al. 2011,

Payne et al. 2011b, 2014) to test the prediction that rainfall would induce a shift in the way these animals use space, allocate activity, or both. Body activity has been shown to correlate with set-net catchability (Gannon et al. 2014), so we also examined archival set-net catch data to test for longer-term responses to rainfall frequency in these 2 species. The response of commercial catch rates to rainfall varies markedly between estuarine species (e.g. decreasing with rainfall for whiting, but increasing for other species; Gillson et al. 2009), so the comparison of our biologging data to catch data for mulloway and whiting was aimed at exploring the role of behaviour in determining fisheries trends.

MATERIALS AND METHODS

Fieldwork

Mulloway represent the largest (up to 1.8 m; Taylor et al. 2006b) predatory fish species inhabiting estuaries in southeastern Australia. They exhibit a generalist-piscivore diet dominated by forage fish and, to a lesser extent, prawns and cephalopods (Taylor et al. 2006a). The smaller-bodied (length at maturity ~24 cm; Burchmore et al. 1988) whiting are benthic carnivores, with diets dominated by polychaete worms and bivalve molluscs (Hadwen et al. 2007). The lack of dietary overlap between the 2 species suggests they are unlikely to exhibit competition for food resources. Whiting are considered a very successful bait type for mulloway among fishers in New South Wales (N. L. Payne pers. obs.), so while we could find no evidence for predation of whiting by mulloway in the published literature, it is possible that mulloway represent a predatory threat to co-habiting whiting.

A total of 9 mulloway (540 to 1200 mm total length, average mass 3115 g) and 10 whiting (308 to 382 mm total length, average mass 325 g; see Table A1 in the Appendix for details of individual fish) were captured by hook and line throughout the Clyde River estuary (35.704° S, 150.179° E; Fig. 1) from October 2012 to May 2013. Fish were implanted with acoustic accelerometers containing a tri-axial acceleration and depth sensor (VemcoTM), after Walsh et al. (2012). Briefly, fish were individually anaesthetised via immersion in water containing 50 mg l⁻¹ Aqui-S (Aqui-S Ltd.; concentrations were determined for the study species) immediately post-capture, and transmitters were inserted into the body cavity via a 15 to 20 mm ventral incision, which was made with a surgical scalpel and sealed with surgical sutures. To aid in re-

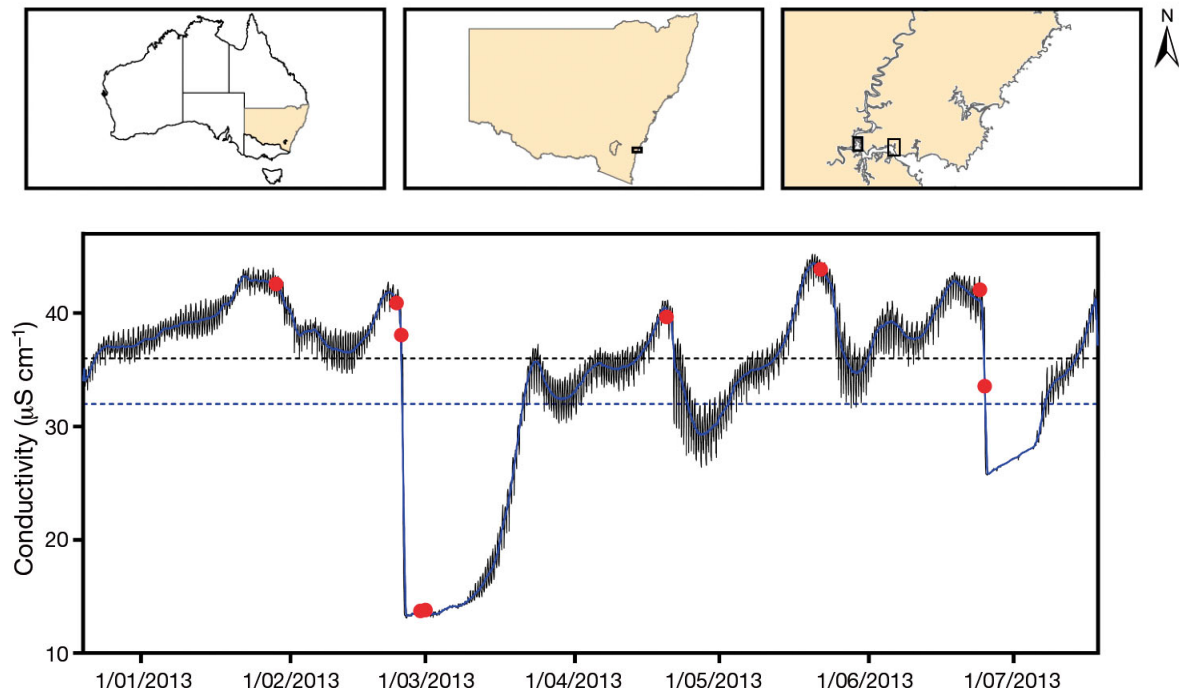


Fig. 1. Top panels: study site and location of acoustic arrays in the Clyde River, New South Wales. Bottom panel: changes in conductivity at the upstream acoustic array throughout the monitoring period. Solid black line: raw values in which the tidal cycle is evident; solid blue line: smoothed dataset used in linear modeling. Horizontal dashed lines indicate the threshold values (blue = $32 \mu\text{S cm}^{-1}$; black = $36 \mu\text{S cm}^{-1}$) used to group data for display in Fig. 2. Red dots: rain events $>20 \text{ mm}$

covery from surgery, each fish was injected with an antibiotic (oxytetracycline) at 75 mg kg^{-1} fish mass, and gills were continually irrigated with fresh estuary water throughout the surgical procedure. Fish recovered from the anaesthetic in 50 l holding tubs, and were returned to their site of capture as soon as they resumed normal swimming and buoyancy-regulating behaviour. Sedation and recovery periods varied among individuals, but were typically around 10 min, such that most fish were out of their natural habitat for 20 to 25 min in total. Accelerometer transmitters had delays of 2 min, a sampling window of 20 s and an estimated battery life of 240 (mulloway) and 220 d (whiting). Due to their smaller body size, all whiting were implanted with V9AP transmitters (mass 6 g), whereas all mulloway were implanted with V13APs (13 g; www.vemco.com), such that transmitters represented $<2\%$ body mass for all fish.

Tagged fish were monitored by 2 separate arrays of Vemco acoustic receivers: an 'upstream' and 'downstream' array approximately 7 km apart, comprising 15 and 23 receivers, respectively (Fig. 1) configured to record acceleration and depth data from October 2012 to August 2013. Maximum water depth within these 2 areas was generally $<10 \text{ m}$, with some deeper areas (10 to 15 m), particularly where the upstream

array was located. All whiting were captured and tagged within the upstream array, whereas mulloway were captured throughout the estuary. Receivers were spaced 200 to 400 m apart within each array (the nominal range for these transmitters; Payne et al. 2010, 2011a), and all data were retrieved from the receivers in August 2013. An Odyssey data logger (Dataflow Systems) was deployed near the centre of the upstream array (approximately mid-water), which recorded conductivity and temperature every hour for later analysis. The accuracy of this logger was checked by comparing values to those obtained from 6 other loggers deployed throughout the estuary during the study.

Data analyses

A series of linear mixed models were used to examine the influence of time of day (day or night, which was determined from the timing of local sunrise and sunset; www.ga.gov.au/geodesy/astro/sunrise.jsp) and conductivity (as a proxy of rainfall; these data were smoothed with a 24 h running mean to remove the influence of tidal fluctuations; see Fig. 1) on the activity (m s^{-2}) and depth (m) patterns of mulloway and

whiting. All activity or depth data from all individuals were included in our models, with fish ID included as a random effect and time of day and conductivity as fixed factors; results were considered significant at $p < 0.05$. For activity, data collected from both arrays were included in the models, whereas we only included depth data that were collected in the upstream array to control for vertical habitat effects (the range of depths available in the upstream array was not the same as that of the downstream array). We were interested in whether diel activity and depth patterns varied with rainfall, so included the interaction between time of day and conductivity in both models. Activity and depth data were filtered from multiple detections (where multiple receivers recorded the same acoustic transmission) prior to model fitting. Linear models were run on data spanning a period of approximately 8 mo (mid-December 2012 to early August 2014).

Commercial catch data

Set-nets are a passive gear that are held in a fixed position for several hours and rely on fish actively swimming into the nets for capture (see Gray 2002 for details of operation in NSW). As such, an increase in fish swimming activity should positively correlate with an increase in set-net catch per unit effort (CPUE), as was shown for dusky flathead *Platycephalus fuscus* (Gannon et al. 2014). We examined archival mullo-way CPUE from the Clarence River commercial set-net fishery (data were obtained from the NSW Department of Primary Industries Commercial Catch Statistics Database), and compared those data to that of whiting in the same river from Gillson et al. (2009). We also compiled mullo-way data over a similar period as Gillson et al.'s whiting (1998 to 2007), and compared these to estimates of freshwater discharge collected in the upper Clarence River (29.567° S, 152.668° E). To remove seasonal effects, we restricted data to summer/autumn periods (Dec to May), which facilitated robust comparisons with our transmitter data (which were mainly collected over summer and autumn) and the whiting CPUE data (which were reported for autumn; Gillson et al. 2009). In summer/autumn of 2001, a severe flood event in the Clarence River led to low dissolved oxygen levels and a major fish kill in that river (Walsh et al. 2001). This was the only such event that occurred throughout the period of our CPUE data, so we excluded data from that year from our analyses. We calculated mean mullo-way CPUE (kg d^{-1}) and freshwater flow (megalitres, MI

d^{-1}) for summer and autumn in each year, and \log_{10} transformed those data to normalise variances, and to be consistent with the whiting data from Gillson et al. (2009). We then compared mullo-way CPUE and flow data using linear regression.

RESULTS

A total of 77966 and 140344 activity/depth data records were analysed from 9 mullo-way and 5 whiting, respectively (Table A1 in the Appendix). Accelerometer readings from 5 of the 10 whiting originally captured consisted of less than 5 d of data, so were excluded from analysis. The depth sensor on 1 mullo-way (V13AP) was faulty (i.e. consistently produced negative depth values) so these data were also excluded from analysis. Nine rain events (of at least 20 mm rainfall in a 24 h period) that were associated with a significant reduction of estuarine conductivity occurred during our monitoring period (Fig. 1; rain events recorded at Nelligen; www.bom.gov.au/climate).

For transmitter data, the day/night \times conductivity interaction was significant for both activity and depth in both species (Table 1). To graphically explore these interactions, we plotted mean (pooled across all indi-

Table 1. Linear mixed-effects models of mullo-way *Argyrosomus japonicus* and whiting *Sillago ciliata* activity and depth explained by time of day (day/night) and estuarine conductivity ($\mu\text{S cm}^{-1}$). Data were collected via accelerometer transmitters over a period of approximately 8 mo

	β	SE	t	p
Mullo-way activity				
Intercept	0.073	0.025	2.94	0.005
Day/night	-0.185	0.011	-16.26	<0.0001
Conductivity	-0.015	0.001	-28.46	<0.0001
Day/night \times Conductivity	0.008	0.000	22.63	<0.0001
Mullo-way depth				
Intercept	-1.816	3.964	-0.46	0.658
Day/night	9.087	0.448	20.27	<0.0001
Conductivity	0.388	0.022	17.69	<0.0001
Day/night \times Conductivity	-0.295	0.013	-22.72	<0.0001
Whiting activity				
Intercept	-0.818	0.202	-4.05	0.007
Day/night	0.206	0.008	25.66	<0.0001
Conductivity	0.005	0.000	13.33	<0.0001
Day/night \times Conductivity	-0.003	0.000	-13.84	<0.0001
Whiting depth				
Intercept	2.360	0.352	6.72	0.001
Day/night	0.512	0.084	6.10	<0.0001
Conductivity	0.046	0.004	12.31	<0.0001
Day/night \times Conductivity	-0.015	0.002	-6.55	<0.0001

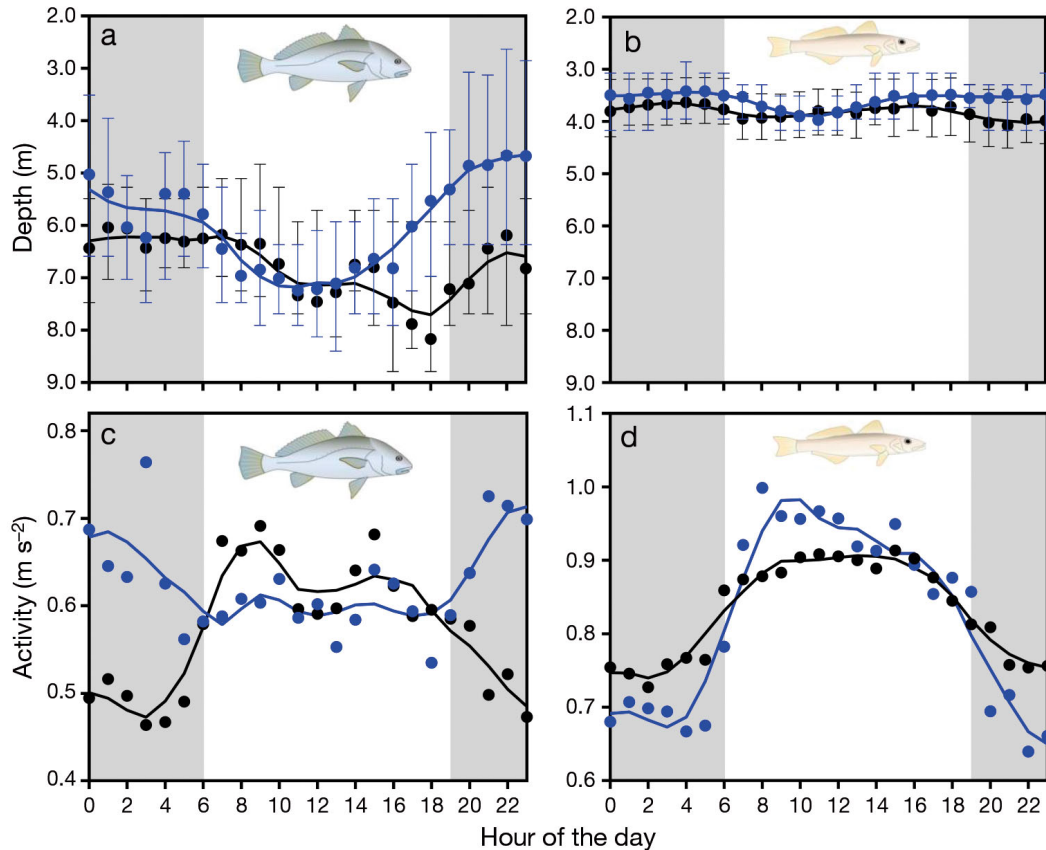


Fig. 2. Mean water depth and body activity for (a,c) mulloway *Argyrosomus japonicus* and (b,d) sand whiting *Sillago ciliata* implanted with accelerometer transmitters. Data are stratified into non-rain periods (i.e. estuarine conductivity $>36 \mu\text{S cm}^{-1}$; black data) and rain periods (conductivity $<32 \mu\text{S cm}^{-1}$; blue data). See Fig. 1 for changes in conductivity throughout the monitoring period. Data were pooled across all individuals ($n = 9$ mulloway and 5 whiting). Grey shading: nighttime. Error bars representing first and third quartiles for depth are shown in (a) and (b) to indicate the degree of overlap in vertical distribution of the 2 species

viduals) depth and activity values for each species during each hour of the day when estuarine conductivity was low ($<32 \mu\text{S cm}^{-1}$ representing rain-affected periods), and high ($>36 \mu\text{S cm}^{-1}$ representing non-rain periods) throughout the entire 8 mo monitoring period. These thresholds (32 and $36 \mu\text{S cm}^{-1}$) were chosen on the basis of trends in conductivity observed during and after rain events (Fig. 1). During normal (non-rain) conditions, mulloway used deeper water than whiting, particularly in the evening (Fig. 2 a,b; black data), and both species were more active during the day than at night (Fig. 2 c,d; black data). During rain-affected periods, mulloway reversed their diel depth and activity patterns, encroaching on shallower depths during the night than during normal conditions (Fig. 2a; blue data), and simultaneously becoming strongly nocturnal (Fig. 2c; blue data). In contrast, rain was associated with a strengthening of activity pattern for whiting, which became more active during the day and less active at

night than during normal conditions (Fig. 2d; blue data). Whiting also inhabited shallower water during rain-affected periods, particularly during the night (Fig. 2b; blue data). Mulloway consistently inhabited deeper water than whiting during both day and night during normal conditions (black data in Fig. 2a versus b), but encroached on whiting vertical habitat at night during rain-affected periods (blue data in Fig. 2a versus b). To indicate the degree of overlap in vertical distribution of the 2 species, error bars representing the first and third quartiles of depth data are shown in Fig. 2a,b.

The relationship between mulloway CPUE and freshwater discharge in the Clarence River from 1998 to 2007 was variable, but the 2 variables were positively correlated ($p < 0.05$, $R^2 = 0.29$; Fig. 3 top panel). This contrasts with the trend for whiting in the same river and over the same period (Gillson et al. 2009), where CPUE was negatively related to freshwater flow (Fig. 3 bottom panel).

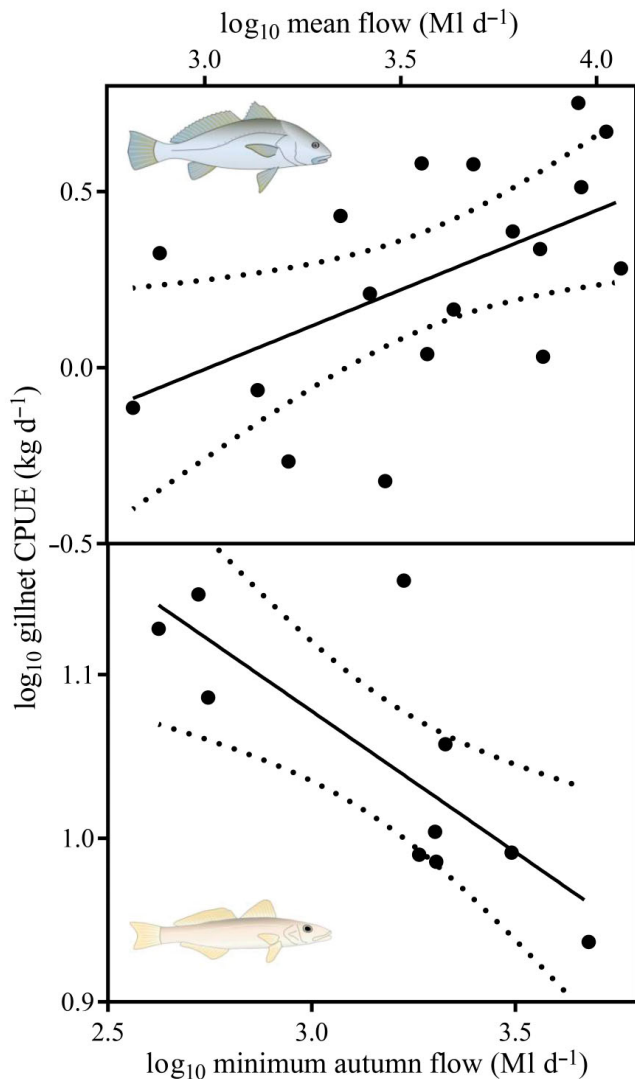


Fig. 3. Influence of freshwater discharge on commercial set-net catch per unit effort (CPUE) for mullet *Argyrosomus japonicus* (top panel) and whiting *Sillago ciliata* (bottom panel). Data for whiting were derived from Gillson et al. (2009), and both regression lines are significant ($p < 0.05$). Dotted lines indicate 95% CI

DISCUSSION

Both species were diurnally active and spatially segregated (in the vertical plane) during normal conditions, with rain preceding an increase in spatial overlap, a switch to nocturnal activity in mullet, and a corresponding decrease in nocturnal activity in whiting. This pattern represents a switch from spatial to temporal segregation, and suggests that rain can lead to dramatic changes in animal behaviour. These changes add to the growing body of evidence that fish can exhibit highly plastic behavioural rhythms

(Metcalf et al. 1999, Sims et al. 2005, Fitzpatrick et al. 2011, Fox & Bellwood 2011, Payne et al. 2013, 2015), but our study is one of the few to identify a link to weather (see Heupel et al. 2003, Sackett et al. 2007). Given predicted future changes in rainfall frequency (Allan & Soden 2008), a better understanding of the consequences of altered niche dynamics associated with weather may be important.

Animals almost always increase refuging or decrease movement when predation risk is high (Lima & Dill 1990, Lima 1998a,b, Kronfeld-Schor & Dayan 2003), and the rain-associated change in whiting behaviour could be a response to the switch toward nocturnal activity in mullet and simultaneous loss of spatial segregation. However, the behavioural responses of both species could be completely independent of one another, and driven by other factors. Rain drives changes in a variety of physico-chemical properties in estuarine systems (e.g. salinity, turbidity and various nutrients), and these changes were likely experienced by both species. It is possible, for example, that a species-specific freshwater-induced energetic burden (i.e. the higher costs of osmoregulation associated with rapid changes in salinity; Dalla Via et al. 1998, Sangiao-Alvarellos et al. 2005) forced whiting to seek refuge from tidal challenges in shallower areas, whereas mullet could opportunistically elevate their foraging effort in response to some other temporarily available prey species. It is difficult to determine whether the change in whiting behaviour is a direct response to a change in predation threat posed by mullet; indeed, we could find no published evidence of whiting in the diet of mullet (Taylor et al. 2006a). However, these 2 species maintain segregation from one another via switches between spatial and temporal partitioning, so a low encounter rate would be expected even if mullet pose a strong predation threat to whiting. Many local fishers believe whiting to be a very successful bait type for targeting mullet, but whether the changing niche dynamics we observed represents a direct predator–prey interaction remains unclear. The importance of indirect predatory effects on prey behaviour are well recognized (e.g. Heithaus 2001, Dill et al. 2003), which highlights the importance of evaluating behavioural changes at the community level.

The addition of alternative resources can strongly influence predator behaviour (Heithaus 2001), and we consider it likely that the switch to nocturnal activity in mullet was driven by a change in optimal foraging conditions. The influence of elevated turbidity (as is expected in estuaries after rainfall) on

fish foraging effort is well recognised (Wellington et al. 2010, Gray et al. 2011, Johannesen et al. 2012), and the movement of a key nocturnal prey item of mulloway (*Metapenaeus macleayi*; Taylor et al. 2006a) was reported to increase immediately after rainfall (Ruello 1973, Glaister 1978). Mulloway may also face increased energetic challenges in line with the drop in salinity, but this could be outweighed by an increase in predation efficiency.

During rainy conditions, the switch to nocturnal activity in mulloway coincided with the opposite pattern for whiting (a strengthening of the diel activity pattern). Interestingly, this divergence is broadly consistent with long term (~10 yr) catch data, with increased rainfall leading to higher catch rates for mulloway but lower catch rates for whiting (Fig. 3). An increase in fish swimming activity should correlate with an increase in set-net catchability, and a recent study found temperature-associated trends in body activity (measured via the same transmitters used in this study; Gannon et al. 2014) were correlated with set-net catch rates for dusky flathead *Platycephalus fuscus*. Timing of set-netting was not reported for our data, but most fishers in NSW prefer to set their nets at night (N. L. Payne pers. obs.), so the divergent shifts in nocturnal body activity after rain (Fig. 2c,d) could largely explain why catchability increases with rainfall for mulloway, but decreases for whiting (Fig. 3). Only part of the geographical distributions of mulloway and whiting overlap, so comparing rain-associated trends in activity or CPUE in regions containing one species but devoid of the other could be a useful way to explore whether changes in whiting behaviour are dependent on changes in mulloway behaviour.

CONCLUSIONS

There are few behavioural changes more drastic than a complete reversal of activity rhythm. This study suggests that rainfall can drive strong behavioural responses in the timing of fish activity, and a switch from spatial to temporal segregation between species. New technologies (such as biologging) provide the opportunity to examine niche segregation models over spatio-temporal scales that previously were not possible, and data over these scales are particularly important for examining the impact of short-term, unpredictable environmental changes like weather. The frequency and magnitude of these disturbances are likely to increase (Allan & Soden 2008), so a mechanistic understanding of how ani-

mals respond to them may prove critical in predicting diverse ecosystem impacts.

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Appendix.

Table A1. Tagging summary and data collected from acoustic accelerometer transmitters implanted in mullet *Argyrosomus japonicus* and sand whiting *Sillago ciliata*. U: sex unidentified

Species	Tagging date (dd/mm/yyyy)	Total length (mm)	Sex	Tag type	Number of depth data (m) (days detected)	Number of activity data (m s ⁻²) (days detected)
<i>A. japonicus</i>	15/11/2012	1200	F	V13AP	8157 (72)	8181 (72)
<i>A. japonicus</i>	5/12/2012	886	M	V13AP	0 (0)	6630 (152)
<i>A. japonicus</i>	6/12/2012	740	M	V13AP	2771 (90)	2801 (90)
<i>A. japonicus</i>	11/12/2012	600	U	V13AP	6517 (88)	6496 (88)
<i>A. japonicus</i>	15/05/2013	540	U	V13AP	2493 (27)	2503 (27)
<i>A. japonicus</i>	17/05/2013	660	U	V13AP	7838 (64)	7695 (64)
<i>A. japonicus</i>	24/05/2013	810	U	V13AP	2620 (18)	2643 (18)
<i>A. japonicus</i>	24/05/2013	688	U	V13AP	2420 (16)	2432 (16)
<i>A. japonicus</i>	24/05/2013	755	U	V13AP	2857 (41)	2912 (41)
<i>S. ciliata</i>	14/11/2012	308	M	V9AP	19155 (188)	18946 (188)
<i>S. ciliata</i>	14/11/2012	355	F	V9AP	507 (2)	501 (2)
<i>S. ciliata</i>	14/11/2012	356	F	V9AP	39648 (188)	39575 (188)
<i>S. ciliata</i>	14/11/2012	346	F	V9AP	59 (19)	39 (19)
<i>S. ciliata</i>	15/11/2012	361	F	V9AP	1495 (5)	1516 (5)
<i>S. ciliata</i>	15/11/2012	333	F	V9AP	505 (2)	497 (2)
<i>S. ciliata</i>	21/11/2012	330	F	V9AP	0 (0)	0 (0)
1 <i>S. ciliata</i>	22/11/2012	375	F	V9AP	2830 (136)	2868 (136)
<i>S. ciliata</i>	29/11/2012	360	F	V9AP	87 (4)	99 (4)
<i>S. ciliata</i>	12/12/2012	382	U	V9AP	8423 (142)	8791 (142)

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