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ORIGINAL PAPER

Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance

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Abstract The influence of anthropogenic disturbance on the behaviour of wild animals is increasingly recognised for terrestrial systems. Data on free-ranging aquatic animals are comparatively scarce, and this represents a problem for estimating the consequences of human disturbance for organism fitness and therefore the functioning of aquatic systems. We used acoustic accelerometer and depth transmitters implanted in wild fish and archival stomach content data to test for relationships between the intensity of boating and the activity levels and foraging efficiency of an estuarine predatory fish, the mulloway *Argyrosomus japonicus*. Increasing boating activity (inferred from week-long trends in underwater noise and local maritime records) was associated with a reduction in activity levels and increased depth distributions of mulloway. Stomach content data from a nearby estuary revealed a far-lower feeding rate and altered diet composition on weekends (when boating activity is greatest) compared to weekdays for this species, and an inferred foraging success rate almost one-third that of weekdays. These data suggest the behaviour and foraging intensity of mulloway is significantly influenced by anthropogenic disturbance. The overall fitness costs of the reduction in foraging success will depend on how readily mulloway can reallocate foraging to less disturbed conditions, and the extent of stress-related responses to disturbance in this species. This study supports earlier predictions that anthropogenic disturbances like noise could have significant impacts on the behaviour and fitness of aquatic animals.

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Introduction

The importance of non-lethal human disturbances on the behaviour and fitness of animals is increasingly recognised. For example, the risk-disturbance hypothesis (Frid and Dill 2002) proposes that animal responses to human activity can be similar to those of real predation risk, and that these anti-predator behaviours come at the cost of other critical activities like foraging or reproduction (Lima 1998a; Lima and Bednekoff 1999; Frid and Dill 2002). Understanding the fitness costs associated with these behavioural responses to human disturbance is emerging as an important pursuit in conservation biology (Berger-Tal et al. 2011; Tuomainen and Candolin 2011; Wildermuth et al. 2013).

In marine ecology, the historical focus of research on impacts of human disturbance has been on fishery harvest

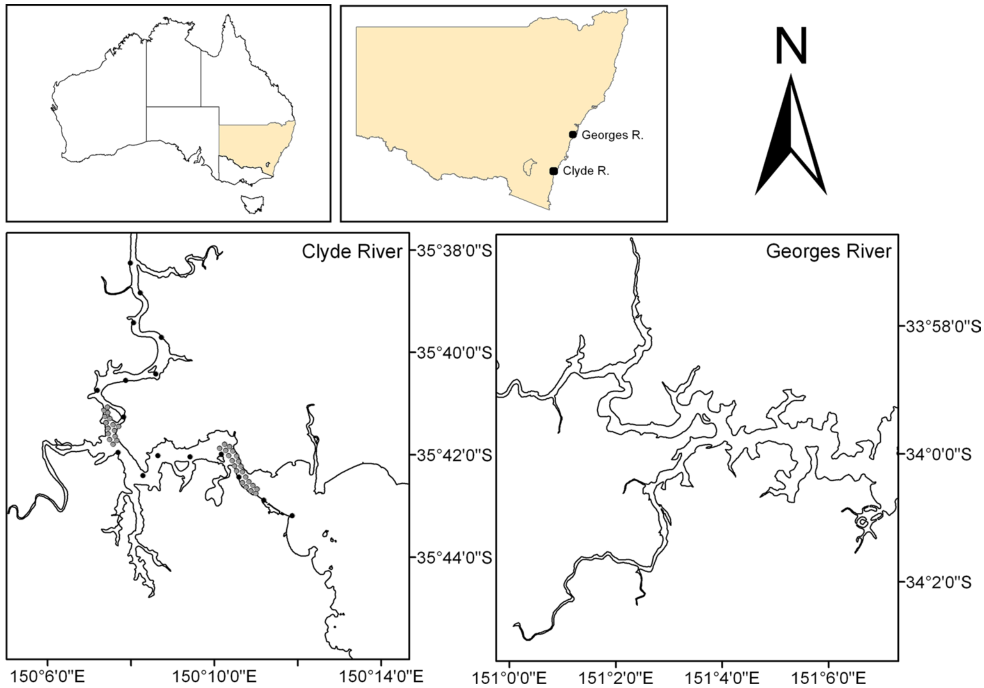

Fig. 1 Location of estuaries from which activity (Clyde River) and diet (Georges River) data were collected. Acoustic receiver positions within the Clyde River are indicated by *grey* (where synchronisation tags were used to infer disturbance levels and activity, and data were collected) and *black* (where activity and depth data were collected; upper reaches of estuary not shown) *dots*

rates and spatial closures (Pauly et al. 1998; Claudet et al. 2008, 2010) or physico-chemical stressors (Russell et al. 2009; Connell et al. 2013). However, other disturbances are receiving increasing attention. Slabbekoorn et al. (2010) combined (largely) terrestrial examples with inductive reasoning to make a convincing case for the potentially broad impacts of human disturbance (noise from boats and other activities) on fish behaviour and fitness, and several earlier studies echo these concerns (e.g. Popper 2003; Popper and Hastings 2009a, b). A variety of laboratory studies have reported diverse impacts of human disturbances like noise on aquatic animal physiology (Lagardere 1982; Smith et al. 2004; Graham and Cooke 2008) and behaviour (Purser and Radford 2011; Bruintjes and Radford 2013; Wale et al. 2013; Kunc et al. 2014), but our understanding of how disturbance affects these parameters in wild aquatic animals is relatively poor (Slabbekoorn et al. 2010). From a behavioural perspective, extrapolation of laboratory findings to natural populations can be inappropriate (Popper and Hastings 2009a), so there is clearly a case for evaluating the effects of human disturbance on free-ranging fishes in their natural environment.

In this study, we used internally implanted accelerometry transmitters to examine relationships between anthropogenic disturbance (boating intensity) and activity levels of a free-ranging predatory fish (mulloway *Argyrosomus japonicus*). Mulloway are endemic to estuarine and coastal regions of southern Australia and South Africa and represent an important commercial and recreational fishery throughout their range. There is anecdotal evidence of noise-related reductions in catcheability in this species, with many fishers employing electric motors rather than noisier petrol engines when targeting mulloway (NLP personal observation). We therefore considered mulloway a useful species with which to examine disturbance impacts. We collected activity (dynamic body acceleration) data from mulloway inhabiting an estuary popular among recreational fishers in south-eastern Australia and compared these data to trends in relative boating intensity. We also examined trends in archival stomach content data from mulloway captured in a nearby estuary for evidence of disturbance-related changes in predation rates.

Methods

Acoustic accelerometry

Work with animals in this study was permitted under University of NSW animal care and ethics permit 11/30A. We used internally implanted acoustic accelerometers to estimate relative activity levels of mulloway (after Payne et al. 2011b, 2013; Gannon et al. 2014). We acknowledge that the behavioural impact of the tagging procedure and selection bias for individuals with a particular personality (e.g. boldness) are untested in this study, but consider the biologging approach insightful nonetheless. Ten mulloway (see Table S1 for fish sizes and tagging dates) were captured via hook and line throughout the Clyde River estuary (35.70°S, 150.179°E; Fig. 1) from November 2012 to May 2013 and implanted with acoustic accelerometers (containing a tri-axial acceleration and depth sensor; model V13AP-1L "activity" algorithm, Vemco™, Halifax, Nova Scotia) following Walsh et al. (2012). Briefly, fish were individually anaesthetised via immersion in a solution containing 50 mg L^{-1} Aqui-S (Aqui-S Ltd., Lower Hutt, New Zealand) immediately post-capture, and transmitters were inserted into the body cavity via a 15–20 mm ventral incision, which was made with a surgical scalpel and sealed with surgical sutures. To aid recovery 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 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. Following earlier recommendations (Cooke and Wagner 2004), all surgery was conducted by trained (theoretical and hands-on) personnel with previous experience in intraperitoneal implantation of telemetry devices in teleosts (NLP and DVM). Accelerometers sampled at five Hz, had a nominal delay (the average time between acoustic transmissions) of two minutes, a sampling window of 20 s and an estimated battery life of 240 days. Depth sensors had a maximum range of 50 m and a resolution of 0.22 m. Tagged fish were monitored via an array of 34 acoustic receivers (model VR2W, Vemco, Halifax, Nova Scotia) spaced approximately 1.2 km apart along the estuary (Fig. 1), with transmitted data successfully recorded when fish were within range of each receiver (approximately 200–300 m; Payne et al. 2011a; How and de Lestang 2012; Stocks et al. 2014). As part of a contemporary study, a further 39 receivers were deployed for most of our monitoring period, and data recorded from those receivers were included in our analyses (Fig. 1). While sections of the river could not be monitored (e.g. >500 m from a receiver, or in very shallow or deep water), this design allowed us to record mulloway behaviour across a broad range of habitats and depths. All data were retrieved from the receivers by the end of August 2013.

Anthropogenic disturbance

Many fishers in the study area use electric trolling motors when specifically targeting mulloway (NLP personal observation), but petrol combustion motors when travelling throughout the estuary. Various non-fishing recreational boaters also operate in the area, and these generally use petrol motors of various power outputs. As such, individual boats and boat activities are likely to represent various levels of "disturbance" to the aquatic environment, and it is often difficult to evaluate the likely disturbance level caused by each boat, even qualitatively (e.g. whether a boat is using a relatively noisy petrol motor or a relatively quiet electric one). As such, simply quantifying boating rates may not provide an accurate measure of disturbance experienced by aquatic animals. Given this, we developed an approach for quantifying relative underwater disturbance by evaluating the performance (measured as relative frequency of acoustic detections) of acoustic positioning systems that were deployed within the Clyde River estuary as part of the contemporary tracking study. These positioning systems comprise an array of VR2W receivers and co-located, fixed-position synchronisation tags (transmitting at 69 kHz, model V16-6L, 10 min average delay between transmissions, Vemco™, Halifax, Nova Scotia;). These positioning systems triangulate the position of acoustic tags within the vicinity of an array, and the synchronisation tags synchronise the internal clock of each receiver (see Espinoza et al. 2011 for details). One array consisted of 23 receivers and synchronisation tags positioned near the mouth of the estuary (35.701°S, 150.18°E), and a second array of 16 receivers and tags was located approximately 7.0 km upstream (35.688°S, 150.128°E; Fig. 1). Both arrays comprised grids of approximately equilateral triangles, with receivers spaced 200–300 m apart, moored 1.5–2 m from the substratum, and in water depths ranging from 4.0 to 10.0 m. Synchronisation tags were attached ~0.5 m above the receivers, such that they were 2–2.5 m above the substratum. The acoustic detection frequency data from the positioning systems were collected from mid-November 2012 to mid-April 2013 (a total of 22 weeks).

Since the probability of receivers successfully decoding acoustic transmissions declines as ambient noise increases (Voegeli and Pincock 1996; Payne et al. 2010; Cagua et al. 2013), the relative frequency of acoustic detections from the synchronisation transmitters can be used as a proxy of relative acoustic disturbance near 69 kHz. Increased boat traffic should reduce acoustic detection frequencies via several mechanisms, including: (a) boat engines (particularly petrol ones) will elevate background reverberation, thereby reducing the ability of receivers to identify the acoustic transmissions at 69 kHz; (b) displacement of water by travelling boats ("wakes") and associated propeller cavitation will increase mixing of air bubbles in the water column, which will increase both absorption and scattering of acoustic signals—an effect shown to significantly reduce detection frequencies when wind is the vector (Gjelland and Hedger 2013); and (c) most sonar devices used by the general public operate at frequencies that include 69 kHz, and this interference can drastically reduce acoustic detection frequencies (pers. comm. Vemco™ technical staff). It is important to note that 69 kHz is above the hearing range of most fish, so our measure of "disturbance" is more a measure of relative boat activity than a direct measure of sound levels that would be detected by fish. To validate the link between boat traffic and our disturbance measure, we examined maritime communication records from the Batemans Bay Marine Rescue Unit 1/10/2012 to 30/6/2013. As a safety precaution throughout Australia, boat users are advised to communicate with similar Units during all outings, and these communications are logged by each Unit. The majority of these records were for offshore excursions, and since we could not be certain that they were exactly representative of upstream (within our acoustic array) excursions, we examined these data graphically rather than undertaking formal analyses.

Data analyses

For the proxy of anthropogenic disturbance (boating activity), all detections from synchronisation tags in both arrays were summed for every 24-h period, and the mean number of total detections on each day of the week (i.e. Sunday–Saturday) was calculated for the entire monitoring period (22 weeks). Since increasing noise reduces detection frequencies (Voegeli and Pincock 1996; How and de Lestang 2012; Cagua et al. 2013), we derived a "noise quotient" (after Simpfendorfer et al. 2008) as the inverse of the centred mean detection frequencies for each day of the week (we calculated the mean detection frequency for each day of the week across the entire monitoring period; centred these data by dividing by the total mean across all days; then calculated the inverse of these seven data). Significant variation in detection frequencies can result from variable wind speeds, diurnal rhythms in biological noise, rainfall, salinity, and several other parameters (Voegeli and Pincock 1996; Payne et al. 2010; How and de Lestang 2012; Cagua et al. 2013; Gjelland and Hedger 2013), so our use of mean day-of-the-week values over a long time series (5 months) was intended to smooth out the majority of this variation and to provide a relative measure of within-week variation in anthropogenic disturbance. These seven noise quotient data (mean values for each day of the week) were assigned to each corresponding activity and depth data for analyses.

Linear mixed models were used to test whether disturbance influenced activity or depth of tagged mulloway ($P < 0.05$), with activity data $\log_{10}$-transformed to achieve a Gaussian distribution, and fish ID included as a random effect.

Diet analysis

Archival dietary data of mulloway from the Georges River (33.977°S, 151.036°E; Fig. 1) were analysed to compare stomach fullness of fish captured on weekdays (Mondays–Fridays; when we expected boat activity would be lowest in that system) and weekends (Saturday–Sunday). Full details of sampling and sample processing are given in Taylor et al. (2006) and are summarised here. Fish were sampled over a period of three years (2003–2005) using an otter trawl, multi-panel gill nets, and the recreational fishery. The stomach and intestinal tract were dissected from the body cavity, the stomach opened, and stomach fullness subjectively estimated as empty (zero) to completely full (five). Contents were sorted, identified, and enumerated, and sorted prey items were freeze-dried for 48 h and the dry weight of each prey type measured. Stomach content data from 2003 to 2005 were combined with data collected from 1977 to 1979 (initially reported in Pease et al. 1981 and later presented in Taylor et al. 2006) and were expressed as per cent composition by weight for five groups representative of the main taxa (mysids, fish, prawns, cephalopods, and miscellaneous invertebrates; Taylor et al. 2006). A total of 278 mulloway were sampled on weekdays and 83 on weekends.

Stomach content data were analysed in two ways. Firstly, gut fullness was compared between weekend and weekday periods for all fish using a *t* test. Secondly, multivariate diet data for fish larger than 50 cm TL (to remove the effect of ontogenetic variation in the diet; Taylor et al. 2006) were expressed as a Bray–Curtis similarity matrix of $\log_e + 1$ transformed data and compared between weekdays and weekends using a single-factor permutational multivariate analysis of variance (PERMANOVA, using Type-III sum-of-squares and unrestricted permutation of raw data). The taxonomic groups contributing to differences between weekdays and weekends were evaluated using similarity percentages analysis. All multivariate analyses were undertaken in PRIMER v 6 with PERMANOVA+ (PRIMER-E, Plymouth, United Kingdom). Time-of-capture data were not recorded for diet data, but since digestion rates of sciaenids are generally less than 16 h (e.g. Gillum et al. 2012), we assumed that stomach contents were representative of food ingested on the day of capture. Data on the timing of peak foraging for this species are unavailable, and we acknowledge that the magnitude of any difference between weekday and weekend diets may be influenced by an interaction between the timing of fish feeding and fisher sampling.

Results

Disturbance levels (inferred from the performance of our acoustic arrays) were highest on Saturdays and Sundays, above average on Fridays, and lowest from Monday–Thursday (Fig. 2). This week-long trend was consistent with boat activity records in the Batemans Bay area (Fig. S1).

A total of 147,459 and 116,096 activity and depth data, respectively, were recorded across all fish across a period of approximately 9 months (Table S1). One fish yielded few data so was excluded from analysis, and a significant

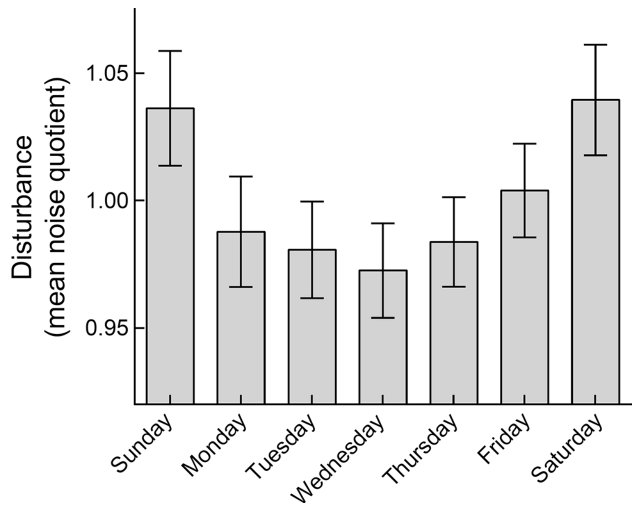

Fig. 2 Anthropogenic disturbance levels in the Clyde River estuary. Disturbance was measured via performance analysis of an array of acoustic transmitters and receivers operating at 69 kHz and gives an indication of relative boating intensity. Data are mean ± SEM for each day of the week

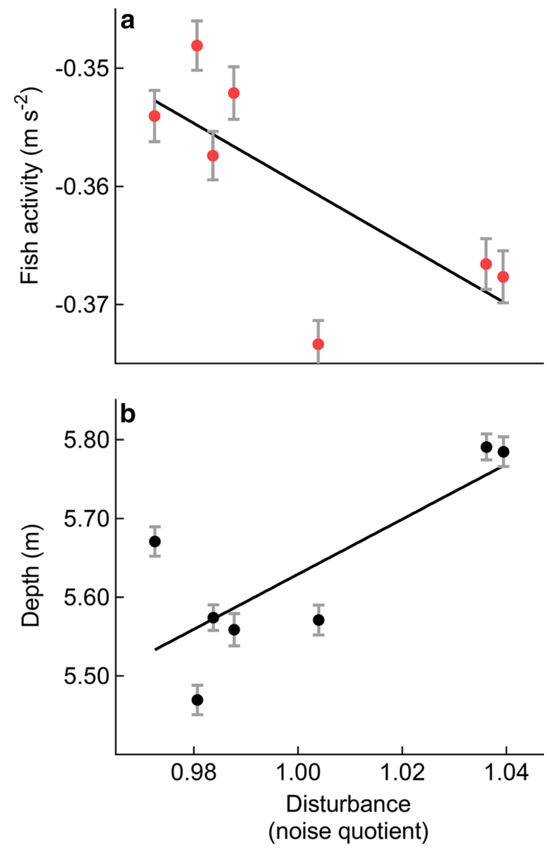

Fig. 3 The influence of disturbance (an indication of relative boating intensity, inferred from noise quotients; Fig. 2) on mean activity and depth of mulloway, which were pooled across all individuals ($n = 9$) for each day of the week for this figure. *Errors* indicate SEM

portion of depth data from another fish (TL 88.6 cm) was erroneous (depth values ≤0 m), and these data were excluded from analyses.

As disturbance increased, mulloway were less active and inhabited deeper water (for activity: $F_{1,147,450} = 56.22$, $P < 0.0001$, Fig. 3a; and for depth: $F_{1,116,087} = 230.61$, $P < 0.0001$; Fig. 3b. Note: linear mixed models were run on the full biologging data set, with mean values [and SEM] for each day shown in Fig. 3 for display only). Individual tagged mulloway varied in their response to disturbance (Fig. 4; for this display, data were grouped into periods of above- and below-average disturbance [Fridays–Sundays and Mondays–Thursdays, respectively, based on noise quotient data; Fig. 2], and centred by subtracting the average activity or depth value of each individual from the mean value for disturbed [Fridays–Sundays] and undisturbed [Mondays–Thursdays] periods), and body size appeared to have little influence on the response to disturbance for both activity (Fig. 4a) and depth (Fig. 4b).

Stomach fullness of historic mulloway data from the Georges River estuary was significantly lower on weekends (Saturdays and Sundays) than weekdays (mean weekend fullness was 39 % of the weekday mean; $t_{359} = 4.2$, $P < 0.0001$, Fig. 5). Given unbalanced sample sizes (278 vs. 83 for weekdays and weekends, respectively), we also compared weekend data to 83 randomly selected samples from weekdays, and the difference was still significant ($t_{164} = 3.5$, $P = 0.001$). Multivariate analyses indicated that the composition of prey assemblages varied between weekdays and weekends ($F_{1,116} = 4.06$, $P = 0.019$), with 59 % of this variation driven by a lower abundance of forage fish (mainly *Hyperlophus vittatus* and *Ambassis jacksoniensis*) in stomachs sampled during weekends (Fig. 5).

Discussion

Increased boating activity was associated with a reduction in activity rates and altered depth distribution of free-ranging mulloway. Interpreting the magnitude of activity suppression during disturbed periods is difficult because our accelerometer transmitters do not provide direct information on discrete behaviours such as the frequency of predation events or flight responses. However, diet data revealed a 61 % reduction in ration on weekends compared to weekdays (Fig. 5), suggesting a major change in predation frequency with elevated disturbance. Diet data were collected in an adjacent estuary several years prior to the biologging data, so directly comparing the magnitude of responses in these data sets may be inappropriate. Nevertheless, the two independent data sets represent persuasive evidence that boating activity

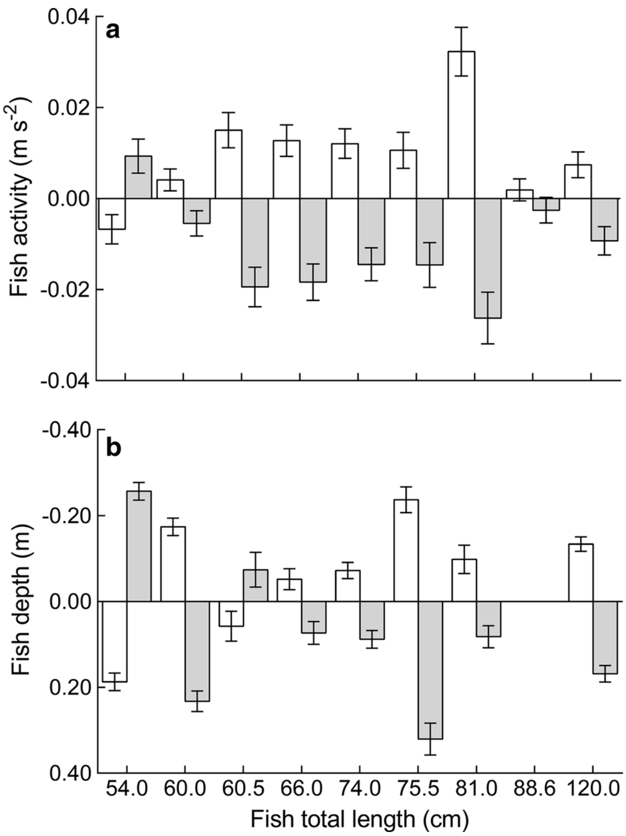

Fig. 4 Mean centred **a** activity and **b** depth of the nine mulloway during conditions of lower than average disturbance (Monday–Thursday; *unfilled bars*) and higher than average disturbance (Friday–Sunday; *filled bars*). Data were stratified into these periods on the basis of the noise quotient data (Fig. 2). *Errors* indicate SEM, and one fish yielded no depth data

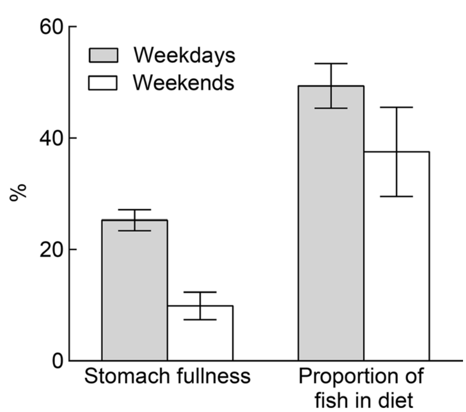

Fig. 5 Mean per cent (±SEM) stomach fullness and relative contribution of fish prey in the diet of mulloway captured in the Georges River from 1977–1979 and 2003–2005 for weekdays (Monday–Friday) and weekends (Saturday–Sunday). $N = 278$ and 83 samples for weekdays and weekends, respectively

can have a significant impact on foraging success of this species.

Non-lethal human disturbances are often perceived as threats by animals, with the risk-disturbance hypothesis (Frid and Dill 2002) predicting that responses to human disturbance (e.g. hiding, fleeing, or increasing vigilance) will be similar to those of predation risk. Animals generally increase refuging or decrease movement when predation risk is high (Lima and Dill 1990; Lima 1998a, b; Kronfeld-Schor and Dayan 2003), so the perception of boating as a threat seems an intuitive model for explaining the reduction in activity and foraging success in mulloway. Several laboratory studies have documented boat noise-associated behavioural changes consistent with increased vigilance in aquatic animals (e.g. in hermit crabs: Chan et al. 2010, three-spined sticklebacks: Purser and Radford 2011, and shore crabs: Wale et al. 2013), and given powered boating will generally be associated with elevated noise levels, and our data are consistent with these laboratory findings. Further, if the altered mulloway behaviour is driven by threat perception, any reduction in foraging intensity will likely be exacerbated by stress, which is a common consequence of noise disturbance (Kight and Swaddle 2011) and can suppress appetites via the corticotropin-releasing factor system in fish (Bernier 2006). These compounding influences of boating activity on foraging may largely explain the considerable differences seen in our stomach content data between heavily disturbed (weekends) and less disturbed (weekdays) periods.

Understanding how behavioural responses translate into fitness costs has been highlighted as a critical avenue for anthropogenic disturbance research (Barber et al. 2010; Francis and Barber 2013), and for conservation biology in general (Berger-Tal et al. 2011; Tuomainen and Candolin 2011; Wildermuth et al. 2013). Foraging success is a fundamental determinant of animal fitness; largely regulating growth rates, fecundity, and a suite of other fitness measures, and our diet data suggest foraging success (relative biomass of prey captured) of mulloway under highly disturbed conditions may be less than half that of less disturbed periods (i.e. weekends vs. weekdays; Fig. 5). At face value, this would represent an overall (week-long) reduction in ration of 26 % compared to a scenario of constant low-disturbance (i.e. if weekend and weekday foraging success were equal), which would likely result in significant fitness costs. However, animals should tend to allocate foraging and anti-predator behaviour in line with temporal variation in risk (Lima and Bednekoff 1999), so the suppression of foraging on weekends may be largely offset by elevated foraging effort during low-risk (weekday) periods.

Foraging is risky when the threat of predation is high, so animals should reduce vigilance and increase resource acquisition under safer conditions to enable increased vigilance (and decreased foraging) under riskier conditions (Lima 1998a, b, Lima and Bednekoff 1999; Higginson et al. 2012). If mulloway perceive disturbance as a threat, they might shift the timing of foraging to deal with temporal variation in boating activity, but laboratory studies with this species suggest feeding frequency has a significant influence on growth rates even when fish are fed to satiation (Kaiser et al. 2011). For example, mulloway fed to satiation twice per day achieved almost 20 % greater mass after 42 days than those fed to satiation once per day (Kaiser et al. 2011). This suggests that a reallocation of feeding intensity could still be associated with significant fitness costs.

The disturbance represented by increased boating activity may affect mulloway behaviour via visual or olfactory cues (the presence of fishing bait or pollutants from boats could be detected by fish and influence their behaviour) or by physical disturbance such as wakes caused by fast-moving boats. However, the increased underwater noise levels generated by boats are likely to play a significant role in the reduction in foraging intensity. The majority of energy from anthropogenic noise sources in water (including ships and fishing vessels) is concentrated within a frequency range that coincides with the hearing abilities of most fish species (i.e. between 10 and 1,000 Hz; Popper and Hastings 2009a, Slabbekoorn et al. 2010), including mulloway (Parsons et al. 2009, 2012), and the potential impacts of anthropogenic noise on fish is increasingly realised. A growing number of laboratory studies suggest this type of disturbance can have diverse impacts on aquatic animals (Graham and Cooke 2008; Purser and Radford 2011; Bruintjes and Radford 2013; Wale et al. 2013; Kunc et al. 2014), but our data extend these findings to the wild, by providing evidence consistent with noise-associated shifts in behaviour of a free-ranging fish. It is important to note that mulloway behaviour may be mediated by behavioural responses of their prey, so future studies that simultaneously monitor disturbance response in both predators and prey could be particularly powerful.

Our data add to the growing body of evidence that anthropogenic disturbance can have significant impacts on aquatic animal behaviour, and probably, fitness. While our biologging approach does not facilitate quantification of foraging time or success per se, some more recent technologies do, and these tools may be instrumental in quantifying the fitness costs of anthropogenic disturbance for aquatic animals. For example, accelerometer loggers coupled with video cameras have successfully quantified predation event frequency in free-ranging penguins (Kokubun et al. 2011; Watanabe and Takahashi 2013; Watanabe et al. 2014), and accelerometers have also been used to estimate the energetic costs of anthropogenic disturbance in scallops (Robson et al. 2012). Combining these new technologies with laboratory experiments (to identify proximate mechanisms of disturbance impacts) may become crucial for understanding consequences of anthropogenic disturbance at the ecosystem level.

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