



# Duration of migration and reproduction in males is dependent on energy reserve in a fish forming spawning aggregations

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**ABSTRACT:** Clarifying the relationship between individual energetic state and reproductive behaviour is essential for understanding the life history strategies of fish as well as for determining fisheries management measures. Many papers have recently been published on fish spawning aggregations (FSAs), in which numerous fish migrate to specific sites for spawning, yet little is known about the relationship between individual energetic state and reproductive behaviour. We tested whether the individual energetic state affected the reproductive behaviour in male white-streaked grouper *Epinephelus ongus*, a species that forms FSAs. Body composition measurement of market specimens suggests that male *E. ongus* feed less and mainly use their lipid reserves for metabolism and testis development during the spawning season. An integrative analysis of body composition and acoustic telemetry data showed that there is a positive relationship between pre-migration lipid density and duration away from the resident area for migration and reproduction (duration away). These results indicate that fatter males with higher lipid density spent longer periods outside of the resident area, which may enhance the susceptibility of these individuals to intensive fishing pressure at the FSA site. Furthermore, the lipid expenditure during the duration away estimated in this study corresponded well with the energy expenditure for metabolism and testis development estimated through the metabolic theory of ecology, suggesting that we could accurately estimate the energy requirement for reproductive behaviours. This study highlights the importance of linking energy reserves to reproductive behaviours in other fishes forming spawning aggregations.

**KEY WORDS:** Epinepheline serranid · Grouper · Metabolic theory · Selective fishing · Spawning aggregation · Spawning migration · Telemetry

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## INTRODUCTION

Animals are assumed to allocate energy to reproduction, growth, and metabolism in a way that maximizes fitness (Roff 1992, Davies et al. 2012). Since reproductive behaviour (e.g. migration, spawning,

competition for spawning territories and partners, nest building, and parental care) is energetically costly, linking individual energetic state with reproductive behaviour is one of the key issues in studies of the life history strategies of fish (Larsson et al. 1990, Roff 1991, Jonsson et al. 1997, Yoneda et al. 2014).

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The link between individual energetic state and reproductive behaviour is also essential to determine fisheries management measures because it leads to detecting behavioural and physiological traits that are linked to higher reproductive success and/or higher fishing vulnerability (Cooke et al. 2007, Sutter et al. 2012, van Overzee & Rijnsdorp 2015).

Over 80 species of marine fish, mainly coral reef fishes, form fish spawning aggregations (FSAs), in which numerous fish migrate to specific sites for spawning (Sadovy de Mitcheson & Colin 2012). The FSAs are typically categorised as resident, in which individuals migrate within or near their home range, or transient, in which individuals migrate well outside their home range (Domeier & Colin 1997, Domeier 2012). Resident FSAs occur at a specific time of day, last at most a few hours, and occur daily for the entire spawning season, whereas transient FSAs occur during specific months of the year and last for days to weeks. It is suggested that transient FSAs are more vulnerable to fishing (Sadovy de Mitcheson & Erisman 2012) because they are more predictable in time and location, they last for longer periods, and a single FSA represents the larger proportion of the annual reproductive effort of the involved individuals (Domeier & Colin 1997, Domeier 2012).

Patterns of energy acquisition and allocation to reproduction are often categorised along the capital–income breeding continuum (Jönsson 1997, Stephens et al. 2009, McBride et al. 2015). Capital breeding species utilise a pre-stored energy reserve for reproduction, while income breeding species utilise energy acquired during the spawning period for reproduction; however, some species are intermediate between these two. The capital–income breeding terminology is often restricted to female egg production in fish biology literature (Kurita 2010, McBride et al. 2015) but has been expanded to the total reproductive effort (including migration, competition for territories and partners, and parental care) of both sexes in other literature (Jönsson 1997, Mysterud et al. 2005, Stephens et al. 2009). In this study, we applied this terminology to describe energy investment patterns for the total reproductive effort of males. In fish forming spawning aggregations, resident spawning species are considered to be close to the income breeding end of the continuum (Choat 2012) because the daily cost for reproduction and migration is directly fuelled by recent feedings (Warner 1995). Presumably, transient spawning species are close to the capital breeding end of the continuum because they store energy to cover the cost for long-distance migrations and long periods at spawning grounds

and because there is a limited number of spawning opportunities per year (Choat 2012, Domeier 2012); however, as far as we are aware, no studies have tested this hypothesis.

Given the potential benefits of breeding in aggregations, including increased mate encounter (Molloy et al. 2012) and fertilization (Gaudette et al. 2006) rates and reduced per capita predation rates on eggs and adults (Krause & Godin 1995), it can be hypothesized that the timing of migration and duration at the FSA site should be synchronous. However, there are demonstrated variations in the timing and duration among and within sexes. Males arrive at spawning grounds earlier and stay longer at the spawning grounds than females in several species (Gladstone 1994, Zeller 1998, Rhodes & Sadovy 2002, Nemeth et al. 2007, Bijoux et al. 2013, Lowerre-Barbieri et al. 2013, Grabowski et al. 2014), and there are large variations in the timing and duration within sexes, specifically in males (Zeller 1998, Rhodes & Sadovy 2002, Robinson et al. 2008, Bijoux et al. 2013, Grabowski et al. 2014). Since males build territories or produce sounds in all species studied in this context (Gladstone 1994, Nordeide & Folstad 2000, Robinson et al. 2008, Nemeth 2012, Samoily 2012, Lowerre-Barbieri et al. 2013), it is plausible that the reason males arrive at FSA sites earlier than females is to attract females. However, given that there are substantial variations in the timing and duration within sexes, the question arises whether the individual energetic state is the implicit factor that drives the variation within sexes.

The white-streaked grouper *Epinephelus ongus* is a commercially important species that forms transient FSAs at specific sites in the Yaeyama Islands, Japan. *E. ongus* forms FSAs around the last quarter moon in 1 or 2 consecutive months between April and June, and evidence suggests that each individual attends the spawning aggregation only once a year (Nanami et al. 2014, Ohta & Ebisawa 2015). Direct underwater observation, histological observation of gonads, and fisheries catch data suggest that the peak spawning date is the last quarter moon (Nanami et al. 2013, 2014, Ohta & Ebisawa 2015). The histological observation of ovaries suggests that the female *E. ongus* spawns more than once per season, and the total number of spawning eggs is determined before the spawning period (multiple batch spawner with determinate fecundity) (Ohta & Ebisawa 2015). *E. ongus* spawn in mating pairs, but subordinate males also sneak into the spawning of the mating pair (Nanami et al. 2013). Forty percent of the annual catch occurs during the spawning season, when fishermen mainly target FSA sites by spear-

fishing (Ohta & Ebisawa 2015). The annual catches in the Yaeyama Islands have decreased by about half in the last 2 decades (Ohta & Ebisawa 2009). Thus, presence at an FSA site makes *E. ongus* more vulnerable to fishing and is the likely cause of the decline in the local population. A previous acoustic telemetry study revealed that, compared to females, males left the release site for the spawning ground earlier and returned to the release site later, and there was a large variation in the duration between the dates of leaving and returning (duration away, which consists of the time for round-trip migrations and residence time at the spawning ground) among males but a small variation among females (Nanami et al. 2014). Additionally, duration away may be related to Fulton's condition factor in males, although it was not statistically significant due to the small sample size ( $r^2 = 0.49$ ,  $n = 8$ ,  $p = 0.053$ ) (Nanami et al. 2014). Considering this fact and that transient spawning species are likely to rely on energy reserve for reproductive behaviours, we hypothesized that male *E. ongus* feed less and rely on energy reserves for reproductive behaviour (i.e. migration, territorial defence, spawning, and daily metabolism), and thus there may be a positive relationship between the pre-migration energy reserve and the duration away. To test these hypotheses, our study consisted of 2 steps, both of which combined body composition measurement and an acoustic telemetry survey (Fig. 1). First, we aimed to elucidate the pattern of energy acquisition and allocation to reproductive behaviour in male *E. ongus* by measuring changes in proximate composition, testis size, and feeding probability over time, as well as migration timings, during the spawning season (Fig. 1a). Second, we aimed to investigate the relationship between the pre-migration energy reserve (i.e. lipid density) and duration away using the relative condition factor (Fig. 1b).

## MATERIALS AND METHODS

### Body composition analysis

To assess the changes in proximate composition, stomach content, and testis size over time during the spawning season, we purchased male *Epinephelus ongus* specimens (47 individuals in total) from commercial catches taken around the coast of the Yaeyama Islands, Japan, 2 to 4 times per week during April and May 2013. Total length (TL, mm), wet body mass (g), testis mass (g), and presence-absence of stomach content were assessed, and then the proxi-

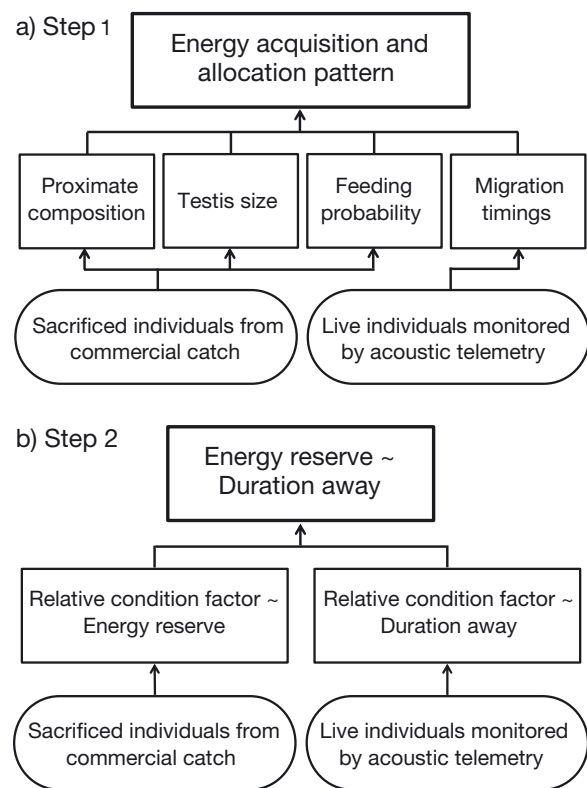


Fig. 1. Flowcharts of the 2 steps in this study, showing (a) the pattern of energy acquisition and allocation to reproductive behaviour in the male *Epinephelus ongus* and (b) the relationship between the pre-migration energy reserve and duration away

mate composition (i.e. lipid and protein of whole body and testis) of 42 individuals was analysed. The remaining 5 individuals were not used for the proximate composition analysis because of time constraints (a large number of specimens were purchased within a few days, and it takes approximately 2 h to separate and homogenise the body parts in each specimen).

The proximate composition analysis was conducted according to standard tables of food composition in Japan 2010 (Anonymous 2010). The muscle, gut, and testis were separated from the *E. ongus* specimens and homogenised using a mortar and food processor. From each homogenate, 1.0 and 0.5 g were subsampled and used to determine lipid and protein content, respectively. The lipid content (g per 100 g wet mass) was analysed by the Soxhlet method. Lipid was extracted with diethyl ether in a Soxhlet extraction device from freeze-dried samples. The protein content (g per 100 g wet mass) was measured by the Kjeldahl method. Homogenate samples were digested with sulphuric acid, the nitrogen content was measured by

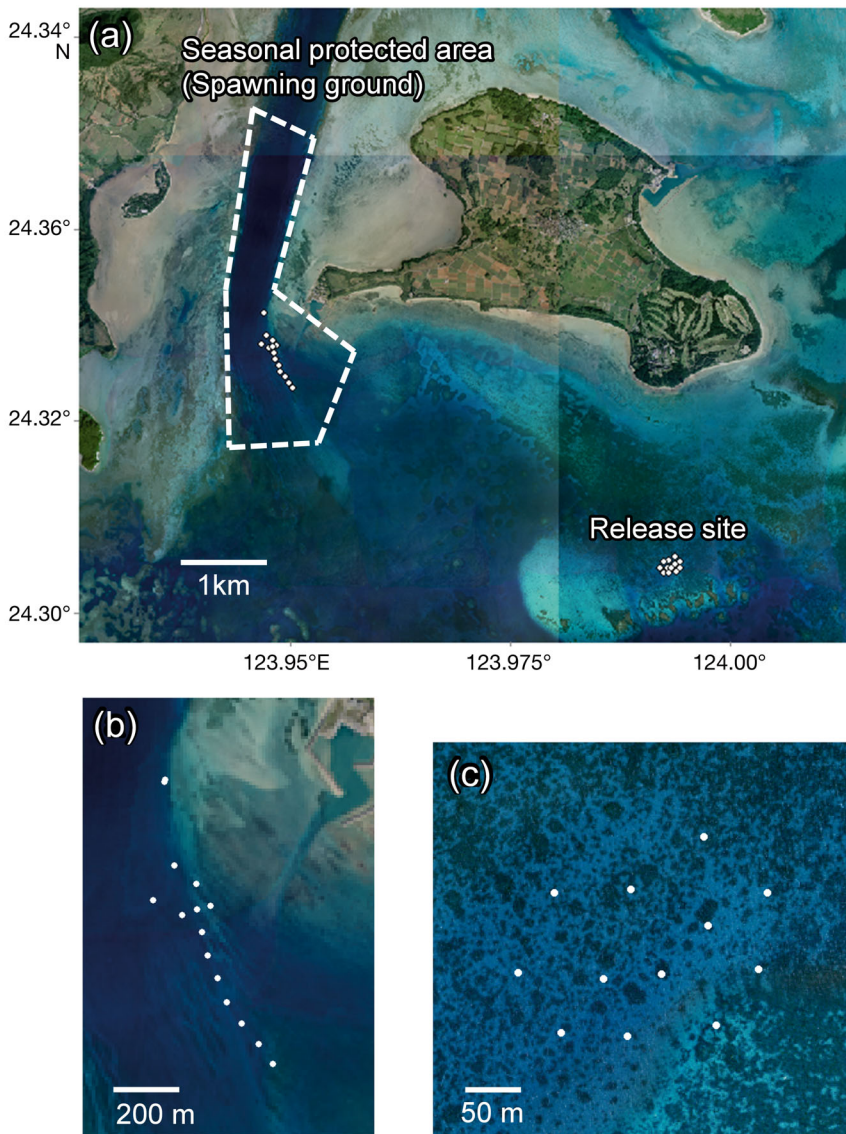


Fig. 2. (a) Study area, with close-ups of (b) the spawning ground and (c) the release site. White dots represent the locations of receivers. Note, there are 2 receivers in the close proximity at the northernmost dot in the spawning ground. The aerial photograph was supplied by the International Coral Reef Research and Monitoring Center, Japan

titration, and the protein content was calculated from the nitrogen content using the conversion factor of 6.25. The above analyses were repeated 2 to 3 times for each homogenised sample to confirm that the analyses were accurate. The testis was generally too small for the proximate composition analysis, and thus the energetic density of the testis was only calculated for 5 individuals obtained on the day when the gonadosomatic index (GSI, %) was at its peak. The calorific coefficients to estimate energy from the proximate composition data were  $39.3 \text{ kJ g}^{-1}$  in lipid and  $17.6 \text{ kJ g}^{-1}$  in protein (Schmidt-Nielsen 1997).

### Acoustic telemetry survey

This survey was conducted in Sekisei Lagoon in the Yaeyama Islands (Fig. 2). Ten male *E. ongus* individuals were monitored during the 2012 spawning season, and 11 individuals were monitored during the 2013 spawning season (Table 1). Approximately 1 mo before the estimated peak spawning date (last quarter moon of May), *E. ongus* were captured by hook and line by scuba divers 5 km southeast of the main spawning ground. The captured specimens were brought to the research vessel, and an acoustic transmitter (V9-2L and V9-2H, Vemco; diameter 9 mm, length 21 mm, weight in air 2.9 g, average signal interval 240 or 300 s, expected battery life 934 or 450 d) was surgically implanted into the abdominal cavity of each fish under anaesthesia using 0.1% 2-phenoxyethanol (see Kawabata et al. 2008 for details of the surgical procedure). During the implantation procedure, morphological characteristics of gonads were visually checked to verify the sex of the specimens. Since the fish were tagged approximately 1 mo before the estimated peak spawning date, when their testes were still small, it was not possible to examine their spawning capabilities by extruding milt. After a 2 h recovery period, the tagged fish were released into the same coral patches where they were captured. A preliminary experiment using dummy transmitters showed no effects of the transmitters

implantations on survival, growth, and spawning (Nanami et al. 2014). After release, signals from tagged fish were monitored using 12 and 15 automated monitoring receivers (VR2 and VR2W, Vemco) deployed around the release site and spawning ground, respectively (Fig. 2). To maximize the probability of detection at the spawning ground, 15 receivers were set up at the core site of the spawning ground, where high densities of *E. ongus* were observed (Ohta & Nanami 2009); however, the detection area of the receivers could cover only a small portion of the whole spawning ground due to the lim-



Table 1. *Epinephelus ongus*. Summary of acoustic monitoring data for tagged fish. TL: total length; BW: body weight; DN<sub>release</sub>: detection number at release site; DD<sub>release</sub>: number of days detected at release site; RI<sub>release</sub>: residency index at release site; DN<sub>spawning</sub>: detection number at spawning ground; DD<sub>spawning</sub>: number of days detected at spawning ground; RI<sub>spawning</sub>: residency index at spawning ground; Tw: water temperature (mean  $\pm$  SD) at spawning ground during duration away. Dates given as yr/mo/d

Year	ID	TL (mm)	BW (g)	Date released	Last date detected	Departure date	Returning date	Duration away (d)	DN <sub>release</sub>	DD <sub>release</sub> (d)	RI <sub>release</sub>	DN <sub>spawning</sub>	DD <sub>spawning</sub> (d)	RI <sub>spawning</sub>	Tw (°C)
2012	M1	272	330	2012/4/9	2012/6/10	2012/5/6	2012/5/27	21	17045	41	1.00	784	7	0.33	26.4 $\pm$ 0.5
	M2	289	356	2012/4/9	2012/6/10	2012/5/2	2012/5/20	18	11227	44	1.00	164	3	0.17	26.1 $\pm$ 0.7
	M3 <sup>a</sup>	306	464	2012/4/9	2012/5/1	2012/4/21	–	–	2387	11	1.00	27	7	–	–
	M4	304	462	2012/4/9	2012/6/10	2012/4/27	2012/5/18	21	10814	41	1.00	10	1	0.05	25.7 $\pm$ 0.8
	M5 <sup>b</sup>	268	292	2012/4/9	2012/6/10	2012/5/7	2012/5/17	10	4684	52	1.00	270	6	0.60	26.3 $\pm$ 0.5
	M6	280	314	2012/4/9	2012/6/10	2012/5/8	2012/5/16	8	13670	54	1.00	141	3	0.38	26.3 $\pm$ 0.5
	M7	245	232	2012/4/9	2012/6/10	2012/5/8	2012/5/18	10	1469	52	1.00	0	0	0.00	26.0 $\pm$ 0.7
	M8	311	448	2012/4/10	2012/6/10	2012/5/1	2012/5/18	17	3420	45	1.00	126	10	0.59	26.4 $\pm$ 0.5
	M9	307	458	2012/4/10	2012/6/10	2012/5/6	2012/5/19	13	3108	49	1.00	2	2	0.15	26.3 $\pm$ 0.5
	M10	284	326	2012/4/10	2012/6/10	2012/5/6	2012/5/17	11	7260	51	1.00	20	5	0.45	26.4 $\pm$ 0.5
2013	M11	297	384	2013/4/2	2013/6/4	2013/4/23	2013/5/16	23	20628	39	1.00	11	4	0.17	24.8 $\pm$ 0.4
	M12	285	340	2013/4/2	2013/6/4	2013/4/27	2013/5/8	11	19433	51	1.00	4	1	0.09	24.5 $\pm$ 0.4
	M13	284	326	2013/4/2	2013/6/4	–	–	–	16371	61	1.00	0	0	–	–
	M14	269	322	2013/4/2	2013/6/4	2013/4/25	2013/5/12	17	20125	45	1.00	4	1	0.06	24.6 $\pm$ 0.3
	M15	265	270	2013/4/2	2013/6/4	2013/4/25	2013/5/8	13	25476	49	1.00	19	6	0.46	24.5 $\pm$ 0.3
	M16 <sup>a</sup>	329	498	2013/4/2	2013/4/29	2013/4/21	–	–	6925	17	1.00	67	5	–	–
	M17	311	442	2013/4/4	2013/6/4	2013/4/27	2013/5/9	12	15706	50	1.00	11	4	0.33	24.5 $\pm$ 0.3
	M18	303	390	2013/4/4	2013/6/4	2013/4/27	2013/5/6	9	3505	53	1.00	0	0	0.00	24.5 $\pm$ 0.4
	M19 <sup>b</sup>	281	338	2013/4/4	2013/6/4	2013/4/27	2013/5/7	10	397	42	0.81	2	1	0.10	24.5 $\pm$ 0.4
	M20	272	260	2013/4/4	2013/6/4	2013/4/30	2013/5/9	9	21854	53	1.00	20	2	0.22	24.5 $\pm$ 0.3
	M21	263	310	2013/4/4	2013/4/27	2013/4/27	–	–	3017	23	1.00	0	0	–	–
Mean $\pm$ SD		287 $\pm$ 20	360 $\pm$ 76	–	–	–	–	13.7 $\pm$ 4.8	10882 $\pm$ 7926	44.0 $\pm$ 12.6	0.99 $\pm$ 0.04	80 $\pm$ 176	3.2 $\pm$ 2.8	0.24 $\pm$ 0.20	25.4 $\pm$ 0.9

<sup>a</sup>Captured at the spawning ground. <sup>b</sup>M5 and M19 were the same individual monitored in 2012 and 2013

ited number of receivers available (Fig. 2). Preliminary testing indicated that the detection range of each receiver at 50% detection probability was 50 to 100 m. See Nanami et al. 2014 for more detailed protocols of capture, tagging, release, and receiver deployment. Water temperature was measured at 1 h intervals by temperature data loggers (HOBO Water Temp Pro v2, Onset Computer) deployed at the release site and the spawning ground. Animal care and experimental procedures were performed in accordance with the Guidelines for Animal Experimentation of Nagasaki University with approval of the Institutional Animal Care and Use Committee.

## Data analyses

### General detection patterns in acoustic telemetry

Data for the 2 periods of 2 mo each (April 11 to June 10 in 2012 and April 5 to June 6 in 2013) were analysed to elucidate the general spatial patterns of male *E. ongus* associated with reproduction. Since false detection could occur when there were multiple tagged fish within a site (www.vemco.com), we removed any single signal detection within a 24 h period in either the spawning ground or the release site (Meyer et al. 2007, Nanami et al. 2014). To assess the general spatial patterns of fish, the detection number (DN) and the number of days detected (DD) were calculated in both the release site (DN<sub>release</sub> and DD<sub>release</sub>) and the spawning ground (DN<sub>spawning</sub> and DD<sub>spawning</sub>). Then, residency indices (RI) were estimated for both the

release site ( $RI_{\text{release}}$ ) and the spawning ground ( $RI_{\text{spawning}}$ ) by the following formulae:

$$RI_{\text{release}} = \frac{DD_{\text{release}}}{\text{Days between first and last detections} - \text{Duration away} + 1} \quad (1)$$

$$RI_{\text{spawning}} = \frac{DD_{\text{spawning}}}{\text{Duration away}} \quad (2)$$

The date when the last signal was detected in the release site before an absence of at least 4 d was regarded as the departure date, and the date when the first signal was detected after their absence was regarded as the returning date (Fig. 3). The duration between departure date and returning date was regarded as the duration away, which consists of the time for round-trip migrations and the residence time at the spawning ground (Fig. 3).

#### Change in body composition

To observe the general trends of changes in energy reserve and testis size over time during the spawning season, we modelled proximate composition and GSI (testis mass per whole body mass, %) as a function of time using a local polynomial regression model (LOESS smoothing) (Zuur et al. 2009a,b, Nunn et al. 2010). The time-series change in feeding probability was assessed by logistic regression, where fish with empty stomachs and with prey items were regarded

as 0 and 1, respectively. In the logistic regression analysis, the linear predictor of the full model was regarded as a cubic polynomial function of time, and the Akaike information criterion (AIC) was used to select the most parsimonious model. To clarify the timings of departure from and returning to the release site in the male *E. ongus*, the change in the proportion of fish in duration away over time was calculated from the migration data obtained through acoustic telemetry in 2013 using the Kaplan-Meier method (Kleinbaum & Klein 1996). The Kaplan-Meier method can include individuals that never undergo the event of interest as sources of censoring data. Censoring allows for the calculation of probability functions without attributing event times. In this study, the departure from and returning to the release site were regarded as events, while the capture by fisherman or the end of the monitoring period were regarded as censoring. The analyses were conducted using R 3.1.0 (R Foundation for Statistical Computing) with the function *loess* for the LOESS smoothing, the function *glm* for the logistic regression, and a custom program for the Kaplan-Meier method.

#### Relationship between energy reserve and duration away

To examine the relationship between the lipid reserve and duration away, we devised a model composed of lipid reserve, body mass, water temperature, and duration away. If the lipid reserve is the main source of energy and is maximally expended during the duration away, the lipid reserve can be expressed as:

$$\text{Lipid reserve} = \text{Duration away} \times \text{Metabolic rate} \quad (3)$$

In general, the resting metabolic rate of the animals can be expressed by a model that combines allometry and temperature-dependent rate (so-called metabolic theory of ecology), in which the metabolic scaling exponent is 0.75 (Gillooly et al. 2001). However, the intraspecific metabolic scaling exponent (0.75) becomes closer to 1 when the activity level is high (Glazier 2009). Male *E. ongus* swim against strong currents and show agonistic behaviours towards conspecific males at the spawning ground (A. Nanami et al. unpubl. data). They also travel 2.2 to 8.8 km to and from the spawning ground and resident area (Nanami et al. 2015). Therefore, the metabolic rate was regarded as an active metabolic rate, and the scaling exponent of the model for the resting metabolic rate, 0.75 (Gillooly et al. 2001), was substituted by 1:

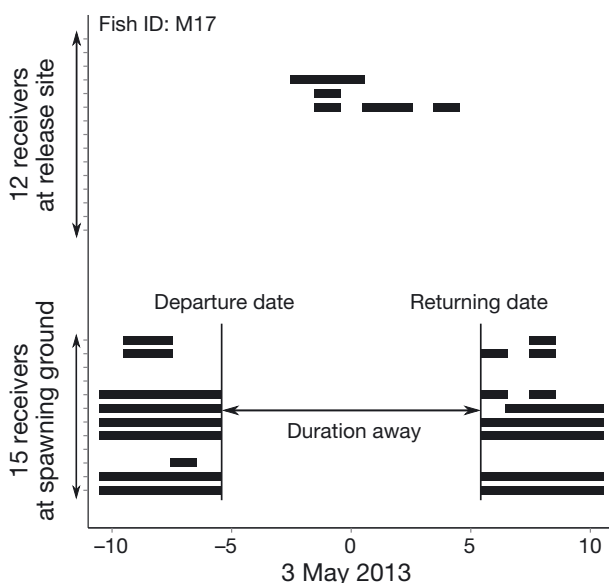


Fig. 3. *Epinephelus ongus*. Typical detection pattern in acoustic telemetry survey, showing the departure date, returning date, and duration away (see 'Materials and methods' for details). Black horizontal bars represent the dates on which receivers detected tagged *E. ongus*

$$\text{Metabolic rate} \propto (\text{Body mass})^1 \times e^{-\frac{E}{k \times Tw}} \quad (4)$$

where  $Tw$  is water temperature;  $E$  is the average activation energy for the rate-limiting enzyme-catalysed biochemical reactions of metabolism, which is relatively constant (approximately 0.6 to 0.7 eV); and  $k$  is Boltzman's constant ( $8.62 \times 10^{-5}$  eV K<sup>-1</sup>). For our application, we use a mean value of 0.65 eV for  $E$ . From Eqs. (3) & (4):

$$\text{Lipid reserve} \propto \text{Duration away} \times \text{Body mass} \times e^{-\frac{E}{k \times Tw}} \quad (5a)$$

$$\frac{\text{Lipid reserve}}{\text{Body mass}} \propto \text{Duration away} \times e^{-\frac{E}{k \times Tw}} \quad (5b)$$

Given that fish experience fluctuating temperature, we let  $Tw$  vary with time. Therefore, the total temperature-dependent metabolism during the duration away is the time integral of the temperature-dependent metabolic rate ( $e^{-\frac{E}{k \times Tw}}$ ). Hence, the temperature-dependent metabolic rate during the duration away can be expressed as:

$$\frac{\int e^{-\frac{E}{k \times Tw}} dTw}{\text{Duration away}} \approx \frac{\sum_{i=1}^n e^{-\frac{E}{k \times Tw_i}}}{n} \quad (6)$$

where  $Tw_i$  is the  $i$ th measurement of water temperature, and  $n$  is the total number of observations of water temperature during the duration away. Thus, from Eqs. (5b) & (6):

$$\frac{\text{Lipid reserve}}{\text{Body mass}} \propto \text{Duration away} \times \frac{\sum_{i=1}^n e^{-\frac{E}{k \times Tw_i}}}{n} \quad (7)$$

Based on Eq. (7), we examined the relationship between the lipid reserve per body mass (lipid density, J g<sup>-1</sup>), duration away, and water temperature. The lipid density was regarded as an objective variable, while duration away and water temperature were regarded as covariates. This was done because the covariate should be known exactly for ordinary linear regression models, and errors can bias the estimated slope to be shallower than the true value (Pearson 1901). Obviously, the lipid density had measurement errors because it was estimated from the relative condition factor (see Eq. 8), while the duration away and water temperature had small errors because they were directly measured by acoustic telemetry and temperature data loggers. Thus, the duration away was regarded as a covariate to examine the relationship between the duration away, water temperature, and lipid density. In addition, it is natural to consider that the duration away and water temperature affect the total lipid expenditure through metabolism. The year (2012 or 2013) was also included as a random factor (Kéry & Schaub 2011) because unknown bio-

logical and physical conditions may cause an inter-annual difference in the relationship. The lipid density of the acoustically tagged individual was estimated from a linear regression with the relative condition factor (Le Cren 1951, Froese 2006):

$$\frac{\text{Lipid reserve}}{\text{Body mass}} \propto \text{Relative condition factor} \quad (8)$$

$$\text{Relative condition factor} \propto 100 \times \frac{\text{Body mass}}{W_E} \quad (9)$$

where  $W_E$  is the length-specific expected body mass predicted from the mass length regression for the population ( $n = 47$ ):

$$W_E = 1.67 \times 10^{-4} \times TL^{2.58} \quad (10)$$

Eq. (7) was fitted using data obtained from acoustic telemetry, and Eq. (8) was fitted using data obtained from the body composition analysis (Fig. 1b). To simultaneously fit these equations, a hierarchical Bayesian model with Markov-chain Monte-Carlo (MCMC) method was used (Kéry & Schaub 2011). The number of draws per chain, thinning rate, burn-in length, and number of chains were set at 200 000, 2, 10 000, and 4, respectively. The deviance information criterion (DIC) was used to select the most parsimonious model. MCMC was conducted using WinBUGS 1.4.3 (The BUGS Project, MRC Biostatistics).

## RESULTS

### General detection patterns in acoustic telemetry

A summary of the acoustic monitoring data for male *Epinephelus ongus* is presented in Table 1. All but 1 fish (M19) were continuously detected by at least 1 receiver per day at the release site during the period except duration away ( $RI_{\text{release}} = 1$ ). M19 was continuously detected at the release site until 5 d after the returning date but was detected intermittently afterwards ( $RI_{\text{release}} = 0.81$ ). These results indicate that the departure and returning dates were accurate in all fish. Ten of the 10 fish (100%) and 10 of the 11 fish (90.9%) departed the release site in 2012 and 2013, respectively. Among the fish that departed, 9 of the 10 fish (90%) and 8 of the 10 fish (80%) were detected at the spawning ground in 2012 and 2013, respectively. Nine of the 10 fish (90%) and 8 of the 10 fish (80%) returned to the release site in 2012 and 2013, respectively. Two fish (M3 in 2012 and M16 in 2013) were captured at the spawning ground by fishermen, 1 fish (M21 in 2013) was not detected after the departure date, and 1 fish (M13 in

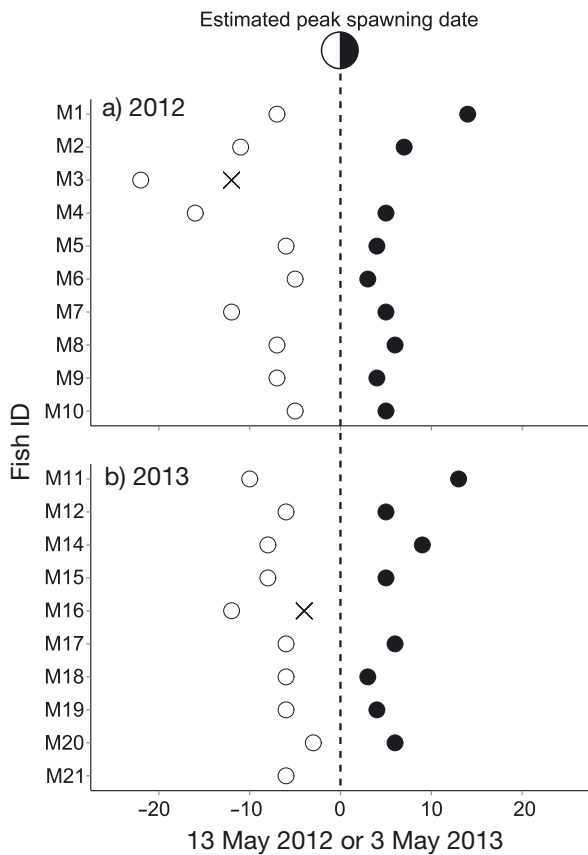


Fig. 4. *Epinephelus ongus*. Departure date (O) and returning date (●). M3 and M16 were captured by fishermen at the spawning ground (x), and M21 was not recorded after departure from the release site. Note that M13 is not shown in the figure because the fish did not depart from the release site throughout the monitoring period

2013) did not depart the release site during the 2 mo period. The fish were only detected intermittently at the spawning ground (Table 1;  $DN_{\text{spawning}}$ , 0 to 784 [range],  $80 \pm 176$  [mean  $\pm$  SD];  $DD_{\text{spawning}}$ , 0 to 10 d,  $3.24 \pm 2.84$  d;  $RI_{\text{spawning}}$ , 0 to 0.60,  $0.24 \pm 0.20$ ), and there was no significant relationship between the duration away and  $DD_{\text{spawning}}$  ( $r^2 = 0.09$ ,  $n = 17$ ,  $p = 0.25$ ). None of the fish left the release site for spawning migration more than once in both years, although the monitoring periods covered the last quarter moon in June.

There were large variations in the departure date, returning date, and duration away in male *E. ongus* (Table 1; Fig. 4). The departure dates were 5 to 22 d ( $9.8 \pm 5.6$  d) and 3 to 12 d ( $7.1 \pm 2.5$  d) before the estimated peak spawning date in 2012 and 2013, respectively. The returning dates were 3 to 14 d ( $5.9 \pm 3.3$  d) and 3 to 13 d ( $6.4 \pm 3.2$  d) after the estimated peak spawning date in 2012 and 2013, respectively. The duration away was 8 to 21 d ( $14.3 \pm 5.0$  d) and 9 to

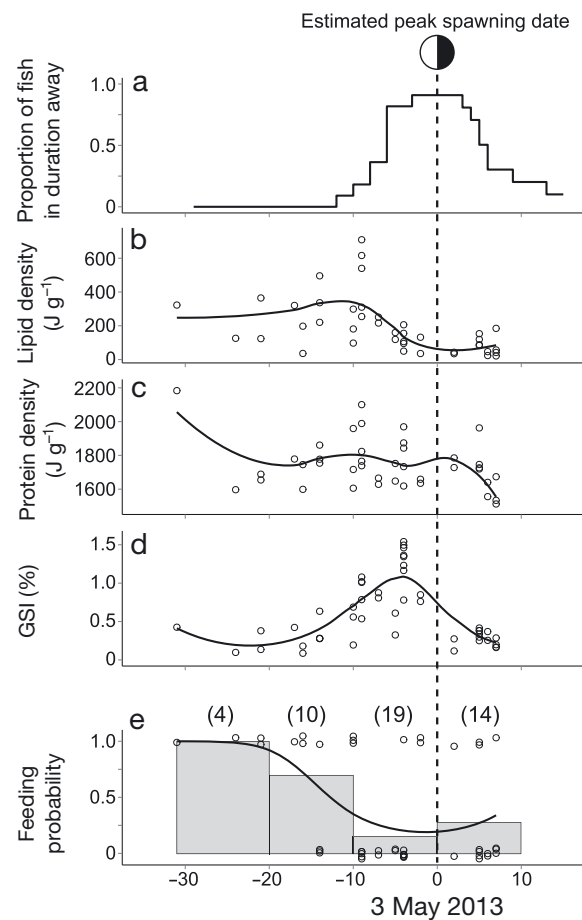


Fig. 5. *Epinephelus ongus*. Time-series of (a) proportion of fish in the duration away (determined by acoustic telemetry,  $n = 11$ ); (b,c) energy density of lipid and protein content, respectively ( $J g^{-1}$ ,  $n = 42$ ); (d) gonadosomatic index (GSI, %,  $n = 47$ ); and (e) feeding probability ( $n = 47$ ). Grey bars in (e) represent the proportion of individuals with prey items in the stomach, and numbers in parenthesis re-present the sample size in each time bin

23 d ( $13.0 \pm 4.8$  d) in 2012 and 2013, respectively. The mean temperatures at the spawning ground during the duration away were  $25.7$  to  $26.4^\circ C$  ( $26.2 \pm 0.2^\circ C$ ) and  $24.5$  to  $24.8^\circ C$  ( $24.6 \pm 0.1^\circ C$ ) in 2012 and 2013, respectively (Table 1).

### Change in body composition

The lipid density decreased from approximately 10 d before through 2 d after the estimated peak spawning date (last quarter of May), corresponding to departure and returning dates, respectively, in earlier individuals (Fig. 5a,b). The protein density only started to decrease when the lipid density neared zero (Fig. 5b,c). The GSI increased from



Table 2. *Epinephelus ongus*. Null and 3 models fitted using a logistic regression, up to a cubic polynomial function of time, to estimate feeding probability. The best-fit model was chosen according to the lowest Akaike information criterion (AIC)

Model	Number of parameters	AIC
Null	1	66.4
Time	2	63.4
Time + Time <sup>2</sup>	3	62.5
Time + Time <sup>2</sup> + Time <sup>3</sup>	4	63.1

approximately 20 to 4 d before the estimated peak spawning date and then sharply decreased (Fig. 5d). The feeding probability sharply decreased around 10 d before the estimated peak spawning date and was very low thereafter (Fig. 5a,e); the lowest AIC was obtained for the model composed of a squared polynomial function of time (Table 2). The values in GSI and feeding probability around the estimated peak spawning date in this study were similar to the values in 2007 to 2009 (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m534p149\\_supp.pdf](http://www.int-res.com/articles/suppl/m534p149_supp.pdf)). The mean energetic density of the testes was  $27.8 \pm 0.5 \text{ J g}^{-1}$  and was composed of  $6.2 \pm 0.2 \text{ J g}^{-1}$  of lipid and  $21.5 \pm 0.5 \text{ J g}^{-1}$  of protein.

### Relationship between energy reserve and duration away

There was a significant positive relationship between relative condition factor and lipid density ( $r^2 = 0.38$ ,  $n = 42$ ,  $p < 0.01$ ; Fig. 6a). There was also a significant positive relationship between relative condition factor and duration away ( $r^2 = 0.39$ ,  $n = 17$ ,  $p < 0.01$ ; Fig. 6b). In the hierarchical Bayesian model, the lowest DIC was obtained for the model composed of only duration away (Table 3). These results indicate that there was a significant positive relationship between duration away and lipid density (Fig. 6c), but water temperature did not significantly affect the relationship.

## DISCUSSION

The decrease in lipid density, decreased probability of food items present in stomachs, and increase in GSI over the spawning season suggest that the fish fed less and mainly used energy reserve for metabolism and testis development during the duration away (Fig. 5). Although the protein density started to

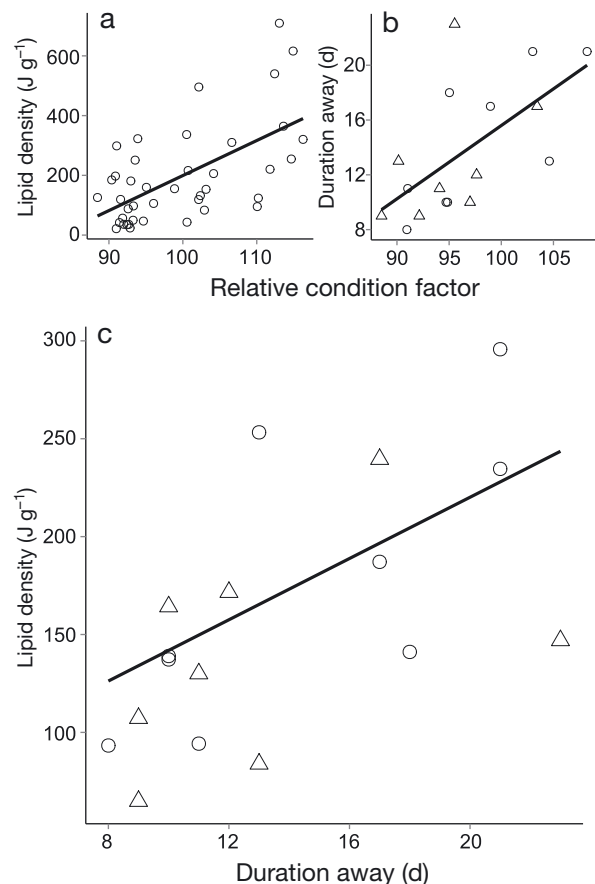


Fig. 6. *Epinephelus ongus*. Relationships between (a) relative condition factor and lipid density ( $n = 42$ ), (b) relative condition factor and duration away ( $n = 17$ ), and (c) duration away and lipid density ( $n = 17$ ). Circles and triangles in (b,c) represent *E. ongus* individuals monitored in 2012 and 2013, respectively

decrease after the lipid density approached zero, this occurred around the returning dates (Fig. 5a–c). These results suggest that the male *Epinephelus ongus* is a capital breeder, or is at least closer to being a capital breeder in the capital–income breeding continuum, and that the lipid was the primary energetic source used. The lipid density and duration away relationship indicated that higher lipid densi-

Table 3. *Epinephelus ongus*. Deviance information criterion (DIC) for each model in the hierarchical Bayesian model

Model	Number of parameters	DIC
Null	1	143
(Duration away)	2	137
(Duration away) $\times \frac{\sum_{i=1}^n e^{-\frac{E}{k \times T w_i}}}{n}$	2	143

ties can be linked to longer times spent for migration and reproduction.

We suggest that the metabolic theory of ecology supports the lipid density and duration away relationship when we include the energy for testis development, as follows. Based on Fig. 6c, the mean daily lipid expenditure was  $7.8 \text{ J d}^{-1} \text{ g}^{-1}$ . A general model, based on fish body mass and temperature (Gillooly et al. 2001), suggested that the resting metabolic rate was  $1.5 \text{ J d}^{-1} \text{ g}^{-1}$ . Metabolic rates during the reproductive activities are considered active rates, since male *E. ongus* migrate 2.2 to 8.8 km to and from the spawning ground and the resident area (Nanami et al. 2015) and show agonistic behaviour towards conspecific males as well as actively swimming against strong currents at the spawning ground (A. Nanami et al. unpubl. data). The active metabolic rates of *E. ongus* in this study (350 g mean body mass) were estimated to be 2 to 3 times the resting metabolic rates (Killen et al. 2007); therefore, the metabolic rate during the reproductive activities was estimated as 3.0 to  $4.5 \text{ J d}^{-1} \text{ g}^{-1}$ . The GSI increased about 1% ( $27.8 \text{ J g}^{-1}$ : lipid,  $6.2 \text{ J g}^{-1}$ ; protein,  $21.5 \text{ J g}^{-1}$ ) during the duration away (13.7 d on average) (Fig. 5d). Energy conversion costs for lipid and protein deposition were reported to be 10 and 79%, respectively, in another grouper (white grouper *E. aeneus*) (Lupatsch et al. 2003); therefore, daily energy expenditure for testis development per body mass was estimated as  $3.6 \text{ J d}^{-1} \text{ g}^{-1}$  for *E. ongus*. The daily lipid expenditure we estimated ( $7.8 \text{ J d}^{-1} \text{ g}^{-1}$ ) falls within the range of the total daily energy expenditure for metabolism and testis development ( $6.6$  to  $8.1 \text{ J d}^{-1} \text{ g}^{-1}$ ).

Contrary to our prediction, there was no significant relationship between the duration away and  $DD_{\text{spawning}}$ . As the duration away consists of the time for round-trip migrations and residence time at the spawning ground, 2 possible explanations may have caused this pattern: (1) There was actually a positive relationship between the duration away and the residence time at the spawning ground, but a substantial individual variation in the time elapsed outside of the detection range of receivers within the spawning ground (Fig. 2) masked the actual pattern. (2) There was a large individual variation in the time elapsed for the round-trip migrations, and thus the duration away did not represent the residence time at the spawning ground. The second explanation is unlikely because, in the case of another species (bluehead wrasse *Thalassoma bifasciatum*) that forms spawning aggregations, there are small individual variations in migration times between the feeding ground and the spawning ground when distances are

the same among individuals (Warner 1995), and the distance between the release site and the spawning ground were the same for all tagged *E. ongus* in this study (Fig. 2). Additionally, fish were detected at the spawning ground only within a limited number of times and days (Fig. 3; Table 1), probably because the detection ranges of receivers could only cover a small portion of the whole spawning ground (Fig. 2). Given these facts, it was more likely that the duration away was representative of the residence time at the spawning ground; however, we acknowledge that we could not detect the actual arrival and departure dates at the spawning ground due to the small area covered by the array of receivers. Further research using a larger number of receivers covering a wider area of the spawning ground is required to confirm this hypothesis.

This study, together with a previous study (Nanami et al. 2014), indicates that the individual variation in duration away is large and dependent on the pre-migration energetic state in males, whereas the variation is small and unrelated to the energetic state in females (see Nanami et al. 2014 and Table S2 in the Supplement for the female data). This sex-specific difference might be related to the different energy allocation tactics of males and females. The previous study on the gonadal histology of *E. ongus* indicated that the peak GSI of males around the peak spawning date was relatively low (functional maturation stage,  $1.1 \pm 0.5$ ), whereas the peak GSI of females was relatively high (hydrated stage,  $22.1 \pm 7.7$ ) (Ohta & Ebisawa 2015). Energy reserve can be allocated to either metabolic cost during the duration away or to gonads, and the individual reproductive potential per season is determined by the number of spawning events and the number of spawning or fertilized eggs per spawning event (Murua et al. 2003, McBride et al. 2015). The number of spawning events is related to the residence time at the spawning ground, but the number of spawning or fertilized eggs per spawning event is not related to the residence time at the spawning ground (Murua et al. 2003, Loher 2011, Grabowski et al. 2014). Thus, it was likely that the male *E. ongus* mainly allocated energy reserve to the metabolic cost for increasing the duration away and possibly also to the testis to increase the number of spawning events, which was related to the residence time at the spawning ground. Alternatively, females may allocate energy reserve to the ovaries to increase the number of eggs per spawning event, which was irrespective of the residence time at the spawning ground.

Our results are significant for the management of *E. ongus*. Fishing has been prohibited in the largest FSA of *E. ongus* (Fig. 2a) for short periods (5 to 10 d) around the last quarter moon of 1 or 2 consecutive months between April and June (estimated peak spawning date) since 2010. This restricted closure period was determined based on the fact that the catchment and reproduction of *E. ongus* were concentrated within a specific lunar phase (Ohta & Ebisawa 2015). Periods of closure can protect some males and most females; however, males that stay longer at the spawning ground will be more vulnerable to fishing. Before the short prohibition periods that began in 2010, males were caught from 1 mo before through 1 wk after the estimated peak spawning date, while most females were caught only during the week of this date (Ohta & Ebisawa 2015). In this study, fisherman caught 2 of 21 tagged males (10%) at the spawning ground, and these 2 captured males were the earliest individuals that left the release site for the spawning ground in 2012 and 2013 (Table 1; Fig. 4). In addition, the duration away of males ( $13.7 \pm 4.8$  d) was longer than that of females ( $8.0 \pm 1.7$  d) (Nanami et al. 2014), and fisherman caught none of the 35 tagged females (see Table S2 for details of the female data). Our observations and those of Ohta & Ebisawa (2015) suggest that fishing pressure was biased towards males and specifically towards fatter males that had higher lipid density, since the residence time at the spawning ground might be longer in these males.

Selective fishing of fatter males has strong potential to negatively impact population size and stability through multiple pathways (Heino et al. 2013, van Overzee & Rijnsdorp 2015). First, selective fishing of males would skew the sex ratio towards females. The skewed sex ratio could reduce the mate encounter rate and sperm availability for females (Shapiro et al. 1994, Rowe & Hutchings 2003, van Overzee & Rijnsdorp 2015), which may lead to a decline in the reproductive success of females. In addition, as *E. ongus* is a protogynous hermaphrodite (Maplestone et al. 2009), the skewed sex ratio could eventually decrease the size at sex reversal and thus decrease the mean size of mature females, as shown in other protogynous hermaphroditic species (Platten et al. 2002, Hamilton et al. 2007). This may in turn decrease the reproductive output of the population because total fecundity (total number of spawning eggs per season) is proportional to the size of females (Ohta & Ebisawa 2015). Second, selective fishing of fatter males would increase the proportion of thinner males in the population. This could decrease the fer-

tilization success of each spawning event because the male condition is related to sperm quality and fertilization success (Rakitin et al. 1999). In addition, the increased proportion of thinner males could affect offspring growth and survival through paternal effects (Green & McCormick 2005). Last, if being fatter is a heritable trait, the selective fishing of fatter males could cause fisheries-induced evolution. The fisheries-induced evolution of life history traits such as size at maturation and growth rate has been reported in many fish species (Jørgensen et al. 2007, Kuparinen & Merilä 2007), and the evolution of behavioural and physiological traits has recently started to be recognised (Cooke et al. 2007, Biro & Post 2008, Uusi-Heikkilä et al. 2008, Sutter et al. 2012). Fisheries-induced evolution could further exacerbate the local population state due to the genetic basis of phenotypic change. When the phenotypic change is based on plasticity, the over-exploited population can rapidly recover after the implementation of fisheries management, whereas when the phenotypic change is based on genetics, the population can only slowly recover after the implementation (Conover et al. 2009, Enberg et al. 2009). Considering these potential threats, an extended closure period to protect fatter males in the *E. ongus* population is recommended.

Finally, our results show a clear relationship between energy reserve and duration away in the male *E. ongus*. Our results further suggest that selective fishing of males with higher lipid density may occur in *E. ongus*. These facts highlight the importance of linking energy reserves to reproductive behaviours in other species forming spawning aggregations.

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