Journal of FISH BIOLOGY

Journal of Fish Biology (2015) **86**, 1396–1415
doi:10.1111/jfb.12649, available online at wileyonlinelibrary.com

Diet and cannibalism in plainfin midshipman *Porichthys notatus*

K. M. Cogliati* † ‡, C. Danukarjanto*†, A. C. Pereira*, M. J. Lau§,
A. Hassan*, A. F. Mistakidis*, B. M. Bolker||¶, B. D. Neff§
and S. Balshine*

**Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON, L8S 4K1 Canada, §Department of Biology, University of Western Ontario, 1151 Richmond Street, London, ON, N6A 5B7 Canada, ||Department of Mathematics & Statistics, McMaster University, 1280 Main Street West, Hamilton, ON, L8S 4K1 Canada and ¶Department of Biology, McMaster University, 1280 Main Street West, Hamilton, ON, L8S 4K1 Canada*

(Received 27 February 2014, Accepted 30 January 2015)

The macroscopic and microscopic diversity of potential food items available in the nests of plainfin midshipman *Porichthys notatus* were quantified and compared with items that were found in the stomach and intestine (digestive tract) of the guarding males. In this species, males occur as one of two possible reproductive morphs: guarder males that care for young and sneaker males that parasitize the courtship and care of guarder males. Although it was predicted that guarder males would have fewer feeding opportunities due to their confinement to the nest, they in fact had more food items in their digestive tracts than did sneaker males and females. Date in the breeding season (a proxy of care duration) and body condition were not correlated with the amount of food consumed by guarder males. The main type of food consumed was *P. notatus* embryos; 69% of all guarder males sampled had cannibalized offspring. By comparing the diet of both sexes and tactics, this study sheds light on some of the strategies designed to cope with the costs of providing parental care.

Key words: alternative reproductive tactics; body condition; food abundance and availability; parental care.

INTRODUCTION

Of the >514 families of fishes, 20% show some form of parental care for offspring (Gross & Sargent, 1985; Mank *et al.*, 2005; Nelson, 2006). Parental care in fishes includes activities such as hiding or guarding embryos, chasing off predators, fanning to ventilate embryos and removing debris or microorganisms from the embryos (Blumer, 1982). Such caring behaviours not only increase rates of offspring development and survivorship, but also carry costs for the caring parent including reductions in survival,

---

‡Author to whom correspondence should be addressed. Tel.: +1 905 525 9140 ext. 26037; email: k.cogliati@gmail.com

†Theses authors contributed equally to this manuscript.

mating opportunities and fecundity (Trivers, 1972; Gross & Sargent, 1985; Smith & Wootton, 1995).

Many of the costs associated with care are a result of decreased opportunities to feed. There can be significant physical deterioration and a reduction of energy stores during care (Marconato & Bisazza, 1988; Smith, 1993; Cooke *et al.*, 2002; Cargnelli & Neff, 2006; Ito *et al.*, 2010). For example, in the stream goby *Rhinogobius* sp., body condition and liver size, two measures of energy stores, both decreased in caring males as the breeding season progressed (Ito *et al.*, 2010). Indeed, 68% of *Rhinogobius* sp. guarding males did not eat during the 4 week period between nest building and egg hatching (Ito & Yanagisawa, 2000; Ito *et al.*, 2010). Decreased body condition can have effects on future growth and survival. For example, individuals in poor condition are more likely to be captured by predators (Fitzgibbon & Fanshawe, 1989; Mesa *et al.*, 1994), while reduced growth can influence future mating opportunities (Andersson, 1994) and fecundity (Balshine-Earn, 1995). One possible response to the decreased opportunities to feed during care is cannibalism of embryos (Rohwer, 1978). Theory suggests that cannibalism can be adaptive even when the parents are related to the consumed offspring, because cannibalism can enable parents to recoup the necessary energy or important nutrients needed to continue caring for the remaining offspring and thus increase the survival of the brood as a whole (Rohwer, 1978; Sargent, 1992; Klug *et al.*, 2006; Klug & Bonsall, 2007).

The high costs of parental care are thought to select for the evolution of alternative reproductive tactics (ART), where some individuals parasitize the care and courtship of other conspecifics (Gross, 1996; Taborsky *et al.*, 2008). ARTs are considered discontinuous variations in behaviours and other traits that represent alternative ways to achieve and maximize fitness (Gross, 1984; Taborsky, 1997). This mating system is especially common among fishes, and typically presents itself as two male reproductive morphs broadly classified as guarder and cuckolder males (Taborsky *et al.*, 2008). Guarder males actively compete for access to resources or females, have secondary sexual characteristics, defend breeding territories and often provide parental care (Caro & Bateson, 1986). In contrast, cuckolder males exploit the investment of guarder males by satellite or sneak-spawning using stealth, speed or female mimicry to gain fertilizations (Taborsky *et al.*, 2008). Cuckolder males do not provide care and invest instead in gonad size and sperm quality (Taborsky, 1998). Using a fish species with well-characterized ARTs, the plainfin midshipman *Porichthys notatus* Girard 1854, the potential costs of lost feeding opportunities associated with parental care by guarder males were quantified and compared across tactics and sexes.

The mating system and caring behaviour of *P. notatus* make it an excellent candidate for investigating the costs of parental care associated with lost feeding opportunities. This fish is a nocturnally active, deep-water species found along the Pacific coast of North America from Sitka, Alaska, U.S.A., to Magdalena Bay, Mexico (Arora, 1948; Walker & Rosenblatt, 1988). The distribution of this species, however, shows a break point along the Oregon coast, with a northern population stretching from Oregon to Alaska and a southern population stretching from Oregon to Mexico (Warner & Case, 1980; Thompson & Tsuji, 1989; Harper & Case, 1999; Cogliati *et al.*, 2014*a*). *Porichthys notatus* males occur as one of the two morphs called either guarder (type I) or sneaker (type II) males; the morphs are anatomically, physiologically and behaviourally distinct (Brantley & Bass, 1994). Guarder males are eight times larger in body mass than sneaker males. They build and defend nests under rocks in the intertidal zone during the spawning period and use acoustic signals to court females (Brantley & Bass, 1994). Females lay all of their eggs in a nest and will leave once spawning is completed, relinquishing all parental duties to the guarder males (Brantley & Bass, 1994). The guarder males will spend up to 4 months caring for the embryos by guarding them from predators, brushing the embryos with their bodies or fins to remove debris and fanning to oxygenate them until they are free-swimming (Arora, 1948; Brantley & Bass, 1994). While providing parental care for their offspring, guarder males are confined to their nest cavity and do not appear to leave (Arora, 1948; Brantley & Bass, 1994). In contrast, sneaker males eschew all courting, territorial and egg-tending behaviour and instead simply steal fertilizations from guarder males when females are present (Brantley & Bass, 1994). Sneaker males invest heavily in gonadal tissue and sperm competitive traits, and have testes that, after controlling for differences in body size, are up to seven times larger than the testes of guarder males (Brantley & Bass, 1994). Spawning takes several hours to complete, after which females and sneaker males leave the nest (Brantley & Bass, 1994). Previous studies of *P. notatus* have anecdotally described aspects of their diet, including an investigation of the luciferin-rich ostracods *Vargula hilgendorfii* that are found in the southern but not in the northern population (Hubbs, 1920; Arora, 1948; Warner & Case, 1980; Sisneros *et al.*, 2009). No detailed analyses of diet content nor of differences in diet between male tactics and between the sexes, however, have been conducted.

In this study, observations were first made to assess food availability in the nests of *P. notatus*. Next, by analysing the number and diversity of items found in the stomachs and intestines (digestive tracts), the diet of guarder males was compared with the observed food availability in the nests. Also, the diet of sneaker males and females (collected opportunistically whenever they were found from within the nests) was compared with that of the guarder males. Three predictions were tested using the observations of food availability and diet. First, because guarding males are confined to the nest during a long parental care period, it was predicted that the body condition of guarding males would decrease over the course of the breeding season (as proxy for the duration of care). Second, as fish body condition deteriorated, food intake would increase. Third, it was also predicted that guarder males, because of their limited foraging abilities during care, would have less food intake than sneaker males and females who are typically in the nest for only a few hours and therefore have more opportunities to feed.

MATERIALS AND METHODS

SAMPLING LOCATIONS

From 10 May 2010 to 15 July 2010, *P. notatus* nests were sampled from rocky beaches during low tide in the intertidal zone in British Columbia, Canada [Ladysmith Inlet: 49° 01′ N; 123° 83′ W and Mill Bay: 48° 63′ N; 123° 53′ W on the eastern coast of Vancouver Island, Fig. 1(a); and Crescent Beach: 49° 04′ N; 122° 88′ W in South Surrey, Fig. 1(b)]. Additionally, from 31 May 2011 to 17 July 2011, nests were sampled from Ladysmith Inlet and Crescent Beach in British Columbia, from Washington [Seal Rock: 47° 71′ N; 122° 88′ W, Fig. 1(c)], and from California [Tomales Bay: 38° 15′ N; 122° 90′ W, Fig. 1(d)]. Samples collected from British Columbia and Washington represent the north population, while samples collected from California represent the south population (Warner & Case, 1980; Cogliati *et al.*, 2014*a*). Note that observations of food availability and the comparison between food availability and guarder male diet were made using samples collected only from British Columbia in 2010 and 2011.

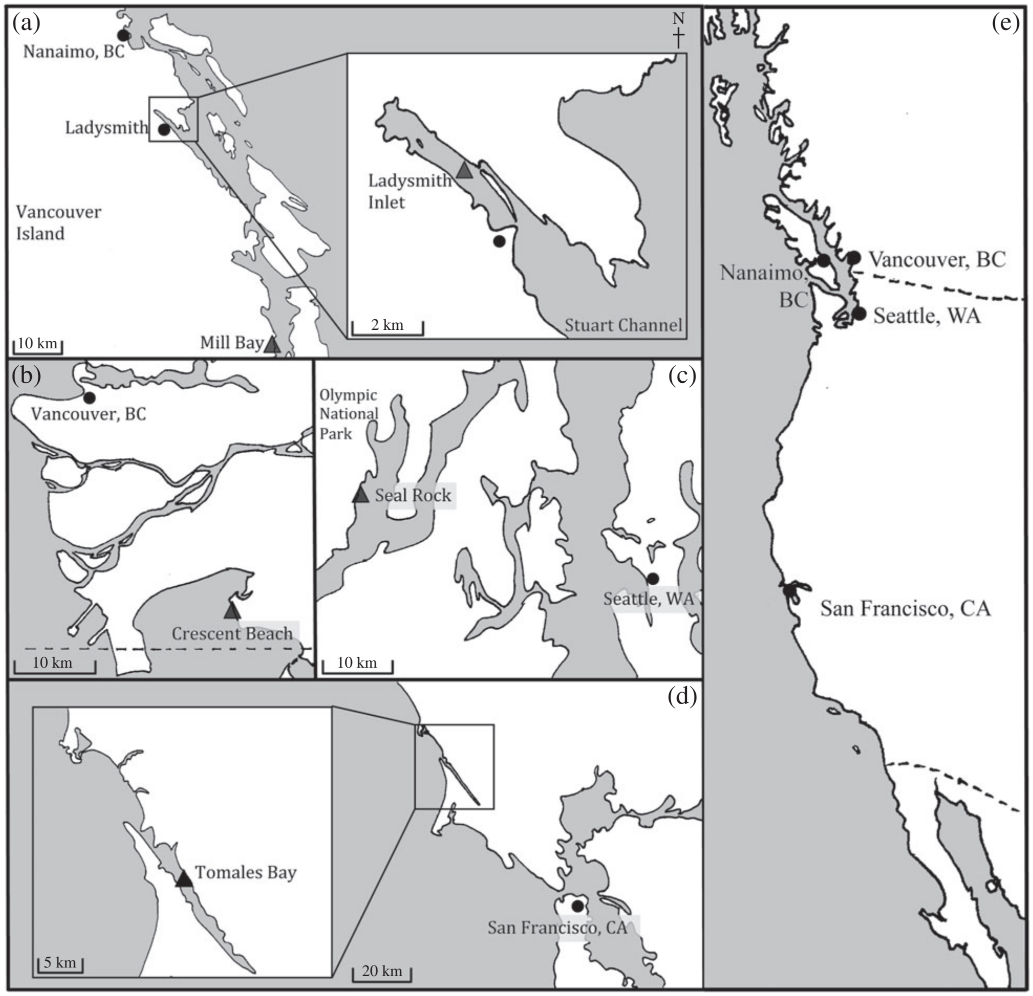

Fig. 1. Location of study sites (▲) along the Pacific coast of North America, with reference cities labelled (●). (a) Ladysmith Inlet and Mill Bay study sites on the east coast of Vancouver Island, south of Nanaimo, BC. (b) The study site at Crescent Beach on the west coast of mainland BC, south of Vancouver. (c) The Seal Rock study site in Puget Sound, south of Strait of Juan de Fuca. This study site is located east of Olympic National Park and west of Seattle, WA. (d) The Tomales Bay study site located on the west coast of California, north of San Francisco. Scales shown at bottom left are specific to each location. (e) The west coast of North America, for reference.

OBSERVATIONS OF FOOD AVAILABILITY IN NESTS

Macroscopic, in nests

To assess possible food resources immediately available to guarder males during the reproductive season, the species diversity in 105 nests across all sites in British Columbia was quantified in June 2010 (Ladysmith Inlet, $n = 69$; Mill Bay, $n = 8$; Crescent Beach, $n = 28$). Individual rocks were overturned to expose the nest cavity, and immediately following the opening of each nest cavity, one researcher conducted a visual count of all mobile organisms, followed by a visual count of the sessile organisms found on the overturned rock surfaces (*i.e.* the ceiling of the nests) and in the cavities/depressions underneath the rock surface. All macroscopic organisms that were quantified within the nests were identified to the lowest possible taxonomic rank.

Microscopic, on broods

To assess the diversity of microscopic food items directly on the embryos across the reproductive season, organisms from the broods of 25 nests were collected in British Columbia in 2011. Early in the breeding season (June), 15 nests were sampled, whereas 10 nests were sampled later in the breeding season (July). To collect the organisms on the broods, a flexible funnel was positioned below the embryos, the embryos were washed using 200 ml of filtered seawater (filtered through a 40 μ cell strainer) and everything on the broods was collected into a small container. These washings were then poured through a square of 65 micron plankton net and the mesh plankton net and its contents were transferred to a 50 ml tube filled with 95% ethanol for storage. Once the washings were collected, the guarder male from each nest was removed and euthanized so that the contents of its digestive tract could be compared with organisms from the washings at the nest. The developmental stage of all offspring found in the nests was also recorded (*i.e.* whether the nest contained eggs only, both eggs and hatched embryos or hatched embryos only). This order of development generally follows the progression of the breeding season; most nests contain eggs early in the season and contain hatched embryos late in the season (Cogliati *et al.*, 2013). Microscopic samples collected were processed in the laboratory.

OBSERVATIONS OF DIET FOR GUARDER MALES, SNEAKER MALES AND FEMALES

A total of 151 fish across all sites and both years were collected from nests and their body mass (in g), total length (L_T in cm) and standard length (L_S in cm) were measured. The sex of each fish was recorded based on the shape of their urogenital papilla, overall colouration and gonads once dissected. Fish were sampled by overturning rocks to locate nests and guarder males, and females and sneaker males were opportunistically collected from the nests. Morph type was determined using criteria that have been well developed for this species, including body size and the gonado-somatic index (I_G: the ratio of gonad mass to body mass; Brantley & Bass, 1994; Bass, 1996). Overall, 123 guarder males, 10 sneaker males and 18 females were sampled. A solution of benzocaine (Sigma-Aldrich; www.sigmaaldrich.com), ethanol and seawater, followed by cervical severance was used to euthanize fish. The digestive tract of each fish was dissected by making an incision from the gills to the anus to remove the whole digestive tract including the intestine, which was then weighed (G_F in g). The contents of the digestive tract were rolled out from the anterior to posterior end using a probe and the contents were preserved in 95% ethanol. The empty digestive tract was then reweighed (G_E) and the mass of the digestive tract contents alone (G_C) was determined, where $G_C = G_F - G_E$. Collected digestive tract samples were processed in the laboratory.

MICROSCOPIC ANALYSIS

The microscopic organisms were quantified for the 25 embryo washings and the digestive tracts of 101 of the 151 *P. notatus* collected from the nests (73 guarder males, 10 sneaker males and 18 females). In this sub-set of 101 digestive tract samples, all females and sneaker males were included, and the 73 guarder male samples used were haphazardly chosen. The researchers who quantified organisms in the nest washings and in the digestive tract samples were blind to the identity of the location of the nest and reproductive type sampled. All organisms caught in the plankton net from the embryo washings were removed by soaking the net for 48 h and rinsing with 95% ethanol. Afterwards, the net was passed under a Nikon SMZ 1500 stereomicroscope fitted with a ×1 WD54 lens (Nikon Instruments Incorporated; www.nikoninstruments.com) and checked for any remaining organisms not removed by the rinsing. Any remaining organisms on the net were added to the sample. Excess ethanol in the sample was decanted with a pipette, leaving each sample in 20 ml of ethanol. This solution was transferred to a gridded 90 mm^2 Petri dish with 13 mm^2 × 13 mm^2 and illuminated using a Fibre-Lite MI-150 High Intensity Illuminator (Dolan-Jenner Industries; www.dolan-jenner.com) under the microscope. Organisms were identified to the lowest feasible taxonomic rank, each type of organism was counted and all organisms were extracted for preservation in 95% ethanol. The preserved digestive tract samples were examined using the same protocols, except that the samples were transferred immediately to the Petri dish without a 48 h soaking period. Following previous studies, invertebrates such as crustaceans, gastropods and zooplankton, as well as *P. notatus* offspring, were classified as food items (Hubbs, 1920; Arora, 1948; Sisneros *et al.*, 2009). Cannibalism had been observed previously by Mensinger & Case (1991) and Sisneros *et al.* (2009) but the extent of this behaviour is yet to be quantified. Abiotic items and plant matter were classified as non-food items. Although plant matter may provide some energy, *P. notatus* are ambush predators (Nelson, 2006). Thus, plant matter is an unlikely component of their diet and rather probably ingested accidentally.

Of the original 151 fish collected, 50 guarder males were not scrutinized for microscopic analysis. Instead, the digestive tracts of these remaining 50 guarder males (from samples collected in British Columbia in 2010) were analysed for instances of cannibalism only. Altogether, rates of cannibalism for guarder males were assessed using the data from these 50 guarder males in addition to the original 73 guarder males scrutinized for whole-digestive tract contents.

CANNIBALISM ANALYSIS

To explore whether guarding males were consuming their own young, whenever instances of cannibalism were detected during examination of the digestive tracts, intact embryos were removed from the samples for genetic analyses. Using standard extraction protocol, DNA was extracted from a sub-set of these embryos and from the associated fin clips collected from the guarder males associated with the nest during field sampling. Sixty-seven embryos found in the digestive tracts of 11 males were genotyped using six microsatellite loci developed for *P. notatus* (Suk *et al.*, 2009; Cogliati *et al.*, 2013). Following the methods outlined in the study of Cogliati *et al.* (2013), fragment analyses were conducted on a capillary sequencer (CEQ 8000, Beckman Coulter; www.beckmancoulter.com) and alleles from each locus were scored based on characteristic peaks. The two-sex paternity model (Neff *et al.*, 2000*a*, *b*; Neff, 2001) was used to calculate a paternity value for each male based on the embryos found in their digestive tracts.

DATA PREPARATION

For each nest, brood and digestive tract examined, three measures were calculated: richness which refers to the number of different organism classifications found per sample, abundance which refers to the total number of organisms found per sample and frequency of occurrence, which refers to the total number of samples in which a specific type of organism occurred. Specifically for the digestive tracts examined, two additional measures were calculated. First, digestive tract mass was used as a measure of overall fullness. For this measure, differences in body mass were controlled for by dividing the mass of the digestive tract contents (G_C) with the eviscerated body mass (M_E). Eviscerated body mass was calculated as the total mass of the fish (M_T) minus the mass of the digestive tract contents ($M_E = M_T - G_C$). Second, the percentage of empty digestive tracts was calculated for both tactics and sexes.

Body condition was characterized by plotting $\log_{10} M_E$ with $\log_{10} L_S$ of the fish and obtaining the residuals from a linear regression (Jakob *et al.*, 1996). A positive value signified an individual in better condition compared with the average and a negative value represented individuals who were on average in poor condition. Following well-established protocols, the hepato-somatic index of each fish was calculated using the formula: $I_H = 100\, M_L\, M_E^{-1}$, where M_L is liver mass (Htun-Han, 1978; Chellappa *et al.*, 1995). The digestive tract mass for one guarder male and the body condition for two females were not collected due to technical problems with the balance in the field.

STATISTICAL ANALYSES

All statistical analyses were performed using JMP 10.0 (SAS Institute Inc.; www.jmp.com), with the exception of the generalized linear models (GLM), which were conducted in R v2.15.2 (The R Foundation for Statistical Computing; www.r-project.org). Data were $\log_{10}$ transformed to reach normality wherever possible and count data (abundance measure) were analysed using negative binomial GLMs (nbGLM) to accommodate the over-dispersed Poisson distributed data. Otherwise, all data that did not conform to normality or that violated the assumption of homogeneity of variance were analysed using non-parametric statistics (Kruskal–Wallis and Wilcoxon tests).

To address the first prediction (body condition deteriorates with the duration of care), linear regressions were used to correlate both measures of guarder male body condition with time in the breeding season. Time in the breeding season corresponded to the Julian date of sample collection. The collection date was used as a proxy for the duration of parental care provided by guarder males, so for example, males collected later in the season were assumed to be from males that had been providing care for longer than the males collected earlier in the breeding season. A linear regression was also used to assess the relationship between condition and digestive tract mass, while condition and food abundance in the digestive tract were assessed using an nbGLM. For the second prediction (as body condition deteriorates, food intake would increase), food availability and guarder male diet were assessed. The availability of food on the broods over the reproductive season was investigated using *t*-tests and ANOVA. Here, early in the season *v.* late in the season as well as the developmental stage of the offspring in the nests were used as categorical predictor variables. Food abundance (in the digestive tract) and digestive tract mass were assessed across the breeding season using nbGLM and linear regression, respectively, with Julian date as the predictor variable. To test the third prediction (guarder males would have less food in their digestive tracts than sneaker males and females), sex and tactic differences in diet were examined using non-parametric tests followed by *post hoc* analyses. For food abundance differences specifically, digestive-tract mass was analysed using ANOVA with a *post hoc* analysis. Finally, parasitic worms and instances of cannibalism were identified in the digestive tracts of these fish. Because these instances were both overdispersed and count data, sex and tactic differences were analysed in these occurrences using non-parametric analyses and nbGLM.

RESULTS

OBSERVATIONS OF FOOD AVAILABILITY IN NESTS

Macroscopic, in nests

In the 105 nests sampled macroscopically, 43 different organisms were identified, with an average of six different types of organisms per nest (richness range: 0–11 types of organisms). Many of the organisms found in nests were also abundant with an average of 91 total organisms per nest (range: 0–1089 organisms). Shore crabs *Hemigrapsus* spp. (present in 88% of nests), hermit crabs *Pagurus* spp. (73% of nests) and barnacles *Balanus glandula* (64% of nests) were by far the most frequently occurring organisms found inside *P. notatus* nests. The 10 organisms with the greatest frequency of occurrence in *P. notatus* nests, along with their abundance values, are plotted in Fig. 2(a).

Microscopic, on broods

On the 25 broods examined, 20 different microscopic organisms were identified. In terms of richness, there were on average seven different organisms per brood (range: 2–12 organisms). The average abundance of organisms found on the broods was 480 per brood (range: 53–2054). Copepods were the most common organisms found on the broods and were present in every nest sampled. The distribution of the 10 organisms with the greatest frequency of occurrence on broods, along with abundance values, is plotted in Fig. 2(b).

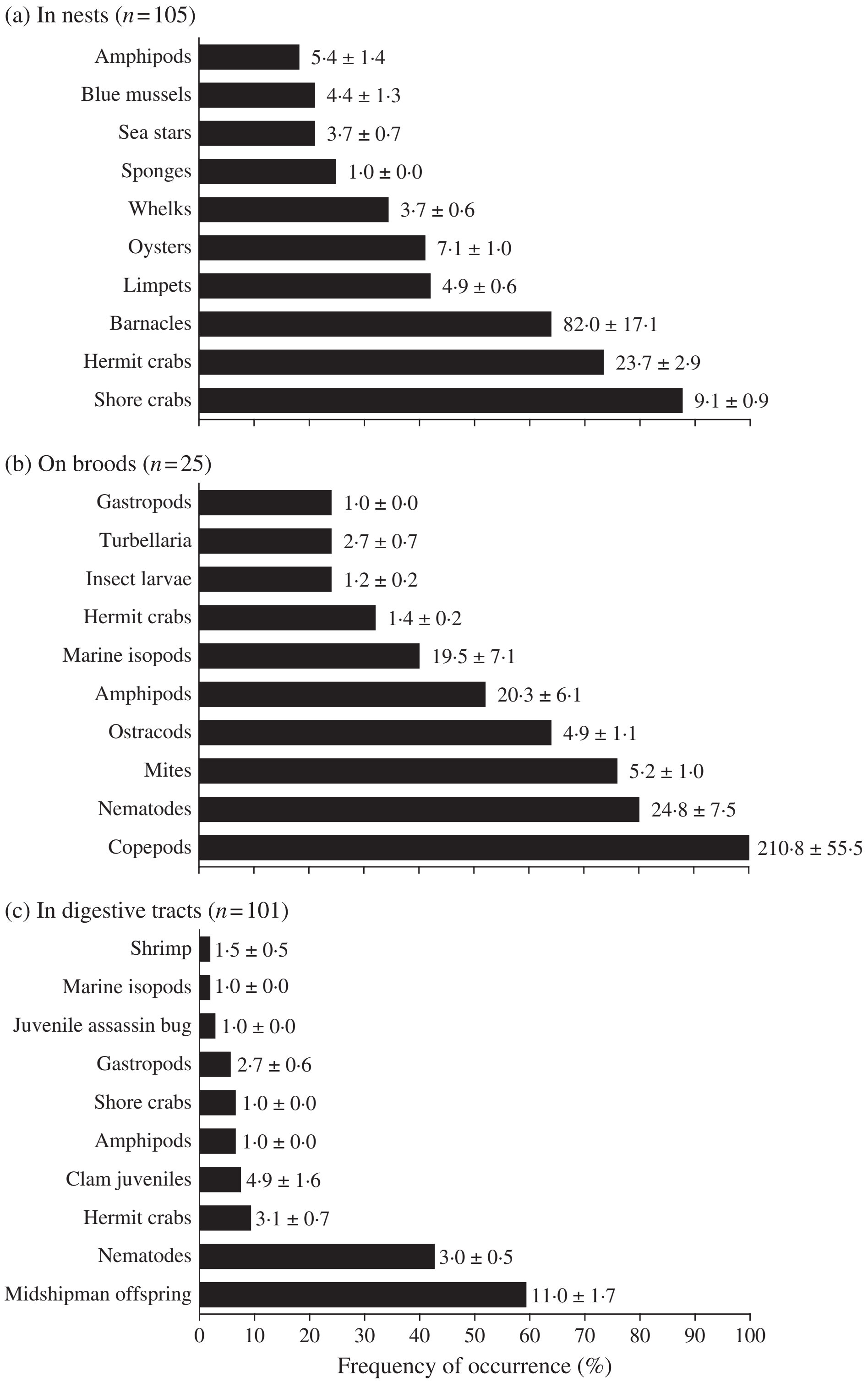

FIG. 2. Frequency of occurrence for the 10 most commonly found organisms (a) in the nests, (b) on the broods and (c) in the digestive tracts of reproductively mature *Porichthys notatus*. Numerical values show the mean ± S.E. abundance of each organism per sample, excluding samples from which the organism was not found.

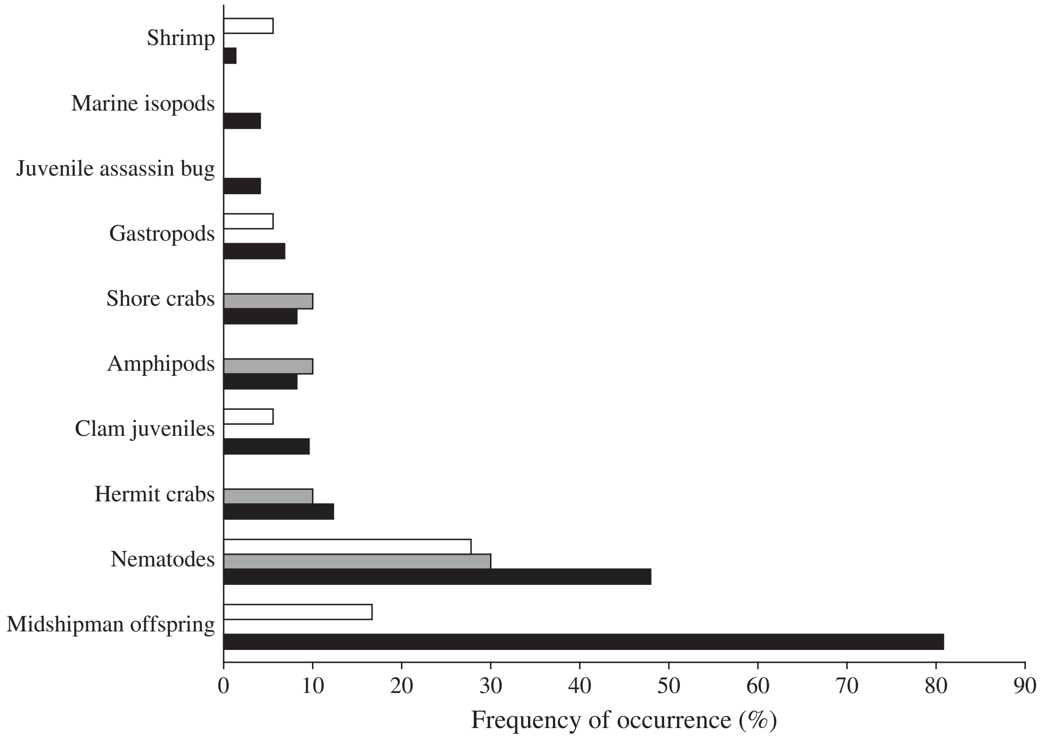

FIG. 3. Frequency of occurrence for the 10 most commonly found organisms in guarder male (■; $n = 73$), sneaker male (▨; $n = 10$) and female (□; $n = 18$) *Porichthys notatus*.

OBSERVATIONS OF DIET FOR GUARDER MALES, SNEAKER MALES AND FEMALES

Across the 101 fish examined in detail for digestive tract content, a total of 50 different items in the digestive tracts were found of which 18 could be classified as food. Five items were various species of parasites (one species of Acanthocephala, one species of Trematoda, one species of Cestoda and two unknown species) and the remaining 27 items were objects such as shell fragments and various classes of sediment and plant matter and so were classified as non-food, as they were probably ingested accidentally. Only food items were considered in the subsequent analyses. Across all samples collected, species richness in the digestive tract was low with an average of two different organisms found (range: 0–5); abundance was also low with an average of nine items per digestive tract (range: 0–67). The distribution of the 10 most frequently occurring organisms in the digestive tracts of fish, along with abundance values, is plotted in Fig. 2(c). Across all fish sampled, 21% of digestive tracts were empty (percentage of empty digestive tracts; 7% of guarder males had empty digestive tracts, 6% of females and 50% of sneaker males). *Porichthys notatus* offspring (eggs, egg casings or hatched embryos) were the most frequent organism found in the digestive tracts and were found in 58% of all the fish examined. The distribution of the 10 most frequently occurring organisms in the digestive tracts separated by sex and tactic type is plotted in Fig. 3.

For guarder males only, richness and abundance were compared across sampling locations (British Columbia, California and Washington). Only guarder males were investigated here as they are represented across all sites while females and sneaker

TABLE I. Digestive tract content breakdown for guarder male *Porichthys notatus* based on sampling location. The table shows the 10 organisms with the highest frequency of occurrence based on all samples (see Fig. 3) and parasites

	British Columbia ($n = 53$)		California ($n = 14$)		Washington ($n = 6$)	
Organism	FO	Mean ± S.E.	FO	Mean ± S.E.	FO	Mean ± S.E.
Shrimp	0	0	1	2·0	0	0
Marine isopods	1	1·0	1	1·0	0	0
Juvenile assassin bug	3	1·0 ± 0·0	0	0	0	0
Gastropods	4	2·3 ± 0·5	1	5·0	0	0
Shore crabs	5	1·0 ± 0·0	0	0	1	1·0
Amphipods	3	1·0 ± 0·0	3	1·0 ± 0·0	0	0
Clam juveniles	5	4·6 ± 2·4	2	3·0 ± 0·0	0	0
Hermit crabs	9	2·9 ± 0·8	0	0	0	0
Nematodes	33	3·1 ± 0·6	1	1·0	1	5·0
Midshipman offspring	45	12·1 ± 2·3	11	8·4 ± 2·0	3	3·0 ± 1·0
Parasites*	30	6·2 ± 3·6	13	896·6 ± 268·6	6	4·7 ± 1·4

n, sample size; FO, frequency of occurrence; values represent the actual number of samples where an organism type was identified. Mean ± S.E., calculated using only samples where organism occurred. Does not include samples where no organism was found.

*Parasites include all species identified (see Table II).

males were collected opportunistically (Table I). There was no effect of sampling location on total abundance of organisms (Kruskal–Wallis: $\chi^2 = 1{\cdot}88$, d.f. = 2, $P > 0{\cdot}05$) and so sampling location was not included in further analyses. There was a significant effect of sampling location on parasite abundance (Kruskal–Wallis: $\chi^2 = 29{\cdot}19$, d.f. = 2, $P < 0{\cdot}001$). Therefore, sampling location was considered when investigating parasites.

COMPARISON OF FOOD AVAILABILITY AND GUARDER MALE DIET

Seven organisms were found on both the broods and in the digestive tracts of guarder males from samples collected in British Columbia only (Fig. 4) and there was a positive correlation in the prevalence of these organisms when the broods and the digestive tracts were compared ($R^2 = 0{\cdot}66$, $n = 7$, 95% C.I. = 0·08 to 0·85, $P < 0{\cdot}05$).

PREDICTION 1: GUARDER MALE CONDITION DETERIORATES ACROSS THE BREEDING SEASON

There was no effect of Julian date on the body condition of guarder males ($R^2 = 0{\cdot}010$, $n = 73$, 95% C.I. = −0·0004 to 0·0010, $P > 0{\cdot}05$) or on their I_H ($R^2 = 0{\cdot}016$, $n = 73$, 95% C.I. = −0·0009 to 0·0030, $P > 0{\cdot}05$). There was also no significant relationship between body condition and food abundance (nbGLM: increase in mean ± S.E. ln food abundance per unit of body condition: 3·5 ± 2·8, $\chi^2 = 1{\cdot}25$, $P > 0{\cdot}05$) nor was there a relationship between body condition and digestive tract mass ($R^2 = 0{\cdot}002$, $n = 72$, 95% C.I. = −2·22 to 1·45, $P > 0{\cdot}05$). A significant positive relationship between liver investment (I_H) and food abundance was observed [nbGLM: increase in ln food abundance

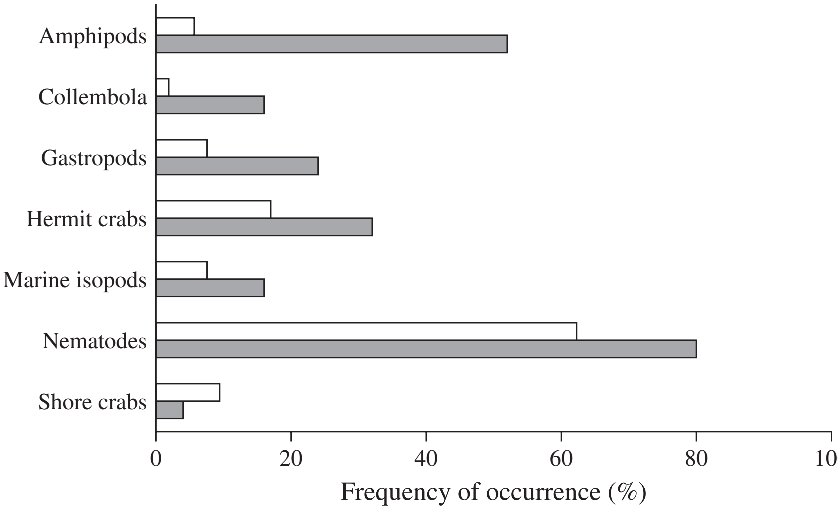

FIG. 4. Comparison of the frequency of occurrence of organisms that were identified both on the broods (▨; $n = 25$) and in the digestive tracts (☐; $n = 53$) of guarder male *Porichthys notatus*.

per unit of liver investment, I_H, +0·54 ± 0·13 (mean ± S.E.), $\chi^2 = 4{\cdot}12$, $P < 0{\cdot}001$], but there was no significant relationship between I_H and digestive-tract mass ($R^2 = 0{\cdot}013$, $n = 72$, 95% C.I. = −0·05 to 0·13, $P > 0{\cdot}05$).

PREDICTION 2: AS BODY CONDITION DETERIORATES, FOOD INTAKE WILL INCREASE

As a result of lengthy parental care in this species, it was predicted that guarder males would eventually begin to consume food later in the breeding season. There was no significant change in food abundance in the digestive tracts of the guarder males over the course of the breeding season [nbGLM: increase in ln food abundance per unit time: 0·002 ± 0·008 (S.E.), $\chi^2 = 0{\cdot}03$, $P > 0{\cdot}05$]. Guarder male digestive tract mass also did not significantly change across the season ($R^2 = 0{\cdot}004$, $n = 72$, 95% C.I. = −0·004 to 0·007, $P > 0{\cdot}05$). Also, no seasonal decline in body condition was observed.

There were significantly more organisms on the broods later in the breeding season (mean ± S.E.: 655 ± 115) compared with early in the breeding season (mean ± S.E.: 218 ± 141; *t*-test: $t_{23} = 3{\cdot}1$, $P < 0{\cdot}01$). When nests were further divided into those containing only eggs (more common in the early part of the breeding season) *v.* those with mainly hatched embryos, the broods with more developed young had significantly more organisms on them than broods with eggs only (ANOVA: $F_{2,22} = 8{\cdot}41$, $P < 0{\cdot}01$). When only the nests from later in the breeding season were examined, those with eggs-only had significantly fewer organisms with a mean ± S.E. of 452 ± 163 ($n = 9$), while the nests with mainly hatched young had a mean ± S.E. of 959 ± 199 organisms ($n = 6$; *t*-test: $t_{13} = 2{\cdot}41$, $P < 0{\cdot}05$). These results suggest that guarding males may more diligently remove organisms from broods of eggs but do not continue to do so for broods of hatched young.

PREDICTION 3: GUARDER MALES WOULD HAVE LESS FOOD IN THEIR DIGESTIVE TRACTS THAN SNEAKER MALES AND FEMALES

There was no difference between females and sneaker males in terms of food abundance in the digestive tract (*post hoc* Wilcoxon: $Z = 0{\cdot}05$, $P > 0{\cdot}05$). Females had $3{\cdot}6 \pm 3{\cdot}0$ (mean ± S.E.) items in their digestive tracts while sneaker males had $1{\cdot}0 \pm 4{\cdot}1$ (mean ± S.E.) items. In contrast, guarder males had $11{\cdot}6 \pm 1{\cdot}5$ items in their digestive tract, and significantly more than either females (Kruskal–Wallis: $\chi^2 = 31{\cdot}52$, d.f. = 2, $P < 0{\cdot}001$; *post hoc* Wilcoxon test: $Z = 4{\cdot}53$, $P < 0{\cdot}001$) or sneaker males [*post hoc* Wilcoxon test: $Z = -3{\cdot}94$, $P < 0{\cdot}001$; Fig. 5(a)]. Guarder male digestive tract mass tended to be two times greater than sneaker male digestive tract mass, although not significantly different [ANOVA: $F_{2,97} = 2{\cdot}71$, $P > 0{\cdot}05$; Tukey's HSD: $P > 0{\cdot}05$; Fig 5(b)]. All other comparisons were not significant (Tukey's HSD: all $P > 0{\cdot}05$).

PARASITES

Five different intestinal parasitic worms were identified in the digestive tracts of the 101 *P. notatus* analysed in detail; 67% of the guarder males sampled had at least one of these parasites. The three most common were Acanthocephala (spiny headed worms), Cestoda (tapeworms) and Trematoda (tissue flukes; Table II). These parasites were often found in large numbers, ranging from one to 2991 individual parasites in a given digestive tract sample. Only Acanthocephala and Cestoda were found in females and sneaker males, with a frequency of occurrence of 50 and 40%, respectively. Guarder males sampled from California had significantly more parasites (mean ± S.E.: $896{\cdot}6 \pm 268{\cdot}6$) than the guarder males sampled from British Columbia ($6{\cdot}2 \pm 3{\cdot}6$) and Washington ($4{\cdot}7 \pm 1{\cdot}4$; Kruskal–Wallis: $\chi^2 = 27{\cdot}03$, d.f. = 2, $P < 0{\cdot}001$; Table I). Guarder males that cannibalized eggs were not more likely to have parasites in their digestive tracts ($\chi^2 = 2{\cdot}4$, d.f. = 1, $P > 0{\cdot}05$). The total number of parasites sampled from guarder males decreased as the season progressed [nbGLM: increase in ln parasite abundance per unit time: $-0{\cdot}041 \pm 0{\cdot}014$ (S.E.), $\chi^2 = 6{\cdot}5$, $P > 0{\cdot}01$]. Because all the parasites identified have complex life cycles with an intermediate host that is typically found in *P. notatus* diets (*e.g.* snails or molluscs), it is likely that the parasites were acquired when the fish ingested an infected intermediate host (Barber *et al.*, 2000).

CANNIBALISM

Of the 151 *P. notatus* whose digestive tracts were examined for signs of cannibalism, 58% had consumed *P. notatus* eggs or hatched embryos. For guarder males, 69% were cannibals and these males consumed on average $7{\cdot}7 \pm 1{\cdot}3$ offspring (range: 1–106 offspring, median of 2). There were no sneaker males that were cannibals, but three females (of 18, or 17%) were cannibals and consumed one, two and 31 offspring, respectively.

Larger guarder males tended to consume more embryos than did smaller guarder males regardless of body condition, although not significantly different [nbGLM: increase in ln embryo number per unit of body length: $+0{\cdot}09 \pm 0{\cdot}05$ (S.E.), $\chi^2 = 1{\cdot}68$, $P > 0{\cdot}05$; increase in ln embryo number per unit of body condition: $+3{\cdot}44 \pm 3{\cdot}49$ (S.E.), $\chi^2 = 0{\cdot}98$, $P > 0{\cdot}05$]. For guarder males, time in the breeding season did not

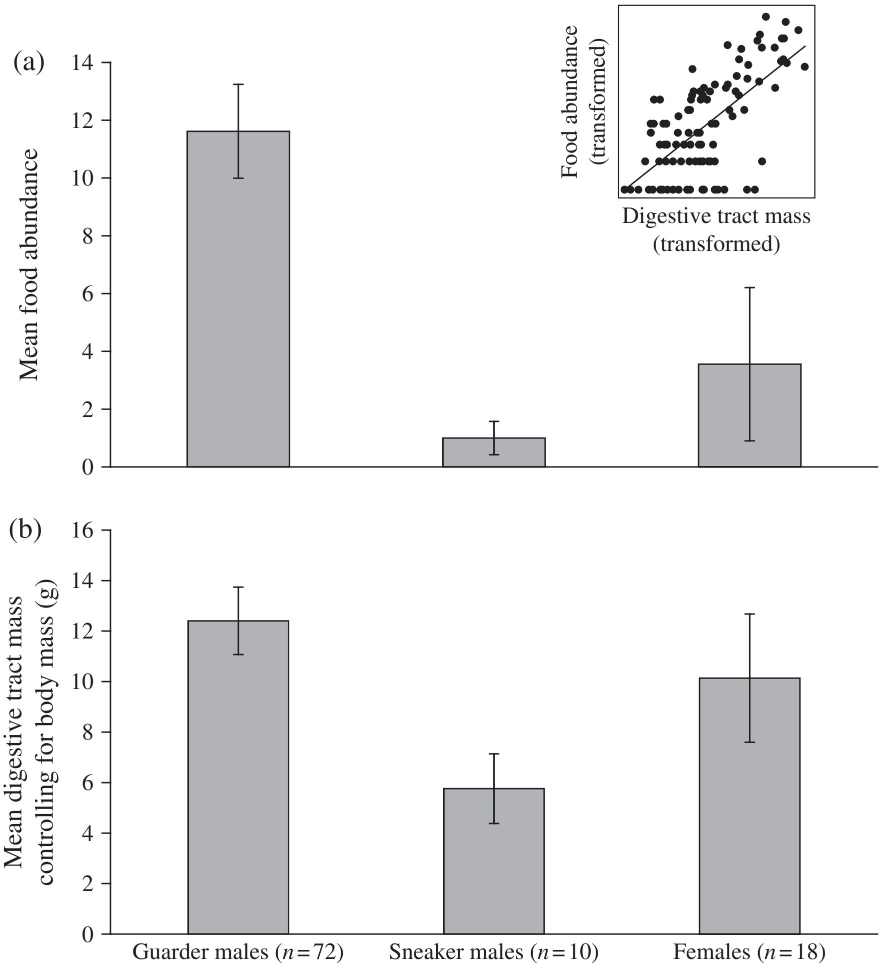

FIG. 5. Comparison among sex and male reproductive types of the (a) mean ± S.E. of total food abundance in the digestive tracts and (b) mean ± S.E. digestive tract content mass controlling for eviscerated body mass (g × 1000) in *Porichthys notatus*. Inset shows the relationship between food abundance and digestive tract mass controlling for body mass. For the inset, a $\log_{10}(x + 1)$ transformation was used for the zero-inflated total food abundance and a $\log_{10}$ transformation for digestive tract content mass. The curve was fitted by $y = 0{\cdot}977x + 2{\cdot}749$ ($R^2 = 0{\cdot}434$).

affect the number of offspring consumed [nbGLM: ln embryo number per unit of time: $+0{\cdot}002 \pm 0{\cdot}01$ (S.E.); $\chi^2 = 0{\cdot}21$, $P > 0{\cdot}05$], nor did the number of young cannibalized vary across stages of offspring development (Kruskal–Wallis: $\chi^2 = 1{\cdot}8$, d.f. = 2, $P > 0{\cdot}05$).

Among the 11 males from which consumed cannibalized embryos were collected from their digestive tracts and genotyped, eight males (72%) were unrelated to the cannibalized embryos. The remaining three males had paternity values of 9, 26 and 100%, respectively. Because the number of embryos consumed and successfully genotyped varied among males (see Table III), these results need to be treated with caution. For example, the male with 100% paternity had only one embryo in its digestive tract. The overall mean paternity, between cannibals and the embryos from their digestive tracts, was 12% (range = 0–100%, median = 0%; Table III).

TABLE II. The various classes of parasites identified in the digestive tracts of *Porichthys notatus*

Parasite class	*O%**	Abundance†	Life cycle‡	Effects§
Acanthocephala (spiny-headed worms)	46	4·9 (range: 1–32)	Complex IH: decapods or other crustaceans	Mass loss Seasonal mortality Intestinal perforation
Cestoda (tapeworms)	25	510 (range: 1–2991)	Complex IH: often snails	Mass loss Intestinal irritation Low reproductive output
Trematoda (tissue flukes)	11	1	Complex IH: often molluscs	Inflammatory response Lowered haemoglobin and haematocrit level
Unknown 1	1	1	–	–
Unknown 2	1	1	–	–

*Frequency of occurrence (*O%*) shows the percent of samples from which the parasite was found, of the 101 possible fish.

†Mean number of parasites found per sample.

‡Complex life cycle includes two hosts. Most common intermediate hosts (IHs) are listed.

§According to [Arai (1969); Möller & Anders (1986); Barber *et al.* (2000)].

TABLE III. Cannibalism data from a set of 11 guarder *Porichthys notatus* males

Male ID	Number of embryos consumed	Number of embryos genotyped	Cannibalism paternity (%)*
1	1	1	0
2	1	1	0
3	1	1	0
4	1	1	0
5	1	1	100
6	10	9	0
7	18	7	0
8	21	1	0
9	22	20	9
10	38	5	26
11	53	17	0

*The percentage of offspring that was compatible with the cannibal father calculated according to the two-sex paternity model in Neff *et al.* (2000*a*, *b*).

DISCUSSION

This study showed that there were food resources available for guarder males in their nests and on their broods. Apart from embryos, however, the digestive tracts examined were relatively empty; guarder males consumed embryos rather than other available surrounding food items. Although it was initially predicted that guarder males, as a result of their caring duties and their long confinement to the nest area, would have fewer opportunities to feed and therefore would have less food in their digestive tracts, the results show the opposite pattern. In general, guarder males consumed more than actively reproducing females and sneaker males. This observed difference was mainly driven by cannibalism by guarder males. For guarder males, food abundance in the digestive tracts was not related to body condition, and both food abundance and digestive tract content mass were not related to time in the breeding season. Based on the observations of this study, these results suggest that all fish collected from nests during the breeding season regardless of sex and tactic are not actively foraging; rather, guarder males with access to embryos appear to consume small numbers of embryos and do so fairly regularly.

The diet of the *P. notatus* has been briefly mentioned in a number of previous studies, reporting that *P. notatus* consume crustaceans and small fishes (Eigenmann, 1892; Hubbs, 1920; Arora, 1948; Hart, 1973). Cannibalism has also been documented anecdotally (Mensinger & Case, 1991; Sisneros *et al.*, 2009). In this study, it was confirmed that reproductively mature *P. notatus* do consume a number of different crustaceans and *P. notatus* embryos, in addition to nematodes and molluscs. Although infrequent, instances of terrestrial insects in the diet of *P. notatus* were observed. There was no evidence of other fish species in their digestive tracts, not even in the form of bony structures or scales. *Porichthys notatus* embryos were both the most abundant food item found and had the highest frequency of occurrence. Many factors, however, could influence abundance and frequency of occurrence for particular organisms found in digestive tract samples, including differences in digestion and evacuation times, and the size of the meal (Bromley, 1994). For example, 85% of eggs that were force fed to Pacific salmon *Oncorhynchus tshawytscha* (Walbaum 1792) were cleared from the digestive tract within 48 h (Garner *et al.*, 2009); a similar digestion time of 48 h for embryos has been observed in *P. notatus* (A. Bose, pers. comm.). Although there are probably differences in digestion and evacuation times among prey items, it is unlikely that the frequency of occurrence and abundance of food items were grossly under or overestimated in reproductively active adults of this species because the majority of the diet items of *P. notatus* consist of hard structures (including egg casings) that would not digest quickly.

Three previous studies noted that the digestive tracts of reproductive *P. notatus* fish located in intertidal zones were largely empty (Hubbs, 1920; Arora, 1948; Sisneros *et al.*, 2009). Although this study mostly agrees with these previous findings, the results of this study also indicate that guarder males are in fact consuming a small amount over the breeding season and the organisms consumed are often found in the nest or on the brood. Similarly, a study of smallmouth bass *Micropterus dolomieu* Lacépède 1802 found that nesting males had food in their stomachs and the authors argued that these sources of food are important to supplement the endogenous energy reserves during care (Mackereth *et al.*, 1999). In contrast to the results of this study, Magnhagen (1986) found that nesting male common goby *Pomatoschistus microps* (Krøyer 1838) consumed significantly less than females, a result attributed to limited mobility of male *P. microps* during the parental care period. In this study, contrary to the third prediction, sneaker males and females in the nests had even lower food intake than the nest guarding males, which may suggest that fish may not eat during spawning but minimal feeding may occur and may be necessary during the care period in this species.

Parental care is a costly behaviour and can result in significant physical deterioration and a loss of energy reserves (Magnhagen, 1986; Marconato & Bisazza, 1988; Lindström & Hellström, 1993; Okuda & Yanagisawa, 1996). As a result, it was initially predicted that guarder males would lose body condition over the reproductive season, and that food intake would increase accordingly. Instead, in this study, no evidence was found for the idea that condition or food intake changed across the season. By consuming a small amount of embryos and other prey items throughout the breeding season, guarder males may be able to retain condition during the parental care period. Cannibalism may be an adaptation to maintain the necessary energy required for performing care and, in part, may explain the observed high frequency of occurrence of partial cannibalism (consuming only part of the brood; Rohwer, 1978; Sargent, 1992; Sargent *et al.*, 1995). Neff (2003) found that male bluegill *Lepomis macrochirus* Rafinesque 1819 in lower body condition were more likely to partially cannibalize their brood, suggesting that this behaviour is important for replenishing energy reserves. In contrast to Neff's (2003) results on *L. macrochirus*, the energy replenishing hypothesis was not supported in this study as no significant relationship between body condition and the number of embryos cannibalized for guarder males was observed (Rohwer, 1978; Sargent, 1992; Sargent *et al.*, 1995; Bose *et al.*, 2014). Conversely, other studies have instead found a positive relationship between condition and number of cannibalized offspring in other species including the long-snout clingfish *Diademichthys lineatus* (Sauvage 1883; Gomagano & Kohda, 2008) and three-spined sticklebacks *Gasterosteus aculeatus* L. 1758 (Mehlis *et al.*, 2009).

If cannibalism is not related to body condition, why then did so many *P. notatus* guarder males consume embryos? The reasons for partial cannibalism vary both within and among species (Smith & Reay, 1991; Klug & Bonsall, 2007). First, parents will often cannibalize in situations where nest size is limited, where offspring are of low quality and quantity, or in situations of low oxygen concentration, facilitating parental investment in remaining offspring (Rohwer, 1978; Sargent, 1992). For example, males of the beaugregory damselfish *Stegastes leucostictus* (Müller & Troschel 1848) consume more embryos in areas of low oxygen, which the authors interpret as an adaptive strategy to ensure the success of remaining embryos (Payne *et al.*, 2002). In *P. notatus*, nest space is limited and guarder males must withstand cyclical environmental perturbations when they remain in the nests at low tide resulting in periods of hypoxia (Sisneros *et al.*, 2009; Craig *et al.*, 2014). These conditions could select for partial cannibalism, and would be adaptive if the remaining uneaten offspring have higher survival as a result of the parental behaviour. Second, parental care theory predicts that cannibalism should increase as the mean paternity to the group of offspring decreases (Trivers, 1972; Whittingham *et al.*, 1992; Westneat & Sherman, 1993). Neff (2003) found that parental male *L. macrochirus* that had more sneaker males present during spawning were more likely to consume part of their brood. Additionally, parental male *L. macrochirus* may be selectively culling unrelated offspring after exposure to olfactory cues from the hatched embryos (Neff, 2003). In *P. notatus*, paternity is commonly lost to both sneaker and cuckolding guarder males, and a high degree of nest takeover has been documented for *P. notatus* especially in the early part of the breeding season (Cogliati *et al.*, 2013, 2014*a*, *b*). Thus, partial cannibalism may be a response by guarder males to reduced paternity. Indeed, this study showed that guarder males were largely unrelated to the embryos they consumed. Although this result could provide preliminary evidence for selective cannibalism, guarder males were also largely unrelated to the embryos in their nest (unpubl. data), suggesting instead that partial cannibalism in *P. notatus* may be in response to taking over a nest.

This is the first comprehensive diet analysis study in a toadfish that determined both food availability and food consumed in reproductively mature individuals. Often, studies that examine diet fail to make comparisons between the sexes or between males adopting different behavioural tactics or to look at diet in relation to food availability. These were important facets of this observational study and accordingly, significant differences in diet between male alternative tactics and sexes were observed. The diet choices were studied in the context of what food was available for guarder males and what items they could possibly acquire based on their presumably limited mobility outside of the nest. Guarder males had many available food options in their nests, but these items were largely untouched. Instead, they fed primarily on *P. notatus* embryos. These cannibal males were also mainly unrelated to the offspring consumed, and are likely to have cannibalized as a result of a nest takeover. Altogether, by comparing the diet of both sexes and tactics in a species with a lengthy and costly parental care period, these results shed light on some of the adaptations and strategies designed to cope with the costs of providing parental care.

A. Bass, M. Marchaterre and J. Sisneros generously assisted with sample permits and site locations in California and Washington. C. Chui, J. Marentette and J. Reynolds helped with data collection in British Columbia. B. Cogswell, R. Cogswell, D. Weatherell, S. Weatherell, M. Balshine, D. Balshine and especially C. Flader and S. Flader kindly provided access to midshipman sampling sites and lodgings for field crew. S. Marsh-Rollo was invaluable for her microscope and analyses training provided for C.D. and A.C.P. S. Marsh-Rollo, D. Rollo and B. Leander helped with identification of organisms. C. O'Connor and C. Dey helped with statistical analysis. This work was funded by the Natural Sciences and Engineering Research Council of Canada (grants to B.D.N. and S.B.).

References

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Arai, H. P. (1969). Preliminary report on the parasites of certain marine fish in British Columbia. *Journal of the Fisheries Research Board of Canada* **26,** 2319–2337.

Arora, H. L. (1948). Observations on the habits and early life history of the batrachoid fish, *Porichthys notatus* Girard. *Copeia* **1948,** 89–93.

Balshine-Earn, S. (1995). The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. *Animal Behavior* **509,** 1–7.

Barber, I., Hoare, D. & Krause, J. (2000). Effects of parasites on fish behaviour: a review and evolutionary perspective. *Reviews in Fish Biology and Fisheries* **10,** 131–165.

Bass, A. H. (1996). Shaping brain sexuality. *American Scientist* **84,** 352–363.

Blumer, L. S. (1982). A bibliography and categorization of bony fish exhibiting parental care. *Zoological Journal of the Linnean Society* **75,** 1–22.

Bose, A. P. H., Cogliati, K. M., Howe, H. S. & Balshine, S. (2014). Factors influencing cannibalism in the plainfin midshipman fish. *Animal Behaviour* **96,** 159–166.

Brantley, R. K. & Bass, A. H. (1994). Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish, *Porichthys notatus* (Teleostei, Batrachoididae). *Ethology* **96,** 213–232.

Bromley, P. J. (1994). The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries* **4,** 36–66.

Cargnelli, L. M. & Neff, B. D. (2006). Condition-dependent nesting in bluegill sunfish *Lepomis macrochirus*. *Journal of Animal Ecology* **75,** 627–633.

Caro, T. M. & Bateson, P. (1986). Organization and ontogeny of alternative tactics. *Animal Behavior* **34,** 1483–1499.

Chellappa, S., Huntingford, F. A., Strang, R. H. C. & Thomson, R. Y. (1995). Condition factor and hepatosomatic index as estimates of energy status in male three-spined stickleback. *Journal of Fish Biology* **47,** 775–787.

Cogliati, K. M., Neff, B. D. & Balshine, S. (2013). High degree of paternity loss in a species with alternative reproductive tactics. *Behavioral Ecology and Sociobiology* **67,** 399–408.

Cogliati, K. M., Mistakidis, A. F., Marentette, J. R., Lau, A., Bolker, B. M., Neff, B. D. & Balshine, S. (2014*a*). Comparing population level sexual selection in a species with alternative reproductive tactics. *Behavioral Ecology* **25**, 1524–1533. doi: 10.1093/beheco/aru147

Cogliati, K. M., Balshine, S. & Neff, B. D. (2014*b*). Competition and cuckoldry: estimating fitness of alternative reproductive tactics in plainfin midshipman. *Behaviour* **151,** 1209–1227.

Cooke, S. J., Phillipp, D. P. & Weatherhead, P. J. (2002). Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. *Canadian Journal of Zoology* **80,** 756–770.

Craig, P. M., Fitzpatrick, J. L., Walsh, P. J., Wood, C. M. & McClelland, G. B. (2014). Coping with aquatic hypoxia: how the plainfin midshipman (*Porichthys notatus*) tolerates the intertidal zone. *Environmental Biology of Fishes* **97,** 163–172.

Eigenmann, C. H. (1892). The fishes of San Diego, California. *Proceedings of the United States National Museum* **15,** 122–178.

Fitzgibbon, C. D. & Fanshawe, J. H. (1989). The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *Journal of Zoology* **218,** 99–107.

Garner, S. R., Heath, J. W. & Neff, B. D. (2009). Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* **66,** 1546–1553.

Gomagano, D. & Kohda, M. (2008). Partial filial cannibalism enhances initial body condition and size in paternal care fish with strong male-male competition. *Annales Zoologici Fennici* **45,** 55–65.

Gross, M. R. (1984). Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In *Fish Reproduction: Strategies and Tactics* (Potts, G. W. & Wooton, R. J., eds), pp. 55–75. London: Academic Press.

Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* **11,** 92–98.

Gross, M. R. & Sargent, R. C. (1985). The evolution of male and female parental care in fishes. *American Zoologist* **25,** 807–822.

Harper, R. D. & Case, J. F. (1999). Disruptive counterillumination and its anti-predatory value in the plainfin midshipman *Porichthys notatus*. *Marine Biology* **134,** 529–540.

Hart, J. (1973). *Pacific Fishes of Canada*. Ottawa, ON: Fisheries Research Board of Canada.

Htun-Han, M. (1978). The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonadosomatic index, hepatosomatic index and condition factor. *Journal of Fish Biology* **13,** 369–378.

Hubbs, C. (1920). The bionomics of *Porichthys notatus* Girard. *American Naturalist* **54,** 380–384.

Ito, S. & Yanagisawa, Y. (2000). Mate choice and cannibalism in a natural population of a stream goby, *Rhinogobius* sp. *Ichthyological Research* **47,** 51–58.

Ito, S., Kanebayashi, M., Sato, A., Iguchi, K., Yanagisawa, Y. & Oomori, K. (2010). Changes in male physiological condition during brooding activities in a natural population of a stream goby, *Rhinogobius* sp. *Environmental Biology of Fishes* **87,** 135–140.

Jakob, E. M., Marshall, S. D. & Uetz, G. W. (1996). Estimating fitness: a comparison of body condition indices. *Oikos* **77,** 61–67.

Klug, H. & Bonsall, M. B. (2007). When to care for, abandon, or eat your offspring: the evolution of parental care and filial cannibalism. *American Naturalist* **170,** 886–901.

Klug, H., Lindström, K. & St. Mary, C. M. (2006). Parents benefit from eating offspring: density-dependent egg survivorship compensates for filial cannibalism. *Evolution* **60,** 2087–2095.

Lindström, K. & Hellström, M. (1993). Male size and parental care in the sand goby, *Pomatoschistus minutus*. *Ethology Ecology and Evolution* **5,** 97–106.

Mackereth, R. W., Noakes, D. L. G. & Ridgway, M. S. (1999). Size-based variation in somatic energy reserves and parental expenditure by male smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes* **56,** 263–275.

Magnhagen, C. (1986). Activity differences influencing food selection in the marine fish *Pomatoschistus microps*. *Canadian Journal of Fisheries and Aquatic Sciences* **43,** 223–227.

Mank, J. E., Promislow, D. E. L. & Avise, J. C. (2005). Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. *Evolution* **59,** 1570–1578.

Marconato, A. & Bisazza, A. (1988). Mate choice, egg cannibalism and reproductive success in the river bullhead, *Cottus gobio*. *Journal of Fish Biology* **33,** 905–916.

Mehlis, M., Bakker, T. C. M. & Frommen, J. G. (2009). Nutritional benefits of filial cannibalism in three-spined sticklebacks (*Gasterosteus aculeatus*). *Naturwissenschaften* **96,** 399–403.

Mensinger, A. F. & Case, J. F. (1991). Bioluminescence maintenance in juvenile *Porichthys notatus*. *Biology Bulletin* **181,** 181–188.

Mesa, M. G., Poe, T. P., Gadomski, D. M. & Peterson, J. H. (1994). Are all prey created equal? A review and synthesis of differential predation on prey substandard condition. *Journal of Fish Biology* **45,** 81–96.

Möller, H. & Anders, K. (1986). *Diseases and Parasites of Marine Fishes*. Kiel: Verlag Möller.

Neff, B. D. (2001). Genetic paternity analysis and breeding success in bluegill sunfish (*Lepomis macrochirus*). *Journal of Heredity* **92,** 111–119.

Neff, B. D. (2003). Decisions about parental care in response to perceived paternity. *Nature* **422,** 716–719.

Neff, B. D., Repka, J. & Gross, M. R. (2000*a*). Parentage analysis with incomplete sampling of candidate parents and offspring. *Molecular Ecology* **9,** 515–528.

Neff, B. D., Repka, J. & Gross, M. R. (2000*b*). Statistical confidence in parentage analyses with incomplete sampling: how many loci and offspring are needed? *Molecular Ecology* **9,** 529–539.

Nelson, J. S. (2006). *Fishes of the World*, 4th edn. New York, NY: John Wiley and Sons, Inc.

Okuda, N. & Yanagisawa, Y. (1996). Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. *Animal Behavior* **52,** 307–314.

Payne, A. G., Smith, C. & Campbell, A. C. (2002). Filial cannibalism improves survival and development of beaugregory damselfish embryos. *Proceedings of the Royal Society B* **269,** 2095–2102.

Rohwer, S. (1978). Parent cannibalism of offspring and egg raiding as a courtship strategy. *American Naturalist* **112,** 429–440.

Sargent, R. C. (1992). Ecology of filial cannibalism in fish: theoretical perspectives. In *Cannibalism: Ecology and Evolution Among Diverse Taxa* (Elgar, M. A. & Cresp, B. J., eds), pp. 38–62. New York, NY: Oxford University Press.

Sargent, R. C., Crowley, P. H., Huang, C., Lauer, M., Neergaard, D. & Schmoetzer, L. (1995). A dynamic program for male parental are in fishes: brood cycling and filial cannibalism. *Behaviour* **132,** 1059–1078.

Sisneros, J. S., Alderks, P. W., Leon, K. & Sniffen, B. (2009). Morphometric changes associated with the reproductive cycle and behaviour of the intertidal-nesting, male plainfin midshipman *Porichthys notatus*. *Journal of Fish Biology* **74,** 18–36.

Smith, C. (1993). The cost of parental care in teleost fishes. PhD Thesis, University of Wales, Aberystwyth, UK.

Smith, C. & Reay, P. (1991). Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries* **1,** 41–64.

Smith, C. & Wootton, R. J. (1995). The costs of parental care in teleost fishes. *Reviews in Fish Biology and Fisheries* **5,** 7–22.

Suk, H. Y., Neff, B. D., Fitzpatrick, J. L. & Balshine, S. (2009). Isolation and characterization of polymorphic microsatellite loci in the plain midshipman fish. *Hereditas* **146,** 204–207.

Taborsky, M. (1997). Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviours? *Behavioral Ecology and Sociobiology* **41,** 361–362.

Taborsky, M. (1998). Sperm competition in fish: bourgeois males and parasitic spawning. *Trends in Ecology and Evolution* **13,** 222–227.

Taborsky, M., Oliveira, R. F. & Brockman, H. J. (2008). The evolution of alternative reproductive tactics concepts and questions. In *Alternative Reproductive Tactics* (Oliveira, R. F., Taborsky, M. & Brockman, H. J., eds), pp. 1–21. New York, NY: Cambridge University Press.

Thompson, E. M. & Tsuji, F. I. (1989). Two populations of the marine fish *Porichthys notatus*, one lacking in luciferin essential for bioluminescence. *Marine Biology* **102,** 161–165.

Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man* (Campbell, B., ed.), pp. 136–179. Chicago, IL: Aldine-Atherton.

Walker, H. J. & Rosenblatt, R. H. (1988). Pacific toadfishes of the genus *Porichthys* (Batrachoididae) with descriptions of three new species. *Copeia* **1988,** 887–904.

Warner, J. A. & Case, J. F. (1980). The zoogeography and dietary induction of bioluminescence in the midshipman fish, *Porichthys notatus*. *Biological Bulletin* **159,** 231–246.

Westneat, D. F. & Sherman, P. W. (1993). Parentage and the evolution of parental behavior. *Behavioral Ecology* **4,** 66–77.

Whittingham, L. A., Taylor, P. D. & Robertson, R. J. (1992). Confidence of paternity and male parental care. *American Naturalist* **139,** 1115–1125.