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Top-down pressure on small pelagic fish by eastern Australian salmon *Arripis trutta*; estimation of daily ration and annual prey consumption using multiple techniques

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A B S T R A C T

Ecosystem-level models that trace flows of mass and energy to quantify species interactions are important tools in whole ecosystem-based approaches to managing marine resources. A critical input parameter for such models is an estimate of the consumption rates and biomasses of prey consumed by fish populations. Here we estimate the annual prey consumption of an abundant coastal piscivore, *Arripis trutta*, which may exert substantial top-down control on its prey over its broad latitudinal range (28–43°S) in the coastal waters off south-eastern (SE) Australia. Three independent techniques were used to estimate annual prey consumption at two environmentally-relevant temperatures, 15 and 20 °C: experimental gastric evacuation experiments (coupled with stomach content analyses); bioenergetics modelling, and; empirical regression modelling. Each technique yielded a similar range of estimates with annual food consumed/biomass (Q/B) ranging from 3.20 to 4.02 at 15 °C and 4.23 to 5.25 at 20 °C. Using an estimated *A. trutta* stock biomass in SE Australia of 10,000 t, total mean annual prey consumption was estimated to be 42,200 t, consisting primarily (93%) of small zooplanktivorous teleosts, particularly Australian sardines *Sardinops sagax* (35%) and scads *Trachurus* spp. (30%). These results indicate that *A. trutta* do possess a top-down influence on the pelagic ecosystem of coastal SE Australia via consumption of considerable biomasses of small pelagic fish. However, despite the use of a maximum regional estimate of *A. trutta* abundance and the presence of at least two other ecologically similar predatory fish species with higher annual prey consumption rates in SE Australian coastal waters, *A. trutta* may remove only a small proportion (~15%) of the estimated spawning biomasses of its major prey species in this region annually. The multiple-technique approach used in this study has for the first time quantified the diet of *A. trutta* in SE Australia and provided broad and repeatable estimates of its annual prey consumption for use in ecosystem models designed to manage coastal fisheries resources in this region.

1. Introduction

The eastern Australian salmon *Arripis trutta* (Bloch & Schneider, 1801) is an abundant, medium-sized pelagic fish species distributed in the coastal marine waters of south-eastern (SE) Australia from southern Queensland to western Victoria and Tasmania (Paulin, 1993; Stewart et al., 2011). *A. trutta* has a strong schooling habit and may form vast schools of up to thousands of tonnes of fish around ocean beaches and areas of exposed coast (Malcolm, 1966). It sustains important commercial fisheries throughout SE Australia, with current landings amongst

the highest historical levels (>2,000 t/year), as well as being a highly-prized recreational sportfish (Stewart et al., 2012).

In addition to their economic importance to fisheries in SE Australia, *A. trutta* is a high trophic level predator as well as prey in nearshore pelagic food webs (Griffith et al., 2011) and should therefore play an important ecological role in the ecosystem. The diet of *A. trutta* in SE Australian coastal waters is dominated (94% by weight) by small pelagic zooplanktivorous teleosts; primarily Australian sardines *Sardinops sagax* (35%) and carangids of the genus *Trachurus* (30%) (Hughes et al., 2013). Adult *A. trutta* in turn are preyed upon by a suite of apex predators like marine mammals (Malcolm, 1966) and sharks (Stewart et al., 2011). Many winter-nesting seabirds are also reliant on feeding *A. trutta* schools to make pelagic prey available to them (Barnes et al., 2004). *A. trutta* are a highly mobile species which undergo seasonal reproductive migrations covering hundreds of km (Malcolm, 1966; Stanley, 1978). They posses relatively fast growth rates and attain

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maturity in 2.2 years at 31 cm FL and a maximum size of 78 cm FL and 7.4 kg (Hartill and Walsh, 2005; Stewart et al., 2011). In combination with observations of the voracious feeding behaviour of *A. trutta* (Hughes et al., 2013), it is therefore likely that *A. trutta* require substantial quantities of prey to accommodate their energy requirements for growth and metabolism.

Consequently, the species have the potential to exert a 'top-down' influence on the nearshore pelagic ecosystem, as has been demonstrated for other pelagic piscivorous teleosts from similar trophic levels in temperate Australia and elsewhere (e.g. Essington, 2003; Glaser, 2011; Griffiths et al., 2007, 2009; Overton et al., 2008). Top-down effects of predation can alter the diversity of ecosystems, realised niches and the relative abundance of species (Glaser, 2011). The influence of pronounced top-down effects can also cause trophic cascades, which impact species at all trophic levels in the food chain (Estes et al., 1998).

Pelagic ecology uses ecosystem-level models that trace flows of mass and energy as a means of quantifying species interactions (e.g. Christensen and Pauly, 1992; Christensen and Walters, 2004) which is highlighted by the ever-increasing global interest in ecosystem-based fisheries management (e.g. Scandol et al., 2005). These models are important tools for managing marine resources, but in order to be effective in predicting the complex ecological interactions in marine ecosystems, many require some essential input parameters, one being an estimate of predation rates of fish populations on their prey (Essington, 2003; Griffiths et al., 2009). Dietary studies based on the physical contents of fish digestive tracts provide such data by quantifying diet composition and prey consumption rates based on daily ration estimates (Griffiths et al., 2007).

Although information on diet composition is readily available for many fish species, estimating prey consumption rates remains problematic because all existing methodologies have important limitations (Chipps and Wahl, 2008; Essington et al., 2001). Stomach content analysis (e.g. Elliot and Persson, 1978) requires extensive sampling, which may not be possible for highly-mobile and widely-dispersed pelagic organisms. Bioenergetics modelling (e.g. Hanson et al., 1997; Hartman and Kitchell, 2008) requires extensive data on the size and temperature dependence of metabolism, which can only be collected from captive fish. Finally, regression models (e.g. Palomares and Pauly, 1989, 1998) can be used to estimate the consumption-biomass ratio of a population, but do not allow prediction of how variation in the size-structure of the population affects predation rates.

The approach presented in this study was to employ all three techniques to provide a range of prey consumption estimates for *A. trutta*: experimental gastric evacuation experiments coupled with stomach content analyses, bioenergetics modelling, and empirical regression modelling. This multi-faceted approach allows for comparison of direct and indirect methods and can provide valuable independent corroboration of laboratory-measured bioenergetics parameters (Olson and Boggs, 1986). This approach has been successfully used to provide evidence of top-down effects of predation on prey in diverse studies ranging from lingcod *Ophiodon elongatus* predation on rockfishes *Sebastes* spp. (Beaudreau and Essington, 2009), to predation on northern anchovy *Engraulis mordax* by albacore *Thunnus alalunga* (Glaser, 2011), and killer whale *Orca orcinus* predation on marine mammals (Williams et al., 2004).

Information on the consumption rates of large pelagic fish in the temperate coastal waters of SE Australia is lacking, particularly in relation to predation on small zooplanktivorous species which are prone to dramatic fluctuations in abundance (e.g. Alheit and Hagen, 1997; Glaser, 2011; Ward et al., 2001). Small pelagic fish species form a critical role as the middle trophic level in many coastal marine ecosystems as important prey for a wide range of predators including fishes, cephalopods, seabirds, pinnipeds and cetaceans (Rogers and Ward, 2007). The lack of knowledge regarding consumption rates on small zooplanktivorous species by large pelagic fish in the temperate waters of SE Australia, coupled with recent concerns over the effects of climate

change on this ecosystem (e.g. Hallegraeff, 2010; Hughes et al., 2013; Johnson et al., 2011; McLeod et al., 2012; Poloczanska et al., 2007), initiated interest in better understanding the consumption rates of *A. trutta* in this region. The objective of this study was therefore to estimate *A. trutta* predation rates, daily ration and annual prey consumption and examine the potential for the species to exert top-down pressure on small zooplanktivorous fishes in this region.

2. Materials & methods

2.1. Daily ration & prey consumption rates

The daily consumption rates of *A. trutta* were estimated using one experimental (direct) and two empirical (indirect) techniques in order to provide a range of values for daily consumption and hence overall annual consumption of prey species. The methods used were: i) experimentally measuring gastric evacuation rates in the laboratory using wild-caught captive fish (Olson and Boggs, 1986; Olson and Mullen, 1986) and then applying this rate to the observed diet of fish sampled in the wild (Hughes et al., 2013); ii) using a bioenergetics model (Fish Bioenergetics 3.0 – The University of Wisconsin) designed to quantify the physiological and ecological constraints to growth and the strength of predator–prey relationships (Hanson et al., 1997; Hartman and Kitchell, 2008); and iii) using an empirical formula derived for multiple regression models for a suite of fishes dependent on shape, size, habitat, temperature and food type (Palomares and Pauly, 1989, 1998). From each technique, it was possible to estimate the amount of food ingested (Q) by a population expressed as a fraction of its biomass (B) per year (Q/B). Based on its distribution, *A. trutta* experiences annual SSTs of between ~13 and 23 °C.[1] Q/B was therefore calculated using each technique at two environmentally relevant temperatures for this region, 15 and 20 °C, to provide a plausible range of values. Q was estimated using diet composition presented in Hughes et al. (2013). The biomass of the *A. trutta* stock in SE Australia is estimated to be between 4,500 and 10,000 t (Hughes, 2012). All calculations were therefore done using an estimated stock biomass for *A. trutta* in SE Australia of 10,000 t as it would give maximum estimates of annual prey consumption of *A. trutta* in SE Australia.

2.1.1. Gastric evacuation experiments

Experimental *A. trutta* were locally caught by rod and line and transported 10–20 at a time in a ~800 L oxygenated tank to the Cronulla Fisheries Research Centre Aquarium Facility on Port Hacking (34°04′S, 151°09′E) within 0.5–2 h of capture. The fish were maintained in captivity in a cylindrical (Ø = 496 cm, depth = 159 cm) 35,000 L flow-through seawater tank with ambient water temperature and photoperiod. Their diet in captivity consisted of a range of small fish, squid and prawns similar to prey found in the stomachs of wild-caught fish (Hughes et al., 2013). Captive *A. trutta* were fed daily. Fish were held in captivity for a period of at least 2 months prior to experiments.

Two gastric evacuation experiments were conducted using these captive fish; the first during the period 21–23 July 2008 at an average water temperature of ~15 °C and the second during the period 30 April–2 May 2009 at an average water temperature of ~20 °C. Initial trials indicated that 2–3 d was the time taken to completely clear the gut following a meal; therefore on both occasions fish were starved for 4 d prior to experiments to ensure they had completely cleared their stomachs. Both *S. sagax* and *Trachurus novaezelandiae* were offered to the fish prior to the experiments; *S. sagax* were readily accepted, however *T. novaezelandiae* were rarely eaten, therefore the experiments were done using whole *S. sagax* only. Each *S. sagax* to be fed to the experimental fish was pre-weighed (to the nearest 0.01 g) and a uniquely-numbered soft plastic bead (6 mm × 8 mm, 0.2 g) was

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[1] NOAA_ERSST_V3 data provided by the NOAA/OAR/ESRL PSD (Boulder, Colorado, USA). http://www.esrl.noaa.gov/psd/.

carefully inserted into its body cavity. This way, the exact quantity of food ingested by an individual could be determined from analysis of the labelled beads present in the fish's stomach. On each occasion the fish were fed to satiation. The elapsed time from feeding to the time the fish was euthanised using an overdose of Aqui-S anaesthetic (Aqui-S New Zealand Ltd) was recorded. Freshly sampled fish were measured (FL) to the nearest mm, and weighed to the nearest g. The entire viscera was then removed from the fish (within 5 min of death), the stomach split open and the *S. sagax* remains contained within weighed to the nearest 0.01 g and the numbers of all beads present recorded.

Following completion of the experiments, gastric evacuation data were represented by plotting the proportion of the meal remaining in the fish's stomachs against time post-feeding (h) and linear functions fitted to the data according to the method described by Olson and Mullen (1986). The integral of these linear functions was then used to calculate the evacuation time (A_i) for *S. sagax* at 15.1 and 19.4 °C in units of proportion/h. A_i represents the average amount of time required to evacuate the average proportion of all *S. sagax* meals in the stomach at any instant in time and does not require an *a priori* assumption of exponential gastric function (Olson and Mullen, 1986).

Daily consumption rates of prey for wild *A. trutta* were then estimated using the methods of Olson and Mullen (1986) where the feeding rate (r̂, g/h) is predicted by dividing the mean wet weight of the stomach contents ($\overline{W}_i$, g – from Hughes et al., 2013) by the average time required to evacuate the average proportion of prey type *i* (A_i – as calculated above). This can be represented in the following model for a predator that consumes a range of prey that are evacuated at different rates:

$$\hat{r} = \sum_{i=1}^{I} (\overline{W}_i / A_i), \tag{1}$$

where *i* refers to each of the prey types consumed by the predator. This represents the prey consumption per hour, so that r̂ is multiplied by the number of hours per day in which the predator feeds to estimate the daily meal (M). Because *A. trutta* are regularly caught both during the day and at night (Hughes, 2012; Stewart et al., 2011), it was assumed that they feed over the entire diel cycle and r̂ was therefore multiplied by 24. Daily ration was then calculated by expressing M as a percentage of the average W_w of fish examined. Daily ration could then be scaled up to give an estimate of Q/B at each experimental temperature. Size related variation in consumption was also investigated amongst three sizes classes of fish: small (S, <20 cm FL), medium (M, 20–40 cm FL) and large (L, >40 cm FL). All empty stomachs were included in the estimation of daily ration because they represent the true proportion of the population that may not have fed prior to capture. Because captive *A. trutta* would not eat food other than *S. sagax*, A_i could only be estimated for this prey item. This was not considered likely to bias results as small pelagic fish (and in particular *S. sagax*) were the most important dietary component for wild *A. trutta* (Hughes et al., 2013), which were assumed to be of similar digestibility to *S. sagax* based on their similar size and functional form. Indeed, it has been shown that gastric evacuation rate does not differ significantly for food types with similar morphology and energy content in other primarily piscivorous species, *Pomatomus saltatrix* (Buckel and Conover, 1996) and *Thunnus albacares* (Olson and Boggs, 1986). This approach has been previously used by many other researchers in the absence of specific A_i estimates for all prey items in the diet (e.g. Griffiths et al., 2007, 2009; Menard et al., 2000; Olson and Galván-Magaña, 2002). The A_i estimate for *S. sagax* was therefore applied to all prey items in the diet, as any potential biases in the calculation of daily ration are likely to be small given the overwhelming influence of small pelagic fishes to the overall diet.

2.1.2. Bioenergetics modelling

Bioenergetics models are commonly used for estimating the consumption rates of fishes and have been parameterized for nearly 80

fish species (Beaudreau and Essington, 2009; Hartman and Kitchell, 2008). The bioenergetics model (Fish Bioenergetics 3.0; Hanson et al., 1997) employed here attempts to use thermodynamic principles to constrain estimates of consumption within energetically plausible ranges for the growth of individual fish (Hunsicker and Essington, 2008; Kitchell et al., 1977). This model is based on the general bioenergetics model formulation of Kitchell et al. (1977) in which energy consumed (*C*) is equal to the sum of energy used in growth, respiration and metabolism on a daily basis as specific consumption rates in J/g of fish:

$$C = G_s + (R + SDA) + (F + U), \tag{2}$$

where G_s represents somatic growth, *R* is respiration, SDA is specific dynamic action (energetic costs due to digestion), *F* is egestion and *U* is excretion. Energy losses due to reproduction were not included in the model.

Somatic growth (G_s — g/d) was calculated based on the von Bertalanffy growth function (VBGF) for *A. trutta* in SE Australia and associated body weights (Hughes, 2012; Stewart et al., 2011). The size ranges of *A. trutta* were determined using the VBGF estimates of size-at-age 0 of 2.33 cm FL and size at maximum longevity (oldest *A. trutta* recorded 12 + years) of 60.16 cm FL (Stewart et al., 2011).

The function for respiration *R* takes the form:

$$R = R_a \cdot W^{R_b} \cdot f\,(\text{Temp}) \cdot \text{ACT}, \tag{3}$$

where R_a and R_b are the intercept and slope of the allometric function for standard respiration, respectively, *W* is the wet weight of the predator and ACT is a constant multiplier that scales standard metabolism to active metabolism. $f\,(\text{Temp})$ is a temperature-dependent respiration function.

It was assumed that *R* increased exponentially with temperature across the range of ambient temperatures experienced by *A. trutta* according to the function:

$$f\,(\text{Temp}) = \exp\!\left(R_q \cdot \text{Temp}\right), \tag{4}$$

where R_q is a coefficient and Temp is the temperature experienced by the predator. R_q approximates Q_{10}, the rate at which standard respiration increases with an increase of 10 °C, and was determined as:

$$R_q = \ln\,(Q_{10}) / 10, \tag{5}$$

The physiological parameters used to estimate *A. trutta* metabolism and energy density (ED - 6,279 J/g) were taken from Hartman and Brandt (1995a, c) as estimated for *P. saltatrix* (Table 1). This species was considered to be an appropriate proxy for *A. trutta* as both species are pelagic schooling perciform teleosts, have similar distributions in Australia (Hutchins and Swainston, 1986), ecology (Silvano and Begossi, 2005), diet (Buckel & Conover 1997), feeding behaviour (Hartman and Brandt, 1995b), spawning migrations (Ward et al., 2003) and trophic positions in coastal Australian waters (Griffith et al.,

Table 1
Nominal parameter values used in the *A. trutta* bioenergetics model. Values used were taken from Hartman and Brandt (1995a, c) as estimated for *P. saltatrix*.

Parameter name	Symbol	Nominal value
Mass-dependent intercept of respiration	R_a	0.00558
Mass-dependent slope of respiration	R_b	−0.264
Temperature-dependent slope of respiration	R_q	0.06925
Activity multiplier	ACT	1
Specific dynamic action	SDA	0.172
Egestion	F	0.104
Excretion	U	0.068
Energy density	ED	6279

2011). As the most important dietary item for *A. trutta* were pelagic teleosts, we used the energy content of *S. sagax* (8,709 J/g – Parrish et al., 2000) as a proxy for the energy content of all teleosts in the diet. Simulations were done at 15 and 20 °C for the estimation of consumption rates (g prey/g predator/d) which were in turn converted to Q/B estimates for small, medium and large *A. trutta*.

2.1.3. Empirical multiple regression modelling

The third method employed to estimate food consumption was to use the empirical formula of Palomares and Pauly (1989, 1998). This formula derives multiple regression models from 108 freshwater and marine fish populations (38 species) for the prediction of Q/B using the population parameters of asymptotic weight, habitat temperature, a morphological variable (caudal fin aspect ratio) and food type as independent variables (Palomares and Pauly, 1998):

$$log Q/B = 7.964 - 0.204\, log W_\infty - 1.965\, T' + 0.083\, AR + 0.532\, h + 0.398\, d, \tag{6}$$

where W_∞ is the asymptotic weight (g), T' is water temperature (°K), AR is the aspect ratio of the caudal fin, and h and d are dummy variables indicating herbivores ($h = 1$, $d = 0$), detritivores ($h = 0$, $d = 1$) and carnivores ($h = 0$, $d = 0$). As *A. trutta* are carnivores (Hughes et al., 2013), h and d were both set to 0. The aspect ratio of the caudal fin AR is a dimensionless, species-specific constant defined by the equation:

$$AR = h^2/s \tag{7}$$

where h is the height of the caudal fin (cm) and s is its surface area (cm^2) extending to the narrowest part of the caudal peduncle. This variable is used to quantify the activity level of fishes and was derived from the observation that active fishes with high metabolism have caudal fins with a high AR, whereas more sluggish fish with low metabolic rates have caudal fins with a low AR (Palomares and Pauly, 1989). AR was measured by photographing the caudal fins of a broad size range of fish and then using image analysis software (ImageJ; U. S. National Institute of Health, Bethesda, Maryland, USA) to measure h and s. An estimate of Q/B was then calculated at 15 and 20 °C.

3. Results

### 3.1. Daily ration & prey consumption rates

3.1.1. Gastric evacuation experiments

On each occasion the experimental fish became satiated after approximately 2.5 min of feeding. Experimental parameters and results are given in Table 2. At ~15 °C, experimental fish consumed 8.2 kg of *S. sagax* (mean individual *S. sagax* weight 40.4 ± 0.4 g). Sixty-three percent of fish sampled contained labelled food remains (mean meal weight 102.0 ± 11.6 g). Time for complete digestion took 50.1 h and A_i was estimated to be 22.59 (Fig. 1). At ~20 °C, 87% of fish sampled had consumed an average *S. sagax* meal of 82.3 ± 8.1 g out of the 7.3 kg offered (mean individual *S. sagax* weight 25.8 ± 0.3 g). Time for complete digestion was 39.34 h and A_i was estimated to be 17.10 (Fig. 1).

Using the evacuation rate (A_i) estimates above, daily ration for *A. trutta* of various sizes and at the two experimental temperatures was calculated (Table 3). The estimated mean daily consumption averaged across *A. trutta* of all sizes (4.7–64.6 cm FL, 1,593.31 ± 21.53 g) was 13.97 ± 0.19 g at ~15 °C and 18.45 ± 0.25 g at ~20 °C. This equated to a daily ration of 0.88 ± 0.01 and 1.16 ± 0.02% of body weight per day (BW/d) at ~15 and ~20 °C respectively. Estimated daily ration was similar for small (1.01 ± 0.04 & 1.33 ± 0.05% BW/d at ~15 and ~20 °C respectively) and large *A. trutta* (0.89 ± 0.01% & 1.18 ± 0.01% BW/d) and was lowest for medium-sized *A. trutta* (0.58 ± 0.01% & 0.77 ± 0.01% BW/d). Estimated annual consumption rates increased with

Table 2
Experimental parameters [temperature (°C), fish size (fork length (FL – cm)) and weight (g), food weight (total and mean – g)] and results [sample sizes, experimental meal weight (g), time for complete digestion (h) and A$_i$ estimates] for *A. trutta* gastric evacuation experiments.

Temperature mean ± SE (range) (°C)	Fish FL mean ± SE (range) (cm)	Fish weight mean ± SE (range) (g)	Total food weight (g)	Food weight mean ± SE (range) (g)	Number of fish sampled	Number of fish that consumed experimental meal	Experimental meal weight mean ± SE (range) (g)	Time to complete digestion (h)	A$_i$ estimate (proportion × h = h)
15.1 ± 0.1 (14.5–15.5)	51.3 ± 0.3 (47.6–55.7)	2,481 ± 54 (1,912–3,281)	8,197.34	40.38 ± 0.36 (23.94–57.02)	45	28	102.02 ± 11.62 (23.94–207.32)	50.10	22.59
19.4 ± 0.1 (17.9–20.9)	53.7 ± 0.2 (50.5–56.9)	3,032 ± 47 (2,600–3,782)	7,331.55	25.81 ± 0.33 (12.21–39.21)	38	33	82.31 ± 8.11 (23.37–206.06)	39.34	17.10
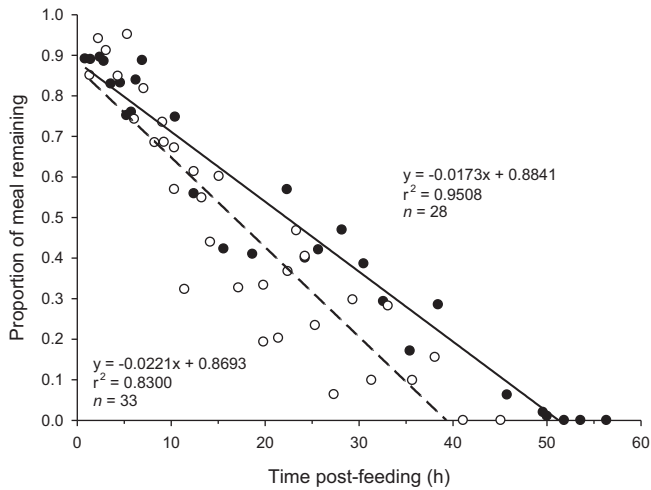
Fig. 1. Proportion of initial wet mass of *S. sagax* recovered from the stomachs of captive experimental *A. trutta* versus time post-feeding (h) at 15.1 °C (●) and 19.4 °C (○). The area beneath the linear relationships estimates (A_i) for *S. sagax* at 15.1 °C (solid line) and 19.4 °C (dashed line) in units of proportion/h. A_i represents the average amount of time required to evacuate the average proportion of all *S. sagax* meals in the stomach at any instant in time. *n* is sample size.

both fish size and temperature from 0.24 ± 0.01 kg/year for small fish at ~15 °C to 9.13 ± 0.01 kg/year for large fish at ~20 °C. The amount of food ingested in a year (*Q*) by *A. trutta* of all sizes combined expressed as a fraction of their biomass (*B*) was therefore calculated to be 3.20 ± 0.04 at ~15 °C and 4.23 ± 0.06 at ~20 °C (Table 3).

3.1.2. Bioenergetics modelling

Using the bioenergetics model simulations described above, daily ration for *A. trutta* of various sizes and at the two experimental temperatures was calculated (Table 4). The estimated mean daily consumption averaged across *A. trutta* of all sizes (2.33–60.16 cm FL) was 12.55 ± 0.74 g at 15 °C and 19.01 ± 1.00 g at 20 °C. This equated to a daily ration of 1.01 ± 0.06 and 1.36 ± 0.07 % of body weight per day (BW/d) at 15 and 20 °C respectively. Daily ration was higher for small ($2.61 \pm 0.03\%$ & $3.63 \pm 0.05\%$ BW/d at 15 & 20 °C respectively) and medium-sized *A. trutta* (1.36 ± 0.01 & $1.90 \pm 0.02\%$ BW/d) and was lowest for large *A. trutta* (0.92 ± 0.01 & $1.28 \pm 0.01\%$ BW/d). Estimated annual consumption rates increased with both fish size and temperature from 0.41 ± 0.01 kg/year for small fish at 15 °C to 10.83 ± 0.12 kg/year for large *A. trutta* at 20 °C. This was equivalent to an overall *Q/B* for *A. trutta* in SE Australia of 3.67 ± 0.22 at 15 °C and 4.98 ± 0.26 at 20 °C (Table 4).

3.1.3. Empirical multiple regression modelling

There was substantial variability in *A. trutta* caudal fin aspect ratio (*AR*) for fish of all sizes (12.9–61.5 cm FL), ranging from 1.775 to 3.143 (Fig. 2). *AR* was not significantly correlated with fish size (r = 0.03, p = 0.34, n = 190) and therefore the average *AR* for fish of all

sizes (2.366 ± 0.022) was used in the multiple regression model. W_∞ was calculated by converting the L_∞ value (62.59 cm FL) estimated in Stewart et al. (2011) and Hughes (2012) to weight using the length–weight relationship for *A. trutta* estimated in Hughes (2012) (Wt = $0.0192(\text{FL})^{2.9666}$, $r^2 = 0.99$, n = 2,300). W_∞ was therefore calculated to be 4,100.27 g. Using the multiple regression model, overall *Q/B* for *A. trutta* was therefore calculated to be 4.02 at 15 °C and 5.25 at 20 °C.

3.1.4. Annual prey consumption in SE Australia

Assuming a 10,000 t population of *A. trutta* in coastal SE Australian waters, the *Q/B* estimates for each technique equated to an estimated annual prey consumption of between 31,991 t (at 15 °C) and 42,271 t (at 20 °C) calculated from the gastric evacuation experiments, between 36,717 and 49,782 t (at 15 °C & 20 °C, respectively) calculated from the bioenergetics model, and between 40,179 and 52,518 t (at 15 °C & 20 °C, respectively) from the multiple regression model. The *Q/B* estimates calculated from each technique were then averaged to give an overall *Q/B* value at 15 °C of 3.63 ± 0.24 and 4.82 ± 0.31 at 20 °C (mean 4.22 ± 0.31)., this equates to overall annual prey consumption of between $36,296 \pm 2,373$ t at 15 °C and $48,190 \pm 3,063$ t at 20 °C (Table 5). Total annual consumption of the primary prey category in the diet, pelagic fishes, ranged from $34,012 \pm 2,224$ t at 15 °C to $45,158 \pm 2,870$ t at 20 °C (mean $39,585 \pm 2,547$ t). Consumption of demersal fishes ranged from 1380 ± 90 t/year at 15 °C to 1833 ± 117 t/year at 20 °C (mean 1607 ± 103 t/year). All other prey categories made much smaller contributions (16–396 t at 15 °C, 22–526 t at 20 °C) to total annual prey consumption. Total mean annual consumption of the two most abundant species in the diet, *S. sagax* and *Trachurus* spp., were $14,614 \pm 940$ & $12,719 \pm 818$ t/year, respectively. Substantial quantities of *Scomber australasicus* (2290 ± 147 t), *Hyperlophus vittatus* ($1,758 \pm 113$ t), *Engraulis australis* ($1,370 \pm 88$ t) and *Sillago flindersi* ($1,075 \pm 69$ t) were also estimated to be consumed each year.

4. Discussion

This study has provided the first information on daily consumption rates and annual consumption of prey species for *A. trutta*. These prey consumption estimates show that *A. trutta* may play a top-down role in the coastal pelagic ecosystem of SE Australia. Using an estimated stock biomass of 10,000 t, *A. trutta* consume an estimated 42,200 t of primarily small schooling zooplanktivorous fishes annually in this region.

The consumption rate estimates presented here were calculated using three independent techniques, two empirical and one experimental, to provide a range of values with associated errors thereby diminishing some of the individual limitations of each methodology. Each technique produced comparable estimates that provide confidence that the estimates are both reliable and repeatable. Most previous work has used a single estimation technique (e.g. Elliot and Persson, 1978), multiple similar techniques (e.g. Buckel & Conover 1997), or applied experimental results derived for one species to other comparable species based on physiological similarities (e.g. Griffiths et al., 2007, 2009; Olson and Galván-Magaña, 2002). Agreement amongst the

Table 3
Fork length (cm), mean body weight (g ± SE), daily consumption (g/d ± SE), ration (%BW/d ± SE), annual prey consumption (kg/year ± SE) and *Q/B* estimate (food consumed/biomass) for small, medium and large *A. trutta* at the two gastric evacuation experimental temperatures (~15 & ~20 °C) for which A_i was estimated.

Size class	Length range (FL cm)	Mean body weight (g)	Experimental temperature (°C)	Daily consumption (g/d)	Daily ration (% BW/d)	Annual consumption (kg/year)	Q/B
Small	4.7–20.0	66.62 (2.30)	15.1 (0.1)	0.67 (0.02)	1.01 (0.04)	0.24 (0.02)	
			19.4 (0.1)	0.88 (0.03)	1.33 (0.05)	0.33 (0.02)	
Medium	20.0–40.0	656.59 (12.31)	15.1 (0.1)	3.81 (0.07)	0.58 (0.01)	1.39 (0.05)	
			19.4 (0.1)	5.03 (0.09)	0.77 (0.01)	1.84 (0.07)	
Large	40.0–64.6	2,119.26 (19.29)	15.1 (0.1)	18.93 (0.17)	0.89 (0.01)	6.91 (0.13)	
			19.4 (0.1)	25.02 (0.23)	1.18 (0.01)	9.13 (0.17)	
Overall	**4.7–64.6**	**1593.31 (21.53)**	**15.1 (0.1)**	**13.97 (0.19)**	**0.88 (0.01)**	**5.10 (0.14)**	**3.20 (0.04)**
			19.4 (0.1)	18.45 (0.25)	1.16 (0.02)	6.74 (0.18)	4.23 (0.06)

Table 4
Fork length (FL – cm), mean body weight (g ± SE), daily consumption (g/d ± SE), ration (%BW/d ± SE), annual prey consumption (kg/year ± SE) and Q/B estimate (food consumed/biomass) for small, medium and large *A. trutta* using simulations of the bioenergetics model at 15 & 20 °C. The size ranges of *A. trutta* were determined using the VBGF estimates of size-at-age 0 of 2.33 cm FL and size at maximum longevity (12 years) of 60.16 cm FL (Hughes, 2012; Stewart et al., 2011).

| Size class	Length range (FL cm)	Body weight (g)	Simulation temperature (°C)	Daily consumption (g/day)	Daily ration (% BW/day)	Annual consumption (kg/year)	Q/B
Small	2.33–20.0	43.57 (0.54)	15	1.12 (0.01)	2.61 (0.03)	0.41 (0.01)	
			20	1.60 (0.02)	3.63 (0.05)	0.58 (0.01)	
Medium	20.0–40.0	542.97 (5.31)	15	7.32 (0.07)	1.36 (0.01)	2.67 (0.03)	
			20	10.42 (0.10)	1.90 (0.02)	3.80 (0.04)	
Large	40.0–60.16	2,301.08 (25.53)	15	21.04 (0.24)	0.92 (0.01)	7.68 (0.09)	
			20	29.69 (0.33)	1.28 (0.01)	10.83 (0.12)	
Overall	**2.33–60.16**	**1,320.79 (73.07)**	**15**	**12.55 (0.74)**	**1.01 (0.06)**	**4.58 (0.27)**	**3.67 (0.22)**
			20	**19.01 (1.00)**	**1.36 (0.07)**	**6.94 (0.36)**	**4.98 (0.26)**

three methods provided improved confidence that the consumption estimates represent a biologically plausible range of annual consumption rates for *A. trutta* in SE Australia.

It is important to note, however, that the estimates of *A. trutta* consumption using gastric evacuation experiments are likely to be conservative. Other studies that have successfully used gastric evacuation experiments to estimate consumption rates have shown that when prey types are structurally similar (e.g. small pelagic teleosts), differences in energy density contribute to prey-specific rates of evacuation (Temming and Herrmann, 2003) with gastric evacuation rates inversely correlated with total lipid content prey items (Olson and Boggs, 1986). The experimental food organism used in this study, *S. sagax*, is likely to have the highest lipid content of the teleosts in the diet of *A. trutta* (Parrish et al., 2000) and thus gastric evacuation rates for all other items are expected to be faster. It is probable therefore that overall actual consumption rates and daily ration for are potentially even higher than the estimates presented here.

Temperature had a significant effect on the gastric evacuation rates (and hence consumption rates) of *A. trutta* with evacuation rates at 20 °C 1.3 times faster than at 15 °C. The influence of water temperature on fish metabolism and rates of meal processing has been studied in a variety of pelagic fish species and has shown that decreased water temperatures result in decreased gastric evacuation and metabolic rates (e.g. Benkwitt et al., 2009; Griffiths et al., 2009; Temming et al., 2002). Consumption rates of carnivorous fishes can vary substantially, but have generally been observed to be between 5 and 25% BW/d (Gillum et al., 2012), with lower rates generally observed for predatory fishes of >1 kg in size (Beaudreau and Essington, 2009). Daily ration estimates for *A. trutta* of all sizes (0.9–1.4% BW/d) were substantially lower than for other similar piscivorous temperate pelagic fish species *Morone saxatilis* (~5% BW/d) and *P. saltatrix* (~6% BW/d) estimated using

bioenergetics modelling in Chesapeake Bay (Hartman and Brandt, 1995b). Daily ration for both *M. saxatilis* and *P. saltatrix* was calculated from maximum consumption rates at optimal temperatures of 20–25 °C, whereas daily ration for *A. trutta* in the present study was calculated from the mean consumption rate at environmentally relevant, but likely sub-optimal temperatures of 15–20 °C. It is therefore likely that *A. trutta* daily ration would be more similar to those calculated for *M. saxatilis* and *P. saltatrix* if maximum consumption rates had been estimated in this study using higher temperatures (>20 °C) in aquaria experiments and model simulations. Daily ration for *A. trutta* was also lower than those for the mainly tropical scombrids *Thunnus tonggol* (1.3–2.3% BW/d: Griffiths et al., 2007), *Euthynnus affinis* (2.0–4.1% BW/d: Griffiths et al., 2009), skipjack tuna *Katsuwonis pelamis* (5.5–9.9% BW/d: Menard et al., 2000; Essington, 2003), albacore *T. alalunga* (3.8% BW/d: Essington, 2003), juvenile bigeye tuna *Thunnus obesus* (4.8% BW/d: Menard et al., 2000) and juvenile *T. albacares* (2.3–9.6% BW/d: Olson and Boggs, 1986; Maldeniya, 1996). The difference in daily ration between these species and many temperate species (including *A. trutta*) is due to the influences of both the high metabolic rates possessed by scombrids (Palomares and Pauly, 1998) in addition to the higher temperatures of the mainly tropical waters in which they are found on prey evacuation rates and hence daily ration. Indeed, even within the family Scombridae, temperate species like southern bluefin tuna *Thunnus maccoyii* and Atlantic bluefin tuna *Thunnus thynnus* have daily ration estimates (0.9–1.0 & 1.0–2.0% BW/d, respectively) much lower than for tropical species and similar to those for *A. trutta* presented here (Essington et al., 2001; Young et al., 1997).

A. trutta daily ration decreased with increasing fish size from 1.0–3.6% BW/d for small fish (<20 cm FL) to 0.9–1.3% BW/d for large fish (>40 cm FL). This pattern has been similarly noted for other pelagic piscivorous species *M. saxatilis* (Hartman and Brandt, 1995b), *T. albacares* (Maldeniya, 1996), *P. saltatrix* (Hartman and Brandt, 1995b), *T. tonggol* (Griffiths et al., 2007) and *E. affinis* (Griffiths et al., 2009). For
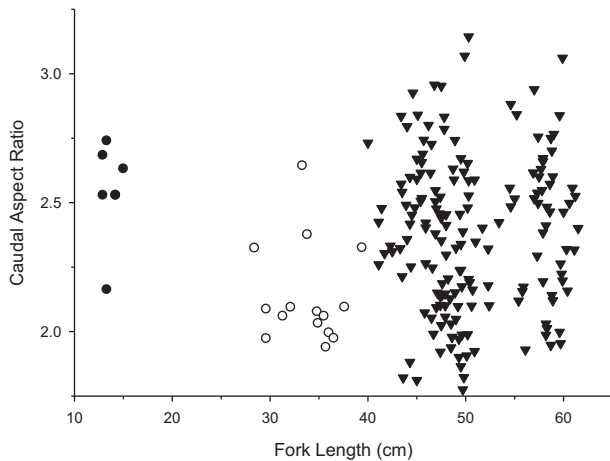
Fig. 2. Caudal fin aspect ratio versus fork length (FL – cm) for small (●, 0–20 cm FL, n = 7), medium (○, 20–40 cm FL, n = 16) and large (▼, >40 cm FL, n = 167) *A. trutta*.

Table 5
Estimated annual consumption (t/year ± SE) of major prey categories by *A. trutta* in south-eastern Australia at 15 and 20 °C (using an estimated stock biomass of 10,000 t). Estimated annual consumption of the two most important species in the diet, *S. sagax* and *Trachurus* spp., are also given.

Prey category	Temperature (°C)		
	15	20	Mean
Pelagic fishes	34,012 (2,224)	45,158 (2,870)	39,585 (2,546)
S. sagax	12,556 (821)	16,671 (1,060)	14,614 (940)
Trachurus spp.	10,928 (714)	14,509 (922)	12,719 (818)
Demersal fishes	1381 (90)	1833 (117)	1607 (103)
Molluscs	16 (1)	22 (1)	19 (1)
Cephalopods	82 (5)	108 (7)	95 (6)
Benthic crustaceans	113 (7)	150 (10)	131 (9)
Pelagic crustaceans	280 (18)	372 (24)	326 (20)
Plants	17 (1)	22 (1)	19 (1)
Miscellaneous	396 (26)	526 (33)	461 (30)
Total	**36,296 (2373)**	**48,190 (3063)**	**42,243 (2718)**

T. tonggol it has been suggested that the decline in daily ration with size may be the result of decreased metabolic demand at sizes greater than that at which the growth rate begins to slow (Griffiths et al., 2007). As a result, larger fish may require relatively smaller amounts of food to meet their metabolic requirements than smaller fish. The decreasing growth rate which occurs with increasing size (Stewart et al., 2011) likely reflects this decrease in metabolic demand and hence daily ration in *A. trutta*. The low daily ration calculated for medium-sized *A. trutta* occurred as an artefact of the high proportion of empty stomachs recorded during analysis of diet composition for this size class of fish (Hughes et al., 2013) and was therefore not likely reflective of a real physiologically-driven pattern.

4.1. Ecosystem & fishery implications

The estimates of prey consumption rates and daily ration presented here suggest that *A. trutta* could potentially play a role in structuring the coastal pelagic ecosystem in SE Australia by consuming between 3.6 and 4.8 times their own biomass of prey annually. Nonetheless, the Q/B estimates presented here are well within the range for some temperate pelagic marine fish species (e.g. 1.52 for European seabass *Dicentrarchus labrax* – 4.08 for marine coho salmon *Oncorhynchus kisutch*: Palomares and Pauly, 1998), but are low compared with other similar sized primarily piscivorous pelagic species from other temperate waters worldwide (e.g. 18.3 for *M. saxatilis* & 10.8 for *P. saltatrix* – Hartman and Brandt, 1995b) and up to an order of magnitude lower than for species with the highest energy demands like scombrids (e.g. *K. pelamis* 32.4, *T. albacares* 19.8, *T. alalunga* 13.4 – Essington, 2003; Australian bonito *Sarda australis* 15.6 – Griffiths et al., 2010).

This suggests that although the *A. trutta* population in SE Australian waters may have a top-down influence through annual consumption of large amounts of primarily pelagic prey, their overall impact relative to their biomass is comparatively low compared with that of other species which occupy similar trophic positions in this region. To our knowledge, biomass estimates for other medium to large-sized pelagic piscivores in SE Australia have not been made, but if populations of comparable medium to large-sized pelagic piscivores like *P. saltatrix*, yellowtail kingfish *Seriola lalandi*, *S. australis*, *K. pelamis* and *Thunnus* spp. occur in biomasses similar to that of *A. trutta* in coastal SE Australian waters, then it follows that, with Q/Bs at least double (Hartman and Brandt, 1995b), and up to 8 times (Essington, 2003) larger than that of *A. trutta*, their annual consumption rates will be correspondingly larger than that of *A. trutta*. For example, a population of *S. australis* ($Q/B = 15.6$; Griffiths et al., 2010) or *K. pelamis* ($Q/B = 32.4$; Essington, 2003) has the potential to consume up to 4.3 and 9 times, respectively, the amount of prey in this region annually compared with that of *A. trutta*.

These findings also may have important implications for the management of both *A. trutta* and small pelagic fishes in SE Australia. The tendency of small pelagic species to aggregate in schools makes them vulnerable to overfishing; high fishing effort levels and variable recruitment amplified by the effects of environmental variability have historically resulted in stock and fishery collapses (Sugihara et al., 2011). Even during periods of high landings during the 1980s (Kailola et al., 1993), annual catches of small pelagic fishes were still smaller than the estimates of *A. trutta* annual prey consumption presented here. When mortality due to predation is incorporated explicitly into population assessment models, estimates of natural mortality can often exceed estimates of harvest mortality, especially for species at low to moderate trophic levels such as small zooplanktivorous fishes (Buckel et al., 1999; Gaichas et al., 2010). Small pelagic fishes in this region are currently harvested at relatively low levels (Ward et al., 2012), and the population of *A. trutta* appears to be relatively stable, despite current historically high commercial landings (Stewart et al., 2012). The dramatic biomass fluctuations in populations of zooplanktivorous fishes seen in many parts of the world (e.g. Atlantic herring *Clupea harengus* and European pilchard *Sardina pilchardus* in the north-east Atlantic:

Alheit and Hagen, 1997; *S. sagax* and *E. mordax* in the California Current System: Glaser, 2011), including southern Australia (*S. sagax* and *E. australis* in the Great Australian Bight: Ward et al., 2001), coupled with changes to large scale oceanography as a result of climate-related warming of coastal SE Australian waters over recent decades (Ridgway, 2007), suggest that similar fluctuations and/or shifts in the populations of zooplanktivorous fishes will almost inevitably occur in this region in the future. The combined stock biomass of the two species which constitute the majority of the *A. trutta* diet, *S. sagax* and *Trachurus* spp., is currently estimated to be 181,000 t in SE Australia (Ward et al. 2012). Our consumption estimates for these two prey species combined (27,300 t; Table 4) therefore represents removal of only a small proportion (~15%) of this biomass annually. Despite this relatively low predation pressure on species which are functionally similar small pelagic zooplanktivores, environmentally-driven variability in the relative abundance of such high biomass trophic groups (e.g. Alheit and Hagen, 1997; Glaser, 2011; Ward et al., 2001) means that there is inherent potential for alterations to the structure and function of the pelagic ecosystem of SE Australia to occur, which may in turn have unexpected effects on populations of piscivorous predator species like *A. trutta* (Cury et al., 2000; Glaser, 2011). Such effects may include diet shifts (e.g. Bulman et al., 2001), changes in abundance (e.g. Cury et al., 2000), emigration (e.g. Crawford, 1999) and increased impacts of commercial harvesting (e.g. Pauly et al., 1998, Cury et al. 2000).

Conversely, the shift in diet of *A. trutta* from pelagic crustaceans to zooplanktivorous fishes which has occurred in recent decades (Hughes et al., 2013) may have already resulted in increased predation pressure by *A. trutta* on zooplanktivorous fishes in this region. If the biomass of *A. trutta* in coastal SE Australian waters remains stable, then it is likely that predation pressure on the suite of prey species will remain relatively temporally constant. However, if the SE Australian *A. trutta* stock mimic the dramatic declines evident in more heavily harvested large predatory species which occupy high trophic levels, like scombrids (e.g. Fromentin, 2009; Murawski, 2010), this may result in an increase in the size of the zooplanktivorous fish population in SE Australia (see modelling in Griffiths et al., 2010). Including accurate and quantified information on predator–prey interactions such as those presented here can reduce the levels of uncertainty in biomass estimates and aid in the development and application of multispecies ecosystem models (e.g 'Ecopath with Ecosim'; Pauly et al., 1998) that are designed to address just these types of questions.

5. Conclusions

Here, we present the first estimates of daily consumption rates and annual consumption of prey species by *A. trutta* in SE Australia using three independent techniques to produce estimates with improved reliability and repeatability compared with the use of a single technique employed alone. Estimates of *A. trutta* annual prey consumption are consistent with the hypothesis that *A. trutta* likely have a top-down influence on small zooplanktivorous fishes in SE Australia. There are, however, several influential factors that make it impossible to assess whether the magnitude of top-down pressure exerted by *A. trutta* on small pelagic fishes, overall, is substantial enough to cause significant fluctuations in the populations of these species. Firstly, we did not explicitly examine the effects of *A. trutta* predation-induced mortality on prey population dynamics. Secondly, we used the upper estimate of *A. trutta* abundance in this region (10,000 t) in order to provide a maximum annual prey consumption estimate; if the stock biomass for *A. trutta* in SE Australia is smaller than 10,000 t then this estimate could be proportionally lower. Thirdly, there are at least two other ecologically similar predatory fish species with annual prey consumption rates that are likely to be considerably higher than that of *A. trutta* present in this region. Finally, estimated annual consumption of key prey species by *A. trutta* is generally a small proportion of estimated spawning biomass in the region (Ward et al., 2012), which also

precludes making a definitive conclusion regarding the extent of potential top-down regulation exerted by *A. trutta* on small pelagic fishes in coastal SE Australian waters.

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