

Evaluating the potential for trophodynamic control of fish by the longfin inshore squid (*Loligo pealeii*) in the Northwest Atlantic Ocean

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Abstract: Many marine apex predator populations have been depleted via targeted fishing, potentially enhancing the productivity of lower trophic-level species such as squid. Squid may be predators of juvenile stages of fish stocks, so fishing could induce compensatory juvenile mortality. Here we evaluate the energetic potential of the longfin inshore squid (*Loligo pealeii*) to exert trophodynamic control on recruitment of several commercially important fish populations. We estimated the population prey consumption of *L. pealeii* by developing bioenergetics and population models based on previously published data. Our predictions of population consumption showed that squid consume high quantities of prey on daily and seasonal time scales. Further, comparisons between our estimates of population consumption and fish recruitment biomass indicate that *L. pealeii* may potentially exert a trophodynamic control on the recruitment success of commercially exploited fish species even if these species are only a minor prey item of squid. Overall, our findings suggest that the predation interactions of *L. pealeii* should be considered when managing and rebuilding fish stocks in the northwest Atlantic continental shelf ecosystem.

Résumé : Plusieurs populations de prédateurs marins situées au sommet du réseau alimentaire ont été épuisées par la pêche ciblée, ce qui favorise potentiellement la productivité des espèces de niveau trophique inférieur, telles que le calmar. Les calmars peuvent être des prédateurs des stades juvéniles des stocks de poissons; la pêche peut donc générer une mortalité des jeunes à cause de l'effet Allee. Nous évaluons ici le potentiel énergétique du calmar totam pour le contrôle trophodynamique du recrutement chez plusieurs populations de poissons d'intérêt commercial. Nous estimons la consommation de proies de la population de *Loligo pealeii* en élaborant des modèles bioénergétiques et démographiques basés sur des données publiées antérieurement. Nos prédictions concernant la consommation de la population montrent que, sur des échelles temporelles journalières et saisonnières, les calmars mangent de grandes quantités de proies. De plus, les comparaisons entre nos estimations de la consommation de la population et la biomasse du recrutement des poissons indiquent que *L. pealeii* peut potentiellement exercer un contrôle trophodynamique sur le succès du recrutement d'espèces de poissons exploitées commercialement, même si celles-ci ne représentent que des proies secondaires pour les calmars. Globalement, nos résultats soulignent qu'il est nécessaire de tenir compte des interactions de prédation de *L. pealeii* lorsqu'on veut gérer et rebâtir les stocks de poissons dans l'écosystème de la plate-forme continentale du nord-ouest de l'Atlantique.

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Introduction

Evidence that predator populations may regulate marine fish recruitment has incited fishery scientists to incorporate trophic interactions into assessments of commercial fish stocks and management strategies (Hollowed et al. 2000; Tsou and Collie 2001; Jurado-Molina et al. 2005). Developing stock assessments that consider the effects of predation interactions on population dynamics requires a characterization of predator-prey relationships and recognition that some important predation interactions may not be apparent unless there is a shift in trophic dynamics provoked by fishing or other mechanisms. For instance, in triangular food

webs, shorter-lived, fast-growing prey species may expand in response to the removal of adult predatory fishes and in turn exacerbate the loss of predator biomass by consuming the younger stages of their predator (Swain and Sinclair 2000; Walters and Kitchell 2001; Lynam et al. 2005). Increased juvenile mortality rates in heavily exploited predator populations could inhibit recruitment success and potentially lead to depensation (Walters and Kitchell 2001). Identifying those prey species that are capable of exerting a trophodynamic control on the early life stage of their exploited predators is an important step toward effectively accounting for predation interactions in fisheries management strategies.

Squid populations can potentially impose a negative impact on the recruitment of commercially harvested fish stocks. In recognition of the voracious feeding habits of squid, previous authors have suggested that squid predation could have a substantial impact on the mortality of juvenile fishes (Maurer and Bowman 1985; Dawe 1988; Rodhouse and Nigmatullin 1996). Commercial fish populations inhabiting the northwest Atlantic continental shelf ecosystem may be particularly vulnerable to predation by squid. The longfin inshore squid (*Loligo pealeii*) is both a predator and a prey

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item of commercially important fishes, many of which have endured decades of heavy exploitation and are considered overfished or recovering (Northeast Fisheries Science Center 2006). Predators of *L. pealeii* include *Pomatomus saltatrix* (bluefish), *Melanogrammus aeglefinus* (haddock), *Pollachius virens* (pollock), *Merluccius bilinearis* (silver hake), and *Paralichthys dentatus* (summer flounder) (Langton and Bowman 1977; Lange 1980; Bowman et al. 2000), and their prey items include the early life stages of gadids, merlucciids, pleuronectids, clupeids, and scombrids (Vovk 1972; Macy 1982; Hunsicker and Essington 2006). *Loligo pealeii* occupies similar habitat as the larval and juvenile stages of these exploited fishes throughout most of the year (Sherman et al. 1984; Able and Fahay 1998), and during this period their ecological role may shift between predator, competitor, and prey (Vovk 1985). Consequently, the trophic interactions of *L. pealeii* may be an important factor dictating the recruitment success of the early life stages of commercial fish populations, particularly during years of high squid abundance.

Estimating the potential for *L. pealeii* to exert trophodynamic control on commercially exploited fish stocks requires estimates of the individual feeding rates of squid, how these rates vary with size and temperature, and the size structure and abundance of the *L. pealeii* stock. A strong energetic link between a predator and prey does not necessarily translate into a strong trophic link (Paine 1980), and estimates of prey consumption alone are not sufficient for determining the top-down effect of squid on fish abundance. A suite of factors needs to be considered, including the functional responses of juvenile fish and squid populations. However, for squid to exert an impact on fish abundance they must consume a high proportion of the available biomass of their prey; thus, quantifying the predation demand of squid is a necessary step for determining whether *L. pealeii* predation may affect fish recruitment. The predation demand of *L. pealeii* has been previously quantified from stomach contents and gastric evacuation rates (Maurer and Bowman 1985). However, these methods require extensive sampling effort and often yield infrequent and highly variable estimates of consumption (Adams and Breck 1990). Also, estimates based on field measurements can be biased, since gastric evacuation rates are influenced by many factors, including predator size, prey type, meal size, and temperature (Adams and Breck 1990).

Bioenergetics models are an alternative method for estimating predation rates. These models attempt to use thermodynamic principles to constrain estimates of consumption within energetically plausible ranges (Winberg 1956; Kitchell et al. 1977). They permit exploration of size- and temperature-dependent consumption, and they have been shown to successfully predict predation rates (Rice and Cochran 1984; Hansson et al. 1996). Further, these models have been used to quantify the effect of predators on their prey resources (Cyterski et al. 2002; Irwin et al. 2003; Roby et al. 2003), evaluate changes in predation demand in response to environmental conditions (Harvey 2005), and estimate population predation responses to alternative harvesting strategies (Kitchell et al. 1997; Essington et al. 2002; Schindler et al. 2002). Similarly, a squid bioenergetics model coupled with published estimates of the size structure

and abundance of the *L. pealeii* population can be used to develop and test hypotheses concerning the potential predatory impact of squid populations on juvenile fishes in response to the effects of commercial fishing, physical forcing, or other factors.

We combined previously published data from various *Loligo* species to parameterize a generic *Loligo* bioenergetics model. The specific objectives of this paper are to (i) synthesize available information on the metabolic expenditures of *Loligo* spp. and develop a simplified bioenergetics model to estimate individual consumption rates of *Loligo*; (ii) apply the bioenergetics model to the *L. pealeii* population along the northwest Atlantic continental shelf (Maine to Cape Hatteras) to estimate the total population consumption in the summer and winter seasons; and (iii) evaluate whether it is energetically plausible for *L. pealeii* to exert a trophodynamic control on the early life stages of commercially exploited fishes. We consider our model an evolving tool that can be used by scientists and managers alike to evaluate prey consumption by *L. pealeii* under various sets of assumptions.

Materials and methods

Bioenergetics model

Bioenergetics models are often used to estimate prey consumption of species with long life spans, age-structured populations, and discrete, annual spawning events. The longfin inshore squid, however, is short-lived (<1 year), spawns year round and has life history traits that are influenced by season (Brodziak and Macy 1996). Namely, winter-hatched squid (November to May) exhibit slower growth rates and longer life spans than summer-hatched squid (June to October; Brodziak and Macy 1996). To accurately account for the unique life history traits of squid, we modeled the *Loligo* energy budget on daily time steps and represented the winter- and summer-hatched squid as winter and summer cohorts, respectively.

We used the following energy balance equation to estimate the consumption rates of *Loligo* (Winberg 1956; Kitchell et al. 1977):

$$(1) \quad C = G + AL + RL + R$$

where C is the consumption rate, G is somatic growth, AL are the assimilation losses, RL is gonadal growth, and R is the metabolic rate (all in $J \cdot g^{-1} \cdot day^{-1}$). We modeled somatic and reproductive growth together as total body growth, i.e., we did not explicitly account for patterns of gonadal tissue loss under the assumption that *Loligo* spp. are largely semelparous (Rocha et al. 2001). The data used to develop the squid energy budget came from a synthesis of previously published data on the bioenergetics of *Loligo* spp. (Table 1). We fit allometric and temperature-dependent functions to these data to estimate winter (November–May) and summer (June–October) hatched squid consumption rates. Further, we ran Monte Carlo simulations to account for potential errors associated with parameter values and estimated the median and 5th and 95th percentiles of individual squid consumption rates. (All nominal parameters and equations that were used in the bioenergetics model are listed in Tables 1 and 2, respectively.)

Table 1. Parameter values and references used in seasonal *Loligo* bioenergetics model.

Parameter	Winter	Summer	Reference
x_{SMR}	103.8484	183.3581	O’Dor 1982; Segawa and Hanlon 1988; Boucher-Rodoni and Mangold 1989;
y_{SMR}	-0.1566	-0.1548	Finke et al. 1996
ACT	2.40	1.85	O’Dor 1982
ED	4166 J·g ⁻¹	4166 J·g ⁻¹	Macy 1980
PED	3800 J·g ⁻¹	3800 J·g ⁻¹	Pedersen and Hislop 2001
AE	0.76	0.76	Wallace et al. 1981; Wells and Clarke 1996
OC	19 J·mL ⁻¹	19 J·mL ⁻¹	Webber and O’Dor 1986
$L(t)$			Brodziak and Macy 1996; Macy and Brodziak 2001
y_{min}	4.63	2.29	
y_{max}	27.07	43.67	
t_{min}	2.563	1.643	
t_{max}	9.725	9.232	
$W(t)$			Northeast Fisheries Science Center 2002
x_w	0.2566	0.2566	
y_w	2.1518	2.1518	

Note: Terms labeled x_{SMR} and y_{SMR} are constants specific to the equations for squid standard metabolic rates; ACT is the activity multiplier; ED is the squid energy density; PED is the prey energy density; AE is the assimilation efficiency; OC is the oxycalorific coefficient; y_{min} , y_{max} , t_{min} , and t_{max} are constants specific to the equations for *L. pealeii* growth rates; x_w and y_w are constants specific to the *L. pealeii* weight-at-length equations.

Table 2. Description of components and equations for generic *Loligo* bioenergetics model.

Component	Description	Equation
SMR	Standard metabolic rate (mL O ₂ ·kg ⁻¹ ·h ⁻¹)	$SMR = x_{SMR} W(t)^{y_{SMR}}$
AMR	Active metabolic rate (mL O ₂ ·kg ⁻¹ ·h ⁻¹)	$AMR = ACT [x_{SMR} W(t)^{y_{SMR}}]$
$L(t)$	Length (cm) at age t (months); pooled sex, winter; pooled sex, summer	$L(t) = y_{min} \exp \left[\ln \left(\frac{y_{max}}{y_{min}} \right) \frac{t - t_{min}}{t_{max} - t_{min}} \right]$
$W(t)$	Weight (g) at length (cm)	$W_L = x_w L^{y_w}$

Note: Terms labeled x and y are constants specific to the equations in which they appear; ACT is the activity multiplier; y_{min} and y_{max} are the predicted sizes of the youngest and oldest individuals, respectively; t_{min} and t_{max} are maximum and minimum observed age (months), respectively.

Assimilation losses are the losses of energy due to egestion, excretion, and specific dynamic action. These energetic values have not been determined for *Loligo* spp., thus we accounted for assimilation losses by multiplying the consumption rate by an estimate of assimilation efficiency (AE). We assumed this value represents the proportion of ingested food that is available for growth, metabolism, and reproduction; therefore, the energy budget can be expressed as

$$(2) \quad AE \cdot C = G + RL + R$$

The estimate of AE in this model is equal to the sum of the published estimate of absorption efficiency for the omastrephid squid *Illex illecebrosus* (0.86; Wallace et al. 1981), and a plausible estimate of the energetic costs associated with specific dynamic action (10% of energy consumed; Wells and Clarke 1996). We assumed that energy loss associated with the excretion of nitrogenous and other waste compounds is negligible compared with the remaining terms in the energy budget (Petza et al. 2006).

Growth rates were taken from size-at-age data presented by Brodziak and Macy (1996) and Macy and Brodziak (2001), and the fitted seasonal, pool-sexed Schnute growth models. The seasonal growth curves account for differences in growth rates of winter-hatched (November to May) and

summer-hatched (June to October) squid. We converted length-at-age to weight-at-age using a published length–weight relationship for *L. pealeii* (Northeast Fisheries Science Center 2002). Daily growth rates were converted from grams to energy units by using the average energy density (ED; J·g⁻¹) of juvenile and adult *L. pealeii* reported by Macy (1980).

Mass-specific metabolic rates were determined by synthesizing previously published data for various species of the genus *Loligo*, including *Loligo opalescens* (O’Dor 1982), *Loligo brevis* (Segawa and Hanlon 1988; Finke et al. 1996), and *Loligo forbesi* (Segawa and Hanlon 1988; Boucher-Rodoni and Mangold 1989). Together, these data provide standard metabolic rates (SMR) of squid across a wide range of body sizes (0.018–1004 g) and temperatures (12 to 24 °C). To determine the SMR of winter-hatched and summer-hatched squid, we standardized the individual metabolic rates to 10 and 18 °C, respectively, by assuming a Q_{10} of two, which is near the average value for *Loligo* spp. (Macy 1980; O’Dor 1982; Wells et al. 1988). The Q_{10} value is the factor by which an organism’s metabolism increases with a 10 °C increase in temperature. We then fit a regression of the temperature-specific metabolic rates against body size to estimate the allometric coefficients for winter and summer SMR equations (Table 2; Fig. 1). The metabolic rates were converted to energy units

($\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) by using an oxycalorific coefficient (OC) of $19 \text{ J}\cdot\text{mL}^{-1} \text{ O}_2$ (Webber and O'Dor 1986).

Some data exist on the swimming speed dependence of metabolism for *Loligo* spp. (O'Dor 1982; Finke et al. 1996; Bartol et al. 2001); however, there is no information on the relationship between metabolic rate and both body mass and swimming speed. Thus, to account for the effect of activity on metabolism, total respiration was modeled using a fixed multiplier of standard respiration (Kitchell et al. 1977). Activity multipliers (ACT) and expressions for seasonal active metabolic rates (AMR) were determined using empirical data from O'Dor (1982). O'Dor (1982) measured the effect of temperature on the metabolic rates of *L. opalescens* at various activity levels. ACT for winter and summer cohorts were calculated as the ratio of the metabolic rates reported for active ($0.20 \text{ m}\cdot\text{s}^{-1}$) and standard ($0 \text{ m}\cdot\text{s}^{-1}$) swimming speeds at 10 and 18 °C, respectively. Both winter and summer AMRs were used to calculate the seasonal energy budgets of *Loligo*.

We converted our estimates of daily energy consumption to mass units (g) by dividing C ($\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) in eq. 2 by the specified prey energy density (PED; Table 1). The PED used in our models is similar to values reported for juvenile groundfish (<10 cm; Pedersen and Hislop 2001). We recognize, however, that squid are generalist predators feeding on crustaceans, fish, and squid, and thus there will be some variation in the energy density of their prey.

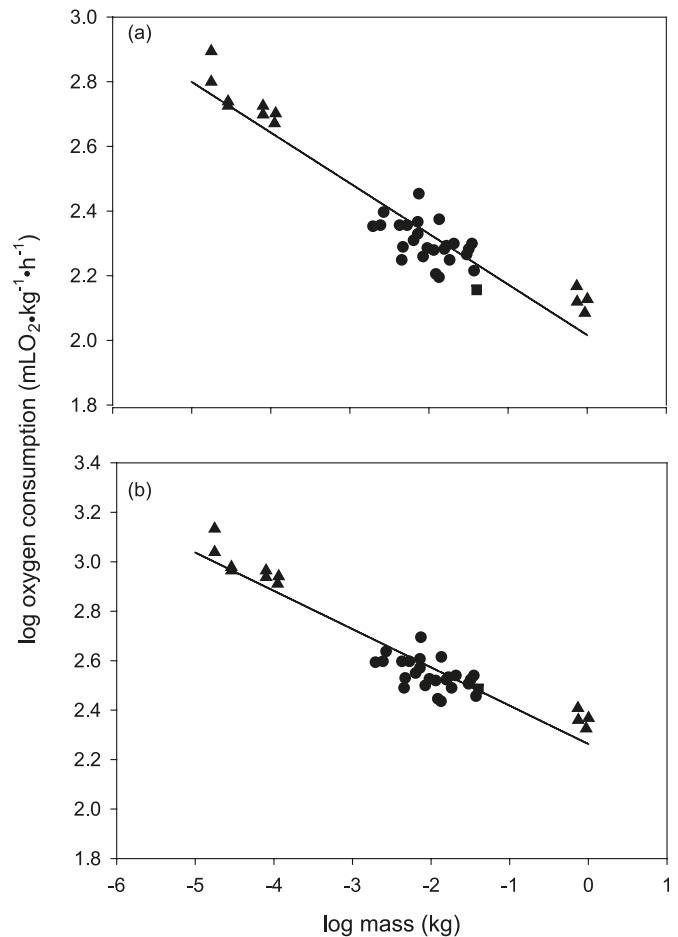
Sensitivity analysis

We measured the sensitivity of the seasonal *Loligo* bioenergetics model to each parameter using the Monte Carlo error analysis method (Bartell et al. 1986). For this analysis, the model parameters were randomly chosen from normal distributions with nominal values set as the mean values (Table 1) and coefficients of variation (CVs) equal to 2%, 10%, or 20% (Bartell et al. 1986). These CVs encompass the levels of parameter variation suggested for error analysis by past authors (Bartell et al. 1986). We ran 1000 iterations of the seasonal bioenergetics models for each CV and evaluated the sensitivity of the average individual consumption rates of squid at sizes capable of piscivory (mantle lengths 9–31 cm) to each model parameter by the parameters' relative partial sums of squares (RPSS; version 11, SYSTAT software Inc., Richmond, California). The RPSS removes the interactive effects of the parameters prior to quantifying deviations in the response variable caused by individual parameter variation, thus providing better estimates of model sensitivity than alternative methods (Bartell et al. 1986).

Population model

We coupled the seasonal bioenergetics model with a seasonal *L. pealeii* age-structured population model to estimate population consumption by *L. pealeii* at lengths capable of piscivory (≥ 9 cm; Hunsicker and Essington 2006). Stock assessments give estimates of total *L. pealeii* biomass, but because feeding rates and diet depends on body size, we need to estimate total biomass by age or size class. We estimated biomass-at-age (day) using a simple algorithm, and most parameter values were borrowed from the Northeast Fisheries

Fig. 1. The standard metabolic rates of *Loligo* spp. over a range of body sizes. Individual metabolic rates were standardized to (a) winter (10 °C) and (b) summer (18 °C) temperatures. Square, *L. opalescens*; triangles, *L. forbesi*; circles, *L. brevis*.



Science Center (NEFSC) *L. pealeii* stock assessment (Northeast Fisheries Science Center 2002).

To determine biomass-at-age, we first calculated survivorship at age (l_a) using the following equation:

$$(3) \quad l_a = l_{a-1} \exp(-Z_{a-1})$$

where Z_{a-1} is the total mortality rate (fishing and natural mortality) of squid at the previous age. To parameterize eq. 3, we used length- and season-specific natural mortality rates (M ; quarter $^{-1}$) from the *L. pealeii* length-based virtual population analysis stock assessment model (Northeast Fisheries Science Center 2002). Length-based estimates were converted to age using the *L. pealeii* seasonal growth curves reported by Brodziak and Macy (1996) and Macy and Brodziak (2001; Table 2). Estimates for juvenile M (≤ 9 cm) were not available and were assumed to be the same as those reported for nonsenescent adults. We used the seasonal F_{\max} values from the *L. pealeii* stock assessment to estimate season-specific fishing mortality rates (F ; quarter $^{-1}$) for adult squid vulnerable to fishing gear (≥ 9 cm; Northeast Fisheries Science Center 2002). The estimates of total mortality (Z) were converted from a quarterly rate to daily rate.

We estimated the proportion of individuals in each age category (n_a) as

$$(4) \quad n_a = \frac{l_a}{\sum_a l_a}$$

and calculated the proportion of total species biomass in each age category (bs_a):

$$(5) \quad bs_a = \frac{\sum_{a \text{ in } s} w_a n_a}{\sum_z w_a n_a}$$

Weight-at-age (w_a) was estimated using the aforementioned growth curves and weight-at-length relationship (Table 2). We then calculated biomass-at-age as the product of bs_a and total population biomass. Published estimates of average minimum and maximum autumn biomass from scaled catch–survey models were included as total population biomass in this model (years 1967–2001; Northeast Fisheries Science Center 2002). We assumed that the NEFSC autumn biomass estimates are the equivalent for all seasons. Lastly, to estimate the population consumption by *L. pealeii*, we multiplied the seasonal estimates of biomass-at-age by the predicted individual consumption rates of *Loligo* at the respective age. We multiplied the individual consumption rates (median values) by the minimum and maximum estimates of biomass-at-age to provide a potential range of *L. pealeii* population consumption.

Potential for predatory impact on juvenile fishes

To explore whether it is energetically plausible for *L. pealeii* to exert a trophodynamic control on juvenile fish populations, we compared our estimates of the total seasonal consumption by *L. pealeii* with the average annual recruitment of five potential fish prey inhabiting similar regions of Northwest Atlantic Ocean. Further, we estimated the proportion of the *L. pealeii* diet consisting of individual fish species (by mass) that would be sufficient to make total seasonal squid consumption equal to the recruitment biomass for that species. To be conservative, we only used our minimum estimates of population consumption in this analysis. We summed the predicted lower bound of daily population consumption for winter and summer cohorts over lengths capable of piscivory (≥ 9 cm) and then multiplied these consumption estimates by 90 days to estimate the lower bound of total seasonal (or quarterly) consumption by potentially piscivorous squid. For this analysis, we made the simplifying assumption that the reported biomass for *L. pealeii* represents an instantaneous measure of the population at a stable age distribution. This assumption is supported by the year-round spawning behavior of *L. pealeii* (Brodziak and Macy 1996) and hence the potential for constant recruitment of squid to the population.

We estimated average annual recruitment biomass for the following five fish stocks: *Melanogrammus aeglefinus* (haddock; age-1, Georges Bank), *Gadus morhua* (Atlantic cod; age-1, Gulf of Maine – Georges Bank), *Merluccius bilinearis* (silver hake; <age-1, Gulf of Maine – Cape Hatteras), *Paralichthys dentatus* (summer flounder; age-0, Gulf of Maine – Cape Hatteras), and *Peprilus triancanthus* (butterfish; age-1, Gulf of Maine – Cape Hatteras). We chose these stocks because the larval–juvenile stages of these stocks are

known to spatially overlap with *L. pealeii* at some time during the year (Sherman et al. 1984; Able and Fahay 1998). Also, stock assessments are available for most of these species, which permits comparison of potential squid predation with recruitment biomass.

We calculated the average recruitment of butterfish over a 10-year period (1990–1999) from annual estimates of recruit biomass published in the stock assessment for this species (Northeast Fisheries Science Center 2004). There are no published estimates of recruit biomass for haddock, Atlantic cod, and summer flounder, but estimates of recruit abundance (number) are available. Thus, we calculated the average abundance of recruitment for these species over the same 10-year period and translated this into recruitment biomass based on the mean weight of recruits published for haddock (Brodziak et al. 2006), Atlantic cod (Mayo and Terceiro 2005; Mayo and Col 2006; O'Brien et al. 2006), and summer flounder (Terceiro 2006). There are no available estimates of biomass or abundance for silver hake recruits; therefore, we used the previously described algorithm to estimate the biomass of silver hake at sizes vulnerable to squid predation (≤ 10 cm, ≤ 0.5 years of age). The parameter values were based on previously published estimates of natural mortality (Brodziak et al. 2001; Tsou and Collie 2001), fishing mortality (Brodziak et al. 2001), and total population biomass (average for 1990–1999; Brodziak et al. 2001). Weight-at-age was determined using the specialized Von Bertalanffy growth function (Pauly 1981), with parameter values borrowed from Helser (1996).

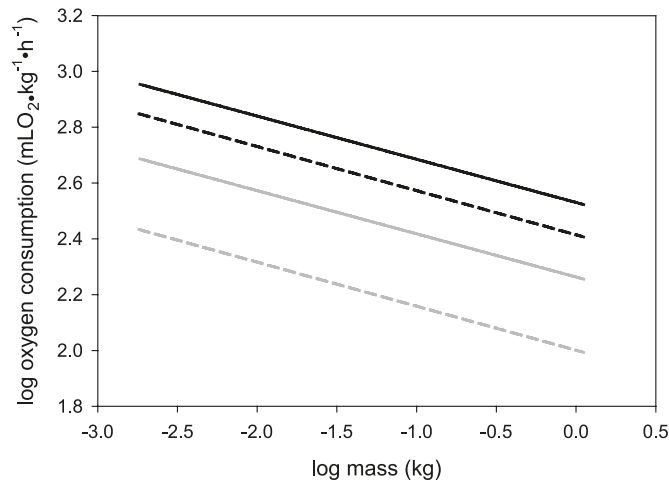
Results

Bioenergetics model

To estimate the allometry of standard respiration for the winter and summer squid cohorts, we fit regressions of temperature-specific metabolic rates of various *Loligo* species against squid body size. The R^2 values of these regressions show that the winter and summer relationships fit the data quite well (Fig. 1). As expected, the metabolic rates over all body sizes were higher when standardized to summer temperatures in comparison with winter temperatures, and the mass-specific metabolic rates were greatest for small squid. We note that the variance in the seasonal SMRs is mostly between squid species and not within species; thus, the observed relationship could be portrayed as species-based. However, the within- and between-species data follow a similar slope, which suggests that the relationship between *Loligo* SMRs and body size reflect the contrasting body sizes of the squid species.

Our estimates of seasonal ACT indicate that the energetic cost of swimming at moderate speeds ($0.20 \text{ m}\cdot\text{s}^{-1}$) is greater for squid exposed to winter temperatures than for those exposed to summer temperatures. Thus, while SMR is substantially greater during summer, AMR differs slightly between summer and winter (Fig. 2). O'Dor (1982) showed that active metabolism is similar across a range of temperatures (10 – 18 °C); however, the difference between standard and active metabolism is greater for those squid exposed to cold temperatures than for those inhabiting warmer water temperatures. As a result, the model produces a counterintuitive prediction that energetic cost of activity is higher in winter

Fig. 2. Comparison between modeled mass-specific standard and active metabolic rates (SMRs and AMRs, respectively) at both winter (10 °C) and summer (18 °C) temperatures. Black solid line, summer AMR; black broken line, winter AMR; grey solid line, summer SMR; grey broken line, winter SMR.



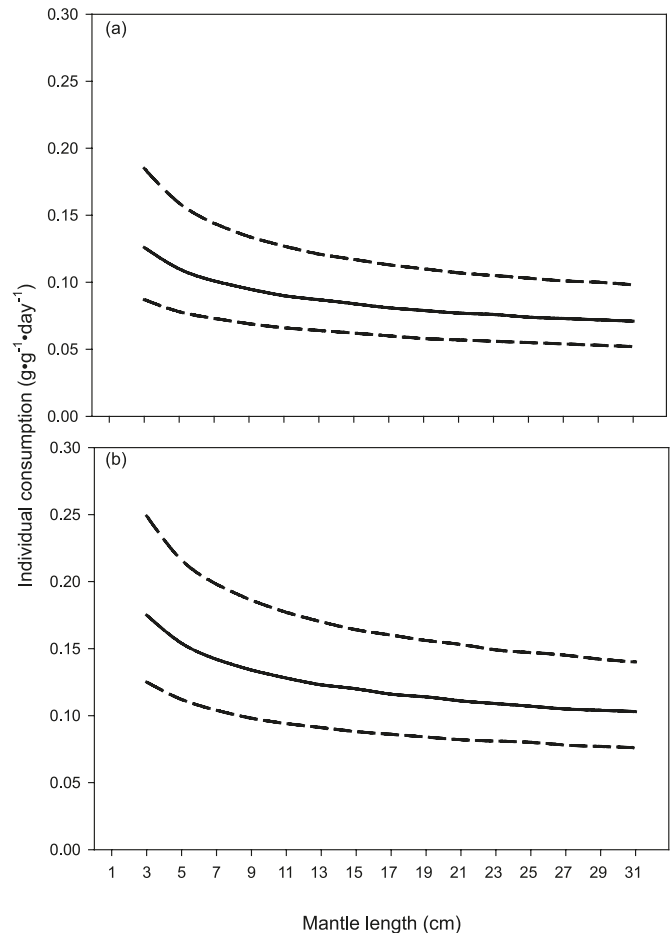
than in summer. This is reflected in the model by the ACT values (Table 1).

The seasonal trends of the predicted individual consumption rates of *L. pealeii* were similar to the trends in predicted metabolic rates. Because the feeding habits of squid are size-dependent, we present our estimates of consumption by length categories (Collins and Pierce 1996; Lordan et al. 1998; Hunsicker and Essington 2006). Overall, the predicted individual consumption rates were higher for the summer cohort (hatched May to October) compared with the winter cohort (hatched November to April), and the consumption rates of small-bodied squid were higher than those of larger squid (Fig. 3). The predicted median winter consumption rates decreased from 0.12 to 0.07 g·g⁻¹·day⁻¹ over increasing squid body size, while the 5th and 95th percentiles ranged from 0.18 to 0.09 g·g⁻¹·day⁻¹ and 0.08 to 0.05 g·g⁻¹·day⁻¹, respectively. The predicted median summer consumption rates ranged from approximately 0.17 to 0.10 g·g⁻¹·day⁻¹ and the 5th and 95th percentiles ranged from 0.25 to 0.14 g·g⁻¹·day⁻¹ and 0.12 to 0.07 g·g⁻¹·day⁻¹, respectively. The predicted cumulative consumption by an individual squid showed a different trend than that of individual consumption rates. For example, we found that by summing the daily consumption (g·day⁻¹) of an individual *Loligo* over lengths capable of piscivory (9–31 cm), the cumulative consumption was approximately 1980 g·recruit⁻¹ for the winter period and 1600 g·recruit⁻¹ for the summer period. The higher estimate of total consumption by a piscivorous squid in the winter period is likely an artifact of the slower growth rate and longer life span of winter-hatched squid compared with summer-hatched squid.

Sensitivity analysis

We tested the sensitivity of the average individual consumption rates of *L. pealeii* at lengths capable of piscivory (9–31 cm) to model parameters using the Monte Carlo error analysis method. We ranked the model parameters by their RPSS to determine which input parameters contributed the

Fig. 3. Seasonal mass-specific consumption rates of *Loligo* plotted against squid mantle length. Estimates were derived using eq. 2. (a) Winter-hatched squid; (b) summer-hatched squid. Upper broken lines, 95th percentile; solid lines, median; lower broken lines, 5th percentile.

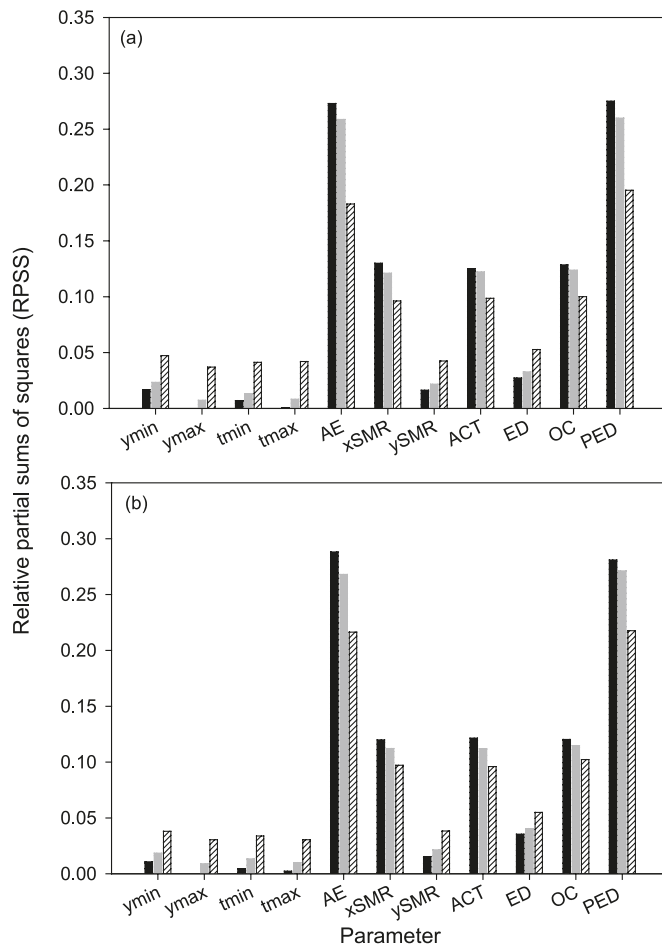


most uncertainty to the average individual consumption rates of *Loligo*. The rank order of the model parameters varied slightly among seasons and under the three levels of uncertainty (2%, 10%, and 20%; Fig. 4). Our results indicated that the winter and summer cohort consumption estimates were most sensitive to AE and PED, while the next most important parameters contributing to model uncertainty were ACT, OC, and χ_{SMR} . The remaining parameters contributed little to the uncertainty in the model outputs. The sum of the $RPSS_{CV=2\%}$ and $RPSS_{CV=10\%}$ winter and summer bioenergetics model parameters were >0.99, which indicates that the linear model described nearly all of the variation in the model output. The $RPSS_{CV=20\%}$ for the winter and summer model parameters dropped to 0.95 and 0.93, respectively, suggesting a greater degree of nonlinearity in the response of model outputs to parameter perturbation.

Population model

To estimate population consumption by *L. pealeii*, we coupled the minimum and maximum estimates of biomass-at-age from the season-specific age-structured population model with the median individual consumption rates predicted from the seasonal bioenergetics model. The winter

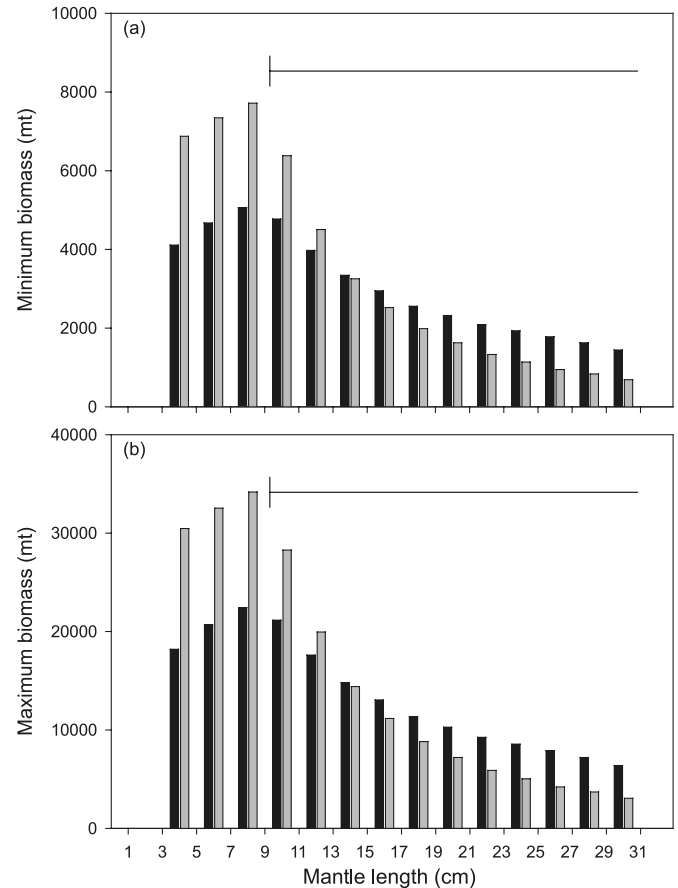
Fig. 4. Relative partial sums of squares (RPSS) for parameters of the seasonal (a, winter; b, summer) *Loligo* bioenergetics model. Three coefficients of variation (CV) were used to test the sensitivity of the average individual consumption rates by *Loligo* (9 to 31 cm) to the model parameters: black, CV = 0.02; grey, CV = 0.10; hatched, CV = 0.20. y_{\min} , y_{\max} , t_{\min} , and t_{\max} are constants specific to the equations for *L. pealeii* growth rates; AE is the assimilation efficiency; x_{SMR} and y_{SMR} are constants specific to the equations for squid standard metabolic rates; ACT is the activity multiplier; ED is the squid energy density; OC is the oxycaloric coefficient; PED is the prey energy density.



and summer biomass estimates of *L. pealeii* were highest within the small to middle size classes and decreased with increasing body size. The predicted biomass estimates of *L. pealeii* at lengths capable of piscivory were higher for the summer cohort than for the winter cohort, ranging from approximately 34 200 to 151 400 t and 27 300 to 121 000 t, respectively (Fig. 5).

The predicted minimum and maximum daily population consumption by *L. pealeii* showed a similar trend to the squid biomass estimates. In general, the predicted population consumption decreased with increasing squid body size. Also, the predicted consumption by larger, piscivorous squid (≥ 9 cm) was higher in the summer period (Fig. 6). Our estimates of total consumption by potentially piscivorous squid ranged from approximately 3400 to 14 800 t-day⁻¹ for the summer and 2100 to 9400 t-day⁻¹ for the winter. Our estimates of population consumption for winter and summer

Fig. 5. Minimum (a) and maximum (b) length-based biomass estimates of *Loligo pealeii* inhabiting the Northwest Atlantic Ocean (see Materials and methods). Black bars, summer cohort (April–September); grey bars, winter cohort (October–March). Black lines indicate the mantle lengths at which *L. pealeii* is capable of piscivory.

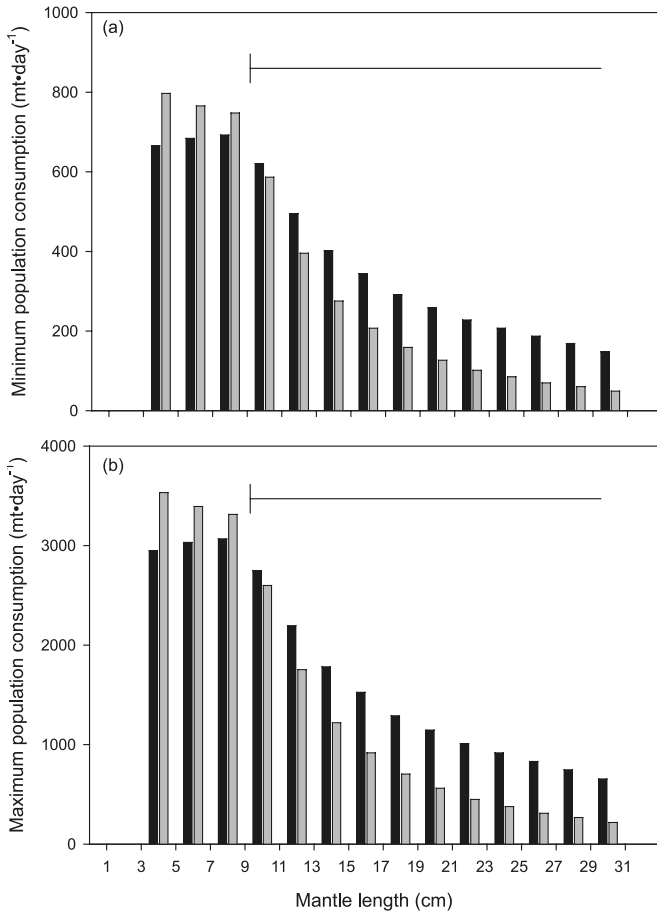


seasons are applicable to spring and autumn seasons, respectively.

Potential for predatory impact on juvenile fishes

In our effort to explore whether large *L. pealeii* (9–31 cm) could have a predatory impact on juvenile fishes, we predicted a minimum estimate of total population consumption by large squid equal to $\sim 306\,000$ and 189 000 t for the summer and winter seasons, respectively. Our estimates of the average annual biomass of recruits of potential fish prey were the following: butterfish (16 250 t), Atlantic cod (9890 t), haddock (8980 t), summer flounder (8290 t), and silver hake (25 500 t). Depending upon the season (i.e., winter–spring versus summer–autumn), the results indicated that total consumption by *L. pealeii* may be roughly 13–18 times greater than the annual recruitment of butterfish; 23–33 times greater than the recruitment biomass of Atlantic cod, haddock, and summer flounder; and 8–12 times greater than silver hake recruitment. Further, our results suggest that 5%–9% and 8%–13% of the *L. pealeii* diet would need to consist of butterfish and silver hake, respectively, for seasonal squid consumption to equal the estimated annual recruitment of these species. Only 3%–5%

Fig. 6. Estimates of total consumption by *Loligo pealeii* over squid mantle lengths during winter (grey bars, October–March) and summer (black bars, April–September) seasons. Consumption was estimated by coupling the seasonal bioenergetics model of *Loligo* with the size-structured population model of *L. pealeii* inhabiting the Northwest Atlantic Ocean. (a) Lower bound; (b) upper bound. Black lines indicate the mantle lengths at which *L. pealeii* is capable of piscivory.

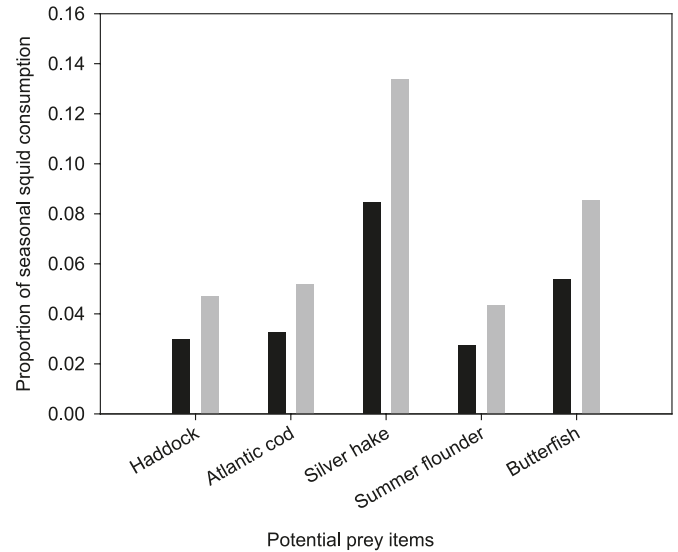


of the squid diet would need to consist of Atlantic cod, haddock, or summer flounder for recruitment biomass to equal seasonal squid consumption (Fig. 7).

Discussion

We developed a seasonal generic *Loligo* bioenergetics model in combination with a seasonal *L. pealeii* age-structured population model to explore whether it is energetically plausible for *L. pealeii* to exert a trophodynamic control on juvenile fishes in the northwest Atlantic continental shelf region. Analyses of our models produced three main findings. First, our predicted consumption rates for individual *Loligo* at sizes capable of piscivory were substantial. The average estimates of individual consumption were 11.5% and 8% squid body mass-day⁻¹ for summer (June–October) and winter (November–May) cohorts, respectively. Second, our predictions of population consumption for *L. pealeii* showed that squid consume high quantities of prey daily. The average estimates within our conservative predictions were 300 and 200 t-day⁻¹ for summer and

Fig. 7. The proportion of the *Loligo pealeii* diet, by mass, that would need to consist of potential fish prey for total seasonal squid consumption to equal fish recruitment. Squid consumption is based on the estimated minimum summer consumption rates (black bars) and minimum winter consumption rates (grey bars) of the *L. pealeii* population inhabiting the Northwest Atlantic Ocean.



winter seasons, respectively. Third, comparisons between our estimates of seasonal population consumption and estimates of juvenile fish recruitment indicated that consumption by *L. pealeii* may greatly exceed the annual recruitment biomass of juvenile fishes and that juvenile fishes need to compose only a small proportion of the *L. pealeii* diet for seasonal squid consumption to equal fish recruitment. Collectively, our findings suggest that *L. pealeii* may potentially exert a trophodynamic control on the recruitment success of commercially exploited fish species even if these species are only a minor prey item of squid.

Our estimates of individual and population consumption rates are consistent with those published in past studies. Previously published estimates of individual feeding rates for juvenile squid range from 13% to >20% body mass-day⁻¹ (Hanlon 1990; Segawa 1990). Published estimates of consumption by squid of commercial size range from 13.1% to 18% squid body mass-day⁻¹ (Karprov and Cailliet 1978; Yang et al. 1986; Erhardt 1991). Our predictions of population consumption rates for *L. pealeii* are similar to the estimates of Maurer and Bowman (1985), although our approach provides a distinct advantage for estimating squid consumption. Maurer and Bowman (1985) estimated squid consumption using daily rations calculated from squid stomach contents analyses and fish gastric evacuation rates. They multiplied the mean daily rations of large size groups by an estimate of the *L. pealeii* standing stock to calculate the population consumption. Their results suggest that *L. pealeii* predation can negatively impact the mortality of juvenile fishes; however, their approach provides coarser estimates of seasonal *Q:B* that are less informative for quantifying the prey demand of potentially piscivorous squid. The relationship between squid body size and consumption is nonlinear, and squid exhibit ontogenetic, size-dependent patterns in

piscivory and predation in general (Collins and Pierce 1996; Lordan et al. 1998; Hunsicker and Essington 2006). To effectively quantify squid consumption on juvenile fishes, it is important take a detailed account of the influence of body size on estimates of squid consumption. Our models incorporate the effects of body size as well as population size structure on *L. pealeii* consumption rates.

Similar to all model outputs, the predicted consumption rates of potentially piscivorous squid from the bioenergetics model deserve careful scrutiny. For our model, we used information from several squid species to estimate values for model parameters, and this type of parameter borrowing has been criticized (Ney 1993). Results of the sensitivity analyses revealed that the model was most sensitive to the estimated values for assimilation efficiency and prey energy density. We estimated assimilation efficiency using the assimilation losses described for the northern shortfin squid (*Illex illecebrosus*) and other cephalopods because the energetic values associated with these losses have not been determined for *Loligo* spp. For prey energy density, we used an averaged value from known fish prey (i.e., Gadiformes) because we were mainly interested in estimating the consumption rates of piscivorous squid. Also, the coarse resolution of squid prey items inhibited our ability to accurately account for the energy densities of their diet. The precision of our model output can be improved with better empirical data on these parameters and others. For example, we used a constant ACT to account for swimming speed dependence on metabolism over all body sizes. It is unlikely that the swimming speed is independent of body size; however, there is no data for which both body mass and swimming speed are accounted for simultaneously. Further, because of the limited empirical data we did not fully explore the influence of temperature on squid consumption rates. We used fixed temperatures to estimate seasonal metabolic rates, although squid are most likely exposed to varying temperatures on daily, weekly, and (or) monthly time scales. Such changes in temperature have been shown to affect an organism's energy budget and hence its energy consumption (Harvey 2005). More information on the energetic expenditures of *L. pealeii* is needed to improve our estimates of prey demand; however, this data is difficult to attain because of the challenge of keeping squid alive in captivity. In reality, a higher precision of individual consumption rates is likely to be overshadowed by the large uncertainty surrounding the estimate of *L. pealeii* population biomass used to estimate population consumption.

Our main motivation for predicting squid population consumption was to evaluate whether *L. pealeii* is capable of exerting a trophodynamic control on juvenile fishes. For this analysis, we used a ratio of squid consumption to fish recruitment biomass as a basis for highlighting potentially vulnerable fish species. Owing to the feeding behavior and high digestion rates of squid, it is difficult to ascertain the energetic contribution, and hence the prey demand, of juvenile fish species from direct estimates of *L. pealeii* diet composition. Thus, ratios of consumption to recruitment are a practical alternative for identifying those species whose recruitment could be dictated by squid predation. This methodology is potentially limited by uncertainties surrounding estimates of *L. pealeii* population consumption

and fish recruitment biomass; however, similar uncertainties will plague alternative methods.

Our analysis showed that seasonal squid consumption could exceed annual fish recruitment by 8- to 33-fold. Atlantic cod, haddock, and summer flounder exhibited the highest consumption to recruitment ratios, and we found that these fishes needed to compose $\leq 5\%$ of the prey composition of the *L. pealeii* population for seasonal squid consumption to equal the annual recruitment of these species. The low recruitment estimates of these species may be attributed to the depleted spawning biomass of the fish populations due to fishing. However, the low estimates could also be an effect of our inability to estimate total recruitment biomass over the entire range of these fish populations along the northwest Atlantic continental shelf because of insufficient stock assessment information (i.e., Atlantic cod and haddock). Silver hake and butterfish have the highest estimates of recruitment biomass and consequently the lowest ratios of squid consumption to recruitment biomass. Our analysis showed that these fishes needed to compose $\leq 13\%$ and $\leq 8\%$ of *L. pealeii* prey composition, respectively, for their recruitment biomass to equal squid consumption. We recognize that we are unable to determine whether these estimates are similar to the actual energetic contributions of juvenile fish species to *L. pealeii* diet composition, and it is not our intention to imply that *L. pealeii* can decimate an entire year class of juvenile fishes. As generalist predators, it is likely that squid prey on multiple fish species, and the strength of their predatory impact will depend on the degree of spatiotemporal overlap between squid and their prey. However, fishes have been found to compose a substantial proportion of the *L. pealeii* diet ($>35\%$ by weight; Vinogradov and Noskov 1979), and Gadiformes, including silver hake, have been identified in *L. pealeii* stomach contents (Maurer and Bowman 1985; Vovk 1985; Hunsicker and Essington 2006). Given these diet studies and the known distributions of squid and juvenile fishes, it seems plausible that *L. pealeii* could exert a trophodynamic control on the recruitment of the aforementioned fishes.

Until recently, predation-mediated recruitment has been a phenomenon observed mainly in fish communities. For example, on Georges Bank it has been shown that predation is a dominant source of mortality of prerecruit fish and that predation can significantly affect the year-class size of some juvenile fishes (Sissenwine et al. 1984; Tsou and Collie 2001). In the Barents Sea, it appears that the survival of capelin (*Mallotus villosus*) is impacted by both herring and cod predation (Hjermmann et al. 2004). Similarly, it has been proposed that medusae can impose a negative impact on the survival and recruitment of North Sea herring through both predatory and competitive interactions with larval herring (Lynam et al. 2005). However, recent findings suggest that squid may also play an important role in predation-mediated recruitment. For example, off the west coast of North America, the jumbo squid (*Dosidicus gigas*) population has recently expanded in both its biomass and its geographical range (Brodeur et al. 2006; Field et al. 2007; Zeidberg and Robinson 2007). This expansion may be a response to warming sea surface temperatures or to fisheries-induced alterations to the trophic structure in this region (Field et al. 2007; Zeidberg and Robinson 2007). The in-

crease in squid abundance has raised concern among scientists because this species is a predator of commercially valuable fishes, including Pacific hake (*Merluccius productus*) (Field et al. 2007). Circumstantial evidence suggests that high squid abundance has a major impact on this groundfish population (Zeidberg and Robinson 2007). Squid populations in other ecosystems, including the Northwest Atlantic, could also benefit from ecosystem changes, and elevated abundances could exacerbate the predatory impact on juvenile fishes in these regions as well.

The potential for squid to impose a top-down forcing on juvenile fishes supports the movement toward more holistic, ecologically-based fisheries stock assessments. In light of the evidence of predation-mediated recruitment in marine ecosystems, scientists have begun to acknowledge that commercial species should be managed with respect to their predator and prey interactions and not as single, isolated species. It is now recognized that the harvest limits of predator and prey species may depend on one another, and as a result predation interactions are being accounted for in various stock assessment models (Hollowed et al. 2000; Tsou and Collie 2001; Jurado-Molina et al. 2005). Our results indicate that the predation interactions of *L. pealeii* are energetically plausible and therefore warrant consideration for managing and rebuilding fish stocks in the northwest Atlantic continental shelf system.

In summary, our results suggest that *L. pealeii* could potentially exert a trophodynamic control on the recruitment success of commercially valuable fishes in the northwest Atlantic continental shelf ecosystem. The predicted individual and population consumption rates provide evidence that seasonal squid consumption could exceed the annual recruitment biomass for some exploited fish species. Further analyses indicate that these fishes would need to compose only a small proportion of the *L. pealeii* prey composition for seasonal squid consumption to equal annual fish recruitment. Our results coupled with the numerous studies of squid feeding habits indicate that squid can exert a predatory impact on the recruitment success of juvenile fishes (Erhardt 1991; Rodhouse and Nigmatullin 1996; Dawe 1988). However, there has not yet been any formal analysis to explore the hypothesis that squid predation and (or) competition acts as an impediment to marine fish recruitment. The findings from our study call for a serious evaluation of this hypothesis, particularly for the many fish populations in the northwest Atlantic region that are depleted and (or) recovering.

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