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Generalized Predatory Impact Model: A Numerical Approach for Assessing Trophic Limits to Hatchery Releases and Controlling Related Ecological Risks

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Rigorous assessment of species and ecosystem biology underpins responsible marine stock enhancement. Estimation of limits to stocking density, based on ecosystem productivity and energetic requirements of stocked species, can be used to gauge the appropriate magnitude of release densities, minimizing waste of resources, and the possibility for adverse stocking effects. A generalized mass-balance model (generalized predatory impact model) for stocking density estimation has been developed. The approach is based around the principles of ECOPATH and accounts for dynamic estimation of stocking-related ecosystem relationships at fine temporal (days) and spatial scales. The main parameter inputs include probability distributions for key biological and life-history traits of stocked species and estimates of primary productivity for the target ecosystem. The energetic requirements of stocked fish are evaluated in terms of growth and mortality as well as ontogenetic transitions in diet, habitat use, morphology, and migration. The theoretical carrying capacity for a stocked species within a given arena is assessed from primary productivity, levels of predation by stocked fish on different trophic groups, and a specified level of acceptable trophic impact. A Monte Carlo analysis of uncertainty is used to provide a probability distribution of stocking densities for a given trophic impact. The model is applied for stocking juveniles of snook (Centropomus undecimalis) *in Sarasota, FL, USA, and mulloway* (Argyrosomus japonicus) *in Georges River, NSW, Australia. The model is useful for estimating an appropriate stocking density when planning pilot-scale fish releases. Such releases should be carefully monitored to validate model assumptions and determine density-dependent and other environmental effects.*

Keywords   trophic impact, trophic level, stocking density, mortality, common snook, mulloway

INTRODUCTION

Increasing pressure on fish stocks worldwide is well documented and is reflected by declining fishery catch relative to

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effort (e.g., Cook et al., 1997; Pauly et al., 2002; Sibert et al., 2006). The long-accepted maximum yearly fisheries production of 80 million tonnes (Gulland, 1970) was exceeded in the late 1980s, and total production has stabilized at around 90 million tonnes since 1990, despite continually increasing effort and improved technology. In reality, while worldwide production has stabilized, continuing increases in fishing effort carry a risk of stock declines and decreased economic productivity

(Beddington et al., 2007). Stock enhancement, sea ranching, or restocking provides an opportunity to increase fishing productivity in some situations through the release of hatchery-reared recruits (Bell et al., 2008).

The release of cultured individuals into estuarine and marine systems is an old concept. Historically, the process has been fraught with many failures where releases were ineffective or had detrimental impacts on wild populations, but there have also been also some fisheries and conservation successes (Hilborn, 1998). Many past failures have arisen due to an incomplete understanding of the ecosystem, the target species, or the fishery, which have led to release programs being developed in inappropriate systems or being operated inefficiently (Taylor et al., 2005). Nonetheless, current concerns about depletion of fish stocks and degradation of aquatic habitats have stimulated a resurgence of interest in fisheries enhancement, and many research programs aimed at responsible implementation of fish releases have emerged in recent years (Bell et al., 2008). Whether releases occur for the purposes of sea ranching, stock enhancement, or re-stocking, the success of such programs is clearly linked to the capacity of the environment to support additional hatchery-reared recruits.

The assumption that recruitment may be limited to a level that does not fully utilize the available carrying capacity is central to stocking-related activities, and this has been addressed at length in the literature (Munro and Bell, 1997; Doherty, 1999; Walters and Martell, 2004; Taylor et al., 2005; Bell et al., 2006). Despite this assumption, carrying capacity is rarely assessed in a quantitative fashion prior to the release of fish, although a limited number of case studies have examined carrying capacity in the context of stock enhancement (Leber et al., 1995; Salvanes et al., 1995; Cooney and Brodeur, 1998; van der Veer et al., 2000; Brennan et al., 2008). Blankenship and Leber (1995) suggested that the carrying capacity of a particular habitat be assessed through pilot releases and subsequent monitoring of density-dependent responses (such as growth, survival, and emigration). While this approach forms an integral component of the responsible approach to marine stock enhancement, the full extent of density-dependent processes, and thus the carrying capacity, will only become evident when high levels of releases are tested. The risk of overstocking therefore remains a concern, particularly where adverse ecological consequences could include displacement of wild stock and other competitors.

The development of detailed, system-specific models of carrying capacity is often beyond the scope of most pilot-scale marine releases. In addition, this may be difficult to estimate where stocking aims to fill the carrying capacity produced when the natural supply of juveniles has failed or is reduced (Stottrup and Sparrevohn, 2007). Consequently, there is a clear need for an approach for establishing release densities for pilot releases, especially when releases are targeted to smaller systems (Taylor and Suthers, 2008). This is particularly important when stocking high-level predators, where there is a potential to have broad impacts across a range of lower trophic levels. It is important to both evaluate these potential effects and the significance of density-dependence in the proposed stocking scenario.

The predatory impact model (PIM) is a decision support tool that was initially designed to estimate the trophic impacts associated with stocking mulloway (*Argyrosomus japonicus*) in the Georges River and to use these values to inform stocking density estimation (Taylor and Suthers, 2008). While the PIM is specific for mulloway, the concept was designed using general relationships published in the scientific literature and relatively minor data requirements that would allow application to other species and systems. This article describes the structure of a generalized version of the PIM (GPIM) and demonstrates application of the model to case studies for mulloway releases in New South Wales, Australia, and snook (*Centropomus undecimalis*) releases in Florida, USA.

Argyrosomus japonicus is an estuarine and coastal predator distributed across the Indian Ocean basin and the western Pacific Ocean (Silberschneider and Gray, 2008; Taylor and Piola, 2008). Mulloway is a carnivore, with small juveniles preying on mysid shrimp common in estuarine habitats (Taylor, 2008); larger juveniles prey on penaeid prawns, and adults primarily prey on zooplanktivorous fishes (Taylor et al., 2006a; Taylor and Mazumder, 2010). The species inhabits inshore and near-shore areas (Taylor et al., 2006b), is fast growing, matures from 51 cm total length (TL), and is currently classified as overfished in New South Wales (Silberschneider et al., 2009). Research into the development of stock enhancement for the species has been underway across several estuaries (Taylor et al., 2009). Common snook (*Centropomus undecimalis*; hereafter referred to as snook) are a coastal warm-water fish of economic importance, which commonly associate with shoreline habitat (Peters et al., 1998). Small snook prey predominantly on small crustaceans, with fish (including anchovies and small sparids) prevalent in the diet from a length of 30 cm (Blewett et al., 2006). Decapod crustaceans, such as penaeid shrimp and portunid crabs, are present in the diet throughout the juvenile stage (Gilmore et al., 1983; McMichael et al., 1989); however, when snook reach maturity, the diet is almost exclusively composed of fish (Blewett et al., 2006). Snook represent one of the top marine sport fish along the Florida coastline (Muller and Taylor, 2006) but are considered overfished (Muller and Taylor, 2006). In addition, fishing mortality rates have continued to increase alongside declining recruitment rates over previous decades, despite strict catch regulations (Muller and Taylor, 2006). This is in part due to catch-and-release mortality, which accounts for a substantial portion of fishing mortality (Taylor et al., 2001; Muller and Taylor, 2006). Stock enhancement research to augment low levels of natural recruitment for snook off Florida's Gulf of Mexico coast is currently underway (Brennan et al., 2005, 2006, 2008).

METHODS

Model Overview

The GPIM is a single-cohort vector-based model that links potential trophic impacts of stocked individuals with estimated ecosystem productivity to inform stocking density estimation and potentially reduce the risk of overstocking and adverse ecosystem consequences (Figure 1). The model also assesses the relative impacts of different stocking scenarios (Taylor et al., 2008), such as comparisons of the outcomes of stocking at different release sizes, release species, and release systems. The model is designed to use parameters that are commonly available from literature or species stock assessments or that can be obtained relatively easily from empirical measurements (Figure 1). The model limits stocking density such that trophic impacts on average do not exceed a specified proportion of total productivity at the trophic level being preyed upon (specified as the trophic impact factor).

Base Model Structure

Fish growth is described by a standard von Bertalanffy growth model and a length–weight relationship:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right),$$

$$W_t = a \cdot L_t^b,$$

where L_t and W_t reflect length and weight as a function of time, respectively, k is the von Bertalanffy growth rate coefficient, L_∞ is the asymptotic length, t_0 is the theoretical age at which $L = $ 0, a and b are the weight coefficient and exponent, respectively, and t is the post-release time step during the model period. These relationships are carried through the model as vectors of length and weight values for the period between age-since-stocking (t_{stock}) and the age at the conclusion of the model period (t_{max}).

Consumption-per-unit-biomass (Q/B) can change with fish length or weight due to greater foraging efficiency, different foraging strategy, or improved allocation and availability of energetic resources. The caudal aspect ratio A generalizes the bioenergetic considerations in the Palomares and Pauly (1998) Q/B model, and it is expressed as a function of fish size rather than as a single value to account for the scaling of metabolism and other associated factors previously mentioned. The caudal aspect ratio is calculated as a function of changing caudal fin height (h) and lateral surface area of the caudal fin (SA) over the model period, according to the following equation (Pauly, 1989):

$$A_t = \frac{h_t^2}{SA_t}.$$

Daily consumption in terms of biomass consumed per gram of consumer (C_t, g g^{-1} d^{-1}) is calculated using a generalized predictor of consumption per unit biomass (Palomares and Pauly, 1998):

$$C_t = \frac{10^{(7.964 - 0.204 \cdot \log W_\infty - 1.965 \cdot T' + 0.083 \cdot A_t + 0.532 \cdot h + 0.398 \cdot d)}}{365},$$

where h and d are logical values; $h = 1$ and $d = 0$ if the species is a herbivore, $h = 0$ and $d = 1$ if the species is a detritivore, and $h = 0$ and $d = 0$ if the species is a carnivore; and W_∞ is the asymptotic weight. T' is the temperature of the water body (T),
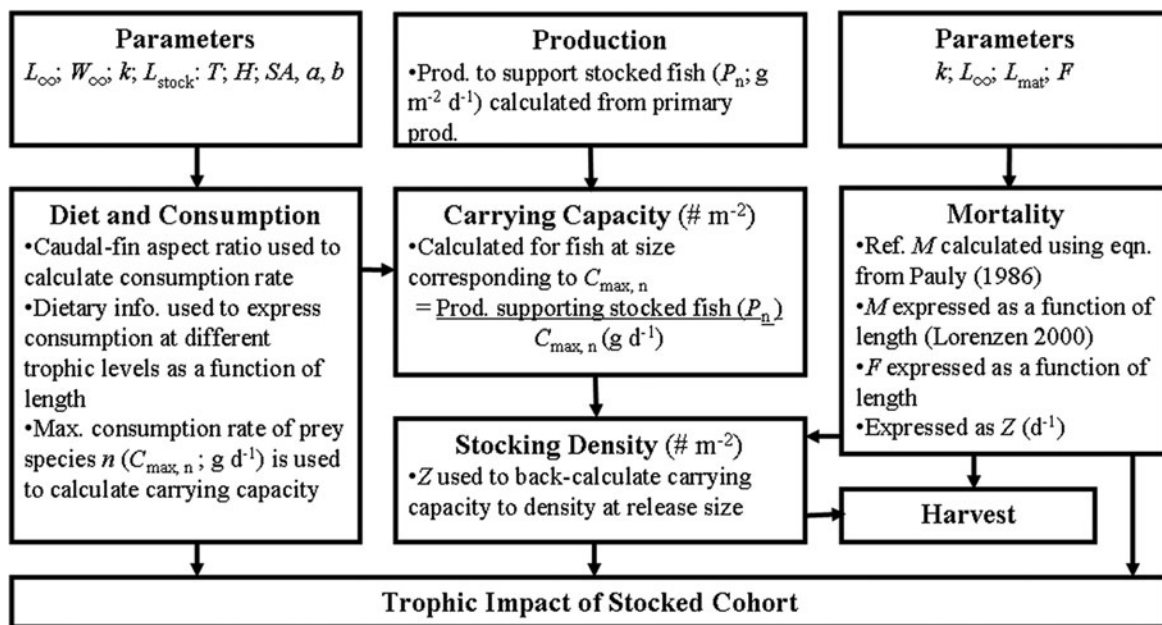

Figure 1 Conceptual layout of GPIM indicating major parameter inputs, main outputs, and information flow through the model.

expressed in Kelvin units using the formula

$$T' = 1000 \cdot (T + 273.15)^{-1}.$$

The model requires empirical information on the proportion of major prey items in the diet and how this varies with length or age. The model is designed such that dietary relationships should be grouped by trophic similarity. For example, if diet moves from primarily herbivorous fish prey to piscivorous fish prey, these data clearly represent an ontogenetic transition between different trophic groups. The trophic group concept allows the model to produce instantaneous estimates of production at specific trophic levels. These dietary relationships are provided for n trophic groups that are important throughout the model period, and the consumption relationship is partitioned into trophic groups according to

$$C_{t,n} = W_t \cdot C_t \cdot D_{t,n},$$

where $C_{t,n}$ (g d^{-1}) is the modeled consumption of a single consumer fish on trophic group n throughout the model period, and $D_{t,n}$ is the proportion of trophic group n in the diet (which may vary throughout the model period, as described above; Taylor and Suthers, 2008). The consumption maxima that occur during the model period are evaluated by the model for n trophic levels and are used to define the maximum instantaneous consumption rate of a single fish on each trophic group and the factor determining the theoretical carrying capacity ($C_{n,\,max}$; Taylor and Suthers, 2008).

The production (P_n) available to support stocked fish is calculated for each trophic group n at the corresponding trophic level using the generalized equation (Pauly and Christensen, 1995)

$$P_n = Pa_n \left(A \cdot P_1 \cdot TE^{TL_n - 1} \right),$$

where Pa_n is the target trophic impact factor (the proportion of production allocated to support stocked fish), P_1 is the wet-weight primary productivity in the area to be stocked, TL_n is the estimated trophic level of trophic group n, TE is the trophic transfer efficiency within the system to be stocked, and A is the area of key habitat (m^2) likely to be used by stocked fish within the model period, which should include at least the foraging arena of the species (Walters and Juanes, 1993; Walters and Martell, 2004).

The parameter Pa_n accounts for the target trophic impact by apportioning the total productivity at each trophic level. The trophic impact factor refers to the upper ceiling of productivity at any particular trophic level that is available to support stocked fish, and the model will simulate trophic limits to stocking density by matching the maximum consumption rate of an individual fish at a particular trophic level (i.e., $C_{n,max}$) to the amount of productivity assigned to support the stocked cohort (i.e., P_n). For example, if an acceptable trophic impact factor was 5% of productivity at trophic level n, Pa_n would be specified as 0.05, and P_n would provide an estimate of upper productivity ceiling at trophic level n, which is assigned to support the cohort

of stocked fish. Thus, the total consumption rate of the cohort, on average, should not exceed this upper limit of productivity. Different values of Pa_n can be specified for each individual trophic level. Specification of Pa_n for any trophic level may depend on the structure of the ecosystem, the objectives of the release program, and/or the magnitude of perceived or actual recruitment limitation. Trophic impact, productivity, and consumption rates for each trophic group n are used to estimate the carrying capacity for stocked fish of the given habitat for the size at which $C_{n,max}$ values occur using the following:

$$CC_n = \frac{P_n}{C_{n,max}}.$$

Where estimates of natural mortality obtained from empirical data are not available for the species, natural mortality is calculated as a function of L_∞, K, and T using the generalized equation of Pauly (1980):

$$M = 10^{-0.0066 - 0.279 \cdot \log L_\infty + 0.6543 \cdot \log k + 0.4634 \cdot \log T}.$$

While this represents the default equation for natural mortality where empirical information is not available, it can be incorporated with other estimators of natural mortality (e.g., Hoenig, 1983; Ralston, 1987) using established methods (Hall et al., 2004) for inclusion in the model.

Several previous studies provide evidence for an allometric relationship between natural mortality and body weight (see Lorenzen, 1996, and references therein). Accounting for this relationship is particularly important in stocked fisheries, where release size is of key interest. Lorenzen (2006) proposed a relationship where natural mortality is inversely proportional to length, which allows natural mortality to be expressed as a function of length at time-after-release (M_t):

$$M_t = M_r \left(\frac{L_r}{L_t} \right),$$

where M_r is the mortality rate at reference length L_r. Mortality rates estimated for recruited fish or those predicted by the Pauly (1980) equation typically correspond to the mortality rate at the size at maturation; hence, M_r was set equal to the estimated value and L_r to equal L_{mat} (Lorenzen, 2011).

Fishing mortality (F_t) is expressed as the product of the fishing mortality (F) for the fully selected length groups and a length-based logistic selectivity curve:

$$F_t = F \cdot \frac{e^{(a + b \cdot L_t)}}{1 + e^{(a + b \cdot L_t)}},$$

where a and b are constants. The above calculation of fishing mortality is dependent on the type of gear used, and alternative selectivity formulas may be substituted if appropriate. For fish species targeted by anglers where selectivity is not well known, the length at which fish recruit to the fishery (usually the minimum length that can be legally retained by the angler) may be substituted for L_{50} in the above equation, which would then provide an approximation of the change in fishing mortality with

size- and time-post-release. The total daily mortality rate Z_t is expressed as the sum of M_t and F_t:

$$Z_t = \frac{M_t + F_t}{365}.$$

The instantaneous daily mortality estimates (Z_t) are used to back-calculate stocking density for each trophic group n at the specified length-at-stocking (L_{stock}) for each carrying capacity estimate using the equation

$$SD_n = CC_n \cdot e^{\sum_{t=t_{stock}}^{t_{c\max n}} Z_t},$$

where CC_n is the carrying capacity calculated for trophic group n, t_{stock} is the age-at-stocking, and $t_{c\max n}$ is the corresponding time-since-stocking (d) at which $C_{\max,n}$ occurred. A global stocking density estimate is produced by averaging the values of SD obtained for each trophic group.

The model also calculates the expected harvest and total impact on the trophic groups over the model period, for the estimated stocking density. The total impact reflects the total biomass consumed by the stocked cohort over the model period and is useful for considering the relative trophic impact per unit yield among release scenarios. The number of fish remaining after time-since-stocking t (d) is calculated for the model period ($t_{stock} \leq t \leq t_{max}$) as

$$N_t = SD \cdot e^{-\sum_{t=t_{stock}}^{t_{c\max n}} Z_t \cdot t},$$

and cumulative biomass harvested (H) is calculated as a function of time-since-stocking for the model period ($t_{stock} \leq t \leq t_{max}$) using a modification of the Baranov catch equation:

$$H = \sum_{t=t_{stock}}^{t_{max}} \frac{F_t}{Z_t} \cdot N_t \cdot (1 - e^{-Z_t}) \cdot W_t.$$

The model then integrates abundance and biomass estimates over the period t_{stock} to t_{max} to determine the total trophic impact (TI) on each trophic group n using the equation

$$TI_n = \sum_{k=t_{stock}}^{t_{max}} N_t \cdot C_{t,n},$$

where N_t and $C_{t,n}$ are the number of fish remaining for each daily time step and daily consumption on trophic group n, respectively. Total trophic impact is determined by summing the impacts on n trophic groups.

Sensitivity Analysis

A MATLAB (MathWorks, Natick, MA, USA) script representing the above model was used for all simulations. A sensitivity analysis was undertaken on key parameters within the model to determine the relative effect of these parameters in driving model predictions. A parameter set for mulloway (*Argyrosomus japonicus*, see description below) was used for these simulations (Table 1). Monte Carlo simulations were used to produce unique parameter sets for each model run, comprising random combinations of either the estimate for each parameter or the estimate ± 10%. Monte Carlo simulations continued until the variance in stocking density estimates stabilized.

Parameters and outputs were standardized such that parameter coefficients directly indicated the first-order effects, and thus the relative importance of the corresponding parameters, following the approach of Kleijen (1997). The standardization process involved first determining the spread (a_h) and mean (b_h) of possible values each parameter h could take:

$$a_h = \frac{h_{max} - h_{min}}{2},$$

$$b_h = \frac{h_{max} + h_{min}}{2},$$

Table 1 Mean (and variations on the mean) for mulloway *Argyrosomus japonicus* used in sensitivity analysis simulations

Parameter	Name	− 10%	Value	+ 10%	Supporting sources
k (L_∞)[a]	Growth growth rate coefficient (asymptotic length)	0.23 (134)	0.26 (122)	0.29 (110)	Silberschneider and Gray (2005)
T	Temperature	15.7	17.4	19.4	Measured from field data (Georges River, Sydney, Australia)
F	Fishing mortality	0.495	0.55	0.605	Silberschneider and Gray (2005)
P_1	Primary productivity	1.24	1.38	1.52	Estimated using the simple estuarine response model (SERM; Baird et al., 2003)
TE	Trophic transfer efficiency	0.09	0.10	0.11	Pauly and Christensen (1995)
TL_1	Trophic level of trophic group 1	2.18	2.40	2.67	Estimated using data in Taylor et al. (2006a)
TL_2	Trophic level of trophic group 1	2.36	2.60	2.88	
TL_3	Trophic level of trophic group 1	2.72	3.00	3.33	

[a]Due to the covariance structure between K and L_∞, these parameters were set as inverse covariates to reduce variance inflation in the sensitivity analysis.

and then calculating a standardized value of parameter h in the parameter set i (x_{ih}):

$$x_{ih} = \frac{z_{ih} - b_h}{a_h},$$

where z_{ih} is the original non-standardized value of parameter h.

Best-fit equations were developed using step-wise regression analysis of parameter combinations against resultant model outputs (Kleijnen, 1997), and competing best-fit equations were evaluated using Akaike information criteria in the open-source statistical package R v. 2.6.1 (Ihaka and Gentleman, 1996). The resulting regression equation provided approximations of the input/output behavior of the simulation model and parameter coefficients that directly indicated the relative importance of parameters in determining stocking density.

Simulation Structure

To account for uncertainty in parameter estimation, the parameters that were identified as significant drivers of the model in the sensitivity analysis were specified in the model as probability distributions. Probability distributions were developed on the basis of mean and error variance estimates from various published sources (Table 2). As K and L_∞ are correlated (Pilling et al., 2002), these parameters were specified as a multivariate probability density function informed by the variance-covariance structure between K and L_∞ in a non-linear fit of the von Bertalanffy growth model to length–age data for each species.

The model was structured as a Monte Carlo analysis of uncertainty (MCAoU), a common approach to assessing risk in ecological systems (Bartell et al., 1992). Each model simulation sampled a value from each parameter's probability distribution until variance in stocking density stabilized, thus producing a probability distribution of stocking density estimates, which corresponded to the specified trophic impact factor. The model also used the relationships described above to estimate the probability distribution for trophic impact and harvest associated with the specified parameter set.

Case Studies to Demonstrate the Application of GPIM

The GPIM was applied to two predatory fish species (*Argyrosomus japonicas* and *Centropomus undecimalis*) to demonstrate the generality of the model structure. These species were chosen because they occupy a similar trophic position but differ in growth, fishing impact, and ecosystem, and there were sufficient existing data to parameterize the model. Simulations for mulloway were performed using temperature measurements and primary productivity estimates in the Georges River, Sydney, Australia, an estuary that has previously been stocked with mulloway (Taylor et al., 2009). Average annual temperatures and associated variance were measured in the river using temperature loggers (Hobo Pendant) from November 2007 to November 2008. A depth-integrated primary productivity estimate and associated variance was estimated for the Georges River using the simple estuarine response model (SERM) described in Baird et al. (2003). Simulations for snook were performed using temperature and primary productivity estimates in the North Creek Estuary (on the basis of previous measurements in the same area, Pomeroy, 1960; Bucolo et al., 2008), Sarasota, Florida, an

Table 2 Parameter values for mulloway *Argyrosomus japonicus* and snook *Centropomus undecimalis* used in GPIM simulations

Parameter	Argyrosomus japonicus		Centropomus undecimalis	
	Estimate	Supporting sources	Estimate	Supporting sources
h	0	Pauly (1989)	0	Pauly (1989)
d	0		0	
a	0.00001679	Silberschneider and Gray (2005)	0.0000044014	
b	2.869		3.1117	Muller and Taylor (2006)
t_0	−0.0552		−0.04	
L_{stock} (cm)	10	Taylor et al. (2009)	8.1	Brennan et al. (2008)
L_{mat} (cm)	51	Silberschneider et al. (2009)	20	Muller and Taylor (2006)
k	$N(0.27, 4.58e^{-5})$	Estimated from length-age data for mulloway stock in NSW[a]	$N(0.35, 8.43e^{-4})$	Estimated from length–age data for snook stocked in Sarasota, FL[b]
L_∞	$N(122.9, 2.6)$		$N(75.1, 12.9)$	
T	$N(17.9, 3.9)$	Measured from field data (Georges River, Sydney, Australia)	$N(22.5, 2.3)$	Measured from field data (North Creek, Sarasota, FL, USA)
F	$N(0.5, 0.1)$	Estimated from Silberschneider and Gray (2005)	$N(0.6, 0.1)$	Estimated from Muller and Taylor (2005)
P_1	$N(1.38, 0.36)$	SERM (Baird et al., 2003)	$N(1.20, 0.37)$	Estimated from Pomeroy (1960) and Bucolo et al. (2008)
TE	$N(0.10, 0.06)$	Pauly and Christensen (1995)	$N(0.10, 0.06)$	Pauly and Christensen (1995)
TL_1	$N(2.4, 0.2)$		$N(2.2, 0.2)$	
TL_2	$N(2.6, 0.3)$	Estimated using data in Taylor et al. (2006a)	$N(2.3, 0.2)$	Estimated using data in Blewett et al. (2006)
TL_3	$N(3.0, 0.3)$		$N(2.5, 0.3)$	

[a]Data made available from NSW Department of Primary Industries length–age databases.
[b]Data made available from snook stock-recapture databases.

estuary in which several pilot snook releases have taken place (Brennan et al., 2005, 2006, 2008).

The parameters and probability distributions for each of these species are presented in Table 2. For case study simulations, A was held constant at 10,000 m^2 to provide a stocking density estimate for 1 hectare of key habitat for each species. Snook recruit to the fishery at a much older age than mulloway, and for this reason, t_{max} (i.e., age at which fish are well recruited to the fishery; conclusion of model period) was set at 1,642 days (approximately 4.5 years) for mulloway and 2,190 days (approximately 6 years) for snook. The results of the simulations are thus specific for the species and geographic area and the fishery that was used to inform the parameter estimates shown in Table 2.

RESULTS

Sensitivity Analysis

The best model produced from the multiple regression and model selection routines included all the key parameters provided to the model (Figure 2) and explained 72% of the variation in the estimated stocking density ($F = 9,815$; $p \ll 0.001$). Results of the sensitivity analysis (Figure 2) indicate that k (von Bertalanffy growth coefficient) had the largest relative positive correlation with stocking density. Fishing mortality (F) and the productivity parameters P_1 and TE also had lower relative positive correlations with stocking density (Figure 2). Both T and TL_n correlated negatively with stocking density. The lowest trophic level (TL_1) was the most influential trophic level on the model results when compared with a moderate influence of the intermediate level (TL_2) and the lowest influence from the high trophic level (TL_3, Figure 2).
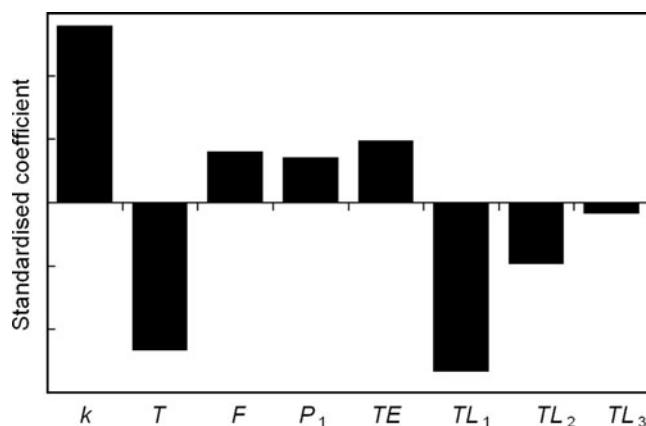

Figure 2 Results of sensitivity analysis for GPIM showing relative impacts of key parameters on model simulations for mulloway (k, von Bertalanffy growth coefficient; T, mean environmental temperature; F, fishing mortality; P_1, primary productivity; TE, trophic transfer efficiency; TL_1, TL_2, and TL_3, tropic levels of three trophic groups). Magnitude of each measurement directly reflects the relative importance of that parameter in driving stocking density.

Case Study Simulations

On the basis of the parameter set provided, the optimal simulated stocking density for mulloway within the Georges River is ~50 fish ha^{-1} at a release size of 100-mm TL (Figure 3A). The mean potential harvest and impact (over the model period) associated with this stocking rate are ~11 kg ha^{-1} (Figure 3B) and ~320 kg ha^{-1} (Figure 3C), respectively, over ~4.5 years. The harvest is also expressed as a mean yield of ~0.24 kg (Figure 3D) harvest per fish stocked in the scenario.

For snook, the optimal stocking density estimated on the basis of the parameter set provided for North Creek is ~660 fish ha^{-1} at a release size of 80 mm standard length (SL, Figure 4A). The mean potential harvest and impact (over the model period) associated with this stocking rate is ~84 kg ha^{-1} (Figure 4B) and ~4,425 kg ha^{-1} (Figure 4C), respectively. A mean yield of ~0.13 kg (Figure 4D) catch per fish stocked is estimated for snook in this scenario. Note that these outputs consider only a single stocking event and do not consider the implications of stocking multiple cohorts in successive year.

DISCUSSION

The GPIM is the first generalized trophic model explicitly aimed at providing estimates of limits to stocking density for stock enhancement or sea ranching scenarios. The GPIM is essentially a synthesis of generalized predictive models that are structured in such a fashion as to provide estimates of parameters of principal interest to managers or scientists involved in fish releases. Taylor and Suthers (2008) first presented the PIM, which was designed to estimate release densities for mulloway. The GPIM developed in the current study draws on the concepts of the original PIM with important improvements. The generalized estimator of consumption (Palomares and Pauly, 1998) remains at the center of the GPIM, and this forms the basis of the estimation of carrying capacity, as proposed in Taylor and Suthers (2008; Figure 1).

The GPIM makes several key advances on the PIM and addresses several key limitations outlined in Taylor and Suthers (2008). The first key limitation of the PIM was the estimation of prey productivity on which stocking density is based. Previously, this relied on empirical measurements or species-specific estimates of prey productivity. The GPIM includes a conventional generalized approach to estimating productivity by including a general trophic productivity model (Figure 1), which relates consumption rates on the specific trophic levels on which the released species feeds to the productivity at these trophic levels (Pauly and Christensen, 1995). This allows the model to account for more generalist feeding strategies, which are often observed in fish populations (e.g., Barnes et al., 2011; Smith et al., 2011). The second major enhancement in GPIM is that it draws on recent publications to include mortality as size-based functions, thus taking into account the relatively high rates of
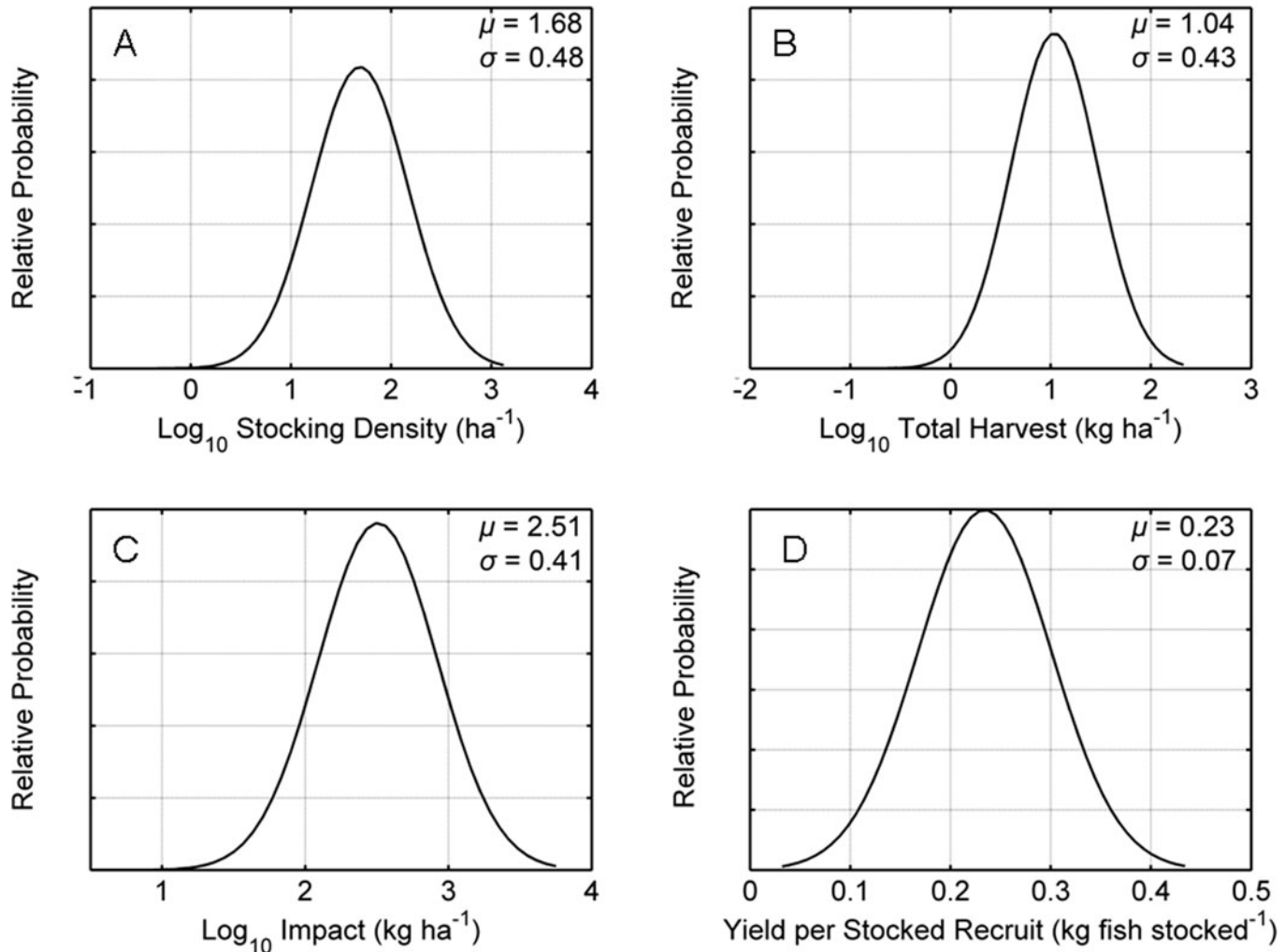
Figure 3 GPIM simulation outputs for mulloway *Argyrosomus japnoicus* released into Georges River, New South Wales, Australia. Relative probability is shown for the four key model outputs: (A) potential stocking density, (B) potential harvest, (C) potential trophic impact, and (D) potential yield per stocked recruit.

natural mortality, which may be experienced by stocked fish in the early stages post-release (e.g., Lorenzen, 2000, 2006). Third, the PIM failed to take account of uncertainty in model parameters. This has been addressed in the GPIM, as key parameters driving model simulations revealed by the sensitivity analysis are now provided as probability distributions, and uncertainty is incorporated through an MCAoU.

Munro and Bell (1997) first suggested that ECOPATH models could be useful for estimating the effects of enhancing recruitment of specific components of an ecosystem, and recent versions of the model allow the incorporation of hatchery stocking into model scenarios (Christensen et al., 2005). There is, however, a paucity of examples in the scientific literature that have employed this model in the context of stock enhancement, although few examples do exist in the gray literature (Christensen, 1994; Rogers and Allen, 2008). This may be because the time and cost required for parameterization and development of a full ecosystem model for the receiving sys-

tem, such as ECOPATH, may be prohibitive at the early stages of stock enhancement or sea-ranching projects. Many of the concepts that underpin the GPIM are drawn from ECOPATH, particularly the trophic level and mass balance concepts and the estimation of consumption (Christensen and Pauly, 1992). Thus, the reduced data requirements for the GPIM allow stocking scenarios to be assessed according to these concepts but without the development of a full ecosystem model, which provides a considerable advantage for developing stocking research programs.

Factors Driving Model Estimations

Results of the sensitivity analysis revealed that growth and temperature are important variables driving the estimation of trophic limits to stocking density in the GPIM. Temperature and growth are key components of the generalized estimators
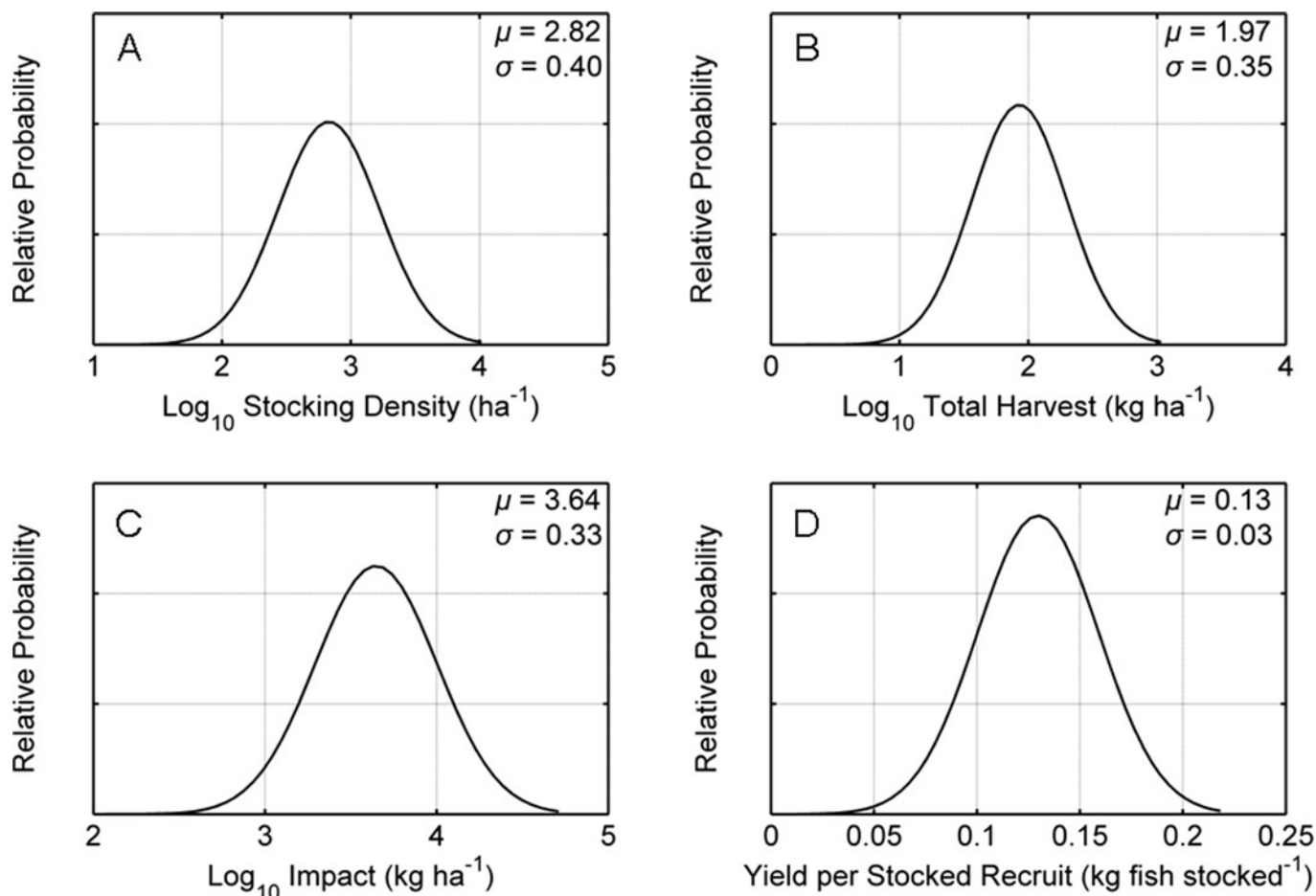
Figure 4 GPIM simulation outputs for snook *Centropomus undecimalis* released into North Creek, Florida, USA. Relative probability is shown for the four key model outputs: (A) potential stocking density, (B) potential harvest, (C) potential trophic impact, and (D) potential yield per stocked recruit.

of mortality (Pauly, 1980) and consumption (Palomares and Pauly, 1998), and the relative relationship of temperature and growth with stocking density can be explained by considering both metabolic theory and mortality during the model period, respectively.

Temperature is negatively related to stocking density through the generalized estimator of consumption per unit biomass. Consumption has a negative relationship with T', which is an inverse measure of temperature (Palomares and Pauly, 1998). Consequently, temperature has an indirect positive relationship with consumption, as individual rates of metabolism are positively temperature dependent (Brown et al., 2004). Thus, higher relative consumption rates lower the number of individuals that the system can support within the specified threshold of trophic impact. The positive correlation between growth coefficient k and stocking density arises due to the cumulative mortality experienced by the cohort during the model period. A higher k and associated faster growth means that the cohort recruits to the fishery at an earlier point in the model period. This means that fish are exposed to fishing mortality over a larger proportion of

the model period (which also contributes to a greater harvest) and, thus, experience greater overall mortality during the model period. The elevated loss of fish from the system during the model period means that a higher stocking density can be supported to fully utilize the trophic resources allocated to support the stocked cohort.

Unsurprisingly, parameters relating to trophic productivity (P_1, TE) positively relate to stocking density. Greater primary productivity (P_1) means a greater mass of carbon is entering the system, thus increasing the relative carrying capacity and stocking density. A greater trophic efficiency (TE) equates to a more efficient passage of carbon between trophic levels, so a larger portion of the biomass synthesized by primary producers is conveyed to the higher trophic levels on which stocked fish are preying. The negative relationship between trophic level (TL_n) and stocking density reflects differences in the relative magnitude of production, which is conveyed to these higher trophic levels. The generalized estimator of productivity (Pauly and Christensen, 1995) shows that the available production decreases with an increasing trophic level, thus producing a

negative relationship between stocking density and the trophic
level of a trophic group appearing in the diet.

Constraining Trophic Impact

The GPIM is intended primarily as a risk reduction tool to
lower the chance of the negative effects on the stocked species'
prey, which may occur as a result of overstocking. Overstock-
ing occurs where the capacity of the receiving system to sup-
port recruits is exceeded and can have effects at the popula-
tion or community level. For example, overstocking grass carp
(*Ctenopharyngodon idella*) in Lake Erhai (China) had adverse
effects at the community level through suppressed growth of
aquatic macrophytes (Li, 1999; Liu et al., 2008). In addition,
Tatara et al. (2011) found that while the stocking of hatchery-
reared steelhead parr (*Oncorhynchus mykiss*) into experimental
streams led to an increase in the composite (hatchery-reared and
natural) population, the emigration of natural steelhead parr led
to an overall decrease in the abundance of natural recruits. Evi-
dence of displacement arising from overstocking is rare in ma-
rine systems, potentially due to the complex experimental frame-
work required to detect population and community changes in
manipulated ecosystems (some good examples can be found in
Leber et al., 1995; Kellison et al., 2003; Brennan et al., 2008;
Eggleston et al., 2008). It should be noted, though, that if fish
survive to reproduce, density dependence may arise, such as
increased mortality or displacement in subsequent generations.

The trophic impact factor, as defined in the context of this
model, is a new concept in stock enhancement, which partially
deals with the potential for impacts on food resources and other
organisms. Recruitment limitation is a key assumption underly-
ing releases of fish into open marine systems (Munro and Bell,
1997; Taylor et al., 2005; Lorenzen et al., 2010); however, it is
rarely quantified and used as a basis for release densities, de-
spite tools being available that explicitly allow this (e.g., Medley
and Lorenzen, 2006). In the GPIM, the trophic impact factor is
largely a subjective parameter, but it is one that can be based
on general knowledge of the receiving system and natural stock
and allows the risk of adverse competitive effects and resultant
displacement or density-dependent effects to be indirectly taken
into account. The simplicity of the parameter and its inclusion in
the GPIM lies in the constraint of stocking density within a des-
ignated acceptable level of trophic impact and evaluation of the
associated outcomes (such as potential harvest). Alternatively,
the GPIM also allows stocking densities, trophic impacts, and
potential harvests to be compared among a range of allowable
trophic impact levels. While there is still some potential risk
of overstocking when using this approach (for example, if the
estimated trophic impact factor is too high for a particular sys-
tem), applying the GPIM approach provides a useful, species-
and system-specific range of stocking density estimates with
which to commence pilot releases. This provides a starting point
for empirical evaluation of the success and effects of stocking,
building on the techniques suggested previously in this section.

Application of the Model Across Species

The current study presents the application of the GPIM to
two carnivorous teleost species; however, there are key features
of the model that facilitate its application to a diverse range of
other marine species, including herbivorous and detritovorous
fish and invertebrates. Adapting the model to herbivorous or
detritivorous fishes is achieved through manipulating the binary
operators h and d in the generalized estimator of consumption
(see Palomares and Pauly, 1998). Similarly, the model can be
converted for use with invertebrates by including an estimate of
gross growth efficiency (e.g., Wolff and Cerda, 1992) in place of
the generalized estimator of consumption, which will account
for the forage resources required to sustain a specific growth rate.

While the model simulations presented here are specific to the
respective systems, fisheries and species for which the parame-
ters are estimated, factors that contribute to the differences ob-
served in model estimates between the two species are worth dis-
cussing. First, snook have a higher recommended stocking den-
sity than mulloway, which is a combination of higher primary
productivity in Florida, the fact that snook feed at a lower trophic
level than mulloway, and a longer model period over which fish
experience mortality (6 years compared with 4.5 years). In ad-
dition, as previously described, the faster growth of snook in
Florida will also act to increase stocking density estimates. The
higher trophic impact estimates observed for snook in Florida
arise from higher stocking density and the longer duration of
the model period (~4.5 years for mulloway versus ~6 years for
snook) during which trophic impacts accumulate. Overall, the
total harvest is greater for snook in Florida as a result of greater
fishing mortality, greater stocking density, and a longer model
period. In contrast, the yield per stocked recruit is slightly higher
for mulloway due to a lower natural mortality.

The GPIM is also useful for evaluating the potential suitabil-
ity of species of differing biological and/or fishery characteris-
tics for a particular system by holding ecosystem characteristics
constant and altering other parameters according to the partic-
ular species. Conversely, the potential outcomes for scenarios
dealing with the release of a single species across different sys-
tems can be also evaluated by providing the model with species-
specific data for each of the particular systems. In addition, the
stocking densities and potential outcomes of stocking different
sized cohorts of fish can also be evaluated using the GPIM,
which is of relevance to evaluating the cost-to-benefit outcomes
of different release scenarios.

CONCLUSIONS

In conclusion, the GPIM represents one of a range of tools
useful in planning stocking programs. This approach also high-
lights the significance of reliable fundamental biological data
on growth, mortality, and feeding ecology in planning release
endeavours. The model is useful for desktop evaluation of

different stocking strategies but does not capture all of the extrinsic processes that may act on stocked populations during and after release. Consequently, complementary approaches (such as EnhanceFish; Medley and Lorenzen, 2006) should also be employed, and model estimates should always be considered a first step in the process. EnhanceFish is based on fishery stock assessment approach and deals explicitly with density-dependence and mortality for both wild and released fish and genetic interactions. Further, the major focus of developing release programs should remain on empirically evaluating pilot-scales releases in the field (e.g., Blankenship and Leber, 1995; Leber et al., 1998; Brennan et al., 2006, 2008; Leber, 2011; Leber and Blankenship, 2012) and validating model estimates. The model provides a starting point for estimating release sizes, and the accuracy of the predictions can be validated by both experimental work and reviewing the results from trial releases. These pilot-scale releases are ideally conducted in a targeted fashion based on a solid understanding of species biology and ecosystem characteristics (e.g., Taylor et al., 2013), which will help to ensure that species requirements are met by the stocked system and improve the survival of stocked fish (Taylor et al., 2009).

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