



## Using experimental ecology to understand stock enhancement: Comparisons of habitat-related predation on wild and hatchery-reared *Penaeus plebejus* Hess

Faith Ochwada-Doyle<sup>a,b,\*</sup>, Charles A. Gray<sup>c</sup>, Neil R. Loneragan<sup>d</sup>, Matthew D. Taylor<sup>a,b</sup>

<sup>a</sup> Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Science, University of New South Wales, NSW, 2052, Australia

<sup>b</sup> Sydney Institute of Marine Science, Building 22, Chowder Bay Road, Mosman, New South Wales, 2088, Australia

<sup>c</sup> Cronulla Fisheries Research Centre, NSW Primary Industries Science and Research, P.O. Box 21, Cronulla, NSW, 2230, Australia

<sup>d</sup> Centre for Fish and Fisheries Research, School of Biological Sciences and Biotechnology, Murdoch University, South Street, Murdoch, Western Australia, 6150, Australia

### ARTICLE INFO

#### Article history:

Received 31 July 2009

Received in revised form 6 April 2010

Accepted 8 April 2010

#### Keywords:

Eastern Australia  
Fisheries management  
Habitat structure  
Macrophyte  
Predation  
Stock enhancement

### ABSTRACT

Marine stock enhancement is often characterized by poor survival of hatchery-reared individuals due to deficiencies in their fitness, such as a diminished capacity to avoid predators. Field experiments were used to examine predation on *Penaeus plebejus*, a current candidate for stock enhancement in Australia. We compared overall survival of, and rates of predation on, wild *P. plebejus* juveniles, naïve hatchery-reared juveniles (which represented the state of individuals intended for stock enhancement) and experienced hatchery-reared juveniles (which had been exposed to natural predatory stimuli). Predation was examined in the presence of an ambush predator (*Centropogon australis* White, 1790) and an active-pursuit predator (*Metapenaeus macleayi* Haswell) within both complex (artificial macrophyte) and simple (bare sand and mud) habitats. Overall survival was lower and rates of predation were higher in simple habitats compared to complex habitats in the presence of *C. australis*. However, the three categories of juveniles survived at similar proportions and suffered similar rates of predation within each individual habitat. No differences in survival and rates of predation were detected among habitats or the categories of juveniles when *M. macleayi* was used as a predator. These results indicate that wild and hatchery-reared *P. plebejus* juveniles are equally capable of avoiding predators. Furthermore, exposure of hatchery-reared juveniles to wild conditions does not increase their ability to avoid predators, suggesting an innate rather than learned anti-predator response. The lower predation by *C. australis* in complex habitats was attributed to a reduction in this ambush predator's foraging efficiency due to the presence of structure. Ecological experiments comparing wild and hatchery-reared individuals should precede all stock enhancement programs because they may identify deficits in hatchery-reared animals that could be mitigated to optimize survival. Such studies can also identify weaknesses in wild animals, relative to hatchery-reared individuals, that may lead to the loss of resident populations.

© 2010 Elsevier B.V. All rights reserved.

### 1. Introduction

Overexploitation, habitat loss and recruitment variability have resulted in global declines in many marine populations of economic importance (Pikitch et al., 2004; Anderson et al., 2008). Modern fisheries management attempts to ameliorate these trends through a range of approaches including habitat restoration, reduction of fishing effort, closures to fishing and stock enhancement (Ludwig et al., 1993; Hilborn, 2007). The latter approach involves releasing large numbers of hatchery-reared individuals into the wild to augment the natural supply of larvae or juveniles and therefore optimize harvests and overcome recruitment-limitation (Bell et al., 2008). Despite its

potential, however, examples of unsuccessful stock enhancement endeavors are alarmingly wide spread (Grimes, 1998; Brown and Day, 2002), and include failed releases of salmon in the United States (Hilborn, 1998), scallops in Australia (Bell et al., 2005) and lobster in the United Kingdom (Addison and Bannister, 1994).

One aspect contributing to the failure of stock enhancement efforts is poor survival of hatchery-reared individuals once released into the wild due to deficits in their behavior and fitness (Davis et al., 2004). Hatchery-reared animals may have a diminished capacity to exploit resources compared to wild animals for two reasons. Firstly, physical, behavioral and physiological traits may be altered by the rearing environment causing characteristics that are essential for survival in the wild, but unnecessary in a hatchery environment, to remain poorly developed (Einum and Fleming, 2001). For example, a regular feeding regime in hatcheries and grow-out facilities may inhibit development of efficient foraging behavior. Secondly, hatchery-rearing may increase the proportion of animals with low genotypic

\* Corresponding author. Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Science, University of New South Wales, NSW, 2052, Australia. Tel.: +61(2)93858269; fax: +61(2)93851558.

E-mail address: [faith.ochwada@student.unsw.edu.au](mailto:faith.ochwada@student.unsw.edu.au) (F. Ochwada-Doyle).

fitness due to the absence of natural selection pressures or production of release animals from a small number of brood-stock (Ryer, 2004; Araki et al., 2007).

A typical trait that may be inhibited as a result of environmental plasticity and reduced genotypic fitness is the ability of individuals to sense and avoid predators (Einum and Fleming, 2001; Stunz and Minello, 2001). The absence of predatory stimuli in hatcheries, for example, may limit development of visual and/or olfactory mechanisms for recognition of predators. Artificial rearing can also induce rapid variations in genotypes that can change protective social behaviors such as facultative schooling (Olla et al., 1998; Álvarez and Nieceza, 2003). If releases are to produce positive outcomes for fisheries, any differential predation mortality between hatchery-reared and wild organisms must be identified, and the underlying causes addressed (Brown and Laland, 2001). Yet, for many candidates for stock enhancement, this issue is rarely examined.

Using manipulative experiments, we compare predation on hatchery-reared and wild *Penaeus plebejus* Hess. Like many other penaeid species, two specific demographic characteristics make this species a prime candidate for stock enhancement. Firstly, *P. plebejus* contributes to an important fishery in temperate southeastern Australia (Ives and Scandol, 2007) and stock enhancement may mitigate recent declines in its catch rates which have been caused by high exploitation rates and loss of habitat (Rothlisberg et al., 1999). Secondly, this offshore spawning species is prone to recruitment-limitation due to its dependence on the nursery habitats provided by estuaries and intermittently closed lagoons. The restricted entrances of intermittently closed lagoons often produce a physical barrier to larval ingress, leading to recruitment-limitation. Stock enhancement may therefore supplement the low natural influx of larvae in such systems (Rothlisberg et al., 1999; Ochwada et al., 2009).

This study is the first to explicitly compare predation on hatchery-reared and wild penaeids. We contrast the survival and rate of mortality due to predation of wild and hatchery-reared *P. plebejus* when exposed to a predatory scorpaenid fish (the eastern fortesque, *Centropogon australis* White, 1790) and a predatory penaeid (the school prawn, *Metapenaeus macleayi* Haswell). Since predation on some penaeids has been shown to vary with the level of habitat complexity due to differences in the type of protection afforded by different habitats (Minello and Zimmerman, 1985; Kenyon et al., 1995; Primavera, 1997; Ochwada et al., 2009), we also contrast mortality due to predation in stocked and wild *P. plebejus* within different habitats.

## 2. Methods

### 2.1. Experimental animals

This study investigated mortality due to predation in three groups of *P. plebejus* juveniles. The first group comprised of wild juveniles (*Wd*) which had spawned naturally and recruited into an open lake on the southeastern coast of Australia that had never been stocked with *P. plebejus*. (Merimbula Lake; 36°53'51" S; 149°53'05" E). These juveniles had therefore been exposed to natural predatory stimuli since hatching. The second group comprised of naïve hatchery-reared juveniles (*Ht<sub>N</sub>*), which were exclusively held in hatchery conditions before use in the experiments. The *Ht<sub>N</sub>* juveniles represented the condition of individuals released for enhancement and were included to examine the sole effect of hatchery-rearing on predation mortality. The third group was introduced to test whether short term exposure of hatchery-reared juveniles to naturally occurring predatory stimuli decreases vulnerability to predation mortality. This treatment comprised of experienced hatchery-reared juveniles (*Ht<sub>E</sub>*) that had been stocked into a closed coastal lake in southeastern Australia (Wallagoot Lake; 36°47'18" S; 149°56'31" E) where they were exposed to the natural environment and any associated predatory

stimuli. Wallagoot Lake has been closed to the ocean, and thus recruitment of *P. plebejus*, for over ten years. Any juvenile *P. plebejus* captured from this lake were therefore stocked individuals.

The *Wd* juveniles were captured in Merimbula Lake using a benthic sled towed by two people over a total period of approximately 21 h. *Wd* juveniles used in each trial were collected from the lake 11–24 h before commencement of each trial. The captured *Wd* juveniles were identified to species level using a dissecting microscope. The mean carapace length (CL) of the *Wd* juveniles retained for the experiments was  $4.72 \pm 0.07$  mm ( $\pm$ SE). Both the *Ht<sub>E</sub>* and *Ht<sub>N</sub>* juveniles were produced at the same time in a commercial hatchery (Rocky Point Aquarium, Gold Coast, Australia) using 97 wild brood-stock (~1:96 male to female sex ratio) collected off central eastern Australia (between 30°16'49" S; 153°12'06" E and 24°45'06" S; 153°01'22" E). Individuals were reared in the hatchery for 18 d to a mean CL of  $4.03 \pm 0.05$  mm ( $\pm$ SE). During this early rearing period, *P. plebejus* were held in 40,000 L parabolic fiberglass tanks at densities of approximately 200,000 individuals/tank<sup>-1</sup> and fed hatchery pellets (1.5 L/tank<sup>-1</sup>/d<sup>-1</sup>) consisting of marine and plant proteins, plant meals, yeast, algae, marine oils, vitamins and antioxidants. Feeding involved dispersing the hatchery pellets over the water-surface in each tank by hand. The tanks lacked any form of substrate or predatory-stimulus. All hatchery-reared juveniles were transported to Sydney airport (33°56'46" S; 151°10'38" E) by air within 10 L of water in sealed plastic bags, which were carried in sealed polystyrene boxes. *Ht<sub>N</sub>* juveniles were then transported by road to Cronulla Fisheries Research Centre (34°04'21" S; 151°08'56" E) where they were transferred to 100 L fiberglass aquaria tanks. *Ht<sub>N</sub>* juveniles were reared within these tanks for an additional 36 d to a mean CL of  $4.62 \pm 0.06$  mm ( $\pm$ SE) for use in the experiments. During this later rearing period, the *Ht<sub>N</sub>* juveniles were held at a density of approximately 400 individuals/tank<sup>-1</sup> in similar rearing conditions as describe above and sustained on the same hatchery pellets described above (60 tank<sup>-1</sup> d<sup>-1</sup>). Approximately 3,000,000 *Ht<sub>E</sub>* juveniles were transported by road from Sydney airport to Wallagoot Lake where they were released. After 36 d, a small proportion of the released *Ht<sub>E</sub>* juveniles were re-captured and retained for the experiment within portable 50 L aerated tanks. The *Ht<sub>E</sub>* juveniles were re-captured from Wallagoot Lake at a mean CL of  $4.79 \pm 0.059$  mm ( $\pm$ SE) using a benthic sled towed by hand. This sampling was conducted by two people over a total period of 19 h. Juveniles from each category were transported to the experimental site in Wallagoot Lake by road within separate aerated 50 L tanks before use in the experiments.

Juvenile *C. australis* with a total length (TL) of  $7.33 \pm 0.88$  cm (mean  $\pm$  SE) and sub-adult *M. macleayi* with a TL of  $8.98 \pm 1.01$  cm (mean  $\pm$  SE) were collected from bare and seagrass habitats in Merimbula Lake using a 10-m beach seine (5 mm mesh size) and coarse mesh dip nets respectively. These species were used as predators because they exhibit two common but distinct foraging behaviors (Ochwada et al., 2009). *C. australis* represents a typical passive ambush predator (Harmelin-Vivien and Bouchon, 1976). In contrast, predators such as *M. macleayi* actively pursue their prey until captured. *C. australis* (Bell et al., 1978) and *M. macleayi* (Ruello, 1973; Dall et al., 1990c) have both also been shown to be effective predators of post-larval and juvenile penaeids (Ochwada et al., 2009). The predators used in each experimental trial were collected 1 d before the trial and housed in separate aerated tanks (50 L) during this period.

### 2.2. Predation experiments

The experiments were conducted in eighteen square, stretch-mesh (2 mm) cages (1 × 1 × 1 m) with enclosed bases within Wallagoot Lake in January, 2009. The experimental sites had a water depth of  $0.5 \pm 0.09$  m (mean  $\pm$  SE), a salinity of  $39.9 \pm 0.03$  (mean  $\pm$  SE) and a water-temperature of  $25 \pm 1.74$  °C (mean  $\pm$  SE). Six cages were established with each of either bare sand (*S*), bare mud (*M*) or artificial macrophyte (*A*) within them. These three habitats represent the most frequently

occurring habitats in the estuaries of southeastern Australia (Roy et al., 2001).

Surface sand and mud were collected from Wallagoot Lake and carefully deposited into the *S* and *M* cages respectively to a depth of 6 cm such that the substratum covered the internal base of each cage. The artificial macrophyte in the *A* cages consisted of a 40-cm long, weighted base attached to 27 vertical blades (25 cm long  $\times$  1.5 cm wide) of AquaMat® (a positively buoyant synthetic matting with a high microscopic surface area). Two weighted bases were covered with a layer of bare sand (6 cm deep) on the internal base of each *A* cage to create an emerging shoot density equivalent to  $\sim 54$  shoots  $m^{-2}$  and a surface area of  $\sim 0.20 m^2 m^{-2}$  of substrate. AquaMat® has been previously shown to effectively simulate the blades and leaves of macrophytes in the wild (Arnold et al., 2005). Prior to preparation of the *A* cages, the AquaMat® was conditioned in a natural seagrass bed in Wallagoot Lake for 17 d to facilitate the colonization of biota. The cages used in each experimental trial were prepared 1 day before the trial.

Three of the cages containing each habitat type were assigned haphazardly (i.e. chosen blindly using a non-probability based selection scheme) as experimental cages and had one predator added to them at the beginning of each experimental trial. The remaining cages did not contain predators and were used simply as controls. Control and experimental cages were assigned haphazardly as either wild, experienced hatchery-reared or naïve hatchery-reared and received either *Wd*, *Ht<sub>E</sub>* or *Ht<sub>N</sub>* juveniles at the beginning of each trial. Three independent replicate trials of the experiment were undertaken ( $n=3$ ) with each predatory species over a total of 24 d. The use of each predatory species was alternated during this time (i.e.: trials 1, 3 and 5 were conducted with *C. australis* as the predator and trials 2, 4 and 6 were conducted with *M. macleayi* as the predator). New substrates and predators were used for each experimental trial and cages were reassigned haphazardly to a treatment at the beginning of each trial.

Before each experimental trial, twenty new *P. plebejus* juveniles from each category were released into their respective cages. This density was chosen based on the stocking densities currently being trialed in southeastern Australian estuaries and took into account estimated rates of mortality directly after a stock enhancement event (Ye et al., 2005). The juveniles were left to settle in the cages for 2 h, after which one predator was added to each experimental cage using a large fine mesh dip net. The control cages only differed from the experimental cages in that they did not have a predator added to them. The control cages allowed quantification of mortality caused by experimental artifacts (e.g. transportation, handling and caging) as opposed to the experimental variable. The process of adding a predator to a cage was simulated in the control cages by submerging an empty dip net that had previously contained a predator into the water for 10 s. After 72 h, each cage was moved intact to the shoreline where the predator within each experimental cage was removed, anesthetized and preserved in formalin. The remaining contents of each cage were emptied into a plastic container and examined to quantify the number of juvenile *P. plebejus* surviving at the end of the experiment. From these numbers, the percentage survival within each treatment and the weekly rate of predation for each category of juveniles within each habitat were calculated. The weekly predation rate was calculated by subtracting the number of juveniles surviving in each experimental treatment from the number of juveniles surviving in each corresponding control treatment, dividing this value by 3 d and then multiplying it by 7 d. This calculation enabled quantification of mortality specifically caused by predation.

### 2.3. Statistical analyses

All statistical analyses were carried out in *Stat graphics Plus 5*. Cochran's Test ( $\alpha=0.01$ ) was used to examine homogeneity of variances among treatments and where variances differed among treatments, data on survival and rates of predation were to be square root-

log-transformed respectively. However, all three data sets had homogeneous variances. Three separate analyses of variance (ANOVAs) ( $\alpha=0.01$ ) were initially used to analyse the data; one to test for differences in survival among categories of juveniles, habitats and predator treatments when *C. australis* was used as the predator, one to test for differences in survival among categories of juveniles, habitats and predator treatments when *M. macleayi* was used as a predator and one to test for differences in rates of predation mortality among categories of juveniles, habitats and the type of predator used. All three factors in the first two ANOVAs, habitat (3 levels; *A*, *S* or *M*), category (3 levels; *Wd*, *Ht<sub>E</sub>* or *Ht<sub>N</sub>*) and predator treatment (2 levels: *present* or *absent*), were fixed. All three factors in the third ANOVA, predator type (2 levels; *C. australis* or *M. macleayi*), habitat (3 levels; *A*, *S* or *M*) and category (3 levels; *Wd*, *Ht<sub>E</sub>* or *Ht<sub>N</sub>*), were also fixed. Where a significant interaction between factors was detected by an ANOVA, Tukey's HSD ( $\alpha=0.01$ ) test was used to compare treatments in a pair-wise manner. Among the more powerful unplanned parametric tests available, Tukey's HSD is one of the only ones that controls for experiment-wise error rates (Day and Quinn, 1989).

To quantify uncertainty in our findings where the ANOVAs and Tukey's HSD tests gave non-significant results, the data from each ANOVA was analysed further using three independent general linear models (GLMs) ( $\alpha=0.01$ ). The GLMs for the data used in the first two ANOVAs took on the general form of;

$$\text{Survival} = \beta_0 + \beta_1 \text{Predator treatment}_{\text{absent}} + \beta_2 \text{Habitat}_A + \beta_3 \text{Habitat}_M + \beta_4 \text{Category}_{HtN} + \beta_5 \text{Category}_{HtE},$$

and the GLM for the data used in the last ANOVA took on the general form of;

$$\text{Predation rate} = \beta_0 + \beta_1 \text{Predator type}_{C. australis} + \beta_2 \text{Habitat}_A + \beta_3 \text{Habitat}_M + \beta_4 \text{Category}_{HtN} + \beta_5 \text{Category}_{HtE},$$

where  $\beta_0$  was each model's intercept and  $\beta_{1-5}$  were the partial regression coefficients for the regressors of each categorical independent variable (i.e.: the factors from the ANOVAs). The reference levels for the variables predator treatment, habitat, category and predator type were *present*, *S*, *Wd* and *M. macleayi* respectively. The  $\beta_i$  values of the regressors for each variable provided estimates of effect size with confidence intervals (CIs). Since effect size CIs that exclude the null hypothesized value (in this case  $H_0: \beta_i=0$ ) indicate that the null hypothesis is not true (Colegrave and Riuxton, 2003; Steiger, 2004), the GLMs allowed us to gauge the biological importance of each variable's effect on survival or predation rate (Cohen, 1988; Thomas, 1997; Nakagawa and Cuthill, 2007).

### 3. Results

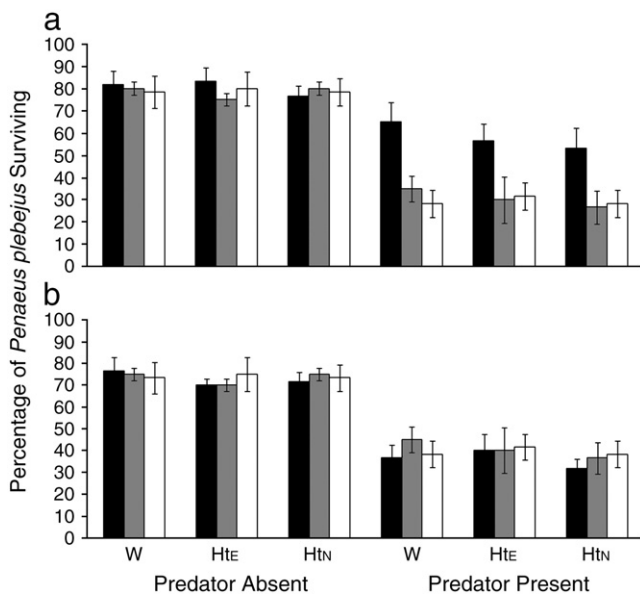
The first two ANOVAs examined differences in the survival of *P. plebejus* among habitats, categories of juveniles and predator-absent or -present treatments for each of the *C. australis* and *M. macleayi* trials. These analyses found that when either predator was absent, survival of *P. plebejus* ranged from 70 to 83% and was significantly higher than survival in the presence of either predator (Table 1 for *M. macleayi* trials; Tukey's HSD for *C. australis* trials;  $P<0.01$ ;  $n=3$ ). For the ANOVA from the *M. macleayi* trials (Table 1), in which the influence of the main effect of predator treatment could be interpreted, the mean square for predator treatment was an order of magnitude greater than that for all other main effects, suggesting that this treatment was crucial to the experiment. Most importantly, survival did not vary between the wild, naïve hatchery-reared and experienced hatchery-reared juveniles or between the artificial macrophyte, bare sand and bare mud in the absence of *C. australis* and *M. macleayi*, (Fig. 1; Table 1).

**Table 1**

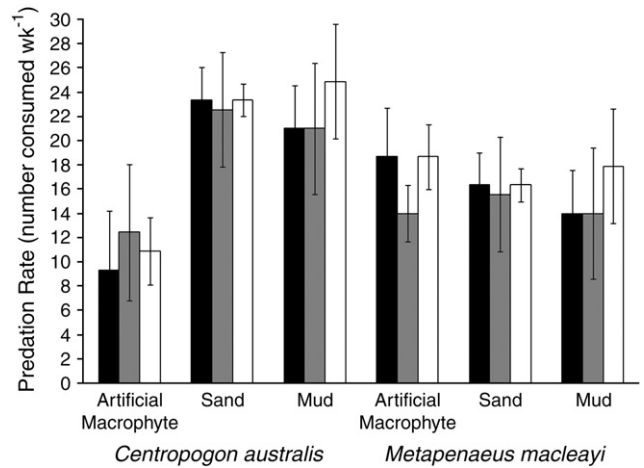
Three-way ANOVAs ( $\alpha=0.01$ ) comparing the survival of wild, experienced hatchery-reared and naïve hatchery-reared *Penaeus plebejus* juveniles within three habitats (artificial macrophyte, bare sand and bare mud) in the presence and absence of either *Centropogon australis* or *Metapenaeus macleayi*.  $n=3$  for each treatment.

Source of variation	Predator							
	<i>C. australis</i>				<i>M. macleayi</i>			
	df	MS	F	p-value	df	MS	F	p-value
Juvenile category (C)	2	78.25	0.61	0.55	2	42.13	0.39	0.68
Habitat (H)	2	1375.46	10.69	$p<0.01$	2	33.79	0.31	0.73
Predator treatment (P)	1	21,400.50	166.28	$p<0.01$	1	16,189.40	148.80	$p<0.01$
C×H	4	41.43	0.32	0.86	4	26.16	0.24	0.91
C×P	2	28.24	0.22	0.80	2	50.46	0.46	0.63
H×P	2	1047.69	8.14	$p<0.01$	2	17.13	0.16	0.85
C×H×P	4	23.38	0.18	0.95	4	17.82	0.16	0.96
Residual	36	128.70			36	108.79		
Total	53				53			

When *C. australis* was present, survival of *P. plebejus* showed no significant variation among wild, naïve hatchery-reared and experienced hatchery-reared juveniles within each of the habitats studied (Fig. 1a; Table 1). However, a significant interaction between habitat and predator treatment was detected (Table 1) and Tukey's HSD indicated that survival was significantly higher in artificial macrophyte (53 to 65%) compared to bare sand (28 to 31%) and mud (27 to 35%) in the presence of *C. australis* ( $P<0.01$ ;  $n=3$ ). When this predator was absent, however, survival was homogenous among the different habitats ( $P>0.01$ ;  $n=3$ ) but significantly higher within each habitat (65–95%) compared to the corresponding predator-present treatments ( $P<0.01$ ;  $n=3$ ). In the trials where *M. macleayi* was present as the predator, survival did not vary significantly between wild, naïve hatchery-reared and experienced hatchery-reared juveniles (Fig. 1b; Table 1). It was also similar among the macrophyte, bare sand and bare mud habitats (Fig. 1b; Table 1). Survival of *P. plebejus* ranged from 31 to 45% in the presence of *M. macleayi* and was significantly lower within each habitat than it was within each corresponding predator-absent treatment (Fig. 1b; Table 1).



**Fig. 1.** Mean ( $\pm$ SE) survival of wild (W), experienced hatchery-reared ( $Ht_E$ ) and naïve hatchery-reared ( $Ht_N$ ) *Penaeus plebejus* juveniles in artificial macrophyte (black bars), bare mud (grey bars) or bare sand (white bars) in the presence and absence of (a) *Centropogon australis* or (b) *Metapenaeus macleayi* as predators.



**Fig. 2.** Mean ( $\pm$ SE) rate at which *Centropogon australis* and *Metapenaeus macleayi* preyed upon wild (black bars), experienced hatchery-reared (grey bars) and naïve hatchery-reared (white bars) *Penaeus plebejus* juveniles (PL) within artificial macrophyte, bare mud and bare sand.

The third ANOVA examined the rate at which *P. plebejus* were preyed upon among different habitats, juvenile categories and in the presence of the two different types of predator. This analysis showed that predation mortality was homogenous among wild, naïve hatchery-reared and experienced hatchery-reared juveniles (Fig. 2; Table 2). However, there was a significant interaction between the type of predator used and habitat (Table 2). Tukey's HSD indicated that in the presence of *M. macleayi*, rates of predation were homogeneous (14.0–19.6 juveniles  $wk^{-1}$ ) among the habitats ( $P>0.01$ ;  $n=3$ ), but in the presence of *C. australis*, rates of predation were significantly lower in artificial macrophyte (9.3–12.4 juveniles  $wk^{-1}$ ) compared to rates in bare sand (22.5–23.3 juveniles  $wk^{-1}$ ) and bare mud (21.0–24.8 juveniles  $wk^{-1}$ ) ( $P<0.01$ ;  $n=3$ ). Within each habitat however, the rates at which *C. australis* and *M. macleayi* preyed upon *P. plebejus* were not significantly different (Tukey's HSD;  $P>0.01$ ).

All three GLMs showed that the observed effect sizes for juvenile category, as estimated from the partial regression coefficients of this variable's regressors, were consistently low ( $\beta_{4-5}<1.21$ ) (Tables 3 and 4). Furthermore, the CIs around each of these effect sizes spanned zero (Tables 3 and 4), indicating that there were no important biological differences between wild, naïve hatchery-reared and experienced hatchery-reared juveniles in terms of survival or rate of predation mortality. The second GLM also showed that the observed effect sizes for habitat were similarly low ( $\beta_{2-3}<0.93$ ) and that their CIs were inclusive of zeros (Table 3), confirming the trivial biological influence of habitat on survival of *P. plebejus* when *M. macleayi* was the predator. Similarly, the final GLM showed that the observed effect size for predator type was low ( $\beta_1=1.30$ ) and that the CI around this

**Table 2**

Three-way ANOVA ( $\alpha=0.01$ ) comparing the rate (number  $wk^{-1}$ ) at which *Centropogon australis* and *Metapenaeus macleayi* preyed upon wild, experienced hatchery-reared and naïve hatchery-reared *Penaeus plebejus* juveniles within three habitats (artificial macrophyte, bare sand and bare mud).  $n=3$  for each treatment.

Source of variation	df	MS	F	p-value
Predator type (PT)	1	90.74	1.92	0.17
Juvenile category (C)	2	20.97	0.44	0.64
Habitat (H)	2	164.04	3.48	0.04
PT×C	2	8.47	0.18	0.84
PT×H	2	262.24	5.56	$p<0.01$
C×H	4	7.06	0.15	0.96
PT×H×C	4	8.47	0.18	0.95
Residual	36	47.18		
Total	53			

**Table 3**

The results of GLMs ( $\alpha=0.01$ ) used to assess the relationship between survival of *Penaeus plebejus* juveniles and predator treatments (present or absent), type of habitat (artificial macrophyte, bare sand or bare mud) and the category of the juveniles (wild, experienced hatchery-reared or naïve hatchery-reared) in trials where either *Centropogon australis* or *Metapenaeus macleayi* were used as predators. The table gives each model's intercept ( $\beta_0$ ) and its standard error (S.E.); the partial regression coefficients ( $\beta_{1-s}$ ) for the regressors of each model's independent variables and their S.E.s; and the upper and lower confidence limits around each of these values.  $n = 3$ .

<i>Centropogon australis</i>	$\beta$ (S.E.)	Lower limit	Upper limit
Intercept	59.35 (1.65)	54.93	63.77
Predator treatment <sub>absent</sub>	19.91 (1.65)	15.49	24.32
Habitat <sub>Artificial macrophyte</sub>	10.09 (2.33)	3.84	16.35
Habitat <sub>Mud</sub>	-4.91 (2.33)	-11.16	1.35
Juvenile category <sub>naïve hatchery-reared</sub>	-2.13 (2.33)	-8.38	4.12
Juvenile category <sub>experienced hatchery-reared</sub>	0.09 (2.33)	-6.16	6.35
<i>Metapenaeus macleayi</i>			
Intercept	56.02 (1.27)	52.59	59.44
Predator treatment <sub>absent</sub>	17.31 (1.27)	13.89	20.74
Habitat <sub>Artificial macrophyte</sub>	-1.57 (1.81)	-6.42	3.27
Habitat <sub>Mud</sub>	0.93 (1.81)	-3.92	5.77
Juvenile category <sub>naïve hatchery-reared</sub>	-1.57 (1.81)	-6.42	3.27
Juvenile category <sub>experienced hatchery-reared</sub>	0.09 (1.81)	-4.75	4.94

effect size was inclusive of zero. This suggests that differences between *C. australis* and *M. macleayi*, in terms of the rate at which they consume *P. plebejus*, are not biologically important.

#### 4. Discussion

One factor that contributes to the failure of stock enhancement programs is uncertainty over the capacity of hatchery-reared animals to fully develop mechanisms for effective predator evasion (Olla et al., 1998; Hawkins et al., 2008). At small spatial and temporal scales, the current study shows that hatchery-reared *P. plebejus* juveniles and their wild con-specifics are equally capable of avoiding the predators *C. australis* and *M. macleayi*. Furthermore, exposure of hatchery-reared juveniles to wild conditions for five weeks does not increase their ability to avoid these predators.

These results differ from those of studies on teleosts which predominantly indicate that naïve hatchery-reared fish suffer higher predation than their experienced or wild counterparts (e.g. Olla and Davis, 1989; Johnsson et al., 1996; Stunz and Minello, 2001). In the presence of predators, exclusively hatchery-reared flounder (*Paralichthys dentatus*) produced from hatchery-reared brood-stock displayed riskier behavior, such as swimming in the water column for longer periods or taking longer to bury themselves among benthos, when compared to wild flounder (Kellison et al., 2000). Furthermore, first-generation hatchery-reared salmon (*Salmo salar*) lacking any exposure to wild conditions displayed lagging physiological responses to predators. The retarded responses included a delayed increase in

**Table 4**

The results of a GLM used to assess the relationship between the rate of predation mortality in *Penaeus plebejus* juveniles and the type of predator used (*Centropogon australis* or *Metapenaeus macleayi*), the type of habitat (artificial macrophyte, bare sand or bare mud) and the category of the juveniles (wild, experienced hatchery-reared or naïve hatchery-reared). The table gives each model's intercept ( $\beta_0$ ) and its standard error (S.E.); the partial regression coefficients ( $\beta_{1-s}$ ) for the regressors of each model's independent variables and their S.E.s; and the upper and lower confidence limits around each of these values.  $n = 3$ .

	$\beta$ (S.E.)	Lower limit	Upper limit
Intercept	17.46 (0.94)	14.93	19.98
Predator type <sub>C. australis</sub>	1.30 (0.94)	-1.23	3.82
Habitat <sub>Artificial macrophyte</sub>	-3.46 (1.33)	-7.03	0.12
Habitat <sub>Mud</sub>	1.34 (1.33)	-2.23	4.91
Juvenile category <sub>Naïve hatchery-reared</sub>	1.21 (1.33)	-2.37	4.78
Juvenile category <sub>Experienced hatchery-reared</sub>	-0.86 (1.33)	-4.44	2.71

ventilation rate indicating a belated realization of the dangers posed by predators (Johnsson et al., 2001; Hawkins et al., 2004). Another previous study compared wild blue crabs (*Callinectes sapidus*) with first-generation naïve hatchery-reared crabs and experienced hatchery-reared crabs (which were conditioned to natural stimuli through release into the wild) and found that all hatchery-reared crabs were slower to adopt protective burying behavior within sediment than wild crabs (Davis et al., 2004; Young et al., 2008). In the above studies, higher rates of predation on the relatively naïve cultured animals were attributed to limited genetic and/or developmental acquisition of the morphological, chemical and behavioral cues used for predator detection and avoidance. This was in-turn attributed to culture in a predator-free environment (Einum and Fleming, 2001; Stunz and Minello, 2001). However, these examples from the literature serve as poor direct comparisons with *P. plebejus* as they relate to animals with different morphologies, behaviors and physiologies from *P. plebejus*. There are currently no examples in the literature of similar studies on penaeids or other closely related species.

The types of deficits in anti-predator mechanisms that may cause higher mortality in hatchery-reared penaeids include retarded escape movements owing to an under-developed telson, reduced chemo-sensory abilities to detect predators (Dall et al., 1990a) or a diminished ability to recognize and develop a behavioral affinity with protective habitat (Ochwada et al., 2009). Although our study did not explicitly examine such deficits in hatchery-reared *P. plebejus*, the similar survival and rates of predation mortality between hatchery-reared and wild *P. plebejus* observed here suggests that these deficits are non-existent or minimal and may not lead to detectable differences in the survival of released individuals in systems dominated by predators like *C. australis* and *M. macleayi*. One possible explanation for the absence of such deficits is that *P. plebejus* is able to evade predators through genetically rather than developmentally acquired traits. This implies that juveniles reared in a predator-free environment would have an innate ability to detect and avoid predators. For the naïve and experienced hatchery-reared juveniles in these experiments, overall genotypic change towards degraded anti-predator mechanisms, due to the absence of natural selection pressures in the hatchery, is likely to have been negligible because the juveniles were produced from wild brood-stock. Even so, similar mortality rates (Hvidsten and Lund, 1988) and fright-responses to predatory stimuli (e.g.: amount of time spent motionless and amount of time spent near substrate) have previously been reported between naïve salmonids bred from multiple generations of cultured individuals and con-specifics that were either similarly reared but had ancestral exposure to predators (Berejikian et al., 2003) or completely wild (Ryer, 2004). These results were attributed to an inherited ability to respond to predators that was robust enough to withstand multiple generations of hatchery-rearing.

Although the hatchery-reared juveniles used here appear to have retained effective genetically acquired anti-predator mechanisms, this may not necessarily be the case for all hatchery-reared *P. plebejus*. Only one male brood-stock was used to produce the juveniles here; a practice that is strongly discouraged for large-scale stock enhancement purposes (Blankenship and Leber, 1995; Taylor et al., 2005). It is possible that this male parent was genetically predisposed to effective predator evasion, resulting in high paternally inherited defense mechanisms among the cultured juveniles. Another wild male parent with lower fitness may have possessed ineffective defense mechanisms and may have consequently produced offspring likely to suffer higher rates of predation. This potential for negative genetic consequences if a single, different male parent had been used highlights the importance limiting the loss of genetic fitness during enhancement by using numerous brood-stock from each sex. Despite *P. plebejus*' apparent inherited capacity to evade *C. australis* and *M. macleayi* given genetically fit or diverse parents, another important consideration for future enhancement events is whether *P. plebejus*'

capacity to avoid other types of predators is equally innate or whether evasion of predators with different foraging techniques compared to *C. australis* and *M. macleayi* is learned.

Predation by *C. australis* on all categories of *P. plebejus* juveniles was lower in the artificial macrophyte compared to the bare habitats. These patterns of predation mortality are consistent with those observed for other penaeids (Minello and Zimmerman, 1985; Kenyon et al., 1995; Primavera, 1997). Juvenile penaeids such as *P. plebejus*, *P. esculentus*, *P. aztecus*, *P. merguensis* and *P. monodon* all exhibit a strong affinity with complex habitat (Minello and Zimmerman, 1985; Kenyon et al., 1995; Primavera, 1997; Ochwada et al., 2009). Coupled with the use of rapid back-ward escape movements afforded by the presence of a fan-like telson, this behavioral association is thought to impede location and capture by predators (Dall et al., 1990b; Kenyon et al., 1995; Almany, 2004). If stock enhancement is proposed for a system in which ambush predators like *C. australis* are abundant, enhancement of penaeids such as *P. plebejus* could be optimized by limiting releases to systems with extensive complex habitats such as macrophyte beds. It should be noted that as many penaeid species increase in size, burrowing into sand appears to become a more common means of predator avoidance than hiding among complex habitats (Hill and Wassenberg, 1993; Liu and Loneragan, 1997). This transition represents a substantial ontogenetic shift and investigating any associated changes in habitat-related predation mortality will assist in developing a more general model for long-term predation mortality of *P. plebejus* in stocked systems.

Although wild and hatchery-reared *P. plebejus* were equally capable of avoiding predation when present independently in artificial macrophyte, the apparent protective nature of complex habitats creates the potential for intra-specific competition for refuge within this habitat when wild and stocked individuals coexist in systems dominated by passive ambush predators. This competition could result in differential predation mortality between the two categories in systems dominated by passive ambush predators. Experiments examining competition between co-existing wild and hatchery-reared *P. plebejus* should therefore be conducted prior to enhancement of *P. plebejus* to determine if enhancement could lead to the loss of stocked populations or the displacement of wild populations. These experiments would ideally examine the effects of predation on the survival and growth of co-existing hatchery-reared and wild individuals as shelter becomes increasingly limited (Underwood, 2007).

When juvenile *M. macleayi* were used as predators, the overall survival and rate of predation mortality of all categories of *P. plebejus* did not differ between the artificial macrophyte and bare habitats. When similar results have been recorded for other penaeids that were prey items, it has been suggested that aspects of the chosen predator's physiology, morphology or behavior make it equally adept at detecting and capturing prey within complex and simple habitats (Minello and Zimmerman, 1983; Primavera, 1997). Whilst predation by passive ambush predators like *C. australis* (Harmelin-Vivien and Bouchon, 1976; Meager et al., 2005) can be significantly reduced by the presence of structure, predators that chase their prey like *M. macleayi* may be unaffected by habitat complexity because they squeeze between structures and occupy the narrow crevices where prey attempt to hide (Dall et al., 1990c; Primavera, 1997).

The mortality of *P. plebejus* was significantly lower in that absence of either *C. australis* or *M. macleayi* compared to when these predators were present. This pattern reflects the successful use of the predator-absent treatments as controls for comparison with the experimental predator-present treatments. Even so, the moderate mortality (17–30%) observed in the absence of either predator warrants discussion because it suggests the presence of artifacts due to transportation and handling of *P. plebejus* or artifacts caused by caging. For the processes of transportation and handling, any introduced artifacts were applied to both the experimental and control treatments. The effects of these artifacts should have therefore contributed equally to the mortality

observed in all treatments allowing unbiased assessment of differences between and among treatments (Peterson and Black, 1994). Although caging was similarly applied to both predator treatments, it is possible that artifacts associated with this particular intervention interacted with the experimental variable. For example the presence of a cage may have altered the predatory behavior of *C. australis* and *M. macleayi*. The use of a procedural cage-less control could have therefore helped to account for artifacts due to caging. However, the mobility of penaeids (relative to slow moving species, such as molluscs, or completely sessile animals) and the inherent difficulties of re-capturing penaeids once released into an un-enclosed area, made it impossible to introduce a cage-less procedural control. In the absence of such a procedural control, our experimental design still enabled us to subtract the number of juveniles surviving in each experimental treatment from the number surviving in each corresponding control treatment when calculating the rate of predation on *P. plebejus*. We were therefore able to separate experimental mortality from mortality due to caging.

In recent years, stock enhancement programs have begun to evolve from poorly investigated and indiscriminate mass releases to those based on scientific theory and precautionary accountability (Leber, 2002; Bell et al., 2008; Taylor and Suthers, 2008). This change must continue to incorporate quantitative experimental studies that compare the ecological attributes of hatchery-reared and wild individuals. Although the present study has shown that hatchery-reared *P. plebejus* juveniles and their wild con-specifics are equally capable of avoiding some predators, the experimental procedure presented here should be applied to other candidates for stock enhancement. Its application may identify deficits in hatchery-reared individuals of other species that could be mitigated before release or deficits in wild individuals that may lead to the loss of resident populations (Davis et al., 2004). This type of work can improve the success of stock enhancement and assist in assessing the risks of this management approach.

## Acknowledgements

This work was completed as part of a PhD candidature and supported in part by grants from the New South Wales Recreational Saltwater Fishing Trust (#L30), the Australian Research Council (#LP0775000) and the New South Wales Department of Primary Industries. The project was carried out with UNSW animal care and ethics approval (#06/88A). We would like to thank A. Poore, UNSW staff and volunteers from the Merimbula Fishing Club for their assistance during the study. We would also like to thank the five anonymous reviewers for their invaluable comments on the original manuscript. [RH]

## References

- Addison, J.T., Bannister, R.C.A., 1994. Re-stocking and enhancement of clawed lobster stocks – a review. *Crustaceana* 67, 131–155.
- Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106, 275–284.
- Álvarez, D., Nicieza, A.G., 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. *J. Fish Biol.* 63, 1565–1577.
- Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J.R., May, R.M., Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835–839.
- Araki, H., Cooper, B., Blouin, M.S., 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318, 100–103.
- Arnold, S.J., Sellars, M.J., Crocos, P.J., Coman, G.J., 2005. Response of juvenile brown tiger shrimp (*Penaeus esculentus*) to intensive culture conditions in a flow through tank system with three-dimensional artificial substrate. *Aquaculture* 246, 231–238.
- Bell, J.D., Burchmore, J.J., Pollard, D.A., 1978. Feeding ecology of a scorpaenid fish, the fortiesque *Centropogon australis*, from a *Posidonia* seagrass habitat in New South Wales. *Aust. J. Mar. Freshw. Res.* 29, 175–185.
- Bell, J.D., Rothlisberg, P.C., Munro, J.L., Loneragan, N.R., Nash, W.J., Ward, R.D., Andrew, N.L., 2005. Restocking and stock enhancement of marine invertebrate fisheries. *Adv. Mar. Biol.* 49, 1–353.

- Bell, J.D., Leber, K.M., Blankenship, H.L., Loneragan, N.R., Masuda, R., 2008. A new era for restocking, stock enhancement and sea ranching of coastal fisheries resources. *Rev. Fish. Sci.* 16, 1–9.
- Berejikian, B.A., Tezak, E.P., LaRae, A.L., 2003. Innate and enhanced predator recognition in hatchery-reared chinook salmon. *Environ. Biol. Fishes* 67, 241–251.
- Blankenship, H.L., Leber, K.M., 1995. A responsible approach to marine stock enhancement. *Am. Fish. Soc. Symp.* 15, 167–175.
- Brown, C., Day, R.L., 2002. The future of stock enhancements: lessons for hatchery practice from conservation biology. *Fish. Fish.* 3, 79–94.
- Brown, C., Laland, K., 2001. Social learning and life skills training for hatchery reared fish. *J. Fish Biol.* 59, 471–493.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*. Lawrence Erlbaum Associates, New Jersey.
- Colegrave, N., Riuxton, G.D., 2003. Confidence intervals are a more useful complement to non-significant tests than are power calculations. *Behav. Ecol.* 14, 446–450.
- Dall, W., Hill, B., Rothlisberg, P., Sharples, D., 1990a. *The Biology of the Penaeidae*. Academic Press, London. 1–488 pp.
- Dall, W., Hill, B., Rothlisberg, P., Sharples, D., 1990b. Predation on Penaeids, *The Biology of the Penaeidae*. Academic Press, London, pp. 357–377.
- Dall, W., Hill, B.J., Rothlisberg, P.C., Staples, D.J., 1990c. Food and Feeding, *The Biology of the Penaeidae*. Academic Press, London, pp. 314–332.
- Davis, J.L.D., Young-Williams, A.C., Aguilar, R., Carswell, B.L., Goodison, M.R., Hines, A.H., Kramer, M.A., Zohar, Y., Zmora, O., 2004. Differences between hatchery-raised and wild blue crabs: implications for stock enhancement potential. *Trans. Am. Fish. Soc.* 133, 1–14.
- Day, R.W., Quinn, G.P., 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59, 433–463.
- Einum, S., Fleming, I.A., 2001. Implications of stocking: ecological interactions between wild and released salmonids. *Nord. J. Freshwat. Res.* 75, 56–70.
- Grimes, C.B., 1998. Marine stock enhancement: sound management or technorogance? *Fisheries* 23, 18–23.
- Harmelin-Vivien, M.L., Bouchon, C., 1976. Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tuléar (Madagascar). *Mar. Biol.* 37, 329–340.
- Hawkins, L.A., Armstrong, J.D., Magurran, A.E., 2004. Predator induced hyperventilation in wild and hatchery Atlantic salmon fry. *J. Fish Biol.* 65, 88–100.
- Hawkins, L.A., Magurran, A.E., Armstrong, J.D., 2008. Ontogenetic learning of predator recognition in hatchery-reared Atlantic salmon, *Salmo salar*. *Anim. Behav.* 75, 1663–1671.
- Hilborn, R., 1998. The economic performance of marine stock enhancement projects. *Bull. Mar. Sci.* 62, 661–674.
- Hilborn, R., 2007. Reinterpreting the state of fisheries and their management. *Ecosystems* 10, 1362–1369.
- Hill, B.J., Wassenberg, T.J., 1993. Why are some prawns found in seagrass? An experimental study of brown (*Penaeus esculentus*) and grooved (*P. semisulcatus*) tiger prawns. *Mar. Freshw. Res.* 44, 221–227.
- Hvidsten, N.A., Lund, R.A., 1988. Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar*, in the estuary of River Orkla, Norway. *J. Fish Biol.* 33, 121–126.
- Ives, M.C., Scandol, J.P., 2007. A Bayesian analysis of NSW eastern king prawn stocks (*Melicertus plebejus*) using multiple model structures. *Fish. Res.* 84, 314–327.
- Johnsson, J.L., Petersson, E., Jonsson, E., Björnsson, B., Jarvi, T., 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Can. J. Fish. Aquat. Sci.* 53, 1546–1554.
- Johnsson, J.L., Hojesjo, J., Fleming, I.A., 2001. Behavioral and heart responses to predation risk in wild and domesticated Atlantic salmon. *Can. J. Fish. Aquat. Sci.* 58, 788–794.
- Kellison, G.T., Eggleston, D.B., Burke, J.S., 2000. Comparative behaviour and survival of hatchery-reared versus wild summer flounder (*Paralichthys dentatus*). *Can. J. Fish. Aquat. Sci.* 57, 1870–1877.
- Kenyon, R.A., Loneragan, N.R., Hughes, J.M., 1995. Habitat type and light affect sheltering behavior of juvenile tiger prawns (*Penaeus esculentus* Haswell) and success rates of their fish predators. *J. Exp. Mar. Biol. Ecol.* 192, 87–105.
- Leber, K.M., 2002. Advances in marine stock enhancement: shifting emphasis to theory and accountability. In: Stickney, R.R., McVey, J.P. (Eds.), *Responsible Marine Aquaculture*. CABI Publishing, Maryland, pp. 79–89.
- Liu, H., Loneragan, N.R., 1997. Size and time of day affect the response of postlarvae and early juvenile grooved tiger prawns *Penaeus semisulcatus* De Haan (Decapoda: Penaeidae) to natural and artificial seagrass in the laboratory. *J. Exp. Mar. Biol. Ecol.* 211, 263–277.
- Ludwig, D., Hilborn, R., Waters, C., 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260, 17–36.
- Meager, J.J., Williamson, I., Loneragan, N.R., Vance, D.J., 2005. Habitat selection of juvenile banana prawns, *Penaeus merguensis* de Man: testing the roles of habitat structure, predators, light phase and prawn size. *J. Exp. Mar. Biol. Ecol.* 324, 89–98.
- Minello, T.J., Zimmerman, R.J., 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated Spartina structure on predation rates. *J. Exp. Mar. Biol. Ecol.* 72, 211–231.
- Minello, T.J., Zimmerman, R.J., 1985. Differential selection for vegetative structure between juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*), and implications in predator–prey relationships. *Estuar. Coast. Shelf Sci.* 20, 707–716.
- Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev. Camb.* 82, 591–605.
- Ochwada, F., Loneragan, N.R., Gray, C.A., Suthers, I.M., Taylor, M.D., 2009. Complexity affects habitat preference and predation mortality in postlarval *Penaeus plebejus*: implications for stock enhancement. *Mar. Ecol. Prog. Ser.* 380, 161–171.
- Olla, B.L., Davis, M.W., 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture* 76, 209–214.
- Olla, B.L., Davis, M.W., Ryer, C.H., 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bull. Mar. Sci.* 62, 531–550.
- Peterson, C.H., Black, R., 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar. Ecol. Prog. Ser.* 111, 289–297.
- Pikitch, E., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, J., 2004. Ecosystem-based fishery management. *Science* 305, 346–347.
- Primavera, J.H., 1997. Fish predation on mangrove-associated penaeids: the role of structures and substrate. *J. Exp. Mar. Biol. Ecol.* 215, 205–216.
- Rothlisberg, P.C., Preston, N.P., Loneragan, N.R., Die, D.J., Poiner, I.R., 1999. Approaches to reseeded penaeid prawns. In: Howell, B.R., Moksness, E., Svasand, T. (Eds.), *Stock Enhancement and Sea Ranching*. Fishing News Books, Oxford, pp. 365–378.
- Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east Australian estuaries. *Estuar. Coast. Shelf Sci.* 53, 351–384.
- Ruello, N.V., 1973. Burrowing, feeding and spatial distribution of the school prawn *Metapenaeus macleayi* (Haswell) in the hunter river region, Australia. *J. Exp. Mar. Biol. Ecol.* 13, 189–206.
- Ryer, C., 2004. Comparison of genetically based antipredator behaviour in hatchery and wild coho fry from a coastal Oregon river: interpreting a negative result. *J. Fish Biol.* 64, 1413–1418.
- Steiger, J.H., 2004. Beyond the F test: effect size confidence intervals and tests of close fit in the analysis of variance and contrast analysis. *Psychol. Methods* 9, 164–182.
- Stunz, G.W., Minello, T.J., 2001. Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 260, 13–25.
- Taylor, M.D., Suthers, I.M., 2008. A predatory impact model and targeted stock enhancement approach for optimal release of mulloway (*Argyroromus japonicus*). *Rev. Fish. Sci.* 16, 125–134.
- Taylor, M.D., Palmer, P.J., Fielder, D.S., Suthers, I.M., 2005. Responsible estuarine finfish stock enhancement: an Australian perspective. *J. Fish Biol.* 67, 299–331.
- Thomas, L., 1997. Retrospective power analysis. *Conserv. Biol.* 11, 276–280.
- Underwood, A.J., 2007. Negative interactions: an overview of competition among marine organisms. In: Connell, S.D., Gillanders, B.M. (Eds.), *Marine Ecology*. Oxford University Press, Melbourne, pp. 101–109.
- Ye, Y., Loneragan, N., Die, D., Watson, R., Harch, B., 2005. Bioeconomic modelling and risk assessment of tiger prawn (*Penaeus esculentus*) stock enhancement in Exmouth Gulf, Australia. *Fish. Res.* 73, 231–249.
- Young, A.C., Johnson, E.G., Davis, J.L.D., Hines, A.H., Zmora, O., Zohar, Y., 2008. Do hatchery-reared blue crabs differ from wild crabs and does it matter? *Rev. Fish. Sci.* 16, 254–261.