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Estimating the efficiency of a small beam trawl for sampling tiger prawns *Penaeus esculentus* and *P. semisulcatus* in seagrass by removal experiments

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ABSTRACT: The efficiency with which a small beam trawl (1 × 0.5 m mouth) sampled postlarvae and juveniles of tiger prawns *Penaeus esculentus* and *P. semisulcatus* at night was estimated in 3 tropical seagrass communities (dominated by *Thalassia hemprichii*, *Syringodium isoetifolium* and *Enhalus acoroides*, respectively) in the shallow waters of the Gulf of Carpentaria in northern Australia. An area of seagrass (40 × 3 m) was enclosed by a net and the beam trawl was repeatedly hand-hauled over the substrate. Net efficiency (q) was calculated using 4 methods: the unweighted Leslie, weighted Leslie, DeLury and Maximum-likelihood (ML) methods. The Maximum-likelihood is the preferred method for estimating efficiency because it makes the fewest assumptions and is not affected by zero catches. The major difference in net efficiencies was between postlarvae (mean ML $q \pm 95\%$ confidence limits $= 0.66 \pm 0.16$) and juveniles of both species (mean q for juveniles in water ≤ 1.0 m deep $= 0.47 \pm 0.05$), i.e. the beam trawl was more efficient at capturing postlarvae than juveniles. There was little difference in net efficiency for *P. esculentus* between seagrass types (*T. hemprichii* versus *S. isoetifolium*), even though the biomass and morphologies of seagrass in these communities differed greatly (biomasses were 54 and 204 g m^{-2}, respectively). The efficiency of the net appeared to be the same for juveniles of the 2 species in shallow water, but was lower for juvenile *P. semisulcatus* at high tide when the water was deeper (1.6 to 1.9 m) (0.35 ± 0.08). The lower efficiency near the time of high tide is possibly because the prawns are more active at high than low tide, and can also escape above the net. Factors affecting net efficiency and alternative methods of estimating net efficiency are discussed.

KEY WORDS: Net efficiency · Beam trawls · Tiger prawns · Seagrass

INTRODUCTION

The distribution and relative abundance of juvenile crustaceans and fish have been studied by sampling with jet nets (Penn & Stalker 1975, Turnbull & Watson 1992), drop traps (Zimmerman et al. 1984) and beam trawls (e.g. Young 1978, Coles & Lee Long 1985, Worthington et al. 1991). Jet nets and drop traps attempt to capture all the animals in an area, whether they are above or buried in the substrate. In contrast, beam trawls, which are towed over the surface of the substrate, catch animals that are on, or disturbed from, the substrate and that could not avoid the net. Beam trawl catch data have been used in studies of long-term changes in relative abundance of crustaceans and fish by standardising the time of sampling to that of known catchability or highest catch rates (e.g. Staples & Vance 1979, Staples et al. 1985). This requires a detailed understanding of how catch rates change with a number of factors, particularly tidal and lunar cycles (see Vance & Staples 1992, Vance et al. 1994).

The juveniles of commercially important penaeid prawns (shrimp) are usually found in nursery habitats in shallow, inshore and estuarine waters (Dall et al. 1990). For example, juvenile brown and grooved tiger prawns *Penaeus esculentus* and *P. semisulcatus* are found on beds of seagrass and algae (Coles & Lee Long 1985, Staples et al. 1985, Vance & Staples 1992), and juvenile brown shrimp *P. aztecus* live in salt marshes (*Spartina alterniflora*) (Zimmerman et al. 1984). As seagrasses in tropical Australia differ markedly in their morphology, some types may provide better habitat for juvenile tiger prawns than others (Poiner et al. 1987, 1989, Loneragan et al. 1994). However, before one can evaluate this hypothesis, it is important to establish whether the sampling device is equally efficient in all seagrass communities.

Most species of prawns bury themselves during the day, and emerge from the substrate and become active at night (Dall et al. 1990, Wassenberg & Hill 1994). Juvenile prawns are therefore usually sampled with small beam trawls at night (e.g. Young 1978, Turnbull & Watson 1992, O'Brien 1994). The efficiencies of different beam trawl nets have been compared (McNeill & Bell 1992, Turnbull & Watson 1992) and the daytime efficiency of a beam trawl has been estimated for *Penaeus aztecus* in salt marshes (Zimmerman et al. 1984). However, we know of no estimates of the efficiency of beam trawls in different seagrass beds.

Both the efficiency of a net and the size of the population it is sampling can be estimated by 'removal experiments', whereby an area is repeatedly sampled over a relatively short time interval (e.g. Ricker 1975, Schnute 1983, Joll & Penn 1990). Removal experiments, and the Leslie-DeLury techniques of data analysis, assume that the population is closed, and that the catchability of the target species is constant throughout the sampling period (Ricker 1975). Maximum-likelihood techniques have also been applied to the data from removal experiments to estimate net efficiency and population size (e.g. Seber & Le Cren 1967, Schnute 1983, Riley & Fausch 1992).

In this study we used removal methods to estimate the efficiency of a small beam trawl at night in different seagrass beds. The efficiency with which this net captured newly settled *Penaeus esculentus* and *P. semisulcatus* postlarvae (i.e. the first benthic stages) was compared with that for capturing juveniles. Its efficiency at capturing juvenile *P. semisulcatus* in deeper water (i.e. at high tide) was compared with its efficiency in shallower water (i.e. at low tide). The efficiency of the net was calculated by different methods (Leslie, DeLury, Maximum-likelihood) and the biases in these methods are discussed.

MATERIALS AND METHODS

Removal experiments. Removal experiments were used to estimate the efficiency of a small beam trawl at 2 intertidal seagrass beds (North West Reef and Black Stump Bay) in northwestern Groote Eylandt (13 to 14° S, 135 to 137° E), and 1 intertidal seagrass bed in the Embley River (12° 40′ S, 141° 50′ E) in the northeastern Gulf of Carpentaria, Australia. Only 1 seagrass community type was found at each site and thus the effects of site and seagrass type cannot be separated. The main species of seagrass at North West Reef was *Thalassia hemprichii*. The dominant seagrasses at Black Stump Bay were *Syringodium isoetifolium* and *Cymodocea serrulata* and in the Embley River, the main seagrass was *Enhalus acoroides* (see Table 1). At least 2 areas of seagrass were sampled at each site to provide an estimate of within-seagrass-bed variation.

Prawns were sampled at night at all sites because this is the time when juvenile tiger prawns are most active and beam trawl catches are highest (Vance 1992, Vance & Staples 1992, Vance et al. 1994). Sampling was carried out between the spring and neap stage of the tidal cycle. The experiments at North West Reef were completed in January 1984 and those at Black Stump Bay in February 1984, both during the first quarter of the moon. The Embley River studies were completed in January 1991 during the last quarter of the moon.

The dimensions of the beam trawl used in the removal experiments were: mouth 1 m wide and 0.5 m high; body of the net, 2.5 m long with 2 mm mesh; cod-end, 1 m long with 1 mm mesh.

This net was repeatedly hand-hauled over a 40 m long × 3 m wide area of seagrass, marked out by posts and enclosed by a 2 m deep net, made of 6 mm mesh. The enclosure net was set around the posts while rowing a small dingy to create as little disturbance as possible. A dingy was moored at each end of the rectangle. The beam trawl was hand-hauled along the length of the rectangle, with 3 hauls required to completely sweep the enclosed area (up one side, down the middle, up the other side of the rectangle). Any catch was removed from the cod-end before the start of the next haul. Each 40 m haul took about 75 s to complete, which is about the same towing speed as that used when this net is towed by a small boat (ca 0.5 to 0.6 m s^{-1}). The sequence of trawls was repeated until the rectangle had been swept 5 times (i.e. 15 trawls) within 75 to 90 min in all experiments, except one (North West Reef, Expt 2), when only 3 sweeps (i.e. 9 trawls) could be made before dawn.

Each removal experiment was completed on a previously untrawled area of seagrass. Two experiments were carried out at both Black Stump Bay and North West Reef. A total of 6 experiments (3 at high and 3 at low tide) were completed in the Embley Estuary on 3 consecutive nights, to investigate the influence of water depth on the efficiency of the net.

Measurements. The prawns from each trawl were placed on ice and taken to the laboratory where they were identified, counted and measured (carapace length, CL) to the nearest 1 mm under a dissecting microscope. Although the postlarvae of the tiger prawn group (<3 mm CL) could be distinguished from other penaeid postlarvae groups (e.g. banana prawns *Penaeus merguinensis* and *P. indicus*, king prawns *P. latisulcatus* and *P. longistylis*, and greasy prawns *Metapenaeus* spp.), they could not be identified to species. Juvenile tiger prawns ≥3 mm CL were identified from the characteristics outlined by Grey et al. (1983). Mean carapace lengths were calculated for juvenile tiger prawns (≥3 mm CL) for each removal experiment where more than 25 prawns were caught.

Seagrass. Samples of seagrass were collected from North West Reef in December 1983, from Black Stump Bay in February 1984 and from the Embley River in November 1990. The sampling methods are described in Poiner et al. (1987). The total surface area of each species of seagrass was calculated from the sum of the surface areas of the leaves, stems and shoots. The mean total surface area, shoot density and above-ground biomass of seagrass per m^2 were calculated for each site. The above-ground biomass for each species or taxon of algae was also calculated at each site, and summed to determine the total above-ground biomass for algae.

Calculation of net efficiency. Postlarvae and small juvenile prawns may have been able to emigrate from, or immigrate into, the enclosed seagrass area. However, because the experiments were completed within 90 min, we have assumed that emigration and immigration from the enclosure were negligible. In addition, laboratory studies of juvenile *Penaeus esculentus* behaviour show that small tiger prawns move only short distances when disturbed (Kenyon 1993) and thus there was probably relatively little movement through the enclosure net in response to the passage of the beam trawl.

The data from the removal experiments were analysed as a special case of the Leslie-DeLury methods because equal units of effort were used to make the successive catches (Ricker 1975, Joll & Penn 1990). Each group of 3 trawls that completely swept the rectangle (1 sweep) was used as the standard unit of effort, and the catch was the total catch from these 3 trawls. Only those experiments in which at least 25 individuals were caught were analysed to estimate net efficiency; this limited the data for postlarvae and juvenile *Penaeus esculentus* to Groote Eylandt experiments, and the data for juvenile *P. semisulcatus* to Embley River experiments. Full details of the notation and equations used to calculate net efficiency are given in the Appendix. A brief description of each method is given below.

Leslie's method: This method is based on a linear regression of catch per unit effort (CPUE) on the cumulative catch to the start of the ith sweep (see Ricker 1975, p. 151). A weighted Leslie regression was also calculated using the inverse of the catches as the weight for each point (see also Crittenden 1983).

DeLury's method: This method is based on the regression of ln(CPUE) in each sweep on the cumulative effort (E). Zero sweeps, which were only recorded on the last sweep of an experiment, were not included in these analyses.

Maximum-likelihood method: Schnute (1983) assumes that on the ith sweep of the enclosure, each remaining prawn is exposed to capture with the same probability q independently, i.e. the ith catch has a binomial distribution. The catchability q is usually unknown and we assume that it is constant over the fishing interval i, which leads to Model 1 of Schnute (1983).

Comparisons of net efficiencies. Only pairwise comparisons were possible between size groups (i.e. postlarvae and juveniles), species of juvenile prawn, and seagrass types because catch rates of one or more groups were too low to allow broader comparisons to be made using analysis of covariance. The means and standard errors of $\hat{q}$ and $\hat{N}_0$ from each method of calculation (i.e. Leslie, weighted Leslie, DeLury and Maximum-likelihood) were calculated for postlarvae (both species combined), juvenile *Penaeus esculentus*, and juvenile *P. semisulcatus* at low and high tide. Differences in the Maximum-likelihood estimates of q were calculated and Z-statistics (using the pooled variance) were used to test for differences in net efficiency and for constructing the 95% confidence intervals. The following comparisons in Maximum-likelihood net efficiency were made: (1) between seagrass types for postlarvae and juvenile *P. esculentus*; (2) between postlarvae and juvenile *P. esculentus*; (3) between high and low tide (i.e. deep and shallow water) for juvenile *P. semisulcatus*; and (4) between juveniles of *P. esculentus* and *P. semisulcatus* in different seagrass types.

RESULTS

Salinity, temperature and seagrass

During the removal experiments mean temperature of the bottom waters ranged from 28.9 (Embley Estuary, low tide) to 30.6°C (North West Reef) and mean salinity from 33.2 (Black Stump Bay) to 36.5‰ (North West Reef) (Table 1). Water depth was less than 1.2 m

Table 1. Summary of environmental and macrophyte data for removal experiments. Values represent means, or means ± 1 SE. Seagrass data for January 1991 in the Embley River were collected in November 1990. Surface area of seagrass is per m^2 of substrate. AGB: above-ground biomass; *Thalassia*: *T. hemprichii*; *Syringodium*: *S. isoetifolium*

Variable	Groote Eylandt		Embley River	
	North West Reef	Black Stump Bay	Low tide	High tide
Date:	Jan 1984	Feb 1984	Jan 1991	Jan 1991
Environment				
Temperature (°C)	30.6	29.4	28.9 ± 0.5	29.3 ± 0.4
Salinity (‰)	36.5 ± 0.04	33.2 ± 0.39	35.3 ± 0.4	35.1 ± 0.5
Mean depth (m)	0.85 ± 0.25	0.95 ± 0.04	0.40 ± 0.08	1.75 ± 0.11
Macrophytes				
Seagrass AGB (g m^{-2})	54.0	204.1	75.5	
Surface area (m^2)	1.63	7.52	2.28	
Shoot density (n m^{-2})	816.6	6357.8	2493.0	
Main species by AGB (%)	*Thalassia* (67.8)	*Syringodium* (73.9)	*Enhalus acoroides* (98.0)	
Algae AGB (g m^{-2})	99.1	37.3	0	

during the studies on postlarvae and 1.0 m for juvenile *Penaeus esculentus* at the Groote Eylandt sites. The mean water depths on the Embley River seagrass bed were about 0.4 at low tide (range = 0.2 to 0.5 m) and 1.8 m at high tide (range = 1.6 to 1.9 m).

The mean above-ground biomass of seagrass ranged from 54 g m^{-2} (*Thalassia hemprichii*) at North West Reef to 204 g m^{-2} (mainly *Syringodium isoetifolium* with some *Cymodocea serrulata*) at Black Stump Bay (Table 1). The density of seagrass shoots at North West Reef was about a third of that at Black Stump Bay and one-eighth of that at the Embley River. At this latter site, *Halodule uninervis*, a small thin seagrass with many shoots, comprised 2% of the above-ground biomass but was found at very high shoot densities. Algae, mainly *Caulerpa microphylla*, were a significant component of the total above-ground biomass of all macrophytes at North West Reef (Table 1).

Carapace lengths and catches from removal experiments

The mean CL for juvenile *Penaeus esculentus* (range of means = 6.7 to 7.5 mm) and *P. semisulcatus* (range = 6.4 to 7.6 mm) were very consistent at the 3 sites and in

Table 2. *Penaeus esculentus* and *P. semisulcatus*. Total numbers of postlarvae (both species combined) and juvenile prawns caught in each sweep of the enclosure by a small beam trawl and total catches for each experiment. NWR: North West Reef; BSB: Black Stump Bay; Embley: Embley River; *Thalassia*: *T. hemprichii*; *Syringodium*: *S. isoetifolium*; *Enhalus*: *E. acoroides*. *Only 3 sweeps conducted

Expt no.	Site, seagrass, tidal state	Date	Sweep 1	2	3	4	5	Total catch
Postlarvae		**1984**						
1	NWR, *Thalassia*	Jan	109	24	8	5	8	154
2	NWR, *Thalassia*	Jan	45	15	7	*	*	67
3	BSB, *Syringodium*	Feb	21	5	2	1	0	29
4	BSB, *Syringodium*	Feb	43	5	3	2	0	53
Juvenile *P. esculentus*		**1984**						
1	NWR, *Thalassia*	Jan	19	9	5	3	0	36
3	BSB, *Syringodium*	Feb	72	16	6	15	6	115
4	BSB, *Syringodium*	Feb	16	11	9	4	1	41
Juvenile *P. semisulcatus*		**1991**						
5	Embley, *Enhalus*, low tide	Jan	50	28	26	1	12	117
6	Embley, *Enhalus*, low tide	Jan	81	59	7	6	3	156
7	Embley, *Enhalus*, low tide	Jan	24	18	3	9	5	59
8	Embley, *Enhalus*, high tide	Jan	16	19	10	7	2	54
9	Embley, *Enhalus*, high tide	Jan	39	15	21	10	8	93

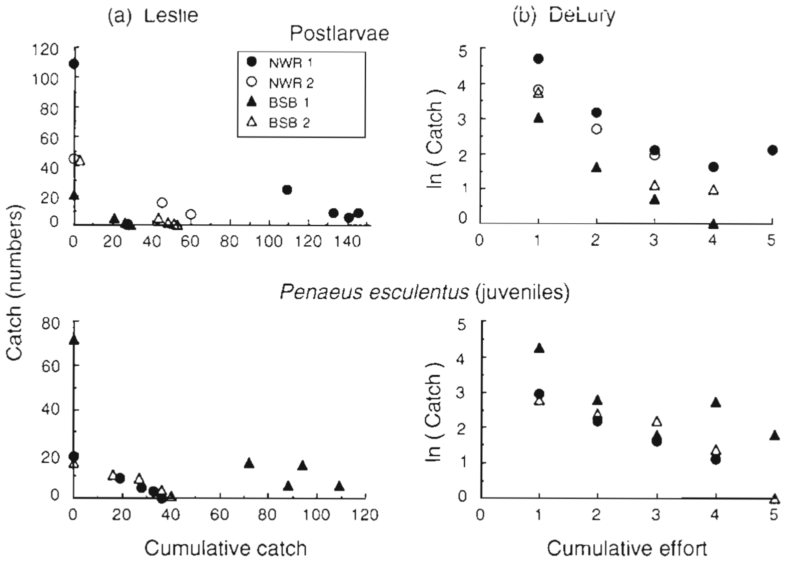

Fig. 1. *Penaeus esculentus* and *P. semisulcatus*. (a) Leslie and (b) DeLury relationships for postlarvae (both species combined), and juvenile *P. esculentus* from removal experiments with a small beam trawl

the different experiments. Most *P. esculentus* (92%) and *P. semisulcatus* (82%) were less than 10 mm in CL.

Only experiments where the total number of individuals exceeded 25 were used in the analysis of the removal experiments (Table 2): 4 experiments met this criterion for postlarvae (of both species combined), 3 for juvenile *Penaeus esculentus* and 5 for juvenile *P. semisulcatus*, all in the Embley River (Table 2). There were no experiments in which 25 juveniles of both tiger prawn species were caught.

Catches of postlarvae in the first sweep of the enclosure ranged from 67 to 81% of the total catch of postlarvae in each experiment, while those of juvenile *Penaeus esculentus* ranged from 39 to 63% of the total catch (Table 2). Catches of juvenile *P. semisulcatus* ranged from 30 to 52% of the total catch in each experiment (Table 2).

Estimates of net efficiency

The regressions used to obtain the parameters to estimate *q* for the Leslie and weighted Leslie models were significant, or close to significant (i.e. $0.05 < p \leq 0.10$) in all cases (Figs. 1 & 2). The first point in some of the Leslie regressions $(0, C_1)$ was well separated from subsequent points, which grouped closely together (Expts 1 and 3; Fig. 1, Table 2). The unweighted Leslie estimates of *q* differed most from the weighted estimates in these cases (Table 3).

In general, the DeLury equation did not fit the data as well as the Leslie equation (Figs. 1 & 2). Thus, not all 12 DeLury regression equations were significant: 7 were significant at $p = 0.05$; 2 at $0.05 < p \leq 0.10$; and 3 were not significant at $p = 0.10$. High standard errors were recorded for the DeLury estimates of *q* for postlarvae in Expts 1 and 4, for *Penaeus esculentus* in Expt 3, and for *P. semisulcatus* in Expts 5 and 7 (Table 3). In these experiments, high proportions of prawns (>60%) were caught in the first 1 or 2 sweeps of the enclosure (Table 2, Figs. 1 & 2).

The estimated efficiencies of the beam trawl calculated by each of the 4 methods (Leslie, weighted Leslie, DeLury and Maximum-likelihood) were always higher for postlarvae than for juvenile *Penaeus esculentus* or juvenile *P. semisulcatus* (Table 3). Estimates of net efficiency for juveniles of *P. esculentus* and those for *P. semisulcatus* at low tide were similar in magnitude and, in all cases except 1 (DeLury, Expt 7), were higher than the estimated efficiencies for *P. semisulcatus* at high tide (Table 3).

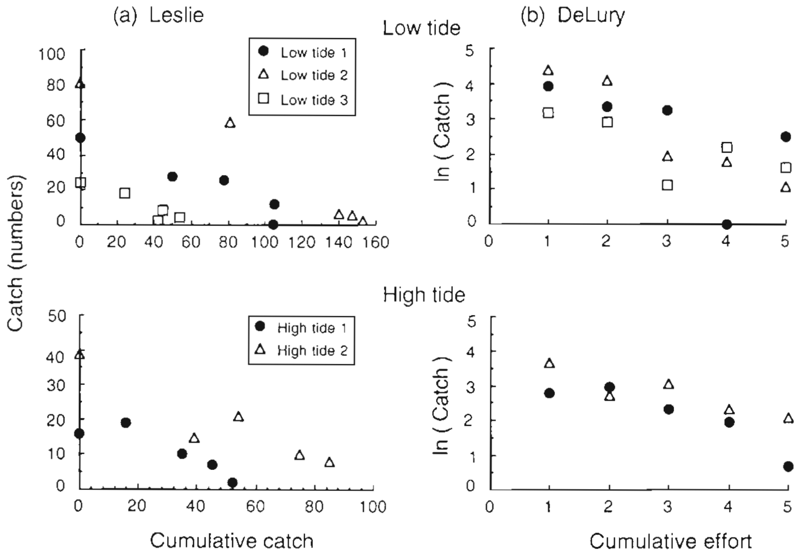

Fig. 2. *Penaeus semisulcatus*. (a) Leslie and (b) DeLury relationships for juvenile prawns from removal experiments with a small beam trawl

Table 3. *Penaeus esculentus* and *P. semisulcatus*. Estimates of the absolute value of the efficiency q (±1 SE) with which a small beam trawl captured tiger prawns in different seagrass beds during removal experiments. NWR: North West Reef; BSB: Black Stump Bay; Embley: Embley River; *Thalassia*: *T hemprichii*; *Syringodium*: *S. isoetifolium*; *Enhalus*: *E. acoroides*

Expt. no.	Site, seagrass, tidal state	Leslie	Weighted Leslie	DeLury	Maximum-likelihood
Postlarvae					
1	NWR, *Thalassia*	0.73 ± 0.04	0.67 ± 0.10	0.51 ± 0.17	0.63 ± 0.04
2	NWR, *Thalassia*	0.64 ± 0.03	0.63 ± 0.04	0.61 ± 0.06	0.66 ± 0.06
3	BSB, *Syringodium*	0.72 ± 0.02	0.70 ± 0.04	0.64 ± 0.08	0.63 ± 0.15
4	BSB, *Syringodium*	0.82 ± 0.04	0.74 ± 0.09	0.64 ± 0.19	0.71 ± 0.29
	Mean	0.73	0.69	0.60	0.66
Juvenile *P. esculentus*					
1	NWR, *Thalassia*	0.51 ± 0.02	0.53 ± 0.05	0.46 ± 0.03	0.51 ± 0.10
3	BSB, *Syringodium*	0.63 ± 0.09	0.49 ± 0.16	0.41 ± 0.19	0.51 ± 0.04
4	BSB, *Syringodium*	0.36 ± 0.04	0.41 ± 0.04	0.49 ± 0.10	0.43 ± 0.07
	Mean	0.50	0.48	0.45	0.49
Juvenile *P. semisulcatus*					
5	Embley, *Enhalus*, low tide	0.40 ± 0.07	0.50 ± 0.13	0.51 ± 0.36	0.40 ± 0.04
6	Embley, *Enhalus*, low tide	0.54 ± 0.08	0.56 ± 0.08	0.59 ± 0.11	0.59 ± 0.03
7	Embley, *Enhalus*, low tide	0.39 ± 0.09	0.37 ± 0.15	0.34 ± 0.20	0.38 ± 0.06
	Mean low tide	0.44	0.48	0.48	0.46
8	Embley, *Enhalus*, high tide	0.29 ± 0.08	0.33 ± 0.07	0.41 ± 0.11	0.36 ± 0.07
9	Embley, *Enhalus*, high tide	0.35 ± 0.08	0.30 ± 0.08	0.30 ± 0.08	0.34 ± 0.05
	Mean high tide	0.32	0.32	0.36	0.35

The Maximum-likelihood net efficiencies (q) for postlarvae and juvenile *Penaeus esculentus* did not differ between the seagrasses at North West Reef and Black Stump Bay (Table 4). The overall mean Maximum-likelihood net efficiency (±95% confidence limits, C.L.) for postlarvae was 0.66 ± 0.16, while that for juvenile *P. esculentus* was 0.49 ± 0.09. While the Maximum-likelihood net efficiency for juvenile *P. semisulcatus* at low tide (0.46 ± 0.05) was significantly higher than that at high tide (0.35 ± 0.08), it did not differ from that for juvenile *P. esculentus* (Table 4). The overall mean net efficiency for juvenile tiger prawns (i.e. both *P. esculentus* and *P. semisulcatus*) in water less than 1.0 m deep (0.47 ± 0.05) was significantly lower than the overall mean for postlarvae (Table 4).

Table 4. *Penaeus esculentus* and *P. semisulcatus*. Mean (±95% confidence limits, C.L.) Maximum-likelihood estimates of net efficiency q, and the results of comparisons between means. NWR: North West Reef; BSB: Black Stump Bay; Embley: Embley River; *Thalassia*: *T hemprichii*; *Syringodium*: *S. isoetifolium*; *Enhalus*: *E. acoroides*; ns: not significant

Comparison	Mean q ± 95% C.L.	Z-value	p
Postlarvae			
NWR, *Thalassia*	0.64 ± 0.07	0.16	ns
BSB, *Syringodium*	0.67 ± 0.32		
Mean	0.66 ± 0.16		
Juvenile *P. esculentus*			
NWR, *Thalassia*	0.52 ± 0.20	0.50	ns
BSB, *Syringodium*	0.47 ± 0.08		
Mean	0.49 ± 0.09		
Juvenile *P. semisulcatus*			
Embley, *Enhalus*, low tide (≤0.5 m)	0.46 ± 0.05	2.20	<0.05
Embley, *Enhalus*, high tide (≥1.6 m)	0.35 ± 0.08		
Juveniles			
P. esculentus, *Thalassia*, and *Syringodium*	0.49 ± 0.09	0.54	ns
P. semisulcatus, *Enhalus*, low tide	0.46 ± 0.05		
Mean (≤1.0 m)	0.47 ± 0.05		
Life stage			
Postlarvae, *Thalassia*, and *Syringodium*	0.66 ± 0.16	6.64	<0.001
Juveniles (both species, ≤1.0 m)	0.47 ± 0.05		

Estimates of initial population size

The Leslie, weighted Leslie and Maximum-likelihood estimates of the initial population size were within 10 prawns of the total catch in all cases, except Expt 5 (*Penaeus semisulcatus* at low tide; Table 5). By contrast, the DeLury estimates were lower than the total catch by 10 or more prawns in 5 experiments (postlarvae, 1 and 4; *P. esculentus*, Expt 3; *P. semisulcatus*,

Table 5. *Penaeus esculentus* and *P. semisulcatus*. Estimates of the initial population size of tiger prawns and the total catch from a small beam trawl during removal experiments. NWR: North West Reef; BSB: Black Stump Bay; Embley: Embley River; *Thalassia*: *T. hemprichii*; *Syringodium*: *S. isoetifolium*; *Enhalus*: *E. acoroides*

Expt no.	Site, seagrass, tidal state	Leslie	Weighted Leslie	DeLury	Maximum-likelihood	Total catch
Postlarvae						
1	NWR, *Thalassia*	148.2	149.9	120.7	155.0	154
2	NWR, *Thalassia*	69.8	70.6	70.3	70.0	67
3	BSB, *Syringodium*	28.8	29.1	27.1	30.0	29
4	BSB, *Syringodium*	51.9	52.7	41.4	54.0	53
Juvenile *P. esculentus*						
1	NWR, *Thalassia*	37.4	36.7	38.9	37.0	36
3	BSB, *Syringodium*	109.0	113.0	99.7	118.0	115
4	BSB, *Syringodium*	46.9	43.4	43.4	43.0	41
Juvenile *P. semisulcatus*						
5	Embley, *Enhalus*, low tide	125.7	108.4	100.3	127.0	117
6	Embley, *Enhalus*, low tide	161.8	157.3	143.7	157.0	156
7	Embley, *Enhalus*, low tide	63.3	60.2	60.7	65.0	41
8	Embley, *Enhalus*, high tide	67.2	60.6	58.7	61.0	54
9	Embley, *Enhalus*, high tide	104.2	109.1	107.4	107.0	93

Expts 5 and 6), and exceeded the total catch by more than 10 prawns for *P. semisulcatus* in Expt 7 (Table 5).

DISCUSSION

Calculating net efficiency

Few estimates of absolute efficiency have been made for the nets that are used to catch fish and crustaceans in inshore marine and estuarine nursery habitats (Allen et al. 1992). In our study, we used removal experiments to estimate the efficiency of a beam trawl for capturing small tiger prawns in 3 of the tropical seagrass communities in the Gulf of Carpentaria, northern Australia. The Maximum-likelihood method of estimating efficiency or catchability (q) from removal experiments is the preferred one because it makes the fewest assumptions, and poses no computational problems when no individuals are caught (Schnute 1983). Although the computation for the Maximum-likelihood method appears to be more complicated than those for the Leslie and DeLury methods, the calculations are readily completed when the maximisation is for only 1 parameter. Our results show that the DeLury estimates of both q and N_0 become unreliable when q is high and the catches decline to low values during an experiment (see also Seber & Le Cren 1967, Ricker 1975). When catches are very high in the first sweep of the net, the unweighted Leslie gives higher estimates of q than the Maximum-likelihood.

Differences in net efficiency between sizes of prawns and types of seagrass

The results from our study provide initial estimates of net efficiency for a beam trawl net in capturing small tiger prawns. The catches of postlarve and juveniles were not sufficient in each experiment to permit direct comparisons between the different size classes or between species. In addition, we were not able to sample the full range of seagrass types in the Gulf of Carpentaria. However, the estimates of efficiency and comparisons of net efficiency show some important trends. The efficiency of the small beam trawl at night differed more between postlarvae (<3 mm CL) and juvenile (≥ 3 mm CL) tiger prawns than between different types of seagrass, which differed greatly in their structure and biomass. Efficiency was higher for the postlarvae of tiger prawns (mean ML = 0.66) than for juvenile *Penaeus esculentus* (0.49) or juvenile *P. semisulcatus* (0.47) in shallow water (≤ 1.0 m deep). The higher net efficiency for postlarvae may be because postlarvae rarely bury in the substrate, even on unvegetated habitats (Kenyon 1993), and they may not move as quickly as juveniles to avoid the net.

In shallow water (≤ 1.0 m deep), net efficiency did not differ significantly between the juveniles (mainly 3 to 10 mm CL individuals) of the 2 species of tiger prawns. The Maximum-likelihood estimates of net efficiency for juvenile *Penaeus esculentus* and juvenile *P. semisulcatus* were higher in shallow (mean $q = 0.47$) than deeper water (1.6 to 1.9 m deep, mean $q = 0.35$). Moreover, the highest Maximum-likelihood estimate of q for juvenile tiger prawns was obtained when the water was only 0.2 m deep. In the field, catches of juvenile tiger prawns are greater at low than at high tide (Vance & Staples 1992, Vance et al. 1994). As juvenile tiger prawns in the laboratory are more active at high than at low tide (Vance 1992), the lower catches and net efficiencies at high tide could result from the prawns being distributed throughout the water column when they are more active. The prawns can also avoid the net in water deeper than 0.5 m by moving above its path, as well as to the side and below it.

Although our estimates of net efficiency were made by repeatedly hand-hauling the beam trawl, estimates from towing the beam trawl from an outboard-powered dingy are likely to be similar, i.e. at low tide, efficiency for capturing postlarvae is likely to be higher than that for juveniles, which in turn would be greater than that for juveniles at high tide. Towing nets by outboard dingy creates more disturbance in the path of the net, particularly in shallow waters, than hand-hauling. However, small tiger prawns move only short distances when disturbed, often to the nearest vegetation (Kenyon 1993). Thus, the efficiency of outboard-towed beam trawls may be close to that of a hand-hauled net.

Different species of prawns respond to light in varying degrees and, as a consequence, the proportion of the population that is buried during the day and night varies between species (Penn 1984, Wassenberg & Hill 1994). The response of prawns to light and their degree of nocturnal activity has important implications for the proportion of prawns that will be caught by a net during the day. The daytime efficiency of a small beam trawl for capturing brown shrimp *Penaeus aztecus* was estimated at 23%, based on comparisons of catches in a beam trawl and drop trap of known efficiency (Zimmerman et al. 1984). Since the catch rates of juvenile tiger prawns during the day, when the prawns are more often buried, are about half those at night (N. R. Loneragan, CSIRO Division of Fisheries, unpubl. data), the daytime efficiency of our net may also be about 25%.

Our results for *Penaeus semisulcatus* show that the efficiency of the net can vary in adjacent areas of the same seagrass bed on consecutive nights (range for Maximum-likelihood q at low tide = 0.38 to 0.59). The net efficiency of a commercial otter trawl for large western king prawns *P. latisulcatus* ranged from 31 to 53% in 2 experiments on adjacent sandy areas (Joll & Penn 1990). This variation in efficiency was thought to be due to variation in the amount of light reaching the substrate between the 2 experiments. Experimental studies have shown that large *P. latisulcatus* respond more strongly to light than large tiger prawns (Wassenberg & Hill 1994). The net efficiency for juvenile tiger prawns is therefore likely to be less sensitive to changes in light than that for king prawns.

Because of the small range of water temperatures in our study, the changes in net efficiency are not likely to be due to differences in water temperature. However, in subtropical and temperate regions, net efficiency could vary greatly with temperature. Prawns spend more time buried and are less active at lower (particularly <18°C) than higher temperatures (Hill 1985). The efficiency of seine nets for capturing some species of fish also varies with temperature (Allen et al. 1992).

The relative net efficiency of both small and large beam trawls can vary markedly between different species of fish and crustaceans (Warburton 1989, McNeill & Bell 1992). A large beam trawl net (3 m in width) was more efficient at capturing juvenile *Penaeus esculentus* than several other species of crustaceans and fish (Warburton 1989), possibly because juvenile *P. esculentus* tend to stay in the seagrass, particularly when disturbed.

Approaches to estimating net efficiency

Our experiments suggest that if beam trawl catches of tiger prawns are standardised by the depth of sampling, comparisons can be made between catch rates in different types of seagrass. The strategy we used for estimating efficiency could not, however, be used to estimate net efficiency in deep water. Our estimates of net efficiency need to be confirmed by using different methods and net efficiency should also be estimated in different seagrass communities. In addition to the type of removal experiments we used, net efficiency has been estimated by: (1) comparing catch rates between 2 methods — one with known efficiency (Zimmerman et al. 1984); (2) removal experiments with marked individuals (Ricker 1975); and (3) removal experiments in which all remaining individuals are collected at the end of an experiment by using a toxicant, such as rotenone (Allen et al. 1992). Unfortunately, postlarvae and early juvenile stages of tiger prawns are too small to be tagged and apparently, they are not affected by rotenone. The suggestion that artificial seagrass beds could be seeded with individuals to provide alternative estimates of the efficiency of beam trawls warrants investigation (McNeill & Bell 1992).

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Appendix. The notations and equations used to calculate net efficiency

N_0	Initial population size before trawling
N_i	Expected number in the population remaining after the ith sweep of the enclosure
q	Proportion of the population caught during each sweep
C_i	Expected catch during the ith sweep
T_i	$\sum_{j=1}^{i} C_j$, the sum of the expected catches including the ith sweep
k	Total number of sweeps of the enclosure

In this study we are mainly interested in estimating the catch efficiency (q), and secondarily in estimating the initial population size (N_0), where:

$$N_i = N_{i-1} - C_i \quad \text{and} \quad C_i = q\,N_{i-1};\ i = 1, 2, \ldots, 5$$

In the equations below, a variable with a ^ indicates that it is an observed variable, or that it has been estimated from the observed data.

Leslie's method
Clearly:

$$C_i = q(N_0 - T_{i-1}),$$

where T_0 is defined to be 0 and the first regression point is therefore $(0, C_1)$. The regression equation can now be written in the form of $y = a + bx$, with $a = q\,N_0$ and $b = -q$. The estimates of q and N_0 are therefore: $(\hat{q}) = -\hat{b}$ and $\hat{N}_0 = -\hat{a}/\hat{b}$.

The estimate of q is unbiased as the expectation of $\hat{q} = q$.

DeLury's method
Simple algebra leads to:

$$C_i = q(1-q)^{i-1} N_0$$

Using natural logarithms, we derive:

$$\ln C_i = i \ln(1-q) + \ln[q\,N_0/(1-q)].$$

This regression function can then be written in the form of $y = a + bx$, with

$$a = \ln[qN_0/(1-q)] \text{ and } b = \ln(1-q).$$

The estimates of (q, N_0) are therefore

$$\hat{q} = 1 - e^{\hat{b}},\ \hat{N}_0 = e^{\hat{a}+\hat{b}}/(1-e^{\hat{b}})$$

The underlying model is that $\ln \hat{C}_i$ has an error term with a normal distribution $N(0, \sigma^2)$. However, $1 - e^{\hat{b}}$ is not an unbiased estimate of $q = 1 - e^{b}$ and the corrected estimate of q to the first order is given by:

$$\hat{q}_c = 1 - e^{\hat{b}}(1 - r_\alpha^2/2),$$

where r_α is the standard error of $\hat{b}$ (see Lindley 1965, p. 134–136).

Maximum-likelihood method
If k sweeps of the enclosure are made, the maximum-likelihood estimate of q is given by:

$$\hat{q}_c = \hat{T}_k/(k\,\hat{N}_0 - \sum_{i=1}^{k-1} T_i).$$

Therefore, maximising the likelihood can be made with respect to 1 parameter (N_0). The estimate of q can be obtained after $\hat{N}_0$ is found.

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