

## Comparison of an enclosure drop trap and a visual diving census technique to estimate fish populations in eelgrass habitats

I. C. Bobsien and H. Brendelberger

Department of Limnology, Institute of Zoology, Christian-Albrechts-University, Kiel, Germany

### Abstract

In shallow vegetated aquatic habitats exceeding 2 m depth, conventional methods to determine fish abundances are of limited success. In this study, the sampling qualities of 2 methods for investigating the fish community associated with the eelgrass *Zostera marina* were tested: a newly developed enclosure drop trap (ET) operated from the water surface and a visual diving strip transect technique. The construction and the sampling procedure of the enclosure trap are described in detail. Both sampling procedures were performed simultaneously at the same eelgrass sampling site at depths between 2 and 5 m. The comparison revealed deficiencies in relative catch efficiency for both methods. Limitations with respect to bottom-dwelling forms are obvious for the ET and with respect to the Syngnathidae and Gasterosteidae for the visual diving census. Abundance estimates of pelagic, schooling species were highly variable with both methods. Correction coefficients for the different behavioral categories of eelgrass fish were calculated. The fish species composition showed good agreement between the 2 methods, but the number of species on each sampling occasion was consistently higher in the ET catches. The length class frequency distributions estimated by the divers corresponded approximately with direct measurements of fish from the ET catches. The methods complemented one another and can be recommended for simultaneous deployment to get accurate quantitative estimates of eelgrass fish populations. The relative capture efficiency of the enclosure trap can be incorporated to improve abundance measurements of small fish in *Zostera marina* beds without the help of divers.

### Introduction

The seagrass beds of shallow water ecosystems are important habitats because of their trophic and nursery functions for many fish and crustaceans throughout the world (Watson et al. 1993; Murphy et al. 2000). These functions also mean that they are considered of paramount economic value (Costanza et al. 1997). At the same time, however, most seagrass beds are threatened by aspects of coastal environmental degradation. Short and Wyllie-Echeverria (1996) reported reduced water clarity and related factors caused by increasing anthropogenic inputs as the most serious cause of seagrass habitat loss worldwide. The factors related to water clarity

included nutrient loading, eutrophication, water quality, pollution, and turbidity. Scientific research may provide the impetus for the protection, restoration, and conservation of these diverse communities and resources. In this context, reliable quantitative methods to determine fish and macroinvertebrate abundances in submerged aquatic vegetation are of special importance.

Eelgrass beds in the Baltic Sea typically occur at depths of 1 to 6 meters (Boström et al. 2003). In these shallow areas conventional quantitative methods to determine fish abundances are of limited success. Passive collection devices such as gill nets are unsuitable for quantitative sampling because the catches cannot be clearly related to a distinct area and time, although they are useful for collecting qualitative information about fish communities (Edgar and Shaw 1995) or to document the migration of larger fishes (Sogard et al. 1989).

Traditionally, seagrass community studies employ seines and trawls for sampling small epibenthic animals in coastal waters down to 10 and 20 m depth, respectively. Trawls and seines provide a rapid assessment of large areas and comparable data for a broad range of conditions and habitats. But they are also known for their high operating cost, lack of replicability, and destructive effect on vegetated habitats (Edgar et al.

### Acknowledgments

This research was funded by the environmental foundation Deutsche Bundesstiftung Umwelt (DBU). We would like to thank Thomas Walter and Michael Bachmann for assembling the enclosure trap and Uwe Küchler (Rolladen-Küchler Company, Kiel) for putting two roller shutters at our disposal. We also thank Klaus Kreyelkamp for developing an accurate scale drawing of the enclosure trap, Björn Thoma and Michael Teßmann for help with the underwater diving census, and Kerstin Maczassek for collecting and analyzing eelgrass samples. Eileen J. Cox kindly helped to improve the English.

2001). Further drawbacks are the difficulties in assessing defined sampling areas and the low, variable catch efficiencies, depending on species, fish behavior, fish size, macrophyte biomass, bottom type, trawl size, mesh size, net clogging, and towing speed (Kjelson and Johnson 1978; Parsley et al. 1989; Pierce et al. 1990; Wennhage et al. 1997).

Traps that rapidly enclose a clearly defined area have been increasingly used to sample fish populations in shallow-water habitats because they are a precise and accurate means to obtain quantitative estimates of fish assemblage abundance and biomass in vegetated habitats (Kushlan 1981; Jacobsen and Kushlan 1987; Jordan et al. 1997). The absolute efficiency of drop traps can be estimated in shallow block net separated areas with known fish densities (Kushlan 1981; Jordan et al. 1997), and they have often been used to estimate the relative efficiency of seines and trawls (Freeman et al. 1984; Dewey et al. 1989; Wennhage et al. 1997).

Enclosure traps, including drop-traps (Kahl 1963; Kushlan 1974; Gilmore et al. 1978; Pihl and Rosenberg 1982; Pihl Baden and Pihl 1984; Nellbring 1985), drop-nets (Hellier 1958; Mosely and Copeland 1969; Kjelson et al. 1975; Adams 1976), buoyant pop-nets (Larson et al. 1986; Serafy et al. 1988; Dewey et al. 1989; Connolly 1994), lift-nets (Higer and Kolipinski 1967; Rozas 1992), and throw-traps (Kushlan 1981; Jacobsen and Kushlan 1987; Chick et al. 1992; Jordan et al. 1997), provide instantaneous samples and are considered to be the most efficient sampling devices for small fishes and invertebrates in shallow-water habitats less than 1.5 m deep (Kushlan 1981; Jordan et al. 1997). But only a few complex and labor-intensive buoyant drop- and pop-nets with floating frames are usable at depths of 2 to 5 m (Mosely and Copeland 1969; Larson et al. 1986; Serafy et al. 1988). The major disadvantages of these systems are the need for divers to set or to clear the traps, the additional bottom structure (pop-nets) that can attract or repel organisms, and the long equilibration time (hours to a day) after setting.

Other techniques, such as the visual diving census (VDC), provide a powerful tool to estimate fish abundance. The diving census method was first described by Brock (1954) and has been applied especially for coral reefs. Subsequently, the VDC has been used under a wide range of environmental conditions to investigate the fish fauna of the Baltic Sea, including submerged vegetation (Jansson et al. 1985; Thetmeyer 1998). VDC has also been applied in Mediterranean seagrass beds (*Posidonia oceanica*) compared to trawling, and biases associated with these techniques are well documented (Brock 1982; Harmelin-Vivien and Francour 1992; Edgar et al. 2004). VDC is considered to be an accurate technique and is widely accepted for estimating fish abundances under clear water conditions in different habitat types. The success of this method depends on the experience of the divers; rapid and accurate determination of the fish species encountered is necessary. Experience is even more critical in seagrass beds where most resident fishes are rather small, camouflaged, and many show cryptic behavior.

The aim of the present study was to design a quantitative collection technique that adequately reflects the abundances of small fish in temperate eelgrass beds. For this purpose, we constructed a portable enclosure drop-trap (ET) that operates without the help of divers.

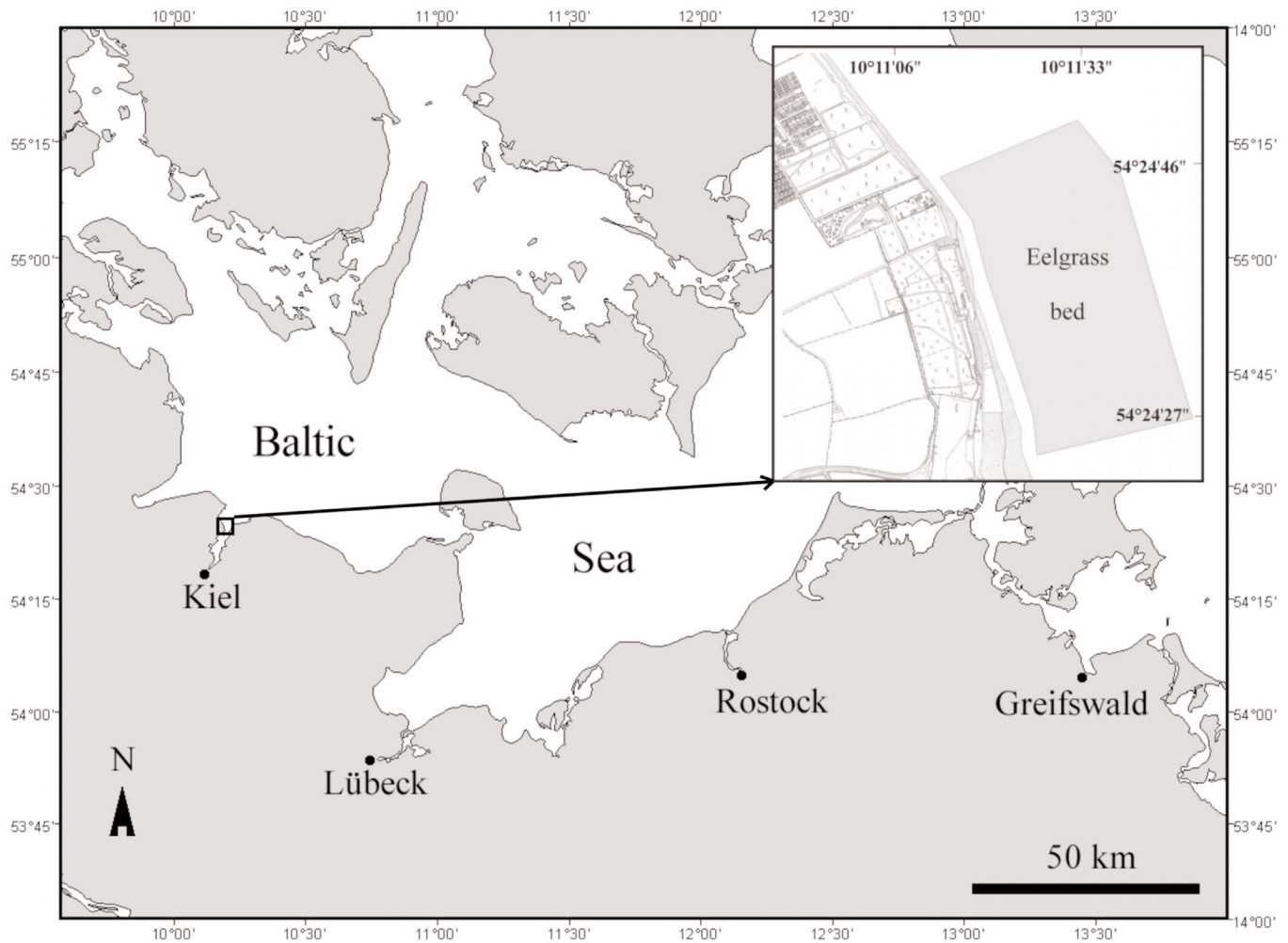
Information about gear catch efficiency is important for adjusting catch data and providing more accurate estimates of fish abundances. We therefore quantified the catch efficiencies of the ET relative to estimates obtained by the VDC technique. Correction coefficients for typical seagrass-dwelling fishes of five different behavioral categories (guilds) were calculated by comparing animal abundance supplied by the two methods. Further species richness, diversity, and size composition were compared. Additionally, the abundance of the dominant shore crab (*Carcinus maenas* Linnaeus, 1785) was recorded. Abundance estimates by 2 divers were compared to correct for personal bias.

### Materials and procedures

*Area investigated and environmental conditions*—The comparative study was carried out in a monotypic eelgrass meadow (*Zostera marina* Linnaeus, 1758) on the northwest coast of the outer Kiel Fjord in the Baltic Sea, Germany (Figure 1).

The eelgrass bed extended over 23 ha in depths of 2 to 5 m and was interrupted by small, unvegetated, sandy patches. The study site was exposed to wind and waves, with sediment conditions ranging from coarse (< 3 m depth) to fine sand or muddy silt (> 3 m depth), lacking big stones. The structural components of the eelgrass meadow were investigated by divers on 16 August, 25 September, and 27 October 2003 (Table 1). Fish census and ET catches were carried out simultaneously on 21 August, 25 September, and 27 October 2003 between 9 am and 7 pm.

*Description of the sampling methods*—**Enclosure trap.** Square-profiled (12 × 12 mm, 1.2 mm thick) aluminum bars were welded together to form a frame (Figure 2D; 2.0 × 1.0 × 0.6 m) with stabilizing elements (Figure 2C and L) and a sealable, 2-part lid (Figure 2A). Frame and lid were built with open-end bars, allowing air to escape from the cavities during sampling procedures. The lid, attached with hinges to the frame, is kept sealed using elastic bands with hooks, facilitating a quick closing and opening of the trap. Knotless white nylon net material (Figure 2B), 6 mm mesh size, covers the frame and lid. The underside is free of netting. The bottom edge is bordered by an aluminum flange (Figure 2H, 100 mm high, 2 mm thick). An adjustable-length steel pin (Figure 2G) is located at each bottom corner to prevent the ET from sliding over the ground during the closing procedure. By pulling the shutter ropes (Figure 2F), the roller shutter (Figure 2K), led by a guide rail (Figure 2E), unwinds and closes the underside of the ET. The roller shutter (Figure 2K) consists of a shaft (Figure 2I) with a strap roll (Figure 2M) to wind up the roller shutter segments. It was purchased as unit (Rolladen-Küchler Company Kiel, Germany), including the shaft with strap roll, the roller shutter segments, the covering, and the guide rails. During sampling the ET is suspended with



**Fig. 1.** Study area showing the location of the eelgrass bed in the outer Kiel Fjord.

4 ropes from a buoy (lift, 20 kp), and it is balanced horizontally in the water column using 4-kg lead weights (Figure 2J). The total weight of the enclosure trap is 36 kg. A remote trigger mechanism on a release rope frees the trap from the buoy, and the ET descends to the bottom at approximately  $1.5 \text{ m s}^{-1}$ . The enclosed area is  $2 \text{ m}^2$ .

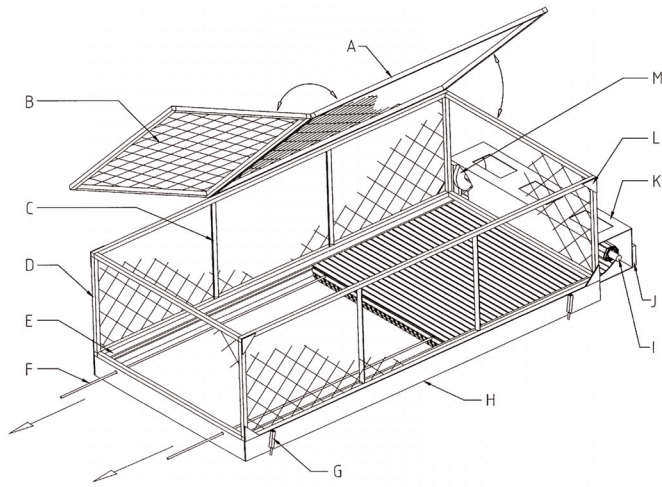
**Sampling procedure.** Sampling requires a small boat (4 m) or flat-bottomed punt with an outboard engine and 2 operators. The ET is aligned perpendicularly to the side of the boat so that 1 person can operate each side of the trap. Once the boat is positioned over the sampling ground, the ET is carefully pushed into the water. It then hangs below the buoy and is balanced horizontally in the water column. Equilibration time after pushing the ET into the water is 1 to 3 min depending on wind and wave action while the boat and ET drift in the water. The release rope is pulled when the boat has drifted 10 to 15 m away from the ET, minimizing disturbance by the boat. The lowered drop trap then encloses a  $2\text{-m}^2$  area including eelgrass and its associated fauna. When the shutter rope is pulled, the

roller shutter closes the underside 10 cm above the sediment. The shutter rope (20 m) allows closure without lifting the ET from the bottom. In preliminary tests divers did not observe any lift or tilt of the ET during the closure procedure. It was not necessary to clip weights onto the shutter rope to ensure its horizontal alignment. During the closure, flexible rubber lips

**Table 1.** Structural characteristics of the *Zostera marina* meadow sampled.

Eelgrass structure	n	Sampling date 2003		
		16 Aug	25 Sept	27 Oct
Shoot density, per $\text{m}^2$	30	$381 \pm 95$	$315 \pm 113$	$293 \pm 97$
Shoot length, mm	100	$490 \pm 183$	$474 \pm 145$	$500 \pm 139$
Leaf area, $\text{dm}^2 \text{ m}^{-2}$	100	$42 \pm 23$	$48 \pm 31$	$34 \pm 19$
Above-ground biomass, $\text{g m}^{-2}$	30	$98 \pm 72$	$109 \pm 69$	$68 \pm 48$
Below-ground biomass, $\text{g m}^{-2}$	30	$154 \pm 92$	$131 \pm 64$	$75 \pm 75$

Biomass values are given as dry mass per unit area. Values are arithmetical means  $\pm$  SD; n = number of replicates sampled.



**Fig. 2.** Aluminum enclosure drop trap for sampling small epibenthos in eelgrass beds. Double-headed arrows demonstrate the function of the divided lid. White-headed arrows indicate the pull direction of the shutter rope to close the trap. See text for further explanations.

(50 × 30 × 3 mm) brush across the sediment, depressing the macrophytes, disturbing the demersal fauna and thus guiding animals into the trap. The rubber lips, manufactured of fiber-reinforced nitril-butyl rubber mats and fixed to the first roller shutter segment, are aligned at right angles to the sediment, blocking the space between the sliding door and the sediment. While the ET closes, the rubber lips are slightly deflected across the depressed eelgrass plants. Irregularities in the seabed, such as small stones (< 50 mm in height) draw the lips aside, after which they swing back to their former positions, not allowing fish to escape easily. Minor depressions in the seabed allow the lips to straighten and thereby also sweep the ground. Major depressions are insufficiently cleared. The closed ET is then lifted up and pulled into the boat. The lid allows quick and easy removal of all organisms and debris. The roller shutter must then be rewound to prepare the ET for further sampling. In previous tests the capture procedure, especially the descent behavior and the closure, was monitored by 2 divers. The well-balanced ET was never observed to hit the ground at an angle or to roll over. The sliding door mechanism runs smoothly and worked perfectly in unvegetated areas (sandy ground) as well as in heavily vegetated *Z. marina* beds. The capture qualities of the ET were tested to a maximum depth of 5 m and to maximum eelgrass densities of approximately 600 shoots m<sup>-2</sup>.

Subsequently, the ET has successfully completed more than 1000 drops without any damage to its construction. Material costs amount to approximately US \$800, including US \$360 for the roller shutter (US \$180 per m<sup>2</sup>) and US \$440 for remaining material costs. It took 35 hours to assemble the first prototype of the ET.

During the comparative study described here, a total of 90 drops were performed, which correspond to 180 m<sup>2</sup> of eelgrass

area. Five trap drops were pooled to give blocks of 10 m<sup>2</sup>. Animal abundances were compared with abundances within 10 m<sup>2</sup> transect segments inspected by divers (see below). Catch efficiencies were also calculated from these 10-m<sup>2</sup> block samples. The fish caught with the trap were anesthetized with benzocaine (ethyl 4-aminobenzoate) and immediately preserved in 96% ethanol. They were counted, identified to species level, and measured to the nearest millimeter. Size frequency distributions of directly measured fish were compared with size estimates obtained by the divers.

**Visual diving census.** The underwater visual census technique was carried out in accordance with the diving census procedure described by Jansson et al. (1985). On each sampling occasion, a lead-weighted 60-m transect line, marked in meter increments and subdivided into 10-m transect segments, was set across the sampling area in 2 to 5 m of water. Both ends of each line were fixed to the bottom with 5-kg lead weights, and additional line segments passed to surface marker buoys. Two experienced census divers swam slowly and quietly on both sides of the line counting, identifying, and recording all fishes and the shore crabs within a strip of 0.5 m on both sides of the line and within the water column above. (Previous investigations had shown that inspection fields greater than 0.5 m markedly increased the probability of double counting.) Hidden fish were found by carefully parting the vegetation and turning shells and stones. Most fish species were measured against a centimeter ruler. The duration of the diving census varied between 3 and 4 hours for a 60-m<sup>2</sup> eelgrass area. Abundance and size-structure were noted on a white plastic sheet, 0.5 m in length, which was used as both a notepad and reference width for the inspected transect. The 10-m transect segments were assumed to be independent of each other within each 60-m block. To compare abundances and catch efficiency, the 10-m transect segments (10 m<sup>2</sup> eelgrass area) were compared to 5 sampling blocks of the ET. The diving census began at least 45 min after the deployment of the transect lines. All counting and measuring was undertaken by the same 2 divers. Statistical comparisons of the different counts were performed for total fish and shore crab abundances to detect any personal bias.

**Behavioral and microhabitat categories**—Five categories (A through E) were chosen to characterize the microhabitat preference and reflect the feeding mode and behavior of dominant species in the eelgrass meadows of the western Baltic Sea. The classification was developed from personal observations and gut content analysis: (A) fast-moving planktivorous fish feeding above the canopy and sheltering below it; (B) slower-moving fish living under the leaf canopy; (C) faster-moving fish living under the leaf canopy; (D) fish living on the sediment; and (E) shore crab living on and hiding in the sediment.

**Quantitative comparison**—The catch efficiency of the ET was determined relative to the VDC technique according to a method described by Salthaug (2002). The catch efficiency (*r*) of one sampling method relative to another can be estimated

**Table 2.** Number (*N*) in decreasing order, proportion, and range of total length (TL) of species detected by ET and VDC technique in a *Z. marina* eelgrass bed during August, September, and October 2003.

Behavioral category	Family	Species	Method	<i>N</i>	%	TL, mm
	Teleostei					
A	Gobiidae	<i>Gobiusculus flavescens</i>	ET/VDC	565	44.2	15-36
D		<i>Pomatoschistus minutus</i>	ET/VDC	367	28.7	20-84
		<i>Gobius niger</i>				
B	Syngnathidae	<i>Nerophis ophidion</i>	ET/VDC	174	13.6	103-256
C	Gasterosteidae	<i>Spinachia spinachia</i>	ET/VDC	71	5.5	63-140
C		<i>Gasterosteus aculeatus</i>	ET/VDC	47	3.7	20-75
B	Syngnathidae	<i>Syngnathus typhle</i>	ET/VDC	32	2.5	42-237
D	Zoarcidae	<i>Zoarces viviparus</i>	ET/VDC	10	0.8	120-300
B	Syngnathidae	<i>Syngnathus rostellatus</i>	ET	4	0.3	100-113
D	Cottidae	<i>Taurulus bubalis</i>	ET/VDC	3	0.2	37-43
D		<i>Myoxocephalus scorpio</i>	VDC	2	0.2	113-127
C	Labridae	<i>Ctenolabrus rupestris</i>	ET/VDC	2	0.2	47-51
D	Gadidae	<i>Gadus morhua</i>	VDC	1	0.1	120
	Sum			1278	100.0	15-300
	Decapoda					
E	Portunidae	<i>Carcinus maenas</i>	ET/VDC	371	—	carapace length > 20 mm

*Pomatoschistus minutus* and *Gobius niger* were combined due to uncertain discrimination in the visual diving census.

by taking the abundance ratio between the methods when they are sampling on the same density of organisms under comparable conditions:

$$r = N_{ET} N_{VDC}^{-1} \quad \text{for } N > 0 \quad (1)$$

where  $N_{ET}$  is the species abundance estimated by enclosure trap and  $N_{VDC}$  the abundance estimated by VDC. To ensure as equal a density of organisms as possible, the ET sampling and VDC were conducted simultaneously in the same place. The median of the relative catch efficiency ( $r$  values) was used as an estimator.  $x$  values were calculated and plotted on frequency graphs to show outliers and variability of the comparative study. To eliminate the problem of asymmetry, the  $r$  values between 0 and 1 were adjusted by transformation to the same scale as values above 1. A useful transformation is given in Salthaug (2002):

$$\begin{aligned} x_1 &= r - 1 && \text{for } r \geq 1 \\ x_2 &= -(r^{-1}) + 1 && \text{for } r < 1 \end{aligned} \quad (2)$$

where  $x$  values corresponding to  $r$  values below 1 become negative. Values of 0 indicated no differences in catch efficiency between the sampling methods.

The fish diversity reflected by the 2 methods was quantified by the Shannon-Weaver index ( $H'$ ). The Shannon-Weaver index of diversity (Krebs 1999) was calculated from

$$H' = -\sum_{i=1}^S (p_i) (\log_e p_i) \quad (3)$$

where  $S$  is the number of species in the sample and  $p_i$  the proportion of the  $i$ th species. The species number (richness) was also recorded.

**Schooling behavior**—Some fish species aggregate in large schools within eelgrass meadows, and density estimates from diving census or ET sampling may deviate substantially from the true density, depending on the presence or absence of a school along the transect or in the drop area of the ET. For this reason, these species were sometimes excluded from the analysis (see below).

**Statistical analysis**—The total fish abundances and abundances for the shore crab, *C. maenas*, obtained by each method and pooled over the sampling period were compared with sign test to detect differences in sampling efficiency (Salthaug 2002). Total fish abundances were compared, including and excluding the two-spotted goby (*G. flavescens*), which exhibited major fluctuations in catches due to its swarming behavior. The sign test was also applied to the different behavioral groups established for the eelgrass fish community. Differences in total fish abundances between sampling dates and sampling methods were analyzed by Kruskal-Wallis test. The Wilcoxon signed rank test was used to evaluate differences in abundance estimates between the 2 divers performing the VDC.

### Assessment

**Fish community and species richness**—A total of 1278 fish individuals were counted, 548 with the ET and 730 with the diving census. Thirteen fish species from 7 families were recorded by the combination of the 2 methods. The size spec-

**Table 3.** Comparison of species composition, numbers of fish, and shore crabs as well as richness and diversity detected with enclosure trap (ET) and visual diving census (VDC) during comparative sampling of 60-m<sup>2</sup> eelgrass bed in 2003.

Species	21 Aug		25 Sept		27 Oct		Sum	
	ET	VDC	ET	VDC	ET	VDC	ET	VDC
<i>N. ophidion</i>	23	4	40	0	84	23	147	27
<i>S. rostellatus</i>	1	0	2	0	1	0	4	0
<i>S. typhle</i>	9	0	17	0	4	2	30	2
<i>G. niger/P. minutus</i>	37	168	34	104	7	17	78	289
<i>G. flavescens</i>	18	8	150	357	33	0	201	365
<i>G. aculeatus</i>	33	0	12	1	0	0	45	1
<i>S. spinachia</i>	12	4	12	12	11	20	35	36
<i>T. bubalis</i>	1	0	0	2	0	0	1	2
<i>M. scorpio</i>	0	0	0	0	0	2	0	2
<i>Z. viviparus</i>	4	2	2	2	0	0	6	4
<i>G. morhua</i>	0	0	0	1	0	0	0	1
<i>C. rupestris</i>	0	1	1	0	0	0	1	1
Sum	138	187	270	479	140	64	548	730
Richness	9	6	9	7	6	5	10	11
Diversity	1.82	0.47	1.41	0.71	1.13	1.30	1.65	1.09
<i>C. maenas</i>	56	77	28	96	15	99	99	272

*P. minutus* and *G. niger* were combined due to uncertain discrimination during the visual diving census.

trum of the fish ranged from 15 to 300 mm (Table 2). The relative frequencies of species determined with both methods differed considerably. The rank order obtained by the combination of the 2 methods indicated that the Gobiidae were the most frequent species, followed by *Nerophis ophidion* (Syngnathidae) and the Gasterosteidae, namely *Spinachia spinachia* and *Gasteosteus aculeatus* (Table 2).

The semipelagic two-spotted goby, *G. flavescens*, was by far the most common species, by both VDC and ET. The VDC method recorded the demersal gobies, *G. niger* and *P. minutus*, as the second most frequent species, whereas the straight-nosed pipefish, *N. ophidion*, was the second most frequent species determined with the ET (Table 3).

Only minor differences in species composition were seen between the methods. *M. scorpio* and *G. morhua* were detected only by the diving census method, whereas *S. rostellatus* was exclusively detected with the ET. The portunid crab, *C. maenas*, was also very common in the eelgrass meadow but was underrepresented in the ET catches (Table 3). The number of species and their abundances varied greatly with sampling date and method. In September, the divers found high numbers of swarming two-spotted gobies (*G. flavescens*) feeding above the transects. In August and October, no such aggregations were observed and thus only some or no *G. flavescens* were found. On each sampling occasion the species richness recorded with the ET was consistently higher than with the VDC counts, but the divers recorded a total of 11 fish species compared to 10 by the ET method (Table 3). If the total number of species recorded by the 2 methods ( $S = 13$ ) is assumed to be the closest approximation to the actual species number, an average of

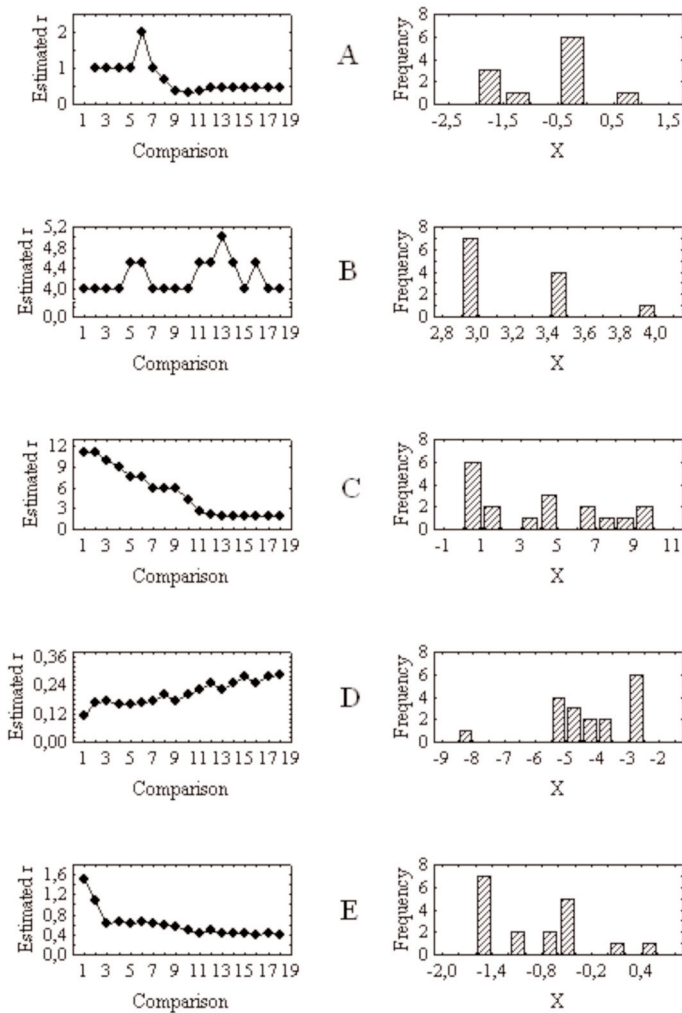
69% (August and September) and 46% (October) of the species richness was captured with the ET and only 54% (August and September) and 38% (October) by VDC.

**Diversity**—The Shannon-Weaver diversity index calculated for both methods showed divergent trends over the sampling period, with increasing values for the VDC and decreasing values for the ET. In August and September, ET catch diversity exceeded that established by the diving census, but in October this trend was reversed (Table 3). These differences could be related to the relatively low species richness but high numbers of *G. flavescens* and demersal gobies detected by the divers, affecting evenness and thereby diversity. Total species richness decreased in October, as detected by both methods, but the ET diversity index was lower (Table 3). This was not explained by richness but by the relatively high abundances of *N. ophidion* and *G. flavescens* captured by the ET, affecting evenness. The ET appears to reflect the biological diversity and species richness much more accurately than the VDC.

**Abundance**—Significant differences in total fish abundances obtained by the 2 methods occurred only in October [ $H_{(1,n=12)} = 7.99$ ;  $P = 0.005$ ], where the ET catch characteristics were superior to the VDC technique. Both the ET [ $H_{(2,n=18)} = 8.67$ ;  $P = 0.01$ ] and the VDC [ $H_{(2,n=18)} = 15.19$ ;  $P = 0.005$ ] detected significant difference in fish abundance between the sampling occasions.

Mean total numbers and total fish abundances determined with the ET were lower than values obtained by the VDC method, but the efficiency values were not significantly different, independent of the presence of *G. flavescens* (Tables 4 and 5).

The statistical analysis revealed the selective features of the 2 methods based on the behavioral classifications and



**Fig. 3.** Frequency graphs of the  $x$  values and estimated relative catch efficiency ( $r$ ) for the chronologically increasing number of comparisons made between ET and VDC. Results are shown for behavioral classifications and microhabitat preferences: *G. flavescens* (A), Syngnathidae (B), Gasterosteidae (C), bottom-dwelling Gobiidae (D), and portunid crab *C. maenas* (E). Note that the scales differ.

microhabitat categories of the fish. These results should be used to improve the abundance estimates derived from both methods.

**Relative catch efficiency—*G. flavescens*.** For the shoaling two-spotted goby, *G. flavescens* (category A), no significant differences in the relative catch efficiency were found, but relative efficiency values indicated restricted catch characteristics for ET (Table 5). The estimated efficiency values declined slightly during the experiment but remained stable after 9 simultaneous comparisons. Frequency graphs of the  $x$  values showed minor positive and negative variations (zero indicated no differences in efficiency), but several negative values misalign the weighting toward negative  $x$  values (Figure 3A). To

obtain improved abundance estimates for *G. flavescens*, the catches made by the ET should be multiplied by 1.6.

**Syngnathidae.** As expected, the Syngnathidae (category B) were detected with high relative efficiency by the ET, significantly higher than the diving census (Table 5). All median efficiency values ranged between 4 and 5, indicating the severe limitations of the VDC method for phytomimetic and well-camouflaged fish hiding motionless in dense vegetation, escaping the attention of the divers. Variation in the frequency graph is low and limited to values between 3 and 4 (Figure 3B). The abundance estimates obtained by a diving census should be corrected by multiplying abundance values for Syngnathidae by a factor of 4.0.

**Gasterosteidae.** The Gasterosteidae (category C) are composed of the fifteen-spined stickleback, *S. spinachia*, and the three-spined stickleback, *G. aculeatus*. *Spinachia spinachia* was recorded in similar total abundances by both methods. Significant differences in relative catch efficiency (Table 5), however, were attributed to *G. aculeatus*, which seems to avoid the divers and thus is rarely detected. During the sampling period from August to October, the ET abundances decreased, whereas the diving census abundances increased (Table 3). These contrasting trends with decreasing differences in abundance estimates during the study period led to consistently decreasing efficiency values. Variations of  $x$  values in the frequency graphs indicate the better detection characteristics of the ET (Figure 3C). VDC abundance estimates for the three-spined stickleback in eelgrass beds should be corrected by a factor of 1.8.

**Bottom dwellers.** The comparison revealed the serious limitations of the ET for estimating bottom-dwelling fish (category D). Significant differences in relative detection efficiency between the methods were discovered for the demersal Gobiidae, represented by *P. minutus* and *G. niger*, which seem able to avoid capture by the ET (Table 5). The relative efficiency values increased during the study (Figure 3D) due to decreasing differences in abundance between the methods over the sampling period (Table 3). The frequency graphs of the  $x$  values showed 1 outlier, but consistently negative values, supporting the general findings of the comparison. Abundance estimates by the ET should be adjusted by a factor of 1.7.

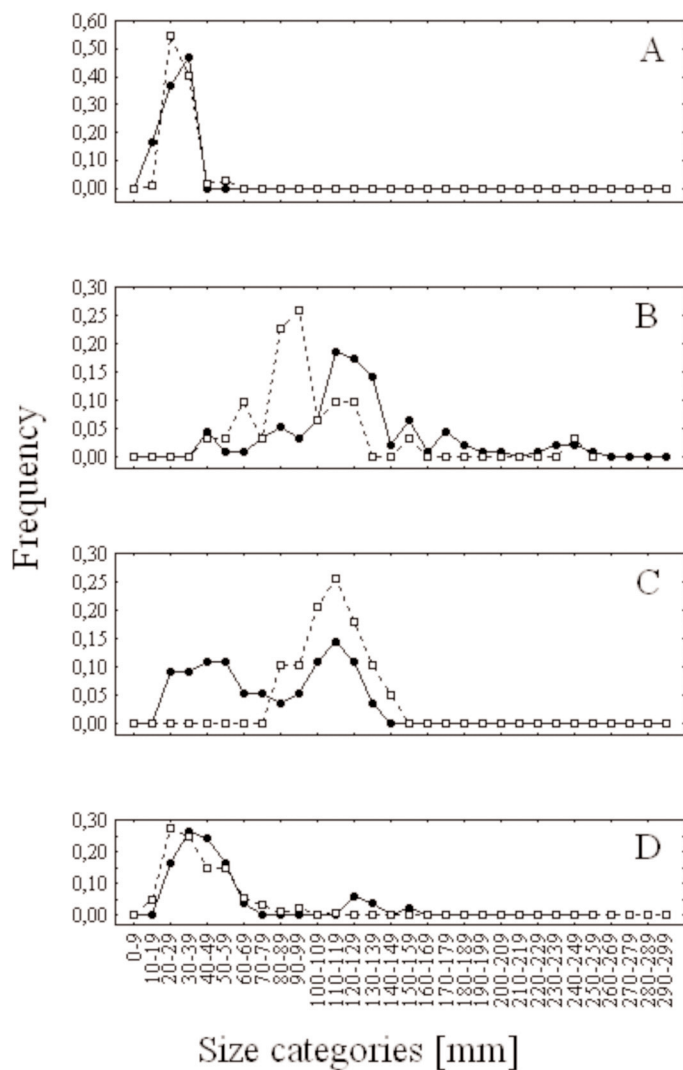
***C. maenas*.** Significant differences in relative detection efficiency between the methods were also discovered for the shore crab, *C. maenas* (Table 5), which seems to be able to avoid capture by the ET. The median of the efficiency values remained relatively stable after 11 comparisons, indicating minor variation in catch efficiency between the methods over the sampling period (Figure 3E). Variation in the frequency graphs included positive as well as negative  $x$  values, with more negative numbers (Figure 3E). The correction value suggested for the shore crab is 1.6 for the ET.

**Divers.** The abundance estimates for fish did not differ significantly between the divers, and variability was small compared to variability between sampling occasions (Table 4). Sig-

**Table 4.** Total sampled area, total number, and total abundance ( $n = 18$ ) as well as abundance ( $n = 6$ ) of fish and shore crab (*C. maenas*) obtained by ET and VDC in 2003 in an eelgrass bed at Kiel Bight.

Method	Area, m <sup>2</sup>	Number, N	Abundance, N m <sup>-2</sup>	Abundance, N m <sup>-2</sup>		
				21 Aug	25 Sept	27 Oct
ET	180	548	3.0 ± 1.4	2.3 ± 0.9	4.5 ± 1.2	2.3 ± 0.8
VDC	180	730	4.1 ± 3.5	3.1 ± 0.6	8.0 ± 3.5	1.1 ± 0.4
ET (without <i>G. flavescens</i> )	180	347	1.9 ± 0.1	2.0 ± 0.5	2.0 ± 0.5	1.8 ± 0.6
VDC (without <i>G. flavescens</i> )	180	365	2.0 ± 1.0	3.0 ± 0.8	2.0 ± 0.6	1.1 ± 0.2
ET ( <i>C. maenas</i> )	180	99	0.6 ± 0.3	0.9 ± 0.4	0.5 ± 0.2	0.3 ± 0.2
VDC ( <i>C. maenas</i> )	180	272	1.5 ± 0.2	1.3 ± 0.6	1.6 ± 0.6	1.7 ± 0.4

Abundance values are means ± SD.



**Fig. 4.** Size-frequency distribution based on in situ estimates of fish size by VDC transect technique (●) and directly measured fish size obtained by ET sampling (□). Results are shown for behavioral classifications and microhabitat preferences: *G. flavescens* (A), Syngnathidae (B), Gasterosteidae (C), and bottom-dwelling fish (D).

nificant statistical differences in abundance estimates occurred only for the shore crab (*C. maenas*) in October 2003 (Table 6).

**Visual estimate of fish length**—The size-frequency distribution based on estimated sizes was in good agreement with the directly measured individuals. For this reason the use of 10-mm interval size classes for the length measurements of the divers is justifiable. The data illustrate that the divers were able to estimate fish sizes with a high degree of precision. However, the curves for the Gobiidae (Figure 4A and D) based on visual estimates were shifted slightly to the left, indicating that divers tend to underestimate the length of these fish. Suboptimal agreement of length frequency distributions between the methods was found for the Syngnathidae and the Gasterosteidae (Figure 4B and C). Larger individuals (> 160 mm long) of the Syngnathidae were rarely found during the diving census counts (Figure 4B), indicating a lower detection efficiency for adult pipefish. The Gasterosteidae showed converse results. Smaller *G. aculeatus* and *S. spinachia* (< 80 mm long) were rarely detected by the divers (Figure 4C). Whereas *G. aculeatus* was almost absent from the divers' counts, probably due to its avoidance response, juvenile *S. spinachia* were not seen because of their camouflaged behavior and coloration.

## Discussion

In this investigation the catch efficiency of a newly constructed enclosure drop trap, which operates without the help of divers, was compared with a visual diving census technique carried out simultaneously in an eelgrass bed of the Baltic Sea. The methods differ in their characterization of the fish fauna. Differences were found in the rank order of frequent fish species. The fish species spectrum represented by both methods was consistent with results of other investigations of shallow water habitats in the Baltic Sea (Winkler and Thiel 1993; Bischoff et al. 1997; Thetmeyer 1998). This was true for species richness as well as abundance (Jansson et al. 1985; Hunter-Thomsen et al. 2002). More than 30 fish species can be found in the shallow waters of the western Baltic Sea (Gründel 1980; Thetmeyer 1998). Thetmeyer (1998) surveyed 8 stations at 2, 4, and 8 m depth with visual diving transect census and 17 stations with beam trawl (3 m beam length, 1 cm mesh size)

**Table 5.** Efficiency values ( $r$ ) of the ET relative to the VDC transect technique and results from statistical comparison (sign test).

Behavioral category	$r$	$n$	$Z$	$P$
A	0.44	18	0.52	0.61
B	4.00	18	4.00	0.0001
C	1.83	18	2.12	0.03
D	0.28	18	3.53	0.0004
E	0.39	18	3.40	0.0007
Total (A–D)	0.76	18	0.24	0.81
Total (B–D)	1.05	18	0.49	0.63

at approximately 6 m depth. The VDC detected 1 to 10 fish species at each site, sampling  $3 \times 25$  m strip transects of 2 m width. The beam trawl found 1 to 14 species at each station. These results are in accordance with the richness detected by both methods in this study. The species richness detected by the ET was negligibly higher on each sampling occasion compared with the diving census technique. Only minor differences in species composition were obtained over the sampling period by the 2 methods; the visual census detected 11 and the ET 10 species (Table 3). Diversity, evenness, and time course of abundances showed contrasting results, with diversity and evenness values for the pooled data being higher from the ET than from the VDC technique. No differences in efficiency in terms of total fish abundance were found (Table 5), but significant differences were found with regard to the behavioral classifications of the eelgrass fish assemblage. These results indicate that the new ET yields consistent and adequate predictions about the fish community structure and abundance in eelgrass beds.

**Selectivity and fish behavior—Pelagic species.** The common semipelagic *G. flavescens*, which aggregates in large schools above the eelgrass canopy, was detected with low relative efficiency by the ET although there were no significant differences between the methods (Table 5). Fast-swimming, pelagic, schooling species are generally underrepresented in enclosure traps (Rozas and Minello 1997). Depending on the presence or absence of the schools, density estimates from the 2 methods varied greatly between sampling occasions. Numerous replicate hauls and observations are required to avoid this bias, although another approach is to exclude schooling pelagic fish from analysis because of the data distortion they cause (Edgar et al. 2001).

**Crypsis and avoidance.** Bias may be introduced because of the differential visibility of fish. Small cryptic fish can be underestimated by more than an order of magnitude by the visual diving census, even with meticulous searches of small areas (Brock 1982; Willis 2001). Pipefish of the family Syngnathidae were among the most frequent species captured by the ET in this study (Table 3). The Syngnathidae are characterized by an ambush feeding mode or a slow approach to prey. Their slow movements and crypsis make it difficult for the

**Table 6.** Statistical comparison of the total fish and shore crab (*C. maenas*) abundances estimated by the 2 divers during VDC.

Sampling date 2003	category	$n$	$t$	$Z$	$P$
21 Aug	Total fish	12	36	0.24	0.81
	Shore crab	12	11	1.05	0.29
25 Sept	Total fish	12	36	0.24	0.81
	Shore crab	12	19	1.24	0.21
27 Oct	Total fish	12	11	1.36	0.17
	Shore crab	12	0.0	2.80	0.005

$n$  = number of replicate samples.

divers to quantify these species. In particular, adult individuals > 160 mm long were rarely discovered by the divers (Figure 4), because of their perfect camouflage coloration and the behavior of adults compared to juveniles. On the other hand, the ET efficiently captured these cryptic forms, which are often closely associated with the eelgrass and show a low escape response. Small individuals may, however, have escaped the ET owing to their morphology. Although the inspection field of each diver was only 0.5 m wide, phytomimetic Syngnathidae were significantly underestimated compared with the ET method (Table 5), which caught 6 times more Syngnathidae than were detected by the visual diving census.

Other small fish, like the frequent Gasterosteidae, were slightly underestimated by the diving census method. The fifteen-spined stickleback, *S. spinachia*, was detected in similar abundances by both methods, indicating low avoidance response and good perception by the divers. In contrast, the three-spined stickleback, *G. aculeatus*, exhibited the lowest detectability and was almost absent from VDC counts. The ET, however, showed *G. aculeatus* to be a frequent eelgrass inhabitant, fourth in the frequency of fish species (Table 3). A pronounced avoidance response of *G. aculeatus* to the silhouette and the noise of divers, noted by Jansson et al. (1985), was also found in this study. Significant differences in relative catch efficiency for the Gasterosteidae between the 2 methods was directly related to the avoidance response of *G. aculeatus*. Because the ET operates vertically, it does not seem to induce any pronounced avoidance response in *G. aculeatus*.

**Demersal fauna.** The bottom-dwelling fish (mostly Gobiidae) and the shore crab, *C. maenas*, were caught with significantly reduced efficiency by the ET compared with the visual census (Table 5). These results are in general accordance with published data, e.g., Rozas and Minello (1997), who stated that sedentary, nonschooling animals are generally underrepresented in enclosure trap catches.

The avoidance response of benthic Gobiidae to divers seems to be less pronounced than in the three-spined stickleback, but demersal Gobiidae particularly hide in seafloor irregularities and depressions and partly escaped the ET. The avoidance reactions of the Gobiidae occur horizontally, close to the ground; only 28% of bottom-dwelling Gobiidae were guided vertically into the ET.

Shore crabs are able to hide by burying themselves in the sediment, a feature that may explain the reduced relative catch efficiency of the ET. Only 39% of the shore crabs were detected by the ET compared with the diving census (Table 3).

**Species identification**—A major problem of the visual diving census was the species identification in situ. Notably the bottom-dwelling juvenile Gobiidae, *P. minutus* and *G. niger*, could not easily be distinguished by the divers (Ellund et al. 1980). In situ identification of *P. minutus*, *P. microps*, and *P. pictus* appeared almost impossible, but *P. microps* and *P. pictus* are assumed to be absent from the study area because neither was found during intensive ET sampling attempts in the same eelgrass bed over 2 years. Demersal Gobiidae were pooled in the bottom-dwelling fish category. Uncertainties with respect to other rare species could be overcome by capturing with small dip nets for identification, but this method is not applicable to highly abundant species like the Gobiidae. The ET, in contrast, provides (a priori) the possibility of definitive identification of the captured animals.

**Mesh size**—The 6 mm mesh size used in this investigation excluded quantitative sampling of larval and juvenile stages. Smaller mesh sizes were not tested, but would presumably increase the early faunal stages in the catches although they may also affect the descent of the trap.

**Diver variability**—Edgar et al. (2004) pointed out that the diving strip transect technique used in this investigation is not greatly affected by variability between divers. However, other authors suggested that the variability between divers confounded the analysis of diving census data (Thompson and Mapstone 1997). In this study the variation between the 2 divers was tested and found not to be significantly different (except for *C. maenas* in October) and to be relatively low (Table 6) compared to the variability between sampling dates.

**Visual size estimates**—During the visual diving census fish were measured against a centimeter ruler and the results were compared to direct measurements of the fish captured with the ET. The census divers were found to be capable of making precise size estimates, but with a slight tendency to underestimate the size of small fish (Figure 4). Major differences in size-frequency distribution occurred only for the Syngnathidae and the Gasterosteidae, but this may be due to the low numbers of Syngnathidae and *G. aculeatus* detected by the VDC. Edgar et al. (2004) found that divers' size estimates become increasingly inaccurate as fish size deviates from 300 mm. Fish < 175 mm long were underestimated by about 20% and fish > 400 mm long were overestimated by about 10%.

### Comments and recommendations

In the present investigation some general drawbacks of the ET were found: (1) solid and irregular sediment with big stones made sampling impossible, (2) disturbance involved with the sampling procedure and rough seas may increase the avoidance response of fish due to the noise, shadows, and vertical movements of the ET within the water column, (3) the shut-

ter mechanism worked inadequately if the pull direction of the shutter rope was not more or less parallel to the long axis of the trap, (4) the catches were highly variable due to the small sampling area of the ET, (5) the trap is unsuitable for adequately sampling larger areas, and (6) the ET is not suitable for catching larger fishes.

On the other hand, the enclosure trap has several advantages over other assessment techniques: (1) the portable trap is relatively cheap and can be used in dense *Z. marina* beds, < 600 shoots m<sup>-2</sup>, (2) it can yield a relatively high number of replicates and allows repeated sampling at short time intervals from relatively small areas or the experimental plots essential in coastal monitoring programs and scientific research, (3) the trap enclosed a defined area, important for quantitative assessments, (4) it could be used at depths down to 5 m without the help of divers, (5) it collected relatively clean samples, minimizing time-consuming sorting, (6) high spatial resolution allowed the determination of indices of dispersion, and (7) the fish were collected live and with minimal trauma, making possible live release and facilitating identification, accurate length and weight measurements, and gut content analysis.

The enclosure trap as presented here is a useful sampling device for the rapid and easy assessment of the fish community in eelgrass beds. The correction coefficients for different behavioral groups and species facilitate quantitative sampling of small common eelgrass nekton. The limitations and suitability of the visual diving census for detecting the different behavioral categories of small fish in dense eelgrass beds are now better understood. The enclosure trap and visual diving census methods are complementary and their simultaneous use can be recommended to obtain accurate quantitative estimates of eelgrass fish populations. Data on the relative capture efficiency of the enclosure trap can be used to improve abundance measurements of small fish in *Z. marina* eelgrass beds without the help of divers.

### References

- Adams, S. M. 1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. *J. Exp. Mar. Biol. Ecol.* 22:269-291.
- Bischoff, K., K. Quitschau, and H. Schöne. 1997. Zum Vorkommen ausgewählter Tierarten in den Seegraswiesen vor Timmendorfer (Insel Poel). *Meer und Museum* 13:62-64 (in German).
- Boström, C., S. Baden, and D. Krause-Jensen. 2003. The seagrass of Scandinavia and the Baltic Sea, pp.27-35. *In* The World Atlas of Seagrasses. E. P. Green and F. T. Short, Eds. Berkeley, CA, University of California Press.
- Brock, V. E. 1954. A preliminary report on method of estimating reef fish populations. *J. Wildl. Manage.* 18:297-308.
- . 1982. A critic of the visual census method for assessing coral reef fish populations. *Bull. Mar. Sci.* 32:269-276.
- Chick, J. H., F. Jordan, J. P. Smith, and C. C. McIvor. 1992. A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. *J. Freshwater Ecol.* 7:353-361.

- Connolly, R. M. 1994. Comparison of fish catches from buoyant pop net and beach seine net in a shallow seagrass habitat. *Mar. Ecol. Prog. Ser.* 109:305-309.
- Costanza, R., and others. 1997. The values of the world's ecosystem services and natural capital. *Nature* 387:253-260.
- Dewey, M. R., L. E. Holland-Bartels, and S. J. Zigler. 1989. Comparison of fish catches with buoyant pop nets and seines in vegetated and nonvegetated habitats. *N. Am. J. Fish. Manage.* 9:249-253.
- Edgar, G. J., H. Mukai, and R. J. Orth. 2001. Fish, drabs, shrimps and other large mobile epibenthos: measurement methods for their biomass and abundance in seagrass, p. 255-270. *In* Global Seagrass Research Methods. F. T. Short and R. G. Coles, Eds. Amsterdam, Elsevier Science.
- , N. S. Barrett, and A. J. Morton. 2004. Biases associated with the use of underwater visual census technique to quantify the density and size-structure of fish populations. *J. Exp. Mar. Biol. Ecol.* 308:269-290.
- and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size structure and production of fishes in Western Port, Victoria. *J. Exp. Mar. Biol. Ecol.* 194:53-81.
- Ellund, A.-M., G. Sundmark, and S. Thorman. 1980. The identification of *Pomatoschistus pictus*, *P. microps*, and *P. minutus* (Gobiidae, Pisces). *Sarsia* 65:239-242.
- Freeman, B. J., H. S. Greening, and J. D. Oliver. 1984. Comparison of three methods for sampling fishes and macroinvertebrates in a vegetated freshwater wetland. *J. Freshwater Ecol.* 2:603-609.
- Gilmore, R.G., and others. 1978. Portable tripod drop net for estuarine fish studies. *Fish. Bull.* 76:285-289.
- Gründel, E. R. 1980. Ökosystem Seegrasswiese: Qualitative und quantitative Untersuchungen über die Struktur und Funktion einer *Zostera*-Wiese vor Surendorf (Kieler Bucht, Westl. Ostsee). Ph. D. thesis, University of Kiel, Germany.
- Harmelin-Vivien, M. L., and P. Francour. 1992. Trawling or visual censuses? Methodological bias in the assessment of fish population in seagrass beds. *Mar. Ecol.* 13:41-51.
- Hellier, T. R., Jr. 1958. The drop-net quadrat, a new population sampling device. *Publ. Inst. Mar. Sci. Univ. Tex.* 5:165-168.
- Higer, A. L., and M. C. Kolipinski. 1967. Pull-up trap: a quantitative device for sampling shallow water animals. *Ecology* 48:1008-1009.
- Hunter-Thomsen, K., J. Hughes, and B. Williams. 2002. Estuarine-open-water comparison of fish community structure in eelgrass (*Zostera marina* L.) habitats of Cape Cod. *Biol. Bull.* 203:247-248.
- Jacobsen, T., and J. A. Kushlan. 1987. Sources of sampling bias in enclosure fish trapping: effects on estimates of density and diversity. *Fish. Res.* 5:401-412.
- Jansson, B.-O., G. Aneer, and S. Nellbring. 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. *Mar. Ecol. Prog. Ser.* 23:31-43.
- Jordan, F., S. Coyne, and J. C. Trexler. 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m<sup>2</sup> throw trap. *Trans. Am. Fish. Soc.* 126:1012-1020.
- Kahl, M. P., Jr. 1963. Technique for sampling population density of small shallow-water fish. *Limnol. Oceanogr.* 8:302-304.
- Kjelson, M. A., and G. N. Johnson. 1978. Catch efficiencies of a 6.1-meter otter trawl for estuarine fish populations. *Trans. Am. Fish. Soc.* 107:246-254.
- , W. R. Turner, and G. N. Johnson. 1975. Description of a stationary drop-net for estimating nekton abundance in shallow waters. *Trans. Am. Fish. Soc.* 104:46-49.
- Krebs, C. J. 1999. *Ecological Methodology*, 2nd ed. Benjamin/Cummings, Menlo Park, CA.
- Kushlan, J. A. 1974. Quantitative sampling of fish populations in shallow freshwater environments. *Trans. Am. Fish. Soc.* 103:348-352.
- . 1981. Sampling characteristics of enclosure fish traps. *Trans. Am. Fish. Soc.* 110:557-562.
- Larson, E. W., D. L. Johnson, and W. E. Lynch. 1986. A buoyant pop net for accurately sampling fish at artificial habitat structures. *Trans. Am. Fish. Soc.* 115:351-355.
- Mosely, F. N., and B. J. Copeland. 1969. A portable drop-net for representative sampling of nekton. *Publ. Inst. Mar. Sci. Univ. Tex.* 14:37-45.
- Murphy, M. L., S. W. Johnson, and D. J. Csepp. 2000. A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. *Alaska Fish. Res. Bull.* 7:11-21.
- Nellbring, S. 1985. Abundance, biomass and seasonal variation of fish on shallow soft bottoms in the Askö area, northern Baltic proper. *Sarsia* 70:217-225.
- Parsley, M. J., D. E. Palmer, and R. W. Burkhardt. 1989. Variation in capture efficiency of a beach seine for small fishes. *N. Am. J. Fish. Manage.* 9:239-244.
- Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1990. Sampling littoral fish with seine: corrections for variable capture efficiency. *Can. J. Fish. Aquat. Sci.* 47:1004-1010.
- Pihl Baden, S., and L. Pihl. 1984. Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, Western Sweden. *Ophelia* 23:65-90.
- Pihl, L., and R. Rosenberg. 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, Western Sweden. *J. Exp. Mar. Biol. Ecol.* 57:273-301.
- Rozas, L. P. 1992. Bottomless lift net for qualitative sampling nekton on intertidal marshes. *Mar. Ecol. Prog. Ser.* 89:287-292.
- and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* 20:199-213.
- Saltaug, A. 2002. Quantitative comparison of aquatic sampling gears. *Sarsia* 87:128-134.
- Serafy, J. E., R. M. Harrell, and J. C. Stevenson. 1988. Quantitative sampling of small fishes in dense vegetation: design

- and field testing of portable "pop-nets." *J. Appl. Ichthyol.* 4:149-157.
- Short, F. T., S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conserv.* 23:17-27.
- Sogard, S. M., G. V. N. Powell, and J. G. Holmquist. 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. *Bull. Mar. Sci.* 44:179-199.
- Thetmeyer, H. 1998. Umweltmonitoring in Schleswig-Holstein. Kleinfische der Ostseeküste. Monitoring-Bericht 1998, pp. 57. Landesamt für Natur und Umwelt des Landes Schleswig-Holsteins, Flintbek (in German).
- Thompson, A. A., and B. D. Mapstone. 1997. Observer effects and training in underwater visual surveys of reef fishes. *Mar. Ecol. Prog. Ser.* 154:53-63.
- Watson, R.A., R. G. Coles, and W. L. Lee Long. 1993. Simulation estimates of annual yield and landed value for commercial penaeid prawns from a tropical seagrass habitat, Northern Queensland, Australia. *Aust. J. Mar. Freshw. Res.* 44:211-219.
- Wennhage, H., R. N. Gibson, and L. Robb. 1997. The use of drop traps to estimate the efficiency of two beam trawls commonly used for sampling juvenile flatfishes. *J. Fish Biol.* 51:441-445.
- Willis, T. J. 2001. Visual census methods underestimate density of and diversity of cryptic reef fishes. *J. Fish Biol.* 59: 1408-1411.
- Winkler, H. M., and R. Thiel. 1993. Beobachtungen zu aktuellen Vorkommen wenig beachteter Kleinfischarten an der Ostküste Mecklenburgs und Vorpommerns (Ostdeutschland). Rostock. *Meeresbiol. Beitr.* 1:95-104 (in German).

*Submitted 20 May 2005*

*Revised 2 October 2005*

*Accepted 29 November 2005*