Marine Biology Research
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713735885

Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia

Jan Arie Vonk [ab]; Marjolijn J. A. Christianen [a]; Johan Stapel [ac]
[a] Department of Environmental Science, Radboud University Nijmegen, Nijmegen, the Netherlands [b] Department of Freshwater and Groundwater, National Institute for Public Health and the Environment (RIVM), Bilthoven, the Netherlands [c] Present address: Royal Netherlands Academy of Arts and Sciences, Amsterdam, the Netherlands

First published on: 26 February 2010

To cite this Article Vonk, Jan Arie, Christianen, Marjolijn J. A. and Stapel, Johan(2010) 'Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia', Marine Biology Research,, First published on: 26 February 2010 (iFirst)

To link to this Article: DOI: 10.1080/17451000903233789

URL: http://dx.doi.org/10.1080/17451000903233789

Marine Biology Research
2010, 1–10, iFirst article

ORIGINAL ARTICLE

Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia

JAN ARIE VONK[1,2]*, MARJOLIJN J. A. CHRISTIANEN[1] & JOHAN STAPEL[1,3]

[1]*Department of Environmental Science, Radboud University Nijmegen, Nijmegen, the Netherlands;* [2]*Department of Freshwater and Groundwater, National Institute for Public Health and the Environment (RIVM), Bilthoven, the Netherlands;* [3]*Present address: Royal Netherlands Academy of Arts and Sciences, Amsterdam, the Netherlands*

Abstract
Motile fauna species in two mixed-species seagrass meadows with different canopy structure were studied on an uninhabited island in the Spermonde Archipelago, Sulawesi, Indonesia. The main focus of the study was to assess the edge effect and seasonal abundance of macrobenthic invertebrates. Fish and infauna densities were determined as well. Fauna was counted using permanent transects (macrobenthic invertebrates), visual census (fish species), and sediment cores (infauna). Both meadows had a comparable distribution of motile fauna species with polychaetes (35% of total abundance), bivalves (27%) and sipunculids (25%) accounting for the largest part of the total faunal abundance. The closed canopy meadow (high seagrass leaf biomass) had an overall higher faunal abundance compared with the open canopy meadow (low seagrass leaf biomass) (1133 vs. 751 individuals m^{-2}). Although infauna abundance was comparable between the meadows, macrobenthic invertebrates (crustaceans, echinoderms, and molluscs) and fishes were more abundant in the closed canopy meadow, with only a few individual species more abundant in the open canopy meadow. The effect of distance from the meadow edge on macrobenthic invertebrate abundance was significant, with higher abundances towards the interior of the seagrass meadows, but for fish abundance no significant differences were found. Effects of seasonality (rainy vs. dry season) on macrobenthic invertebrate abundance were only significant for molluscs. We concluded that macrobenthic invertebrate abundance was most influenced by seagrass canopy structure, followed by meadow edge effects, and least by seasonality. Comparisons of faunal abundance in seagrass meadows need thus to include information on these three variables.

Key words: *Fish, infauna, macrobenthos, seagrass–fauna interactions, tropical seagrasses*

Introduction

The Indo-Pacific region is characterized by large, often multi-species seagrass meadows (Nienhuis et al. 1989; Tomascik et al. 1997; Kuriandewa et al. 2003; Kiswara et al. 2009). Seagrass meadows provide substrate in the water column which attracts many fauna species for shelter, food availability or settling opportunities. The settlement of epiphytic species, macrobenthic invertebrates, infauna, and fish in seagrass meadows results in habitats with higher production, diversity and abundance than unvegetated areas (Ogden 1980; Orth et al. 1984; Edgar & Shaw 1995; Hemminga & Duarte 2000). Many of these species are of significant economic importance, such as shrimps and prawns (Tomascik et al. 1997). Dominant faunal groups living in most tropical Indo-Pacific meadows include sea urchins (echinoderms), bivalves, crustaceans and fishes (Erftemeijer et al. 1993; Alcoverro & Mariani 2004; Unsworth et al. 2007a,b; Vonk et al. 2008).

The abundance of fauna in seagrass meadows can be influenced by different environmental conditions that include seagrass canopy structure, distance relative to the meadow edge, and seasonality. Increase in habitat complexity due to the seagrass canopy (i.e. higher seagrass density or aboveground biomass) is assumed to result in higher faunal abundance due to reduced predation risk and enhanced food supply (Howard et al. 1989; Hyndes

*Correspondence: Jan Arie Vonk, Department of Environmental Science, Institute for Wetland and Water Research, Faculty of Science, Radboud University Nijmegen, PO Box 9010, NL-6500 GL Nijmegen, the Netherlands. E-mail: javonk@gmail.com
Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

(Accepted 31 July 2009; Published online 1 March 2010)

ISSN 1745-1000 print/ISSN 1745-1019 online
DOI: 10.1080/17451000903233789

et al. 2003; Unsworth et al. 2007a). Fauna species present in seagrass meadows also migrate from (and to) nearby coral or sandy areas for food and/or shelter. This behaviour results in increased abundances near the edge of the seagrass meadows, especially for fish species (Dorenbosch et al. 2005; Gullström et al. 2008; Smith et al. 2008). In the Indo-Pacific many of these fish species feed on invertebrates (Tomascik et al. 1997), and the increased predation pressure near the edge of the meadow can influence the abundance of invertebrates (Peterson et al. 2001; Boström et al. 2006). Seasonality (rainy vs. dry season) can influence faunal abundance in tropical meadows throughout the reproduction cycle (Robertson & Duke 1987; Bos et al. 2008). However, the conditions during the rainy season can be more stressful (more wind and wave activity) for macrobenthic invertebrates living in the often shallow water seagrass meadows.

The influence of distance from the meadow edge and seasonality on faunal abundance are poorly studied in tropical mixed-species meadows in the Indo-Pacific, but it can be an important variable when faunal abundances of different meadows are compared. The aim of this study is to determine the influence of distance from the meadow edge and of seasonality on faunal abundance of different groups in two mixed-species seagrass meadows with different canopy structure in Sulawesi, Indonesia. We focused on the abundance of macrobenthic invertebrates, since information on this group is scarce and relatively larger effects are expected, but also the abundance of fish species and infauna was determined.

Materials and methods

Study area

We studied species in two adjacent seagrass meadows on the island of Bone Batang (4°90' S; 119°18' E), located 15 km offshore in the Spermonde Archipelago. This consists of a large group of coral islands and submerged reefs on the continental shelf along the west coast of South Sulawesi, Indonesia (see Vonk 2008, for details of the island). The area has a diurnal tide and the rainy season in this area lasts from November to April (Erftemeijer & Herman 1994). Bone Batang has an intertidal sandy shoal with a surrounding reef flat and is protected by a barrier reef on the wave-exposed site and large coral boulders on the less-exposed site. An extensive multi-species seagrass meadow covers the reef flat, which consists of coarse carbonate sand and coral rubble. The two selected adjacent seagrass meadows had significantly different total seagrass density and aboveground biomass (Table I). The meadows were therefore quantified as closed (high seagrass leaf biomass) and open canopy (low seagrass leaf biomass) structure, respectively, and consisted mainly of the co-occurring seagrass species *Thalassia hemprichii* (Ehrenberg) Ascherson, 1871, *Halodule uninervis* (Forsskål) Ascherson, 1882, and *Cymodocea rotundata* Ehrenberg & Hemprich ex Ascherson, 1870. The chosen meadows were subtidal (0.2–0.5 m below extreme low water-level spring tides) and located on the less-exposed site of the island, with few scattered coral lumps (<0.3 m diameter) present. Although uninhabited, the island was used by fishermen from neighbouring islands for fishing activities and selective collection of invertebrate species.

Faunal abundance

Macrobenthic invertebrates were determined in permanent transects, fish were surveyed using visual census, and infauna was counted from sediment cores. In each of the meadows three permanent transects were pegged out. The transects with marking poles on the corners were perpendicular to the edge of the meadow, 15 m long and 1 m wide, and started 2 m from the seaward edge. All measurements were carried out in these permanent transects (or alongside for the infauna cores). Macrobenthic invertebrate abundances (>1 cm) were determined by temporarily dividing permanent transects into 15 quadrats of 1 m^2. All visible species were counted on 11 occasions (five times during the rainy season and six times during the dry season) between October 2004 and November 2005. On five occasions the sizes of these invertebrates were measured. All fauna species observed and collected were identified to species level when possible. Other taxonomic units (family, order) were used when higher resolution was not possible. Infauna abundance (species >0.1 cm) was determined from 12 core samples, taken from the sediment in both meadows using a core sampler (16 cm diameter, 20 cm depth) between May and July 2005. The core was washed out over a 0.1 cm sieve and infauna species were collected. Sponge fragments were discarded.

Fishes were counted with visual census using SCUBA, snorkelling and a stationary point-count method (Polunin & Roberts 1993). Because of underwater visibility (range 6–15 m), 5 m quadrats were surveyed using a 5 m rope as a reference for quadrat size. After placing the line, the observer waited for 3 min to minimize disturbance. For 10 min all fish species within or passing through the quadrat were counted. The observer spent the first 7 min on the edge and moved for the last 3 min

Table I. Seagrass specifications (mean ± SE) for the closed and open canopy meadow; shoot density (# m^{-2}) and biomass of leaf, rhizome and root (g DW m^{-2}). Significant differences between the meadows are denoted using letters (data from Vonk 2008).

Meadow canopy	Seagrass species	Density shoot	Biomass leaf	Rhizome	Root
Closed	*T. hemprichii*	604 ± 43	43.1 ± 3.1^{A}	260.5 ± 18.6	66.9 ± 4.8
	H. uninervis	2424 ± 115^{A}	46.5 ± 2.2^{A}	136.9 ± 6.5^{A}	54.2 ± 2.6^{A}
	C. rotundata	879 ± 51^{A}	28.4 ± 1.7^{A}	63.9 ± 3.8^{A}	42.2 ± 2.5^{A}
	Total	$\mathbf{3904 \pm 103^{A}}$	$\mathbf{118.0 \pm 3.3^{A}}$	$\mathbf{461.3 \pm 17.7^{A}}$	$\mathbf{163.3 \pm 5.1^{A}}$
Open	*T. hemprichii*	799 ± 65	32.9 ± 2.7^{B}	282.2 ± 23.0	84.9 ± 6.9
	H. uninervis	1178 ± 157^{B}	8.1 ± 1.1^{B}	74.6 ± 10.0^{B}	32.6 ± 4.4^{B}
	C. rotundata	378 ± 43^{B}	5.5 ± 0.6^{B}	20.6 ± 2.4^{B}	10.9 ± 1.2^{B}
	Total	$\mathbf{2355 \pm 130^{B}}$	$\mathbf{46.5 \pm 2.1^{B}}$	$\mathbf{377.4 \pm 16.7^{B}}$	$\mathbf{128.4 \pm 4.7^{B}}$

over the quadrat to search for fish hiding within the canopy. Care was taken that fishes moving regularly in and out of the quadrat were not counted more than once. Fish were classified into 2.5 cm size classes using an underwater slate. At both ends and in the middle of each permanent transect fish abundance was determined monthly between April and July 2005. Surveys were conducted at high tide, when water movement was minimal, to standardize for possible tidal effects on the fish assemblage.

Statistics

All counted data were transformed before statistical analysis. We used the square root transformation of the counted value plus 0.5 (Sokal & Rohlf 1995). For all encountered fauna species the differences in abundance between the closed and open canopy meadow were analysed using *t*-tests. For fish abundance, the meadow-edge effect was analysed using ANOVA. The effects of canopy structure, distance from the meadow edge, and seasonality on the abundance of macrobenthic invertebrate groups (crustaceans, echinoderms, and molluscs) were analysed using MANOVA, followed by linear regression for significant meadow edge effects. Effects of seasonality (rainy vs. dry season) for individual macrobenthic invertebrate species were analysed using *t*-tests.

Results

Abundance

The closed canopy meadow had a higher total faunal abundance compared with the open canopy meadow (1133 vs. 751 individuals m^{-2}). Both studied meadows had a comparable distribution of fauna species with polychaetes (35% of total abundance), bivalves (27%) and sipunculids (25%) accounting for the largest part of the total faunal abundance (Table IIA). Including Nynantheae (4.7%), most of these species were small infauna species. Crustaceans (5.1%), echinoderms (2.5%) and large bivalves (*Atrina vexillum* and *Pinna muricata*) were the main groups of invertebrate species living (partly) above the sediment. Total fish abundance accounted for 0.5% of total faunal abundance. Fish species with the highest abundance in the meadows were large schools of small juvenile *Atherinomorus lacunosus* and Clupeidae, the herbivorous species *Calotomus spinidens* and *Leptoscarus vaigiensis*, the omnivorous species *Siganus canaliculatus*, and the zoobenthivorous species *Cheilio inermis*, *Gerres oyena*, *Pomacentrus adelus* and *Stethojulis strigiventer* (Table IIB).

Canopy structure

The large bivalves *Atrina vexillum*, *Pinna muricata*, *P. bicolor*, *Malleus albus*, *Isognomon pernum* and *Modiolus micropterus*, all sea urchins, the sea star *Protoreaster nodosus* and the shrimp *Neaxius acanthus* were significantly more abundant in the closed canopy meadow compared with the open canopy meadow (Table IIA). Alpheid shrimps were the only invertebrate species more abundant in the open canopy meadow. Total fish abundance was significantly higher in the closed canopy meadow compared with the open canopy meadow ($t = 2.44$, $d = 70$), as well as certain individual fish species (*Atherinomorus lacunosus*, *Cheilio inermis* and *Stethojulis canaliculatus*). Some fish species were more abundant in the open canopy meadow (*Anampses caeruleopunctatus*, *Halichoeres chloropterus*, *Pomacentrus adelus* and *S. strigiventer*). Infauna abundance remained comparable for the two meadow types.

Edge effect

The effect of distance from the meadow edge on macrobenthic invertebrate groups was clear for molluscs in the closed canopy meadow (Table III, Figure 1). Their abundance towards the interior increased significantly and almost 60% of the total variation was explained by distance from the edge for this group in the close canopy meadow (linear regression; $F_{1,493} = 708.7$, $p < 0.001$).

Table II. Invertebrate (A) and fish (B) abundance (individuals 10 m^{-2}) counted in the closed and open canopy meadow in sediment cores (c; $n = 12$ cores), in permanent transects (t; $n = 495$ quadrats) or by visual census (v; $n = 36$ areas) and their sizes (cm), with authorities of genera or species indicated in parentheses. Significant differences in abundances between the closed and the open canopy meadow are marked (*t*-test; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

A			Closed canopy meadow				Open canopy meadow				
			Size		Abundance		Size		Abundance		
Invertebrates			Mean	Range	Mean	*SE*	Mean	Range	Mean	*SE*	
Crustaceans											
	Alpheus sp. **	t			0.28	0.07			0.81	0.04	(Fabricius, 1798)
	Dardanus sp.	t			0.28	0.09			0.28	0.01	(Paulson, 1875)
	Neaxius acanthus ***	t			18.44	0.83			7.07	0.32	(Milne Edwards, 1878)
	other crustaceans	c			426.3	30.71			455.9	48.26	
Molluscs											
Bivalvia	*Atrina vexillum* ***	t	8.7	2–16	33.49	1.38	6.2	3–9	0.12	0.01	(Born, 1778)
	Cardiidae	c			106.6	20.57			0		
	Codakia tigerina	c			284.2	26.85			82.89	16.13	(Linnaeus, 1758)
	Isognomon pernum ***	t	3.4	1–6	4.34	0.43	1		0.02	0.00	(Linnaeus, 1767)
	Lioconcha hieroglyphica	c			71.05	18.99			0		(Conrad, 1837)
	Lucinidae 1	c			1457	79.39			1285	116.5	
	Lucinidae 2	c			106.6	15.13			165.8	27.00	
	Malleus albus ***	t	9.2	3–20	4.87	0.39	11.7	1–20	1.31	0.06	(Lamarck, 1819)
	Modiolus micropterus *	c			284.2	36.11			0		(Deshayes, 1836)
	Paphia undulate	c			71.05	12.90			41.45	11.96	(Born, 1778)
	Pinna bicolor ***	t	9.5	4–15	3.66	0.30	7.5	4–10	0.14	0.01	(Gmelin, 1791)
	Pinna muricata ***	t	5.8	2–15	71.15	2.69	5	1–9	0.44	0.02	(Linnaeus, 1758)
	Tridacna sp.	t	6.7	5–12	0.20	0.10	9	8–10	0.14	0.01	(Bruguière, 1797)
Gastropoda	*Aplysia* sp.	t			0.04	0.04			0.16	0.01	(Linnaeus, 1767)
	Conus sp.	t			0.10	0.04			0.14	0.01	(Linnaeus, 1758)
	Cypraeidae	t			0.14	0.05			0.24	0.01	
	Lambis sp.	t			0.04	0.03			0.06	0.00	(Röding, 1798)
	Littorinidae	c			532.9	70.32			538.8	75.93	
	Nudibranchia	t			0.24	0.09			0.08	0.00	
	Pyrene sp.	t			0.18	0.07			0.16	0.01	(Röding, 1798)
	other gastropods	t			0.67	0.13			0.79	0.04	
Cephalopoda	*Loligo duvauceli*	v			0		9		0.31	0.25	(Orbigny, 1848)
Echinoderms											
Asteroidea	*Protoreaster nodosus* *	t	13.8	4–76	0.75	0.12	11.6	4–30	0.42	0.02	(Linnaeus, 1758)
Echinoidea	*Diadema setosum* ***	t	3.9	1–14	1.15	0.18	3.1	1–5	0.40	0.02	(Leske, 1778)
	Mespilia globulus ***	t	2.3	1–4	4.51	0.46	4.3	4–5	0.12	0.01	(Linnaeus, 1758)
	Tripneustes gratilla ***	t	6.7	2–11	15.52	0.70	7.3	3–10	7.64	0.34	(Linnaeus, 1758)
	T. gratilla (juveniles)	c			106.6	20.57			82.89	16.13	
	other sea urchins **	t	4.3	1–8	0.48	0.12	3.3	2–6	0.12	0.01	
Holothuroidea		c			0				82.89	16.13	
	Synapta maculata	t	19.3	10–40	0.08	0.04	90	80–100	0.06	0.00	(Chamisso & Eysenhardt, 1821)

Table II (*Continued*)

A			Closed canopy meadow				Open canopy meadow			
			Size		Abundance		Size		Abundance	
Invertebrates			**Mean**	Range	**Mean**	***SE***	**Mean**	Range	**Mean**	***SE***
Ophiuroidea		t	**10.3**	3–17	**2.40**	*0.31*	**9.7**	1–20	**2.53**	*0.11*
Other invertebrates										
	Aciculata (Polychaeta)	c			**1101**	*56.05*			**870.4**	*128.8*
	Canalipalpata (Polychaeta)	c			**2949**	*180.3*			**1782**	*176.3*
	Platyhelminthes	t	**2.1**	1–4	**0.20**	*0.06*	**2.5**	1–4	**0.42**	*0.02*
	Sipuncula	c			**2735**	*155.0*			**1907**	*104.3*
	Nynantheae (>10mm) *	t	**7.7**	4–10	**0.32**	*0.12*	**2.5**	2–3	**0.04**	*0.00*
	Nynantheae (<10mm) **	c			**817.1**	*67.70*			**165.8**	*47.86*

B			Closed canopy meadow				Open canopy meadow				
			Size		Abundance		Size		Abundance		
Fish species			**Mean**	Range	**Mean**	***SE***	**Mean**	Range	**Mean**	***SE***	
Osteichthyes											
Apogonidae	*Cheilodipterus quinquelineatus*	v			**0**		**3.0**		**0.11**	*0.11*	(Cuvier, 1828)
Atherindae	*Atherinomorus lacunosus* **	v	**4.0**	2–6	**56.89**	*18.63*	**4.2**	4–6	**9.44**	*4.02*	(Forster, 1801)
Aulostomidae	*Fistularia commersonii*	v			**0**		**28.0**		**0.01**	*0.01*	(Rüppell, 1838)
Balistidae	*Rhinecanthus verrucosus*	v	**16.1**	14–18	**0.17**	*0.05*	**16.7**	15–18	**0.08**	*0.03*	(Linnaeus, 1758)
Belonidae	*Tylosurus crocodilus crocodilus*	v	**45.0**	40–50	**0.14**	*0.12*			**0**		(Péron & Lesueur, 1821)
Centriscidae	*Aeoliscus strigatus*	v	**12.0**		**0.04**	*0.04*			**0**		(Günther, 1861)
Clupeidae		v	**3.5**	2–7	**16.17**	*6.60*	**3.0**	2–4	**11.11**	*5.31*	
Gerreidae	*Gerres oyena*	v	**15.0**	8–30	**0.33**	*0.17*	**10.9**	6–15	**0.62**	*0.30*	(Forsskål, 1775)
Haemulidae	*Plectorhinchus gaterinus*	v			**0**		**15.0**		**0.01**	*0.01*	(Forsskål, 1775)
Hemiramphidae	*Hemiramphus far*	v			**0**		**22.8**	18–28	**0.06**	*0.06*	(Forsskål, 1775)
Labridae	*Anampses caeruleopunctatus* **	v	**18.0**		**0.01**	*0.01*	**14.5**	10–20	**0.18**	*0.05*	(Rüppell, 1829)
	Cheilinus fasciatus	v			**0**		**15.0**		**0.01**	*0.01*	(Bloch, 1791)
	Cheilinus trilobatus	v	**8.1**	3–16	**0.19**	*0.05*	**7.6**	3–13	**0.26**	*0.06*	(Lacepède, 1801)
	Cheilio inermis **	v	**18.9**	6–35	**1.46**	*0.22*	**16.4**	3–29	**0.73**	*0.10*	(Forsskål, 1775)
	Choerodon anchorago	v	**17.0**	10–25	**0.13**	*0.04*	**16.9**	10–22	**0.12**	*0.03*	(Bloch, 1791)
	Halichoeres chloropterus ***	v	**6.7**	3–12	**0.17**	*0.05*	**8.4**	3–18	**0.63**	*0.10*	(Bloch, 1791)
	Halichoeres scapularis	v	**11.3**	6–15	**0.03**	*0.02*			**0**		(Bennett, 1832)
	Halichoeres schwartzi	v	**8.0**		**0.02**	*0.02*	**7.3**	5–9	**0.10**	*0.04*	(Bleeker, 1847)
	Stethojulis strigiventer *	v	**5.9**	3–9	**0.29**	*0.09*	**5.6**	3–8	**0.69**	*0.16*	(Bennett, 1832)
	Thalassoma lunare	v	**9.4**	7–13	**0.06**	*0.03*	**11.8**	6–20	**0.07**	*0.03*	(Linnaeus, 1758)
Lethrinidae	*Lethrinus harak*	v	**4.0**		**0.03**	*0.03*	**10.0**	8–12	**0.06**	*0.06*	(Forsskål, 1775)
	Lethrinus ornatus	v	**5.0**	2–7	**0.37**	*0.23*	**6.3**	4–8	**0.11**	*0.05*	(Valenciennes, 1830)
Mullidae	*Parupeneus barberinus*	v	**13.5**	6–18	**0.04**	*0.02*	**10.3**	6–20	**0.13**	*0.05*	(Lacepède, 1801)
	Upeneus tragula	v	**17.3**	12–21	**0.07**	*0.03*	**16.5**	13–21	**0.04**	*0.02*	(Richardson, 1846)
Nemipteridae	*Pentapodus trivittatus*	v	**16.6**	13–21	**0.39**	*0.05*	**16.6**	10–20	**0.28**	*0.05*	(Bloch, 1791)

Table II (*Continued*)

B			Closed canopy meadow				Open canopy meadow				
			Size		Abundance		Size		Abundance		
Fish species			**Mean**	Range	**Mean**	***SE***	**Mean**	Range	**Mean**	***SE***	
Pomacentridae	*Chromis* sp.	v	**3.2**	2–8	**0.28**	*0.12*	**2.2**	1–7	**0.28**	*0.09*	(Cuvier, 1814)
	Pomacentrus adelus *	v	**4.8**	3–9	**0.36**	*0.13*	**4.2**	3–8	**0.78**	*0.14*	(Allen, 1991)
Scaridae	*Calotomus spinidens*	v	**23.0**	10–30	**0.53**	*0.07*	**15.2**	4–29	**0.51**	*0.17*	(Quoy & Gaimard, 1824)
	Leptoscarus vaigiensis	v	**10.3**	2–18	**0.23**	*0.06*	**7.2**	3–22	**0.39**	*0.14*	(Quoy & Gaimard, 1824)
	Scarus sp.	v	**13.0**	4–20	**0.14**	*0.08*	**11.8**	5–15	**0.17**	*0.10*	(Bleeker, 1849)
Serranidae	*Epinephelus* sp.	v			**0**		**16.5**	16–17	**0.02**	*0.02*	(Bloch, 1793)
Siganidae	*Siganus canaliculatus* *	v	**13.3**	5–20	**0.74**	*0.34*	**14.3**	14–15	**0.07**	*0.04*	(Park, 1797)
	Siganus doliatus	v	**10.0**		**0.03**	*0.03*	**10.1**	6–17	**0.08**	*0.04*	(Guérin-Méneville, 1829)
	Siganus guttatus	v			**0**		**11.0**		**0.02**	*0.02*	(Bloch, 1787)
Tetradontidae	*Arothron manilensis*	v			**0**		**17.0**		**0.02**	*0.02*	(De Procé, 1822)
	Canthigaster compressa	v	**5.0**		**0.01**	*0.01*	**4.0**		**0.04**	*0.03*	(De Procé, 1822)
	Canthigaster solandri	v			**0**		**3.0**		**0.01**	*0.01*	(Richardson, 1845)

Besides the abundance of crustaceans in the open canopy meadow (linear regression $F_{1,493} = 1.001$, $p = 0.32$), the abundance of the other groups of macrobenthic invertebrates also changed significantly from the edge towards the interior of the seagrass meadows. However, in all these cases on average only 2% of the total variation was explained by the edge effect (linear regression: molluscs in open canopy $F_{1,493} = 50.77$, $p < 0.001$; echinoderms in closed canopy $F_{1,493} = 5.395$, $p = 0.021$, in open canopy $F_{1,493} = 21.63$, $p < 0.001$; crustaceans in closed meadow $F_{1,493} = 18.26$, $p < 0.001$). Total fish abundance showed no significant edge effect in either meadow (Figure 2).

Seasonality

Significant differences in the abundance of the molluscs, but not for crustaceans or echinoderms were observed between rainy and dry seasons (Table III, Figure 3). The effect of seasonality was also smaller compared to the edge effect and canopy structure (largest effect). Focusing on individual macrobenthic invertebrate species showed that the bivalves *Isognomon pernum* ($t_{988} = -7.051$, $p < 0.001$) and *Tridacna* sp. ($t_{988} = -2.635$, $p = 0.009$), the echinoderms *Protoreaster nodosus* ($t_{988} = -2.492$, $p = 0.013$), *Synapta maculata* ($t_{988} = -2.429$, $p = 0.015$) and ophiuroidae ($t_{988} = -2.948$, $p = 0.003$) were all more abundant during the dry season, while only undefined gastropod species ($t_{988} = 3.127$, $p = 0.002$) were more abundant in the rainy season.

Discussion

We found a large edge effect (explaining 60% of total variation) for the abundance of molluscs in the closed canopy meadows, while for the other groups (crustaceans and echinoderms) or in the open canopy meadow only a very small edge effect (explaining <2% of total variation) on the abundance was observed. The abundance of invertebrate groups always increased towards the interior of the seagrass meadows. This effect may be caused by increased food availability towards the interior of the meadow (Boström et al. 2006) or increased predation pressure near the meadow edge (Peterson et al. 2001). The seagrass canopy structure was comparable over the length of the studied transects, thus primary food availability is less likely to induce this effect. Fish migrating from and to nearby coral areas, which is observed in many tropical meadows (e.g. Unsworth et al. 2007b; Gullström et al. 2008), can result in higher foraging activities near the edge. However, we observed no significant edge effect on fish abundance, in contrast to other studies in

Table III. Estimated influence of seagrass canopy, distance from meadow edge and seasonality (rainy vs. dry) on the abundance of macrobenthic invertebrate groups using MANOVA (DF = 1930 in canopy and seasonality, DF = 14,930 in edge). The effect size of the variables is given as η^2 (denoted using font style: ***large*** $\eta^2 \geq$ ***0.14***; **medium 0.06** $\leq \eta^2 <$ **0.14**; *small 0.01* $\leq \eta^2 <$ *0.06*; not significant $\eta^2 < 0.01$).

	Crustaceans		Echinoderms		Molluscs	
Dependent variable	F	p	F	p	F	p
Seagrass canopy	**103.4**	<0.001	***171.5***	<0.001	***3949***	<0.001
Meadow edge	**4.473**	<0.001	*2.889*	<0.001	***67.97***	<0.001
Seasonality	1.417	0.23	3.679	0.055	*9.662*	<0.001

tropical (Dorenbosch et al. 2005; Gullström et al. 2008) and temperate (Smith et al. 2008) meadows. Thus, both seagrass aboveground biomass and fish predation do not explain the observed differences in macrobenthic invertebrate abundance from the edge to the middle in our studied meadows.

Intertidal seagrass meadows in this tropical area show large seasonal variations in aboveground biomass due to daytime exposure during low-water levels and desiccation of the leaves (Erftemeijer & Herman 1994). Therefore, we chose subtidal meadows, with no seasonal trend in seagrass aboveground biomass (Vonk 2008), to minimize the effects of canopy changes on seasonal faunal abundance. We observed only a small effect of seasonality on macrobenthic invertebrate abundance in this study. Besides higher total abundance of molluscs in the dry season, only a few individual species showed significant differences in abundance between the seasons. In the few studies that are available, seasonal trends are observed for macrobenthic invertebrate abundance in Indo-Pacific meadows. Bos et al. (2008) encountered lower abundance of the sea star *Protoreaster nodosus* during some months of the year, caused by the reproduction cycle and migration of juveniles of this species. For pelagic crustacean abundances, Robertson & Duke (1987) observed significant differences over seasons in tropical Australian meadows. From large numbers of dead echinoderms in the shallows after storms during the rainy season, we expected to observe seasonal effects for this group, but none were found. More studies are

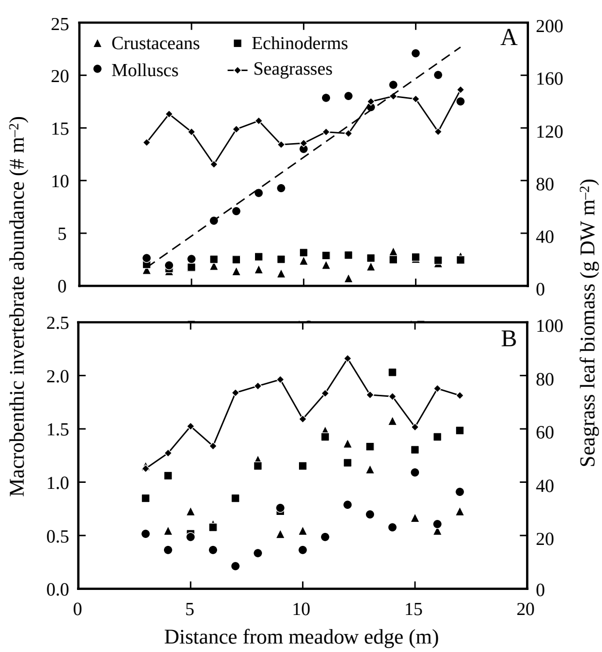

Figure 1. Mean abundance of macrobenthic invertebrate groups (>1 cm) living (partly) above the sediment, counted using transects in the closed (A) and the open (B) canopy meadow at different distances from the meadow edge ($n = 33$). Only the significant regression lines for molluscs in the dense canopy meadow is shown ($R^2 = 0.59$), since the other significant edge effects explained less than 2% of the total variance.

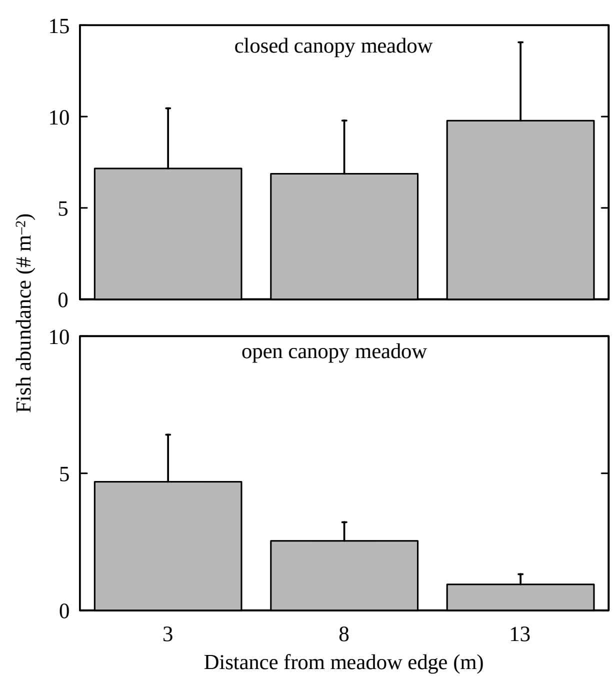

Figure 2. Mean total fish abundance (+ SE) counted at different distances from the edge of the meadow in the closed (top) and the open (bottom) canopy meadow using visual census ($n = 12$). No significant differences in fish abundance were found in both meadows (ANOVA, closed canopy $F_{2,33} = 0.20$, $p = 0.82$; open canopy $F_{2,33} = 2.99$, $p = 0.06$).

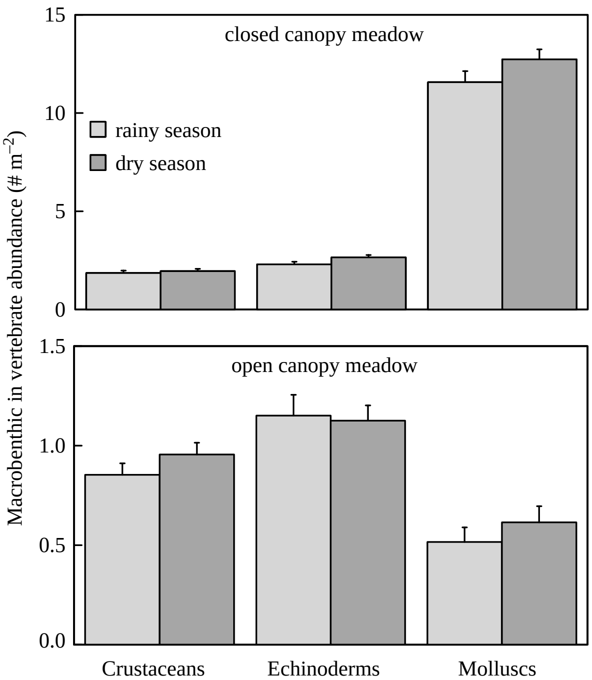

Figure 3. Mean abundance (+ SE) of macrobenthic invertebrate groups (>1 cm) living (partly) above the sediment, counted using transects in the closed (top) and the open (bottom) canopy meadow during the dry season ($n=270$) and rainy season ($n=225$). Only for total mollusc abundance significant difference between the rainy and dry season were observed (see Table III).

needed to determine seasonal changes in abundance for the most important groups of macrobenthic invertebrates living in these Indo-Pacific meadows.

The seagrass density and biomass of the studied meadows were comparable with other studies on tropical meadows (Nienhuis et al. 1989; Erftemeijer & Herman 1994; Vermaat et al. 1995; Kuriandewa et al. 2003). The faunal abundances of the seagrass meadows presented in this study were directly influenced by human fisheries activities. Although the island Bone Batang was uninhabited, people from neighbouring islands frequently visited the island. Human activities on the island included year round selective collection of invertebrates by hand and fishing activities performed with a variety of gear, ranging from large fine nets for small juvenile fish to line fishing for large top predators. However, due to the nearby presence of large coral boulders, no large beamtrawls or beach seine nets were used. The collected invertebrates were mostly holothuroids, large gastropods and some bivalve species. The abundance of these first two groups of invertebrates was low compared with less disturbed meadows (e.g. Nienhuis et al. 1989), and it is likely that this is directly influenced by the fishing activities.

The most abundant fauna species present in the seagrass meadows were small infauna species, with no significant difference in abundance between both meadows. This could be caused by the comparable belowground seagrass biomass of the meadows. Infauna species may be inhibited by heavy rhizome mats and are inversely related to belowground biomass (Stoner 1980). Epiphytic invertebrates had low abundance and patchy distribution, but were present within the meadows. Bryozoa and sponges occurring on seagrasses were only observed as small local patches within the meadow, but none of these patches occurred within the transects used in this study.

As expected from previous studies, we observed that the abundance of macrobenthic invertebrates was higher in the closed canopy meadow (high seagrass leaf biomass) compared to the open canopy meadow (low seagrass leaf biomass). Increased habitat complexity and food availability, and lower predation risks associated with the closed seagrass canopy may be the main reasons for the higher abundance of these organisms (Orth et al. 1984; Peterson et al. 2001; Jackson et al. 2006). Besides being more abundant in the closed canopy meadow, large bivalves like *Atrina vexillum* and *Pinna muricata* also enhanced faunal abundance by creating habitats for other invertebrate species, as shown for mussels (*Modiolus americanus* Leach, 1815) in *Zostera* meadows (Valentine & Heck 1993). Their shells were used by sea urchins for shelter, by bivalves for attachment, and by crustaceans for shelter. The only invertebrates preferring the open canopy were Alpheid shrimps, confirmed by increased densities reported in open *Thalassia hemprichii* dominated meadows (Erftemeijer et al. 1993; Stapel & Erftemeijer 2000; Unsworth et al. 2007a). These shrimps depend on visual guarding by symbiotic gobies, which may be hampered in closed canopies.

Most fish species encountered in our meadows were zoobenthivorous species, comparable to other tropical Indo-Pacific meadows (Unsworth et al. 2007b; Gullström et al. 2008). Significantly higher total fish abundance in closed canopy meadows is also observed in other tropical meadows (e.g. Tomascik et al. 1997; Gullström et al. 2008). The significantly higher densities of *Siganus canaliculatus* and of juvenile *Atherinomorus lacunosus* in the closed canopy meadow may be explained by lower predation pressure, while larger specimens of herbivorous fish like *Calotomus spinidens* and *Leptoscarus vaigiensis* (Scaridae) may prefer closed canopy meadows due to increased food availability (Hyndes et al. 2003; Jackson et al. 2006). However, not all fish species prefer closed canopy meadows and habitat preference remains distinct between species (Hyndes et al. 2003; Salita et al. 2003). Zoobenthivorous species, such as *Anampses caeruleopunctatus*, *Halichoeres chloropterus*, *Stethojulis strigiventer* and *Pomacentrus adelus*, preferred the open canopy meadow, with only *Cheilio inermis* preferring the dense canopy. This preference of larger benthic predators for more open canopies has been shown before (e.g. Salita et al. 2003), and is linked to an increased foraging efficiency (Jackson et al. 2006).

We conclude that besides the expected strong effect of seagrass canopy on macrobenthic invertebrates, distance from the meadow edge influenced their abundance, whereas the influence of seasonality was only small. Closed canopy structure and increasing distance from the edge both increased the macrobenthic invertebrate abundance. This indicates that differences in abundances can occur on a relatively small scale in seagrass meadows. For fish only increased canopy structure influenced their abundance, with no significant edge effect observed. We conclude that for motile fauna species the structure of the seagrass canopy and location within the meadow strongly influences their abundance. Comparing faunal abundances in different tropical seagrass meadows has to include a description of the canopy structure, the position relative to the meadow edge, and possibly seasonality to prevent misinterpretation of faunal abundance variation due to these environmental factors.

Acknowledgements

We thank Piet Nienhuis, Christian Mulder and both anonymous reviewers for comments on the manuscript, Alfian Noor for administrative arrangements in Indonesia, and Klaas Strating, Marjolein Pijnappels, and Saido for assistance with sampling. This research was funded by NWO-WOTRO grant W86-168, Schure-Beijerinck-Popping grant SBP/JK/2005-44 and the Department of Environmental Science, Radboud University Nijmegen.

References

Alcoverro T, Mariani S. 2004. Patterns of fish and sea urchin grazing on tropical Indo-Pacific seagrass beds. Ecography 27:361–65.

Bos AR, Gumanao GS, Alipoyo JCE, Cardona LT. 2008. Population dynamics, reproduction and growth of the Indo-Pacific horned sea star, *Protoreaster nodosus* (Echinodermata; Asteroidea). Marine Biology 156:55–63.

Boström C, Jackson EL, Simenstad CA. 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine Coastal and Shelf Science 68:383–403.

Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G. 2005. Distribution of coral reef fishes along a coral reef–seagrass gradient: Edge effects and habitat segregation. Marine Ecology Progress Series 299:277–88.

Edgar GJ, Shaw C. 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. Journal of Experimental Marine Biology and Ecology 194:53–81.

Erftemeijer PLA, Drossaert WME, Smekens MJE. 1993. Macrobenthos of two contrasting seagrass habitats in South Sulawesi, Indonesia. Wallaceana 70:5–12.

Erftemeijer PLA, Herman PMJ. 1994. Seasonal-changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. Oecologia 99:45–59.

Gullström M, Bodin M, Nilsson PG, Öhman MC. 2008. Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. Marine Ecology Progress Series 363:241–55.

Hemminga MA, Duarte CM. 2000. Seagrass Ecology. Cambridge: Cambridge University Press. 298 pages.

Howard RK, Edgar GJ, Hutchings PA. 1989. Faunal assemblages of seagrass beds. In: Larkum AWD, McComb AJ, Sheppard SA, editors. Biology of Seagrasses: A Treatise on the Biology of Seagrass with Special Reference to the Australian Region. Amsterdam: Elsevier, p 536–64.

Hyndes GA, Kendrick AJ, MacArthur LD, Stewart E. 2003. Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. Marine Biology 142:1195–206.

Jackson EL, Attrill MJ, Rowden AA, Jones MB. 2006. Seagrass complexity hierarchies: Influence on fish groups around the coast of Jersey (English Channel). Journal of Experimental Marine Biology and Ecology 330:38–54.

Kiswara W, Behnke N, van Avesaath P, Huiskes AHL, Erftemeijer PLA, Bouma TJ. 2009. Root architecture of six tropical seagrass species, growing in three contrasting habitats in Indonesian waters. Aquatic Botany 90:235–45.

Kuriandewa TE, Kiswara W, Hutomo M, Soemodihardjo S. 2003. The seagrasses of Indonesia. In: Green EP, Short FT, editors. World Atlas of Seagrasses. Hong Kong: University of California Press, p 171–82.

Nienhuis PH, Coosen J, Kiswara W. 1989. Community structure and biomass distribution of seagrasses and macrofauna in the Flores Sea, Indonesia. Netherlands Journal of Sea Research 23:197–214.

Ogden JC. 1980. Faunal relationships in Caribbean seagrass beds. In: Phillips RC, McRoy CP, editors. Handbook of Seagrass Biology, an Ecosystem Perspective. New York: Garland STPM Press, p 173–98.

Orth RJ, Heck KL, Vanmontfrans J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator prey relationships. Estuaries 7:339–50.

Peterson BJ, Thompson KR, Cowan JH, Heck KL. 2001. Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering. Marine Ecology Progress Series 224:77–85.

Polunin NVC, Roberts CM. 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100:167–76.

Robertson AI, Duke NC. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology 96:193–205.

Salita JT, Ekau W, Saint-Paul U. 2003. Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. Marine Ecology Progress Series 247: 183–95.

Sokal RR, Rohlf FJ 1995. Biometry. New York: W.H. Freeman & Co. 887 pages.

Smith TM, Hindell JS, Jenkins GP, Connolly RM. 2008. Edge effects on fish associated with seagrass and sand patches. Marine Ecology Progress Series 359:203–13.

Stapel J, Erftemeijer PLA. 2000. Leaf harvesting by burrowing alpheid shrimps in a *Thalassia hemprichii* meadow in South Sulawesi, Indonesia. Biologia Marina Mediterranea 7:282–85.

Stoner AW. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bulletin of Marine Science 30:537–51.

Tomascik T, Mah AJ, Nontji A, Moosa MK 1997. The Ecology of the Indonesian Seas. Part II. Singapore: Periplus Editions. 1388 pages.

Unsworth RKF, De Grave S, Jompa J, Smith DJ, Bell JJ. 2007a. Faunal relationships with seagrass habitat structure: A case study using shrimp from the Indo-Pacific. Marine and Freshwater Research 58:1008–18.

Unsworth RKF, Wylie E, Smith DJ, Bell JJ. 2007b. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuarine. Coastal and Shelf Science 72:81–88.

Valentine JF, Heck KL. 1993. Mussels in seagrass meadows: Their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico. Marine Ecology Progress Series 96:63–74.

Vermaat JE, Agawin NSR, Duarte CM, Fortes MD, Marbà N, Uri JS. 1995. Meadow maintenance, growth and productivity of a mixed Philippine seagrass bed. Marine Ecology Progress Series 124:215–25.

Vonk JA. 2008. Seagrass nitrogen dynamics – growth strategy and the effects of macrofauna in Indonesian mixed-species meadows. PhD thesis, Radboud University Nijmegen, Nijmegen, 192 pages.

Vonk JA, Pijnappels MHJ, Stapel J. 2008. *In situ* quantification of *Tripneustes gratilla* grazing and its effects on three co-occurring tropical seagrass species. Marine Ecology Progress Series 360:107–14.

Editorial responsibility: David McKinnon