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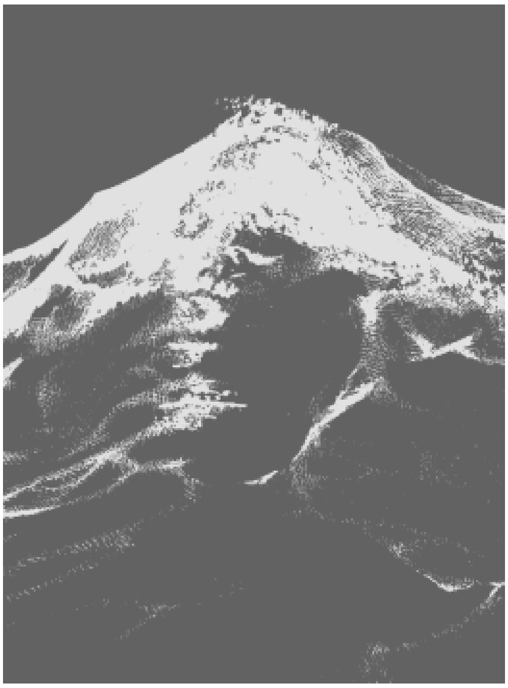

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Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf

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Abstract. A total of 8200 stomach samples was collected from 102 fish species caught by trawl or gillnet during research surveys on the south-eastern Australian shelf from 1993 to 1996. Diet compositions were analysed based on percentages of wet weight of prey. Of the total fish examined, 70 species had sufficient stomach samples (i.e. >10) for further analysis. Ten trophic guilds were identified from cluster analysis. Benthic prey dominated the diets. However, analysis on a subset of 28 abundant species that were commercially and ecologically important, showed that pelagic prey was dominant, particularly for 12 quota species. This suggests that pelagic production contributes significantly to the trawl fishery production. Further analysis on the diets of these 28 species found that although fish was more important than invertebrate prey, there was no evidence of significant predation on commercially important species (quota species) by other fish species. A food web diagram was constructed, mostly based on the diet compositions, guild structure and relative abundance of commercially and ecologically important fish species, to show major trophic interactions of the shelf ecosystem.

Introduction

The south-eastern Australian shelf, off Victoria and New South Wales (NSW) (Fig. 1), has been supporting demersal fisheries since the early 1900s (Tilzey 1994). Over 22 species are being harvested, with average annual fishery landings of ~25 000 t (Tilzey 1999). However, ecological interactions among these harvested species and between the harvested species and other abundant species have not been well studied. Since most fish are harvested by demersal trawls, we initially believed that benthic production would be the most important contribution to fishery production, whereas pelagic contributions, from either on or off the shelf, were believed to be relatively minor. Also, predation on harvested species, which could provide additional information on relative importance of fishing effects on the demersal fish communities, is poorly understood.

Between 1993 and 1997, CSIRO Marine Research conducted intensive investigations of factors that affect fishery production on the south-eastern Australian shelf (Bax *et al.* 1999; Bax and Williams 2000; Williams and Bax 2001). The project was multi-faceted and investigated the association of fish assemblages with habitats, and the influences of physical and chemical variables of the habitat in the biological attributes of the assemblages (papers in this issue). This paper presents the major parts of the project results on the diets and trophic guilds of commercially and other abundant or potentially piscivorous fish species. Specifically, the aims of this study were: (1) to describe the diets of ecologically and commercially important fish species in the shelf; (2) to identify the trophic guild structure of the fish community; (3) to compare the relative importance of pelagic and benthic contributions to the fishery production by comparing pelagic and benthic prey sources of commercial species; and (4) to evaluate the magnitude of predation on commercially important (quota) species. A conceptual food web model was also constructed, based on the diet compositions and the guild structure of the

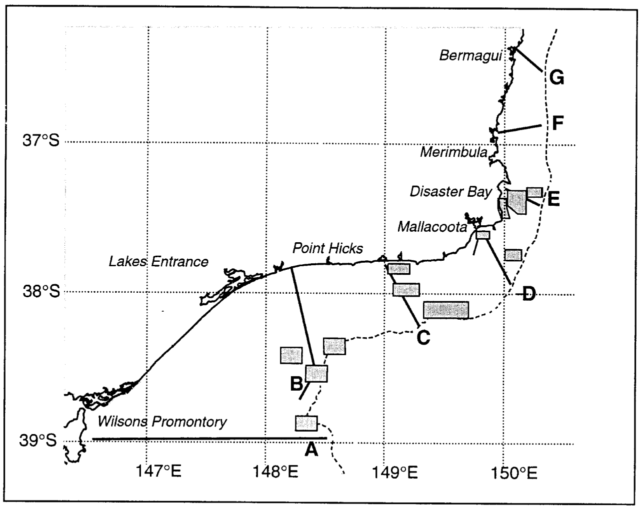

Fig. 1. Map of study area off south-eastern Australia, showing locations of transects A–G (bold lines) and mesohabitat study areas (greyed boxes).

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important species, to illustrate important trophic interactions in the shelf.

Methods

Study area

The study area was from Wilsons Promontory on the southern Victorian coast to Bermagui on the NSW coast in the south-eastern Australia continental shelf. The total area represented was about 23 900 km^2 within a depth range of 40–200 m. The sampling design had two phases: broad scale surveys and focussed area surveys. For the broad scale surveys, seven transects were sampled, each transect consisting of stations spaced at 25 m, 40 m, 80 m, 120 m and 200 m depths across the shelf (Fig. 1). For the focussed area surveys, sampling was focussed within six study areas or mesohabitats. Within these mesohabitats, 17 macrohabitats were defined at a finer scale. Details of the sampling locations and strategies are described in Bax and Williams 2000 and other papers (this volume). Fish were caught by bottom trawls in the broad scale surveys or by traps or gillnets in the focussed area surveys. Only data from the bottom trawls and gillnets were used in the analysis because trapped fish would have eaten bait. Data from the broad scale surveys and the focussed area surveys are combined in the analysis.

Sample collections

Surveys were conducted on the FRV *Southern Surveyor* during July–August 1993 (winter), August–September 1994 (spring), April–May 1996 (autumn) and November–December 1996 (summer), to cover seasons. Collections were made throughout each survey for the broad scale and focussed area studies. Where possible, a range of depths, time, geographical locations and size of fish was sampled for each species. From each bottom trawl, stomachs were removed from up to 10 fish per selected species. Fish that were obviously net-feeding were not selected. A maximum of 50 stomachs per species per cruise was taken. Additional samples were collected during commercial boat surveys in macrohabitats with non-trawl gear during June through October 1994, September 1995, May 1996 and January 1997. Large stomachs were frozen at –20°C and small stomachs were preserved in 10% formalin. Biological details such as length, weight and sex of sampled fish were recorded.

In the laboratory, stomachs were assessed for fullness and then dissected. Prey items were identified to the lowest possible taxon. Items were counted, blotted on absorbent paper to remove excess moisture and weighed (to 0.001 g in the case of very small items). Fish digested beyond recognition were identified from otoliths if possible. Squid beaks were identified by Dr C. C. Lu (formerly Museum of Victoria). No attempts were made to back-calculate sizes of animals from otolith or beak sizes.

Diets were described by determining the proportions of prey by wet weight in stomachs containing food, as this best represented trophic flows. Prey items were aggregated to 14 categories for further analyses. The functional categories were generally based on taxonomy and primary habitat except in the case of megabenthos that comprised two phyla, Mollusca and Crustacea. A similar system was used by Fujita *et al.* (1995) when examining shelf fishes off northern Japan. Justification for categorization was drawn from references such as Last *et al*. (1983), Bulman and Blaber (1986), Blaber and Bulman (1987), Gomon *et al*. (1994), Jones and Morgan (1994) and personal communication with CSIRO colleagues. Since over 800 prey items were identified, only the major taxa comprising the functional categories are listed in Table 1. Some taxa may comprise species that are categorized in different functional groups, e.g. Caridea, Ascidiacea, Macrouridae.

Data analysis

Overall, 217 species were caught during these surveys and stomachs were taken from 102 species (Bax *et al.* 2000). From this total, we chose 70 species for analysis because we were able to take sufficient numbers of stomach samples, usually more than 10 (Table 2). Initial analysis showed that sample variability was high between and within samples for some species. Therefore, all samples for a species were amalgamated in the analysis to represent an overall diet composition.

A cluster analysis was used to classify the 70 species into groups, which we assumed to represent trophic guilds. In the cluster analysis, the three unknown prey categories—fish, invertebrate and crustacean—were pro-rated across the appropriate prey categories to maximize the data available for use in the cluster analyses. We

Table 1. Functional prey categories and major prey taxa used to aggregate prey data in diet analyses of 70 fish species from the south-eastern Australian shelf

Species were identified from the taxa listed. Note that some taxa occur in more than one functional group

Functional group	Major taxa comprising functional groups
Benthic invertebrates	Echinodermata, Ascidiacea, Ectoprocta, Cnidaria, Branchiopoda, Gastropoda, Porifera, Sipuncula, Platyhelminthe, Echiura
Polychaetes	Polychaeta
Benthic crustaceans	Isopoda, Caprellidae, Gammaridae, Cyclopoida, Harpacticoida, Cumacea, Ostracoda, Stomatopoda
Megabenthos	Anomura, Brachyura, Homolidae, Caridea, Octopoda, Sepioida
Benthic fish	Bothidae, Callionymidae, Congridae, Elasmobranchii, Gerreidae, Gobiesocidae, Gonarynchidae, Macrorhamphosidae, Monacanthidae, Moridae, Opichthidae, Ophidiidae, Pempheridae, Pinguipedidae, Platycephalidae, Pleuronectidae, Rajidae, Scorpaenidae, Sillaginidae, Syngnathidae, Triglidae
Benthopelagic fish	Berycidae, Carangidae, Chlorophthalmidae, Gempylidae, Macrouridae, Ophididae, Percichthyidae, Platycephalidae, Scorpaenidae, Serranidae, Trichiuridae, Zeidae
Pelagic fish	Argentinidae, Congridae, Emmelichthyidae, Idiacanthidae, Malacosteidae, Myctophidae, Phosichthyidae, Scombridae, Scorpaenidae, Sternoptychidae
Pelagic invertebrates	Ascidiacea, Thaliacea, Teuthoidea, Nautiloidea, Cnidaria
Pelagic crustaceans	Penaeidae, Sergestidae, Caridea, Euphausiacea, Mysida, Calanoida, Cyclopoida, Hyperiidae
Unknown fish	Unidentifiable fish remains
Unknown crustaceans	Unidentifiable crustacean remains
Unknown invertebrates	Unidentifiable invertebrate remains other than crustacean
Unknown	Unidentifiable remains
Other	Sediment, macroalgae, seagrasses

assumed that this method based on the known diet components of the individual species, would best represent their diets. The unknown category was not pro-rated because it could not provide additional information. In the cluster analysis, we used Bray-Curtis dissimilarity coefficients with an average linkage clustering algorithm (SPSS Version 6.1, 1994).

A subset of 28 species was chosen for which we determined the relative importance of benthic and pelagic sources of prey, and the importance of quota fish species as prey. This subset consisted of 12 quota species and a further 16 'important' species (Table 2). We selected important species based on their high relative abundance in our surveys and their high representation in diets of the species analysed. The subset contributed between 44% and 76% of fish biomass caught in the broad scale trawl surveys, depending on area, and 78% of the biomass caught by trawl from the mesohabitat sites (see Bax *et al.* 2000 for more detail). Benthopelagic prey were classed as pelagic sources for this analysis as our diet data showed that for many species, most of their food was pelagic.

A food web was constructed for the shelf ecosystem. This will serve as a conceptual model for the trophic interactions of the system. We based the food web on the diet data and derived guild structure from the analysis, relative abundance of species and importance to the commercial fisheries in the shelf system. The model emphasized details in fish species with simplified components in the low trophic levels (plankton and benthic invertebrates). It does not include higher trophic levels such as seals, birds, tuna or large pelagic sharks.

Results

General description

Of the 70 species, about one-third was piscivorous (Table 3). Within families, diets could vary markedly between species. For example, in the dory family, three of the four dories were piscivores, *Zeus faber*, *Zenopsis nebulosus* and *Cyttus australis*, whereas *Cyttus novaezelandiae* ate only pelagic crustaceans. In the Triglidae, three species, *Chelidonichthys kumu*, *Lepidotrigla vanessa* and *Pterygotrigla polyommata* ate mainly benthic fish whereas the two others were invertebrate feeders: *Lepidotrigla mulhalli* was a benthopelagic feeder and *Lepidotrigla modesta* was a benthic feeder. In the *Caelorinchus* species, *C. mirus* was a benthic piscivore, *C. australis* was an omnivore and *C. parvifasciatus* and *C. fasciatus* were polychaete specialists.

Fish within families used not only very different prey but also different sources i.e. either pelagic or benthic. In the Scorpaenidae, both *Helicolenus percoides* and the closely related perch species, *Helicolenus barathri*, ate fish, pyrosomes, crabs, cephalopods and shrimps but the former ate a larger proportion of pelagic prey. In contrast, *Neosebastes scorpaenoides* ate more benthic prey such as crabs, gastropods and benthic fish. In the Serranid family, the *Caesioperca lepidoptera* ate benthic invertebrates such as ascidians, coral and polychaetes and pelagic shrimps, copepods and pyrosomes. In contrast, *Caesioperca rasor* and *Lepidotrigla pulchella* were piscivores, probably benthopelagic, and *Apogonops anomalus* was a pelagic piscivore.

Family members might also eat similar prey taxa but from different sources, such as in the previous example of the piscivorous perches. Both flatheads, *Neoplatycephalus richardsoni* and *Platycephalus bassensis*, were piscivores, but the former ate benthopelagic fish whereas the latter ate benthic fish.

Species that foraged in the same part of the water column could use different prey taxa. For example, the pelagic species, *Trachurus declivis* and *T. novaezelandiae*, ate largely myctophids and euphausiids. Similarly, *Centroberyx affinis* ate predominantly *Apogonops anomalus* and the same euphausiids. However, both warehous, *Seriolella* species, ate mostly pyrosomes.

Some species specialized in quite specific prey items; the warehous in pyrosomes, and as an example of exclusive piscivores, *Genypterus blacodes*, *Lepidoperca pulchella* and *Rexea solandri* all ate predominantly fish but from benthic, benthopelagic and pelagic origins, respectively.

Guild structure

Overall diets were calculated, and prey items were amalgamated into the broad prey categories for cluster analysis (Table 3). From the dendrograms the nine guilds produced were identified at a dissimilarity level of 70% (Fig. 2), including a group of species whose diet consisted predominantly of unknown prey. These species probably did not group into more descriptive groups because not enough data were available to describe their diets reliably. A few species could be misappropriately clustered because the reproportioned data might misrepresent their real feeding preferences, i.e. benthic, benthopelagic or pelagic. Also, these data were based on proportions by weight that might overemphasize larger, rarer prey items or underemphasize smaller, more common prey items, and so give a false impression of the guild to which the fish actually belongs.

Omnivores were species that ate a variety of invertebrate prey in dominant proportions and included fish at greater than 10%. Benthopelagic omnivores specializing in megabenthos and benthic crustaceans were *Caelorinchus australis*, *Helicolenus percoides*, *H. barathri*, *Squalus megalops* and *Mustelus antarcticus*. *Pseudolabrus psittaculus* was probably also a benthopelagic omnivore but ate a high proportion of unknown prey. Also specializing in megabenthos and small crustaceans was a group of epibenthic invertebrate feeders including *Urolophus* species and two benthic omnivores, *Raja* sp. A and *Neosebastes scorpaenoides*. The last two ate fish in low proportions (between 10% and 50%), which may account for why they were not differentiated from the epibenthic invertebrate feeders in the analyses. These two groups differentiated at about 65% dissimilarity.

Polychaete specialists were included invertebrate feeders *Parequula melbournensis* and *Narcine tasmaniensis* and

Table 2. Common and scientific names and numbers of stomach samples for the 70 fish species from the south-eastern Australian shelf

The list is divided into three parts: 12 quota species (commercial fishery); 16 ecologically important species (abundant species); and the remaining 32 species. The species in the first two parts comprise the subset used in detailed analyses

Species name	Common name	No. stomachs containing food	No. stomachs examined
Quota species			
Centroberyx affinis	Redfish	379	485
Genypterus blacodes	Pink ling	93	111
Helicolenus percoides	Ocean perch	572	848
Nemadactylus macropterus	Jackass morwong	327	552
Neoplatycephalus richardsoni	Tiger flathead	171	350
Pseudocaranx dentex	White trevally	27	72
Rexea solandri	Gemfish	6	12
Seriolella brama	Blue warehou	80	130
Seriolella punctata	Silver warehou	283	462
Sillago flindersi	Eastern school whiting	52	222
Zenopsis nebulosus	Mirror dory	19	59
Zeus faber	John dory	120	29
Ecologically important species			
Apogonops anomalus	Three-spined cardinal fish	79	115
Caesioperca lepidoptera	Butterfly perch	53	65
Cephaloscyllium laticeps	Draughtboard shark	93	14
Chlorophthalmus nigripinnis	Cucumberfish	210	242
Cyttus australis	Silver dory	103	149
Lepidotrigla mulhalli	Deepwater gurnard	130	165
Macrorhamphosus scolopax	Common bellowsfish	236	254
Meuschenia scaber	Velvet leatherjacket	66	87
Synchiropus calauropomus	Common stinkfish	121	142
Urolophus paucimaculatus	Sparsely-spotted stingaree	147	154
Helicolenus barathri	Deep ocean perch	54	74
Latris lineata	Striped trumpeter	12	22
Nemadactylus douglasi	Grey morwong	19	22
Platycephalus bassensis	Sand flathead	13	42
Squalus megalops	Spikey dogfish	130	190
Trachurus declivis	Jack mackerel	345	586
Other species			
Allomycterus pilatus	Deepwater burrfish	17	24
Arothron firmamentum	Starry toadfish	11	11
Atypichthys strigatus	Mado sweep	24	31
Azygopus pinnifasciatus	Banded-fin flounder	10	20
Caelorinchus australis	Southern whiptail	24	24
Caelorinchus fasciatus	Banded whiptail	25	36
Caelorinchus mirus	Gargoyle fish	58	58
Caelorinchus parvifasciatus	Faint-banded whiptail	12	13
Caesioperca rasor	Barber perch	11	18
Chelidonichthys kumu	Red gurnard	25	25
Cyttus novaezelandiae	New Zealand dory	40	40
Diodon nicthemerus	Globefish	80	114
Emmelichthys nitidus nitidus	Redbait	78	89
Galeorhinus galeus	School shark	3	12
Kathetostoma canaster	Speckled stargazer	23	23
Kathetostoma laeve	Common stargazer	15	16
Latridopsis forsteri	Bastard trumpeter	20	20
Lepidoperca pulchella	Eastern orange perch	6	25
Lepidotrigla modesta	Minor gurnard	119	129
Lepidotrigla vanessa	Butterfly gurnard	20	20
Meuschenia freycineti	Sixspined leatherjacket	72	72

Mustelus antarcticus	Gummy shark	7	17
Narcine tasmaniensis	Tasmanian numbfish	37	37
Neosebastes scorpaenoides	Ruddy gurnard perch	30	30
Notolabrus tetricus	Bluethroat wrasse	6	9
Ophthalmolepis lineolata	Maori wrasse	11	13
Pagrus auratus	Snapper	13	17
Paramonacanthus filicauda	Leatherjacket	9	10
Parequula melbournensis	Silverbelly	10	10
Parma microlepis	White ear	1	5
Pempheris multiradiatus	Common bullseye	10	26
Pseudolabrus psittaculus	Rosy wrasse	12	14
Pterygotrigla polyommata	Latchet	20	22
Raja sp. A	Longnose skate	63	63
Scomber australasicus	Blue mackerel	48	59
Scorpis lineolata	Silver sweep	8	8
Squatina australis	Australian angel shark	37	47
Thyrsites atun	Barracouta	174	24
Trachurus novaezelandiae	Yellowtail horse mackerel	10	10
Urolophus cruciatus	Banded stingaree	132	132
Urolophus sp. A	Kapala stingaree	7	7
Urolophus viridis	Green-back stingaree	120	120

also benthic omnivores *S. flindersi* and *Nemadactylus macropterus*.

Meuschenia freycineti, *Meuschenia scaber* and *Synchiropus calauropomus* were included in the group of epibenthic invertebrate feeders and omnivores that ate invertebrates other than crustaceans.

The groups containing the benthic and benthopelagic piscivores clearly differentiated in the dendrogram grouping. These groups ate more than 50% fish, and in most cases more than 80%. *Zeus faber*, *Zenopsis nebulosus*, *Pagrus auratus*, *Kathetostoma laeve*, *Thyrsites atun*, *Galeorhinus galeus* and *Neoplatycephalus richardsoni* were virtually exclusive piscivores.

Pelagic invertebrate feeders, *Seriolella punctata* and *S. brama*, fed mostly on pyrosomes. *Cyttus novaezelandiae* and *Paramonacanthus filicauda* and *Pempheris multiradiata* were pelagic crustacean feeders, whereas *Trachurus declivis* and *Centroberyx affinis* included fish in their diets, and were classified as omnivores.

Apogonops anomalus and *Scorpis lineolata* were pelagic piscivores. *Scomber australasicus* also clustered as a piscivore but might be better classified as a pelagic omnivore since it ate mostly pelagic invertebrates such as ascidians, pyrosomes and salps and less than 40% fish.

Prey sources

In the full data set of 70 species, more than half the species, i.e. 37, relied on benthic foods as their major food source. In contrast, pelagic prey sources dominated in 18 of the 28 commercial or abundant species (Plate I). Furthermore, the diets of nine of the 12 quota species, i.e. *R. solandri*, *Z. nebulosus*, *S. brama*, *S. punctata*, *C. affinis*, *Z. faber*, *P. dentex*, *H. percoides* and *N. richardsoni*, were dominated by pelagic prey sources. The species that ate predominantly benthic prey were *S. flindersi*, *N. macropterus*, *G. blacodes*, *L. mulhalli*, *U. paucimaculatus*, *H. barathri*, *M. scaber*, *P. bassensis*, *S. calauropomus* and *N. douglas*i, of which the first three were quota species. Prey of *M. scolopax* was largely unidentified (70%) but likely to have also been benthic.

Piscivory on quota species

The majority of the 28 commercial or abundant species were piscivorous. Fish comprised more than 50% of the diets of 12 species and more than 30% of 15 species (Table 4). However, of all the fish-eaters, 27 of the 28 species, only four ate more than 1% of quota species. The highest proportions were found in the diets of *L. lineata* where 17% of the diet was *Helicolenus* species and in *Z. faber* where 10% of the diet was *C. affinis*. *N. richardsoni* ate over 5% of *S. flindersi* and 2% of *G. blacodes*. Also of interest was that *T. declivis*, a non-quota species, was eaten in large amounts by *Z. faber* (43%), *Z. nebulosus* (50%) and *C. laticeps* (34%).

Food web

In the food web diagram (Fig. 3), the 70 fish species were grouped into 16 trophic boxes. These groupings were largely based on the diet compositions (Table 3), similarities of life history and growth patterns, importance to the commercial fisheries and ecological importance (relative abundance). The groupings, however, were very arbitrary. All fish boxes, except the small fishes one, were intended to represent interactions between adult or subadult fishes. Juvenile fishes were pooled in the small fish box. The additional six prey categories were added to represent major prey groups for both benthic and pelagic prey sources. Arrows connecting boxes represent major food web

Table 3. Diets of fish from the south-eastern Australian shelf expressed as percentage by weight for 14 prey categories
See text for details of each prey category (* denotes <1% and – denotes prey is absent)

Predator	Other	Benthic invertebrate	Polychaeta	Benthic crustacean	Megabenthos	Benthic fish	Benthopelagic fish	Pelagic invertebrate	Pelagic crustacean	Pelagic fish	Unknown invertebrate	Unknown crustacean	Unknown fish	Unknown
Quota species														
Centroberyx affinis	*	*	*	2	5	2	26	*	35	7	–	20	3	*
Genypterus blacodes	*	2	*	*	9	69	9	7	1	*	*	*	2	*
Helicolenus percoides	*	2	1	8	9	21	9	32	1	2	–	1	13	1
Nemadactylus macropterus	*	5	43	11	7	1	5	1	9	*	–	5	5	8
Neoplatycephalus richardsoni	*	*	*	1	2	39	23	*	*	16	–	1	18	–
Pseudocaranx dentex	–	*	*	5	9	*	60	–	*	–	–	*	*	25
Rexea solandri	–	–	–	–	–	–	15	–	–	–	–	–	79	6
Seriolella brama	*	*	*	*	–	*	–	71	*	–	11	*	*	16
Seriolella punctata	*	*	*	*	*	–	–	83	*	–	–	*	*	16
Sillago flindersi	–	18	45	1	1	3	–	1	*	–	1	1	23	7
Zenopsis nebulosus	–	–	–	–	*	–	51	–	–	45	–	–	3	*
Zeus faber	*	*	*	*	*	11	67	2	*	10	–	*	11	–
Ecologically important species														
Apogonops anomalus	*	–	*	–	1	–	–	*	12	23	–	3	60	1
Caesioperca lepidoptera	–	3	*	*	*	–	–	41	4	–	–	5	*	46
Cephaloscyllium laticeps	*	4	*	*	28	5	42	6	–	1	–	2	11	–
Chlorophthalmus nigripinnis	3	7	3	2	10	1	–	24	21	–	3	7	8	11
Cyttus australis	*	*	–	*	1	40	48	*	4	–	–	1	5	*
Lepidotrigla mulhalli	–	1	*	20	25	*	–	*	28	–	–	23	1	1
Macrorhamphosus scolopax	3	4	4	15	3	*	–	1	3	–	*	52	*	14
Meuschenia scaber	5	58	3	*	2	–	–	2	*	–	*	1	–	29
Synchiropus calauropomus	26	38	7	2	9	–	–	*	*	–	*	8	*	11
Urolophus paucimaculatus	*	3	17	7	27	*	–	*	1	–	–	38	*	7
Helicolenus barathri	*	8	12	21	9	5	4	5	5	1	–	7	19	3
Latris lineata	–	2	–	*	*	28	45	4	–	–	–	–	20	–
Nemadactylus douglasi	*	2	3	3	82	–	–	–	*	–	–	1	5	3
Platycephalus bassensis	–	1	*	–	1	66	–	6	–	–	–	–	25	–
Squalus megalops	–	4	1	*	23	13	10	18	*	*	*	1	28	1
Trachurus declivis	1	1	*	*	*	*	*	1	31	18	–	32	13	2
Other species														
Allomycterus pilatus	–	38	–	20	25	–	–	1	–	–	–	15	*	–
Arothron firmamentum	2	20	3	8	*	–	–	1	13	–	–	19	–	33
Atypichthys strigatus	*	*	–	*	*	*	–	9	*	–	–	*	83	7
Azygopus pinnifasciatus	–	87	8	1	–	–	–	*	–	–	–	1	1	1
Caelorinchus australis	–	*	24	13	25	21	–	9	1	–	–	6	1	–
Caelorinchus fasciatus	–	17	32	5	22	–	–	*	2	–	–	9	*	13
Caelorinchus mirus	–	1	1	5	10	–	–	*	2	–	–	9	59	13
Caelorinchus parvifasciatus	–	36	51	1	5	–	–	–	–	–	–	3	2	3
Caesioperca rasor	–	5	–	*	–	*	–	11	8	–	–	2	70	4
Chelidonichthys kumu	4	3	*	–	1	87	2	1	–	–	–	–	1	*
Cyttus novaezelandiae	–	–	–	–	–	–	–	–	95	–	–	5	–	–
Diodon nicthemerus	*	50	2	8	38	–	–	1	–	–	–	–	–	*
Emmelichthys nitidus nitidus	–	*	–	*	*	–	–	27	18	–	–	14	4	37
Galeorhinus galeus	–	*	–	1	2	7	42	1	–	15	–	*	32	–
Kathetostoma canaster	–	*	–	*	4	16	76	1	–	–	–	–	3	*
Kathetostoma laeve	–	*	–	*	1	44	39	*	–	–	–	*	16	–
Latridopsis forsteri	3	4	1	10	2	–	–	–	–	–	–	6	–	75
Lepidoperca pulchella	–	1	–	–	–	–	–	*	*	–	–	1	98	*

Lepidotrigla modesta	*	*	4	10	63	1	–	–	9	2	–	10	*	*
Lepidotrigla vanessa	–	*	–	*	11	71	–	*	4	–	–	1	13	*
Meuschenia freycineti	2	61	4	3	16	–	*	7	–	–	1	3	1	2
Mustelus antarcticus	–	*	*	1	35	*	9	46	–	–	–	7	2	–
Narcine tasmaniensis	–	12	84	2	1	–	–	–	*	–	1	*	–	1
Neosebastes scorpaenoides	–	23	–	8	50	16	–	*	–	–	–	*	2	–
Notolabrus tetricus	–	41	–	–	18	–	–	29	–	–	–	2	6	5
Ophthalmolepis lineolata	–	18	–	–	6	–	–	–	–	–	–	*	69	6
Pagrus auratus	–	4	–	*	–	7	89	*	–	–	–	*	*	–
Paramonacanthus filicauda	–	1	*	–	–	–	–	*	26	–	–	73	–	*
Parequula melbournensis	–	18	64	4	*	–	–	–	–	–	–	1	–	13
Parma microlepis	*	16	*	–	–	–	–	1	–	–	–	–	–	83
Pempheris multiradiatus	–	–	20	*	*	–	–	*	76	–	–	3	–	1
Pseudolabrus psittaculus	–	32	–	–	–	–	–	–	1	–	–	17	27	23
Pterygotrigla polyommata	–	–	–	–	20	65	3	*	–	–	–	*	12	–
Raja sp. A	*	*	*	1	46	44	*	1	1	–	–	2	4	1
Scomber australasicus	–	*	*	*	–	–	–	35	5	–	–	22	38	1
Scorpis lineolata	*	–	2	–	–	–	–	18	*	–	–	–	80	–
Squatina australis	*	1	*	1	*	20	5	1	*	2	–	*	70	*
Thyrsites atun	–	–	–	*	*	12	64	*	1	4	–	*	19	*
Trachurus novaezelandiae	–	–	–	1	–	–	–	*	8	–	–	1	–	89
Urolophus cruciatus	*	21	42	5	15	–	–	*	*	–	*	9	–	7
Urolophus sp. A	–	*	*	16	57	–	–	–	8	–	–	14	–	4
Urolophus viridis	*	2	16	11	30	*	–	–	3	–	*	30	3	6

interactions. The apex predators appeared to be dogfish (which included small sharks), dories, ling, flathead and a group of large fish including *Chelidonicthys kumu*, *Latris lineata* and *Pagrus auratus* (see Table 2 for scientific or common names).

Discussion

The study of guild structure in community ecology has become popular to illustrate the internal organization of communities (Jaksic and Medel 1990). The term guild has been defined as the ' .. term [which] groups together species, without regard to taxonomic positions, that overlap significantly in their niche requirements' (Root 1967 cited in Jaksic and Medel 1990). Studies of guild structure are generally restricted to single phylogenetic groups, such as the fishes in this study, but they provide basic structures from which further analysis of food web and linkages to other components of ecosystems can be derived. Definition of guild structure is no doubt dependent on aggregations of data, such as prey groupings (see below for more discussion), and on statistical methods used for classifications. We believe that the analysis broadly represented the guild structure of this system.

The guild assignments of species in this study were mostly the same as those determined in other studies in this region. *Apogonops anomalus*, *Genypterus blacodes* and *Helicolenus percoides* were assigned to similar guilds in a study on the upper slope off eastern Tasmania (Blaber and Bulman 1987). On the other hand, we assigned *T. declivis* to the pelagic omnivore guild, whereas Blaber and Bulman (1987) assigned it to the pelagic piscivore guild. The difference here is mainly due to the contribution of fish in diets. In this study, the contribution of fish was 38%, if we converted wet weight to energy terms, compared with 90% energy in the Tasmanian study. If we had used energy terms, we would also have assigned it to the pelagic piscivore group according to our criteria. It is also possible that differences in diet could be due to depth or locality differences. Young *et al.* (1993) and Williams and Pullen (1993) found that the diets of *T. declivis* caught at similar depths to this study were dominated by *Nyctiphanes australis*, a neritic euphausiid known as krill, during autumn. They suggest that *T. declivis* might aggregate when krill is abundant but switch to other abundant prey such as mesopelagic fishes. Similar results were also found in the early slope study (Blaber and Bulman 1987).

In this study, we did not consider the relative abundances of either predators or prey, although their importance can be seen from the *T. declivis* example. Variation in diet could be due to seasonality in predator or prey abundance, ontogenetic shifts in diet, depth and location. Since we did not examine these variations here, the results presented in this paper should be considered as overall averages of diet compositions and guild structure of the system. Detailed descriptions of the diets of these species, as related to fish size, depth and habitat types, are certainly possible and will be analysed further in separate papers.

Although nearly half the fish in the subset of 28 species were highly piscivorous—more than 50% of their diet was fish—very little of the fish component comprised quota species. However, it is not known if a significant portion of the unidentified fish component might have been quota

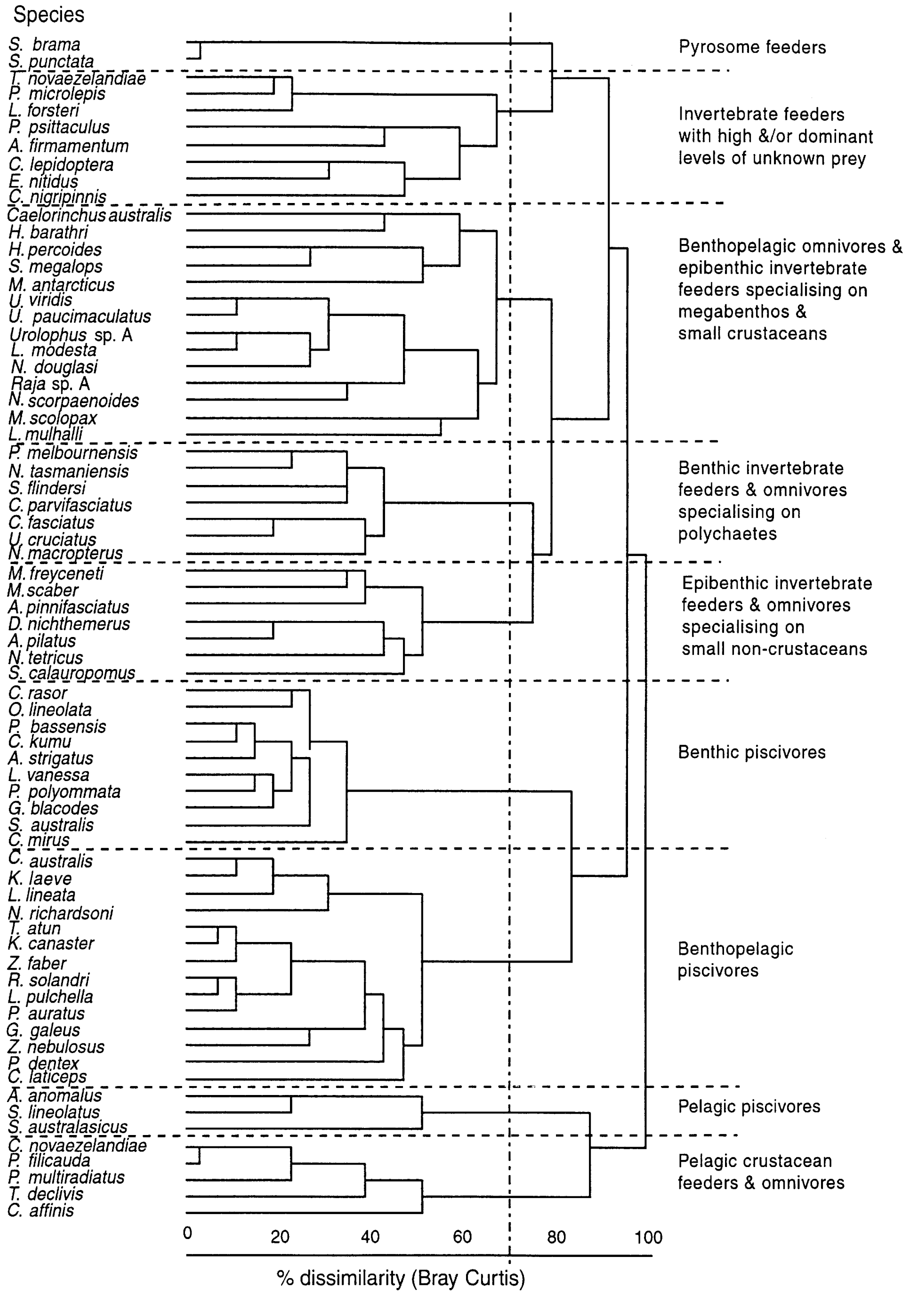

Fig. 2. Cluster dendrogram, based on Bray–Curtis dis-similarity measures of diet composition, of 70 fish species from the south-eastern Australian shelf.

species, particularly juveniles that would be more rapidly digested and unidentifiable than larger fish. It is obvious that juveniles are preyed on because we detected *N. richardsoni* feeding on *G. blacodes* that were probably the young of the year. Similarly, *Latris lineata* were probably feeding on juvenile *Helicolenus percoides*. In these cases, the relative consumption in numbers is much higher and predators could be consuming a significant proportion of the prey species' year class.

In our study, the diet of the overall community is nearly equally split between benthic and pelagic prey sources. It is expected that benthic associations are more common in fish assemblages in shallower water and that deeper species are more generalist feeders (Mauchline and Gordon 1985). Despite this, the large majority of the 12 commercial fishes in our study, relies very much on pelagic prey. Since these 12 species comprised up to 52% of the fish biomass caught in the broad scale surveys and 21% of fish caught in the

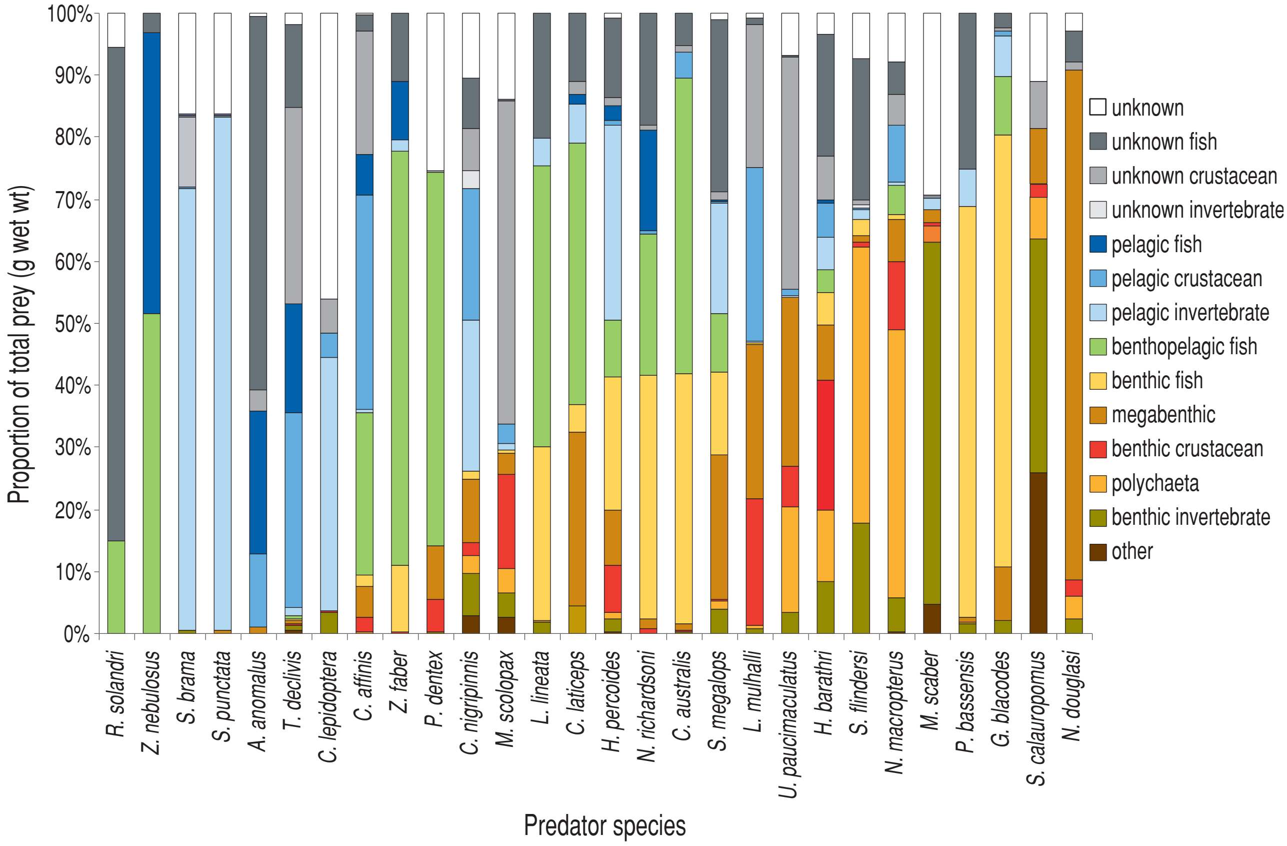

Plate I. Diet composition based on wet weight of prey for 28 fish species from the south-eastern Australian shelf. They include 12 quota species (commercial fishery) and 16 ecologically important species (see Table 2 for detailed list). Cool colours indicate pelagic prey sources and warm colours indicate benthic sources.

mesohabitats, the importance of pelagic production to the overall community becomes much more significant. Mesopelagic prey were also important to demersal fish in other coastal shelf waters (Fujita *et al.* 1995), and in deeper waters on the upper- and mid-slope (Pearcy and Ambler 1974; DuBuit 1978; Sedberry and Musik 1978; Mauchline and Gordon 1984*a*, 1984*b*, 1984*c*; Bulman and Blaber 1986; Houston and Haedrich 1986; Blaber and Bulman 1987; Gordon and Mauchline 1990). The pelagic prey of these predator species is often very abundant (Targett 1981; Bulman and Blaber 1986; Fujita *et al.* 1995) and this abundance might contribute to the reduction of competition between the predators.

The dependence on pelagic food sources, and *T. declivis*, by the species in our subset of commercially and ecologically important species, adds an interesting dimension to management of multi-species fisheries. Much of this pelagic prey was fish. Understanding the trophic structure and interactions is fundamental to understanding the dynamics of the ecosystem. Although the methodology and completeness of available information are often grossly inadequate (Pimm *et al.* 1991), food web analysis and modelling can provide better information for ecosystem management problems.

Fundamental to food-web analyses is the appropriateness of the pooling or aggregation of prey taxa. Here we used ‘functional groupings’ as the preferred method because we could consider size, mobility, taxa and habitat. We assumed that predators were more likely to be generalists than specialists in response to prey availability but that certain preferences such as habitat (i.e. source) or size might also be important. The resulting guilds might be too coarse and not reflect the ways in which species partition their niches. However, other factors not considered, such as depth and locality, may also be equally important. Further food web analysis may prove that these groupings need modifying.

The only previous food web structure designed for species in the same area of the SEF shelf was that of Parry *et al.* (1990). They examined trophic interactions of species from 7 to 30 m and from 30 to 50 m. Their study is based on only 12 species and a small numbers of stomach samples. Our study covers a much broader depth range, from 25 m to

Table 4. Percentage by weight of total, quota species, *T. declivis* and other fish in the fish component of the diets of 27 fish-eating species from the south-eastern Australian shelf

The quota species (indicated by *) are commercial fishery species. The 27 species are within the 28 species subset (see Table 2)

Prey type	Total fish	Quota fish	*T. declivis*	Other fish
L. lineata	93.5	17.4		76.1
**Z. faber*	97.9	11.3	43.0	43.6
**N. richardsoni*	96.4	7.8	0.7	87.9
C. laticeps	58.9	6	33.5	19.4
**C. affinis*	37.0	0.9		36.1
**N. macropterus*	10.8	0. 5		10.3
C. australis	93.3	0.4		92.9
P. bassensis	91.4	0.2		91.2
T. declivis	31.4	0.2		31.2
S. megalops	50.8	0.1		50.7
**G. blacodes*	81.3	0.1		81.2
**Z. nebulosus*	100	0	50.4	49.6
**R. solandri*	94.4	0		94.4
A. anomalus	83.1	0		83.1
**P. dentex*	60.4	0		60.4
**H. percoides*	45.6	0	4.7	40.9
**H. barathri*	28.7	0		28.7
**S. flindersi*	25.6	0		25.6
C. nigripinnis	9.2	0		9.2
N. douglasi	5.0	0		5.0
L. mulhalli	1.2	0		1.2
M. scolopax	0.6	0		0.6
U. paucimaculatus	0.2	0		0.2
C. lepidoptera	0.2	0		0.2
**S. brama*	0.2	0		0.2
**S. punctata*	0.2	0		0.2
S. calauropomus	0.1	0		0.1

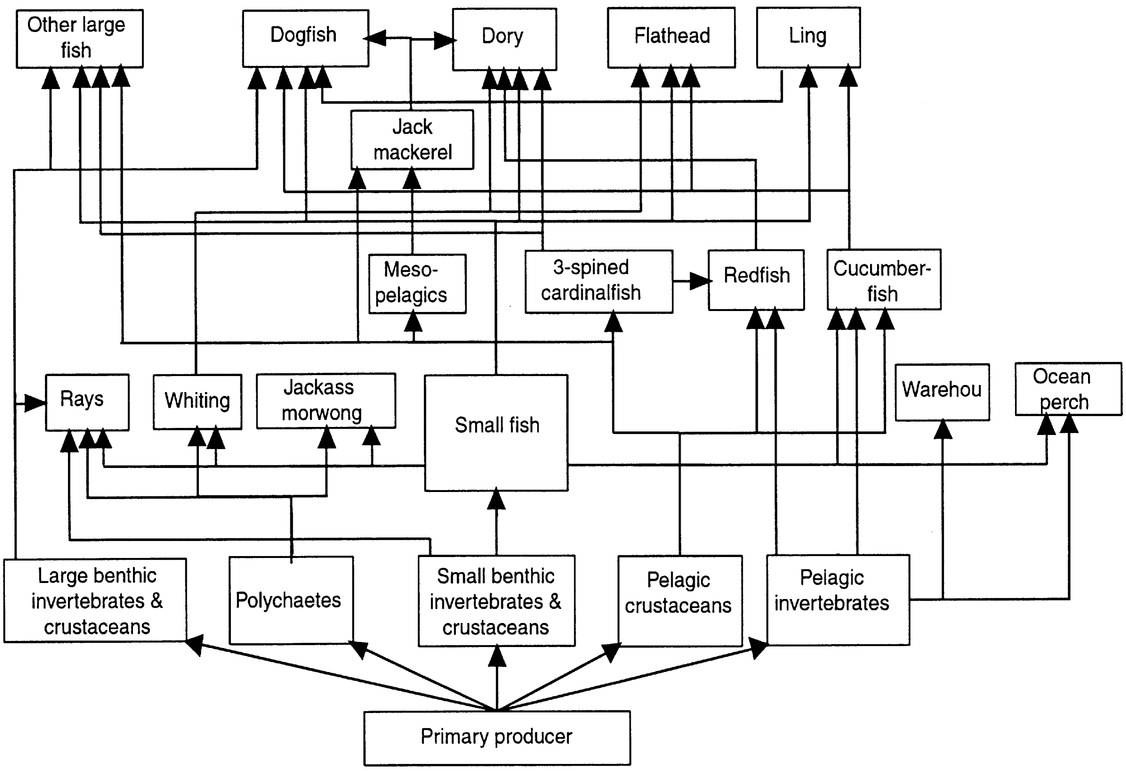

Fig. 3. Food web diagram for the south-eastern Australian shelf.

200 m, and combines all depths. We also examined a larger number of species and stomach samples. Despite this, flathead, dogfish and rays appear dominant in both studies. In our study we deliberately chose to treat certain species separately because of their importance, e.g. quota species, and so our food web was devised with further analysis of energy flows and significant interactions in mind.

In demersal ecosystems such as the SEF shelf, where prey species are diverse and their production can be driven by the outer shelf production, tightly coupled predator–prey interactions are unlikely because predators can switch to more abundant prey, or switch from pelagic to benthic prey or vice versa. We found that although there appeared to be many species of apex predators, none was abundant enough to be considered as a 'keystone' predator. Similarly, large sharks, marine mammals and birds were not considered to be keystone predators either. Such a lack of 'keystone' species is common in other marine systems (Jennings and Kaiser 1998). This suggests that the fishery may play an important role in determining fish community structure. This is commonly seen in many other marine systems (Jennings and Kaiser 1998; Hall 1999).

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References

Bax, N., and Williams, A. (eds) (2000). Habitat and fisheries production in the South East Fishery ecosystem. Final Report to Fisheries Research and Development Corporation. (CSIRO: Hobart, Australia.)

Bax, N., Williams, A., Davenport, S., and Bulman, C. (1999). Managing the ecosystem by leverage points: a model for a multispecies fishery. In 'Ecosystem Approaches for Fisheries Management'. Proceedings of the 1998 Wakefield Symposium on Ecological Considerations in Fisheries Management. pp. 283–303. (Alaska Sea Grant College Program.)

Bax, N., Williams, A., and Gowlett-Homes, K. (2000). Biological communities. In 'Habitat and Fisheries Production in the South East Fishery Ecosystem'. (Eds N. Bax and A. Williams.) Final Report to Fisheries Research and Development Corporation. (CSIRO: Hobart, Australia.)

Blaber, S. J. M. and Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345–56.

Bulman, C. M., and Blaber, S. J. M. (1986). Feeding ecology of *Macruronus novaezelandiae* (Hector)(Teleostei: Merluciidae) in south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **37**, 621–39.

DuBuit, M. H. (1978). Alimentation de quelques poissons téléostéens de profondeur dans la zone du seuil de Wyville Thomson. *Oceanologica Acta* **1**, 129–34.

Fujita, T., Kitagawa, D., Okuyama, Y., Ishito, Y., Inada, T. and Jin, Y (1995). Diets of the demersal fishes on the shelf off Iwate, northern Japan. *Marine Biology* **123**, 219–33.

Gomon, M. F., Glover, J. C. M., and Kuiter, R. H. (eds)(1994). 'The Fishes of Australia's South Coast.' (State Print: Adelaide, Australia.) 992 pp.

Gordon, J. D. M., and Mauchline, J. (1990). Depth-related trends in diets of a seep-sea bottom-living fish assemblage of the Rockall Trough. In 'Trophic Relationships in the Marine Environment'. Proceedings of the 24th European Marine Biology Symposium. (Eds M. Barnes and R. N. Gibson.) pp. 439–52. (Aberdeen University Press: Aberdeen.)

Hall, S. J. (1999). 'The Effects of Fishing on Marine Ecosystems and Communities.' (Blackwell Science: London.) p. 274.

Houston, K. A., and Haedrich, R. L. (1986). Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, northwest Atlantic Ocean. *Marine Biology* **92**, 563–74.

Jaksic, F. M., and Medel, R. G. (1990). Objective recognition of guilds: testing for statistically significant species clusters. *Oecologia* **82**, 87–92.

Jennings, S., and Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. In 'Advances in Marine Biology'. (Eds J. H. S. Baxter, A. H. Southward and P. A. Tyler.) pp. 203–343. (Academic Press: London.)

Jones, D. S. and Morgan, G. J. (1994). 'A Field Guide to Crustaceans of Australian Waters.' (Reed: Sydney, Australia.) 216 pp.

Last, P. R., Scott, E. O. G., and Talbot, F. H. (1983). 'Fishes of Tasmania.' (Tasmanian Fisheries Development Authority: Hobart, Australia.) 563 pp.

Mauchline, J., and Gordon, J. D. M. (1984*a*). Feeding and bathymetric distribution of the gadoid and morid fish of the Rockall Trough. *Journal of the Marine Biological Association U. K.* **64**, 657–65.

Mauchline, J., and Gordon, J. D. M. (1984*b*). Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. *Journal du Conseil International pour l'Exploration de la Mer* **41**, 239–47.

Mauchline, J., and Gordon, J. D. M. (1984*c*). Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology* **81**, 107–21.

Mauchline, J. and Gordon, J. D. M. (1985). Trophic diversity in deep-sea fish. *Journal of Fish Biology* **26**, 527–35.

Parry, G. D., Campbell, S. J., and Hobday, D. K. (1990). Marine resources off east Gippsland, southeastern Australia. Marine Science Laboratories Technical Report No. 72. 166 pp.

Pearcy, W. G., and Ambler, J. W. (1974). Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep Sea Research* **21**, 745–59.

Pimm, S. L., Lawton, J. H., and Cohen, J. E. (1991). Food web patterns and their consequences. *Nature* **350**, 669–74.

Sedberry, G. A., and Musick, J. A. (1978). Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the USA. *Marine Biology* **44**, 357–75.

Targett, T. E. (1981). Trophic ecology and structure of coastal Antarctic fish communities. *Marine Ecology Progress Series* **4**, 243–63.

Tilzey, R. D. J. (1994). Introduction. In 'The South East Fishery'. (Ed. R. D. J. Tilzey.) pp. 15–40. (Bureau of Resource Sciences: Canberra, Australia.) 360 pp.

Tilzey, R. D. J. (ed.) (1999). 'The South East Fishery 1998, Fishery Assessment Report Compiled by the South East Fishery Assessment Group.' (Australian Fisheries Management Authority: Canberra, Australia.) 199 pp.

Williams, A., and Bax, N. J. (2001). Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**, 513–36.

Williams, H., and Pullen, G. (1993). Schooling behaviour of jack mackerel *Trachurus declivis* (Jenyns) observed in the Tasmanian Purse-seine fishery. *Australian Journal of Marine and Freshwater Research* **44**, 577–87.

Young, J. W., Jordan, A. R., Bobbi, C., Johannes, R. E., Haskard, K., and Pullen, G. (1993). Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia. *Marine Biology* **116**, 9–18.

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