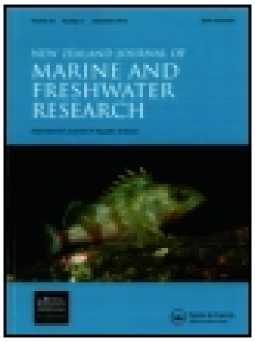

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Food resource use among five flatfish species (Pleuronectiformes) in Wellington Harbour, New Zealand

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Abstract Gut content analyses of 1068 samples from flatfish in Wellington Harbour were carried out to determine patterns of food resource use among five species co-occurring there. Diets differed between species and, for some species, varied with location, season, and time of day. Two broad patterns of food resource use were recognised. Firstly, four species *(Rhombosolea plebeia, R. leporina, Peltorhamphus novaezeelandiae, Pelotretis flavilatus)* fed on benthic infauna and epifauna while the fifth species *(Arnoglossus scapha)* fed on benthic epifauna and pelagic organisms. Secondly, three species *(R. plebeia, R. leporina, P. novaezeelandiae)* had relatively diverse diets which closely overlapped while two species *(P. flavilatus, A. scapha)* had relatively narrow diets and little dietary overlap. The same species show different patterns of food resource use elsewhere in New Zealand; it is proposed that local conditions contribute to the observed patterns in Wellington Harbour.

Keywords Pleuronectiformes; co-occurring species; food resource-use; New Zealand; *Rhombosolea; Peltorhamphus; Pelotretis; Arnoglossus*

INTRODUCTION

Fifteen species of flatfish (Pleuronectiformes) are found in New Zealand waters (Ayling & Cox 1982), eleven of which belong to the Pleuronectidae (subfamily Rhombosoleinae); four belong to the Bothidae. Co-occurrence of two or more rhombosoleinid species in coastal waters and inlets is common in New Zealand (Webb 1973; Roper 1981) but little is known of patterns of food resource use among them.

Studies of flatfish in the Northern Hemisphere have shown that co-occurring species tend to be from different feeding groups, viz., fish-feeders, crustacea-feeders, polychaete/mollusc-feeders (de Groot 1971) thereby minimising competition for food (Lande 1973; Stickney et al. 1974; Kravitz et al. 1977; Pearcy & Hancock 1978; Steinarsson 1979). Flatfish species in each feeding group defined by de Groot (1971) are characterised by their morphological and behavioural adaptations to feeding. The morphological adaptations are considered secondary to the primary asymmetry, which develops during the larval stage of flatfish (Norman 1934) and reflects their bottom-dwelling mode of life (Norman 1934; Yazdani 1970; Tsurata & Omori 1976).

Although food resource use among co-occurring flatfish species has not been studied in New Zealand, several accounts of the gut contents of a range of species exist, including some sampled at the same location (e.g., Graham 1956; Webb 1973; Roper 1981). On the basis of Graham's account, de Groot (1971) placed the New Zealand Pleuronectidae in the crustacea or polychaete-mollusc feeding groups and the Bothidae in the fish feeding group. More recent accounts agree with this general division although the placing of different rhombosoleinid species into each group varies as feeding habits within a species appear to differ geographically (Webb 1973; Mines 1975; Roper 1981).

Seven flatfish species co-occur in Wellington Harbour, and a preliminary description of their gut contents (Mines 1975) suggested considerable overlap among four rhombosoleinid species *(Rhombosolea plebeia, R. leporina, Peltorhamphus novaezeelandiae,* and *Pelotretis flavilatus).* Two other dwarf rhombosoleinid species *(Peltorhamphus tenuis,* and *P. latus)* and a species of Bothidae *(Arnoglossus scapha)* fed on entirely different prey.

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The presence of seven flatfish species in Wellington Harbour and the overlap in diet among four of them prompted a more comprehensive investigation of their feeding habits and the possible mechanisms of food resource division among them (Livingston 1981). The study focused on adult populations of *R. plebeia*, *R. leporina*, *P. novaezeelandiae*, *P. flavilatus*, and *A. scapha*. The two dwarf species of *Peltorhamphus* were omitted from the study since their size (< 100 mm total length) excludes them from competition with adults of the other species (> 150 mm total length). Feeding habits of juvenile flatfish and dwarf species did not form part of the study.

This paper presents the dietary composition and diet variation of five flatfish species with season, tidal cycle, night-day cycle, and location in Wellington Harbour.

METHODS AND MATERIALS

Study area

Wellington Harbour (Fig. 1) forms a relatively sheltered basin with a surface area of about 80 km^2, and is connected to Cook Strait by a narrow channel. Most of the harbour shoreline to the north, east, and south consists of sandy beaches, while the western shoreline consists of a reclamation bank and port facilities. The harbour floor slopes steeply down to an almost level bottom at a mean depth of 20 m (Gilmour 1960).

The tide floods in a clockwise direction and ebbs in an anti-clockwise direction (Brodie 1958). Temperature, salinity, and turbidity of Wellington Harbour water have been described by Booth (1975); shoreline and subtidal sediments by van der Linden (1967).

Rough ground, underwater power cables and shipping channels in Wellington Harbour restrict trawling to the northern and eastern parts of the harbour. For this study, the area sampled was considered in three sectors (Fig. 1), the North Sector being the shallowest region and receiving most turbid freshwater discharge from the Hutt River. The South Sector has relatively clear water and receives a greater influx of oceanic water from Cook Strait.

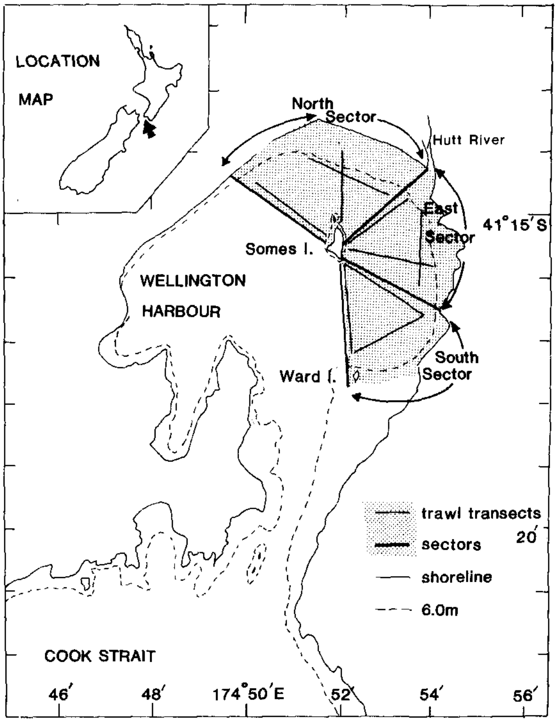


Fig. 1 Sampling area and trawl transect positions.

Collection and examination of material

Fish were caught from each sector with an otter trawl (cod end to centre of ground rope 15 m; wing mesh 140 mm; cod-end mesh 114 mm) towed from RV *Tirohia*. The net was towed at an average speed of three knots for 30–40 min in each haul. Sampling took place at least once a month between September 1976 and September 1977. Two additional excursions were made during March and July 1978 to increase the sample sizes of some of the less abundant flatfish species. Because of unfavourable weather conditions, not all sectors were sampled on each occasion. Following capture of the flatfish, the entire gut and its contents were immediately excised and placed in 10% buffered formalin.

Rhombosolea plebeia, *R. leporina*, *P. novaezeelandiae*, and *P. flavilatus* have simple tubular alimentary canals with little morphological distinction between oesophagus, stomach, or intestine. Although fragmented, the food items were identifiable from all parts of the gut and analyses involved the entire gut contents of these species. Food positioned in the anterior one-third of the gut was defined as freshly ingested and in the posterior two-thirds of the gut as partially digested. Percentage fullness of each gut was calculated as a percentage of the length of gut containing food divided by the total length of the gut. The contents from each gut were sorted into major taxonomic groups: ophiuroids, crustaceans, polychaetes, molluscs (with shell), mollusc siphons, coelenterates, and fish. The relative volume of each group within the gut sample was assessed semi-quantitatively, using the points method (Hyslop 1980). Identification of individual items was then made to species level where possible. The presence of each prey type was noted and counts of individual items made. Not all items were complete, thus counts did not necessarily reflect ingestion of whole animals. In the case of ophiuroids, the central discs were counted since individuals were highly fragmented. Freshly ingested ophiuroid material showed that the fish tended to swallow the bulk of the animal intact, perhaps losing some of the arm extremities. In the case of maldanid polychaetes, counts represent the number of worm tails only — complete worms were rarely taken. Other polychaetes were taken intact. Mollusc siphons and cnidarian remains could not be quantified in terms of numbers of whole animals.

In contrast with the rhombosoleinids, the alimentary canal of *A. scapha* is complex with clearly defined regions. Food items in the stomach generally consisted of complete items and, provided digestion had not proceeded too far, were easily identified and counted. Gut content analyses of *A. scapha* involved stomach contents only.

Table 1 Grouping of principal prey types as "infauna", "epifauna", or "pelagic".

Infauna

Largely sedentary organisms that live in permanent or temporary burrows below the sediment–water interface. In the gut of the flatfish, each organism invariably had evidence of mud or tube remains around its body.

Polychaetes	*Paraprionospio pinnata* *Glycera americana* *Lumbrinereis* sp. *Sigalion* sp. *Nephthys* sp. *Asychis trifilosa* *Asychis theodori* *Onuphis aucklandensis*[§]
Crustacea	*Macrophthalmus hirtipes*

Epifauna

Organisms that live in or on the sediment surface that make excursions from their burrows and could therefore be taken when away from their burrows. Mud or burrow remains of these species were absent in the guts of flatfishes.

Polychaetes	*Onuphis aucklandensis*[§]
Crustacea	*Ampeliscidae* *Lysianassidae* *Jaxea novaezealandiae*
Cnidaria	One unidentified species

Pelagic

Organisms that can be captured up in the water column.

Crustacea	*Periclimenes yaldwyni*
Fish	*Engraulis australis*

[§] Specimens of *O. aucklandensis* classed as infauna were enclosed by a mud tube, while those classed as epifauna had no tube remains around their bodies.

Data analyses

The problems of gut content analysis reviewed by Hynes (1950) and Hyslop (1980) were heeded, and to offset biases associated with any one procedure, three methods of analysis were adopted:

Percentage frequency of occurrence: %f.o. = $n/N \times 100$, where n is the number of fish in which a particular prey type (species in most cases) occurred and N is the total number of fish in that sample; calculated for both major taxonomic groups and individual prey types.

Percentage numerical frequency: %n.f. = $i/I \times 100$, where i is the number of individuals of a particular prey type that occurred in sample N, and I is the total number of individuals of all prey types counted in sample N; calculated for both major taxonomic groups and individual prey types.

Percentage relative volume: %r.v. = $w/W \times 100$, where w is the estimated relative volume of a particular prey type out of the total food volume W (maximum of 20 score points) in the gut of individual fish; calculated for major taxonomic groups only.

It was considered that %f.o. would provide a measure of constancy of a prey type within the diet, %n.f. would provide a measure of the most frequently consumed prey type, and %r.v. would indicate which prey type formed the bulk of the diet. Because of problems in counting mollusc siphons and cnidarian remains (see above), only %f.o. and %r.v. were recorded for these prey types.

Percentage dietary overlap (after Tyler 1972) was used as a measure of similarity of diet among the flatfish examined: % dietary overlap = $O/T \times 100$, where O is the observed number of co-occurrences of prey types between predator species and T is the total number of co-occurrences possible among predator species.

Variation of diet with time of year and point of capture in the harbour were investigated using %f.o. Tidal and diel feeding cycles in the Rhombosoleinae species were studied by estimating the proportion of fish with fresh food in their guts (food located in the first third of the gut was classed as fresh). This approach eliminated problems of digestion rates and time lags. Feeding cycles in *A. scapha* were examined by the presence/absence of food in the stomach.

Presentation of results

Data are presented in tabular and graphical form. Raw data not given here are available in Livingston (1981). The terms "major taxonomic group" and "prey type" refer to two levels of analysis in comparing diet composition. The terms "principal and secondary diet components" are used in a

Table 2 Species list of prey items consumed by flatfish species in Wellington Harbour (n.d., not determined).

	R. plebeia		*R. leporina*		*P. novaezeelandiae*		*P. flavilatus*		*A. scapha*	
Prey	%f.o.	%n.f.	%f.o.	%n.f.	%f.o.	%n.f.	%f.o.	%n.f.	%f.o.	%n.f.
POLYCHAETA										
SIGALIONIDAE										
Sigalion sp.	20.3	2.5	2.1	1.0	2.5	<1	0.9	<1	-	-
POLYNOIDAE										
Polynoe sp.	1.6	<1	-	-	-	-	-	-	-	-
GLYCERIDAE										
Glycera americana (Leidy, 1853)	11.6	0.6	14.6	2.6	9.9	<1	-	-	-	-
Ophioglycera sp.	0.4	<1	-	-	1.2	<1	-	-	-	-
NEPHTYIDAE										
Aglaophamus sp.	4.6	<1	-	-	-	-	-	-	5.1	<1
Nephthys sp.	17.6	<1	4.2	?	1.2	<1	-	-	3.4	<1
ONUPHIDAE										
Onuphis aucklandensis Augener, 1924	46.0	6.1	5.3	1.4	61.2	34.9	1.4	95.6	3.4	<1
LUMBRINEREIDAE										
Lumbrinereis sp.	5.6	<1	1.1	-	9.9	<1	0.9	<1	-	-
ARABELLIDAE										
Arabella sp.	2.3	<1	-	-	-	-	-	-	-	-
SPIONIDAE										
Paraprionospio pinnata (Ehlers, 1901)	6.9	3.3	22.1	39.4	6.2	4.8	1.8	-	-	-
ORBINNIDAE	1.1	<1	-	-	-	-	-	-	-	-
PHYLLODOCIDAE	0.7	<1	-	-	-	-	-	-	-	-
GONIADIDAE	0.4	<1	-	-	-	-	-	-	-	-
CAPITELLIDAE										
Capitella capitella Blainville, 1828	0.2	<1	-	-	-	-	-	-	-	-
MALDANIDAE										
Asychis trifilosa Augener, 1926	53.4	13.4	4.2	1.0	22.2	4.9	0.9	<1.0	3.4	<1
Asychis theodori Augener, 1926	21.3	3.3	-	-	5.2	<1	0.9	<1	3.4	<1
PECTINARIIDAE										
Pectinaria sp.	-	-	1.1	<1	-	-	-	-	-	-
OTHER POLYCHAETA	14.1	-	9.5	-	-	-	1.8	-	-	-
CRUSTACEA										
PALAEMONIDAE										
Periclimenes yaldwyni Holthuis, 1959	1.2	<1	-	-	6.2	<1	-	-	52.5	53.0
THALASSINOIDAE	0.5	<1	1.1	<1	-	<1	0.9	<1	-	-
LAOMEDIIAE *Jaxea novaezealandiae* Wear & Yaldwyn, 1966	24.6	1.6	1.1	<1	17.3	1.4	-	-	-	-
HYMENOSOMATIDAE										
Halicarcinus sp.	-	-	5.3	<1	13.6	1.8	-	-	-	-
OCYPODIDAE *Macrophthalmus hirtipes* (Jacquinot, 1852)	14.3	1.8	71.6	43.0	35.8	13.7	4.4	1.3	-	-
AMPELISCIDAE	29.6	2.3	5.3	<1	3.7	<1	-	-	-	-
LYSIANASSIDAE	6.1	<1	5.3	1.8	16.0	1.8	0.9	<1	-	<1
UNIDENTIFIED CRUSTACEA	1.1	5.4			1.2		1.8		-	-
CNIDARIA Burrowing type (sp. undet.)	-	-	6.3	10.8	-	-	2.1	3.1	-	-
TUNICATA?	-	-	-		9.9	4.7	-	-	-	-
MOLLUSCA										
NUCULIDAE										
Nucula hartvigiana Pfeiffer, 1864	17.6	<1	20.0	3.0	3.7	0.1	1.8	0.5	-	-
mollusc siphons (sp. undet.)	-	-	21.0	n.d.	-	n.d.	-	n.d.	-	-
ECHINODERMATA										
OPHIUROIDEA										
Amphiura rosea Farquhar, 1894	99.2	59.4	-	-	28.4	32.0	-	-	-	-
PISCES										
ENGRAULIDAE										
Engraulis australis (White, 1790)	-	-	-	-	-	-	-	-	64.4	47.3
PLEURONECTIDAE										
Peltorhamphus sp.	-	-	-	-	-	-	-	-	3.4	<1

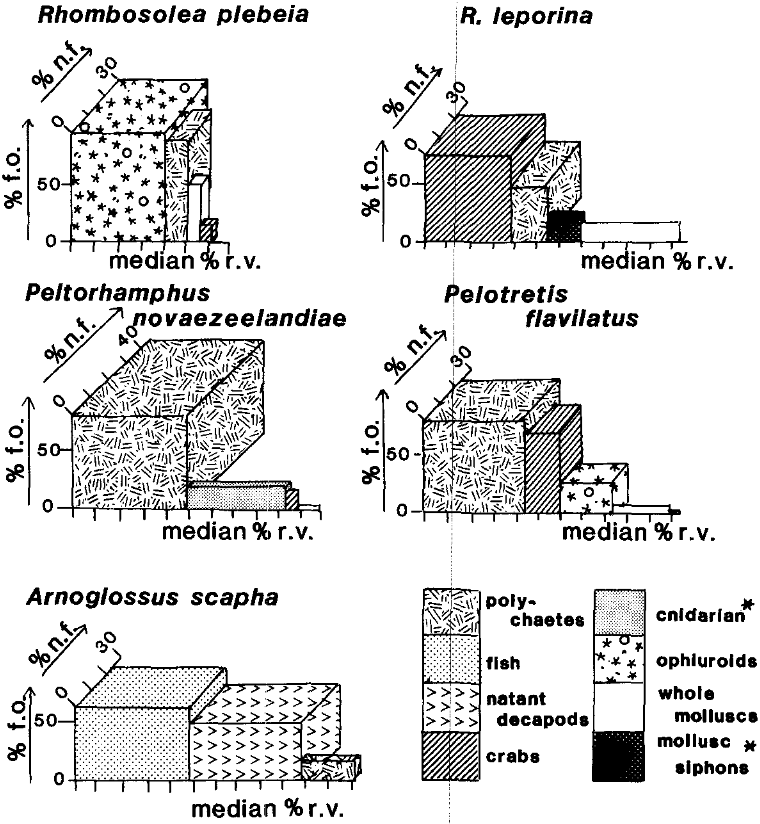


Fig. 2 Major taxonomic groups consumed by flatfish species in Wellington Harbour. x-axis: 20% increment % relative volume median; y-axis: % frequency of occurrence; oblique axis: % numerical frequency. * %f.o. and %r.v. values only.

general sense based on the combined quantifications of %f.o., %n.f., and %r.v. Fishes are described as specialised or generalised feeders according to the relative diversity of their diets, and as benthic or pelagic feeders depending on the location of the principal prey at the time of capture (Table 1). Prey types are classed as "infauna", "epifauna", or "pelagic" according to where they occur relative to the sediment/water column interface. The terms food choice and selection are used in the sense that the fish do not eat their food by random selection. Availability of prey refers to numerical abundance and functional availability to the fish species in question; for example, benthic infauna are essentially unavailable to fish ill-equipped for feeding on the seafloor.

RESULTS

A total of 1068 flatfish were taken for gut content analyses. Of these, 621 were *R. plebeia* (15–45 cm total length, TL), 116 were *R. leporina* (20–39 cm TL), 98 were *P. novaezeelandiae* (15–45 cm TL), 130 were *P. flavilatus* (20–39 cm TL), and 103 were *A. scapha* (20–35 cm TL). At least 82% of rhombosoleinid guts contained food, but only 52% of *A. scapha* stomachs contained food.

Diet composition

Major taxonomic groups dominating the diet of each flatfish species differed (Table 2; Fig. 2). *R. plebeia* fed principally on ophiuroids while *R. leporina* fed principally on crustaceans. Both *P. novaezeelandiae* and *P. flavilatus* fed on polychaete worms, however, worms in the gut contents of *P. novaezeelandiae* were infauna, while those identified in *P. flavilatus* were epifauna (Table 2). *A. scapha* had a diet consisting almost equally of small fish and shrimps (Fig. 2). These principal food types dominated the respective diets of each species in terms of %f.o., %n.f., and %r.v., suggesting that the same food types comprised the most constant, most frequently taken, and greatest biomass in the diet of each flatfish species.

A comparison of the %f.o. of individual prey types showed that the dominant taxonomic groups largely comprised a single species, but secondary taxonomic groups gave diversity to the diet (Table 2). For example, *A. rosea* was the only ophiuroid species eaten by *R. plebeia*, but 17 species of polychaetes and at least eight species of crustaceans contributed secondarily to the diet. *R. plebeia, P. novaezeelandiae*, and *R. leporina* had the most diverse diets in descending order. *P. flavilatus* and particularly *A. scapha* diets were far less diverse (Table 2).

Overlap in diet

Percentage overlap in diet was greatest among the Rhombosoleinae, the three most similar being *R. plebeia, R. leporina*, and *P. novaezeelandiae* at the prey species level (31.3% overlap, Table 3). Differences between the rhombosoleinids and *A. scapha* reflect choice of main prey items (%f.o. >10) associated with the seabed and water column respectively (Table 4). The separation between *P. flavilatus* and the other three rhombosoleinids largely reflects differences in diet diversity but also choice of *Onuphis aucklandensis* as epifauna rather than as infauna as determined by the presence/absence of polychaete tube remains in the gut.

Variation in diet with location of capture

Of the 1068 flatfish taken for gut content analyses, 49% were from the East Sector (Table 5), which reflects the higher abundance of rhombosoleinid species in trawl catches from there (Mines 1971). Both *R. plebeia* and *P. flavilatus* were taken from the South Sector, while *R. plebeia, R. leporina*, and

Table 3 Percentage dietary overlap of food types with percentage frequency of occurrence >10 among flatfish in Wellington Harbour (see text for derivation).

	R. plebeia	*R. leporina*	*P. novaezeelandiae*	*P. flavilatus*	*A. scapha*
R. plebeia	–	21.4%	46.1%	9.0%	0%
R. leporina	–	–	16.7%	0%	0%
P. novaezeelandiae	–	–	–	11.1%	0%
P. flavilatus	–	–	–	–	0%
A. scapha	–	–	–	–	–

Table 4 Food resource use among flatfish in Wellington Harbour based on percent frequency of occurrence >10%.

Prey	*R. leporina*	*P. novaezeelandiae*	*R. plebeia*	*P. flavilatus*	*A. scapha*
Infauna					
Paraprionospio pinnata	+				
Nucula hartvigiana	+		+		
Macrophthalmus hirtipes (in burrow)	+	+	+		
Glycera americana	+	+	+		
Onuphis aucklandensis (in tube)		+	+		
Lumbrinereis sp.		+			
Asychis trifilosa		+	+		
Amphiura rosea		+	+		
Asychis theodori			+		
Sigalion sp.			+		
Nephthys sp.			+		
Epifauna					
Mollusc siphons	+				
Halicarcinus sp.		+			
Lysianassidae		+			
Jaxea novaezealandiae		+	+		
Ampeliscidae			+		
Tunicate?			+		
Onuphis aucklandensis (out of burrow)				+	
Cnidaria				+	
Pelagic					
Periclimenes yaldwyni					+
Engraulis australis					+

P. novaezeelandiae were collected in significant numbers from the North Sector. In contrast to the rhombosoleinid species, *A. scapha* predominated in the South Sector.

A comparison of diets of flatfish captured from North, East, and South Sectors showed that principal food types (Table 5) dominated the diets in all areas of the harbour. Some of the secondary types, however, differed markedly in their importance between sectors in terms of frequency of occurrence. Food types of greater than 20% difference between sectors included *A. trifilosa (R. plebeia)*, mollusc siphons and *P. pinnata (R. Leporina), A. rosea, M. hirtipes, A. trifilosa, J. novaezealandiae* and *Halicarcinus (P. novaezeelandiae), P. yaldwyni (A. scapha)*. The differences were generally greatest between North/East Sectors and the South Sector and probably reflected the unequal sample sizes between sectors to some extent. The occurrence of a particular prey item in the diets of flatfish in any one sector, however, was not necessarily consistent. For example, the %f.o. of *J. novaezealandiae* in the guts of *R. plebeia* was greatest in North and East Sectors while in the guts of *P. novaezeelandiae*, %f.o. was greatest in the South Sector.

Seasonal cycles

No obvious seasonal trends in the presence or absence of food in the gut were observed, although the percentage of all species of flatfish with food in their gut varied from 22 to 100%. The greatest fluctuation occurred in the feeding pattern of *A. scapha*. The least fluctuation in feeding patterns was observed for *R. plebeia* where 83% or more contained food in their gut all year. Small sample sizes may have obscured seasonal patterns.

Seasonal changes in dominant food types were found in *R. leporina* and *A. scapha*. A reduction in the intake of crabs *(M. hirtipes)* by *R. leporina* during Spring 1977 was accompanied by an increase in mollusc siphons (Fig. 3). The change in dominance from *E. australis* to *P. yaldwyni* in the diet of *A. scapha* during autumn, and the reversal in spring was quite pronounced.

Secondary food types showing positive correlation with change in %f.o. of principal food items with time were *Ampelliscidae* and *A. rosea* and to some extent *M. hirtipes* eaten by *R. plebeia*, and *A. rosea* and *O. aucklandensis* eaten by *P. novaezeelandiae*. Negative correlation was noticeable for *A.*

Table 5 Percent frequency of occurrence of main food types eaten by flatfish in each sector of the study area; §, guts empty; number of flatfish in parenthesis.

Main prey types in diet of each flatfish sp.	North Sector	East Sector	South Sector
R. plebeia	(206)	(293)	(123)
Amphiura rosea	78	92	94
Onuphis aucklandensis	51	47	35
Asychis trifilosa	41	63	51
Ampeliscidae	34	29	24
Asychis theodori	25	23	12
Jaxea novaezealandiae	25	29	13
Macrophthalmus hirtipes	21	14	4
R. leporina	(42)	(70)	(4)§
Macrophthalmus hirtipes	69	75	–
mollusc siphons	42	7	–
Glycera americana	11	20	–
Paraprionospio pinnata	3	35	–
P. novaezeelandiae	(17)	(72)	(9)
Onuphis aucklandensis	82	75	63
Amphiura rosea	26	14	50
Macrophthalmus hirtipes	18	44	0
Asychis trifilosa	9	19	63
Jaxea novaezealandiae	0	19	25
Halicarcinus sp.	0	15	25
P. flavilatus	(18)	(78)	(34)
Onuphis aucklandensis	93	81	76
Cnidaria	13	23	21
A. scapha	(2)	(13)	(82)
Engraulis australis	80	50	59
Periclimenes yaldwyni	0	25	57

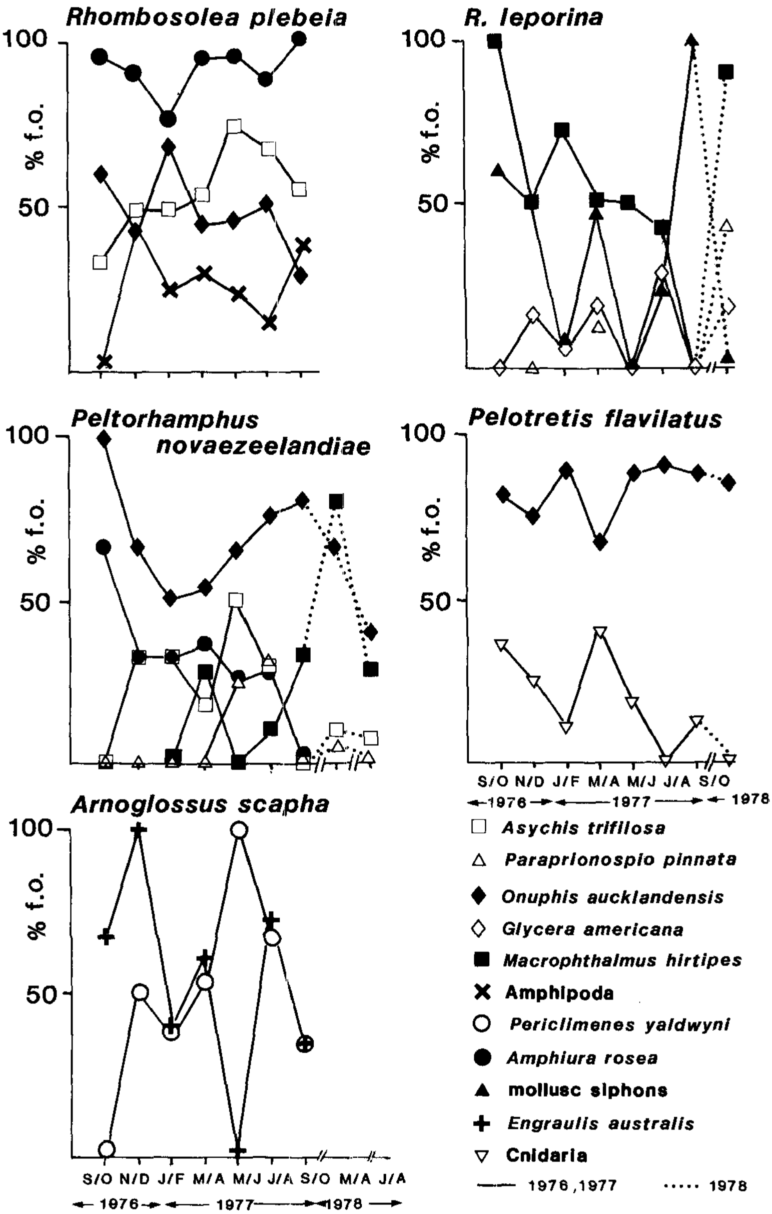


Fig. 3 Seasonal changes in dominant prey items (x-axis: sampling periods).

rosea and *O. aucklandensis* eaten by *R. plebeia*, and *M. hirtipes* eaten by *P. novaezeelandiae*.

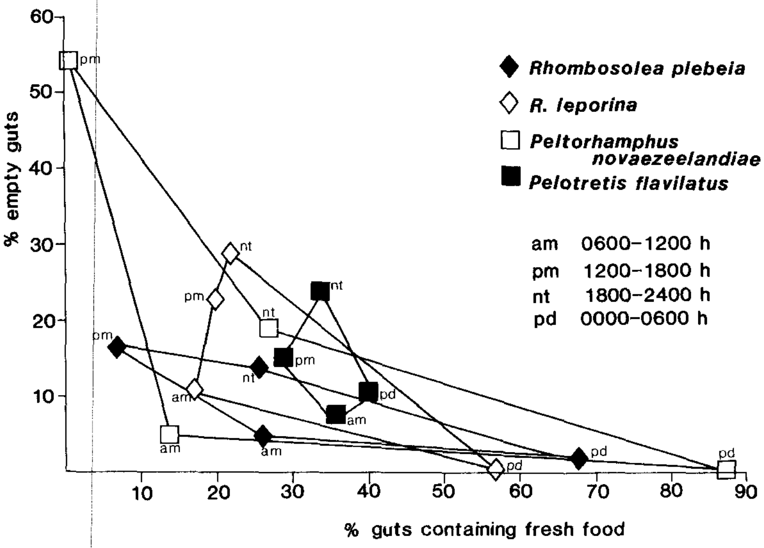
Diel and tidal feeding cycles

A comparison of gut fullness and state of digestion at different times of day and night, and of the tidal cycle showed that feeding in *R. plebeia, R. leporina*, and *P. novaezeelandiae* was primarily nocturnal (Fig. 4). No diel cycles of gut fullness were detected for *P. flavilatus* or *A. scapha* and tidal cycles did not appear to be linked with gut fullness in any consistent pattern.

DISCUSSION

Dietary differences among flatfish in Wellington Harbour reflect differences in the location of the prey relative to the bottom sediments, the relative activity of the prey species, and the morphological

Fig. 4 Diel changes in stomach fullness and prey "freshness" of flatfish in Wellington Harbour.



and behaviourial differences of the flatfish, as summarised in Fig. 5. The results also indicate that *R. plebeia, R. leporina*, and *P. novaezeelandiae* feed largely at night and the only species for which marked seasonal changes in diet were detected, was *A. scapha.*

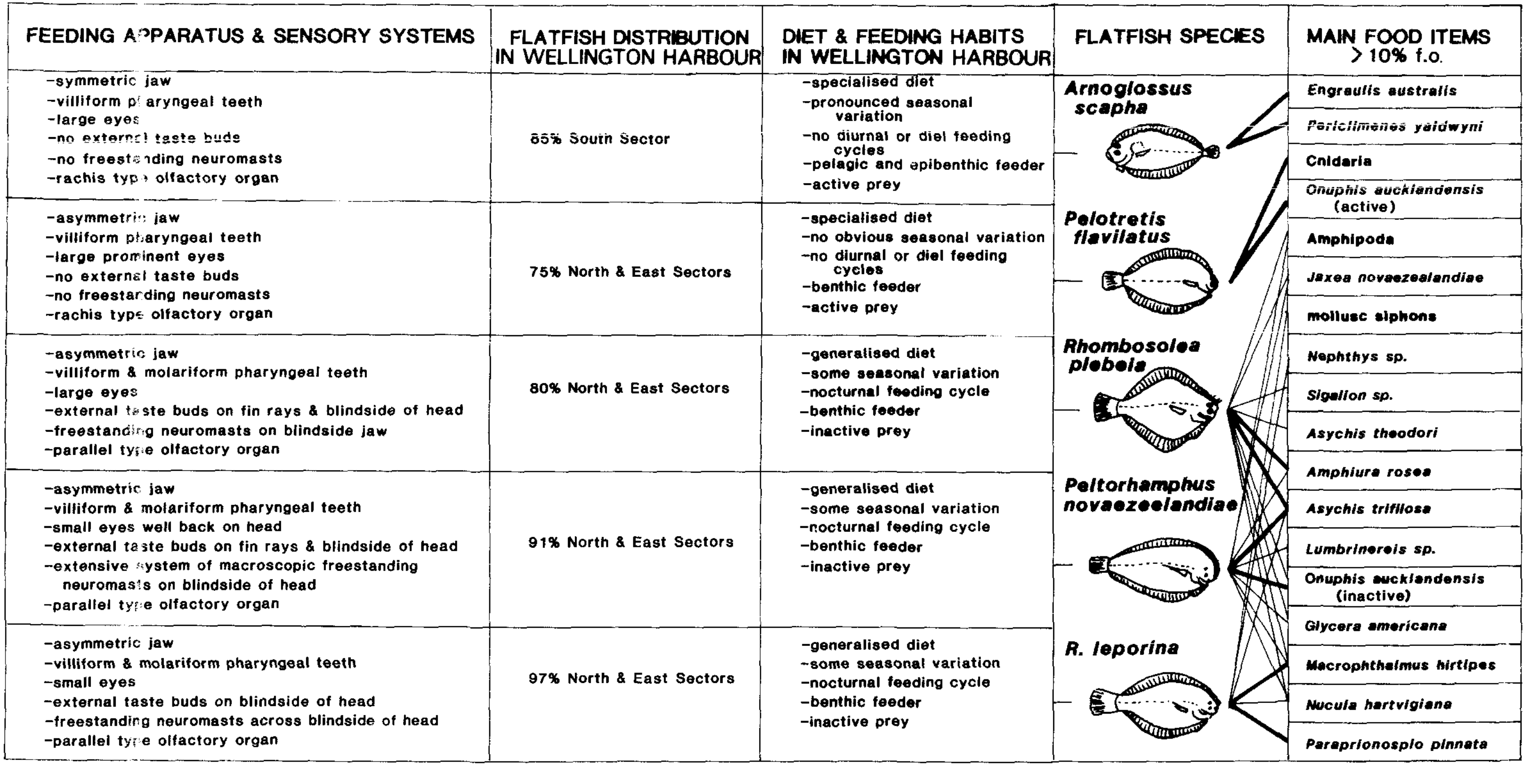
The non-random distribution of flatfish species in the Harbour may be related to sediment types and water depth (e.g., Pearcy 1978) or associated with distribution of prey in different sediment types (Petersen 1911; Jones 1952; Pearcy & Hancock 1978; Steinarsson 1979; Jewet & Feder 1981). As a group, the Rhombosoleinae are generally found in shallow coastal waters while *A. scapha* are generally found in deeper waters (Graham 1956). The South Sector is the deepest part of Wellington Harbour and the subtidal sediments are dominated by coarse grained material eroded from Somes Island and Ward Island (van der Linden 1967). The offshore sediments of the North and East Sectors are fine grained in comparison; however, little is known of the sediment preferences of these flatfish species. It is apparent that, in Wellington Harbour, the Rhombosoleinae were most common in areas underlain by fine sediments whereas *A. scapha* was most common in deeper water with coarser grained sediments.

Although dietary components differed slightly depending on which part of the harbour flatfish had been captured in, two broad patterns of food resource division are apparent (Fig. 5). The most obvious separation is between *A. scapha*, feeding on active mid-water prey, and the other four species which fed on organisms in or on the seabed. The second pattern separates *R. plebeia, R. leporina*, and *P. novaezeelandiae*, with their diverse, closely overlapping diets consisting of benthic infauna, from *P. flavilatus* and *A. scapha* which have specialised diets of one or two main species taken on or above the sediment surface.

A comparison of the morphology of the feeding apparatus (jaws, dentition, gill rakers) and the extent of sensory development (eye size, eye position, external taste buds, superficial neuromast systems, fin ray specialisation) and brain lobe morphology (Livingston 1981) provides some explanation for the observed division of food resources (Fig. 5). The close overlap in diet and nocturnal feeding habits of *R. plebeia, R. leporina*, and *P. novaezeelandiae* suggest that these species were feeding primarily non-visually, using their external taste buds and superficial neuromast systems to locate food, while *A. scapha* and *P. flavilatus* were feeding visually.

Aquarium studies confirmed that *R. plebeia* and *P. flavilatus* maintained visual contact with prey while *R. leporina* and *P. novaezeelandiae* did not (Livingston 1981). The relative diversity of infaunal organisms taken by the non-visual feeders and overlap in diet of these species suggests that these flatfish gulp at the sediment upon detection of suitable prey. This activity has been observed among many benthic feeding flatfish species elsewhere (e.g., Summers 1980). The relatively narrow, specialised diets of *P. flavilatus* and *A. scapha* are typical of visual feeders (de Groot 1971).

Comparison with data available from other parts of New Zealand showed that quite different patterns occur. *Rhombosolea plebeia* and *P. flavilatus* as well as *A. scapha* are described as feeding on fish and other active prey such as shrimps in Otago coastal waters (Graham 1956). Overall, there is



FEEDING APPARATUS & SENSORY SYSTEMS	FLATFISH DISTRIBUTION IN WELLINGTON HARBOUR	DIET & FEEDING HABITS IN WELLINGTON HARBOUR	FLATFISH SPECIES
-symmetric jaw -villiform pharyngeal teeth -large eyes -no external taste buds -no freestanding neuromasts -rachis type olfactory organ	85% South Sector	-specialised diet -pronounced seasonal variation -no diurnal or diel feeding cycles -pelagic and epibenthic feeder -active prey	***Arnoglossus scapha***
-asymmetric jaw -villiform pharyngeal teeth -large prominent eyes -no external taste buds -no freestanding neuromasts -rachis type olfactory organ	75% North & East Sectors	-specialised diet -no obvious seasonal variation -no diurnal or diel feeding cycles -benthic feeder -active prey	***Pelotretis flavilatus***
-asymmetric jaw -villiform & molariform pharyngeal teeth -large eyes -external taste buds on fin rays & blindside of head -freestanding neuromasts on blindside jaw -parallel type olfactory organ	80% North & East Sectors	-generalised diet -some seasonal variation -nocturnal feeding cycle -benthic feeder -inactive prey	***Rhombosolea plebeia***
-asymmetric jaw -villiform & molariform pharyngeal teeth -small eyes well back on head -external taste buds on fin rays & blindside of head -extensive system of macroscopic freestanding neuromasts on blindside of head -parallel type olfactory organ	91% North & East Sectors	-generalised diet -some seasonal variation -nocturnal feeding cycle -benthic feeder -inactive prey	***Peltorhamphus novaezeelandiae***
-asymmetric jaw -villiform & molariform pharyngeal teeth -small eyes -external taste buds on blindside of head -freestanding neuromasts across blindside of head -parallel type olfactory organ	97% North & East Sectors	-generalised diet -some seasonal variation -nocturnal feeding cycle -benthic feeder -inactive prey	***R. leporina***

MAIN FOOD ITEMS > 10% f.o.
Engraulis australis
Periclimenes yaldwyni
Cnidaria
Onuphis aucklandensis (active)
Amphipoda
Jaxea novaezealandiae
mollusc siphons
Nephthys sp.
Sigalion sp.
Asychis theodori
Amphiura rosea
Asychis trifilosa
Lumbrinereis sp.
Onuphis aucklandensis (inactive)
Glycera americana
Macrophthalmus hirtipes
Nucula hartvigiana
Paraprionospio pinnata

Fig. 5 Summary of food resource use and morphological variation among flatfish species in Wellington Harbour. (Thick lines indicate dominant prey items).

considerable overlap and diversity among the diets of the same five species as examined in Wellington Harbour (Graham 1956). Similarly, *P. flavilatus* and *A. scapha* are reported as feeding on polychaetes and ophiuroids. On the basis of dietary composition, flatfish in Wellington Harbour could be categorised under de Groot's (1971) system as fish-feeders *(A. scapha)*, crustacea-feeders *(R. leporina)* and polychaete/mollusc-feeders *(R. plebeia, P. novaezeelandiae, P. flavilatus)*. In Otago coastal waters, de Groot (on the basis of Graham's work) described *R. plebeia* as a crustacea-feeder (Graham 1956; de Groot 1971). In the Avon-Heathcote Estuary, the prey of *R. plebeia, R. leporina*, and *P. novaezeelandiae* are principally crustaceans (Webb 1973). Clearly the morphology and behavioural flexibility of these five flatfish species do not necessarily limit food selection to the types of prey consumed in Wellington Harbour.

Flatfish species distribution varies with salinity, temperature, oxygen tension, and sediment type (e.g., McCracken 1963; Roper 1979). Although these factors probably vary between Wellington Harbour, Otago Harbour, and the Avon-Heathcote estuary, such variation is unlikely to be of sufficient magnitude to explain the differences in patterns of use of food resources. It is expected that flatfish diets differ with locality and sediment type according to potential prey organisms occurring in each area (e.g., Mulicki 1947; Jones 1952; Pearcy & Hancock 1978). Flatfish species also tend to feed on more abundant prey items and often change their diets according to the seasonal fluctuations in abundance of these organisms (e.g., Powles 1965; Klimova & Ivankova 1977). The major food items consumed by each species are relatively abundant in Wellington Harbour although their local availability may vary accordingly. The benthic community in Wellington harbour is described as an *Amphiura rosea–Echinocardium australis* community (Morton & Miller 1973). Such communities usually have an abundance of *A. rosea, M. hirtipes*, and *G. americana* in addition to other macrofauna (Powell 1937). *Amphiura rosea* reaches relatively high densities (mean 78/m^2) in both fine sediments and the relatively coarse sediments of the South Sector (McKoy 1970). *Engraulis australis* eggs, larvae, and prejuveniles are more abundant in the South Sector than in any other area of the harbour (Frentzos 1980) and it is likely that adult *E. australis* are also more abundant in the South Sector. The shrimp *P. yaldwyni* is more abundant in the South Sector in association with the coarse sediment that lies between Somes Island and Ward Island (H. Packer, Victoria University, pers. comm.).

Fish species which dwell in zones of high turbidity or areas of low illumination such as caves frequently have well-developed near-field sensory systems, as in *R. plebeia, R. leporina*, and *P. novaezeelandiae*, that are used for prey location (Moore 1950; Gosline 1971). High turbidity has been demonstrated to reduce the efficiency of prey capture by visual feeding flatfish, and to influence food selection in the field (Moore & Moore 1976). The open coast of Otago has relatively deep water overlying coarse sands, and is likely to be far less turbid than the Avon-Heathcote estuary — which is a shallow river-mouth system — or Wellington Harbour which has relatively turbid waters as a result of resuspended fine bottom deposits (Booth 1975). It is therefore highly probable that conditions in Wellington Harbour and the Avon-Heathcote estuary favour non-visual feeding among *R. plebeia*, and particularly *R. leporina* and *P. novaezeelandiae*. As *P. flavilatus* and *A. scapha* do not have external taste buds or superficial neuromast systems, I consider these two species to be primarily visual feeders although the olfactory organs and lateral line systems presumably supplement vision to some extent. It is significant that visual-feeding flatfish observed elsewhere, feeding on items such as ophiurids, were visually attracted to the cloud of sediment produced by movements (Weber 1965). In Wellington Harbour, a cloud of sediment produced by such movements of prey is unlikely to be clearly visible.

Although non-visual feeders among flatfish tend to have less selective diets than visual feeders (Stickney et al. 1974), this does not provide sufficient explanation for the differences in diversity of diet between the non-visual and visual feeding flatfish in Wellington Harbour since the same flatfish species in Otago Harbour feed on a wide range of food types. One possibility is that the turbid conditions may reduce availability of even abundant prey types to the visual feeders.

It has been shown that the diets of co-occurring species tend to overlap when food resources are abundant, and become more restricted when food resources are scarce (e.g., Keast 1970). This has been interpreted by some (e.g., Tyler 1972) to imply that as food resources become scarce, "competition" for food increases. Depending on the competitive ability of each species, prey are eaten according to the ability of a fish species to capture one particular prey item over another (e.g., Tyler 1972). However, competition or more importantly significant levels of competition cannot be precisely defined or directly measured (Connell 1980). Studies measuring overlap of resource utilisation or "niche breadth" merely indicate areas of potential competition (Colwell & Futuyama 1971; Feinsinger et al. 1981; Linton et al. 1981). The percentage overlaps in diet presented in this work suggest that individualistic responses rather than food resource partitioning through patterns of food resource division between adult flatfish in Wellington Harbour as suggested by Ebeling & Laur (1986). In other studies, morphometrics of closely similar species have been quantitatively compared using overlap ratios to show where morphological differences may enable them to exploit their food differently with space and time (e.g., Ricklefs & Cox 1977; Gatz 1979). But differences, for example, in mouth size between *P. flavilatus* and other Rhombosoleinids do not appear to influence what size of the polychaete *O. aucklandensis* is consumed by either species, and do not necessarily indicate an area of divergence in feeding habits. It is possible that competitive interactions occur among newly metamorphosed flatfish as their densities on the sea floor peak following spawning periods. The feeding habits of juvenile flatfish are known to alter with prey densities (e.g., Wyatt 1972; Kiorboe 1978) and flexibility in feeding methods at this stage could be advantageous.

Competition is potentially a major selective force in the process of evolution (Connell 1980). It is suggested that even under conditions of limited food supply, each flatfish species in Wellington Harbour has sufficiently flexible feeding habits to prevent exclusion of other species through competition for food.

Among most groups of co-occurring flatfish species, dietary separations (Stickney et al. 1974; Kravitz et al. 1977; Steinarsson 1979), spatial separations (Pearcy & Hancock 1978) or temporal separations (Lande 1976; Guelpen & Davis 1979) are generally considered to be important factors enabling these potential competitors to co-exist without the exclusion of one or other species. Turbid conditions and the ability of the flatfish to respond under such conditions may influence the patterns of food resource use among *R. plebeia, R. leporina, P. novaezeelandiae, P. flavilatus,* and *A. scapha* in Wellington Harbour.

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